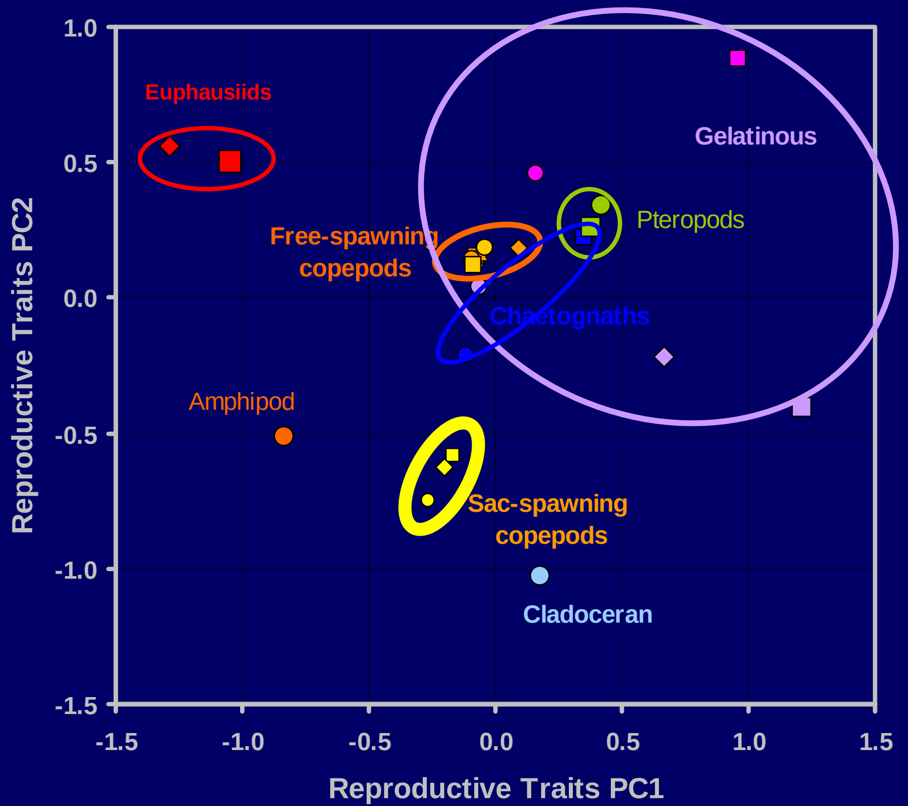
Classification of Zooplankton Life History Strategies



Dave Mackas[1] and Jackie King[2]

Fisheries & Oceans Canada

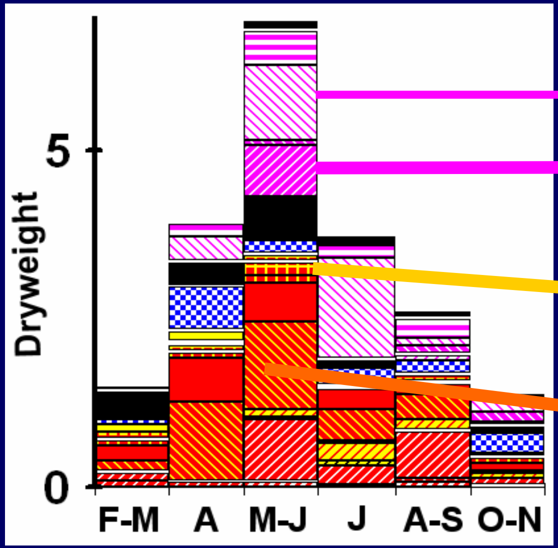
[1]Institute of Ocean Sciences & [2]Pacific Biological Station

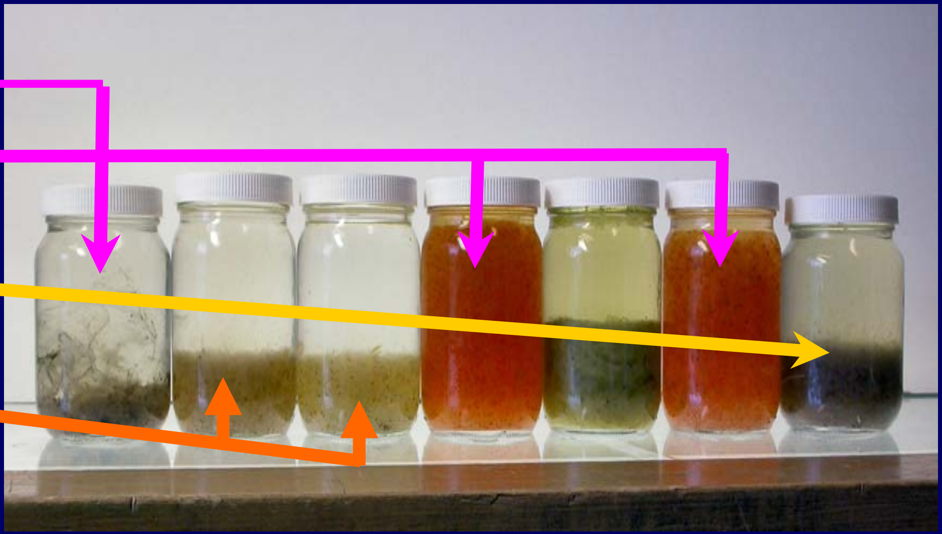
Outline of Talk:

- 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.

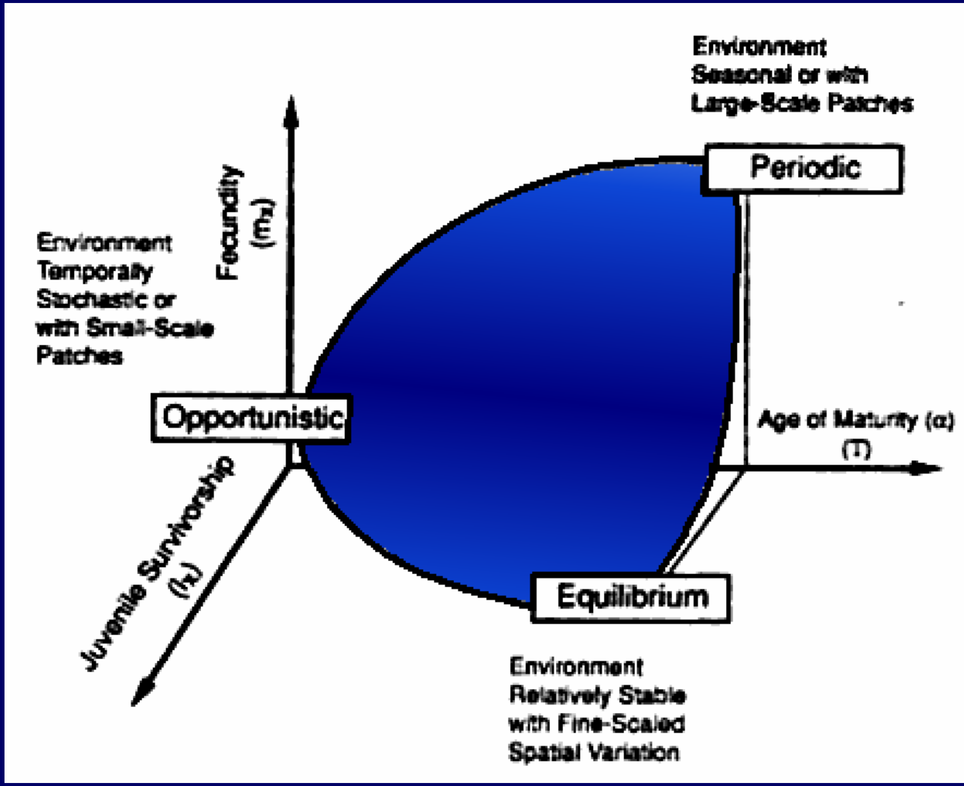
- Investment in survival and ability to compete

(Doesn't not 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')

LHS of Marine Invertebrates

(summary from Ramirez-Llorda 2002)

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

Historical Background: What about zooplankton??

Intensive research on individual traits within 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 <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:
23 spp. routinely present & occasionally dominant in northern California Current System

Free-spawning copepods:
- *Calanus marshallae, C. pacificus, Metridia*

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

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

Euphausiids:
- *Euphausia pacifica, Thysanoessa spinifera*

Hyperiid amphipod:
- *Parathemisto pacifica*

Cladoceran:
- *Evadne*

Chaetognaths:
- *'Sagitta' elegans, Eukrohnia*

Shelled Pteropods:
- *Limacina, Clio*

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

Ctenophore:
- *Pleurobrachia*

Scyphozoan medusa:
- *Aurelia aurita*

Choice 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?

‘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?

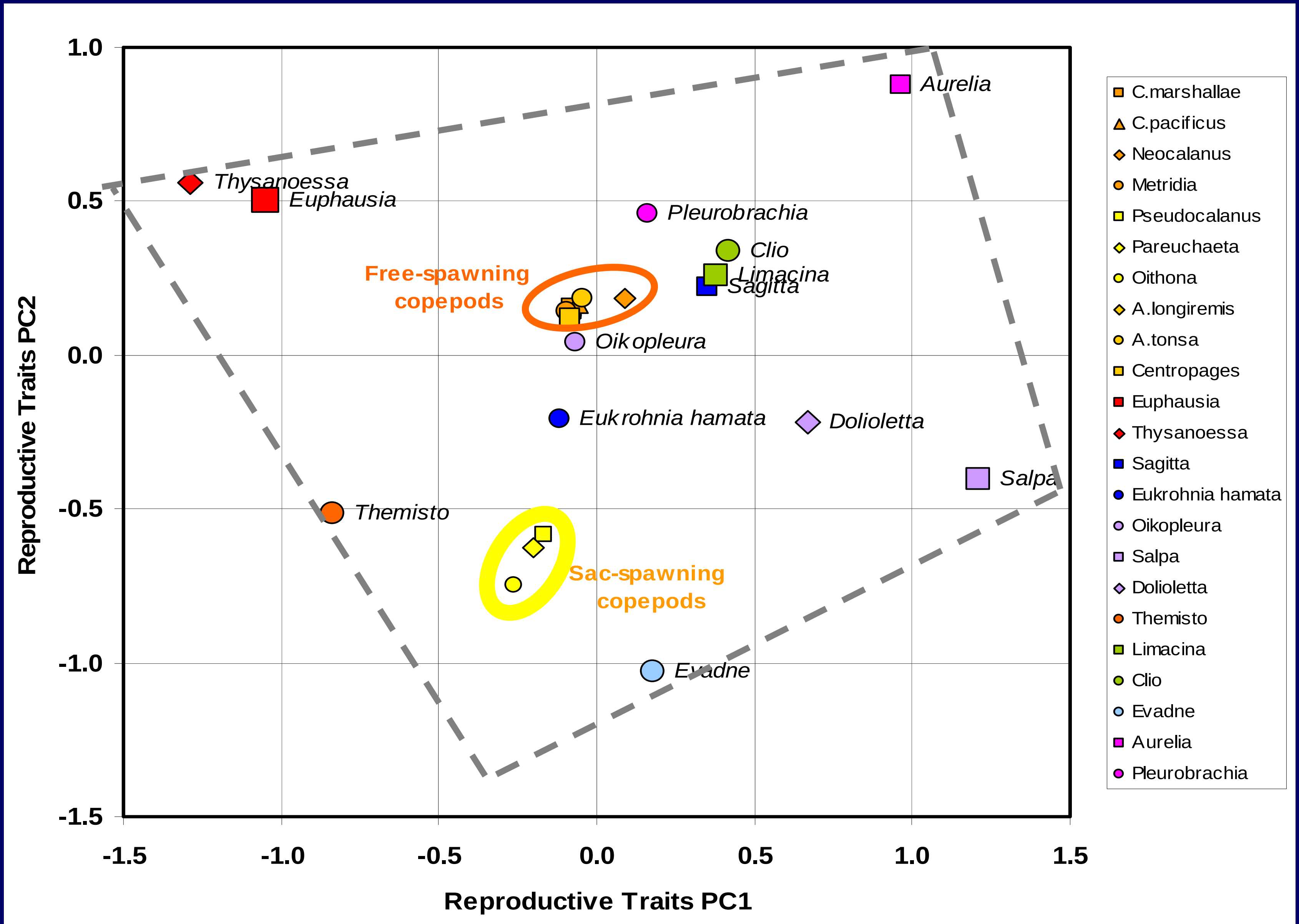
Ordination Results

PCoA on reproductive traits

- First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	42.37	29.05
Eigenvector		
log Fecundity	2.15	3.28
r (per day)	1.83	-0.67
Lifespan (years)	-4.23	1.67
Iteroparous/Semelparous	-2.66	-0.39
Mode of reproduction	3.00	-0.05
Parental brooding	-0.09	-3.85

PCoA on reproductive traits



PCoA of reproductive traits

High *r* & fecundity

Long life span

Semelparous

Reproduction mostly sexual

Relatively low *r*

Long life span

Iteroparous

High *r*, Short-life span

Semelparous

Alternating stages

Reproduction mostly vegetative, parental attachment

Low fecundity

Iteroparous/Semelparous

Some hermaphrodites

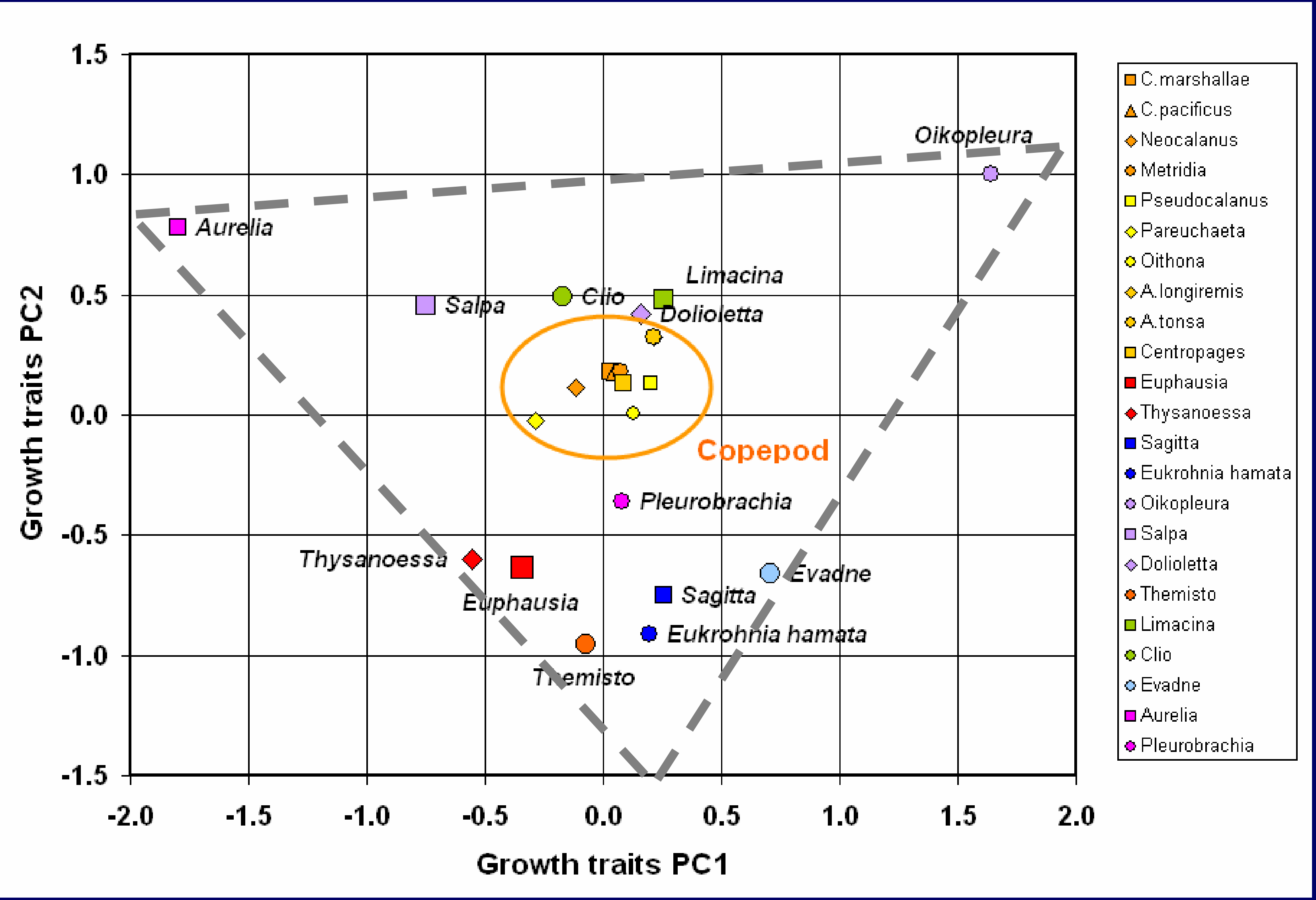
Parental brooding

PCoA on growth traits

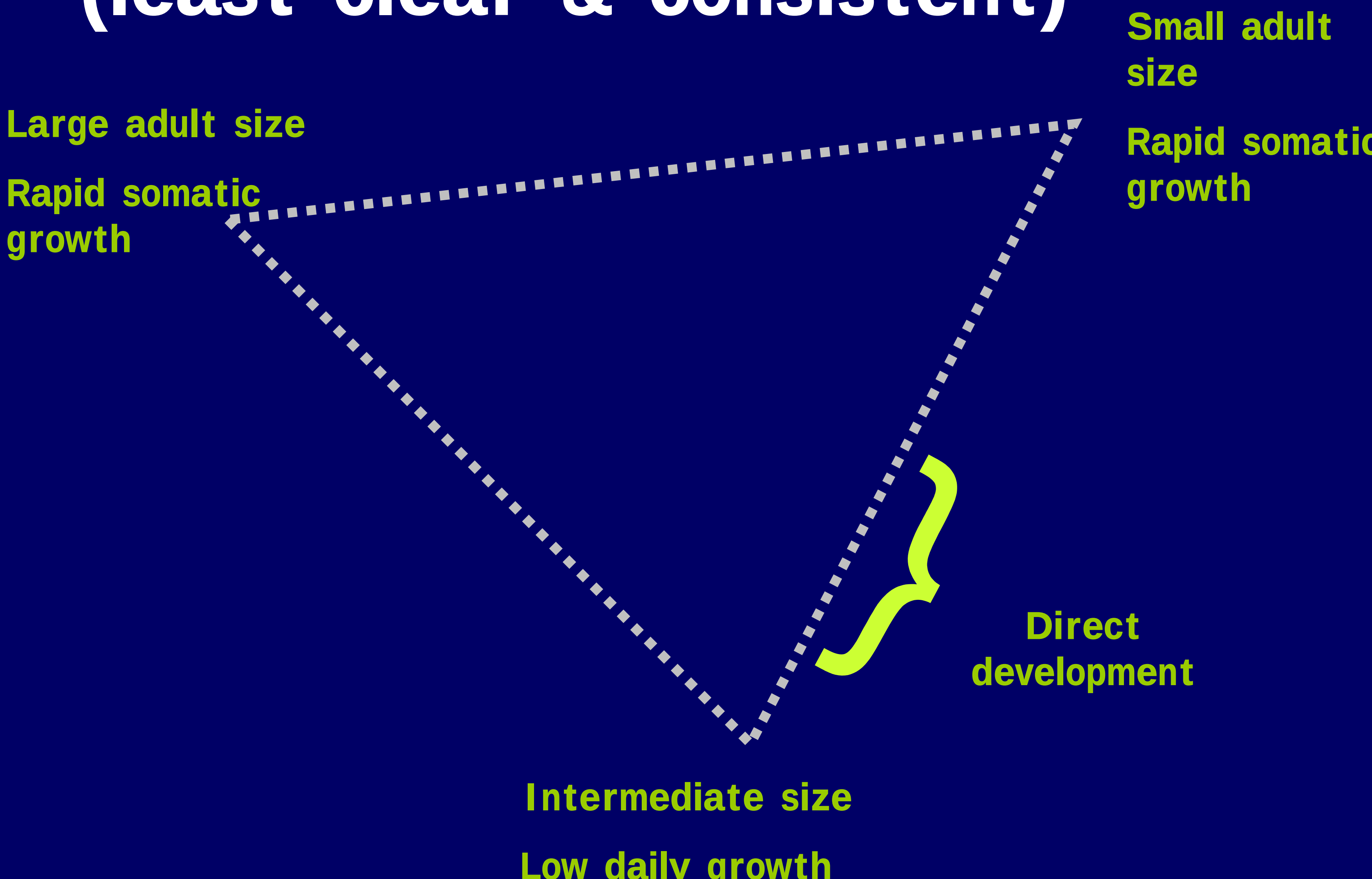
- First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	55.62	44.38
Eigenvector		
log Adult size (dry weight)	-3.99	0.13
Somatic growth (per day)	2.12	3.02
Proportion of life as juvenile/adult	1.86	-3.15

PCoA on growth traits



PCoA of growth traits (least clear & consistent)

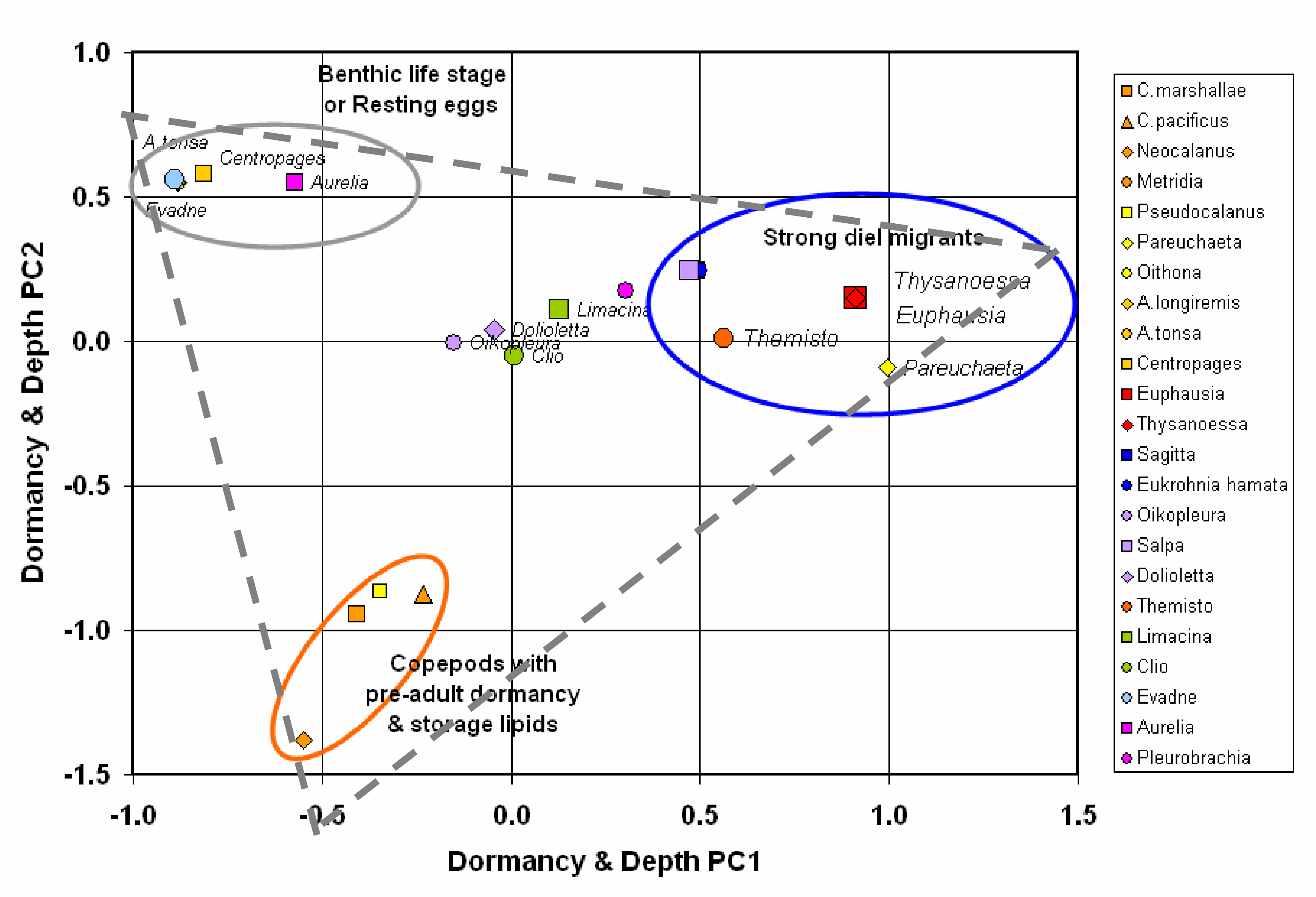


PCoA on ‘refuge’ traits

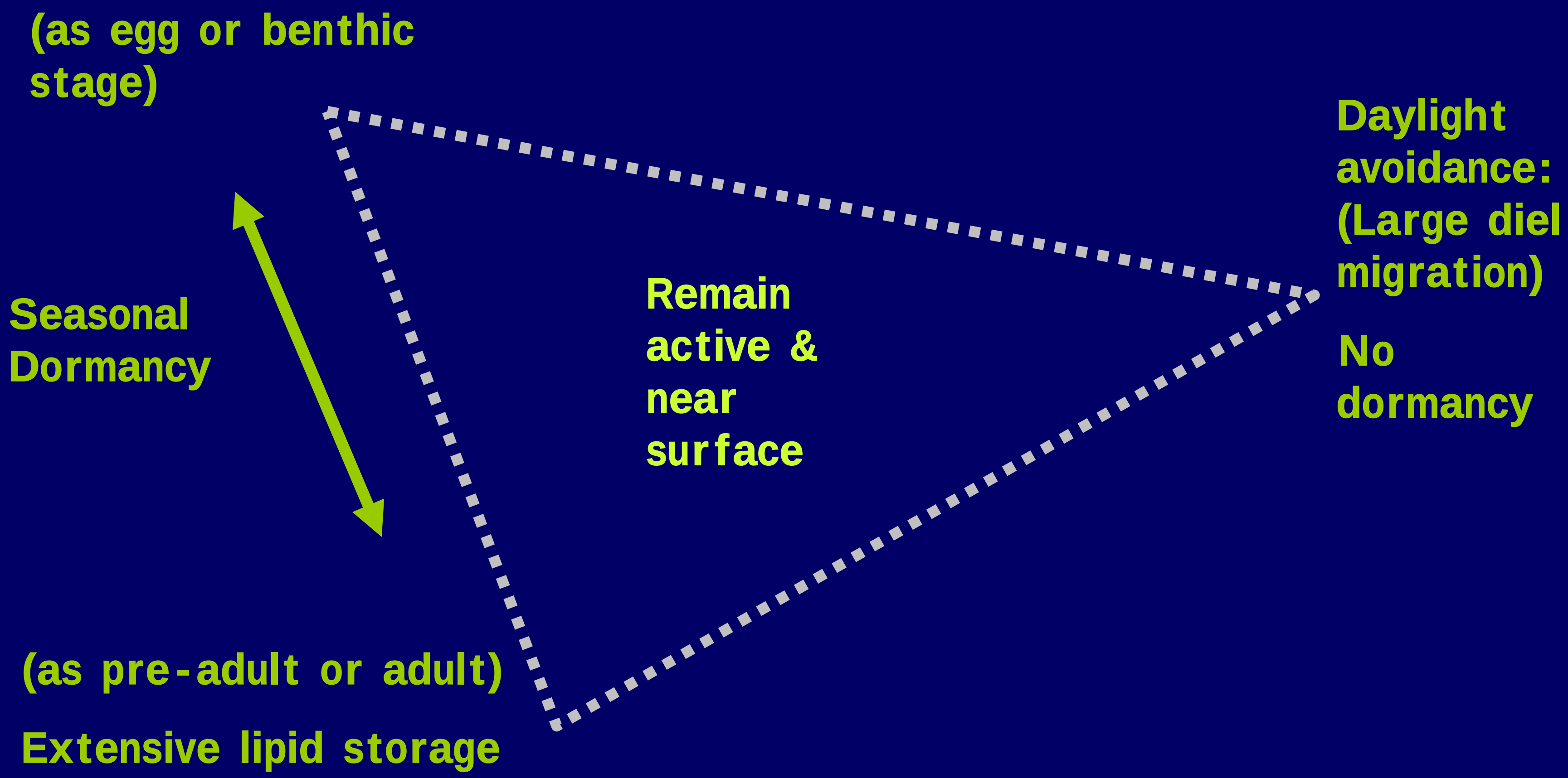
First 2 coordinates are significant

	PCo1	PCo2
Percent Variation	47.18	35.87
Eigenvector		
Extent of diel migration	0.87	0.61
Ontogenic migration	0.08	-0.46
Dormancy	-0.61	-0.26
Storage of lipids	0.45	-0.46
Benthic stage	-0.79	0.56

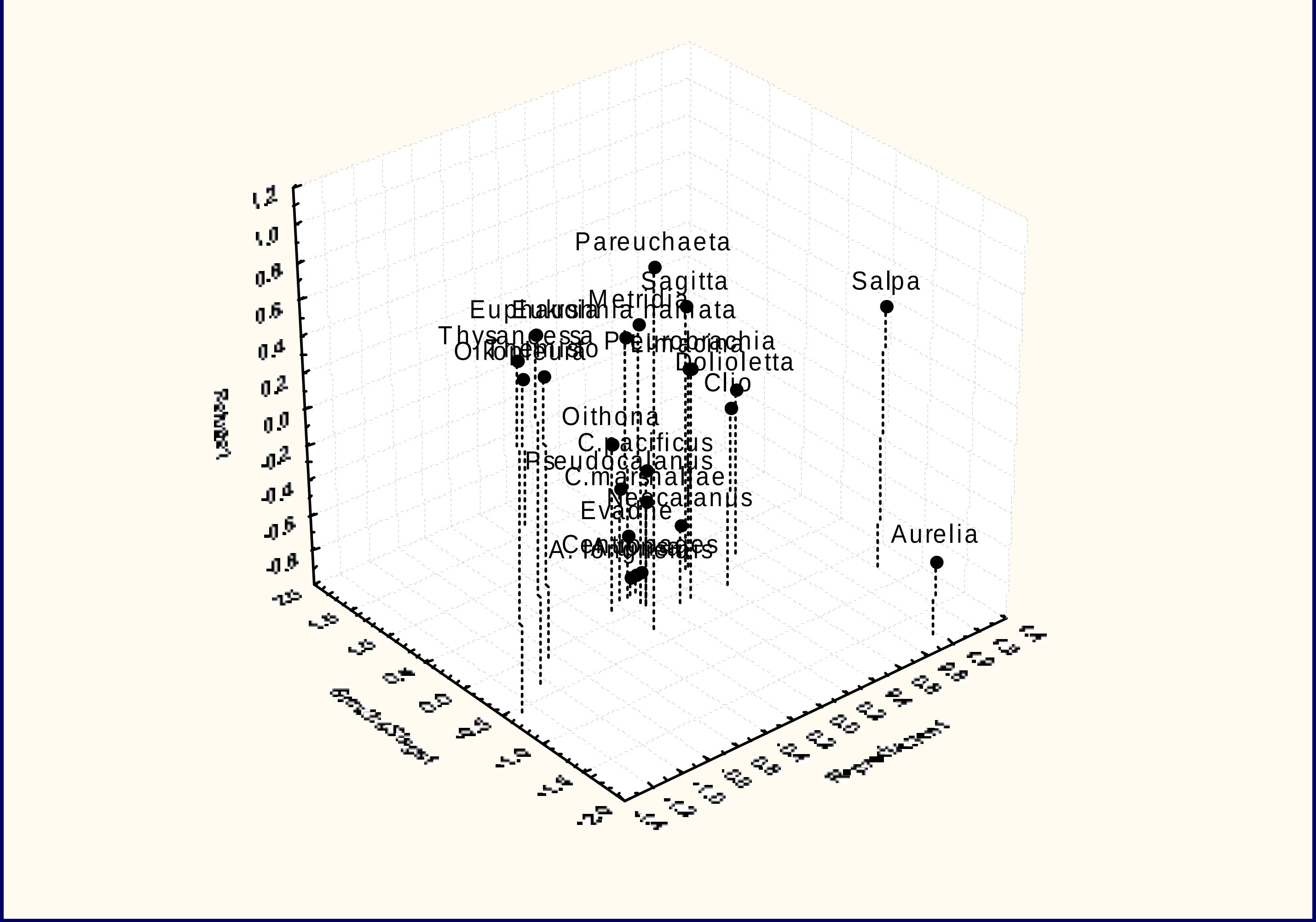
PCoA of refuge traits



PCoA on refuge traits

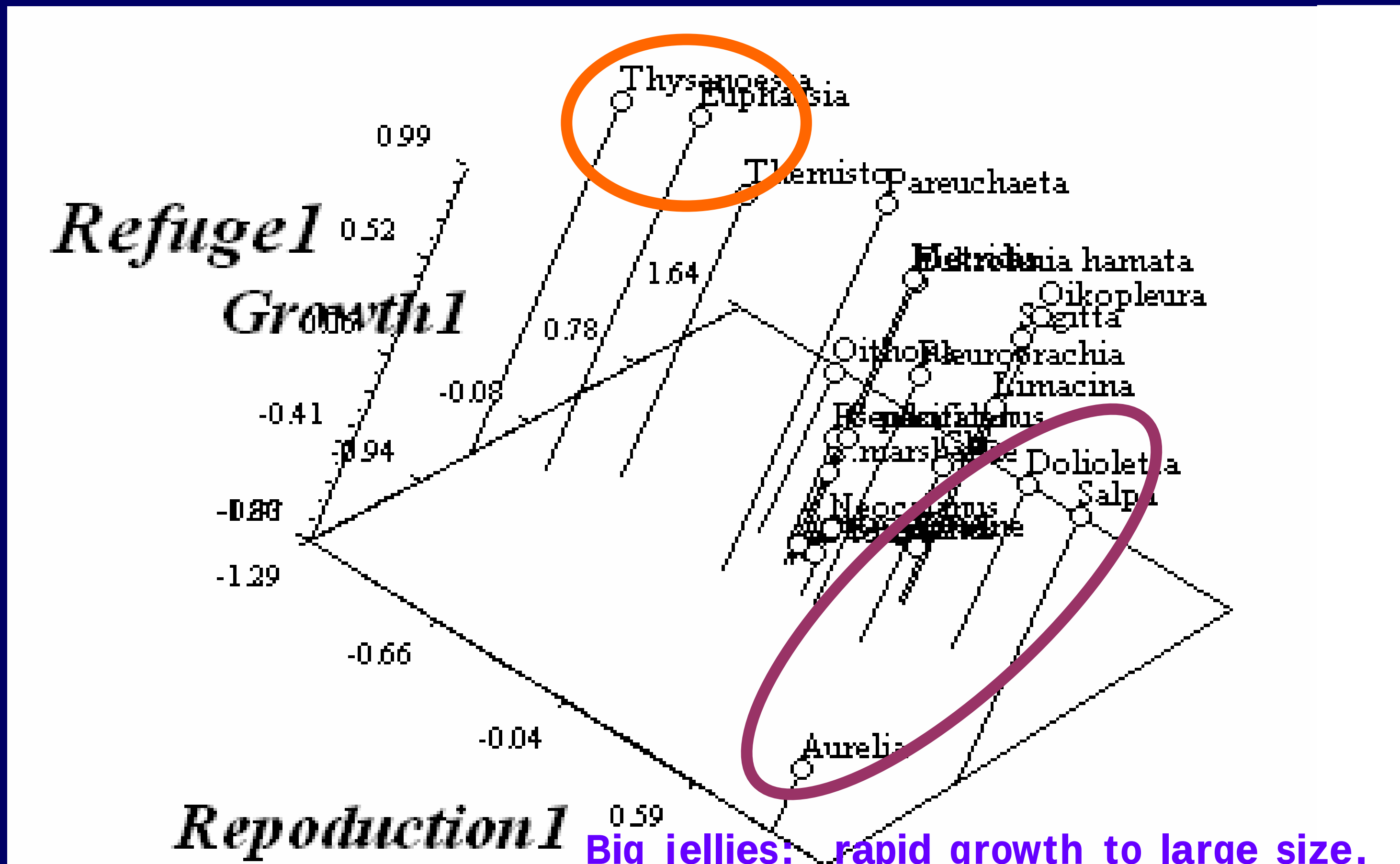


3D views – Lead axis from each PCoA

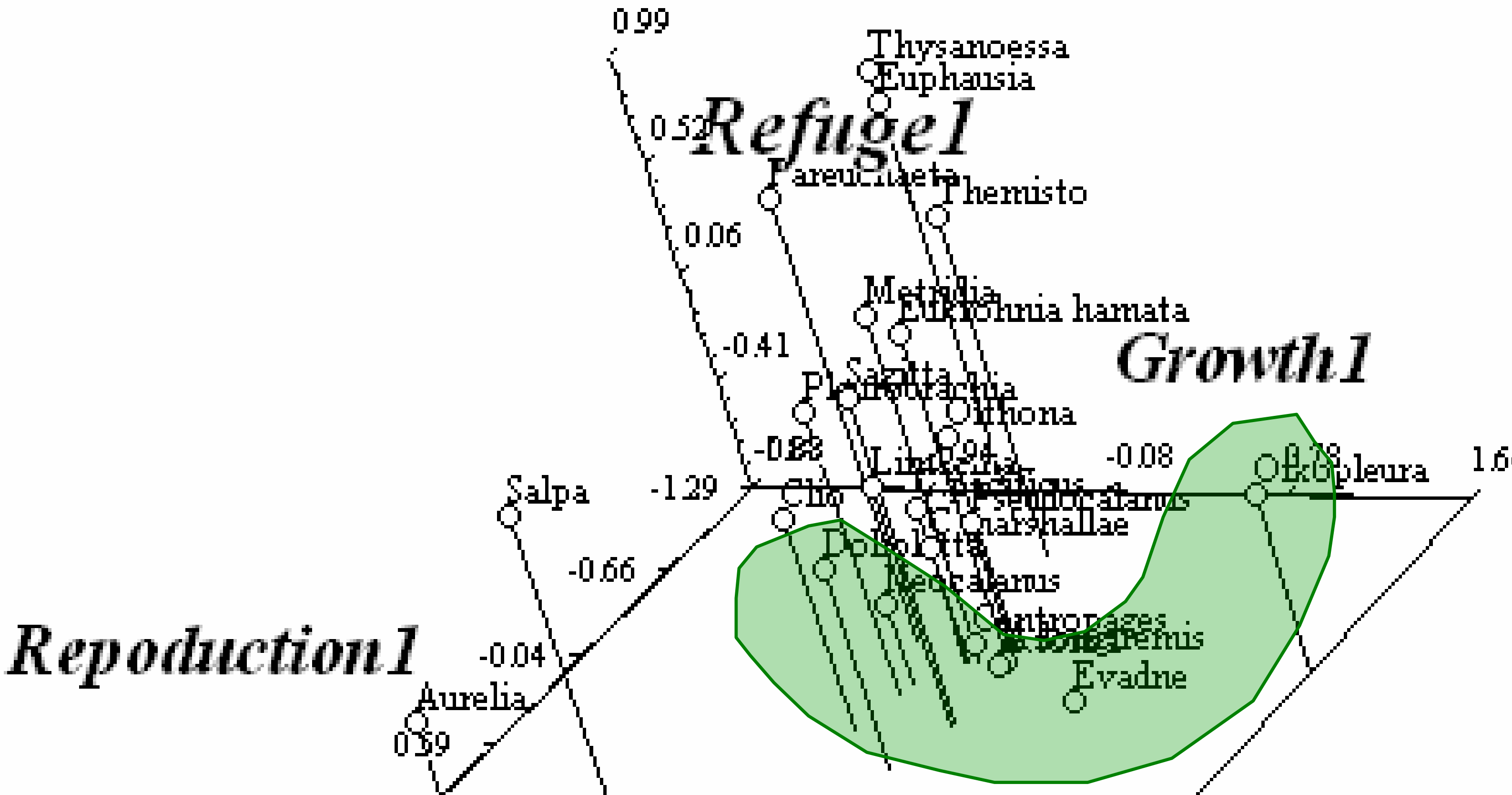


Big crustaceans: Large diel migration, no dormancy, long-lived.

iteroparous, dioecious - e.g. *Euphausia, Thysanoesa, Thermisto*



Big jellies: rapid growth to large size, alternating sexual/vegetative reproduction, no dormancy e.g. *Aurelia, Salpa*



“Coastal opportunists”:
Small jellies & crustaceans
Rapid growth & reproduction
Often resting eggs
e.g. *Evadne*, *Oikopleura*, *Acartia*, *Dolioletta*

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)

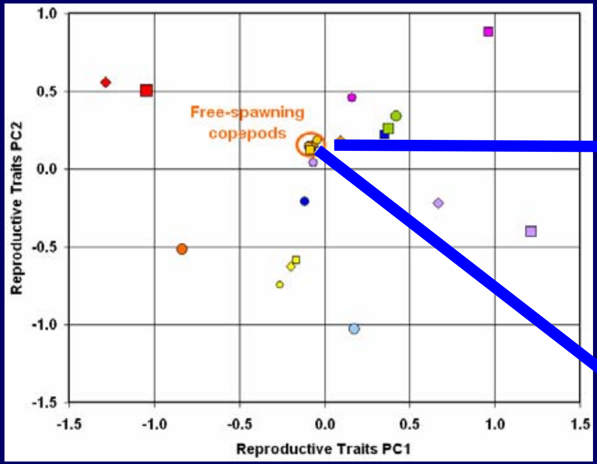
– Slow decorrelation by ‘equilibrium’ and ‘periodic’ groups (time series contain gradual trends and multi-year fluctuations)

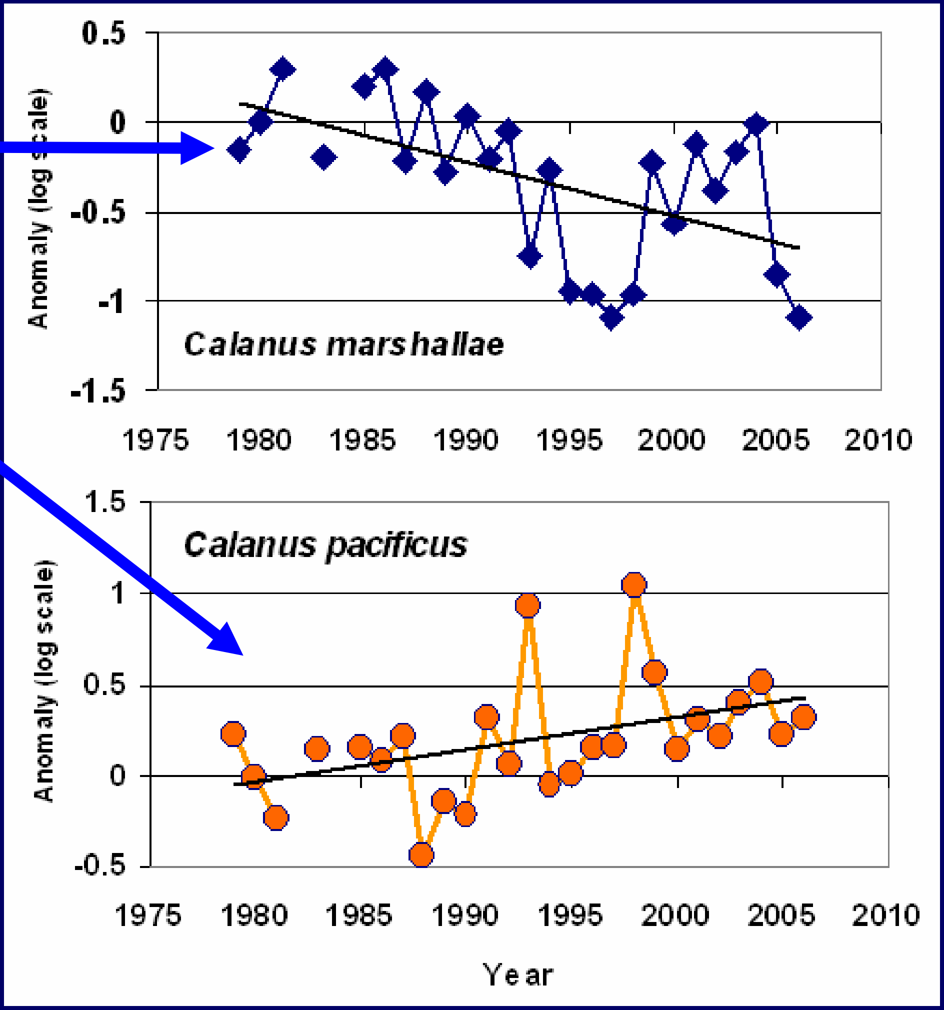
Comparison with Time Series-Results

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

- Anticorrelation <u>within</u> LHS clusters
- Differences in amplitude & time scale <u>between</u> LHS clusters
- Differences in time scale <u>within</u> LHS clusters

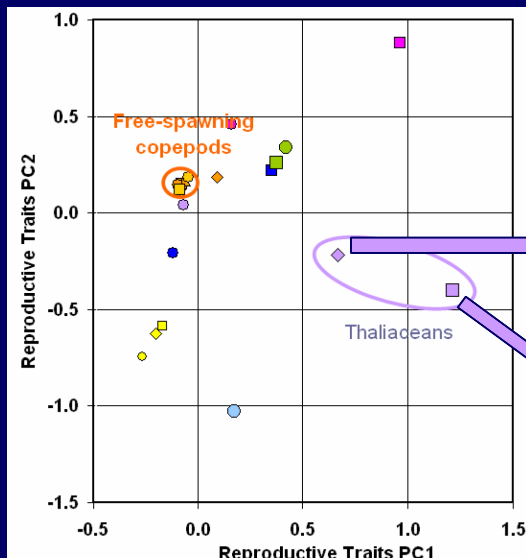
Anticorrelation within LHS clusters

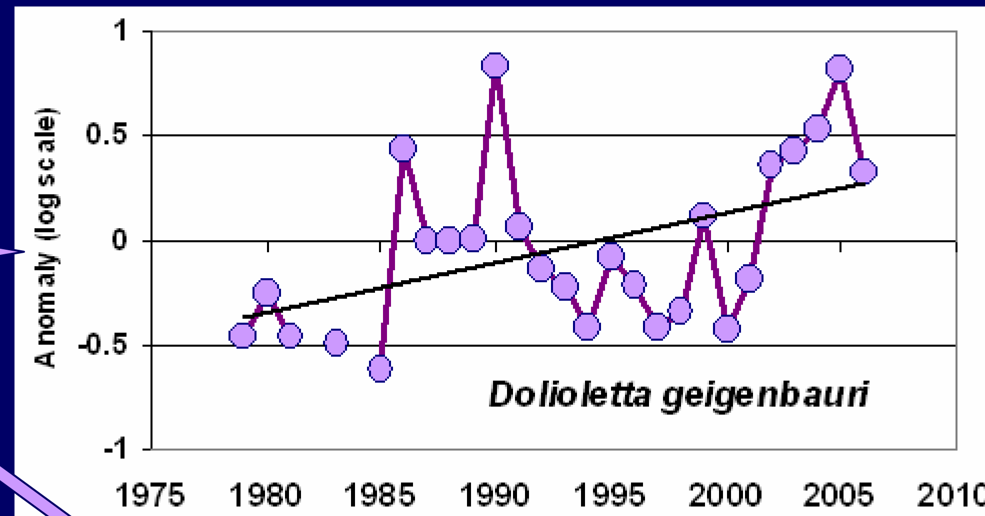


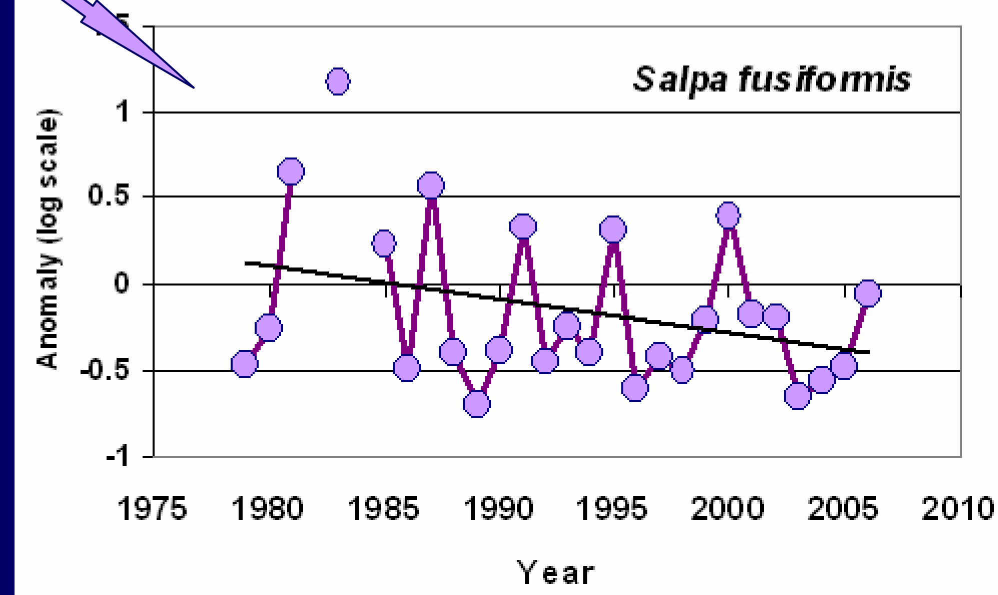


Species replacement, driven by shifting faunal boundaries, not by LHS difference

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



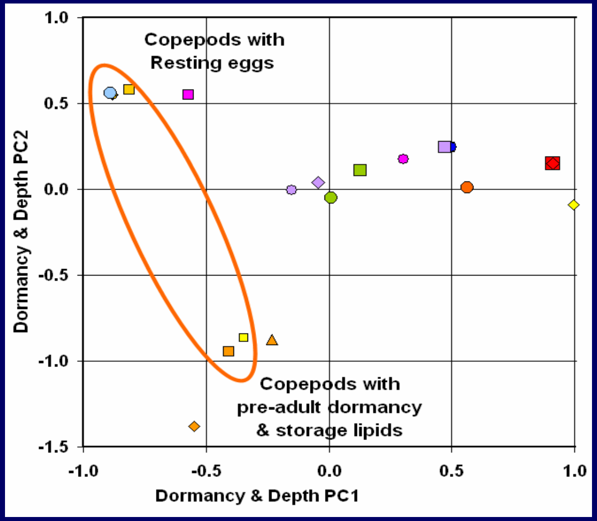


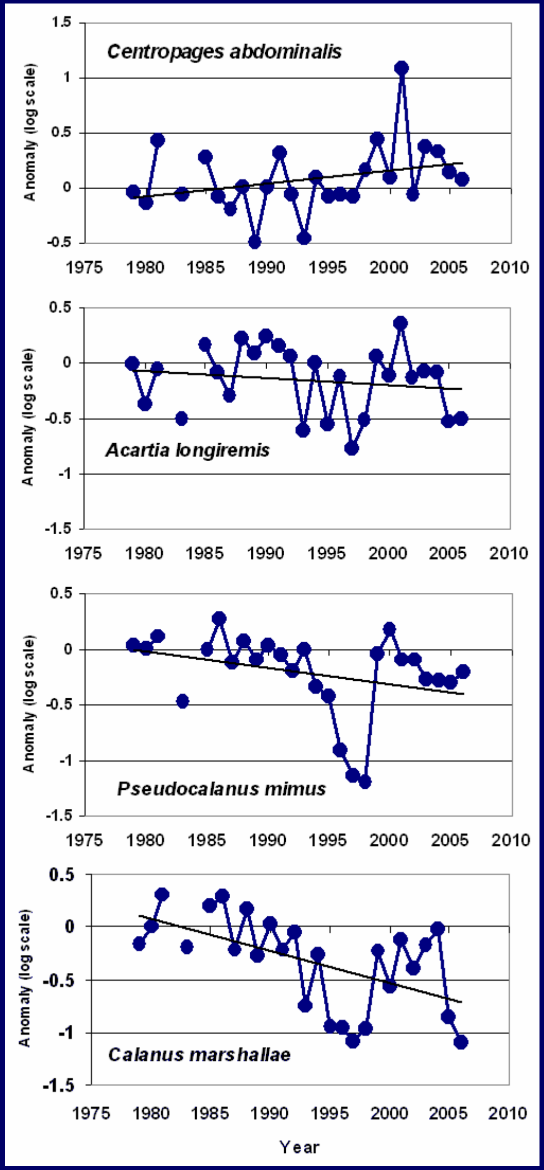


Salp time series definitely ‘spikey’

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 (e.g. cladocerans similar to doliolids)
- 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 our classification & quantification of multi-phase LHS (sexual-asexual, active-dormant, planktonic-benthic, direct development vs. metamorphosis)
- Include more taxa
- Compare with other regions