Ransom A. Myers (RAM) Ian Jonsen, Joanna Flemming Greg Breed, Chris Field Mike James Don Bowen

State-Space Models for Movement and Habitat Use

FMAP (Future of Marine Animal Populations) http://fish.dal.ca Dalhousie University Halifax, Canada



James, Eckert, Myers Mar. Bio. 2005



### **Imperial Mathematician**





Kepler's elliptical orbit for Mars.



### **Imperial Mathematician**

24 Young of Year Grey Seals see Greg Breed's talk

### **Argos Satellite Telemetry Data**

Getting more out of the data

Goals of State-Space analysis

- Infer true locations from noisy data
- Account for error w/out loss of information
- Infer behaviour, test hypotheses



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Jonsen, Flemming and Myers (2005) Ecology 86: 2874-2880

### Data Filtering & State Estimation Jonsen et al. 2005. Ecology 86:2874-2880



Jonsen, Flemming and Myers (2005) Ecology 86: 2874-2880



#### Noisy Data: ad-hoc Filtering Extreme values removed prior to analysis



#### State-Space Filtering is Fundamentally Different Location estimates w Cls & parameter estimation



#### State-Space Filtering is Fundamentally Different Location estimates w Cls & parameter estimation

# $\mathbf{Y}_{1} \mathbf{Y}_{2} \mathbf{Y}_{3} \mathbf{Y}_{4} \mathbf{Y}_{5} \mathbf{Y}_{6} \mathbf{Y}_{7} \mathbf{Y}_{8} \mathbf{Y}_{9} \mathbf{Y}_{10} \mathbf{Y}_{11} \mathbf{Y}_{12} \dots \mathbf{Y}_{T}$



We also carried out likelihood analysis

This is Sir Ronald Fisher

 $\alpha_1 \alpha_2 \alpha_3 \alpha_4 \alpha_5 \dots \alpha_T; \gamma, \sigma, \tau$ 

#### State-Space Filtering is Fundamentally Different Location estimates w Cls & parameter estimation



# What are State Space Models

- Analysis of sequential data observed with error
- Estimate unobservable states from error-prone observations
- Simultaneously deal with process variability & estimation error
- Accomodates non-Gaussian errors, nonlinear dynamics, and other complexities in the data
- Accomodates missing observations

# Why State Space Models?

- Simply one of the key "right ways" to think about many modern problems
- Engineers, Economists, Oceanographers use this approach
- State-space models used for: Tracking moving objects Shooting down missiles Predicting stock market trends Predicting global circulation patterns Speech recognition



# The First State-Space Model: the Kalman Filter

Process Model :

Measurement Model :  $x_k = M_k y_k + v_k$ 

 $y_{k+1} = A_k y_k + u_k$ 

- Used to estimate state variables, not dynamical parameters
- Can be applied to non-stationary processes.
- Measurement noise and process noise are white and Gaussian.
- Dynamics are linear.

### State-Space Concept



## **State Space Models**

### **Measurement Equation**

- Relates imperfect observations to true position
- Estimate ARGOS error with ε

### **Transition Equation**

- Predicts next position from behavioral model

Error function  $y_t = h(\alpha_t, \varepsilon_t)$ observed true location location

 $\alpha_{t} = f(\alpha_{t-1}, \eta_{t}; \gamma)$ 

movement function

parameters

What is important about the transition equation?

$$\alpha_t = f(\alpha_{t-1}, \eta_t; \gamma)$$

The state variable is random variable, and should NOT be thought of as a simple number. The above equation can be better interpreted as the probability of a given state value  $\alpha_t$ . Thus, we write the state as a Greek letter,  $\alpha_t$ . Consider the simplest model where the mean for the next time period is a simple multiple of this years state.

$$p(\alpha_t | \alpha_{t-1}) = \mathcal{N}(\alpha_{t-1} \gamma, \sigma)$$

What is important about the state equation?

$$\alpha_t = f(\alpha_{t-1}, \eta_t; \gamma)$$

The state variable is random variable, and should NOT be thought of as a simple number. We write the state as a greek letter,  $\alpha_t$ 

How is this programmed with BUGS

mean[t] <- f(alpha[t-1]; γ)
alpha[t] ~ dlnorm (mean[t], sigma)</pre>

This symbol means "is distributed as", and implies that alpha[t] is a random variable.



1<sup>st</sup> location = release point

# *eg.* release location estimated with GPS

Apply dynamics (transition eqn)

**Observe a location with error** 

Integrate over predicted & observed densities (Bayes Rule)

Updated prediction becomes prior for next time step

## Software

## WinBUGS: Bayesian Analysis Using Gibbs Sampling



This is the innovation likelihood

# Movement (Transition) Equation First difference correlated random walk

$$d_{t} = \gamma T(\theta)d_{t-1} + N_{2}(0,\Sigma)$$
  
$$\alpha_{t} = \alpha_{t-1} + d_{t}$$

### **Observation Equation**

 $y_t = t$ -distribution ( $\alpha_t$ ,  $\sigma_t$ ,  $\upsilon_t$ )

Plus an algorithm to regularize estimated locations in time

## Movement (Transition) Equation



**Observation Equation** 

## $y_t = t$ -distribution ( $\alpha_t$ , $\sigma_t$ , $\upsilon_t$ )

 $\alpha_t$ 

 $y_t$ 

### Dealing with Complex Data Argos telemetry data

- Observations made irregularly through time
- Observation errors non-Gaussian (extreme values)
- Observation errors vary through time

#### "Ideal" Data Regular time intervals with constant Gaussian errors, & no missing data



#### "Real" Data Irregular time intervals with varying non-Gaussian errors, & missing data



# Sources of Uncertainty

- Estimation error
  - Data observed with error
  - Errors can be non-Gaussian



Satellite telemetry





## Argos location errors



data from Vincent et al. 2002

## Argos errors follow *t*-distributions:



Jonsen, Flemming, Myers, Ecology, 2005



### Tag Precision

 $y_t = t$ -distribution ( $\alpha_t$ ,  $c\sigma_t$ ,  $\upsilon_t$ )

• for each location class is assumed known (Vincent et al. 2002, Jonsen et al 2005)

**C** is an estimated parameter that scales the variance to each tag

Best tags are **1000's** of times more precise than the worst tags

Best tags in a single lot can be **100's** of times more precise than worst tags from a lot





65°W 64°W 63°W 62°W 61°W 60°W 59°W

State-space models allow you to think about things, that it is very difficult to think about otherwise

## Navigation: Estimating the "Circle of Confusion"

Flemming et al. in press. Environmetrics


Regularized Track of Turtle 18284



Longitude

Corresponding GC Route





It is essential to treat groups of animals simultaneously for maximum utility of the data.

# Leatherback turtles are unique in that they expose their pineal spot to sunlight.



# Turtles are close to the surface during the day during migration



### Examining Diel Migration Behaviour in Leatherbacks



Jonsen, James Myers. in review. Journal of Animal Ecology



### Hierarchical Bayes State-Space Model (HB SSM)



### **HB SSM**



### **Conventional Approaches Do Not Work**



Log ratio of day to night speeds δ

### Results are consistent with the hypothesis that the pineal spot improves navigation.



## Dynamics of behavior is very nonlinear, to determine hot spots and foraging

- Solution: Markov switching models between behavioral modes
- Dynamics within a behavioral mode is linear

## State-Space Switching Models





Federal Reserve Bank of St. Louis *Review*, July/August 2005, 87(4), pp. 435-52.



# Summary

- State-space models allow you to think about problems which have no conventional solution
- Fundamentally different approach to analysis of complex, error-prone data emphasis on estimation of "true" states, biological parameters and uncertainty
- Models can be fit to other types of sequential movement data (GPS, Archival tags)

## The Future

- Better incorporation of oceanographic data
- Model testing, statisticians do NOT know how to compare models with non-Gaussian errors
- More "user friendly" (i.e. less "user angry" methods). This would include an easy to use library with a variety of possible behaviour.

### Critical Spatial/Temporal Models Tools

Ransom A. Myers (RAM) Dalhousie University, Canada

Pew Global Sharks Assessment FMAP (Future of Marine Animal Populations) Sloan Census of Marine Life

http://fish.dal.ca Lenfest Foundation

# What was the most common large animal in the world? (perhaps this one was)





### Loss of sharks in the Gulf of Mexico 300 fold decline – no one noticed



Oceanic Whitetip captures per 10,000 hooks

Baum and Myers, 2004 Ecology Letters

Circumstantial evidence of oceanic whitetip sharks being common in the Gulf of Mexico



# **Critical Modeling Tools**

- Generalized linear models with negative binomial error
- Generalized linear mixed effects models to standardize old and new surveys



- **a**. Northern Gulf of Mexico bottom shrimp trawl survey
- b. NMFS offshore bottom trawl survey
- c. NMFS inshore bottom trawl survey
- d. Southeast U.S. SEAMAP bottom shrimp trawl survey
- $\boldsymbol{e}.$  North Carolina Institute of Marine Sciences longline survey
- f. Crooke commericial longline data
- μ. Meta-analytic mean

#### Loss of Dusky Sharks in the Eastern US



### Consequences of "protection" since 1993: Rate of decline has increased:



Instantaneous rate of change in abundance

Change in trend since 1993

## **Critical Modeling Tools**

Surveys vary in time, and the sharks move seasonally up and down the coast

We used a generalized linear mixed effect model with negative binomial errors to describe the seasonal movement up and down the coast by allowing the seasonal harmonics to be an interaction, i.e. latitude and harmonics.

# Reduce fishing mortality for sensitive species for survival of the species



Source: Myers and Worm 2005. Phil. Trans. R. Soc. B 360:13-20 Proportional reduction of fishing mortality

1.0

Dusky shark. Source: NMFS

# **Critical Modeling Tools**

- Calculus
- Generalized linear models

Hammerhead sharks

#### Sphyrna lewini





Science. Jan. 2003. J.K. Baum, R.A. Myers, D.G. Kehler, B. Worm, S.J. Harley, P.A. Doherty

## Results



# **Critical Modeling Tools**

- Development of a new regression model that does not use "zeros" (we believe the fishermen sometimes lie).
- Robustness analysis that show results are robust to alternative assumptions







Area

# Same results for trawl surveys in Gulf of Mexico



Shepherd and Myers Ecology Letters 2005

### Same results for trawl surveys in Gulf of Mexico



Shepherd and Myers Ecology Letters 2005

#### **Decline of Mediterranean Sharks**



#### **Decline of Hammarhead sharks**



Boero F. & A. Carli 1979 – Boll. Mus. Ist. Biol. Univ. Genoa (47)

#### **Decline of Mediterranean Sharks**

#### By catch associated with a Tuna Trap In Tirrenian Sea



"Tonnarella di Baratti"




Hammerhead shark

#### Smooth-hound



# **Critical Modeling Tools**

 Repeat analysis world wide using a metaanalytic approach



## Critical Modeling tools:

- Generalized linear models to standardize historical surveys, e.g. diurnal differences
- Mapping historical surveys on recent Stratified Random design









Latitude



Latitude













Longitude

















Catch Per Hundred Hooks, Year = 1970



Catch Per Hundred Hooks, Year = 1971





Catch Per Hundred Hooks, Year = 1973



Catch Per Hundred Hooks, Year = 1974





Catch Per Hundred Hooks, Year = 1976





Catch Per Hundred Hooks, Year = 1978







## **Critical Modeling Tools**

• Plot the data and think for yourself

#### Common patterns of decline


## Critical Modeling tools:

 Nonlinear Mixed Effect Models to Describe Common Patters

#### Totally Stupid Reasons for not Believing the Obvious

- You ignore research surveys.
- Removing Large Predators Couldn't Possibly Affect Survival of Other Fish.
- Fishing Couldn't Possibly Affect the Size of Tuna.
- Fishermen are so stupid they cannot use satellite data to find tuna.
- Fishermen are so stupid that they don't improve their gear.

These estimates are conservative: Fishermen are smarter (GPS, satellite information, ACDP (Acoustic Current Doppler Profiler)).



Locations of a leatherback turtle over a two week period tagged by my student Mike James that maintains its position within a cold core ring (somehow).

#### **Study area**



## Analysis repeated using independent research data







Yellowfin tuna – equitorial Pacific

#### Change in body size







Mean mass (kg)

## Critical Modeling tools:

 Generalized linear mixed effects models to standardize historical surveys for depth and soak time

#### Loss of sharks in the Gulf of Mexico 300 fold decline – no one noticed





Oceanic Whitetip captures per 10,000 hooks

#### What about prey fish?



Illustration taken from the book "Encyclopedia of Canadian Fishes" by Brian W. Coad with Henry Waszczuk and Italo Labignan, 1995,

## Explosion of Pomfrets in the Gulf of Mexico ~1000 fold increase – no one noticed



Pomfret captures per 10,000 hooks

Many thanks to NMFS for data and advice

#### The Rise of the Marine Mesopredators





Pelagic Sting Ray Pteroplatytrygon violacea



Photos from Phillip Colla, photography

## Explosion of Pelagic Stingrays in the Gulf of Mexico ~1000 fold increase – no one noticed



1950's 1990's Pelagic stingray captures per 10,000 hooks

Many thanks to NMFS for data and advice



#### Major shrimp stocks in the North Atlantic



## Cod and shrimp biomass in the North Atlantic:



Year



Worm and Myers, Ecology 2003

Shrimp biomass (Thousand tonnes)

#### Step 2: Random-effects metaanalysis



## **Critical Modeling Tools**

- Random effects meta-analysis
- Corrections for temporal autocorrelations
- Corrections for spatial autocorrelaitons
- Modeling of environmental (bottom up) effects



#### Blue marlin (*Makaira nigricans*)



#### Sailfish (*Istiophorus albicans*)

1.5 **Blue Marlin** Sailfish Mean 1.0 number of fish per 100 0.5 hooks 0.0 1960 1980 1990 2000 1970 Year











## **Critical Modeling Tools**

• Hierarchical Bayes State-Space Models

#### Loss of species density per decade

- Displayed is the number of tuna and billfish species that are found on a standard longline with 1000 hooks
- The time series runs from 1952-1999
- It shows how large hotspots are disappearing over time and how few concentrations of diversity remain today

After data from: Worm B, Sandow M, Oschlies A, Lotze HK, Myers RA (2005) Global patterns of predator diversity in the open oceans. **Science** Aug. 2005.



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-1369



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-136



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-136



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-13



Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-136

# Critical Modeling Tools: Rarefaction diversity

•Compare diversity between cells with different sample size

•Species richness: Expected number of species per 50 individuals

•Species density: expected number of species per 1000 hooks





Bluefin Tuna / 1000 hooks 1960


Bluefin Tuna / 1000 hooks 1970



Bluefin Tuna / 1000 hooks 1980



Bluefin Tuna / 1000 hooks 1990

### Tagging also shows bluefin restricted to N Atlantic



Source: Block et al. 2005. Nature 434: 1121-1127

# Global decline in ocean predator diversity

- Increasing catches
- Decreasing diversity
- Long-term decline linked to fishing
- Yearly variability linked to climatic changes

Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-1369



## ENSO affects diversity across entire Pacific

Species richness

Blue marlin catch rates



Slope of  $\Delta_t$  with ENSO

Source: Worm, Sandow, Oschlies, Lotze, Myers 2005. Science 309:1365-1369

# Understand oceanographic drivers of diversity

- Patterns of diversity were explained by
  - Mean temperature
  - Fronts and eddies
  - Oxygen



Source: Worm et al. 2005. Science 309:1365-1369

## **Critical Modeling Methods**

- Spatial regression with anisotropic spatially correlated errors
- We used SAS Proc MIXED (and the generalized linear model additions) which are very fast, and easy to use.

# Use remaining hotspots for global conservation

- Consistent patterr of species richnes and density
- Five major hotspo
  - U.S. east coast
  - Hawaiian chain
  - Southeast Pacific
  - Australian east co
  - Sri Lanka



Source: Worm et al. 2005. Science 309:1365-1369

## Protect diversity hotspots in national waters

 Special places where many species aggregate

- Key habitats
- Food supply

Worm Lotze Myers 2003. PNAS 100:9884-9888



## Validate hotspots across species groups







Source: Worm et al. 2005. Science: 309:1365-1369

### Simulating area closures

- Hotspot closure reduces catch of threatened species
- Displacement issues must be considered
- Fishing effort needs to be reduced as well



Worm Lotze Myers. 2003. PNAS 100:9884-9888

## **Critical Modeling Method**

• Simulation methods

The First Collective Act of Humanity was to save the great whales –

despite massive denial

we can do
the same for the remaining
virgin areas of the oceans
and for the great sharks.





#### LOSS OF SOILSHEIF CIAMS SOUTH OF LONG ISTAND





#### Meta-analysis of cownose ray trends



### Increase in small sharks: sharpnose shark





Strong, W.R. Jr; Snelson, F.F. Jr; Gruber, S.H. Copeia 1990, 836-839

#### **GREAT HAMMERHEAD SHARK PREDATION UPON SPOTTED EAGLE RAY**

Photo by Demian ChapmanD. D. Chapman and S. H. Gruber, 2002 Bull. of Mar. Sci. 70: 947–952

### Loss of hammerheads from surveys



Shepherd and Myers, 2005, Ecology Letters

Dusky shark



Generalized linear model results						
	Estimate	StdErr	р	k/scale		
Abundance	-0.169	0.0171	5.67e-23	4.28		
Length	-0.0105	1.4e-3	8.85e-14	18.8		

#### Great hammerhead



Generalized linear model results							
	Estimate	StdErr	р	k/scale			
Abundance	-0.143	0.0812	0.079	1.96			
Lenath	-7.19e-3	0.0707	0.919	1			

**Bull shark** 



	Estimate	StdErr	р	k/scale
Abundance	-0.172	0.0443	9.99e-5	4.28
Length	-0.0136	5.e-3	6.69e-3	63.2





















Instaneous rate of change in abundance with time

### Experimental Results of Pete Peterson and Sean Powers in North Carolina



## Loss of Bay Scallops with Cownose Ray Fall Migration



Mortality of almost 100% during fall migration of cownose rays



August bay scallop density

## Excluding cownose rays allow the survival of bay scallops.









Trophic Cascades: Consequences of the loss of top predators may be greater than we think The First Collective Act of Humanity was to save the great whales –

despite massive denial

we can do
the same for the remaining
virgin areas of the oceans
and for the great sharks.



### Past use of State-Space Models for Movement

- Models by David Brillinger in 1998 showed migration across oceans using a directional random walk on a sphere.
- John Sibert used "almost linear" Kalman filter models to improve popup tags locations (see U. of Hawaii website)
- Morales, Haydon, Friar, Holsinger, Fryxell (Ecology 2004) used hidden Markov models



### Blue marlin (*Makaira nigricans*)



### Sailfish (*Istiophorus albicans*)
1.5 **Blue Marlin** Sailfish Mean 1.0 number of fish per 100 0.5 hooks 0.0 1960 1980 1990 2000 1970 Year











Not only have large predators declined by at least a fact 10, but mesopredators have often increased by at least a factor of 10.

FMAP (Future of Marine Animal Populations)part of the Sloan Census of Life http://www.fmap.caPew Global Sharks Assessmenthttp://www.globalsharks.ca



(9) Baum et al. (2003): Northwest Atlantic.

Not only have large predators declined by at least a fact 10, but mesopredators have often increased by at least a factor of 10.

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### Special Case of State-Space Models: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- α: hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
  - The initial state distribution  $P(\alpha_1)$
  - The transition model P( $\alpha_t \mid \alpha_{t-1}$ )
  - The observation model P(  $Y_t \mid \alpha_t$  )

#### **State Space Models**

Maximize likelihood to estimate model parameters  $\gamma$  ob

observed location

true location

Error function

Use Markov Chain Monte Carlo methods in WinBugs

 $\alpha_t = f(\alpha_{t-1}, \eta_t; \gamma)$ 

 $y_t = h(\alpha_t, \varepsilon_t)$ 

movement function

parameters

#### State-Space Models

#### Process model

true location  $\alpha_{t+1} = f$ (true location  $\alpha_t$ , parameters, process variability)

**Observation model** observed location  $\mathbf{y}_t = h(\text{true location } \alpha_t, \text{ observation error})$ 

#### State-Space Models

#### Process model

true location  $\alpha_{t+1} = f$ (true location  $\alpha_t$ , parameters, process variability)

#### Observation model

observed location  $\mathbf{y}_t = h(\text{true location } \alpha_t, \text{ observation error})$ 

#### **Location Estimates**



# This represents a different way of thinking

# How are animals different from particles?

- They have free will
- They have "inertia", they tend to keep going the same direction.
- They have different behaviours

# Why State Space Models

- This is simply one of the key "right ways" to think about many key modern problems:
- Engineers, economists, oceanographers, and speech recognition scientists, use modifications of this idea;
- If you want to shoot down a missile, you use a state space model.

When migrating leatherbacks spend more time close to the surface during the day.





From James, Ottensmeyer, and Myers (in review)



#### **Economometrics:**

# How our analysis differs:

- We use a large amount of prior information on the accuracy of locations, i.e. they are described by "heavy tailed" distributions.
- We model the performance of each transmitter, because there are very clear differences among transmitters.
- We use the first state-space model of switching for movement implemented for an ecological problem.
- First meta-analytic approach which combines information from different tracts using a hierarchical random-effects meta-analytic approach.

# Making Switching Models Work

 Meta-analysis greatly improves the estimates because relative few transitions are observed for each track. In the Bayesian approach, both the parameters ?? and the values of the states (α<sub>1</sub>, α<sub>2</sub>, ..., α<sub>T</sub>) are viewed as random variables.

## What is Kalman Filtering Used For?

- What is it used for?
- Tracking missiles
- Tracking heads/hands/drumsticks
- Extracting lip motion from video
- Lots of computer vision applications
- Economics
- Navigation

#### First Measurement



#### Second Measurement



#### **Combine Estimates**





#### **Combined Estimates Conditional Density Function** $N(\hat{x}, \hat{\sigma}^2)$ $\hat{x} = \hat{x}_2$ $=\sigma_2^2$ -2 0 2 8 12 6 10 14 4

#### But suppose we're moving

# Not *all* the difference is error Some may be motion KF can include a motion model Estimate velocity and position

-2

10

# Switching Models

- Does not work well on one animal
- Works well if animals have the same switching parameters (this is the same as a fixed effect meta-analysis).
- We would like to have a hier. model, where parameters are random variables.

#### Applications







GPS

Satellite orbit computation

Active noise control



Tracking

## **Examples - Target tracking**

The state process consists of the position, velocity, and acceleration coördinates (9 dimensions in all) of a ballistic or steered target (i.e rocket or missle); randomness in the state process may come from interactions with the atmosphere, or from evasive maneuvers. Observations consist of data from radar and infrared sensors, and prior knowledge of the initial location of the target; observation noise comes from background noise sources such as clutter, or internal thermal noise in the sensor.

#### Examples: Weather and Ocean Prediction

Nonlinear filtering theory allows new data to be assimilated into the differential equations which drive a numerical model of the ocean and/or atmosphere.

### Examples

 Asset Pricing - Each component of the state is the value of some asset or derivative, or else an underlying interest rate; the observations consist of data on specific sale prices of related assets at a sequence of times.

#### Different short behavors

# Why state-space models?

- Only method that models time series structure with missing values.
- Models estimation error.
- Models non Gaussian errors.
- Models nonlinear relationships.
### Further advantages

• Switching models

#### What about Levy flights? Heuristic, but not mechanistic.



# State space models

- State variables
- parameters
- forcing functions
- rules of change
- the state variables in the future depend upon the current state, the parameters (constants), any external perturbations (the forcing functions), and the rules of change

## State variables

- The complete description of the current state of the system -- complete enough that you can "rebuild" the system with this amount of information
- examples the number of animals in the population - the age structure of a population, the presence or absence of species in a community matrix ....

#### Parameters

- Do not change over time and are the constants that describe the rates or limits
- intrinsic rates of growth, carrying capacity, survival rates, fecundity rates etc.

# Forcing functions

- Natural or anthropogenic factors that affect the state
- weather impacts on survival or reproduction
- harvesting
- These are "external" to the model -- that is we don't attempt to describe the dynamics of these factors

# Rules of change

• The equations that describe how the state variables change over time in relation to the current values of the state, the parameters, the the forcing functions.

• 
$$S_{t+1} = f(S_t, p, u_t)$$

# A simple state space model Logistic growth

- Numbers next year are number this year + net production, minus removals
- $N_{t+1} = N_t + rN_t(1 N_t/k) C_t$
- N is the population size
- r is the intrinsic rate of increase
- k is the carrying capacity
- C is the catch

# Quiz #1

- Take a piece of paper
- From this logistic growth model
- 1 what are the state variable(s)
- 2 what are the parameter(s)
- 3 what are the forcing function(s)
- 4 what are the rules of change

#### The answer

- The state variable is the population size
- The parameters are the intrinsic rate of increase r, and the carrying capacity k
- The forcing function is the catch
- The rules of change is the equation

# Components of rules of change

- Logical relationships
  - statements that are true by definition
  - numbers next year = numbers this year +
    births deaths + immigration emigration
  - also known as tautologies
- Functional relationships
  - specify the relationship between a rate and a state variable or something related to a state variable (survival as a function of density)

# For logistic growth model

- A logical relationship
  - number alive next year is number alive this year plus net production minus catch
- The functional relationship - net production =  $rN_t(1-N_t/k)$

#### STATE PROCESS

 The primary object of study is a Markov process, X, whose probability law is known, but which cannot be observed directly. It serves as a model for the true state of the system under study; hence X is called the state process. The simulation below shows a real-valued process; in practice X may be high-dimensional, with values in a manifold or metric space.

#### OBSERVATIONS

- At certain times t[1],t[2],... (perhaps continuously), some function of the state, corrupted by noise, is observed. For example, observations might be of the form
- Yt[n]=h[Xt[n],Vt[n]]
- where h is a continuous function, and Vt[1],Vt[2],... are independent random variables, independent of X.

#### Structural Equation Modelling (SEM)

Minimise the difference between the observed (S) and implied ( $\Sigma$ ) covariances by adjusting the path coefficients (B)



 $x^{T}$ .x is the implied variance covariance structure  $\Sigma$ 

C contains the residual variances (u,v,w) and covariances

The free parameters are estimated by minimising a [maximum likelihood]

# **Modeling Sequential Data**

- Sequential data arises in many areas of science & engineering
- Types of data sources:
  - Time series, generated by a dynamical system
  - Sequence generated by one-dimensional spatial process
- On- line analysis vs. Off-line analysis

# **Classical Solutions**

- Classic approaches to time-series prediction
  - Linear models: ARIMA(auto-regressive integrated moving average), ARMAX(autoregressive moving average exogenous variables model)
  - Nonlinear models: neural networks, decision trees
- Problems with classic approaches
  - prediction of the future is based on only a finite window
  - it's difficult to incorporate prior knowledge
  - difficulties with multi-dimensional inputs and/or outputs

# **State-Space Models**

- Assumptions:
  - There is some underlying hidden state of the world (query) that generates the observations (evidence), and evolves in time, possibly as a function of our inputs
  - Models are first-order Markov, i.e.,

 $P(X_t | X_{1:t-1}) = P(X_t | X_{t-1})$ 

observations are conditional first-order Markov

 $\mathsf{P}(\mathsf{Y}_t \mid \mathsf{X}_t, \mathsf{Y}_{t-1}) = \mathsf{P}(\mathsf{Y}_t \mid \mathsf{X}_t)$ 

- Time-invariant or homogeneous
- The goal: computing of the belief state:

The belief on the hidden state of the world given the observations up to the current time y1:t and inputs u1:t to the system, P(X | yS1:t, u1:t)

• State-space model must define a prior  $P(X_1)$ , a state-transition function,  $P(X_t \mid X_{t-1})$ , and an observation function,  $P(Y_t \mid X_t)$ 

# **SSM:** Representation

Hidden Markov Models (HMMs):

Xt is a discrete random variables

Kalman Filter Models (KFMs):

Xt is a vector of continuous random variables

Dynamic Bayesian Networks (DBNs): more general and expressive language for representing state-space models

## **SSM: Inference**

- A state-space model defines how X<sub>t</sub> generates Y<sub>t</sub> and X<sub>t</sub>.
- The goal of inference is to infer the hidden states (query)
  X<sub>1:t</sub> given the observations (evidence) Y<sub>1:t</sub>.



# **SSM: Inference (cont.)**

- Inference tasks:
  - Filtering (monitoring): recursively estimate the belief state using Bayes' rule
    - prediction: computing  $P(X_t | y_{1:t-1})$
    - updating: computing  $P(X_t | y_{1:t})$
    - throw away the old belief state once we have computed the prediction ("rollup")
  - Smoothing: estimate the state of the past, given all the evidence up to the current time
    - Fixed-lag smoothing (hindsight): computing  $P(X_{t-1} | y_{1:t})$  where 1 > 0 is the lag
    - Fixed-interval smoothing (offline): computing  $P(X_t | y_{1:T})$  for all
  - Prediction: predict the future
    - Lookahead: computing  $P(X_{t+h} | y_{1:t})$  where h > 0 is how far we want to look ahead  $1 \le t \le T$
  - Viterbi decoding: compute the most likely sequence of hidden states given the data
    - MPE (abduction):  $x_{1:t}^{*} = \operatorname{argmax} P(x_{1:t} | y_{1:t})$

# **SSM: Learning**

- Parameters learning (system identification) means estimating from data these parameters that are used to define the transition model P( X<sub>t</sub> | X<sub>t-1</sub> ), the observation model P( Y<sub>t</sub> | X<sub>t</sub> ) & the prior P(X<sub>1</sub>)
- The usual criterion is maximum-likelihood(ML)
- The goal of parameter learning is to compute

- 
$$\theta^*_{ML} = \operatorname{argmax}_{\theta} P(Y|\theta) = \operatorname{argmax}_{\theta} \log P(Y|\theta)$$
, where

$$\log P(Y \mid \theta) = \log \prod_{m=1}^{N_{train}} P(y_{1:T}^m \mid \theta) = \sum_{m=1}^{N_{train}} \log P(y_{1:T}^m \mid \theta)$$

- Or  $\theta^*_{MAP}$  = argmax  $_{\theta} \log P(Y|\theta) + \log P(\theta)$  if we include a prior on the parameters
- Two standard approaches: gradient ascent and EM(Expectation Maximization)
- Problem: Hidden variables complicate finding of the globally optimal parameters
- Structure learning: more ambitious

#### HMM: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- X: hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
  - The initial state distribution  $P(X_1)$
  - The transition model P( $X_t | X_{t-1}$ )
  - The observation model P( $Y_t | X_t$ )

### **HMM: Hidden Markov Model**



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- HMM is the simplest DBN
  - a discrete state variable with arbitrary dynamics and arbitrary measurements

### Special Case of State-space Models: Hidden Markov Model



- one discrete hidden node and one discrete or continuous observed node per time slice.
- α: hidden variables
- Y: observations
- Structures and parameters remain same over time
- Three parameters in a HMM:
  - The initial state distribution  $P(\alpha_1)$
  - The transition model  $P(\alpha_t | \alpha_{t-1})$
  - The observation model P(  $Y_t | \alpha_t$  )

#### HMM: Hidden Markov Model





# **KFM: Kalman Filter Model**

- KFM has the same topology as an HMM
- all the nodes are assumed to have linear-Gaussian distributions

**X**<sub>2</sub>

Y<sub>2</sub>

X<sub>1</sub>

**Y**<sub>1</sub>

 $x(t+1) = A^*x(t) + v(t),$ 

v ~ N(0, Q) : process noise, x(0) ~ N(X(0), V(0))

$$\mathbf{y}(t) = \mathbf{C}^* \mathbf{x}(t) + \mathbf{w}(t),$$

- $w \sim N(0, R)$ : measurement noise
- Also known as Linear Dynamic Systems (LDSs)
  - a partially observed stochastic process
  - with linear dynamics and linear observations: f(a + b) = f(a) + f(b)
  - both subject to Gaussian noise
- KFM is the simplest continuous DBN
  - a continuous state variable with linear-Gaussian dynamics and measurements

## All Roads Lead From Gauss 1809



"... since all our measurements and observations are nothing more than approximations to the truth, the same must be true of all calculations resting upon them, and the highest aim of all computations made concerning concrete phenomenon must be to approximate, as nearly as practicable, to the truth. But this can be

- accomplished in no other way than by suitable combination of more
- observations than the number absolutely requisite for the determination of
- the unknown quantities. This problem can only be properly undertaken
- when an approximate knowledge of the orbit has been already attained,
- which is afterwards to be corrected so as to satisfy all the observations
- in the most accurate manner possible."
- •
- From Theory of the Motion of the Heavenly Bodies Moving about the Sun in Conic Sections, Gauss, 1809

•

#### What does a Kalman filter do ?

• The Kalman filter propagates the conditional density in time.



# How does it do it ?

- The Kalman filter iterates between two steps
   Time Update (Predict)
  - Project current state and covariance forward to the next time step, that is, compute the next a priori estimates.
  - Measurement Update (Correct)
    - Update the a priori quantities using noisy measurements, that is, compute the a posteriori estimates.

$$\hat{y}_k = \hat{y}_k^- + K_k \left( x_k - M_k \hat{x}_k^- \right)$$

• Choose  $K_k$  to minimize error covariance

You can ask questions and think about questions you can not otherwise.

- Circle of confusion
- Turtle speed at night
- Are there modes, or "behavioural states" in their behaviour.

#### **Random Effect Model**



#### Weights in Canadian waters



Nesting female morphometrics: St. Croix, U.S.V.I. Boulon et al. 1996. Chelonian Conserv, Biol. 2:141-147. Lines fit by constant slope analysis of covariance after log transformation.

Turtles are 33% heavier in Canadian coastal areas versus on the nesting beach



Male leatherback movements

- not previously described
- annual migratory cycle that includes movement between temperate foraging areas and tropical breeding areas

James, Eckert and Myers Marine Biology (*in press*)








### A Switching SSM

# Switching model, estimates switches b/w 2 behavioural states





Year

Lewison et al. 2004 Ecology Letters







Swordfishing fleet at anchor, Neils Harbour, Cape Breton. -13.

#### Mike James Andrea Ottensmeyer



### Identification of high-use areas and threats to leatherback sea turtles in northern waters

James, Ottensmeyer and Myers Ecology Letters (2005)



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tience as some line got fouled in the rapid hauling, or an obstreperous fellow in the depths below made off with the best part of a valuable line. To an unsophisticated observer our crew, | leave you in the lurch when the prize is almost

Fish, like women, are a very uncertain institution, and their tastes are equally unaccountable. When you least expect it, off they sail and



GAFFING A SHARK.

within your grasp; at least such has proved my sailor's experience with them. Thus it was that, while we were merrily hauling up the denizens of Whale Deep, the supply suddenly gave out-either our bait had cloyed on their palates, or, what is quite as likely, they began to smell a submarine rat, and regarded the sudden upward movement of their companions with wellgrounded suspicion. As if by simultaneous agreement they suddenly ceased to bite, and after wooing them in vain for a couple of days, we resolved to weigh and head for the northward.



### Questions?

- What are the fundamental changes in a community that occur after the apex predators are removed?
- Have lower trophic levels responded?
- How can we carry our a meta-analysis in different communities that may not be independent?

## Major shrimp stocks in the North Atlantic



# Cod and shrimp biomass in the North Atlantic:



Year



Worm and Myers, Ecology 2003

Shrimp biomass (Thousand tonnes)

## Step 2: Random-effects metaanalysis













#### There is much less than 10% of cod left -



Fitting a simple model to crazy data can yield reliable, and very powerful conclusions



#### Newspaper reports of sharks in Croatia

# With training, "experts" can ignore the most obvious of data:

- 1872 Man's head and leg and dolphin in stomach
- 1872 8 Great White Sharks reported caught
- 1888 Woman's body and lamb in stomach
- 1894 Preserved at Zagreb Nat. Hist. Mus.
- 1926 Woman's shoes, laundry in stomach
- 1946 Pig of 10 kg in stomach
- 1950 Encounter during eating a dead calf
- 1954 Attack on boat
- 1975+ -No sightings.

Newspaper reports of sharks in Croatia





#### Community Changes on St. Pierre Bank

Myers and Worm 2003 Nature



#### Spatial Loss of Cod History

TRAC

W MALEN MALEN



FIG. 21.—Recaptures to October, 1934, of cod tagged in the Jeddore Rock to Egg Island area, N.S., in May, 1934.



FIG. 18.—Recaptures in May to October, 1934, 1935, 1936 and 1937, of cod tagged near Halifax in June, 1934.



FIG. 15.—Recaptures during "summers" of 1927, 1928, 1929 and 1930 of cod tagged off Shelburne, N.S., during September and the first day of October, 1926.

## Identification of high-use areas and threats to leatherback sea turtles in northern waters

James, Ottensmeyer and Myers Ecology Letters (2005)





#### Global changes in species diversity

joint work with Boris Worm Dalhousie University