Seasonal reproduction in a fluctuating energy environment

Insolation-driven synchronized broadcast spawning in corals

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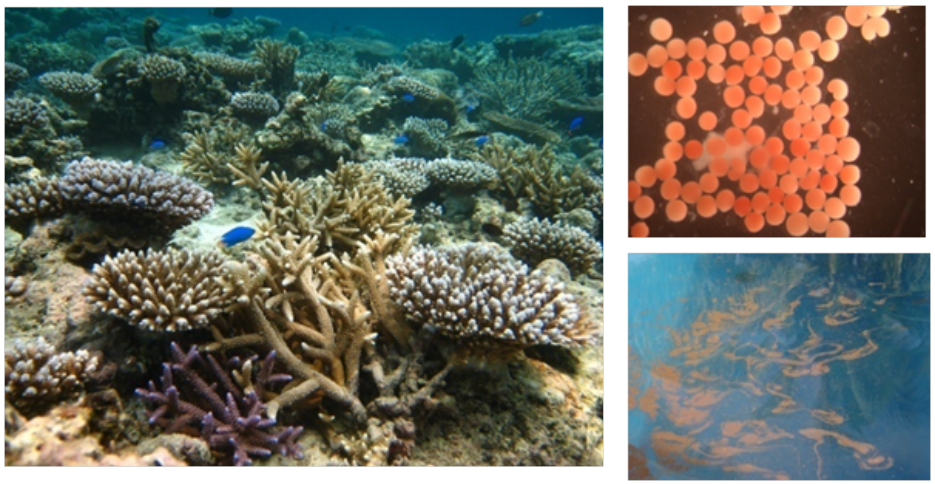
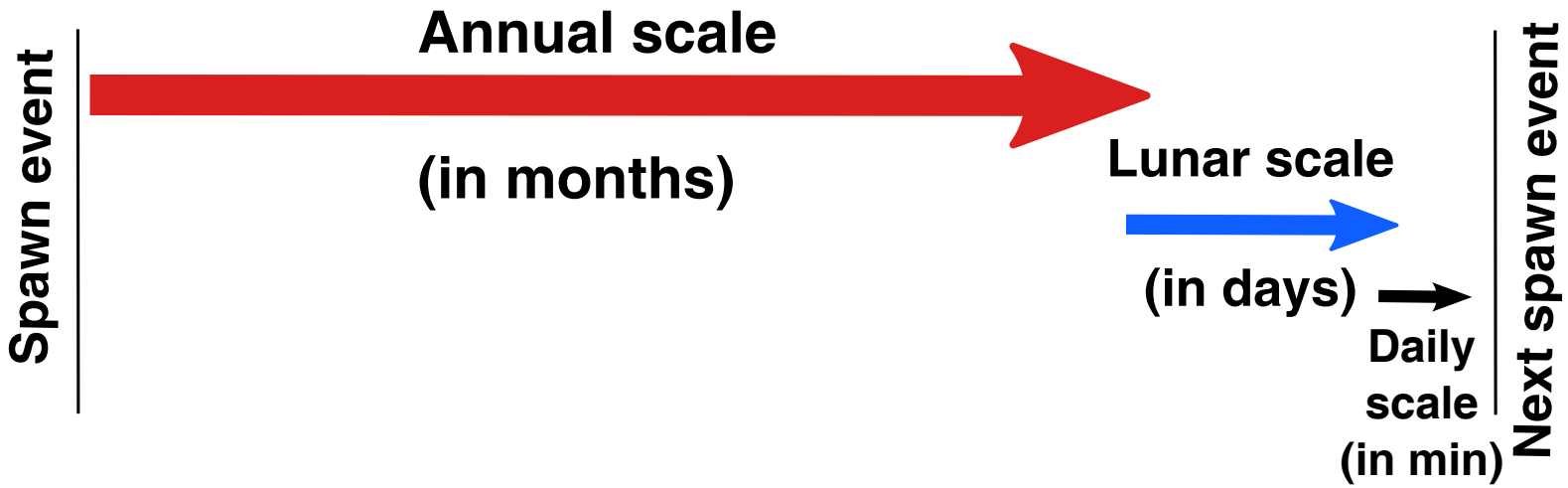
Biology of broadcast spawning

- Corals are a keystone species in reef (marine) ecosystem
- Many corals reproduce by *broadcast spawning*
  - Highly synchronized
- Understand capability of some environmental signals to produce tight synchrony



Coral reef (left) and spawn slicks (right) in Republic of Palau

Cascade of timing mechanisms



Different time-scales of operating mechanisms

Hypothesis: Cascade responsible for producing synchrony

Factors hypothesized to affect spawn timing

Entrainment or phase-locking

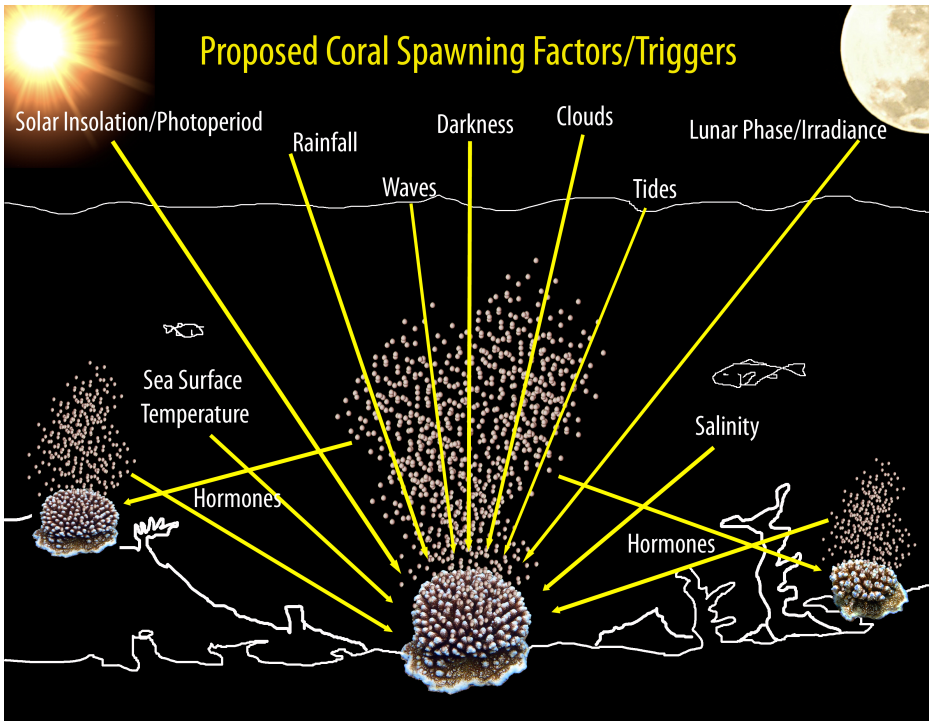
Effected by external periodic driver

e.g., insolation, sea surface temperature, tides, wind, salinity,...

Synchrony

Coherence via interaction (or coupling)

e.g., hormonal signaling



Bioenergetic considerations

- Reproduction requires a lot of energy
- Gametogenesis occurs over a period of 6-9 months
- >90% coral energy needs satisfied by symbiotic algae

Hypothesis

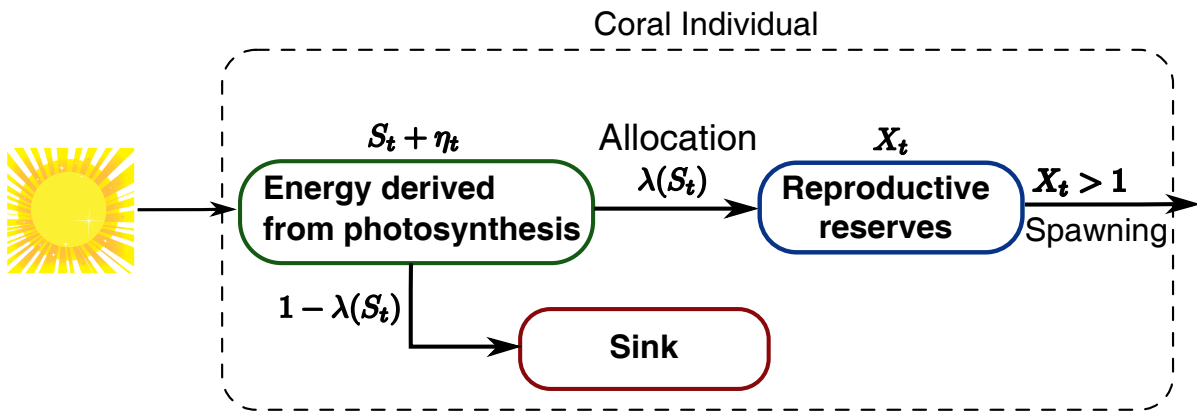
Solar insolation via photosynthetic algae key to spawning in the annual timescale

Central question: insolation-driven entrainment

- Can annually periodic insolation rhythms entrain the coral?
  - with fluctuations (noise) in insolation
  - limiting spawning to 1 month window, where finer scale mechanisms can take over
- What biologically-consistent mechanisms can achieve this?
- How narrow a spawning window can these achieved?

Stochastic integrate-and-fire model

- Abstraction of dynamic energy budget model of coral symbiosis[1]



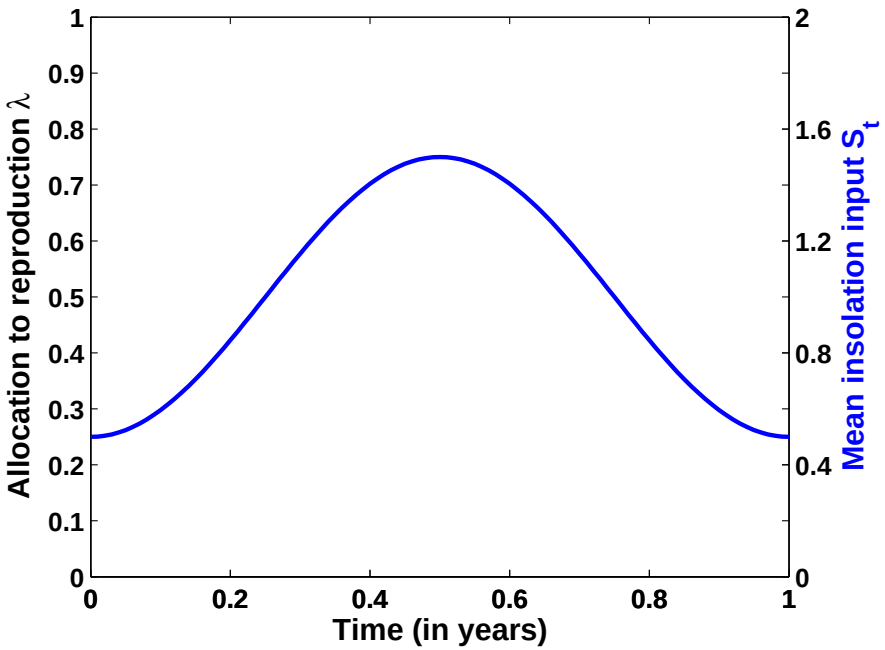
Stochastic integrate-and-fire bioenergetic model

- One state - reproductive reserves - model

[1] Muller, E.B., Kooijman, S.A.L.M., Edmunds, P.J., Doyle, F.J. and Nisbet, R.M., "Dynamic energy budgets in syntrophic symbiotic relationships between heterotrophic hosts and photoautotrophic symbionts," Journal of Theoretical Biology 259 (2009) 44-57.

Biologically consistent energy allocations $\lambda(S_t)$

1. Switched allocation $\Longrightarrow$ Allocate if energy input is increasing
2. Proportional allocation $\Longrightarrow$ Allocate fixed fraction of energy input



Mean insolation

Biologically consistent energy allocations $\lambda(S_t)$

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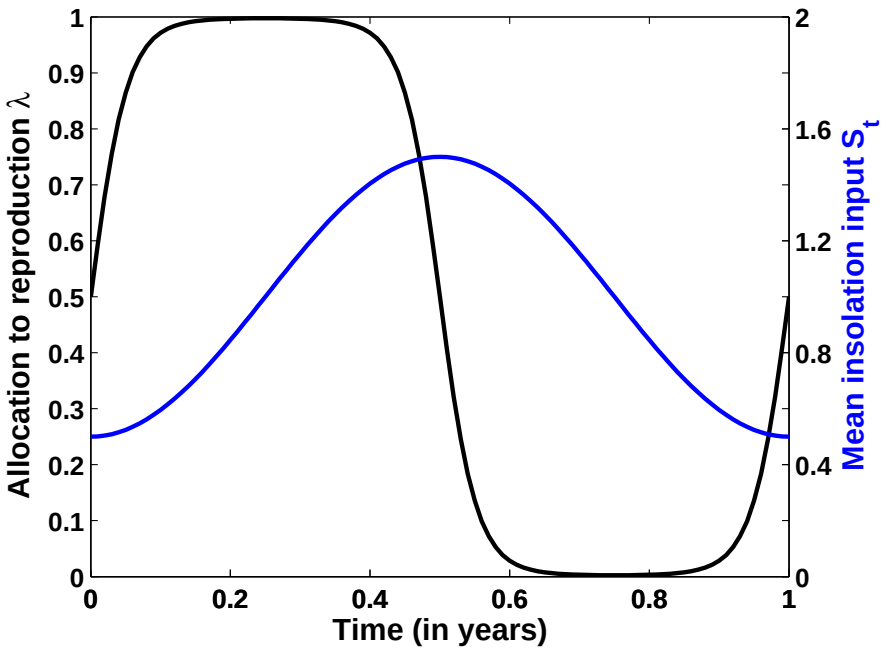

Switched allocation

Biologically consistent energy allocations $\lambda(S_t)$

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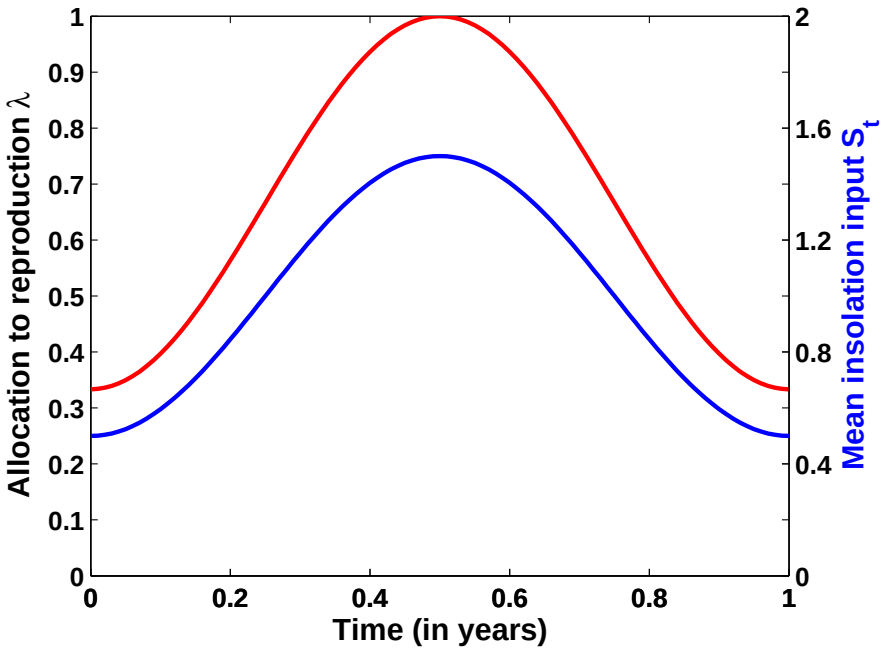
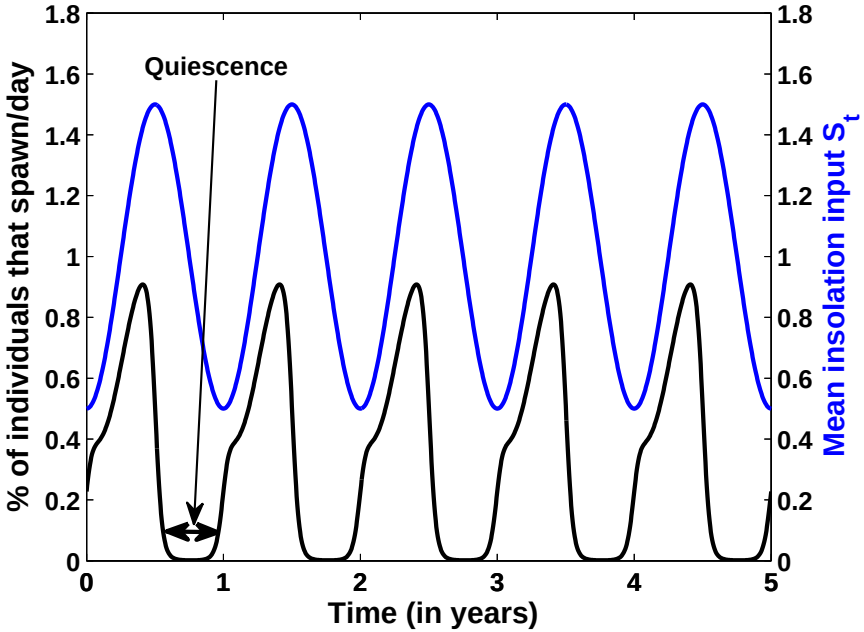
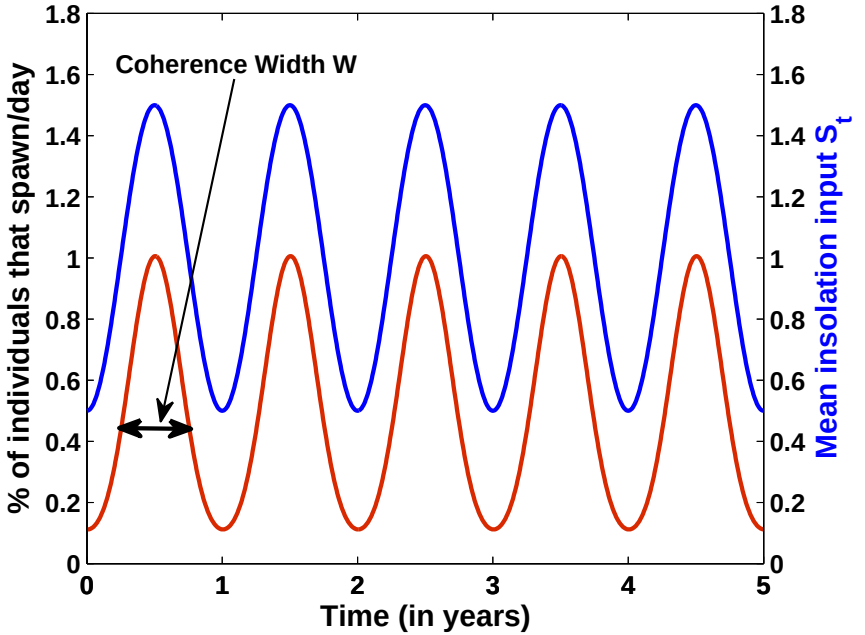


Proportional allocation

Purely input-dependent allocations do not work



1. Switched allocation (W = 66 days)



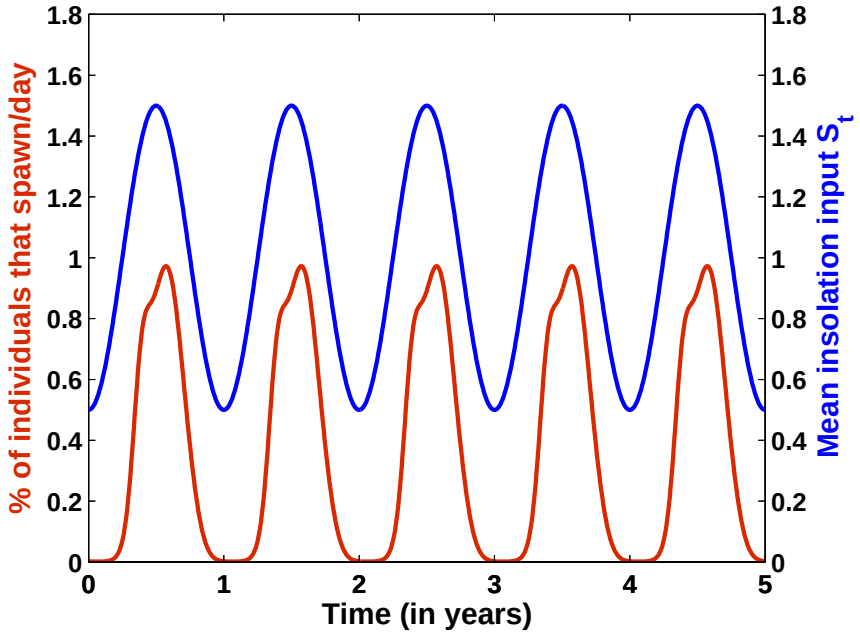
2. Proportional allocation (W = 72 days)

Either broad spawning pattern and/or no quiescence

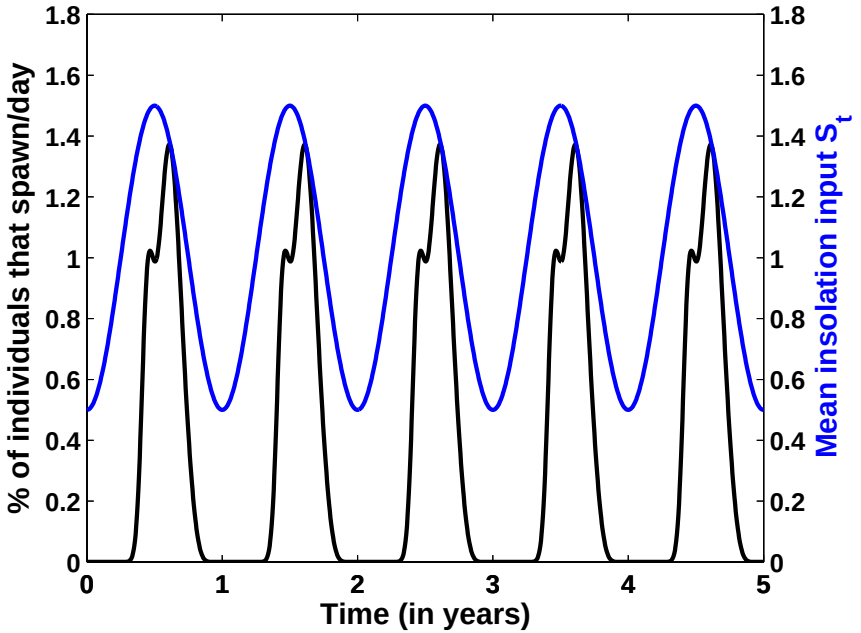
Reserves that require maintenance

- Additional energy needed to maintain reproductive apparatus
- **Maintenance types**
  - **A.** Linear maintenance
  - **B.** Seasonally varying maintenance
- With allocation 2. (proportional allocation)

Feedback through maintenance produces desired entrainment



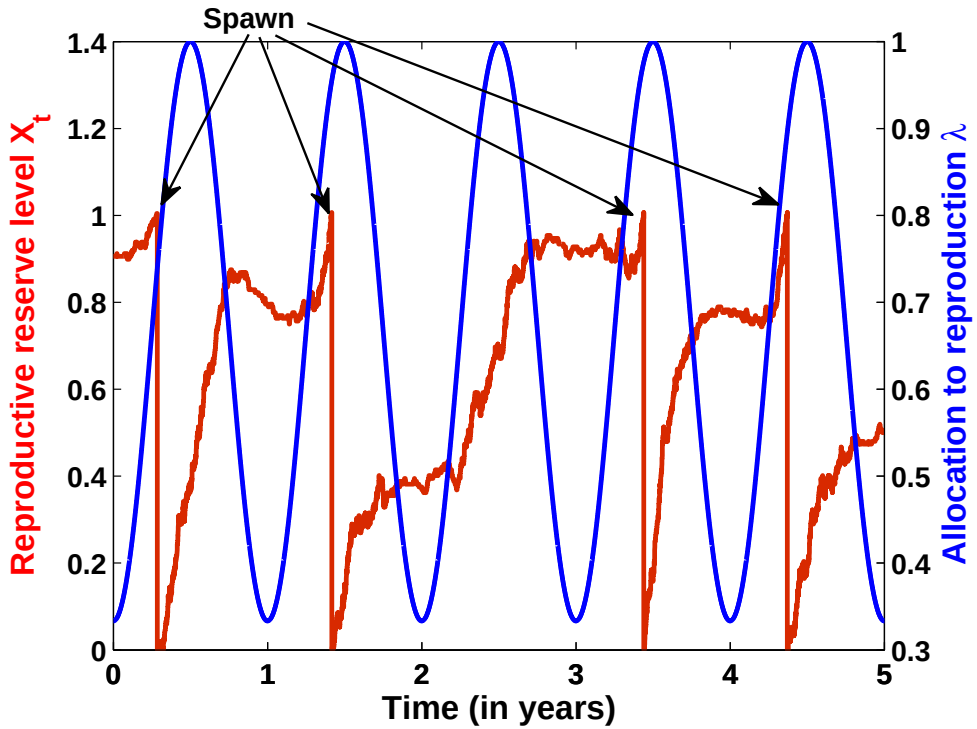
A. Linear maintenance (W=42 days)



B. Seasonally varying maintenance (W=35 days)

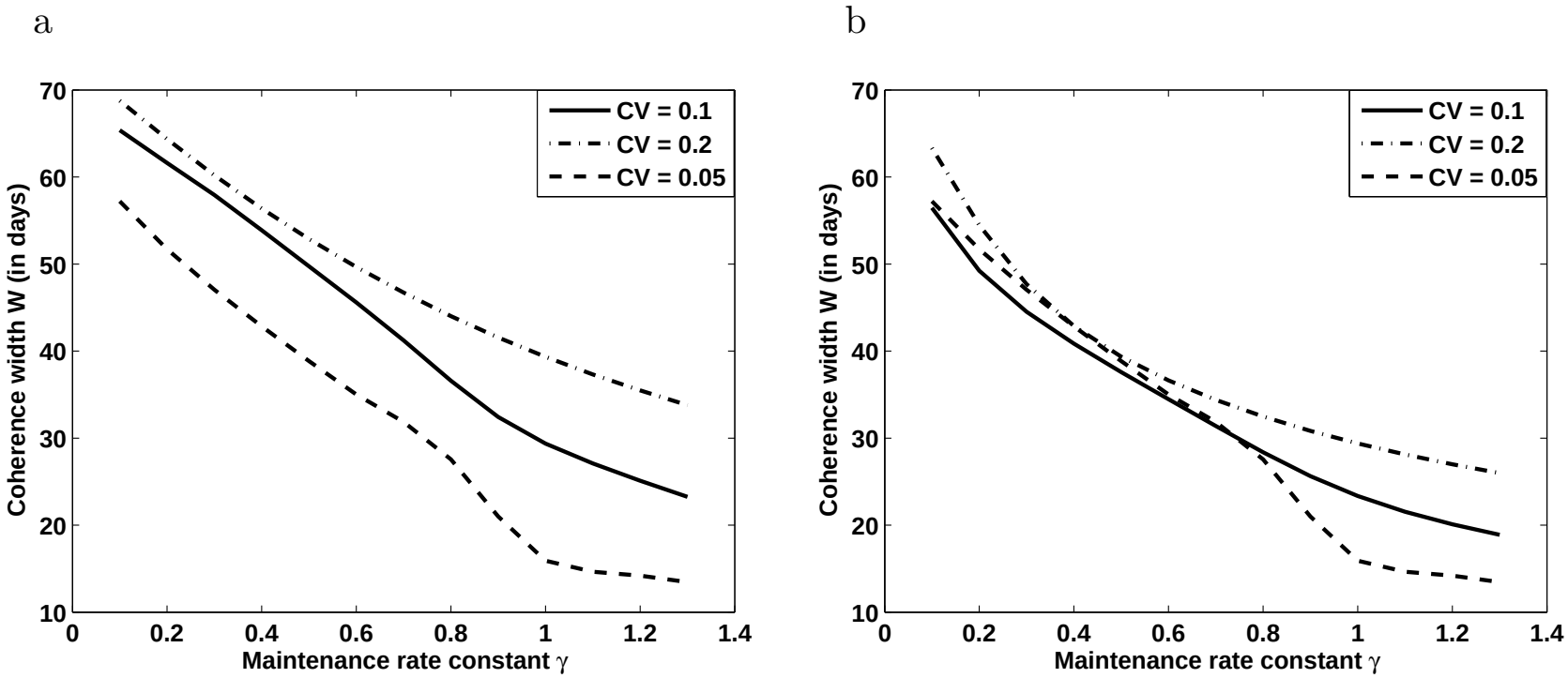
- Entrainment to about one lunar cycle with quiescence

Prediction 1: Coral individuals skip spawning in certain years



Reserve level for one coral under seasonally varying maintenance and proportional allocation

Prediction 2: Tighter coherence with more energy spent



Linear (left) and seasonally varying (right) maintenance for different input noise levels (CV)

Conclusions and Future Work

- Information about reproductive state, i.e., maintenance, entrains coral to about a month in the annual timescale
- Such mechanisms work in the presence of noise (robust)
- Trade-off between expending more energy and tighter spawning coherence
- Future Work
  - entrainment at shorter time scales
  - coupling between corals
  - connect model to biological measures of reproductive state

Implications beyond corals

Simple abstract model is applicable to other synchronized phenomena

- Division of marine phytoplankton – current work
  e.g., Doyle and Poore (1964)
- Masting or seeding in trees
  e.g., Satake and Iwasa (2000, 2002), Lyles et al. (2009)
- Seasonal insect emergence
  e.g., Gurney, Crowley and Nisbet (1992)

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For more information:

B. Ananthasubramaniam, R. M. Nisbet, D. E. Morse and F. J. Doyle III, “Integrate-and-fire Models of Insolation-driven Entrainment of Broadcast Spawning in Corals”, *Theor. Eco.*, In Press, doi:10.1007/s12080-010-0075-z