

The importance of the *M. diaphragmaticus* to the duration of dives in the American alligator (*Alligator mississippiensis*)

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Abstract

We tested the hypothesis that the crocodylian *M. diaphragmaticus* extends the duration of dives by disabling this muscle in a group of juvenile American alligators and comparing the duration of their dives to the duration of the dives of animals in which the muscle remained intact. We studied the groups while they were fasting, 1 h after they had eaten a meal with a density that was either greater or less than water, and at 22 and 28 °C. We found that the duration of dives was longer for the control group compared to animals without a functional *M. diaphragmaticus*, both when fasting and after having consumed the denser meal. The warmer temperature significantly decreased the duration of the dives for both groups, as did eating in general. The preponderance of these data indicates that transection of the *diaphragmaticus* reduced time spent underwater, but the mechanism for this reduction is unknown. Lack of a functional *diaphragmaticus* could impair the animals' ability to inspire sufficient air to support the dive, but we think this explanation is unlikely because both groups were able to float at the surface and thus needed to reduce lung volume to dive. An alternative explanation is that the effect on duration is a consequence of an impairment of a locomotor rather than ventilatory function of the muscle.

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Introduction

Crocodylians have a fascinating and complex way of breathing. Like other amniotes they use costal ventilation, but inspiration can be supplemented by pelvic aspiration and a form of diaphragmatic ventilation (Fig. 1) that is not homologous with mammalian diaphragmatic breathing (Naifeh et al., 1970; Gans and Clark, 1976; Farmer and Carrier, 2000). It is unclear when the crocodylian diaphragmatic muscle evolved or why crocodylians need several different mechanisms to

supplement inspiration. In a previous study of the role of the *M. diaphragmaticus* in inspiration (Uriona and Farmer, 2006), we transected the muscle in a group of juvenile alligators and left it intact in a second group. While the animals were sitting quietly on land, we gave them hypercapnic gas to breathe to induce maximal breaths (vital capacity) under two conditions: when they were fasting and after they had eaten. We did not find a significant difference in vital capacity between the groups when they were fasted, indicating that the animals do not always need this muscle to take large breaths. In contrast, after the animals had eaten a meal we found significantly smaller vital capacities in the transected group, suggesting that the *M. diaphragmaticus*

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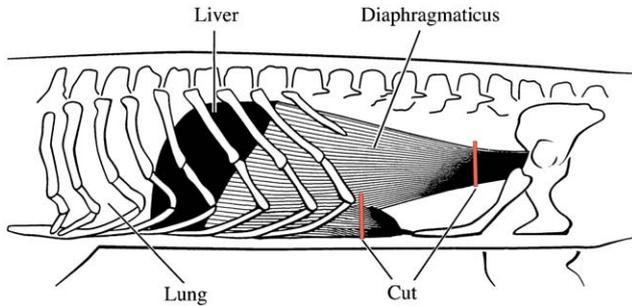


Fig. 1. Illustration of the crocodilian *M. diaphragmaticus*, which originates ventrally on the caudal-most gastralia and laterally on the ilium and inserts on the liver, which is mechanically connected to the lungs. The *diaphragmaticus* contributes to inspiration through caudal translation of the viscera, including the large stomach and liver, which in turn pulls on the lungs and increases the thoracic volume. To disable the muscle, we transected both the ventral and lateral portions of the muscle. Figure modified with permission from Farmer and Carrier (2000).

is important for vital capacity when the respiratory system is stressed (Uriona and Farmer, 2006). However, we only studied breathing while the animals were on land. American alligators are highly aquatic in their lifestyle, spending 18–41% of their time underwater (Seebacher et al., 2005). Thus it is possible that the *M. diaphragmaticus* is very important for inspiration in an aquatic setting (Gans and Clark, 1976). When the animals are submerged, the hydrostatic pressure on the thoracoabdominal cavity might reduce their ability to inspire. Furthermore, because the amount of air in the lung will presumably influence the duration of a dive, we hypothesized that animals with an intact *M. diaphragmaticus* would dive for longer periods, especially in the postprandial state, than individuals who have had this muscle transected (Uriona and Farmer, 2006), but this hypothesis remains untested.

A small difference in the ability to stay submerged may have important ramifications for juvenile crocodilians because they take refuge from predators such as birds and raccoons under water. Although adult crocodilians have few if any nonhuman predators, rates of predation are high on juveniles; more than 50% of hatchlings die before the age of 1 year (Woodward et al., 1987). Thus there could be strong positive selection for an ability to increase the duration of dives while retaining the capacity to eat large meals, which presumably facilitates rapid growth. Juvenile alligators voluntarily eat meals as large as 10–15% of their body mass (Uriona and Farmer, 2006). In this light we hypothesized that animals with an intact *M. diaphragmaticus* would on average dive for longer periods in the postprandial state than individuals that have had this muscle transected (Uriona and Farmer, 2006). We

undertook this study of importance of *M. diaphragmaticus* to the duration of dives to test this hypothesis.

Materials and methods

Animal care

We obtained embryos of American alligators (*Alligator mississippiensis* Daudin 1801) from the Rockefeller Wildlife Refuge (Louisiana, USA). After hatching, we housed the animals ($n = 14$) in 378-l tanks until they reached 3 years of age, at which point we transferred them to 38-l glass aquariums with 3–4 animals per aquarium. The temperature of the aquaria was 25 °C and basking platforms and full-spectrum lights were present. The animals experienced a 12 h:12 h light:dark cycle. The animals were fed *ad libitum* a diet of Mazuri crocodilian diet (PMI Nutrition International, Brentwood, MO, USA).

Experimental design

As hatchlings, the animals were randomly divided into two groups of seven individuals each. In one group we transected the *diaphragmaticus* muscle. In the second group we randomly selected three individuals and performed a sham surgery. In this study and in previous experiments (Uriona and Farmer, 2006) no statistical difference ($p > 0.05$) in vital capacity or in the duration of dives was seen between the sham-operated animals and the non-operated animals and so these data were pooled. Both sham- and *diaphragmaticus*-transected animals were 3 years recovered from surgeries before the experiments were performed.

During data collection one of three groups consisting of equal numbers of control and transected animals (4–6 animals per group) were placed in a 284-l aquarium (122 cm × 45 cm × 61 cm; $L \times W \times H$) filled three quarters full of water. Animals were observed for 30 min before the duration of their dives was measured. Pilot experiments showed that many of the animals preferred to float at the surface rather than dive. We therefore attached a mass equaling 2.5% of the animal's body mass with a slender piece of tape under the jaw of the animal and this was effective in motivating diving behaviors without taxing the animals' ability to freely move about the aquarium. The criteria for selecting dives for analysis are described below in the section on data collection and analysis. We measured the duration of the dives for each animal while at a body temperature of 22 °C under the following conditions: in the fasted state (6 days fasted), 1 h after having eaten a buoyant meal (Mazuri crocodilian diet), and 1 h after having eaten a non-buoyant meal (the hearts and gizzards of

chickens). The animals preferred the buoyant food and two individuals from the control and transected groups refused to eat the non-buoyant food. Thus the sample size is smaller for the non-buoyant meal at 22 °C than for the buoyant meal at 22 °C. Furthermore, although we wished to study the effects of a warm temperature (28 °C) on dive time in all of these physiological states, because of the difficulty in convincing the animals to eat the non-buoyant meal we omitted this meal at 28 °C.

At 22 °C, seven dives (criteria for the dives are described below) from all the animals were recorded in the fasted state and the following day seven more dives from all the animals were recorded after the animals had been given an hour to eat a buoyant meal. We repeated this protocol two more times, with a week between each feeding, for a total of 21 dives studied for each animal in each of the fasted and fed states. At the time of these experiments, control animals weighed between 156 and 306 g (242.9 ± 23.3 g; mean \pm s.e.) and the transected animals weighed between 198 and 313 g (273.1 ± 16.1 g; mean \pm s.e.).

One month after completing the experiments, we repeated the protocol but at 28 °C. At the time of these experiments, control animals weighed between 194 and 385 g (295.2 ± 29.1 g; mean \pm s.e.) and the transected animals weighed between 257 and 338 g (320.6 ± 13.3 g; mean \pm s.e.). Following these experiments we again lowered the temperature to 22 °C and followed the procedure described above after feeding a non-buoyant meal. At the time of these experiments, control animals weighed between 219 and 440 g (336.3 ± 35.9 g; mean \pm s.e.) and the transected animals weighed between 314 and 408 g (362.8 ± 11.7 g; mean \pm s.e.).

The specific gravity of the buoyant and non-buoyant meals was determined by comparing the weight of the food in air to that in water. To obtain the weight of the food in water we placed the food in a cage, which was suspended from a hanging scale (Ohaus triple beam balance, Florham Park, NJ, USA), and then submerged the cage in water.

Surgery

Animals were lightly anaesthetized by enclosure in a box with a rag soaked in isoflurane. Once drowsy, they were intubated and ventilated with a small animal ventilator (CWE Inc., Ardmore, PA, USA) using air that had passed through an isoflurane vaporizer (Draeger, Luebeck, Germany). The level was initially set at 4%, but was reduced to 0.5% for the majority of the surgery. All surgeries were performed using sterile technique. With the animal in the supine position, the ventral and lateral regions of the abdomen were disinfected with Betadine (Purdue Pharma, Stamford, CT, USA) and the animal was draped with a sterile

cloth. An incision was made along the ventral midline of the animal to expose the ventral portion of the *diaphragmaticus*. With the experimental animals the muscles were cleared of veins (e.g. lateral abdominal) and transected. Two lateral incisions were made cranial to the pelvic girdle. The attachment of the *diaphragmaticus* to the ilium was identified and this portion of the muscle transected. With the sham surgeries, the same cutaneous incisions were made and the muscles were identified but not transected. All incisions were closed with suture. The animals were treated both with a topical antibiotic and intraperitoneal injections of antibiotics (Baytril; Bayer, Leverkusen, Germany) and kept dry until the incisions had healed. During this time they were given water orally every day.

Data collection and analysis

Animals were weighed before and after feeding and the percent body mass ingested was recorded. An observer who was naive regarding whether or not the animals had a transected *diaphragmaticus* recorded dive times with a stopwatch. Only dives longer than 1 min and not over 20 min were analyzed. Dives lasting for less than 1 min consisted mainly of swimming, and for this reason were removed from the analysis. A dive longer than 20 min was only seen with three animals and in each case represented an outlier for statistical purposes.

We analyzed the durations of the dives lasting between 1 and 20 min for normality and examined the effects of meal size and body size using linear regressions. We used a repeated measures analysis of variance (Statistex 8.1) to analyze the effects of transecting the *diaphragmaticus* as well as temperature on average dive time. We used a one-tailed Students *t*-test to study the effects of transecting the *diaphragmaticus* and temperature on average maximal dive time. For all statistical tests a *p*-value of less than 0.05 was treated as significant. The values reported are mean and maximal dive times \pm standard error for the control and *diaphragmaticus*-transected animals for the fasted and fed states at 22 and 28 °C and with the different meals at 22 °C. The maximal dive times were obtained by averaging the longest dives measured during each of the trials and is therefore an average maximal dive time.

All experiments were approved by the University of Utah Animal Care and Use Committee.

Results

The duration of dives lasting between 1 and 20 min had a normal distribution. The results of the linear regression of dive time and body mass or dive time and

Table 1. Linear regression for dive time to body mass or the mass of the meals.

Temperature (°C)	State	Regressed	Slope	R ²
22	Fasted	DT vs. M	$y = 0.0032x$	0.0045
22	Fed+	DT vs. M	$y = 0.0026x$	0.0095
22	Fed–	DT vs. M	$y = -0.0019x$	0.0033
22	Fed+	DT vs. %	$y = -8.8567x$	0.0029
22	Fed–	DT vs. %	$y = -34.9870x$	0.0843
28	Fasted	DT vs. M	$y = 0.0013x$	0.0028
28	Fed+	DT vs. M	$y = 0.0013x$	0.0085
28	Fed–	DT vs. %	$y = -4.6346x$	0.0154

DT, dive time; Fed+, fed buoyant meal; Fed–, fed non-buoyant meal; M, body mass (kg); %, percent body mass ingested.

the mass of the meals showed no effect on dive time due to the body mass of the animals used in these experiments and the size of the meals consumed (Table 1). When fed the buoyant meal for the 22 and 28 °C experiments, the control group consumed 9.4% and 5.5% of their body mass on average, respectively, and the *diaphragmaticus*-transected animals consumed 7.2% and 4.6% of their body mass, respectively. When fed the non-buoyant meal for the 22 °C experiments, the control group and *diaphragmaticus*-transected group consumed 5.0% and 5.2% of their body mass, respectively. The specific gravity of the buoyant meal was 0.666 and the specific gravity of the non-buoyant meal was 1.125.

Experiments at 22 °C

Both the control and the *diaphragmaticus*-transected animals were able to stay positively buoyant at the surface of the water in both the fasted and fed state when fed either buoyant or non-buoyant meals. In the fasted state the control animals had significantly longer dives on average (1.06 min longer) than the *diaphragmaticus*-transected animals. Similarly, after eating a non-buoyant meal, the control animals had significantly longer dives than the *diaphragmaticus*-transected animals; the control animals on average dove for 4.27 ± 0.08 min and the *diaphragmaticus*-transected animals, 3.33 ± 0.10 min. In contrast, after eating a buoyant meal, there was no significant difference in the average dives. No significant difference in the maximal dive times between the two groups was observed for the fasted and fed state regardless of the meal fed (Fig. 2).

The control animals had significantly shortened mean and maximal dive times when comparing the buoyant meal to the fasted state (Fig. 3). The control animals had a mean dive time of 5.20 ± 0.12 min when fasting and 3.27 ± 0.15 min after eating the buoyant meal. The maximal dive times for these animals were 11.10 ± 1.47 min when fasting and 6.15 ± 0.47 min after

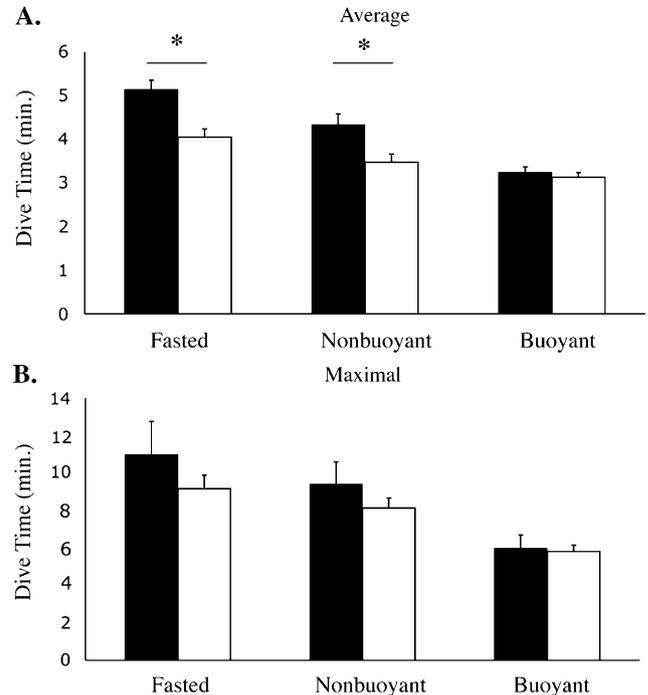


Fig. 2. (A) Graphs of average \pm SEM dive time for control animals (dark bars) and *diaphragmaticus*-transected animals (open bars) at 22 °C when fasting ($n = 7$ for both groups), after eating non-buoyant food (hearts and gizzards of chickens, $n = 6$ for both groups) and buoyant food (Mazuri crocodilian diet, buoyant food, $n = 7$ for both groups). (B) Graphs of maximal \pm SEM dive times for control animals (dark bars) and *diaphragmaticus*-transected animals (open bars) at 22 °C when fasting, after eating non-buoyant food and buoyant food. The symbols * identify statistically significant differences between groups with statistical significance set at $p \leq 0.05$.

eating the buoyant meal. The same trends were seen with the *diaphragmaticus*-transected animals. The average dive time in the fasting state, 4.16 ± 0.11 , was significantly longer than when fed a buoyant meal, 3.19 ± 0.06 min (Fig. 3). The difference between the maximal dive times for this group was also significantly different when comparing the fasted and fed (buoyant meal) states, with values of 9.16 ± 0.45 and 5.59 ± 0.19 , respectively (Fig. 3).

Three dives from three different fasting individuals were not analyzed because they all lasted longer than 20 min; these dives were approximately twice as long as any other dives recorded for that same individual. One control animal dove for 30.33 min and two *diaphragmaticus*-transected animals dove for 23.38 and 22.41 min.

Experiments at 28 °C

Again both groups of animals were able to stay positively buoyant at the surface of the water in the fasted and fed (buoyant food only) state. We found no statistically significant differences between the control

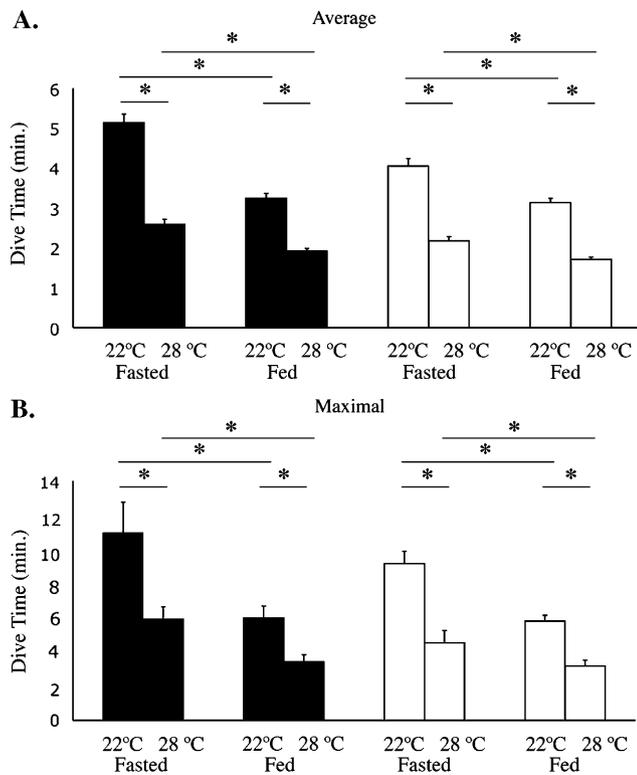


Fig. 3. (A) Graphs of average \pm SEM dive time for control animals (dark bars, $n = 7$) and *diaphragmaticus*-transected animals (open bars, $n = 7$) at 22 and 28 °C in the fasted and fed state (buoyant food). (B) Graphs of maximal \pm SEM dive time for control animals (dark bars) and *diaphragmaticus*-transected animals (open bars) at 22 and 28 °C in the fasted and fed state (buoyant food). The symbol * followed by a solid bar identifies statistically significant differences between dive times at 22 °C compared to 28 °C and dive duration when fasted compared to when fed, with statistical significance set at $p \leq 0.05$.

and *diaphragmaticus*-transected animals in average and maximal dive times in both the fasted and fed state. However, both average and maximal dive times were significantly shorter at 28 °C than at 22 °C for control and *diaphragmaticus*-transected animals (Fig. 3). The control animals experienced a significantly different average dive time when comparing the fasted and fed states, with an average dive time of 2.46 ± 0.07 min when fasting and 2.06 ± 0.04 min when fed a buoyant meal. After eating, maximal dive times for control animals were also significantly shorter, with fasted animals diving 6.02 ± 0.42 min and fed animals 3.42 ± 0.25 min. Like the control animals the *diaphragmaticus*-transected animals had a significantly shorter average dive times in the fed state, with the fasting dive times equaling 2.19 ± 0.06 and fed dive times of 1.51 ± 0.03 min (Fig. 3). The maximal dive time for this group was also significantly different when comparing the fasted and fed states, with values of 4.48 ± 0.42 and 3.28 ± 0.18 , respectively (Fig. 3). There were no dives over 20 min at 28 °C.

Discussion

In general, the duration of the dives we measured accords well with prior studies of diving in crocodylians (Table 2, Grigg et al., 1985; Wright, 1987; Wright et al., 1992). We saw a decrease in duration with increasing temperature and we saw a decrease in duration after the animals had eaten, which we hypothesized would occur (Uriona and Farmer, 2006). Although a predicted result, it is noteworthy that this is the first study to empirically test the effect of feeding on the duration of dives, at least as far as we are aware. Because we studied diving just 1 h after the animals ate, the mechanical effects of eating were probably more influential than a postprandial increase in metabolism, which peaks in alligators around 36 h after feeding when held at 30 °C (Busk et al., 2000), and rises even more slowly at cooler temperatures (Farmer et al., 2008). We also predicted and observed dives of longer duration in the group of animals with intact diaphragmatic muscles than in the group in which the muscles had been disabled. However, several observations cast doubt on our idea that the underlying mechanism is an impaired ability to take large breaths when the ventilatory system is mechanically stressed (Klein et al., 2003).

The hypothesis that impairment of the ventilatory function of the *diaphragmaticus* reduces dive duration is refuted by several observations. First, all animals from both groups were able to float at the surface at will, both when fasting and after having eaten. Evidently, the animals could take large enough breaths in these states to remain buoyant. To stay submerged without actively swimming or clinging to the tank, which the animals did not do in this study, requires the animals to have a specific gravity equal to or greater than water and, therefore, they must have exhaled some of the gases of the lung before they dove. Thus the animals were not diving after having inspired a maximal breath but were diving after having either exhaled or inhaled to this lesser but desired lung volume. Second, little if any difference in duration of the dives was predicted to occur between these groups when in the fasting state, when presumably the animals can inspire without difficulty, yet the difference we measured was most pronounced when the animals were fasting. Third, the results for each group of animals differed depending upon whether the density of the meal was greater or less than water.

Reptiles can adjust the volume of gas in the lung to control specific gravity (Jackson, 1969). Jackson (1969) found that when floats or weights were attached to the shell of turtles the animals corrected the experimental displacements of their specific gravity by changing the volume of air in the lungs. Our results comparing a meal of Mazuri gator chow to one of meat are consistent with these studies because when the alligators ate gator chow

Table 2. Reported dive times for different members of the crocodylian family.

Animal	Mean dive time (min)	Maximum dive time (min)	Number of animals	Mass (kg)	Water temp. (°C)	Condition	Reference
<i>Crocodylus porosus</i>	3.08±1.87	–	5	2.25±0.74	25	Undisturbed captive	Wright et al. (1992)
<i>Crocodylus porosus</i>	19.6±1.8	–	5	2.25±0.74	25	Disturbed captive	Wright et al. (1992)
<i>Crocodylus porosus</i>	4.7±0.3	–	4	2.59±0.30	25	Undisturbed captive	Wright (1987)
<i>Crocodylus johnstoni</i>	21.7±3.1	95.0±10.6	5	9.88±1.97	–	Wild	Seebacher et al. (2005)
<i>Crocodylus porosus</i>	2.6±0.3	30	1	9.7	–	Wild	Grigg et al. (1985)
<i>Alligator mississippiensis</i>	5.20±0.12	11.10±1.47	7	0.24±0.02	22	Disturbed captive	Present study

they had significantly shorter dive times than after consuming a meal of meat. This suggests they compensated for the change in specific gravity that accompanied feeding on the buoyant gator chow by reducing lung volume; however, the *diaphragmaticus* was not necessary for this adjustment of specific gravity. Thus another explanation is requisite to explain the difference in dive duration between the control and the *diaphragmaticus*-transected groups.

We think the difference in the duration of the dives between these groups is a consequence of impairing a locomotor function of the *diaphragmaticus* rather than the ventilatory function of the muscle. Although the lungs of crocodylians are important reservoirs of oxygen and the *diaphragmaticus* can play a role in filling the lungs, activation of this muscle also affects aspects of locomotion in water, particularly pitch and roll, independent of breathing (Uriona and Farmer, 2008). Activity in the *diaphragmaticus* is observed when the alligators are not inspiring (the head is underwater) coincident with a head-down tail-up tilt.

By pulling the lungs caudad the *diaphragmaticus* can shift the center of buoyancy caudad and therefore help tilt the tail up and the head down. Thus alligators appear to use the *diaphragmaticus* to control posture and maneuverability when in water. This role of the *diaphragmaticus* in locomotion may explain the differences in the duration of the dives between the control and *diaphragmaticus*-transected animals. Animals with an intact *diaphragmaticus* may be able to pull the lungs further caudad, making a head-down descent easier than it is for animals that are unable to contract the *diaphragmaticus*. Animals with a transected *diaphragmaticus* might compensate for this impairment on maneuverability by inspiring smaller volumes of air into the lungs, and would on average have dives of shorter duration. The observation that a buoyant meal decreases the difference in dive duration between animals with and without a functioning *diaphragmaticus*

further supports this hypothesis because an increase in the buoyancy of the abdominal region would move the center of buoyancy toward the tail and facilitate a head-down maneuver independent of the activity of the *diaphragmaticus*.

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