



THEME SECTION

Technological innovation in marine ornithology

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INTRODUCTION

The coming of age of marine ornithology

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ABSTRACT: The founders of the at-sea study of marine birds were scientists who had the opportunity to go to sea on cruises designed for other purposes. Likewise, the first studies of seabirds in colonies were parts of larger expeditions or programs. Data were obtained by direct observation and manual recording in the field. With the advent of the miniaturization of electronics, data acquisition has become largely automated, the types of questions addressed are more sophisticated, and the analysis of large data sets has greatly advanced. As the field has matured, at-sea observations have become collaborative efforts between ornithologists and traditional oceanographers, and colony studies have begun to address fundamental questions of evolution and ecology. The continued development of devices that reveal the behavior and physiology of free ranging birds provides exciting opportunities for the expansion of marine ornithology.

KEY WORDS: First World Seabird Conference · Remote sensing · Technological advances · Seabirds

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Marine ornithology is a relatively young science, but it has come a long way from the early days of colony studies based on expeditions to collect eggs, and at-sea observations made from whaling ships (Murphy 1914, 1936). Indeed, the early days of mar-

ine ornithology were defined by resourcefulness with, for example, Wynne-Edwards (1935) making observations from a passenger ship crossing the Atlantic Ocean. Although Jespersen (1930) was perhaps the first to quantify the distributions of seabirds

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at sea with respect to an oceanographic variable (zooplankton biomass), the at-sea study of seabirds did not become an active branch of marine science until the 1950s and 1960s with the pioneering work of Kuroda (1955), Bourne (1963), Brown (1968), Jehl (1973), and Pocklington (1979), among others. Likewise, the study of the breeding biology and reproductive ecology of seabirds gained momentum in the early 1960s and 1970s with seminal work by Ashmole & Ashmole (1967, 1968), Ashmole (1971), Bédard (1969), and others. It may be hard to realize in today's world of electronic devices, but almost all data gathered at sea before the mid-1980s were recorded on sheets of paper, and most colony data were gathered either by handling the birds or by sitting in blinds for hours waiting to record salient bits of behavior.

In 2010, the Pacific Seabird Group hosted the First World Seabird Conference in Victoria, British Columbia, and we decided that it would be a good time to examine how marine ornithology had advanced since its beginnings, and the role that technological innovations had played in various aspects of the study of marine birds. We solicited 9 contributions for a theme session entitled 'Technological and Analytical Innovation in Seabird Research', with topics ranging from progress in at-sea studies of seabirds (Ainley et al. 2012, this Theme Section), through smart tags attached to birds to elucidate at-sea behavior (Wilson & Vandenberg 2012, this Theme Section) to food consumption studies (Karnovsky et al. 2012, this Theme Section), stress hormones, genetics (Taylor & Friesen 2012, this Theme Section), as well as conservation issues.

The changes in methodology over the past decades have been profound. New, automated systems are permitting more data to be gathered, more quickly and with less effort. The assessment of accuracy has been improved, along with the precision of measurements. New chemically-based approaches to genetics, physiology and diet studies have emerged. Behind almost all of these advances is the development of computing power and the miniaturization of all things electronic. Without the increased capacity of everyday electronics incorporated in, for example, mobile phones, many of the gadgets used in seabird studies that we now take for granted would not be possible. Perhaps as important, improved computing power and increased sophistication in the manipulation and analyses of data have resulted in the ability to work with data sets the size of which was unimaginable 3 decades ago. These advances are revealing much that we have wanted to know about the evolution, behavior and ecology of marine birds. In many

cases, these same devices are also telling us much about the oceans in general, and the parts of the oceans used by birds in particular. The contributions to this Theme Section provide a taste of the wide range of topics covered at the First World Seabird Conference, and insight into the growing interconnections between marine ornithology and other branches of marine science.

Contemplation of the future in a field as vibrant and fast-moving as marine ornithology is always exciting. The ability to assess the position of a bird to within a fraction of a meter will allow assessment of the use of territory space in a way heretofore impossible, and if several birds are so 'marked' it will become possible to ascertain interactions with neighboring birds, chicks and potential predators. We might be able to understand what makes a good parent, what makes a good territory, and how the dynamics of interactions among territory holders define the milieu of the colony. More refined genetic studies will allow identification of relationships among birds on a colony as well as between colonies. Perhaps we will be able to answer some of the questions about kin selection and natural selection in the evolution of coloniality. Studies of how individual birds use the ocean are likely to accelerate. High-resolution multi-frequency echo-sounding equipment is now readily available and affords the opportunity to quantify the movements of birds underwater with respect to their prey field (Benoit-Bird et al. 2011). In the near future we should be able to ask about the prey fields in places where birds choose to feed and where they inspect the water column but do not tarry to forage. We can also expect strong advances in devices designed to track where a bird has gone, in or out of the water, and how the vagaries of movement relate to the structure of the aquatic environment. Coupled with simultaneous measures of physiology, the energetic costs and benefits of foraging habitat selection will be elucidated. Indeed, advances in technology promise to tell us exactly where and when birds have swallowed every prey item, and the energy expended to acquire it. That said, it seems doubtful that instruments will replace bird observers on sea-going vessels. Not only are the challenges of form recognition formidable, limiting the use of electronic scanners, but there is the added benefit of building collegial relationships with fellow scientists on multi-disciplinary cruises. Personal contacts on shipboard are important for the establishment of inter-disciplinary research, and besides that, no amount of electronic gadgetry is going to replace the value of good friends.

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Adding the ocean to the study of seabirds: a brief history of at-sea seabird research

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ABSTRACT: We review the history of how research directed towards marine ornithology has led to an appreciation of seabirds as highly specialized marine organisms. Beginning with R. C. Murphy (Pacific), V. C. Wynne-Edwards (Atlantic), and associates in the early 1900s, the research approach grew from an emphasis on seabird single-species ecology to an appreciation of interacting species assemblages and finally to seabirds being considered as important components of marine food webs. After a slow, drawn-out beginning, the initial main impetus for developing the field was a need to map seabird abundance and distribution tied to understanding impacts of continental shelf resource exploitation. Coalescing during the 1970s to 1980s to facilitate this line of research were 6 factors: (1) ability to identify birds at sea; (2) standardization of techniques to quantify abundance; (3) resources and techniques for mapping; (4) appreciation of how scale affects seabird relationships to hydrographic features and patchy prey; (5) development of computing power and appropriate statistics; and (6) seabird biologists becoming embedded in, as well as organizing, multidisciplinary marine research projects. Future advances in understanding the role of seabirds in marine food webs will be made by seabird biologists participating in multidisciplinary projects using grid-like surveys relative to oceanographic features in combination with instrumentation that reveals the finer details of seabird foraging behaviors.

KEY WORDS: At-sea surveys · Food-web structure · Foraging ecology · Seabird · Seabird habitat

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THE FOUNDATIONS

Our appreciation of the marine ecology of seabirds, as opposed to their nesting ecology and behavior, began with scientists such as Jespersen and Wynne-Edwards in the Atlantic and Murphy in the Pacific. Working in the early part of the 20th century, all identified patterns in seabird distributions at sea. Wynne-Edwards (1935) proposed classifying seabirds into coastal, off-shore, and pelagic groups based on his observations in the North Atlantic. Jespersen (1924) collected information on plankton and seabirds on research cruises in the Atlantic; he noted a relationship of birds with distance to land but also

postulated that some of the variation in seabird distribution he observed was related to variation in food resources. Murphy, working in the Pacific basin, went to coastal South America and in addition participated in several cruises to the adjacent Southern Ocean aboard whaling vessels; he was seeking to provide context to the multitude of specimens residing in major museums, particularly the American Museum of Natural History (AMNH) that employed him and still has one of the largest collections of seabird specimens in the world. Also available to him were the field notes and specimens amassed by Beck who, after being commissioned by the California Academy of Sciences and AMNH, ventured into the

waters off California, around the Galapagos, and elsewhere in South (and North) America, by hitching rides on fishing vessels or rowing his dory well off the coast (see, for instance, Beck 1910). Murphy's summary of the 1000s of his, Beck's, and others' specimens and their marine context can be found in the 2-volume treatise, 'The oceanic birds of South America' (Murphy 1936). In these 2 volumes, discussing the waters and their avifauna surrounding South America (including the Atlantic, Pacific, and Caribbean basins, as well as the Southern Ocean), Murphy introduced seabird aficionados to oceans that are partitioned by fronts into water masses, each with a characteristic seabird species assemblage and overall seabird density. This treatise by Murphy constituted the first synthesis of seabird ecology, having 31 pages of references, citing works dealing with all oceans (including work in the North Atlantic by Jespersen 1929 and Wynne-Edwards 1935). Pocklington (1965) found application of Murphy's findings to the delineation of species assemblages by water mass in the Indian Ocean, as since have others elsewhere in the world ocean (e.g. Bourne & Warham 1966 in understanding occurrence patterns of *Macronectes*). Insights into Murphy's at-sea experience can be found in 'A log-book for grace: whaling ship Daisy, 1912–13', written well after his ocean traveling was completed (Murphy 1965).

Almost 4 decades later, Ashmole (1971) summarized what was known about seabirds near to island shores, in a book chapter entitled 'Seabirds and the marine environment,' based on his work in the 1960s. Ashmole's classification of seabird foraging methods is still in use today. Otherwise, studies of seabird marine ecology were given little attention until the 1970s when the designation of Exclusive Economic Zones (EEZs) by coastal countries and a push to develop petroleum resources became constrained by legislation such as the US National Environmental Policy Act of 1970. Due to that legislation, environmental impact assessments for activity on federal lands (in this case, the continental shelf) were required. At that point, surveys of the coastal ocean were needed to describe seabird abundance and distribution, and the 'golden age' of at-sea studies of seabirds began (Appendix 1). Though not propelled by legislation, efforts in other countries also led to seabird assessments and atlases elsewhere at this time (M. L. Tasker pers. comm.; Appendix 1).

Not only with these ship and airplane surveys did we begin to learn about seabirds at sea, but in the process marine ornithology added community ecology, i.e. the description of recurring species as-

semblages and species associations, to its otherwise largely autecological emphasis. Grid-like and transect-driven survey efforts continued for a few decades, branching eventually into a few studies of actual seabird interactions with prey and ocean (not just atlases of horizontal distribution). Then in the late 1990s and 2000s, with the maturation of technology such as satellite, global locating system (GLS), and global positioning system (GPS) tracking and miniaturization of devices enabling the recording of dive behavior, in conjunction with remote sensing of surface features, none of which requires going to sea, increasing numbers of seabird ecologists began a return to single-species studies. Seabird movements were now being plotted against remotely-sensed ocean properties, rather than being observed in the marine environment.

During the 'golden age' of at-sea studies, we learned a great deal about the place of seabirds in their true element: the ocean where they spend 90% of their existence and for the exploitation of marine resources for which most of their morphology has evolved. Herein, we review this history in some detail, in part to complement the recent paper by Tremblay et al. (2009). Those authors sampled the seabird literature and described various broad trends in marine bird research over the past several decades by using an electronic key-word search that included positional data and at least 1 environmental variable (e.g. sea surface temperature, SST).

FIRST ANALYSIS OF SEABIRDS AT-SEA STUDIES

The main findings of Tremblay et al. (2009), analyzing trends based on frequency of papers discussing seabirds and spatial habitat features, including both indirect (instrument deployment from land) and direct (at-sea observation) efforts to understand seabird marine ecology, can be summarized as follows:

(1) Clumping studies by 5 yr bins beginning in 1970 and ending in 2005, it is evident that at-sea effort began slowly but in the most recent decades has accelerated. As a subjective, qualitative check, the frequency of our own papers involving direct at-sea work loosely paralleled the upward trend that Tremblay et al. (2009) described, although the increase was not as steep (Fig. 1).

(2) Marine research efforts were entirely ship-based up until the early 1970s, then added aerial surveys through 1990s. Thereafter, land-based instrument attachment became the preferred means to learn about seabird at-sea movements.

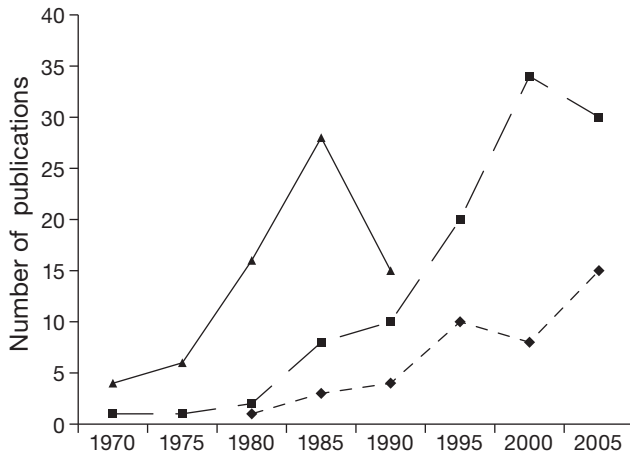


Fig. 1. Growth in the prevalence of at-sea studies judged by number of publications by 5 yr bin: (—) Tremblay et al. (2009); (---) authors' publications based on direct, at-sea work (those not included in Tremblay); (---) Scientific Committee for Antarctic Research (SCAR) list compiled in 1996 (papers not in Tremblay and mostly from non-western-European, non-North American journals). Tremblay et al. (2009) detailed 106 direct (shown) and 112 indirect marine studies in the period 1970 to 2005

(3) Real time, *in situ* measurements of seabird habitat comprise at least 60% of the effort in each 5 yr bin, with indirect measures (remote sensing) appearing in the mid-1980s and contributing a third by 2000.

(4) The habitat feature of choice is SST (25% of studies).

(5) To summarize and analyze results, statistical and spatial modeling of various types appeared in the 1980s, and is now the preferred tool used to understand seabird presence with respect to ocean features.

We note that 1 especially important topic not treated by Tremblay et al. (2009) is how the quantity, quality, and dispersion of prey affects seabird occurrence. This topic, though it treats seabirds as wholly marine organisms (e.g. Brown 1980), is rarely investigated in most seabird 'marine' studies. Most of the latter operate under the assumption that seabirds are generalist predators and that physics and physical parameters explain enough about where the birds find food. This means that very few of the many papers by Hunt, Piatt, Spear, Veit, and their colleagues, investigating foraging behavior and diet from an at-sea perspective, and none of the papers by Nevitt, investigating multi-sensory foraging strategies including the role of olfaction, were included by Tremblay et al. (2009). It would take a book to summarize this literature, even that of Hunt alone; indeed, one could start with Stabeno et al. (2005), Ladd et al. (2005), Jahncke et al. (2005), Vlietstra et al. (2005), Hunt & Stabeno

(2005), work backward, and spend several weeks reading about seabirds' roles in polar food webs, especially that of the Bering Sea. For now, instructive summaries of seabird foraging ecology were provided by Ballance et al. (2001) and, especially, Shealer (2002).

FACTORS THAT SHED LIGHT ON THE RELATIONSHIP BETWEEN OCEANOGRAPHY AND SEABIRDS

To understand how we have learned about why seabirds occur where they do and what they are doing while there, one has to keep in mind the progression or evolution of research foci that began with studies investigating single species, or 'autecology,' to 'community ecology' (synecology), and finally to 'ecosystem ecology.' During the 1960s, before the period studied by Tremblay et al. (2009), there was ample effort toward logging individual seabird species' occurrence on the ocean in terms of presence-absence and relative abundance. Many of these data gathered were from 'ships of opportunity' as is readily apparent in Tuck's (1980) book, 'A guide to seabirds on the ocean routes.' During that early period, the US National Museum of Natural History (USNMNH), funded by the US Army which was interested in birds as disease vectors, undertook an intensive investigation of seabird colonies throughout the South Pacific. The effort was called the Pacific Ocean Biological Survey Program (POBSP), headed by P. Humphries and J. Church, and it included the logging of birds seen on passages among the islands and not-to-interfere participation in fisheries and oceanographic research cruises. This resulted in several publications, the most notable being King's (1974) work, 'Pelagic studies of seabirds in the central and eastern Pacific Ocean,' composed of several chapters, some of them atlas-like, treating different species or species groups. Second to Murphy's work, this was a pioneering study. Earlier work by King (1970) was among the first in which seabird biologists participated in oceanographic research cruises.

The efforts of the 1960s were mainly descriptive. Much of the work involved biologists from non-western European or North American countries. In fact, the later peak and falloff among these studies exhibited in Fig. 1 was to a large extent due to the disintegration of the Soviet Republic; basic natural history research took a major hit as the USSR collapsed. As it was, we did not begin to understand why certain species occurred where they did until work in the 1970s

looked at seabird distributions at sea in relation to weather patterns (Manikowski 1971, 1975) and water masses (Brown et al. 1975, Pocklington 1979). In fact, the work by Brown et al. (1975) and Pocklington (1979) quantified the ideas of Murphy. Pocklington (1979) may have been among the first seabird papers to ever appear in a mainstream marine biology journal, now the norm for at-sea studies. From this period on, at least 6 coalescing paths of investigation have contributed to the evolution of seabird studies as we know them today. These 6 paths are discussed below.

(1) What bird is that?

In the 1960s and 1970s, crossing the oceans, one had to carry several kilograms of books, including Murphy (1936), as 'field guides;' or at least one of us had to (D.G.A.; see Gill 1967 for a similar opinion). The best guides available were the 'Preliminary field guides' by King (1967) as well as Watson (1965) and Watson et al. (1963) of USNMNH (based mostly on specimens) written to assist the POBSP biologists, and the Peterson Field Guide series, which were useful only in coastal waters. Alexander's (1955; a much less useable version appearing in 1928) 'Birds of the ocean' was also important to include in one's at-sea library. It was not until the appearance of Harper & Kinsky's (1978) 'Southern albatrosses and petrels: an identification guide,' that we had the first seabird guide written by people who had actually spent a good deal of time at sea, and thus knew of the difficult viewing conditions typically experienced, in this case in waters around New Zealand and elsewhere in the Southern Ocean. Identifying birds at sea became possible without needing a library at sea! Their effort, as well as that of the qualitative data on seabird occurrence of the 1950s to 1970s, finally culminated in the 'bible' of seabird identification at sea, Harrison's (1983) 'Seabirds: an identification guide.' However, seabird identification is not static. The era of genetic analyses since the 1990s has led to the splitting of many 'species,' to which very able observers have been playing catch-up in order to identify field-visible identification characteristics (e.g. Robb et al. 2008, Howell 2009, Howell et al. 2010). This revolution has led to discovering new ranges for species, sometimes bigger and unexpected (e.g. Bailey et al. 1989, Pyle et al. 1993, Brinkley et al. 2000). A revised version of Harrison (1983) that reflects current taxonomies is now critically needed. The recent volume by Howell (2012) is now the standard to emulate.

(2) Techniques for collecting quantitative data

Until the paper by Tasker et al. (1984), with some exceptions, seabird data were largely qualitative presence-absence with large birds, e.g. albatrosses, over-emphasized because they could be seen farther away than small birds, e.g. storm-petrels. After reviewing the previously used methods, Tasker et al. (1984) proposed a standardized technique of using well defined strips, i.e. 300 m wide, with search effort broken temporally into fixed time segments, i.e. 'snap shots.' The Southern Ocean BIOMASS effort sponsored by the Scientific Committee for Antarctic Research (SCAR) collected data in 10 min bins, 1 in each hour of ship transit, with reports coming from different sectors of the Southern Ocean (e.g. Abrams 1985, Ryan & Cooper 1989, Bretagnolle & Thomas 1990). These data were compiled into species maps, which when compiled became 'atlases' (see next section). It was not until the continental shelf oil development studies that continuous transects became more common, due to the use of aerial surveys (e.g. Briggs et al. 1987, Schneider et al. 1987), but also used in ship-based ecological surveys as well, e.g. of the Ross Sea (Ross Ice Shelf Project, RISP; Ainley et al. 1984) and of the eastern tropical Pacific (EPOCS; Spear et al. 1995, Ribic et al. 1997).

It was recognized early on (e.g. Gould et al. 1982) that the issue of bird 'flux' needed to be statistically controlled because more birds are counted that are flying opposite to ship travel than those flying with the ship, and fast-flying species are over-counted relative to slow-flying ones or birds sitting on the water. The problem was identified by Tasker et al. (1984), who proposed using the 'snapshot' approach to avoid this bias (also see Gould & Forsell 1989). A further solution to correct for flux, based on bird and ship speed and direction, was proposed by Gaston & Smith (1984), but correction for flux became more widely used as a result of Spear et al. (1992; also see Spear & Ainley 1997). While there is still debate about the conditions under which one technique might be better than the other (e.g. continuous counts when seabirds are in low densities and snap-shot methods when there are high densities; also see van Franeker 1994), both of these techniques led to higher precision of surveys. In particular, the use of at-sea data was used to estimate population size of burrowing species for which population estimation is difficult to accomplish (Clarke et al. 2003); this latter work to date is the only one that tested the agreement between at-sea census results compared to island-based censuses. Precision was also achieved

by the development of line transect methodology (Burnham et al. 1980), although the collection of distance and angle data precludes the use of this technique for species other than single, special-status species, such as marbled murrelets *Brachyramphus marmoratus* (Ralph et al. 1995; also see Tasker et al. 1984) or species standing on ice such as penguins (Southwell & Low 2009).

(3) Mapping at-sea seabird distributions

We touched on this briefly above in reference to the 'golden age' of at-sea studies. Huge resources were put into mapping seabird and other biota in areas where offshore oil development had been proposed. The studies were done before lease sales were held. Examples are the Outer Continental Shelf Assessment Project (OCSEAP) and the Programme Intégré pour le Recherche des Oiseaux Pélagiques (PIROP). Shelf waters could not be leased by governments to oil companies until environmental impact studies (EIS) were completed, and those could not be completed until the potentially affected biota were mapped. In fact, many seabird biologists were employed to do this, which in itself was a first, as before EIS requirements only university professors were paid, with their students, to conduct seabird studies as part of basic rather than applied research. The EIS effort relative to offshore oil development also led, in large part, to the founding of the Pacific Seabird Group.

The mapping needed in EISs led to the production of seabird atlases, which now cover much of North American and European coastal waters (Appendix 1). The first were those by Brown et al. (1975, with updates in 1977 and 1986), but if one now searches the web using the words 'seabird atlas' one will receive, currently, 229 000 entries (which would also likely include seabird colony catalogs). These atlases are essentially grids in which relative or absolute abundance of each species is shown relative to coastal and bathymetric features. The information for most of these atlases is contained in data bases that are readily available, and are now used, for instance, in assessments of oil spill impacts and are often updated (Appendix 1). A good example is Briggs et al. (1987), which has since been repeatedly updated for a portion of the California coast where oil exploration is still active (Mason et al. 2007). Consistent with the need for rapid assessment of damage during oil spills, surveys like those reported in the latter 2 publications are now mostly done by aircraft.

Those data, too, were used subsequently by NOAA (2008) for purposes of marine sanctuary management plans. Globally, there is presently an increasing effort to incorporate the distribution of seabirds at-sea into planning and the identification of candidate areas for consideration of Marine Protected Areas (MPAs) in coastal areas (e.g. Sala et al. 2002), and at regional (Lombard et al. 2007) and ocean basin (Harris et al. 2007, Trebilco et al. 2008) scales. In Europe, a coalition of researchers formed European Seabirds at Sea (ESAS), which combined the results of most European at-sea studies into 1 data base. This is accomplished in North American waters by contractors to NOAA (e.g. Compilation of Data At-Sea, CDAS). These data banks have been used in efforts to invoke ecosystem-based management in fisheries, in both Europe (International Council for the Exploration of the Sea, ICES, Working Group on Seabird Ecology) and less successfully in the Pacific (PICES); the majority of the ICES data, however, are colony based, which is not covered in the present review.

Perhaps most critically, it is important to note that these atlases provide valuable baseline historical data for current and future surveys, should they be repeated, to assess the predicted effects and unexpected consequences of climate change or other drivers on marine ecosystems.

(4) Attention to scale

The scale at which we perceive seabirds in the context of ocean features had been recognized from the beginning (e.g. Murphy 1936), but once hypothesis testing was introduced in seabird research (see next section) it had to be addressed specifically. In one of the first review papers, Hunt & Schneider (1987), following Schneider & Duffy (1985), synthesized the ideas of scale in relation to the biology and physics of marine phenomena (Hauray et al. 1978) as it applied to seabirds at-sea. In part recognizing the importance of scale came about in attempts to match bird patches with prey patches determined by acoustics (e.g. Schneider & Piatt 1986). Various large data bases have since been useful in further applications of scale to seabird occurrence relative to ocean features (e.g. Ford et al. 2004, Huettmann & Diamond 2006). This path has not progressed much beyond the ideas discussed by Hunt & Schneider (1987). Advances in statistical techniques (discussed in the next section) have the potential for informing a deeper understanding of the role of scale in seabird-prey ecology (e.g. Logerwell et al. 1998).

(5) Statistics and controlling factors

Initial attempts to understand factors affecting seabird distributions related bird species occurrence to simple ocean features (SST and sea surface salinity [SSS]), not necessarily collected simultaneously (Brown et al. 1975, Pocklington 1979, Abrams & Griffiths 1981). There was also the limitation of access to computers and the software to analyze the seabird data. In fact, some data compilations, such as those led by W. Bourne in the Northeast Atlantic in the 1970s, were never properly written up because of being overwhelmed by the 'too much data' problem (M. L. Tasker pers. comm.). The first computer taken to sea by D.G.A. and G. Divoky was fitted into a steamer trunk, having been made from a kit in L. Karl's garage; it accompanied those biologists on a cruise from Long Beach, California, USA, to McMurdo Station, Antarctica, in 1977, making the process of data entry much easier than all the coding of data sheets that went on previously. It did not take long for this advance to be overtaken by the continuing computer revolution: direct data entry from the ship's bridge (Updegraff & Hunt 1985).

Then with the issue of scale being incorporated into analyses, and the development of ever more powerful (and smaller) computers, seabird researchers played a game of catch-up to the rapid evolution then underway in statistics, somewhat as follows, in a movement that increasingly emphasized community ecology (multi-species assemblages): (1) contingency tables were used (Haney 1986a), along with multivariate statistics (Ribic & Ainley 1988/89), to look at how species assemblages use different water masses; (2) seabird densities relative to ocean properties began to be modeled, initially as a Gaussian function of SST (Abrams & Lutjeharms 1986); (3) correspondence analysis was used to model non-linear relationships between seabirds and physical oceanographic variables (Abrams & Underhill 1986); (4) cluster analysis and multivariate statistics were used to delineate latitudinal ocean features and multi-species assemblages (Ribic & Ainley 1988/89). By the 1990s, continuing into the 2000s, spatial statistics came into use, including the use of spatial point patterns (O'Driscoll 1998) and spatial error structures in linear models (Ainley et al. 1998). Advances in the linear model (e.g. generalized linear models) allowed the use of other error structures (beyond Gaussian) and incorporated nonlinear relationships beyond polynomial forms (e.g. generalized additive models; Woehler et al. 2001). Advances in model selection (e.g. Akaike's information criterion, Bayesian Infor-

mation Criterion) allowed researchers to test competing non-nested models and move beyond reliance on p-values (Chapman et al. 2004). Further development of computer power allowed even more sophisticated analyses to look for and understand occurrence of individuals and species assemblages relative mainly to physical features and to explore patterns in the data rather than relying on specified statistical models (e.g. classification and regression trees, Ribic & Ainley 1997). Computer-based techniques have developed whereby habitat models can be constructed to (reliably) fill in gaps of spatial coverage on the basis of species' correlations with specific habitat features (e.g. Raymond & Woehler 2003, Nur et al. 2011). For more examples of modern statistical techniques used in at-sea marine ornithology, see Tremblay et al. (2009).

(6) Seabirds as part of the ecosystem

Seabirds finally attained the status of bona fide marine organisms (i.e. the respect of other marine biologists) when seabird biologists began to embed themselves into at-sea biological oceanography and fisheries projects. The first was Processes of the Bering Shelf (PROBES) in the 1980s, being also among the first investigations of seabirds and fronts. With such studies, it became apparent that the relationships of seabird at-sea distribution to seabird prey (e.g. type, abundance, patchiness), and not just physical features, were important (Hunt & Schneider 1981, Kinder et al. 1983, Hunt et al. 1990, Hunt & Harrison 1990). Another, somewhat coincident investigation was RINGS, a study of Gulf Stream warm- and cold-core rings, on which seabird researchers piggy-backed (Haney 1986a,b,c, 1987). These sorts of ecosystem efforts launched a search for seabird-prey associations, especially using acoustics to quantify the patchiness of prey usually with single seabird species in mind (e.g. Woodby 1984, Obst 1985, Piatt 1990, Veit et al. 1993, Mehlum et al. 1999, Fauchald et al. 2000). The study by Veit et al. (1993) is interesting when compared to that of Hunt et al. (1992), who used the same prey data base but different correlates, and taken together presented somewhat confounding patterns of seabird occurrence near South Georgia colonies. At the least, these studies showed further, independent of scale, the complexity in dealing with seabirds and their supposed prey patches. The subject in fact has been taken even to being resolved by fractal analysis (Russell & Hunt 1992)!

An appreciation of seabirds as marine organisms, and their role in food webs, was finally achieved in the late 1980s when seabird biologists became active participants in multi-researcher investigations, playing a role in project and cruise design. The first was Antarctic Marine Ecosystem Research in the Ice Edge Zone (AMERIEZ), a multi-ship, multi-season, multi-investigator study of physics and biology of the Antarctic marginal ice zone. A seabird biologist was actually co-chair of the steering committee and chief scientist of one of the vessels, thus helping to direct the entire sampling effort. Much about the marine biology of seabirds was learned (e.g. Fraser & Ainley 1986, Ainley et al. 1986, 1992, Rau et al. 1992).

Coincident with that effort, though not one that is full-on multidisciplinary, Hunt and associates put together cruises in 1983 to 1986 that included zooplankton sampling using both acoustics and nets (Hunt & Harrison 1990, Hunt et al. 1990), and expanded the effort to include a physical oceanographer for cruises in 1991 and 1992 in the western Aleutians (see Hunt et al. 1998). This paper was slow to complete, but was successful in closely integrating birds, plankton, and physics at the same space and time scales (a precursor to Global Ocean Ecosystems Dynamics, GLOBEC, see below). This was followed by a National Marine Fisheries Service (NMFS) eastern tropical Pacific tuna–porpoise assessment program, again with seabird or top predator biologists playing a central role in planning, this time investigating the ecology of tuna and their associates (birds, mammals). The project related species densities to *in situ* and satellite-generated ocean properties, like chlorophyll (Ballance et al. 1997, 2006). Another multi-investigator example is Baseline Research on Oceanography, Krill, and the Environment (BROKE), which conducted an extended cruise to determine how ocean circulation off East Antarctica affected the occurrence of top predators and their prey (Nicol et al. 2000).

Finally, with the passing of the 20th and arrival of the 21st century, the international program GLOBEC was formed to investigate some problematic fishery questions, specifically what happened to Atlantic cod *Gadus morhua* (study area is George's Bank); what happened to Pacific salmon *Oncorhynchus* spp. (study area is the northern California Current); and what happened to Antarctic krill *Euphausia superba* (study area is the western Antarctic Peninsula; www.globec.org; Hofmann et al. 2004, Batchelder et al. 2005)? GLOBEC sought to understand the dynamics of middle-trophic level species (coincidentally, seabird prey), in conjunction with temporal and spatial

ocean variability, as key to learning why major fish stocks were changing. Seabirds (and marine mammals) were seen by this program as being fundamental to answering those questions, given their competition with or predation of these fish. Therefore, marine ornithologists were members of steering committees. By this time, the computer revolution that had aided the analysis of seabird (and other large) data sets, as well as adding remote sensing capabilities, had also led to the ability to collect biological and physical ocean data in real time, which could help to explain the occurrences of seabirds and their prey in a way never before imagined. This was accomplished through towed arrays (SeaSoar, Biomapper) having acoustics and other electronic sensors to quantify in a continuous fashion such variables as chlorophyll and its depth maximum, SST, SSS, thermocline and pycnocline depth, and dynamic height, as well as biomasses of fish and invertebrates among several size classes. Given that all data were continuously collected, any scale of variation could be investigated at least through the meso-scale. The current effort involves the construction of 'end-to-end' food-web models, in which one back-calculates trophic connections starting at the top of the food web. A number of publications to date have resulted, showing that, indeed, seabirds and large fish, both being mesopredators, interact in important ways that help to structure the food webs of which they are a part (Chapman et al. 2004, Ainley et al. 2005, 2009, Ribic et al. 2008, Ainley & Hyrenbach 2010).

THE FUTURE

As noted by Tremblay et al. (2009), studies of seabirds' interactions with the oceans have recently been evolving from Eulerian (grid-like) to Lagrangian (particle-like) as researchers in increasing numbers turn to the wonders of electronic miniaturization to investigate seabird movements both over and within the sea in the context of variables easily quantified spatially by remote sensing (e.g. SST, chlorophyll, sea level height, sea ice cover). The grid-like and ecosystem studies, such as AMERIEZ and GLOBEC, provided validation for the collection of these variables via remote sensing to explain seabird occurrence. Actually, though, what has been happening is that marine ornithology is reverting to its initial roots of investigating the autecology of individual species, but with much more sophistication and detail and over every possible scale. The much steeper ascent in the numbers of marine-related papers in the broader

community compared to our own effort of direct at-sea effort (see Tremblay et al. 2009) bespeaks the rise in the use of high-technology in the seabird field, in a sense beginning to overwhelm at-sea research.

Most remotely-sensed data are at relatively coarse spatial and temporal scales, which may prevent the sensing technology from detecting features of interest to foraging birds. The latter are likely to be operating at much finer scales. However, this coarseness can work for at-sea studies by reducing the complexity of the habitat for researchers, and may be particularly useful for our understanding of species that cross ocean basins where we cannot integrate the environmental heterogeneity at such large spatial and temporal scales. It is the balance between environmental heterogeneity and 'homogeneity' that is critical for analyses (e.g. Shaffer et al. 2006, Raymond et al. 2010). Fundamentally it boils down to what biological questions are being investigated. Being explicit about scale in the development of the questions (e.g. conceptual models) may help determine what might actually be reasonable to try to answer as well as what tools might be useful (e.g. remotely-sensed data or not). There is a need for both approaches—the coarse, top-down approach that provides a context or framework and understanding of the detailed, fine-scale data obtained from instrumented birds. We can undertake research using either approach, but integration of the 2 is the key to further developing a full appreciation of the interaction of seabirds and the marine environment.

As it is, atlas-type seabird data (Eulerian) are being applied in the identification of major seabird 'hot-spots.' This information will be invaluable for identifying and supporting stretches of the ocean that should be designated as MPAs (Harris et al. 2007) or managing human activities in other ways (e.g. NOAA 2008). Such data are especially valuable when combined with Lagrangian data to identify true foraging areas, separating foraging from commuting individuals (e.g. Ballard et al. 2011).

Unfortunately, the use of remotely-sensed ocean variables is also once again diverting our efforts away from placing seabirds in the ocean as important members of multispecies communities and important players in food-web structuring. While the Lagrangian approach has been invaluable in addressing problems related to single, often special-status species (the source of funding) or special scenarios (e.g. by-catch), it is getting away from an ecosystem perspective, which is needed for application of ecosystem-based management of marine resources. Whether the pieces can be put together some day remains to

be seen (see below). Only a few studies, such as those by Grémillet et al. (2008), Takahashi et al. (2008), or Pichegru et al. (2010), have matched satellite tracking with the assessment of prey distribution, but even in those cases, too, we are dealing with single seabird species devoid of any interactions with other predators, competitors, or facilitators in the ocean.

Remaining for the future are efforts that combine Eulerian and Lagrangian strategies, thus, to reveal the 3-dimensional (3D) spatial use by predatory fish, seabirds and marine mammals, as interacting species, within a well quantified 3D prey field. In other words, a GLOBEC-type study in which the main bird, mammal, and fish predators are being tracked within a well quantified and varying distribution of prey, i.e. the ultimate study of marine predator-prey patch use. In that way the competition and facilitation that is part of these predators' exploitation strategies can be revealed (see Ainley et al. 2005, 2009). On the other hand, time may be drawing short to undertake such projects as ship costs rise, and oceanographers, themselves enamored by the electronic revolution, resort more and more to autosubs and sea gliders to understand physical and biotic variability in the ocean. On such ocean-going vehicles, which can stay deployed for months and thus are ideal for oceanographers' purposes, no room exists for seabird sighting.

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Appendix 1. Compilation of at-sea seabird atlases that provide information on distribution, including 'hotspots' of high seabird concentration; many have associated data bases. Very few of these are included in the Literature Cited

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Technological innovation in archival tags used in seabird research

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ABSTRACT: The first archival tags were used on seabirds in the 1960s. Since that time, when recording systems were primitive, various technological advances, culminating in solid state devices, have provided the seabird research community with extraordinarily sophisticated and powerful tags. This work documents the progress and development of archival tags used on seabirds. Major advances and the insights that these have provided into seabird behavioural ecology are highlighted, followed by an examination of the current limitations to our ability to study seabird ecology and speculation on what the future will bring to this exciting and dynamic field.

KEY WORDS: Archival tags · Seabirds · Ecology · Behaviour · Loggers · Review

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INTRODUCTION

Mankind is not well adapted to study most marine animals in their natural environment without the aid of technology. Debatably though, seabirds are easier to study than other marine animals. Being virtually all flighted, they are generally highly conspicuous, even at sea, and have incited comment and fascination for years (e.g. Murphy 1936). In addition, many seabirds are colonial and so constitute an obvious part of the landscape in some of the world's coastal regions. Against this, the volant species travel fast, and often range far out to sea, which makes them problematic to follow, while the flightless species tend to be inconspicuous at sea and are hard to study because they are such adept divers. It is hardly surprising, therefore, that early studies of seabirds were almost entirely devoted to their life in the colony (e.g. Stonehouse 1975) even though documentation of the behaviour of birds at sea was understood to be pivotal to understanding their ecology and role in ecosystems (Croxall 1987).

Ironically, the same features that lent themselves to the study of seabirds on land also made seabirds natural subjects for the deployment of automatic re-

ording devices to determine their at-sea behaviour. In 1965, Gerald Kooyman and colleagues attached the first depth recorder to a free-ranging marine mammal, the Weddell seal *Leptonychotes weddelli* (Kooyman 1965), documenting that this animal could dive hundreds of metres deep and demonstrating the power of recording technology to explain the behaviour of elusive animals at sea. Aside from the advantage of their large size (and therefore the capacity to carry the large tags), however, marine mammals were problematic because the recovery of deployed devices necessitates that equipped animals return to a predictable location, something that most marine mammals do not do, unlike nesting seabirds. During these early archival tag years, the biggest disadvantage that seabirds had compared to marine mammals for the use of the technology was their considerably smaller mass. However, the penguins, whose heaviest representative, the emperor penguin *Aptenodytes forsteri*, weighs ca. 32 kg (Williams 1995), represent a substantial departure from the seabird norm. It is therefore unsurprising that the first seabird equipped with archival tag technology was indeed from this species (Kooyman et al. 1971), that it was the technology pioneer Gerald Kooyman who

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did it, and that during the following few years the only seabirds on which loggers were deployed were the large, robust, colonial, ground-nesting and flightless penguins (Kooyman et al. 1982, Adams & Brown 1983, Lishman & Croxall 1983, Wilson & Bain 1984). This is not to say that penguins are exempt from deleterious device effects, as many studies show (e.g. Ropert-Coudert et al. 2000b, 2007, Beaulieu et al. 2010). Indeed, device size and mass have been, and will always be, problematic for seabirds, with scientifically and ethically unacceptable behavioural and physical changes induced by tags acting as the ultimate deterrent to their use (see 'A sober moment—the flipside of gadgets').

Since Kooyman's early work, archival tag technology for seabirds has advanced dramatically. This approach now allows seabirds to be followed virtually whenever and wherever they go to sea and thereby eliminates many of the biases in land- or ship-based observations, the accuracy of which are very dependent on environmental conditions (Duffy 1983, Schneider & Duffy 1985). Archival tag technology has enabled the measurement of everything, from the size of individual prey items swallowed (Wilson et al. 1992a, 1995c) to the space use by migrating birds over years (González-Solís et al. 2007, Egevang et al. 2010). This paper looks back at the developments in seabird-attached logging technology over the 40 yr since Kooyman et al. (1971) first published on the diving capacities of the emperor penguin and attempts to highlight important developments and how these have enabled researchers to gradually reveal the at-sea secrets of these most conspicuous yet most elusive of marine animals.

This review focuses on recording units (also known as archival tags or loggers) although a few brief references are made to transmitting devices. The latter have a separate developmental history, which is described very briefly here. Transmission telemetry started with very high frequency (VHF) tags. Position was simply given via triangulation of signals received by 2 spatially separated receiving stations (cf. Kenwood 1987). Signal attenuation and line-of-sight operating conditions limit the distance over which this telemetry can be used (Kenwood 1987); both of these are problematic in the marine environment because radio waves are not transmitted through seawater. Thus no signals are received from diving birds, and the signals of birds on the sea surface may be attenuated by the swell. Nonetheless, researchers have tracked seabird movement using this approach (Sirdevan & Quinn 1997, Whittier & Leslie 2005) and even used the cessation of signals

during diving to deduce dive/pause intervals (Wanless et al. 1993). Although the problem of seabirds ranging too far from land to be tracked by land-based receiving stations (Adams & Navarro 2005) was sometimes solved by researchers following in boats or aircraft (Heath & Randall 1989, Hébert et al. 2003), some birds cover such large tracts of ocean so fast that this too has its limitations. This problem was partially solved when researchers were able to use platform transmitter terminals (PTTs), which transmit to orbiting satellites using the Argos system (Taillade 1992) that detects position anywhere on the planet (e.g. Jouventin & Weimerskirch 1990). The Argos system is limited, however, in the number of positional fixes that can be taken per day (e.g. Georges et al. 1997) and positional accuracy is variable, being generally no better than a few hundred metres at best (see e.g. Weimerskirch et al. 1992, Brothers et al. 1998, Wilson et al. 2002b). These 2 limitations have now been largely mitigated by global positioning systems (GPS) which derive the tag position using radio-waves from orbiting satellites (von Hünenbein et al. 2000, Hulbert & French 2001). Calculated bird positions are good to within a few metres (Grémillet et al. 2004, Ryan et al. 2004) and updated positions can be derived at any time, except when the bird is underwater. The only real limitation on temporal or spatial resolution is the size of the battery package, because appreciable amounts of power are needed to determine position (Rose et al. 2005, Meyburg & Fuller 2007). Most applications of GPS technology on seabirds use this radio transmission technology in combination with loggers to store the positional data, which are retrieved when the bird is recaptured at the colony (e.g. von Hünenbein et al. 2000, Freeman et al. 2010), i.e. a hybrid of transmission telemetry and the logging approach.

DEVELOPMENTAL STAGES

Tags on animals and the problems of recording

There are 2 concepts that were important in the development of archival tag technology for seabirds. One was that animals could carry any sort of foreign body, something that had evolved in the carrier pigeon era and was routinely adopted by researchers using VHF telemetry by the 1960s (Cochran & Lord 1963, Kenward 1987, 2001). The other was that the foreign body carried could actually record information autonomously. Although modern technology accepts this as given, in the first half of the 20th cen-

tury data of any sort was generally stored by ink on paper. In the biologists' realm, notebooks and ink chart recorders were at the core of this. Although such methods are inappropriate for wild animals, it is unsurprising that Gerry Kooyman's first depth recorder for Weddell seals used an analogous method, recording data using a scribe on a rotating drum which had been covered by carbon from smoke, with the scribe actually scratching a trace in the smoked layer (Kooyman 1965).

In-depth view of seabird foraging

Although penguins are large seabirds, the first attempts to record data from them at sea required a much smaller system than that developed for seals by Kooyman and colleagues. Per Scholander had proposed using an ingenious system developed by Lord Kelvin in the mid-1880s (Scholander 1940, cited in Kooyman 2004, 2007) for recording depth by ships, whereby a plumb line was used to assess the likelihood of running aground while navigating in uncharted areas. An air-filled capillary tube, closed at one end, acts as a depth gauge: with increasing depth (and therefore pressure), water is forced into the air-filled space, travelling up the tube, being expelled again when the depth decreases. If the capillary tube is dusted with a water soluble dye, the system shows the maximum depth attained over a period of time (Fig. 1). Kooyman and colleagues first used this on penguins in the 1960s (Kooyman et al. 1971) and it has been used on a large variety of seabirds many times since (e.g. Montague 1985, Burger & Wilson 1988). The system is still in use today, particularly on the smaller species such as

storm petrels *Hydrobates pelagicus* (e.g. Albores-Barajas et al. 2011).

Despite its limitations, this first recording system for seabirds at sea revealed penguins to be able to dive to depths that far exceeded previous thinking, and demonstrated that these birds must have remarkable physiological mechanisms allowing them to withstand very high pressures and to breath-hold for the presumed extended periods of time necessary to reach those depths (Kooyman 1975, Kooyman et al. 1982). The 'dusted capillary tube depth gauge' was so small, robust and cheap that it could be deployed on a large range of diving seabird species and, over time, this instrument was applied on other, much smaller, species. As with the first penguins, it has been demonstrated that diving seabirds tend to substantially exceed the expectations of researchers. For example, 180 g Cassin's auklets *Ptychoramphus aleuticus* can dive to 43 m (Burger & Powell 1990) while 420 g wedge-tailed shearwaters *Puffinus pacificus* can dive to 66 m (Burger 2001).

The recording of a single maximum depth in diving seabirds over a specified period of time has profound physiological implications but may give a very biased view of ecologically relevant depths (Burger & Wilson 1988, Whitehead 1989). In a further developmental step, in order to determine norms rather than extremes of depth use, the capillary tube system was modified by positioning a radioactive bead of phosphorus on the water-air interface and the tube was placed on X-ray film sealed inside a waterproof sachet (Wilson & Bain 1984). The position of the phosphorus, a measure of depth, exposed the adjacent film, darkening it more the longer it spent at any position. Careful densitometer readings showed the total amount of time that the device spent at any depth (Wilson & Bain 1984) (Fig. 2a). This specific approach was only ever used on the African penguin *Spheniscus demersus* (Wilson 1985), but it spawned the development of depth gauges using light on film rather than radioactivity (Wilson et al. 1989) (Fig. 2b). These systems showed that, although the maximum depths reached by diving seabirds may be exceptional (for an extensive compilation see the Penguin book online database of diving records at <http://polaris.nipr.ac.jp/~penguin/penguiness/>), the time spent at depth tended to decrease with increasing depth (Wilson et al. 1991a, Chappell et al. 1993, Wanless et al. 1993, Zimmer et al. 2010). There are two reasons for this: (1) diving birds tend to terminate their dives at shallow depths more often than deep, and (2) in addition, accumulated time underwater is greater at shallower depths because birds always

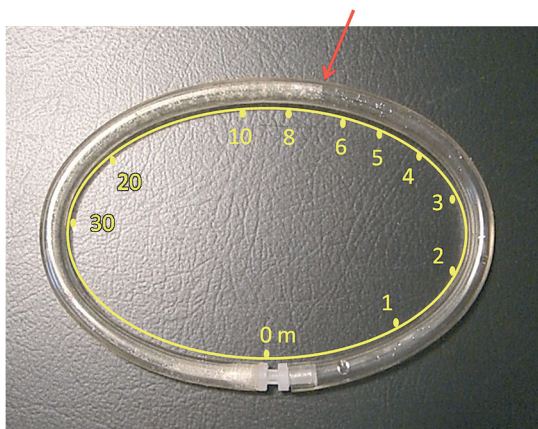


Fig. 1. Capillary depth gauge with water soluble dye showing the maximum dive depth of 7 m (red arrow) reached by a crowned cormorant *Phalacrocorax coronatus*

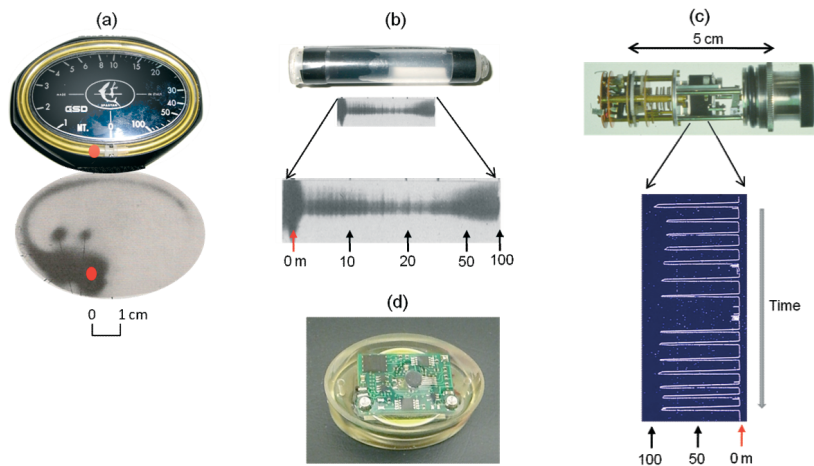


Fig. 2. Four different generations of time-depth recorders used on seabirds: (a) a capillary depth gauge modified so that a radioactive bead exposes film (Wilson & Bain 1984); (b) a modified syringe fitted with light-emitting diode to expose film (Wilson et al. 1989); (c) a compressible bellows system attached to stylus scribing on a rotating drum (Naito et al. 1990); (d) a modern, solid-state depth gauge (Cefas G6, e.g. Elliott 2011). The red circles and arrows indicate 0 m depth

have to start and finish their dives at the surface, travelling through the surface waters, even if they are foraging at greater depths (Zimmer et al. 2010). The accumulation of time underwater for transit as well as foraging meant that time-at-depth recording devices could not easily ascribe time underwater specifically to foraging or transit.

A solution to this was demonstrated elegantly by a Japanese researcher, Yasuhiko Naito, who built a modified, very miniature analogue of the Kooyman (1965) Weddell seal continuous dive recorder (Fig. 2c). A diamond-tipped stylus scratched an ultra-thin line (<8 μm) on carbon-coated paper (<10 μm thick) as it wound over time from one spool to another. The stylus moved across the film width with depth, creating a trace that effectively mirrored the depth use over time for periods of days (the original system used for birds had a very slow scroll rate [$0.024 \text{ mm min}^{-1}$] and so had deployment periods of up to 20 d) (Naito et al. 1990) (Fig. 2c). This system was deployed extensively on a large number of penguins (e.g. Williams et al. 1992, Croxall et al. 1993, Watanuki et al. 1997) and cormorants (e.g. Croxall et al. 1991, Kato et al. 1992) (Fig. 3). It did much to create the important concept of the 'dive profile', effectively a graphical representation of depth on the y-axis (usually with increasing depth descending) and time on the x-axis (Simeone & Wilson 2003, Halsey et al. 2007). The ability to record depth continuously had profound consequences for the understanding of seabird behaviour underwater. Researchers realized not only that dives typically consisted of a descent, bottom and ascent phase (Naito et al. 1990) but also that dives were variously grouped into types according to the shapes they made in the dive profile (cf. Leboeuf et al. 1988, Wilson 1991). In fact, continuous depth recording is still in use today with much more sophisticated logging systems but ones which, as far as

depth versus temporal accuracy is concerned, are actually little better than the original Naito et al. (1990) unit. U-shaped, V-shaped and W-shaped dives have been documented (Croxall et al. 1993, Wilson et al. 1996) with the steepness of the vertical arms in the dive profiles indicating rate of change of depth, a measure of the putative 'interest' of birds in the different water strata. Transit can be reasonably well differentiated from foraging in loggers that record depth continuously and there seems little doubt now that small undulations in the depth profile of the bottom phase are generally due to prey pursuit and/or capture (e.g. Charrassin et al. 2001, Simeone & Wilson 2003, Bost et al. 2007, Hanuise et al. 2010).

The continuously recording depth gauge not only gave useful information about the way seabirds used depth, it also provided fundamental data about the periods spent at the surface between dives. The relationship between dive depth and dive duration had been examined by simple observation as long ago as

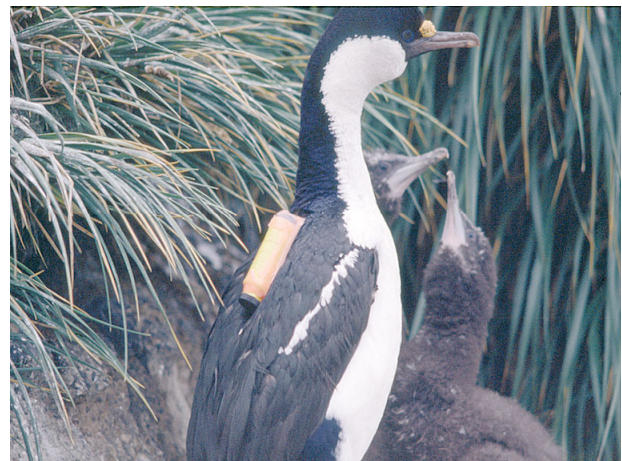


Fig. 3. Imperial shag *Phalacrocorax atriceps* wearing one of Yasuhiko Naito's early time-depth recorders (see Fig. 2c)

1924 (Dewar 1924), as was, later, the relationship between dive duration and surface pause (e.g. Cooper 1986). However studies had to be conducted from convenient vantage points, primarily from the coast, and were thus restricted to birds diving in shallow water, which was not necessarily the norm. The continuously recording depth gauge allowed researchers to examine the durations of all dives, how they relate to depth, and how long it takes birds to recover from the dives before they dive again (cf. Burger et al. 1993, Wanless et al. 1993). Such work can examine dive performance and surface pauses from a physiological standpoint, and may attempt to formalise processes affecting the rates of oxygen uptake and carbon dioxide removal (Croll et al. 1992, Burger et al. 1993); as well seeking explanations for the commonly observed accelerating surface duration with dive duration (Ydenberg & Forbes 1988, Ydenberg & Guillemette 1991, Wanless et al. 1993) by invoking anaerobic dives and the production of lactate (Boyd 1997, Kooyman & Ponganis 1997, 1998).

Finally, by their nature, continuously recording depth gauges allow examination of depth use over a range of temporal scales. Thus, researchers have been able to examine how dives may vary over the course of foraging trips and how they relate to ecological variables, notably time of day (e.g. Williams et al. 1992).

Interface with electronics

The first fully electronic devices used on seabirds were crude but, nevertheless, heralded a fundamental change in the way information from seabirds was recorded. An ingenious development whereby the system could be constructed by biologists rather than electrical engineers involved a simple modification of quartz watches. David Cairns and colleagues prepared the watches so that seawater would short-circuit the progression of the liquid crystal-displayed time and fitted them to guillemots *Uria* sp. in such a way that the time display could be seen (Cairns et al. 1987b). By careful observation of the birds at their colonies, noting the displayed time when the auks left the colony and returned, these workers could determine the time spent underwater during the foraging trip (Cairns et al. 1987a).

In a further development, Wilson & Achleitner (1985) built an electronic counter into a propeller system which, when placed on an African penguin, rotated with distance as the bird swam, giving a single value at the end of the foraging trip of how far the bird had travelled over the whole foraging trip.

With the development of electronics, devices recording single data points were rapidly superseded by ones capable of storing multiple data points, even if, in the first instance, they could not do so continuously over time, as the Naito et al. (1990) depth gauge had done. The interface between old-style data recording and the more sophisticated solid-state devices which recorded parameters as a proper function of time was a multiple maximum depth recorder, first used by Kooyman et al. (1982). This unit simply recorded the number of dives made by a bird that exceeded a certain depth threshold. There were nominally 5 depth thresholds and these were set to cover the whole depth range exploited by the species. Its first use was on penguins smaller than those from the genus *Aptenodytes*, chinstrap penguins *Pygoscelis antarctica* (Lishman & Croxall 1983), and although it served to demonstrate remarkable diving capacities in some of the smaller penguin species, it was rapidly eclipsed by more advanced systems that recorded data with a proper time base.

Solid-state technology

By the end of the 1980s, the electronics consumer industry had produced accessible, accurate, quartz-based clocks and memory chips, both elements that could be built into seabird loggers to record parameters as a proper function of time. This development also signalled the time when most biologists stopped inventing devices themselves, leaving the increasingly complicated task to electronic engineers. From that moment on, the capacities of seabird archival tags have followed well-defined trends, mirroring demands for enhanced sophistication by the consumer market, for example for ever smaller mobile phones with increasing functionality, with the result that seabird tags have become smaller while delivering increasingly detailed information about bird activities at sea.

Changes in capacities in solid-state devices

The primary constraint limiting seabird archival tag performance is size and/or mass. So the adoption of 'better' systems primarily reflects the availability of technology that performs a specific function while being minimally sized, requiring reduced power and causing minimal impacts to the seabird carrier. The inception and subsequent widespread use of surface-mounted technology (Prasad 1997) reduced the

size of components used within circuits but minimal power use was, and still is, particularly important because the lower the power required, the smaller the battery needed. Even today, batteries in seabird loggers are a major part of the overall volume and mass. Nonetheless, solid-state systems in seabird loggers have shown a dramatic decrease in power consumption over the last 2 decades while continually increasing performance. For example, it takes energy to write data into a memory but seabird loggers with roughly comparable batteries used e.g. 16 KB memories in 1992 (Wilson et al. 1993a) and today use 1 GB (Wilson et al. 2008). Likewise, current drain was such that few solid-state seabird devices used in the 1990s could be deployed for more than 1 to 2 wk (e.g. Kooyman et al. 1992, Jouventin et al. 1994), whereas today some of the smallest, such as some light geolocation tags weighing less than 5 g, can operate over years (Afanasyev 2004), and thus give insights into the movements of some species over the full annual cycle (e.g. Phillips et al. 2006, González-Solís et al. 2007, Guilford et al. 2009) (Fig. 4). The power requirements of the various sensors have also decreased, which means that deployment durations can be increased and/or that the recording frequency can be increased. The first solid-state seabird loggers to record with a proper time base typically stored data once every 10 or 15 s (e.g. Wilson et al. 1993a). This rather crude timescale as a measure of bird behaviour is, in many ways,

analogous to protocols used by behavioural ecologists involving instantaneous scans of their study animals (e.g. Van Oort et al. 2004, O'Driscoll et al. 2008). The value of the data depends critically on the duration of the behaviour relative to the sample interval. Where behavioural sequences have durations similar to that of the scan interval, the study can only document the percentage time engaged in this activity or its incidence over the course of the day rather than giving details of its precise length (cf. Boyd 1993, Wilson et al. 1995b). More particularly, since sensors in seabird loggers actually return values of some parameter, such as depth, rather than a binary-type return, such as 'the bird is underwater', sampling interval is critical in defining the form of the behaviour. This is amply illustrated by the effect of the temporal resolution on the definition of the dive profile. Sampling at intervals of 10 s would give 19 points for the mean dive length of a king penguin *Aptenodytes patagonicus* of ca. 190 s (Moore et al. 1999), but only 2 for the little Penguin *Eudyptula minor* with a mean dive duration of 21 s (Bethge et al. 1997), and miss most dives made by Peruvian boobies *Sula variegata* at around 2 to 3 s (Ludynia et al. 2010). So, not only would a sampling regime of 10 s be inadequate to define the descent, bottom and ascent phases of most dives made by little penguins but, where surface intervals are shorter than 10 s (cf. Bethge et al. 1997), this temporal resolution would not even be enough to define the length of most dives because adjacent dives would tend to run together (Wilson et al. 1995b).

The descriptions of dive durations and dive profiles are affected by more than just the temporal resolution, however. They are also critically affected by resolution of the actual recorded information, something that has also improved over the years. It is notable that many authors detailing information on the durations and depths of penguin dives disregard any that do not exceed 3 m (e.g. Bost et al. 1994, Moore et al. 1999, Radl & Culik 1999, Falk et al. 2000, Deagle et al. 2008). This may reflect, in part, a perception that such 'surface' dives are irrelevant for actual feeding, something that is certainly not true for Adélie *Pygoscelis adeliae*, chinstrap *P. antarctica*, gentoo *P. papua* or African penguins (R. P. Wilson unpubl. data), although it may be for the habitually deeper diving species such as the king and emperor penguins (e.g. Rodary et al. 2000, Zimmer et al. 2008b). However, the omission of shallow dives is more likely to be due to a combination of the limited ability of the recording system to resolve depth accurately and the drift that values recorded by transducers display when the bird is at the water surface.

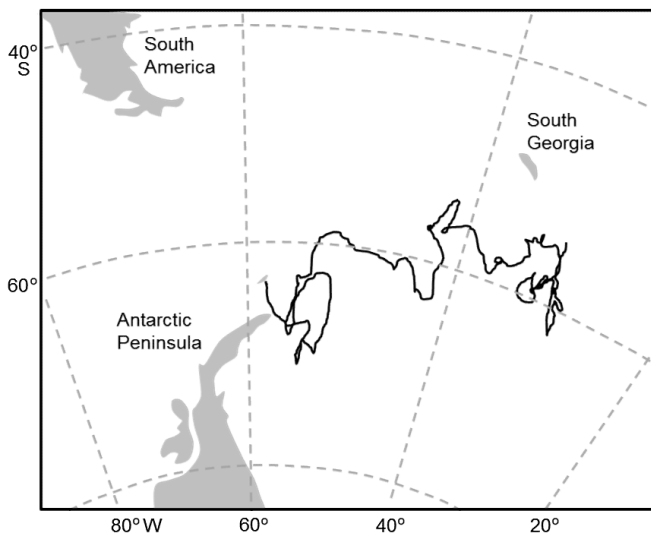


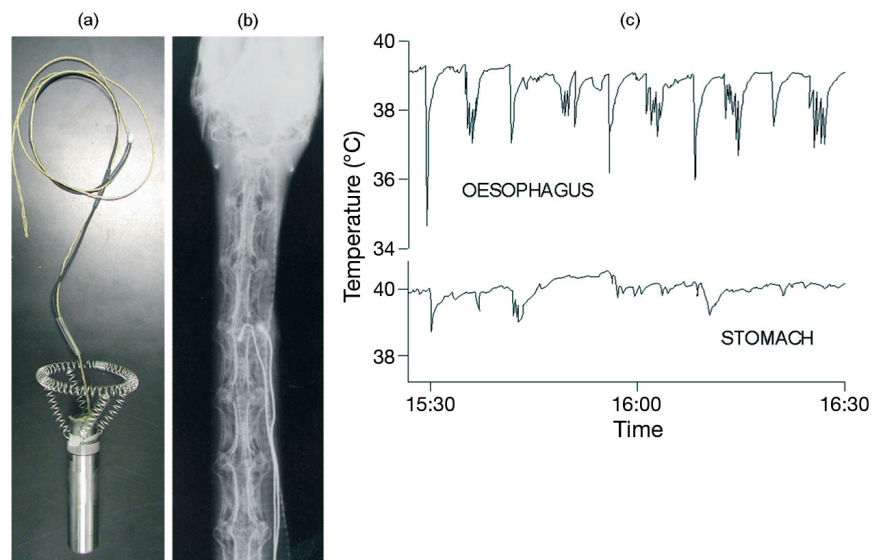
Fig. 4. Post-breeding and over-winter movements of a chinstrap penguin *Pygoscelis antarctica* from King George Island (located at the most westerly part of the track) as determined using geolocation. This was the first multi-month (5) track obtained for a seabird using this technology. For more details see Wilson et al. (1998)

Assuming perfect transducer functioning, 8-bit resolution will only give a depth reading to the nearest ca. 2 m if the maximum recordable depth is 500 m. With increasing resolution, however, researchers should be able to give more credence to near-surface dives, which is important for a proper understanding of seabird foraging ecology. Aside from potentially being used for foraging, near-surface dives are commonly used by penguins for commuting (Williams et al. 1992, Bengtson et al. 1993, Wilson 1995) and, as such, constitute an appreciable proportion of both their time and energy allocation while at sea. This latter is particularly pertinent because buoyancy effects due to the compression of air with depth make near-surface swimming particularly energetically expensive (Wilson et al. 1992b).

Although depth use by seabirds is probably the most examined aspect of their marine ecology as determined by logger technology, the increase in temporal and absolute resolution that has come with developments in the solid-state industry has enabled researchers to resolve a suite of ever smaller and more fleeting changes in seabird behaviour, which, far from being trivial, can be pivotal for understanding seabird ecology. For example, the earliest measurements of stomach temperature to determine when endothermic seabirds ingest ectothermic prey took place once every 8, 16 or 32 s (Wilson et al. 1992a), resulting in a very coarse time-based resolution of prey swallowing. Arguably, better temporal resolution would not have helped in this case because of the delay in heat-state transfer between prey and device (Wilson et al. 1995c). However higher sampling frequencies for temperature sensors enabled researchers to move the trans-

ducers from the stomach to the oesophagus and thus not only to determine precisely when prey was ingested, but also the resolution of much smaller prey items than in the stomach system (Ancel et al. 1997, Ropert-Coudert et al. 2000a, Charrassin et al. 2001, Hanuise et al. 2010) (Fig. 5). The capacity to sample parameters with ever greater accuracy and higher frequencies has enabled researchers to ask questions that were unthinkable just a decade or 2 ago and which, depending on recording frequency, relate to entirely different aspects of seabird biology. For example, low frequency measurement (e.g. ca. 1 Hz) of acceleration can give information on body posture and thus behaviour (Yoda et al. 1999), allowing the time/behaviour budget of penguins to be resolved (Yoda et al. 1999, 2001). Higher frequencies (e.g. ca. 30 Hz) allow resolution of faster events (Ropert-Coudert & Wilson 2004), such as foot-strokes in shags (Watanuki et al. 2005) and flipper beats in penguins, which has allowed researchers to examine how seabirds invest effort in swimming with respect to depth and consequent changes in buoyancy (e.g. Sato et al. 2002, Watanuki et al. 2003) or how cormorants modulate wing beat frequency as a function of meal size (Sato et al. 2008). Even higher recording frequencies of acceleration (ca. 300 Hz) show the complexity of rapid processes such as the wing beat (e.g. Fig. 6). Although not yet examined critically, the higher frequency wave signals within the major heave signal that corresponds to the wing beat (Fig. 6) are presumably due to particular muscular, bone/joint configurations and wing morphology (Pennycuick 1990, 1996) and may indicate food load, feather condition or flight conditions (Fig. 6).

Fig. 5. (a) Stomach temperature sensor housed within a titanium cylinder (with retaining spring to hinder regurgitation) combined with oesophageal temperature sensor, at the end of the wound cable. (b) X-ray of the location of the oesophageal sensor in a king penguin *Aptenodytes patagonicus* (cf. Hanuise et al. 2010). (c) Prey ingestion indicated by drops in the temperature profile recorded by oesophageal and stomach thermistors (from Ropert-Coudert et al. 2001)



Sensor development

The advances in recording frequency, sensor resolution and power consumption would have had little impact on our understanding of seabird ecology if they had not been accompanied by a substantial development of various miniature, low-power sensors. Modern transducers are powerful, and the data they record have provided inputs to 2 primary lines of research. One approach uses the specific function of the transducer in its own right, while the other uses it as a proxy for something else. For example, temperature transducers have disclosed fascinating information on temperature per se. Measurement of seabird internal temperature (Woakes et al. 1995) has, inter alia, stimulated debate about deep body temperature cooling to enhance diving capacity (Handrich et al. 1997). Measurements showing the overall flexibility of seabird body temperatures have led to propositions that the costs of homeothermy may be offset by storing muscle-generated heat (Wilson & Grémillet 1996), while measurement of external temperature (Koudil et al. 2000, Watanuki et al. 2001) has enabled researchers to define the environment in which birds operate and the metabolic consequences of this (Croll & McLaren 1993, Handrich et al. 1997, Enstipp et al. 2006, Niizuma et al. 2007). The proxy approach has, in contrast, used changes that occur in environmental temperature to infer seabird behaviour, for example to detect when birds are on the water or flying (e.g. Tremblay et al. 2003). In a further development, this has been combined with bird geographic position (often derived using transmission technology) to map the temperature properties of seabird foraging areas in 2 (Weimerskirch et al. 1995) or 3 dimensions (e.g. Charrassin et al. 2004).

Sensors that respond to light are an excellent example of the value of measuring a parameter as a proxy for some other process. The measurement of environmental light has been useful to determine burrow use in hole-nesting species (Wilson et al. 1995a) and to define the conditions of ambient light under which visual predators, such as penguins, can operate (Wilson et al. 1993b, Zimmer et al. 2008a). However its most widespread and revealing use has been in helping to determine seabird position by allowing determination of day length and local mid-day, as a function of the day of the year, giving latitude and longitude, respectively (Wilson et al. 1992b, Hill 1994). This global location sensing or geolocation technique has spawned a large number of studies that have revealed the extraordinary distances that some species may travel during the annual cycle (e.g.

Shaffer et al. 2006, Egevang et al. 2010). Latterly, in a recent example of a double proxy, Green et al. (2009b) even reconstructed the routes of macaroni penguins *Eudyptes chrysolophus* using internal loggers which could not record light but could document a proxy for it. Here, Green et al. (2009b) recorded dive depth versus time of day because macaroni penguins only swim as deeply as they can see, so the changes in light at the water surface, which were themselves a proxy for bird position, were reflected in the changing depth use of the foraging birds.

The work by Green et al. (2009b) was based on implanted devices. This has been, and likely always will be, the province of a select few. Today, researchers, and particularly physiologists, use a variety of implanted devices to measure parameters such as lactate as well as the more conventional body temperature (Ponganis 2007, Ponganis et al. 2010). Essentially pioneered for seabirds by Pat Butler (Butler & Woakes 1979 and references therein), the implantation approach, which has been particularly useful for measurement of heartbeat rate without having to deal with signal noise coming from skeletal muscles (Kuroki et al. 1999), has necessitated a high degree of sophistication in the electronics. Indeed, heartbeat rate researchers were already using complex electronics to transmit heartbeat rate from seabirds in 1982 (Butler & Woakes 1982), and to store data in 1995 (Woakes et al. 1995), when many researchers using external tags were still reliant on mechanical systems. Although useful as a direct measure, recordings of heartbeat rates in diving seabirds were also important in fuelling discussions about how this measure related to dive physiology (Kooyman & Ponganis 1998) and the more general value of heartbeat rate as a proxy for metabolic rate (Butler 1993). The finding that heartbeat rate increases with increasing metabolic rate (Bevan & Butler 1992, Bevan et al. 1994, Green et al. 2001), coupled with the fact that implanted loggers can be kept in place for months (Butler et al. 1998, Guillemette et al. 2002, Green et al. 2004), has enabled research into the metabolic costs of specific activities such as flight (e.g. Weimerskirch et al. 2000) and diving (e.g. Froget et al. 2004) as well as the more generic costs of, for example, incubation (e.g. Weimerskirch et al. 2002), brooding (e.g. Green et al. 2002) and chick-rearing (e.g. Bevan et al. 2002). Indeed, the heartbeat rate technique has even recently been used to derive food consumption by macaroni penguins throughout the annual cycle (Green et al. 2009a), something that is currently impossible by any other means.

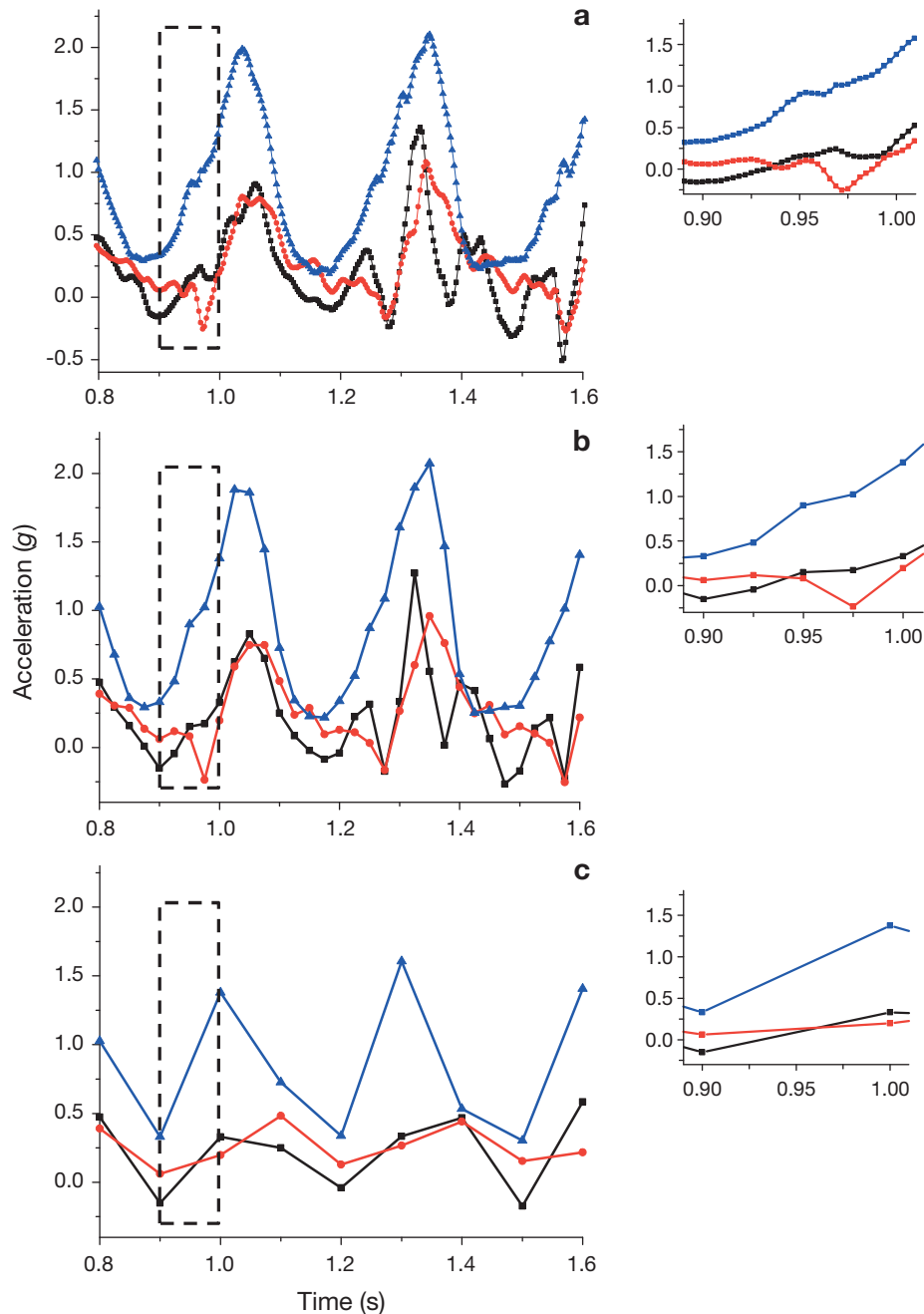


Fig. 6. Acceleration signals recorded by a logger mounted dorsally on a northern gannet *Morus bassanus*: (▲) heave; (●) surge; (■) sway. Two wing beats are (a) resolved at 320 Hz and then subject to thinning so that they can be presented at apparent recording rates of (b) 40 Hz and (c) 10 Hz. The insets to the right show a small (comparable) section from the 3 recording scenarios (dashed boxes) to illustrate how smaller amplitude, higher frequency wave patterns (perhaps due to the precise mechanisms of musculo-skeletal functioning during the wing beat cycle) are lost with decreasing recording frequency

Over the last few years, metabolic rate, at least that associated with movement, has become accessible using another proxy, and one that can be derived using tri-axial acceleration transducers in externally-attached devices (Wilson et al. 2006). Here, body movement is quantified by the dynamic acceleration

which correlates linearly with rate of oxygen consumption (Gleiss et al. 2010 and references therein). This relationship seems to hold, in cormorants at least, irrespective of whether birds are swimming, diving or walking (Gomez Laich et al. 2011). An advantage of accelerometry over heartbeat rate as a

proxy for metabolic rate lies in the short time periods over which the energy expenditure can be determined; so that, for example, not only can the cost of the descent, bottom phase and ascent of dives be estimated e.g. in penguins, but also the cost of pursuit of individual prey (Wilson et al. 2010). This in turn will provide inputs to standard cost/benefit analyses of behavioural ecology, with quantification approaching, or exceeding, those used in experimental manipulation of terrestrial birds (Shepard et al. 2009). Importantly, since accelerometer signals also code for animal behaviour (Yoda et al. 2001, Watanabe et al. 2005, Shepard et al. 2008b, Sakamoto et al. 2009a), the same transducers can provide information on the timing, incidence, extent, intensity and energetic cost of behaviours. Determination of the activity-specific metabolic rate of free-living seabirds has long been problematic (cf. Nagy et al. 1984, Birtfriesen et al. 1989, Furness & Bryant 1996) but this is changing due to the development of tri-axial accelerometer loggers. Combination of these with, for example, depth (e.g. Shepard et al. 2008b) or altitude (e.g. Weimerskirch et al. 2005) transducers, should help us put the behaviour into an ecological context so that modellers, given the suite of behaviours that seabirds have at their disposal and their costs, can examine the consequences of adopting particular strategies.

Considered combination of sensors in seabird archival tags can yield more than the simple sum of each of the sensors. An example of this is in dead-reckoning, or vectorial calculation of animal movements (Wilson & Wilson 1988, Wilson et al. 1991b), made possible by geomagnetic sensors that allow derivation of bird heading during travel (Shiomi et al. 2008). Using this together with estimates of speed (e.g. Ropert Coudert et al. 2002, 2006, Shepard et al. 2008a), the movements of seabirds can be determined with very fine (relative; sub-metre [Wilson et al. 2002b]) resolution, even when they are underwater (Wilson 2002, Shiomi et al. 2008, 2010), where the more commonly used GPS systems (which rely on radio-signals from satellites) cannot function. The seamless nature of dead-reckoned tracks together with their high temporal resolution (Wilson et al. 2007a) mean that they have particular potential for determining behaviour from the precise form of the track. Currently, the most sophisticated behavioural analyses associated with seabird tracks are based around using some metric, such as first passage time (Johnson et al. 1992), to examine area restricted search (ARS) (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005, Suryan et al. 2006). Although the concept of ARS is clearly fundamental to the way

some seabirds forage, the spatial resolution of tracks and the ability to determine bird behaviour are critical in identifying what is genuinely ARS and what is possibly just a change in travel mode (e.g. from flight to paddling) resulting in a decrease in translocation rate. This could result either from a change in search strategy or just be a consequence of the bird resting at the sea surface. Fine scale dead-reckoning tracks coupled with transducers that code for behaviour, such as accelerometers, will do away with this uncertainty and allow researchers to examine ARS as a function of travel mode and, therefore, scale, in an unbiased manner.

Beyond derivation of bird heading during travel, sensors for determining magnetic field strength have also been used to create proxies for a number of important activities. This is done by equipping birds with the sensors on a body part adjacent to another that moves with respect to it, on which a minute magnet is placed. The position of the moving body part (e.g. the lower mandible in the beak, the wing, the cloaca) with respect to the immobile part (e.g. the upper mandible or body) is given by the magnetic field strength perceived by the sensor. (Fig. 7). High sampling rates (typically >10 Hz) allow such systems to determine, for example, every single breath that seabirds take (Wilson et al. 2003), when they defaecate (Wilson et al. 2004) and when and how much birds consume (Wilson et al. 2002a). This approach has led to estimates of food consumption that far exceed those previously projected, at least for the Magellanic penguin *Spheniscus magellanicus* (Wilson et al. 2007b). It has also strengthened the idea that some diving seabirds anticipate their proximate dive depth and inhale accordingly, so as to have near



Fig. 7. Imperial shag *Phalacrocorax atriceps* fitted with an inter-mandibular magnetic sensor unit that records beak openings

neutral buoyancy at operating depths (Sato et al. 2002, Wilson & Zimmer 2004). In addition, this technology has indicated that some penguins load their bodies with oxygen according to the perceived likelihood of prey consumption based on the number of prey they have caught in the previous dive (Wilson 2003). As powerful as this approach may appear, its substantial weakness is currently the link between the sensor and the logger, which takes the form of a cable which can be easily broken (Bost et al. 2007, Liebsch et al. 2007, Hanuise et al. 2010). This will change when loggers become small enough to be fitted to the body part that is currently just the site for the sensor.

Finally, following the pioneering work of Marshall (1998), who used cameras on pinnipeds, cetaceans and turtles, some seabird researchers have been using miniature cameras on free-living birds to give a visual picture of the environment around the animals (e.g. Takahashi et al. 2004, Watanuki et al. 2008, Sakamoto et al. 2009b) (Fig. 8). Although currently limited to taking pictures relatively infrequently (e.g. once every 15 s), and therefore subject to the analogous sampling frequency problems of the early loggers, this approach is fundamentally different from any other logger system because it allows researchers to look outside the bird. Previously, the closest that workers have come to examining the environment has been in bird-borne transducers that sample directly at the bird/environment interface, with all the associated problems (Wilson et al. 2002b). The range of camera loggers is dictated only by the visi-



Fig. 8. Northern gannets *Morus bassanus* interacting with, and around, conspecifics documented by a bird-borne camera placed on the tail. Photo from a study by S. Patrick and S. Votier (unpubl.) on the foraging behaviour of northern gannets

bility of the medium through which the birds are moving so they have been used underwater to assess which substrate types shags *Phalacrocorax aristotelis* forage over (Watanuki et al. 2008) and to study prey fields (Takahashi et al. 2008), as well as to look at intra-specific (Takahashi et al. 2004) and inter-specific foraging associations (Sakamoto et al. 2009b) and even to assess interactions with shipping (Grémillet et al. 2010). A disadvantage of this approach lies in the non-standardization of the visual field, which varies according to the transparency of the medium (particularly in water), but also according to how much of the visual field is taken up by portions of the bird (particularly the head). The restrictions on the visual field of the camera means that non-documentation of an event, for example the presence of a vessel (Grémillet et al. 2010), does not mean that one is not there, although documentation of it is obvious proof that it is. A new conceptual approach will be required to overcome this problem, although careful use of fish-eye lenses may mitigate it to some extent. A final drawback of camera systems is that many hours are currently required to examine the data, the vast majority of data stored being worthless. Sophisticated analytical software should make this task more manageable in the future.

Software development

The problems of data analysis from camera loggers are not unique to camera systems. The large amounts of data gathered by multiple-channel loggers increasingly necessitate special software to deal with them. Standard spreadsheets such as Excel (<http://office.microsoft.com/en-us/excel/>), with currently a maximum of 32000 graphable points, are unhelpful given that the analytical basis for most seabird data recording systems is graphical. ORIGIN (www.originlab.com) and IGOR-Pro (www.wavemetrics.com) are vastly superior programs for this but, given the relatively complex computations necessary to derive, for example, a dead-reckoned track from geomagnetic, pressure and speed data (Shiomi et al. 2008), the seabird community really needs bespoke software. Some tag manufacturers such as Wildlife Computers (www.wildlifecomputers.com) provide special software for e.g. analysis of depth traces but the increasing number of different applications of accelerometers, such as for behavioural or energetic analysis, makes this an ever-expanding task. The R-environment (www.r-project.org) and Matlab (www.mathworks.com) are applicable, and allow

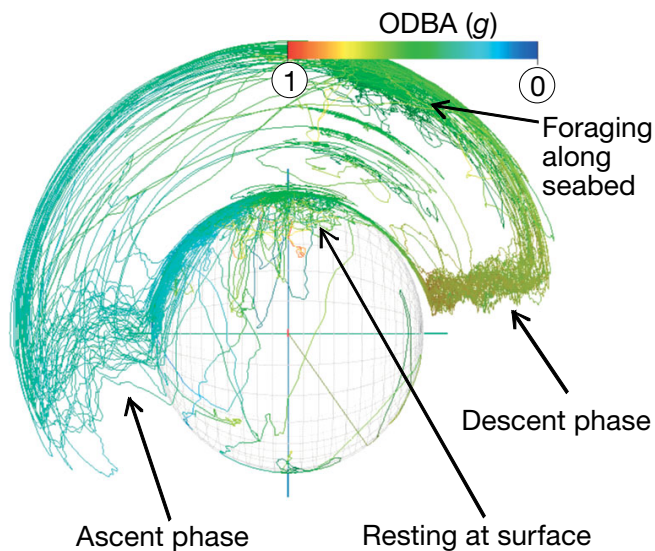


Fig. 9. Screenshot of an output of a program (CRYSTAL BALL; Grundy et al. 2009) to visualize changes in behaviour adopted by an imperial cormorant *Phalacrocorax atriceps* during multiple dives and resting periods at the surface between them. The lines on the outside of the globe indicate animal body angle (the horizontal axis bisecting the globe is the pitch while the vertical axis bisecting the globe is the roll) so that lines on the right hand side of the globe indicate head-down posture (e.g. descent—the green umbilical chord), those on the left hand side indicate 'head-up' posture (e.g. ascent—the blue, more diffuse, umbilical chord), while those in the middle (concentrated around the 'North pole') indicate body angle deviating little from level. A measure of dive depth is given by the distance of the lines into space, away from the globe (all points on the globe surface are from behaviours that occur when the bird is at the water surface). A measure of how hard the bird was working via overall dynamic body acceleration (ODBA from 0 to 1 g; cf. Wilson et al. 2006) is given by the colour (red = most intense, blue = least intense)

people to share analytical protocols, but these may simply not be fast enough to deal with the many millions of data items gathered by multi-channel loggers. The approach taken by Sakamoto et al. (2009a) may set a trend in providing freeware for use by the seabird research community, in this case Ethographer which works in IGOR Pro, to help determine behaviours (<http://sites.google.com/site/ethographer/download>). We may hope so. The future will determine whether the faster processors in computers will allow even programs like IGOR Pro to function rapidly enough with the increasingly larger datasets or whether we will have to revert to bespoke software written in a highly efficient computer language such as C++ (Grundy et al. 2009). Finally, complex data require complex analysis, but that this can be greatly facilitated by software that visualizes the data

in a revealing manner. Spherical scatter plots represent such an approach, and are the basis behind a program called CRYSTAL BALL (Grundy et al. 2009), which translates the 3 acceleration axes into a graph that can display 6 or 7 dimensions so that they are all visible in one moving image (Fig. 9). Certainly, the future will need more of this.

THE FUTURE

Smaller size, bigger capacity

The future of archival tags in seabird research looks set to follow existing trends. Devices will become ever smaller and ever more powerful with respect to what they can record so that, ultimately, it will be possible to equip even the smallest seabirds such as storm petrels (Hydrobatidae) with units that detail the minutiae of their lives. Critically, reduction in size and mass will also help reduce deleterious device effects (cf. Bowlin et al. 2010, Vandenabeele et al. 2011). Some of the analytical work will be processed in the device but much will be left to a suite of, hopefully coherent, programs developed for the research community.

The future will see the lives of seabirds being probed in increasing detail, coupled with the development of a more holistic approach, as researchers realise that it is possible to determine bird activities precisely, as well as their costs in terms of energetics and time (cf. Shepard et al. 2009) and their consequences. Understanding how the biotic and abiotic environment affects seabirds, as well as modelling the costs and benefits of different strategies available to birds, must be primary goals in a changing world where prediction is becoming paramount. We have never had such extraordinary capacity for acquiring difficult knowledge about the lives of enigmatic seabirds. Let us hope that our ability to use the data is on a par with the technology that lets us acquire it.

A sober moment—the flipside of gadgets

The euphoria of discovery using animal-attached tags must be tempered with the certainty that seabirds with attached devices do not behave in a manner identical to unequipped conspecifics (Paredes et al. 2005, Ropert-Coudert et al. 2007, Beaulieu et al. 2010, Saraux et al. 2011). Even discounting ethics, which we should not (Hawkins 2004), the value of data acquired by animal-attached devices depends critically on the data either being representative or at

least allowing us to determine what 'representative' is. In our desire for knowledge, and to demonstrate exciting discoveries, which may enhance our own publication record, we will have to walk the line between deployment of unacceptably large devices (e.g. Wilson et al. 1986, Watanuki et al. 1992, Culik et al. 1994, Whidden et al. 2007) and the need for data that is of value from scientific, ethical and conservation perspectives. Our teetering along this line in the past has brought us to where we are now, with a better understanding of seabirds at sea than ever before. We should not let the rush of advances cloud our judgment in the future.

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From lavage to lipids: estimating diets of seabirds

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ABSTRACT: Understanding seabird marine habitat affinities, at-sea behavior, variability in reproductive success, migratory patterns, phenology, and other life history traits depends primarily on knowledge of the prey that they consume. Traditionally, estimating diets has been done through classification and enumeration of prey remains found in stomach contents of seabirds collected at sea, as well as chick meals, pellets, and feces collected at breeding colonies. These techniques have the advantage of high taxonomic resolution of prey, but suffer from biases due to the underestimation of soft-bodied or small prey that are digested completely and overestimation of prey with durable parts that are retained for long periods of time. Recent innovations in 2 biochemical assays of seabird tissues—stable isotope and fatty acid analyses—have greatly expanded knowledge of seabird diets and have advanced our understanding of the ways in which seabirds can indicate inter-seasonal, annual, decadal, and longer shifts in oceanographic conditions over varying spatial scales. Advances in statistical approaches to these data have provided new ways in which prey can be identified and quantified. When applied in combination, these 3 techniques (traditional diet sampling, and stable isotope and fatty acid analyses) have the potential to reveal pathways of energy flux across marine ecosystems and to provide new insight into marine ecosystem dynamics. We review the basic principles of these approaches to determining seabird diet and emphasize the need for more formal conceptual and statistical integration of methods to advance this field.

KEY WORDS: Diet · Seabird · Stable isotope · Isoscape · Mixing models · Bayesian · Quantitative fatty acid signature analysis · QFASA

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INTRODUCTION

Diet forms the critical link between seabirds and the biotic and abiotic components of their environment. Linking variability in oceanographic conditions with the array of measurements we make on seabirds (e.g. reproductive success, chick growth rates, recruitment, survival, at-sea distributions, diving behavior, stress levels, energetic expenditures, body condition, phenology) requires understanding the type, amount, and quality of prey that seabirds consume. Furthermore, a profound understanding of seabird diets is critical to the conservation of these marine top predators. Assessment of seabird diets can elucidate factors causing population declines (e.g. Becker & Beissinger 2006) and can identify par-

ticular prey (e.g. Cury et al. 2011) or foraging areas (e.g. Louzao et al. 2011) that need protection.

Traditionally, estimating diets has been done through collection of ingested prey when seabirds are at breeding colonies. This technique can reveal the type and number of prey, but can be biased towards prey with durable parts. Biochemical assays of seabird tissues such as stable isotope (Hobson et al. 1994) and fatty acid (FA) signature analysis (Iverson et al. 2007) have provided insight into trophic levels of diet, how diets shift over time (e.g. diets during winter when seabirds are often inaccessible) and regions (e.g. benthic versus pelagic, and specific migratory routes), and have elucidated differences between adult and chick diets (Hobson 1993, Hobson et al. 2002a,b, Karnovsky et al. 2008). However, these biochemical

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approaches are limited in their ability to assess prey type and the quantity of prey consumed when diverse prey from similar trophic levels or with similar FA compositions are eaten. Nevertheless, the careful quantification of stomach contents in conjunction with these biochemical techniques has advanced our understanding of the ways in which seabirds can indicate inter-seasonal, annual, decadal, and longer shifts in oceanographic conditions and over varying spatial scales. These innovations in assessing diets are expanding the types of questions that can now be answered. Integration of these approaches is the next frontier in evaluating seabird life history.

TRADITIONAL METHODS

Background

Traditional assessment of seabird diets at colonies usually involves the identification and enumeration of prey found in stomachs, regurgitates, feces, pellets, and gular pouches, or observations of food provisioned to chicks (see Duffy & Jackson 1986, Barrett et al. 2007). Here we describe the techniques briefly with an emphasis on the limitations and recent innovations of each method.

Measurements of diets using traditional diet sampling techniques reflect the food ingested over short time scales (hours to days) prior to sampling (e.g. Karnovsky et al. 2003). Furthermore, diet sampling at the colony is usually restricted to the spring or summer, which is the chick-rearing period when adults return to land (e.g. Chérel et al. 2002) and prey delivered to chicks could differ from those ingested by adults (e.g. Shealer 1998).

Biases in this method stem from the rapid digestion of some types of prey and the retention of other types of prey or hard parts. Soft-bodied prey are often digested rapidly and are underestimated (e.g. Polito et al. 2011). Furthermore, some species of seabirds that have gizzards retain hard parts such as squid beaks for extended periods (Furness et al. 1984). Another complication is that retention may not be complete, and numbers of squid can be over- or underestimated depending on the part of the squid beak (upper or lower beak) used in estimating the number of squid consumed (Xavier et al. 2011). Prey that have small or fragile hard parts are often excreted or digested completely and are therefore underestimated (Van Heezik & Seddon 1989, Xavier et al. 2011). Even though fish otoliths resist digestion because they are made of an aragonite form of

calcium carbonate and otoline (Gon & Heemstra 1990), small otoliths can be digested completely. In a study of captive little penguins *Eudyptula minor*, Gales (1988) found that otolith length and weight decreased as the resident time in the penguin increased. Van Heezik & Seddon (1989) found that smaller otoliths were digested faster in yellow-eyed penguins *Megadyptes antipodes*. Thus, fish that have small otoliths can be underestimated in diets. However, careful attention to these biases can reveal much about the foraging strategies of seabirds. For example, Spear et al. (2007) recorded stomach fullness, differential digestion of prey, and levels of erosion of otoliths and squid beaks found in seabird stomachs. They used this to reveal which seabirds fed nocturnally, the previous day, within the study area, scavenged, or fed in association with subsurface predators (Spear et al. 2007).

Direct observation

Diet sampling at the breeding colony usually occurs during the breeding season when seabirds return regularly to feed their growing chicks. From early on, researchers took advantage of the fact that some species carry prey in their bill. Prey can be identified, the size can be estimated, and the frequency of delivery to chicks is easily observed. Pearson (1968) elucidated the ecological differences amongst 3 species of terns in this manner. Long-term observations of birds at the same colony can reveal inter-annual shifts in the prey base around the colony. For example, Gaston et al. (2003) observed the fish carried back to chicks by thick-billed murres *Uria lomvia* from 1980 to 2002. They observed a shift from ice-dependent Arctic cod *Boreogadus saida* to more boreal species, which was coincident with the decline in ice around the colony. Several technological innovations have increased the efficiency and accuracy of collecting these data. For example, Larson & Craig (2006) used 'digiscoping' (the use of a digital camera held up to spotting scopes or binoculars) to photograph terns returning with fish in their bills. These digital photographs allowed them to estimate size more accurately and identify the prey and to more easily confer with fish biologists on fish identification. These data showed that the terns took a greater diversity of fish than previously known. All manner of handheld digital recording devices have been employed to aid in the recording of observations of food delivery at colonies. For example, as part of a long-term study of common murres *U. aalge* on the Farallones Islands, California, USA, biologists record

the fish size and species as well as bird identity (from bands and known nest sites) with hand-held electronic recorders (Palm Pilot; R. Bradley pers. comm.), and digital programs are now available for multiple device types (e.g. HanDbase4, DDH Software).

Analysis of pellets

Some seabirds regurgitate pellets containing the undigested hard parts of the prey they consumed. Collection of pellets is a non-invasive way of assessing diets (e.g. Duffy & Laurenson 1983). Harris & Wanless (1992) analyzed the otoliths from pellets of European shags *Phalacrocorax aristotelis* and found that they relied on an unexpected food source, lesser sandeels *Ammodytes marinus*. A major drawback of using pellets is possible bias. Lindsay & Meathrel (2008) recorded partially consumed prey and the prey identified in pellets of Pacific gulls *Larus pacificus* at several colonies. They found that their estimates of prey consumption based on these indirect measures greatly underestimated the amount of prey consumed and were heavily biased towards the large prey that had hard parts. Nevertheless, using pellets alone, they were able to identify a wide range of prey species from diverse taxonomic groups (crabs, mussels, invertebrates, fish, and other seabirds).

Gular pouch, regurgitates, and stomach lavage

Some seabirds (e.g. little auks *Alle alle*) bring food back to their chicks in a sublingual gular pouch. These diet samples can be removed easily with a finger or a small spoon (e.g. Karnovsky et al. 2003). Other species readily regurgitate upon capture (e.g. Cassin's auklet *Ptychoramphus aleuticus* and thin-billed prion *Pachyptila belcheri*), which can then be collected (e.g. Abraham & Sydeman 2006, Quillfeldt et al. 2010). Still others swallow their prey into their stomachs (e.g. penguins, procellariiforms, gulls). In his study of herring gulls *Larus argentatus*, Hunt (1972) found that voluntary regurgitations by chicks gave biased samples due to being incomplete. He found that by inserting his index finger into the proventriculus and scooping out the food, he was able to extract complete diet samples. In addition, these samples can be extracted through stomach lavage techniques (e.g. Ainley et al. 2003, Miller et al. 2009, Neves et al. 2011). Stomach lavage (also known as stomach flushing or water offloading) involves the introduction of saltwater into the stomach of the bird

with a tube and then flushing out the contents of the stomach (Wilson 1984). Stomach lavage has greatly expanded the understanding of diets of seabirds that regurgitate food back to chicks and is a great advance over killing birds to examine their stomach contents (e.g. Volkman et al. 1980) or the use of emetics (Jablonski 1985). While impacts of stomach lavage may vary with different species, Robertson et al. (1994) found that Adélie penguin *Pygoscelis adeliae* adults did not alter their foraging behavior after flushing, and their chicks grew normally.

Analysis of guano

Hard parts such as otoliths and squid beaks are often excreted by seabirds. By sorting through guano, these can be extracted, identified, and measured, and the fish and squid component of the diets can be assessed. Because these hard parts can accumulate in the colony over time, long-term diet shifts can be assessed if different layers of the ornithogenic soil can be dated. McDaniel & Emslie (2002) were able to assess changes in diets of Adélie penguins over 6000 yr by measuring otoliths and squid beaks recovered from different layers of Adélie penguin colonies. Genetic analysis of guano has begun to be used to identify seabird prey. For example, the seasonal transition from krill diets to myctophids was detected in the DNA found in macaroni penguin *Eudyptes chrysolophus* guano (Deagle et al. 2007). Despite the appeal of this non-invasive technique, several challenges remain; there is often very little amplifiable DNA in guano, and clone libraries of specific primers of prey species are currently lacking (Deagle et al. 2007). Analysis of fecal DNA from captive little penguins fed known diets revealed that each fish species undergoes differential digestion, which influences detection in excreted DNA (Deagle et al. 2010). However, Deagle et al. (2010) found that digestion rates were constant across individuals, so there is potential for correction factors to be developed to estimate quantities of different prey consumed using this technique.

Taxonomy

One of the strengths of traditional diet sampling is the provision of taxonomic content of the diets examined. However, identifying the prey that are recovered or observed with traditional diet sampling techniques often requires extensive knowledge of the taxonomy of prey species. As prey are often partially

digested, this requires knowledge of diagnostic fragments (e.g. Quillfeldt et al. 2010). Field guides of many components of seabird prey, such as fish bones and squid beaks, are available (e.g. Hecht 1987, Hansel et al. 1988, Xavier & Cherel 2009). The ability to view and measure prey seen through the microscope on a computer screen allows researchers to save images and electronically send them to experts (Reinalda et al. 2010). However, access to taxonomists is often the limiting factor in prey species identification. Worldwide, there has been a decline in the number of trained taxonomists (Pearson et al. 2011).

Measurements

Stomach contents are often characterized by 2 measures, percent occurrence and average percent of total contents. Percent occurrence reflects the frequency with which birds consumed a particular taxon. Average percent of total reflects the average numerical proportion of each taxon. Another commonly used measure is percent biomass based on wet weight measurements (e.g. Cherel et al. 2002). Hard parts such as otoliths, squid beaks, and bones provide identifiable remains and can be included in the percent occurrence and average percent total measurements but often make up a small fraction of the wet weight of the prey in the stomach sample. In some cases, it is possible to use regressions of prey morphometrics to infer the original size and mass of the fish or squid consumed (e.g. Cherel et al. 2002).

Diet studies in which comparisons are made among stomach contents have benefitted enormously from the application of statistical techniques that allow for group comparisons. Principal component analysis (PCA) in conjunction with ANOVA allows the identification of statistically significant differences amongst groups (e.g. Fig. 1, see also Spear et al. 2007). Distance measures such as multi-dimensional scaling and cluster analyses provide evidence of which groups have more similar diets (e.g. Fig. 2). These techniques can utilize frequency of occurrence, average percent of total, or prey biomass data.

Future directions

Despite the biases in traditional diet sampling, application of these techniques is the only way that specific taxonomic information can be known. Collecting samples can often be done with minimal disturbance to the birds (gular pouch contents, pellets,

direct observations). Therefore, even with known limitations, consistent application of traditional sampling techniques can provide critical information when comparing spatial, temporal, and demographic effects on diet. Recommendations to advance the use of these techniques include:

(1) Producing photographs and field guides of type specimens, and sharing these data freely to make the specialized knowledge of taxonomists more readily applicable. For example, the work by Xavier & Cherel (2009) is available without charge from the British Antarctic Survey.

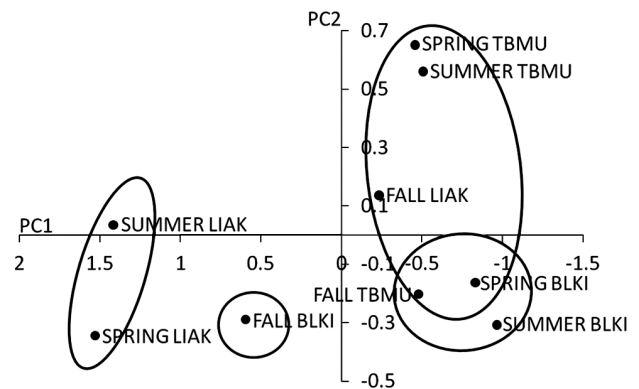


Fig. 1. Principal component analysis (PCA) comparing percent occurrence of prey among 8 combinations of seasons/species of seabirds foraging in the North Water Polynya. Prey composition of species groups enclosed in the same circle were not significantly different (Sidak multiple comparison tests, $p > 0.05$) BLKI: black-legged kittiwake *Rissa tridactyla*; TBMU: thick-billed murre *Uria lomvia*; LIAK: little auk *Alle alle* (Karnovsky et al. unpubl.). Based on data presented by Karnovsky et al. (2008)

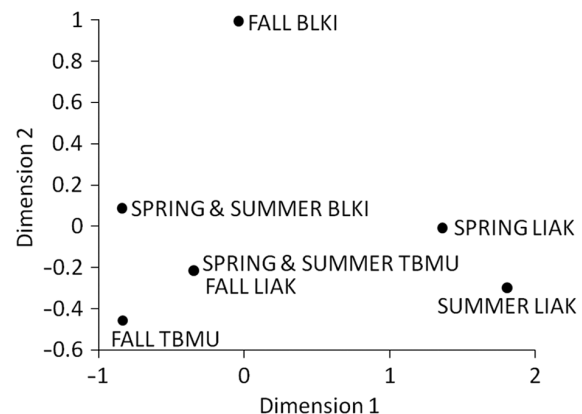


Fig. 2. Multi-dimensional scaling (MDS) plot based on the distance matrix derived from a cluster analysis of the percent frequency occurrence of prey that were eaten by the same species/seasons as in Fig. 1 (Karnovsky & Hunt unpubl.). Based on data presented by Karnovsky et al. (2008)

(2) Collection and archiving of prey voucher specimens. Many regressions for mass and length of fish are based on very few fish specimens. Furthermore, there are still many fish and squid whose otoliths and beaks are undescribed.

(3) Continued development of the identification of prey from DNA in feces.

STABLE ISOTOPES

Background

From the earliest isotopic analyses of seabird tissues over 20 yr ago (Hobson 1987, Schaffner & Swart 1991), researchers have embraced this approach to decipher the nutritional ecology of seabirds. There has been an exponential increase in the use of such measurements using a variety of seabird and prey tissues, ranging from temperate (Bearhop et al. 2000, Hipfner et al. 2010) to tropical (Awkerman et al. 2007, Cherel et al. 2008) and polar regions (Hodum & Hobson 2000, Hobson et al. 2002a,b, Quillfeldt et al. 2010, Phillips et al. 2011). These investigations followed from earlier use of isotopic analyses of marine systems (Owens 1987, reviewed by Michener & Schell 1994). Several authors have provided overviews of the use of stable isotope methods in seabird investigations (Forero & Hobson 2003, Barrett et al. 2007, Bond & Jones 2009) or more general use of stable isotope techniques in avian or mammalian ecology (Inger & Bearhop 2008, Tollit et al. 2010, Hobson 2011). Here we focus on recent developments and future directions emerging in this rapidly changing field of study.

The primary use of stable isotopes in seabird ecological studies has been the establishment of trophic position and region of feeding (e.g. Fig. 3). These efforts, for the most part, have been based on the measurement of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of seabirds and their prey, and are based on the documented isotopic discrimination between diet and seabird tissues and knowledge of baseline isotopic signatures in the in-shore and pelagic foodwebs used by birds (reviewed by Bond & Jones 2009). Isotopes of a variety of other elements (e.g. O, H, S, Hg, Pb, Sr) can be used effectively in marine systems, especially as additional tracers of source inputs, but these applications are still relatively infrequent (Rubenstein & Hobson 2004, Hobson 2011). More recently, isotopic measurements have been used to infer migratory movements, connectivity, and seasonal interactions based largely on increasing delineation of marine isoscapes

or spatial patterns in foodweb isotopic signatures across the oceans (West et al. 2010). Increased use of captive seabirds raised on known or manipulated isotopic diets has also provided new insights into the role of physiology and growth on isotopic values in seabird tissues and into mechanisms controlling the behavior of isotopes *in vivo* (Williams et al. 2007). The recent development of isotopic mixing models based on Bayesian techniques has contributed greatly to more robust estimates of dietary inputs that better propagate known sources of error (Parnell et al. 2010).

Trophic level (TL) and source of feeding

The placement of individuals or populations to trophic level (TL) using stable isotopes is possible because the assimilation of elements from one TL to another involves a reasonably predictable change in the ratio of heavier to lighter isotopes for several elements. This is due to a variety of physiological processes that ultimately involve rate-limiting steps. Thus, the identification of these tissue- and element-specific isotopic discrimination factors is fundamental to the application of the approach. The conversion

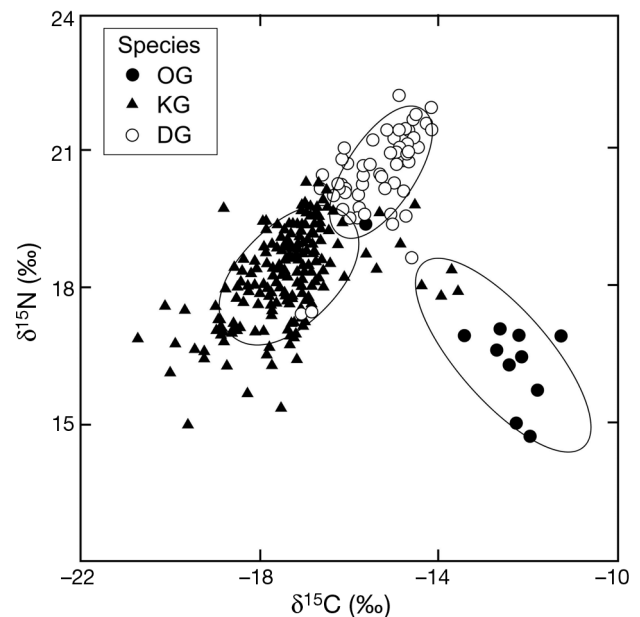


Fig. 3. *Larus atlanticus*, *L. dominicanus*, and *Leucophaeus scoresbii*. Isotopic segregation of 3 sympatric large gulls from coastal Patagonia, Argentina. OG: Olrog's gull, KG: kelp gull, DG: dolphin gull. The figure illustrates the power of the isotope approach for delineation of communities related to trophic positions and relative use of benthic vs. pelagic feeding. Gaussian bivariate ellipses based on whole blood of chicks (after Forero et al. 2004)

of isotope data to actual TL depends upon the assumption that we know enough about the isotopic composition of primary producers (i.e. phytoplankton) at the base of the foodweb of interest, or that we can identify a key organism in the foodweb of interest whose TL and isotopic value are known. Thus, if primary producers are considered, we have

$$TL_c = 1 + (\delta X_c - \delta X_p) / \Delta TL \quad (1)$$

where TL_c is the TL of the consumer of interest, δX_c is the isotopic composition of the consumer, δX_p is the isotopic composition of primary producers, and ΔTL is the average tissue-specific isotopic discrimination factor between TLs for the marine foodweb of interest. The problem is that we rarely, if ever, are able to derive an accurate estimate of δX_p . This is because we usually sample particulate organic matter rather than 'pure' phytoplankton. Also, we know that the isotopic composition of phytoplankton can change throughout the season depending on sea surface temperature and nutrient availability (Michener & Schell 1994, Montoya 2007).

A more practical approach has been to assume that we can anchor a foodweb to an organism whose TL is assumed to change little, such as an herbivorous copepod or any organism at TL 2. In such cases, we have:

$$TL_c = 2 + (\delta X_c - \delta X_h) / \Delta TL \quad (2)$$

where δX_h is the isotopic composition of the obligate herbivore chosen. However, even in this case, many 'herbivorous' zooplankton also ingest micro-zooplankton, thereby blurring the boundaries between strict herbivores and primary carnivores from an isotopic perspective.

The first generation of seabird dietary investigations using stable isotopes to determine TL relied heavily on these models (Hobson & Welch 1992, Hobson 1993, Hobson et al. 1994, Forero et al. 2004, Hedd & Montevecchi 2006). This led to an interest in just how accurate estimates of isotopic discrimination values were.

Inferring TL and source of feeding from stable isotopes necessitates the use of an accurate diet–tissue isotopic discrimination factor (e.g. $\delta^{15}N$, $\delta^{13}C$). Dietary models are based on the application of such discrimination factors between diet and consumer tissues in a simple arithmetic manner, and sensitivity analyses have shown the problems that can arise if inappropriate discrimination factors are assumed (Caut et al. 2008a). Fortunately, meta-analyses of data based on captive studies across a broad range of taxa have provided reasonable estimates for a number of

marine applications (Kelly 2000, Post 2002) and have revealed patterns associated with metabolic pathways of voiding nitrogenous waste (Vanderklift & Ponsard 2003). Bond & Jones (2009) provided a summary of the $\delta^{15}N$ and $\delta^{13}C$ estimates derived from captive studies on a variety of tissues (e.g. blood and feathers). Evans Ogden et al. (2004) provided similar estimates for a marine-associated shorebird, and Polito et al. (2009) reviewed isotopic discrimination factors associated with seabird egg components.

Recent studies have emphasized the importance of dietary quality and quantity in driving isotopic discrimination in animals, especially for N (Robbins et al. 2005, Martínez del Rio et al. 2009). These studies suggest that high-quality diets, namely those providing the most limiting amino acid (AA), result in lower $\delta^{15}N$ values, and attempts have been made to provide calibration algorithms relating $\delta^{15}N$ to diet quality (Robbins et al. 2005, see also Caut et al. 2008b). These corrections may be useful for omnivores that have access to a wide range of diets of varying N content. However, seabirds feeding on marine sources of protein (invertebrates, fish, mammals, birds) almost certainly meet their N requirements adequately through these sources, and we predict only relatively small effects of diet quality on seabird isotopic discrimination. Thus, for seabirds, more interest has been aimed at how other factors may influence $\delta^{15}N$ and $\delta^{13}C$, such as the effects of growth rate and dietary intake in chicks versus adults, nutritional stress, and aspects of metabolic routing also common to other taxa.

Severe catabolism of body proteins, typical of fasting or starvation, increases $\delta^{15}N$ values in a variety of bird tissues (Hobson et al. 1993), and individuals that have been salvaged from wrecks or oil spills are not suitable for dietary reconstructions, especially those involving metabolically active tissues (Sanpera et al. 2008). For healthy wild birds, contrasting diets of provisioning adults and chicks using stable isotope assays has provided information on adult diets as well as those of more easily sampled chicks. Using captive or controlled studies of wild alcids, Williams et al. (2007) and Sears et al. (2009) demonstrated that growth rate and amount of food intake of young can affect tissue $\delta^{15}N$ values, independent of diet $\delta^{15}N$ value. While this effect was relatively small (up to 0.7‰ in $\delta^{15}N$ and ~0.3‰ in $\delta^{13}C$), it does reveal potential sources of variance in isotope ratios of chicks in wild populations. These authors suggested that the depletion in tissue $\delta^{15}N$ values with growth rate and reduced dietary intake was due to an increase in N use efficiency. Thus, isotopic conse-

quences of protein catabolism in fasting birds seems to be opposite to the effect of more subtle and likely more natural variation in nutrition and growth experienced by chicks. We also know that growing chicks will typically have more urea in blood plasma than adults and that this might depress chick blood $\delta^{15}\text{N}$ values (Bearhop et al. 2002). Together, such age-related effects on chick tissue $\delta^{15}\text{N}$ values are likely to bias chick values to be lower than those of adults with the same diet. Woo et al. (2008) found no dietary difference between chicks and adult thick-billed murrets *Uria lomvia* at a low Arctic colony based on similar blood $\delta^{15}\text{N}$ values, a conclusion that may need to be revisited.

Isotopic turnover

Elemental or isotopic turnover determines the period of integration over which diets contribute to tissue synthesis. In most dietary studies, we assume that an organism is in equilibrium with its diet or local food web, but this may or not be the case, depending on the movement history of the individual and the tissue chosen. The most useful estimates of tissue turnover have been provided by captive experiments in which birds have been switched from one diet to an isotopically different diet, and patterns of isotopic change in the tissue of interest are recorded. The resulting patterns of isotopic change in tissues fit an exponential decay model, and so the half life of a given element in a tissue can be readily derived (Hobson & Clark 1992). More recently the derived parameter, residency time of an element in tissue, has been used (Martínez del Rio & Anderson-Sprecher 2008). For most avian applications, we have a reasonably good idea of these turnover rates for most tissues of interest, such as blood plasma, blood cells, whole blood, muscle, and liver. Both growth and catabolic components of tissue turnover rates follow an allometric relationship, which allows extrapolation to species of different body mass (Carleton & Martínez del Rio 2005, Martínez del Rio et al. 2009). Seabird researchers can thus estimate isotopic turnover rates for their species and tissue of interest, although further controlled studies using species of various sizes are still needed.

A major recent development in our understanding of isotopic turnover in animals has been provided by the application of graphical methods previously designed to trace inputs from individual radionuclides to a mixture. Using this approach, Cerling et al. (2007) demonstrated that turnover patterns can be

the result of combined fast and slow turnover pools. This approach promises greater insight into the physiology of birds in general and metabolic routing in particular. Further captive diet-switch experiments that examine origins of specific dietary or endogenous proteins and their relative rates of incorporation into tissues will be the next generation of turnover experiments.

Mixing models

In cases where the isotopic composition of dietary alternatives is known, isotopic mixing models can be used to estimate the relative proportion that each contributes to consumers. The key parameter in such models is the diet–tissue discrimination factor for each isotope used in the model. Currently, the major weakness of dietary isotope models is their assumption of perfect mixing of dietary elements. Dietary macronutrients undergo differential routing, but mixing models do not automatically consider this. This is a particular weakness of dealing with bulk tissues rather than individual compounds. Thus the $\delta^{15}\text{N}$ axis really represents a ‘protein axis,’ since N only occurs in dietary protein and N atoms end up in proteins in the consumer. In marine systems, the $\delta^{13}\text{C}$ axis, however, can be more difficult to interpret if C in dietary lipids contributes to consumer proteins and lipids. Typically, lipids are removed before bulk tissue analyses and are dealt with in separate pathways (Cherry et al. 2011). Procellariiform seabirds that feed their young prey stomach oils may be a special case involving much greater transfer of lipid carbon to body tissues and so may require special consideration when applying stable isotope methods (Thompson et al. 2000, Cherel et al. 2005).

A major breakthrough in the way animal ecologists deal with isotope mixing models was provided by a probabilistic approach where there are more isotopically distinct dietary sources than isotopes to provide a unique mathematical solution (i.e. when the number of sources exceeds the number of isotopes by >1). This allowed ecologists to define ranges of possible solutions, information that can also be extremely valuable (Caut et al. 2008c). The pioneering work of Phillips & Koch (2002) and Phillips & Gregg (2003) in isotopic mixing models has been followed by Bayesian mixing models. A key advantage of these models is the ability to apply prior knowledge of diets, based on stomach content data, observation, or other means. In a Bayesian framework, the use of informed priors can greatly enhance our ability to

accurately predict dietary contributions based on isotope data. In addition, recent models allow a much better means of dealing with error in dietary estimates, allowing error propagation and ultimately sensitivity analyses related to key parameters such as the diet–tissue isotope discrimination factor. Species- and age-specific discrimination factors should be used whenever possible because inter- and intra-specific variations in these values can affect model results (Bond & Diamond 2011). Currently, there are 3 primary (free) software products dealing with isotope-based mixing models. SIAR is based on R and allows for concentration-dependent mixing models (Parnell et al. 2010). MixSIR is based on Matlab but at least until recently did not allow a concentration-dependent option (Moore & Semmens 2008). SISUS is an extremely user-friendly frequentist-based option (<http://statacumen.com/sisus/>). Seabird biologists are exploring the use of these mixing models to advantage (Votier et al. 2010, Polito et al. 2011).

Isotopic niche

With biplots of seabird tissue $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ (e.g. Fig. 3), differences in isotopic niche space can be seen. This approach can be extrapolated to multi-dimensional or multi-isotopic niche space (Bearhop et al. 2004, Newsome et al. 2007), and allows estimation of niche segregation or overlap among species, sexes, or age groups (e.g. Forero et al. 2002, 2005), and potentially, niche changes seasonally, spatially, or in response to changes in resource availability. This approach is also suited to study whether populations are comprised of specialists, generalists, or both (Bearhop et al. 2004, Layman et al. 2007, Woo et al. 2008). In well constrained systems (e.g. within an isotopically well defined and understood marine food web) and where all of the basic components of isotopic differences among individuals other than diet can be accounted for (molt phenology, isotopic discrimination factors, periods of isotopic integration), the isotopic niche concept remains interesting. However, there are assumptions that need to be emphasized in any such approach.

If 2 species, constrained to a given system, differ in their isotopic niche space, then it is likely that they also differ in

their realized ecological niche space. However, if 2 species overlap, then it is less obvious that they occupy the same ecological niche because different dietary species (e.g. forage fish) can overlap extensively isotopically. The correct interpretation of isotopic niche changes thus requires a detailed knowledge of the isotopic nature of alternative dietary items and of how baseline isotopic patterns may change spatially. This remains a daunting challenge. A more parsimonious approach is to restrict attention to so-called ‘trophic niches’ using $\delta^{15}\text{N}$ measurements, as already discussed (e.g. Hedd et al. 2010), but again, researchers should always consider the possibility of variable $\delta^{15}\text{N}$ baselines in marine isoscapes (e.g. Jaeger et al. 2010b, Jaeger & Chérel 2011). We suggest that seabird researchers more critically consider whether isotopic differences or similarities can always be translated to useful estimates of dietary or ecological niches.

Marine isoscapes

Stable isotope methods can be used to track movements of seabirds or to identify feeding regions, because marine food webs are not isotopically homogeneous in space and time. This approach has been used in terrestrial systems (Hobson & Wassenaar 2008, West et al. 2010) and more recently in marine systems (Fig. 4; Graham et al. 2010). Minami & Ogi

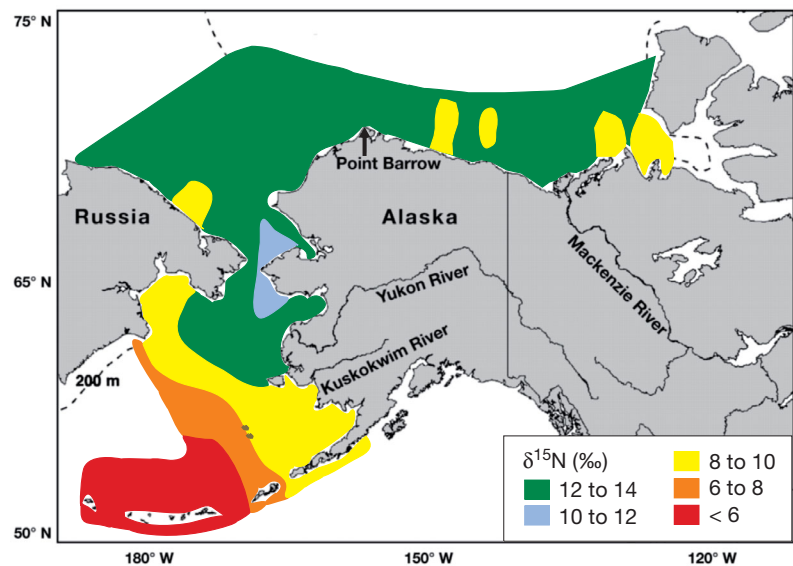


Fig. 4. $\delta^{15}\text{N}$ copepod isoscape of the Bering, Chukchi and Beaufort Seas illustrating the often highly structured isotopic nature of marine food webs, which can be used to delineate seabird origins. Isotopic structure must be considered when modeling trophic level over large regions (from Schell et al. 1998)

(1997) were the first to explore this approach for seabirds by examining migratory dynamics in sooty shearwaters *Puffinus griseus* in the North Pacific. They noted that tissue $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ muscle values of immature shearwaters changed in time and space, and they associated these patterns to regions of the Pacific with areas of upwelling that were consistent with the migratory behavior of this species. More recently, the strong isotopic structure of marine food webs in the Southern Ocean, which show pronounced depletion especially in ^{13}C with latitude, has informed the analysis of movements of several species of seabirds once they departed from colonies (Quillfeldt et al. 2005, 2008, 2010, Cherel & Hobson 2007, Phillips et al. 2009, Roscales et al. 2011). For Cory's shearwater *Calonectris diomedea diomedea* breeding in the Mediterranean, Ramos et al. (2009a) provided an analysis of $\delta^{15}\text{N}$, $\delta^{13}\text{C}$, and $\delta^{34}\text{S}$ in flight feathers to reveal a spatiotemporal gradient in molt sequence which could ultimately be related to movements off western Africa during the non-breeding season.

The placement of individual seabirds to geographic regions using marine isoscapes in the absence of known persistent and major isotopic gradients remains a daunting task. However, recent research is encouraging. Stable-C isotope values in primary production are sensitive to ambient water temperature, and $\delta^{13}\text{C}$ values in tissues of sessile and migratory marine animals are well correlated with sea surface temperatures (Barnes et al. 2009, MacKenzie et al. 2011). This creates the possibility of producing year-specific marine isoscapes based on remotely-sensed water temperature. As our understanding of key mechanisms controlling the isotopic composition of primary productivity increases, our ability to construct marine isoscapes relevant to seabird studies will increase (Graham et al. 2010, Barnes et al. 2011). Finally, the combination of several assays in addition to tissue isotope values of consumers can result in greater resolution of placement. This was demonstrated by Gómez-Díaz & González-Solís (2007), who combined morphological, genetic, stable isotope, and trace element analyses to assign a suite of pelagic seabirds to origin.

Our ability to link stable isotope values with locations of birds at sea has been greatly enhanced by the recent development of spatial tracking devices such as geolocators (e.g. Jaeger et al. 2010b) or GPS tags (e.g. Votier et al. 2010). These devices provide information on movement patterns during the non-breeding season, as the birds move to isotopically distinct regions while they sequentially replace their

feathers (e.g. González-Solís et al. 2011). Shorter-term movements during foraging trips in the breeding season can be assessed with the combined use of tracking devices and stable isotope analysis of a tissue with shorter turnover such as blood (e.g. Rayner et al. 2010). However, regional marine isoscapes may not show sufficient structure over regions of interest to assign foraging locations. For example, seabirds breeding in the NE Atlantic did not show regional-scale biogeographic differences in stable isotope values despite inter-colony variation in feeding locations (Roscales et al. 2011). A major challenge in using tracked seabirds as a means of describing marine isoscapes is the fact that it is still difficult to tease out the isotopic effects of changes in diet and changes in baseline isotope values.

Compound-specific approaches

The vast majority of stable isotope investigations in ecological studies have used the isotopic measurement of bulk tissues (e.g. feather keratin, muscle, lipids, blood). Increasingly, there is interest in the isotopic composition of individual compounds such as AAs or FAs, which can now be measured through gas chromatographic isotope-ratio mass spectroscopy. Individual AAs show isotopic discrimination with TL, while others are invariant. The magnitude of isotopic discrimination associated with those AAs that do show TL effects appear to be constant. McClelland & Montoya (2002) determined that the difference in $\delta^{15}\text{N}$ between glutamate and phenylalanine in a consumer was 7‰ and could be used to estimate the relative trophic position of the consumer. Popp et al. (2007) used this approach by measuring $\delta^{15}\text{N}$ values of trophic (alanine, aspartic acid, and glutamic acid) and source (glycine, phenylalanine) AAs in yellowfin tuna *Thunnus albacares* to estimate tuna TL:

$$\text{TL} = 1 + (\delta^{15}\text{N}_{\text{Glutamic acid}} - \delta^{15}\text{N}_{\text{Glycine}})/7 \quad (3)$$

Should this relationship hold for marine food webs in general, this compound-specific approach will form a reliable means of determining trophic relationships and source of feeding in birds and will form the basis of a second generation of seabird trophic studies. However, recent investigations by Lorrain et al. (2009) on the isotopic composition of phenylalanine and glutamate in penguin blood suggest that the trophic enrichment factor between these AAs differs from 7‰, and more research is warranted.

While the laboratory analysis of individual compounds is involved and expensive, there are some

key advantages over bulk tissues with the next generation of trophic modeling. Chief among these is that such compounds often have well defined metabolic pathways that are well understood and which involve no or well-constrained isotopic discrimination (Evershed et al. 2007). The nature of metabolic routing of key dietary components strongly suggests that the current difficulty of high variance related to isotopic discrimination and routing can be overcome by adopting an isotopic compound-specific approach to deciphering animal diets by using stable isotopes (Federer et al. 2010). For AAs, it is now clear that some differ little in their $\delta^{15}\text{N}$ values through food webs, whereas others change dramatically. This appears to be unrelated to whether such AAs are essential or non-essential, but instead likely corresponds to the ease with which they exchange N during trans-amination events (Wolf et al. 2009). By evaluating which AAs are variant and invariant in seabirds, the isotopic measurement of individual AAs in seabirds and their food webs promises to provide a much more reliable trophic model. Advantages of the isotopic analysis of individual FAs is less clear but likely will relate to the establishment of invariant signatures of source. Moreover, by using FA isotope analyses, a more quantitative estimate of contributions of sources of primary productivity over the use of FA analyses alone may be possible (e.g. Budge et al. 2008).

Other isotopes

We have emphasized here the use of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ measurements in seabird dietary studies, but it is worth considering the potential use of isotopes of other elements. $\delta^{34}\text{S}$ measurements have been used to characterize source of food in a variety of marine organisms. This isotope can be very useful in segregating pelagic versus inshore or benthic food webs and is very useful for delineating estuarine versus marine habitats (Peterson & Fry 1987, Rubenstein & Hobson 2004, Hebert et al. 2008, Moreno et al. 2010). Bird feathers are a particularly useful material for $\delta^{34}\text{S}$ analysis because they contain high concentrations of this element.

In terrestrial systems, $\delta^2\text{H}$ and $\delta^{18}\text{O}$ measurements are especially useful for assigning birds to origins (Hobson & Wassenaar 2008). It has been assumed that these isotopes will be less useful in marine systems, where their values relative to the international standard, Vienna Standard Mean Ocean Water, are by definition 0. However, isotopes of these elements

are sensitive to temperature and freshwater influences in coastal regions and may prove to be useful components of marine isoscapes (see Schaffner & Swart 1991, Ramos et al. 2009b, Hobson et al. 2010). Finally, there are a host of heavier elements that have been poorly investigated, but which show promise in future seabird applications, especially those related to source of feeding or transport of contaminants. These include the isotopes of Pb (Stewart & Outridge 2003), Sr (Font et al. 2007, Hobson et al. 2010), and, more recently, Hg (Point et al. 2011). The improved availability of analytical instruments like inductively coupled plasma mass spectrometers will now accelerate research in these areas.

Analytical methods and nomenclature

Differences in analytical approaches may affect interpretation of isotopic data. Foremost among these is the issue of lipid extraction of tissues prior to analysis. Since lipids are more depleted in ^{13}C than other macromolecules, the differential presence of lipids in tissues can significantly affect tissue $\delta^{13}\text{C}$ values. Because lipids are typically metabolically routed to either lipid stores or to energy production, the removal of lipids from analyses allows isotopic interpretations based largely on proteinaceous pathways for most marine consumers without the confounding factor of variable lipid contents. Some debate over whether or how to remove lipids has emerged, since some lipid extraction approaches can result in slight changes to tissue $\delta^{15}\text{N}$ values, due to the loss of some proteins. One solution is to split samples and run half for $\delta^{13}\text{C}$ with lipid removal and the other half without lipid extraction for $\delta^{15}\text{N}$ measurements. Alternatively, one may use a *post hoc* correction for differential lipid content based on the elemental C:N ratio (e.g. Post et al. 2007, Logan et al. 2008, but see Oppel et al. 2010). Where seabird researchers are particularly interested in tissue $\delta^{13}\text{C}$ values, a lipid-free $\delta^{13}\text{C}$ value will be most useful. Importantly, seabird biologists should be careful when comparing isotope data among studies that have used different sample pretreatment protocols.

The measurement of $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ in organic materials is routine, with good agreement among most laboratories. However, the measurement of $\delta^2\text{H}$ and $\delta^{18}\text{O}$ is challenging, due to the fact that there are no internationally accepted standards for the measurement of non-exchangeable H in organic materials. Some laboratories have gone to great lengths to address this problem through the development of in-

house standards (Qi et al. 2011), but others have not paid enough attention to this issue, and researchers must be careful when comparing data for these elements on organic materials.

The reporting of analytical error associated with isotopic measurements also varies among authors. Ideally, researchers will quote both the results of within-run replicate measurements of appropriate organic standards that span the range of their unknowns and are of similar material, as well as the long-term statistics of these standards over numerous runs (Jardine & Cunjak 2005). Actual (‰) values of routine lab standards should be reported. Authors should refrain from reporting isotope measurements to more than 1 significant figure, since this is in keeping with actual measurement precision. Further recommendations on data reporting can be found in Bond & Hobson (in press).

Future directions

The typical lack of taxonomic information on seabird diets that are better evaluated through the use of stomach content and FA analysis does not detract from the continued use of stable isotope methods in seabird ecological studies. Rather, the strengths of the isotope approach are complementary to these other approaches. Isotopic assays of tissues within the same individual provide information on diet that spans temporal ranges over days to months prior to sampling. No other technique provides this deep archival or retrospective capability and, of course, such methods can be applied to historic (Hobson & Montevecchi 1991, Hobson et al. 2004, Becker & Beissinger 2006, Emslie & Patterson 2007, Norris et al. 2007), as well as contemporary seabird trophic investigations. Moreover, isotopic ratios integrate many behavioral and environmental events that ultimately describe the isotope space occupied by an individual and can be an appropriate means of examining competitive overlap and exclusion among individuals and populations (Bearhop et al. 2004, Newsome et al. 2007, Jaeger et al. 2009). The relative ease of sampling and laboratory analyses of the common stable isotopes of C, N, and S, together with the low cost of analyses, are powerful incentives to use isotopic assays in seabird dietary and ecological investigations. The following are some recommendations to move this field forward:

(1) Refinement of our understanding of the variance associated with tissue-specific isotopic discrimination factors that link seabirds to their diet. Studies

can be both field and laboratory based and can evaluate the effects of diet quality, growth stage, fasting, and environmental variables (Martínez del Río et al. 2009, Bond & Diamond 2011). Where considerable doubt remains about the validity of trophic models based on derived isotopic discrimination factors, researchers are encouraged to conduct sensitivity analyses using Bayesian-based mixing models.

(2) Trophic models based on isotopic differences between isotopically invariant and variant AAs need to be investigated further (Fig. 5). Continued research on the advantages of $\delta^{13}\text{C}$ and $\delta^2\text{H}$ analyses of individual FAs in seabirds and their eggs is also encouraged (Hobson 2011).

(3) Individual seabirds whose molt origins at sea have been established through independent means such as the use of satellite tags or geolocators must be sampled for isotopic assays. While spatial and temporal changes in diet need to be considered, the use of tissues from the tracked individuals will contribute to ground-truthing of marine isoscapes. Researchers should investigate isotopic measurements other than the more traditional $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and $\delta^{34}\text{S}$ assays. However, for those isotopes whose

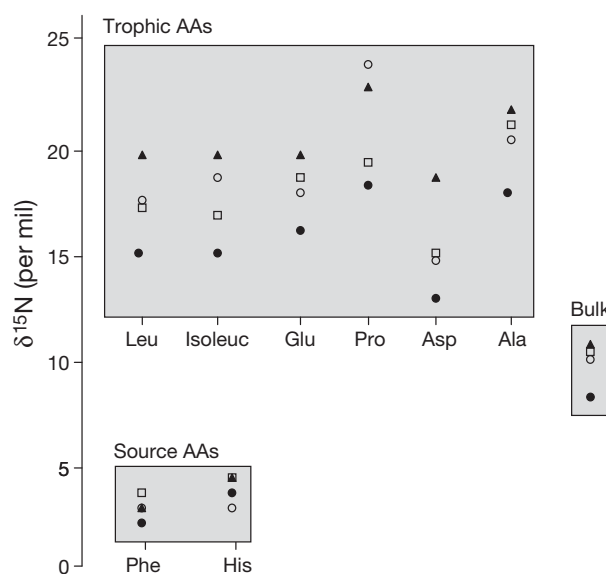


Fig. 5. Stable-nitrogen isotope values of individual amino acids (AAs) and bulk tissues of northern rockhopper penguin *Eudyptes chrysocome moseleyi* (○), southern rockhopper penguin *E. c. chrysocome* (●), king penguin *Aptenodytes patagonicus* (□), and Adélie penguins *Pygoscelis adeliae* (▲). Source AAs are relatively invariant between trophic level (TL) and can be used to track variation in baseline isotope food web samples, whereas trophic AAs are enriched in ^{15}N trophically. The difference between source and trophic AAs can be used to derive absolute trophic level in seabirds and other marine consumers (from Lorrain et al. 2009)

behavior in foodwebs is less certain (e.g. regarding isotopic discrimination within food webs, metabolic routing, etc.), emphasis should be placed on controlled studies using captive animals to first establish basic principles.

FATTY ACIDS

Background

FAs comprise the majority of lipids found in all organisms. Their great diversity, conservation of structure during digestion, biochemical restrictions to synthesis and modification, and in some cases unique origins among plants and animals, have fostered research ranging from elucidating phylogenetic patterns in metabolism and biosynthesis to determining food web structure in complex marine ecosystems. Several reviews provide extensive background on the origins, structure, analysis, and use of FAs in tracing trophic relationships (Dalsgaard et al. 2003, Iverson et al. 2004, Budge et al. 2006, Iverson 2009, Tollit et al. 2010). We focus on the most recent advances and new directions, as well as challenges to further developing these techniques.

All FAs are composed of chains of carbon atoms with associated hydrogen atoms, most commonly in even-numbered straight chains of 14 to 24 carbons with 0 to 6 double bonds, with a terminal methyl (-CH₃) end and a terminal carboxyl (-COOH) end. Double bonds are usually separated by a single methylene group (CH₂, i.e. methylene interrupted), and thus FAs are named by their carbon number: number of double bonds and location (n-x) of the double bond nearest the terminal methyl group (the position of which is conserved), with all other double bond positions known to occur accordingly (e.g. 18:3n-3). In rare cases, FAs can also be non-methylene interrupted and are named instead with each double bond position identified by Δ relative to the carboxyl end (e.g. 20:2 Δ 5,11). The array of FAs in marine ecosystems is complex, with about 70 FAs routinely identified in any given organism or tissue (Iverson 2009). Several characteristics of FAs and their storage patterns make them very useful tracers of predator diets and marine foodweb structure (e.g. Cook 1996, Budge et al. 2006, Iverson 2009).

(1) Organisms are limited in their ability to biosynthesize, modify chain length, and introduce double bonds in FAs. Most biosynthesis of unique FAs occurs in primary producers and ectothermic consumers at the bottom of the food chain, whereas limitations in

these processes are most pronounced with increasing phylogenetic order, culminating in endothermic, non-ruminant vertebrates. Additionally, the propensity in endotherms, such as seabirds, for modifying FAs, even if the capacity exists, is greatly reduced when FAs are abundant, such as in prey inhabiting marine ecosystems.

(2) Unlike dietary proteins and carbohydrates, which are completely broken down during digestion, FAs are generally not degraded unless used immediately for energy. Instead, FAs are released from ingested lipid molecules (principally dietary triacylglycerols [TAG] but also wax esters [WE] from some prey), and are taken up into adipose tissue and reintegrated into TAG for storage in a conservative manner.

(3) Animals have a large capacity to store fat, which can be subsequently or alternately mobilized for short- or long-term energy demands. Thus, ingested FAs bioaccumulate in predator fat stores, principally adipose tissue. Thus, sampling predator fat storage reservoirs allows examination of the integration of FA ingestion over time.

In seabirds, the key lipid reservoirs and those most directly influenced by diet are adipose tissue and, in procellariiforms (e.g. albatrosses, shearwaters, fulmars, petrels), also stomach oils. Adipose tissue represents the integration of FAs from diet over time, after having undergone digestion and some metabolic processing. In contrast, stomach oils are produced from recent prey lipids ingested via a unique anatomical and physiological process (Roby et al. 1989), and have not been digested and have undergone minimal metabolic processing (Wang et al. 2007, Richoux et al. 2010). Although dietary FAs can also be isolated from blood, overall blood FA component is dominated by FAs produced endogenously, unless the bird has very recently (i.e. within hours) consumed a meal. In the latter case, the FAs from diet are carried for a short time in portomicrons (large triglyceride-rich lipoproteins) prior to uptake by tissues, which must be isolated from the other blood lipids to examine dietary FA intake from the last meal only (e.g. see Cooper et al. 2005).

Qualitative approaches to investigation of foraging patterns

FAs can be used to study trophic relationships and food webs of seabirds in several ways, with interpretations depending on the tissue sampled. The most common approaches—and with the longest history by far—are using FAs qualitatively or semi-quantita-

tively to examine empirically determined differences among predators in levels of specific FAs or in complete arrays of FAs (FA signatures; Iverson 1993), which indicate differences in diet(s) among individuals, populations, and species. Additionally, if something is known about unique or unusual FA characteristics or ratios of specific FAs in certain prey, it may then be possible to attribute the predator differences to consumption of specific prey, especially if there is other evidence available from traditional diet analyses (e.g. stomach contents) or from stable isotope information. Specific FAs have been referred to as 'biomarkers' for distinguishing certain food sources, e.g. by differentiating primary producers and bacteria, indicating certain primary consumers such as copepods, identifying markers of carnivory, or distinguishing terrestrial versus marine sources (e.g. Fig. 6; reviewed by Dalsgaard et al. 2003, Budge et al. 2006, Iverson 2009).

While unusual levels of certain FAs or ratios among FAs can sometimes be attributed to only 1 or a few prey types and thus indicate their importance in the diet of a consumer, this possibility is rare in higher TL predators such as seabirds. FAs originating at the base of the food web become ubiquitous throughout higher levels, and as TLs increase, the ability to use a single FA or ratio of FAs to trace feeding to a specific food type is greatly reduced. Thus, in higher predators such as seabirds, there are few 'biomarker' FAs, which by definition should be unique to only a single or several prey items and traceable directly to con-

suming that prey. Although it may be easier to trace diet items using marker FAs or ratios in seabirds that feed on primary consumers (e.g. least auklets, Fig. 6) than in piscivores, there may still be the problem of most prey items sharing a similar suite of FAs (albeit at differing levels, depending on the prey type and species). However, in the unique case of procellariiforms, another compound at the whole lipid level can be used as a type of biomarker. Only certain prey species synthesize and store FAs in WE rather than as TAG, and in some ecosystems, WE may be confined to only 1 or a few prey species (e.g. copepods, myctophids). Since procellariiform stomach oils have not undergone digestion, the presence of WE can be used as confirmation of consumption of those prey species that make WE, and also provides the opportunity to examine different time scales of dietary integration by comparing with FAs in adipose tissue TAG, which represent consumption over a longer time frame (Wang et al. 2007, Iverson 2009).

Despite the various limitations discussed above, evaluating variation in FAs and FA signatures among individuals and populations of seabirds remains a promising, qualitative, way to investigate trophic interactions and to detect dietary differences. Differences in FA patterns among individuals and populations translate directly to differences in dietary intake, even if that dietary intake is not fully elucidated. For instance, FAs have been used in such qualitative or semi-quantitative ways to investigate spatial and temporal differences in foraging patterns as well as to confirm general resource use of a number of seabird species (e.g. Dahl et al. 2003, Connan et al. 2005, Iverson et al. 2007, Käckelä et al. 2007, 2010, Springer et al. 2007, Karnovsky et al. 2008, Williams et al. 2008, Wang et al. 2009, Ronconi et al. 2010). When such FA patterns are used in combination with other diet information (e.g. direct observation, stomach contents, stable isotopes), results are compelling (e.g. Connan et al. 2007, Iverson et al. 2007, Springer et al. 2007, Karnovsky et al. 2008, Ronconi et al. 2010). This qualitative use of FAs provides valuable information that is likely not possible to obtain otherwise, but, it will generally not allow specific interpretation of seabird diet composition.

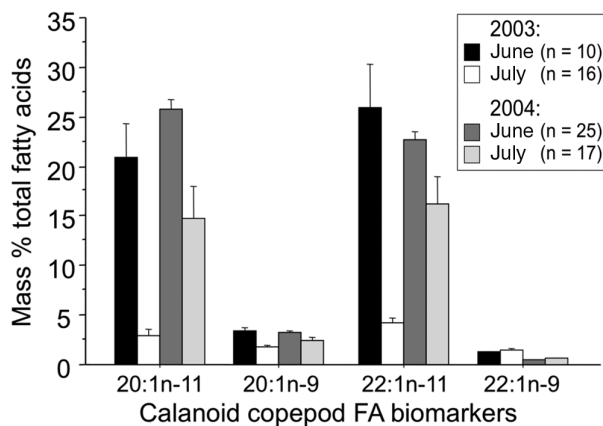


Fig. 6. *Aethia pusilla*. Copepod fatty acid (FA) biomarkers (mean \pm SE) in adipose tissue from adult least auklets in the 2003 and 2004 breeding seasons on St. Paul Island, Alaska (USA). The high levels of these biomarkers in early June of both years indicate that copepods had been abundantly available for several weeks. By July in both years, the decline in these FAs was consistent with the relative timing of the decline of copepods documented in each year, and illustrates the sensitivity of FA signatures to changes in diet, which indicate environmental changes. Data from Springer et al. (2007)

Quantitative estimation of diets

The existence of clearly distinguished patterns of FAs (FA signatures) among different prey species or types in a given ecosystem (e.g. Budge et al. 2002, Iverson et al. 2002, Piche et al. 2010), combined with

the understanding that FAs are predictably deposited in predator adipose tissue, raises the possibility of quantifying diets by determining the most likely mixture of prey signatures that could account for the predator's FA signature. This is the area of greatest current interest and innovation (Iverson 2009). Quantitative FA signature analysis (QFASA; Iverson et al. 2004) is a first-generation statistical tool developed to determine the weighted mixture of prey species FA signatures that most closely resembles that of the predator's FA stores, thereby inferring its diet. With comparable underpinnings, QFASA is in principle similar to mixture models developed for stable isotopes (e.g. Phillips & Koch 2002, Phillips & Gregg 2003). Assuming appropriate sampling of predator and prey lipids (reviewed by Budge et al. 2006, Iverson 2009), QFASA proceeds by applying experimentally derived weighting factors (calibration coefficients, CCs) to individual predator FAs to account for the effects of predator metabolism on FA deposition. It then takes the average FA signature of each prey species (or group), and estimates the mixture of prey signatures that comes closest to matching that of the weighted predator's FA stores by minimizing the statistical distance between that prey species mixture and the weighted predator FA profile. Lastly, this proportional FA mixture is weighted by the fat content (i.e. relative FA contribution) of each prey species to estimate the proportions of each prey in the predator's diet (Iverson et al. 2004).

The use of CCs to account for imperfect mixing of all ingested prey FAs into adipose tissue due to metabolism effects in the predator overcomes some of the problematic assumptions of complete dietary mixing as in the early isotopic mixing models (see 'Stable isotopes: mixing models'). CCs are determined from captive validation studies in which a predator consumes a single diet over a period long enough for complete FA turnover, assuming then that the FA signature of the predator's lipid stores will resemble the diet FA signature as much as possible and any differences can be attributed to metabolic processing of individual FAs. To date, seabird adipose tissue CCs have been estimated in chicks of common murrets and tufted puffins *Fratercula cirrhata* and in adults of Steller's eiders *Polysticta stelleri*, spectacled eiders *Somateria fischeri* and yellow-legged gulls *Larus michahellis* (Iverson et al. 2007, Williams et al. 2009, Wang et al. 2010, Käkälä et al. 2010). Although the CCs estimated from the various studies share many similarities (including some similarities with CCs determined for marine mammals; Iverson 2009), it is not yet known whether differences

are due to species, age (adult versus chick), feeding regime, and/or study effects. Additionally, while CCs are critical to the accurate performance of QFASA, they remain a relatively simple mathematical attempt to describe potentially complex biochemistry. Thus, further captive validations will be extremely useful in advancing this aspect of QFASA. Additionally, Wang et al. (2007) proposed the possibility of using stomach oil FAs in procellariiforms to estimate adipose tissue CCs in the same individuals if on long-term constant diets (i.e. using stomach oil as proxy for prey), since little to no metabolic processing appears to have occurred. Alternatively, Wang et al. (2007) suggested the potential for using stomach oil FAs directly without CCs to estimate recent diet using QFASA.

Besides CCs, perhaps the next most important issue to using QFASA is building an appropriate and comprehensive prey database and sampling all species sufficiently to allow quantitative evaluation of within- and between-species variability to confirm the ability to reliably differentiate prey species in the QFASA model (e.g. Iverson et al. 2004, Budge et al. 2006, Iverson 2009). Depending on the ecosystem and logistics, this can be a daunting task. Additionally, depending on the complexity of the array of prey species and shared ecology, it is unlikely that all individual species in an ecosystem can be differentiated from one another based on their FA signatures. Thus, the onus is on the researcher to make decisions based upon empirical evidence, testing, and evaluation of potential confounding of prey species and which species to include, exclude, or group based on ecological equivalence and taxonomy (e.g. Piche et al. 2010). This is also where the use of multiple tools in diet analyses can be extremely informative (see also 'Future directions' below).

The other issues that remain important for interpretation of seabird diets using FA signatures include which FA subset should be used in the QFASA model. Not all FAs provide information on diet, and certainly FAs that provide no link to diet should be removed (see Iverson et al. 2004). Beyond that, the FA subset to use will also depend on accuracy of measurements and confidence in trace FA measurement, as well as reliability with which CCs for specific FAs are measured. Secondly, a better understanding is needed of the time frames of FA turnover in fat stores and thus the time frame of dietary history they represent. Several controlled studies have been conducted that begin to address this in seabirds (Williams et al. 2009, Wang et al. 2010). However, how these time frames differ during periods of fat storage versus high-energy use is not known. The pre-

cise time frame of food consumption that stomach oils represent is also unclear. Despite these issues, QFASA estimates of diet have now been validated in captive common murre and red-legged kittiwake *Rissa brevirostris* chicks and adult Steller's and spectacled eiders in diet trials involving relatively simple diet mixtures (3 to 5 prey species; Iverson et al. 2007, Wang et al. 2010). Although, in principle, diet estimates using QFASA versus stomach content analyses would not be expected to be identical, given the different time frames they represent and other method-associated biases, the comparison of both can prove informative and has served as validation of QFASA in free-ranging adult common murres, thick-billed murres, red-legged kittiwakes, and black-legged kittiwakes involving a complex ecosystem-wide mixture of prey species (Fig. 7; Iverson et al. 2007).

Future directions

The original QFASA model of Iverson et al. (2004) is a first-generation mixing model, which explicitly incorporates information on predator metabolism and prey fat content into the statistical estimation

procedure. As stated above, the current model has several absolute requirements, which need to be further evaluated and verified. In addition to these issues are those of the evolution, refinement, and improvement of the QFASA model. The following include recommendations in advancing the use of FAs to understand seabird diets.

Further evaluation of QFASA model components

(1) Prey FA catalogues or 'libraries' are required for the modeling of any predator diet, but these cannot just be collections of prey that are blindly included in model estimations. Prey FA signatures not only differ across species, but can also vary within species over spatial and temporal scales or within demographic groups such as in juveniles and adults that have different feeding patterns (e.g. Iverson et al. 2002). This variation must be investigated to determine the actual effect on diet estimates using QFASA and hence the creation of appropriate within or among prey species separations or groupings. Additionally, given the onerous task of building any prey database for a given predator, collaboration among researchers

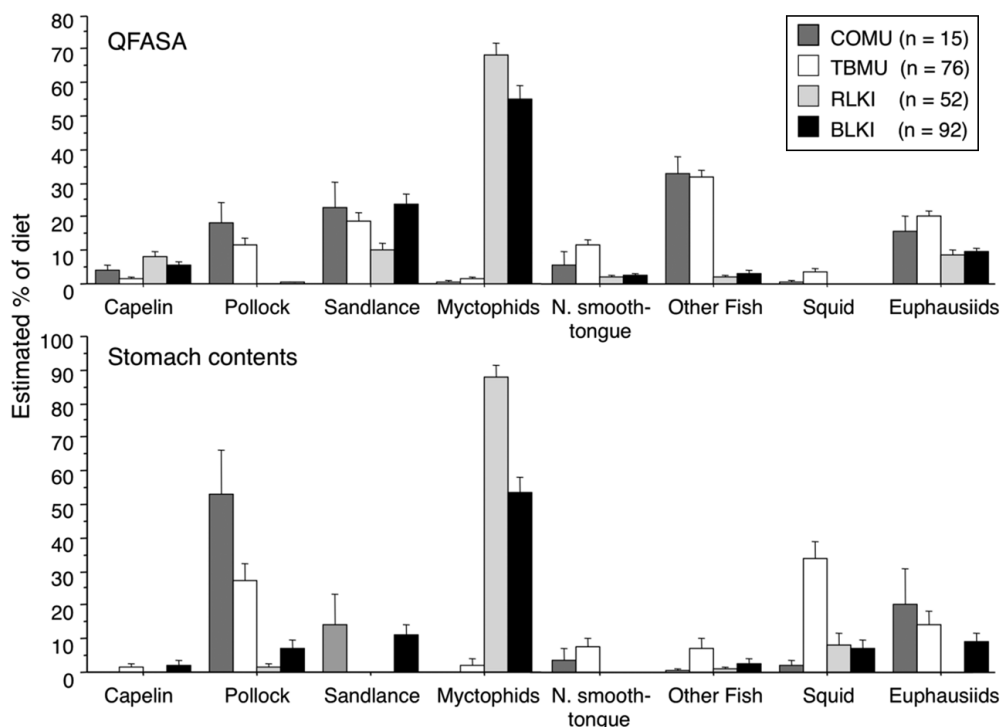


Fig. 7. Diet estimates of free-ranging common and thick-billed murres (COMU, TBMU) and red- and black-legged kittiwakes (RLKI, BLKI) ($n = 235$) in the Bering Sea using quantitative fatty acid signature analysis (QFASA) modeled on 161 prey representing 15 species, in comparison with stomach content analysis in the same individuals (mean \pm SE). Only prey species appearing in diet estimates are presented. Reproduced from data in Iverson et al. (2007)

to develop a global reference database of prey FA signatures across different studies that span different ecoregions and time scales would greatly aid the advancement and use of QFASA.

(2) Further captive validation studies to determine CCs across species continue to be of paramount importance. The outputs of the QFASA model are extremely sensitive to the CCs used and a better understanding or refinement of the effects on CCs of species, age (i.e. adults versus growing chicks), and diet (e.g. high versus low fat; prey with widely different FA signatures) would improve the application of QFASA to estimating diets. Such studies will also be important for improving determination of the time frame that estimated diets represent in seabirds.

(3) Finally, through the above-mentioned further captive validation studies, a refinement in determination of the most appropriate FA subsets to use in QFASA will improve the accuracy of diet estimates.

Advanced FA mixing models

The current QFASA model provides point estimates of diet, using average prey FA signatures, with the large amount of variability in prey FA profiles captured using a bootstrapping procedure to compute standard errors for diet composition vectors (Iverson et al. 2004). In subsequent work, Stewart (2005) developed a means to produce interval estimates of diet, exploring alternative ways to summarize prey by random sampling and re-sampling, and also exploring a means of estimating goodness of fit with compositional data. However, in both methods, no other prior information was incorporated in the mixing models. Most recently, effort has been focused on developing a Bayesian approach to the mixing model, which allows for incorporation of prior information on diet composition and prey FAs when available and, perhaps more importantly, gives an accurate account of uncertainty (Blanchard 2011). Additionally, it allows diet estimations to be made at both the population level as well as with the individual predator. The Bayesian method provides more accurate diet estimations when using synthetic data sets. However, in real predators, the multicollinearity of prey FAs—that is, where prey species have similar FA compositions—remains an issue (Blanchard 2011). Strategies for dealing with this issue are discussed, but clearly, explicitly incorporating more prior information from other sources should improve the accuracy of diet estimates.

FA-stable isotope-specific analyses

As discussed previously, like FAs, stable isotope signatures are transferred in largely predictable ways from the diet to the predator. But isotopically distinct dietary sources do not always exist and there can also be multicollinearity in prey FAs among species. To deal with such issues in both methods, the possibility of coupling the analysis of FAs and stable isotopes should be a new frontier in elucidating diet. That is, by analyzing the stable isotopes of individual FAs, we may better be able to trace FA patterns to prey at various TLs and perhaps incorporate such information into various mixing models. This was demonstrated in a preliminary study by Budge et al. (2008), which allowed the use of mass balance calculations to estimate the contributions of ice algae versus water-column phytoplankton to sequentially higher TLs, culminating in seabirds and marine mammals. This accomplishment could not have been possible using FA signatures alone. Given the success of this attempt to trace carbon sources from the very bottom to the very top of a food web, it should be possible to use such a combination of techniques to answer more simple questions in differentiating direct prey species of seabird predators.

CONCLUSIONS

While each of the 3 techniques for determining seabird diets and ecological position can be used on its own, when they are applied in combination, oftentimes the limitations inherent in each of the techniques can be overcome. For example, traditional stomach content analysis can be used to validate shifts in diets determined from stable isotope or FA analysis. Likewise, stable isotope and FA analysis can be used to confirm dietary patterns suggested by stomach content findings. Karnovsky et al. (2008) found that little auks shift their TL up in the fall; their FAs then resembled the signatures of black-legged kittiwakes, and their stomach contents included prey that were found only in those species at that time of year. In a similar fashion, Connan et al. (2010) combined all 3 techniques to reveal that provisioning Tasmanian short-tailed shearwaters *Puffinus tenuirostris* feed in Antarctic waters (stable isotope analysis) on myctophids (FA) when self-feeding, which is in contrast to the euphausiid-dominated diets they collected for chicks.

A significant challenge in combining several analytical techniques to examine seabird diet and

the source of feeding clearly is the statistical integration of disparate information. Currently, Bayesian and likelihood methods of examining this question seem best suited to the use of probabilistic models. Such approaches will allow the use of informative priors to guide model estimates. For example, stomach content data can be used to inform stable isotope and FA model estimates (Moore & Semmens 2008). Likewise, Polito et al. (2011) found that Bayesian isotope mixing models could not estimate the fish component of penguin diets accurately without incorporating the results of stomach content analysis. They used the estimates of the relative contribution of specific fish species with similar TLs to refine their 2-source isotopic mixing model. Application of stomach content analysis alone underestimated the biomass contribution of fish to the penguin diets, which were better assessed using stable isotope analysis. Their study showed how integrating the 2 methods greatly enhanced their ability to quantify penguin diets through the use of Bayesian mixing models (Polito et al. 2011).

In addition to enhancing understanding of shifts in oceanographic conditions through the study of seabird diets, these data are critical for the development of conservation strategies for seabirds. For example, Ramos et al. (2011) were able to predict how management strategies would impact different colonies of yellow-legged gull *Larus michahellis*, through an inter-colony comparison of stable isotopes in feathers. Critically endangered Balearic shearwaters *Puffinus mauretanicus* showed geographic variation in stable isotopes of feathers, which gave support for particular foraging areas to become Marine Protected Areas (Louzao et al. 2011). Maranto et al. (2011) used FA biomarkers to identify the colony origins of terns killed at inland dams as part of a lethal control program meant to protect juvenile salmonids. Their results showed that the birds feeding at the dams were not of local origin so extirpation of the colony closest to the dam would not be effective in protecting salmonids (Maranto et al. 2011).

We are confident that the next decade will see the formal development of such multiple-technique approaches to seabird dietary studies within a strong analytical framework. More and more, we are also witnessing the use of multiple tools together to answer fundamental questions related to diet and source of feeding. Rather than relying on a single tool, such studies provide a 'weight of evidence' approach to dietary investigations.

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Use of molecular genetics for understanding seabird evolution, ecology and conservation

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ABSTRACT: Information on genetic variation within and among populations of highly mobile organisms such as seabirds is necessary for understanding their evolution and ecology, and can be a tool for conservation. Recent developments in molecular genetics, including efficient mutation-detection methods and automated sequencing, are providing detailed genetic information for non-model organisms. Furthermore, theoretical advances such as coalescent theory and molecular assignments are providing powerful tools to determine species' historical and contemporary abundance, distributions and movements. We review advances for studying phylogenetics, population genetics, hybridization, ecology and conservation in seabirds and summarize recent studies in each field. All fields will benefit from larger data sets and more sophisticated analytical methods. Phylogenetic studies will provide a more robust determination of evolutionary history, while studies of population genetics and hybridization will be elevated to genomic-level avenues of inquiry. Ecological studies may benefit from improved molecular assignments, and conservation-focussed studies will benefit from an increased understanding of seabird evolution and ecology. In addition, we highlight that combination of new molecular and analytical tools with data on morphology, behaviour and movements is especially powerful for understanding seabird evolution and ecology, and for aiding conservation.

KEY WORDS: Gene flow · Hybridization · Molecular assignments · Population genetic structure · Phylogeography · Phylogenetics · Population size · Review

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INTRODUCTION

If you are interested in evolution and ecology, why study seabirds? As a group, seabirds possess a number of extreme life history characteristics that make them particularly good model organisms for DNA-based research into evolution and ecology: they can travel great distances, thus violating assumptions of many population divergence and speciation models, yet they generally exhibit natal philopatry (return to the site of birth to reproduce); and, although their breeding sites can be difficult to access, seabirds generally breed in large colonies from which sufficient samples can be collected for robust genetic analyses. Additionally, seabirds tend to be behaviourally complex, and their reliance on the marine environment makes them good candidate species

to study in relation to climate change and other anthropogenic effects. This review explores uses of molecular genetics for understanding seabird evolution and ecology, and highlights the usefulness of this research to understanding broader evolutionary and ecological questions.

Early studies of morphology, behaviour and ecology of seabirds provided much information on their evolution, including estimates of genetic relationships among populations, species and higher taxa (e.g. Storer 1952, van Tets 1965, Nelson 1970, Strauch 1985, see also review by Schreiber & Burger 2002). However, the genetic basis of morphological and behavioural characters is generally unknown, and inferences are limited to patterns, rather than ecological and evolutionary processes. Subsequently, molecular tools such as protein electrophoresis and

DNA–DNA hybridization provided more direct information on population genetic structure, hybridization and phylogenetic relationships (e.g. Sibley 1970, Sibley & Ahlquist 1990). For example, protein electrophoresis revealed the very close genetic related-

ness of some *Larus* spp. (white-headed gull; Snell 1991), and indicated that Atlantic puffins *Fratercula arctica* from different colonies are genetically similar, despite significant differences in body size (Moen 1991).

Table 1. Summary of 2nd and 3rd generation DNA sequencing methods and platforms

Method	Description	Cost
2nd generation (next generation)		
454 pyrosequencing	Parallelized version of pyrosequencing Pyrosequencing uses luciferase to generate light for detection of individual nucleotides added to the growing DNA strand Uses emulsion PCR (DNA amplified inside water droplets; each droplet contains 1 DNA template attached to 1 primer-coated bead, which forms a clonal body) DNA can be extended >1 nucleotide at a time	Cheaper than Sanger sequencing; shorter read length than Sanger, longer than Illumina and SOLiD
Illumina (Solexa)	Sequencing based on reversible dye-termination DNA molecules attach to primers on a slide — causes formation of local clonal bodies (bridge PCR) Four types of reversible terminator bases added to reaction, nucleotides that are not incorporated are washed away Images taken of the fluorescently labeled nucleotides Dye and terminal 3' blocker chemically removed — allows next cycle to begin DNA only extended by 1 nucleotide at a time	Cheaper than 454 pyrosequencing, similar price to SOLiD; shorter read length than both Sanger and 454
SOLiD	Sequencing by ligation DNA amplified by emulsion PCR before sequencing Resulting beads (each contains only copies of the same DNA molecule) deposited on slide Pool of oligonucleotides of fixed length labeled according to sequenced position; annealed and ligated Preferential ligation for matching sequences produces signal informing nucleotide at that position	Cheaper than 454 pyrosequencing, similar price to SOLiD; shorter read length than both Sanger and 454 pyrosequencing, comparable read length to Illumina
3rd generation (next-next generation)		
Ion semiconductor	Sequencing based on detection of hydrogen ions released during DNA polymerization, rather than optical methods System uses a microwell plate (different DNA in each well), wells are flooded with a single type of nucleotide, if nucleotide incorporates a hydrogen ion, it is released and read as the correct base Multiple bases can be added simultaneously if they are the same type	Cheaper and faster than any 2nd generation platform, similar read length to 454 pyrosequencing,
DNA nanoball	Rolling circle replication amplifies small fragments of genomic DNA into DNA nanoballs Sequencing by ligation (unchained) used to determine nucleotide sequence	Low cost compared to other methods, but short read lengths
Helioscope™ single molecular	Extension based sequencing (1 nucleotide at a time as with Sanger sequencing) Uses DNA fragments with added poly-A tail adaptors Cyclic washes with fluorescently labeled nucleotides occur, and reads are performed by Helioscope sequencer	Low cost compared to other methods, but short read lengths
Single molecular real time (SMRT™)	Sequencing by synthesis approach with unmodified polymerase and fluorescently labeled nucleotides	Relatively low cost; 1000 bp read lengths

Table 2 (this and following page). Summary of computer programs for analysis of molecular data, modified from Tables 1 & 2 in Excoffier & Heckel (2006), with the addition of programs for phylogenetic and ecological investigations. POPG, population genetics; POPD, population dynamics; HYB, hybridization; PHY, phylogenetics. MULT, multi-allelic markers (no specific mutation model assumed); DNA, sequence data; STR, short tandem repeat also known as microsatellites (stepwise mutation assumed); hapSTR, linked SNP and STR markers; SNP, single nucleotide polymorphism; FREQ, frequency data; AFLP, amplified fragment length polymorphism; DIST, distance matrix; RAPD, random amplified polymorphic DNA

Program	Discipline	Functions	Data type	Platform	Source
Structure	POPG, POPD, HYB	Uses genotypes from multiple markers to determine underlying genetic structure among a set of individuals; can detect immigrants; use in assignment studies	MULT	Java	Pritchard et al. (2000)
NewHybrids	HYB	Designed for the analysis of a single hybrid population; samples can only come from 2 parental populations	MULT	Windows, Linux	Anderson & Thompson (2002)
IM, IMA, IMA2	POPG, HYB	Isolation model testing; multiple versions with migration, 2 population model can estimate divergence time, ancestral population size, divergence time, and migration	DNA, STR, hapSTR	DOS, MacOS	Nielsen & Wakeley (2001), Hey & Nielsen (2004, 2007)
DIYABC	POPG, HYB	Make inferences based on Approximate Bayesian Computation; graphical interface	STR	Windows, Linux	Cornuet et al. (2008)
Migrate	POPG, POPD, HYB	Estimates the effective population sizes and migration rates of 2 constant populations using non-recombining sequences, microsatellite data, or enzyme electrophoretic data	DNA, SNP, STR, MULT	DOS, MacOS, Linux	Beerli & Felsenstein (1999) Beerli & Palczewski (2010)
Bayes Ass+	POPG	Uses multilocus genotypes to estimate contemporary migration between populations	MULT	Windows, MacOS, Linux	Wilson & Rannala (2003)
Cfit	HYB	Fits genotypic and phenotypic data to equilibrium cline models	MULT	Windows	Gay et al. (2008)
ClineFit	HYB	Fits genotypic data to equilibrium cline models	MULT	Windows, MacOS	Porter et al. (1997)
BAPS	POPG	Assigns individuals to genetic clusters; can consider them immigrants or descendants from immigrants	MULT	Windows	Corander et al. (2003, 2004)
GeneClass2	POPG	Uses multilocus genotypes to assign individuals to populations and detect immigrants	MULT	Windows	Piry et al. (2004)
Geneland	POPG	R package that takes into account spatial positions of individuals when detecting population subdivisions	MULT	R	Guillot et al. (2005)
Arlequin	POPG	Multi-use population genetics software environment; computes indices of genetic diversity, F -statistics, Hardy-Weinberg Equilibrium, etc.	DNA, SNP, STR, MULT, FREQ	Windows	Excoffier et al. (2005)
DnaSP	POPG	Estimates several measures of DNA sequence variation within and between populations including linkage disequilibrium, recombination, gene flow and gene conversion	DNA, SNP	Windows	Librado & Rozas (2009)
FSTAT	POPG	Multiple functions – F_{ST} estimates, etc.	STR, MULT	Windows	Goudet (1995)
GDA	POPG	Multiple functions; basic indices of genetic diversity	AFLP, MULT	Windows	Lewis & Zaykin (2002)
Genepop	POPG	Multiple function; basic indices of genetic diversity	STR, MULT	DOS	Raymond & Rousset (1995)
GENETIX	POPG	Multiple function; basic indices of genetic diversity	MULT	Windows	Belkhir et al. (1996–2004)
MEGA	POPG	Multiple function; basic indices of genetic diversity	DNA, DIST	Windows	Tamura et al. (2011)
MSA	POPG	Multiple function; basic indices of genetic diversity	STR, MULT	DOS, MacOS, Linux	Lipman et al. (1989)
SPAGeDi	POPG	Computes genetic distance between populations, inbreeding, kinship, relatedness	STR, MULT	DOS, Windows, MacOS, Linux	Hardy & Vekemans (2002)
BATWING	POPG	Generation Bayesian inference, demographic history, population splits	STR, SNP	DOS, MacOS, Linux	Wilson & Rannala (2003)
COLONISE	POPG	Uses multilocus genotypes to study patterns of colonization events in population histories	MULT	Windows	Foll & Gaggiotti (2005)

(continued on next page)

Table 2 (continued)

Program	Discipline	Functions	Data type	Platform	Source
LAMARC	POPG	For estimating the historical demographics of a number of populations	DNA, SNP, STR	DOS, MacOS, Linux	Kuhner (2006)
MSVAR	POPG	For estimating the historical demographics of a number of populations (expansions and bottlenecks)	STR	DOS, Linux	Beaumont (1999)
Hickory	POPG	Software for analysis of geographic structure in genetic data. Estimates F-statistics from dominant or co-dominant marker data	AFLP, RAPD, MULT	Windows, Linux	Holsinger (1999)
BOTTLENECK	POPG	Detects recent effective population size reductions	MULT	Windows	Cornuet & Luikart (1996)
GENETREE	PHY	Phylogeny reconstruction	DNA	DOS	Griffiths & Tavaré (1994)
PARENTE	POPD	Paternity analysis of genetic data	STR, SNP	Windows	Cercueil et al. (2002)
CERVUS	POPD	Paternity analysis of genetic data	STR, SNP	Windows	Marshall et al. (1998)
PATRI	POPD	Paternity analysis of genetic data	STR, SNP, RFLP	Windows, Linux	Nielsen et al. (2001)
PROBMAX	POPD	Paternity analysis of genetic data	STR, SNP	DOS	Danzmann (1997)
BAlI-Phy	PHY	Phylogeny reconstruction	DNA		Redelings & Suchard (2005)
BayesPhylogenies	PHY	Phylogeny reconstruction	DNA		Page & Meade (2004)
BEAST	PHY	Phylogeny reconstruction	DNA		Drummond & Rambaut (2007)
BUCKy	PHY	Phylogeny reconstruction	DNA		Ané et al. (2007)
Mesquite	PHY, POPG, POPD	Phylogeny reconstruction	DNA		Maddison & Maddison (2011)
MrBayes	PHY, POPG	Phylogeny reconstruction	DNA		Huelsenbeck & Ronquist (2001)
PAML	PHY	Phylogeny reconstruction	DNA	Windows, Unix, Linux, MacOS	Yang (1997)
PAUP*	PHY	Phylogeny reconstruction	DNA	Windows, Unix, MacOS	Swofford (2002)
PHYLIP	PHY	Phylogeny reconstruction	DNA	Windows, DOS, MacOS	Felsenstein (1989)
TOPALi	PHY	Phylogeny reconstruction	DNA	Java	Milne et al. (2004)
Treefinder	PHY	Phylogeny reconstruction	DNA	Java	Jobb et al. (2004)

Increasingly sophisticated DNA-based technologies, especially sequencing methods (Table 1), in combination with new approaches to data analysis (Table 2; Excoffier & Heckel 2006) are now allowing researchers not only to infer genetic relationships among populations and species, but also to address previously intractable questions in both evolution and ecology (Table 3, Fig. 1). Topics now accessible to researchers include (1) rediscovery of species thought to be extinct (e.g. Steeves et al. 2010), (2) identification of speciation events driven by mechanisms previously thought to be improbable (e.g. Friesen et al. 2007a), (3) coevolutionary dynamics of seabirds, their parasites and their immunogenetics

(e.g. McCoy et al. 2005a, Bollmer et al. 2007), (4) understanding why some seabirds exist as highly differentiated populations while others exhibit little genetic differentiation across large distances (e.g. Morris-Pocock et al. 2010, Taylor et al. 2010a; see also review by Friesen et al. 2007b), (5) estimates of historical and contemporary population sizes and movements (e.g. Peery et al. 2008, Boessenkool et al. 2010), and (6) definition of population units for conservation (e.g. Friesen et al. 2005). Additionally, the developing field of ecological genomics (Dupont et al. 2007, Mitchell-Olds et al. 2008, Stapley et al. 2010) is enabling researchers to determine the genetic underpinning of morphological and physiological

Table 3. Potential advances in major sub-disciplines of marine ornithology due to advances in molecular genetics, in particular new sequencing technology and new analytical techniques

Sub-discipline	Advance
Phylogenetics	Genome-level phylogeny construction Larger marker sets Community phylogenetics
Population genetics	Larger marker sets Population genomics Gene expression studies Multispecies approaches Seascape genetic approaches
Hybridization	Larger marker sets Hybridization genomics Candidate genes for reproductive isolation Gene expression studies
Ecology	Demographic estimate accuracy Genetic basis of sexual traits and signaling Movement and local adaptation Genetics of adaptation
Conservation	Higher accuracy molecular assignments Functional differences between populations (gene expression) Disease screening, toxicology

variation in a number of taxa (e.g. McCracken et al. 2009, Sætre & Sæther 2010, Schluter et al. 2010) including seabirds (e.g. Baião et al. 2007).

Advances in other taxa are highlighting key areas of research relevant to the study of seabird evolution and ecology, particularly advances in avian model systems like the *Ficedula* flycatchers (Sætre & Sæther 2010). Thus, research is coming full-circle, with molecular studies providing insight into the genetic basis of morphological and behavioural characters that were once used to infer the genetic relationships among populations and species. As sequencing technology improves and costs decrease, the development of genomic resources for seabirds will also play an increasing role in seabird conservation (Frankham 2010). These advances are particularly timely, as many species are listed as threatened or endangered, global fish stocks continue to decline, and numerous, generally unknown, consequences of climate change are set to impact many seabirds (Grémillet & Boulinier 2009).

Here we review molecular genetic methods for studying seabird evolution and ecology, and then

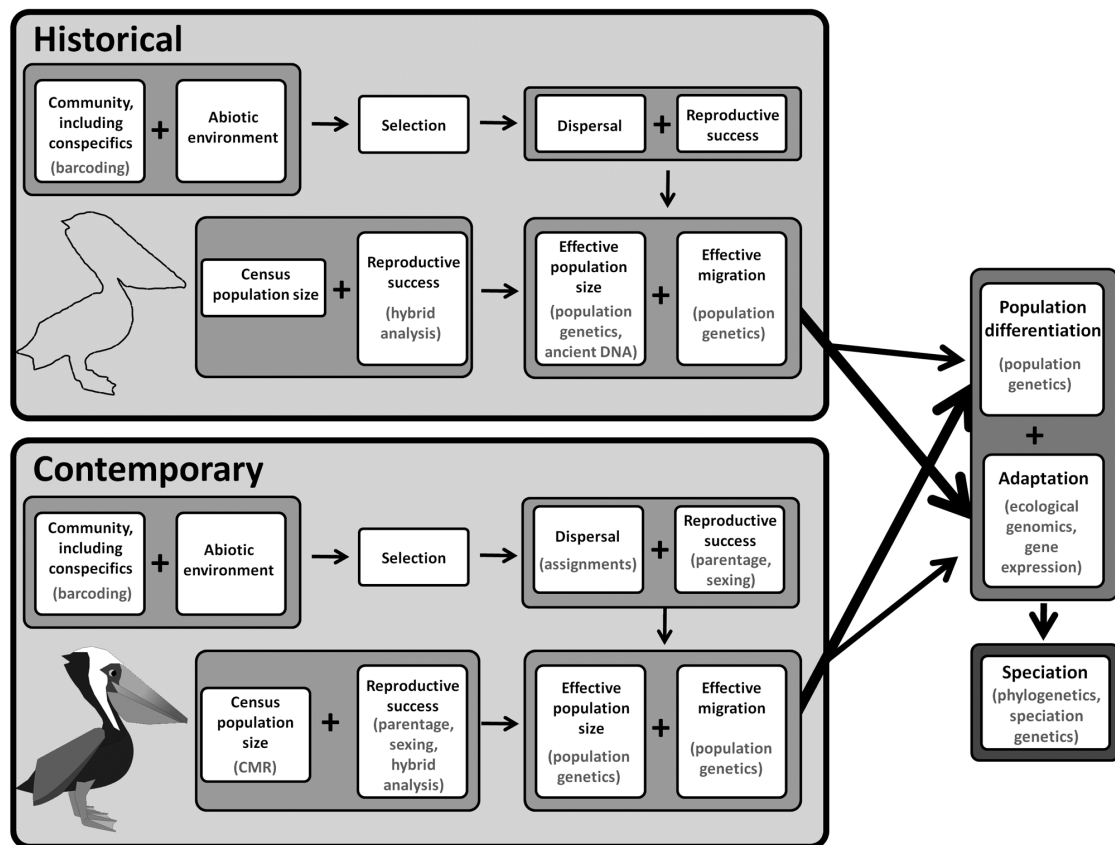


Fig. 1. Applications of molecular tools (in parentheses) for the study of seabird evolution and ecology. Arrow thickness indicates the presumed strength of causal relationships

Table 4. Types of molecular markers used in studies of evolution and ecology, the source of genetic variation, potential uses, and costs of analysis; devel.: development; screen.: screening; mod.: moderate

Marker type	Source of variation	Uses	Cost (devel.)	Cost (screen.)	Notes
mtDNA					
Restriction fragment length polymorphism (RFLP)	Lengths of fragments due to substitutions at restriction sites and in intervening sequences	Population genetics, phylogenetics	Low	Mod.	Superseded by direct sequencing (see following marker type)
Direct sequencing	Any mutation	Population genetics, hybridization, phylogenetics	Low	Low	Inferences restricted by unusual inheritance (matrilineal, no recombination), but high mutation rate makes it useful for recent and/or rapid evolution events
Nuclear DNA					
Minisatellite DNA (classical fingerprinting)	Numbers of repeat units within a fragment	Kinship, individual identification	Low	Mod.	Superseded by use of microsatellite DNA
Randomly amplified polymorphic DNA (RAPD)	Presence/absence of fragments due to substitutions in PCR priming sites and intervening sequences	Kinship, population genetics	Low	Low	Repeatability tends to be poor; some journals will not accept RAPD data; dominant inheritance complicates some inferences
Amplified fragment length polymorphism (AFLP)	Presence/absence of fragments due to substitutions in PCR priming sites, restriction sites, and intervening sequences	Population genetics, hybridization	Low	Low	Dominant inheritance complicates some inferences
Microsatellite DNA; intersimple sequence repeat (ISSR), short tandem repeat (STR)	Numbers of repeat units within a fragment	Kinship, population genetics, hybridization	Mod.	Low	Widely used, but becoming superseded by direct sequencing; vulnerable to homoplasy
Single nucleotide polymorphisms (SNPs)	Any mutation, but usually a substitution	Potential kinship via phylogenetics, but usually population genetics, hybridization	High at present	Low	Highly repeatable; source of variation is usually known
Direct sequencing	Any mutation, but usually a substitution	Population genetics and phylogenetics, but also kinship, hybridization	Low	Mod. at present	Highly repeatable; source of variation is usually known; screening cost is decreasing rapidly

draw examples from studies of phylogenetics, population genetics, hybridization and ecology (Table 3, Fig. 1). For each section, we outline traditional approaches, highlight examples using new molecular tools, and explore how traditional and molecular methods can be combined. We also give an overview of applications of molecular methods to conservation. This paper is not a comprehensive review of all molecular genetic work currently being conducted on seabirds; it is meant to highlight a few areas of research and to expose some ideas about future directions in seabird research.

MOLECULAR GENETIC METHODS

Information about an organism's evolution and ecology is retained in its DNA, and recent methods, especially those based on coalescent theory and Bayesian statistics, let us extract and understand this information. Numerous methods have been developed to assay DNA variation indirectly (several recent reviews, e.g. Baker 2000, Avise 2004; Table 4). One of the earliest methods to be developed was DNA fingerprinting, in which restriction enzymes (bacterial enzymes that recognize and cut short frag-

ments of DNA, typically 4 to 6 base pairs [bp] long) and agarose gel electrophoresis are used to screen individuals for variation in the number of repeats of a 20 to 25 bp unit. Restriction enzymes also can be used to detect mutations resulting in restriction fragment length polymorphisms (RFLPs) in short fragments of purified DNA such as mitochondrial DNA (mtDNA). These methods of mutation detection have been largely superseded by tools based on polymerase chain reaction (PCR), or DNA amplification. Common techniques include analysis of amplified fragment length polymorphisms (AFLPs), which uses a combination of restriction enzymes and PCR to detect sequence variation, and microsatellite analyses, which use specially designed PCR primers to amplify gene regions that tend to vary in the number of short (typically 2 to 6 bp) repeating units (Table 4).

Indirect methods of mutation detection such as AFLPs and microsatellite screening have the advantage that large numbers of individuals can be assayed quickly and relatively inexpensively. However, these tools are being replaced by direct sequencing of target genes, and analyses of single nucleotide polymorphisms (SNPs—single base pair replacements, insertions or deletions; Vignal et al. 2002, Coates et al. 2009). New sequencing methods are making SNP discovery and direct sequencing much easier and will greatly increase genetic tools for seabird studies (our Table 1; Tautz et al. 2010, Helyar et al. 2011). Financial costs of generating and mapping genomic level SNP datasets, or of identifying variable microsatellites are no longer prohibitive (see reviews by Hudson 2008, Shendure & Ji 2008, Tautz et al. 2010). Numerous studies of seabird evolution and ecology have used DNA sequencing to assess phylogenetic relationships (e.g. Pereira & Baker 2008, Jesus et al. 2009, Patterson et al. 2011), population differentiation (e.g. Morris-Pocock et al. 2008, Gómez-Díaz et al. 2009, Hailer et al. 2011; see review by Friesen et al. 2007b) and hybridization (e.g. Pacheco et al. 2002, Gay et al. 2007, 2008b, Taylor et al. 2010b), and to estimate population parameters such as migration rates or population sizes (e.g. Boessenkool et al. 2010). New sequencing methods now enable whole genomes to be sequenced within months (Hudson 2008, Mitchell-Olds et al. 2008, Shendure & Ji 2008, Thomson et al. 2010, Ekblom & Galindo 2011), although the full genome of a seabird species has yet to be assembled. The potential for genomic level seabird research to contribute to the larger picture in evolutionary biology is huge, particularly given recent findings regarding population divergence, hybridization, and speciation in a num-

ber of seabird species (see 'Population genetics and phylogeography' and 'Hybridization' below).

The drawbacks associated with using molecular genetic tools for studying ecology and evolution are rapidly being overcome (Hudson 2008). Previously, molecular genetic tools could be slow and expensive to adapt to particular research projects, and they often provided little information about functional variation or behaviour (but see e.g. Baião et al. 2007, McCracken et al. 2009). Until recently, assembling enough variable markers was also difficult for numerous seabird species: traditional, first generation sequencing methods suggested that variable markers are less common in birds than in other taxa (Baker 2000). New sequencing methods (summarized in Table 1; see reviews by Schuster 2008, Shendure & Ji 2008) are revolutionizing the study of ecology and evolution and have essentially removed the limitations outlined here (Hudson 2008, Tautz et al. 2010, Gardner et al. 2011); generating large, variable SNP or microsatellite datasets is now a possibility for any species. Additionally, the development of large genomic resources for seabirds will allow more directed studies that can target genes responsible for functional variation and possibly even the genetic underpinnings of behaviour, as has been done in other groups of organisms (Barrett 2010, Hubbard et al. 2010, Stapley et al. 2010, Toth et al. 2010).

Coalescent-based approaches that utilize Markov chain Monte Carlo (MCMC) methods and likelihood-based inference (implemented in Isolation with Migration: IM, Isolation with Migration Analytic: IMA, and Isolation with Migration Analytic 2: IMA2; see Table 2), and, more recently, approaches utilizing Approximate Bayesian Computation (ABC; Cornuet et al. 2008) (Table 2) are rapidly increasing our ability to robustly evaluate hypotheses about population divergence, and to infer population history (Hey 2006, Hey & Nielsen 2007, Csilléry et al. 2010, Lopes & Beaumont 2010, Pinho & Hey 2010). These approaches allow us to robustly estimate divergence times, historical and contemporary population sizes, rates of gene exchange during divergence, and to evaluate competing divergence scenario hypotheses. A number of seabird research groups are now utilizing larger (10+ markers) datasets and have recently developed analytical methods (Peucker et al. 2009, Lopes & Boessenkool 2010, Morris-Pocock et al. 2010, 2011, Taylor et al. 2011a, Welch et al. 2011).

DNA-based investigations of seabird evolution and ecology have the greatest power when combined with traditional methods, for example, by comparing variation in AFLPs with band returns to infer meta-

Table 5. Examples of studies in which molecular data were combined with other types of data to enable new insights into seabird evolution, ecology or conservation. AFLP: amplified fragment length polymorphism

Species	Molecular marker(s)	Additional tool(s)	Inference	Source
Cory's shearwater <i>Calonectris diomedea</i>	Microsatellites	Morphometrics, stable isotopes, trace metals	Individuals could be assigned to breeding colonies with 86% accuracy	Gómez-Díaz & González-Solís (2007)
Procellariiformes	Allozyme, DNA-DNA hybridization, DNA sequence	Morphology, behaviour, life history	More comprehensive inclusion of species than in previous phylogenies	Kennedy & Page (2002)
Phalacrocoracidae	mtDNA	Osteology	Cliques' of compatible characters suggest similar selective pressures	Holland et al. (2010)
Atlantic puffin <i>Fratercula arctica</i>	Allozymes	Morphometrics	Geographic variation in body size is due to environmental effects	Moen (1991)
Band-rumped storm-petrel <i>Oceanodroma castro</i>	mtDNA, microsatellites	Morphometrics, vocalizations	Divergence in morphology and vocalizations of seasonal populations precedes divergence in neutral molecular markers	Smith & Friesen (2007), Bolton et al. (2008), Deane (2011)
Black-legged kittiwake <i>Rissa tridactyla</i>	Microsatellites	Microsatellite variation in ticks	Kittiwakes prospecting among local colonies results in gene flow for kittiwakes but not ticks	McCoy et al. (2005b)
Wandering albatross <i>Diomedea exulans</i>	AFLP	Band returns	Populations are demographically but not genetically isolated	Milot et al. (2008)
Laysan albatross <i>Phoebastria immutabilis</i>	mtDNA, microsatellites	Band returns	Rare migration prevents genetic divergence of populations and enables colonization of new sites despite generally strong philopatry	Young (2010)
Cook's petrel <i>Pterodroma cookii</i>	mtDNA	Light-based data loggers, stable isotopes	Genetic divergence between colonies is ultimately the result of differences in non-breeding distributions and breeding times	Rayner et al. (2011)
Glaucous-winged gull <i>Larus occidentalis</i> and western gull <i>Larus glaucescens</i>	mtDNA, microsatellites	Plumage colouration Bare-part colouration	Restricted introgression of phenotypic traits compared to neutral markers – indicating selection on phenotypic traits and a role in isolation the species	Gay et al. (2008)

population dynamics (e.g. Milot et al. 2008), by combining morphometrics with isotope and genetic data to assign birds killed during winter to breeding populations for impact assessment (e.g. Gómez-Díaz & González-Solís 2007), or by using tracking data in concert with genetic estimates of gene flow in investigations of mechanisms of population differentiation (detailed in 'Ecology' below and in Table 5).

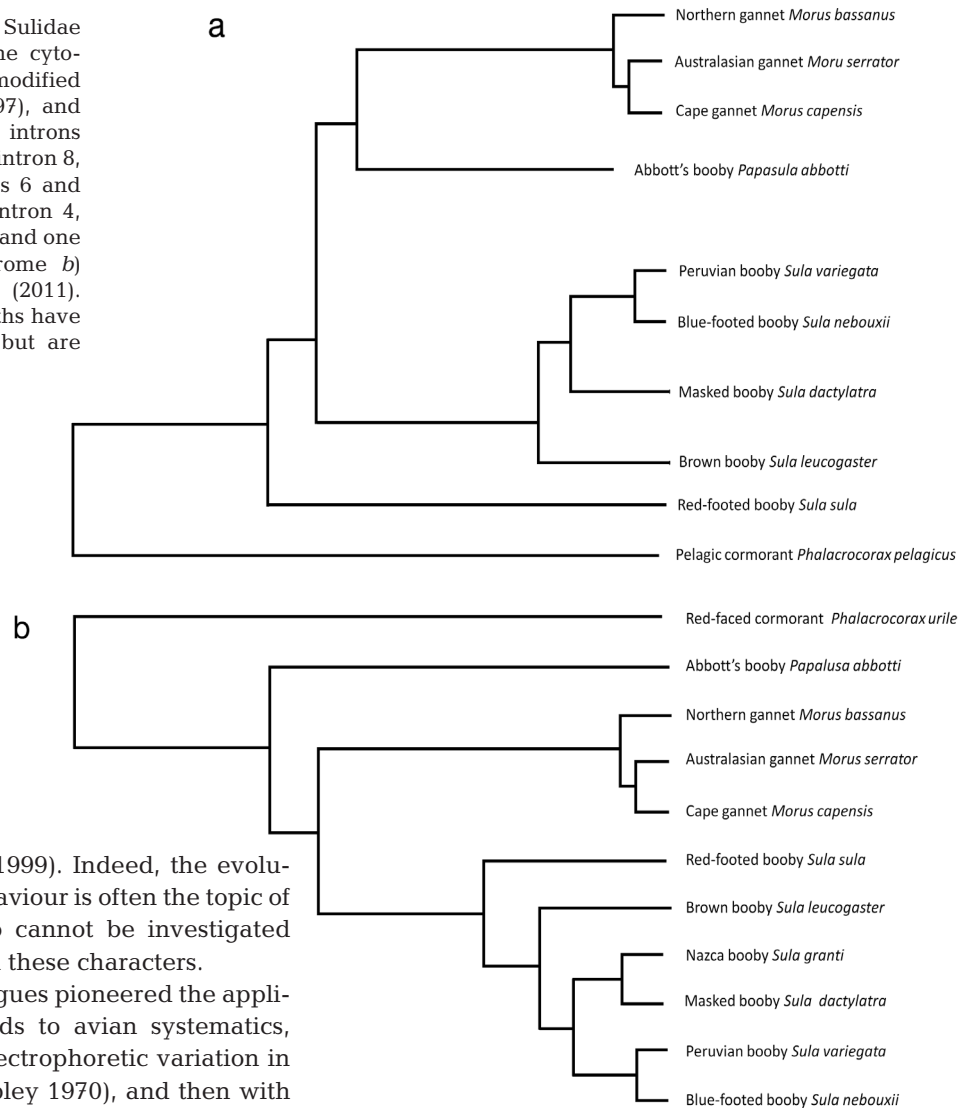
PHYLOGENETICS

Phylogenetics, the study of the evolutionary relationships among organisms, attempts to construct a tree that is representative of the true evolutionary history of a group of organisms. The tree can then aid investigations of taxonomy, character evolution (e.g. mating rituals, or clutch size) and diversification (e.g.

mechanisms of speciation; Avise 2004). However, unless the phylogenetic relationships among species are well resolved, evolutionary hypotheses cannot be reliably tested.

Traditional methods for phylogenetic reconstruction for seabirds rely on external and internal morphology, behaviour, and fossils. Studies based on these methods have provided significant insights into seabird evolution and ecology. For example, behavioural characters, morphology, osteology and allozymes have been used to evaluate evolutionary relationships within the Alcidae, Stercorariidae and Pelecaniformes (van Tets 1965, Strauch 1985, Watada et al. 1987, Kennedy et al. 1996, Chu et al. 2009, Smith 2010). However, the genetic basis for these characters is not usually known, and morphology and behaviour may differ between populations because of selection, phenotypic plasticity, or environmental

Fig. 2. Phylogenetic tree for the Sulidae (a) based on a fragment of the cytochrome *b* gene (gene tree) modified from Friesen & Anderson (1997), and (b) based on multiple nuclear introns (d-crystallin intron 7, a-enolase intron 8, ornithine decarboxylase introns 6 and 7, triosephosphate isomerase intron 4, and lipoprotein lipase intron 2) and one mitochondrial marker (cytochrome *b*) modified from Patterson et al. (2011). Node support and branch lengths have been removed for simplicity, but are high throughout



induction (Barbraud et al. 1999). Indeed, the evolution of morphology and behaviour is often the topic of interest in a study, and so cannot be investigated using phylogenies based on these characters.

Charles Sibley and colleagues pioneered the application of molecular methods to avian systematics, first with their studies of electrophoretic variation in egg white proteins (e.g. Sibley 1970), and then with their very comprehensive DNA–DNA hybridization work (Sibley & Ahlquist 1990). The first phylogenetic studies of seabirds based on DNA sequence data used single markers to infer evolutionary relationships. For example, Nunn et al. (1996) used sequence of the mitochondrial cytochrome *b* gene to generate a phylogeny of 14 albatross species, and Nunn & Stanley (1998) used cytochrome *b* sequences to evaluate evolutionary relationships among 85 species of procellariiform seabirds. Similarly, Friesen & Anderson (1997) used cytochrome *b* sequences to infer a phylogeny for the Sulidae (Fig. 2a), and Kennedy et al. (2005) used mitochondrial sequences to reconstruct evolutionary relationships among darters, cormorants and boobies.

Using a single genetic marker like albumin, or multiple markers from a non-recombining unit like mtDNA, for phylogenetic reconstruction can misrepresent the evolutionary relationships among organ-

isms, because single-gene trees do not necessarily represent the species' true history (Maddison 1997, Degnan & Rosenberg 2006, 2009). Recent advances in sequencing technology have allowed researchers to expand genetic datasets, and developments in phylogenetic analyses now allow researchers to estimate species trees using coalescent theory and Bayesian statistics (Table 2; e.g. Bayesian Estimation of the Species Tree [BEST], Liu 2008). These advances together led to the Tree of Life web project, which started in 1996, but has since expanded with these advances (Maddison & Maddison 1996).

Several recent phylogenetic studies of seabirds illustrate the utility of multilocus datasets. For example, Abbott's booby *Papasula abbotti* is ecologically, morphologically, and behaviourally distinct from other species in the Sulidae (Nelson 1978), and its placement within the family was unclear until recently.

Patterson et al. (2011) used 5 nuclear introns and a mitochondrial marker to estimate a species tree using BEST (Fig. 2b). They found that Abbott's booby was basal to all other members of the Sulidae and likely diverged from the group about 22 million years ago. Interestingly, the results were broadly congruent with van Tets (1965) phylogenetic reconstruction based on behaviour.

In a similar study, Kennedy et al. (2009) used multiple unlinked loci to evaluate the phylogenetic position of the Galapagos cormorant *Phalacrocorax harrisi*, an ecologically and morphologically unique member of the Phalacrocoracidae. Although this species is the only phalacrocoracid that has lost the ability to fly and was previously placed in its own genus, results from Kennedy et al. (2009) indicate that the Galapagos cormorant is most closely related to 2 species that are common and broadly distributed in North America: the double-crested cormorant *P. auritus* and the neotropic cormorant *P. brasilianus*.

Kennedy & Page's (2002) procellariiform phylogeny provides an excellent example of synergy through the combination of different analytical approaches. These authors used 7 incomplete phylogenies based on behaviour, DNA–DNA hybridization, isozymes, life history, morphology, and DNA sequence data to generate a supertree for the Procellariiformes. In another example, Holland et al. (2010) compared strongly supported but incongruent trees based on osteological versus molecular data for the cormorants and shags. Their study found 'cliques' of compatible morphological characters, suggesting groups of taxa under similar selective pressures. Although Cohen et al. (1997) provided a discussion of difficulties in combining morphological, behavioural, and genetic data to construct phylogenies, future researchers should attempt to construct phylogenies based on multiple nuclear and mitochondrial loci and, ideally, combine traditional approaches in phylogeny construction. Studies such as these are needed for other groups of seabirds, and will aid future investigations of both character evolution and mechanisms of diversification in seabirds.

POPULATION GENETICS AND PHYLOGEOGRAPHY

Understanding population genetic structure (the extent to which local populations differ genetically) helps researchers understand many aspects of evolution and ecology (Fig. 1). For example, some seabird species exhibit dramatic geographic variation in morphology and behaviour while others do not (e.g.

Storer 1952, Ainley 1980, Power & Ainley 1986, del Hoyo et al. 1992, 1996, Baião et al. 2007). Examining population genetic structure in these species can help determine the adaptive significance (if any) of geographic variation in life history, morphology, physiology and behaviour; how, where and why the variation originated; how populations are connected or what prevents them from being connected; and how species multiply. Furthermore, population differentiation is the first step towards speciation in most speciation models (Coyne & Orr 2004). Consequently, many population genetic studies explore the evolutionary histories of seabirds to understand the speciation history. A subfield of population genetics, phylogeography, studies the correspondence between phylogeny and geography, and can provide insights into evolution and ecology (Avise et al. 1987, Avise 1994).

Studies of morphology, physiology, and behaviour help elucidate population genetic structure. For example, geographic variation in plumage and morphometrics is more extensive in *Cephus* spp. (guillemots) than in *Uria* spp. (murre). Storer (1952) proposed that this difference is a result of differences in dispersal: guillemots nest in small colonies distributed linearly along coastlines and probably do not disperse far from colonies during the non-breeding season, whereas murre nest in a small number of large colonies, and generally migrate seasonally. However, as in phylogenetic studies, the genetic basis of morphological and behavioural characters is not usually known (but see Baião et al. 2007): even if individuals or populations are morphologically similar, they may differ genetically (e.g. Friesen et al. 1996a, Morris-Pocock et al. 2008, Hailer et al. 2011).

Protein electrophoresis also has provided useful insights into population structure and evolution (Baker 2000, Avise 2004). For example, protein variation suggests that thick-billed murre *Uria lomvia* form kin groups within colonies (Friesen et al. 1996b). In contrast, Moen (1991) found little geographic variation in allozymes among Atlantic puffins from throughout the northeast Atlantic, despite significant variation in body size. Protein electrophoresis yields data rapidly and is inexpensive to conduct; however, birds must be captured and sometimes sacrificed, proteins degrade easily, protein variability is often insufficient to be useful, and some variation is under selection (potentially violating assumptions of neutral mutation theory) and thus may not reflect true evolutionary history (Baker 2000).

Initial uses of DNA to study seabird population differentiation focused on mtDNA (e.g. Pitocchelli et al. 1995), because its unusual mode of inheritance and

relatively high mutation rate make it sensitive to changes in population size and migration rate (Wilson et al. 1985, Baker 2000, Avise 2004, Eda et al. 2008, Rains et al. 2011). Increasingly however, studies of population differentiation, phylogeography, and speciation are using large multilocus datasets of SNPs, microsatellites and sequence data (Table 3) to provide a more complete picture of contemporary versus historical population sizes and dispersal rates (Fig. 1; e.g. Peery et al. 2010, Hailer et al. 2011). For example, Techow et al. (2010) used cytochrome *b* and 6 microsatellite loci to examine the phylogeography and speciation history of giant petrels *Macronectes* spp. Their analyses revealed a complex history that involved population fragmentation, periods of population expansion, and secondary contact.

Population genetic analyses of seabirds have also benefitted from multispecies approaches, at both the seabird (i.e. analyzing multiple species of seabirds) and organismal (i.e. analyzing multiple species of seabird and other non-avian taxa) levels (e.g. parasites). Parasites are useful for studying long-lived species such as seabirds (Nieberding & Olivieri 2007), and multispecies approaches utilizing parasites have increased our understanding of the constraints on the genetic structure and the movements of seabirds (e.g. McCoy et al. 2005b, Gómez-Díaz et al. 2007). McCoy et al. (2005b) compared population genetic structure in black-legged kittiwakes *Rissa tridactyla* with one of their ectoparasites (the tick *Ixodes uriae*). Population genetic structure was much stronger in the ticks than in the kittiwakes, and, given the life history of the ticks, McCoy et al. (2005b) inferred that local movements of kittiwakes during the breeding season result in gene flow for the kittiwakes but not the ticks. Similarly, multispecies approaches at the seabird level have allowed researchers to detect common factors responsible for the presence or absence of population structure (important for making predictions for unstudied species, or informing conservation decisions) (reviewed in Friesen et al. 2007b), and the potential for multispecies approaches is very high given the aforementioned advances in sequencing technology and data analysis techniques.

The strongest population genetic and phylogeographic seabird studies are synergistic and combine molecular data with demographic data, morphology, and/or behaviour to elucidate mechanisms of population differentiation in seabirds. Our goal should be combining this approach with larger, more robust genetic datasets, as some researchers are doing already—though not yet at the scale made possible by

new sequencing methods. For example, by comparing variation in AFLPs with band returns, Milot et al. (2008) showed that populations of wandering albatrosses *Diomedea exulans* are demographically but not genetically isolated. In another synergistic study, Rayner et al. (2011) used geolocator-based tracking, isotopes, and DNA-based methods to examine contemporary and historical populations of Cook's petrel *Pterodroma cookii*, reporting that genetically distinct populations are segregated during the non-breeding season. They suggested that habitat specialization during the non-breeding season may lead to breeding asynchrony, which may restrict gene flow between the populations in conjunction with philopatry (Rayner et al. 2011).

Further studies such as these are needed to understand mechanisms of diversification and adaptation in seabirds, especially in relation to anthropogenic disturbances such as climate change. We see an opportunity for seabird evolutionary biologists and ecologists to move from population genetic to population genomic level studies (Hudson 2008, Tautz et al. 2010, and see Viner & Mitchell 2010 entire issue). Larger, more robust genetic datasets, combined with the ecological knowledge of many seabird researchers, will make population genomic studies more informative as they relate to the mechanisms that generate seabird diversity, than present population genetic studies. The possibility of expanding analyses to examine genes responsible for divergence or to explore differences in gene expression (transcriptomics) between closely related species (e.g. physiological differences, Hedgecock et al. 2007), should be pursued by seabird researchers, especially given the extreme physiology of this taxonomic group and the potential importance of physiological differences in relation to divergence events. These avenues of inquiry will contribute more generally to our understanding of population divergence and speciation and be valuable to the broader evolutionary biology community.

Recently, the term 'seascape genetics' has been used to describe population genetic studies of marine organisms that examine how environmental variables (e.g. ocean currents, ocean productivity) influence differentiation (e.g. Skillings et al. 2011, Amaral et al. 2012, see review by Selkoe et al. 2008; the terrestrial equivalent, 'landscape genetics', is reviewed in Sork & Waits 2010; see also Special issue on landscape genetics Vines & Mitchell 2010). Although no seabird studies to date have explicitly used the term 'seascape genetics', seabird researchers are generally cognizant of the effects of oceanic environmental variables such as fronts, eddies, and climatic phe-

nomena like El Niño on seabird population genetics (Steeves et al. 2003, 2005a,b, Morris-Pocock et al. 2008, Hailer et al. 2011, Rayner et al. 2011, Taylor et al. 2011a). Future population genetic studies of seabirds would benefit from including these variables explicitly, to ensure seabird population genetic studies remain on par with studies of other marine organisms.

HYBRIDIZATION

Hybridization can be either a creative or a destructive force in evolution (Harrison 1993, Allendorf et al. 2001). Global rates of hybridization are increasing and have contributed to species extinctions in a number of taxonomic groups, but have led to the establishment of new species in others (Brumfield 2010). Regardless of the outcome, documenting hybridization and understanding how it affects seabirds is an important aspect of seabird ecology and evolution, but is potentially erroneous without data from multiple, unlinked genetic markers. Hybridization also has conservation implications. For example, as climate change alters marine habitats a number of temperate seabird species may expand their ranges towards the poles. The evolutionary and conservation implications of these range shifts are unknown; however, studies of other species suggest that range shifts may increase hybridization rates (Kelly et al. 2010).

Traditional studies of hybridization in seabirds involved reports of birds with unusual plumage patterns (e.g. Cairns & DeYoung 1981), or geographic variation in morphology and/or allozyme allele frequencies (e.g. Bell 1996). These studies are complicated by the fact that back-cross hybrids, and even F1 hybrids, can be difficult to distinguish from parental species based on morphology (e.g. Friesen et al. 1993). Researchers now have the ability to generate sufficiently large genetic datasets (see above; Table 1) and possess appropriate computer programs to characterize hybridization between species thoroughly (see 'Molecular genetic methods' above and the following paragraph; Table 2; Gay et al. 2007, 2008, 2009, Taylor et al. 2010a, 2011b).

Although hybridization is generally considered rare in seabirds, an increasing number of studies are documenting hybridization and interspecific gene flow using multilocus cline and coalescent-based analyses (e.g. Reinhardt et al. 1997, Gay et al. 2007, 2008, Brown et al. 2010, Carneiro et al. 2010, Taylor et al. 2010b, 2011b, Taylor 2011). Molecular markers can also aid in determining whether an individual has

hybrid ancestry, how many generations ago hybridization occurred, and which species was maternal vs. paternal. Several recent studies of seabird hybridization illustrate the utility of using molecular markers.

An example comes from Taylor's (2011) analysis of hybridization between blue-footed boobies *Sula nebouxii* and Peruvian boobies *Sula variegata*. Taylor (2011) used a multilocus data set and cline analysis to examine introgression and to characterize the hybrid zone. He found that blue-footed and Peruvian boobies hybridize, but that pre- and postzygotic barriers are well established, particularly in light of the recent divergence of this species pair (Patterson et al. 2010). Additionally, Taylor et al. (2010b) and Taylor (2011) used a multilocus dataset to determine that morphologically aberrant individuals within the hybrid zone are most likely first generation hybrids and that the majority of hybridization between blue-footed and Peruvian boobies takes place between female Peruvian boobies and male blue-footed boobies, with subsequent backcrossing primarily between female hybrids and male blue-footed boobies. Finally, Taylor (2011) evaluated the likelihood that this species pair diverged from their common ancestor with gene flow, and found that a divergence with gene flow scenario was more likely than divergence without gene flow, using the isolation with migration model implemented in IMA. A dataset generated using new sequencing methods would significantly improve the ability of any study similar to the one completed by Taylor (2011) to explore the evolutionary history of a species pair, particularly given the low level of genomic divergence detected in this other studies using the current datasets.

A synergistic investigation of seabird hybridization was conducted successfully by Gay et al. (2007, 2008, 2009). They used multiple unlinked genetic markers, morphological characters, and cline analyses to determine the nature of the hybrid zone for each species pair. White-headed gulls appear more prone to hybridization than most other seabirds, possibly because of recent divergence and subsequent secondary contact between morphologically and behaviourally similar species (discussed in Gay et al. 2007, 2008, 2009). Gay and colleagues were able to document introgression at neutral loci and subsequently compared the rate of introgression of neutral loci with phenotypic introgression. They inferred that selection against phenotypic introgression is strong in both hybrid zones, and that sexual selection may be important for maintaining the species barriers.

Seabird researchers interested in hybridization should take a synergistic approach whenever possi-

ble. Future investigations of hybridization in seabirds will benefit from larger, genome-spanning datasets, and approaches that target functional differences between hybridizing species. As with hybrid-zone research on other non-model organisms, seabird researchers should seek to determine the genetic regions, and ultimately genes, responsible for reproductive isolation.

ECOLOGY

Tracking population fluctuations and dispersal patterns is important for understanding how species respond to natural and anthropogenic stressors. Such information is critical both for understanding ecology and evolution, and for conservation (see next section). Capture-mark-recapture (CMR) studies (banding or ringing) help to clarify population relationships and dynamics, and the technology required for banding studies is relatively cheap (e.g. Nisbet 1989, Wooller et al. 1992, Wanless et al. 2007). For example, a long-term banding study of blue-footed boobies *Sula nebouxii* on Isla Isabel, Mexico, revealed that individuals are more faithful to their first nest site than their natal site and may have a 'dispersal phenotype' (Kim et al. 2007). This behaviour is not shared by other members of the Sulidae and would not have been predicted based on long-term banding of the Nazca booby *S. granti*, a close relative of the blue-footed booby, in the Galapagos (Huyvaert & Anderson 2004). Banding has also revealed long distance movement between seabird colonies and a general trend of natal philopatry in many seabirds (Wooller et al. 1992). More recently, GPS tracking has provided previously unattainable high-resolution data on seasonal and daily movements (Grémillet & Boulinier 2009, Wilson & Vandenabeele 2012, this Theme Section). Unlike banding, tracking studies require expensive equipment and have only recently become common in the literature. Both banding and tracking require extensive effort and are virtually impossible for secretive species.

DNA-based methods allow researchers to assign individuals to genetic populations and to estimate population parameters like dispersal and population size in non-invasive ways (e.g. using moulted feathers, fecal samples, scavenged carcasses). Most notably, molecular assignments can provide insights into movements with minimal disturbance to individuals. Molecular assignments involve using an individual's multilocus genotype to infer its origin (Manel et al. 2005). If an individual's genotype clusters with high

probability with individuals from a different sampling site, that individual is likely a migrant. Molecular assignments are most successful when populations are significantly genetically differentiated (i.e. $F_{ST} > 0.1$) but can be used even when populations are only weakly differentiated (i.e. $F_{ST} < 0.05$) (e.g. Peery et al. 2008, Hall et al. 2009).

Although using molecular assignments to identify dispersal events can require large numbers of samples from many populations and so can be logistically challenging, this method is increasingly common in the seabird literature (e.g. Boessenkool et al. 2009, Schlosser et al. 2009) and often provides insights unavailable from banding data. Rare dispersal events, which are difficult to detect if band returns are low, may be captured in the multilocus genotype of an individual. For example, Boessenkool et al. (2009) used multilocus assignments in their study of yellow-eyed penguins *Megadyptes antipodes* and found evidence of rare migration events that would not likely have been detected otherwise. Similarly, Hall et al. (2009) used molecular assignments to characterize dispersal patterns in marbled murrelets *Brachyramphus marmoratus* in central California, and Faria et al. (2010) used both molecular assignments and methods based on coalescent theory to infer source-sink dynamics in South American terns *Sterna hirundinacea*. In an innovative modification of molecular assignments known as parent-offspring dyad analysis, Peery et al. (2008) determined that the central California population of marbled murrelets is a demographic sink.

Application of molecular assignments to species for which extensive CMR and/or tracking data exist is an especially promising but largely unused method to elucidate the connection between evolution and ecology, e.g. by disentangling the relative effects of historical versus contemporary seabird movements on local adaptation, or inferring the effect of non-breeding distributions on population differentiation and speciation (Friesen et al. 2007b). For example, band returns indicate that Laysan albatrosses *Phoebastria immutabilis* are strongly philopatric to natal breeding colonies, making them highly vulnerable to anthropogenic disturbance. However, geographic variation in mtDNA and microsatellites suggests that Laysan albatrosses have sufficient dispersal over longer timeframes to maintain population genetic variation and enable rapid colonization (Milot et al. 2008, Young 2010, Rayner et al. 2011). We could not find any studies that combine data from molecular markers and satellite tracking, highlighting the need for research using this combination of methods.

DNA-based methods allow seabird researchers to census populations through non-invasive molecular 'mark-and-recapture'. Rudnick et al. (2008) presented the method in their study of non-breeding imperial eagles *Aquila heliaca* in Kazakhstan. Direct counts of eagles in the Naurzum Zapovednik suggested that fewer than 32 individuals used the area; however, analysis of moulted feathers using the program MARK indicated a roosting population of 308 individuals (Rudnick et al. 2008). Although this approach has yet to be conducted on seabirds, the utility of the method and the nature of seabird roosting areas (numerous feathers available for sampling) suggest that it may be useful. Population sizes and changes in size can also be estimated indirectly by applying genetic theory to molecular variation. For example, deviations in heterozygosities from values predicted at mutation-drift equilibrium can be used to infer recent population increases or declines using programs such as BOTTLENECK (Cornuet & Luikart 1996) and FLUCTUATE (Kuhner et al. 1998). Using this approach, Birt et al. (2012) found support for census results suggesting that Xantus's murrelets *Synthliboramphus hypoleucus hypoleucus* on Guadalupe Island, Mexico, have declined over the last century, and by comparing variation in contemporary and historical samples of yellow-eyed penguins, Boessenkool et al. (2010) estimated an effective size an order of magnitude lower than the census size for the southern population than for the northern population.

Additionally, DNA-based methods allow the evaluation of sex-specific questions, since the sex of a bird can now be determined with relative ease, using only a blood or feather sample. Given that many seabirds are sexually monomorphic, and that morphological details are not always recorded during sample collection, molecular sexing of seabirds is invaluable. Indeed, a search of the literature highlights the prevalence of this method in recent years: over 400 papers on seabird ecology and evolution have used molecular sexing since 2002. The questions addressed by these studies are highly diverse and include investigations of physiological ecology (e.g. Giudici et al. 2010), breeding investment and foraging (e.g. Torres et al. 2011), sociochemical compounds (e.g. Leclaire et al. 2012), sex-specific foraging behaviour (e.g. Weimerskirch et al. 2006), disease transmission (e.g. Wojczulanis-Jakubas et al. 2011), and the utility of morphology or behaviour in sex determination of wild birds (Zavalaga et al. 2009).

Finally, DNA-based methods are useful for investigations of parentage and kinship in seabirds.

Microsatellites and SNPs can be used to generate genealogies, to detect extra pair paternity, and to assign offspring to adults when sampling is sufficient. The literature on this topic is vast and new sequencing methods will aid the development of the variable markers required for paternity assignment (e.g. Baião & Parker 2009, Wojczulanis-Jakubas et al. 2009, Huyvaert & Parker 2010).

CONSERVATION

In addition to providing managers with better understanding of seabird evolution and ecology, molecular genetic methods can aid conservation (recent reviews: Allendorf & Luikart 2007, Frankham 2010, Haig et al. 2011). Probably the most important direct contribution at present involves defining units of conservation. To be most effective, species-level conservation must be based on sound taxonomy: failure to recognize reproductively isolated species can result in loss of diversity. Taxonomy was traditionally based on morphology and ecology, but recent studies have unveiled several examples of mistaken taxonomy such as 'cryptic' species that are similar in appearance and ecology but that represent reproductively isolated, sometimes ancient lineages (e.g. Friesen et al. 1996a, Bolton et al. 2008, Rayner et al. 2011). The New Zealand storm petrel *Oceanites maorianus* provides an example. Presumed extinct for 150 years, birds similar to the New Zealand storm petrel were documented off New Zealand in 2003. Analyses of variation in both mtDNA and a nuclear intron confirmed that these birds belonged to the same taxon as the type specimen and that represents a distinct species (Robertson et al. 2011).

In addition, most conservation legislation recognizes phenotypically, ecologically and/or genetically distinct populations of vertebrate species as worthy of protection (e.g. 'distinct population segments' under the US Endangered Species Act; 'diagnosable units' under the Canadian Species at Risk Act). The rationale is that loss of these populations would result in loss of some of the species' genetic resources, including potential local adaptations, and that such populations may be genetically and demographically isolated from each other. Distinct populations are often termed evolutionarily significant units (ESUs), and may be identified from unique molecular, morphological, behavioural or ecological characteristics (e.g. Moritz 1994, Fay & Nammack 1996). Marbled murrelets illustrate the importance of defining distinct population segments. Murrelets breeding in

Washington, Oregon and California were originally treated as a threatened population segment, distinct from British Columbia and Alaska birds (USFWS 1992), but when molecular studies failed to find genetic differences between these regions (Friesen et al. 2005), distinct population status was removed; the viability of the species is now being evaluated as a single unit.

Additionally, local populations may be demographically but not genetically isolated from each other. Such populations may have sufficient dispersal to prevent genetic differentiation and local adaptation, but not enough to function as a single demographic unit. Thus, birth rates, death rates, and other demographic parameters may differ. Such populations are often referred to as management units (MUs) and may be recognized from differences in allele frequencies at molecular markers (e.g. Moritz 1994). Results from molecular studies often provide insights not expected from ecological data. For example, the high dispersal ability of the yellow-eyed penguin *Megadyptes antipodes* suggests that the species represents a single demographic unit, but differences in frequencies of mitochondrial haplotypes and microsatellite alleles, and results of assignment tests indicate that birds breeding on New Zealand's South Island are demographically isolated from those elsewhere and should be treated as a separate MU (Boessenkool et al. 2009).

Molecular markers can also aid conservation. For example, estimates of effective population size are needed both to assign species to conservation categories and to develop recovery plans; these estimates are often one or more orders of magnitude lower than census sizes (e.g. yellow-eyed penguins; Boessenkool et al. 2010). Molecular markers can identify hybrid individuals and their descendants (see 'Hybridization' above), and so aid recovery plans by allowing managers to exclude hybrid individuals from captive breeding programs, or from the population if maintenance of genetically pure populations is a conservation goal (e.g. Haig et al. 2004). Population markers can also help to assess the population-specific effects of anthropogenic disturbances (e.g. oil spills, Riffaut et al. 2005; fisheries by-catch, Walsh & Edwards 2005). Gómez-Díaz & González-Solís (2007) provide an example of the synergistic application of molecular genetics with other tools for impact assessment. They were able to assign individual *Calonectris* spp. shearwaters that had been caught in long-line fisheries in the Mediterranean to their population of origin with 86 to 100% accuracy using morphometrics, stable isotopes, trace metals, and

multilocus genotypes. As DNA technology becomes more accessible, many new applications to conservation are emerging (e.g. disease screening, Ishak et al. 2008; toxicology, Haig et al. 2011).

CONCLUSIONS

Studies of phylogenetics, population genetics, hybridization, speciation and ecology in seabirds have improved our understanding of evolution, ecology and conservation, and this can only grow as more seabird research groups incorporate DNA-based analyses including new sequencing technologies into their investigations. Seabird research in evolutionary biology has the potential to contribute in a significant way to evolutionary biology, given the ecological knowledge of seabird researchers, advances in sequencing technology and data analysis, and the fact that collection of a sufficient number of samples for robust genetic analyses is usually a possibility for colonially nesting organisms.

DNA-based methods are providing seabird researchers with tools to address previously intractable questions about seabird evolution and ecology. Although the majority of new genetic resources were not developed specifically for seabirds, advances in sequencing technology and analytical methods are resulting in improved genetic and genomic resources for seabirds within the capabilities of many seabird research groups. Many seabird researchers do not include genetic data in their studies; however genetics can provide versatile tools to aid in studying evolution, ecology and conservation of seabirds (Table 3, Fig. 1). Some molecular methods are still being optimized, but the potential applications of molecular markers will likely increase as DNA-marker generation becomes cheaper and faster, and methods of data interpretation become increasingly sophisticated. Results of studies that combine molecular markers with other tools will be especially useful to understanding the evolution, ecology and conservation not only of seabirds but also of other highly mobile organisms in a rapidly changing world.

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