APPENDIX O

APEX: 96163O

Statistical Review of APEX Study Designs and Analyses: 1996

Project Number: 97163 O

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Study History: The Alaska Predator Ecosystem Experiment (APEX) in Prince William Sound, Alaska required use of sampling designs whose analyses are not commonly available for biological field studies. The design included systematically located unequal length transects and collection of spatially correlated data on abundance, distribution, and biomass of forage fish and abundance and distribution of sea birds. Analyses include estimation of resource selection functions and adjustment for the correlated data. Beginning in 1995, we provided review of and advice for the non-standard study designs in order to help insure that appropriate statistical inferences can be made during the analysis phase of the studies. We also provided advice and assistance during statistical analyses of 1995 data and report preparation for some of the individual projects within APEX.

Abstract: Modifications were made in sampling designs and overall study protocols for the 1997 field season in collaboration with Principal Investigators of the other APEX projects. Custom computer software was developed for analysis of spatially correlated acoustic survey data. Statistical analyses were recommended for some of the APEX projects to insure that statistical inferences are justified by the 1995 and 1996 data collection procedures. Results of interactions with the APEX projects are included in the annual reports, study protocols, and detailed project descriptions submitted by the Principal Investigators.

Key Words: statistical analysis, spatially correlated data, protocols, study design.

Modifications were made in the sampling design for collection of the 1996 acoustic survey data to included random placement of survey blocks in the near-shore areas of Prince William Sound in collaboration with Dr. Lew Haldorson and Dr. Tom Shirley, Project 97163A, Forage Fish Distribution. These blocks were sampled with transects running at approximately 45 degrees to the shoreline during the acoustic survey. The off-shore acoustic survey in 1996 was conducted according to the same design as used in 1995 to provide comparable data. We developed custom software for analysis of the spatially correlated data collected in 1995 and 1996. These computer programs were used by Mr. Ken Coyle for assistance in analysis of the 1995 acoustic data and are currently being used for analysis of the 1996 near-shore and off-shore acoustic data. Analyses for abundance and distribution foraging sea birds in relation to schooling fish followed statistical procedures specifically developed for study of resource selection by animals in collaboration with Dr. William Ostrand, Project 97163B.

Interaction with these and other APEX projects included review of study protocols for the 1997 field season and general advise on statistical analysis for data collected in 1995 and 1996

The individual Principal Investigators are primarily responsible for issuing the reports on 1995 and 1996 data from the various projects within APEX. Results of our interactions with the Principal Investigators are contained within those reports.

APPENDIX Q

APEX: 96163Q

Exxon Valdez Oil Spill
Restoration Project Annual Report

The Factors That Limit Seabird Recovery In The EVOS Study Area: A Modeling Approach

Restoration Project 97163Q
Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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March 1997

The Factors That Limit Seabird Recovery In The EVOS Study Area: A Modeling Approach

Restoration Project 97163Q
Annual Report

Study History: The project effort was initiated in February 1997 as a new project. Field work is not direct component of this project, which relies on the data gathered by all other APEX projects as well as data in the literature.

Abstract: We use mathematical models to assess ways in which food supply could be affecting recovery of seabirds in the EVOS study area. The models address foraging effort and success as it relates to breeding productivity. In the first year of effort we will concentrate on developing models for Pigeon Guillemots and Black-legged Kittiwakes in Prince William Sound. Results will test the degree to which food limitation is affecting recovery, indicate the mechanisms by which this could come about, and identify the scale at which interactions are occurring between food availability and the colonies being studied by APEX. Moreover, results should help to "aim" the APEX research effort so that sufficient data are collected to fulfill the overriding APEX objective: to understand the ways in which food supply is limiting seabird recovery.

Key Words: *Exxon Valdez*, Pigeon Guillemots, Black-legged Kittiwakes, foraging effort, population growth, mathematical modeling.

Project Data: (will be addressed in the final report)

Citation: Ainley, D. G., R. G. Ford and D. C. Schneider. 1997. The factors that limit seabird recovery in the EVOS study area: a modeling approach., *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 97163Q), Anchorage, Alaska.

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Executive Summary

We use mathematical models to assess ways in which food supply could be affecting recovery of seabirds in the EVOS study area. Thus, we are addressing the main APEX (Alaska Predator Experiment) hypothesis that food supply is limiting recovery of certain avian populations from the *Exxon Valdez* oil spill. We present here the general outline of the mathematical models, with lists of parameters to be included. Eventually data inputs will comprise information from the field components of APEX. supplemented with data published elsewhere.

Introduction

The general hypothesis of the APEX project is that a change in the relative abundance of forage fish species has prevented recovery of injured avian populations in Prince William Sound. Within this general hypothesis a series of ten working hypotheses are being investigated. The data being collected to test these hypotheses differ in temporal and spatial scale. Some additional data at the time scale of decades exist. However, most of the data are at much smaller scales than the general hypothesis, which is at the scale of decades (time for recovery in long-lived species) and at the spatial scale of the entire sound. Statistical inference can be used to bridge some but not all of the gap. The remainder will be bridged by the same methods used in oceanography (Figure 1), where hypotheses are stated at a specific scale, hypotheses are constrained by conservation laws, and ratios of rates are used to identify the importance of competing processes. This approach integrates the available information, bridges the gap from data to the hypothesis, and identifies variables that need to be linked. The model output will allow avian recovery rates to be evaluated in relation to prey availability, using data and knowledge gathered for this ecosystem.

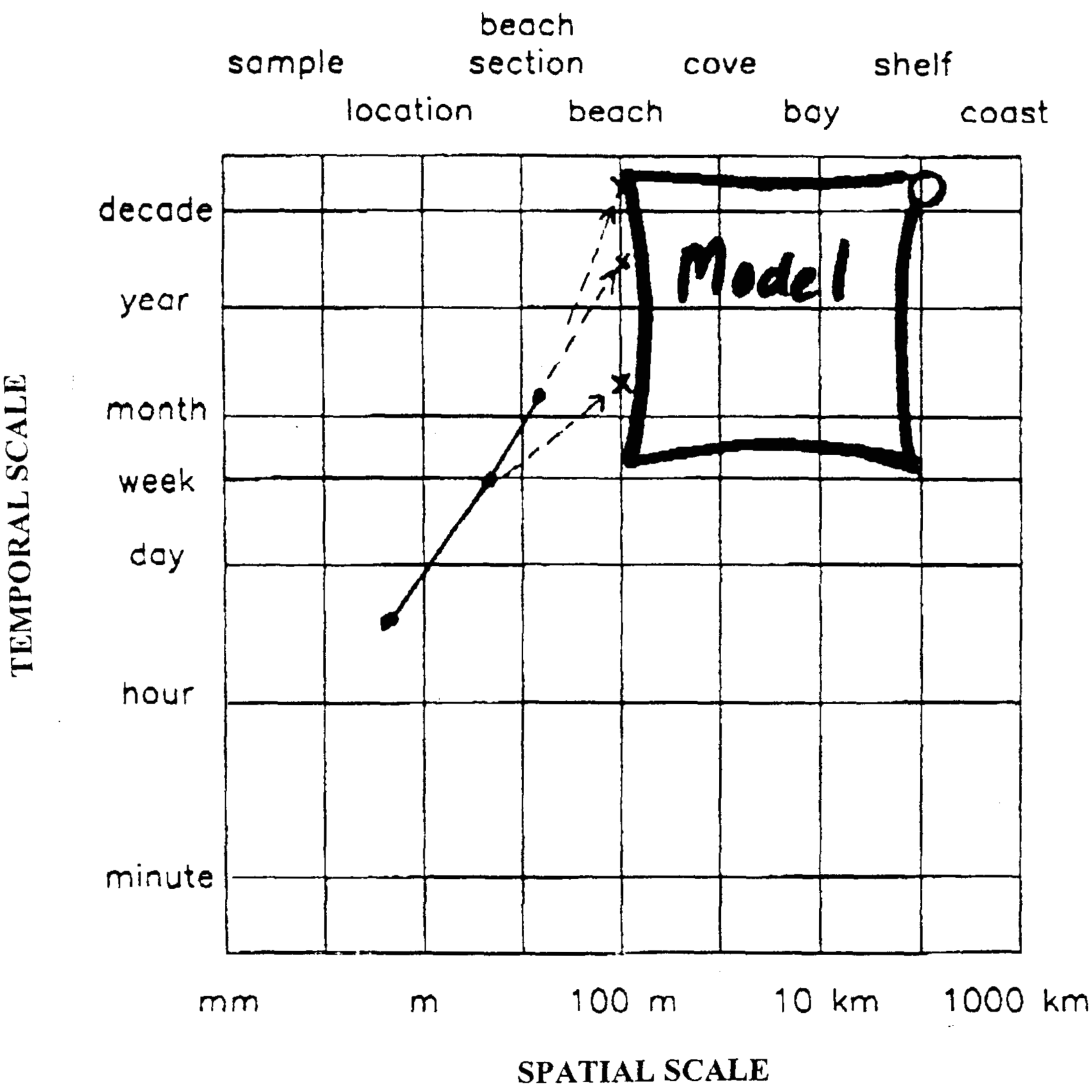
Objectives

Hypotheses to be evaluated by mathematical modeling using existing data, under the null hypothesis:

1. Annual survivorship, age of first breeding, foraging range, feeding frequency of chicks, and reproductive success are not related to food availability. We hypothesize that feeding frequency of chicks and breeding success in large colonies should be lower than in small colonies.

2. No differences in 1 will be evident in pre- and post-spill comparisons, where possible.

Figure 1. Scope of APEX general hypothesis (circle), of available data on Pigeon Guillemot feeding rate (solid lines), of statistical inference (dotted line), and of the model (box).



Methods

The approach will be iterative, beginning with existing verbal models of population dynamics and foraging distribution, including recent findings by APEX investigators. From this a preliminary outline for an integrated computational model will be developed and presented to the APEX investigators and referees. The model will consist of a demographically structured spatial model linked to a spatially structured foraging model. The model will be revised as needed, then data sources for each functional relation in the model will be listed. The model will then be coded. Initial runs will be used to identify relative sensitivity to parameters. Which relationships, for example, have the largest influence on population change and rates of recovery? These results will be presented for discussion and revision as needed. The revised model will be used to guide further testing of working hypotheses. The model will then be used to quantify rates of recovery relative to changes in prey base. Because the model is based on dynamics, it can be used to calculate energy exchange from prey to avian populations through time, including average energy exchange before and after 1989.

Results and Discussion

A demographically structured model linked to a spatially structured foraging model was chosen for several reasons. First and most importantly, the APEX general hypothesis concerns demographics (recovery) in relation to prey distribution. Further, such an approach was successfully applied by Ford et al (1982) for the Pribilof Island colonies and by Nur et al. (1993) for central California colonies. Finally, it is recognized that any long term monitoring program must include demographics, which prevail over other sources of change in avian density at decadal time scales (see below).

Based on findings by APEX investigators, the following conceptual changes were made in the model developed by Ford et al (1982). First, longer term optimality, based on learning or territoriality, was introduced as an alternative to search based on short-term optimality. Evidence for consistent patterns of foraging site usage comes from work in Prince William Sound (PWS) on Pigeon Guillemots (Kuletz 1983) and Black-legged Kittiwakes (Irons 1992). Second, new habitat variables were introduced, notably distance from shore, depth, and substrate type. Pertinent evidence includes the observed restriction of foraging to nearshore areas in PWS, the absence of a strong advective regime in the inner part of the sound, the association of sandlance and juvenile herring with specific habitats in shallow water, and linkage of kittiwakes to shallow water features that increase the local rate of prey resupply near the sea surface. Deeper water species (notably murres and procellariids) are absent from PWS suggesting that foraging mechanisms in relation to habitat differ from the system of shelf break currents and shallow sea fronts that were modeled at the Pribilof colonies. Third, conservation laws were used to make complete listings of processes that alter seabird density at multiple scales. Important components were then identified by comparing rates at the scale of the hypothesis.

Black-legged Kittiwakes and Pigeon Guillemots were chosen because more data exists on these than other species. The guillemot is listed by the EVOS trustees as not recovered.

Spatial scale. A 5 km^2 grid was considered sufficiently detailed for PWS, which extends roughly 100 km from north to south and east to west. A smaller grid scale may be necessary within 10 km of the coast, based on the finding that the bulk of foraging on energy rich fish species occurs in this habitat, with much lower foraging activity offshore.

Time scale: Available data limited the model to time steps of two seasons (breeding vs non-breeding) with a 10 day time step during the breeding season.

Once the avian species, spatial scope, and temporal scope of the model were identified, the components of the general hypothesis were quantified.

BOX 1. Quantification of the APEX general hypothesis.

"Change in forage fish has prevented recovery of some avian populations."

"Avian population" was defined as the number of a species within grid cell of area A = 5 km^2, where:

$$N = \text{count}/5\ km^2 = \#/5\ km^2$$

"Change in avian population" was defined as an instantaneous rate, resulting in components ($r = b - z$) consistent with the demographic literature, where:

$$\text{dotN} = 1/N \ * \ dN/dt = \%/\text{unit time}$$

"Forage fish" from the point of view of predators was defined as the energy available to a bird species within the area of each grid cell, where:

$$\mathbf{E} = \text{Sum over depth of } \mathbf{spE} * \mathbf{B.prey} = kJ/g * g/m^3 = kJ/5\ km^2$$

E for kittiwakes was defined as the energy density within the surface layer, 1 m by 5 km, based on acoustic estimates immediately below this layer. **spE** is the specific energy (kJ/g) of the resource, **B.prey** is the biomass concentration (g/m^3) of the resource. **E** for Pigeon Guillemots was defined as the energy density either within the water column or at the bottom, in water less than 50 m in depth.

"Change in forage fish" was defined as the instantaneous rate of change in energy density available to a bird species within the finite area of each grid cell, again to produce component variables consistent with the demographic literature:

$$\mathbf{dotE} = 1/E \ * \ dE/dt = \%/\text{time within each grid cell.}$$

The general hypothesis was cast in quantitative terms on a fixed (Eulerian) grid, where dynamics were computed in discrete time steps within finite volumes. This means that dynamics are first expressed as instantaneous rates, such as the familiar expressions for instantaneous mortality (**z** in the fisheries literature), recruitment (**b** in the ecological literature), or net rate of increase (**r** = b - z). These rates are then integrated over finite volumes and areas to obtain averages over volumes or areas (r.o = b.o - z.o). Conservation laws for numbers, mass, and energy were used to obtain a complete listing of concomitant rates. An expression for energy exchange was written for each bird species and each of its important prey. The relative importance of these concomitant rates was evaluated by taking ratios at the scale of the hypothesis. Application of a conservation law for numbers and energy produces a complete listing of all sources of change in avian density **dotN.o** and change in resource density **dotE.o** of fish.

dotN.o	=	b.o - z.o + F.o
	=	recruitment - mortality + movement(flux)
change in density	=	demographic change + kinematic change

dotE.o	= dot spE	+ dotM	+ b.o	- z.o	+ F.o
	change in specific energy with age	+ somatic growth	+ recruitment from parent cohort	- death within known cohort	+ movement

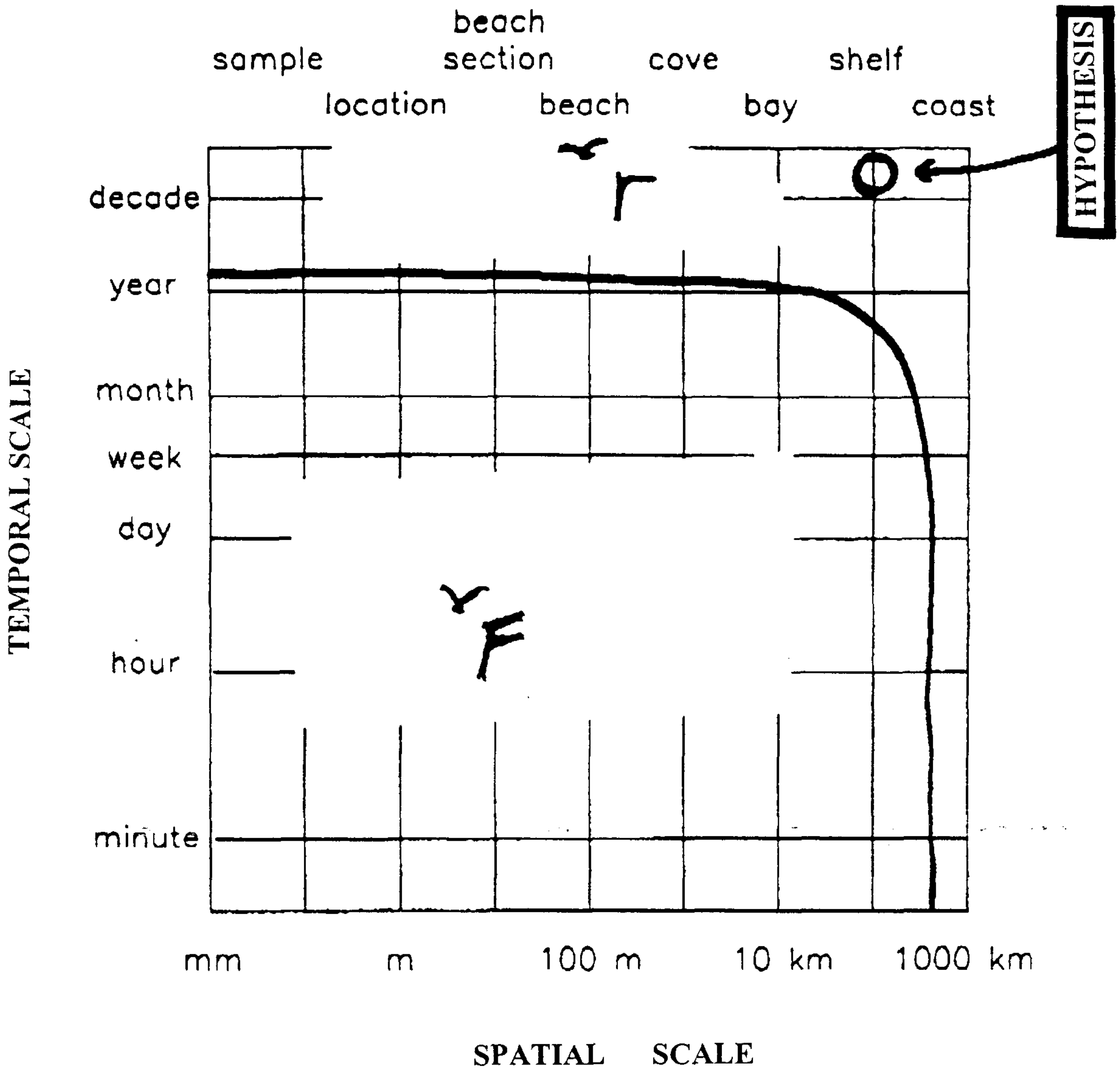
Once a complete listing was obtained, the next step was to identify which components could be treated as constants at the time and space scale of the hypothesis. Order of magnitude values were assigned to each component of change in resource density **dotE.o**, based on knowledge of the biology of sand lance, herring, and capelin.

dot spE	= <1%/decade	(limited decadal change in kJ/g)
dotM	= <10%/decade	(limited decadal change in body size)
b.o	= >100%/decade	(100% change in recruitment possible)
F.o	= >100%/decade	(doubled migration into PWS possible)

The conclusion from this was that specific energy **spE** and body mass **M** could be taken as single values for each prey species. For **spE** and **M**, short term measurements (lower left part of Figure 1) could be applied at scale of the hypothesis (upper right part of Figure 1). For prey that do not migrate into and out of PWS (possibly sand lance), recruitment **b.o** and mortality **z.o** will be more important than movement, **F.o**, which can be ignored at the scale of PWS. At smaller scales, within PWS, redistribution at decadal scales would need to be considered. For highly migratory species such as capelin and herring, both demographics (**b.o - z.o**) and movements at the scale of PWS would need to be considered.

Similar analysis was made for the components of **dotN.o**, change in avian density, at the scale of the hypothesis. At the time scale of a half year, 100% of a migratory population vacates the breeding range, while mortality will be of the order of 10% during the nonbreeding season. The ratio **r/F** = (10%/halfyear)/(100%/halfyear). At this time scale, movements prevail (**r/F** < 1). At the time scale of a year or more seabird colonies change little in distribution; a figure as high as 1%/year would be surprising in any breeding population in PWS. At the time scale of a year, **r/F** = (10%/year)/(1%/5 year). The ratio **r/F** exceeds unity and demographics prevail over kinematics (movements). For Black-legged Kittiwakes, Figure 2 shows the relative importance of movement and demographics as a function of space and time scale. The conclusion from this analysis was that demographics cannot be ignored, at the scale of the APEX general hypothesis.

Figure 2. Scope diagram for demographics vs kinematics of Black-legged Kittiwakes.



The data available for marine birds were sufficiently detailed to allow an age or stage specific treatment of recruitment and death. The demographic model was structured around the transition points listed in Table 1. A stage was defined as the time between two transition points. Survival within each stage was defined as proportion surviving from one transition point to the next (Table 2). Death rate, **D,** within a stage was defined as the proportion removed. Recruitment rates, **b**, total mortality rates **ztot**, and predation rates **zpred** were calculated from survival and mortality, as shown in Table 3. Instantaneous rates were calculated because these, unlike crude survival and death rates, can be summed over areas, over sources, and over time periods.

Table 1. Transition points used in age structured model of population size.

attempts	=	nest built
eggs	=	egg laid
hatch	=	chick hatched live
fledge	=	check departed nest alive
new adults	=	chick returned alive to breed
adult@fledge	=	adult alive at date of fledge
adult@next attempt	=	adult returned alive after breeding

Table 2. Stage specific survival and death rates used in the age structured model of avian population size.

SURVIVAL RATES

S.nest	= attempts	= #nests/pair in colony
S.egg	= egg production	= number eggs/nest
S.chick	= egg hatch	= number hatch/number eggs
S.subad	= chick production	= number fledged/number hatched
S.ad1	= subadult survival	= first breeders/number fledged
S.ad2	= breeding survival	= returned breeders/first breeders
S.ad.n	= adult survival	= breeders at age n/breeders at n-1

DEATH RATES

D.nest	= nest failure	= failed pairs/total pairs
D.egg	= egg loss	= eggs lost/eggs laid
D.chick	= chick loss	= chicks lost/chicks hatched
D.subad	= subadult loss	= subadults lost/chicks fledge
D.ad1	= 1st breeder loss	= 1st breeders lost/1st breeders marked
D.ad2	= 2nd breeder loss	= 2nd breeders lost/2nd breeders marked
D.ad.n	= breeder loss	= breeders lost/breeders marked

Table 3. Instantaneous rates of recruitment **b**, total mortality **ztot**, and predatory mortality **zpred** computed from the proportions in Table 2.

RECRUITMENT

b.egg	= ln S.nest + ln S.egg
	= eggs/pair
b.subad	= yr^{-1} * (lnS.nest + lnS.egg + lnS.chick + lnS.subad).
	= subadults/pair

MORTALITY

ztot.nest	= -ln S.nest
ztot.chick	= -ln S.chick
ztot.subad	= -ln S.subad
ztot.ad1	= -ln S.ad1
ztot.ad2	= - ln S.ad2
ztot.ad.n	= - ln S.ad.n

LOSS RATES

nest failure	= ztot.nest - 1 = (nest - pair)/pair
egg loss	= ztot.chick - 1 = (hatch - eggs)/eggs
chick loss	= ztot.subad - 1 = (fledge - hatch)/hatch
subadult loss	= ztot.ad1 - 1 = (return - fledge)/fledge
first breeder loss	= ztot.ad2 - 1 (return - 1st tries)/1st tries
breeder loss	= ztot.ad.n - 1 (returned - breeder)/breeders

PREDATION RATES

zpred.egg
zpred.chick
zpred.subad
zpred.ad1
zpred.ad2
zpred.ad.n

These demographic rates are related to prey resource density **E** via adult intake rates (**dotE.int** = kJ/day) and delivery rates to chicks (**dotE.deliv** = kJ/day), as in Table 4. The quantitative relation between avian demographic rates (including recovery) and fish resource density **E** was then expressed in both verbal (Table 5) and graphical (Figure 3) forms.

Table 4. Definition of adult intake **dotE.int** and chick delivery **dotE.deliv**.

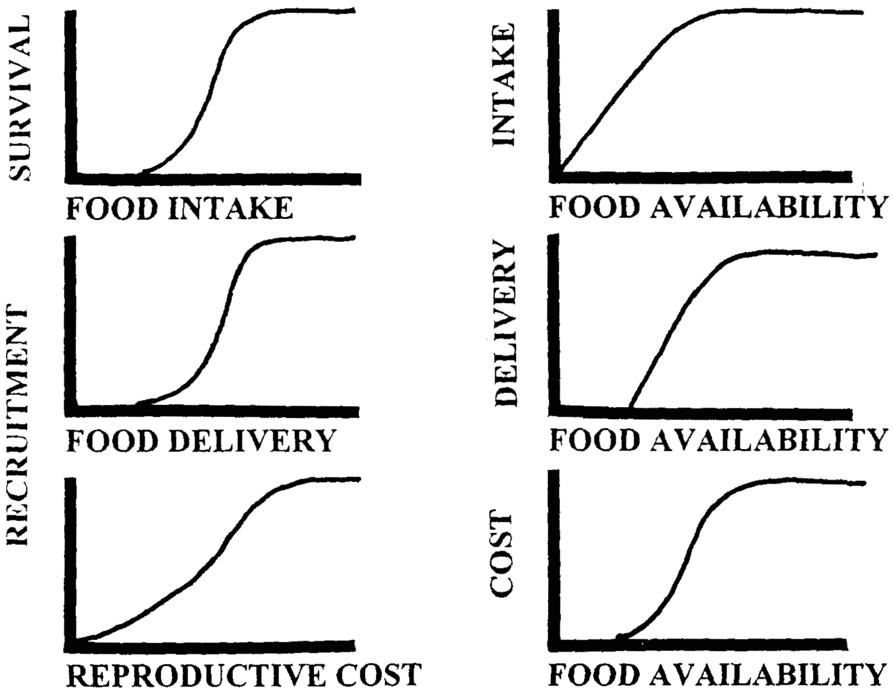
dotE.int	= F.rate * C.att * C.succ * C.energy	= kJ/day
F.rate	= trips/day	= foraging rate
C.att	= attempt/trip	= capture attempts
C.succ	= captures/attempt	= capture success
C.energy	= kJ/capture	= energy value of capture
dotE.deliv	= F.rate * M.meal * spE.meal	= kJ/day
F.rate.deliv	= trips/day	= foraging rate
M.meal	= g/trip	= meal size
spE.meal	= kJ/g	= meal value

Table 5. Verbal statement of relation of variables, for APEX general hypothesis.

A1. Survival to next stage depends on (intake, predation, other)
A2. Recruitment depends on (delivery, predation, other)

B1. Intake depends on (resource quality spE, density E, other)
B2. Delivery depends on (resource quality spE, density E, other)
B3. Delivery depends on (distance from colony, other costs)

Figure 3. Graphical expressions of the relation of variables, for the APEX general hypothesis; shapes of curves provisional.



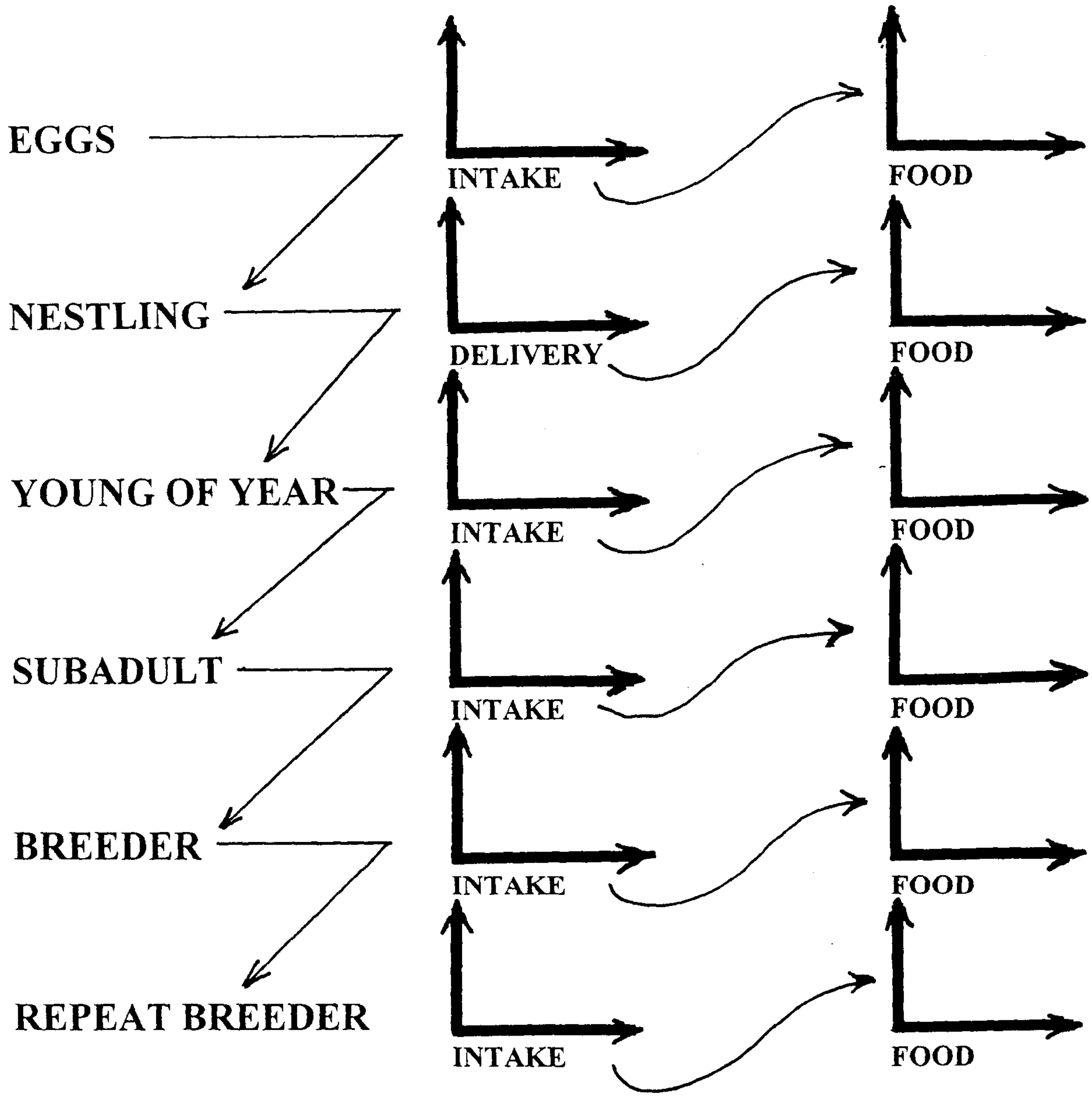
Based on discussions with APEX investigators, several variables (Table 6) were considered potentially important in affecting intake and delivery rates of food. These variables were resource distribution **E**, relative abundance of prey with high specific energy **spE** = kJ/g, and costs of food delivery, including time to find food. Travel time will in turn depends on foraging tactics (information center, traplining, etc).

Table 6. Variables considered to be potentially important in affecting food intake **dotE.int** by birds, or delivery **dotE.deliv** to chicks.

E	=	resource density	= kJ/5 km^2
B.prey.pel	=	local resource concentration in water	= g/m^3
B.prey.benth	=	local resource concentration at bottom	= g/m^3
spE.high/spE.low	=	ratio of high to low energy density species	= (kJ/g)/(kJ/g)
Cost of capture (kJ/day)			
L.prey	=	distance between prey	= m
A.school	=	school area	= m^2
FMR	=	field metabolic rate	= kJ/day
Cost of delivery (kJ/delivery)			
L.colony	=	distance from colony	= km

These variables and relationships were developed in discussion with several investigators before the APEX review in February 1997. The resulting model structure was presented to APEX investigators and referees during the February review meeting. The model was presented first in rough outline (Table 5, Figure 3), then in more detailed form, shown in Figure 4.

Figure 4. Age structured model, showing relation of survival (or recruitment) to intake (or delivery), together with relation of intake (or delivery) to resource distribution E (food).



Investigators agreed on the concept of using non-linear relations between demographic rates and intake/delivery. The preferred form of the relation was generally sigmoidal ("buffers"), following those sketched by Cairns (1987). The available data (Ainley et al. 1995; Anker-Nilsson 1996) are consistent with this form of relation. Based on et al. 1995; Anker-Nilsson 1996) are consistent with this form of relation. Based on comments from investigators, a few modifications were made. Three additional variables (Table 7) were suggested as being important, via effects on subsequent survival.

Table 7. Hypotheses concerning variables that potentially affect future survival.

HYPOTHESES

C1. post breeding survival depends on (effort to breed)

C2. post breeding survival depends on (weight loss)

C3. sub adult survival depends on (weight at fledge)

C4. sub adult survival depends on (condition at fledge)

VARIABLES

dotE.effort	= kJ/season (delivered + ingested)	= effort to breed
deltaM.adult	= g/adult - mean(g/adult)	= weight loss (gain)
dotM.chick	= g/day	= chick growth rate
M.subad	= g/fledgling	= weight at fledge
cond.fledge	= gram/cm	= condition at fledge

The third variable in Table 7 corrects weight at fledging for degree of development, measured as wing length at time of fledging, a rough proxy for age. A derived measure (with units of $gram^2/(\ln(cm))^2$) is also being used. An effort will be made to find a more biologically interpretable measure. One possibility is to use wing length as a proxy for age, then fit the chick growth data to model with biologically interpretable parameters, such as a von Bertalanffy growth curve.

Once the model was identified, the next step was to list the available data. These data (Tables 8,9,10) will be used to define the form of the relation between variables, to estimate average values of each variable, and to estimate parameters relating one variable to another.

Table 8. Data for Black-legged Kittiwakes in Prince William Sound. Source is either no data, historical data, or APEX protocols for data collection and reporting, listed by sub-project letter. JD = Julian date; (A) = archeology (will require time to assemble).

SYMBOL	UNITS	SOURCE	LOCATION	TIME
POPULATION SIZE AND TRENDS				
N.colony	pairs/colony	E,hd	all colonies	JD
N.sea	birds/km^2	E,hd	coastline	JD
SURVIVAL				
S.nest	egg success/nest built	E	3 colonies	JD
S.egg	clutch size/nest with eggs	E	3 colonies	JD
S.chick	eggs hatched/eggs laid	E	3 colonies	JD
S.subad	fledged/chicks hatched	E	3 colonies	JD
S.ad1	adults returning/chicks fledged	E	1 colony	JD
S.ad2	---		-	
S.ad.n	adults returning/adults banded	E	1 colony	JD
MORTALITY DUE TO PREDATORS				
Dpred.nest	----	-		
Dpred.egg	losses/egg laid	D.Irons(A)	3 colonies	JD
Dpred.chick	losses/chick hatched	D.Irons(A)	3 colonies	JD
Dpred.subad	----	-		
Dpred.ad1	----	-		
Dpred.ad2	----	-		
Dpred.ad.n	losses/breeding pair	F.Bassett(Th.)	1 colony	JD

Table 8. Continued....

SYMBOL	UNITS	SOURCE	LOCATION	TIME
OTHER VARIABLES				
deltaM.adult	g/adult (end of season)	E	1 colony	JD
dotM.chick	g/day	E	3 colonies	JD
M.subad	g/fledgling	E	3 colony	JD
cond@fledge	gram/cm (winglength)	E	3 colony	JD
dotE.effort	kJ/season	E(A)		
dotE.int	kJ/day	E(A)		
F.rate	trips/day	D.Irons	1 colony	JD
C.att	attempt/trip	E	1 colony	JD
C.succ	captures/attempt	B	lat/long	JD
C.energy	kJ/capture	B,E	PWS	JD
dotE.deliv	kJ/d	(A)		
F.rate.deliv	trips/day	B,E	PWS	JD
M.meal	g/trip	E	1 colony	JD
spE.meal	kJ/g	E	1 colony	JD
L.prey	km	E,B	1 colony	JD
A.school	km^2	B	PWS	JD
FMR	kJ/kg	D.Irons	1 colony	JD
L.colony	km	E	1 colony	JD

Table 9. Data for Pigeon Guillemots in Prince William Sound. Source is either no data, historical data from K.Kuletz at one colony (KK), colony atlas (FWS), or APEX protocols for data collection and reporting, listed by subproject letter. JD = Julian date; (A) = archeology (will require time to assemble).

SYMBOL	UNITS	SOURCE	LOCATION	TIME
POPULATION SIZE AND TRENDS				
N.colony	pairs/colony	FWS	all colonies	
N.colony	pairs/colony	F,G,KK	2 colonies	JD
N.sea	birds/km^2	E,F,KK	coastline	JD

Table 9. Continued....

SYMBOL	UNITS	SOURCE	LOCATION	TIME
SURVIVAL				
S.nest	egg sites/pair	F,G,KK	2 colonies	JD
S.egg	eggs/site	F,G,KK	2 colonies	JD
S.chick	chicks/nest site	F,G,KK	2 colonies	JD
S.subad	fledged/chicks hatched	F,G	2 colonies	JD
S.ad1	adults returning/chicks fledged	F,G,KK	2 colonies	JD
S.ad2	---		-	
S.ad.n	adults returning/adults banded	F,G,KK	2 colonies	JD
MORTALITY DUE TO PREDATORS				
Dpred.nest	----		-	
Dpred.egg	egg loss/nest site	F,KK	1 colonies	JD
Dpred.chick	chick loss/nest site	F,KK	1 colonies	JD
Dpred.subad	----		-	
Dpred.ad1	----		-	
Dpred.ad2	----		-	
Dpred.ad.n	losses/pair	F,KK	1 colony	JD
OTHER VARIABLES				
deltaM.adult	g/adult (end of season)	G	2 colony	JD
dotM.chick	g/day	F,G	2 colony	JD
M.subad	g/fledgling	F,G	2 colony	JD
cond@fledge	gram/cm (winglength)	F,G	2 colony	JD
dotE.effort	kJ/season	(A)		
dotE.int	kJ/day			
F.rate	trips/day	F,G	2 colony	JD
C.att	attempt/trip			
C.succ	captures/attempt	B	lat/long	JD
C.energy	kJ/capture	B	PWS	JD
dotE.deliv	kJ/day	G	2 colonies	JD
F.rate.deliv	trips/day	F,G	2 colonies	JD
M.meal	g/trip	F,G	2 colonies	JD
spE.meal	kJ/g	(A)		
L.prey	km	B	lat/long	JD
A.school	km^2	B	lat/long	JD
FMR	kJ/day			
L.colony	km	E,B	lat/long	JD

Table 10. Prey data for Black-legged Kittiwakes and Pigeon Guillemots in Prince William Sound. Source is either no data, NVP = nearshore vertebrate predator protocol, SEA project, or APEX protocols for data collection and reporting, listed by subproject letter. JD = Julian date; (A) = archeology (will require time to compile).

SYMBOL	UNITS	SOURCE/TYPE	LOCATION	TIME
M.prey.pel	g/m^3	A/acoustic	3 block	JD
		B/acoustic	PWS	JD
		SEA/aerial	PWS	JD
spE.pel	kJ/g	G		
M.prey.benth	g/m^2	NVP/acoustic (A)	PWS	JD
		NVP/seine (A)	PWS	JD
		F/seine (A)	1 colony	JD
		W.Barbour/quadrat (A)	intertidal	JD
		ADF&G/shrimp trawl (A)		
		UAF (A)	kelp beds	
spE.benth	kJ/g	G		

Discussion and Conclusions

1. The APEX general hypothesis could be readily cast in quantitative terms.

2. In seabirds, demographic rates prevail over kinematic (movement) rates at the scale of the APEX general hypothesis. Demographic variables will need to be estimated, in relation to prey intake and delivery, in order to test the APEX general hypothesis.

3. Data exist to estimate nearly all demographic parameters in 3 colonies of Black-legged Kittiwakes and 2 colonies of Pigeon Guillemots in Prince William Sound.

4. Post fledging and post breeding mortality (s.ad1, s.ad.n) need to be estimated in multiple years, starting in 1997.

5. Concomitant data are needed to estimate parameters relating uptake/delivery to small scale resource density E, for both species. Concomitant measures of the following variables need to be made in multiple years, starting in 1997.

-Capture rates (C.att, C.succ, C.energy) in relation to prey density E = kJ/area.

-Prey intake (dotE.int = kJ/day) and delivery rates (dotE.deliv = kJ/day) relative to variation in resource density E and quality (spE.high/spE.low).

6. Prey intake (dotE.int) by adults needs to be estimated for the pre-breeding, incubation, chick rearing, and post breeding periods.

7. The feasibility of use field metabolic rate (FMR) to measure prey intake of both species in relation to resource density, delivery rate, and energy content (spE) of chick meals should be examined.

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Literature Cited

Ainley, D.G., W. J. Sydeman and G.J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Mar. Ecol. Progr. Ser. 118: 69-79.

Anker-Nilsson, T., R. Barrett and J. Krasnow. 1996. Long- and short-term responses of seabirds in the Norwegian and Barent's seas to changes in stocks of prey fish. Internatl. Symp. Role Foragefish Mar. Ecosys., Nov 1996. Alaska Seagrant, Univ. Alaska Fairbanks [Abstract}.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5: 261-267.

Ford, R.G, J. A. Wiens, D. Heinemann & G.L. Hunt, Jr. 1982. Modeling the sensitivity of colonially breeding marine birds to oil spills: guillemot and kittiwake populations on the Pribilof Islands, Bering Sea. J. Appl. Ecol. 19:1-31.

Kuletz, K. 1983. Mechanisms and consequences of foraging behavior in a poulation of breeding pigeon guillemots. M.Sc. Thesis, Univ. California, Irvine.

Irons, D.B. 1992. Aspects of foraging behavior and reproductive biology of the Black-legged Kittiwake. PhD Diss., Univ. California, Irvine.

Nur, N., R.G. Ford & D.G. Ainley. 1993. Computer model of Farallon seabird populations. Natl. Ocean. Atmosph. Admin., Gulf Farallones Natl. Mar. Sanct., Contract CX-8140-1-0019. San Francisco CA.