Ecology, Diversity and Biogeography of the Abyss and the CCZ

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Pew workshop on Design of Marine Protected Areas for Seamounts and the Abyssal Nodule Province in Pacific High Seas
23-26 October, 2007
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 °C)
- High hydrostatic pressure
- Often physically very stable *(low currents)*
- Much of structure biogenic *(fragile)* or nodules
- Hard substrates *(nodules)* harbor a distinct fauna

4500 m Equatorial Pacific

5600 m Central North Pacific

Xenophyophore
*(10 cm)*

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

From R. Carney
- 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

Surface deposit feeder

Subsurface deposit feeder

Crustaceans

Isopod

Amphipod
- Enigmatically, very high **local** species diversity –

80 - 100 macrofaunal species per $m^2$

Abyssal deep sea

~ 50 spp per 100 individuals

Despite low habitat complexity – Rivals most diverse ecosystems
Also, surprisingly diverse “charismatic” megafauna in CCZ:

Nautile dives June 04, > 20 spp. in few km$^2$
- High local diversity but low habitat complexity compared to many other locally diverse ecosystems

~ 100 species macrofaunal species m⁻² sediment
HIGH GLOBAL DEEP-SEA DIVERSITY?

Global Biodiversity Estimates

- Freshwater (Described)
- Terrestrial (Described)
- Marine (Described)
- Marine
- Soils & Sediments (all taxa)
- Tropical Insects
- Deep-Sea Sediments (macrofauna)

Snelgrove and Smith 2002
Abyssal fauna very poorly sampled and described!

Total abyssal records (3000 – 6000 m) at species/genus level in OBIS
2) Ecological Impacts of Nodule Mining
Nature of Mining Impacts:

- **International Seabed Authority** set up by UNCLOS to manage seabed and resources as “the common heritage of mankind,” including **environmental protection**

- Eight exploration contracts currently registered with ISA
- Seven in CCZ
- Each claim 75,000 km²
**Physics Impacts:**

### Direct Strip-Mining Effect:
- Remove nodules, ~5 cm of sediment in >5-m swathes
- Remove nodule habitat, kill most infauna, alter geochemistry
- Could impact ~300 – 600 km² yr⁻¹ (~10,000 km² over 15 yr)

### Sediment-Plume Deposition:
- Entomb benthos
- Dilute deposit-feeder food
- Clog filter-feeding apparatus
- Could affect ~50,000 km² over 15 years of operation
- Chronic plume effects not evaluated (bad for suspension feeders)

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Oebius et al. (2001)
Heterogeneous distribution of nodules will be reflected in mining patterns – mining will directly impact 20-30% of target area.

Plume disturbance could impact large proportion of mining claim over 15 yr mining operation.

Size and relative position of potential mining blocks in the French pioneer area, N. Pacific Ocean (modified from Lenoble 1999).
Species extinction as a function of habitat loss, based on species-area relationships (e.g., Nifle and Mangel, 2000)

For species restricted to scales of mining claims (of order 50,000 km²), extinctions are likely
What do we know about biological impacts?

**LOCAL-SCALE IMPACTS**

*A number of experimental studies, all small in intensity and spatial scale compared to actual mining, e.g.*

1) DISCOL Experiment (Thiel *et al.*, 2001) – dragged plows on 8-m frame

- disturbed ~20% of 11 km²
- resampled over 7 years

![Plow cuts (disturbed) 50 cm](image)

![Relatively undisturbed](image)
Results of plowing in DISCOL & others: few mm of deposition

Dramatic declines in abundance & diversity of macrofauna and megafauna within 11 km² after 7 years

- Redeposited layer low in food quality (Fukushima & Kuboki, 2000)
Insights from revisiting test-mining tracks in 2004:

OMCO Track
~1.5 m wide
~10 cm deep

Appears very fresh

When was it created?
Insights from revisiting test-mining tracks in 2004:

**OMCO Track**
- ~1.5 m wide
- ~10 cm deep
- Appears very fresh

When was it created?

**1978**

Little change in 26 years!
CONSERVATION ISSUES FOR NODULE MINING

Mining impacts will involve very large scales & long recovery times

Important to setup MPA’s prior to mining!

Primary MPA goals:

1) Protect representative and critical habitats
2) Prevent species extinctions

!!! Only recommendations on MPA’s date from NRC (1984):
- based on limited biodiversity and biogeographic data
3) General Abyssal Biogeography – Forcing processes?

1) Particulate organic carbon flux - probably most important

Annual Primary Production - 1998 - 1999
Note that gradient in particulate organic carbon flux in CCZ region is steeper from south to north than from east to west.
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
4) Hydrostatic pressure???

5) Flow/topography interactions -- Isolation by continents, sills and mid-ocean ridges
General Abyssal Biodiversity/Biogeography Patterns -

(Brief survey – more complete synthesis = goal of CeDAMar.
Also, keep in mind very poor sampling coverage!)

“Regional” species diversity:

North Atlantic – upper abyssal max

? Other Basins?

Figure 19-5  Variation in species richness along the depth gradient of the ocean (data compiled by Rex, 1981). Species richness is an estimate for samples of 50 individuals. (See Hurlbert, 1971, for method)
Species level patterns?

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
MEGAFAUNA (> 2 cm) –

Bentho-pelagic fishes – large and mobile, 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) (Coryphaenoides 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.
Invertebrate megafauna – e.g., **Elasipod holothurians** (Hansen, 1975; Billet, 1991; Bluhm and Gebruk, 1999)

- From widespread trawling stations (mostly)

1) > 100 deep-sea species

2) ~40 abyssal endemics *(spp. radiation?)*

3) 6 cosmopolitan species (15%)

4) 18 spp. restricted to single basins *(4 rare)*

5) 3 local endemic abyssal species beneath upwelling zones

**Elasipod Conclusions:**

- Well developed abyssal fauna
- Most spp. widely distributed
- Endemism related to high POC flux
- Pelagic dispersal of lecithotrophic larvae important
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 appears 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
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 – Aurospio dibranchiata
   (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
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
MEIOFAUNA – limited species-level data, mixed picture
(42 – 300 µm)

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?

Nematoda – deep-sea biogeography very poorly known

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

2) Abyssal endemics? Kaplan Project - Abyssal Radiation?
Yellow shading cover centers of discrete abyssal provinces (hadal provinces = variously colored lines). Based primarily on Vinogradova (1997) and Sokolova (1997). The abyssal provinces occur at water depths of 3000 – 6000 m, and the hadal provinces below 6000 m. Note that the CCZ falls on the boundary between two, and possibly three, likely zoogeographic provinces.
4) Biodiversity and Biogeography of the Clarian-Clipperton Zone

POLYMETALLIC NODULES EXPLORATION AREAS IN THE PACIFIC OCEAN
AREAS UNDER CONTRACT WITH THE INTERNATIONAL SEABED AUTHORITY AND AREAS RESERVED FOR THE AUTHORITY

“The Area” is defined as “the seabed and ocean floor and subsoil thereof, beyond the limits of national jurisdiction” (1982 United Nations Conventions on the Law of the Sea article 1, paragraph 1(1)). The chart of the Area is indicative only of claimed and potential maritime limits.

Legend
- Contractor Areas
  - COMRA (China)
  - DORD (Japan)
  - Government of Korea
  - IFREMER/AFERMOD (France)
  - Interscience
  - Yachtkrologia (Russian Federation)
  - FGKNR (Germany)
- Reserved Areas

Clipperton Island (France)
Colima (Mexico)
Isla de Revillagigedo (Mexico)
Hawaii (USA)
Biodiversity, species ranges, and gene flow in the abyssal Pacific nodule province: predicting and managing the impacts of deep seabed mining ("KAPLAN PROJECT")

Funded by The Kaplan Fund & the International Seabed Authority

Investigators:

Craig R. Smith, John Lambshead, Gordorn Paterson, Alex Rogers, Andy Gooday; Hiroshi Katazato, Myriam Sibuet, Joelle Galeron, Karsten Zengler

Project Goals:

To begin to evaluate biodiversity levels, geographic ranges, & rates of gene flow for three key benthic faunal components within the abyssal Pacific (nodule province).

1) Use molecular methods and combined with standard taxonomy to estimate the number of polychaete, nematode and foraminiferal species at 3 stations spaced at ~1500-km intervals.

2) Use state-of-the-art molecular and morphological techniques to begin evaluate species overlap and rates of gene flow over scales of 1500 - 3000 km.

3) Broadly communicate our findings to the scientific and mining-management communities.
- 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 4º seawater, 95% EtOH; also some in formalin for morphology)

- Merging taxonomy with previous sampling programs

Cruises in:
- Feb-Mar 2003 – USA, New Horizon
- Feb 2004 – Japan, Umitaka-Maru
- May-Jun 2004 – France, L’Atalante

(85 days at sea)
We are intercalibrating Kaplan data with collections of undescribed species from previous studies to allow regional synthesis (ongoing, funded through CeDAMar)

* Existed in 1984 when NRC made first rough MPA recommendations
**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 ≤ 0.05, Chi square test)*

Proportion of Amphinomids significantly lower in Kaplan Central than Kaplan East *(p < 0.025)*
KAPLAN Foraminiferan Studies

Andrew Gooday, Fusae Nozawa, Nina Ohkawara, Hiroshi Kitazato

‘Resigella-like’ form 1

12,513 stained live specimens sorted from Site E, 3686 specimens from Site C
The foraminifers at the Kaplan East and Central sites are predominately agglutinated, dominated by monothalamous and Komokiacion forms.

Dominant monothalamous foram species at Station E

Dominant komokiacion species at Station E
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.

Conclusion:

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

Tiny, undescribed psammosphaerid overwhelmingly abundant at Kaplan Site C but not found at Site E 1500 km away (N. Ohkawara)
Kaplan nematodes:
(Lambshead, Lunt, Floyd, Elce, Smith & 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 > 3 bps

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

- 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
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) could 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.
Tiny, undescribed agglutinated sphere (psammosphaerid) that is overwhelmingly abundant at the Kaplan Central Site C (625 of all intact specimens) but not found at Site E (SEM photographs by Ms Nina Ohkawara, JAMSTEC)
Census of Diversity of Abyssal Marine Life (CeDAMar)

GOALS:
- Coordination of standard field sampling programs
- Synthesis of abyssal biodiversity and biogeography
  (including intercalibration of “working species” collections)
Questions ?
Family composition of macrofaunal polychaetes from Kaplan Station E (Top) and Station C (Bottom).
Rex et al., in press. Global bathymetric pattern of standing stock and body size in the deep-sea benthos.

Standing stock corrected for latitude and longitude (n=2310 from a total of 128 studies)
Fig. 6.3. Distribution of surface-sediment types in the deep Pacific Ocean. Modified from Berger.
For those areas studied in detail (e.g., the Santa Catalina Basin (Fig. 6.1) (Smith and Hamilton, 1983) and the base of the central California slope at 4100 m (Station M, Fig. 1) (LaRue et al., 1996; Beaulieu, 2002)), more than 50 macrofaunal species have been recorded within a site.

The macrobenthos (i.e., animals passing through a 2 cm mesh but retained on a 300μm sieve) of the California slopes and basins consists of a high diversity of taxa, especially polychaetes, agglutinat- ing foraminifers, bivalves, crinoids, tanaids, and entomostracans (Jumars, 1975; Levin et al., 1991; Kubert and Smith, 1992). Macrafan community abundance (5000 to 10 000 m⁻²; Table 6.1) and biomass (4 to 8 mg wet weight m⁻²) (K.L. Smith and Hinga, 1983; C.R. Smith and Hessler, 1987) are low relative to most shelf communities; but local species diversity on the California slope can be extraordinarily high. For example, at 1230 m depth in the San Diego Trough (Fig. 6.1), a sample of 50 macrofaunal polychaetes is likely to contain more than 30 species (Fig. 6.7) and a 0.25 m² patch of seafloor typically contains more than 100 species of macrofauna (Jumars and Gallagher, 1982). In contrast, a typical soft-sediment intertidal assemblage includes fewer than 50 species in an area of 0.25 m² (Staelgrove and Smith, 2002). In fact, local macrofaunal diversity of California slope sediments is high even by deep-sea standards and rivals that of structurally much more complex, species-rich habitats such as coral reefs (Staelgrove and Smith, 2002).

The meiofauna (animals passing through a 300μm sieve and retained on one of 42μm) are an abundant but relatively poorly studied component of the slope benthos. Nematodes, calcareous and agglutinating Foraminifer, and harpactioid copepods abound in this size class, with Foraminifer and nematodes probably
Location of the stations of the projects DIVA, ANDEEP, BIOZAIRE and the planned German-Brazilian cooperation.
roughly 100 and 1000 m (Wiseman et al., 1992), and along the Peru–Chile margin at depths of tens to hundreds of meters (Diaz and Rosenberg, 1995). Partially enclosed basins may also contain bottom water with little or no oxygen at depths far below the oxygen-minimum zone if the deepest point of entry into the basin (i.e., its sill depth) falls within this zone; this is because the densest water entering the basin comes from the sill depth, and thus fills all deeper levels. Several such low-oxygen basins (e.g., the Santa Barbara, Santa Monica and San Pedro Basins) occur in the borderland region off southern California (Emery, 1960).

**Sinking flux of particulate organic carbon**

The primary source of food material for deep-sea communities, excluding hydrothermal vents and cold seeps, appears to be the rain of organic particles, ranging from individual phytoplankton cells to dead whales, sinking from the euphotic zone (Chapter 2). The organic matter in the smaller of these particles degrades and is consumed by midwater animals during transit through the water column, generally yielding a very low flux of food to the deep-sea floor. Consequently, benthic assemblages of the abyss are among those with the poorest supply of food and the smallest biomass on the Earth’s solid surface. As might be expected in an energy-poor ecosystem, the total biomass in many size-classes of benthos (e.g., the meiofauna, macrofauna and megafauna) on the deep-sea floor often is correlated with the annual rate of the rain of particulate organic carbon (Fig. 6.4; Rowe et al., 1991; C.R. Smith et al., 1997). In fact, it has been suggested that the biomass in certain benthic size classes, in particular the macrofauna, might be useful as an index of the annual flux of labile particulate organic carbon to the deep-sea floor (C.R. Smith et al., 1997); time series monitoring of abyssal benthic biomass might be employed, for example, to elucidate changes in the deep flux of particulate organic carbon (and the oceanic carbon cycle) in response to global climate change.

Two factors exert primary control on the sinking flux of particulate organic carbon to the ocean floor.
MICROBES – High diversity, but “everything is everywhere”?!?
(Atkins, 2000; Schenkenberg et al., 2005)

GENERAL SPECULATIONS?:

Modal Abyssal Species Ranges by Size Class
Most CCZ macrofaunal species are small, delicate deposit feeders (esp. surface deposit feeders)
At no site is
- But also include **large, delicate** surface deposit feeders and a few suspension feeders

- Psychropotes longicauda

- Glass sponge & brisingids

- Central CCZ

- 5000 m
- Enigmatically, very high local species diversity –

80 - 100 macrofaunal spp per m$^2$

Abyssal deep sea

~ 50 spp per 100 individuals

Despite low habitat complexity – Rivals most diverse ecosystems
Also, surprisingly diverse “charismatic” megafauna in CCZ:

Nautile dives June 04, > 20 spp. in few km²
HIGH GLOBAL DEEP-SEA DIVERSITY?

Global Biodiversity Estimates

Number of Species ($\times 10^6$)

- Freshwater (Described)$^1$
- Freshwater$^1$
- Terrestrial (Described)$^2$
- Terrestrial$^2$
- Marine (Described)$^3$
- Marine$^3$
- 10$^9$ bacteria?
- 10$^8$ nematodes?
- Erwin (1982)
- Thorson (1971)
- Grassle & Maciolek (1992)
- May (1992)
- Poore & Wilson (1993)

Soils & Sediments (all taxa)

Tropical Insects

Deep-Sea Sediments (macrofauna)

Snelgrove and Smith 2002
However, abyssal nodule provinces also vast in size –
- most common habitats extend for 1000’s of km
- species ranges potentially broad compared to mining disturbance

Extinctions unlikely?
Nature of Mining Threat:
- **International Seabed Authority** setup by UNCLOS to manage seabed and resources as “the common heritage of mankind,” including *environmental protection*

- Seven exploration contracts currently registered with ISA
- Six in CCZ
- Each claim 75,000 km²
Time is now ripe to rigorously design MPA’s for the CCZ because:

1) 6-fold more sampling data now/soon available (with intercalibration)

2) Very recent application of molecular techniques to resolve species ranges (e.g., Kaplan – ISA project)

3) Development by ISA of Geologic Model of CCZ

4) Legal framework for MPA’s exists in the International Seabed Authority

* Existed in 1984
One characteristic differs from abyss:

High levels of endemism on 100 - 1000 km scale

Lord Howe, Norfolk, & Tasmanian Seamounts
Richer de Forges et al. (2000)

1000 km ➔ ~ 4% overlap, 3000 km ➔ 0% overlap
Time is ripe for seamount synthesis & MPA design:

- Many new seamount data available

- International recognition of seamount biodiversity and deleterious trawling impacts
3) Taxonomy based only on morphological analyses

-Recent DNA-based analyses suggest many cryptic species in deep sea.

E.g., based on morph. *Chaetozone setosa* is cosmopolitan.

Data from Adrian Glover

Common in -
- CCZ,
- Cal. Slope,
- NE USA & European coastal zones
Kaplan Project Sampling to Date (85 days at sea!)

USNEL: 13 (9 Etoh, 4 Form.)
Multicores: 10

USNEL: ~17 (8 Etoh, 9 Form.)
Multicores: 12

USNEL: 12+ (6 Etoh, 6 Form.)
Multicores: 10

PIONEER INVESTORS ALLOCATED AREAS FOR EXPLORATION OF POLYMETALLIC NODULES IN THE PACIFIC OCEAN

- COMRA (China)
- DORD (Japan)
- IFREMER/AFRENOD (France)
- INTEROCHEANMETAL (Bulgaria, Cuba, Czech Rep., Russian Fed., Slovak Rep., Poland)
- YUZHMORORGOLOGIA (Russia Fed.)
- KORDI (Korea)
- RESERVED AREAS FOR THE INTERNATIONAL SEABED AUTHORITY
Different facies have different megafaunal and macrofaunal community structure → substantial km-scale habitat heterogeneity