

Diet studies of seabirds: a review and recommendations

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We review the different methods that are used to collect dietary data from marine birds. We consider their limitations and practicalities and emphasize critical data gaps in our knowledge of the feeding ecology of seabirds (namely diets outside breeding seasons). To enhance comparability of findings among studies, species, and oceanographic regions, we make recommendations on standards for the reporting of results in the literature.

Keywords: foodwebs, large predators, oceanographic comparisons, seabird diet sampling.

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Introduction

Seabirds are integral components of marine ecosystems and, besides being the subject of general scientific interest, are excellent indicators of changes in the marine environment (Furness and Monaghan, 1987; Furness and Camphuysen, 1997). For example, seabird data give early indications of fluctuations in fish stocks and oceanographic conditions (Montevecchi, 1993; Frederiksen *et al.*, 2004), and monitoring programmes for seabirds have been implemented in many parts of the world to investigate these relationships. In its broad sense, monitoring can be defined as "the process of gathering information about system state variables at different points in time for the purpose of assessing system states and drawing inferences about change in state over time" (Yoccoz *et al.*, 2001). The systems of interest here are typically seabird populations, and the state variables include breeding population size, reproductive success, adult survival, and seabird diets, but can also include broader foodweb and ecosystem extrapolations.

Many methods are used to study seabird diet. Some are based on opportunism whereby samples are collected *ad hoc*, e.g. from watching food uptake directly or by collecting dropped fish, regurgitated food, or faeces. Others take a more systematic approach through regular collections or sightings made within a specified time. Techniques vary greatly and range from the direct killing of birds to inspect their stomach contents through to totally non-invasive and repeatable observations of fish-carrying birds. Indirect methods include observations of feeding flocks, analyses of faeces or regurgitated food remains, or tissue collection for

stable isotope or fatty-acid analyses. All methods have, however, biases of one kind or other (Duffy and Jackson, 1986; Rodway and Montevecchi, 1996; Carss *et al.*, 1997; González-Solís *et al.*, 1997; Andersen *et al.*, 2004), and almost all methods and studies refer to the short breeding season when birds are readily accessible on or near land. When seabirds are not breeding and are dispersed along the coasts and over the open seas, there is no completely satisfactory non-destructive method for sampling their diets. Consequently, far too little is known about what and how much seabirds eat when they are at sea, or how the diets of immature birds and non-breeding birds compare with those of breeding adults or chicks.

The variable approaches to diet sampling and the different formats of data presentation often make it difficult to assess shifts in diets over time or spatial patterns in the exploitation of particular prey. Consistency is required to allow comparisons of the size and energetic content of prey items to be made, and a detailed reporting of techniques (methods) used to calculate, for example, prey body size and weight from prey fragments is very important. There is also a need to be as clear and informative as possible with respect to taxonomy, a subject that is constantly being revised and refined.

This review of diet sampling methods and our recommendations on how to report results in a standard manner are an outgrowth of work conducted by the ICES Working Group on Seabird Ecology meetings in 2006 and 2007. We describe the methods used

to sample seabird diets and trophic relationships, and provide recommendations for standardizing and enhancing the comparability of data collections and reporting.

Dietary sampling methods

Stomach sampling/regurgitations

To assess the diets of seabirds directly, it is necessary to obtain or extract items from the digestive tract where they may be found in the oesophagus, crop, proventriculus, gizzard, or small intestine. Generally, the only items retained in the gizzard are hard parts such as bones, shells, exoskeletons, polychaete jaws, and squid beaks. Everything from the proventriculus to the oral cavity can often be sampled by lavage (see below) without harming the bird, whereas sampling the gizzard or intestine is only possible from dead, dissected specimens. Once the food samples are obtained, they can be sorted and identified, and measurements, e.g. weight, linear dimensions, volume, taken. Size of digested prey can often be estimated from measurements of undigested hard parts such as otoliths, bullae, bones, shells, and polychaete or squid beaks, but the accuracy depends greatly on the amount of digestion and wear of these items (see section on Pellets below).

Dead birds

Shooting birds at sea is one way of obtaining dietary data. Shooting has, however, the obvious limitation of killing the birds, which raises ethical issues, especially in relation to species of conservation concern. Moreover, a substantial fraction (often 30% or more of birds shot at sea) do not contain any food items other than bony fragments in the gizzard (RRV and G. L. Hunt, unpublished data from South Georgia and the Bering Sea). Therefore substantial numbers need to be shot to obtain an adequate sample. For these reasons, shooting is becoming increasingly unacceptable as a sampling tool. In addition, because many seabirds feed socially, shooting a sample of birds at a single location may give a misleading indication of diet that may vary between aggregations. Consequently, shooting as a sampling tool can rarely achieve a representative picture of the spatial and temporal variation in diet. However, birds shot for other reasons, e.g. for pollutant analyses, harvesting (such as the Newfoundland murre, *Uria* spp., hunt), or shot as pests (although those killed at, for instance, aquaculture sites may provide very biased data), have been used for diet studies (e.g. Rowe *et al.*, 2000). Other sources of dead birds are oil spills, bycatches in fishing gear, and beached carcasses of oiled or wrecked birds (e.g. Blake, 1983; Lorentsen and Anker-Nilssen, 1999; Ouweland *et al.*, 2004), although birds from the last group have very often starved to death and yield few or biased data. Dead birds often arrive on beaches in a trickle, e.g. as a result of chronic oil pollution, or may hit a coastline *en masse* after an oiling incident, or a wreck following extended extreme weather (e.g. Stenhouse and Montevecchi, 1996). Such large-scale events should be seized for diet studies whenever possible, because they often provide large samples across a range of species from the same time and location (Ouweland *et al.*, 2004). In some oil spills, specimens may be sequestered for litigation purposes (Carter *et al.*, 2003), and, unless sufficient excess material is available, they become impossible to access for years after the incident. Efforts should, however, be made to ensure that they can be used after litigation, because they are often then discarded.

Once the birds are retrieved, the stomach or entire digestive track should be removed as soon as possible, and preferably

frozen. Preservation in ethanol is a poor option because it leads to tissue discolouration, which can be problematic in identification of some small prey. The use of formaldehyde, even when buffered, is strongly discouraged owing to health concerns and because otoliths quickly dissolve in it. During the subsequent analysis, allowance must be made for the differential digestion of food items in different portions of the digestive track. Items in the crop can be near intact, but the further an item progresses through the system, the more it is digested and consequently the more difficult it may be to identify and measure accurately. Items in the gizzard may be retained for a considerable time; sometimes until they are forcibly regurgitated as a pellet (see below). Squid beaks or polychaete jaws, for example, may be retained for a month or longer (Jackson and Ryan, 1986; van Heezik and Seddon, 1989; Pütz, 1995), so such retention needs to be taken into account when estimating dietary composition based on dissected dead birds and/or regurgitated samples. As the soft parts of squids or polychaetes are digested quickly, the beaks or jaws in the gizzard are often the only evidence of their presence in the diet. Using the number of these items in the gizzard will, nevertheless, likely overestimate their proportional contribution because of their long retention times, so such counts need to be weighted (e.g. Duffy and Jackson, 1986). There is also need to consider interspecific variation in this. Some seabirds, such as gulls (*Laridae*) and skuas (*Stercorariidae*), empty the gizzard from time to time by regurgitating pellets of indigestible material, whereas others, such as procellariiforms, rarely do so, so may retain hard parts of prey in the gizzard for many months.

Regurgitations

Some birds, especially nocturnal petrels and shearwaters (*Procellariidae* and *Hydrobatidae*, respectively), when attracted to lights at night become disorientated and land on a ship's deck or the ground. To lessen weight or as a panic response, they often vomit the contents of the upper digestive tract. At breeding colonies, stormpetrels can also be caught in mist-nests where they will regurgitate or can be induced to regurgitate (Montevecchi *et al.*, 1992; Hedd and Montevecchi, 2006). Sampling this way can be especially valuable because it may be the only way to obtain dietary information from birds at sea and/or outside the breeding season. The problem with this technique of sampling outside the breeding season is that it is entirely opportunistic and dependent on weather conditions, because birds are much more likely to be attracted to lights during foggy, overcast, and/or rainy weather. Nevertheless, such sampling can produce valuable information on the food types available at prey patches at sea.

Other species such as gannets (*Sulidae*), cormorants (*Phalacrocoracidae*), gulls, and terns (*Sternidae*) at or near the nest or on their way to feed chicks often regurgitate food held in the proventriculus if disturbed. Chicks may also spontaneously regurgitate in response to disturbance, or can be easily stimulated to regurgitate. Such samples are often only partly digested material and readily identifiable in the field (e.g. from gannets, cormorants) or on return to the laboratory (gulls, kittiwakes, *Rissa* spp.). Another advantage is that this type of sampling can be repeated (using the same or different birds) through the breeding season. Hard body parts (otoliths, bones, etc.) are also often not worn by digestion (although there are different digestion rates among opaque and hyaline otoliths; Jobling and Breiby, 1986), so allowing reliable determinations of prey size. Note, however, that the proportion of ingested items in the regurgitations varies, so the

amount regurgitated cannot be used as an estimate of meal size. Another limitation of this method is that the disturbance involved in some breeding colonies reduces the numbers of visits possible. There may also be biases where some food types are easy to regurgitate whereas others are not.

Stomach lavage, emetics

If a bird does not regurgitate voluntarily, the upper digestive tract can be sampled without harming the bird by flushing the contents with water. This process, referred to as lavage, stomach flushing, or water offloading, involves pumping water through a tube inserted in the oesophagus of a bird and catching the regurgitated contents in a bag, sieve, or bucket (Wilson, 1984; Ryan and Jackson, 1986). A latex tube is inserted deep into the bird's oesophagus, and water (preferably salt water) pumped (using a syringe) in the other end of the tube. If working in cold regions, the water should be slightly heated to avoid cold stress. The bird is then inverted over a suitable receptacle into which the water and stomach contents are emptied. The process may be repeated to ensure as complete an emptying of the gastric system as possible (Neves *et al.*, 2006). Note that in some countries, the use of this method may require a licence.

One limitation of lavage relates to how the birds are captured, because many birds vomit immediately upon being captured, so appear to be empty upon having their stomachs flushed. It has also proved difficult to use in some groups of seabird that do not regurgitate food to offspring, e.g. auks, though see Wilson *et al.* (2004).

Birds do not always eject all the contents of the upper gut tract during lavage, and can sometimes be induced to do so using an emetic (Ryan and Jackson, 1986). Emetics can, however, increase the risk of harming birds, especially if used by inexperienced researchers, so their use is not recommended.

Excrement

Bird excrement has been used in various ways to reconstruct diets. Hard parts from prey, such as bones, scales, eggs or otoliths of fish, parts of the exoskeletons of crustaceans, squid beaks and jaws and setae of nereid worms, calcite plates and spines of echinoderms, or shell hinges of molluscs may all survive digestion and are often excreted. If such parts are recognizable and still bear a relationship with original prey size, they may be used to identify prey and reconstruct prey size. This method has been applied to many different mammalian piscivores, most notably pinnipeds and otters, *Lutra lutra* (Pierce *et al.*, 1991; Tollit *et al.*, 1996, 2004; Kingston *et al.*, 1999; Andersen *et al.*, 2004). Seabirds that excrete such remains are also candidates for similar studies and many have been carried out on omnivorous gulls and skuas (Andersson and Götmark, 1980; Ambrose, 1986; Kubetzki *et al.*, 1999; Kubetzki and Garthe, 2003), piscivorous ducks (Anatidae; Rodway and Cooke, 2002), mollusc-eating seaduck (Swennen, 1976; Nehls, 1989; Nehls and Ketzenberg, 2002; Leopold *et al.*, 2007), benthos-feeding waders (Scolopacidae; Dekinga and Piersma, 1993; Scheiffarth, 2001), and other birds (e.g. Ormerod and Tyler, 1991; Taylor and O'Halloran, 1997). Relatively few such studies have, however, been carried out on other seabird taxa (e.g. terns, Veen *et al.*, 2003; Stienen *et al.*, 2007).

Advantages of the method are that it is non-invasive and simple. Furthermore, large sample sizes can be processed and time-series built by repeated sampling schemes. Given that different methods often reveal different prey types, studying remains in excrement could reveal prey species previously unknown,

e.g. *Nereis* jaws in sandwich tern (*Sterna sandvicensis*) excrement (Stienen *et al.*, 2007). Genetic analyses of faecal or scat samples may also be used to identify the sex of the predator (Reed *et al.*, 1997).

Being widely used and with samples readily available, the method has also been extensively tested against other methods of diet study (Prime and Hammond, 1987; Dellinger and Trillmich 1988; Cottrell *et al.*, 1996; Taylor and O'Halloran, 1997). Such tests have demonstrated that studies of excrement, like many other indirect methods covered here, are unlikely to reveal all prey taken by the predator. Some prey are easily fully digested, and some birds also use other means to rid themselves of prey hard parts, e.g. through regurgitation of pellets (see below). Moreover, some parts survive better than others and some prey may be completely overlooked or greatly underestimated. For example, sandeel (Ammodytidae) otoliths appear in the faeces of great black-backed gulls (*Larus marinus*), but otoliths of gadoid fish too large to pass through the intestine are voided in pellets (RWF, unpublished data). Another disadvantage is that excrement is unlikely to be collected at sea, unless a suitable platform on which they are deposited is available for sampling (Camphuysen and de Vreeze, 2005). Also, processing faecal samples can be unpleasant, although several washing methods have been developed (Bigg and Olesiuk, 1990), and estimating prey size from their remains is also time-consuming compared with measuring whole fish in a bird's oesophagus. The identification of prey from their remains, be they faecal or regurgitates, requires good identification guides (Härkönen, 1986; Watt *et al.*, 1997; Leopold *et al.*, 2001) and/or reference collections.

Pellets

Several seabirds regurgitate indigestible prey remains in discrete pellets. These may be collected and the remains sorted, using methods similar to those described earlier. Pellet analysis has been used widely on cormorants and shags (*Phalacrocorax* spp.; Kennedy and Greer, 1988; Barrett *et al.*, 1990; Hald-Mortensen, 1995; Derby and Lovvorn, 1997; Grémillet and Argentin, 1998; Leopold *et al.*, 1998; Olmos *et al.*, 2000), gulls (Meijering, 1954; Spaans, 1971; Wietfeld, 1977; Garthe *et al.*, 1999b; Kubetzki *et al.*, 1999; Kubetzki and Garthe, 2003), skuas (Votier *et al.*, 2004, 2006, 2007), terns (Favero *et al.*, 2000; Granadeiro *et al.*, 2002; Veen *et al.*, 2003; Bugoni and Vooren, 2004; Mauco and Favero, 2005), black skimmers (*Rhynchops niger*; Naves and Vooren, 2006), and other birds such as waders, kingfishers (Alcedinidae), and dippers (*Cinclus cinclus*; Swennen, 1971; Jost, 1975; Cairns, 1998). Being widely used and with samples readily available, particularly from cormorants, the method has been tested extensively both with captive birds fed known diets (Votier *et al.*, 2001), and against other diet study methods (Brugger, 1993; Harris and Wanless, 1993; Russell *et al.*, 1995; Trauttmansdorff and Wassermann, 1995; Zijlstra and van Eerden, 1995; Suter and Morel, 1996; Casaux *et al.*, 1997, 1999; Votier *et al.*, 2003).

Like faeces collection, the method is non-invasive and simple and can provide large samples over time, although finding pellets is often restricted to breeding colonies or roosts. However, species such as gulls aggregate in mixed groups, especially at roosts and resting sites, so that pellets can sometimes not be allocated to a specific species. Pellets can be collected from any dry surface such as offshore lighthouses and platforms, or even specially designed floating pellet-collecting devices (Gagliardi *et al.*, 2003), and are

available throughout the year (Johansen *et al.*, 2001). Pellet data can provide a quantitative index of diet composition, and on the assumption that birds generally eject one pellet per day (as generally with cormorants) or one pellet per meal (as often with gulls and skuas), and that the pellet contains the hard parts of all prey eaten, it is possible to convert this index to a rough estimate of the quantitative composition of diet (Johansen *et al.*, 2001; Votier *et al.*, 2001, 2003, 2007). There are, however, few field verifications of the numbers of pellets produced per day (e.g. in cormorants; Hüppop and Fründt, 2002). Moreover, Johnstone *et al.* (1990) showed that the proportion of otoliths recovered in shag pellets varied greatly from day to day and according to the species of fish ingested, and that measurements of otoliths sometimes gave misleading estimates of fish size. As a consequence, pellet analysis is better used for determining diet composition than for quantification of consumption (Carss *et al.*, 1997).

Many different prey types have been found in pellets, including unexpected ones (e.g. Leopold and van Damme, 2003), suggesting that most prey can be assessed using the method. Some comparative studies have, however, clearly indicated that the hard parts of small prey may not end up in the pellets, but rather in excrement (e.g. Veen *et al.*, 2003). As in excrement studies, some prey items do not leave hard parts in pellets, and processing pellets and reconstructing the numbers of prey and prey sizes is time-consuming.

Further problems arise as a result of the possibility of secondary consumption of prey by a seabird, i.e. the pellet may contain remains of prey present in the digestive tract of the fish or other organism consumed by the seabird. For example, Johnson *et al.* (1997) suggested that the invertebrate prey found in the pellets of double-crested cormorants (*Phalacrocorax auritus*) were prey of the fish consumed and not of the cormorants themselves. This source of error may also be relevant in studies of faeces or regurgitated remains and in analyses of dead birds containing partly or completely digested material. In general, however, fish stomachs appear to contain few hard parts of prey, and although bivalve or gastropod molluscs may be identified as secondary prey, the problem is probably small (Arnett and Whelan, 2001).

Food dropped in the colony

Fish or other food items dropped by adults returning to the colony or dropped by chicks during feeding may be found on the ground or on breeding ledges, where they can be collected and identified. They are, however, poor indicators of food choice. In mixed colonies, the species that dropped the food is generally unknown, and those dropped by chicks may be unrepresentative of the fish normally eaten. For example, guillemot and tern chicks often reject fish that are too large or too difficult to swallow, or those dropped by adults (often non-breeding birds) may not be representative of those caught by chick-provisioning adults (Atwood and Kelly, 1984; Harris and Wanless, 1985). A further source of bias is that dropped fish are often readily found and eaten by other seabirds in the area, probably with the most conspicuous items disappearing first.

Observations and collection of food from fish-carrying species

Some seabird species bring whole fish (and rarely other food items) carried openly cross- or lengthwise in the bill to their chicks and some seaduck bring large prey items to the surface before swallowing them. With practice and for species carrying

single or few fish (e.g. terns, auks), it is often possible to identify such food items from a distance using binoculars or a telescope as the bird stands in the colony or sits on the water (Birkhead and Nettleship, 1987; Leopold *et al.*, 1992; Harris and Wanless, 1995; Rodway and Montevecchi, 1996; Barrett, 2002; Larson and Craig, 2006). It is also possible to estimate prey size in relation to bill length.

In some cases, identification of fish (and estimates of their size) carried by birds into the breeding colony can be controlled by subsequently catching the observed birds and collecting the fish (see below). For single-prey loaders that carry fish lengthwise in the bill, such as guillemots (*Uria* spp.), the fact that the head of the fish may be carried at different depths in the bird's oesophagus, so reducing the observed length of fish in the bill, needs to be taken into account. For species carrying many small fish (e.g. puffins), species identification and quantification is also possible (and often used), but the possibilities for observation error are larger (Rodway and Montevecchi, 1996).

The main advantage of being able to make direct observations of fish is the possibility of collecting large samples without any disturbance to the birds. If the species breeds in dense colonies, e.g. guillemots, advantages are the simplicity of the method, and the possibility to make many observations over short periods, and hence to document short-term temporal and spatial (within or between colonies) variations in prey choice.

The main disadvantage of the method is the possibility of mis-identifying the prey with no possibility of later confirmation. This is even more of a problem for species carrying many small (even larval) fish, because numbers and sizes are easily misjudged, although this shortcoming can be partly overcome by still or video photography of fish being carried in the bill (Larson and Craig, 2006). Such records will allow subsequent confirmation of identification by fish experts and more accurate estimates of prey size.

A preferable alternative is to sample the fish directly by capturing the fish-carrying birds (see Rodway and Montevecchi, 1996). In large colonies, fish-carrying common (and less often Brünnich's) guillemots on their way to the nest site can be caught easily using a hoopnet on the end of a pole (fleyg) or noose pole once they have landed on or near the site (Birkhead and Nettleship, 1987; Davoren and Montevecchi, 2003). Fish-carrying puffins (and razorbills, *Alca torda*) can also be caught with fleyg or mist nets as they arrive at or circle past the colony, or with a noose pole once they have landed (Wanless *et al.*, 2004). Because small fish, fry, or larvae are easily lost in vegetation or crevices in rocks, sampling sites should be chosen with care. Trimming the vegetation or placing plastic sheeting under the mist net will also reduce such loss.

For burrow-nesting species, a second method is to block the entrances of 20–30 burrows for 1–2 h using a screen (of wire or plastic netting) a short distance inside, or a fishnet placed over the entrance (Sanger and Hatch, 1987; Finney *et al.*, 2001), and then to collect any fish dropped. One problem is that the samples are sometimes damaged as the adult tries to get past the screen. Sealing the chick's bill shut using a pipecleaner such that it cannot pick up the food dropped by the adult has been tried successfully (Harding *et al.*, 2002), but such activities raise ethical concerns. These direct methods involve some disturbance of the adults, but the collection of fish has the great advantage of allowing accurate quantitative studies of prey composition (either by number, weight, or energy content) in that the fish are whole

and often very fresh (even at times alive) when brought into the colony. Collecting fish can also demonstrate highly selective foraging by seabirds that may not be evident from field observation of fish-carrying birds. For example, Barrett and Furness (1990) found that common guillemots fed chicks almost exclusively ripe female capelin (*Mallotus villosus*) and rarely brought in either spent female or male capelin.

Either method (observation or collection) is, however, limited to the chick-rearing period which, for guillemots and razorbills, may last only 4–5 weeks between the hatching of the first egg and the fledging of the last chick. For terns and some auks, however, the method may also be used to determine food choice and quality during the courtship period early in the breeding season. How representative the fish fed to mates are of the general diet of the species is, though, largely unknown (see Discussion).

Recently, detailed observations of seabirds feeding at sea, following a standardized protocol (Camphuysen and Garthe, 2004), have revealed prey choice in some detail. Although many prey captures, particularly of small prey items, may be overlooked, such studies provide additional information by revealing the food source and the location directly (Schwemmer and Garthe, 2005, 2006).

Biochemical methods

Biochemical methods of determining seabird diet have several advantages over more traditional methods. Diet sampling by conventional methods most often indicates what the individual seabird has just eaten and therefore may not reflect “average” or typical diet if temporal variability is high. In contrast, stable isotope ratios and fatty acid signatures in bird tissues both integrate diet information over space and time (ranging from days to months; Hobson *et al.*, 1994). Additionally, the often large biases associated with sampling gut contents or regurgitations through differential digestion of soft and hard parts do not apply to these indirect methods. A major value of using chemical assays is that they provide a means of assessing adult trophic interactions and diets during breeding and, importantly, non-breeding periods (e.g. Hedd and Montevecchi, 2006). Furthermore, combining the use of biochemical methods with conventional sampling can allow more detailed interpretation of diet in situations where either method on its own may give misleading results (Bearhop *et al.*, 2001; Hedd and Montevecchi, 2006).

Stable isotope analysis

Examining tissue levels of different stable isotopes has been used extensively in avian feeding ecology studies (e.g. Hobson and Welch, 1992; Hobson, 1993; Hobson *et al.*, 1994; Sydeman *et al.*, 1997). The method is based on the fact that stable isotope ratios of nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) in tissues pass from prey to predator in a predictable manner. For nitrogen, the ratio of the heavier (and rarer) isotope to the lighter one increases at a rate of ~3–5 parts per thousand between each trophic level in marine systems, such that the method can be used to indicate the trophic level of the predator, though not the specific items in the diet. Although complex, stable isotope methodologies are now fairly routine and laboratories around the world offer this service at a reasonable cost. They do, however, require voucher samples from hypothesized foraging areas, which may be difficult over long distances, including migration, and long time-scales (see below).

As the metabolic rates of various tissues differ, stable isotope ratios reflect trophic levels at different time- (and hence spatial) scales, from days for “fast” tissues (e.g. plasma) to months for “slow” ones (e.g. feathers; Hobson *et al.*, 1994; Bearhop *et al.*, 1999, 2002). Stable isotope analysis of “slow” tissues provides an opportunity to assess diet during times of the year not normally covered by traditional diet sampling at seabird breeding colonies. Also by analysing small pieces of feathers grown in the non-breeding season, assessments of autumn, winter, and spring diets can be possible, depending on the species’ moulting chronology (Cherel *et al.*, 2002; Hedd and Montevecchi, 2006). The method also permits assessment of the trophic interactions of extinct and ancient birds through the collection of tissues (e.g. bone collagen) at archaeological sites (e.g. Hobson and Montevecchi, 1991). The stable isotope analysis of museum material can be a powerful tool to assess the historical impact of fisheries, or of oceanographic changes (Thompson *et al.*, 1995; Becker and Beissinger, 2006; Hilton *et al.*, 2006).

Although carbon isotope ratios change less between trophic levels than those of nitrogen, they are useful in providing a general idea of how far from shore or in which oceanographic regions the bird has fed. For seabirds that feed only in marine environments, ^{13}C is enriched in relation to ^{12}C in nearshore compared with offshore waters and from high latitudes towards the equator (Rau *et al.*, 1982; Goericke and Fry, 1994; Cherel *et al.*, 2000). Because $^{13}\text{C}/^{12}\text{C}$ ratios differ strongly between marine and terrestrial/fresh-water foodwebs, they can also be informative for seabirds that consume prey from both these different environments (e.g. many gull species, or great cormorants, *Phalacrocorax carbo*), where a two-source mixing model can be used to assess the proportions of protein derived from marine and fresh-water systems (Bearhop *et al.*, 1999). Although less pronounced than the difference between terrestrial and marine signals, possible differences in the isotopic signatures of pelagic and demersal fish could probably be used to identify the presence of the latter (often obtained as trawl fishery discards) in the diet of seabirds that normally feed primarily on pelagic fish or zooplankton (Furness *et al.*, 2006). Through their reflection of oceanographic gradients associated with latitude, carbon signals can also provide insight into the movements and winter habitat use of wide-ranging species (e.g. Hedd and Montevecchi, 2006).

Quantitative fatty acid signature analysis

A relatively new method used to probe the diets of marine organisms takes advantage of the facts that (i) the fatty acid composition of prey species is diverse (among species) and characteristic (within species), (ii) long-chain (i.e. >14 units) fatty acids pass relatively un-degraded to predators, and (iii) the predator ultimately stores prey fatty acids in adipose tissue, which can be sampled non-destructively using biopsy (Iverson *et al.*, 2004). As relatively few fatty acids are synthesized by the predators themselves, dietary vs. intrinsic fatty acids can be distinguished. This technique has advantages over the use of stable isotopes because actual diet composition rather than just trophic level can be assessed (Käkelä *et al.*, 2006, 2007). The potential of using the two techniques in combination offers a possibility for more powerful dietary analyses.

A problem inherent in the fatty acid technique is that predator diets usually contain more than one prey species, such that the signatures are often complex and cannot be examined just by eye. Moreover, variability of fatty acid signatures between individuals

of prey species, and intrinsic predator fatty acid production and metabolism sometimes need to be taken into account when interpreting the predator signatures. Iverson *et al.* (2004) outline a statistical modelling technique that was successful in estimating known diet composition of marine seals and mink (*Mustela vison*), and more recently, Iverson *et al.* (in press) confirmed the applicability of fatty-acid analyses to seabirds. The technique is also demanding because a fatty acid database of all possible prey is needed to interpret predator signatures accurately. The database for seabird diets in the Atlantic will no doubt expand over the next few years (and is already doing so in Alaska; Iverson *et al.*, in press). It is also important to calibrate the metabolic shifts in fatty acid signatures between the consumer seabird and its food (Käkelä *et al.*, 2005). The availability of software to perform the statistical modelling requirement of the method would aid its general applicability.

Serological methods

Serological methods also have the potential for detecting species-specific markers in digested prey items. The enzyme-linked immunosorbent assay (ELISA) has been used to identify invertebrate tissue, but it requires extensive laboratory effort to produce specific antisera to the range of potential prey species (Freeman and Smith, 1998). Trials to identify fish and molluscan prey of jackass penguins (*Spheniscus demersus*) also noted problems with cross-reactivity (Walter *et al.*, 1986).

Pierce *et al.* (1990) tested the use of serological methods to identify fish prey in the diets of marine mammals, and antisera were raised to muscle protein extracts of three fish species. The antisera were tested for reactions with protein extracts from raw and *in vitro* digested fish muscle, the stomach contents of captive bottlenose dolphins (*Tursiops truncatus*) fed known diets, digestive tract contents of grey seals (*Halichoerus grypus*) and common seals (*Phoca vitulina*) that contained hard remains of known prey species, and the excrement of captive seals provided known diets. Atlantic salmon (*Salmo salar*) antisera were sufficiently strong and specific to be used for identification of salmonid proteins in digestive tract contents of marine mammals, and were potentially applicable to the screening of seal faeces. Antisera raised for Atlantic cod (*Gadus morhua*) and herring (*Clupea harengus*) were less successful, however, owing to low specificity and low titre, respectively.

Notwithstanding, there is potential to develop this methodology further, but because of the large number of prey species in most seabird diets and the need for a reference database, serological methods may ultimately turn out to be too expensive.

Gel electrophoresis and iso-electric focusing of proteins

Walter and O'Neill (1986) tested the use of polyacrylamide gel electrophoresis to identify the prey consumed by jackass penguins. They found that different prey species could be recognized up to 6 h after ingestion. Freeman and Smith (1998) used iso-electric focusing to identify fish tissue in diets samples of Westland petrel (*Procellaria westlandica*). Some 45% of the stomach samples produced clear protein-banding patterns, and more than half of these were identified as species common in fishery waste. Proteins in the other samples were presumably too digested for this technique. Freeman and Smith (1998) claimed that iso-electric focusing is comparatively quick and inexpensive, and

particularly useful for diet studies where the flesh eaten is likely to be relatively undigested at the time of sampling. Despite this claim, and the fact that the method is used widely in fisheries studies, neither this method nor gel electrophoresis has been used widely in seabird diet studies.

DNA of prey in faeces

The DNA of prey present in animal faeces may also provide a valuable source of information for dietary studies. Deagle *et al.* (2005) tested whether prey DNA could be detected reliably in faeces samples from captive Steller sea lions (*Eumetopias jubatus*). Most of the DNA obtained came from the predator, but prey DNA could be amplified using prey-specific primers. The four prey species fed in consistent daily proportions throughout the trial were detected in >90% of the faeces DNA extractions. Deagle and Tollit (2007) analysed faeces from captive sea lions fed a diet containing three fish species (50%, 36%, and 14% by weight) using real-time PCR to quantify mtDNA in undigested tissue and in the faecal samples. The percentage composition of fish mtDNA extracted from tissue corresponded reasonably well with the weight of fish in the mixture, but the results indicated that there are prey-specific biases in DNA survival during digestion. However, both studies highlighted an approach also applicable to seabirds that can identify prey species accurately and that is not dependent on prey hard parts surviving digestion.

Food sampling below feeding birds Fish/plankton hauls and acoustic signals under seabird feeding frenzies

When flocks of intensively feeding seabirds (planktivores or piscivores) are encountered, sampling the sea for potential food items can provide information on the potential prey locally available (Grover and Olla, 1983; Skov *et al.*, 1989; Baars *et al.*, 1990; Piatt, 1990; Camphuysen, 1999; Frengen and Thingstad, 2002; Schwemmer and Garthe, 2006). Food may be sampled by taking fish or plankton hauls at the site, or acoustically. Whereas fish hauls are often taken opportunistically, in other words only when feeding frenzies of seabirds are encountered, it would be useful also to sample control sites, i.e. at similar locations away from the feeding frenzies. Additional information can be gained through the use of echosounders that reveal the locations and sizes of prey patches (Veit *et al.*, 1993; Veit, 1999) but usually not species composition (but see Madureira *et al.*, 1993), which generally requires verification by trawling.

Benthos sampling below flocks and feeding sites of seaduck, cormorants, and shags

Flocks of seaduck that reside for a longer period at a certain location are likely to feed there on benthic prey. Because benthic prey often stays at the same place (possible exceptions being fish eggs, amphipods, and other epibenthos), such locations may be sampled with bottom grabs, dredges, nets, SCUBA, cameras on remotely operated vehicles, or other devices to assess available potential prey. In situations where one prey type is numerically dominant and suitable as food, it may be inferred that this potential prey is also the actual prey taken. Examples are given in Birt *et al.* (1987), Leopold *et al.* (1995), Kube (1996), and Degraer *et al.* (1999).

Archaeological: guano, middens, and mummies

Hard parts of pellets or faeces can be conserved in sediments (Martini and Reichenbacher, 1993). Hence, geological deposits, including guano layers in recent and abandoned seabird colonies (Rand, 1960) or archaeological sites may contain information on the diets of seabirds in the past (Emslie *et al.*, 1998). Perhaps even more spectacular, although of little relevance to modern diet studies of seabirds, prey remains are sometimes found in fossil seabirds (Mayr, 2004). Both these types of studies could be particularly informative in considerations of long-term ocean climate change.

Application of data loggers

Whereas all the methods outlined above address the identification of the food items taken, few provide sound quantitative data concerning how much food is eaten. Recent approaches using data loggers not only provide data on how much food, but also when (and sometimes even where) food is ingested. Such methods involve the capture and recapture of birds to deploy and then to download the data and/or remove the devices. So far, stomach temperature loggers have been most commonly applied. Their use is based on the principle that the ingestion of cold prey (fish, cephalopods, etc.) by warm-blooded seabirds leads to a temporary drop in temperature in the digestive tract (Wilson *et al.*, 1992). From the magnitude of the temperature drop and the time it takes to re-warm the stomach and contents, the amount of food can be estimated (Wilson *et al.*, 1995). The method has been applied successfully to a variety of seabirds, including penguins, albatrosses, cormorants, and gannets (Grémillet and Plös, 1994; Wilson *et al.*, 1995; Garthe *et al.*, 1999a). A major problem with the technique is that the detection works very well for single, large prey items, but less well for multiple prey items, especially small ones. In the worst case, small fish such as sandeels or small chupeids cannot be detected at all after the stomach has partly filled, so that both information on timing of feeding and amount of food can be masked (Wilson *et al.*, 1995; Wanless *et al.*, 2005a, b). However, some studies have been able to quantify prey consumption. To avoid the masking effect of prey lying in the stomach on top of the device, two other technologies were developed that try to detect prey ingestion in the bird before the prey enters the stomach. Ancel *et al.* (1997), Charrassin *et al.* (2000), and others applied sensors in the oesophagus that record prey ingestion while the prey moves from the beak of the birds towards the stomach. Wilson *et al.* (2002) recently devised a mandibular sensor that records changes in sensor voltage as a function of intermandibular angle. Captive feeding trials showed that prey weight can be determined with reasonable accuracy, and there has been some indication that prey type can be resolved if the recording frequency is high enough (Wilson *et al.*, 2002). Heart-rate monitors have been used on black-browed albatrosses (*Diomedea melanophris*) and white-chinned petrels (*Procellaria aequinoctialis*) (Bevan *et al.*, 1995) to detect feeding on the principle that heart rate increases in response to ingestion and preliminary digestion of food. Back-mounted miniaturized digital still-camera loggers have recently been fitted to seabirds nesting on the Isle of May and foraging underwater (Watanuki *et al.*, 2007). These cameras provide valuable information on the detailed foraging behaviour of the birds, and further development and application of this novel technology for seabird foraging studies is anticipated.

Presentation of data

Besides standard methods of sampling, a unified approach to the presentation of results is needed. Duffy and Jackson (1986) reviewed methods for analysing and presenting dietary data, and this is still an excellent reference 20 years after its publication. The main objectives of seabird diet analyses are (i) to compare diet composition between species, times, and sites, and (ii) to quantify the consumption rate of a predator on its prey to species level and, for fish prey often also age class, sex, and reproductive condition (e.g. gravid). Hence, the data have to be presented in a way to fulfil these aims and to allow interstudy comparison.

Data collections and presentations are based on research objectives. For example, research questions may focus on foodwebs and prey consumption by avian predators, or on chick growth and fledging success. In the latter instance, more emphasis is placed on the sizes of food loads fed to chicks and how these change over time. Researchers may also be interested in the nutrient and organic composition and the energy densities of chick feeds. These analyses have proved very informative in demonstrating decreases in the condition of forage species, likely reflecting broader bottom-up foodweb effects (Davoren and Montevecchi, 2003; Wanless *et al.*, 2005a, b). When parents feed their offspring whole, relatively undigested fish, chick diets may be more directly and easily related to prey consumption assessments.

It is also essential to report the sites and times of sample collections, because prey species vary widely, often irregularly, over space and time. The diets of conspecific seabirds can vary considerably among colonies and oceanographic regions (Schneider and Hunt, 1982; Barrett *et al.*, 1987; Montevecchi *et al.*, 1992; Garthe *et al.*, 2007), as well as seasonally (e.g. Barrett *et al.*, 1987; Hedd and Montevecchi, 2006). Seabirds are opportunistic and to a certain extent capture the prey that is available; therefore, estimates of spatial and temporal variability in data need to be presented. Single-day or single-location data are all too often presented as representative of a species (see Brown *et al.*, 1981).

Qualitative data/taxonomy

Prey items are usually identified to the lowest achievable taxonomic level (order, family, genus, species, and sometimes subspecies). In the absence of a standardized world list of animals and plants, and given the frequent changes in nomenclature following advances in taxonomic research, an author should always try to accommodate future scientists by stipulating the references used to identify prey. It should also be made clear in publication what taxonomic conventions were followed, so that readers can understand what taxa are listed, knowing that nomenclature may change in years to come. A full list of reported taxa should be added as an (electronic) appendix of each diet study, to facilitate future use and comparisons, including at least the class of all prey items, and when possible also order, family, genus, and (sub)species, such as exemplified in Table 1. Such a list should also include the common name of prey items, because they may have been used elsewhere in the paper. A minimum requirement would be an accurate list of the different taxa found, because in later meta-analyses, it is important to know exactly the taxonomic level to which species were identified when comparing lists from different species or sites. For example, a category "unidentified polychaetes" may comprise only a single species, a few species, or even some dozen species, which makes a big difference when

Table 1. Example of an appendix in a hypothetical diet study listing prey items found and reported, including insects, crustaceans, worms, molluscs, bony fish, and plants.

Class	Order	Family	Genus	Species
Insecta	Ephemeroptera	—	—	—
Insecta	Diptera	—	—	—
Insecta	Diptera	Muscidae	<i>Musca</i>	<i>domestica</i>
Insecta	Coleoptera	Carabidae	<i>Poecilus</i>	<i>versicolor</i>
Insecta	Coleoptera	Coccinellidae	—	—
Malacostraca	Decapoda	Corystidae	<i>Corystes</i>	<i>cassivelaunus</i>
Malacostraca	Decapoda	Canceridae	<i>Cancer</i>	<i>pagurus</i>
Polychaeta	Phyllodocida	Nereidae	<i>Nereis</i>	<i>virens</i>
Polychaeta	Phyllodocida	Nereidae	<i>Nereis</i>	<i>diversicolor</i>
Oligochaeta	Terricola	Lombricidae	<i>Lumbricus</i>	<i>terrestris</i>
Bivalvia	Cardiacea	Cardiidae	<i>Cerastoderma</i>	<i>edule</i>
Bivalvia	Mactracea	Mactridae	<i>Spisula</i>	<i>subtruncata</i>
Bivalvia	Tellinacea	Tellinidae	<i>Macoma</i>	<i>baithica</i>
Osteichthyes	—	—	—	—
Osteichthyes	Clupeiformes	Clupeidae	<i>Clupea</i>	<i>harengus</i>
Osteichthyes	Clupeiformes	Clupeidae	<i>Sprattus</i>	<i>sprattus</i>
Osteichthyes	Gadiformes	Gadidae	<i>Merlangius</i>	<i>merlangus</i>
Osteichthyes	Scorpaeniformes	Triglidae	<i>Trigla</i>	<i>lucerna</i>
Osteichthyes	Pleuronectiformes	—	—	—
Osteichthyes	Pleuronectiformes	Bothidae	<i>Arnoglossus</i>	<i>laterna</i>
Osteichthyes	Pleuronectiformes	Solidae	<i>Solea</i>	<i>solea</i>
Dicotyledones	Tubiflorae	Convolvulaceae	<i>Convolvus</i>	—
Spermatopsida	Vitales	Vitaceae	<i>Vitis</i>	<i>vinifera</i>
Liliopsida	Poales	Poaceae	—	—
Liliopsida	Poales	Poaceae	<i>Triticum</i>	—
Liliopsida	Poales	Poaceae	<i>Ammophila</i>	<i>arenaria</i>

comparing species numbers. If different taxa were identified down to differing taxonomic levels, comparisons have to take this into consideration. Also, a possible bias caused by different stages of digestion for different taxa may cause severe errors. Ignoring unidentifiable diet components is likely to bias against more rapidly digestible material (Duffy and Jackson, 1986). The same holds, of course, for quantitative analyses.

Quantitative data

Prey lists should be extended to make at least some estimates of the abundance of the different taxa found. The easiest (and fastest) way is to note in how many "sample-units" the respective food item occurred, i.e. in what percentage of pellets, stomachs, etc., which should be termed "frequency of occurrence". However, regarding the large differences in size of prey items in many seabird species, e.g. copepods vs. fish in fulmars (*Fulmarus glacialis*; Furness and Todd, 1984), or amphipods and other small crustaceans vs. fish in Brünnich's guillemot (Lønne and Gabrielsen, 1992), better measures to quantify food should also be applied if possible. Dietary data can be quantified in terms of numbers of individuals per taxon (resulting in "numerical abundance") or by biomass estimates per taxon if there are means to count individuals and/or to estimate their volume or weight. Because many prey items will be partly or largely digested and therefore incomplete, there is a need to convert numbers of individual prey items to the (minimum/maximum) number of

individual prey of a given size and weight. Any documentation should clarify the techniques used to estimate the size and weight of individual prey (e.g. the regression equations used to calculate fish size from otoliths dimensions, or to estimate shrimp size from particular measurements of claws or carapace). Documentation of prey size should preferably include length frequency distributions (histograms), because these will often reveal the age distributions of fish taken as well as the range (minimum and maximum), the mean (with standard deviation or error) and the median size of prey (including the quartiles), and sample size. Biomass given as wet weight is preferable to dry weight, but it should be given with caution, because prey may dehydrate when transported in the beaks of parent birds returning food to colonies (Montevecchi and Piatt, 1987). Conversion factors between wet and dry weights should be quoted.

Several indices and methods to compare species or sites have been published. Pinkas (1971), Pitcher (1980), Bigg and Perez (1985), and Day and Byrd (1989) developed various indices of relative importance, Duffy and Jackson (1986) listed a variety of diversity indices, and Swanson *et al.* (1974) describe how to weight diet samples mathematically. Diet similarity (or overlap) among samples can be determined, for instance using percentage composition by weight and Morisita's index of diet similarity, which expresses similarity as a percentage (Baltz and Morejohn, 1977). Other niche parameters that can be calculated if frequencies are available are niche breadth or niche overlap (Colwell and

Futuyma, 1971; Mühlenberg, 1989). Also, more sophisticated statistics such as cluster analysis or multidimensional scaling may be applied for categorizing dietary data (Lønne and Gabrielsen, 1992; Kubetzki and Garthe, 2003). All these methods require that the original data are presented in a comparable manner (see above). Again, it is extremely important to have the diet analysed down to the same taxonomic level to achieve comparable data and to allow for differences in digestibility.

Discussion

Differences in diet between adults and chicks, breeders and non-breeders

When analysing and evaluating studies of seabird food, there is often bias resulting from a non-representative sampling design. Because it is extremely difficult to sample diet of seabirds at sea, it is not surprising that the vast majority of studies on seabird feeding ecology is restricted to the breeding sites and seasons. Moreover, even the comparatively few studies that have compared the diets of adults to chicks or of breeders to non-breeders have almost all revealed substantial differences in diet.

Seabirds provisioning chicks face different constraints from those when self-feeding and, as a result, chick food normally differs from the food eaten by adults (Ydenberg, 1994; Dierschke and Hüppop, 2003). Small chicks may be unable to ingest large prey (Shealer, 1998), and parents flying with prey visible in their bills may be subject to kleptoparasitism (Veen, 1977; Furness, 1978; Burger and Gochfeld, 1991; Ratcliffe *et al.*, 1997) or face aerodynamic or gravity constraints. Moreover, prey otherwise "optimal" or "ideal" for adults may be available only at distances from colonies that outweigh their caloric or nutritional advantages (Weimerskirch, 1998). These constraints all lead to a shift in adult diet away from prey optimal for chick rearing, so reducing the possibilities of determining the former in the breeding colonies. Optimal foraging theory, or more precisely, central-place foraging theories (Orians and Pearson, 1979) predict that:

- (i) single-prey loaders (such as guillemots or terns) should bring larger, and in energetical terms richer, prey to their chicks than they swallow themselves (Wilson *et al.*, 2004; Sonntag and Hüppop, 2005);
- (ii) multiple-prey loaders (such as many smaller auks that can carry several fish in their bill, Procellariiformes that convert prey to stomach oil, or seabirds that ferry multiple prey in their crop and/or stomach) should optimize their energy load per trip, particularly if trips are long, or few and far between (Ydenberg, 1994; Davoren and Burger, 1999).

Optimizing energy load may be achieved by selecting fatty fish such as clupeids, sandeels, capelin, or mackerel (*Scomber scombrus*), but also by selecting larger or gravid fish, because these generally contain more energy per item and per gramme (Montevecchi and Piatt, 1984; Hislop *et al.*, 1991; Lawson *et al.*, 1998). Parents need to sustain themselves and should therefore attempt to allocate their resources optimally between themselves and their chicks. Those that need only to feed themselves may satisfy their daily needs with small or lean prey, if easily available, but parents that need to invest heavily in prey transport will benefit from being selective (Mehlum, 2001). Optimal prey allocation may lead to starvation of young if adult survival or fitness is at risk in years where food is scarce or of poor quality. Seabirds are generally long-lived, and would rather desert their offspring when

conditions turn bad than risk a reduction in their own survival and hence their lifetime reproductive potential (Erikstad *et al.*, 1998, but see also Davis *et al.*, 2005). Therefore, they only continue to feed young when resources are adequate. When single-prey loaders feed their young, the allocation of food between parents and chicks could, in theory, take the form of optimal sharing (Leopold *et al.*, 1996; Davis *et al.*, 2005; Sonntag and Hüppop, 2005), i.e. the parents ingest all small prey, and fly off only with large prey, with the threshold being determined by their relative needs. Alternatively, parents could fulfil their own needs first, before switching to chick provisioning. Studies that simultaneously examine adult and chick diet are rare in seabirds (Brown and Ewins, 1996; Davoren and Burger, 1999; Dierschke and Hüppop, 2003; Wilson *et al.*, 2004). Parental foraging tactics investigated with bird-borne tracking and activity devices and sensors that record prey intake (e.g. Weimerskirch, 1998; Wilson *et al.*, 2002; Garthe *et al.*, 2007) will help shed light on the behavioural decisions that underlie these dietary patterns.

Breeding birds without chicks include birds that still have eggs or birds that have lost their clutch or brood. Birds with chicks bring in food that is higher in energetic density than the food taken by birds without chicks (Keijl *et al.*, 1986; Noordhuis and Spaans, 1992; Brown and Ewins, 1996; Ojowski *et al.*, 2001). Mehlum (2001) showed that common guillemots and Brünnich's guillemots that bring fish to their young can have much smaller prey, e.g. euphausiids, as their staple diet when self-feeding. This may also be the case in the pre-fledging period of common guillemots shortly after the chick has left the breeding shelf and is being fed at sea by the male parent (Anker-Nilssen and Nygård, 1987). Other studies in the non-breeding season, i.e. away from the colonies and not connected to chick-provisioning, suggest that seabirds then take a larger variety of prey, including many species that are relatively low in energy density (Bradstreet and Brown, 1985; Hedd and Montevecchi, 2006), and often at a lower trophic level (Bearhop *et al.*, 2001).

The diet of adults may vary through the breeding period or may differ between sexes, reflecting changing demands through the seasons (Spaans, 1971; Pierotti and Annett, 1987, 1991; Pons, 1994), or even between individuals. For example, Niebuhr (1983) observed that female herring gulls in the pre-laying period preferred mussels, which provided calcium for egg-shell formation, whereas males fed on refuse. Despite the greater energetic value of refuse, mussel specialists produced more offspring, and their chicks were larger at all developmental stages than those of refuse specialists (Pierotti and Annett, 1987). Individual feeding preferences provide additional variability (McCleery and Sibly, 1986), necessitating large sample sizes.

At seabird colonies, there is generally a high proportion of non-breeding adults (Aebischer, 1986; Pons and Migot, 1995; Warham, 1996; Grunsky-Schöneberg, 1998). These are immatures and adults that skip breeding for a year (or more), which might extenuate energetic constraints and hence increase lifetime reproduction and overall fitness (Cailadine and Harris, 1997; Cam *et al.*, 1998; Bradley *et al.*, 2000). Again, owing to different demands and constraints, their diets likely differ from those of breeders. Diets may therefore differ within individuals over time, and between individuals at any one time and place given different constraints and opportunities (opportunistic feeding).

The major problem with seabird diet studies to date is the lack of knowledge concerning the food of birds at sea away from the colonies, i.e. outside the breeding season, and for non-breeding

and immature birds. Most species of seabird spend most of their lives offshore, so many of the data on the diet of non-breeding seabirds are derived from beached birds or from birds drowned in fishing nets. In general, feeding can be more opportunistic outside the breeding season because birds are not forced to stay near their breeding sites or to provision chicks. Hence, food composition is more varied outside the breeding season (Spaans, 1971; Halley *et al.*, 1995; Ainley *et al.*, 1996; Ouweland *et al.*, 2004; Ludynia *et al.*, 2005).

Seabird diet and threats to seabirds

It is widely accepted that a great threat to seabirds currently is longline bycatch mortality. This affects many species of scavenging seabird, especially albatrosses, with 19 of the 21 species of albatross considered to be under threat of extinction as a result of unsustainable mortality caused by fisheries (Phillips *et al.*, 2006; Bull, 2007). Better understanding of scavenging seabird diets and feeding ecology is an important part of understanding this impact, and of developing mitigation measures or management to reduce the possibility of interaction. Biochemical approaches in particular may help to indicate how important longline baits are as food for scavenging seabirds, and the use of data loggers and satellite transmitters may provide a better understanding of the foraging behaviour of scavenging seabirds in relation to fishing vessel locations and activities. In addition, it is clear that scavenging seabirds may benefit from fishery waste (offal and discards), and that the suitability of this waste can vary dramatically according to regional variations in fishery management practice and regulations (Furness *et al.*, in press). Profound changes in fisheries, such as the introduction of a zero discard policy after many years of high rates of discarding, may have important implications for scavenging seabirds, but also for other smaller seabirds on which these scavengers may feed when deprived of discards (Votier *et al.*, 2004). Monitoring seabird diets during such periods of changing fishery management will be an important aspect of "ecosystem-wide management" and may best be done using a combination of biochemical and direct conventional approaches.

Another major concern is the reduction in food availability to seabirds that may result from climate change or fisheries (Tasker *et al.*, 2000; Furness 2002, 2003; Wanless *et al.*, 2007). Here again, monitoring of seabird diets, including the size and energetic quality of prey items (Wanless *et al.*, 2005a, b) over a series of years will help to determine how diets vary as a function of food fish abundance, and may indicate the necessary minimum biomass of food fish required to sustain healthy populations of seabirds in particular ecosystems.

Seabird diet in the context of ecosystem function and management

Cairns (1987) introduced an integrated approach to the use of seabirds as indicators of marine food supplies, and later (Cairns, 1992) stressed the need for closer collaboration between seabird biology and fisheries science to benefit the conservation of both birds and fish. With increasing concern over the conservation of marine ecosystems that sustain intensive fishing effort (Pauly *et al.*, 2005), the need to monitor the diets of seabirds and to incorporate seabird populations within regional models of marine ecosystems is becoming even clearer.

Many seabirds are excellent, wide-ranging samplers of small fish that are difficult to sample adequately by traditional survey methods, e.g. because the fish are schooling or keep to nearshore

nursery areas inaccessible to seagoing vessels. In terms of timeliness, cost-efficiency, and accuracy, data on seabird diets may therefore often prove to be valuable indicators of fish recruitment that are well-suited for incorporation in or for tuning fisheries assessment models (Barrett, 1991; Cairns, 1992; Litzow *et al.*, 2000; Lewis *et al.*, 2001).

Karpouzi *et al.* (2007) estimated that seabirds of the world consume ~96 million tonnes of food each year, compared with a total catch by marine fisheries of ~120 million tonnes. Although Karpouzi *et al.* (2007) were able to map in considerable detail the geographical hotspots for consumption by seabirds, they could find data on diet composition for just half the world's seabird species; data had to be guessed for the other half. Moreover, for most species, the only data on diet are for birds sampled during the breeding season, and often only for chick diet, so these global or regional ecosystem energetics models are forced to use limited, probably biased, data on diet composition. Even within regions where seabird research has been particularly detailed, as in the North Sea, there are few data on the diet of most species of seabird during winter, and these limitations constrain quantitative assessments of food consumption at an ecosystem level. It is to be hoped that a combination of the newly developing biochemical methods, conventional sampling, and the use of new data loggers (including camera loggers) may provide the opportunity to determine winter diets of the most abundant seabirds in the near future.

Overview and summary

Valuable information about feeding ecology, foodwebs, and oceanographic variability can be garnered from dietary studies of marine birds. Many species of seabird are excellent, wide-ranging samplers of small fish and crustaceans that are difficult to sample adequately by traditional survey methods. Many target fish species exhibit vessel and gear avoidance, or occur in surface waters in hydroacoustically invisible zones and/or in near-shore nursery areas outside the range of seagoing vessels (Montevecchi, 1993). Many of the species consumed by seabirds are not commercially exploited so are ignored by surveys supporting fisheries management. Yet these "non-commercial" species often come to be exploited commercially and are then overfished (Pauly *et al.*, 1998). Seabird samplers can also provide insights into changes in the ecology of such unexploited species and also at times provide key information about ocean climate change independent of direct fishery influences (Field *et al.*, 2007; Montevecchi, in press). In terms of providing early warning signals, cost-efficiency, and precision, seabird diets have often provided useful information about fish recruitment that is well suited for incorporation in fisheries management models (Hislop and Harris, 1985; Barrett, 1991; 2002; Hatch and Sanger, 1992; Roth *et al.*, 2007).

Owing to the considerable variability in the methods with which dietary data can be collected and reported, there is often a lack of comparability among findings that can hinder more comprehensive and broader application. By reviewing and evaluating these methods and their limitations, and by making recommendations from standardization in the reporting of results, our aim has been to increase the information value and comparability of seabird diet data collected by marine ornithologists and to further extend their usage in marine ecology, fisheries research, and in biological and physical oceanography.

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