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# CARDIAC RESPONSES TO DABBING AND DIVING IN THE MALLARD, *ANAS PLATYRHYNCHOS*<sup>1</sup>

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Mallards typically dabble for their food in shallow water. However, in the northern climate, shallow ponds freeze in winter, and mallards may be forced to dive for food in deep water. We have mimicked these feeding behaviors by confining mallards to shallow (0.3 m deep) and deep (1.0 m) artificial ponds. Heart rate was monitored from the ducks during these behaviors telemetrically. Dabbles lasted an average of  $3.0 \pm 1.0$  s ( $\pm$ SD), with a maximum of 9 s, and heart rate changed little during head immersion. Dives had a mean duration of  $6.2 \pm 2.1$  s with a maximum of 11.6 s. Heart rate after 2-s submergence was nearly the same, at 250 beats  $\cdot$  min<sup>-1</sup>, regardless of pre-dive heart rate. In other words, if pre-dive heart rate was low ( $<200$  beats  $\cdot$  min<sup>-1</sup>), there was a diving tachycardia; whereas, when pre-dive heart rate was high ( $>300$  beats  $\cdot$  min<sup>-1</sup>), there was a noticeable diving bradycardia. This cardiac response to voluntary diving was nearly eliminated by bilateral section of the vagal baroreceptor nerves. In true diving ducks (*Aythya* sp.), heart rate after 2-s submergence is positively correlated with heart rate in the immediate pre-dive period, and this relation is unaffected by baroreceptor denervation. Obviously, mallards differ markedly from true diving ducks not only in cardiac adjustments to diving but also in their control.

## INTRODUCTION

Ducks are commonly divided into two groups, divers and dabblers, but probably all dabbling ducks dive when they are very young, and even adult dabbling ducks dive for food far more frequently than is generally acknowledged. Foraging dives by mallards (*Anas platyrhynchos*), black ducks (*A. rubripes*), African black ducks (*A. sparsa*), pintails (*A. acuta*), Bahama pintails (*A. bahamensis*), shovelers (*Spatula clypeata*), New Zealand brown ducks (*A. auklandica chlorotis*), gadwalls (*A. strepera*), cape teal (*A. capensis*), gray teal (*A. gibberifrons*), wood ducks (*Aix sponsa*), and mandarin ducks (*A. galeculata*) have been observed (Kutz 1940; Dean 1950; Mylne 1954; Chapman, King, and Webb 1959; Kear and Johnsgard 1968; Bourget and Chapdelaine 1982). Dives may be made to

depths greater than 3 m (Kutz 1940). Mean dive times are approximately 5 s (Dean 1950; Bourget and Chapdelaine 1982), with maximum dive times of 10 s (Chapman et al. 1959; Bourget and Chapdelaine 1982). Bourget and Chapdelaine (1982) suggested that dabbling ducks spending the winter in northerly regions may be forced to dive for food because shallow water is more likely to be frozen over during cold spells.

The heart rate response to forcible submergence of a restrained dabbling duck is characterized by a gradual slowing of the heart and an increase in peripheral resistance (Butler and Jones 1982). This response is virtually eliminated by sectioning the carotid body nerve (Jones and Purves 1970), indicating that it is brought on by the progressive hypoxemia and hypercapnia associated with the breath-hold dive. In contrast, in diving ducks such as the red-head (*Aythya americana*), bradycardia develops immediately on submergence and is inhibited by spraying a local anesthetic over the external and internal nares (Furilla and Jones 1986). Hence nasal receptors, which contribute only to apnea in dabbling ducks (Bamford and Jones 1974), have an important cardiovascular influence in diving ducks.

Although ducks can withstand many minutes of forced submergence, in nature

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most voluntary dabbles and dives are extremely short. Dabbles seldom exceed 5-s duration, and dives are usually less than 20 s. Voluntary head submersion by dabbling ducks causes little or no change in heart rate (Furilla and Jones 1986). This is not surprising, given that the periods of submergence are too short to cause sufficient changes in blood gas tensions to stimulate systemic chemoreceptors. On the other hand, heart rate changes would be expected in divers submerging voluntarily as soon as the nasal receptors contact water. While this appears to be the case, close correlation of heart rates broadcast from ducks by telemetry with cine films of diving behavior shows that, some seconds before the dive, both breathing and heart rates increase, and heart rate then falls just before rather than actually on submergence (Butler and Woakes 1979, 1982; Woakes and Butler 1983). The first cardiac interval in voluntary dives is usually the longest, and heart rate then rises to stabilize in the range of 100–200 beats  $\cdot$  min<sup>-1</sup> within 2–5-s submergence (Furilla and Jones 1987). This is very different from the response in forced dives, when heart rate falls to about 20 beats  $\cdot$  min<sup>-1</sup> in a similar time period (Furilla and Jones 1986).

It has been suggested that the pre-dive hyperventilation and tachycardia are correlates of the high aerobic energy demands in voluntary dives in that these maneuvers serve to flush CO<sub>2</sub> from and load O<sub>2</sub> into the blood and pulmonary oxygen stores (Butler 1985). Butler (1985) has suggested that the high heart rates in voluntary dives are the expression of a balance between the cardiovascular responses to forced diving and to exercise in air, with the balance being tipped toward the exercise response. Consequently, what cardiac adjustments to diving would be expected in dabbling ducks that have been trained to make voluntary dives? This study was undertaken to investigate the nature of these cardiac adjustments in the dabbling duck (*A. platyrhynchos*) and the underlying mechanisms bringing about these adjustments.

#### MATERIAL AND METHODS

Two male mallards and one female Pekin duck (*Anas platyrhynchos*) were used to record the cardiac response to voluntary

dabbling. Five mallards (two male and three female) were used in the voluntary diving observations. Heart rate was obtained telemetrically using EKG transmitters (Narco Biosystems, Downsview, Ont.). The transmitter was sterilized with benzalkonium chloride (Zephiran, 1:750, Winthrop Laboratories, Aurora, Ont.). A midline incision was made in the skin and body wall over the abdomen after anesthetizing the area by injection of Xylocaine. Bipolar loop electrodes were placed on the pericardium, and the transmitter was placed in the peritoneal cavity. The peritoneal cavity was then closed with surgical silk. After surgery, 125 mg of Ampicillin (Penbritin, Ayerst Laboratory, Montreal) was administered i.m., and the birds were allowed 1 day to recover before being placed on the pond.

For dabbling, the ducks were placed in a 0.8 (w)  $\times$  2.8 (e)-m fiberglass tank with water 0.3 m deep and a 0.8  $\times$  0.8-m platform at one end. Only those dabbles lasting longer than 3 s were used in data analysis. This was done to ensure that the heart rate was not changing at the 2-s mark as the result of any activity associated with surfacing. The EKG signal was received on a Narco FM-Biotelemetry receiver, stored on magnetic tape, and simultaneously displayed on a pen recorder. On playback, heart rates were obtained either by measuring the cardiac intervals by hand or electronically by using a cardi tachometer.

For diving, the mallards were placed singly in a 0.8 (w)  $\times$  1.8 (e)-m fiberglass tank with water 1.0 m deep and with a 0.8  $\times$  0.4-m platform at one end. Food was scattered on the surface and quickly sank. For the first week, the birds ate only that food that could be reached before it sank. If the bird did not dive after 1 wk, a small amount of food was placed on the platform daily. The amount of food was kept small to maintain the health of the animal while preserving the hunger drive. The duck was removed from the tank if diving had not begun by the end of the second week. The ducks' behavior was recorded on a Canon VR-40 VHS video recorder using a JVC GX-N4 camera. Once diving had begun, an EKG transmitter was implanted, and the signal was placed on one of the audio tracks of the video recorder. The videotape was reviewed at high speed. When a dive was

observed, the tape was played at normal speed, and the audio signal was displayed on a pen recorder. Heart rate was obtained from the EKG using a cardi tachometer. Only those dives lasting longer than 4 s were used in data analysis so that heart rate at 2 s of the dive was unaffected by the activity of surfacing. The transmitters were removed after data collection.

A  $\beta$ -blocker with a long half-life was used to test the effect of sympathetic influences on the pre-dive and dive heart rates. Nadolol (Corgard, Squibb Montreal), a nonselective  $\beta$ -blocker with a half-life of 24 h was used in preference to propranolol, which has a half-life of only 2 h (Gilman, Goodman, and Gilman 1980). Nadolol was administered orally to one mallard—4 mg on the first day followed by 2 mg daily for 2 additional days. This treatment was repeated using the same protocol about one week later. The  $\beta$ -blockade was judged to be effective because pre-dive heart rate was usually less than 300 beats  $\cdot$  min<sup>-1</sup>.

Four mallards were used to study the effect of baroreceptor denervation on the cardiac response to voluntary diving. All surgery was performed under general anesthesia (20 mg  $\cdot$  kg<sup>-1</sup> sodium pentobarbital, Somnotol, MTC Pharmaceuticals, Mississauga, Ont.). Entry to the thoracic cavity was gained through the interclavicular air sac. In three ducks the left baroreceptor nerve was sectioned approximately 1.5 cm distally from the nodose ganglion, and the right nerve was sectioned near the pulmonary vein at a point where the nerve turns ventrally and medially toward the heart. After denervation, the air sac was closed with surgical silk and the skin was sutured over the repaired air sac. The ducks were allowed 1 wk to recover and then placed on the diving tank. When diving resumed, the EKG transmitter was implanted, using the same procedure as for intact ducks. In one duck, the nerves were exposed during initial surgery and a loop of thread was placed around each nerve. One end of each thread was anchored to the skin high in the neck after the wound was closed. After heart rate data were collected for this condition (sham operated), the duck was again anesthetized, and the threads were slowly pulled through the wound sectioning the nerves. Hence, the duck acted as its own control for baroreceptor denervation. The duck was

returned to the tank on the following day, and data collection started when diving resumed. Chronic barodenervation is usually accompanied by high heart rates (Jones et al. 1983), and Nadolol was used to reduce pre-dive heart rates in this group.

The effectiveness of denervation was tested by injecting 25  $\mu$ g of phenylephrine into the brachial vein while monitoring blood pressure from the brachial artery and noting the presence or absence of a fall in heart rate. At the end of observations, the animals were killed with a lethal dose of sodium pentobarbital and baroreceptor nerve section checked postmortem. One of the four mallards underwent a bradycardia following administration of the vasoconstrictive drug. The postmortem inspection revealed that only the left baroreceptor nerve was sectioned.

Pre-dive heart rate was determined 1 s before submergence, and dive heart rate was determined 2 s after submergence. The data are shown as least-squares regressions with the 95% confidence limits of the slope and the standard error of estimate (Zar 1984). The slopes were tested for significance ( $P < .05$ ) against slopes of either 0 or 1, using the  $t$ -statistic.

## RESULTS

When dabbling voluntarily, heart rate did not change noticeably, although the slope of the regression line is significantly different from one (figs. 1, 2A). Large changes in heart rate were rare, and these were not always related to the moments of submersion or emersion. The mean duration of submergence was  $3.0 \pm 1.0$  (SD) s with a maximum of 9 s; however, the large majority of dabbles were less than 3 s and were therefore not used in this analysis.

The time required to dive to the bottom of the tank and return to the surface was approximately 2 s. Dive time increased during the first week of diving from 2 s to 6 s, and the combined mean of all ducks after the first week was  $6.2 \pm 2.1$  s with a maximum dive time of 11.6 s.

When voluntarily diving, the ducks showed little or no anticipatory increase in heart rate before the dive even if the pre-dive heart rate was low (fig. 2B). The heart rate was lowest before the first of a series of dives and increased progressively between subsequent dives. Pre-dive heart rates ranged

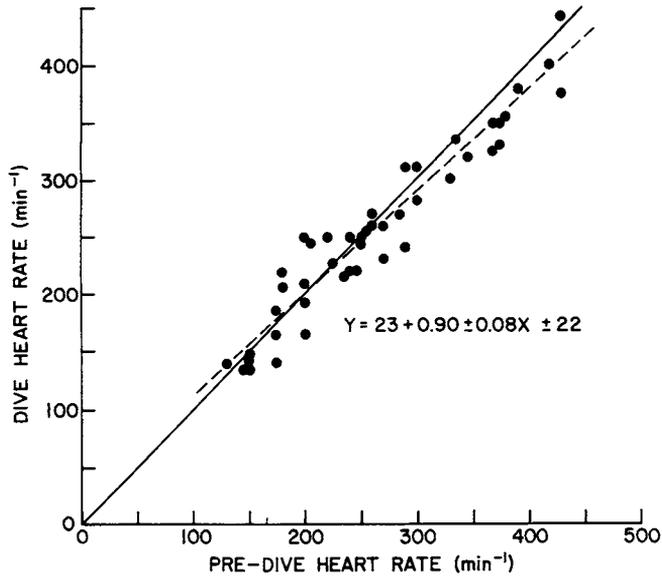


FIG. 1.—The relationship between presubmergence and submerged heart rate during voluntary dabbling when the head was underwater for over 3 s. The broken line represents the regression of these data. In this and all other figures, the line passing through the origin represents the line of identity.

from 150 to 500 beats  $\cdot$  min $^{-1}$  (fig. 3A). In one duck, the mean dive time was  $7.7 \pm 1.2$  s, the dive:pause ratio was one, and pre-dive heart rate rapidly increased to 500 beats  $\cdot$  min $^{-1}$  during a series of dives. The duck represented by the data in figure 4 (solid circles) had a low dive:pause ratio ( $\ll 1$ ). The heart rate of this duck was usually above 400 beats  $\cdot$  min $^{-1}$  immediately after a long dive ( $>9$  s), but the duck rested at the surface for more than 10 s, during which heart rate decreased. Consequently, the rate before the next dive was never higher than 350 beats  $\cdot$  min $^{-1}$ .

The heart rate at 2 s into the dive was nearly the same regardless of the pre-dive rate. The combined data from three mallards (50 dives each) show that dive heart rate was about 250 beats  $\cdot$  min $^{-1}$  (fig. 3A). When the data for each animal were analyzed separately, the regression lines of two of the three ducks were not significantly different from zero, but the regression line for the third duck was significantly different from zero. The regression lines, for individual ducks or all ducks together, cross the line of identity, indicating that the heart rate increased in dives when pre-dive heart rate

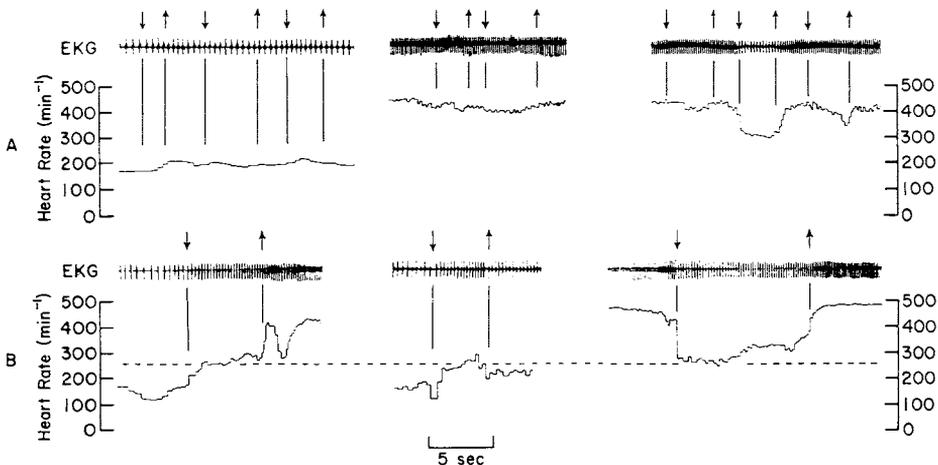


FIG. 2.—EKG and cardiometer traces from mallards. A, Dabbling; B, diving. The broken line at 250 beats  $\cdot$  min $^{-1}$  represents the typical heart rate at 2 s into dives. There is no typical heart rate for dabbles.

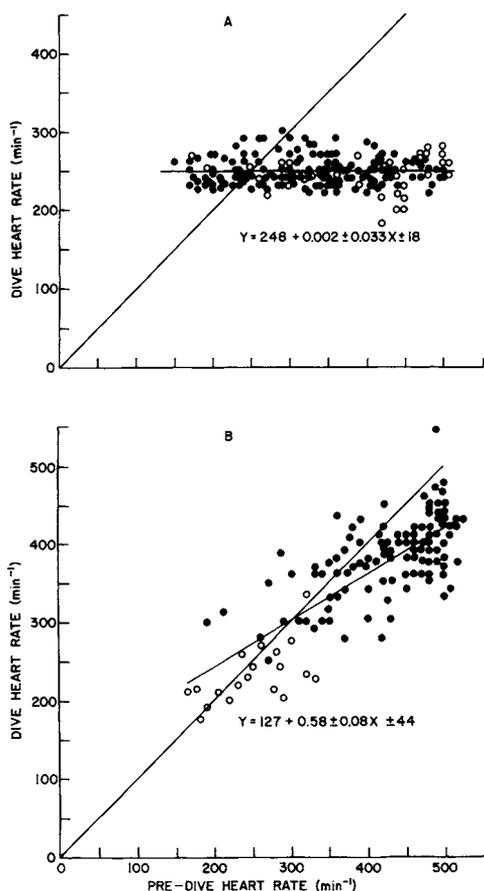


FIG. 3.—The relationship between pre-dive and dive heart rate. *A*, During voluntary dives of three intact mallards (solid circles) and one sham operated mallard (open circles); *B*, voluntary dives of three barodenergated ducks without  $\beta$ -blockade (solid circles) and following  $\beta$ -blockade with nadolol (open circles). The regression equation, with 95% confidence limits of the slope and the standard error of the estimate, is given.

was low while it decreased in dives when pre-dive heart rate was high (figs. 2*B*, 3*A*, 4).

Baroreceptor denervation altered the relationship between pre-dive and dive heart rate (fig. 3*B*). The regression line now approaches, although is significantly different from, the line of identity (fig. 3*B*). The duck that had only one baroreceptor nerve sectioned (fig. 4) gave a response between that of intact ducks and those ducks whose baroreceptor nerves were sectioned bilaterally (fig. 3*B*).

#### DISCUSSION

When diving ducks (*Aythya* sp.) dive voluntarily, there is always a fall in heart

rate, and the dive heart rate is positively correlated with the pre-dive rate (Furilla and Jones 1986). This fall in heart rate appears to result from a constant increase of vagal output regardless of the pre-dive heart rate, while the variability of pre-dive and dive heart rates is probably set by the amount of cardiac sympathetic activity present during each dive (Furilla and Jones 1987). In contrast, mallards appear to be regulating heart rate during the early stages of the dive, with the regulated rate being approximately 250 beats  $\cdot$  min $^{-1}$ . The adjustment in heart rate must be vagally mediated because the cardiac sympathetic nerves are incapable of bringing about rapid changes in heart rate (Furilla and Jones 1987). Consequently, in dives, not only is the amount of change of vagal activity variable, but the direction of change depends on the pre-dive rate.

The heart rate response to voluntary dabbling shown by the mallard is puzzling. There is no doubt that chemoreceptors are responsible for the cardiovascular adjustments to forced diving (Jones and Purves 1970; Lillo and Jones 1982), so it is not surprising that little or no cardiac adjustment occurred during short periods of head submersion. However, Furilla and Jones (1986) showed that, when the duck's heart rate was high just before a forced dive, heart rate fell rapidly to approximately 146 beats  $\cdot$  min $^{-1}$ . Evidence from voluntarily dabbling geese (Kanwisher, Gabrielsen, and Kanwisher 1981) and Pekin ducks (Gabrielsen 1985) also indicates changes in heart rate to approximately 150 beats  $\cdot$  min $^{-1}$  on submersion, with heart rates of 200–300 beats  $\cdot$  min $^{-1}$  during the short breathing period. Although observations from this study reveal some changes in heart rate during dabbles, heart rate did not fall to 150 beats  $\cdot$  min $^{-1}$  with any regularity. In fact, figure 2*A* shows that the presence of a bradycardia was unpredictable, while the rate of fall of cardiac frequency was variable.

As with mallards, penguins show no anticipatory tachycardia, but, unlike mallards, penguins show little or no cardiac adjustments to voluntary submergence (Butler and Woakes 1984). Penguins are almost neutrally buoyant, while dabbling ducks are far more buoyant than diving ducks (Den-

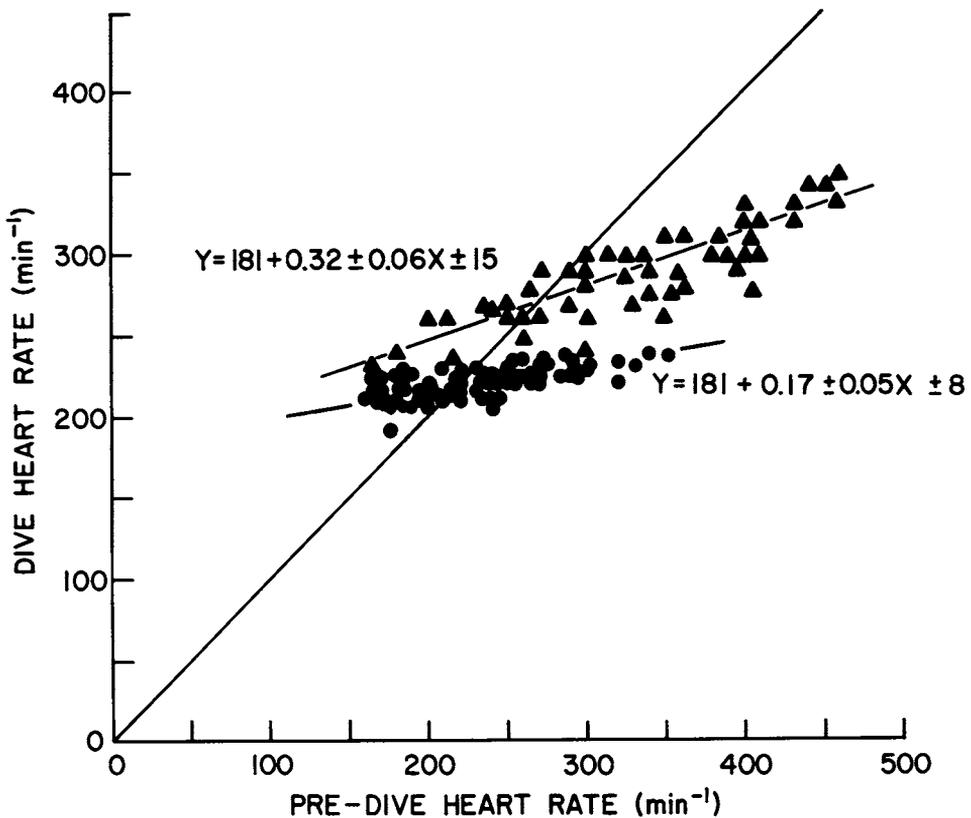


FIG. 4.—The relationship between pre-dive and dive heart rate from one mallard before (solid circles), and after denervation of the left baroreceptor nerve (solid triangles). The regression equations for heart rate data before and after unilateral barodenervation are given below and above the regression lines, respectively. These data are from the same bird and are not included in the previous figure.

ner [1946] in King 1966) and must work harder to dive. In fact, two of the five ducks used in the present study seemed unable to submerge fully without the aid of the wings but, once underwater, they switched to leg propulsion. Consequently, a pre-dive tachycardia would be expected in mallards if the pre-dive tachycardia seen in diving ducks is in anticipation of a high level of exercise during submergence.

The cardiac response to voluntary diving in mallards is greatly reduced by bilaterally sectioning the baroreceptor nerves, but not by unilateral section. This contrasts with diving ducks, such as the redhead (*Aythya americana*), in which barodenervation has no effect on the cardiac response to voluntary submergence (Furilla and Jones 1987). Information concerning heart rate is undoubtedly carried in duck baroreceptor nerves (Jones 1973), but whether ducks—or any animals—use this information to regulate heart rate, rather than arterial

blood pressure, is unknown. It is unfortunate that our knowledge of the adjustments to submergence is limited to heart rate because if arterial pressure is being maintained during the dive, it may be that the system is responding to, and correcting for, changes in pressure brought about by alterations in total peripheral resistance. Since mallards are leg-propelled divers, the change in total resistance may be largely the result of modifications in hind limb perfusion. There is no evidence, however, for or against arterial pressure being maintained, and, if it is not, heart rate itself is the likely regulated variable. Other factors must be involved, however, because the slope of the regression after baroreceptor denervation is markedly different ( $0.58 \pm 0.08$ ) from 1. Even so, it is clear from this and other studies of voluntary dabbling and diving in birds that few generalizations can be made regarding not only the cardiovascular adjustments to submergence but also their control.

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