frontiers | Frontiers in Marine Science

TYPE Mini Review
PUBLISHED 09 June 2025
DOI 10.3389/fmars.2025.1605709

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OPEN ACCESS

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RECEIVED 03 April 2025
ACCEPTED 19 May 2025
PUBLISHED 09 June 2025
CORRECTED 11 June 2025

CITATION
Kraus SD (2025) Til death do us part? The critical value of long-term marine mammal studies. *Front. Mar. Sci.* 12:1605709. doi: 10.3389/fmars.2025.1605709

Til death do us part? The critical value of long-term marine mammal studies

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Long term studies in ecology and biology have been essential for addressing significant evolutionary and ecological questions. Long term marine mammal studies face different challenges, but are proving critical to ocean policy. New technologies combined with long term marine mammal studies provide important information on trends in population biology, anthropogenic stressors, climate change, and oceanographic regime shifts.

KEYWORDS
long-term studies, marine mammals, ecology, evolution, longevity

Ecologists have long sought to address the challenges of identifying natural population dynamics and evolutionary processes through extended multi-year studies of animals, plants, and their ecological support systems (Likens, 1989). Biologists working in plant ecology were perhaps the earliest to recognize the value of long-term studies to address evolutionary questions, for example, succession, niche specialization, competition, reproductive success, and responses to disturbance (Rees et al., 2001). Such work is made feasible because plants don't move much, and individuals can be tracked throughout their lives.

In vertebrate groups, researchers tackling the same questions also realized that answers would only be available by following animal populations or ecosystems for extended periods of time. Clutton-Brock and Sheldon (2010) parsed long-term studies into two categories, population assessments and individual-based studies. Ornithologists may have been the first to keep multi-year population records of bird colonies (Wooller et al., 1992; Lack and Lack, 1966). Terrestrial mammal researchers were quick to follow with multi-year studies of primates, ungulates, ursids, and rodents (see: Clutton-Brock and Sheldon, 2010) as well as large mammalian carnivores (Smith et al., 2017). Ornithologists banded birds, which provided data for population estimates, but required frequent recaptures at the nesting sites. Biologists studying terrestrial mammals used a variety of artificial marking and catch and release techniques, including collars, ear tags, brands, and dyes with some success. However, studies based upon individual recognition using natural markings didn't emerge until the 1960's, primarily in large mammals that were difficult to catch and tag, and in which large size meant that large identifying features were distinguishable from a distance (Schaller, 1963; Goodall, 1968; Pennycuick and Rudnai, 1970; Clutton-Brock and Guiness, 1975; Festa-Bianchet et al., 2019).

In the marine mammal world, the International Whaling Commission (IWC) attempted to track population trends from harvesting data for decades, documenting long-term sequential population declines from catch statistics in species after species of large whale (Rocha et al., 2014; Smith, 1984). In the 1920's, the IWC also developed a program using "Discovery tags", which were designed to be implanted in whales and retrieved after the whale was harvested. The Discovery tagging program did elucidate the movements of several large whale species, but was never statistically robust enough for population assessments (Rand et al., 2024). Although the IWC's history demonstrates a resounding failure of commercially based wildlife management, the science of marine mammal population assessments was advanced significantly by the IWC's explorations of alternative assessment methods, including surveys. In pinnipeds, studies also used artificial markings, including flipper tags, brands, and dyes (Laws, 1952), some of which are continued today. Recent advances in computer aided pattern analysis is enabling individual identification from natural markings in some populations (Cheeseman et al., 2022; Thompson et al., 2022).

The use of natural markings in individual-based studies of cetaceans began in the 1970's with the recognition that whales and dolphins could be photographically identified from dorsal fins (killer whales: Bigg, 1982; coastal dolphins: Würsig and Würsig, 1977), a combination of natural markings and tags or brands (bottlenose dolphins: Irvine et al., 1981; Wells and Scott, 1990; Scott et al., 1990; Wells, 2014), tail patterns in humpbacks (Katona et al., 1979), skin coloration in blue whales (Sears et al., 1990), and callosity patterns in right whales (Whitehead and Payne, 1978; Payne, 1986; Kraus et al., 1986). In 1990, the International Whaling Commission published a collection of papers that demonstrated the utility and maturity of individual identification methods across every cetacean taxonomic group (Hammond et al., 1990). The papers in that publication also identified the potential uses of individual identification for assessing population size, social structure, migrations, reproductive rates, survival, and behavior, as well as interactions with predators and human activities. Currently, hundreds of marine mammal studies around the world use photographs of individually recognizable animals to assess population trends, demography, behavior, and habitat use patterns.

Mann and Karniski (2017) defined long-term studies as those lasting 10 years or more. Given the diversity of population dynamics and longevity of marine mammals, it may be more appropriate to define long-term studies in the context of the subject-species longevity and generation length, since life history parameters change as animals age and transition through life stages. Following the IUCN (2001) definition of generation length, only the Phocoenids and some river dolphins have generations of less than ten years (Taylor et al., 2007). Studies on animals for periods less than a generation length run the risk of mis-interpreting or over-generalizing findings, and will miss the consequences of variability in age-related changes in reproduction and mortality, as well as long-term environmental changes in habitat or anthropogenic influences.

However, long-term studies are notoriously hard to maintain (Schradin and Hayes, 2017; Hayes and Schradin, 2017). Government funding agencies tend to have short-term management needs, and may focus on getting immediate answers to those questions. The one notable exception is the U.S. National Science Foundation, which maintains the Long-Term Ecological Research Program (LTER) and the Long-Term Research in Environmental Biology (LTREB) programs to study of ecological and population phenomena. Both programs emphasize studies of ecosystem functions, and while the LTER supports many marine field sites, it does not fund single-species studies. Outside of the US, there are some sources of limited long-term funding from governments and foundations, but these are limited. Occasionally a crisis (e.g., the *Deepwater Horizon* oil spill) and litigation will lead to longer-term support for some species, although that might only last 10 years. Private non-profit or foundation support also tends to run out of interest after a period of time. These funding vagaries lead the principal investigators committed to maintaining such programs to spend much of their time chasing funding. In addition, the longevity of the study animal may exceed the duration of a scientists' career or motivation, which means both funding and succession plans are necessary.

Finally, the amount of data management required can be daunting. For example, in their more than 50 year bottlenose dolphin study, the Sarasota Dolphin Research Program team has collected over 1.1 million identification photographs (ca 184,000 individual identification records of over 6,000 animals), 300,000 hours of acoustic recordings, and nearly 900 blood samples. In addition, the prey studies for this work collected over 770,000 fish (141 different species) in nearly 1,400 purse seine sets (Berens McCabe et al., 2021). The data collection, management, and analysis tools for this quantity of information did not exist when the study started, and researchers have had to develop those tools and computer programs over time.

These funding and data management challenges should not discourage the next generation – the benefits, both scientifically, and in terms of career path options, are extremely rewarding and productive, and can profoundly influence scientific and conservation goals in the entire field (Gulland, 2021). One testament to this is the over 350 scientific publications produced by the Sarasota bottlenosed dolphin team over the period of this long-term study (an average of 7 per year)!.

Clutton-Brock and Sheldon (2010) identified six strengths that long-term, individual-based studies have provided ecologists and evolutionary biologists. They include 1), analysis of development and aging, 2), variation in breeding ecology and evolution of life histories, 3), quantification of social structure, 4), calculations of lifetime fitness measures, 5), quantitative genetics and estimates of selection, and 6), the linkage of measures 1–5 between generations.

I would add two important strengths to single-species long-term studies. The first is the power of such studies for early detection of ecosystem changes and shifting habitat-use baselines. This is a recognized value in long-term ecosystem studies, but because marine mammals exploit a variety of trophic levels, they are particularly well-suited to early warnings of ecosystem shifts in areas where concurrent long-term environmental studies do not exist (i.e. most marine and aquatic habitats). The second is the power of long-term studies on a single species to identify changes in life history parameters, habitat use patterns, and behavior, in response to anthropogenic pressures. In this case, changes in human development near shore, boat and shipping traffic, coastal runoff including agricultural chemicals, and environmental accidents (e.g., oil spills), are all increasing in heavily populated areas. Climate change is shifting both the phenology and the patterns of migration and habitat use (Jones and Driscoll, 2022). Several studies have shown these impacts on multiple species, and the Wells et al. (2025) paper in this issue summarizes a long-term study on *Tursiops* that has rigorously grappled with all of these questions. The value of long-term research in both terrestrial and marine ecosystems is no longer in doubt. These programs have contributed inordinately to our understanding of evolutionary processes (Stroud and Ratcliff, 2025; Cocciardi et al., 2024), ecology (Blanc and Thrall, 2024; Hughes et al., 2017), the effects of climate change (Crespo, 2022; Jones and Driscoll, 2022), the effects of pollutants (Kucklick et al., 2022), social behavior (Clutton-Brock, 2021; Elliser and Herzing, 2016; Whitehead and Rendell, 2014), disturbance ecology (Carome et al., 2022; Gaiser et al., 2020), population consequences of animal health (Rolland et al., 2016), and the effects of anthropogenic and natural stressors (Knowlton et al., 2012; Pirotta et al., 2023).

One additional benefit of long-term studies on marine mammals is the use of experimental methods that augment the core program. For example, drone technology is now being used to assess body condition, social behavior, habitat use, and assist individual identification in numerous species (Álvarez-González et al., 2023). For the last 60 years, biological samples collected from free-swimming marine mammals have been used to conduct genetic, pollutant, or stable isotope analyses. Subsequent analytical techniques were applied to questions about reproduction (hormones), health, and disease (Lanyon and Burgess, 2019). More recently, advances in high-throughput molecular methods allow the application of genomics, transcriptomics, epigenomics, proteomics, and metabolomics to marine mammal biology (Mancia, 2018). All of these advances have benefited from long-term individual-based studies where animal histories were known, so the data could be linked with sex, age, and reproductive stage, providing cross validation that is grounded in previously established population biology (see Duffield and Wells, 2023). As demonstrated in this special issue, integrating the results of these new methods leads to a more complete picture of species-relevant biological drivers, and the effects of various natural and anthropogenic stressors.

Given the important information derived from long-term marine mammal research, how will it be possible to promote such studies going forward? There seem to be four fundamental components to successful long-term studies.

First, a dedicated (or possibly crazy) scientist needs to be committed to fundraising, managing staff and fieldwork, and publishing over a long period of time. That period of time will vary, but perhaps the generation length of the species under study is a good starting place. In most cases this will be 10+ years, although for many larger species, generation lengths can approach 2 decades. Since we know there are changes in individual life history parameters as animals age, it may be appropriate to use the species mean longevity as a guide, although that means a comprehensive long-term study may require many decades of work. Kudos and sympathies to scientists who study Bowhead whales, which likely live to over 200 years! Less taxing options for long-term studies may include research that collects data intermittently, e.g., intensively for three years with several years between those focused periods (e.g. Filby et al., 2014; Wang et al., 2024). While there is a risk of missing major population-wide events (e.g., a disease, or red tides), such an approach can provide a long-term overview of population dynamics in the face of anthropogenic disturbance or habitat changes.

Second, the successful long-term maintenance of a research program is probably most secure with institutional or community support, either from zoological parks and/or aquaria, consortia of scientists, or dedicated grass-roots non-profits. Institutional support may be partly financial, which stabilizes scientists over the long term, but most important is a commitment to curating the data and any biological samples for the long term. For those species with very long lives, the biological questions may only be answered in time frames that exceed a researcher's career (see Breed et al., 2024). Thus, an institutional home may be the only way to guarantee the continuity of many studies over decades. This is not a trivial commitment, and institutions need to be able to demonstrate benefits of supporting such work. Zoos, aquaria, and academic institutions can justify this on the basis of a commitment to global conservation, and that in turn can benefit philanthropic fundraising efforts. In this regard, public support for long-term research really matters, especially if these programs are leveraged to enhance science education and public support for oceanic conservation.

Third, successful long-term studies continue to evolve around the core data collection. Principal investigators should seek out collaboration, employ new technological advances, and be open to upending "conventional wisdom" as new findings emerge and are validated (Gulland, 2021). One benefit of an institutionally curated archive of data and samples is that new technologies and analytical methods applied to older samples can sometimes yield remarkable biological insights. Recent developments in genetic, epigenetic, stable isotope analyses, metabolomics, immune and disease testing, as well as advances in statistics and modelling, open a wide range of new methods that may be applicable to older samples and datasets (see Mancia, 2018).

Finally, long-term studies would benefit tremendously from changes in the way that funding agencies and scientists are thinking about this type of biological research. Many government funding agencies are motivated by immediate management questions, and may provide support for scientists to answer those questions in the shortest amount of time. Open ended funding? Not so much. Foundations are frequently interested in their ability to show "impact" from funding, either for conservation or scientific reasons, but that focus can lead to short-term awards, where results can be highlighted in annual reports with some regular frequency. Rarely are these sources of funding likely to commit financial support for the long term. Scientists may be partly at fault here. Who is going to support us if we say, "Well, it will take me ten years, and we don't know what we'll find, but it will be scientifically terrific!" The solution to funding may be straightforward for all stakeholders. Scientists engaged in long term research on a particular marine mammal must keep the variety of funders' goals in mind. It is relatively easy to address management goals while engaged in most long-term studies, and to provide managers with regular updates that are relevant to them. For management purposes, it is easy to imagine addressing somewhat universal marine mammal problems: bycatch, fisheries conflicts, pollution, or acoustic disturbance, as examples. For foundations, it is also relatively easy to integrate conservation or scientific discovery into a long-term study, provided there is a steady flow of analyses, incorporating new ideas and methods. For those concerned about their careers, well-managed and collaborative long-term studies yield so much information on such a variety of topics, it is not difficult to maintain a stream of meaningful publications that will move the field forward. As part of the multi-variate challenges to long-term studies, it is incumbent upon scientists to show that long-term studies contribute to a variety of critical policy questions as well as scientific ones (see Hughes et al., 2017).

Both government agencies and private philanthropy would be well-served to recognize the well-documented value of long-term studies to the management, conservation, and scientific understanding of marine mammals and their ecosystems. The contents in this special issue and the many other publications cited here show the importance and potential of keeping a core research program on a single species going over decades. Multiple creative and rigorous programs have been able to take advantage of core long-term research programs to expand scientific horizons far beyond what any of us could have imagined 50 years ago. The results have informed many aspects of basic marine mammal biology, but also yielded deep insights into oceanic ecology, mammalian life history, and marine mammal/human interactions. These core long-term marine mammal studies have also allowed for the development of new analytical approaches to fundamental biological questions, helped address critical policy and management issues, and provided extensive baseline data from which we will be able to evaluate the ongoing changes in oceanic ecosystems long into the future.

When should a long-term study end? There may be natural end-points, when principal investigators retire, or unavoidable ones, either related to funding or politics, or due to shifts in habitat use by the study species, or even local extinctions. One ending criterion could be when new discoveries and publications reach an asymptote, suggesting that the returns on any further scientific investment will be limited. Given the rapidity of climatological changes in oceanic habitat, as well as ongoing scientific advances in new study and analysis methods, this seems unlikely. One alternative strategy is to put a program on hiatus for a period of time, then recapitulate the early study's data collection and analysis at a later date. This approach can reveal significant shifts in population biology, but may not be able to identify the causes.

But perhaps this is the wrong question. What would we have lost if the Sarasota Bay dolphin study had been stopped 10 years ago? Since 2015, the publication of ca. 80 papers includes significant work on pollutants, acoustics, microbiology, automated individual identification, plastics ingestion, physiology, and much more. In this particular case, the scientific losses would have been huge. One under-appreciated feature of long-term studies is that the rate of discovery and publication appears to increase across time, due to the addition of new collaborators and new analytical methods. The synergy that occurs by combining multiple disparate datasets (e.g. individual identifications, reproductive histories, genetics, etc.) leads to discoveries that were unimaginable historically. This alone argues for support of long-term studies of durations well beyond what we might expect. The longevity of any research program should be dependent upon the quality and quantity of the science it produces. In that light, the Sarasota Bay dolphin study, and many of the other long-term single species marine mammal studies cited here, are outstanding exemplars of such research, and should continue well into the future.

Author contributions

SK: Writing – review & editing, Conceptualization, Writing – original draft.

Funding

The author(s) declare that no financial support was received for the research and/or publication of this article.

Conflict of interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

Correction note

This article has been corrected with minor changes. These changes do not impact the scientific content of the article.

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