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**Gill surface area in relation to growth rates and maximum size
in sharks**

Hata, David N., Ph.D.

The College of William and Mary, 1993

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Ann Arbor, MI 48106

GILL SURFACE AREA IN RELATION TO GROWTH
RATES AND MAXIMUM SIZE IN SHARKS

A Dissertation

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

by

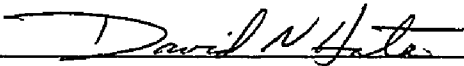
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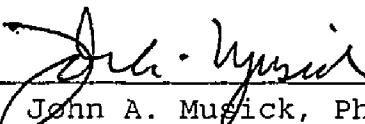
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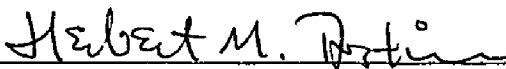


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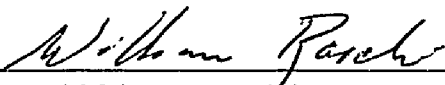
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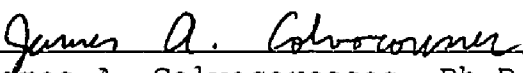
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DEDICATION

This work is dedicated to my parents for their continued support, both emotional and financial, throughout my seemingly eternal quest to reach a higher level of unemployment. They have withstood more than they should have (or probably wanted to).

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My friends have made me what I am today, and I will get them back for it.

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ABSTRACT

The most commonly used equation to describe size at age in fishes is the von Bertalanffy growth equation (VBE): $L_t = L_\infty(1 - \exp(-K(t - t_0)))$. The VBE assumes that growth rate is based on the balance of anabolic and catabolic processes: $dW/dt = HW^d - kW^m$. Anabolism, kW^d , is considered proportional to gill surface area ($A = rW^d$), and a "generalized" VBE (GVBE) has been previously determined: $L_t = L_\infty(1 - \exp(-KD(t - t_0)))^{1/D}$, where $D = b - bd$ and b is from $W = qL^b$. The growth rate may be rewritten in terms of gill area, A , as $dW/dt = kA/(A_\infty/W_\infty^m) - kW^m$ (Text Equation 15). This study examined the hypothesis that growth rate was proportional to gill area and that maximum size was determined by a critical ratio, A_∞/W_∞ .

Gill areas were examined for sandbar and tiger sharks. Values of the gill area coefficient, d , obtained here and for other species were fit to the GVBE using a modified Ford-Walford equation (OFW) to calculate GVBE parameters. The GVBE was also fit using Equation 15. Length at age data sets for sandbar, tiger, dusky, blue, white, and shortfin mako sharks were obtained from literature sources.

The adequacy of the GVBE is dependent on the data set. The OFW produced realistic results for seven data sets, but produced unrealistic L_∞ estimates for three other data sets. Text Equation 15 produced realistic results for five data sets, but not for two other data sets.

A_∞/W_∞ for the lamnid sharks are greater than for the carcharhinids, and within the carcharhinids, A_∞/W_∞ for tiger, dusky and blue sharks are similar, but greater than for sandbar sharks. Sandbar sharks may compensate for the lower A_∞/W_∞ by greater ventilation volumes and/or higher blood oxygen affinity. Growth in individual sandbar sharks was not correlated with individual gill areas.

The results support the contention that species- or population-specific $dW/dt \propto A/W$, and that decreasing A/W results in asymptotic growth. However, other factors may obscure or supersede the influence of individual variability in gill area on individual growth characteristics.

GILL SURFACE AREA IN RELATION TO GROWTH
RATES AND MAXIMUM SIZE IN SHARKS

INTRODUCTION

Studies on growth in fishes generally rely on some kind of mathematical expression to describe size (weight or length) at age. Equations intended to be purely descriptive or predictive may be useful if they adequately perform their function, and if interpretation of them does not make assumptions beyond that. A disadvantage of such empirically derived representations is that they lack any physiological significance and cannot be used to investigate biological variations in growth, such as that due to food supply (Beverton and Holt 1957). An expression that combines accurate descriptive/predictive properties and biological foundation and which can be incorporated into theoretical population models would be preferred. Several formulas, such as the Gompertz and Brody Equations, exist, although Beverton and Holt (1957) rejected them because they lacked any physiological basis.

The most commonly applied equation that satisfies these requirements, at least in some cases, is that developed by von Bertalanffy (1938). The von Bertalanffy growth equation is based on the physiological balance of anabolic (synthesis of native protein) and catabolic (degradative) processes, the former defined as a function of surface, the latter as a function of volume or mass.

Anabolism is dependent on both food and oxygen supply, while catabolism, precisely pre-oxidative catabolism, is dependent solely on weight (Pauly 1981). The von Bertalanffy equation assumes determinate growth and that the balance of anabolism and catabolism leads to decreasing growth rate and eventually to some asymptotic length or weight, L_{∞} or W_{∞} , giving

$$L_t = L_{\infty}(1 - e^{-K(t - t_0)}) \quad (1)$$

where L_t is length at time t , K is a "metabolic" coefficient of growth, and t_0 is the theoretical age at which $L = 0$ if growth always followed the same equation. However, pre-metamorphic or in-utero growth should not be assumed to follow the same growth pattern as in later life, and t_0 represents a simple time reference for the growth curve.

The equation is derived from

$$dW/dt = HW^d - kW^m \quad (2)$$

where dW/dt is the rate of growth in weight, H and k are coefficients of anabolism and catabolism, respectively, d relates anabolism to some limiting surface, and m relates catabolism to weight. The von Bertalanffy equation as originally presented assumes isometric growth, where a surface is related to length squared, mass is related to length cubed and catabolism is a constant dependent only on mass, so $d = 2/3$ and $m = 1$, and the coefficient $K = k/3$.

In analysis of the equation, several authors have

based their arguments on food conversion and the digestive area as the limiting surface (Beverton and Holt 1957; Ursin 1967; Ricker 1975; 1979). Fry (1957) suggested that the respiratory area, rather than digestive area, might be the growth limiting surface. Others have stated that growth is indeterminate, and non-asymptotic equations should be developed (Parker and Larkin 1959; Paloheimo and Dickie 1965; Knight 1968; Roff 1980). It is arguable that, in some instances, the von Bertalanffy growth equation provides a poor fit to the data, either in its predictive ability or determination of the asymptotic length. In his analysis of the von Bertalanffy equation Pauly (1981) argued that it was valid, and that the limiting surface was respiratory. Pauly (1981) generalized the original equation which, based on limited data, assumed that the limiting surface increased in proportion to a constant 2/3 power of weight ($d = 2/3$), and allowed the power to vary. He reanalysed one data set for bluefin tuna and found that the recalculated L_{∞} agreed well with the observed maximum length, much better than the original value which was more than 1.5 times the observed maximum. Pauly (1981) presented the "generalized" von Bertalanffy equation as

$$W_t^D = W_{\infty}^D (1 - e^{-(3KD/b)(t - t_0)})^b \quad (3)$$

$$L_t = L_{\infty} (1 - e^{-KD(t - t_0)})^{1/D} \quad (4)$$

The constant D is determined from equations relating anabolism and weight to length:

$$S = pL^a \quad (5)$$

$$W = qL^b \quad (6)$$

$$D = b - a \quad (7)$$

where S is some surface across which substances required for anabolism enter the body, p, q, a, and b are coefficients. Combining Equations 2, 6 and 7 gives

$$L_{\infty} = q^{-1/b} [H/k]^{1/D} \quad (8)$$

$$W_{\infty} = (H/k)^{1/(1-d)} \quad (9)$$

Ursin (1967) stated that k was independent of asymptotic size, but that H or d or both depended on maximum size. Because pre-oxidative catabolism depends on weight, and weight is related to length as above, the "metabolic" factor D represents a balance of anabolism and catabolism (Pauly 1981). Taylor (1962) derived the same "generalized" von Bertalanffy equation as Pauly (1981) (Equation 3 above), but fit D to empirical data, stating that no evidence supports either gill area or intestinal area as the limiting surface.

Metabolism is dependent on temperature, so both H (and W_{∞} and L_{∞} from Equations 8 and 9 above) and k (and therefore K) vary with temperature (Taylor 1962; Ursin 1967). Pauly (1981) equated K to environmental stress factors which reduce growth from the maximum potential. The relationship between growth rates, maximum size and temperature is well noted (e.g. Gunter 1950; Beverton and Holt 1957; Ricker 1979). Oxygen consumption in cod, Gadus

macrocephalus, was greater at 7°C than at 4 or 10°C (Paul et al. 1988). Similarly, growth rates of brown trout, Salmo trutta, were found to be greatest at intermediate temperatures, and decreased at low and high temperatures (Elliot 1975a; 1975b). Temperatures associated with greatest growth rates in brown trout decreased as food supply decreased from maximum ration to just above maintenance ration (Elliot 1975a; 1975b).

Beverton and Holt (1957) suggested that food supply and population density affect W_{∞} , but not K . Individual growth increases with decreasing population density if the food supply per-capita resultantly increases. Although this would indicate the digestive tract as the limiting surface, Pauly (1981) contended that food conversion efficiency is ultimately dependent on oxygen supply. Even if the food supply is unlimited, the assimilation or burning of the food energy requires oxygen. Food supply and oxygen are interactive growth-limiting factors (Brett 1979). Oxygen consumption in cod is greater for fed fish than unfed ones, and O_2 consumption increases for several days following one-time feeding episodes in cod and aholehole, Kuhlia sandvicensis (Muir and Niimi 1972; Paul et al. 1988). Swift (1963) stated that growth rates in salmonids are not effected by oxygen concentration. However, this applies only above a certain critical oxygen concentration (Brett 1979). Food consumption and conversion rates decrease below

a certain oxygen concentration in largemouth bass and northern pike (Stewart et al. 1967; Adelman and Smith 1970). The limiting effect of reduced oxygen supply is shifted to lower concentrations when food rations are restricted (Brett 1979). The major factor of this "respiratory dependence" is the amount of water passed over the gills (Fry 1957). Alternatively, this may be considered as the amount of gill area over which water is passed.

The growth of gill area relative to weight is generally expressed as

$$A = rW^d \quad (10)$$

$$\log (A) = \log (r) + d \log (W) \quad (11)$$

where A is the gill area, W is fish weight, and r and d are coefficients, r representing the gill surface area at 1 unit of weight (g, kg, etc.), and d generally being 0.5 - 0.95. Although Pauly (1981) stated that fish attaining a larger weight generally have larger values of d, while smaller fish have values of 2/3 or less, Palzenberger and Pohla (1992) found no correlation among a wide range of species reported in the literature. Gill surface area can be similarly expressed in relation to length, as done by Price (1931), so that $A = S$ (Equation 5). When S (= A) and W increase isometrically with length, $a = 2$, $b = 3$, $d = 2/3$, and $D = 1$, producing the original, or "specialized", von Bertalanffy equation above (Pauly 1981).

Combining Equations 2, 5, 6, and 10, and setting $S = A$

for gill area relative to length, produces

$$\begin{aligned}
 A &= rW^d \\
 A &= r(qL^b)^d \\
 pL^a &= rq^d L^{bd}
 \end{aligned}
 \tag{12}$$

$$a = bd \tag{13}$$

From Equation 7, $D = b - bd$.

If d is less than unity, the relative gill area, A/W , decreases with weight. If $d = 1$, Equation 2, in terms of length, becomes $dL/dt = L(E - K)$, where $E = Hp/bq$.

Integrating gives the exponential growth equation $L_t = L_0 e^{(E-K)t}$ (Taylor 1962). However, the exponential equation is concave upward (assuming E and K are constant), in contrast to the typical convex pattern of growth in post-metamorphic fishes. This would empirically exclude values of $d = 1$, at least in post-metamorphic fishes. Values of $d > 1$ have been calculated in early life stages of fish (pre-metamorphosis), generally $< 0.05 - 1.0$ g (Pauly 1981; Oikawa and Itazawa 1985; Hughes and Al-Kadhomi 1988). Oxygen consumption has not been found to differ between life stages, suggesting that other surfaces, such as skin and finfolds, also act in larval respiration (Pauly 1981; Hughes and Al-Kadhomi 1988).

A linear relationship between $\log(A)$ and $\log(W)$ apparently exists throughout the weight range of various species, so d is constant. Assuming gill area is proportional to oxygen consumption (Q), the oxygen supply

should decrease to some level just sufficient for maintenance metabolism (Pauly 1984). Some evidence indicates that A is indeed proportional to Q (Hughes 1972; DeJager and Dekkers 1975). However, gill surface area may only be indicative of oxygen consumption during active metabolism, whereas the entire area is not used during rest (Hughes 1984). The metabolic rate, in terms of oxygen consumption, follows the same relationship to weight as gill area:

$$Q = vW^x \quad (14)$$

Active metabolism in sockeye salmon is proportional to $W^{0.96} - W^{0.999}$, depending on temperature, whereas resting metabolism is proportional to $W^{0.78} - W^{0.914}$ (Brett 1965; Brett and Glass 1973). Similarly, oxygen consumption in northern pike, Esox lucius, is proportional to $W^{0.80}$ at rest, and $W^{0.99}$ at maximum sustained activity (Armstrong et al. 1992).

Laboratory studies on elasmobranchs have indicated that water flow volume may vary between hemibranchs, suggesting that oxygen extraction is not proportional to hemibranch area, so total gill area is not representative of oxygen consumption. Piiper and Schumann (1967) observed a higher Po_2 of expired water at the first gill slit of Scyliorhinus stellaris than the other slits, implying oxygen extraction was less, and attributed this to a higher water flow/blood flow ratio in the first gill slit. In

stationary S. canicula water entering the mouth is expired through the posterior three gill slits, whereas water entering the spiracle leaves via the anterior two slits (Hughes 1960). Grigg (1970) reported that the first gill slits of Heterodontus portjacksoni, which has reduced spiracles, can be used for water intake, though normally water enters through the mouth. Hemibranch respiratory areas may not be proportional to the relative volume of water passing over the gills, based on parasite distribution and gill area per arch (Paling 1968; Hughes 1984). However, water flow over the gills may be abnormal in resting or restrained animals (Fishman 1967; Hughes 1984).

The von Bertalanffy equation has been applied to many elasmobranchs, including Isurus oxyrinchus, Carcharodon carcharias, Prionace glauca, Galeocerdo cuvier, Carcharhinus obscurus, and C. plumbeus (Stevens 1975; Lawler 1976; Pratt and Casey 1983; Cailliet et al. 1985; Casey et al. 1985; Branstetter et al. 1987; Natanson 1990). Holden (1974) modified Equation 1 for elasmobranchs to estimate K without requiring length at age data. Using the apparently false assumption (Pratt and Casey 1990) that pre- and post-natal K were the same, and given the length of gestation, T, length at conception, L_t , and birth, L_{t+T} , and maximum observed length, L_∞ , he estimated K from

$$L_{t+T}/L_\infty = 1 - e^{-KT}$$

Springer (1960) suggested that carcharhiniform growth may be determinate in some Carcharhinus and Negaprion, but indeterminate in Sphyrna and Galeocerdo. Compagno (1988) stated that, at least for some carcharinoids, growth is actually indeterminate but appears determinate because of decreasing growth rates. Although some studies indicate growth rate decreases through life to some constant rate, some tagging evidence suggest that growth is determinate, with rates approaching zero (Thorson and Lacy 1982; Gruber and Stout 1983; Casey et al. 1985).

Gill surface area studies on elasmobranchs determined typical values of d from 0.74 to 0.97 (Hughes 1972; Hughes 1977; Hughes 1978; Emery and Szczepanski 1986; Hughes et al. 1986). This implies that growth is determinate, since A/W decreases with weight. The slow decrease in A/W at larger weights when $d < 1$ or when d approaches unity may simulate a constant ratio ($d = 1$) and erroneously lead to the conclusion of indeterminate growth. If d is not constant throughout the weight range, but increases, then values of $d \geq 1$ would allow for indeterminate growth. Emery and Szczepanski (1986) found that endothermic sharks had a greater gill area per weight than ectothermic sharks, although values of d were not greater. The oxygen consumption coefficient x (Equation 14) is 0.80 for Scyliorhinus spp. (Winberg 1960). In comparison, values of d are 0.96 and 0.78 for S. canicula and S. stellaris,

respectively (Hughes 1972; Hughes et al. 1986). Oxygen consumption data from three free-swimming Sphyrna lewini produced a value of x (Equation 14) = 0.93 (Howe 1988).

The hypothesis to be considered is that anabolism is limited by respiratory surface, and that the supply of oxygen, hence the ratio of gill area to size (length or weight), decreases with size ($d < 1$), so that growth rate decreases in proportion to decrease in A/W or A/L . If L_{∞} or W_{∞} exists, it is determined by some critical ratio, whereby further growth is prevented by lack of sufficient oxygen supply to support it - i.e. anabolism cannot counterbalance the increased catabolism of additional growth. If $d > 1$, growth rate would increase, at least until the ratio reaches some value where anabolism is maximum, wherein growth rate would become constant. This possibility is unlikely, at least in post-natal elasmobranchs.

From Equations 2 and 9, the instantaneous growth rate is defined by

$$dW/dt = kW_{\infty}^{D/b} W^d - kW^m$$

Substituting for W^d and W_{∞}^d produces

$$dW/dt = kA/(A_{\infty}/W_{\infty}^m) - kW^m \quad (15)$$

which for $m = 1$ becomes

$$dW/dt = k/(A_{\infty}/W_{\infty}) [A - W(A_{\infty}/W_{\infty})]$$

Relative gill surface area with respect to weight, A/W , follows the relationship

$$A/W = rW^{d-1}$$

For values of $d < 1$, this represents a decreasing relative oxygen supply, the rate of which is determined by the magnitude of the departure of d from 1.

Energy (food) consumed (C) may be partitioned into total metabolic output (R), fecal (F) and excretory waste loss (U), and energy gain (G) (Kitchell 1983):

$$C = R + F + U + G$$

Total metabolism and waste loss correspond to routine maintenance costs (M), and energy gain consists of both somatic and gonadal growth.

Oxygen consumption (Q) may be equivalently partitioned into components representing routine metabolism (including waste loss) (Q_M) and somatic and gonadal growth (Q_G). Assuming oxygen consumption is proportional to gill surface area, this becomes

$$\begin{aligned} A &= A_M + A_G \\ A_G &= A - A_M \\ A_G &= A - r_M W^{d(M)} \end{aligned}$$

If an asymptotic weight exists as dictated by the von Bertalanffy equation for $d < 1$, at W_∞ , the corresponding gill surface area, A_∞ , can supply only enough oxygen for routine metabolism:

$$\begin{aligned} A_\infty &= A_M \\ A_G &= 0 \\ A_\infty/W_\infty &= A_M/W_\infty \\ A_\infty/W_\infty &= r_M W_\infty^{d(M)} / W_\infty \end{aligned}$$

If $d(M) = 1$,

$$A_{\infty}/W_{\infty} = r_M$$

$$A_M = (A_{\infty}/W_{\infty})W$$

For any weight less than W_{∞} , $A/W > A_{\infty}/W_{\infty}$, and growth is supported by the "excess" gill area

$$A_G = A - (A_{\infty}/W_{\infty})W$$

From Equation 15

$$dW/dt = k/(A_{\infty}/W_{\infty})A_G$$

Theoretically, the instantaneous growth rate is proportional to the potential for growth as described by gill area if $d(M) = m = 1$.

The purposes of this study are to:

1. examine the relationship of gill surface area to length and weight:

$$A = pL^a \text{ (Equation 5)}$$

$$A = rW^d \text{ (Equation 10)}$$

under the hypothesis that a and d are constants following Equation 13.

2. examine the relationship of changes in growth rate to changes in gill surface area to weight ratios under the hypothesis that $dW/dt \propto A_G$.

MATERIALS AND METHODS

The sandbar shark, Carcharhinus plumbeus, is a coastal-pelagic carcharhinid distributed worldwide in temperate and tropical waters (Compagno 1984), and is the most abundant shark in the Chesapeake Bight (Musick and Colvocoresses 1986). The sandbar shark is a relatively large species: the reported maximum length of males is 224 cm total length (TL), and of females is 239 cm, possibly up to 300 cm TL (Compagno 1984). Springer (1960) believed that growth was determinate in this species. Growth studies have been conducted on the Atlantic coast, producing von Bertalanffy equation parameters (Casey et al. 1985). The predicted maximum lengths of 312 cm TL (257 cm fork length: FL) for males and 363 cm TL (299 cm FL) for females are much larger than observed, suggesting that d may deviate substantially from the $2/3$ defined in the original von Bertalanffy equation.

The tiger shark, Galeocerdo cuvier, is similarly a cosmopolitan temperate and tropical carcharhinid of coastal-pelagic waters (Compagno 1984), and is fairly common in Chesapeake Bight experimental long-line collections (Musick and Colvocoresses 1986) and tournament landings. The observed maximum length of males is 370 cm TL. Females reportedly attain lengths greater than 550 cm,

possibly up to 740 cm (Compagno 1984) However, most females do not exceed 430 - 500 cm (Compagno 1984), and reported lengths above 600 cm are unsubstantiated (Randall 1992). Springer (1960) believed that growth was indeterminate in the tiger shark. Branstetter et al. (1987) calculated an L_{∞} of 388 cm TL for Gulf of Mexico specimens and 440 cm for Atlantic coast specimens.

Sharks were collected from long-lining cruises and from shark tournament returns. Specimens were measured for total and standard length (TL and SL) in centimeters (cm) and weight in kilograms (kg), and sex was determined. Weight was not determined for some specimens, so their weights were estimated using length-weight regressions from VIMS collection records (Table 1). Lengths reported in the literature were also converted using these equations.

A total of 16 sandbar and 8 tiger sharks were examined. These included 12 female sandbar sharks 66 to 170 cm SL (88 - 225 cm TL) and 4 males 65 to 134 cm SL (87 - 177 cm TL). Four male tiger sharks ranged from 88 to 272 cm SL (125 cm TL - 354 cm TL) and four females ranged from 70 to 218 cm SL (103 - 302 cm TL). In addition, two blue sharks, Prionace glauca, 171 and 185 cm SL (226 and 248 cm TL), two blacktip sharks, C. limbatus, 91 and 97 cm SL (127 and 130 cm TL) and one dusky shark, C. obscurus, 160 cm SL (214 cm TL) were examined.

One side of the branchial basket, usually the left,

Table 1. Length-weight regressions used in text. Lengths are in cms and weights are in kgs. Sources for equations for blue, dusky, shortfin mako and white sharks are indicated.

X	Y	INTERCEPT	SLOPE	N	r^2
SANDBAR					
TL	SL	1.31	0.746	574	0.996
TL	FL	1.96	0.818	664	0.994
SL	FL	1.13	1.092	574	0.998
LOG SL	LOG WT	-4.994	3.109	422	0.991
LOG TL	LOG WT	-5.308	3.081	419	0.989
LOG FL	LOG WT	-5.163	3.125	420	0.990
TIGER					
TL	SL	-13.51	0.797	26	0.996
TL	FL	-8.93	0.849	31	0.996
SL	FL	5.14	1.065	26	0.999
LOG SL	LOG WT	-4.839	2.980	22	0.991
LOG TL	LOG WT	-5.884	3.255	24	0.991
LOG FL	LOG WT	-5.212	3.093	30	0.993
DUSKY (Natanson 1990)					
TL	FL	-2.2973	0.8352	167	0.99
LOG TL *	LOG TW	-5.313	3.029	80	0.985
BLUE (Stevens 1975)					
LOG TL	LOG WT	-5.894	3.208		
SHORTFIN MAKO (Pratt and Casey 1983)					
TL	FL	1.931	0.929	179	0.99
(Compagno 1984)					
LOG TL	LOG WT	-5.316	3.10		
WHITE (Compagno 1984)					
LOG TL	LOG WT	-5.363	3.14		

* from data in appendix

was removed and stored in 10% Formalin. The right side was used if the left side was damaged during capture. Bilateral symmetry was assumed, so that the gill areas on the left and right sides of the body were considered to be equal (Hughes, et al. 1986). This assumption permitted the examination of only one side. That estimate was then doubled to obtain the total gill area. No correction was applied for fixative effect, although Oikawa and Itazawa (1985) calculated a shrinkage coefficient of 5.7% for carp gill areas fixed in 10% Formalin. Gill area-weight regression slopes should not be affected by shrinkage, although intercepts are (Hughes 1990). Gill slit heights, in millimeters, were measured from one side of 12 sandbar, 7 tiger and all additional shark species, and doubled to account for both sides of the shark.

For each side there are g hemibranchs; in the sandbar and tiger sharks this consists of one posterior hemibranch on the hyoid arch, and an anterior and posterior hemibranch separated by a septum on each of four branchial arches for a total of $g = 9$ hemibranchs. For each hemibranch, the length (L_h) of the first and last six filaments, and every other or every third filament between was determined to the nearest 0.1 or 1 mm using a dial caliper or ruler, respectively. Lengths of filaments not directly measured were determined by linear interpolation. For one tiger shark in which all filaments on one side were measured, the

total filament length calculated from measurements of every third filament differed by no more than 0.1% from the complete measurement for each hemibranch, and by only 0.04% overall. However, abbreviated measurements were always less than complete measurements, due to the convexity of filament lengths. As the number of unmeasured filaments between measured filaments increases, the amount of underestimation may become considerable.

A systematic sample of $p \geq 12$ filaments from at least one hemibranch was usually selected. When fewer than 12 filaments were selected systematically, additional filaments were randomly selected to obtain a total of 12 filaments. Several hemibranchs were examined in a selected subsample of specimens to determine if the relationship between filament area and filament length was constant between hemibranchs.

Filaments consisted of exposed lamellae and lamellae under a branchial canopy as observed in other elasmobranch species (Benz 1984). This study only examined exposed lamellae in area estimates because those under the branchial canopy were not considered to contribute to respiration.

Selected filaments were excised, placed on a glass slide, and examined under a dissecting microscope. Filament length (L'_h) was measured again in optical micrometer units (OMUs: 1 OMU = 0.67 mm) because excised length often

differed from in situ length. The h th filament ($h = 1$ to p) was divided into $k = 2$ or 3 strata of approximately equal length (L'_{hi} , $i = 1$ to k). When a filament was less than 30 OMUs, it was usually divided into 2 strata. Two or three counts ($= x_{hi}$) of the number of lamellae per unit length (n_{hij}) were made in each stratum to estimate the total number of lamellae in the i th stratum (N_{hi}) and for the filament (N_h). Usually a sample of $m_{hi} = 3$ lamellae was randomly selected by position (OMUs) within each stratum. For example, a filament $L_h = 33.4$ mm in situ and 47.2 OMUs excised ($L'_h = 31.7$ mm) was cut into basal, medial and distal strata of $L'_{h,1-3} = 15.6, 15.5$ and 16.1 OMUs (23.3, 23.1 and 24.0 mm), respectively. For the basal stratum, counts of 10 lamellae/0.84 mm, 10/0.80 and 10/0.82 ($n_{h,1,1-3} = 11.9, 12.5$ and 12.2 lamellae/mm) were made from the basal, medial and distal portions of the section, and 3 positions, 118, 128 and 48 OMUs were randomly selected from a possible 156 positions (10 x OMU). Counts of lamellae and random positions were similarly selected from the medial and distal strata from, respectively, 155 and 161 possible positions. A section, usually consisting of 2-4 lamellae was excised with a razor blade from the filament sections as close as possible to the selected positions. The selection of 2-4 lamellae insured that at least one was undamaged.

Counts of lamellae/mm and area measurements were made

using a BioSonics Optical Pattern Recognition System which digitized a dissecting microscope image obtained via a video camera. Video images could be measured for distances and areas using computer software calibrated to the image with a stage micrometer.

The area of one side of the j th lamella (a'_{hij}) was assumed to be exactly equal to that of the other side, so that the total area of the lamella is $a_{hij} = 2a'_{hij}$. The area of stratum i , a_{hi} , and of filament h , a_h , and their variances are

$$\begin{aligned} A_{hi} &= N_{hi} \bar{a}_{hi} \\ s^2(\bar{a}_{hi}) &= [\Sigma (a_{hij} - \bar{a}_{hi})^2] / (m_{hi} - 1) \\ s^2(A_{hi}) &= N_{hi} (N_{hi} - m_{hi}) s^2(\bar{a}_{hi}) / m_{hi} \\ A_h &= \Sigma A_{hi} \\ s^2(A_h) &= \Sigma s^2(A_{hi}) \end{aligned}$$

where

$$\begin{aligned} \bar{a}_{hi} &= \Sigma a_{hij} / m_{hi} \\ N_{hi} &= L'_{hi} \Sigma n_{hij} / x_{hi} \end{aligned}$$

For the example above,

$$\begin{aligned} N_{h,1} &= 23.3(11.9+12.5+12.2)/3 = 284 \text{ lamellae} \\ a'_{h,1,1} &= 0.89; a_{h1,1} = 1.78 \text{ mm}^2 \\ a'_{h,1,2} &= 0.95; a_{h1,2} = 1.90 \text{ mm}^2 \\ a'_{h,1,3} &= 0.65; a_{h1,3} = 1.30 \text{ mm}^2 \\ A_{h,1} &= 284.3(1.78+1.90+1.30)/3 = 472 \text{ mm}^2 \\ s^2(\bar{a}_{h,1}) &= 0.101 \\ s^2(A_{h,1}) &= 284(284-3)0.101/3 = 2687 \end{aligned}$$

Analysis of covariance was used to determine if the

regression relationship of filament area to filament length differed between hemibranchs. Bartlett's test was used to determine if the regression variances differed between hemibranchs. All nine hemibranchs were examined from one G. cuvier, and eight hemibranchs were examined from one C. plumbeus. In addition, two or three hemibranchs were examined from several other specimens of each species.

Gill area estimates were conducted in two ways. The first method (A) assumed no significant difference in slopes or intercepts between hemibranchs within each specimen (see RESULTS). Data were pooled to obtain a single regression slope and intercept for each specimen, which were then applied to all filaments from all hemibranchs of that specimen.

Visual examination of scatter-plots indicated that $s(A_h)$ was proportional to A_h , so filament area and length were transformed to the regression form

$$\log(A_h) = c + B \log(L_h)$$

The regression results from the sample were then applied to all filaments to estimate the total gill area:

$$A = 4 \sum A_h$$

The gill area estimated from the measured filaments was multiplied by 4 to obtain the total area, A, to account for lamellae on both sides of each filament, and for the other side of the branchial basket which was not measured.

Ninety-five percent confidence intervals of A were

determined by calculating the 95% prediction intervals (Montgomery and Peck 1982) of individual filaments and summing.

Method B assumed no significant difference in slopes between hemibranchs within specimens or between specimens. However, differences in intercepts between anterior and posterior facing hemibranchs within specimens and between specimens were assumed (see RESULTS). It was further assumed that the intercepts were correlated with standard length. The multiple regression model assumed the form:

$$\log (A_h) = B_0 + B_1 * SL + B_2 * HEMI + B_3 * \log(L_h)$$

where B_x are coefficients, SL = standard length and HEMI = an indicator variable, with a value of 0 for posterior facing hemibranchs and 1 for anterior facing hemibranchs.

Total gill area was then calculated as

$$A = 4 \sum 10^{(A_h)}$$

The above methods of determining total gill area were compared with that of Hughes (1966). Under this method (C), usually every fifth filament is measured to obtain an overall estimate of the total filament length, L. From a sample of filaments - e.g. every twentieth on a holobranch, three lamellae are measured from each filament, one each from the base, middle and tip, and bilateral areas are determined and averaged over all filaments (a). The number of lamellae/mm (n) is determined from three counts from each filament and averaged. The total gill area is then

estimated as

$$A = 4 * L * n * a$$

The present study used filament lengths as measured above, the means of all estimates of lamellae/mm and lamella areas, with up to nine measurements per filament for both counts and areas.

Once the gill surface area (A) was estimated for the sample of sharks it was regressed against weight (W) and length (L) in the form

$$A = rW^d$$

$$\log(A) = \log(r) + d \log(W)$$

$$A = pL^a$$

$$\log(A) = \log(p) + a \log(L)$$

Evaluation of the generalized von Bertalanffy growth equation utilized gill surface area equations determined for sandbar and tiger sharks in this study and equations determined for shortfin mako, Isurus oxyrinchus, white, Carcharodon carcharias, dusky, Carcharhinus obscurus, and blue sharks, Prionace glauca, by Emery and Szczepanski (1986). Both studies used specimens fixed in 10% Formalin, so any shrinkage was considered equal between studies.

Empirical values of D and d were derived from back-calculated length at age data for shortfin mako, white, blue, dusky, sandbar, and tiger sharks (Stevens 1975; Lawler 1976; Pratt and Casey 1983; Cailliet et al. 1985; Casey et al. 1985; Branstetter et al. 1987; Natanson 1990)

using the modified Ford-Walford equation (Taylor 1962; Pauly 1981)

$$L_{t+1}^D = m + n \cdot L_t^D$$

The parameter D is practically bounded by 0 ($d = 1$) and b ($d = 0$). The best empirical fit was determined as the D that resulted in the largest r^2 value. These empirical estimates of D were then applied to generalized von Bertalanffy growth equations (Equations 3 and 4 above) where $n = e^{-KD}$ and $m = L_\infty(1 - n)$. Values of t_0 were fit by minimizing the sum of squared deviates (observed length - predicted). Observed values of d obtained here and by Emery and Szczepanski (1986) were also fit to the modified Ford-Walford equation. Empirically derived estimates of D and von Bertalanffy equation parameters were compared with those obtained from observed values of d . Values of K are not directly comparable between different values of D, but following the modified Ford-Walford equation, values of KD are equivalent. Usually only ages represented by two or more individuals were included. Calculated values of L_∞ and W_∞ were compared with observed maxima (Compagno 1984). Lengths were converted to weights using equations presented in Table 1.

For derivations of the generalized von Bertalanffy equation using Equation 15, observed growth rates, dW/dt , were estimated from length at age data reported in the literature, converted to weight as $(W_t - W_{t-z})/z$ where $z =$

time between formation of the birth mark and first winter mark or time between subsequent winter marks (1 year). Using gill surface area equations, K and W_{∞} were empirically estimated from Equation 15 by forced regression through the origin:

$$dW/dt = \beta_1(3A) + \beta_2(3W)$$

where $\beta_1 = (W_{\infty}/A_{\infty})K$

$$\beta_2 = K$$

The parameter t_0 was estimated by minimizing the sum of squared deviations of predicted length at age from observed.

The formation of vertebral bands in young sandbar sharks is apparently annual, at least through about 104 cm TL, based on laboratory studies (Branstetter 1987) and aquarium specimens (Casey et al. 1985). However, annual periodicity has not been validated in older individuals. Casey and Natanson (1992) found much slower growth in sandbar sharks based on tag-recapture specimens than reported by Casey et al. (1985).

Values of dW/dt can be determined from tag-recapture data as $(W_r - W_t)/t$ where W_r is weight at recapture, W_t is weight at tagging, and t is time at liberty. K can be estimated from the regression coefficients without requiring exact knowledge of ages. Tag-recapture data for sandbar sharks (Casey and Natanson 1992) and blue sharks (Stevens 1976; 1990) were used to estimate K and W_{∞} , which

were compared with estimates from other methods. Values of dW/dt were regressed against the mid-point weights $(W_r - W_t)/2$ calculated from lengths at tagging and recapture, and the associated predicted gill area. Data used in regressions for sandbar sharks excluded values of $dW/dt > 5$ kg/yr. Data for blue sharks excluded values of $dW/dt < 0$. Equations were fit to estimated lengths at birth of 40 cm for blue sharks and 51.4 cm (44 cm FL) for sandbars to obtain t_0 .

Vertebrae for age determination were obtained from 13 C. plumbeus used to determine gill area in order to examine whether individual gill surface areas affected growth. Vertebrae were obtained from only 4 tiger sharks, so age determination was not attempted from them. A segment of two or more vertebrae was removed from the spinal column anterior to the first dorsal fin and either stored in 10% Formalin or frozen. For examination, individual vertebrae were separated and cleaned of any remaining tissue, then air-dried. A longitudinal section was obtained by cutting a portion of the vertebra with a fine-toothed saw. The exposed face was polished to near the center with 240-320 grit wet/dry sandpaper, then fixed to a microscope slide with thermoplastic cement. The remaining portion of the vertebra was then removed to leave a section approximately 0.5 mm thick. The exposed face was polished with 400 grit wet/dry sandpaper then buffed with aluminum oxide powder.

Finished sections were examined under a dissecting microscope and measurements were made using the BioSonics Optical Pattern Recognition System following Casey et al. (1985).

Regression of standard length (SL) on vertebral radius (VR) produced the equation

$$SL = 0.006 + 0.0726*VR$$

The regression intercept was not significant so the Dahl-Lea direct proportion method was used to back-calculate vertebral marks to ages as

$$SL_c = VR_c (SL_i / VR_i)$$

where SL_i and SL_c are length at mark i and at capture, and VR_i and VR_c are vertebral radius at mark i and at capture, respectively. Age at capture was estimated by assuming the first annulus was formed at an assigned birth date of 1 June, and that subsequent marks were formed on an arbitrary 1 January date (Casey et al. 1985). Therefore, the first winter mark is formed at an age of 0.58 years, and a shark captured on 1 July with 6 annuli (1 birth and 5 winter marks) was 6.08 years of age.

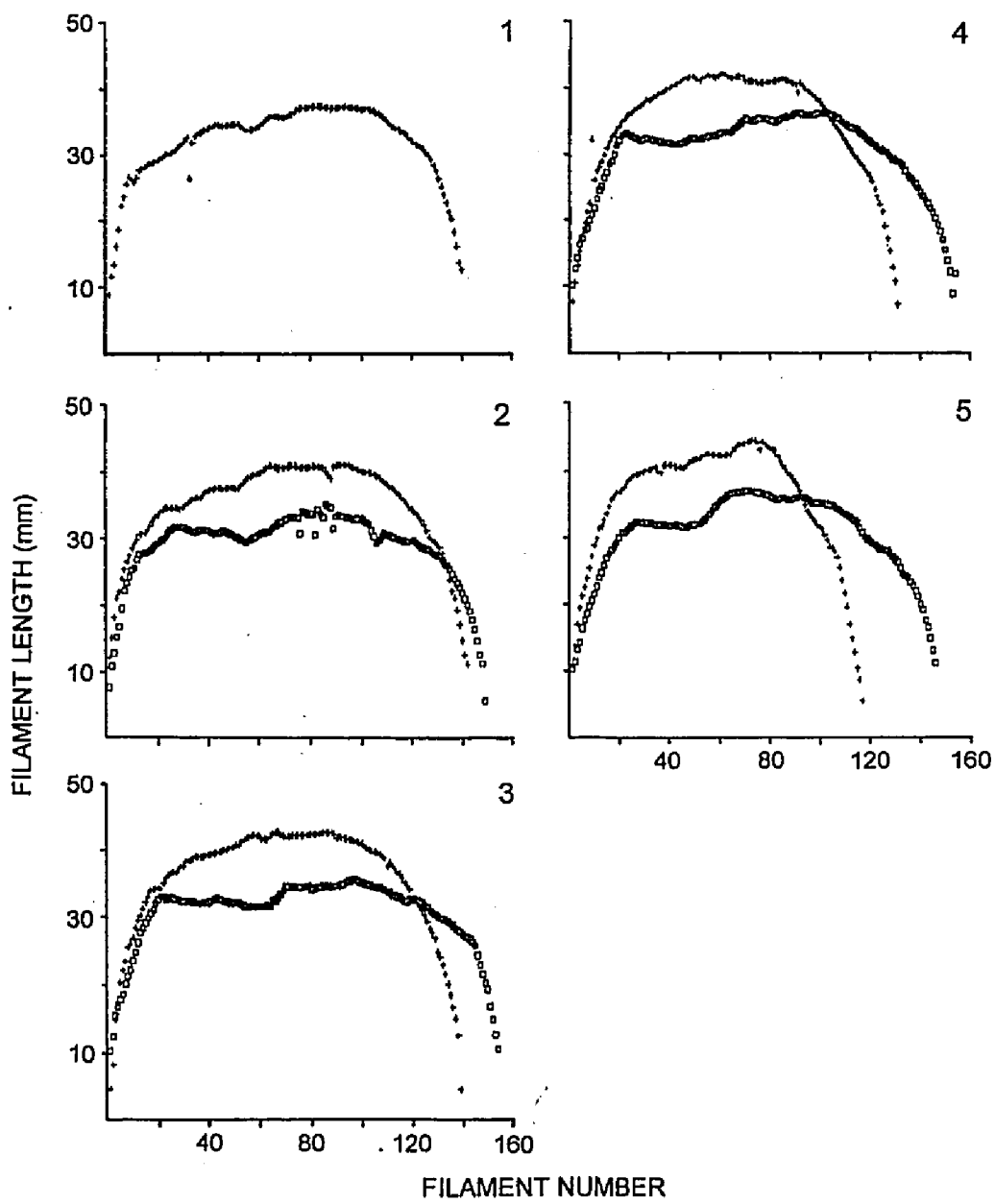
RESULTS

Gill Surface Area

Sandbar Shark:

In the sandbar shark the longest gill filaments were generally found on the posterior-facing, odd-numbered, hemibranchs (1, 3, 5, 7, 9). However, the number of filaments on anterior-facing, even-numbered, hemibranchs (2, 4, 6, 8) were greater than on the posterior-facing hemibranch for a given holobranch (Fig. 1). Filaments rapidly increased in length from the hemibranch origin. On posterior facing Hemibranchs 1 and 3 the longest filaments occurred on the descending limb of the arch. Generally, the longest filaments occurred progressively toward the middle of the arch from Hemibranch 5 to 9. In anterior facing hemibranchs, following an initial rapid increase in filament length, lengths leveled off or decreased slightly from approximately Filaments 30 through 60. In general, on anterior facing hemibranchs the longest filaments occurred on the descending arch limb. There were occasional irregularities in filament appearance. Filaments were occasionally truncated, either by defect or mechanical damage (Fig. 1, Hemibranch 1). Parasitism was frequently apparent, especially in larger individuals, commonly resulting in scarring or truncation of filament tips (e.g.

Figure 1. Lengths of gill filaments for each holobranch on the left side of a sandbar shark specimen. Crosses denote posterior-facing hemibranchs, squares denote anterior-facing hemibranchs. The first filament is the most dorsal on that hemibranch.



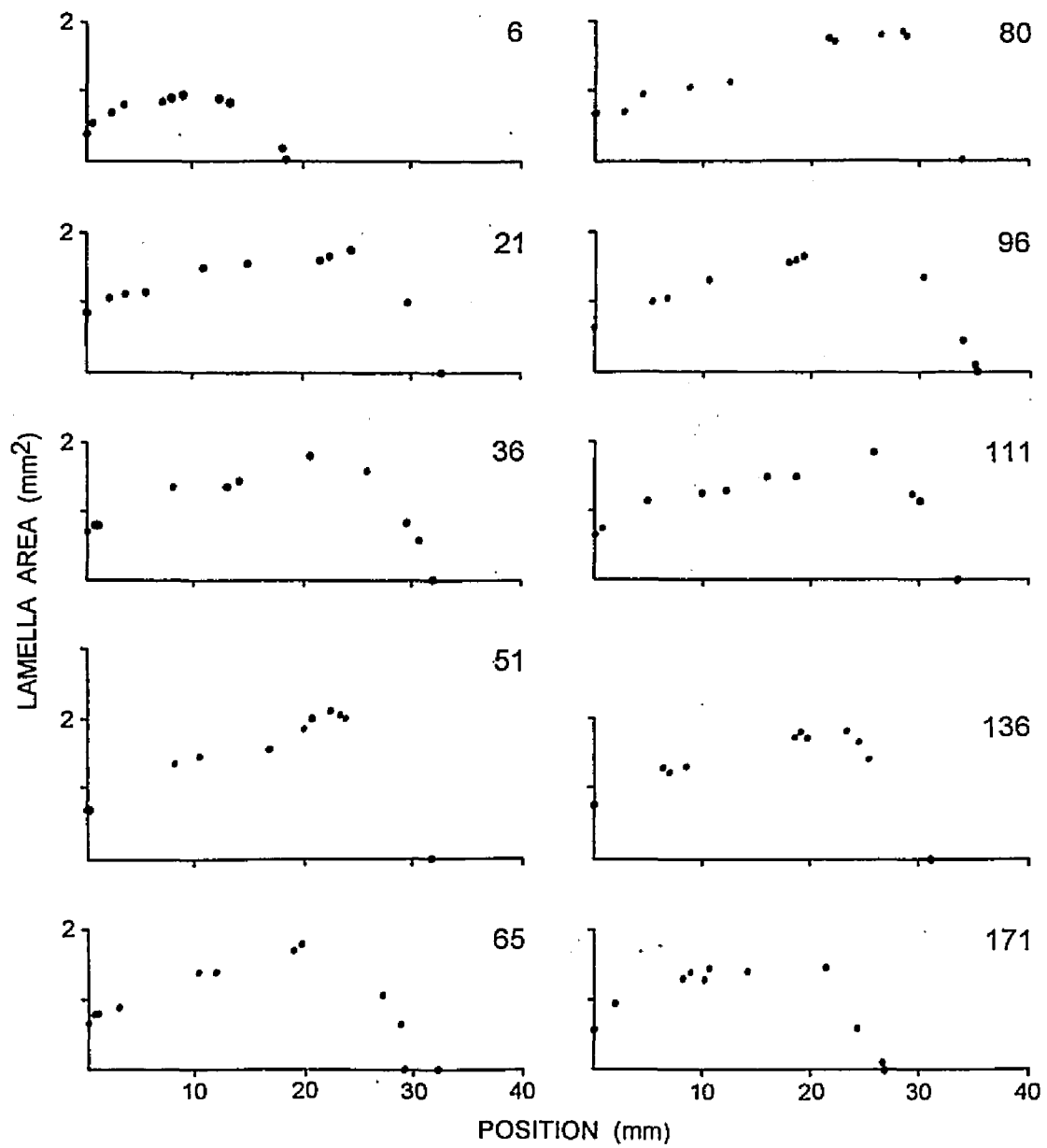
Hemibranch 2). Some filaments were forked, resulting in a greater effective length (Hemibranch 7). Fusion of filaments in some specimens was apparently due to healing after some mechanical damage.

Lamella areas of select filaments on Hemibranch 4 are illustrated in Figure 2. Following emergence from the branchial canopy, lamellar area gradually increased. Maximum lamellar area occurred at 2/3 to 4/5 of filament length, then rapidly decreased toward the filament tip. As seen in Filament 65, filament tips were occasionally scarred with no lamellae present.

The total number of filaments on one side of the branchial basket ranged from 1253 to 1306. There was no significant correlation between number of filaments and size of the individual. However, the mean and total length of filaments were positively correlated with standard length ($r = 0.9831$ and 0.9867 , respectively), indicating that increases in gill area with size are due to changes in filaments themselves, rather than to increases in numbers of filaments.

For one specimen the sample size of lamellae selected was approximately proportional to number of lamellae. One lamella was selected for each five OMUs, with a minimum of three lamellae randomly selected from each section. Therefore, three lamellae were selected from sections < 15 OMUs, (total $m_h = 9$ lamellae from total filament length < 45

Figure 2. Bilateral surface areas of the first, last and randomly selected lamellae from selected filaments on the fourth hemibranch shown in Figure 1. Filament number is denoted in upper right corner. Positions are indicated as distance from the base of the filaments.



OMUs) four from sections 15-20 OMUs and five from sections 20-25 OMUs. Total filament areas were estimated from maximum $m_{hi} = 1, 2, 3$ and 4 by including only the first 1, 2, 3 and 4 lamellae in randomly selected order and compared with area estimates for the maximum $m_{hi} = 5$ selected. Regression MSEs decreased as sample size increased from one to three lamellae (Fig. 3a). Although variances apparently increased from the minimum at $m_{hi} = 3$, this was likely due to random selection rather than a real phenomenon. Even with maximum sample sizes of four or five, sample sizes of some filaments were only three or four. Regression variances would be even lower if all sample sizes were the maximum. Standard deviations of estimated total filament area for five filaments in which $m_{hi} = 5$ were plotted as lamellae were randomly added to the estimate and showed a fairly steady decrease (Fig. 3b). Therefore, a sample size of $m_{hi} = 3$ was selected as a balance of cost (time) and accuracy.

Typically, lamellae were selected from the side of the filament visible as it was placed with the tip to the right. From the specimen used above for sample size determination, area estimates were made from the "typical" side of seven systematically sampled filaments from Hemibranch 5 and from the "opposite" side of seven filaments. Analysis of covariance (Table 2) did not reveal any significant difference in regression slopes or

Figure 3. a: Variance (MSE) of regressions of $\log(\text{filament area})$ on $\log(\text{filament length})$ as the number of lamellae measured increases from one to five per section (three sections per filament). b: standard deviations ($s(A)$) of calculated filament area for five filaments as the number of lamellae measured increases from one to five per section.

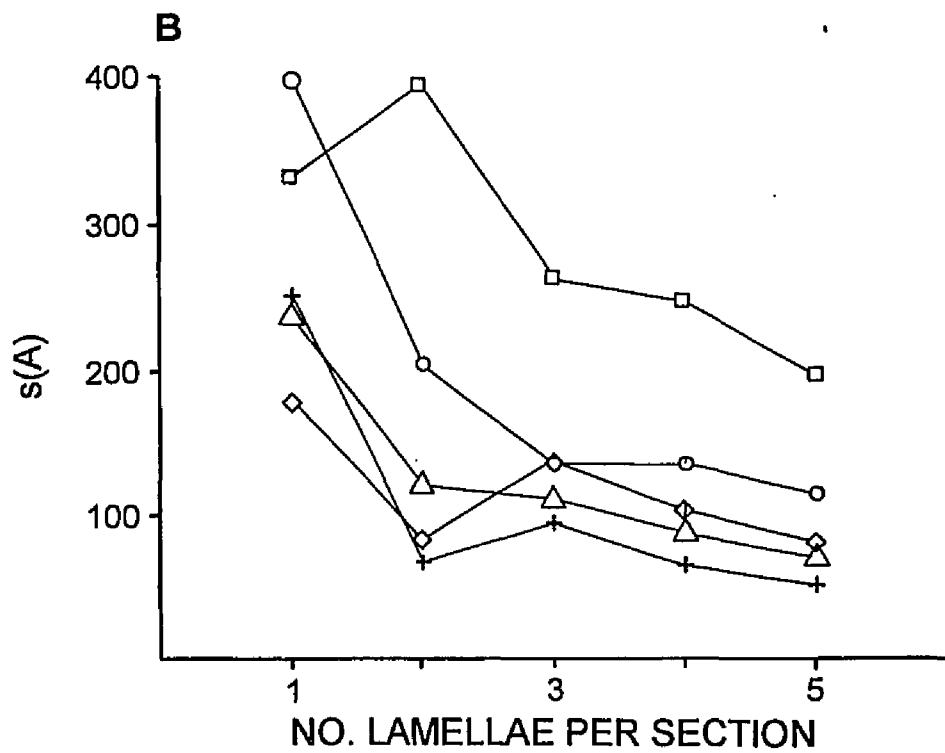
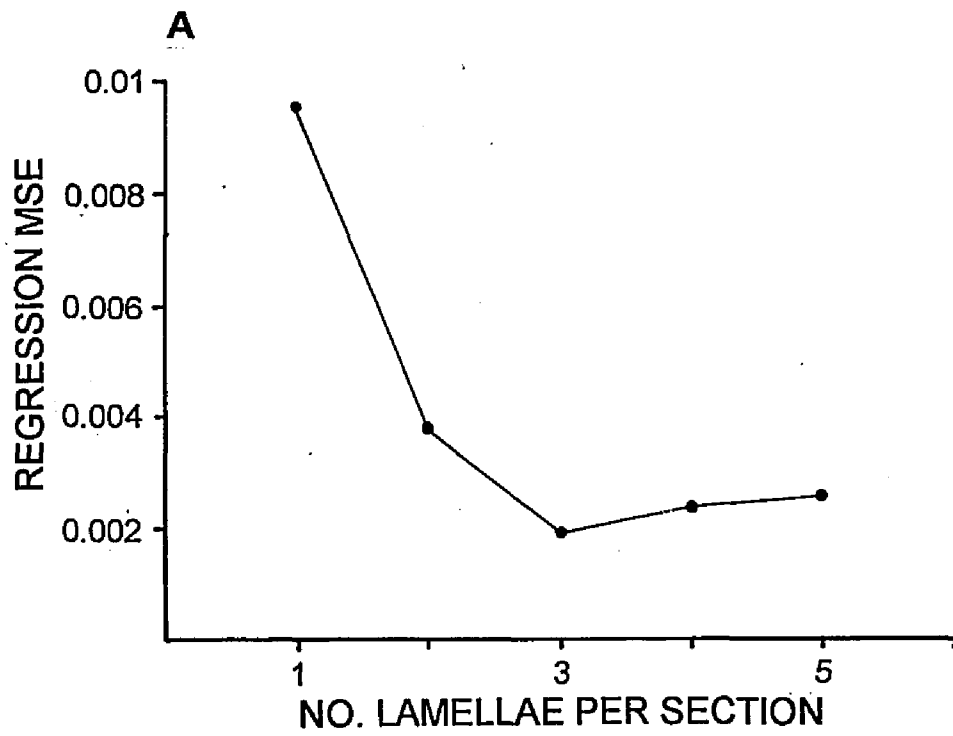


Table 2. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for measurements on the "typical" (T) and "opposite" (O) sides of filaments on Hemibranch 5 from a sandbar shark specimen. B denotes Bartlett's test statistic. Tests were conducted at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
R5T	7	1.5783	0.0032	1.7111	0.406	0.22	1.07	0.24
R5O	7	1.8167	0.0021	1.7111	0.420			

intercepts. Therefore, estimates made from the "typical" side were considered representative of both sides.

Analysis of covariance did not reveal any consistent difference in the relationship of the number of lamellae and filament length among hemibranchs. Regression slopes and intercepts of log-transformed data were not significantly different among hemibranchs in some specimens, but were different in others (Table 3).

Similarly, there were no consistent relationships between mean lamella area and filament length among hemibranchs. Regression slopes and/or intercepts of log transformed data were significantly different for some specimens, but not for others (Table 4). However, in specimens in which slopes were equal, there was a tendency for intercepts to be higher in even-numbered hemibranchs than in odd-numbered hemibranchs, whether the difference was significant or not.

Analysis of covariance indicated consistent relationships between filament area and filament length between hemibranchs (Table 5). There was a significant difference in regression slopes among Hemibranchs 4, 5 and 9 in the original data set for one specimen. However, this difference was due to one short filament, which, as an endpoint for the regression line, had a strong influence. No significant difference in slopes was observed when that filament was deleted from the data set. For one specimen in

Table 3. Results of analysis of covariance of regressions of number of lamellae (y) on filament length (x) for sandbar sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{01} : all variances equal; H_{02} : all slopes equal; H_{03} : all intercepts equal.

HEMI	N	SLOPE	MSE	ADJ. SLOPE	ADJ. INT.	H_{01} B	H_{02} F	H_{03} F
L4	14	0.7815	0.0009	-	-	3.88*		
L5	14	0.6910	0.0003	-	-			
R8	12	0.7247	0.0004	0.7302	1.495	3.69	0.16	0.24
L9	12	0.7469	0.0001	0.7302	1.499			
L4	12	0.9877	0.0006	0.9651	1.140	4.66	1.08	0.74
L5	12	0.8674	0.0001	0.9651	1.134			
L9	12	0.9722	0.0005	0.9651	1.145			
L4	12	0.8314	0.0010	0.8217	1.409	5.93	0.39	0.52
L5	12	0.7900	0.0002	0.8217	1.407			
L9	11	0.8566	0.0004	0.8217	1.417			
L4	12	0.8403	0.0008	-	-	7.00*		
L5	16	0.7501	0.0002	-	-			
L1	10	1.0274	0.0005	-	-	1.48	5.57*	
L4	13	0.9850	0.0003	-	-			
L5	13	0.8098	0.0002	-	-			

Table 3. Continued.

HEMI	N	SLOPE	MSE	ADJ.	ADJ.	H _{O1}	H _{O2}	H _{O3}
				SLOPE	INT.	B	F	F
L4	13	1.1032	0.0004	-	-	2.42	5.52*	
L5	13	0.8548	0.0001	-	-			
L9	12	0.8757	0.0002	-	-			
L1	13	0.7836	0.0001	0.8087	1.345	10.41	1.33	2.47*
L2	12	0.8142	0.0003	0.8087	1.360			
L3	12	0.7427	0.0001	0.8087	1.363			
L4	12	0.7813	0.0006	0.8087	1.370			
L5	12	0.7737	0.0003	0.8087	1.369			
L6	12	0.8518	0.0001	0.8087	1.365			
L7	12	0.8340	0.0003	0.8087	1.354			
L8	12	0.8348	0.0009	0.8087	1.363			

Table 4. Results of analysis of covariance of regressions of mean lamella area (y) on filament length (x) for sandbar sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
L4	13	0.8749	0.0041	0.9855	-1.307	0.01	2.40	9.55*
L5	13	1.1516	0.0043	0.9855	-1.225			
R8	12	0.9598	0.0012	-	-	4.10*		
L9	12	1.1911	0.0047	-	-			
L4	11	1.0890	0.0014	1.0059	-1.045	2.26	0.59	6.72*
L5	12	0.8690	0.0009	1.0059	-1.084			
L9	12	1.0330	0.0026	1.0059	-1.106			
L4	12	1.1892	0.0040	1.1572	-0.361	0.51	2.59	1.26
L5	12	1.2841	0.0057	1.1572	-1.702			
L9	11	0.7303	0.0036	1.1572	-1.666			
L4	12	0.9373	0.0036	0.9026	-0.945	0.77	0.04	1.72
L5	16	0.8800	0.0022	0.9026	-0.974			
L1	10	1.2538	0.0016	1.1471	-1.192	4.07	0.22	3.25
L4	13	1.1049	0.0021	1.1471	-1.203			
L5	13	1.1197	0.0058	1.1471	-1.248			

Table 4 (continued).

HEMI				ADJ.	ADJ.	H _{O1}	H _{O2}	H _{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
L4	13	0.5856	0.0023	-	-	0.98	4.60*	
L5	13	1.0457	0.0038	-	-			
L9	12	1.2760	0.0022	-	-			
L1	13	1.2444	0.0054	1.1513	-1.296	2.88	1.22	2.21*
L2	12	1.0682	0.0058	1.1513	-1.267			
L3	12	1.0517	0.0041	1.1513	-1.316			
L4	12	1.2972	0.0029	1.1513	-1.256			
L5	12	1.0880	0.0047	1.1513	-1.307			
L6	12	1.1228	0.0039	1.1513	-1.265			
L7	12	1.3329	0.0110	1.1513	-1.343			
L8	12	0.8656	0.0026	1.1513	-1.267			

Table 5. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for sandbar sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
L4	14	1.9881	0.0085	-	-	5.17*		
L5	14	2.4390	0.0021	-	-			
R8	12	1.6846	0.0015	1.7467	0.208	3.07	1.68	9.12*
L9	12	1.9381	0.0048	1.7467	0.133			
L4	11	1.9183	0.0014	1.9378	0.149	2.35	1.37	6.46*
L5	12	1.7365	0.0008	1.9378	0.105			
L9	12	2.0053	0.0024	1.9378	0.091			
L4	12	2.0207	0.0022	1.9789	-0.267	2.05	2.88	2.42
L5	12	2.0742	0.0052	1.9789	-0.295			
L9	11	1.5870	0.0023	1.9789	-0.239			
L4	12	1.7778	0.0035	1.6883	0.457	0.67	0.30	2.19
L5	16	1.6302	0.0022	1.6883	0.425			
L1	10	2.2813	0.0020	2.0771	-0.039	1.88	1.15	1.45
L4	13	2.0901	0.0024	2.0771	-0.024			
L5	13	1.9296	0.0048	2.0771	-0.062			

Table 5 (Continued).

HEMI	N	SLOPE	MSE	ADJ.	ADJ.	H _{O1}	H _{O2}	H _{O3}
				SLOPE	INT.	B	F	F
L4	13	1.6890	0.0027	2.0559	-0.027	0.40	2.77	2.03
L5	13	1.9006	0.0034	2.0559	-0.060			
L9	12	2.1518	0.0023	2.0559	-0.069			
L1	13	2.0281	0.0054	1.9601	0.049	2.85	1.43	2.84*
L2	12	1.8825	0.0045	1.9601	0.093			
L3	12	1.7945	0.0043	1.9601	0.046			
L4	12	2.0786	0.0026	1.9601	0.114			
L5	12	1.8618	0.0038	1.9601	0.062			
L6	12	1.9748	0.0040	1.9601	0.099			
L7	12	2.1670	0.0117	1.9601	0.011			
L8	12	1.7005	0.0038	1.9601	0.097			

which filaments were measured from eight hemibranchs, there was no significant difference in slopes but there was a significant difference in intercepts. When regression slopes were equal, anterior facing hemibranchs usually had a higher intercept, whether or not the difference was significant. Although most comparisons were conducted on two or three hemibranchs, this difference was consistent in the specimen in which eight hemibranchs were examined.

Analyses of regression slopes indicated no significant differences for anterior facing hemibranchs or posterior facing hemibranchs (Tables 6 and 7). Furthermore, when pooled within specimens, there was no significant difference in slopes among specimens (Table 8).

Individual slopes and intercepts for anterior and posterior facing hemibranchs were visually examined for patterns. Intercepts were significantly correlated with standard length, although slopes were not (Fig. 4). There was no significant difference in slopes of regressions of intercepts on standard length for anterior and posterior facing hemibranchs ($F = 3.27$, $df = 1, 20$).

The apparent equality of filament area/length slopes allowed the use of a single pooled slope. Method B produced the multiple regression equation presented in Table 9. All coefficients were significant. Similar forms of the equation were applied to the number of lamellae and mean lamella area for each filament. The indicator variable was

Table 6. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for sandbar sharks for even-numbered (anterior-facing) hemibranchs, pooled within specimens (SPEC). B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

SPEC	N	SLOPE	MSE	ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
				SLOPE	INT.	B	F	F
CP001	14	1.8571	0.0076	1.8852	0.095	4.80	1.25	45.33*
CP010	12	1.6846	0.0015	1.8852	0.023			
CP011	11	1.9183	0.0014	1.8852	0.230			
CP012	12	2.0207	0.0022	1.8852	-0.161			
CP013	12	1.7778	0.0035	1.8852	0.164			
CP014	48	1.8983	0.0036	1.8852	0.211			
CP015	13	2.0901	0.0024	1.8852	0.264			
CP016	13	1.6890	0.0027	1.8852	0.224			
CP017	9	1.5201	0.0013	1.8852	0.178			

Table 7. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for sandbar sharks for odd-numbered (posterior-facing) hemibranchs, pooled within specimens (SPEC). B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

SPEC				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
CP001	14	2.0460	0.0010	2.0265	-0.193	6.05	0.95	45.31*
CP002	11	2.0414	0.0011	2.0265	0.154			
CP005	12	1.9237	0.0017	2.0265	0.010			
CP006	19	2.0938	0.0045	2.0265	-0.169			
CP007	15	2.1703	0.0035	2.0265	-0.110			
CP008	14	2.2319	0.0021	2.0265	-0.208			
CP009	12	2.1552	0.0094	2.0265	-0.318			
CP010	12	1.9381	0.0048	2.0265	-0.270			
CP011	24	1.9529	0.0017	2.0265	-0.044			
CP012	23	1.9460	0.0051	2.0265	-0.328			
CP013	12	1.7778	0.0035	2.0265	-0.046			
CP014	49	1.9966	0.0065	2.0265	-0.057			
CP015	23	2.0502	0.0037	2.0265	0.026			
CP016	25	2.0877	0.0030	2.0265	-0.020			
CP017	14	1.7096	0.0025	2.0265	-0.079			
CP019	14	2.0324	0.0060	2.0265	-0.064			

Table 8. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for sandbar sharks, odd- (O) and even-numbered (E) hemibranchs pooled within specimens. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

SPEC		N	SLOPE	MSE	ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
					SLOPE	INT.	B	F	F
CP001	E	14	1.857	0.0076	1.986	-0.051	3.52	1.33	47.31*
CP001	O	14	2.046	0.0010	1.986	-0.130			
CP002	O	11	2.041	0.0011	1.986	0.226			
CP005	O	12	1.924	0.0017	1.986	0.079			
CP006	O	19	2.094	0.0045	1.986	-0.113			
CP007	O	15	2.170	0.0035	1.986	-0.047			
CP008	O	14	2.232	0.0021	1.986	-0.151			
CP009	O	12	2.155	0.0094	1.986	-0.268			
CP010	E	12	1.685	0.0015	1.986	-0.111			
CP010	O	12	1.938	0.0048	1.986	-0.211			
CP011	E	11	1.918	0.0014	1.986	0.075			
CP011	O	24	1.953	0.0017	1.986	0.021			
CP012	E	12	2.021	0.0022	1.986	-0.275			
CP012	O	23	1.946	0.0051	1.986	-0.277			
CP013	E	12	1.778	0.0035	1.986	0.015			
CP013	O	12	1.778	0.0035	1.986	0.015			
CP014	E	48	1.898	0.0036	1.986	0.063			
CP014	O	49	1.997	0.0065	1.986	0.004			
CP015	E	13	2.090	0.0024	1.986	0.113			
CP015	O	23	2.050	0.0037	1.986	0.089			
CP016	E	13	1.689	0.0027	1.986	0.076			
CP016	O	25	2.088	0.0030	1.986	0.041			
CP017	E	9	1.520	0.0013	1.986	0.024			
CP017	O	14	1.710	0.0025	1.986	-0.015			
CP019	O	14	2.032	0.0060	1.986	0.001			

Figure 4. Plot of intercepts, adjusted for common slope, of regressions of filament area on filament length against standard length. Data were pooled within anterior-facing (circles) and posterior-facing (crosses) hemibranchs for each specimen.

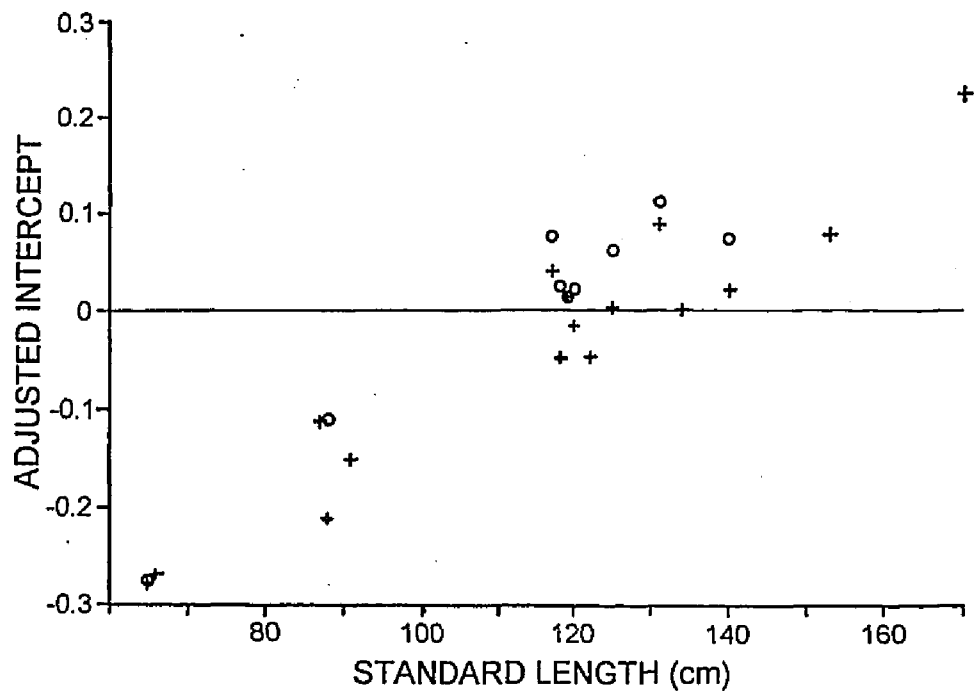


Table 9. Parameter estimates for regressions of log transformed total filament area estimates (AREA), mean lamella area (MEAN LAM AREA) and total number of lamellae (NO. LAMELLAE) for all sandbar sharks combined (see METHODS). SL denotes standard length (cm) of individual sharks, HEMI is an indicator variable denoting odd-numbered (posterior-facing) and even-numbered (anterior facing) hemibranchs. FIL L denotes log transformed filament length. COEFF denotes parameter estimate, $s(\beta)$ denotes standard error of the parameter estimate.

DEPENDENT VARIABLE	INDEPENDENT VARIABLE	COEFF	$s(\beta)$	T-TEST	MSE	r^2	N
AREA	INTERCEPT	-0.5876					
	SL	0.0528	0.0079	6.73		0.0058	445
	HEMI	0.0044	0.0002	22.78			
	FIL L	2.0096	0.0262	76.63			
MEAN LAM AREA	INTERCEPT	-2.0185					
	SL	0.0534	0.0082	6.51		0.0064	445
	HEMI	0.0052	0.0002	25.65			
	FIL L	1.1757	0.0274	42.90			
NO. LAMELLAE	INTERCEPT	1.4301					
	SL	-0.0008	0.0001	-11.41		0.0007	445
	FIL L	0.8344	0.0092	90.73			

not significant in calculating the number of lamellae. However, it was significant in estimating mean lamella area, indicating that differences in total filament area among hemibranchs are due to mean lamella area rather than number of lamellae.

Total gill surface areas estimated from the three methods were similar (Table 10; Fig. 5). Ninety-five percent confidence intervals obtained from Method A encompassed the estimates from the other methods. Analysis of covariance indicated that the regression equations (Table 11) for the three methods did not differ significantly in slope ($F = 0.024$; $df = 2, 42$) or intercept ($F = 2.405$; $df = 2, 44$). All slope estimates are within one standard error of $d = 1$.

Total gill slit heights (GSH) increase approximately isometrically with standard length ($GSH = 4.665 \cdot SL^{0.992}$; $s(\beta) = 0.055$; $r^2 = 0.970$; $n = 12$). GSH were also proportional to total gill areas ($GSH = 3.818 \cdot A^{0.319}$; $s(\beta) = 0.022$; $r^2 = 0.953$) (Fig. 6).

Tiger shark:

As in the sandbar shark, filament lengths were greatest in the posterior facing hemibranchs. Within each "type" of hemibranch (anterior and posterior facing), maximum filament lengths increased from the first to the last hemibranch (Fig. 7). Variation in filament length

Table 10. Estimates of total gill surface areas (mm^2) for sandbar sharks from Methods A, B and C (see RESULTS) with upper and lower 95% confidence limits (U95 and L95) for Method A.

SEX	SL	TW	METHOD A		L95	METHOD B		METHOD C	
			AREA	U95		AREA	AREA	AREA	AREA
M	65	4.2	856868	1158463	633796	909700	933065		
F	66	4.9	865723	1461181	512969	892108	1004059		
F	87	11.7	2314227	3301793	1621952	2137411	2607290		
M	88	10.5	2037950	2826664	1469364	2154304	2267539		
F	91	12.5	2447345	3272878	1830059	2472031	2517054		
F	117	27.7	5543015	7288516	4215579	4717448	5862656		
M	118	28.7	4482834	6433390	3123753	5457910	4649025		
F	119	29.5	5078971	6666477	3870101	5230525	5362988		
F	120	33.1	6185480	7999443	4783282	6211661	6629662		
F	122	28.1	4778538	6499601	3513185	5422524	5668053		
F	125	36.3	6192835	8846248	4335315	6055824	6139198		
F	131	40.4	8198570	10792503	6228188	7255220	8158945		
M	134	38.6	6890513	10350483	4587945	7880585	8055039		
F	140	47.6	7402946	9457539	5794752	8335594	7889349		
F	153	57.5	13385784	16749722	10698040	15662077	15288184		
F	170	99.8	18404371	24247480	13972163	19379230	23005013		

Figure 5. Plot of $\log(\text{gill surface area})$ against $\log(\text{total weight})$ for sandbar sharks by the three methods of estimation. Squares denote Method A, crosses denote Method B, and circles denote Method C.

Table 11. Parameter estimates for regressions of log transformed gill surface areas (mm^2) on log transformed weight (kg) and standard length (cm) for sandbar sharks. r and p are intercepts and d and a are regression slopes from text Equations 5 and 10. $s(d)$ and $s(a)$ denote standard errors of slope estimates. The coefficient of determination, r^2 , is not to be confused with the regression intercept, r .

	DF	10^r	d	$s(d)$	MSE	r^2
Weight:						
METHOD A	14	5.287	0.986	0.0266	0.0015	0.9899
METHOD B	14	5.289	0.996	0.0410	0.0036	0.9768
METHOD C	14	5.321	0.990	0.0369	0.0029	0.9809
	DF	10^p	a	$s(a)$	MSE	r^2
Length:						
METHOD A	14	0.320	3.089	0.0950	0.0020	0.9869
METHOD B	14	0.241	3.136	0.1139	0.0028	0.9818
METHOD C	14	0.328	3.104	0.1203	0.0031	0.9794

Figure 6. Plot of $\log(\text{gill slit height})$ against $\log(\text{gill surface area})$. '+' denotes sandbar sharks, squares denote tiger sharks, circles denote blacktip sharks, diamonds denote blue sharks, and 'x' denotes the dusky shark.

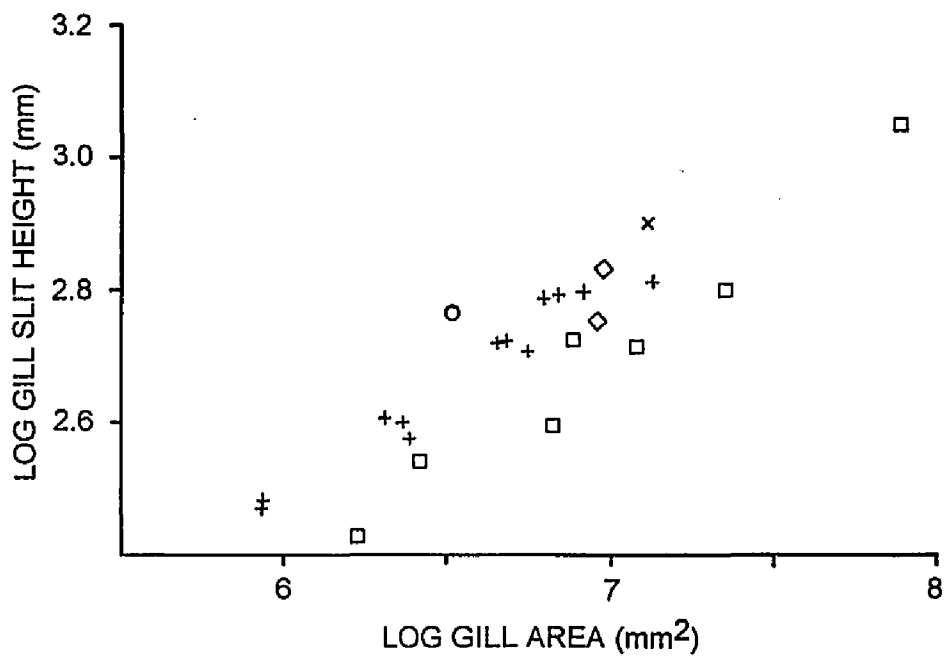
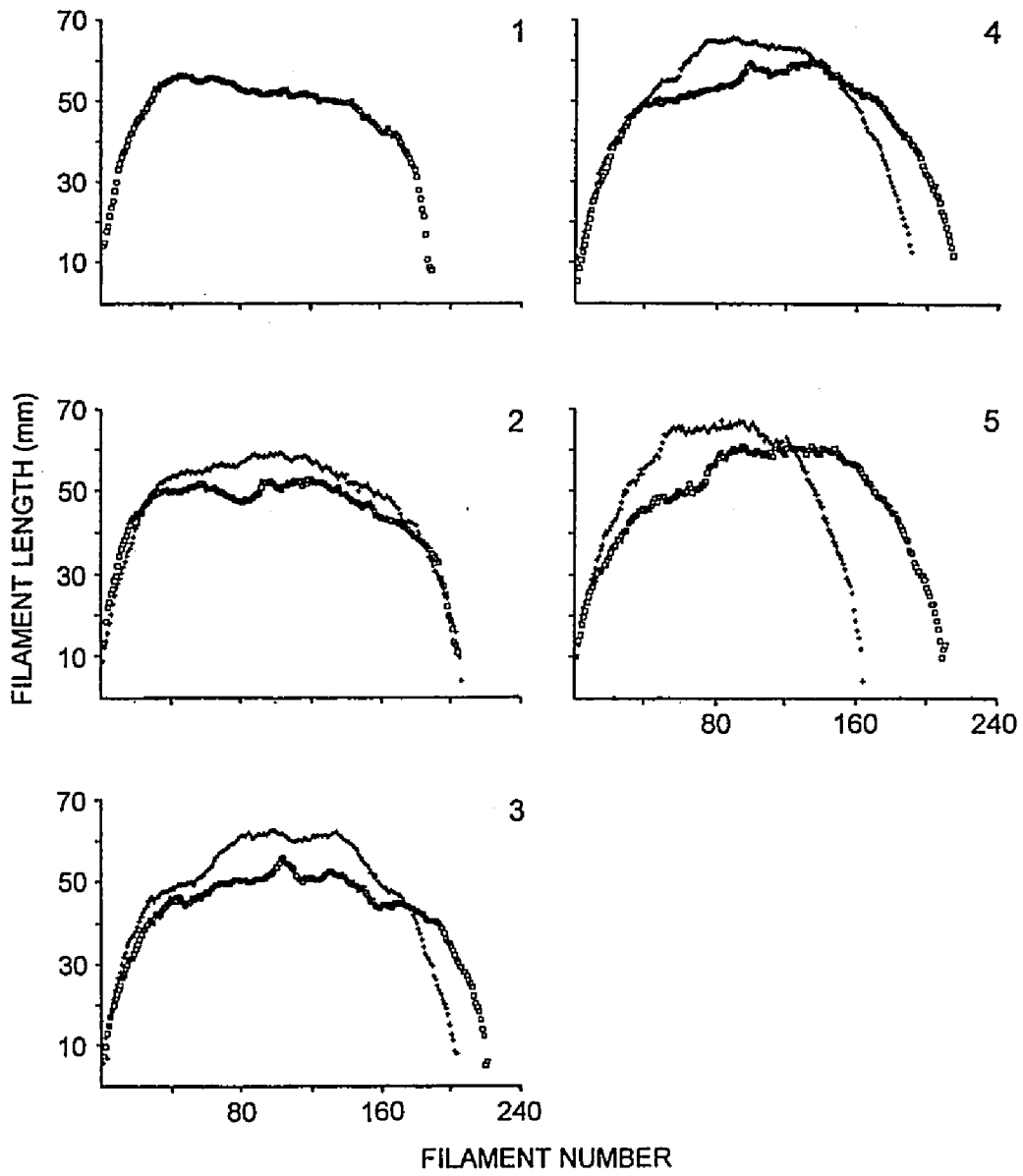


Figure 7. Lengths of gill filaments for each holobranch on the left side of a tiger shark specimen. Crosses denote posterior-facing hemibranchs, squares denote anterior-facing hemibranchs. The first filament is the most dorsal on that hemibranch.



along the hemibranch was similar to that in sandbar sharks, although the plateau in lengths on anterior facing hemibranchs was apparent only after Hemibranch 4 and was not as pronounced. Although not indicated in Figure 7, filament truncation, forking and fusion occurred as in the sandbar shark.

The total number of filaments on one side ranged from 1747 to 1818. As in the sandbar shark, there was no apparent correlation between number of filaments and weight of the individual. The mean and total length of filaments were positively correlated with standard length ($r = 0.9964$ and 0.9973 , respectively).

Analysis of covariance did not reveal any consistent difference in the relationship of the number of lamellae and filament length among hemibranchs. Regression slopes and intercepts differed among hemibranchs in some specimens but not in others (Table 12).

Similarly, there were no consistent relationships between mean lamella area and filament length among hemibranchs. Regression intercepts were significantly different for some specimens, but not for others (Table 13).

Analysis of covariance did not reveal any consistent differences in the relationship of filament area and filament length among hemibranchs. While intercepts differed among hemibranchs in one specimen, there was no

Table 12. Results of analysis of covariance of regressions of number of lamellae (y) on filament length (x) for tiger sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{01} : all variances equal; H_{02} : all slopes equal; H_{03} : all intercepts equal.

HEMI	N	SLOPE	MSE	ADJ. SLOPE	ADJ. INT.	H_{01} B	H_{02} F	H_{03} F
R1	12	0.4511	0.0004	-	-	13.77	2.80*	
R2	12	0.5231	0.0010	-	-			
R3	12	0.7470	0.0006	-	-			
R4	12	0.7466	0.0022	-	-			
R5	12	0.3043	0.0007	-	-			
R6	12	0.5520	0.0015	-	-			
R7	11	0.5553	0.0005	-	-			
R8	12	0.8945	0.0026	-	-			
R9	21	0.9082	0.0063	-	-			
L6	14	0.8180	0.0004	0.8456	1.322	0.12	0.48	0.35
L7	13	0.8597	0.0005	0.8456	1.327			
L4	14	0.8832	0.0004	0.8597	1.264	2.56	0.20	22.50*
L5	13	0.8485	0.0009	0.8597	1.310			
R4	12	0.9021	0.0002	-	-	1.15	6.97*	
R5	12	0.7134	0.0002	-	-			
R6	12	0.8554	0.0003	-	-			
R7	13	0.7856	0.0002	-	-			

Table 13. Results of analysis of covariance of regressions of mean lamella area (y) on filament length (x) for tiger sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI	N	SLOPE	MSE	ADJ. SLOPE	ADJ. INT.	H_{O1} B	H_{O2} F	H_{O3} F
R1	12	0.8411	0.0033	1.8591	-0.516	6.02	0.86	2.95*
R2	12	1.2088	0.0049	1.8591	-0.530			
R3	12	0.8372	0.0053	1.8591	-0.551			
R4	12	0.5404	0.0052	1.8591	-0.539			
R5	12	0.0247	0.0010	1.8591	-0.584			
R6	12	0.8348	0.0035	1.8591	-0.553			
R7	11	0.8902	0.0064	1.8591	-0.603			
R8	12	0.7196	0.0160	1.8591	-0.618			
R9	21	0.7195	0.0082	1.8591	-0.607			
L6	14	1.2696	0.0038	1.3730	-1.842	1.99	0.49	1.49
L7	13	1.4261	0.0089	1.3730	-1.879			
L4	14	0.5053	0.0044	0.8074	-0.581	1.11	3.29	1.55
L5	13	0.9513	0.0083	0.8074	-0.621			
R4	12	1.4678	0.0026	-	-	15.76*		
R5	12	1.2872	0.0289	-	-			
R6	12	1.2004	0.0036	-	-			
R7	13	1.1719	0.0045	-	-			

difference in other specimens (Table 14). For one specimen in which filaments were measured from all nine hemibranchs there was no significant difference in slopes or intercepts.

Analyses of regressions of filament areas on filament lengths indicated no significant differences in slopes for anterior facing hemibranchs or posterior facing hemibranchs within individuals (Table 14). However, when data were pooled within specimens, slopes were significantly different among specimens (Tables 15 and 16).

Method B produced the multiple regression equation presented in Table 17. All coefficients were significant. As in the sandbar shark, the indicator variable was not significant in calculating the number of lamellae. However, it was significant in estimating mean lamella area, indicating that differences in total filament area among hemibranchs are due to mean lamella area rather than number of lamellae, as in sandbar sharks.

Total gill surface areas estimated from Method A, B and C were similar (Table 18; Fig. 8). Ninety-five percent confidence intervals obtained from Method A encompassed the estimates from B and C. Regression equations were similar between methods (Table 19) in slope ($F = 0.150$; $df = 2, 18$) and intercept ($F = 0.142$; $df = 2, 20$). As in the sandbar shark, slopes were not significantly different from $d = 1$.

Analysis of covariance for regressions of log

Table 14. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for tiger sharks by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI	N	SLOPE	MSE	ADJ. SLOPE	ADJ. INT.	H_{O1} B	H_{O2} F	H_{O3} F
R1	12	1.2922	0.0042	1.5583	0.795	7.68	0.79	1.26
R2	12	1.7319	0.0055	1.5583	0.839			
R3	12	1.5842	0.0069	1.5583	0.785			
R4	12	1.2871	0.0102	1.5583	0.771			
R5	12	0.3290	0.0021	1.5583	0.752			
R6	12	1.3869	0.0038	1.5583	0.779			
R7	11	1.4456	0.0066	1.5583	0.741			
R8	12	1.6142	0.0247	1.5583	0.740			
R9	21	1.6277	0.0165	1.5583	0.756			
L6	14	2.0876	0.0046	2.2186	-0.520	0.37	0.87	1.23
L7	13	2.2859	0.0067	2.2186	-0.552			
L4	14	1.3886	0.0044	1.6671	0.683	1.90	2.47	0.03
L5	13	1.7999	0.0101	1.6671	0.689			
R4	12	2.3699	0.0035	2.0632	-0.242	0.86	1.30	4.49*
R5	12	2.0548	0.0030	2.0632	-0.264			
R6	12	2.0557	0.0056	2.0632	-0.236			
R7	13	1.9575	0.0045	2.0632	-0.322			

Table 15. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for tiger sharks for even-numbered (anterior-facing) hemibranchs, pooled within specimens. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{01} : all variances equal; H_{02} : all slopes equal; H_{03} : all intercepts equal.

SPEC				ADJ.	ADJ.	H_{01}	H_{02}	H_{03}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
GC001	48	1.569	0.0114	-	-	3.79	4.58*	
GC002	14	2.088	0.0046	-	-			
GC003	14	1.389	0.0044	-	-			
GC004	24	2.126	0.0046	-	-			
GC005	4	2.132	0.0006	-	-			
GC006	4	2.386	0.0071	-	-			
GC007	4	1.977	0.0004	-	-			

Table 16. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for tiger sharks for odd-numbered (posterior-facing) hemibranchs, pooled within specimens (SPEC). B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

SPEC				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
GC001	68	1.569	0.0086	-	-	7.19	4.96*	
GC002	13	2.286	0.0067	-	-			
GC003	13	1.800	0.0101	-	-			
GC004	24	1.995	0.0044	-	-			
GC005	12	2.126	0.0034	-	-			
GC006	8	1.944	0.0010	-	-			
GC007	8	1.943	0.0013	-	-			
GC008	12	2.054	0.0036	-	-			

Table 17. Parameter estimates for regressions of log transformed total filament area estimates (AREA), mean lamella area (MEAN LAM AREA) and total number of lamellae (NO. LAMELLAE) for all tiger sharks combined (see METHODS). SL denotes standard length of individual sharks, HEMI is an indicator variable denoting odd-numbered (posterior-facing) and even-numbered (anterior facing) hemibranchs. FIL L denotes log transformed filament length. COEFF denotes parameter estimate, s(B) denotes standard error of the parameter estimate.

DEPENDENT VARIABLE	INDEPENDENT VARIABLE	COEFF	S(B)	T-TEST	MSE	R ²	N
AREA	INTERCEPT	-0.3550					
	SL	0.0031	0.0002	19.77	0.0096	0.9620	271
	HEMI	0.0378	0.0123	3.08			
	FIL L	1.8571	0.0375	49.51			
MEAN LAM AREA	INTERCEPT	-1.7872					
	SL	0.0035	0.0002	22.50	0.0092	0.9303	271
	HEMI	0.0432	0.0120	3.59			
	FIL L	1.0513	0.0367	28.68			
NO. LAMELLAE	INTERCEPT	1.4275					
	SL	-0.00036	0.00007	-5.54	0.0017	0.9355	271
	FIL L	0.8083	0.0155	52.11			

Table 18. Estimates of total gill surface areas (mm^2) for tiger sharks from Methods A, B and C (see RESULTS) with upper and lower 95% confidence limits (U95 and L95) for Method A.

SEX	SL	TW	METHOD A		L95	METHOD B		METHOD C	
			AREA	U95		AREA	AREA	AREA	AREA
F	70	4.1	1666800	2137039	1300046	1835759	1777597		
M	88	8.2	2629487	3638184	1900960	3241146	3093051		
F	112	17.7	6661250	9359539	4740889	5939934	6606156		
F	112	20.0	7657564	9972158	5880708	6910250	7728538		
M	151	45.1	11983587	17262589	8319167	13344043	12496590		
M	185	82.6	22419349	35214750	14273268	22166720	23235843		
F	218	134.8	38944208	59003180	25706425	39536823	38104724		
M	272	200.6	77908167	91880872	66060812	89538148	73650367		

Figure 8. Plot of $\log(\text{gill surface area})$ against $\log(\text{total weight})$ for tiger sharks by the three methods of estimation. Squares denote Method A, crosses denote Method B, and circles denote Method C.

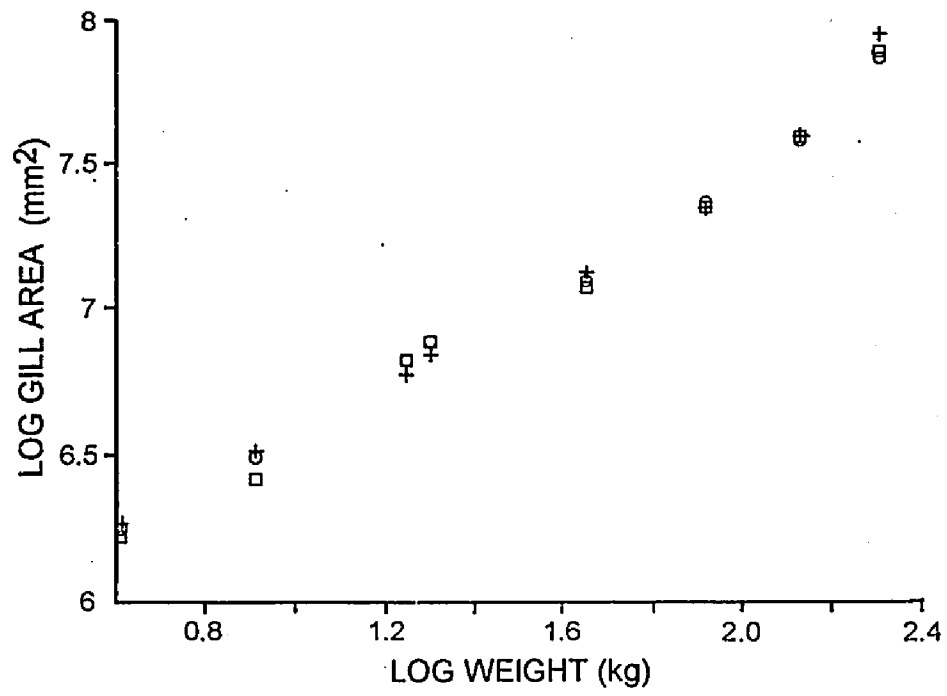


Table 19. Parameter estimates for regressions of log transformed gill surface areas (mm^2) on log transformed weight (kg) and standard length (cm) for tiger sharks. r and p are intercepts and d and a are regression slopes from text Equations 5 and 10. $s(d)$ and $s(a)$ denote standard errors of slope estimates. The coefficient of determination, r^2 , is not to be confused with the regression intercept, r .

	DF	10^r	d	$s(d)$	MSE	r^2
Weight:						
METHOD A	6	5.605	0.946	0.0473	0.0056	0.9852
METHOD B	6	5.631	0.941	0.0533	0.0070	0.9811
METHOD C	6	5.668	0.912	0.0383	0.0036	0.9896
	DF	10^p	a	$s(a)$	MSE	r^2
Length:						
METHOD A	6	1.065	2.791	0.1195	0.0041	0.9891
METHOD B	6	1.090	2.788	0.0915	0.0024	0.9936
METHOD C	6	1.288	2.692	0.0869	0.0022	0.9938

transformed total gill area on total weight indicated no significant difference in slopes between species, although intercepts were different (Table 20). Likewise, intercepts of log transformed total filament length and mean number of lamellae per millimeter on total weight differed significantly between species. However, neither regression slopes nor intercepts of mean lamella area on total weight were significantly different.

The ratio of gill area to weight (A/W) for sandbar sharks is nearly constant through the weight range examined due to the proximity of d to unity (Fig. 9). The decrease in predicted A/W is more evident for tiger sharks as d departs from unity.

As in the sandbar sharks, total gill slit heights (GSH) increased approximately isometrically with standard length ($GSH = 4.336 * SL^{0.973}$; $s(\beta) = 0.114$; $r^2 = 0.936$; $n = 7$). GSH were also proportional to total gill areas ($GSH = 1.781 * A^{0.351}$; $s(\beta) = 0.032$; $r^2 = 0.961$) (Fig. 6). Although GSH for tiger sharks were slightly greater at a given length than for sandbar sharks, GSH were less than for sandbar sharks for a given gill area. If GSH is an indication of ventilation volume, e.g. $GSH^3 \propto$ water volume (cm^3/hr), the larger GSH suggests that sandbar sharks can pass a greater amount of water over a given gill area ($cm^3/hr/mm^2$) than can tiger sharks (Fig. 10).

Table 20. Results of analyses of covariance between tiger (GC) and sandbar (CP) sharks for total gill surface area in mm^2 (TOTAL AREA), mean lamella area in mm^2 (MN LAM AREA), mean number of lamellae per millimeter of filament length (# LAM/mm) and total filament length in mm (TOTAL FIL L) on weight (kg). All variables were log transformed. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{01} : all variances equal; H_{02} : all slopes equal; H_{03} : all intercepts equal.

			ADJ.	ADJ.	H_{01}	H_{02}	H_{03}
	N	SLOPE	MSE	SLOPE	INT.	B	F
TOTAL AREA							
GC	8	0.9460	0.0056	0.9644	5.577	3.74	0.66
CP	16	0.9856	0.0015	0.9644	5.317		132.0*
TOTAL FIL L							
GC	8	0.3162	0.0004	0.3231	4.402	0.02	0.66
CP	16	0.3311	0.0004	0.3231	4.147		887.4*
# LAM/mm							
GC	8	-0.1097	0.0003	-0.1200	1.266	0.03	1.53
CP	16	-0.1319	0.0004	-0.1200	1.284		4.51*
MN LAM AREA							
GC	8	0.7058	0.0027	0.7444	-0.654	0.07	2.55
CP	16	0.7890	0.0033	0.7444	-0.654		<0.01

Figure 9. Plot of ratios of gill surface area/total weight against total weight. '+' denotes sandbar sharks, squares denote tiger sharks, circles denote blacktip sharks, diamonds denote blue sharks, and 'x' denotes the dusky shark.

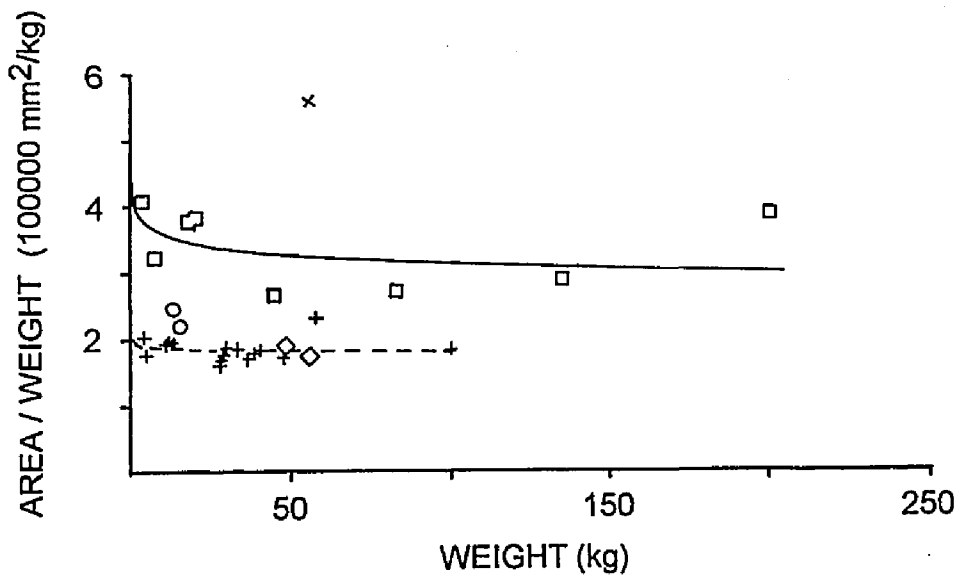
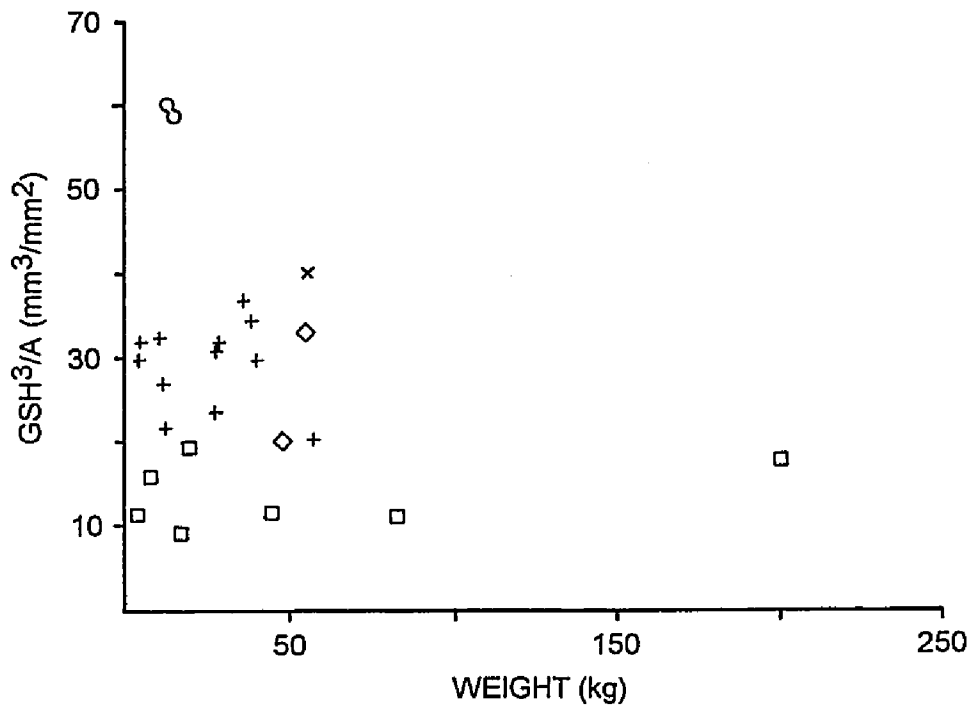


Figure 10. Plot of ratio of cube of total gill slit height/gill surface area (GSH^3/A) against total weight. '+' denotes sandbar sharks, squares denote tiger sharks, circles denote blacktip sharks, diamonds denote blue sharks, and 'x' denotes the dusky shark.



Other Species:

The total number of filaments on one side were 1318 and 1338 for the blacktip sharks, 1880 for the dusky, and 1300 and 1341 for the blue sharks. As in the sandbar shark, filament lengths were generally greatest in the posterior facing hemibranchs, although numbers of filaments were usually greater on anterior facing hemibranchs.

Analysis of covariance for blacktip sharks did not indicate a consistent difference in the relationship of the number of lamellae and filament length between Hemibranchs 4 and 5. Slopes differed within one specimen but not the other. No significant differences were found for regression slopes for the one dusky or two blue sharks, although intercepts differed for one blue shark (Table 21).

Slopes of regressions of mean lamella area on filament length differed between hemibranchs for the two blacktip sharks. Regression slopes did not differ for the dusky or blue sharks, although intercepts differed for the dusky shark (Table 22).

Analysis of covariance indicated that regression slopes of filament area on filament length differed between hemibranchs for both blacktip specimens (Table 23). Slopes and intercepts did not differ significantly for the one dusky shark and one blue shark, but slopes differed for the other blue shark.

Total gill surface areas estimated from Method A and C

Table 21. Results of analysis of covariance of regressions of number of lamellae (y) on filament length (x) for other shark species by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
BLACKTIP:								
L4	14	0.7810	0.0005	-	-	2.86	19.18*	
L5	12	0.4796	0.0015	-	-			
L4	14	0.7576	0.0004	0.7764	1.4724	0.28	0.58	2.92
L5	12	0.7940	0.0003	0.7764	1.4851			
DUSKY:								
R4	12	0.9522	0.0004	0.7572	1.4688	0.25	3.75	1.01
R5	12	0.7344	0.0006	0.7572	1.4784			
BLUE:								
L4	12	0.7844	0.0003	0.7469	1.4259	0.89	3.72	5.79*
L5	12	0.7028	0.0001	0.7469	1.4412			
L4	14	0.6890	0.0003	0.6794	1.5281	1.08	1.14	1.31
L5	12	0.6291	0.0001	0.6794	1.5354			

Table 22. Results of analysis of covariance of regressions of mean lamella area (y) on filament length (x) for other shark species by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
BLACKTIP:								
L4	14	1.4153	0.0035	-	-	0.78	5.47*	
L5	12	1.0683	0.0060	-	-			
L4	14	1.5724	0.0056	-	-	0.39	12.67*	
L5	12	0.9407	0.0038	-	-			
DUSKY:								
R4	12	1.1650	0.0052	1.4762	-	2.01	1.26	13.10*
R5	12	1.5125	0.0020	1.4762	-			
BLUE:								
L4	12	1.0888	0.0043	1.2161	-1.333	1.00	2.65	0.05
L5	12	1.3656	0.0022	1.2161	-1.328			
L4	14	1.5487	0.0022	1.5100	-1.834	1.52	2.55	0.98
L5	12	1.3075	0.0010	1.5100	-1.852			

Table 23. Results of analysis of covariance of regressions of filament area (y) on filament length (x) for other shark species by hemibranch. Hemibranch (HEMI) prefixes denote left (L) or right (R) side of specimen examined. B denotes Bartlett's test statistic. An asterisk (*) denotes significance at $\alpha = 0.05$. H_{O1} : all variances equal; H_{O2} : all slopes equal; H_{O3} : all intercepts equal.

HEMI				ADJ.	ADJ.	H_{O1}	H_{O2}	H_{O3}
	N	SLOPE	MSE	SLOPE	INT.	B	F	F
BLACKTIP:								
L4	14	2.1963	0.0003	-	-	1.68	17.16*	
L5	12	1.5479	0.0003	-	-			
L4	14	2.3300	0.0039	-	-	0.09	14.85*	
L5	12	1.7347	0.0032	-	-			
DUSKY:								
R4	12	2.1172	0.0040	2.2333	-0.418	0.45	0.19	12.20*
R5	12	2.2469	0.0026	2.2333	-0.498			
BLUE:								
L4	12	1.8732	0.0036	1.9629	0.0924	0.40	1.44	0.79
L5	12	2.0684	0.0024	1.9629	0.1132			
L4	14	2.2378	0.0012	-	-	0.03	5.04*	
L5	12	1.9366	0.0014	-	-			

were similar, although areas calculated using Method C were always greater (Table 24). Gill areas for the three species were comparable to areas of sandbar sharks of similar weight (Fig. 11). However, gill areas calculated for the dusky and blue sharks are less than predicted by Emery and Szczepanski (1986). Average lamella areas and number of lamellae/mm for blacktip and blue sharks were similar to values predicted by equations for sandbar sharks (Table 20). In contrast, the mean lamella area for the dusky shark was less, and the number of lamellae/mm was greater, than predicted from Table 20.

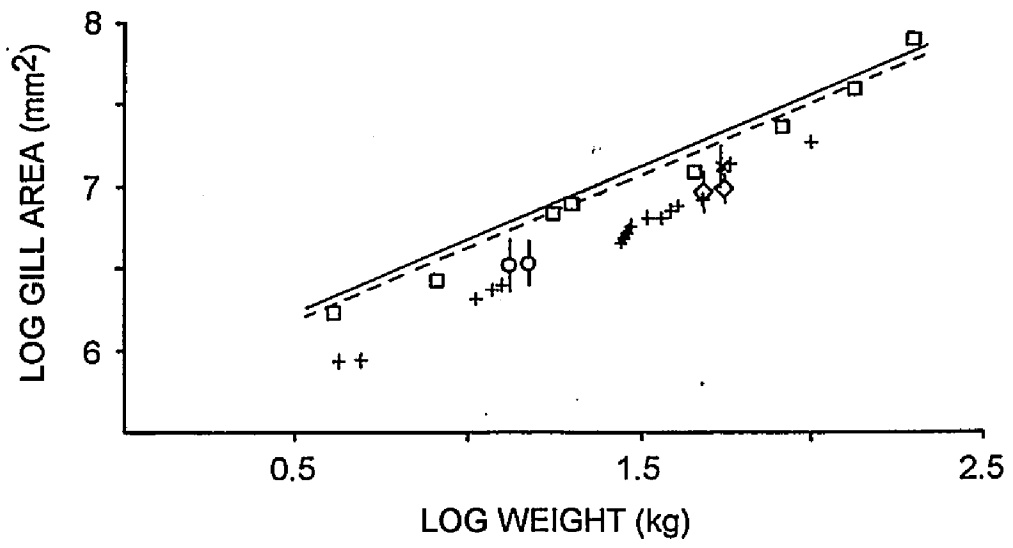
The ratio of gill area to weight for the dusky shark was the largest of any specimen examined here (Fig. 9). A/W for the blacktip sharks were intermediate to sandbar and tiger sharks, and the ratio for the blue sharks were similar to sandbar sharks.

The relationship between total gill slit height and gill area for the blue sharks appears similar to that for sandbar sharks (Fig. 6). GSH for the blacktip sharks was greater for a given gill area than for sandbar or tiger sharks. GSH for the dusky shark appears slightly greater than for sandbar sharks. The ratio GSH^3/A was greatest for the blacktip sharks, whereas the ratio for blue sharks was similar to that for sandbar sharks and, for the dusky shark, only slightly greater than for sandbar sharks (Fig. 10). This suggests that blacktip, and possibly dusky,

Table 24. Estimates of total gill surface areas (mm^2) for other shark species from Methods A and C (see RESULTS) with upper and lower 95% confidence limits (U95 and L95) for Method A. Parameters for Method C are total filament length in millimeters (TOTAL FIL LEN), mean number of lamellae/millimeter (LAM/mm), and mean bilateral lamella area (MN LAM AREA) in mm^2 .

SEX	SL	TW	AREA	METHOD A U95	L95	TOTAL FIL LEN	LAM/mm	MN LAM AREA	METHOD C AREA
Blacktip:									
M	91	13.2	3250871	4799293	2216499	33340.4	15.65	1.71	3568822
M	97	15.0	3294793	4527565	2398086	35276.4	15.98	1.61	3623064
Dusky:									
F	160	55.7	12912551	17578069	9504433	82631.1	13.03	3.28	14117213
Blue:									
F	171	48.1	9097382	12155467	6815124	50552.1	11.80	4.15	9890884
M	185	55.3	9483279	11518543	7809550	53752.2	11.12	4.22	10093912

Figure 11. Plot of $\log(\text{gill surface area})$ against $\log(\text{total weight})$ for all species examined. '+' denotes sandbar sharks, squares denote tiger sharks, circles denote blacktip sharks, diamonds denote blue sharks, and 'x' denotes the dusky shark. Vertical bars indicate 95% confidence limits.



sharks may respire a greater relative water volume ($\text{cm}^3/\text{hr}/\text{mm}^2$) than blue, sandbar or tiger sharks.

Age and Growth

Von Bertalanffy growth parameters estimated from empirical and observed values of D are given in Table 25. Growth parameters were fit to data using $D = 1$, the original von Bertalanffy equation (OVB), for comparison. Parameters for sandbar and tiger sharks were fit using d calculated from Methods A and B above. No empirical D was calculated for the dusky or blue shark because no maximum r^2 was obtained. In other species there was usually little difference in the r^2 of the empirically derived Ford-Walford equation (EFW) and that using the observed d (OFW). Likewise, there was usually little difference in the fit of the von Bertalanffy equations within the data ranges used, although the equations usually diverged beyond that range. Sums of squared deviates (SSE) usually indicate that EFW parameters fit the lengths at age better than OFW parameters. However, for the white sharks the OFW resulted in a smaller SSE than did the EFW.

Von Bertalanffy growth parameters calculated from Equation 15 using observed values of D are given in Table 25. No parameters were estimated for dusky (Lawler 1976) or mako sharks because regression coefficients were not significant. No parameters are given for blue sharks because the regression resulted in a negative K .

Table 25. Von Bertalanffy growth equation parameters estimated by various methods (see text). Values of r^2 are from the modified Ford-Walford equation or text Equation 15. Maximum lengths are from Compagno (1984). Data were obtained from references given in Methods.

SPECIES	REFERENCE	r^2	d	D	L_∞ cm TL	\bar{W}_∞ kg	K	KD	t_0	A_∞/W_∞ mm ² /kg	SSE
SANDBEAR CASEY ET AL. MALES	EMP D	0.9901	0.870	0.40	239.5	105.3	0.2695	0.1078	-7.28	-	198.5
	D = 1	0.9895	0.675	1	299.6	210.0	0.0546	0.0546	-3.47	-	178.9
	OBS D	0.9899	0.996	0.012	217.6	78.4	12.0617	0.5203	-27.22	191171	247.4
	OBS D	0.9899	0.986	0.043	219.1	80.1	3.3663	0.1452	-19.36	182116	242.1
	EQN 15	0.4233	0.996	0.012	209.5	69.8	11.0754	0.1365	-30.58	190829	687.7
	EQN 15	0.4228	0.986	0.043	209.5	69.8	3.1155	0.1344	-21.88	181801	726.8
	OBS MAX				224						
SANDBEAR CASEY ET AL. FEMALES	EMP D	0.9982	0.572	1.32	435.1	663.0	0.0183	0.0242	-2.70	-	566.7
	D = 1	0.9980	0.675	1	336.5	300.4	0.0465	0.0465	-3.76	-	601.8
	OBS D	0.9958	0.996	0.012	238.5	103.9	11.0381	0.1360	-29.39	190388	1195.3
	OBS D	0.9959	0.986	0.043	240.1	106.2	3.0761	0.1327	-20.83	181606	1157.3
	EQN 15	0.6885	0.996	0.012	288.2	186.4	7.4466	0.0918	-43.38	190335	673.3
	EQN 15	0.6892	0.986	0.043	289.3	188.6	2.0932	0.0903	-30.42	180154	664.6
	OBS MAX				234-239						

POSSIBLY 300

Table 25. continued.

SPECIES	REFERENCE	r^2	d	D	L_{∞} cm TL	W_{∞} kg	K	KD	t_0	A_{∞}/W_{∞} mm^2/kg	SSE
SANDBAR LAWLER FEMALES	EMP D	0.9988	0.507	1.52	549.4	1360.1	0.0074	0.0113	-2.95	-	84.9
	D = 1	0.9986	0.675	1	275.4	162.0	0.0547	0.0547	-4.25	-	122.8
	OBS D	0.9971	0.996	0.012	196.9	57.6	12.8480	0.1583	-26.30	189652	365.7
	OBS D	0.9972	0.986	0.043	198.2	58.8	3.5846	0.1546	-18.95	182908	351.6
	EQN 15	0.7180	0.996	0.012	309.9	233.1	5.4291	0.0668	-59.83	188595	464.7
	EQN 15	0.7192	0.986	0.043	312.0	238.0	1.5190	0.0655	-42.24	179360	457.1
SANDBAR CASEY AND NATANSON	TAGGING		0.996	0.012	221.4	82.7	5.8855	0.0724	-55.50	191130	
	TAGGING		0.986	0.043	221.8	83.1	1.6628	0.0717	-38.97	182022	
TIGER (ATL) BRANSTETTER ET AL.	EMP D	0.9994	0.644	1.16	433.6	501.0	0.0928	0.1076	-1.71	-	494.9
	D = 1	0.9994	0.693	1	423.6	464.2	0.1216	0.1216	-2.08	-	551.1
	OBS D	0.9980	0.946	0.176	384.7	339.3	1.1856	0.2084	-7.39	294001	898.4
	OBS D	0.9981	0.941	0.192	385.3	341.1	1.0749	0.2064	-7.08	303082	889.1
	EQN 15	0.5529	0.946	0.176	408.6	412.8	1.0158	0.1788	-8.59	290903	1264.5
	EQN 15	0.5548	0.941	0.192	408.8	413.6	0.9249	0.1776	-8.18	299654	1247.0
	OBS MAX			550							
TYPICALLY 430-500											
TIGER (GULF) BRANSTETTER ET AL.	EMP D	0.9993	0.398	1.96	472.2	661.1	0.0384	0.0753	-0.37	-	26.7
	D = 1	0.9976	0.693	1	392.4	361.9	0.1853	0.1853	-1.33	-	376.9
	OBS D	0.9924	0.946	0.176	358.6	269.8	1.7829	0.2842	-4.88	297661	844.7
	OBS D	0.9925	0.941	0.192	359.1	271.1	1.6168	0.3105	-4.67	307215	832.9
	EQN 15	0.5834	0.946	0.176	397.5	377.3	1.2759	0.2246	-6.95	292319	1486.9
	EQN 15	0.5867	0.941	0.192	397.7	378.1	1.1616	0.2230	-6.63	301244	1466.0

Table 25. continued.

SPECIES		r^2	d	D	L_{∞} cm TL	W_{∞} kg	K	KD	t_0	A_{∞}/W_{∞} mm^2/kg	SSE
DUSKY	EMP D	-	-	-	-	-	-	-	-	-	-
LAWLER	D = 1	0.9940	0.670	1	1904.1	41803.4	0.0057	0.0057	-8.65	-	294.6
FEMALES	OBS D	0.9954	0.88	0.363	546.4	952.6	0.1142	0.0415	-17.87	270725	350.1
	EQN 15	-	-	-	-	-	-	-	-	-	-
	OBS MAX				365						
					POSSIBLY 400						
DUSKY (INDIAN)	EMP D	-	-	-	-	-	-	-	-	-	-
NATANSON	D = 1	0.9979	0.670	1	493.1	698.0	0.0303	0.0303	-7.63	-	1696.4
FEMALES	OBS D	0.9987	0.88	0.363	431.4	465.6	0.1423	0.0517	-17.53	295012	1110.6
	EQN 15	0.2550	0.88	0.363	368.4	288.8	0.2286	0.0831	-10.24	312418	2549.4
DUSKY (ATL)	EMP D	-	-	-	-	-	-	-	-	-	-
NATANSON	D = 1	0.9990	0.670	1	386.2	333.0	0.0461	0.0461	-7.12	-	1499.1
FEMALES	OBS D	0.9994	0.88	0.363	365.2	281.2	0.1818	0.0661	-15.73	313418	874.4
	EQN 15	0.5629	0.88	0.363	336.0	218.4	0.2636	0.0958	-10.04	323069	1764.3
DUSKY (ATL)	EMP D	-	-	-	-	-	-	-	-	-	-
NATANSON	D = 1	0.9988	0.670	1	430.6	463.1	0.0405	0.0405	-6.87	-	329.3
MALES	OBS D	0.9991	0.88	0.363	385.7	331.8	0.1804	0.0656	-14.96	307255	155.9
	EQN 15	0.3521	0.88	0.363	365.8	282.4	0.2154	0.0783	-12.29	313251	277.6

Table 25. continued.

SPECIES	REFERENCE	r ²	d	D	I _∞ cm TL	W _∞ kg	K	KD	t ₀	A _∞ /W _∞ mm ² /kg	SSE
BLUE STEVENS	EMP D D = 1	- 0.9504	- 0.688	- 1	- 2071.5	- 55544.6	- 0.0163	- 0.0163	- -1.89	- -	- 298.8
	OBS D	0.9587	0.88	0.385	419.8	331.0	0.4446	0.1712	-3.85	273921	325.5
	EQN 15	-	-	-	-	-	-	-	-	-	-
	OBS MAX	-	-	-	-	-	-	-	-	-	-
					383						
					POSSIBLY 480-650						
BLUE STEVENS	TAGGING		0.88	0.385	267.0	77.6	0.8145	0.3134	-2.10	325987	
WHITE	EMP D	0.9990	0.904	0.30	716.8	4013.0	0.2780	0.0834	-12.00	-	333.6
CAILLIET	D = 1	0.9988	0.682	1	1129.8	16746.1	0.0289	0.0289	-5.06	-	301.7
ET AL.	OBS D	0.9989	0.77	0.722	882.8	7719.7	0.0687	0.0496	-6.74	544317	310.6
	EQN 15	0.8558	0.77	0.722	763.1	4877.8	0.0933	0.0674	-5.08	604934	949.4
	OBS MAX	-	-	-	640						
					POSSIBLY >800						
MAKO	EMP D	0.9865	0.606	1.22	485.0	1022.9	0.0802	0.0979	-0.84	-	1479.5
PRATT AND	D = 1	0.9864	0.677	1	443.4	774.8	0.1327	0.1327	-1.11	-	1596.1
CASEY	OBS D	0.9861	0.74	0.806	417.3	641.5	0.2059	0.1660	-1.44	1071817	1747.3
	EQN 15	-	-	-	-	-	-	-	-	-	-
	OBS MAX	-	-	-	-	-	-	-	-	-	-
					394-400						

Estimates of L_{∞} for male sandbar sharks by the EFW (240 cm) and OFW (218-219 cm) and by Equation 15 (210 cm) using data from Casey et al. (1985) are reasonable compared to the observed maximum length for males (ca. 224 cm). The EFW and OFW are nearly identical within the age range used (Fig. 12a). Equation 15 deviated substantially from observed sizes, because of the wide scatter of observed dW/dt at weight (Fig. 12b). The OVB produced a much larger estimate of L_{∞} (300 cm). The empirical d (0.870) was smaller for males than observed (0.986-0.996), but not unreasonable.

The asymptotic length for female sandbar sharks obtained from the EFW (435 cm; $d=0.572$) and from the OVB (337 cm; $d=0.675$) using data from Casey et al. (1985) are much larger than the observed maximum. Asymptotic lengths calculated from the OFW for females (239-240 cm TL, depending on d) are comparable to the observed maximum (ca. 240 cm) (Fig. 13a). The estimate of $L_{\infty} = 288-289$ cm obtained from Equation 15 (Casey et al. 1985) appears too large, but is comparable to a possible maximum length of 300 cm. The OFW may underestimate growth rates (dW/dt) at larger weights, whereas Equation 15 may overestimate dW/dt (Fig. 13b).

The OFW produced lower estimates of L_{∞} using data from Lawler (1976) (197-198 cm) (Fig. 14a). The asymptotic length from the EFW (549 cm; $d=0.507$) is apparently too

Figure 12. a: Back-calculated length at age and von Bertalanffy growth curves for male sandbar sharks. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Casey et al. (1985)

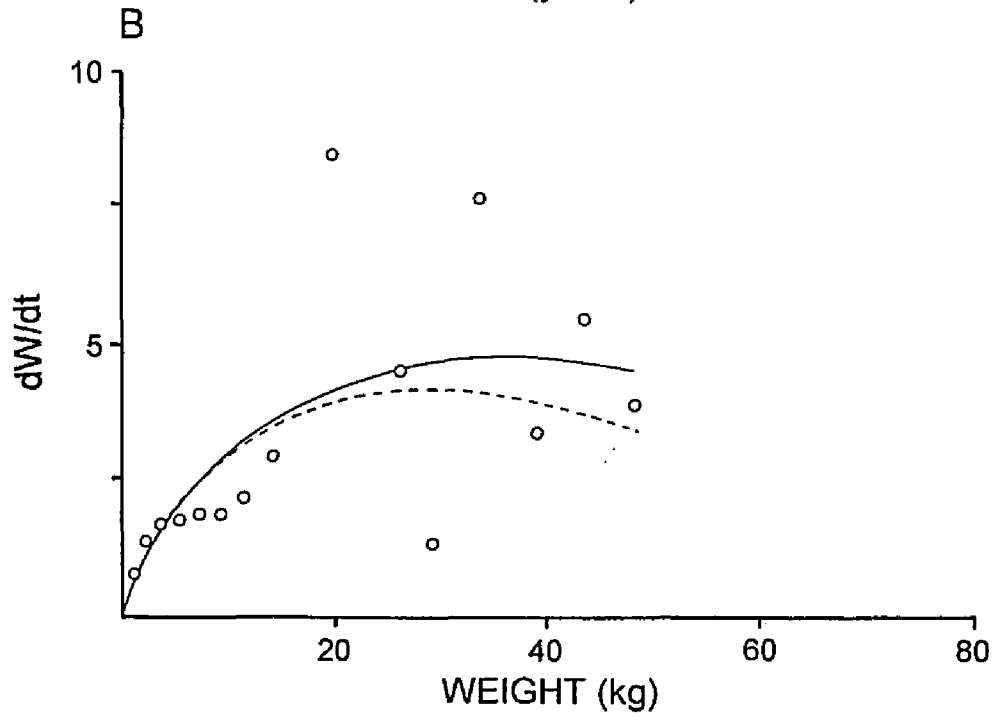
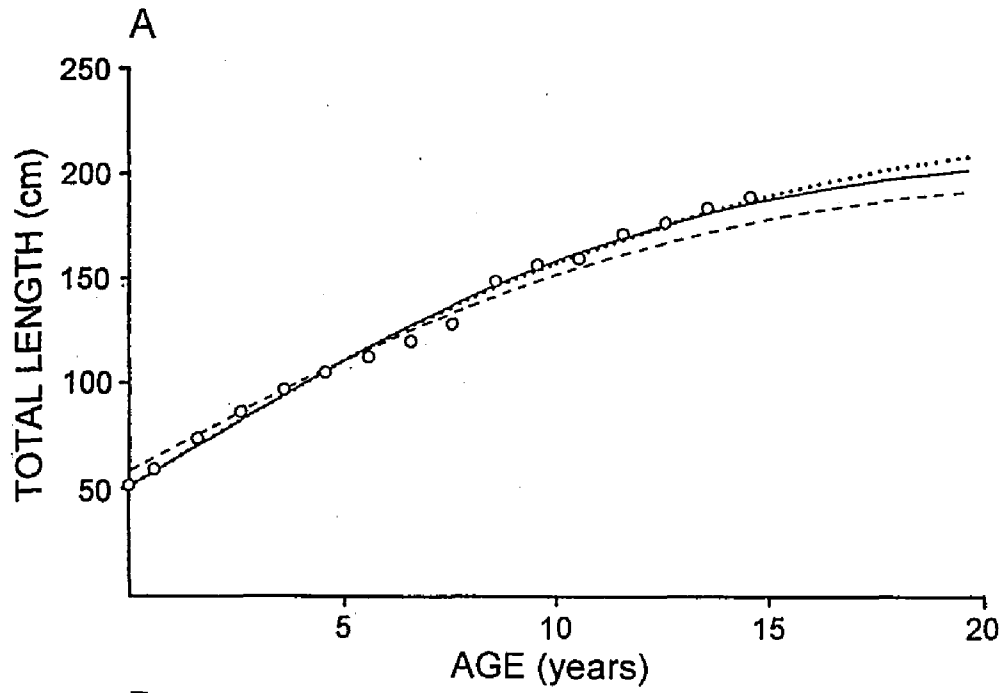


Figure 13. a: Back-calculated length at age and von Bertalanffy growth curves for female sandbar sharks. b: observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Casey et al. (1985).

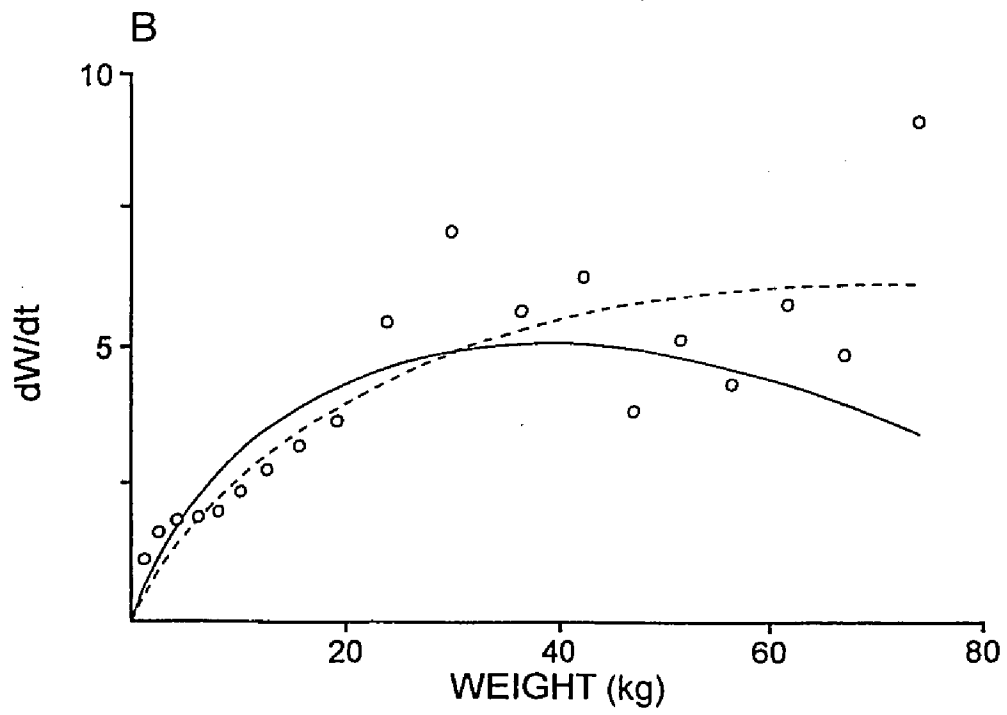
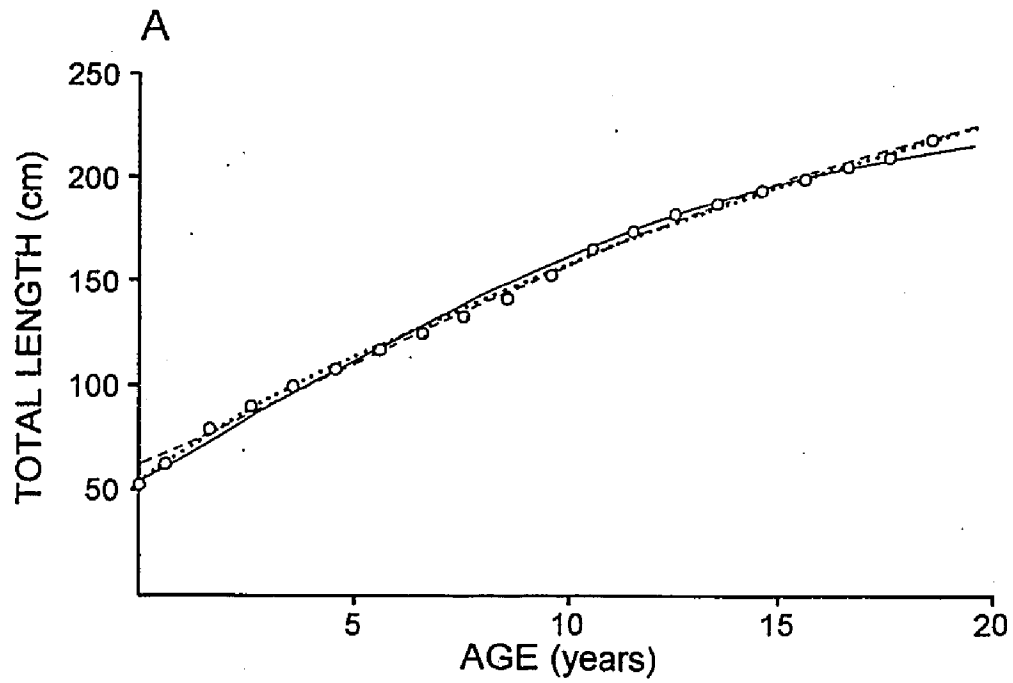
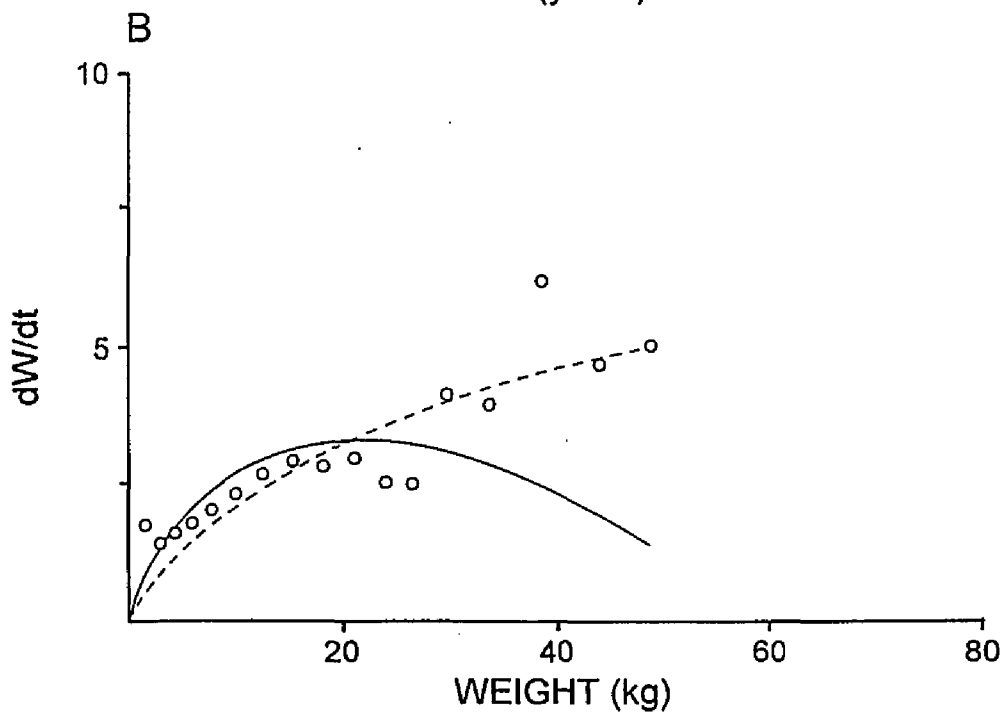
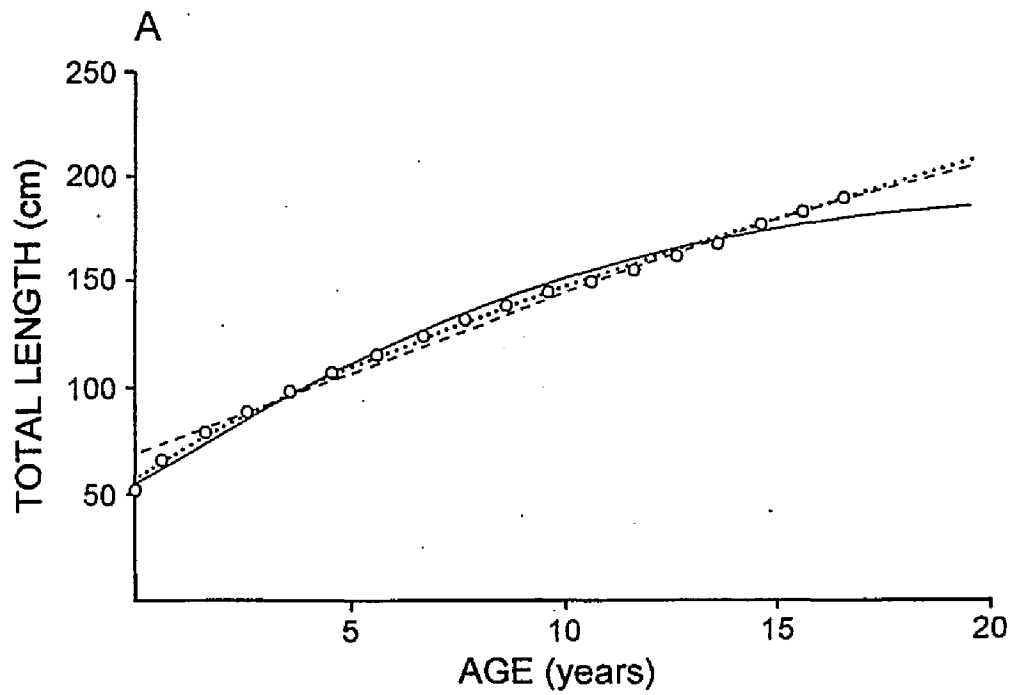


Figure 14. a: Back-calculated length at age and von Bertalanffy growth curves for female sandbar sharks. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Lawler (1976).



large, probably because of the nearly linear growth. Equation 15 produced similar estimates of L_{∞} (310-312 cm) to those of Casey et al. (1985), and fit growth in weight better than did the OFW (Fig. 14b). Empirically estimated d for females from Casey et al. (1985) and Lawler (1976) were much smaller than observed (0.986-0.996), and probably unrealistic.

Asymptotic lengths calculated for tiger sharks (359-472 cm TL) were smaller than the observed maximum (550 cm), regardless of region or equation used. Both the OVB and the OFW produced lower estimates of L_{∞} than did the EFW for both regions (Figs. 15a and 16a), and underestimated even the lower typical maximum lengths. The EFW compared more favorably with the typical maxima (434-472 cm compared to 430-500 cm). Asymptotic lengths obtained from Equation 15 were also low compared with observed maxima. However, Equation 15 fit growth in weight data better than the OFW, especially at larger weights (Figs. 15b and 16b). Empirically derived estimates of d for Atlantic (0.644) and Gulf sharks (0.398) were much smaller than observed values (0.941-0.946).

The asymptotic lengths calculated from the OFW for female dusky sharks (Lawler 1976) (556 cm) and Indian Ocean female dusky sharks (Natanson 1990) (431 cm) are greater than the observed maximum (Figs. 17a and 18a). However, L_{∞} for Atlantic Ocean females (365 cm) and males (386 cm)

Figure 15. a: Back-calculated length at age and von Bertalanffy growth curves for tiger sharks from the Gulf of Mexico. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Branstetter et al. (1987).

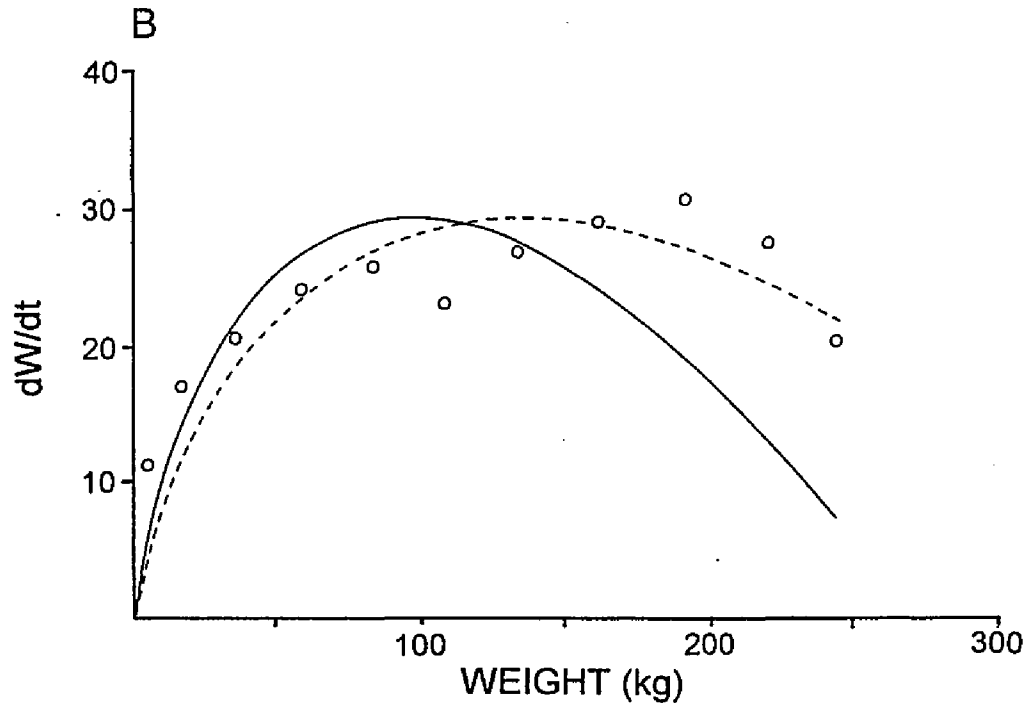
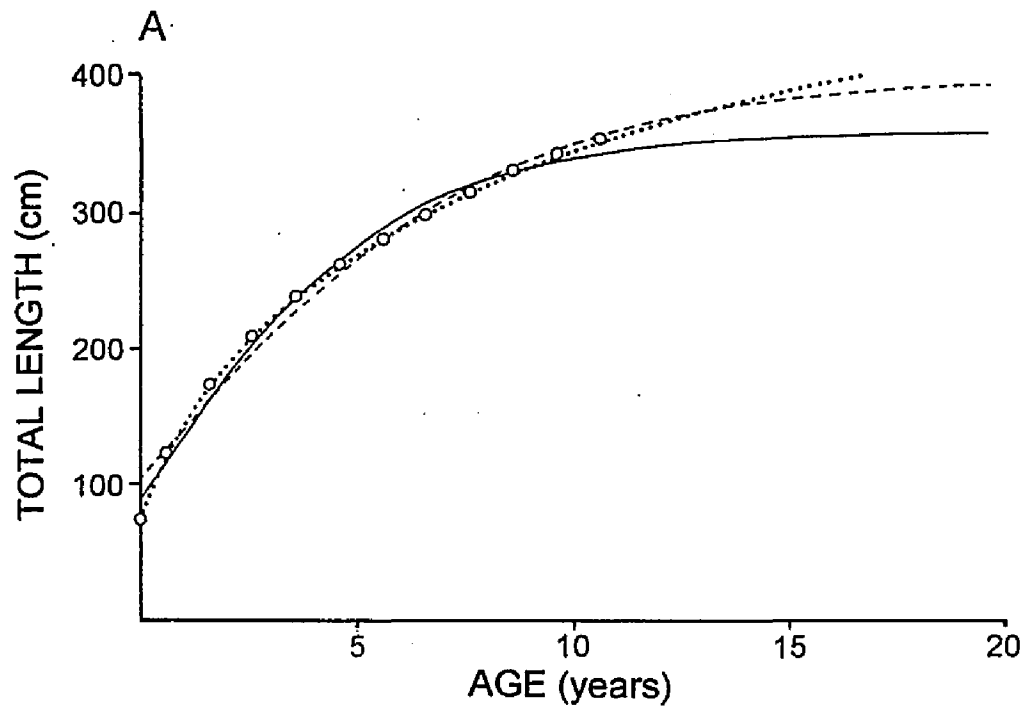


Figure 16. a: Back-calculated length at age and von Bertalanffy growth curves for tiger sharks from the Atlantic. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Branstetter et al. (1987).

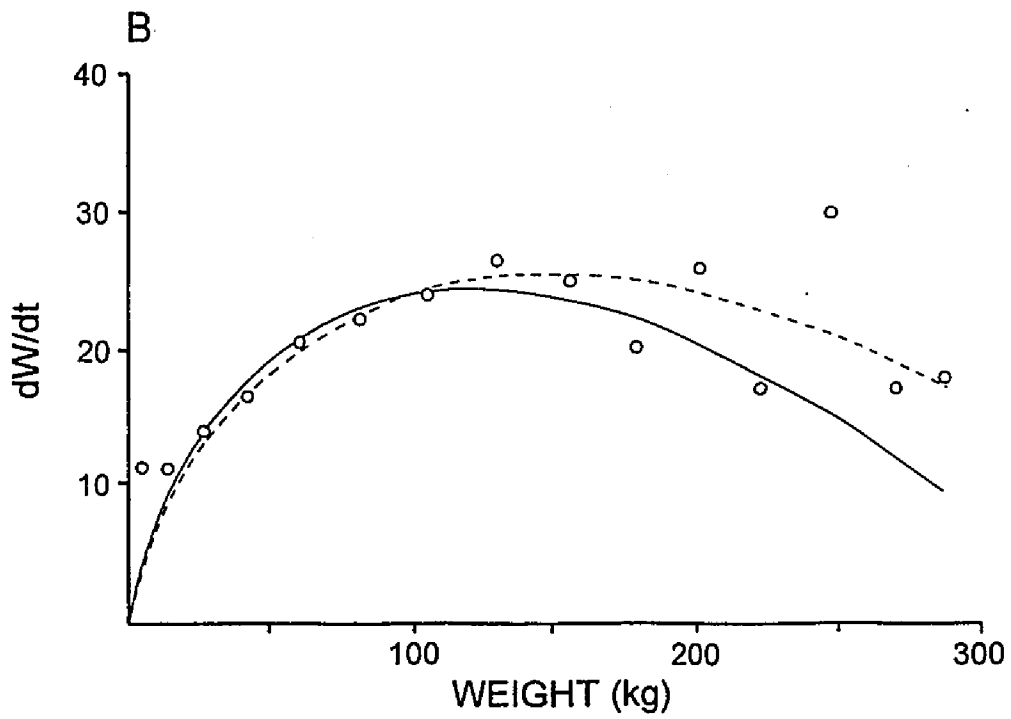
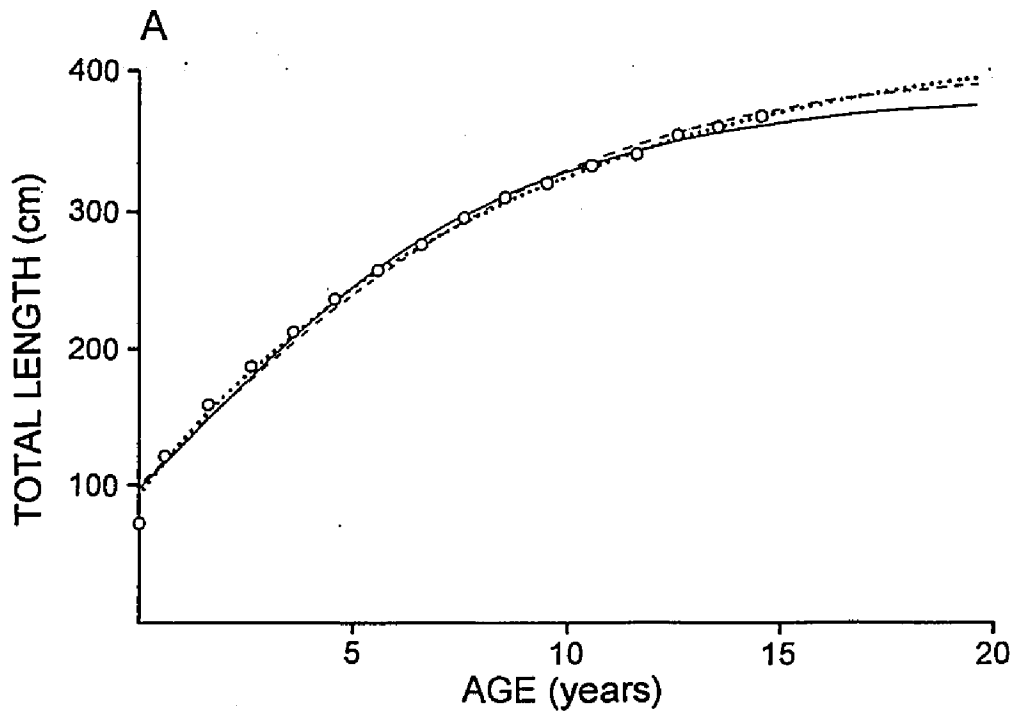


Figure 17. a: Back-calculated length at age and von Bertalanffy growth curves for female dusky sharks from the Atlantic. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW). Data from Lawler (1976).

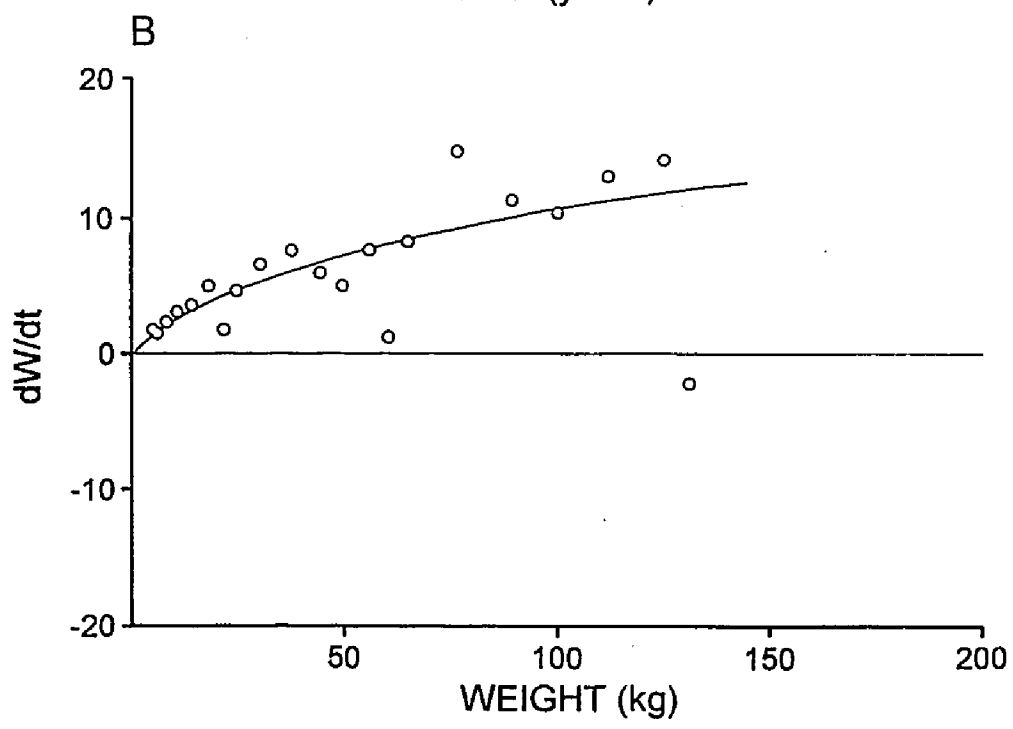
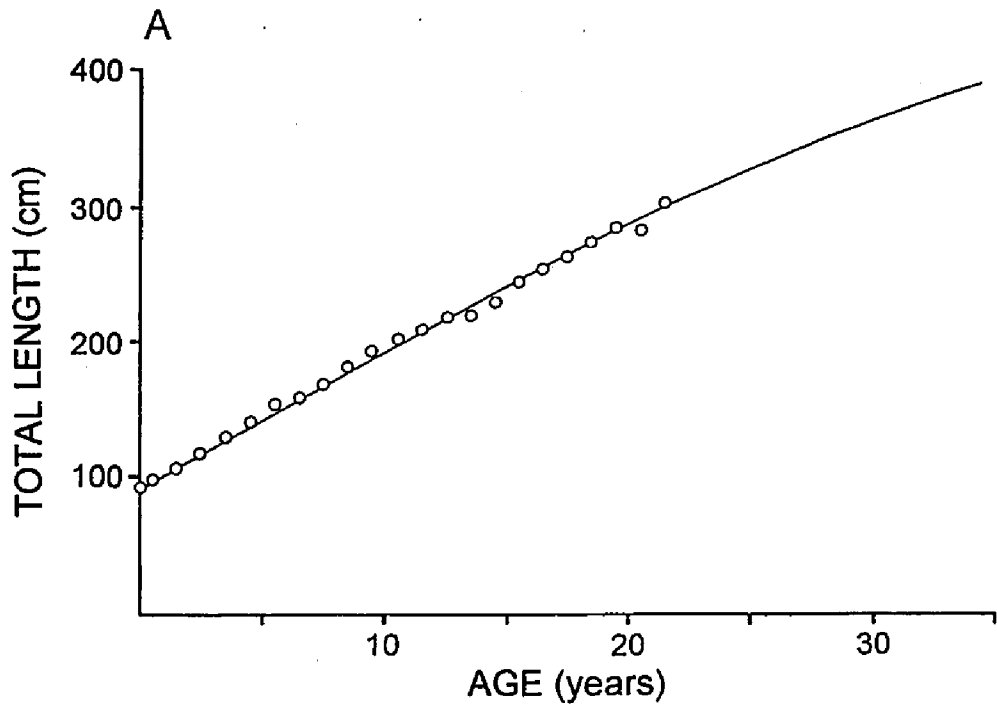
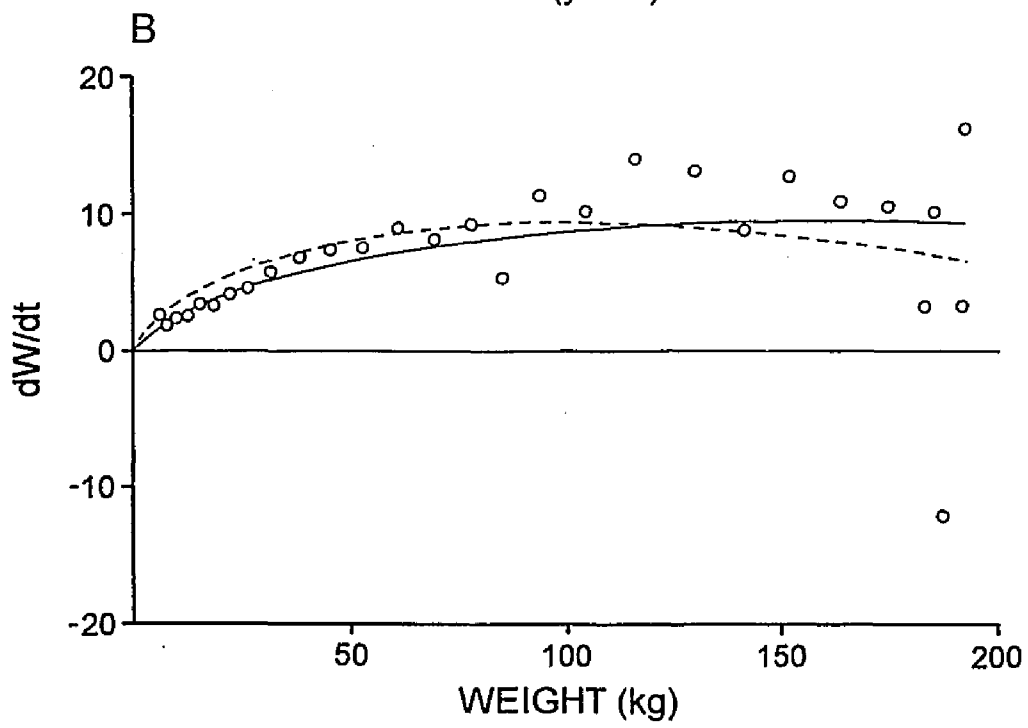
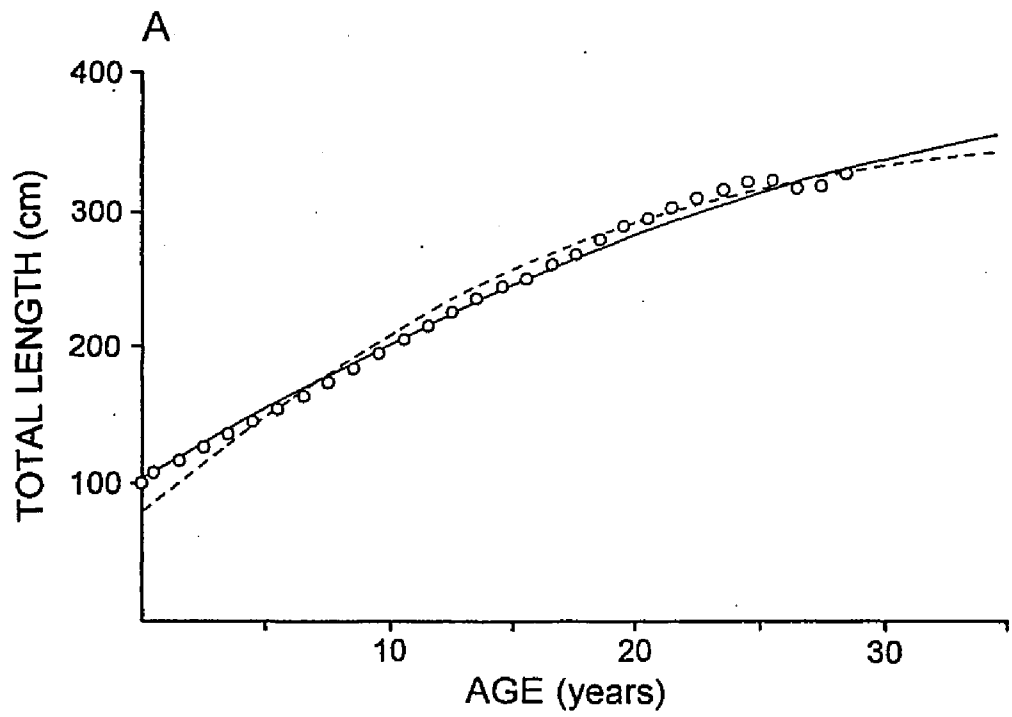


Figure 18. a: Back-calculated length at age and von Bertalanffy growth curves for female dusky sharks from the Indian Ocean. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dashed line = Equation 15. Data from Natanson (1990).



(Natanson 1990) are reasonable given a maximum length of 365-400 cm (Figs. 19a and 20a). The OVB produced an extreme estimate of L_{∞} for the dusky using data from Lawler (1976) (1904 cm). Asymptotic lengths for Indian Ocean females and Atlantic Ocean males were also too large. The L_{∞} estimated from Equation 15 for Atlantic Ocean females (Natanson 1990) (336 cm) slightly underestimates the maximum length, but apparently fits weight growth data better at larger weights than does the OFW (Fig. 19b). Asymptotic lengths from Equation 15 for Indian Ocean females (368 cm) and Atlantic Ocean males (366 cm) are close to the observed maximum. Lawler's (1976) OFW fits weight growth data well (Fig. 17b), despite the large L_{∞} , and probably suffers from a lack of larger (older) fish.

The asymptotic length estimated from the OFW for the white shark (883 cm) is much larger than the observed maximum. Calculated L_{∞} by the EFW and Equation 15 for white sharks (717 and 763 cm, respectively) are likewise greater than the observed maximum of 600-640 cm, although the maximum may be as large as 800 cm. All three equations fit observed length at age data well (Fig. 21a). Both the OFW and Equation 15 fit weight growth data well (Fig. 21b), but apparently suffer from a lack of larger fish. In contrast, the L_{∞} obtained from the OFW for mako sharks (417 cm) and blue sharks (420 cm) are reasonable compared with the observed maxima, considering the lack of older fish (Figs.

Figure 19. a: Back-calculated length at age and von Bertalanffy growth curves for female dusky sharks from the Atlantic. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dashed line = Equation 15. Data from Natanson (1990).

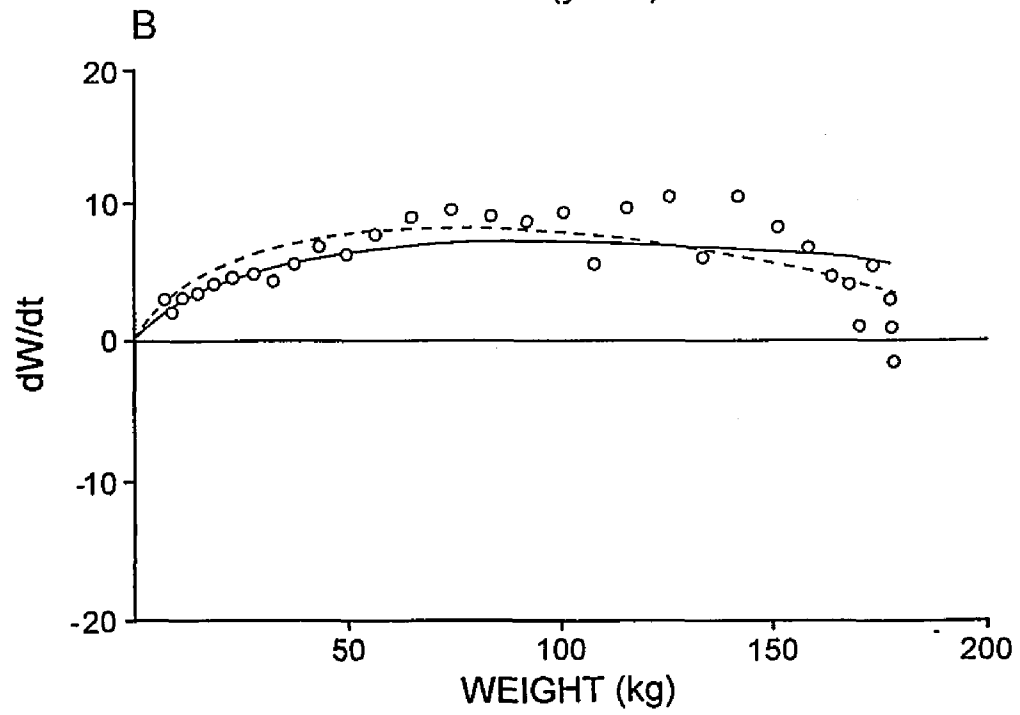
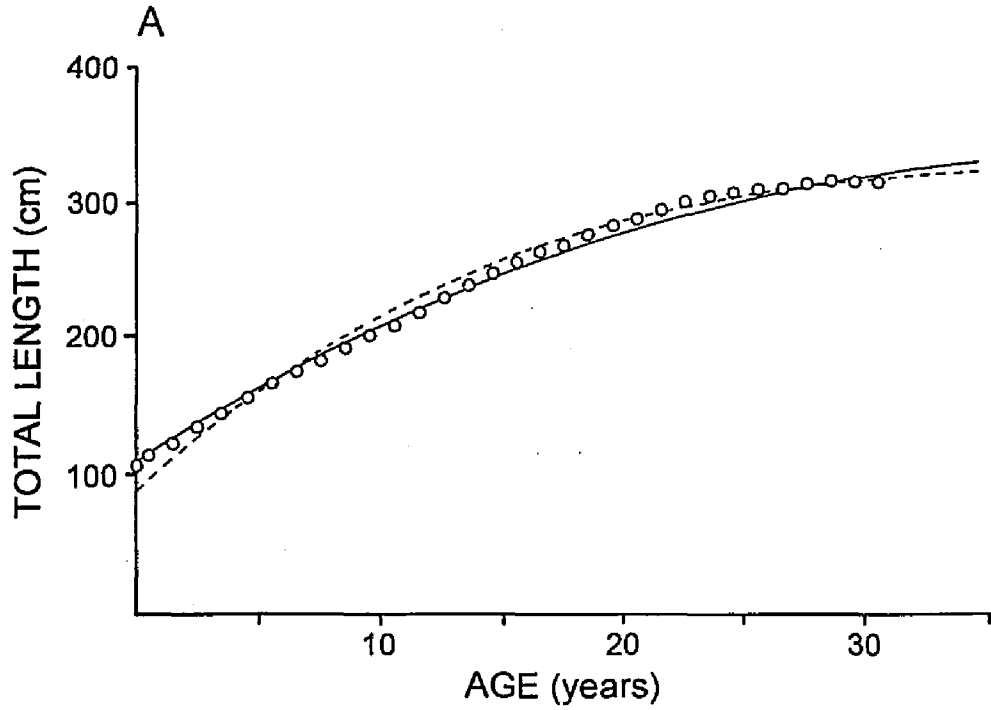


Figure 20. a: Back-calculated length at age and von Bertalanffy growth curves for male dusky sharks from the Atlantic. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dashed line = Equation 15. Data from Natanson (1990).

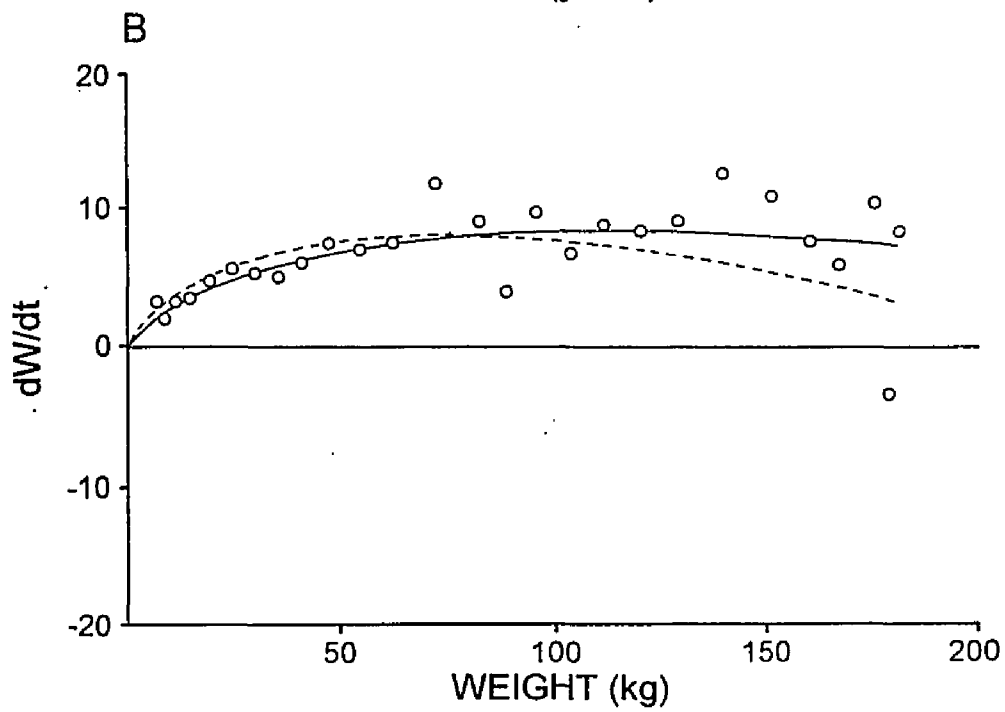
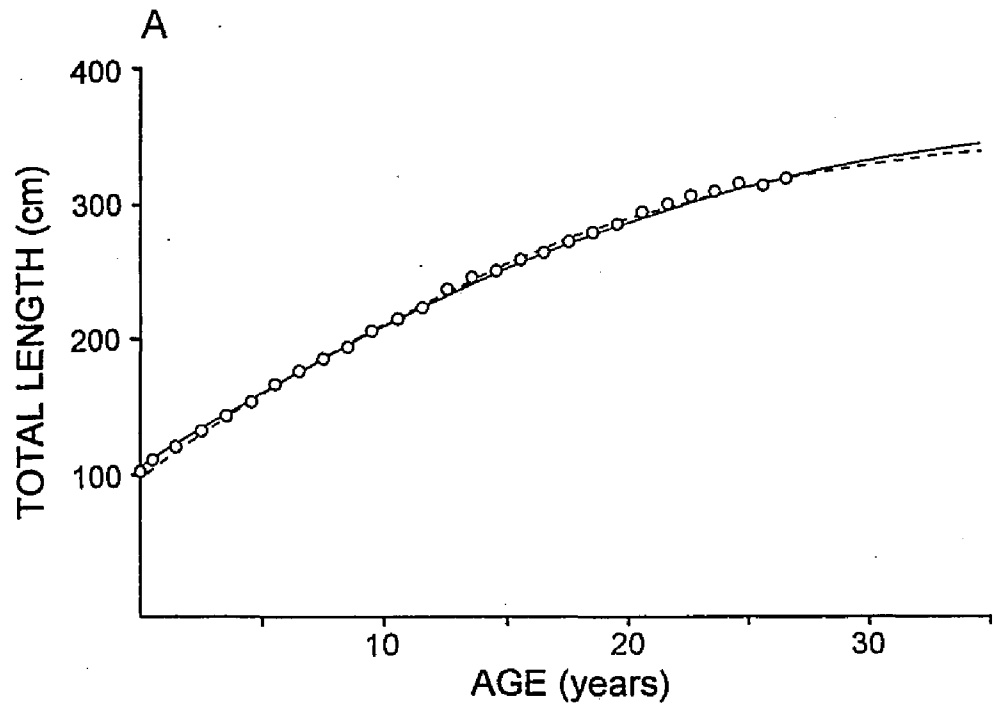
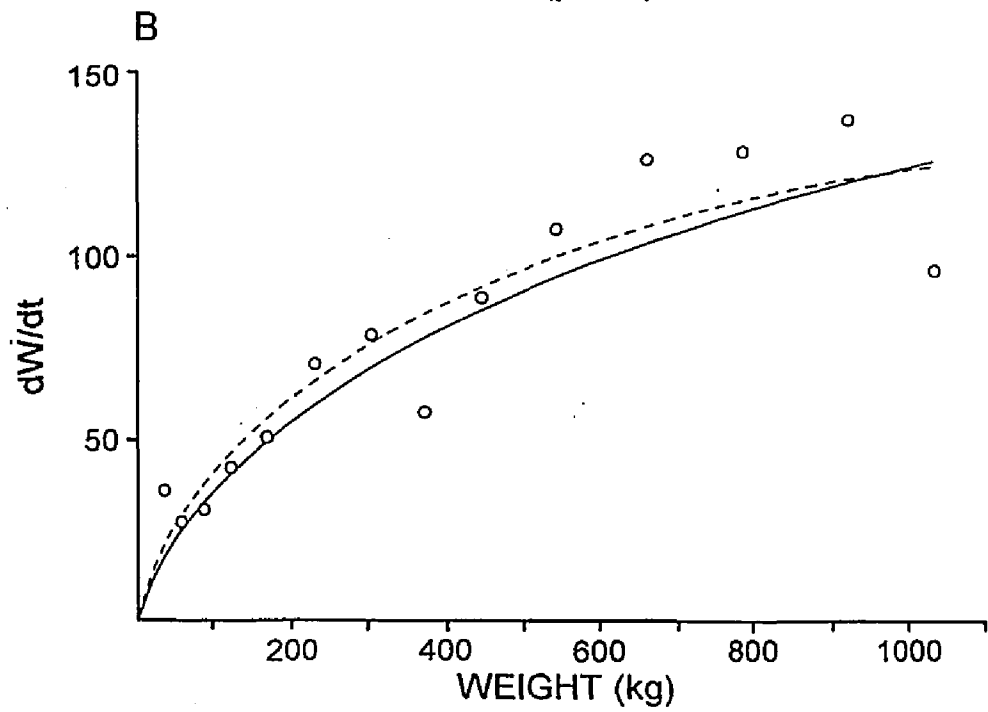
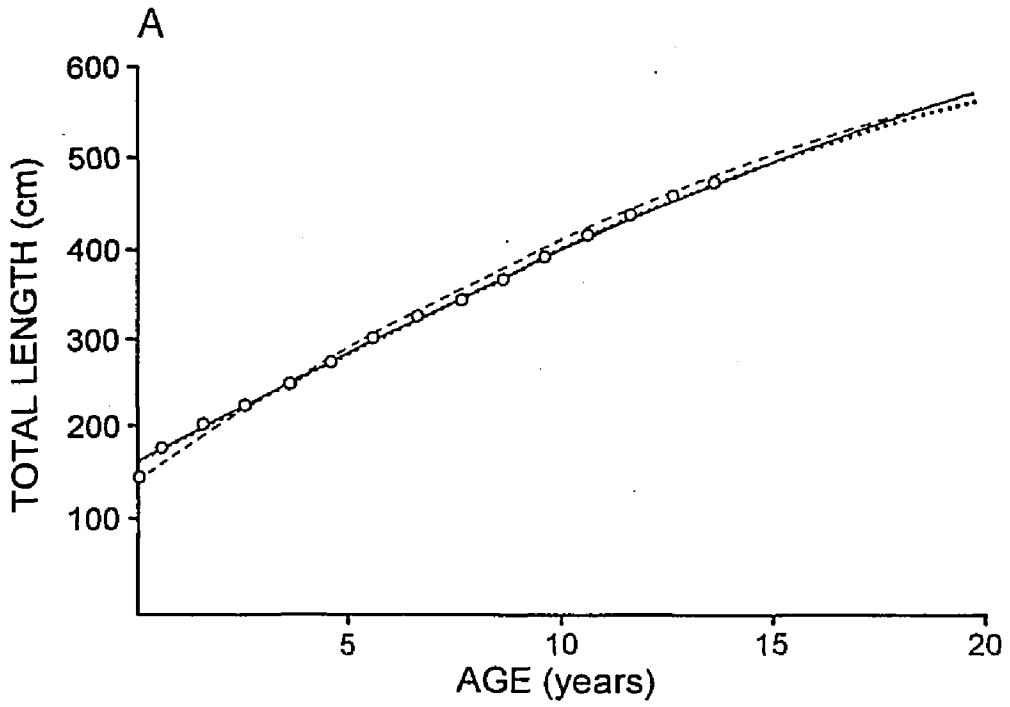


Figure 21. a: Back-calculated length at age and von Bertalanffy growth curves for white sharks. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW), dashed line = Equation 15. Data from Cailliet et al. (1985).



22a and 23a). The OFW fit weight growth data reasonably well for both species (Figs. 22b and 23b), although there was considerable scatter in dW/dt at larger weights for makos, and a lack of data for blue sharks. The L_{∞} obtained from the EFW for the mako shark (485 cm) is considerably larger than the observed maximum. The OVB produced extreme estimates of L_{∞} for the white (1130 cm) and blue (2072 cm) sharks.

Apparently, the adequacy of the modified von Bertalanffy equation is dependent to a large degree on the data set. For the sandbar, Atlantic Ocean dusky (Natanson 1990), mako and blue sharks the observed d (OFW) produced realistic results. In contrast, the OFW produced unrealistic asymptotic lengths for Atlantic (Lawler 1976) and Indian Ocean (Natanson 1990) dusky sharks and white sharks. All methods consistently underestimated the maximum length for tiger sharks. The length at age data for the tiger sharks shows more of an asymptote than do the data for the other species. The original von Bertalanffy equation ($D = 1$) performed poorly for the sandbar, dusky, blue and white sharks, as a result of the departure of the "true" D from unity. The extreme values of L_{∞} from both the OFW and OVB from Lawler's (1976) length at age data for the dusky shark reflect a fairly constant growth rate, with no indication of a decreasing rate at greater ages. This may be due to errors in identifying annuli or a lack of a

Figure 22. a: Back-calculated length at age and von Bertalanffy growth curves for mako sharks. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed d from Ford-Walford equation (OFW), dotted line = empirical D (EFW). Data from Pratt and Casey (1983).

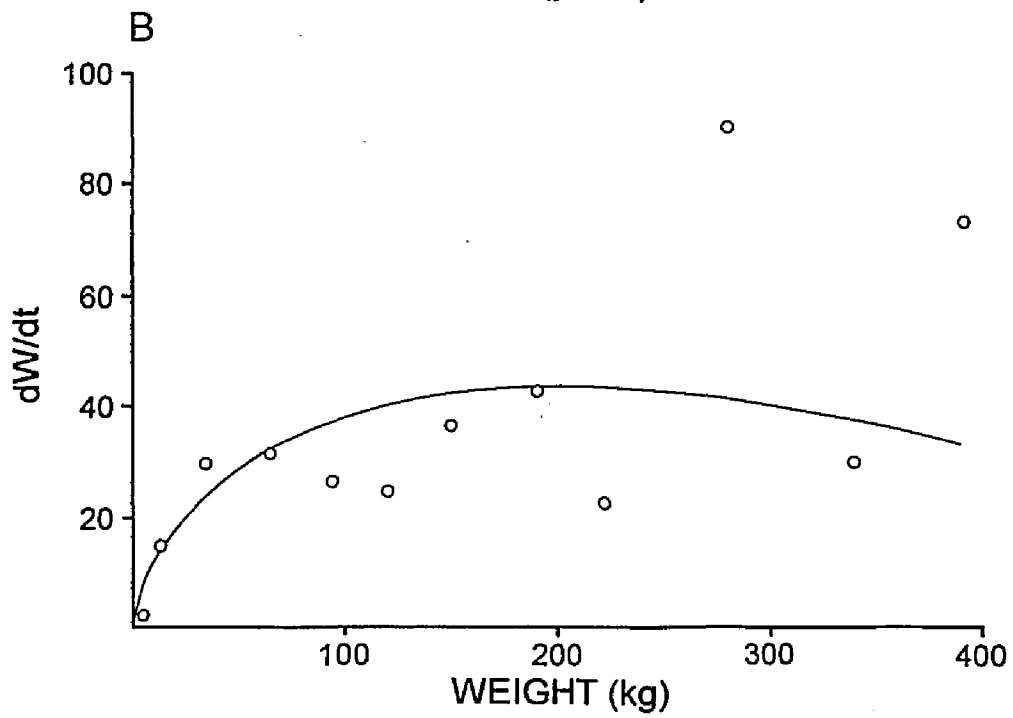
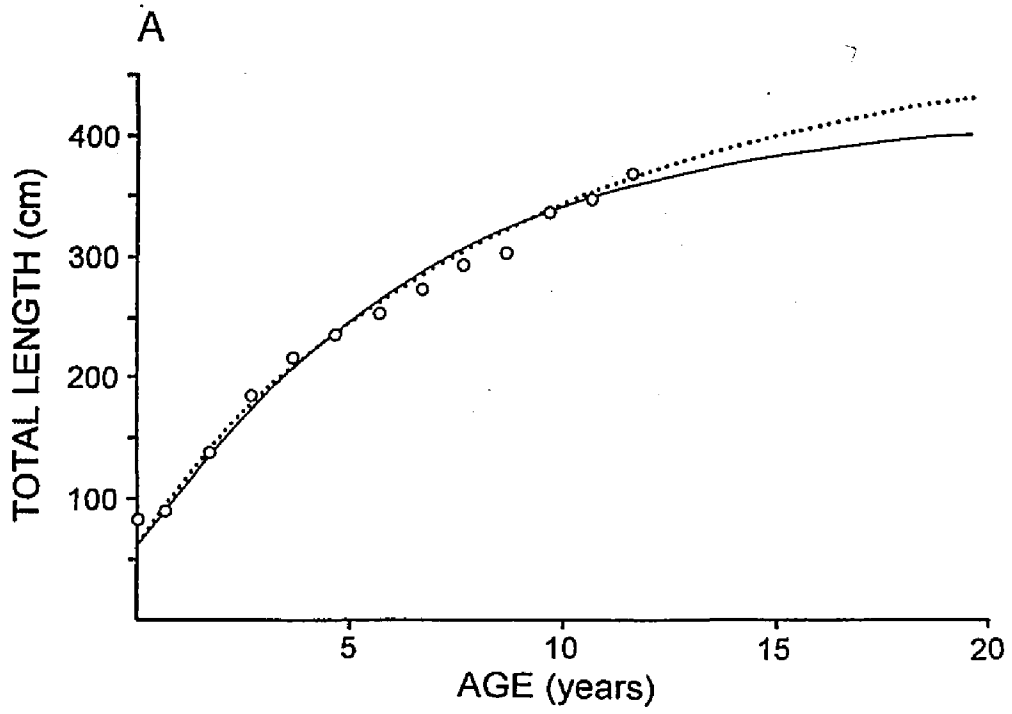
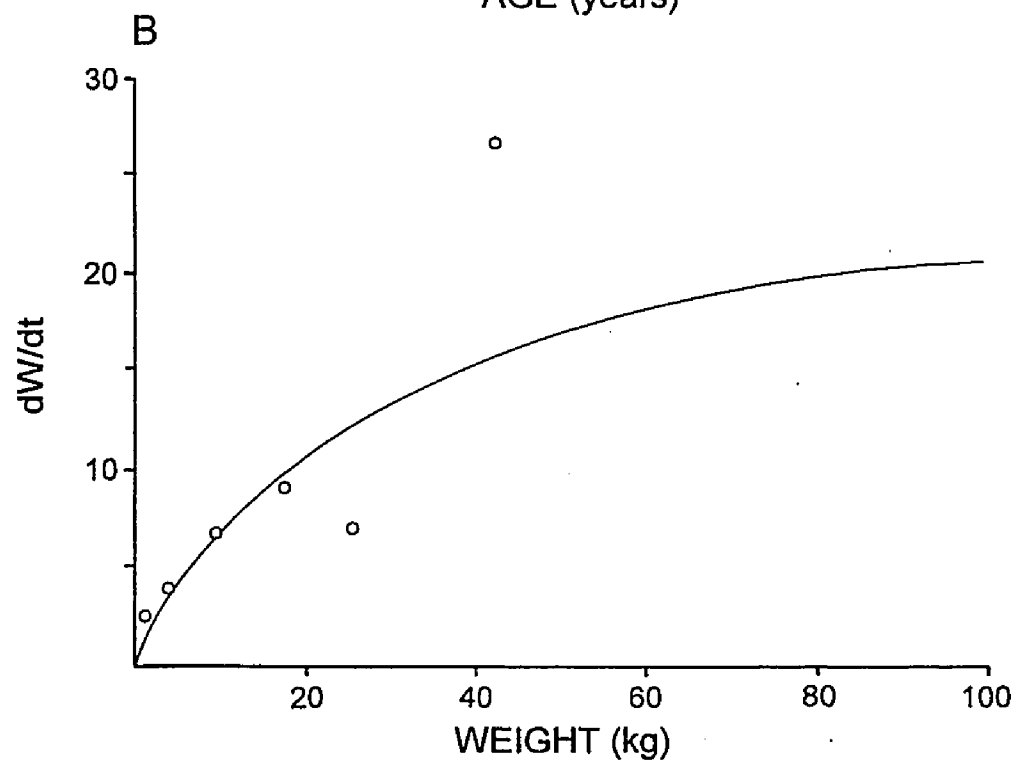
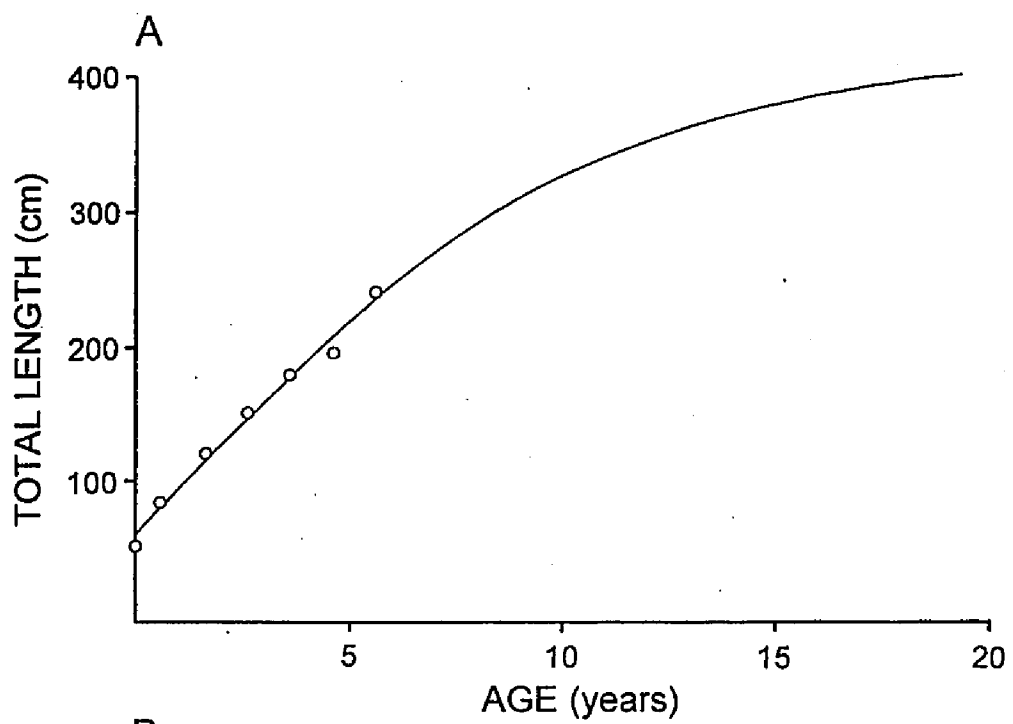


Figure 23. a: Back-calculated length at age and von Bertalanffy growth curves for blue sharks. b: Observed and calculated growth rate (kg/yr) by weight. Solid line = observed and from Ford-Walford equation (OFW). Data from Stevens (1975).



sufficient number of older, larger individuals in the sample.

Von Bertalanffy growth parameters calculated from Equation 15 using tagging data are given in Table 25. For both the sandbar and blue shark there was considerable variability in calculated dW/dt (Figs. 24 and 25), although regression coefficients were significant. The asymptotic length of blue sharks obtained from tagging data (267 cm) is much smaller than the reported maximum length, whereas KD is nearly twice that obtained from length at age data. The asymptotic length obtained for sandbar sharks is comparable to the observed maximum, but the calculated KD is much lower than that calculated from length at age data. By arbitrarily assuming that one vertebral mark is formed every two years, the von Bertalanffy equation from tagging data is in reasonable agreement with Casey et al.'s (1985) length at age data (Fig. 25).

Although asymptotic lengths vary between methods in some instances, and from observed maxima, estimates of A_{∞}/W_{∞} from observed gill area-weight relationships are more similar (Table 25). When compared with the carcharhinid sharks, the estimates of A_{∞}/W_{∞} for the lamnid species are greater, indicating a higher metabolism required for endothermy (Fig. 26). Within the carcharhinids, A_{∞}/W_{∞} for sandbar sharks (ca. 18×10^4 - 19×10^4 mm^2/kg) are lower than for tiger (29×10^4 - 30×10^4 mm^2/kg),

Figure 24. a: Von Bertalanffy growth curve for sandbar sharks obtained from tagging data. Back-calculated lengths at age (Casey et al. 1985) assuming one vertebral mark is formed per one and two years are given for comparison. b: Observed and calculated growth rate (kg/yr) by weight from tagging data. Data from Casey and Natanson (1992).

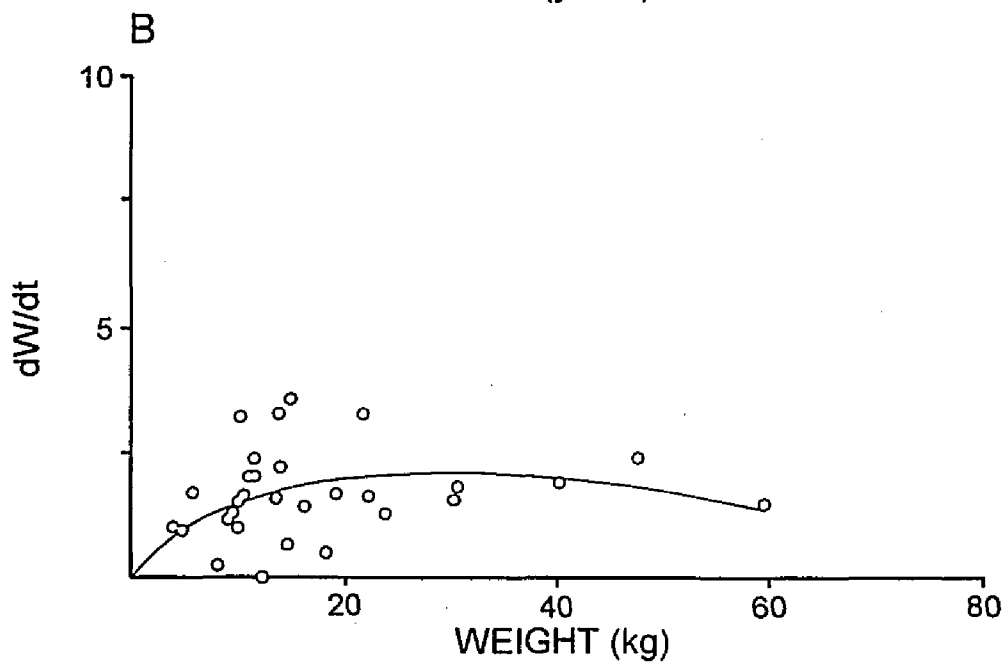
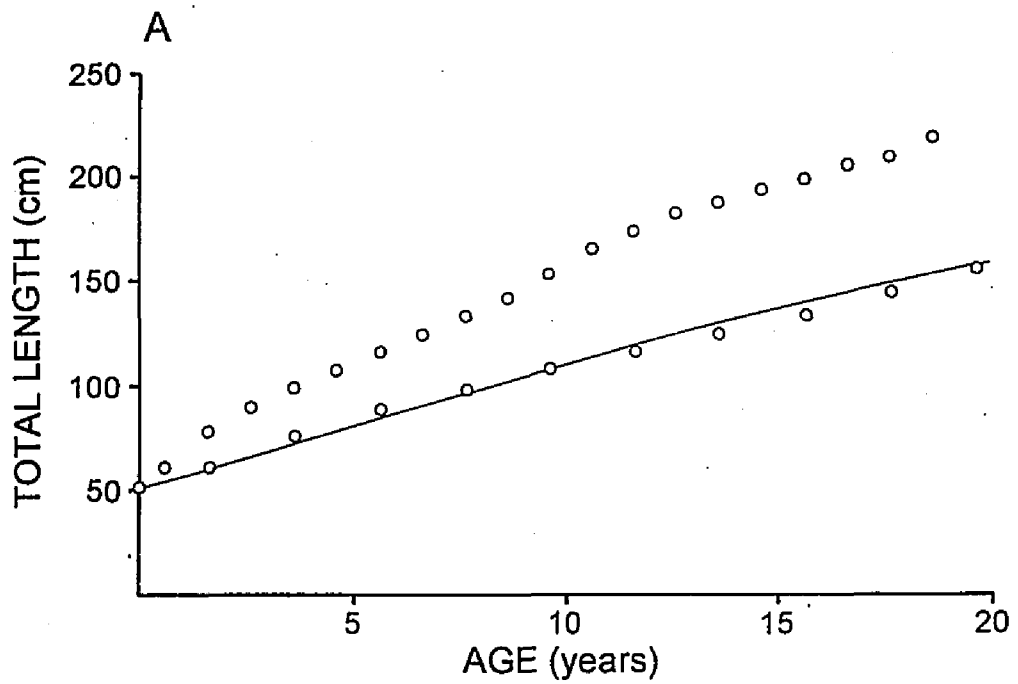


Figure 25. a: Von Bertalanffy growth curve for blue sharks obtained from tagging data. Back-calculated lengths at age and von Bertalanffy growth curve (dotted line; see Fig. 19) given for comparison. b: Observed and calculated growth rate (kg/yr) by weight. Data from Stevens (1976; 1990).

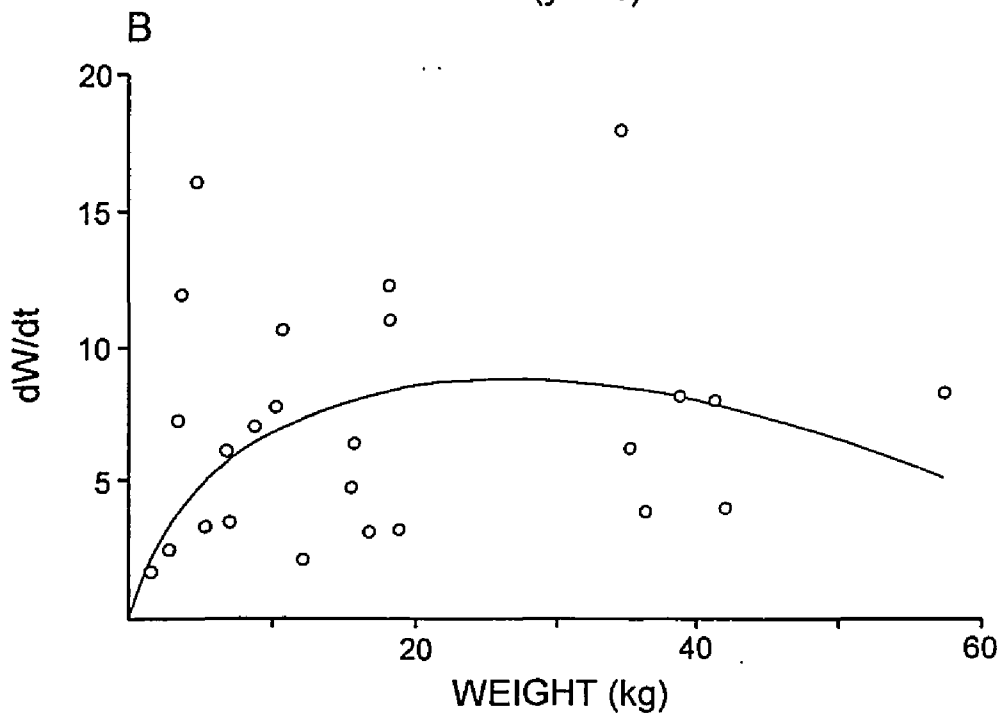
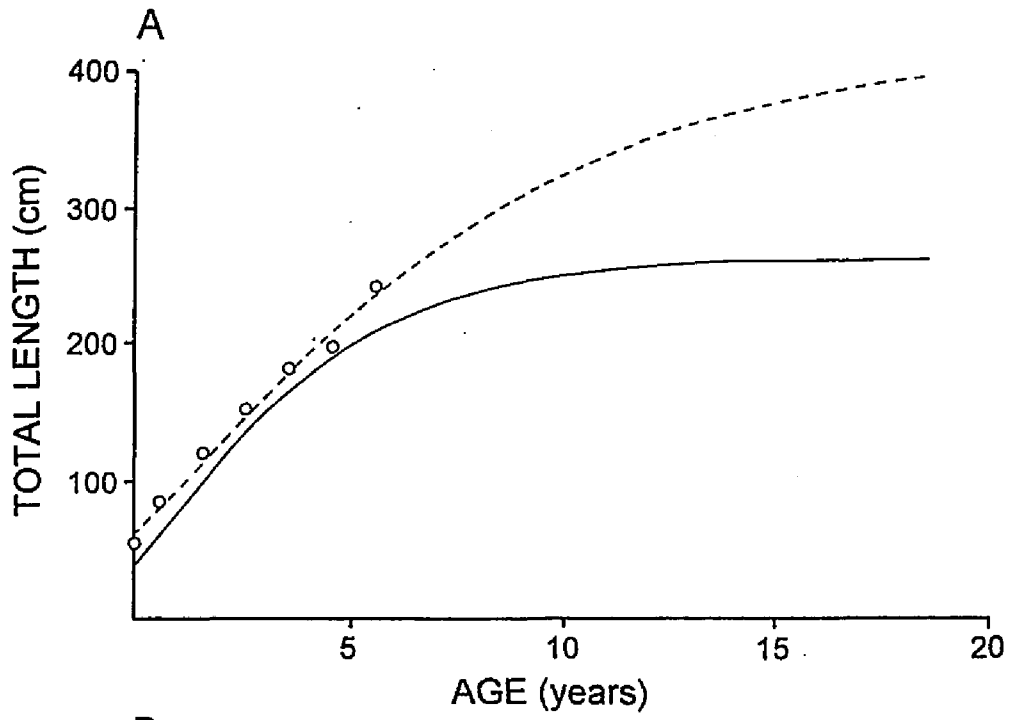
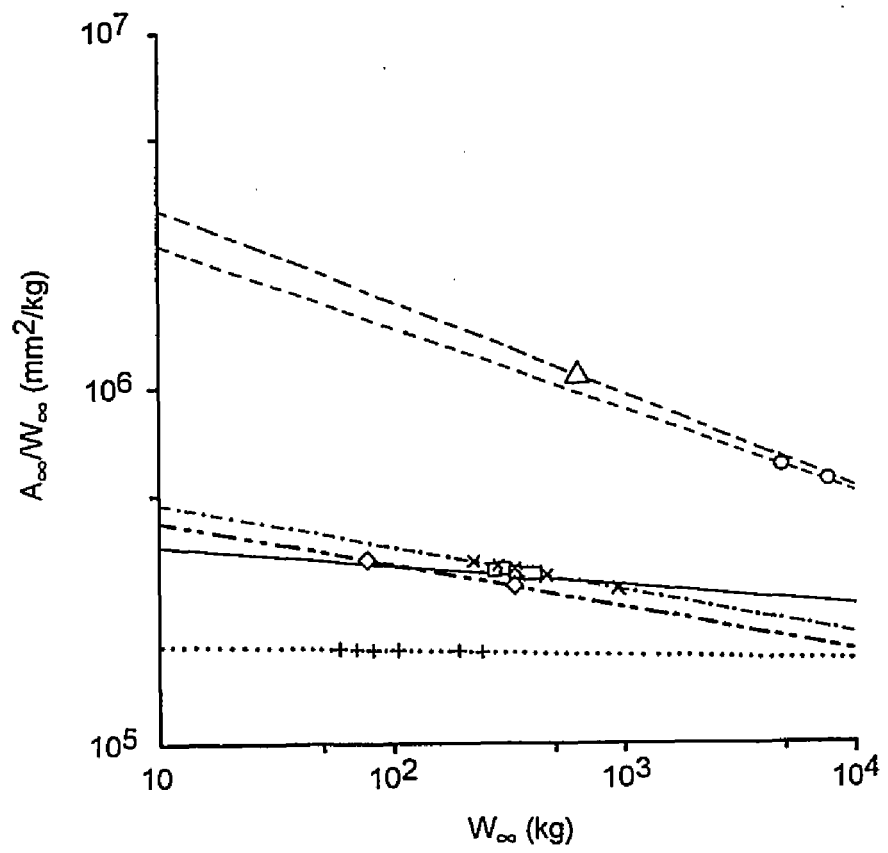


Figure 26. Plot of A_{∞}/W_{∞} against asymptotic weight (W_{∞}) for all species examined. '+' denotes sandbar sharks, squares denote tiger sharks, diamonds denote blue sharks, 'x' denotes dusky sharks, circles denote white sharks, and the triangle denotes shortfin mako sharks. Lines indicate predicted values from equations presented in the text or from Emery and Szczepanski (1986). Only values from method A are presented for sandbar and tiger sharks for clarity.



dusky ($27 \times 10^4 - 32 \times 10^4 \text{ mm}^2/\text{kg}$) or blue sharks ($27 \times 10^4 - 33 \times 10^4 \text{ mm}^2/\text{kg}$), indicating lower apparent metabolic requirements. However, the gill areas obtained here for two blue sharks suggest a lower regression intercept than obtained by Emery and Szczepanski (1986). By extension, this would suggest that A_{∞}/W_{∞} for that species may be as low as for sandbar sharks. Within data sets, K increased with A_{∞}/W_{∞} among different methods (Table 25), but there was no apparent correlation among data sets.

The 13 sandbar sharks used in the gill area study and examined for age ranged from 65 to 140 cm SL. Calculated ages ranged from 3.3 to 16.3 years at capture. The best fit of the modified Ford-Walford equation to the mean back-calculated lengths at age from all specimens was determined at $D = 0.97$ ($d = 0.685$) and gave the parameter estimates $K = 0.0848$, $t_0 = -2.75$ and $L_{\infty} = 178.5$ cm SL. Application of the D calculated from gill areas produced estimates of $K = 4.3206$, $t_0 = -15.15$ and $L_{\infty} = 144.6$ for Method A ($D = 0.043$), and $K = 15.4415$, $t_0 = -21.32$, and $L_{\infty} = 143.9$ for Method B ($D = 0.012$).

Generalized von Bertalanffy equations using the empirical and observed D were applied to weight using Equation 3. Residuals of the gill area-weight regressions were plotted against deviations of observed weight at age from predicted. Correlation coefficients were not significant for either the empirical fit ($r = 0.4149$; $t =$

1.51; $df = 11$) or the observed d ($r = 0.3227$; $t = 1.13$; $df = 11$) to Method A residuals. However, residuals of the von Bertalanffy equation using Method B ($D = 0.012$) were negatively correlated with the Method B gill area residuals ($r = -0.5271$; $t = -2.057$; $df = 11$). The negative correlation indicates that individuals with gill areas larger than predicted for that weight are smaller at age than predicted. This is in apparent contradiction to the expectation that individuals with larger gill areas would be larger at age.

There is no apparent correlation between individual growth and gill surface area. Modified Ford-Walford equations were applied to back-calculated lengths at age for individuals older than 6 years using $D = 0.0123$. There was no significant correlation between individual Method B gill area residuals and K values ($r = 0.0170$; $t = 0.042$; $df = 6$) or L_{∞} ($r = -0.1073$; $t = -0.264$; $df = 6$).

DISCUSSION

The results of the gill area study support the original hypothesis that gill surface area increases at a constant rate with size and that the ratio of gill area to weight (A/W) decreases with weight ($d < 1$). Despite the proximity to unity, the values of d result in decreasing A/W , although the rate of decrease is low for sandbar sharks. Furthermore, through Equation 15, the age and growth studies presented here support the contention that species-specific or population-specific growth rates decrease with decreasing A/W , and that the decreasing A/W results in asymptotic growth, even as d approaches 1. Notwithstanding the diversity of literature sources, the gill area studies and age and growth results support Pauly's (1981) contention that growth, at least for species, sexes or populations, is limited by respiratory surface, and indicate that maximum weight is determined by a critical ratio, A_{∞}/W_{∞} . However, a number of factors affect the interpretation of the results, such as the validity of the gill area measurements and the assumption that gill area is proportional to oxygen consumption. Errors in length at age estimates or conversions to weight, sampling bias, and individual variability in growth characteristics also affect conclusions. Although applied

specifically to sharks, the theories and equations examined in this study should be applicable to teleosts as well.

Gill surface area slopes (d) found in this study are similar to those found in some other elasmobranch species, but larger than in other species. Estimated slopes are 0.97, 0.937 and 0.961 for Scyliorhinus canicula, Raja clavata and Torpedo marmorata (Hughes 1972, Hughes 1977; Hughes 1978). However, values of d obtained for S. stellaris, white, shortfin mako, blue, and dusky sharks are 0.779, 0.77, 0.74, 0.88, and 0.88, respectively (Hughes et al. 1986; Emery and Szczepanski 1986).

In contrast to the slopes found here by different methods (0.986 - 0.996), Emery and Szczepanski (1986) obtained a slope of 0.74 for the sandbar shark. This difference may be due to differences in estimates of mean lamella areas. Hughes' (1966) method of area determination, $A = 4 * L * n * a$, may be rewritten as

$$A = 4(\alpha_1 W^{\beta_1})(\alpha_2 W^{\beta_2})(\alpha_3 W^{\beta_3})$$

$$A = 4\alpha_1 \alpha_2 \alpha_3 W^{\beta_1} W^{\beta_2} W^{\beta_3}$$

$$A = 4\alpha_1 \alpha_2 \alpha_3 W^{(\beta_1 + \beta_2 + \beta_3)}$$

The regression slope, d, is equal to $(\beta_1 + \beta_2 + \beta_3)$ where β_1 , β_2 and β_3 are the slopes relating weight to total filament length, mean number of lamellae/mm and mean lamella area. Slopes obtained from this study are, respectively, 0.3311, -0.1319 and 0.7890, whereas Emery and Szczepanski (1986) calculated slopes of 0.40, -0.13 and 0.48. Slopes for mean

lamella area differed substantially between studies. Both studies utilized Formalin preserved specimens, so possible deformation of lamellae from preservative shrinkage should not differ by much. The regression slope of mean lamella area on weight for tiger sharks is similar to those for Scyliorhinus canicula, Raja clavata and Torpedo marmorata (Hughes 1972, Hughes 1977; Hughes 1978), and not significantly different from that found here for sandbar sharks, so slopes found here do not appear unrealistic. Furthermore, mean lamella areas found here for the dusky and blue sharks are comparable to areas predicted by Emery and Szczepanski (1986). Visual examination of Emery and Szczepanski's (1986) regressions indicate that all parameters, including mean lamella area, for their largest specimen were less than for the next four largest specimens. This end point may have had a significant influence on the regression slopes.

In contrast, the difference between gill areas calculated for blue sharks in this study and areas predicted from Emery and Szczepanski (1986) is apparently due to differences in total filament lengths. The total gill areas, as well as total filament lengths obtained here, are less than predicted by regression equations in Emery and Szczepanski (1986), whereas mean lamellae/mm were greater than predicted. Average lamella areas were nearly identical to those predicted by regression equations in

Emery and Szczepanski (1986), and the number of filaments was within the range they found.

Differences in mean lamella areas and total filament areas between anterior and posterior facing hemibranchs have not been previously reported in elasmobranchs. Although mean lamella areas differ among the hemibranchs, slopes of regressions of mean lamella area on weight should not be affected in Hughes' (1966) method of gill area estimation, as long as sampling is consistent among specimens. However, intercepts would be affected, and care should be taken to insure that hemibranch differences are adequately represented.

The results of Method B suggest that sampling methodology may be simplified. The equation parameters (Tables 9 and 18) can be estimated from a limited sample representative of the species size range. These results could then be extrapolated to a larger sample in which only the filament lengths are measured. The most time consuming part of this study was the dissection and measurements of lamellae. Slopes of regressions of filament area on filament length did not differ significantly among individuals for sandbar sharks, but did differ among individual tiger sharks. However, use of the pooled slope in Method B resulted in estimates of r and d similar to those obtained using individual slopes in Method A. This method may also eliminate some of the sampling or

measurement error variability among individuals.

There was little difference in estimates of r and d from the three methods. However, Method C used the same randomly selected lamellae as the other methods, so any bias would be consistent among methods. Any bias should be less than would occur from nonrandom selection.

The hypothesis examined in this study makes some important assumptions: measured gill area is proportional to the effective gill area and the effective gill area is proportional to oxygen consumption. Hughes (1966) suggested that the respiratory surface area was only 60-70% of the total measured gill area, but Randall (1970) suggested the functional area in resting trout may be as low as 20% of the measured area. The actual vascular surface area of lamellae in Ophiodon elongatus is 88% of the total measured area (Farrell 1980). If functional surface area is a constant fraction (C_{funct}) of the total measured area,

$$A_{\text{funct}} = C_{\text{funct}} A_{\text{meas}}$$

$$A_{\text{funct}} = C_{\text{funct}} r W^d$$

the intercept is affected, but not the slope.

Oxygen consumption is typically greater during active metabolism than during rest (e.g. Brett 1965; Brett and Glass 1973; Armstrong et al. 1992). In rainbow trout with a 27-30% reduction in their gill area, maximum swimming speed and oxygen consumption was reduced, although oxygen consumption at rest and at lower swimming speeds were not

affected (Duthie and Hughes 1987), indicating that the entire gill area is not required at all times. There is little information on active respiration rates in sharks. Data for three juvenile scalloped hammerhead sharks indicate that during normal activity oxygen consumption is proportional to $W^{0.93}$ (Howe 1988).

Swimming speed, U , is related to body length, L , in the form of the equation $U = \delta L^\beta$. Weihs (1977) calculated that energetically optimal swimming speed, U_o (cm/sec) = $6.9FL^{0.43}$. Blake (1983) calculated that under turbulent flow $U_{turb} \propto L^{0.39}$. Observations on free-swimming bull and sandbar sharks correspond to $\beta = 0.43$ (Weihs et al. 1981). Parsons (1990) obtained a similar equation of $4.9TL^{0.496}$ cm/sec for bonnethead sharks, Sphyrna tiburo. The coefficient for swimming speed, $\beta = 3/14(5x-3)$ for turbulent flow (Wu 1977), where x is the coefficient for oxygen consumption in Equation 14. Assuming turbulent flow, and that for normal activity $d = x$, $\beta = 0.414$ at $d = 0.986$ for sandbar sharks and 0.365 at $d = 0.941$ for tiger sharks, in reasonable agreement with Weihs' coefficient. Given this admittedly tenuous association, it is assumed here that gill area is proportional to oxygen consumption during normal activity.

This study also assumed that the gills were the only respiratory surface. Cutaneous respiration in resting Scyliorhinus canicula may account for a negligible portion

of the total resting respiration (Toulmond et al. 1982) or as much as 10% of the total (Nonnotte and Kirsch 1978). It is assumed here that cutaneous respiration accounts for a small fraction of the total during normal activity and is negligible, averaged over normal activity, relative to branchial respiration.

Respiratory and/or circulatory parameters may change due to long-term osmotic changes. Average lamellar areas in Oncorhynchus mykiss held in seawater are greater, and water-blood barrier thickness is less than in those held in freshwater, producing an oxygen diffusing capacity in seawater 3.6 times greater than in freshwater (Laurent and Hebibi 1989), despite the decreasing solubility of oxygen in water (α) with increasing salinity. In a step-wise transfer from 33 to 15.2 ‰, Chan and Wong (1977) observed no change in oxygen consumption in free-swimming lipsharks, Hemiscyllium plagiosum, after acclimation, although oxygen consumption dropped immediately after transfer began. Burke (1974) found no difference in hemoglobin oxygen affinity (P_{50}) between bull sharks, Carcharhinus leucas, in fresh and salt water.

Oxygen consumption may be increased by increasing the respiratory area, decreasing the distance across which oxygen must pass, or increasing the oxygen activity gradient across the gills (Randall 1970). The oxygen gradient may be increased by raising the partial pressure

of oxygen (P_{O_2}) in water (increasing ventilation rate) or by lowering the blood P_{O_2} (high haemoglobin oxygen affinity). The lower P_{50} (pressure at which blood or haemoglobin is 50% saturated) of sandbar sharks indicates that haemoglobin oxygen affinity is much greater than that of blue sharks (Pennelly et al. 1975). Values of P_{50} obtained for other shark species (Table 26), although determined under different conditions, are also greater than for the sandbar, which may explain, in part, the apparent lower A_{∞}/W_{∞} for sandbar sharks. In contrast, P_{50} for the endothermic mako shark is similar to that of the ectothermic species, and does not indicate a higher oxygen affinity.

Other haematological characteristics support the higher metabolism of the endothermic sharks, but do not help explain the apparent lower metabolism of sandbar sharks. Haemoglobin concentrations ([Hb]: g/100 ml) and hematocrit (Hct: vol%) are fairly constant among elasmobranchs of varied activity levels (Baldwin and Wells 1990; Wells et al. 1992), although higher values of Hct and [Hb] may be associated with more active species (Johansson-Sjöbeck and Stevens 1976). Blood oxygen carrying capacity may be increased by increasing Hct and [Hb], and mean cell haemoglobin concentration ($MCHC = 100[Hb]/Hct$) may serve as a useful index of blood oxygen transport potential (Wells and Baldwin 1990). Hct and [Hb] in the

Table 26. Haematological characteristics for various shark species.

Species	Ref	Hct	[Hb]	MCHC	P ₅₀	pH	C ^o
<i>I. oxyrinchus</i>	F	32.4	-	-	10.6	7.6	25
<i>I. oxyrinchus</i>	G	40.8	14.3	36.9	-	-	-
<i>C. carcharodon</i>	G	36.0	13.5	37.9	-	-	-
<i>A. vulpinus</i>	G	37.4	13.6	36.0	-	-	-
<i>N. acutidens</i>	J	13.0	3.6	27.7	12.3	7.4	25
<i>N. acutidens</i>	J	-	-	-	9.9	7.8	25
<i>N. acutidens</i>	H	18.2	5.5	30.0	-	-	-
<i>G. cuvier</i>	G	19.8	6.5	33.8	-*	-	-
<i>G. cuvier</i>	I	-	-	-	~10*	7.6	20
<i>P. glauca</i>	E	22.3	5.7	25.7	-	-	-
<i>P. glauca</i>	G	15.2	5.0	33.2	-*	-	-
<i>P. glauca</i>	D	-	-	-	~10*	~7.5	20
<i>C. melanopterus</i>	J	17.0	4.1	24.3	17.9	7.4	25
<i>C. melanopterus</i>	J	-	-	-	11.1	7.8	25
<i>C. melanopterus</i>	H	17.1	4.1	24.3	-	-	-
<i>C. leucas</i>	C	-	-	-	11	7.4	25
<i>C. leucas</i>	C	-	-	-	17	6.8	25
<i>C. leucas</i>	A	21.6	(marine)	-	-	-	-
<i>C. leucas</i>	A	23.3	(freshwater)	-	-	-	-
<i>C. leucas</i>	B	22.8	(freshwater)	-	-	-	-
<i>C. obscurus</i>	G	18.2	6.2	34.5	-	-	-
<i>C. plumbeus</i>	G	14.9	5.1	35.0	-*	-	-
<i>C. plumbeus</i>	D	-	-	-	~6	~7.5	20

References:

- A Thorson 1962
- B Thorson et al. 1973
- C Burke 1974
- D Penelly et al. 1975
- E Johansson-Sjöbeck and Stevens 1976
- F Wells and Davie 1985
- G Emery 1986
- H Baldwin and Wells 1990
- I Scholnick and Mangum 1991
- J Wells et al. 1992

* estimated from figure.

endothermic white, shortfin mako and common thresher, Alopias vulpinus, sharks are much greater than those of ectothermic species such as the sicklefin lemon, Negaprion acutidens, tiger, blacktip reef, Carcharhinus melanopterus, bull, dusky and sandbar sharks (Table 26) (Johansson-Sjöbeck and Stevens 1976; Wells and Davie 1985; Emery 1986; Wells et al. 1992). MCHC values are more similar among species (Johansson-Sjöbeck and Stevens 1976; Emery 1986; Baldwin and Wells 1990; Wells et al. 1992), although sandbar sharks approach the higher values of endothermic sharks, and might approach the oxygen transport potential of those species.

If total gill slit height (GSH) is an indication of ventilation volume, then a greater GSH for a given gill area may increase the ventilation rate ($\text{cm}^3/\text{hr}/\text{mm}^2$) and provide for greater oxygen consumption. The higher GSH of sandbar sharks for a given gill area, compared with tiger sharks, may explain the difference in A_{∞}/W_{∞} between those species. The higher GSH^3/A for the blacktip sharks and possibly the dusky shark would provide for greater oxygen consumption and support a higher metabolism than suggested by A_{∞}/W_{∞} .

Empirical estimates of the generalized von Bertalanffy growth parameters depend on the accuracy of the input data. Slight variations in calculated length at age would be expected to change the "best fit" value of d . Such errors may be due to the method of back-calculation or variation

in the assignment of the time of birth and annulus formation. Variations in b and d have small effects on L_{∞} , but substantial effects on K , as indicated by the differences in K for male sandbar sharks. Furthermore, the parameters are based on data averaged over several year classes. Variability in biotic and abiotic factors would result in variability in growth parameters, among year classes and even among individuals.

Equation 15 and the associated von Bertalanffy parameter estimates are subject to errors from several sources. This method is more sensitive to the length-weight relationship than the modified Ford-Walford equation. Errors in weight estimation from lengths may produce large errors in dW/dt estimates, due to the heteroscedastic nature of the length-weight relationship. Weights at smaller lengths are more sensitive to errors in the length-weight intercept. Such errors may account for the lack of fit of Equation 15 to the smallest weights. As weights increase, the variability in dW/dt increases, possibly because sizes at age are averaged over progressively fewer individuals with progressively larger variance. These problems are evident in the typically greater SSE from Equation 15 than from the Ford-Walford equation. Also, there was generally no strong evidence of decreasing dW/dt at greater weights in some species, so L_{∞} was extrapolated from the variable end of the data range. In view of the

potential problems, Equation 15 performed reasonably well compared to the Ford-Walford equation, supporting the hypothesis that gill area influences growth.

The wide variation in observed dW/dt from tagging data may likewise be due to several factors. There may have been errors in determining lengths at tagging, as suggested by the apparent decrease in lengths of some blue sharks upon recapture. Although these decreases were omitted from analysis, it cannot be assumed that all apparent increases were accurate. Three apparent outliers in the sandbar shark data ($dW/dt > 5$) were, none the less, within the range of values for the length at age data. However, their presence resulted in a nonsignificant regression. Inclusion of those points would have increased K . In some instances time at liberty was on the order of several years. Over long-term, the mid-point weight may not accurately reflect the "mean" weight for placement of dW/dt on the weight axis. Likewise, the calculated dW/dt may not reflect the true mean over that time span. In addition, severe damage may occur during capture, which can lead to reduced growth rates, so rates deduced from tagging studies may be minimal estimates (Davenport and Stevens 1988).

The results obtained for sandbar sharks indicate the effect of data sets used. The modified Ford-Walford equation and observed d (OFW) performed well with the data from Casey et al. (1985), but apparently underestimated L_{∞}

for data from Lawler (1976). The empirical estimate of d (0.870) for males was close to the observed value, so the L_{∞} was similar. In contrast, the empirical values of d for females (0.507 and 0.572) were much lower than the observed, and consequently the L_{∞} was greatly overestimated. Asymptotic lengths using the observed d were closer to the observed maximum than those calculated using $D = 1$ (OVB) with data from Casey et al. (1985), but the opposite was true for the data from Lawler (1976). Equation 15 performed well for males, but may have overestimated L_{∞} for females using both data sets. Given the potential errors involved, the results were more consistent than expected, and not unreasonable if sandbar sharks attain 300 cm (Compagno 1984). Likewise, L_{∞} from tagging data was comparable to the observed maximum. Although KD from tagging data was considerably lower than from length at age data, it is comparable to K (0.046) obtained by Casey and Natanson (1992).

The OFW produced asymptotic lengths less than those calculated by Branstetter et al. (1987) for tiger sharks from the Gulf of Mexico (388 cm) and Atlantic coast (440 cm) and much less than the observed maximum (550 cm). They reported typical maximum lengths of 380-420 cm from the literature, more in agreement with their L_{∞} , but still larger than that obtained from the OFW for Gulf tiger sharks here. DeCrosta et al. (1984) calculated an L_{∞} of 437

cm TL for Hawaiian specimens, in agreement with that for Atlantic specimens (Branstetter et al. 1987). In data sets such as for tiger sharks, in which decreasing growth rates at older ages are evident, the asymptotic length is more rigidly fixed, and variation in D does not substantially alter estimates of L_{∞} . Similarly, the descending phase of dW/dt in Equation 15 produced an L_{∞} close to that obtained from the Ford-Walford equation.

The asymptotic length for blue sharks obtained by Stevens (1975) (423 cm TL) is similar to that found here by the OFW (420 cm). The K calculated by Stevens (0.110) is only slightly less than KD reported here (0.1712). Both asymptotic lengths are greater than the observed maximum length of 383 cm (Compagno 1984), but are reasonable if blue sharks attain greater lengths of 480 cm. The disparity between calculated and observed maximum lengths may be due to the relatively short age range (7 yr) used. Cailliet et al. (1983) obtained a much lower L_{∞} (266 cm) using data through age 9 years and attributed the difference from Stevens (1975) to methodology. However, they did not exclude the possibility of population differences. Tanaka et al. (1990) calculated an L_{∞} of 304 cm for females and 369 cm for males. The L_{∞} calculated here from tagging data (267 cm) is close to that obtained by Cailliet et al. (1983), although KD obtained here (0.3134) was larger than K they reported (0.223).

The L_{∞} calculated here for white sharks from the OFW (883 cm) is much larger than the largest reliable observed length (640 cm) although they may attain lengths of 800 cm, and lengths >900 cm have been reported (Randall 1973; Cailliet et al. 1985). The L_{∞} and KD obtained from Equation 15 (763 cm and 0.0674) are more reasonable given a maximum length of 800 cm, and close to those calculated by Cailliet et al. (1985) (764 cm and 0.058).

The L_{∞} obtained here for shortfin mako sharks by the OFW (417 cm) is much larger than obtained elsewhere, but only slightly greater than the observed maximum (400 cm). Pratt and Casey (1983) reported asymptotic lengths of 373 cm TL (345 cm FL) for female and 327 cm (302 cm FL) for males. Cailliet et al. (1983) calculated an L_{∞} of 321 cm. The KD calculated here (0.1768) is similar to K obtained by Pratt and Casey (1983) (0.266 for males, 0.203 for females), but much larger than that reported by Cailliet et al. (1983) (0.072).

Observed maximum lengths much greater than the typical maximum may be due to individual variation in growth characteristics. The variation in observed sizes at age implies differences in growth rates (K or KD), and by extension, variation in individual maximum attainable length, L_{∞} . From Equations 8 and 9, L_{∞} and W_{∞} increase as k (and K) decreases (for a given H), so individuals with lower K values than average may reach greater than average

ultimate sizes. In addition, the von Bertalanffy equation is based on growth in weight, and the corresponding asymptotic length is an average. The increased variance in the weight-length relationship at larger sizes suggests that extreme lengths are not necessarily associated with comparably extreme weights. From the standard error of the weight-length regression slope (0.0646) for tiger sharks (Table 1), 95% confidence limits for the weight of a 550 cm individual are 468-2541 kg: the lower limit equals the mean weight predicted for a 424 cm individual. Therefore, deviations in calculated L_{∞} from the observed maximum, as in tiger and blue sharks, do not necessarily indicate a failure in the von Bertalanffy equation - they may simply reflect, in part, the variability in individual growth characteristics and variability in weights possible at larger sizes. Differences in observed and predicted maximum lengths, as well as lengths at age, may also be due to errors in calculations of length at age or bias in sampling.

Calculated values of t_0 were quite large, especially in the sandbar sharks. However, t_0 is merely a time reference and should not be interpreted biologically (e.g. as an indication of gestation period). While t_0 may be interpreted as the age at which length is zero if growth always followed the von Bertalanffy equation, growth in utero cannot be considered equal to growth post-partum.

Furthermore, the generalized von Bertalanffy equation includes an inflection point which is dependent on D . The inflection point, t_i , departs from t_0 as D departs from 1 (Pauly 1981). For species such as the sandbar and tiger sharks, in which d is close to unity and D is small, a large t_0 would be expected. As d approaches $2/3$ and D approaches unity, as in the white and shortfin mako sharks, t_0 approaches t_i , and would be expected to approach $t=0$. Finally, the parameter is dependent on the data set used. A close fit to observed lengths at age may project the equation to a large t_0 , regardless of the value of D . This is evident in the sandbar shark data, where the growth during the first year after birth is much less than that in-utero.

As stated above, the "stress factor", K (Pauly 1981), is a population average, and individual fish have unique values of K . Likewise, unique values of K may be associated with populations or sexes, as in the tiger and sandbar sharks. Variations in K may account for the differences in growth rates, without variations in d (or D). This does not preclude the possibility of population differences in d , as such variability has been found in teleosts (Palzenberger and Pohla 1992). K may vary within populations, over seasons or over "life phases". Moreau (1987) reviewed the seasonal aspect of K . Casey et al. (1985) observed a reduction in growth rate of sandbar sharks around age 6

years, followed by an increase, concurrent with abandonment of the inshore nurseries. They suggested that some limiting factor prompted the offshore movement. Such a factor may be equated to "stress", which reduces K.

Assuming that values of d found for other elasmobranchs are approximately correct, the range of values do not support Pauly's (1981) suggestion that d is proportional to maximum weight. However, the values may be indicative of life-styles. Slopes greater than 0.94 were obtained for the benthic Raja clavata and Torpedo marmorata. Slopes were 0.941-0.946 and 0.986-0.996 for tiger and sandbar sharks, 0.88 for both the blue and dusky sharks, and 0.77 and 0.74 for the shortfin mako and white sharks. Hydrodynamic and feeding considerations indicate that sandbar and tiger sharks are relatively slow swimming species, whereas the dusky shark is a more active species, and the mako is a highly active shark (Raschi and Musick 1984). The blue shark is hydrodynamically adapted to a less active lifestyle than might be expected (Raschi and Musick 1984), and cruises at speeds intermediate to the predicted optimal and that required to sustain minimal lift (Scharold 1989).

The difference between Scyliorhinus canicula (0.97) and S. stellaris (0.779) may indicate different life-styles of the two species, or errors in area estimation. Food habits of the two species (Compagno 1984) do not indicate

greater or lesser activity in either species. Red muscle comprises a greater proportion of total muscle mass than white muscle in highly active species (Webb 1975). Red muscle comprises 18% of the muscle mass in the caudal region of S. canicula, compared to 22% in the blue shark, and 12.4% in S. stellaris (Greer-Walker and Pull 1975; Bone 1978), indicating S. canicula may be slightly more active than its congener, contrary to the suggestion here that it would be less active.

While individual variability exists, this study was not able to correlate such variability in growth with variability in gill areas. The negative correlation between weight at age residuals and Method B gill surface area residuals found in this study is in disagreement with the expectation that individuals with larger than average gill areas would be larger than average at age (positive correlation). Although Method B reduces individual measurement variability, such variability may be real, and not due to measurement error. The positive, albeit nonsignificant, correlation from Method A follows expectation and may be more realistic. Additionally, errors in age determination and differences in individual life histories may have confounded the results.

In summary, the results of this study support the contention that large scale growth rates, such as for species or populations, are proportional to gill area.

However, a number of factors may affect individual growth, such as food supply or hormones, which may obscure or supersede individual variability in gill areas. The fact that the same gill area equation is applicable to different sexes and regions, would support the idea that individual variability is due to other biotic or abiotic factors, since other factors would necessarily account for the population differences.

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