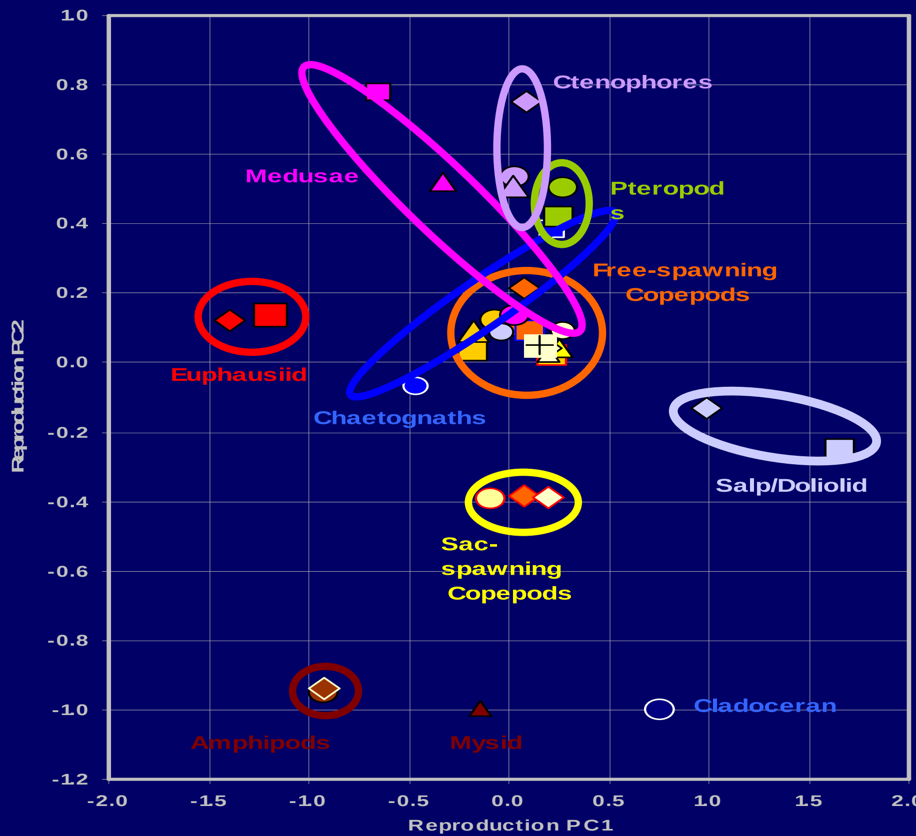
Classification of Zooplankton Life History Strategies



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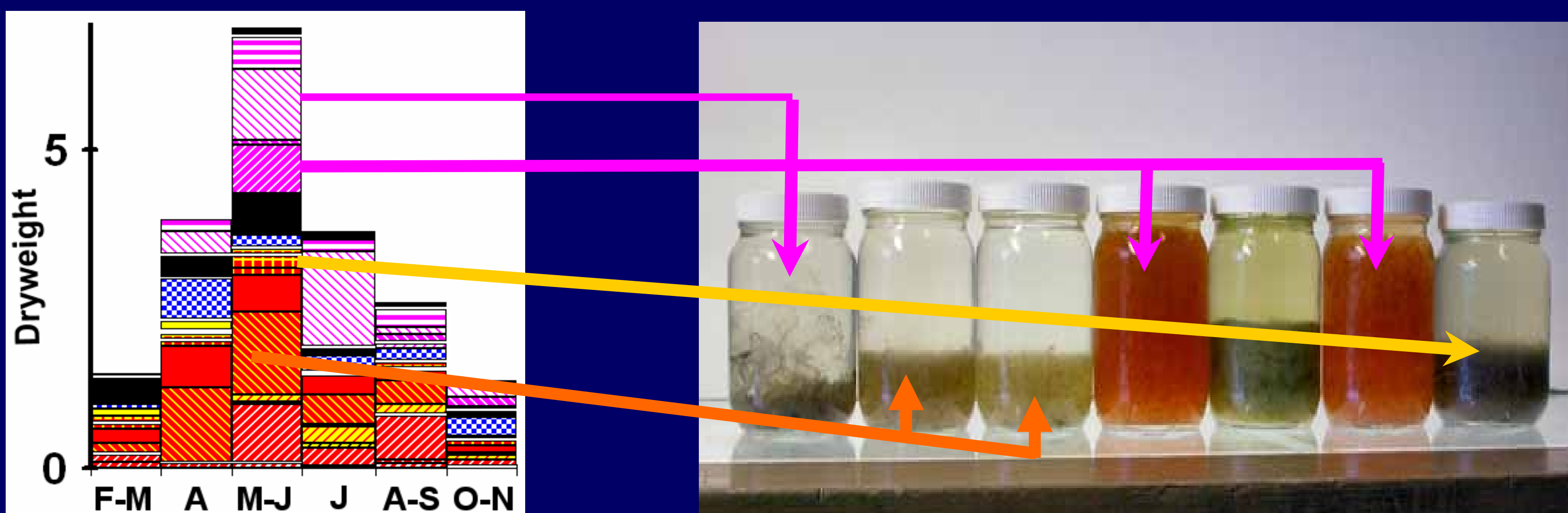
Outline of Talk:

- Motivation for the analysis
- LHS theory - historical summary
- Ordination of zooplankton LHS traits
  - Analysis methods
  - Choice of traits
- Results & Interpretations
- Comparison to anomaly time series

Motivation: Understanding “who wins”

Zooplankton communities include many species & strategies. A few are usually dominant, others always rare, others show intense, unpredictable ‘outbreaks’



Ave. climatology vs. Ugly(?) Reality

Historical Background (1)

r vs. *K* theory (e.g. Pianka 1970, Levins 1968)

- Investment in reproduction, rapid growth & dispersal

vs.

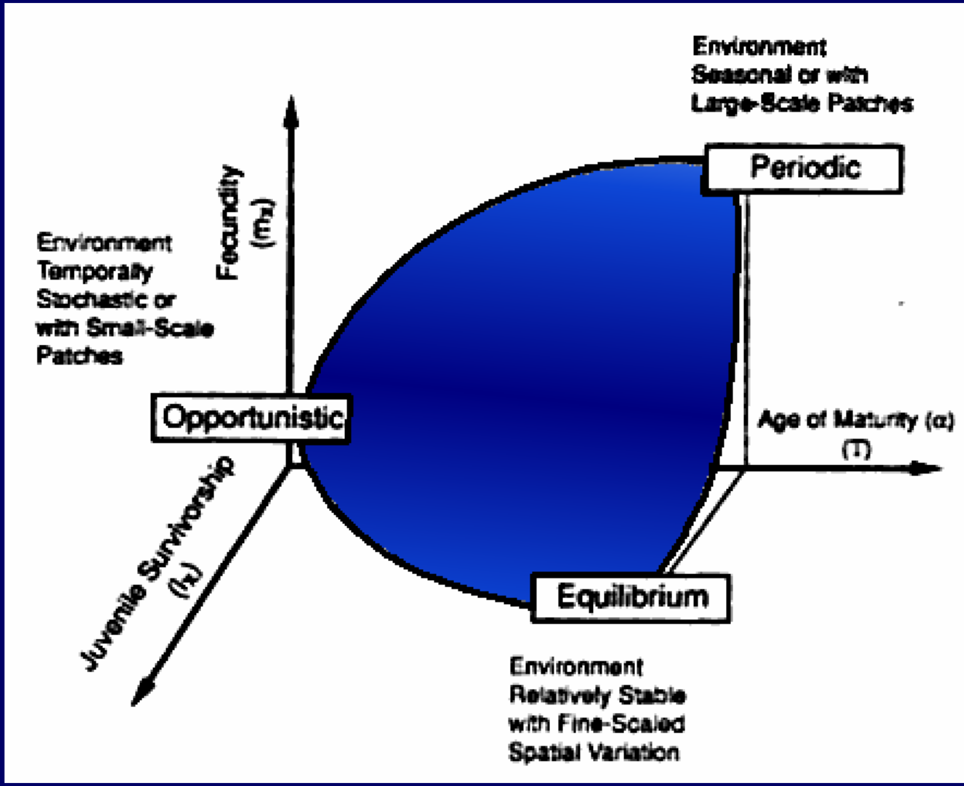
- Investment in survival and ability to compete

(Doesn't consider age structure within the population, nor constraints imposed by morphology)

Historical Background (2)

Demographic Theory

(e.g. Winemiller & Rose, 1992)



Three end-members:

'Opportunist' - quick turnover (≈ *r* strategy)

'Equilibrium' – high survival rate, especially of juveniles (≈ *K* strategy)

'Periodic' – fecundity very high, but reached at older age (betting on eventual 'big win')

(Subsequent analyses identify additional LHS classes: 'Salmonid', 'Intermediate')

Historical Background: What about zooplankton??

Intensive research on individual traits <u>within</u> a few major taxonomic groups

- Egg number and survival for free- vs. sac-spawning copepods
- Egg production vs. food availability
- Brooding
- Seasonal dormancy & resting eggs

So far, little inter-group comparison

Our approach:

Multivariate ordination of LHS

(Principal Coordinates Analysis (PCoA) of species-species distance matrix derived from species-traits matrix, King & McFarlane 2003)

to identify:

- Life-history traits that covary across taxa
- Taxa that share similar strategies

Issues and obstacles encountered:

- Qualitative diversity of zooplankton LHS is <u>much</u> greater than for fish
- Within-species plasticity of some traits
- Information gaps for some life stages (especially survival rate) ➨ often cannot do LxMx integration

(Nevertheless, <u>can</u> rank/classify taxa on each trait. This is sufficient for PCoA ordination)

Choice of taxa: 36 temperate-subarctic marine spp.

(many are present & occasionally dominant in northern California Current System)

Free-spawning copepods:
- ***Calanus marshallae, C. pacificus, C. finmarchicus, Neocalanus plumchrus, Metridia, Temora, Paracalanus, Eucalanus, Rhincalanus***

Sac-spawning copepods:
- ***Pseudocalanus, Pareuchaeta, Eurytemora, Oithona similis***

Copepods with resting eggs:
- ***Acartia longiremis, A. tonsa, A. hudsonica, Centropages, Temora, Eurytemora***

Euphausiids:
- ***Euphausia pacifica, Thysanoessa spinifera***

Hyperiid amphipod:
- ***Parathemisto pacifica***

Gammariid amphipod:
- ***Calliopius laevisculus***

Cladoceran:
- ***Evadne***

Chaetognaths:
- ***'Sagitta' elegans, Eukrohnia***

Shelled Pteropods:
- ***Limacina, Clio***

Planktonic tunicates:
- ***Salpa fusiformis (salp)***
- ***Dolioletta (doliolid)***
- ***Oikopleura (appendicularian)***

Ctenophores:
- ***Pleurobrachia, Mnemipopsis, Beroe***

Scyphozoan medusa:
- ***Aurelia aurita***

Hydrozoan medusae:
- ***Aglantha digitale, Aequorea***

Three categories of LHS traits:

‘Reproductive’:

- Log Fecundity
- r (per day)
- Lifespan (years)
- Iteroparous vs. Semelparous
- Mode of reproduction:
  - Separate sexes?
  - Hermaphroditic?
  - Parthenogenetic?
  - Alternating sexual/vegetative?
- Parental brooding:
  - Free spawning
  - Retain eggs
  - Retain larvae

‘Growth’:

- Log Adult size
- Somatic growth rate
- Fraction of lifespan in ‘adult’ body form

‘Refuges’ (Depth & Dormancy):

- Extent of diel migration
- Ontogenic migration?
- Dormancy
  - As egg
  - As adult/late juvenile
- Lipid storage?
- Benthic stage?

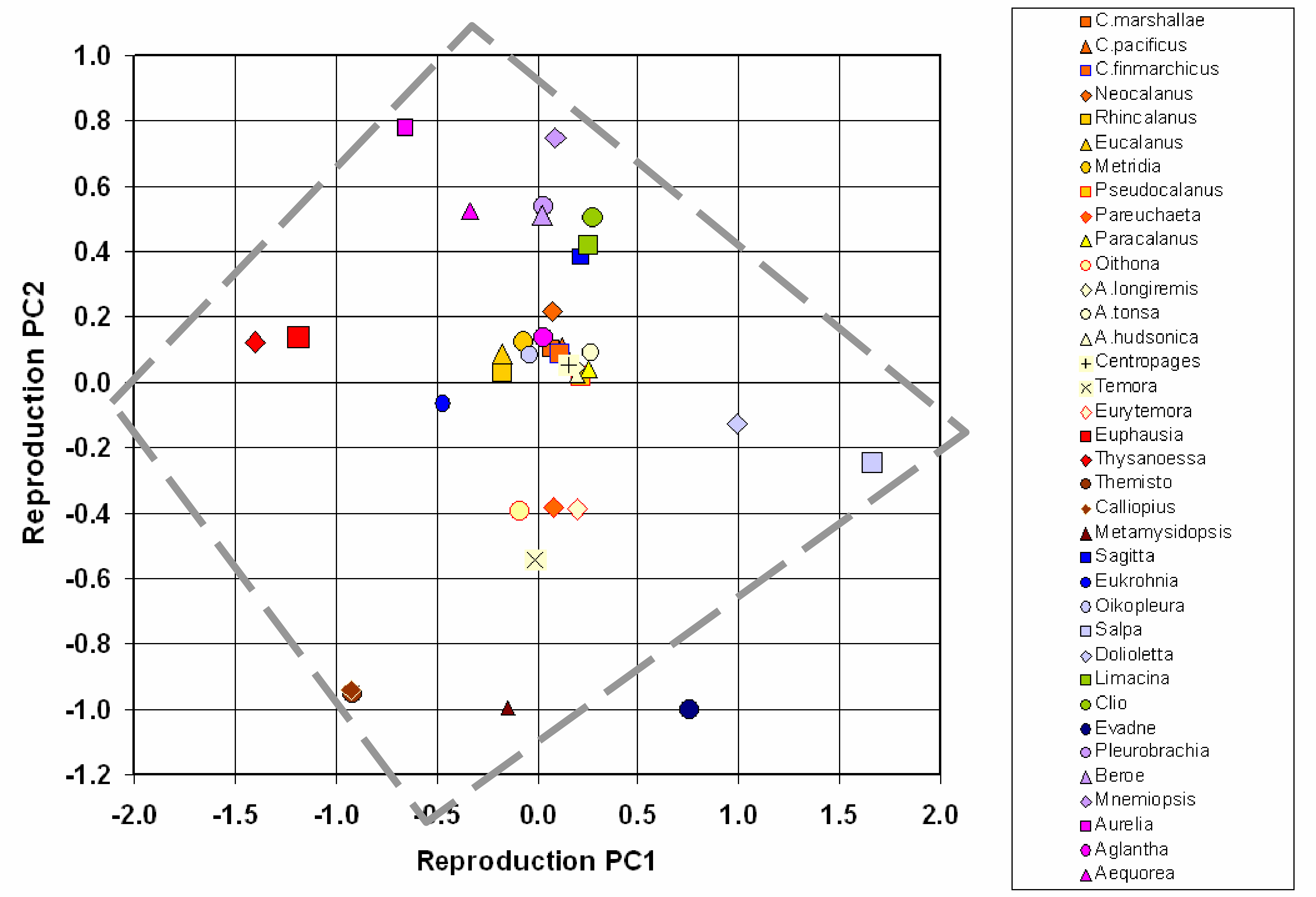
Ordination Results

PCoA on reproductive traits

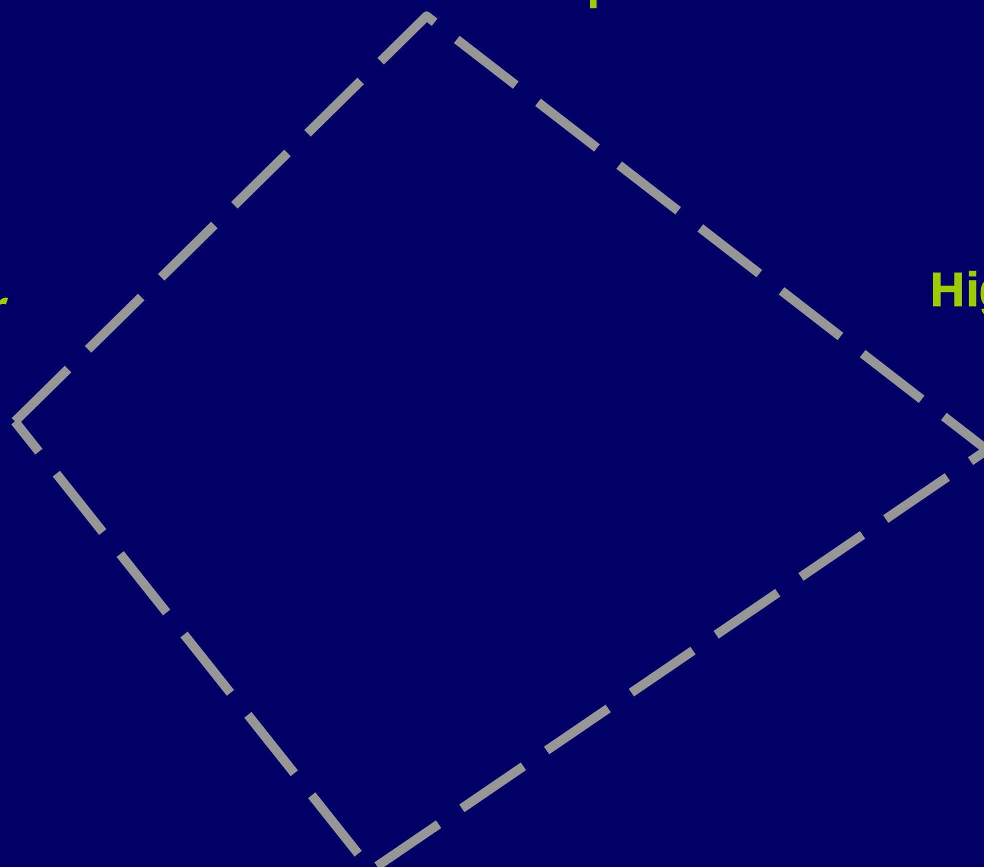
- First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	43.64	30.18
Eigenvector		
log Fecundity	0.66	4.49
r (per day)	4.61	-0.95
Lifespan (years)	- 4.95	0.75
Iteroparous/Semelparous	- 3.41	-1.47
Mode of reproduction	2.32	1.45
Parental brooding	0.76	-4.27

Ordination of reproductive traits



Ordination of reproductive traits

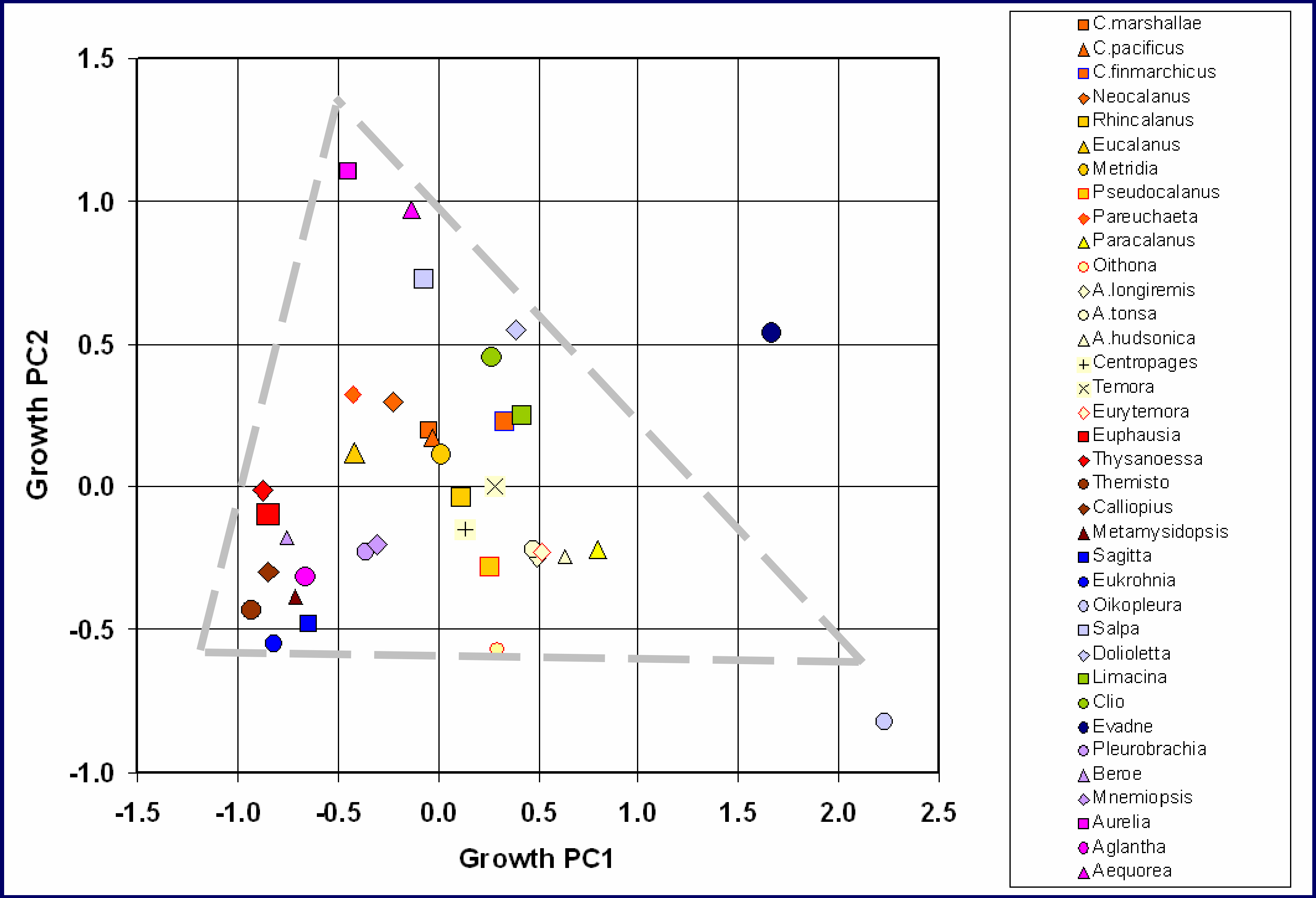


PCoA on growth traits

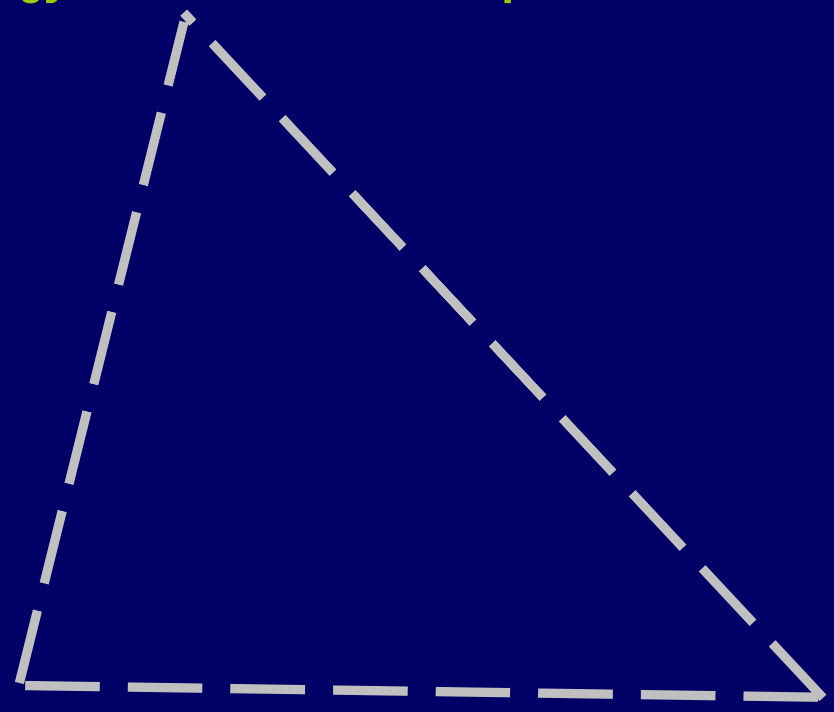
- First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	71.82	28.18
Eigenvector		
log Adult size (dry weight)	-3.38	2.93
Somatic growth (per day)	5.74	0.37
Proportion juvenile/adult	-2.36	-3.30

Ordination of growth traits



Ordination of growth traits

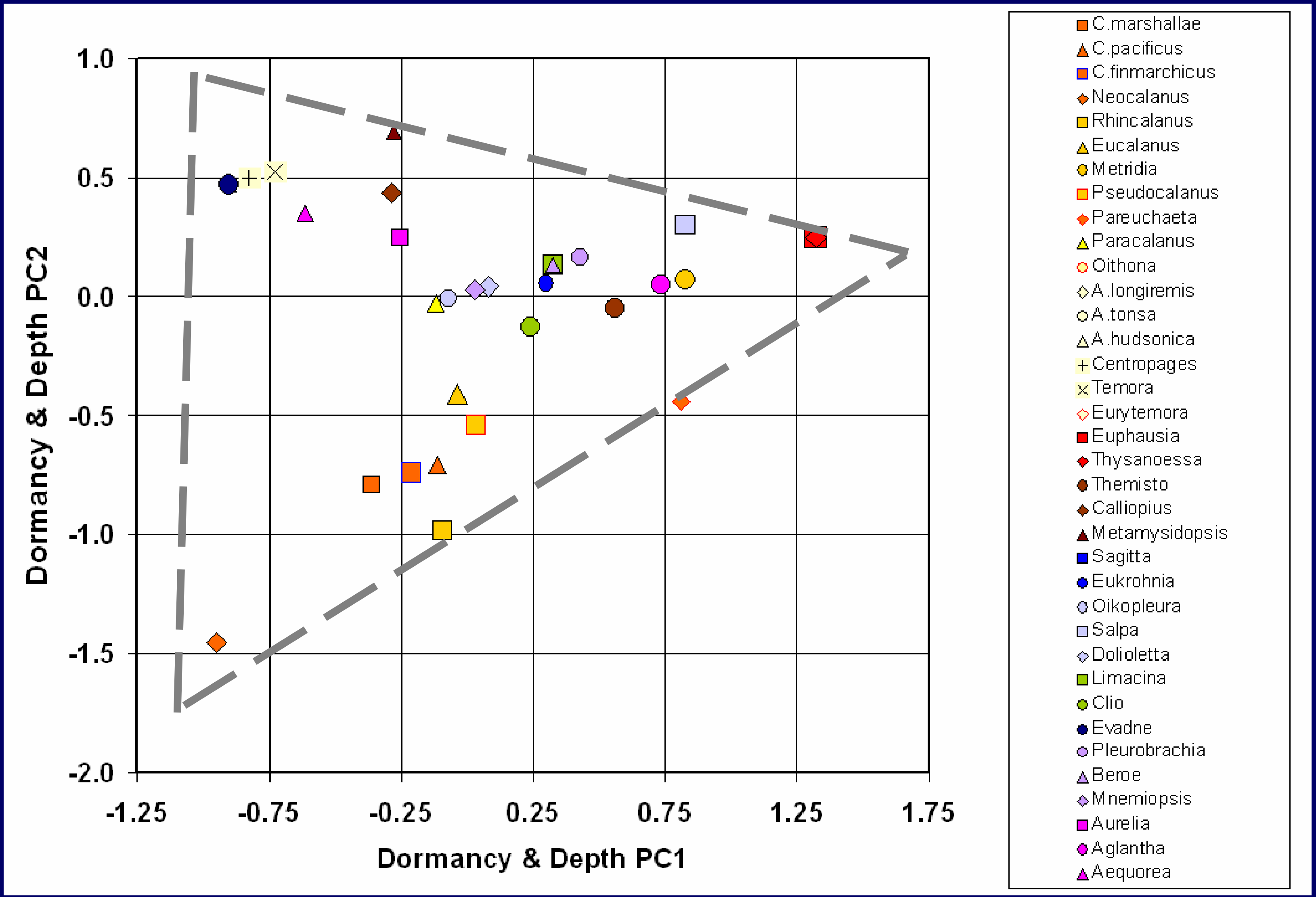


PCoA on refuge traits

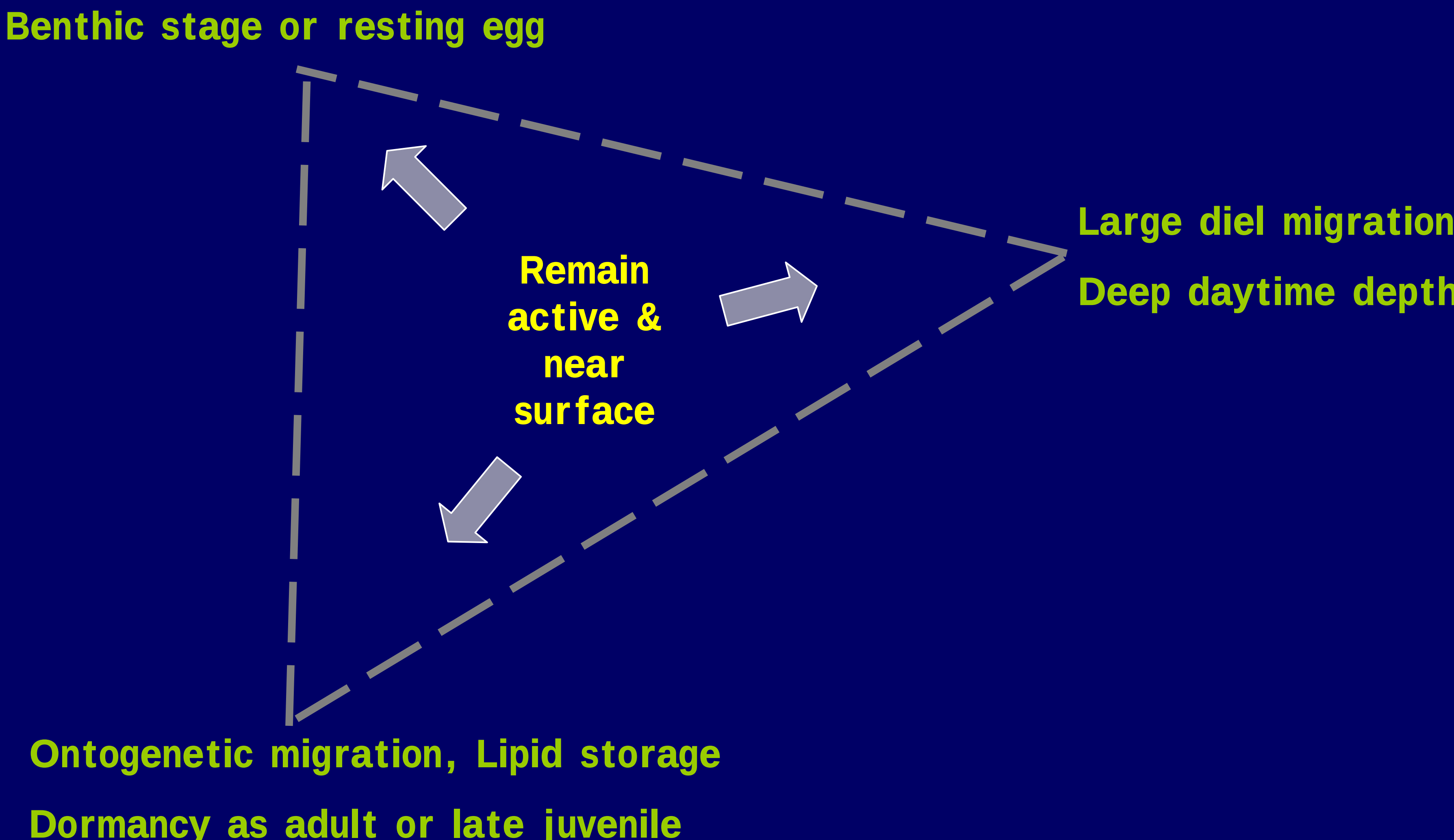
- First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	49.86	28.68
Eigenvector		
Extent of diel migration	4.87	1.74
Ontogenic migration	-1.19	-2.58
Dormancy	-4.34	-1.14
Storage of lipids	-0.01	-3.64
Benthic stage	-4.14	4.86
Daytime depth	4.81	0.75

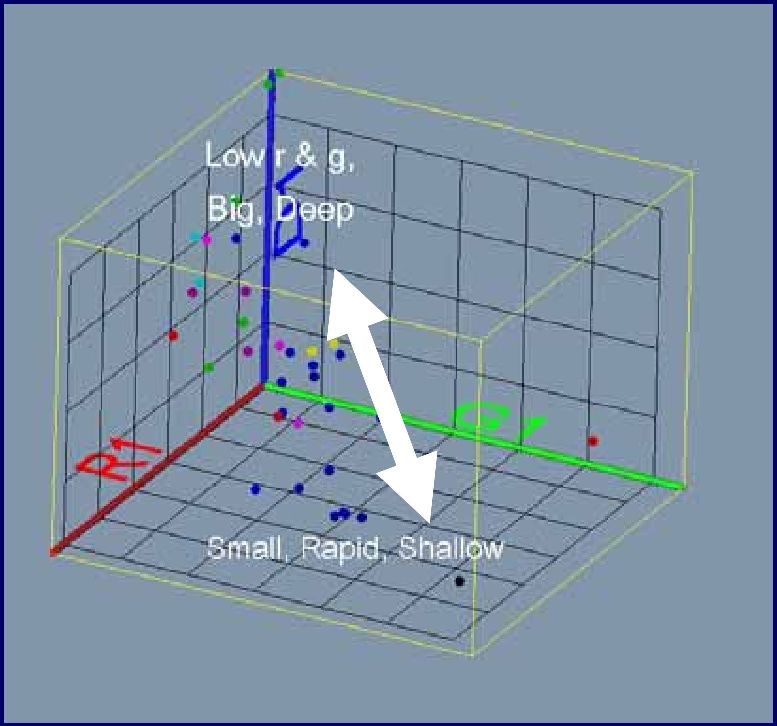
Ordination of refuge traits

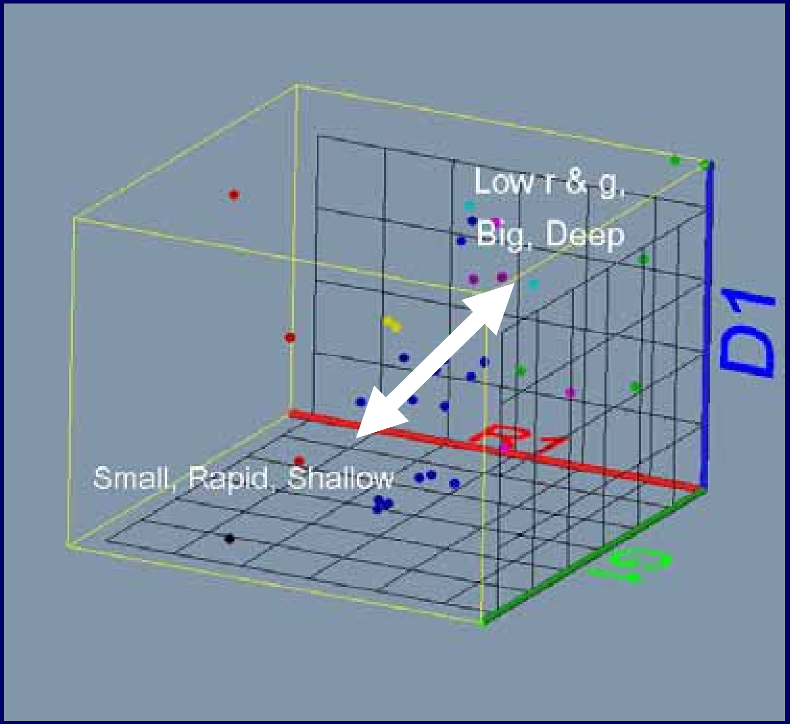


Ordination of refuge traits

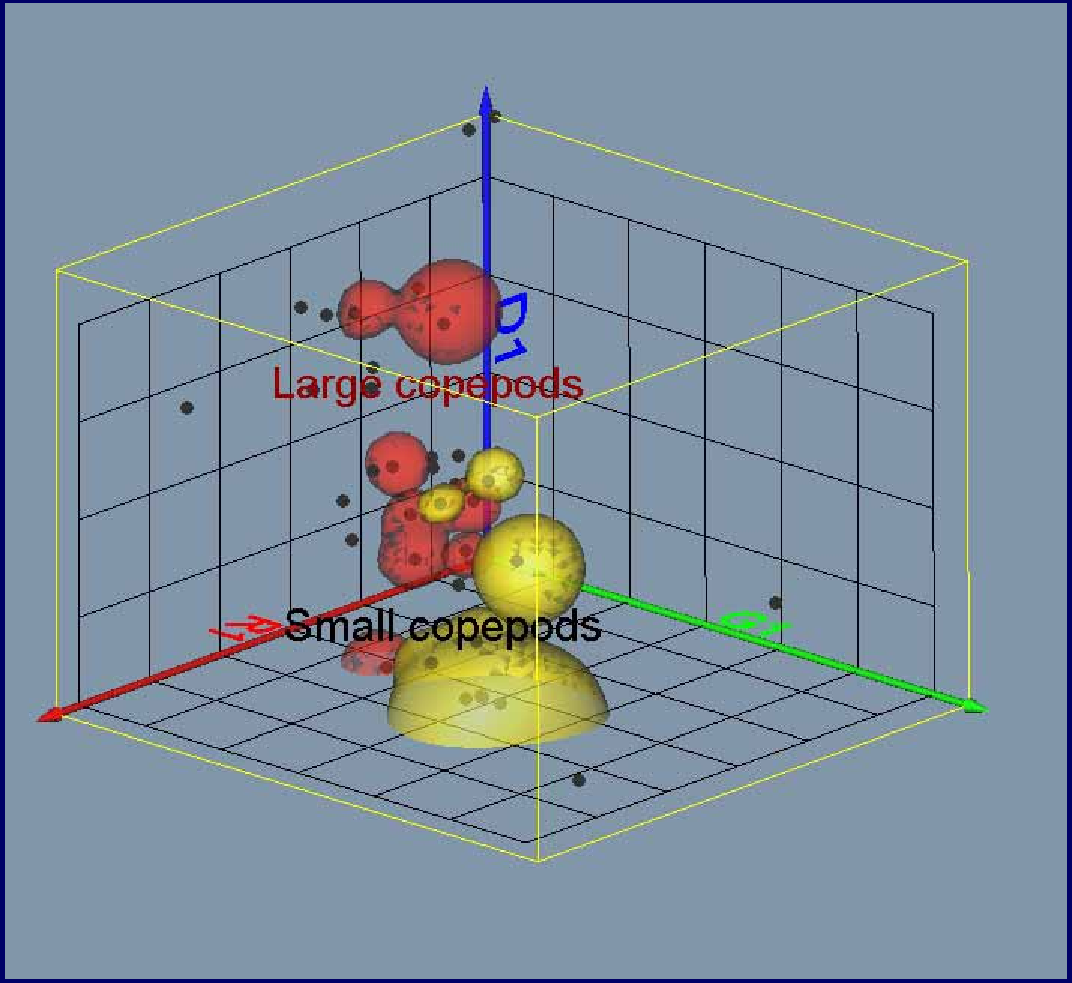


Scores on lead axes from each PCoA are intercorrelated, mostly due to size dependence of rates

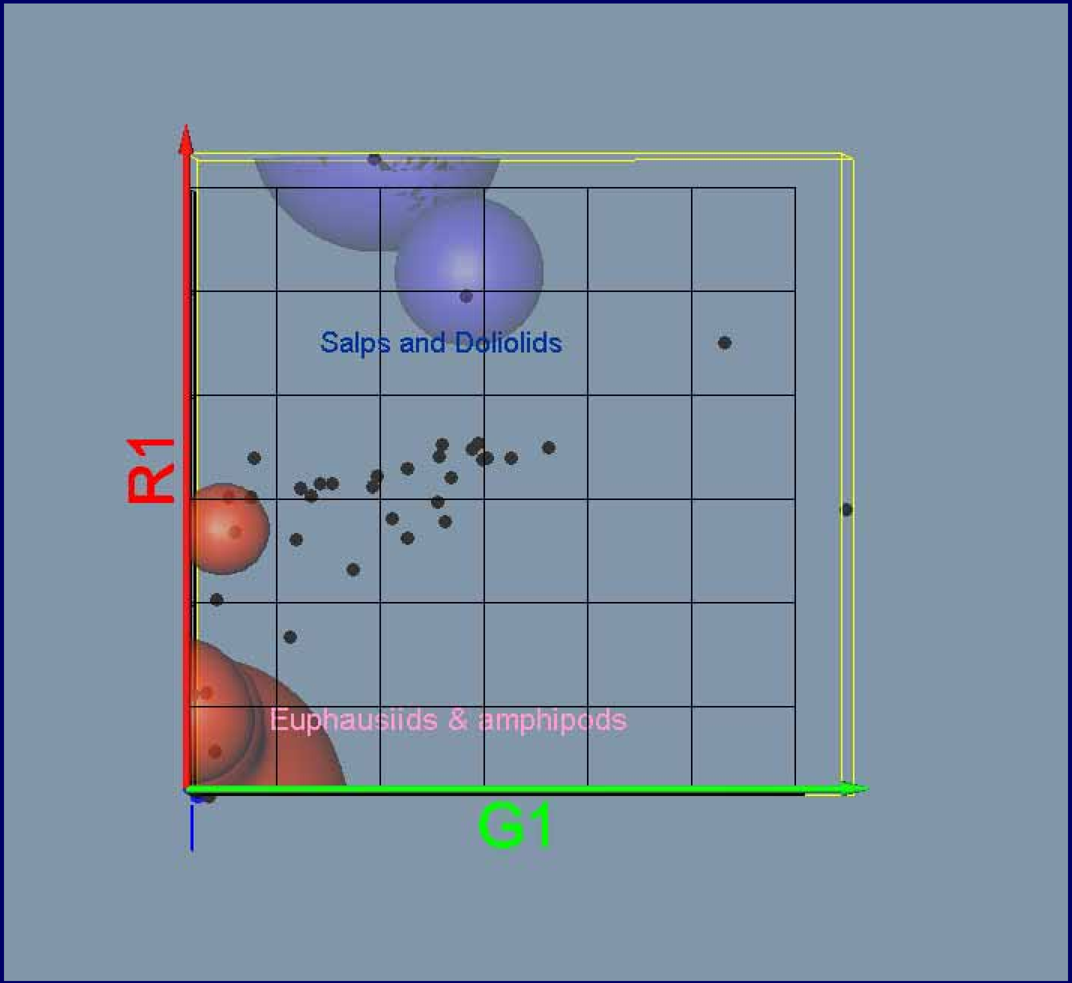




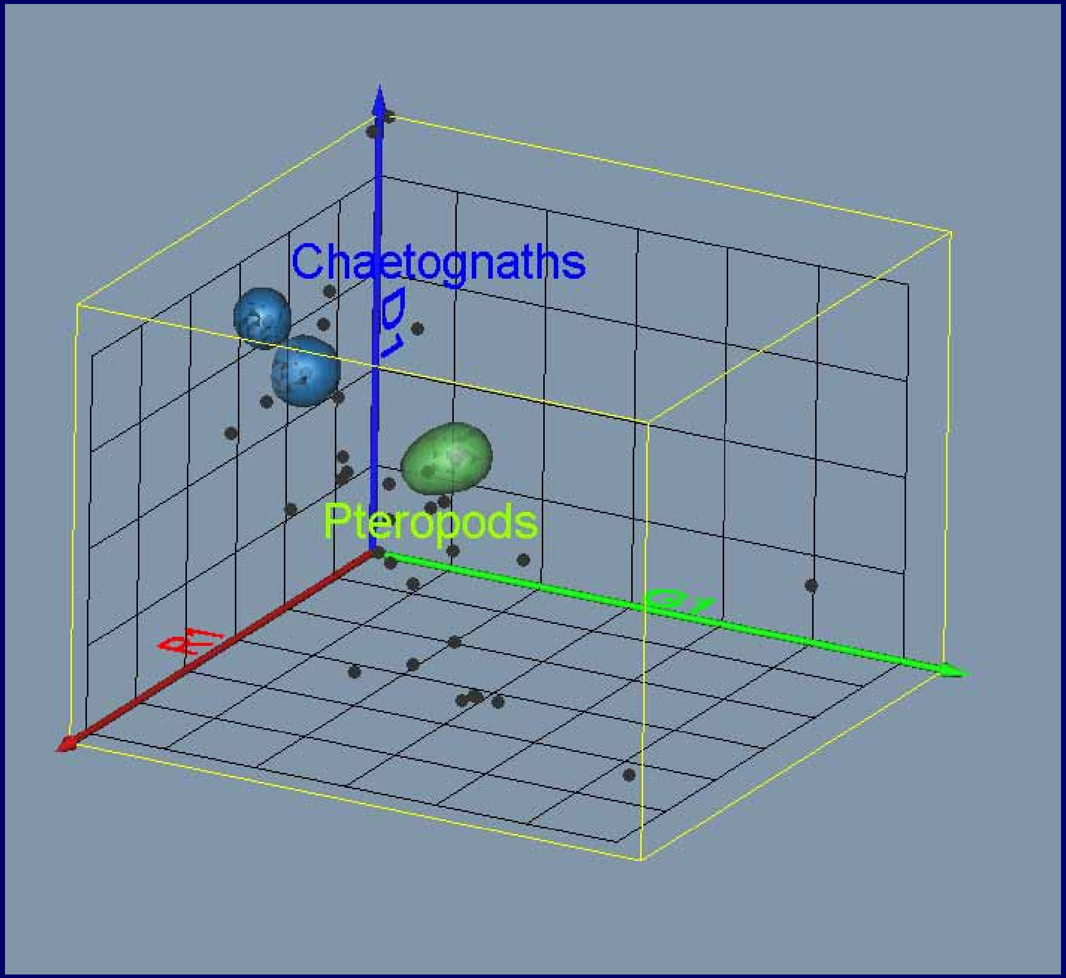
Additional 3D views – Clusters sharing taxonomic & morphologic similarity: (I) Large vs. small copepods



Additional 3D views – Clusters sharing taxonomic & morphologic similarity: (II) Large crustaceans vs. Salps/Doliolids



Additional 3D views – Clusters sharing taxonomic & morphologic similarity: (III) Chaetognaths vs. Pteropods



Comparison with Time Series - Initial expectations:

Sign of response correlated with LHS?

- Some LHS favored during some ocean ‘regimes” (response to environmental change similar within a LHS cluster)

Time scale of response correlated with LHS

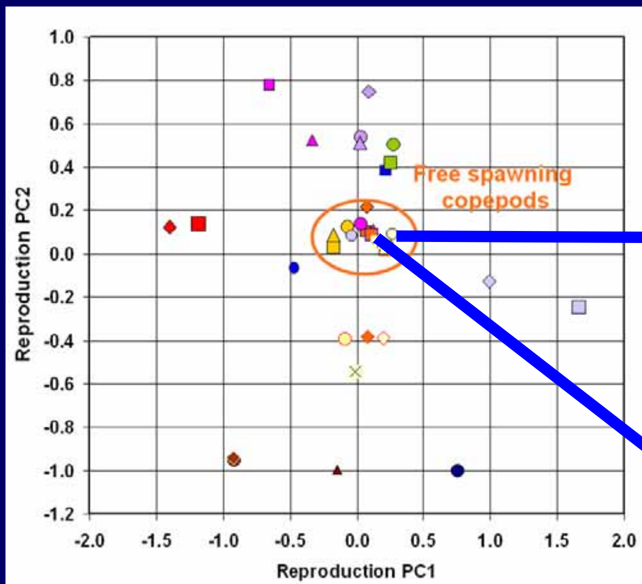
- Rapid decay of temporal autocorrelation by ‘opportunists’ (=spikey time series)
- Slow decorrelation by ‘equilibrium’ and ‘periodic’ groups (time series contain gradual trends and multi-year fluctuations)

Comparison with Time Series-Results

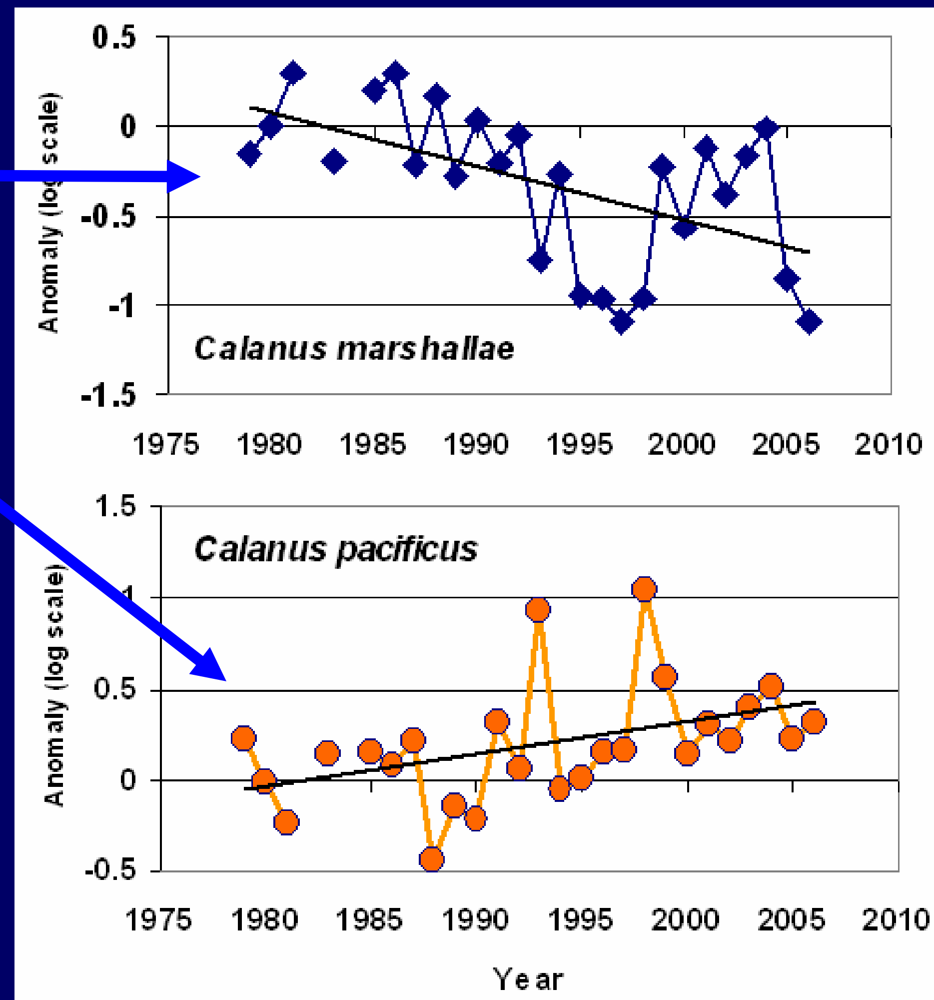
Interesting, but more complicated than "expectation". Anomaly time series provide examples of:

- Anticorrelation within LHS clusters
- Differences in amplitude & time scale between LHS clusters
- Differences in time scale within LHS clusters

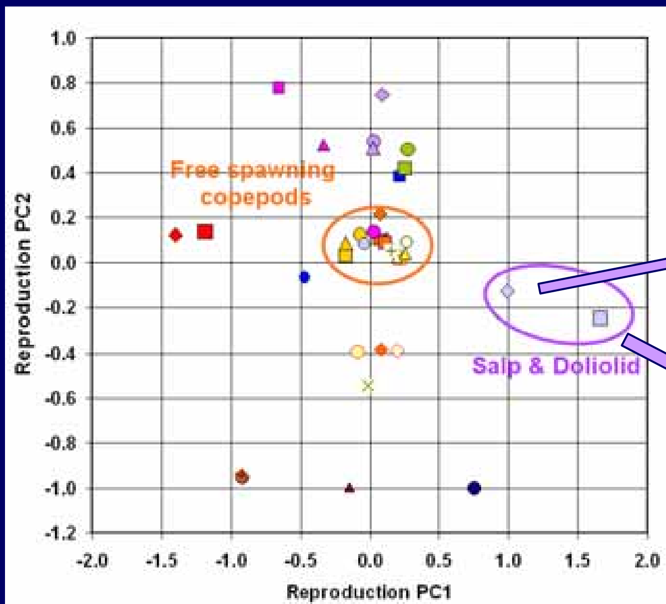
Anticorrelation within LHS clusters

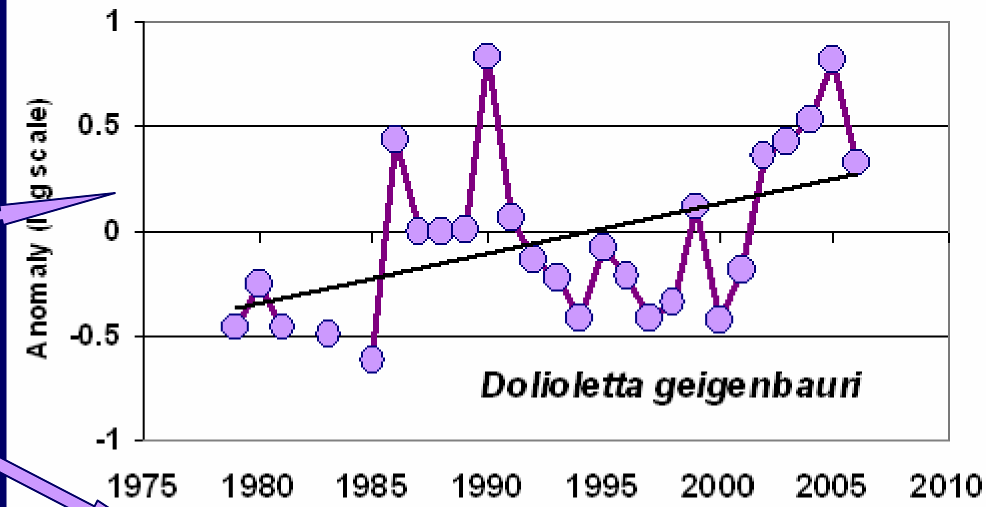


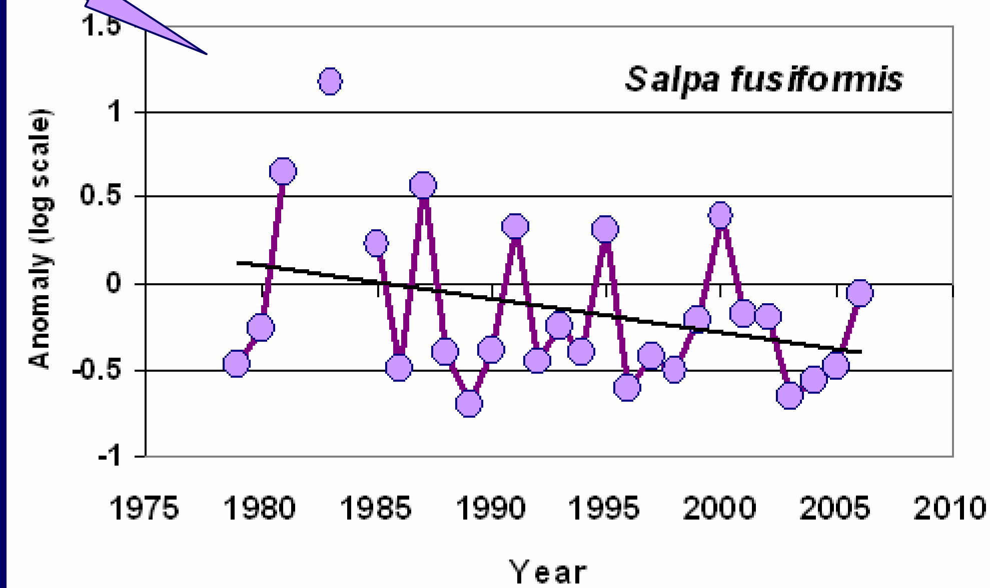
Species replacement, driven by shifting faunal boundaries, not by LHS difference



Contrasts of sign & time scale <u>within</u> LHS clusters (2)



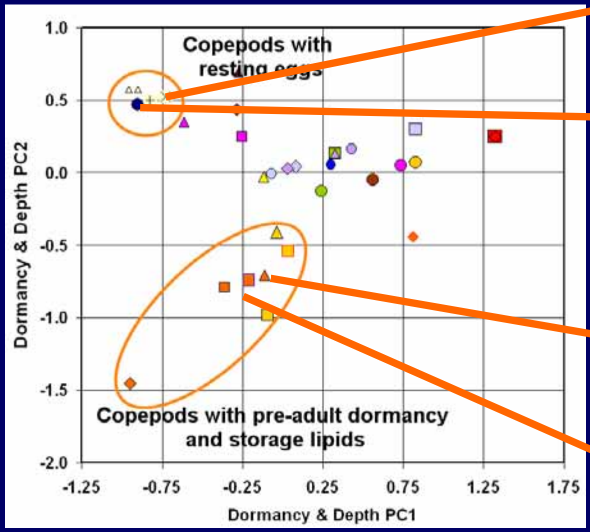


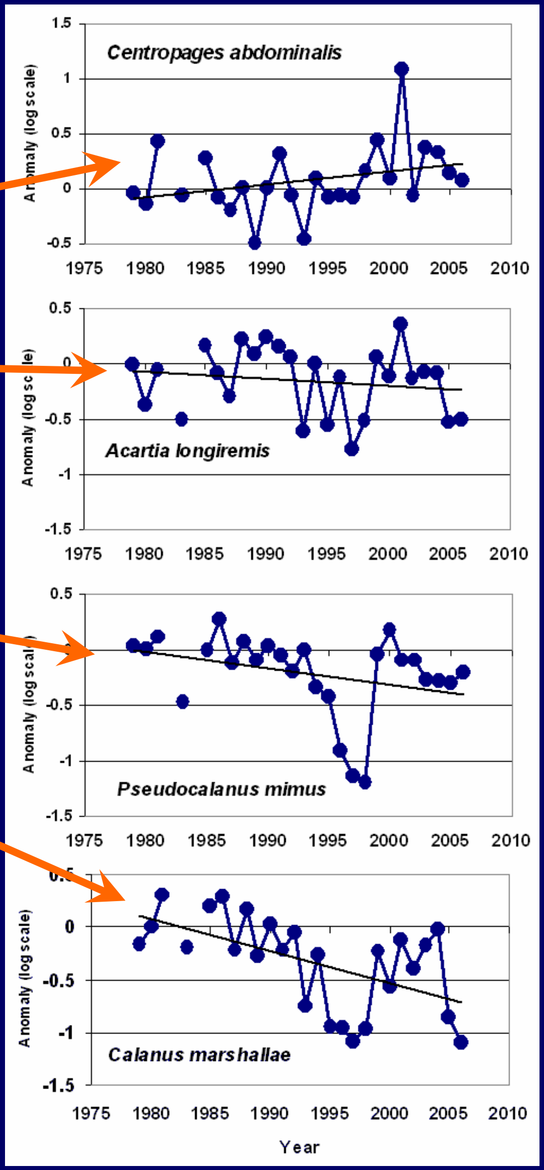


Salp time series definitely 'spikey'

Doliolid time series more like the copepods

Gradients of amplitude & time scale between LHS clusters





Trend and 'Regime' responses within 'cool water' zoogeographic cluster are modulated by reproductive and dormancy strategies

Summary

- PCoA ordination summarized variability among zooplankton life history strategies
- ALL observed strategies persist locally and are represented ~globally
- LHS clusters map strongly onto taxonomy, but with some surprises
- Interannual change (in our region) is dominated by shifting zoogeographic affinity, but modulated by LHS (True elsewhere?)

Future Directions

- Include within-species plasticity of LHS ('point' ➨'range' description of traits)
- Improve classification & quantification of multi-phase LHS (sexual-asexual, active-dormant, planktonic-benthic, direct development vs. metamorphosis)
- Include more taxa
- Compare with other regions

BIG thanks to the following for advice & data:

- Mary Arai & Jenny Purcell (medusae)
- Carol Lalli (pteropods)
- Jaime Gomez-Gutierrez, Tracy Shaw, Leah Feinberg & Bill Peterson (euphausiids)
- Andrew Hirst (growth rate theory)
- Xenia Kosobokova (chaetognaths)
- Moira Galbraith (size & abundance trends)

Spares & extras

LHS of Marine Invertebrates

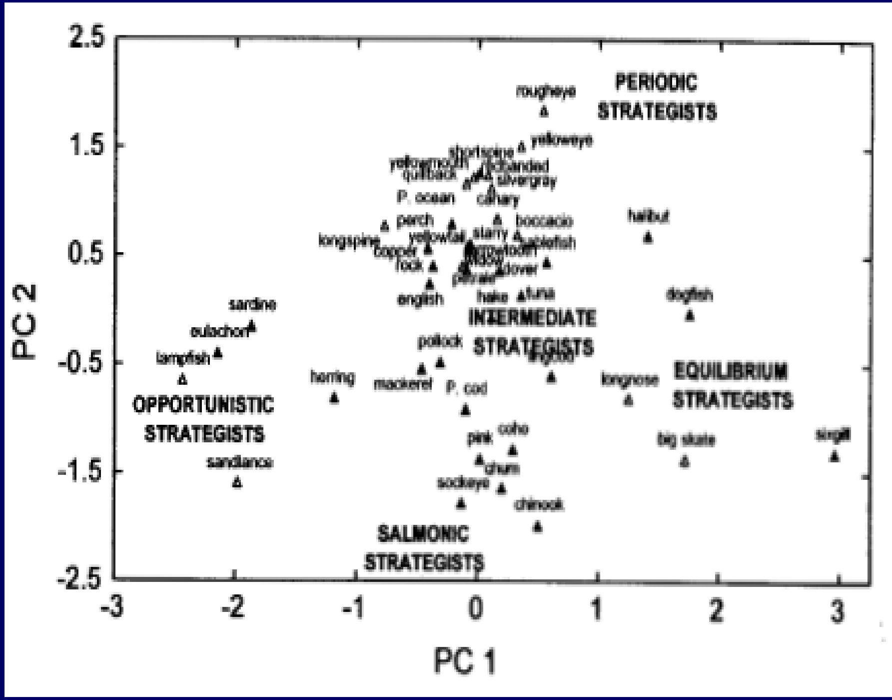
(summary from Ramirez-Llorda 2002)

- Most comparisons have been among benthic taxa
- Tradeoffs of fecundity vs. other modes of parental investment (egg size, brooding, ….)
- Effects of food availability
- Gradients with increasing latitude and depth (fewer and larger eggs)

Historical Background (3)

Fish LHS refinements

(e.g. King & McFarlane 2003)



Two additional clusters:

‘Salmonid’ – resemble ‘opportunistic’ but large adults & eggs; split life cycle between ocean & FW

‘Intermediate’ – resemble ‘periodic’ but shorter life span and lower fecundity