A MATHEMATICAL CONSIDERATION ON THE FUNCTION OF BALEEN PLATES AND THEIR FRINGES

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ABSTRACT

Many have suggested that baleen fringes are adapted to the food that is caught and strained by baleen whales. A study reported here suggests that the situation is slightly more complicated.

In balaenopterid whales, the baleen is arranged so that when the jaws are opened more than about 15 degrees, the mouth becomes open all the way to the rear of the mouth, making filtration impossible, but allowing freedom of movement in the jaws when the whale is making large gulps. The baleen plates are curved, which makes them rigid in the center of the baleen row, while making them flexible around the margin, which is interpreted as producing a sealing zone that prevents openings from developing in the baleen while the whale is straining his food.

The fringes, of taxonomic interest, vary in characteristics in the same whale. There are actually at least 2 different kinds in the fin whale—a large kind and a small kind. The fringes give the baleen plate an internal structure that is grainy, like wood. This brings about a striking phenomenon—the more acutely the plate's edge cuts across this grain, the fewer fringes can be produced by the plate in this region. Therefore, where the plate edge is very steep, as in the right whales, the diameter of the fringe must be very small to make up for this shortcoming. A sei whale was found where the angle was zero degrees between the edge and the grain, and correspondingly, no fringes at all were on the plate at this level.

A mathematical formula was developed that relates fringe characteristics with baleen plate characteristics. Several shortcomings to this formula are mentioned.

INTRODUCTION

As is fairly well known, the whalebone whales have a specialized feeding structure involving hardened, keratinized palatal rugosities* (Barge, 1936, p. 43)

* There has been some doubts expressed in the literature as to what constitutes the true mammalian palate in the whalebone whales, with Cuvier and a number of authors believing that the baleen stands upon the regular mammalian palate, while Eschricht believed that the regular palate took in only that surface exposed within the area covered by the baleen, the latter area being thus a new addition to the mammalian palate. The matter was last considered by Freund in 1912, who decided that the baleen were to be considered what Cuvier had held them to be—palatal rugosities standing upon the regular mammalian palate.

Sci. Rep. Whales Res. Inst.,
No. 28, 1976, 37–55.

extended into the form of a series of transversely arranged plates on each side of the upper jaw (Tomilin, 1957, p. 6). Teeth are only present during a transient embryonic stage (Ridewood, 1922). The palatal plates, also known as baleen or whalebone, and popularly called "gills" or "strainers" by those involved in the whale fishery, are more related to hair in structure and composition than to bone, which the term whalebone deceptively implies. Whalebone is composed of a large number of hairlike tubules arranged in parallel and cemented together by a matrix or marrow which becomes broken up on the internal edge of the

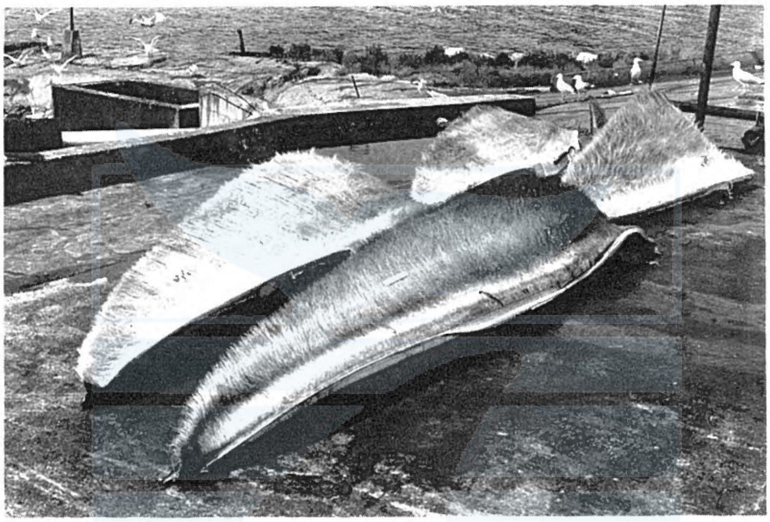

Fig. 1. The left baleen rows of a fin whale (in front) and of several sei whales (to the left and behind).

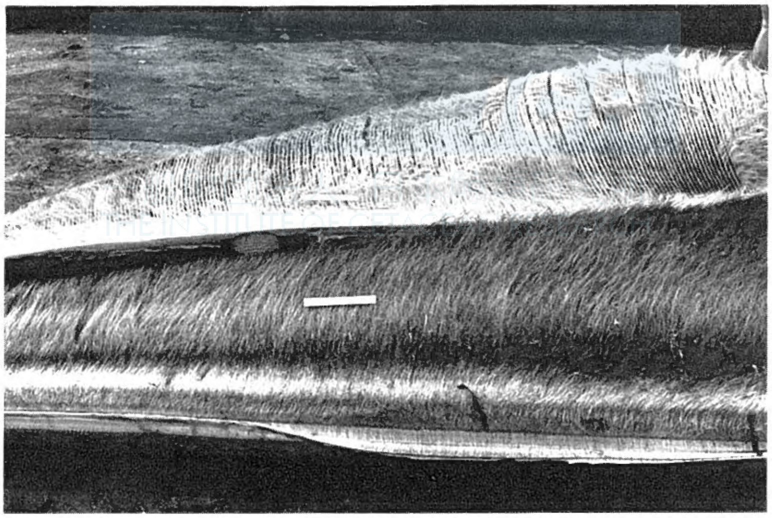

Fig. 2. The fringes and baleen of a fin whale (in front) and a sei whale (behind).

plate by friction against the tongue which releases the tubules, that then form a tangled fringe along the border of the plate (Turner, 1873; Tullberg, 1833; Tomilin, 1957 (1967)). These freed tubules are usually referred to as bristles or fringes. Since the term "bristle" is also used for the sensory hair fibers or vibrissae found on the surface of the head and jaws in whalebone whales, as well as for the bristle-like anterior serial homologs for the baleen plates in the front of the palate, the term "fringe" is used here. The fringes obstruct the slitlike spaces between the palatal plates, and form a layer or screen on the internal margin of the plates, typically concealing the latter from view from within the mouth (Figs. 1 and 2). The baleen plates and fringes are known to differ in several ways from species to species, so that they have taxonomic value, while it has also been suggested that the characteristics of the palatal plates and the fringes are adapted to the nature of the food taken by each species, depending on whether the food is minute, consisting of copepods (right whales and sei whales), or krill, a Euphausid crustacean (blue whale), or fish (fin whale, minke whale, humpback whale) (Tomilin, 1957; Nemoto, 1959; and personal observations made on northwest Atlantic whales). It is generally held that finer fringes are necessary for trapping finer sizes of plankton, and that coarser fringes are needed for imprisoning fish and krill (Nemoto, 1959, p. 155). Nemoto believes further that it is the fringe fineness and not the fringe density that influences or is correlated with food preferences.

WHALEBONE FORM AND CONFIGURATION

The whalebone, as already mentioned, is composed of a series of plates that form a uniformly graded series from the front of the mouth, or tip of the snout, to a level somewhat behind the eye, on a greatly enlarged palate. In all baleen whales, the baleen on either side of the mouth is separated at the rear by the median palatine keel, while in front, the baleen is separated by a space in the right whales (Eschricht and Reinhardt, 1861; Nemoto, 1959), while they are joined by a series of coarsely bristle-like serial homologs to the palatal plates in the balaenopterid whales or rorquals, the latter term being understood to include the genus *Megaptera*. This crossband is called among other things the *Zwischenband* by Freund in his studies of the cetacean palate (loc. cit.). The zwischenband has been presumed to have a functional significance, although this function is not yet known. In bulk, it is only a tiny fraction of the entire structure of baleen on the palate, so that its consequences would seem to be minimal. It is probably a secondary condition, for it is absent in the gray whale as well as in right whales.

The skull has a long, flattened rostrum to support this straining apparatus which is entirely confined to the oral cavity. The absence of a cheek, in which place there lies exposed a spacious vestibulum oris s. pariacoel in front of the angle of the mouth, permits the angle of the mouth to lie very far posteriorly, behind the eye, giving the head a reptilian appearance that has been recognized by others (von Schulte, 1916). The cheek's absence is correlated with the absence of cheek teeth and any form of mastication. The enormous palate is supported by specialized processes of the maxillary bone that reach backward, and which have been described by G. S. Miller (1923) as a part of the telescoping of the cetacean skull.

Transversely, the baleen is separated into a single dominating large triangular plate, that tends *en masse* to close the oral cavity on each side from above, and a number of ribbonlike medial platelets, of variable form, that are short and occupy a linear zone between the main lateral plates externally and the smooth median palatal crest or keel that forms a prominent longitudinal arch along the middle of the roof of the mouth. The terminology for these variable features of the baleen has been discussed by Williamson (1973). In the fin whales of the northwest Atlantic, the medial platelets are coalesced into a small triangular platelet that sometimes even fuses with the main lateral plate. The baleen closes the entire side of the mouth, except for an oval opening in front, when the jaws are opened on the order of 10 to 15 degrees. It is interesting to note that an opening of the mouth greater than this quickly or abruptly opens the mouth cavity all the way to the rear, and thus completely frees the lower jaw from the whalebone on the upper jaw. The lower jaw, thus freed, is allowed to adopt any number of configurations permitted by an intramandibular kinesis, to which it is known to be adapted (Lillie, 1910, p. 99). These facts have led to two contrasting hypotheses related to feeding in the rorquals; the first is continuous feeding supposed while the jaws are open on the order of 10 to 15 degrees, and the second is the supposition of intermittant "gulping" or engulfment of dense swarms of the prey. The smallness of the forward aperture in the rorquals when the jaws are open 10 to 15 degrees argues against the continuous mode of feeding in the rorquals, for filter-feeding vertebrates have a clearcut tendency to develop large mouths that are closed on the side. Nearly all the anatomical structures that are here described and elsewhere during this study all suggest that the rorquals feed by the engulfment of swarms of prey, rather than by true filter-feeding, which seems to be confined to the bowhead and the right whales, where there is also a large opening formed in the front of the mouth.

The main lateral plate of the rorqual palate approximates a right triangle whose short base is lodged within a matrix on the ventral surface of the palate, and whose other edge stands externally, so that the hypotenuse sweeps along the internal face of the plate and produces and supports the fringes that line the internal border of the baleen (Fig. 3). The triangle has a curve along its length, causing the apex of the plate, which projects downward into the oral cavity, to be situated further laterally than the lateral edge of the plate's base secured to the rostrum. This character of the baleen plates in the rorquals forces a complication upon the jaw kinetics which has not been generally recognized; namely, the mandibular rami must rotate around the baleen during opening and closing of the mouth. This rotation may be seen in whales brought

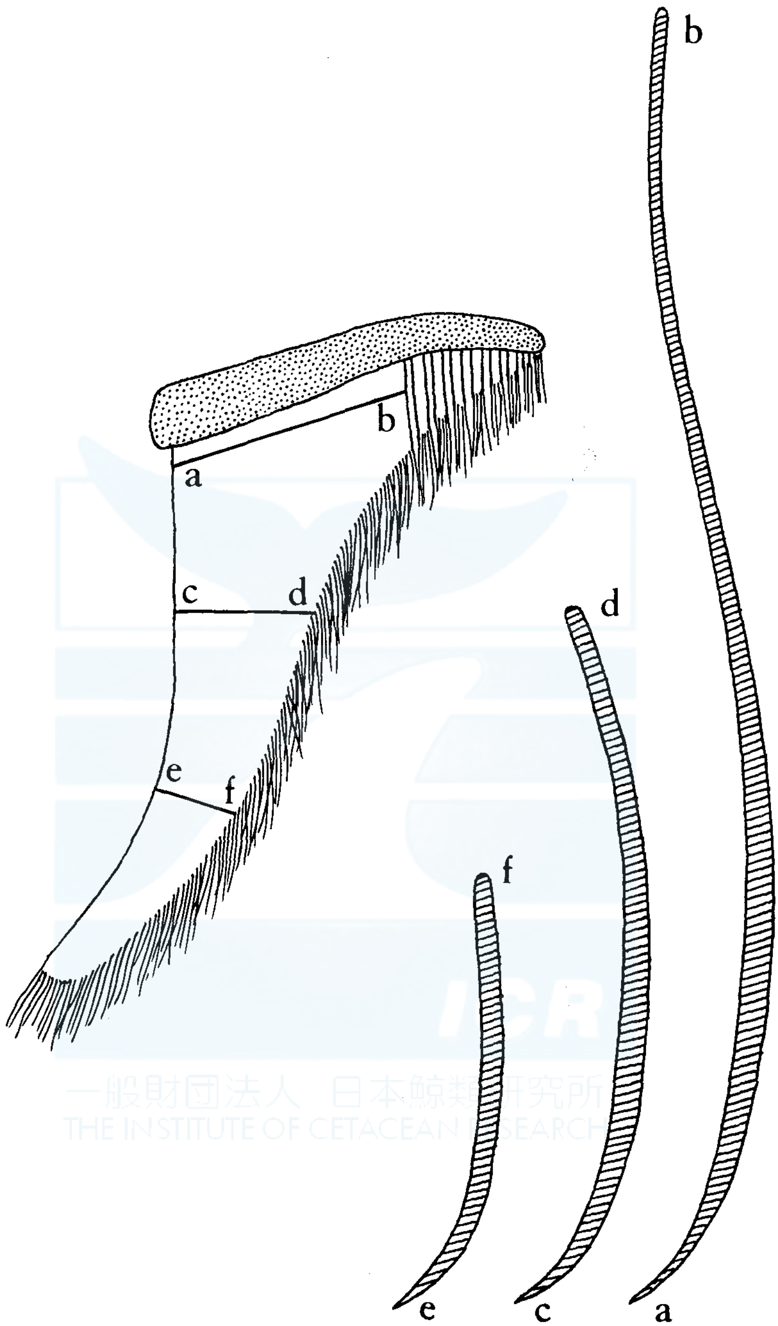

Fig. 3. A sei whale baleen plate and its curvatures, diagrammatically shown.

up and processed during flensing, and is controlled by the adducter jaw musculature, as was demonstrated by Lillie (loc. cit. p. 99). This complication is not indicated in the classical diagrams demonstrating the feeding mechanism of balaenopterid whales, where the outward sweep of the whalebone is usually not indicated. This is by and large due to the fact that these diagrams were based on foetal material, where the outward sweep of the adult stage had yet to appear. The baleen appears relatively late in embryonic life, so that its general configuration can only be seen in postnatal specimens.

In cross-section, the plates show another bend or curve, that was earliest recognized by Scoresby in the bowhead (1810, p. 579). In the rorquals the plates are concave posteriorly and convex anteriorly, giving a sinuous course to the slitlike spaces that pass between consecutive plates (Fig. 3). This curve has been found to give rigidity to each plate, and at least makes them resist deformation in the central area of the baleen when considerable pressure is brought to bear on them. This circumstance must be considered as applicable only to the rorquals, for the extremely flexible plates of balaenid whales suggests an entirely different situation, as has been recognized by Nemoto (loc. cit. p. 154) and Tomilin (1957). In the rorquals, the lateral edge of each plate terminates as a thin blade with a sharp edge, which on the other hand is relatively flexible and yielding, and curved rather sharply to the rear. When the mouth closes to less than 15 degrees, these edges are apparently pressed together, closing or reducing the spaces between the plates. When the mouth is slightly open, the spaces are apparently closed ventrally and left open dorsally to convey exiting water away from the cavity of the mouth, especially through the spacious vestibulum oris lying immediately in front of the angle of the mouth posteriorly.

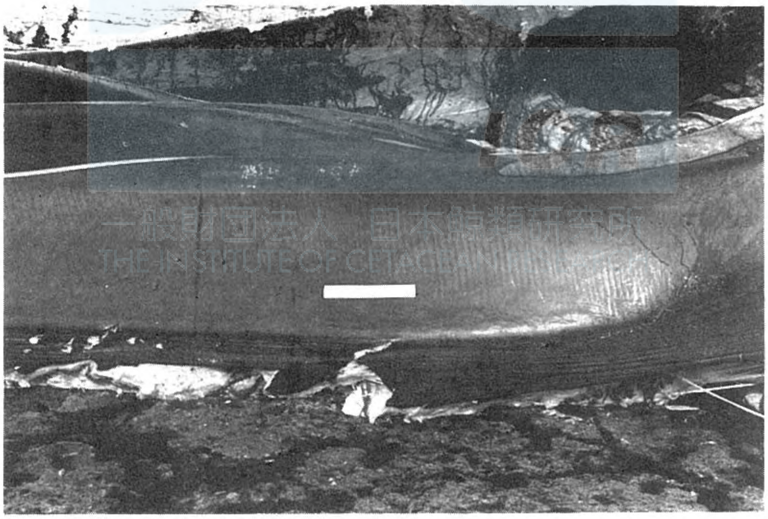

Fig. 4. A closeup view of the ridged surface contours on the medial face of a fin whale mandible. The ruled marker is 6 inches or approximately 15 centimeters.

In this way an effective seal can be made between the baleen and the lower jaw while food is being strained out of the water. These relations are fairly plain when one examines the baleen *in situ* on fresh specimens. The close or intimate relation indicated above between the palatal plates and the lower jaw can be further demonstrated by the typical presence of furrows and ridges impressed upon the medial face of the lower jaw, which matches the pattern and spacing of the baleen plates, and suggests considerable pressures brought to bear between the lower jaw and the distal region of the whalebone in balaenopterid whales (Fig. 4). These furrows and ridges on the mandible are not a post mortem artifact of towing the whale in for processing, as this produces patches of freshly exposed dermis next to zones where the baleen is shredded into long ribbons along its grain.

Whereas the palatal plates of the balaenopterids are relatively short, sturdy, and apparently subjected to considerable stresses, the whalebone plates of the right whales are very long, narrow, and straplike, and extremely flexible, even in dried specimens. What flexibility the rorqual baleen has is lost when preserved as a dry specimen.

CHARACTERISTICS OF THE FRINGES

The fringes are formed by abrasion of the tongue against the edges of the palatal plates. In life they are limp, extremely flexible, and elastic, capable of being stretched a good fraction of their length without breaking. This is not the case in dried study specimens. The fringes lie freely against the baleen in any direction, according to the current conditions that might dominate in their vicinity of the mouth. A randomly-woven net or mat thus has a tendency to form over a large portion of the plates, where intricate entanglement forces the fringes to stay close to the margins of the plates for much of the fringes' length. This tangling tends to vanish along the distal apex of the baleen, and along the medial margin, where the small medial platelets stand adjacent to the exposed palatine crest.

The fringes vary in characteristics along the edge of the palatal plates, and may actually be classified into different sorts (Figs. 5 and 6), which produces a complication that must eventually be reckoned with when quantitative relationships or taxonomic criteria are developed for more detailed comparison of fringes and fringe density between whale species.*

The fringes along the apex or distal tip of the baleen are stiff and coarse, and do not become tangled. The whalebone matrix may be slow to erode away from the fringes here, or else a process of splitting in the plate takes place here, to help bring about making larger and stiffer filaments, which helps give the ventral margin of the baleen the appearance of a brush along its length (Figs. 1 and 2). As already remarked, this portion of the baleen is apparently trapped

* Rund (1940, p. 6, figs. 2 and 3) illustrates these two sizes of fringe for a fin whale.

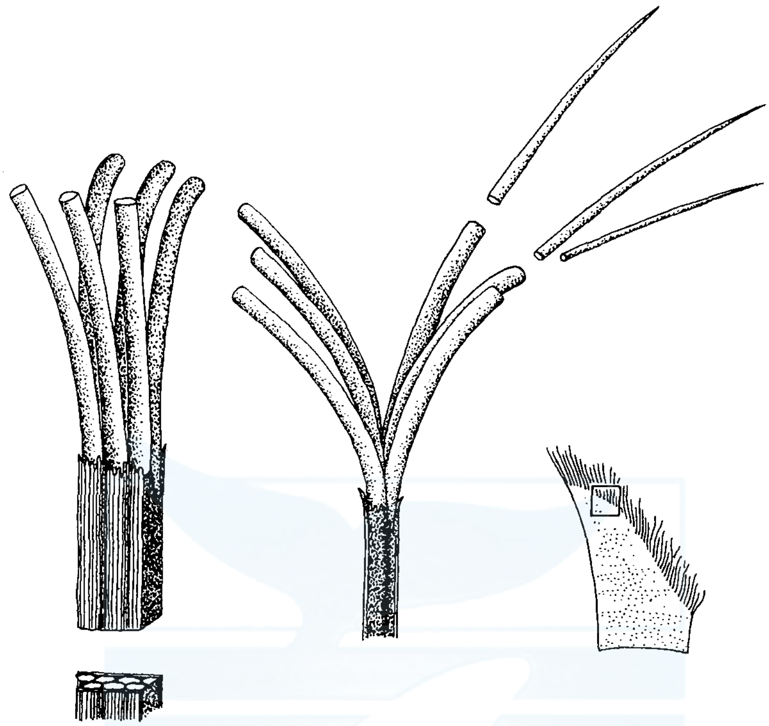

Fig. 5. The characteristics of the fringes from the distal region of the baleen plates of a fin whale. Only one large type of fringe is present.

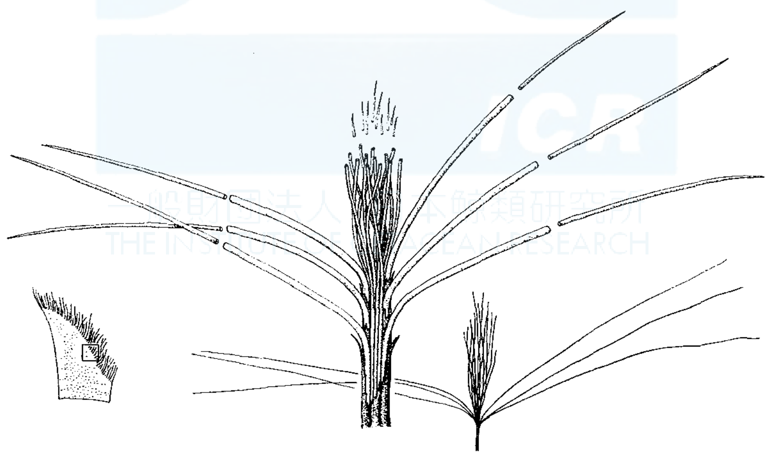

Fig. 6. The characteristics of the fringes from a more proximal portion of a baleen plate from a fin whale. The fringes are arranged into two kinds in three series, a smaller kind of fringe being intercalated between the two outer rows of large fringes.

between the floor of the mouth and the tongue medially and the lower jaw laterally during feeding, effectively sealing the opening between the lower jaw below and the palatal plates above with an extremely dense set of stiff coarse fringes. Toward the median line, coarse fringes persist somewhat in the fin whale, as two layers, adjacent to each face of the plate, giving the face a grained, grooved appearance to its surface. These fringes gradually become finer as the medial side of the plate is reached. Between these two layers of long and coarse fringes there appears a finer, shorter type of fringe, which the rest of the thickness of the plate supplies, so that the thicker the plate is locally, the more of these finer fringes are accommodated (Fig. 6). They may be as short as one centimeter or even less, in contrast with the coarser variety, that often reaches 20 centimeters in length. The finer fringes come to dominate in number medially, giving the baleen of the fin whale a fine white silky appearance (occasionally with black patches of pigmentation that interrupt this texture with a darker shade of fringes). The most medial fringes are supported weakly by rows of medial platelets, in such a manner that slight pressure applied to the layer of fringes here, as produced by the palm of one's hand, causes the collapse of the ribbons or platelets of whalebone underlying the fringes. This region of the baleen also appears to be relatively densely fringed, although it has yet to be demonstrated objectively. It may also be interpreted as a zone of sealing, where the complex of fringes and whalebone platelets collapses during the feeding cycle to form a mildly water-resistant barrier that prevents openings from developing and enlarging into the thinner screen supported by the main lateral plates. By various means the fringes also appear to increase in density toward the front of the mouth (by the closer approximation of plates) and posteriorly (both by closer approximation of plates and change in plate configuration). In this way the whalebone appears to be completely surrounded by a region that prevents the development of openings in its margin while filtration is taking place (see also below). It is here suggested that not the entire screen surface of the baleen takes part in the actual act of filtration, but only a semiovoid area in the central and rearward portion of the whalebone. At any rate, the marginal area takes on a second function, if it does filtration as well, of acting as an intermediate sealing area that prevents openings from appearing and growing while the food is being strained from the water. This consideration would prevent a simple relation from appearing when a comparison is attempted between the total screen areas of different species of mysticete whales for the purpose of attempting to determine relative feeding efficiencies between species, unless the filtering, active portion of the baleen is proportionate throughout all the rorqual species.

In a relationship with water isomorphic or similar to Ohm's law for electric currents, water is determined to flow along the path of least resistance, and so would seem to be mostly confined to the central region of the whalebone series, where the fringe density appears to be minimum (see also below), and where the plates are most rigid and most widely separated, so that closure between plates during stress cannot ordinarily take place. The relative contributions of these two factors, first the plates themselves locally closing around the margins to shut out a water current, and second the relative different densities of fringes around the baleen, has yet to be determined. In the event that the second factor should prove to be relatively significant, methods of determining or calculating fringe density would be needed to establish the part that the fringes play during the feeding cycle. That a current regime is set up within the mouth that involves water flowing along the path of least resistance, which can be structurally controlled to some degree, has previously been suggested in relation to the function of the gill slits and gill rakers of fishes (Galbraith, 1967).

Certain of the relations between the fringes and the palatal plates are demonstrated in Table 1, where fringe counts were made along with other measurements, of three consecutive plates taken from approximately the middle of the row of a 56-foot male fin whale taken by the Atlantic Whaling Co. at Williamsport, Newfoundland, in 1972. Each plate was divided horizontally, or perpendicular to its grain, or the course of the tubules within its substance, into 3 centimeter ribbonlike units. For each such unit, the number of fringes it contributed along the plate edge was counted. This was converted into a density per transverse centimeter. Secondly, it is important to note that the inner edge of the plate cuts the grain of the tubules at an angle, so that the fringes, relatively dense when considered per transverse or horizontal distance, are thinned out by having to be spread along a longer edge than this, over a variable length. This relationship holds for all whalebone whales, and has notable consequences for the narrow plates of the right whales.

Thus, as the table shows for the first fin whale plate, in the ribbonlike unit between 12 and 15 centimeters from the medial edge of the plate, a total of 285 fringes, or 95.1 per transverse centimeter, both of the coarse and fine variety, pass to the edge of the plate. Since, however, the edge of the plate makes an angle of only about 11.5 degrees with the tubule grain at this location, the edge of the plate corresponding to this portion of the baleen is 15.2 centimeters long, to produce a density of only 18.8 fringes per direct centimeter of edge. The sine of 11.5 degrees is approximately .197, and, correspondingly, 3 cm./15.2 cms. is .197, and $.197 \times 95.1$ fringes per transverse centimeter yields the observed 18.8 fringes per direct edge centimeter. Thus the steeper the edge of the plate, and the more acutely it cuts the angle of the plate's grain, the more thinned out are the fringes. Thus, as can be seen in the table, the thinnest densities tend to occur along the middle of the edge of the plate, where the plate is steepest, notwithstanding the fact that it is also relatively thick in cross-section here as well, and so relatively densely fringed when considered by transverse or horizontal units of distance. Local irregularities in plate form, which commonly occur, prevent a perfectly smooth trend in fringe densities as taken along the plate's edge. The tables somewhat weakly suggest an increase in density distally, but this emerges from the increased fringe size that predominates here. Likewise, the increase in density is only weakly suggested medially. Here the

TABLE 1. FRINGE AND PLATE PARAMETERS MEASURED FOR THREE CONSECUTIVE BALEEN PLATES TAKEN FROM THE MIDDLE OF THE BALEEN ROW OF A 56-FEET MALE FIN WHALE TAKEN IN NEWFOUNDLAND, 1972. FOR FURTHER EXPLANATION OF THE PARAMETERS SET FORTH IN THIS TABLE, SEE THE TEXT.

	Position of plate portion counted	Number of fringes in 3 transverse or horizodtal cms.	Number of fringes in 1 transverse centimeter	Length along edge corresponding to the 3 cm counted	Number of fringes per cm. of direct edge	Plate thickness in mm.	Sin θ
baleen plate no. 1	0- 3	102	34.1	3.9	26.2	1.35	.769
	3- 6	124	41.3	7.1	33.8	1.95	.423
	6- 9	170	56.7	9.3	18.3	2.75	.323
	9-12	194	64.6	10.3	18.8	3.23	.291
	12-15	285	95.1	15.2	18.8	3.70	.197
	15-18	264	88.0	14.1	18.7	3.75	.213
	18-21	211	70.3	8.1	26.1	3.49	.371
	21-24	135	45.0	8.1	16.8	3.02	.371
	24-27	85	28.4	3.7	26.6	2.80	.937
baleen plate no. 2	0- 3	118	39.4	4.0	45.0	1.69	.750
	3- 6	137	45.7	7.5	18.3	1.94	.400
	6- 9	187	62.3	9.6	19.5	2.03	.312
	9-12	234	77.9	11.0	21.3	2.42	.273
	12-15	314	104.5	14.6	21.5	3.52	.206
	15-18	305	101.5	14.6	20.9	3.89	.206
	18-21	213	71.0	8.0	26.6	3.54	.375
	21-24	157	52.4	8.2	19.2	2.80	.366
	24-27	79	22.3	3.0	26.3	2.47	1.000
	27-30	22	7.3	3.0	7.4	1.11	1.000
baleen plate no. 3	0- 3	124	41.3	4.2	29.5	1.40	.714
	3- 6	134	44.7	7.6	17.6	2.00	.395
	6- 9	184	61.4	9.1	20.2	2.20	.329
	9-12	229	76.3	10.6	21.6	3.05	.283
	12-15	308	102.8	13.6	22.7	3.20	.220
	15-18	294	97.9	14.1	20.9	3.52	.213
	18-21	204	71.3	8.7	23.5	3.49	.345
	21-24	146	48.6	8.6	17.0	2.68	.349
	24-27	88	29.3	3.6	24.5	2.58	.833

plates are relatively more numerous than their counterpart main lateral plates, and so provide a surplus of fringes in the medial palatal zone.

It will also be found that plate thickness is positively correlated with the number of fringes per transverse or horizontal centimeter of plate for these three fin whale plates. This correlation is only weakly developed for the fin whale, however, due to the presence of two different kinds of fringes. There is one linear regression from the lateral edge of the plate to its center, where the large fringes dominate and the plate is relatively thicker to support them, and another regression from the center to the medial edge, where the finer fringes dominate. A stronger correlation may perhaps be found in other whales, if there is not the same strong distinction between two different classes of fringes.

QUANTITATIVE CONSIDERATIONS

The fringes of the whalebone are the functional portion of the baleen, that actually take part in capturing or imprisoning the food. The mechanism apparently varies with the food item. Copepods and other minute plankton may be strained out of the water somewhat inefficiently by sang mechanisms, while larger krill and fish are more easily and effectively retained by being too large to pass between the fringe filaments and are thus imprisoned within the oral cavity, much as the food of many fish is impounded in the branchial chamber by the gill rakers. If the fringes were absent, most of this food, including fish, could probably escape between the palatal plates, that are more to be considered a structural support for the layer of fringes which permits at the same time an exit for water passing through the screen. This "fishproof" filter is comparable in design with that of the whale shark, *Rhineodon typus*, which was described and figured by Gudger in 1941. This filter may be contrasted with that of the basking shark, *Cetorhinus maximus*, the latter depending in part on the aid of mucus secretion to help snag food out of the water. That mucus often figures in filter feeding indicates the innate inefficiencies that are usually present in true filter feeding mechanisms. Kawamura (1974) has presented evidence indicating a similar inefficiency probably being present in the straining mechanism of the sei whale. The whale shark, with its "fishproof" filter is known to prey on fish schools (Gudger, 1915), while the basking shark is confined to feed on more relatively inert plankton (Schnakenbeck, 1955), since its filter apparatus is not particularly effective in restraining fish, as is also the case with the filter-feeding Mississippi paddlefish, *Polyodon spathula*, (Imms, 1904). Due to the effect of a boundary layer in moving fluids, snagging mechanisms in filtration apparatuses are likely to be inefficient (for a reference to boundary layer phenomena, cf. Schlichting, 1968).

The denser the layer of fringes, the more effectively it retains food, but the harder it is to pass water through it and out between the plates, so that fringe density has a minimum and maximum level between which there must lie an optimum condition. This optimum condition will have a certain degree of inefficiency, depending upon the type of food. The density of fringes covering the baleen palatal plates seems to be controlled by a number of factors, no one of which necessarily may stand out from species to species, according to the preliminary observations so far made on various whalebone whales. That fringe density is apparently correlated with the hydrodynamics of the whale's feeding mechanism implies what Nemoto (loc. cit.) suggested, that fringe density is not primarily correlated with food type (p. 155).

Fringe density can be formulated in several different ways: either as the total surface area of fringes per unit of screen surface, or as the total fringe volume per unit of screen area. It may also be conceived as a total length of fringes confined to each unit of area. Comparison between right whales and sei whales with such balaenopterid species as the fin whale shows that fringe radius plays an important role in affecting the density. This excludes the density parameter expressed as the total length of fringes confined to each unit of area from consideration. The fact that fringe filaments can be approximated as narrow circular cylinders allows the implication that volume is kept at a minimum while fringe surface area is made large. Volume density would indicate the quantity of material obstructing the passage of food out through the baleen plates, and could also be correlated perhaps with another potentially useful parameter, porosity. Surface area density on the other hand would indicate the physical interaction possible between the fringes and the water passing through them. Doubling the volume by doubling fringe length doubles the surface area as well. Doubling fringe radius on the other hand quadruples the volume while only doubling the surface area, thus making the volume version of the parameter more sensitive to variations in fringe size. This quadrupled fringe volume density can be easily appreciated in comparing the baleen of the sei whale with that of the fin whale (Figs 1 and 2). Note that the denser and more coarsely fringed surface of the baleen in the fin whale quite effectively conceals the plates lying underneath. This effect is best brought out by considering fringe density as the total volume of fringe filaments per unit of screen surface area. At any rate, the expressions for fringe volume and fringe surface area differ simply by a factor of r, the fringe radius, when expressed as proportionalities.

We thus define the density as being proportional to the average volume, V, of a fringe, and the number of fringes, n, present:

$$d \propto Vn. \qquad (1).$$

The average volume of a fringe, approximated as a circular cylinder, is proportional to the square of fringe radius, r, and the average fringe length, l:

$$V \propto r^2 l. \qquad (2).$$

The number of fringes per unit of area is dependent upon several factors, which are as follows:

$n \propto 1/w$, where w is the space between plates. Other factors being fixed, doubling the width between plate halves the remaining finge density.

$n \propto b$, where b is the width of the palatal plate's edge. Other factors being fixed, twice the plate edge thickness is assumed to acommodate twice the number of fringes provided by the plate. This can only be approximate, however, for as shown for the fin whale discussed above, there are 2 kinds of fringes involved, and doubling the thickness would affect only 1 of the 2 kinds involved, or both to different proportions.

$n \propto p$, where p is the density of fringe tubules per unit of transverse or horizontal section area of the plate (see also the discussion above, regarding Table 1). Doubling p doubles the number of fringes per unit area. This seems to be achieved in life by usually decreasing the average fringe radius, so that there is a tendency for p to be in part a variable dependent on r, and vice versa, which complicates this analysis, since it involves finding a formula for fringe density based on independent variables.

$n \propto \sin\theta$, where θ is the angle that the plate's margin forms with the vertical. (See also the discussion above regarding Table 1) Doubling $\sin\theta$ doubles the quantity of plate supporting a given surface area of the screen, and thus doubles the number of fringes arising in that area.

Combining these four proportionalities yields

$$n \propto p\frac{b}{w}\sin\theta\,. \tag{3}$$

Substituting (2) and (3) into (1) yields

$$d \propto r^2 l p \frac{b}{w}\sin\theta$$

or

$$d = k r^2 l p \frac{b}{w}\sin\theta \tag{4}$$

for some unknown constant of proportionality, k. Dimensional analysis of (4) shows that k has no physical dimensions.

Of the factors appearing in formula (4), several seem to be less variable than the remaining ones, although this is based on preliminary observations. In particular, w, the width between plates seems liable to least variation from one species to the next, although in any one individual, it tends to decrease by about half its value toward the front of the mouth and to the extreme rear. When too narrow, the space prevents easy flow of water through the baleen, whereas when too wide, it cannot satisfactorily support the fringes. In the latter case, the fringes are prone to disentangle and wash between the plates, opening up gaps among them. This has been observed to happen post mortem in several sei whales, which seem especially prone to show this variably developed, and in a fin whale (Fig. 8).

There is next to be considered the possibility of a web of interrelationships which would complicate the significance of formula (4), which is based in form on the ideal that all factors on the right-hand side are all independent variables. Placing these 6 variables on which fringe density depends into the simplest scheme, Figure 7, there emerges a set of ten possible complicating interrelationships, of which three seem at present to exist.

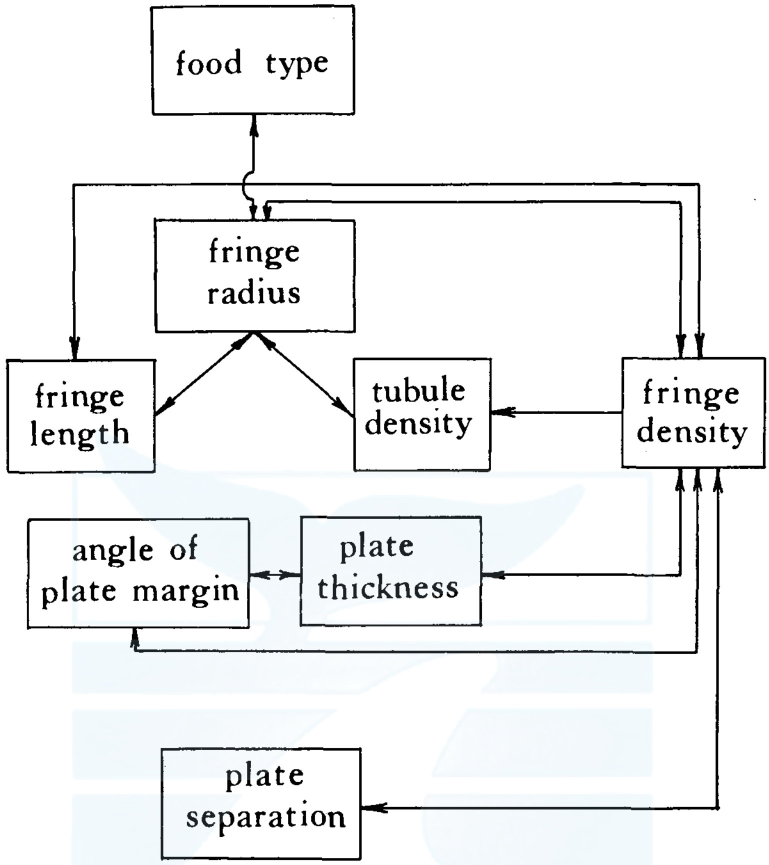

Fig. 7. The simplest scheme of interrelationships observed up to now in the characteristics of baleen plate form and configuration and fringe characteristics. For discussion, see text.

(1) Fringe radius-fringe length. It seems probable that increasing fringe radius entails an increase in fringe length, by virtue of making the fringe stronger and more resistant to wear. Graphing as a histogram the fringes of a fin whale yields a somewhat bimodal distribution of lengths, one mode long, for the fringes of larger radius, and another mode, among the shorter fringes, for those of smaller radius.

(2) Plate thickness-angle of plate margin. In balaenopterid whales, there appears to be valid grounds for believing that plate thickness increases with the angle of the plate's margin, first as an artifact of wear, and secondly as an element of design, an effect that strengthens the plate in that portion of the baleen where rigidity is necessary to keep the screen of the whalebone functional.

(3) Fringe radius-tubule density. In right whales especially, where there is a very steep plate angle less than 10 degrees, the tubule density of the plate

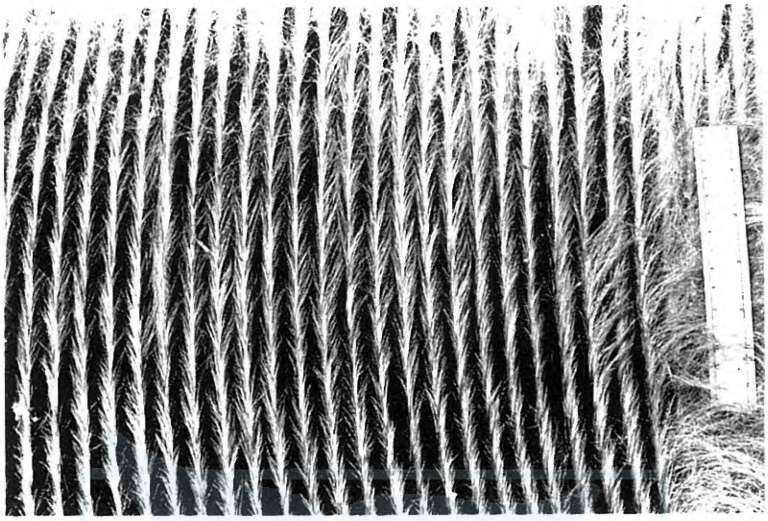

Fig. 8. Sei whale baleen, showing the manner in which the fringes may on occasion wash between the plates, which could result in feeding inefficiencies if of common occurrence. Such regions are extensively present in the sei whale baleen shown in fig. 2.

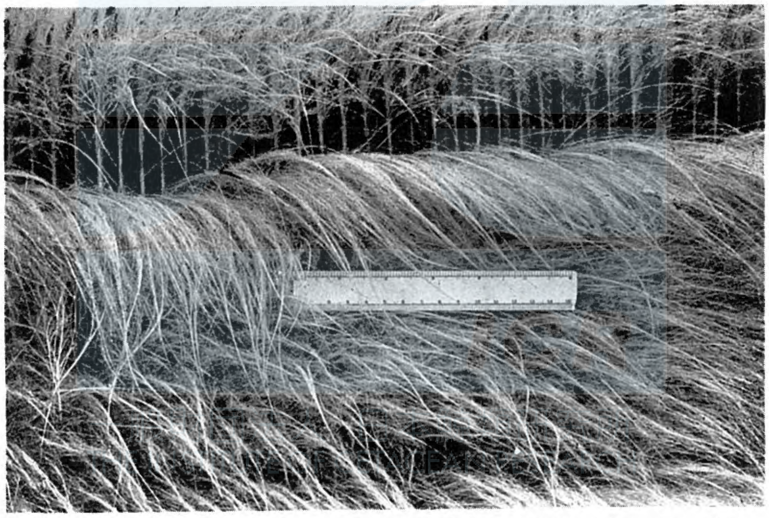

Fig. 9. A growth pace in a sei whale, from which no fringes arise. This zone is due to a weak development of the tubule matrix during that year's growth. The angle of the plate is here so steep that it is actually parallel to the grain of the plate.

must increase sharply to provide enough fringes to accommodate the long and very steep border of the plate. This has been made possible by a sharp reduction in the fringe radius, which is thus related to the increase in tubule density. On the other hand, if fringe diameter is the primary variable of concern, where it must be small to function well with the food concerned, then the plate must apparently have a steep angle to prevent the density of fringe filaments from exceeding an optimum level. In all events the fineness of the fringes of the right whale are correlated with the very narrow plate shape, whether or not they are truly correlated with the prey taken.

Formula (4) conveniently summarizes several of the phenomena that have been above noted in the baleen studied of the various species. One more instance is worth noting, regarding the sei whale. An individual was taken at Blandford, Nova Scotia, which shows the extreme consequences of the "right whale effect", where steepness of the plate's margin makes it difficult to develop a satisfactory supply of fringes along the border. By formula (4), an angle of zero degrees, which has a sine value of zero, implies that fringes disappear from that area entirely. Such regions have in fact been found in the steeper regions of the sei whale baleen, where, for one exceptional pace of growth, no fringes arise from the plate at all. This is matched more proximally with a bluntly-angled "step", where, by the formula, and as is evident in the photograph of Fig. 9, a proportionally greater density of fringes arises.

CONCLUSIONS

1. There exist the following variables associated with the parameter of fringe density in whalebone whales:
   a. fringe radius
   b. fringe length
   c. tubule density of the plate
   d. palatal plate thickness
   e. angle of plate margin
   f. separation between plates.
2. These six variables may be combined to produce a formula expressing fringe density as volume per unit of surface area. The use of this formula is made complicated by at least 3 relations observed between the following variables:
   a. fringe radius—fringe length
   b. plate thickness—angle of plate margin
   c. fringe radius—tubule density.
3. In particular, the plate form is correlated with fringe characteristics by the presence of a trigonometric relation between the angle of the plate's margin and fringe density, and by plate thickness and fringe density.
4. The fineness of fringes is a sensitive variable that is correlated with plate shape. If fringe fineness is truly correlated with the food taken, it is also correlated with the angle of the baleen plate's inner margin, and thus with plate form.
5. The lateral edge of the baleen plate in rorqual whales follows a curve that sweeps outward, and which is everywhere closely related with the medial

face of the mandible when the mouth is closed. This relation is substantiated by the presence of furrows and ridges on the inner face of the mandibles (fin whale), which closely correspond to the configuration of the baleen.

6. The baleen plates are thickened and arched in several planes, and this provides a rigidity that resists closure of the plates by collapse in the central area of the baleen. This rigidity is in contrast strikingly absent around the margins of the baleen screen, which suggests the presence of a sealing zone that prevents gaps from developing during the feeding cycle.

ACKNOWLEDGMENTS

This study was carried out while taking advantage of facilities and materials kindly provided by Dr. Edward D. Mitchell of the Fisheries Research Board of Canada.

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