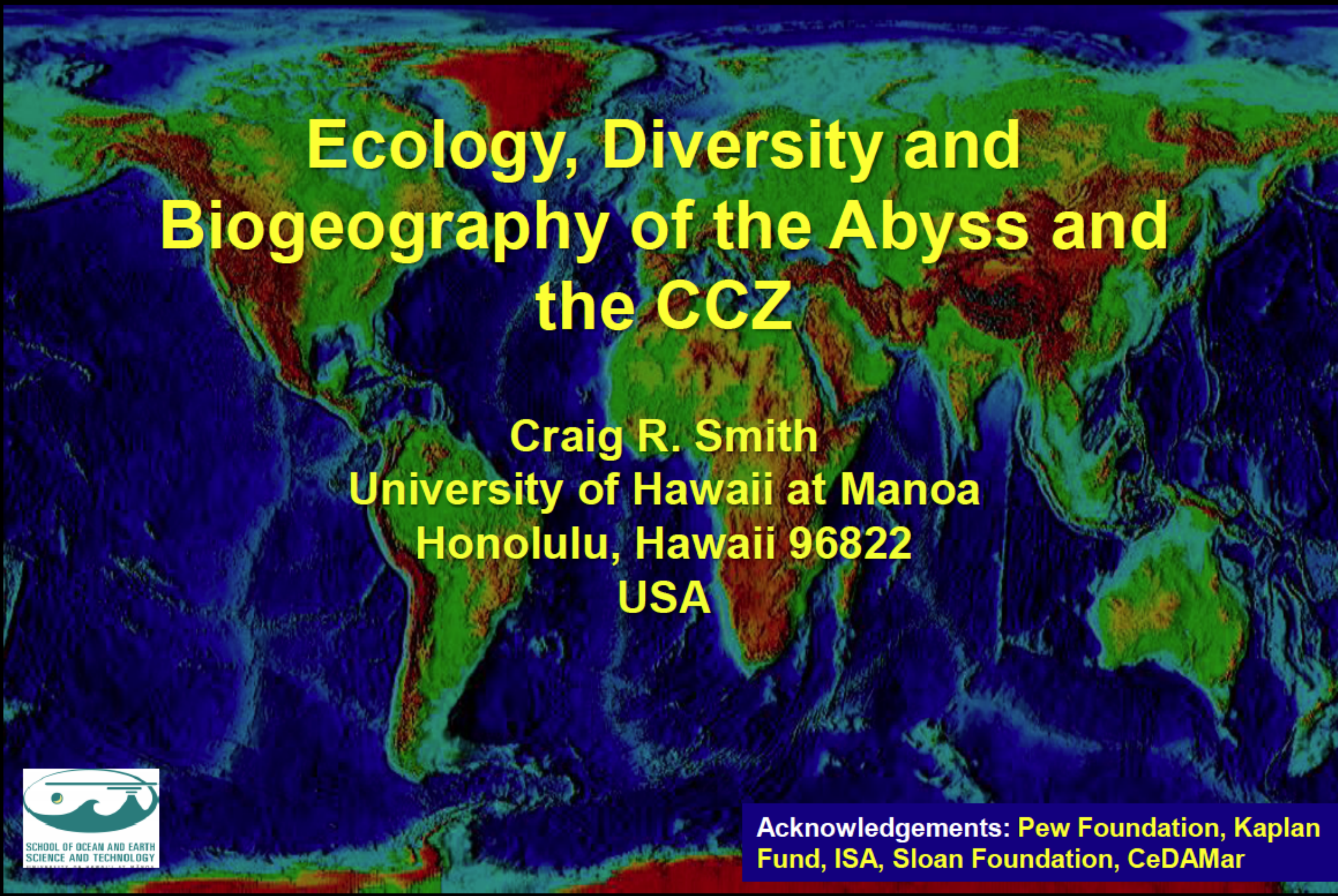
Biology of Manganese Nodules

The abyssal habitat
The fauna of the abyss
Biogeography of the abyss
CCS nodule province
    The Kaplan project
Nodule fauna

Extra special thanks to Craig Smith for sharing his presentation:



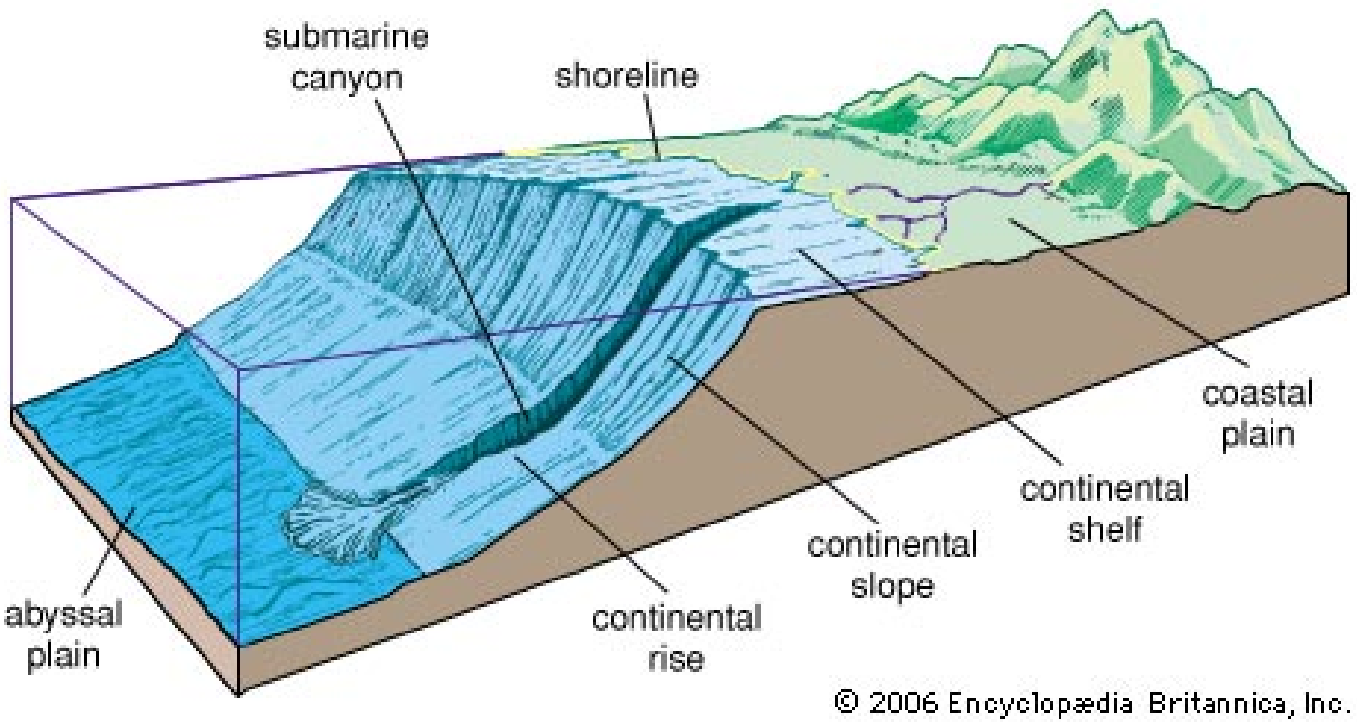
Reminder:
Characteristics of the deep ocean

- Absence of sunlight
- Temperatures around freezing
- Average salinity
- High dissolved oxygen
- Extremely high pressure
- Slow bottom currents (except abyssal storms)
- Low food supply

Especially true of the Abyss

Where are the abyssal plains?

- past the continental slope and rise
- typically 2,200 m to 5,500 m
- 40% of the ocean floor is abyssal plain
- sedimentation is slow ~2 cm every 1000 years



1) Nature of Abyssal Benthic Ecosystem - Seafloor (3000 – 6000 m) = Vast (the big blue)

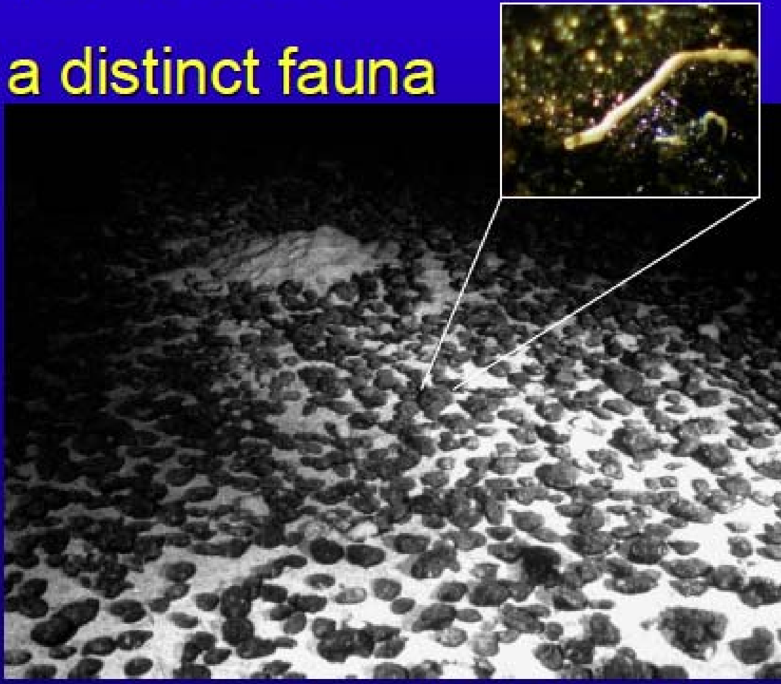
54% of Earth's surface!

Ecological Characteristics of Abyssal Seafloor –

- Mostly plains of sediment (sand to clay)
- Low temperature (-1.0 to 2.0 ^{o}C)
- High hydrostatic pressure
- Often physically very stable (low currents)
- Much of structure biogenic (fragile) or nodules
- Hard substrates (nodules) harbor a distinct fauna

L. Levin


4500 m Equatorial Pacific


5600 m Central North Pacific

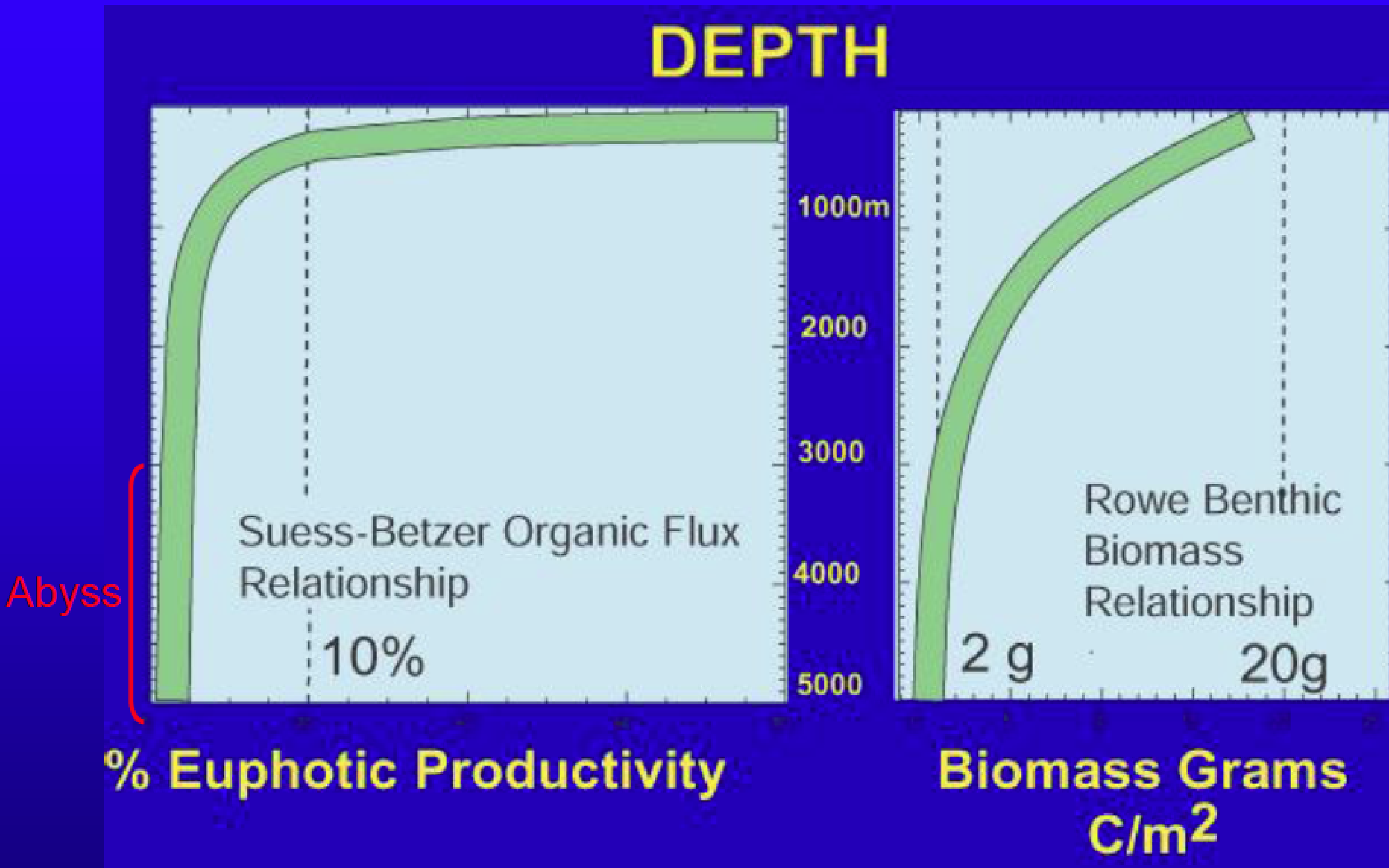
Life in an abyssal plain

- Stable homogeneous environment
  (temperature, salinity, low currents, little turbulence, always dark, very little change in environment over large distances)
- Largest ecosystem on earth
  (expansive soft bottom substrate)
- Stability selects for incredible biodiversity
- Biomass = low
  There are many different species, BUT the number of individuals in each species may be small per area sampled.
- Food limitations can be severe

Dendrotionid Isopod

Tripod fish: Biozaire bathypterois

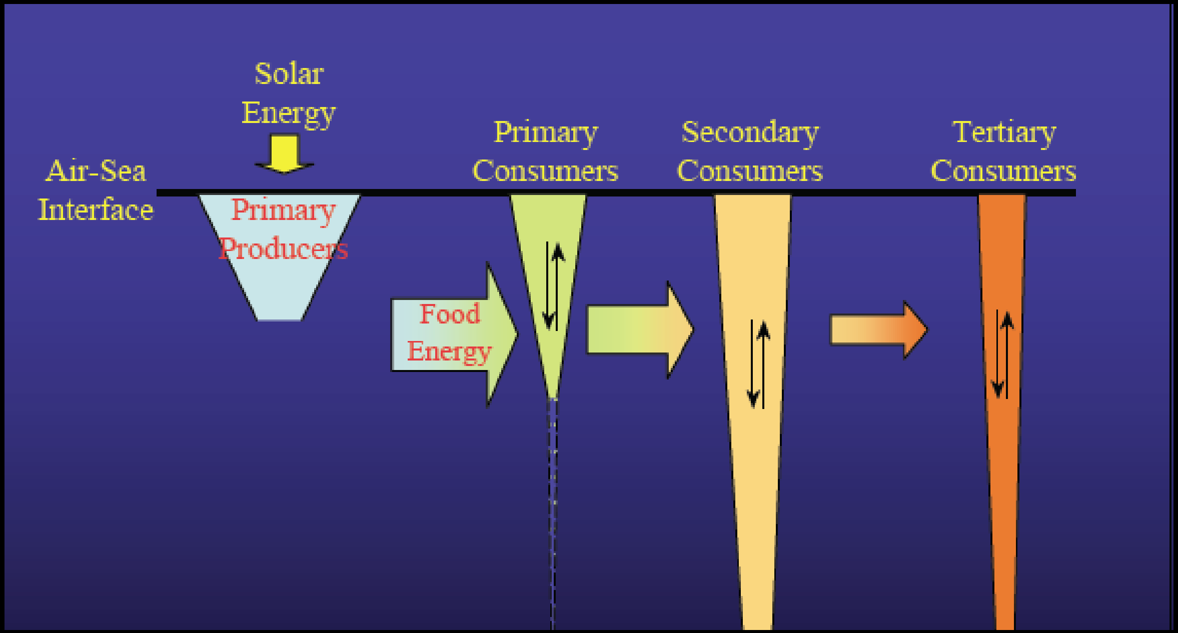
Food from sinking POC flux ⟶ *"Food Limited"*



- Biomass, production, growth rates, recolonization rates very low, all controlled by the flux of sinking POC

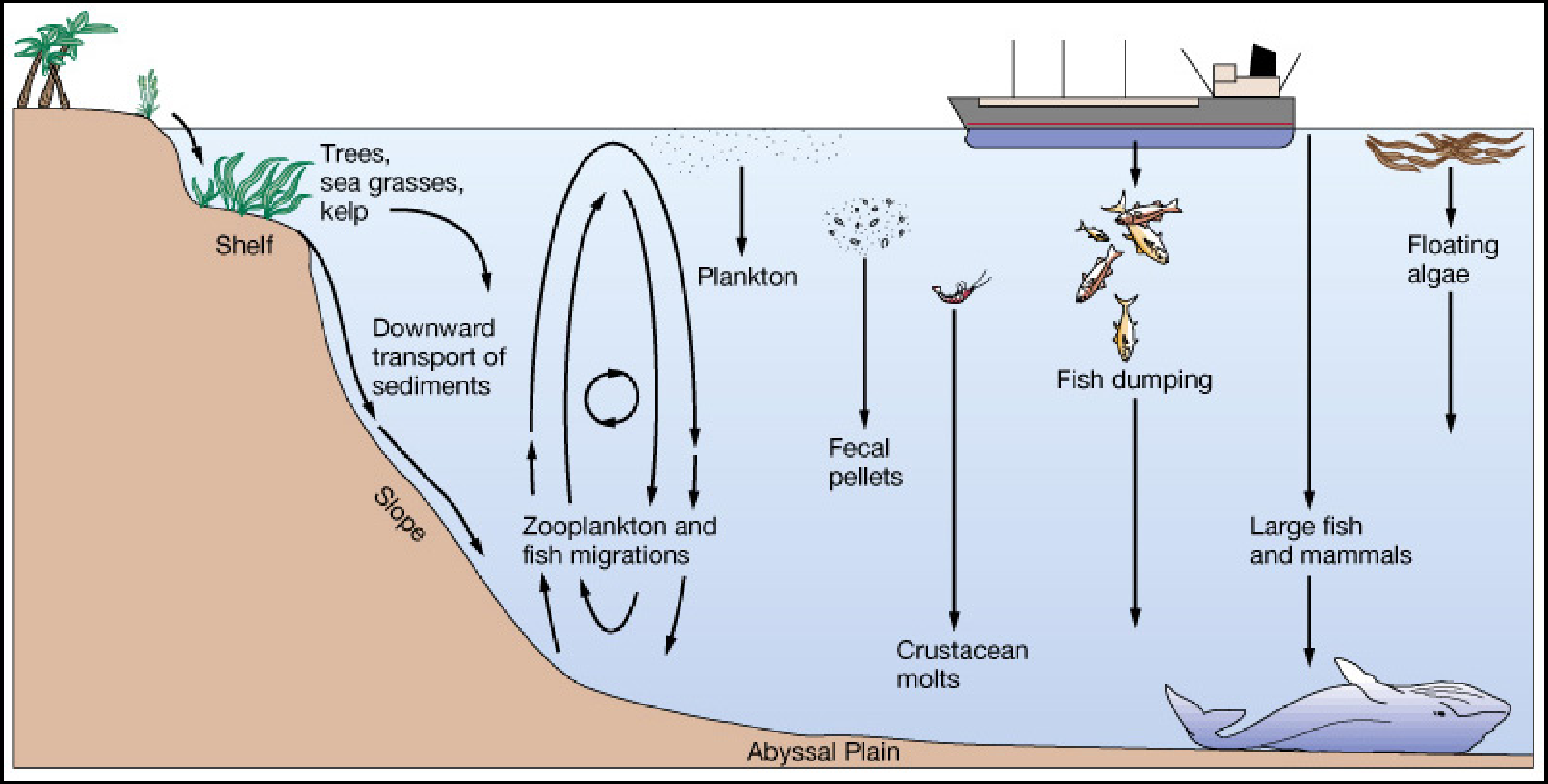
From R. Carney

Food to the Abyss



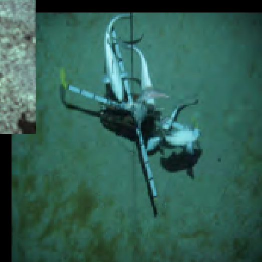
- Passive detrital rain
- Remains of plankton, fecal pellets, moults
- Plant debris and animal carcasses
- Small, light particles (bacteria etc.) remain suspended indefinitely
- Dissolved organic matter (DOM) derived from POM (usually refractory)

Food sources for abyssal deep-sea organisms:
- Surface primary productivity



Food to the Abyss can be patchy in space and time

Seabed photographs showing massive accumulations of phytodetritus on the abyssal sea floor (Billett et al. 1983).



Rapid microbial response by barophilic bacteria to freshly deposited phytodetritus (Lochte and Turley 1988)

http://pcwww.liv.ac
•uk/earth/crozet/images/Fig1.jpg

Responses to Food Falls

(challenging the paradigm of constancy)

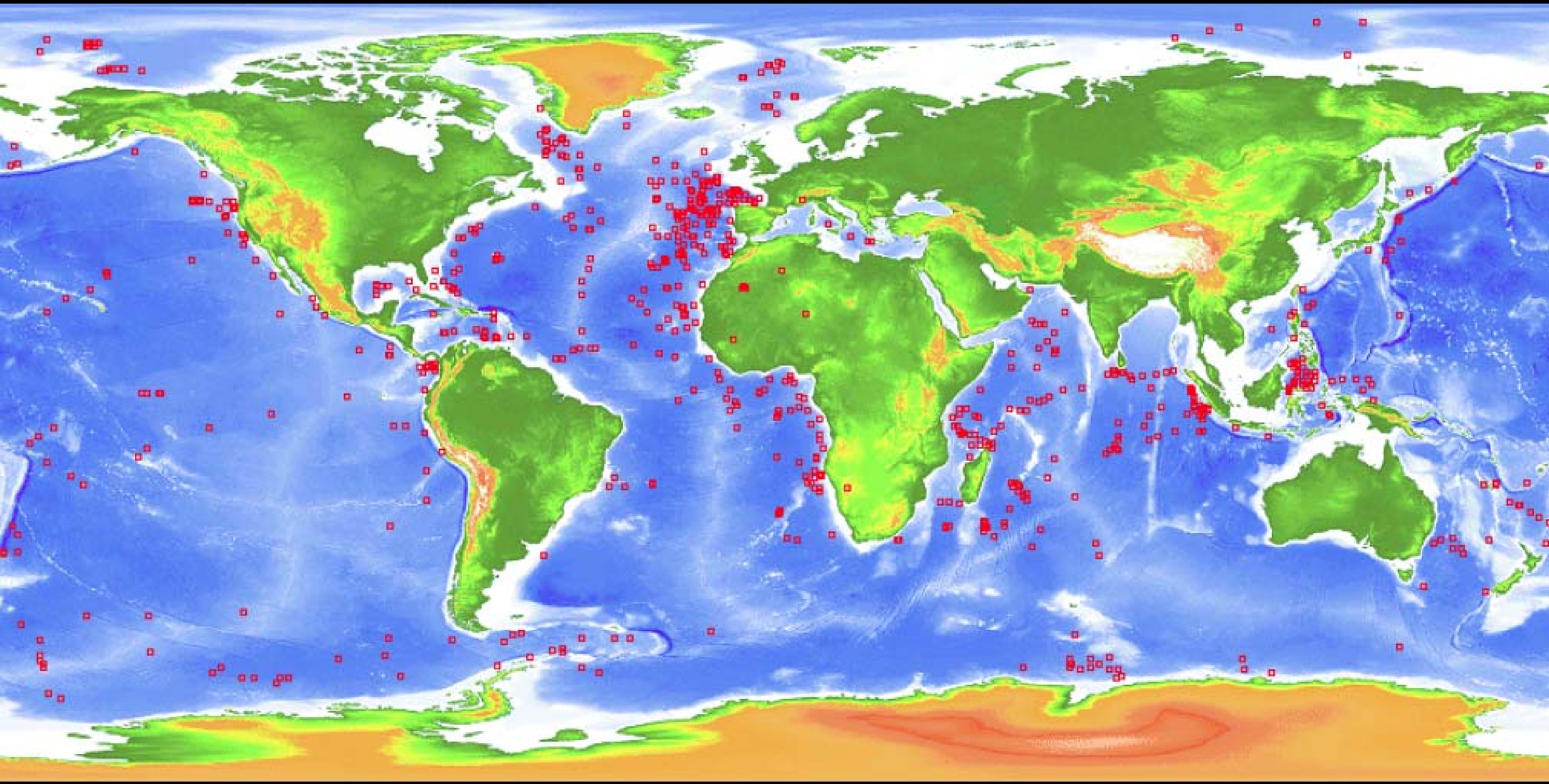
- Scavengers attack dead animal fall

  (Isaacs and Schwartzlose, 1975)

Hagfish, lyssianasid amphipods, isotopods, brittle stars

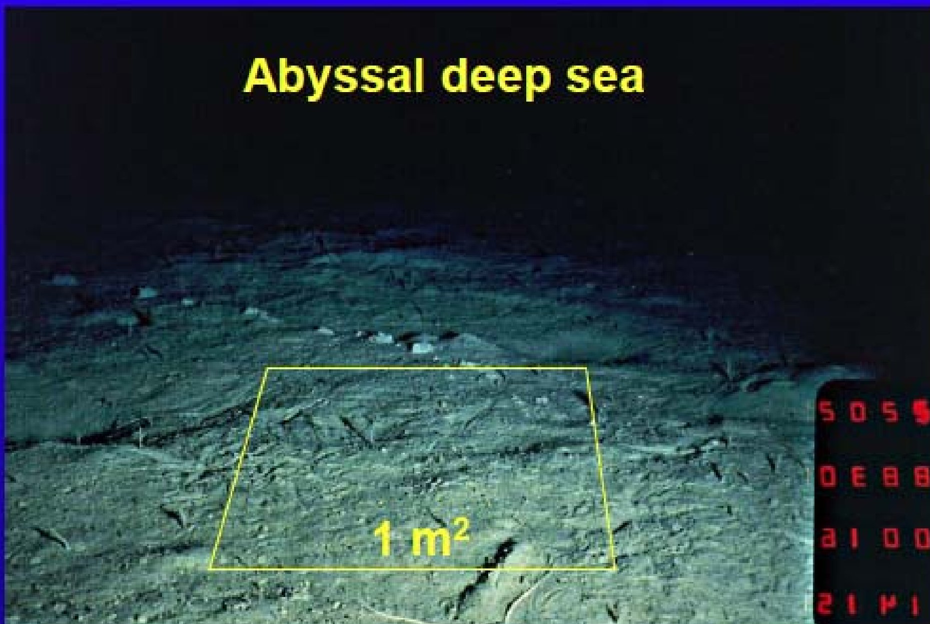
Abyssal fauna very poorly sampled and described!

Total abyssal records (3000 – 6000 m) at species/genus level in OBIS

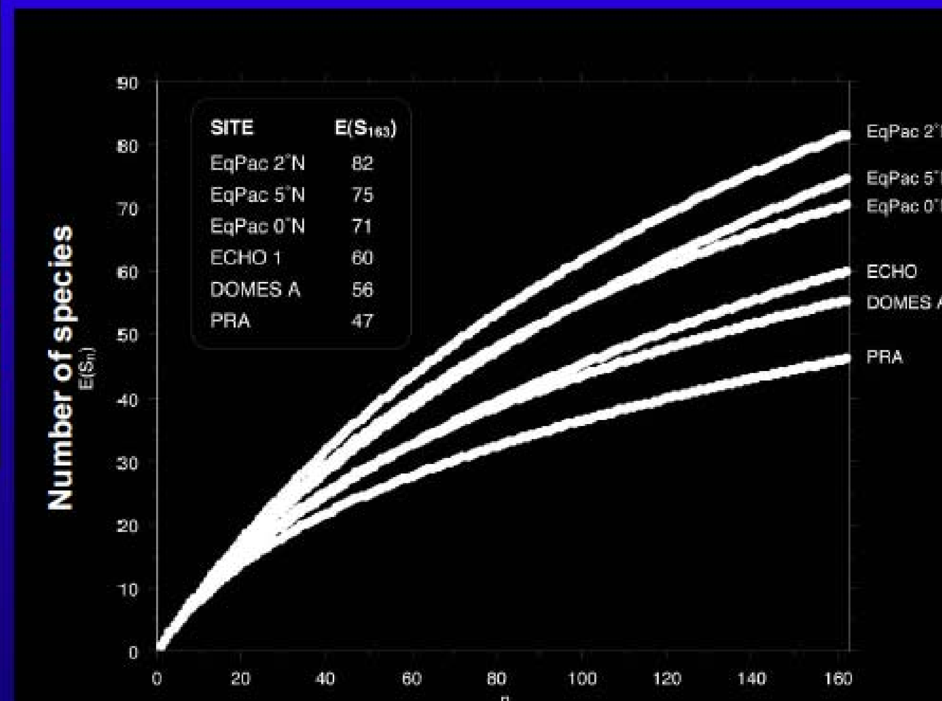


- Enigmatically, very high local species diversity –

80 - 100 macrofaunal species per m²



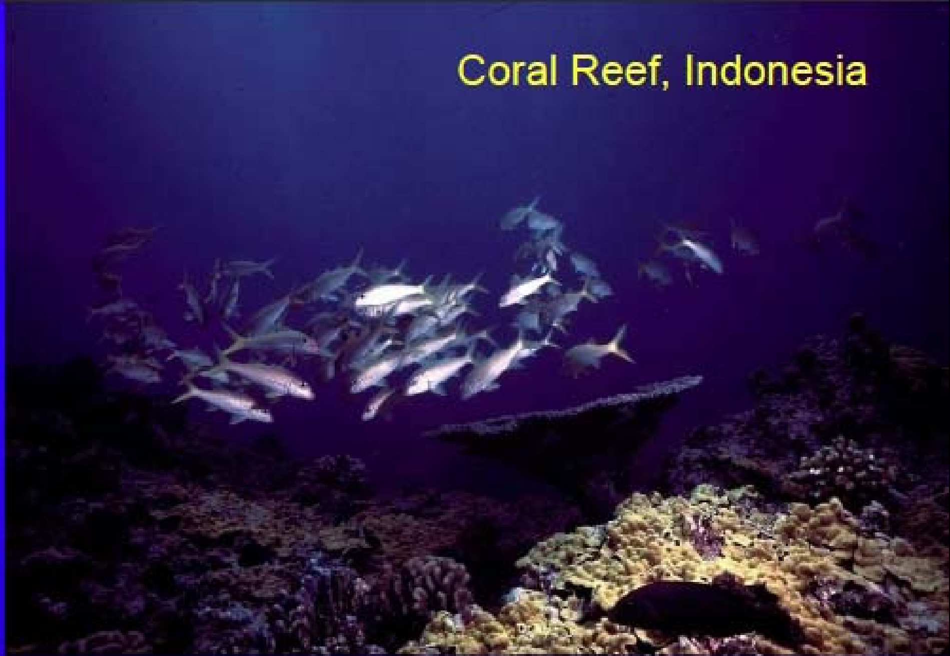
~ 50 spp per 100 individuals



Number of individuals

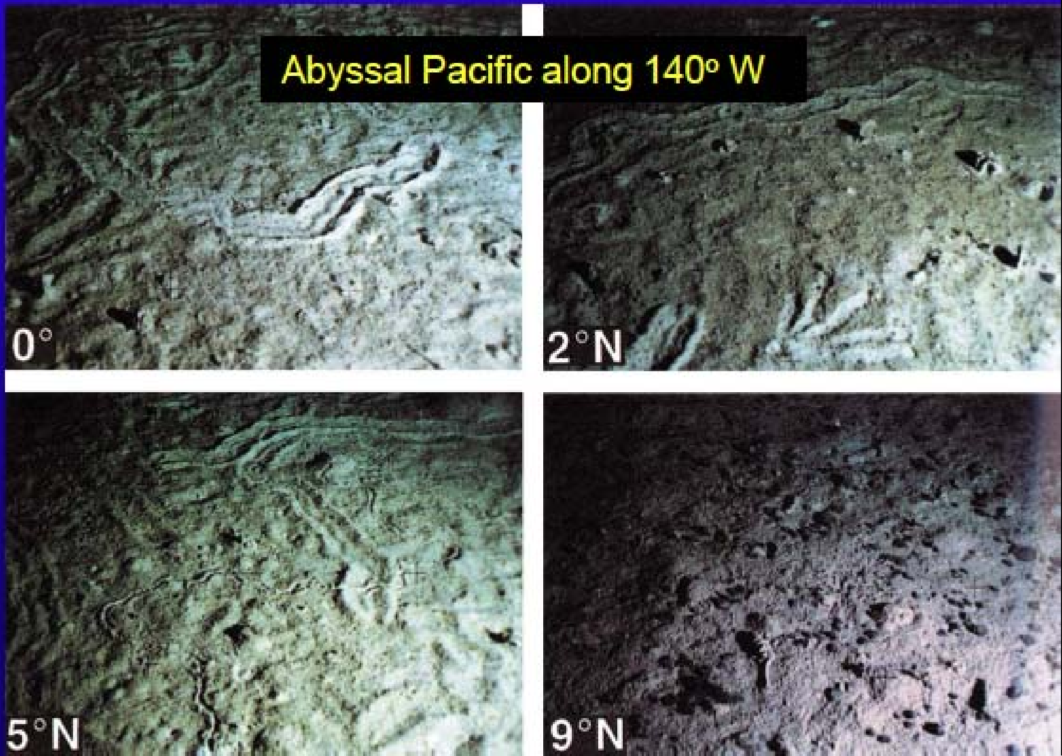
Despite low habitat complexity – Rivals most diverse ecosystems

Rainforest, Costa Rica



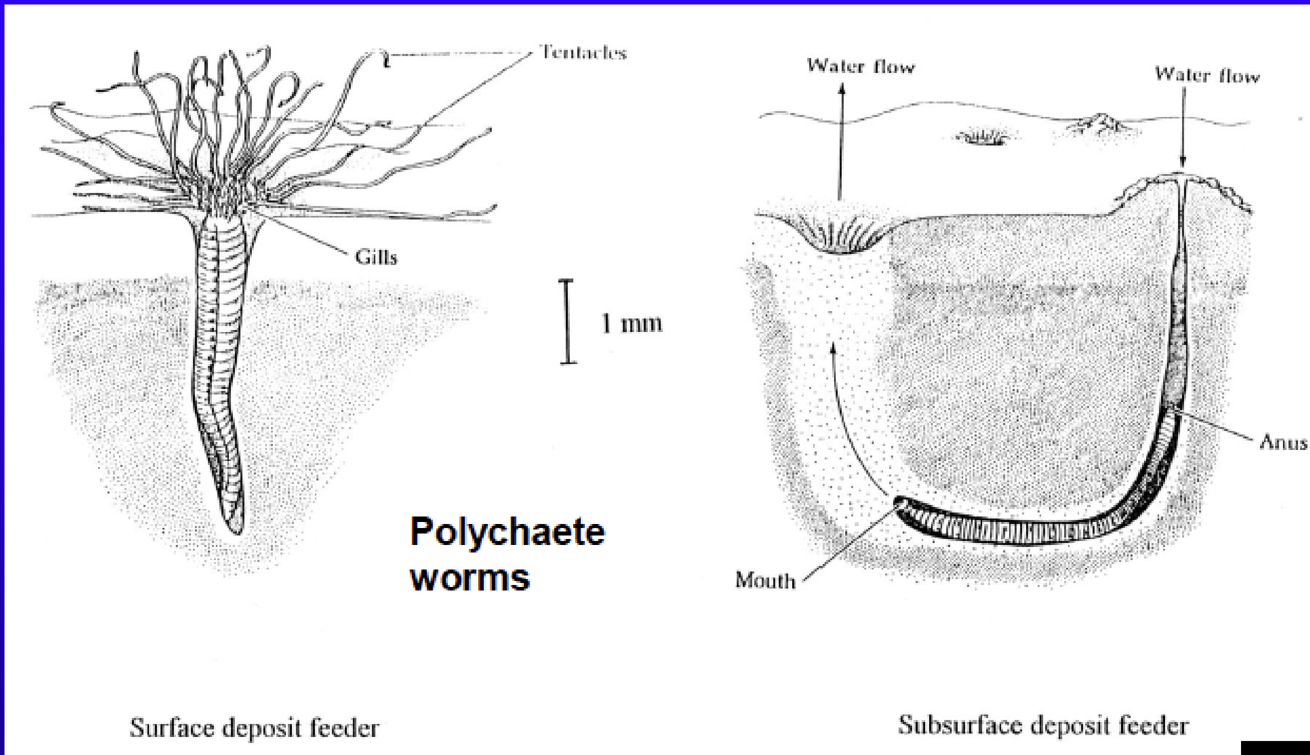
-High local diversity but low habitat complexity compared to many other locally diverse ecosystems

~ 100 species macrofaunal species m $^{-2}$ sediment

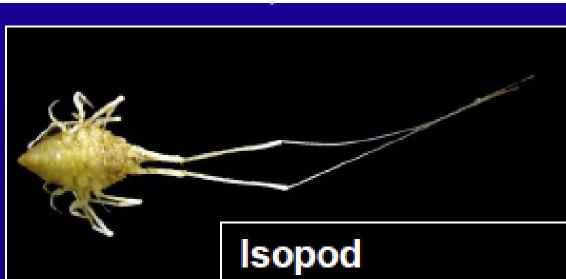


- Much of abyssal fauna = *small, delicate* deposit feeders (esp. surface deposit feeders) but also suspension feeders living on nodules

Examples of macrofauna (300 µm – 3 cm)



Polychaete worms



Isopod

Crustaceans

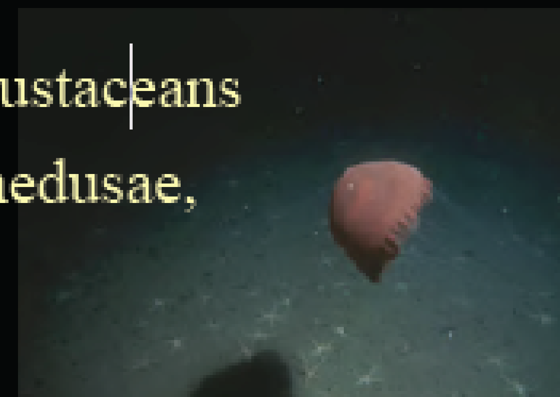
Amphipod

Consumer Groups

- **Sediment community** - bacteria, protozoans, nemat polychaetes, bivalves, crustaceans

- **Epibenthic megafauna** - holothurians, ophiuroids, asteroids, gastropods, sponges

•**Benthopelagic animals** - fishes, squid, large crustaceans



•**Plankton** - bacteria, protozoans, crustaceans, medusae, chaetognaths

Life in the deep abyss

- In general there is high diversity, even in food limited abyssal plains
- Megafauna (big enough to see) includes:
  - Mobile omnivorous fishes, cehalopods (squid and octopuses), amphipods, and shrimp
  - Mobile deposit feeders such as holothurians (sea cucumbers) and starfish
  - Non-mobile suspension feeding glass sponges, anemones and other cnidarians
  - Xenophyophores- Giant protozoans

Life in the deep abyss

- Xenophyophores-
  - Weird giant agglutinating protozoans
  - Provide habitat for other organisms
  - The ones in nodule provinces are not well studied, but likely to yield additional specialized species of smaller animals

Life in the deep abyss

- The Macrofauna (too small to see easily, bigger than about 0.3 mm) are very diverse in the sediment. Most are surface deposit feeders and can have hundreds of different species in one locality
  - Polychaetes (bristle worms) are the most abundant and diverse
  - Taneid and isopod crustaceans are next
  - Also bivalve molluscs (tiny clams), can be quite abundant

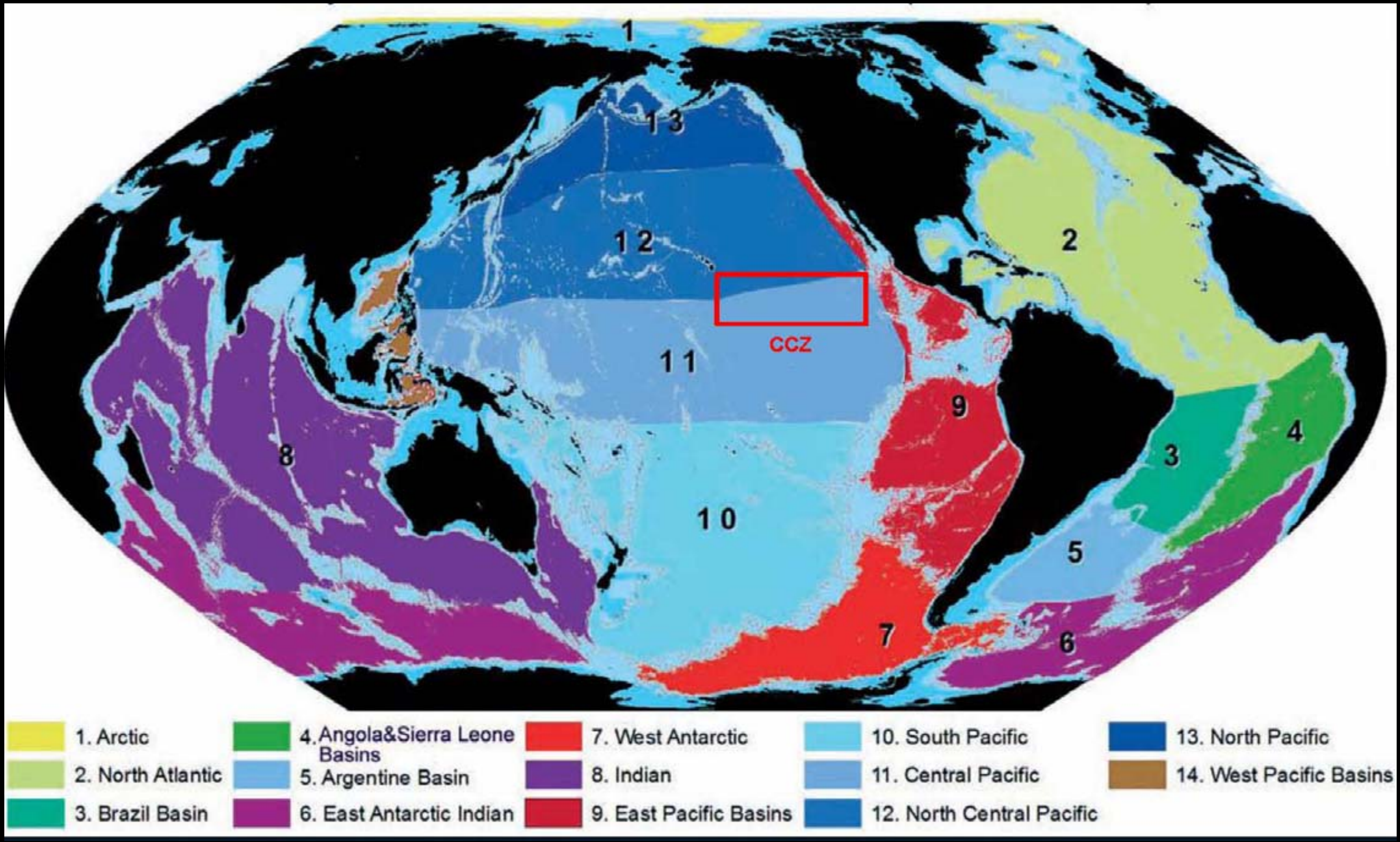
Life in the deep abyss

- The Meiofauna (tiny animals between 0.03 and 0.3 mm) are also quite diverse in the sediment and can be very abundant numerically.
  - Foraminifera (a protozoan) are the most abundant and diverse group
  - Nematodes are also very abundant
    - (up to 100,000 worms per m^2)
  - A variety of bivalve molluscs (tiny clams), can be also abundant

Life in the deep abyss

- The Microbiota (mostly bacteria) can constitute the highest proportion of the biomass in the sediments
  - About 1.4 grams carbon per m2
    - 10 times more than the macrofauna
    - 100 times more than the nematode worms

Biogeography of the abyss (400 – 5500 m depth)

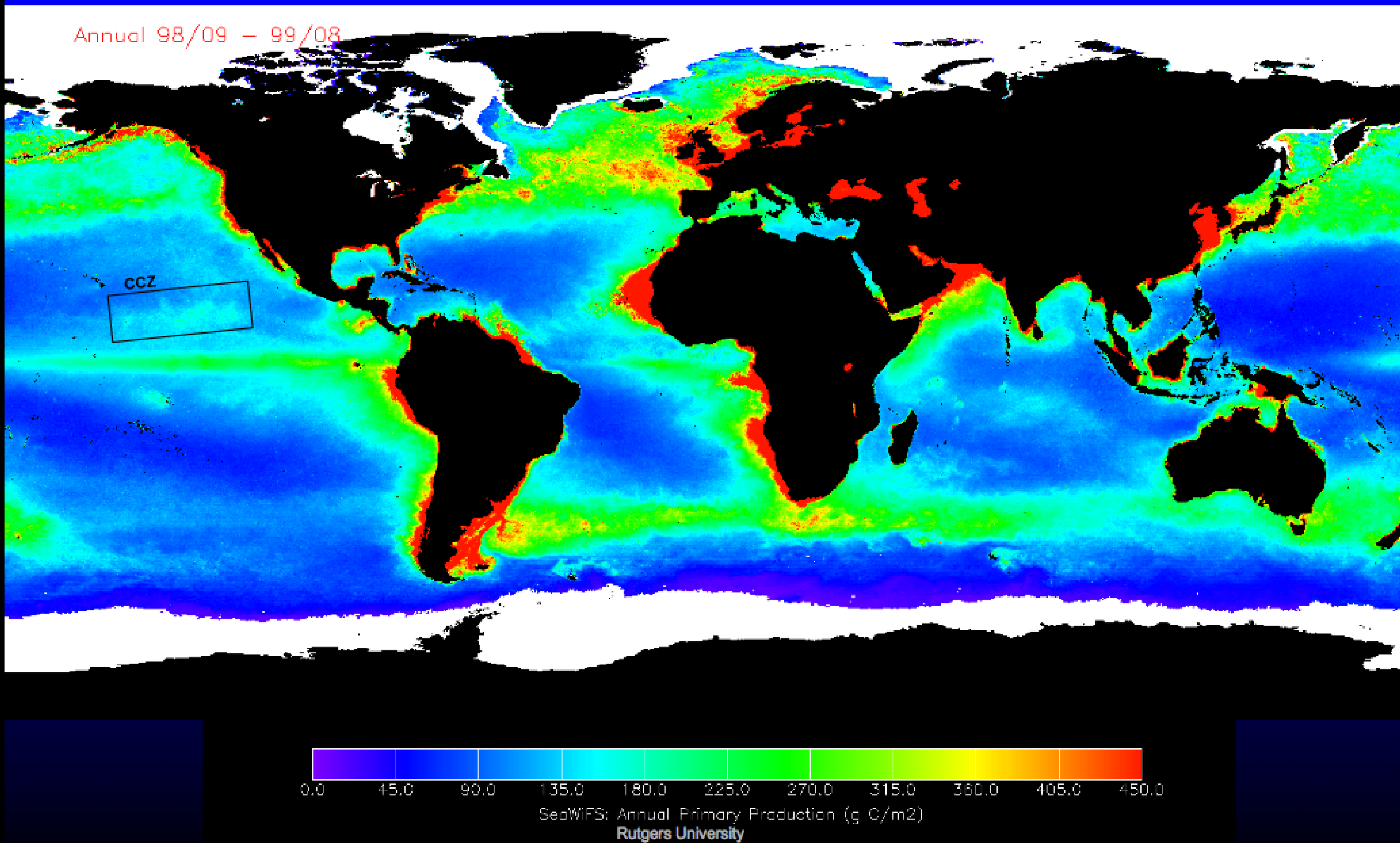


Very large provinces of a very large ecosystem!

What drives the biogeographic patterns in the Abyss?

1) Particulate organic carbon flux - probably most important

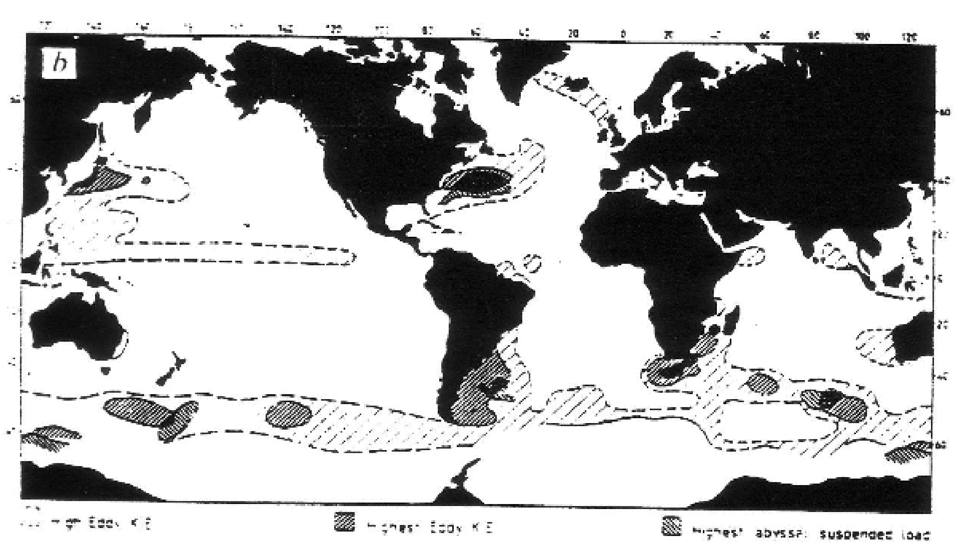
Annual Primary Production - 1998 - 1999



What drives the biogeographic patterns in the Abyss?

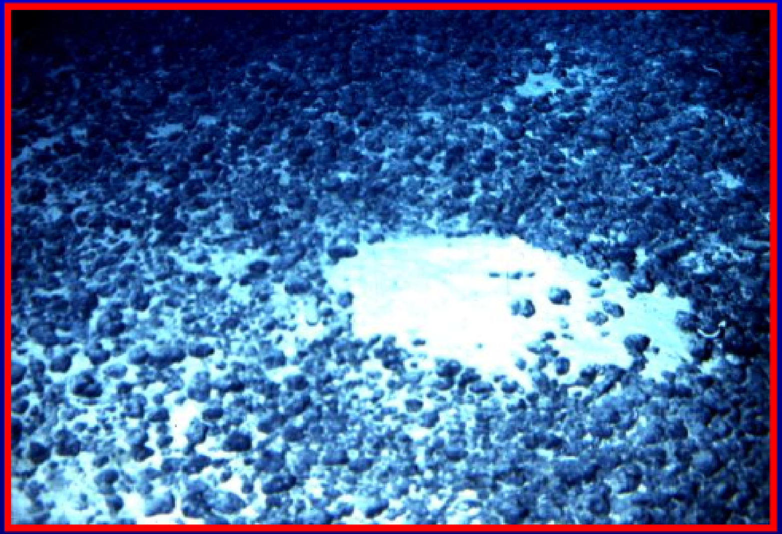
2) Flow regime

Abyssal areas of potentially high flow and sediment transport



Hollister and McCave, 1984

3) Substrate type (especially presence/absence of hard substrate)



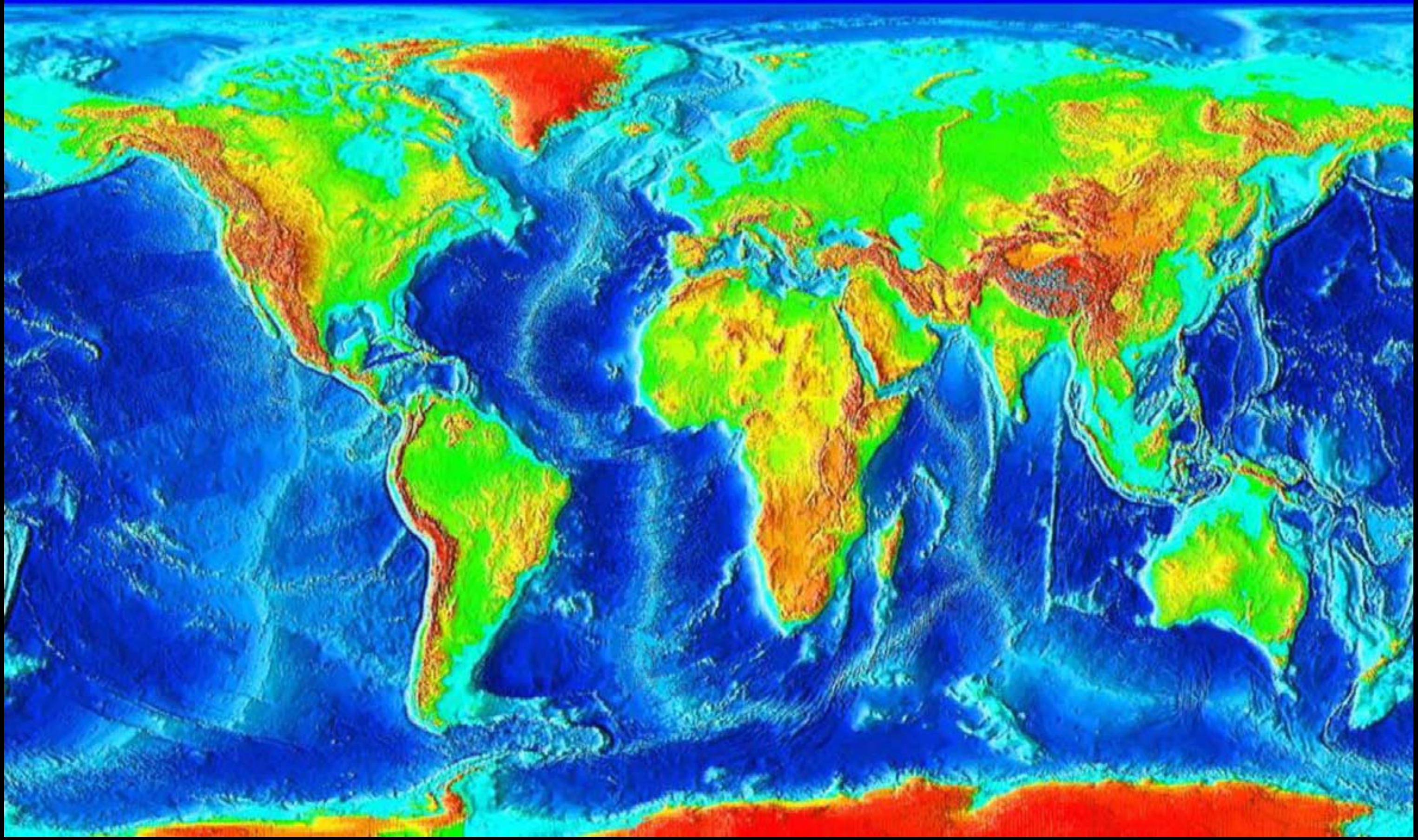
Nodules, 4100 m Pacific

What drives the biogeographic patterns in the Abyss?

4) Hydrostatic pressure??? (upper and lower limits to the abyss?)

5) Flow/topography interactions -- Isolation by continents, sills and mid-ocean ridges

[6) Historical processes]



What about species level patterns in the Abyss?

In most marine ecosystems – biogeographic patterns related to adult body size & mobility, and larval dispersal abilities

For representative taxa in each size class (megafauna to meiofauna) will ask:

1) How many deep-sea species are known?

2) Are there abyssal endemics?

3) Are there cosmopolitan abyssal species?

4) What proportion are restricted to single basins?

5) Are there local endemics?

Answers are fundamental to assessing extinction risks in the abyss

What about species level patterns in the Abyss?

MEGAFAUNA (> 2 cm) –

Bentho-pelagic fishes – large and moblie, use as e.g. Macrouridae (rattails) (Source: Jeff Drazen complied from many references)

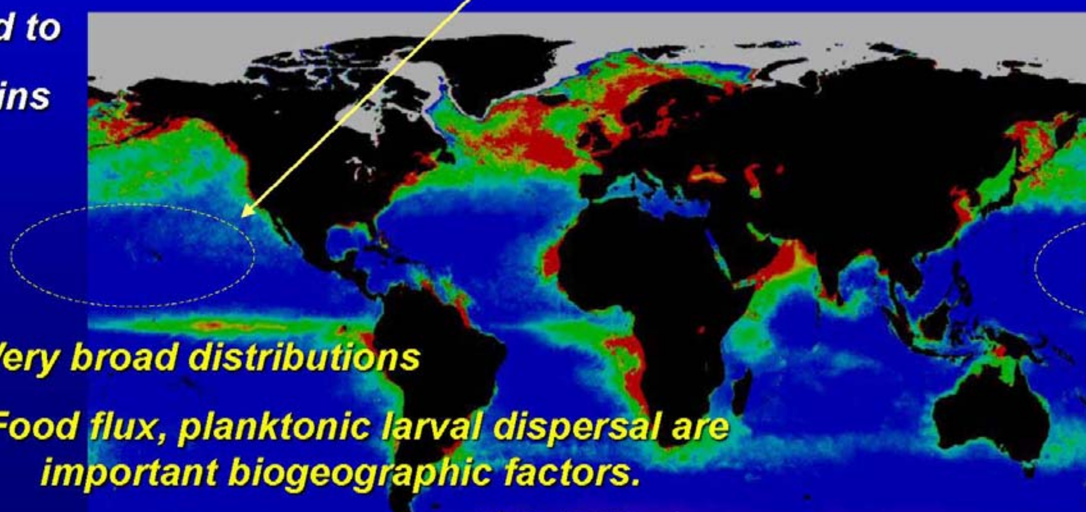
1) *300 deep-sea species (only 9 abyssal species)*

2) *One abyssal endemic (beneath N. Pacific oligotrophic gyre)*

(Coryhaenoides yaquinae)

3) *One cosmopolitan species*

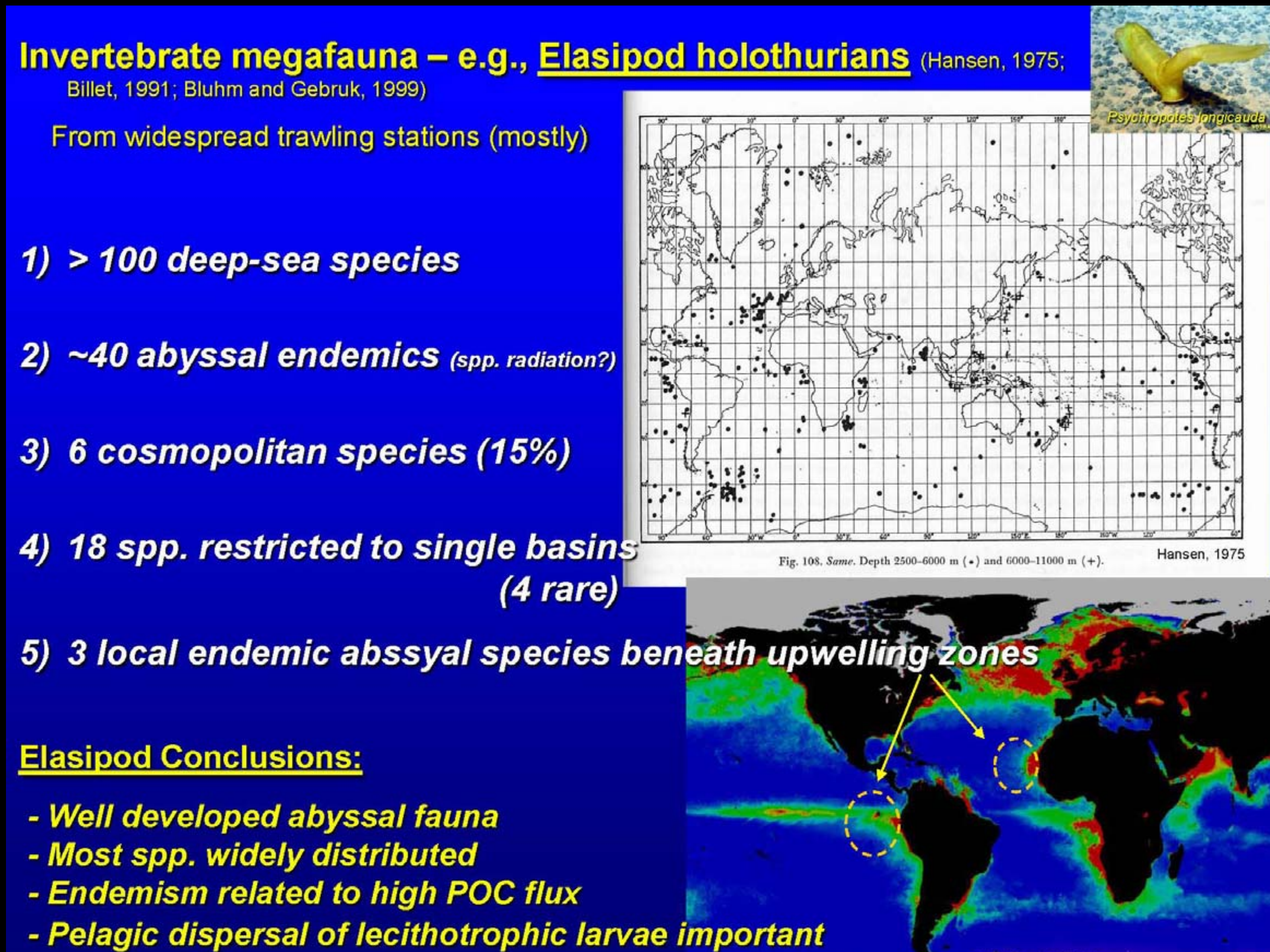
4) *4 species restricted to single basins*



Fishy Conclusions: *- Very broad distributions*

- Food flux, planktonic larval dispersal are important biogeographic factors.

What about species level patterns in the Abyss?



What about species level patterns in the Abyss?

MACROFAUNA (2 cm - 300 μm) **– more speciose, more restricted ranges than megafauna**

Asellote Isopods (peracarid crustaceans, or "pouch shrimp")

1) >>500 deep-sea species (Wolff , 1962: Wilson, 1987; Brandt, 2005)

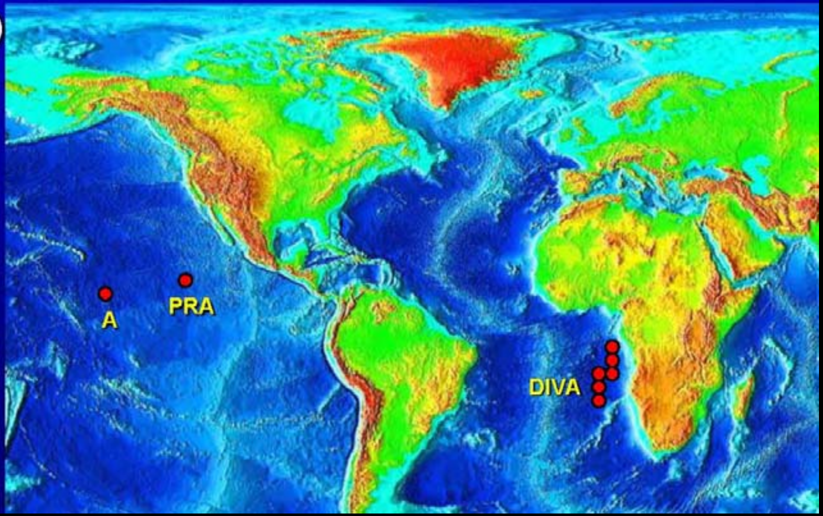
2) Potentially hundreds of abyssal species (adaptive radiation)

3) Cosmopolitan species few percent of abyssal diversity

4) Local endemism very common –

- Wilson, 1987 – only 20% overlap between sites A and PRA (131 spp., spacing ~ 2000 km)

- Brandt et al., 2005 - DIVA (spacing ~500 km)
  - 100 spp. isopods (240 spp. peracarids)
  - ~ 50% from only one station (most rare)



Isopod (peracarid) Conclusions:

- ***Species richness very high***
- ***Abyssal radiation evident***
- ***Endemism common?***
- ***Grossly undersampled***

What about species level patterns in the Abyss?

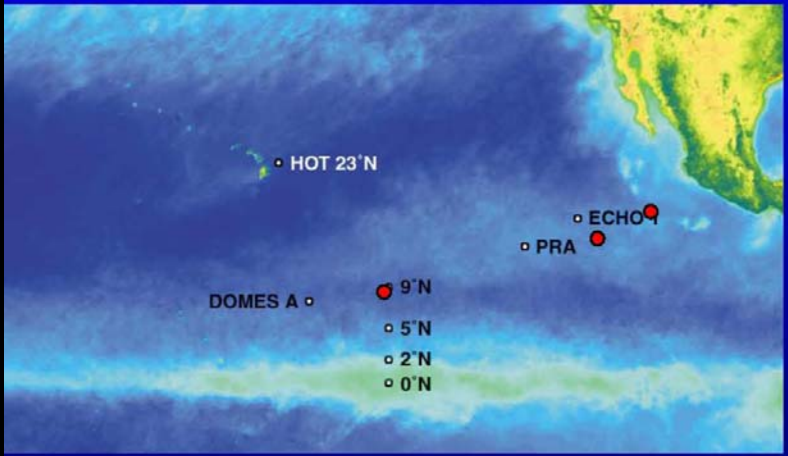
Polychaete worms – broad range of repro. strategies

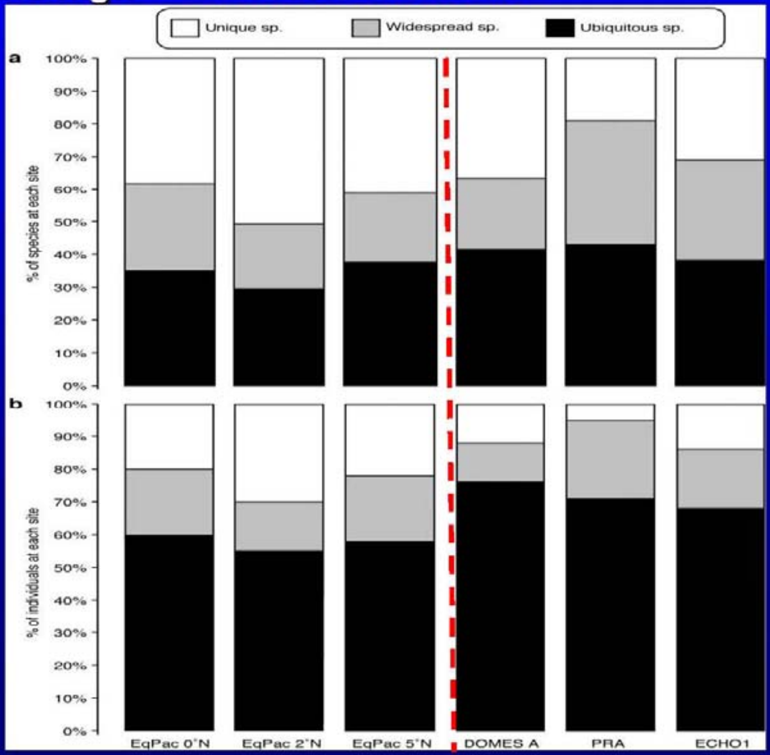
1) >200 species from single deep-sea regions – global richness??
(e.g., Glover et al., 2001, 2002)

2) Abyssal endemics? - likely, but taxonomy poorly known *(>90% undescribed)*

3) Some abyssal species could be cosmopolitan – *<u>Aurospio dibranchiata</u>*
(Glover, Mincks, Paterson, Smith – unpublished data)

4) Species turnover over 500-1000 k seems high – 20-50% endemism?





May be due to very poor sampling - most species are rare and at no site is species accumulation asymptote approached

Glover et al., 2002

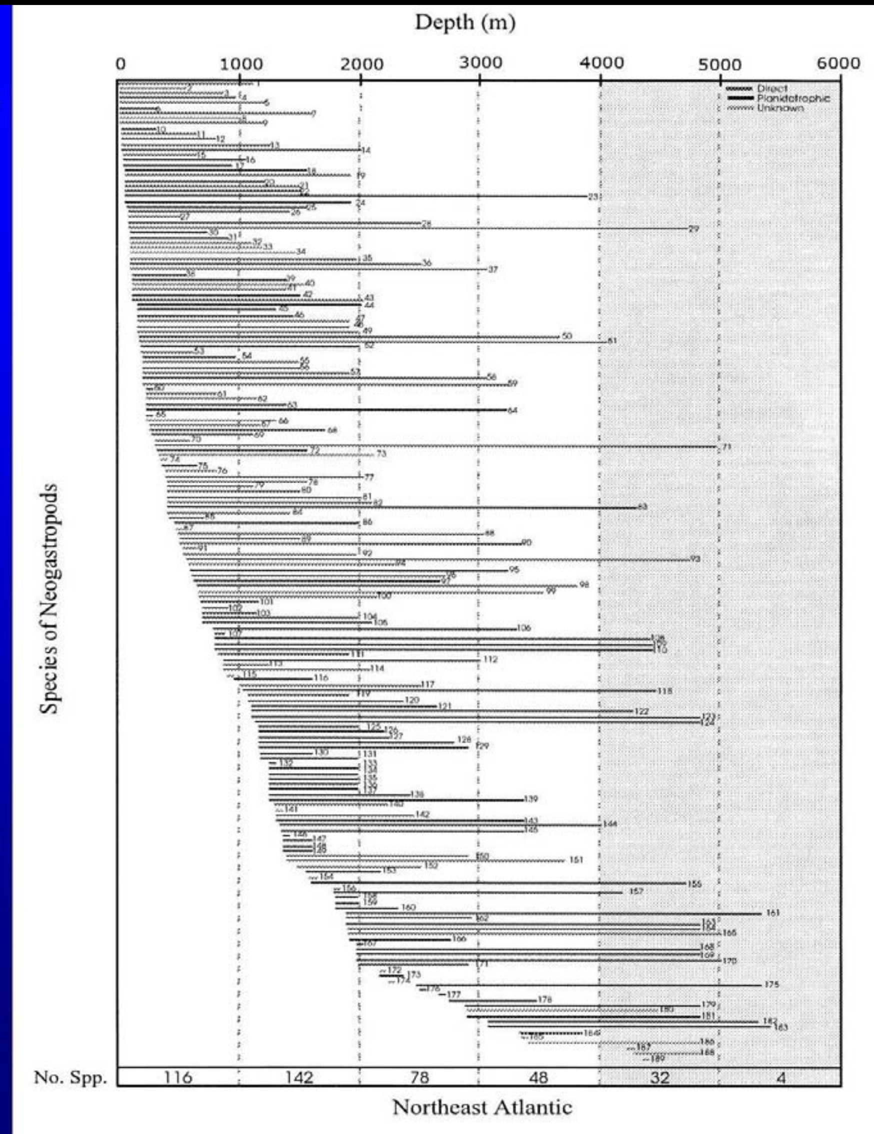
What about species level patterns in the Abyss?

Neogastropods in North Atlantic – different pattern

- *Broad depth distributions*
- *Few species restricted to abyss → abyssal sink!*
- *Are most non-reproductive refugees from shallow depths?*
- *Many with planktotrophic development*

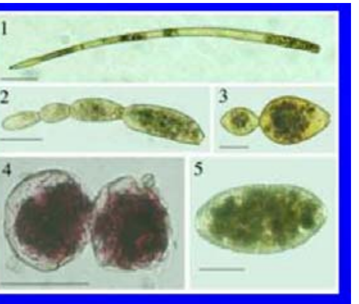
NEEDS TESTING IN PACIFIC!!!

Rex et al., 2005



What about species level patterns in the Abyss

MEIOFAUNA – limited species-level data, mixed picture
(42 – 300 μm)



Foraminifera

Foraminifera – (From Gooday, pers. comm.)

1) *~500 deep-sea species known*

2) *High local diversity (> 250 spp. per site)*

3) *Some species cosmopolitan (depth ranges > 4000 m!)*

? High local, but low global diversity?

Nematode

Nematoda – deep-sea biogeography very poorly known

1) *High local diversity (100's of spp. per site)*

2) *Abyssal endemics? Kaplan Project - Abyssal Radiation?*

Conclusions from the Abyss:

1) Biogeographic patterns vary with body size, taxon and life histories ⟶ need to consider representative range of the organisms in MPA design.

2) In some groups (isopods, elasipods, nematodes?) there is evidence of abyssal radiation and novel evolutionary lineages, in others (gastropods) there may be an abyss “sink”.

3) Some groups (e.g., peracarids) appear to have surprisingly restricted distributions, e.g., to portions of the CCZ, but at present we cannot resolve rarity from endemism.

4) Intercalibration of working species collections, and merging of morphological and molecular taxonomy, urgently needed.

Obstacles to Further Abyssal Biogeographic Synthesis:

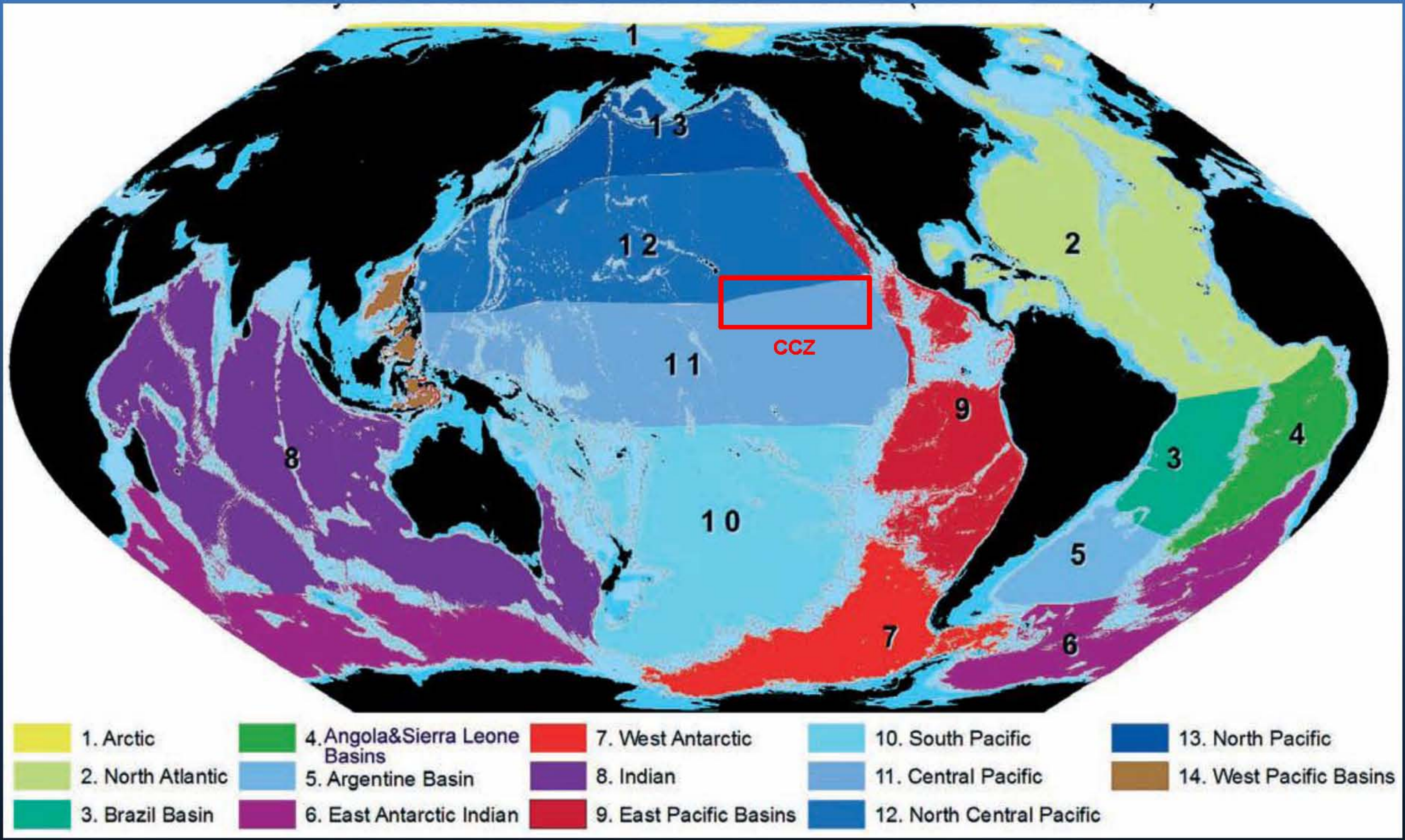
1) > 90% of abyssal diversity is in undescribed species, and there is little intercalibration of working species between programs

2) Undersampling: How can we distinguish rarity from endemism?

3) Potentially large number of cryptic species, especially in polychaetes and nematodes - need combined studies of morphological and molecular taxonomy (DNA barcoding)

4) Patterns of population connectivity are essentially unknown, making it very difficult to recognize source and sink populations

Hypothesized Biogeographic Provinces of the Abyssal Ocean (3500-6500 m)



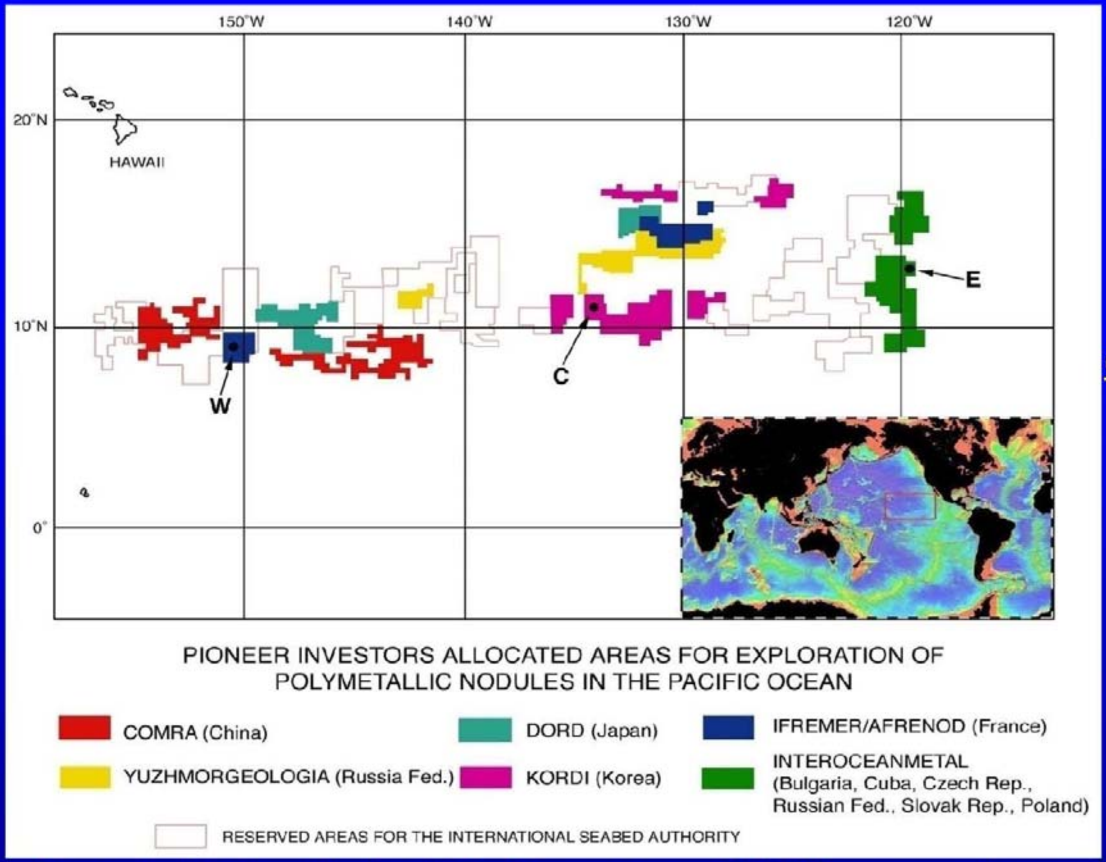
Note that the CCZ falls on the boundary between two, and possibly three, likely zoogeographic provinces.

UNESCO. 2009. *Global Open Oceans and Deep Seabed (GOODS) – Biogeographic Classification*. Paris, UNESCO-IOC. (IOC Technical Series, 84.)

The Kaplan Project and ISA report: Still the best source of data and most complete study. Available on line and copies are coming for all of you.

Some additional data is included in my conclusions.

Kaplan Project



Cruises in:

- Feb-Mar 2003 –USA, New Horizon
- Feb 2004 – Japan, Umitaka-Maru
- May-Jun 2004 – France, L'Atalante

(85 days at sea)

- Sampled intensively at 3 sites across CCZ for many taxa (collected 14-20 BC's for macrofauna, ~10 multicores for meiofauna and microflora per site)
- Used new, "DNA-friendly" sampling techniques (sieving in cold room with 4° seawater, 95% Etoh; also some in formalin for morphology)
- Merging taxonomy with previous sampling programs

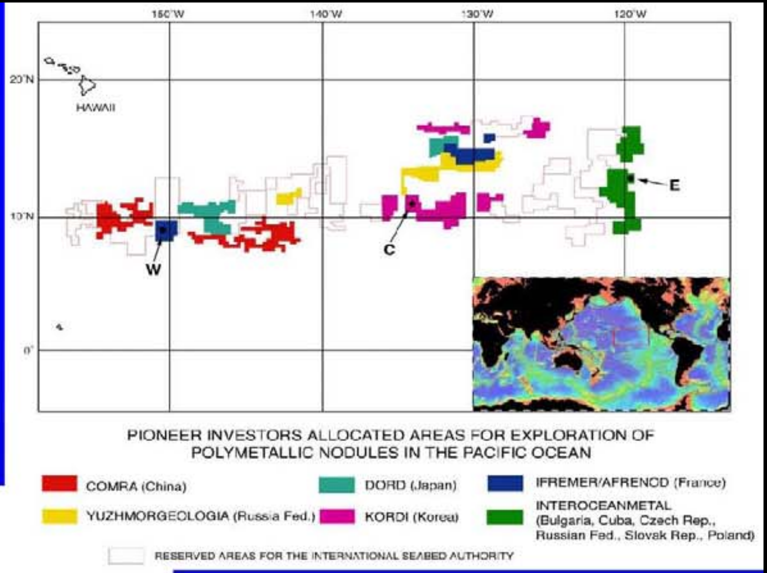
Kaplan Project

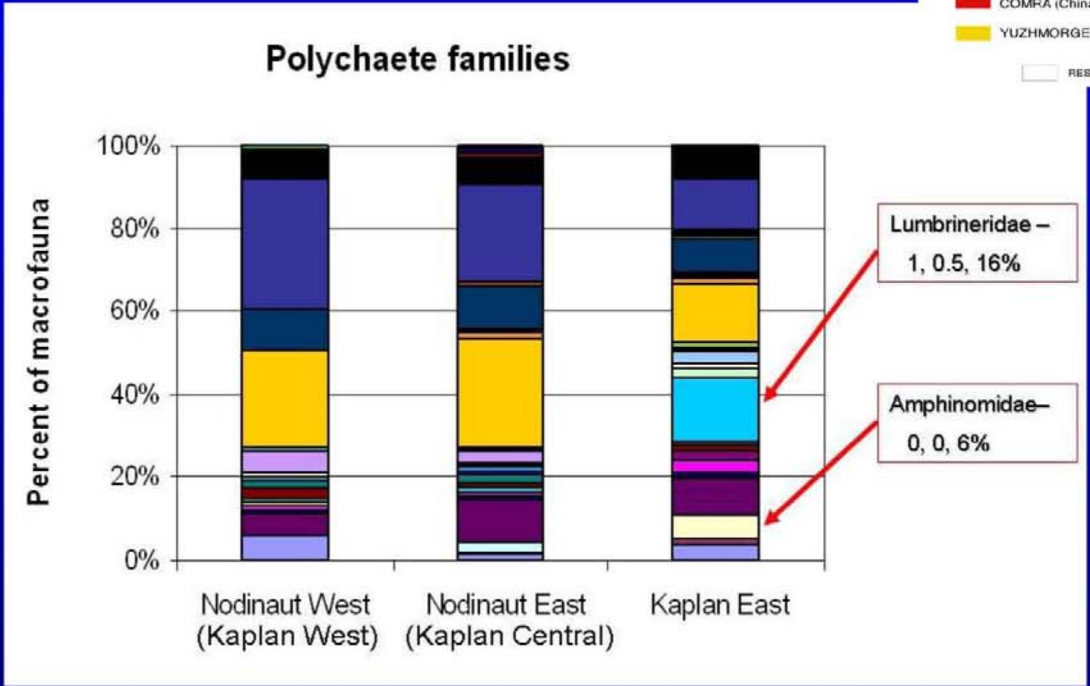
RESULTS:

Three sites in CCZ (~1500 km apart)

- ***Major differences in polychaete fauna at family level*** *(Kaplan Project, unpub.)*

- ***Driven by productivity gradient?***



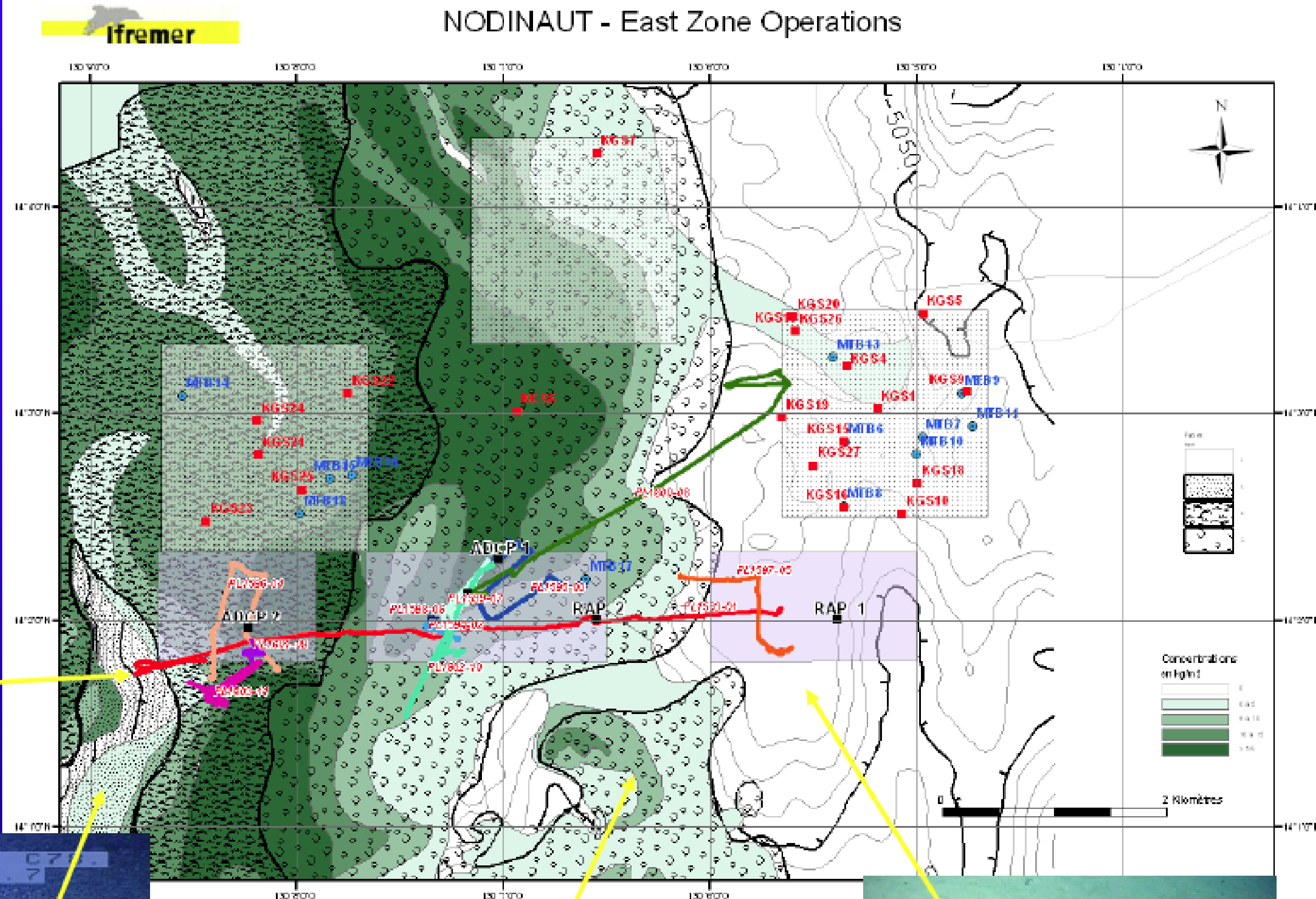


Proportion of lumberinerids significantly lower in Kaplan Central and West ($p \leq 0.05$, Chi square test)

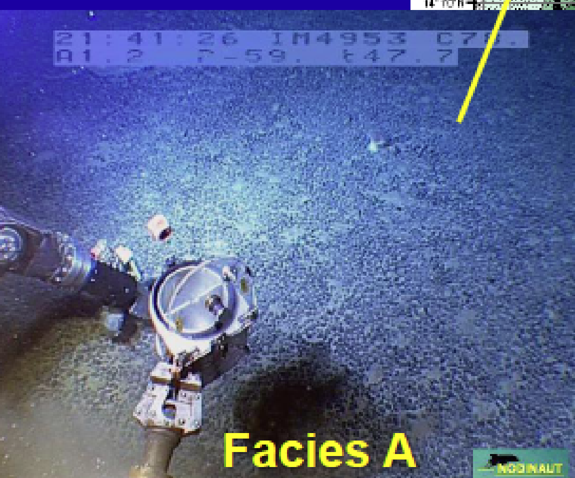
Proportion of Amphinomids significantly lower in Kaplan Central than Kaplan East ($p < 0.025$)

There is significant Habitat Heterogeneity at scales of 1-100 km in the abyss (Kaplan site C)

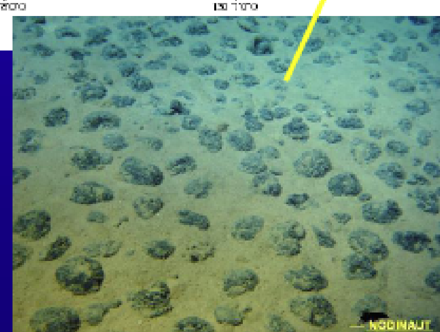
Nodule abundance: 0 to >15 kg m^{-2}



Bare Scarp



Facies A

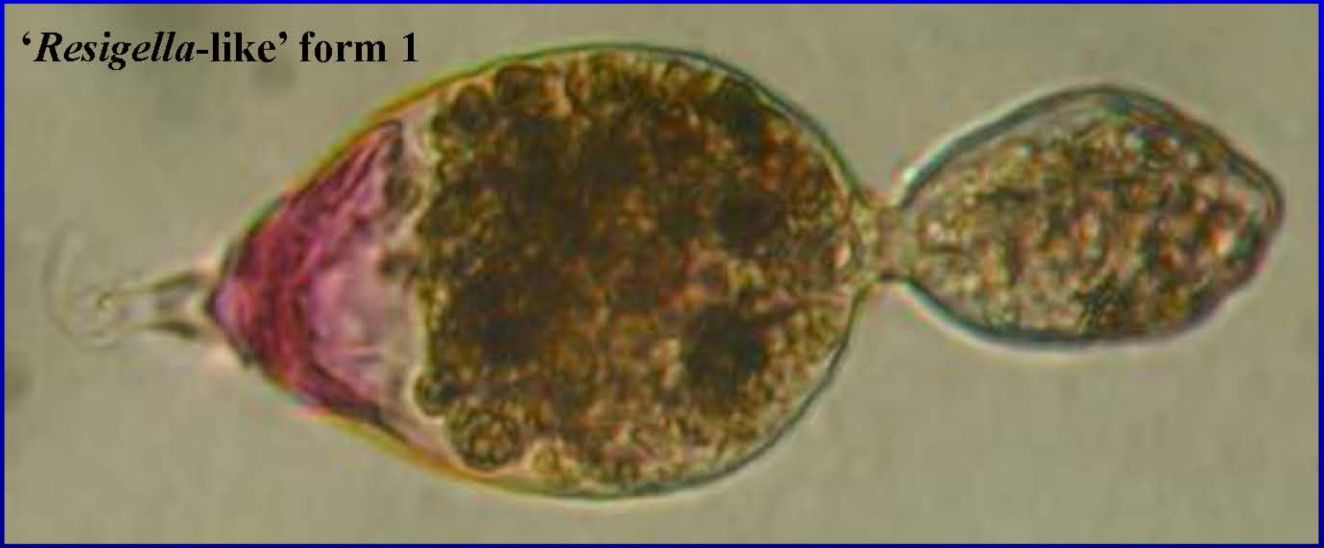


Facies C

Facies 0

KAPLAN Foraminiferan Studies

Andrew Gooday, Fusae Nozawa, Nina Ohkawara, Hiroshi Kitazato



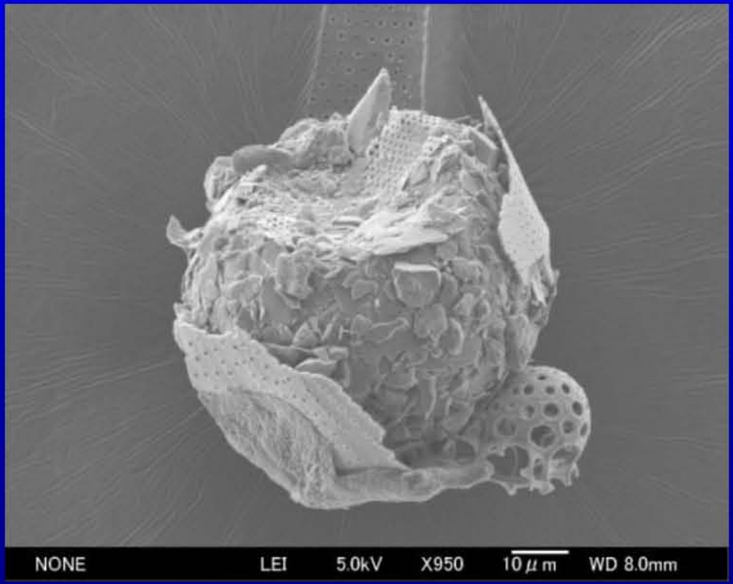
12,513 stained live specimens sorted from Site E, 3686 specimens from Site C

Comparison Between Kaplan Sites:

Total species at sites E and C combined = 300

~ 29 species shared between sites (underest.)

Still, dominant species at site C (62% of abundance) not found at E, and vice versa.



Tiny, undescribed psammosphaerid overwhelmingly abundant at Kaplan Site C but not found at Site E 1500 km away (N. Ohkawara)

Conclusion:

Significant turnover of major components of the foraminiferan fauna over scales of roughly 1000 km across the CCZ.

Kaplan nematodes:

(Lambshead, Lunt, Floyd, Elce, SmithΦ & Rogers, in prep.)

-Amplified 18S rRNA genes (500 bps) from **97 nematode specimens** from Kaplan E and W sites

-**73 MOTUs (putative species**) differing by $\geq$ 3 bps

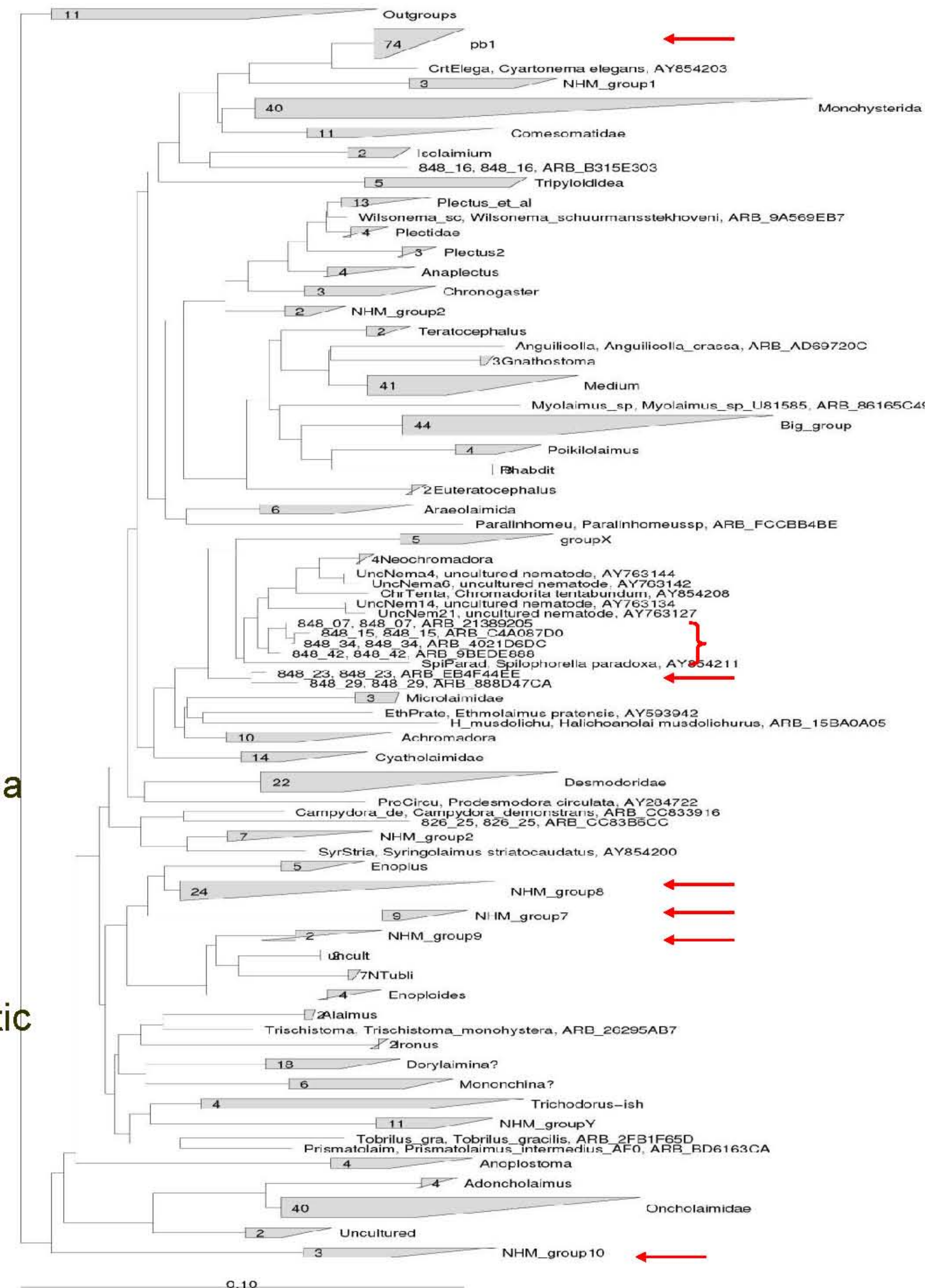
-Only 3 MOTUs fall within bar coded shallow water genus *Daptonema* (Monhysteroidea)

-Most of the deep-sea MOTUs fall into distinct, monophyletic groups e.g., clusters in Oncholaimoidea, Enoploidea and Chromadoroidea.

-Suggests:

1) Novel abyssal lineages hidden by cryptic morphology

2) numerous unique abyssal nematode taxa may result from adaptive radiation



Nodule habitat and fauna

- Although defined by the presence of nodules, most of the biodiversity is in the soft sediment
  - High levels of local biodiversity of tiny animals (macrofauna and meiofauna)
  - Strong evidence for regional differences within CCFZ
  - In general very poorly known (but lots of current work)
  - Many new species discovered from almost every collection
    - (1 new species of polychaete found for each 1.3 sequenced in the Kaplan project)

Side note: although molecular analyses finds scary numbers of species, it will also facilitate much more time and financially efficient inventories

Nodule habitat and fauna

Megafauna: Low density, moderate diversity, no current evidence for regional scale endemicity

Nodule habitat and fauna

There is a distinct nodule fauna as well

- On the order of ˜70 species so far
- Mostly foraminiferans (protozoans), but also small filter-feeding animals: sponges, polychaetes, molluscs, bryozoans
- Different animals seem to specialize on different nodule surface textures
- Recent data suggests some regional variation within CCZ

The report of the Kaplan project to the ISA (2007) and the subsequent recommendations for establishment of marine protected areas treat this subject very thoroughly and although the basic messages have not been changed by subsequent publications there is a good amount of work going on now.