Gills and kidneys in ureosmotic regulation in euryhaline skates

PATRICK PAYAN, LEON GOLDSTEIN, AND ROY P. FORSTER

Gills and kidneys in ureosmotic regulation in euryhaline skates. Am. J. Physiol. 224(2): 367-372. 1973.—The purpose of this study was to determine the simultaneous rates of branchial and renal urea excretion in skates (Raja erinacea and R. radiata) gradually adapted to seawater or half-diluted seawater or acutely transferred to 75% seawater. Branchial excretion did not change significantly following acute transfer to 75% seawater. In skates gradually adapted to 50% seawater, branchial urea excretion decreased from 57 μmoles/100 g × hr to 20, in direct relation to the reduction in plasma urea concentrations from 589 μmol to 227. Hence, there appears to be no change in the permeability of gill glands to urea during adaptation. Both during acute transfer to 75% seawater and in skates gradually adapted to 50% seawater, urea fluxes and renal urea clearances increased as much as 10-fold. Branchial water effluxes measured with HTO were approximately the same in both intact and hypophysectomized skates adapted either to seawater or to 50% seawater. Thus, in gills of these species, contrary to certain other elasmobranchs, there is no change in either diffusional water permeability or in urea permeability during adaptation to environmental dilution.

Methods

The two species of skates studied (Raja erinacea and Raja radiata) were caught in Frenchman's Bay, Maine. These fish (male and female), ranging between 400 and 1,300 g, were kept in a common aquarium in running seawater where the average temperature was 13 ± 1°C. The fish were fed during the entire period of experimentation. Fish were

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adapted to the diluted seawater in the common aquarium, following the same program as that used and described by Goldstein and Forster (4) (dilution of 100% seawater to 50% in 5 days).

**Branchial excretion of urea.** The branchial effluces of urea were measured with the aid of an isotopic technique (urea-14C) in fish that had had their urinary pore catheterized the preceding day (those adapted to 100% seawater and those submitted to acute environmental dilution) or their cloaca catheterized (skates gradually adapted to the half-diluted seawater). Two hours after the intravenous injection of radioactive urea (10 μc/kg) into the caudal vein, the fish was placed in an aerated aquarium containing a known volume of external medium (3-4 liters according to the weight of the fish). The aquarium was surrounded by running seawater to maintain a constant bath temperature (13 ± 1 C). For the acute transfer experiments, after a control period of 4-6 hr in 100% seawater, the fish was quickly immersed in 75% seawater for 4 hr. External bath samples of 1 ml were removed every hour. Three blood samples were taken at the start, at the time of transfer, and at the end of the experiment. These were drawn into heparinized syringes by caudal puncture or with the aid of a PE-10 catheter (inserted the previous day in the caudal artery).

In the fish adapted to the half-diluted seawater, urea effluces were followed over a period of 4 hr by removing 1-ml samples of external medium every hour. At the end of the experiment, blood was drawn by puncture of the caudal artery. The radioactivity of these samples of the external medium as well as that of the plasma was analyzed by addition of scintillation fluid (Aquasol, New England Nuclear) and counting in a liquid scintillation counter (Nuclear-Chicago). The radioactivities of these different samples were corrected for quenching, using an external standard. The concentration of plasma urea was determined by the Archibald method as previously described (5).

The branchial efflux of urea (expressed in μmoles/100 g X hr) is equal to the ratio of the radioactivity in the external medium (in counts/min divided by the average specific radioactivity in the plasma in counts per minute (counts/min) per μ mole expressed per 100 g body wt X hr.

The branchial clearance of urea (C, urea μl/100 g X hr) was calculated by dividing the branchial efflux (in μmoles/100 g X hr) by plasma concentration of urea (in μmoles/μl). The coefficient of branchial permeability of urea by diffusion, P, urea (in cm/sec), is equal to P, urea = f, /AC, where f, stands for the efflux of urea (in μmoles/100 g X sec), A for the branchial surface (in cm²/100 g), and C for the plasma concentration of the urea (in μmoles/ml). Thus, the following equation is obtained:

\[
P_{\text{urea}} = \frac{10^{8}}{3,600} \times \frac{1}{A} \times C_{b, \text{urea}}
\]

**Renal excretion of urea.** These experiments were carried out on skates in which the cloaca was catheterized the day prior to the experiment with the aid of a large catheter attached to a collection balloon. It is possible, therefore, that the liquid collected was slightly contaminated by the intestinal and rectal fluid. It is likely, however, that the fluid collected was mainly urine. Concerning contamination by the intestine, it is generally believed that the elasmobranchs do not drink at all or very little (8, 14). In addition, we never noted the presence of feces in our collected specimens. On the contrary, it is quite likely that our specimens contained rectal fluid. To our knowledge, no study has been carried out on the rectal secretion in the skates, which have a rectal gland notably smaller than those of sharks. In the latter, the rectal fluid contains very little urea (2) In addition, our results were similar to those obtained by Goldstein and Forster (4) in the skates in which the urinary pore was catheterized. It is concluded, therefore, that the excretion of urea thus measured was essentially of renal origin.

During acute transfer experiments, there were two urine collection periods: the first 4 hr before the transfer and the second 3 or 4 hr after transfer. A blood sample was taken at the beginning and at the end of the experiment by caudal puncture. In the skates adapted to 50% seawater, we collected urine for 4 hr; then the blood was withdrawn by caudal puncture. The urine flow (expressed in μl/100 g X hr) was determined volumetrically.

**Diffusional flow of water.** Tritiated water (HTO), 12 μc/kg, was injected intramuscularly about 30 min before the beginning of the experiment to allow the isotope to be distributed uniformly in the water space of the fish. The fish was then placed in an aquarium containing a known volume of aerated external medium (1-2 liters, according to the weight of the fish). The aquarium was immersed in running water which acted as a refrigerator to maintain the temperature of the experimental bath constant (13 ± 1 C). Bath samples of 1 ml were withdrawn every 15 min for 2 hr, then at the end of 4 hr to determine the value of the external radioactivity at equilibrium. After the addition of scintillation fluid (Aquasol, New England Nuclear) to the samples, they were counted in a liquid scintillation counter (Nuclear-Chicago). Graphical analyses of the curves obtained for the appearance of the radioactivity in the external medium (in counts/min per ml), as a function of the time in hours, permitted calculation of the value of the rate of renewal of the external water of the fish (in % hr⁻¹) (9). We have measured the hourly rate of turnover of water in the normal and hypophysectomized fish adapted to two different salinities: seawater and half-diluted seawater.

Hypophysectomy was carried out on skates that had been slightly anesthetized (5 min in seawater containing 3 g/L MS 222). Using a cork borer, a hole was cut in the roof of the buccal cavity at the level of the hypophysis which was then aspirated. Experiments were conducted 21 days or more after ablation of the hypophysis. The hypophysectomy was confirmed by dissection at the end of the experiment.
UREOSMOTIC REGULATION IN SKATES

cm/sec) was calculated by the relation:

$$P_{os} = \frac{F_{net}}{A \times \Delta C}$$

where \( F_{net} \) (in mmoles/sec) is the net osmotic flow across the gills, \( A \) is the gill area (in cm²/100 g), and \( \Delta C \) (in mOsm/kg) is the osmotic gradient between internal and external media.

RESULTS

Table 1 shows the variations of plasma urea concentrations and osmotic pressures during experimental dilution of the external medium. The urea concentration of plasma increased significantly 4 hr after acute transfer into 75% seawater. In the fish that had been gradually adapted to 50% seawater, a diminution of 42% was observed when compared to the controls in 100% seawater. Plasma osmotic pressure decreased by 32% in the fish adapted to 50% seawater. Initially the osmotic gradient in 100% seawater was 7 mOsm/kg; immediately after the transfer it increased to 226, and 4 hr after the transfer it was reduced to 177. It is interesting to note that the skates fully adapted to 50% seawater maintained an osmotic gradient between their external and internal media, which was steeper than that prevailing in skates adapted to 100% seawater (135 against 7 mOsm/kg).

Branchial urea efflux in skates studied under different experimental conditions is shown in Table 2. Following acute transfer (100–75% seawater), urea chemical gradient decreased from 389 to 371 mM and branchial efflux increased slightly, but not significantly \((P < 0.1\) by paired-data analyses; mean difference \(\pm\) SEM = +14 ± 7.0 for six fish). Figure 1 shows a typical experiment illustrating that urea efflux by the gills does not change during the 4 hr after acute transfer. However, in skates adapted to 50% seawater, branchial excretion diminished by two-thirds compared to controls in 100% seawater (Table 2); the urea efflux decreased from 57.0 to 19.8 μmoles/hr. This decrease in branchial urea excretion paralleled the reduction in chemical gradient of urea across the gills (389 vs. 227 mM). Goldstein and Forster (4), using the same species, found a branchial excretion on the order of 23 μmoles/100 g X hr for skates in 100% seawater. This difference may be due to the fact that our fish were fed, whereas those in the experiments by Goldstein and Forster were not. By way of comparison, it may be noted that Payan and Maetz (8) found in Scyliorhinus canicula a branchial efflux of 21.4 ± 4.08 (n = 4) μmoles/100 g X hr (experiments carried out at 16°C), and Boylan (1) found the branchial excretion of urea in Squalus acanthias (common spiny dogfish) to be about 23 μmoles/100 g X hr at 16°C. In the present study the branchial clearances of urea (\(C_{b,area}\)) for skates adapted to

### Table 1. Effect of environmental dilution on plasma urea levels and osmotic pressure in skate, R. erinacea

<table>
<thead>
<tr>
<th>Seawater</th>
<th>Plasma Urea concn, mM</th>
<th>External Medium Osmotic pressure, mOsm/kg</th>
<th>Δ(Internal – External) mOsm/kg</th>
</tr>
</thead>
<tbody>
<tr>
<td>100%</td>
<td>389 ± 2.4 (4)</td>
<td>932 ± 11.0 (4)</td>
<td>7.0 ± 4.8 (4)</td>
</tr>
<tr>
<td>75%</td>
<td>371 ± 4.3 (4)</td>
<td>883 ± 13.4 (4)</td>
<td>706 ± 2.0 (4)</td>
</tr>
<tr>
<td></td>
<td>* P value* &lt;0.01</td>
<td></td>
<td>177 ± 12.6 (4)</td>
</tr>
<tr>
<td>50%</td>
<td>227 ± 26.3 (5)</td>
<td>632 ± 12.6 (5)</td>
<td>135 ± 2.62 (5)</td>
</tr>
<tr>
<td></td>
<td>* P value† &lt;0.001</td>
<td></td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Values are means ± SE. Numbers of animals per group are shown in parentheses. Animals in 100 and 50% seawater were fully adapted. Animals in 75% seawater were studied during the first 4 hr after transfer. * Group in 75% seawater compared to group in 100% seawater. † Group in 50% seawater compared to group in 100% seawater.

### Table 2. Effect of environmental dilution on renal and branchial urea excretion in skate, R. erinacea

<table>
<thead>
<tr>
<th>Seawater</th>
<th>Kidneys, μmoles/100 g X hr</th>
<th>Gills, μmoles/100 g X hr</th>
</tr>
</thead>
<tbody>
<tr>
<td>100%</td>
<td>2.2 ± 0.54 (4)</td>
<td>57.0 ± 9.64 (6)</td>
</tr>
<tr>
<td>75%</td>
<td>11.3 ± 1.17 (4)</td>
<td>71.1 ± 19.41 (6)</td>
</tr>
<tr>
<td></td>
<td>* P value* &lt;0.001</td>
<td>&lt;0.3 NS</td>
</tr>
<tr>
<td>50%</td>
<td>23.4 ± 5.81 (5)</td>
<td>19.8 ± 3.99 (5)</td>
</tr>
<tr>
<td></td>
<td>* P value† &lt;0.02</td>
<td>&lt;0.02</td>
</tr>
</tbody>
</table>

Values are means ± SE. Numbers of fish per group are shown in parentheses. NS: not significant \((P > .05)\). * Group in 75% seawater compared to group in 100% seawater. † Group in 50% seawater compared to group in 100% seawater.
100 and 50% seawater were, respectively, 142 ± 22.1 (n = 6) and 94 ± 34.7 (n = 5) μl/100 g X hr. The difference in these two values is not statistically significant due to the large spontaneous variation among individual skates.

Transfer from 100 to 75% seawater brought about an immediate increase of urine flow from 29.1 to 168.5 μl/100 g X hr (Table 3). In the skates adapted to 50% seawater, the urinary output was increased ninelfold. The following urinary concentrations of urea were found in fish adapted to 100% seawater, to 50%, and in those having undergone acute transfer for 4 hr in 75% seawater, respectively: 77 ± 19.4 (n = 4), 85 ± 20.7 (n = 5), and 82 ± 14.6 (n = 4) mm. The renal excretion of urea was significantly increased during the 4 hr after the transfer into 75% seawater. Figure 1 illustrates a typical experiment in which urea excretion by the kidney increased from 2 to 9 μmoles/100 g X hr, whereas efflux via the gill was similar in the two media. In skates adapted to half-diluted seawater, the renal excretion of urea increased 10-fold (Table 2). Renal clearance of urea increased fivefold 4 hr following transfer into 75% seawater. The average diffusional water fluxes for skates in 100 and 50% seawater were 52.6 and 52.3 ml/100 g X hr, respectively. The average diffusional water fluxes for skates in 100 and 50% seawater were 52.6 and 52.3 ml/100 g X hr, respectively. Table 4 also shows the results obtained in the hypophysectomized skates. Hypophysectomy had no significant effect on the rate of turnover of internal water across the gills of skates adapted to the two different salinities. In these calculations the water space was considered to be unaltered after hypophysectomy.

### DISCUSSION

The results obtained in this study concerning the adaptation of *R. erinacea* to dilute external media confirm previous observations by Goldstein and Forster (4). In this species, dilution of the external medium produces a decrease of the internal osmolarity due primarily to reduction of the internal urea concentration. This diminution may be achieved either by an increase of branchial and renal urea elimination, by decreased endogenous production of urea, or both. The present study dealt mainly with the role of the gills in urea elimination.

During gradual (5 days) adaptation to 50% seawater, plasma urea concentrations fell from an average of 389 to

### TABLE 3. Effect of environmental dilution on renal function in skate, *R. erinacea*

<table>
<thead>
<tr>
<th>Seawater</th>
<th>$V_i$ μl/100 g X hr</th>
<th>GFR μl/100 g X hr</th>
<th>Renal Clearance of Urea μl/100 g X hr</th>
<th>Excreted Filtered %</th>
</tr>
</thead>
<tbody>
<tr>
<td>100%</td>
<td>29.1 ± 2.46</td>
<td>62 ± 18</td>
<td>5.6 ± 1.44</td>
<td>6 ± 2</td>
</tr>
<tr>
<td>75%</td>
<td>168.5 ± 51.52</td>
<td>(4)</td>
<td>(4)</td>
<td>&lt;0.05</td>
</tr>
<tr>
<td>$P$ value*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50%</td>
<td>274.2 ± 41.06</td>
<td>290 ± 110</td>
<td>108.8 ± 26.99</td>
<td>34 ± 7</td>
</tr>
<tr>
<td>$P$ values†</td>
<td></td>
<td></td>
<td></td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Values are means ± se. Numbers of fish per group are shown in parentheses. $V_i$ = urine flow. * Group in 75% seawater compared to group in 100% seawater. † Group in 50% seawater compared to group in 100% seawater. † Values are taken from Goldstein and Forster (4).

### TABLE 4. Diffusional water fluxes in intact and hypophysectomized skates, *R. erinacea* and *R. radiata*, adapted to different salinities

<table>
<thead>
<tr>
<th></th>
<th>100% Seawater</th>
<th>50% Seawater</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Controls</td>
<td>Hypo</td>
</tr>
<tr>
<td>$\lambda$, %/hr</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(7)</td>
<td>(7)</td>
</tr>
<tr>
<td>$d$, ml/hr X (100 g)$^{-1}$</td>
<td>64.2 ± 1.91</td>
<td>64.1 ± 2.78</td>
</tr>
</tbody>
</table>

Values are means ± se. Numbers of fish per group are in parentheses. $\lambda$ = turnover rate of internal water. $d =$ diffusional water permeability.

**FIG. 2.** Appearance curves of HTO in external bath of *R. erinacea* and *R. radiata* adapted to 100 and 50% seawater. External radio-activity is plotted in percent of equilibrium value ($Q_{eq}$) against time in hours. Bottom graph illustrates method employed to calculate turnover rate of internal water ($\lambda$ in %/hr). Diminution of external salinity did not affect water turnover rate.
227 mm. The theoretical quantity of urea that the organism must eliminate during this period to lower the plasma concentration to 227 mm (taking into account the increase in the urea space from 82 to 91 ml/100 g) is (389 × 82 – 227 × 91)/120 hr = 77 μmoles/100 g × hr. During acute transfer of skates from 100 to 75 % seawater, branchial excretion increased from 57 to 77 μmoles/100 g × hr, and renal excretion was 11 μmoles/100 g × hr, total excretion increasing from 59 to 82 μmoles/100 g × hr. These results suggest that following acute dilution of the external medium total excretion of urea increases only slightly; renal elimination increases significantly, but this is a minor route of excretion. There is no evident increase at the more important branchial site. In skates gradually adapted to 50 % seawater, the branchial efflux of urea was 20 μmoles/100 g × hr and renal excretion was 23 μmoles/100 g × hr. The latter in this case represents 54 % of the total excretion of urea, whereas it was only 4 % in the animals originally adapted to 100 % seawater. In skates adapted to 50 % seawater, the kidney plays an important role as the gills with respect to the elimination of urea. However, total excretion of urea is essentially unchanged during both acute transfer and adaptation of skates to dilute seawater and, therefore, cannot account for reduction in plasma urea concentration during environmental dilution. Thus, as suggested previously by Goldstein and Forster (4), a rapid decrease of the rate of synthesis of urea must play an important role in reducing the internal urea level.

The coefficient of branchial permeability of urea in the skates adapted to the 100 and 50 % seawater was calculated to be 1.0 × 10⁻² and 0.7 × 10⁻² cm/sec, respectively, assuming a branchial surface in the skate similar to that given by Boylan (1) for Squalus acanthias (370 cm²/100 g). Thus, P_urae does not seem to be significantly diminished by dilution of the external medium. This suggests that decreasing the chemical gradient of urea between the external and internal media leads to a reduction in the rate of branchial excretion of urea without a significant modification of the permeability of this membrane to urea. On the other hand, renal clearance of urea is significantly increased in the skates adapted to the diluted seawater (Table 3). These results suggest that branchial urea excretion is a passive mechanism correlated to the chemical gradient existing across the gills. In contrast, the kidney seems to modulate the urea excretion in a much more active manner as a function of the osmoregulatory needs of the organism.

In the marine elasmobranchs the osmotic gradient between the strongly saline environment and the plasma across the branchial membrane is generally very small. It follows that even if the branchial osmotic permeability were large, which is the case in Squalirrhinus canicula (9), the net osmotic flow across the gills would be minimal. In a fish in equilibrium with respect to its water balance, the branchial net osmotic flow across the gills is equal to the difference between the entries of water (drinking) and the losses of water (urinary and rectal outputs). In the elasmobranchs, the rate of drinking may be considered to be negligible (14). The net osmotic flow across the gills is therefore approximately equal to the sum of the renal and rectal outputs, i.e., the cloacal output, which was in fact measured in our experiments. In skates adapted to 100 % seawater, this output was very low (29.1 μl/100 g × hr), an observation which is in accord with the existence of a small osmotic gradient (7 mOsm/kg). By way of comparison the following outputs are listed together with the corresponding osmotic gradient across the gills. For Squalirrhinus canicula the corresponding values are 28.5 μl/100 g × hr and 10 mOsm/kg; for Squalus acanthias they are 50 μl/100 g × hr and 70 mOsm/kg, respectively. The transfer into diluted seawater imposes an increased osmotic gradient across the gills; entry of water dilutes the internal medium following transfer. Titration of blood hemoglobin 4 hr after acute transfer into 75 % seawater confirmed this. As Table 3 indicates, the response of the kidney to the water loading was immediate, urinary output during 4 hr after acute transfer being increased fivefold. Urinary output was also markedly elevated in skates gradually adapted to half-diluted seawater. A ninefold increase in urine flow occurred compared to skates adapted to 100 % seawater, thus confirming previous observations by Goldstein and Forster (4) in the same species. The elevated urinary output was due in part to the large osmotic gradient across the gills (135 ± 2.69 mOsm).

In order to compare the coefficients of osmotic permeability of the gills of skates in the two media, the net osmotic flow (in μmoles/100 g × sec) was related to the osmotic gradient (in mOsm/kg). Unfortunately, the inaccuracy of the determination of the osmotic gradient in the animals adapted to 100 % seawater (7 ± 4.8 mOsm/kg) (n = 4) did not permit this comparison to be made with a great deal of precision. The average coefficient of osmotic permeability in skates adapted to the 50 % seawater, taking 370 cm²/100 g for the branchial surface, was P = 0.84 × 10⁻⁴ cm/sec. This value is significantly lower than that obtained in the European dogfish Squalirrhinus canicula (9), which was found to have an osmotic permeability coefficient of 8.1 × 10⁻⁴ cm/sec.

These values for osmotic permeability of the gills paralleled those for diffusional water permeability. Table 5 shows that the water turnover rate in R. erinacea and R. radiata is lower than in certain other elasmobranchs studied by Payan and Maetz (9). Whereas S. canicula and R. montagui are strictly marine elasmobranchs, R. erinacea, R. radiata, and Torpedo marmorata are forms that adapt readily to a dilute environment. Thus, the gills of strictly marine elasmobranchs seem to have higher diffusional permeability for water than elasmobranchs capable of adapting to dilute seawater, and the differences have a significant bearing on

**Table 5. Diffusional water fluxes in elasmobranchs and teleosts**

<table>
<thead>
<tr>
<th>Elasmobranchs</th>
<th>ω, %·hr⁻¹</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Squalirrhinus canicula</td>
<td>156.6 ± 13.08 (n = 14)</td>
<td>Payan and Maetz (9)</td>
</tr>
<tr>
<td>Raja montagui</td>
<td>167 ± 11.1 (n = 4)</td>
<td>Payan and Maetz (9)</td>
</tr>
<tr>
<td>Torpedo marmorata</td>
<td>97 ± 0.5 (n = 4)</td>
<td>Payan and Maetz (9)</td>
</tr>
<tr>
<td>Raja erinacea and Raja radiata</td>
<td>64.2 ± 1.91 (n = 4)</td>
<td>Present work</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Teleosts</th>
<th>ω, %·hr⁻¹</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carassius auratus FW</td>
<td>51.1 ± 3.9 (n = 10)</td>
<td>Motoi et al. (6)</td>
</tr>
<tr>
<td>Serranopsis scriba SW</td>
<td>23.8 ± 1.2 (n = 10)</td>
<td>Motoi et al. (6)</td>
</tr>
</tbody>
</table>

Values are means ± se. Numbers of fish per group are shown in parentheses. FW = freshwater. SW = seawater. ω = turnover rate of internal water.
the ecology of the fishes. Table 4 indicates that branchial
diffusional water permeability was identical in skates
adapted to full-strength and to 50% seawater. According to
unpublished observations on two other euryhaline elasmo-
branchs, Negaprion brevirostris and Torpedo marmorata, no
effect of different external salinities on branchial diffusional
water permeability was observed. In contrast, in the steno-
haline S. canicula adapted to 85% seawater, the water
permeability was observed. In contrast, in the steno-
haline S. canicula adapted to 85% seawater, the water
turnover rate decreased significantly from 157 to 78%/hr (9).
These results suggest that the hypophysis intervenes to regulate the water permeability of the
gills in the dogfish Scyliorhinus adapted to 100 and 85%
seawater, whereas this kind of hormonal control of branchial
water flux is nonexistent in the skates R. erinacea and R.
radiata.

In skates, R. erinacea and R. radiata adapted to the two
media (100 and 50% seawater), hypophysectomy did not
change the water turnover rate (Table 4). In contrast,
hypophysectomy in Scyliorhinus canicula was previously
found to lower the rate of internal renewal of water from
157 to 89%/hr (9). These results suggest that the hypoph-
ysis intervenes to regulate the water permeability of the
gills in the dogfish Scyliorhinus adapted to 100 and 85%
seawater, whereas this kind of hormonal control of branchial

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