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Introduction

J. P. CROXALL

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 OET, UK

The last decade or so has been a period of unrivalled progress in our quantitative understanding of the processes of energy flux in marine systems. Not surprisingly, much of this research has been directed to questions and topics relevant to the management of commercial fisheries. Nevertheless, this has also served to focus attention on those natural components of the system, such as seabirds and seals, which might compete with, or prey upon, commercially important species (e.g Furness, 1982; Nettleship, Sanger & Springer, 1984).

Understanding predator–prey relationships requires much information about the diet, distribution and bioenergetics of both predators and prey and on the detailed nature of their interactions. Such data are not easy to acquire, even for terrestrial systems where direct, simultaneous observation and experimentation is possible. In pelagic marine systems, wide-ranging predators operate in a vast, ever-changing three-dimensional environment. Study and sampling under these conditions are severely constrained by the limitations of operating from research vessels and shore stations. However, a number of major studies have recently been undertaken to assess the role of top predators, especially seabirds, as consumers in productive marine systems.

This book, which originated from a symposium on 'Seabirds and nutrient cycles' at the XVIII International Ornithological Congress in Moscow (Croxall, 1986), presents results from a selection of these studies, covering a broad geographical range from Arctic (Chapters 10, 11), north temperate (Chapter 11), tropical–subtropical (Chapters 12–14), south temperate (Chapter 14) and sub-Antarctic (Chapter 15) regions. These illustrate both the general features, and different views, of the role of seabirds in a variety of marine ecosystems.

To complement these case-studies of particular seabird communities and to provide a broader perspective concerning many of the species involved, the first part of the book treats in detail the feeding ecology of the main seabird groups and reviews a number of topics of fundamental importance to understanding the interactions of seabirds with their marine environments.

Most of this book – and especially the reviews of feeding ecology – is concerned with four seabird groups: penguins (Sphenisciformes); albatrosses, petrels, storm petrels and diving petrels (Procellariiformes); pelicans, gannets and boobies, frigatebirds, tropicbirds and cormorants (Pelecaniformes); and auks, or alcids (Alcidae). This assemblage totals nearly 200 species; about another 100 species (mainly terns, gulls and sea ducks), which derive nearly all their food from the sea, are not considered in any detail here. This was partly an arbitrary decision to keep the volume within bounds but also reflects the fact that few of these species both venture far from land and are also sufficiently abundant to have any major impact on marine resources.

There are a number of major questions relating to predators in the context of their interactions with prey. 1. How many are there? 2. What do they eat? 3. How much energy (i.e. food) do they need? 4. When, where (and how) do they take their prey?

This volume seeks to deal with the nature of seabird diets, when and how they catch prey and, in respect of the case-studies, where these activities are concentrated, at least at certain times of the year. Detailed information on the current status of all the world's seabirds (Croxall, Evans & Schreiber, 1984) and on seabird energetics (Whittow & Rahn, 1984) has recently been published. These topics are not covered here.

Because the early chapters of this book review the characteristics of the marine environment (Chapter 2), seabirds' adaptations and abilities for flight (Chapter 3) and diving (Chapter 4) and their adaptations for feeding at sea (Chapters 6–9), this introduction need only briefly summarise various aspects of the life style of seabirds.

Although oceans cover 60% of the earth's surface, only 2–3% of the world's birds have been able to exploit them effectively. This suggests that it is no simple matter for birds to live at sea especially perhaps because they must spend considerable time ashore when they breed. It is not surprising, therefore, that amongst birds, seabirds show a number of quite extreme biological and ecological adaptations and features.

In general, seabirds are larger than land birds and lay eggs that are also larger, but not disproportionately so. Seabirds also lay small clutches and in three groups (Procellariiformes, Fregatidae, Phaethontidae) all species produce only a single egg, proportionately larger than the eggs of species with larger clutches. Large eggs tend to take a long time to hatch and seabirds, in particular many tropical species and all Procellariiformes, show very extended incubation periods compared with other birds. This feature and the relations between egg size, yolk content, embryonic growth rate and other aspects of incubation are treated in Whittow & Rahn (1984). Egg formation is also a lengthy process in seabirds (Grau, 1984) with yolk deposition taking up to 30 days and the lag period (between yolk completion and laying) lasting up to 10 days (cf one day in chickens).

Similarly, rearing chicks to independence lasts a long time in seabirds, often 2 months or more and up to about one year in the King Penguin *Aptenodytes patagonicus*. Only for the auks are short periods typical; in this family a few species have highly precocial young, which depart to sea with their parents when only 2–3 days old. However, such chicks receive extensive parental care at sea. Post-fledging parental care is also typical, even for well-grown offspring that may be capable of some independent feeding, in the case of pelicans, boobies, cormorants, frigatebirds and at least one species of tropicbird. It is very rare in penguins, Procellariiformes (only occurring in tropical albatrosses) and auks (except for the precocial murrelets and possibly the Little Auk (Dovekie) *Alle alle*). The topic is reviewed by Burger (1980).

It will be clear from this that seabirds tend to have long breeding seasons. In extreme cases, this period, from arrival at the colony in order to commence pre-breeding courtship activities until the time when chicks become independent, may last more than a year (e.g. in King Penguins, several albatrosses and frigatebirds). If successful in rearing a chick such species breed less frequently than annually. Most other species, however, breed once each year.

Seabirds are long-lived, with an adult survivorship that is rarely less than 80% per year, typically around 90% and attains 95% in many Procellariiformes, some gannets and some auks. They also show considerably deferred sexual and/or social maturity and the mean ages at which reproduction starts in albatrosses (and possibly frigatebirds) are the oldest recorded in birds. Sexual maturity in albatrosses is attained at earlier ages but the acquisition of a partner (which involves spending substantial periods ashore – and hence not feeding) takes several further years. All this suggests that the acquisition of experience, presumably initially learning to find and capture food and later forming pair-bonds with a partner, is a key feature of the early life of seabirds. While the majority

Table 1.1. *Some mean demographic and biological characteristics of the main families of seabirds*

Group	No. of species	Adult weight (kg)	Age (years) at first breeding	Adult annual survival rate (%)	Clutch size	Incubation period (days)	Chick-rearing period (days)
Sphenisciformes							
Spheniscidae (penguins)	16–18	4–12(–40)[a]	4–8	75–85(–95)[a]	1–2	33–62	50–80(–350)[b]
Procellariiformes							
Diomedeidae (albatrosses)	14	2–4(–12)[c]	7–13	92–97	1	60–79	116–150(–280)[c]
Procellariidae (petrels)	*c.* 70	0·15–2·3(–7)[d]	4–10	90–96	1	43–62	42–120
Hydrobatidae (storm petrels)	20	0·03–0·05	*c.* 4–5	*c.* 90+	1	40–50	55–70
Pelecanoididae (diving petrels)	4	0·1	2–3	75–80	1	46–56	45–55
Pelecaniformes							
Pelecanidae (pelicans)	2[e]	3·5	3–4	*c.* 85	2–3	30	55–60
Sulidae (gannets, boobies)	9	1–3·5	3–5	90–95	1–2(–3)[f]	41–56	90–120(–170)[g]
Phaethontidae (tropicbirds)	3	0·5–0·8	?	?	1	41–44	60–90
Fregatidae (frigatebirds)	5	0·7–1·5	?*c.* 9–10	?	1	44–55	140–170+
Phalacrocoracidae (cormorants)	29	1–5	4–5	85–90	2–3	25–30	60–90
Charadriiformes							
Alcidae (auks)	22	0·1–1·0	2–5	80–93	1–2	29–42	(2[h]–)15–50

[a] Emperor Penguin *Aptenodytes forsteri*. [b] Emperor Penguin 170 days; King Penguin *A. patagonicus* 350 days. [c] Great albatrosses. [d] Giant petrels *Macronectes* spp. [e] There are 6 other, essentially non-marine, species. [f] Boobies. [g] Red-footed Booby *Sula sula* to 140 days; Abbott's Booby *S. abbotti* to 170+ days; [h] *Synthliboramphus* murrelets.

of seabirds are monogamous and pair for life (although some divorces occur even in such species), there is evidence that most species of booby and frigatebird change partners more regularly.

Some of these features are summarised for each of the families treated in this book in Table 1.1. Within each family there is a considerable range of adaptions, perhaps particularly in the auks, but there is not space to treat this in detail here. Many aspects of the general biology and ecology of seabirds have been reviewed by Nelson (1980); the emphasis in the rest of this volume must remain with feeding ecology.

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