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Tooth Replacement Rates of the Sharks *Triakis semifasciata* and *Ginglymostoma cirratum*

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With one figure

Abstract

Leopard Sharks, *Triakis semifasciata* (specimens of 123 and 124 cm total length) have a replacement rate of 9 to 12 days and a Nurse Shark, *Ginglymostoma cirratum* (specimen of 151 cm total lenght) of 28 days. Tooth replacement, generally, is a growth process. The replacement rates depend, in the same way as other growth processes, on the age of the animals, on their diet, and probably also on seasonal changes. The replacement process is continuous; teeth are shed, even if they are not worn. On the other hand, even if functional teeth break out or are heavily damaged, the replacement rates will not be increased.

Experiments

Data about tooth replacement rates in sharks are of great importance for the understanding of certain ecological and physiological aspects of these animals. Additionally they can be used for calculating the growth rates of these animals (Moss 1967, 1972; Wass 1973). However very few data are available so far, and the factors which influence the growth rates are hardly kown.

For measuring replacement rates individual teeth have to be marked in captive specimens; there are basically three different techniques of marking:

1. Staining of the calcifying teeth with the fluorescing Tetracycline. In vertebrates the Tetracyline is injected intraperitoneally. This method, used by Applegate (1967), Märkel and Laubier (1968) and Boyne (1970), has two serious drawbacks: (a) in order to check the position of the marked teeth the animals have to be killed and the jaws have to be prepared out. Thus each dentition can be checked only once. (b) in a given tooth file calcification takes place in several neighboring teeth at the same time. Thus several teeth will afterwards be found to fluoresce, and it is very difficult to determine the exact position of the teeth at the time when the injection took place.

2. Prasad (1945) removed whole parts of the dentition of live rays in order to show that a replacement of the teeth takes place. Ifft and Zinn (1948) extracted up to 22 functional teeth in *Mustelus canis* and stained remaining teeth with silver nitrate. They waited until the gaps were filled with replacement teeth. It is difficult to tell how the animals were affected by such an operation. (The death of numerous animals during the experiment probably did not result directly from the tooth extraction). It can be assumed however, that loss of teeth does not increase or stimulate the tooth replacement rates.

3. Teeth can be marked by clipping their cusps with wire cutters (Moss 1967; Wass 1971, 1973). This method has probably no adverse effect on the animals, and it allows quick and exact identification of the marked teeth. It has the drawback that it can only be applied in sharks with cuspidate teeth.

Three sharks were available to us:

a) *Triakis semifasciata* Gigard, 1854, two male specimens of 123 and 124 cm length. Before the experiments, they had been kept in the Waikiki Auquarium in Honolulu for 4 years. They are approximately 5 years old. The size of their claspers, which are 8.5 and 9.5 cm long (measured from the notch which separates the pelvice fins from the claspers to the tip of the claspers), seem to indicate that the animals are close to maturity.

b) *Ginglymostoma cirratum* (Bonnaterre, 1788), one female specimen. It had been kept in a private aquarium in Honolulu for several years (no data are available), before it was moved to the Waikiki Aquarium in February 1974.

The experiments were conducted in the spring of 1976. For the experiments the animals were kept in an open tank 6 m in diameter and 1.5 m in depth at the Kewalo Basin Laboratory of the National Marine Fisheries Service in Honolulu/Hawaii. Mr. R. Shomura, Direktor of the Service, gave his permission and Mr. A. Dixon and the late Mr. T. Byles provided technical help. Every second day they were fed to satiation with squid.

For operation and observation the sharks were transfered to a smaller holding tank, with 150 to 200 ppm of the anaesthetic Piscaine. After 5 to 10 min the animals could be handled; afterwards it took them approximately 10 to 20 min to recover from the anaesthetic. The tooth cusps of up to 17 teeth were clipped with wire cutters without damaging the rest of the teeth. The animals were checked every few days. The observations were carried out for 5 weeks with the Leopard Sharks and for 3 months with the Nurse Shark, which had a much slower replacement rate.

For reasons mentioned above we used the third method of marking of the teeth. In the two Leopard Sharks we clipped the cusps of 14 and 16 teeth in the upper jaws, all of which were in the second position, that is immediately behind the most labial teeth.

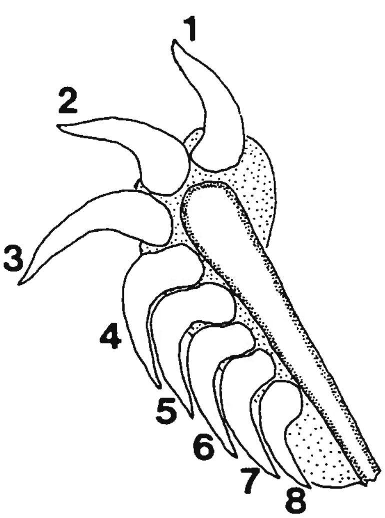

Fig. 1. Schematical cross-section through a shark jaw, indicating the positions of the functional tooth and its replacement teeth. It is herewith proposed that the positions of the teeth in one family are numbered from the oldest (the functional) tooth to the younger tooth.

The time was noted until all of them moved into the first position, and then until all of them were shed. In the Nurse Shark 17 teeth of the third position in the upper jaw were clipped and the time noted till they reached the second position, then the first position and then finally were shed. This method allowed a fairly exact determination of the time required to move one position, because three values of tooth movement rate could be obtained. The three sharks survived the experiment in good health.

The numbering of tooth positions is explained in fig. 1: In each tooth file (= tooth family) the most labial tooth has position number 1. This numbering is used irrespective of the numbers of functional teeth and replacement teeth in a given tooth file.

In the Leopard Sharks it takes 9 to 12 days for a tooth to move one tooth position, that is to move into the position of its immediate predecessor. In the Nurse Shark a given tooth moves one position in approximately 28 days.

Discussion

Tooth replacement in polyphyodont dentitions is the result of a growth process, namely the growth of the dental lamina (Kerr 1919; Osborn 1974; Reif 1976). The exact mechanism of the transport of the teeth over the jaw cartilage, however, is still obscure (see Poole and Shellis 1976, for a detailed discussion). The finding that the tooth replacement is a growth process, however, allows the proposal of several hypotheses:

a) Formation of the teeth and their transport over the jaw is a continuous process. The velocity of the transporting belt, and thus the tooth replacement rates, slow down during aging. Wass (1973) showed that the mean functional tooth life in *Carcharhinus milberti* slows down from 18 days in young animals to 38 days in older animals (In the Carcharhinidae only a single tooth is functional at a given time. Hence Wass's "mean functional tooth life" is in this case the same as our "time required to move one position". In *Triakis*, *Ginglymostoma* and many other genera more than one tooth is functional. If in a given genus six teeth of the same tooth family are functional at the same time, then the mean functional tooth life is six times as long as the time to move one position). In *Carcharhinus menisorrah* there seems to be an increase from approximately 20 days to approximately 32 days in mean functional tooth life (Wass 1971). These are all the data available so far.

b) The replacement rates can be influenced by varying the amount of food provided to the animals. Moss (1967) showed that in starved young Lemon Sharks the replacement rates are 10.0 days in the upper jaw and 9.2 days in the lower jaw, compared with 7.8 days in the upper jaw and 8.2 days in the lower jaw in animals which were fed to satiation. Boyne 1970, showed on the basis of a Tetracycline study that the replacement rate was 14 days in young Lemon Sharks. The difference between Moss's and Boyne's results can have several explanations: The Tetracycline method is not very accurate and the experiments could have been performed with different diets or in different seasons, etc.

c) In regions with strong seasonal temperature differences the replacement rates change with the seasons. (No date are available so far).

d) The replacement rates are different in different taxa. This is obvious from the available data. The following data have not yet been mentioned in this text:

Scyliorhinus caniculus, approximately 5 weeks, in winter, size of the specimens not mentioned. Tetracycline study (Mörkel and Laubier 1968).
Heterodontus francisci, 3 to 4 weeks, size of the specimens no mentioned, Tetracycline study (Applegate 1967).
Raja undulata (the only batoid which was studied so far), 4 weeks, starved animals, Tetracycline study (Märkel and Labourg 1968).

e) The tooth replacement process is independent of demand: functional teeth will automatically be shed according to the growth velocity, even if they are not yet worn. On the other hand, even if many functional teeth break out at the same time, the replacement rates will not be increased. No feedback loop has yet been discovered which could slow down or increase replacement rates according to demand. On the basis of the knowledge of growth processes is it not very likely that such a feedback loop exists at all.

f) There is no possibility to fill a certain gap in the functional series without moving the whole tooth set. In most dentitions the roots of neighboring tooth families imbricate, thus preventing any relative movement between the tooth families. The lack of mobility probably exists as well in those dentitions in which neighboring tooth families are separated. This assumption is based on histological observations of the tooth "transporting belt" (called tooth band by Poole and Shellis 1976), a thin tissue layer which lies between the tooth anchoring fibers and the jaw cartilage (unpublished results of Nobiling and Reif).

g) The velocity of the transporting belt is probably the same in any region of the dentition. The teeth are being replaced at the same rate all over the whole dentition of one jaw. According to hypothesis (f) one tooth family can never be moved without moving the whole tooth set. A relative movement of the tooth families is thus not possible, but there could still be a velocity gradient from the symphysis to the distal end of the dentition. Several observations point to the fact that such a gradient does not exist in shark dentitions (except perhaps for *Heterodontus portusjacksoni*, *H. japonicus* and *H. zebra*. see Reif, 1976):

1. The most distal teeth which we marked in our experiments were about midway between symphysis and the distal end. Within this stretch no velocity gradient could be discovered.
2. Many shark genera have well developed longitudinal rows (rows of teeth which run in the longitudinal axis of the jaws, perpendicular to the direction of the tooth families). Examples are: *Squalus*, lower jaw teeth of *Etmopterus*, *Dalatias*, *Isistius* (with the neighboring teeth wedged together), and *Ginglymostoma*, where neighboring teeth are spatially separated. In all these cases a velocity gradient would lead to a tilting of the longitudinal rows.

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Zusammenfassung

Zahn-Austauschraten wurden gemessen bei Leopardenhaien, *Triakis semifasciata* (Exemplare von 123 und 124 cm Gesamtlänge) und bei einem Ammenhai, *Ginglymostoma cirratum* (Exemplar von 151 cm Gesamtlänge). Hierzu wurden die Spitzen einiger Zähne mit einer Zange entfernt und gewartet, bis die so markierten Zähne ausgefallen waren. Bei den Leopardenhaien beträgt die Zeit, die ein Zahn benötigt, um eine Position vorzurücken, 9—12 Tage, bei dem Ammenhai 28 Tage. Diese Daten werden verglichen mit den wenigen anderen Daten, die über Zahnaustauschraten bei Haien vorliegen.

Zahnaustausch bei polyphyodonten Gebissen, generell, ist ein Wachstumsprozeß. Er hängt wie andere Wachstumsprozesse ab vom Alter des Organismus, von der Nahrung und wahrscheinlich auch von jahreszeitlichen Rhythmen. Der Zahnaustausch ist stets ein kontinuierlicher Prozeß. Das führt dazu, daß oft Zähne ausgeworfen werden, die noch nicht abgenutzt sind. Auf der anderen Seite gibt es keinen Hinweis darauf, daß bei überdurchschnittlicher Belastung der Zähne und bei Ausbrechen von Zähnen die Zahnaustauschgeschwindigkeit erhöht wird.

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