THE EXPLOITATION OF NATURAL ANIMAL POPULATIONS

Edited by
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AND

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PREFACE

For the theme of the Second Symposium of the British Ecological Society, the Programme Planning Committee decided upon some aspect of animal population ecology. 'The exploitation of natural animal populations' was finally chosen as a subject likely to bring together those interested in a wide variety of animals and both theorists and practical ecologists.

In all, 130 ecologists, from ten countries, attended, and these included not only those concerned with exploited animals but also a number interested in other fields of population ecology such as economic entomology. The discussions benefited greatly as a result.

Through the kindness of the Council of the Durham Colleges in the University of Durham, the meeting was held in Durham and the formal sessions took place in the Applebey Lecture Theatre. Most of the participants were accommodated in St Mary's College and Grey College, where much informal discussion took place. On the evening of 28th March a series of films relevant to the theme of the meeting were shown, but proceedings really began on the following morning when Professor Cragg, in his dual capacity as host and President welcomed the participants and introduced the Symposium.

Invited papers were read during the three days that followed. These have been printed here in the order in which they were delivered, and in substantially the same form, although the printed versions are naturally rather longer and contain more supporting detail than could be presented verbally. All the papers were followed by discussions, and there were also three sessions devoted to discussion alone: together these occupied about half the time of the Symposium. The records of the discussions are based on notes made at the time and later edited and somewhat shortened, and all these have been approved by the contributors before publication.

In any Symposium of this kind many people assist in one way or another, and the Society, the organizers, and the editors are grateful for all the help they have received. The Council and members of staff of the Durham Colleges, and in particular Professor Cragg, contributed greatly to the enjoyment of the meeting by their hospitality and efficient share in the organization. We received invaluable co-operation and help from people consulted in the planning stage, and from the contributors, including those who opened

discussions. We are also grateful to the sponsoring organizations who made it possible for several speakers and participants to attend the Symposium.

E. D. Le Cren
M. W. Holdgate

INTRODUCTION

Although most human communities have now passed from a purely hunting economy to a pastoral and agricultural one, the capture of wild or semi-wild animals is still an important activity. Fish provide a substantial part of the protein eaten by many peoples, and predominate in the diet of some, and molluscs, birds, land mammals, whales and seals all contribute their quota. It is common knowledge that many of these important natural resources have been grossly over-exploited in the past, and that the manner in which they are now harvested often leaves much to be desired. Ultimately the rational management and development of wild populations may lead to much fuller human control and near-domestication, but for the forseeable future we are likely to continue to rely on wild animals for some of our food and raw materials.

In addition, the capture of certain wild animals or fish has a recreational value, and this kind of sport has assumed a considerable political and economic importance in the more highly developed countries. It is not surprising therefore that there has been considerable economic and popular support for the study of exploited animals. Applied biologists, whether working on game animals or on species which are important sources of food and raw materials, like fish, whales, seals and certain sea birds, have been responsible for much of the research and many of the advances in population ecology. In this they have been aided by economic entomologists concerned with agricultural pests and disease vectors. To the contributions of these ecologists must be added those made by mathematicians and theorists and those resulting from the study of experimental populations in the laboratory. All these approaches have been concerned in one way or another with the dynamics of animal populations.

Although the exploitation of a particular species or group of animals involves many specific and practical problems, all such exploitations are intimately bound up with fundamental population ecology. This interaction between the specific and the general can be seen in the papers in the first three parts of the Symposium that deal with particular animals such as herrings, cockles, grouse, partridge, duck or whales. Some of the population factors involved seem to be peculiar to the type of animal: others are of wider relevance, and an attempt is made, especially in the discussions, to discover and define these fundamental points of similarity and difference.

The different approaches that have been adopted by the workers on different groups, the different population parameters they try to measure, and the different terminology they use, all tend to impede the fruitful comparison of results obtained for various kinds of animals. These difficulties of comparison will be apparent to any reader, and are themselves considered in the discussions. For example, it is not easy to observe marine fish in their natural habitat and sea fisheries deal with a bulk product largely assessed by weight. It is not surprising that fishery biologists have tended to concentrate their approach on the mass population dynamics of fish and their food. Conversely it is easier to observe the behaviour of individual birds or land mammals than to count them and obtain statistics on mortality rates and the like, so ornithologists and mammalogists have tended to build up their information from individual field observations rather than the statistical analysis of large samples. Insect ecologists find both approaches beset by difficulties and have to contend with special problems of their own: for example the absence of overlap in the generations of many insect species, which makes their numbers tend to fluctuate rather violently. Environments and populations alike differ in their stability, and the extent and consequences of these differences are argued about in several of the discussions.

Comparative population dynamics also suffers from a lack of the necessary data, and some of this deficiency has arisen because biologists have not always known what the essential parameters are. A detailed, comparative analysis of population parameters within one group is one approach which may lead to a clearer recognition of what data are vital, and hence to a simplification of practical problems of observation. Holt attempts such an analysis for fish.

A resilience to artificial population changes seems to be a prerequisite if a species is to be exploited successfully. Although some resilience may be a characteristic of all species, not all have been able to contribute a substantial yield to man and yet show no long-term decline in abundance. The reactions of populations to exploitation can, however, be used as evidence as to whether or not all populations possess natural regulatory mechanisms, and should throw light on how such mechanisms operate. Nikol'skiĭ reviews the features of fish populations which can be considered as adaptive and compensatory, and several other papers contribute evidence on population regulation. The relative importance of factors intrinsic to the population and extrinsic environmental factors in the control of populations is still a moot point, as is apparent from the discussions.

Progress in the understanding of population dynamics in relation to exploitation has been much assisted by the use of mathematical models. As is discussed on p. 379, some form of model is essential for almost any advance,

but the true mathematical model may produce, by mathematical argument, deductions and implications unlikely to have been discovered by other means. Such deductions can then be tested against reality, or used to make practical recommendations and forecasts. The latter has been accomplished successfully for fish populations, and some of the main approaches to the design and use of such models are discussed by Gulland, and in a more general way by Watt.

Another approach to understanding through simplification is by the use of laboratory populations. Here environmental complexity can be reduced to a minimum, and the combination of model and experiment used to test theory as, for example, Slobodkin uses experiments with *Daphnia* and *Hydra* to investigate the efficiency of exploitation.

The ultimate aim for rational human use of a population must be to obtain an efficient maximum (and economic) long-term yield. The simpler fishery models are concerned only with the efficient utilization of the fished stock, but more sophisticated and comprehensive considerations must include the whole population in all life stages and eventually the whole biota. Long-term trends and the factors controlling the numbers of young fish are described by Beverton, while Le Cren discusses the efficiency of the reproductive and recruit-rearing processes.

In most population investigations there comes a time when consideration has to be extended beyond intra-specific factors to inter-specific relationships and to the environment. Little is known about the balance of closely related species and how it may be affected by the exploitation of one or more of them, but Lindström and Nilsson contribute a paper on the probable competitive interactions of whitefish species in the same lake. In some situations man finds himself competing with predators for the same prey species: such a situation would arise if African plains game were cropped as a major protein source in the manner foreshadowed in Pearsall's paper. Such a conflict can produce practical complications when the predators are themselves of aesthetic or commercial value to man. The grey seal is considered by some naturalists to be worthy of protection, but Rae regards it as a serious predator on valuable fish. Lockie attempts an assessment of the relative importance of man and the grey seal as predators of salmon, and Shearer illustrates one way out of such conflicts by describing some practical measures to protect salmon nets from seals. The discussion following these papers seems to indicate that more real information on the population parameters of both seals and fish is needed before judgement can be given.

One might think that nature conservation would invariably involve protection against exploitation for the species or community that is being preserved, but in practice some degree of cropping is often essential,

especially where natural population controls have been artificially removed. Pearsall considers that the rational management and exploitation of wild animals is potentially the most efficient form of land use in the African plains, where present agricultural and pastoral practises tend to destroy environmental fertility.

The economic and practical importance of wild animals provides abundant justification for the study of their populations by ecologists, but there are also other reasons. The large scale on which exploited animals are taken provides the biologist with abundant samples for study, and when some record has been kept of the catches, invaluable statistical information about secular changes in abundance may be available. An ecologist studying other organisms, who has to collect his own samples every week for fifty years may well feel envious! Furthermore, observation alone of a relatively stable population will not usually lead to an understanding of its regulatory mechanism: some kind of disturbing influence is needed. Climatic trends or year to year variations may be useful, but artificially induced disturbances can be much more revealing. Exploitation by man is such a disturbance and can often constitute an experiment in population dynamics. (Paradoxically, it was the *cessation* of fishing in the North Sea during the two world wars that revealed many of the effects of exploitation on fish populations.)

The exploitation of animals thus provides ecologists with financial support to work on a wide range of animal species, abundant material to study, and experiments to observe. The following pages may be offered as a sample of what population ecologists have made of these opportunities, and how far they have progressed towards an understanding of the scientific basis of the response of natural animal populations to exploitation.

CONTENTS

THE POPULATION DYNAMICS OF DIFFERENT KINDS OF EXPLOITED ANIMALS

PROBLEMS CONCERNING THE POPULATION DYNAMICS OF THE ATLANTIC HERRING (*CLUPEA HARENGUS* L.) WITH SPECIAL REFERENCE TO THE NORTH SEA

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INTRODUCTION

For centuries the fisheries for herring (*Clupea harengus* L.) have contributed a major share of the total fish harvest in European waters. In the years 1950–5, the annual herring yield for all European countries averaged about two million metric tons, which was approximately one-third of the yield of about six million tons of all species. The events in these fisheries are, therefore, of major importance to the herring industries and the economies of the major fishing nations of Europe, including the United Kingdom.

The regions from which these harvests are taken in the north-east Atlantic range from the north coast of Iceland and the Barents Sea in the north to the English Channel in the south, and from the west coast of Iceland in the west to the Baltic in the east. However, two areas are of outstanding importance; the west coast of Norway and the North Sea. The first of these is the centre of the Norwegian winter fishery, between January and April, which reached peak yields of over a million metric tons in the years 1950–5; the second is the centre of a great international fishery, pursued throughout the year by the herring fleets of Germany, Holland, the United Kingdom, Sweden, Denmark, Belgium, France, Poland and the U.S.S.R., which together produced about three-quarters of a million metric tons annually in the years 1950–5.

The results of long-term biological investigations of the herring exploited in these regions have established that these two major fisheries are based on different herring 'tribes'. The Norwegian fishery exploits the oceanic 'Atlanto-Scandian', spring spawning 'tribe' which has its spawning grounds on the coastal banks along the Norwegian west coast, and its main adult feeding grounds in the deep, oceanic region between Norway and Iceland. The North Sea fishery, on the other hand, is centred principally on a summer–autumn spawning 'tribe' which has its spawning grounds on banks in the

northern, central and southern regions of the North Sea, and whose distribution is bounded by the continental slope in the north and east. Only in the 'fringe' region of the northern North Sea has any substantial overlap in the distributions of these tribes been detected in the forty to fifty years of intensive herring research in this area. Therefore, for fishery assessment purposes, the 'Atlanto-Scandian' tribe can be discounted as a substantial source of supply for the North Sea herring fishery, and as a factor governing the fluctuating yields from it, and vice versa, at least during the present century. The approximate boundaries between the two tribes and the region of overlap between them are shown in Fig. 1.

Throughout their long histories, these two fisheries have been characterized by marked long- and short-term fluctuations and trends in landings. The most striking of these have been the 'herring periods' of the Norwegian (and Swedish west coast) fishery; they have taken the form of alternate periods of high and low yield, which can be traced in the Norwegian and Swedish statistical records, back to at least the sixteenth century. The most recent 'low' in the Norwegian fishery occurred towards the end of the nineteenth century, when, between 1860 and 1875, the annual landings fell from about one million hectolitres to 200 hectolitres. An equally large and rapid rise took place early in the twentieth century, and by 1913 the annual yield had risen again to over a million hectolitres.

Marked fluctuations are also reflected in the early and later catch records of the North Sea, and neighbouring herring fisheries. In some notable instances (e.g. Firth of Forth; western English Channel) these have been of sufficient magnitude, and the period of low yield sufficiently sustained to cause the complete collapse of a traditional fishery, while in others they have resulted in sharp changes in the 'success' of the fisheries.

This 'property' of the European herring fisheries had a marked and lasting influence on the attitude of early and later herring scientists to the relative importance of natural and man-made factors in governing the yield from them. Man-made influences (i.e. fishing) tended to be regarded as of relatively small importance. This attitude persisted during the period of decline of many of the important demersal fisheries, and the rapid growth of quantitative studies of the dynamics of the exploited demersal stocks in the inter-war and early post-war years. Throughout this period the European herring stocks were generally regarded as underfished, but subject to wide natural fluctuations in abundance, distribution and habits. As a consequence, the kind of scientific data collected on the herring fisheries remained largely qualitative in nature.

Since the second world war, however, disturbing events in some components of the North Sea fishery have caused an urgent reappraisal to be

made of this long standing viewpoint and attention to be paid to the population dynamics of the exploited herring stocks. In this period major changes have taken place in the nature and size of the herring fisheries in the North

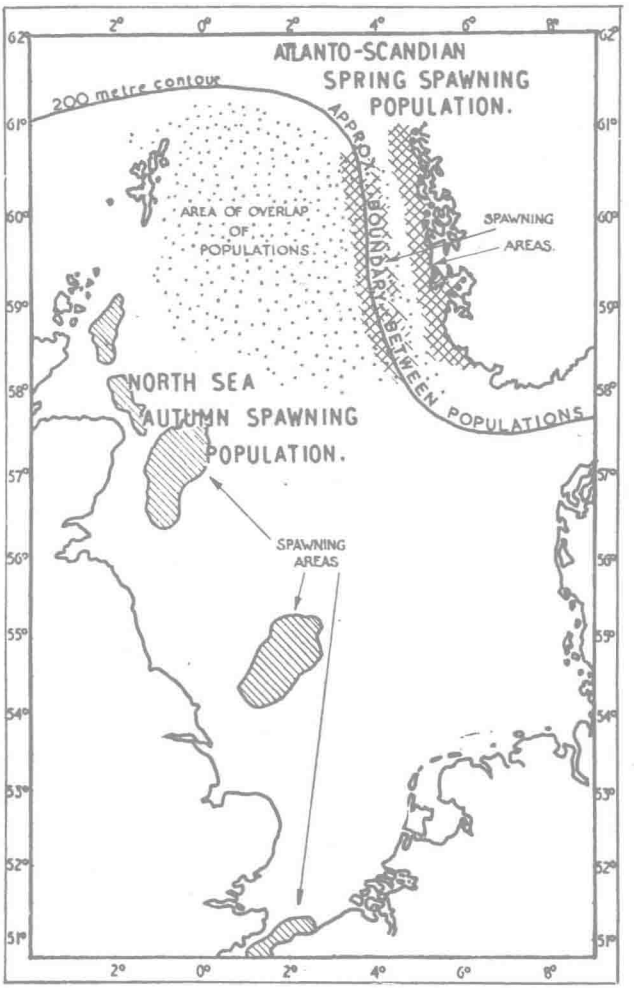

FIG. 1.—Approximate boundaries and area of overlap between North Sea and Atlanto-Scandian herring tribes.

Sea; the British component of this fishery at East Anglia has declined alarmingly; changes have taken place in the abundance and composition of the exploited stock, and changes have been detected in certain of the bio-