Environmental stochasticity in ecology and evolution

Easton R White

QE Proposal

1 Dec 2016

Outline

- How I got here
- Background on environmental stochasticity
- Ch. 1: Role of seasonality in ecology
- Ch. 2: Evolution of phenology
- Ch. 3: Designing marine protected areas under uncertainty
- Ch. 4: Sea star wasting disease
- Timeline

RESEARCH | OPEN ACCESS

Modeling the population dynamics of lemon sharks

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The role of spatial structure and landscape heterogeneity in driving local extinctions

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Contributed Paper

Shifting elasmobranch community assemblage at Cocos Island—an isolated marine protected area

Easton R. White,* § Mark C. Myers,† Joanna Mills Flemming,‡ and Julia K. Baum*

*Department of Biology, University of Victoria, P.O. Box 1700 STN CSC, Victoria, BC, V8W 2Y2, Canada
†Department of Biology, University of Northern Iowa, 144 McCollum Science Hall, Cedar Falls, IA, 50614-0421, U.S.A.
‡Department of Mathematics and Statistics, Dalhousie University, 6316 Coburg Road, P.O. Box 15000, Halifax, NS, B3H 4R2, Canada

Ch 0: Environmental stochasticity

- Ubiquitous in natural systems
- Definitions
- Why it matters
- Past modeling work
- Lewontin and Cohen
- Climate change moving forward

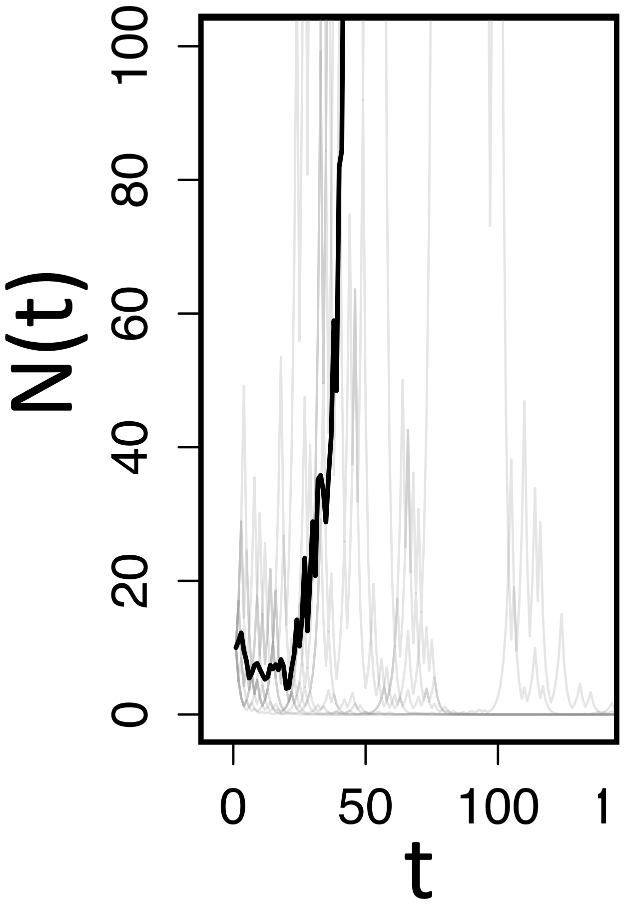
Environmental stochasticity

- Definition: environmental stochasticity would include dynamic abiotic or biotic factors that may affect many individuals of that population similarly (Lande et al. 2003)
- May include factors like temperature, precipitation, snowfall, pathogens, resource pulses, other species, or human activity (Boyce et al. 2006, Yang et al. 2008, Smith et al. 2011, Lawson et al. 2015)

Lewontin and Cohen (1969)

N (t+1) = R(t)N (t)

$$R(t) = \begin{cases} 1.7 \text{ w/ prob } 0.5 \\ 0.5 \text{ w/ prob } 0.5 \end{cases}$$



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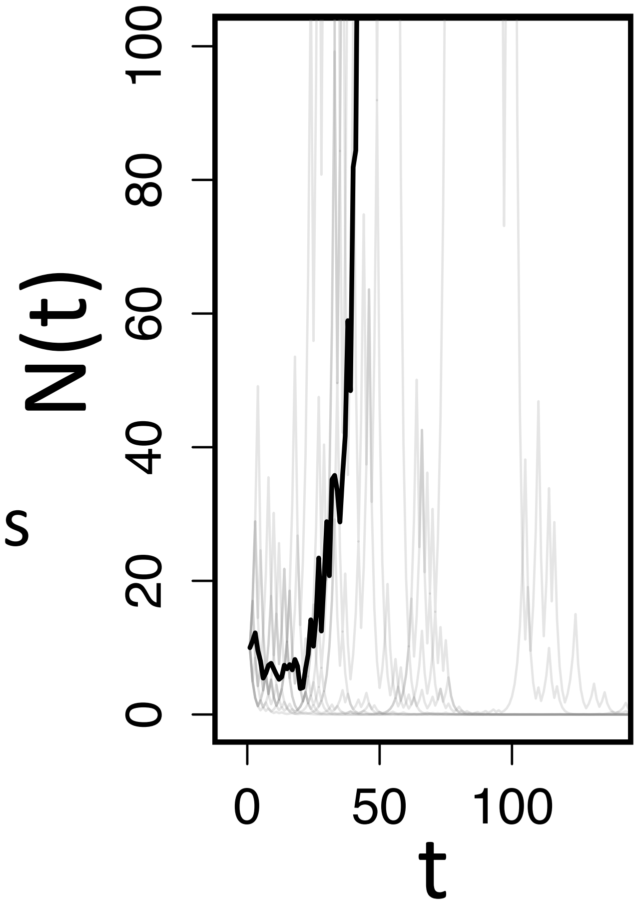
Stochastic growth rate depends on both mean and variance of environmental noise



Environmental stochasticity

- Climate change is expected to increase the variability in several environmental drivers (Vasquez et. al 2015)

- In most cases, environmental stochasticity would be expected to decrease population growth, increasing extinction risk

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Seasonality definition

A form of environmental stochasticity where a variable experiences regular and predictable changes which recur each year

Seasonality definition

A form of environmental stochasticity where a variable experiences regular and predictable changes which reoccur each year

Temperature
Precipitation
Salinity
Wind
Photoperiod
Resource pulses
Upwelling
Human activity

(Fretwell 1972, Altizer et al. 2006, Stevenson et al. 2015)

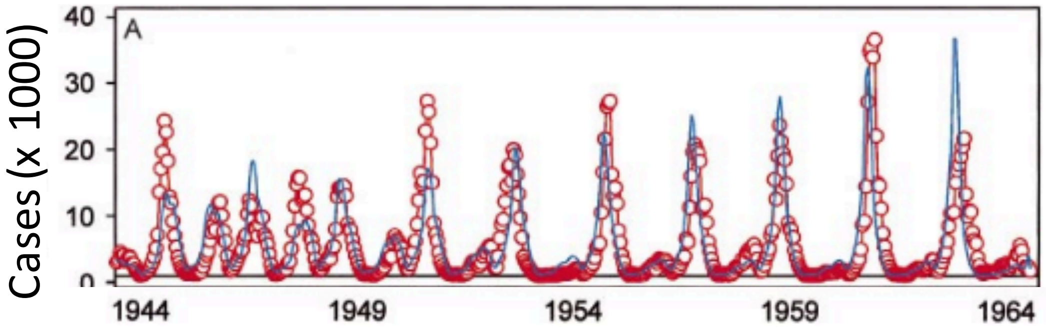
Where has seasonality been overlooked in ecology?

How do modeling results change with the inclusion of seasonal forces?

Where has seasonality been important?

Epidemiology

Measles in the UK



Grenfell et al. 1995

Where has seasonality been important?

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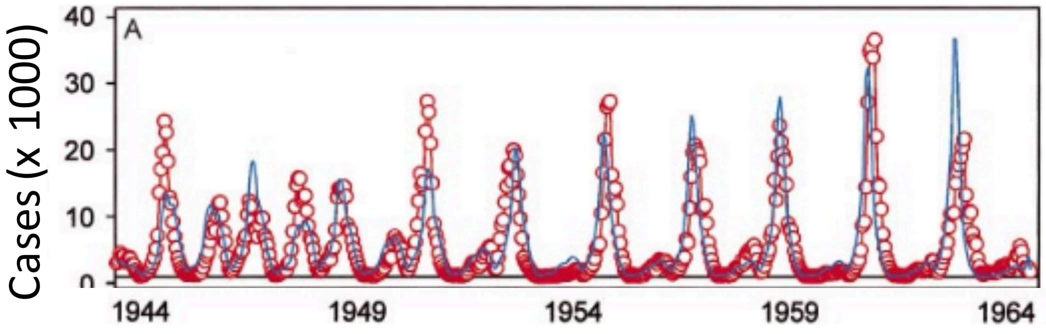


Grenfell et al. 1995

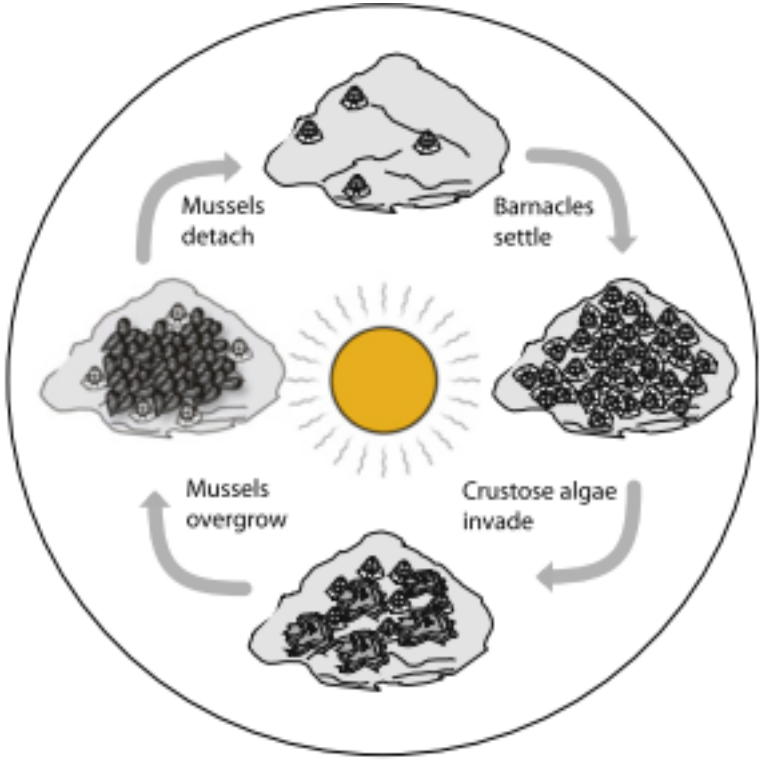
Ecology

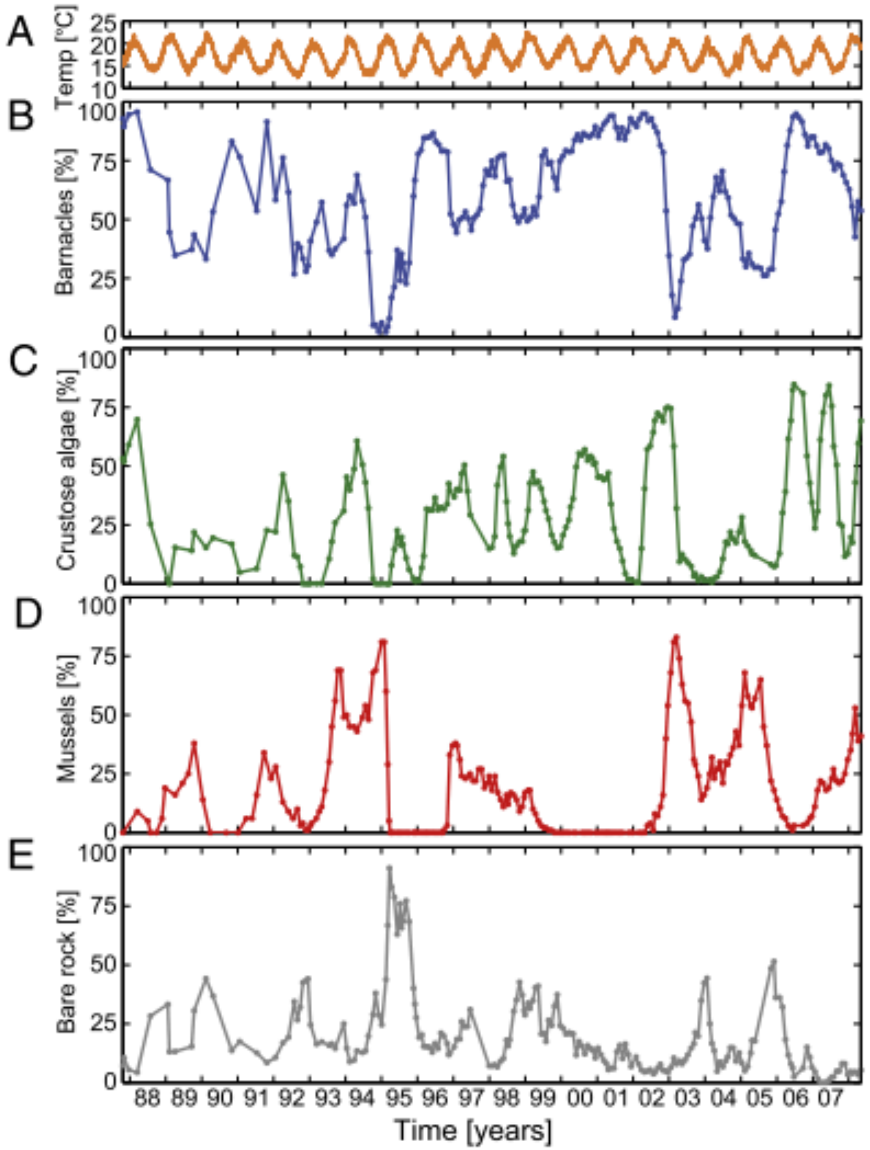
- Phenology (Forrest & Miller Rushing 2010)
- River systems (Power et al. 2008)
- Species interactions (Taylor et al. 2013)
- Animal migration (Shaw & Couzin 2013)
- Food web ecology (McMeans et al. 2015)
- Succession (Beninca et al. 2015)

Modeling seasonality

Modeling approach	Description
Hybrid models	Combines discrete time (between years) and continuous time (within season) models
Impulsive differential equations	Short term perturbations
Numerical methods	Numerical tools can be used to approximate solutions of complicated population models
Periodic matrices	Different transition matrices for each season
Floquet theory	Allows a measurement of invasion rates in strictly periodic environments (Klausmeier 2008)
Successional state dynamics	Approach to modeling seasonally forced food webs as series of state transitions (Klausmeier 2010)
Nonautonomous system of differential equations	Set of differential equations with external forcings
Individual based models	Simulate dynamics of individuals and examine how this scales up to population or community scales

Where has seasonality been important?

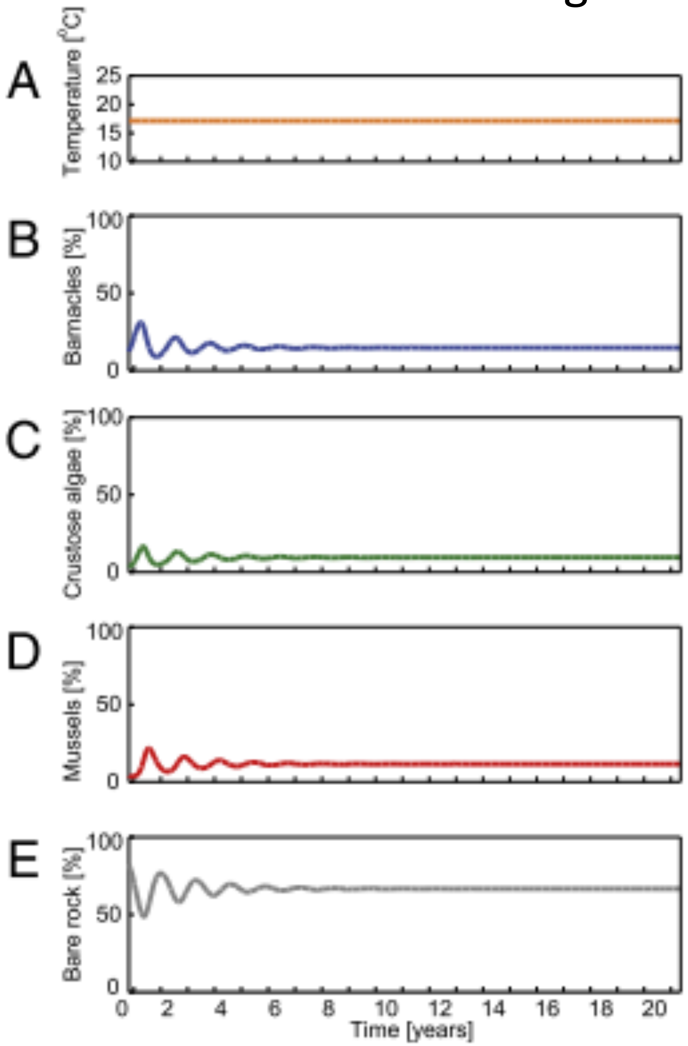




(Beninca et al. 2015)

Basic population models with seasonal forcing terms

No seasonal forcing



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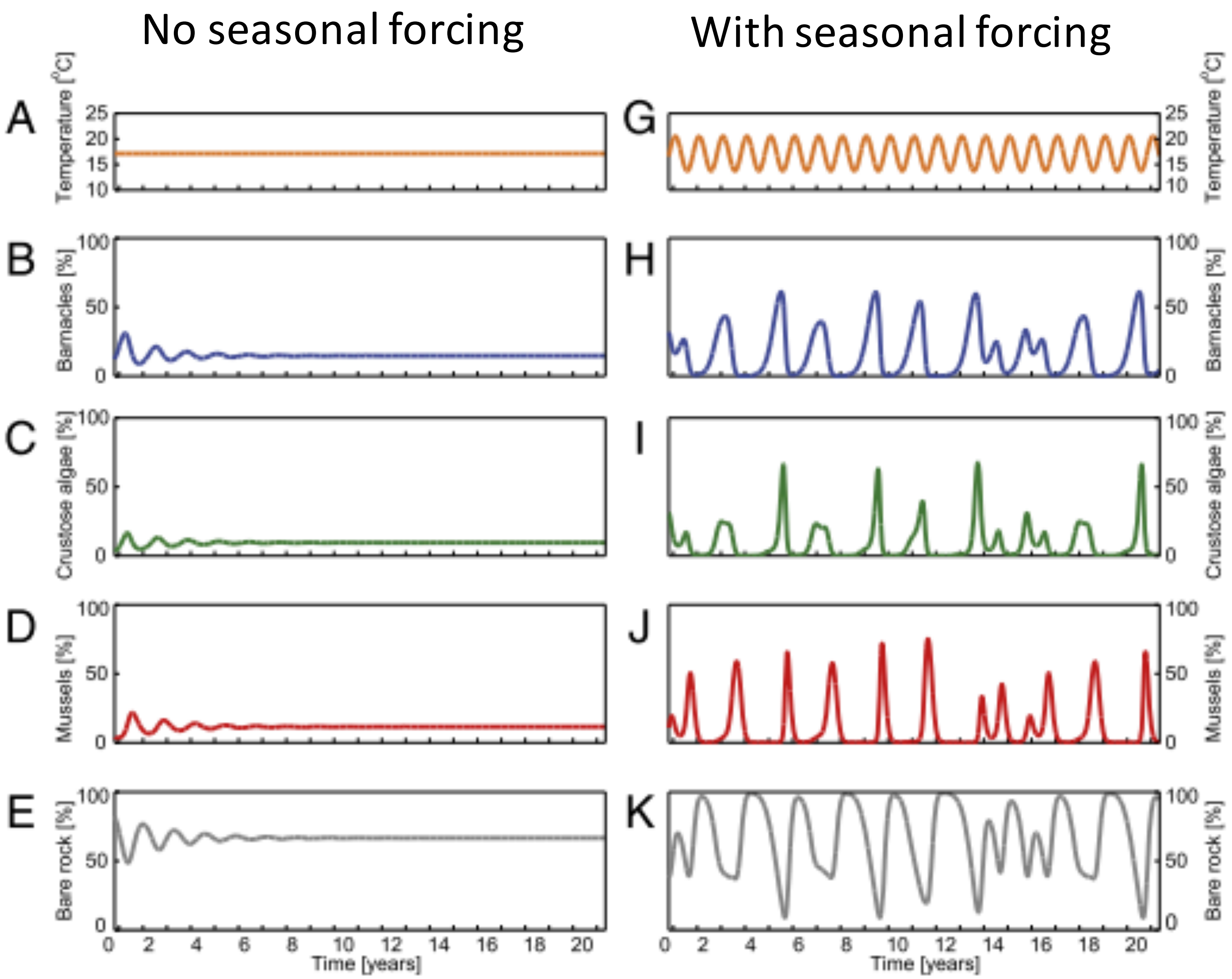
Basic population models with seasonal forcing terms



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Conclusions

- In order to study seasonality, need detailed data across years and several times within each year

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- Mathematical models with seasonality may predict very different dynamics

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- Mathematical models with seasonality may predict very different dynamics

- Seasonality can be the largest source of environmental variability that organisms face in the context of ecological or evolutionary dynamics

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Chapter 2: Evolution of phenology under environmental variability

- Big questions and setup
- Climate change
- Evolutionary dynamics
- Adaptive dynamics
- Pikas
- PIPs then summary figures

Timing of events has changed for many species

- Hibernation timing for ground squirrels in Canada (Reale et al. 2003)
- Migrating birds in Europe (Both, Visser, and others)
- Day of first flowering for many plants (Ibanez et al. 2010)

- Bird–Caterpillar–Plant system in the Netherlands (Both et al. 2009)

What timing of reproduction should evolve for organisms in variable environments?

How will selection pressures on reproductive timing change with climate change?

How is reproductive timing affected by climate change?

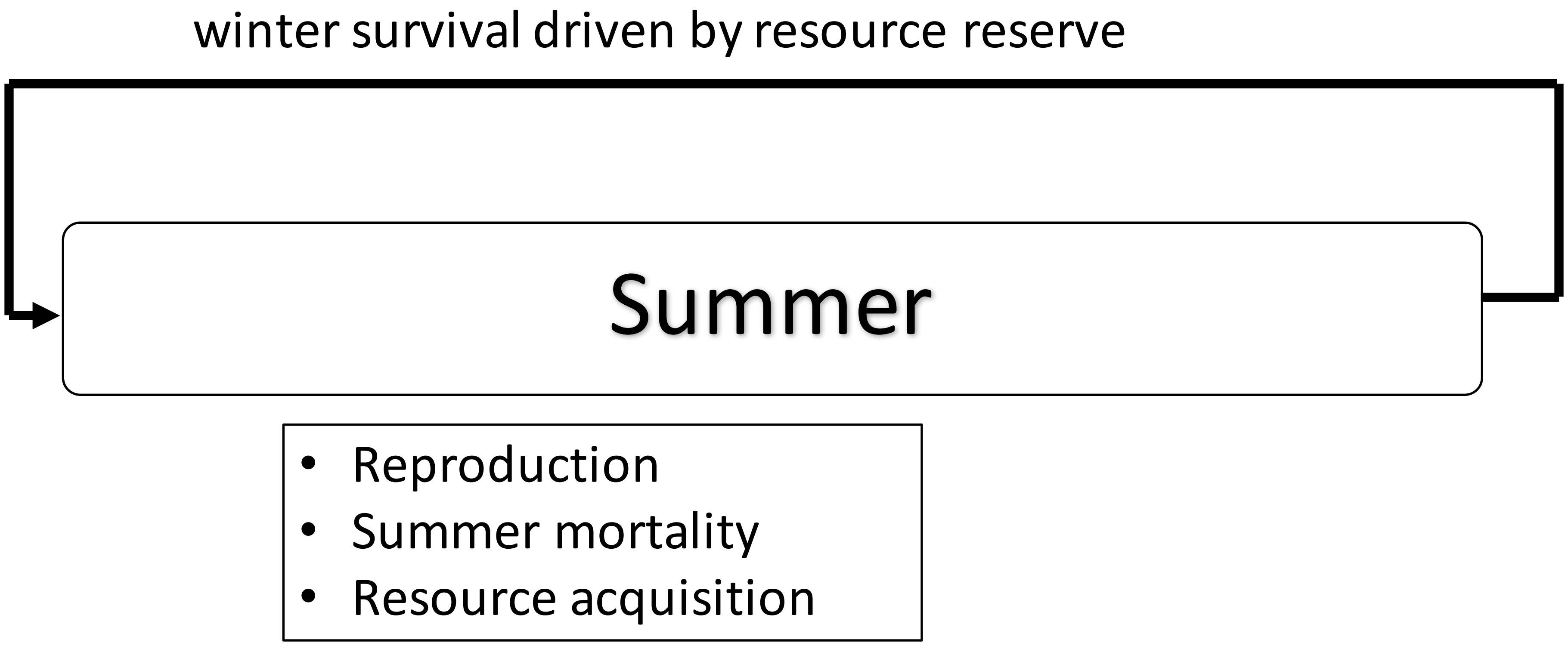
collared pika
(*Ochotona collaris*)

How is reproductive timing affected by climate change?

collared pika
(*Ochotona collaris*)

- Consider them a model species
- Have data available (Franken et al. 2004)
- Possibly threatened by climate change, because of their biology and location

General Model



Within-season dynamics

$$
\begin{array}{lrcl}
\text{Snow depth:} & \frac{d}{dt}E(t) & = & eE(t), \\
\text{Adult density:} & \frac{d}{dt}A(t) & = & -u_A A(t), \\
\text{Juvenile density:} & \frac{d}{dt}J(t) & = & -(u_J + u_E \frac{E(t)}{K+E(t)})J(t), \\
\text{Adult haypile size:} & \frac{d}{dt}B_A(t) & = & w_A \frac{a_A R(t)}{1+a_A h_A R(t)} - \beta_A B_A(t), \\
\text{Juvenile haypile size:} & \frac{d}{dt}B_J(t,\tau) & = & w_J \frac{a_J R(t)}{1+a_J h_J R(t)} - \beta_J B_J(t), \\
\text{Plant biomass:} & \frac{d}{dt}R(t) & = & rR(t)(1 - \frac{R(t)}{K_R}) - A(t)\frac{a_A R(t)}{1+a_A h_A R(t)} - J(t)\frac{a_J R(t)}{1+a_J h_J R(t)}
\end{array}
\quad (1)
$$

Within-season dynamics

Juvenile mortality depends on snow depth

$$
\begin{aligned}
&\text{Snow depth:} && \tfrac{d}{dt}E(t) &&= eE(t), \\
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\end{aligned}
\tag{1}
$$

Birth pulse

$$
\begin{aligned}
\text{Births of juveniles:} \quad & J(\tau) &&= \alpha(E,\tau)A(\tau) \\
\text{Juvenile resource reserve at birth:} \quad & B_J(\tau) &&= 0
\end{aligned}
\tag{2}
$$

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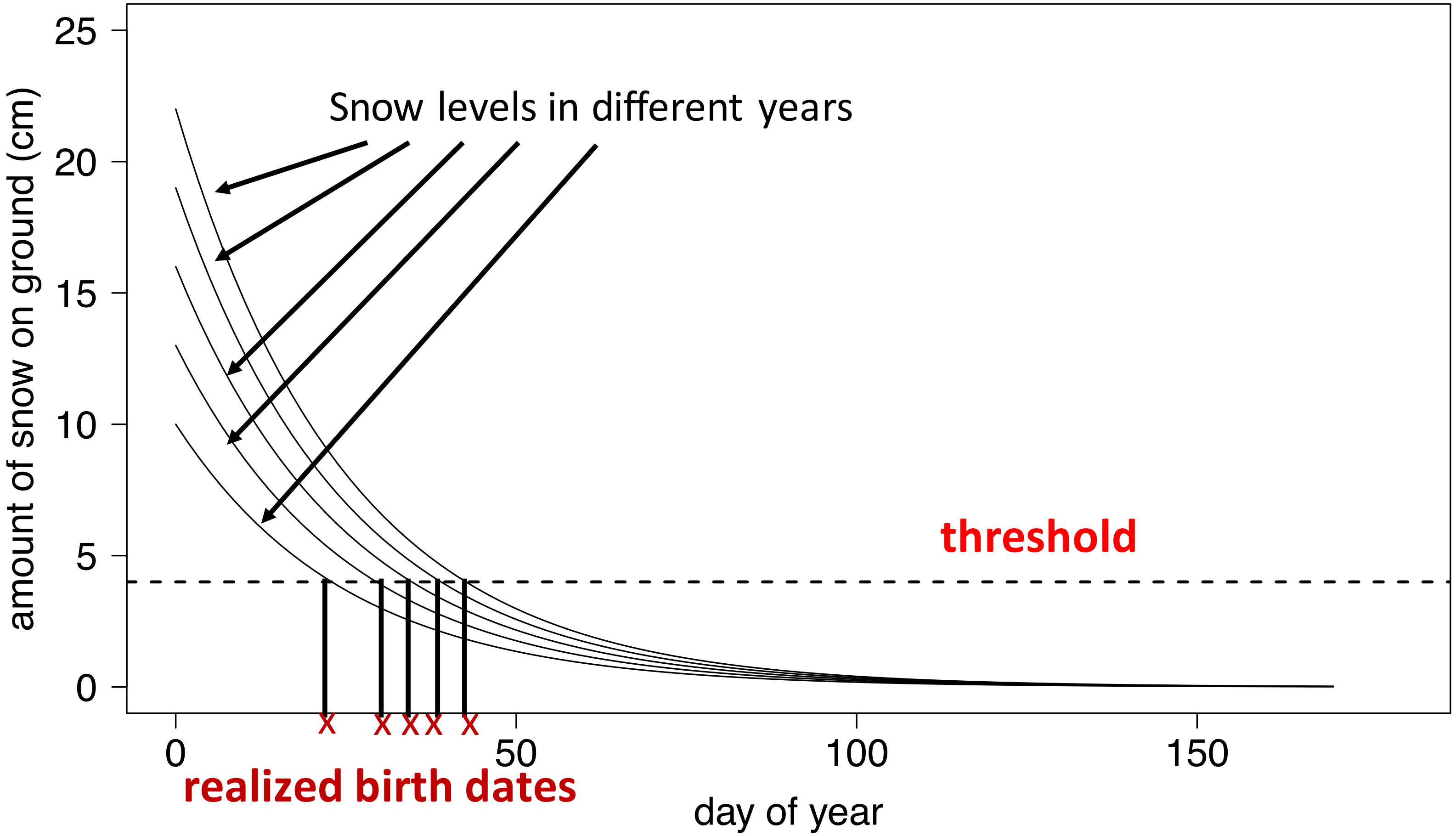
Between-season dynamics

$$\begin{aligned}
\text{Environment initial condition:} \quad & E(0) && \sim \text{random variable,} \\
\text{Adult density initial condition:} \quad & A_{n+1}(0) && = A_n(1)\tfrac{\sigma_A B_A(1)}{k_A + B_A(1)} + J_n(1,\tau)\tfrac{\sigma_J B_J(1)}{k_J + B_J(1)}, \\
\text{Juvenile density initial condition:} \quad & J_{n+1}(0) && = 0, \\
\text{Adult resource reserve initial condition:} \quad & B_A(0) && = 0, \\
\text{Juvenile resource reserve initial condition:} \quad & B_J(0) && = 0, \\
\text{Resource initial condition:} \quad & R(0) && = R^{ini}
\end{aligned} \tag{3}$$

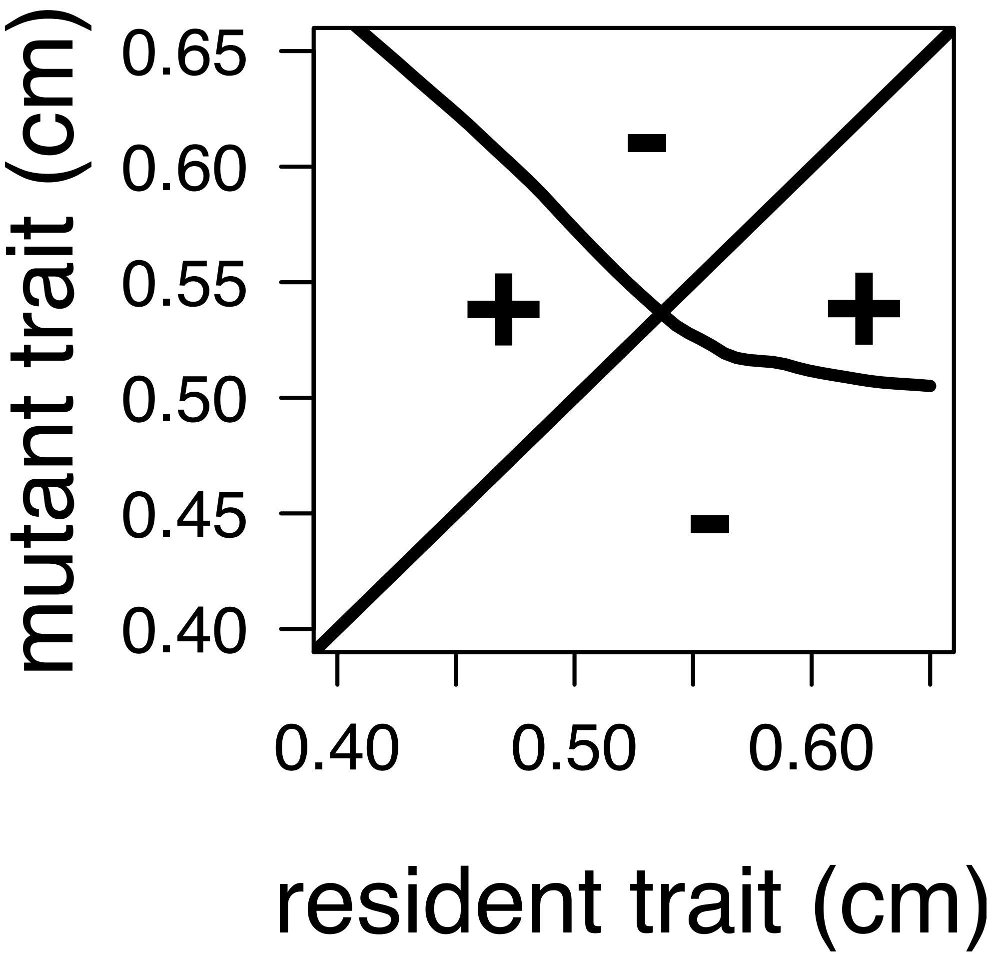
Reproductive timing cue based on snow depth



Adaptive dynamics

- We ignore genetic component (timescale separation between evolutionary and ecological timescales)
- Instead use game theoretical approach, which allows for frequency dependence (Diekman 2004, Brannstrom et al. 2013)

Pairwise invasibility plot



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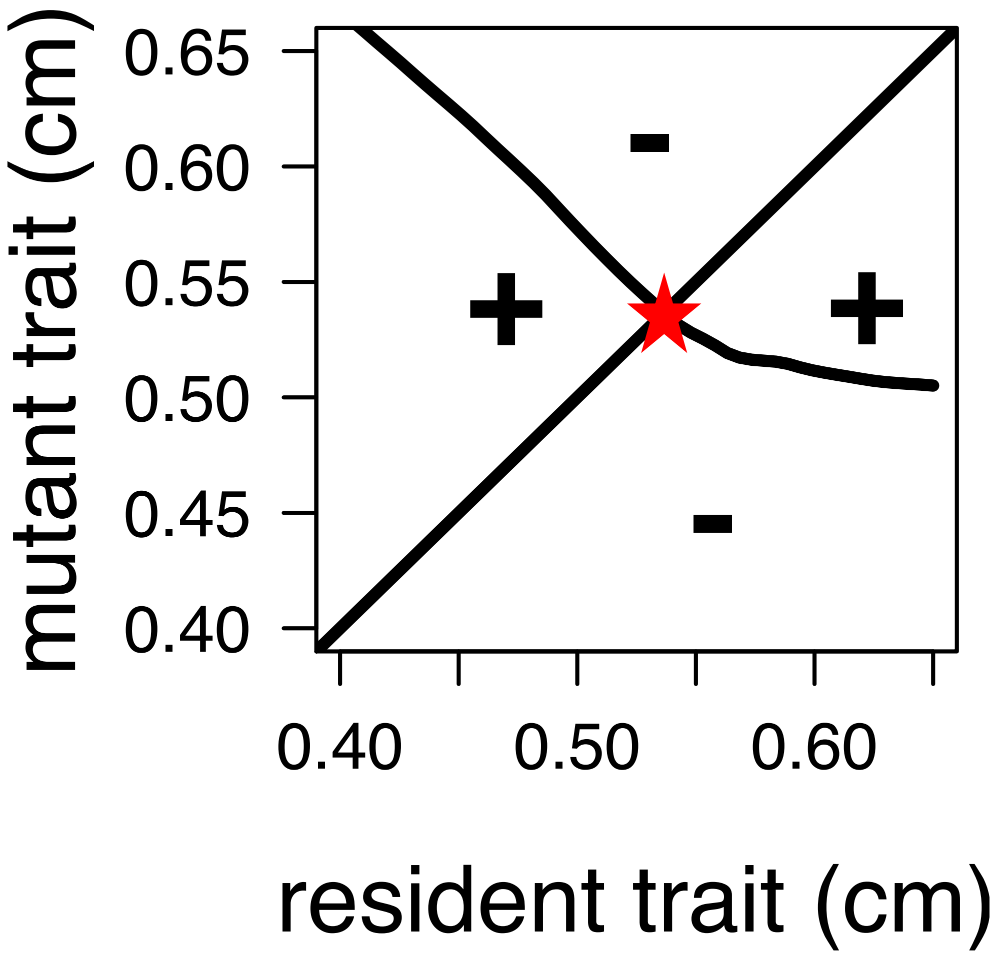
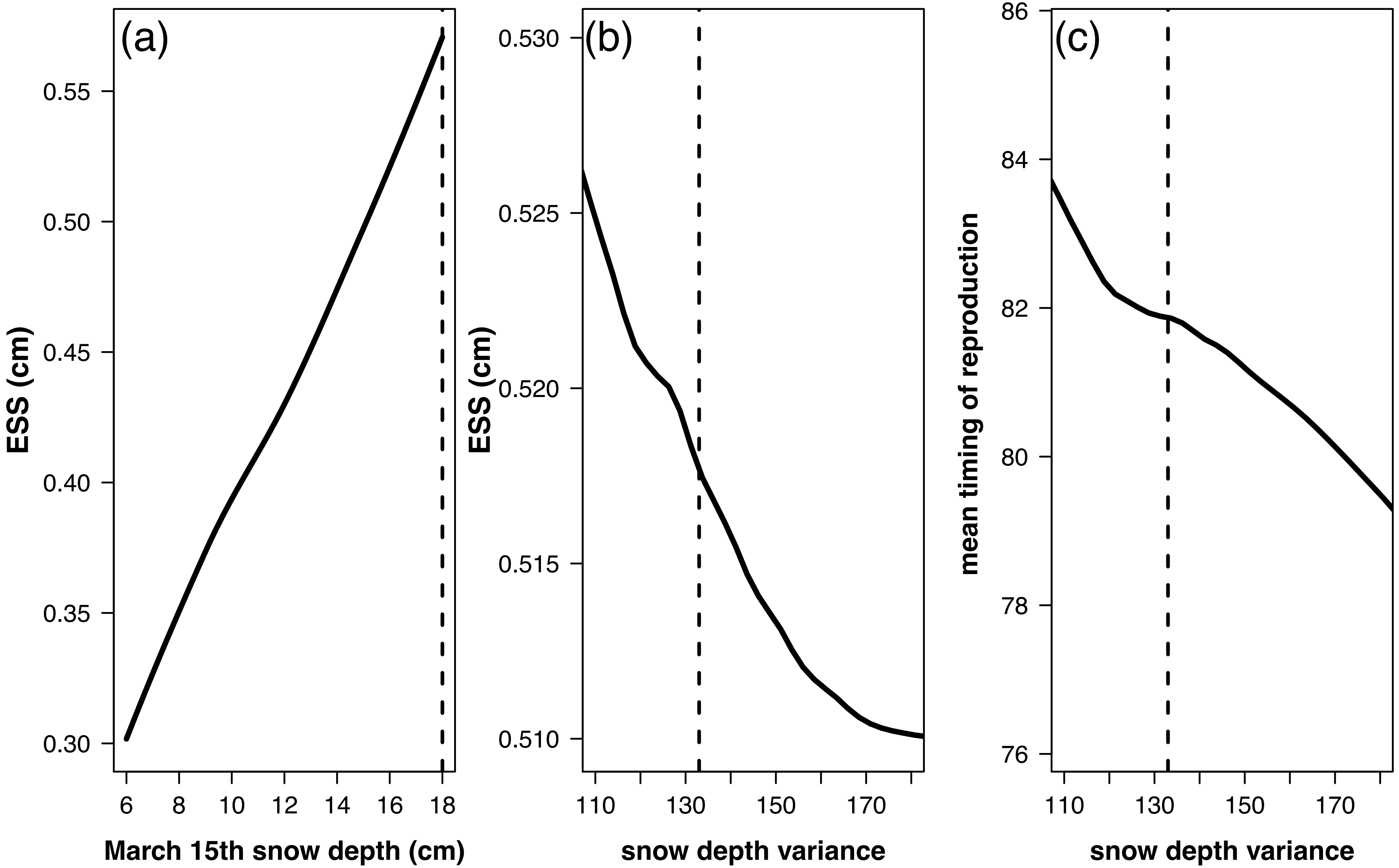


Predicted ESS



Conclusions

- Environmental-based cue was more realistic than timing-cue
- Earlier spring timing predicts advancement of reproductive timing, but increased variability in spring timing selects for later reproductive timing (depends on model conditions)
- Including environmental stochasticity can reverse model predictions

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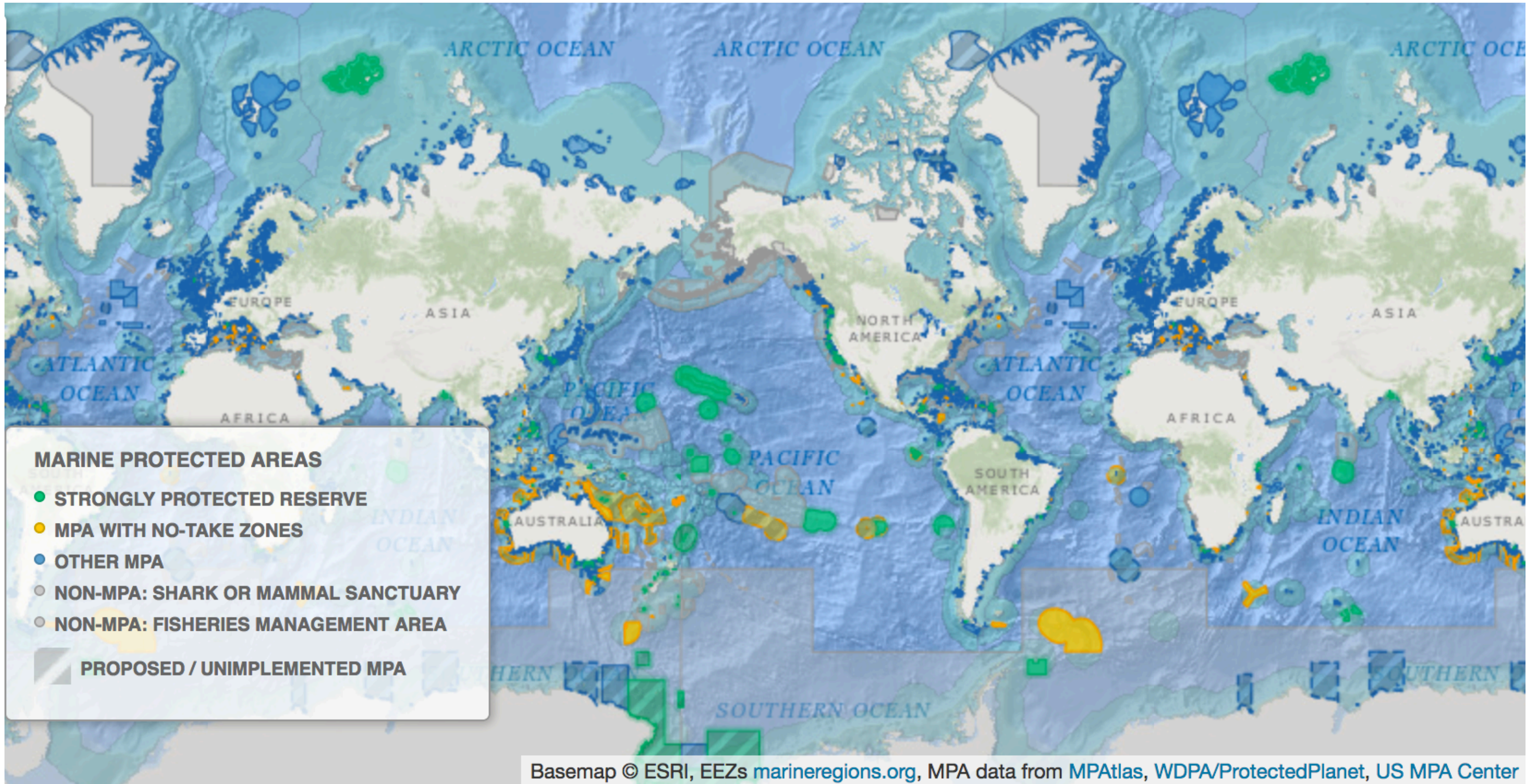
Chapter 3: Designing marine reserves for resilience to extreme events

- Introductin
- Big questions here
- Theoretical approaches
- Empirical examples
- Future directions

MPA history and motivation

- Proliferation of MPAs in past few decades as ecosystem-based management (Lester et al. 2009, Edgar et al. 2014)



MPA history and motivation

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- A lot of past work on spacing and size guidelines (Botsford et al. 2001, Hastings & Botsford 2003, Hastings & Botsford 2006, Baskett et al. 2007, White & Rogers-Bennett 2010, White et al. 2010, Brown et al. 2015)

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- Various approaches to design MPAs in Australia, California, and elsewhere (Brown et al. 2015)

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- Various approaches to design MPAs in Australia, California, and elsewhere (Brown et al. 2015)
  - Static approach (e.g. MARXAN) – not worried about persistence
  - Dynamic (often bio economic) approaches – examine connectivity and persistence (White et al. 2014)

MPA objectives

- Need to be very clear about objectives of MPAs
- What should we maximize?
  - Resilience
  - Robustness
  - Harvesting
  - Biodiversity

Uncertainty in MPA design

- Recruitment and dispersal are both highly variable (White & Rogers-Bennett 2010, Williams & Hastings 2013)
- Rare events (often driven by anthropogenic factors) are hard to predict

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  - Including catastrophes (Allison et al. 2003, Wagner et al. 2007, McGilliard et al. 2011)

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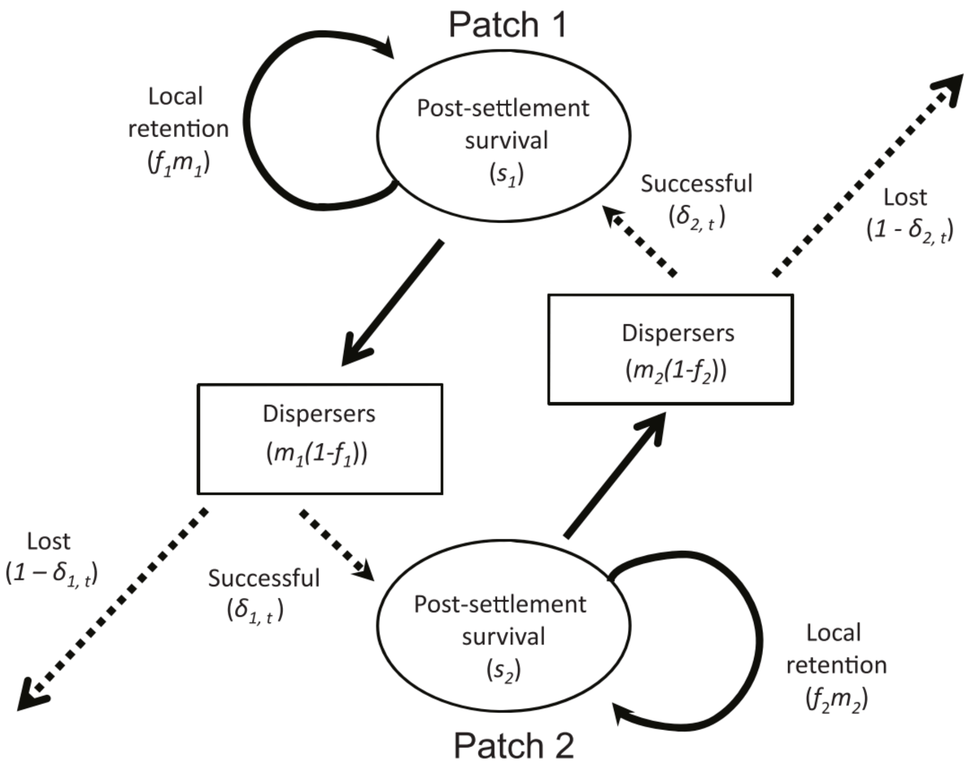
- Including uncertainty can change management recommendations (Cabrel et al. 2016)
- Adaptive management may be best strategy

How do we design MPAs given high levels of uncertainty?

How does the frequency and magnitude of rare events affect the design of MPAs?

Theoretical approach

- Discrete time, spatially explicit, and probably age/size structured (citations)

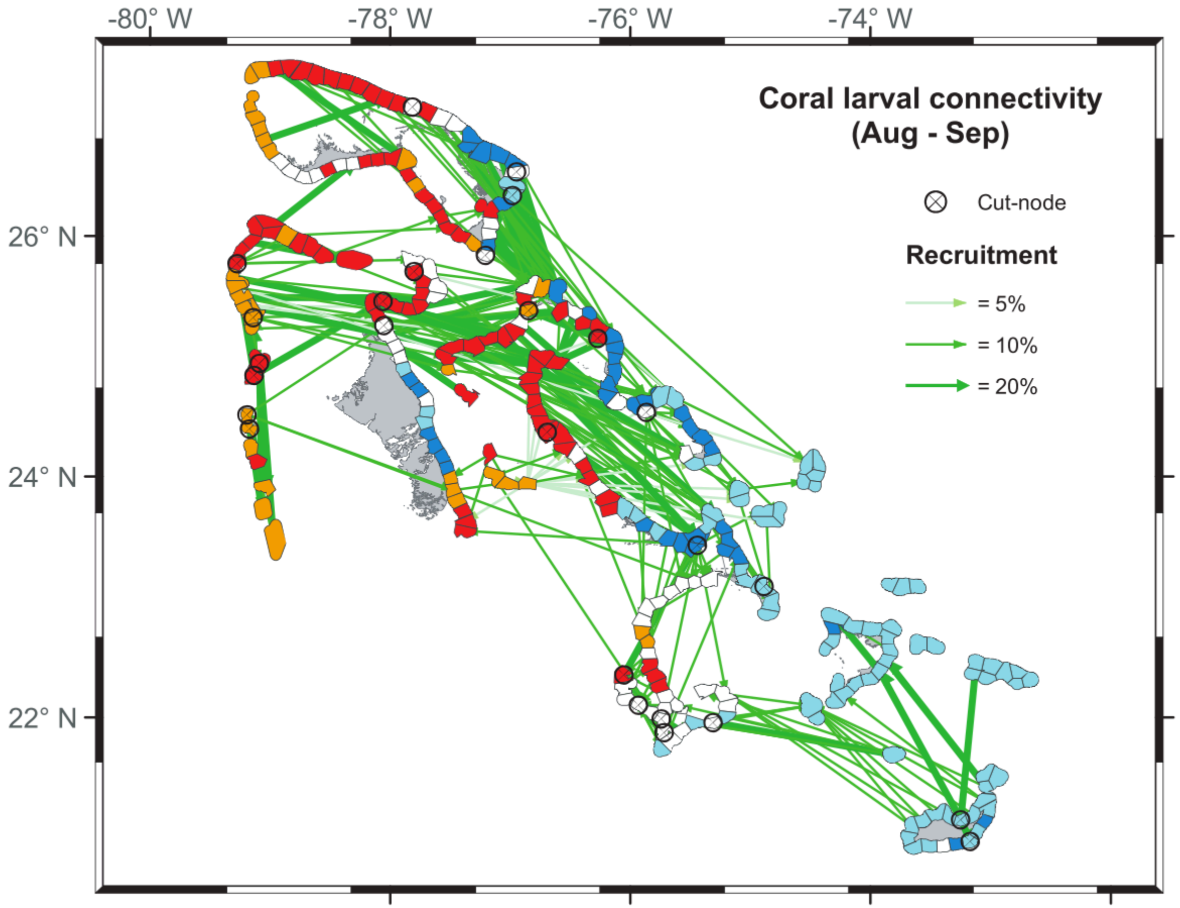


Potential empirical examples

- Coral reefs in the Caribbean
- Fishery dynamics off of California

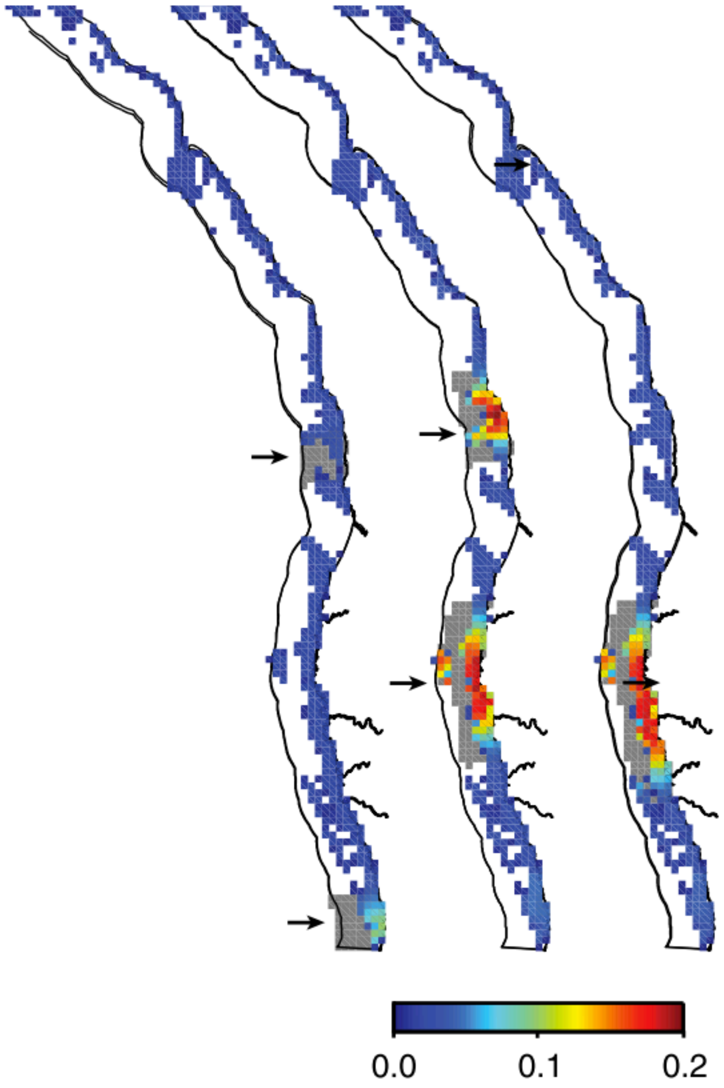
Coral reef example

- Past work has examined MPA design in static (MARXAN framework, Mumby et al. 2011)
- Need to account for environmental variability (hurricanes, bleaching)



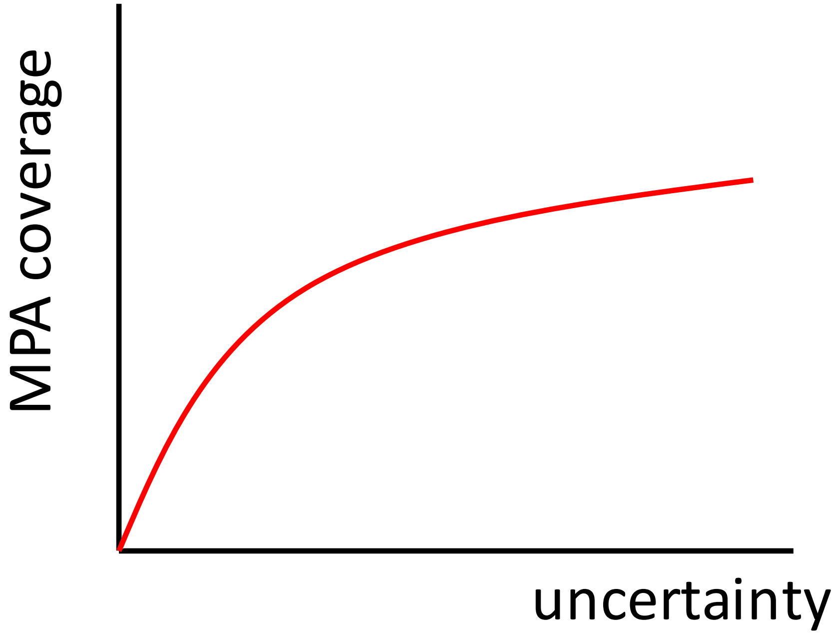
California fishery example

- California MPA system (White et al. 2010, 2013, Botsford et al. 2014)
- Should account for variability in recruitment and dispersal (especially in unusual conditions, like El Nino)



Possible results

- Including environmental stochasticity into models of MPA design will produce different results than those that ignore this uncertainty



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- Models will likely result in more area need in MPAs and more closely spaced
- Multiple sets of disturbances may interact with one another

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- Models will likely result in more area need in MPAs and more closely spaced
- Multiple sets of disturbances may interact with one another

- High levels of uncertainty may require that you use adaptive management strategy

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Chapter 4: Modeling sea star wasting disease

- Introduction
- Big questions here
- Simple model
- Potential results
- Future directions

Disease, conservation biology, and climate change

- Disease risk is not usually incorporated into conservation biology (Lafferty & Gerber 2002)
  - Can dramatically decrease population size and have community-level effects
  - E.g. Caribbean urchin *Diadema antillarum in 1983*

- Climate change is expected to have a number of effects on disease risk:
  - Pathogen growth and reproduction (Harvell et al. 2002 Harvell et al. 2009)
  - Host susceptibility
  - Species interactions

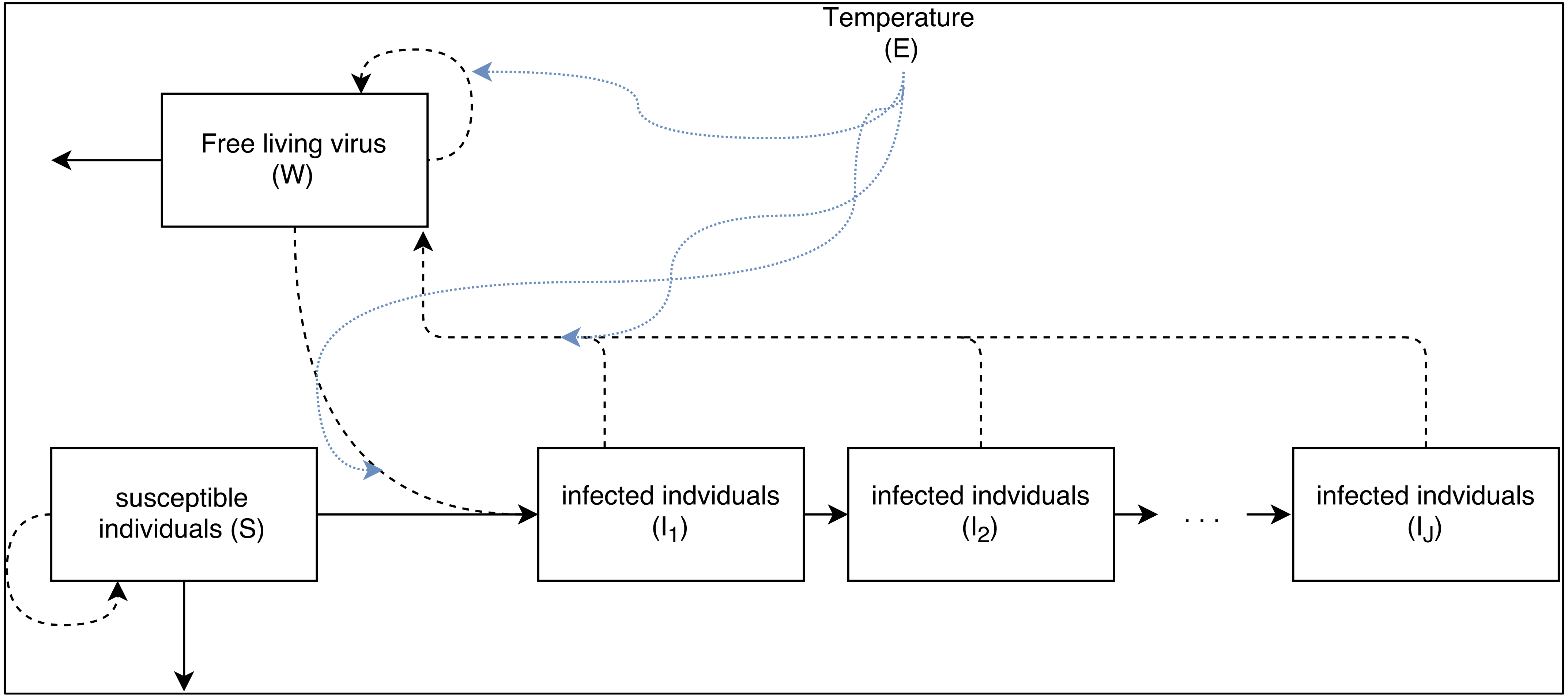
Sea star wasting disease

- Outbreak first noticed in summer of 2013, which was unusually warm in many places
- Affects over 20 species of sea stars
- Longterm data available from MARINe program (UCSC)
- Caused by a virus (Hewson et al. 2014)
- Larger stars showed disease signs sooner than juveniles, but diseased juveniles died more quickly

Is the disease spatially spread, environmentally-triggered, or both?

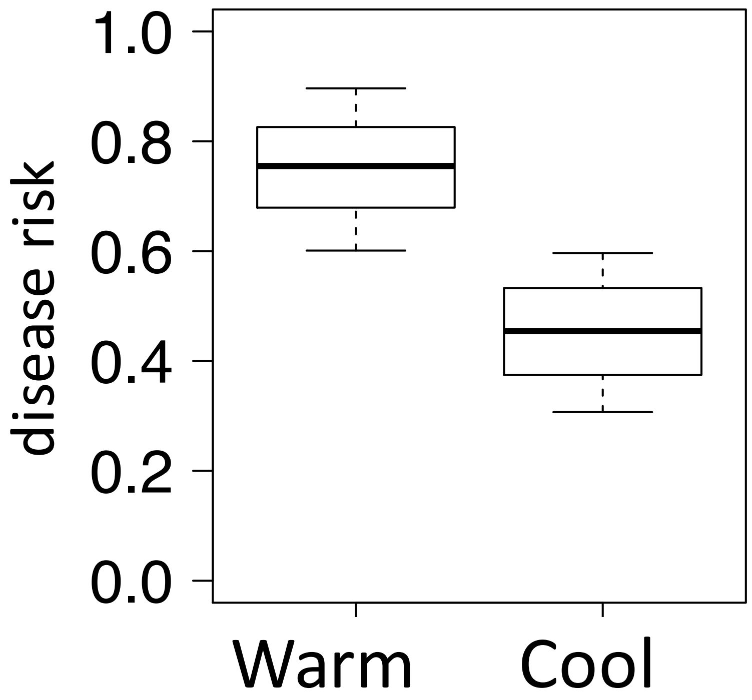
What management actions may be appropriate?

Proposed modeling framework



Possible results

- High densities or warming may promote disease outbreaks



Possible results

- High densities or warming may promote disease outbreaks
- If the disease is environmentally-triggered, we could use temperature to predict future outbreaks (Maynard et al. 2016)

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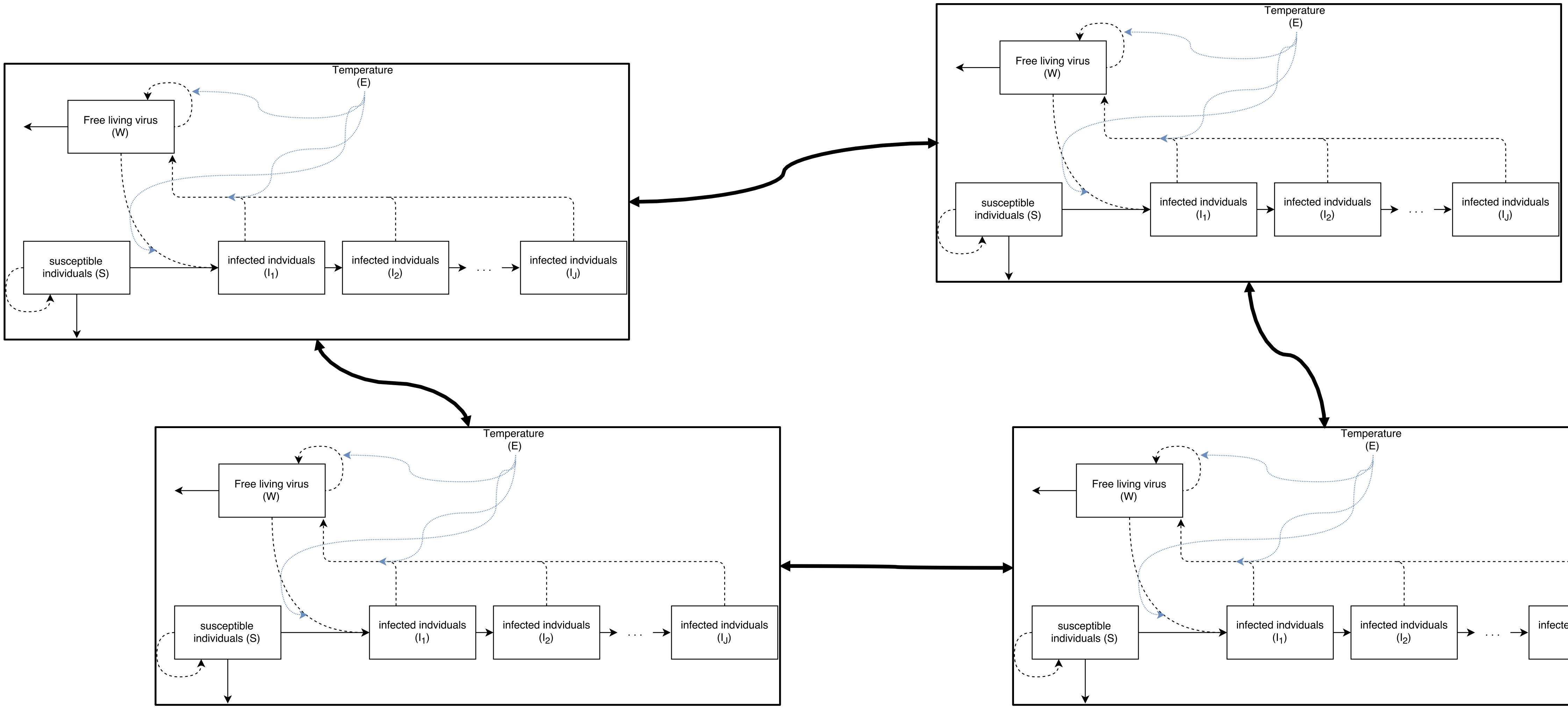
- High densities or warming may promote disease outbreaks
- If the disease is environmentally-triggered, we could use temperature to predict future outbreaks (Maynard et al. 2016)
- Culling in spatial framework may be appropriate

Spatial modeling (Sokolow et al. 2009)



Broader implications

- Including environmental stochasticity into models can alter, or even reverse, predictions of deterministic models
- Environmental stochasticity, or uncertainty more generally, needs to be taken into account by managers and conservation biologists
- Adaptive management may be only way forward given large levels of uncertainty

My timeline

Names	Spring 2016	Summer 2016	Fall 2016	Winter 2017	Spring 2017	Summer 2017	2017-2018	Summer 2018
Chapter 1	Lit Review and Writing		Finish Writing					
Chapter 2	Lit Review and Writing	At IIASA	Finish Writing					
Chapter 3			Lit Review	Collect Data	Modeling	Modeling	Analysis and Writing	Defend
Chapter 4			Lit Review			Data and modeling	Analysis and Writing	Defend

Additional slides

General phenology model

$$
\begin{array}{llcl}
\text{Environment:} & \frac{d}{dt}E(t) & = & h(E(t)), \\
\text{Adult abundance:} & \frac{d}{dt}A(t) & = & -A(t)u_A(A(t)), \\
\text{Juvenile abundance:} & \frac{d}{dt}J(t,\tau) & = & -J(t,\tau)u_J(E(t),\hat{J}(t)), \\
\text{Non-mature juvenile abundance:} & \frac{d}{dt}J^i(t) & = & -J^i(t)u_J^i(E(t),\hat{J}(t)), \\
\text{Adult resource reserve:} & \frac{d}{dt}B_A(t) & = & f_A(c_A(R(t)),B_A(t)) - \delta(B_A(t),s(t,E(t))) \\
 & & & -g_A(B_A(t)), \\
\text{Juvenile resource reserve:} & \frac{d}{dt}B_J(t,\tau) & = & f_J(c_J(R(t)),B_J(t,\tau)) - g_J(B_J(t,\tau)), \\
\text{Non-mature juvenile resource reserve:} & \frac{d}{dt}B_J^i(t) & = & f_J^i(c_J(R(t)),B_J^i(t)) - g_J(B_J^i(t)), \\
\text{Resource level:} & \frac{d}{dt}R(t) & = & k(R(t)) - A(t)c_A(R(t)) - \hat{J}(t)c_J(R(t))
\end{array}
\tag{1}
$$

$$
\begin{array}{llcl}
\text{Births of juveniles:} & J(\tau,\tau) & = & A(\tau)\alpha(s(\tau,E(\tau))), \\
\text{Juvenile resource reserve at birth:} & B_J(\tau,\tau) & = & B_J^{ini}(B_A(\tau))
\end{array}
\tag{2}
$$

General phenology model

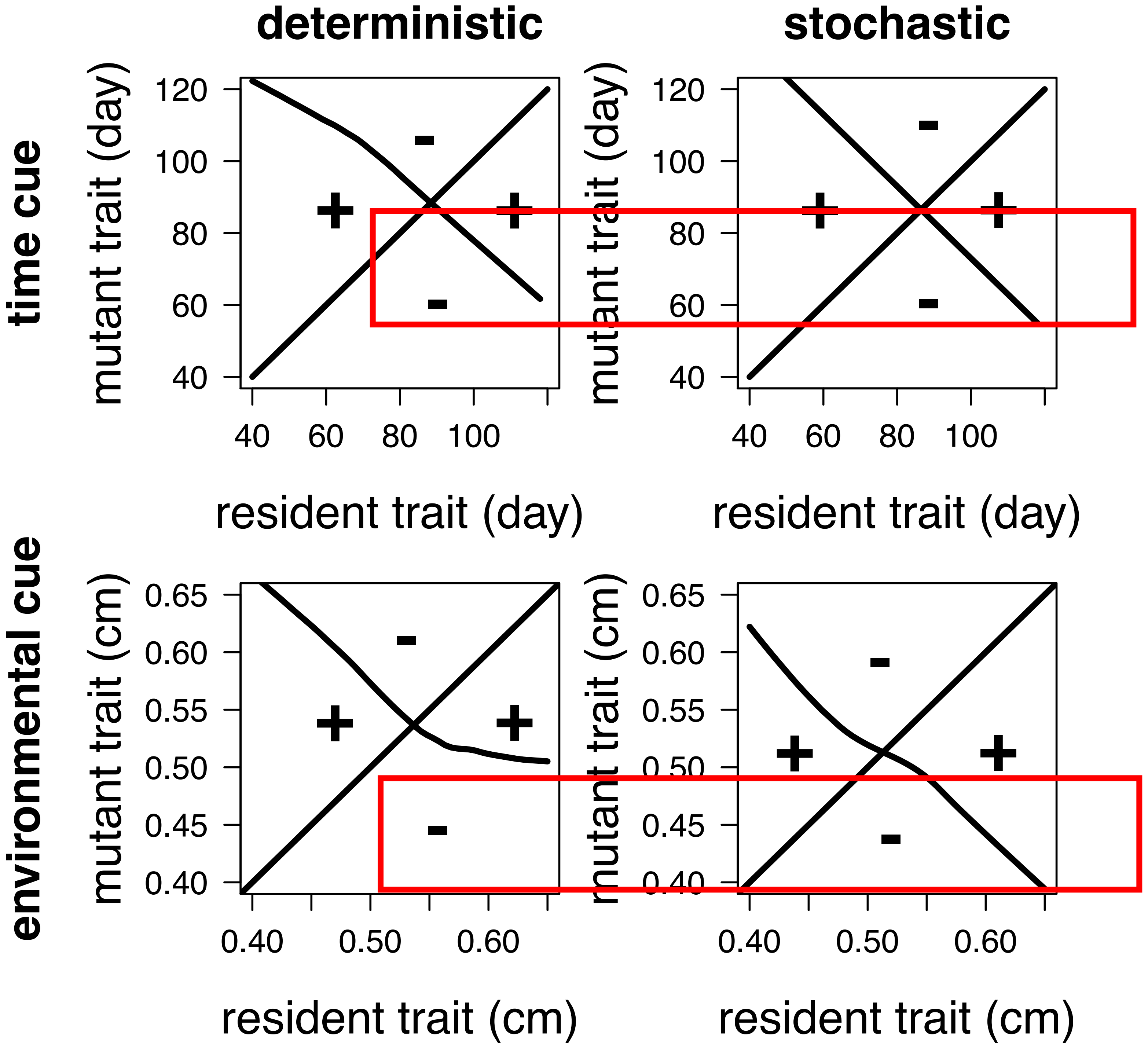
$$
\begin{array}{llcl}
\text{Environment:} & E(0) & \sim & \text{random variable,} \\
\text{Adult abundance:} & A_{n+1}(0) & = & l_A(B_A(1), A_n(1))A_n(1) \\
 & & & + \int_0^1 m l_J(B_J(1,\tau), J_n(1,\tau))J_n(1,\tau)d\tau \\
 & & & + \sum_{i=1}^{N} m l_J^i(B_J^i(1), J_n^i(1))J_n^i(1) \\
\text{Non-mature juvenile abundance:} & J_{n+1}^1(0) & = & \int_0^1 (1-m) l_J(B_J(1,\tau), J_n(1,\tau))d\tau, \text{when } i = 0, \\
\text{Non-mature juvenile abundance:} & J_{n+1}^{i+1}(0) & = & (1-m) l_J^i(B_J^i(1), J_n^i(1))J_n^i(1), \text{when } i > 0,\ i < N, \\
\text{Adult resource reserve:} & B_A(0) & = & B_A^{ini}, \\
\text{Non-mature juvenile resource reserve:} & B_J^i(0) & = & B_J^{i,ini}, \\
\text{Resource:} & R(0) & = & R^{ini}
\end{array}
\tag{3}
$$

Pika model parameters

Notation	Parameter	Units	Estimate	Reference
e	decay parameter for snow depth	1/time	-0.04	Environment Canada
$E[0]$	average snow depth on March 15th	cm	18.00	Environment Canada
σ_E	standard deviation of snow depth on March 15th	none	12.00	Environment Canada
u_A	adult mortality rate	1/time	-0.001	Smith (1978), Supp. Mat.
u_J	summer mortality rate of juveniles with no snow present	1/time	-0.01	Supp. Mat.
u_E	maximum summer mortality rate of juveniles with snow present	1/time	-0.50	Supp. Mat.
K	half-saturation constant for $E[t]/(K+E[t])$	cm	15.00	Supp. Mat.
w_J	conversion of resources into resource reserve	reserve/(grams consumed)	0.33	Smith and Ivins (1984)
β_J	decay of body condition	1/time	-0.001	Dearing (1997)
w_A	conversion of resources into resource reserve	reserve/(grams consumed)	0.33	Smith and Ivins (1984)
β_A	decay of body condition (change in haypile size without renewal)	1/time	-0.001	Dearing (1997)
r	intrinsic rate of growth	1/time	0.044	McIntire and Hik (2005)
K_R	carrying capacity per meter squared	grams	150.00	McIntire and Hik (2005)
a_A	per capita adult attack rate	area/time	1.50	Supp. Mat.
a_J	per capita juvenile attack rate	area/time	1.50	Supp. Mat.
σ_A	max adult over winter survival	none	0.90	COSEWIC (2011)
K_A	half saturation constant for adult over winter survival	reserve	2500.00	Morrison et al. (2009)
σ_J	max juvenile over winter survival and maturation probability	none	0.90	COSEWIC (2011)
K_J	half saturation constant for juvenile over winter survival and maturation probability	reserve	2500.00	Morrison et al. (2009)
$s(t)$	number of offspring per year	# female offspring/female	1.50	Smith and Weston (1990)

Table 1: Default model parameters derived from literature or calculated in the supplementary material for the Collared pika (*Ochotona collaris*) population at Ruby Ridge, Yukon, Canada.

Comparing cues and deterministic vs stochastic scenarios



MPA additional material

Sea star wasting additional material

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