BRIDGING THE GAP BETWEEN ORNITHOLOGY AND FISHERIES SCIENCE: USE OF SEABIRD DATA IN STOCK ASSESSMENT MODELS[1]

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Abstract. Seabirds and marine fish share habitats and food webs, but there is too little contact between the disciplines that study them. Fish stock assessment models, designed for use on teleost fishes with high fecundity, high recruitment variability, and continued growth throughout life, may be strengthened by inclusion of seabird data. In some circumstances seabird-based indices of prey abundance could assist in calibration of sequential population analysis of fish stocks. Seabird energy acquisition rates, equivalent to fisheries catch per unit effort, are the most promising avian indicators of stock size. Seabird data may be useful in predicting recruitment of commercial fisheries and in improving estimates of natural fish mortality. The impact of seabird predation on fish stocks depends on the age of targeted fish and their subsequent growth and mortality. Yield-per-recruit analyses, derived from fisheries science, suggest that under plausible conditions the impact of seabird predation on fish stocks may be amplified by avian preference for small prey. Increased collaboration between seabird biology and fisheries science will benefit conservation of both birds and fish.

Key words: Seabird biology; fisheries biology; stock assessment; prey indicators; marine abundance indices; time budgets.

INTRODUCTION

The lives of air- and water-breathing vertebrates of the world's oceans are intimately entwined through physical proximity and trophic dependencies. But the same close relations do not exist among scientists who specialize in marine vertebrates; instead, professional affinities follow taxonomic, rather than ecological, lines.

The theme of this paper is that seabird and fisheries biology have much to gain from each other's data and insights. Fisheries biology is a mature discipline, having been active since the turn of the century in support of commercial fisheries conservation and management (Cushing 1981). Seabird biology is an upstart in the marine field, and has only recently broken from its land-bound traditions to apply new mathematical, electronic, and physiological techniques to investigations of birds at sea (Croxall 1987). This new research has suggested that seabirds play central roles in marine food webs (e.g., Huntley et al. 1991), and that as wide-ranging and highly visible predators they have potential as indicators of fish abundance (Cairns 1987).

This paper examines potential applications of

seabird data to fisheries stock assessments and methods of fisheries analysis which could help clarify the impact of seabirds on their prey. Work toward the integration of seabird data with fisheries models is proceeding rapidly in several areas (e.g., Sparholt 1990; Bailey et al. 1991); the present paper is designed to encourage further endeavors. An ancillary goal is to review features of fish populations and assessment techniques which must be understood for successful integration of seabird and fisheries data. The fisheries literature is vast and daunting, and many of its key elements are grasped by few outsiders (Larkin 1978).

ESSENTIAL FEATURES OF FISH POPULATION DYNAMICS

The problems and possibilities of managing marine fish stocks stem from the life history traits of marine teleost fishes, which differ in many respects from typical vertebrate patterns (Larkin 1978, Rothschild 1986). The generalizations below apply particularly to mid- to high-latitude shoaling species, which are the chief prey of many seabirds.

Marine teleosts generally produce large numbers of eggs which pass through larval and juvenile stages before reaching sexual maturity at
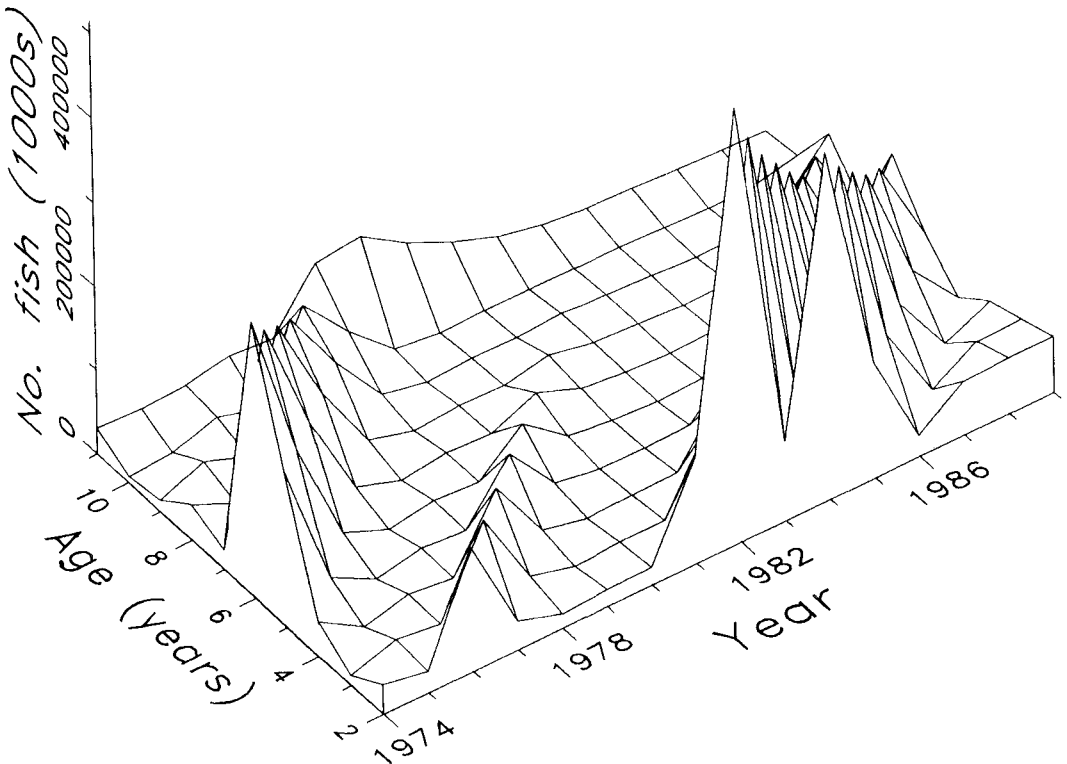
FIGURE 1.   Number by age of herring caught in the west coast Newfoundland herring fishery, 1973–1989. Note the strong ridges formed by the 1968, 1980, and 1982 year classes, and the paucity of fish from other years. Data from McQuinn and Lambert (1990).

ages typically ranging from two to several years. Growth, although reduced after the onset of sexual maturity, continues throughout life and somatic weight may increase several-fold after sexual maturity.

Because of high and variable mortality in early life, there are large annual fluctuations in the number of young fish recruiting (i.e., reaching fishable size) to a fishery (Rothschild 1986). Varying strengths of year-classes can be tracked by aging fish through otolith or scale ring counts (Summerfelt and Hall 1987). This variation is illustrated by the west Newfoundland herring (*Clupea harengus*) fishery where the majority of fish caught between 1973 and 1989 came from only four year-classes (Fig. 1; McQuinn and Lambert 1990). Because of the great variation in early mortality the size of a recruiting cohort usually bears little relation to the size of its parental stock (Cushing 1981).

The biomass of a fish cohort depends on the interaction between mortality and continued growth. Cohort biomass is commonly modeled with von Bertalanffy growth equations (Busacker et al. 1990). Figure 2 (upper curves) shows the typical pattern of biomass elaboration, with mass peaking in the early years of adulthood and then declining as the effects of mortality overtake those of growth.

FISH STOCK ASSESSMENT TECHNIQUES

Sequential population analysis. The most commonly used stock assessment technique is sequential population analysis (SPA) and its variants virtual population and cohort analyses (Gulland 1965, Pope 1972, Megrey 1989). SPA assumes an absence of immigration and emigration and requires a fishery of long duration that is sufficiently intense to affect the population. Figure 3 outlines the major steps of an SPA-based assessment. I will first describe the input data necessary for this approach and then deal with SPA itself.

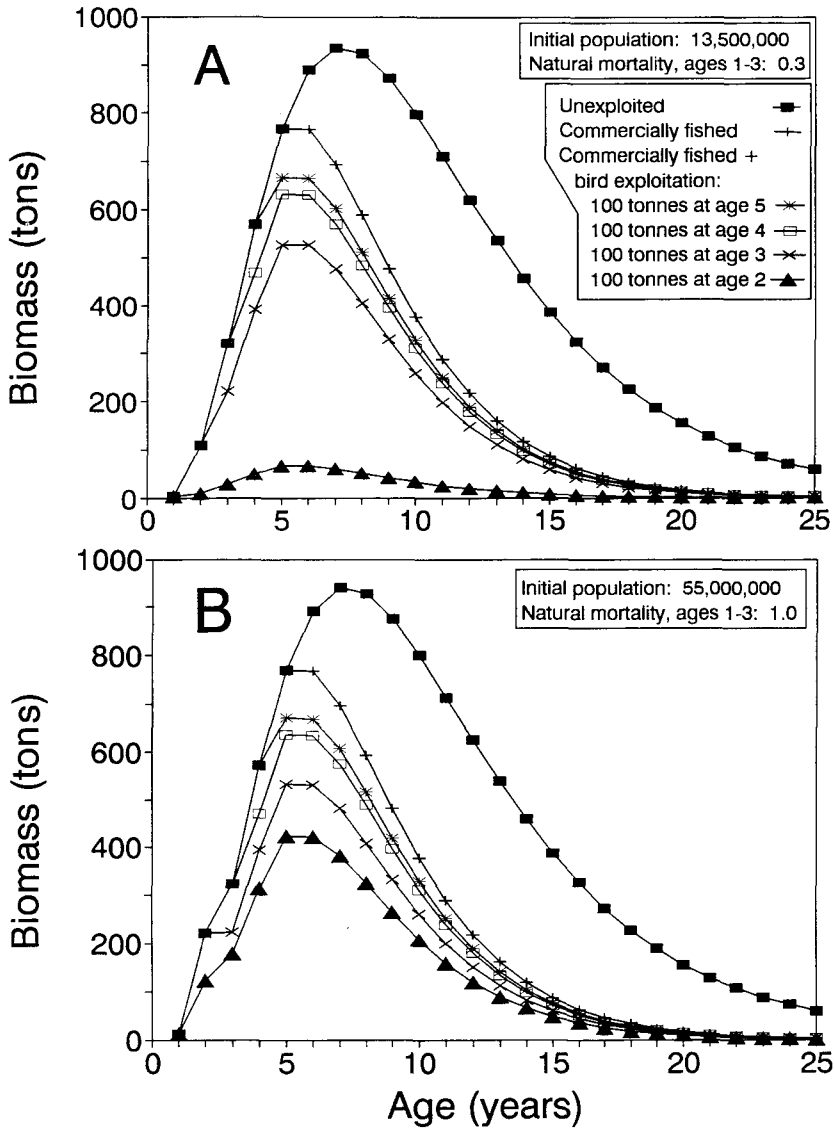SPA uses as input a catch-at-age matrix, an

FIGURE 2.   Change of biomass with age in a hypothetical winter flounder cohort. Population at age 1 is assumed to be 13,500,000 fish in A and 55,000,000 fish in B. Growth follows von Bertalanffy parameters given by Vaillancourt et al. (1985). Instantaneous mortality due to causes other than bird or fishery exploitation is 0.3 and 1.0 at ages 1–3 in A and B, respectively, and 0.2 thereafter in both A and B. In commercially fished populations instantaneous fishing mortality is 0.15 after age 5. The effects on cohort biomass of avian predation of 100 tons of fish of various ages are shown.

index of stock abundance, and a natural mortality rate. The catch-at-age matrix gives the number of fish caught of each age during each year (Stephenson 1988). This is derived from landing statistics and from aged fish from commercial samples (Doubleday and Rivard 1981a). Figure 1 shows a catch-at-age matrix in three-dimensional form. Abundance indices are typically derived from catch per unit effort (CPUE) of commercial fisheries or research surveys (Doubleday and Rivard 1981b). CPUEs from various gear types, seasons, and areas can be integrated into a combined index by a multiple regression technique (the multiplicative model,
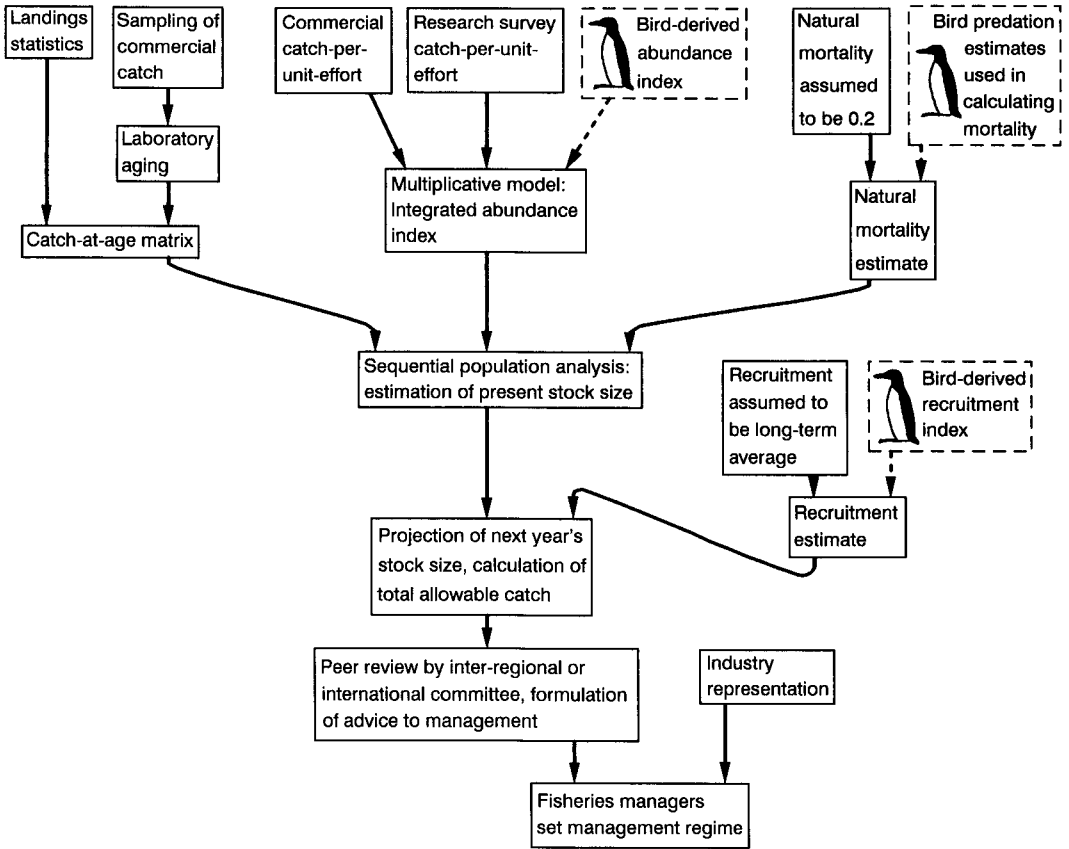
FIGURE 3.   Structure of an analytical stock assessment. Elements in solid boxes show typical current practice; elements in dashed boxes show potential uses of seabird data in stock assessments.

Gavaris 1980). Natural mortality is difficult to measure and is often chosen subjectively (Hildén 1988).

SPA can be understood by considering a hypothetical population in which all mortality is due to fishing (O'Boyle 1988). If the number of fish caught of each age is recorded each year, the cumulative catch of a particular cohort is an estimate of the total size of that cohort. This estimate will asymptotically trend towards true cohort size as the number of years increases.

Fish populations are affected by natural as well as fishing mortality, so natural mortality rates are used to adjust cumulative catches to improve estimates of cohort size (Winters 1988). Cumulative summation works well for cohorts whose life span is nearly ended, but underestimates size of younger cohorts that have not been extensively fished. This problem is tackled by iteratively regressing population estimates against in-

dependent abundance indices, a process known as calibration. A recent fishing mortality rate is arbitrarily picked, which allows populations of each age to be calculated for all the years of the catch-at-age matrix. The best estimate of present population is found by iteratively varying this fishing mortality and measuring explained variation in the regression between the stock abundance index and the calculated population-at-age. Present stock size is taken as the calculated population when explained variation peaks.

Once the current size and age structure of the stock has been estimated by SPA, stock status for the following year is projected (Gascon 1988). Because the abundance of young fish below commercial size is rarely known, the size of the recruiting year class is set at the mean of previous years. The conflicting effects of fish growth and mortality on cohort biomass (see Fig. 2) are examined in a yield-per-recruit analysis, which es-

timates the fishing mortality that would maximize yield from the stock. A total allowable catch based on these considerations is then recommended to stock managers.

Acoustic estimates. The leading alternative to SPA is the direct estimation of biomass from hydroacoustic surveys (MacLennan and Simmonds 1992). This is based on knowledge of acoustic reflectivity (target strength) of fish and measurements of strength of echoes returning from fish schools. Since target strength varies with size and species, biological samples are required to confirm species identification and determine fish size and age structure. Acoustic surveys yield information equivalent to the "sequential population analysis" box in Figure 3; procedures thereafter are similar to those of SPA-based assessments. In practice acoustics are often used jointly with analytical assessments. Acoustic estimates may serve as abundance indices for SPA calibration, and commercial sampling data may be used in projections of acoustic biomass estimates.

Surplus production models. Surplus production models require no age-structured stock information (Ricker 1975). These models assume that an unexploited fish population will increase along a predictable curve to reach a stable carrying capacity, and that a fishing intensity producing maximum sustainable yield can be calculated from this curve. In practice, fish populations rarely follow a smooth curve to a stable equilibrium and surplus production models are now uncommon in stock assessments (Larkin 1977, Walters 1987).

APPLICATION OF SEABIRD DATA TO FISHERIES ASSESSMENT MODELS

Abundance indices. It has frequently been proposed that data derived from seabirds may indicate abundance of their prey (Cairns 1987; Monaghan et al. 1989b; Montevecchi, in press). Such indicators could potentially be used for calibration of sequential population analysis of fish stocks.

An ideal indicator of stock size has the following characteristics: (1) it responds directly to stock variations and is immune to influence from other sources; (2) it permits detection of changes in stock size at all stock levels; and (3) it can be used to generate an abundance index that is linearly related to absolute stock size. Potential indicators can be divided into those based on pop-

ulation and reproductive parameters and those based on time and energy budgets. These types have different characteristics and are considered separately below.

Population and reproduction parameters that have been suggested as stock indicators include adult survivorship, egg size, clutch size, breeding success, chick growth, chick fledging weight, adult weight, and guano production (Anderson and Gress 1984, MacCall 1984, Cairns 1987, Croxall et al. 1988, Croxall 1989). However, all of these parameters can be influenced by factors unrelated to food supply (see Cairns 1992) and their utility is also reduced by zones of constancy with respect to prey abundance and by difficulties in establishing a relation with absolute stock size.

Figure 4 plots putative relations between prey supply and several seabird reproductive and population parameters (Cairns 1987, Williams and Croxall 1990). Because adult seabirds have high annual survivorship except during extreme prey scarcity (Croxall and Rothery 1991, Cairns 1992), survivorship indicates food abundance only when food is very scarce. At other times survivorship is constant or nearly so with food supply, and so has no value as an indicator.

When food supplies are very poor breeding success will be constant at zero (Fig. 4; Drent and Daan 1980). When food supplies are favorable, breeding productivity may also be constant over a broad range of food abundances. This occurs because birds appear to "buffer" the effects of varying food supplies by adjusting their foraging effort to maintain constant levels of parental care (Burger and Piatt 1990). Behavioral buffering may have similar stabilizing effects on chick growth (Hamer et al. 1991). Reproductive success and chick growth may indicate food supply within a certain range; i.e., food supply is above the minimum for survival of some chicks but below the level where parents can readily exceed chick needs (Fig. 4). However, brood adjustment may act to decouple food supply from growth parameters. Williams and Croxall (1990) reported that fledging weights of Gentoo Penguin (*Pygoscelis papua*) chicks declined with size of parental food loads. They attributed this paradox to high mortality during food-scarce years of one of the two chicks in the brood, which allowed the surviving sibling to increase its food intake.

In the absence of immigration and emigration, the integration of survivorship and reproductive success is population growth. This parameter has
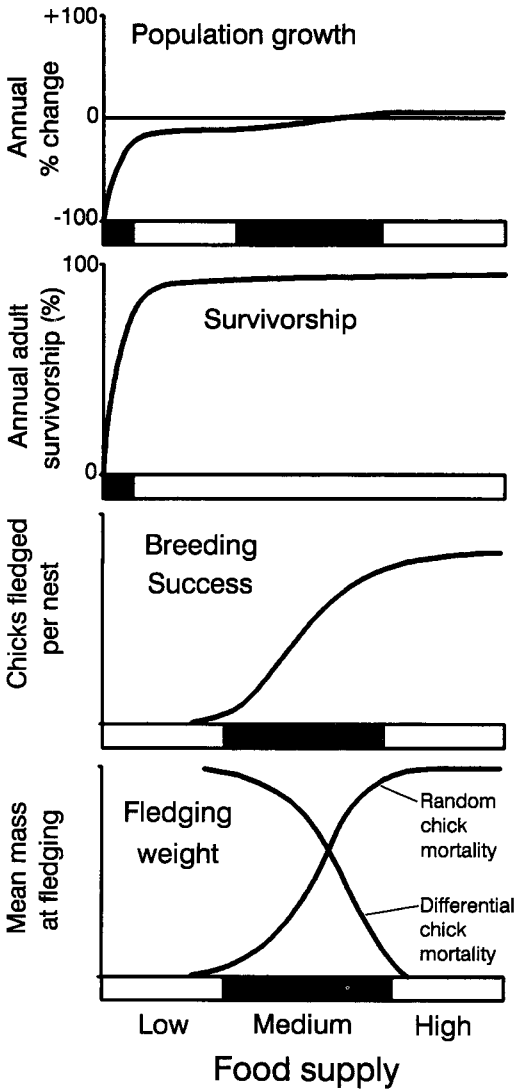
FIGURE 4. Hypothesized relations between food supplies and seabird population and reproductive parameters. Bars at the base of panels indicate zones of prey availability where seabird parameters are likely to indicate food supply. In the bottom panel the curve labeled differential chick mortality gives fledging weights where chicks in poor condition suffer high pre-fledging mortality in poor food years, thus leaving more food for surviving siblings (Williams and Croxall 1990).

two zones of co-variation with food supply: one at very low food abundances where adult survivorship falls, and one at intermediate levels of food abundance where breeding success varies with food supply (Fig. 4).

The zones of variation of population and reproductive parameters tend to occupy the lower and middle ranges of food supply (Fig. 4), hence the simultaneous use of several parameters may qualitatively indicate trends in this part of the spectrum. However it appears unlikely that population or reproductive parameters can provide a quantitative indicator that operates at all levels of food supply.

Use of time and energy budgets provides an alternative to reproduction- and population-based food indicators (Eberhardt 1977, Estes et al. 1986). As endotherms with high metabolic rates, seabirds must maintain energetic equilibrium within a relatively small range of body weights (Birt-Friesen et al. 1989, Croll et al. 1991). Time devoted to feeding should thus be linked to food supplies as foraging time is adjusted to maintain energy equilibrium under varying feeding conditions.

The easiest way to infer foraging time is to measure colony attendance, which should increase as favorable feeding conditions release time that can be spent at the nest (Gaston and Nettleship 1982, Burger and Piatt 1990). However, if time unneeded for foraging is spent mostly at sea (as is the case for Common Murres, *Uria aalge*, Cairns et al. 1987b), colony attendance will only approximately reflect feeding time.

Recent advances in instrumentation now make it possible to directly measure time budgets of birds at sea (Trivelpiece et al. 1986, Cairns et al. 1987a, Jouventin and Weimerskirch 1990). In addition, time-energy studies based on the doubly-labeled water technique (Weathers et al. 1984, Goldstein 1988) allow accurate measurement of energy use. If both energy needs and foraging time are known for an animal in energetic equilibrium, it is possible to calculate the rate of energy acquisition while foraging. This is equivalent to the catch per unit effort of fisheries science.

This approach can be illustrated by the Northern Gannet (*Sula bassanus*). Birt-Friesen et al. (1989) showed by simultaneous measurements of time and energy use that this plunge-diving seabird consumes 144 kJ hr^{-1} while at the colony or sitting on the water and 349 kJ hr^{-1} while flying. Foraging time is equivalent to flight time because prey are located from the air. The nest is normally guarded by one parent (Montevecchi and Porter 1980); time spent accompanying the partner at the nest or sitting on the water can therefore be considered a buffer which varies according to needs of foraging time. Calculations of energy acquisition must also consider chick
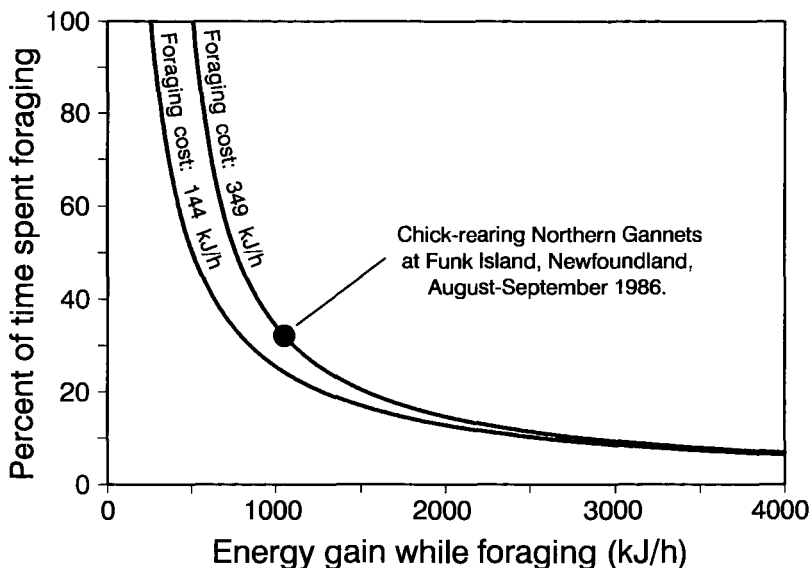
FIGURE 5. Calculated relation between energy gain while foraging and percent time foraging required to maintain energy equilibrium in Northern Gannets in the middle of the chick-rearing period. See Appendix for equation. The species' foraging cost is 349 kJ hr^{-1} (Birt-Friesen et al. 1989) and each parent must also supply 1,800 kJ day^{-1} to its nestling (Montevecchi et al. 1984). Assimilation efficiency is 0.8 (Furness 1978). The dot indicates percent foraging time observed in the field (Birt 1987). Time foraging is also plotted for foraging costs of 144 kJ hr^{-1} (equivalent to costs of sitting on the water or at the colony, Birt-Friesen et al. 1989).

needs. Northern Gannets feed their single chicks 3,600 kJ days^{-1} at the six-week midpoint of their nestling period (Montevecchi et al. 1984).

Figure 5 plots the relation between energy acquisition rate and the amount of foraging time needed to maintain energy equilibrium (see Appendix for derivation of equations). Foraging time rises rapidly when acquisition rate is low; a bird that gains 800 kJ hr^{-1} while foraging can meet its energy needs by spending 50% of its time foraging but if energy acquisition falls to 530 kJ hr^{-1}, foraging time must rise to 24 hr day^{-1}. In August–September 1986 chick-rearing gannets at Funk Island, Newfoundland, spent 31% of their time in flight (Birt 1987), which corresponds to an acquisition of 1,080 kJ hr^{-1}. Foraging time also increases with the cost of foraging relative to other activities, particularly when energy acquisition is slow (Fig. 5).

Calculation of seabird energy acquisition rate from time budgets requires knowledge of activity-specific metabolic rates which can be determined by regression analyses of time allocation against energy use (Nagy et al. 1984, Birt-Friesen et al. 1989). Energy measurements by the doubly-labeled water method are highly accurate but may have to be repeated to cover geographic and other variations (Montevecchi et al. 1992). Once activity-specific metabolic rates are established energy acquisition rates can be calculated from time allocations which can be measured relatively cheaply by digital immersion timers or radio transmitters (Wanless et al. 1985, Cairns et al. 1987a). These acquisition rates can be used directly as CPUE in stock abundance indices.

Energy acquisition rates are likely to most accurately reflect stock size at intermediate ranges of food availability. When prey are very abundant, a large change in energy acquisition rate will result in only a small change in percent foraging time (Fig. 5), which will magnify the effect of measurement errors. When food is very scarce the assumption of energy equilibrium may be violated, and per capita energy needs may rise because of decreases in insulative body fat (Brodie and Pàsche 1982). Moreover, time budget measurements may be impossible if food shortages force colony abandonment (Schreiber and Schreiber 1989). When stocks are extremely low the best indicator of food abundance may be adult survivorship (Ainley et al. 1988) or adult weight and condition index (Monaghan et al. 1989a).

Natural mortality. Natural mortality is gen-

erally set at a constant value in fisheries assessments (Fig. 3), although seabirds and other fish predators are highly size, and therefore age, selective (e.g., Swennen and Duiven 1977). Mortality due to specific predators can be estimated through diet data and bioenergetics models of food needs (Furness 1978, Harwood and Croxall 1988). If geographic area of this exploitation can be established (not always easy; see Bourne 1983), bird-caused mortality to the stock can be estimated.

A second approach to inclusion of seabird mortality in fisheries assessments is a form of SPA known as multispecies virtual population analysis (MSVPA) (Shepherd 1988, Pope 1989). MSVPA uses dietary information to estimate predation rates within and among fish species and hence refine natural mortality estimates. Unlike standard SPA, MSVPA allows mortality rates to vary among ages and among years according to estimated predation intensity. The most extensive implementation of MSVPA has been the North Sea, where predation calculations have shown that fish may consume as much biomass of commercial stocks as the fishery itself (Daan 1987). MSVPA models can also be extended to include estimates of seabird predation rates on fish (Sparholt 1990). MSVPAs are still in the experimental stage but their use and influence seem destined to grow (Kerr and Ryder 1989).

Recruitment indices. Because seabirds frequently prey on fish below commercial size, they are potential predictors of subsequent recruitment to commercial stocks. Ideally seabird data would provide a quantitative indicator of pre-recruit cohort size according to the methods suggested for SPA calibration. However, most fisheries assessments contain no recruitment predictors other than the long-term mean, so even qualitative bird-derived estimates of pre-recruit abundance may improve accuracy of stock projections.

There are numerous examples of seabird predation on small fish which could potentially provide recruitment predictors. The strong correlation reported by Monaghan et al. (1989b) between number of tern chicks available for banding and subsequent recruitment of sand lance (*Ammodytes* sp.) is most promising in this regard. Other recruitment predictors might come from murres feeding on capelin (*Mallotus villosus*) in Newfoundland (Burger and Piatt 1990) or from Rhinoceros Auklets (*Cerorhinca mono-*

cerata) preying on herring in British Columbia (Vermeer and Westrheim 1984).

Yield-per-recruit analyses. Seabird predation on fish stocks is typically estimated by bioenergetics models as tons removed within a geographic area (e.g., Wiens and Scott 1975, Furness 1978, Croxall et al. 1984). Although such estimates are commonly expressed as percentage of local fish production (Croxall 1987), the impact of bird predation depends crucially on avian prey size selection and the growth and mortality schedules of the fish population.

Bird impact on fish stocks can be modeled using yield-per-recruit analyses similar to those used to calculate the level of fishing intensity that optimizes yield. I illustrate this approach by simulating biomass changes of winter flounder (*Pseudopleuronectes americanus*), a significant prey of cormorants (*Phalacrocorax* spp.) in the Gulf of St. Lawrence (Cairns et al. 1991). Figure 2 tracks biomass of a flounder cohort using known growth curves (Vaillancourt et al. 1985) and assuming instantaneous natural mortality due to non-avian sources of 0.2 after age 3 and fishing mortality of 0.15 after age 5. Because juvenile mortalities are poorly known but are likely higher than adult mortality (Pope and Knights 1982), effects of two levels of juvenile mortality are modeled. Age 1 populations are adjusted for variation in juvenile mortality so as to achieve similar levels of peak cohort biomass.

The impact of avian harvest of 100 metric tons from this hypothetical stock increases sharply with selection of younger fish, and with the assumption of a low non-avian juvenile mortality (Fig. 2). When bird exploitation targets age 2 fish and non-avian instantaneous juvenile mortality is set at 0.3 (equivalent to 26% annual death rate), bird predation reduces peak biomass by 91% (Fig. 2A). In this scenario, the birds remove so many small fish that few ever reach commercial size. When birds target age 5 fish, the same harvest results in only a 13% reduction in peak biomass. Here, bird impact on the stock is much less because cohort biomass has already grown substantially before avian harvest.

Figure 2B shows the effects of bird harvest when non-avian instantaneous juvenile mortality is 1.0 (63% annual death rate). Impact on the stock is reduced under this assumption because most of the small fish taken by birds would have succumbed to natural mortality in the absence of avian predation. In these trials avian removal

of 100 tons of age 2 and age 5 fish causes peak biomass to drop by 45 and 13%, respectively.

It has been suggested (e.g., Cairns et al. 1991) that seabird preference for small fish reduces competition with the fishery. However, this analysis shows that under plausible conditions, impact on stocks can be magnified by preference for early year classes, and that a small avian harvest may have a larger effect on stock biomass than a much greater harvest of older fish by the commercial fishery.

DISCUSSION

Fisheries biology is a mature science with a vast literature and deeply rooted traditions. What can the newly minted discipline of avian marine ecology offer this monolith? To answer this we must understand that many of the models and tenets of fisheries biology are hard to confirm experimentally and "faith plays an accordingly large part in fisheries science" (Larkin 1978). Part of the challenge is that reliable data are often surprisingly difficult to collect. Among the pitfalls of fisheries data are biases in commercial CPUE due to increased fishing power (Baird et al. 1990) and deliberate misreporting of landings or effort (McQuinn 1987). Other factors affecting fish populations may be outside the traditional perimeter of fisheries data gathering, which is based on commercial and research fishing. In particular the distribution and abundance of juvenile fish, which are often difficult to capture in conventional fishing gear, is poorly known for many commercial stocks (e.g., Chadwick et al. 1990).

Standard assessment approaches encounter the greatest difficulty in short-lived pelagic species (Csirke 1988), which are often the chief prey of both seabirds and important commercial fishes. When assessments cannot reliably characterize a stock, both seabirds and the fishery are put at risk. Declines of capelin in Newfoundland (Brown and Nettleship 1984) and the Barents Sea (Vader et al. 1990) had important consequences to seabird populations, but it has proven difficult to accurately measure these declines and determine their causes (Carscadden 1984, Hamre 1988). Inclusion of seabird data will by no means resolve all assessment difficulties (Bailey et al. 1991) but conventional techniques alone are unlikely to be successful where seabirds are major predators.

As Hunt et al. (1991) point out, seabird foraging violates statistical rules of sampling be-cause birds concentrate on particular sites where prey is most available. In addition, seabird catch rates reflect prey availability, not absolute abundance. These difficulties do not obviate the use of seabird data as stock indicators because commercial fishing fleets, upon whose catch rates many stock assessments are based, also concentrate on local prey aggregations and use fishing methods which are highly selective (Pope 1988, Abrahams and Healey 1990, Winters and Wheeler 1990). Abundance indices based on research surveys observe statistical niceties but surveys usually involve only one vessel and hence suffer from small sample size. There is no perfect indicator of fish stocks; under some circumstances seabird-based indices may be useful supplements to currently available tools, but they will not replace them.

Many temperate or polar seabird populations are monophagous or nearly so. Such populations are the best substrates for developing seabird-based indices because seabird parameters should respond to availability of the major prey. Where seabirds feed on several species, the relative importance of various prey in the diet may indicate prey availability on a dichotomous presence/absence scale (Montevecchi et al. 1988a). However development of interval scales of prey abundance in euryphagous species will be confounded by prey switching unless clear hierarchies of prey preference can be established.

Seabird parameters have been used to infer both spatial and temporal variation in food supplies (e.g., Ricklefs et al. 1984, Burger and Piatt 1990). Until relations between seabird parameters and food supplies are firmly established, prey indication is likely to be most reliable at single sites where ecological conditions other than food supply are similar over time and where standard monitoring protocols can be maintained (Estes 1990, Garshelis et al. 1990).

The linking of seabird biology to fisheries management programs will require new orientations in field research. Much of seabird ecology has developed from long-term monitoring of breeding parameters at single colonies (Wooler et al. 1992). Long-term monitoring programs should be expanded to incorporate independent measures of prey abundance which will permit testing of hypothesized relationships between seabird parameters and prey supplies. Such tests are most practical where colony foraging range is sufficiently small to allow accurate estimation of

abundance of prey available to breeding birds. Fine-scale SCUBA (Birt et al. 1987), acoustic (Safina and Burger 1988, Burger and Piatt 1990), and trawl (Currie and Comeau 1989) surveys seem the most promising methods of measuring local prey abundance. Use of stock estimates from regular fisheries assessments is an alternative to the colony-specific approach (Anderson and Gress 1984, Crawford and Shelton 1978), but the lack of spatial and temporal correspondence between stock assessment zones and colony foraging areas may obscure relationships (Croxall 1987).

Some data useful to fisheries assessments may be derived from small additions to present seabird research. However, the large-scale monitoring programs necessary for full integration of seabird trophic interactions into marine resource models are likely to be expensive by traditional norms of seabird funding. Such costs are nevertheless small when compared to assessment-related fisheries research. For example, a major fish stock typically absorbs several weeks of research vessel time annually at a cost (in United States dollars) of $10,000–20,000 day^{-1}, plus extensive commitment of sampling, laboratory, and analytical personnel. If the utility of seabird data in fish stock assessment can be demonstrated, reassignment of even a small fraction of fisheries budgets would substantially boost resources available to seabird monitoring.

The generation of seabird data that can be used in current assessments is but one step towards management models that encompass the interests of marine predators as well as those of commercial fishermen. Multispecies models such as MSVPA may become part of the official assessment process in some areas. Seabird biologists should seek participation in inter-disciplinary efforts to implement such models; the recently formed Seabird/Fisheries Study Group within the International Council for the Exploration of the Sea is an apt forum. Where seabirds prey on pre-recruit year-classes of commercial species, such models should incorporate yield-per-recruit analyses to estimate the influence of seabirds on prey stock size. Under some conditions of avian preference and fish growth and mortality, small seabird harvests may have major impacts on fish stocks (Fig. 2). Seabird bioenergetics models, grafted to MSVPA, could assist in estimating bird-induced fish mortality (e.g., Sparholt 1990). Multispecies models could also use seabird parameters in stock abundance indices.

The emphasis on quantitative models should not overshadow the contribution to fisheries science of qualitative seabird studies. Because seabirds often sample species and size-ranges that are unavailable to commercial and research gear, they may provide valuable information on migration, distribution, and life history (e.g., Berruti and Colclough 1987, Montevecchi et al. 1988b, Ridoux 1988). Such studies are likely the most valuable avian contributions to fisheries science to date.

This paper has focused on potential contributions by seabird biology to fisheries management. Such benefaction is not solely altruistic because seabirds suffer substantial risk when fish are overexploited or managed without regard to natural predators (Furness and Ainley 1984). The flowering of avian marine ecology in the 1980s has shown that seabirds are a major component of the marine community. For seabirds to maintain this standing in the face of increasing pressures on marine resources requires that seabird data and seabird interests be integrated into marine management models. The bridging of the traditional chasm between fisheries and seabird biology offers the best chance that this will occur.

ACKNOWLEDGMENTS

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APPENDIX

Derivation of formulas relating time spent foraging to energy gain while foraging.

For an animal in daily energetic equilibrium, the sum of energy gained (G) is equal to the sum of energy expended (Ex) over 24 hours divided by assimilation efficiency (A). If the animal is provisioning young its contribution to their energy requirements (C) must also be included:

$$\Sigma\, G = \frac{\Sigma\, Ex}{A} + C. \tag{1}$$

Energy gained per day is the product of gain per hour while foraging (G_{for}) and daily foraging time in hours (t_{for}). Daily energy expenditure is the sum of the products of activity-specific expenditure rates $(Ex_{act_1}, Ex_{act_2}, \ldots)$ and time spent in each activity $(t_{act_1}, t_{act_2}, \ldots)$, all divided by assimilation efficiency, plus the contribution to brood provisioning:

$$G_{for}t_{for} = \frac{\displaystyle\sum_{i=1}^{i=n} Ex_{act_i}t_{act_i}}{A} + C. \tag{2}$$

Consider an animal which maintains energetic equilibrium by foraging just long enough per day (t_{for}) to meet its energy requirements. The remaining time is spent in various activities whose time allocation per day is fixed $(t_{act_1}, t_{act_2}, \ldots)$, and in a buffer (t_{buf}) activity which expands or contracts with changes in foraging time. The daily energy budget is:

$$G_{for}t_{for} = \frac{Ex_{for}t_{for}}{A} + \frac{\displaystyle\sum_{i=1}^{i=n} Ex_{act_i}t_{act_i}}{A} + \frac{Ex_{buf}\left(24 - t_{for} - \displaystyle\sum_{i=1}^{i-n} t_{act_i}\right)}{A} + C. \tag{3}$$

Energy gain rate while foraging is therefore:

$$G_{for} = \frac{Ex_{for}}{A} + \frac{\displaystyle\sum_{i=1}^{i=n} Ex_{act_i}t_{act_i}}{t_{for}A} + \frac{Ex_{buf}\left(24 - t_{for} - \displaystyle\sum_{i=1}^{i=n} t_{act_i}\right)}{t_{for}A} + \frac{C}{t_{for}}. \tag{4}$$

We now rearrange terms to determine foraging time per day:

$$G_{for}t_{for} - \frac{Ex_{for}t_{for}}{A} + \frac{Ex_{buf}t_{for}}{A} - \frac{24Ex_{buf}}{A} + \frac{Ex_{buf}\displaystyle\sum_{i=1}^{i=n} t_{act_i}}{A} = \frac{\displaystyle\sum_{i=1}^{i=n} Ex_{act_i}t_{act_i}}{A} + C \tag{5}$$

$$t_{for}\left(G_{for} - \frac{Ex_{for}}{A} + \frac{Ex_{buf}}{A}\right) = \frac{\displaystyle\sum_{i-1}^{i-n} Ex_{act_i}t_{act_i}}{A} + \frac{24Ex_{buf}}{A} - \frac{Ex_{buf}\displaystyle\sum_{i=1}^{i=n} t_{act_i}}{A} + C \tag{6}$$

$$t_{for} = \frac{\displaystyle\sum_{i=1}^{i-n} Ex_{act_i}t_{act_i} + Ex_{buf}\left(24 - \displaystyle\sum_{i=1}^{i=n} t_{act_i}\right) + AC}{G_{for}A - Ex_{for} + Ex_{buf}}. \tag{7}$$