Predicting patterns of stress and mortality in intertidal invertebrates: applications of biophysical ecology in a changing world

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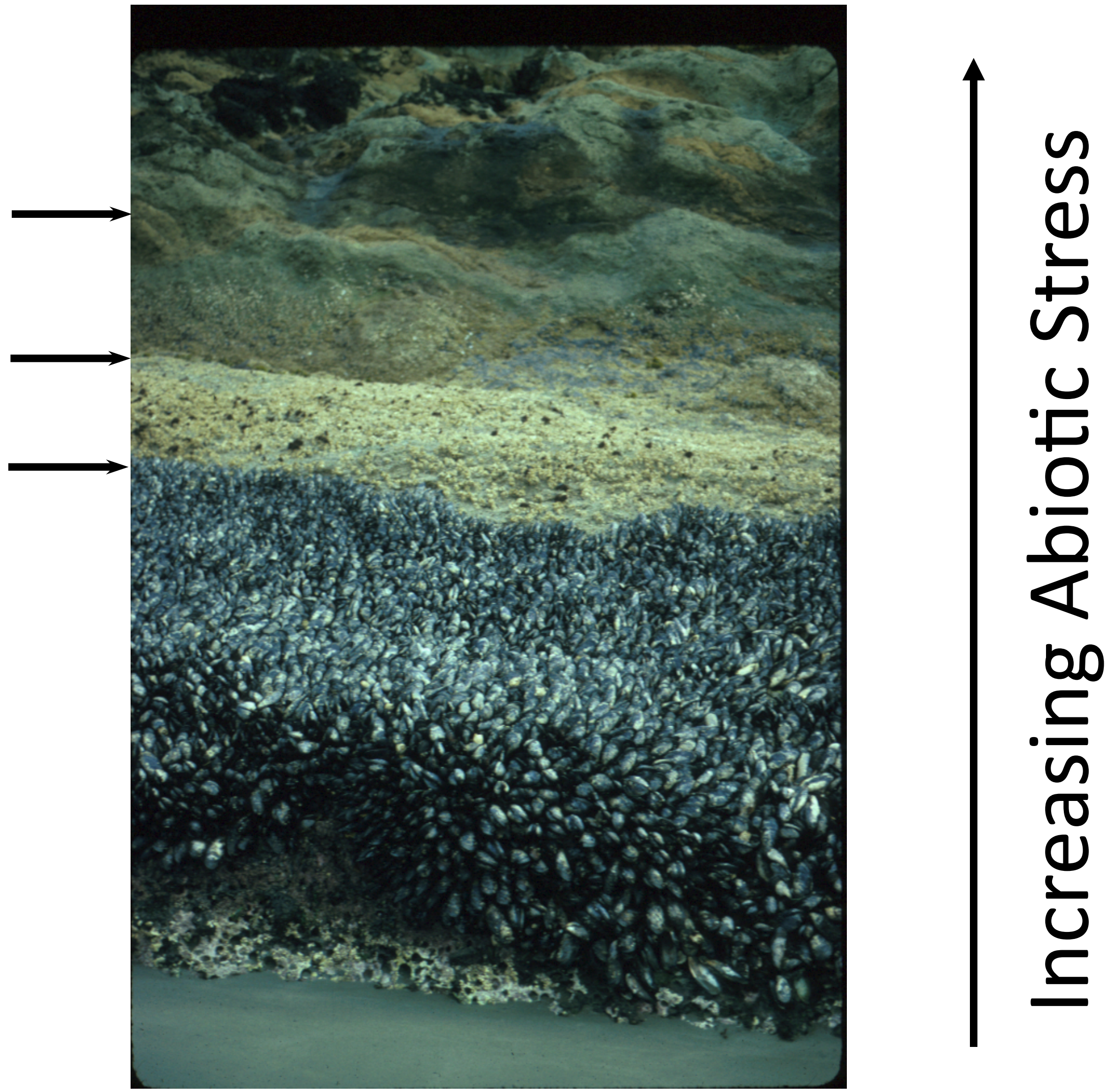
Zonation: intertidal ecosystems have long served as models for examining role of weather in driving patterns of distribution



Observed changes in intertidal ecosystems

- Mass mortality around the world (e.g. Harley 2008)
- Latitudinal shifts of up to 50km/decade (reviewed in Helmuth et al. 2006)

New molecular approaches

- Many organisms are living "close to the edge" (e.g., Somero, Pörtner)
- Even well within range boundaries, conditions may be suboptimal, even though no evidence of lethality (Beukema, e.g.)
- *This means that slight increases in stress may lead to sudden collapses along significant portions of ranges*

How do we predict where this might occur??

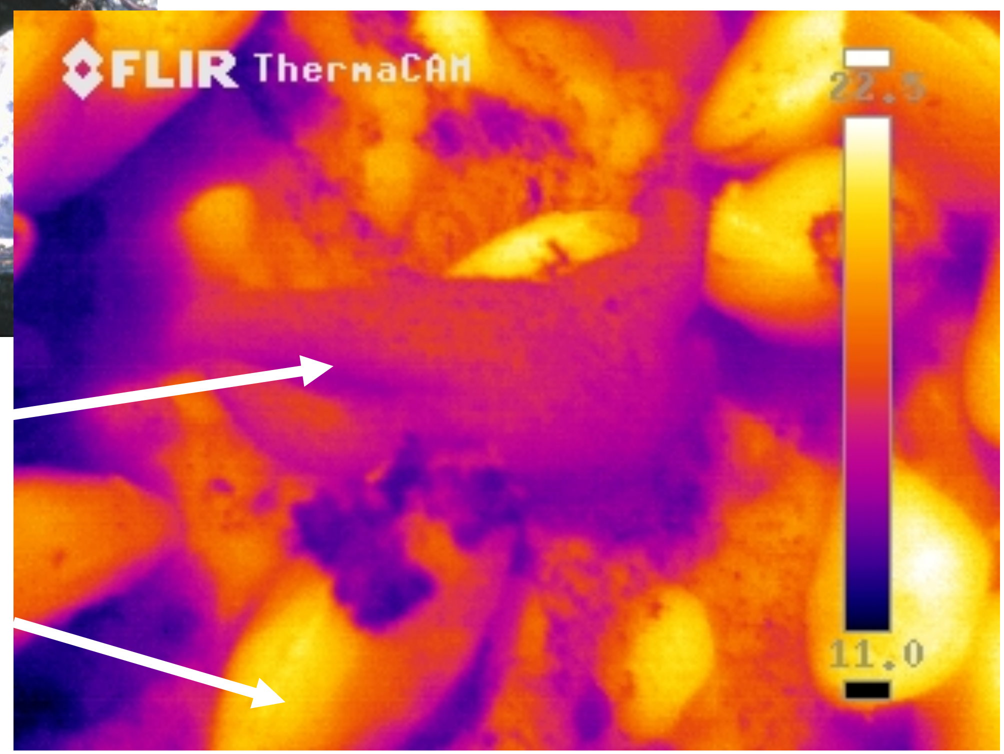
- Most niche models are based on correlations with large-scale environmental variables; i.e. realized niche space of organism
- Can we create a framework that not only considers niche space based on functional traits of the organism, but also can forecast sublethal processes such as growth and reproduction as well as survival?

"Habitat" vs. "niche"

- Habitat: Physical place where an organism lives and the ambient conditions in that habitat; e.g. rock with given oxygen levels and flow
- Environment: Habitat after organism interacts with it (e.g. behavioral choice- burrow at night)
- Niche: subset of environment that drives physiology, *as experienced by the organism*

After Kearney 2006 *Oikos* 115

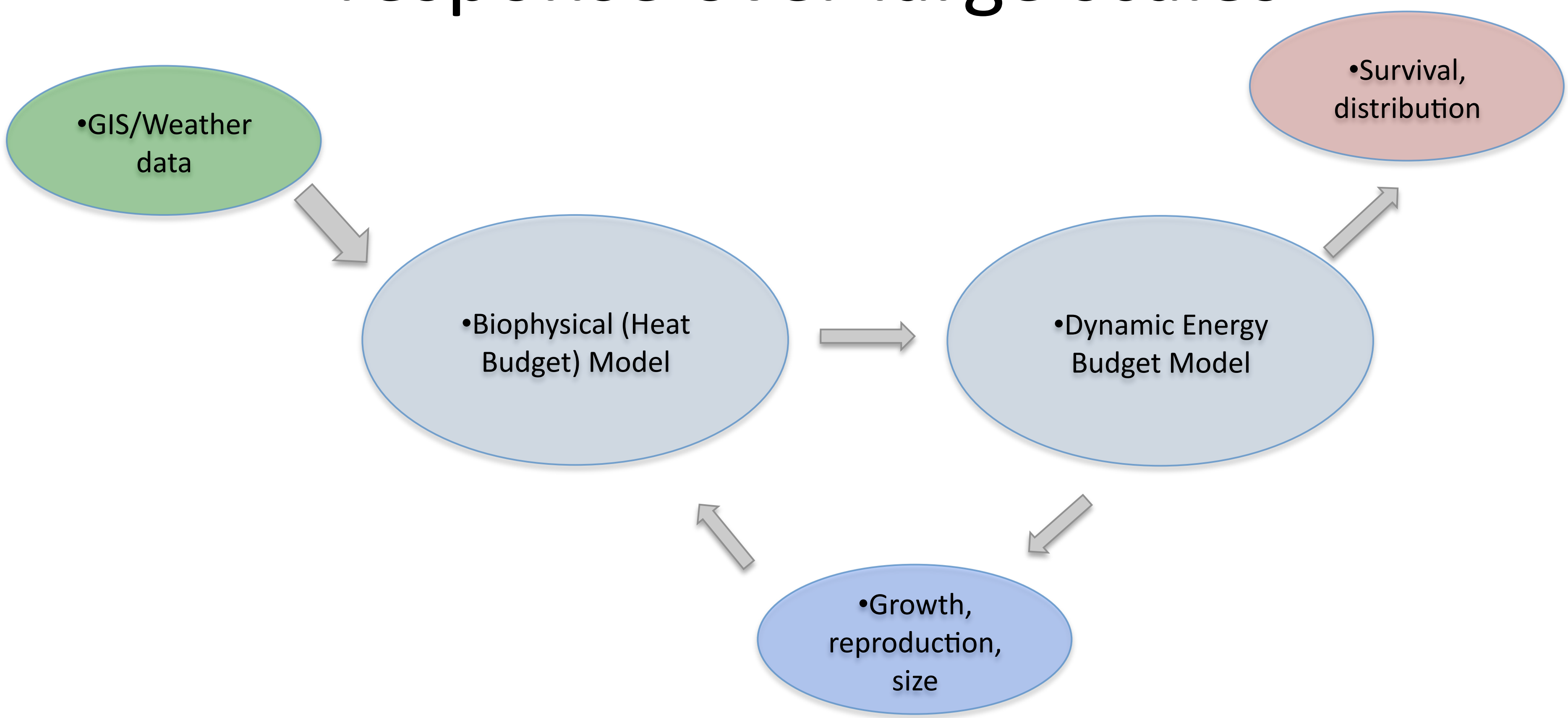
Two intertidal organisms exposed to identical microclimates can experience different body temperatures



Seastar at ~12°C

Mussel at ~21°C

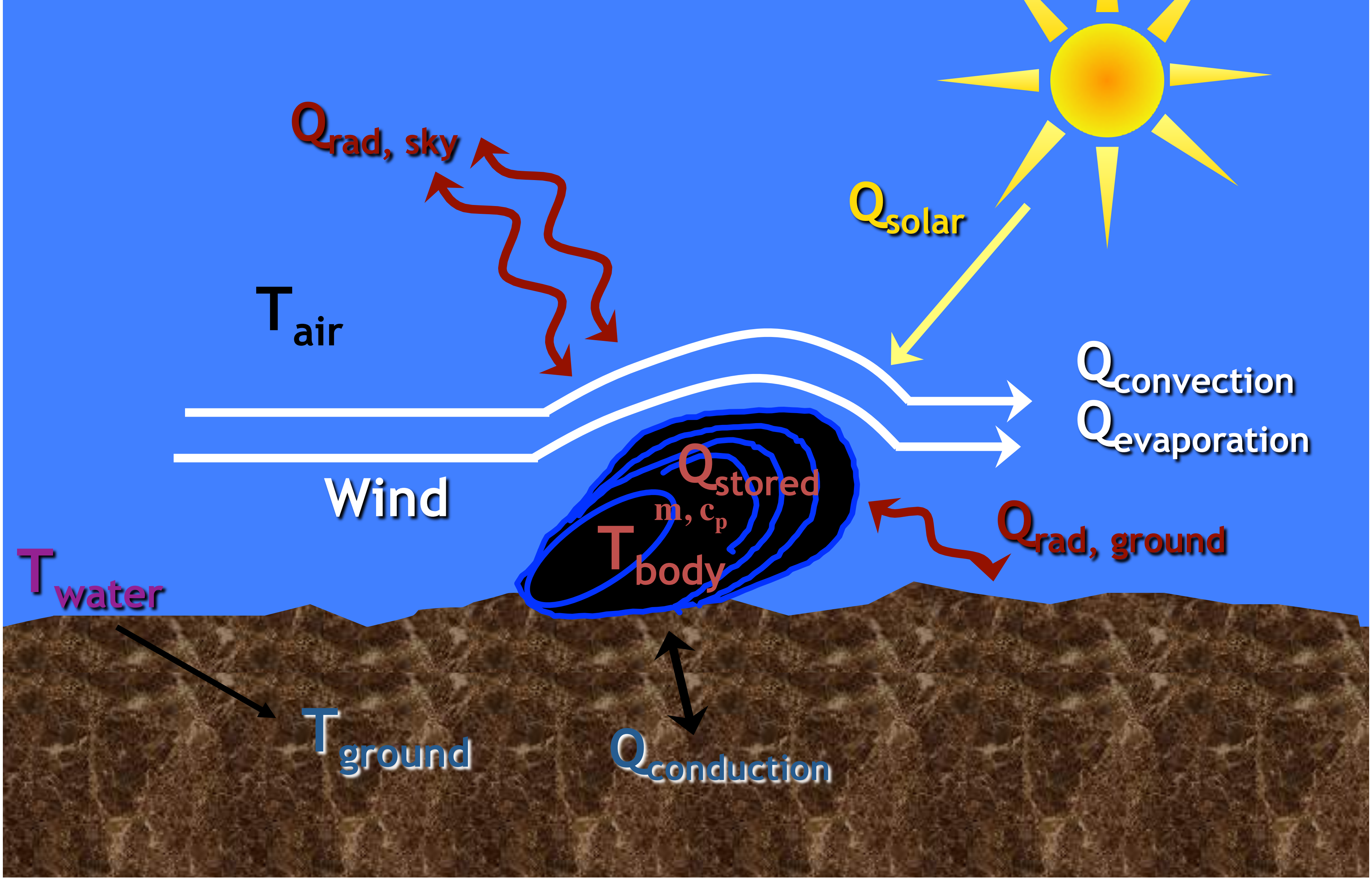
Linking weather to physiological response over large scales



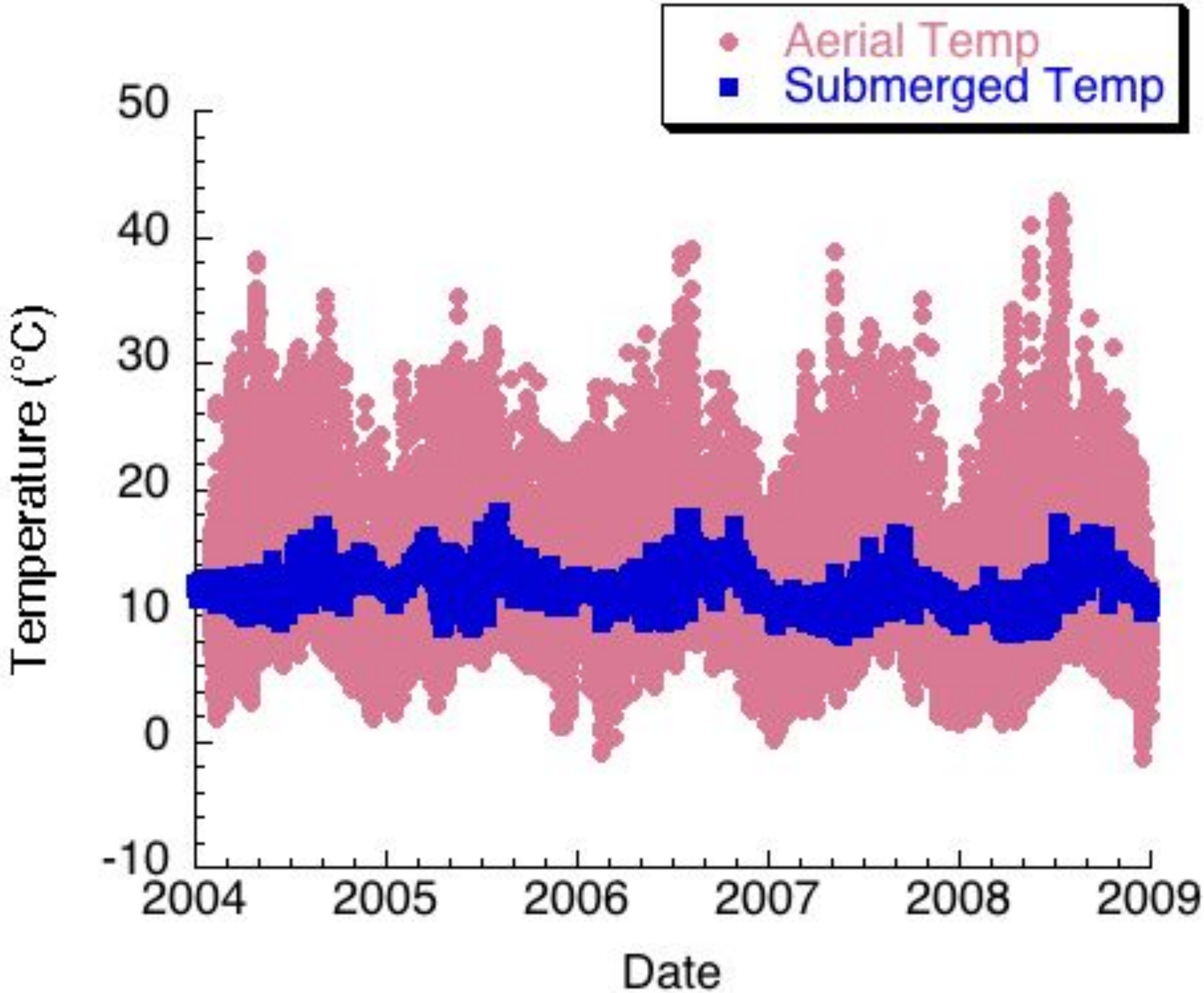
Kearney, Simpson, Raubenheimer and Helmuth 2010, PTRS, in press.

Biophysical Ecology (Heat budget modeling)

Heat In – Heat Out = Heat stored

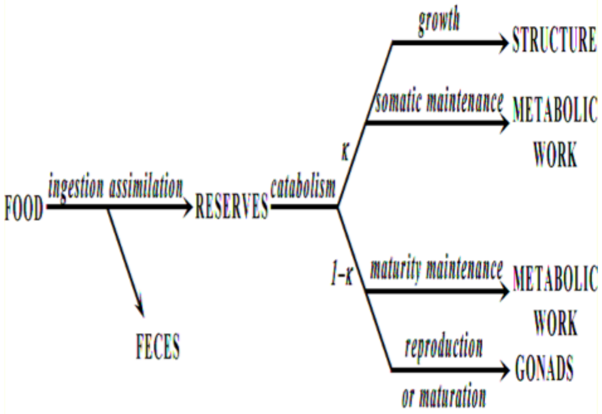


Bodega Bay Mussel Temperatures



Dynamic Energy Budgets

Mike and Gianluca did this part….



Feeding rate:

$J_X = \{J_{XAm}\}L^2 f$

with $f = X/(X + \{J_{XAm}\}/\{F_m\})$

Length in a constant environment:

$L = L_\infty - (L_\infty - L_0)\mathrm{e}^{-r_B t}$

with $r_B = [p_M]/3(\kappa f[E_m] + [E_G])$ and $L_\infty = \kappa f \kappa_X \mu_{XA}\{J_{XAm}\}/[p_M]$

Reproduction rate:

$R = p_r r_B\left(gL_\infty L^2 + fL^3 - (f+g)L_p^3\right)$

with $p_r = 3[E_m](1-\kappa)/E_0$ and $g = [E_G]/\kappa[E_m]$

Respiration rate:

$J_O = \alpha\{J_{XAm}\}L^2 + [p_M]\left(\beta L^3 + \gamma L_p^3\right)$

α, β and χ are compound parameters independent of maintenance and assimilation

Toxic effect on maximum specific searching rate:

$$\{F_{m,C}\} = \frac{\{F_m\}}{1+\frac{([M_Q]-[M_{\mathrm{NEQ},F}])_+}{K_F}} \text{ or } \{F_{m,C}\} = \frac{\{F_m\}}{1+\frac{(C-C_{\mathrm{NEC},F})_+}{C_{K,F}}}$$

Toxic effect on maximum specific feeding rate:

$$\{J_{XAm,C}\} = \frac{\{J_{Xm}\}}{1+\frac{([M_Q]-[M_{\mathrm{NEQ},F}])_+}{K_F}} \text{ or } \{J_{XAm,C}\} = \frac{\{J_{Xm}\}}{1+\frac{(C-C_{\mathrm{NEC},F})_+}{C_{K,F}}}$$

Toxic effect on maintenance rate:

$$[p_{M,C}] = [p_M]\left(1+\frac{([M_Q]-[M_{\mathrm{NEC},M}])_+}{K_M}\right) \text{ or } [p_{M,C}] = [p_M]\left(1+\frac{(C-C_{\mathrm{NEC},M})_+}{C_{K,M}}\right)$$

Impact on asymptotic size because of effect on maintenance and feeding rates:

$$L_{\infty,C} = \frac{L_\infty}{\left(1+\frac{([M_Q]-[M_{\mathrm{NEQ},F}])_+}{K_F}\right)\left(1+\frac{([M_Q]-[M_{\mathrm{NEC},M}])_+}{K_M}\right)} \text{ or}$$

$$L_{\infty,C} = \frac{L_\infty}{\left(1+\frac{(C-C_{\mathrm{NEC},F})_+}{C_{K,F}}\right)\left(1+\frac{(C-C_{\mathrm{NEC},M})_+}{C_{K,M}}\right)}$$

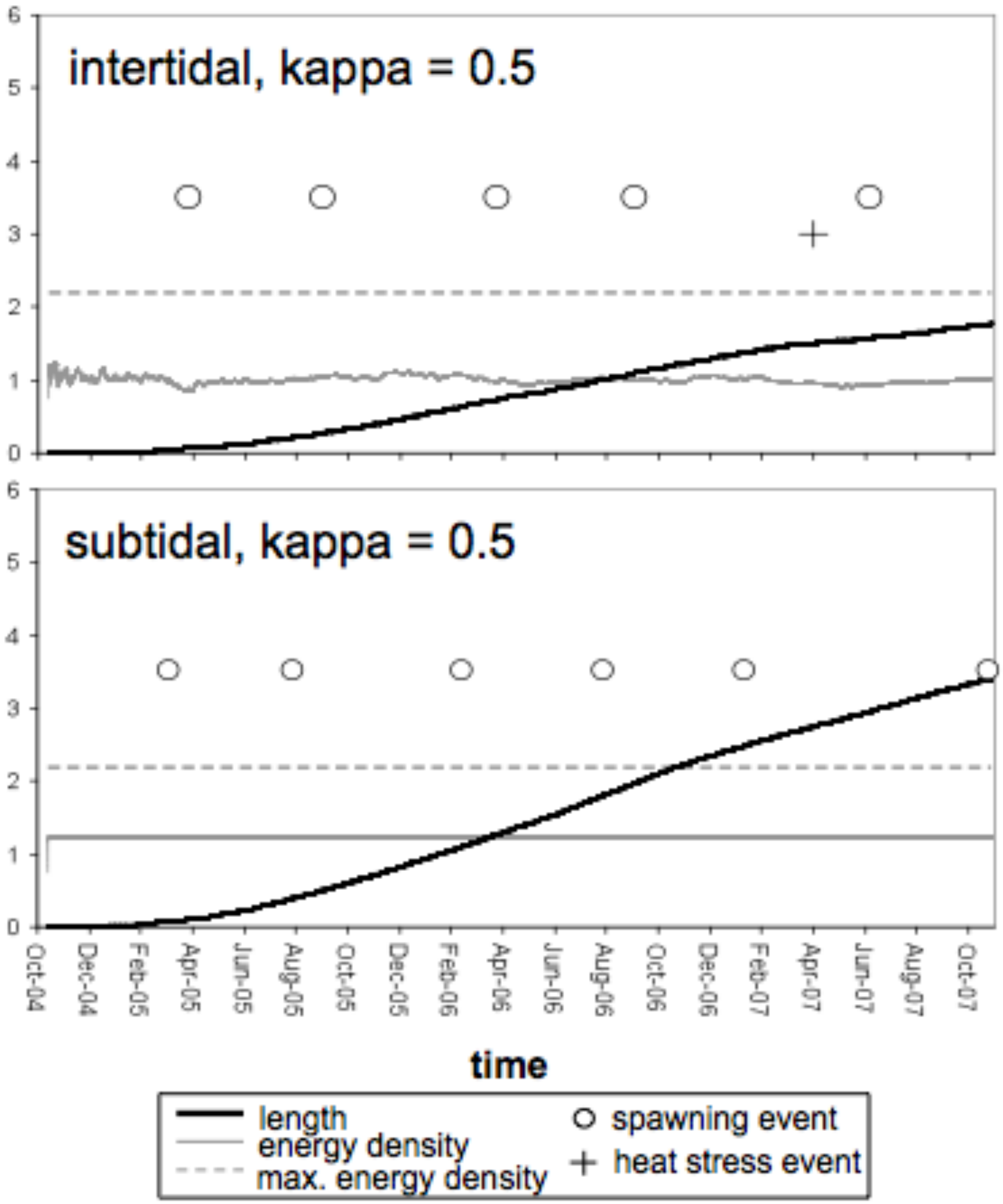
Lotka-Euler equation

$$1 = \int_0^\infty R\mathrm{e}^{-(r+h)t}\,\mathrm{d}t$$

C	#/V	Ambient toxicant concentration
$C_{K,F}$	#/V	Toxicant scaling concentration for effects on feeding
$C_{K,M}$	#/V	Toxicant scaling concentration for effects on maintenance
$C_{\mathrm{NEC},F}$	#/V	No-effect concentration for feeding
$C_{\mathrm{NEC},M}$	#/V	No-effect concentration for maintenance
C_X	#/L^3	Toxicant density in food
E_0	e/#	Energy cost to produce an egg
$[E_g]$	e/L^3	Volume-specific cost of growth
$[E_m]$	e/L^3	Maximum energy reserve density
f	–	Scaled functional response
$\{F_m\}$	#/$L^2 \cdot t$	Surface-specific maximum food searching rate
$\{F_m\}$	#/$L^2 \cdot t$	Surface-specific maximum food searching rate with toxicants
g	–	Energy investment ratio
h	$1/t$	Specific mortality rate
J_O	#/t	Oxygen consumption rate
J_X	#/t	Ingestion rate
$\{J_{XAm}\}$	#/$L^2 \cdot t$	Surface-specific maximum ingestion rate
$\{J_{XAm,C}\}$	#/$L^2 \cdot t$	Surface-specific maximum ingestion rate with toxicants
k_d	$V/L^2 \cdot t$	Surface-specific uptake rate of ambient toxicants
k_e	L/t	Toxicant elimination rate
k_X	$L^3/L^2 \cdot t$	Surface-specific uptake rate of toxicants in food
K_F	#/$L^2 \cdot t$	Toxicant scaling body burden for effects on feeding
K_M	#/L^3	Toxicant scaling body burden for effects on maintenance
L	L	Body length
L'	L	Length increase from reaching puberty to first egg clutch
L_0	L^b	Initial length
L_∞	L^b	Asymptotic or ultimate length
$L_{\infty,C}$	L	Asymptotic or ultimate length with toxicants
L_p	L	Length at puberty
$[M_Q]$	#/L^3	Body burden
$[M_{\mathrm{NEQ},F}]$	#/L^3	No-effect body burden for feeding
$[M_{\mathrm{NEQ},M}]$	#/L^3	No-effect body burden for maintenance
p	#/V	Log likelihood profile parameter
$\{p_{Am}\}$	#/$L^2 \cdot t$	Surface-specific maximum assimilation rate
p_r	#/L^3	Compound parameter for reproduction
$[p_M]$	#/$L^3 \cdot t$	Volume-specific maintenance rate
$[p_{M,C}]$	#/$L^3 \cdot t$	Volume-specific maintenance rate with toxicants
r	$1/t$	Specific population growth rate
r_B	$1/t$	Von Bertalanffy growth rate
$r_{B,C}$	$1/t$	Von Bertalanffy growth rate with toxicants
R	#/t	Reproduction rate
t	t	Time
X	#/V	Food density
α	#/#	Compound parameter related to oxygen consumption
β	#/e	Compound parameter related to oxygen consumption
γ	#/e	Compound parameter related to oxygen consumption
δ_M	L/L	Shape correction factor converting cubed biovolume to body length
κ	–	Fraction of catabolic power energy spent on maintenance and growth
κ_X	–	Assimilation efficiency
Λ	–	Negative log likelihood
μ_{XA}	e/#	Chemical potential of food

(slide courtesy Erik Muller)

Bodega Bay, California, mussel *Mytilus californianus*

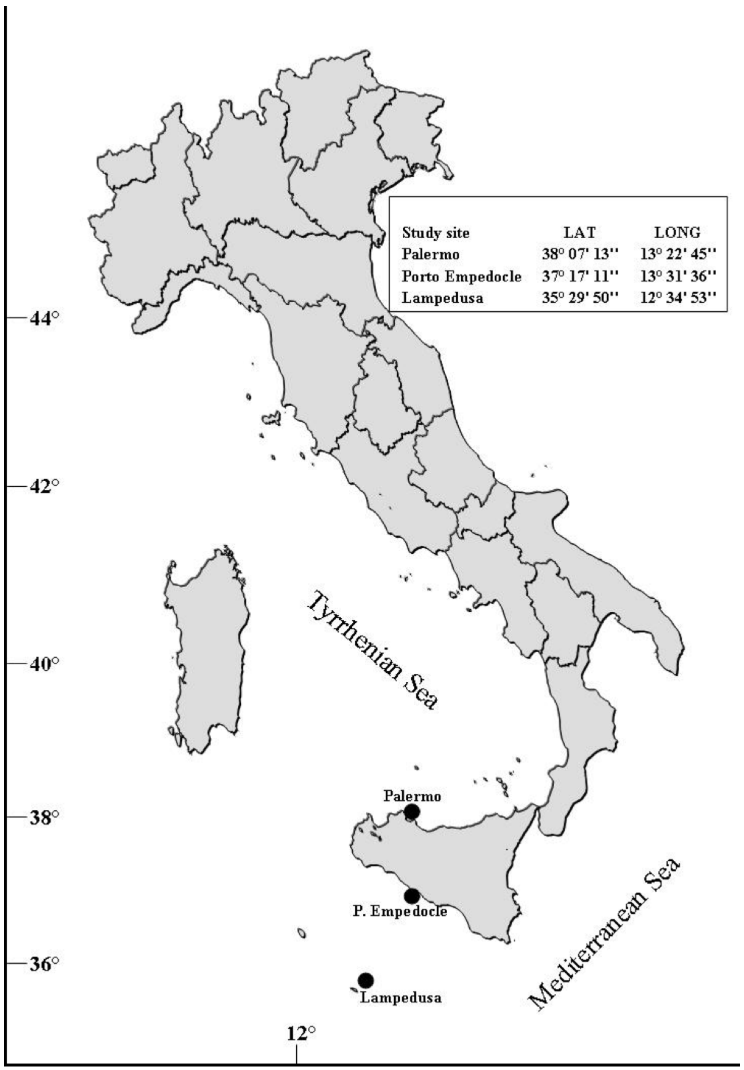


5 Spawning events
1 Heat stress events
Max length 1.8 cm

6 Spawning events
0 Heat stress events
Max length 3.1 cm

Kearney et al., 2010

Mytilus galloprovincialis in the Mediterranean



- Lethal aerial exposures limit distribution in Palermo
- At Porto Empedocle and Lempedusa (more *southern* sites) repeated exposures to elevated but sublethal temperatures set intertidal limits

Sará et al., in review

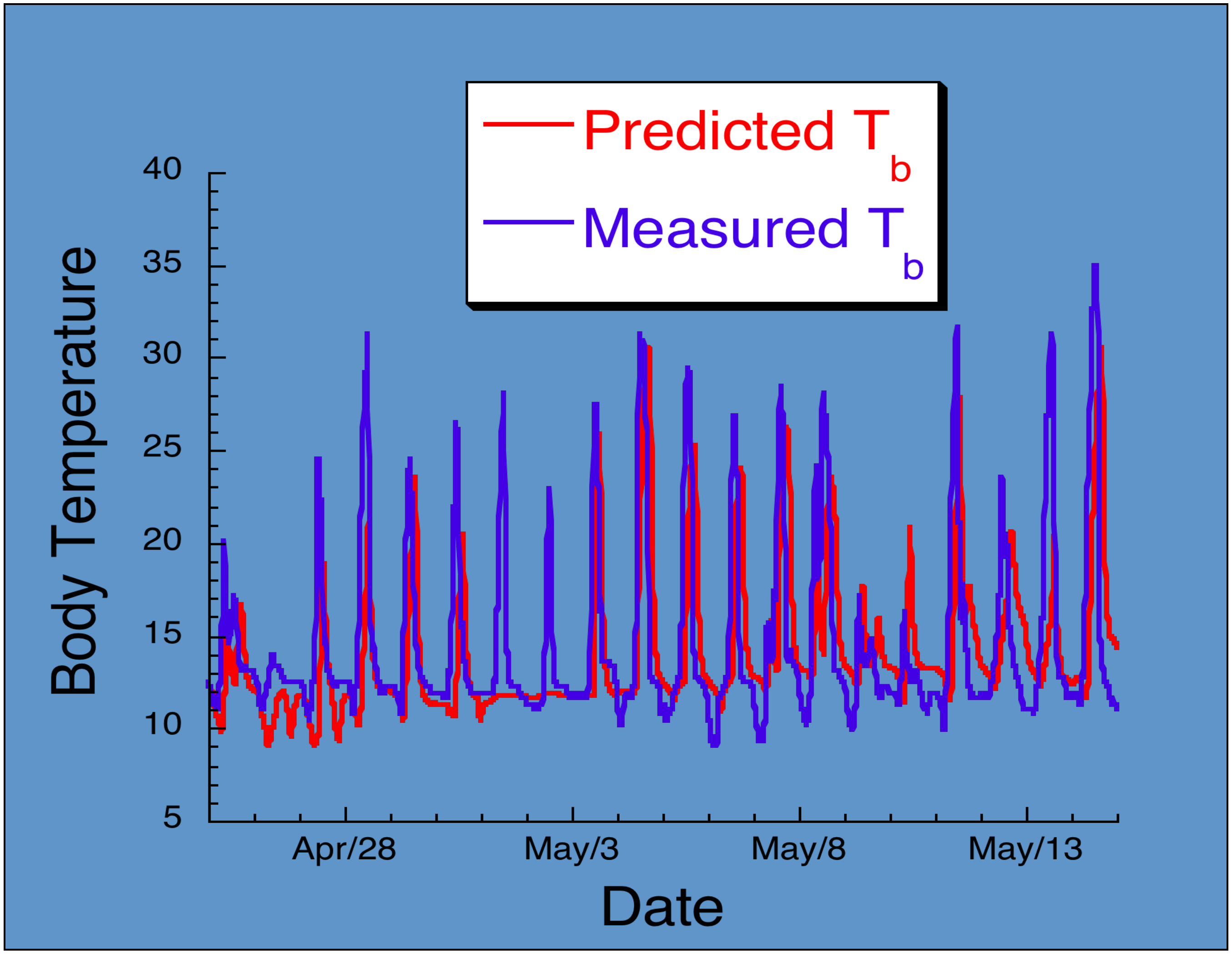
Applications

- Biophysical approaches can describe the niche space of an organism based on functional traits
- DEB theory can predict not only mortality but also growth and reproduction, potentially predicting "trouble spots" before lethality occurs

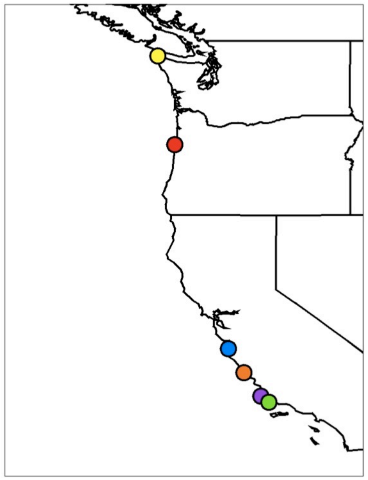
But it isn't that simple of course

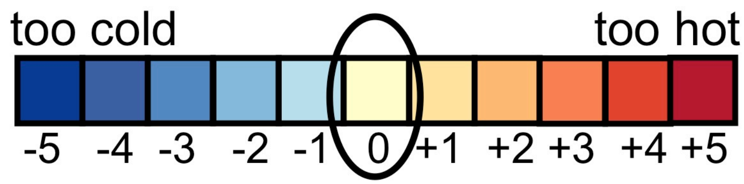
- There is a lot we don't know about intertidal organisms
- Intertidal mussels can undergo either aerobic or anaerobic metabolism depending on duration of exposure, relative humidity, etc.
- They also incur a "debt" during low tide that is repaid during high tide
- We still need to refine the DEB approach for intertidal organisms

Biophysical models are best viewed as probablistic

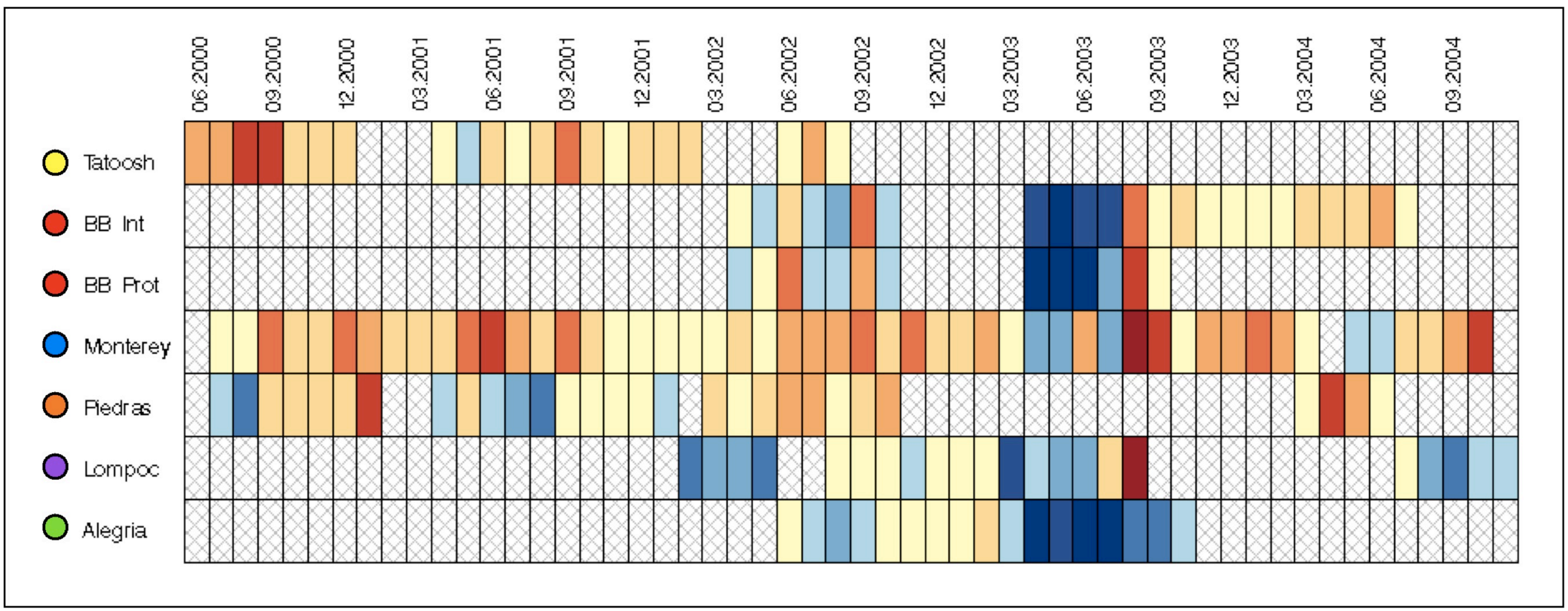


Hindcast Model Performance *vs.* Field Data



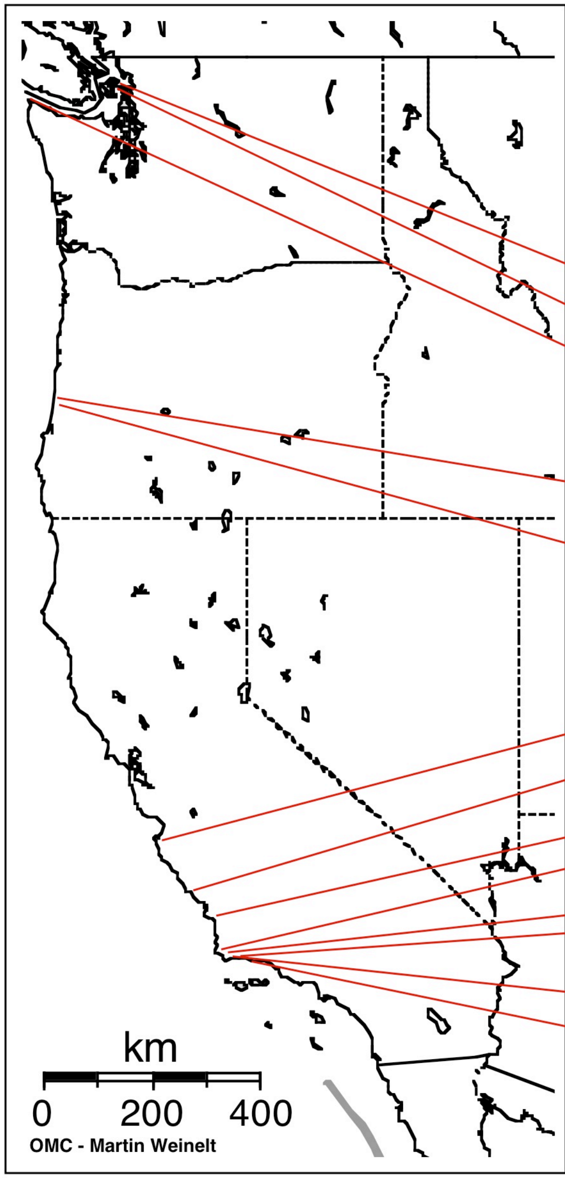


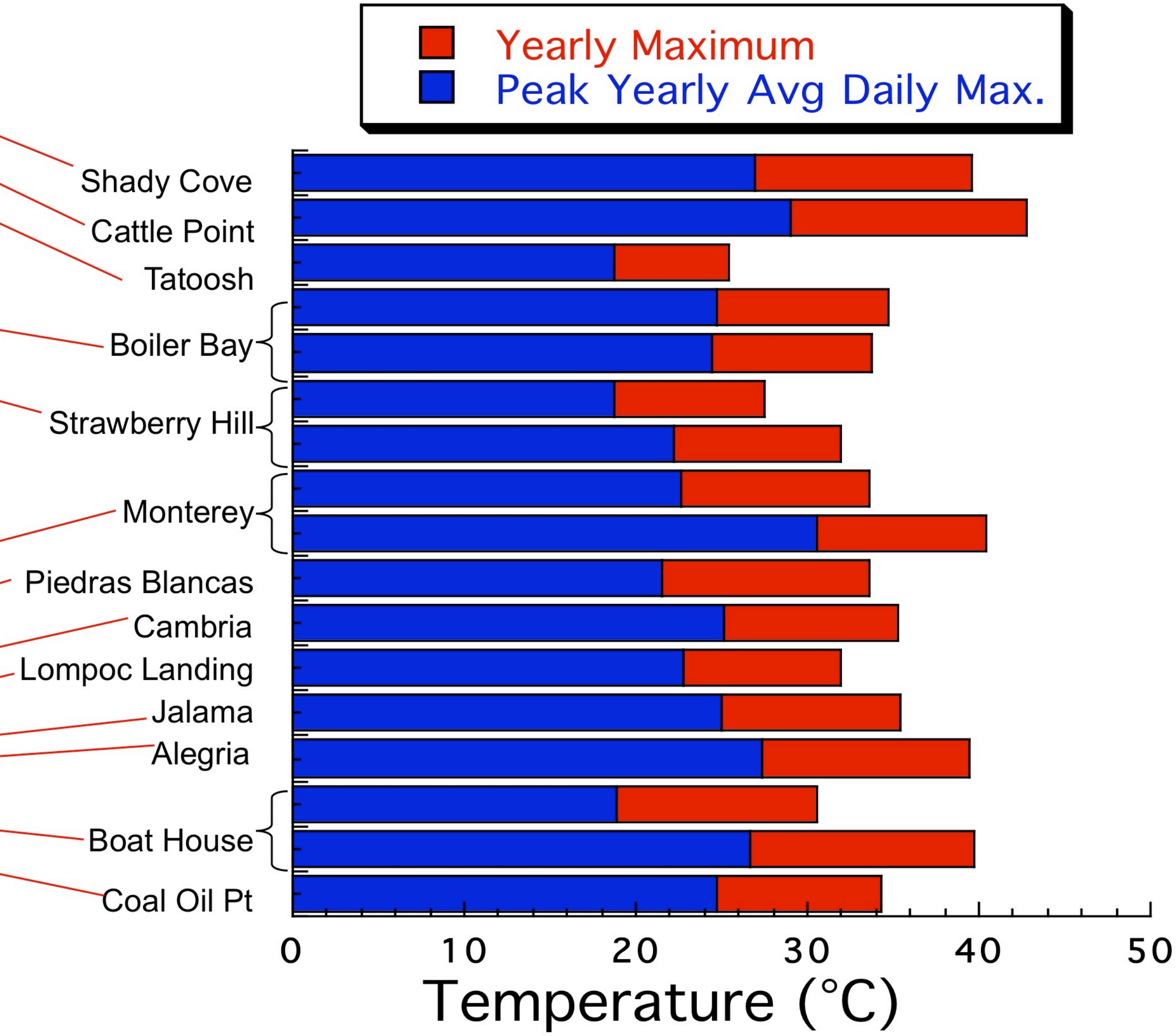
Difference in Monthly Average Maximum



(Gilman et al., *PNAS* 2006)

Thermal mosaic over a large geographic range





(Helmuth et al. 2006 *Ecol Monogr*)

Where we go from here

- Geographic maps of mortality, stress and growth
- Comparative maps between species-> species interactions
- Forecasts of physiological response and ecological response (tipping points?) using GCMs

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