1

Introduction

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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
Introduction

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

<table>
<thead>
<tr>
<th>Group</th>
<th>No. of species</th>
<th>Adult weight (kg)</th>
<th>Age (years) at first breeding</th>
<th>Adult annual survival rate (%)</th>
<th>Clutch size</th>
<th>Incubation period (days)</th>
<th>Chick-rearing period (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Sphenisciformes</strong></td>
<td></td>
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<tr>
<td>Spheniscidae (penguins)</td>
<td>16–18</td>
<td>4–12(−40)</td>
<td>4–8</td>
<td>75–85(−95)</td>
<td>1–2</td>
<td>33–62</td>
<td>50–80(−350)</td>
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<tr>
<td><strong>Procellariiformes</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Diomedeidae (albatrosses)</td>
<td>14</td>
<td>2–4(−12)</td>
<td>7–13</td>
<td>92–97</td>
<td>1</td>
<td>60–79</td>
<td>116–150(−280)</td>
</tr>
<tr>
<td>Procellariidae (petrels)</td>
<td>c. 70</td>
<td>0.15–2.3(−7)</td>
<td>4–10</td>
<td>90–96</td>
<td>1</td>
<td>43–62</td>
<td>42–120</td>
</tr>
<tr>
<td>Hydrobatidae (storm petrels)</td>
<td>20</td>
<td>0.03–0.05</td>
<td>c. 4–5</td>
<td>c. 90+</td>
<td>1</td>
<td>40–50</td>
<td>55–70</td>
</tr>
<tr>
<td>Pelecanoidae (diving petrels)</td>
<td>4</td>
<td>0.1</td>
<td>2–3</td>
<td>75–80</td>
<td>1</td>
<td>46–56</td>
<td>45–55</td>
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<td><strong>Pelecaniformes</strong></td>
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<tr>
<td>Pelecanidae (pelicans)</td>
<td>2*</td>
<td>3.5</td>
<td>3–4</td>
<td>c. 85</td>
<td>2–3</td>
<td>30</td>
<td>55–60</td>
</tr>
<tr>
<td>Sulidae (gannets, boobies)</td>
<td>9</td>
<td>1–3.5</td>
<td>3–5</td>
<td>90–95</td>
<td>1–2(−3)</td>
<td>41–56</td>
<td>90–120(−170)</td>
</tr>
<tr>
<td>Phaethontidae (tropicbirds)</td>
<td>3</td>
<td>0.5–0.8</td>
<td>?</td>
<td>?</td>
<td>1</td>
<td>41–44</td>
<td>60–90</td>
</tr>
<tr>
<td>Fregatidae (frigatebirds)</td>
<td>5</td>
<td>0.7–1.5</td>
<td>?c. 9–10</td>
<td>?</td>
<td>1</td>
<td>44–55</td>
<td>140–170+</td>
</tr>
<tr>
<td>Phalacrocoracidae (cormorants)</td>
<td>29</td>
<td>1–5</td>
<td>4–5</td>
<td>85–90</td>
<td>2–3</td>
<td>25–30</td>
<td>60–90</td>
</tr>
<tr>
<td><strong>Charadriiformes</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Alcidae (auks)</td>
<td>22</td>
<td>0.1–1.0</td>
<td>2–5</td>
<td>80–93</td>
<td>1–2</td>
<td>29–42</td>
<td>(2b−) 15–50</td>
</tr>
</tbody>
</table>

*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; *Synthliboramphus* murrelets.
Introduction

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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References
2

Scale-dependent processes in the physical and biological environment of marine birds

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Introduction

A major goal of pelagic bird studies is to understand the determinants of bird distribution and abundance. Seabirds inhabit a highly heterogeneous environment, in which physical processes are a function of scale (Stommel, 1963). Large-scale processes include major circulation patterns in ocean basins; intermediate-scale processes include differentiation of water masses and movements of large gyres; and small-scale processes include eddies that may be only a few meters across. Because most chemical and biological processes in the ocean are driven by physical processes, they are also a function of scale. In this chapter we discuss seabirds in the context of scale-dependent variability in their physical and biological environment.

Prey distribution is one likely determinant of bird distribution, and investigators have attempted to measure and correlate bird and prey numbers. Jesperson (1930) made daily counts of birds while zooplankton were sampled over 1000 km × 1000 km segments of the North Atlantic. These bird and plankton abundances were highly correlated (Ricklefs, 1973), with a remarkable explained variance ($r^2 = 0.76$) for a pelagic bird study. On a smaller scale, Woodby (1984) used hydroacoustic surveys of euphausiids (Thysanoessa sp.) in the southeastern Bering Sea and found a correlation between regions with acoustic echoes and the presence of murres Urta sp. in one of two years. However, he did not demonstrate that the murres were foraging on the source of the echoes. In the Antarctic, Obst (1985) used a depth sounder for a hydroacoustic survey and correlated the presence of birds and swarms of Euphausia superba, their principal food. Identification of the echo source was made by net hauls and SCUBA investigations. In the Bay of Fundy phalaropes concentrate near an upwelling off Brier Island (Brown, Barker & Gaskin, 1979). The phalaropes
feed on copepods which are brought to the surface by tidal currents sweeping over a shallow sill and are subsequently concentrated by a convergence front.

In contrast to these investigations, most pelagic bird studies have not included direct correlations between bird and prey abundance. There are several reasons. Bird studies are usually made from ships on other business and there is no chance to stop and sample prey or to assess bird diets. Many prey taken by birds are hard to sample using traditional plankton nets and trawls (Ashmole & Ashmole, 1968). Fish, squid and even euphausiids move too rapidly to be sampled quantitatively by this gear. Hydroacoustic survey methods promise to alleviate this problem. Additionally, because most seabirds are opportunistic predators that partition marine resources on the basis of habitat (water masses) rather than by prey type (Ainley, 1980), it is difficult to know which prey to sample. Once we have a better knowledge of prey distribution, it will then be crucial to understand how physical and chemical processes control prey productivity, patchiness and availability to birds. Conversely, because bird distribution and abundance reflect oceanic conditions, and because concentrations of birds are relatively easily observed, information on birds may be used by individuals in other oceanographic disciplines for locating features of interest (Gudkov, 1962; Ashmole & Ashmole, 1968; Zelickman & Golovkin, 1972).

While the pelagic distribution of birds may be closely tied to prey distribution, other behavioral, morphological or energetic constraints can disrupt this relation. Flight performance, related to wing loading and aspect ratios, may set morphological limits on distribution related to the predictability of winds of some minimum (or perhaps maximum) velocity (Bailey, 1968; Pennycuick, 1982; Ainley & Boekelheide, 1983). Cormorants are limited in their seaward dispersal by the wetability of their feathers (Rijke, 1968), while the distribution of birds with different styles of foraging (plunge diving versus pursuit diving) depends not only on food availability, but also on water clarity (Ainley, 1977). Finally, birds commuting between foraging areas or to and from a colony pass over water masses not used for foraging, thereby diminishing our ability to determine avian use of specific water masses (Ainley, 1980; Ainley, O’Connor & Boekelheide, 1984). This problem is exacerbated by birds that forage nocturnally but are censused during the day. Thus, in considering the role of physical events in patterning bird distribution, we cannot ignore patterns, unrelated to water-mass properties, generated by the other aspects of seabird biology (Pielou, 1960).
Scale-dependent processes in the marine environment

Spatial and temporal scales of variability
It is difficult to interpret observations of an isolated part of a system without some idea of the scale and structural organization of the whole (Hutchinson, 1953). Without prior experience, we cannot tell whether a particular observation is typical, or is a rare occurrence. Likewise, unexplained variance, noise at one scale, may be due to pattern at a different scale.

Stommel (1963) recognized the importance of scale and illustrated the relation between the temporal and spatial scales of several different physical processes in the ocean. Subsequently, Haury, McGowan & Wiebe (1978) modified Stommel’s type of diagram to show the time/space scales of variability of zooplankton biomass (Fig. 2.1). The patterns of greatest concern to marine ornithologists fall between B (swarms) and H (biogeographic provinces).

If we are to document quantitative relations between seabirds and oceanographic processes our sampling effort must reflect the scales of these processes (Crowley, 1977). When there is little spatial or temporal variation in a phenomenon, relatively few samples may describe it adequately. If there is considerable variation occurring at different scales then sampling must be increased (Stommel, 1963). Interactions between events at different scales confuse our ability to identify simple patterns, and these interactions may have biological importance.

Fig. 2.1. Temporal and spatial scales of physical and biological events in the ocean (after Haury et al., 1978, with permission of the authors and Plenum Press).
Sampling program design has recently gained prominence as oceanographers found that sampling effort affects their conclusions concerning the scale and variance of phenomena (Kelley, 1976; Dayton & Tegnor, 1984). Continuous sampling or at least frequent sampling at a scale much less than the smallest periodicity of interest (space or time) is critical (Platt & Denman, 1975). When the sampling interval is too large, the shortest fluctuations in the data cannot be resolved, and an apparent periodicity larger than the true periodicity will be obtained. Failure to perceive patches due to sampling at too large a scale can reduce apparent variability because variance generated at smaller scales is overlooked (Cassie, 1959; Crowley, 1977). In a computer simulation study and subsequent field study, Wiebe (1971, 1972) found that increasing the sampling effort (in his case, net size and tow length), increased the precision of population estimates because the variance of the estimates was an inverse function of the number of plankters ‘caught’.

Patchiness in plankton is likely to be important in understanding patchiness in bird distribution. Birds can prey directly on plankton; in other cases prey organisms, such as anchovies, can respond to plankton patchiness (Visser et al., 1973). It is important to know the scales of prey patchiness because small prey frequently are ‘useful’ to predators only when they are concentrated (Golovkin, Shivokolobov & Garkavaya, 1972; Gaskin, 1976; Brodie, Sameoto & Sheldon, 1978; Lasker, 1979).

Steele (1978) proposed a simplified representation of the scale of patchiness in marine systems in which the temporal and spatial scale (ambit) at which organisms live increases with successively higher levels in the food chain (Fig. 2.2). In this conceptualization, life span is the critical feature of the time scale. Phytoplankton move over a distance of a few kilometers during periods of 1–10 days. Fish occupy or visit areas with bounds of the order of 1000 km over a period of 300–2000 days.

Although Steele (1978) restricts the use of the term ambit to the space used during an organism’s lifetime, Haury et al. (1978) define ambits as ‘the sphere of action…of individuals over days, weeks, lifetimes’. This introduction of a variable time scale is important, particularly for long-lived organisms, because the physical scale relevant to their ecology or population biology will vary greatly with temporal scale between daily feeding bouts, breeding or wintering seasons, and oceanographic events influencing lifetime distribution or survival. While lifetime ambits can be large for organisms at higher trophic levels, their distributions may be highly localized or patchy over short periods of time, such as during foraging. This
increased short-term patchiness in high trophic-level prey is of consequence for top-level carnivores (Steele, 1980).

The control of phytoplankton patchiness is a complex function of growth, grazing and water mixing, interacting with factors that cause zooplankton to aggregate where barriers (fronts) limit dispersal. Vertical displacements in the water column have greater effect on photosynthesis than similar sized horizontal displacements, due to steeper gradients in light, nutrients and oxygen in the vertical (Owen, 1981). Thus phytoplankton and zooplankton have evolved structures and mechanisms for controlling their vertical position. In contrast, physical factors play a large role in structuring plankton patches horizontally and in time (Steele, 1976; Haury et al., 1978). The minimum horizontal distance over which phytoplankton growth can maintain patch structure against horizontal turbulent diffusion is of the order of a few kilometers (Platt, 1972; Steele, 1976). At smaller scales, water turbulence (eddies) controls their distribution. Eddies smaller than a few kilometers in diameter and of less than a week’s duration tend to break up biological patterning, while larger, longer-lived eddies may contribute to it (Owen, 1981).

The distribution of zooplankton relative to phytoplankton, and their interactions, are important because the chlorophyll content of water samples is frequently the only indicator marine ornithologists have of

Fig. 2.2. Temporal and spatial scales of lifetime ambi of various marine organisms: phytoplankton (P), zooplankton (Z) and fish (F) (after Steele, 1976, with permission of the author and Plenum Press).