LECTURE NOTES
Theoretical Biophysics, Tuesday, June 9, 2019
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http://ib.berkeley.edu/labs/koehl

Suggested reading:

1. When to use mechanistic vs. phenomenological models:
    pp. 39-43 in: Koehl, Chapter 3 in *Perspectives in Ecological Theory*, R. May, J. Roughgarden, S. Levin [Eds.]
   (I've provided a pdf for posting for you, or you can download it from this page of my website: https://ib.berkeley.edu/labs/koehl/koehl-publist.html)

2. Pros, cons, and usefulness of optimization:
    Chapter on optimization in: Oster, G. F. and E. O . Wilson, *Caste and Ecology in Social Insects*. Monographs in Population Biology Vol. 12

3. Example of our approach:
    Koehl, M. A. R. and Cooper, T. (2015) Swimming in an unsteady world. Integr. Comp. Biology 55: 683-697. doi:10.1093/icb/icv092
   (I've provided a pdf for posting for you, or you can download it from my https://ib.berkeley.edu/labs/koehl/koehl-publist.html)

   More examples listed here: https://ib.berkeley.edu/labs/koehl/resint/mass.html

References I promised to provide to some of you during discussions over lunch or coffee:
Motions of bodies of different shapes, swimming vs. passive, in turbulence:
    Pujara, N, M. A. R. Koehl, and E. A. Variano (2018) Rotations and accumulation of ellipsoidal microswimmers in isotropic turbulence. J. Fluid Mechanics 838: 356-368.
   (pdf on this page: https://ib.berkeley.edu/labs/koehl/koehl-publist.html)

How sniffing (antennule flicking) affects the temporal pattern of odor signals intercepted by lobsters vs. crabs in a turbulent odor plume, and how temporal patterns provide information about position in the plume.
    Reidenbach, M.A. and M. A. R. Koehl (2011) The spatial and temporal patterns of odors sampled by lobsters and crabs in a turbulent plume. J. Exp. Biol. 214: 3138-3153.(pdf here: https://ib.berkeley.edu/labs/koehl/koehl-publist.html)

Model of branching in transport systems (there are many specific studies of plants, animals, cities, etc. that grew from this approach):
    West, G. B., J. H. Brown, B.J. Enquist. (1997) A General Model for the Origin of Allometric Scaling Laws in Biology. Science 276:122-126. DOI:10.1126/science.276.5309.122

   A brief overview is in: West, G.B. and J. H. Brown (2004) Life's universal scaling laws. Physics Today **57**: 36. doi.org/10.1063/1.1809090

Lecture outline:

1. Why should biologists care about YOUR work?
   How can you make your theories useful to understanding biological, ecological, or evolutionary processes?

2. Traps for physicists modeling biological systems
   -- Fitness?
   -- Is energy the right "currency" for your system?
   -- Is optimality useful?

3. Traps for experimental biologists and for theorists
   Organisms and processes occur in environments that can affect them: physical, chemical, biological

(example from our work: "Moving through a turbulent environment: Embedding models in real-world data")

4. Exercise for YOU:

For the system you are studying, answer these questions.

a) Which features of the environment are important (i.e. can affect the process you are modeling)?

b) How do the important features of the environment vary in space and time?

c) What are the relevant spatial and temporal scales of environmental variation for YOUR question?

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Lecture:

My field is biomechanics (e.g. structural design, biomaterials, dynamics of organisms) and biofluiddynamics (physics of swimming, flying, fluid transport in bodies, etc.)

-- Our work sits at the interface between biology and physics/engineering/mathematics
-- I am an experimentalist, but I collaborate with theorists.

1. Why should biologists care about YOUR work?

How can you make your theories useful to understanding biological, ecological, or evolutionary processes? How can you work make an impact in the field of biology?

I'm a professor in a biology department. **When I ask many of my colleagues whey they ignore theoretical work, here are some of the answers they give me**:

a. The model does not answer an important biological question.
   or
   The theorist is trying to answer a question that e answered years ago with experimental work.

b. We can't relate the model to real biological questions because:
   -- the assumptions are unrealistic,
   -- the parameters used do not relate to anything in the real world that we can understand or measure,
   -- the models make predictions that cannot be tested experimentally (because what is predicted does not relate to anything in the real world, or because it is technically too difficult or time consuming to make the necessary measurements.

c. We can't understand the talks given by theorists (slide after slide of Greek symbols that are not defined) or their papers (pages and pages of math beyond what we have studied without explanations in words of what processes the different parts of the equations are describing).

So........ What can YOU do so that your theoretical work will make a difference in the field of biology?

a. Talk with biologists, go to their meetings, take in introductory undergraduate class in the broad area of biology that you are studying ------->

   ...to find our what the important <u>un</u>solved questions are.

(If you think you have an important unsolved question that biologists should be thinking about, then go to their meetings and give really clear talks about your ideas about that question. Convince them why it is important and why it is exciting!)

b. Collaborate with biologists who have the right expertise in the system you are modeling...

   1) ... so you can use sensible parameters (parameters that relate to something in the real world that can be measured), and realistic ranges of values for those parameters

   2) ... so you don't ignore things that are known to be important when you make the simplifying assumptions for your model

   3) ... so your model makes predictions that can be tested

c. Decide if a mechanistic or a phenomenological model is the best choice for the question(s) you are addressing.
(We discussed this in class. Suggested reading #1 goes through these issues in more detail)

d. When you give talks to biologists or write papers you want them to read, think hard about how to communicate clearly to someone in a different field.
-- Tell them what biological question your theory addresses and why they should care about this
-- Tell them why your simplifying assumptions are OK
-- If you can show the results of an equation on a graph, that is easier for a biologist to understand than an equation.
-- If you must show an equation, define the symbols and use words to say what each part of the equation represents.
--Avoid math and physics jargon
-- Have very clear take-home messages so they can go tell their colleagues in words what it is that you discovered with your theoretical approach

Why would a biologists want to collaborate with YOU?
What can theory do for biologists?

a. We can do "experiments" using your model that are not possible with real organisms

b. By varying parameters and doing sensitivity analyses, you can tell biologists which factors are really important and which ones make little difference. Then the biologists can focus their time and energy on the important factors (since it takes a lot of time and effort to make biological measurements and do experiments).

c. Your theory can describe quantitatively a mechanism hypothesized by you or by the biologists. Biologists pose hypotheses and do experiments to try to reject those hypotheses. If you model can predict the outcome of a manipulation of the system that allows a hypothesis to be tested, that is incredibly useful to biologists.

2. Warning about some traps that theorists (with training in math or physics, but not biology) can fall into when they venture into biology:

a. What is "fitness"?

> ...how many surviving kids you produce relative to everybody else of you species in your population...

To be fit you have to: 1) survive long enough to reproduce, AND
2) produce a lot of offspring that survive

...so optimal performance of some function is NOT fitness (although it may contribute to fitness)

b. Is energy the right "currency" for your system?
example: Shrimp devote a lot of muscle mass (the part you eat) to a very energy-costly tail flip that enables them to jump away on isolated occasions from predators. Energy-efficient swimming would not permit them to survive long enough to reproduce).

For your system, think about the aspects of performance that are most important to both survival and to having enough energy to make babies.

c. Are optimization models useful?
(The most clear and enlightening discussion I have seen of this is the chapter on optimization modeling in suggested reading #2)

Joke: Two guys are hiking in the mountains and suddenly they see a big grizzly bear lumbering towards them. One guy starts running but his friend yells, "Why are you running? You can't outrun the bear!" The fellow who is running calls back, "I don't have to outrun the bear. I only have to outrun you!"
The point is that organisms often are not optimal - they just have to be good enough to survive.

We had a discussion about why organisms might not be optimal:
-- Trade-offs between different functions
(example: Long tail feathers can hinder flight performance or make it costly, but girl birds of a particular species really like those long tails and choose to breed with the guys who have them.)

-- Evolution takes time, so the population has not reached optimal performance yet

-- the environment (and thus what optimal performance is) may change more rapidly than organisms can evolve

3. Traps for lab biologists AND theorists
The organisms and processes we studied evolved in and currently function in environments: Physical, chemical, biological

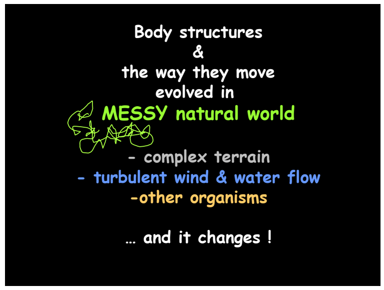
(Examples: The function of the neurons we heard about in yesterday's lecture depends on the chemistry of the medium around them. The motion of microscopic organisms in the real world depends on the ambient fluid flow in which they are swimming.)

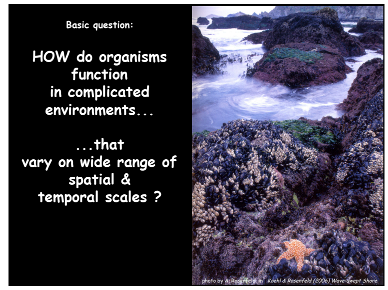
Can you really understand how a biological process works if your theory or experiments ignore the conditions in their environments?

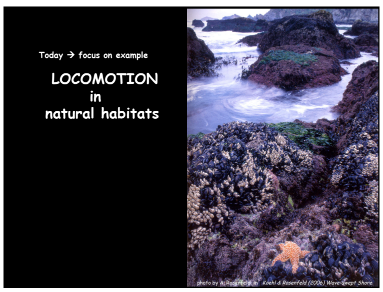
For your system, what are the important environmental factors that affect performance? How do those factors vary in space and time, and which spatial and temporal scales are relevant to the process you are studying?

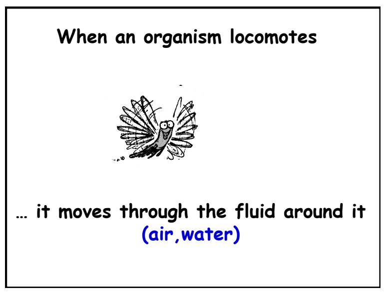
Here is an example from my research:

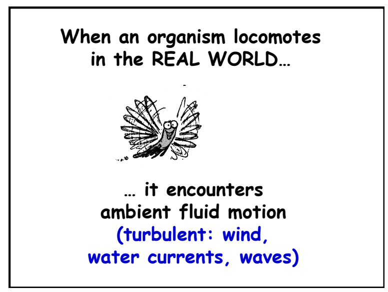

Moving through a turbulent environment:
Embedding models in real-world data
Mimi Koehl
University of California, Berkeley
photo by A. Rosenfeld, in Koehl & Rosenfeld (2006) Wave-swept Shore

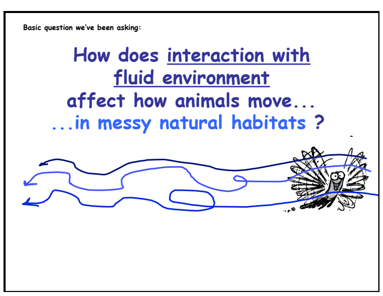

Body structures
&
the way they move
evolved in
MESSY natural world
- complex terrain
- turbulent wind & water flow
-other organisms
… and it changes !

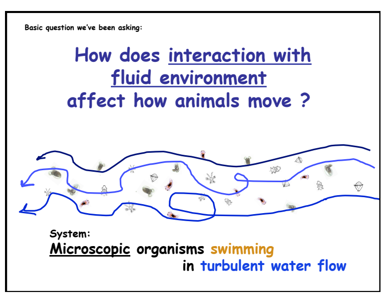

Basic question:
HOW do organisms
function
in complicated
environments...
...that
vary on wide range of
spatial &
temporal scales ?

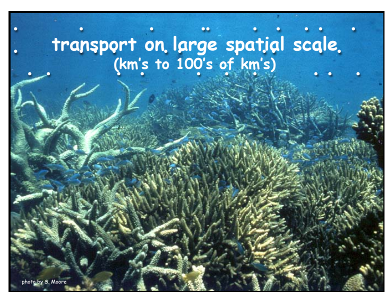

Today → focus on example
LOCOMOTION
in
natural habitats

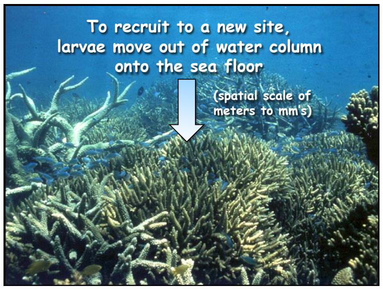

When an organism locomotes
… it moves through the fluid around it
(air,water)

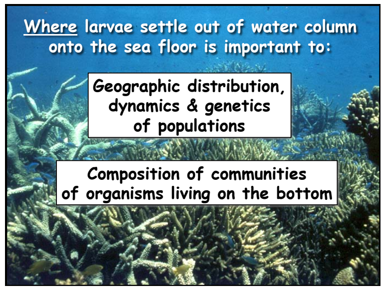

When an organism locomotes
in the REAL WORLD…
… it encounters
ambient fluid motion
(turbulent: wind,
water currents, waves)

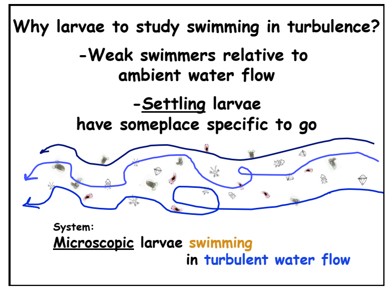

Basic question we've been asking:
How does interaction with
fluid environment
affect how animals move...
...in messy natural habitats ?

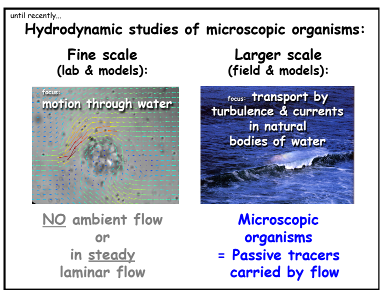

Basic question we've been asking:
How does interaction with
fluid environment
affect how animals move ?
System:
Microscopic organisms swimming
in turbulent water flow

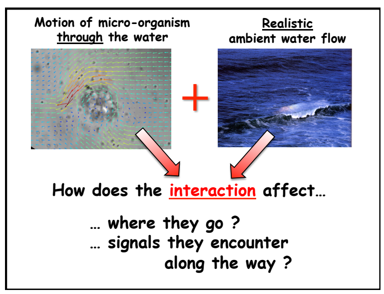

transport on large spatial scale
(km's to 100's of km's)

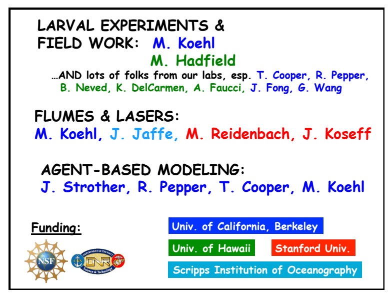

To recruit to a new site,
larvae move out of water column
onto the sea floor
(spatial scale of
meters to mm's)


Where larvae settle out of water column
onto the sea floor is important to:
Geographic distribution,
dynamics & genetics
of populations
Composition of communities
of organisms living on the bottom


Why larvae to study swimming in turbulence?
-Weak swimmers relative to
ambient water flow
-Settling larvae
have someplace specific to go
System:
Microscopic larvae swimming
in turbulent water flow


until recently...
Hydrodynamic studies of microscopic organisms:
Fine scale
(lab & models):
focus:
motion through water
Larger scale
(field & models):
focus: transport by
turbulence & currents
in natural
bodies of water
NO ambient flow
or
in steady
laminar flow
Microscopic
organisms
= Passive tracers
carried by flow


Motion of micro-organism
through the water
Realistic
ambient water flow
+
How does the interaction affect...
... where they go ?
... signals they encounter
along the way ?


LARVAL EXPERIMENTS &
FIELD WORK: M. Koehl
M. Hadfield
...AND lots of folks from our labs, esp. T. Cooper, R. Pepper,
B. Neved, K. DelCarmen, A. Faucci, J. Fong, G. Wang
FLUMES & LASERS:
M. Koehl, J. Jaffe, M. Reidenbach, J. Koseff
AGENT-BASED MODELING:
J. Strother, R. Pepper, T. Cooper, M. Koehl
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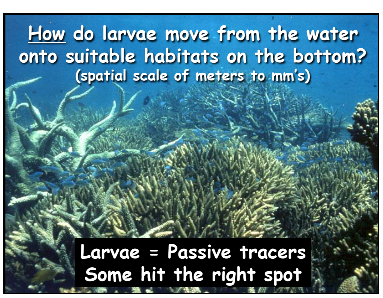
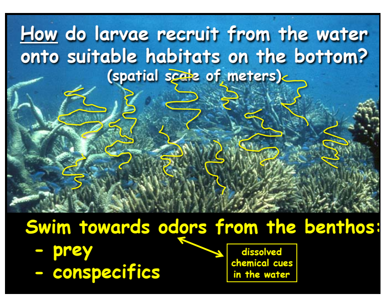
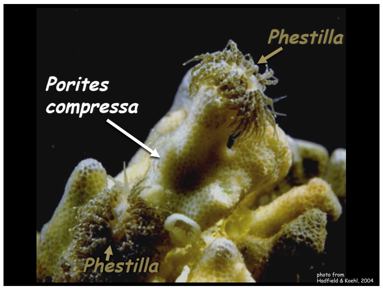
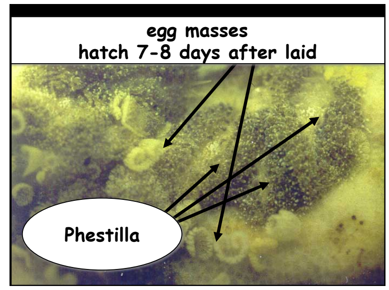
Univ. of Hawaii
Stanford Univ.
Scripps Institution of Oceanography

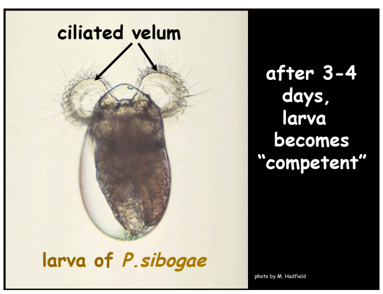

How do larvae move from the water
onto suitable habitats on the bottom?
(spatial scale of meters to mm's)
Larvae = Passive tracers
Some hit the right spot

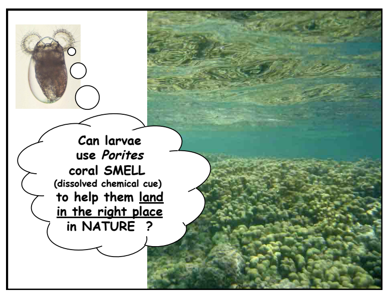

How do larvae recruit from the water
onto suitable habitats on the bottom?
(spatial scale of meters)
Swim towards odors from the benthos:
- prey
- conspecifics
dissolved
chemical cues
in the water


Phestilla sibogae







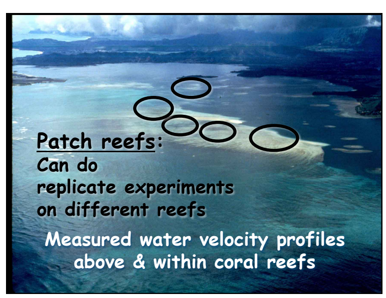


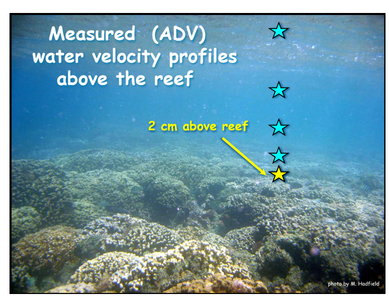
Can larvae use SMELLS (dissolved cues) to help them land in the right place in NATURE ?

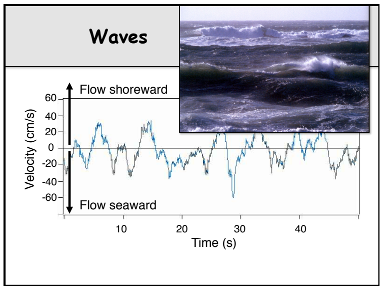
1. Water flow in the field?
2. Dispersal of dissolved coral smell?
3. Larval behavioral responses to dissolved coral smell?

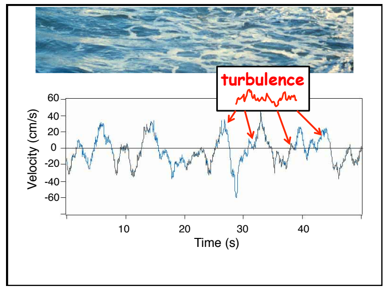
Do responses to coral smell affect where larvae land in ambient water flow?

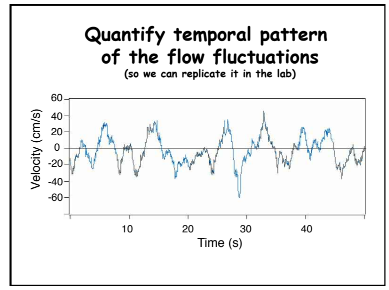
1. Water flow in the field?

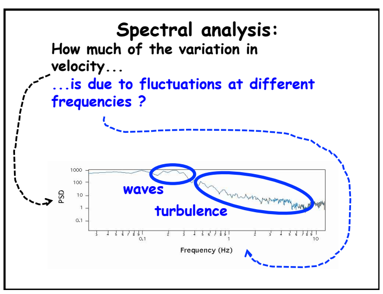


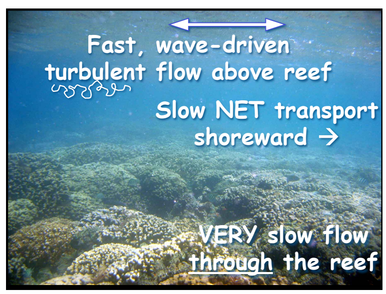


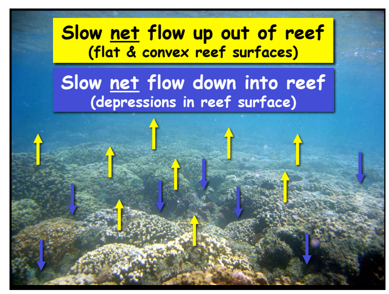

Waves
Flow shoreward
Flow seaward
Velocity (cm/s)
Time (s)

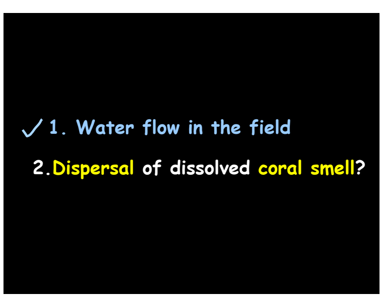

turbulence
Velocity (cm/s)
Time (s)

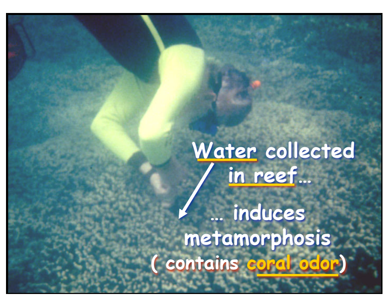

Quantify temporal pattern of the flow fluctuations
(so we can replicate it in the lab)
Velocity (cm/s)
Time (s)

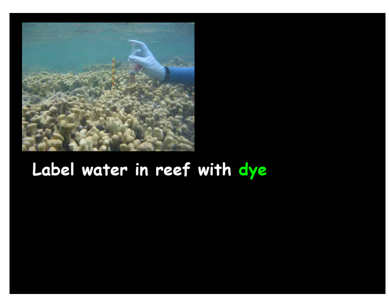

Spectral analysis:
How much of the variation in velocity…
…is due to fluctuations at different frequencies ?
waves
turbulence
PSD
Frequency (Hz)

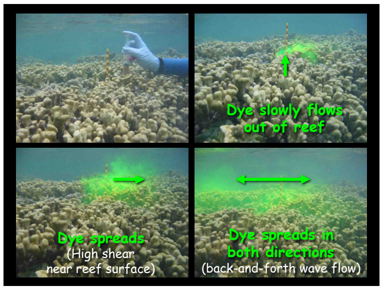

Fast, wave-driven turbulent flow above reef
Slow NET transport shoreward →
VERY slow flow through the reef

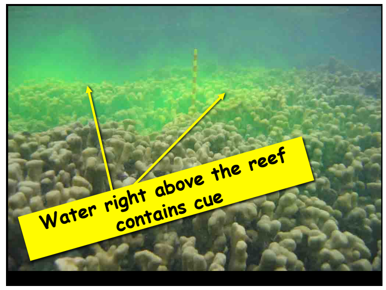

Slow net flow up out of reef
(flat & convex reef surfaces)
Slow net flow down into reef
(depressions in reef surface)

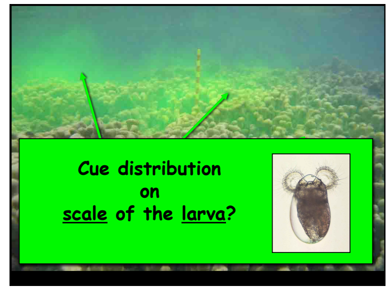

✓ 1. Water flow in the field
2. Dispersal of dissolved coral smell?

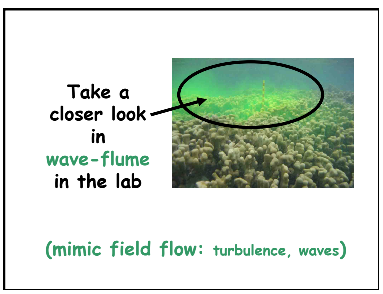

Water collected in reef…
… induces metamorphosis
(contains coral odor)

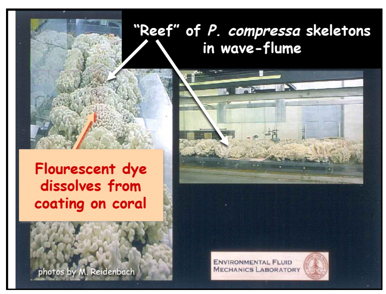

Label water in reef with dye

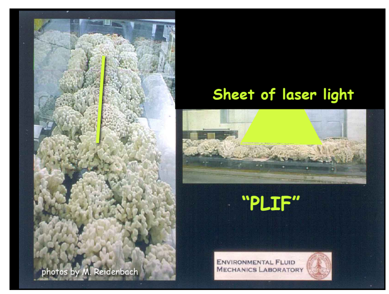


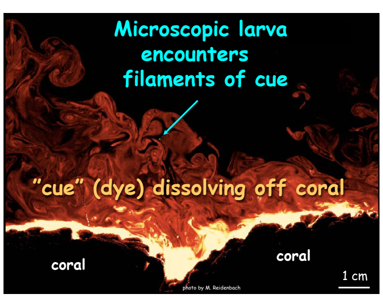








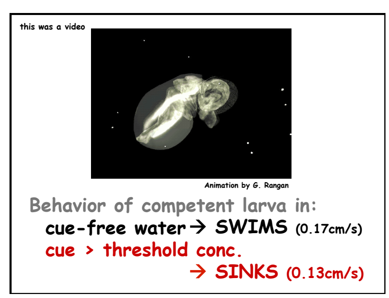




√ 1. Water flow in the field

√ 2. Dispersal of dissolved cues

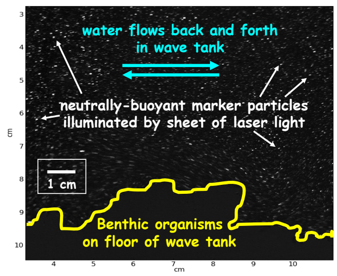
3. Behavioral responses of competent larvae to dissolved cue ?

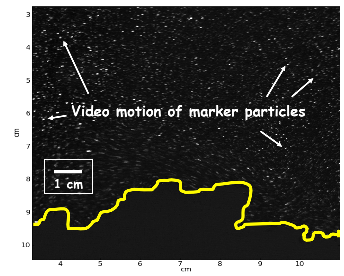


1. Water flow in the field?
2. Dispersal of dissolved cue?
3. Larval behavioral responses to dissolved cue?

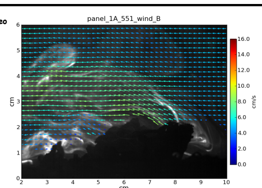
Do responses to cue affect where larvae land when carried in ambient water flow?

Flow on scale of mm's carries larvae



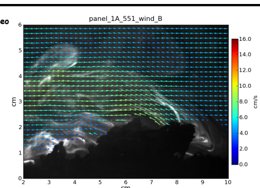


this was a video

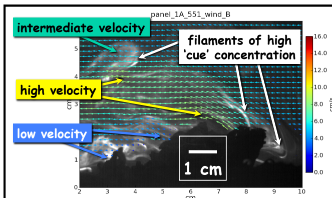


instantaneous velocity vectors (PIV)
(Red – fast) (Blue – slow)
& instantaneous "cue" concentrations (PLIF)
(lighter pixels – higher concentrations)

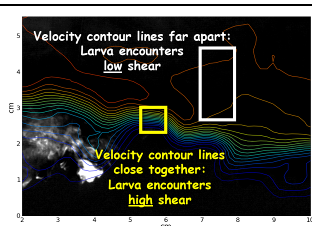
this was a video



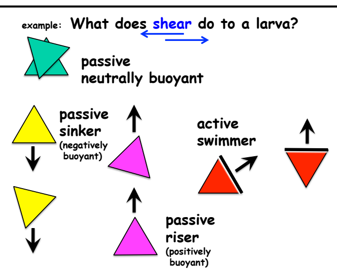
Velocity vectors & "cue" concentrations
CHANGE with time (0.1 – 1 seconds)

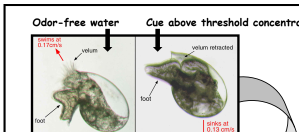


Velocity & "cue" concentrations
VARY on fine spatial scale (0.1mm's – cm's)

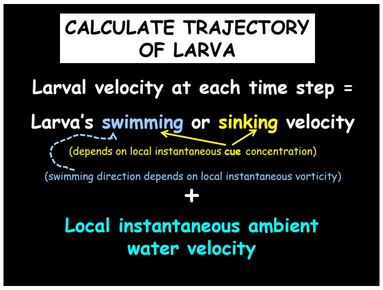


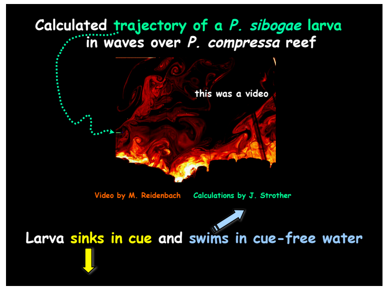
Shear varies rapidly (≤ seconds)
on spatial scales of mm's – cm's

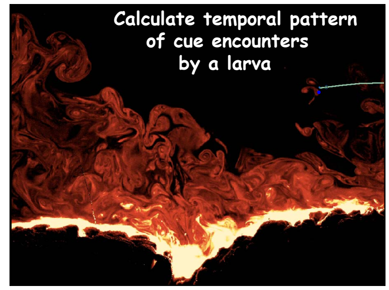


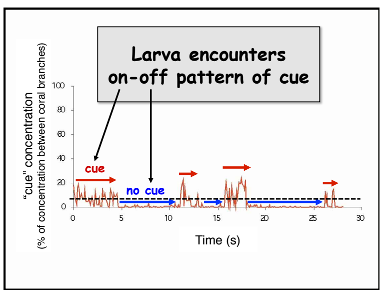


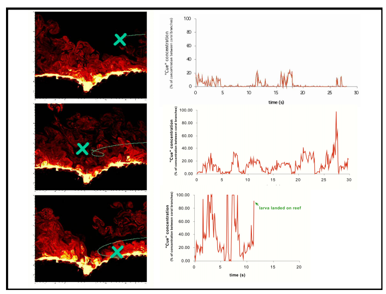
Put model "larvae"
with
this behavior
into
PLIF/PIV videos

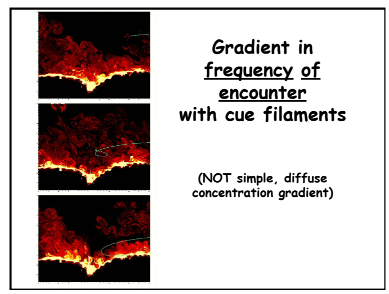

CALCULATE TRAJECTORY
OF LARVA
Larval velocity at each time step =
Larva's swimming or sinking velocity
(depends on local instantaneous cue concentration)
(swimming direction depends on local instantaneous vorticity)
+
Local instantaneous ambient
water velocity

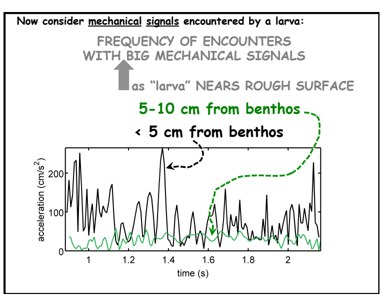

Calculated trajectory of a P. sibogae larva
in waves over P. compressa reef
this was a video
Video by M. Reidenbach
Calculations by J. Strother
Larva sinks in cue and swims in cue-free water

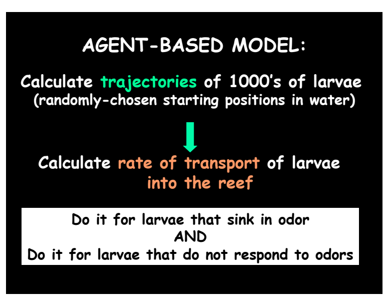

Calculate temporal pattern
of cue encounters
by a larva

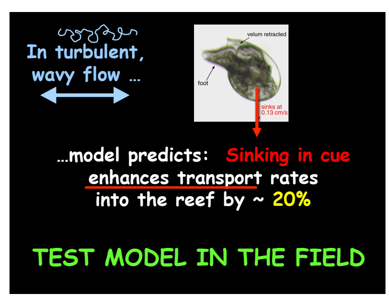

Larva encounters
on-off pattern of cue
"cue" concentration
(% of concentration between coral branches)
100
80
60
40
20
0
cue
no cue
0
5
10
15
20
25
30
Time (s)




Gradient in
frequency of
encounter
with cue filaments
(NOT simple, diffuse
concentration gradient)

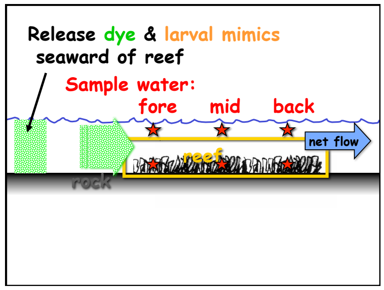

Now consider mechanical signals encountered by a larva:
FREQUENCY OF ENCOUNTERS
WITH BIG MECHANICAL SIGNALS
as "larva" NEARS ROUGH SURFACE
5-10 cm from benthos
< 5 cm from benthos
acceleration (cm/s²)
200
100
0
1
1.2
1.4
1.6
1.8
2
time (s)

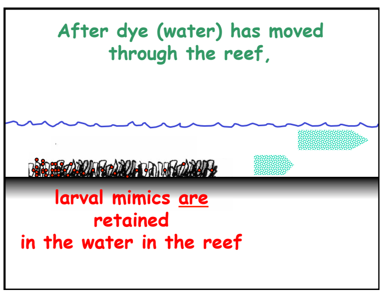

AGENT-BASED MODEL:
Calculate trajectories of 1000's of larvae
(randomly-chosen starting positions in water)
Calculate rate of transport of larvae
into the reef
Do it for larvae that sink in odor
AND
Do it for larvae that do not respond to odors


In turbulent,
wavy flow ...
velum retracted
foot
sinks at
0.13 cm/s
...model predicts: Sinking in cue
enhances transport rates
into the reef by ~ 20%
TEST MODEL IN THE FIELD

MODEL ASSUMES:
Larvae that sink into reef
are retained in water
within reef

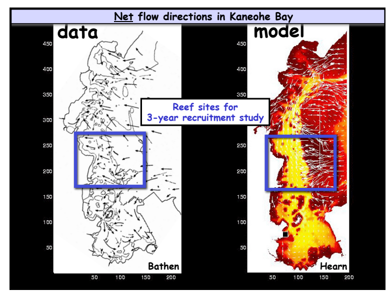
FIELD TEST:
Release larval mimics upstream
of reefs.
Are they retained
in water within reefs?





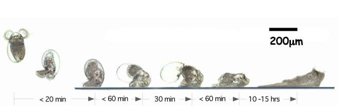
MODEL PREDICTS:
More larvae land on
seaward part of reef

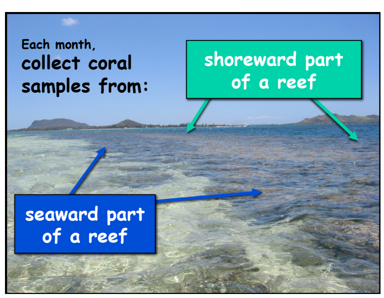
FIELD TEST:
Is *Phestilla* recruitment
greater on
seaward parts of reefs?



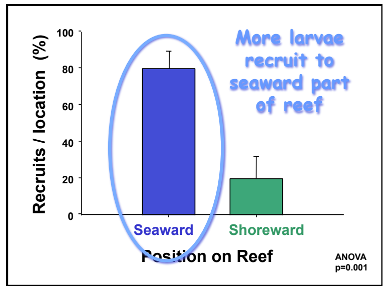
Problem: New recruits are
really tiny !

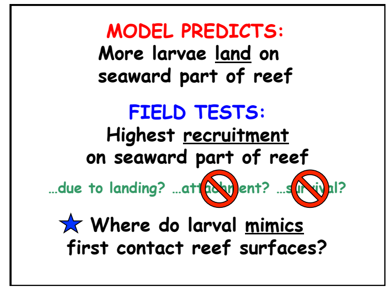
(We can't see them on coral.)

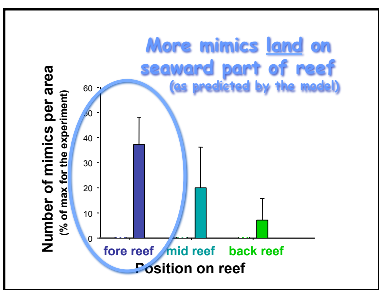


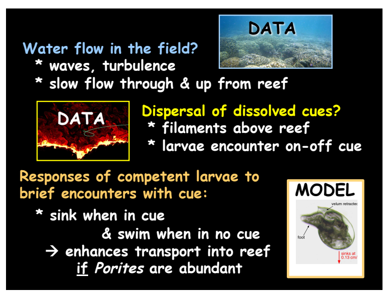


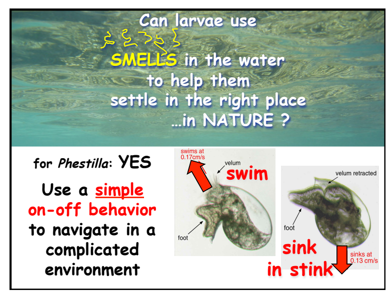

After 2 weeks,
(slugs ~6 mm)
counted # Phestilla
per kg coral

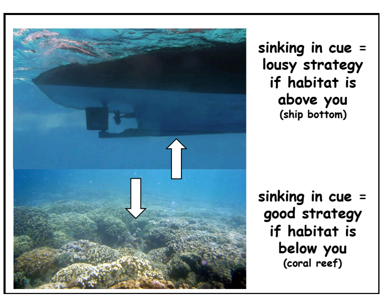

More larvae recruit to seaward part of reef
Recruits / location (%)
100
80
60
40
20
0
Seaward
Shoreward
Position on Reef
ANOVA
p=0.001


MODEL PREDICTS:
More larvae land on seaward part of reef
FIELD TESTS:
Highest recruitment on seaward part of reef
…due to landing?
Where do larval mimics first contact reef surfaces?

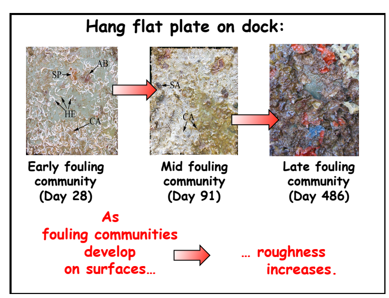

More mimics land on seaward part of reef
(as predicted by the model)
Number of mimics per area
(% of max for the experiment)
60
40
30
20
10
0
fore reef
mid reef
back reef
Position on reef

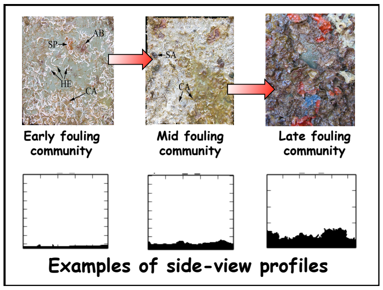

DATA
Water flow in the field?
* waves, turbulence
* slow flow through & up from reef
DATA
Dispersal of dissolved cues?
* filaments above reef
* larvae encounter on-off cue
Responses of competent larvae to brief encounters with cue:
* sink when in cue
& swim when in no cue
→ enhances transport into reef
if Porites are abundant
MODEL

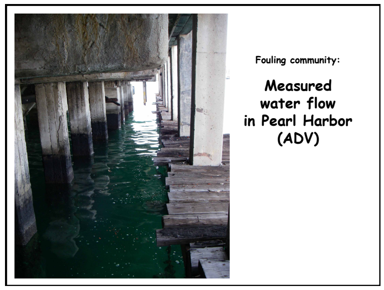

Can larvae use
SMELLS in the water
to help them
settle in the right place
…in NATURE ?
for Phestilla: YES
Use a simple on-off behavior to navigate in a complicated environment
swim
velum
foot
velum retracted
foot
sink
in stink

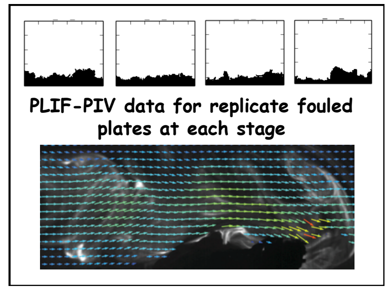

sinking in cue = lousy strategy if habitat is above you
(ship bottom)
sinking in cue = good strategy if habitat is below you
(coral reef)

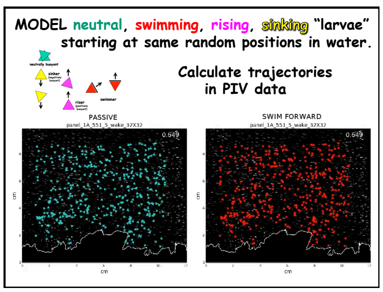

"Fouling" community on ships & docks:
How do microscopic larvae carried in the water land on surfaces ABOVE them or NEXT TO them in harbors ?

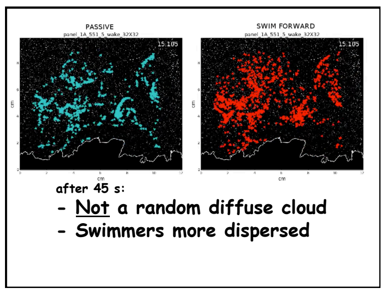

Hang flat plate on dock:
SP
AB
HE
CA
SA
CA
Early fouling community (Day 28)
Mid fouling community (Day 91)
Late fouling community (Day 486)
As fouling communities develop on surfaces…
… roughness increases.

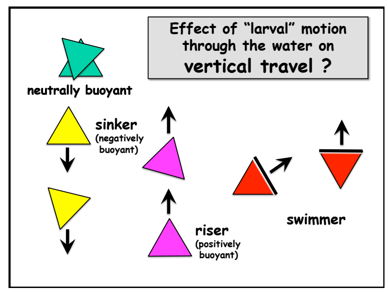

Early fouling community
Mid fouling community
Late fouling community
Examples of side-view profiles

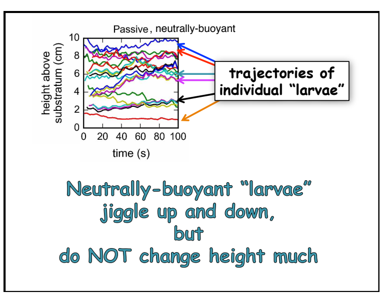

Fouling community:
Measured water flow in Pearl Harbor (ADV)

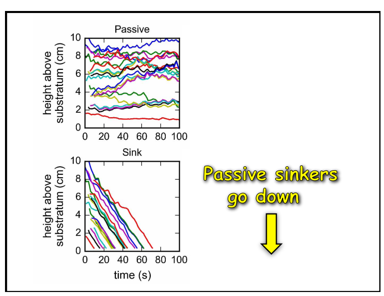

PLIF-PIV data for replicate fouled plates at each stage

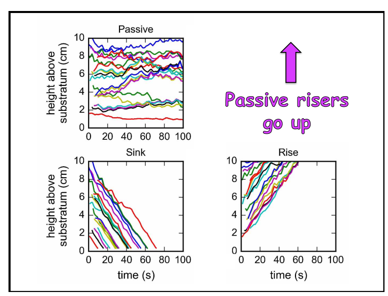

MODEL neutral, swimming, rising, sinking "larvae" starting at same random positions in water.
Calculate trajectories in PIV data
PASSIVE
SWIM FORWARD

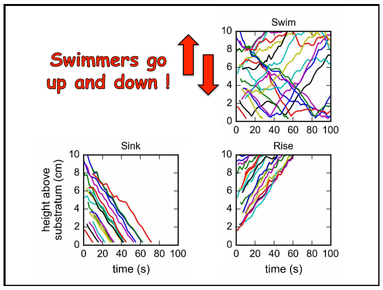

PASSIVE
SWIM FORWARD
after 45 s:
- Not a random diffuse cloud
- Swimmers more dispersed

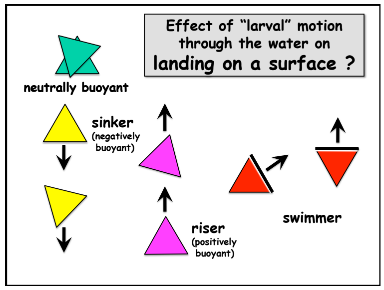

Effect of "larval" motion through the water on vertical travel ?
neutrally buoyant
sinker (negatively buoyant)
riser (positively buoyant)
swimmer

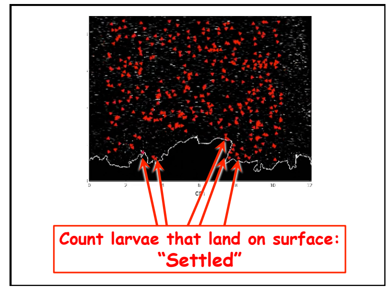

Passive, neutrally-buoyant
height above substratum (cm)
time (s)
trajectories of individual "larvae"
Neutrally-buoyant "larvae" jiggle up and down, but do NOT change height much

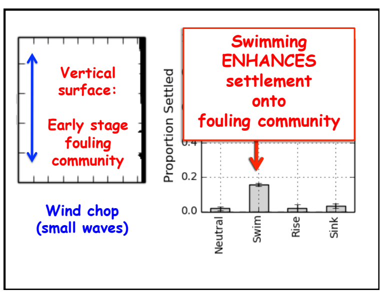

Passive
Sink
height above substratum (cm)
time (s)
Passive sinkers go down

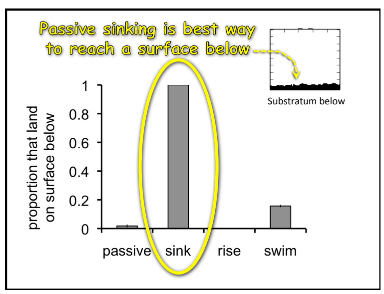

Passive
Sink
Rise
height above substratum (cm)
time (s)
Passive risers go up

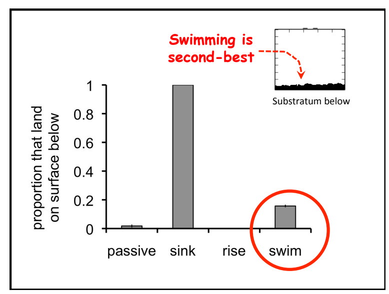

Swimmers go up and down !
Swim
Sink
Rise
height above substratum (cm)
time (s)

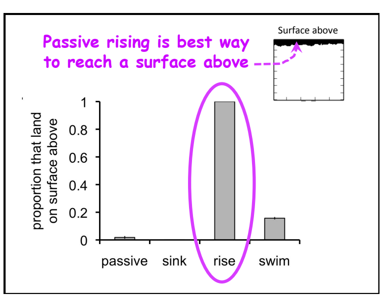

Effect of "larval" motion through the water on landing on a surface ?
neutrally buoyant
sinker
(negatively buoyant)
riser
(positively buoyant)
swimmer

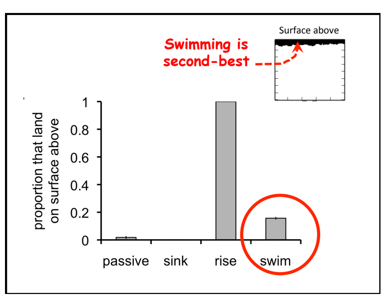

Count larvae that land on surface:
"Settled"

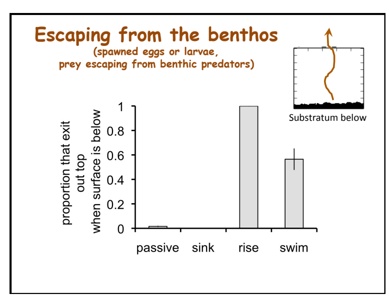

Vertical surface:
Early stage fouling community
Wind chop
(small waves)
Swimming ENHANCES settlement onto fouling community
Proportion Settled
Neutral
Swim
Rise
Sink


Passive sinking is best way to reach a surface below
Substratum below
proportion that land on surface below
passive
sink
rise
swim

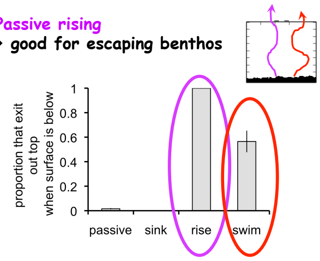

Swimming is second-best
Substratum below
proportion that land on surface below
passive
sink
rise
swim


Passive rising is best way to reach a surface above
Surface above
proportion that land on surface above
passive
sink
rise
swim


Swimming is second-best
Surface above
proportion that land on surface above
passive
sink
rise
swim


Escaping from the benthos
(spawned eggs or larvae, prey escaping from benthic predators)
Substratum below
proportion that exit out top when surface is below
passive
sink
rise
swim

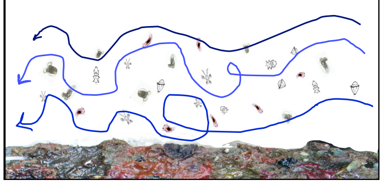
Passive rising
→ good for escaping benthos



Let's sum up what we've learned so far by asking:

WHY SWIM ?

… when you are a tiny, slow, wimpy larva tumbled in turbulent boundary layer



WHY SWIM ?

Swimming & passive rising
→ best escape from benthos

Swimming
→ best landing on vertical surfaces

Swimming
→ second-best landing on surfaces above or below
(passive rising best) (passive sinking best)

WHY SWIM ?

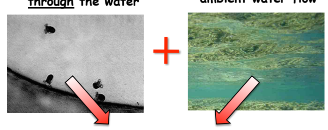
Swimming & passive rising
→ best escape from benthos

Swimming
→ best landing strategy if surface location is unpredictable

summarize:

Motion of micro-organism through the water

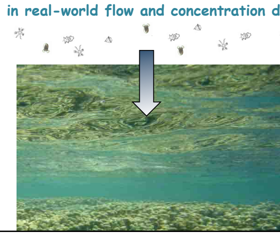
Realistic ambient water flow



How does the interaction affect where they go ?

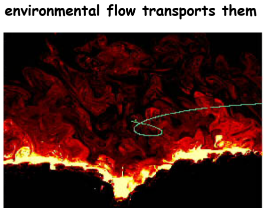
One way to address this question:

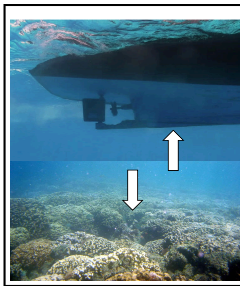
Embed models of behavior in real-world flow and concentration data



we learned...

Behavior of microscopic organisms can bias how environmental flow transports them





Swimming in signal = good strategy if habitat location not predictable (e.g. fouling community)

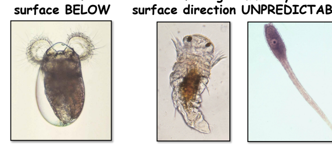
Sinking in signal = good landing strategy if habitat is below you (e.g. coral reef)

test this

How do real larvae react to rapidly-fluctuating
chemical
mechanical
signals that indicate a surface is nearby?

coral reef: surface BELOW

fouling community: surface direction UNPREDICTABLE

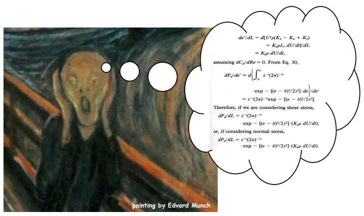


Phestilla sibogae SINK

Hydroides elegans always SWIM

Phallusia philippinensis start to SWIM let me end by saying

Reaction of many biologists to mathematical biology:

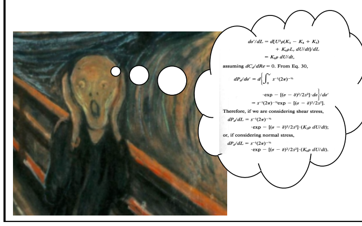


the example I discussed today showed

What modeling can do for me (biologist):

1. Allows me to run "experiments" not possible in real world
2. Tells me which parameters are most important (... worth measuring or studying)
3. Enables me to test hypothesized mechanisms & general principles (quantitative expression of an idea → testable predictions)

How many biologists react to mathematical biology



This biologist's perspective on mathematical biology