

# Modelling relationships among fisheries, seabirds, and marine mammals

by Robert W. Furness

Zoology Department, Glasgow University, Glasgow  
G12 8QQ, Scotland, UK

## 1. Abstract

Calls for culls of seals or seabirds to increase fishery yields have been based on the projection of captive studies of food intake to field populations. Such estimates make a number of unsupported assumptions and lack statistical confidence limits. More precise computations can be made, based on generalized bioenergetics equations. Modelling indicates that seabirds in several ecosystems consume 20–30% of annual pelagic fish production, so are potentially in competition with commercial fisheries. Such estimates require sound knowledge of population size and flux, activity budgets, foraging ranges, and diets as well as data on fish production. Detailed studies of single-species populations could be used to validate the results of bioenergetics modelling. However, partitioning fish consumption between competing interests does not in itself allow detailed predictions of changes that will result from human manipulation. A number of empirical studies indicate that population responses to a reduced food supply depend on a spectrum of factors, particularly species life history and interspecific relationships.

## 2. Résumé

Les demandes d'abattage de phoques ou d'oiseaux de mer pour accroître le rendement de la pêche s'appuient sur la transposition d'études sur l'ingestion d'aliments en captivité à des populations sauvages. Ces estimations posent un certain nombre d'hypothèses non vérifiées et sont dépourvues de limites de confiance statistiques. Il est possible de faire des calculs plus précis en s'appuyant sur des équations généralisées de bioénergétique. La modélisation révèle que les oiseaux de mer de plusieurs écosystèmes consomment 20 à 30 % de la production annuelle de poissons pélagiques, ce qui en fait des concurrents potentiels pour la pêche commerciale. Ce genre d'estimation nécessite une parfaite connaissance de la taille des populations et de leurs mouvements, des budgets d'activité, de la distribution des aires d'alimentation et des régimes alimentaires ainsi que des données sur la production de poissons. Des études détaillées sur les populations à espèce unique pourraient servir à confirmer les résultats de la modélisation bioénergétique. Toutefois, le partage de la consommation de poissons entre les divers intérêts en jeu ne permet pas comme tel de prédire fidèlement les changements qui résulteraient de l'intervention humaine. Un certain nombre d'études empiriques révèlent que les réactions des populations à une réduction de l'approvisionnement alimentaire dépendent

de toute une gamme de facteurs, en particulier du cycle biologique des espèces et des rapports interspécifiques.

## 3. Introduction

This paper reviews the usefulness and limitations of quantitative estimation of the energy requirements of seabird and marine mammal populations, as a step towards understanding the interactions between these predators and their prey populations, and outlines the complex ecosystem relationships that need to be elucidated in order to allow the construction of models capable of predicting effects of perturbations of fish stocks on their natural predators.

Increasing human exploitation of fish stocks throughout the world has led to a focusing of attention on the management of marine ecosystems to maximize their yield to people. Rather than treating each fish population as if it were an isolated stock, as earlier fisheries biologists tended to do, it has become clear that we must manage whole ecosystems in order to optimize the yields of different commercially valuable organisms. Recent investigations of fisheries and stock changes have demonstrated the importance of competition and predator–prey interactions among species of fish (Andersen and Ursin 1977), and revealed management problems involving interactions between several trophic levels (May *et al.* 1979). Seabirds and marine mammals are often top predators in marine ecosystems, and as such are potential competitors with commercial fisheries. Where it is believed that this competition may result in serious and avoidable financial loss to commercial fisheries, an assessment of economic impact of seabirds and seals is a prerequisite to sensible management. Such assessment is most easily made by estimating the population energy requirement, and converting this to food consumption from information on the composition of the diet.

A knowledge of the quantities of food consumed by seabirds and marine mammals is also useful in the search for causal relationships between changes in marine ecosystem structure, induced by environmental changes or overfishing, and changes in the sizes of seabird and mammal populations. With increasing utilization of marine resources there have been demonstrable changes in the structure of many marine ecosystems, and these will inevitably influence populations of non-target species through alterations in the availability, quantity, or quality of their food supplies.

Although we are able to estimate the food consumption of populations, construction of models to simulate the effects of food shortage on seabird population biology is a



much more difficult task. I shall discuss this problem after reviewing the simpler energetics studies.

#### 4. Energy budgets

Broadly speaking, the approaches to quantifying the food consumption of seabird and marine mammal populations can be separated into three groupings, of increasing precision:

1. Combination of population census data with studies of food consumption by captive, or sometimes, free-living, animals;

2. Construction of simulation models combining population data and bioenergetic equations derived by controlled laboratory experimentation; and

3. Direct measurement of metabolic rate in free-living animals. I shall consider the use of these methods for estimating population food consumption (1) by marine mammals and (2) by seabirds.

##### 4.1. Marine mammal energy budgets

###### 4.1.1. Combination of census data and captive feeding studies —

The controversial proposals to cull grey seals (*Halichoerus grypus*) at colonies around Britain provide a good example of the approach used to estimate the quantity of exploited fishery resources consumed by seals and the consequential loss of potential fishery catch. Annual consumption of each prey species by the seal population is estimated from three sets of data: (1) the total number of seals of all ages in the population; (2) the average quantity of food consumed per seal per day; (3) the proportion, by weight, of each species in the diet.

Adult grey seals cannot be counted at sea or at breeding colonies as they are never all together, and the proportion present at any particular time is unknown. The size of the population has to be estimated from counts of pups and life-table statistics (Summers 1978). The ratio of pup numbers to total population size depends on adult survival rate, fecundity, juvenile survival rate, neo-natal mortality, time spent ashore by pups before putting to sea, and the extent of the breeding season. Detailed life-table data are available only for the increasing Farne Islands population, and conversion of pup counts to population size for other areas extrapolate from the Farnes data, assuming that these mortality and fecundity data are applicable to the other populations. The validity of this procedure is dubious, and it is not possible to attach confidence limits to the estimates of total population size. It can be suggested that the mid 1970s pup production of 19 000 individuals at British colonies represents a population size of 70 000 animals, and comparisons with earlier counts indicate a 6–7% increase per annum (Summers 1978).

With presently available techniques, the daily food intake of seals cannot be measured in the field. Such studies would be almost impossible to conduct owing to the pelagic distribution of seals outside the breeding season. Owing to their rapid digestion of food, analysis of stomach contents cannot give reliable information on feeding rates, although this may give an indication of maximum meal size. The assessment of food consumption has been limited to studies of seals kept in captivity. A detailed survey of pinniped species kept in captivity recorded daily food intake of 6–10% of body weight (Keyes 1968), and similar results have been obtained for porpoises (Sergeant 1969). Rae

(1960) and Parrish and Shearer (1977) used an average value of 7 kg per grey seal per day, applying for every day of the year, for the total, all-age, population of grey seals breeding in the British Isles. This was based on observed intake in captivity, and is at the lower end of the range 6–10% of mean body weight. However, grey seals fast for up to 6 weeks during the breeding season, and lose weight, and it is debatable whether captive feeding rates can be applied to wild animals, which are likely to be more active than those in captivity and are less likely to overeat.

###### 4.1.2. Use of bioenergetic equations for marine mammals —

Grenfell and Lawton (1979) used bioenergetic equations provided by Lockyer (1976) to estimate resting metabolic rates (*RMR*) of marine mammals from their body weights. Lockyer (1976) obtained the relationship:

$$RMR \text{ (kcal/day)} = 126.2 W^{0.75} \text{ (s.e. 0.035)}$$

(where *W* is body weight in kg, 1 kcal = 4.19 kJ) from studies using a variety of whales and seals. To convert this to field metabolic rates (*FMR*) Grenfell and Lawton (1979) multiplied *RMR* by a factor of 2, with lower limit of 1.5 and upper limit of 3. Hinga (1979) concluded that the field energy requirements of large whales are approximately 1.5 times *RMR*.

To *FMR* must be added costs of tissue production and assimilation. Humphreys (1979) found an average annual production by large mammals equalling 3.4% of energy assimilation. Assimilation efficiency (conversion of food ingested into assimilated energy) is about 80% in most carnivorous mammals (Lawton 1970). Using Grenfell and Lawton's method, the energy requirement of a grey seal weighing 110 kg would be 12 000 kcal/day, equivalent to about 11 kg of fish/day, if a conversion factor of 2 is used to obtain *FMR* from *RMR*. This suggests that the 7 kg/day estimated from captive feeding studies may be a conservatively low value when calculating total food intake by the population.

###### 4.1.3. Estimated impacts of grey seals on fish stocks —

Grey seal diet has been examined by stomach sampling from animals caught by or in the vicinity of nets or whitfish boats, mainly along the Scottish east coast. This doubtless biases the data in favour of commercially exploited fish species. Little is known of the seasonal or geographical variation in grey seal diet, but it seems likely that cephalopods and sandlance (*Ammodytes marinus*) are important in the diet of grey seals in Orkney and Shetland, where very little stomach sampling has been attempted (Rae 1960). Fishery biologists have tended to discount this bias as insignificant, but in fact it is an unknown and possibly very considerable one.

The final problem is estimation of the loss of potential fishery catch. This can be estimated given the exploitation rate of the fishery for each species consumed and on the assumption that the fish consumed would, if not eaten, be available to the fisheries in the same manner as those not subject to seal predation. For most fish stocks in British waters the rate of exploitation (defined as fishing mortality rate/total mortality rate) is high, in excess of 0.5, and stocks are depleted as a result. Of course, a proportion of the grey seal's diet will be small fish not yet recruited into the commercial fishery and this cannot be adequately assessed at present owing to the biased nature of stomach samples collected to date and to the tendency for much of the stomach contents to be partly digested.



As a result of all these uncertainties, no precise estimate of either the amount of fish consumed by grey seals or the loss of potential fishery catch can be made. Total population size and mean body weight are unlikely to be in error by as much as 50%, but daily food intake may be at least 50% more or less than estimated, and dietary composition of all grey seals throughout the whole year may be very different from that of the samples collected. In view of this, it is little more than speculation to use these data to calculate the impact of grey seals on British fisheries, but Parrish and Shearer (1977) nonetheless suggested that fish consumption by grey seals amounted to 112 000 t/year, and that this, according to the available dietary information, represented a loss of catch to the fishing industry in the mid 1970s of 56 000 t, equivalent to US\$30 million and 5–10% of the total fish catch taken within the UK's fishery limits.

## 4.2. Seabird population food requirements

4.2.1. *Field estimation of seabird food consumption* — In many seabird communities one or two species are numerically dominant and are also responsible for almost all the food consumption of the community. Field observations show how many feeding trips each adult makes per day and how much food is carried in an average meal. Multiplication of these by the number of adults and the number of days that the birds spend at the colony each summer gives the food consumption by the population over the breeding season. Many practical difficulties arise with this method. For example, numbers of feeding trips per day vary seasonally and in relation to brood size and chick age. Non-breeders spend only part of the summer at the colony and take less food than breeders. Even so, this direct approach has been used in a number of early attempts to quantify food consumption by seabirds, particularly with large colonies of Common Murres (*Uria aalge*) and Thick-billed Murres (*Uria lomvia*). At the Seven Islands Reserve, Murman coast, Barents Sea, Kaftanovski (1951) estimated adult food intake at 30 g/day. Also on the Murman coast, Belopolskii (1961) estimated adult food consumption at about 60 g/day and chicks' consumption at 20 g/day. On Novaya Zemlya, Uspenski (1956) calculated that adults take 100 g/day and chicks 35–40 g/day, while Tuck and Squires (1955) at Akpatok Island, Ungava Bay, estimated that adults ate 220 g/day and, from feeding experiments, determined that chicks consumed 13.4 g/day for each gram increase in body weight, or the equivalent of about one-half their body weight in food per day. Although some of the differences between these estimates may be due to variations in climate, food availability, adult activity budgets, or the calorific value of the food taken, such empiric calculations of food consumption are clearly only able to provide an order of magnitude estimate for the food consumption of the seabird communities studied by these authors.

4.2.2. *Bioenergetics models* — The use of bioenergetics equations is reviewed by Kendeigh *et al.* (1977) and the application of bioenergetics modelling in estimating the potential impact of granivorous passerines on the ecosystem is reviewed by Wiens and Dyer (1977). Bioenergetics modelling aims to obtain the values for the numerous parameters of breeding biology and to couple these with generalized bioenergetics equations, computed for passerines or non-passerines, to calculate the daily energy budget of a population. Thus, values obtained under controlled laboratory conditions are projected to free-living populations with

specified activity patterns, biology, and environment. The extensive literature on seabird populations and biology makes this an obvious approach to adopt when considering their impact on fish stocks.

Metabolism can be most precisely defined and measured in terms of the basal metabolic rate (*BMR*). This is the rate of energy utilization by animal tissues at rest and unstimulated by food assimilation or digestion or by low or high temperature. In the field, animals never exist at their *BMR*, as they are usually digesting food and not at complete rest, so basal metabolism is not appropriate for bioenergetics modelling. A more useful measure is "existence metabolism" (*EM*). This is defined as the rate of energy utilization by caged birds able to undertake limited locomotor activity (but not flight) and that are maintaining a constant mass and not undergoing reproduction, moult, growth, or migratory restlessness. Kendeigh (1970) gave logarithmic allometric equations for *EM* of 13 passerine and 5 non-passerine species. Within these categories species followed a common relationship, implying that the *EM* of any seabird species can be calculated from a knowledge of its mass, and the ambient temperature.

Wiens and Scott (1975) based their simulation of Oregon seabird energetics on Kendeigh's equations derived from studies of five non-passerines (a duck, a goose, and three pheasant species). I also used these equations as the basis of a simulation of a Shetland seabird community energy budget (Furness 1978), but pointed out the wide confidence interval associated with Kendeigh's equations, such that these provided the main source of error in the model. Since 1970, extensive studies of *EM* have been carried out with a wide variety of species. Kendeigh *et al.* (1977) confirmed the differences between passerines and non-passerines, and showed that the relationships were identical for almost all orders of non-passerines. Based on 40 or more species of non-passerine the regressions have much smaller standard errors than those used by Wiens and Scott (1975) or Furness (1978). For a typical seabird this would be about 1% rather than the 15–25% resulting from the Kendeigh (1970) equations. Allometric equations have also been derived for other activities of free-living birds, so that activity budget data may be converted to energy expenditure (Kendeigh *et al.* 1977).

The activities likely to make the most substantial contributions to seabird population energy budgets are foraging, provisioning of chicks, adult moult, and egg production. Energy costs of flapping flight have been accurately measured (Kendeigh *et al.* 1977). Energy costs of gliding flight and surface swimming have been determined for a small number of species and are about twice resting metabolism (Prange and Schmidt-Nielsen 1970, Baudinette and Schmidt-Nielsen 1974). No data are available for the costs of swimming or flying underwater, a feeding technique widely employed by seabirds. This provides a major potential error in the calculation of foraging costs. Furness and Cooper (1982) assumed that the costs of underwater swimming were similar to the costs of sustained flight. Given the uncertainties over the allocation of foraging time to different activities, such an assumption is unlikely to provide a major source of error in the modelling process, and it seems likely that both flapping flight and underwater foraging have similar energy costs close to the physiological maximum of which the bird is capable.

Chick energy budgets were computed by Kendeigh *et al.* (1977) from empirical data derived mainly from detailed studies of House Sparrows (*Passer domesticus*) and



Black-bellied Tree-ducks (*Dendrocygna autumnalis*). Regression of the daily energy budget on body mass of the young birds showed good agreement between species in spite of the wide variety of species and modes of development.

Adult moult costs depend on the mass of feathers replaced, which is proportional to body mass to the power 0.96 (Turcek 1966). Feather replacement in the House Sparrow costs 185 kcals per bird (Kendeigh *et al.* 1977) so the cost of moult may be approximated by the equation:

$$\text{Moult cost} = 8.3 W^{0.96} \text{ (kcals)}$$

where  $W$  is the body mass in grams. This is the only equation available for estimating seabird moult costs and is likely to be inaccurate as it is based on the study of a single passerine species. However, moult costs are a very small part of a seabird population energy budget (Williams *et al.* 1977, Furness and Cooper 1982).

The cost of egg production is calculated from the fresh mass of the egg at laying, the calorific value of the egg (averaging 1.3 kcals/g wet mass [King 1973, Schreiber and Lawrence 1976]) and the efficiency of egg production from body reserves, taken to be 73% (El-Wailly 1966, King 1973).

While it is desirable to have more precise knowledge of the energy costs of these various activities, the accuracy of a simulation model is limited not so much by these bioenergetics equations, but mainly by imprecisions in the estimates of seabird population sizes and the foraging activity budgets of adults (Furness and Cooper 1982).

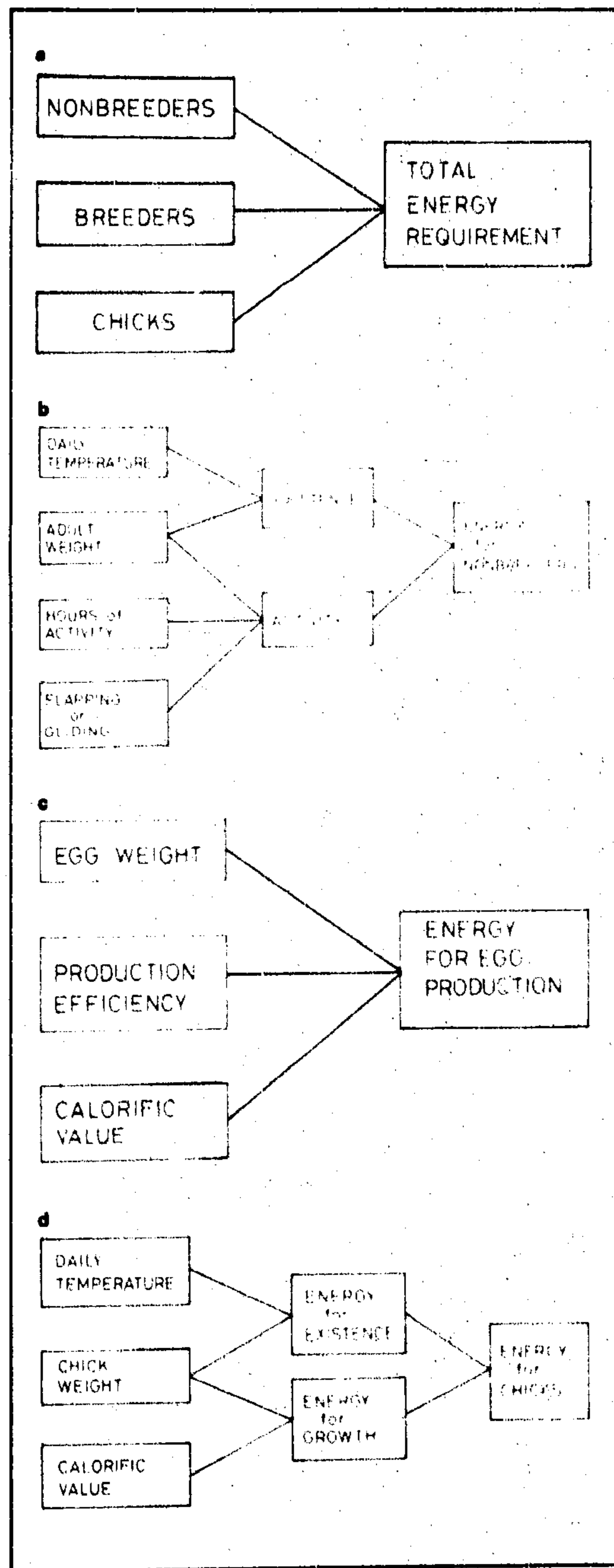
The major inputs and computations for a typical model are shown in Figures 1a-d. Many inputs can be given with great precision. For example, chick weight in relation to age can be closely modelled by growth equations (Fig. 2). In contrast, some parameters are difficult to specify. Adult body weight is an important input, but may show dramatic seasonal variation (Fig. 3).

Model sensitivity can be explored by altering each input or bioenergetics parameter value in turn by 1% and recording the percentage change in the output estimate of total population energy requirement. Parameter sensitivity is defined as the percentage change in output value resulting from a 1% change on an input value. Almost all parameters have sensitivity values of considerably less than one (Figs. 4 and 5). Their exact magnitude depends to some extent on the biology of the species. The Skua (*Catharacta skua*) is a seabird with a fairly high body mass, which spends only a few hours foraging each day during its 5-month breeding season. The Arctic Tern (*Sterna paradisaea*) weighs less, spends only 3 months at the breeding site and at least one adult of each pair is foraging throughout most of the daylight period. In the case of the Skua the model is most sensitive to the estimation of existence metabolism, numbers of individuals in the population, and food utilization efficiency. For the Arctic Tern the model is most sensitive to the activity budget of adults, numbers in the population, and food utilization efficiency. Determination of sensitivity values should be carried out whenever this type of simulation modelling is undertaken as it indicates which parameters must be precisely known to give output results with small standard errors.

Model accuracy can be estimated by using a Monte Carlo technique (Furness 1978). Using the bioenergetics equations in Kendeigh *et al.* (1977) the 95% confidence interval for the model estimate of population energy requirement of Shetland or South African seabirds is about

Figure 1

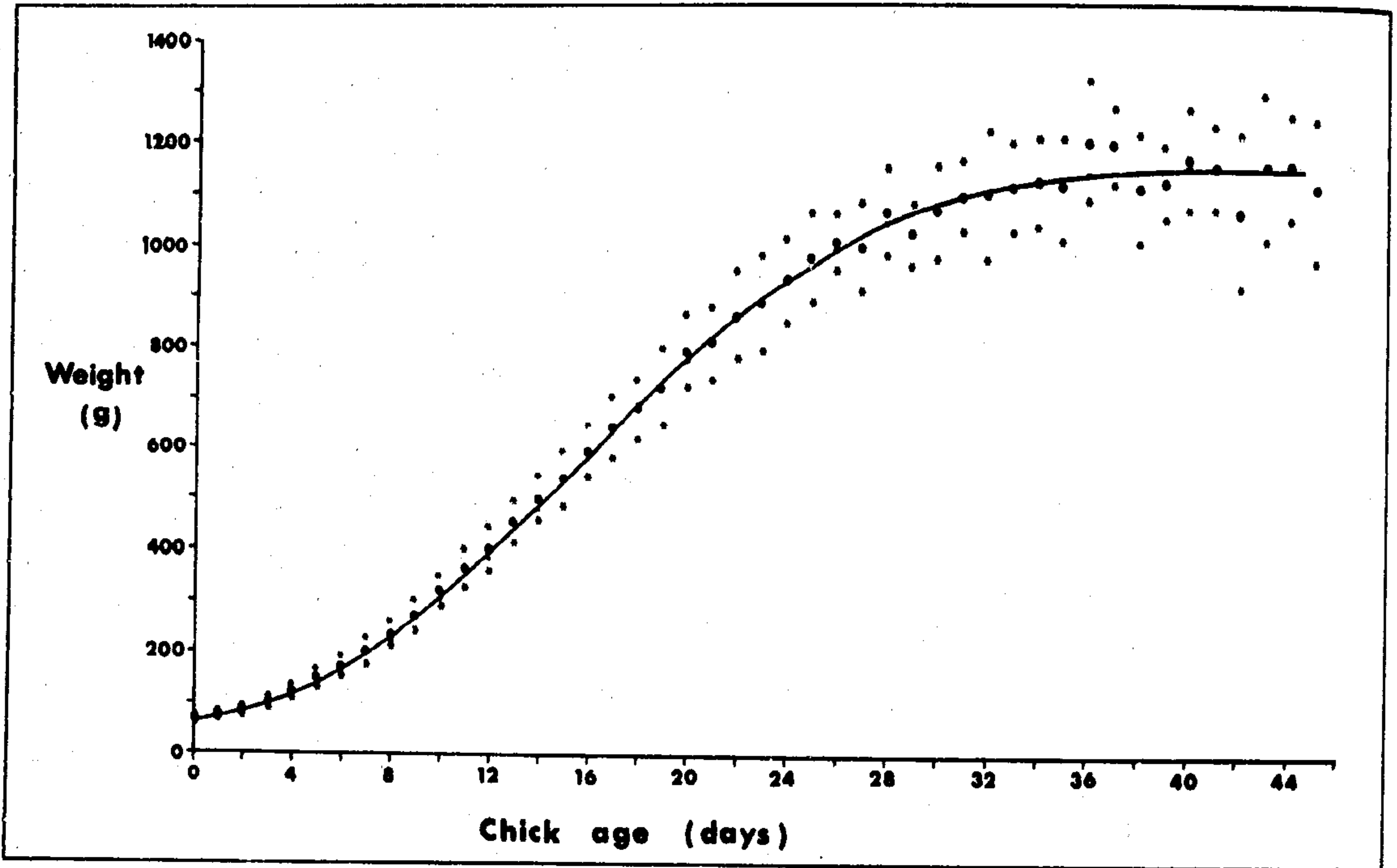
Components of a seabird bioenergetics model: (a) population total comprises non-breeders, breeders, and chicks; (b) inputs for non-breeders; (c) inputs for breeders also include costs of egg production; (d) inputs for chicks. Note that refinements to include costs of moult, change in adult weight, or incubation have been ignored for simplicity.



**Figure 2**

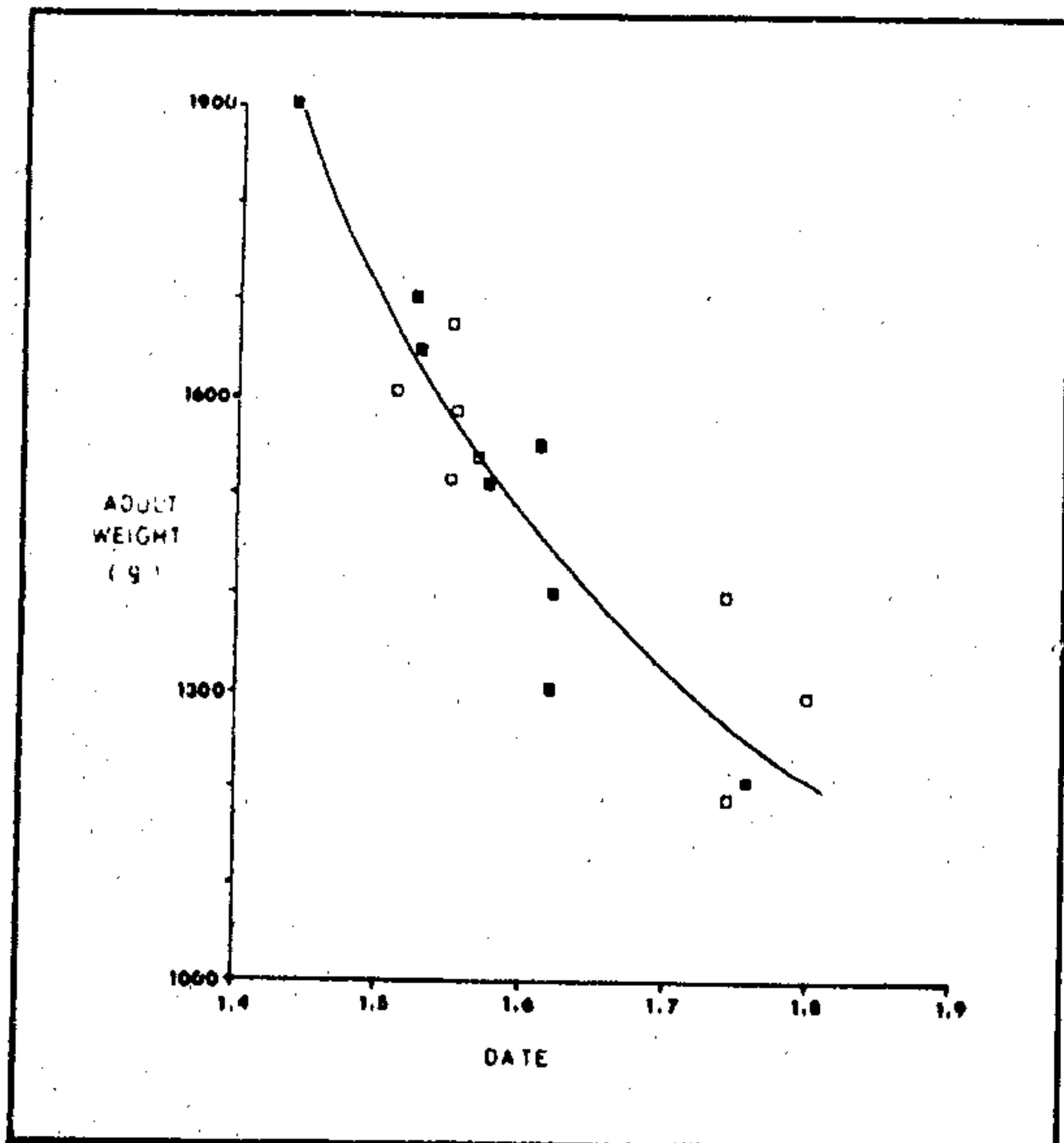
Growth of Skua chicks: mean weights (dots) and upper and lower 66% confidence intervals for individual weights (stars) are shown for 1255 measurements of chicks of known age hatched between 20 May and

20 June 1975. The line represents the logistic equation of best fit, used in bioenergetics modelling:  $w = 1167.08 / (1 + 16.955e^{-0.176t})$ , where  $w$  is chick weight in grams and  $t$  is the age in days



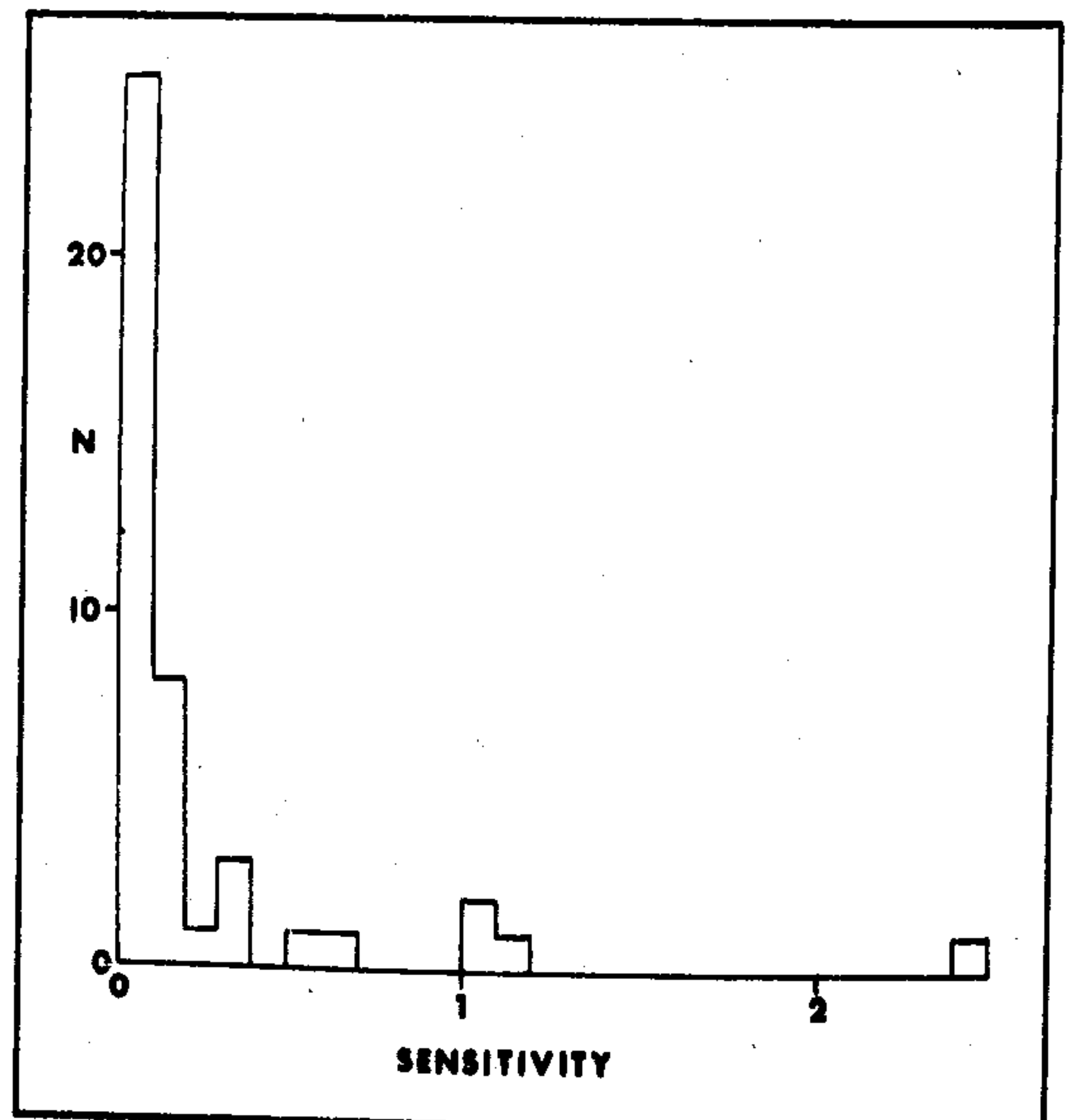
**Figure 3**

Weights of adult Skuas on Foula through the breeding season: breeding birds solid squares, non-breeders open squares



**Figure 4**

Model sensitivity (see text) to errors in the 44 parameters for Skua input data



plus or minus 30% of the mean (Furness and Cooper 1982). Further improvements in model precision are limited by the parameters population size, food utilization efficiency, and adult activity budget. As seabird populations can rarely be censused to an accuracy better than plus or minus 20% (Harris 1976) it is pointless to attempt to refine the model further unless the aim is to examine seasonal patterns of energy expenditure or the proportions used in different activities or by different parts of the population.

Adult existence requirements are equal to, and often much greater than requirements for foraging activity (Table 1). In Shetland, energy requirements of chicks or non-breeders are very small in comparison to the requirements of the breeding adults, even around the middle of the breeding season when numbers of non-breeders at the islands reach a maximum and chick food requirements peak (Fig. 6). The same pattern was found in a study of the energy requirements of seabird populations in South Africa (Furness and Cooper 1982). Adult existence accounted for 50–70% of the total population annual energy requirement, while the costs of moult and egg production represented less than 3% for each species (Table 2).

**4.2.3. Direct field measurements of metabolism** — Direct field measurements of food consumption or individual metabolism can be made using a number of recently developed and sophisticated techniques, but none of these has yet been applied to seabirds. Injection of radioisotopes of elements whose excretion rate is correlated with the rate of metabolism, injection of doubly labelled water ( $D_2O^{18}$ ), and heart-rate biotelemetry all have potential (Furness 1982). Development of these techniques would provide a useful direct measurement of seabird population energetics, which could be used to validate the much simpler and cheaper use of bioenergetics models.

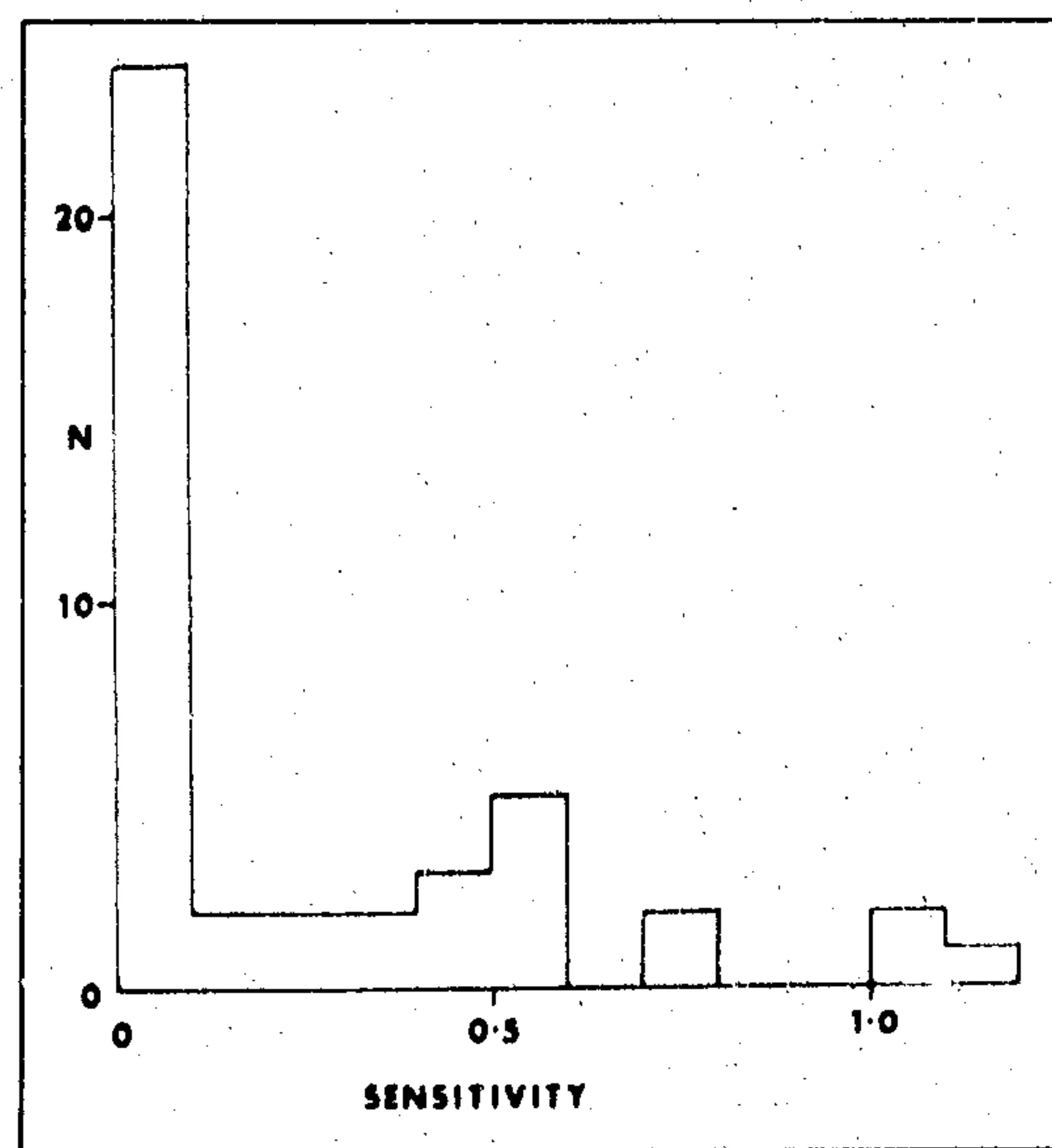
#### 4.3. Conclusions from bioenergetics modelling

Further research into the activity budgets of seabirds will be necessary to improve the accuracy of bioenergetics models. Further research is also essential in order to determine the foraging ranges of seabirds from breeding colonies. Population energy requirements can only be set in context if the diets and foraging ranges of the seabirds are

also known and there are data on the production of fish stocks within the foraging areas of the birds. Knowledge of seabird diets is often poor, and information on seabird foraging ranges is particularly limited.

Wiens and Scott (1975) estimated that the seabirds of coastal Oregon consumed 22% of the annual fish production. Furness (1978) estimated that the seabirds of Foula, Shetland, consumed about 29% of the fish production within a 45-km radius of the colony, and Furness and Cooper (1982) estimated that the seabirds of the southern Benguela system in the mid 1970s consumed 20% of the pelagic fish biomass. Seabird predation is clearly quantitatively important in some marine ecosystems and may potentially compete with fishing interests. The increases in

**Figure 5**  
Model sensitivity for Arctic Tern input parameters



**Table 1**

Energy budgets of seabird populations estimated from bioenergetics modelling: Skua and Arctic Tern populations at a Shetland colony during the breeding season alone (from Furness 1978)

Population component	Energy allocation	Skua		Arctic Tern	
		Expenditure, million kcal/yr*	% of budget, breeding season	Expenditure, million kcal/yr	% of budget, breeding season
Breeder	existence	188.1	60.0	45.6	40.6
	activity	67.7	21.6	51.8	46.2
	egg production	1.2	0.4	0.5	0.4
	total	257.0	82.0	97.9	87.2
Non-breeders	existence	21.4	6.8	2.0	1.8
	activity	5.6	1.8	2.2	2.0
	total	27.0	8.6	4.2	3.8
Chicks	existence	21.1	6.7	8.4	7.5
	growth	8.4	2.7	1.7	1.5
	total	29.5	9.4	10.1	9.0
Population	total	313.5	100.0	112.2	100.0

\*1 kcal = 4.19 kJ.

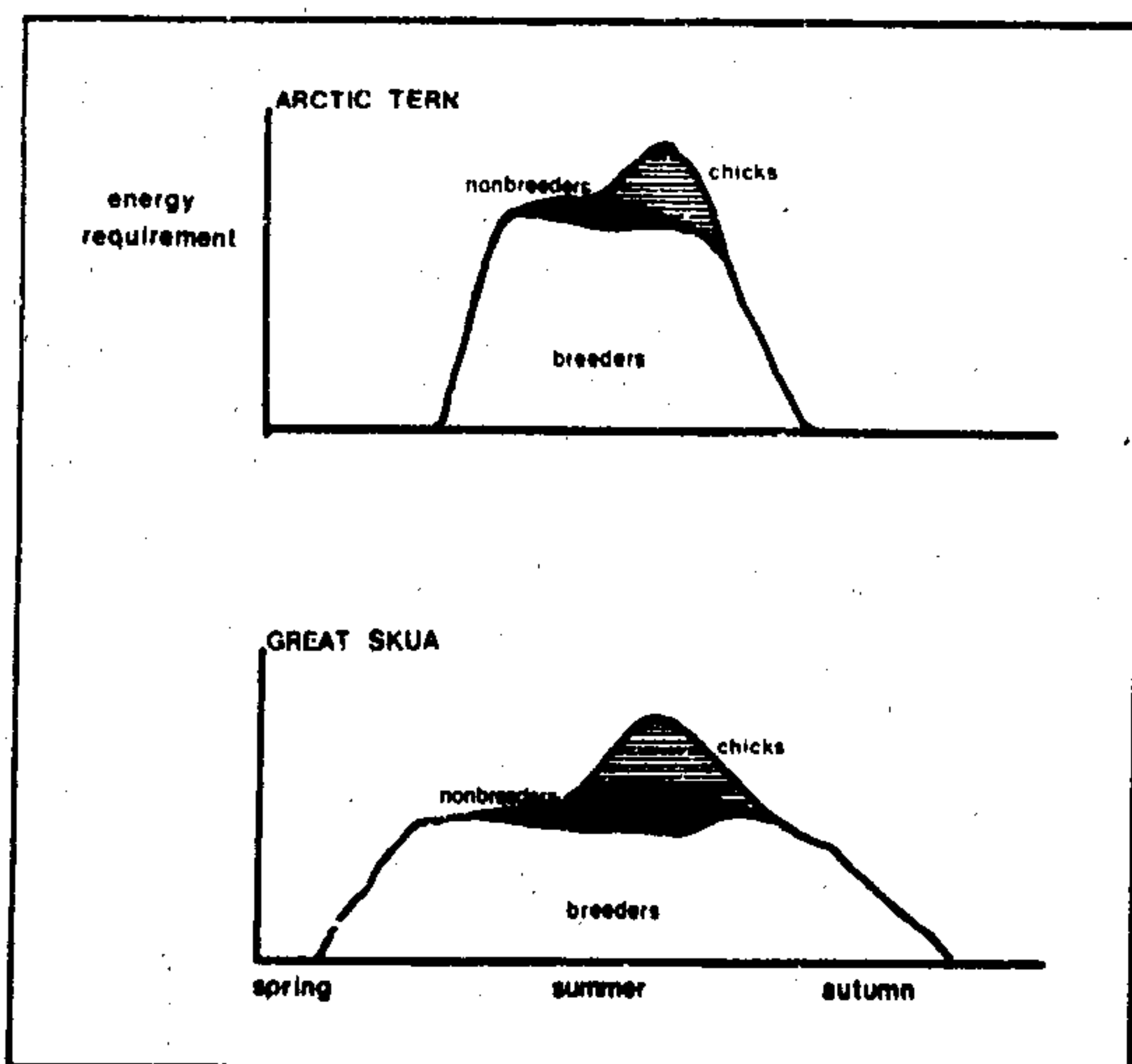


seabird populations in Scotland (Furness, this volume), decreases of seabirds in southern Africa (Burger and Cooper, this volume), increases of seabirds and seals in the Antarctic (Croxall and Prince 1979), decreases of guano birds in Peru (Santander 1980), and breeding failure of alcids in the west of Norway (Lid 1981) can all be attributed to major switches in composition of fish stocks in these areas. Although the high predation rates of these seabirds help to explain their rapid response to changes in the marine ecosystem, it is not possible to make predictions about the changes in seabird population sizes from bioenergetics models alone. Consideration also has to be given to interspecific relationships and effects of food shortage or excess on different aspects of population biology. No satisfactory models of these relationships have yet been constructed, but they are a logical sequel to bioenergetics modelling in order to gain further insight into relationships between seabird populations and fish stocks. For the remainder of this paper I shall consider the ways in which seabird populations are influenced by changes in food availability.

**Table 2**  
Energy budgets of seabird populations estimated from bioenergetics modelling: seabirds in the southern Benguela system (from Furness and Cooper 1982). Energy expenditure in  $\text{kJ} \times 10^3/\text{year}$

Energy allocation	Jackass Penguin		Cape Gannet		Cape Cormorant	
	Expenditure	% of budget	Expenditure	% of budget	Expenditure	% of budget
Adult existence	229.4	71.4	101.9	50.7	72.1	63.6
Adult foraging	62.1	19.4	72.7	36.1	32.3	28.5
Chicks	24.6	7.6	22.2	11.0	6.2	5.4
Adult moult	4.9	1.5	4.3	2.1	2.8	2.5
Egg production	0.4	0.1	0.1	0.1	0.05	0.0
Population total	321.7	100	201.2	100	113.4	100

**Figure 6**  
Seasonal patterns in the energy requirements, while resident at the colony, of breeding, non-breeding, and young Skuas and Arctic Terns at Foula, Shetland, as estimated by bioenergetics modelling. The spring increases and autumn decreases are due to the arrival and departure of birds at the colony.



## 5. Effects of food shortage on seabird communities

### 5.1. Mechanisms

Food shortage can influence seabird population dynamics by reducing breeding success or increasing adult mortality or delaying age of first breeding, or a combination of these. Seabirds are generally long-lived, and few studies have accurately measured their adult survival rates, let alone annual variations in survival rates or variations in survival related to colony size, population density, or food availability. Coulson and Wooller (1976) showed that the annual survival rate of adult breeding Black-legged Kittiwakes (*Rissa tridactyla*) fell as the study colony increased in size and density, and they associated this change with increasing competition, particularly for nest sites in the larger colony. Ollason and Dunnet (1983) have shown that annual changes in numbers of Northern Fulmars (*Fulmarus glacialis*) nesting on a small island in Orkney depend mainly on year-to-year variations in recruitment rate, which appears to correlate with food availability. Adult survival rate has shown little variation and does not correlate with changes in breeding numbers.

A consequence of culling Herring Gulls (*Larus argentatus*) has been a reduction in the age of first breeding (Chabrzyk and Coulson 1976, Duncan 1978). Nesting of younger birds is presumably possible due to reduced competition, although the relative roles of social behaviour and increased food per bird are unclear. The hormonal basis of such release is described by Carrick and Murray (1964), who implicate food reserves as the trigger for maturation.

Many studies have indicated that food availability is one of the main determinants of breeding success in seabird populations. Harris and Hislop (1978) showed that Atlantic Puffins (*Fratercula arctica*) select larger fish and species of high calorific value to feed chicks. Chick growth and fledging weights were highest when the diet consisted mainly of sprats (*Sprattus sprattus*), whereas in years when young whiting (*Merlangus merlangus*) were fed to chicks their growth was poorer. Food quantity and quality tended to be better at the Isle of May than at St. Kilda. Rates of increase of the two colonies parallel these differences in food availability, although there is little evidence that variations in fledging weight resulting from food shortage alter Atlantic Puffin survival or subsequent return to the colony (Harris 1982).

Food availability to chicks may also influence breeding success in an indirect way. Atlantic Puffin breeding success is greater on sloping habitat than on flat habitat on Great Island, Newfoundland, as a result of the interaction between food availability and gull interference. Hungry chicks spend more time at the burrow entrance, exposing themselves to a higher risk of gull predation. Frequency of chick feeding was lower on flat habitat because gulls were able to kleptoparasitize food-carrying adults more successfully there, so that chicks on the flat habitat were more likely to suffer food shortage (Nettleship 1972). The complicated interaction between habitat, food availability, and the interspecific relations indicates the difficulty of relating seabird community dynamics to food supplies.

Brood-size-reduction is a strategy employed by a number of seabird species. This is clearly correlated with food availability, and optimizes fledgling production in relation to food supply (Hahn 1981). Procter (1975) showed that the older chick in broods of the South Polar Skua



(*Catharacta maccormicki*) would attack and kill the younger if deprived of food for a period of time. Young (1963) found that it was exceptional for the younger chick to survive to fledging when food was in short supply. The closely related Skua in the North Atlantic regularly rears both chicks to fledging. The population is currently growing rapidly under favourable conditions provided by the whitefish industry and increased sandlance stocks (Furness and Hislop 1981) so that chicks even in supernormal broods rarely go short of food. Haymes and Morris (1977) found that Herring Gulls at Lake Erie were able to rear supernormal broods without increased brood reduction or predation because they were able to make use of human-supplied artificial food sources in addition to their natural food supply, while Hunt (1972) found that chicks fed on garbage and fish waste grew faster than those in more isolated colonies where only natural foods were available. Hunt and Hunt (1976) found that Glaucous-winged Gull (*Larus glaucescens*) chick survival correlated closely with growth rate and both were determined largely by food availability.

Thus, several studies have shown the importance of food availability, directly or indirectly, in determining breeding success. Modelling seabird population responses to changes in fish stocks would require a theoretical framework allowing relationships between food availability and breeding success, as well as adult survival rate and age of first breeding, to be quantified. I know of only one such model at present. Using a combination of central place foraging theory (Hamilton and Watt 1970, Orians and Pearson 1979) and a deterministic simulation model of Common Murre feeding rate and chick growth, Ford *et al.* (1982) concluded that the breeding success of a Common Murre population would fall steeply with a food density reduction of only 10–30%, and a reduction of food availability of 40% or more would lead to total reproductive failure. Overfishing of fish stocks can easily lead to a stock density reduction of this magnitude (Hempel 1978) so that serious effects on seabird population dynamics could be expected.

Our lack of data on the relationships between food availability and adult survival rate or age of recruitment preclude similar modelling of these aspects of population dynamics. Further studies of the relative roles of breeding success, recruitment, and adult survival on seabird population change are required before reliable models of population dynamics can be constructed. In addition, influences of interspecific effects need to be taken into account, which will prove even more difficult to incorporate into a simulation model.

## 5.2. Examples of the influences of food availability on seabird populations

Having discussed the need to construct models to investigate the influences of changing fish stocks on seabird communities, and the problems in measuring effects of food availability on parameters of population dynamics, I shall finish by describing a few documented examples of fishery–seabird interactions.

Lid (1981) has reviewed the history of alcid breeding success and population change in west Norway over the last 25 years. He showed that Atlantic Puffins, Common Murres, and Razorbills (*Alca torda*) have not decreased noticeably in numbers during this period, but since 1969 all species have shown dramatically reduced breeding success

compared with earlier years, while average weights of adult Atlantic Puffins also seem to have decreased. Lid (1981) attributes these changes to the reduction in Norwegian spring-spawning herring (*Clupea harengus*) stocks from 10 million metric tons in 1958 to 0.5 million metric tons by 1969, as a result of overfishing. At the same time the catches of sandlance in Norwegian waters have grown from less than 10 000 t in the 1960s to 150 000 t by the end of the 1970s. These two species were the main prey of the alcids in the 1960s and their disappearance from the diet seems to be the cause of the alcids' recent breeding failures. The model proposed by Ford *et al.* (1982) would predict total breeding failure with this scale of reduction in food availability.

Similar relationships can be seen particularly well in the Benguela ecosystem, where seabird numbers can be estimated from historical records of guano yields and census counts (Crawford and Shelton 1978; Burger and Cooper, this volume). Of particular interest is the differential response of the three main groups of seabirds. Cape Gannets (*Sula capensis*) are strong fliers and travel considerable distances from breeding colonies in search of food. Cormorants (*Phalacrocorax* spp.) have wettable plumage and are weak in flight so their range is rather smaller. Jackass Penguins (*Spheniscus demersus*) are flightless and travel short distances from their colonies to feed. Intense exploitation of pilchards (*Sardinops ocellata*) and the larger age classes of pelagic species in general (Crawford 1981), has reduced food availability to these seabirds. Cape Gannets have been able to exploit waste from demersal trawlers working far offshore and increase their foraging range to exploit distant fish shoals, but Jackass Penguins have been unable significantly to alter their foraging ranges or diets. As a result, Jackass Penguins have shown a much greater population decline than have Cape Gannets (Burger and Cooper, this volume). A similar differential effect of food shortage has been noted in Peru, where the Guanay Cormorant (*Phalacrocorax bougainvillii*) has suffered much higher mortality rates and population decrease than the Peruvian Booby (*Sula variegata*) as a result of the reduction of anchovy (*Engraulis ringens*) stocks (Jordan and Fuentes 1966, Nelson 1978, Santander 1980). In this case too, the broader ecological niche of the booby probably gave it an advantage when food became short.

Pearson (1968) showed that the proportion of available time spent in foraging decreased with increasing body size in the seabird community on the Farne Islands, Northumberland. If this rule is generally applicable then the smallest species are likely to be most severely affected by food shortage as they have little opportunity to increase their foraging effort. Similarly, dominance hierarchies at feeding sites behind whitefish trawlers may result in some species suffering a disproportionate reduction in food supply when availability decreases (Furness and Hislop 1981).

## 6. Conclusions

Bioenergetics modelling provides useful quantitative assessments of the impact of seabird communities on fish stocks and suggests the likelihood of changes in fishery practices or fish-stock sizes affecting seabird numbers. However, it is not clear which aspects of population biology would be altered by food shortage, or what interactions would take place between seabird species. Simple predictions would be that species with specialized feeding methods and a high dependence on the food that has been



reduced in availability would be likely to decline in numbers. Species with restricted foraging ranges, low in the feeding status hierarchy, or of small size are particularly at risk. It is to be hoped that focusing of attention on this complex subject will lead to the development of more sophisticated predictive models and the monitoring of seabird population biology in areas where fisheries are particularly intense.

## 7. Literature cited

- Andersen, K.P.; Ursin, E. 1977.** A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Medd. Dan. Fisk. og Havunders. N.S.* 7:319-435.
- Baudinette, R.V.; Schmidt-Nielsen, K. 1974.** Energy cost of gliding flight in Herring Gulls. *Nature* 248:83-84.
- Belopolskii, L.O. 1961.** Ecology of sea colony birds of the Barents Sea. (Transl. from Russ.) *Isr. Programme for Sci. Transl. Jerusalem*. 346 pp.
- Burger, A.E.; Cooper, J. This volume.** The effects of fisheries on seabirds in South Africa and Namibia.
- Carrick, R.; Murray, M.D. 1964.** Social factors in population regulation of the Silver Gull *Larus novaehollandiae* Stephens. *C.S.I.R.O. Wildl. Res.* 9:189-199.
- Chabryk, G.; Coulson, J.C. 1976.** Survival and recruitment in the Herring Gull *Larus argentatus*. *J. Anim. Ecol.* 45:187-203.
- Coulson, J.C.; Wooller, R.D. 1976.** Differential survival rates among Kittiwake Gulls *Rissa tridactyla* (L.). *J. Anim. Ecol.* 45:205-213.
- Crawford, R.J.M. 1981.** Catch per standard-boat-day and deployment of effort in the South African purse-seine fishery, 1964-1976. *Investl. Rep. Sea Fish. Inst. S. Afr.* 122:1-24.
- Crawford, R.J.M.; Shelton, P.A. 1978.** Pelagic fish and seabird inter-relationships off the coasts of South-West and South Africa. *Biol. Conserv.* 14:85-109.
- Croxall, J.P.; Prince, P.A. 1979.** Antarctic seabird and seal monitoring studies. *Polar Rec.* 19:573-595.
- Duncan, N. 1978.** The effects of culling Herring Gulls (*Larus argentatus*) on recruitment and population dynamics. *J. Appl. Ecol.* 15:697-713.
- El-Wailly, A.J. 1966.** Energy requirements for egg laying and incubation in the Zebra Finch *Taeniopygia castanotis*. *Condor* 68:582-594.
- Ford, R.G.; Wiens, J.A.; Heinemann, D.; Hunt, G.L. 1982.** Modelling the sensitivity of colonially breeding marine birds to oil spills: guillemot and kittiwake populations on the Pribilof Islands, Bering Sea. *J. Appl. Ecol.* 19:1-32.
- Furness, R.W. 1978.** Energy requirements of seabird communities: a bioenergetics model. *J. Anim. Ecol.* 47:39-53.
- Furness, R.W. 1982.** Competition between fisheries and seabird communities. *Adv. Mar. Biol.* 20:225-307.
- Furness, R.W. This volume.** Seabird-fisheries relationships in the north-east Atlantic and North Sea.
- Furness, R.W.; Cooper, J. 1982.** Interactions between breeding seabird and pelagic fish populations in the Southern Benguela Region. *Mar. Ecol. Prog. Ser.* 8:243-250.
- Furness, R.W.; Hislop, J.R.G. 1981.** Diets and feeding ecology of Great Skuas *Catharacta skua* during the breeding season in Shetland. *J. Zool. Lond.* 195:1-23.
- Grenfell, B.T.; Lawton, J.H. 1979.** Estimates of the krill consumed by whales and other groups in the Southern Ocean: 1900 and the present. Unpubl. manusc. rep. to the Int. Un. for Conserv. of Nat. and Nat. Resour. Gland, Switzerland. 27 pp.
- Hahn, D.C. 1981.** Asynchronous hatching in the Laughing Gull: cutting costs and reducing rivalry. *Anim. Behav.* 29:421-427.
- Hamilton, W.J.; Watt, K.E.F. 1970.** Refuging. *Ann. Rev. Ecol. Syst.* 1:263-286.
- Harris, M.P. 1976.** The seabirds of Shetland in 1974. *Scott. Birds* 9:37-68.
- Harris, M.P. 1982.** Seasonal variations of fledging weight in the Puffin *Fratercula arctica*. *Ibis* 124:100-103.
- Harris, M.P.; Hislop, J.R.G. 1978.** The food of young Puffins, *Fratercula arctica*. *J. Zool. Lond.* 185:213-236.
- Haymes, G.T.; Morris, R.D. 1977.** Brood-size manipulations in Herring Gulls. *Can. J. Zool.* 55:1762-1766.
- Hempel, G. 1978.** North Sea fisheries and fish stocks — a review of recent changes. *Rapp. et P.-V. Reun. Cons. Int. Explor. Mer* 173:145-167.
- Hinga, K.R. 1979.** The food requirements of whales in the southern hemisphere. *Deep Sea Res.* 26A:569-577.
- Humphreys, W.F. 1979.** Production and respiration in animal populations. *J. Anim. Ecol.* 48:427-453.
- Hunt, G.L. 1972.** Herring Gull population dynamics: the significance of man's waste products. *Int. Ornithol. Congr. The Hague. Proc.* (15):652.
- Hunt, G.L.; Hunt, M.W. 1976.** Gull chick survival: the significance of growth rates, timing of breeding, and territory size. *Ecology* 57:62-75.
- Jordan, R.; Fuentes, H. 1966.** Las poblaciones de aves guaneras y su situación actual. *Inst. del Mar de Peru* 10:1-31.
- Kaftanovski, Yu.M. 1951.** Birds of the murre group of the eastern Atlantic. Studies of the fauna and flora of the USSR. *Moscow Soc. of Nat.* 28:1-170.
- Kendeigh, S.C. 1970.** Energy requirements for existence in relation to size of bird. *Condor* 72:60-65.
- Kendeigh, S.C.; Dol'nik, V.R.; Gavrilov, V.M. 1977.** Avian energetics. Pages 127-204 in Pinowski, J.; Kendeigh, S.C. eds. *Granivorous birds in ecosystems*. IBP. Vol. 12. Cambridge Univ. Press. Cambridge.
- Keyes, M.C. 1968.** Nutrition of pinnipeds. Pages 359-395 in Keyes, M.C. ed. *Behaviour and physiology of pinnipeds*. Appleton. New York.
- King, J.R. 1973.** Energetics of reproduction in birds. Pages 78-107 in Farner, D.S. ed. *Breeding biology of birds*. Nat. Acad. of Sci. Washington. 515 pp.
- Lawton, J.H. 1970.** Feeding and food energy assimilation in larvae of the damselfly *Pyrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). *J. Anim. Ecol.* 39:669-689.
- Lid, G. 1981.** Reproduction of the Puffin on Rost in the Lofoten Islands in 1964-1980. *Cinclus* 4:30-39.
- Lockyer, C.H. 1976.** Growth and energy budgets of large baleen whales from the southern hemisphere. *Advis. Comm. on Mar. Resour. Res. Sci. Consult. on Mar. Mammals. Food and Agr. Org. Rome*. 40 pp.
- May, R.M.; Beddington, J.R.; Clark, C.W.; Holt, S.J.; Laws, R.M. 1979.** Management of multispecies fisheries. *Science* 205:267-277.
- Nelson, J.B. 1978.** The Sulidae: gannets and boobies. Oxford Univ. Press. Oxford. 1012 pp.
- Nettleship, D.N. 1972.** Breeding success of the Common Puffin (*Fratercula arctica* L.) on different habitats at Great Island, Newfoundland. *Ecol. Monogr.* 42:239-268.
- Ollason, J.; Dunnet, G.M. 1983.** Modelling annual changes in numbers of breeding fulmars, *Fulmarus glacialis*, at a colony in Orkney. *J. Anim. Ecol.* 52:185-198.

Orians, G.H.; Pearson, N.E. 1979. On the theory of central place foraging. Pages 155-177 in Horn, D.J.; Stairs, G.R.; Mitchell, R.D. eds. Analysis of ecological systems. Ohio State Univ. Press. Ohio.

Parrish, B.B.; Shearer, W.M. 1977. Effects of seals on fisheries. Int. Council for the Explor. of the Seas (Cm 1977/M:14). Anacat Comm. 5 pp.

Pearson, T.H. 1968. The feeding biology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37:521-552.

Prange, H.D.; Schmidt-Nielsen, K. 1970. The metabolic cost of swimming in ducks. J. Exp. Biol. 53:763-777.

Proctor, D.L.C. 1975. The problem of chick loss in the South Polar Skua *Catharacta maccormicki*. Ibis 117:452-459.

Rae, B.B. 1960. Seals and Scottish fisheries. Mar. Res. 1960(2):1-39.

Santander, H. 1980. The Peru current system. 2. Biological aspects. Pages 217-227 in Proc. Workshop on the phenomenon known as 'El Nino.' UNESCO. Paris.

Schreiber, R.W.; Lawrence, J.M. 1976. Organic material and calories in Laughing Gull eggs. Auk 93:46-52.

Sergeant, D.E. 1969. Feeding rates of Cetacea. Fiskdir. Skr. Ser. Havunders 15:246-258.

Summers, C.F. 1978. Trends in the size of British grey seal populations. J. Appl. Ecol. 15:395-400.

Tuck, L.M.; Squires, H.J. 1955. Food and feeding habits of Brunnich's Murre (*Uria lomvia lomvia*) on Akpatok Island. J. Fish. Res. Board Can. 12:781-792.

Turcek, F.J. 1966. On plumage quantity in birds. Ecol. Polska. Ser. A 14:617-634.

Uspenski, S.M. 1956. The bird bazaars of Novaya Zemlya. (Transl. from Russ.). Transl. Russ. Game Rep. No. 4. Queen's Printer. Ottawa. 159 pp.

Wiens, J.A.; Dyer, M.I. 1977. Assessing the potential impact of granivorous birds in ecosystems. Pages 205-266 in Pinowski, J.; Kendeigh, S.C. eds. Granivorous Birds in Ecosystems. IBP. Vol. 12. Cambridge Univ. Press, Cambridge.

Wiens, J.A.; Scott, J.M. 1975. Model estimation of energy flow in Oregon coastal seabird populations. Condor 77:439-452.

Williams, A.J.; Siegfried, W.R.; Burger, A.E.; Berruti, A. 1977. Body composition and energy metabolism of moulting Eudyptid Penguins. Comp. Biochem. Physiol. 56A:27-30.

Young, E.C. 1963. The breeding behaviour of the South Polar Skua. Ibis 105:203-233.