Size and species-based analyses of food webs

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Species identity, body size and trophic role

Estimating trophic level

Approaches:

Nitrogen stable isotope analysis to estimate trophic level (as $\delta^{15}N$) for:

- individuals
- species
- size classes

Mean fractionation per trophic level is typically $3.4^{0}/_{00}$ (SD $1.1^{0}/_{00}$) and designated as $\Delta\delta^{15}N$

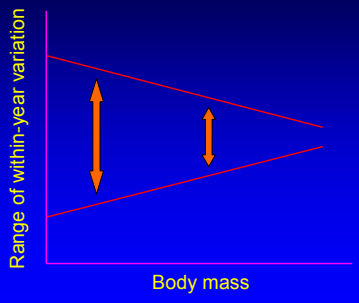
Warning: validation and sensitivity analysis essential

Size and species-based analyses of food webs

- Species identity, body size and trophic role
- Mean size and individual size
- Size-structure in food webs
- Applications of size-based methods

Species identity, body size and trophic role

Estimating trophic level- seasonal variation in $\delta^{15}N$



Species identity, body size and trophic role

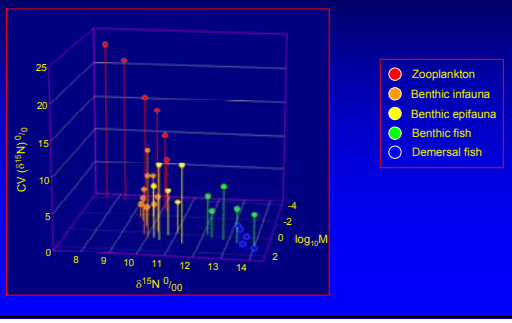
Focus on:

Exploring relationships between species identity, body size and trophic level

Linking these relationships to patterns of energy use by species and communities

Species identity, body size and trophic role

Estimating trophic level- seasonal variation in $\delta^{15}N$

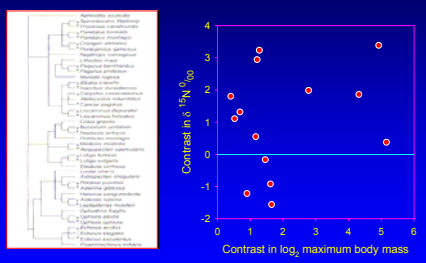


Species identity, body size and trophic role

Relationships between mean body size and trophic level

Species identity, body size and trophic role

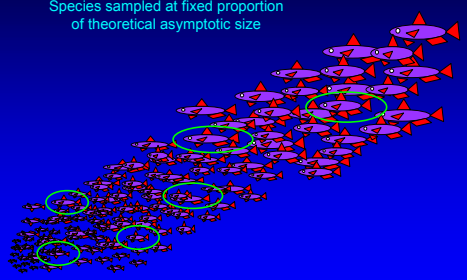
Relationships between $\delta^{15}N$ and body size: comparative approach



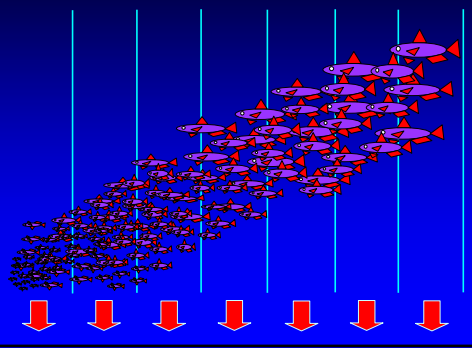
Source: Marine Ecology Progress Series 226: 77-85 (2002)

Species identity, body size and trophic role

Species sampled at fixed proportion of theoretical asymptotic size

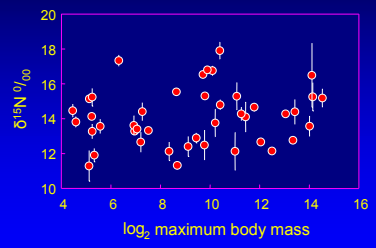


Species identity, body size and trophic role



Species identity, body size and trophic role

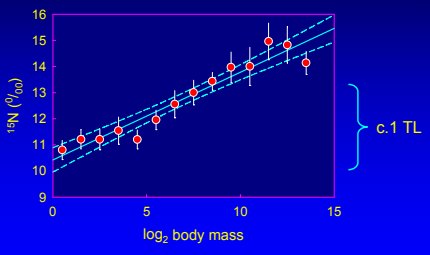
Cross species relationships between $\delta^{15}N$ and body size



Source: Marine Ecology Progress Series 226: 77-85 (2002)

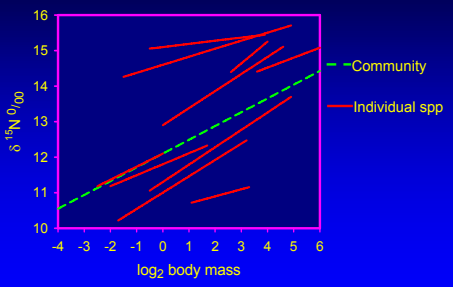
Species identity, body size and trophic role

'All individuals' relationships between $\delta^{15}N$ and body size



Source: Marine Ecology Progress Series 226: 77-85 (2002)

Species identity, body size and trophic role



Mean size and individual size

Mean size of often used as a proxy for a species' attributes

Does it reflect patterns of energy use in a consistent way?

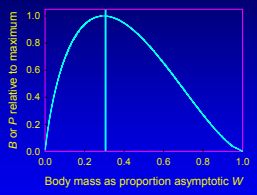
Species identity, body size and trophic role

Species' relationships between $\delta^{15}N$ and body size

Source: J Anim Ecology 76: 72-82 (2007)

Mean size and individual size

The body size at which a population attains maximum biomass (B) can be expressed as a function of the natural mortality and growth rate



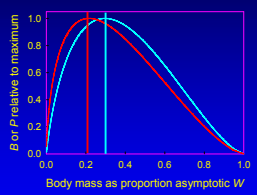
Source: Holt (1958) ICNAF Spec Publ. 1

Species identity, body size and trophic role

Body mass at trophic level 4.3

Mean size and individual size

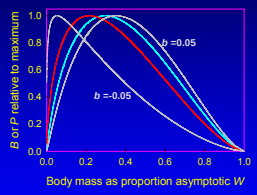
Related expressions can be derived for the body size at which the energy required to support a population is greatest (W_{me})



Source: J Animal Ecology 76: 72-82 (2007)

Mean size and individual size

Related expressions can be derived for the body size at which the energy required to support a population is greatest (W_{me})



The relationship between W_{me} *and* W_{∞} depends on transfer efficiency (ε), the relationship between body size and trophic level (b), natural mortality (M) and the growth rate (k)

Source: J Animal Ecology 76: 72-82 (2007)

Size-structure in food webs

Mean size and individual size

Relationships between $\delta^{15}N$ and body size

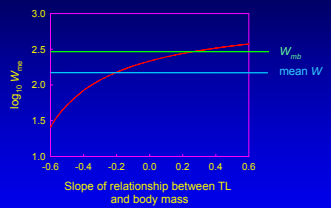
Source: J Anim Ecology 76: 72-82 (2007)

Size-structure in food webs

- Relationship with patterns of energy flux
- Evidence for component energy pathways
- Consequences of oversimplification

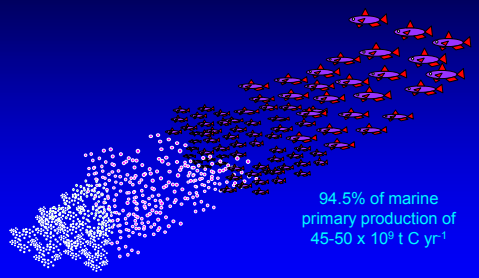
Mean size and individual size

W_{me} as a function of b in relation to mean weight and W_{mb}



Mean size is not consistently related to the energetic requirements of a population

Size-structure in food webs

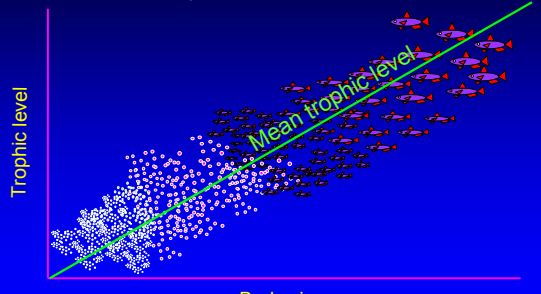


94.5% of marine primary production of 45-50 x 10^9 t C yr^{-1}

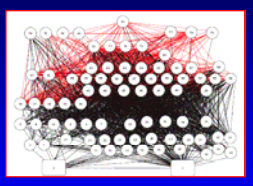
After: Sheldon, Kerr, Boudreau, Dickie, Pope and others

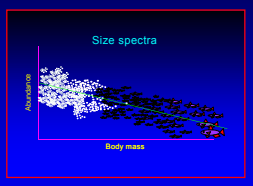
Size-structure in food webs

Body size and trophic level



Size-structure in food webs

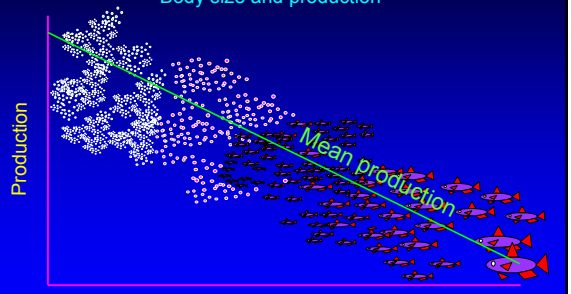




Source: Link (2002) Mar Ecol Prog Ser 230: 1-9

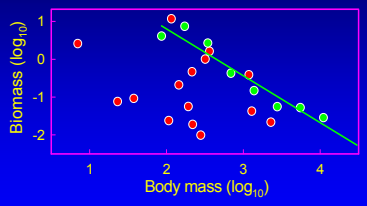
Size-structure in food webs

Body size and production



Size-structure in food webs

Size-spectra: all individuals binned by body mass class, not mean body mass vs mean biomass



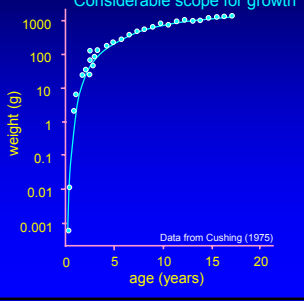
Size-structure in food webs

Why do we see the observed patterns?

Small primary producers

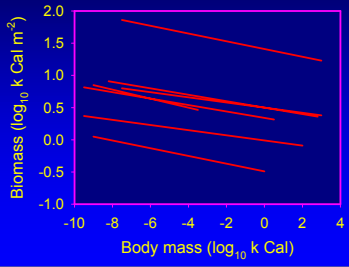
Size-based predation

Considerable scope for growth



Size-structure in food webs

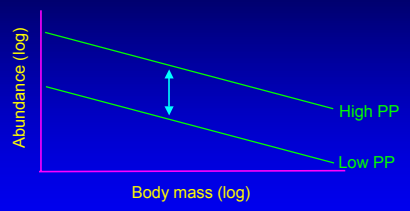
Size spectra



Source: Boudreau and Dickie (1992) Can J Fish Aquat Sci 49: 1528-1538

Size-structure in food webs

Size spectra



Source: Boudreau and Dickie (1992) Can J Fish Aquat Sci 49: 1528-1538

Size-structure in food webs

Predicting size-spectrum slopes from energy availability

In size structured food webs, energy use will decrease with M as a function of TE and PPMR

Source: Cyr (2000) and Brown & Gillooly (2003) PNAS 100: 1467-1468

Size-structure in food webs

Slopes of size-spectra are relatively predictable from knowledge of the energy available to different size classes of animals

Size-structure in food webs

Predicting size-spectrum slopes from energy availability

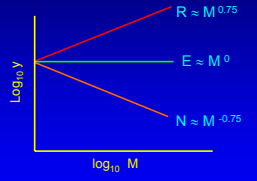
In size structured food webs, energy use will decrease with M as a function of TE and PPMR

….. and thus estimates of TE and PPMR, coupled with scaling theory, might be used to predict the slopes of size-spectra

Source: Brown & Gillooly (2003) PNAS 100: 1467-1468

Size-structure in food webs

Predicting size-spectrum slopes from energy availability



In communities that share a common energy source, energy use may be independent of body mass:

the energy equivalence hypothesis of Damuth (1981)

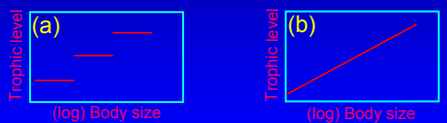
But, in size structured food webs, individuals do not share a common energy source

Source: Damuth (1981) Nature 290: 699-700

Size-structure in food webs

Predicting size-spectrum slopes from energy availability

This approach can be developed and applied to food webs where trophic levels are not discrete (a), but a continuous linear function of body size (b)



Source: Jennings & Mackinson (2003) Ecology Letters 6: 971-974

Size-structure in food webs

Predicting size-spectrum slopes from energy availability

Testing the theory:

Estimate abundance and trophic level of all animals of 2- 512 g in a size-based food web:

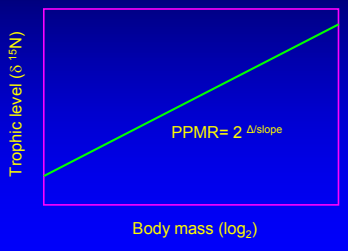
Fish: acoustics, otter and beam trawls

Invertebrates: beam trawls, cores and dredges

… in order to determine the slope of the size-spectrum, TE and PPMR

Size-structure in food webs

Predicting predator-prey body mass ratios (PPMR)

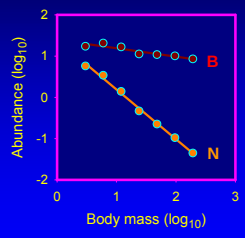


Source: Marine Ecology Progress Series 240: 11-20 (2002)

Size-structure in food webs

Predicting size-spectrum slopes from energy availability

Testing the theory:



Scaling of B	
Observed	Predicted
M -0.20	M -0.24
Scaling of N	
Observed	Predicted
M -1.20	M -1.24

Source: Jennings & Mackinson (2003) Ecology Letters 6: 971-974

Size-structure in food webs

Predicting predator-prey body mass ratios (PPMR)

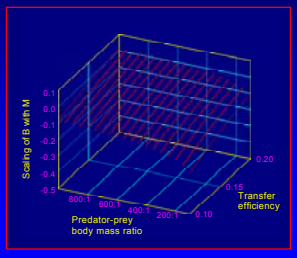
The advantage of stable isotope-based approach is that it gives community average PPMR and integrates variation through time, but

1) sampling requirements are prodigious
2) relatively few applications to date

Diet data provide a complementary approach and good global coverage (Cohen et al., 1993; Brose et al., 2005; Barnes et al., 2008)- although they tend to be collected over short time periods

Size-structure in food webs

Effects of changing PPMR and TE on the predicted slope of the size-spectrum



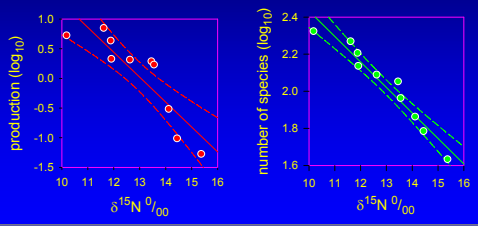
… therefore quite strong constraints on possible slopes in real systems

Size-structure in food webs

Estimating transfer efficiency and species numbers at different trophic levels

Transfer efficiency= $10^{\Delta * slope}$

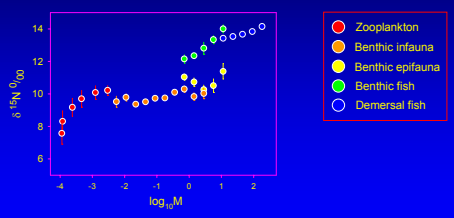
Ratio predator diversity: prey diversity = $10^{\Delta * slope}$



Source: Marine Ecology Progress Series 240: 11-20 (2002)

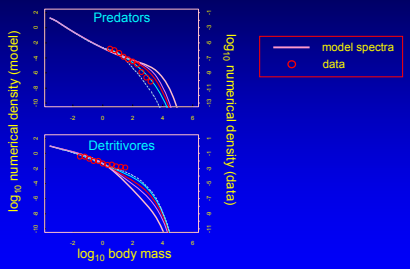
Size-structure in food webs

Trophic level vs body mass relationships in subsets of the food web



Size-structure in food webs

Dynamic model of coupled predator and detritivore spectra



Source: Blanchard et al (submitted)

Size-structure in food webs

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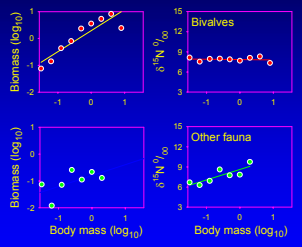
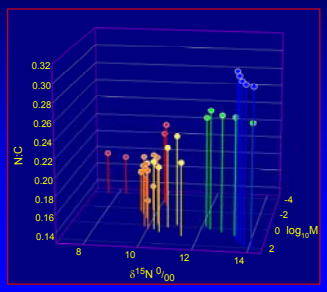


The more positive SS slopes for bivalves are consistent with the prediction that energy is shared

Source: Oecologia 150: 282-290 (2006)

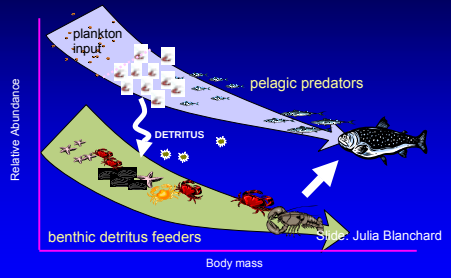
Size-structure in food webs

Body size and stochiometry



Size-structure in food webs

Accounting for coupling in models



Source: Blanchard et al (submitted)

Applications

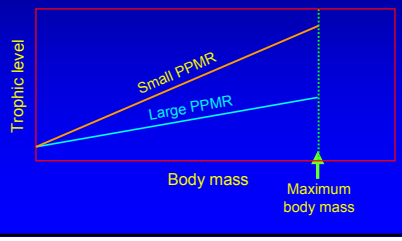
Simplified size-based representations of food webs allow application of the methods despite:

1. Variations in species composition
2. Differences in the physical environment

Applications

Factors affecting food chain length

In a community of given size and species composition, maximum food chain length will be longer when predator-prey body mass ratios are smaller



Linking food chain length and environment

Results

Mean predator-prey body mass ratios are smaller in more variable environments

Mean predator-prey body mass ratios are smaller in longer food chains

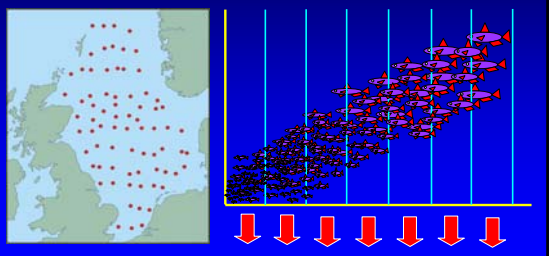
So, we predict that stable environments are associated with steeper size-spectra

Consequence: less available production for a given primary production in more stable environments

Source: Proc Roy Soc B 270: 1413-1417 (2003)

Linking food chain length and environment

1. Estimate PPMR from size-based $\delta^{15}N$ analysis of tissue samples at 75 stations throughout the North Sea



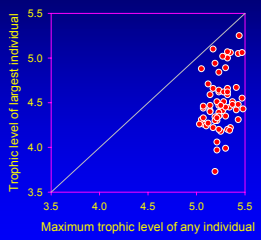
Linking low and high trophic levels

Regularities in the processes that determine size structure allow for wide-ranging application of size-based methods-despite variations in species composition and environment

There are now several examples of approaches that use these regularities as a basis for linking phytoplankton production to production at higher trophic levels (Maury et al., 2007; Blanchard et al. subm)

Linking food chain length and environment

2. Estimate maximum food chain length at the same stations based on $\delta^{15}N$ vs length relationships for all species



Source: Proc Roy Soc B 270: 1413-1417 (2003)

Global biomass estimates

Inputs:

Primary production

Temperature

Predator-prey size ratios

Transfer efficiency

Global biomass estimates

Locate midpoint of phytoplankton size range, based on relationship between total and picoplankton production

↓

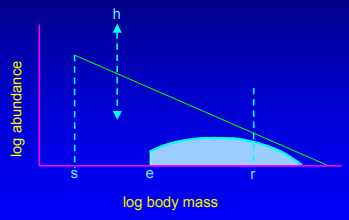
Define biomass at midpoint size class (and hence spectrum intercept) from transfer efficiency, body mass and temperature

↓

Define slope of size spectrum from transfer efficiency and predator-prey mass ratio

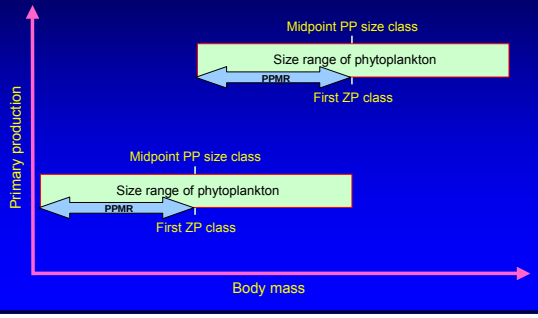
Global biomass estimates

Separating the fishy component



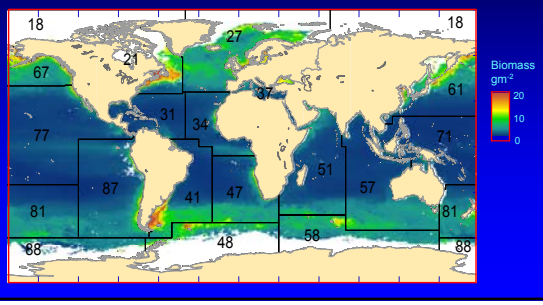
Global biomass estimates

Establishing intercepts of size- spectra



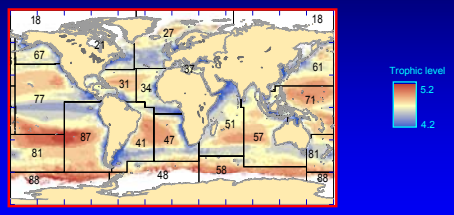
Global biomass estimates

Fish biomass



Global biomass estimates

Variation in food chain length



Source: relationships based on Agawin (2000) Limn Ocean 45: 591-600

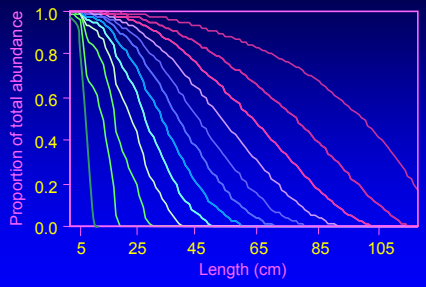
Size and species-based analyses of food webs

Some thoughts about the future

1. How do determinate and indeterminate growth patterns influence the contribution of size and species identity to observed food web structures and processes?
2. How do we incorporate species identity into size-based analyses and models? and should we account for variability in competitive ability among species classified by size?

Including species identity in size-based models

e.g. Duplisea & Bravington, Pope et al, Hall et al, Andersen & Beyer



Source: Pope et al (2006) ICES J Mar Sci 63: 1029-1044

Size and species-based analyses of food webs

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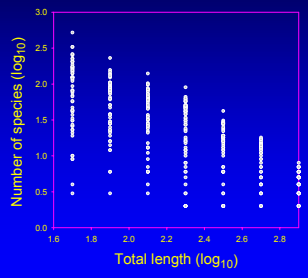
2. How do we incorporate species identity into size-based analyses and models? and should we account for variability in competitive ability among species classified by size?
3. How should we retain information on the size distributions of individuals in food web analysis?

Including species identity in size-based models

Next steps- account for species relative abundances and variation in species specific traits



Size and species-based analyses of food webs

… but not to forget that the 'right' level of complexity- and the emphasis given to body size or species identity- depends on the questions we want to address

… and the preferred accuracy or precision of the answer

Including species identity in size-based models

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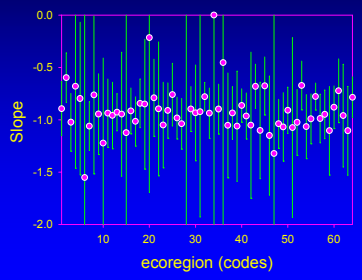

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