DEDUCTIONS CONCERNING THE AIR BLADDER AND THE SPECIFIC GRAVITY OF FISHES.

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The function of the air bladder in fishes has been a subject of discussion since the time of Aristotle, all manner of uses having been suggested for it—flotation adjustment, sense organ, manometer, barometer, respiration reservoir, sound producer, steering device, and the like. The most obvious function is that having to do with adjusting the equilibrium of the fish in water, and, knowing as we do the bewildering diversity of modification of most other organs among the thousands of species of fishes which are known, it is not at all surprising that the air bladder has also been adapted to perform many functions other than the principal and obvious one. For a brief description of the air bladder of fishes and a discussion of its functions see Tower (1902), Goodrich (1909), and Günther (1880).

It is not necessary in the present connection to consider the various secondary functions of the air bladder. The mere fact of its presence necessarily affects the specific gravity of fishes, and it is on this point that this discussion centers.

The specific gravity of the fat-free substance of salt-water fish (including backbone, but not the head and viscera) can be shown to be about 1.076. For the present purpose that figure will be taken for the whole fat-free fish. Full sea water has a specific gravity of about 1.026. A 10 kg. fish, fat-free and exclusive of air bladder or other spaces, would have a volume of $\frac{10000}{1.076}=9293$ cc. In order to be in equilibrium with sea water of the specific gravity mentioned, it should displace $\frac{10000}{1.026}=9746$ cc. An air bladder or other space of $9746-9293=453$ cc. is necessary to give the fish the required displacement. For water of increasing salinity, from pure fresh water to most concentrated sea water, the following table shows the corresponding air-bladder volume necessary to float each 10 kg. of fish whose specific gravity is 1.076:

Specific gravity of water.	Volume of air bladder.	Pressure in air bladder, millimeters mercury.	Specific gravity of water.	Volume of air bladder.	Pressure in air bladder, millimeters mercury.
	Cc.			*Cc.*	
1.000	706	760	1.020	511	1,030
1.005	657	817	1.025	463	1,159
1.010	608	882	1.026	453	1,188
1.015	559	959	1.030	416	1,289

This table shows that if fish live in and are adjusted to fresh water and if they travel seaward it will be necessary for the air bladder to become smaller. In those fishes in which the air bladder is closed (as in all the Acanthopteri, or spiny-rayed species, which are typically marine) the volume may presumably be reduced by resorption of some gas in the blood and the discharge of it into the sea, or the gas volume may be compressed, in which case the pressures developed in the air bladder corresponding to the various salinities are shown in the table in terms of millimeters of mercury, the assumption being made that when the fish is adjusted in fresh water its air-bladder pressure is 1 atmosphere (760 mm.). In nearly all the teleost fishes, except the spiny-rayed fishes, the air bladder is provided with a pneumatic duct connecting either with the alimentary canal or with the exterior. Presumably, excess of gas may be expelled through this duct. Some of our most important species, such as salmon, shad, and herring, have this duct.

If the fish lives in and is adjusted to sea water and travels in the direction of a diminishing salinity gradient, the conditions are entirely different, for in this case a migration toward fresh water will demand an enlarging air bladder. If, however, the air bladder is at 1 atmosphere when the migration begins, then the pressure must become less than 1 atmosphere, or a partial vacuum must be established in the air bladder, which seems quite improbable. As an alternative to this we may suppose the gas to be absorbed into the blood from the surrounding sea water and discharged into the air bladder. Apart from the physicochemical and physiological difficulties involved in this gas transference against pressure, it is obvious that the mere pumping of gas into the air bladder will be without influence on the specific gravity of the fish if it merely develops pressure and will be effective only in so far as it actually expands or stretches the fish to a larger size. This method of reducing specific gravity appears quite as improbable as the method that would involve a partial vacuum. Unless some other means is found the fish will have to maintain itself afloat by constant muscular effort if it goes to water of a lower salinity.

The specific gravity of a fish varies with the amount of fat present in the tissue. In fact, Bull (1896, 1897) investigated the possibility of determining the fatness of fish quickly and simply by determining the specific gravity of the fish, and his results, while not altogether satisfactory, are promising. The foundation of this work is, of course, the fact that the specific gravity of fish fat or oil is less than 1 (usually about 0.925), while that of fat-free substance is greater than 1 (about 1.076), that is, fats float on water, while fat-free fish substance sinks. When amounts by weight (W_1 and W_2) of two substances of different specific gravities (S_1 and S_2) are combined, the resultant specific gravity of the whole (S_{1+2}) is given by the formula[1]:

$$S_{1+2}=\frac{W_1+W_2}{\frac{W_1}{S_1}+\frac{W_2}{S_2}}=\frac{S_1S_2(W_1+W_2)}{W_1S_2+W_2S_1}.$$

On a percentage basis (where $W_1+W_2=100$):

$$S_{1+2}=\frac{100\ S_1S_2}{W_1S_2+W_2S_1}.$$

[1] The formula for this relation given by Bull (1897, p. 641), $\frac{Ff+Tt+V1}{100}$, is in error. In this formula F and f, T and t, V and 1 are, respectively, the weight and specific gravities of fat, dry susbtance, and water.

Calculating the specific gravities of a fish on the two figures assumed above (0.925 for fat, 1.076 for fat-free substance), we have the following specific gravities of fish with increasing percentage of fat:

Per cent of fat.	Specific gravity of fish.	Per cent of fat.	Specific gravity of fish.
0	1.0760	14	1.0519
2	1.0726	16	1.0486
4	1.0692	18	1.0453
6	1.0656	20	1.0419
8	1.0621	22	1.0385
10	1.0587	29.34	1.0260
12	1.0553	46.55	1.0000

Thus, a fish which increases in fat content diminishes in specific gravity. At 29.34 per cent fat the fish without air bladder would be in equilibrium with sea water and at 46.55 per cent fat (if it were possible) would float in fresh water without air bladder.

How does the air bladder react to those changing specific gravities? As the fish grows fatter the air bladder must occupy less and less space, as shown in the following table. This table begins with a 10 kg. fish without fat and shows how the air bladder must change as the fish adds fat, so that each weight has the percentage of fat indicated, the other constituents of the fish remaining constant.

Fat in fish (per cent).	Total weight of fish.	Specific gravity of fish substance.	Volume of solid fish substance.	Displacement necessary to float fish in sea water, specific gravity= 1.026.	Air bladder volume necessary.
	a	b	$c=\left(\frac{a}{b}\right)$	$d=\left(\frac{a}{1.026}\right)$	$c-d$
	G.		Cc.	Cc.	Cc.
0	10,000	1.0760	9,293	9,746	453
2	10,204	1.0726	9,513	9,945	432
4	10,416	1.0692	9,741	10,152	411
6	10,638	1.0656	9.983	10,368	385
8	10,869	1.0621	10,233	10,593	360
10	11,111	1.0587	10,495	10,829	334
12	11,363	1.0553	10,767	11,075	308
14	11,628	1.0519	11,054	11,323	279
16	11,904	1.0486	11,351	11,602	251
18	12,195	1.0453	11,666	11,886	220
20	12,500	1.0419	11,997	12,183	186
22	12,820	1.0385	12,335	12,495	160
29.34	14,152	1.0260	13,793	13,793	0

These figures demonstrate clearly that as the fish becomes fatter the specific gravity of the fish substance diminishes and the necessary air-bladder volume becomes smaller and smaller. Thus, in a fish of 22 per cent fat (which is not uncommon in herring and salmon) the fish would be in equilibrium with sea water (specific gravity = 1.026), with scarcely more than a third (160 cc.) as much air-bladder volume as would be required for a fish free from fat. At 29.34 per cent fat the fish would be in equilibrium with sea water without an air bladder. Thus, fat can take the place of the air bladder and make the latter unnecessary.

We saw above that a fish must find some means of increasing its displacement if it is to migrate from salt water to fresh water and not sink. With the several increments of fat the fish would be in equilibrium with water of the specific gravities shown below without any change of air bladder volume of 453 cc. per 10 kg. body weight.

Per cent of fat.	Specific gravity of water.	Per cent of fat.	Specific gravity of water.
0	1.0260	14	1.0097
2	1.0239	16	1.0084
4	1.0217	18	1.0062
6	1.0193	20	1.0040
8	1.0171	22	1.0025
10	1.0158	25.3	1.0000
12	1.0127		

It appears from these figures that a fish living at sea and accumulating fat would find itself more at home physically in fresher water without the necessity of enlarging the air bladder. May this not be the influence which directs salmon and shad from salt water to the mouths of rivers? Indeed, it seems unavoidable to conclude that such difficulties in navigation as are introduced by 20 per cent and more of fat must have a profound influence on the movements of the fish. The changes that take place in composition of salmon have been extensively studied. The fluctuations of body composition of the salmon at different stages of the life cycle were studied by Miescher-Ruesch (1880), Paton (1898), Greene (1914, 1919), and those of the herring by Hjort (1914).

Briefly, the career of the Atlantic salmon at sea is as follows: Two or two and one-half years getting its growth, developing muscle and bony tissue (a period obviously of high body specific gravity), then in the third year the accumulation of much fat, whereupon the fish moves to fresh water in the fourth year, when the spawning migration is performed. The large accumulation of fat is consumed in the development of the reproductive organs and in supporting the fish during the journey in fresh water when no food is taken. We do not know so much of the shad as we do of the salmon, but what information we have agrees in a general way with the above.

Apparently, therefore, the fish can not well go into fresh water before a sufficient quantity of fat has been accumulated, because of difficulties in keeping afloat. After the fish has accumulated the fat there would seem to be a strong influence directing it to fresh water.

There is another possible means of overcoming the excessive buoyancy of fat in sea water. That is, the fish may descend until the pressure of the water, by reducing the volume of the air bladder, reduces the displacement of the fish to the necessary extent. This reduction of displacement, with increase in specific gravity, must always occur, in any event, when a fish containing an unprotected air bladder descends. The deeper the fish goes into the water the more easily it descends, the excess weight of the fish becoming greater and greater. If the fish begins to rise, the excess weight over displacement, which must be overcome by muscular exertion, becomes less. The effect to be realized from this cause depends, however, on the volume of air bladder present when the fish is at the surface, for, obviously, when, say, 500 cc. of gas is compressed to 250 cc., a greater difference in specific gravity will result than when 100 cc. of gas is compressed to 50 cc., though the same amount of pressure would be required in either case. Therefore, in a fish whose air bladder had been reduced (if such reduction really occurs) in response to accumulating fat, the effect on specific gravity of diving would be correspondingly reduced.

In the following table there is shown for the several percentages of fat the corresponding depth to which a fish must descend in fresh and salt water, respectively, so that the pressure of the water would equalize the displacement by compressing the air bladder. There is also given the excess weight in grams over the displacement which the body of a 10 kg. fish would acquire by diving 10 m. in water whose density is 1.026 if the fish is in equilibrium at the surface.

Per cent fat.	Depth for equilibrium, fresh water.	Depth for equilibrium, sea water, specific gravity=1.026.	Load in excess of displacement, 10 meters depth.	Per cent fat.	Depth for equilibrium, fresh water.	Depth for equilibrium, sea water, specific gravity=1.026.	Load in excess of displacement, 10 meters depth.
	Cm.	*Cm.*	*G.*		*Cm.*	*Cm.*	*G.*
0	....	....	253	12	486	474	158
2	50	49	....	14	644	628	....
4	105	102	211	16	831	810	130
6	182	177	....	18	1,094	1,066	....
8	266	259	186	20	1,582	1,542	96
10	368	358	....	22	1,881	1,833	....

The air bladder is present in the great majority of fishes. In the Selachii it is absent, in the teleosts it is generally present, although the Heterosomata or flatfishes, Xiphias, the swordfish, Menticirrhus, all the Alepocephalidæ, and a few other families or genera are without air bladders. In all the spiny-rayed fishes (which are typically marine) the air bladder when present has no outlet duct in the adult fish. Any reduction in volume of the air bladder must therefore be accompanied, at least temporarily, by pressure. The pressure might be relieved by absorption of gas into the blood. It does not seem at all unlikely that the varying salinities of ocean water guide such fishes as the mackerel, tuna, herring, bluefish, sharks, and many others. Temperatures, oxygen and CO_2 content, plankton, and other food supply have been studied as directing influences, but it is difficult in every case to show what the immediate effect of the influence is on the fish. In the case of specific gravity the direct effect is obvious and unavoidable.

It would be exceedingly unsafe to make assumption as to what method the fish uses to maintain itself in equilibrium with the water. We know from the work of Tower (1902) and others that the composition of the gas in the air bladder of fishes varies. It contains more and more oxygen with increasing depths, so that fishes taken from great depths have nearly pure oxygen in the air bladder. It was shown that the air bladder very probably performs an important respiratory function. Certainly the loading into the blood stream or the removing therefrom of large quantities of gas could not possibly fail to have a profound effect on the physiological functions of the fish even if fatal embolisms did not occur.

The following conclusions are drawn:

1. Fish on migrating from water of low salinity to that of high salinity may adjust specific gravity by reducing the size of air bladder. In the reverse direction there is no apparent means for voluntary adjustment.

2. As a fish puts on fat its body specific gravity diminishes, *pari passu*, and in proportion to the amount of fat present (*a*) its navigation in salt water is more difficult; (*b*) fresher water is better suited as a physical medium. Until a certain amount of fat is accumulated migration from salt to fresh water must be difficult or impossible.

3. Reduction of volume of air bladder may possibly be effected by (*a*) resorption of gas from bladder to blood and expulsion through gills; (*b*) direct expulsion of gas through pneumatic duct (except in Acanthopteri); (*c*) diving, whereby hydrostatic pressure reduces the volume. The effect produced by diving a given depth is proportional to the absolute volume of the air bladder.

4. Diminishing specific gravity consequent upon increasing fatness probably constitutes a strong directive influence governing the movements of fishes, both marine and anadromous.

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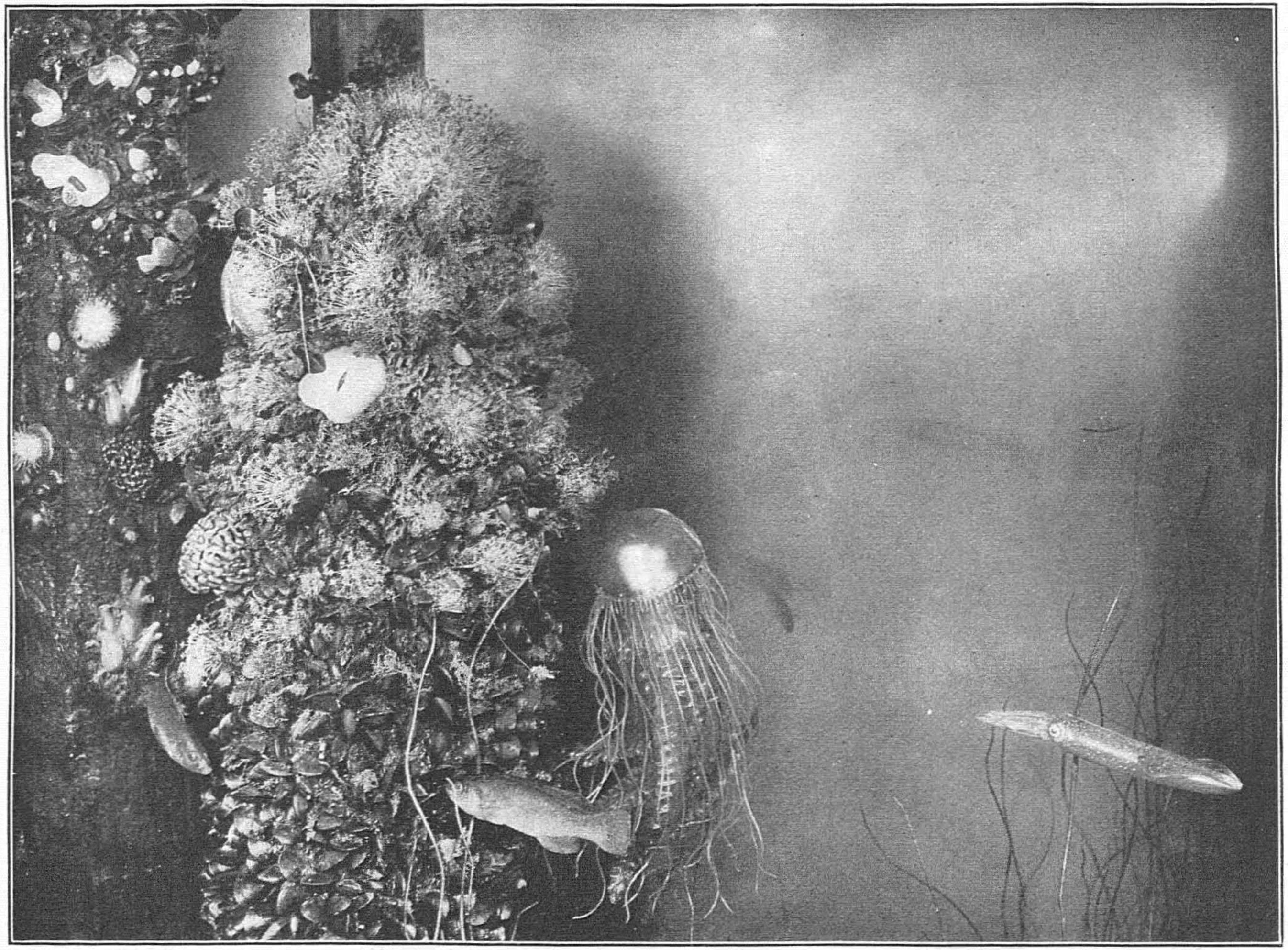

FIG. 99.—Sea mussels growing on a wharf pile at Vineyard Haven, Marthas Vineyard, Mass. Closely associated with the shellfish are hydroids, sea anemonies, sea pork, and sea squirts. Two small fish, cunners, are in the act of browsing on the shellfish. A jellyfish and squid are shown to the right of the colony. (Photograph of a model on exhibit at the American Museum of Natural History, New York. Photograph by courtesy of the American Museum of Natural History.)

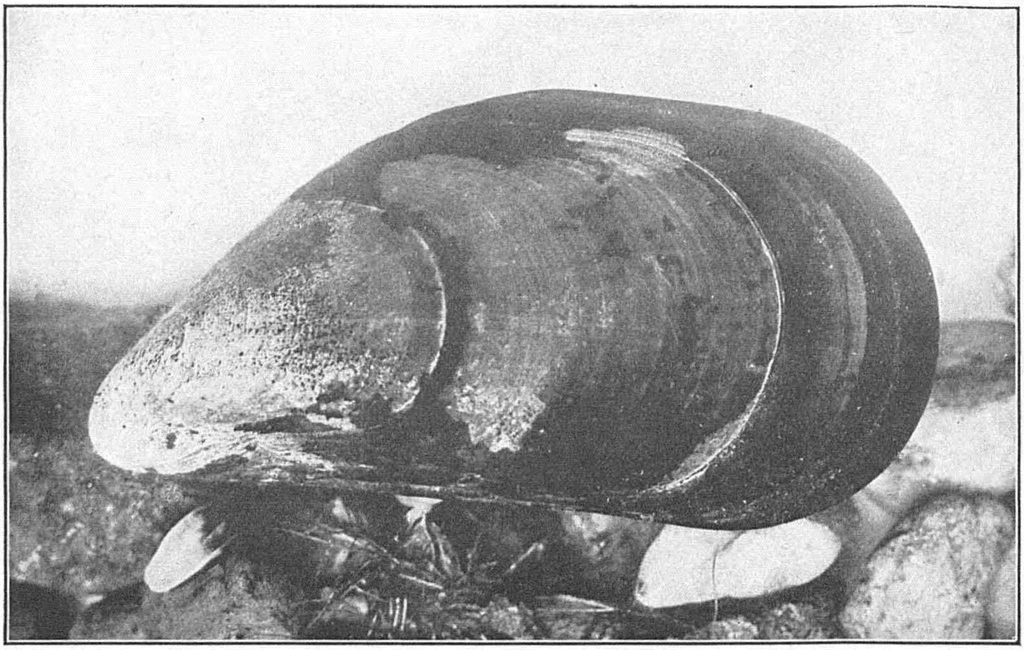

FIG. 100.—The sea mussel *Mytilus edulis* Linnaeus, showing foot distended and attachment by byssus.

FIG. 101.—A bed of sea mussels in Menemsha Pond, Marthas Vineyard, Mass., exposed at low tide. Each square yard of surface is covered with more than a bushel of the shellfish.