

THORACIC COLLAPSE AS AFFECTED BY THE *RETIA THORACICA* IN THE DOLPHIN

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Abstract. The carcass of a subadult female *Delphinus* was placed in a hyperbaric chamber and subjected to two simulated dives each equivalent to 69.7 m. In one dive the thorax was in its natural state, and in the other 100 ml of water had been injected into each pleural cavity. Various morphometric measurements of the thorax were taken before, during, and after each dive.

Results indicate that if fluid is located in the same position as the *retia thoracica*, the shape of the thorax is affected when submitted to diving, but not surface, pressures. The overall collapse of the chest is greater during partial infusion of the pleura, exhibiting exceptional compression in the ventral area. The engorged thoracic rete apparently affects the degree and pattern of thoracic collapse and thereby reduces the amount of displacement stress exerted upon the abdominal organs when the animal is subjected to the high ambient hydrostatic pressures encountered during normal diving.

Diving mammals	Thoracic shape
<i>Retia thoracica</i>	Weddell seal

Dives of the Weddell seal, *Leptonychotes weddelli*, have been recorded to depths of 600 m (Kooyman, 1965), and those of the sperm whale, *Physeter catodon*, to 1500 m (Heezen, 1957). The hydrostatic pressures at these depths (60-150 atm, respectively) require specialized physiological and anatomical adaptations of the common thoracic system of the mammal to accommodate this diving behavior. Ridgway (1972) has stated that the following specific adaptations appear to be of primary importance for deep diving: (1) flexible thoracic structure that allows the thorax to collapse as the hydrostatic pressure increases; (2) large distensible veins, venous sinuses, and *retia mirabilia* that can engorge with blood and fill space as respiratory air is compressed; (3) lungs whose structure contains large amounts of elastic tissue which is stretched upon inspiration and at exhalation allows the lungs to become atelectic without separating from the chest wall; and (4) a resilient trachea that allows the respiratory passages to collapse beyond the limits of the sea-level dead-space volume. The degree of development of these specialized characteristics

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varies considerably among species of marine mammals, depending upon the requirements for deep diving (Ridgway, 1972).

Photographs of a bottlenose dolphin, *Tursiops truncatus*, at a depth of 300 m clearly show thoracic collapse; this process becomes evident at 10 m and is quite pronounced at 60 m (Ridgway *et al.*, 1969). It is only the ventral aspect that appears to collapse. If the process occurs in the dorsal region, it is not apparent.

The delphinid gross thoracic anatomy appears to be well suited to direct the collapse towards the ventral portions. The aquatic environment eliminates the requirement for the ribs to support functionally the internal organs against the pull of gravity. Delphinid ribs reflect this reduction of their support role, being of a generally more delicate structure than those of a terrestrial mammal of equivalent body weight. Near their vertebral ends, the ribs are more robust than at their sternal ends. The ribs are also anteroposteriorly compressed at the vertebral ends, but dorsoventrally compressed at their sternal ends. The rib anatomy alone contributes rigidity to the dorsal aspect of the thorax and flexibility to the ventral aspect. The epaxial musculature, which occupies about one-third of the dorsoventral thickness of this area of the body, also contributes to the inflexibility of the dorsal portion. The thoracic rete mirabile is also located in the vertebral area and the turgescence of the rete during diving may possibly augment the resistance of this part of the chest cavity to collapse.

The thoracic rete mirabile is found only in the Cetacea (Barnett *et al.*, 1958). It extends from the first thoracic vertebra to the first lumbar vertebra and is oriented between and ventral to the ribs; it is supplied by the intercostal, posterior thoracic, and a branch of the internal carotid arteries, while the efferent vessels are the spinal meninges arteries (Viamonte *et al.*, 1968). The arterioles, containing much elastic tissue (Harrison and Tomlinson, 1963), are imbedded in a loose connective tissue stroma with few accompanying veins (Simpson and Gardner, 1972). The tissue of the thoracic rete is highly elastic (Nakajima, 1961).

The present experiment was designed to assess one of the functions of the *retia arteriales mirabilia thoracica* when engorged during thoracic collapse. The turgescence of this engorged structure should increase the inflexibility of the dorsal thorax, and thereby require a greater portion of the thoracic collapse to occur in the ventral part of the chest.

Materials and methods

A carcass of the common dolphin, *Delphinus cf. delphis*, (identified as NUC 156-8) was obtained from a chartered research tuna purse seine operation off the coast from San Diego, California, in September, 1971. It had died in the net and was kept in cold storage (-13°C) for 6 months prior to this experiment. It was an immature female weighing 21.3 kg and with a snout-fluke notch length of 122 cm. Adults of the species are commonly 75 kg in weight and 2.5 m in length (Walker, 1968).

Radiographs of the animal were taken the day prior to the experiment to insure that neither the thoracic cavity nor lungs contained any fluid. It was then immersed

in a tank of room-temperature water to thaw. Previous experience had shown that 24 hours were adequate to completely thaw a specimen of this size.

A standard double-lock diving recompression chamber with 100 psi capacity was used (interior dimensions of approximately 60" diameter and 96" length; Dixie Corporation, Baltimore, Md.). Before the animal was placed in the hyperbaric pressure chamber for testing, a longitudinal subcranial incision was made and the arytenoepiglottoidal cartilage was securely tied to prohibit any escape of air from the lungs during the tests.

The animal was placed dorsal side down on the floor of the chamber and not immersed in water. Measurements of four dimensions were taken before, during, and after each of two simulated dives. The specimen was measured by U.S. Navy-certified divers whose experience with deep dives eliminated any effects of nitrogen narcosis and allowed them to take reliable measurements to the nearest one-half centimeter. The axial circumference was measured with a tape measure, the dorsoventral thickness with an X-ray caliper rule, and the thoracic widths at two locations along the axillary circumferential line with a set of outside calipers. The positions at which the two thoracic widths were taken were 15 and 25 cm circumferential distance from the mid-dorsal. The latter measurement was across the axillae and subsequent dissection showed this location to be just ventral to the articulation

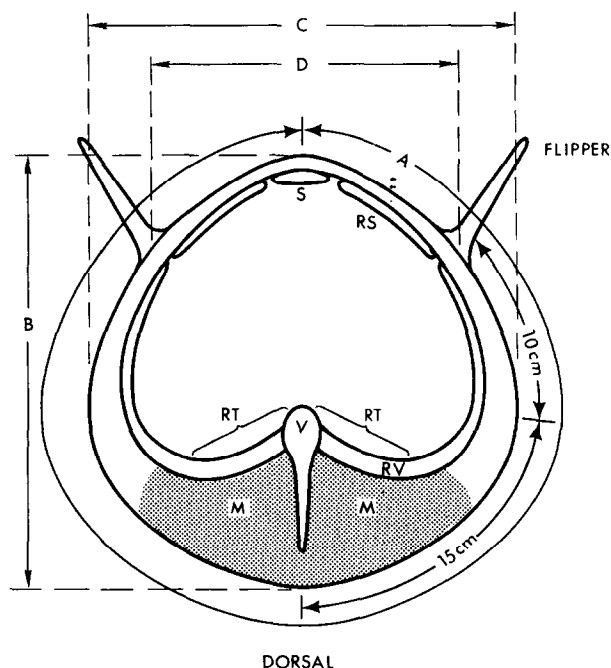


Fig. 1. Diagram of a cross-section through the thorax of the dolphin at the axilla. Points between which measurements were made and some general anatomy are shown. A, circumference; B, dorsoventral thickness; C, width at ribs; D, width at axilla; M, epaxial musculature; RT, *retia thoracica*; RS, sternal ribs; RV, vertebral ribs; S, sternum; V, vertebra.

between the vertebral and sternal ribs. The thoracic width measured at 15 cm was just ventral to the major bend of the rib as it leaves the vertebral column and curves ventrally toward the sternum (fig. 1). The specimen was not handled or moved during or between the test dives.

The simulated dives were both to depth 69.7 m (7 atmospheres). The first dive was performed with the thorax in an unaltered condition. Before the second dive, 100 ml of deionized water were injected into each pleural cavity with a 35-ml syringe fitted with a 16-gauge needle to simulate engorgement of the rete. The needle remained inserted but stoppered while the syringe was reloaded. During injection, positive pressure was maintained on the fluid in the syringe so that when the needle passed through the flesh and entered the cavity, the resistance to injection was noticeably decreased and all the water was confidently placed inside the thoracic cavity. After retraction of the needle, the absence of any gas or fluid escaping from the injection site indicated that the tissue had sealed tightly over the needle hole.

Upon later dissection, 100 ml of water were poured into one side of the thoracic cavity. As in the tests, the specimen was lying on its back. The fluid settled into the depression formed by the dorsal arching of the ribs immediately lateral to the rib-vertebra articulations. The fluid level was not even high enough to cover completely all the structures of the rete on the vertebrae, indicating that *in vivo* retial engorgement is probably not greatly different from the simulated volume of 100 ml of water.

Results

The shape of the thorax was different between the dry condition and when the water was injected. With fluid in the cavity, the thorax became dorsoventrally shallower, and more constricted across the chest, while the circumference and width across the ribs remained constant (table 1). The greatest percentage of change was the axillary width—more than four times greater than the next largest change (table 2).

The average dimensions taken at surface pressure showed negligible change between the dry and injected conditions (table 3).

TABLE 1

Comparison of the two sets of thoracic measurements during simulated dives of a *Delphinus*

	Dive I*			Dive II**		
	Before	During	After	Before	During	After
Depth of dive (m)	0	-69.7	0	0	-69.7	0
Circumference (cm)	68.5	61.5	69.0	69.5	62.0	69.5
Dorsal-ventral (cm)	19.5	17.5	18.5	19.0	16.5	19.0
Width (ribs) (cm)	22.5	20.0	22.0	22.0	20.0	22.0
Width (axillary) (cm)	18.0	19.0	17.0	18.0	15.0	17.5

* Without injection of water.

** With water injected.

TABLE 2

Change of measurements in percent between dry and injected conditions in simulated dives

	A*	B**	Difference (A-B)
Circumference	-10.6	-10.8	0.2
Dorsal-ventral	-7.9	-13.2	5.3
Width (ribs)	-10.1	-9.1	-1.0
Width (axillary)	+8.6	-15.5	24.1

* A: $\frac{(\bar{x}_i \text{ at surface}) - (\bar{x}_i \text{ at } -69.7 \text{ m})}{(\bar{x}_i \text{ at surface})} \times 100$ without injection of water.

** B: $\frac{(\bar{x}_i \text{ at surface}) - (x_i \text{ at } -69.7 \text{ m})}{(\bar{x}_i \text{ at surface})} \times 100$ with water injected.

TABLE 3

Change in average measurements between dry and injected conditions at surface pressures

	A (cm)*	B (cm)**	Difference (%) (A-B)/A \times 100
Circumference	68.75	69.50	-1.1
Dorsal-ventral	19.00	19.00	0.0
Width (ribs)	22.25	22.00	1.1
Width (axillary)	17.50	17.75	-1.4

* A: Without injection of water.

** B: With water injected.

Discussion

This experiment was designed to test a hypothesis regarding the type, not the degree, of mechanical effects of certain anatomical structures. It is believed that a larger sample size for statistical purposes would not affect the conclusions. In the wild, *Delphinus* has been recorded to dive to 256.6 m with an average depth of 63.6 m (Evans, 1971). The simulated depth of 69.7 m used in this experiment is well within the known range for adults.

Cetaceans dive after inspiration so their lungs are full of air at the onset of a dive (Ridgway *et al.*, 1969). That most of the air remains in that part of the respiratory tract which is deeper than the arytenoepiglottoidal cartilage, has been indicated in the work of Coulombe *et al.* (1965). To insure that condition during the present experiment, this structure was tied securely in the closed position.

PLEURAL CAVITY DISPLACEMENT

The lung volume of a 170-kg delphinid, *Tursiops truncatus*, has been determined

to be 12.5 l when the animal is at the water's surface (Irving *et al.*, 1941). If it is assumed that the same relationship of lung volume-to-body weight exists for *Delphinus*, the lung volume of the 21.3 kg experimental animal was 3.04 l.

According to Boyle's Law ($P_1V_1 = P_2V_2$), the experimental pressure of 7 atm would compress the lungs of the specimen to a volume of 0.43 l. The abdominal viscera and thoracic wall would have to supplant 86% of the original pleural cavity volume. With 0.20 l of the pleural cavity occupied by the engorged thoracic rete, the volume subject to temporary displacement is reduced to 79%.

If, however, immature individuals of 122 cm in size dive to only 35 m, thoracic collapse and pleural cavity displacement would be reduced and the effect of the engorged rete would be increased. Without engorgement of the thoracic rete, 75% of the initial pleural cavity volume would be filled by the lower viscera and the compressed chest. With engorgement of the rete to 0.20 l, it is necessary to displace only 65%. The thoracic rete, when filled with blood, can have a notable effect on the degree of thoracic collapse and anterior displacement of the abdominal viscera while the animal is in a diving mode.

THORACIC COLLAPSE

The shape of the thorax collapsing under high hydrostatic pressure does not appear to be of uniform distortion. Published photographs (Ridgway *et al.*, 1969) indicating

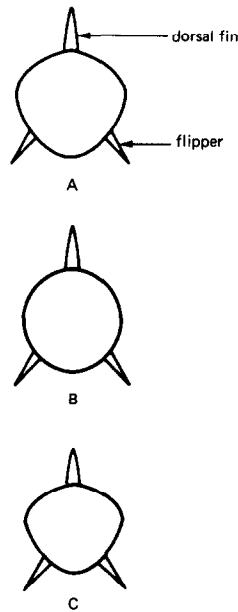


Fig. 2. Diagram illustrating change in shape of the dolphin thorax during various simulated diving conditions. A, at surface pressure with no fluid in the pleural cavities; B, at 7 atmospheres of pressure with no fluid in the pleural cavities; C, at 7 atmospheres of pressure with 100 ml of water in each pleural cavity.

greater collapse in the ventral aspect were confirmed by the results of the present experiment. The vertebral ribs and sternal ribs articulate on the ventral-lateral region of the thorax. Each joint forms a V-pattern directed caudally. Compression of the chest wall in this region would make the V-pattern of the joints more acute, move them to the posterior, and reduce the ventral width of the chest. The measurement across the chest of the experimental animal appeared to be the one most influenced by simulated retial engorgement (table 2).

The cross-sectional form of the dolphin thorax is roughly that of an egg: dorsally broader and ventrally narrower. Under pressure and without the simulated retial engorgement, this egg shape tends to become more circular. However, with 200 ml of fluid in the region of the thoracic rete, the egg shape of the chest becomes exaggerated; the ventral portion becomes much narrower. Collapse of the chest wall seems to increase when the retial volume is enlarged (fig. 2). The abdominal viscera, therefore, should be less displaced and under reduced stress during this condition.

Conclusions

The *retia mirabilia thoracica* and its total function in the biology of cetaceans remain basically unexplained. Cunningham (1877) and Nakajima (1961) have independently suggested that the structure serves as a cushion for shocks to the spinal cord and also maintains a constant thermal environment for that part of the nervous system. The thoracic rete may also serve as a shunt through which the blood may flow while bypassing the muscles during diving (H. Erickson, cited in Scholander, 1940). Nagel *et al.* (1968), with their investigation of the pressure-damping effect on cerebral circulation, have presented one other possible function. The results of the present experiment indicate yet another function: influence on the collapse pattern of the thorax.

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References

- Barnett, C. H., R. J. Harrison and J. D. W. Tomlinson (1958). Variations in the venous systems of mammals. *Biol. Rev.* 33: 442-487.
- Coulombe, H. N., S. H. Ridgway and W. E. Evans (1965). Respiratory water exchange in two species of porpoise. *Science* 149: 86-88.
- Cunningham, D. J. (1877). The spinal nervous system of the porpoise and dolphin. *J. Anat. Physiol. (London)* 11: 209-228.

- Evans, W. E. (1971). Orientation behavior of delphinids: Radio telemetric studies. *Ann. N. Y. Acad. Sci.* 188: 142–160.
- Harrison, R. J. and J. D. W. Tomlinson (1963). Anatomical and physiological adaptations in diving mammals. In: *Viewpoints in Biology*, edited by J. D. Carthy and C. L. Duddington. London, Butterworth & Co., Ltd., pp. 115–168.
- Heezen, B. C. (1957). Whales entangled in deep sea cables. *Deep Sea Res.* 4: 105–116.
- Irving, L., P. F. Scholander and S. W. Grinnell (1941). The respiration of the porpoise, *Tursiops truncatus*. *J. Comp. Physiol.* 17: 145–168.
- Kooyman, G. L. (1965). Maximum diving capacities of the Weddell seal, *Leptonychotes weddelli*. *Science* 151: 1553–1554.
- Nagel, E. L., P. J. Morgane, W. L. McFarland and R. E. Galliano (1968). Rete mirabile of dolphin: Its pressure-damping effect on cerebral circulation. *Science* 161: 898–900.
- Nakajima, M. (1961). In regard to the rete mirabile of the cetacea. (In Japanese). *Toho Med. Acad. J.* Vol. 8, No. 4.
- Ridgway, S. H., B. L. Scronce and J. Kanwisher (1969). Respiration and deep diving in the bottlenose porpoise. *Science* 166: 1651–1654.
- Ridgway, S. H. (1972). Homeostasis in the aquatic environment. In: *Mammals of the Sea: Biology and Medicine*, edited by S. H. Ridgway. Springfield, Charles C. Thomas Publ. Co., pp. 590–747.
- Scholander, P. F. (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skr.* Nr. 22.
- Simpson, J. G. and M. B. Gardner (1972). Comparative microscopic anatomy of selected marine mammals. In: *Mammals of the Sea: Biology and Medicine*, edited by S. H. Ridgway. Springfield, Charles C. Thomas Publ. Co., pp. 298–418.
- Viamonte, M., P. J. Morgane, R. E. Galliano, E. L. Nagel and W. L. McFarland (1968). Angiographic studies in living dolphin. *Am. J. Physiol.* 214: 1225–1249.
- Walker, E. P. (1968). *Mammals of the World*. Baltimore, John Hopkins Press, p. 1114.