Stable Isotope Ecology

Chapter 1 Introduction

College of Marine Sciences Shanghai Ocean University

2017

Glossary

1. Fractionation : 分馏; 分画; 분류
2. Photosynthesis: 光合作用；光合成；광합성
3. Spectrograph：光谱仪；スペクトログラフ；분광기
4. Herbivore：草食动物；草食動物；초식 동물
5. Carnivore：肉食动物；肉食動物；육식성의
6. Niche：生态位；ニッチ；벽감
7. Otolith：耳石；耳石；이석

From Google translate

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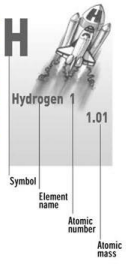
PERIODIC TABLE of the ELEMENTS

DEPARTMENT OF SCIENCE AND TECHNOLOGY

ALKALI METALS
ALKALI EARTH METALS
TRANSITION METALS
OTHER METALS
OTHER NONMETALS
HALOGENS
NOBLE GASSES
RARE EARTH METALS

At room temperature the element is:
Gas
Liquid
Natural solid
Man-made solid [synthetic]

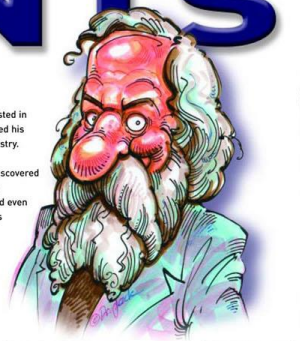


DMITRI MENDELEYEV (1834 – 1907)

The Russian chemist, Dmitri Mendeleyev, was the first to observe that if elements were listed in order of atomic mass, they showed regular (periodical) repeating properties. He formulated his discovery in a periodic table of elements, now regarded as the backbone of modern chemistry.

The crowning achievement of Mendeleyev's periodic table lay in his prophecy of then, undiscovered elements. In 1869, the year he published his periodic classification, the elements gallium, germanium and scandium were unknown. Mendeleyev left spaces for them in his table and even predicted their atomic masses and other chemical properties. Six years later, gallium was discovered and his predictions were found to be accurate. Other discoveries followed and their chemical behaviour matched that predicted by Mendeleyev.

This remarkable man, the youngest in a family of 17 children, has left the scientific community with a classification system so powerful that it became the cornerstone in chemistry teaching and the prediction of new elements ever since.
In 1955, element 101 was named after him: Md, Mendelevium.



IA 1	IIA 2	IIIB 3	IVB 4	VB 5	VIB 6	VIIB 7	VIII 8	VIII 9	VIII 10	IB 11	IIB 12	IIIA 13	IVA 14	VA 15	VIA 16	VIIA 17	VIII A 18
1 H Hydrogen 1 1.01																	2 He Helium 2 4.00
2 lithium 3 6.94 Li	4 Be Beryllium 4 9.01											5 B Boron 5 10.81	6 C Carbon 6 12.01	7 N Nitrogen 7 14.01	8 O Oxygen 8 16.00	9 F Fluorine 9 19.00	10 Ne Neon 10 20.18
3 Na Sodium 11 22.99	12 Mg Magnesium 12 24.31											13 Al Aluminium 13 26.98	14 Si Silicon 14 28.09	15 P Phosphorus 15 30.97	16 S Sulphur 16 32.06	17 Cl Chlorine 17 35.45	18 Ar Argon 18 39.95
4 K Potassium 19 39.10	20 Ca Calcium 20 40.08	21 Sc Scandium 21 44.96	22 Ti Titanium 22 47.88	23 V Vanadium 23 50.94	24 Cr Chromium 24 52.00	25 Mn Manganese 25 54.94	26 Fe Iron 26 55.85	27 Co Cobalt 27 58.93	28 Ni Nickel 28 58.69	29 Cu Copper 29 63.55	30 Zn Zinc 30 65.39	31 Ga Gallium 31 69.72	32 Ge Germanium 32 72.61	33 As Arsenic 33 74.92	34 Se Selenium 34 78.96	35 Br Bromine 35 79.90	36 Kr Krypton 36 83.80
5 Rb Rubidium 37 85.47	38 Sr Strontium 38 87.62	39 Y Yttrium 39 88.91	40 Zr Zirconium 40 91.22	41 Nb Niobium 41 92.91	42 Mo Molybdenum 42 95.94	43 Tc Technetium 43 (98)	44 Ru Ruthenium 44 101.07	45 Rh Rhodium 45 102.91	46 Pd Palladium 46 106.42	47 Ag Silver 47 107.87	48 Cd Cadmium 48 112.41	49 In Indium 49 114.82	50 Sn Tin 50 118.71	51 Sb Antimony 51 121.76	52 Te Tellurium 52 127.60	53 I Iodine 53 126.90	54 Xe Xenon 54 131.29
6 Cs Caesium 55 132.91	56 Ba Barium 56 137.33	Lanthanide Series	72 Hf Hafnium 72 178.49	73 Ta Tantalum 73 180.95	74 W Tungsten 74 183.85	75 Re Rhenium 75 186.21	76 Os Osmium 76 190.23	77 Ir Iridium 77 192.22	78 Pt Platinum 78 195.08	79 Au Gold 79 196.97	80 Hg Mercury 80 200.59	81 Tl Thallium 81 204.38	82 Pb Lead 82 207.20	83 Bi Bismuth 83 208.98	84 Po Polonium 84 (209)	85 At Astatine 85 (210)	86 Rn Radon 86 (222)
7 Fr Francium 87 (223)	88 Ra Radium 88 (226)	Actinide Series	104 Rf Rutherfordium 104 (261)	105 Db Dubnium 105 (262)	106 Sg Seaborgium 106 (263)	107 Bh Bohrium 107 (262)	108 Hs Hassium 108 (265)	109 Mt Meitnerium 109 (266)									

La Lanthanum 57 138.91	Ce Cerium 58 140.12	Pr Praseodymium 59 140.90	Nd Neodymium 60 144.24	Pm Promethium 61 (145)	Sm Samarium 62 150.36	Eu Europium 63 151.96	Gd Gadolinium 64 157.25	Tb Terbium 65 158.92	Dy Dysprosium 66 162.50	Ho Holmium 67 164.93	Er Erbium 68 167.26	Tm Thulium 69 168.93	Yb Ytterbium 70 173.04	Lu Lutetium 71 174.96
Ac Actinium 89 227.02	Th Thorium 90 232.03	Pa Protactinium 91 231.03	U Uranium 92 238.02	Np Neptunium 93 (237)	Pu Plutonium 94 (244)	Am Americium 95 (243)	Cm Curium 96 (247)	Bk Berkelium 97 (247)	Cf Californium 98 (251)	Es Einsteinium 99 (254)	Fm Fermium 100 (257)	Md Mendelevium 101 (258)	No Nobelium 102 (259)	Lr Lawrencium 103 (260)

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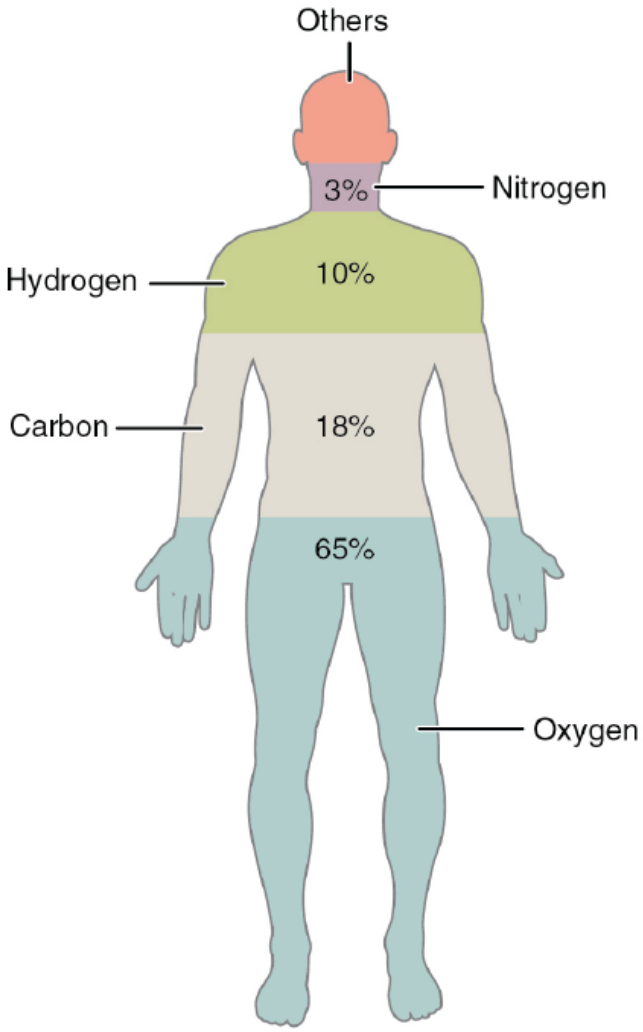
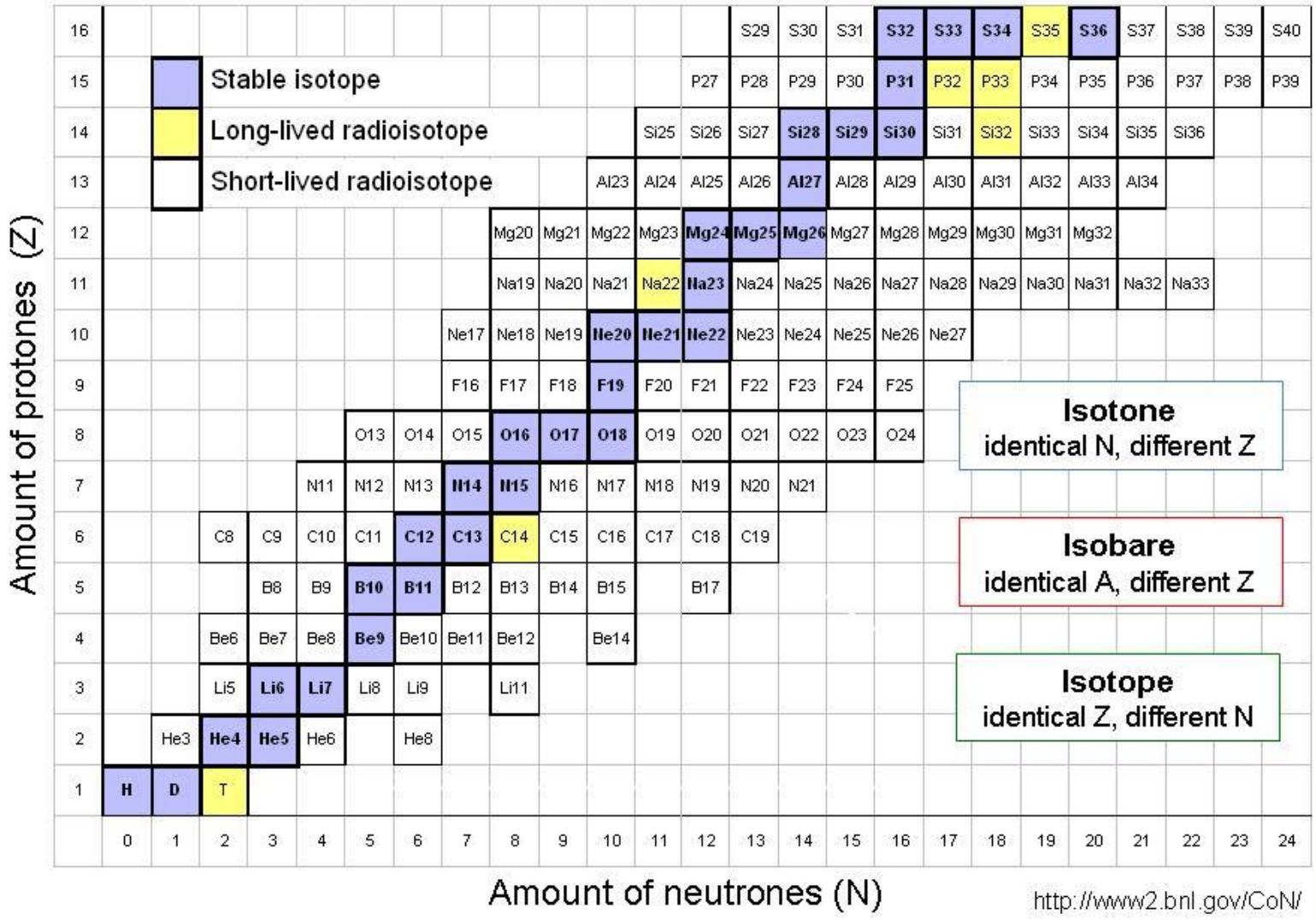
Elements



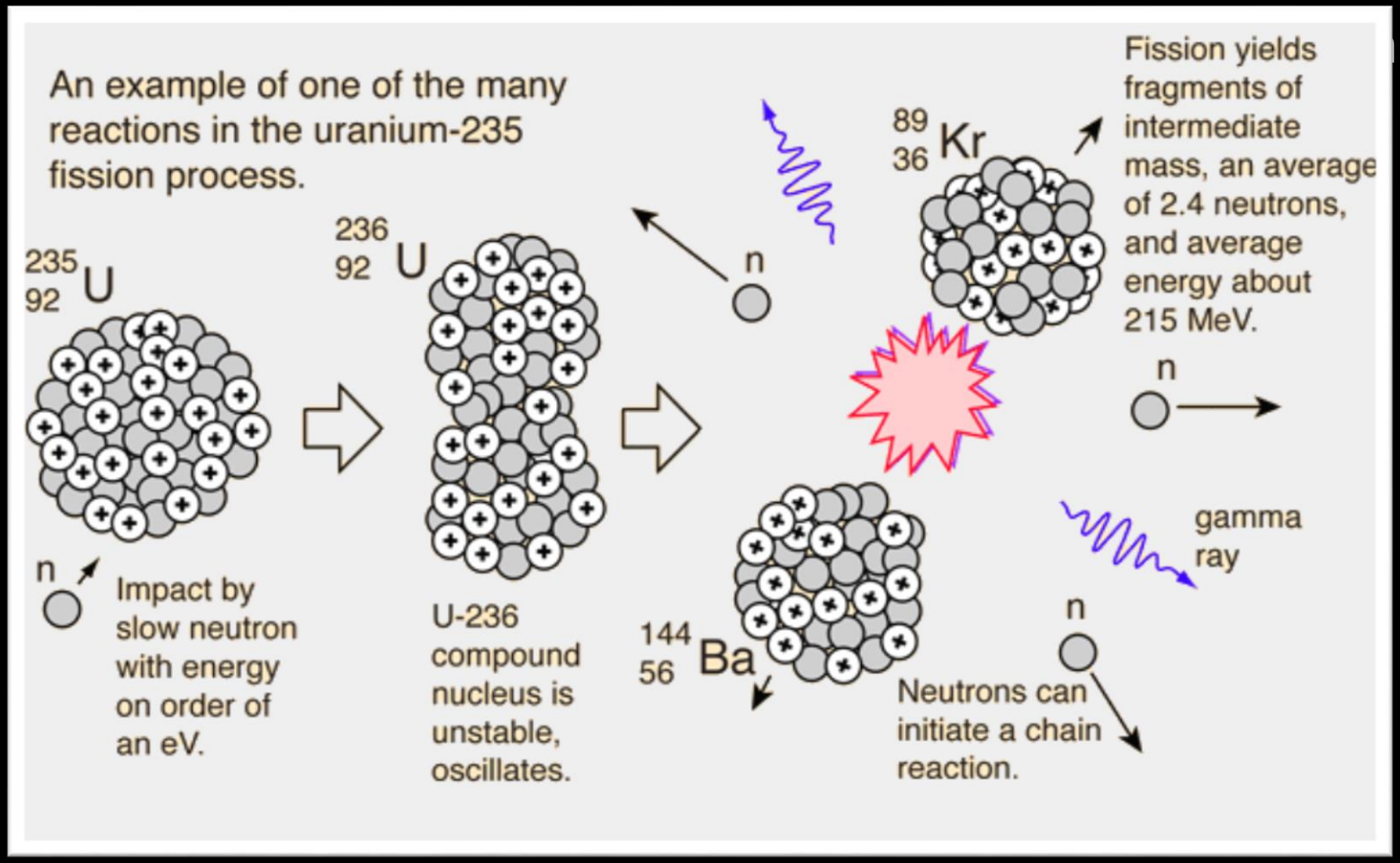
Element	Symbol	Percentage in Body
Oxygen	O	65.0
Carbon	C	18.5
Hydrogen	H	9.5
Nitrogen	N	3.2
Calcium	Ca	1.5
Phosphorus	P	1.0
Potassium	K	0.4
Sulfur	S	0.3
Sodium	Na	0.2
Chlorine	Cl	0.2
Magnesium	Mg	0.1
Trace elements include boron (B), chromium (Cr), cobalt (Co), copper (Cu), fluorine (F), iodine (I), iron (Fe), manganese (Mn), molybdenum (Mo), selenium (Se), silicon (Si), tin (Sn), vanadium (V), and zinc (Zn).		less than 1.0

Isotopes

$$ {}^{A}_{Z}X_{N} \qquad A = Z+N $$

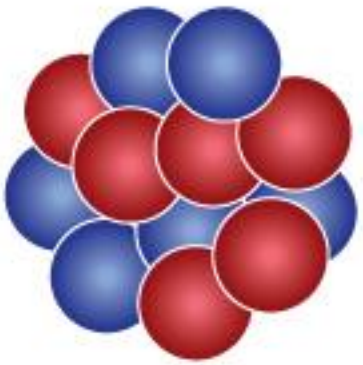


Isotope

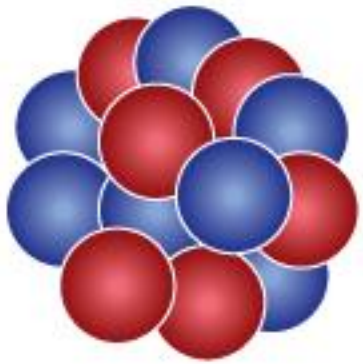

An example of one of the many reactions in the uranium-235 fission process.
235 92 U
n
Impact by slow neutron with energy on order of an eV.
236 92 U
U-236 compound nucleus is unstable, oscillates.
n
89 36 Kr
Fission yields fragments of intermediate mass, an average of 2.4 neutrons, and average energy about 215 MeV.
n
gamma ray
144 56 Ba
n
Neutrons can initiate a chain reaction.

Isotopes and Their Elements

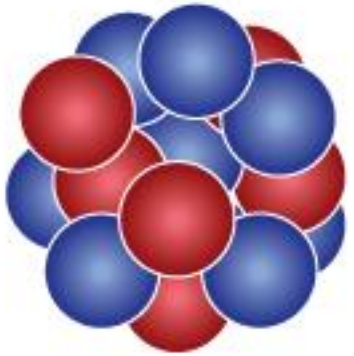
- er
- c
  nt



carbon-12
98.9%
6 protons
6 neutrons



carbon-13
1.1%
6 protons
7 neutrons

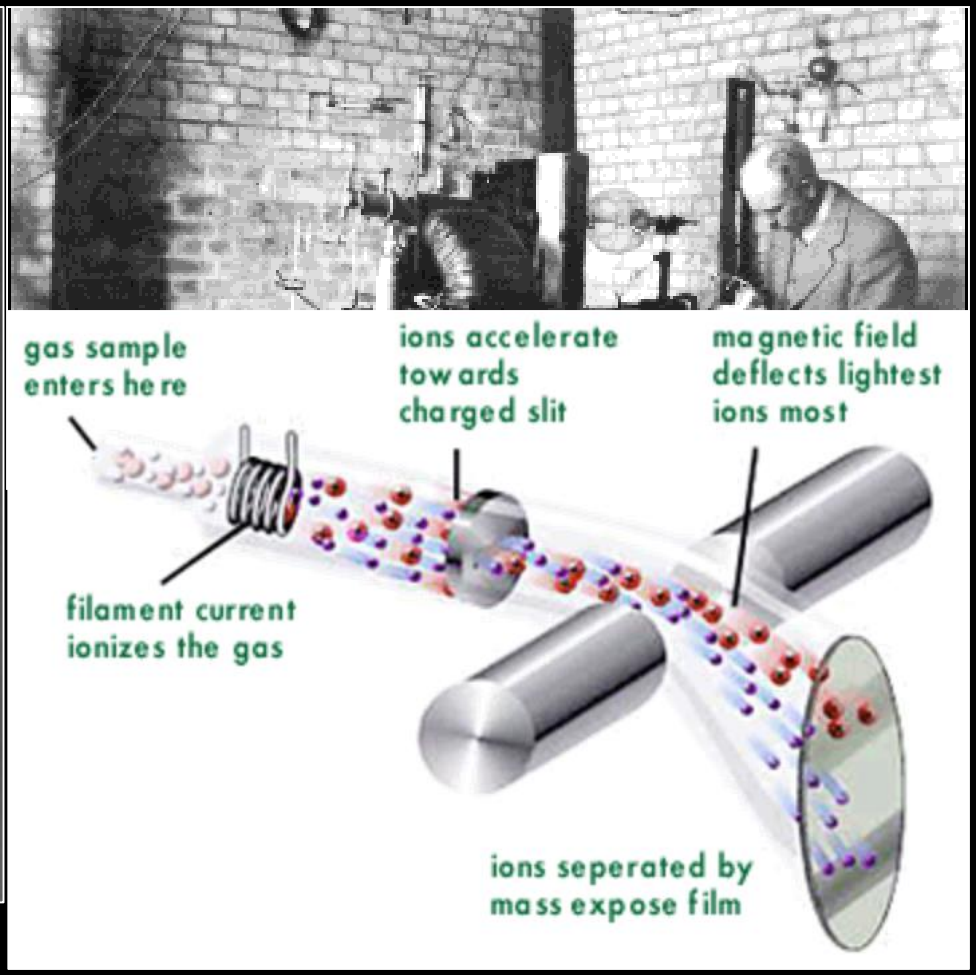


carbon-14
<0.1%
6 protons
8 neutrons

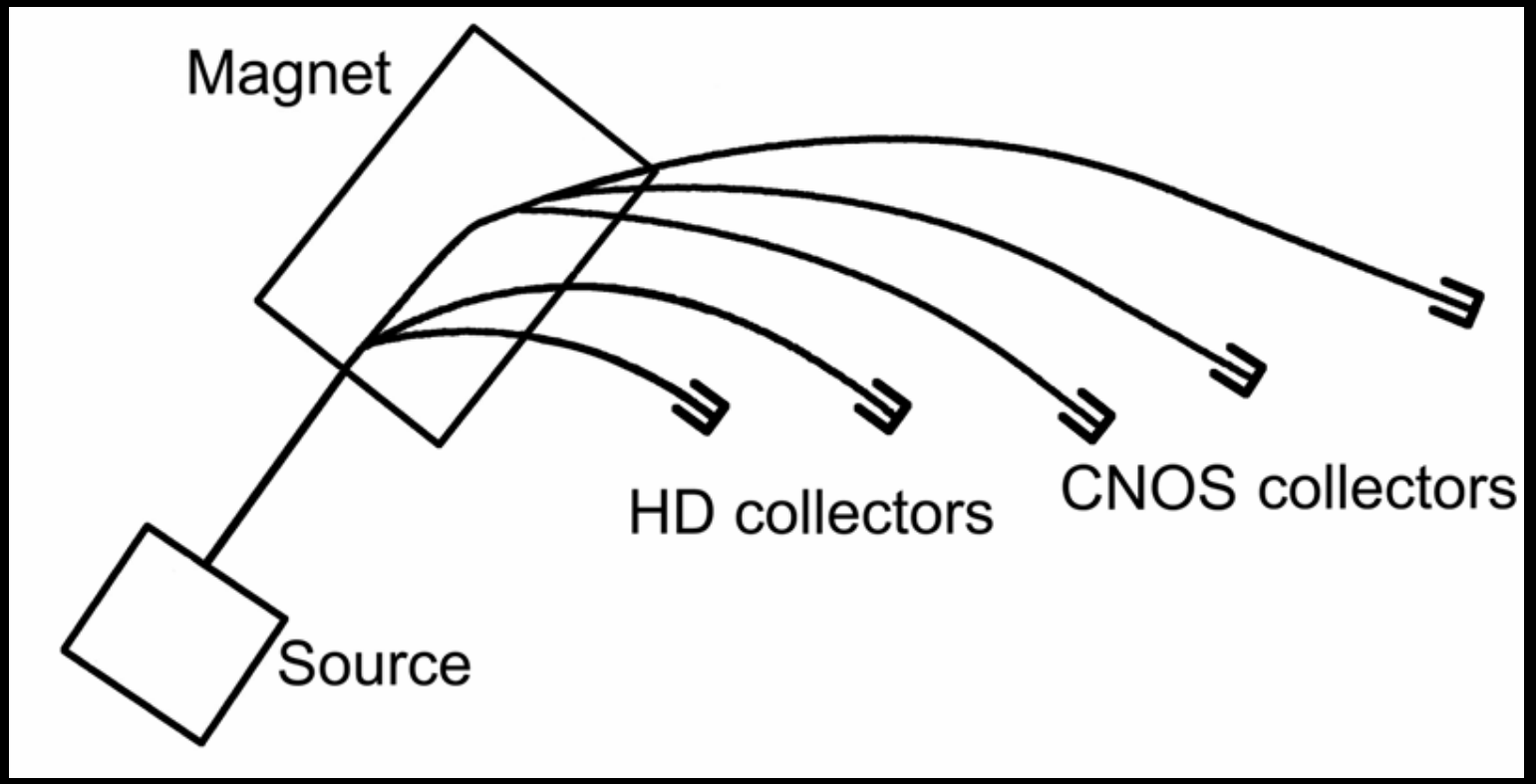
Isotopes and Their Elements

- Frederick Soddy first introduced the term "isotope" in a formal way during a speech to the British Royal Society on Feb 27, 1913. He won the 1921 Nobel Prize in Chemistry for "his investigations into the origin and nature of isotopes".

Francis W. Aston



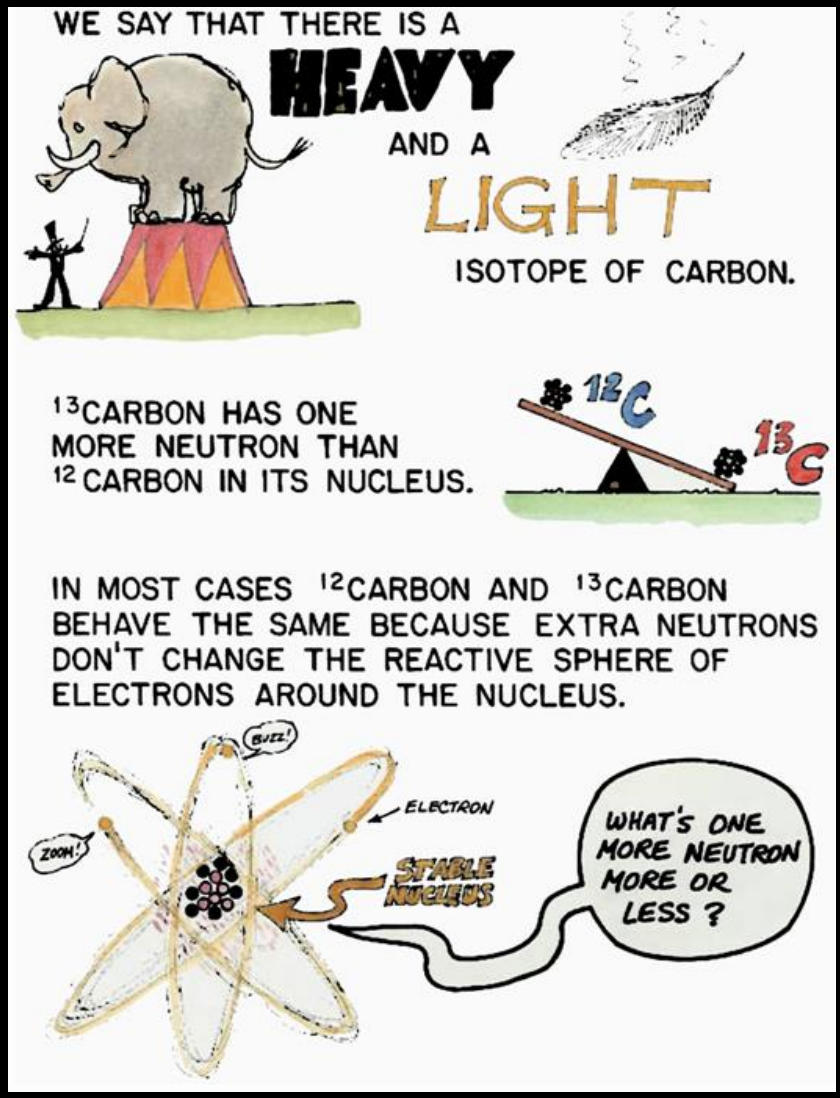
One neutron is measurable



Stable isotope

Stable isotope

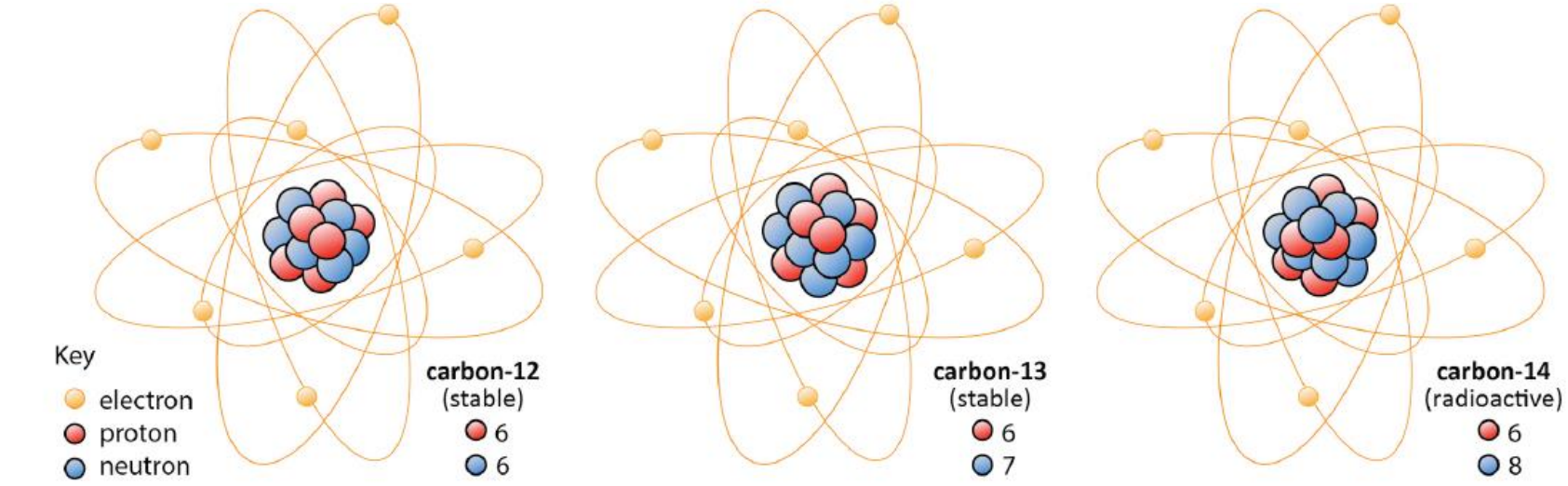
- Stable isotopes are safe isotopes that do not decay and unlike the radioactive isotopes, are not at all hazardous to human health. In fact, stable isotopes are quite abundant and natural parts of each one of us.



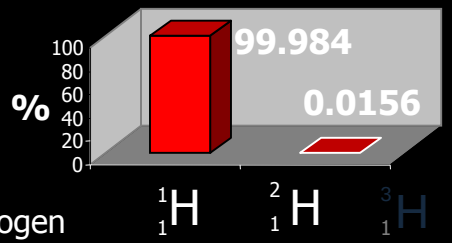
Stable Isotope

^{32}S	^{33}S	^{34}S	^{36}S
31.97207	32.97145	33.96786	35.96708
95.02%	0.75%	4.21%	0.02%
Stable	Stable	Stable	Stable

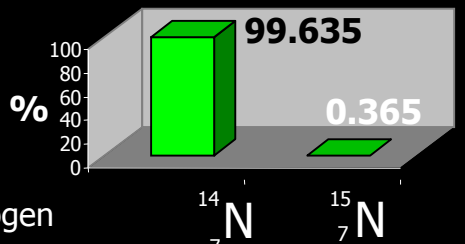
^{1}H	^{2}H	^{3}H
1.00794	2.0141	$t_{1/2}$ =12.32yrs
99.985%	0.015%	
Stable	Stable	Cosmogenic/ anthropogenic



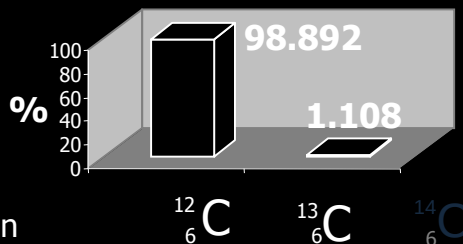
^{14}N	^{15}N	^{12}C	^{13}C	^{14}C	^{16}O	^{17}O	^{18}O
14.00307	15.0001	12.00000	13.00335	14.0	15.9949	16.9991	17.9991
99.63%	0.37%	98.89%	1.11%	$t_{1/2}$ = 5715yrs	99.76%	0.04%	0.20%
Stable	Stable	Stable	Stable	Radioactive Cosmogenic/ anthropogenic	Stable	Stable	Stable



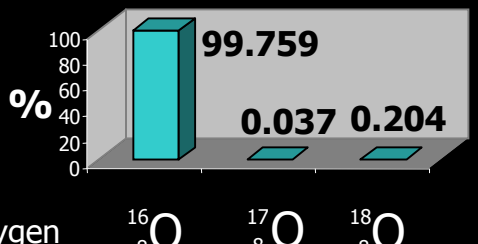
Hydrogen $^{1}_{1}H$ $^{2}_{1}H$ $^{3}_{1}H$



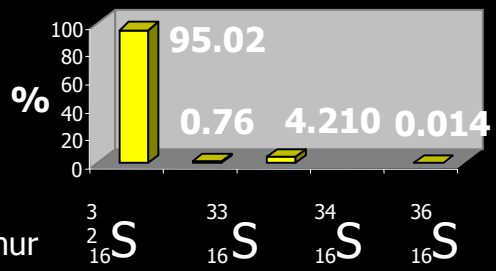
Nitrogen $^{14}_{7}N$ $^{15}_{7}N$



Carbon $^{12}_{6}C$ $^{13}_{6}C$ $^{14}_{6}C$

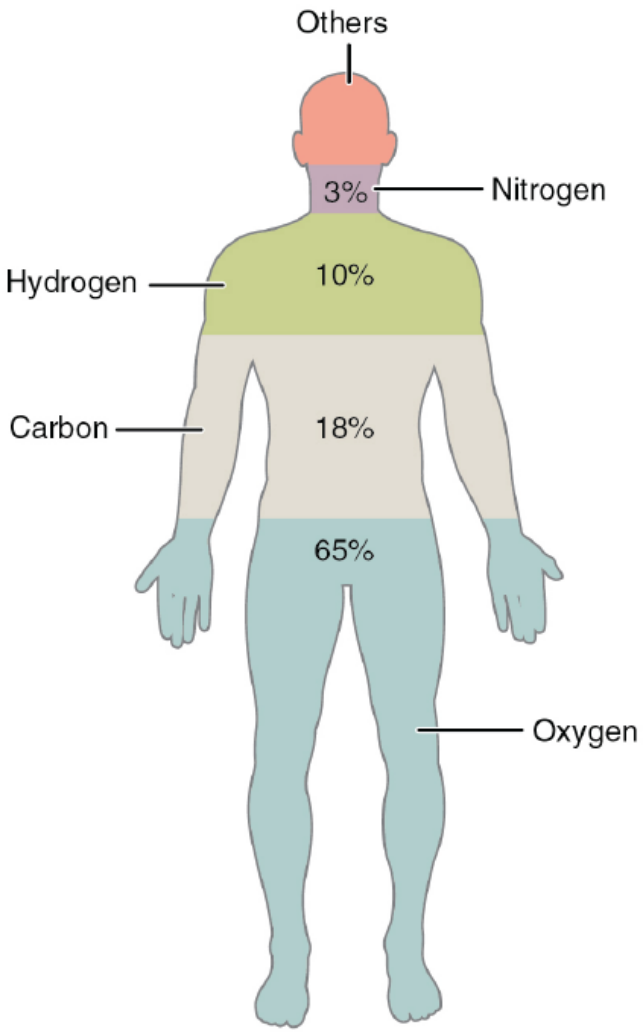


Oxygen $^{16}_{8}O$ $^{17}_{8}O$ $^{18}_{8}O$



Sulphur $^{32}_{16}S$ $^{33}_{16}S$ $^{34}_{16}S$ $^{36}_{16}S$

You Are What You Eat



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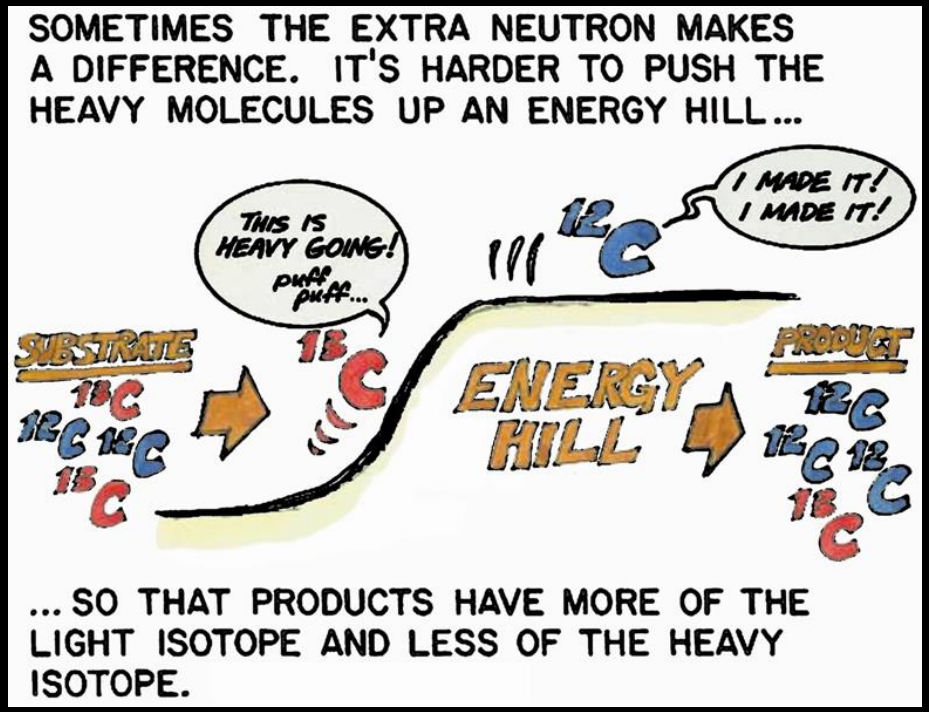
Mixing and Fractionation

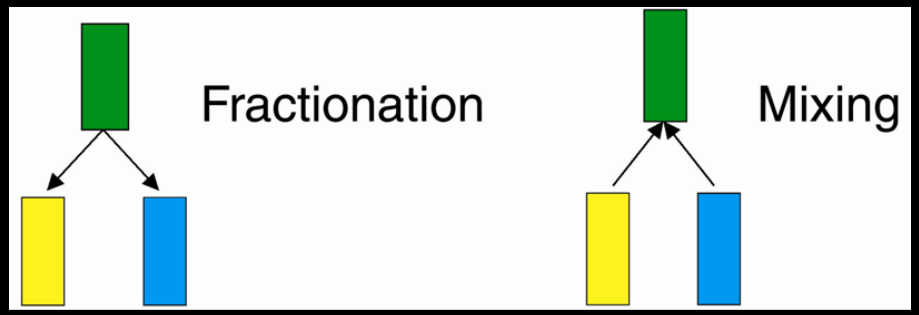
- In kinetic reactions, the light isotopes usually react faster.



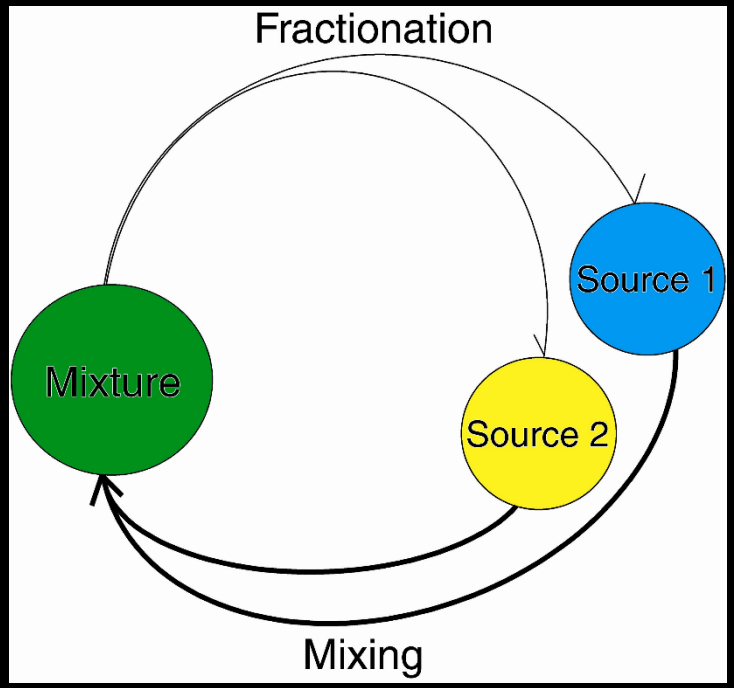
The extra neutron does make a very slight difference in some reactions; having an extra neutron usually results in slower reactions. This reaction difference is fractionation.

Mixing and Fractionation

- In kinetic reactions, the light isotopes usually react faster.
- In exchange reactions, heavy isotopes concentrate where bonds are strongest.



Fractionation splits apart mixtures to form source materials. These sources recombine via mixing. There is a strong general analogy between isotopes and colors, so that isotopes can be thought of as dyes or tracers. In this color example, fractionation separates green into yellow and blue components, with conversely yellow and blue mix to form green.



Fractionation

1. Fractionation: higher atomic mass means they are conserved during chemical reactions (evaporation, assimilation)
2. In kinetic reactions, the light isotopes usually react faster
3. In exchange reactions, heavy isotopes concentrate where bonds are strongest.
4. The isotope ratio of a consumer will reflect that of its prey
5. Used to infer ecological activities or animal migration.

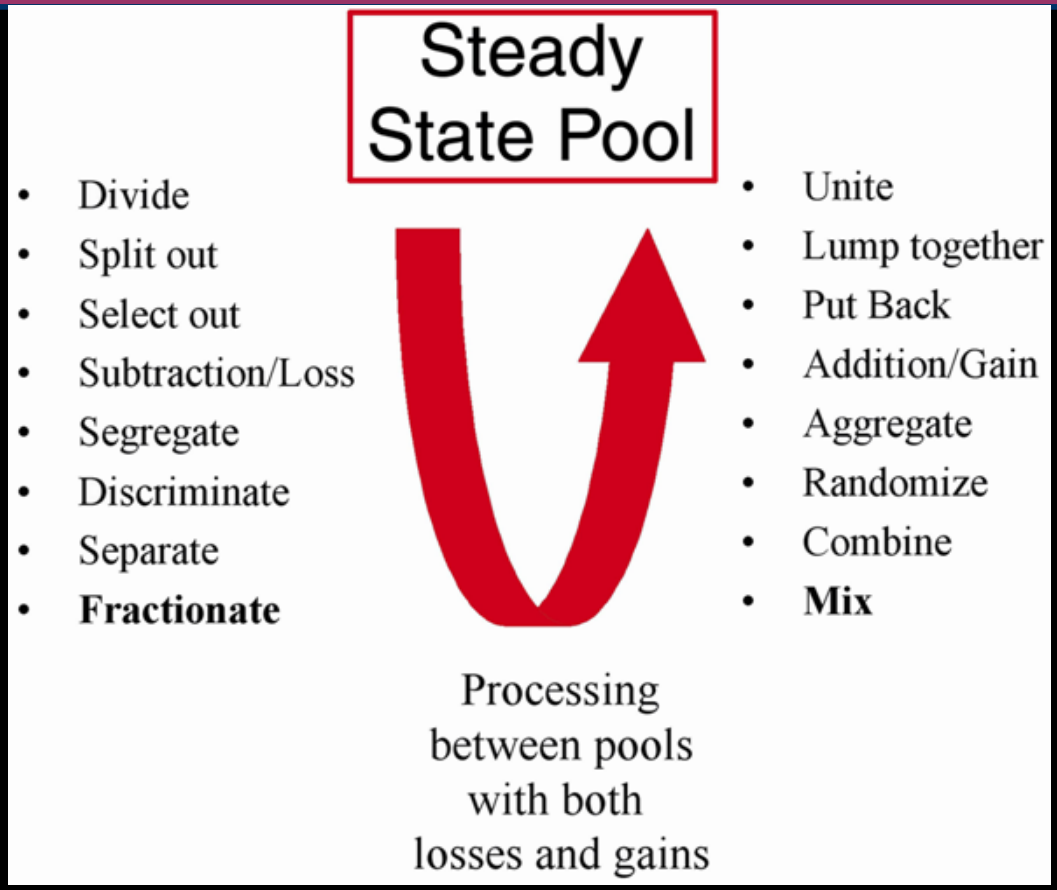
What is fractionation?

- Fractionation occurs during reactions and is commonly denoted by the Greek symbol Δ.
- The simplest equation of fractionation applies to a reaction where a product is formed from a source material,

$$\delta_{\mathrm{PRODUCT}} = \delta_{\mathrm{SOURCE}} - \Delta,$$

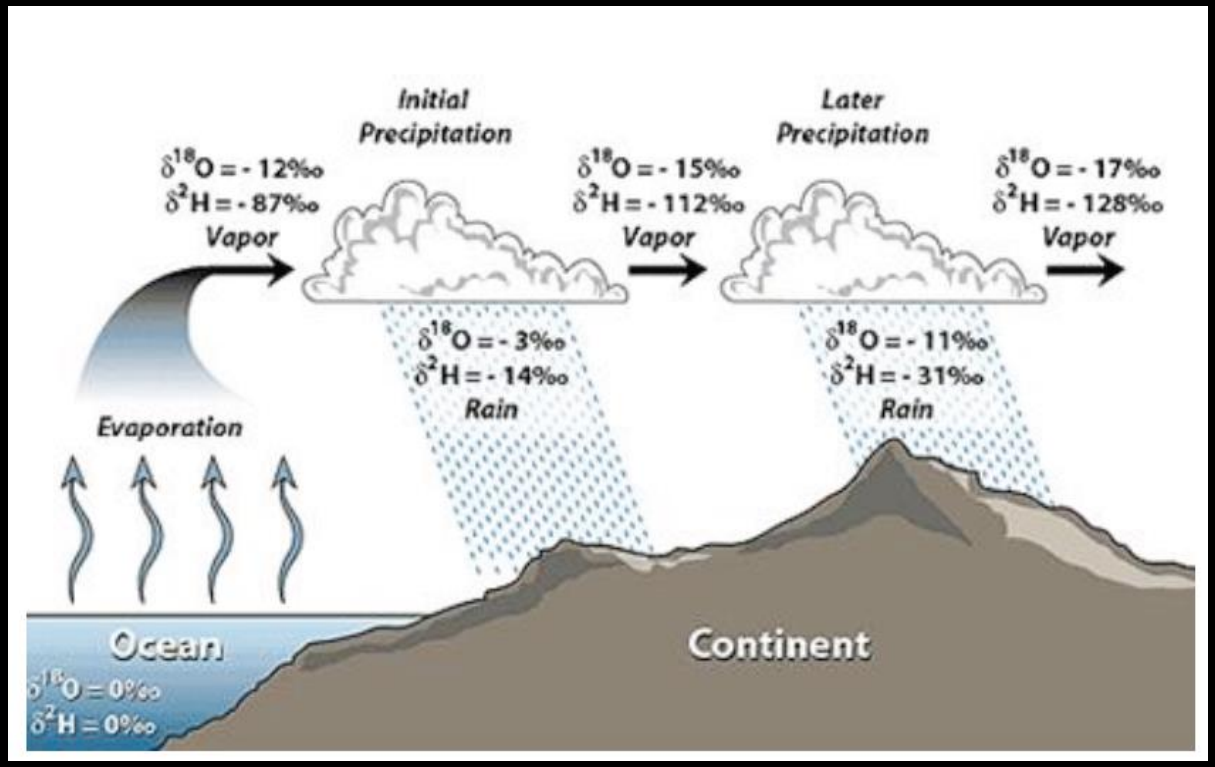
$$\Delta = \delta_{\mathrm{SOURCE}} - \delta_{\mathrm{PRODUCT}}.$$

Mixing and Fractionation



Fractionation and mixing together control isotope cycling and circulation. There are many words to use when thinking about isotope “fractionation” or “mixing”, and as long as you remember that these words do not imply human intervention, control or intent, most of these words can help you understand isotope cycling.

Why is fractionation useful



Terminology-Delta notation

Stable isotope measurement are presented as ratio relative to a known standard

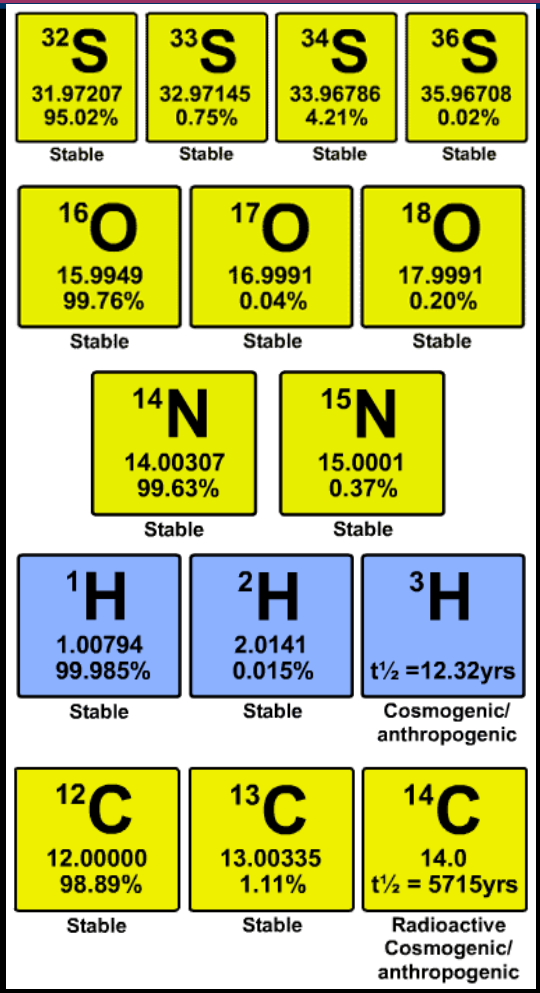
$$\delta^{a}X = \left(\frac{{}^{a}R_{x} - {}^{a}R_{std}}{{}^{a}R_{std}} \right) \times 1000$$

$$\delta^{13}C_{Sample} = \left\{ \frac{\left(\frac{^{13}C}{^{12}C}\right)_{Sample}}{\left(\frac{^{13}C}{^{12}C}\right)_{Reference}} - 1 \right\} * 1000$$

‰=per mill

Why are stable isotope useful

- 5 most commonly used isotopes in ecological research are carbon (^{13}C), nitrogen (^{15}N), hydrogen (^{2}H), oxygen (^{18}O) and Sulphur (^{34}S).
- Each isotope can be used to infer different ecological relationship.



Reference Standards

	Ratio, H/L	Value	%H	%L
Standard Mean Ocean Water	$^{2}H/^{1}H$	0.00015576	0.15574	99.984426
SMOW	$^{17}O/^{16}O$	0.0003799	0.03790	99.76206
	$^{18}O/^{16}O$	0.0020052	0.20004	99.76206
PeeDee Belemnite (PDB)	$^{13}C/^{12}C$	0.011180	1.1056	98.8944
and Vienna-PDB (VPDB)	$^{17}O/^{16}O$	0.0003859	0.0385	99.7553
	$^{18}O/^{16}O$	0.0020672	0.2062	99.7553
Air (AIR)	$^{15}N/^{14}N$	0.0036765	0.36630	99.63370
Canyon Diablo Troilite (CDT)	$^{33}S/^{32}S$	0.0078772	0.74865	95.03957
and Vienna-CDT	$^{34}S/^{32}S$	0.0441626	4.19719	95.03957
	$^{36}S/^{32}S$	0.0001533	0.01459	95.03957

Stable isotope in trophic ecology

You are <u>What</u> you eat (± a little bit)

Isotope Circulation in the Biosphere

- Photosynthesis is one of the important reactions governing isotope circulation in the biosphere.

Nitrogen ($\delta^{15}N$)

Ecology, 83(3), 2002, pp. 703–718

USING STABLE ISOTOPES TO ESTIMATE TROPHIC POSITION: MODELS, METHODS, AND ASSUMPTIONS

DAVID M. POST[1,2,3]

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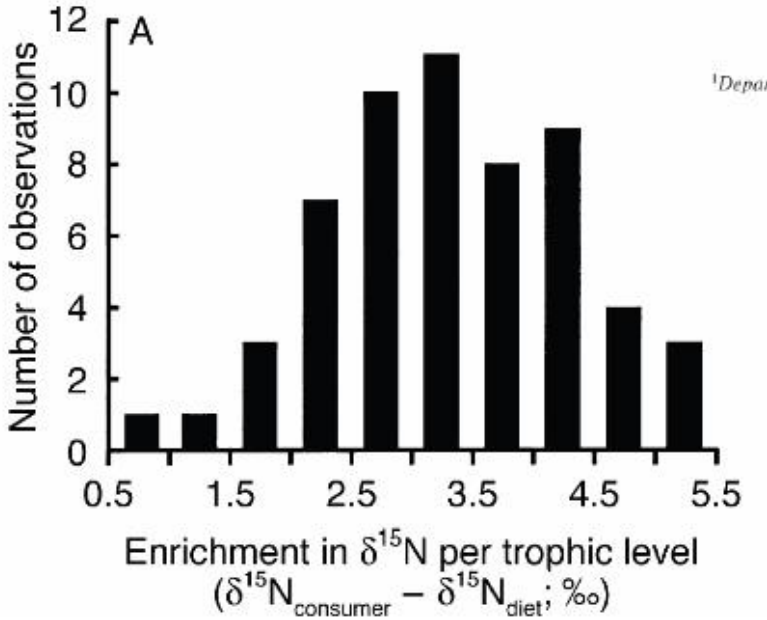
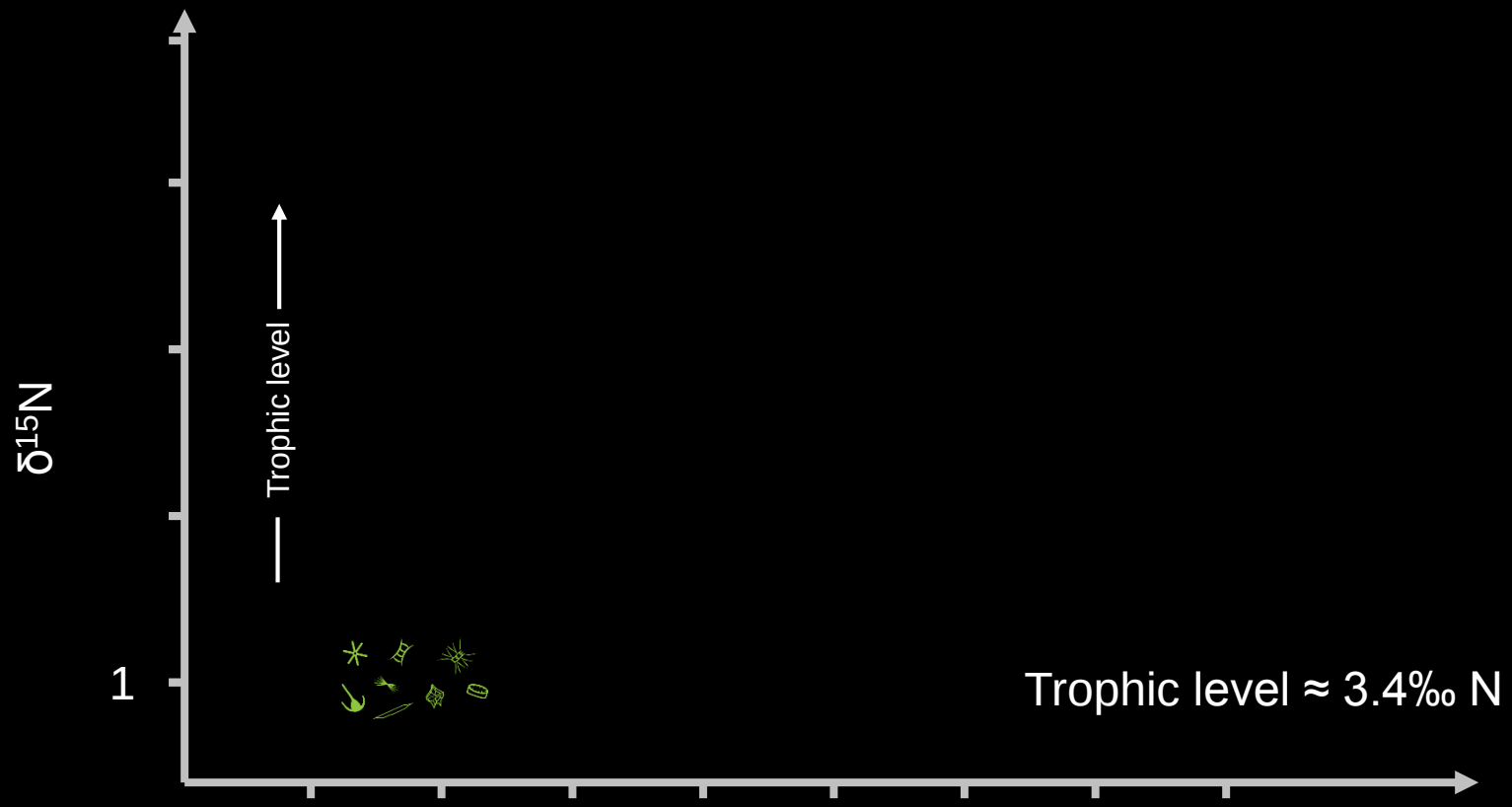
[2]*Institute for Ecosystem Studies, Box AB, Millbrook, New York 12545 USA*

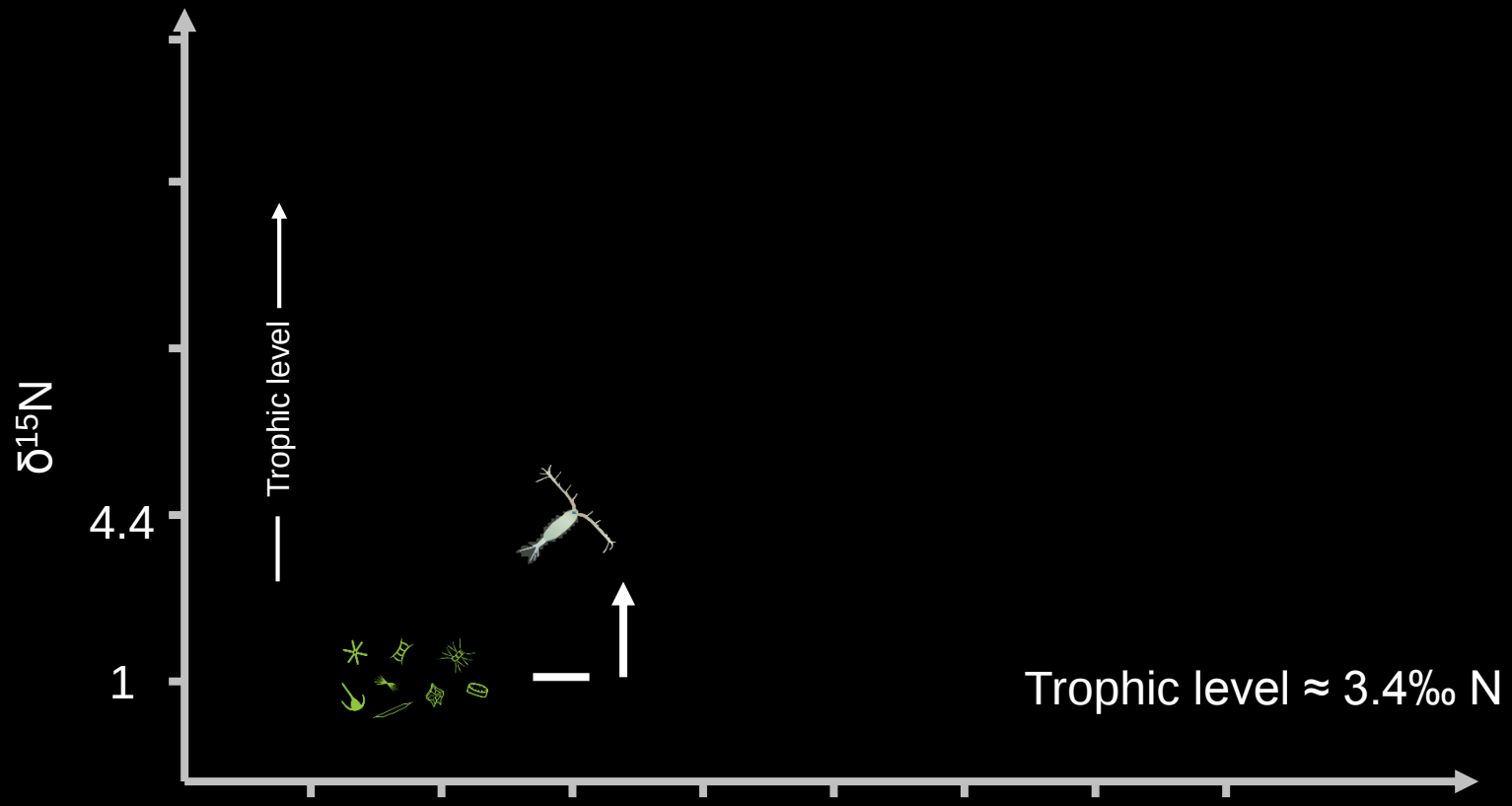


Enrichment ≈ 3.4‰ per trophic level

Nitrogen ($\delta^{15}N$)



Nitrogen ($\delta^{15}N$)



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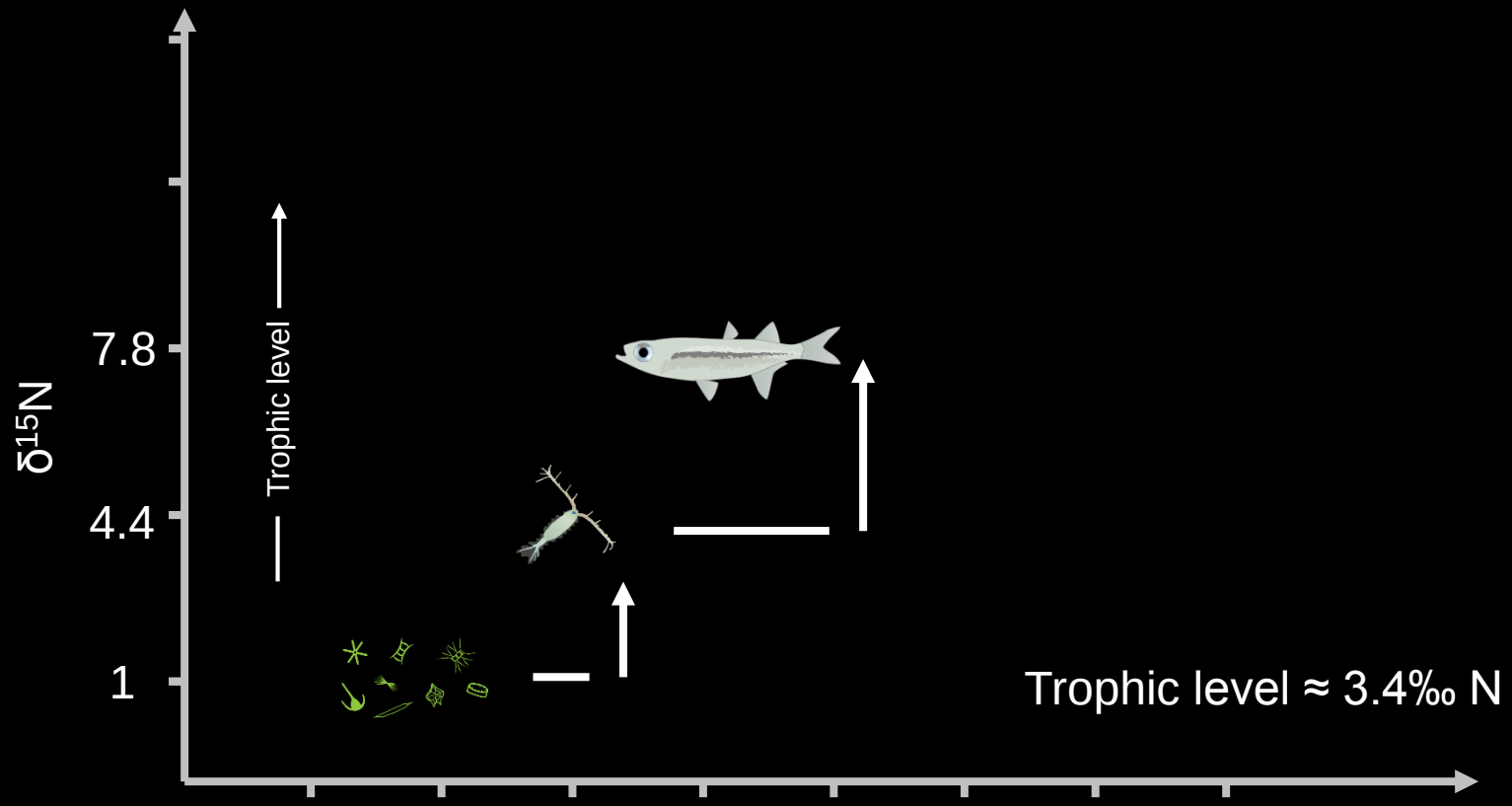

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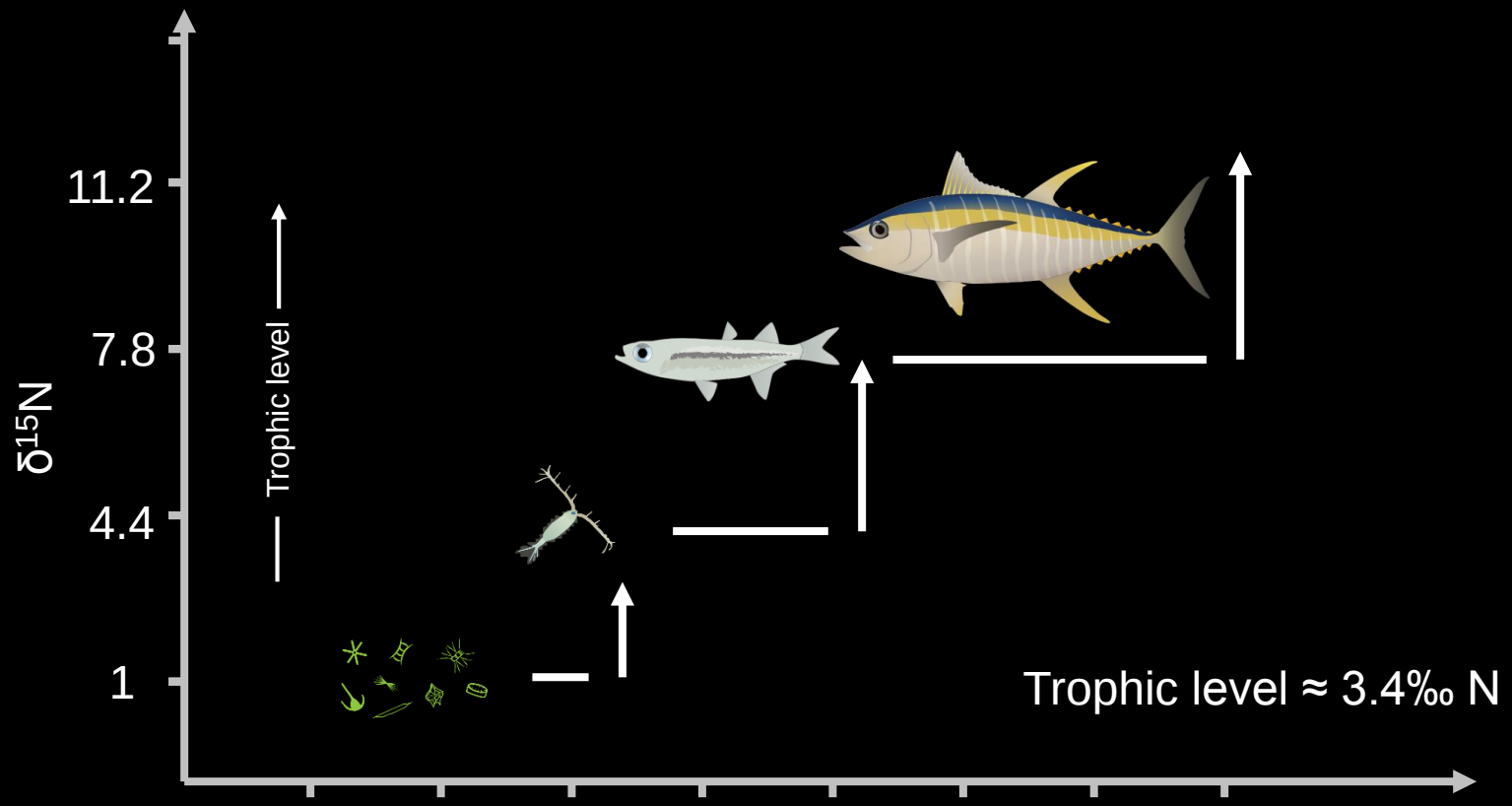
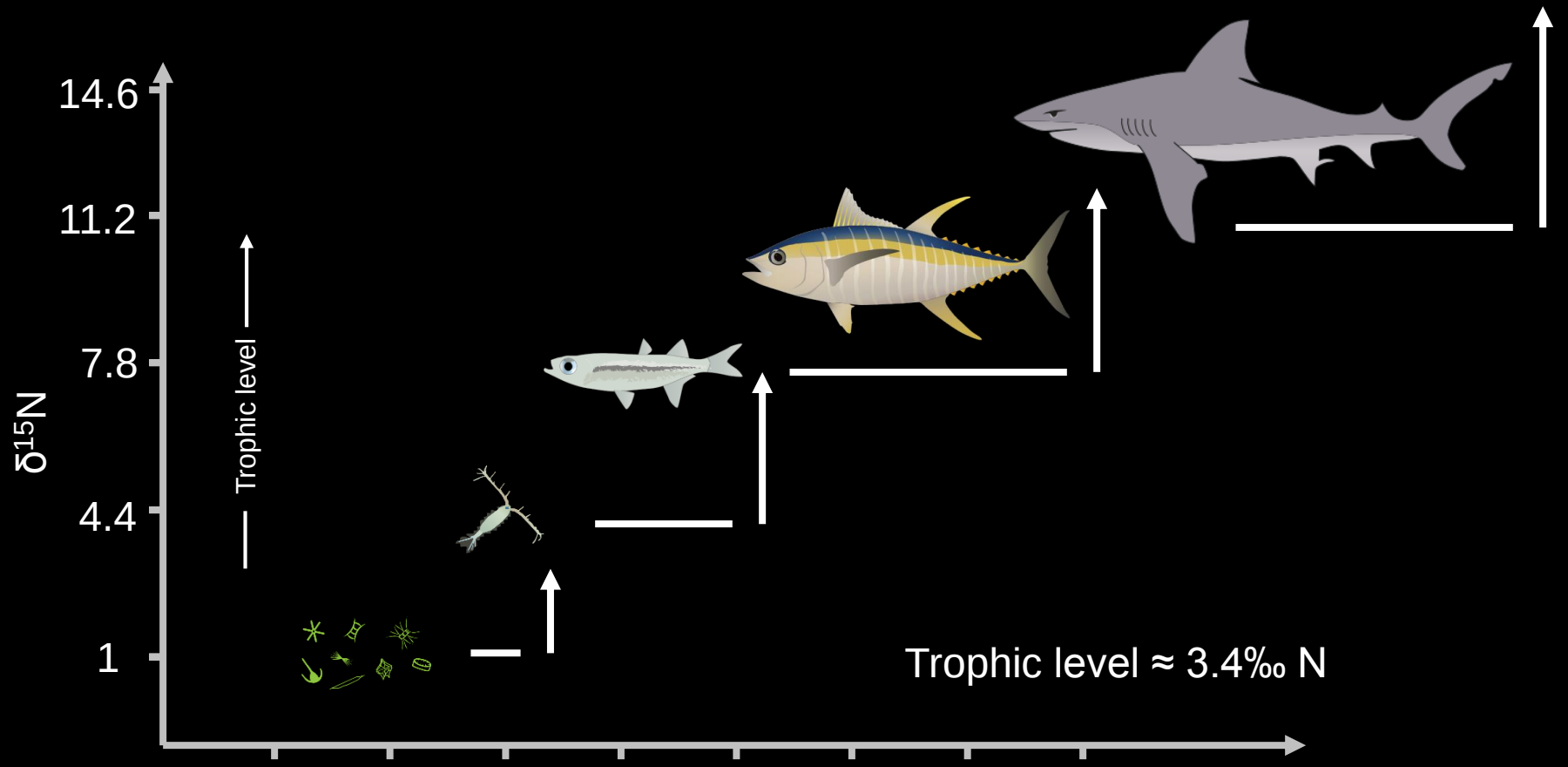
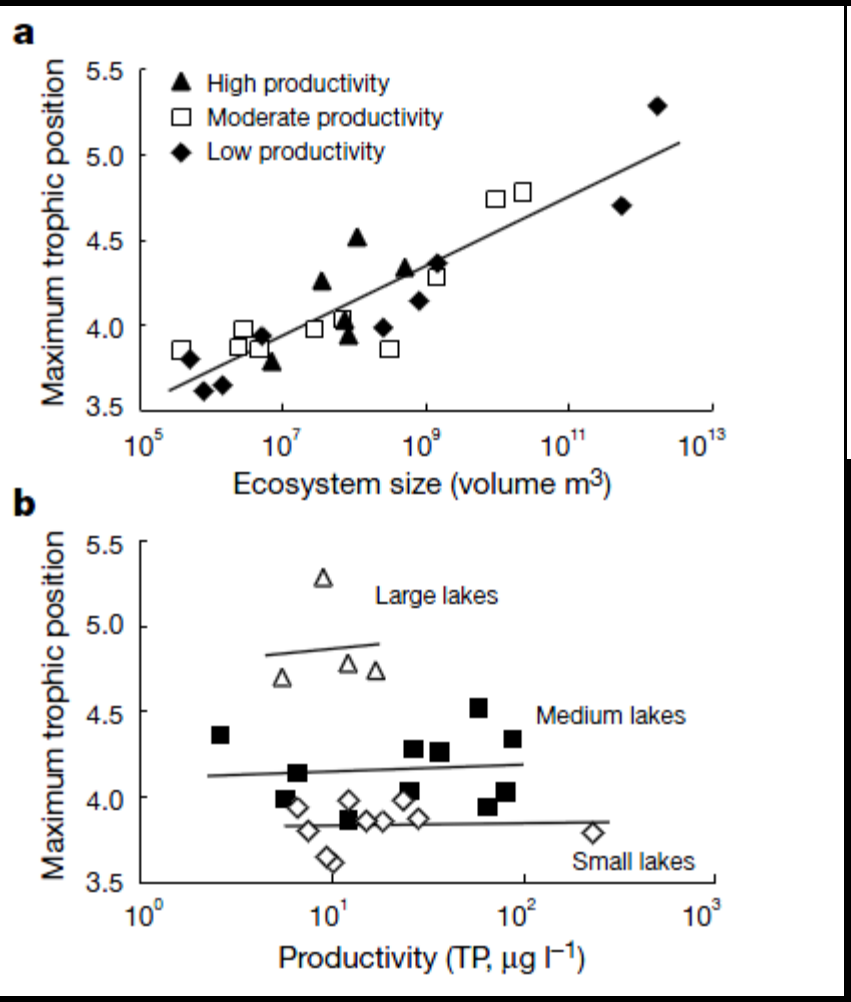


Nitrogen ($\delta^{15}N$)



Nitrogen ($\delta^{15}N$)



letters to nature

Acknowledgements

We thank A. K. Singh, S. Merkel and J. Hu for discussions and assistance. The work was supported by IGPP-LANL and NSF.

Correspondence and requests for materials should be addressed to H.-R.W. (e-mail: wenk@seismo.berkeley.edu).

Ecosystem size determines food-chain length in lakes

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Finally, we used stable isotope techniques to estimate maximum trophic position (MTP), a variable that is conceptually similar to mean food-chain length[10]. Because MTP is a continuous variable, we can detect subtle changes in food-chain length within the naturally occurring range of ecosystem size and productivity.

Stable isotope ratios of nitrogen and carbon are powerful tools for evaluating tropic structure and energy flow in ecological communities[21]. The $\delta^{15}N$ of an organism is typically enriched by 3.4‰ (±1‰) relative to its diet[22], and can be used to determine the trophic position of an organism. In contrast, $\delta^{13}C$ changes little as carbon moves through the food web and can be used to evaluate the ultimate sources of energy for an organism[21,23]. In lakes, $\delta^{13}C$ is particularly useful for differentiating between the two major sources of available energy: littoral (near shore) production from attached algae and detritus, and pelagic (open water) production from phytoplankton[24]. In our study lakes, the difference between littoral and pelagic $\delta^{13}C$ was between 2 and 10‰ (mean, 6.5%), with littoral $\delta^{13}C$ enriched in ^{13}C relative to pelagic $\delta^{13}C$.

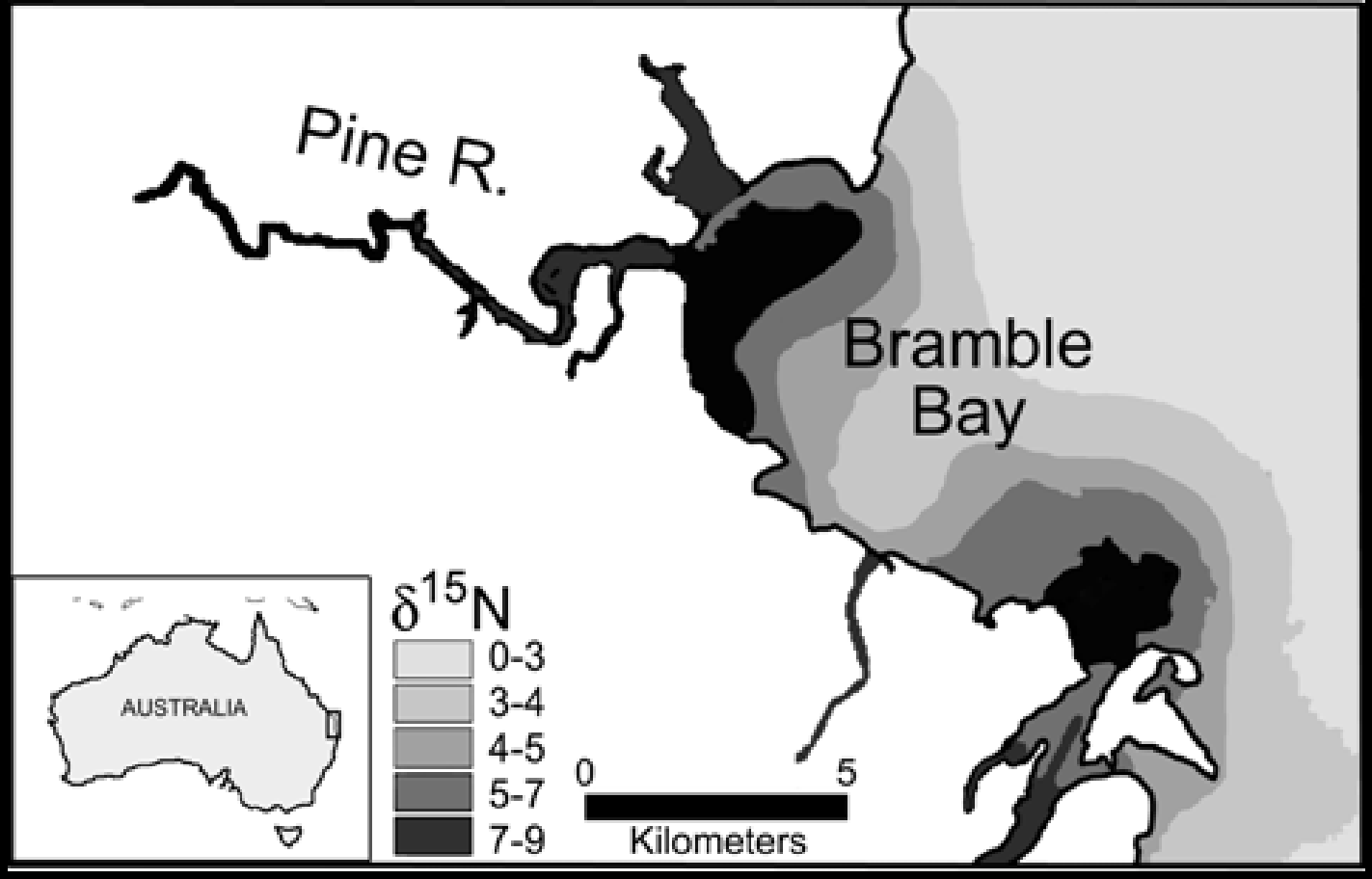
Stable isotopes provide a continuous measure of trophic position

Food chain length and maximum trophic position are positively related to ecosystem size.

Post et al. 2000, *Nature*

Nitrogen ($\delta^{15}N$)

- Large isotope contrasts might be expected between lakes in which primary production is limited by N (little fractionation by phytoplankton) versus P (abundant N → large possible fractionations during N uptake by phytoplankton).Where phytoplankton have different $\delta^{15}N$ values than terrestrial vegetation, the nitrogen isotopes may function as source markers for organic pollution.
- This approach has been successfully applied in marine environments. There is a wide range reported for nitrogen isotope



$\delta^{15}N$ values of algae in Moreton Bay, Australia. High $\delta^{15}N$ values along the western shore indicate N pollution inputs from watershed rivers and local sewage treatment facilities. The coastal pollution plumes are hard to identify by conventional measurements of ammonium and nitrate nutrients, because tides rapidly disperse nutrients and algae use up the nutrients during growth in algal blooms of the region. But the isotope values persist as nutrients are incorporated into the algae, tracing the nitrogen linkage to coastal inputs. Results are contoured for macroalgae that were incubated 4 days *in situ* at approximately 100 sites in September 1997, then analyzed for $\delta^{15}N$ (Costanzo et al. 2001). This $\delta^{15}N$ work continues now as a monitoring technique termed "sewage plume mapping" (Costanzo et al. 2005).

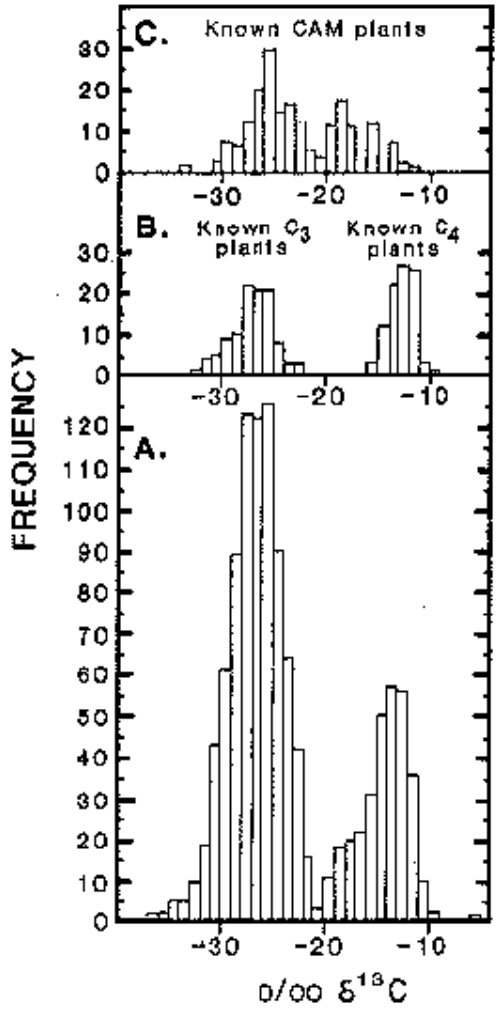
The Carbon Cycle

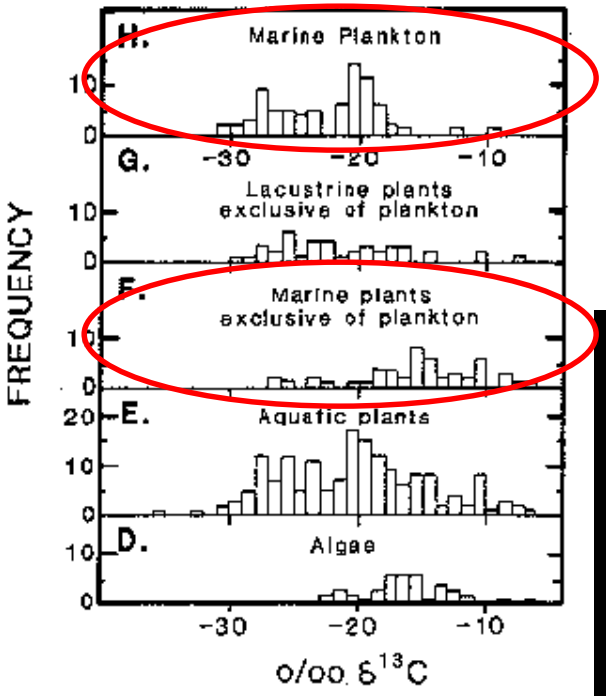
- The carbon cycle involves active exchanges of CO_2 among the atmosphere, terrestrial ecosystems and the surface ocean.
- The $\delta^{13}C$ value of atmospheric CO_2 is decreasing in response to inputs of ^{13}C depleted CO_2 from fossil fuel plus biomass burning and decomposition. Over the past 100 years the decrease may have been almost 1‰, from about −7‰ to −8‰. Carbon uptake by the dominant C_3 plants on land involves a net fractionation of about 20‰ between the atmospheric CO_2 and plant biomass (−28‰). Carbon uptake by C_4 plants, mainly tropical and salt grasses, involves a small net fractionation of about 5‰.

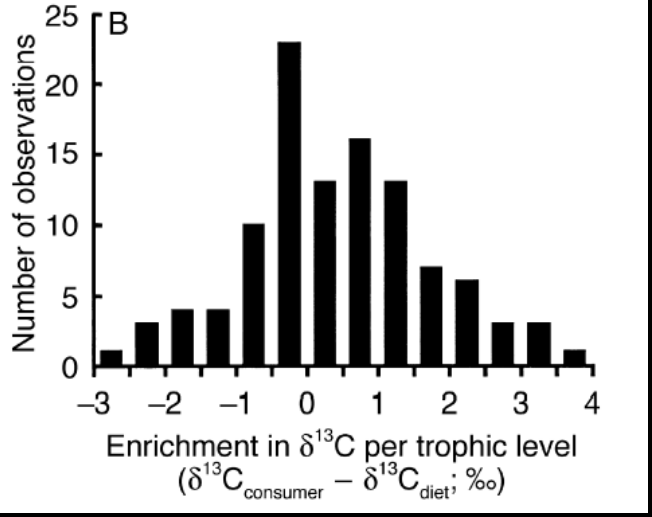
The Carbon Cycle

- The exchange of CO_2 between the atmosphere and the surface of the ocean involves an equilibrium chemical fractionation between atmospheric CO_2 (−8‰) and the total CO_2 (ΣCO_2, mostly bicarbonate) in surface ocean water (about 1‰).
- The withdrawal of carbon to form carbonates involves small isotope fractionations whereas uptake of dissolved inorganic carbon in planktonic photosynthesis involves larger kinetic fractionation that results in algal values of about −19 to −24‰. Both the dissolved and the particulate organic matter in the oceans predominantly have a marine planktonic origin.

Carbon ($\delta^{13}C$)

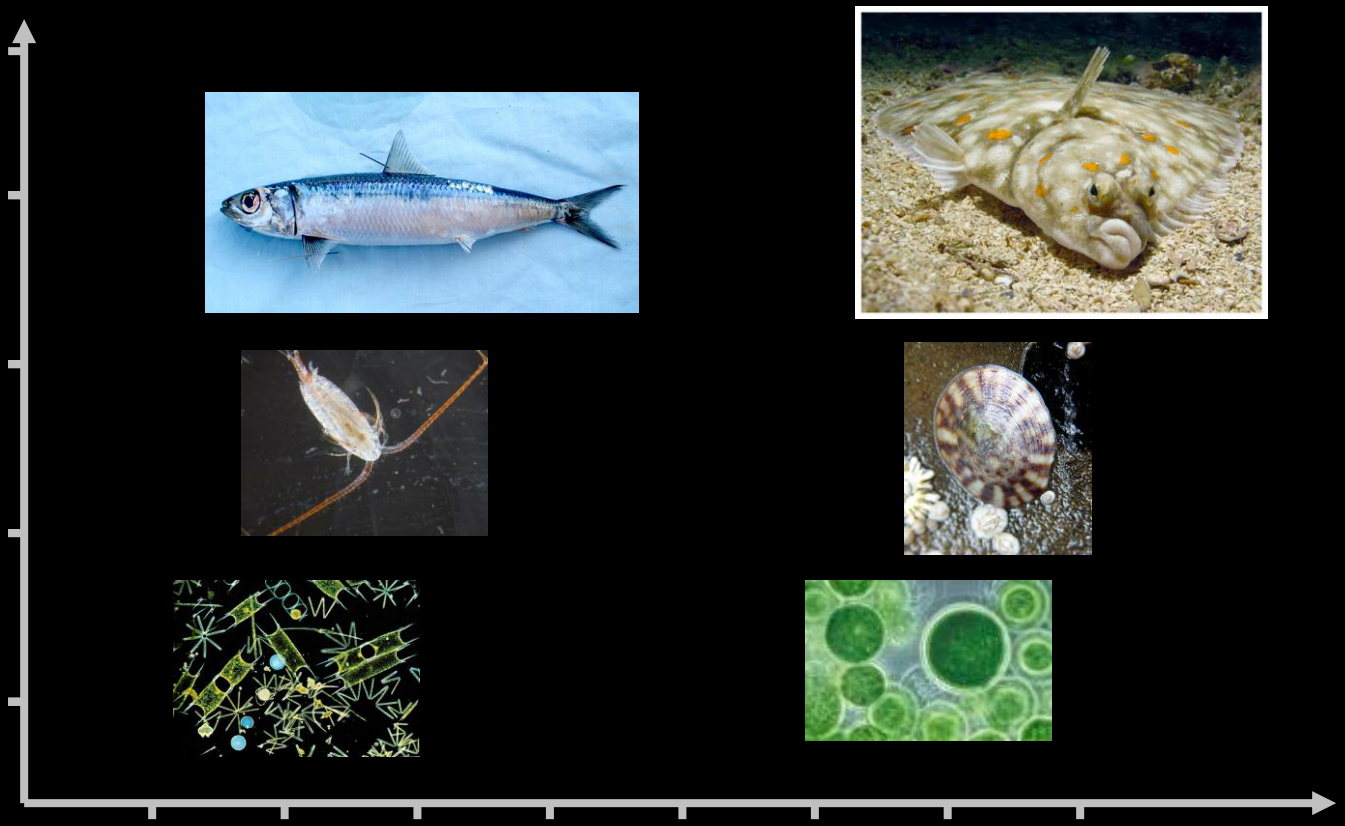




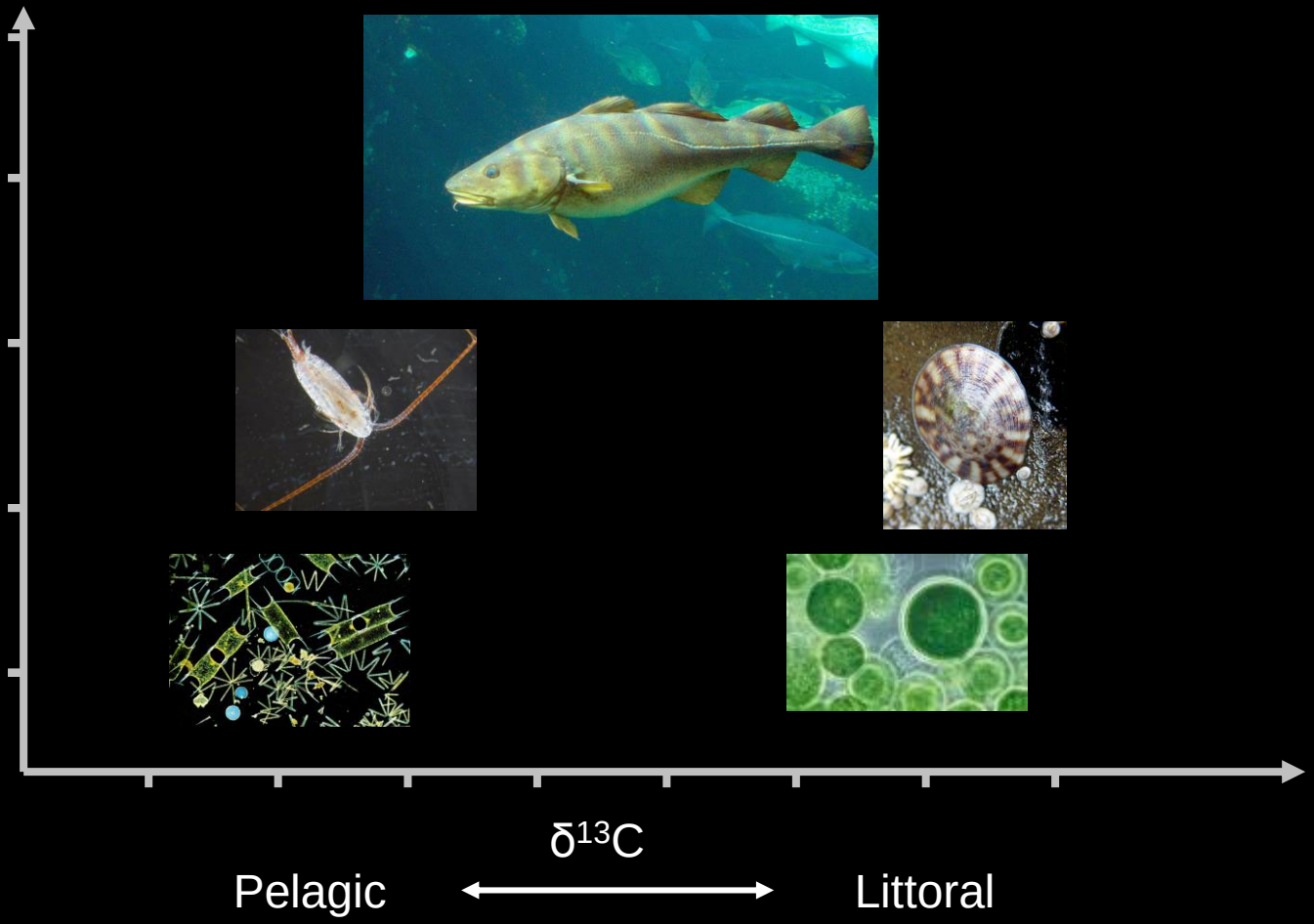


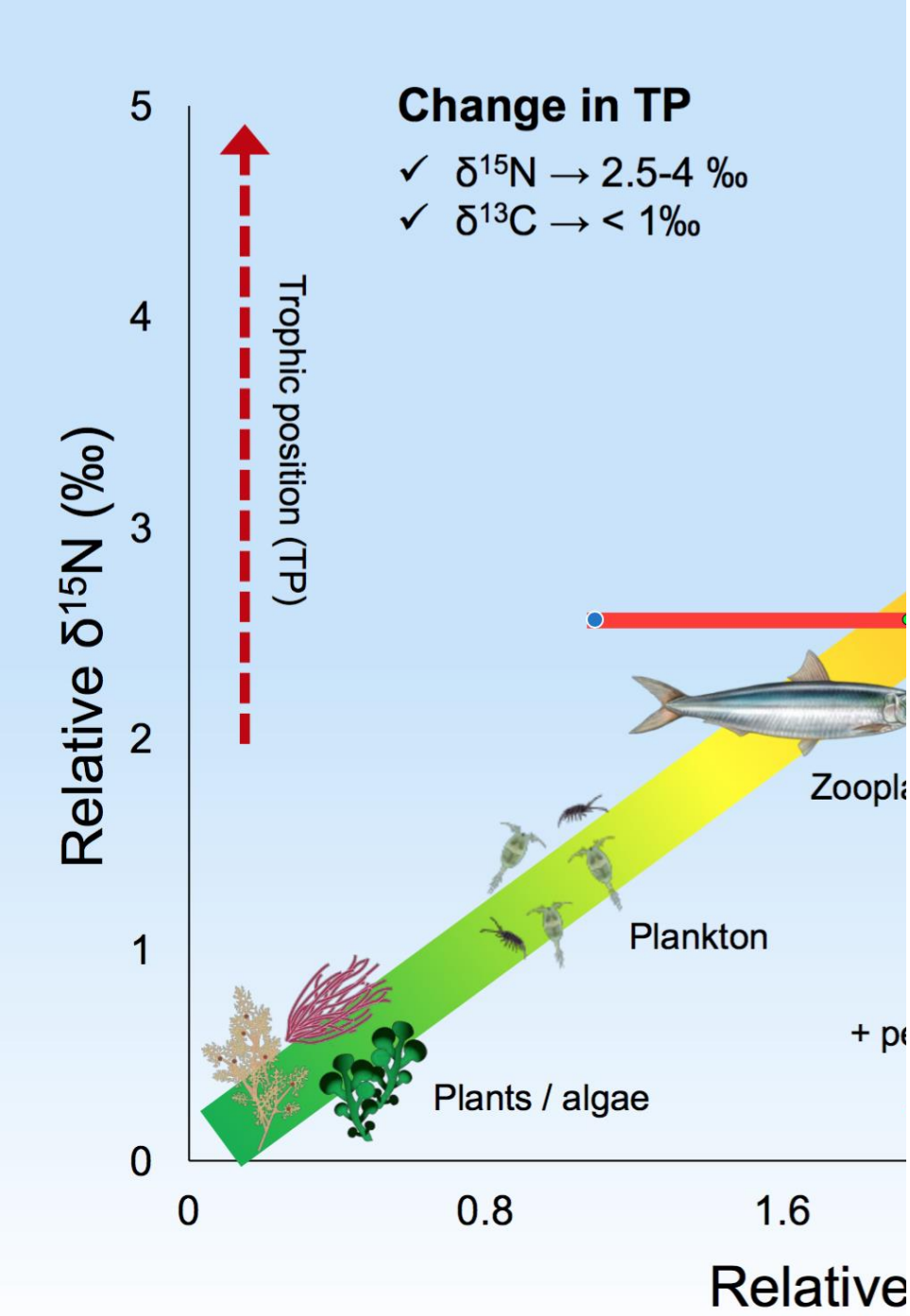
Trophic enrichment: 0~1‰

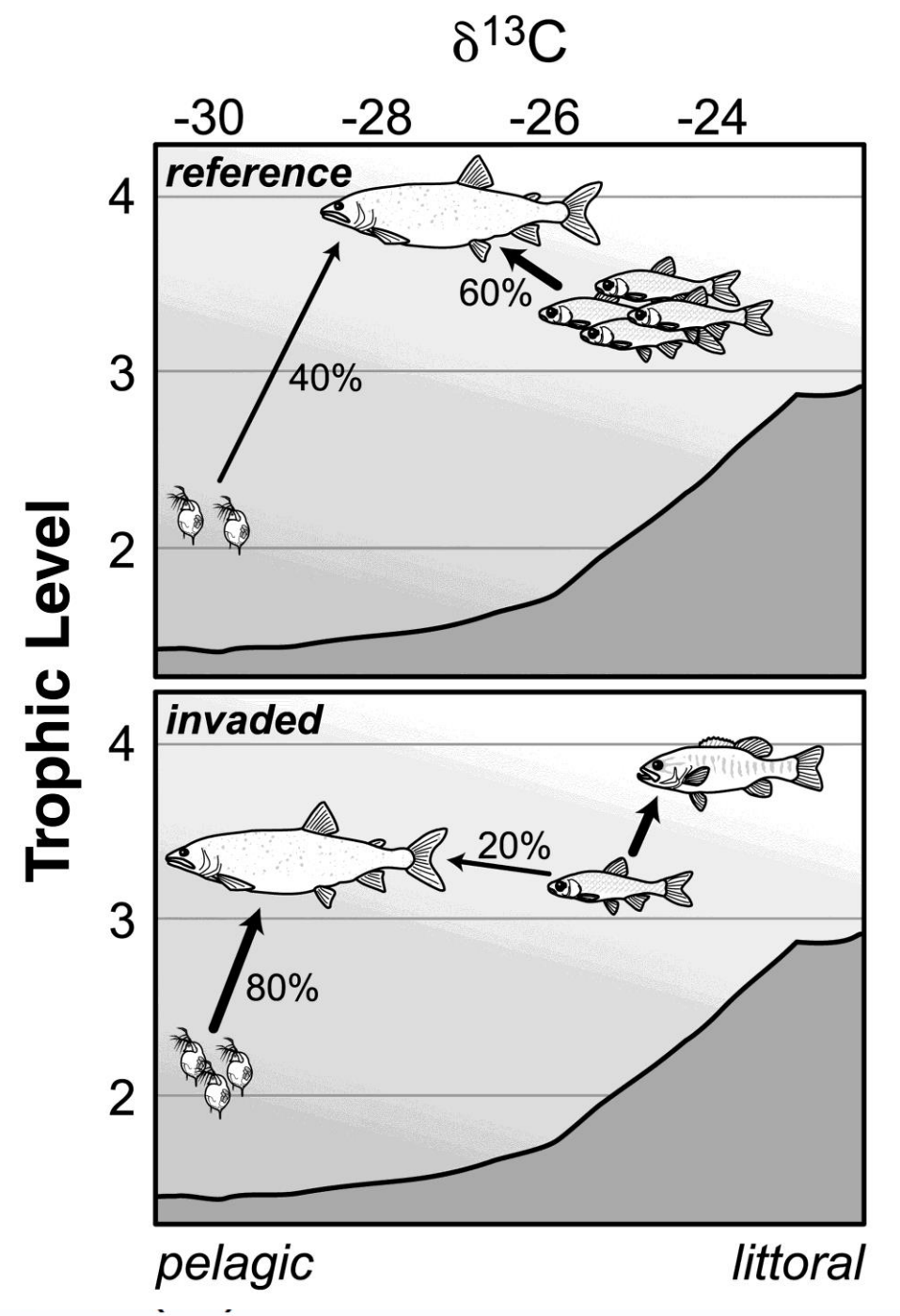
Carbon ($\delta^{13}C$)



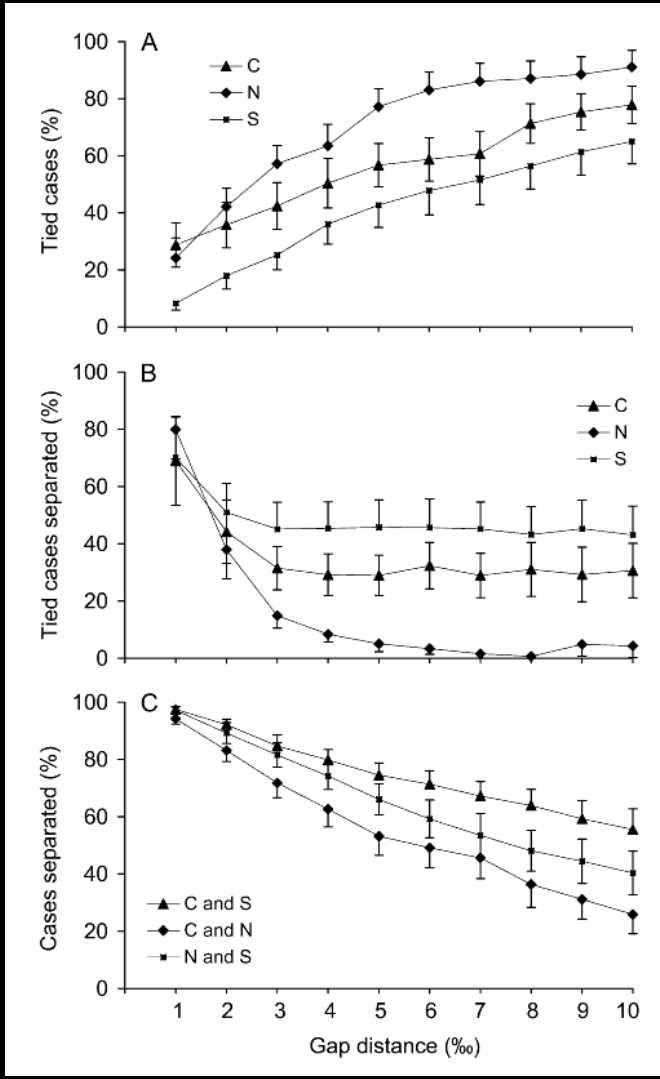
Carbon ($\delta^{13}C$)




Change in TP
✓ δ15N → 2.5-4 ‰
✓ δ13C → < 1‰
Trophic position (TP)
Relative δ15N (‰)
5
4
3
2
1
0
0
0.8
1.6
Relative
Zoopla
Plankton
+ pe
Plants / algae


δ13C
-30
-28
-26
-24
Trophic Level
reference
40%
60%
invaded
20%
80%
4
3
2
pelagic
littoral

Sulfur ($\delta^{34}S$)



Oecologia (2004) 138: 161–167
DOI 10.1007/s00442-003-1415-0

METHODS

Rod M. Connolly · Michaela A. Guest ·
Andrew J. Melville · Joanne M. Oakes

Sulfur stable isotopes separate producers in marine food-web analysis

Additional isotopes give more power to discriminate between sources

Hydrogen (δ^2H)

Hydrogen (δ^2H)

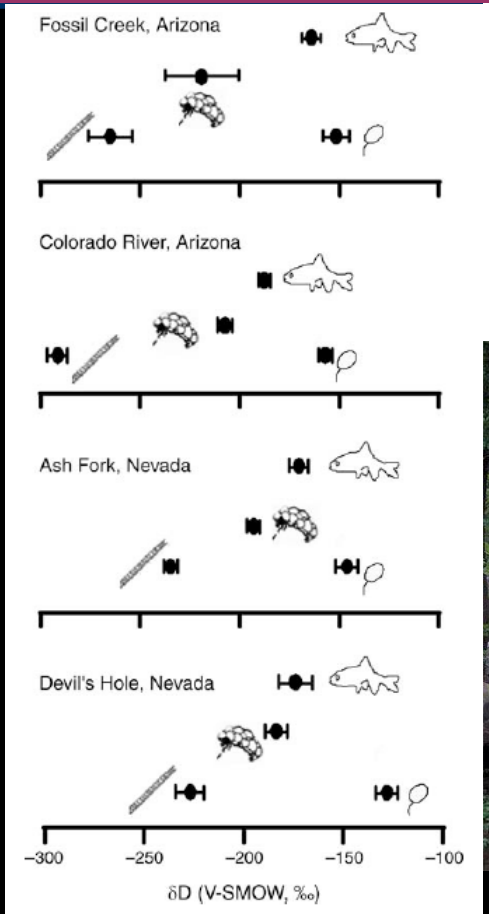


FIG. 1. Consistent differences in δD between algae (bottom left symbol) and leaf litter (bottom right symbol) in four aquatic ecosystems, showing intermediate status of benthic invertebrates and fish. Approximate trophic position is indicated by vertical position in each graph. Values are means ± SE. V-SMOW (Vienna Standard Mean Ocean Water) is an international standard for the hydrogen isotopic composition of water.

Ecology, 88(6), 2007, pp. 1587–1592

MEASURING TERRESTRIAL SUBSIDIES TO AQUATIC FOOD WEBS USING STABLE ISOTOPES OF HYDROGEN

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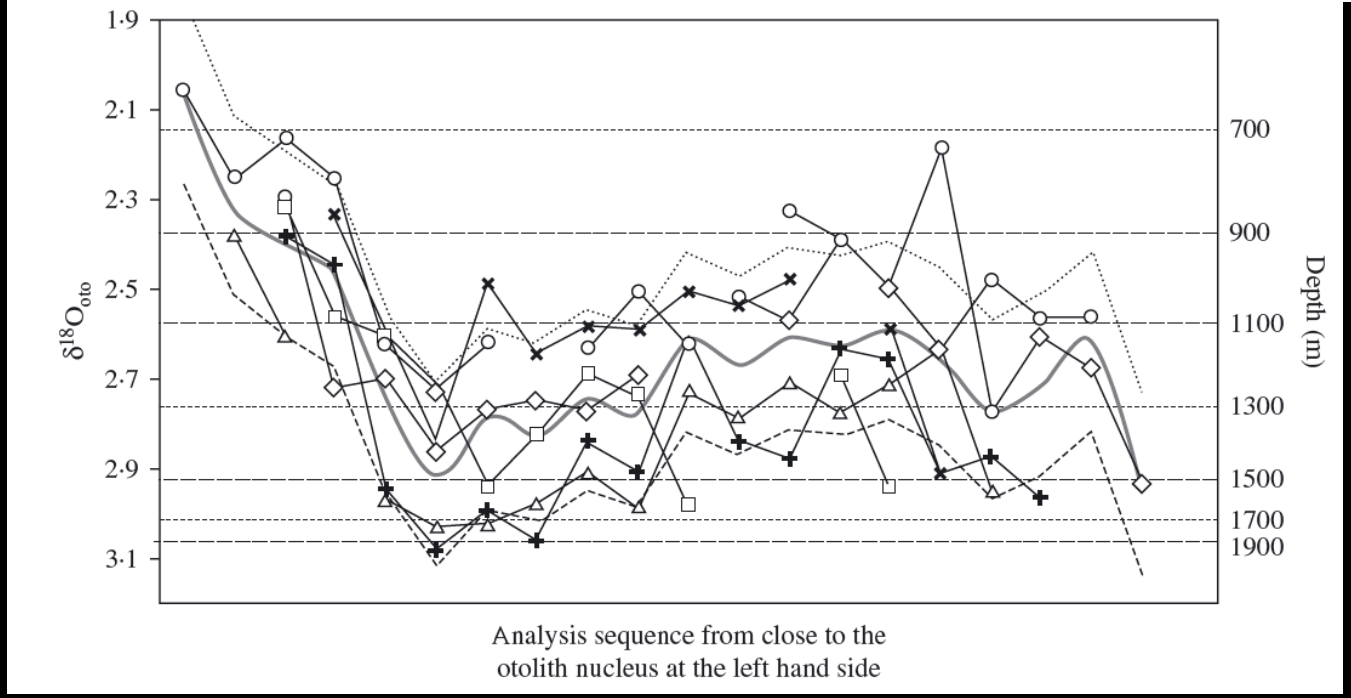
Powerful tool in river ecology
Limited applications in marine (to date…)

Oxygen ($\delta^{18}O$)

Identifying migrations in marine fishes through stable-isotope analysis

C. N. TRUEMAN*, K. M. MACKENZIE AND M. R. PALMER

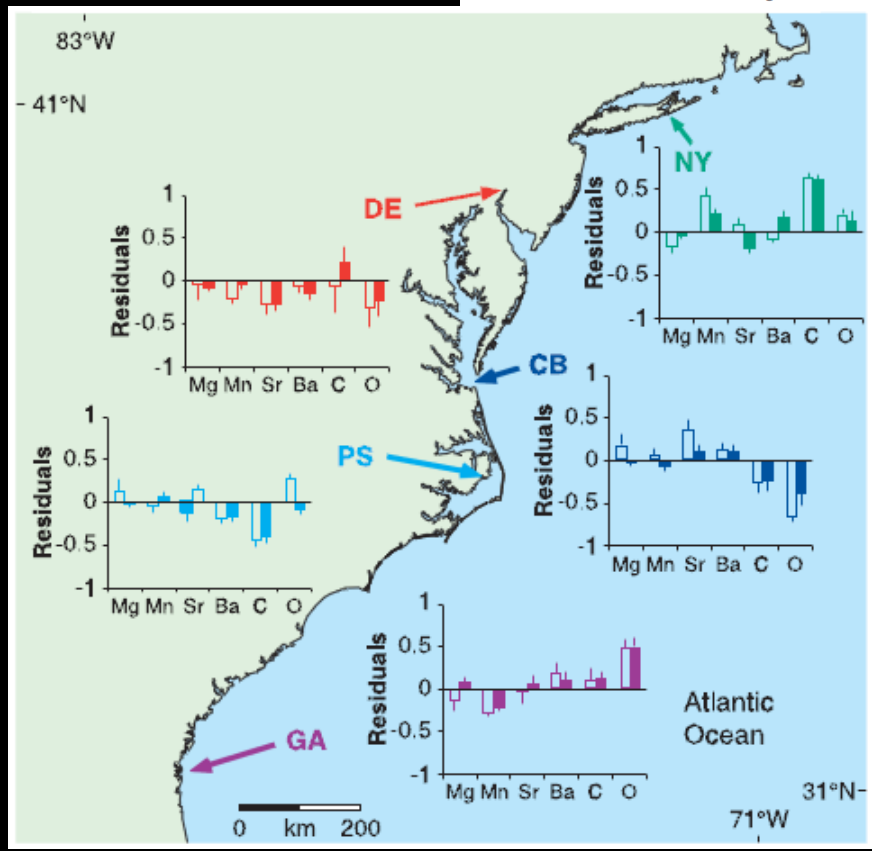
Ocean and Earth Science, National Oceanography Centre, Southampton, University of Southampton, Waterfront Campus, Southampton SO14 3ZH, U.K.

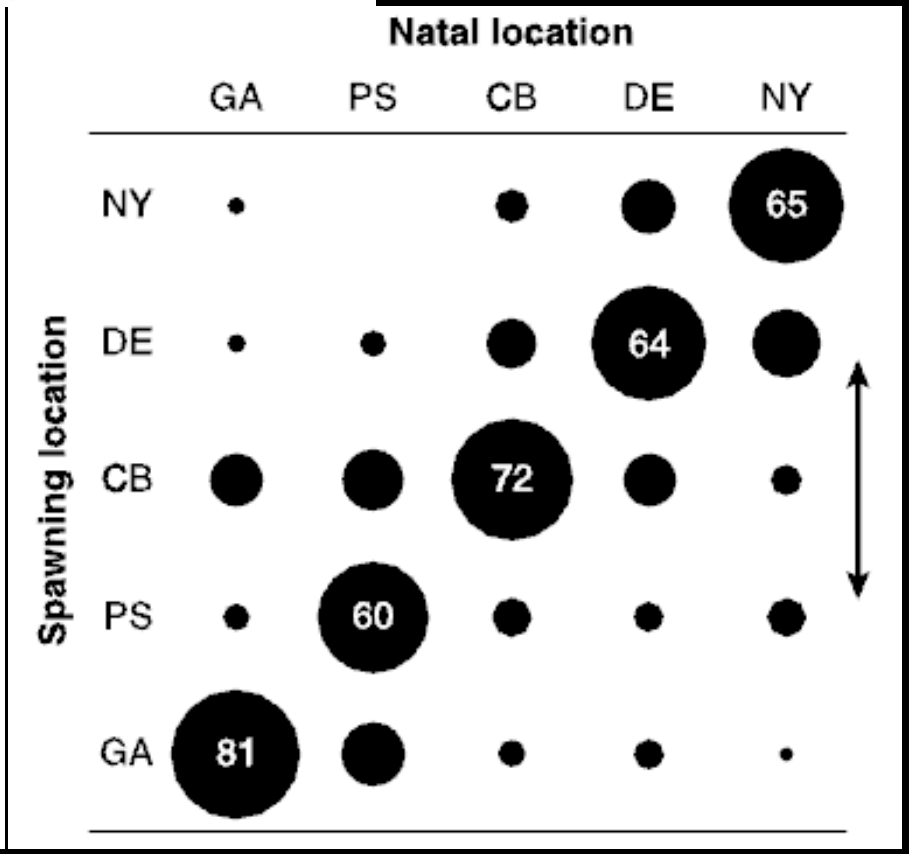


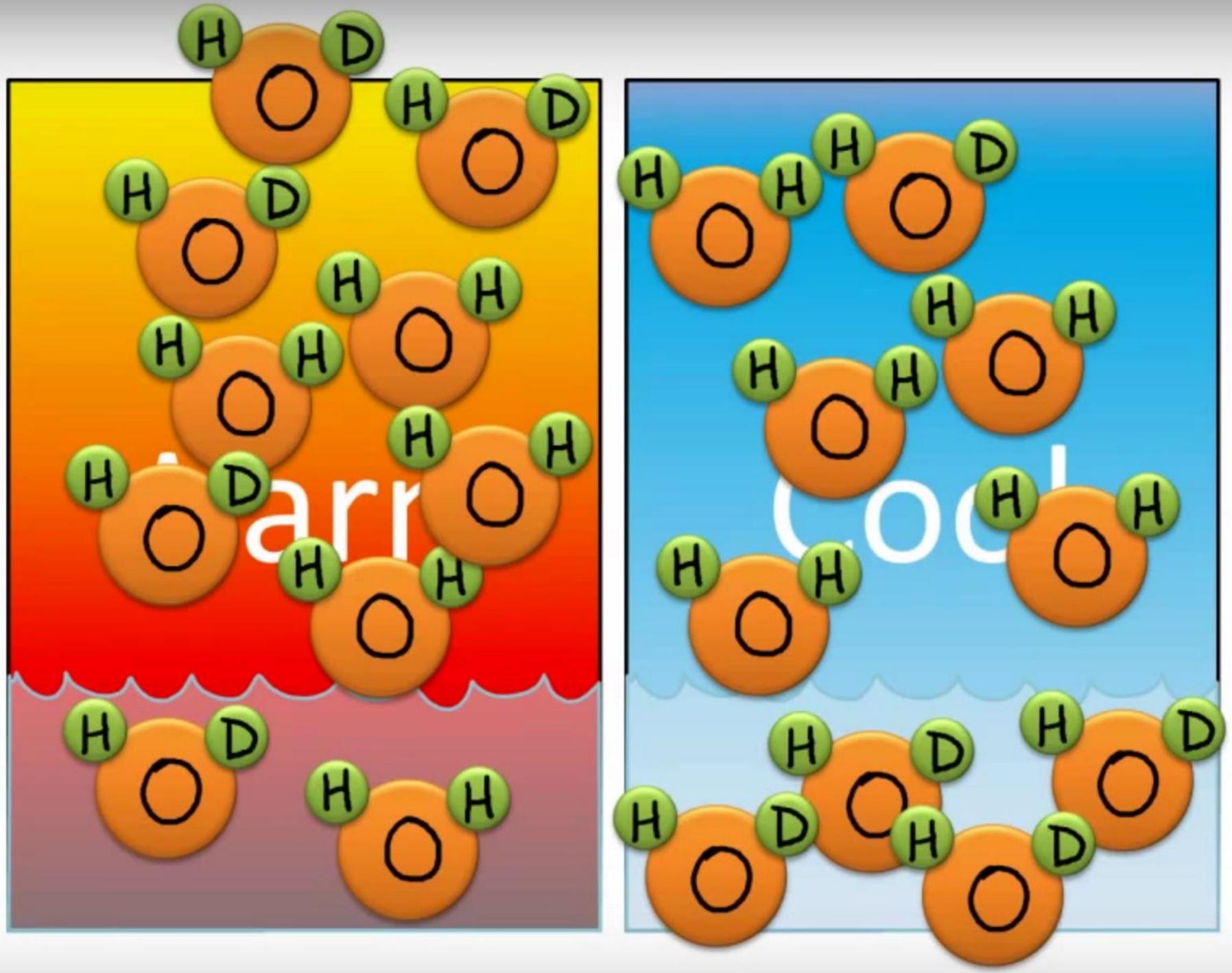
Oxygen ($\delta^{18}O$)

Natal Homing in a Marine Fish Metapopulation

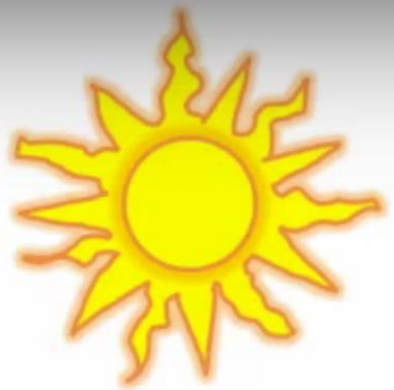
Simon R. Thorrold,[1]*† Christopher Latkoczy,[2] Peter K. Swart,[3] Cynthia M. Jones[1]

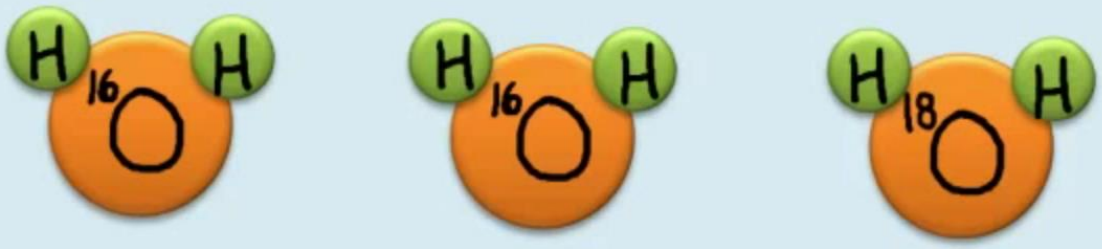




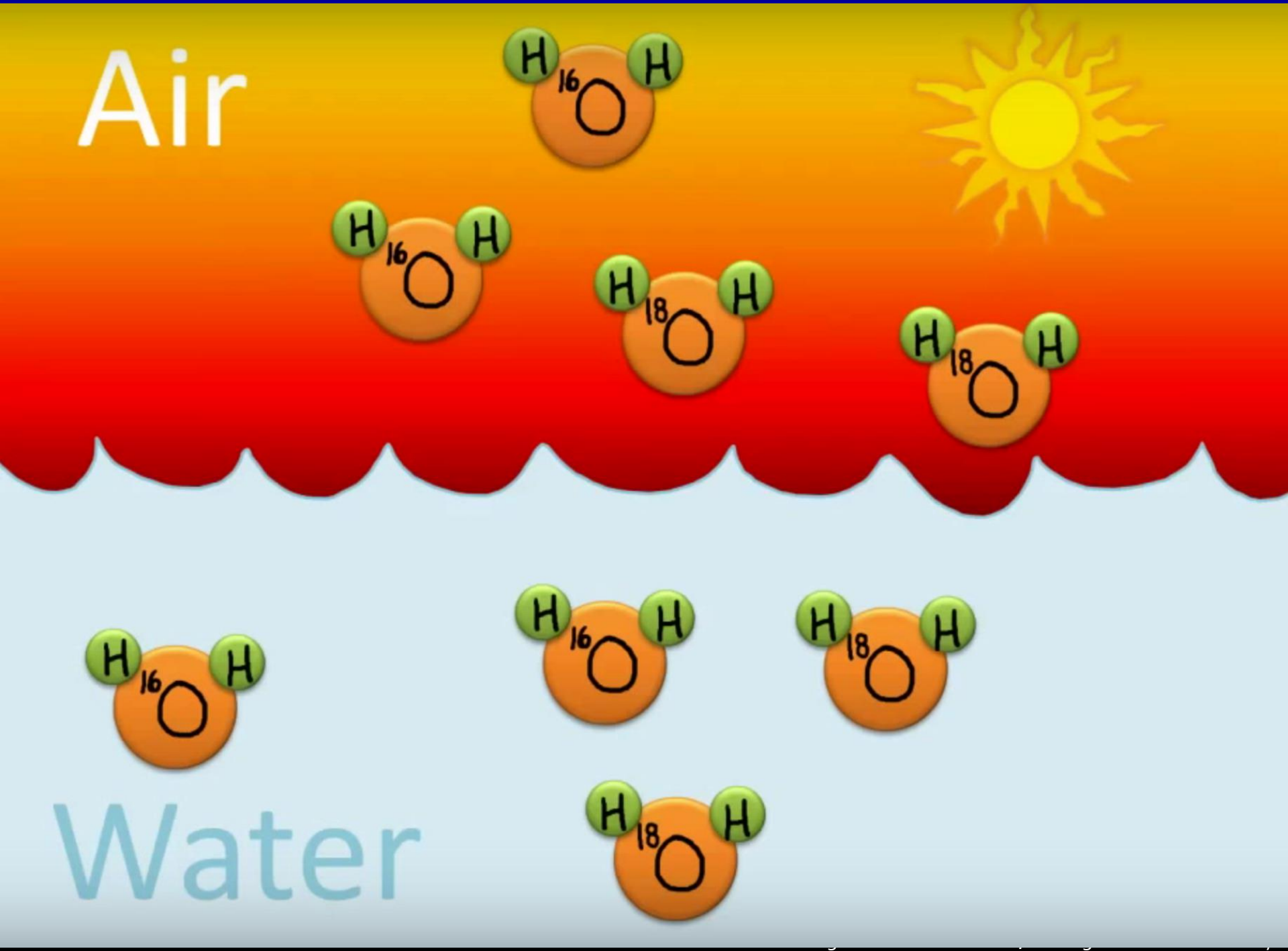

Warm
Cool

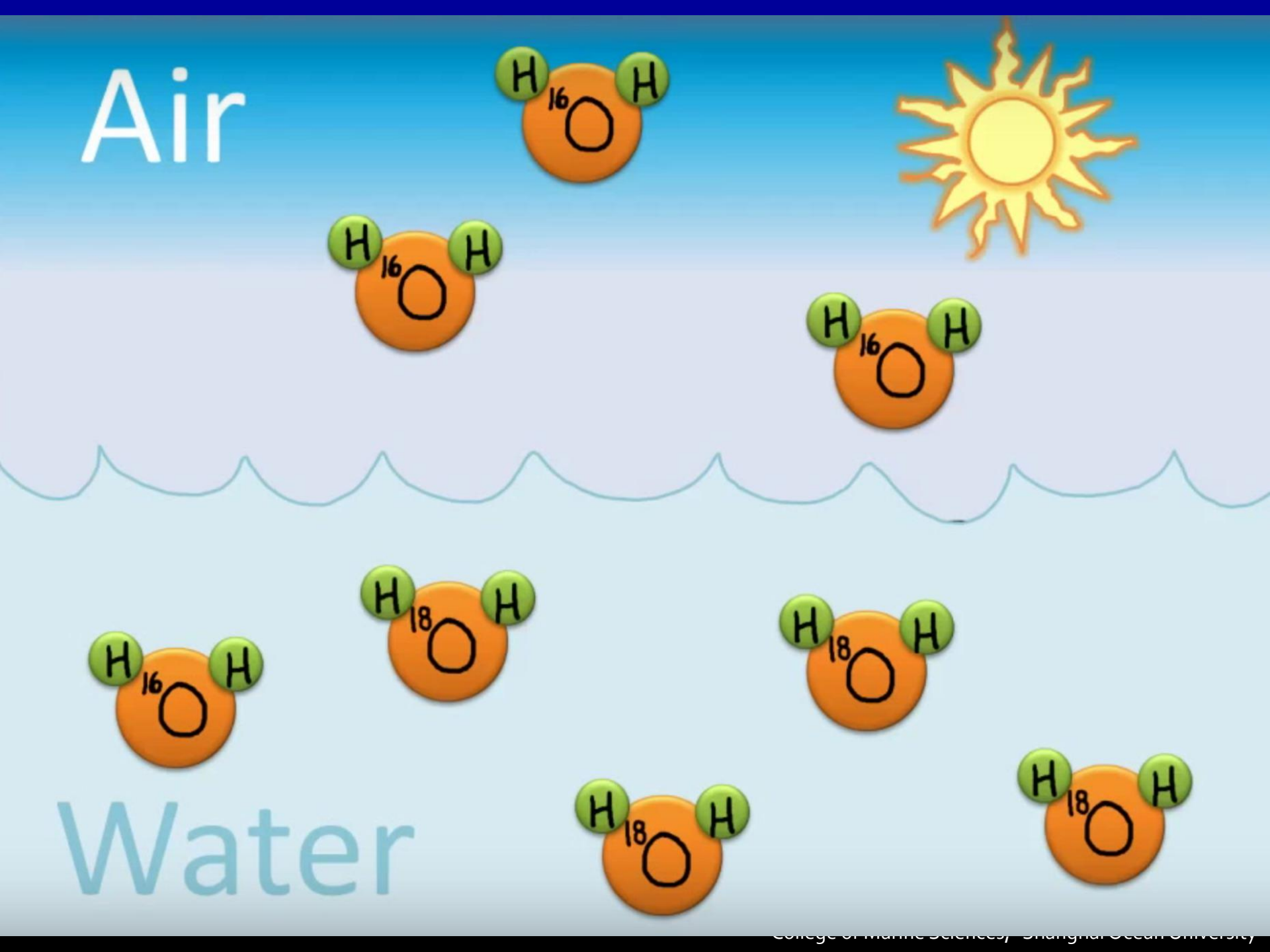
Air





Water


Air
H 16 O H
H 16 O H
H 18 O H
H 18 O H
H 16 O H
H 16 O H
H 18 O H
H 18 O H
Water


Air
H 16 O H
H 16 O H
H 16 O H
H 16 O H
H 18 O H
H 18 O H
H 18 O H
H 18 O H
Water

$\delta^{18}O$ ‰

$\delta^{18}O = (((^{18}O/^{16}O \text{ of a sample})/(^{18}O/^{16}O \text{ of a standard})) - 1) \times 1000$

$\downarrow \delta^{18}O = \downarrow {}^{18}O/^{16}O = \downarrow T$

$\uparrow \delta^{18}O = \uparrow {}^{18}O/^{16}O = \uparrow T$

$\downarrow \delta^{18}O = \downarrow {}^{18}O/^{16}O = \uparrow T$

$\uparrow \delta^{18}O = \uparrow {}^{18}O/^{16}O = \downarrow T$

$\delta^{18}O$ ‰

$\delta^{18}O = (((^{18}O/^{16}O \text{ of a sample})/(^{18}O/^{16}O \text{ of a standard})) - 1) \times 1000$

$\downarrow \delta^{18}O = \downarrow {}^{18}O/^{16}O = \downarrow T$

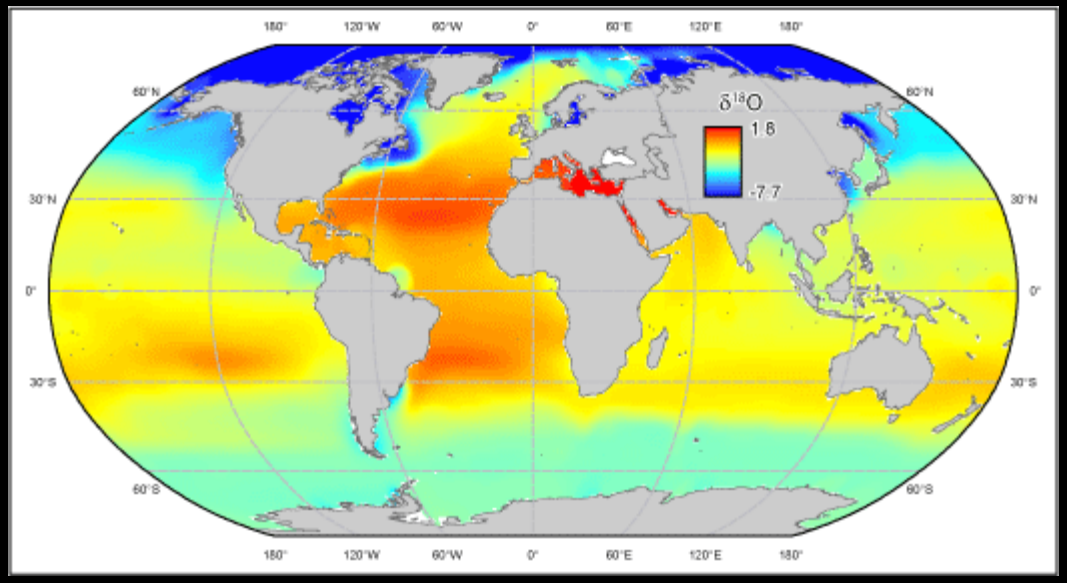
$\uparrow \delta^{18}O = \uparrow {}^{18}O/^{16}O = \uparrow T$

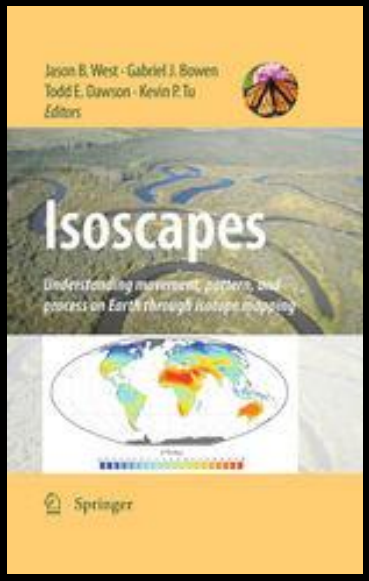
$\downarrow \delta^{18}O = \downarrow {}^{18}O/^{16}O = \uparrow T$

$\uparrow \delta^{18}O = \uparrow {}^{18}O/^{16}O = \downarrow T$

Isoscape

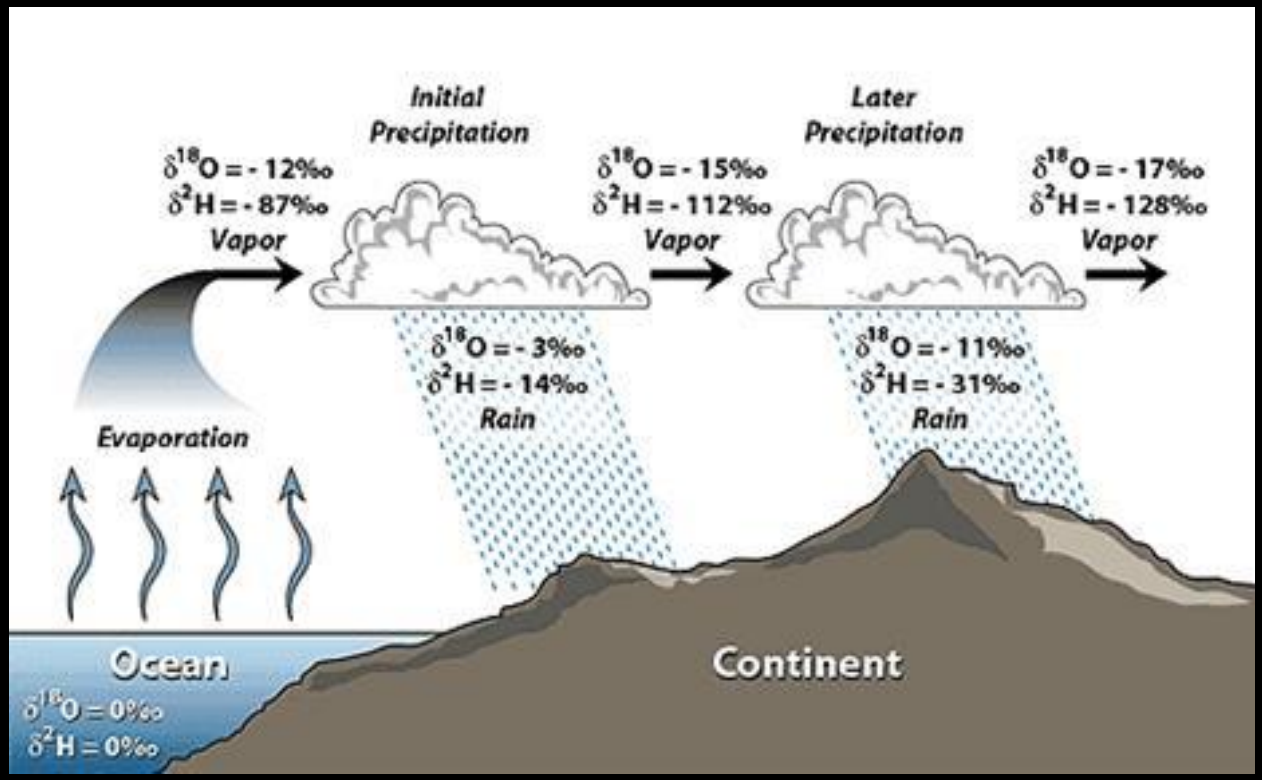
You are Where you eat.



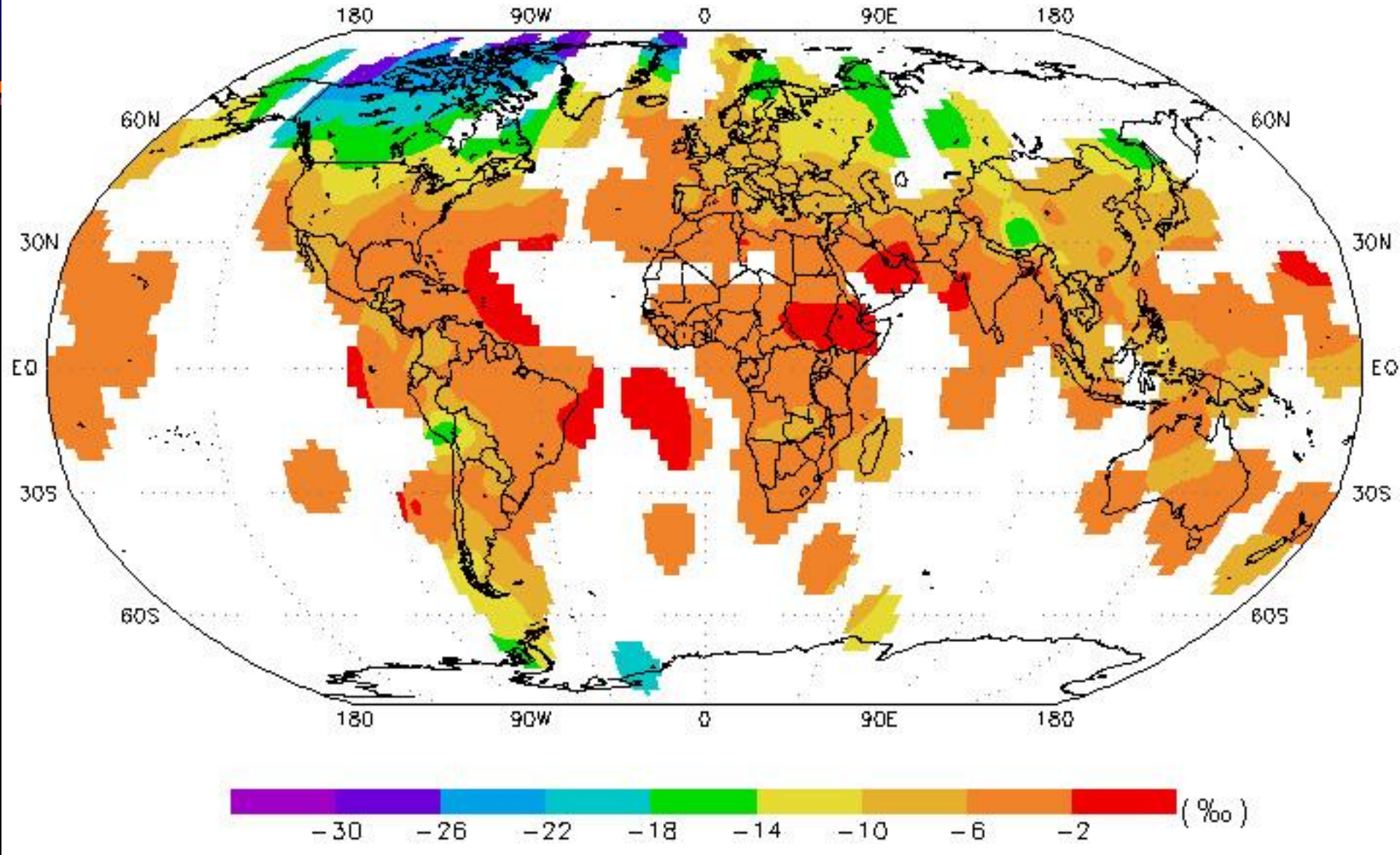


Isoscape

You are Where you eat.

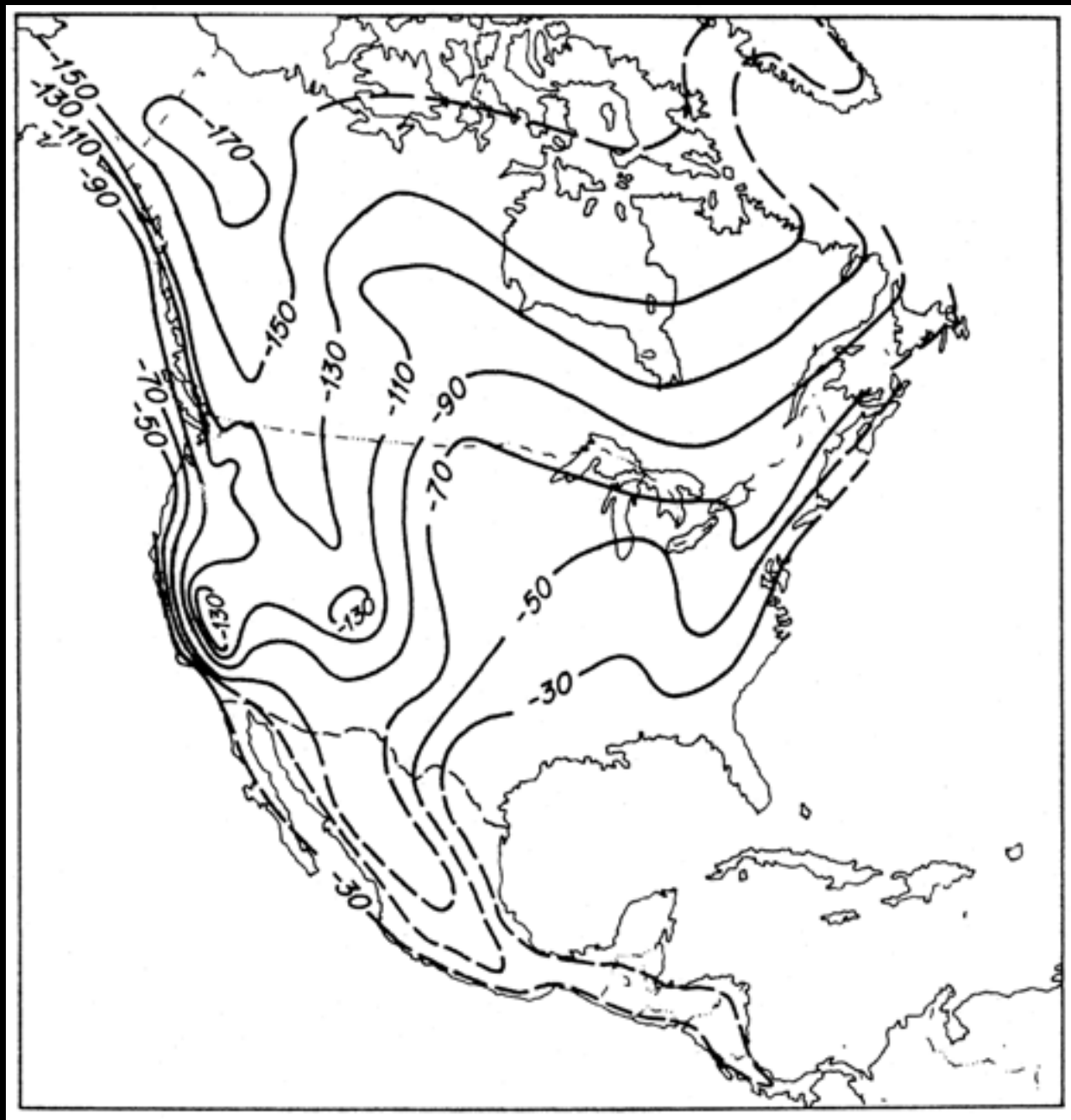


Weighted Annual $\delta^{18}O$



Isotope map of North America for precipitation δD values. Plant and animal δD values reflect this continental-level map.

Fry B. 2006. *Stable Isotope Ecology*



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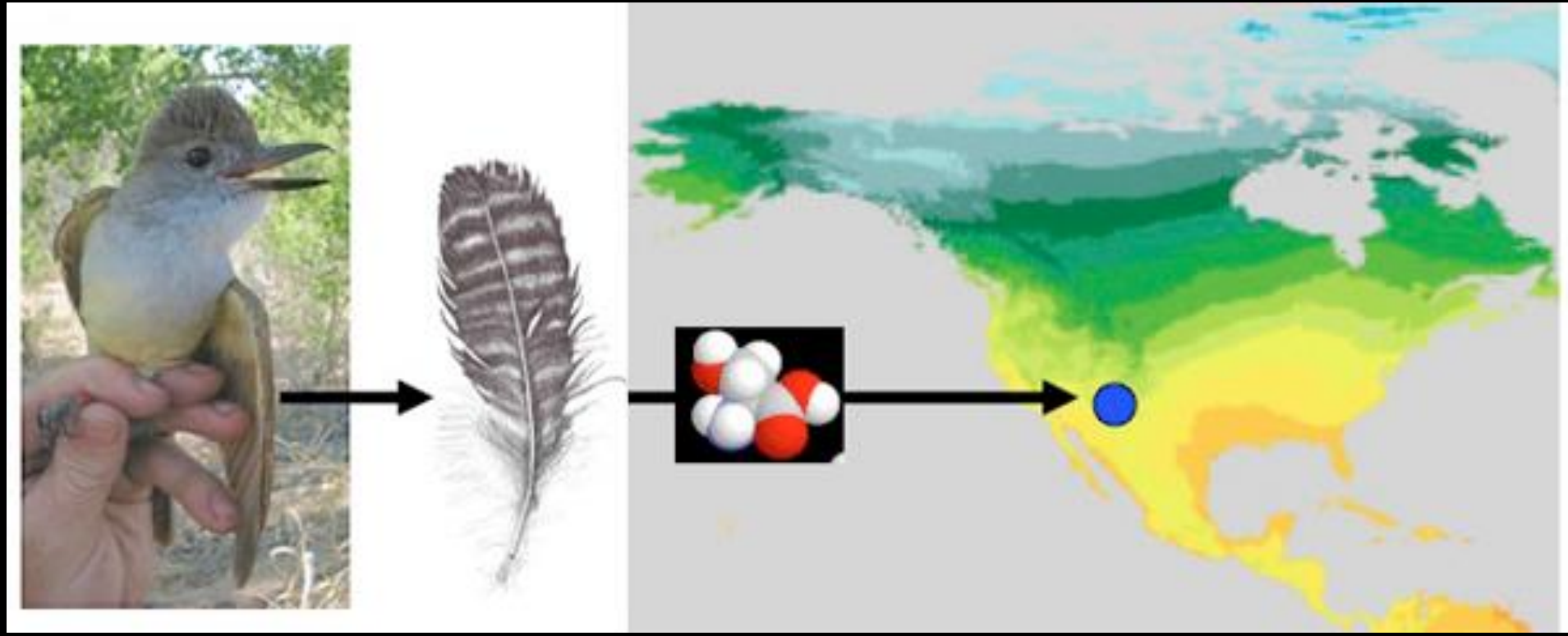


Isoscape

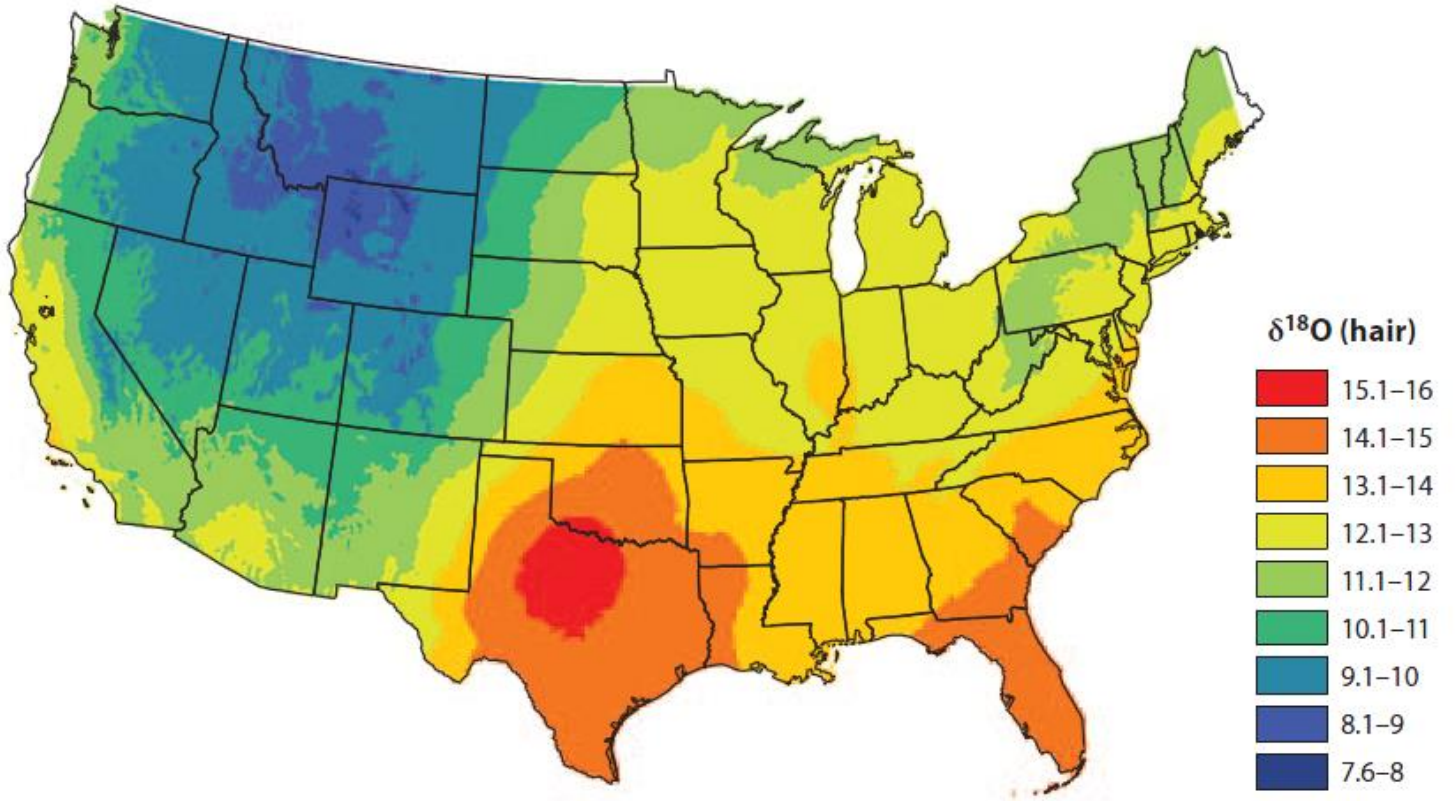


Figure 11

$\delta^{18}O$ isoscape for modern human hair. Map values are estimated based on a modeled isoscape for tap water and a regression model relating observed hair and drinking-water isotope ratios from sample sites in 18 states. Figure reprinted from Ehleringer et al. (2008).

Tissue turnover rates

You are <u>When</u> you eat!

Tissue turnover rates

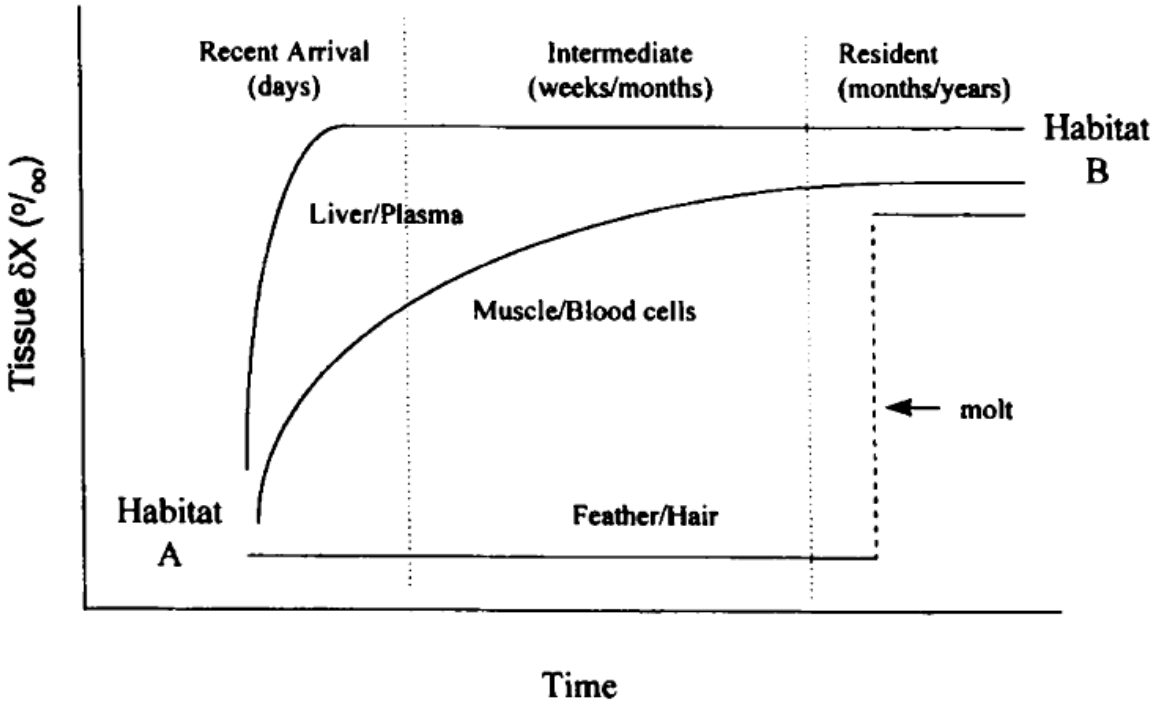


Fig. 2 Depiction of the changes in stable isotope (*X*) values expected when a bird or mammal hypothetically moves between biomes (*Habitat A* vs *Habitat B*) that are isotopically distinct. Contrasting stable isotope values across tissues can provide information on the residency time of an individual in habitat B providing tissue turnover rates and times of molt are known

Oecologia (1999) 120:314–326

Keith A. Hobson

Tracing origins and migration of wildlife using stable isotopes: a review

Tissue turnover rates

The Condor 94:181–188

ASSESSING AVIAN DIETS USING STABLE ISOTOPES I: TURNOVER OF ^{13}C IN TISSUES[1]

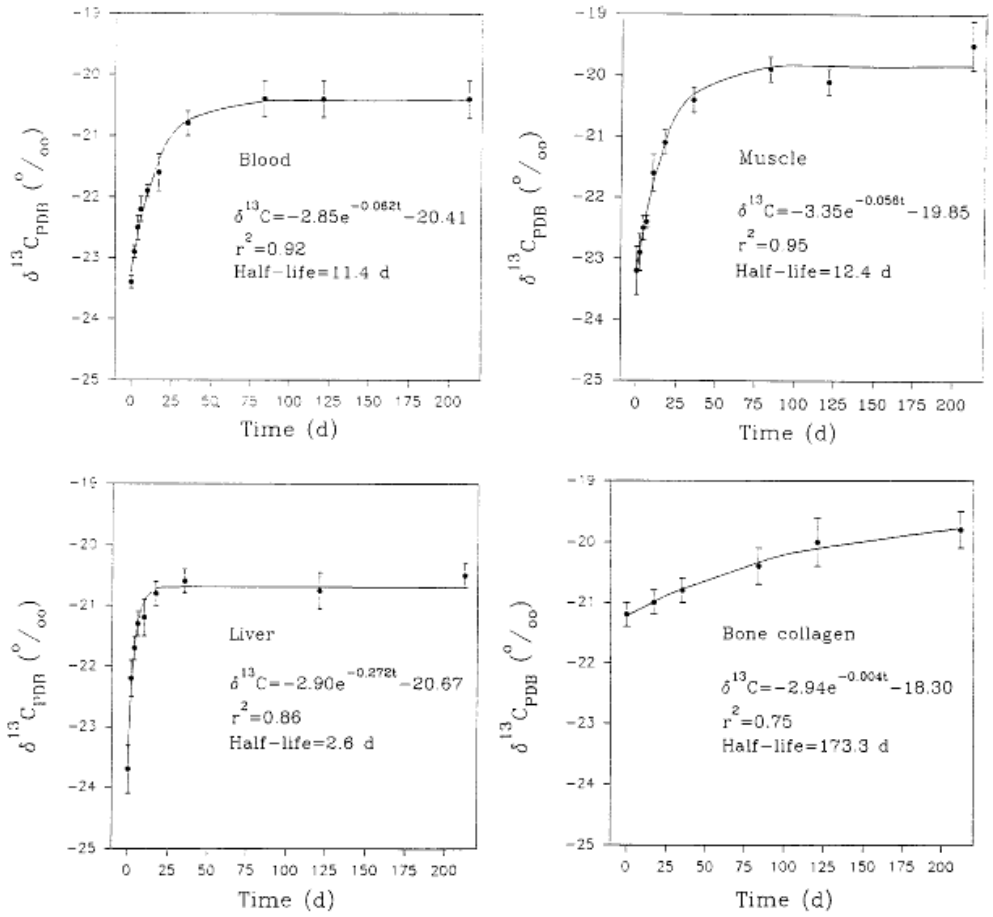


FIGURE 1. Stable-carbon isotope exponential models for quail tissues. Data are means (closed circles) ± SD (vertical lines) and sample sizes are $n = 3$ for each point.

Tissue turnover rates

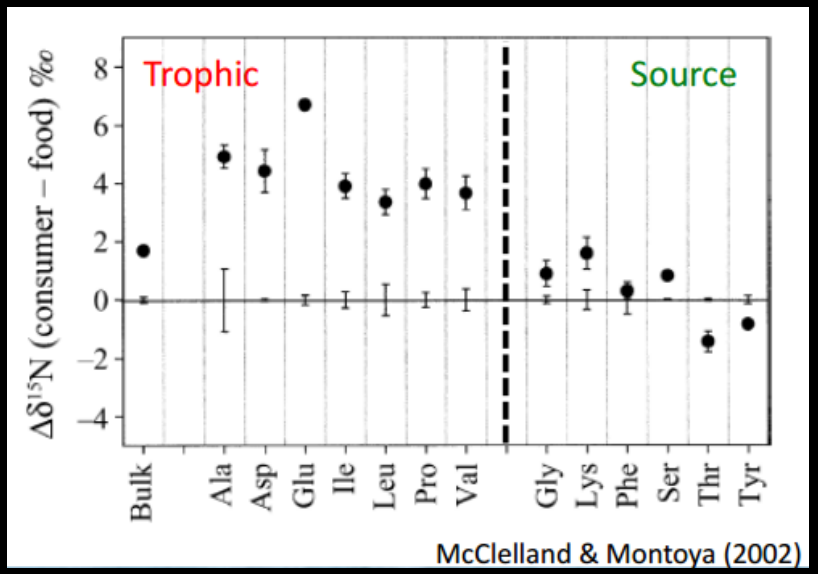
Timeframe	Tissue
Hours	Breath, stomach content
Days	Blood plasma, scat
Weeks	Liver, organ
Month - Season	Muscle, blood (whole), hair, fur, feather, collagen
Lifetime	Bone carbonate, inert materials (scale)

Sampling

- Sample prey items over a longer time frame than consumers
- Sample consumers at end of growing season to reflect resource use through that period.

Compound- Specific Stable Isotope

- For highly migration animals
- Protein
  Amino acids (AA)



"Trophic" Amino Acids

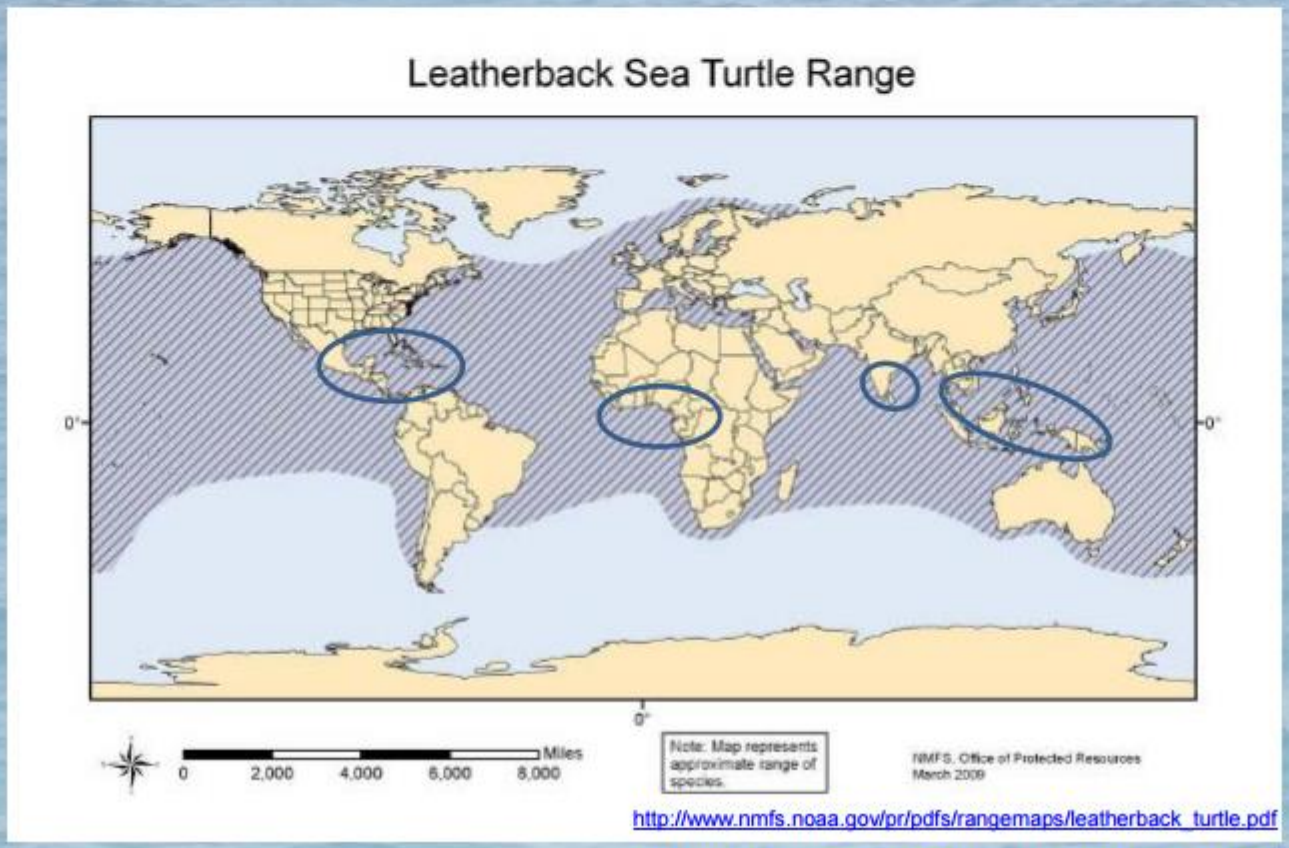
Carbon/nitrogen bond cleaved causing enrichment of ^{15}N during metabolism
These AA enriched in ^{15}N through food web
Eg: Glutamic, alanine, aspartic acid

"Source" Amino Acids

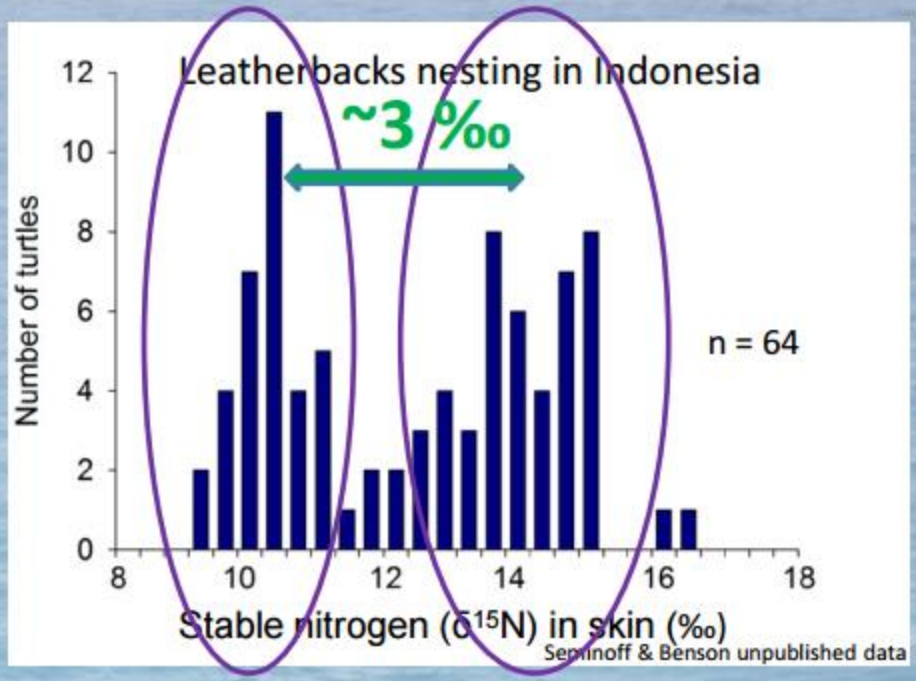
Do not undergo transamination reactions during metabolism
Retain $\delta^{15}N$ composition of base food web
Eg: Phenylalanine, lysine, threonine

Leatherbacks (*Dermochelys coriacea*)

- Nest in tropical beaches
- Display natal beach homing
- Forage over vast areas at high latitudes
- Exclusively feed on gelatinous prey



Challenge of bulk isotopes: Leatherbacks in Pacific

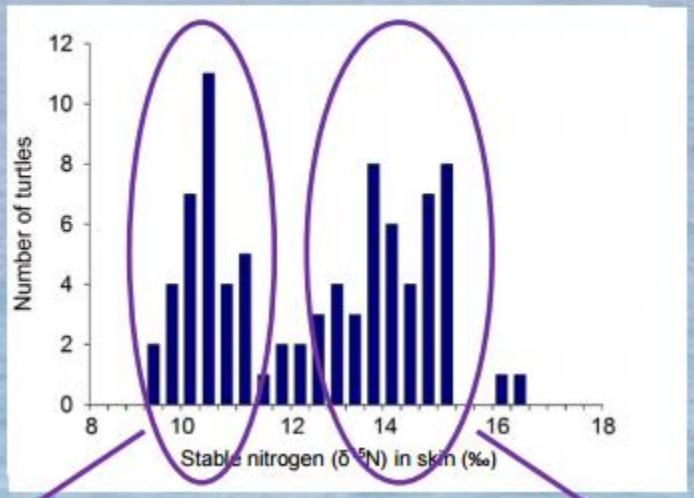


Interpretations:

1. Two feeding populations feeding at different trophic levels (~3‰ difference)
2. Two feeding populations feeding in areas with different nitrogen cycling regimes

THIS IS A JOB FOR AA-CSIA!

Application of AA-CSIA: Leatherbacks in Pacific



Derivatized AA
Analyzed GC-IRMS

Skin samples:

n = 3

Source AA: phe = 4.2 ± 0.7 ‰
Trophic AA: glu = 17.7 ± 0.4 ‰

n = 3

Source AA: phe = 7.2 ± 0.3 ‰
Trophic AA: glu = 21.0 ± 0.1 ‰

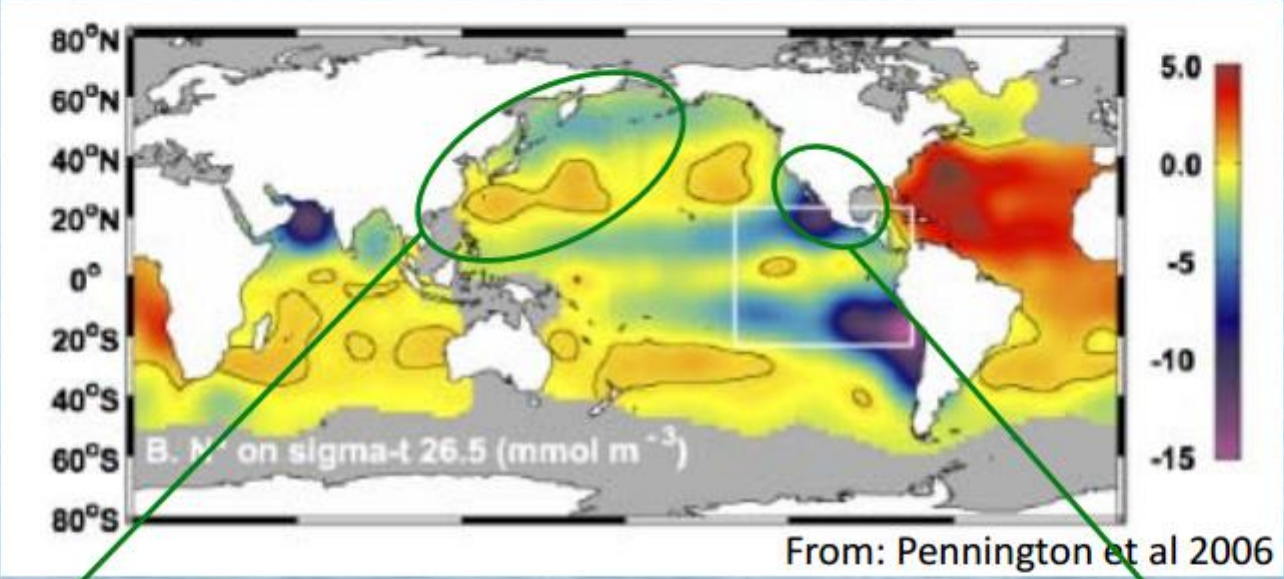
$$TP_{Glu\text{-}Phe} = \frac{\delta^{15}N_{Glu} - \delta^{15}N_{Phe} - 3.4}{7.6} + 1$$

Trophic Position (AA) = 2.33 ± 0.1

Trophic Position (AA) = 2.36 ± 0.1

Application of AA-CSIA: Trace different sources of N

Map of N* for the Pacific



From: Pennington et al 2006

Source AA: phe = 4.2

Source AA: phe = 7.2

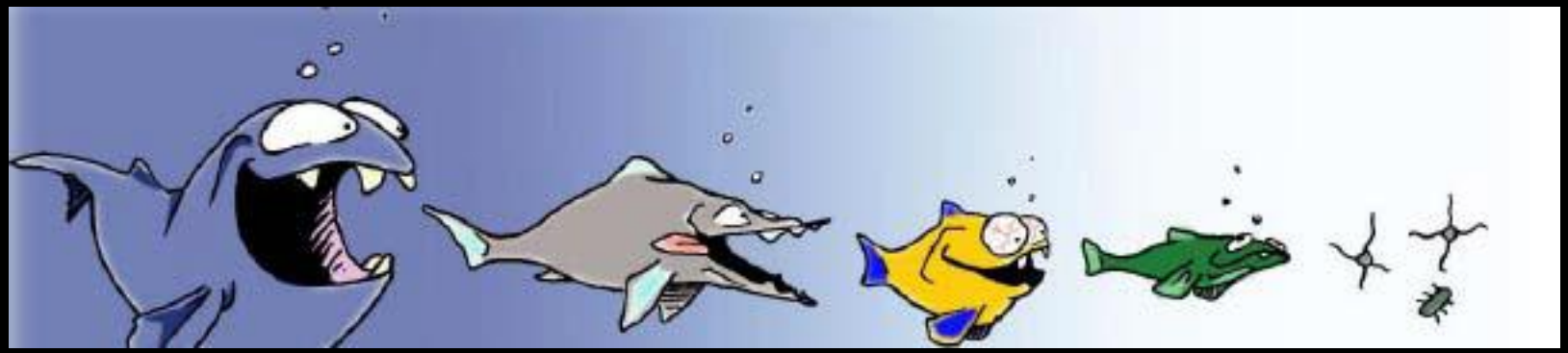
N* is a Redfield N:P ratio derived such that:

N* > 1 nitrogen fixation dominates ($\delta^{15}N$ <5 ‰)

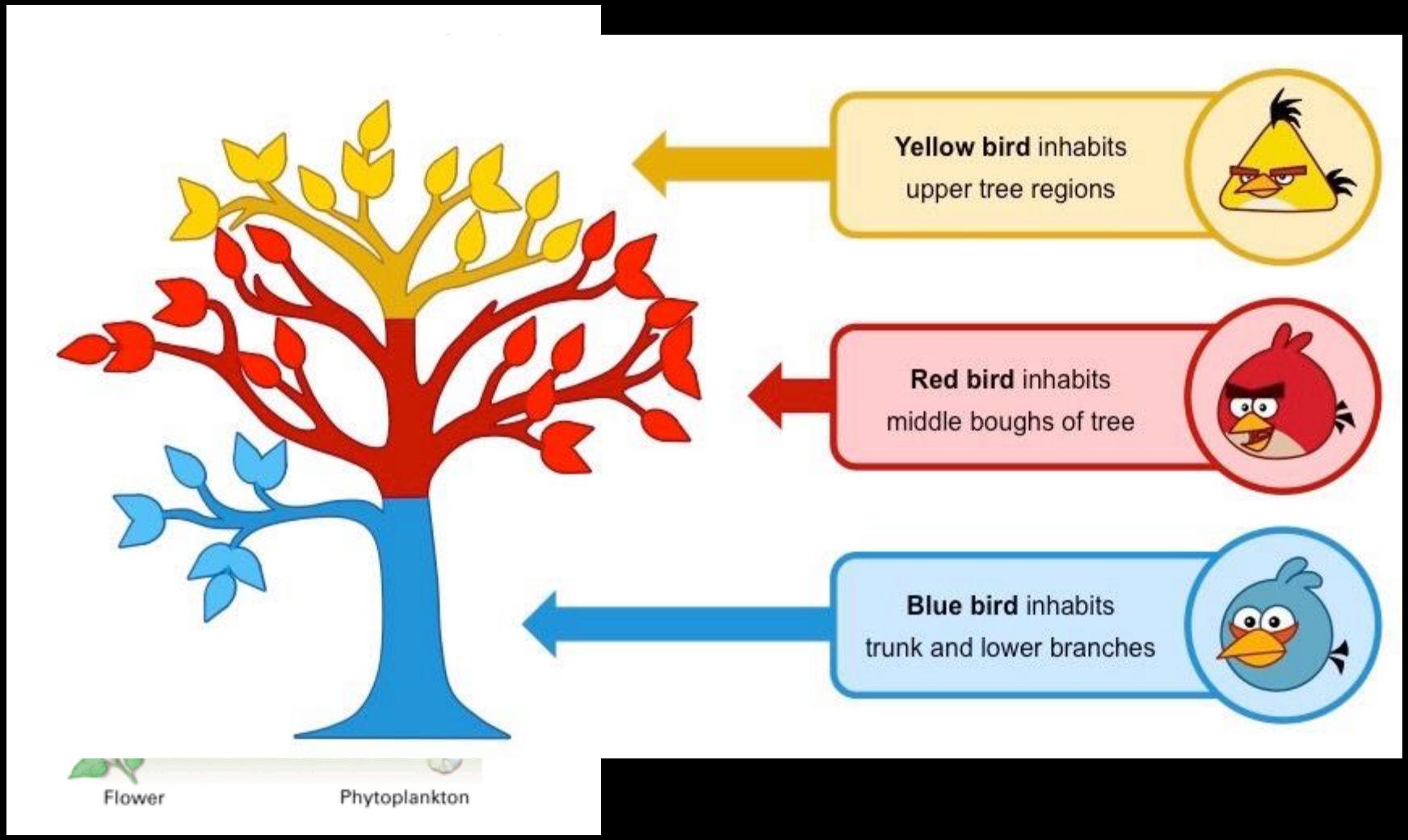
N* < 1 denitrifcation dominates ($\delta^{15}N \approx$ 5-15 ‰)

Isotopes and food webs

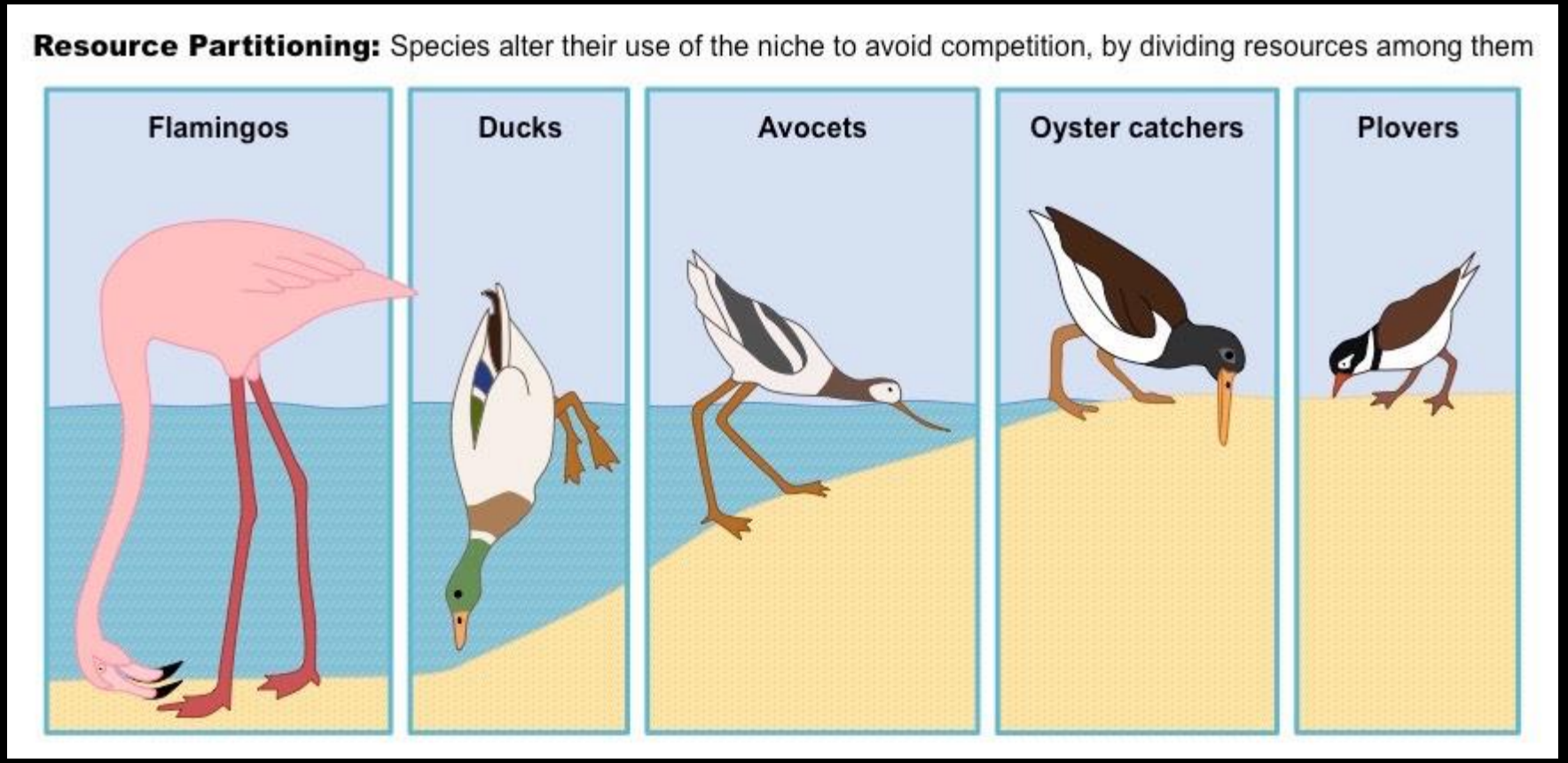
- You are How you eat!



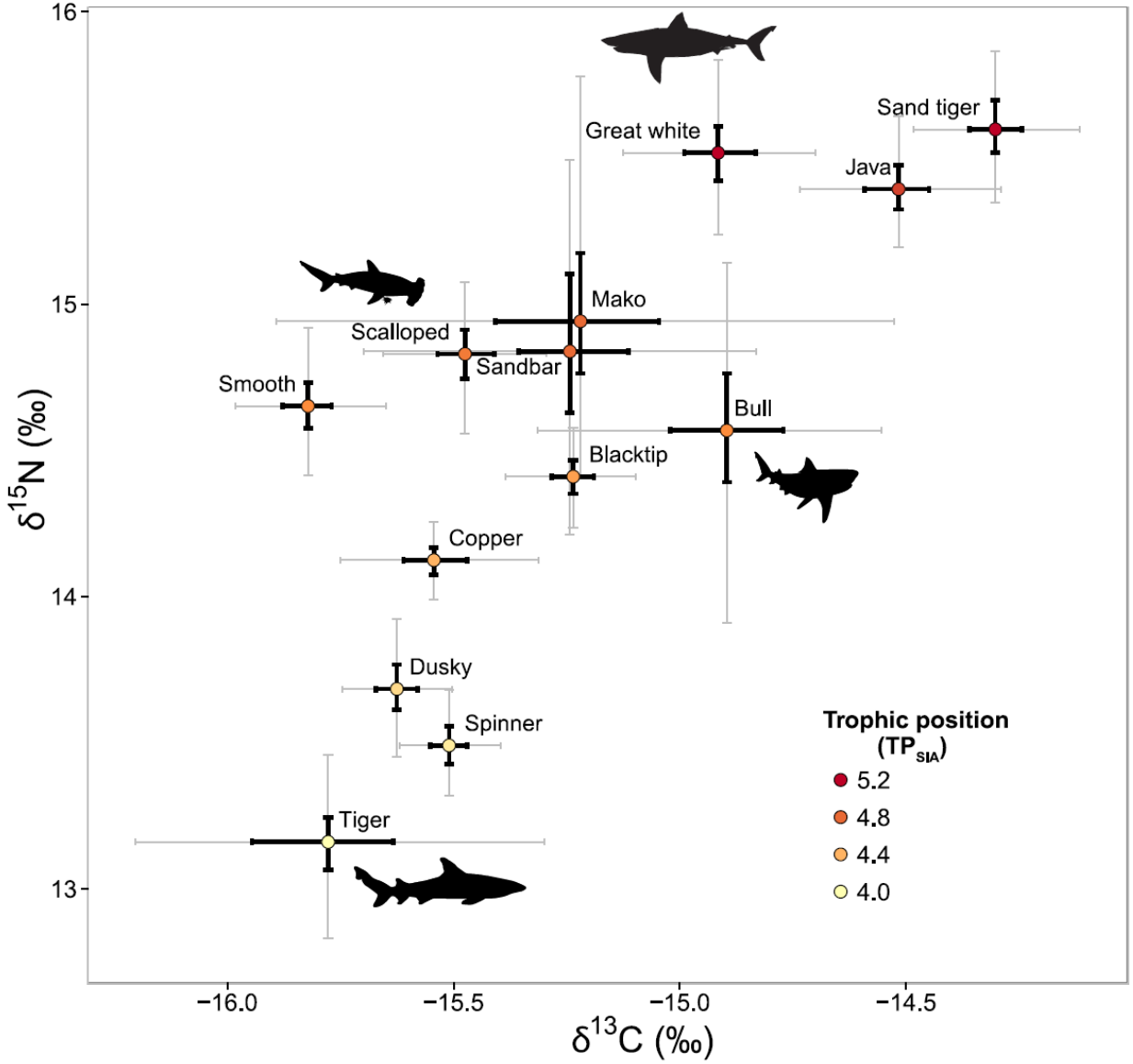
Trophic niche----Trophic level

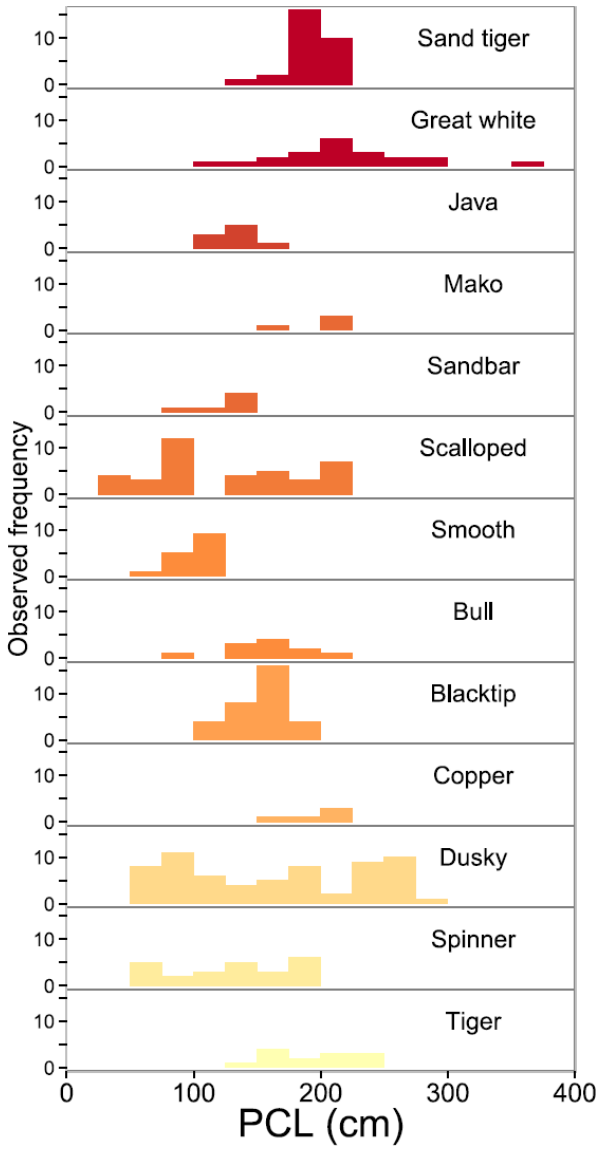


Trophic niche----Diet



- Organisms can forage at the same trophic level but feed on different prey types


16
15
14
13
δ^{15}N (‰)
−16.0
−15.5
−15.0
−14.5
δ^{13}C (‰)
Great white
Sand tiger
Java
Mako
Scalloped
Sandbar
Smooth
Bull
Blacktip
Copper
Dusky
Spinner
Tiger
Trophic position
(TP_{SIA})
5.2
4.8
4.4
4.0


Observed frequency
Sand tiger
Great white
Java
Mako
Sandbar
Scalloped
Smooth
Bull
Blacktip
Copper
Dusky
Spinner
Tiger
0
100
200
300
400
PCL (cm)

Trophic Niche----Niche width

Specialist

Narrow niche width
-Herbivore
-Carnivore

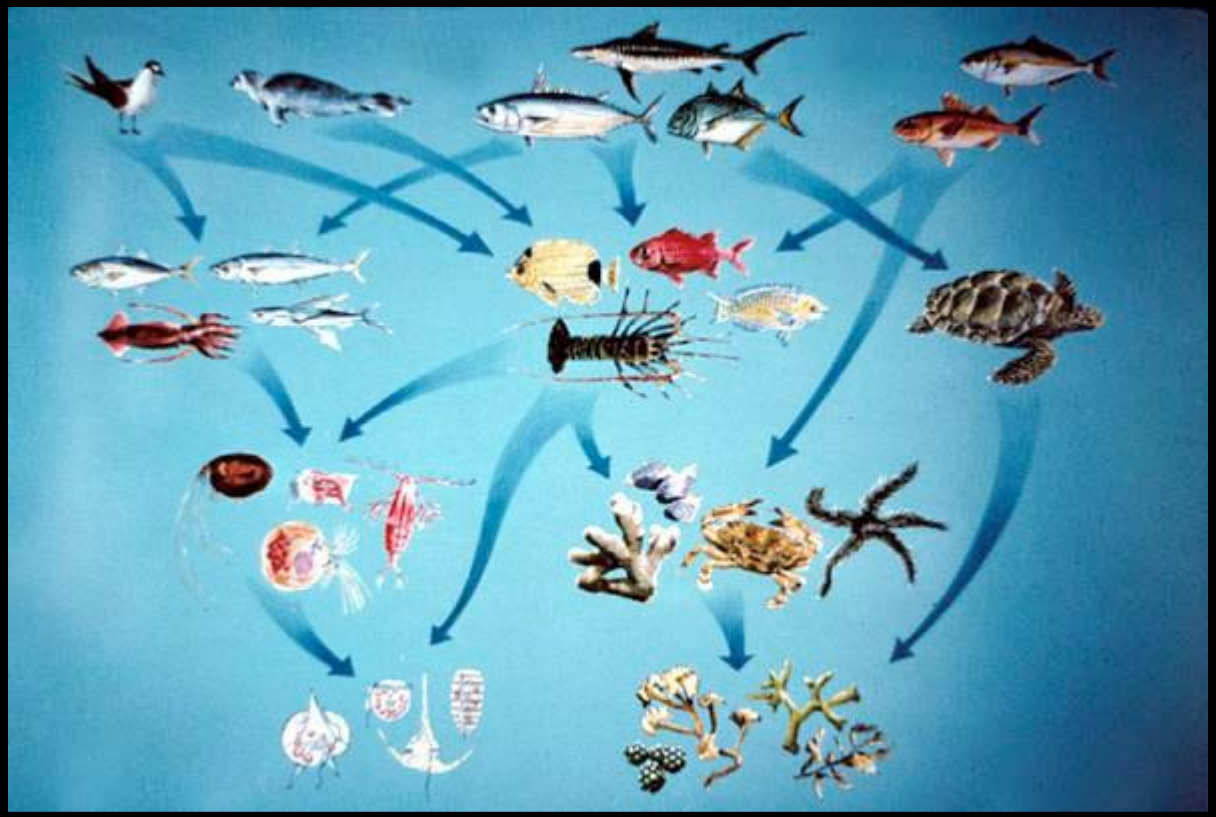
Generalist

Broad niche width
-Omnivore

Trophic Niche- Food web

Specialist Generalist Specialist

Trophic level



Pelagic Benthic

A niche for isotopic ecology

Seth D Newsome[1*], Carlos Martinez del Rio[2], Stuart Bearhop[3], and Donald L Phillips[4]

Fifty years ago, GE Hutchinson defined the ecological niche as a hypervolume in n-dimensional space with environmental variables as axes. Ecologists have recently developed renewed interest in the concept, and technological advances now allow us to use stable isotope analyses to quantify these niche dimensions. Analogously, we define the isotopic niche as an area (in δ-space) with isotopic values (δ-values) as coordinates. To make isotopic measurements comparable to other niche formulations, we propose transforming δ-space to p-space, where axes represent relative proportions of isotopically distinct resources incorporated into an animal's tissues. We illustrate the isotopic niche with two examples: the application of historic ecology to conservation biology and ontogenetic niche shifts. Sustaining renewed interest in the niche requires novel methods to measure the variables that define it. Stable isotope analyses are a natural, perhaps crucial, tool in contemporary studies of the ecological niche.

Front Ecol Environ 2007; 5(8): 429–436, doi:10.1890/060150.01

Ecology, 88(1), 2007, pp. 42–48

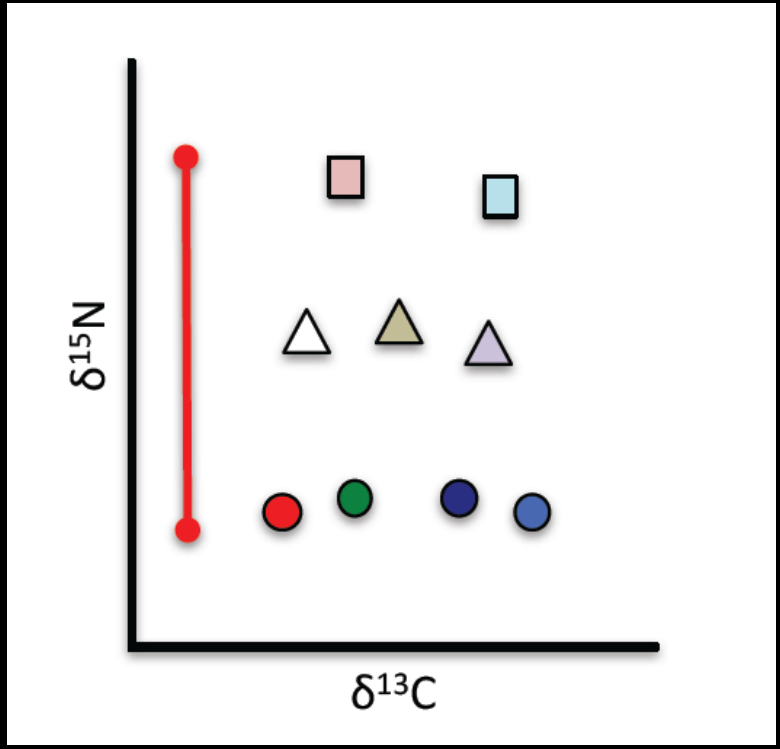
CAN STABLE ISOTOPE RATIOS PROVIDE FOR COMMUNITY-WIDE MEASURES OF TROPHIC STRUCTURE?

CRAIG A. LAYMAN,[1,5] D. ALBREY ARRINGTON,[2] CARMEN G. MONTAÑA,[3] AND DAVID M. POST[4]

[1]*Marine Science Program, Department of Biological Sciences, 3000 NE 151st Street, North Miami, Florida 33181 USA*
[2]*Loxahatchee River District, 2500 Jupiter Park Drive, Jupiter, Florida 33458-8964 USA*
[3]*Universidad de Los Llanos Ezequiel Zamora, UNELLEZ, Guanare, Apartado Postal 3310 Venezuela*
[4]*Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520-8106 USA*

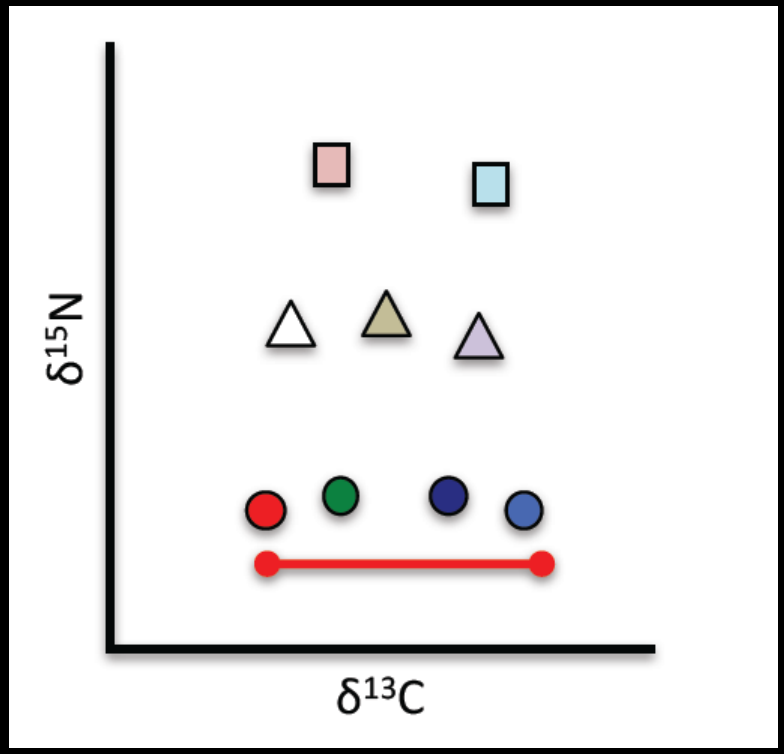
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web



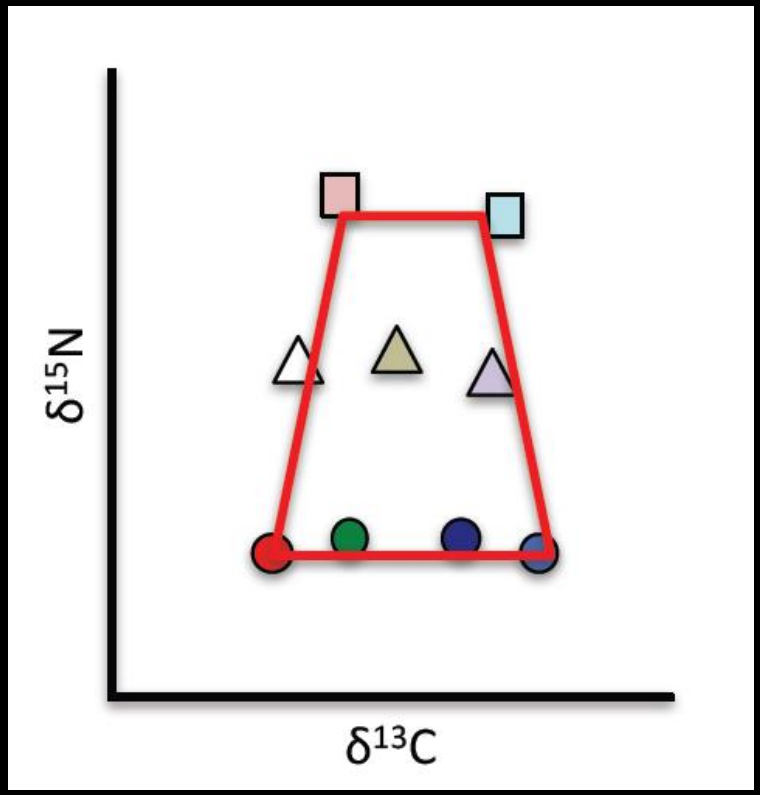
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web
2. CR
   $\delta^{13}C$ range- Breadth of resource use



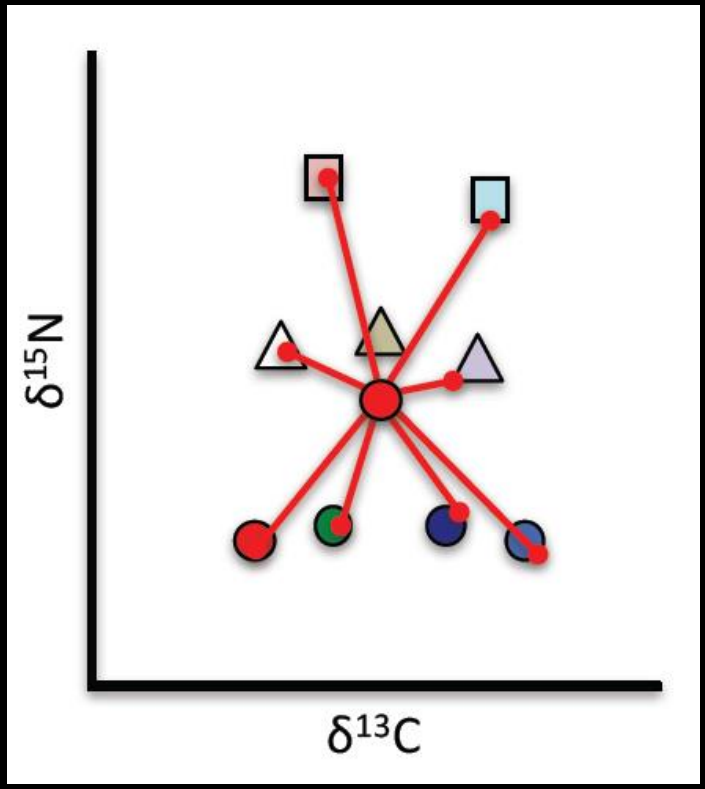
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web
2. CR
   $\delta^{13}C$ range- Breadth of resource use
3. TA
   Total area-Size of food web in δ space.



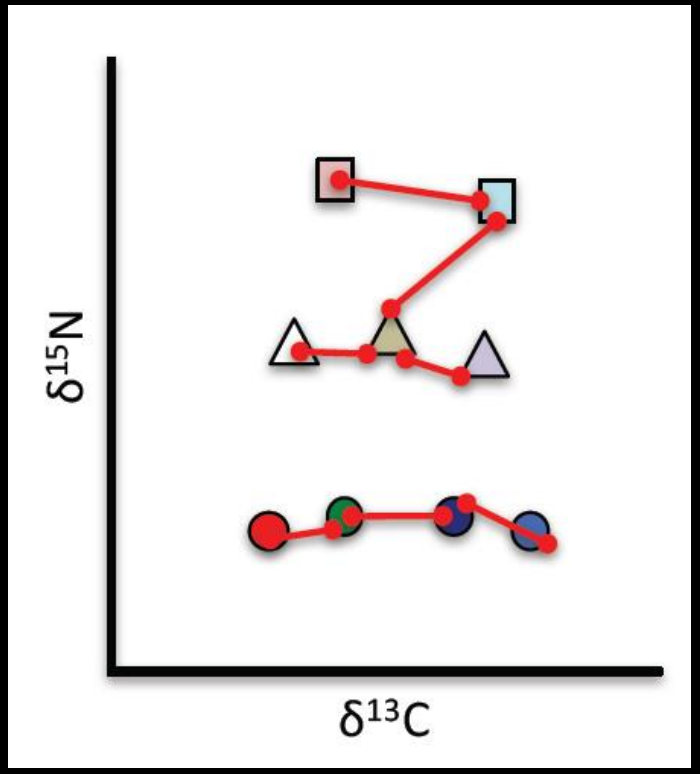
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web
2. CR
   $\delta^{13}C$ range- Breadth of resource use
3. TA
   Total area-Size of food web in δ space.
4. CD
   Mean distance to centroid



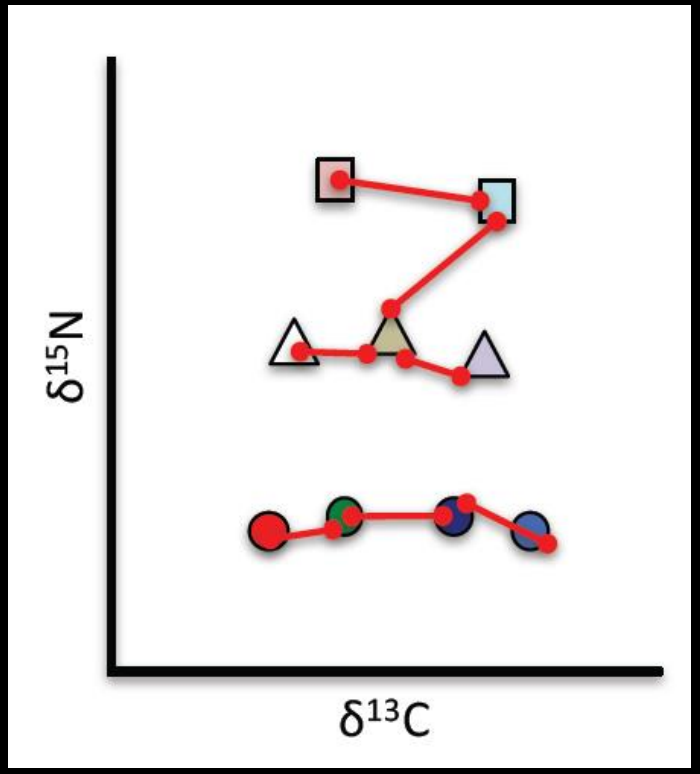
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web
2. CR
   $\delta^{13}C$ range- Breadth of resource use
3. TA
   Total area-Size of food web in δ space.
4. CD
   Mean distance to centroid
5. NND
   Mean nearest neighbor distance



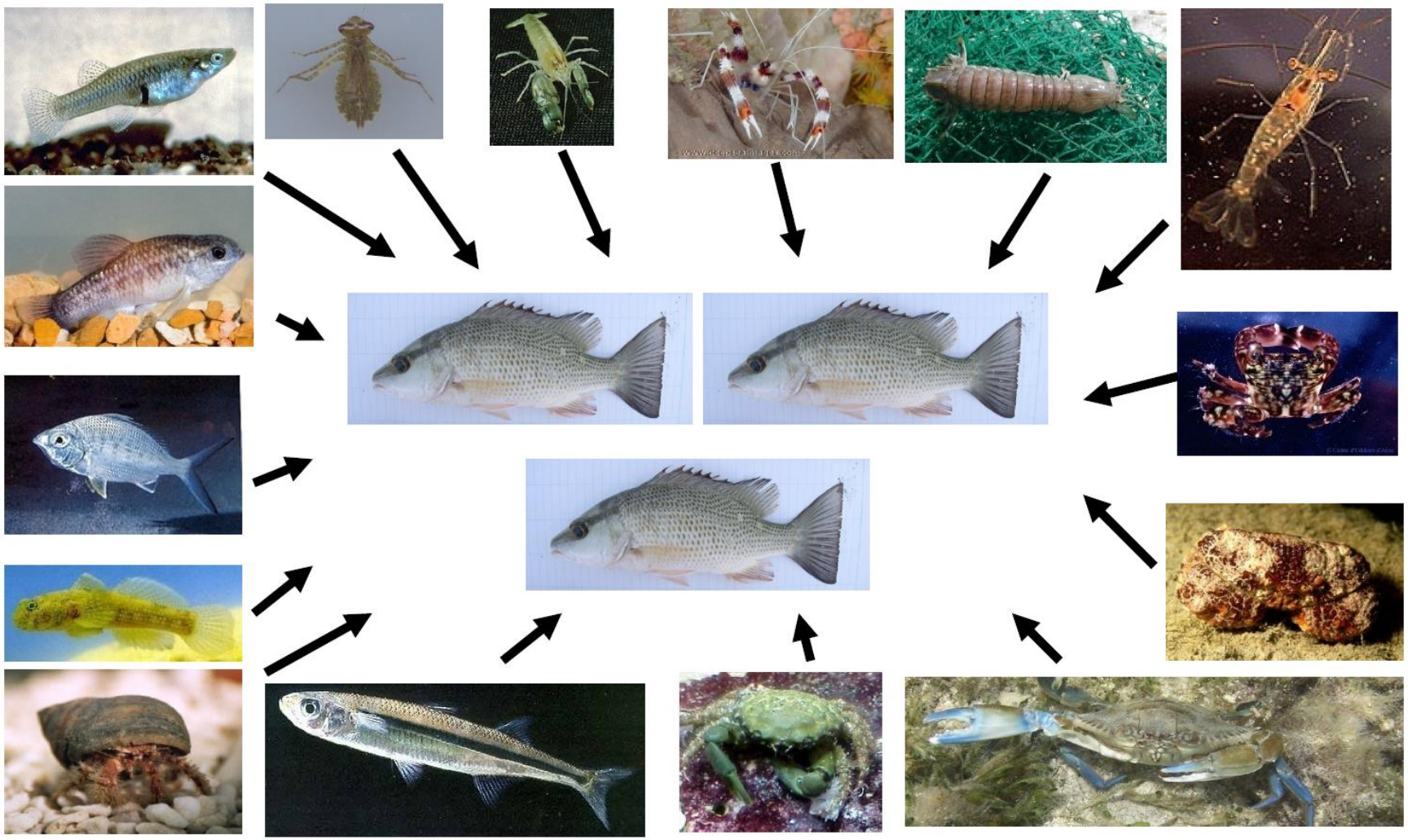
Layman matrics

1. NR
   $\delta^{15}N$ range- Trophic height of food web
2. CR
   $\delta^{13}C$ range- Breadth of resource use
3. TA
   Total area-Size of food web in δ space.
4. CD
   Mean distance to centroid
5. NND
   Mean nearest neighbor distance
6. SDNND
   SD nearest neighbor distance

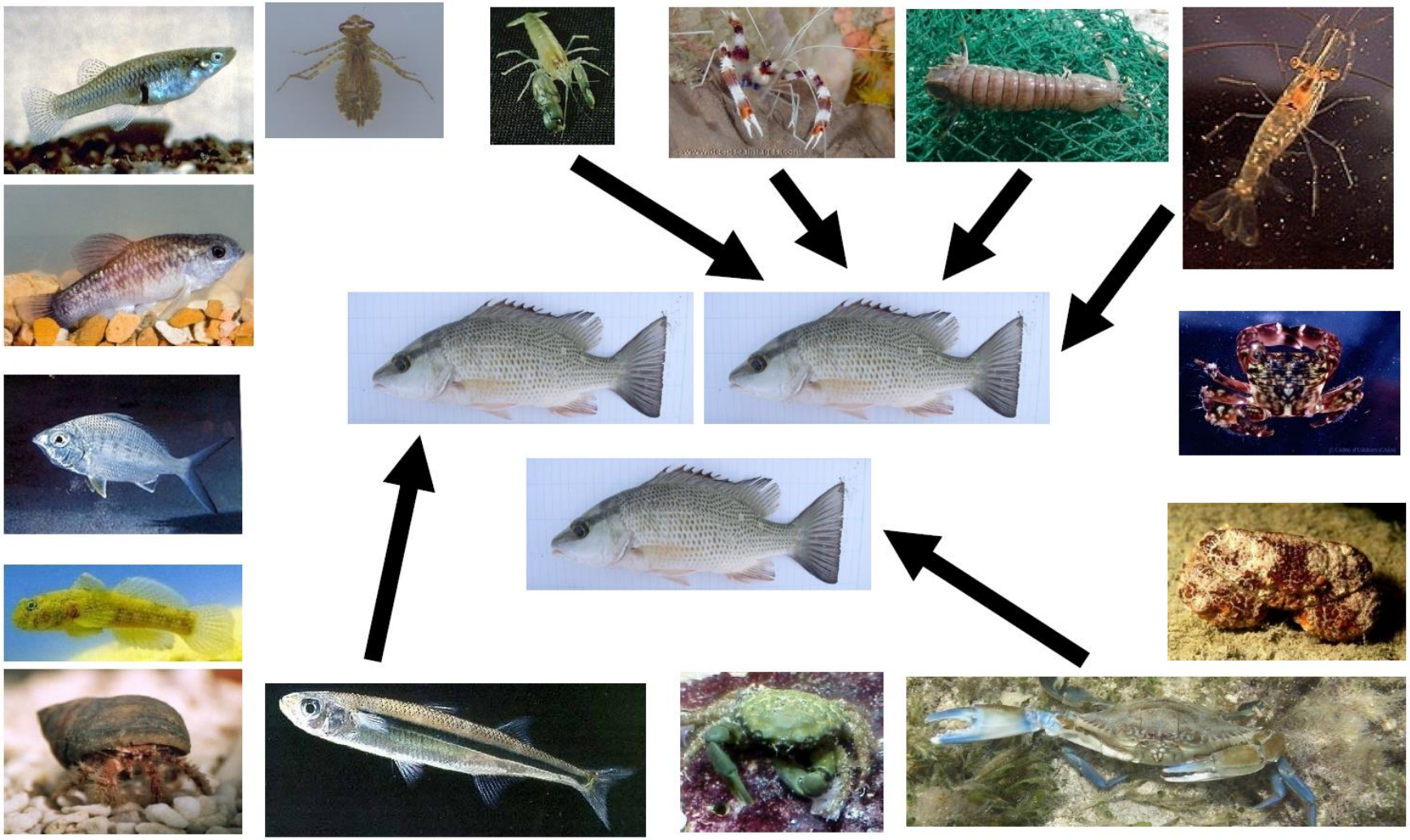


"Generalist" population:

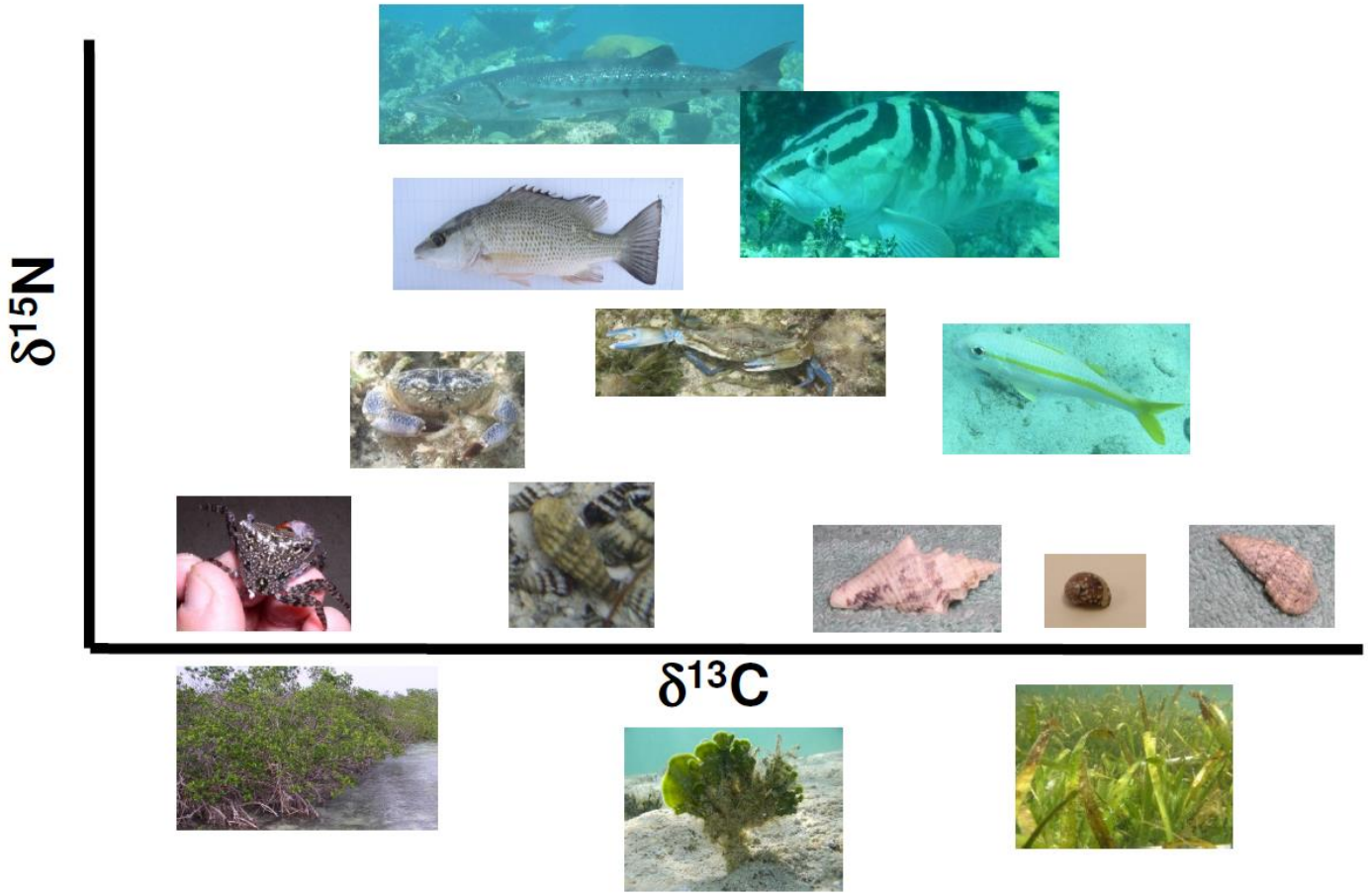
(1) *All* individuals have *variable* diet



“Generalist” population:
(2) Individual specificity in diet



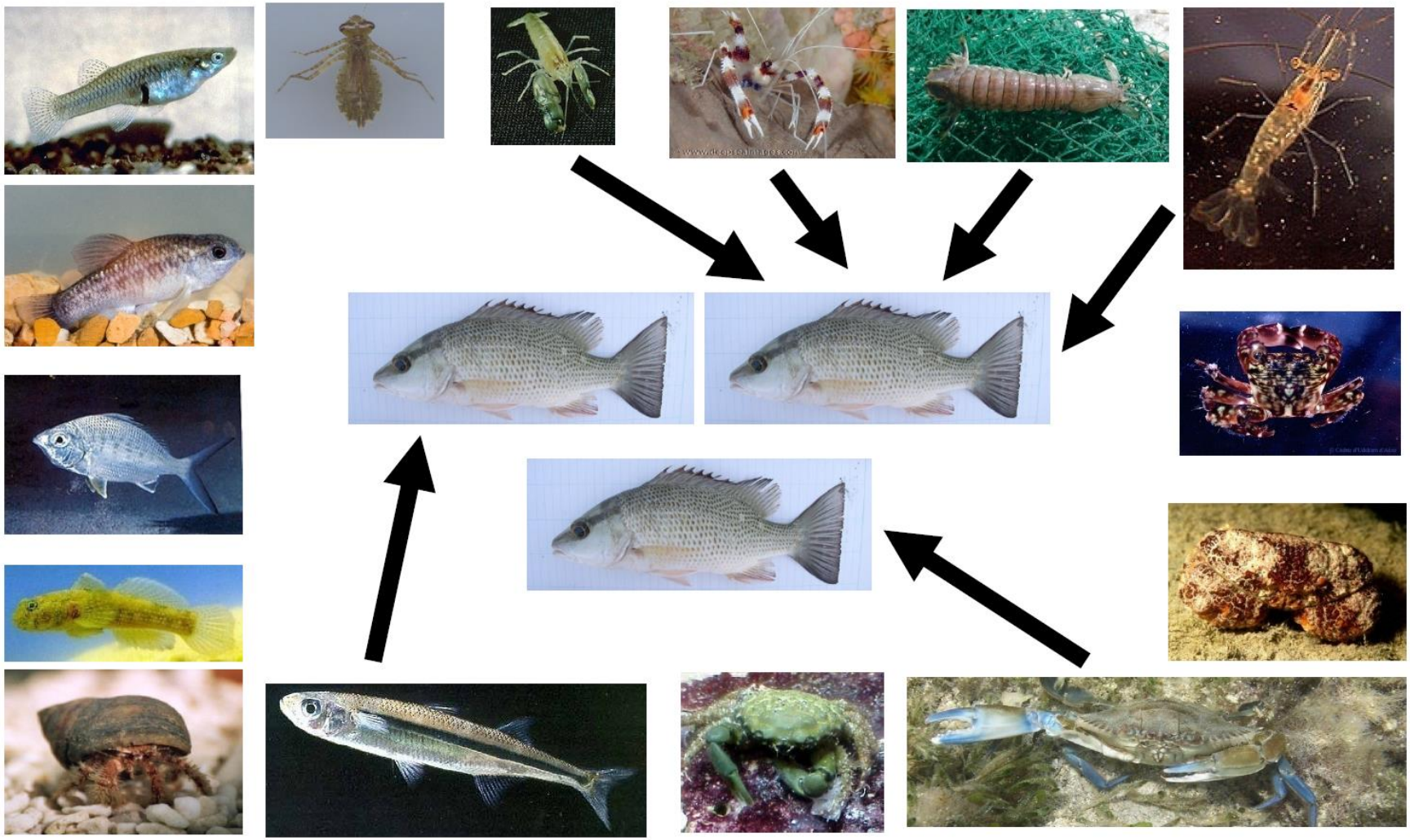
$\delta^{15}N$ - $\delta^{13}C$ Bi-plots as "Niche" Space



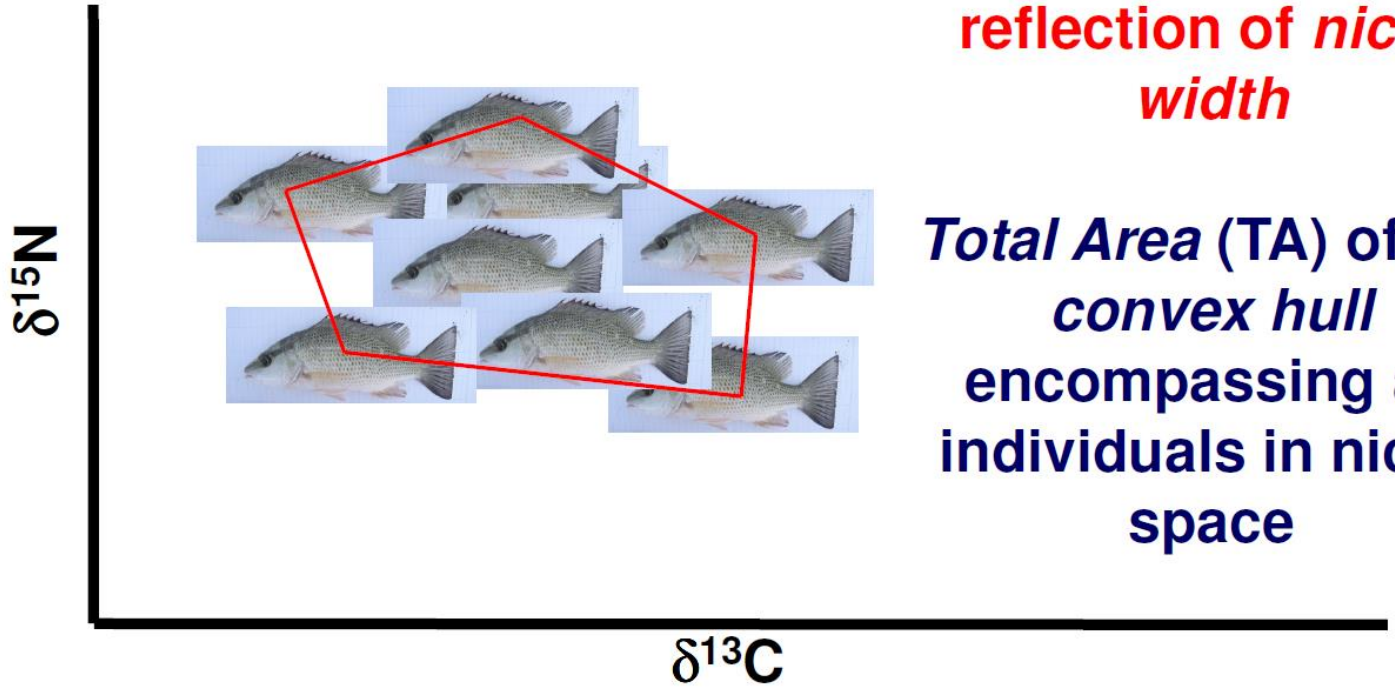
Position in bi-plot space a representation of that species *trophic niche*

Core Question #2

High Degree of Intraspecific Niche Variation Suggests Individual Specialization



Trophic Niche Width



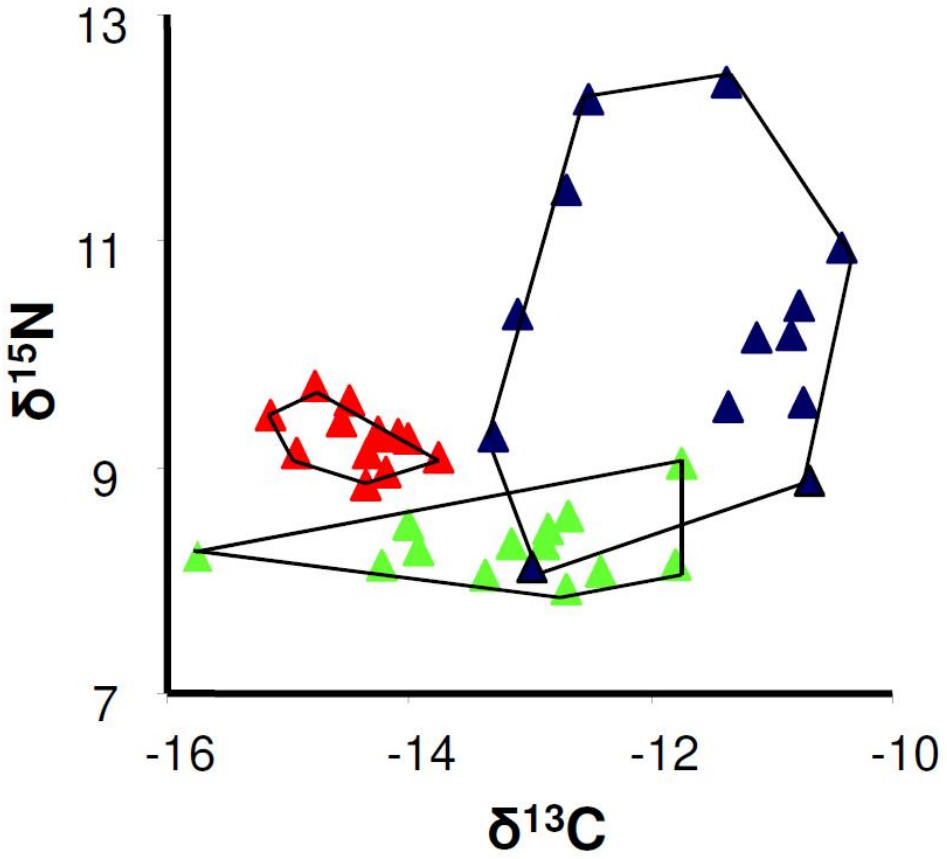
This variation is a reflection of *niche width*

***Total Area* (TA) of the *convex hull* encompassing all individuals in niche space**

One of a series of metrics to quantitatively describe food web structure

Layman et al., *2007, Ecology*
Layman and Post, *2008, Ecology*

Niche Width Across Fragmentation Gradient



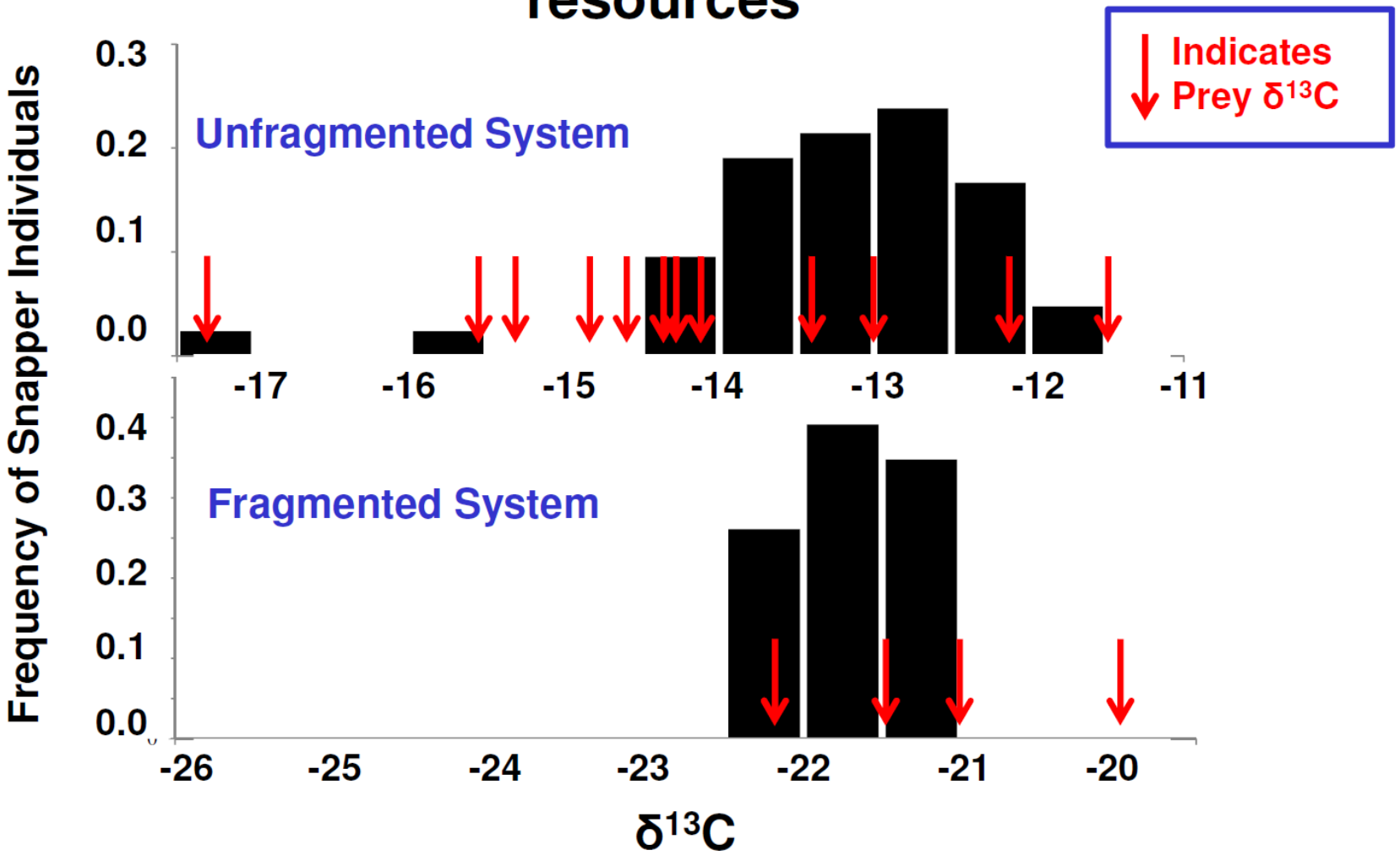
% Fragmented	Niche Width
0	8.9
51	2.5
99	0.6

13 from each creek system

Core Question #2

Layman et al., *2007, Ecology Letters*

Snapper niche diversity tracks diversity of prey resources



Core Question #2

Layman et al. *Unpublished Data*

Jackson ellipse

Ecology, 88(1), 2007, pp. 42–48

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CRAIG A. LAYMAN,[1,5] D. ALBREY ARRINGTON,[2] CARMEN G. MONTAÑA,[3] AND DAVID M. POST[4]

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Journal of Animal Ecology

British Ecological Society

Journal of Animal Ecology 2011, **80**, 595–602

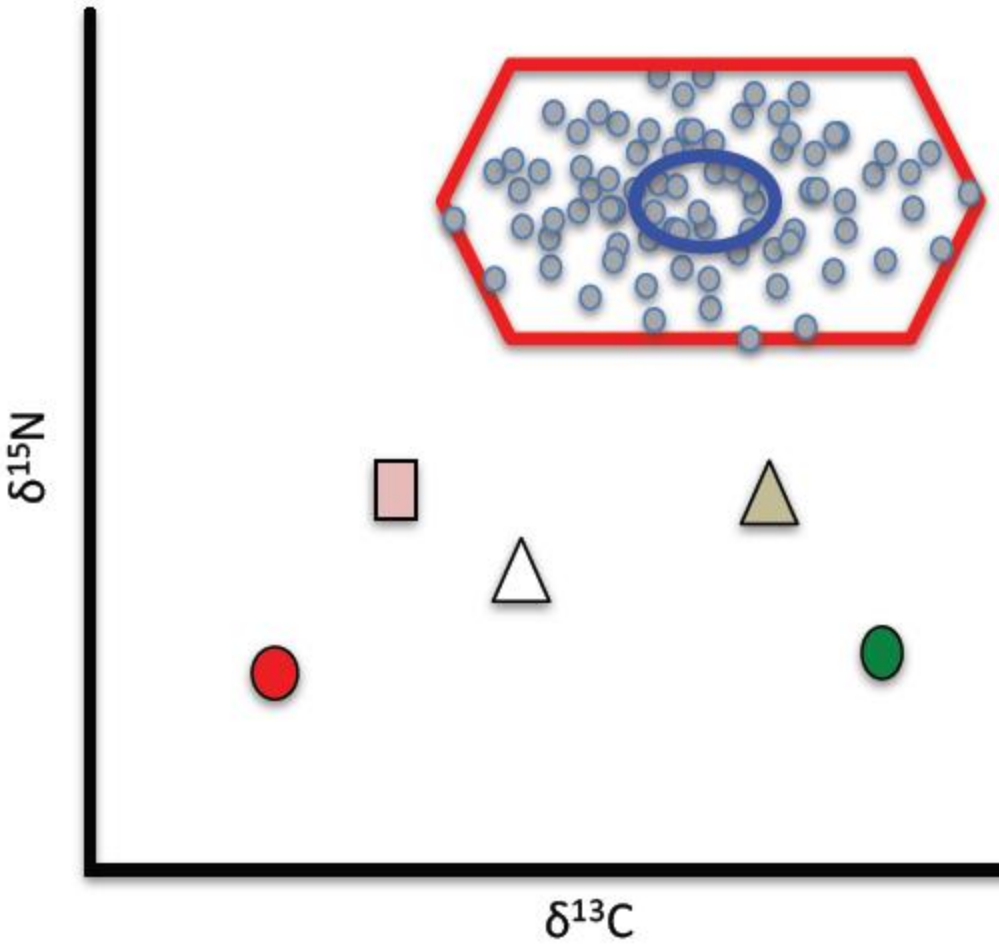
doi: 10.1111/j.1365-2656.2011.01806.x

Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R

Andrew L. Jackson[1]*, Richard Inger[2], Andrew C. Parnell[3] and Stuart Bearhop[2]

[1]*Department of Zoology, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland;* [2]*Centre for Ecology & Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, Cornwall, TR10 9EZ, UK; and* [3]*Department of Statistics, School of Mathematical Sciences, University College Dublin, Dublin 4, Ireland*

Jackson ellipse



TA – Total niche

SEA – Realised niche

SIA using R

- MixSIAR
- SIBER
- SIDER
- SIAR
- Http://github.com/AndrewLJackson

Experimental design

- What is your question?
- Diet, migration, trophic interactions
- Individual, population, community, ecosystem
- Seasonal variation
- Know your system?
- Which & how many isotopes, better resolution with more than C & N
- Baselines

Baselines

- The foundation of every isotope study
- Strong baseline supports stone results
- Devote time, effort and $$$ to developing a thorough and reliable baseline
- Sample primary producers
- Collect invertebrates at lowest feasible taxonomic level
- Include temporally significant resources (MDN)?

Preservation

- All preservation methods effect isotope ratios, but some have a greater effect than others…

- Drying (48hrs 60℃)
- Freezing (Best way)
- Ethanol and Formalin (No)

SIA applications in SHOU

- Freshwater ecosystem
  Lake fish
  Lake Food web structure
- Marine Ecosystem
  Squids
  Sharks

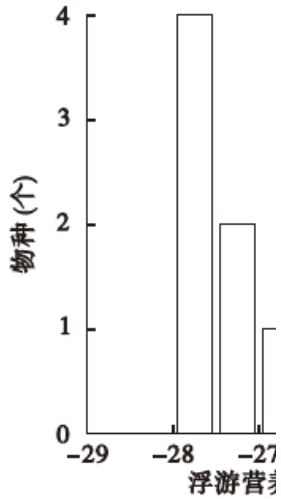
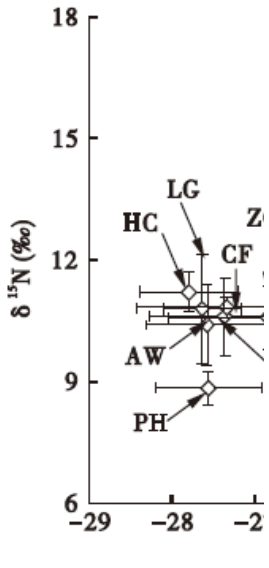


图 2　东太湖主要物

Fig. 2　δ[13] C freque
Lake Taihu



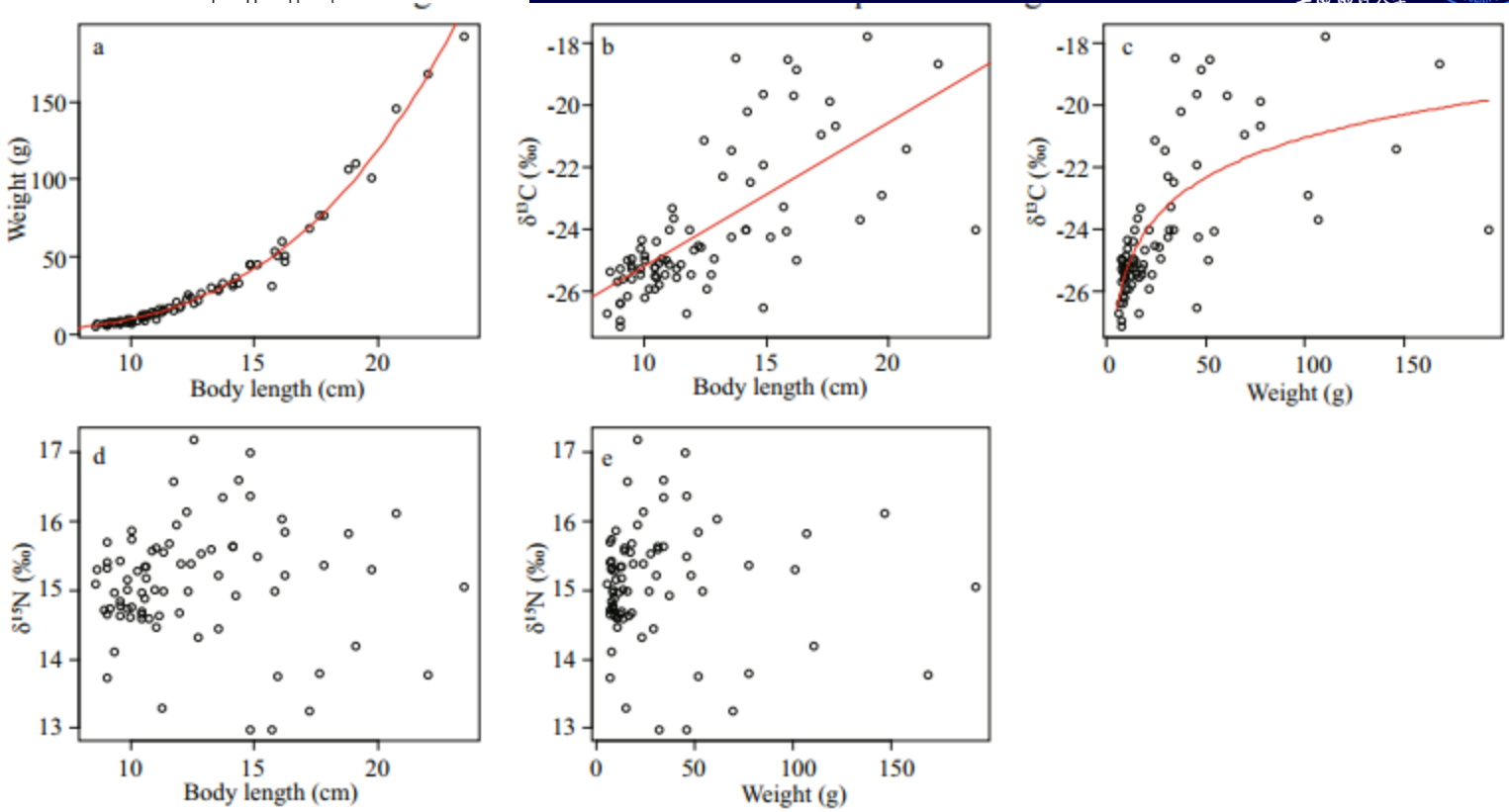


Fig.2 Relationship between *Cultrichthys erythropterus* weight and standard length (a), muscle δ[13]C and standard length and weight (b, c), and muscle δ[15]N and body length and weight (d, e) in East Lake Taihu

Red lines represented the significant relationships.

图 3　东太湖食物网结构

Fig. 3　Food web structure of the East Lake Taihu

Chinese Journal of Oceanology and Limnology

http://dx.doi.org/10.1007/s00343-017-6225-z

Spatial variations in food web structures with alternative stable states: evidence from stable isotope analysis in a large eutrophic lake*

LI Yunkai (李云凯)[1,2], ZHANG Yuying (张毓颖)[2], XU Jun (徐军)[3], ZHANG Shuo (张硕)[1,**]

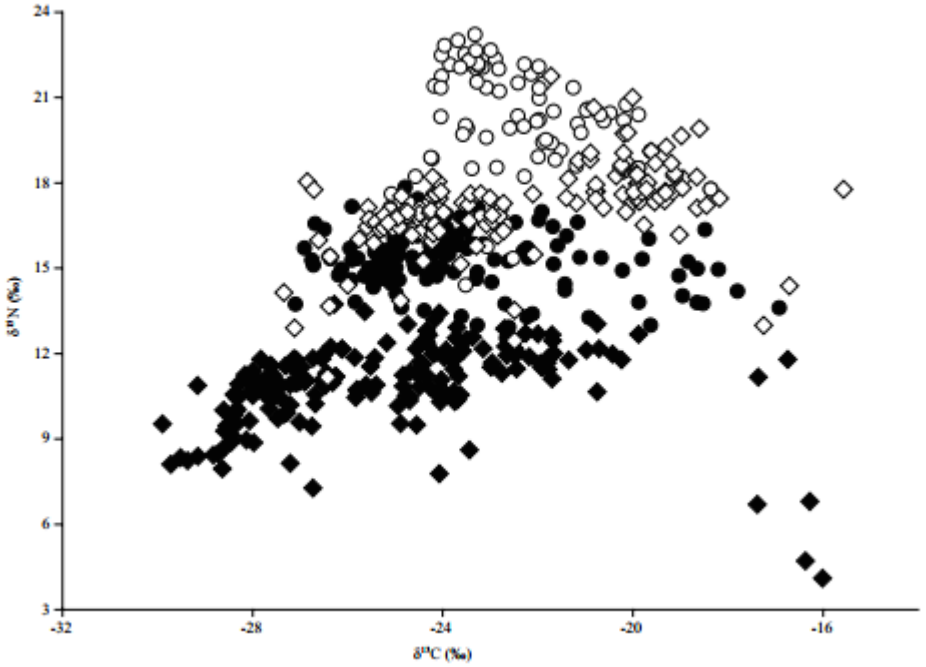


Fig.2 $\delta^{15}N$ and $\delta^{13}C$ values of organisms sampled in Meiliang Bay (MB) and East Taihu Lake (ETL)

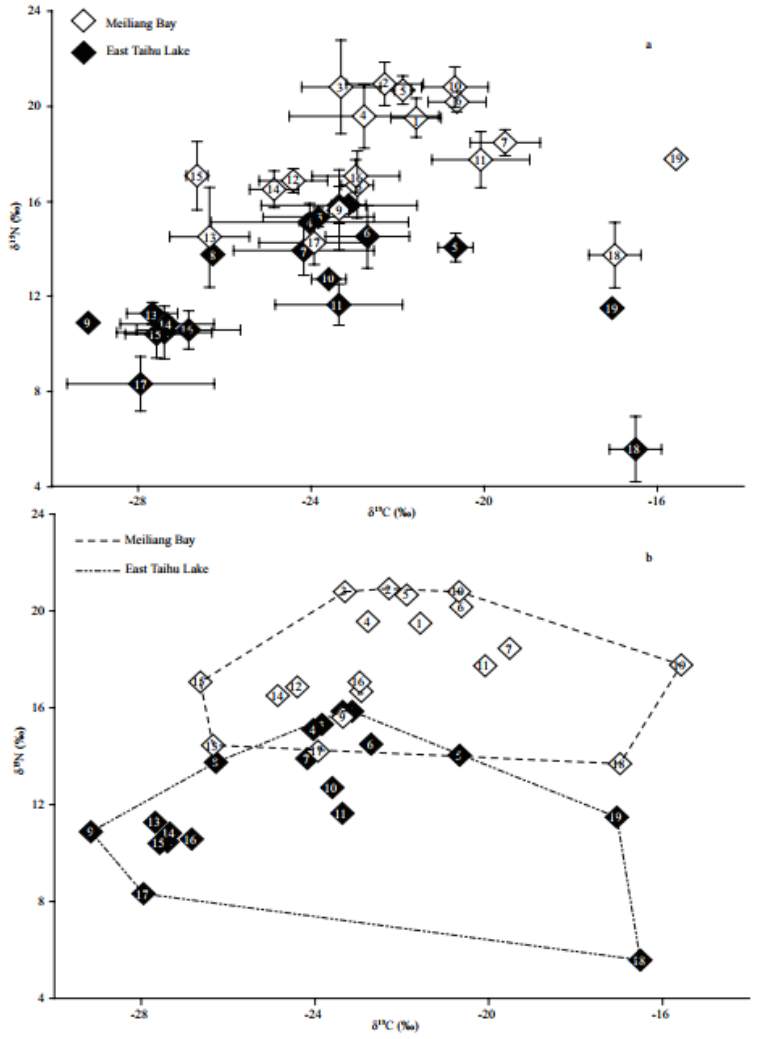


Fig.3 Mean values (±SD) of $\delta^{15}N$ and $\delta^{13}C$ of species sampled in Meiliang Bay (MB) (hollow diamond) and East Taihu Lake (ELT) (black diamond) (a); total area (convex hull area) of $\delta^{15}N$ and $\delta^{13}C$ bi-plots of MB and ETL of Taihu Lake (b)

Species code: 1: *Silurus* spp. 2: *Erythroculter ilishaeformis*; 3: *Coilia ectenes taihuensis*; 4: *Cultrichthys erythropterus*; 5: *Pelteobagrus fulvidraco*; 6: *Carassius auratus*; 7: *Cyprinus carpio*; 8: *Aristichthy snobilis*; 9: *Hypophthalmichthys molitrix*; 10: *Exopalaemon modestus*; 11: *Bellamya aeruginosa*; 12: *Corbicula fluminea*; 13: *Hyriopsis cumingii*; 14: *Unio douglasiae*; 15: *Anodonta woodiana*; 16: Zooplankton; 17: Phytoplankton; 18: *Potamogeton maackianus*; 19: *Myriophyllum spicatum*.

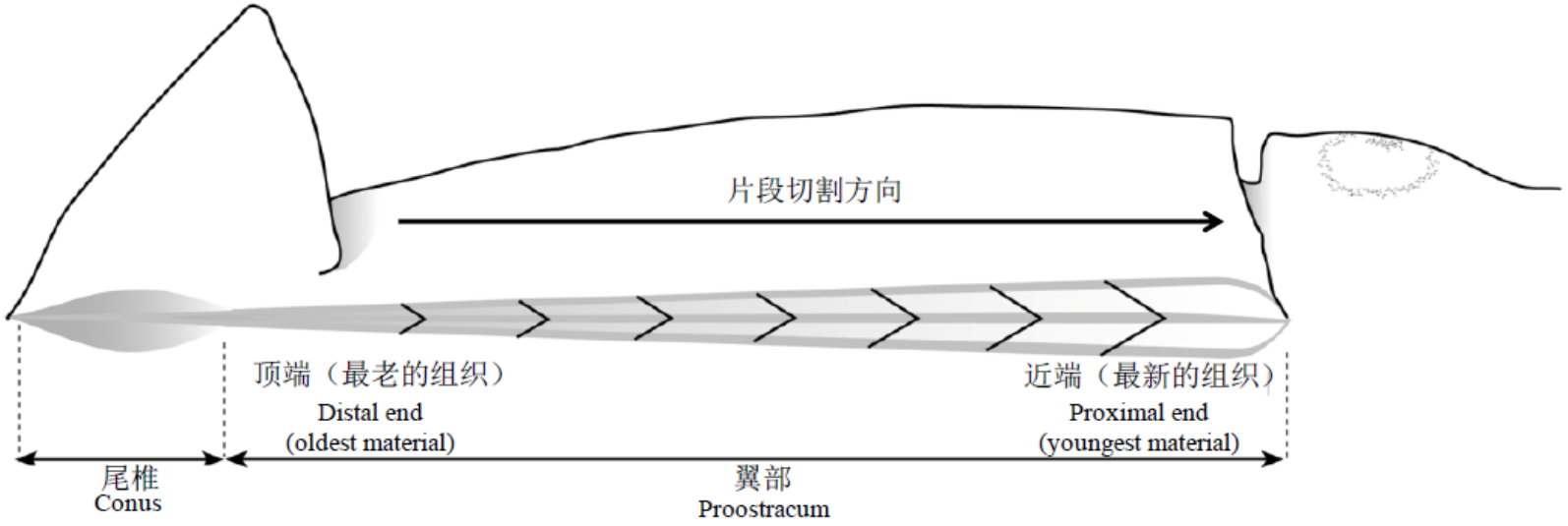
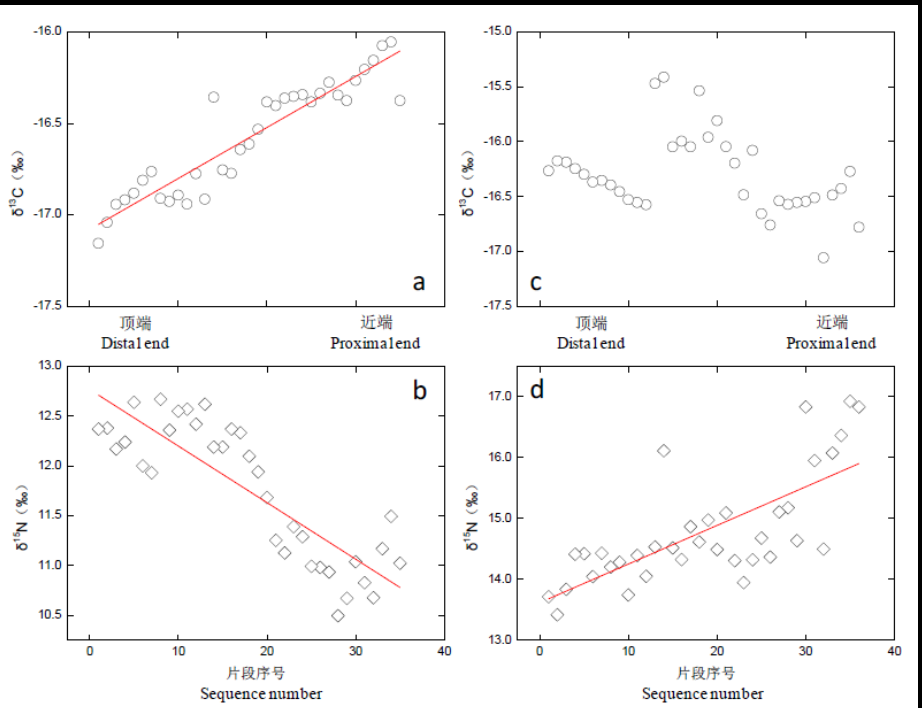


图 1.茎柔鱼内壳横截图

Fig.1 Transverse screenshots of jumbo squid gladius



注：图中红线代表的是稳定同位素值同切割片段序号（即生活史过程）存在显著线性关系

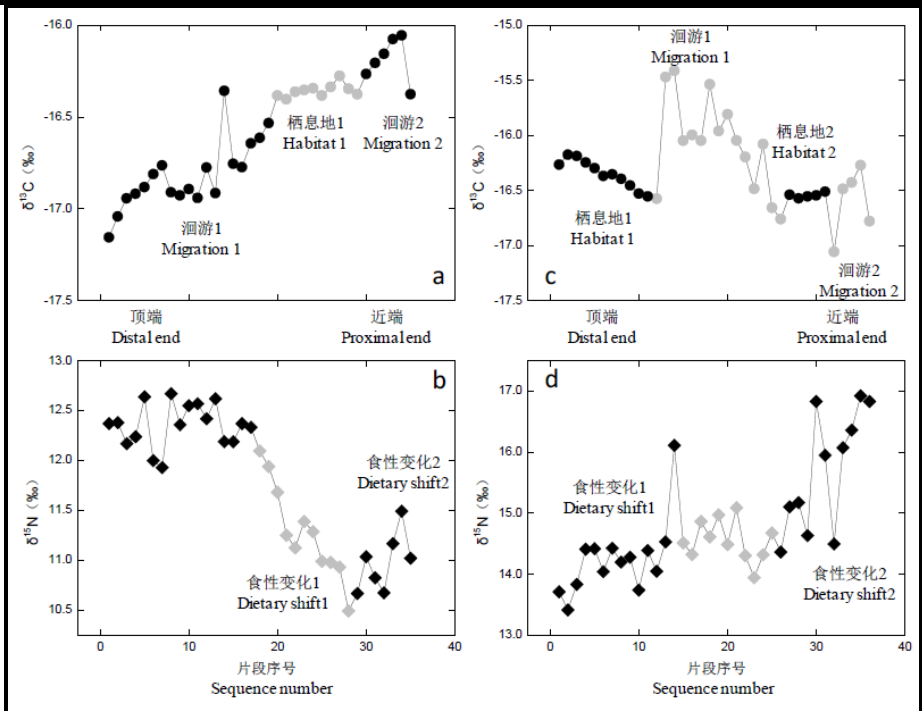


图 3 茎柔鱼 A（图 a, b）茎柔鱼 B (图 c, d) 生活史中的洄游和栖息地变化

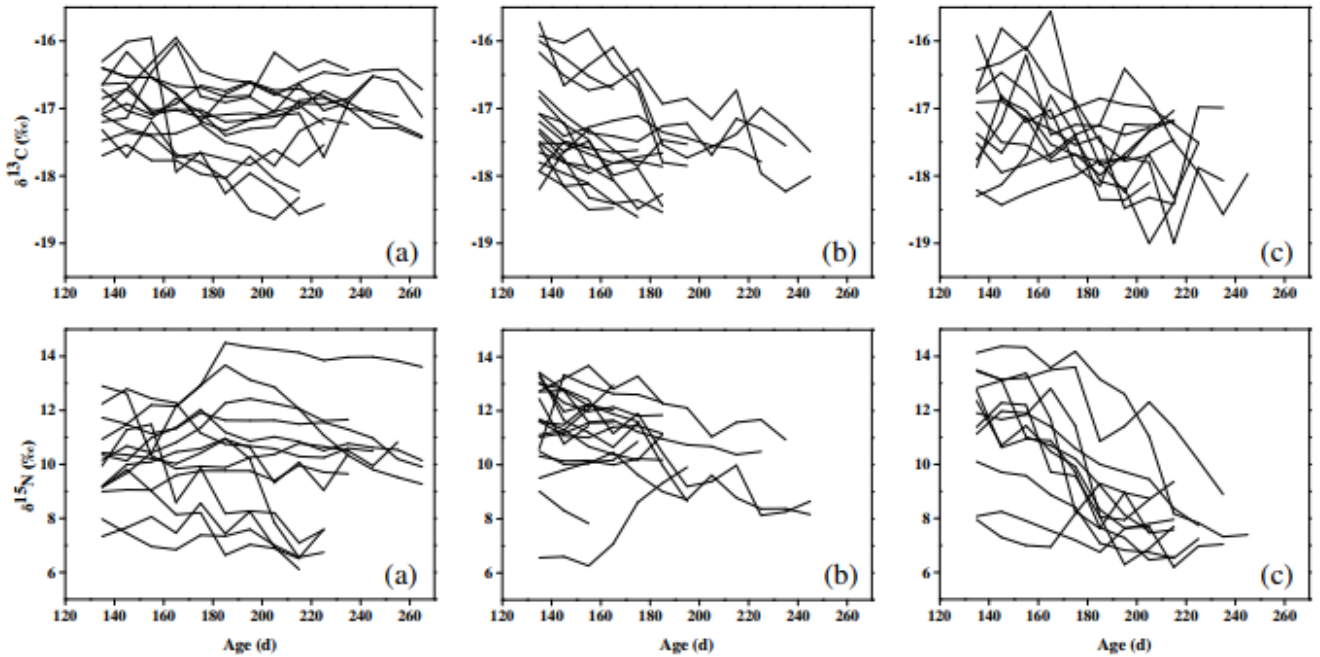


Fig. 4. The $\delta^{13}C$ and $\delta^{15}N$ values along the proostracum of *D. gigas* from 2009 (a), 2013 (b) and 2014 (c).

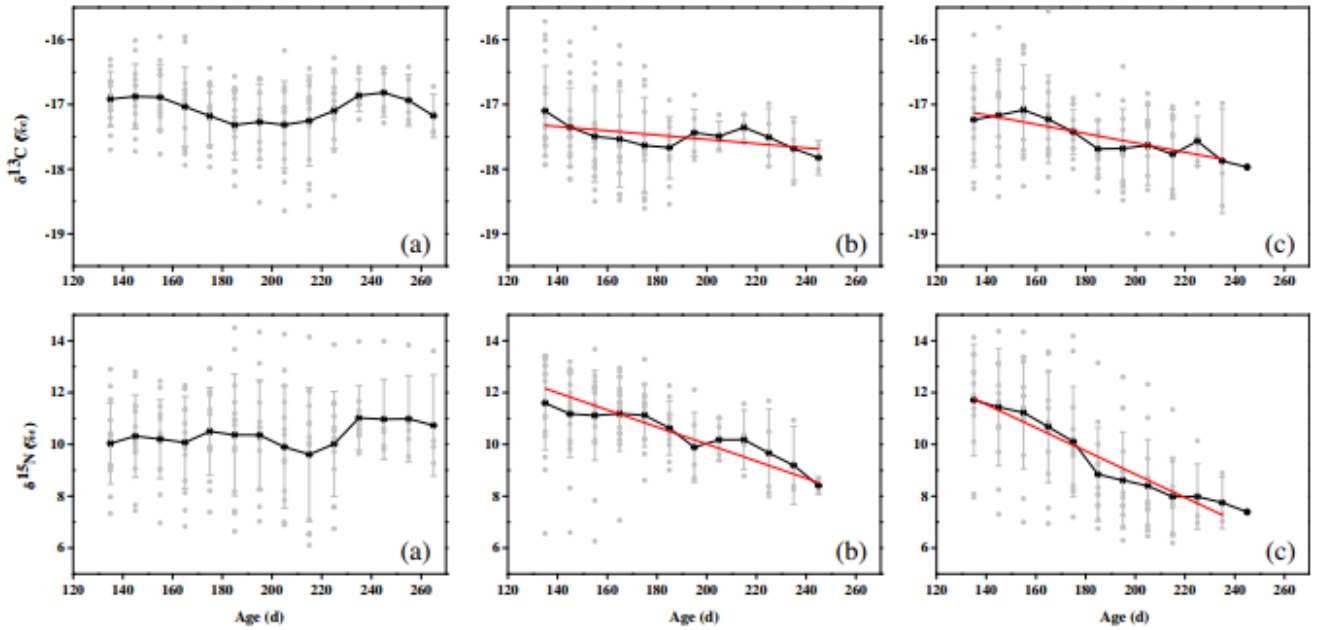
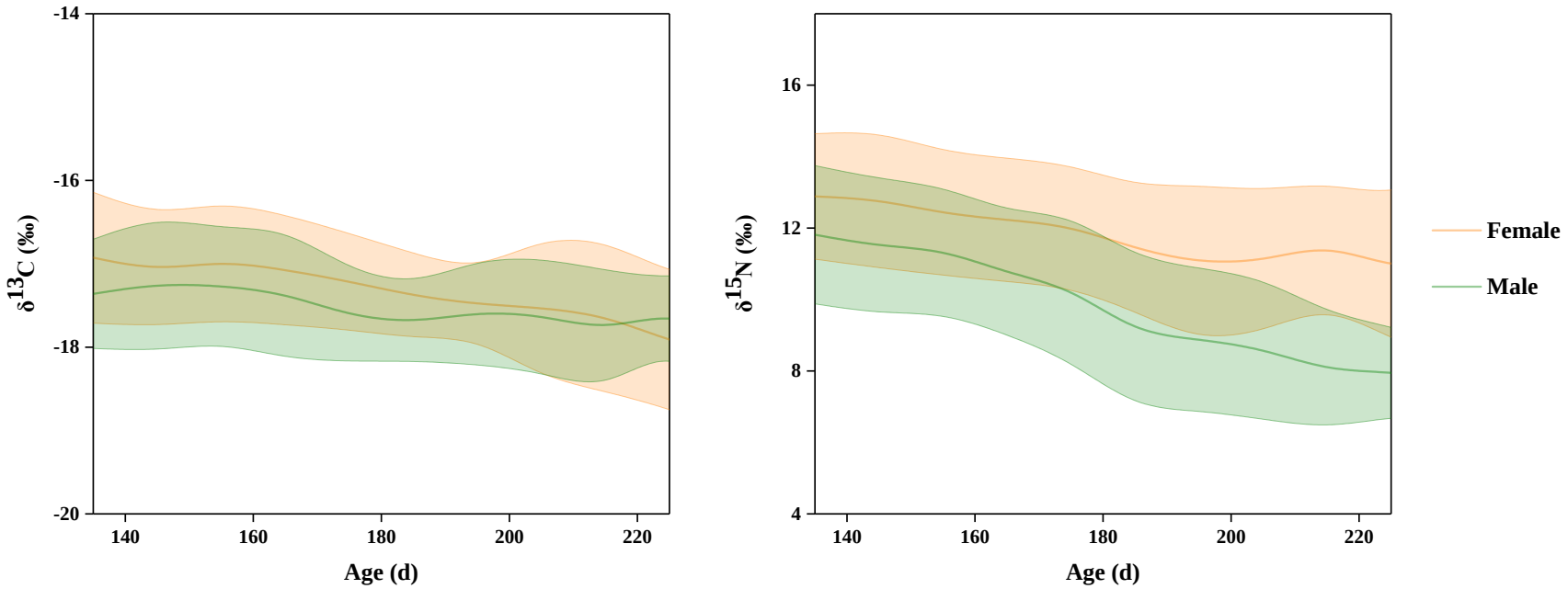


Fig. 5. Ontogenetic time series of $\delta^{13}C$ and $\delta^{15}N$ and mean (1SD) values for each ten-day period of 2009 (a), 2013 (b) and 2014 (c). Lines represent significant relationships.

Squid

2. Different isotopic trends between sex

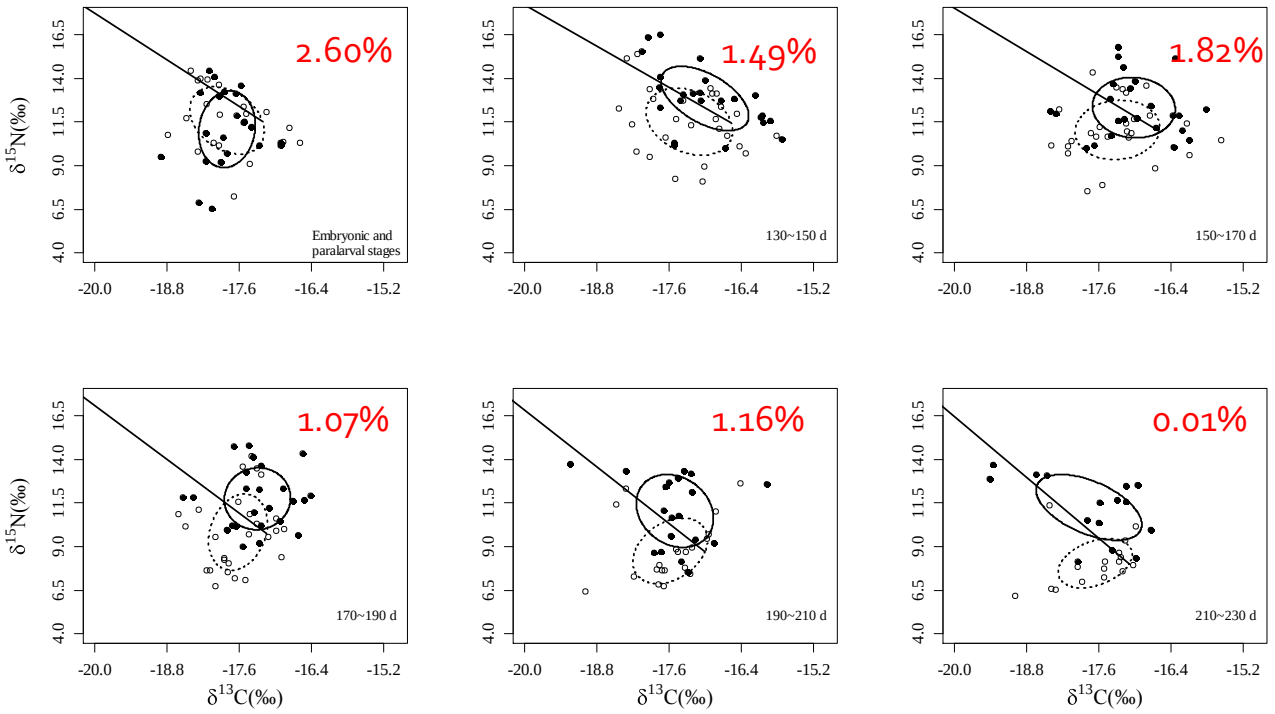


female *n*=12； male *n*=13； N=232

Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*

Squid

3. Sexual Segregation in trophic niche



Submitted to *Canadian Journal of Fisheries and Aquatic Sciences*

Research Article

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(wileyonlinelibrary.com) DOI: 10.1002/rcm.7396

Urea and lipid extraction treatment effects on $\delta^{15}N$ and $\delta^{13}C$ values in pelagic sharks

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[1]College of Marine Sciences, Shanghai Ocean University, 999 Huchenghuan Rd., Shanghai 201306, China
[2]Marine Sciences Program, School of Environment, Arts and Society, Florida International University, 3000 NE 151st, North Miami, FL 33181, USA
[3]Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Avenue, ON, N9B 3P4, Canada

RATIONALE: Stable isotope analysis (SIA) provides a powerful tool to investigate diverse ecological questions for marine species, but standardized values are required for comparative assessments. For elasmobranchs, their unique osmoregulatory strategy involves retention of ^{15}N-depleted urea in body tissues and this may bias $\delta^{15}N$ values. This may be a particular problem for large predatory species, where $\delta^{15}N$ discrimination between predator and consumed prey can be small.
METHODS: We evaluated three treatments (deionized water rinsing [DW], chloroform/methanol [LE] and combined chloroform/methanol and deionized water rinsing [LE+DW]) applied to white muscle tissue of 125 individuals from seven pelagic shark species to (i) assess urea and lipid effects on stable isotope values determined by IRMS and (ii) investigate mathematical normalization of these values.
RESULTS: For all species examined, the $\delta^{15}N$ values and C:N ratios increased significantly following all three treatments, identifying that urea removal is required prior to SIA of pelagic sharks. The more marked change in $\delta^{15}N$ values following DW (1.3 ± 0.4‰) and LE+DW (1.2 ± 0.6‰) than following LE alone (0.7 ± 0.4‰) indicated that water rinsing was more effective at removing urea. The DW and LE+DW treatments lowered the %N values, resulting in an increase in C:N ratios from the unexpected low values of <2.6 in bulk samples to ~3.1 ± 0.1, the expected value of protein. The $\delta^{13}C$ values of all species also increased significantly following LE and LE+DW treatments.
CONCLUSIONS: Given the mean change in $\delta^{15}N$ (1.2 ± 0.6‰) and $\delta^{13}C$ values (0.7 ± 0.4‰) across pelagic shark species, it is recommended that muscle tissue samples be treated with LE+DW to efficiently extract both urea and lipids to standardize isotopic values. Mathematical normalization of urea and lipid-extracted $\delta^{15}N_{LE+DW}$ and $\delta^{13}C_{LE+DW}$ values using the lipid-extracted $\delta^{15}N_{LE}$ and $\delta^{13}C_{LE}$ data were established for all pelagic shark species. Copyright © 2015 John Wiley & Sons, Ltd.

The stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in shark tissues provide a powerful tool to investigate important ecological questions regarding movement,[1,2] foraging strategies,[3,4] trophic position,[5,6] reproduction[7] and multi-species interactions.[8,9] Their application is based on the premise that, as predators consume prey, the carbon and nitrogen stable isotope ratio values of those predators fractionate systematically throughout the food web. Specifically, the change in $\delta^{13}C$ values of the predator are conservative (0–1‰), relative to the prey eaten, allowing identification of basal productivity or foraging locations;[10] while the $\delta^{15}N$ values show a more prominent increase per trophic step (2–5‰), providing a method to quantify the trophic position (TP) of predators and to estimate food chain length.[11–13]

When examining carbon stable isotope ratios, lipids in animals' tissues are a source of measurement uncertainty.[14] Lipids are depleted in ^{13}C relative to protein and carbohydrates;[15] consequently, the higher the tissue lipid content, the more negative the $\delta^{13}C$ value of the organism irrespective of diet or foraging location. Lipid removal or correction is therefore recommended to standardize data among species within a food web.[16] This procedure is widely adopted across a range of aquatic animal groups including teleost fish,[17,18] cephalopods,[19] crustaceans,[20] marine mammals[21] and elasmobranchs.[1,22,23]

Compared with most aquatic species, elasmobranchs adopt a unique osmoregulation mechanism.[24] Elasmobranchs maintain urea ($CO(NH_2)_2$) and trimethylamine oxide (TMAO; C_3H_9NO) in their tissues for osmotic balance. These soluble nitrogenous compounds may artificially lower $\delta^{15}N$ values in shark tissues confounding data interpretation as they are considered to be ^{15}N-depleted.[3,25,26] Furthermore, inter/intra-specific variations in the concentrations of urea and TMAO in body tissues of different species/life-stages that fluctuate depending on ambient salinity can bias comparisons among species.[27–29] This may be a particular problem for large predatory species, where $\delta^{15}N$ discrimination between predator and consumed prey can be small.[30] Similar to lipid extraction, the removal of urea and TMAO from shark muscle is therefore recommended prior to SIA.[25]

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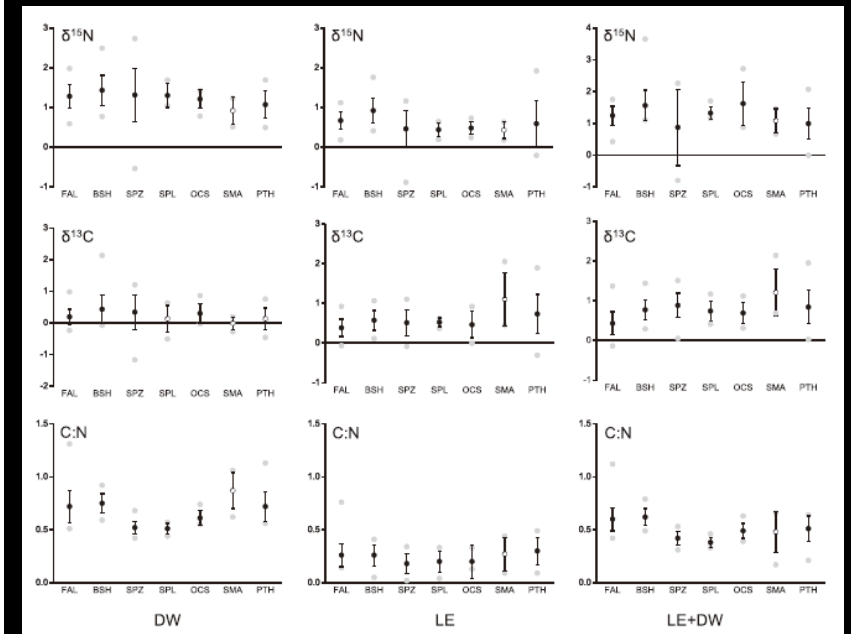

Figure 1. Calculated differences in $\delta^{15}N$ and $\delta^{13}C$ values and C:N ratios among treatments (deionized water (DW)), lipid extraction (LE), lipid extraction combined with deionized water rinsing (LE+DW) and untreated (Control) shark muscle tissue for each species. Solid grey circles are minimum and maximum values for each species. Solid black circles and open black circles are mean values (±SD) with significant and non-significant paired Student's t-tests or Wilcoxon signed rank tests, respectively (Table 3). For species codes and sample sizes, see Table 1.

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Quantifying ontogenetic stable isotope variation between dermis and muscle tissue of two pelagic sharks

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ABSTRACT: Comparative analysis of isotope values from different tissues can capture temporal variation in the trophic and foraging behavior of difficult to study large marine predators, revealing either uniform or variable ecological roles over time. The isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of dermis, and muscle tissue of silky *Carcharhinus falciformis* and blue sharks *Prionace glauca* sampled in the northeast central Pacific were analyzed to quantify ontogenetic inter- and intra-tissue isotopic variation. Consistent differences in $\delta^{15}N$ values occurred between dermis and muscle tissue for both species (2.5 ± 0.4‰ and 2.1 ± 0.3‰, respectively), while tissue differences in $\delta^{13}C$ values were more variable between species (2.3 ± 0.6‰ and 0.7 ± 0.6‰, respectively), likely a result of tissue composition. The overall $\delta^{15}N$ and $\delta^{13}C$ values of dermis and muscle were highly correlated for blue sharks and for silky sharks with the exception of silky shark $\delta^{13}C$ values. This pattern indicates that dermis isotope values are able to provide a proxy for muscle tissue, similar to that previously reported for fin, accepting dermis-specific diet–tissue discrimination factors. Tissue-specific ontogenetic isotopic variation for the silky shark, and the low regression slope value between dermis and muscle $\delta^{13}C$ values, however, may suggest that dermis and muscle tissue have different isotopic turnover rates. These data demonstrate that dermis yields valuable isotope data to examine the trophic ecology and feeding/movement behavior of sharks, but further work is required to address dermis-specific turnover rates and diet–tissue discrimination factors.

KEY WORDS: Pelagic shark · Stable isotope · Dermis

INTRODUCTION

In recent years, our understanding of the temporal and spatial variation in trophic roles and foraging dynamics of shark species has improved based on the application of carbon and nitrogen stable isotopes (Matich et al. 2010, 2011, Hussey et al. 2011, Kim et al. 2012a). Compared to the instantaneous 'snapshot' of dietary information obtained from gut content analysis, stable isotope analysis (SIA) allows examination of feeding behaviors integrated over numerous time periods (Martínez del Rio et al. 2009, Willis et al. 2013). For example, the isotopic composition of different metabolic tissues with diverse turnover rates can provide dietary information integrated over short (weeks, using plasma; Matich et al. 2011) to long (months to years, using muscle; MacNeil et al. 2005) periods. Consequently, inter-tissue stable isotope comparisons can examine dietary shifts and variation in trophic position of species (MacNeil et al.

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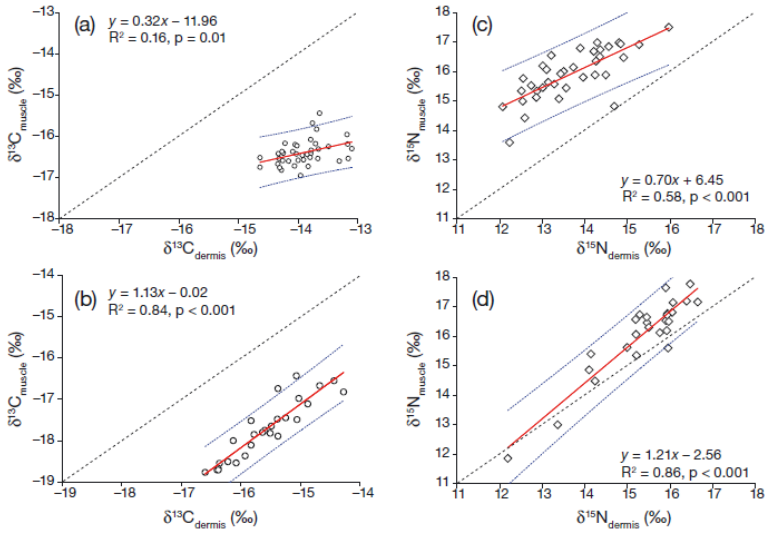

Fig. 2. Comparison of $\delta^{13}C$ (open circle) and $\delta^{15}N$ (open diamond) values between skin and muscle tissue of (a,c) silky shark *Carcharhinus falciformis* (n = 39) and (b,d) blue shark *Prionace glauca* (n = 26). The dashed black line depicts the 1:1 isotopic relationship between the 2 tissues. The solid red lines indicate the regression slope for significant relationships, while the blue dashed lines represent the 95% confidence intervals of the regression analysis

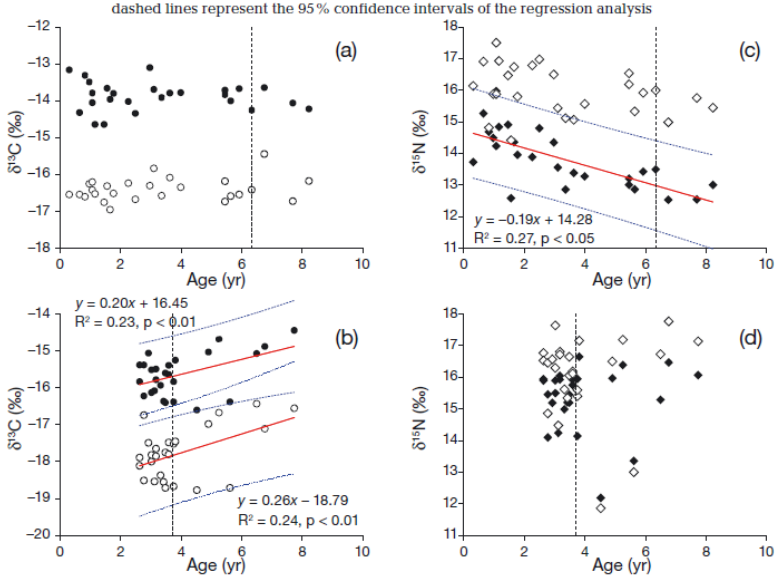

Fig. 3. Relationship of (a,b) $\delta^{13}C$ and (c,d) $\delta^{15}N$ values from paired samples of skin (solid circle and diamond) and muscle (open circle and diamond) and age for (a,c) silky shark *Carcharhinus falciformis* (n = 39) and (b,d) blue shark *Prionace glauca* (n = 26) sampled in northeast central Pacific. Solid red lines indicate the regression slope for significant relationships, while the blue dashed lines represent the 95% confidence intervals of the regression analysis. The vertical black dashed lines indicate age at 50% maturity

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Trophic interactions among pelagic sharks and large predatory teleosts in the northeast central Pacific

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ABSTRACT

Sharks are considered to play important roles in structuring marine ecosystems, consequently understanding their trophic ecology and interactions with other marine predators is required. In the central Pacific Ocean, whether the trophic roles of pelagic sharks are complementary or redundant to large teleost predators remains unclear. In this study, stable carbon and nitrogen isotope analysis were used to examine the isotopic niche overlap of eight pelagic shark species and six pelagic teleost predators, including tuna and billfish. Large intra-specific variation and minimal inter-specific variation in both $\delta^{15}N$ and $\delta^{13}C$ values were observed among sharks and teleosts. Moreover, there was a high degree of trophic overlap among pelagic shark and teleost species, with the exception of the blue shark, the $\delta^{13}C$ values of which indicated a much longer foraging time in the purely pelagic waters. Moreover, although the stable isotopic data suggested that the pelagic sharks in the study area share similar prey and habitats with other pelagic predators, such as tuna and billfish, blue sharks and shortfin mako sharks did not show isotopic overlap with these predators. These data highlight the diverse roles among pelagic sharks, supporting previous findings that this species complex is not trophically redundant; but further studies on the diet and fine-scale habitat used are required to verify this hypothesis.

1. Introduction

Pelagic sharks are primary bycatch species of longline fisheries operating in open ocean ecosystems and are prone to high fisheries mortality rates (Kitchell et al., 2002; Schindler et al., 2002). Their typically large pectoral fins render them attractive to the shark fin industry, to which they contribute a substantial percentage of total species traded (Clarke et al., 2006). But as k-selected species, pelagic sharks possess several biological attributes (low growth rate, late maturity, and low fecundity) that make them vulnerable to overfishing (White et al., 2012) and limit their recovery potential (Walker, 1998). The standardized catch rate of silky sharks (*Carcharhinus falciformis*) in the North Pacific Ocean, for example, was estimated to have decreased by 91.7% between 1950 and 1997 with the onset of commercial fishing (Baum and Myers, 2004). Pelagic sharks also range across poorly monitored regions (Gilman et al., 2008), therefore the annual global catch rate reported to the Food and Agriculture Organization of the United Nations (FAO) is likely largely underestimated (Clarke et al., 2006; Ferretti et al., 2010). More than 50% of pelagic species are currently considered threatened worldwide (Dulvy et al., 2008).

Conservation and management of pelagic sharks involves two key issues, consideration of their unique evolutionary characteristics in relation to biodiversity importance and global conservation priorities and mitigating over exploitation in fisheries to maintain the integrity of their ecological role in marine food webs (Kitchell et al., 2002). Most large shark species feed at or near the top of marine food webs; however, their trophic roles are thought to vary significantly among ecosystems, species and contexts (Heithaus et al., 2008; Kiszka et al., 2015). Declines in the abundance of large sharks have the potential to induce trophic cascades in coastal and demersal ecosystems (Ferretti et al., 2010), yet it remains unclear how their removal impacts the trophic structure of pelagic communities in open-ocean ecosystems (Ward and Myers, 2005; Kiszka et al., 2015).

To date, only one study has directly examined the effect of removing large pelagic sharks on ecosystem structure, finding conflicting results. Through an Ecopath with Ecosim model, Kitchell et al. (2002) identified limited effects of removing pelagic sharks on the overall fish community when assigning a standardized trophic level of approximately 4.5. Model results suggested compensatory effects of shark removal by other large teleost predators that have faster biomass turnover rates, such as tuna and billfish. When variable trophic roles among large and small sharks were considered within the model, however, non-linear effects were observed with negative consequences for ecosystem structure. Inter-specific variation in habitat use (Rabehagasoa et al., 2012), diet (Kiszka et al., 2014) and trophic complexity (Kiszka et al., 2015) is observed among pelagic sharks supporting the latter model predictions, but uncertainties over their ecological role/s remain. Specifically,

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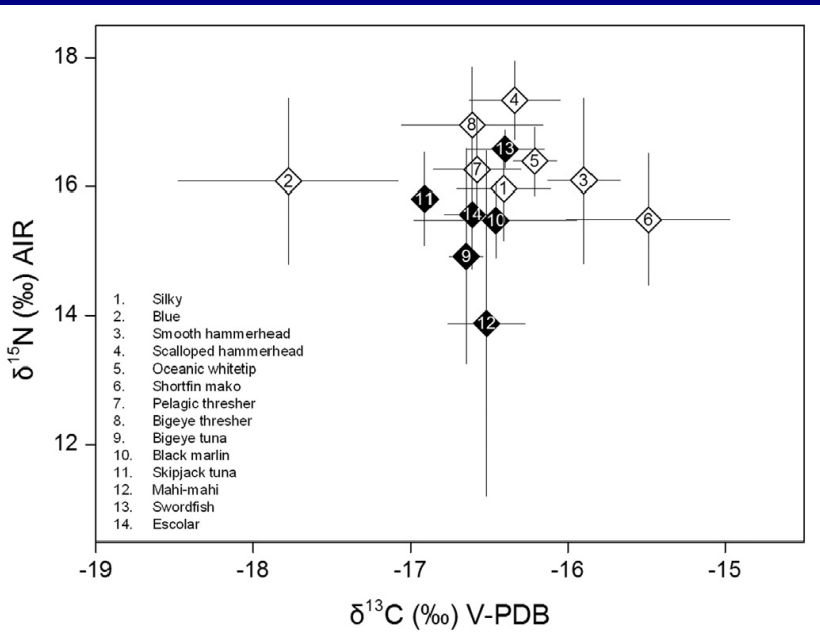

Fig. 2. A biplot of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) for pelagic sharks (open diamonds) the large predatory teleosts (black diamonds) of the northeast central Pacific pelagic community.

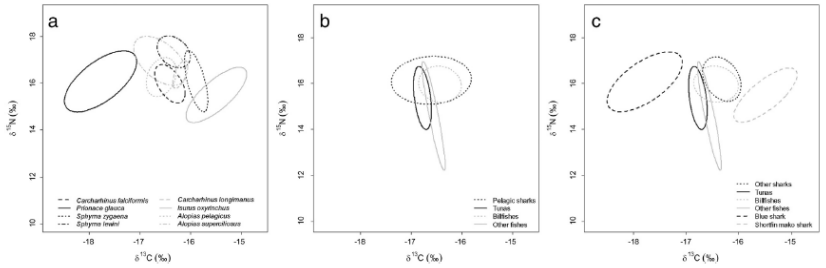

Fig. 3. Stand ellipse areas corrected for sample size (SEAc) of pelagic sharks (a), pelagic guilds (b), and pelagic guilds with blue sharks and shortfin mako sharks separated from the pelagic shark guild (c).

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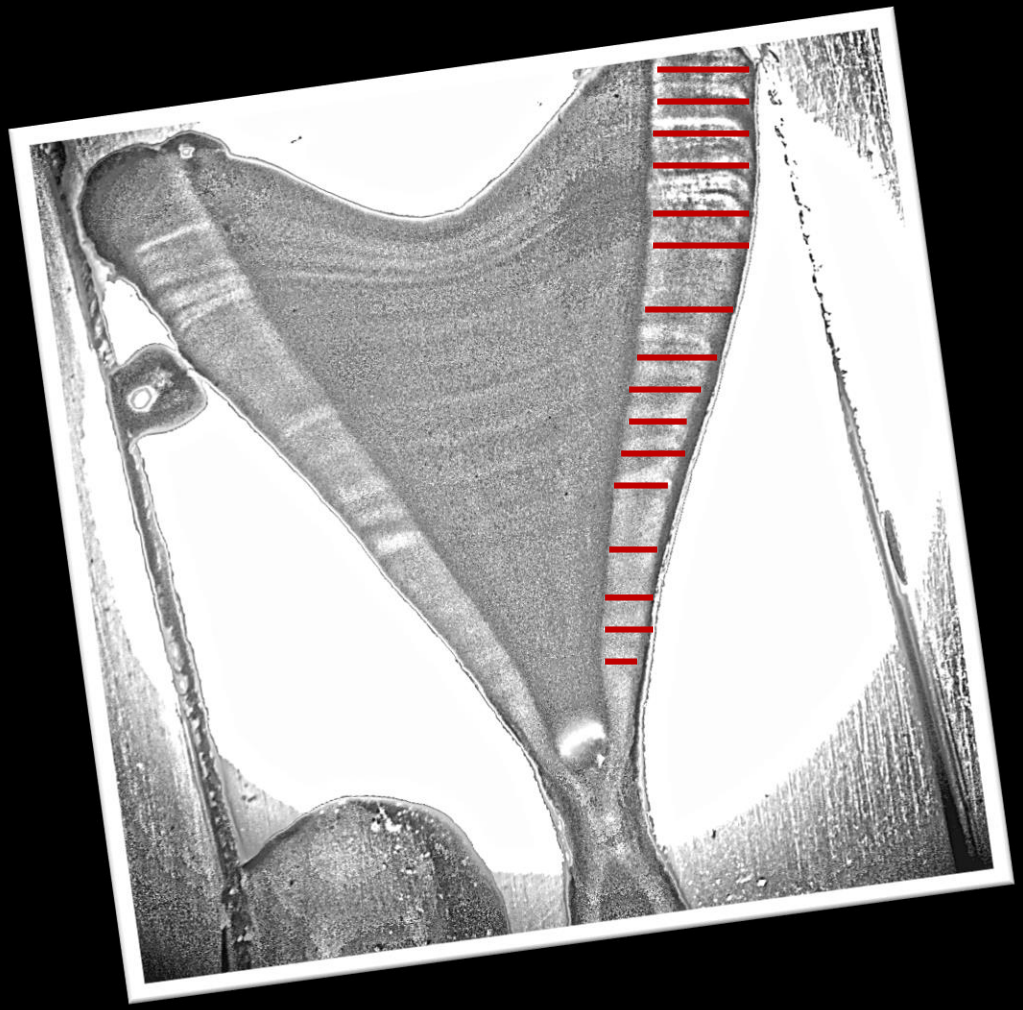
Age and growth



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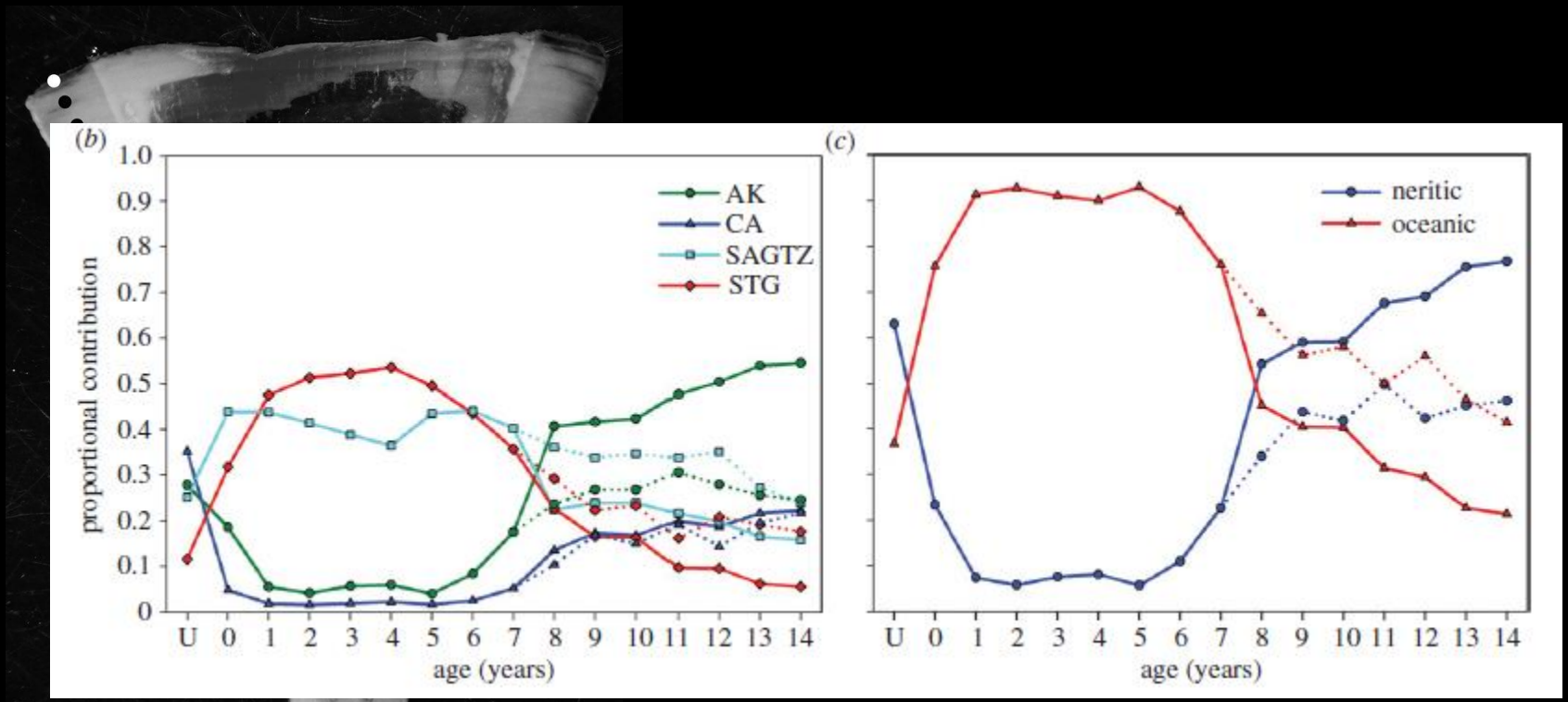

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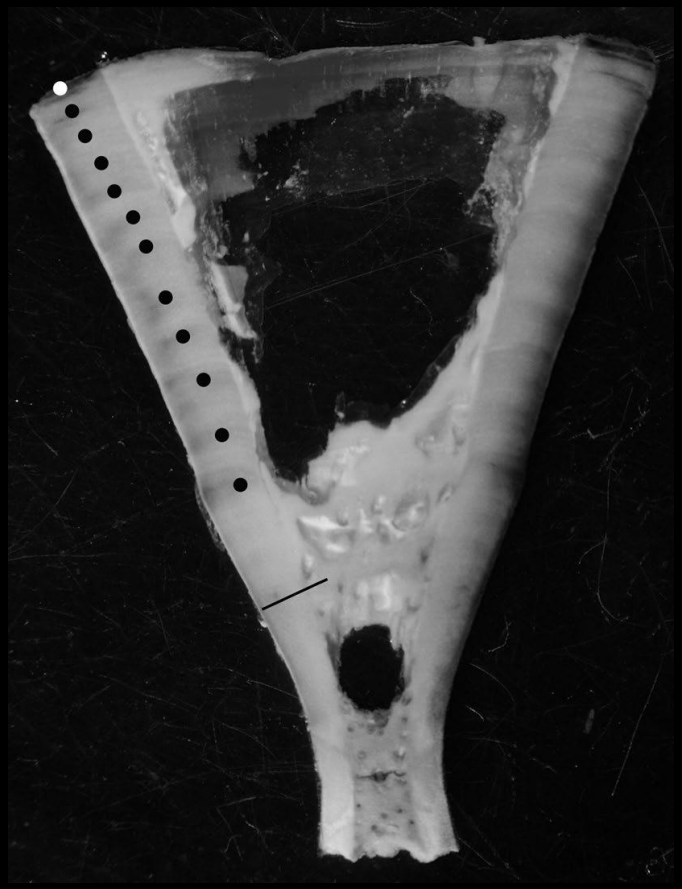

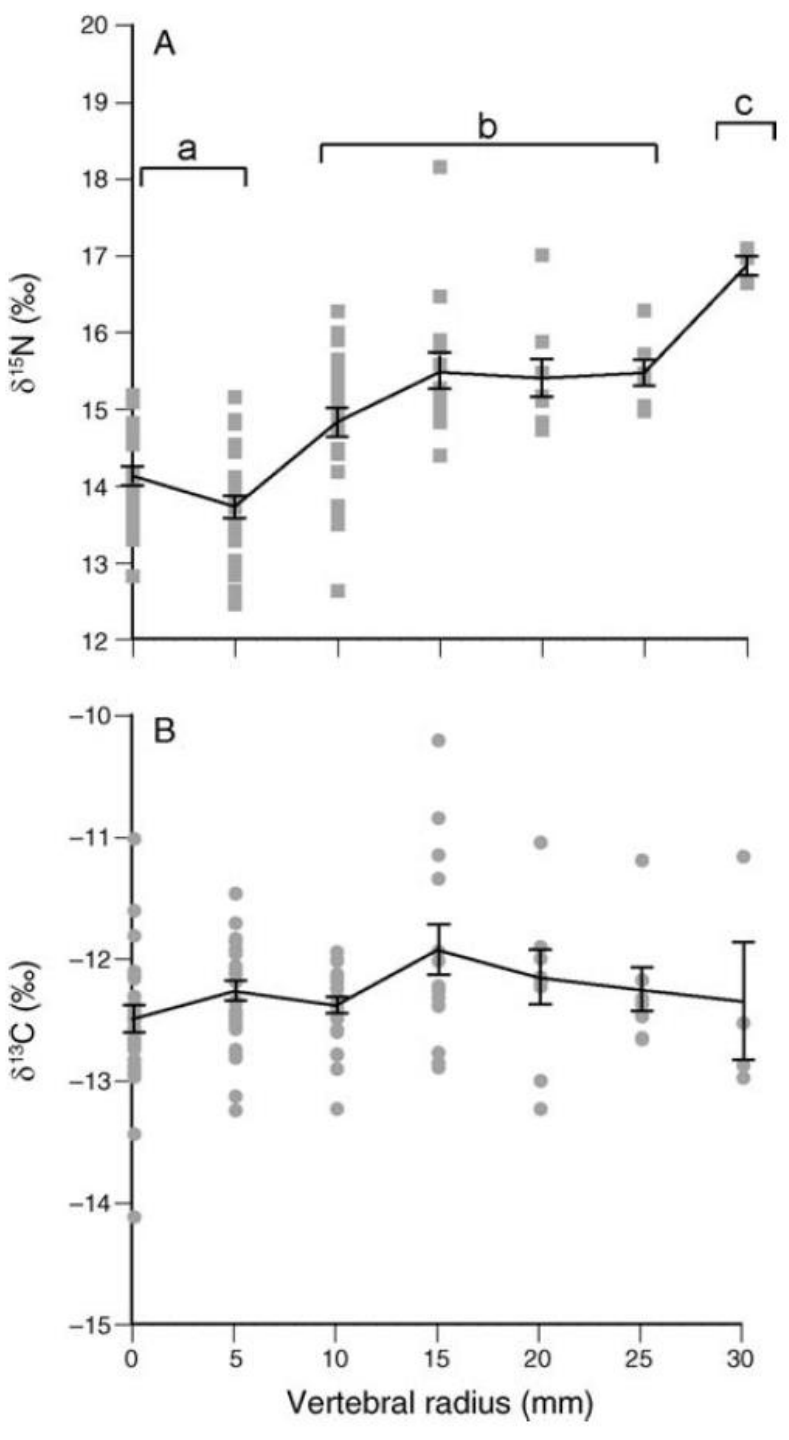

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