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SENSITIVITY TO PRESSURE CHANGES IN TELEOSTS LACKING SWIM-BLADDERS

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QUTOB (1962) has recently confirmed the view (Koshtojanz & Vassilenko, 1937) that sensitivity to changes in hydrostatic pressure is one of the functions of the swim-bladder. It may therefore be of interest that we have observed clear evidence of sensitivity to such changes in certain larval teleosts which lack swim-bladders. These observations comprise some on larvae of *Pleuronectes platessa* L. carried out at Port Erin, Isle of Man, by one of us (A.L.R.) and some on larvae of *Centronotus gunnellus* (L.) studied at Menai Bridge, Anglesey, by the others (S.Z.Q. & E.W.K.J.).

These species are believed to lack swim-bladders at all stages of their development. Kyle (1913) and Ehrenbaum (1905) have described the larvae. We confirmed the absence of swim-bladders from the larvae we studied by careful examination under dissecting microscopes. The tissues were transparent and swim-bladders or indeed gas vesicles of extremely small size would have been easily visible if any had been present. Furthermore we subjected the larvae to pressures as low as 700 mb. below atmospheric. The larvae remained normally orientated and negatively buoyant under these conditions, whereas those of *Blennius pholis*, when similarly but less drastically treated, behaved very differently. At reduced pressure, the *Blennius* larvae evidently suffered over-expansion of the swim-bladders which they possess at that stage, tended to float up out of control and swam head downwards in a very agitated manner.

The youngest *Pleuronectes* larvae tested for pressure sensitivity were at stage 2 according to the definition of Shelbourne (1957), i.e. the yolk sac was resorbed but the notochord was still straight. Other larvae tested were at early stage 3, with the notochord bent but the eyes still placed symmetrically and the total lengths ranging from 7.25 mm. to 9.25 mm. with a mean of 8.3 mm.; late stage 3, with similar characters but lengths ranging from 9.0 mm. to 11. 75 mm. with a mean of 10.5 mm.; stage 4, with the left eye started to move but not reached edge of head ; and stage 5, with the left eye on or over the edge of the head. In testing for pressure sensitivity, batches of the larvae were placed in a tall perspex tank 60 cm. deep and 2.5 cm. square in cross-section (Rice, 1961). They were subjected to alternate periods of high and low pressure by raising and lowering one end of a flexible tube, connected to the vessel and filled for part of its length with mercury. Four experiments were carried out, using larvae ranging from stage 2 to stage 4 inclusive. The lighting was from overhead and produced an intensity of about 400 lux at the top of the tank. Water temperatures lay between 11° and 13°. At a pressure of two atmospheres the larvae swam upwards strongly and collected in the upper half of the tank. When the pressure was reduced to one atmosphere they swam less strongly and tended to sink. To illustrate this behaviour, the numbers swimming above half-depth were recorded every

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minute. The results of four experiments are shown in Table 1. The increases in numbers of larvae above half-depth at the higher pressures were significant in each experiment, with P < 1.0%.

TABLE 1

Larvae of *Pleuronectes platessa* in a tall vessel were subjected to pressures of one and two atmospheres alternately, the pressure being changed generally at intervals of 5 min. The numbers swimming above half-depth (30 cm.) recorded at intervals of 1 min. are given below with arrows to indicate the sequence of pressure changes and observations. Total numbers in each batch a, b, c and d, were :—

	(a) seven stage 2 larvae		(b) eleven early stage 3 larvae		(c) twelve late stage 3 larvae		(d) ten stage 4 larvae	
	1 *At.*	2 *Ats.*	1 *At.*	2 *Ats.*	1 *At.*	2 *Ats.*	1 *At.*	2 *Ats.*
					5		5	
					5	9	5	
					5	11	5	
					4	11	5	
					4	10	5	
					4	9	5	
		6	9					
	6	6	9	11	4			
	5	6	9	11	3			4
	3	6	9	11	3			6
	3	6	9	11	3			8
	3	6	9	11	4			7
	4	3	8	9	2			4
	4	4	6	9	3			7
	4	5	7	10	3			8
	4	5	7	11	3	7		8
	4	5	8	11	4	7		7
means	3.9	5.4	8.18	10.5	3.68	7.53	3.5	6.6

On the other hand stage 5 larvae, which had adopted the benthic habits of the adult fish, remained close to the bottom of the tank for most of the time and showed no tendency to move upwards at increased pressures.

Recently hatched larvae of *Centronotus gunnellus* were observed in thick-walled, conical glass flasks. Their usual habit was to swim slowly and more or less vertically, head upwards. They were denser than seawater, but their swimming just counteracted their tendency to sink. Batches of larvae, totalling 25, were given routine pressure changes which were initially very small, corresponding to 5 or 10 cm. of seawater, by carefully manipulating a compressed air supply, connected to the top of the flask. These had no appreciable effect (Table 2), but somewhat larger changes of pressure had a significant effect (P <: 2 % at changes equivalent to 25 cm. of seawater). When the pressure was increased the larvae swam somewhat more strongly, generally upwards. When it was decreased they became less active and allowed themselves to sink. The response to decreased pressure was particularly striking. The larvae which had previously swum into the upper half of the flask sank down again quite quickly. Swimming upward in response to an increase in pressure was a more gradual process. Evidently the principal mechanism in depth regulation is the general constancy in swimming speed and although this may readily be slowed or stopped through linkage to the pressure-sensitive system, it can be increased only within economical limits.

TABLE 2

When 25 larvae of *Centronotus gunnellus* were subjected to gradually increasing changes in pressure, imposed at intervals of a minute, the numbers swimming above half-depth (5 cm.), recorded at 15 second intervals, were as follows. Time in minutes is recorded in brackets.

	At. p.-k-					*-?*At. + 5 cm. water*					*At.p.<r*					*->At. + 10 cm. water*			
sees. (mins.)	15	30	45	60		15	30	45	60		15	30	45	60		15	30	45	60
(1)	11	14	11	12	(2)	9	10	11	9	MID	9			9	(12)	10	13	10	9
(3)	10	10	13	7	(4)	11	13	10	10	(13)	8			8	(14)	9	10	12	12
(5)	11	11	6	8	(6)	8	11	10	12	(15)	10			9	(16)	8	7	7	7
(7)	9	9	7		(8)	13	11	11	13	(17)	6			7	(18)	9	8	7	9
(9)	12	11	9	12	(10)	11	9	10	11	(19)	9	9	11	11	(20)	**7**	**12**	**8**	**7-**
means	11	11				10	11	10	11							9	10		

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	At. />.<-					*-^•At. + 25 cm. water*					*At.p.^r*					*->At. + 50 cm. water*			
(21)	6	5	6	8	(22)	12	13	11	11	>(31)	8	6	8	8	(32)	15	13	15	11
(23)	11	7	8	9	(24)	10	10	13	11	(33)	10	8	11	9	(34)	12	13	12	13
(25)	9	11	9	10	(26)	10	11	10	10	(35)	8	6	5	5	(36)	8	8	11	10
(27)	9	9	9	9	(28)	10	8	11	8	(37)	9			5	(38)	6	9	10	10
(29)	8	9	11	8	(30)	11	10	8	7-	(39)	5			4	(40)	7	7	7	9-
means		8	9			11	10	11	9							10	9	11	10

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	At.p.<r					*->At. + 1 M.*					*At.p.<r*					*->At. +6M*			
(41)	9	6	10	10	(42)	9	13	11	13	>(51)	6	6	6	6	(52)	16	16	18	20
(43)	9	8	9	7	(44)	10	13	14	15	(53)	10	8	6	6	(54)	14	16	16	15
(45)	8	5		5	(46)	10	.9 .	11 .	11	(55)	8	7	6	7	(56)	13	15	16	16
(47)	8	10			**(48)**	**10**	**12**	**14**	**13**	(57)	8	6	6	6	(58)	10	11	14	14
(49)	8	7			(50)		11	11	13.	(59)	6	4	6	7	(60)	14	15	16	17
means	8	7	7	7		9	12	12	13							13	15	16	16

The *Centronotus* larvae were not so obviously sensitive to small changes as were larvae of *Blennius pholis*, which possessed swim-bladders. When those were given a similar routine of pressure changes (Table 3), they gave significant responses to changes equivalent to 5 and 10 cm. of seawater, P being < 2.5% and <: 0.1% respectively. Their behaviour thus displayed a sensitivity similar to that recorded for other teleosts with swim-bladders (Harden-Jones and Marshall, 1953). They differed from *Centronotus* larvae in that they re-orientated themselves and swam actively downwards after decreases in pressure. It might be expected, of course, that such larvae, which must try to maintain buoyancy equilibrium with a basically unstable system of control, would respond very readily to small fluctuations in pressure. That *Centronotus* larvae do not respond so readily does not necessarily mean that they cannot perceive such small fluctuations, which would have less significance for them.

The method of perceiving such changes in the absence of a gas organ is far from clear, but the ability to do so is widespread amongst invertebrates (Hardy & Bainbridge, 1951 ; Knight-Jones & Qasim, 1955 ; Baylor & Smith, 1957 ; Rice, 1961).

Digby (1961) and Enright (1962) have recently discussed mechanisms which may be involved.

TABLE 3

When 25 larvae of *Blennius pholis* were subjected to gradually increasing changes in pressure, imposed at intervals of a minute, the numbers swimming above half-depth (5 cm), recorded at 15 second intervals, were as follows. Time in minutes is recorded in brackets.

Atmospheric p.<——>*At. + 5 cm. water*										*Atmospheric p.<r*					•*At. + 10 cm.*				
sees. (mins.)	15	30	45	60		15	30	45	60		15	30	45	60		15	30	45	60
(1)	0	1	0	0	(2)	0	3	2	0	Mil)	1	1	1	2	(12)	4	8	5	3
(3)	0	1	1	2	(4)	2	3	2	1	(13)	2	1	2	2	(14)	2	5	4	3
(5)	1	0	2	2	(6)	3	3	2	2	(15)	1	1	0	0	(16)	2	4	4	3
(7)	1	0	2	1	(8)	1	2	2	1	(17)	1	1	2	4	(18)	4	8	6	4
(9)	1	3	5	2	(10)	2	5	3	1-	(19)	1	2	2	2	(20)	6	6	4	3-^
means	0.6	1	2	1.4		1.6	3.2	2.2	1		1.2	1.2	1.6	2.4		3.6	6.2	4.6	3.2
•y *Atmospheric p.* <-——> *At. + 25 cm.*										*Atmospheric p.* <——>*At. + 50 cm*									
(21)	2	1	3	2	(22)	8	14	8	7	•>(31)	0	1	1	0	(32)	11	13	10	9
(23)	1	1	1	1	(24)	3	5	5	5	(33)	2	1	0	0	(34)	7	9	7	7
(25)	2	2	2	2	(26)	3	6	5	3	(35)	3	0	0	0	(36)	7	8	5	6
(27)	1	2	2	2	(28)	6	10	7	6	(37)	2	0	0	1	(38)	8	7	3	5
(29)	1	0	1	1	(30)	3	4	2	3--	(39)	1	1	0	0	(40)	8	11	6	8->
means	1.4	1.2	1.8	1.6		4.6	7.8	5.4	4.8		1.6	0.6	0.2	0.2		8.2	9.6	6.2	7
y *Atmospheric p.* <-——>*At. + 1 M.*										*Atmospheric p.* <- >*At. + 6M.*									
(41)	0	0	1	0	(42)	11	19	17	15	•>(51)	1	0	1	1	(52)	18	24	23	21
(43)	5	2	0	0	(44)	11	11	11	12	(52)	7	2	0	0	(54)	13	21	21	17
(45)	3	0	1	0	(46)	10	14	11	6	(55)	8	2	0	0	(56)	10	17	16	18
(47)	1	0	1	2	(48)	' 8	12	11	11	(57)	6	2	1	0	(58)	13	16	19	15
(49)	1	0	0	0	(50)	12	14	9	10-'	(59)	5	4	1	0	(60)	11	17	12	11
means	2	0.4	0.6	0.4		10	14	12	11		5.4	2	0.6	0.2		13	19	18	16

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