ARTICLE

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Where does the air go? Anatomy and functions of the respiratory tract in the humpback whale (*Megaptera novaeangliae*)

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ABSTRACT

Air is a limited resource under water. Pressure changes during diving and ascent further affect buoyancy and sound production/transmission by changing air volumes, densities, and shapes of air spaces and vibration pathways. This paper will focus on how humpback whales use air, and the respiratory tract adaptations that help overcome these challenges. These highly modified respiratory tract tissues function to shunt air to increase oxygenation for extending breath-hold time, conserve and recycle air, maintain hearing at depth, generate sound for communication and navigation, transmit vibrations to water, mitigate noise, support air spaces from collapsing, regulate chamber volumes, produce bubbles as visual signals, control air release as a tool to trap prey, modify center of gravity, regulate buoyancy, and reduce energy expenditure during locomotion. The humpback whale is able to utilize air in an aquatic environment in ways that allow it to support a wide range of unique behaviors.

RÉSUMÉ

L'air est une ressource limitée sous l'eau. Les changements de pression au cours de la plongée et de la remontée affectent la flottabilité et la production / transmission des sons en changeant les volumes d'air, les densités et les formes des espaces aériens et des voies de vibration. Cet article se penche sur la façon dont les baleines à bosse utilisent l'air ainsi que les adaptations des voies respiratoires qui participent au processus. Les tissus des voies respiratoires sont hautement modifiés et fonctionnent de manière à shunter l'air pour augmenter l'oxygénation afin de prolonger le temps d'apnée, de conserver et de recycler l'air, de maintenir l'audition en profondeur, de générer des sons pour la communication et la navigation, de transmettre des vibrations à l'eau, d'atténuer le bruit, d'empêcher les espaces devant contenir l'air de s'effondrer, de réguler les volumes des chambres, de produire des bulles servant de signaux visuels, de réguler la libération de l'air qui servira d'outil pour piéger des proies, de modifier le centre de gravité, de réguler la flottabilité, et enfin de réduire les dépenses d'énergie lors de la locomotion. La baleine à bosse utilise l'air dans un milieu aquatique de manière à assurer une multitude de comportements uniques.

INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are air-breathing mammals adapted to fully aquatic life. They are able to perform many functions underwater, including swimming, feeding, excreting, communicating, mating, birthing, nursing, and sensing their surroundings (Reidenberg 2007). One function, however, remains restricted to the surface: breathing. However, their simple "blow" is in sharp contrast to the complex respiratory tract hidden within their bodies.

Air (actually it is a mixed gas that is not necessarily atmospheric "air", as the molecular composition will vary depending upon the respiratory phase) is moved throughout the humpback whale's respiratory tract. What happens to that air? It is used for respiration, hearing, communication, navigation, visual displays, feeding, air conservation and recycling, locomotion, and buoyancy control, among other behaviors. The humpback whale respiratory tract consists of lungs, trachea, larynx, nasopharynx, bony nasal cavities, external nasal cavities, and blowholes, with air sac extensions into the pterygoid air sacs or "sinuses" (under the skull, near the ear) and the laryngeal sac (ventral to the larynx). This study explores the various air-containing spaces in the humpback whale, including the tissue folds, valves, and muscles that regulate these spaces, and how these structures are used for so many different functions.

MATERIALS AND METHODS

It is not feasible to observe internal respiratory tract anatomy in live humpback whales, as these methods generally utilize invasive approaches or internal imaging technologies (e.g., computerized axial tomography or CT scanning, magnetic resonance imaging or MRI, ultrasound scans) that are difficult or currently impossible to deploy in a field situation on wild, large-bodied whales. Therefore, this study uses post mortem anatomical findings to reconstruct the properties of the living tissues and derive the functions of the respiratory tract.

Observations were made from postmortem dissections of humpback whales. Twelve specimens were studied: four adults (all females), three juveniles (one female and two males), and five calves (three females, two males). No whales were killed for this

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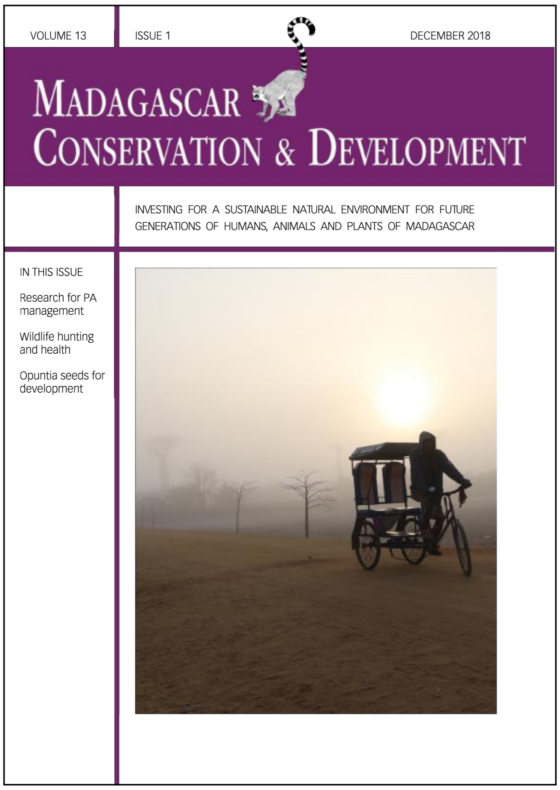

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study. All specimens were obtained after death.

One whale was found beach stranded on the east coast of Madagascar, and was collected and examined by the scientific team of the Cetamada organization. This is the first scientific specimen of a mysticete larynx collected in the Indian Ocean. The remaining eleven whales were from the Atlantic Ocean, and were found beach stranded along the northeast coastline of the United States of America (USA), specifically in the states of New York and Massachusetts. Specimens from these whales were collected and distributed through the Marine Mammal Health and Stranding Response Program (MMHSRP) of the National Marine Fisheries Service (NMFS) under the National Oceanic and Atmospheric Administration (NOAA), USA. Response to and examination of these stranded whales (including collecting tissue samples from the carcass) were authorized under NMFS permit No. 932-1905/MA-009526 in accordance with the Marine Mammal Protection Act. Tissue specimens are maintained under a letter of authorization from NMFS NOAA to possess and receive marine mammal hard and soft parts for comparative anatomy research (issued to the author). Specimen transfers were approved and arranged by the state Regional Stranding Coordinators of the MMHSRP: Riverhead Foundation for Marine Research and Preservation (New York), Atlantic Marine Conservation Society (New York), and the New England Aquarium (Massachusetts).

Visual inspection was made of the external nares (blow holes), including limited exposure of the nasal plugs and lateral plates that surround the nasal openings. The blowhole tissues were removed for further dissection from one male calf.

Laryngeal samples were taken whole whenever possible, including most of the trachea. Specimens varied greatly regarding degree of freshness or decomposition. Each larynx specimen was removed from the whale carcass using standard butchering techniques (knives and retracting hooks), occasionally assisted by use of heavy machinery to move or retract adjacent tissues. Whenever possible, the larynx was removed along with the hyoid bone (the attached bone was often used as a handle to assist in retracting the larynx out from the carcass). The larynx was then put into a holding container (plastic bag or plastic tub) and brought back to our laboratory for preservation by either freezing or immersion in formalin (10% formaldehyde solution).

Laryngeal dissections were carried out to assess the anatomy of the muscles, cartilages and joints, and soft tissues associated with sound production. Most larynges were initially cut along the dorsal midline and each side retracted laterally to reveal the ventral lumen including the laryngeal sac. The bisection was continued into the ventral aspect for some specimens, dividing the larynx in the midsagittal plane into left and right halves. Once photographs were taken, some specimens had the vocal folds (U-fold) removed so they could be prepared for future MRI or CT scanning. The rest of the specimen was then defleshed to assess the cartilaginous skeleton.

Visual assessments of pulmonary anatomy were made whenever possible while on site during the dissections of stranded whales. In many cases, limitations on dissection time prevented a full necropsy. In many dissections, the thoracic cavity was only partially opened, and thus lungs were not fully exposed. Lungs were thus usually examined in situ. No whole lung specimens were recovered for further dissection.

RESULTS

Specimens ranged in size (straight linear length from rostrum tip to notch between flukes) from 538cm to 1550cm. Specimen data are given in Table 1.

The humpback whale respiratory tract consists of lungs, trachea, larynx, nasopharynx, bony nasal cavities, external nasal cavities, and blowholes, with air sac extensions into the pterygoid air sacs or "sinuses" (under the skull, near the ear) and the laryngeal sac (ventral to the larynx). The larynx is interlocked with the nasal cavity, and the digestive pathway passes lateral to this interlock (Figure 1). The lungs are paired, and reside mostly along the dorsal aspect of the thoracic cavity. Interestingly, they are not divided into lobes, even though the primary (mainstem) bronchi do divide into secondary and tertiary bronchi within the lungs.

Tracheal cartilages are irregular in shape and spacing, but are generally of similar thickness. Sometimes they form discrete O-shaped rings, and sometimes they bifurcate or fuse with neighboring rings. Rings closer to the carina tend to be distinct, but rings close to the larynx are usually fused together dorsally and incomplete ventrally. This fusion becomes more pronounced rostrally, where they cannot be distinguished from the cricoid cartilage of the larynx (Figures 2 and 3). The primary (mainstem), secondary, and tertiary bronchi are reinforced by cartilage rings. There is an eparterial bronchus branching into the right lung rostral to the right mainstem bronchus (Figure 4).

The lumen of the tracheo-laryngeal junction contains several parallel and thin soft tissue folds along the ventro-lateral aspect (Figure 4). These folds are gently curved into an S-shape that begins parallel to the trachea (i.e., parallel to the long axis of the trachea but perpendicular to the tracheal cartilage rings) and ends directed towards the lateral edges of the vocal folds (i.e., parallel to the tracheal rings and perpendicular to the long axis of the trachea). There do not appear to be any muscles associated with these S-shaped folds, but they appear to contain tough connective tissue fibers, as they do not decompose as easily as the adjacent mucosal tissues.

A midline thickening is found along the dorsal aspect of the laryngeal lumen (Figures 4 and 5). It appears to be mostly comprised of fatty tissue. We referred to this swelling as a "cushion" due to its soft, compressible texture. The cushion is positioned directly dorsal to the gap between the vocal folds. The cushion's shape is ovoid and elongated in the long axis of the trachea and

Table 1. List of the 12 specimens of humpback whale (*Megaptera novaeangliae*), including age, sex, body length, field ID number, and location of stranding. (Field ID letter codes: NY = Okeanos Ocean Research Foundation, or Riverhead Foundation for Marine Research and Preservation, New York; MH = New England Aquarium, Cape Cod Stranding Network, or International Fund for Animal Welfare, Massachusetts; MAD = Cetamada, East coast of Madagascar)

Age	Sex	Length	Field ID number	Location
Calf	Female	548cm	NY-2411-00	New York, USA
Calf	Female	794cm	NY-881-92	New York, USA
Calf	Male	845cm	MH-96-479-MN	Massachusetts, USA
Calf	Male	not available	MH-98-629-MN	Massachusetts, USA
Calf	Female	850cm	NY-2700-01	New York, USA
Juvenile	Male	960cm	NY-4270-2010	New York, USA
Juvenile	Female	962cm	NY-814-91	New York, USA
Juvenile	Male	not available	AMCS20Mn2017	New York, USA
Adult	Female	1386cm	NY-766-91	New York, USA
Adult	Female	1535cm	NY-2818-2002	New York, USA
Adult	Female	not available	NY-4790-2013	New York, USA
Adult	Female	1550cm	MAD-201601-MNX	Sambava, Mada.

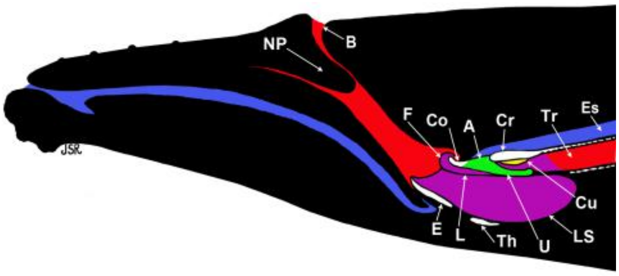

Figure 1. Schematic diagram of a humpback whale head showing the respiratory tract (red), digestive tract (blue), laryngeal lumen (purple), cartilages (white), cushion under the cricoid cartilage (yellow), and U-shaped vocal fold supported by the arytenoid cartilage of the right side (green). (A = arytenoid cartilage, B = blowhole, Co = corniculate cartilage, Cr = cricoid cartilage, Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, Es = esophagus, F = flap of tissue from the corniculate cartilage, L = lip of the vocal fold, LS = laryngeal sac shown partially inflated, NP = nasal plug, Th = thyroid cartilage, Tr = trachea, U = U-shaped vocal fold)

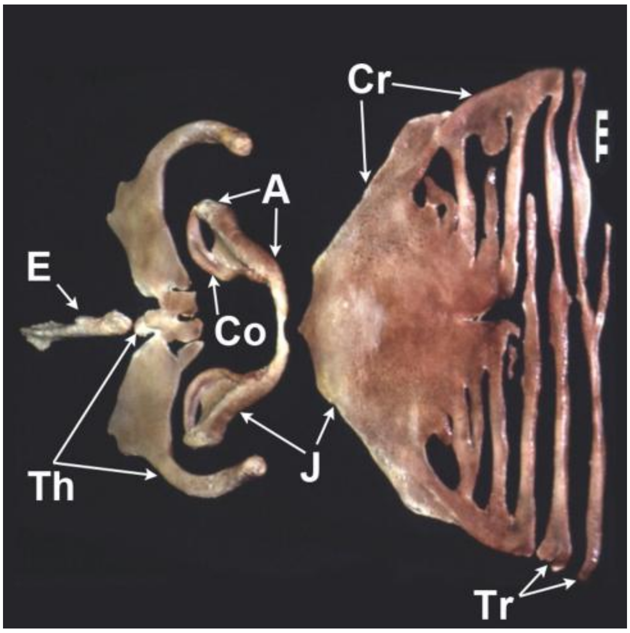

Figure 2. Disarticulated laryngeal cartilages from a juvenile female humpback whale, dorsal aspect. (Rostral is to the left, caudal is to the right, dorsal is exposed, and ventral is hidden. A = arytenoid cartilage, Co = corniculate cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, J = synovial joint between the arytenoid and cricoid cartilages, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm)

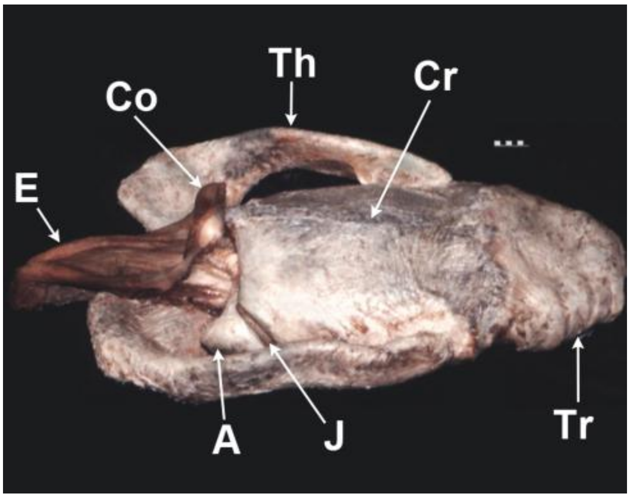

Figure 3. Articulated laryngeal cartilages from an adult female humpback whale, lateral-oblique aspect. (Rostral is to the left, caudal is to the right, dorsal is top, and ventral is bottom of figure. A = arytenoid cartilage, Co = corniculate cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, J = synovial joint between the arytenoid and cricoid cartilages, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm)

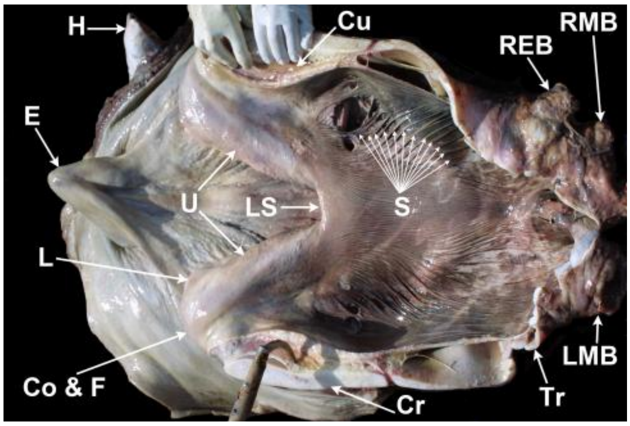

Figure 4. Larynx from an adult female humpback whale, viewed from dorsal aspect. Rostral is to the left, caudal is to the right, cricoid cartilage incised in midline and reflected laterally to expose lumen. (A = arytenoid cartilage, Co & F = corniculate cartilage and flap (they have become soft with decomposition and are draped over edge and disappear ventrally), Cr = cricoid cartilage (retracted on the left by a metal hook, and on the right by two gloved hands), Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, H = hyoid apparatus (probably the thyrohyal portion), L = lip of the vocal fold, LMB = left mainstem (primary) bronchus, LS = laryngeal sac (begins underneath the letters U and LS, but extends in the direction of the arrow under the ligament that joins the two U-shaped vocal folds), REB = right eparterial bronchus (epibronchus), RMB = right mainstem (primary) bronchus, S = S-shaped folds, Tr = trachea, U = U-shaped vocal folds. Note: Although there are some holes in the mucosa due to decomposition, the S-shaped folds remain intact thus indicating they may be comprised of stiffer tissues (more collagen connective tissue fibers?). The many parallel S-shaped folds may direct air from the trachea to the gap between the U-shaped vocal folds)

larynx, being thickest in the midline and tapering laterally, rostrally, and caudally. This ovoid shape is matched to the long gap that runs rostro-caudally between the U-shaped vocal folds in the plane of the glottis (glottic gap). It appears to seal the glottic gap when the vocal folds are raised towards the cushion, or perhaps dampen vocal fold vibrations when making slight contact.

There are three unpaired cartilages (cricoid, thyroid, and epiglottis), and two fused paired cartilages (aryteno-corniculate complex) that comprise the larynx (Figure 2). The cricoid is located dorsally. It is very broad but incomplete ventrally. As previously mentioned, it is fused to the tracheal rings caudally and laterally. The rostro-lateral edges are tapered diagonally away from the midline, and support the synovial joint for the articulation of the arytenoid cartilages (Figure 3).

The midline of the thyroid cartilage is located on the ventral aspect of the larynx, and is positioned closer to the rostral end of the larynx (Figure 2). Its body is relatively small, compared to that found in most other mammals. It does not fold sharply between the two lamina, nor does it have a strong ventral prominence ("Adam's apple"). It does have a notch in the rostral midline that is largely occupied by the epiglottic cartilage (Figure 6). The superior horns (cornua) extend superiorly and curve caudally in an arch that connects to the lateral aspects of the cricoid cartilage (Figure 3).

The epiglottic cartilage is softer than the other cartilages, even in fresh specimens. In decomposed specimens, it appears to decompose faster (perhaps indicating a higher water content and lower degree of perichondrial fibrous tissue), and becomes very flexible (Figure 6). When defleshed, its boundaries are difficult to ascertain, as the edges do not have a thickened covering of fibrous tissues as do the other cartilages. The epiglottic cartilage has many holes throughout its body, giving it a perforated appearance. It is unclear what occupies these holes in life. The overall shape resembles the curved outer walls of a half cylinder (i.e., with a hollow center), with the convex aspect facing rostrally towards the oral cavity, and the concave aspect facing toward the laryngeal aditus. The base is thicker than the apex. The apex is pointed, and directed into the nasopharynx. The rostral aspect (the convex surface) faces the oral cavity, and is covered along the superior aspect by the soft palate. The epiglottis (epiglottic cartilage with its covering flesh) rests posterior to the soft palate, and is positioned in contact with this tissue at rest (Figure 5).

Arytenoid cartilages are paired, and each one is fused to a corniculate cartilage (Figure 2). The aryteno-corniculate complex extends both caudally and rostrally. The caudal extension is comprised of arytenoid cartilage, and supports the tissue of the vocal fold (Figure 1). The distal caudal tip is curved medially and is attached to the other arytenoid cartilage's distal caudal tip by a ligament (likely the homolog of the vocal ligament) (Figure 2). This joining gives the pair of vocal folds the appearance of one continuous U-shaped fold (Figures 4 and 5). The caudal extensions are cylindrical, and give this same shape to the vocal fold tissue that covers them. This tissue has several smaller folds along the dorsal aspect that may indicate some flexibility during vibrations. The tissue covering the medial aspect is smooth and flat, and appears to seal against its pair during adduction. The tissue covering the rostro-ventral region (just before the corniculate portion of the complex) is extended into a thickened lip-like shape (Figures 4 and 5). The "lips" of the opposed pair may part and re-seal, perhaps interrupting airflow to create pulsed sounds. The ventral surface of the vocal folds is continuous with the lateral walls of a ventral diverticulum called the laryngeal sac (vide infra).

The aryteno-corniculate complex extends as the corniculate cartilage rostrally (Figure 2). The corniculate projects superiorly and curves cadually towards the cricoid cartilage. The rostral, convex edge supports a flap of tissue called the corniculate flap (Figures 3 and 5). This tissue projects rostrally as a thin plate. As it is only supported by cartilage caudally, the rostral extension is very flexible. The paired corniculate flaps lie side by side, oriented in the sagittal plane. If the flaps move medially then they contact each other (adduction), and if the flaps are parted laterally then the space between them is enlarged (abduction). They are joined dorsally by a thin tissue that spans the midline. Ventrally, the space between them is continuous with the laryngeal aditus. The two flaps appear to nest into the trough-shaped lumen of the dorso-caudal aspect of the epiglottis.

At the midpoint of the aryteno-corniculate complex, there is a joint surface (on the caudal aspect) that is part of the arytenoid portion of the cartilage complex. Each arytenoid joins the rostro-dorsal edge of the cricoid cartilage at a synovial joint – one on each side of the larynx (Figure 3). The joint is curved, and elongated on a diagonal slope away from the midline. The curved shape enables the cartilage to rock rostrally and caudally, rotating around an axis oriented between left and right. The extension of the joint surface along a diagonal slant allows the cartilage to slide rostro-caudally, while also adducting as it moves rostrally and abducting as it moves caudally. There also appears to be an ability to rock the arytenoid medially and laterally along this diagonal surface, causing the distal (caudal) arytenoid tips to abduct or adduct.

Each arytenoid has a projection on the lateral aspect called a muscular process (Figure 3). The muscular process supports the posterior and lateral cricoarytenoid muscles. Manual manipulation of the joint reveals that the posterior cricoarytenoid can pull the

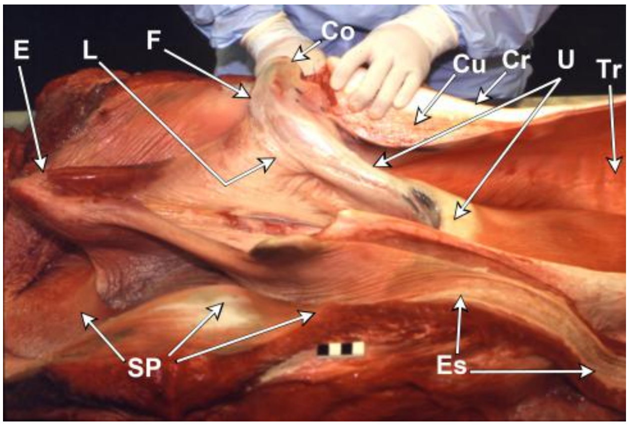

Figure 5. Larynx from a juvenile male humpback whale, viewed from lateral-oblique aspect. Rostral is to the left, caudal is to the right, cricoid cartilage incised in midline and reflected laterally to expose lumen. (Co corniculate cartilage, Cr = cricoid cartilage (retracted on the right by two gloved hands), Cu = cushion under the cricoid cartilage, E = epiglottic cartilage, Es = esophagus, F = flap of corniculate cartilage, L = lip of the vocal fold, SP = soft palate (note epiglottis lifted up so is not in direct contact with area indicated by left arrow, and note additional center and right arrows indicating extension around corniculate cartilage as palatopharyngeal sphincter, that was cut in the dorsal midline, exposing the musculature above the scalebar), Tr = trachea, U = U-shaped vocal folds. Scale bar: each black or white square = 1 cm. Note: the cushion is positioned directly above the vocal folds, and matches the gap between them in length. The cushion may serve as a valve blocking airflow between the laryngeal sac and the trachea, or may dampen vibrations from the U-shaped vocal folds)

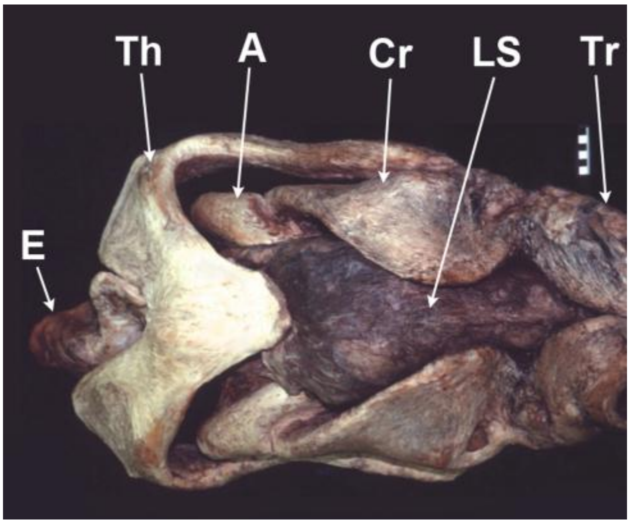

Figure 6. Articulated laryngeal cartilages from an adult female humpback whale (same specimen shown in figure 3), ventral aspect. Rostral is to the left, caudal is to the right, dorsal is hidden, and ventral is exposed. (A = arytenoid cartilage, Cr = cricoid cartilage, E = epiglottic cartilage, LS = laryngeal sac, Th = thyroid cartilage, Tr = trachea. Scale bar: each black or white square = 1 cm. Note: some of the laryngeal sac is hidden underneath the thyroid cartilage in the midline. However, the bulk of the laryngeal sac is positioned in the gap caudal to the thyroid cartilage and between the lateral aspects of the cricoid cartilage)

muscular processes towards the midline, perhaps resulting in rotation of the vocal folds. Further manipulation of the joint reveals that the lateral cricoarytenoid can pull the muscular processes laterally, parting the vocal folds. There is also an interarytenoid muscle between the base of each corniculate extension. Squeezing the arytenoids together in the direction of this muscle's fibers causes adduction of the vocal folds and corniculate flaps. The cricothyroid muscle was not manipulated, but the fiber direction indicates that it can bring the base of the thyroid cartilage closer to the cricoid. It is unclear what this action accomplishes, but it may collapse the laryngeal lumen and laryngeal sac. Manual pressing of the V-shaped thyroid cartilage against the ventral aspect, where there is no other cartilage support (as the cricoid is incomplete ventrally), collapses the laryngeal sac (Figure 6).

The musculature of the thyroarytenoid and/or vocalis appear to be extended circumferentially around the laryngeal sac. This is verified by the presence of the recurrent laryngeal nerve innervating the sac's musculature. The circumferential muscle layer surrounding the laryngeal sac is very thick, and appears to be a forceful means of contracting the sac (independent of thyroid cartilage compression). No intrinsic laryngeal muscles were observed that can expand the sac. Extrinsic muscles were not fully dissected as they were always severed from the sternum and sometimes detached from the hyoid. Remnants of their attachments indicate that when they pull the larynx rostrally (e.g., hyoepiglotticus, thyrohyoid) they can extend the laryngeal sac in the rostro-caudal axis, and when they pull it caudally (e.g., sternothyroid, sternohyoid) they can help compress it.

The laryngeal sac is a ventral diverticulum located below the vocal folds (Figures 1 and 6). The glottic gap is the entrance to the laryngeal sac's lumen (Figure 4). The lateral walls are supported dorsally by the arytenoid cartilage extensions inside the vocal folds. The laryngeal sac extends caudally under the trachea. There are no tracheal cartilages immediately above the laryngeal sac. This may allow the sac to distend into the tracheal lumen from below and narrow the trachea's volume. The deflated laryngeal sac (including its thick musculature) occupies a volume that is approximately equal to that of the trachea and larynx, and appears to be able to swell to an even greater volume. During dissection, it was apparent that the combined volume of the collapsed laryngeal sac and larynx was very close to the volume of one whole (mostly deflated) lung, but likely can double in size and inflate to a volume close to the total of both lungs. The laryngeal sac has a row of pits on either side in the caudal region of the lumen. It is unclear what is inside the pits. The left and right sides of the sac are joined in the midline at a median raphe. This raphe is supported by a ligament that connects caudally in the midline to the ligament between the caudal tips of the vocal folds, and connects rostrally in the midline to the caudal edge of the thyroid cartilage. It appears to be the remainder of the homolog of the fused vocal ligaments. This homology is supported by the presence of the internal laryngeal branch (sensory portion) of the superior laryngeal nerve innervating the mucosal surface of the laryngeal sac on either side. As in other mammals, this sensory branch only innervates the larynx superior/rostral to the level of the glottis.

The rostral aspect of the larynx (unpaired epiglottis and paired corniculate cartilages with their flaps) is inserted into the nasopharynx (Figure 1). The opening into the larynx (laryngeal aditus) is thus aimed at the nasal region. The soft palate is extended laterally around the epiglottic and corniculate cartilages, and connects behind them, forming a circular sphincteric valve (palatopharyngeal sphincter) sealing the entrance to the nasopharynx (Figure 5). The soft palate's mass is much larger anteriorly than it is posteriorly, and contains musculature that can tighten its grip around the epiglottic and corniculate cartilages. This appears to help seal the aditus from incursions of water or food during swallowing or other open-mouthed behaviors. The epiglottis can be removed from behind the soft palate, and inserted into the mouth. Although it is difficult to bend the epiglottis in a fresh specimen, this movement into the oral cavity is easily accomplished when the soft palate (rostral portion of the palatopharyngeal sphincter) is lifted superiorly manually.

Above the nasopharynx are the openings to the paired bony nasal passageways at the bottom of the skull (posterior choanae). These two cylindrical chambers are angled superiorly in a diagonal rostro-dorsal plane. The bony nasal passageways widen as they approach the top of the head, and terminate in two separate blowhole openings. The blowholes are protected from water incursions by a prominent rostral ridge that serves as a splash-guard, deflecting water laterally (Figure 1). The blowholes (nostrils, external nares) are valvular, and can be closed by opposing the lateral surface towards the medial surface. This tissue is stiffened by cartilage plates that are moved by facial muscles. In addition the nostrils can be completely sealed by the nasal plugs. Each plug is a curved tongue-like structure that is inserted into the nasal passageway. It can be retracted during breathing, but at rest it remains covering the passageway, thus sealing it from water (Figure 1). Facial muscles are responsible for retracting the plugs anteriorly to open the blowholes.

DISCUSSION

AIR SHUNTING. During respiration (inhalation and exhalation), the air moves between the blowholes and the lungs, following the most direct pathway. When the whale is submerged, air inspired into the lungs is likely to become oxygen depleted relatively quickly. The whales may be able to extend their breath holding time by shunting air between the lungs and other respiratory spaces. This would allow the whale to turn over the oxygen-depleted "used" air in the lungs, exchanging it for more oxygen-rich "unused" air that was previously trapped in non-respiratory spaces (nasal cavities, respiratory diverticulae, larynx, and trachea). Shunting oxygen-rich air from these spaces to the lungs may allow continued gas exchange to occur, effectively giving the whale additional breaths underwater.

The shunting mechanism appears to involve pushing air back and forth between two flexible-walled spaces that can alternately stretch and recoil. The parallel nasal passageways through the skull are not likely to be involved in such shunting because their walls are not flexible since they are constrained by bone. However, the lungs and the soft-sided laryngeal sac are perfect for this function. As the diaphragm contracts, air is drawn from the nose, past the larynx, through the trachea, and into the lungs. No more air can move in from the nostrils while underwater. Air is also unlikely to move in from the mouth, even if it were held above water, because the oral cavity is usually isolated from the respiratory tract (Reidenberg and Laitman 2007a). This isolation of the two pathways is an essential cetacean adaptation that prevents drowning during underwater open-mouthed behaviors (Reidenberg and Laitman 1987). Instead, additional respiratory-like movements may occur through shunting of air between various chambers. As air is unlikely to move back into the rigid nasal region, shunting probably occurs between the lungs and laryngeal sac. Air is may be diverted from the full lungs (through thoracic intercostal muscle contractions compressing the ribs together and shrinking lung volume) and into an expanding laryngeal sac, located ventral to the larynx. Capturing the air in the sac ensures that it is not lost to the environment (conserved) and therefore can be used again (recycled). Once the laryngeal sac is fully expanded, it can compress via contraction of its circumferential musculature, evacuating its gas back through the larynx and trachea and to the lungs. The volume of the laryngeal sac is at least as large as one lung (Reidenberg and Laitman 2010), and possibly can be expanded to match the volume of both lungs. If so, compression of the sac would expel laryngeal sac air back into both lungs, filling them completely. This shunting most likely occurs when dive depths pressures are relatively shallow and ambient pressure does not force complete collapse of the airways.

Of course, the degree of expansion of any of these spaces is subject to the forces of ambient pressure. The lungs collapse and gas volumes shrink with increasing ambient pressure during a dive (Kooyman and Ponganis 1998). Presumably, there is a depth (and therefore pressure) at which these air spaces will completely collapse, and shunting will no longer be possible. The expandable laryngeal sac may therefore also function as an accessory air reservoir, allowing the whale to compensate for the effects of pressure. It may use these reserves to add volume to the essential air chambers, thereby maintaining a functional volume (e.g., for vocalizations) under conditions in which the more typical respiratory space volumes would have otherwise completely collapsed.

Maintaining essential air spaces at depth is also important for hearing, as the tympanic membrane (ear drum) and ossicles (ear bones) cannot vibrate to transmit sounds unless they are suspended in an air-filled chamber. In this mechanism, sound vibrations are likely received by fat associated with the lower jaw (Yamato et al. 2012). This is the mechanism toothed whales use for sound reception (Koopman et al. 2006). The sound is then transmitted to the fat/tissue interface of the tympanic membrane. Movement of the tympanic membrane (that is extended into a structure often called the "glove finger"), causes vibration of the attached ossicles that, in turn, vibrate the oval window and the fluid within the cochlea (Ketten 2000). Different frequencies (i.e., sound wavelength) and magnitudes (i.e., sound amplitude) are then detected by the specialized hair cell receptors of the cochlea that then transmit the signal to the brain. As air spaces collapse, some of the remaining air is preferentially held in the pterygoid air sac (Reidenberg and Laitman 2008). This air sac is located under the skull and connects with the middle ear space. Air fills this sac through a connection with the pharynx. As the pharynx collapses at depth, what little air remains is likely shunted into the pterygoid sac. As the pterygoid sac then begins to collapse, its remaining air is shunted in turn to the middle ear. Diving depth may thus be limited to ranges where hearing is still functional because the middle ear airspace has not yet collapsed. Alternatively, another hearing mechanism may be used that avoids the necessity of maintaining a middle ear air space. This would enable the whale to dive even deeper, reaching depths where the pterygoid air sac would completely collapse. This alternative mechanism uses vibrations that are conducted along the bone of the skull directly to the ear (Cranford et al. 2010, Cranford and Krysl 2015).

SOUND PRODUCTION AND TRANSMISSION. Humpback whales are well known for their elaborate songs, sung by the adult males predominantly in a range between 40Hz and 4kHz (Au et al. 2001, 2006, Mercado et al. 2003, Herman et al. 2013). Singing behavior occurs in both the northern and southern hemisphere humpback whales and, although all whales in a given population sing the same song at the same time, neighboring populations are influenced through cultural transmission to sing the same song (Clapham 2017). As mammals, whales have inherited a pneumatic sound generating system, similar to what land animals use. This presents a major transmission problem underwater, as sound waves generated in air by vibrations of the vocal folds (vocal "cords") do not transfer to water. Through evolution, humpback whales and other baleen whales (mysticetes) have developed a unique larynx (voice box) with vocal fold homologs that are fused caudally (called "U-shaped fold") that enables them to generate and then transfer sounds to water (Laitman and Reidenberg 1999, Reidenberg and Laitman 1999, 2007b). Air passing from the lungs to the trachea is diverted away from the usual path to the blowholes. Instead, it is directed 90 degrees inferiorly away from the nasal cavities and towards the throat region. The air passes through a gap between the U-shaped vocal folds. The vocal folds are also re-oriented 90 degrees (compared to terrestrial mammals) so that they are parallel to the long axis of the trachea. Interestingly, a similar configuration also occurs in toothed whales (odonotcetes), except that the reorientation of vocal folds parallel to airflow occurs in the opposite direction (Reidenberg and Laitman 1988, 1999). Air passing between these folds should cause the tissues to vibrate, generating sound (Mercado et al. 2010, Adam et al. 2013, Cazau et al. 2013).

Note that while singing is typically done by adult males, the females and juveniles have also been recorded making sounds. These sounds are more social, including mother-calf calls or feeding calls that coordinate the upward lunge through a bubble-net. The same anatomy described for song production is likely used for these calls as well. Further work is needed to elucidate the specific sounds that can be generated by the various parts of the vocal apparatus (vide infra on corniculate flaps).

Unlike terrestrial mammals, whales must transfer sound energy to water. Any sound waves generated in the air spaces of the head are "lost" as they are not transmitted out of the whale and into water. Rather, it is the vibrations within the tissue itself that are likely propagated to water. These vibrations appear to be transferred to the laryngeal sac tissue that is attached immediately ventral to the vocal folds. As the walls of the sac vibrate, they move the overlying blubber and skin of the throat region that is made more flexible by the presence of expandable throat grooves. The laryngeal sac and the overlying blubber and skin then pulse, like a drum-head, transferring these pressure waves directly to the water. As flesh is very close in density to water (it is largely comprised of water), there is relatively little transmission loss. This makes it more efficient than the terrestrial mechanism of transferring vibrations from tissue to air.

The many axes of movement of the vocal folds, and their geometry, likely plays a major role in determining the qualities of the produced sounds. Versatility of vocal fold movements may indicate nimble muscular control, and pulse speed (frequency) and intensity (amplitude) may indicate robust fitness. Thicker and longer folds likely produce lower frequency and louder amplitude sounds. As such, the vocalizations may be a true advertisement of the whale's health, stamina, agility, and size, and therefore may be very important in mate competition/selection and in establishing social hierarchy.

The head-down position of singing whales may also assist in directing the sound waves in a trajectory that allows maximum propagation away from whale. In the head-down position, the laryngeal sac faces outward, rather than inferiorly towards the sea floor. As the laryngeal sac vibrates the overlying blubber and skin, the pulses transferred to the water would be directed horizontally. Additional vibrations may also occur through pulses directed at the air columns of the nasal cavities (like a pipe organ). These pulses may move the nasal plugs and emit sounds dorsally (that would be directed horizontally, in the opposite direction from the laryngeal sac, in a head-down position). Alternatively, the bony walls of the nasal cavities may vibrate and send pulses through the skull to be transmitted circumferentially from the head to the water. These air-containing resonant spaces may contribute to the overall quality of the emitted sound (Mercado et al. 2010).

A second sound production mechanism may occur in the larynx at the site of the corniculate flaps. These flattened tissues are aligned side-by-side, and can be parted by air flowing between them. As air flows past, these tissues likely clap against each other, generating pulsed sounds. It is unclear how these pulses are transmitted outside the head, although it is possible that they are either transmitted inferiorly by the attached vocal folds to the laryngeal sac, or that they are propagated superiorly along the walls of the nasal cavity. Having a dual sound source may explain some of the unusual sounds humpback whales can generate.

There are several other points of constriction along the respiratory tract (vide infra on valves), and vibration of any of these may generate sound. Perhaps some dual or multiple energy peaks of whale sounds are generated in a manner similar to how a bagpipe works. If a fundamental frequency is made at the laryngeal sac (similar to the bagpipe's main "bag"), then overtones may be created by adjusting structures downstream of the compressive forces on the laryngeal sac (similar to fingers on the holes of one pipe, harmonics in the other pipes). In some ways, it is reminiscent of overtone singers (or Mongolian throat singers) who generate laryngeal fundamental frequencies, and then create higher frequency overtones by adjusting airflow through the mobile constrictions made by opposition of the tongue, soft palate, and pharyngeal wall.

While it is generally assumed that sounds are made as air flows egressively (away from the lungs), it is also possible that sounds may be made on the ingressive flow (towards the lungs). In this case, contraction of the laryngeal sac may drive the system by increasing sac pressure thus sending air flowing back to the lungs. Air rushing past any constrictions in the respiratory tract would generate vibrations for sound production.

It is important to note the role of the laryngeal sac in extending the length of a vocalization. In a closed system, the volume of air is limited. With rigid walls, the flow of air can only occur until both sides reach equilibrium. Once flow stops, so does sound production. However, if the air-receiving chamber is flexible, then flow time (and therefore vocalization length) can be extended until the distensible chamber reaches full capacity. Therefore, the laryngeal sac, being a highly distensible chamber, facilitates longer songs because the expansion delays pressurization of the respiratory system.

VALVES. The laryngeal sac also may function as a valve when it is fully inflated, an idea originally proposed for the bowhead whale's larynx (Schoenfuss et al. 2014). As the sac is located directly underneath the cartilage-free region of the trachea, this tissue is very flexible. Expansion of the sac may therefore raise the ventral tracheal wall, thereby creating a valve as it collapses the tracheal lumen. Schoenfuss et al. (2014) proposed that this arrangement forced air to only be shunted between the laryngeal sac and the nasal region. This is difficult to accept, as the bony nasal passageways in the skull do not have flexible walls that can expand to accommodate the air from the sac. Rather, we propose that the inflated laryngeal sac does not completely obstruct the trachea.

Rather than serving as a valve that blocks airflow in the trachea, it is possible that the upward bulge of the inflated laryngeal sac simply divides the trachea in the midline into two lateral chambers. This might enable simultaneous bi-directional flow, and therefore continuous sound production, as air on one side may flow ingressively towards the lungs while on the other side it may flow egressively towards the larynx. This idea is slightly flawed, however, because continuous flow would imply a steady contraction of both sac muscles and intercostal muscles. This cannot happen, because contraction of both structures would simply compress the total volume and raise the pressure, rather than send the air flowing in a particular direction. It could only work if the division extends all the way to the carina and allows one lung to inflate while the other deflates. This implies unilateral thoracic wall contraction. This theory is still not ideal because it is unclear how a single laryngeal sac could accommodate bidirectional flow. Rather, the inflated laryngeal sac's effect on the trachea may simply be a mechanism to compensate for volume loss at depth due to raised ambient pressure. Maintaining lateral air channels, however, would still allow flow to occur between the laryngeal sac and the lungs (although it is unlikely to be simultaneously bi-directional). The rationale for collapsing the trachea in this manner is that it allows airflow even though the total air volume is shrinking due to the higher pressure at depth.

TRACHEAL FOLDS. The trachea's lumen has a series of thin parallel tissue folds along the lateral aspects that direct airflow in an S-shaped pattern. The folds appear to act like sails on a sailboat, or blades on a turbine. As the airflow passes along these folds, they become stiffened and are pushed laterally. In this manner, the folds appear to act as buttresses for the tracheal walls, helping to rigidify them. Since the S-shaped folds are curved (like the cupped blades of a fan), the vector of force from the airflow hitting the folds appears to be directed rostro-laterally, forcing the tracheal wall outwards. The airflow is then reflected off this curved surface in a rostro-medial direction, towards the vocal folds. Therefore, the curving shape of the parallel series of folds helps to simultaneously push the walls laterally while directing air towards the vocal folds. Without such lateral support, the entire trachea would collapse and shut off all airflow at depth, and likely prevent any vocalizations. The unusual anatomy of this part of the trachea therefore indicates that extra support is given to the lateral passageways to hold the passageways open (despite rising ambient pressure forcing volume collapse), and thus enable airflow for vocalizations.

Another possible function of the tracheal folds is to reduce "noise" generated by airflow passing over the textured surface of the tracheal lumen. The small ridges created by the tracheal rings can disrupt laminar airflow and generate turbulence along the edges, in turn generating accidental noise. Since the tracheal folds are oriented perpendicular to the tracheal rings, they could break up this accidental noise and thus contribute to a "cleaner" output of intentional sounds.

LARYNGEAL FOLDS AND FLAPS. The valvular action of the U-shaped vocal folds closes the glottic gap and the inflated laryngeal sac compresses the lumen of the trachea. However, there are two other sites of constriction in the respiratory passageways: opposition of the epiglottis and corniculate flaps, and opposition of the lumenal surface of the dorsal cricoid cartilage with the glottic gap between the vocal folds. Epiglottic-corniculate flap opposition can obstruct flow between the larynx and the nasopharynx or nasal cavities. If the two corniculate flaps are opposed to each other, then the only path for air to leave the larynx is for it to flow rostro-superiorly over the lumenal surface of the epiglottis. This part of the epiglottis is trough-shaped. While it can channel air rostro-superiorly towards the nasal cavities, it can also be blocked by opposition with the corniculate cartilage's flaps. If these opposed pair of flaps are nested into the epiglottic concavity, then the channel will be closed. This would restrict air to flowing only between the larynx/laryngeal sac and the trachea/lungs (via the glottic gap between the vocal folds).

Opposition of the cricoid and glottic gap is accomplished by a thickening of the midline lumenal surface of the cricoid cartilage. This thickened "cushion" fits exactly into the concavity of the glottic gap between the vocal folds. When opposed, air cannot flow between the vocal folds, effectively sealing the laryngeal sac from the larynx, trachea, and lungs. Air in the sac would only be able to flow rostro-superiorly towards the nasal cavities. Likewise, air from the lungs would have to bypass the laryngeal sac and instead also flow towards the nasal cavities. As the cushion is in the midline, and does not obstruct the lateral tracheal channels, air could flow around this connection. It would then flow between the corniculate flaps (assuming they are not nested into the epiglottis) and towards the nasal cavities. Another potential function would be to dampen vocal fold vibrations when making slight contact.

BUBBLE RELEASE. Another interesting function of the respiratory tract is its role in generating a visual signal of released bubbles. Bubbling behaviors (e.g., nets, clouds, curtains) occur in both the northern and southern hemisphere humpback whale populations (Clapham 2017). Generally, air is not released during sound production because that would waste the air and prevent it from being recycled for re-use. The blowholes are closed by nasal plugs in the relaxed state, and energy is only spent to occasionally open them for intermittent breaths (Buono et al. 2015). However, when a visual signal of bubbles is necessary, the nasal plug muscles can be contracted, withdrawing the plugs to allow release of air from the blowholes. This creates a column of bubbles or, if the whale is swimming, can create a curtain or wall of bubbles. Such bubble walls are used to signal other whales, usually as an aggressive display. Alternatively, when nasal air release is combined with an upward spiral swimming motion, it can be used to make a bubble net that can trap and concentrate fish for feeding (Sharpe and Dill 1997). Air may also be emitted from the mouth. This appears to occur when the epiglottis is withdrawn from behind the soft palate and is inserted into the oral cavity, and then the tongue is raised to push air out through the sieve of the baleen plates (Reidenberg and Laitman 2007a). This causes the airstream to break into many tiny bubbles called a bubble cloud. This latter function is useful in generating an aggressive visual display, or can be used as a smoke screen or camouflage that disrupts echolocation signals from predatory toothed whales such as orcas or pseudorcas.

BUOYANCY. Air, being less dense than water, is also useful for regulating buoyancy. It is not surprising, then, that whales may adjust their buoyancy by changing the volume of air in various chambers of respiratory tract. Many diving mammals exhale before descent to ensure the body has negative buoyancy and limited exposure to the high partial pressures of gases that could lead to decompression sickness when submerged (Withers et al. 2016). Reducing the air volume makes the whale heavier, allowing it to sink, and increasing the air volume keeps the whale buoyant, allowing it to rest at the surface. This dynamic adjustment in buoyancy requires releasing or acquiring air. However, whales need to keep air in their respiratory tract for sound production, and therefore do not exhale before diving. They must therefore rely upon dynamic internal adjustment of their center of gravity and through movement create a change in buoyancy relative to ambient pressure. They can accomplish this through minor adjustments in the chambers where the air is stored that shift the center of gravity and enable a more energy efficient dive or ascent (Reidenberg and Laitman 2008). If most of the air is shunted to the lungs, then the head becomes heavier than the thorax, and the whale's head will begin to sink. As the head points down, this initiates the dive behavior. Very little tail thrusting may be necessary to continue this ascent, for as the whale begins diving, the ambient pressure rises. This compresses the volume of air in the lungs, and makes the whale heavier so it should sink passively. The opposite may happen on ascent. If the whale shifts the small volume of air available at depth to the nasal region, then the head becomes lighter than the thorax. This will help point the head towards the surface. A few thrusts of the tail may be necessary to begin the ascent, but as the whale rises, the air volume begins to expand. This makes the whale more buoyant and should help lift it passively towards the surface.

Humpback whales appear to have the ability to confine air into various chambers of the respiratory tract (due to the multiple valve sites). Given that at least one of these chambers has muscular control of its volume (the laryngeal sac), it is reasonable to infer that the volume in that chamber can be independently regulated through such muscular contraction. This means that the whale may be able to adjust its buoyancy independently of, or in addition to, the effects of ambient pressure on the volume of air in that chamber (Gandilhon et al. 2015). Such independent control may give the whale a unique mechanism for adjusting its buoyancy. One major advantage of this independent control is the ability to increase the force propelling the whale to the surface. Such increase in buoyancy reduces the need for great energy expenditure to raise the whale up. This would be very useful in a favorite mode of humpback whale feeding: lunges. The energy spent in acquiring prey shouldn't exceed the energy gained from digesting prey. Using buoyancy gained from independent expansion of respiratory spaces would help make lunge feeding an energy efficient activity. There would be evolutionary selection for such a feeding behavior because it results in a net gain in energy acquired. Breaching may simply be an extension of this behavior. Independent adjustment of buoyancy may enable rapid ascent with relatively little fluke movements, relative to what would normally be necessary to propel a whale's full body above the water's surface against the force of gravity.

CONCLUSION

The respiratory tract of the humpback whale is a dynamic system that appears to serve several functions besides respiration. There are many highly modified chambers, tissue folds, and valves that can maintain or modify air spaces and surrounding tissues, some in conjunction with, and some independently of, extreme changes in pressures during diving and ascent. These highly modified respiratory tract tissues function to shunt air to increase oxygenation for extending breath-hold time, conserve and recycle air, maintain hearing at depth, generate sound for communication and navigation, transmit vibrations to water, mitigate noise, support air spaces from collapsing, regulate chamber volumes, produce bubbles as visual signals, control air release as a tool for trapping prey, modify center of gravity, regulate buoyancy, and reduce energy expenditure during locomotion. The humpback whale is not only arguably the most talented singer among all whales, it is also able to utilize air in an aquatic environment in ways that allow it to support a range of other unique behaviors.

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