



齿鲸生物声呐：进展与展望

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摘要 本文以齿鲸生物声呐系统结构与组织特性、发声与声发射调控过程、声信号特性与声接收过程为出发点开展综述, 旨在增强本领域对齿鲸生物声呐优越探测性能的了解, 为人工声呐的发展提供基于生物智能探测技术的参考. 声呐对于水下安全保障和海洋经济建设意义重大. 主动声呐在浅海探测目标时由界面干扰造成的强混响会导致探测距离短、目标识别率低等问题. 齿鲸经过自然选择形成天然的生物声呐系统在浅海强混响下具备优越的目标探测性能. 其镶嵌在鼻腔的声唇与脂肪组织形成的络合物在气流冲击下会振动发出声信号, 经上颌骨、气囊与软组织联合调控形成波束, 往外辐射进行回声定位与目标探测, 通过下颌区域接收目标回波. 齿鲸会综合回波时频信息进行目标识别. 齿鲸生物声呐探测过程中包含复杂的动态变化, 涉及信号调控与波束调控, 且调控过程与探测距离息息相关. 本文可为发展基于齿鲸生物声呐的仿生探测与感知技术提供新思路.

关键词 齿鲸, 生物声呐, 动态调控, 浅海混响

声音是人类感知世界的手段之一, 所谓“知声而不知音者, 禽兽是也”^[1]. 声学是研究声波如何产生、传播和接收的学科^[2]. 经过长期发展, 声学已经从理论走向应用, 发展出来的技术包括超声无损检测、医学超声成像以及水声声呐^[3]. 声波在水中传播时的衰减小于电磁波, 是现有水下远距离信息获取与传播的主要方式^[4]. 水声主动声呐的工作原理就是通过发射声波在水中传播, 接收目标的反射波, 并分析目标物理特性与运动信息, 实现水下目标探测^[3,4]. 被动声呐则是通过被动接收信号, 从而获取信息, 实现目标探测. 现有声呐技术的发展依赖声学理论、材料学、电子学科与仿生等交叉学科的研究.

自然界中存在利用声波在水中的传播进行探测与通讯的齿鲸生物声呐系统, 其优越的探测性能可启发人类优化人工声呐系统设计^[5,6]. 美国海军长期以来支持科学家开展齿鲸等生物声呐系统的目标探测研究,

旨在从生物声呐工作原理中寻找改进人工声呐的方法. 20世纪50年代, 研究人员发现海豚能在漆黑、浑浊的水中寻找渔网中的出口^[7], 随后通过一系列实验发现海豚能在水下发出声信号、感知超声波^[8-10], 并分辨目标的能力^[11,12]. Norris等人^[13]发现眼部被遮挡的海豚依旧能够依靠声波完成任务. 齿鲸的发声依靠前庭囊(vestibular sac)开口的深处的声唇^[14,15]. 鼻腔(nasal passage)的前侧和后侧分别拥有一个声唇(phonetic lips), 分别被称为前背滑囊(anterior dorsal bursae)和后背滑囊(posterior dorsal bursae)^[14], 与脂肪组织相连, 被包在结缔组织鞘(theca)中. 声唇位于喷水孔下方20~70 mm处^[16]. Madsen等人通过高时空分辨率测量声唇振动过程, 结果表明海豚通过气流在鼻腔流动, 激发声唇振动, 振动产生的信号覆盖海豚回声定位及通讯信号频段^[17]. Au等人^[18-21]发现多种齿鲸亚目海豚科生物声唇振动产生的信号经过上颌骨(upper jaw)、软组织与气

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囊(air sac)的调控均能在头部外形成指向性声波束。

自Aroyan等人^[22]在1992年利用有限元数值模型开展数值模型研究海豚波束形成与变化以来,国内外的科学家结合仿真研究了不同齿鲸生物前额的上颌骨、鼻道和气囊以及软组织结构在声波波束形成过程中的作用^[22-36]。其中鼻道与气囊结构主要起反射作用,上颌骨可同时作为反射结构与固体界面波传播通道,而软组织可在一定程度上实现声波的聚焦作用^[32]。齿鲸生物声呐系统能自适应调控发声过程,可根据背景环境调控探测脉冲强度、频率与脉冲间隔实现对不同鱼群、不同材质与不同尺寸目标的探测与识别^[8,33,34]。齿鲸生物声呐系统的优越探测性能也启发人们开展仿生研究,包括新概念声学仿生超材料、仿生声调控系统与仿生探测技术^[32,37-40]。这些充分表明研究齿鲸声呐系统工作机制能助力人工仿生声呐系统发展。本文将对齿鲸生物声呐发射系统的解剖结构、生物声呐发声与调控、声呐信号特性以及生物声呐接收过程进行叙述,形成的一些结论和建议预期可为后续相关研究提供一定借鉴。

1 齿鲸生物声呐系统结构特性

齿鲸生物演化出高度特化的声呐系统,通过整合鼻道腔体、前庭囊、下颌气窦(air sinus)、额隆(melon)、下颌脂肪(mandibular fat)、结缔组织(connective tissue)、肌肉组织(muscle)、上颌骨与下颌骨(mandible)等不同组织结构调控声波发射与接收。这些组分的几何形态、空间尺寸与声学特性参数会影响声波传导过程、外部声场的波束特性以及声接收过程。齿鲸生物声呐声发射系统的核心组件集中分布于前额区域,而其声接收系统位于下颌区域。为揭示其结构多样性,计算机断层扫描(computed tomography, CT)被广泛应用于齿鲸生物声呐系统的扫描与重建过程。图1给出江豚(*Neophocaena phocaenoides*)、中华白海豚(*Sousa chinensis*)、小抹香鲸(*Kogia breviceps*)、短肢领航鲸(*Globicephala macrorhynchus*)、喙鲸(*Ziphius cavirostris*)、宽吻海豚(*Tursiops truncatus*)等典型齿鲸物种声呐系统结构的三维扫描与重建结果^[25,41-49]。

尽管不同齿鲸种类体型差异显著,但其声呐系统存在相似性^[14,44,50-55],其中声发射系统的额隆组织构成前额区的主要成分,其外周由结缔组织包绕,形成声速、密度梯度分布特性。不同齿鲸生物在各个结构的尺寸与形状上存在差异。东亚江豚(*Neophocaena asiae-*

orientalis sunameri)、宽吻海豚(*T. truncatus*)、短肢领航鲸(*G. macrorhynchus*)、喙鲸(*Z. cavirostris*)、中华白海豚(*S. chinensis*)的声源尺寸较小且鼻道呈左、右对称分布。而小抹香鲸(*K. breviceps*)的鼻腔呈现明显的左右不对称性^[48,51]。短肢领航鲸(*G. macrorhynchus*)、喙鲸(*Z. cavirostris*)、小抹香鲸(*K. breviceps*)等物种的上、下颌骨大于中华白海豚(*S. chinensis*)等海豚科物种。然这些海豚科生物的下颌骨及听小骨的体积比例却呈现出比小抹香鲸(*K. breviceps*)大的趋势。这一结果表明齿鲸生物声呐系统的结构多样性,也为理解不同物种在声信号产生与辐射机制上的适应性分化提供了重要的形态学依据。

基于CT数据的三维重建可为声场建模提供几何框架^[22,28],CT扫描获取的电子密度系数亨氏单位(hounsfield unit, HU)为量化组织特性及重建整个头部的声学参数特性提供了媒介。Soldevilla等人^[47]测量了柯氏喙鲸(*Z. cavirostris*)新生幼体头部组织的物理特性,并发现CT成像的HU值与密度、声速显著相关。因此,利用少量的组织切片声学参数与其HU之间的线性关系,结合CT扫描数据可获取整个头部的声速、密度、声阻抗等特性分布。目前开展组织切片测量的物种包括柯氏喙鲸(*Z. cavirostris*)、长江江豚(*Neophocaena asiaeorientalis*)、中华白海豚(*S. chinensis*)、短肢领航鲸(*G. macrorhynchus*)、小抹香鲸(*K. breviceps*)、宽吻海豚(*T. truncatus*)、抹香鲸(*Physeter macrocephalus*)、东亚江豚(*N. a. sunameri*)、长吻真海豚(*Delphinus capensis*)^[24,26-28,32,51,55-60],其中许多物种实现了声学特性参数反演与重建^[25,32,41,43,45,52]。声速分布重建结果(图2)表明齿鲸的前额声呐系统的声速存在显著的梯度特性,其额隆核心区的平均声速为1200~1400 m s⁻¹之间,低于外围肌肉,而结缔组织的平均声速、平均密度最高。额隆在前额形成低密度、低声速、低声阻抗的核心结构,可完成声波聚焦的功能。综上,齿鲸前额存在结构分层,中心为低声速的脂肪性额隆,外围包裹高声速的肌肉与结缔组织。这些数据为构建齿鲸前额声发射与声接收模型提供了重要的物理参数。

2 齿鲸生物声呐发声与调控机制

科学家基于齿鲸声呐系统的解剖结构揭示其发声机制,如图3所示。Evans和Prescott^[56]在1966认为海豚通过喉咽振动产生通讯声信号,通过鼻道及相关气流循环产生脉冲声。后续实验测量与解剖结构都表明鼻道

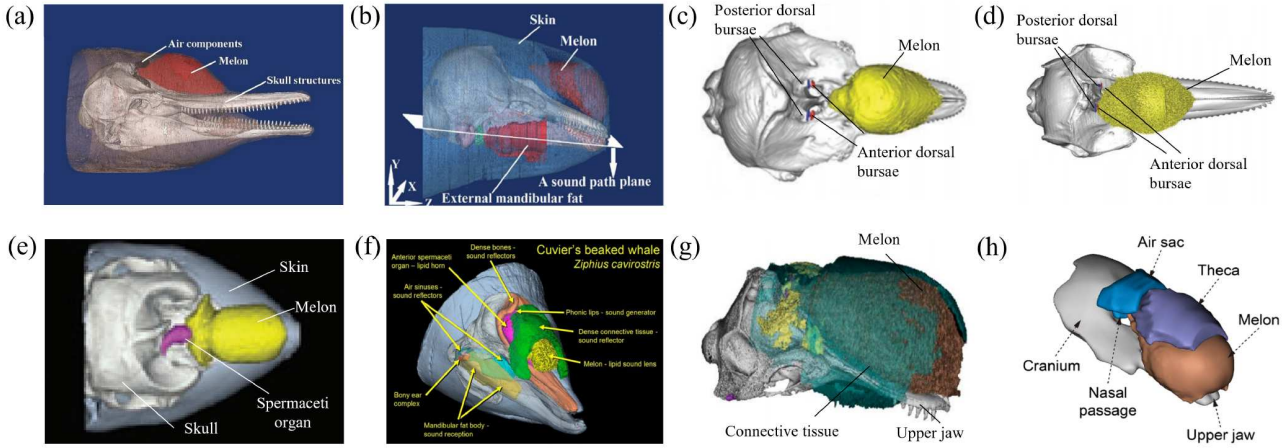


图1 齿鲸头部声呐系统结构三维重建. (a) 中华白海豚(*S. chinensis*)^[41], (b) 东亚江豚(*N. a. sunameri*)^[32], (c) 鼠海豚(*Phocoena phocoena*)^[42], (d) 宽吻海豚(*T. truncatus*)^[42], (e) 小抹香鲸(*K. breviceps*)^[43], (f) 柯氏喙鲸(*Z. cavirostris*)^[44], (g) 短肢领航鲸(*G. macrorhynchus*)^[45], (h) 白鲸(*Delphinapterus leucas*)^[46]

Figure 1 Three-dimensional reconstructions of several odontocetes. (a) Indo-Pacific humpback dolphin (*S. chinensis*)^[41], (b) finless porpoise (*N. a. sunameri*)^[32], (c) harbor porpoise (*P. phocoena*)^[42], (d) bottlenose dolphin (*T. truncatus*)^[42], (e) pygmy sperm whale head (*K. breviceps*)^[43], (f) Cuvier's beaked whale (*Z. cavirostris*)^[44], (g) short-finned pilot whale (*G. macrorhynchus*)^[45], (h) beluga (*Delphinapterus leucas*)^[46]

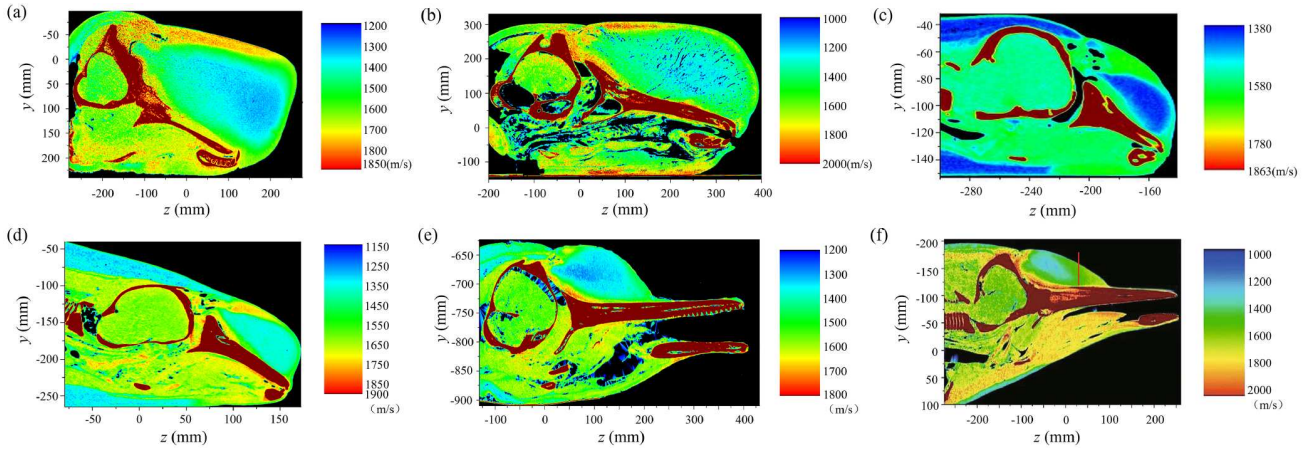


图2 齿鲸声发射系统垂直截面声速分布特性. (a) 小抹香鲸(*K. breviceps*)^[48], (b) 短肢领航鲸(*G. macrorhynchus*)^[45], (c) 长江江豚(*N. asiaorientalis*)^[25], (d) 东亚江豚(*N. a. sunameri*)^[32], (e) 中华白海豚(*S. chinensis*)^[41], (f) 短吻真海豚(*Delphinus delphis*)^[52]

Figure 2 Reconstruction of sound speed in a vertical section of odontocetes' sonar system. (a) Pygmy sperm whale head (*K. breviceps*)^[48], (b) short-finned pilot whale (*G. macrorhynchus*)^[45], (c) Yangtze river finless porpoise (*N. asiaorientalis*)^[25], (d) East Asian finless porpoise (*N. a. sunameri*)^[32], (e) Indo-Pacific humpback dolphin (*S. chinensis*)^[41], (f) short-beaked common dolphin (*Delphinus delphis*)^[52]

系统才是齿鲸发出声音的位置^[57-59]。Cranford等人^[14,60]发现长吻原海豚(*Stenella longirostris*)鼻道通气孔壁的四个脂肪体与相邻组织构成“声唇”，并可调节形状来调控发声。Cranford等人^[14]随后对19种齿鲸的40多个样本进行分析，提出适用于所有齿鲸的气动发声机制，即气流通过鼻道及气腔系统挤压后，驱动其振动产生声脉冲。Wood^[8]和Dubrovsky等人^[61]通过设计弹性环-气管模型模拟声唇振动，产生了时长、峰值频率、

带宽等参数接近海豚真实信号的脉冲，从物理建模角度验证该机制的科学性。通过控制气流与模型可分别产生短时回声定位脉冲(click)和具有谐波特性的哨声(whistle)信号，支持发声可调^[61,62]。

长期以来，研究人员认为多数齿鲸左、右鼻道对称分布，具有两套声唇，分别用来产生click与whistle信号^[14,60]。2023年，Madsen等人^[17]在*Science*发表论文表明齿鲸拥有一个基于鼻腔气流驱动的发声系统，其功能

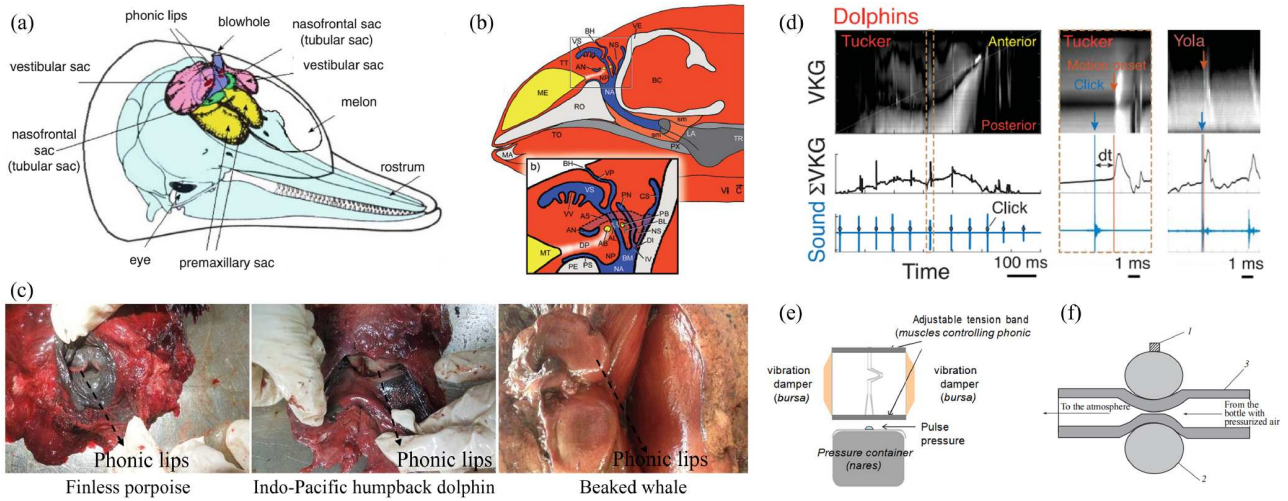


图3 齿鲸声源振动模型与发声机制。(a) 海豚发声与声调控相关结构^[35]；(b) 鼠海豚(*P. phocoena*)发声相关结构^[30]；(c) 三种齿鲸声唇解剖结构^[51]；(d) 海豚发声过程鼻腔动态图像与水听器信号^[17]；(e) 海豚声唇侧向振动模型^[35]；(f) 气动致声物理模型^[61]

Figure 3 Vibration models of sound sources and sound production mechanisms in odontocetes. (a) Sound production anatomy in the dolphin^[35]. (b) Sound production anatomy in the harbor porpoise (*P. phocoena*)^[30]. (c) Phonic lips of three odontocete species^[51]. (d) Videokymography images and hydrophone signal in the nares of two dolphins during sound production^[17]. (e) Striking model for phonic lips^[35]. (f) Schematic view of the underwater part of the physical model of air-driven click production for odontocetes^[61]

类似于喉部和鸣管发声。齿鲸位于不同声区的组织振动会分别产生探测信号和交流信号，从而为产生不同类型功能信号提供了形态学基础。从鼠海豚(*P. phocoena*)到抹香鲸(*P. macrocephalus*)等物种都会利用“气动致声”来产生回声定位脉冲，进一步揭示了齿鲸该机制的适用性。但其精细调控与多信号协同生成仍是未来探索的重点方向，尤其是生物如何根据需求产生通讯信号与探测信号。像小抹香鲸(*K. breviceps*)等物种因何不发出具有调频、谐频特性的通讯whistle信号仍需开展后续研究。

此外，齿鲸声源虽左、右呈现结构对称，然其尺寸存在一定差异。Frainer等人^[42]、McKenna等人^[43]和宋忠长^[51]发现中华白海豚(*S. chinensis*)、长吻真海豚(*D. capensis*)、热带斑海豚(*Stenella attenuata*)及短肢领航鲸(*G. macrorhynchus*)的声源与额隆后侧衔接方式有所差异。东亚江豚(*N. a. sunameri*)的声源未与额隆后侧的脂肪组织形成直接衔接^[51]。Cranford等人^[23]认为声源的振动能量可通过其与额隆的接触界面进行传递，并进一步经由额隆组织向前方辐射声波。除东亚江豚(*N. a. sunameri*)外，其余物种的声源均与额隆后侧的脂肪组织形成明确的解剖学连接，暗示其声波传导路径可能遵循类似的生物物理机制^[51]。然而，东亚江豚(*N. a. sunameri*)独特的声源-额隆分离结构提示其可能存在不同于其他齿鲸的局部声传播特性。

声源振动发声后，声波在头部的传播是分步骤的，头骨、额隆等结构在传中发挥作用，并最终通过前额传入水中形成波束，如图4所示。声波沿软组织传播时，上颌骨会形成界面波传导效应，与来自软组织通道的声波叠加向前传播。头骨可同时作为声波反射器与波导。齿鲸气囊系统开口于喷孔，向下连至咽喉，多数齿鲸有三对气囊，结构左右对称但尺寸存在差异。齿鲸前额软组织的声速和密度由内而外呈梯度分布(图2)，主要起声波导、抑制旁瓣作用，并与水阻抗匹配，增强声波辐射效率。这些发现进一步凸显了齿鲸生物声呐在进化中体现出来的一致性，不同尺寸的齿鲸通过多相声结构可将声波调控形成指向性波束，其辐射尺寸与声呐信号的频率及指向性之间存在关联^[63]。

3 齿鲸生物声呐信号特性

齿鲸发出的声呐探测信号时长为微秒量级，不同齿鲸差异明显^[6,63~75]。研究人员早期将齿鲸生物声呐探测信号分为宽带脉冲和窄带、高频脉冲^[6]。近来研究发现齿鲸生物声呐信号的复杂性，江豚(*N. phocaenoides*)同时具备发出窄带、高频脉冲与宽带脉冲的能力^[66,74]。而喙鲸(*Z. cavirostris*)会发出频率调制的回声定位脉冲信号^[69,70]。Jensen等人^[63]提出齿鲸生物声呐探测信号可分为4类，如图5所示。第一类为抹香鲸科(*Physeteridae*)发出的低频、宽带脉冲信号，其峰值频率会低于

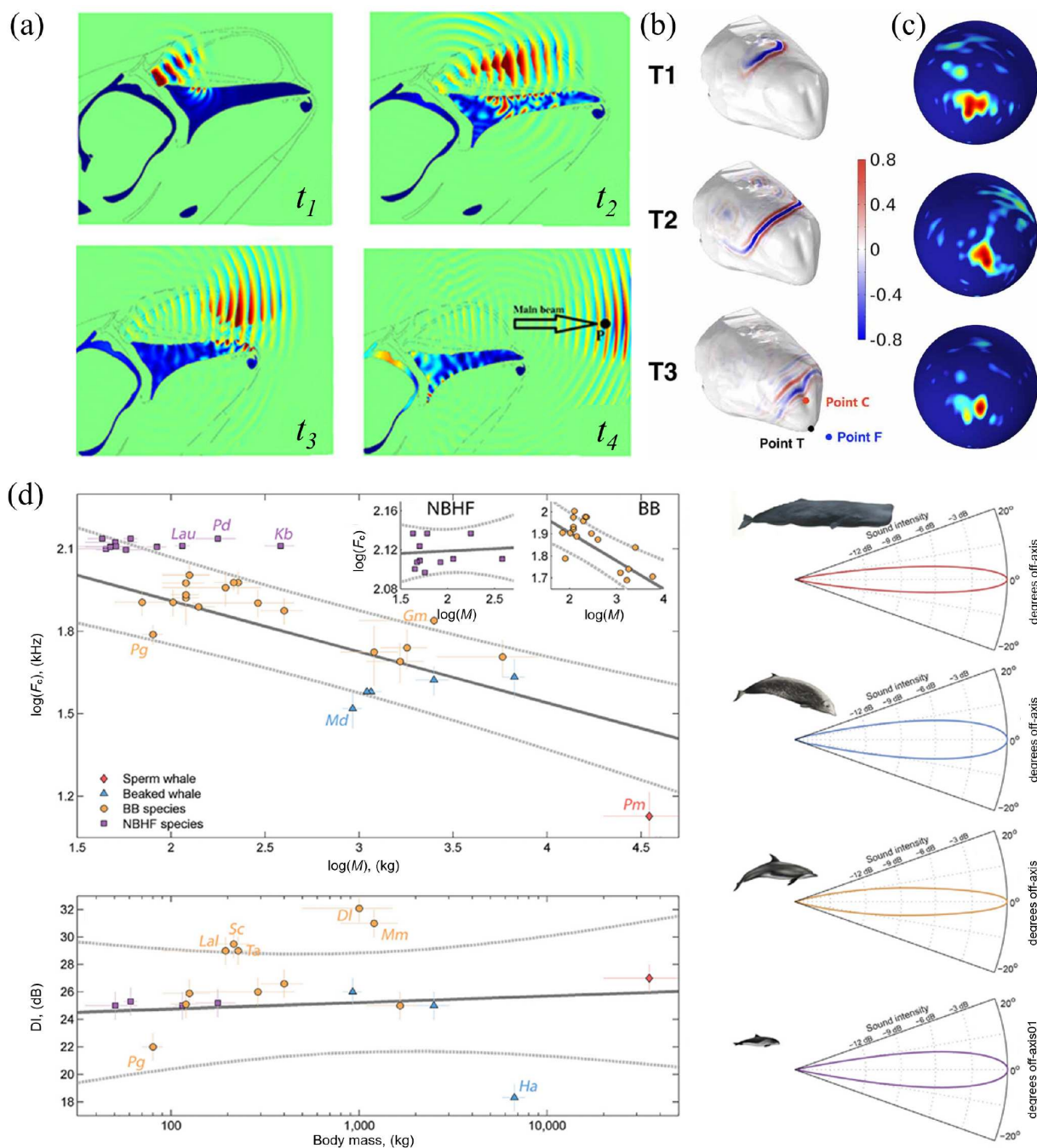


图4 齿鲸发射系统声传播与波束特性。(a) 东亚江豚(*N. a. sunameri*)头部声传播过程^[32]；(b) 里氏海豚(*Grampus griseus*)头部三维声传播过程^[31]；(c) 白鲸(*D. leucas*)左侧、右侧单声源与双声源辐射60 kHz声波波束特性分布^[46]；(d) 齿鲸尺寸与发声频率、波束指向性指数对应关系^[63]。NBHF: 窄带高频；BB: 宽带

Figure 4 Sound propagation in the odontocetes' biosonar system and the resulting beam patterns. (a) East Asian finless porpoise (*N. a. sunameri*)^[32]. (b) Risso's dolphin in three dimensions (*Grampus griseus*)^[31]. (c) Transmitting beam patterns for the left-source, right-source, and dual-source cases of the beluga whale (*D. leucas*)^[46]. (d) Relationships between the Biosonar Frequency and body mass, Sonar beam directivity index DI and body mass across the odontocetes^[63]. NBHF: narrowband high-frequency; BB: broadband

20 kHz, 这种声音会在其头部内反射形成多脉冲信号^[68]。第二类为喙鲸科(*Ziphiidae*)发出的调频脉冲信

号, 峰值频率为30~40 kHz范围内^[69,70]。第三类为大多数海豚科(*Delphinidae*)生物发出的高频、宽带脉冲信

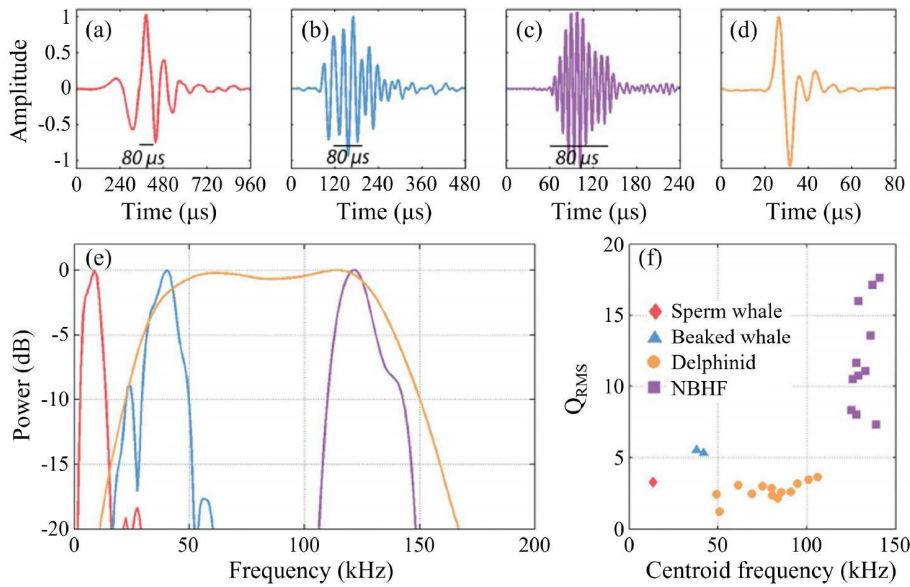


图5 齿鲸回声定位脉冲波形及特性^[63]. (a) 抹香鲸(*P. macrocephalus*); (b) 喙鲸(*Z. cavirostris*); (c) 港湾鼠海豚(*P. phocoena*); (d) 宽吻海豚(*T. truncatus*); (e) 四种齿鲸回声定位信号频谱; (f) 齿鲸主轴信号不同中心频率对应质量因数 Q_{RMS} (中心频率与均方根带宽比值)

Figure 5 Acoustic properties of odontocetes' clicks^[63]. (a) Sperm whales (*P. macrocephalus*); (b) beaked whales (*Z. cavirostris*); (c) harbor porpoise (*P. phocoena*); (d) bottlenose dolphin (*T. truncatus*); (e) spectrums of the echolocation clicks; (f) quality factor Q_{RMS} (defined as the centroid frequency divided by the root-mean-square bandwidth) as a function of click centroid frequency for on-axis biosonar signals

号, 其峰值频可从40 kHz变化至超过 120 kHz^[6,63~65,71]; 而最后一类为鼠海豚(*P. phocoena*)、弗朗西斯科海豚(*Lagenodelphis hosei*)、倭抹香鲸(*Kogia simus*)和小抹香鲸(*K. breviceps*), 以及斑纹海豚属(*Lagenorhynchus*)和黑白海豚属(*Cephalorhynchus*)的六个物种等发出的窄带、高频脉冲信号^[66,72~75].

齿鲸发出的探测脉冲声源级高, 可超过220 dB, 实现远距离探测. 在浑浊海水里捕猎时, 复杂海洋环境和水声信道会使猎物迅速脱离视线. 因此, 齿鲸进化声波束形成与调控能力. 能量集中的声波束有利于追踪远距离猎物, 但靠近猎物时, 窄波束会成为劣势, 导致猎物偏离波束范围. Wisniewska等人^[33]记录到鼠海豚(*P. phocoena*)靠近目标时能扩大探测视角. 齿鲸进行目标探测时, 会减小信号强度, 同时加快信号发射速率, 以低能量、高重复率的声呐脉冲信号串更新猎物信息. 齿鲸会调整发射脉冲串的脉冲间隔、中心频率、峰值频率和带宽等参数, 迅速更新目标信息. 齿鲸目标探测是个复杂的动态过程, 存在显著调控行为, 主要体现在脉冲串动态变化中^[75~93], 如图6所示. 齿鲸的脉冲串可分为三大类, 其中第一类为常规回声定位脉冲串 Regular click train, 主要用于自由游动与目标探测过程中的导航和定位, 具有最大的脉冲间隔(ICI). 第二类为

Buzz脉冲串, 通常是捕猎过程中觅食成功的标志^[76~78], 此外Buzz的功能已扩展到行为学, 如求偶与个体交流等^[79,80], 其ICI显著低于常规脉冲串^[81~83]. 第三类为Burst pulse, 通常发生在求偶、攻击性、协调合作等过程中^[79,84~89]. 齿鲸声呐信号产生的核心是鼻腔气流驱动声唇振动, 通过调控声唇振动模式与鼻腔气压, 可调控信号特性^[17]. 产生探测信号时, 声唇覆盖层与脂肪囊松弛且多处于闭合状态, 鼻腔内高压气流促使声唇短时开放并碰撞式自激振动, 形成黏膜波触发压力波, 生成短脉冲、宽频带、高强度的超声探测信号; 产生低频信号时, 声唇被拉长, 脂肪囊比覆盖层更僵硬, 开放时间延长, 鼻腔气压较低、气流适中, 声唇振动平缓, 形成低频、谐波丰富的通信信号. 两种信号的切换由中枢神经调控: 探测时保障鼻腔高压、控制声唇闭合以缩短气流冲击时间; 交流时降低气压、放松声唇张力以延长冲击时间^[17].

这三种类型脉冲串通常根据ICI设定相应的阈值进行划分, 划分标准与发声齿鲸种类和地点均有关. 对中国南海北部湾野生印度太平洋座头鲸(*Megaptera novaeangliae*)发声统计发现ICI划分阈值为4.9和15.5 ms, Regular click train的ICI最大, Burst pulse次之, Buzz最小^[79]. 有的研究中将ICI大于10 ms的脉冲串认定为Reg-

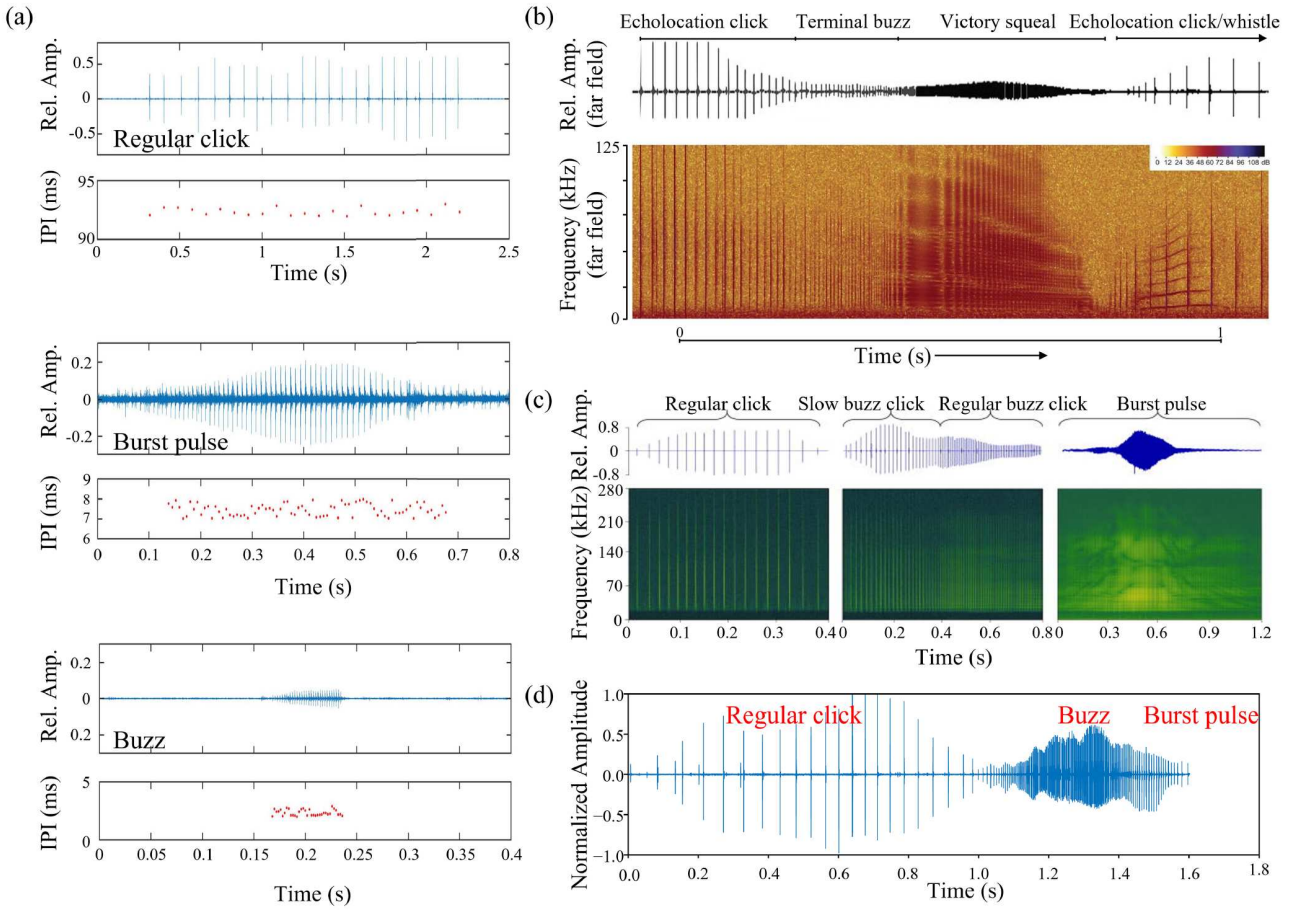


图6 齿鲸的Regular clicks, Burst pulses和Buzzes信号。(a) 北部湾中华白海豚(*S. chinensis*)^[79]；(b) 宽吻海豚(*T. truncatus*)^[77]；(c) 白吻海豚(*Lagenorhynchus albirostris*)^[91]；(d) 厦门湾中华白海豚。Rel. Amp.: 相对幅度

Figure 6 Regular clicks, Burst pulses, and Buzz signals of odontocetes. (a) Indo-Pacific humpback dolphins (*S. chinensis*) in Beibu Gulf^[79], (b) bottlenose dolphins (*T. truncatus*)^[77], (c) white-beaked dolphins (*Lagenorhynchus albirostris*)^[91], (d) Indo-Pacific humpback dolphins (*S. chinensis*) in Xiamen Bay. Rel. Amp.: relative amplitude

ular click脉冲串，而Buzz为ICI小于10 ms的脉冲串^[90-92]。Burst pulse则定义为离散的脉冲串，ICI均小于10 ms。Martin等人^[93]将ICI大于13 ms的脉冲串归为Regular click脉冲串，Burst pulse的ICI小于10 ms，而将ICI小于13 ms之间且紧接Regular click的信号定位为Buzz。齿鲸的脉冲串特性可反映其动态探测阶段，其中第一阶段为靠近阶段，齿鲸回声定位脉冲声信号的ICI明显大于第二阶段的扫描阶段。随目标距离减小，探测进入扫描阶段，ICI减小。在不同探测阶段，齿鲸探测脉冲幅度、中心频率、时长、带宽等参数均是动态变化，体现齿鲸目标探测的调控与策略多样性。

这些信号的动态变化与齿鲸所面临的环境息息相关，如何量化其功能特征是亟待开展的工作。Jiang等人^[94]利用模糊度函数分析了长肢领航探测信号，结果

表明其具备优秀的距离分辨率与多普勒容限，可支撑其精准区分目标与距离。陈晟等人^[95]利用模糊度函数分析对比宽吻海豚在不同环境下发出的探测信号特性，结果表明水池环境下的信号更长、频率更低、带宽更窄，更有利于抗混响，而自然环境下的信号更短，更利于目标分辨。这些研究为后续进一步研究齿鲸生物声呐探测提供新视角，并更加接近实际场景，同时为仿生声呐探测信号设计提供参考。

4 齿鲸生物声呐接收

齿鲸存在多个声接收通道^[94-100]，如图7所示。早期研究认为声波主要通过外耳道进入声接收系统。Norris发现声波从下颌脂肪进入头部，经下颌骨后部盘骨区域进入内部脂肪，再传至听小骨，形成“jaw hearing”声

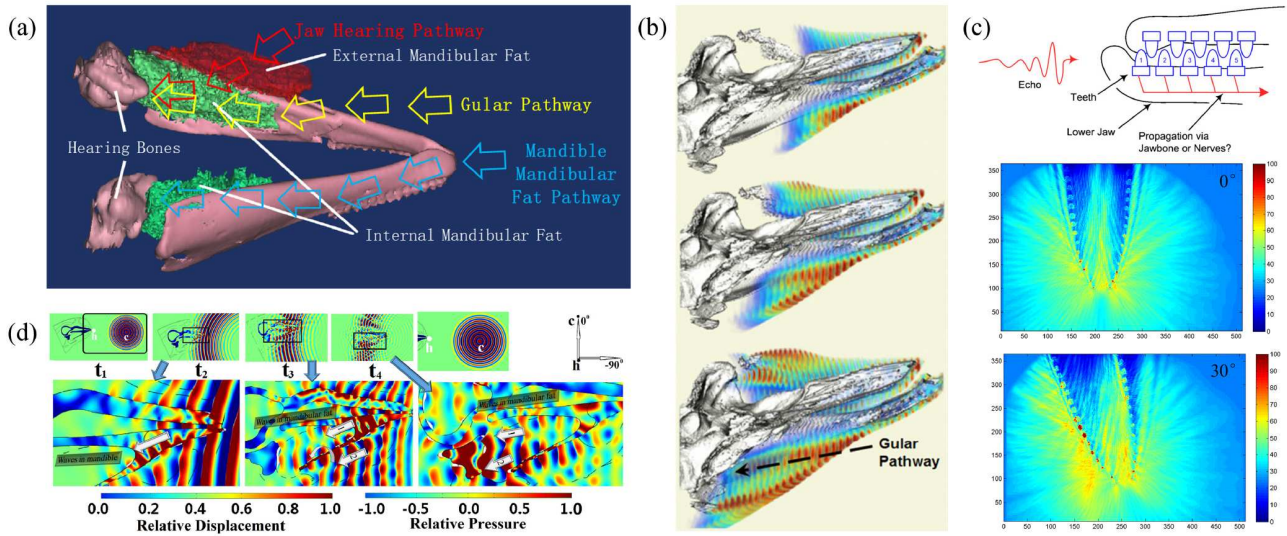


图7 齿鲸声接收通道。(a) 齿鲸三种声接收通道^[99]；(b) 喉部通道^[49]；(c) 牙齿通道^[101]；(d) 下颌听觉通道和下颌骨-下颌脂肪通道^[99]

Figure 7 Sound reception pathways in odontocetes. (a) Three sound reception pathways in odontocetes^[99]; (b) gular pathway^[49]; (c) tooth pathway^[101]; (d) jaw hearing pathway and mandible-mandibular fat pathway^[99]

接收理论。下颌脂肪的声阻抗与水匹配,可减少声传播能量损失。此外,声波还可通过两侧下颌骨之间的软组织进入接收系统,形成“gular pathway”声接收通道。下颌骨前侧的尖端也可作为声接收窗口接收声波。Jiang等人^[94]、陈晟等人^[95]和Mooney等人^[96]测量发现灰海豚(*Grampus griseus*)等三种齿鲸的上颌骨前端声接收响应较强。东亚江豚(*N. a. sunameri*)的声接收数值模型表明,声波会刺激下颌骨前侧发生振动,形成骨传导声波,再传至下颌骨内侧脂肪,最终作用于听小骨,即齿鲸存在由下颌骨与下颌骨内侧脂肪形成的声接收通道^[97]。而齿鲸的牙齿在声接收过程中也起着一定作用^[98~101]。

Aroyan等人^[22]在1992年用计算机断层扫描技术构建真海豚声接收系统有限差分模型以来,数值模型被广泛用于齿鲸声发射与接收研究。如图8所示,声接收过程与声波入射方向相关,不同声接收通道存在联合作用效应。不同方向入射的声波在听小骨的声接收幅值存在差异,会形成声接收指向性。齿鲸声接收指向性主要体现在接收同侧声波性能优于异侧,前侧接收灵敏度高于其他方向^[101~103]。声接收指向性特性呈现出明显的频响特性。白鲸(*D. leucas*)数模仿真结果表明,低频声信号由于波长较长,表现出强声透射^[46]。在5 kHz时,左、右耳朵单波束方位角均为90°。随着频率的增加,方位角逐渐趋近于0°(中线)。双耳束的方位角始终介于两耳单耳束的方位角之间。而最优的声接收

仰角都位于水平线以下,表明其声接收具有显著指向性。

下颌骨、气窦以及下颌脂肪在声接收中起着相应作用^[103~106],如图8所示。江豚(*N. phocaenoides*)的下颌脂肪可以显著增强在54 kHz的前向声接收能量^[106]。Aroyan表明下颌脂肪有助于增强前向声接收波束幅度,会提升声接收前向指向性^[104]。下颌骨存在显著的聚焦特性,有助于形成同侧声接收最优方位角度。Cheong等人^[107]在2025年的最新研究研究结果表明50 kHz范围内,低声速的下颌脂肪通过折射显著增强声信号前向接收指向性。Ou等人^[108]研究发现江豚(*N. phocaenoides*)气窦能有效隔离从后侧、上侧和异侧传到听小骨的声波,从而形成前侧、下侧和同侧的声接收优势。在100 kHz时,有气窦模型的指向性指数为5.64 dB,比无气窦模型的指向性指数4.12 dB高1.5 dB。气窦增加了不同方向声信号的接收差异,有效地为听小骨提供声学隔离,从而增强了以正面、同侧和前侧为主导的声接收过程。这些研究表明了齿鲸声接收通道的多样性与复杂性,其中气窦、下颌骨与下颌脂肪在声接收指向性的形成与调控中起着重要作用。

声接收指向性可在一定程度上提升抗噪能力,然无法完全克服强噪声干扰。水下噪声对齿鲸声接收的主要影响为听觉掩蔽和听觉阈值偏移。研究显示,人为噪声(如船舶噪声)会显著降低宽吻海豚的交流效率,即便海豚通过延长信号时长、提高信号幅度也无法抵消

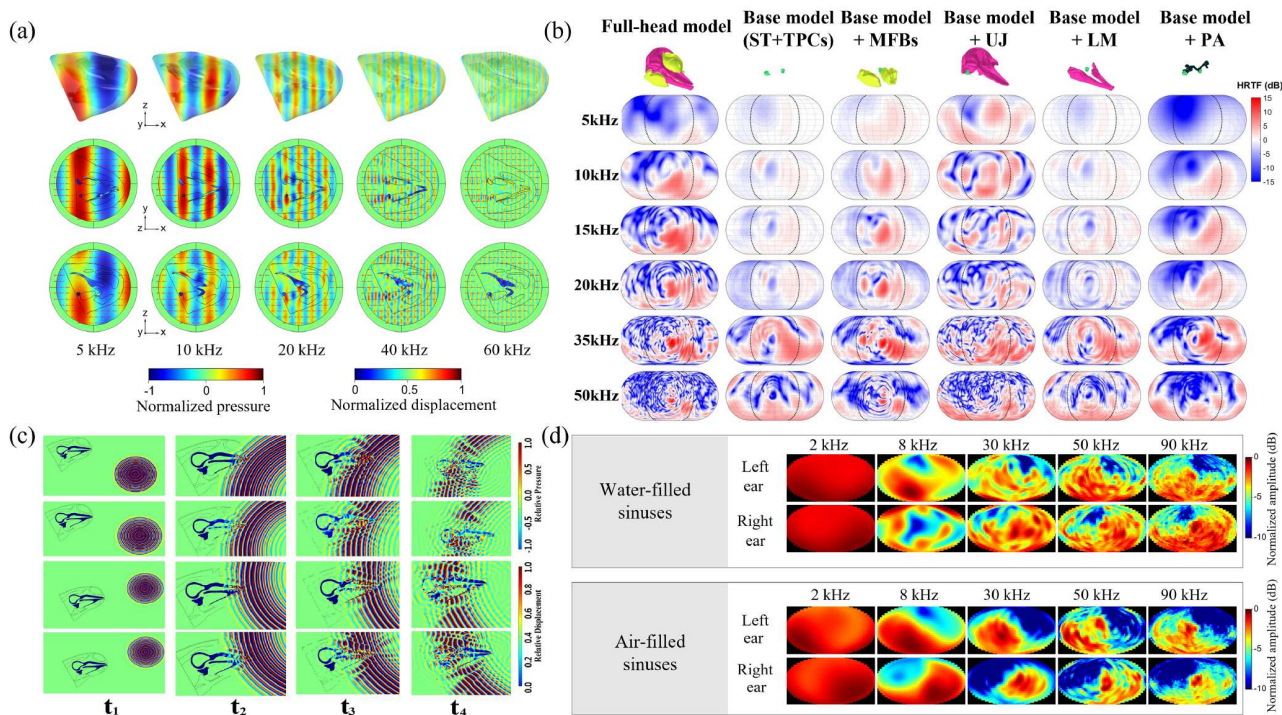


图8 齿鲸声接收过程与声接收指向性。(a) 白鲸(*D. leucas*)声接收过程^[46]；(b) 宽吻海豚(*T. truncatus*)不同结构组合声接收指向性对比^[105]；(c) 东亚江豚(*N. a. sunameri*)声接收^[97]；(d) 长江江豚(*N. asiaeorientalis*)无气窦(上)与完整模型(下)在不同频点声接收指向性对比^[106]。ST: 非脂肪软组织；TPCs: 听骨复合体；MFBs: 下颌脂肪；UJ: 上颌-颅骨复合体；LM: 下颌骨；PA: 鼓周及翼状气窦

Figure 8 Sound reception in odontocetes and the influence of the various structures on directivity. (a) Sound reception in beluga whale (*D. leucas*)^[46]. (b) Sound reception directivity in bottlenose dolphin (*T. truncatus*)^[105]. (c) Sound reception in East Asian Finless Porpoise (*N. a. sunameri*)^[97]. (d) Sound reception directivity in Yangtze finless porpoise (*N. asiaeorientalis*) (top: without air sinuses; bottom: full model)^[106]. ST: nonfat soft tissues; TPCs: tympano-periotic complexes; MFBs: mandibular fat bodies; UJ: upper jaw-skull complex; LM: lower mandible; PA: peribullar and pterygoid air volumes

干扰。船舶噪声还会通过声学掩蔽压缩其有效交流空间。目前，齿鲸回声定位与噪声掩蔽的相互作用研究仍较匮乏，且多数基于圈养动物，相关结论在野外环境的适用性需进一步验证。

5 展望

齿鲸生物声呐探测原理复杂，涵盖结构、信号、波束与策略等多方面调控。在结构方面，齿鲸拥有特化的生物声呐系统，由多种组织结构协同调控声波的发射与接收。不同齿鲸在鼻道、颌骨等结构上存在差异，为物种声信号的差异性提供了形态学依据。齿鲸头部声学参数重建表明其前额呈分层结构，中心脂肪性额隆声速最低，能聚焦声波；在发声机制与波束调控方面，现有研究已表明齿鲸发声核心是鼻道系统，通过气流挤压鼻道“声唇”振动产生声脉冲。声波经前额传播时，头骨起反射和波导作用，前额梯度软组织可抑制旁瓣，并与水进行阻抗匹配，最终形成指向性波束；在信

号方面，齿鲸体现多脉冲动态调控的生物智能特性。浅海环境中，齿鲸会随探测距离变化动态调整探测脉冲串的声学参数。在远距离和近距离探测时，会发射不同类型脉冲串，提升目标探测效率。在声接收方面，齿鲸包含三个声接收通道，会形成声接收指向性。下颌脂肪可增强前向接收指向性，下颌骨有聚焦声波的作用，而气窦能声学隔离、扩大方向接收差异，增强声接收指向性。

齿鲸生物声呐的研究近年来得到大力发展，然而国内外关于齿鲸在混响干扰下的目标探测研究主要集中在声波束与信号测量方面，而波束形成与调控、多脉冲动态调控背后的抗混响及目标匹配特性机理仍存很大研究空间。齿鲸声呐的研究重点需围绕下述方向开展：在结构层面，需进一步解析气囊在齿鲸实际探测过程中的形态，并深度挖掘不同齿鲸的结构尺寸、形态与信号特性之间的关联性；在波束研究方面，需重点探索齿鲸基于生物声呐结构与材料特性的动态声

波束调控和混响抑制过程,揭示齿鲸如何依据环境与目标来调控波束;在信号研究层面,需重点探索齿鲸基于多脉冲调控的目标探测与识别机制,结合人工智能与大数据处理,进一步挖掘齿鲸声呐信号动态调控过程;在声接收层面,需重点研究齿鲸如何利用与融合来自不同声接收通道的信息,并同时深入探索从物理声接收通道到内耳神经通道之间的耦合.受限于研究手段,齿鲸声呐在深远海的发声、波束调控以及目

标探测研究较少.如抹香鲸(*P. macrocephalus*)等深潜物种在高压、低温环境的声呐系统形态,组织结构声速、密度特性,波束动态变化特性以及适应环境与目标的发声调控等方面均亟待研究.最后,基于齿鲸生物声呐探测原理的仿生探测技术目前还处于应用探索阶段,如何启发仿生探测技术,提升人工声呐在浅海混响、深海高压、低温极端环境下的目标探测性能是研究的重点.

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Summary for “齿鲸生物声呐: 进展与展望”

Odontocetes biosonar: progress and prospect

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Odontocetes (toothed whales) have developed an exceptionally sophisticated biosonar system through millions of years of evolution, enabling highly efficient navigation, foraging, and communication in acoustically complex underwater environments. In particular, odontocete biosonar demonstrates outstanding detection capability in shallow-water regions, where artificial sonar systems often experience severe degradation due to strong interface reverberation. The efficiency and robustness of this natural sensing system provide a compelling biological paradigm for addressing fundamental challenges in underwater target detection, localization, and recognition. Consequently, elucidating the mechanisms of odontocete biosonar is not only of central importance to marine bioacoustics but also provides critical inspiration for the development of next-generation bionic acoustic technologies relevant to maritime security and marine economy development.

This review synthesizes current research on odontocete biosonar from multiple perspectives, including anatomical specialization, sound production, beam formation and control, signal characteristics, and sound reception pathways. The exceptional performance of odontocete biosonar is attributed to a highly integrated and functionally specialized anatomical architecture. Sound production originates at the phonic lips/dorsal bursae embedded within the nasal cavity, which serve as the primary acoustic source. Surrounding tissues, such as the fatty melon and a series of air sacs, exhibit pronounced spatial heterogeneity in acoustic impedance. This structural complexity facilitates acoustic coupling between the sound source and surrounding tissues and contributes to effective beam shaping. Biosonar signals are generated through the vibration of the phonic lips driven by pressurized airflow within the nasal system, and odontocetes exhibit a high degree of active control over this process. By regulating air pressure and phonic lip tension, odontocetes can dynamically adjust key signal parameters, including amplitude, inter-click interval, and frequency composition, thereby adapting biosonar emissions to varying environmental conditions and task demands. Beyond sound generation, the coordinated interaction among the melon, air sacs, and skull enables odontocetes to project highly directional forward acoustic beams. Increasing evidence suggests that beamwidth and beam orientation can be actively modulated without head movement. This capability is likely achieved through muscular control of the melon's shape and changes in the volume and configuration of the air sacs, allowing real-time adjustment of acoustic radiation patterns in response to target range. Sound reception in odontocetes is primarily mediated by the mandible and specialized fatty tissues located in the lower jaw region. These tissues can form multiple distinct acoustic pathways that channel returning echoes toward the tympano-periotic complexes. Such a multi-path reception architecture may enable the simultaneous extraction and integration of temporal, spectral, and spatial information from echoes.

By reviewing the co-evolved mechanisms of sound production, dynamic beam control, and multi-path reception, this work highlights how odontocete biosonar provides a biological blueprint for mitigating reverberation effects in shallow-water environments. Future research should move toward integrative, mechanism-driven investigations that explicitly link biosonar structure, acoustic function, and perceptual outcome. In particular, advancing our understanding of how dynamically reconfigurable anatomical components, such as the air sacs and melon, collectively regulate sound radiation and beam patterns under varying environmental and target conditions remains a critical priority. Equally important is elucidating how odontocetes exploit sequences of biosonar signals and fuse information from distributed reception pathways to achieve robust target detection and identification. Extending such studies to deep-diving species and extreme oceanic environments will further clarify the adaptive limits of biosonar. Ultimately, translating these biological mechanisms into bionic sonar architectures and intelligent sensing strategies will be essential for improving artificial sonar performance. Overall, this review bridges biological insight and engineering application, providing a foundation for the development of next-generation bionic underwater acoustic sensing and detection technologies.

odontocetes, biosonar, dynamic control, shallow water reverberation

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