N O T I C E

THIS DOCUMENT HAS BEEN REPRODUCED FROM
MICROFICHE. ALTHOUGH IT IS RECOGNIZED THAT
CERTAIN PORTIONS ARE ILLEGIBLE, IT IS BEING RELEASED
IN THE INTEREST OF MAKING AVAILABLE AS MUCH
INFORMATION AS POSSIBLE

HYDRODYNAMIC ROLE OF FISH SQUAMOSAL INTEGUMENT AS AN ANALOG OF THE SURFACES DIRECTLY FORMED BY THE TURBULENT FLOW
REPORT 2. HYDRODYNAMIC FUNCTION OF SQUAMOSAL INTEGUMENT

A. F. Kudryashov and V. V. Barsukov

1. Report No. NASA TM 75400	2. Government Accession No.	3. Recipient's Catalog No.
4. Title and Subtitle Hydrodynamic role of fish Squamosal Integument as an Analog of the surfaces directly formed by the turbulent flow		5. Report Date DECEMBER 1980
		6. Performing Organization Code
7. Author(s) A.F. Kudryashov, V.V. Barsukov		8. Performing Organization Report No.
		10. Work Unit No.
9. Performing Organization Name and Address SCITRAN Box 5456 Santa Barbara, CA 93108		11. Contract or Grant No. NASw- 3198
		13. Type of Report and Period Covered Translation
12. Sponsoring Agency Name and Address National Aeronautics and Space Administration Washington, D.C. 20546		14. Sponsoring Agency Code

15. Supplementary Notes

Translation of "O gidrodinamicheskoy roli cheshuynogo pokrova ryb kak analoga poverkhnostey, neposredstvenno sformirovannykh vikhrevym potokom, Soobshcheniye 2. Gidrodinamicheskaya funktsiya cheshuynogo pokrova", Zoologicheskiy Zhurnal, Vol. 46, No. 4, 1967a, pp 556-566

16. Abstract

The stream flowing round the slowly swimming squama-free fish can be laminized with the aid of the external slime coat alone. The slime of the fish with well developed squamae can laminize the stream together with the squamatic integument. Adjustments preventing a loss of the slime during laminization are better developed in the fastest squama-free fishes.

17. Key Words (Selected by Author(s))	18. Distribution Statement Unlimited - Unclassified

19. Security Classif. (of this report) Unclassified	20. Security Classif. (of this page) Unclassified	21. No. of Pages 20	22. Price

ii

HYDRODYNAMIC ROLE OF FISH SQUAMOSAL INTEGUMENT AS AN
ANALOG OF THE SURFACES DIRECTLY FORMED BY THE TURBULENT
FLOW

REPORT 2. HYDRODYNAMIC FUNCTION OF SQUAMOSAL INTEGUMENT

A. F. Kudryashov* and V. V. Barsukov*

In the first report we noted the similarity in the irregularities   /556**
of the fish skin that consists of typical cycloid or ctenoid squamae to
the irregularities on the surfaces that are directly formed by the tur-
bulent flow in inorganic nature, particularly in the river beds where
such formations have been studied most completely.

We are attempting here to give a preliminary explanation for the
indicated similarity. We are also attempting to raise certain questions
that follow from this approach to an understanding of the functional
importance of the squama.

One can currently only advance a working hypothesis on the hydro-
dynamic role of the squamosal integument after replacing the shortage
of factual data with a certain number of assumptions, and even after
placing one of them as the basis of the hypothesis.

The initial point of our hypothesis is that slime and the squama are
parts of the same mechanism. This follows from the analogy of the
squamosal integument to the surfaces directly formed by the turbulent
flow.

However, as far as we know, the hydrodynamic function of the slime
remains unclear. This is evidently influenced a great deal by the experi-
ments of Richardson (1935) and Gero (1952). Both authors completely or

1

almost completely negate such a function of slime. We will return again to these experiments later. Now we have to start from the assertion that has little proof, but was advanced long ago and is often repeated. This assertion states that the slime must have a hydrodynamic function.

The analogy between the particles of slime on the surface of the fish and the particles of soil on the surfaces formed by the flow in river beds of course canno. be complete. It is known that the specific weight of slime is roughly equal to the specific weight of water. The transfer of its particles can therefore hardly reduce the energy of the turbulent formations. It can evidently be reduced by the separation of particles, and most likely, mainly only by the formation of projections on the surface of the slime, which is considerably more viscous than the water (Richardson, 1935)[1]. These projections are similar to the waves created by the wind in a very shallow basin with a noneroding bottom. In both cases we are concerned with a movable roughness that is capable of reducing the intensity of vortex formation as opposed to a fixed roughness.

The turbulent formations that follow one after another on the surface of the fish body must possess the effect of displacement (Patrashev, 1953; Nikitin, 1963). The force of displacement of a vortex directed towards the side where the direction of stream velocity and the circumference of the vortex velocity coincide is expressed by the kinetic energy of the vortex formation $\frac{\gamma u^2}{2g}$ (where γ--specific weight of water, u--characteristic velocity of vortex formation, in particular the longitudinal velocity of the vortex movement). The force of vortex displacement F that acts on the separated slime particle with an area of cross section ω_4 equals

$$F \quad \frac{1}{2g} \omega_4 \tag{1}$$

where λ--angle between the direction of the longitudinal velocity movement of the vortex and the force of vortex displacement. The influx

------

[1]The viscosity of slime possibly changes correspondingly to the changes in viscosity of water. For example, in freshly caught Anarhichas (Anarhichadidae) the viscosity of slime rises very noticeably with a drop in air temperature. This is evident in the movable arm of the slide gauge: the colder the weather, the more difficult it is to move the arm on the scale that is covered with slime, with other conditions equal.

of slime and the formation of a projection on its surface begin from
that moment when F begins to surpass the force of viscosity re-
straining the slime, i.e., $F \geq P$. Here the force of viscosity re-
straining the slime on the surface of the epidermis equals $P = \sigma_c \cdot d_b \cdot 1$, (2),
where σ_c--breaking stress of slime; 1--linear dimension, $d_t \cdot 1$--area of
stress surface of separated slime particle.

Thus,

$$\frac{\gamma \cdot u^2}{2g} \cdot \frac{\omega_1}{\cos \lambda} = \sigma_c \, d_b \cdot l \qquad (3)$$

from which

$$\frac{u^2}{2g \cdot d_b} = \frac{\sigma_c \cdot l \cdot \cos \lambda}{\gamma \cdot \omega_1} \qquad (4)$$

Something similar is observed during the turbulent
flow around sandy ridges in a river bed. Instead of the forces of
viscosity that restrain the slime from forming projections on the sur-
face, forces of gravity are active that restrain the particles of sand.

The faster the fish moves, the higher the projections must be on the
slime integument that develop under the influence of vortex formations,and
the greater the danger of separation of these projections, and conse-
quently, the loss of an excessively large amount of slime. This danger
could be reduced if the main mass of the slime projection (as was shown
above, similar to a wind wave) could be replaced by something hard. In
order to guarantee this replacement the squama must imitate, in shape,
dimensions and movements, the largest "slime waves" that in the given
hydrodynamic pattern could develop spontaneously if the slime were not
separated. Secondary irregularities on the wave surface can be imitated
by irregularities in the elastic epidermis that are governed by the
influence of the hard sclerites located under them.

As was stated above, the distance between the sclerites and the
dimensions of the squamae are linked to the shape of the fish body and
the velocity of its movement by the same law as the dimensions of the
irregularities and the ridges on the secondary surface are linked with
the shape of the latter and the velocity of the flow. The irregu-
larities and ridges, in possessing unchanged characteristics during a
steady-state pattern, nevertheless constantly change position according

3

of slime and the formation of a projection on its surface begin from that moment when F begins to surpass the force of viscosity restraining the slime, i.e., $F \geq P$. Here the force of viscosity restraining the slime on the surface of the epidermis equals $P = \sigma_c \cdot d_b \cdot 1$, (2), where σ_c--breaking stress of slime; 1--linear dimension, $d_t \cdot 1$--area of stress surface of separated slime particle.

Thus,

$$\frac{\gamma \cdot v^2}{2g} \cdot \frac{\omega_1}{\cos \lambda} \quad \sigma_c \cdot d_b \cdot l \tag{3}$$

from which

$$\frac{u^2}{2g \cdot d_b} \quad \frac{\sigma_c \cdot l \cdot \cos \lambda}{\gamma \cdot \omega_1} \tag{4}$$

Something similar is observed during the turbulent flow around sandy ridges in a river bed. Instead of the forces of viscosity that restrain the slime from forming projections on the surface, forces of gravity are active that restrain the particles of sand.

The faster the fish moves, the higher the projections must be on the slime integument that develop under the influence of vortex formations, and the greater the danger of separation of these projections, and consequently, the loss of an excessively large amount of slime. This danger could be reduced if the main mass of the slime projection (as was shown above, similar to a wind wave) could be replaced by something hard. In order to guarantee this replacement the squama must imitate, in shape, dimensions and movements, the largest "slime waves" that in the given hydrodynamic pattern could develop spontaneously if the slime were not separated. Secondary irregularities on the wave surface can be imitated by irregularities in the elastic epidermis that are governed by the influence of the hard sclerites located under them.

As was stated above, the distance between the sclerites and the dimensions of the squamae are linked to the shape of the fish body and the velocity of its movement by the same law as the dimensions of the irregularities and the ridges on the secondary surface are linked with the shape of the latter and the velocity of the flow. The irregularities and ridges, in possessing unchanged characteristics during a steady-state pattern, nevertheless constantly change position according

3

to the vortex formations. On the greatest part of the fish the squamae almost do not move along the fish body, but their movement upwards from the body and downwards towards the body can imitate to a certain measure the advance of the ridges over the secondary surface.

Under the influence of fluctuations in the pressure of the turbulent flow around the fish, the squamosal surface can arch (without breaking contact between the squamae), forming longitudinal and transverse waves. The dimensions of these waves, judging from every-   /558 thing, are closely linked to the dimensions and shape of the body, the open section of squamae, of sclerites, and the viscosity and quantity of slime and the movement velocity, in the same way as the size of the ridges in the river beds depends on the depth of the flow, its velocity, the size of the sand particles and the dimensions of the secondary surface.

The main feature of both phenomena is the waves of a certain size that run over the body surface. They correspond to the turbulent fluctuations of the flowing stream, reducing the hydrodynamic resistances. One can adopt for the length of the running wave the doubled length of the open section of the squamula, and as the width of the wave one can adopt the doubled width of the given section as was done in report I.

The waves running over the squamosal fish surface only accompany the turbulent fluctuations in the boundary layer. After each wave, in its trough, a turbulent zone cannot help but form which has a decelerating effect on the fish. This effect could be eliminated by moving the turbulent zones in a transverse direction, from the trough of one wave to the trough of another, to a distance equal to the width of the open section of the squama. We assume that such movements occur during the rotational movement of the fish body. As one can assume from the research of A. Magnan and A. Saint-Lague (1929) and others the indicated movements, slight and not very noticeable, consist of periodic screwing in of the anterior portion of the body and simultaneous unscrewing of the posterior part the amount of a turn. Analogous phenomena are also observed in river beds where tranverse currents exist (Kudryashov, 1959).

4

All the previous discussions touched on the squama located on the greatest section of the fish body, i.e., at the site with the least lateral bends during movement as compared to those located behind the parts of the torso and especially the tail (Bainbridge, 1963), whose surface first becomes concave then convex. Here the length of the open parts of the squama in relation to the unchanging distance between the sclerites is first reduced then increased. To a certain degree these changes respond to the relationship reflected in report I in figure 4, and namely, that with a relative reduction in the momentary stream velocity on the concave side the ratio $\frac{21_r}{db}$ is reduced. With a relative increase in this velocity on the convex side the ratio is increased.

Since the centrifugal forces acting on the particles of water press the particles that are moving with great velocity towards the concave surface and deviate them from the convex, the vortex formation on the concave side of the body must be intensified, and on the convex side-- reduced (Walters, 1962). In the concavities of the fish body large turbulences are formed. Part of their energy is re-used by the fish by repelling from them (Rosen, 1961). One can hardly doubt that the squama participates in the formation and use of these turbulences, and also, during travel against the current, in the use of the turbulences that develop in the river without the participation of the fish (Osborne, 1961; Ohlner, 1964). This role of the squama, however, has not been clarified. One can only note that the turbulences that are analogous to those in the concavities of the fish body, but with axes of rotation arranged horizontally (i.e., according to the arrangement of the surface that is flowed around) are also observed in an order close to the staggered in both the river beds formed directly by a turbulent flow and their laboratory models (Kudryashov, 1959, 1960).

It still remains to clarify the hydrodynamic importance of the radial channels on the open section of the squama. It is not understood what the reasons are for the lack of sclerites on it, without considering the zone neighboring the overlying squamae in the herring, salmon and certain other fish. It is not clear what the importance is of the differences in the sclerites: usually these are concentric cylinders,

but in certain species they travel transverse to or along the squama. It is still not clear what the importance is of the small additional squamulae that are very widespread in many groups of fish, in particular /559 in the herring, cod, pomakantids, rosefish, halibut and others; or the importance of the very great distances between the sclerites in the regenerating squamae as compared to the neighboring normal ones; or the importance of the differences in structure that are present in any fish, and especially in the dimensions of the squamae from different parts of the body (not to mention the role of the enlarged squamae in the bases of the thoracic, abdominal, tail fins and on the abdominal fin of certain fish, see Aleyev, 1959, 1963).

We moreover analyzed the work of the squamosal integument only with a constant velocity of motion, while in many fish movement is formed of alternating accelerations and decelerations (Houssay, 1912; Harris, 1936; Nursall, 1958; Hollands and Alderdice, 1958). Here the laminizing role of the squama should be especially pronounced during the decelerations, and this of course requires a more complicated analysis.

We have been concerned until now with the passive work of the squamosal integument. However, fish with cycloid, and possibly, even with ctenoid squamae most likely are also capable of active control of them. This is indicated by one accidental observation: in a live bream (41 cm long and weighing 1.3 kg) cleaned of squamae and wetted with concentrated solution of sodium chloride, longitudinally pulsing waves passed over the body and spread over the entire height of the body. The wave length comprised two lengths of the open section of the squamulae that were distant from the given site. Here the body did not bend. We do not know which muscle fibers could induce similar movements. This question requires special research.

The fish skin and each squama are abundantly supplied with nerves (Chugunova et al., 1961; Whitear, 1952). T' : fish usually acts in a very pained manner to the extraction of a squamula: the carp, for example, responds calmly to the taking of blood, tagging and even pricking of the back muscle. Stripping of part of the squamae in the merlang reduces the return of tracers three-fold (Beverton et al., 1959).

6

Swimming silver salmon die from such injuries (Yevropeytseva, 1957) and the very same occurs, as is assumed, in the sea during tagging of red salmon (Black, 1957). At the same time the loss of part of the squamae without human participation is a very common phenomenon for fish, including those just named. In any of the species of the genus Sebastodes and Sebastes it is hard to find an adult fish where regenerated squamulae do not comprise the greater part of the squamae. The hydrobiologists who have worked in the northern seas know well that at the sites of large accumulations of herring the plankton nets sometimes catch many of their squamulae, more than plankton. It is most likely that these squamulae are lost by the fish mainly not as a result of injury, but during adaptation of the squamosal integument to the changing exterior.

The noncorrespondence of the squamosal integument to the changed body volume can primarily develop in the case of the drastic exhaustion of the fish due to a shortage of food, strong infestation with parasites, etc. In the rosefish (Sebastes) the fatty deposits that are usually fairly great behind the greatest body section, especially in the rear end of the torso, are reduced in a direction towards the head and tail (Brandes and Ditrich, 1958). When the fish are emaciated, if we are speaking only of the second growth of the squamosal "armor", the replacement of the old squamulae apparently had to occur fairly uniformly in the area of the greatest girth and be reduced from the end of the torso to the head and tail.

In fact, under the thoracic fin, near its base, there are always much fewer regenerating squamulae than above the fin. In the latter case there are often noticeably fewer than before the tail fin. The dispersal of squamulae is apparently linked to the hydrodynamic role of the integument.

K. Müller (1953) writes that there are more regenerating squamae in trout with a poor growth rate. He doubts the mechanical loss of squamulae where new ones rise up in their place. However the possibility is not excluded that such a loss nevertheless appears on the scene as the final act of dispersal of the squamula that does not satisfy the more hydrodynamic requirements. It is possible that the fish rub on

each other and on the substrate in order to get rid of such squamulae that are   ready to fall out under the influence of some internal processes: from their squamulae and not only from parasites as was assumed until now.

Despite the numerous unanswered questions, we nevertheless have the right to draw the conclusion that the squama works with average velocities of movement of the fish. It was apparent from the relationships stated above that both with a reduction and an increase in the velocities a trend is noted towards the reduction in the dimensions of the squama. This evidently results in the end in a reduction in the squama.

All the fish that are equipped only with squamae that are reduced, small, not overlapping and submerged into the skin, or do not have squamae at all, and have a well developed slime integument are slow swimmers, as far as we know. Many of them are capable of short, fast surges, which however, are not the usual method of motion. These include many fish with a more or less "ordinary" body shape, such as the fish from the branch of scorpion fish of the family Scorpaenidae Coccotropus-steam (Matsubara, 1943), many kerchaks and fish from the families close to them and others. This includes all the very elongated, eel-   /5 or ribbon-shaped fish, as well as the fish of average enlongation but swimming with a great amplitude of the lateral bends ("swimming wave"): catfish, burbot, dog salmon of the genus Anarhichas and many others (Matveyev, 1945; Grinberg, 1950, Barsukov, 1959). Their slime formation is noticeably intensified as compared to the squama-free fish that swim with smaller amplitude of bends.

With low velocities of movement that are characteristic for these fish, the stream can evidently be laminized stronfly and without support from the squama.[2] On short, fast surges the acceleration itself should promote laminization (Chestnoy, 1961; Aleyev, 1963).

Even for this last reason the experiments of Richardson (1935) and Gero (1952), who attempted to establish the effect of slime on the motion velocity of fish according to the rate of drop in the models and who arrived at negative results, cannot be considered convincing.

----
[2]An analogous phenomenon is observed in river beds in the smooth phase of movement of detritus, when ridges are not formed.

The situation is aggravated by the fact that the models naturally did not make bends that are characteristic for the swimming fish. When such experiments are set up in the future the following should be considered: in fish with squamae the slime can evidently display its hydrodynamic function completely only in joint operation with the squamosal integument. The latter, as is clearly seen from the aforementioned, can hardly function normally not only in a dead or anesthesized, but even in a sick fish.

It is indicative that in fish fry the squama always appears first of all along the lateral line (Hjort, 1914; Kassner, 1963, and many others), i.e., where the velocity of the stream, as we assumed, is the greatest, and most often on the tail (Van Oosten, 1957; Balon, 1958 and many others), where the vortex formation should be especially strong.

In many fast-moving fish from the suborder of mackerels, the squama on the body again disappears (often with the exclusion of a "girdle" made of modified squamae on the greatest section). Walters (1962) believes that in the given case the laminization of the stream becomes disadvantageous since the danger of separation of the boundary layer increases. During such separation the resistance increases more strongly than during the rise in the turbulent pattern. Nevertheless, in the swordfish with its record velocities the system of laminization is apparently present (see below). Marshall (in Bainbridge, 1961) assumes that the integuments of the tuna that are rich in fatty interlayers like the integuments of very fast marlins, are similar in structure to the dolphin skin and laminize the boundary layer like the latter. This type of laminization possibly is similar in principle to that in other fish who swim without body bends or almost without them (not counting the file-fish we will discuss below). The integuments of these fish carry a system of channels filled with special fluid and opening to the outside by numerous pores.

In the latter case it is not important whether these fish swim extremely fast like the swordfish, or slowly like Desmodema polysticla (Trachipteridae; Walters, 1963). They do not have squamae. In all other

fish that swim without body bends there are no cycloid nor ctenoid
squamae.

The system of channels and pores is apparently more advantageous
than the system of surface slime-squama, but it can only function in
the absence of such body bends that could influence the position of the
fluid in the channels.[3]

The fact that the squama operates on an average amplitude of bends
is apparently linked to its other function, the limiter of these bends
(Grinberg, 1950; Barsukov, 1960). It is hardly accidental that the
number of longitudinal rows of squamae on the fish is closely linked   /561
to the number of vertebrae, especially in fish with fairly large
squamae (Hjort, 1914, et al.),while the closed part of the squama is
greatly strengthened by sclerites. There are usually more here than on the
open section (Wallin, 1957; Galkin, 1958; Koo and Earl, 1963 and many
others). It is possible that to some extent this is why in fish fry
the squama usually appears first of all in the tail section (see above).
An increase in the velocity of movement both in ontogenesis and in
phylogenesis of fish is most often linked to the reduction in ampli-
tude of the lateral bends and the transfer of its greatest percentage
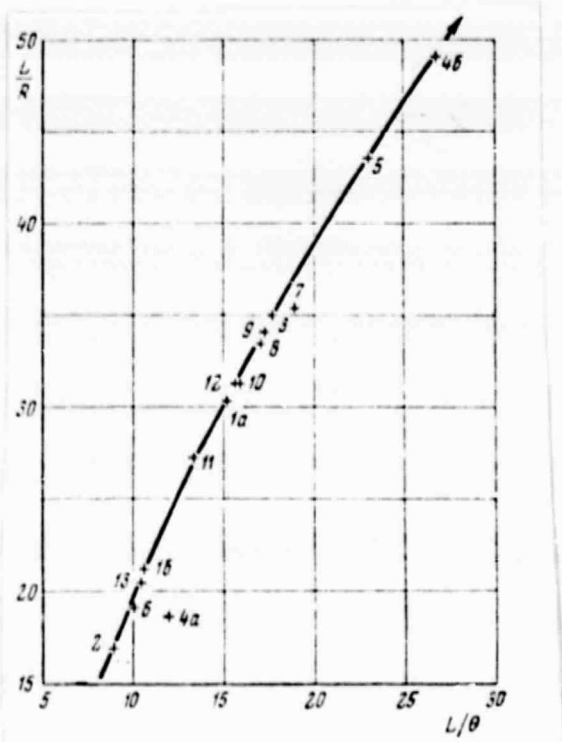of work to the tail fin (Nursall, 1958a; Barsukov, 1960a; Aleyev, 1963).

In Desmodema and the swordfish the system of channels filled with
special fluid evidently acts similarily to the surface slime integument.
However it has the difference that the slime is not drawn in over the
entire body surface, but only in the channels, through the pores, so
that its loss, which is inevitable at high velocities of movement, is
limited. The analogy with the surfaces that are spontaneousl' ~rmed
by the turbulent stream is preserved here also in the most ge   ıl
features. On the graphs that reflect the dependence of the ma. uvered
qualities of the fish body[4] on its relative elongation $\frac{L}{B}$, i.e.,

---

[3]The swordfish swims almost without bends due to the small and very
fast beats of the tail fin, while Desmodema uses undulations of the
long tail fin. In the young Desmodema there are squamae,but then they
disappear together with the epidermis and dermis (Walters, 1963).

[4]Without fins; with a reduction in the index of maneuverability the
maneuverability increases.

$$\frac{L}{R} = 14.73 \cdot \frac{L}{\ell} - 27 \qquad (5)$$

(figure) and the dependence of the relative elongation on the dynamic characteristics $V^2/2gB*$ (fig. 3 in report I) the swordfish falls on the same curves as the fish with squamae. These curves are a continuation of analogous curves for the formations made by the stream in river beds.
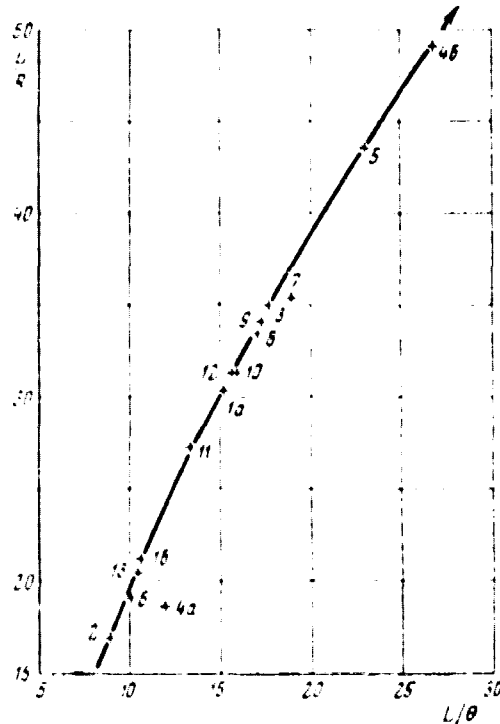

Dependence of Index of Maneuverability of Fish Body on Relative Elongation of Body

As for the fish with squamae, whether they are ctenoid or cycloid, the analogy with the surfaces directly formed by the turbulent flow remains correct for both. The pike perch that has ctenoid squamae does not differ significantly from the other fish we have studied who have cycloid squamae (figure, as well as figures 4-6 in report I).

The difference between the ctenoid squama and the cycloid in a hydrodynamic respect is evidently very small. On the open section of such a squamula, nearer to the edge, spinules with adsorbed apex are arranged in staggered order. The valleys between them are comparable in

$$\frac{L}{R} = 14.73 \cdot \frac{L}{\theta} - 27 \qquad (5)$$

(figure) and the dependence of the relative elongation on the dynamic characteristics $V^2/2gB^*$ (fig. 3 in report I) the swordfish falls on the same curves as the fish with squamae. These curves are a continuation of analogous curves for the formations made by the stream in river beds.

Dependence of Index of Maneuverability of Fish Body on Relative Elongation of Body

As for the fish with squamae, whether they are ctenoid or cycloid, the analogy with the surfaces directly formed by the turbulent flow remains correct for both. The pike perch that has ctenoid squamae does not differ significantly from the other fish we have studied who have cycloid squamae (figure, as well as figures 4-6 in report I).

The difference between the ctenoid squama and the cycloid in a hydro-dynamic respect is evidently very small. On the open section of such a squamula, nearer to the edge, spinules with adsorbed apex are arranged in staggered order. The valleys between them are comparable in

11

dimensions to the vortex formations following on the body surface. However, the double row of sharp spinules arranged in staggered order on the very edge of the squama, with thin membrane stretched between them, judging from everything, fulfills some special task.[5]

The ctenoid squama in a hydrodynamic respect on the average is pos- /562 sibly less complete as compared to the cycloid. In the experiments of Ol'mer (1964) the fish with cycloid squama, the roach and redfin, in moving against the current could use the force of water movement and preferred the experimentally created turbulent zone. The perch with its ctenoid squama did not do this. The eddies restricted its movement. It soon became tired and "began to anchor," pressing towards the bottom. The surges of the perch for food are quick as lightning but short (Girsa, 1962). The pike perch is much more mobile than the perch. It is the most mobile fish with ctenoid squama from our fresh-water and semi-anadromous fish, however it does not like to make such large passages like many semi-anadromous fish with cycloid squama that are fairly similar in dimensions (Volga herring, many whitefish, and others). The sea pike perch (Lucioperca marina) also does not make large migrations (Lovetskaya, 1946). Among the numerous species of Sebastodes, in the species that, judging by body shape, are the most mobile (for example, S. goodei, S. jordani, S. entomelas and S. paucispinis) the squama is generally smaller than in the less mobile fish, while the spinules are smaller r the squamae of the same size.

The possibility is not exluded that the spinules on the ctenoid squama are normally residues of a special type of laminization of the stream with the help of the spinules that are securely fastened to the immobile base. Such type of laminization, judging from everything, was characteristic for the armor made of hanoid squamae that gave rise to the ctenoid and cycloid squamae (Van Oosten, 1957; Grinberg, 1961 and others). Such spinules are clearly evident on the squamae of polypterus and the armored pike (Van Oosten, 1957, fig. 2,3). In a typical case the spinules of the placoid squama from which the hanoid originates, or of the modified osseous, comprise the main part of the squama. Their shape can be very diverse (Bertin, 1958; McCormick et al., 1964; and

---

[5] In the not very mobile Black Sea scorpion fish, in contrast to its relative the sea perch, the spinules do not replace each other on the edge of the squama with growth, but grow constantly, become very long, and by interconnecting with the osseous connectors form a large part

12

others). This type of laminization is widespread in the shark, and only in a few bony fish that are scattered over different orders is it encountered in a developed form (many Balistoidea, Luvarus, Macroramphus, Achiropsetta fry and others, G. Wahlert and H. Wahlert, 1964; Andriyashev, 1960; Bertin, 1958; Van Oosten, 1957). It is apparently also implemented with the participation of slime. There is more slime in the less mobile forms (Matveyev, 1945).

Such type of laminization is generally more universal than the "slime-ctenoid or cycloid squama" system. It is encountered in fish swimming with great body bends and those without them at all, slow and very fast like certain sharks. Nevertheless, in our opinion, the best swimmers among the sharks must be very inferior in velocity to the best swimmers among the bony fish. Generally this type of laminization, judging from everything, is more primitive, but in some special conditions it provides an advantage since in certain bony fish it develops secondarily. In a separately taken individual it is possibly the optimal in a narrower range of velocities than laminization with the help of the mobile squama in fish of similar shape and dimensions, and in this sense is less universal.

The ctenoid squama is always considered a formation that is later than the cycloid squama. This is mainly only because it is encountered much more often among the higher groups of bony fish than among the lower. However, on the same basis, no one considers a later acquisition to be spawning,and not viviparity that is encountered primarily, and in a more developed form exclusively, among the lower fish (sharks).

The combination of a high level of development of some systems of organs with a low level of development of others is a very common phenomenon in the organic world. For a proper judgment as to whether the spinules on the ctenoid squama, in their typical form, are a neoplasm, or whether they originate from the hanoid squama of the predecessor and were preserved after undergoing a number of transformations like a residue of an ancient type of structure,it is necessary first of all to make a deeper study of their function in the modern fish, and from this viewpoint to trace the evolution of spinules in fossil fish.

of the open sector of the squama. They are very similar in position to the bony fins of the open section of the squamulae in certain makrurils, as well as on the epithelial fins of Gobio albipinnatus (Banarescu, 1961).

It is possible that normally this is a residue of an ancient type
of structure, and that at such a stage of reduction its loss
does not have a basic importance. In fact the ctenoid squama differs
in general structure from the cycloid incomparably less than both to-
gether differ from the hanoid, and the latter from the placoid. The
so-called cycloid stage of development of the ctenoid squama, from the
establishment of the squamula to the appearance of the first spinules
on it, in certain species and groups of species could have been
lengthened during evolution, and in the end completely displaces the
ctenoid stage.

In conclusion it remains to say that it is not at all excluded that   /
besides the functions associated with movement, the cycloid, and especi-
ally the ctenoid squama in other fish can also fulfill a protective
function, although not as pronounced as in bony plates of the sturgeon
and the hanoid squama of the armored pike, the armor of the kuzovok,
poacher, sea pipe-fish and skin-carp, the shields of sticklebacks, etc.
L. P. Sabaneyev (1959), for example, asserts that the hard squama of
especially large river perch cannot be penetrated by any spear. By the way
in fish that laminize the stream with the help of spinules attached on
a fixed base, the spinules also can have a protective function that some-
times begins to dominate, as is observed in fakakhy (Tetrodontoidei),
related to the file-fish (Balistoidei) and kuzovok (Ostracioidei).

As for the slime, besides the hydrodynamic function it undoubtedly
has a protective function, and a very versatile one. This is well known
from the many works that are not given here due to a shortage of space.

The multiple nature of the functions of organs and their parts is
extremely characteristic for living organisms (Severtsov, 1939; Mat-
veyev, 1945a, and others). Under certain conditions in some of them
any one of the functions can have an advantage over the others, making
the appropriate corrections in them. Here we have attempted to dis-
cuss only the hydrodynamic functions of the integuments in their
purest form.

Nevertheless our brief survey provides a certain idea about the functional importance of the main direction in the evolution of the squamosal integument in fish. Judging from everything, the main function of the placoid squama was a hydrodynamic function. The protective function began to dominate when the placoid squamae, having merged into the larger hanoid, formed an armor. Later, parts of this armor, very much lightened, and most important,having obtained mobility, were transformed into ctenoid and cycloid squamae. The hydrodynamic function again became the primary, but now fulfilled the work better. The range of hydrodynamic patterns in which it can be implemented was narrowed however.

Conclusion

Fish with well-developed slime integument, but with poorly developed squama, or completely squama-free, swim slowly, although many of them are capable of short, fast surges. Slime release is especially abundant in fish that swim with a large amplitude of lateral bends. The stream that flows around the fish is laminized, judging from everything, only with the help of slime. The surface of these fish possibly reveals the greatest analogy to the surfaces of nonliving nature that are directly formed by turbulent flows.

The fish that are equipped with normally developed ctenoid or cycloid squamæ lying on top of each other move with average velocity, with average amplitude of bends. In these fish the slime laminizes the flow with the cooperation of the squamosal integument. The shape, structure and movements of the squamae apparently replace the shape, structure and movements of the slime projections to a considerable measure. These projections already had to appear during the sucking in of the slime by the turbulent formations, if the slime here could have been retained on the body surface. Therefore the shape, dimensions of the open part of the squama and the distance between the sclerites on it are linked by such hydromechanical relationships to the shape, dimensions and motion velocity of the fish that mainly remain correct even for bodies of nonliving nature directly formed by the turbulent flow, in particular, in river beds where the shape and dimensions of the secondary formations and the flow velocity are analogously linked to the shape

and dimensions of the ridges and irregularities.

The fish that swim without lateral bends or almost without them are
species deprived of the typical integument made of cycloid and ctenoid
squamae. The external slime integument is replaced in them (if one does
not consider the file-fish and fish close to them) by a network of
channels filled with fluid that open to the outside by numerous small
pores. In certain fish, perhaps, it is replaced by a system of fatty
interlayers. This mainly includes the fastest fish. The analogy of
their surfaces to the surfaces of nonliving nature directly formed by
a turbulent flow is apparently preserved in general features.

In sharks, polypterus, armored pike, and secondarily in certain
bony fish from different orders (in particular in file-fish) a special
type of laminization of the flow with the help of spinules is well
developed. These spinules are strongly attached to a fixed base and
are apparently also linked in operation to the external slime integument.
This type of laminization is encountered in slow and fairly fast fish
that swim with strong lateral bends and without them at all, i.e., on
the whole with a larger range of hydrodynamic patterns than the slime-
ctenoid or cycloid squama system. However in separately taken indi-
viduals that are similar in shape and body dimensions, but differ in
squamosal structure, the laminization with the help of the spinules is
the optimal, apparently, in a smaller range than laminization with the
help of the mobile squama. The spinule of the ctenoid squama possibly
is normally a residue of that type of laminization inherited from the
hanoid, and in the final analysis from the placoid squama of the pre-
decessors.

Between the indicated main types of laminization of the flow there
exist numerous transitions, and many deviations caused by the dominance
of some different function and not the hydrodynamic one.

Evolution of the squamosal integument in fish, judging from every-
thing, occurred in the following main direction: dominance of the
hydrodynamic function (placoid squama) → dominance of the protective
function (armor made of hanoid squamae that developed by merging of the

16

placoid) → new dominance of the hydrodynamic function (significantly lightened ctenoid and cycloid squama with mobility) in a more complete expression that was not so widespread as previously.

It goes without saying that the hypotheses we have advanced require the most thorough critical verification.

Bibliography

Aleyev, Yu. G. "Functional Importance of Alae and Homologous Formations to Them in Fish," Tr. Sevastopol'sk. biol. st. AN SSSR, ["Proceedings of Sevastopol' Biol. St. USSR Acad. of Sci."], Vol. 11, 1959. Funktsional'nyye osnovy vneshnego stroyeniya ryby ["Functional Fundamentals of External Fish Structure"], Moscow, 1963.

Andriyashev, A. P. "New Fish Families for Antarctica. Report 3. Pelagic Flatfish Fry (Pisces, Bothidae)on the Shores of Antarctica," Zool. 39, 7, 1960.

Barsukov, V. V. "Family of Dog Salmon (Anarhichadidae)," Fauna SSSR, ["Fauna of the USSR"], vol. 5, 1959, Moscow. "Age of the Ob' Whitefish and Certain Theoretical Questions," Zool. zh., Vol. 39, Issue 10, 1960. "Motion Velocity of Fish," Priroda, No. 3, 1960a.

Galkin, G. G. "Atlas of Squama of Freshwater Bony Fish," Izv. Vses. n. in-ta ozern. i rechn. rybn. kh-va, 46, 1958.

Girsa, I. I. "Effect of Changing Light Intensity on Accessibility of Food Organisms for Predatory Fish," Vopr. ikhtiol., 2, 1 (22), 1962.

Grinberg, M. N. "Dependence of Dimensions of Bony Fish Squama on Body Shape and Nature of Movement," Zool. zh. Vol. 29, Issue 5, 1950. "Ontogenesis of Squama in Bony Fish," Zool. zh. Vol. 40, Issue 2, 1961.

Yevropeytseva, N. V. "Transition to Rolling State and Rolling of Young Salmon," Uch. zap. Leningr. in-ta, 44, 223, 1957.

Kudryashov, A. F. "Reproduction of Bed of Secondary Type under Laboratory Conditions," Tr. Gos. gidrol. in-ta ["Proc. of State Hydrol. Inst."] 69, 1959. "Results of Certain Experiments to Study Bed Processes on Eroding Models," Tr. III Vses. gidrol. s"yezda ["Proc. III All-Union Hydrol. Congress"], V, Gidrometeoizdat, 1960.

Lovetskaya, A. A. "Knowledge of Biology and Fishing of Sea Pike Perch of Azerbaidzhan," Rybn. kh-vo, 10-11 , 1946.

Matveyev, B. S. "Correlation between Skeleton-forming and Glandular /565 Function of Fish Skin in Ontogenesis and Phylogenesis," Dokl. AN SSSR, 49, 7, 1945. "System of Correlative Changes in Shape,

Function and Medium in the Evolution of Animals," Zool. zh. vol.
24, No. 1, 1945a.

Nikitin, I. K. Turbulentnyy potok i protsessy v prirodnoy oblasti
["Turbulent Flow and Processes in Nature"], Kiev, 1963.

Natrashev, A. N. Gidromekhanika ["Hydromechanics"], Moscow, 1953.

*abaneyev, L. P. Zhizn' i lovlya presnovodnykh ryb ["Life and Catching
of Freshwater Fish"], Kiev, 1959.

*evertsov, A. N. Morfologicheskiye zakonomernosti evolyutsii ["Morpho-
logical Laws of Evolution"], Moscow, 1939.

*estnoy, V. N. "Maximum Motion Velocities of Fish," Rybn. kh-vo, 9, 1961.

Chugunova, N. I.; Assman, A. V.; and Makarova, N. P. "Growth and Dynamics
of Fatness in Fish as Adaptive Processes (Based on Experimental Study
of Carp in Volga Delta)," Tr. in-ta morfol. zhivotnykh ["Proc. of
Inst. of Animal Morphol."], 39, 1961.

Bainbridge, R. "Problems of Fish Locomotion, Vertebrate Locomotion,
London, 1961. "Caudal Fin and Body Movement in the Propulsion of
Some Fish," J. Exptl. Biol., 40, 1, 1963.

Balon, E. "Development of the scales of the Danube carp,"
Zool. Anz, 160, 3-4, 1958.

Banarescu, P. "Further systematic studies on gabio (pisces,
cyprindaw), especially in the Danube basin," Vestn. Ceskosl.
Zool. Spolec (Acta Soc. Zool. Bohemoslovenicae), 25, 4, 1961.

Bertin, L. "Cutaneous glands and luminous organs," Traite Zool,
13, 1958.

Beverton, R. J.; Gulland, J. A. and Margetts, A. K. "Whiting Tagging.
How the Tag Return Rate is Affected by the Condition of the Fish
When Tagged," J. Council Perman. Intern. Explorat. Mer., 25, 1, 1959.

Black, E. C. "Alternation in the Blood Level of Lactic Acid in Certain
Salmonid Fishes following Muscular Activity. III. Sockeye Salmon,
Oncorhinchus nerca," J. Fisch. Res. Board, Canada, 14, 6, 1957.

Grandes, C. H. and Ditrich, R. "Relationship between fat content,
water content and fat distribution of commercial fish."
Veroff. Inst. Meeresforsch, Bremerhaven, Vol. 3, 1958.

Gero, D. R. "The Hydrodynamic Aspects of Fish Propulsion," Amer. Mus,
Novitat., No. 1601, 1952.

Harris, J. E. "The Role of Fins in the Equilibrium of the Swimming Fish.
I. Wind-Tunnel Test on a Model of Mustelus canis (Mitchell)," J.
Exptl. Biol., 13, 4, 1936.

*Illegible in foreign text

18

Hjort, J. "Fluctuations in the Great Fisheries of Northern Europe," Rapp. proces. verb., Reunions, 20, 1914.

Hollands, M. and Alderdice, D. F. "The Effect of Temperature on the Cruising Speed of Young Sockeye and Coho Salmon," J. Fish. Res. Board of Canada, 15, 4 1958.

Houssay, F. "Driving shape and stability of fish," Coll. de morphol,dyn., 4, 1912.

Kassner, J. "Studies on the Morphogenesis of Scales in the Rainbow Trout (Salmo irideus (Gibb)," Zool. polon., 13, 3-4, (1964).

Koo, T. S. and Earl, F. "Circulus Height and Related Morphology of Sockeye Salmon Scales as Determined from Sections," Res. Fish. Univ. Washington, Contr., No. 166, 1963.

*agnan, A. and Sain-Lague, A. "Theory of fish," Services techniques de l'aeronautique, Bull. Technique, 58, Paris, 1929.

*atsubara, K. "Studies on the Scorpaenoid Fishes of Japan, Anatomy, Phylogeny and Taxonomy, I, II, Trans. Sigenkagaku Kenkyusyo, 1, Tokyo, 1943.

McCormick, N. W.; Allen, T.; and Young, C. W. Shadows in the Sea, London, 1964.

*aller, K. "Scale deformations for trout, Salmo trutta L and its interpretation," Inst. Fresh-Water res. Drottningsholm, Ann. rep. 1, 1952.

*ursall, J. R. "A Method of Analysis of the Swimming of Fish," Copeia, 2, 1958.

*nlmer, W. "Relationship between body shape and motion medium for fish in standing water," Zool. Jb., 81, 2, 1964.

Osborne, M. F. "The Hydrodynamical Performance of Migratory Salmon," J. Exptl. Biol., 38, 2, 1961.

Richardson, E. G. "The Physical Aspects of Fish Locomotion," J. Exptl. Biol., 13, 1, 1935.

*osen, M. W. "Experiments with Swimming Fish and Dolphins," Pap. Amer. Soc. Mech. Engrs. 61-WA-203, 1961.

Van Oosten, J. "The Skin and Scales," in Physiology of Fishes, ed. by M. E. Brown, N. Y. London, 1957.

Wahlert, G., von, and Wahlert, H. von. "A peculiar scale configuration for the bone fish Balistes bursa and a hydrodynamic explanation," Naturwissenschaften, 51, 2, 1961.

---

*Illegible in foreign text

Wallin, O. "On the Growth, Structure and Developmental Physiology of   /566
    the Scales of Fishes," Inst. Fresh-Water Res. Drottingsholm, 38,
    1957.

Walters, V. "Body Form and Swimming Performance in the Scombroid Fishes,"
    Amer. Zoolgist, 2, 1962. "The Trachypterid Integument and a
    Hypothesis on its Hydrodynamic Function," Copeia, 2, 1963.

Whitear, M. "The Innervation of the Skin of Teleost Fishes," Quart. J.
    Microscop. Sci., 93, 1952.