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Contributions of Photographs to Cetacean Science

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Abstract

Over four decades ago, a short paper demonstrated how photographs of free-swimming dolphins could be used to reveal scientific information about cetaceans. That paper, and a few others published during the same time period, illustrated a research technique that has become foundational in the field of marine mammalogy and resulted in a cascade of science. Photographs can be used to identify individuals, providing insights into movements, migrations, site fidelity, school structure and stability, and abundance. Photographs can be used to estimate group size and improve the precision of abundance estimates. Photographs can characterize reproductive output at the population level. Photographs allow for quantification of morphology, yielding insights into classification at a variety of taxonomic levels; and they provide a means to assess the condition and health of individual animals. And photographs can provide insights into behavior. The information photographs convey and their applications to cetacean research are ever-increasing. Ultimately, photographs have provided a high-quality and relatively inexpensive means to increase the knowledge base for most cetacean species in all of the oceans of the world through research conducted by scientists of developed and developing nations, and through citizen science conducted by non-scientists.

Key Words: cetaceans, photo-identification, mark-recapture methods, line-transect methods, eastern tropical Pacific, school size calibration, photogrammetry

Introduction

In 1977, a short paper published in the journal *Science*, "The Photographic Determination of Group Size, Composition, and Stability of Coastal Porpoises (*Tursiops truncatus*)" (Würsig & Würsig, 1977), documented results of a 21-mo study conducted on common bottlenose dolphins along a small section of the Argentinian coast. Fifty-three individuals moved through the area in subgroups that averaged 15 animals in size. A stable group of the same five animals was identified; these five were joined by other individuals whose identities varied through time. The full results were published the following year (Würsig, 1978).

It was a simple and relatively basic set of results, but the Würsig & Würsig (1977) study has become influential because of the methods documented in that paper. Using 35-mm cameras and telephoto lenses, they took photographs of individual dolphins from land and small boats and discovered that the trailing edge of the dorsal fin of many individual dolphins was uniquely nicked and scarred, and those patterns remained distinctive for at least the 2-y duration of the study (Figure 1). This allowed them to identify individual animals and track them through time, revealing details of their movements and associations with other individuals.

The ability to resight individuals based on unique markings and document them through photographs was a tool that biologists were discovering around the world on a variety of species at the same time that the Würsigs were studying dolphins in Argentina (e.g., Schevill & Backus, 1960; Katona et al., 1979; Bigg, 1982; Payne et al., 1983). This general realization that photographs could be used to reveal information about cetaceans has resulted in a cascade of science. Photographs can be used to identify individuals, providing insights into movements, migrations, site fidelity, school structure and stability, and abundance. Photographs can be used to estimate group size and provide a means to improve the precision of abundance estimates. They can characterize reproductive output at the population level. Photographs allow for quantification of morphology, yielding insights into classification at a variety of taxonomic levels and providing a means to assess condition and health of individual animals. And photographs can provide insights into behavior. Herein, I provide an overview of some of the many ways that photographs have been used to further our understanding of cetacean biology.

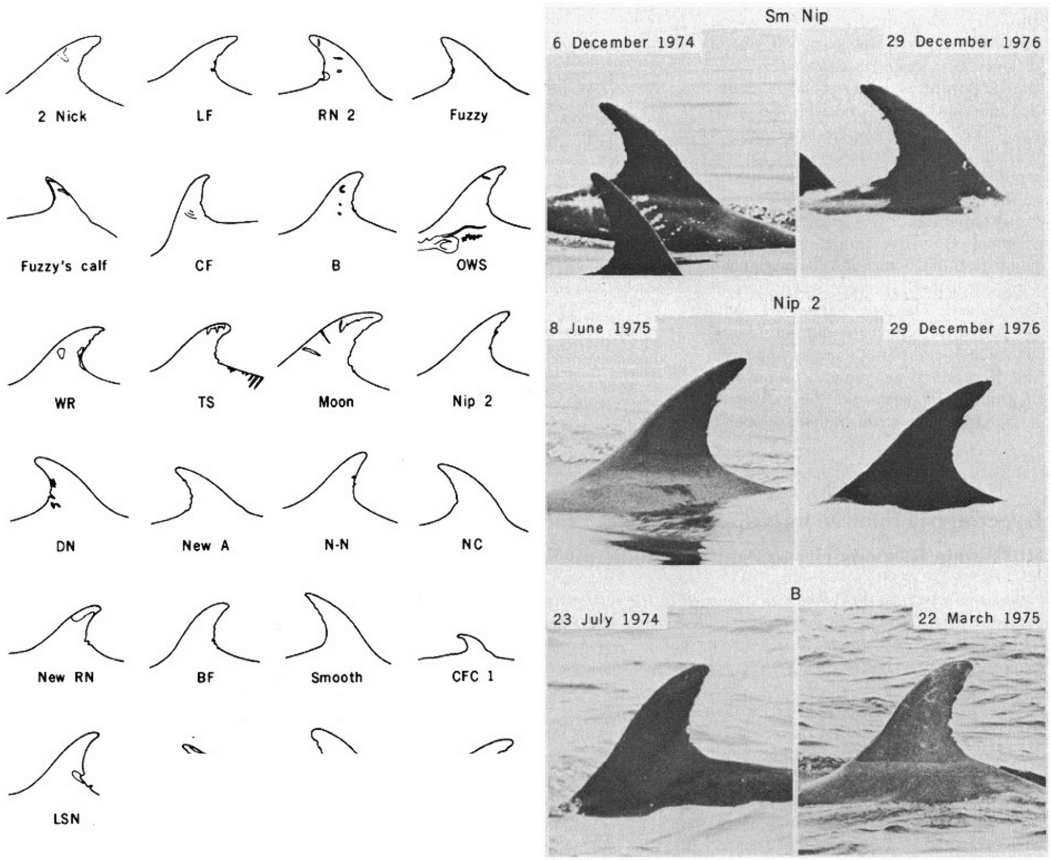

Figure 1. Photographs can be used to identify individuals. Examples of variations in fin size, shape, pigment variation, and scars and nicks of bottlenose dolphins (left), and photographs of three individuals identified using these marks and resighted through time (right) are shown here. From Würsig & Würsig (1977).

Photographs Can Be Used to Identify Individuals

Many cetaceans are born with or acquire distinctive markings that are unique at the individual level and change minimally or not at all throughout their lives. Examples include nicks and scars on the dorsal fins, pectoral fins, or flukes of common bottlenose dolphins (*Tursiops truncatus*), sperm whales (*Physeter macrocephalus*), and fin whales (*Balaenoptera physalus*); distinct pigmentation patterns on the dorsal or ventral fluke surfaces of blue (*Balaenoptera musculus*), humpback (*Megaptera novaeangliae*), gray (*Eschrichtius robustus*), and killer (*Orcinus orca*) whales; and unique placement and development of callosities on the rostra of right whales (*Eubalaena* spp.). This is powerful information. Photographs of these individuals can provide clarity on movements, migrations, and site fidelity (e.g., Calambokidis et al., 2002a; Weller et al., 2012; Swartz, 2018). They can reveal social structure and social stability (e.g., Bigg et al., 1990; Weinrich, 1991; Ramp et al., 2010; Franklin, 2012; Ford, 2018; Whitehead, 2018), and they allow for estimation of abundance (e.g., Barlow et al., 2011).

Movements, Migrations, and Site Fidelity

Once photographically identified, an individual can be spatio-temporally tracked with subsequent photographs (e.g., Würsig & Würsig, 1977). This simple, inexpensive, non-invasive method has led to major advances in our understanding of various cetacean species' movements, migrations, and site fidelity. Photographs are particularly influential when compiled into catalogs so that researchers can compare individuals identified in their study areas with individuals identified elsewhere. The number of photo-identification catalogs, from local to ocean-basin scales, is ever-increasing as is the number of species for which they exist (e.g., Payne, 1986; Arnbom, 1987; Defran et al., 1990; Calambokidis et al., 2002b; Calambokidis & Barlow, 2004; Olson, 2012; Towers, 2015).

These catalogs can yield surprising results; discoveries pertaining to gray whales provide an example. Eastern Pacific gray whales calve in lagoons along the west coast of Baja California, Mexico, and migrate north along the coast of North America to feeding grounds in the Bering, Chukchi, and Beaufort Seas (Swartz, 2018). A separate and genetically distinct population, western Pacific gray whales (LeDuc et al., 2002), feeds in the Okhotsk Sea. This latter population has been monitored using photo-identification methods since the mid-1990s, and these photographs have confirmed seasonal and interannual site fidelity and philopatry (site fidelity by many individuals first identified as young-of-the-year; Weller et al., 2012). Historic evidence indicates that western Pacific gray whales migrated south along the coasts of eastern Russia, the Korean Peninsula, and Japan to the south China Sea to calve. Photographs have confirmed some of these movements (Weller et al. 2008, 2016), though contemporary data are scarce, in part because the population is Endangered with the most recent estimate at about 200 individuals (Weller et al., 2012; Cooke, 2018).

Weller et al. (2012) compared photo-identification images of gray whales between three catalogs: one containing images of 181 western Pacific gray whales feeding in the Okhotsk Sea (Weller et al., 1999); a second containing images of 1,064 eastern Pacific gray whales feeding along the coast of North America between northern California and the Gulf of Alaska (Calambokidis et al., 2002b); and the third containing 2,514 images of, presumably, eastern Pacific gray whales photographed in Laguna San Ignacio, a calving lagoon along the coast of western Baja California, Mexico (Weller et al., 2012). These comparisons revealed that six of the Okhotsk Sea individuals were photographed along the coast of North America, and another four were photographed in Laguna San Ignacio (Figure 2). These remarkable observations, based on photographs, confirmed that at least some western Pacific gray whales migrate to the eastern Pacific, that some travel to the calving lagoons of the west coast of Mexico, and that our

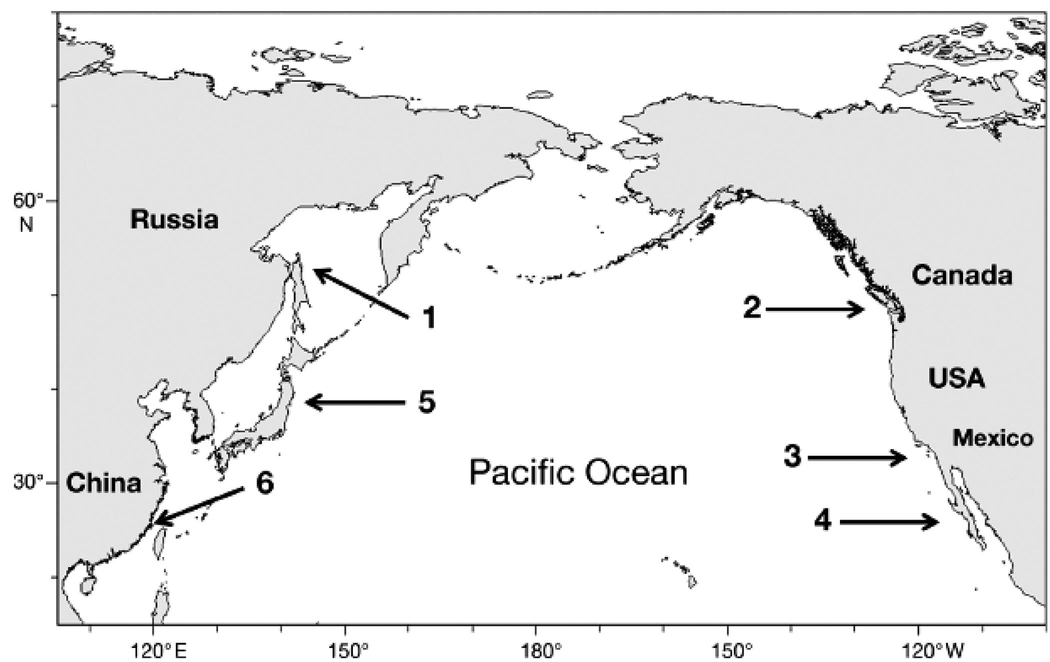

Figure 2. Photographs can reveal surprising details regarding movements and migration patterns. The range of gray whales showing feeding and purported calving grounds for the western North Pacific population (1, 5 & 6), and feeding and calving grounds for the eastern North Pacific population (2, 3 & 4) is shown here. Six individuals were photographed in both areas 1 and 2, and another four were photographed in both areas 1 and 4, revealing that our understanding of movement and migration patterns of gray whales is far from complete. From Weller et al. (2012).

understanding of movement and migration patterns of gray whales is far from complete.

Social Structure and Stability

Once photographically identified, an individual's associations with others can be spatio-temporally tracked. This has proven to be particularly insightful for learning about social structure and stability. In locations where populations can be reliably accessed and studied, photographic observations have revealed information about social structure that is remarkably detailed. Killer whales provide a good example. Photographs have revealed that killer whales are highly social with a group structure characterized by matrilines: a female, her sons and daughters, and the offspring of her daughters (Ford, 2018). In the case of the eastern North Pacific fish-eating "resident" killer whales, these matrilines can contain as many as five generations of related individuals and are highly stable; no permanent dispersal of individuals has been observed over decades of research (Bigg et al., 1990; Ford, 2018). Eastern North Pacific mammal-eating, "transient" killer whales exhibit matrilines of much smaller size and with lower stability; offspring can disperse for extended periods or permanently when they reach maturity, and lone individuals, particularly males, are often observed (Baird & Whitehead, 2000).

There are other examples of complex social structure in cetacean species, the details of which are based on data provided from individuals recognized via photographs of their individual markings (and, in some cases, augmented by molecular genetic analyses). Sperm whales occur in matrilineally related social units consisting of about 10 females and their young. These units tend to remain stable throughout the life of the individual. Units have preferred associations with each other (Whitehead, 2018). Pilot whales (*Globicephala* spp.) form groups of 10 to 20 individuals with close matrilineal associations. These groups are stable with individuals maturing in their natal group and remaining there for life (Olson, 2018). And bottlenose dolphins form cooperative male alliances to sequester and control the movements of females (Connor et al., 1992, 1999).

Photographic identification data have also been used to confirm a lack of social structure. This seems to be the rule for mysticetes in general. Apart from the female–calf association that typically lasts less than 1 y, most associations between individuals within a given species are temporary and brief (Tyack, 1986). Humpback whales, among the best studied of the mysticetes, are usually characterized as occurring in small, unstable groups (Clapham, 2018), although some stable associations on the feeding grounds that span multiple years have been documented (Weinrich, 1991; Ramp et al., 2010). A set of photographs taken 3 y apart at the same location clearly shows the same two humpback whales (an adult male and adult female, the latter with a calf each time) migrating side-by-side off the eastern coast of Australia (Franklin, 2012) and provides additional support that photographic identification of individuals can continue to reveal surprises about cetacean social structure and stability.

Abundance

Photographs allow for estimation of abundance through analytical methods collectively referred to as *mark-recapture*. Briefly, a sample of individuals is captured (photographed) and marked (individually identified through distinct features on the photographed dorsal fins, backs, rostra, and/or flukes). On a subsequent occasion, a second sample of individuals is similarly captured (photographed) of which a number are already marked (previously photographed and recognizable through distinct markings). If a number of assumptions are met, the proportion of marked animals in the second sample should equal the proportion of marked animals in the population (Hammond, 2018). Abundance has been estimated using photographs and mark-recapture methods for many cetacean species, including humpback (Barlow et al., 2011), blue (Calambokidis & Barlow, 2004), sperm (Matthews et al., 2001), and northern bottlenose (*Hyperoodon ampullatus*; Barlow et al., 2005) whales, and common bottlenose (Read et al., 2003), humpback (*Sousa* spp.; Karczmarski et al., 1999), and Hector's (*Cephalorhynchus hectori*; Gormley et al., 2005) dolphins on geographic scales that range from highly localized to entire ocean basins.

Among the more remarkable examples of ocean basin mark-recapture research is the Structure of Populations, Levels of Abundance and Status of Humpbacks (SPLASH) project (Calambokidis et al., 2008). This was a multiyear (2004-2006), multinational effort designed to estimate abundance of humpback whales in the entire North Pacific Ocean based on a dedicated photo-identification study that representatively sampled all six known breeding and all six known feeding populations. Barlow et al. (2011) used 9,948 high-quality individual identifications from photographs of the ventral surface of humpback whale flukes taken from a variety of platforms to estimate that this population numbered 21,808 (CV = 0.04), which is higher than any previous estimates, even exceeding some estimates of pre-whaling abundance.

In 2010, the U.S. National Oceanic and Atmospheric Administration (NOAA) Fisheries conducted a status review of humpback whales worldwide (Bettridge et al., 2015). Five Distinct Population Segments under the Endangered Species Act were identified in the North Pacific. One was subsequently down-listed (from Endangered to Threatened), and another was de-listed (from Endangered to Not at Risk; Figure 3). A critical underpinning of this decision, and chronicling a recovery success story, was the abundance estimates of these populations made possible through photographs.

Photographs Can Be Used to Estimate Group Size

Photographs are regularly used to estimate group size. Commonly photographed marine taxa for these purposes are those occurring in groups on land: surface-nesting seabirds on breeding colonies and pinnipeds hauled out on rookeries (e.g., Loughlin et al., 1984; Bowen et al., 1987; Schiavini & Yorio, 1995; Goebel et al., 2015). Cetaceans are typically visible only at the water surface, and determining group size is particularly challenging because the animals are always moving; an unknown fraction is under water at any moment, and groups can be large, numbering hundreds to thousands, depending on the species (Gerrodette et al., 2018).

An exceptional example of how photographs are used to estimate cetacean group size pertains to dolphins in the eastern tropical Pacific (ETP). Abundance estimates are made with data collected aboard research vessels using line-transect methods (Gerrodette & Forcada, 2005). School size is a critical parameter for abundance yet particularly challenging to estimate because schools frequently avoid ships or fragment as a ship approaches (Archer et al., 2010). Gerrodette et al. (2018) documented calibration of school size estimates made independently by observers at sea with photographs of a subset of those same schools simultaneously photographed from manned aircraft. Accuracy of school size estimates varied widely among observers. Most observers tended to underestimate (69% of observer estimates were less than the photo count) and that tendency increased with group size. For spotted dolphins (*Stenella attenuata*), the difference between the mean of 59 observer estimates and true group size ranged from an underestimate of 11 to 42% (for groups of 50 and 500 animals, respectively). Distribution of the means of the posteriors ranged from estimates of 131.7 to 201.8 for groups of 500 animals. Averaged over all species, underestimates ranged from < 1% for groups of 25 animals to a mean of 47% for groups of 500 animals. Precision of group size estimates was low, and estimates were highly variable among observers for the same group.

Calibration factors derived from these photographs are applied to observer estimates of school size that are an important parameter in abundance estimation and in estimating trends in abundance over time (Gerrodette & Forcada, 2005; Gerrodette et al., 2008). The application of these results, greatly strengthened by the use of photographs, has been particularly far-reaching. Ultimately, these abundance estimates have formed the basic underpinnings for the designation of some dolphin stocks in the ETP as Depleted under the U.S. Marine Mammal Protection Act (MMPA) and for upholding the "Dolphin Safe" label found on cans of tuna in food stores throughout the United States and in many other nations.

Photographs Can Characterize Reproductive Output at a Population Level

Photographs can provide a wealth of information on reproductive output at the school level. Cramer et al. (2008) analyzed aerial photographs taken from a helicopter between 1987 and 2003 of 160 schools of eastern spinner dolphins (*Stenella longirostris orientalis*) and northeastern offshore pantropical spotted dolphins (*Stenella attenuata attenuata*) to obtain number of calves in a school and animal length as a proxy for age (using photogrammetric methods, see next section; Figure 4). From these photographs, Cramer et al. counted over 20,000 dolphins and measured more than 1,500 individuals to obtain two measures of reproductive output: (1) proportion of adult dolphins with calves and (2) length at which calves disassociated from their mothers. (The latter was used as a proxy for weaning, assuming that the disassociation captured in the photographs was permanent.)

Both dolphin stocks are listed as Depleted under the MMPA due to historically high incidental mortality in the yellowfin tuna (*Thunnus albacares*) purse-seine fishery (Lo & Smith, 1986; Wade, 1995; Wade et al., 2007). Cramer et al. (2008) found that the annual number of purse-seine sets on dolphins was a significant predictor of proportion of adult dolphins with calves and length of calf at disassociation for northeastern offshore spotted dolphins. The relationship was inverse for both metrics.

The implications of these photographs and the data they provided were profound. Cramer et al. (2008) concluded that because northeastern offshore spotted dolphins are the primary species targeted by dolphin sets in the tuna purse-seine fishery, the link between fishing intensity and both measures of reproductive output for this stock indicates that the fishery has had population-level effects beyond the incidental kill reported by observers aboard the fishing vessels. Cramer et al. further speculated that the decline in reproductive output was among the proximate causes of the failure of dolphin populations to recover at rates expected after reduction of high incidental

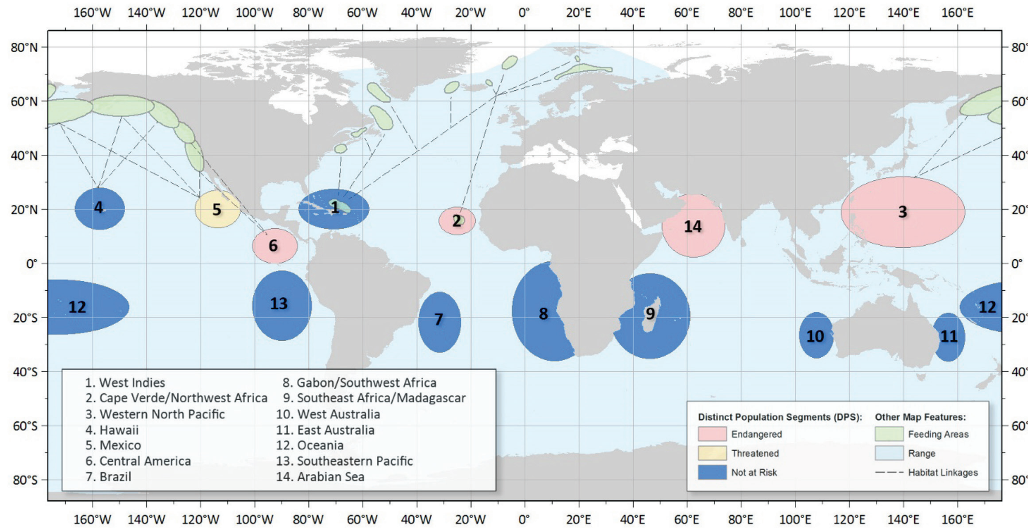

Figure 3. Photographs allow for estimation of abundance through mark-recapture methods. Distinct Population Segments (DPS; numbered circles) identified for humpback whales and linkages to feeding areas (green ellipses) are shown here. Mark-recapture estimates of abundance in the North Pacific based on photographs were an important component in the decision to down-list DPS #5 from Endangered to Threatened and de-list DPS #4 from Endangered to Not at Risk. Figure reproduced from NOAA Fisheries (2018); www.nmfs.noaa.gov/pr/species/mammals/whales/humpback-whale.html.

Figure 4. Photographs can characterize reproductive output at a population level. This aerial photograph of a school of spotted dolphins (*Stenella attenuata*) and eastern spinner dolphins (*Stenella longirostris orientalis*) in the eastern tropical Pacific (ETP) clearly shows that cow–calf pairs can be easily identified (red circle). (Photo courtesy of Southwest Fisheries Science Center, NOAA Fisheries)

mortality due to bycatch in the tuna purse-seine fishery (Gerrodette & Forcada, 2005; Gerrodette et al., 2008). To date, these conclusions have not been disproven.

Photographs Allow for Quantification of Morphology

Photogrammetry is the process of making measurements from photographs. It has broad applications—for example, in the construction of maps, in medical and industrial research, and for military intelligence. Photogrammetry can also allow for precise quantification of morphology and, in this context, photographs have made significant contributions to cetacean science.

Photogrammetric measurements to quantify morphology can be made from photographs taken laterally from the sea surface or land, or vertically from the air, but the latter is more common in cetacean science. Briefly, in vertical photographs, the relationship between the size of an object and its image is determined by the ratio of the focal length of the lens and the distance from the camera to the object (Perryman & Lynn, 1993). If focal length is kept constant, the ratio can be determined by the altitude from which the photograph was taken; and if measurement of altitude is precise, morphological measurements can be accurate to within 2 to 3 cm, and typically less (Perryman & Lynn, 1993). This is powerful information. Morphological information is the basis for describing new species/subspecies. It can also serve as an index of health in conjunction with a baseline and/or time series for comparison.

Identification of Species/Subspecies

Skeletal morphology is the basis of mammalian taxonomy. Although new methods are increasingly being used to clarify cetacean taxonomy (e.g., Rosel et al., 2017), morphology remains the basis for describing new species and subspecies of cetaceans. Obtaining morphological data required for traditional taxonomy is difficult for many cetaceans. Consequently, approximately three quarters of the currently recognized extant cetaceans have no described subspecies, and an estimated 40 cetacean taxa likely have undescribed taxa nested within them (Taylor et al., 2017). Photogrammetry provides a means to obtain morphological data without skeletal specimens and for broad opportunities to clarify cetacean taxonomy. Three examples of the many available in the literature are included below.

Pitman et al. (1987) described the appearance and distribution of a distinctive but unidentified species of *Mesoplodon* known only from two dozen at-sea sightings in the ETP—an animal referred to as *Mesoplodon* species A. For more than another decade, this species would remain unknown. Photographs allowed resolution to this mystery. Using a helicopter (carried aboard a research vessel surveying the same region from which *Mesoplodon* species A sightings were known), Pitman & Lynn (2001) obtained aerial photographs of this animal. From these images, Pitman & Lynn were able to document two distinct color morphs and a correlated incidence of scarring, which they attributed to sexual dimorphism between adult males, and females and young, as well as details of tooth placement in males. They confirmed that wounds of cookiecutter sharks (*Isistius* sp.) healed with white scars (not true for all mesoplodonts). These features—the color and scarring pattern, rostrum length, and position of teeth of adult males—matched those in photographs of a single mesoplodont that stranded in Paracas, Peru, in 1955. Tentatively identified as *Mesoplodon bowdoini*, Pitman & Lynn (2001) confirmed it as *Mesoplodon* species A. Finally, Pitman & Lynn used photographs of 24 individuals of *M.* species A from 13 separate sightings to obtain morphometric data for age and sex classes to reveal that the size of this animal was smaller than any *Mesoplodon* described to date, except one—*Mesoplodon peruvianus*. Taken together, the data from these photographs provided compelling evidence that *M.* species A is, in fact, *M. peruvianus*.

Fisheries observers collected data from hundreds of thousands of dolphins incidentally killed in the early years of the tuna purse-seine fishery in the ETP. Analyses of skeletal and external morphology of spinner dolphins led to the description of two subspecies: (1) the eastern spinner dolphin and (2) the Central American spinner dolphin (*S. longirostris centroamericana*; Perrin, 1990). Perryman & Westlake (1998) analyzed photographs taken from a helicopter carried aboard a research vessel and obtained precise morphological measurements for spinner dolphins. They found two unique morphotypes that corresponded to the known subspecies. Unexpectedly, they also found a third that was intermediate in size between the two and had a distinct and relatively localized distribution. Based on data from these photographs, Perryman & Westlake proposed that this form may represent a new subspecies, which they provisionally named the Tres Marias spinner dolphin. (This form has yet to be formally described as a subspecies [Committee on Taxonomy, 2017].)

In the early 1980s, two groups of Soviet researchers independently proposed two new species of killer whale based on data from specimens killed in Antarctic waters by Soviet whalers (Mikhalev et al., 1981; Berzin & Vladimirov, 1982). Because no holotype specimens existed, these descriptions were discounted by the scientific community. Pitman & Ensor (2003) subsequently described three ecotypes of killer whales from Antarctic waters based on field observations, which they designated as Types A, B, and C. Pitman et al. (2007) used photographs taken from a helicopter to determine total length of Type C killer whales, a fish-eating ecotype known from the southern Ross Sea. They confirmed it as one of the smallest killer whales known (Figure 5), comparing lengths with Soviet whaling data showing that adult female and male Type A killer whales had total lengths (distance between tip of upper jaw and notch of fluke) that were 1 to 2 m and 2 to 3 m greater than Type C, respectively. It was data from these photographs, therefore, that provided morphological evidence for what Pitman et al. described as a dwarf form of killer whale in Antarctica, with a degree of size dimorphism that they proposed could result in reproductive isolation. Subsequent genetic analysis has confirmed this reproductive isolation (Foote et al., 2016).

Condition and Health

Morphology can provide a clear index of body condition. Perryman & Lynn (2002) used vertical aerial photographs of gray whales migrating along the California coast to measure total length, width at widest point, distance from tip of rostrum to widest point, and fluke width. They found ratios based on width and length were sensitive to condition. Specifically, parturient southbound females were widest relative to their length, and northbound cows with calves were the narrowest. This ratio for migrating whales that were not parturient or associated with a calf showed that southbound individuals were significantly wider than northbound individuals photographed approximately 2 mo later, indicating that these predictable but relatively small changes in condition associated with fasting during migration can be reliably detected based on visual observations of morphology as documented in photographs.

Derived from photographs, these morphological indices can be correlated with environmental factors to provide insights into possible drivers of health. This offers the opportunity to proactively manage a population before declines in health result in mortality. A sophisticated example is found in Endangered southern resident killer whales (SRKW), a population that has been shown to be food-limited, with their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*), identified as a key covariate for survival and reproduction (Parsons et al., 2009; Ward et al., 2009; Ford et al., 2010). Fearnbach et al. (2011) used aerial photographs obtained from a helicopter to measure total length of SRKW and linked

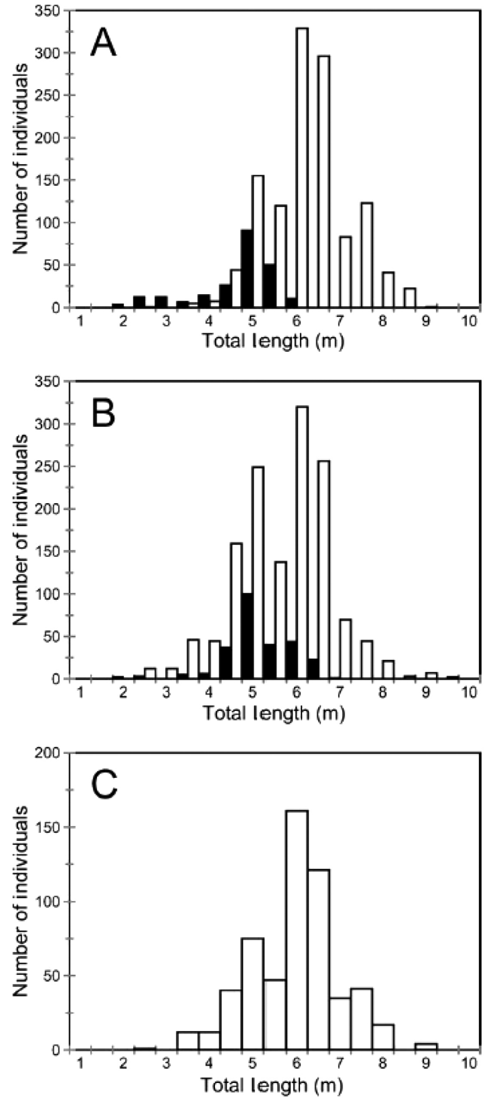

Figure 5. Photographs can be used to confirm morphological differences between ecotypes. Shown here are total lengths of killer whales based on data from (A) Soviet Antarctic whaling (white) and photogrammetric measurements of Antarctic Type C (black); (B) North Atlantic/Norway (white) and Norway coastal waters (black); and (C) Japan coastal waters. Photographs clearly confirm that the Antarctic Type C is a dwarf form of killer whale. From Pitman et al. (2007).

these data to individually identifiable animals tracked through time. They showed that adults older than 30 y were 0.3 m longer than adults younger than 30 y for both males and females; Fearnbach et al. hypothesized that a long-term reduction in food availability may have reduced early growth rates and subsequent adult size in recent decades. Subsequently, Fearnbach et al. (2018) developed an index based on the ratio of head width and distance between the blowhole and dorsal fin using aerial photographs obtained from a helicopter. They applied this ratio to 44 individuals (26 females and 18 males) photographed 5 y apart to assess between-year changes. Eleven individuals had significant declines over the 5-y period, and two of these died shortly after being photographed, suggesting a link between this ratio and health. Eleven of 16 killer whales that changed condition were reproductive-aged females, whereas no adult males showed changes in condition, suggesting that changed condition is reflected in the increased energetic costs of lactation to reproductive females (Noren, 2011), as well as the nutritional help provided to adult males through prey sharing (Ford & Ellis, 2006; Foster et al., 2012; Wright et al., 2016). Aerial photographs and the indices of health that they provide are currently being used to investigate options for adaptive management in near-real time to proactively attempt to recover this SRKW population.

Photographs Provide Insights into Behavior

Because cetaceans spend so much of their time under water, conventional visual observation methods are limited with respect to the data they provide regarding behavior. Photographs have changed this, increasingly contributing to our knowledge of cetacean behavior in a variety of contexts. Four examples, each providing increasingly remarkable insights, are provided below.

Cetacean interactions with fisheries and the resulting impacts are widely recognized. The nature and extent of these interactions are increasingly revealed in photographs. For example, Baird et al. (2015) used photographs to investigate interactions with longline fisheries for three discrete populations of false killer whales (*Pseudorca crassidens*) in waters around Hawaii in the central tropical Pacific. Photo-identification catalogs exist for all three populations, and they assessed scarring patterns on or near the dorsal fins for individual animals. Baird et al. found significant differences between populations in the percentage of individuals scarred by fisheries interactions, the highest being 7.5% of individuals from the Endangered Main Hawaiian Island population. All individuals of known sex were female, suggesting a sex bias in fisheries interactions and a disproportionate impact of these interactions on population dynamics.

The prevalence and ecological impact of killer whale predation on large whales has long been debated, largely because attacks are rarely witnessed (Pitman et al., 2017). Photographs have increasingly provided data to contribute a resolution to this debate. Specifically, images from photo-identification catalogs of humpback whales have been analyzed for killer whale tooth rake marks and used to infer the prevalence of attacks (Naessig & Lanyon, 2004; Mehta et al., 2007; Steiger et al., 2008). The frequency of rake-mark occurrences in some populations ranges as high as 20 to 40%; although in the largest study, less than 7% of whales acquired additional rake marks after the first time they were photographed. These data support the general conclusion that killer whales regularly attack humpback whale calves and juveniles but rarely adults. Calf mortality from these attacks can apparently be significant, however. Gabriele et al. (2001) used photographs to compare the number of individually identified humpback mothers with calves on their breeding grounds with the same mothers whose calves were not present later in the same year on their feeding grounds. From these photographic records, Gabriele et al. inferred that calf mortality ranged between 15 and 24%.

Durban & Pitman (2012) provided the first evidence of migration for Antarctic killer whales using satellite tags. They documented fast (> 12 km/h) and direct movements away from Antarctic waters by six killer whales tagged near the Antarctic Peninsula, five of which moved to subtropical waters off Uruguay and Brazil in surface waters ranging from -1.9° to 24.2°C. Whales traveled slower in warmest waters, but there was no clear indication from swim speed or direction to indicate calving or prolonged feeding. Movements were aseasonal; whales departed Antarctic waters during an 80-d period between February and April. Unexpectedly, one whale returned to within 40 km of its tagging site at the onset of austral winter in June. Another whale made a 109-d non-stop round trip of almost 9,400 km in only 42 d. (Transmission time for all tags ranged from 9 to 109 d.) The adaptive significance of such movements was suggested to be what these scientists termed *physiological maintenance migrations*. They proposed that skin regeneration in subfreezing Antarctic waters would result in unsustainable heat loss and that movements to warmer waters would allow for this physiological requirement. In support of this extraordinary idea, they included between-year photographs of two individually identified Type B (Pitman & Ensor, 2003) killer whales, both photographed in Antarctic waters, and each showing variable diatom coverage (heavy and light; the latter presumably just after return from tropical waters), despite similar seasonality to each sighting. Photographs, therefore, provided strong evidence for this hypothesis that continues to be investigated by additional research.

While conducting research in Antarctica, Pitman & Durban (2009) witnessed three puzzling encounters between Type B killer whales (Pitman & Ensor, 2003) and adult humpback whales. In all three instances, the humpback whales were bellowing loudly, slapping the water with their tails and flippers, and charging at and around the killer whales. The research was conducted in collaboration with a BBC (British Broadcasting Corporation) documentary film crew, and the high-end BBC cameras revealed an astonishing view of the third encounter. When reviewed in slow motion, it was clear that the killer whales were attacking a Weddell seal (*Leptonychotes wedellii*), that a pair of humpback whales had inserted themselves into their midst, that the seal swam frantically toward the humpbacks, and that one rolled onto its back with the seal on its chest. As the water rushed off the humpback with the seal now safely above the sea surface, the humpback used its flipper to deliberately prevent the seal from being washed back into the ocean where it would be once again vulnerable to the attacking killer whales (Figure 6). It was this still photograph from this film clip that led to further investigation; and, in 2017, Pitman et al. (2017) documented 115 accounts of interactions between humpback and killer whales from all world oceans. Their synthesis revealed that humpbacks interfered with killer whales attacking other humpbacks, three other species of cetacean, six species of pinniped, and one teleost fish, and they proposed that humpback whales regularly exhibited what could only be characterized as interspecific altruism.

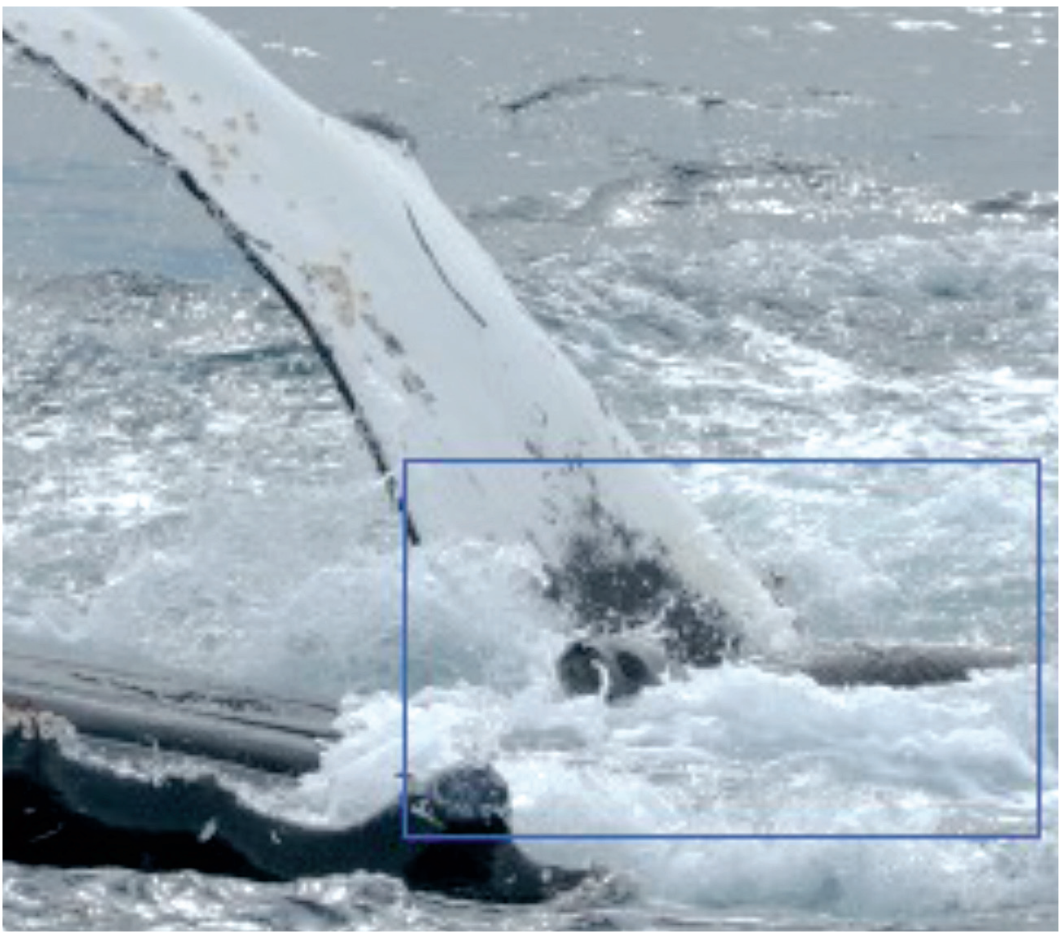

Figure 6. Photographs provide insights into behavior. This photograph shows a Weddell seal (*Leptonychotes wedellii*) on the ventral side of a humpback whale (*Megaptera novaeangliae*). The whale is using its flipper to prevent the seal from being washed off into the sea where a group of attacking killer whales (*Orcinus orca*) are waiting. From Pitman & Durban (2009).

Conclusions

The revelation by Würsig & Würsig (1977) and others working with killer whales, right whales, and humpback whales (e.g., Schevill & Backus, 1960; Katona et al., 1979; Bigg, 1982; Payne et al., 1983) that photographs can provide valuable information has resulted in a cascade of science. Photographs allow insights into movements, migrations, site fidelity, school structure and stability, abundance, reproductive output, taxonomy, condition and health, and behavior. The information conveyed in photographs and applications to cetacean research is ever-increasing (e.g., photographs have also contributed to our understanding of distributional shifts, unusual morphotypes, color variates, hybrids, and injuries from ship strikes). High-quality cameras are now relatively inexpensive and facilitate access to cetacean morphology, behavior, and distribution, allowing opportunities in cetacean research for scientists in all nations, developed and developing. Photographs allow for continued access to a wealth of knowledge about cetaceans worldwide. Perhaps most importantly, as anthropogenic pressures on marine ecosystems and cetaceans increase, photographs make science accessible to non-scientists. We cannot protect what we do not know, and the increasing number of individuals engaged with cetaceans through their cameras, through citizen science or pure recreation (Figure 7), provides optimism for our future.

Dedication

It was a weekday afternoon. I was on a west coast tour of graduate school possibilities. Not knowing a lot about what I wanted from my graduate experience, I did know that I wanted to be a professional scientist. I was a hard worker. I would give the next few years everything I had. I walked out of Dr. Würsig's office stunned. He would take a chance on me!

Today, I remain certain that Moss Landing Marine Lab and my master's degree with Bernd was a defining moment in my professional

Figure 7. Photographs make cetacean science accessible to non-scientists. Passengers aboard the Lindblad *National Geographic Explorer* in Antarctic waters photograph killer whales. (Photo by L. T. Ballance; courtesy Lindblad/National Geographic Expeditions)

development. The culture was supportive and passionate. I was encouraged to become involved, delve deeply, live and breathe science, *think*. Bernd had LOTS of students! He was pulled in many directions, but he was there at pivotal points in my graduate years: the trip to Mexico to help me get my fieldwork started; the dinner with colleagues and students (I got up to clear the table and he whispered "You are here as a scientist—remember that."); and my first talk at a professional conference: "Never apologize at the beginning of a talk," he told me when my practice talk began with "I'm sorry I am not better at speaking Spanish." (I took out that beginning sentence—and won the Best Student Paper Award.)

Now, almost 30 years later, I am the science director for a group of 70 marine mammal and turtle biologists with an annual budget of almost $10M. I am a Professor at Scripps Institution of Oceanography with my own graduate students and teaching responsibilities. I have been privileged to conduct fieldwork in the California Current, Bering Sea, tropical Pacific, Maldives, Mekong River, Antarctic Peninsula, and Ross Sea.

I believe that changing the future through influencing others is among the most powerful contributions one can make to this world. Bernd's science has clearly and significantly influenced the broader world. And his mentorship gave me my professional start and set the course of my rewarding career. This paper is dedicated to his legacy.

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