that these structures serve in buoyancy control.

The occurrence of cloacal bursae among various turtle families has been surveyed (*11*) and is of some interest in regard to possible buoyancy control. In general, cloacal bursae are found in semiaquatic, freshwater turtles (such as *Pseudemys*) but are absent in the highly aquatic, bottom-dwelling soft-shelled turtles (Trionychidae), in shallow-water mud and musk turtles (Kinosternidae), and in the terrestrial tortoises (Testudinidae). In none of the latter families would buoyancy control represent a particularly useful adaptation. However, cloacal bursae are also absent from the marine turtles although these forms would be expected to possess some buoyancy control.

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Respiration and Deep Diving in the Bottlenose Porpoise

Abstract. *A bottlenose porpoise was trained to dive untethered in the open ocean and to exhale into an underwater collecting funnel before surfacing from prescribed depths down to 300 meters. The animal was also taught to hold its breath for periods up to 4 minutes at the surface and then blow in the funnel. Alveolar collapse is probably complete at around 100 meters, and little pulmonary respiratory exchange occurs below that depth. Thoracic collapse was observed visually at 10 to 50 meters and by underwater television to 300 meters.*

Sperm whales appear to be able to dive to at least 1500 m (*1*), and Weddell seals are known to reach 600 m (*2*). In spite of being air breathers, these true marine mammals have considerable three-dimensional freedom in the sea. To make such dives, they must be able to tolerate the pressures of these depths (60 to 150 atm), and they must also be able to hold their breath much longer than land mammals. We have studied these problems with a trained porpoise in the open sea.

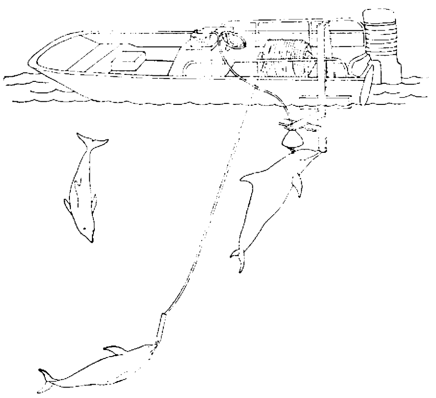

Fig. 1. The experimental setup for deep-diving experiments in the open ocean. The porpoise dives down when the go signal is turned on. He pushes the plunger on the end of the diving test switch, turning the go signal off, and then returns to exhale into the funnel before surfacing.

Scholander (*3*) proposed that alveolar collapse would occur in diving mammals at a depth of about 100 m. Such collapse prohibits gaseous exchange during deep dives and possibly protects the animal from decompression sickness and nitrogen narcosis.

Fiebiger (*4*) suggested that the unique, smooth muscular sphincters of cetacean bronchioles functioned to entrap air in the alveoli. This air would remain in contact with respiratory epithelium during deep dives. We tested both hypotheses in a species that has these sphincters (*5*) and provided further information on diving depths of porpoises, a point of contention (*6, 7*).

The experiments were carried out with a male bottlenose porpoise *Tursiops truncatus*, 2.25 m long and weighing 138 kg. This animal ("Tuffy") has participated in numerous studies, including the Navy Sealab II experiment (*8, 9*), and has been employed to find and mark underwater equipment containing acoustic beacons. For this study two tasks were taught. The first required the porpoise to dive on acoustic command to a switch located at the end of a cable. Tuffy was required to press the switch turning the sound off and to return to the surface and exhale into an inverted water-filled funnel with the large opening about 50 cm below the surface (Fig. 1). He was also taught to breath hold just under the surface, again in response to a sound, and to exhale into the funnel on command. Thus expired air could be collected from any depth or duration of dive that the porpoise was willing to make.

Tuffy was trained to work with divers on the ocean bottom, and we took advantage of this to have him swim rapidly back and forth between two divers at 20 m depth so that expired air could be collected after exercise at that depth. He could also be commanded to come to, and exhale into, the funnel on any breath after a deep dive or after a surface breath hold. Thus we collected air samples of breaths from the 3rd to the 15th after a dive, from the 3rd to the 15th after a surface breath hold, and from random breaths during normal leisurely swimming. We also interrupted hyperventilation, which occurred in anticipation of deep dives, to collect expired air samples.

For deep-diving experiments Tuffy was released from his pen to swim beside a small outboard-powered boat to a diving site up to 8 km offshore. The porpoise usually took up a position in the boat's stern wave and thus actually "surfed" for most of the trip.

The deep-diving device consisted of an acoustic beacon, off switch, temperature sensor, and pressure transducer in a housing at the end of 308 m of five-wire marine cable. A control box in the

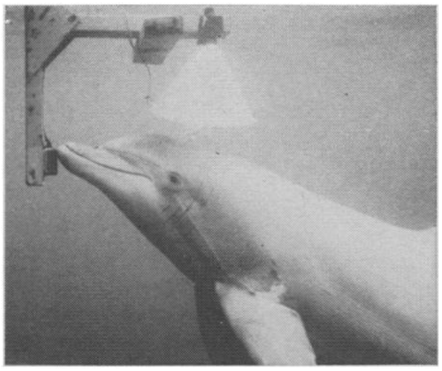

Fig. 2. Porpoise exhales into the funnel just below the surface.

boat which registered depth and temperature had a switch for the dive signal, and gauges. A hydrophone permitted us to monitor the acoustic signal from the deep-dive device.

When the porpoise returned to the surface and exhaled, the respiratory gas displaced the water in the funnel (Fig. 2); a stopcock was then opened, and water pressure forced the gas through polyethylene tubing into a lubricated 100-ml glass syringe. The first 100 ml was disposed of through a three-way stopcock, and the second 100 ml was collected for analysis. Duplicate samples were taken on each funnel full of air.

Initial analyses were done on a Scholander analyzer (*9*). With this experience we felt secure in using a less laborious method. This involved an infrared CO_2 analyzer (Godart capnograph) in series with a nitrogen analyzer (*9*). The oxygen content was determined by subtracting the sum of the CO_2 and N_2 values from 99 percent (100 minus 1 percent inert gas). The instruments were calibrated before and after each day's analyses with gas that had been analyzed on a Haldane apparatus.

Table 1. Percentage of oxygen and carbon dioxide in the porpoise's expired breath after dives to 200 m. Each line represents a figure from a different dive. On one dive the breath was collected on the first exhalation, on the next the ninth, followed by the third, and so on randomly.

Exhalation	Oxygen (%)	Carbon dioxide (%)
1st	5.4 ± 0.4	5.7 ± 0.5
3rd	11.9 ± 1.9	8.2 ± 0.6
6th	13.0 ± 1.2	7.5 ± 0.4
9th	13.2 ± 1.4	6.3 ± 0.7

The animal made 370 deep dives, over 120 breath holds at the surface, and four dives in which he swam back and forth between two divers on the bottom at 20 m. The pulmonary oxygen was much greater after dives to depth than after the surface breath holds of identical periods of time (Fig. 3). After rapid swimming at a depth of 20 m, the exhaled oxygen was considerably less than after a dive to 200 m requiring a similar amount of time and at least as much exercise. Carbon dioxide values for dives of 100 to 300 m were almost identical. Values of carbon dioxide for all dives were much lower than for surface breath holds.

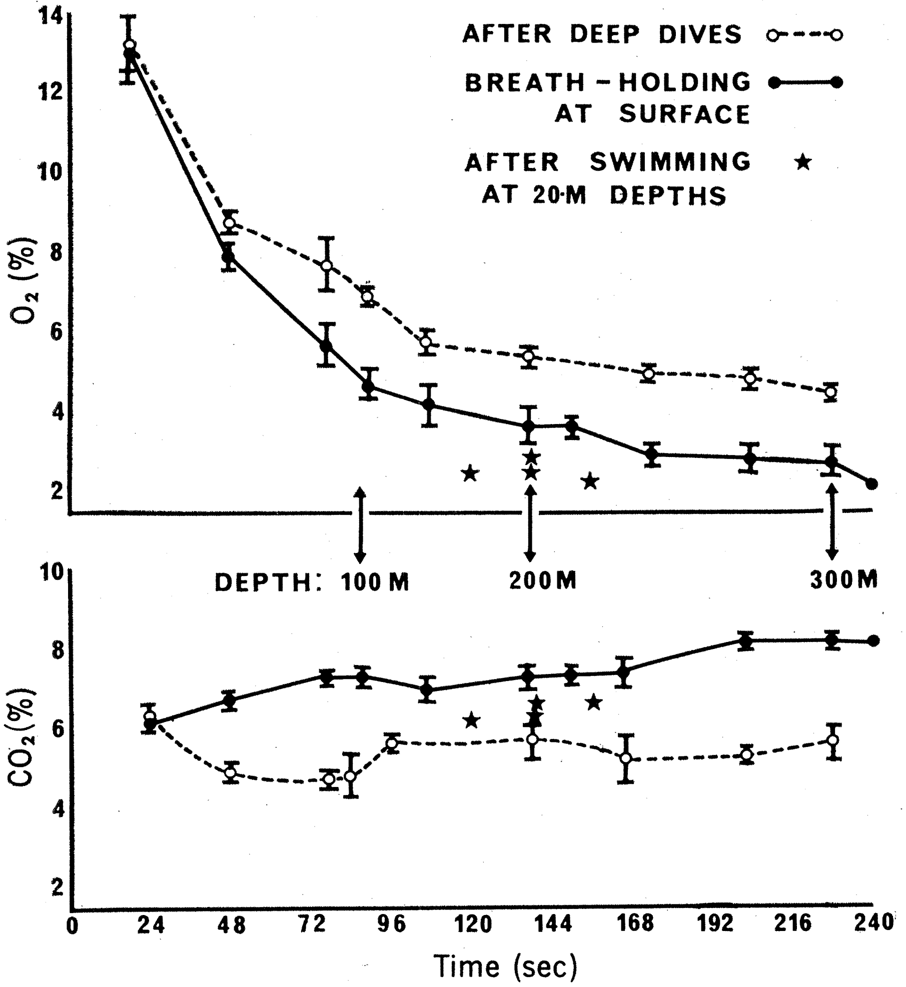

Fig. 3. Oxygen and carbon dioxide in porpoise breath after deep dives, after breath holding just under the surface, and after swimming at a depth of 20 m. Each point represents 7 to 20 dives or surface breath holds. The arrows indicate the average times and points on each graph that represent or correspond to dives of 100, 200, and 300 m.

Increasing depth with its greater pressure should be forcing more of the oxygen into the blood, yet less is used. This indicates that some of the gas in the lungs is isolated from the alveoli. The animal expires explosively, and much of the gas is not caught in the funnel. In spite of this we usually caught at least 3 liters. There clearly had been no great absorption of nitrogen.

It is obvious from close observation of the 370 dives and from the fact that Tuffy returns from depth and exhales several liters of air that he dives on inspired air. Numerous authors have suggested that all marine mammals dive on expiration (*10*). This appears to be true for Weddell, elephant, and harbor seals but not for porpoises.

Tuffy's tidal air, measured by having him exhale into a large calibrated canister, ranged from 5 to 6 liters. If we assume that tidal air is 80 percent of respiratory volume, then his volume is about 7 liters. At 300 m all of the air in Tuffy's lungs must be compressed into a volume of 200 to 260 ml. This volume is smaller than that of the trachea and bronchi, to say nothing of the nares and nasal sacs. When a large porpoise (200 kg) died at our facility, we inserted an endotracheal tube in an attempt to revive him. When this failed, we measured respiratory volume by first inflating the animal and then deflating as much as possible. The measured respiratory volume was 11 liters. The body with deflated lungs weighed 10 kg under water. On full inflation the body was just about neutral or very slightly buoyant. Pressure chamber tests on the fully inflated, freshly excised porpoise lungs indicated that the bronchi and trachea also collapse at depth. The interlocking cartilages of the trachea are heavy and strong, but structured in such a way as to make the trachea resilient rather than rigid (*11*). The bony nares seem to be the only structure of the respiratory system not collapsible, and their volume is no more than 50 ml. The air sinuses of the head contain vascular plexi that probably expand at depth in the same manner as proposed for seals and sea lions (*12*). Man is limited in the depth of his breath-hold dives by his ability to make such pulmonary and circulatory adjustments (*13*).

As the porpoise dives, the thorax starts to collapse. Divers have observed this at only 10 m, and by 60 m thoracic collapse is quite apparent. We have also observed this with underwater television. The lungs have a great deal of elastic tissue, and the flexible rib cage gives the porpoise a resilient thorax that continuously changes shape (Fig. (4).

From the porpoise's behavior and his echolocation clicks (*14*), it appeared that he knew approximately where the dive switch was by echolocating on it as it was lowered into the ocean and by listening to its acoustic beacon when the "go" signal was activated. Prior to dives of more than 150 m the porpoise always hyperventilated by taking three to ten breaths in rapid succession after the go signal was given. It appeared that he always achieved a certain minimum state of ventilation before he dived. This was not the case with surface breath holds on which he rarely hyperventilated. During the surface breath holds the porpoise had no way of knowing how long a breath hold would be required. To be rewarded he had to hold his breath until the breath hold command was turned off and the command to blow in the funnel was turned on. For deeper dives the porpoise hyperventilated even when the first dive of the day was to a depth of 250 or 300 m. Thus the hyperventilation cannot be accounted for by the animal's tiring after sever 1 successive dives or by his anticipation of deeper dives due to having made a series of dives that continued to increase in depth.

In one 34-minute session the porpoise made ten dives to 200 m. Twelve minutes and 52 seconds were spent at depths in excess of 100 m. In another such session 12 dives were made in 58 minutes and about 15 minutes were spent below 100 m. Between dives the porpoise would blow 8 to 15 times in 1 minute and dive again. Random expired air samples were collected (Table 1). Analysis on subsequent breaths after such dives gave values of about 13 percent oxygen but 7.5 to 9 percent carbon dioxide for the first few breaths after the dive. By the eighth to tenth breath after the dive, the content (O_2 + CO_2) of exhaled air was usually back to normal and the porpoise was willing to dive again. This unloading of CO_2 is compatible with measurements made on restrained porpoises (*3*).

The porpoise is not considered to be a good diver. The maximum voluntary breath hold that we have recorded was 7 minutes 15 seconds for a female in a pressure chamber, and 6 minutes for another female at the surface (*6*). Irving *et al.* (*15*) and Elsner *et al.* (*16*) observed maximum times of 6 minutes and 4 minutes 42 seconds, respectively. Tuffy has voluntarily held his breath on numerous occasions for over 4 minutes. His maximum effort has been 4 minutes 45 seconds.

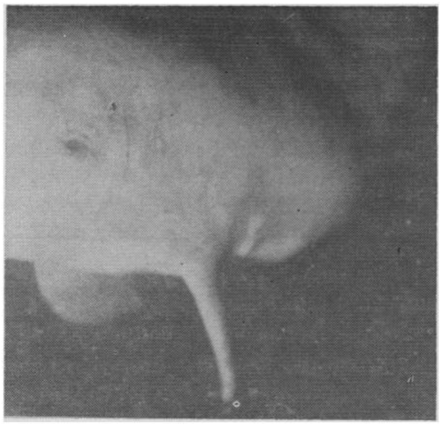

Fig. 4. The porpoise pushing the plunger of the diving test switch at a depth of 300 m. Thoracic collapse is apparent especially in the area behind the left flipper. The picture was taken with an underwater camera that was triggered when Tuffy pushed the plunger.

The extremely nonlinear decrease in partial pressure of oxygen in the lung with time indicates a nonlinear rate of oxygen supply. After 2 minutes the pO_2 of the expired gas is less than 0.05 atm. The oxygen-loading curve of the blood (*17*) implies very little oxygen capacity at these low values. Thus, during the final 2 minutes of a dive or a surface breath hold, the animal's cardiovascular system is functioning poorly as an oxygen-transport system.

In the expired breath 2 percent oxygen means an even lower concentration in the alveoli, for breath from the entire respiratory system is pooled. All the possible errors in our handling also appear to be in the direction of increasing the oxygen in the samples. We must conclude that the porpoise can tolerate very low concentrations of oxygen (3 percent or less) for 1 to 2 minutes.

Our data can be used quantitatively to estimate the extent of the decreased oxygen supply. The animal required about 90 seconds more to make a round trip to 300 m over the time it took to dive 200 m. In this time the oxygen content fell from 5.4 to 4.5 percent. We can assume this was the major flow of oxygen to the animal during this period. It amounts to 0.6 percent of lung volume per minute.

Swimming at the surface, Tuffy breathes three times per minute. The oxygen content in each breath is reduced by 8 percent (21 to 13 percent). Therefore, he consumes about 24 percent of tidal volume per minute (roughly 1340 ml/min). During the deeper part of a dive, oxygen is supplied to him 40 times more slowly than it is at the surface. Figures for surface breath holding are even lower for the final 90 seconds. The porpoise can withstand an alveolar oxygen supply 2.5 percent of normal for this much time.

We cannot completely discount the possibility of the porpoise drawing on an additional store of oxygen such as an isolated pool of oxygenated blood. It seems more likely that a nearly complete anaerobicity exists throughout the animal, including, at least partially, the brain. The small supply of oxygen indicated by our data should be barely enough for the heart. The initial adaptation of *Tursiops,* and most likely other marine mammals, has been to tolerate a much greater degree of temporary deprivation of oxygen in the tissues than terrestrial species can.

Prolonged breath holding is necessary for staying beneath the surface for extended periods. It alone does not allow the animal to go deep. This comes from adaptations in structure that provide flexibility so that air is compressed away from the alveoli during the period of increasing pressure of a dive. Nitrogen is prevented from going into solution in significant quantities, and the animal avoids any problem of the bends. Our data substantiate this earlier hypothesis.

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18. This work was made possible through the outstanding cooperation and performance of a singularly unique *Tursiops truncatus* that we named "Tuffy" because of his humanlike frailty of occasionally displaying an ill temper. We thank F. G. Wood who aided in all phases of the project; Drs. J. G. Simpson and J. Collins, and R. Pierce who reviewed the manuscript; T. Dohms and Dr. H. Chiodi who performed the Haldane analyses; and J. Walton and the Naval Missile Center's photographic unit for the pictures.

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Dialects in Elephant Seals

Abstract. *Threat vocalizations of male elephant seals* Mirounga angustirostris *vary among four populations on islands off the coast of California and Baja California, Mexico. Males at San Nicolas Island in Southern California emit sound pulses at more than double the rate of males at Año Nuevo Island, 528 kilometers north. Mean pulse rates at San Miguel Island and Isla de Guadalupe (408 and 944 kilometers south of Año Nuevo, respectively) are intermediate to these two. Pulse rate is homogeneous within each population and consistent in the same individual. Other properties of the calls which separate populations are pulse duration and embellishment of the initial or terminal pulse in a series. These geographical differences in vocal behavior resemble local dialects in birds and humans.*

Consistent differences in the predominant song or call of adults from different populations of the same species are called local dialects. The phenomenon has been described and studied most intensively in birds and has significance for diverse topics such as speciation, learning, and social communication (*1*). The only mammal in which dialects have been demonstrated is man (*2*). We now report differences in the threat vocalizations of males from different breeding populations of northern elephant seals *Mirounga angustirostris*.

During their 3-month breeding season, adult males haul themselves out of the water on island rookeries along the coasts of California and Mexico, and compete aggressively with each other for status in social hierarchies. Threat behavior is important in maintaining hierarchical relations between males. High-ranking bulls also threaten lower ranking bulls to keep them away from females. As a result, a few of the highest ranking males in each hierarchy do most of the breeding (*3*). A male threatens another male by elevating his head and forequarters and emitting a series of approximately 3 to 15 sound pulses which are loud, low-pitched, and guttural (*4*). After a pause in which the elevated posture is maintained, the vocalization may be repeated. The usual result is that the threatened animal moves away. Thus, threat calls enable one male to displace another with a minimum expenditure of energy. They are the predominant vocalizations of males and occur frequently throughout the breeding season.

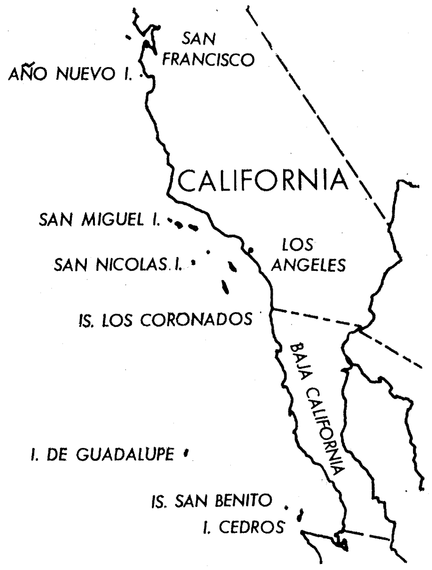

Fig. 1. Islands where northern elephant seals were known to breed in 1969.

We recorded threat vocalizations of full-grown males during the 1968 and 1969 breeding seasons at four major rookeries (*5*): Año Nuevo Island, San Miguel Island, San Nicolas Island, and Isla de Guadalupe (Fig. 1). The only large rookery not sampled is located on Islas San Benito, off the coast of central Baja California. Tape recordings were made from December through February with a Uher Report L recorder and a Uher M514 microphone; overall frequency response of the system was from 70 to 14,000 hz. Marked individuals were identified on the tape when possible.

Temporal analysis of all records was made by displaying uninterrupted series of pulses, called "bursts," on a Tektronix type RM 564 storage oscilloscope. The number of discrete pulses in a burst was counted, and the duration of each burst measured directly on the oscilloscope face as the interval between the peak of the first and last pulse. Wave-form analyses of recordings selected for minimum background noise were made with a Fairchild model 708A oscilloscope, and sound spectrograms were made with a Raytheon Rayspan spectrum analyzer and a Granger model 9010 electrostatic recorder.

We measured variation in pulse rate within individuals and between individuals both during a single season and from one season to the next, using 317 recordings of 43 adult males at Año Nuevo Island. Pulse rate was constant for each individual; 12 males for which we obtained 20 to 45 records apiece exhibited mean pulse rates of approximately 1.0 pulse/sec and standard deviations ranging from 0.04 to 0.09. Change in pulse rate from one year to the next was determined in two ways: by selecting randomly a single vocal burst from each of 23 males in 1968 and comparing this distribution to one similarly collected on 20 different males in 1969, and by comparing the pulse rates of 7 males on which we had records in two consecutive years. The first comparison yielded a mean rate of 0.97 pulse/sec with a