SEABIRD-FISHERIES INTERACTIONS: EVALUATION WITH DIMENSIONLESS RATIOS

DAVID C. SCHNEIDER
Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, A1B 3X7 Canada

DAVID C. DUFFY
The Seatuck Foundation, Box 31 Islip, New York 11751 USA

ALEC D. MACCALL
Southwest Fisheries Science Center, 3150 Paradise Drive, Tiburon, California 94920 USA

DANIEL W. ANDERSON
Wildlife and Fisheries Biology, University of California, Davis, California 95616 USA

Abstract. Marine bird populations interact with fisheries in a variety of ways, with diverse outcomes. Evaluation of these outcomes requires a means of comparison across cases, and a means of identifying the relative importance of concomitant processes at relevant space and time scales. We describe a general quantitative framework that permits comparison of quantitative findings among studies of seabird-fisheries interactions. We then review the results of seabird-fisheries studies within this framework. We discuss the use of ad hoc ratios and dimensional analysis to make decisions about competing processes at relevant space and time scales.

INTRODUCTION

The diversity of interactions of marine bird populations with fisheries (Duffy and Schneider *in press*) includes provision of offal to birds, removal of predators that take the same prey as seabirds, reduction in seabird prey heavily fished by commercial fleets, use of seabirds to locate fish, use of seabirds as bait, near sinking of a fishing vessel by birds, fertilization of coastal waters with guano, reduction in fishery landings due to prior removal by seabirds, piracy by seabirds, and seabird mortality in nets. Outcomes range from positive through neutral to negative for both birds and humans. Examples of all 9 possible outcomes in a two way classification (positive, neutral, negative for birds) x (positive, neutral, negative for humans) occur (Duffy and Schneider *in press*).

Effective seabird conservation depends upon accurately identifying the causes of negative outcomes. The problems that arise in identifying negative effects on marine birds arise in many wildlife managment situations: the time and space scales of causes are unknown, the relative importance of concomitant processes is unknown, and the applicability of other cases to the problem at hand is unknown. In this paper we describe a comprehensive quantitative framework that addresses problems of scale, competing processes, and comparability of results from multiple studies. We show that the framework can be used to review and compare studies of seabird-fisheries interactions. We then demonstrate the use of dimensionless ratios to evaluate competing processes. Dimensionless ratios currently in use will be compared to those arising from dimensional analysis.

QUANTITATIVE FRAMEWORK

The interaction of seabirds, humans, and their marine prey is highly diverse, with elements of interference competition, scramble competition, predation, parasitism, and mutualism (Duffy and Schneider *in press*). These interactions occur primarily at the interface of two fluids, the atmosphere and the ocean, which are in constant motion. Thus, elements of fluid dynamics, ethology, and demography all contribute to changes in seabird populations, and are important in understanding seabird-fisheries interactions. These elements can be incorporated into a single quantitative framework (Schneider 1991) in which the rate of change in local abundance results from demographic, ethological, and fluid processes (Table 1). After commenting briefly on trends in the density and spatial

TABLE 1. Marine bird population interactions with fisheries equations relating state factor distributions to dynamic variables. The equations state, in measurable quantities, that local density changes $[\dot{Q}]$ of vessels, birds or nekton, result from the appearance of new vessels or animals $\dot{R}$, loss or death $\dot{D}$, divergence or convergence due to directed movements $\nabla_h \cdot \boldsymbol{u}$ relative to the surrounding fluid, and divergence or convergence due to passive drift in the atmosphere $\nabla_h \cdot \boldsymbol{u}_{Atm}$ or in the ocean $\nabla_h \cdot \boldsymbol{u}_{Oc}$. The rate of change in density $[\dot{Q}]$ has the same dimensions (% time^{-1}) as the several dynamic terms on the right side of the equation. Terms are defined in greater detail in Appendix 1.

State factor	Distribution		Demography	Ethology	Fluid dynamics		
Fishing Vessels	$[\dot{Q}_V]$	=	$\dot{R}_V - \dot{D}_V$	$- \nabla_h \cdot \boldsymbol{u}_V$	$- \nabla_h \cdot \boldsymbol{u}_{Atm}$	$- \nabla_h \cdot \boldsymbol{u}_{Oc}$	(1)
Nekton	$[\dot{Q}_N]$	=	$\dot{R}_N - \dot{D}_N$	$- \nabla_h \cdot \boldsymbol{u}_N$		$- \nabla_h \cdot \boldsymbol{u}_{Oc}$	(2)
Birds	$[\dot{Q}_B]$	=	$\dot{R}_B - \dot{D}_B$	$- \nabla_h \cdot \boldsymbol{u}_B$	$- \nabla_h \cdot \boldsymbol{u}_{Atm}$	$- \nabla_h \cdot \boldsymbol{u}_{Oc}$	(3)

dynamics of fishing vessels (Table 1, equation 1) and on general knowledge of the density and dynamics of nekton (Table 1, equation 2), we review brefly what is known about each of the terms in equation 3 (Table 1), which relates distribution ($[\mathring{Q}_B]$) to the demographics ($\mathring{Q} = \mathring{R}_B - \mathring{D}_B$) and kinematics ($\mathring{A} = - \nabla_h \cdot u_B - \nabla_h \cdot u_{Atm} - \nabla_h \cdot u_{Oc}$) of marine bird populations.

Demographics and spatial dynamics of fishing vessels

All of the dynamic terms in equation 1 (Table 1) have changed in the last century toward greater concentration of fishing effort, measured by $[\mathring{Q}_V]$. Effort has increased under the combined action of technological advances, economic forces and political pressures (Cushing 1975). The number of new vessels has increased ($\mathring{R}_V > 0$), a development permitted by advances in ship design, and driven by the economics of open fisheries, which distribute the cost of entry over all vessels, rather than placing it on the entrant (Gordon 1954). Vessel loss $\mathring{D}_V$ has decreased due to advances in navigational technology and weather forecasting. Rate of convergence of fishing power $-\nabla_h \cdot u_V$ into limited areas of high fish abundance has increased through ever more effective use of information on ocean conditions and fish movements (Yudovich and Baral 1968). This trend is now being furthered with the use of larger-scale information from satellites. The development of fish-reducing plants in the early part of this century, followed by placement of these plants on ships in the 1930's (McEvoy 1986), contributed to the convergence of fishing power on highly mobile schooling organisms (notably clupeid fishes, squid, and krill), which are important prey of seabirds. Increases in vessel size and advances in ship design have reduced the influence of wind and currents $\nabla_h \cdot u_{Atm} + \nabla_h \cdot u_{Oc}$ on fishing activities.

Population assessment of nekton

Quantitative knowledge of marine nekton (fish, squid, decapods, and euphausiids) decreases moving from left to right in equation 2 (Table 1). Much is known about spatial and temporal change in density; recruitment is the best studied process, mortality is less understood, and movements are least understood. One important negative finding is that recruitment ($\mathring{R}_N$) in many nekton populations is unrelated to abundance $[Q_N]$ at the scale of the entire stock, except that $\mathring{R}_N$ does decrease at very low values of $[Q_N]$ (Cushing 1975). With respect to management, another important finding is that demersal fish composed of multiple year classes can be managed (leaving aside economic and political pressures) by ignoring movements and recruitment, and concentrating instead on yield-per-recruit and the problem of growth overfishing (Gulland 1989). This strategy does not work with schooling pelagics because of their behavior (Csirke 1988), because of the greater concentration of production into fewer cohorts, and because of the tendency of fishing to reduce the number of cohorts in a population (Radovich 1981).

Rate of change in avian density

Information on avian density $[Q_B]$ at sea has increased rapidly in the last two decades. Despite the increase, knowledge of patterns of change in density at sea lags considerably behind that for colonies. Seasonal changes at sea (Shuntov 1972, Powers 1983, Schneider et al. 1987) appear to be as large as those at colonies. Changes have been measured at the scale of 10^2 km or less. At this scale, changes are generally due to movements ($\dot{A}$), rather than demographic changes ($\dot{Q}$). Changes in avian density at this scale have been linked to release of offal from trawlers (Fisher 1952, Trukhin and Kosygin 1987, Abrams 1983), and the collapse of capelin stocks (Erikstad et al. 1990). The evidence for offal-related changes in distribution at this scale (Blake 1984) is not compelling (Furness et al. 1988) and other explanations are equally tenable (Brown 1970). At a much smaller scale, changes in density near trawlers are unquestionably due to the production of offal (Furness et al. 1988).

A number of studies have compared changes in density [$\dot{Q}_B$] measured at colonies with changes in fish density [$\dot{Q}_N$], which are estimated at the spatial scale of the stock, usually > 10^2 km, and often > 10^3 km. A relation has been reported in some cases (Duffy 1983*a*, Springer 1991) but not others (Bailey and Hislop 1978), or only at some locations within an area (Burger and Cooper 1984). At a still smaller scale (Monaghan and Zonfrillo 1986) the numbers of breeding terns in the Firth of Clyde was associated with an index of the abundance of larval herring. Cairns (1987) proposed that [$\dot{Q}_B$] was related to prey abundance only if prey abundance was low. This was corroborated at Røst, in Norway, where [$\dot{Q}_B$] = -8% yr^{-1} in puffins (Anker-Nilsson and Lorentsen 1990) and -3.3% yr^{-1} in murres (Vader et al. 1990) since the collapse of herring stocks. Further support comes from changes in diet associated with several local fishery failures in eastern Newfoundland (Montevecchi et al. 1987). The assumption implicit in these comparisons is that movements of breeding birds between colonies are negligible ($\dot{A}$ = 0) and hence that observed change in abundance reflects demographic changes ($\dot{Q}$).

Avian recruitment

Most seabird research has focused on recruitment ($\dot{R}_B$) because this can be measured directly at the colony, either as number of chicks fledged, or as eggs produced, modified by mortality until fledging. Annual recruitment, defined in this way, varies considerably from place to place (Hunt et al. 1986). Annual recruitment also varies among species within colonies (Brown and Nettleship 1984, Springer 1991) and from year to year. Causes of temporal and spatial variation in $\dot{R}_B$ include pesticides (Anderson and Gress 1984), parasites (Duffy 1983*b*), weather, and prey availability (Furness 1984, Hislop and Harris 1985). The colony at Røst, in Norway, provides one of the clearest examples of the effects of prey availability on $\dot{R}_B$. Recruitment in puffins has been zero due to chick starvation (Lid 1981, Anker-Nilsson 1987) in nearly every year since the late 1960's when the herring stock collapsed from the interacting pressures of fishing and natural mortality (Jakobsen 1985, Rottingen 1985). A relation between recruitment and local fishing pressure also has been reported in the Shetland Islands (Monaghan et al. 1989) and the California Current before 1970 (Anderson and Gress 1984). Contradictory information (Springer 1991, Hatch et al. *in press*) precludes any firm conclusion about the role of fishing in suppressing kittiwake recruitment in the Bering Sea.

Avian mortality

Mortality rates ($\mathring{D}_B$) of seabirds are on the order of 10% yr^{-1} or less once birds begin breeding. Observations away from the colony (Bailey and Davenport 1972, Blake et al. 1984) suggest that this mortality may be episodic and highly localized, rather than occuring as a steady decay in numbers. One source of mortality is drowning in gill nets (Jones and DeGange 1988), especially among alcids (Carter and Sealy 1984, Piatt and Reddin 1984, Piatt et al. 1984, Vader et al. 1990). These mortalities are estimated as numbers killed (D), rather than rates ($\mathring{D}$), because the source populations are unknown. In the North Pacific, for example, estimates of loss to salmon nets are on the order of 0.1 to 0.8 x 10^6 per year (Ogi 1984, King 1984, DeGange et al. *in press*). Many of the murres in this total may come from the Aleutian Islands, and so net mortality may acccount for a substantial fraction of total mortality in these populations (King 1984). Murre losses to gill nets in California was stated to be large enough to affect local colonies (Jones and DeGange 1988). No rates were reported and the loss has now been regulated. In the southern Benguela Current, $[\mathring{Q}_B] < 0$ for African penguins, while $\mathring{R}_B > 0$. Wilson et al. (1988) hypothesize that $\mathring{D}_B > \mathring{R}_B$ during a period of high spatial overlap of purse seiners with juvenile penguins. A high ratio of $[\mathring{Q}]$ to $\mathring{R}_B$ in a colony of wandering albatross has been attributed to net mortality $\mathring{D}_B$ (Weimerskirch and Jouventin 1987). Mortality due to fishing activity also occurs when birds are used for bait (Collins 1884), but no quantitative estimates are available for current fisheries. McIntosh (1903) suggested that direct mortality due to fishing activities may be large enough to offset competition with fisheries; i.e., that the ratio $\mathring{D}_{B\rightarrow V} / (\mathring{R}_{max} - \mathring{R}_{B|V})$ exceeds unity, where $\mathring{R}_{B|V}$ denotes fledging rate in the presence of fishing vessels taking the same prey. Fishing could, in theory, decrease mortality $\mathring{D}_B$ by releasing offal, especially for large bodied fish (Furness et al. 1988).

Avian movements

Little is known about avian movements relative to the surrounding fluid ($- \nabla_h \cdot u_B$). Simultaneous observations of numbers and flight direction at a series of coastal points (Blomqvist and Peterz 1984) and tracking of individuals (Jouventin and Weimerskirch 1990), suggest that net movement results from behavioural interactions with the surrounding fluid ($\nabla_h \cdot u_B = f(\nabla_h \cdot u_{Atm} + \nabla_h \cdot u_{Oc})$). Winds ($\nabla_h \cdot u_{Atm}$) affect bird movements (Blomqvist and Peterz 1984), alter attendance at colonies (Birkhead 1978), and may interact with the aerodynamic performance of a species to modify rate of prey supply to chicks (Uttley et al. 1989). Oceanic currents ($\nabla_h \cdot u_{Oc}$) affect bird movements directly in the case of swimming birds (Brown 1985), or indirectly by concentrating prey. The effects of atmospheric motions and ocean circulation on movements and contact rates between seabirds, fishing vessels, and nekton are largely unknown.

DIMENSIONLESS RATIOS

The relative importance of competing processes listed in equations 1-3 (Table 1) can be evaluated through the construction of dimensionless ratios. We might, for example, take the ratio of recruitment ($\mathring{R}_B$) to death rates ($\mathring{D}_B$) to evaluate the relative importance of these processes in a given situation (Ford et al. 1982). Several dimensionless ratios have been used to evaluate the impact of seabirds on prey stocks. These ratios, named for convenience after the authors who used or devised them, are the Schaefer, Wiens, and Bourne ratios (Duffy and Schneider *in press*). Schaefer (1970) compared the catch rate by birds to the catch rate by fishing vessels. The resulting ratio ($Sf' = D_{N\rightarrow B}/D_{N\rightarrow V}$) scales one source of mortality to another. Literature values of Sf' range from 0.003 (Furness and Barrett 1985), to 87 (Harrison and Seki 1987). The spatial overlap and the spatial scale of catches by birds and fish vessels are rarely known; this may be one source of variation in literature values.

The Wiens ratio (Wiens and Scott 1975) Wi' is $D_{N\rightarrow B}/P_N$ where P_N is production of fish during time period of consumption $D_{N\rightarrow B}$. The Wiens ratio based on mass (rather than numbers) ranges from 0.04 (Bourne 1983) to 0.37 (Springer and Roseneau 1985).

Bourne (1983) argued that advective resupply was substantial relative to prey consumption near the Shetland Islands, but provided no quantitative estimates of either rate. The concept can be quantified as a Bourne ratio (Br'), here defined as the instantaneous loss of nekton to birds, relative to resupply by currents ($\mathring{D}_{N\rightarrow B}/\nabla_h \cdot u_{Oc}$). This ratio scales a demographic rate to a kinematic rate. At South Georgia Island krill consumption by the seabird colony has been estimated at 80% of the standing stock per month (Croxall and Prince 1987), or 2.7% day^{-1}. Advective resupply comes to 16% day^{-1}, using a typical current speed of 3 m s^{-1}, and a foraging radius of 80 km. The resulting ratio is 2.7/16 = 0.17, which indicates that resupply exceeds consumption of krill around South Georgia. In Hudson Bay, advective resupply within a foraging radius of 160 km comes to 1.9% day^{-1}, based on an average current speed of 0.07 m s^{-1} (Cairns and Schneider 1990). Assuming a catch of 30% of stock over a 90 day breeding season, the Bourne ratio would be 0.16, indicating that advective resupply exceeds consumption rate.

Dimensional analysis

A complete set of ratios can be obtained by dimensional analysis (Bridgman 1922). The method is simple. One sets up a two-way table with all variables of interest listed along one side (rows) and all fundamental dimensions along the other side (columns). One then writes the appropriate exponent in each cell (e.g., +2 in the length column for a variable that is an area). This generates the dimensional matrix. The object is to form dimensionless ratios, i.e. combinations of variables, that reduce all cells in the matrix to zero. This can be accomplished by linear algebra (Langhaar 1980), or equivalently by the successive elimination method of Taylor (1974). The latter is readily grasped from an example (Appendix 2).

The results of a dimensional analysis depend on the initial choice of quantities. If we choose number of recruits R, number of deaths D, velocity of individuals relative to the fluid $\boldsymbol{u}_I$, velocity of the fluid relative to the earth $\boldsymbol{u}_F$, change in area occupied $\mathring{A}$, and rate of demographic change $\mathring{Q}$, then dimensional analysis results in three dimensionless ratios (Appendix 2). The three ratios are M' the ratio of demographic rates to divergence (movement), R' the ratio of locomotory to fluid (passive) motions, and D' the ratio of instantaneous recruitment and death rates. Diffusive (random) movements are often an important component of fluid motions ($\nabla_h \cdot u_{Atm} + \nabla_h \cdot u_{Oc}$). If a diffusive term had been included in the list of variables, then a fourth dimensionless ratio would result, the ratio of diffusive to directed motions A'.

As an example of the formal use of these ratios, M' (demography relative to kinematics) can be used to diagnose whether demographic factors (recruitment and death) or kinematic factors (e.g., shifts or contraction in range) should be further investigated as responsible for an observed decline in density ($[\mathring{Q}_B] < 0$. For marine birds, values for the numerator ($\mathring{Q} = \mathring{R}_B - \mathring{D}_B$) *can be obtained from colony studies of mortality and recruitment* rates. Literature values vary, but do not appear to depend on spatial scale. Kinematic values ($\mathring{A}$) for birds can be obtained from flight speeds, if the spatial scale of analysis is small (flight speed x time). Flight speeds decrease with increase in scale, because birds do not fly continuously, nor in straight lines over periods of days (Jouventin and Weimerskirch 1990). Consequently, short-term flight speeds cannot be used to calculate kinematic values at larger scales. Kinematics at seasonal time scales can be calculated from speeds realized between points along the migratory route (Moissan and Sherrer 1973).

For the nektonic prey of marine birds, demographic rates ($\mathring{Q}$) can be obtained from direct measurements in well-studied species, or from allometric equations relating mortality or recruitment rates to body size (Peters 1983). Kinematic rates over short distances can be calculated from allometric equations relating swimming speed to body size. For the same reasons as with birds, kinematic values of nekton at larger scales cannot be calculated *from short-term swimming speeds.* Turning frequency and duration of halts will determine how average speed decreases with increasing spatial and temporal scale.

The ratio of recruitment to mortality rates D' can be used to diagnose the long-term effect of an environmental perturbation on a population. Ford et al. (1982) calculated the recovery time of seabird populations around the Pribiloff Islands at several levels of oil-induced mortality, using the best available demographic and distributional data. Considerable care is needed in calculating recruitment rates, because mortality rates in seabirds decline rapidly with age between time of fledging and time of first reproduction (Jouventin and Weimerskirsch 1988). Consequently, recruitment measured as number of individuals fledged will differ considerably from recruitment measured as number of offspring that reach breeding status. In a population that is maintaining itself, D' is expected to be close to unity if R_B is taken as recruitment to the breeding population. However, if R_B is taken as fledging rate, then D' is expected to exceed unity by a factor roughly proportional to the number of years of active breeding. This is because fledging rate exceeds recruitment to the breeding population. Deviations from these expectations indicate that a population is not maintaining itself.

We can also ask whether empirical ratios or ratios derived from dimensional analysis provide new insights into seabird-fisheries interactions. To do this we examined a relatively well studied situation: fishermen, pelicans, and anchovies in the California Current system (Anderson et al. 1980, Anderson and Gress 1984). Beginning with 3 empirical ratios, we found that for the brown pelican (*Pelecanus occidentalis*) all three ratios take on very small values because consumption by pelicans is small relative to anchovy catch by vessels, to anchovy production, or to anchovy drift past colonies (Anderson et al. 1980). The implicit scale of these comparisons is fairly large because of the mobility of anchovies. Consequently, the effect of a single predator on a dominant species is negligible.

D' the ratio of recruitment to death, did reflect major changes in pelicans, anchovies, and fishermen. The pre-1970 decline and post-1970 recovery of pelicans coincided with a change in D' from less than unity prior to 1970 to greater than unity afterward (Anderson et al. 1975). For anchovies the D' ratio went through 3 phases: $D' = 1$ through the late 1960's and early 1970's, $D' > 1$ during the mid-1970's, D' slightly < 1 since, reflecting major changes in stock size at this time scale. The ratio D' for fishing vessels has been generally low in the U. S., but during the 1980's in Mexico the ratio became much greater than unity resulting in a build-up of a fleet at Ensenada; this resulted in a brief but intense anchovy fishery (Walls 1992) that collapsed in 1990. Thus, the ratio D' reflected the dynamics of change in numbers of pelicans, anchovies, and vessels at fairly large (>100 km) spatial scales.

The ratio of active to passive motions R' is large in vessels, pelicans, and anchovies, except under unusual conditions such as storms. This ratio offered little insight into interactions of pelicans, anchovys, and fishermen in the California Current system.

The ratio of demographics to kinematics M' is highly seasonal in pelicans; at the spatial scale of the foraging radius around colonies the ratio switches from much greater than unity in the breeding season, when populations are tied to colonies (Anderson et al. 1982), to much less than unity outside the breeding season, when birds move away from colonies. Similar seasonal changes occur in anchovies, which become concentrated in the southern California Bight by spawning and feeding constraints. This suggests that seasonal drops in M' of pelicans may be tied to seasonal drops in M' of anchovies. For vessels, the ratio of demographic to kinematic rates tends to be much less than unity except during the opening of a new fishery (large recruitment of vessels), or during the collapse of a fishery (large loss of vessels from the fishery). The ratio of kinematics of vessels to kinematics of fish also appears to be important, because vessels are constrained by the location of home ports, and function more efficiently when the movements of anchovies are restricted. Thus kinematic ratios of prey and predator, and the underlying energetics, may be at least as important as the ratio of demographics to kinematics within a prey or predator. Our conclusion, from examining the case of the brown pelican in south California, was that ratios of the kinematics of prey and predator cannot be ignored in understanding the dynamics of seabird fisheries interactions. A framework based on ratios within populations allowed interpretation of trends in population sizes of pelicans, anchovies, and vessels, but was too restrictive for providing insight into seabird-fishery interactions. It would be useful to undertake a similar evaluation for another system, such as alcids feeding on plankton, where passive fluid motions become important.

DISCUSSION

Comparison of ratios derived from dimensional analysis of a problem can provide information on the relative importance of competing processes. Comparison of several ratios is particularly important in cases where there are a number of competing processes, and a single ratio does not provide full information on all processes. The ratio of recruitment to mortality D' needs to be evaluated, for example, in view of the importance of the ratio of demographic to kinematic rates (M'). If kinematic rates predominate ($M' \ll 1$), then the ratio of recruitment to mortality (D') will be less important (and less readily interpreted) than if demographic rates predominate ($M' \gg 1$).

The use of ratios is no substitute for determining the mechanism responsible for an observed decrease in a seabird population (Duffy et al. 1987). However, ratios can serve as a guide to research needed to identify causes. Ratios also indicate the relative importance of competing processes. The value of the method lies in permitting a comprehensive, rather than piecemeal, evaluation of complex ecological problems. The absence of dimensional analysis from quantitative ecology does not reflect inapplicability of the method.

The goal of research is to make reliable calculations to support decisions on conservation of marine birds. Based on our review of the literature within a comprehensive quantitative framework, several research needs have been identified. One need is for a better understanding of how processes (recruitment, death, active and passive divergence) depend on spatial and temporal scale. A second need is to identify functional relationships between terms (e.g., relation of avian recruitment ($\dot{R}_B$) to change in nekton density ($[\dot{Q}_N]$). A third need is to develop formal models of key functional relationships, with explicit treatment of spatial and temporal scales. The philosophical basis for this approach is that direct measurement is expensive and logistically impossible in many cases; the only alternative is reliable calculations from related parameters, within a consistent theoretical framework.

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APPENDIX 1. *Definition and relationship of variables.*

Q	Quantity of vessels Q_V, birds Q_B, or nekton Q_N. Dimensions are either count or mass.
A	Area occupied by Q_V, Q_B, or Q_N. Dimensions are length^{-2}
$[Q]$	Density of vessels $[Q_V]$, birds $[Q_B]$, or nekton $[Q_N]$. Dimensions are length^{-2} or mass·length^{-2}.
$[\dot{Q}]$	Instantaneous time rate of change of $[Q]$. $[\dot{Q}] = [Q]^{-1}\, d[Q]/dt$, where t = time. Dimensions are % time^{-1}.
$\dot{A}$	Instantaneous time rate of change in area occupied. Dimensions are % time^{-1}.
$\mathbf{u}$	velocity of Q in directions x and y, with respect to fixed Cartesian grid on the surface of the earth. $\mathbf{u} = (\delta x/\delta t \;\; \delta y/\delta t)$. Dimensions are length time^{-1}.
$\mathbf{u}_{Atm}$	velocity of atmosphere in direction x and y, with respect to fixed grid on the surface of the earth.
$\mathbf{u}_{Oc}$	velocity of ocean in direction x and y, with respect to fixed grid on the surface of the earth.
$\mathbf{u}$	velocity of vessels $\mathbf{u}_V$, birds $\mathbf{u}_B$, or nekton $\mathbf{u}_N$ with respect to surrounding fluid (atmosphere or ocean). Dimensions are length time^{-1}.
R	instantaneous rate of recruitment of vessels (R_V), birds (R_B), or nekton (R_N). Dimensions are % time^{-1}.
D	instantaneous rate of loss of vessels (D_V), birds (D_B), or nekton (D_N) ($D_N=Z$ of Ricker [1975]). Dimensions are % time^{-1}.
$D_{N\to V}$	instantaneous loss rate of nekton (fish) to vessels. F of Ricker (1975). Dimensions are % time^{-1}.
$D_{N\to B}$	instantaneous loss rate of nekton (fish) to birds. *Dimensions are % time*$^{-1}$.
$\nabla_h \cdot \mathbf{u}$	horizontal divergence of units of quantity Q moving at velocity $\mathbf{u}$.
$\nabla_h \cdot \mathbf{u} = (\delta u/\delta x \;\; \delta v/\delta y)$.	Dimensions are % time^{-1}.
$Sf' = D_{N\to B}/D_{N\to V}$.	Shaeffer ratio, the instantaneous loss to birds, relative to instantaneous loss to fishery. Estimated as food demands of birds, divided by vessel catch (Schaefer 1970).
$Wi' = D_{N\to B}/P_N$.	Wiens ratio, where P_N is production of fish during time period of consumption $D_{N\to B}$ (Wiens and Scott 1975).
$Br' = D_{N\to B}/\nabla_h \cdot \mathbf{u}_{Oc}$.	Bourne ratio, the instantaneous loss of nekton to birds, relative to resupply by currents (Bourne 1983).

APPENDIX 2. Dimensional analysis.

The quantities of interest are: number of deaths (D), number of recruits (R), velocity of individuals relative to the fluid (u_I), velocity of the fluid relative to the earth (u_F), change in area occupied ($\dot{A}$), and rate of demographic change ($\dot{Q}$). The primary quantities are: length (L), time (T), numbers of individuals (#). The dimensional matrix is:

$$\begin{array}{lcccccc} & D & R & u_I & u_F & \dot{A} & \dot{Q} \\ L & 0 & 0 & 1 & 1 & 0 & 0 \\ T & 0 & 0 & -1 & -1 & -1 & -1 \\ \# & 1 & 1 & 0 & 0 & 0 & 0 \end{array}$$

Dividing through by column 1 (D), the revised matrix becomes:

$$\begin{array}{lccccc} & R/D & u_F/R & u_I/R & \dot{A}/R & \dot{Q}/R \\ L & 0 & 1 & 1 & 0 & 0 \\ T & 0 & -1 & -1 & -1 & -1 \\ \# & 0 & -1 & -1 & -1 & -1 \end{array}$$

Dividing through by row 2 (u_I/R), the revised matrix becomes:

$$\begin{array}{lcccc} & R/D & u_I/u_F & \dot{A}/u_F & \dot{Q}/u_F \\ L & 0 & 0 & -1 & -1 \\ T & 0 & 0 & 0 & 0 \\ \# & 0 & 0 & 0 & 0 \end{array}$$

Dividing through by row 3 ($\dot{A}/u_F$), the final matrix becomes:

$$\begin{array}{lccc} & R/D & u_I/u_F & \dot{Q}/\dot{A} \\ L & 0 & 0 & 0 \\ T & 0 & 0 & 0 \\ \# & 0 & 0 & 0 \end{array}$$

Dimensional analysis results in the following ratios[1]:

$M^f = \dot{Q}/\dot{A}$, Ratio of demographic rates to divergences (movements);
$R^f = \nabla_h \cdot u_I \,/\, (\nabla_h \cdot u_{Atm} + V_h \cdot u_{Oc})$, Ratio of locomotory to fluid (passive) motions;
$D^f = R/D$, Ratio of recruits to deaths.

An additional ratio results if diffusive motions are included:

A^f = ratio of diffusive and inertial motions.

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[1] The idea of scaling active to passive motions occurred while watching a 2-year old child in a typical Newfoundland windstorm (winds 100 km hr^{-1}). The ratio was less than unity, and increased to greater than unity as the child grew older (larger). The choice of symbols is based on first initials of 4 children: Maggie Schneider, Reed Schneider, Dominique Duffy, and Alexander Duffy.