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Whale temples are unique repositories for understanding marine mammal diversity in Central Vietnam

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Abstract. In recent decades, several studies and reviews have contributed new data on marine mammal composition and distribution in Vietnam, including surveys of whale temples along the coast in the southern part of the country. Whale temples have amassed a sizeable number of specimens that have been used as a valuable source of information concerning marine mammals in Vietnam. Previous studies have examined some whale temples in southern Vietnam, but contents of whale temples along the whole coast of Vietnam have not been fully documented. Here we surveyed 18 whale temples in the central part of Vietnam in Đà Nẵng, Quang Nam, Quang Ngai, and Thừa Thiên-Huế Provinces, an area that had not been scientifically documented previously. We identified and measured 140 individual marine mammals from 15 species, four families, and two orders (Artiodactyla, Sirenia). By far the most numerous species encountered (n=41) was the inshore Indo-Pacific finless porpoise (*Neophocaena phocaenoides*). We also encountered >10 skulls of two other taxa: bottlenose dolphins (*Tursiops* sp.) and the Indo-Pacific humpback dolphin (*Sousa chinensis*). Other delphinid species included *Stenella longirostris*, *S. attenuata*, *Globicephala macrorhynchus*, *Grampus griseus*, *Feresa attenuata*, *Pseudorca crassidens*, *Lagenodelphis hosei*, and *Delphinus delphis tropicalis*. We identified one specimen of humpback whale (*Megaptera novaeangliae*) and three of Omura's whale (*Balaenoptera omurai*), increasing the number of records of the recently described Omura's whale in Vietnam to five. In addition, we identified three skulls or partial skulls of the dugong (*Dugong dugon*) in varying conditions, documenting their historical presence in an area where they are no longer present. These records further underscore the importance of whale temples both as places of historical culture and reverence, and important repositories of biodiversity data, from which information on former and current marine mammal distributions can be derived.

Key words. whales, dolphins, Cetacea, natural history, dugongs, South China Sea

INTRODUCTION

Knowledge of marine mammal community composition and distribution in Southeast Asia remains poorly characterised despite its large diversity of marine mammals, which includes many threatened species such as the Irrawaddy dolphin (*Orcaella brevirostris*), Indo-Pacific finless porpoise (*Neophocaena phocaenoides*), and Indo-Pacific humpback dolphin (*Sousa chinensis*) (Jefferson et al., 2017; Minton et al., 2017; Wang & Reeves, 2017). In recent decades, several studies and reviews have contributed new data on the marine mammal composition and distribution in Vietnam through surveys (Smith et al., 1997, 2003; Hines et al., 2008; Vu et al., 2017), documentation of strandings via social media (Vu & Ponnampalam, 2018; Vu et al., 2020), specimens held in scientific institutions (Lloze, 1973; Van Bree & Duguy, 1977; Smith et al., 1995, 1997; Andersen & Kinze, 2000; Pham et al., 2014, 2015), and specimens held in whale temples along the coast of Vietnam (Smith et al., 1995, 1997; Andersen & Kinze, 2000; Beasley et al., 2002; Honma & Kato, 2002; Jefferson, 2002; Jefferson & Van Waerebeek, 2002, 2004; Pham & Nguyen, 2013; Vu et al., 2017, 2020).

Whale temples (Lang Ông) have been recognised as extraordinary repositories of natural history information regarding marine mammals in Vietnam (Smith et al., 1995, 1997; Vu et al., 2020). Their main function, of course, is as a place of veneration for local communities of the whale spirit known as "Cá Ông" or "Lord Fish" (also known as "Nam Hải Đại Vương" or "Nam Hải Đại Tướng Quân"), who is represented as a benevolent whale that assists fishers in times of need at sea, including rescuing capsized individuals from

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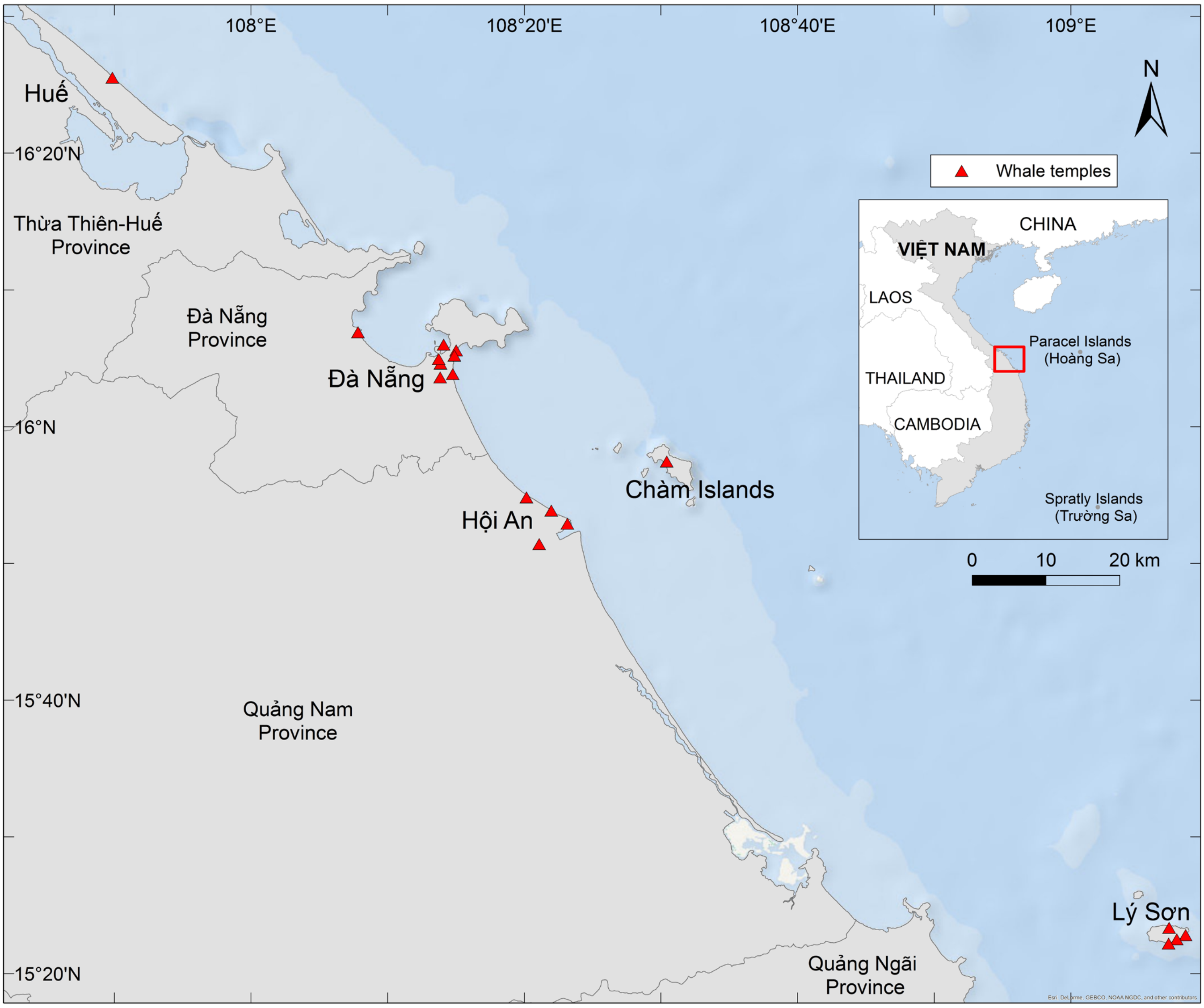

Fig. 1. The locations of whale temples visited during this study in central Vietnam marked with red triangles.

drowning (Lantz, 2009). Fishers often ask for the protection of Cá Ông before going out to sea and when encountering rough weather (Kiem, 1996). Whale temples are dispersed along the coastline of southern and central Vietnam and are central to many fishing communities (vạn chài), where festivals centred on whale worship are known to occur at specific times of year (Kiem, 1996). In an act of respect to Cá Ông, local fishing communities keep the bones of stranded or bycaught marine mammals in temples after initial burial and exhumation (Kiem, 1996; Smith et al., 1997; Lantz, 2009). The finding of a stranded animal by a fisher is often seen as good fortune (Kiem, 1996). Every temple is slightly different in practice and what may be identified as a "whale" may vary from village to village, with some villages including other marine mammals such as dugongs among interments (Smith et al., 1997).

Consequent to these practices, whale temples have amassed a sizeable number of specimens that have been used as a valuable source of information concerning marine mammals in Vietnam. In a pioneering study, Smith et al. (1995, 1997) initiated a broad survey of whale temples and scientific repositories across southern Vietnam with a focus on the temples of Phú Quốc, the Mekong Delta, and near Nha Trang. Smith et al. (1995, 1997) identified 18 marine mammal species from whale temples, some of which were the first records from Vietnam noted in the Western scientific literature. In addition to species identification, whale temples have proven to be important repositories in studies of intraspecific variation. Several studies have taken detailed measurements of skulls from whale temples to examine broader patterns of morphology within *Neophocaena* spp., *Orcaella* spp., *Delphinus delphis tropicalis*, and *Sousa* spp. (Beasley et al., 2002; Jefferson, 2002; Jefferson & Van Waerebeek, 2002, 2004).

However, the contents of whale temples along the whole coast of Vietnam have not been fully surveyed. As noted above, previous studies surveyed whale temples in parts of the south (Smith et al., 1995, 1997; Vu et al., 2017), but did not observe temples in the central part of the country around the Đà Nẵng and Hội An regions, which have a rich history of whale worship that is under increasing threat from expanding tourism in the region (Lantz, 2009; Parnwell, 2013). Some temples in the region have been moved to make way for luxury hotels, and there is some evidence that traditional practices are being eroded (Lantz, 2009; Parnwell, 2013). In addition, cetaceans are undergoing increasing threats in the South China Sea from overfishing (Li et al., 2020), which could lead to local extirpation of some species from this region before their presence or abundance are fully characterised. Our main aims in this study were to survey existing whale temples in central Vietnam near Đà Nẵng and Hội An to identify and catalogue marine mammal specimens and refine knowledge of cetacean occurrences in the country.

METHODS

Temple visitation. From 28 August to 3 September 2018, the authors (MRM, LV, CWP, TAT, SHK, STAR, EH) visited 18 whale temples in central Vietnam, including eight in or near Đà Nẵng, four in the vicinity of Hội An (Quang Nam Province), one in Cù Lao Chàm Islands (Quang Nam Province), four on Lý Sơn Island (Quang Ngai Province), and one southeast of Huế city (Thừa Thiên-Huế Province) (Fig. 1). In many cases, temples were identified ahead of time and visits were arranged with temple keepers or community members. In some cases, temples were located via word of mouth from other temple keepers, members of the local community, or Google Maps. Upon finding these temples, permission for visitation was obtained from the local communities and/or the temple keeper. Following a workshop on marine mammals of Vietnam, students from the Animal Physiology class of Dr Vy at the University of Đà Nẵng assisted us at two temples (DN2019-T1 and DN2019-T4). Global positioning satellite (GPS) coordinates and description of the contents were taken for each temple (Table 1). During these visits, the authors also discussed reporting of stranded whales with local community members and distributed marine mammal stranding response posters.

Identification and measurement of skulls. With the help of temple keepers and local community members, bones were located and moved to flat areas for photographing and measurement. As time allowed, the authors photographed most skulls, as in most cases, these could be determined to species. For each individual skull, we photographed the dorsal, ventral, and lateral views using Fujifilm X-T1 and a Fujinon 60mm macro lens. For some temples, such as HUE2019-T1, in which skulls were sealed in glass boxes, we could not take measurements and just identified skulls to species as accurately as possible given the conditions. In cases where individual specimens were too large, such as those from mysticetes, we photographed key potential diagnostic characters when they could be observed, for example, the lack of an acromion process of the scapula in *Megaptera novaenagliae* or the movement of the parietal bones laterally onto the supraorbital process of the frontal in *Balaenoptera omurai*. When possible, for many odontocete skulls, we took ten standard measurements in mm using callipers. This is a reduced set of standard odontocete cranial measurements, as we were generally allowed at most two hours in temples, and many times substantially shorter than that. Measurements taken were as described in Perrin (1975): condylobasal length (1), rostral length (2), rostral width (3), rostral width at midlength (5), zygomatic width (14), internal nares width (27), pterygoid length (28), length of upper left tooth row (32), tooth count, upper left (33), and tooth count, lower left (35). Numbers in parentheses correspond to those measurements listed in Perrin (1975). Subsequent comparison and identification of skulls to the lowest taxonomic level were confirmed by MM, CWP, and TAJ.

RESULTS

Description of temples. All 18 temples (Table 1, Fig. 1) were generally located near the coast, ranging from temples within former fishing villages swallowed up by the urban expansion of Đà Nẵng (DN2019-T1, DN2019-T4) or development along the coast near Hội An (HA2019-T2), to more rural fishing villages (HA2019-T4, HUE2019-T1). Temples ranged in the degree of active reverence by the local community. One temple near the centre of Đà Nẵng (DN2019-T4) had been turned into a small museum with an attached coffee shop and explanatory signage describing the distinct culture of whale temples with some photos of past strandings (Fig. 2A). Although many bones were present, DN2019-T4 probably had not been an active site of collection for some time. In contrast, the temple in the Cham Islands was the site of vibrant worship by the local community, and temple keepers told stories of collections of marine mammals at this temple going back hundreds of years. Multiple temples on Lý Sơn showed evidence of recent burials of stranded cetaceans outside the temple (Supplemental Fig. 72).

Temples usually consisted of a central building (Fig. 3), in which bones were placed on top, inside, or behind the altar mostly in urns, sealed boxes, or glass-walled boxes (Fig. 4A, C). In a few temples, exposed bones were placed directly on or behind the altar (DN2019-T4, HA2019-T4; Figs. 2A, 4B) or on open shelves (DN2019-T1). In temples with mysticete remains, bones were stored without cover in rooms behind the altar or piled within the main room of the temple itself (DN2019-T3, LS-2019-T2, LS-2019-T4; Supplemental Fig. 71). In one temple (CI2019-T1), bones were piled together in a large above-ground tomb and temple keepers indicated that some may date from over 100 years ago (Fig. 4D). Perhaps the most elaborate temple (HA2019-T4) featured a central building that was built on top of a life-sized model of a Vietnamese fishing boat (Fig. 2B).

Marine mammal records. We examined at least 140 individual skulls or skull fragments, and we were able to identify 15 marine mammal species from four families (Delphinidae, Phocoenidae, Balaenopteridae, Dugongidae) in two orders (Artiodactyla, Sirenia) (Table 1). We also identified bones belonging to domestic cattle at HA2019-T4 and LS2019-T4 and those of an unidentified sea turtle (Chelonioidea) at HUE-2019-T1. Photos of most marine mammal specimens in dorsal, ventral, and lateral views

Table 1. List of temples examined with codes referred to in the text, geographic coordinates, Vietnamese names, number of species identified, minimum estimate of the number of skulls, and notes on each temple.

Temple Codes	Coordinates	Temple Name (if known)	Number of species identified	Minimum estimate of number of skulls	Notes
DN2019-T1	16°06′00″N 108°14′06″E	Đền Thờ Thần Nam Hải	6	25	
DN2019-T2	16°04′37″N 108°13′52″E	Lăng Ông	7	9	
DN2019-T3	16°05′35″N 108°15′01″E	Lăng Thờ Ngư Ông Làng Nam Thọ	2	2	Possibly more skulls present
DN2019-T4	16°03′35.6″N 108°13′50.5″E	Lăng Ông Vạn Tự Chánh Nam Hải	5	12	Now a small museum with attached coffee shop
DN2019-T5	16°05′12″N 108°14′53″E	Lăng Thờ Ngư Ông Phường Mân Thái	1	2	
DN2019-T6	16°03′51″N 108°14′46″E	Miếu Lăng Ông	1	1	
DN2019-T7	16°04′57″N 108°13′44″E	Lăng Ông Phường Nại Hiên Đông	0	0	
DN2019-T8	16°06′54″N 108°07′50″E	Dinh Cô Hồn Nam Ông	4	27	Multiple skulls and bones in jars
CI2019-T1	15°57′27.3″N 108°30′25.8″E	Ông Ngư	5	20	
HA2019-T1	15°52′54.0″N 108°23′09.0″E	Lăng Tiêu Diện	3	8	Possibly more skulls present
HA2019-T2	15°53′51.6″N 108°21′58.7″E	–	0	0	No skulls (one large vertebrae; several small bones)
HA2019-T3	15°54′49.4″N 108°20′09.4″E	Lăng Ông	0	1	
HA2019-T4	15°51′24.6″N 108°21′05.4″E	Lăng Ông Bốn Vạn Duy Vinh	4	26	Many skulls in poor condition; domestic cattle bones also on altar
LS-2019-T1	15°23′21.2″N 109°07′11.5″E	Lăng ông Ngư	0	0	Did not enter; whale buried out front
LS-2019-T2	15°22′42.0″N 109°08′26.5″E	Lăng Tân	1	1	
LS-2019-T3	15°22′29.7″N 109°07′44.9″E	Lăng ông Ngư	0	0	Did not enter; whale buried out front
LS-2019-T4	15°22′30.4″N 109°06′11.9″E	Lăng Tân	0	2	Skull fragments; postcranial
HUE-2019-T1	16°25′31.2″N 107°49′51.0″E	Lăng Ông Ngư	3	6	Sea turtle bones also present

Fig. 2. A, the central altar of DN2019-T4, Đà Nẵng; B, temple near Hội An, HA2019-T4 in the shape of a Vietnamese fishing boat.

Fig. 3. Six examples of central buildings of traditional whale temple complexes. A, HA2019-T2, Hội An; B, DN2019-T6, Đà Nẵng; C, DN2019-T7, Đà Nẵng; D, DN2019-T1, Đà Nẵng; E, HA2019-T1, Hội An; F, DN2019-T1, Đà Nẵng.

Table 2. List of taxa identified from fifteen temples across Central Vietnam with genus and species if known, family, total number, temples where each taxon can be found, and citations of other records from Vietnam for each species.

Genus	Species	Family	Total Number	Temples	Other records from Vietnam
Delphinus	*delphis tropicalis*	Delphinidae	2	Đà Nẵng (T1, T4)	Smith et al., 1997; Jefferson & Van Waerebeek, 2002
Feresa	*attenuata*	Delphinidae	1	Cham Islands (T1)	Smith et al., 1997
Globicephala	*macrorhynchus*	Delphinidae	3	Đà Nẵng (T1, T5)	Smith et al., 1997, 2003
Grampus	*griseus*	Delphinidae	1	Đà Nẵng (T4)	Smith et al., 1997
Lagenodelphis	*hosei*	Delphinidae	3	Đà Nẵng (T2, T3), Hội An (T1)	Smith et al., 2003; Vu et al., 2020
Pseudorca	*crassidens*	Delphinidae	3	Hội An (T4)	Smith et al., 1997
Sousa	*chinensis*	Delphinidae	12	Đà Nẵng (T2, T8), Hội An (T4), Huế (T1)	Smith et al., 1997, 2003; Jefferson & Van Waerebeek, 2004; Pham et al., 2015
Stenella	*attenuata*	Delphinidae	6	Đà Nẵng (T1, T4), Cham Islands (T1), Hội An (T4)	Smith et al., 1997, 2003; Pham et al., 2015
Stenella	*longirostris*	Delphinidae	1	Đà Nẵng (T1)	Smith et al., 1997, 2003
Stenella	sp.	Delphinidae	5	Đà Nẵng (T1, T8), Hội An (T4)	–
Tursiops	*aduncus/truncatus*	Delphinidae	22	Da Nang (T1, T2, T4, T8), Cham Islands (T1), Hội An (T1)	Smith et al., 1997, 2003; Zhou & Qian, 1985
Unknown	sp.	Delphinidae	28	Đà Nẵng (T1, T2, T6, T8), Cham Islands (T1), Hội An (T1, T3), Huế, Lý Sơn	–
Neophocaena	*phocaenoides*	Phocoenidae	41	Đà Nẵng (T1, T2, T3, T5, T6, T8), Cham Islands (T1), Hội An (T4), Huế	Smith et al., 1997, 2003; Jefferson, 2002
Balaenoptera	*omurai*	Balaenopteridae	2	Đà Nẵng (T4)	Pham & Nguyen, 2013; Vu et al., 2017
Megaptera	*novaeangliae*	Balaenopteridae	1	Lý Sơn (T2)	Smith et al., 1997
Unknown	sp.	Balaenopteridae	6	Đà Nẵng (T4, T5), Cham Islands (T1), Lý Sơn (T4)	–
Dugong	*dugon*	Dugongidae	3	Đà Nẵng (T8), Cham Islands (T1)	Tranngocloi, 1962; Van Bree & Duguy, 1977; Smith et al., 1997; Vo et al., 2005; Perrin et al., 2005; Hines et al., 2012

Fig. 4. A, collection of urns with marine mammal skulls from DN2019-T8, Đà Nẵng; B, central altar of HA2019-T4, Hội An; C, central altar of DN2019-T5 (Đà Nẵng) with glass casket of bones in the background; D, large tomb at the temple CI2019-T1 on the Cham Islands.

are shown in Supplemental Figs. 1–71. A complete list of marine mammal species found at each temple is shown in Supplemental Table S1 with their respective field ID numbers.

By far the most common species encountered was the Indo-Pacific finless porpoise (*Neophocaena phocaenoides*); we were able to identify 41 skulls from Đà Nẵng, Cham Islands, Hội An and Huế (Fig. 5A, B). In DN2019-T8, 16 out of 28 skulls belonged to *N. phocaenoides*. The next most common cetacean was the bottlenose dolphin (genus *Tursiops*). Both *T. aduncus* and *T. truncatus* are known to be present in the region, and differentiation between them can be challenging (Smith et al., 1997; but see Wang et al., 2000). However, we believe that the overwhelming majority of bottlenose dolphin skulls belong to *Tursiops aduncus* (Indo-Pacific bottlenose dolphin), such as DN2019-T1-005 shown in Fig. 5C, D. We identified two skulls (DN2019-T2-008; CI2019-T1-005) as *Tursiops truncatus* (common bottlenose dolphin) based on the large size of the skull and lack of convexity in the rostral portion of the premaxilla. Wang et al. (2000) was able to differentiate these species in the South China Sea using a measurement of the length from tip of rostrum to the apex of the premaxillary convexity; however, as we did not take this measurement, identification of *Tursiops* specimens remain tentative. The third most common species was the Indo-Pacific humpback dolphin (*Sousa chinensis*), with records from Đà Nẵng, Hội An, and Huế (Fig. 5E, F). Other definitive delphinid skull identifications included two *Stenella* species (*S. attenuata* and *S. longirostris*), *Lagenodelphis hosei*, *Pseudorca crassidens* (all three skulls from HA2019-T4), *Feresa attenuata*, *Globicephala macrorhynchus*, *Delphinus delphis* (all appear to be *D. d. tropicalis*) and *Grampus griseus*. Representative skulls of each of these species, except *S. longirostris* are shown in Fig. 5G–T. Five other skulls were identified to the level of the genus *Stenella* and it is likely they belong to *S. attenuata*, *S. longirostris*, or *S. coeruleoalba*. Mostly due to incomplete and fragmentary remains, 26 skulls were only able to be identified to the level of Delphinidae.

We found at least nine individual remains of baleen whales in five places, the temples DN2019-T4 (n=4) and DN2019-T5 (n=1) in Đà Nẵng, CI2019-T1 in the Cham Islands (n=1), and at two temples on Lý Sơn Island (n=3). DN2019-T4 contained two skulls of Omura's whale (*Balaenoptera omurai*) (Fig. 6; Supplemental Figs. 34, 35, 38), both noted by the presence of a parietal bone which overlays the dorsal aspect of the supraorbital process of the frontal, two small foramina at the suture between the parietal and squamosal, and a broad, squarish posterior end of the ascending process of the maxilla (Wada et al., 2003; Yamada et al., 2008). At DN2019-T4, we also observed two incomplete rorqual skulls

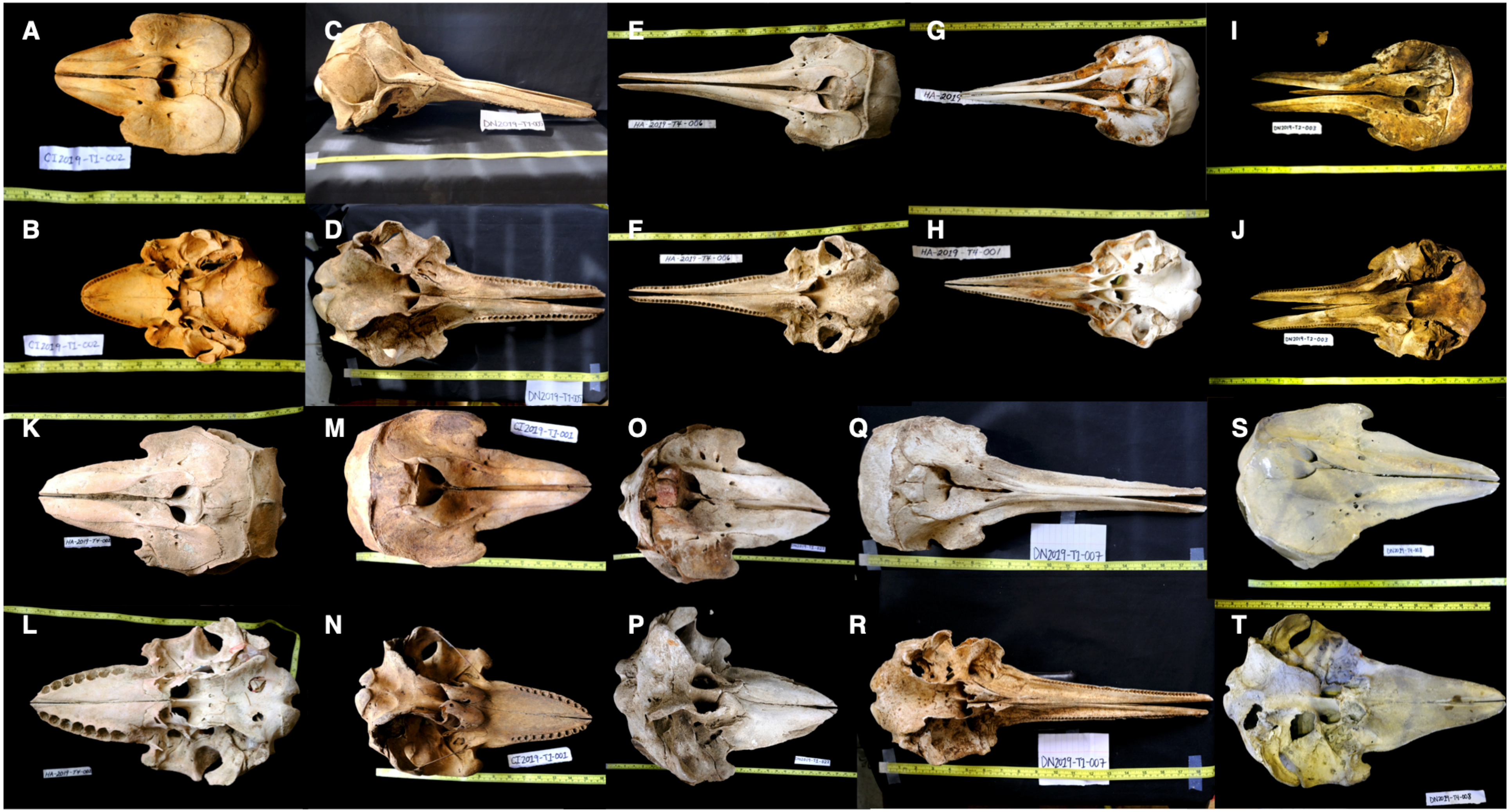

Fig. 5. A selection of odontocete skulls, highlighting most of the species identified during the survey. All photographs of additional specimens can be viewed in the Supplemental Information. A, dorsal view of the skull of CI2019-T1-002, *Neophocaena phocaenoides*; B, ventral view of the skull of CI2019-T1-002, *Neophocaena phocaenoides*; C, dorsal view of the skull of DN2019-T1-005, *Tursiops aduncus*; D, ventral view of the skull of DN2019-T1-005, *Tursiops aduncus*; E, dorsal view of the skull of HA2019-T4-006, *Sousa chinensis*; F, ventral view of the skull of HA2019-T4-006, *Sousa chinensis*; G, dorsal view of the skull of HA2019-T4-001, *Stenella attenuata*; H, ventral view of the skull of HA2019-T4-001, *Stenella attenuata*; I, dorsal view of the skull of DN2019-T2-003, *Lagenodelphis hosei*; J, ventral view of the skull of DN2019-T2-003, *Lagenodelphis hosei*; K, dorsal view of the skull of HA2019-T4-002, *Pseudorca crassidens*; L, ventral view of the skull of HA2019-T4-002, *Pseudorca crassidens*; M, dorsal view of the skull of CI2019-T1-001, *Feresa attenuata*; N, ventral view of the skull of CI2019-T1-001, *Feresa attenuata*; O, dorsal view of the skull of DN2019-T1-022, *Globicephala macrorhynchus*; P, ventral view of the skull of DN2019-T1-022, *Globicephala macrorhynchus*; Q, dorsal view of the skull of DN2019-T1-007, *Delphinus delphis* (long-beaked form); R, ventral view of the skull of DN2019-T1-007, *Delphinus delphis* (long-beaked form); S, dorsal view of the skull of DN2019-T4-008, *Grampus griseus*; T, ventral view of the skull of DN2019-T4-008, *Grampus griseus*.

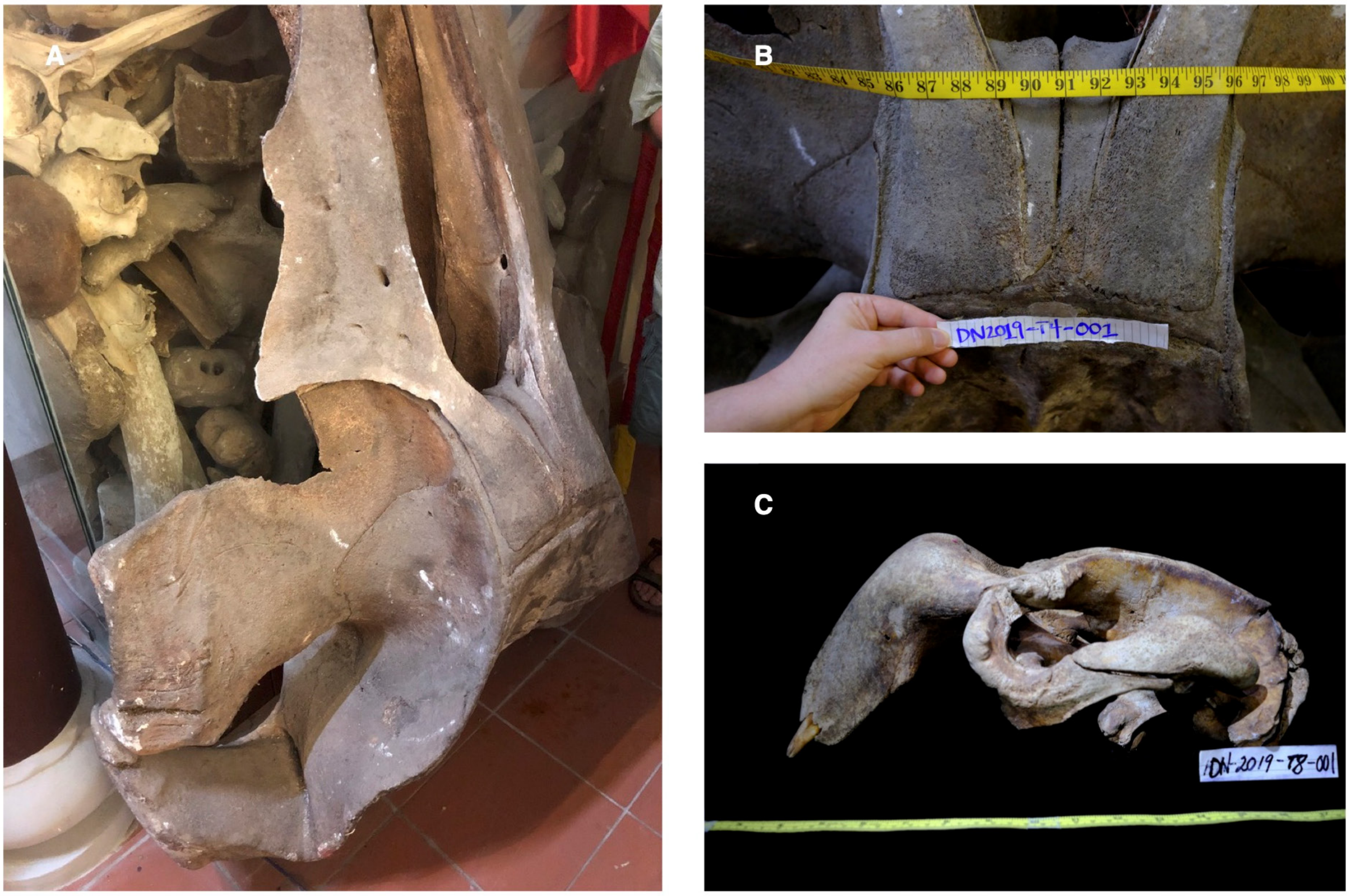

Fig. 6. A, left dorsolateral view of the skull of DN2019-T4-001, *Balaenoptera omurai*; B, dorsal view of the vertex of the skull of DN2019-T4-001, *Balaenoptera omurai*; C, left lateral view of the skull of DN2019-T8-001, *Dugong dugon*.

(Balaenopteridae) that we were unable to identify to species (Supplemental Figs. 45, 46). At LS2019-T2 on Lý Sơn, we observed bones from a large balaenopterid with a fragmentary skull that we were able to identify as a humpback whale (*Megaptera novaeangliae*) from the lack of an acromion process on the scapula (True, 1904). At LS2019-T4, the sign in front of the temple indicated the presence of three large whales; however, we were only able to confirm at least two very large balaenopterid individuals with incomplete skulls.

Finally, we encountered at least three individual dugongs (*Dugong dugon*) from two separate temples, CI2019-T1 (n=2) and DN2019-T8 (n=1). At CI2019-T1, we encountered one fragment of a dugong skull with a partial tusk as well as two isolated partial tusks, which implied a minimum of two individuals. The skull and mandible of DN2019-T8-001 were completely intact (condylobasal length of 388 mm), and erupted tusks measured an average of 18.61 mm, indicating a mature male.

Measurements. We were able to take measurements for 52 odontocete skulls, representing some of the most complete skulls encountered. Measurements and tooth counts of representative skulls are shown in Table 3. Due to the large sample size, for *Neophocaena phocaenoides* (n=13) and *Tursiops aduncus* (n=18), we show average measurements and counts. A complete list of measurements for all individuals is shown in Supplemental Table S1.

DISCUSSION

Odontocetes in Central Vietnam. The most common species encountered in our survey were odontocetes from shallow-water or nearshore environments, with more than 52% of specimens encountered identified as *Neophocaena phocaenoides* (n=41), *Tursiops* sp. (n=22), or *Sousa chinensis* (n=12). As these are the most dependent on nearshore environments, their carcasses would be more likely to wash up on shore. However, both *Neophocaena phocaenoides* and *Sousa chinensis* are among the toothed whales with the highest risk of bycatch worldwide by small-scale gill net fisheries (Temple et al., 2021), and it is very likely that their high numbers are the result of frequent bycatch in the region. Indeed, one study of bycatch in gillnet fisheries in Vietnam identifies five distinct species of dolphins caught as bycatch, although it does not name which species (Chu, 2001). While *Stenella longirostris* and *Delphinus delphis* can occur in more coastal environments (Jefferson et al., 2015), they were poorly represented in the whale temples observed in this study. Smith et al. (1997) also identified *N. phocaenoides*, *Tursiops* sp., and *S. chinensis* as among their four most commonly documented cetaceans. However, their numbers of *Delphinus delphis* specimens were much higher (n=17), most of these from the region around Nha Trang, over 400 km south of Hội An. This discrepancy in sampled remains could represent a true difference in relative abundance of *Delphinus delphis* in the waters off Vietnam. Nha Trang is much closer to the continental shelf and during

Table 3. Selected skulls with a subset of the standard small cetacean measurements of Perrin et al. (1975). Abbreviations: UR, upper right; NE, not examined. Mean measurements of skulls are reported at the bottom for *Neophocaena phocaenoides* (n=13) and *Tursiops aduncus* (n=18).

ID Number	Genus	Species	1. CBL (mm)	2. Rostral length (mm)	3. Rostral width (mm)	5. Rostral width mid-length (mm)	14. Zygomatic width (mm)	27. Internal nares width (mm)	28. Pterygoid length (mm)	Upper tooth row length	Tooth count, Upper left
DN2019-T2-008	*Tursiops*	*truncatus* (?)	525	277.4	140	85.9	244.6	74.1	78.4	239	25
CI2019-T1-005	*Tursiops*	*truncatus* (?)	525	278.7	116.4	65.1	230.1	61.9	NA	239	24
DN2019-T1-019	*Stenella*	*attenuata*	367	235	86	44.7	167	47	46	196	36
DN2019-T4-005	*Stenella*	*attenuata*	431	236	103	48	180	51	58	210	34
CI2019-T1-004	*Stenella*	*attenuata*	438	224.3	86.6	41.2	167.9	47.9	61.2	202.8	33
HA2019-T4-001	*Stenella*	*attenuata*	412	243.1	90.7	44.9	180	47.2	NE	214.7	37–38
DN2019-T1-009	*Stenella*	*longirostris*	343	222	71	42.6	143	37	49	200	40+
DN2019-T3-001	*Lagenodelphis*	*hosei*	430	235.6	120.3	70.3	224.6	62.9	92.3	212.2	43 (UR)
DN2019-T2-003	*Lagenodelphis*	*hosei*	428	236.5	123.7	78.5	211.5	66.2	78.3	212.7	41
DN2019-T2-007	*Sousa*	*chinensis*	502	306.1	110.6	48.7	207.6	68	65.6	267.7	35
HA2019-T4-006	*Sousa*	*chinensis*	538	326	115	47	219	67	64	283	34
DN2019-T4-008	*Grampus*	*griseus*	506	250	199	104	321	76	NE	NE	0
DN2019-T4-010	*Delphinus*	*delphis*	430	279.55	81.2	40.32	163.01	NE	NE	231.13	NE
DN2019-T1-007	*Delphinus*	*delphis*	436	294.28	87.02	41.92	168.61	44	66	258.09	54
CI2019-T1-001	*Feresa*	*attenuata*	432	180.9	122.6	84	232.8	56.3	81.4	117.9	10
HA2019-T4-002	*Pseudorca*	*crassidens*	525	254	176.5	140.3	320	83.2	NE	211.9	8
HA2019-T4-003	*Pseudorca*	*crassidens*	572	276	197.7	NE	350	NE	NE	250	9

	Genus	Species	1. Mean CBL (mm)	2. Mean rostral length (mm)	3. Mean rostral width (mm)	5. Mean rostral width midlength (mm)	14. Mean zygomatic width (mm)	27. Mean internal nares width (mm)	28. Mean pterygoid length (mm)	Mean upper tooth row length	Mean tooth count, upper left
	Neophocaena	*phocaenoides* (n=13)	214.395	76.33846154	72.91153846	55.20307692	137.6191667	43.84166667	28.46666667	64.97	17.90909091
	Tursiops	*aduncus*(?) (n=18)	473.667	276.1717647	114.0617647	57.64866667	222.8988235	60.861	61.40666667	231.6205882	24.83

the summer, the Southern Vietnam Upwelling event produces productive cooler waters in this region (Wu et al., 2019). In other parts of the world, *Delphinus delphis* is generally found in concert with moderate to strong upwelling events (Au & Perryman, 1985; Ballance & Pitman, 1998; Jefferson et al., 2009).

Neophocaena phocaenoides is found in tropical and subtropical waters of <50 m in depth, areas which are under intense pressure from human activities such as fishing and coastal development (Wang & Reeves, 2017). Due to their small size, they are exceptionally vulnerable to being caught in gillnets (Jefferson & Curry, 1994; Park et al., 2015; Wang & Reeves, 2017; Temple et al., 2021). However, population estimates and specific threats to *Neophocaena phocaenoides* in Vietnam are unknown at present. Vessel surveys in the Mekong River Delta in 1995 observed large numbers of gillnets and stake nets set perpendicularly along the channels (TAJ, personal observation), and such fisheries are likely to have had devastating impacts on the finless porpoise population(s) in Vietnam. Strandings and bycatch records suggest this species may be found all along the coast of Vietnam (LV, personal observation), and the high number of *Neophocaena phocaenoides* specimens in temples may indicate a greater need for specifically monitoring marine mammal bycatch and mitigating gillnet use in the region.

The average size of *N. phocaenoides* skulls (214.395 mm; Table 3) in this study is similar to those measured from south-central Vietnam by Jefferson (2002). *Neophocaena phocaenoides* specimens found in the northern South China Sea (including central Vietnam), Hong Kong and Taiwan tend to be larger than specimens from lower latitudes such as the Mekong River Delta of Vietnam, Malaysia, Thailand, and India (Jefferson, 2002). This could imply a genetic divergence with a boundary centred in Vietnamese waters. Although extensive genetic work has been accomplished in East Asia (Yang et al., 2002; Chen et al., 2010; Li et al., 2013; Lin et al., 2014; Zhou et al., 2018), few studies have captured genetic data in the large range of *N. phocoaenoides* extending from Vietnam to the Persian Gulf (Jayasankar et al., 2008; Lin et al., 2017). As far as we know, no studies have addressed the genetic diversity and phylogeography of the Indo-Pacific finless porpoise in Southeast Asia. This should be a top priority to further understand and diagnose evolutionary significant units to inform conservation across the wide range of this threatened species.

Both species of *Tursiops* occur in the region; however, skulls of the two species, *T. truncatus* and *T. aduncus*, can be difficult to distinguish in the region unless discriminant functions are used (Wang et al., 2000). Under our time constraints, we were unable to take a full suite of measurements, so we tentatively identified *Tursiops* skulls based on size and degree of the convexity of the premaxilla on the rostrum (Jefferson et al., 2015). *Tursiops aduncus* is the more coastal and smaller of the species, and we infer that most of the skulls belong to *T. aduncus* due to their size and the convexity of the premaxillae at the midpoint of the rostrum (n=18). However, two skulls (DN2019-T2-008, CI2019-T1-005) were larger, more robust, and lacked convex premaxillae as compared to those attributed to *T. aduncus* (Table 3), and we tentatively referred them to *Tursiops truncatus*. Wang et al. (1999) analysed control region sequences of both *Tursiops* species from China and found a deep split between species in the region. A recent large-scale genetic analysis of the genus *Tursiops* using RADSeq clearly demarcated *T. aduncus* and *T. truncatus* as distinct reciprocally monophyletic lineages using large samples from multiple regions (Moura et al., 2020). However, they did not include any samples from Southeast Asia, and it is unclear where Southeast Asian populations of either species might fit into the global phylogeography of the genus.

Sousa chinensis is another coastal specialist that reaches its highest abundance in waters near estuarine outputs and tidal channels (Parra & Jefferson, 2018). This species has been well-studied in China (Jefferson et al., 2017), but is just beginning to be more widely studied in Southeast Asia (Hoffman et al., 2015; Minton et al., 2016; Kuit et al., 2019) and its relative abundance and occurrence in Vietnam is still unclear. In this study, it was our third most commonly encountered species, and along with results from Smith et al. (1997), it seems that *S. chinensis* is a relatively common species that strands, at least in the southern two-thirds of the country. *Sousa chinensis* is also probably common along the coast of the northern third of Vietnam as well. Smith et al. (2003) encountered at least three individuals in surveys in the Gulf of Tonkin, all of which were inshore near Hạ Long Bay, and Pham et al. (2015) documented at least one taxidermy specimen at the nearby Đồ Sơn Marine Museum. Using habitat modelling, Huang et al. (2019) and Wu et al. (2021) predicted the area near Hạ Long Bay to be highly suitable habitat year-round for *Sousa chinensis*, with several areas in the southern Gulf of Tonkin to be highly suitable during wet seasons. Although Jefferson & Van Waerebeek (2004) used several skulls measured at whale temples in their study of geographic variation in skull morphology of the genus, the genetic connectivity of *S. chinensis* outside China is not well-known. Mendez et al. (2013) used mitochondrial and nuclear data to examine phylogeography across the entire range of the genus *Sousa*; they included samples from the nearby Gulf of Thailand which, although distinct, grouped closely with Chinese samples. Further analyses using more control region sequences confirm there is a distinct mitochondrial clade in the Gulf of Thailand (Zhao et al., 2021), with some evidence from whole genomes that samples from Thailand represent a distinct population (Zhang et al., 2020). Where Vietnamese individuals fit into the growing phylogeographic picture of *Sousa* is an open question that needs further investigation.

A number of delphinid species found in our survey include those that usually reside in deeper waters. These include *Lagenodelphis hosei*, *Globicepala macrorhynchus*, *Feresa attenuata*, *Pseudorca crassidens*, *Grampus griseus*, and *Stenella attenuata*. At least three of these species (*L. hosei*, *G. macrorhynchus*, *S. attenuata*) were identified in offshore surveys of Vietnam, as discussed in Smith et al. (2003). Vu et al. (2020) reported several specimens of *L. hosei* in Vietnam (including DN2019-T3-001); here we add one additional specimen to this list (DN2019-T2-003). In a recent survey of deep waters off Hainan, China, and near the Paracel Islands (Hoàng Sa) in the South China Sea, an area about 350 km northeast from Central Vietnam, researchers identified many of these species including *G. griseus*, *G. macrorhynchus*, *S. attenuata*, and *L. hosei*, and suggested that the northern South China Sea is an important calving ground for deeper-water species (Lin et al., 2020). Liu et al. (2019) also determined that *S. attenuata* was the most common cetacean that stranded on nearby Hainan Island, China, from 1978 to 2016, and *G. macrorhynchus*, *P. crassidens*, and *G. griseus* were species with documented strandings during this period as well.

Mysticete diversity and Omura's Whale in Vietnam. At least eight mysticete whale species are known to be or predicted to be present in Vietnam (Smith et al., 1997; Pham & Nguyen, 2013; Pham et al., 2014). Here we were able to conclusively identify at least two species, *Megaptera novaeangliae* and *Balaenoptera omurai* from remains in the temples. This study contributes two more records (DN2019-T4-001, DN2019-T4-004) to the growing number of specimens of *B. omurai* from Vietnam. To our knowledge, the first record of *B. omurai* described from Vietnam was a whole skeleton present at a whale temple in Phổ Thạnh, Quảng Ngãi Province (Pham & Nguyen, 2013). Vu et al. (2017) described another skull of *B. omurai* from a whale temple on Phú Quốc Island in Kiên Giang Province near the border with Cambodia. Although not part of our study area, we visited the Quảng Ninh Historical Museum (Bảo tàng Quảng Ninh) in Hạ Long, Quảng Ninh Province in the northern part of the country off the famous Hạ Long Bay, and would like to note the presence of a fifth *B. omurai* specimen in the form of a mounted skeleton on display there (Supplemental Figs. 73, 74).

Balaenoptera omurai was first described using both genetic and morphological data from the Sea of Japan, Solomon Islands, and Cocos Islands (Wada et al., 2003). Since this time, documentation of its presence has continued to expand to South and Southeast Asia, Australia, the western Indian Ocean, and the tropical Atlantic (Cerchio et al., 2019). Yamada et al. (2006, 2008) described several osteological specimens as *B. omurai* from areas surrounding Vietnam, including Taiwan (n=7), Thailand (n=3), and Philippines (n=24), expanding its range across the South China Sea and Southeast Asia. Sightings have also been documented from mainland China, Taiwan, Thailand, Malaysia, and the Philippines (Wang et al., 2006; Adulyanukosol et al., 2012; Ponnampalam, 2012; Wang, 2012; Cerchio et al., 2019). The growing number of records suggest *Balaenoptera omurai* might be a common sight off Vietnam; perhaps future surveys in the Gulf of Tonkin and South China Sea may provide living photographic evidence of its presence.

Dugongs in Vietnam. The current presence of dugongs is only verified from southwestern Vietnam (Phú Quốc and possibly Thổ Chu) and the Côn Đảo Archipelago (Marsh et al., 2002; Phan, 2003; Vo et al., 2005; Hines et al., 2008), although Perrin et al. (2005) mentions they are also present north of Hạ Long Bay near the Chinese border. Based on records from whale temples and accounts of captures, dugongs were once found off Phú Quý Island (Nguyen et al., 2000), the south-central coast (Khanh Hoa and Binh Tuan Provinces) (Smith et al., 1997; Hines et al., 2012), and Quảng Ninh, Nghệ An and Quảng Bình provinces in the north (Smith et al., 1997; Vo et al., 2005; Hines et al., 2012). Historically there is a record of a capture of a dugong near Nha Trang >400 km to the south of Đà Nẵng (Tranngocloi, 1962); however, Vo et al. (2002) state that dugongs are not currently present near Nha Trang. Our records of three dugongs from CI2019-T1 and DN2019-T8 indicate that dugongs were present in Central Vietnam with individuals likely present off the Cham Islands and near Đà Nẵng Bay at some point in the past. To our knowledge, there is no evidence that dugongs are currently in these areas; however, Cao et al. (2012) show some evidence of seagrass beds still present in Đà Nẵng Bay, which supports the potential for dugong presence here in the past and perhaps the potential for recolonisation. Undoubtedly dugongs were much more common along the coast of Vietnam in the recent past and their decline and apparent extirpation along most of the coast of Vietnam is likely due to a combination of direct hunting, bycatch, and the destruction of seagrass habitats (Dung, 2003; Vo et al., 2005; Hines et al., 2008). Seagrass and submerged aquatic vegetation along the coast of Vietnam have been severely reduced over that past 20 years (Cao et al., 2012; Tran et al., 2020). The reduction of seagrass environments and absence of the dugong also seems to be the case in nearby Hainan Island, China (Wang et al., 2007). These whale temple records of dugongs underline the importance of whale temples in recording past abundance of marine mammals in particular areas of the Vietnamese coast. Poommouang et al. (2021) identified a unique mitochondrial clade centred on Southeast and East Asia; Vietnamese specimens could represent valuable sources for future DNA analyses to broaden this analysis.

Whale Temples: Past, Present, and Future. Whale temple culture and marine mammal worship in Vietnam is a unique example of a cultural practice that has emerged as a result of interactions between marine mammals and humans. It is unique within Southeast Asia and we know of no other similar practices in the region. The belief in a benevolent whale spirit possibly dates back to the 14th century or before, when the Champa Empire still controlled the central region of Vietnam. It was amplified during the Nguyễn Dynasty in the early 19th century, with the legend of whales aiding the future emperor Gia Long by rescuing him from pursuit by an enemy navy (Kiem, 1996). The new emperor then issued an order that declared all marine mammals as sea gods and sacred animals (Kiem, 1996). In Vietnam today, this belief could potentially contribute to positive outreach actions regarding conservation of marine mammals in the country although interviews of fishers are currently underway by some of the authors. The respect of Vietnamese artisanal fishers toward marine mammals has created a cultural taboo against hunting or harming marine mammals that persists into the present. However, whale worship is under threat as temples are moved to make way for luxury hotels and younger members of fishing communities move to cities (Lantz, 2009; Parnwell, 2013). This could result in fewer specimens deposited in temples and therefore decrease the prospect of long-term use of whale temples as a monitoring tool. CBES (Center for Biodiversity Conservation and Endangered Species) led by Long Vu has set up a monitoring network that is responding to strandings with the help of local fishing communities. Interviews of temple keepers and individuals in Vietnamese fishing communities were taken by some of the authors of this paper in order to assess attitudes toward marine mammals and will be presented at a later date. We hope that conservation efforts can take advantage of this already existing belief among artisanal fishers to promote the protection of marine ecosystems and aid in the establishment of sustainable development practices.

Robineau (1998) favourably compared the marine mammals contained within whale temples to the largest collections in natural history museums throughout the world, and indeed their scientific usefulness to the study of marine mammals is invaluable. The survey of whale temples introduces a simple method to collect information concerning marine mammals that is unique within Southeast Asia, a region in which strandings and bycatch can be difficult to monitor. Indeed, there are still limitations, as some temples do not provide access, and in many temples, bones may be cremated after a certain amount of time due to overcrowding (Lantz, 2009; LV, personal observation). In addition, data on whale temple specimens can be incomplete; recent strandings or bycaught animals are sometimes noted by some temple keepers, but many older specimens lack data. Conditions of animals are not recorded upon stranding, so it is difficult to monitor potential causes of death. This is a limitation in monitoring the true scale of potential effects of fishing or other human impacts. In the future, an in-depth exploration and cataloguing of whale temple specimens along the entire coast of Vietnam is necessary to add an expanding number of records to the documentation of marine mammal occurrences in Vietnam. Although surveys have been completed in certain parts of southern Vietnam, many temples remain to be surveyed. In concert with interviews of fishing communities associated with whale temples, knowledge of past and current distributions could fill in gaps in knowledge needed for better stewardship and conservation of existing marine mammal populations off Vietnam. Further studies should work with community members and build their capacity to collect bone or tooth samples of whale temple remains to examine the population structure of Vietnamese marine mammals and their relationships to Southeast and East Asian populations. Recent studies have used genetic sequences generated from bone to study population genetics and phylogeographic structure of marine mammals (Plön et al., 2019). To our knowledge, there have been few cetaceans from Vietnam that have had any DNA data sequenced (Genbank accession numbers JQ814471–JQ8144713 being the exception). This approach, combined with renewed marine surveys, should help to reveal much needed data regarding marine mammals in a rapidly changing region.

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