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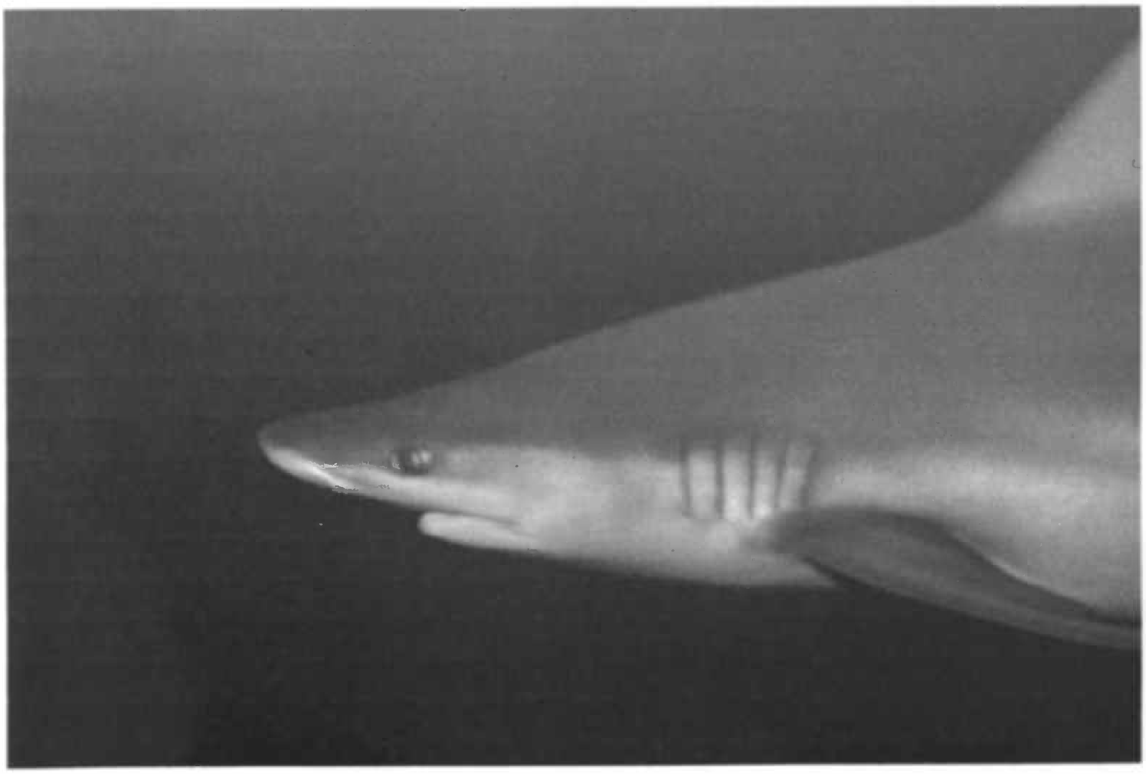

by Angelina Y. den Besten

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Abstract:

Diet is an important factor in keeping captive sharks alive. If not all necessary nutritional components such as proteins, lipids, carbohydrates, vitamins and trace elements are available to the shark in adequate amounts, deficiencies can occur that can lead to diseases, growth disorders or even death. It is essential that sharks will be fed a varied diet consisting of different species of fish and a multivitamin tablet.

Of course not only the quality but also the quantity of food is essential to maintain the health of captive sharks. As example two different calculations for amount of food in % body weight (BW) per week is made. It appears that a sandbar shark, *Carcharhinus plumbeus*, of 34.0 kg should eat about 6% BW. These calculations are based upon the assumption that the growth rate is stable throughout the life of a shark and the weight of the shark is known. The weight of a shark can be estimated as is shown in several diagrams that show weight versus length or weight versus age curves. Also the assumption of stable growth is discussed since there seem to be growth stages throughout the life of a shark.

A factor that also plays a role in the amount of food needed by a shark is the metabolic efficiency which is influenced by its own factors such as glide/rest period, gastric evacuation rate and total gut passage time and absorption efficiency.

This paper is concluded with an overview of known feeding schedules and a brief conclusion.

Contents:

Introduction:

Keeping sharks in captivity is something that can not be done by just anyone. Without proper expertise a shark will soon die after it has been captured. Catching, handling and moving a shark to its new home takes a lot of money and knowledge. Despite this it is tried to study sharks in captivity since there natural environment usually prevents a close study and due to the shyness of the shark which causes it to flee when disturbed.

Gurber and Keyes (1981) describe several ways to capture, handle and transport sharks. It is essential that the duration of the process is kept as short as possible to minimize stress for the shark. One of the least stressfull techniques for capturing a shark is cast netting or the use of a handline or trotline. It is essential during the whole process that the shark is kept horizontally to prevent stress and damage to the shark. Of course the tonic immobility (also known as animal hypnosis) found by Henningsen (1994) is always useful during transport and in captive husbandry. It is known to occur in wide variety of taxa and has been shown in 10 species of sharks. The tonic immobility may last up to approximately 5 minutes.

If the shark survives the trip to its new home, it can take a while before the shark starts feeding (5 days for a 9 foot tiger shark – 5 months for a 10 foot tiger shark) (Clark 1963). In general, small species of sharks and the young of large species of shark seem to take food in captivity sooner than larger sharks do. Besides tank size and water quality of course also the issue of what food to feed in what amount rises.

Historically, nutritional requirements of sharks have been extrapolated mainly from studies done on bony fishes (Halver 1972) and studies on the bioenergetics of the lemon shark, *Negaprion brevirostris* (Gruber 1984; Cortes 1987; Schurdack and Gruber 1989; Cortes and Gruber 1990; Wetherbee *et al* 1990).
The aim of this paper is to give an overview of food composition, known diet compositions as well as stomach contents. This, together with the known growth rates in different life stages, weight increases, and some extrapolated bioenergetic calculations, should enable any shark keeper to estimate the right amount of food to feed any shark.

In this paper the main focus will be on three species of sharks, the sandbar shark *Carcharhinus plumbeus*, the blacktip shark *Carcharhinus limbatus* and the silky shark *Carcharhinus falciformis*, since these will be displayed at the ocean which is currently under construction at Burger's Zoo in Arnhem.

Importance of diet:

Together with a proper environment, diet is one of the most important factors in keeping sharks alive and healthy in captivity. Adequate food, vitamin and mineral supplementation is necessary to assure that sharks grow at a rate similar to that obtained in the wild (Stoskopf 1993). This was sustained in experiments with *Negaprion brevirostris* by obtaining a captive growth rate of 9 - 12 cm/yr while the growth rate for specimens measured in the wild was 14 - 18 cm/yr. The growth rate of a captive shark is thus suggested to be an indicator for its health. Increased intake of nutrients directly increases the growth rate until growth rates levels off at high rations. Slow growth rates are due to the low level of food consumption which may be limited by a slow rate of digestion (Stoskopf 1993).
In order to formulate a proper formula for a balanced shark diet, data must be obtained about the quality and quantity of the diet. This formula should include an energy source plus adequate essential amino acids, essential fatty acids, and vitamins and minerals to promote normal growth and to ensure the health of the shark (Halver 1976).

Diet composition:

A diet can contain several nutritional components such as protein, lipids, carbohydrates and vitamins and minerals. Each of the components has a function in a diet, although some are more important than the others. For instance, after digestion, energy becomes available to a shark in the form of proteins, lipids and to a lesser extent carbohydrates. Single nutritional deficiencies rarely manifest themselves and most information about deficiencies has to be extrapolated from that of other fishes. Stated below are the functions for each of the dietary components.

Proteins

Proteins are the major organic materials in most animal tissues, making up about 67 – 75% of the total on a dry weight basis. Proteins supply the shark continuously with amino acids after the protein is hydrolyzed. These amino acids can then be absorbed from the intestinal tract. Amino acids are used to synthesize new proteins which are used to build new tissues or to repair old or damaged tissues (Stoskopf 1993).

Proteins in the body tissues are built using approximately 23 amino acids These can be divided into essential and non essential amino acids. Studies on bony fishes have shown that the ten essential amino acids are; arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine (Gruber and Keyes 1981; Stoskopf 1993).

If not enough protein can be obtained by a shark a rapid reduction in weight will occur. A weight loss of about 1% of their in air body weight per day is observed when sharks are experimentally fasted. If weight falls below about 80% the damage is irreversible (Gruber and Keyes 1981). Finally the shark will die from starvation. Protein deficiencies can be caused by not enough food available or competition for food, digestive problems, parasites and poor quality of proteins. Symptoms are retarded growth, cachexic, emaciated body with a disproportionately large head,

wrinkled and blotchy skin and ragged fins (Stoskopf 1993). Additional feeding will prevent death as long as no more than 20% body weight has been lost.
If an access of proteins is provided, the shark will metabolize this to produce energy.

Fish as a group are fundamentally different from other vertebrate animals in that they require more dietary proteins (Tacon and Cowey 1985; Wilson and Halver 1986). Mammals and birds require 12 – 25% protein whereas fish require 35 – 55% (Bowen 1987).
The utilization of dietary protein is affected mainly by its amino acid pattern, by the level of protein intake, by the caloric content of the diet and by the physiological state of the shark (Stoskopf 1993). As an essential energy source for some critical body organs and tissues, certain amino acids are readily converted to glucose. Fish are more dependent on amino acids as precursors of glucose than most other animals due to the fact that carbohydrate is not prevalent in their natural diet and they have a limited ability to metabolize it. A portion of the dietary protein is always used as an energy source in the form of glucose.

Lipids

The two general functions that are fulfilled by lipids are first of all the major role they play in providing energy. The second function is that they are involved in maintaining the structural integrity of biological membranes (Stoskopf 1993).
Lipids can be hydrolyzed into 4 products, diglycerides, monoglycerides, glycerol and free fatty acids (Smith 1980; Robinson and Mead 1973). Fatty acids are used for oxidation in fishes and are composed from triglycerides.
Most fishes store large quantities of lipids and especially triglycerides in their muscles and liver. This is especially true for sharks. The liver is not only used as a storage for energy but also as buoyancy control since sharks have no swim blatter like most fishes (Stoskopf 1993). This, together with limited calcification of the skeleton, urea and methylamines (Withers *et al* 1994) and of course swimming movements, compensate for the lacking swim blatter. Due to this double function of the liver it is very important maintain it an appropriate fatty liver level by feeding oily fish species such as mullet, jacks and blue runners (Clark 1963). If too much fish is fed the shark can develop fatty liver syndrome.
Lipids are, just as proteins, highly digestible (Stoskopf 1993). Lonolenic acid and lonoleic acid seem to be the only essential fatty acids (Kabata 1985). Fatty infiltration can be observed if there is a lack of these two essential fatty acids. This may or may not be similar to the lipoid liver disease that has been observed in other fish diseases (Smith 1979; Gruber and Keyes 1981). Fatty infiltration can be cured by supplementing vitamin E (Smith 1979).

Carbohydrates

The natural diet of most sharks contains relatively few carbohydrates. The small amount of carbohydrates that are ingested are derived from muscle glycogen and are used as a source of energy. Digestion of carbohydrates is related to structural complexity; simple saccharides are easily digested, whereas starches are poorly digested by sharks (Smith 1971; Shimeno *et al* 1977).

Vitamins

Vitamins are organic compounds required in trace amounts by most forms of life for normal growth, reproduction and health. Vitamin requirements depend on the intake of other nutrients, species, size and environmental stress (Stoskopf 1993). The exact vitamin requirements for sharks are not yet known although Stoskopf (1993) provides a list of dietary supplements (Table 1). This list is based upon the requirements of marine fishes but is modified for sharks by as well Gruber and Keyes (1981) as Stoskopf (1993) although in both cases it is not stated in what manner this is done. In general, vitamin deficiencies lead to growth disorders and an unhealthy appearance like a wrinkled and blotchy skin or ragged fins (Stoskopf 1993). Especially for sharks on display an unhealthy appearance is not desirable. Many aquaria try to prevent this by supplementing a multivitamin tablet to the diet of their sharks (Gruber and Keyes 1981; Stoskopf 1993; Schmid and Murru 1994).

Table 1; Dietary supplements for captive sharks (Gruber and Keyes 1981; Stoskopf 1993).

Dietary addition	Dosage (per kg Animal Weight per Week)
A	3570 IU
B_1	210.0 mg
B_2	0.39 mg
B_6	0.23 mg
B_{12}	0.9 mg
C	37.5 mg
Calcium pantothenate	0.6 mg
Choline	Trace
D	150 IU
E	37.5 IU
Ferrous gluconate	11.25 mg
Folic Acid	Trace
Inositol	Trace
Kelp (Iodine)	18 μg
Niacin	0.6 mg

Trace elements

Minerals perform important roles in osmoregulation, intermediary metabolism and formation of the teeth, skeleton and scales (Lall 1981). Required minerals are calcium, cobalt, fluorine, iodine, iron, manganese, magnesium, phosphorus, selenium, and zinc. Only trace amounts are necessary and this makes it very difficult to study the requirements of sharks for trace elements. Some minerals can be absorbed from the aqueous environment via skin and gills as well as via intestinal absorption (Anonymous 1983). Most mineral deficiencies are probably caused by poor water quality or inadequate food consumption as can be observed when food is mainly fed in the form of filets and no additional supplements are given (Stoskopf 1993). Usually a single multivitamin tablet, which also contains trace elements is included in the diet once a week. It is thought that this supplementation helps in preventing deficiencies.

An iodine deficiency has been implicated in goitre, which is also known as thyriod hyperplasia (Lloyd 1995; Uchida and Abe 1987). Symptoms of goitre are a ball-like swelling on the lower jaw, in the flat throat area, which will eventually prevent the shark from eating and death can be the next step. In the Ueno Zoo in Japan goitre has successfully been treated after raising the iodine concentration in the tank water to 0.1 mg/l, twice the concentration found in local seawater. Since this raise, six years ago, no signs of goitre have been observed (Uchida and Abe 1987). Although this method has proven to be effective Lloyd (1995) does not recommend it because of the chance that the unstable potassium iodine complex will be solvated in accordance with the temperature of the tank water or other changing factors. The possibility exists that due to this too much iodine will be released in a short span of time. High concentrations of iodine could prove to be lethal to the sharks and other animals in the tank.
The National Aquarium in Baltimore has achieved success in the treatment of goitre by adding a supplement of 6 mg iodine per kg of fish body weight per week to the diet. The Blackpool Sea Life Centre treated goitre by adding iodine salts in an amount of 40mg KI/60 kg per week to the diet of their sharks. In 12 weeks the swelling reduced with 65%. This, together with the increase of water change in the tanks for long-term management, should be sufficient to prevent and/or treat goitre. (Lloyd 1995)

Fish composition

The composition of the diet should resemble the diet consumed in the wild by that species. The diet will mainly be composed of bony fishes that can be imitated by feeding fresh or frozen fish. With frozen fish one should note that the nutritional content of the fish is less than in fresh fish (Stoskopf 1993). This also goes for feeding filets.

Several studies involving stomach contents have been done on sharks species. Castro (1996) studied the stomach contents of *Carcharhinus limbatus* of the South East United States. He analyzed 174 specimens and found in 85 individuals (49%) an empty stomach. Unidentifiable small bony fish remains were found in 30 cases (17%). Furthermore, in 24 cases (14%) menhaden (*Brevoortia tyrannus*) was found and in 6 cases (3%) shrimp trawl bycatch (shrimp heads and very small bony fish) was found. Derived from this can be that in 76.0% fish remains were found and in 8.5% crustaceans were found. In 96% of the cases only one type of prey was found in the stomach. Generally it can be said that Carcharhinid sharks feed mainly on small bony fishes. This is also found by Stillwell and Kohler (1993) in their survey of *Carcharhinus plumbeus* off the North Eastern coast of the United States.
Stevens and McLoughlin (1991) report for a sample of 29 specimens of *C. plumbeus* in North Australian waters a diet that also contains mainly small bony fishes (80%) but next to that consists of mollusks (32%) and crustaceans (16%). In an survey done on 181 specimens they found 88% fish, 22% cephalopods, 8% crustaceans and only 1% mollusks. This contradicts the statement made by Springer (1960) which classifies *C. plumbeus* as a discriminating feeder.

Stevens and McLoughlin (1991) also report on the diet of *Carcharhinus falciformis* in the North Australian waters. It primarily feeds on pelagic and inshore teleosts but also some cephalopods and crustaceans can be found. It is not quit clear where this knowledge came from since no numeric data was given or a source is mentioned.

Clark (1963) reports that many aquaria feed a combination of mullet, jacks, blue runners, and other oily fish. Some aquaria vary this diet with crustaceans, squid, octopus, and even cooked mussels. Fish species that are fed to the bull shark *Carcharhinus leucas* in the research facility of Sea World of Florida, Orlando, Florida are Pacific mackerel (*Scomber japonicus*), Atlantic bonito (*Sarda sarda*), Blue runner (*Caranyx chrysos*) and/or Atlantic herring (*Clupea harengus*) (Schmid and Murru 1994). Crow *et al* (1991) feed their blacktip reefshark *Carcharhinus melanopterus*, previously frozen smelt (*Mallotus villosus*), herring (*Clupea harengus*) and squid (*Loligo* sp).
Generally the idea arises that the shark will eat just about anything presented to him. The main concern for aquaria should be to present the shark with a varied diet of oily fishes, squid and crustaceans according to availability and cost.

Bioenergetics:

Estimate of daily ration

An important factor in a diet is the caloric value of the food. Stillwell and Kohler (1993) have tried to make an estimate of daily ration for *Carcharhinus plumbeus*. They used two different methods to calculate a value for daily ration. One method is based on a calculated routine metabolic rate and the other one on the basic energy equation of Winberg (1956),

$$C = 1.37\ (R+G)$$

where C = energy of food consumed, R = total energy of metabolism, G = metabolic energy in terms of growth, and the coefficient 1.37 represents the 27% of food energy lost through excretion and dissipation such as heat (Brett and Groves 1979).

A metabolic rate for *Carcharhinus plumbeus* is not known so, for this purpose, assumed is that the routine metabolic rate of the spiny dogfish *Squalus acanthias* (Brett and Blackburn 1978) was appropriate for *C. plumbeus*. Adjusting for an increase in temperature to 18.5 °C (J.C. Casey, Narragansett Lab. NMFS Northeast Fish. Sci. Cent., unpubl. Longline data) and using a Q_{10} of 2.2, a metabolic rate of 95.9 mg O_2/kg × h was derived. Using an oxycalorific equivalent of 3.25 cal/mg O_2 cited for fishes (Elliott and Davidson 1975), the routine metabolic expenditure is 311.7 cal/kg × h or 7.48 kcal/kg × d. This amounts to 254.3 kcal/d for *C. plumbeus* with an average weight of 34.0 kg.
To compensate for the food energy lost through excretion, *C. plumbeus* would have to consume 10.2 (7.48 × 1.37) kcal/ kg × d. Now if the weight of the shark is known the daily caloric intake can be calculated. An average *C. plumbeus* weighing 34.0 kg BW would require 346.8 (10.2 × 34.0) kcal/d. If we consider the average caloric value of the foods eaten to be 1.195 kcal/g (Steimle and Terranova 1985) the energy intake in terms of food mass amounts to 290.2 g/d (346.8/1.195) or 0.85% of average body

weight (BW) per day which is about 6% BW per week. The difficulty with this method is to estimate the weight of the shark which will be discussed in the next paragraph.

To employ the Winberg (1956) energy equation, for the second method, a value for G based on average growth in weight estimate of 3.72 g/d for juveniles and adults (Casey and Natanson 1992) was calculated. Questions can be asked for the validation of one value for different life stages and thus growth stages. This will be discussed further in the paragraph "growth in life stages".
Using an average caloric value of shark flesh of 1.01kcal/g (Sidwell *et al* 1974) the daily increase in caloric content due to growth is 3.75 kcal/d (3.72 × 1.01). Schmid and Murru (1994) used a value of shark flesh of 1.4 kcal/g in their bioenergetics study. Known is that this value was derived from the study done by Gruber (1984) on the lemon shark *Negaprion brevirostris*, in contrast to Stillwell and Kohler (1993) who do not list from which species this value is derived. Using the value of 1.4 kcal/g the daily increase in caloric content amounts to 5.2 kcal/d (3.72 × 1.4). Substituting the energy values for metabolism and growth in the equation gives an energy value for food consumed of 353.5 kcal/d (1.37 [254.3 + 3.75]) or 295.8 g/d (Food energy = 1.195 kcal/g) for Stillwell and Kohler (1993) and 355.5 kcal/d (1.37 [254.3 +5.2]) or 297.5 g/d for Schmid and Murru (1994). The final difference of 1.7 g/d is not very big. Daily ration then is equal to 0.87% of BW/d or 6 % BW per week in the case of Stillwell and Kohler (1993) and about the same for Stillwell and Kohler (1993). The problem that arises with this method is that a shark does not exhibit equal growth throughout it's life. Of course, if the growth of a certain life stage is known, this method can be used to calculate the daily ration of a shark. As stated before, growth rates during different life stages will be discussed in a later paragraph.

Weight

Some data on shark weight is known. Kohler *et al* (1995), summarizes length and weight ranges for 13 species of sharks among which are *Carcharhinus falciformis* and *Carcharhinus plumbeus*. The fork length range for *C. falciformis* ranges from 73/78 to 196/212 cm with a weight range of 4 to 88 kg. For *C. plumbeus* the fork length range is 44/45 to 183/201 cm with a weight range from 1 to 68/104 kg. In both cases the females grow the largest and heaviest. A relationship found by Kohler *et al* (1995) between length and weight is

$$WT = (a)FL^{b}$$

in which WT is the total weight in kg of an animal with fork length FL in cm. Calculations were done for both species. For *C. falciformis* a value of $a = 1.5406 \times 10^{-5}$ and $b = 2.9221$ was calculated. The values of $a = 1.0885 \times 10^{-5}$ and $b = 3.0124$ were calculated for *C. plumbeus*. For both species no difference between sex was made since there was no significant difference in slope or intercept of the length/weight relationships. Of course the length of a shark brings along another estimate, but this is one that is slightly better to resolve. Also more information is available on length/ age relationships in sharks (Killam and Parsons 1989; Casey and Natanson 1992; Bonfil *et al* 1993; Sminkey and Musick 1995 and Wintner and Cliff 1996).

Castro (1996) reports on the maximum length and weight of two *Carcharhinus limbatus*, one male of 1,892 mm TL with a weight of 38.55 kg and a female of 1,930 mm TL with a weight of 49.55 kg. Castro (1996) comes up with a weight/length relationship for males and females of

$$W = (2.512 \times 10^{-9})\, L^{3.1253}$$
$$N = 183,\ r^2 = 0.989$$

In which weight (W) is in kg and length (L) is in mm. No difference between the male and female was made probably because of the small sample size and there appears to be no difference between the sexes (Fig. 1A and 1B).

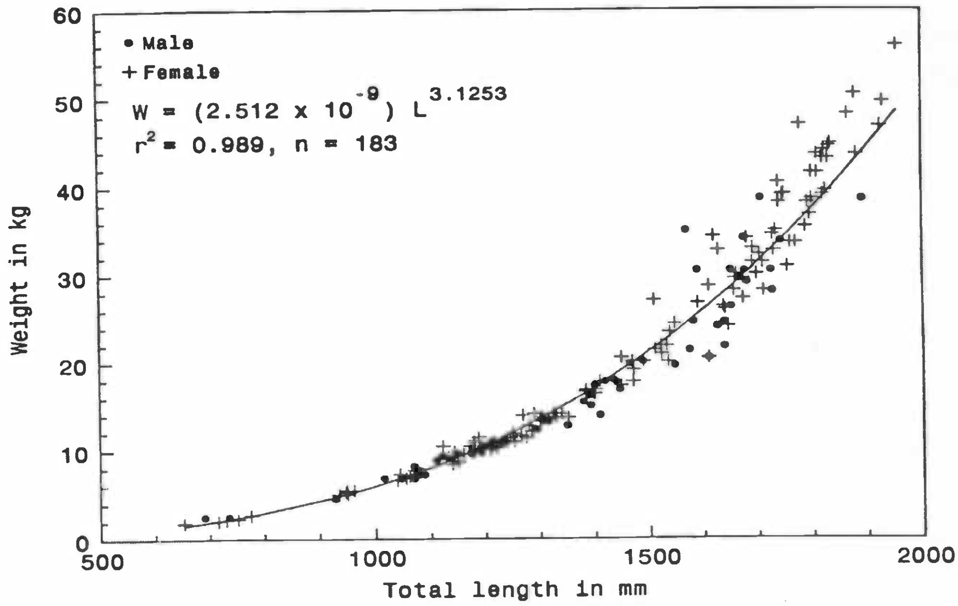

Figure 1A; Total length versus whole weight of two *C. limbatus* (one male, one female) (Castro 1996).

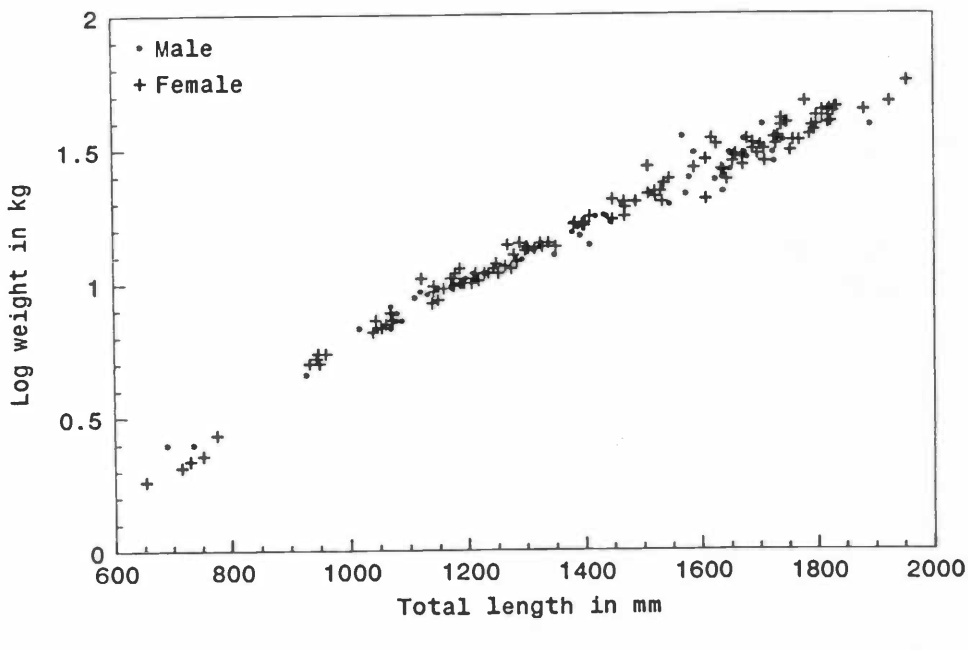

Figure 1B; Log of length versus log of weight of two *C. limbatus* (one male, one female) (Castro 1996).

Killam and Parsons (1989) found a nonlinear relationship between shark age and weight for *C. limbatus*. They discriminated between males and females, something which was not done by Schmid and Murru (1994), Kohler *et al* (1995) and Castro (1996). Found was that the relationship for females $(W)_f$ and males $(W)_m$ significantly fitted with a $P < 0.05$. W is given in kg and r = number of translucent vertebral rings.

$$(W)_f = 42.68/1 + \exp^{-(0.540 \times r) - 3.14}$$
$$r = 0.962,\ N = 69$$

$$(W)_m = 27.83/1 + \exp^{-(0.550 \times r) - 2.58}$$
$$r = 0.974,\ N = 48$$

Growth in length and weight of *C. limbatus* appears to reach an asymptote at approximately 10 years of age at different weights for males and females (Fig 2A and 2B).

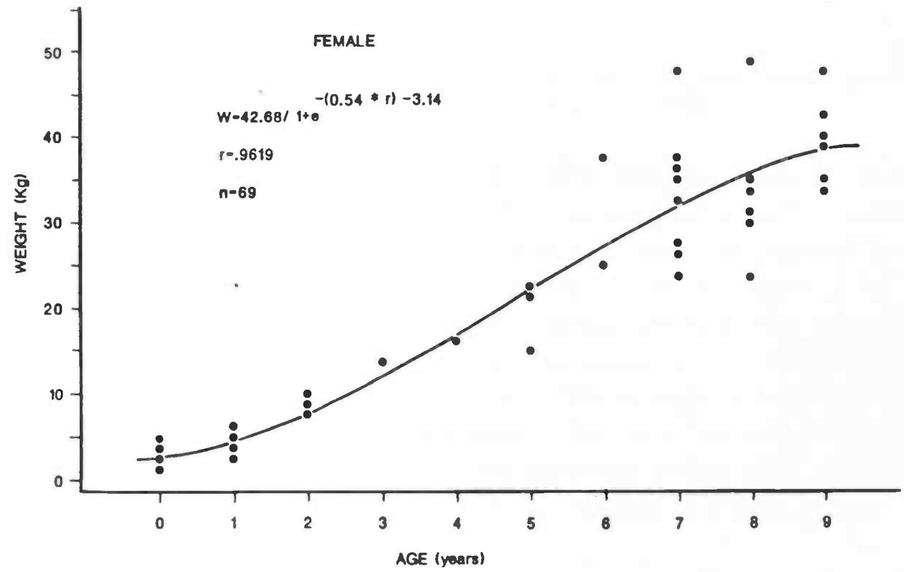

Figure 2A; Age – weight relationship for female *C. limbatus*; logistic growth equation provided a significant fit tot the data ($P < 0.05$) (Killam and Parsons 1989).

Apparently females attain is greater length at the same age as do males since there is no difference in sex in length/weight relationships but there is a difference in sex in age/weight relationships.

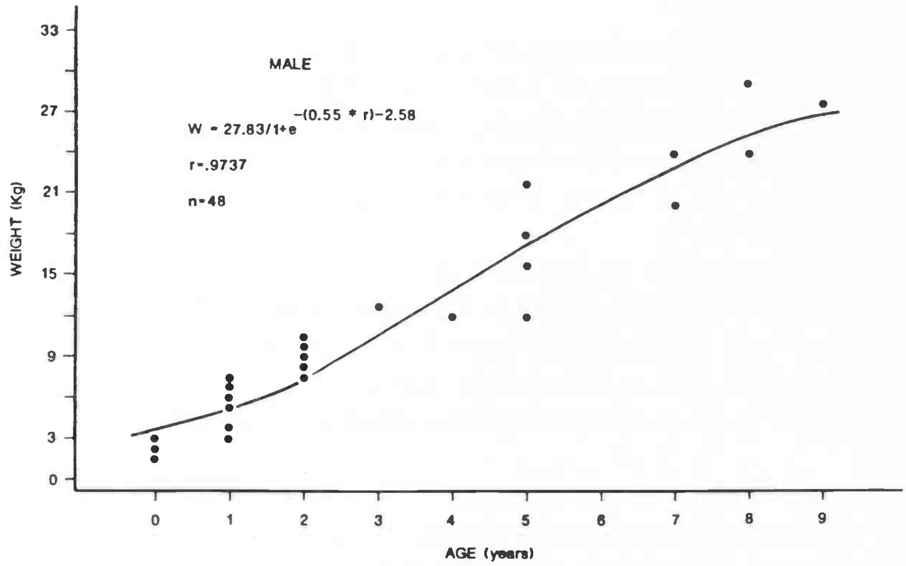

Figure 2B; Age – weight relationship for male *C. limbatus*; logistic growth equation provided a significant fit for the data (P < 0.05) (Killam and Parsons 1989).

In a study of bioenergetics on the bull shark, *Carcharhinus leucas*, by Schmid and Murru (1994), a weight gain of 0.9 kg/month was recorded in the fourth year. This increased to 1.2 kg/month in the fifth year and then decreased to 0.5 kg/month during the sixth year. Weight gain continued to decrease to a gain of 0.2 kg/month during the ninth year. Again no difference was made between the male and the four females. When looking at figure 3 there appears to be no difference either but this is not tested by Schmid and Murru (1994). This would be hard since only one male was used in this study, but maybe they should exclude this male since Killam and Parsons (1989) found a big difference between males and females. Although this could only go for *C. limbatus* or maybe *C. leucas* is the exception.

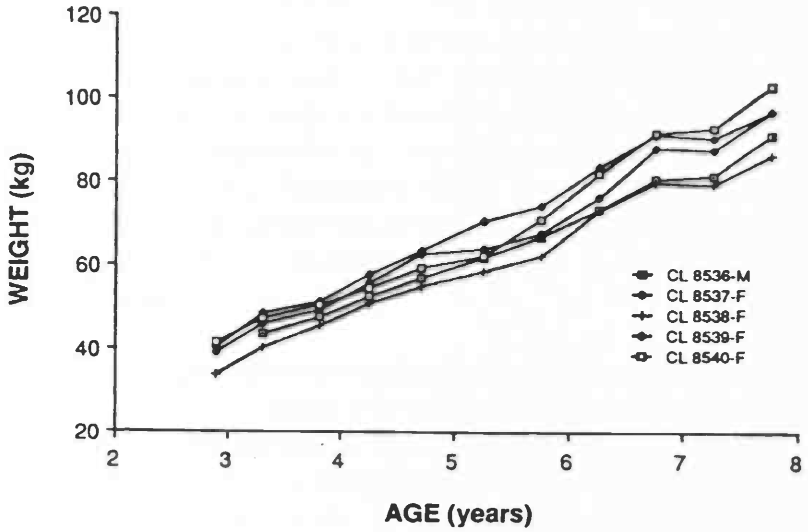

Figure 3; Weight increase for five *C. leucas*. M is male, F is female. (Schmid and Murru 1994).

It appears that growth in terms of weight gain reaches a maximum around the fifth year after which it levels of.

Growth in life stages

During different stages in their lives, sharks show different growth speeds. Sminkey and Musick (1995) found that a *Carcharhinus plumbeus* of 3.3 years of age grew with a speed of 2.1 cm/year. Casey *et al* (1985) expected a growth rate of 7 cm/year and the expected growth rate in this study were 5 cm/year. So the actual growth speed was about half to one third of that of the expected rate.

For *Carcharhinus falciformis*, 5 different growth rate stages were distinguished by Bonfil *et al* (1993). These consisted of 13 cm during the first 6 months (26 cm/year), 19 cm/year during the following 3 years (age 0.5 to 3.5), 15 cm/year in the next three years (age 3.5 to 6.5), 11 cm/year for age 6.5 to age 10.5 and 6 cm or less per year for the rest of their lives. Clearly growth rates level off at higher age.

Killam and Parsons (1989) conducted a growth study on *Carcharhinus limbatus*. They divided the life of a shark up into three stages, juvenile (≤ 120 cm TL), adolescent (immature) and adult (mature), in which TL represents the total length. Juveniles reached a growth rate of 19 – 21 cm TL/year, adolescents a rate of 9 – 10 cm TL/year, whereas adults only grew with a rate of 3 – 4 cm TL/year. They also specified early growth rates in the juvenile stage. Three length classes were distinguished; 68 – 93 cm TL with a growth rate of 2.5 cm/month (30.0 cm/year), 93 – 111 cm TL with a rate of 21.0 cm/year and a class of 111 – 120 cm TL with a growth rate of 19.2 cm/year. At age 10 an asymptote in growth seems to be reached. Wintner and Cliff (1996) found a growth rate for *C. limbatus* of 24 cm/year for the first three years. Adolescent sharks until age 6/7 grew with a rate of 11 – 13 cm/year. After maturity, adults grew with a rate of 5 – 6 cm/year. These growth rates are higher than those found by Killam and Parsons (1989). Brandstetter (1987) found growth rates of 15 cm/year for juveniles, 8 cm/year for adolescents and 4 – 5 cm/year for adults. A possible explanation for these different findings might be that three different populations are reviewed. Wintner and Cliff (1996) studied specimens from the east coasts of South Africa, while Killam and Parsons (1989) studied specimens from Tampa Bay Florida. Brandstetter studied specimens from the northwestern Gulf of Mexico. Wintner and Cliff (1989) also used a second method. With this method growth rates of 23 cm/year for juveniles, 10 –11 cm/year for adolescents and 3 cm/year for adults were found. These are closer to the findings by Brandstetter (1987) and Killam and Parsons (1989). Maybe the second method used by Wintner and Cliff (1989) overestimates growth and/or underestimates age. Brandstetter (1987) suggests that *C. limbatus* is smallest in the North West Atlantic and largest in the Indian Ocean.

Clearly growth rates are not stable throughout the life of a shark. Going back to the paragraph about estimating the daily ration of a shark one can conclude that it not valid to calculate an estimate with one general growth rate for juveniles and adults. So first of al the accurate current growth rate needs to be obtained before a good ration estimate can be made. Of course also other energy requiring processes such as maturing need to be reviewed before an actual estimate is made. Another factor which should be reviewed is the efficiency that is established by ingesting the food.

Metabolic efficiency

Metabolic efficiency can be influenced by several factors. A factor that plays a role in captive husbandry is the swimming pace (Gruber and Keyes 1981). As stated before, unlike most bony fishes, all sharks lack a swimblatter. Together with a fatty liver they must generate lift by forward motion or else sink to the bottom. Many pelagic sharks hardly ever encounter solid barriers during their normal activities so no quick maneuvering considering depth is necessary. These species are hard to keep especially when their "normal" swimming strategies are interrupted. Klay (1977) has provided a possible explanation with his hypothesis about a "glide/rest period". This is the distance an "efficiently" swimming shark covers without muscular contraction. The primary cause of mortality in captive pelagic sharks might be that their habitat disables them from a complete "glide/rest period". Thus in a tank that is to small, the shark encounters a wall before ending a complete "glide/rest period" which makes it stall. This makes a shark use more energy, since he contracts his muscles earlier and more often than when swimming in incomplete periods. Swimming inefficiently lowers the metabolic efficiency and will eventually exhaust the shark.

Another factor that influences the metabolic efficiency is the gastric evacuation rates (the time from ingestion to complete gastric emptying) and total gut passage time (the time from ingestion to compete gastrointestinal tract emptying). This directly influences the amount of food consumed and the nutrients obtained from food. The longer the meal is in the digestive tract, the longer it is subjected to the processes of enzymatic digestion and absorption and, the greater the amount of nutrients absorbed (Windell 1978). It is likely that methodological differences, including food type, temperature, field conditions and so forth, influence these processes. The average time for complete gastric evacuation of a meal measured for teleosts is about 12 hours (Fange and Grove 1979). Based on the few actual measurements and partial measurements of gastric evacuation, it is apparent that a substantially longer period of time is required for food to be completely eliminated from the stomach of sharks than for teleosts. Stoskopf (1993) suggests a positive relationship between ration level and total gut passage time.

Absorption efficiency is also a factor that can influence the metabolic efficiency. Absorption efficiency is a measure of the ability of an organism to digest and absorb nutrients from food (Buddington 1979). The quality of food and the adequacy with which an animal's digestive physiology is extracting energy is reflected in the amount of nutrients absorbed which represents the energy extracted from the food (Brafield and Llewellyn 1982). Absorption efficiency is one of the main indicators of the nutrient value in fish foods and has been used extensively in the evaluation of different foodstuffs and for the formulation and improvement of diets for cultured fishes (Cho *et al* 1985). Absorption efficiencies may range from 62 to 83% for energy, 76 to 88% for organic matter and 76 to 87% for dry matter. Absorption efficiencies increase as energy increases and decline at the highest level of intake (Stoskopf 1993).

Of course their can also problems with absorbing food due to damage which has occurred to the valvular intestine. The periodic occurrence of the intestinal eversion, in which folds of the scroll valve intestine are prolapsed through the cloaca and unrolled, appears to be a natural flushing mechanism of the intestine documented for

8 species of carcharhinid sharks (Crow *et al* 1990). During this brief eversion process, and if sharks are closely confined, as is often the case in holding tank conditions, the exposed intestinal tissues are potentially vulnerable to attack and bite wound injury from other sharks. Crow *et al* (1991) reports nine cases of acute mortality in *Carcharhinus melanopterus* that resulted from severe laceration to complete amputation of large sections of, or the entire, scroll valve intestine. The cause of death in sharks may result from shock, hemorrhage, and electrolyte imbalance (Crow *et al* 1991). Of course the ability to absorb nutrients is also effected and does not help to sustain a healing process. Shark stock density and tank design are thought to be contributing factors to the occurrence of valvular intestinal biting syndrome (Crow *et al* 1991) and can thus help prevent the occurrence.

Feeding in captive husbandry:

Regularity and amount

Schmid and Murru (1994) feed their *Carcharhinus leucas*, twice a week , adding a multivitamin tablet to each first feeding and letting them eat ad libitum the second feeding. Two days separated the two feedings per week. The overall mean food consumption was 3.4% body weight per week (s.d. = 0.7, range 2.1 – 4.5%).
Clark (1963) suggests that anything between one feeding three times a week to as much as several feedings daily is all right. Crow *et al* (1991) have sustained good results with *C. melanopterus* by feeding 10 – 12% body weight per week of previously frozen smelt (*Mallotus villosus*), herring (*Clupea harengus*), and squid (*Loligo* sp.). Of course frozen fish contains a lower nutrient value and should be fed more to saturate the nutrient requirements of the shark (Gruber and Keyes 1981; Stoskopf 1993). The advantage of feeding frozen fish is the minimalization of transmission of disease organisms (Gruber and Keyes 1981).
Gruber and Keyes (1981) observed a consumption of 25% body weight per week in the lemon shark after a short period of food deprivation. Keyes (Gruber and Keyes 1981) also found that food consumption of a large lemon shark can decline to 8% body weight when they are placed in a large tank. This agrees with the theory suggested by Klay (1977) linking glide/rest periods together with metabolic efficiency. A shark in a large tank is more likely to be able to complete a full period than one in a small tank so swimming is metabolically more efficient and the intake of food reduces. Stoskopf (1993) feeds his lemon sharks 2.0 – 2.5 % BW per day, two to three times per week. This amounts to 4.0 – 7.5% BW per week. The values fed by Stoskopf (1993) lay in the same range as the value of 6% BW per week found in the paragraph about bioenergetics as an estimate for daily ration.

Conclusion:

If the growth rate and the weight of a shark can be estimated than the amount of food required by that shark can be calculated. Of course this is under the assumption that that the modified metabolic rate is accurate. This should be further investigated and the value of 95.9 mg O_2/kg should be adjusted accordingly. Of course new methods that can more accurately estimate the weight of a shark should always be used. Another factor that could use some more research is the exact difference in quality between fresh fish and frozen fish or fish filets to help make an estimate for weekly ration when these sorts of food are used.

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