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Marine Mammal Fishery Interactions: <u>Modelling and the Southern Ocean</u> (contribution of IUCN) J.R. Beddington and W.K. de la Mare Department of Biology, University of York. U.K.

### Background

The exploitation of marine mammals played a fundamental role in attracting attention to the Antarctic in the nineteenth century. In the light of the decimation of the stocks of whales in this century it is often overlooked that some species of marine mammals in the Southern Ocean were virtually extirpated in the nineteenth century. Fur seals, elephant seals and right whales fall into this category, although in terms of ecological effects, these are more likely to have been of local rather than global significance.

The more significant impact on the Antarctic ecosystems will have come from the depletion of the stocks of great whales and this story is by now so familiar that it requires no more than the briefest recapitulation here.

The era of modern whaling began in the Antarctic in 1904. In the early period whaling was from land-based stations in the South Atlantic and the main target was humpback whales though some blue and fin whales were also taken. Some Antarctic stocks of humpback whales were also exploited in their wintering grounds in lower latitudes.

In 1925 the first Discovery expedition marked the beginning of serious marine research in relation to whales and krill in the Antarctic. However, more significantly, 1925 also saw the introduction of the first factory ship with a stern slipway and by 1930 the industry was in the main pelagic and the most important target species was the blue whale. By World War II it was already apparent that significant inroads were being made into the stocks of blue whales (Mackintosh, 1942) and by the time the stock was protected by the IWC in 1964 the stock, which is thought to have numbered originally around 200,000 animals, had been reduced to no more than a few thousands.

When whaling resumed after the war, fin whales formed an increasing

proportion of the catch and became the mainstay of the industry throughout the 1950s and 1960s when catches consistently exceeded 25,000 fin whales per year. Eventually these stocks were reduced to the point where they were no longer commercially significant and sei whales became the chief target of the industry. These however were very quickly depleted and today only a remnant of the pelagic whaling industry operates on the smallest of the rorquals, the minke whale.

In all, the biomass of baleen whales was reduced from around 40-50 million tonnes before 1930 (Laws, 1977) to perhaps less than 5 million tonnes today. However, it should be mentioned that these figures may not reflect the true change in biomass because most estimates of initial and current population sizes are based on catch per unit effort (CPUE) methods, which are problematic. For example, recent research (Beddington, 1979; Fowler 1980; Cooke, 1984) has shown that these methods will underestimate population declines with typical whaling CPUE data.

Nonetheless, taking these figures at face value suggests that the biomass of baleen whales in the Antarctic is now around 40 million tonnes less than it was in the pristine state and Laws (1977), from considerations of the food requirements of whales, calculates that the amount of food (mainly krill, Euphausia superba) eaten by baleen whales will have declined by around 150 million tonnes per year.

However, sperm whales have also been heavily exploited in the Southern Hemisphere and a disproportionate share of the catch has come from large males which migrate to high latitudes. It is much more difficult to obtain estimates of the degree of depletion of sperm whales in the Southern Hemisphere but in some areas the declines are considerable (Cooke, de la Mare and Beddington, 1983).

The significance of sperm whale depletion, though smaller than that of the baleen whales in terms of biomass, may be comparable in the magnitude (but not direction) of its effect on the ecosystem because of their high

trophic level. We return to this theme below.

Predator Prey Interactions

There is a number of possible ways that the interaction between krill and its marine mammal predators can be viewed. Such views will determine the goals for management and ultimately the practice of management. Accordingly a brief review of the three main possibilities is appropriate.

One possibility is to consider the marine mammals as pests, which by their predation on krill reduce its potential for producing a sustainable harvest.

A second possibility is that both marine mammals and krill are potentially harvestable resources and that a final choice of harvesting levels will be determined by an intermix of social and economic factors.

Finally, the marine mammals may be considered as species requiring conservation in their own right and the krill fishery may be thought of as a particular type of habitat deterioration.

Whatever the views of the interaction, a decision to manage in this instance is in part based on the belief that marine mammals can affect the yield of fisheries and that fisheries for their food supply can affect the dynamics of marine mammals. This problem is explored in more detail elsewhere in this volume (Beverton, 1984), but it is pertinent to consider it in the context of the Southern Ocean system here. The main management instrument in the Southern Ocean is the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). The relevant part of this Convention is Article II, which reads:

 The objective of this Convention is the conservation of Antarctic marine living resources.

- 2. For the purposes of this Convention, the term 'conservation' includes rational use.
- 3. Any harvesting and associated activities in the area to which this Convention applies shall be conducted in accordance with the provisions of this Convention and with the following principles of conservation:
  - (a) prevention of decrease in the size of any harvested population to levels below those which ensure its stable recruitment. For this purpose its size should not be allowed to fall below a level close to that which ensures the greatest net annual increment;
  - (b) maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine living resources and the restoration of depleted populations to the levels defined in sub-paragraph (a) above; and
  - (c) prevention of changes or minimization of the risk of changes in the marine ecosystem which are not potentially reversible over two or three decades, taking into account the state of available knowledge of the direct and indirect impact of harvesting, the effect of the introduction of alien species, the effects of associated activities on the marine ecosystem and of the effects of environmental changes, with the aim of making possible the sustained conservation of Antarctic marine living resources.

Clearly there are a number of problems in interpreting the precise scientific meaning of certain portions of the text. In particular it is hard to interpret unless, following Edwards and Heap (1981), distinction is made between:

- species in the low trophic levels which form the food base for species in higher tropic levels (e.g. zooplankton, particularly krill);
- 2. species at intermediate trophic levels which prey on the species of the low trophic level but are themselves subject to significant predation by the top trophic level (e.g. squid and fish);
- 3. species at the top trophic levels which prey on levels 1. and 2. but are not themselves subject to significant natural predation (e.g. whales, seals and birds).

With this distinction, it is possible to recognise that top predators may only be adequately treated by the articles if levels of 'maximum net productivity' are interpreted as those occurring when some specific amount of krill are harvested. To put the problem in simple terms, in the absence of exploitation of their food supply, top predators will have some population level at which their net productivity is at a maximum. If their food supply is exploited then there will be a new and lower population level at which their net productivity will be maximised. Hence there is a range of possible protection levels for top predators and the precise level will be determined by the level of krill harvesting: the higher the level of krill harvest the lower the protection level. This would appear to be against the spirit of the convention and hence some interpretation which avoids this ambiguity is necessary. An obvious choice is the level that is defined when no krill are harvested. In any case, it has proved to be very difficult in the case of marine mammals to determine where such levels might be and in practice it is more likely that an arbitrary percentage of pristine abundance will be more useful.

There are a number of other scientific problems of interpretation of this text, which are really only illuminated by the use of a model of the system. Indeed the problem discussed above has been addressed with a particularly simple model of the interaction between the trophic levels in mind.

# Scientific Questions Posed by the Convention

The text of the Convention raises a variety of complex scientific problems. One whole set of problems is concerned with the interpretation and likely behaviour of the system under different types of perturbation. It is in this context that simple theoretical models can play a useful role. In some of the other problems and in particular in any practical area where precise quantitative answers are required, models of a different type are required. In this section we consider in light of simple theoretical models, the likely behaviour of the system. In the following sections we consider the way in which the quantitative estimates necessary for practical management can be obtained.

# Theoretical Models

In a series of papers (May, Beddington, Clarke, Holt and Laws, 1979; Beddington and May, 1980; Beddington and Cooke 1982) various authors have reviewed simple models of components of the Southern Ocean system.

It is inappropriate to review these here and readers interested in the technical detail of the models are referred to the original work. In this paper we describe the conceptual background of the models and then go on to consider the changes that might be expected in the system on the basis of these models.

In essence these models employ simple predator prey models framed in differential equations based on density dependent processes and assume that the unexploited system is in equilibrium.

In the discussion that follows we will frequently refer to Maximum Sustainable Yield (MSY), not because it is likely to be a practically achievable objective but, because of its familiarity, it is a useful concept around which to develop discussion. In addition, for all practical purposes the MSY level can be equated with the level of 'maximum net productivity' referred to in the Convention.

# Krill - Whales

This simple model assumes that the population growth rate of the predator species is determined by the abundance of the prey relative to the abundance of predators. The level of predation by whales on krill is proportional to the abundance of each. Such a model is general in the sense that a whole variety of similar models will produce similar predications to the following:

- There is no unique solution to the level of MSY for either predator or prey when both are harvested. The sustainable yield for one depends on the harvesting rate of the other.
- Population growth rates of the predators should increase following their depletion. For example in the case of the baleen whales following commercial whaling.
- 3. Krill abundance should increase when predator abundance is reduced and predator abundance decline when krill abundance is reduced.
- 4. Harvesting the prey at a level close to the 'surplus': (the difference between the amount eaten before predator depletion to that after predator depletion), could produce overexploitation of the prey.

Krill - Whales - Seals

A variant of the krill-whale model allows there to be more than one species of predator at the same trophic level. This model implies that:

 Calculation of the MSY level for any one species involves specifying the harvest level for both other species. Hence there is further ambiguity in the interpretation of the convention text which requires clarification.

2. Following depletion of one predator both the prey and the other predators should increase in abundance. This parallels the situation in the Southern Ocean with respect to the guild of baleen whales and to other predators such as seals, birds, squid and fish.

Krill - Cephalopods - Sperm Whales

This model extends the prey-predator model to predators at more than one trophic level. In the context of the Southern Ocean, predation by the cephalopod community (presumed to be on krill) is offset by predation by sperm whales on cephalopods. This model implies that:

- Following depletion of the top predator the intermediate predator increases in abundance and hence increases its predation on the prey and prey abundance decreases.
- Recovery of the top predator or harvesting of the intermediate predator will increase prey abundance.

One of the key parameters in all of these models is the extent to which the various species actually compete for the same food source. In general, one would expect that competition is limited in the pristine system, though in a severely perturbed system this may no longer be so.

This brief review of the implications of the simple models poses interesting questions about the Southern Ocean ecosystem. Following depletion of both baleen whales and sperm whales we may expect some increase in the cephalopod community, which benefits from reduced competition and predation. It is possible that the balancing effect of increased predation from the various competitors of the exploited baleen whales could have resulted in any outcome in the range of no change in krill abundance over time to a net increase in abundance. For example, increases in other animals such as fish, cephalopods or birds could take up part or all of the krill no longer consumed by the baleen whales.

How the various components in the system react to a change depends critically on the time scale of the response of the various predators on krill. There is little direct evidence to indicate what the response rates might be for marine mammals in the Southern Ocean. Typically, changes in large mammal populations may be expected to occur at a few per cent a year, though the Antarctic fur seal has shown a capacity for increase somewhat greater than this (Payne, 1977). In contrast, the cephalopods could be expected to have short generation times and relatively high fecundity and hence could change in abundance markedly in a rather short time. Accordingly the response of the community may be difficult to detect.

It is thus possible that the community of cephalopods could be playing a central role in the behaviour of the ecosystem. Unfortunately, there is considerable ignorance about even the natural history of these species. The numbers of marine mammals and birds which feed on squid imply that they are quite abundant, yet they are rarely taken in net hauls and hence the possibility of directly investigating these species poses a formidable problem.

In this situation, simple conceptual models have a role to demonstrate the possible behaviours and their effects on the rest of the system. However, it is clear that if progress is to be made in answering quantitative questions it is necessary to move to the alternative sources of information. These could be via the indirect effects of major changes in the abundance of krill on the marine mammal predators of krill.

# Practical Considerations

The implementation of the Convention raises a number of scientific problems of a more practical nature. Leaving aside questions of how to estimate the abundance of krill and where to set catch limits, Article II of the Convention implies that we have to determine some procedures for ensuring that the marine mammals are not being adversely affected by fisheries. Some insight into the nature of these problems can be gained from

considering some present difficulties in interpreting the current status of marine mammals in the Antarctic from existing data collected from both research activities and commercial whaling operations.

The idea that the depletion of the larger species of baleen whales has led to a competitive release of other marine mammals (and birds) has been around for some time (for example, Sladen, 1964; Gambell, 1973). On the basis of the simple theoretical models discussed above this is one of the types of effects predicted. However, there is a paucity of data which will admit any reliable quantification of such effects. What was once regarded as strong evidence for a marine mammal per capita krill surplus was from observed trends in the demographic rates of baleen whales and crabeater seals.

There are considerable quantities of data on pregnancy rates for the major exploited whale species. However, these data were collected from commercial whaling operations and this has led to a considerable degree of statistical confounding of the data, such that a totally unambiguous interpretation of trends shown by the data is not possible. A number of factors affect apparent pregnancy rates such as time of season of capture, latitude of capture and so on (Gambell, 1973; IWC, 1979). Indeed even the nationality of the inspectors collecting the data seems to reflect different reporting efficiencies (Grenfell, 1981; Mizroch and York, 1983).

Viewed simply as a time series by pooling the data across time of season, latitudinal zone, country taking the catch and so on, these data do show an increase in pregnancy rate, which is what would be expected from the reduction in intra-specific competition due to exploitation. If one takes into consideration the effects of different factors which may account for some of the observed features of the data, these can produce different interpretations. For example, Grenfell (1981) fitted a linear model to the data for blue fin and sei whales which corrected for a number of factors including: month of capture, latitudinal zone and country. This analysis showed qualitatively the same increasing trends as the simple pooling procedures in pregnancy

rate and this was statistically significant. In another analysis of these data for fin whales, Mizroch and York (1982) fitted a model which corrected for a change in length structure of the catches as well and this generally did not show statistically significant trends.

It is not helpful in this discussion to debate the minutiae of the interpretation of confounded statistics, it is more important to note the lesson that such problems can arise from data collected incidentally to a commercial fishery. Left to themselves, commercial fisheries seek to optimise their catch rates and thus the data they collect may be of diminished scientific value, particularly if important trends are to be recognised at an early stage. The other important conclusion is that there is at least the possibility that pregnancy rates offer the potential to show changes in the status of the whale populations.

A much more significant type of evidence for competitive release in the Antarctic was thought to be found in data on demographic parameters of some species of marine mammals which occurred even though they were not subject to any significant exploitation in the period when these changes were apparently taking place. The most striking examples of such changes come from the analysis of earplugs in whales and teeth in seals. These materials, when sectioned, show a number of laminae which in young animals are diffuse and irregular and in older animals become well-defined and regularly spaced (Laws, 1953; Hewer, 1964; Lockyer, 1972). The total number of laminae are related to the age of the animal and the point where the laminae become well-defined is termed the transition layer. The age at which this transition occurs is thought to be associated with the attaining of sexual maturity. Thus in principle, each animal has a record of its age and the age at which it reached sexual maturity. Hence, by plotting year of birth against the ages at maturity for a large sample of animals any trend in ages of attaining sexual maturity would be shown.

However, recent studies have shown that this method of analysis may not give a reliable indication and in fact the method may be fundamentally

flawed (Cooke and de la Mare, 1982, 1983). Some evidence that this is the case has been found for minke whales (IWC, 1984) and even more strongly so in crabeater seals (Bengtsen and Laws, 1983). There are a number of mechanisms which could cause spurious declines to be deduced from this method of analysis and these are discussed in Cooke and de la Mare (1982, 1983) but these are too complex to review here.

The more important consideration is the evidence which demonstrates the unreliability of the method. In 1983 a workshop was held under the auspices of the International Whaling Commission on the reliability of age determination in minke whales and particular attention was paid to determination in trends in the age at sexual maturity from the transition layer analysis. A number of different workers read a sample of ear plugs for age and transition layer and quite good agreement was obtained between readers for the total age of the animals, but the overall agreement on transition layers was poor. At the extreme, the correlation between transition layer readings for some readers was negligible, but the declining trend in age at transition layer from these different readings was virtually identical. This means that the trend is not dependent on the signal perceived from the ear plugs by the different readers and this indicates that there are mechanisms in the reading process which are not as yet understood. However, this result supports the possibility that the observed trends in minke whales are an artifact of the method.

The most convincing evidence that the transition layer method is flawed comes from Bengtsen and Laws (1983). The analysis of transition layers from crabeater seals sampled in the early part of the 1960's showed a decline in the age at sexual maturity. However, an analysis of the samples collected in 1980 showed exactly the same pattern of decline but shifted in time by an amount equal to the time between the samples. Since the apparent trend depends on the year in which the samples are collected, it can be concluded that the trends in age at maturity deduced from transition layers in crabeater seals are also an artifact of the method.

Whatever the answer to these questions, the important point is that

we do not have clear indications of the nature and extent of competition between krill predators in the Antarctic. This does not consitute evidence that such competition does not occur but it does mean that we are not in a position to estimate the strength of competition between species. Lacking such data it is unlikely that we could propose and test models which would give reliable predictions about the actual effects of the depletion of the great whales.

These problems also indicate some of the difficulties that may be faced in the future in determining trends in demographic parameters. This would not be so serious if we could reliably detect small changes in abundance of a given species. Unfortunately, this too is now being seen to be an area with considerable practical difficulties. The major problem is that the inherent variability in typical indices of abundance can mask trends until a very large change has taken place or a very long time series of data have been collected (de la Mare, 1984). This will still apply even for properly designed surveys because animals have patchy distributions and this results in high sampling variability.

This problem is exacerbated by the well-known problem that simple indices of abundance may not be linearly related to total population size. Moreover, recent studies have shown that even very detailed indices of abundance based on recorded searching time may still not be linear with stock size (Zahl, 1982; Cooke, 1984). This is another manifestation of the patchy distribution of animals. These problems are particularly marked in the estimate of whale population sizes from catch data and this is why we are now rather uncertain as to the magnitudes of the declines in the whale populations in the Southern Ocean.

The estimation of trends in whale population size from catch rates depends on commercial whaling, the future of which is in doubt. In any case, there have not been any catches of blue, humpback, fin or sei whales for a number of years and it is unlikely that these populations will have recovered to exploitable levels for some considerable time into the future.

In principle, sightings surveys such as those carried out under the International Decade of Cetacean Research (IDCR) programme can give the requisite information. However, some methodological problems remain to be solved (de la Mare and Cooke, 1984; IWC, 1984b) and also more problematically the indications are that the inherent variability in the results (IWC, 1984b) is such that the same problem arises in reliably detecting trends in abundance.

Thus we find ourselves in the situation where the system to be managed has been significantly perturbed and our information about the effects of the perturbation is not sufficient to give quantitative insight into the effects of various management actions. It follows that our future management procedures must be designed in such a way that we will acquire the required information and at the same time not impose significant risks that some component of the system will be adversely affected to an extent not reversible over a time scale of two or three decades as required by the Convention.

## Information Needs for Assessing Marine Mammal Fishery Interactions

The theoretical models discussed earlier give us some insight into the management principles which will have to be developed if the impact of a krill fishery is not to have a deleterious effect on the population levels of marine mammals. Clearly the Convention implies that a krill fishery is not to prevent the recovery of the severely depleted baleen whale populations to their level of maximum net productivity.

However, converting the principles into a scientifically based management system requires the identification of objective scientific measures of the state of the system and the setting of criteria on which management decisions will be taken. The preceding discussion on our uncertainty about the current state of the system indicates some of the practical difficulties in detecting changes in the system, particularly if management advice is to be timely and thus not require dramatic changes in catch levels.

The design of such a management system presents formidable but not necessarily insuperable scientific problems. The necessary first step in this process must be to gain a better understanding of the interaction between the marine mammals and their prey.

A number of the papers contributed to this volume have raised the problem of identifying the diet of marine mammals, many species of which are polyphagous. In the Southern Ocean the system is <u>prima facie</u> simpler because of the predominance of krill as the major prey species. However, as we have indicated there are a number of problems in assessing any effects of interaction in spite of this natural simplification.

Although rare in normal fisheries practice, the appropriate way to acquire requisite information is by statistically designed experiments. Unfortunately, in a system as large and as perturbed as the Southern Ocean the scale of the experiments is rather daunting. However, as we alluded to earlier, the history of exploitation in the Southern Ocean shows that complete reliance on data collected incidentally to commercial operations is unwise. Such data alone may only yield ambiguous statistical relationships which are often open to a number of alternative interpretations.

A possibility that might be considered is the regulation of the commercial fisheries by the management body in such a way that it implements a designed experiment. Ideally, specification of areas and catch levels from those areas give the possibility of giving different experimental treatments to different areas and the effects of these can be monitored. Such an approach implies that one of the treatments is for there to be no exploitation in some areas to provide suitable experimental 'control'. Conceptually, specifying different levels of exploitation around different land based breeding colonies of a gregarious species and monitoring breeding success would constitute such an experiment.

This approach obviously requires very considerable cooperation between the management body and the fisheries and the degree of regulation implied in the type of experiment above may not support a commercially

viable fishery. In such a case the minimum objective must be to have some substantial reference areas closed to fishing.

The land-based marine mammals, at least in principle, offer the opportunity for monitoring their demographic rates and in some cases, abundance. However, the problems of obtaining similar information for oceanic species such as the great whales are clearly more difficult. As there is no longer commercial whaling on the blue, humpback, fin and sei whales (and this could be the case for minke whales if the moratorium on commercial whaling becomes effective in 1986) it is probable that there will be no information available on whale demographic rates. As we discussed earlier, the direct monitoring of whale abundance is not likely to give the requisite information over a short time scale and thus monitoring responses to krill fishing in the great whales will be practically very difficult.

One suggestion that has been made to overcome these problems is that there are some species which can serve as indicators (the idea is reviewed in Green-Hammond, Ainley, Siniff and Urquhart, 1983). To be of practical use such a species would have to be land-based and thus relatively easily monitored and to respond to a depletion of a shared food supply in a way similar to the oceanic predator. There are a number of reasons for doubting that such a paradigm would provide an indefinitely long-term solution to the problem. For example, land-based predators have a limited foraging range, particularly during the breeding season. The patchy distribution of krill implies that the krill available to the different species will vary widely within the same general area. Even within the feeding range of the indicator species, a fundamental problem remains with this concept. That is the problem of detecting and calibrating the relationship between the species.

This approach could however give grounds for some optimism in establishing an interim procedure that will meet the objectives of the Convention. It is likely that the initial impact of krill harvesting on the marine mammal community will be most noticeable in those species that

are restricted in their range. This is because such species cannot compensate for changes in local abundance of their food supply by movement. Accordingly, detectable changes in the health of the populations of landbased predators may foreshadow changes in the whales. For it seems unlikely that the oceanic species will respond as immediately to a decrease in food supply when they have the opportunity to range widely in their search for food. One possibility therefore, is for the management regime to ensure that some fishing occurs in experimental reference areas and that the fishing intensity outside these areas is not more than that inside.

### The Role of Models

From the preceding it should be clear that there are several classes of models, each of which have their particular uses and shortcomings. The value of theoretical models is that they give insight into the system, they make predictions into what kinds of phenomena might be observed and finally they provide a framework for reconciling the observations and thus give a starting point for refined models. In general, such models do not give useful quantitative predictions about specific aspects of the system, for example, catch limits. In fact this may not even give correct qualitative predictions; in one sense their role is to generate the hypotheses to be tested by observation.

The second class of models that we define here are estimation models which are fitted to data to produce estimates of parameters. The aim of such models and their associated parameters is to encapsulate some aspect of the system under consideration and in particular to produce quantitative estimates about the system such as yields or demographic parameters of particular species. There is a very wide range of such models, for example surplus production models, growth models, population esimators based on catch per unit effort and so on. Such models are designed to incorporate few parameters and as such may not always be applicable in a particular set of circumstances nor give a good fit to the data. The practical problem however, is a well-known one, the generality of a model can be increased and thus give a better fit to the data by adding more parameters but at the expense of

being less certain about the individual values of the resultant parameter estimates. The role of this class of models in the management of resources is obvious.

We categorise the third class of models as strategic simulation models which we see as forming a link between theoretical system models and estimation models. The most important role of such models is to evaluate strategies for the acquisition of information about a system and hence management decisions. This is an aspect of resource management which has been rather neglected but this should not belie its importance particularly in the emergence of the approach to management adopted for the Southern Ocean.

The management required in the Antarctic seeks (amongst others) to limit the impact of a krill fishery on marine mammals and thus the role of strategic simulation models is fundamental in how to go about giving effect to this objective. There are, in essence, three sources of information about the ecosystem relevant to the problem, namely historical information, commercial catch statistics and data from scientific surveys. Of course nothing can be done about the 'experimental design' of historical information but this cannot be said of the planning of data gathering in the future. Scientific surveys are expensive and the amount of resources available for such work will inevitably be limited. In this context the crucial role of strategic simulation modelling is as an aid in planning experimental programmes in a way which optimises the information gained about the system for the amount of scientific resources available. Of particular importance is to indicate how much research effort is required, given a range of models (hypotheses) of the system, to determine whether some effect is occurring, to some specified level of precision. A related consideration is how commercial operations can be integrated into the management system to maximise the scientific utility of commercial catch statistics and thus avoid some of the problems of statistical confounding alluded to earlier.

Thus, in the context of marine mammal fisheries interactions in the Antarctic, the theoretical models give guidance as to what sort of phenomena

to look for, the strategic simulation models indicate how to look for them and the estimation models are the tools which summarise the observations for practical purposes. Such a process can be recursive. One thing should be clear from this discussion, modelling cannot substitute for experimentally rigorous observation. Conversely, unguided observation provides only data not insight.

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