Succession: ecological processes structuring vent communities

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Deep Ocean Exploration Inst. WHOI
Ocean Life Inst. WHOI

Definitions of Succession

- Predictable change in community structure that produces changes in ecosystem (Odum 1969)
- Sequence of changes initiated by disturbance (Ricklefs 1990)
- Non-seasonal, directional and continuous pattern of colonization and extinction on a site by species popuations (Begon et al. 1996)

Models of succession

- **Environmental gradients** Drury and Nisbet 1973
  - different life-history characteristics
- **Chronic Disturbance** Horn 1975
  - disturbance can create patches to be colonized by available larvae
- **Facilitation, Tolerance, Inhibition** Connell and Slatyer 1977
  - change in cause of mortality
  - competition vs. external factors
- **Resource-ratio (R*) Hypothesis** Tilman 1988
  - change in relative competitive abilities

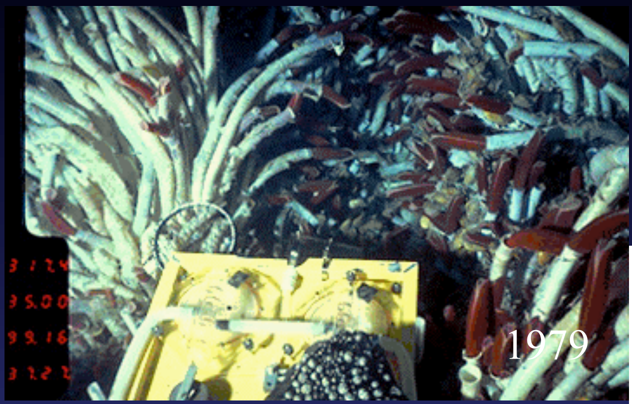
“Classic” Mechanisms of Succession

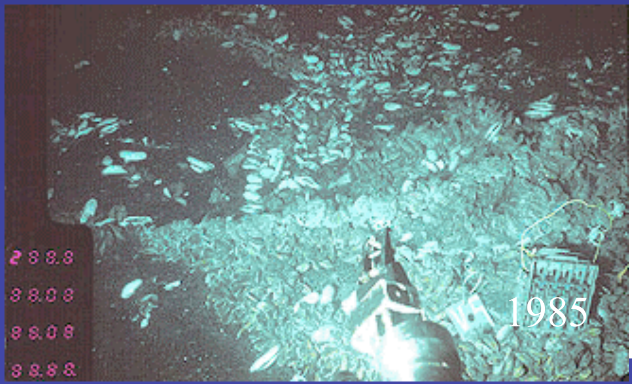
- **Facilitation:** Early occupants change the abiotic environment in a way that makes it comparatively less suitable for themselves and more suitable for the recruitment of others.

- **Tolerance:** Later species are able to tolerate lower resource levels and can grow to maturity in the presence of early species, eventually out-competing them.

- **Inhibition:** Species resist invasion of competitors. Later species gradually accumulate by replacing early individuals, only when they die.

"Succession" at Vents
Galápagos Rift





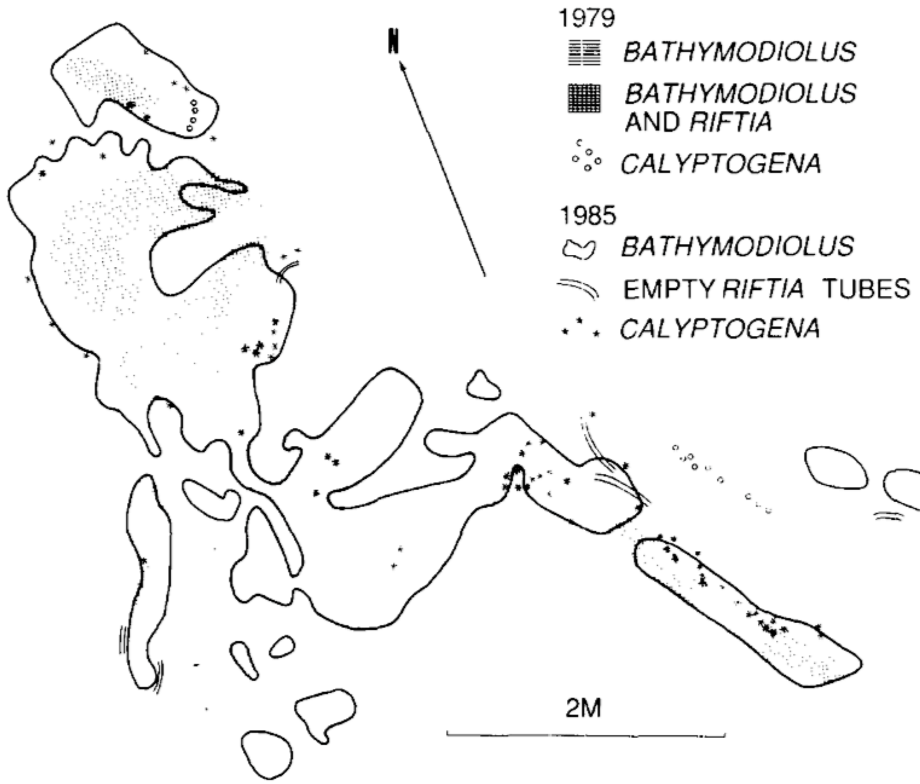
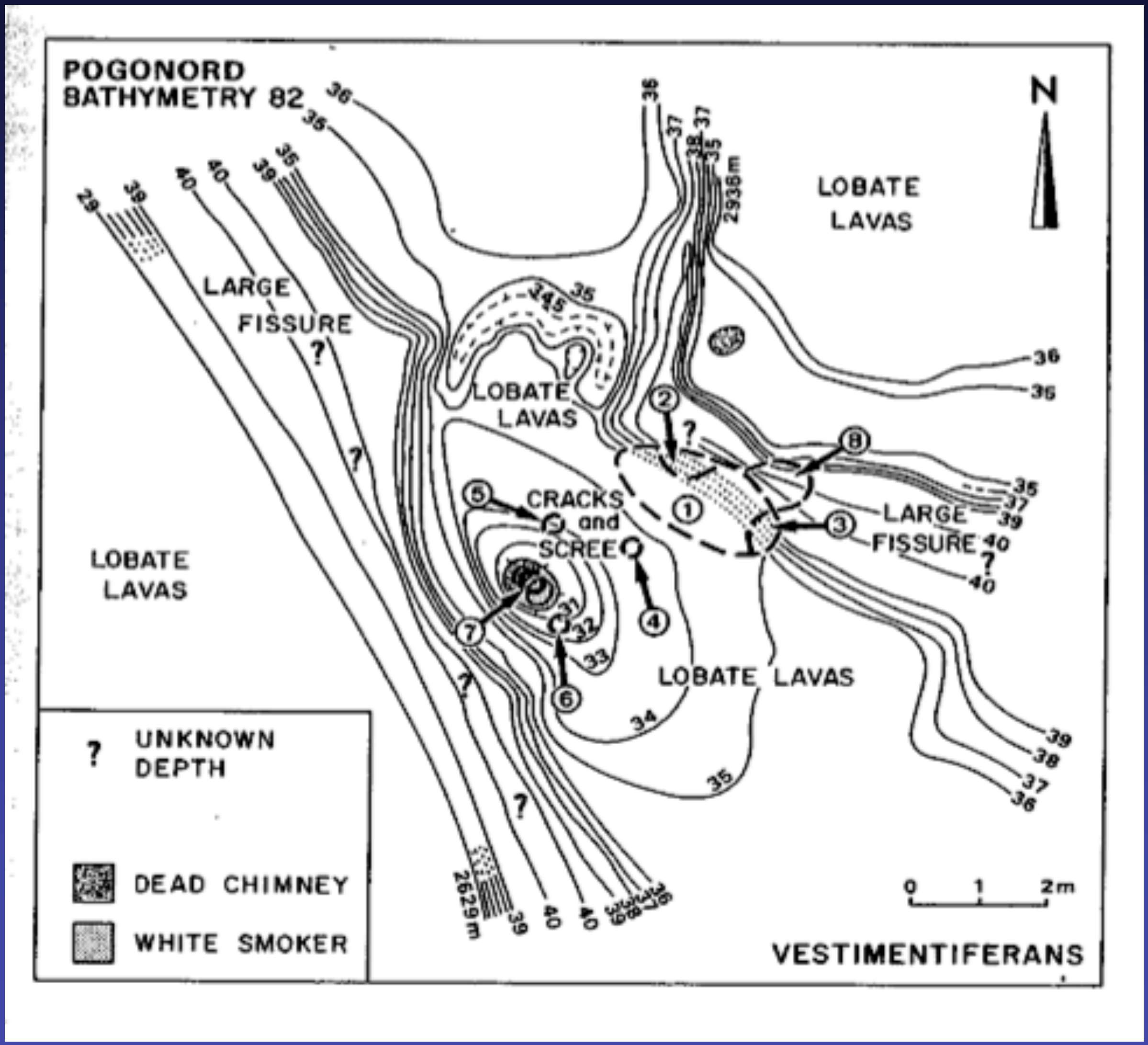


Fig. 3. Distribution in 1979 and 1985 of megafaunal hosts to cheomoautotrophic bacteria at clumps along meridian C.0, from 5.5 to 7.0 on the map in Fig. 1. The patterns for *Bathymodiolus* and living *Riftia* have been simplified.

Hessler et al. 1988

East Pacific Rise

13°N

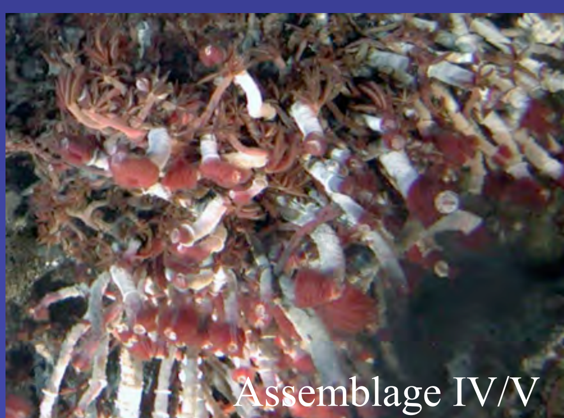


Patterns of recovery
After disturbances:

- lava collapse
- organismal sampling

Fustec et al. 1987

Juan de Fuca Ridge



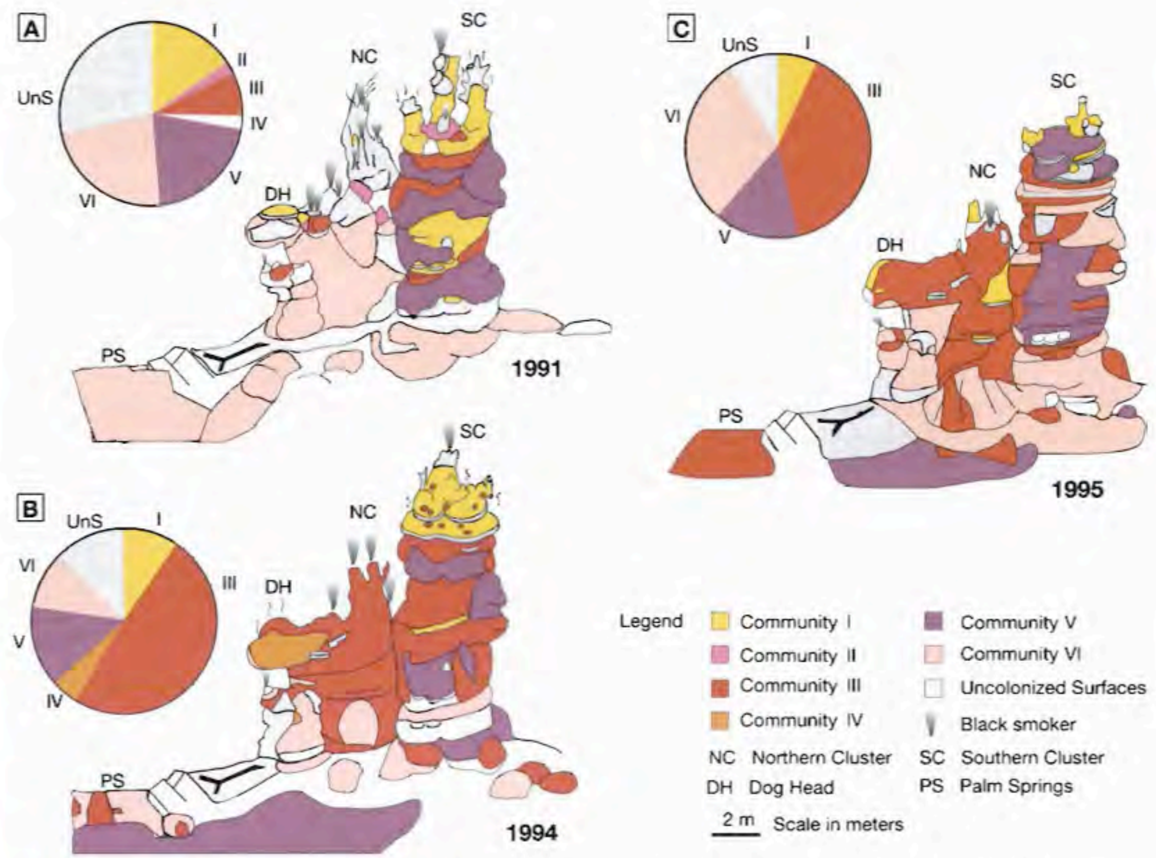
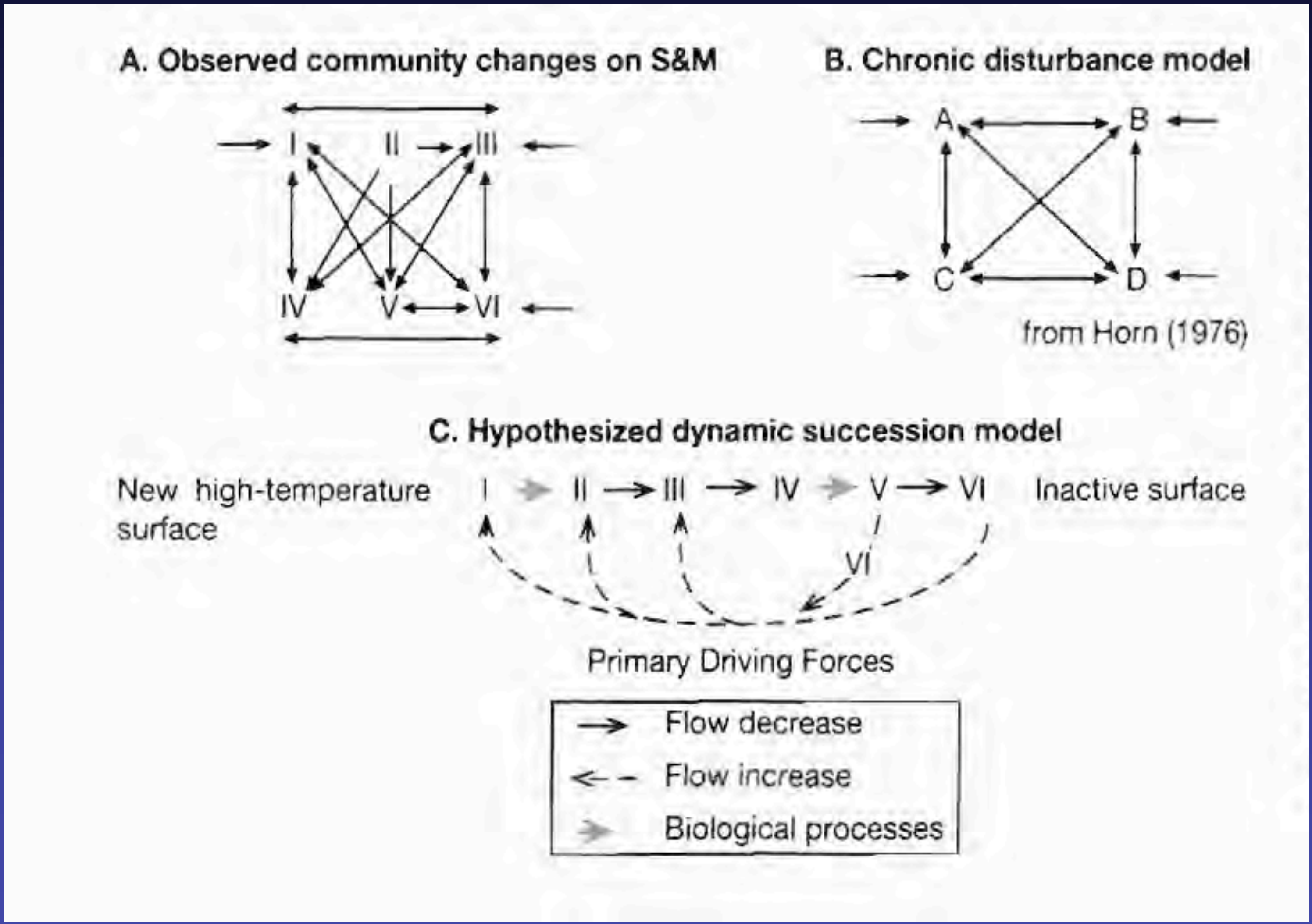


Fig. 3. Community spatio-temporal distribution maps of the west face of S&M: (A) 1991 (July); (B) 1994 (July); (C) 1995 (July). White zones represent unmapped areas. Pie diagrams summarize relative distribution of communities and uncolonized surfaces on the sulfide edifice for the different years

Sarrazin et al. 1997

Patterns correlated with fluid flux



Juan de Fuca Ridge

Sarrazin et al. 1997

Co-Axial Seamount

1993 volcanic eruption
"snowblowers"
abundance of hyperothermophiles

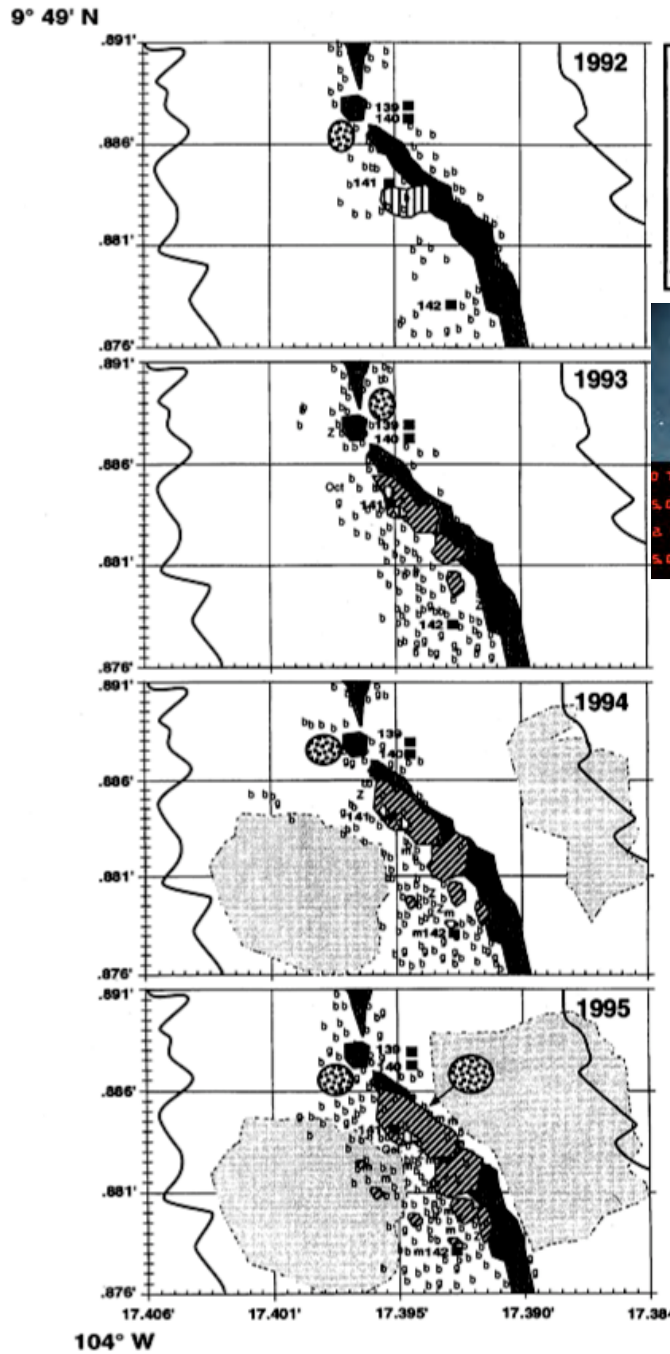
1994 *Ridgeia piscesae* tubeworms
Paralvinella pandorae polychaetes

1995 *Ridgeia* tubeworms grew, *P. pandorae* (smaller)
P. palmiformis (larger)

Patterns of recovery after disturbances:
- eruption

Tunnicliffe et al. 1997

East Pacific Rise 9°50’N



Shank et al. 1998

Patterns of recovery after disturbances:

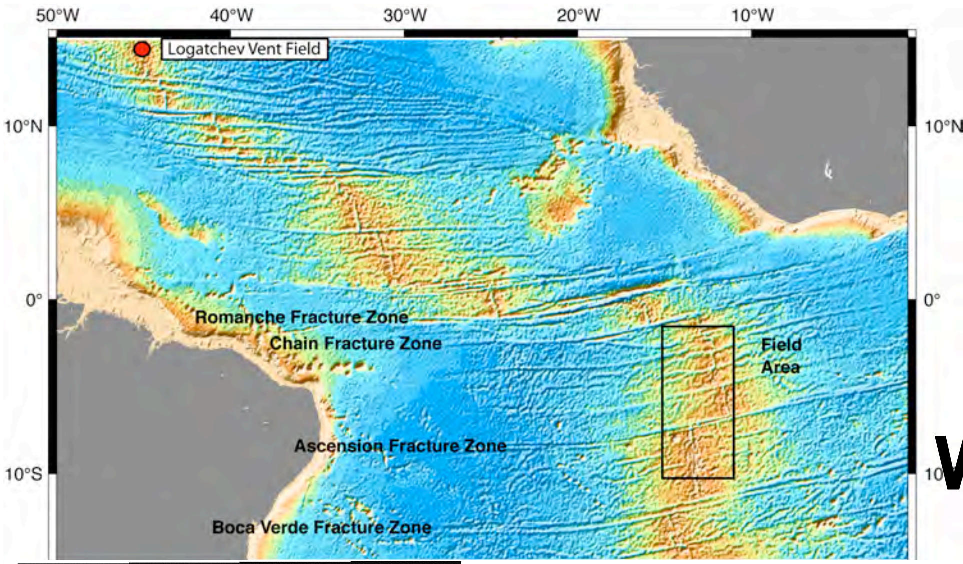
- eruption

Mid-Atlantic Ridge

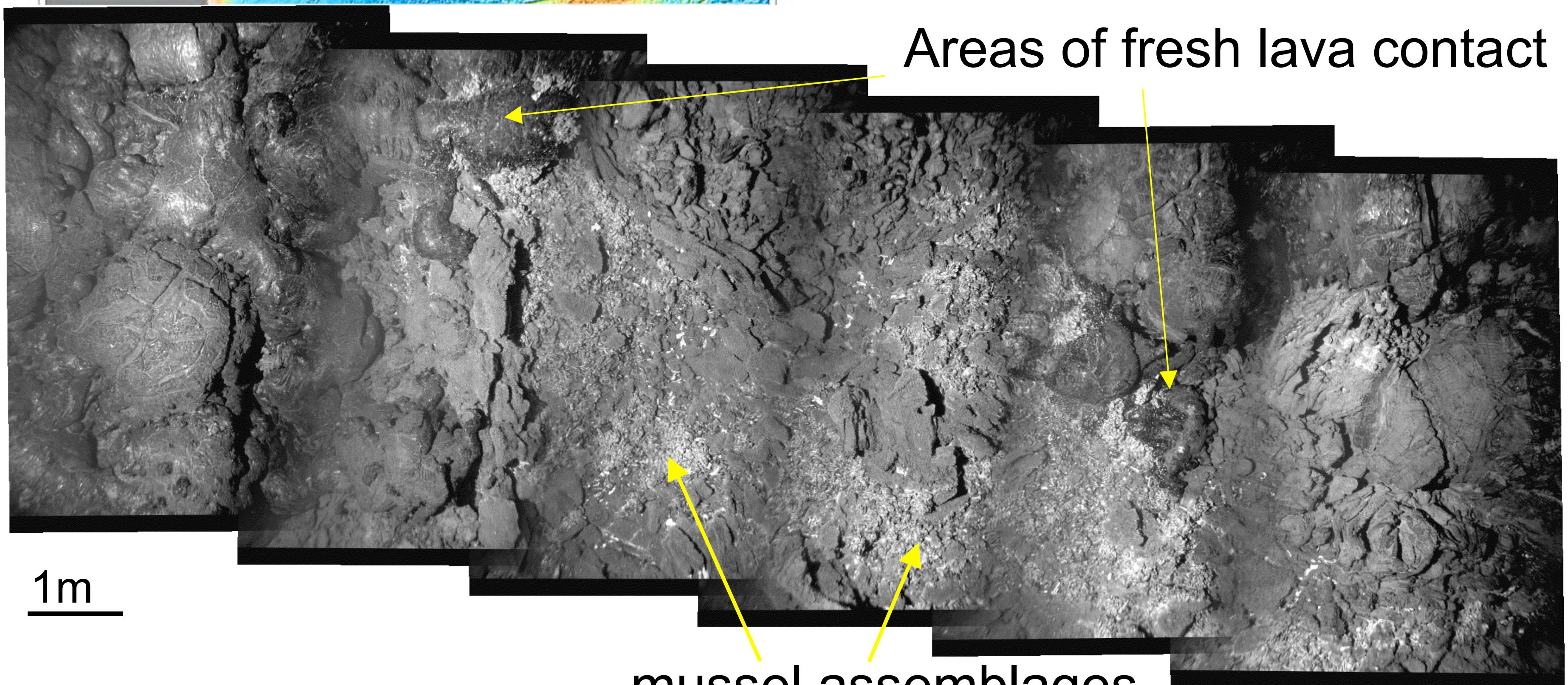
- Broken Spur Copley et al. 1997
  - Interannual variation
  - Shrimp at low density
  - No change in 15 months
- TAG Copley et al. 1999, 2007
  - Subannual variation
  - After drilling
    - Shrimp density shifted with fluid flow
    - Anemones did not change
  - Similar shrimp abundance/composition in 1994/2004

Slow-spreading rate, less disturbance… temporal stability in community structure

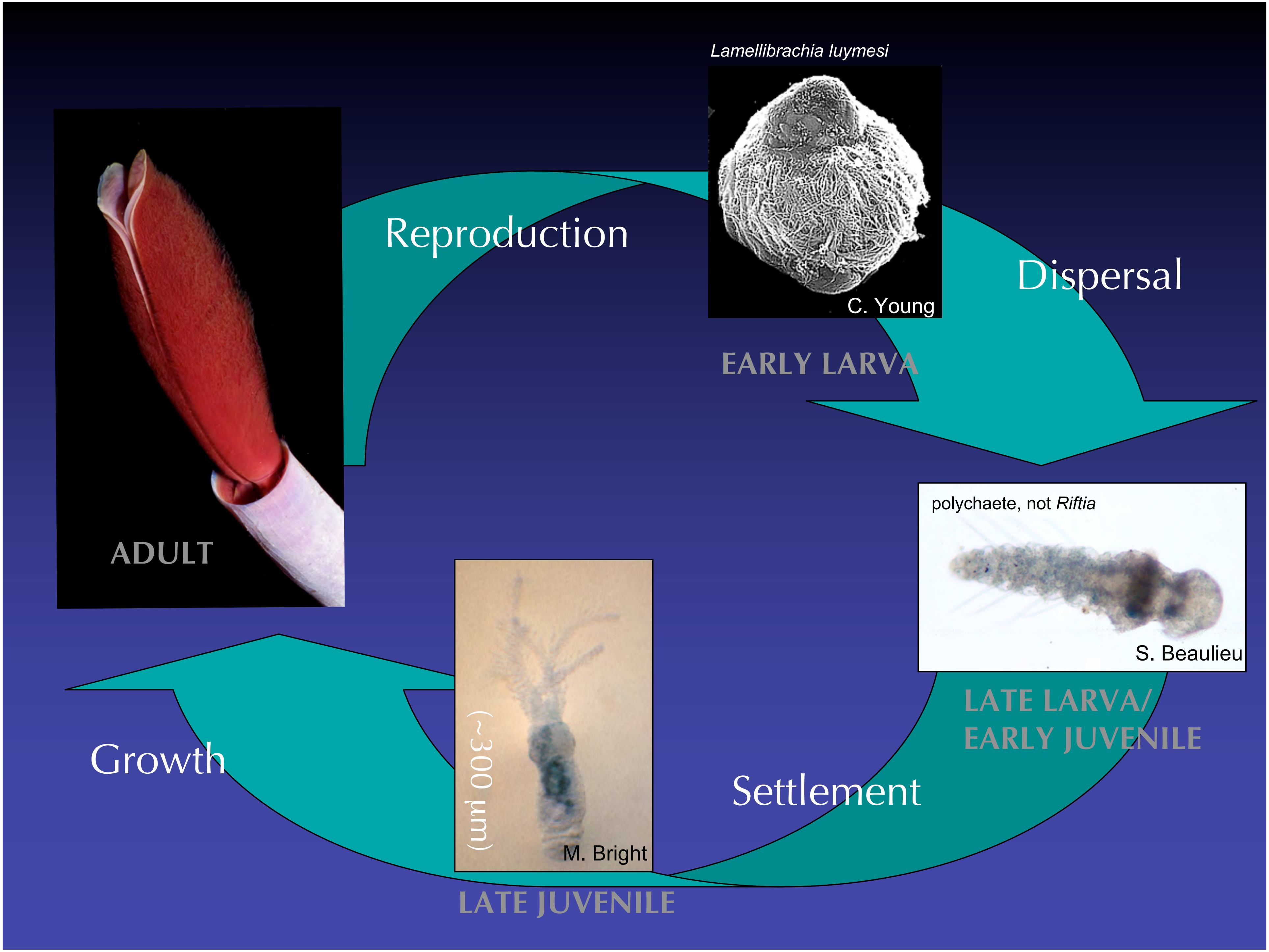
Southern Mid-Atlantic Ridge



Wide Awake Mussel Field



Shank et al (in prep)


Lamellibrachia luymesi
C. Young
Reproduction
Dispersal
EARLY LARVA
ADULT
polychaete, not Riftia
S. Beaulieu
LATE LARVA/
EARLY JUVENILE
Growth
(~300 µm)
M. Bright
Settlement
LATE JUVENILE

Major Controls on “Succession”

- Habitat suitability (e.g., substrate, chemistry)
- Realized dispersal, larval availability, distance from source populations
- Physiology and ecology of larvae, colonists, adults
- Geochemical and biological influences affecting community structure (e.g., resources and competition)

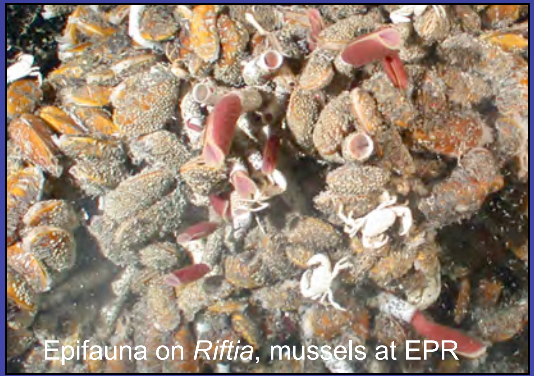
Succession

(geochemical and biological factors)

Stacks of *Lepetodrilus fucensis* at JdFR

- Microhabitat conditions
- Microbial alteration of the habitat

- Biological interactions (positive and negative)
  - JdFR
    - Gregarious settlement of gastropods (*Lepetodrilus* and *Provanna*)
    - Post-settlement mortality of polychaetes (*Amphisamtha* and *Parougia*)
      Kelly et al. 2007
  - EPR
    - Facilitation of conspecifics by serpulid polychaetes
    - Inhibition of colonists by gastropods and a dorvelleid polychaete
      Mullineaux et al. 2003
    - Predation by fish on gastropods and amphipods
      Micheli et al. 2001
    - Habitat provision by foundation species
      Govenar and Fisher 2007



Epifauna on *Riftia*, mussels at EPR

Chemical-Biological Interactions

Evidence for vent fluid chemistry as structuring force

1. Abrupt geochemical change

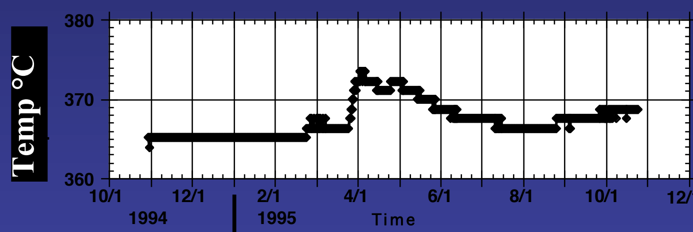
1991

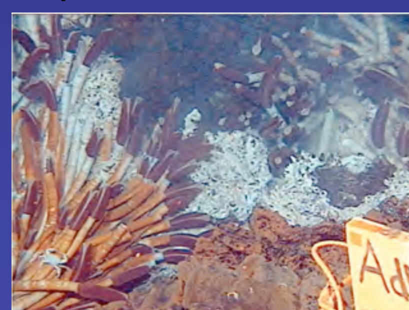
1994

1995

Shank et al. 1998
Von Damm & Lilley 2004

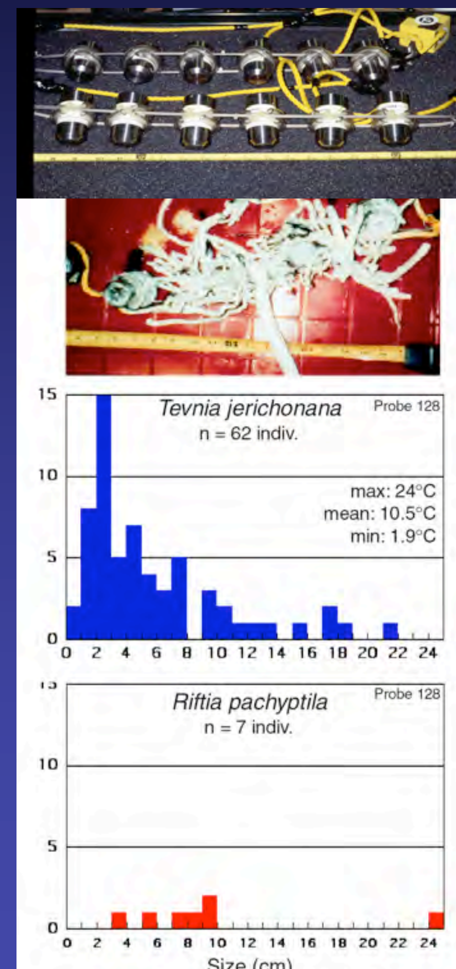
2. Crustal cracking event



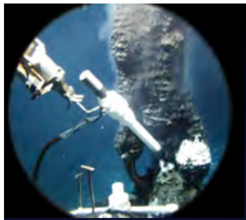


Sohn et al. 1996
Fornari et al. 1998

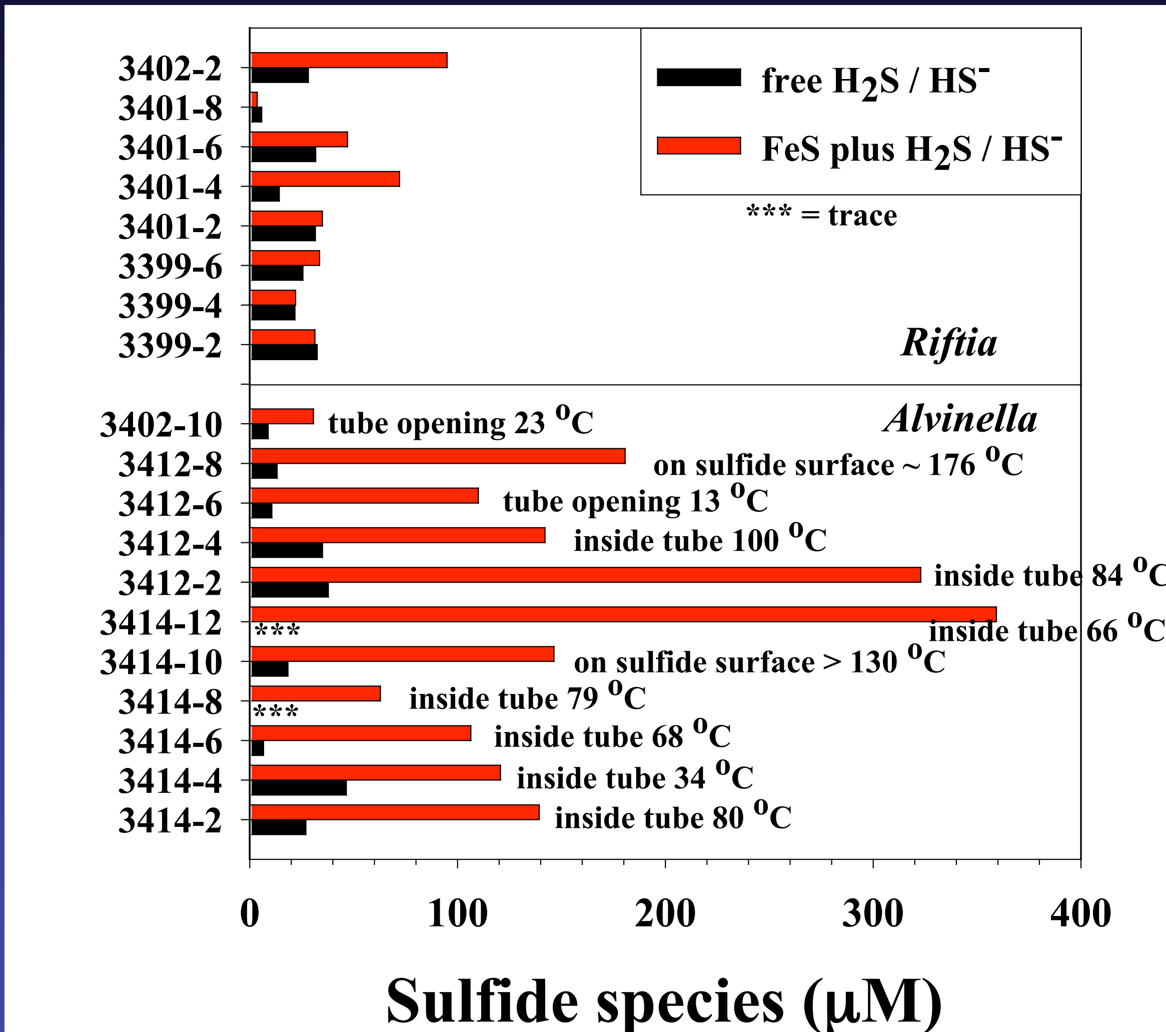
3. Colonization preference



Shank et al. 1997



Microhabitat Comparison of Free H_2S / HS^- (*in situ*) and Total Sulfides



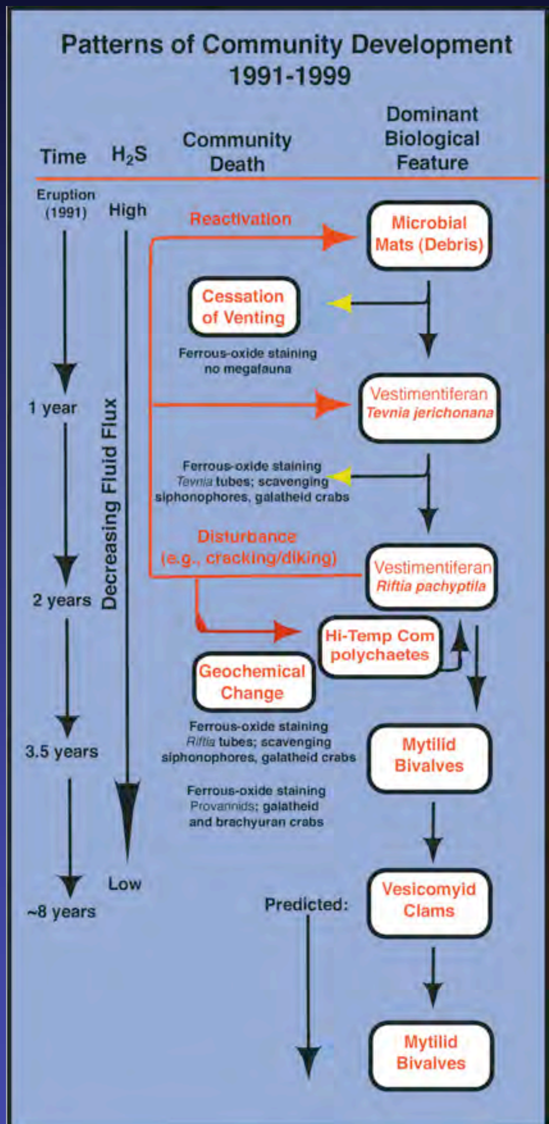
Luther et al. 2001

***Riftia* - H_2S predominates**
Lower T°C; higher pH

***Alvinella* - FeS predominates**
Higher T°C; lower pH
Total sulfide higher

Chemical-Biological Interactions

Patterns correlated with fluid chemistry



Shank et al. 1998

- Snowblowers, bacterial mats associated with vigorous diffuse-flow
- Crabs, limpets respond to productivity
- Tubeworms first sessile metazoans among diffuse-flow
- Bivalves colonize within a few years and overgrow tubeworms
- Serpulids and filter-feeders increase in area as fluid flux wanes

East Pacific Rise

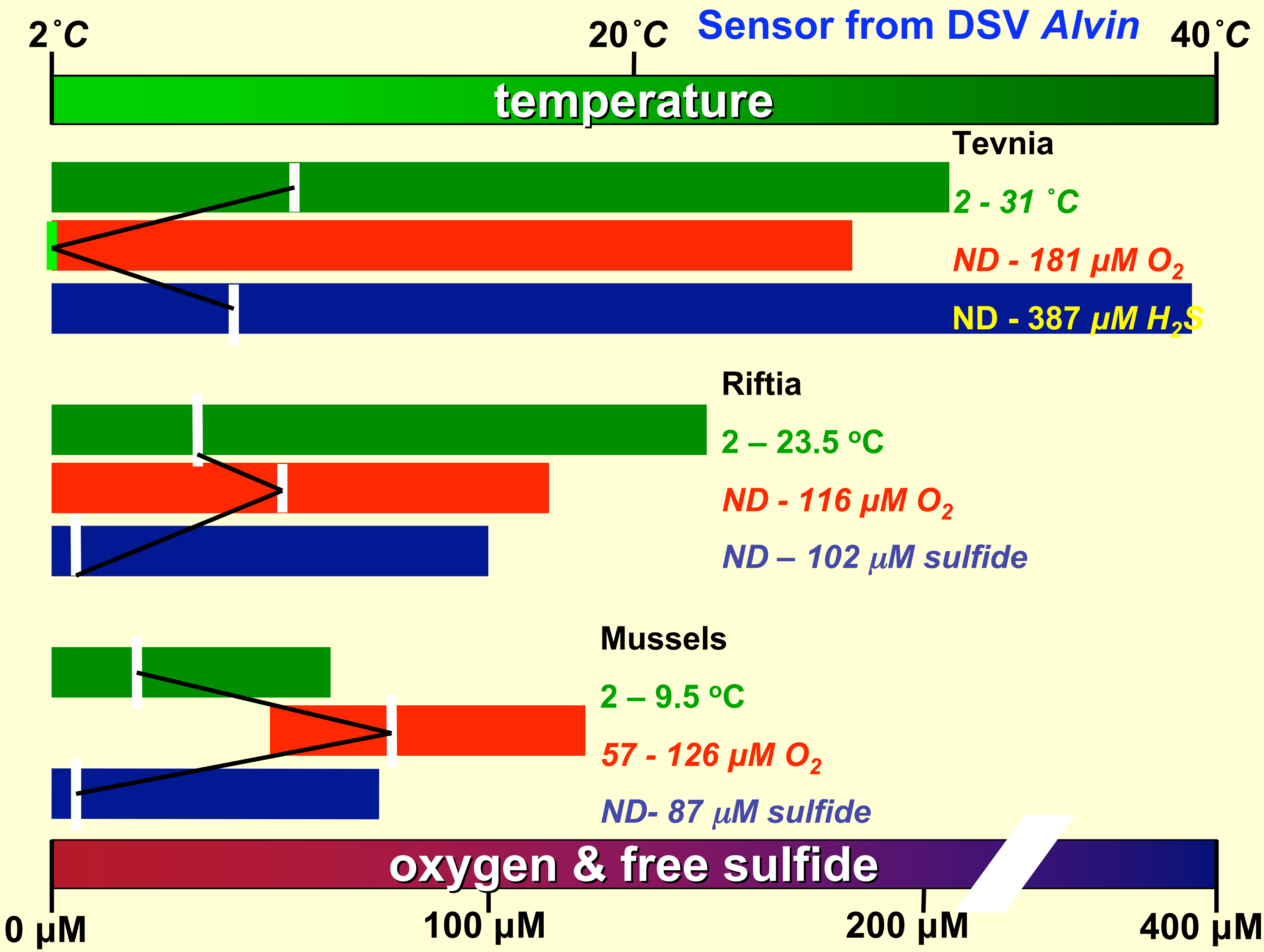
“Succession” studies as a framework

- Gaps and challenges in our understanding
- Integrated temporal experiments
- Consequences of succession on genetic diversity
- Geo-bio-chemical interactions

Fundamental Gaps in Our Understanding

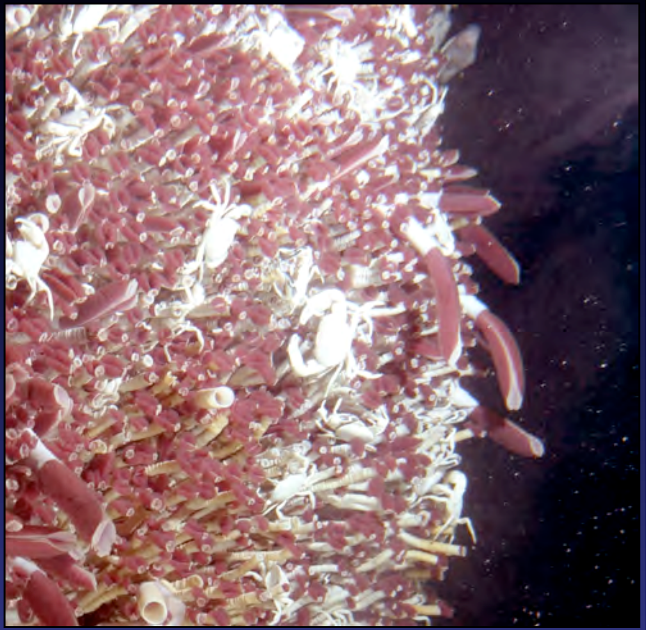
- Physiology of life-history stages in species
- <u>Habitat conditions associated w/ individual species</u>
- Disturbance frequency and geo-chem-bio response
- Interaction between free-living microbes and fauna

2007 - 9° 50’ N East Pacific Rise (all data)



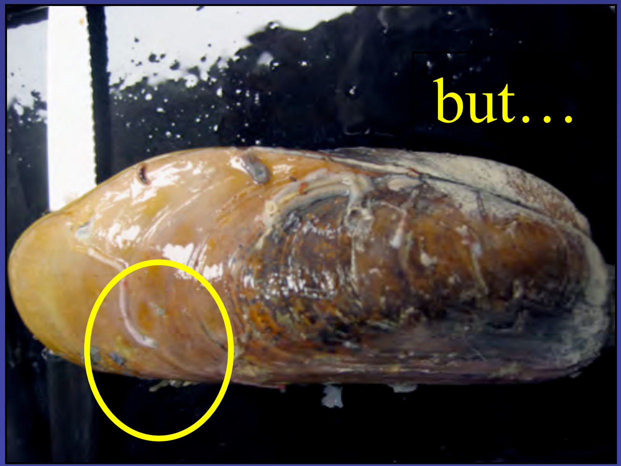
Tevnia and *Riftia*

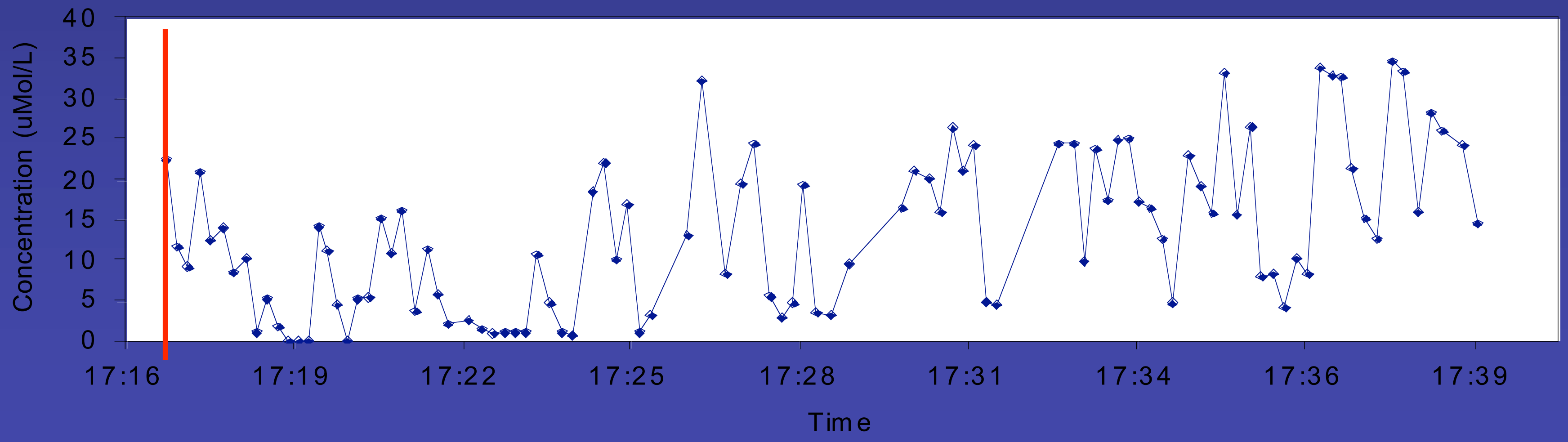
- Biological interactions
  - Facilitation by *Tevnia?;* overgrowth by *Riftia?*
- Different life-history strategies
  - Reproduction
  - Growth rates
- Different physiologies
  - Plume morphology
  - Blood-binding capabilities?



Riftia and mussels

- Physical overgrowth
  Hessler et al. 1988
- Resource competition
  Johnson et al. 1994
- Filter-feeding of larvae





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Concentration (uMol/L)
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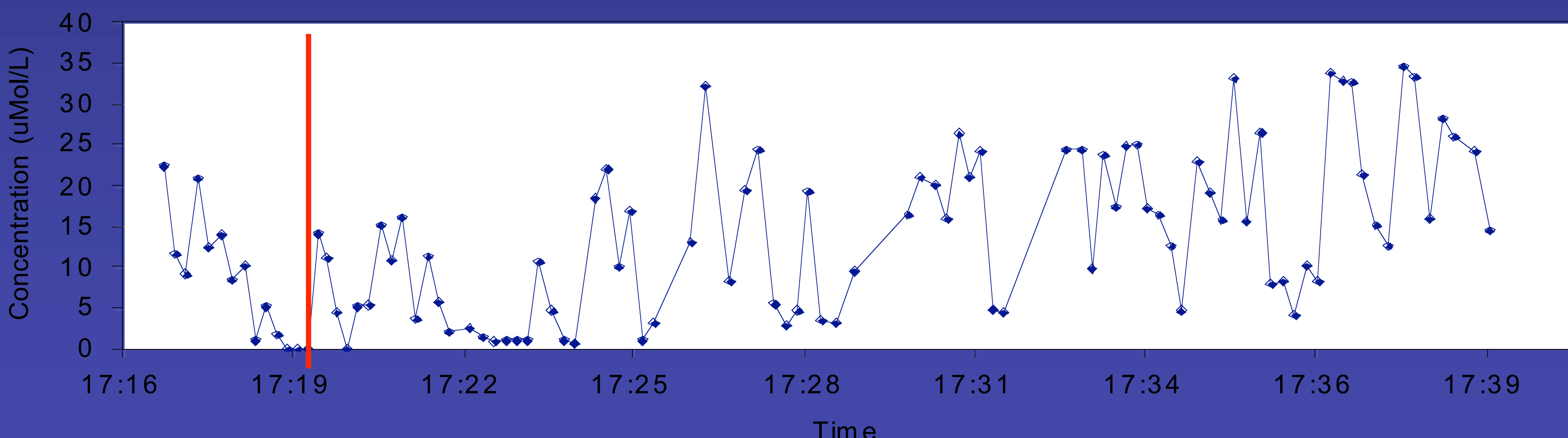
Time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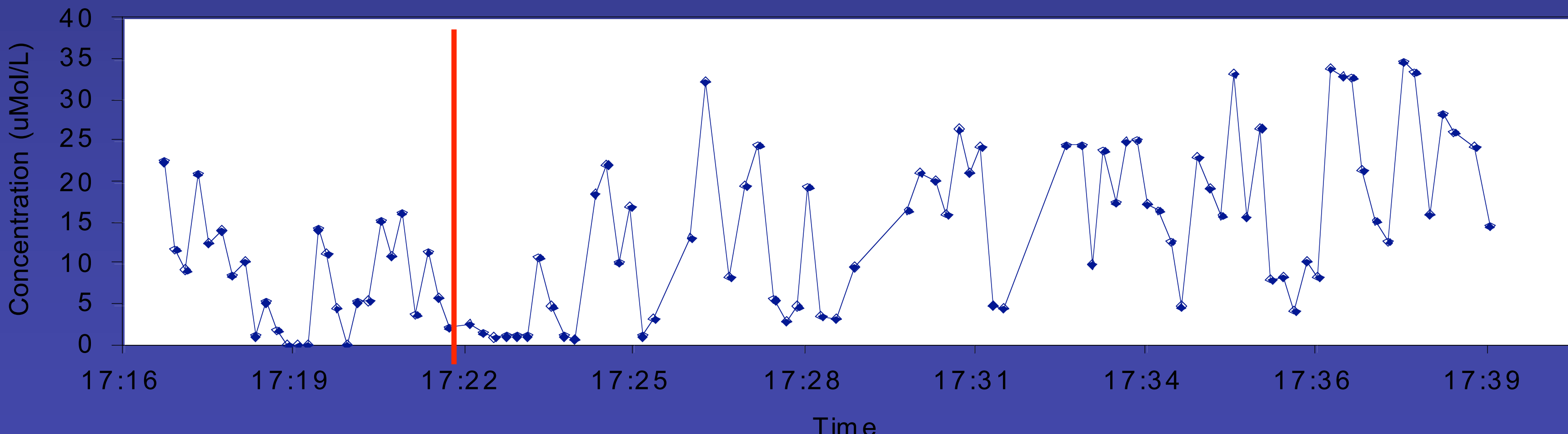
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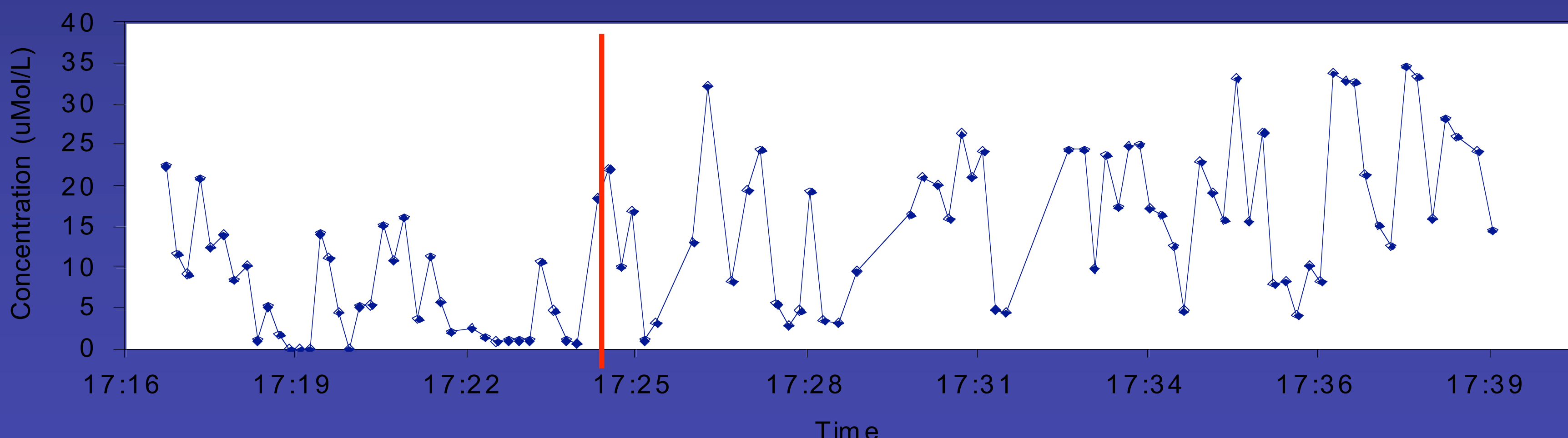

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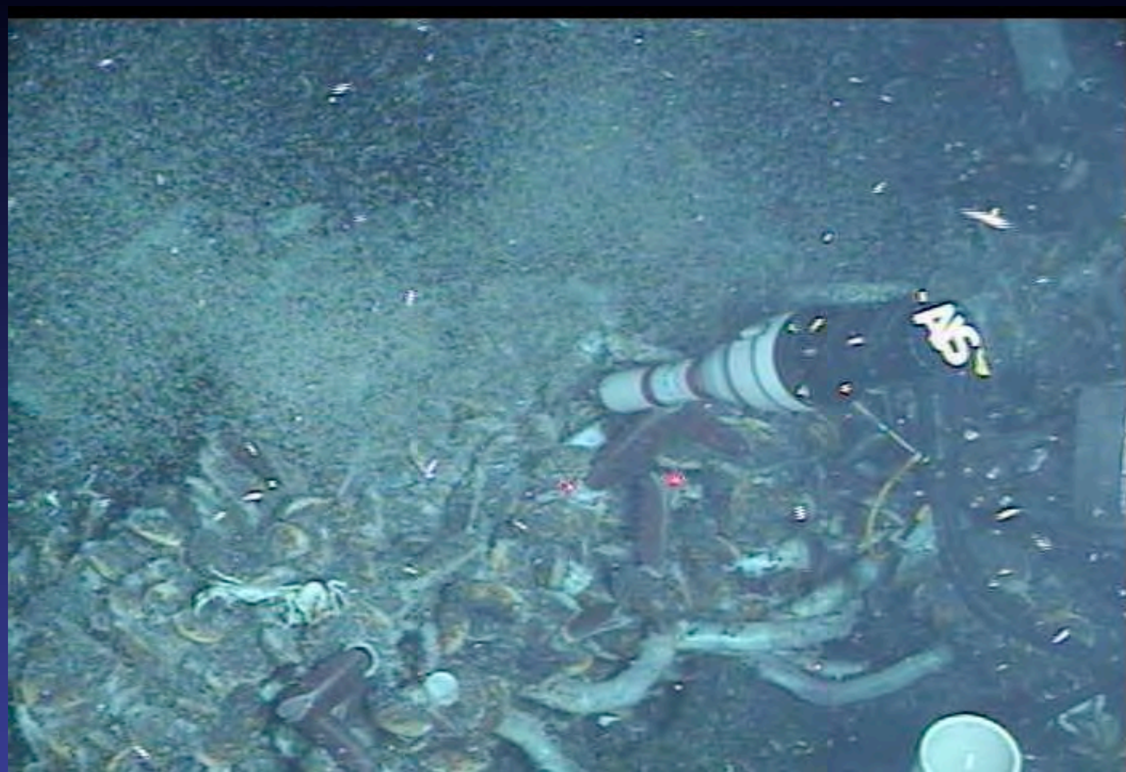

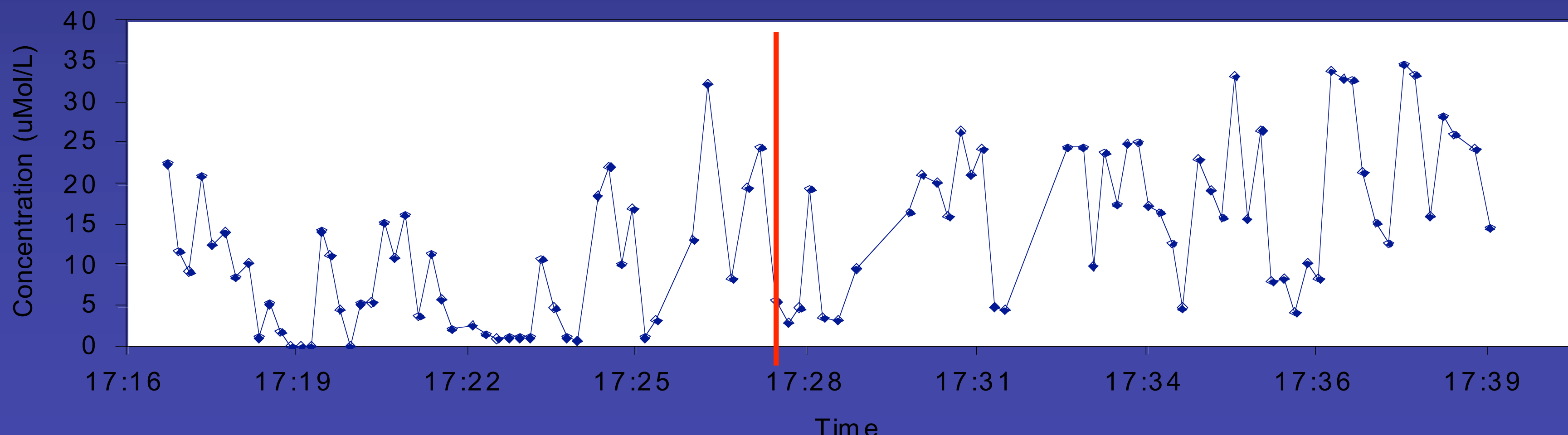

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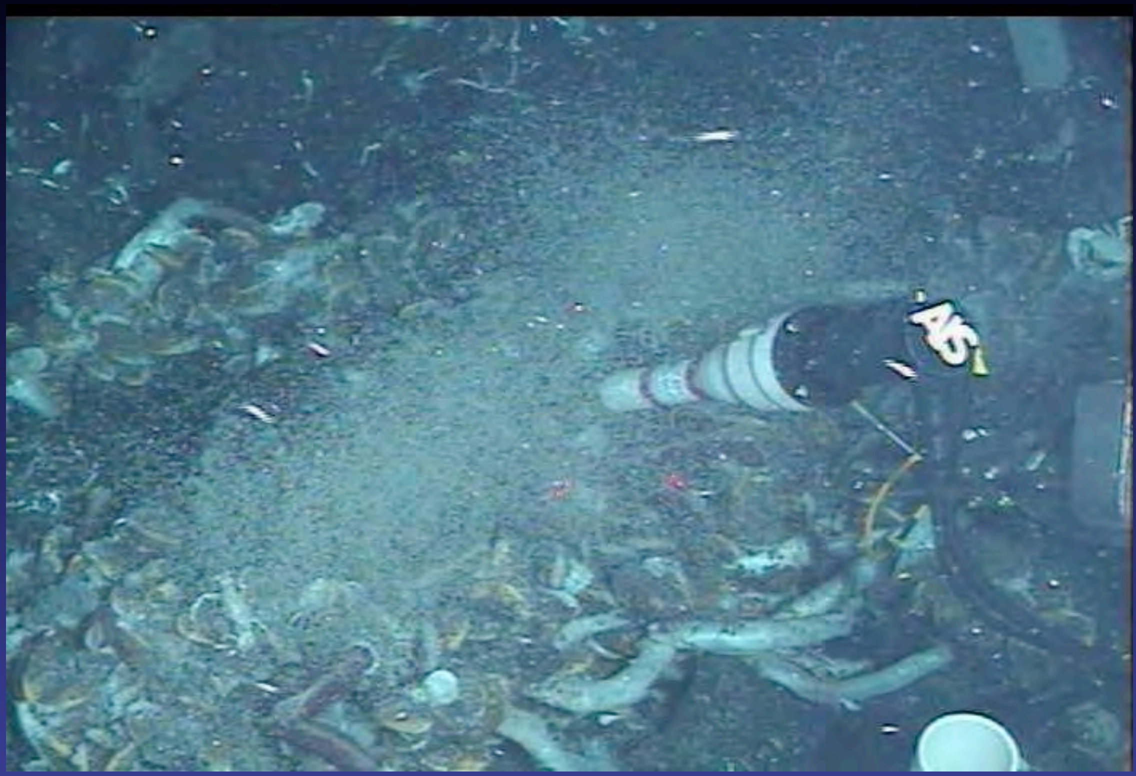
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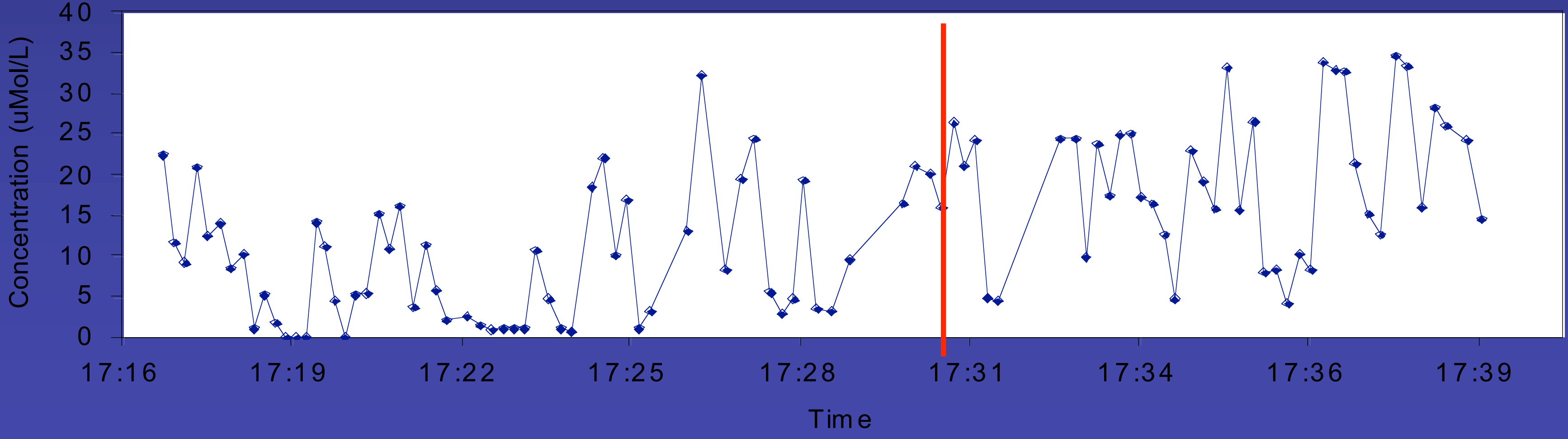
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Fundamental Gaps in Our Understanding

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- Disturbance frequency and geo-chem-bio response
- Interaction between free-living microbes and fauna

Timeline of disturbance (9˚50'N, EPR)

1989	Discovery of 9°50'N venting areas Tubeworm Pillar active
1991	Eruption Dominance of snowblowers and mats Dead *Riftia* at Tubeworm Barbeque
1992	Secondary eruption Dominance of *Tevnia*
1993	Magmatic diking Tubeworm Pillar black smoker Dominance of *Riftia*
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1997	Ty/Io black smokers emerge Tica diffuse flow, few *Riftia*
2002	Rusty *Riftia* fauna absent
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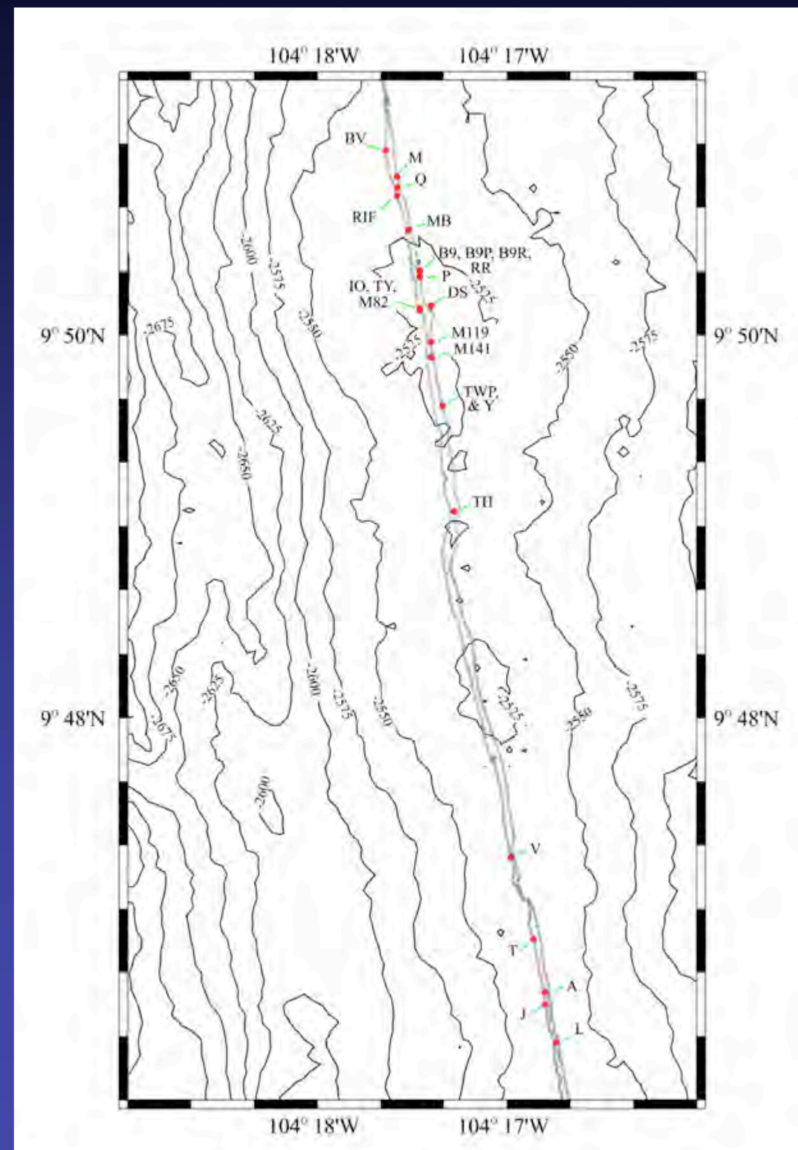
2005-06	Eruption Extinction of Alvinellid Pillar, M Vent, Q Vent, & Tica smoker New areas of diffuse flow
2007	Extensive *Tevnia* colonization Limited *Riftia* presence



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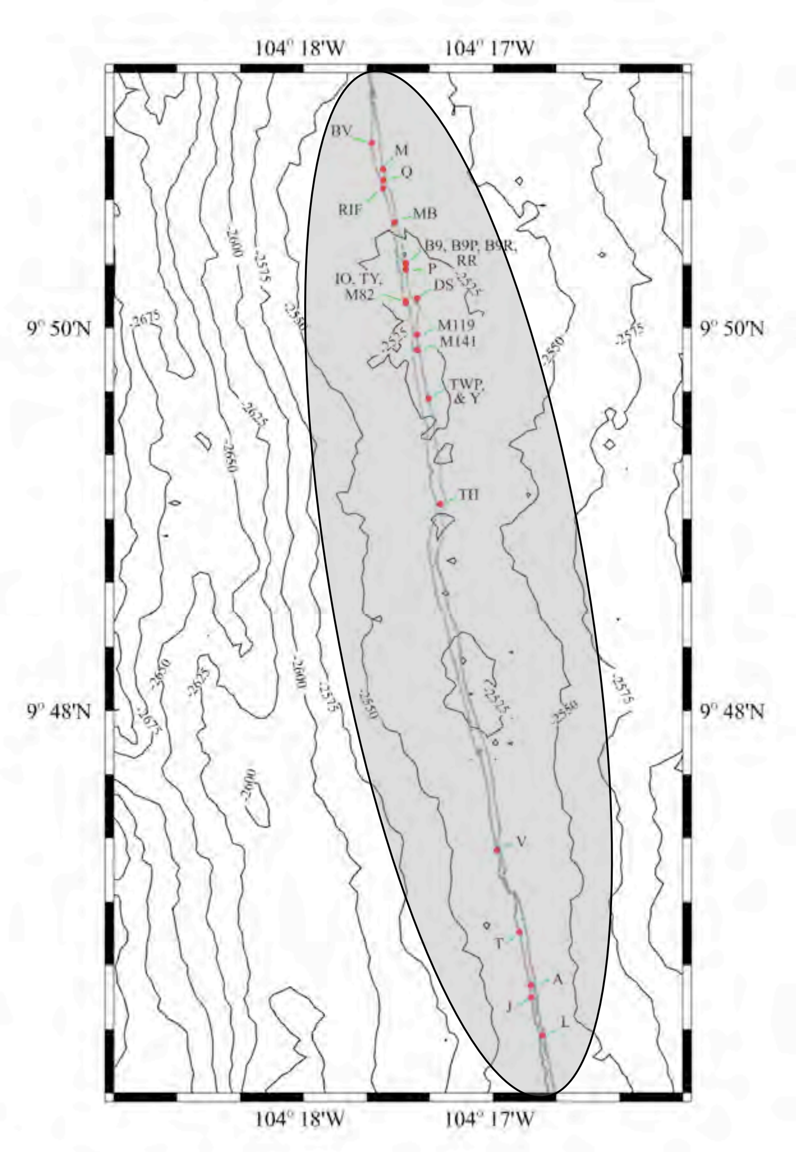

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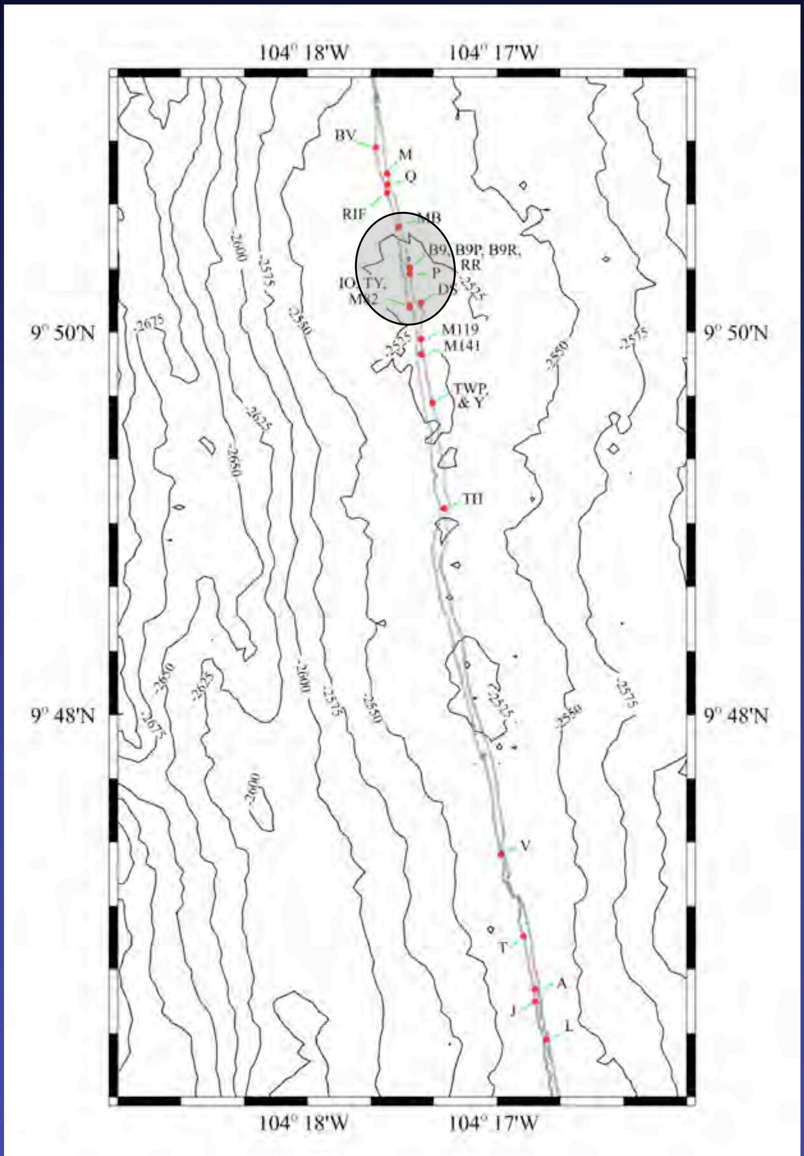

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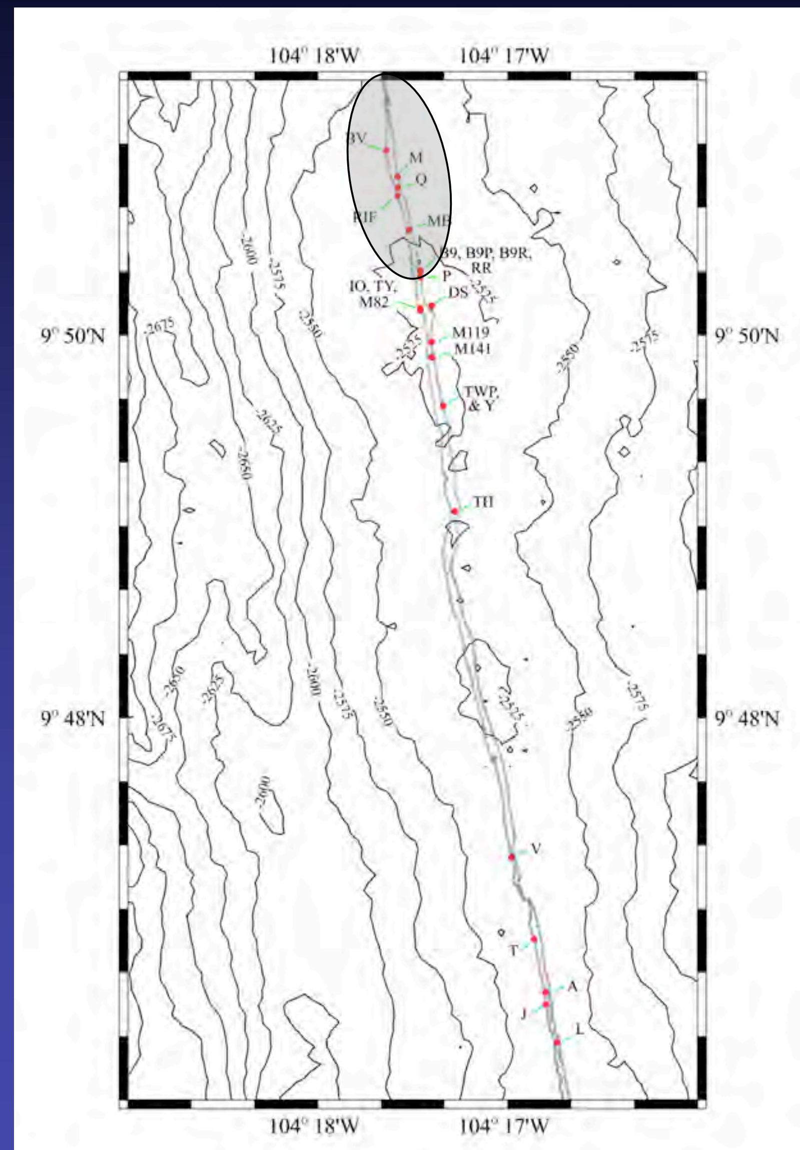

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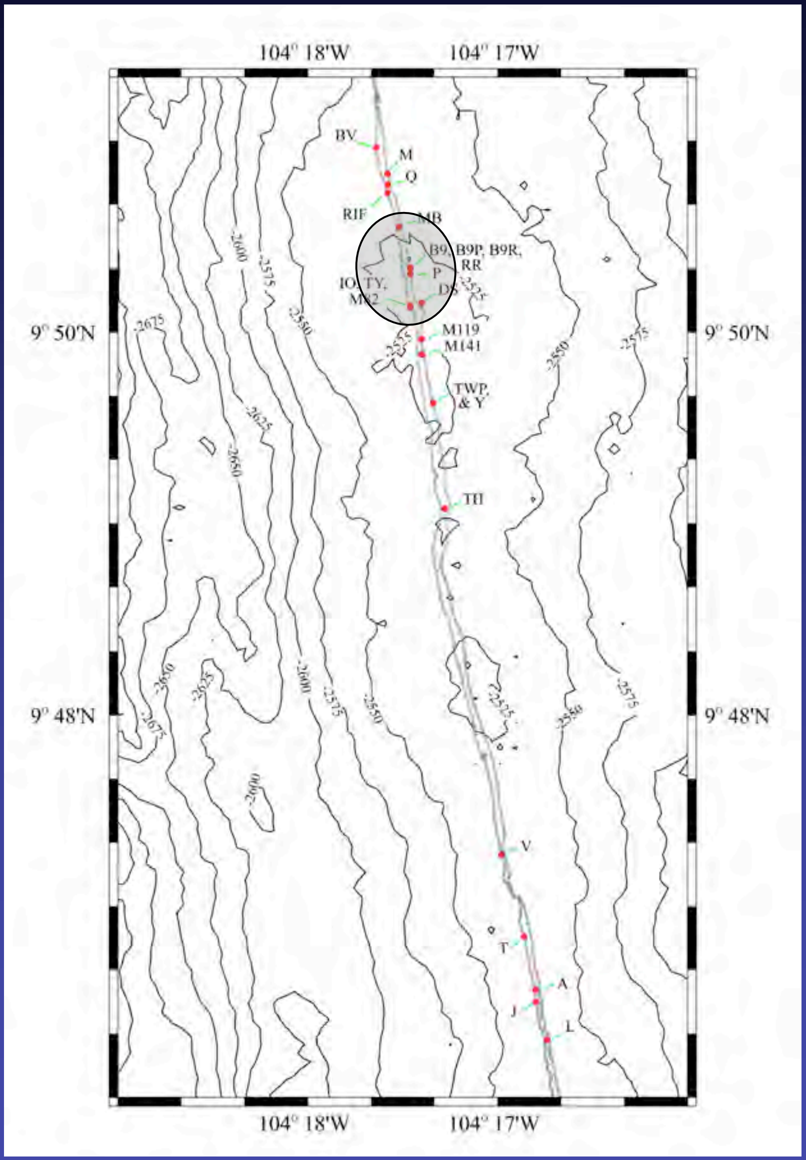

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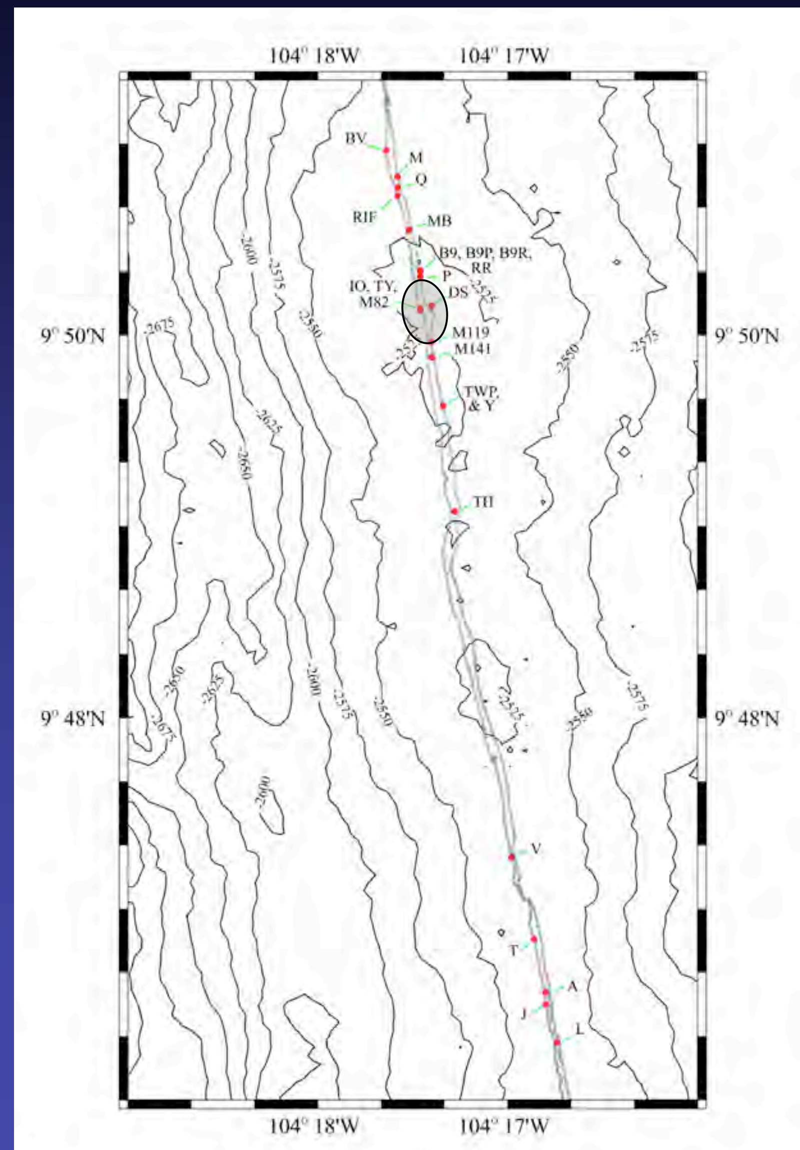

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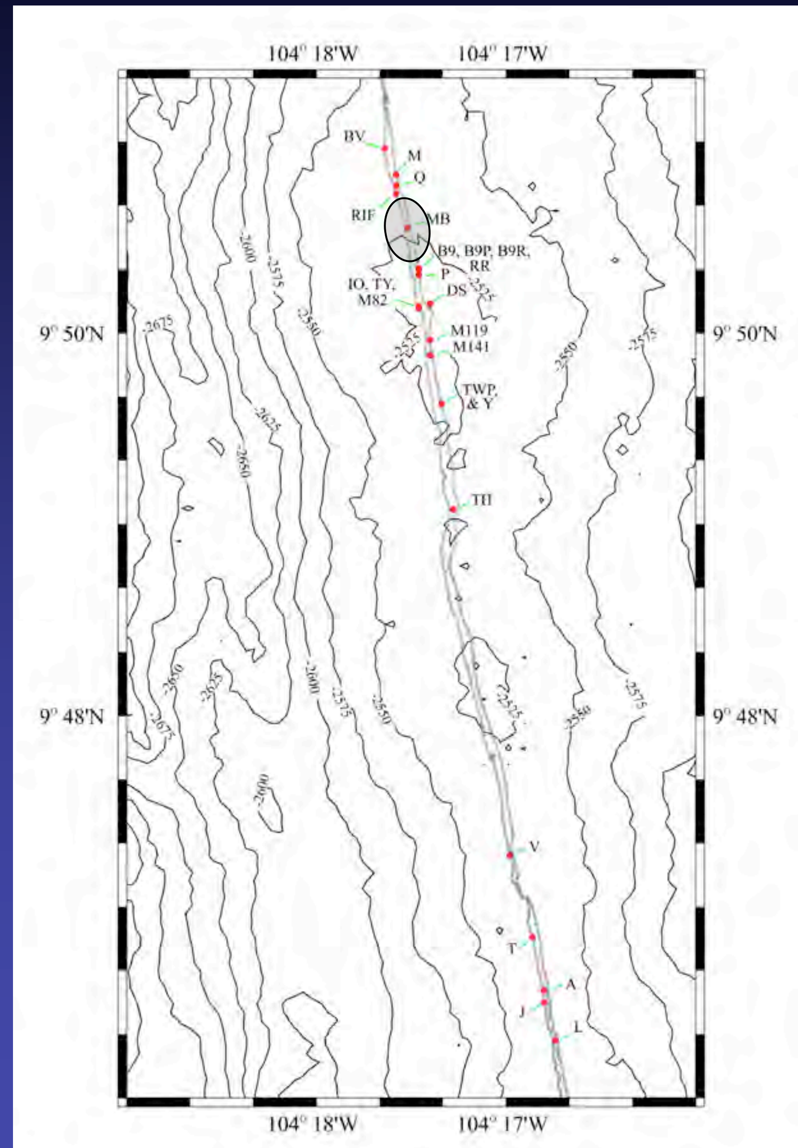
2005-06	Eruption Extinction of Alvinellid Pillar, M Vent, Q Vent, & Tica smoker New areas of diffuse flow
2007	Extensive *Tevnia* colonization Limited *Riftia* presence



Timeline of disturbance (9˚50’N, EPR)

1989	Discovery of 9°50'N venting areas Tubeworm Pillar active
1991	Eruption Dominance of snowblowers and mats Dead *Riftia* at Tubeworm Barbeque
1992	Secondary eruption Dominance of *Tevnia*
1993	Magmatic diking Tubeworm Pillar black smoker Dominance of *Riftia*
1994	Emergence of *Bathymodiolus* & serpulids
1995	Cracking event Serpulid worms & brachyuran crabs Overgrowth of *Riftia* by mussels Rusty *Riftia* area
1997	Ty/Io black smokers emerge Tica diffuse flow, few *Riftia*
2002	Rusty *Riftia* fauna absent
2003	Tica black smoker emerges Tubeworm Pillar flow cessation
2004	Mussel Bed waning Tubeworm Pillar inactive
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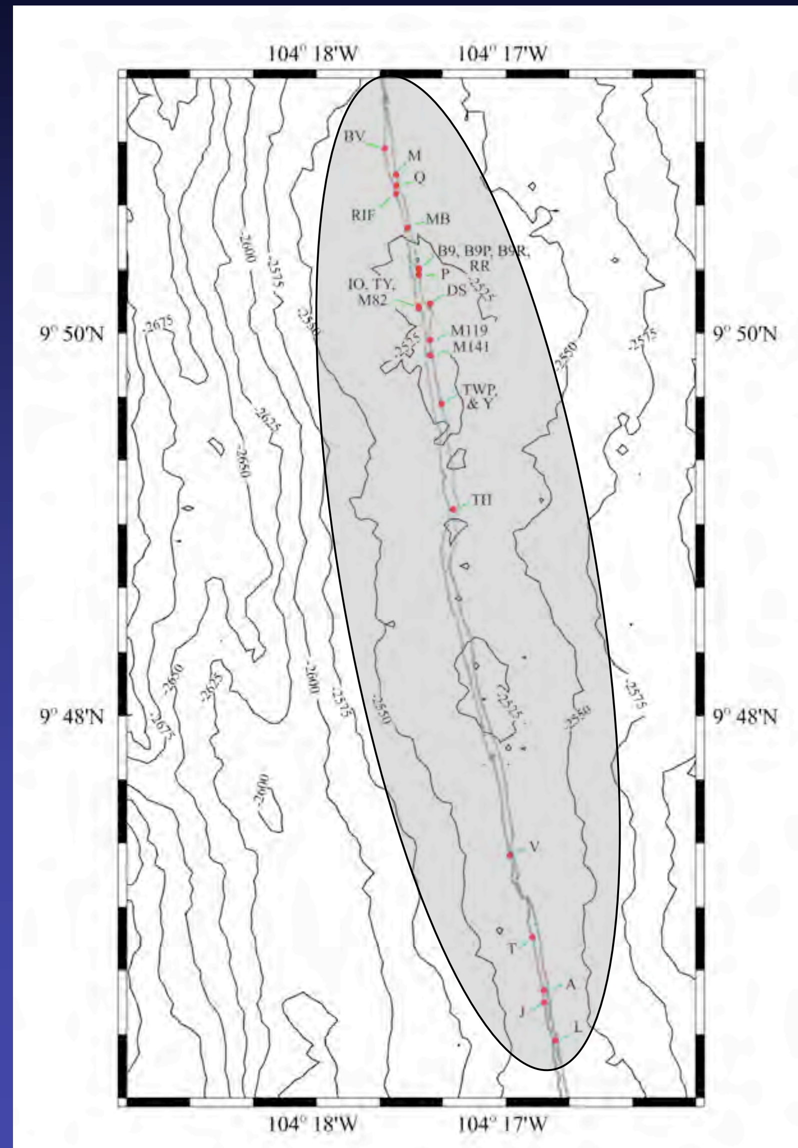
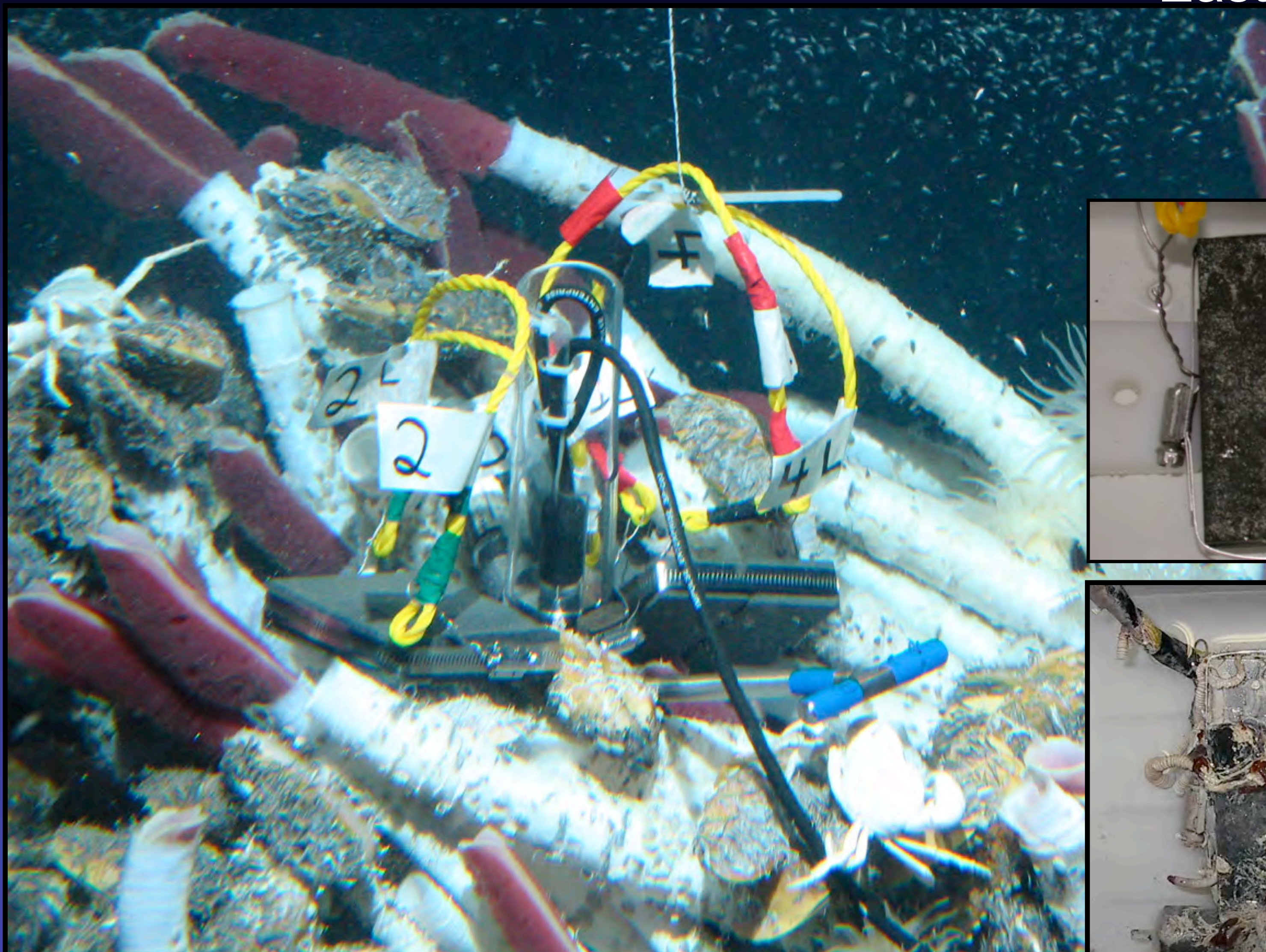


Fundamental Gaps in Our Knowledge

- Physiology of life-history stages in species
- Habitat conditions associated w/ individual species
- Disturbance frequency and geo-chem-bio response
- Interaction between free-living microbes and fauna

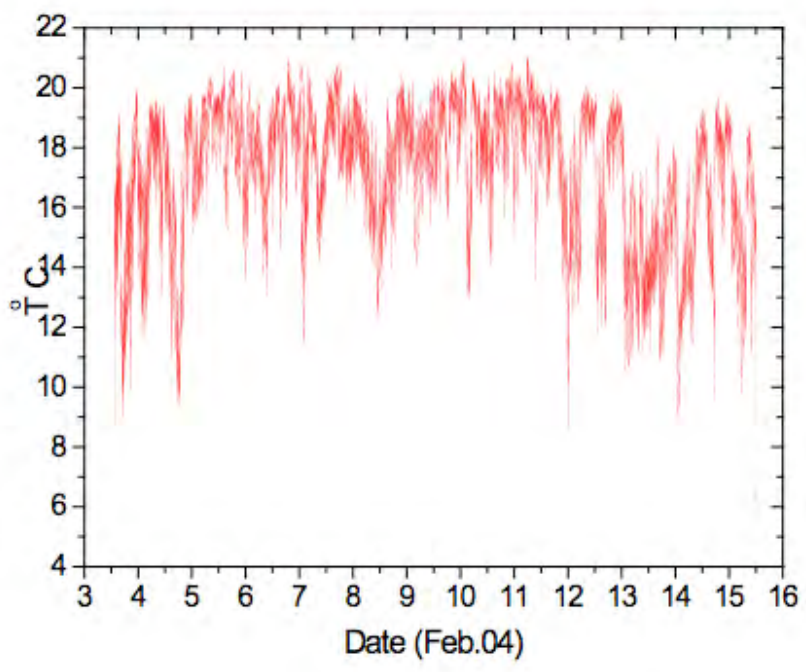
(In-situ, co-located, coincident characterization on ecological timescales)

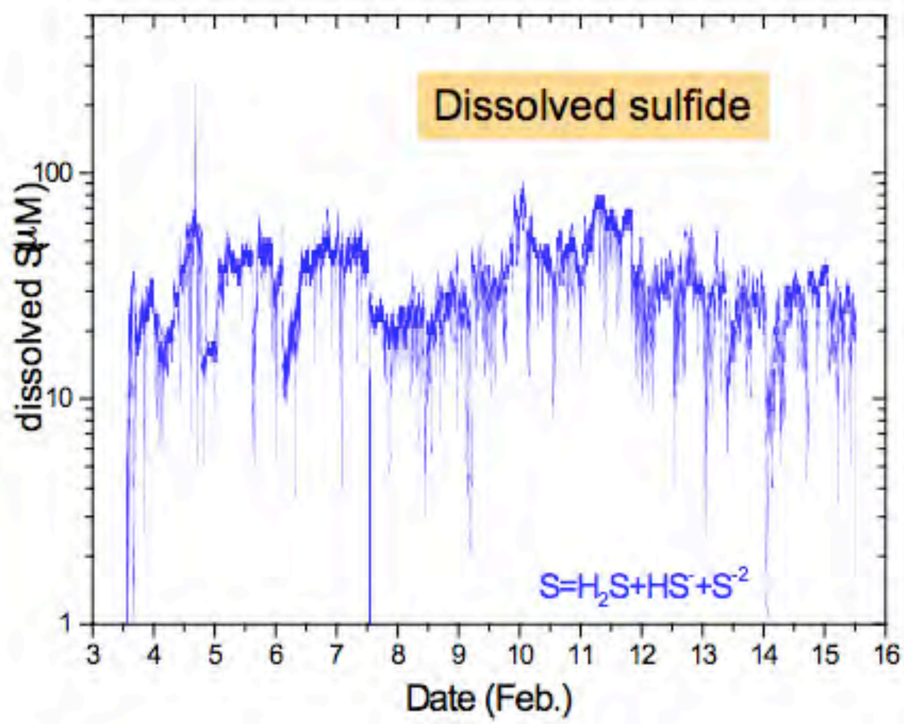
East Pacific Rise
Tica
2004

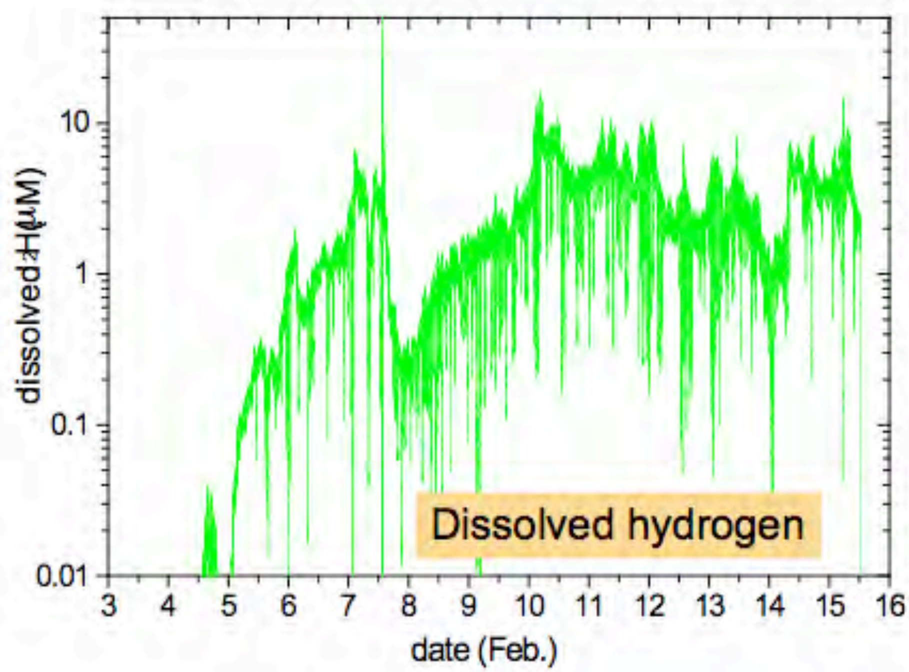


Collaborators: Beaulieu, Ding, Seyfried, Sievert

In situ sensor measurements: pH, dissolved H_2 and H_2S Electrodes (5 second intervals)

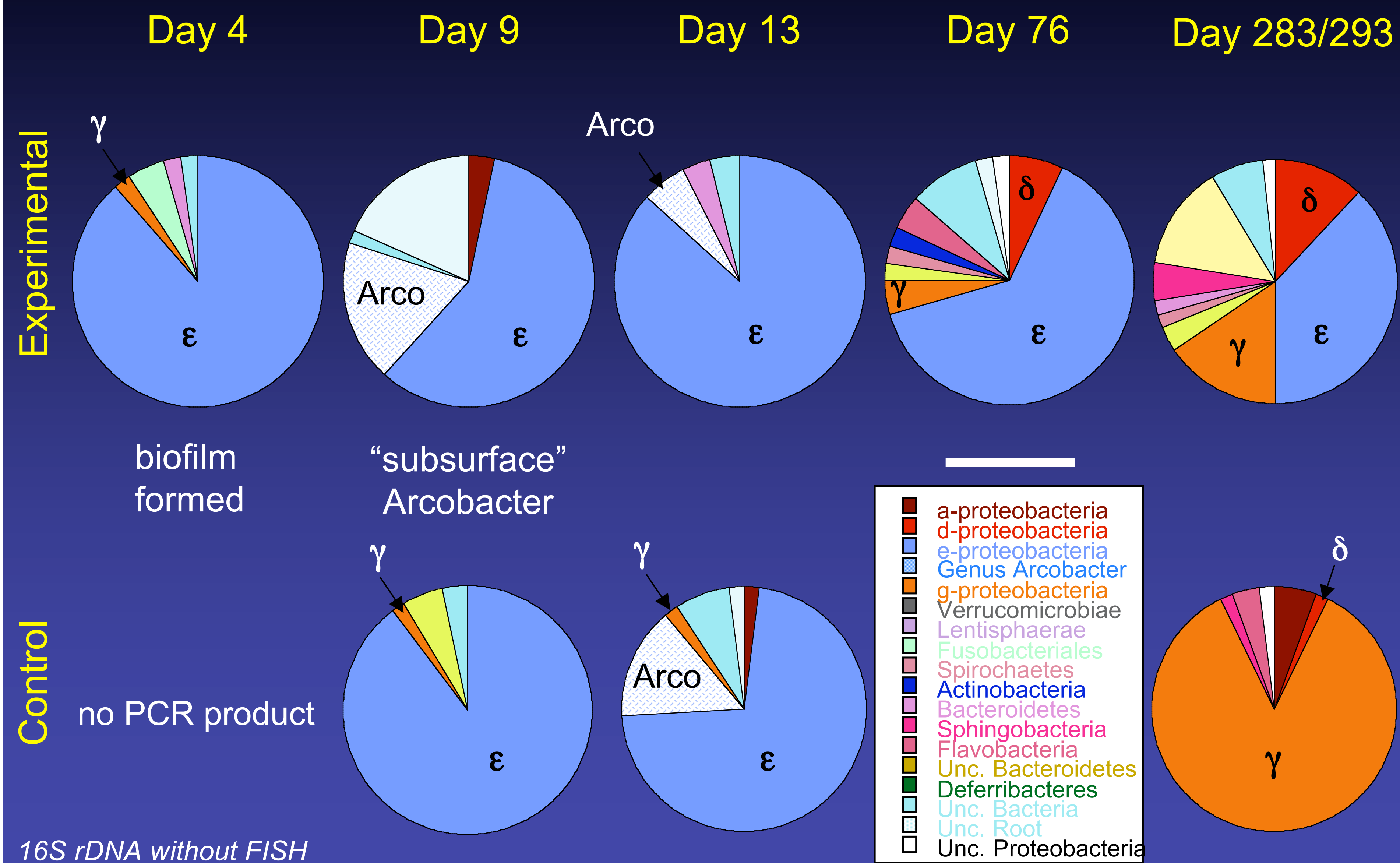






Collaborators: Beaulieu, Ding, Seyfried, Sievert

Early Microbial "succession" on Native Basalt



16S rDNA without FISH

Collaborators: Beaulieu, Ding, Seyfried, Sievert

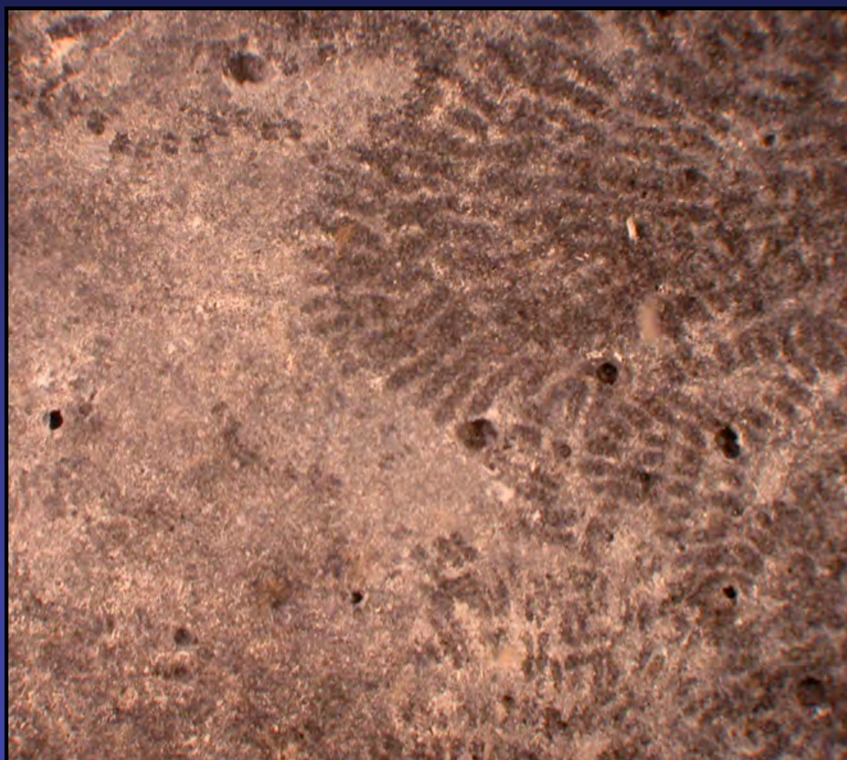
Repeatable Succession? -see Lara Gulman's poster

Limpet “tracks”?
(scraped by limpets feeding on the biofilm?)

4-day panel, Expt site

9-day panel, Expt site

Limpet (*Lepetodrilus* sp.) 1.5mm



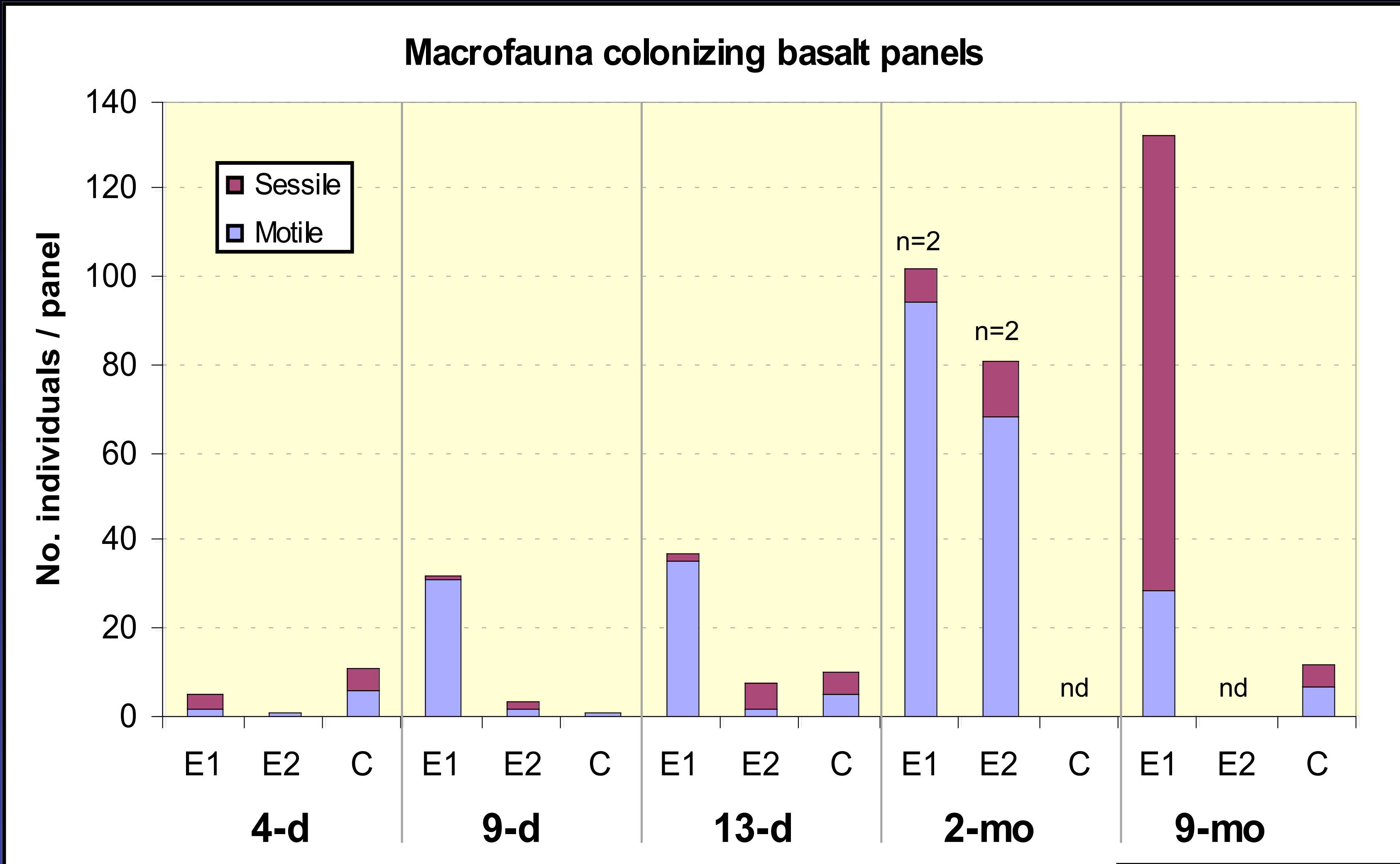
8X

10mm

20X

Small-scale spatial patchiness in microbial succession

Collaborators: Beaulieu, Ding, Seyfried, Sievert



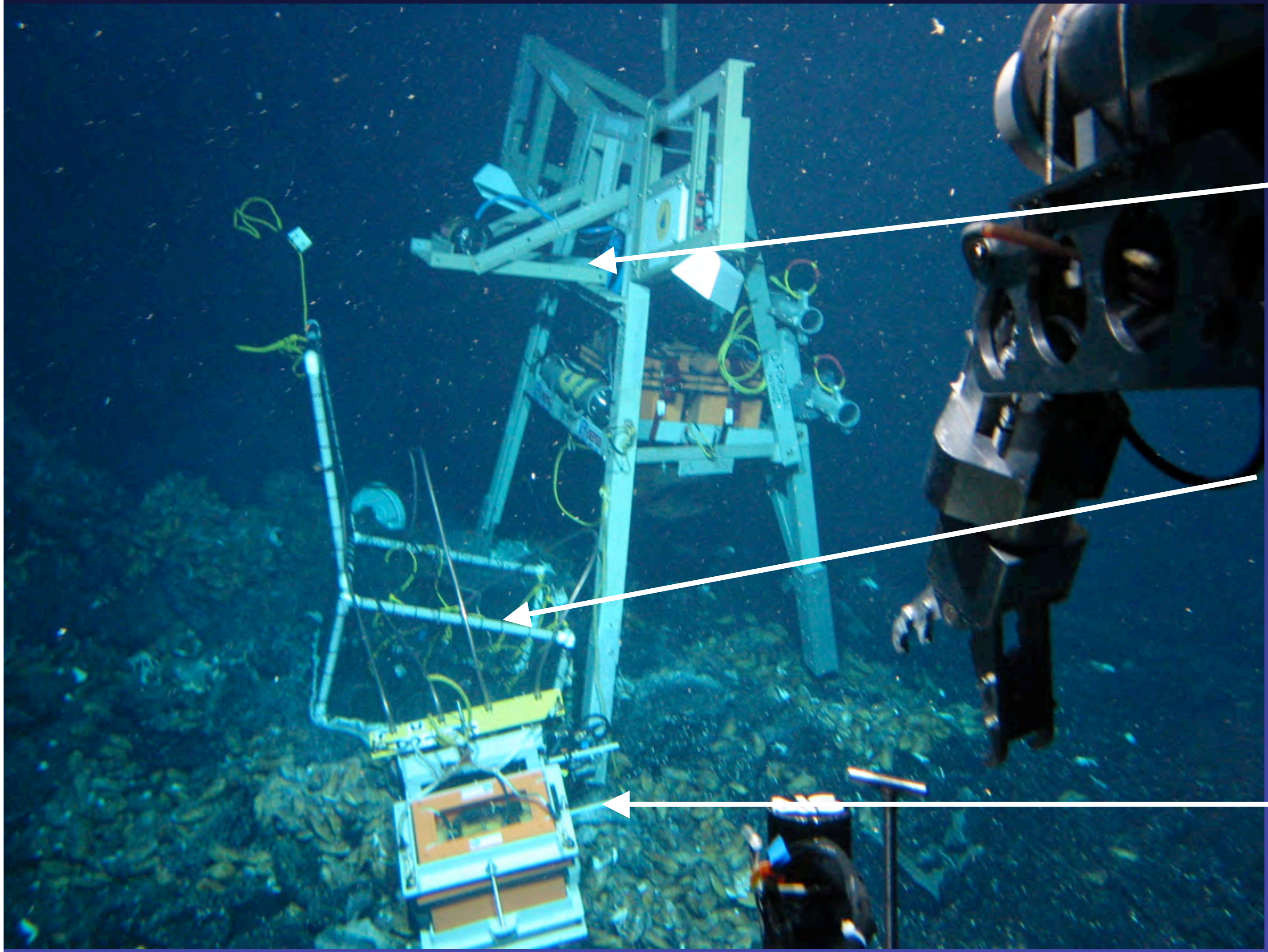
4 days

25 species
7 sessile

9 months

Collaborators: Beaulieu, Ding, Seyfried, Sievert

ISEA at a mussel bed with underwater time-lapsed camera

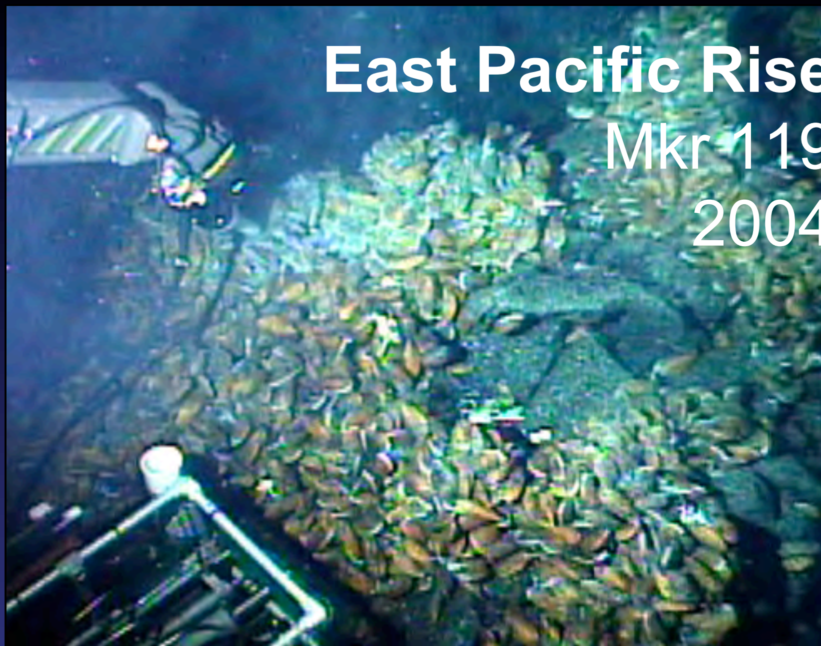


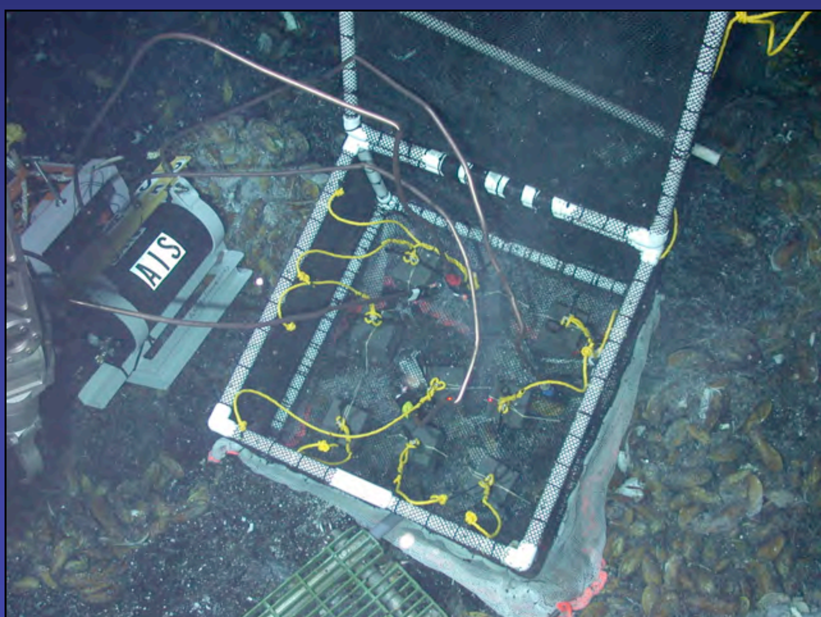
Time-lapse camera

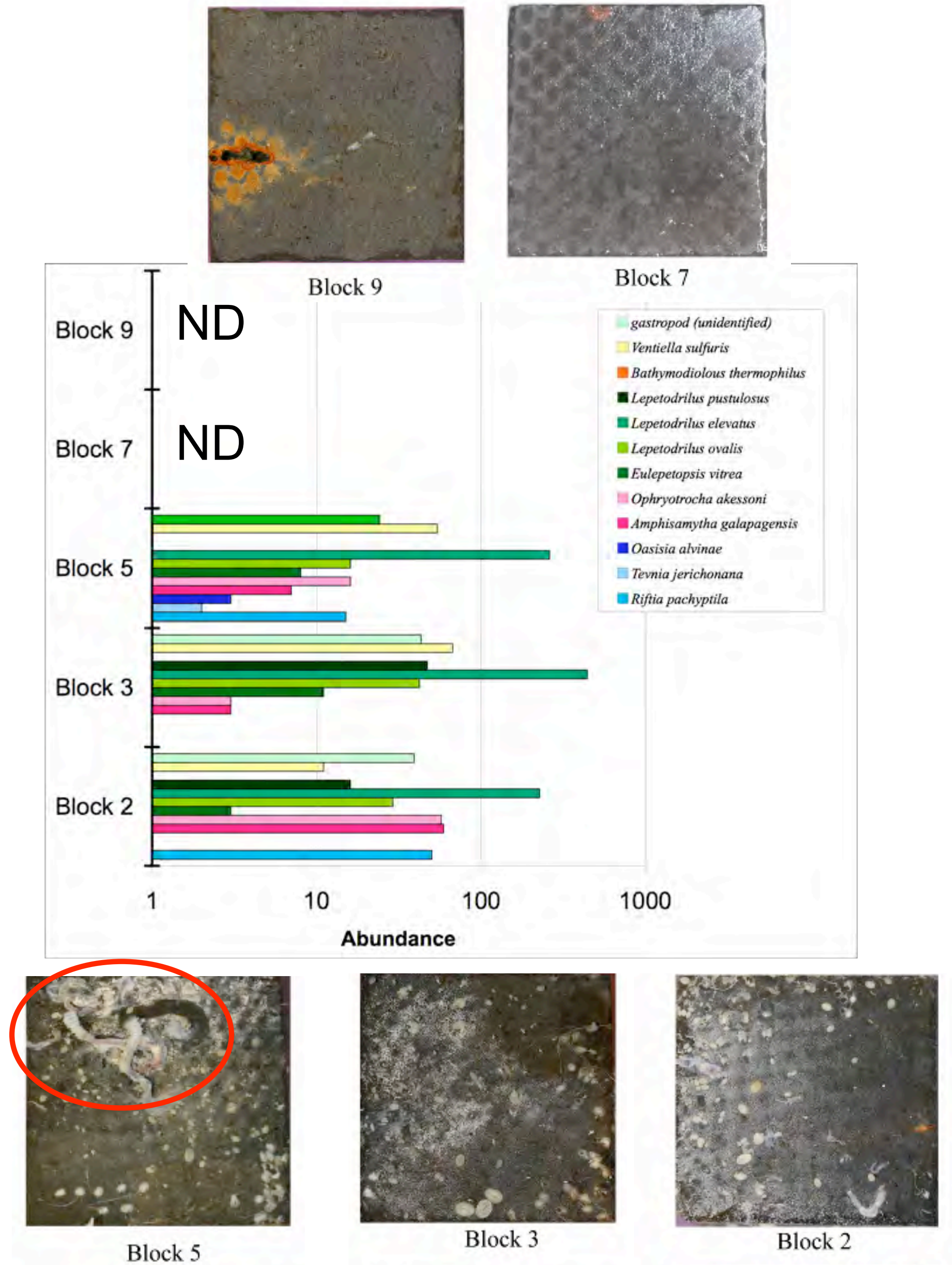
Mussel exclusion cage with electrodes

AIS In-situ Electrochemical Analyzer

Collaborators: Luther, Lutz, Tolstoy, Vetriani

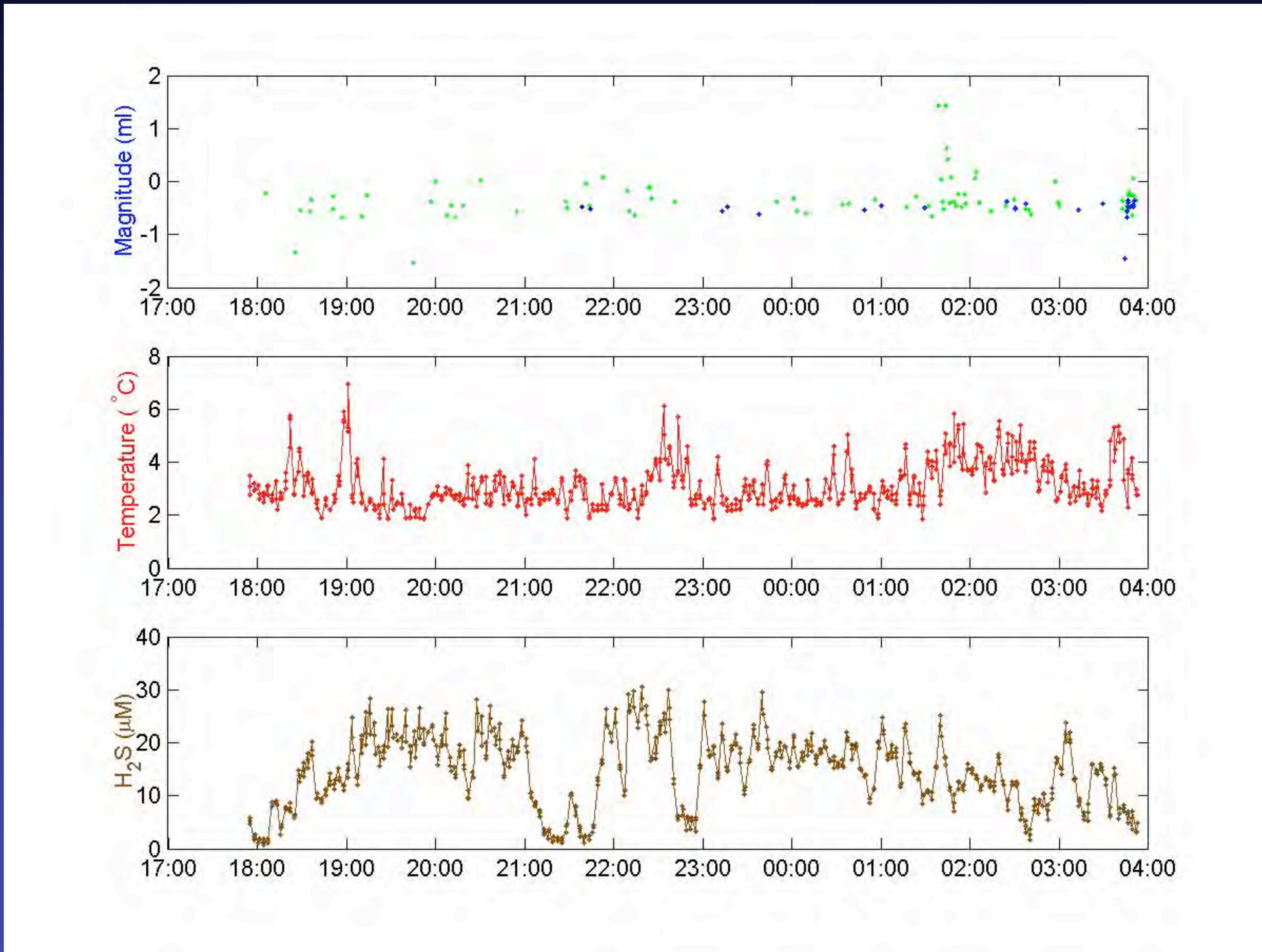






Collaborators: Luther, Lutz, Tolstoy, Vetriani

Correlation of seismic events, T°C, and $\sum H_2S$



Collaborators: Luther, Lutz, Tolstoy, Vetriani

"Seismic delivery" of nutrients?

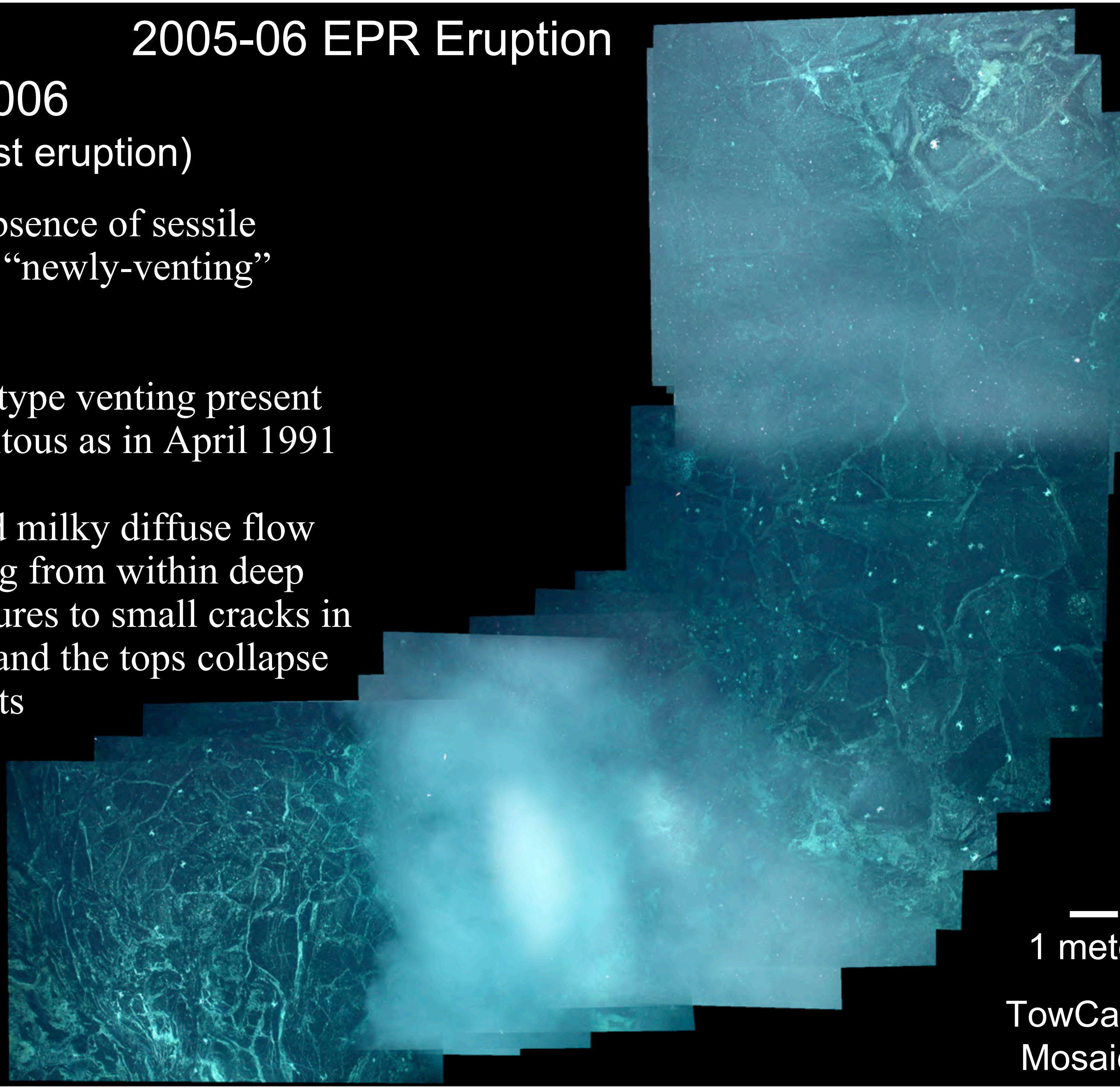
2005-06 EPR Eruption

May 2006
(~6 months post eruption)

- The notable absence of sessile megafauna in “newly-venting” areas

- Snow-blower type venting present but not ubiquitous as in April 1991

- Newly-formed milky diffuse flow vents ranging from within deep pits and fissures to small cracks in sheet flows and the tops collapse lava remnants



1 meter

TowCam Mosaic

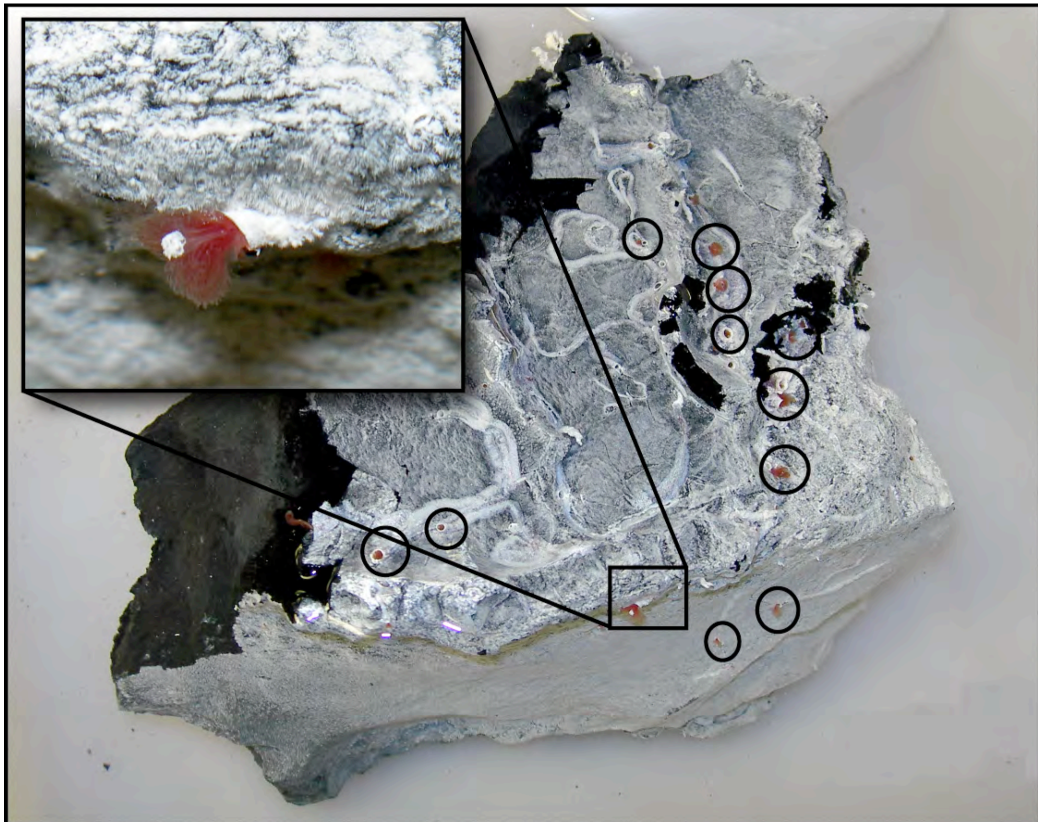
November 2006
~12 months after eruption

Tevnia up to 37cm in length

30°C to 74°C fluids
>1 mmol/kg H_2S

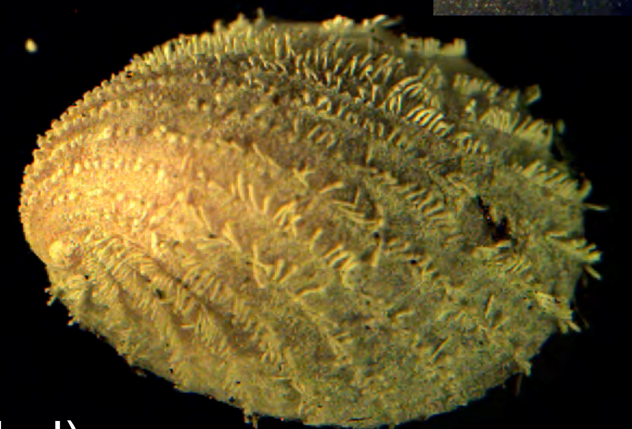
8 associated species
of gastropods, amphipods,
copepods, and polychaetes

June 2006
~7 months post eruption

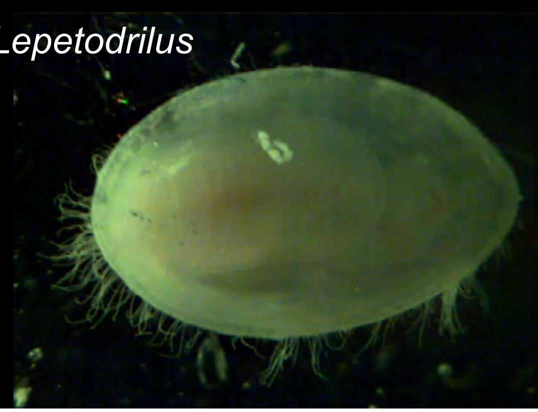


Basalt collected in June 2006
Individual *Tevnia jerichonana* colonists (circled)
Inset shows *Tevnia* < 3mm in length (max. 4 cm)

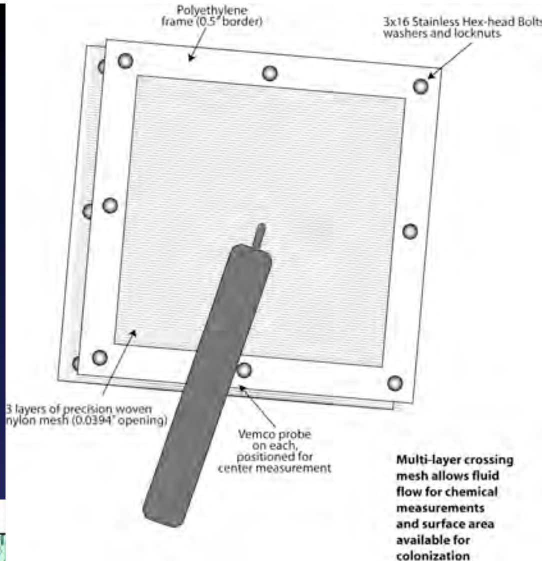
Tevnia jerichonana

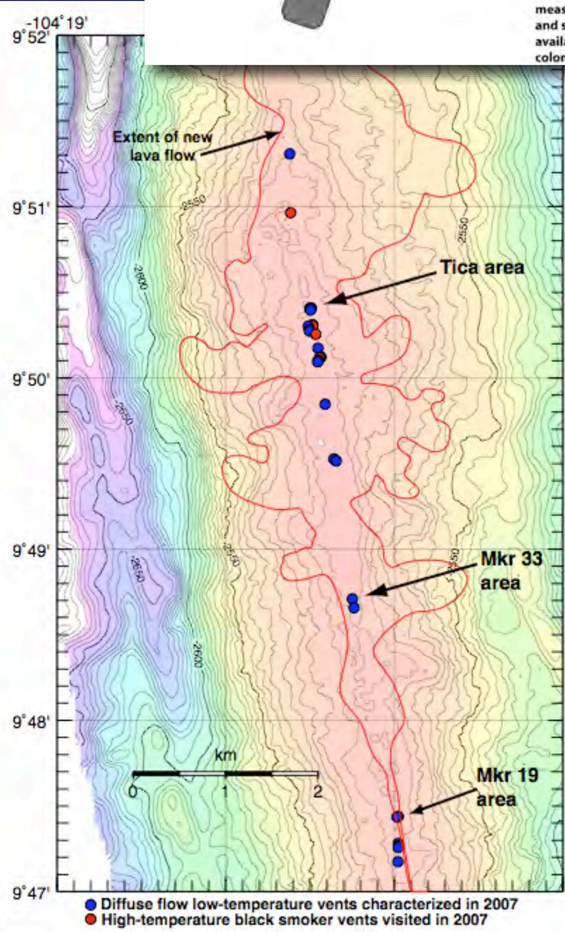


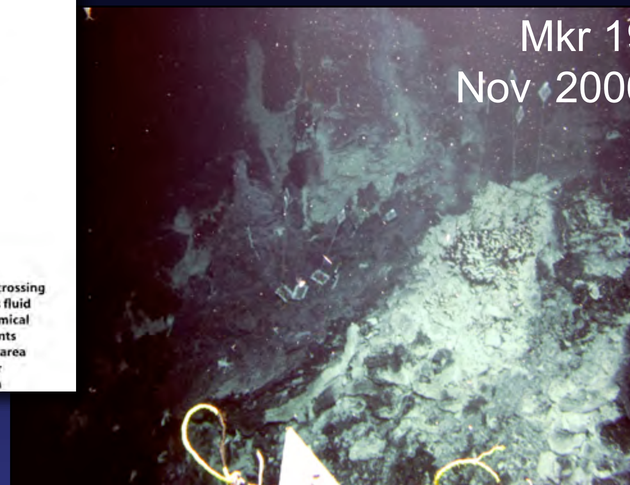
Ctenopelta porifera

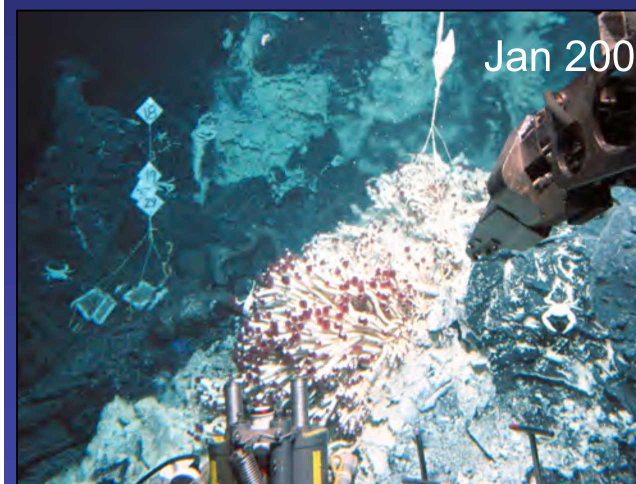


TAMS Integrated Expts





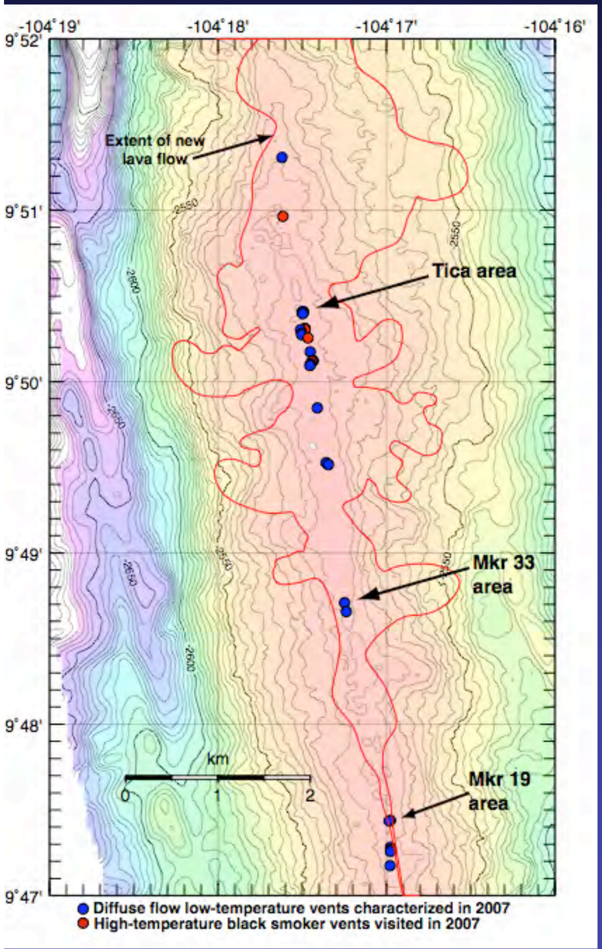




Temporal Autonomous Multidisciplinary Substrates

Collaborators: Bright, Govenar, Luther, Lutz, Vetriani

TAMS Integrated Expts
"TamTown" and "Mkr 19" sites



	Tamtown (6 months)		Marker 19 (6 weeks)	
	Treatment (TAM8)	Control (TAM5)	Treatment (TAM20)	Control (TAM29)
Temperature (° C)	3.85 (1.08)/ 5.9(0.70)[1]	3 (0)/ 2.65 (0.24)[2]	7.17 (0.57)	2.78 (0.27)
O_2 (uM)	39.50 (34.11)/ 4.65 (20.79)	50.65 (3.74)/ 49.81 (4.76)	ND	78.52 (12.90)
H_2S (uM)	ND/ 21.14 (9.36)	1.32 (0.48)/ 0.87 (0.19)	54.18 (19.31)	2.53 (0.26)
AVS (uM)	8.34 (14.28)/ 34.17 (12.56)	ND	98.68 (29.75)	ND

	Tamtown (6 months)		Marker 19 (6 weeks)	
	Treatment (TAM8)	Control (TAM5)	Treatment (TAM20)	Control (TAM29)
Vestimentiferans	+ (n = 7)		+ (n = 7)	
Bathymodilus thermophilus	+ (n = 1)			
Lepetodrilus spp.	+++	+	+	+
Paralvinella pandorae			+	
Polynoids	+	+		+
Ophryotrocha akessoni	+	+	+	+
Ventiella sulfuris	+	+	+++	+
Dahlella caldariensis			+	
Copepods	+	+	+	+
Ostracods	+	+		
Nematodes	+	+	+	+
Forams	+	+	+	+

Collaborators: Bright, Govenar, Luther, Lutz, Vetriani

Stainless steel mesh microbial colonization devices were designed and used to collect concentrated biomass for RNA work

After 7-day post-eruptive deployment at Mk 33 (30°C)

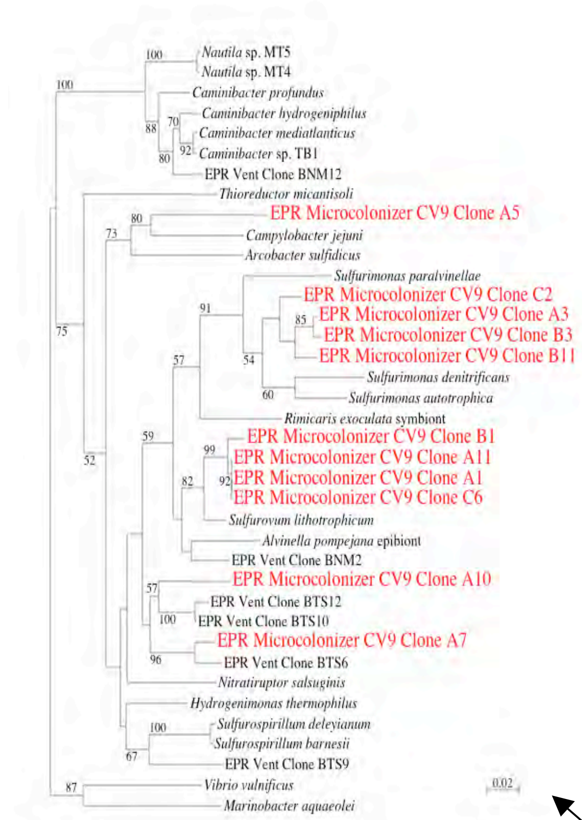


Figure 3. Phylogenetic analysis of reverse transcribed 16S rRNA from ε-*proteobacteria* collected on an artificial substrate deployed in diffuse venting in January 2007.

RNA extraction → **DNAase treatment** → **Reverse transcription (cDNA synthesis) and PCR** → **Cloning and sequencing of 16S rRNA transcripts** → **Phylogenetic analysis**

Collaborators: Govenar, Luther, Lutz, Vetriani

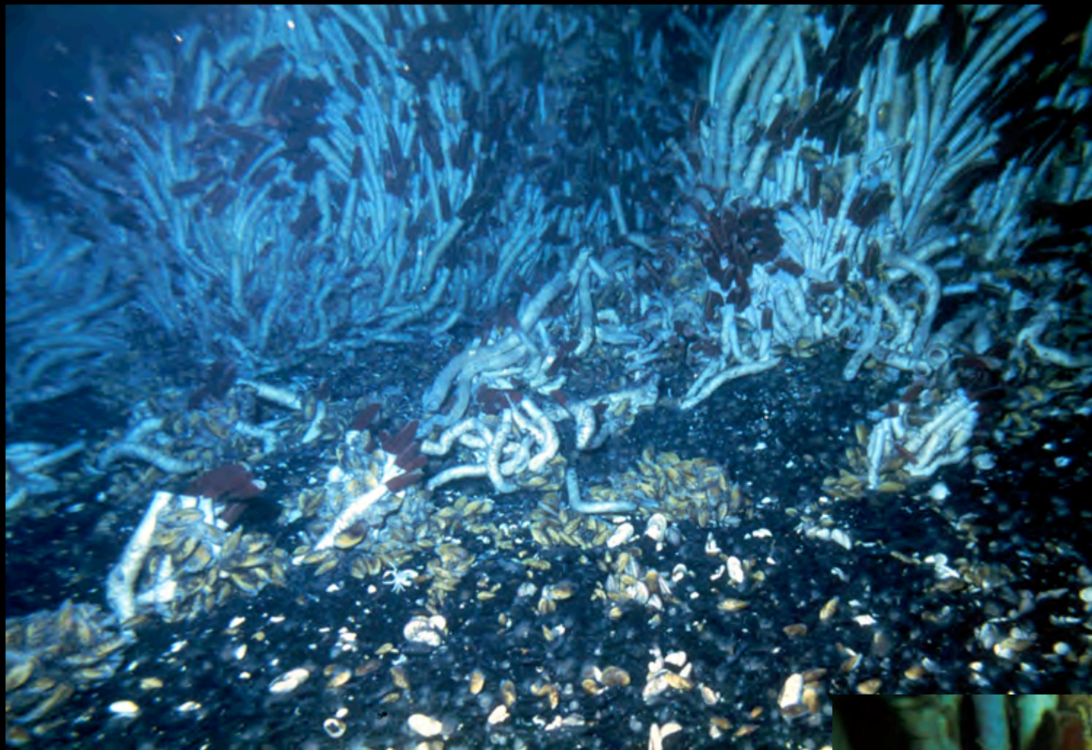
Microcolonizer recovered after a 17-day deployment at Tica showing juvenile tubeworms embedded in a mat of colonizers dominated by epsilon-proteobacteria

Heterotrophic bacteria detoxify ionic mercury …facilitate colonization?

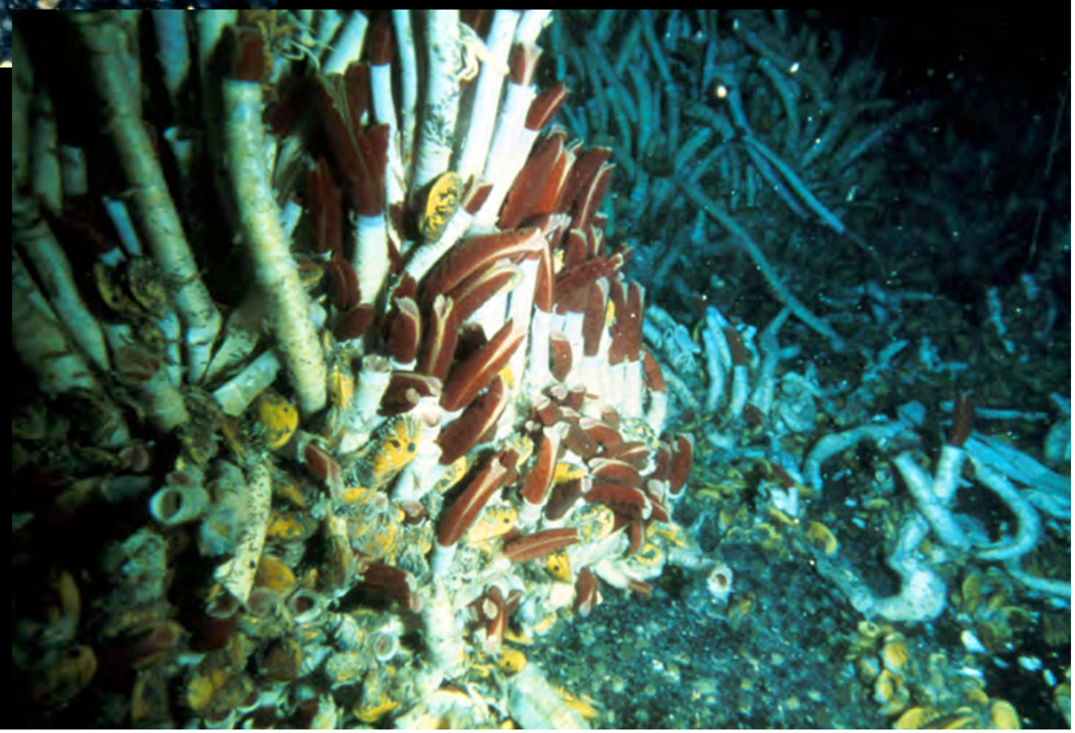
Vetriani et al 2005

“Succession” as a framework

- Gaps in our understanding
- Ongoing integrated temporal experiments
- Consequences of succession on genetic diversity
- Future geo-bio-chemical interactions



Galápagos Rift
Rose Garden
1979



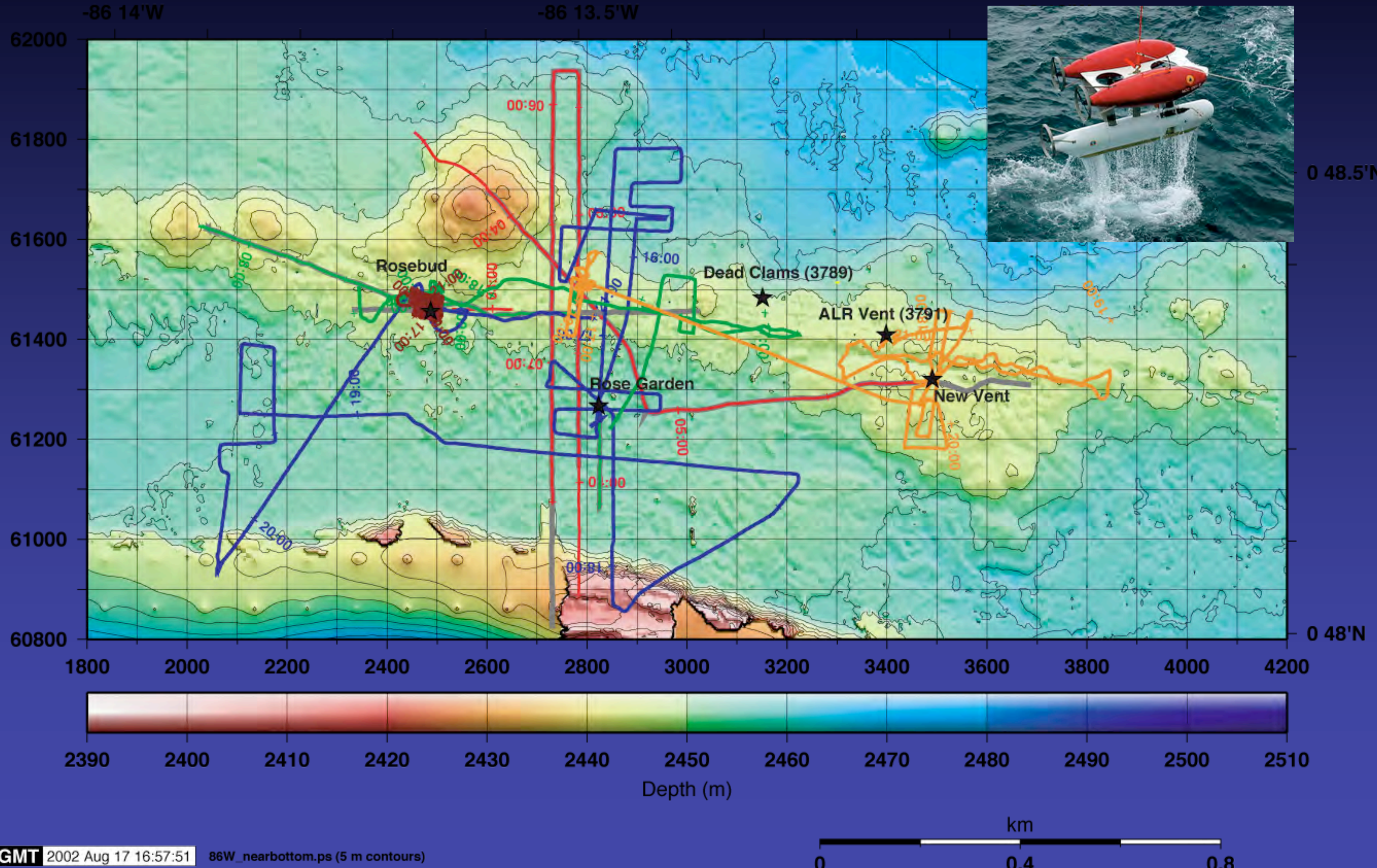
Visited in 1979, 1985, 1988, and 1990

14 seafloor markers and experiments
~7 stacks of Alvin dive weights were observed when visited in 1990

….until 2002

Shank et al. 2003

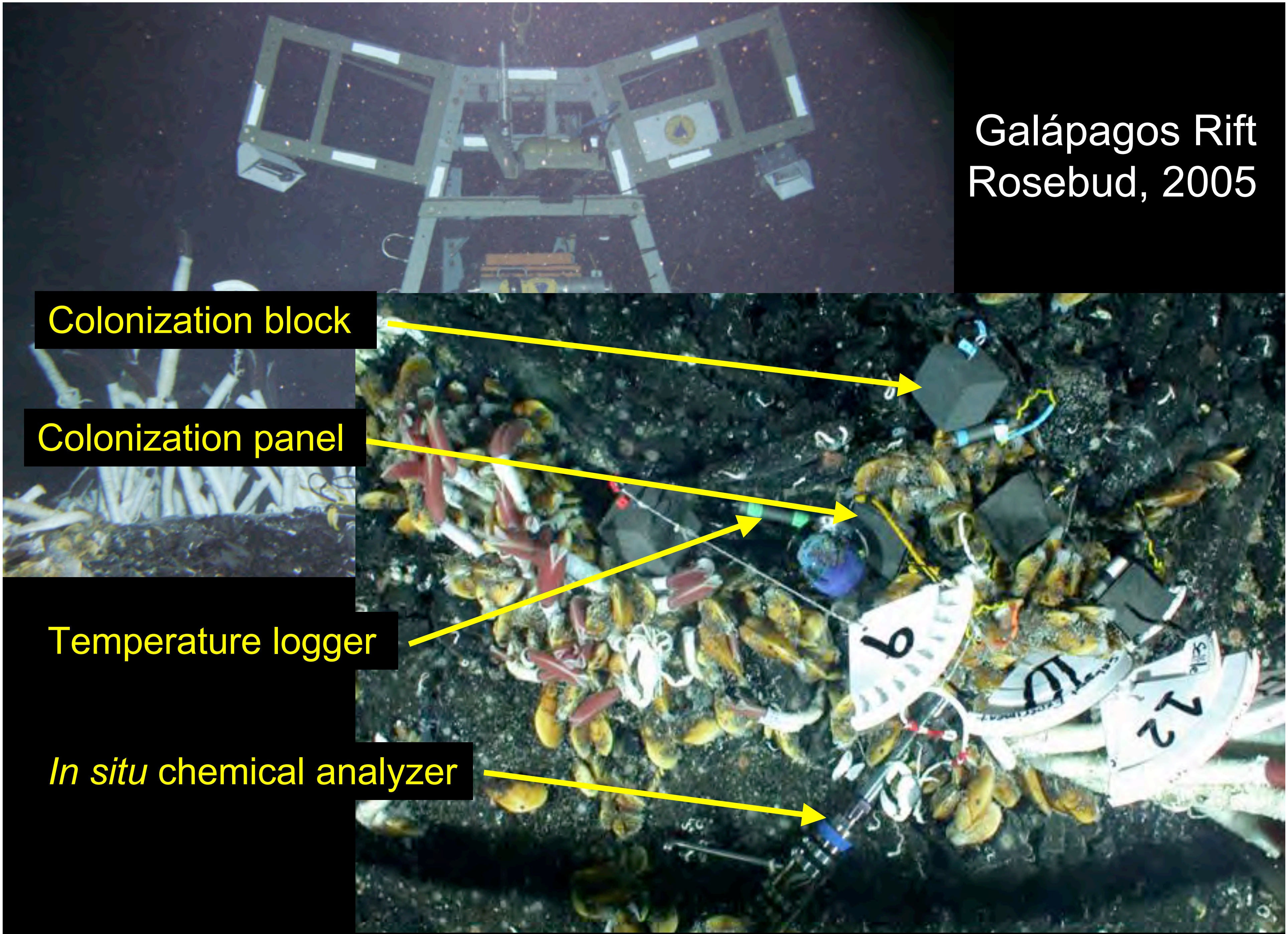
ABE microbathemetry, Alvin tracks, and TowCam lines



675kHz sonar; 5m horizontal; 1m vertical resolution

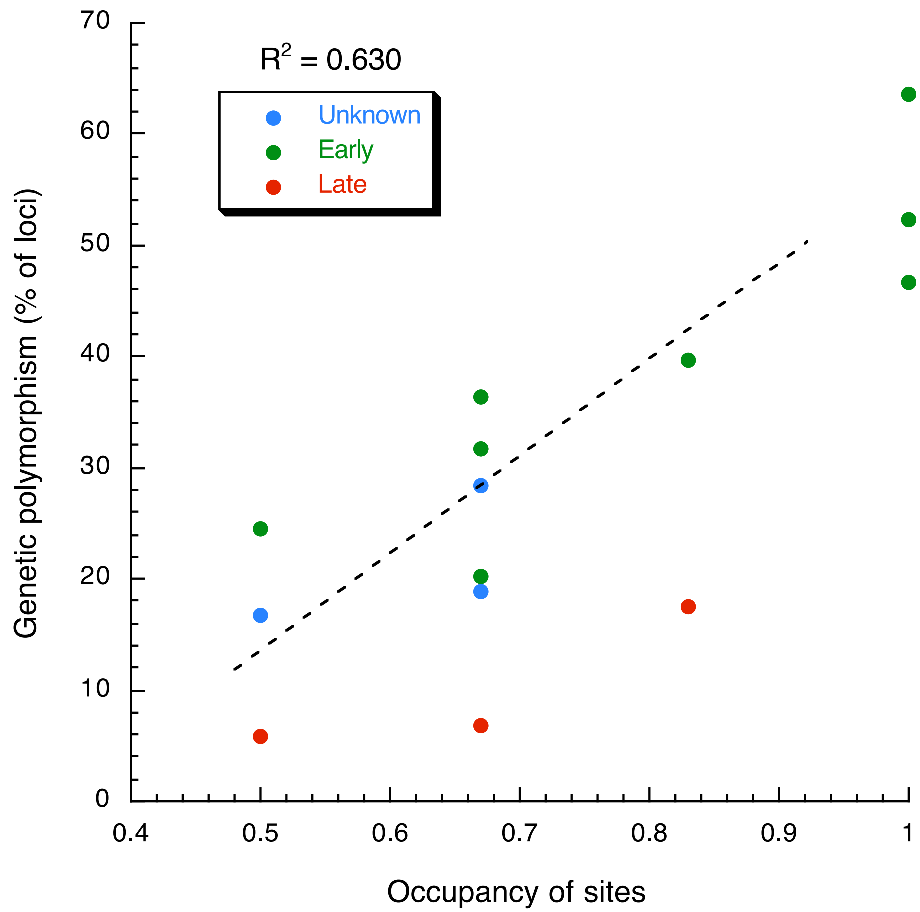
Shank et al. 2003


Shank et al. 2003



Collaborators: Ding, Fornari, Govenar, Seyfried, Ward

Genetic Diversity of Vent Species



Species	Occupancy	Order	P_{95}	Reference
Vestimentiferans				
R. pachyptila	1.00	early	52.4	1
R. piscesae	1.00	early	46.7	2
T. jerichonanae	0.50	early	24.5	3
O. alvinae	0.67	-	28.4	3
Polychaetes				
P. grasslei	1.00	early	63.5	4
A. pompejana	0.67	early	36.4	4
A. caudata	0.67	early	31.7	4
Bivalves				
C. magnifica	0.50	late	5.9	5
B. thermophilus	0.67	late	6.9	6
Limpets				
E. vitrea	0.83	late	17.5	7
L. pustulosus	0.67	-	18.8	7
L. elevatus	0.67	early	20.3	7
L. galriftensis	0.50	-	16.7	7
Amphipods				
V. sulfuris	0.83	early	39.6	8

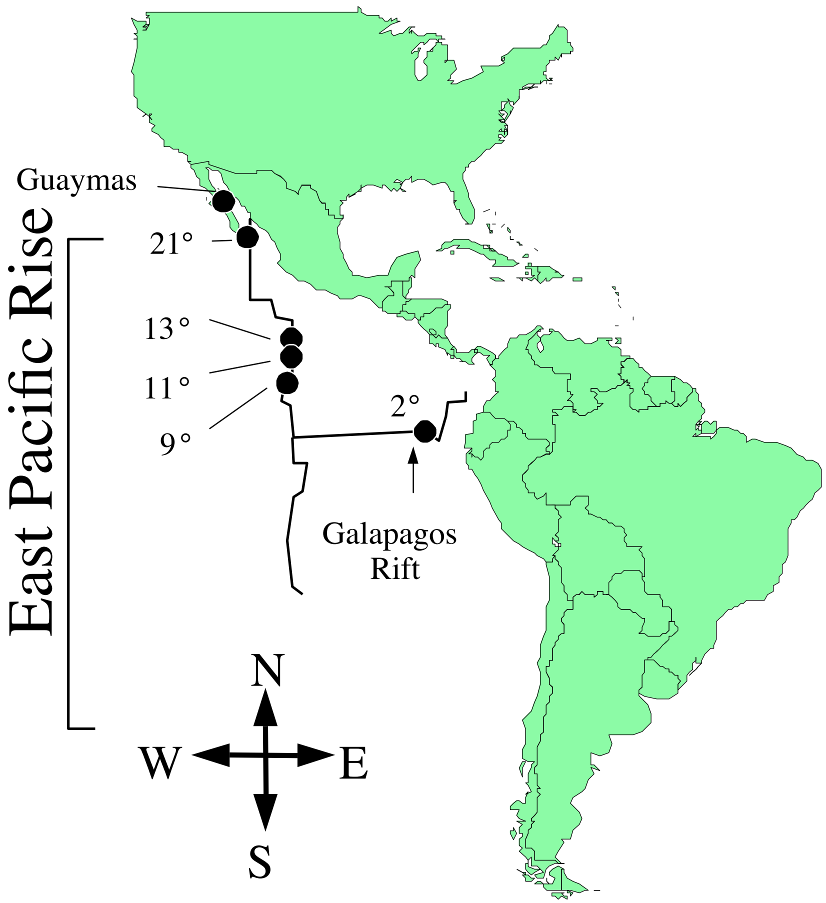
References: (1) Black et al. 1994; (2) Southward et al. 1996; (3) Black et al. 1998.; (4) Jollivet et al. 1995; (5) Karl et al. 1996 ; (6) Craddock et al. 1995; (7) Craddock et al. 1996; (8) France et al. 1992.

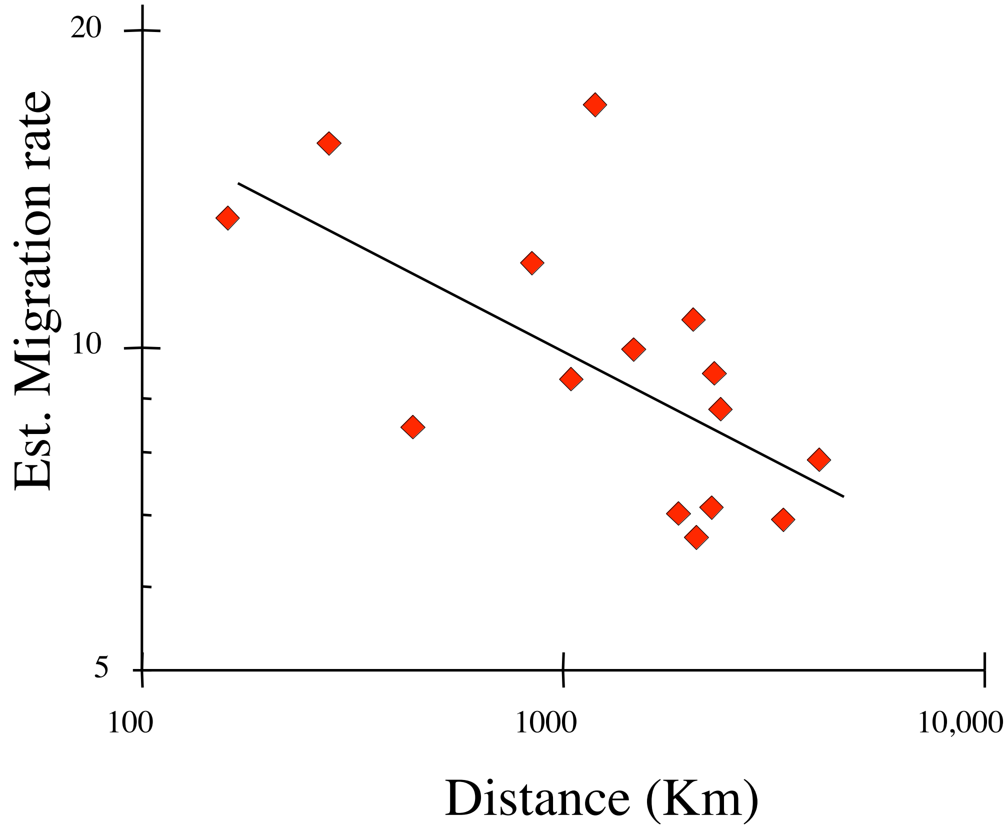
high rates of habitat disturbance and a species' position in ecological successions may affect levels of genetic diversity

Vrijenhoek, Shank, and Lutz 1998

Inferring Dispersal via Population Genetics

The vestimentiferan tubeworm, *Riftia pachyptila*

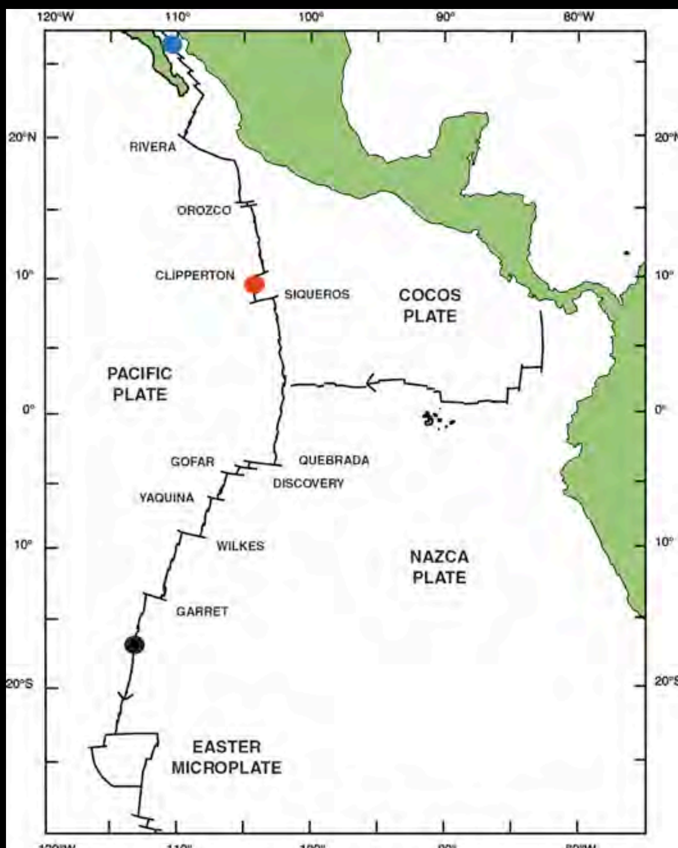




Reject expectations of "island model" of dispersal
Consistent with stepping-stone model
Inference: a species with more limited dispersal abilities

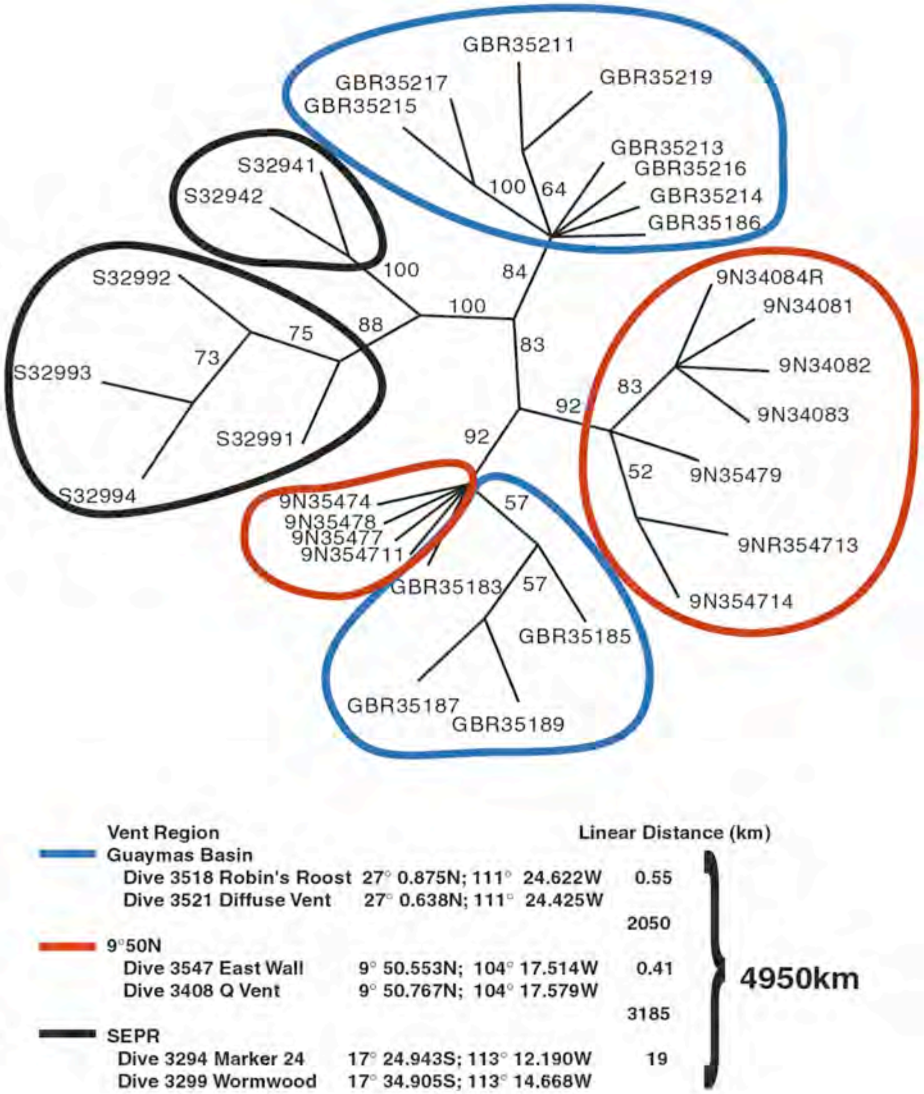
Black et al., 1994

Riftia pachyptila



East Pacific Rise

AFLP
Parsimony Tree
500 bs reps



Shank and Halanych 2007

Genomic Fingerprints: Amplified Fragment Length Polymorphisms

Galápagos Rift

June 2005

To investigate patterns of biological, geological, and geochemical temporal change

June 2002

• comparison with different spp pool

Recovery of recently-settled *Riftia*

55% < 4mm long

Riftia pachyptila

Results

630 loci (94% polymorphic)

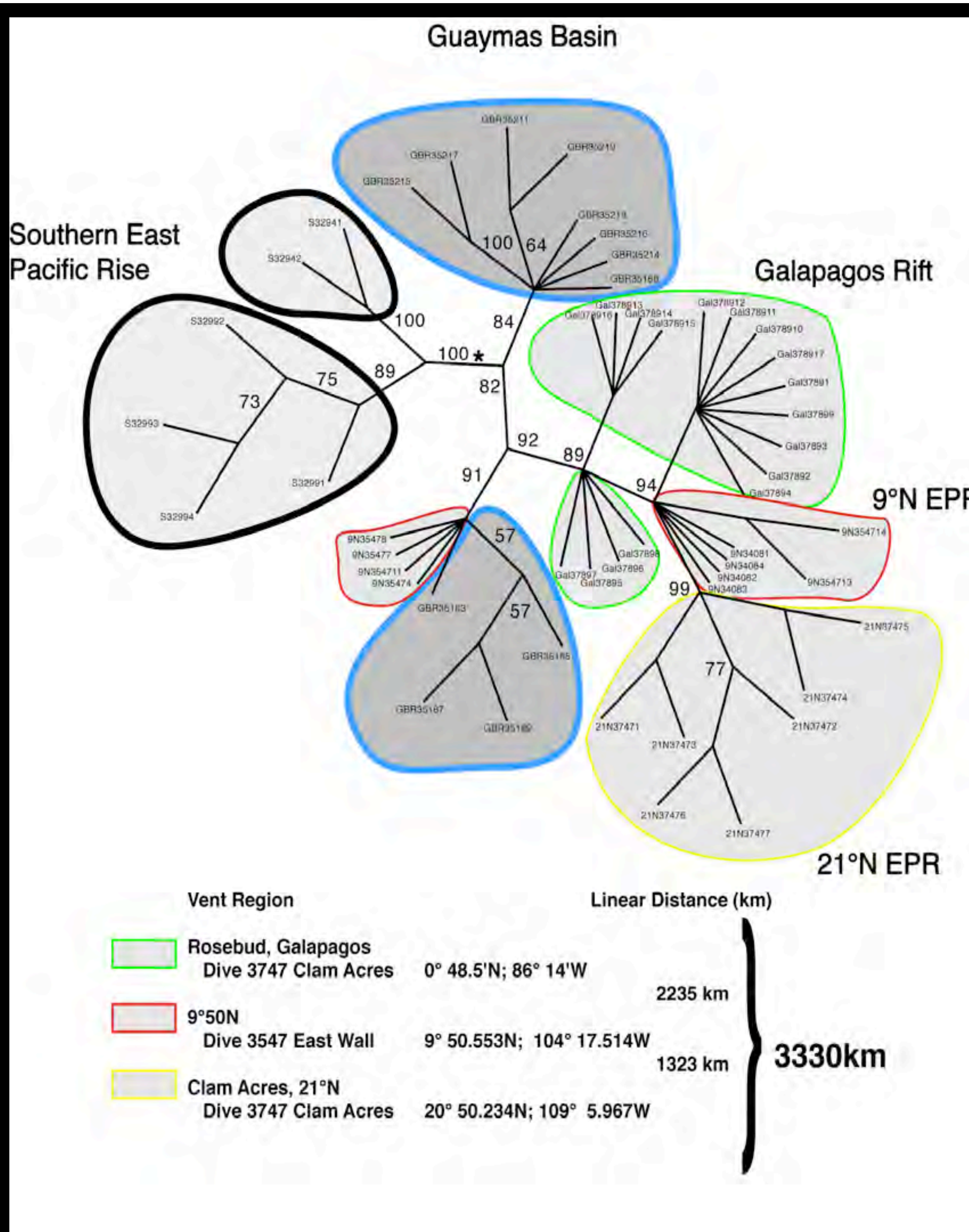
Each ind. = unique fingerprint/haplotype

Each assemblage = genetically distinct

Genetic structure correlated w/ geography

Polytomies (stars) = individuals <10 cm

(DNA msats= See Abby Fusaro's poster)



Shank and Halanych 2007

“Succession” as a framework

- Gaps in our understanding
- Integrated temporal experiments
- Consequences of succession on genetic diversity
- Geo-bio-chemical interactions

Gene Expression Studies

Understanding interaction between organism (function) and the environment

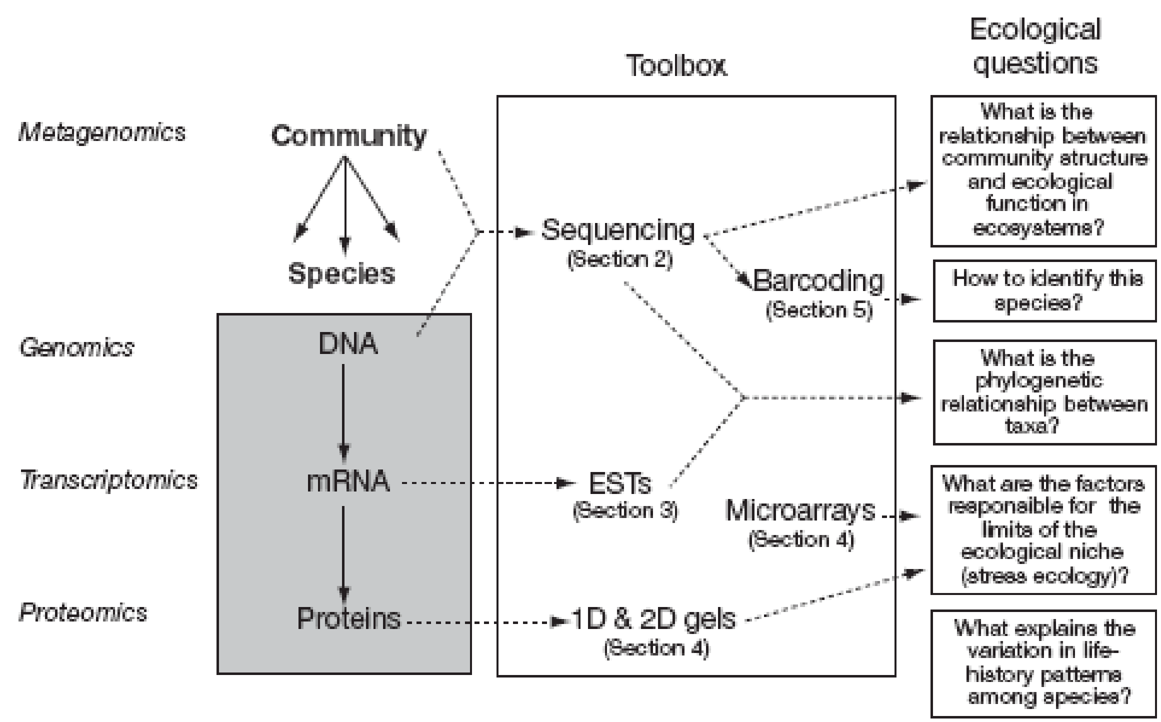


Fig. 1. Links between genomic tools and ecological questions

Dupont, 2007

Gene Expression Studies

Gene expression represents the physiological state of an organism's interaction with it's environment

- What genes are responsible for larval competence/recruitment?
- What genes govern chemoautotrophic production?
- What host genes regulate symbiont function?
- What genes are responsible for adaptive advantages?

Gene Expression Studies

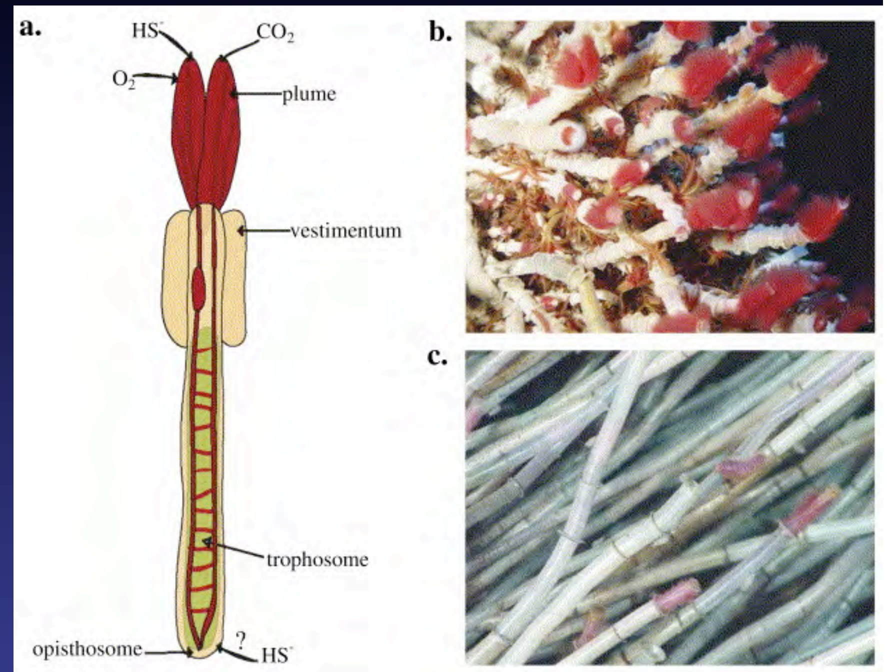
Links between ecological questions and genomic tools

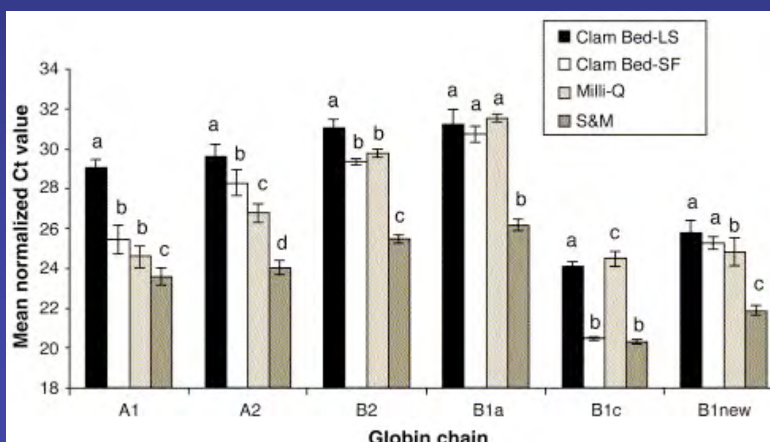
Few Examples:

- Assimilatory citrate reductases for biosynthesis
- Thiosulfate reductases for sulfur/thiosulfate reduction
- ATP sulfurylase for sulfide oxidation in symbionts
- RubisCO and ATP lyase for carbon (CO_2) fixation
- Response to oxidative stress in colonists, juveniles, adults (Calvin cycle vs reductive tricarboxylic acid cycle in *Riftia* symbionts - *Markert et al 2007*)

and global expression patterns for the discovery of functional genes under different environmental/physio-chemical conditions

Ridgea piscesae





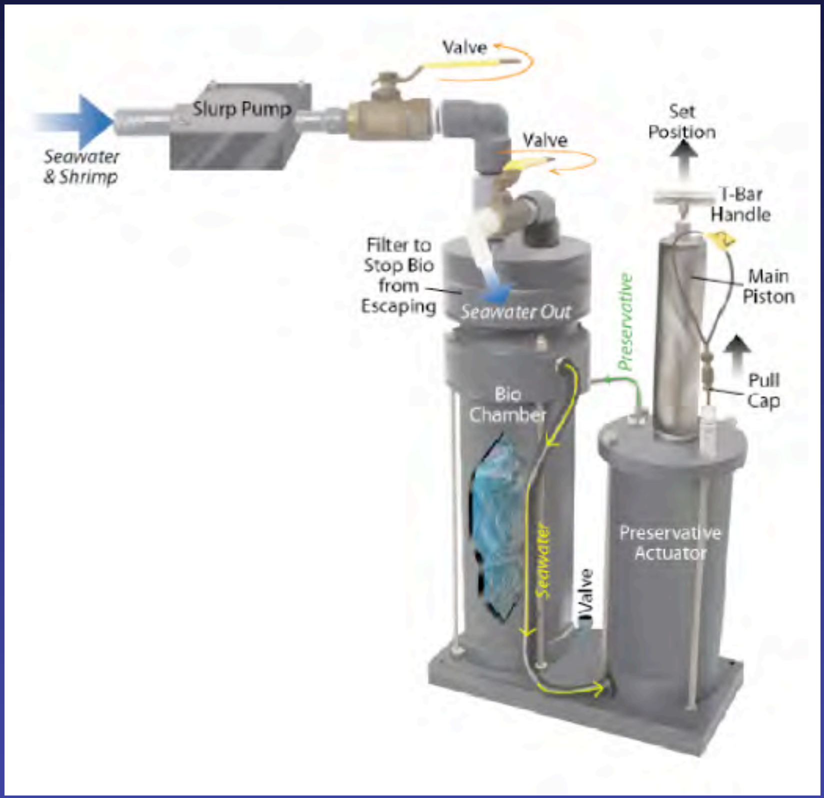
Comparison of site-and phenotype-specific globin chain expression of *R. piscesae*.

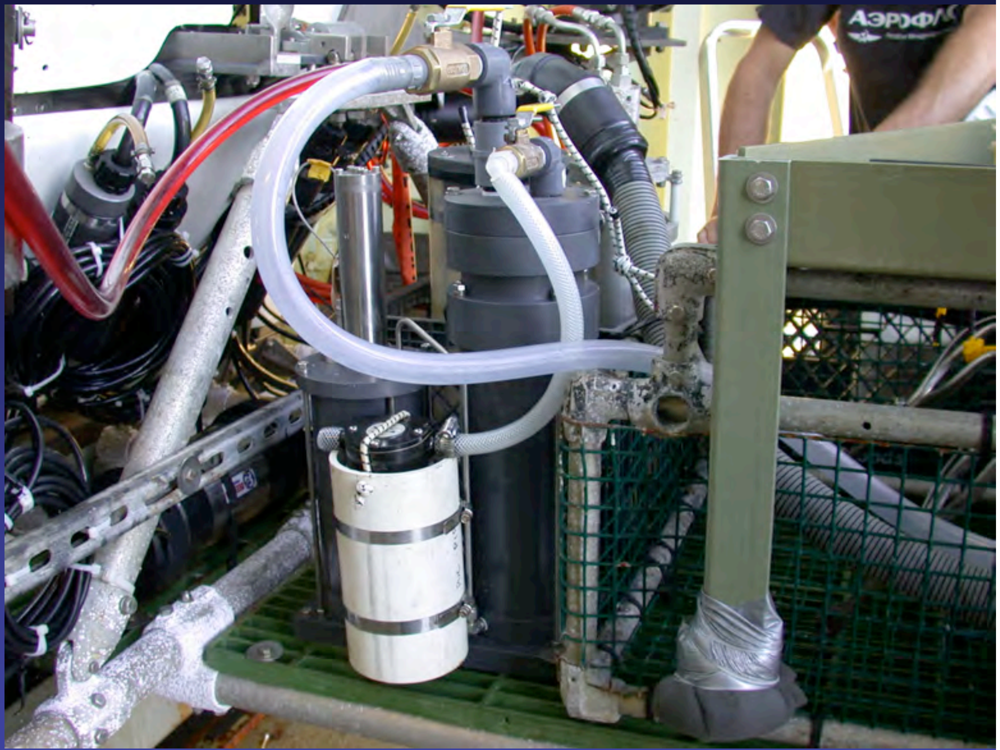
Carney et al 2007

Environmental differences in hemoglobin expression

- expression 12 x higher in short-fat than long-skinny
- different habitat conditions influence phenotype, gene expression, and physiological state

Gene Expression Studies





Enzymatic Sampler

Mounted on Alvin

….Microarray studies looking at thousands of genes
…alvinellids and mussels soon

Parting Perspectives

- No one model of “succession” will suffice- use framework
- Studies of physiology of life-history stages in species
- Habitat conditions associated w/ individual species (T&S)
- Disturbance frequency and geo-chem-bio response
- Interaction of free-living microbes and fauna in chem settings
- Co-located, coincident measurements/expt’al approaches (e.g., gene expression) to determine the physiological and competitive advantages, and the mechanisms of successional change

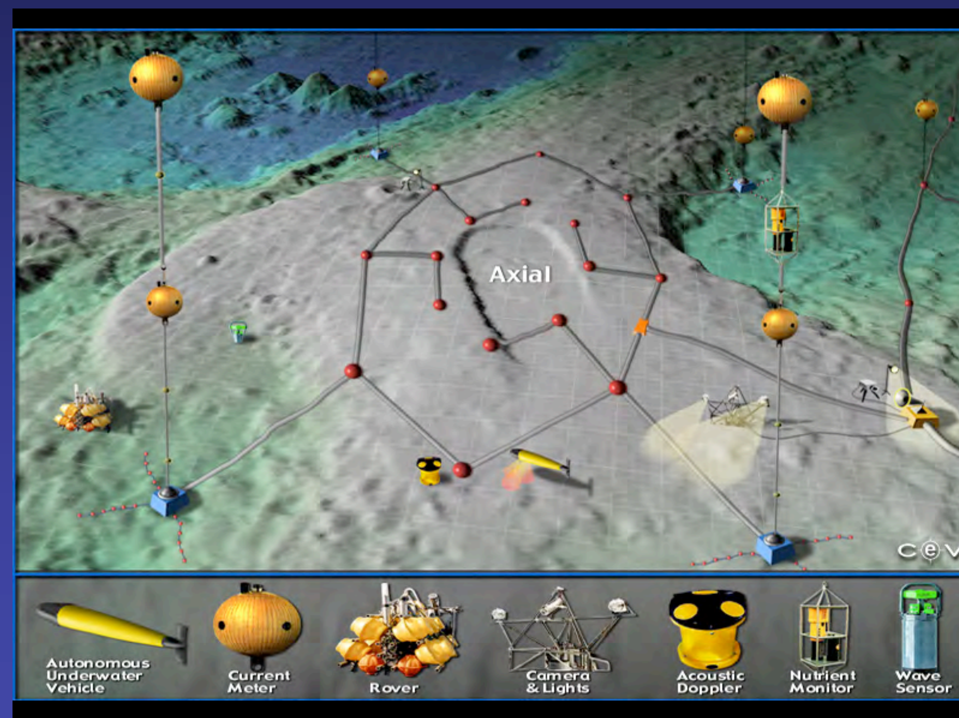
“If we can predict the agents of change, then we can understand the linkages”

Temporal changes occur on scales better studied by observatories

Neptune

J. Delaney

Axial



M. Sturmer

Parting Perspectives

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"If we can predict the agents of change, then we can understand the linkages"

[redacted]