## Have You Wondered?

1. What factors determine where marine organisms live?
2. How the physical environment affects marine organisms?
3. How the growth of marine populations is regulated?
4. What determines the characteristics of marine communities?
5. How energy flow affects the function of an ecosystem?

# 2 Fundamentals of Ecology

- 2.1 The Study of Ecology
- 2.2 Ecology and the Physical Environment
- 2.3 Populations
- 2.4 Communities
- 2.5 Ecosystem: Basic Units of the Biosphere
- 2.6 The Biosphere

# 2.1 The study of Ecology

- The term *ecology* is derived from the Greek word *oikos,* meaning “home,” in reference to nature’s household and the economy of nature. The science of ecology deals with the interactions of organisms with each other and with their environment and how these interactions affect survival and reproduction.

# 2.1 The study of Ecology

- The organisms that inhabit the seas are integrated components of a living network that encompasses the globe.
- Organisms are parts of ecosystems, systems composed of living organisms and their nonliving environment.
- All of the earth's ecosystems taken together compose the *biosphere*.
- The structure of the biosphere is determined by the basic principles of life: the capture of energy, the cycling of nutrients, survival and reproduction, and the process of evolution that has shaped the natural world.

# 2.2 Ecology and the Physical Environ

- Environment--all the external factors acting on the organism
- Abiotic factors
- Biotic factors

*The biotic environment* is the living portion of an organism's environment.

*The abiotic environment* is the physical, or nonliving, environment in which an organism lives.

*Homeostasis* is the internal balance that living organisms must maintain to survive.

GLOSSARY

# HABITAT: Where an organism lives

Figure 2-1 THE CORAL REEF HABITAT. Large habitats, such as the coral reef, can contain many smaller microhabitats. Microhabitats in the coral reef include the crevices in the coral, the sediments surrounding the coral stands, and even the tissues of the organisms themselves.

- Habitat
- Microhabitat

# Maintaining homeostasis

- This internal balancing of factors that occurs in the face of changes in the external environment is called *homeostasis*, and the means of maintaining homeostasis is vital to the life of all organisms
- Ultimately, the ability of organisms to survive in their natural environment depends on their genes and the evolutionary adaptations they have acquired to deal with changing environmental conditions.

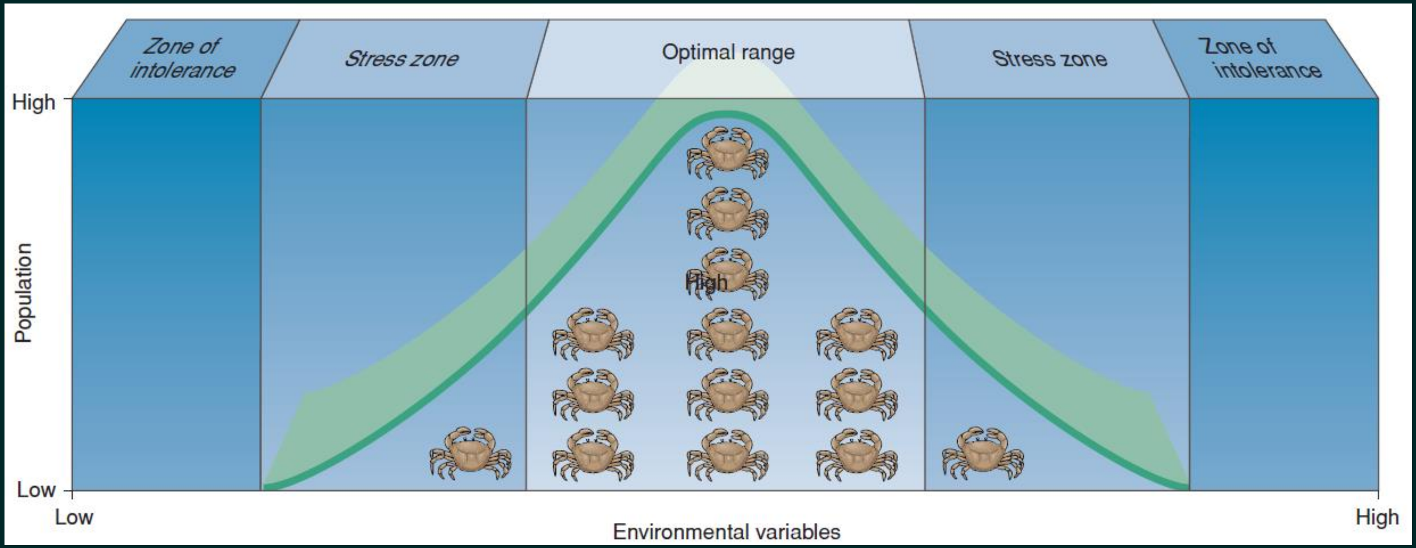


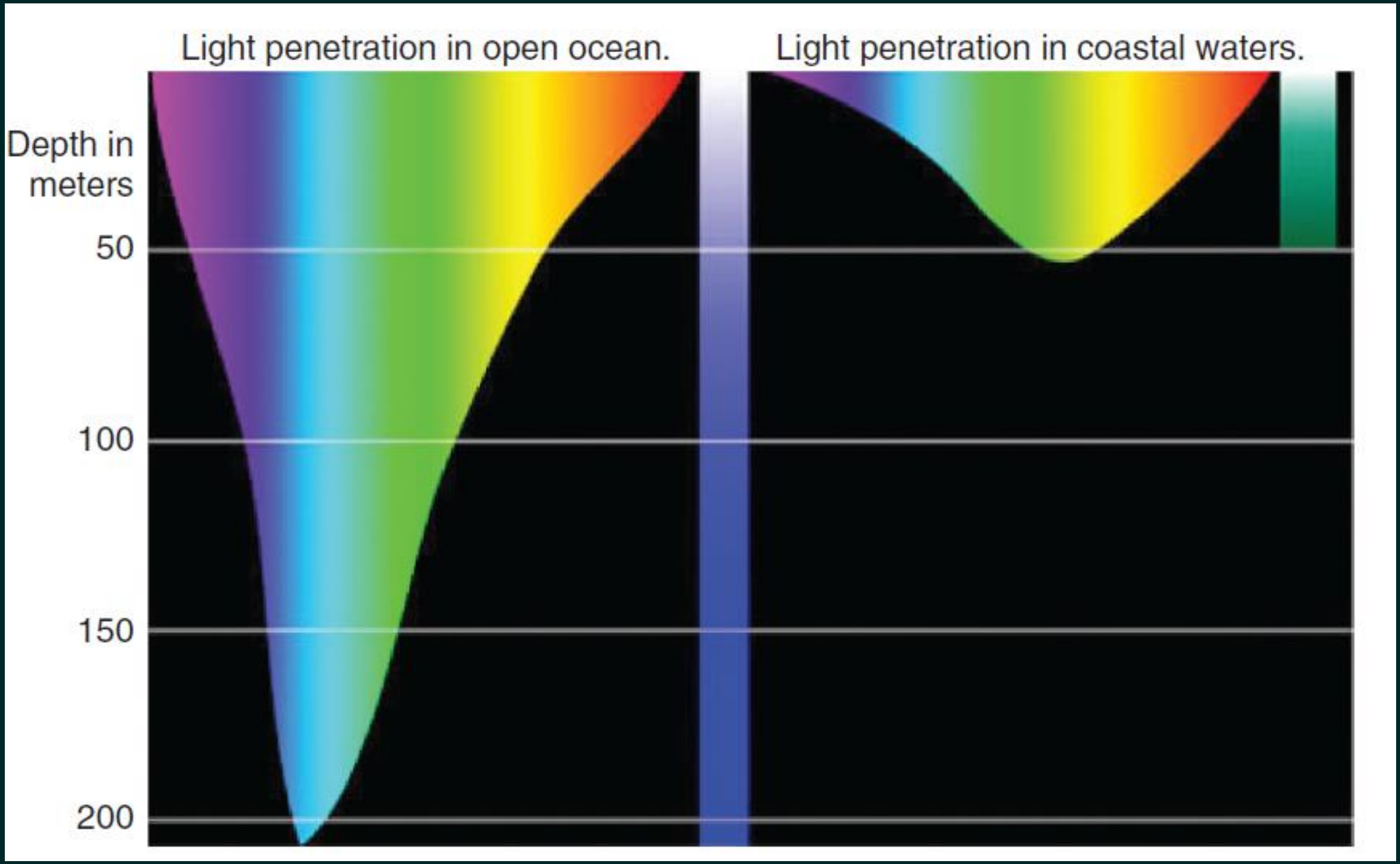

Figure 2-2 OPTIMAL RANGES. An organism survives and reproduces best when environmental factors affecting it fall within an optimal range. Although organisms can live outside of their optimal ranges, they expend more energy maintaining homeostasis, leaving less energy available for reproduction

- Optimal Range
- Zones of stress
- Zones of intolerance

# Physical Environment

- Sunlight
- The largest group of photosynthetic organisms in marine environments are phytoplankton, the mostly microscopic, plantlike organisms and bacteria that float in ocean currents. Phytoplankton, together with seaweeds and plants, are the primary sources of nutrients and energy for marine animals. The distribution of these leading food producers is determined by the available sunlight and nutrients.
- Phytoplankton can migrate vertically.

# Sunlight




(Courtesy of Kyle Carothers, Ocean Explorer, NOAA.)

# Sunlight

$$l_x = l1\ \exp^{(-cx)}$$

(a) Bay Islands (Honduras) coral reef at 2 m depth. (b) Bay Islands (Honduras) coral reef at 20 m depth. (Photographs Martin Speight.)

# Physical Environment

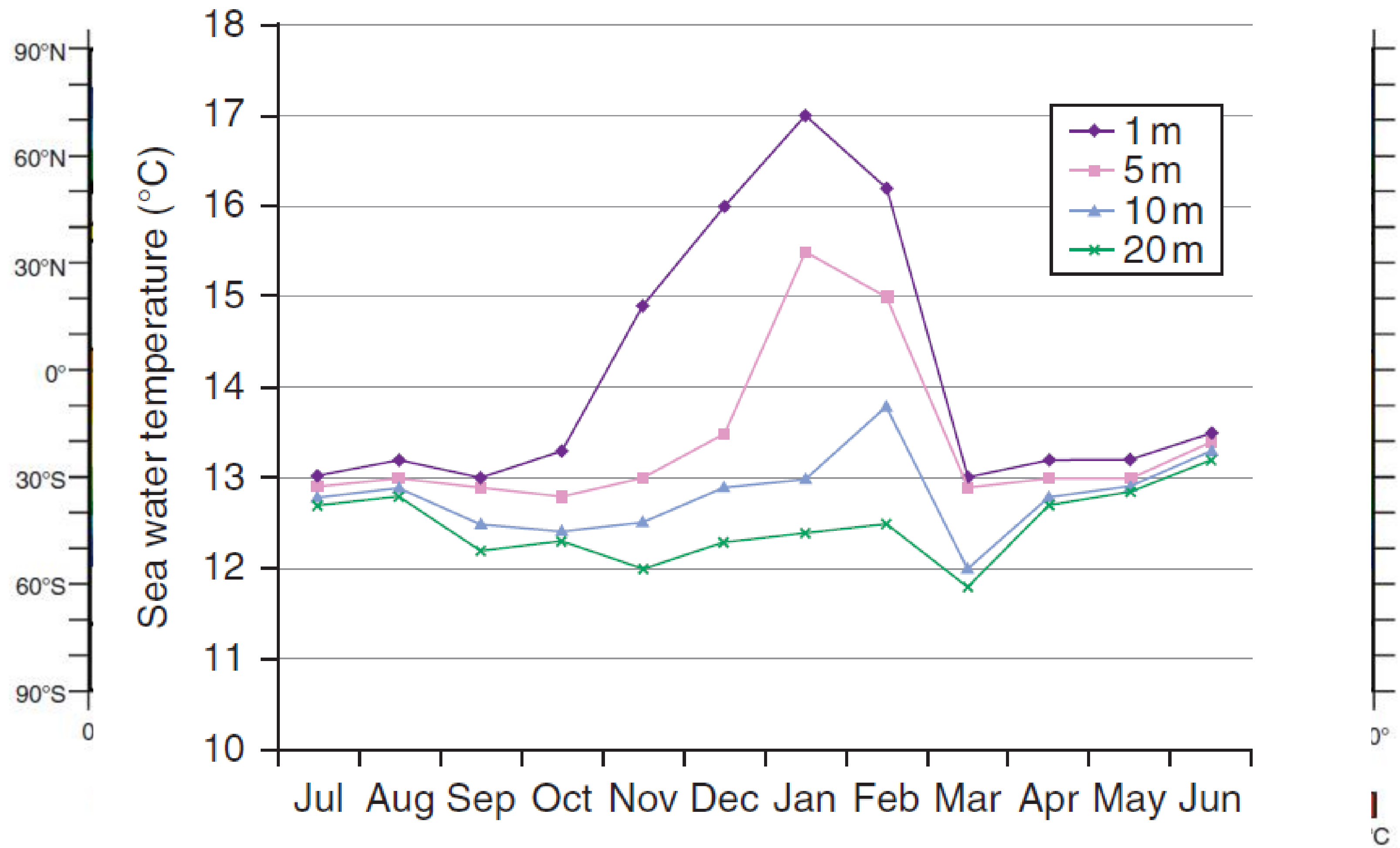
- Temperature
- Ectotherms
- Endotherms

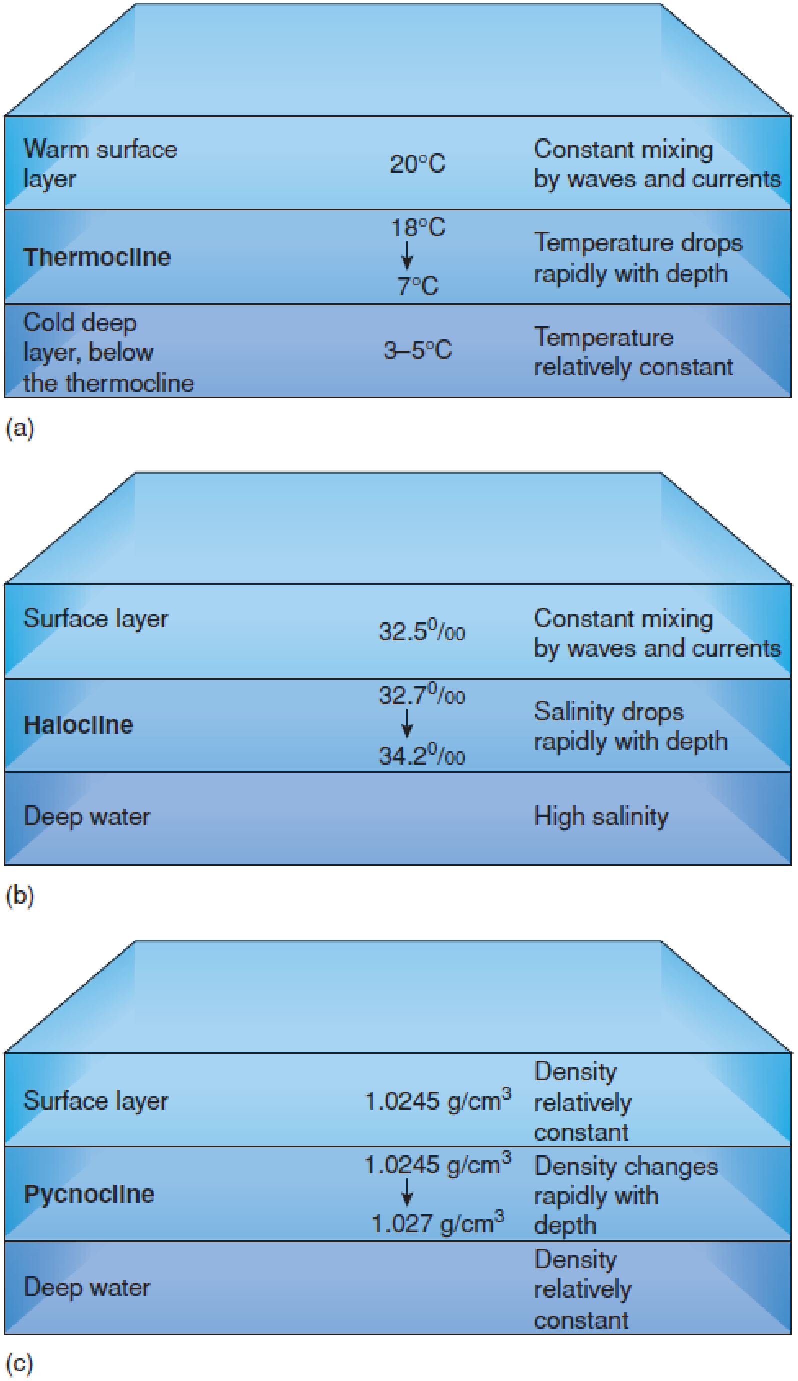

(a)


(b)

Figure 2-3 **TEMPERATURE.** (a) Ectotherms such as this crab obtain most of their body heat from their surroundings. If the environmental temperature rises or falls, so will their body temperature. (b) Endotherms such as this penguin can maintain a constant body temperature by generating heat internally through metabolism. Endotherms are well insulated to prevent excess heat loss.

# Temperature



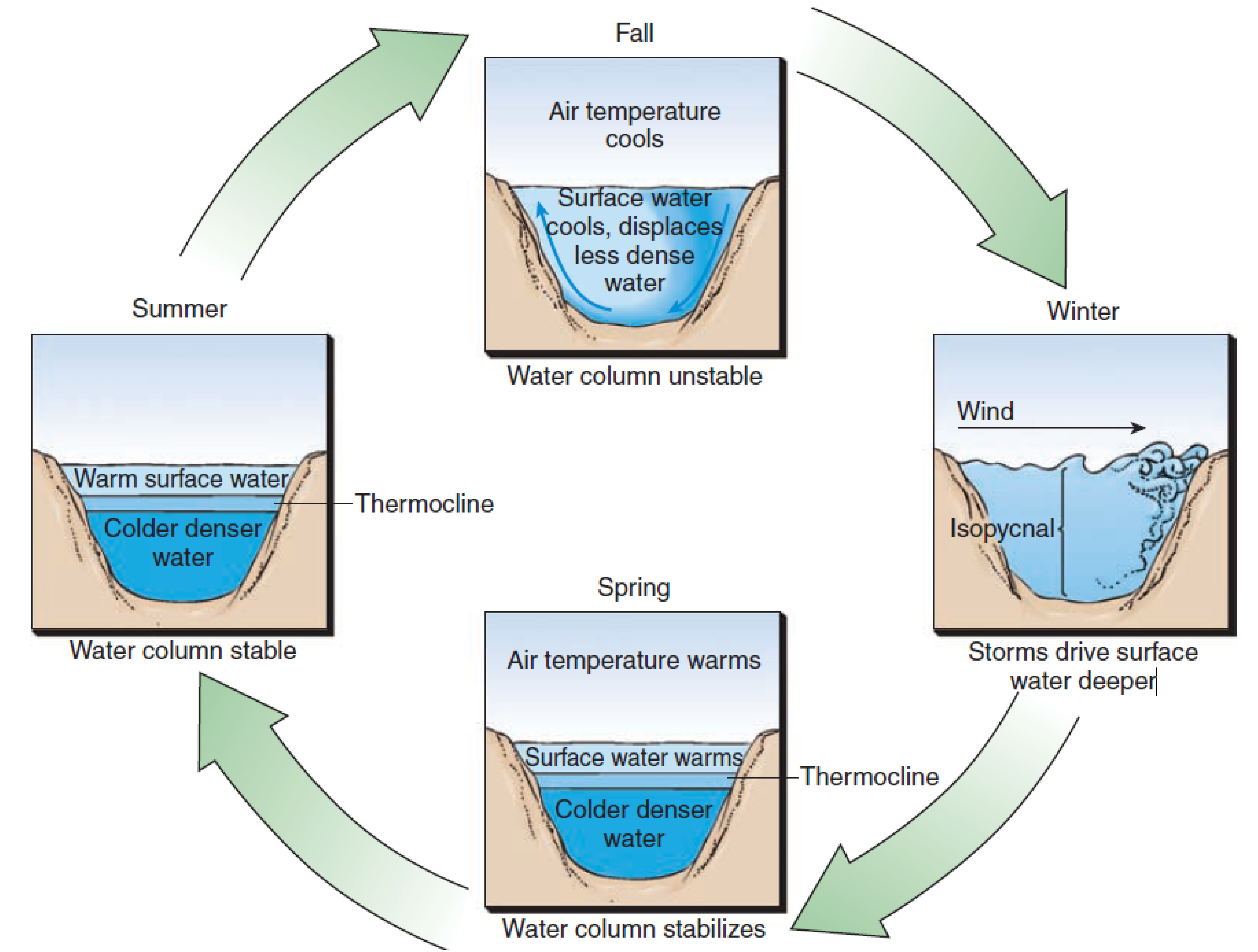



The ***thermocline*** is a zone in the ocean characterized by a rapid change in temperature with increasing depth.
**(温跃层)**

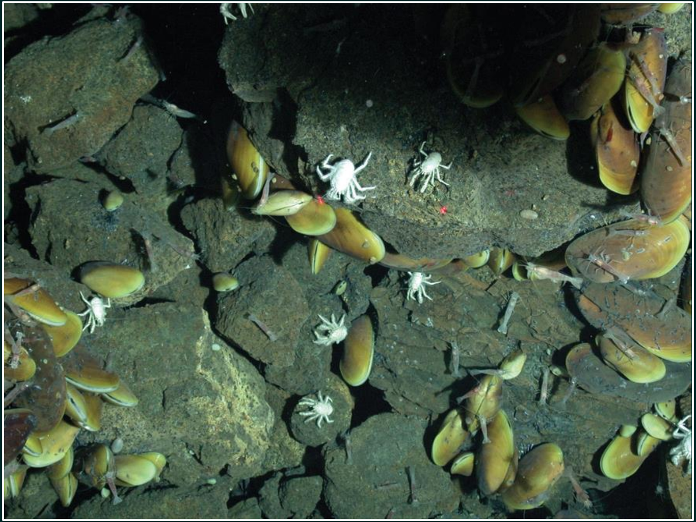
The ***halocline*** is a zone in the ocean that is characterized by a rapid change in salinity with depth.
**(盐度跃层)**

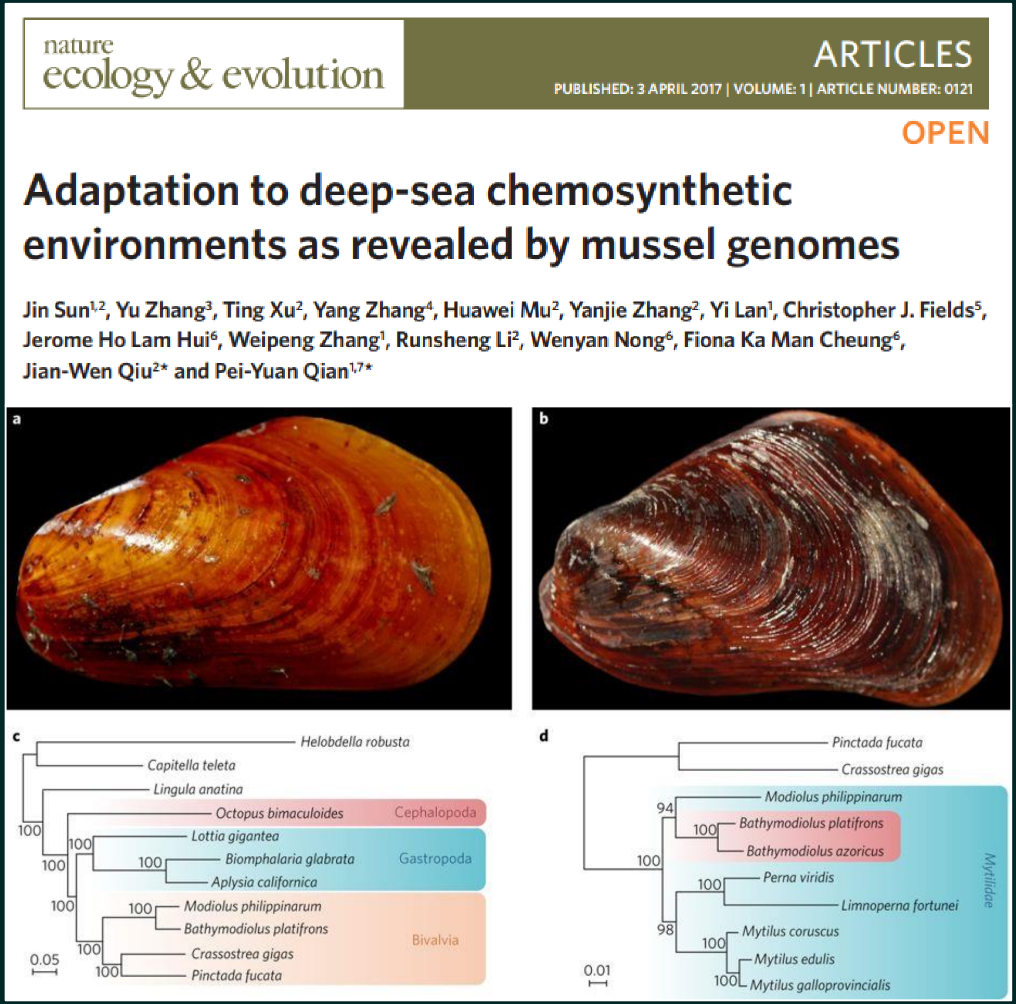
The ***pycnocline*** is a zone in the ocean that is characterized by a rapid change in density with depth.
**(密度跃层)**

GLOSSARY


Fall
Air temperature cools
Surface water cools, displaces less dense water
Water column unstable
Winter
Wind
Isopycnal
Storms drive surface water deeper
Spring
Air temperature warms
Surface water warms
Thermocline
Colder denser water
Water column stabilizes
Summer
Warm surface water
Thermocline
Colder denser water
Water column stable

# Temperature


nature ecology & evolution
ARTICLES
PUBLISHED: 3 APRIL 2017 | VOLUME: 1 | ARTICLE NUMBER: 0121
OPEN

## Adaptation to deep-sea chemosynthetic environments as revealed by mussel genomes

Jin Sun[1,2], Yu Zhang[3], Ting Xu[2], Yang Zhang[4], Huawei Mu[2], Yanjie Zhang[2], Yi Lan[1], Christopher J. Fields[5], Jerome Ho Lam Hui[6], Weipeng Zhang[1], Runsheng Li[2], Wenyan Nong[6], Fiona Ka Man Cheung[6], Jian-Wen Qiu[2]* and Pei-Yuan Qian[1,7]*

# SST

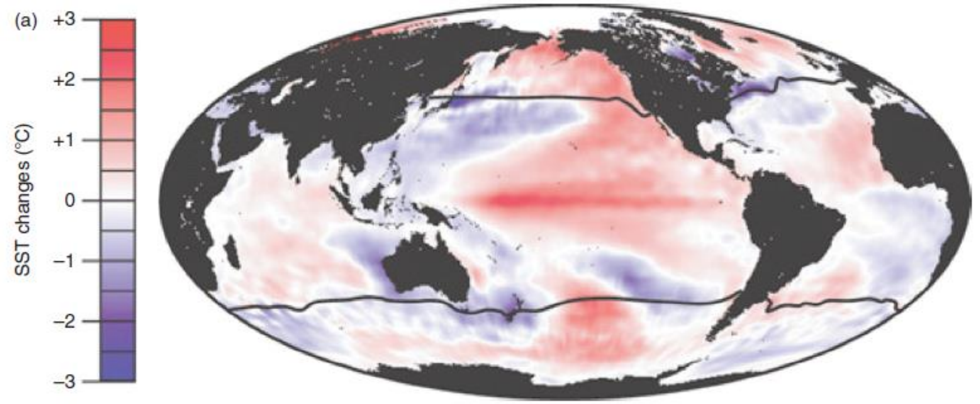



**Figure 1.16**

Global changes in annual average sea surface temperatures (SSTs) for the period 1999 to 2004. (From Behrenfeld et al 2006b; reproduced with permission of *Nature*.)

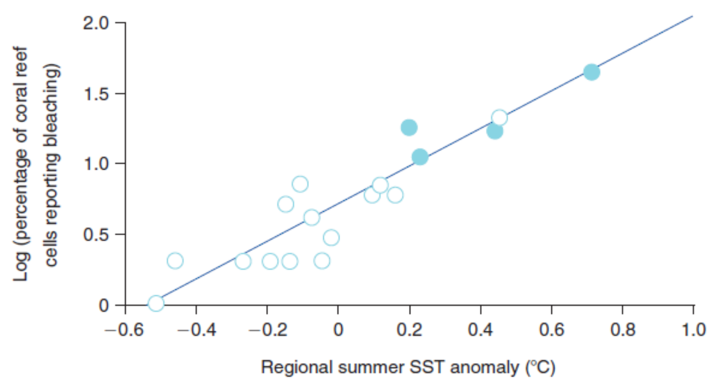



**Figure 1.17**

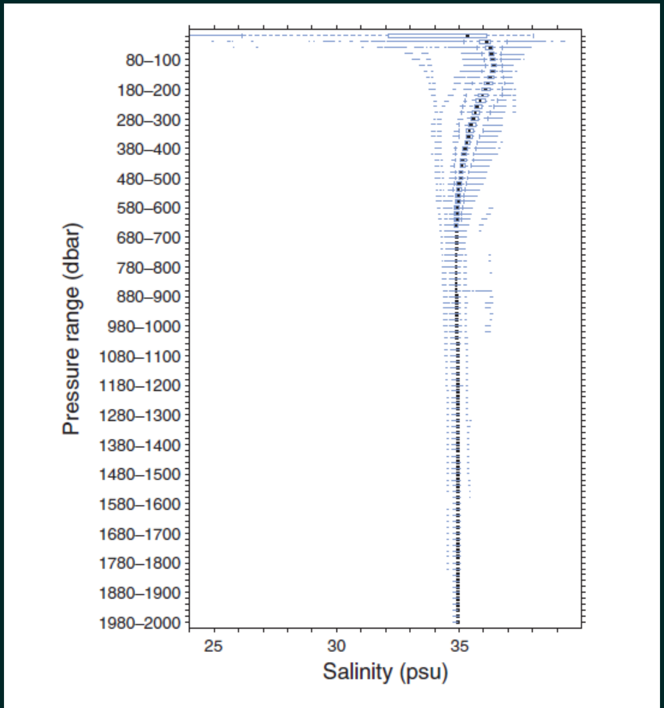
The relationship between the regional SST anomalies and the percentage of coral bleaching. (From McWilliams et al 2005; reproduced with permission of *Ecology* – ESA.) Each data point represents 1 year. Solid circles represent years described in the literature as mass-bleaching events; open circles represent other years.

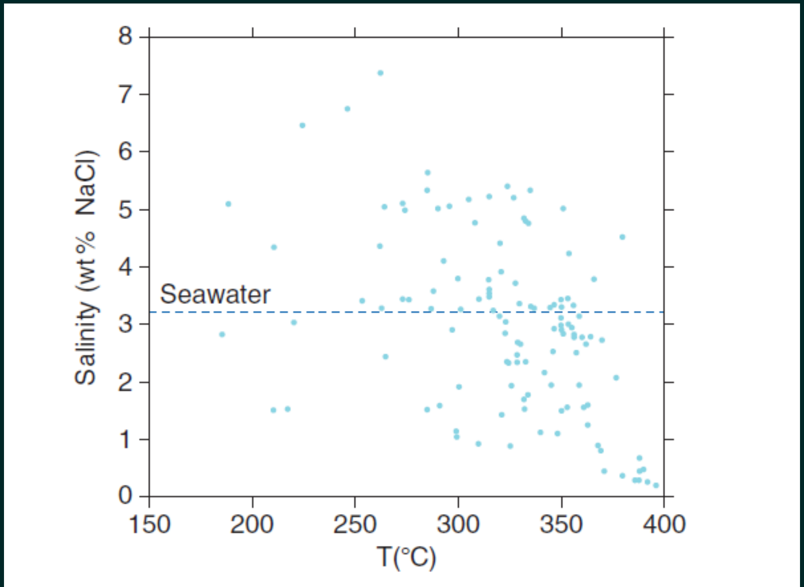
# Physical Environment

- Salinity
  Salinity is measure of the concentration of dissolved inorganic salts in the water.

- Osmosis
  The movement of water across a membrane in response to differences in solute concentration is called *osmosis* which refers to the movement of water across a semipermeable barrier from an area of low solute concentration to an area of high solute concentration.

# Salinity


Pressure range (dbar)
80–100
180–200
280–300
380–400
480–500
580–600
680–700
780–800
880–900
980–1000
1080–1100
1180–1200
1280–1300
1380–1400
1480–1500
1580–1600
1680–1700
1780–1800
1880–1900
1980–2000
25
30
35
Salinity (psu)


Salinity (wt% NaCl)
0
1
2
3
4
5
6
7
8
Seawater
150
200
250
300
350
400
T(°C)

# Defining and measuring salinity

- Salinity is directly proportional to the amount of chlorine in seawater, and chlorine can be measured accurately by a simple chemical analysis, salinity, S, was redefined using chlorinity, Cl, as

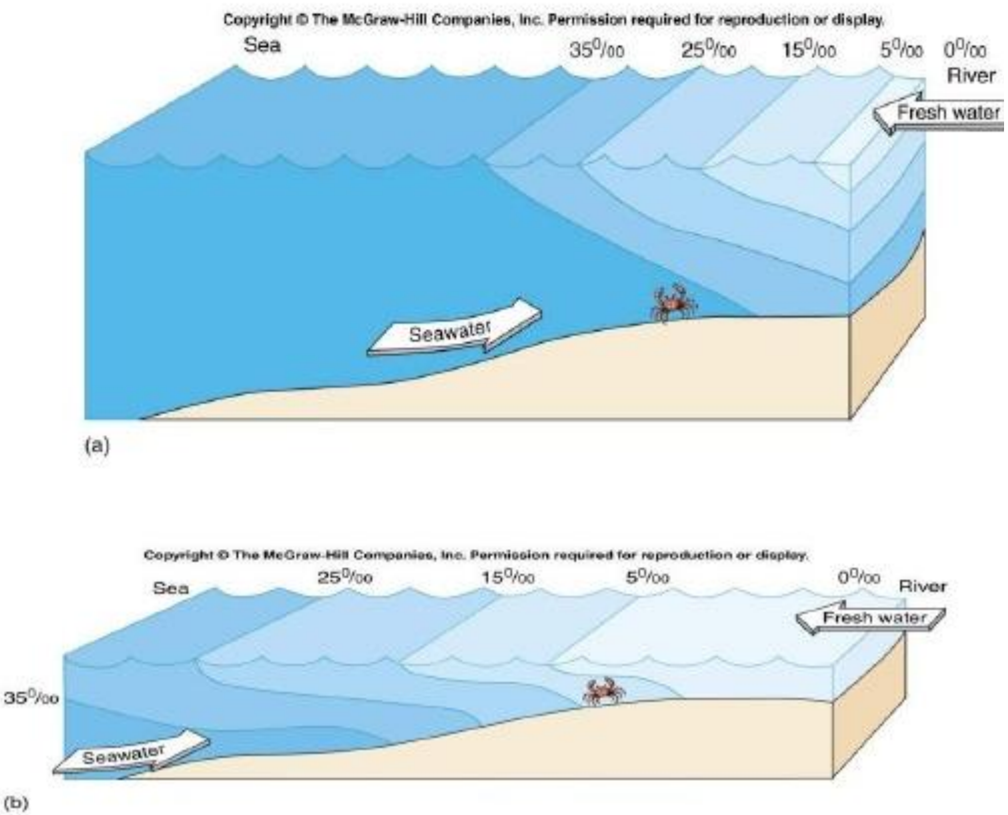
  $S = 1.80655$ chlorinity
- where chlorinity is defined as the mass of silver required to precipitate completely the halogens in 0.3285234 kg of the seawater sample.
- PSU (Practical salinity units) or PSS (Practical salinity scales)

# Defining and measuring salinity

- Conductivity

- refractometers

# Salt wedge



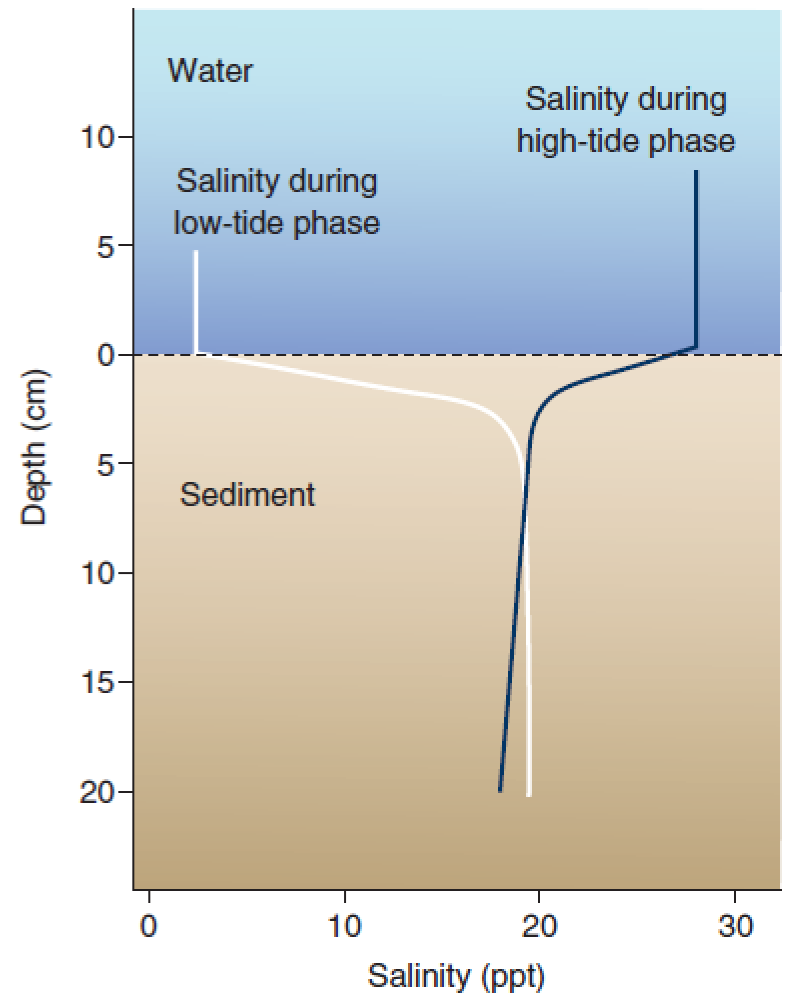




**Figure 1.7**

Variation in the salinity within the water column and within the bottom sediments of an estuary.

# Salinity tolerance

- 8ppt or 30 ppt-stenohaline (狭盐性)


# Salinity tolerance

- Euryhaline (广盐性)


# Physical Environment

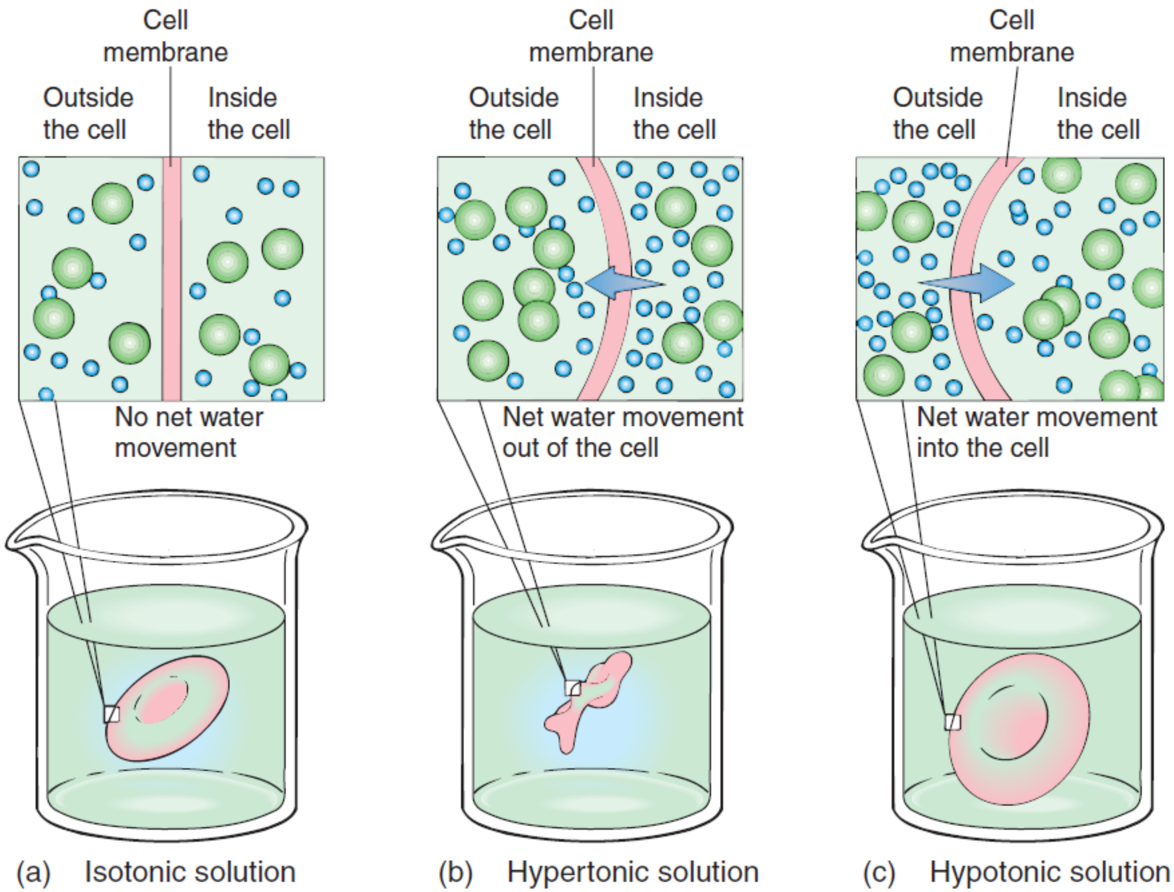
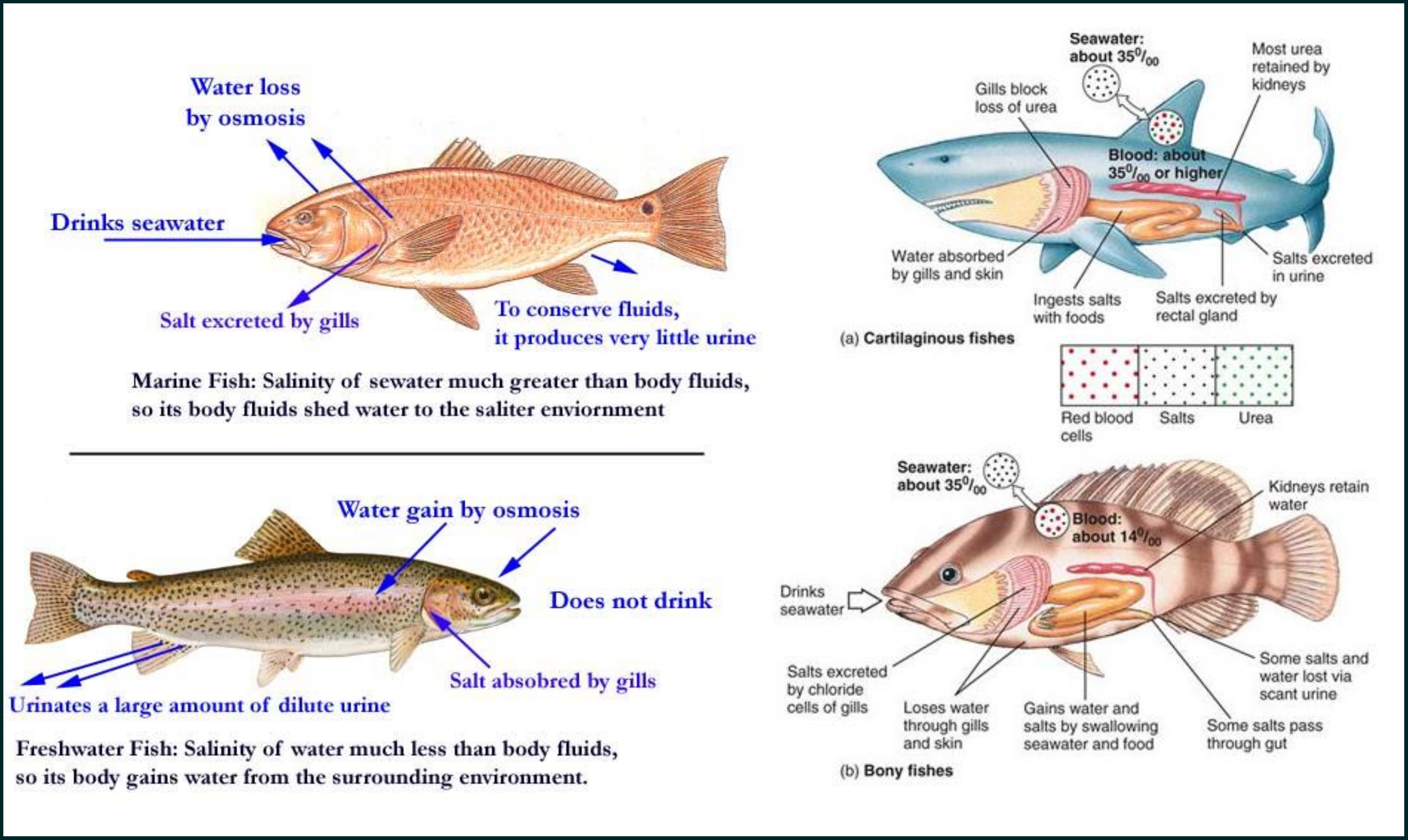



Figure 2-4 **OSMOSIS.** Water tends to move from areas of lower solute concentrations to areas of higher solute concentrations. (a) An isotonic solution contains the same concentration of solute molecules (green) and water molecules (blue) as a cell. Cells placed in isotonic solutions do not change because there is no net movement of water. (b) A hypertonic solution contains a higher concentration of solute than a cell. A cell placed in a hypertonic solution will shrink as water moves out of the cell to the surrounding solution by osmosis. (c) A hypotonic solution contains a lower solute concentration than a cell. A cell placed in a hypotonic solution will swell and possibly rupture as water moves by osmosis from the environment into the cell.

# Osmoregulation of fishes



# Physical Environment

- The pressure at sea level is 760 mm Hg, or 1 atmosphere (14.7 pounds per square inch). Because water is so much denser than air, for every 10 meters (33 feet) below sea level in the ocean, the pressure increases by 1 atmosphere. For instance, the pressure at an average ocean depth of 3,700 meters is 370 atmospheres (2.7 tons per square inch). A wig head lowered to a depth of 4,000 meters, where the pressure is 400 atmospheres, is compressed to approximately one third of its original size

# Physical Environment


**Figure 2-5 PRESSURE.** To demonstrate the pressure in the sea's depths, this wig head, originally the size of a human head, was lowered to a depth of 4,000 meters (13,200 feet). The pressure at this depth is so great that it compressed the Styrofoam to the size you see in this photograph.

# Depth, pressure, and topography

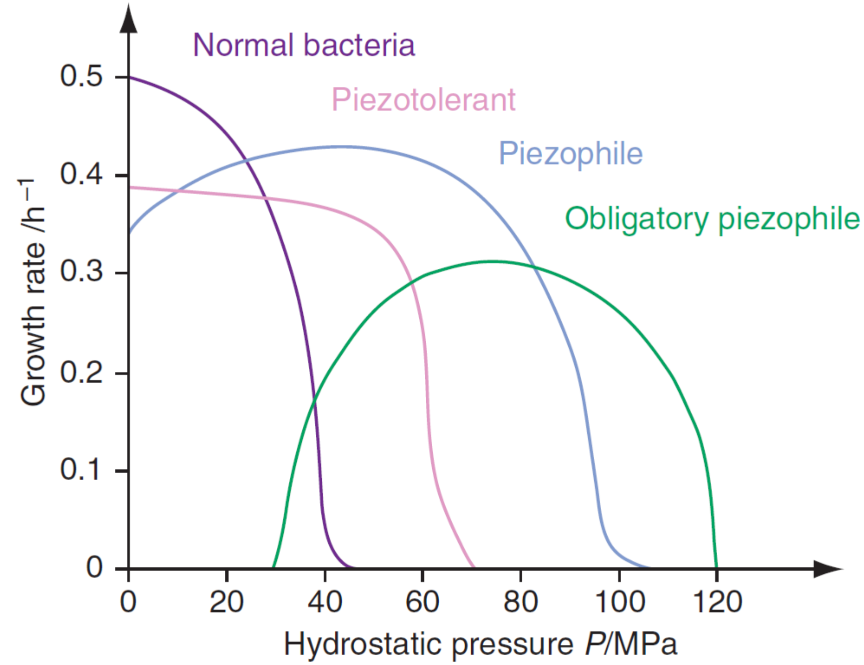
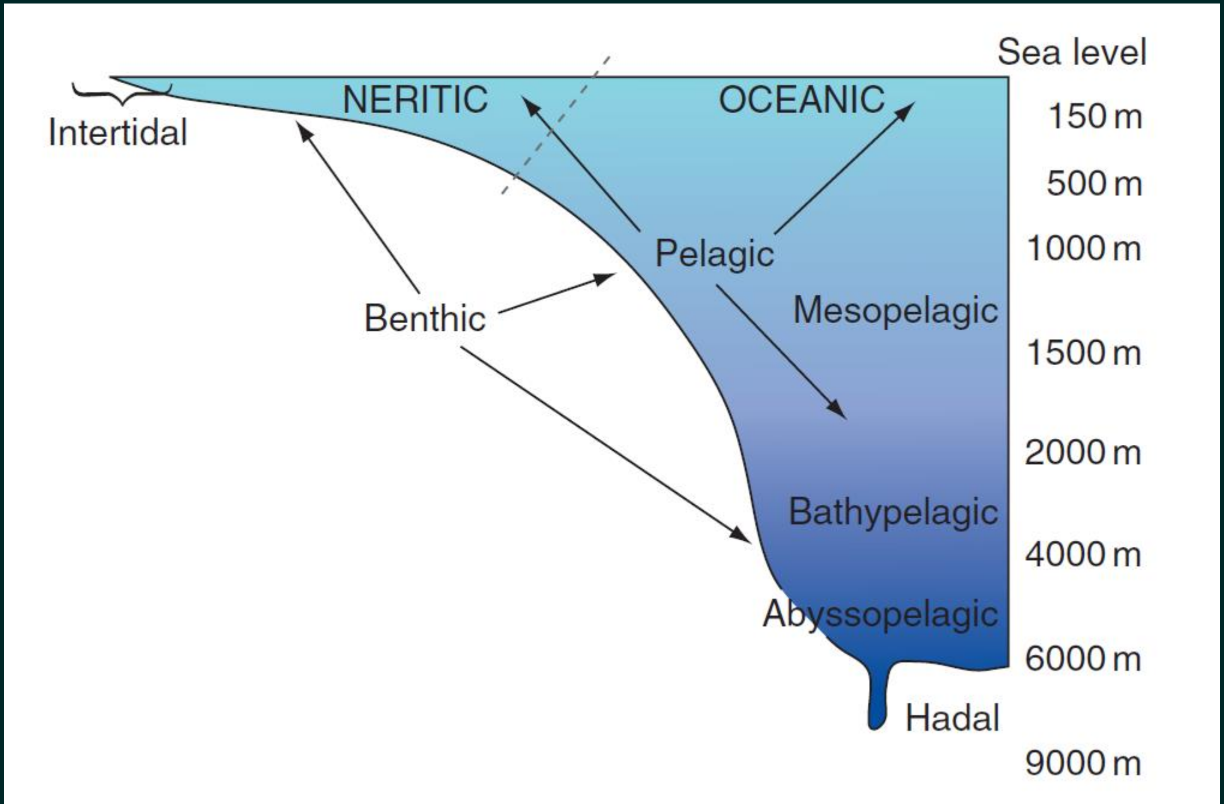



**Figure 1.10**

Definitions of the relationships between growth rate of microorganisms and pressure. Atmospheric pressure (surface) = 0.1 MPa; 120 MPa = 1200 atmospheres or 12,000 m. (After Margesin & Nogi 2004; reproduced with permission of Chemical Society Reviews.)

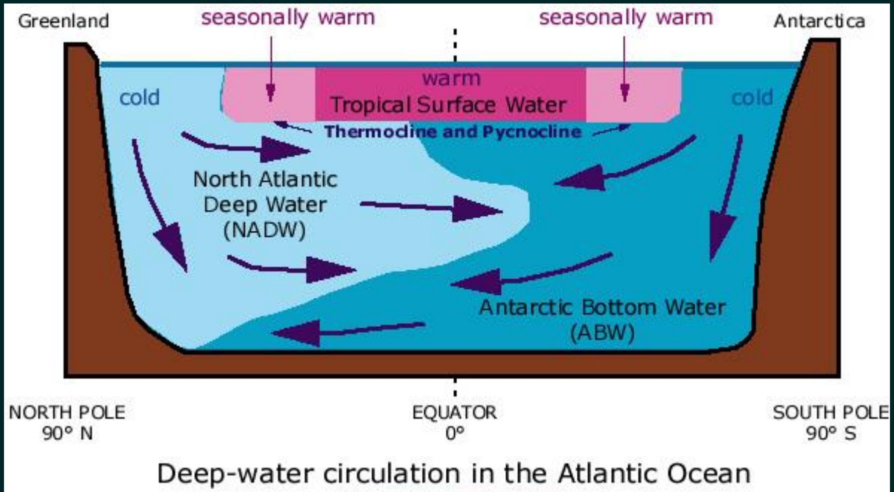
Similar species are partitioning the depth resource resulting in the avoidance of interspecific competition

# Depth


Sea level
Intertidal
NERITIC
OCEANIC
150 m
500 m
1000 m
Pelagic
Benthic
Mesopelagic
1500 m
2000 m
Bathypelagic
4000 m
Abyssopelagic
6000 m
Hadal
9000 m

# Oxygen

- Constant at the surface
- Decrease to 1000m




Deep-water circulation in the Atlantic Ocean

© Alessandro Grippo, 2008

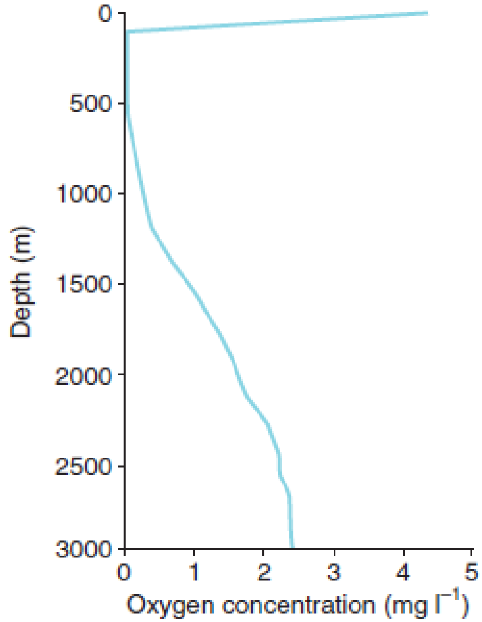



**Figure 1.18**

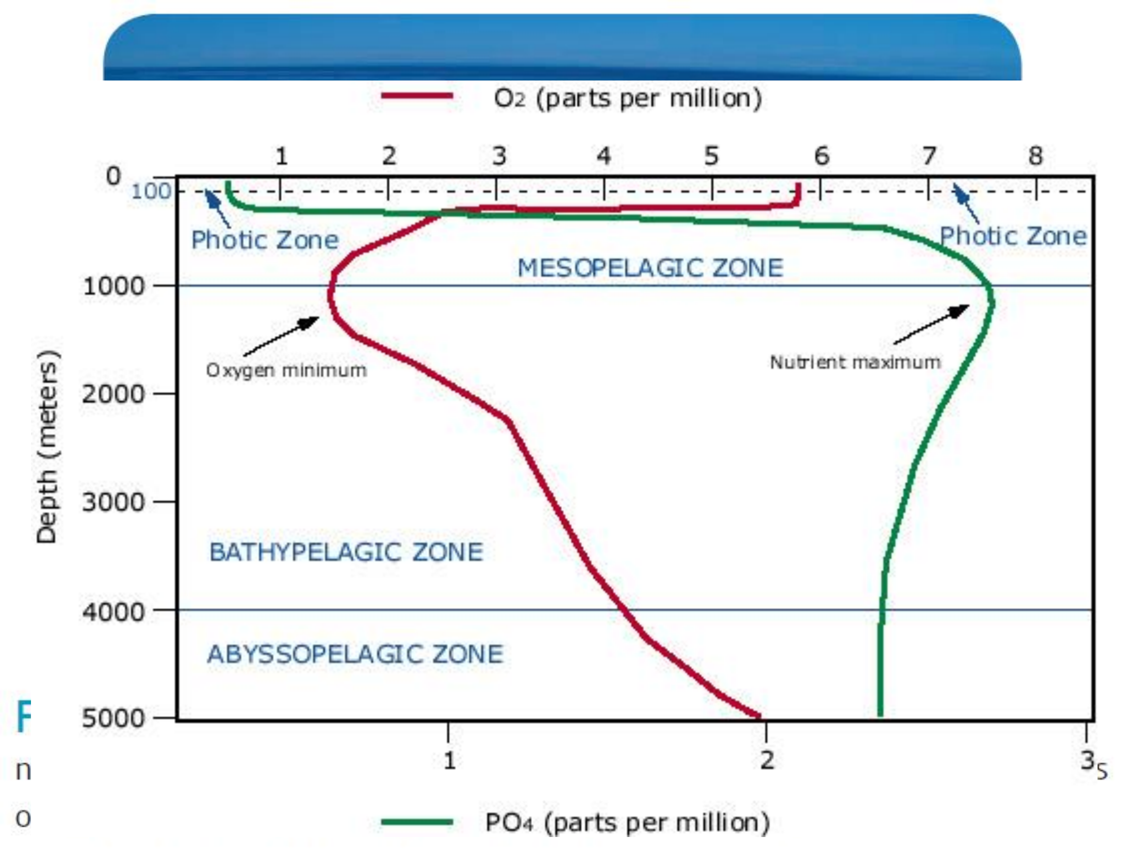
The variation in oxygen concentration with depth in the eastern tropical Pacific Ocean at 13°23'N, 102°27'W. (Modified from Wishner et al 1990.)

# Nutrients

- Organisms need a variety of organic and inorganic materials to metabolize, grow and reproduce. The chemical composition of salt water provides several of the nutrients required by marine organisms. Nitrogen and phosphorous are required by all photosynthesizing plants or plant-like organisms. Other minerals such as calcium are essential for the synthesis of mollusk shells and coral skeletons. Although nutrients are essential for life, excessively high levels of nutrients in sea water can cause eutrophication. This process of nutrient enrichment can lead to vast algal blooms which eventually die and start to decompose. The decomposition may deplete the availably dissolved oxygen in the water, killing fish and other organisms.

# Nutrients

- **Metabolic Requirements**




Tip:
Cooler, less salty water of the open sea contains more oxygen than the warm, saline water in a tide pool

# Elements

- 生命过程所必须元素：
  H, B, C, N, O, F, Na, Mg, Si, P, S, Cl, K, Ca, V, Mn, Fe, Co, Zn, Br, I, etc.
- 对生命可能需要的元素：
  Al, Ti, As, Sn, Pb, Ge, Se, etc.
- 不需要的元素
  He, Li, Be, Ne, Ar, Sc, Cr, Ga, Kr, Rb, Sr, Y, Zr, Nb, Tc, Rn, Rd, Ag, Cd, In, Sb, Te, Xe, Cs, Ba, La, Hf, Ta, W, Re, Os, Ir, Pt, Au, Hg, Tl, Bi, Po, At, Rn, Fr, Ac, Th, Pa, U, etc.

# Tides

- Spring tide and neap tide

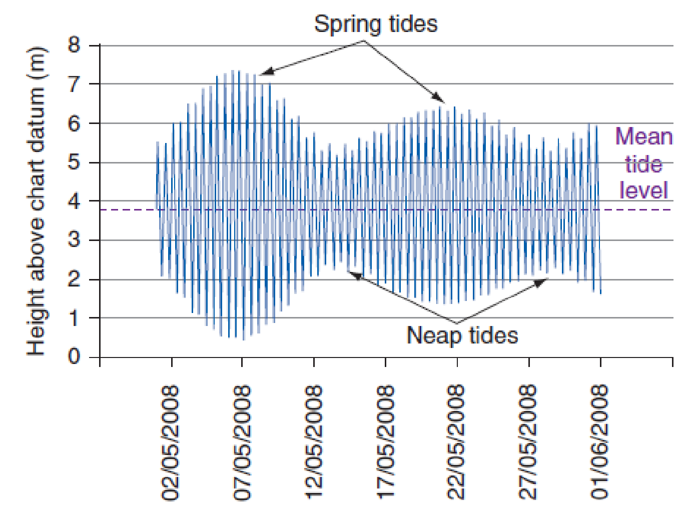
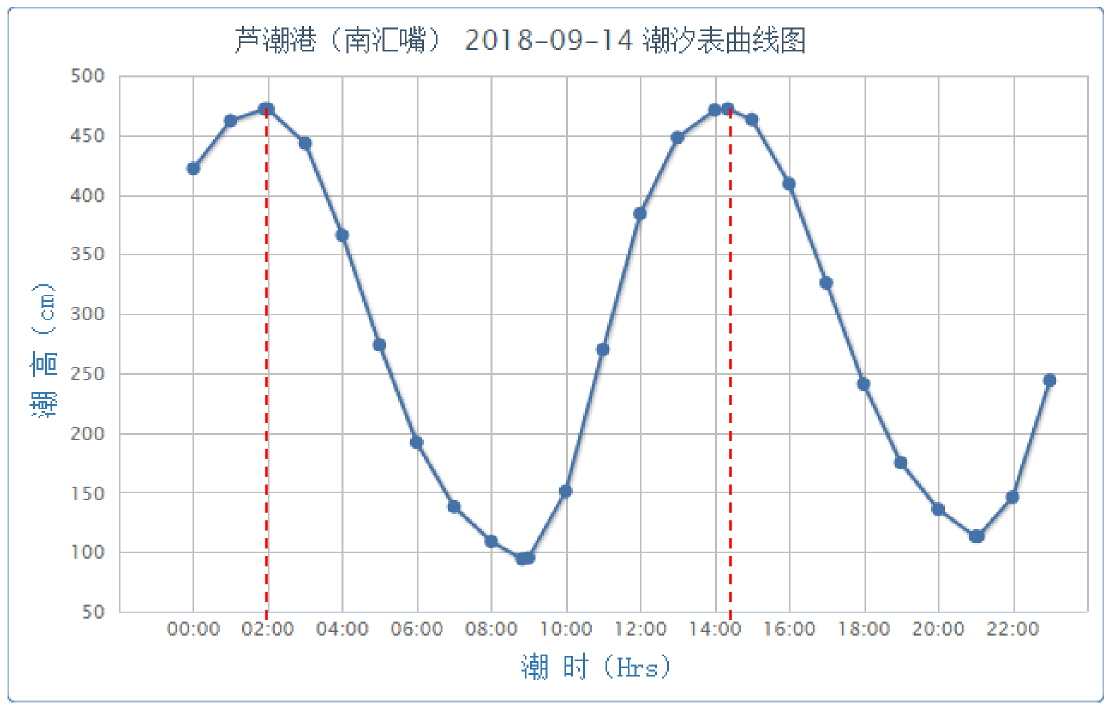



**Figure 1.19**

Typical series of tidal cycles over a month from Milford Haven in Southwest Wales. Chart datum (*y*-axis) is mainly used on nautical charts and is the lowest possible astronomical tide which may never actually be achieved over many years. (Data from 'Tide Plotter', Belfield Software.)



# Thermohaline circulation


**Figure 1.25**

A diagram of the global conveyer belt – the circulation pattern which moves water heat and organisms around the globe. (From Haupt & Seidov 2007 after Brasseur et al 1999; reproduced with permission of Elsevier.)

# Thermohaline circulation

# Climate change

- Two ... re incr ... iño.

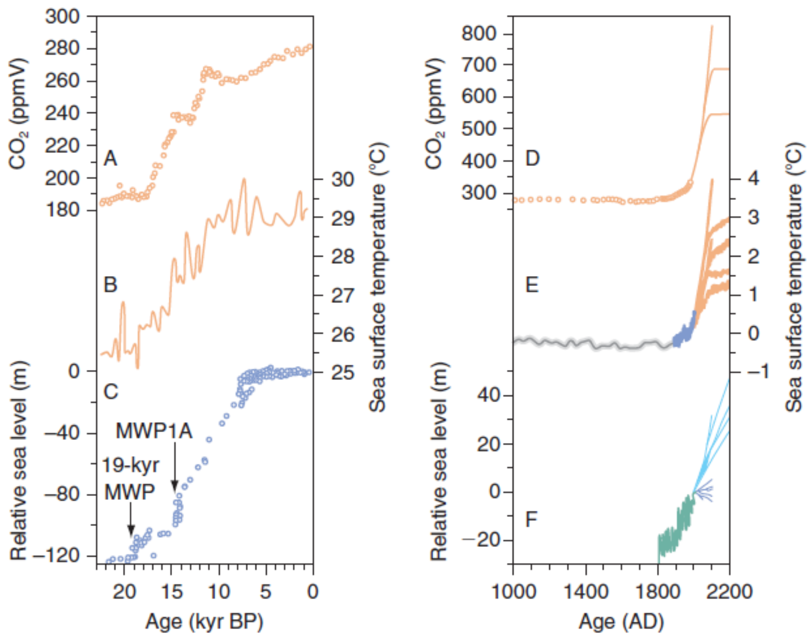
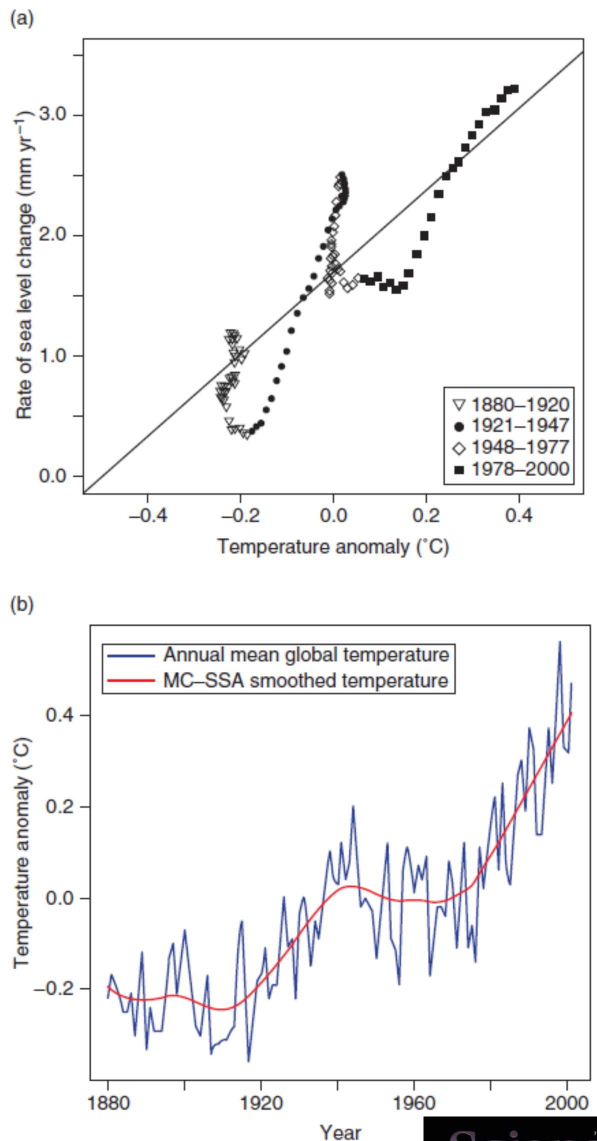




**Figure 1.32**

Time series of key variables encompassing the last interval of significant global warming (last deglaciation) (left) compared with the same variables projected for various scenarios of future global warming (right). (A) Atmospheric $CO_2$ from Antarctic ice cores. (B) Sea surface temperatures in the western equatorial Pacific based on Mg/Ca measured in planktonic forminifera. (C) Relative sea level as derived from several sites far removed from the influence of former ice sheet loading. MWP = meltwater pulse. (D) Atmospheric $CO_2$ over the past millenium (circles) and projections for future increases (solid lines). Records of atmospheric $CO_2$ are from Law Dorne, Antarctica and direct measurements since 1958 are from Mauna Loa, Hawaii. Also shown are three emission scenarios of atmospheric $CO_2$ over the course of the 21st century and subsequent stabilization over the course of the 22nd century. (E) Temperature reconstruction for the Northern Hemisphere from 1000 to 2000 AD (grey time series), global temperature based on historic measurements, 1880 to 2004 (blue time series), and projected warming based on simulations with two global coupled three-dimensional climate models with the use of three emission scenarios (orange time series). (F) Relative sea-level rise during the 19th and 20th centuries from the tide gauge record at Brest, France (green time series), projections for contributions from combined Greenland and Antarctic ice sheets (dark blue time series), and projections from sea-level rise from thermal expansion based on climate simulations shown in (E) (light blue time series). (From Alley et al 2005; reproduced with permission of *Science* – AAAS.)



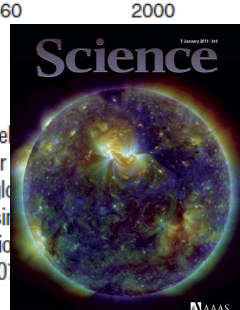
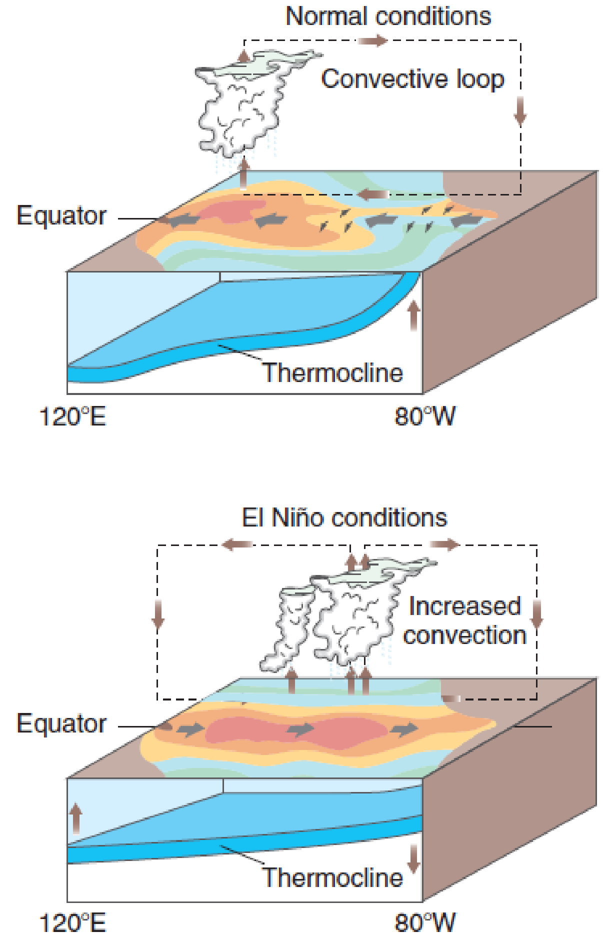




**Figure 1.33**

(a) The relationships of the rate of global mean sea-level ... level surface temperature with the data divided into four ... a different relationship between the variables. (b) The gl... temperature record, annual data and data smoothed usi... The four epochs described in (a) relate to the four sectio... record that can be clearly seen. (From Holgate et al 200... permission of *Science* – AAAS.)




El Niño conditions

Weakened trade winds allow warm water to move eastwards

Thick upper-ocean layer keeps nutrient-rich water from upwelling along the coast of the Americas

Ocean heat released into the atmosphere increases cloud formation and alters path of jetstream

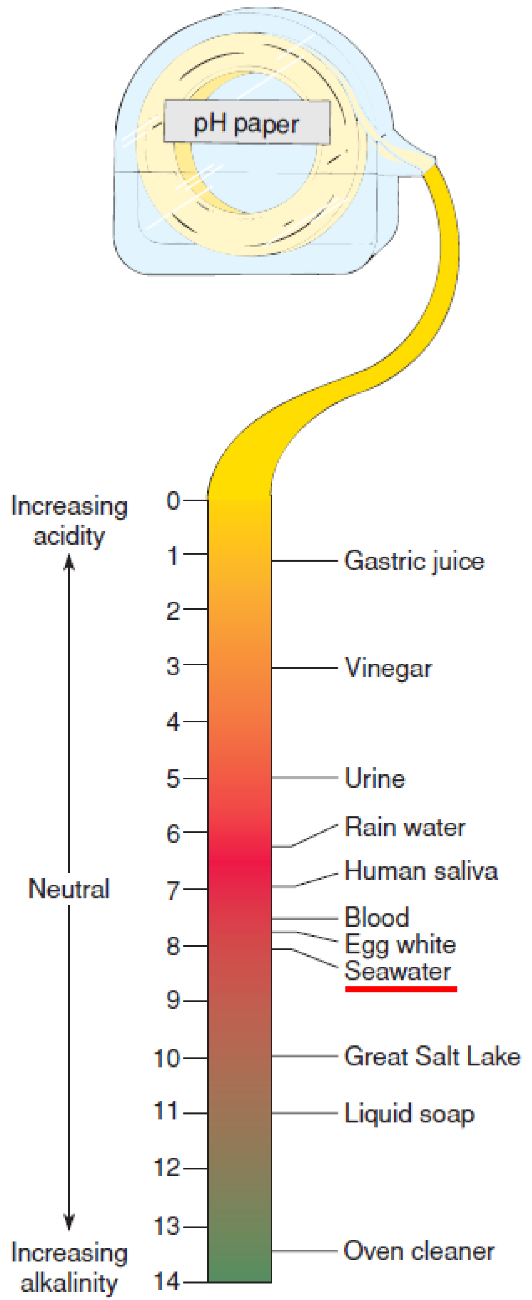
**Figure 1.34**

Marine and atmospheric conditions in the mid-Pacific under normal and El Niño conditions. (Courtesy of NOAA/PMEL/TAO Project Office, Dr. Michael J. McPhaden, Director.)

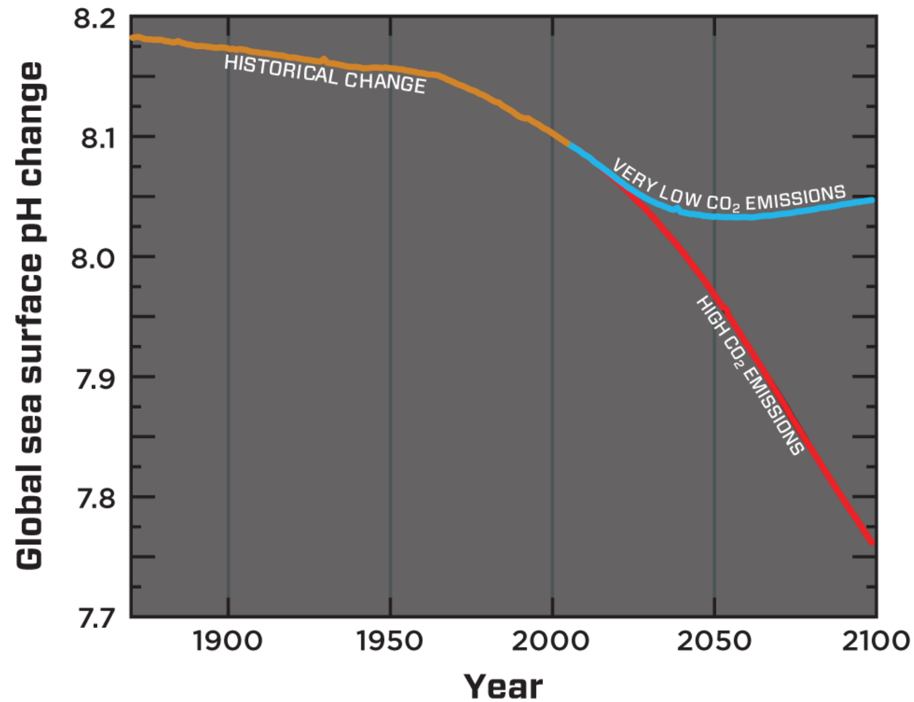
e

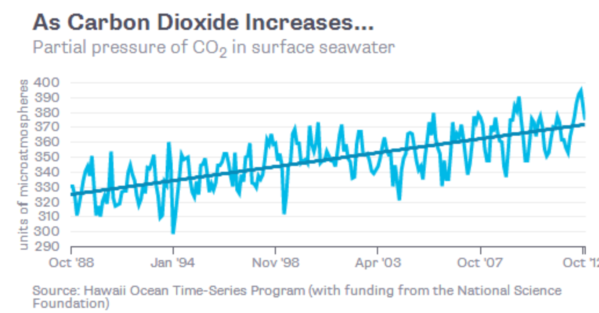
ersity

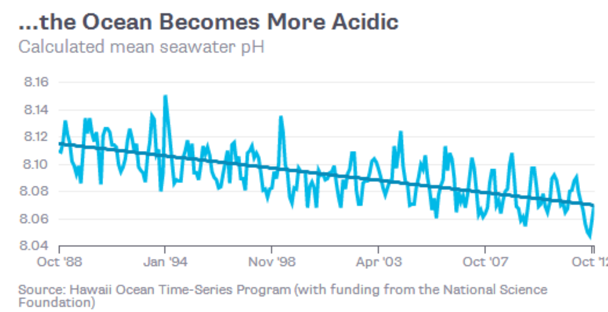
# ENSO


pH paper
Increasing acidity
Neutral
Increasing alkalinity
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
Gastric juice
Vinegar
Urine
Rain water
Human saliva
Blood
Egg white
Seawater
Great Salt Lake
Liquid soap
Oven cleaner

pH scale


Global sea surface pH change
8.2
8.1
8.0
7.9
7.8
7.7
HISTORICAL CHANGE
VERY LOW $CO_2$ EMISSIONS
HIGH $CO_2$ EMISSIONS
1900
1950
2000
2050
2100
Year


As Carbon Dioxide Increases...
Partial pressure of $CO_2$ in surface seawater
units of microatmospheres
400
390
380
370
360
350
340
330
320
310
300
290
Oct '88
Jan '94
Nov '98
Apr '03
Oct '07
Oct '12
Source: Hawaii Ocean Time-Series Program (with funding from the National Science Foundation)

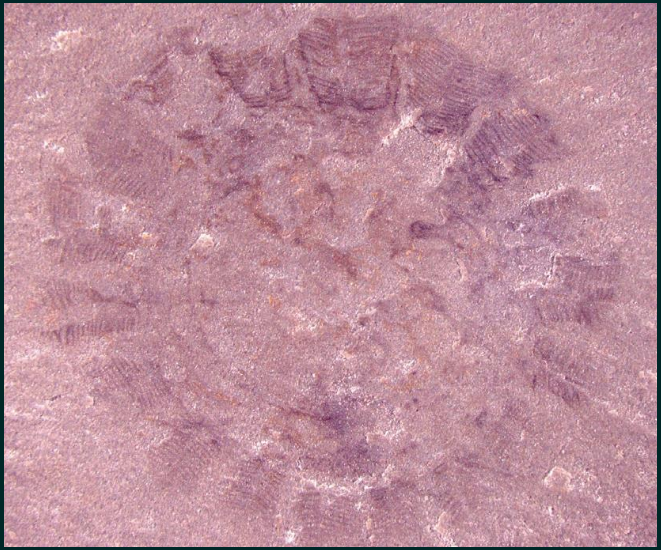

...the Ocean Becomes More Acidic
Calculated mean seawater pH
8.16
8.14
8.12
8.10
8.08
8.06
8.04
Oct '88
Jan '94
Nov '98
Apr '03
Oct '07
Oct '12
Source: Hawaii Ocean Time-Series Program (with funding from the National Science Foundation)

# $CO_2$ and Ocean pH

# Summary

- Clearly there are numerous physical factors and conditions that influence life in the sea. Depth, temperature, salinity, turbidity, velocity, pressure and so on, all combine to produce a myriad of physical and chemical habitats which provide a huge number of combinations and permutations. The oceans are not at all the bland, homogeneous expanse that we might think, and with this in mind, it should be no surprise that the diversity of life in the sea is as rich and varied as the physical conditions in which it lives. This is Biodiversity.

# Marine Biodiversity



# Marine Biodiversity-Past

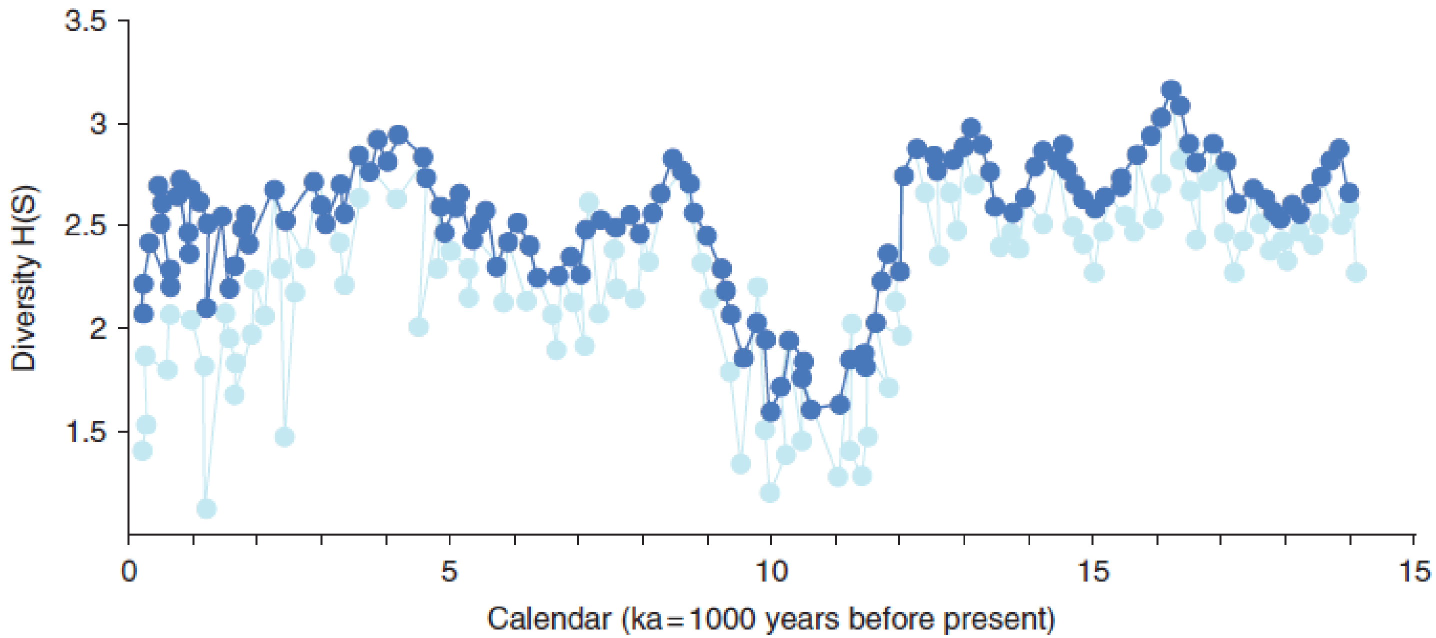



**Figure 2.8**

Ostracod species diversity (Shannon–Wiener index) over the last 20,000 years in northwest Atlantic deep-sea sediment cores. Light blue plots = calculations based on raw census data; dark blue plots based on 3-point moving sum dataset. (From Yasuhara et al 2008; reproduced with permission of Micropaleontology Press.)

# Marine Biodiversity

| REFERENCE | ESTIMATED NUMBER | HABITAT |
|---|---|---|
| Grassle & Maciolek 1992 | 10 million | Deep-sea benthos |
| May 1994 | 0.5 million | Deep-sea benthos |
| Poore & Wilson 1993 | 5 million | Benthos |
| Briggs 1994 | 0.2 million | All sea |
| Reaka-Kudla 1997 | 0.6–0.95 million | Coral reefs |
| Knowlton 2001 | 0.6–9 million | Coral reefs |
| Adrianov 2003 | 20–30 million<br>20–30 million<br>10 million | Macrobenthos<br>Meiobenthos<br>Nematodes |
| Malakoff 2003 | 1 million+ | All taxa/sites |

# Population

- A population is a group of individuals of the same species that occupy a specified area.
- Members of a population interact with each other and are able to breed with each other. They rely on the same resources and are influenced by the same environmental factors.
- In nature, populations are separated from one another by barriers that prevent organisms from interacting or breeding.
- The population, rather than the individual, is the basic unit that many ecologists study.

# Range and Size

- Geographical boundaries.
- Population size.

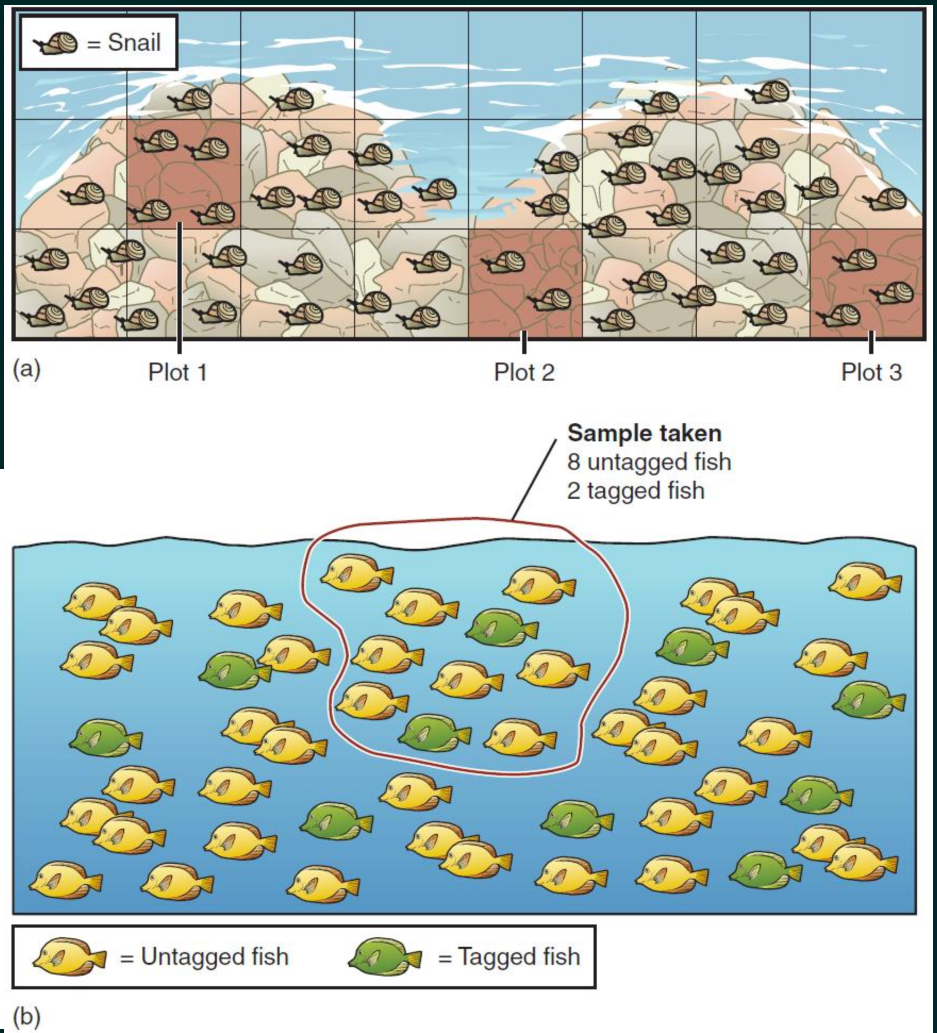
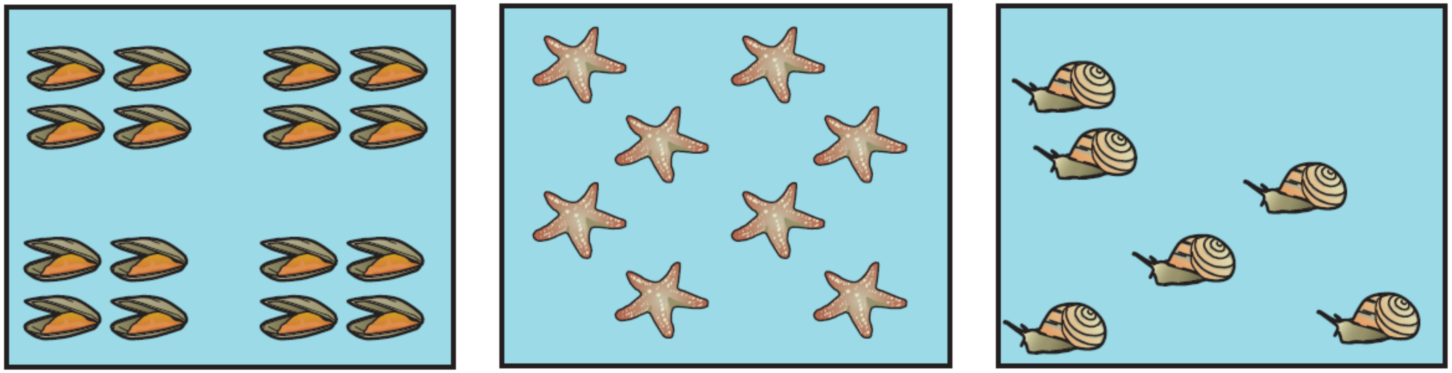



**Figure 2-7 DETERMINING POPULATION SIZE.** (a) We can estimate the number of snails on these coastal rocks by dividing the area into smaller divisions (plots) and then counting the number in several representative plots. We could then find the average number per plot and multiply by the number of plots in the area. (b) The number of fish in this range can be estimated by capturing a sample from the population and marking them with tags. The tagged individuals are then released and allowed to mix with the population. Sometime later another sample is taken and the ratio of tagged to untagged individuals is determined. We assume that this represents the ratio of tagged to untagged individuals in the population. Since we know how many tagged individuals we released into the population, we can estimate the total population size.

# Distribution of Organism



(a) Clumped (b) Uniform (c) Random

Figure 2-8 **DISPERSION PATTERNS.** The pattern of spacing of individuals in a population is known as dispersion. Possible patterns are (a) clumped, (b) uniform, and (c) random.

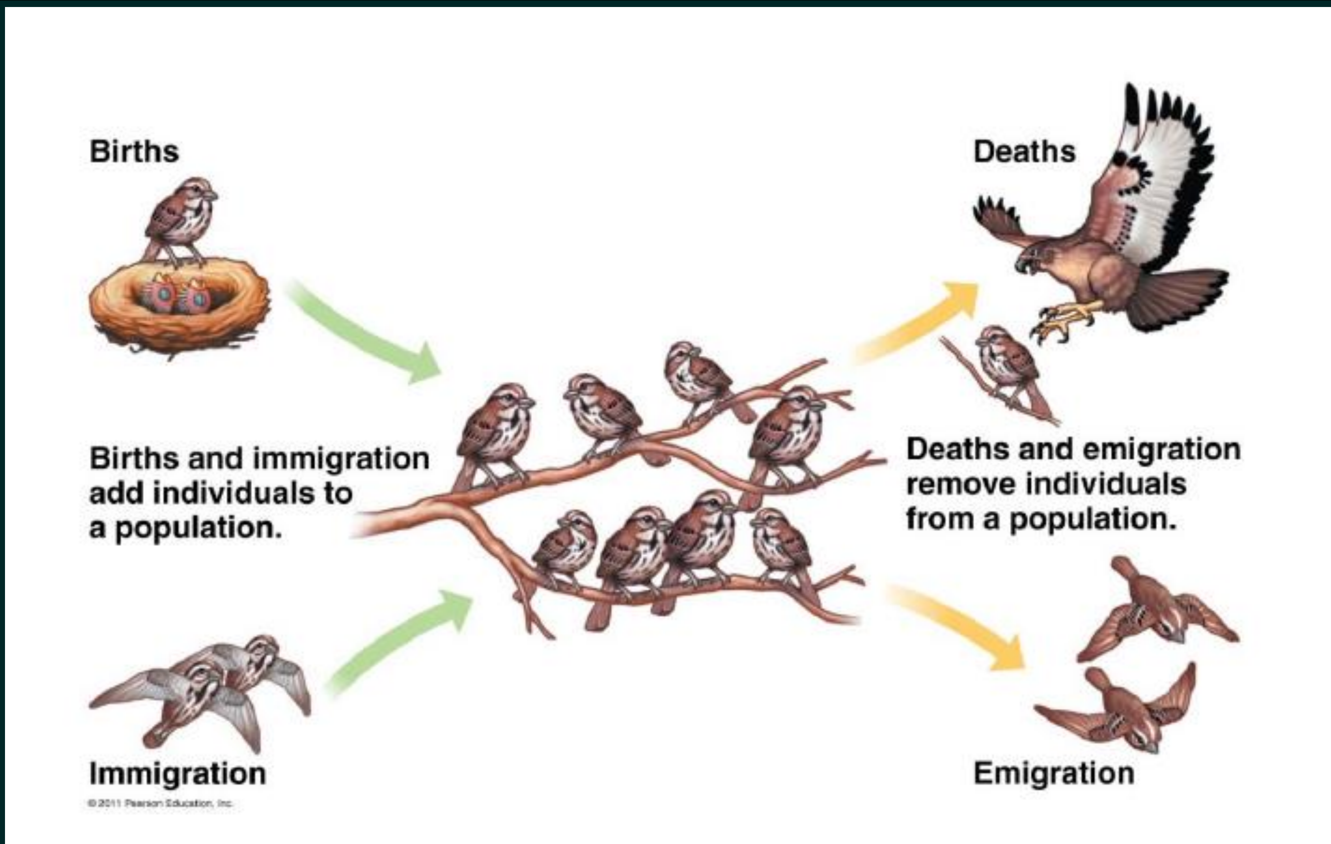
- Population density
- Dispersion: Clumped, uniform and random

Caused by variations in the organism's physical environment.

The results of competition.

Occurs when there is a lack of strong interactions among individuals and is not common in the marine environment

# Change in Population Size



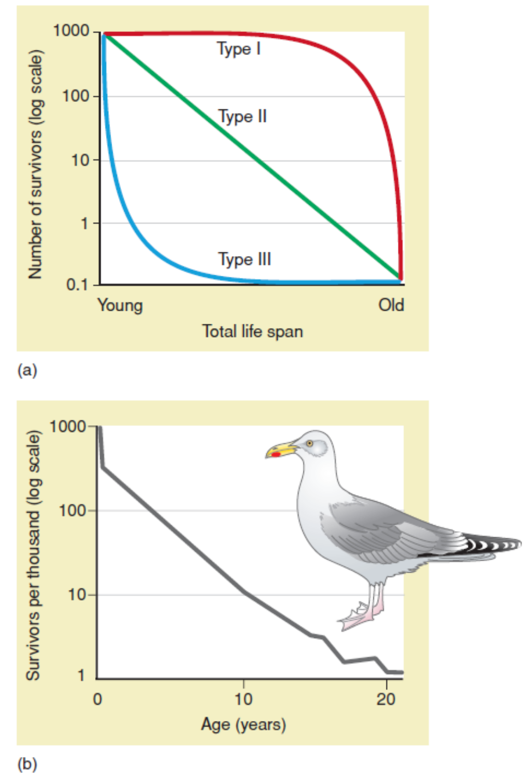
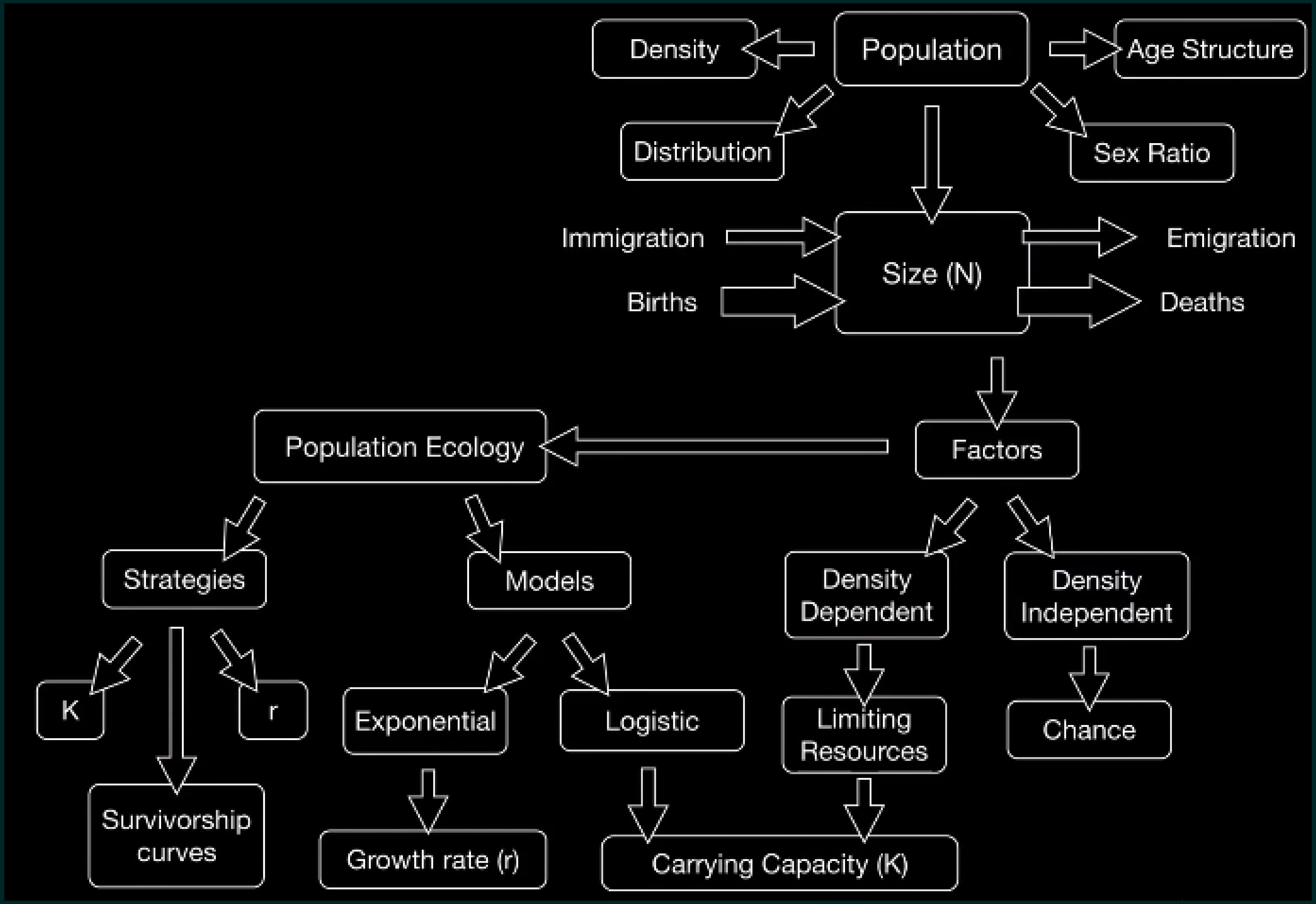




**Figure 2-9** **SURVIVORSHIP CURVES.** (a) Survivorship curves indicate the number of individuals still living at each age from birth to death. Type I curves indicate increased death rates as the organisms age. Type II curves indicate relative constant death rates over time. Type III curves indicate higher death rates among the young but increased survival for those organisms that survive past a certain age. (b) Not all organisms have life histories that conveniently fit one of these three curves in part (a). For instance, herring gulls, *Larus argentatus*, have Type III survivorship curves as chicks and Type II survivorship curves as adults.

# Change in Population Size



# Population Regulation

- Density-dependent factor
- Density-independent factor
- *r-strategists*
- *K-strategists*
- The majority of marine organisms are neither pure r-strategists nor K- strategists but lie somewhere in a continuum between these two extremes.

***Shark reproduce video***

# Population Growth

- Recruitment
- Larval settlement
- J-shaped curve
  (Exponential or logarithmic growth)
- S-shaped curve
  (Logistic growth)
- Carrying capacity

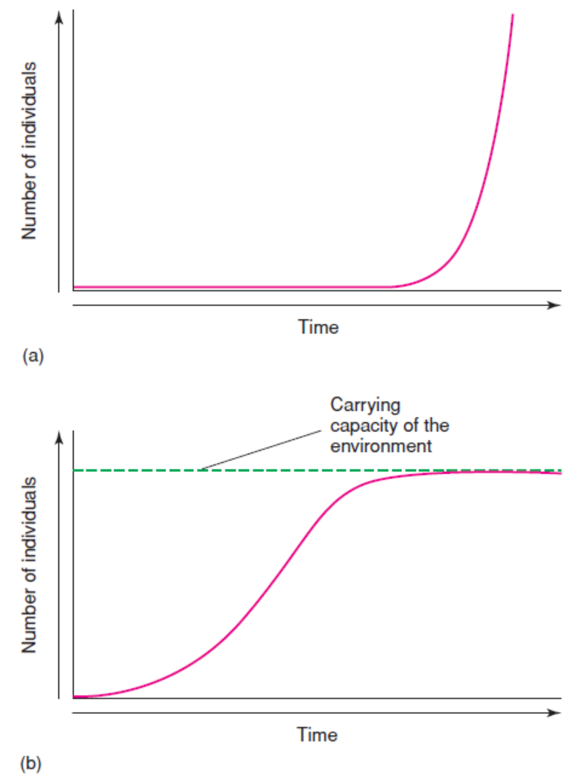



Figure 2-10 POPULATION GROWTH. (a) Under proper conditions, some marine organism populations can grow exponentially. A graph of exponential growth gives a characteristic J-shaped curve. (b) As the growth of a population approaches its carrying capacity, the graph flattens out. As a result, the logistic growth curve shown here has somewhat of an S-shape.

# Population Regulation

- Density-dependent factor
- Density-independent factor
- *r-strategists*
- *K-strategists*
- The majority of marine organisms are neither pure r-strategists nor K- strategists but lie somewhere in a continuum between these two extremes.

***Shark reproduce video***

# r-and K-Selected species

**Table 56.2** Characteristics of *r*- and *K*-Selected Species

| Life history feature | *r*-selected species | *K*-selected species |
|---|---|---|
| Development | Rapid | Slow |
| Reproductive rate | High | Low |
| Reproductive age | Early | Late |
| Body size | Small | Large |
| Length of life | Short | Long |
| Competitive ability | Weak | Strong |
| Survivorship | High mortality of young | Low mortality of young |
| Population size | Variable | Fairly constant |
| Dispersal ability | Good | Poor |
| Habitat type | Disturbed | Not disturbed |
| Parental care | Low | High |

# Population Regulation

- Density-dependent factor
- Density-independent factor
- *r-strategists*
- *K-strategists*
- The majority of marine organisms are neither pure r-strategists nor K- strategists but lie somewhere in a continuum between these two extremes.

***Shark reproduce video***

# Shark reproduce

上海海洋大學
SHANGHAI OCEAN UNIVERSITY
1912-2012

# In Summary

- In ecological terms, a population is a group of the same species that occupies a specific area.
- Factors that affect reproduction and mortality rate such as survivorship and life histories have a significant effect on the size of populations. Populations grow when more organisms are added through reproduction and immigration than are lost through death and emigration. Initially, populations grow quickly, a process known as exponential growth. Such growth cannot be maintained indefinitely.
- Characteristics of the environment, such as space and available food, limit the number of organisms an area can support. This limit is called the carrying capacity of the environment. The carrying capacity is set by density-dependent factors that decrease reproduction or increase mortality rate as a population grows.
- Population growth can also be limited by density-independent factors.

# Community

- A biological *community* is composed of populations of different species that occupy one habitat at the same time.
- The species that make up a community are linked to some degree by competitive relationships, predator-prey relationships, and symbiotic relationships.

A ***community*** is an assembly of populations of different species that occupy the same habitat at the same time.

***Niche*** refers to an organism's role in the environment.

GLOSSARY

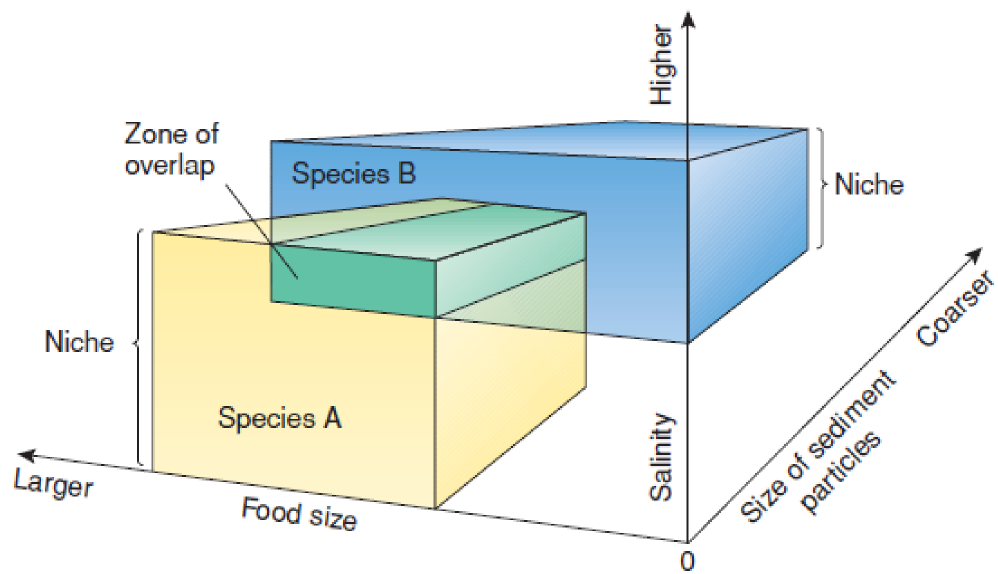
# Community


Figure 2-11 **COMMUNITY.** A community is composed of populations of different species interacting with each other. On this rocky coast populations of limpets, sea anemones, seaweeds, crustaceans, sea stars, and snails all interact with each other in a number of ways to form a balanced community.

# Niche

- What an organism does in its environment is its *niche*.
- A full description of an organism's niche would include the range of environmental and biological factors that affect its ability to survive and reproduce.

**Figure 2-12 A NICHE.** An organism's niche is determined by a variety of abiotic and biotic factors acting together on the organism. This three-dimensional graph shows how several factors (food size, salinity, and size of sediment particles) interact to form niches for two species of burrowing worm. On the basis of this graph, we can see that species A prefers to burrow in substratum composed of smaller sediment particles where the salinity of the water is low and prefers to feed on medium- to large-sized food items. Species B, on the other hand, prefers coarser sediments where the salinity of the water is higher and prefers smaller food items. The zone of overlap indicates the combination of sediments, salinity, and food that would meet the requirements of both organisms.



# Niche

- The niche of an organism is often described as its role in the community. It refers to the environmental conditions and resources that define the requirements of an organism. The broadest niche that an organism can occupy (defined mostly by resource availability and tolerance to abiotic factors) is called its fundamental niche. In reality, organisms often occupy a smaller subset of their fundamental niche because of biological interactions with other species such as competition and predation. This subset is called the realized niche.

# Isotopic niche

Deep-Sea Research I 96 (2015) 49–58

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

## Plasticity of trophic interactions among sharks from the oceanic south-western Indian Ocean revealed by stable isotope and mercury analyses

Jeremy J. Kiszka [a,b,*], Aurore Aubail [b], Nigel E. Hussey [c], Michael R. Heithaus [a], Florence Caurant [b], Paco Bustamante [b]

[a] Marine Sciences Program, Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA
[b] Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS-Université de la Rochelle, Institut du Littoral et de l'Environnement, 2 rue Olympe de Gouges, 17000 La Rochelle, France
[c] Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Avenue, ON, Canada N9B 3P4

ARTICLE INFO

*Article history:*
Received 11 July 2014
Received in revised form
12 November 2014
Accepted 18 November 2014
Available online 28 November 2014

*Keywords:*
Elasmobranchs
Indian Ocean
$\delta^{15}N$
$\delta^{13}C$
Trace elements
Intra-species variations

ABSTRACT

Sharks are a major component of the top predator guild in oceanic ecosystems, but the trophic relationships of many populations remain poorly understood. We examined chemical tracers of diet and habitat ($\delta^{15}N$ and $\delta^{13}C$, respectively) and total mercury (Hg) concentrations in muscle tissue of seven pelagic sharks: blue shark (*Prionace glauca*), short-fin mako shark (*Isurus oxyrinchus*), oceanic whitetip shark (*Carcharhinus longimanus*), scalloped hammerhead shark (*Sphyrna lewini*), pelagic thresher shark (*Alopias pelagicus*), crocodile shark (*Pseudocarcharias kamoharai*) and silky shark (*Carcharhinus falciformis*), from the data poor south-western tropical Indian Ocean. Minimal interspecific variation in mean $\delta^{15}N$ values and a large degree of isotopic niche overlap – driven by high intraspecific variation in $\delta^{15}N$ values – was observed among pelagic sharks. Similarly, $\delta^{13}C$ values of sharks overlapped considerably for all species with the exception of *P. glauca*, which had more $^{13}C$-depleted values indicating possibly longer residence times in purely pelagic waters. Geographic variation in $\delta^{13}C$, $\delta^{15}N$ and Hg were observed for *P. glauca* and *I. oxyrinchus*. Mean Hg levels were similar among species with the exception of *P. kamoharai* which had significantly higher Hg concentrations likely related to mesopelagic feeding. Hg concentrations increased with body size in *I. oxyrinchus*, *P. glauca* and *C. longimanus*. Values of $\delta^{15}N$ and $\delta^{13}C$ varied with size only in *P. glauca*, suggesting ontogenetic shifts in diets or habitats. Together, isotopic data indicate that – with few exceptions – variance within species in trophic interactions or foraging habitats is greater than differentiation among pelagic sharks in the south-western Indian Ocean. Therefore, it is possible that this group exhibits some level of trophic redundancy, but further studies of diets and fine-scale habitat use are needed to fully test this hypothesis.



### 1. Introduction

Sharks are a major component of the top predator guild in open-ocean ecosystems along with tunas, billfish, and cetaceans. These "pelagic sharks" occur from cold temperate to tropical waters, from the surface to 1000 m depth or more (Compagno, 2008) and include some of the most wide-ranging marine predator species (Pitkitch et al., 2008). Their extensive movements and ocean-basin scale migrations are most likely related to oligotrophy and the patchy nature of food resources in open-ocean ecosystems as well as directed movements for social and reproductive purposes. Many pelagic sharks use coastal/continental shelf waters in addition to open oceanic waters throughout ontogeny although certain biological functions, for example, gestation may be restricted to the open ocean (Compagno, 1984; Bonfil, 2008; Nakano and Stevens, 2008). Even though pelagic sharks commonly occur in an environment far from human populations, they commonly overlap and interact with offshore fisheries. Currently, three-quarters of pelagic elasmobranchs are classified as Threatened or near Threatened (IUCN Red List Status), and 11 species are globally threatened with a high risk of extinction (Dulvy et al., 2008). Despite clear evidence for shark population declines, including in oceanic ecosystems (Baum et al., 2003; Myers and Worm, 2003; Ferretti et al., 2010), relatively little is known on the feeding ecology of many species and the ecological importance of this guild is poorly understood (Ferretti et al., 2010; Heithaus et al., 2010; Kitchell et al., 2002).

* Corresponding author at: Marine Sciences Program, Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA. Tel.: +1 305 9194104.
*E-mail address:* jeremy.kiszka@gmail.com (J.J. Kiszka).

http://dx.doi.org/10.1016/j.dsr.2014.11.006


Vol. 17: 83–92, 2012
doi: 10.3354/esr00418

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published online April 27

## Isotopic niches of the blue shark *Prionace glauca* and the silky shark *Carcharhinus falciformis* in the southwestern Indian Ocean

N. Rabehagasoa[1,*], A. Lorrain[2], P. Bach[1], M. Potier[3], S. Jaquemet[4,5], P. Richard[6], F. Ménard[3]

[1]Institut de Recherche pour le Développement (IRD), UMR 212 EME (IRD/IFREMER/UM2), BP 50172, 97492 Ste Clotilde Cedex, La Réunion, France
[2]IRD, UMR LEMAR 195 (UBO/CNRS/IRD), BP 70, 29280 Plouzané, France
[3]IRD, UMR 212 EME, Avenue Jean Monnet, BP 171, 34203 Sète Cedex, France
[4]Université de la Réunion, Laboratoire Ecomar, Avenue René Cassin, 97715 Saint-Denis Cedex, France
[5]IRD, UMR 212 EME, Botany Department, Rhodes University, 6140 Grahamstown, South Africa
[6]Littoral, Environnement et Sociétés, UMR 6250 CNRS-Université de La Rochelle, 17042 La Rochelle, France

ABSTRACT: In the Indian Ocean, the blue shark *Prionace glauca* and the silky shark *Carcharhinus falciformis* represent the 2 main shark bycatch species in pelagic longline and purse seine fisheries, respectively. With the increasing market demand for fins, catches may increase in the future, with potential effects on ecosystem trophic functioning through top-down cascading effects. Knowledge of the species' trophic ecology is therefore crucial but is limited by the lack of data from the Indian Ocean. Stable isotope analysis was therefore performed on muscle tissues ($\delta^{15}N$ and $\delta^{13}C$) of these 2 shark species from the western Indian Ocean. Our study showed that body length, season, and zone effects were relatively small for the 2 species. However, significant $\delta^{13}C$ differences between the 2 species suggest niche partitioning, with silky sharks having a more inshore foraging habitat than blue sharks. Finally, lower muscle $\delta^{15}N$ values were observed in juvenile silky sharks caught by purse seiners around fish aggregating devices (FADs) compared to juveniles caught by longliners. One hypothesis is that FADs could act as an ecological trap for juvenile silky sharks, leading to a position at lowest trophic level for these individuals. However, different foraging habitats could also explain the observed patterns between juveniles. Although preliminary, our results provide a basis for the implementation of species-specific protection and management strategies.

KEY WORDS: Stable isotopes · δ13C · δ15N · Trophic ecology · Niche partitioning · Foraging habitat · Sharks



### INTRODUCTION

Pelagic sharks, which are among the largest predators in the ocean, play an important ecological role in open-sea ecosystems through predation effects on community structure (Estrada et al. 2003, Heithaus et al. 2008, Ferretti et al. 2010). Large pelagic sharks are sometimes the only consumers of a range of meso-predators (Heithaus et al. 2008) such as small elasmobranchs (Wetherbee & Cortés 2004) or some marine mammals. Most shark populations are intensively exploited by large-scale pelagic fisheries (Baum et al. 2003, Campana et al. 2008), leading to marked and rapid declines of the less resilient species, such as carcharhinids. Worldwide, 700 000 to 850 000 t of sharks are caught annually as target species or bycatch, and landings increase at an annual rate of ca. 2% (Camhi et al. 2009, Lucifora et

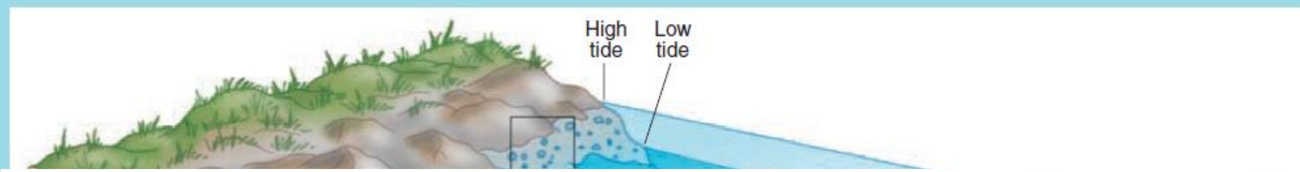
*Email: niriniony.rabehagasoa@ird.fr

# Competition

- When organisms require the same limited resource, such as food, living space, or mates, competition occurs.
- Competition occur between different species – *interspecific*
- Competition occur between members of a single species – *intraspecific* competition


**Figure 2-13 COMPETITION.**
Competition among butterflyfishes is limited by the shape of their mouths, which determines where they can find food and the types of food they can eat. This saddled butterflyfish (*Chaetodon ulietensis)* has a blunt mouth that restricts it to feeding on the surface of corals.

# Connell's Barnacles



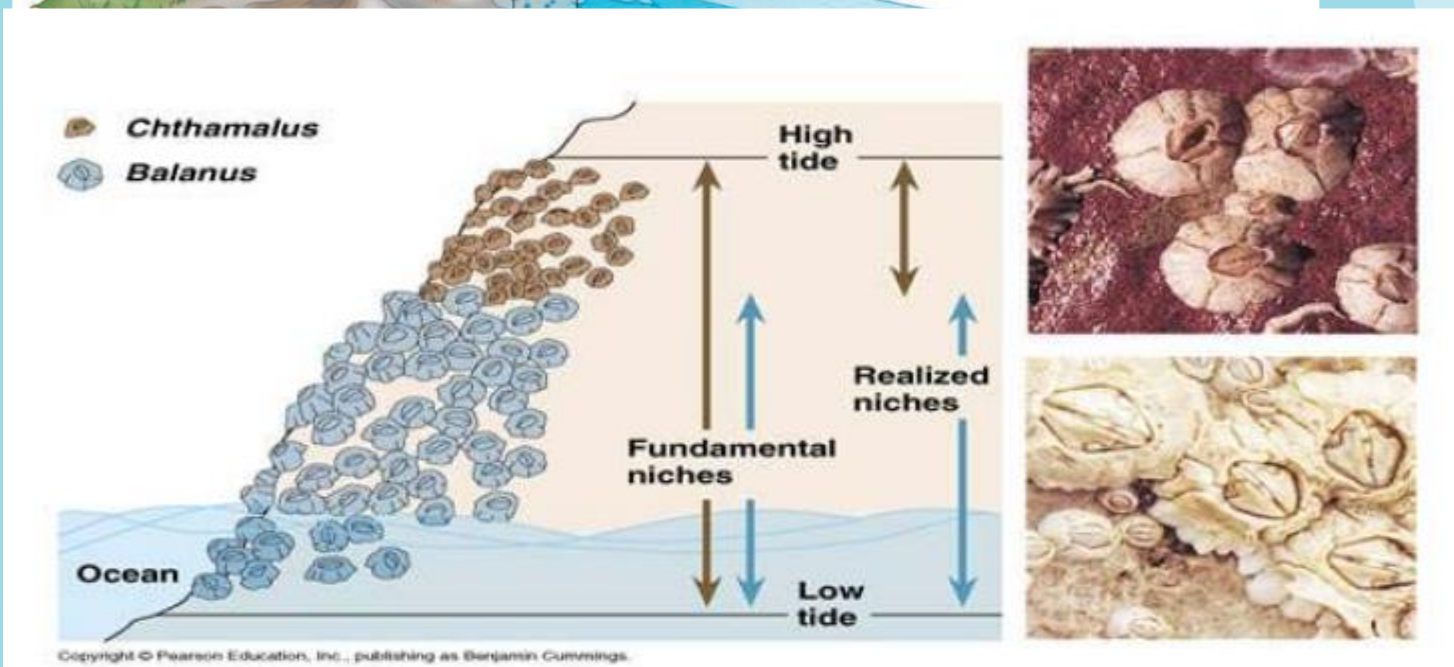




Figure 2-A FUNDAMENTAL VS. REALIZED NICHE. (a) J. H. Connell noted that two species of barnacles in the genera *Chthamalus* and *Semibalanus* live in separate layers on the rocky shores of Scotland. *Chthamalus stellatus* live just above the high tide line and is replaced by *Semibalanus balanoides* beneath this point. (b) When the population of *Chthamalus* was experimentally removed, the population of *Semibalanus* did not colonize the open space. (c) When the *Semibalanus* population was removed, however, *Chthamalus* quickly colonized the open space.

# Symbiosis: Living Together

- Mutualism
- Commensalism
- Parasitism

*Symbiosis* is an intimate living arrangement between two different species.

GLOSSARY


(a) (b) (c)

Figure 2-15 SYMBIOTIC RELATIONSHIPS. (a) Mutualism: a clownfish takes refuge in the tentacles of a sea anemone. (b) Commensalism: Remora fishes attached to this shark gain protection from predators. (c) Parasitism: Nematode worms in the swimbladder of a marine eel derive nutrition from the organ's blood supply and weaken the host.

# Symbiosis

# In Summary

- A community is composed of *populations* of organisms that occupy the same habitat at the same time. The role an organism plays in its environment, in a sense its "profession," is its *niche*. The broadest niche an organism can occupy is its fundamental niche. Interactions with other organisms and the physical environment, however, limit it to a smaller part of the niche called its realized niche. The biological environment of an organism includes interactions with other species, such as *competition*, *predator–prey relationships*, and *symbioses*. The major categories of symbiotic relationships are *mutualism*, *commensalism*, and *parasitism*.

# Ecosystem

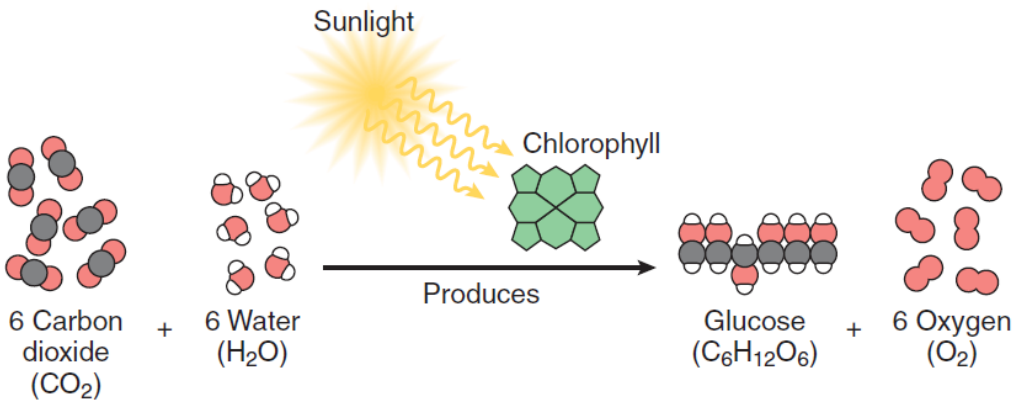
- Energy flow through Ecosystems

All living organisms require energy to live, grow and reproduce. The source of the energy for practically all life on earth is the sun. Organisms that are capable of photosynthesis convert the radiant energy of the sun into the chemical energy of food molecules. The molecules in turn serve as a sources of nutrition for not only photosynthesizers but also the organisms that feed on them. As each organism in turn feeds on another, energy is funneled through levels of the ecosystem.

# Producer

- Some organisms contain special pigment molecules, such as *chlorophyll*, that capture the sun's energy.

**Figure 2-16 PHOTOSYNTHESIS.** In the process of photosynthesis, carbon dioxide and water combine to form a sugar called glucose. Oxygen is a by-product of the reaction. The energy for the process is supplied by sunlight. Special molecules, such as the green pigment chlorophyll, absorb light energy and make it available to power the photosynthetic process. The glucose produced by photosynthesis can be used by the photosynthetic organism as food or to make other important molecules.




- In marine environment, the primary photosynthetic organisms are phytoplankton, seaweeds, and plants. They were called *autotrophs* or *producers.*

# Primary productivity

- Primary productivity refers to the rate at which energy-rich food molecules (organic compounds) are being produced from inorganic materials.

An ***autotroph*** is an organism that is capable of producing its own food; also known as a producer.

***Primary productivity*** refers to the rate at which energy-rich food molecules (organic compounds) are being produced from inorganic materials.

GLOSSARY

# Consumers

- Heterotrophs
- First-order consumers (primary consumers)
- Second-order consumers (secondary consumers)
- *Omnivores*: consumers that feed on both producers and other consumers
- *Detritivores* are organisms that feed on detritus, organic matters such as animal wastes and bits of decaying tissues.
- *Decomposers* are organisms that break down the tissue of dead organisms and help to recycle nutrients.

By N. Hussey

# Food Chains

- In every ecosystem, producers and consumers are linked by feeding relationships called *food chains*.

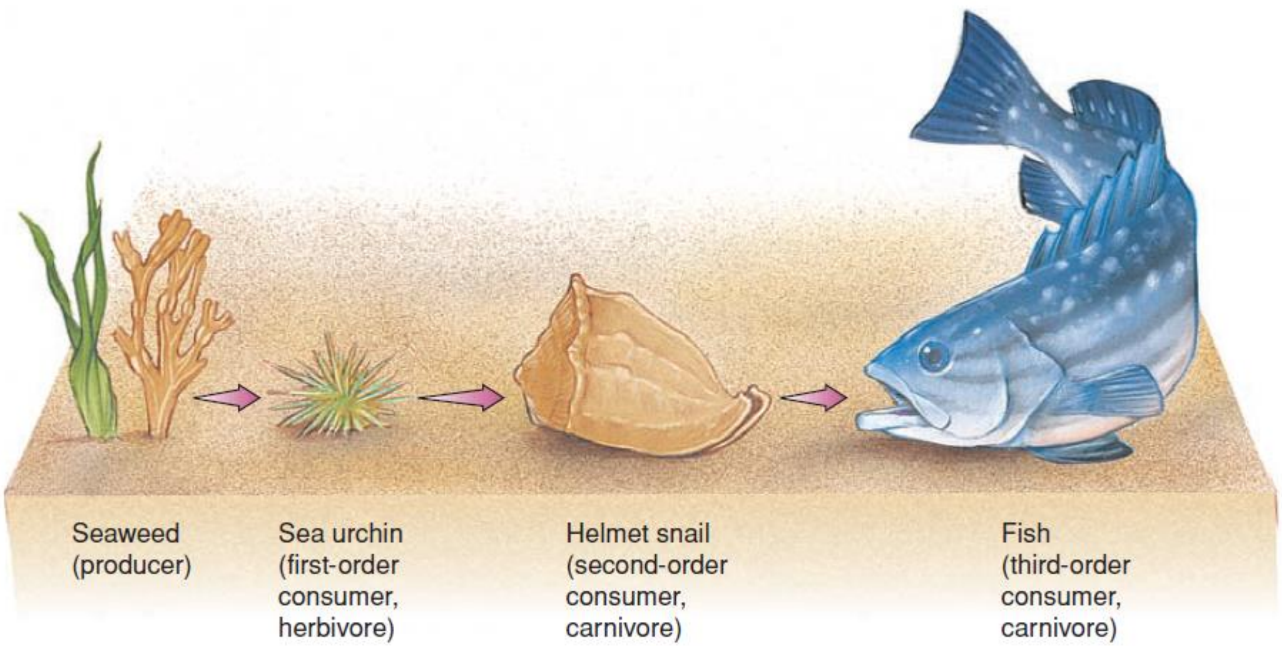



**Figure 2-17 A FOOD CHAIN.** Food chains depict the feeding relationships among a group of organisms as a linear sequence from producers to higher-level consumers.

# Other Energy Pathways

- The phytoplankton may release some of their photosynthetic products into the surrounding seawater. These organic molecules that are lost or released into the water column are referred to as *dissolved organic matter* (DOM).

- *Detritus* represents an enormous supply of energy for marine organisms. The major sources of detritus are decaying plant and algal matter that is not consumed by grazing herbivores, animal wastes, and bits and pieces of animal tissue.

# Food for the Deep

- In the deep ocean, *marine snow* is a continuous shower of mostly organic detritus falling from the upper layers of the water column, plus some inorganic sand and dust.

- 1% or less of digestible biomass that in the sunlit upper surface goes down to the bottom.

# Food for the Deep


Many of the deep sea organism have to adapt to extreme food shortage. They have very low population density and many other adaptations like longevity and very slow growth that these deep sea organisms need to survive

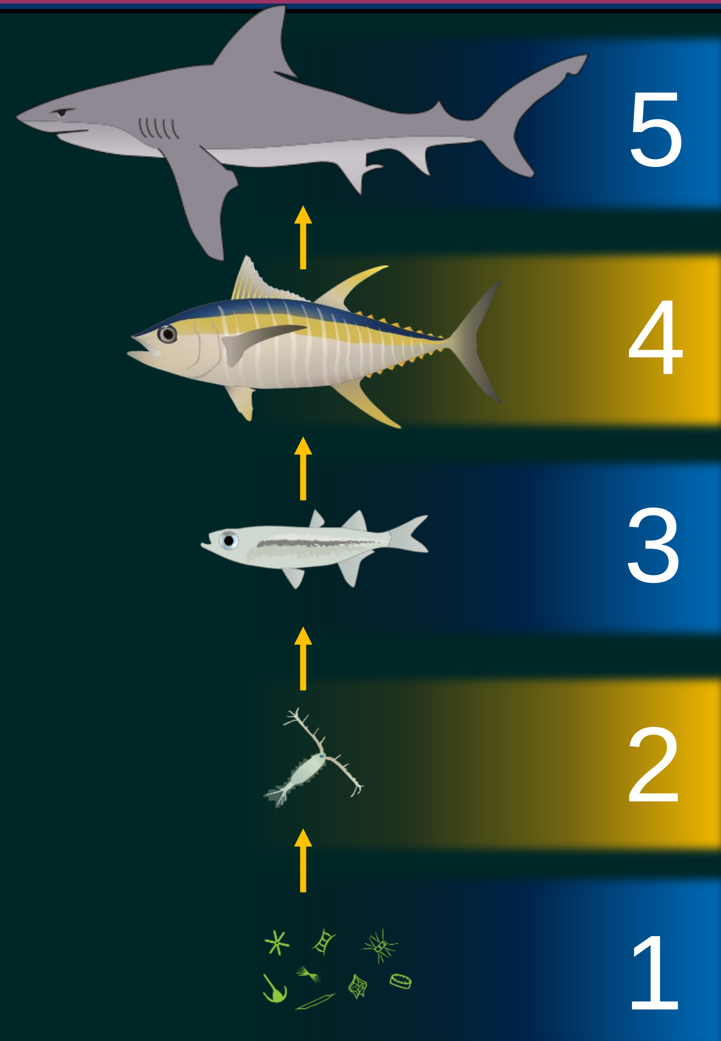
# Marine Food Chains & Webs

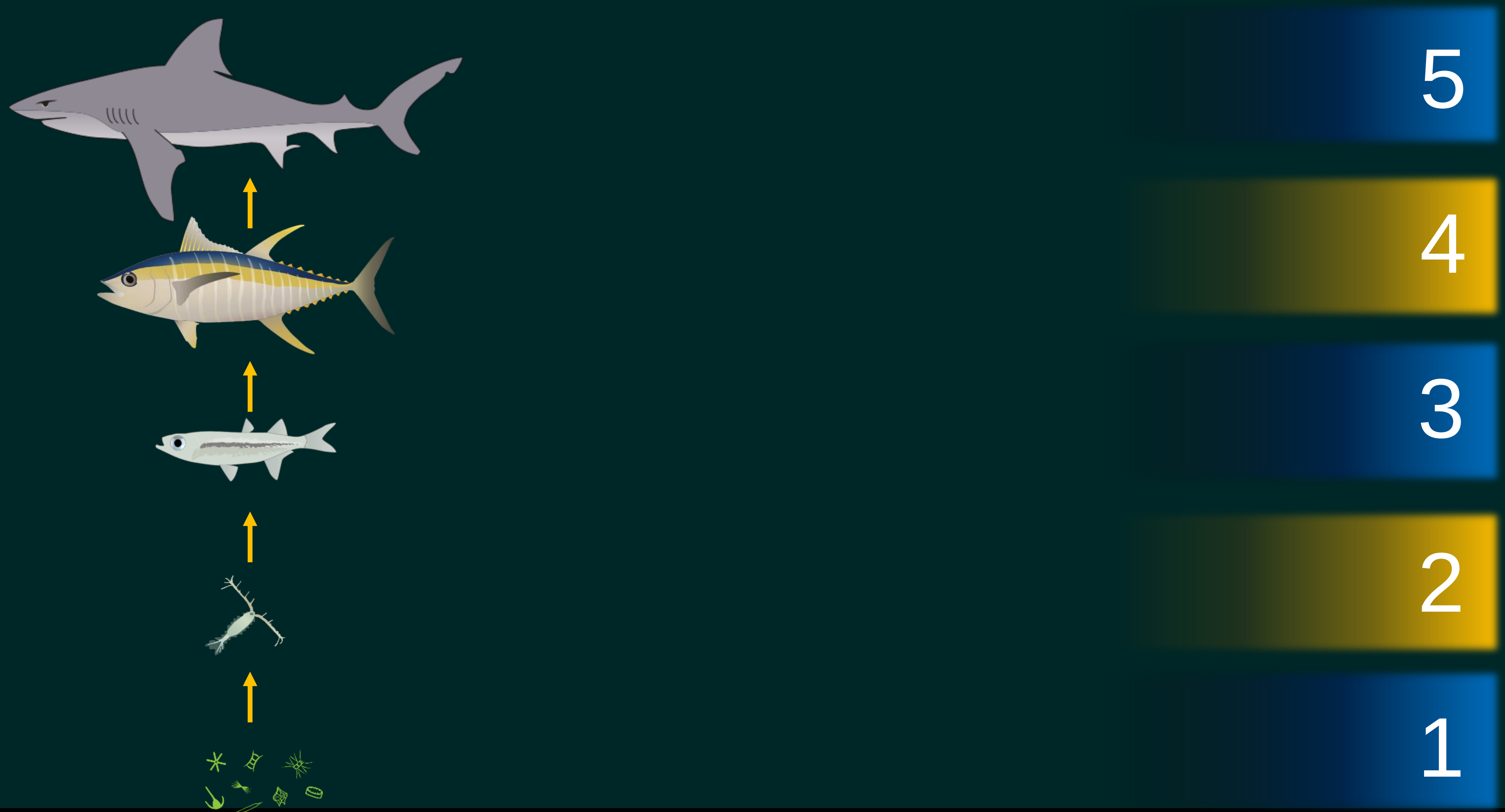
- Producers and consumers are linked by feeding relationships called *food chains*.

  Energy flow through Predator-prey interaction.

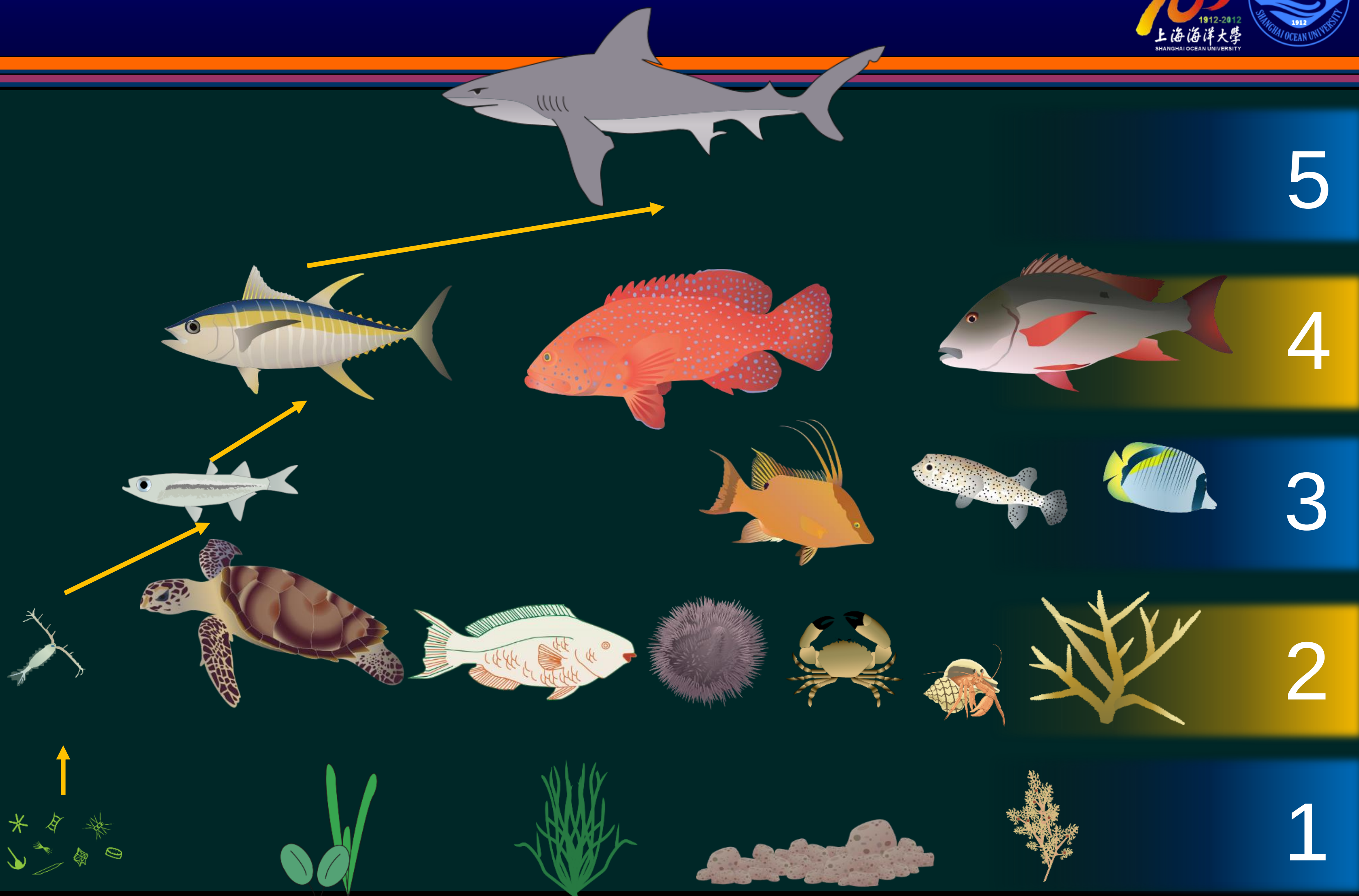
- Trophic level

  is a position in a food chain or food web that indicates an organism's feeding relationships.

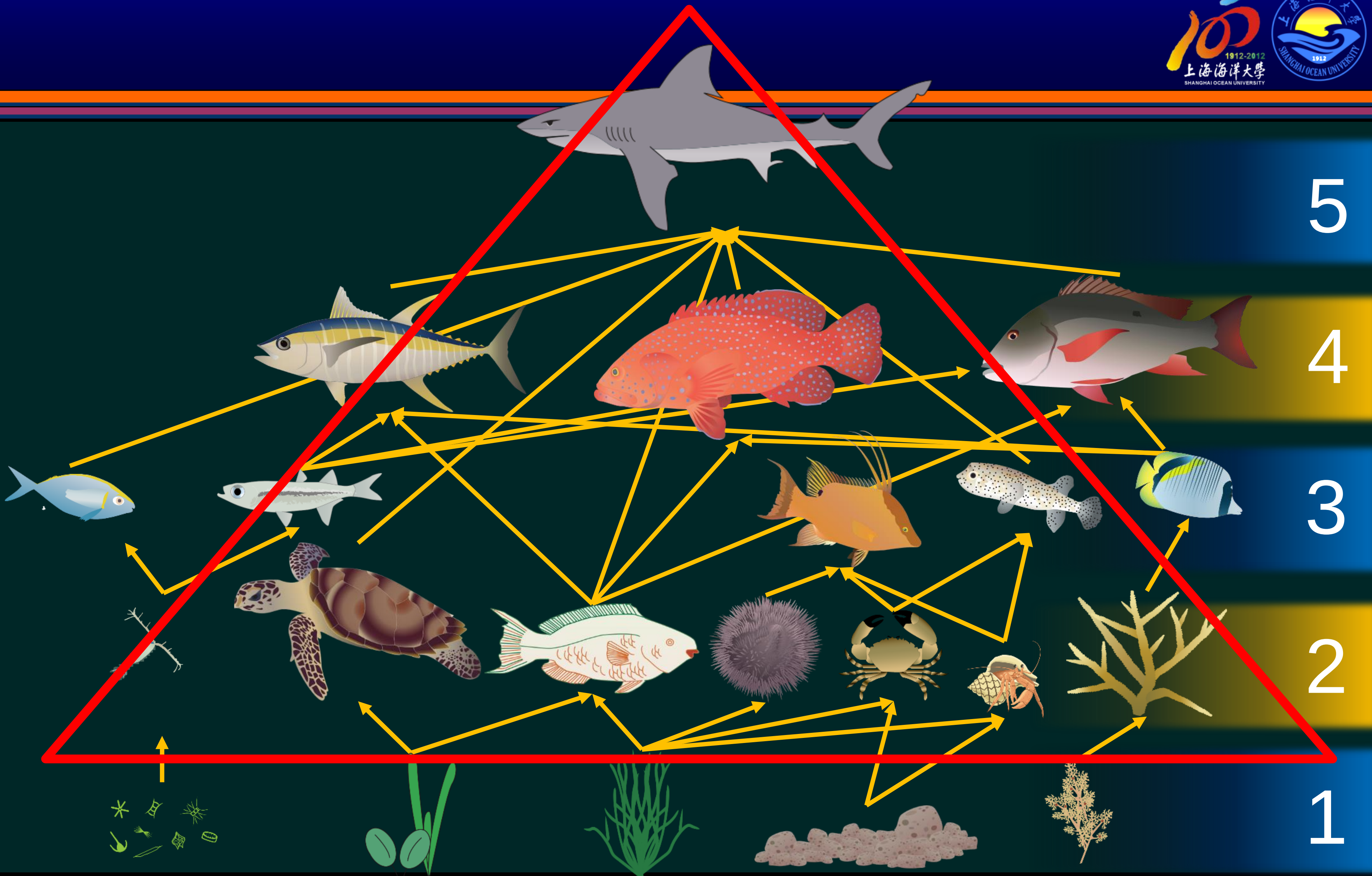




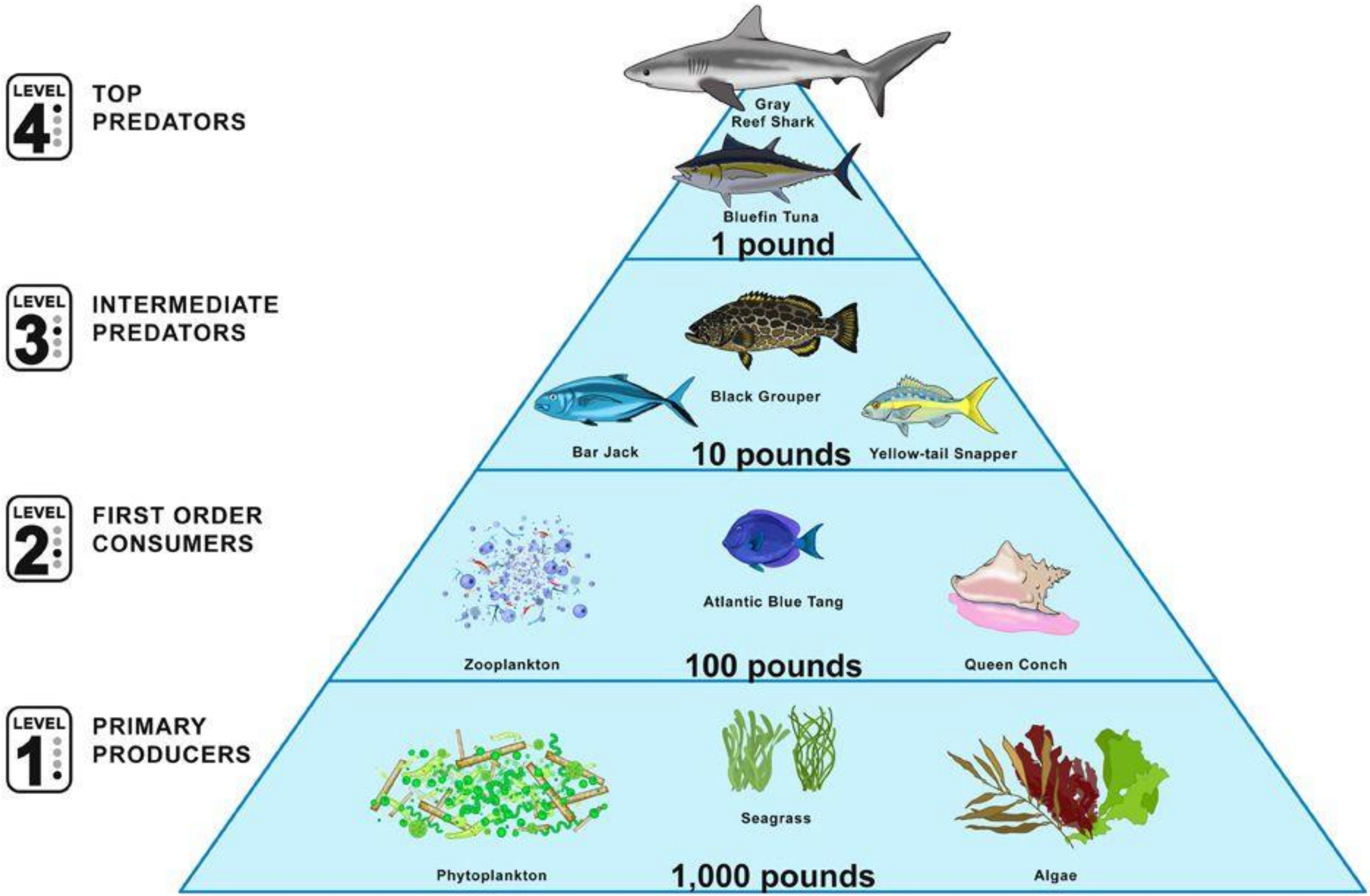

Pics from http://ian.umces.edu/




Pics from http://ian.umces.edu/




Pics from http://ian.umces.edu/


LEVEL 4
TOP PREDATORS
LEVEL 3
INTERMEDIATE PREDATORS
LEVEL 2
FIRST ORDER CONSUMERS
LEVEL 1
PRIMARY PRODUCERS
Gray Reef Shark
Bluefin Tuna
1 pound
Black Grouper
Bar Jack
Yellow-tail Snapper
10 pounds
Atlantic Blue Tang
Zooplankton
Queen Conch
100 pounds
Seagrass
Phytoplankton
Algae
1,000 pounds

# Food webs

- Lindeman (1942) introduced the "energy-efficiency hypothesis"- the fraction of energy entering one trophic level that passes to the next higher level is low (~5-20%,with a mean of 10%)

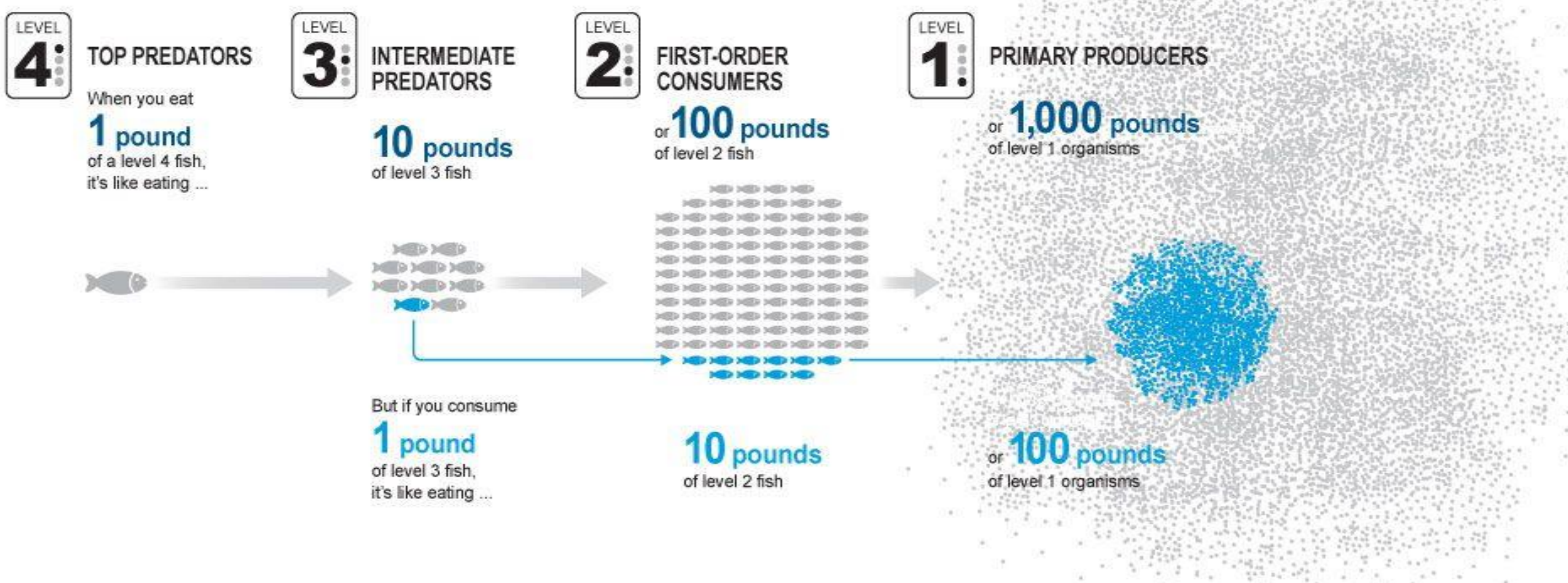
Ecological Efficiency

**GLOSSARY**

***Lindeman's Law*** During the transfer of energy from organic food from one trophic level to the next, only about 10% of the energy from organic matter is stored as flesh. The remaining is lost during transfer, broken down in respiration, or lost to incomplete digestion by higher trophic levels

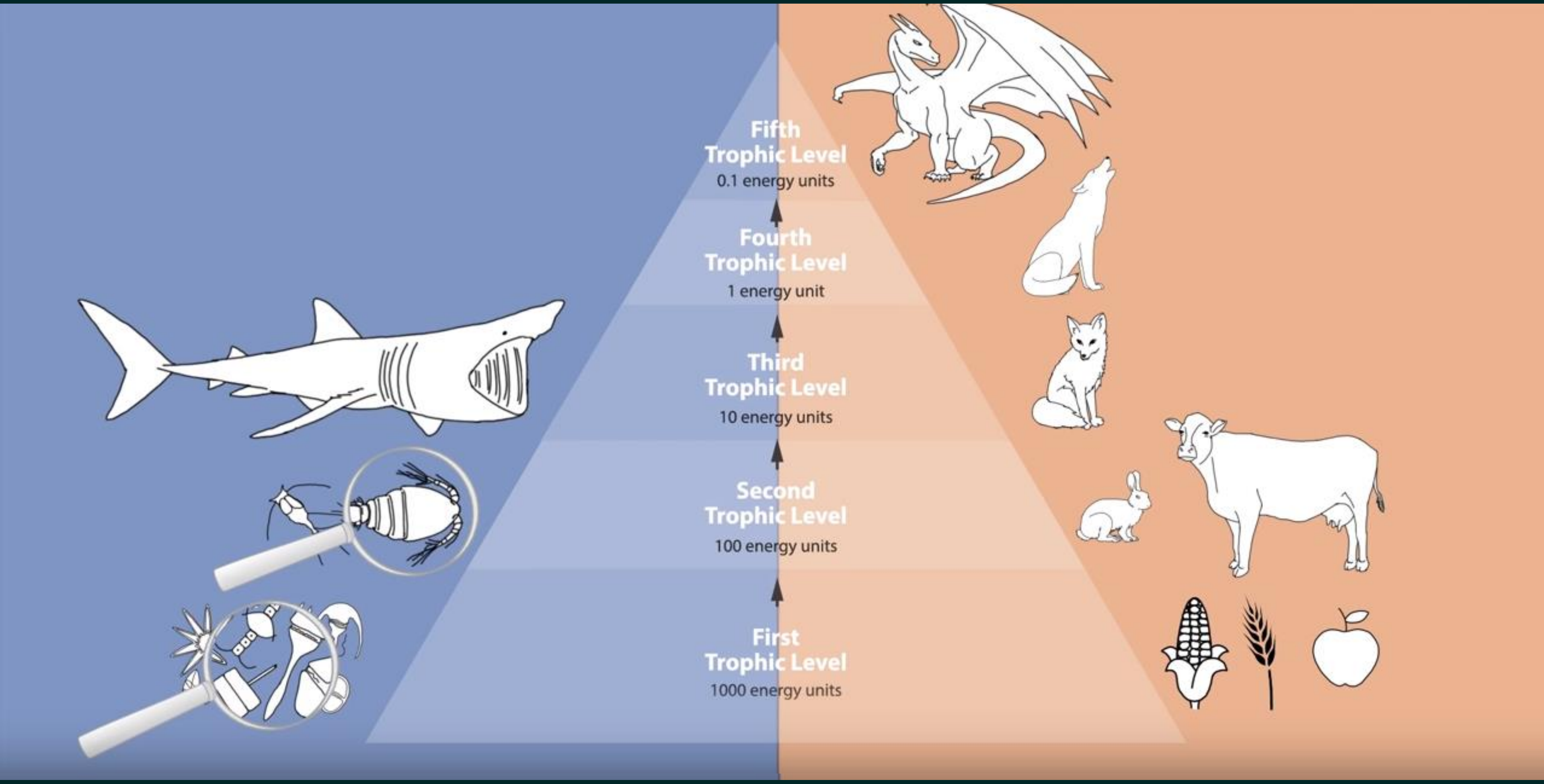
# What We Eat Makes a Difference

A top predator requires exponentially more energy to survive than does a fish at a lower level of the food chain. When wealthy nations catch or buy top predators, they increase their impact on the ocean compared to poor nations, which tend to eat smaller fish.

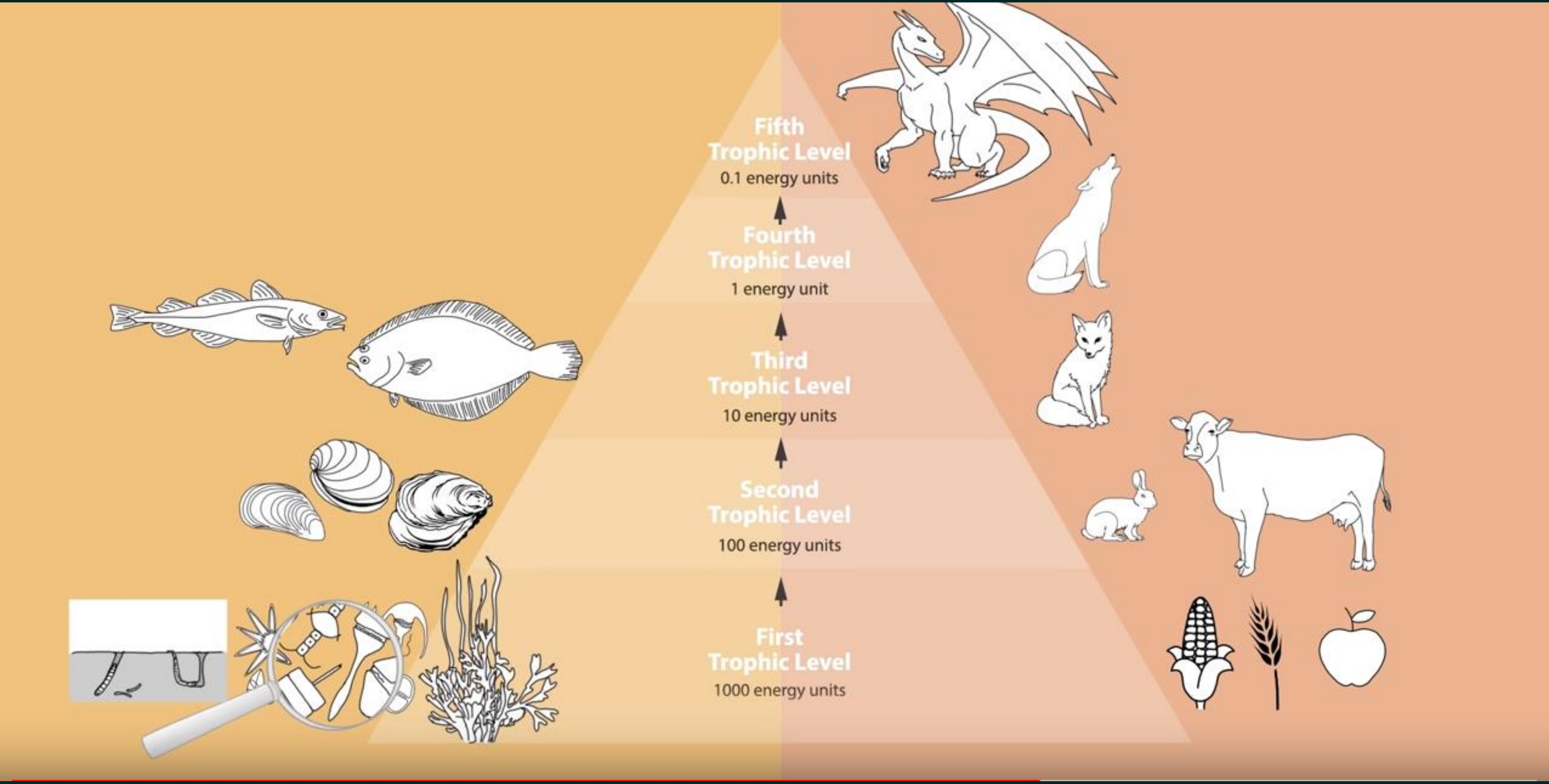



Mariel Furlong, NGM Staff, and Alejandro Tumas
Source: Sea Around Us Project, University of British Columbia Fisheries Centre

# Whale and basking sharks



# Coastal food chain

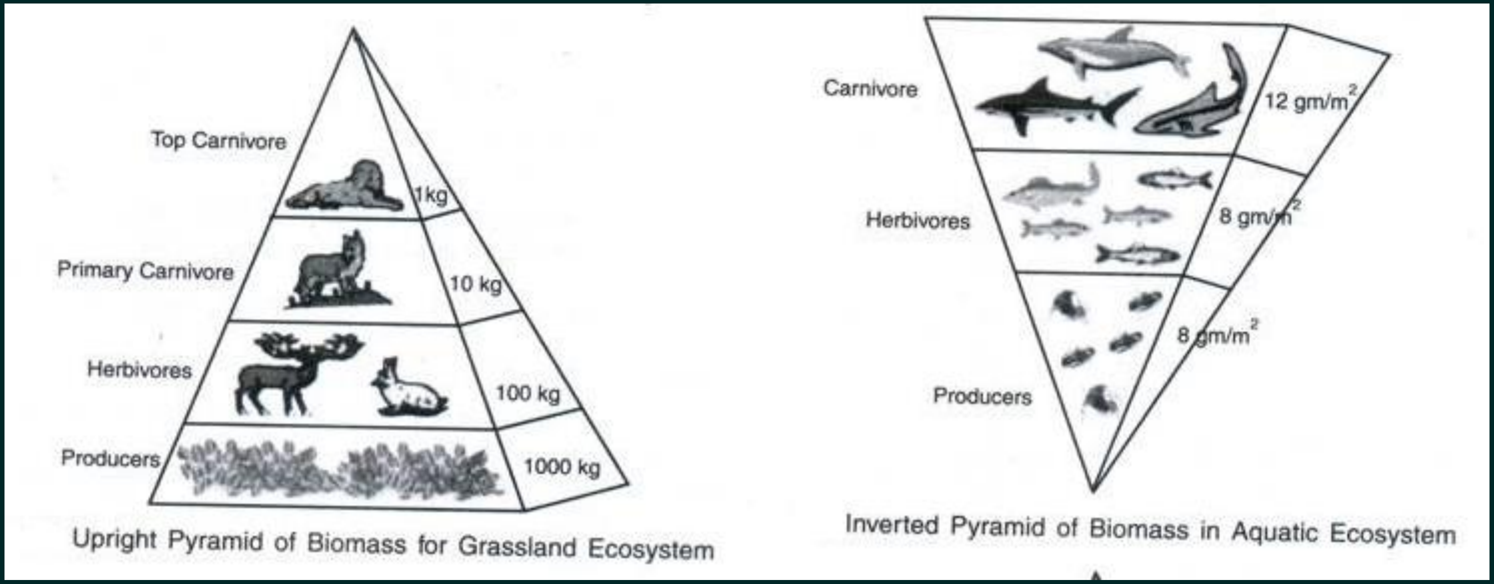


# Oceanic Food Webs

- Food webs in the oceans vary systematically in food chain efficiency, number of trophic levels, primary production

| Food Chain Type | Primary Productivity $gCm^{-2}y^{-1}$ | Trophic Levels | Food Chain Efficiency | Potential Fish Production $mgCm^{-2}y^{-1}$ |
|---|---|---|---|---|
| Open Ocean | 50 | 5 | 10 | 0.5 |
| Continental | 100 | 3 | 15 | 340 |
| Upwelling | 300 | 1.2 | 20 | 36,000 |

# Question??




- Why do aquatic ecosystems have inverted biomass pyramid?

# Mourier et al., 2016

Current Biology
Report

CellPress

## Extreme Inverted Trophic Pyramid of Reef Sharks Supported by Spawning Groupers

Johann Mourier,[1,2,*] Jeffrey Maynard,[1,3] Valeriano Parravicini,[1] Laurent Ballesta,[4] Eric Clua,[1] Michael L. Domeier,[5] and Serge Planes[1,6]
[1]EPHE, PSL Research University, UPVD, CNRS, USR 3278 CRIOBE, 66360 Perpignan, France
[2]Faculty of Science and Engineering, Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia
[3]SymbioSeas and the Marine Applied Research Center, Wilmington, NC 28411, USA
[4]Andromede Oceanology, Place Cassan, 34280 Carnon, France
[5]Marine Conservation Science Institute, 68-1825 Lina Poepoe Street, Waikoloa, HI 96738, USA
[6]Laboratoire d'Excellence CORAIL
*Correspondence: johann.mourier@gmail.com
http://dx.doi.org/10.1016/j.cub.2016.05.058

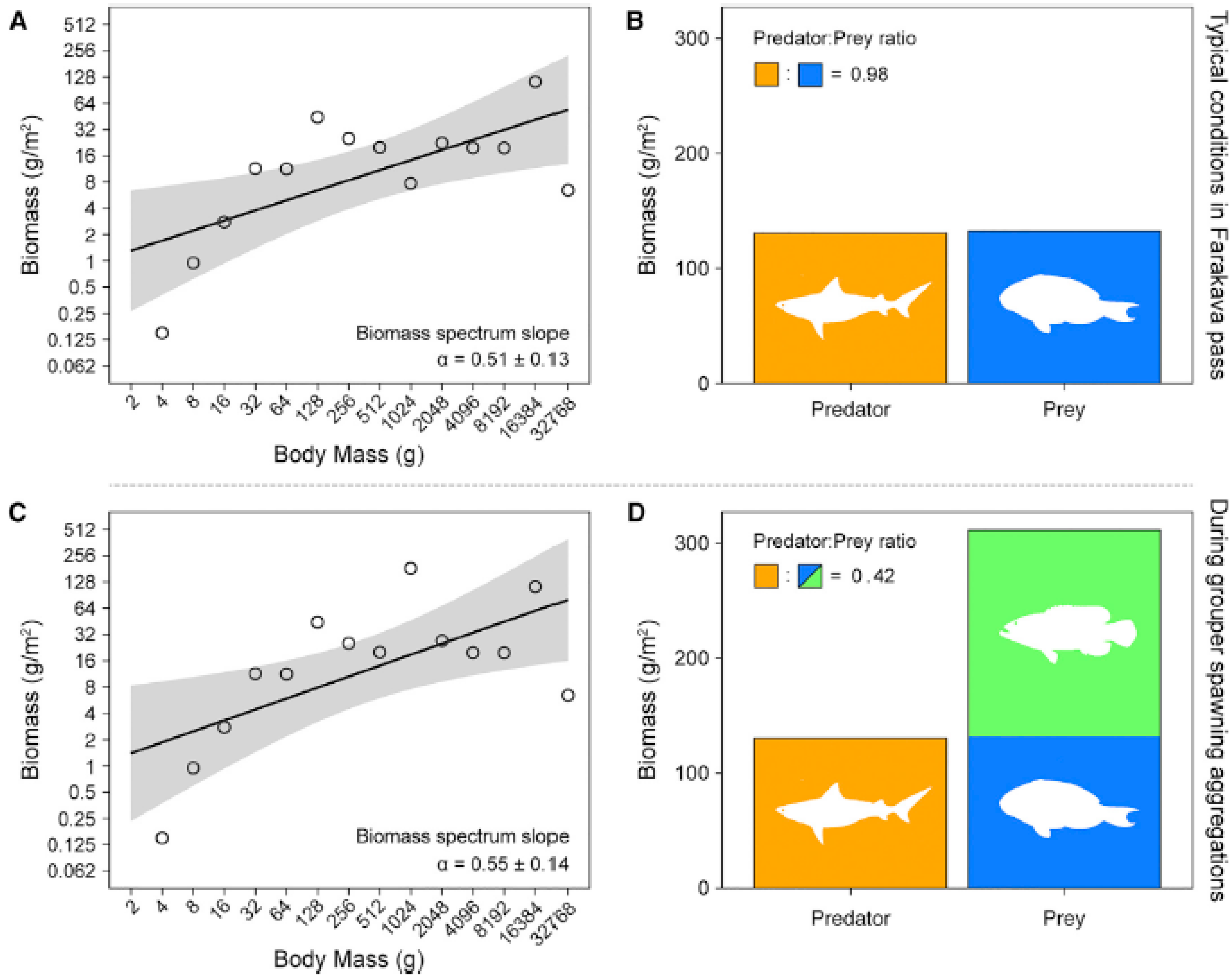



**Figure 2. Trophic Structure and Predator-Prey Dynamics in the Fakarava Pass**

(A) Biomass spectrum of the trophic structure typically observed in the pass is characterized by a positive slope (0.51), indicating an inverted biomass pyramid.

(B) Total shark biomass is similar to the biomass of their potential prey (fish >12.5 cm).

(C) During grouper spawning aggregation, numerous large-bodied fish enter the system, increasing the slope of the biomass spectrum (0.55).

(D) The grouper aggregation decreases the predator-prey ratio by doubling the amount of prey available for sharks.

Gray bands indicate 95% confidence intervals in (A) and (C), and SEMs are given with slope values in (A) and (C). See also Tables S1 and S2.

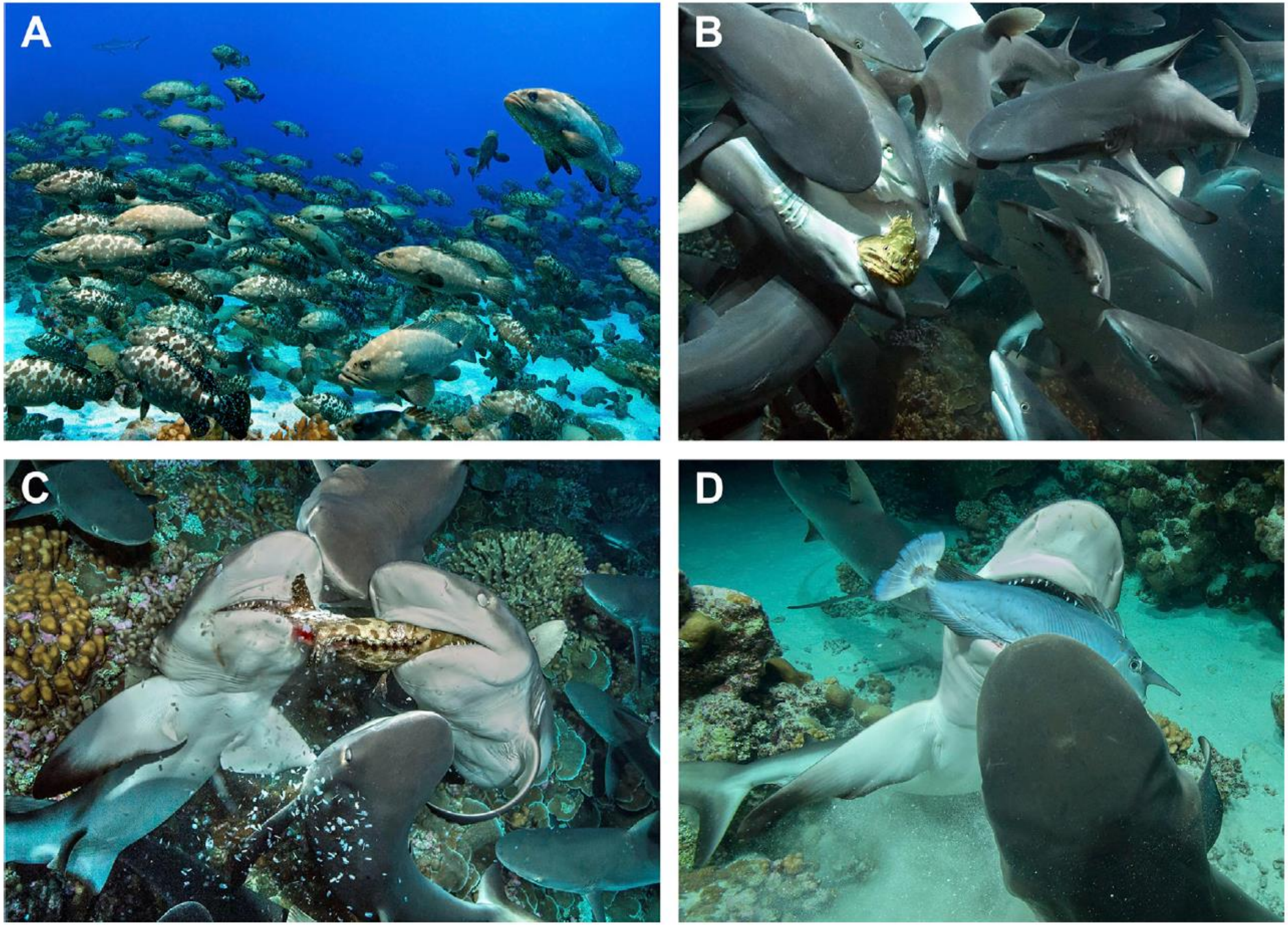



**Figure 4. Photo Examples of Foraging on Fish in the Pass at Night**

(A) Spawning aggregation of *Epinephelus polyphekadion* occurring between full moon of June and July each year.

(B and C) Gray reef sharks foraging at night on *E. polyphekadion*.

(D) Gray reef sharks foraging at night on *Naso annulatus*.

These photos represent natural predation. Lights from cameras are unlikely to have modified the hunting behavior, as the sharks were observed hunting out of light range. Photo © L. Ballesta. See also Figure S3 and Table S3.

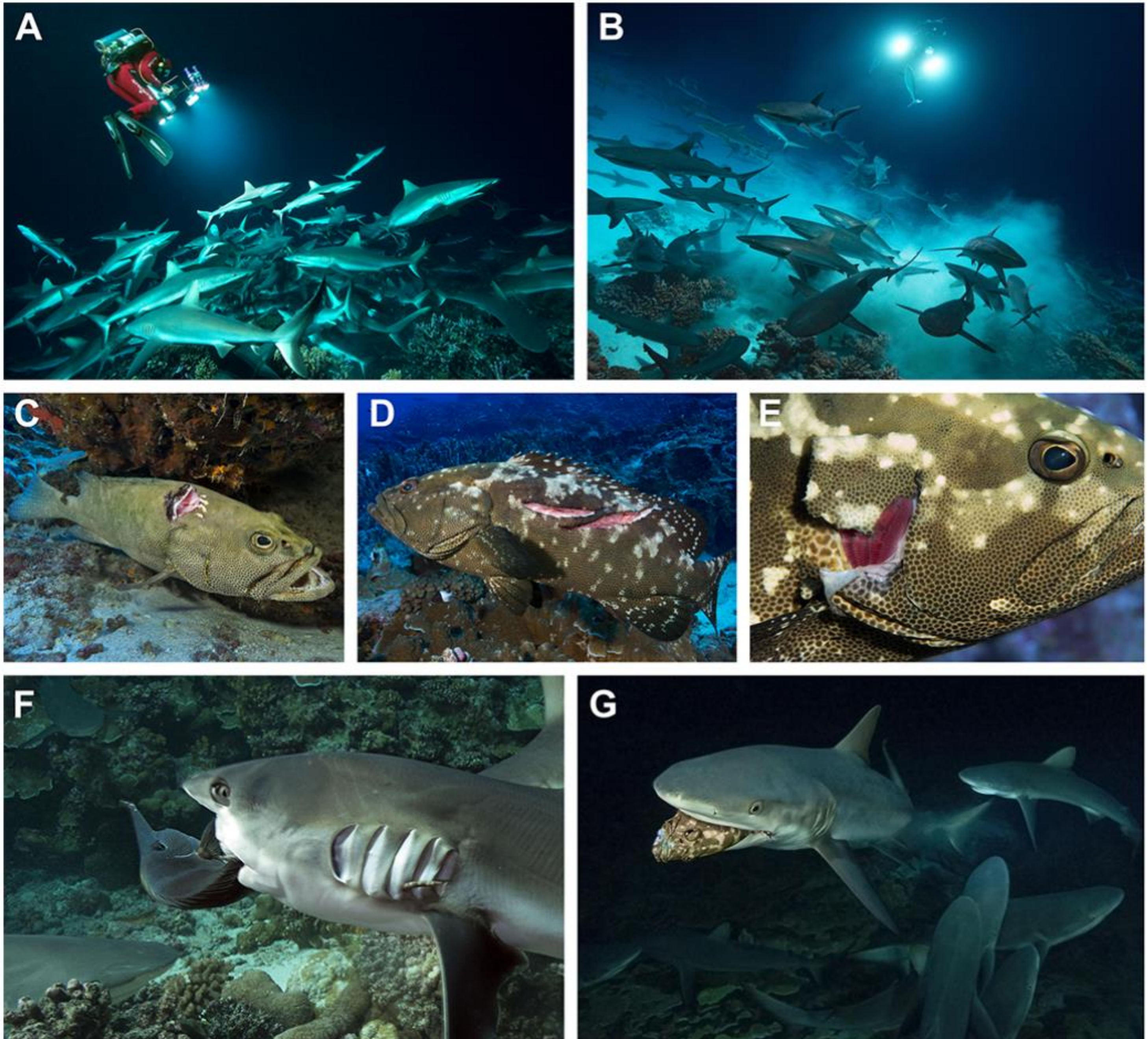
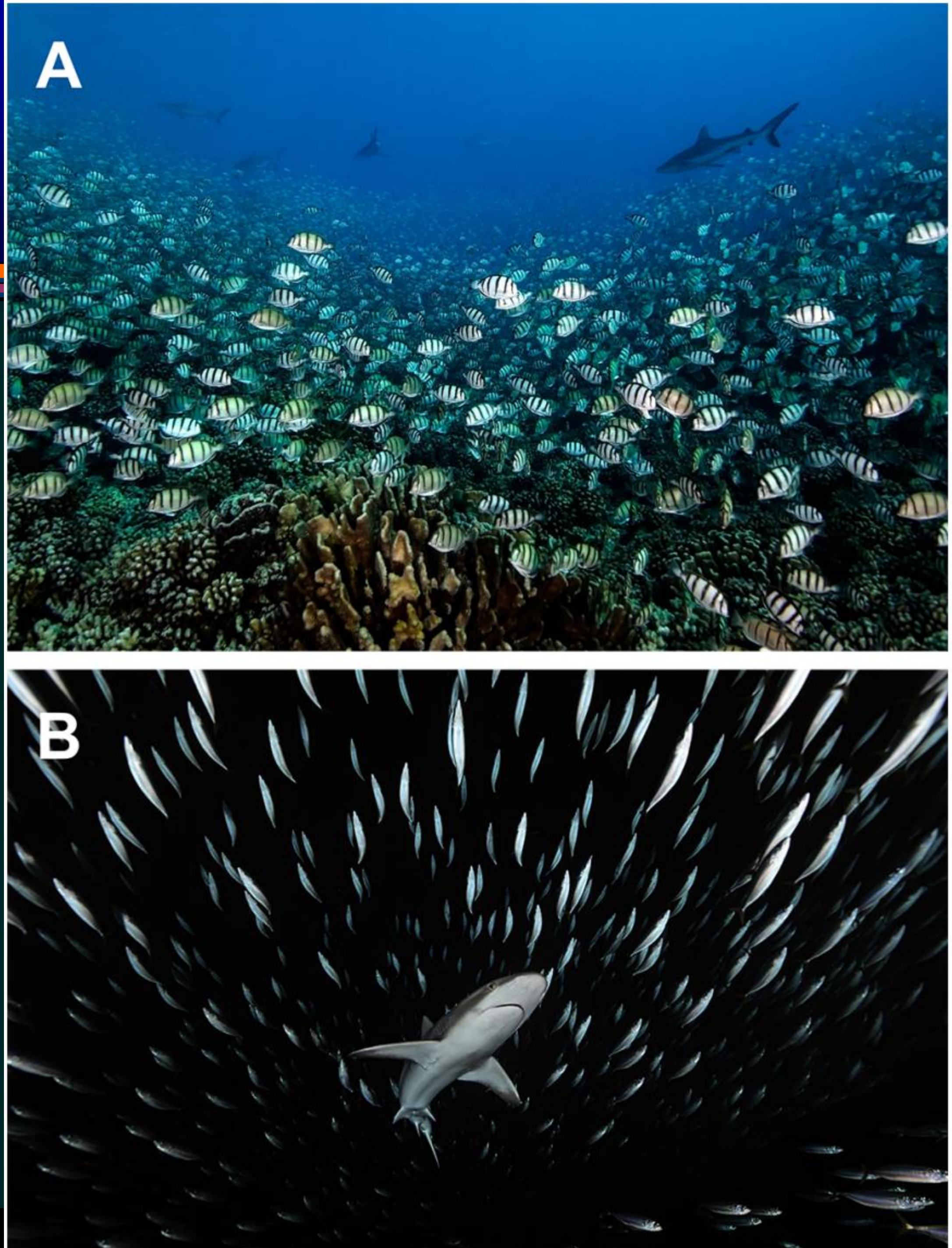



**Figure S3,** ***related to Figure 4*****. Shark foraging activity inferred by behavioral underwater observations using rebreather diving equipment.**

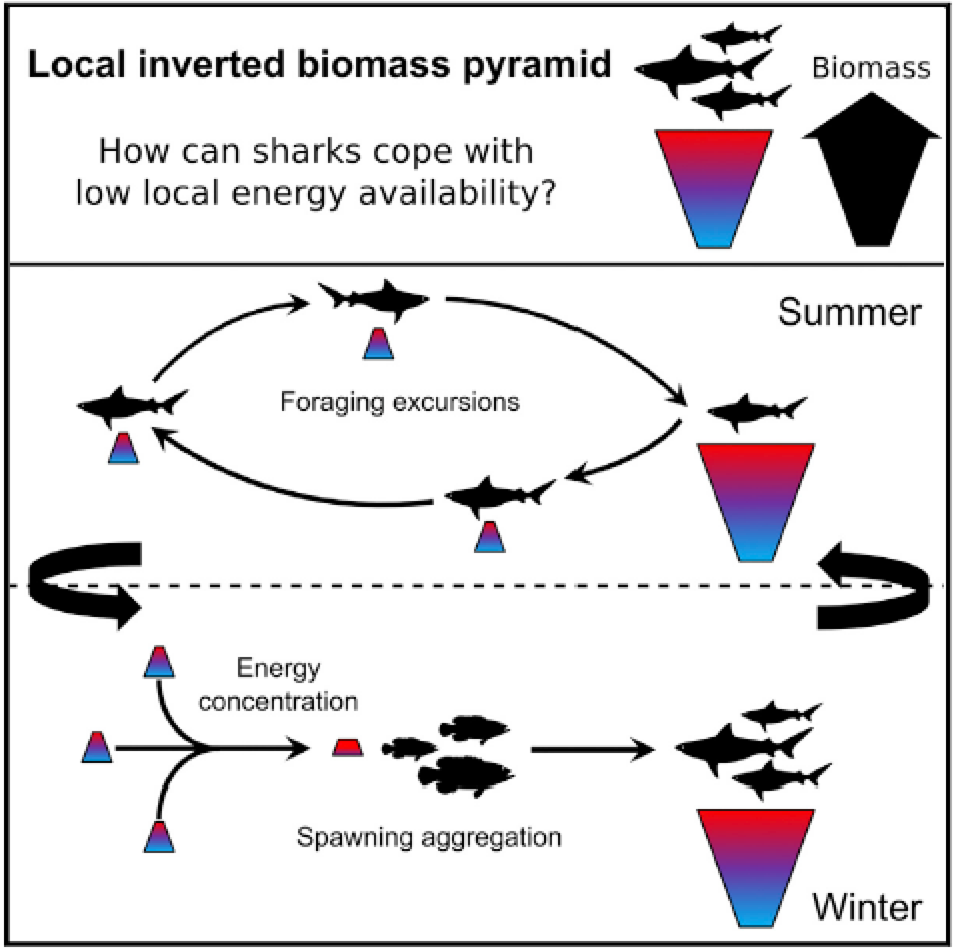

A
B

Report

# Current Biology

## Extreme Inverted Trophic Pyramid of Reef Sharks Supported by Spawning Groupers

### Graphical Abstract





### Authors

Johann Mourier, Jeffrey Maynard, Valeriano Parravicini, Laurent Ballesta, Eric Clua, Michael L. Domeier, Serge Planes

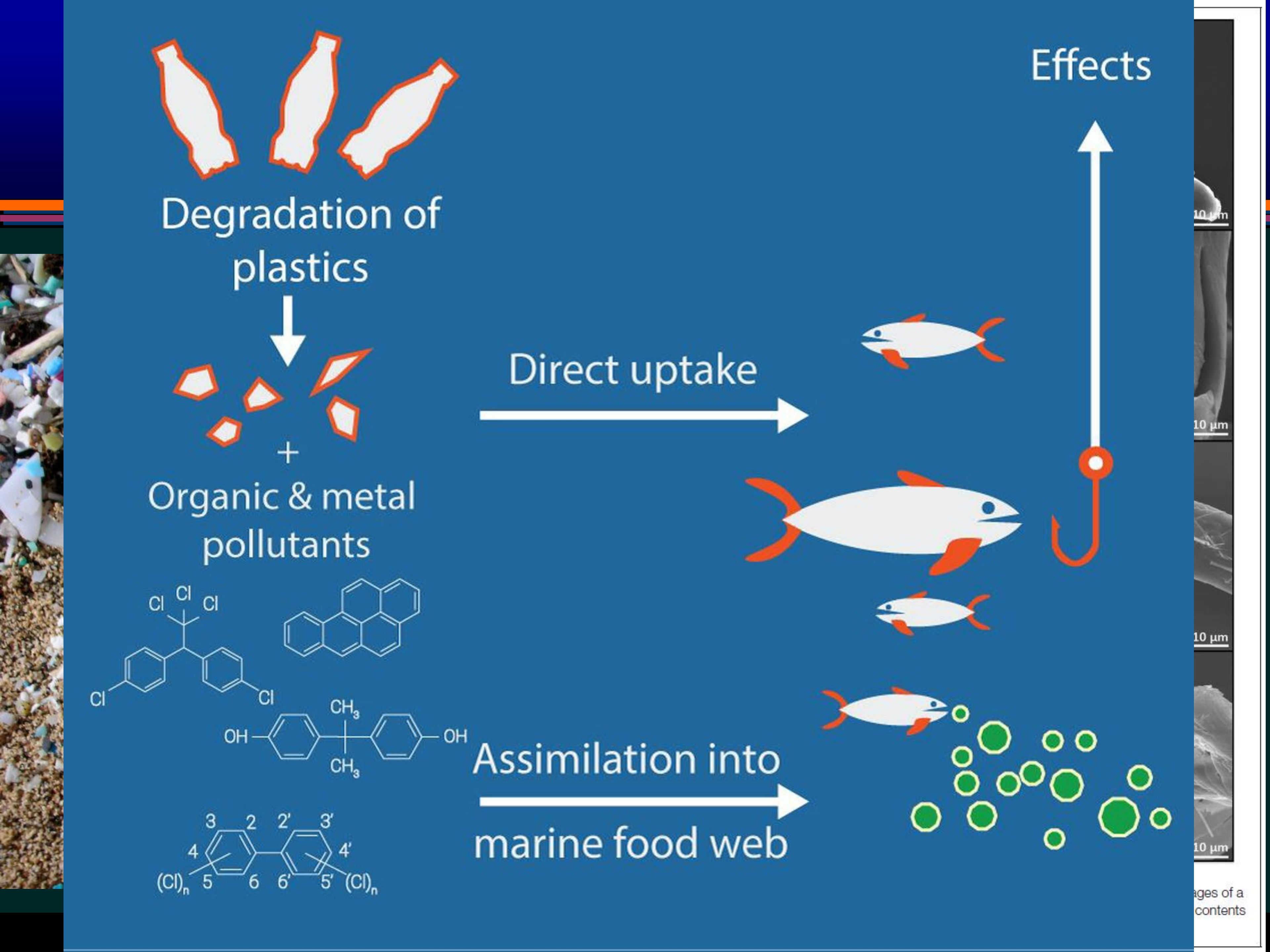
### Correspondence

johann.mourier@gmail.com



### In Brief

Mourier et al. report extremely high shark biomass in pristine Fakarava pass, French Polynesia, producing an inverted trophic pyramid. To escape such constraints, predators typically forage long range on multiple pyramids. This study presents a new mechanism in which subsidies directly come to predators in the form of spawning aggregations.


Effects
Degradation of plastics
Direct uptake
+
Organic & metal pollutants
Cl Cl Cl
Cl Cl
OH CH3 OH
CH3
3 2 2′ 3′
4 4′
(Cl)n 5 6 6′ 5′ (Cl)n
Assimilation into marine food web
10 µm
10 µm
10 µm
10 µm

# Wieczorek et al., 2018

frontiers in Marine Science

ORIGINAL RESEARCH
published: 19 February 2018
doi: 10.3389/fmars.2018.00039

Check for updates

## Frequency of Microplastics in Mesopelagic Fishes from the Northwest Atlantic

*Alina M. Wieczorek*[1,2*], *Liam Morrison*[1], *Peter L. Croot*[1,3], *A. Louise Allcock*[2], *Eoin MacLoughlin*[2], *Olivier Savard*[4], *Hannah Brownlow*[2] and *Thomas K. Doyle*[2,5]

[1] Earth and Ocean Sciences and Ryan Institute, School of Natural Sciences, National University of Ireland Galway, Galway, Ireland, [2] Zoology and Ryan Institute, School of Natural Sciences, National University of Ireland Galway, Galway, Ireland, [3] Irish Centre for Research in Applied Geoscience, Earth and Ocean Sciences, School of Natural Sciences, National University of Ireland Galway, Galway, Ireland, [4] Perkin Elmer, Beaconsfield, United Kingdom, [5] School of Biological, Earth and Environmental Sciences, MaREI Centre, Environmental Research Institute, University College Cork, Cork, Ireland

# RESULTS

A total of 280 fish was captured of which 233 were examined for the presence of microplastics in their gut contents. The most common species amongst the subsampled fish were the

“The key message for us is that our pollution has now reached even the most remote areas and that the plastics may impact key ecological players such as deep-sea fish,” said Wieczorek.


*rafinesquii*, *G.* ... was assessed as being sexually ...

Overall 73 ... their stomachs with *G. denu*... y of occurrence (100%), followed by *S. beanii* (93%) and *L. macdonaldi* (75%)

# Keystone species


Karleskint et al (2009)

- This ochre sea star limits the size of the mussel population in this community. This prevents the mussels from crowding out other species of rock dwellers.
- Paine RT(1995) "A keystone species is a species that has a disproportionately large effect on its environment relative to its abundance".

# Paine's keystone experiment

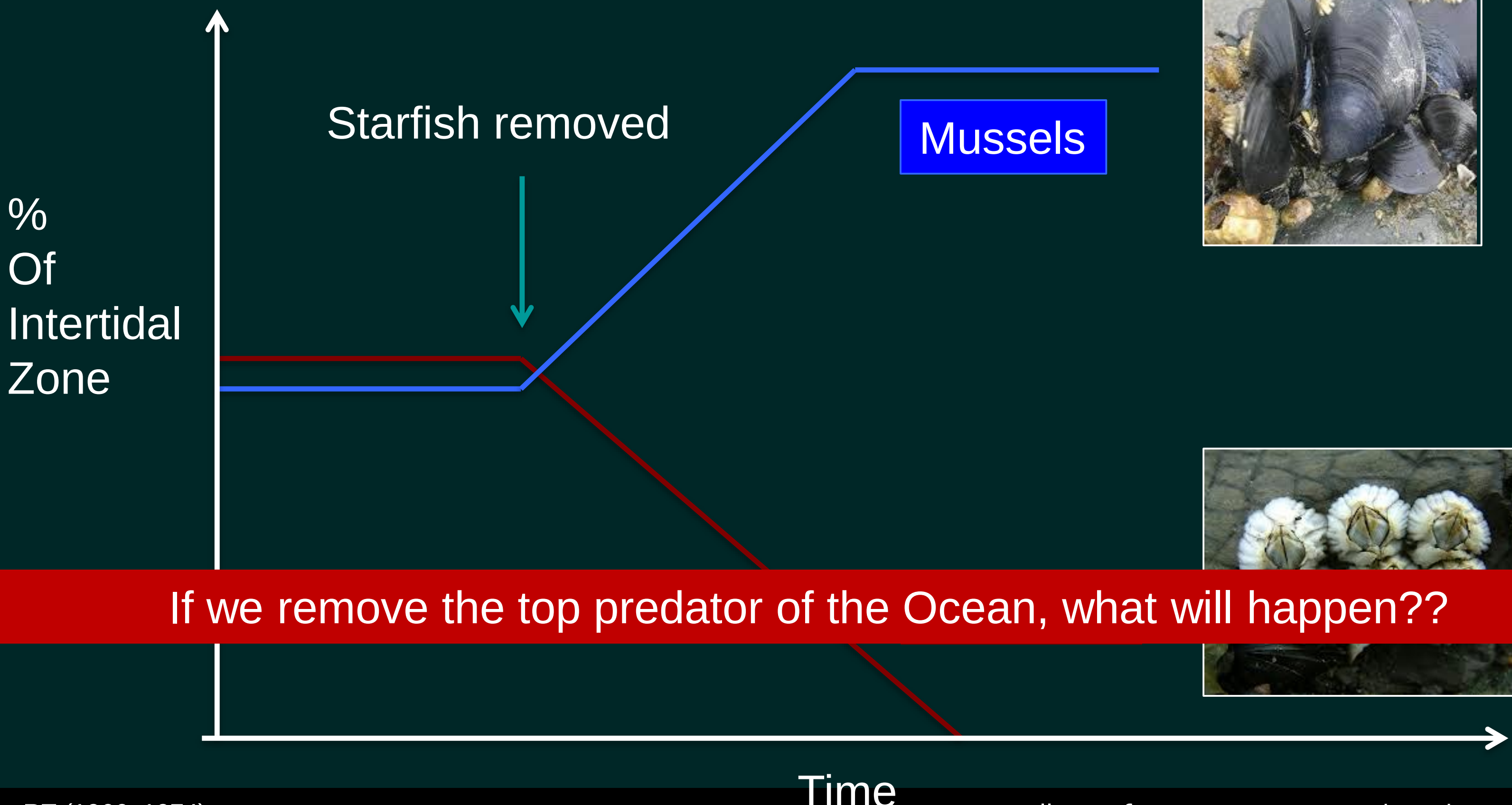
- Predators can allow coexistence of competing prey

Predator


Competitors

# Removal experiment

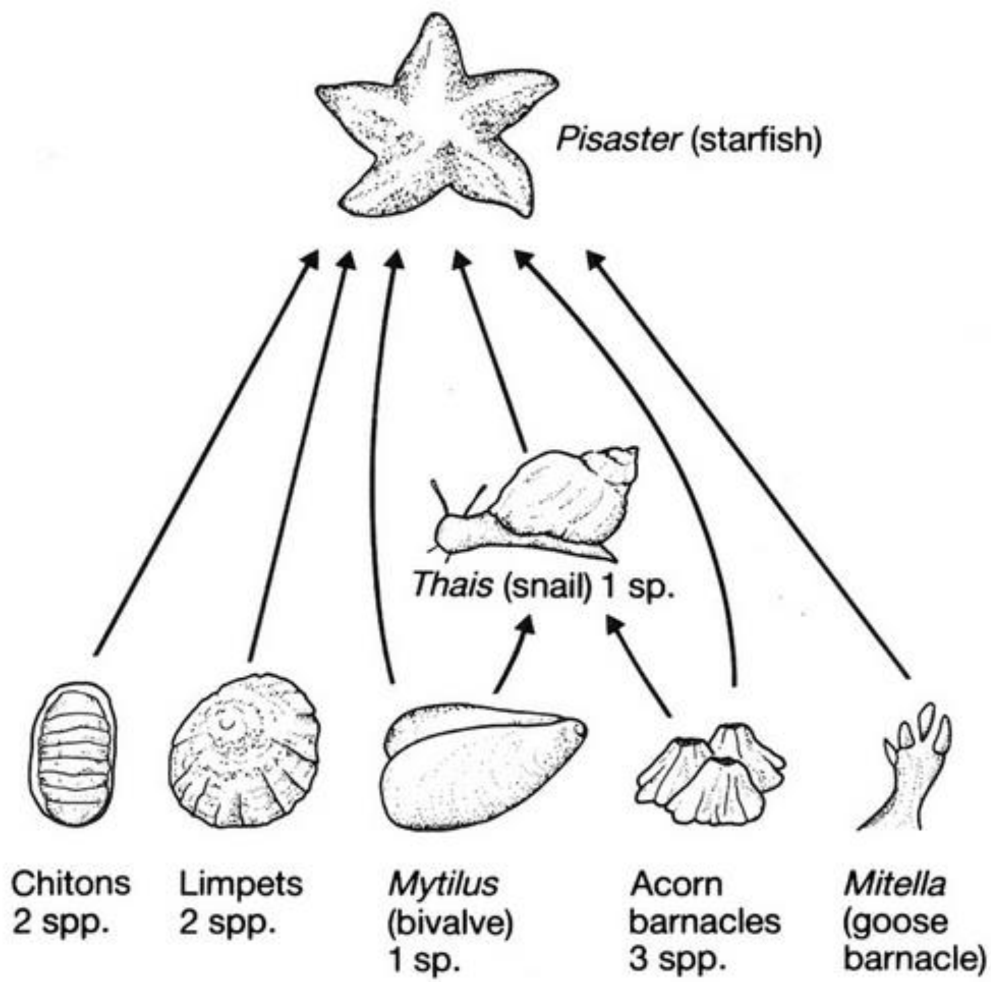
- Mussels are dominant competitors
- Competitive exclusion of barnacles




If we remove the top predator of the Ocean, what will happen??

Paine RT (1966; 1974)

# Paine’s keystone experiment






**The University of Chicago**

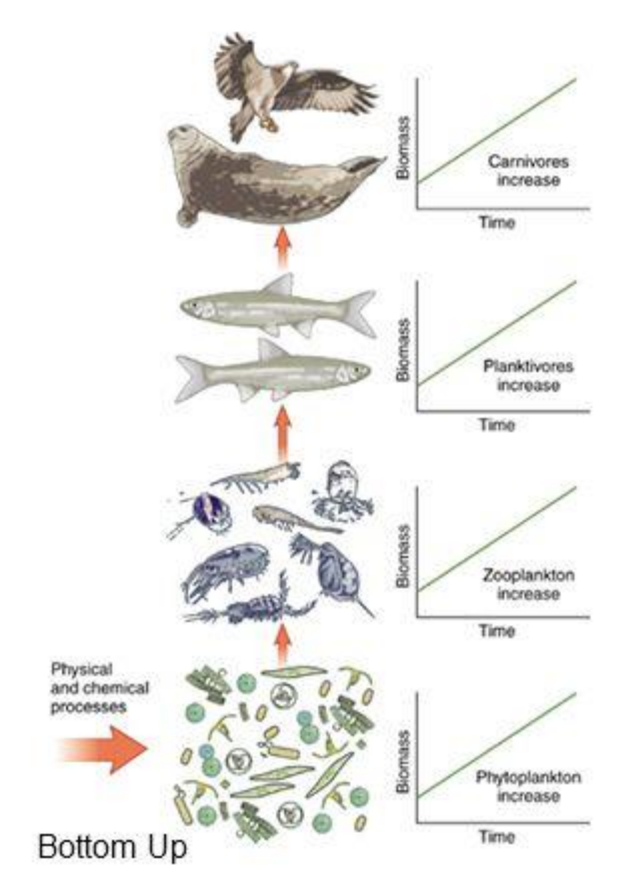
Food Web Complexity and Species Diversity
Author(s): Robert T. Paine
Source: *The American Naturalist*, Vol. 100, No. 910 (Jan. - Feb., 1966), pp. 65-75
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2459379
Accessed: 17-07-2015 14:29 UTC

# Sea Star

# What controls Food Web?

- Traditionally, food webs have been thought of as obeying a kind of supply-side economics: higher productivity of phytoplankton yields higher productivity of zooplankton and on up the chain. Control of food web structure and population dynamics by primary producers us called *bottom-up control*.
- On the other hand, there is evidence that top predators exert control over food web structure and population dynamics. This kind of control is called *top-down control*.
- Control of food web structure and population dynamics by middle trophic levels is called *wasp-waist control*.

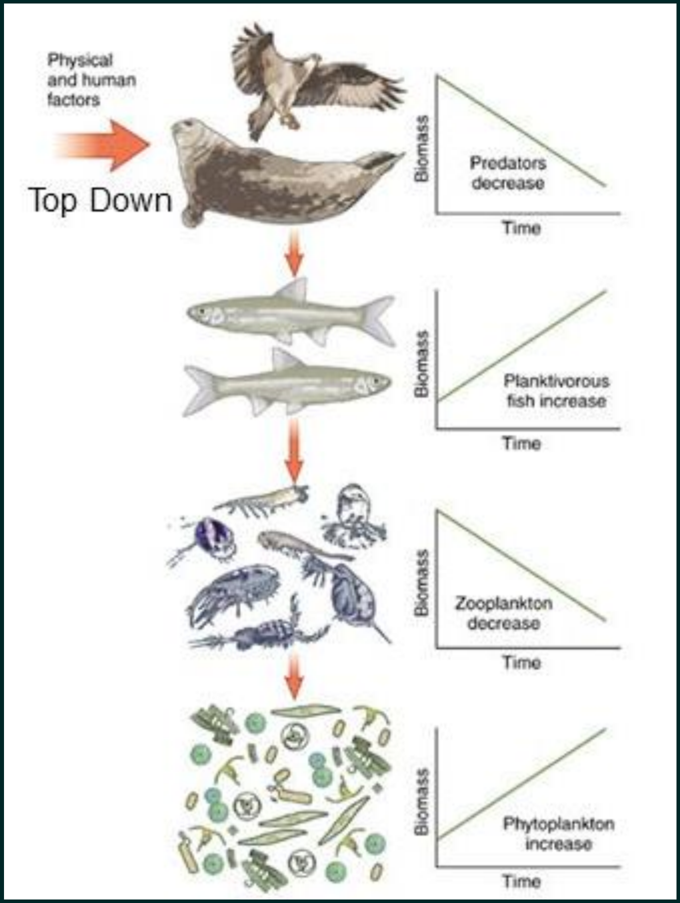
# What controls Food Web?




Bottom-up control of a food web occurs when physical and chemical and human factors drive the growth of autotrophs. In turn, autotrophs supply energy and matter to higher trophic levels. As phytoplankton go, the whole food web goes.

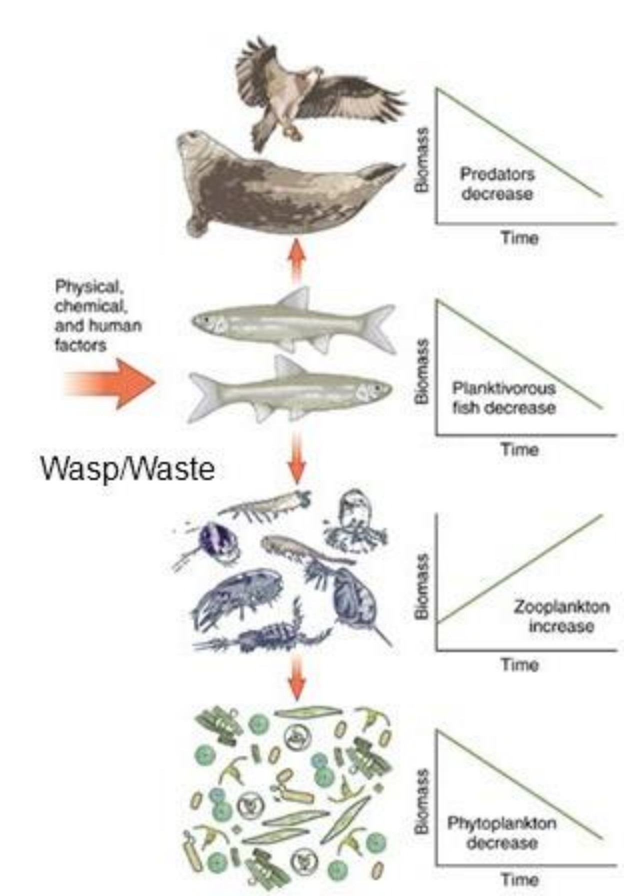
Such as increasing N, P input

# What controls Food Web?




Top-down control of a food web occurs when physical, chemical and human factors control the abundance of top predators. As the top predators decrease, there is a domino effects as lower trophic levels alternatively increase or decrease. As the top predators go, so goes the food web. Such as DDT events, fishing top predators.

# What controls Food Web?




Wasp-waist control of a food web occurs when physical, chemical and human factors regulate middle trophic levels. Control of the abundances of organisms at middle trophic levels controls the trophic levels above and below.

Such as Climate change on sardine fishery.

# *Acanthaster planci*


# Problems

- Eutrophication
- Loss of predators







## Are they important to the Ocean?

# Sharks are important to human

Apex Predators

Meso Predators

Resource Species

Trophic Cascade

***Trophic cascades*** occur when predators in a food web suppress the abundance or alter the behavior of their prey, thereby releasing the next lower trophic level from predation

**GLOSSARY**

*Ecology Letters*, 13: 1055-1071 (**2010**)

Review

# Predicting ecological consequences of marine top predator declines

**Michael R. Heithaus[1], Alejandro Frid[2], Aaron J. Wirsing[1] and Boris Worm[2]**

[1] Department of Biological Sciences, Florida International University, 3000 NE 151st Street, North Miami, FL 33181, USA
[2] Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada

**Recent studies document unprecedented declines in marine top predators that can initiate trophic cascades. Predicting the wider ecological consequences of these declines requires understanding how predators influence communities by inflicting mortality on prey and inducing behavioral modifications (risk effects). Both mechanisms are important in marine communities, and a sole focus on the effects of predator-inflicted mortality might severely underestimate the importance of predators. We outline direct and indirect consequences of marine predator declines and propose an integrated predictive framework that includes risk effects, which appear to be strongest for long-lived prey species and when resources are abundant. We conclude that marine predators should be managed for the maintenance of both density- and risk-driven ecological processes, and not demographic persistence alone.**

## Declines in marine top predators

Predators that occupy high trophic levels in marine habitats, including marine mammals, large teleosts and sharks, have been declining worldwide at a rapid pace [1–4]. Recent estimates suggest that populations of large sharks have declined regionally by 90% or more [3,5]. The status of large tuna, billfish and groundfish [2] and reef-associated predators in human-impacted areas [6] is equally dire. Although the magnitude of some declines is debated, few researchers doubt the generality of sweeping changes to the abundance of upper trophic levels in the oceans. Clearly, accurate prediction of the ecological consequences of these and potential future declines is critical for fisheries and ocean ecosystem management. Ecosystem models currently are the most common method for exploring the wider effects of declining upper trophic levels. These models, however, are driven by detailed system-specific data that might limit the generality of predictions and also preclude parameterization in data-poor situations (Box 1).

Given these concerns, is it possible to make generalized predictions about the likely responses of marine communities to the loss of top predators? Addressing this question requires a functional understanding of how top predators affect the dynamics of marine communities. Recent studies from diverse systems show that predators influence prey populations and communities by inflicting mortality on prey (direct predation) and inducing costly antipredator behavior by their prey (risk effects [7]). Studies in marine systems involving upper trophic level predators, however, have largely failed to consider risk effects. Here we review studies of community rearrangements following marine top predator declines and of how marine predators influence their communities through direct predation and risk effects. Through this synthesis, we build the case that a framework integrating both direct predation and risk effects can achieve improved predictions on the ecological consequences of marine predator declines.

## Marine communities change when top predators decline

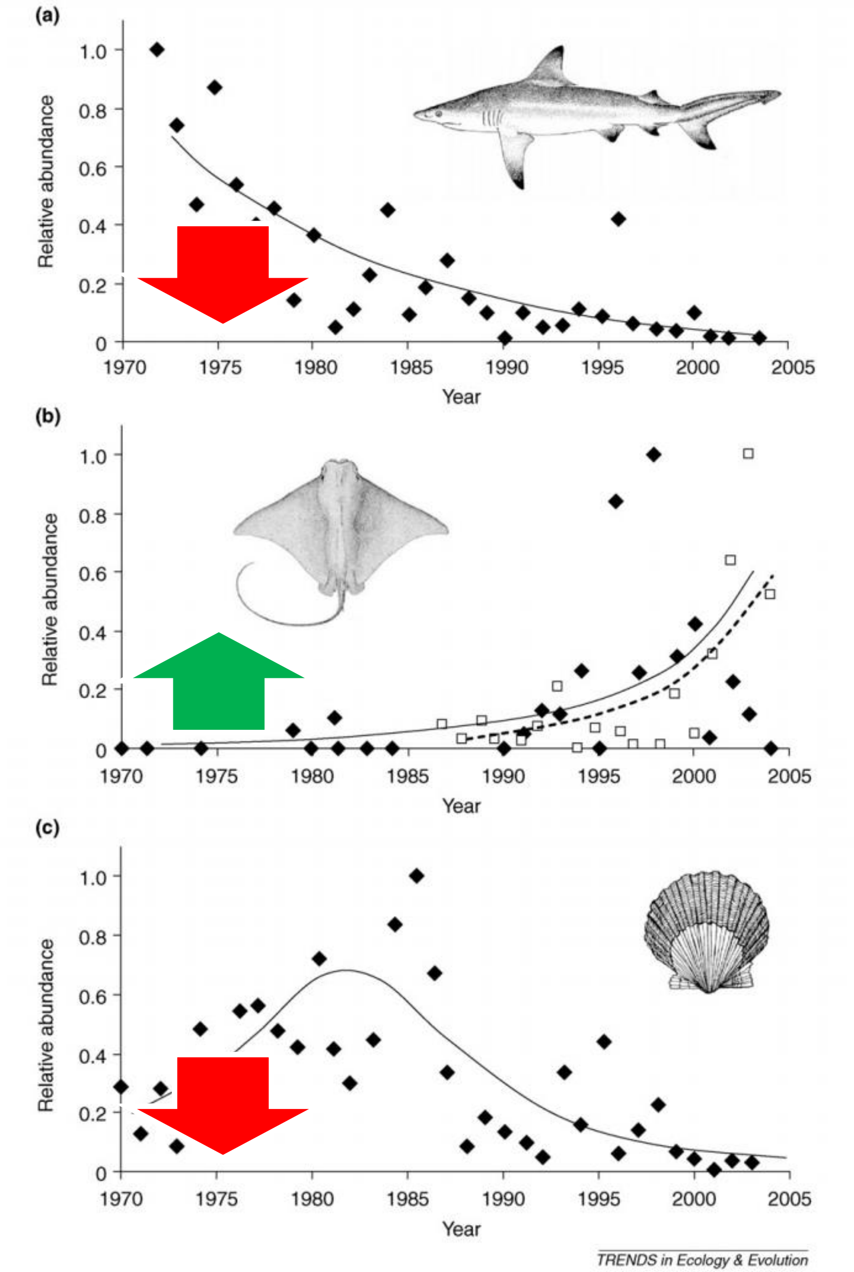
Predicting the ecological consequences of reductions in top predators is, in essence, an inquiry into the importance of top-down processes. From groundbreaking work on rocky intertidal shores [8] to the documentation of the keystone role of sea otters in kelp forests [9] and studies of the indirect effects of bird predation [10], among many other examples, there is little doubt that predators have a fundamental influence on the structure and function of marine communities. Hence, widespread declines of large

### Glossary

**Behaviorally mediated indirect interaction**: occurs when changes in the abundance of one species results in a change in the behavior of a second species (a risk effect) that in turn influences a third species.
**Density-mediated indirect interaction**: occurs when changes in the abundance of one species affect the density of another species through direct predation, which in turn changes densities of a third species.
**Direct predation effect**: effects of predator-inflicted mortality on prey populations.
**Keystone species**: a species that has an impact on community structure disproportionate to its abundance.
**Megagrazers**: large-bodied marine grazers (e.g. green turtles, dugongs and manatees).
**Mesoconsumer**: predators or herbivores in mid-trophic levels. These species are at risk of predation from top predators, and therefore transmit effects of top predators to lower trophic levels.
**Predatory release**: when reductions in the density of top predators causes a numerical increase of their prey.
**Resource species**: in the context of this review, a species that is eaten by mesoconsumers. Depending on the mesoconsumer, resource species are consumers at lower trophic levels (e.g. small teleosts) or primary producers (e.g. seagrasses).
**Risk effect**: changes in prey species (e.g. distribution, energy state, reproductive output) resulting from behavioral responses to the risk of predation.
**State-dependent behavior**: behavioral responses to extrinsic factors (e.g. background level of predation risk) that are assumed to maximize fitness in the context of the physiological (e.g. fat stores), environmental (e.g. resource availability) or other states of the organisms that influence residual reproductive value.
**Trophic cascade**: changes in the relative abundances of multiple species in an ecological community as a result of changes in abundance of one species. Trophic cascades ensue from both direct predation and risk effects of predators.

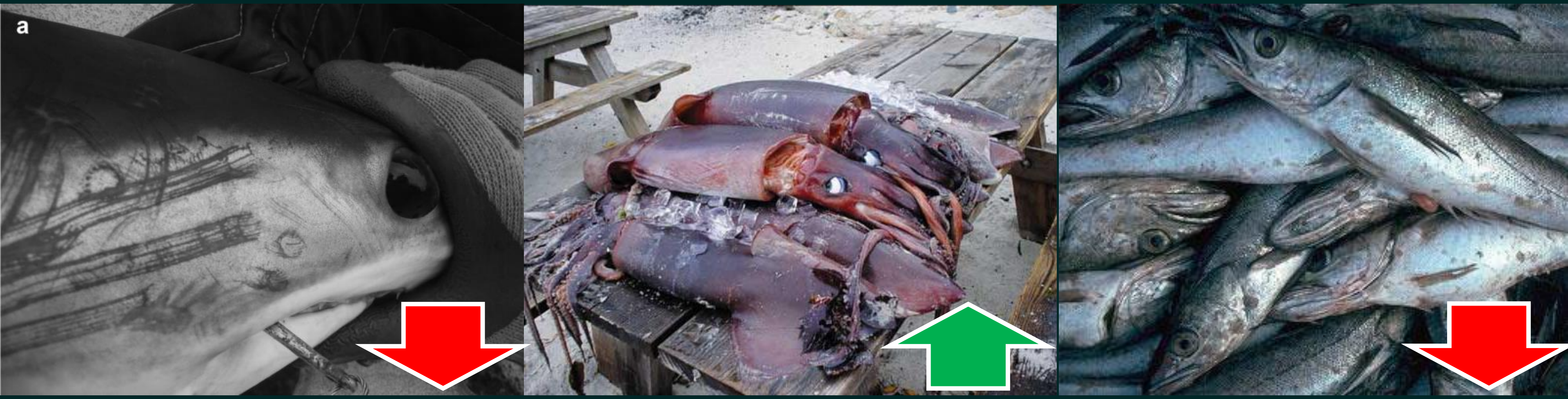
*Corresponding author:* Heithaus, M.R. (heithaus@fiu.edu).


0169-5347/$ – see front matter © 2007 Elsevier Ltd. All rights reserved. doi:10.1016/j.tree.2008.01.003 Available online 4 March 2008




*Trends in Ecology and Evolution,* 23: 202-210 (**2008**)

- Vetter et al. (2008) used data from just about every research technique available to study interactions between the mako and Humboldt squid populations in the California current.




(*PANS*, 2008)

Marine Biology (2002) 140: 237–248
DOI 10.1007/s00227-001-0711-7

**M.R. Heithaus · L.M. Dill
G.J. Marshall · B. Buhleier**

# Habitat use and foraging behavior of tiger sharks (*Galeocerdo cuvier*) in a seagrass ecosystem

Received: 27 November 2000 / Accepted: 31 July 2001 / Published online: 5 October 2001


**Abstract** Understanding the foraging behavior and spatial distribution of top predators is crucial to gaining a complete understanding of communities. However, studies of top predators are often logistically difficult and it is important to develop appropriate methods for identifying factors influencing their spatial distribution. Sharks are top predators in many marine communities, yet no studies have quantified the habitat use of large predatory sharks or determined the factors that might influence shark spatial distributions. We used acoustic telemetry and animal-borne video cameras ("Crittercam") to test the hypothesis that tiger shark (*Galeocerdo cuvier*) habitat use is determined by the availability of their prey. We also used Crittercam to conduct the first investigation of foraging behavior of tiger sharks. To test for habitat preferences of sharks, the observed proportion of time in each habitat for each individual was compared to the predicted values for that individual based on correlated random walk and track randomization methods. Although there was individual variation in habitat use, tiger sharks preferred shallow seagrass habitats, where their prey is most abundant. Despite multiple encounters with potential prey, sharks rarely engaged in prolonged high-speed chases, and did not attack prey that were vigilant. We propose that the tiger sharks' foraging tactic is one of stealth, and sharks rely upon close approaches to prey in order to be successful. This study shows that using appropriate analysis techniques and a variety of field methods it is possible to elucidate the factors influencing habitat use and gain insights into the foraging behavior of elusive top predators.

Communicated by R.J. Thompson, St. John's

M.R. Heithaus (✉) · L.M. Dill
Behavioural Ecology Research Group,
Department of Biological Sciences,
Simon Fraser University, Burnaby,
BC V5A 1S6, Canada

G.J. Marshall · B. Buhleier
National Geographic Television,
Special Projects, Natural History Unit,
1145 17th St, NW, Washington,
DC 20036, USA

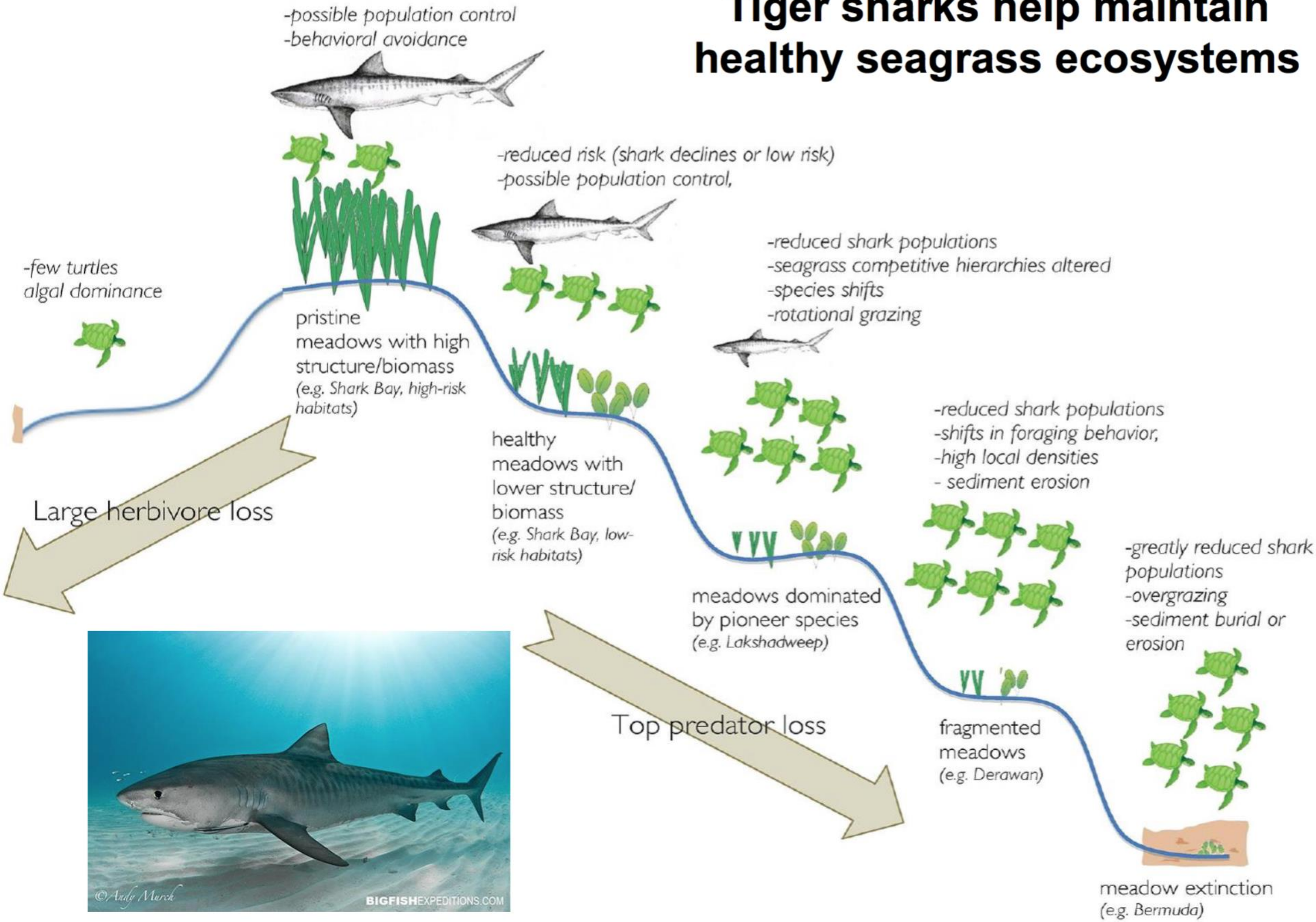
*Present address*: M.R. Heithaus
Center for Shark Research,
Mote Marine Laboratory, 1600 Ken Thompson Parkway,
Sarasota, FL 34236, USA
e-mail: mheithaus@mote.org
Tel.: +1-941-3884441
Fax: +1-941-3884312

## Introduction

Understanding patterns of habitat use and foraging behavior of top predators is important to gaining insight into the dynamics of communities. Patterns of habitat use determine the likelihood of both direct and indirect interspecific interactions, which can influence community structure and stability (e.g. Brown et al. 1999). Therefore, understanding the factors that influence spatial distributions of top predators is critical to predicting the consequences of environmental perturbations and human disturbance on these species and the communities they inhabit. Despite the importance of such studies, it is often difficult to gather data on top predators as they are frequently elusive, have large home ranges, and exist at low population densities. Thus, new methods with meaningful statistical tests could greatly enhance our understanding of top predators in diverse habitats.

Sharks are an example of top predators for which there is little information regarding habitat use and foraging behavior. Yet large sharks may be keystone predators, influencing the structure of ecosystems through predator-prey interactions (e.g. Heithaus 2001a; Simpfendorfer et al. 2001). This study was undertaken to develop methods applicable for gaining insights into their habitat use and to apply new technologies to begin to understand their foraging behavior.

# Tiger sharks help maintain healthy seagrass ecosystems




From Heithaus et al. (2014)

ECOLOGY LETTERS

*Ecology Letters*, (2010) **13**: 1055–1071 doi: 10.1111/j.1461-0248.2010.01489.x

REVIEW AND SYNTHESIS

# Patterns and ecosystem consequences of shark declines in the ocean

Francesco Ferretti,[1]* Boris Worm,[1] Gregory L. Britten,[1] Michael R. Heithaus[2] and Heike K. Lotze[1]

**Abstract**

Whereas many land predators disappeared before their ecological roles were studied, the decline of marine apex predators is still unfolding. Large sharks in particular have experienced rapid declines over the last decades. In this study, we review the documented changes in exploited elasmobranch communities in coastal, demersal, and

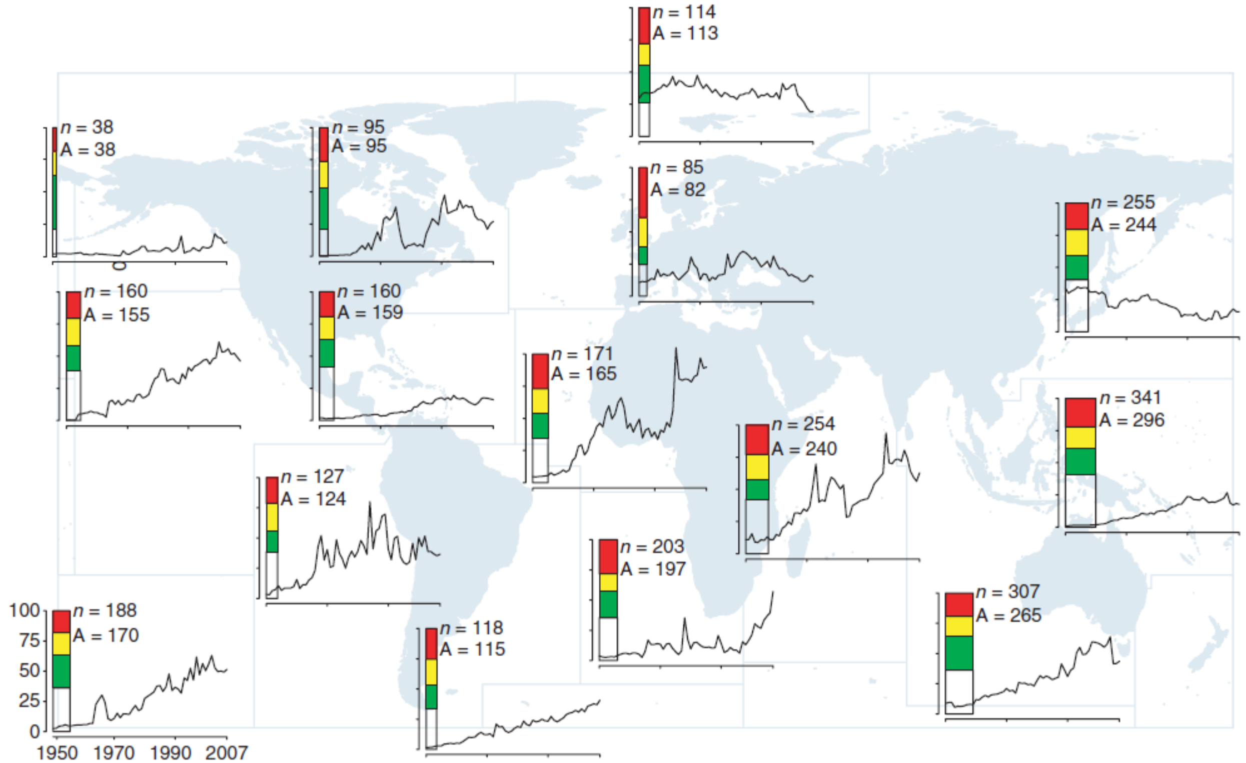



**Figure 2** Global fisheries trends and conservation status of chondrichthyans. Time series refer to landings of sharks, rays and chimeras in thousands of metric tonnes $km^{-2}$ of shelf area since 1950, as reported to the United Nations Food and Agriculture Organization (FAO). Stacked bars represent the global conservation status of all chondrichthyans assessed by the International Union for the Conservation of Nature (IUCN) Shark Specialist Group (Appendix S1, Camhi *et al.* 2009, http://www.redlist.org). Red indicates the percentage of species that occur in a particular FAO area and that are globally assessed as critically endangered (CR), endangered (EN), and vulnerable (VU); yellow indicates near threatened (NT) status and green the percentage of species assessed as least concern (LC). Transparent bars refer to species that are assessed data deficient (DD) or that have not been assessed yet. FAO assessment areas are outlined in light blue on the background map. A list of chondrichthyans occurring in each FAO area was derived from FishBase (http://www.fishbase.org). N, total number of species occurring in that area; A, number of species assessed by IUCN.

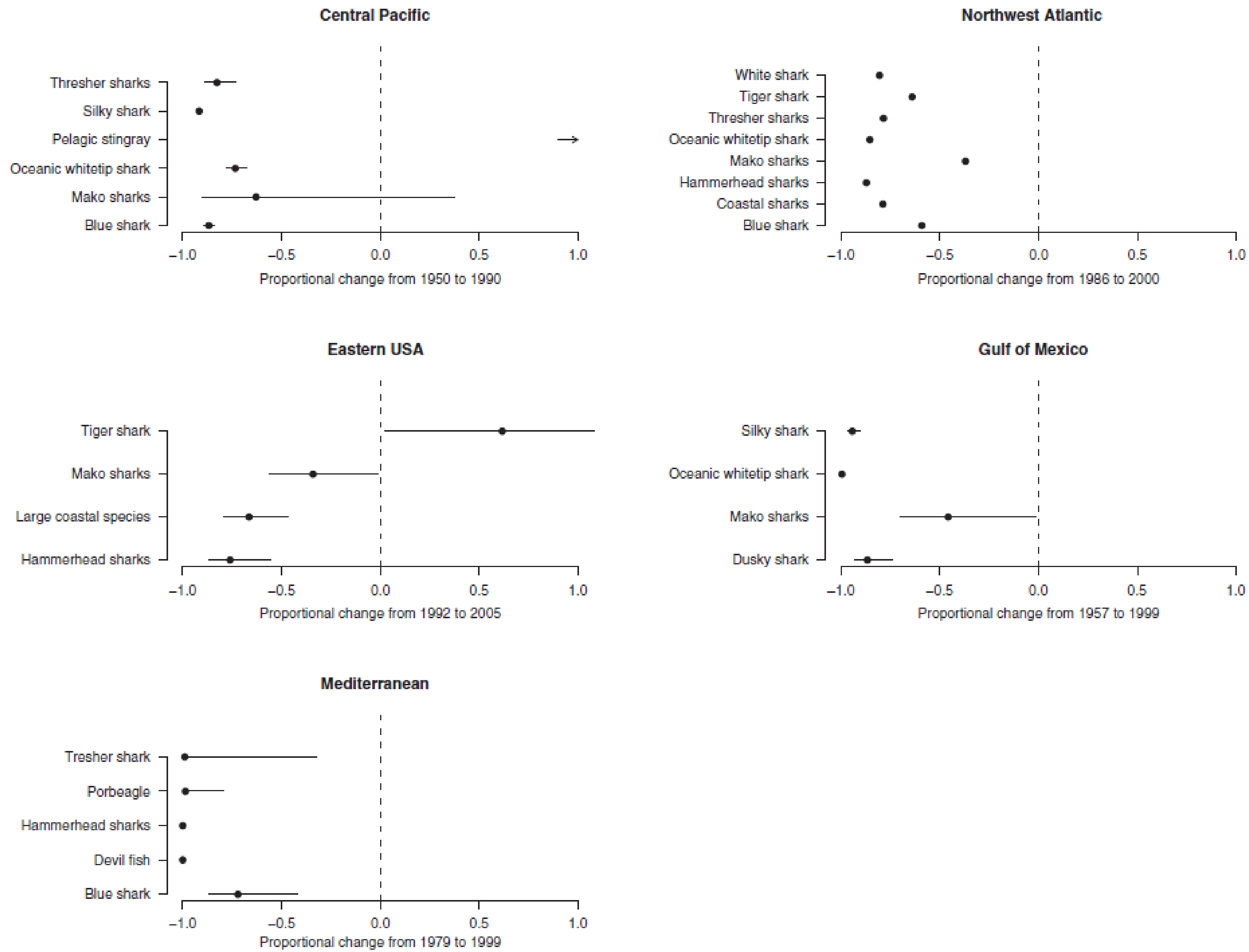



**Figure 5** Relative changes in population abundance of pelagic sharks in the Central Pacific (Ward & Myers 2005), Northwest Atlantic (Baum *et al.* 2003), Eastern USA (Myers *et al.* 2007), Gulf of Mexico (Baum & Myers 2004), and the Mediterranean (Ferretti *et al.* 2008, using the analyses of the Ionian Sea pelagic fishery).

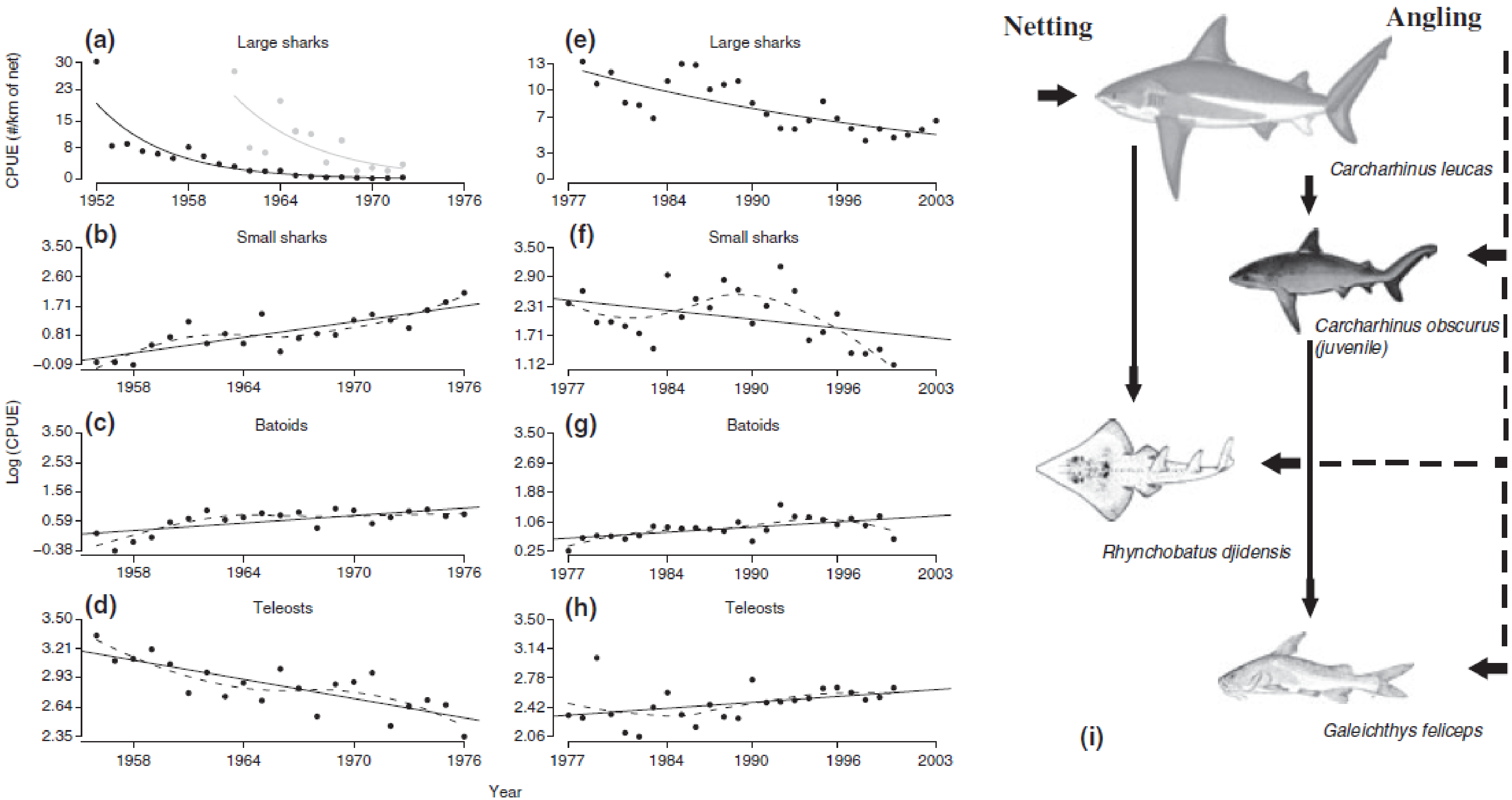



**Figure 6** A possible trophic cascade in the inshore waters of Kwa-Zulu Natal, South Africa. Two periods are contrasted: 1952–1977 and 1978–2003. (a, e) Large sharks caught in shark netting programs (black: Main Beach, grey: Brighton Beach); data were derived from aggregated catches of large sharks species reported in Holden (1977) and Dudley & Simpfendorfer (2006). To be consistent between time periods, the species included in this group in both panels (a, e) are those reported by Holden (1977). Regression lines are: (a) generalized linear models as specified in Fig. 4, and (e) linear models of log(CPUE)~year. Panels (b–d) and (f–h) are time series of log CPUE of small sharks (mostly juvenile dusky sharks), batoids (skates and rays) and teleost fishes from the recreational fishery, as reported by van der Elst (1979) and Pradervand *et al.* (2007). As the fraction of teleosts was not explicitly reported in Pradervand *et al.* (2007), we estimated it by subtracting the elasmobranchs from the total number of fish caught. Solid lines depict linear regressions fitted to log transformed data. Dashed lines represent local regressions (LOESS). The diagram shows common species caught by shark nets and recreational angling, respectively, as well as their trophic relationships. The initial increase of small sharks was thought to be due to predatory release, and their later decline because of increased angling pressure.

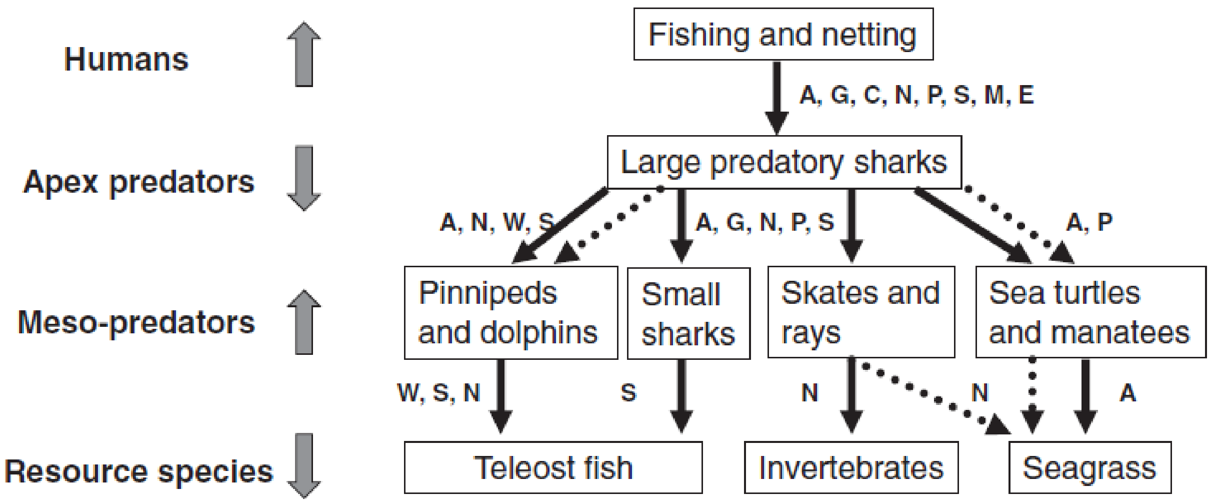



**Figure 7** Documented ecosystem effects of fishing large sharks. Depicted are trophic (solid arrows) and behavioural (dotted arrows) interactions between humans, large and mesopredator elasmobranchs and their prey species. Block arrows represent overall population trends of the various functional groups. Regions in which particular interactions have been documented (see text) are indicated by letters (A, Australia; C, Caribbean; E, Europe; G, Gulf of Mexico; M, Mediterranean Sea; N, North American East Coast; P, Central Pacific; S, South Africa; W, North American West Coast). Note that few studies have documented effects on teleost and cephalopod prey.

# Hydrologic Cycle

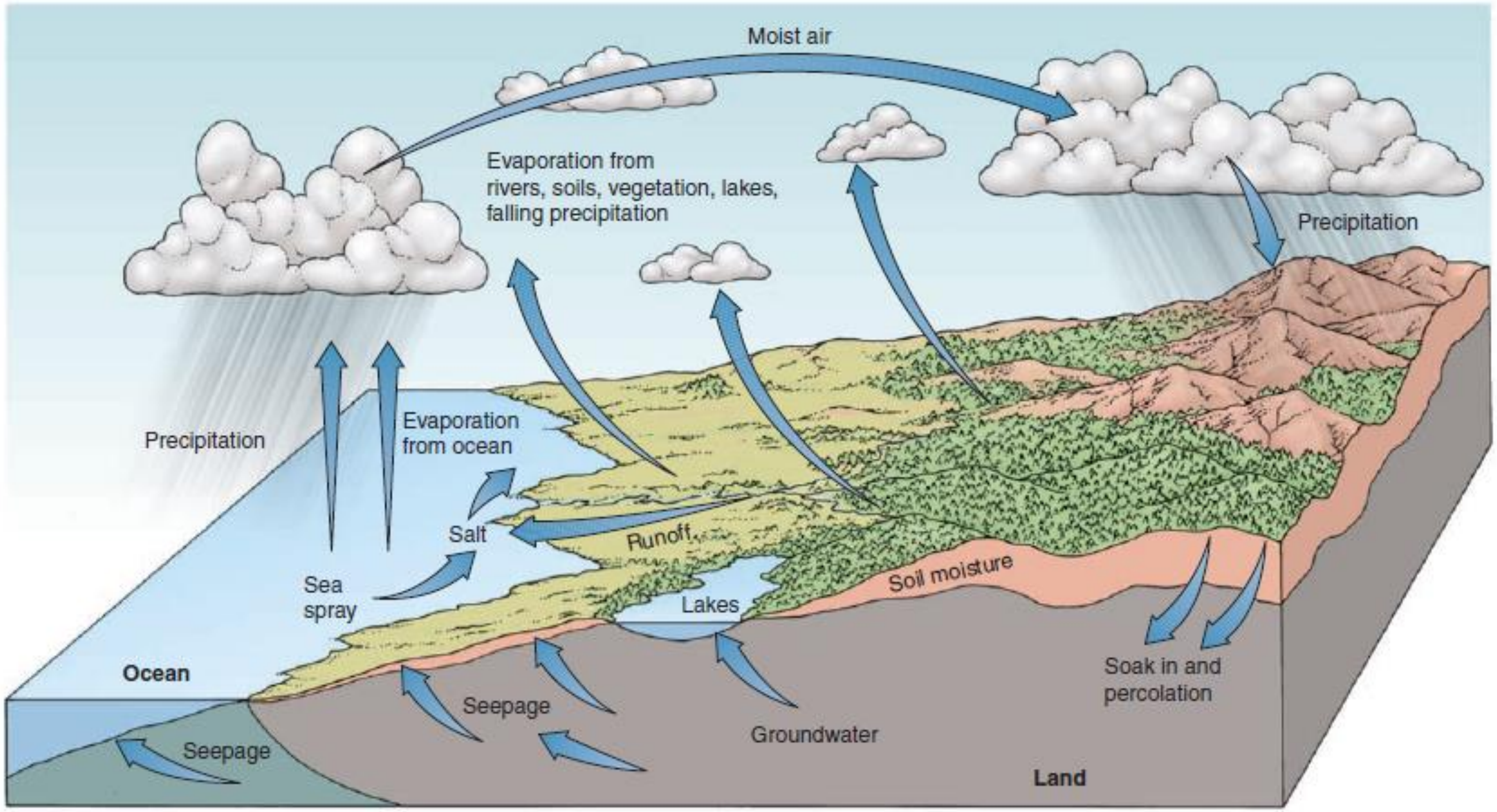



**Figure 2-20 THE HYDROLOGIC CYCLE.** Water leaves the oceans by way of evaporation and returns in the form of precipitation. Rivers and streams collect the precipitation that falls on land and return it to the sea.

# Carbon Cycle

1. Atmosphere (0.03%)
2. Oceans
3. Carbonate rock and petroleum

1. Respiration
2. Decomposition
3. Volcanic eruption
4. Combustion of fossil fuel

# Carbon Cycle

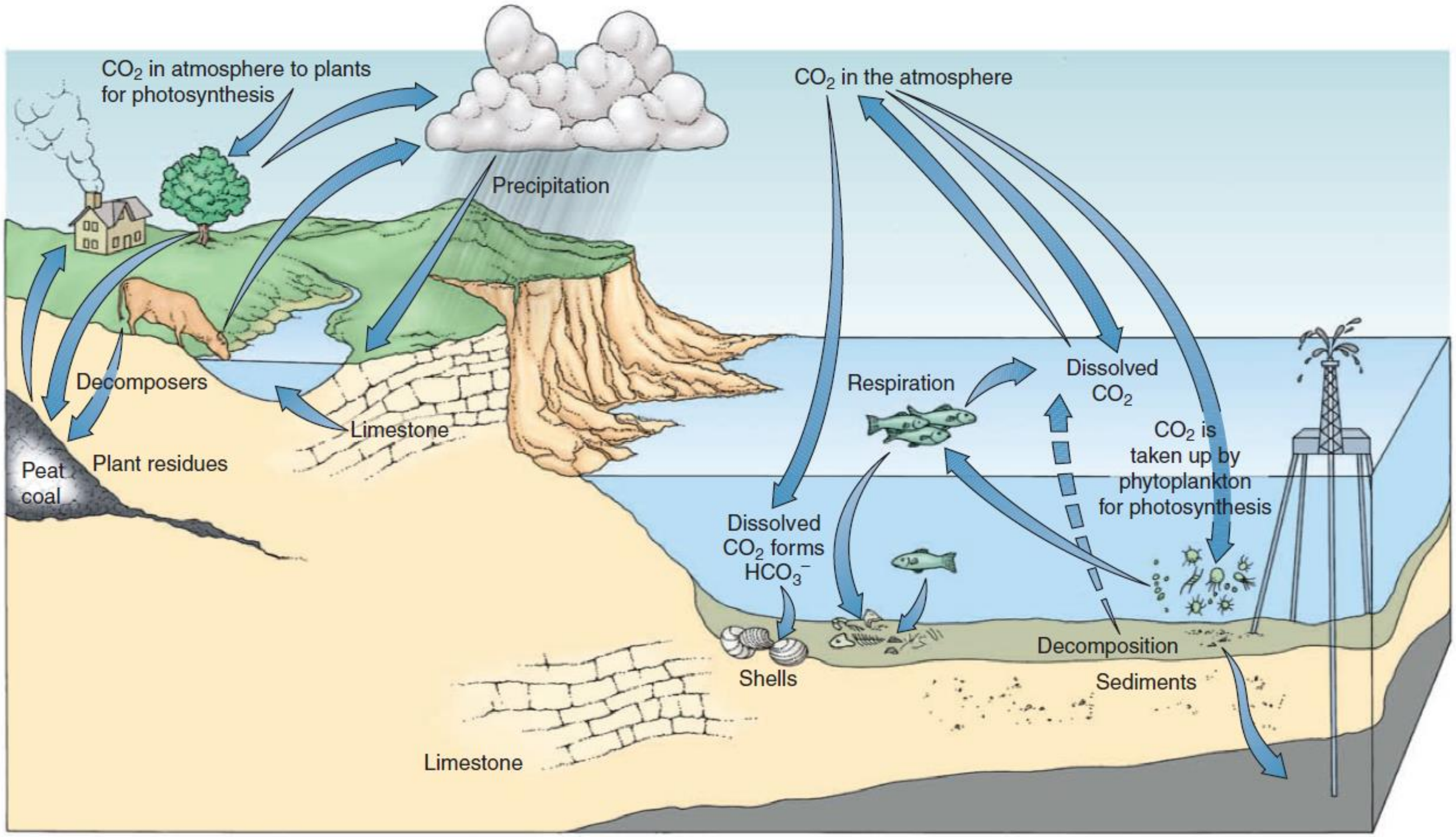



Figure 2-21 THE CARBON CYCLE. Carbon dioxide from the atmosphere that is dissolved in seawater is used by producers to make food through the process of photosynthesis. When the food is metabolized in respiration, the carbon dioxide is returned to the environment. Some carbon dioxide is converted into bicarbonate ions and incorporated into the shells of marine organisms. When these

# Nitrogen Cycle

- Protein and Nucleic acids
- Ammonia, amino acids or nitrates
- Atmosphere and water bodies
- Plants can absorb ammonia and nitrates
- Blue green algae and certain bacteria can fix atmospheric nitrogen into nitrates.---Nitrogen Fixation

# Nitrogen Fixation

Atmospheric nitrogen fixation

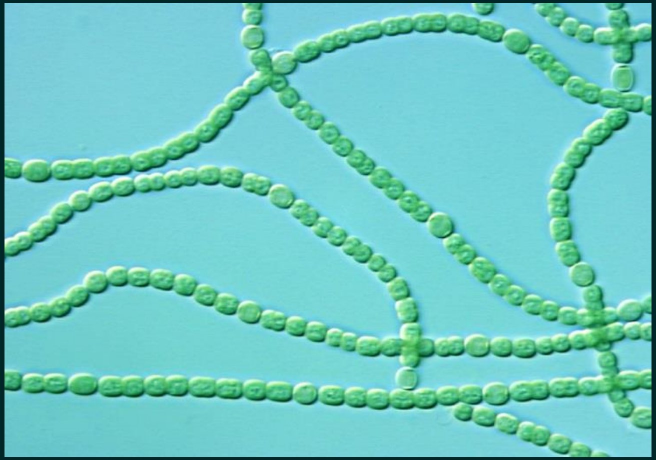
1. During lightening due to high temperature, the atmospheric nitrogen reacts with oxygen and form nitrous oxide ($N_2O$), nitric oxide(NO) and nitrogen peroxide ($NO_2$).
2. These compounds dissolve in rain water to form Nitric acid.
3. They react with alkalies and form nitrates.
4. Plants easily absorb nitrates.

# Nitrogen Fixation

Biological fixation

- Certain bacteria and blue green algae can fix atmospheric nitrogen directly into ammonia.
- Nitrogen fixing bacteria are of two types

1. Free living
2. Symbiotic- Root of Leguminous plant



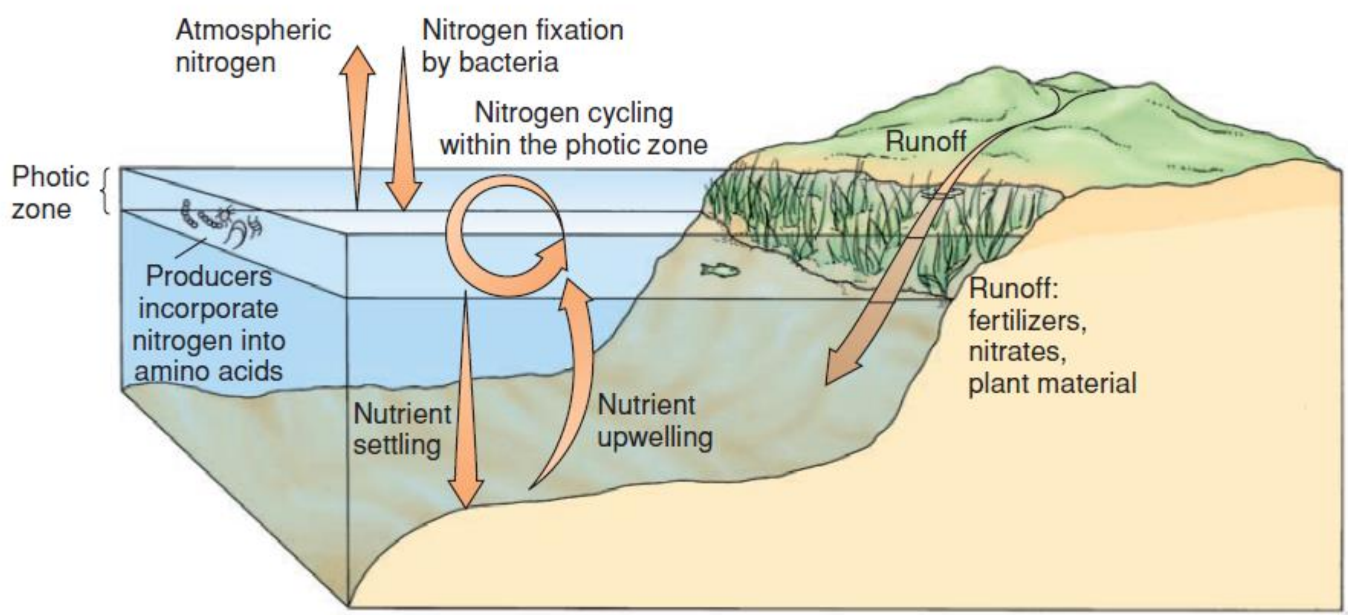
# Nitrogen Cycle

- Nitrification
  Conversion of ammonia into nitrates and nitrites is brought about by the nitrifying bacteria.
- Denitrification
  Bacteria Pseudomonas and Bacillus denitrificants convert nitrate to free nitrogen. This process is called denitrification. Denitrification take place under special conditions in both terrestrial and marine ecosystems. In general , it occurs where oxygen is depleted and bacteria respire nitrates as a substitute terminal electron accepter.

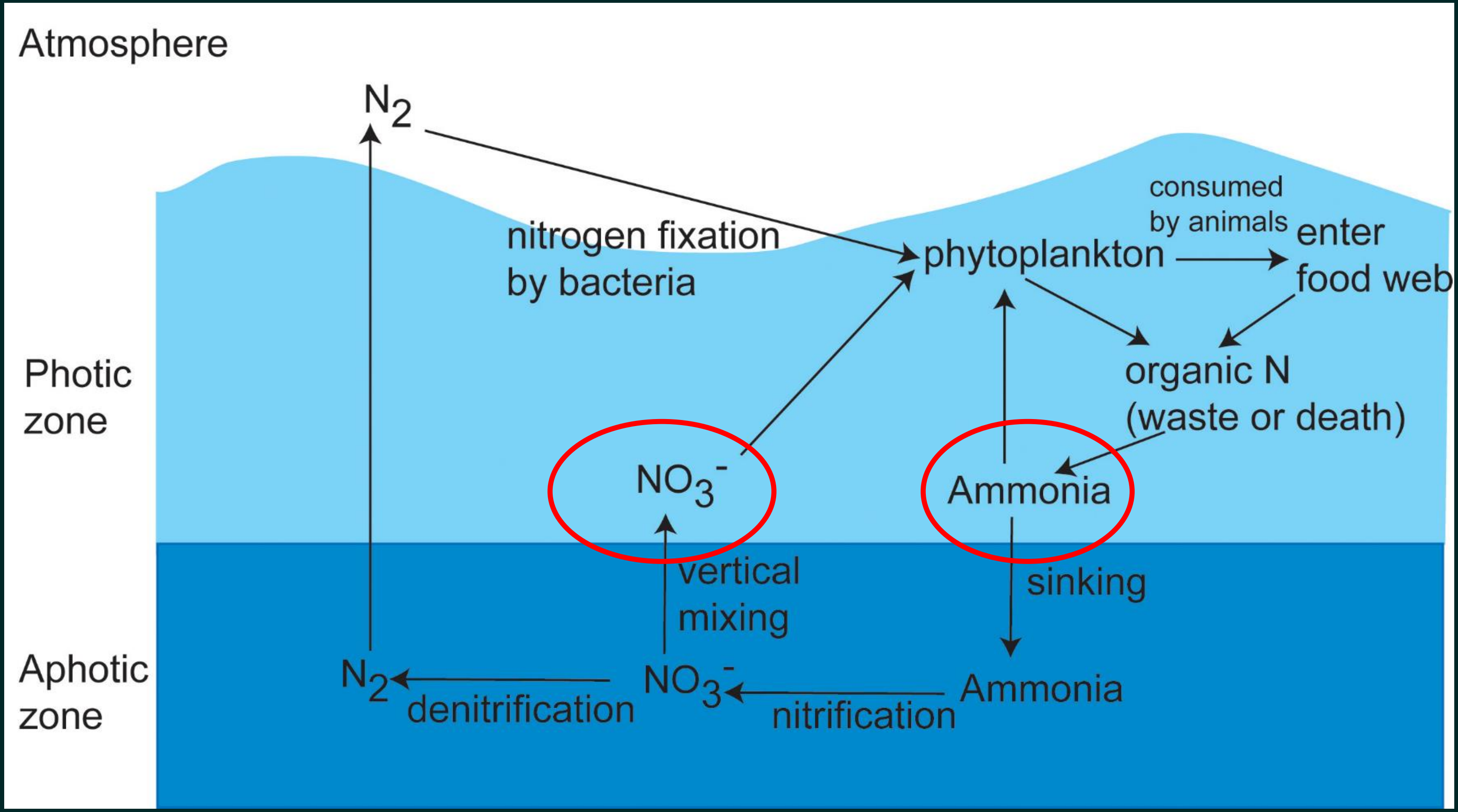
# Nitrogen Cycle

- Ammonia ($NH_3$), ammonium ($NH_4^+$), nitrite ($NO_2^-$), and nitrate ($NO_3^-$)

**Figure 2-22 THE NITROGEN CYCLE.** Upwellings and runoff from the land bring nitrogen into the photic zone, where producers can incorporate it into amino acids. Nitrogen-fixing bacteria in the photic zone can convert atmospheric nitrogen into forms that can be used by producers. Nitrogen is returned to the environment when organisms die or animals eliminate wastes.



# Nitrogen Cycle



nature COMMUNICATIONS

ARTICLE

DOI: 10.1038/s41467-018-03363-0 OPEN

# Ambient nitrate switches the ammonium consumption pathway in the euphotic ocean

Xianhui Sean Wan[1], Hua-Xia Sheng[1], Minhan Dai[1], Yao Zhang[1], Dalin Shi[1], Thomas W. Trull[2], Yifan Zhu[1], Michael W. Lomas[3] & Shuh-Ji Kao[1]

Phytoplankton assimilation and microbial oxidation of ammonium are two critical conversion pathways in the marine nitrogen cycle. The underlying regulatory mechanisms of these two competing processes remain unclear. Here we show that ambient nitrate acts as a key variable to bifurcate ammonium flow through assimilation or oxidation, and the depth of the nitracline represents a robust spatial boundary between ammonium assimilators and oxidizers in the stratified ocean. Profiles of ammonium utilization show that phytoplankton assemblages in nitrate-depleted regimes have higher ammonium affinity than nitrifiers. In nitrate replete conditions, by contrast, phytoplankton reduce their ammonium reliance and thus enhance the success of nitrifiers. This finding helps to explain existing discrepancies in the understanding of light inhibition of surface nitrification in the global ocean, and provides further insights into the spatial linkages between oceanic nitrification and new production.

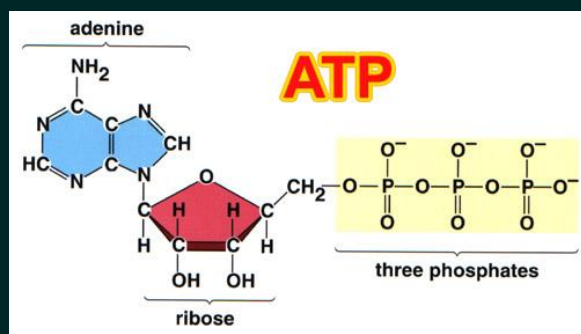
# Phosphorus Cycle

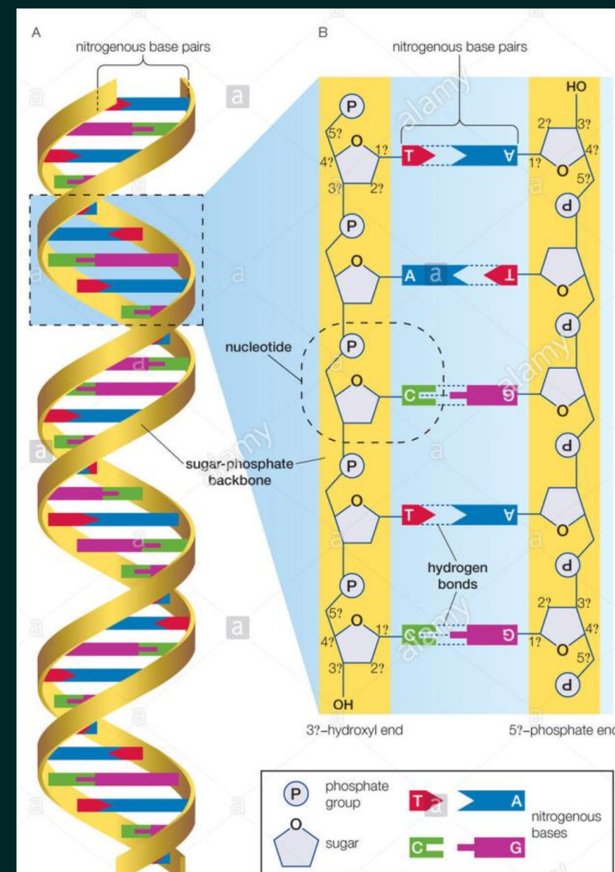
- No phosphorus in atmosphere
- Phosphorus needed to make:

----ATP

----DNA

----lipids

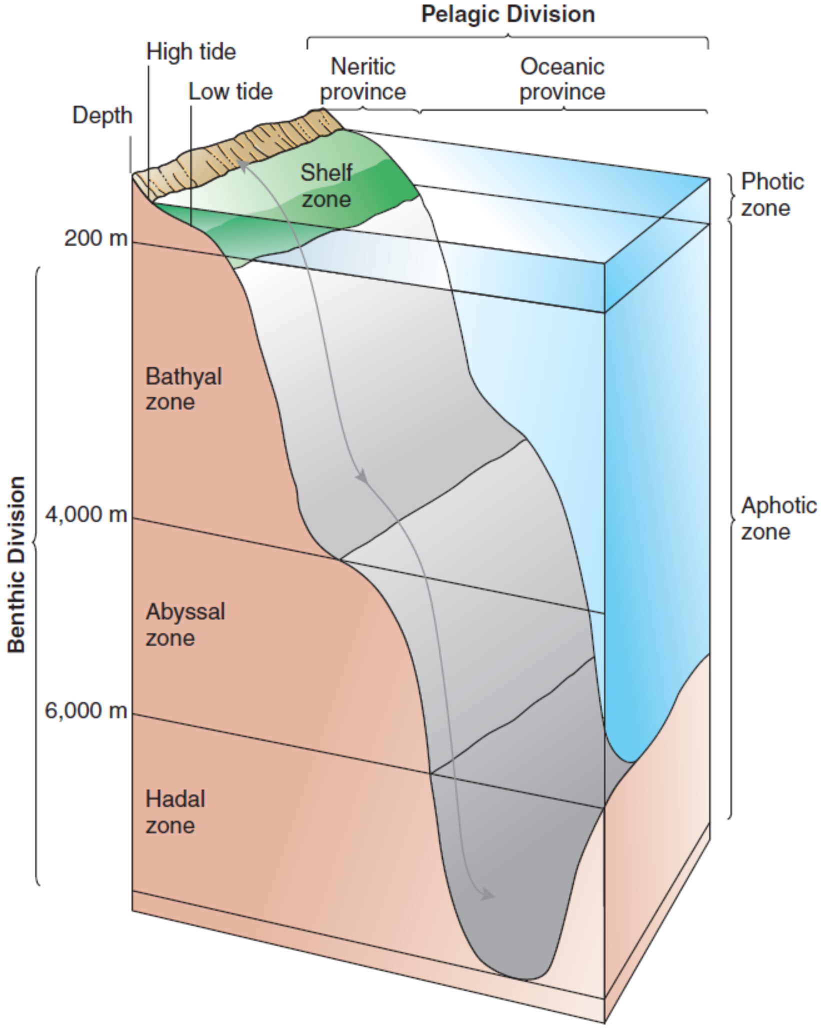


# Phosphorus Cycle

1. Phosphorus released from the weathering of rocks
2. Producers absorb phosphorus through their roots
3. Phosphorus moves up the food chain as animals eat producers
4. Decomposers obtain phosphorus as they feed on dead remains
5. Human Contribution
   Fertilizers and run off with rain

# The Biosphere




Ecologists frequently divide the marine environment into two major divisions: the pelagic division, composed of the ocean's water (the water column), and the benthic division, the ocean bottom. These divisions can be subdivided into zones on the basis of three characteristics: distance from land, light availability, and depth.

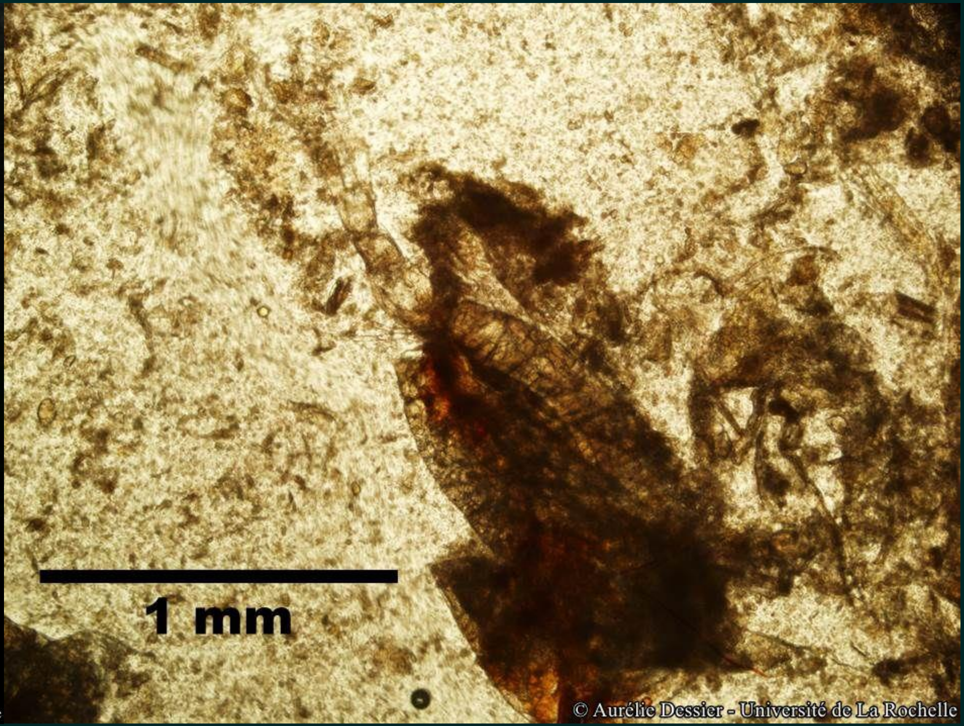
**Figure 2-23 OCEAN DIVISIONS AND ZONES.** Ecologists frequently divide the ocean into two major divisions: the pelagic division, consisting of the water column, and the benthic division, consisting of the sea bottom. The pelagic division can be subdivided based on the availability of sunlight (photic zone and aphotic zone) or distance from the shore (neritic province and oceanic province). The benthic division can be subdivided on the basis of depth (intertidal zone, shelf zone, bathyal zone, abyssal zone, and hadal zone).

# In Summary

- Nutrients are constantly recycled from one generation to the next through biogeochemical cycles. The energy for most life on earth comes from sunlight. Producers capture the energy of sunlight in the chemical bonds of organic molecules. The rate at which these energy-rich molecules are formed is called primary production. Consumer organisms rely on these  molecules as a source of food. In every ecosystem, producers and consumers are linked by feeding relationships called food chains. The ten percent rule of ecology states that the average amount of energy passed from one trophic level to the next is approximately 10%.

# 1. Stomach content analysis


Stomach content of a beached cetecean collected by the French Beaching National Network (RNE).




Observation with a stereomicroscope of a copepod stomach content from a sardine (*Sardina pilchardus*) caught in the Gulf of Biscay continental shelf.

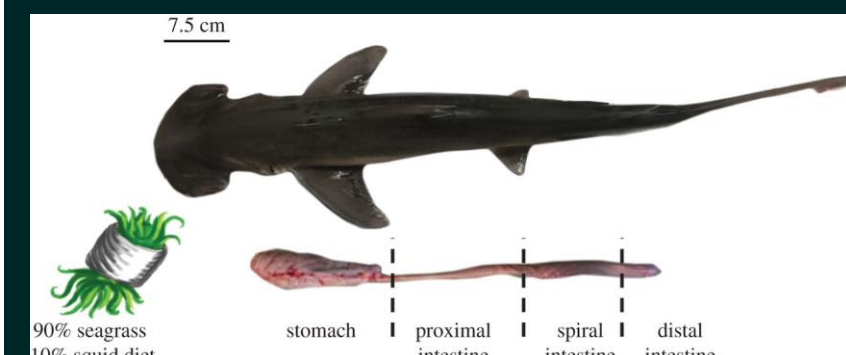
# 1. S

# Omnivorous Sharks?

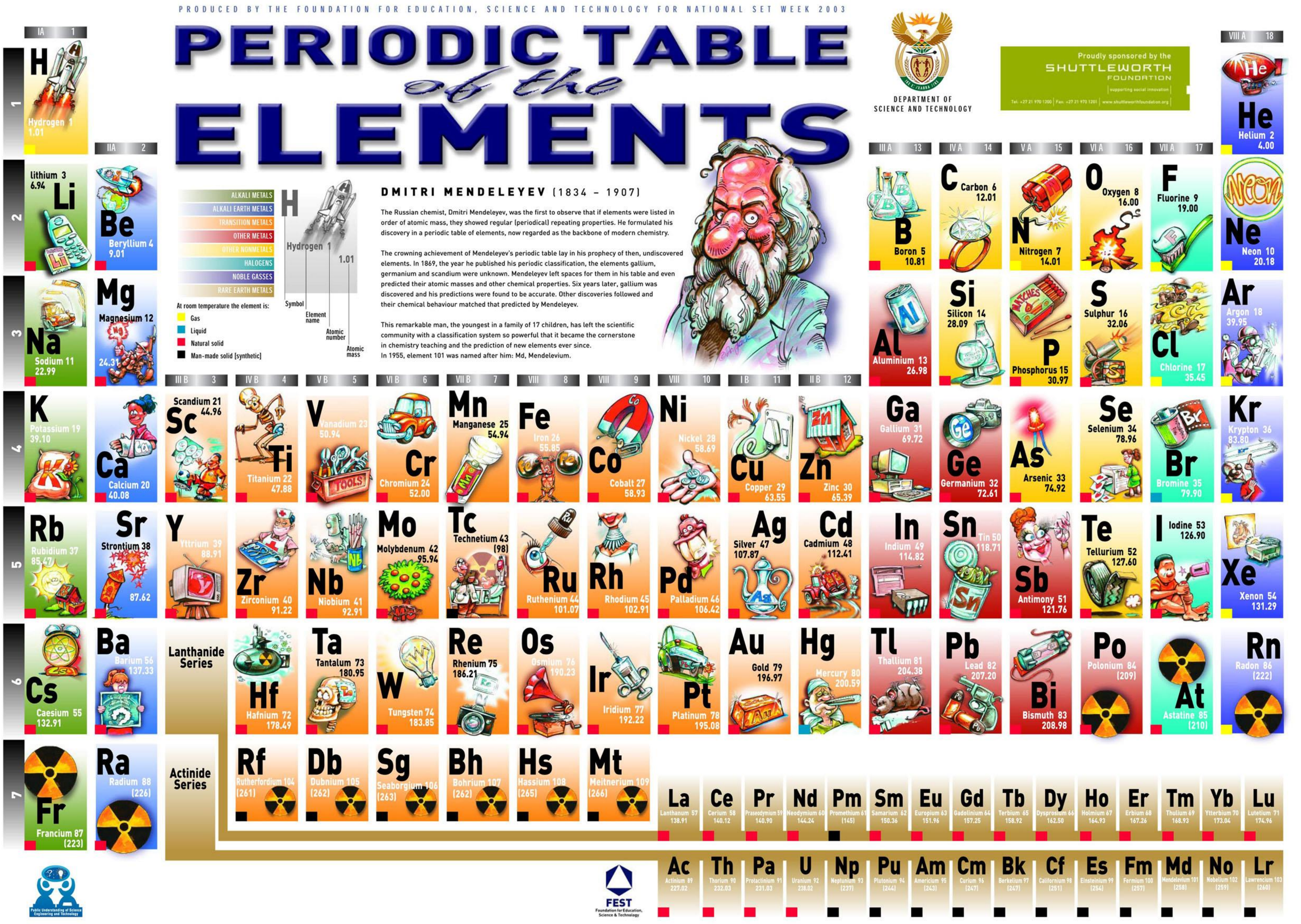
The New York Times

## The Omnivorous Sharks That Eat Grass

Diminutive bonnethead sharks are the first omnivorous sharks known to science, which could change our understanding of what some sharks eat.

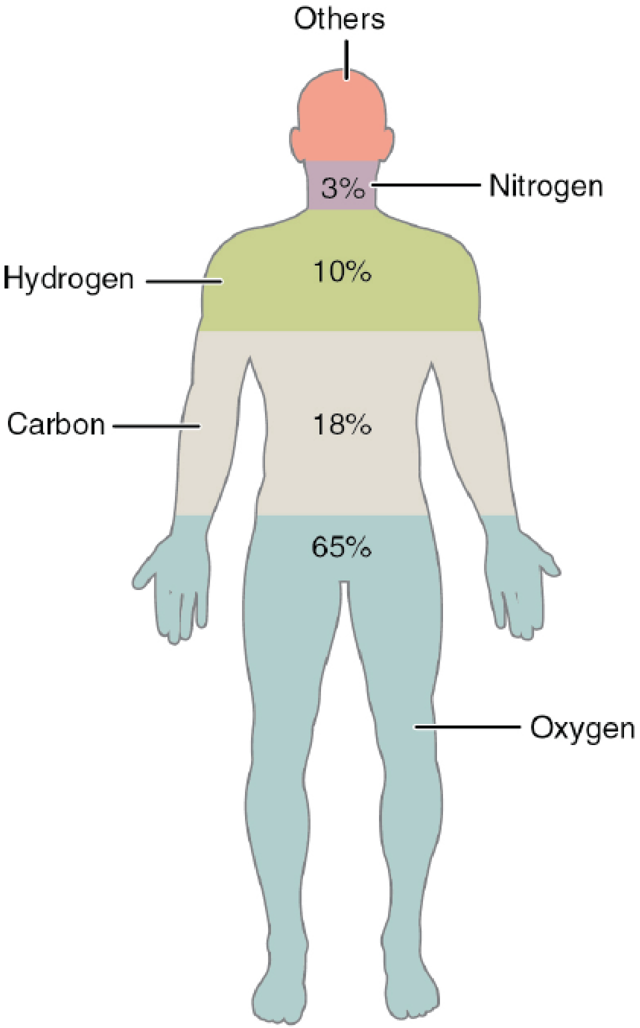



# 2. Stable isotope analysis



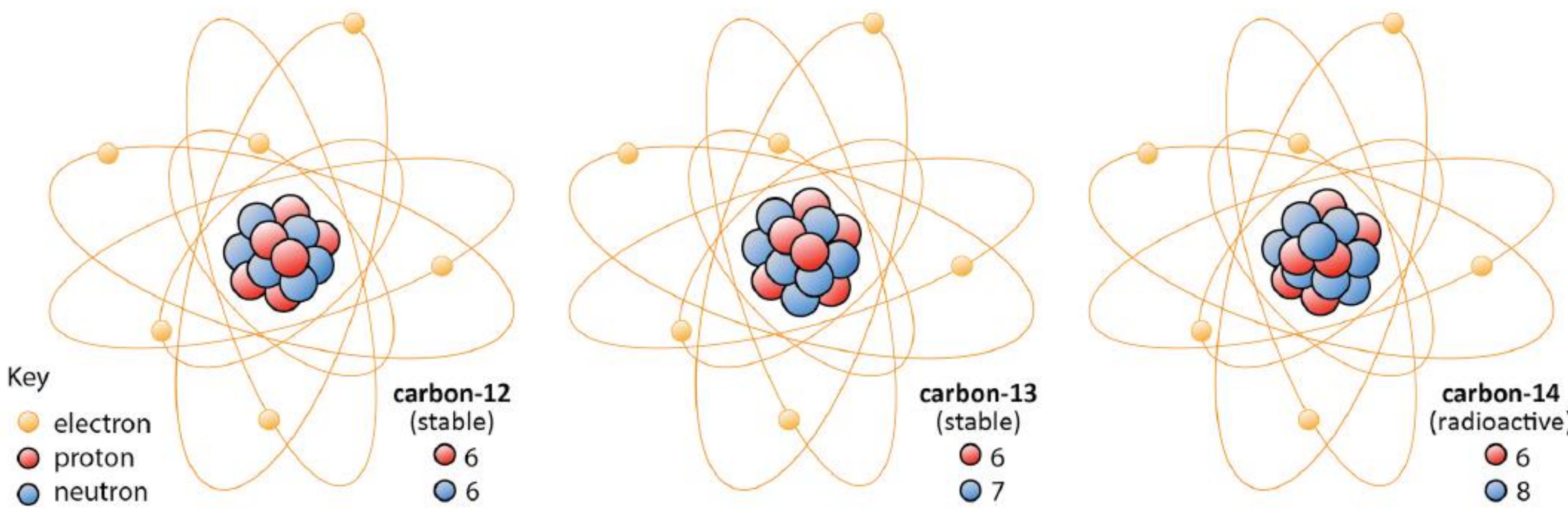
PRODUCED BY THE FOUNDATION FOR EDUCATION, SCIENCE AND TECHNOLOGY FOR NATIONAL SET WEEK 2003
PERIODIC TABLE of the ELEMENTS
DEPARTMENT OF SCIENCE AND TECHNOLOGY
Proudly sponsored by the SHUTTLEWORTH FOUNDATION
DMITRI MENDELEYEV (1834 – 1907)
The Russian chemist, Dmitri Mendeleyev, was the first to observe 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.
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)
H Hydrogen 1 1.01
Symbol
Element name
Atomic number
Atomic mass
IA 1
IIA 2
IIIA 13
IVA 14
VA 15
VIA 16
VIIA 17
VIIIA 18
IIIB 3
IVB 4
VB 5
VIB 6
VIIB 7
VIII 8
VIII 9
VIII 10
IB 11
IIB 12
H Hydrogen 1 1.01
He Helium 2 4.00
Li Lithium 3 6.94
Be Beryllium 4 9.01
B Boron 5 10.81
C Carbon 6 12.01
N Nitrogen 7 14.01
O Oxygen 8 16.00
F Fluorine 9 19.00
Ne Neon 10 20.18
Na Sodium 11 22.99
Mg Magnesium 12 24.31
Al Aluminium 13 26.98
Si Silicon 14 28.09
P Phosphorus 15 30.97
S Sulphur 16 32.06
Cl Chlorine 17 35.45
Ar Argon 18 39.95
K Potassium 19 39.10
Ca Calcium 20 40.08
Sc Scandium 21 44.96
Ti Titanium 22 47.88
V Vanadium 23 50.94
Cr Chromium 24 52.00
Mn Manganese 25 54.94
Fe Iron 26 55.85
Co Cobalt 27 58.93
Ni Nickel 28 58.69
Cu Copper 29 63.55
Zn Zinc 30 65.39
Ga Gallium 31 69.72
Ge Germanium 32 72.61
As Arsenic 33 74.92
Se Selenium 34 78.96
Br Bromine 35 79.90
Kr Krypton 36 83.80
Rb Rubidium 37 85.47
Sr Strontium 38 87.62
Y Yttrium 39 88.91
Zr Zirconium 40 91.22
Nb Niobium 41 92.91
Mo Molybdenum 42 95.94
Tc Technetium 43 (98)
Ru Ruthenium 44 101.07
Rh Rhodium 45 102.91
Pd Palladium 46 106.42
Ag Silver 47 107.87
Cd Cadmium 48 112.41
In Indium 49 114.82
Sn Tin 50 118.71
Sb Antimony 51 121.76
Te Tellurium 52 127.60
I Iodine 53 126.90
Xe Xenon 54 131.29
Cs Caesium 55 132.91
Ba Barium 56 137.33
Lanthanide Series
Hf Hafnium 72 178.49
Ta Tantalum 73 180.95
W Tungsten 74 183.85
Re Rhenium 75 186.21
Os Osmium 76 190.23
Ir Iridium 77 192.22
Pt Platinum 78 195.08
Au Gold 79 196.97
Hg Mercury 80 200.59
Tl Thallium 81 204.38
Pb Lead 82 207.20
Bi Bismuth 83 208.98
Po Polonium 84 (209)
At Astatine 85 (210)
Rn Radon 86 (222)
Fr Francium 87 (223)
Ra Radium 88 (226)
Actinide Series
Rf Rutherfordium 104 (261)
Db Dubnium 105 (262)
Sg Seaborgium 106 (263)
Bh Bohrium 107 (262)
Hs Hassium 108 (265)
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)
FEST Foundation for Education, Science & Technology

# Isotope




| 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 |

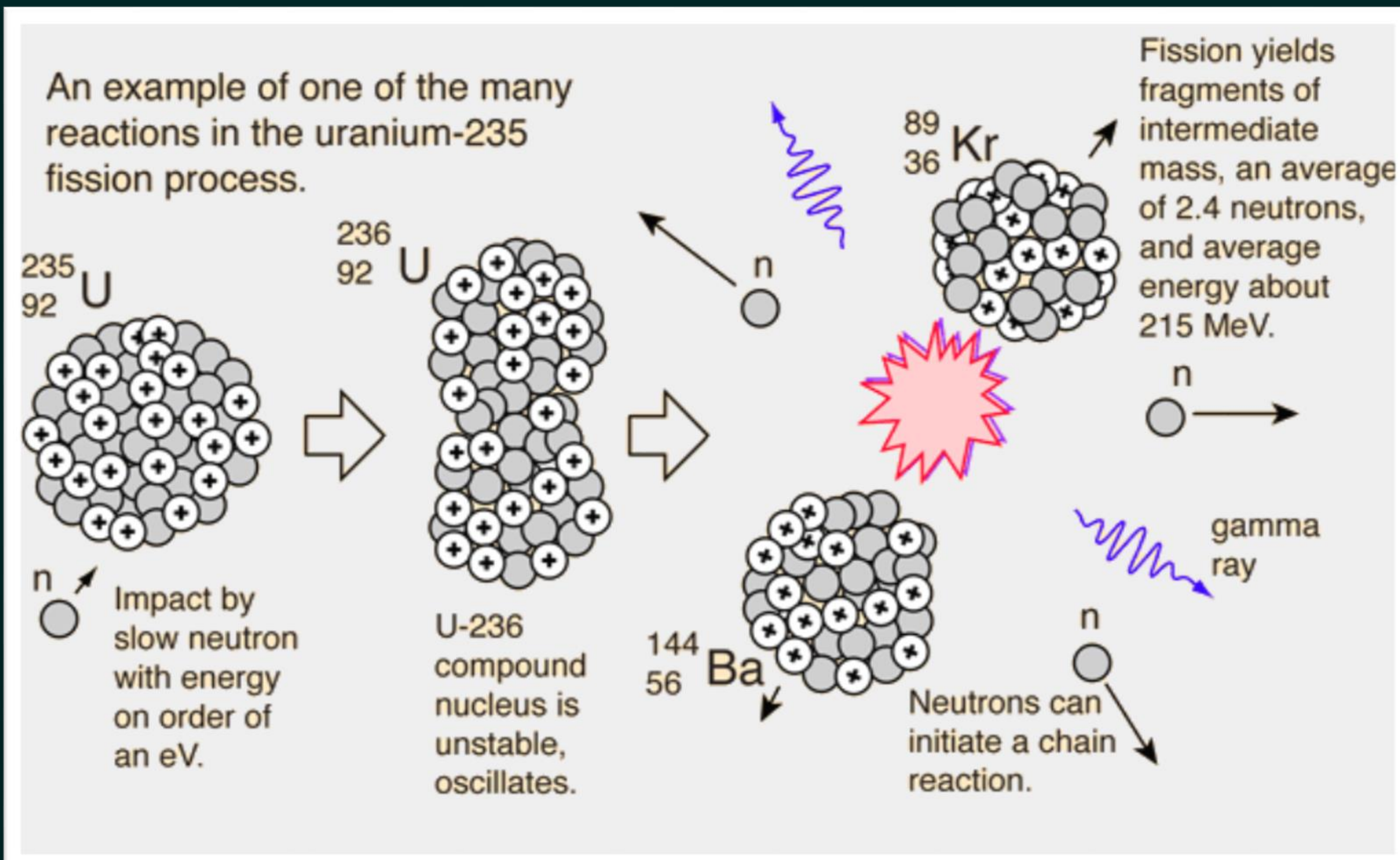
# Isotope



Key
electron
proton
neutron
carbon-12
(stable)
6
6
carbon-13
(stable)
6
7
carbon-14
(radioactive)
6
8

# Isotope

e


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

- Isotopes are forms of the same eleme
of neutrons in the nucleus.
- The word "isotope" comes from cons
table of the elements, and means tha
all occupy the same (*iso*) place (*topos*
- Frederick Soddy first introduced the
formal way during a speech to the Br
Feb 27, 1913. He won the 1921 Nobel
"his investigations into the origin and

# Francis W. Aston

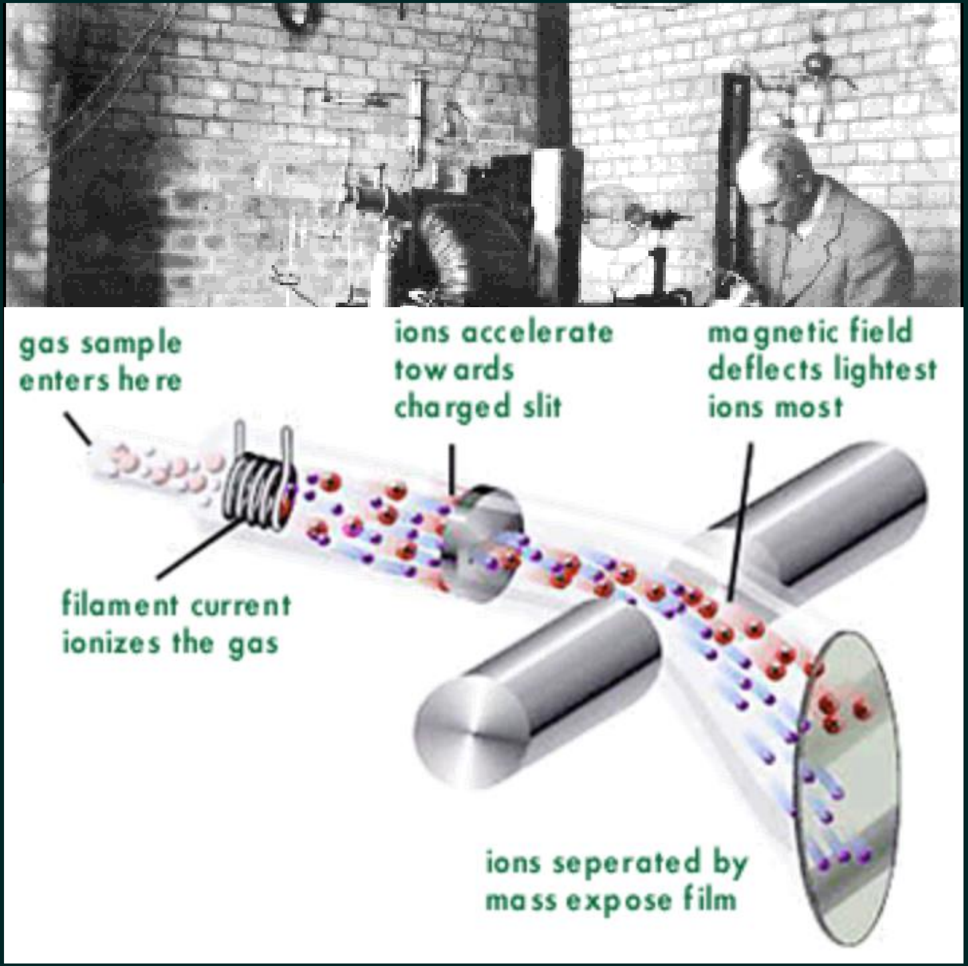
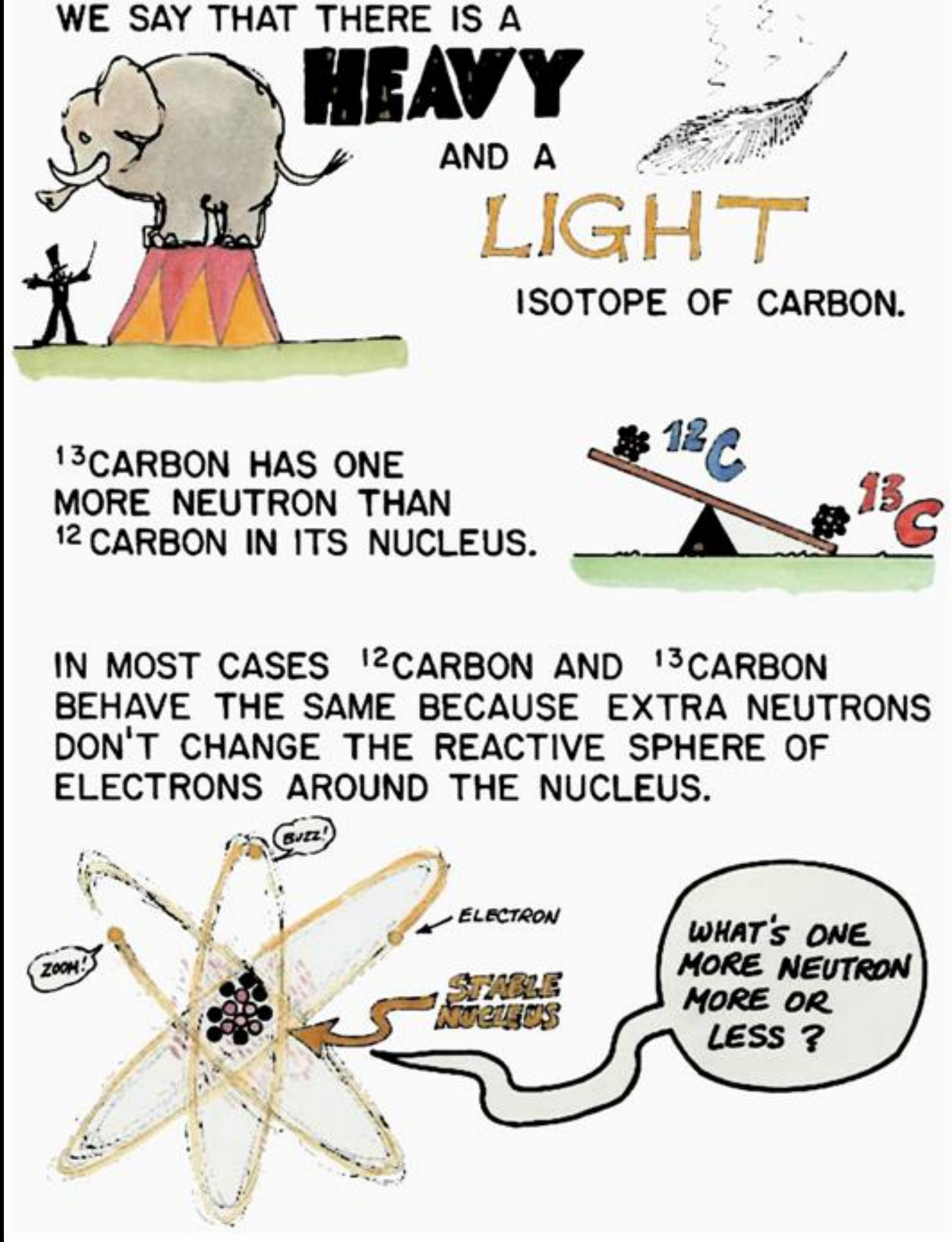


Fig. 1.1. An extra neutron in the $^{13}C$ isotope makes the nucleus more massive or “heavier” than the $^{12}C$ isotope, but does not affect most chemistry that is related to reactions in the electron shell.



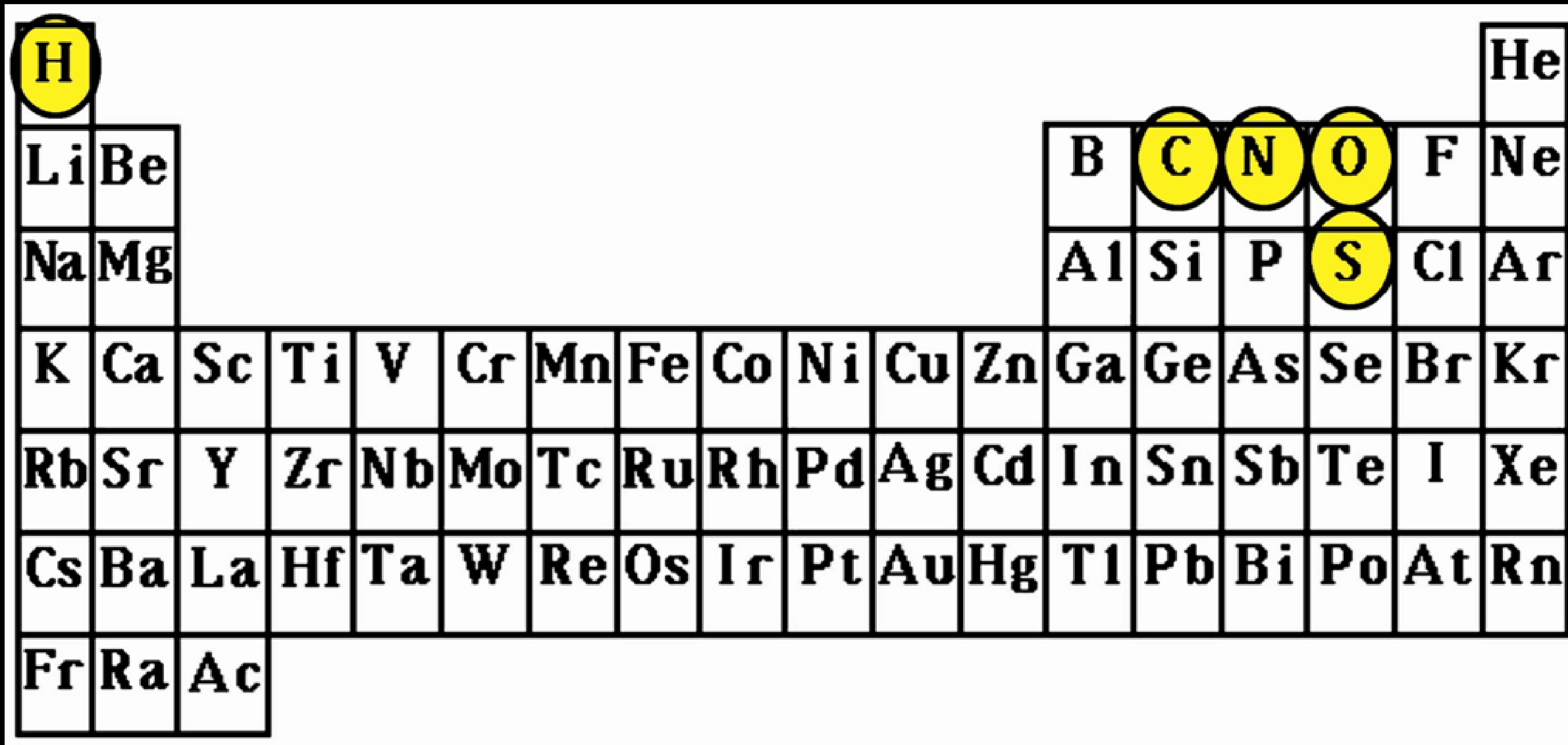
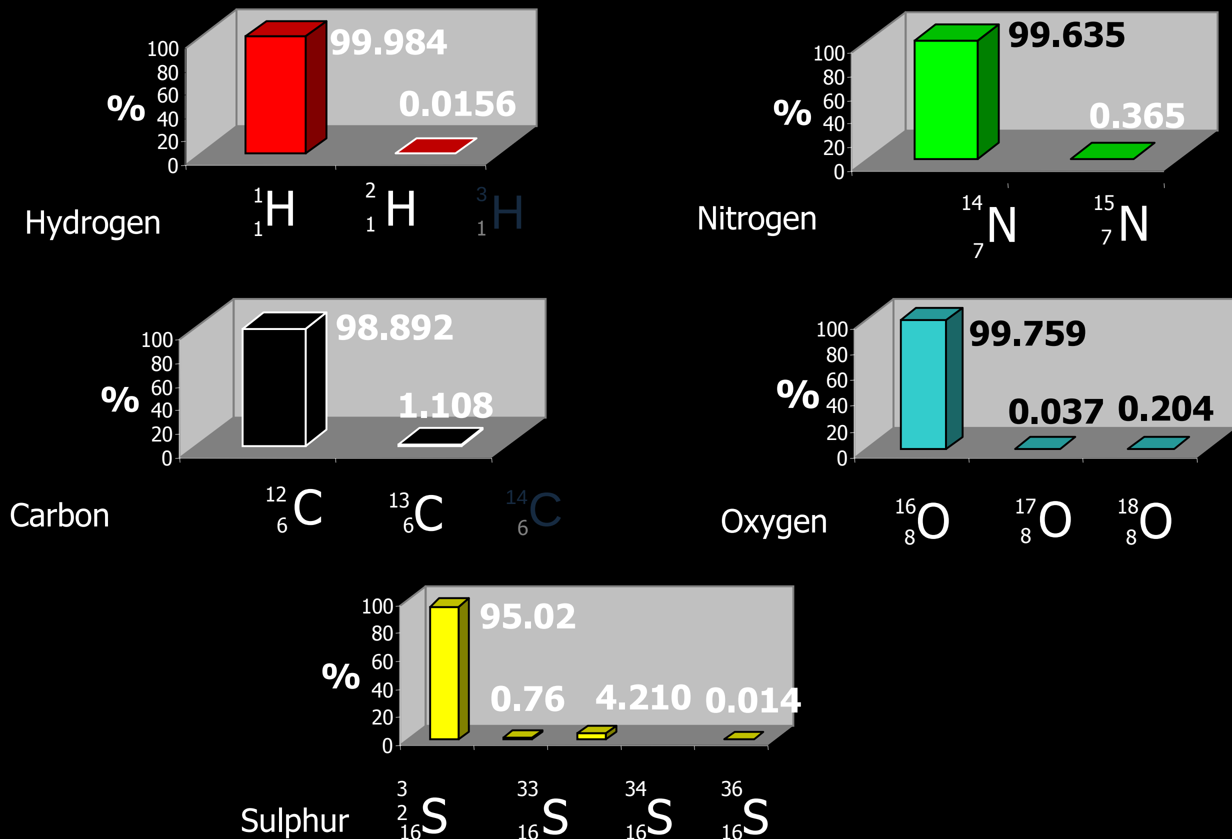



Fig. 1.2. An abbreviated periodic table of the elements. Elements have more than one isotope variety that differ in the number of neutrons. Stable isotopes of the circled HCNOS elements (hydrogen, carbon, nitrogen, oxygen and sulfur) are emphasized in this book. Details about isotopes for many of these elements are available at the website http://wwwrcamnl.wr.usgs.gov/isoig/period/.

# 稳定同位素的自然丰度



Hydrogen
%
100
80
60
40
20
0
99.984
0.0156
$^{1}_{1}H$
$^{2}_{1}H$
$^{3}_{1}H$
Nitrogen
%
100
80
60
40
20
0
99.635
0.365
$^{14}_{7}N$
$^{15}_{7}N$
Carbon
%
100
80
60
40
20
0
98.892
1.108
$^{12}_{6}C$
$^{13}_{6}C$
$^{14}_{6}C$
Oxygen
%
100
80
60
40
20
0
99.759
0.037
0.204
$^{16}_{8}O$
$^{17}_{8}O$
$^{18}_{8}O$
Sulphur
%
100
80
60
40
20
0
95.02
0.76
4.210
0.014
$^{32}_{16}S$
$^{33}_{16}S$
$^{34}_{16}S$
$^{36}_{16}S$

Fig. 1.3. You are what you eat - stable isotopes in a 50 kg human who is composed of mostly of light isotopes with a small amount of heavy isotopes. People are mostly water, so hydrogen and oxygen isotopes dominate at >35kg. Next come C isotopes at >11 kg, then N isotopes. S isotopes are missing – they should be here at about 220g for the light isotope 32S and 10g for the heavy isotope 34S. Have you had your isotopes today? (from Wada and Hattori, 1990; reproduced with permission of CRC Press LLC).

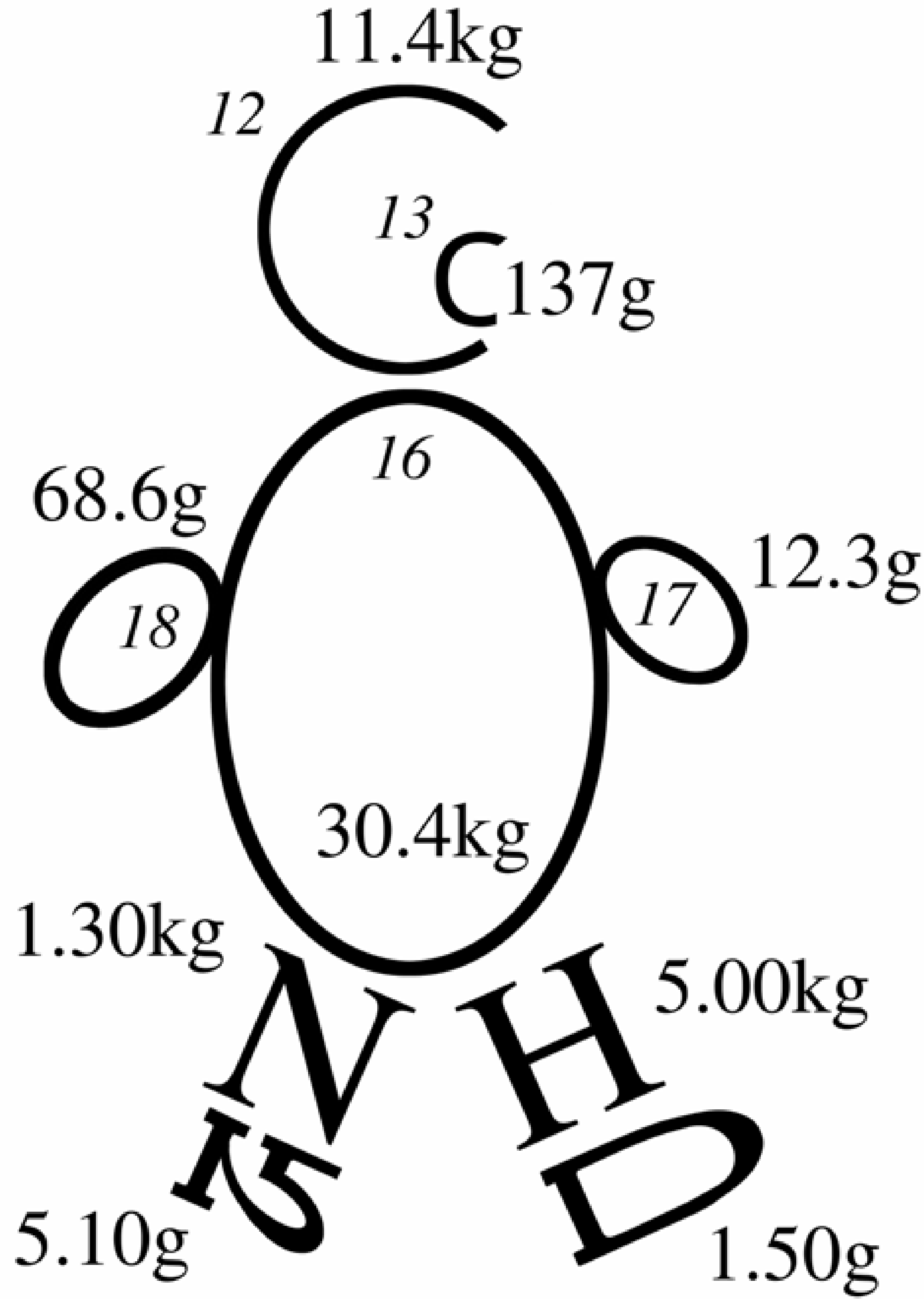


Fig. 1.4. focuses on the five elements (hydrogen, carbon, nitrogen, oxygen and sulfur) and their 13 stable isotopes.

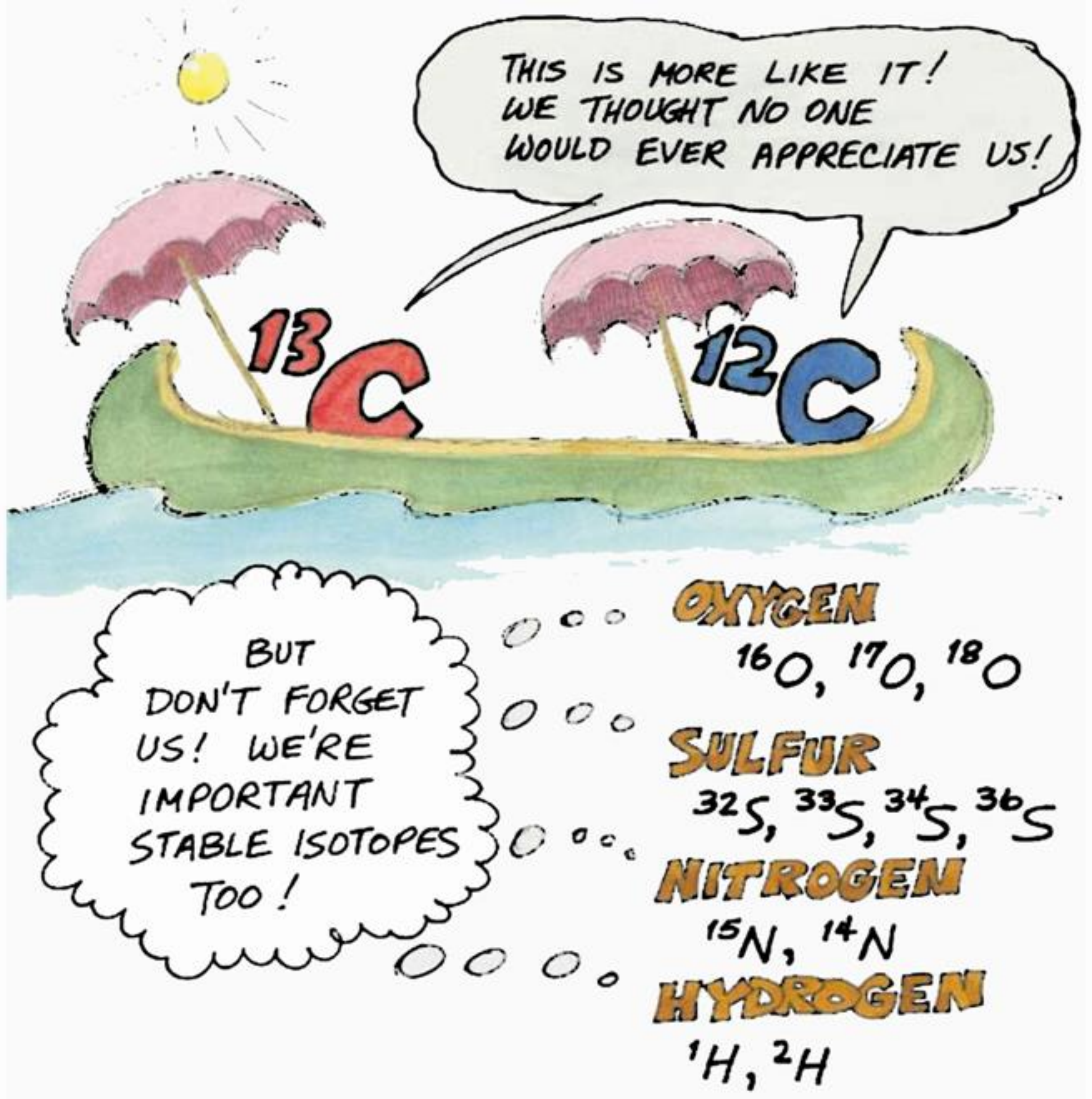
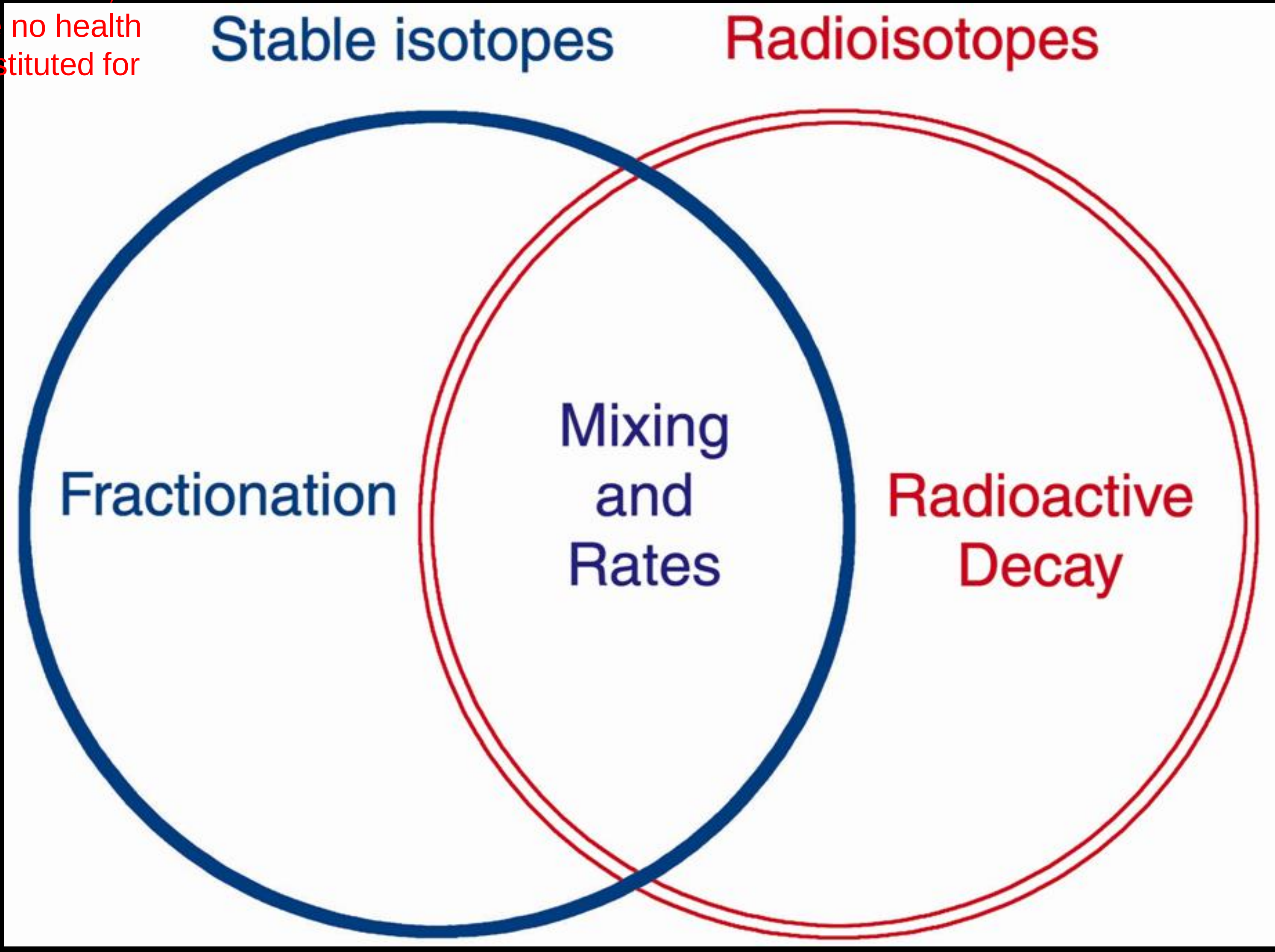


Fig. 1.5. Stable isotopes are especially valuable for studying the origins and cycling of organic matter in the biosphere. Ecologists also use radioisotopes (especially $^{3}H$, $^{14}C$, and $^{32}P$) to study cycling rates and to determine ages. Where possible, stable isotopes that pose no health risk are increasingly substituted for the radioisotopes.



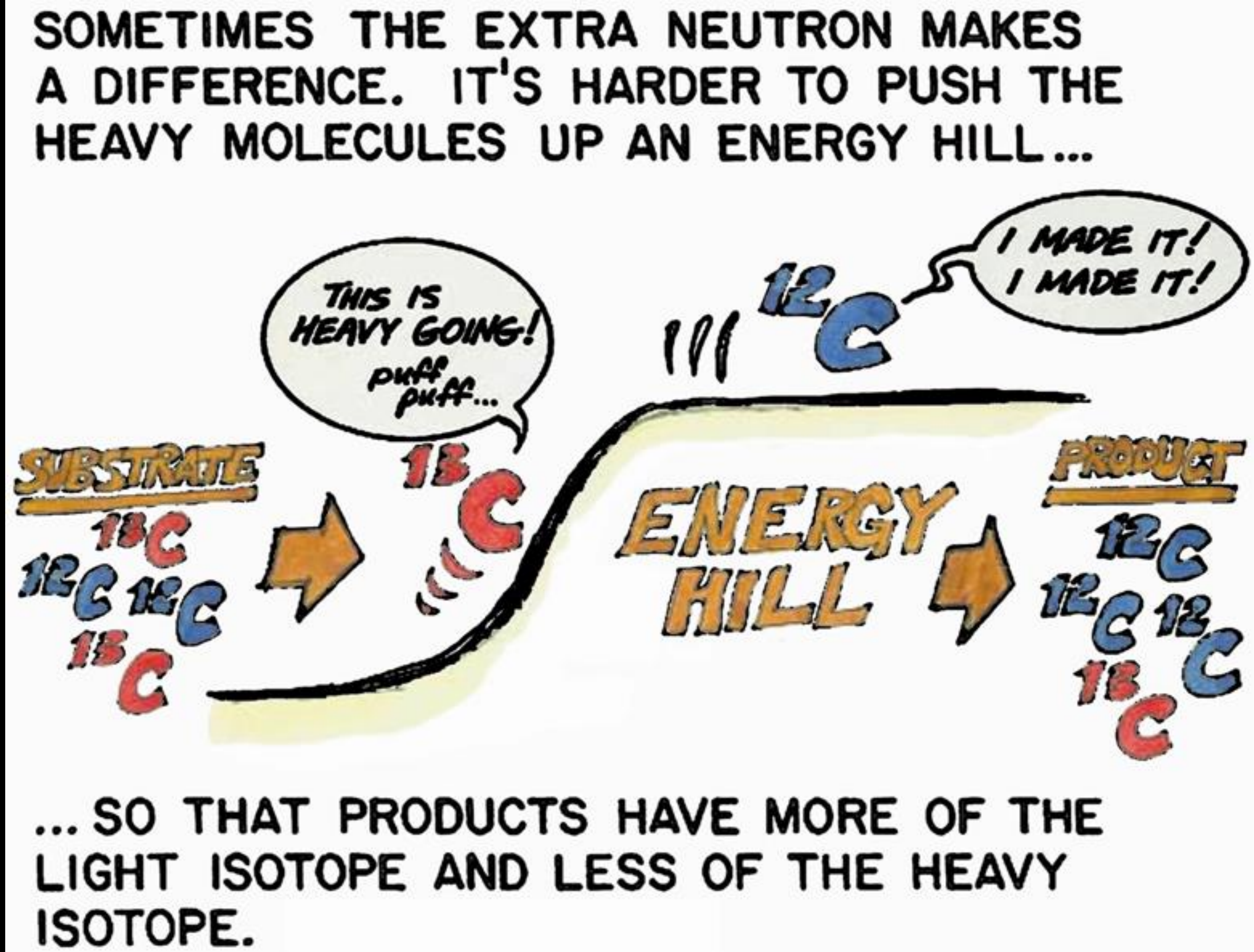



Fig. 1.6. The extra neutron does make a very slight difference in some reactions; having an extra neutron usually results in slower reactions. This reaction difference is fractionation.

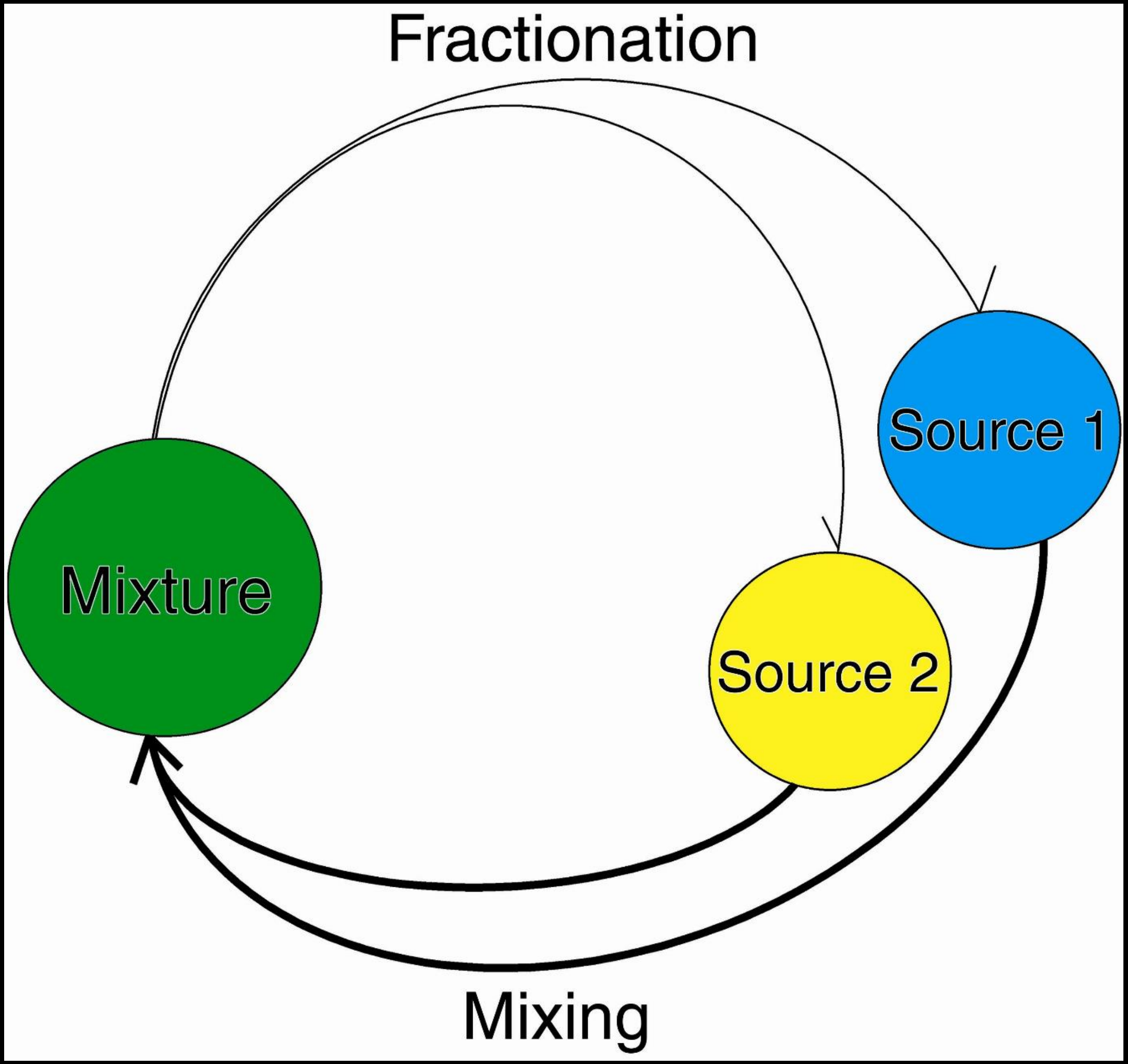



Fig. 1.9. Isotopes cycle via fractionation and mixing, with fractionation splitting apart mixtures to form source materials. These sources recombine via mixing to complete the cycle.

# Stable isotope

# What Stable isotope can do?

*地质*

*(古环境) 海洋*
*水文地理*

*大气*
*气候变化*

*土壤*
*农业环境*

*生态*
*生物地球化学*

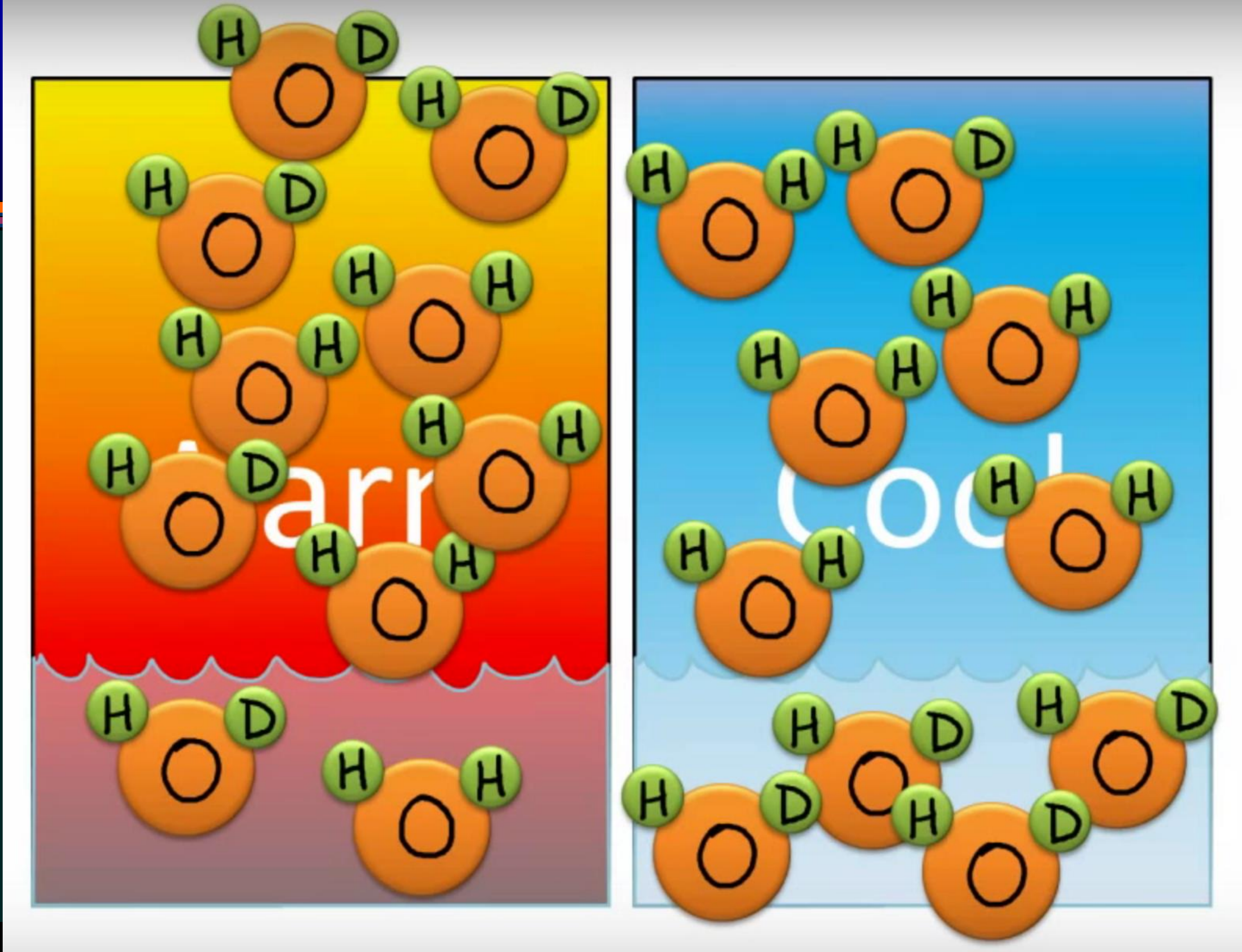
*食品掺假*

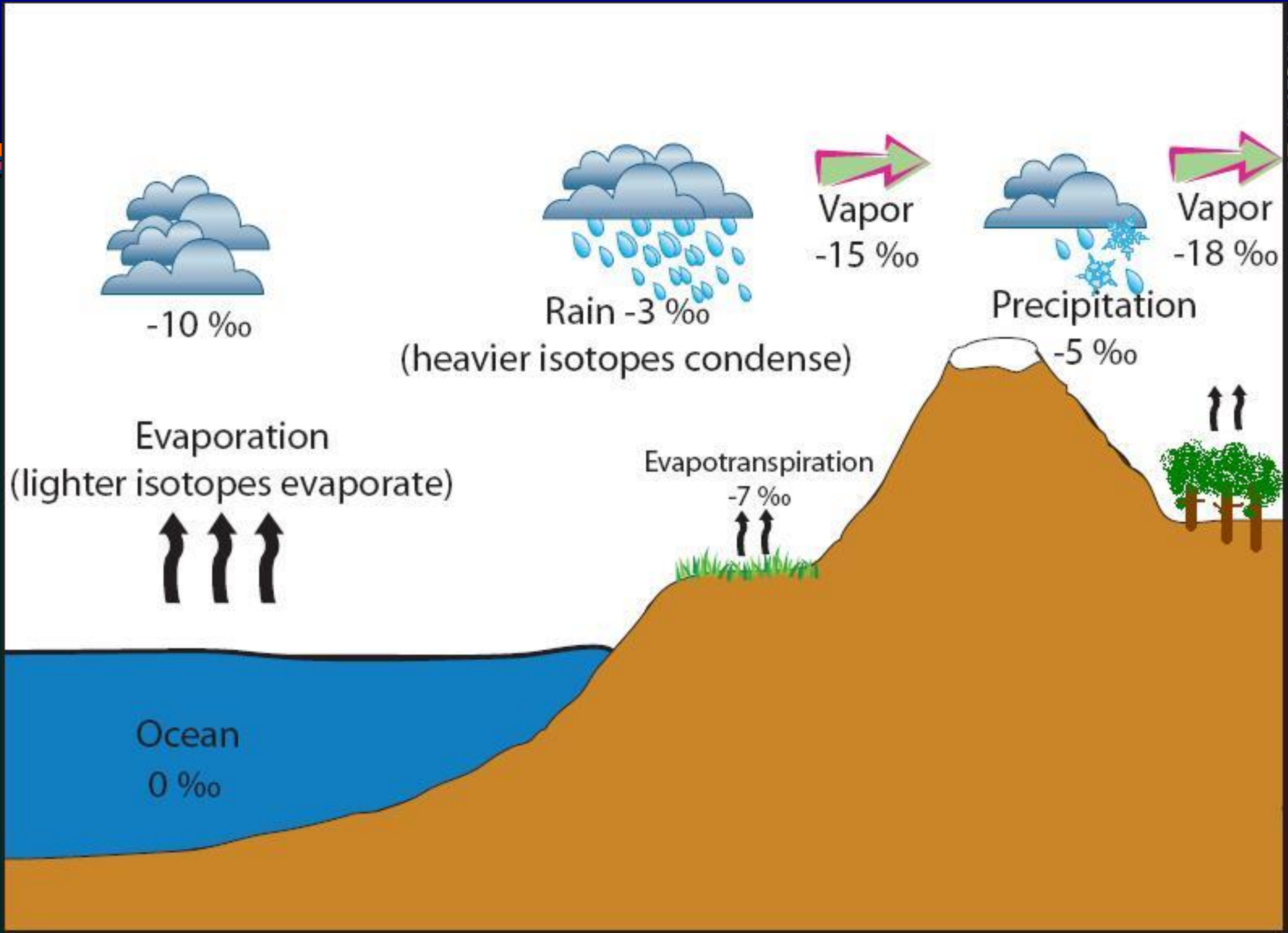
*兴奋剂检测*


*法医鉴定*

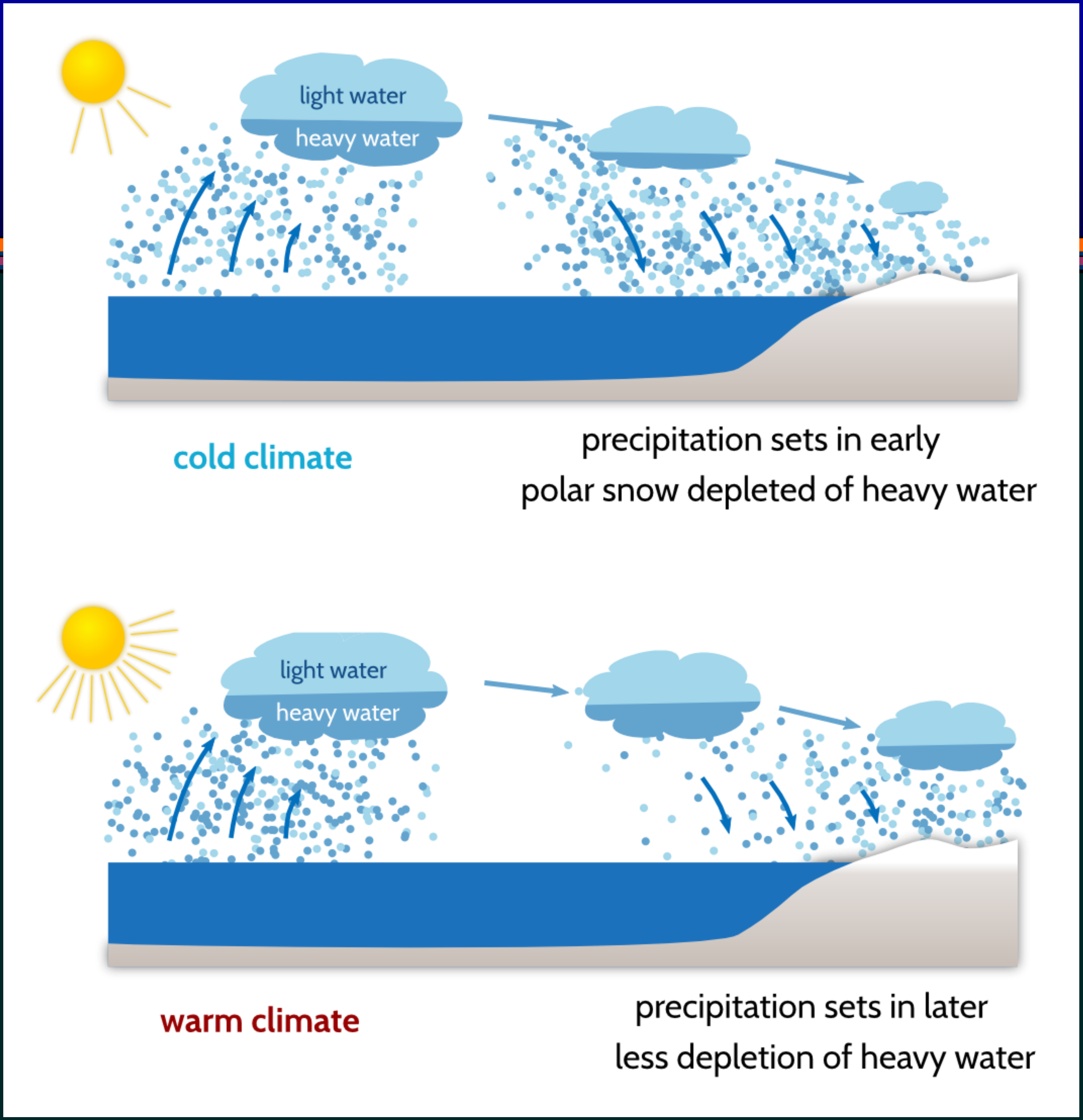
*临床生物学*

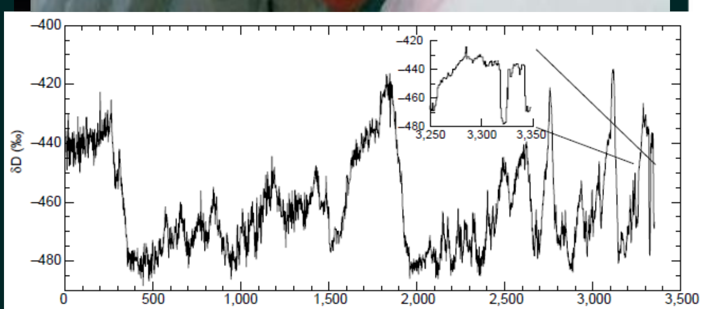
*石油化工*

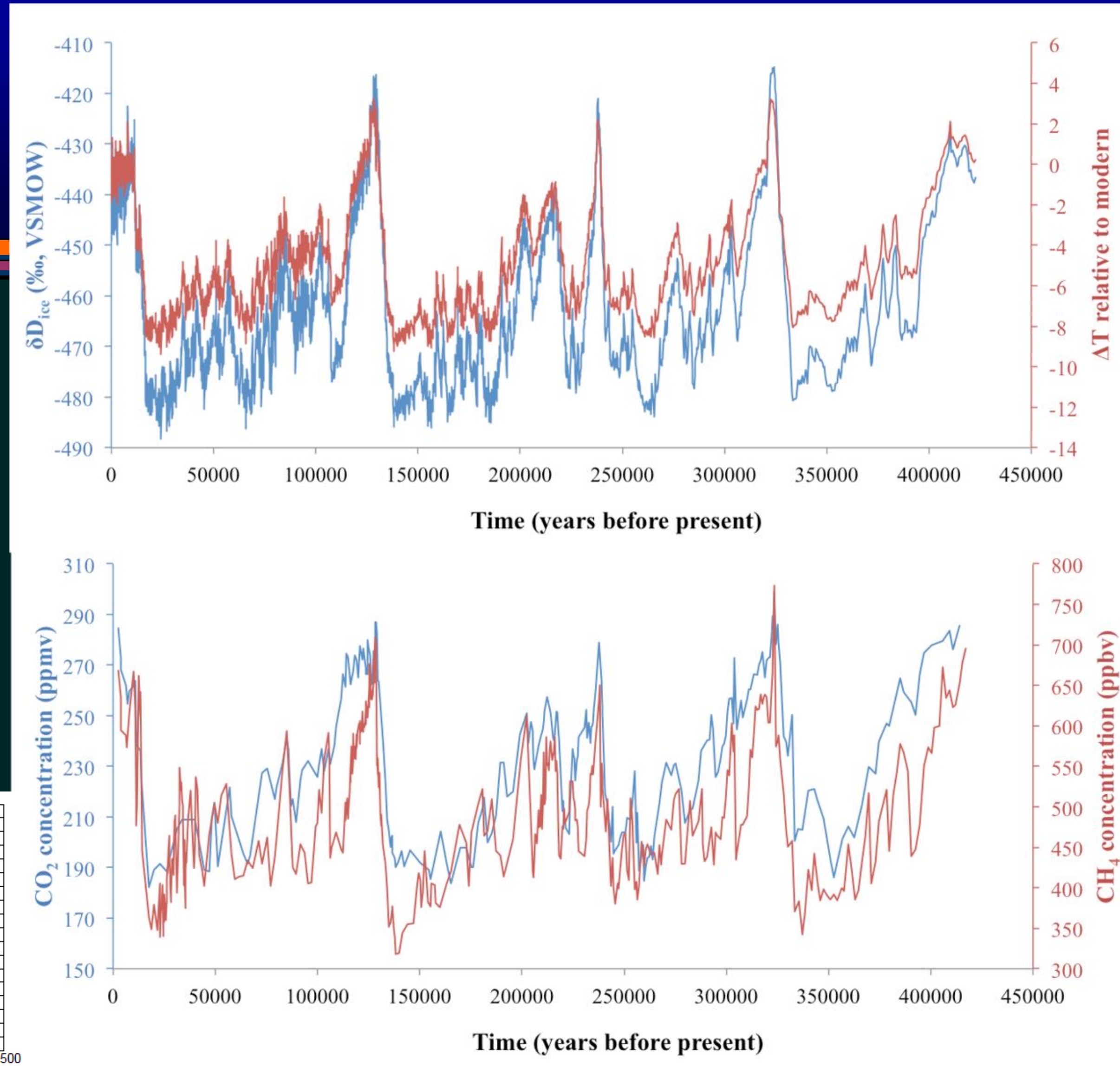




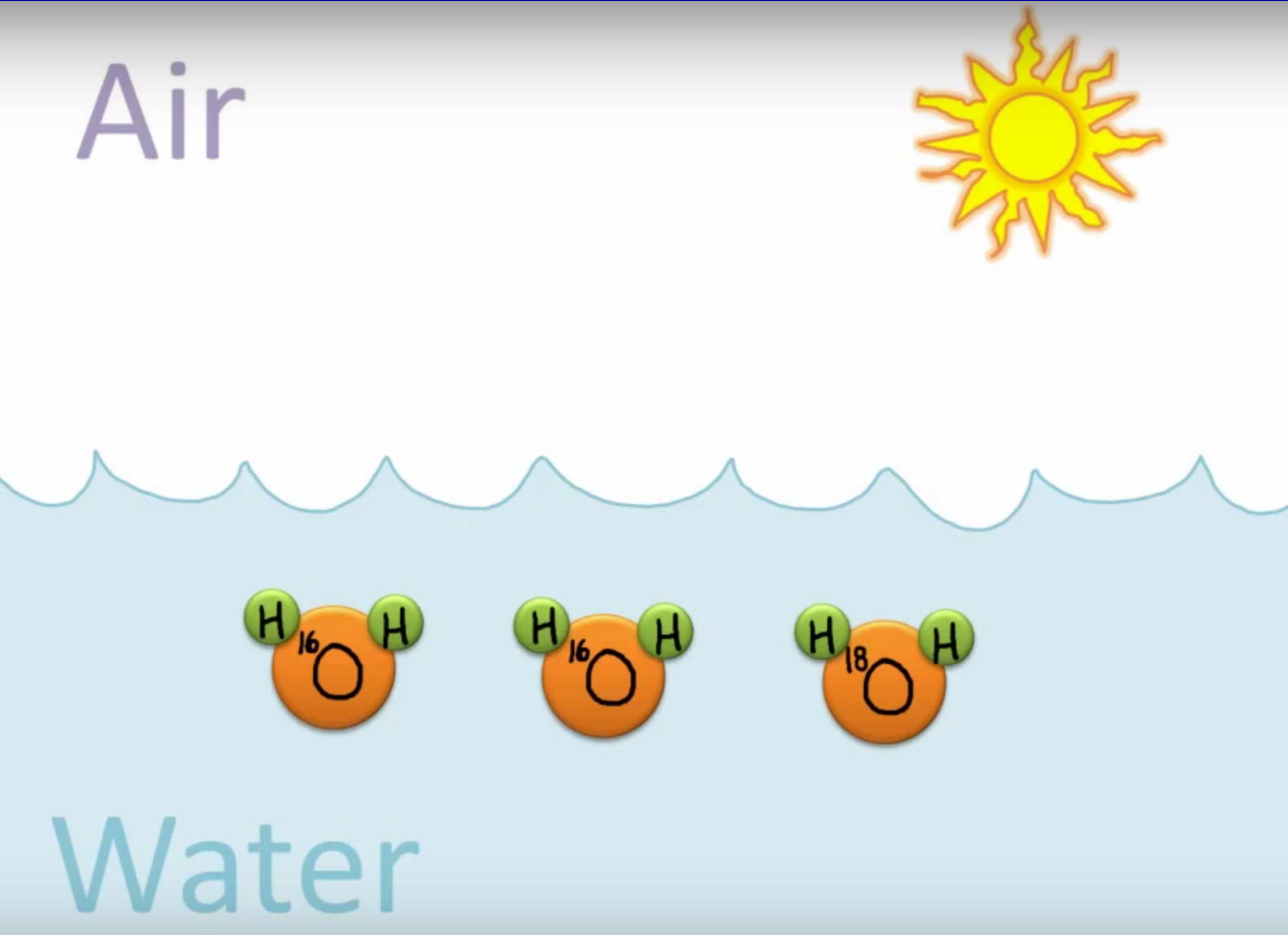
-10 ‰
Rain -3 ‰
(heavier isotopes condense)
Vapor
-15 ‰
Precipitation
-5 ‰
Vapor
-18 ‰
Evaporation
(lighter isotopes evaporate)
Evapotranspiration
-7 ‰
Ocean
0 ‰

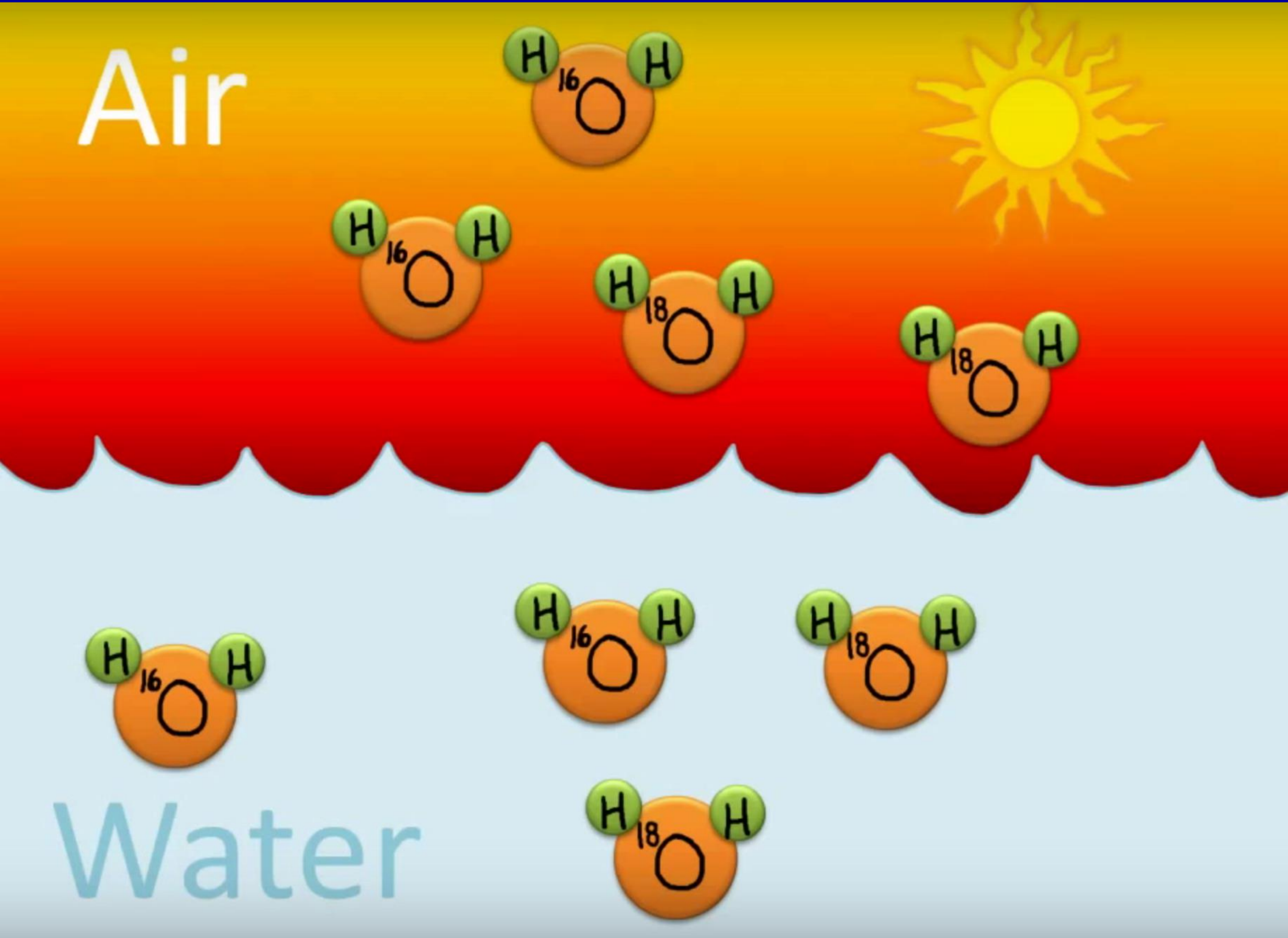

light water
heavy water
cold climate
precipitation sets in early
polar snow depleted of heavy water
light water
heavy water
warm climate
precipitation sets in later
less depletion of heavy water

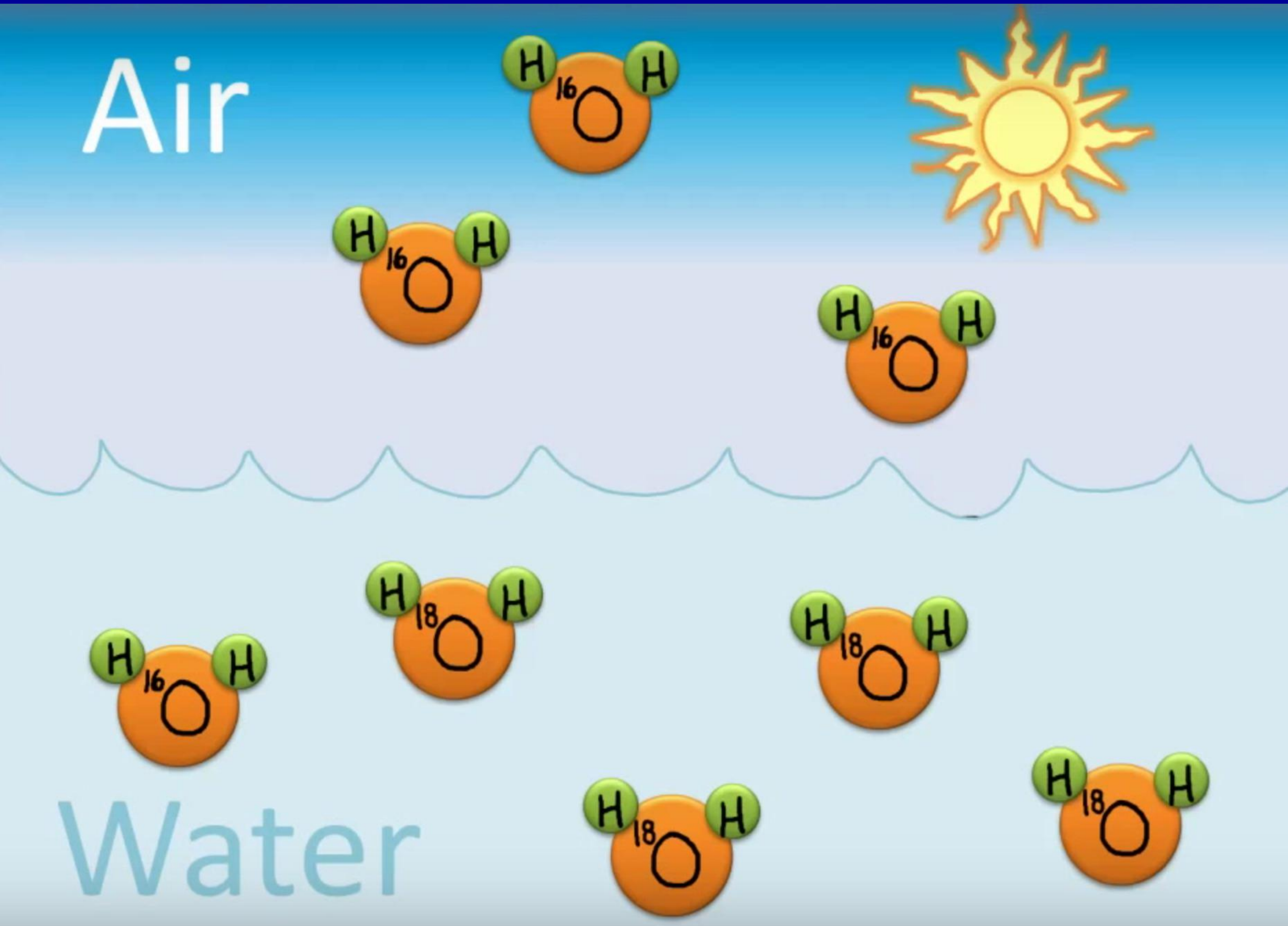



The Vostok ice core record of hydrogen isotopes, temperature and greenhouse gas concentrations in the last 420,000 years (*Petit et al., 1999 in Nature*)


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


Air
Water


Air
Water
H
16O
18O

# $\delta^{18}O$ ‰

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

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

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

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

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

# $\delta^{18}O$ ‰

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

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

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

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

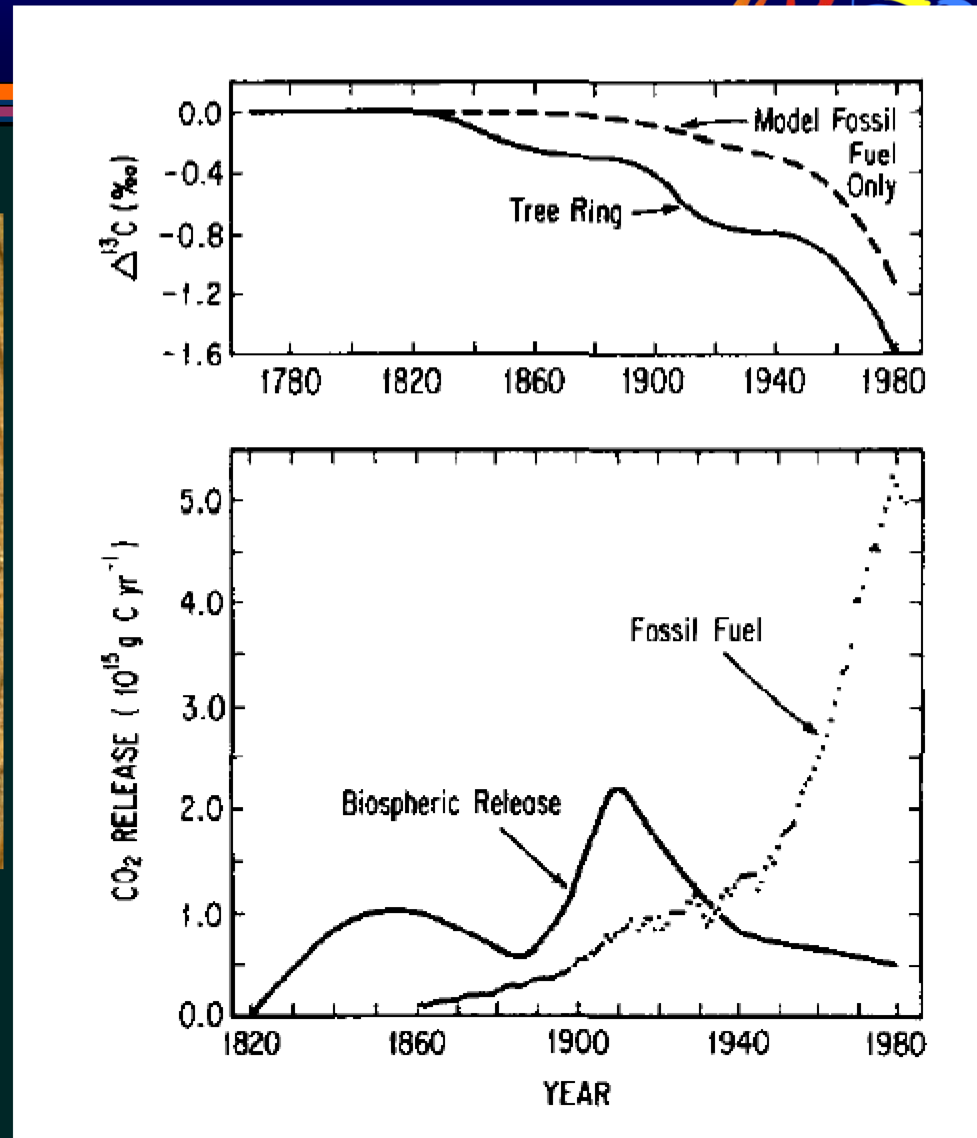
$\uparrow \delta^{18}O = \uparrow {}^{18}O/^{16}O = \downarrow T$

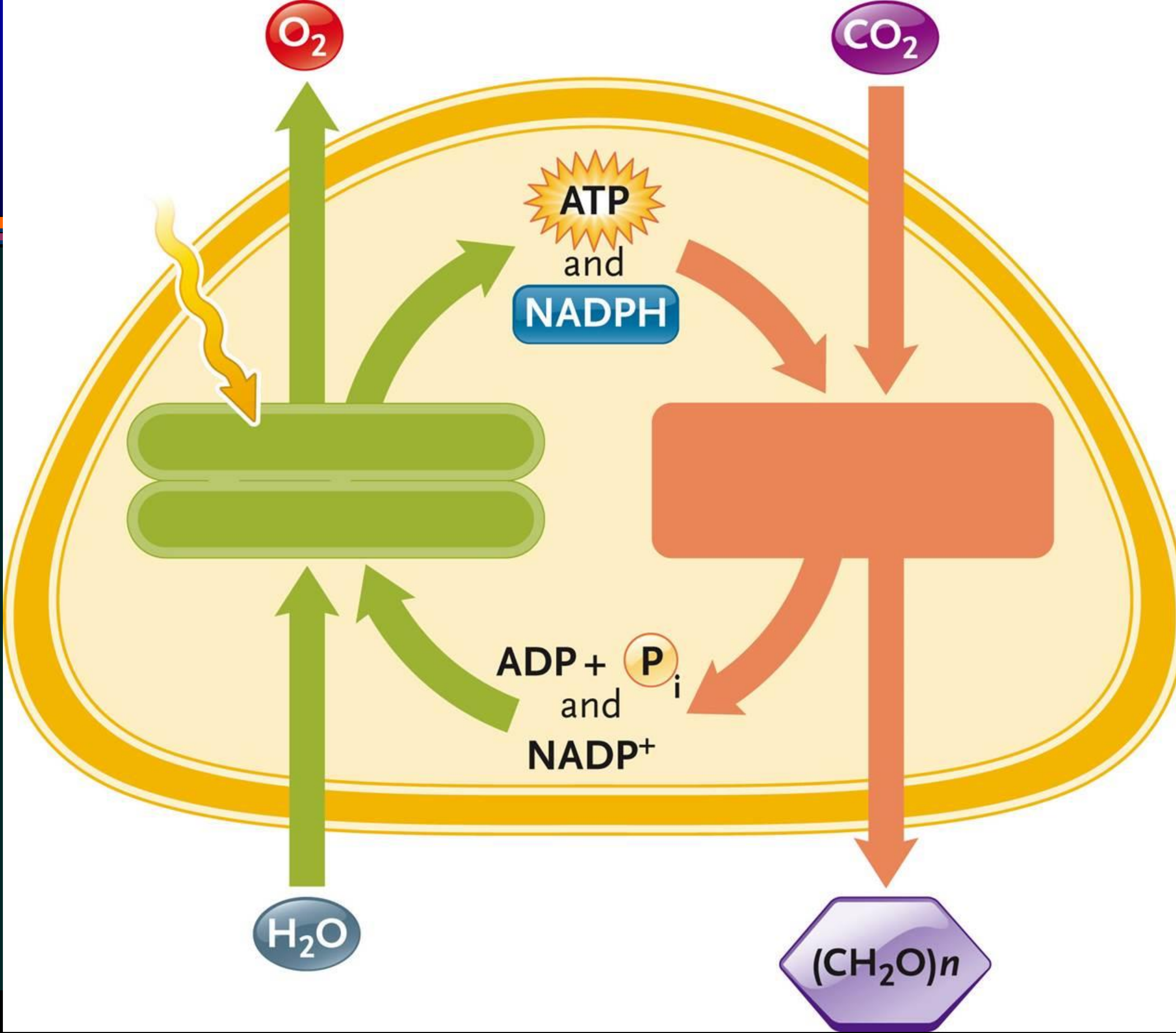
# $\delta^{13}C$ ‰

$\delta^{13}C = (((^{13}C/^{12}C \text{ of a sample})/(^{13}C/^{12}C \text{ of a standard}))-1)\times1000$

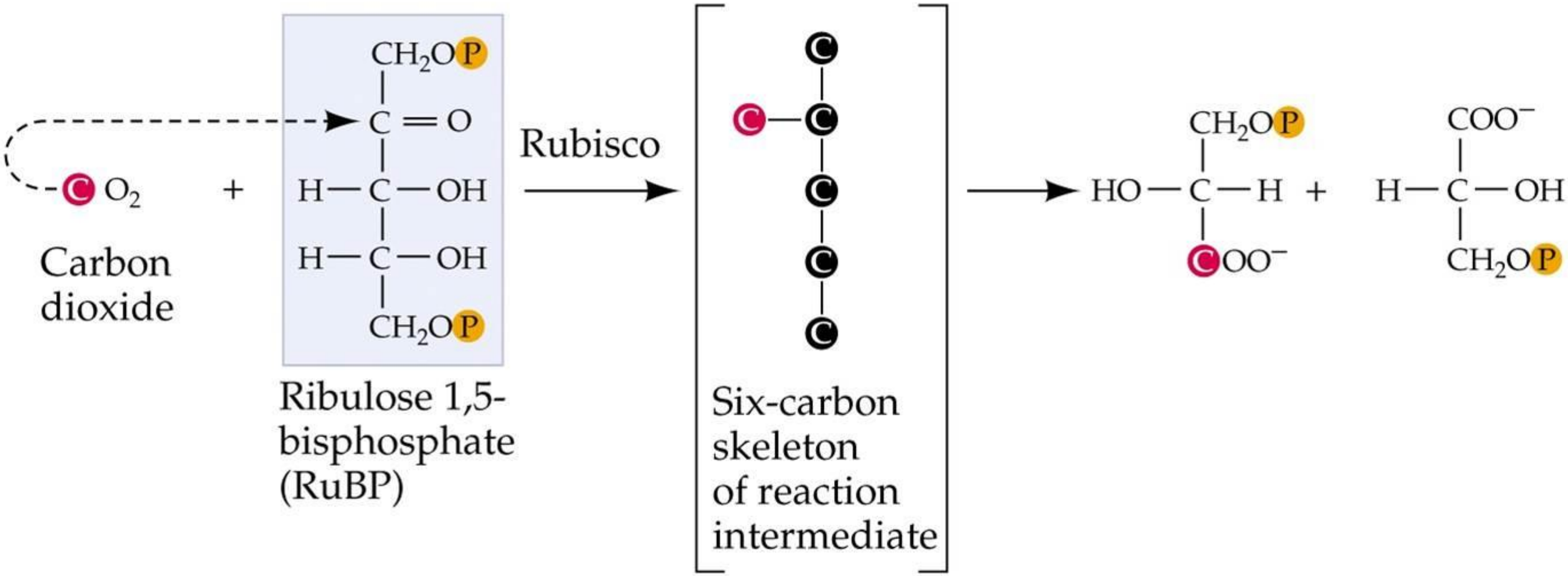
$\downarrow \delta^{13}C = \downarrow {^{13}C}/{^{12}C} = \uparrow CO_2$


Images/Universal Images Group


0.0
-0.4
-0.8
-1.2
-1.6
Δ13C (‰)
Model Fossil Fuel Only
Tree Ring
1780
1820
1860
1900
1940
1980
5.0
4.0
3.0
2.0
1.0
0.0
CO2 RELEASE (10^15 g C yr^-1)
Fossil Fuel
Biospheric Release
1820
1860
1900
1940
1980
YEAR


$O_2$
$CO_2$
ATP
and
NADPH
ADP + P i
and
NADP+
$H_2O$
$(CH_2O)n$

# C3 vs C4

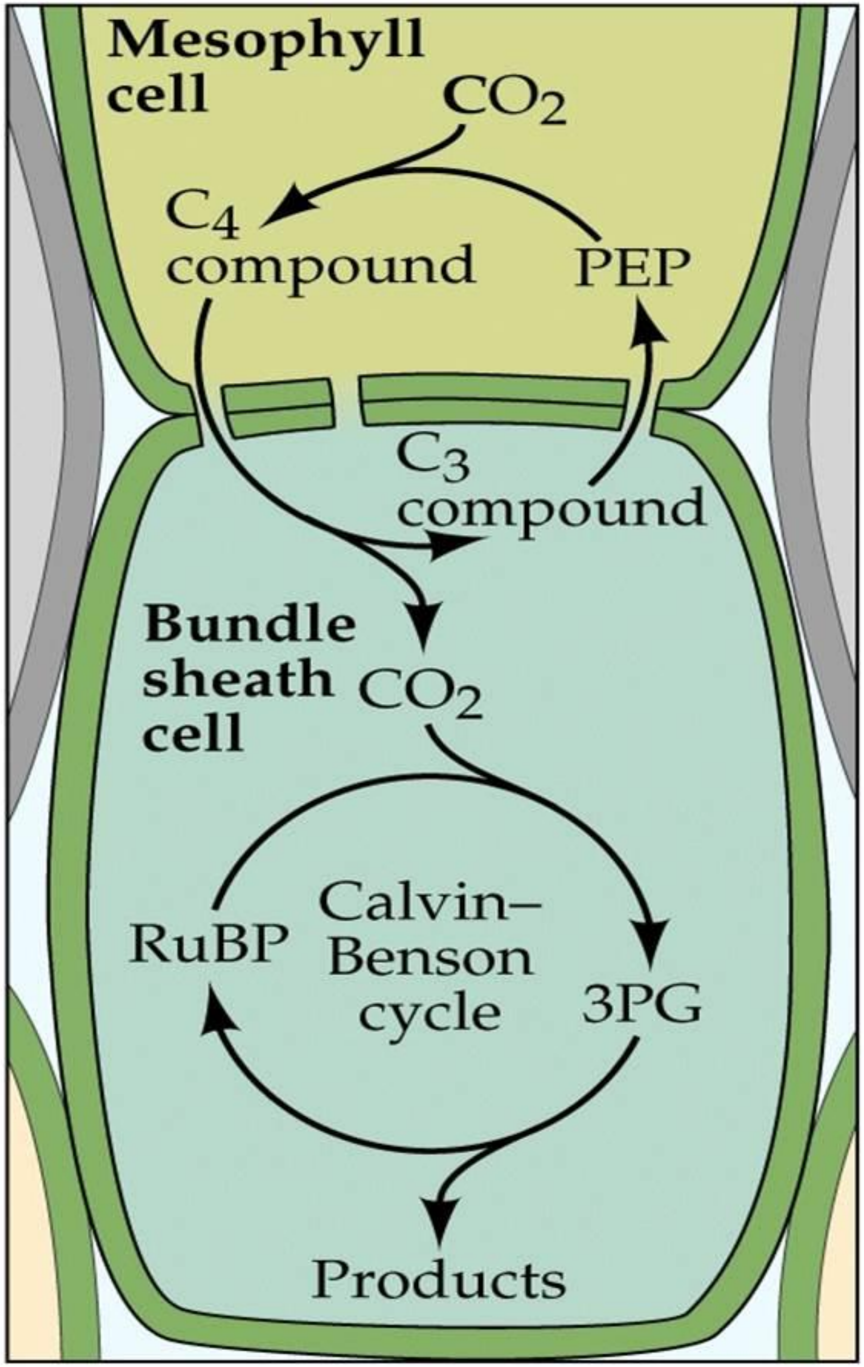


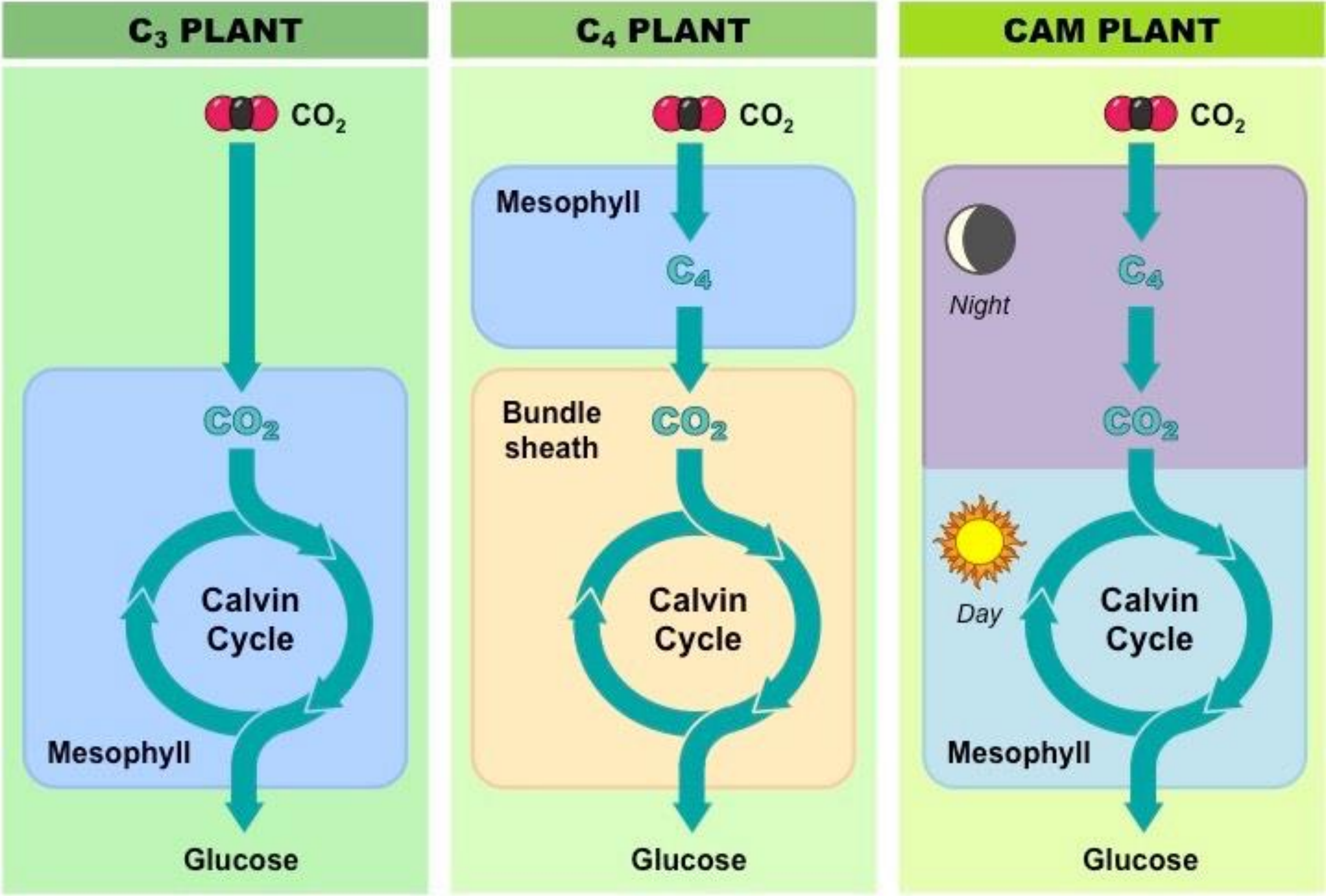



在这个反应中，二氧化碳生成两个三碳的化合物，这就是C3植物的由来。

# C3 vs C4

如图所示，在上面的细胞内，二氧化碳首先被转变为一个四碳的化合物（C4名称的由来），这个化合物被转运到下面的细胞内，再施放二氧化碳，加入到开尔文循环中。



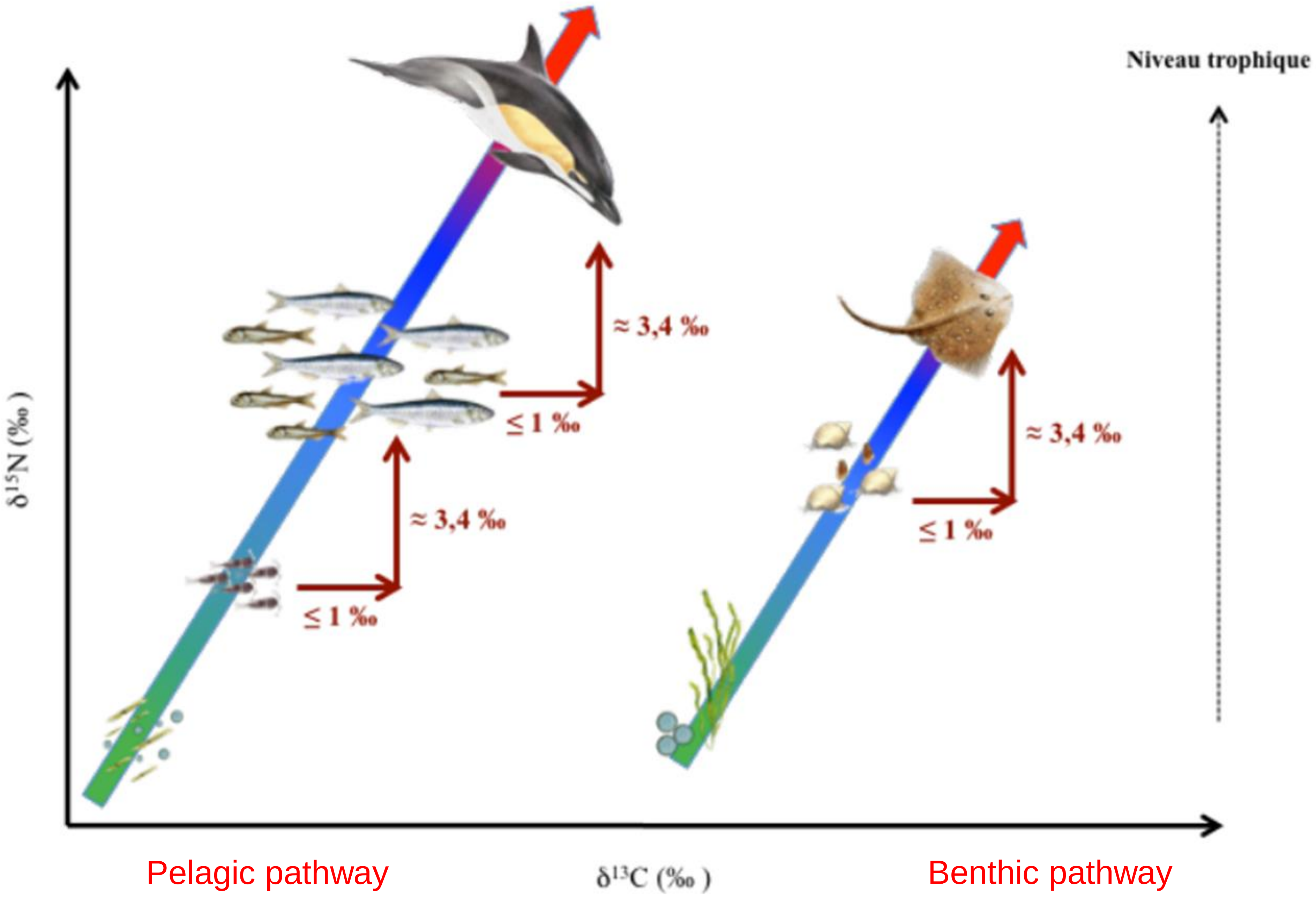

C3 PLANT
C4 PLANT
CAM PLANT
CO2
CO2
CO2
Mesophyll
C4
CO2
Calvin Cycle
Mesophyll
Glucose
Bundle sheath
CO2
Calvin Cycle
Glucose
Night
C4
CO2
Day
Calvin Cycle
Mesophyll
Glucose

# $C_3$ vs $C_4$

- $C_3$植物利用1,5-磷酸核酮糖羧化酶（Rubisco）固定$CO_2$，形成了两个三碳化合物（3-磷酸甘油酸），参与有机物合成。大气中的二氧化碳的碳同位素的值为-8‰，Rubisco酶在固定二氧化碳时会优先选择轻的同位素，即$^{12}C$，从而引起同位素的分馏，$C_3$植物的碳同位素的值的范围是（-34‰~-22‰）。
- $C_4$植物利用磷酸烯醇式丙酮酸羧化酶（PEPC）固定$HCO_3^-$，生成磷酸和草酰乙酸，在不同酶的作用下，草酰乙酸生成了不同的四碳化合物（苹果酸或天冬氨酸），$HCO_3^-$的碳同位素的值为+7‰~+11‰，PEPC固定$^{12}C$和$^{13}C$的速率是差不多的，所以$C_4$植物的碳同位素值的范围是（-17‰～-11‰）。

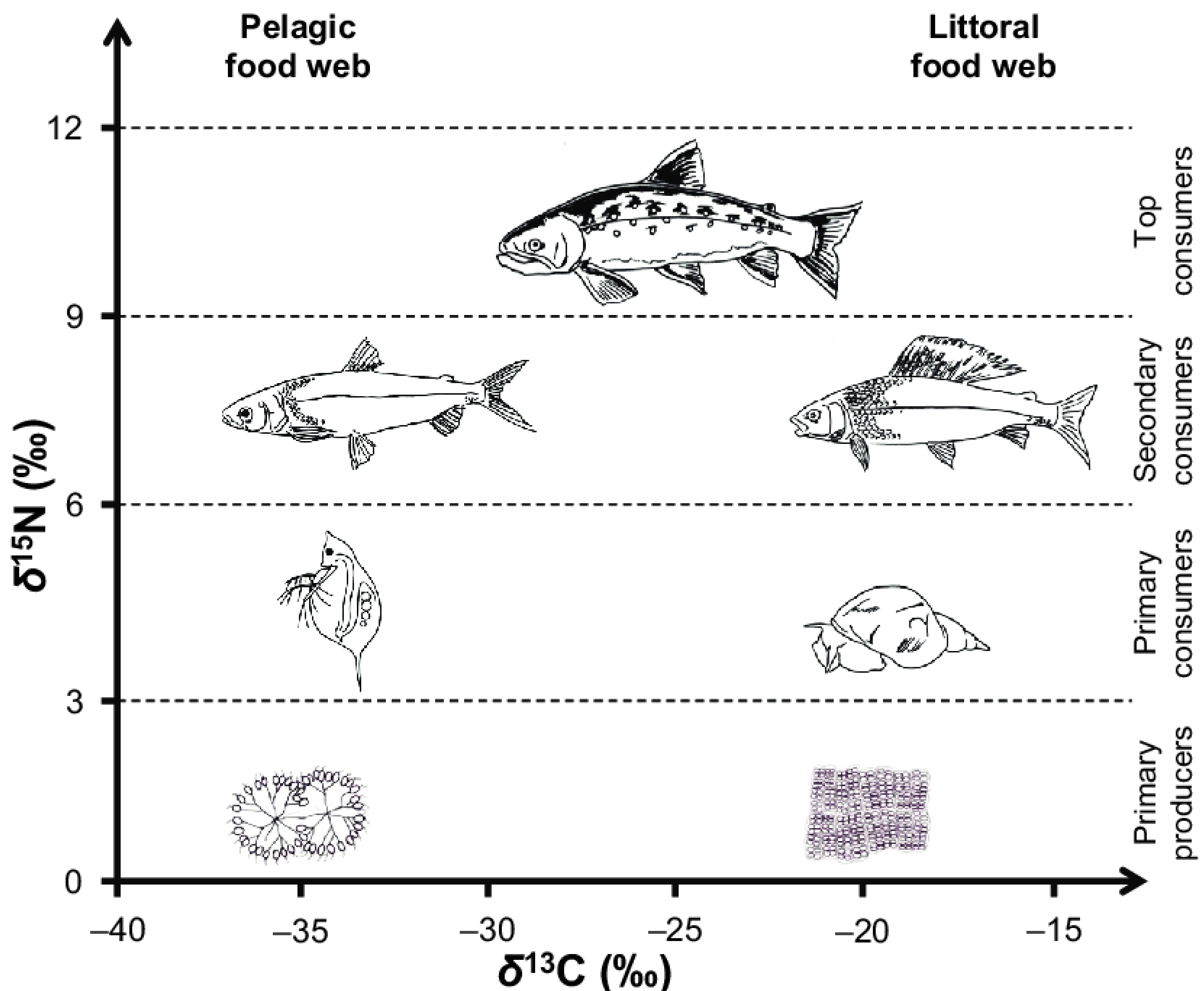
# General Introduction

- It focuses on fundamental principles of mixing and fractionation that govern isotope circulation in the biosphere, and aims to help you understand and use these principles.




Pelagic pathway

Benthic pathway


Pelagic food web
Littoral food web
12
9
6
3
0
δ15N (‰)
–40
–35
–30
–25
–20
–15
δ13C (‰)
Top consumers
Secondary consumers
Primary consumers
Primary producers

# Heithaus et al., 2013

Vol. 481: 225–237, 2013
doi: 10.3354/meps10235

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 7

MARINE ECOLOGY PROGRESS SERIES

## Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem

Michael R. Heithaus[1,*,**], Jeremy J. Vaudo[1,**], Sina Kreicker[2], Craig A. Layman[1], Michael Krützen[2], Derek A. Burkholder[1], Kirk Gastrich[1], Cindy Bessey[1], Robin Sarabia[1], Kathryn Cameron[1], Aaron Wirsing[3], Jordan A. Thomson[1], Meagan M. Dunphy-Daly[4]

[1]Marine Sciences Program, School of Environment, Arts and Society, Florida International University, 3000 NE 151st St., North Miami, Florida 33181, USA

[2]Evolutionary Genetics Group, Anthropological Institute & Museum, University of Zurich, Winterthurerstr. 190, 8057 Zurich, Switzerland

[3]School of Environmental and Forest Sciences, Box 352100, University of Washington, Seattle, Washington 98195, USA

[4]Duke University Marine Laboratory, Nicholas School of the Environment, 135 Duke Marine Lab Road, Beaufort, North Carolina 28516, USA

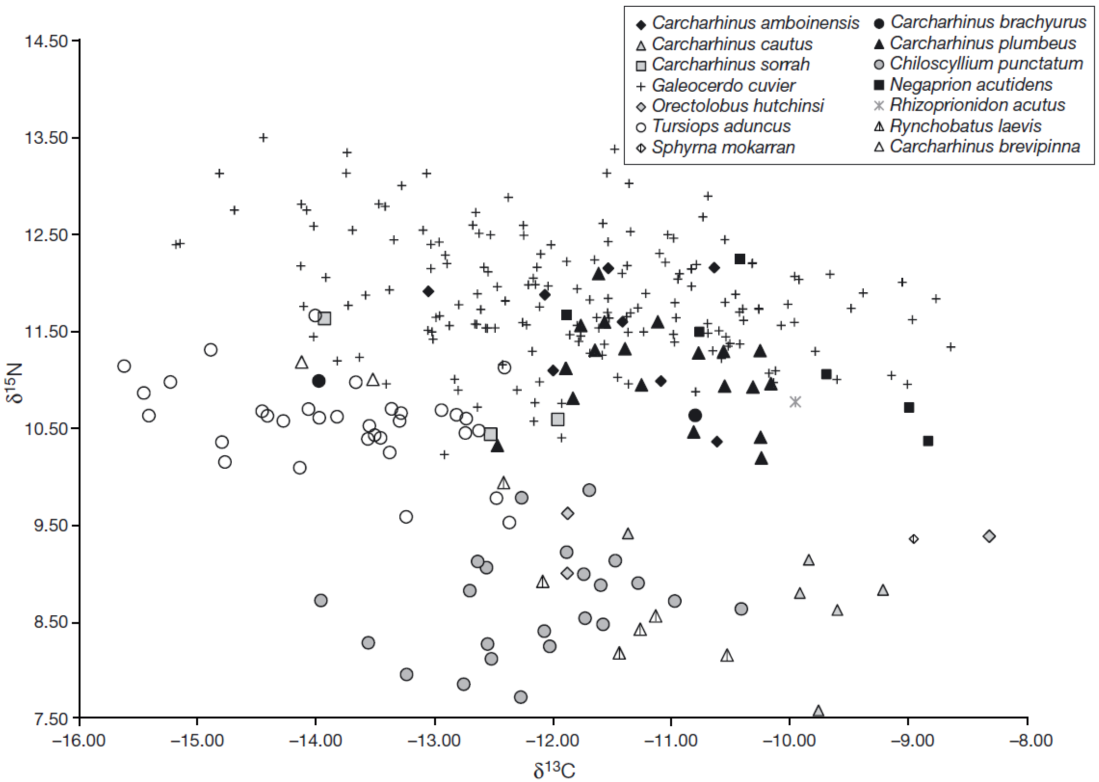



Fig. 1. Isotope values of all individual sharks and dolphins sampled in the Eastern Gulf of Shark Bay, Australia

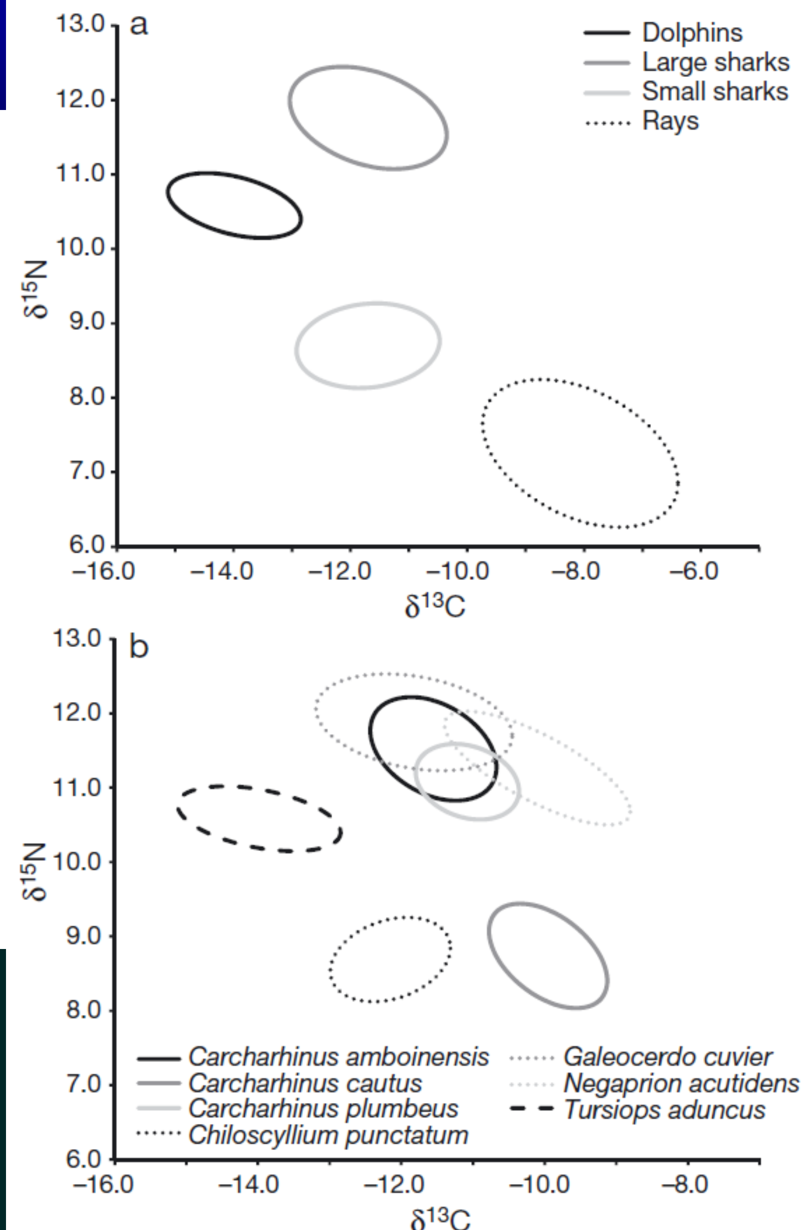



Fig. 3. Standard ellipse areas corrected for sample size (SEAc) of large predators based on (a) guild-level and (b) species-level analyses

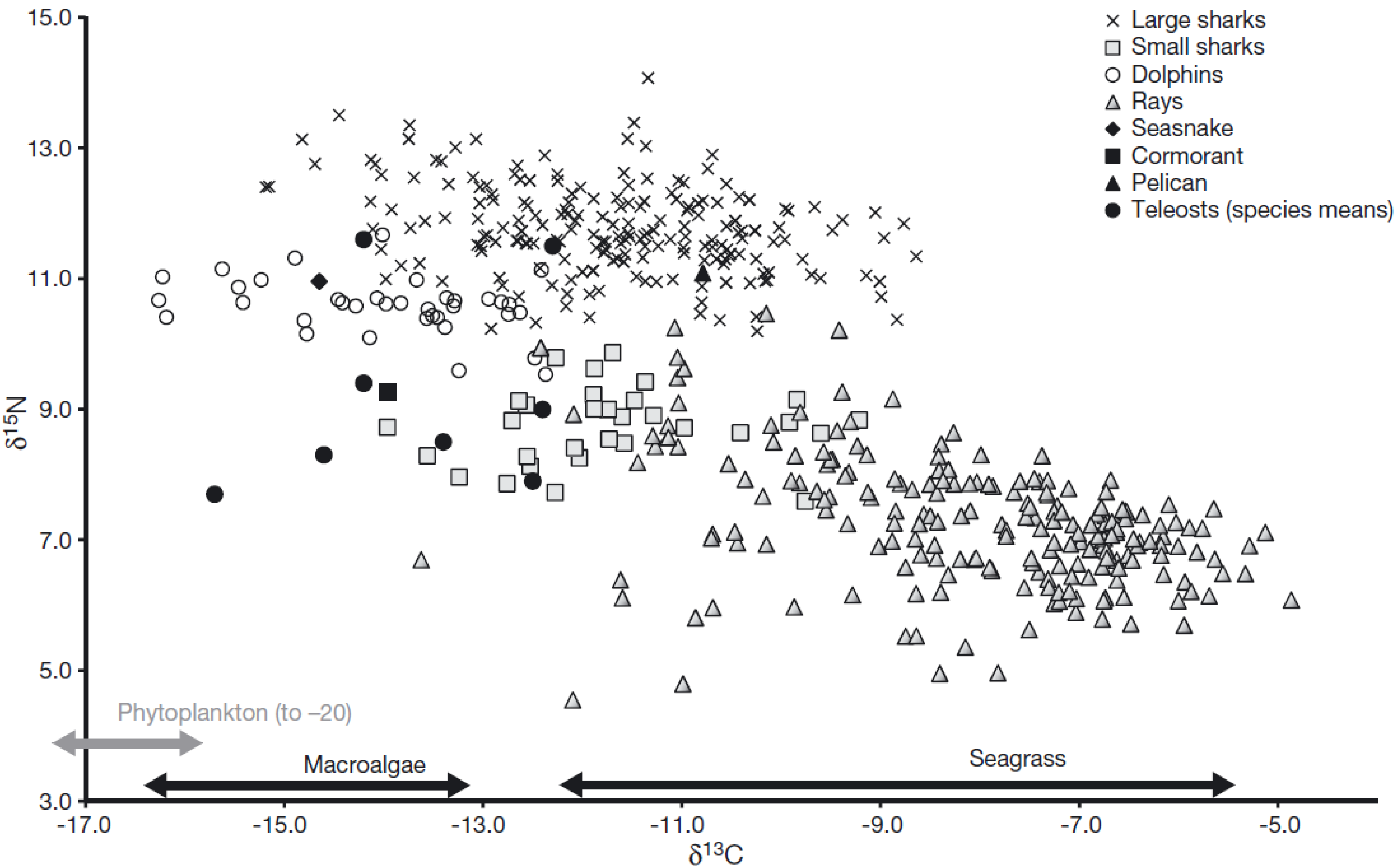



Fig. 5. Isotopic values of large predators (individual values) and representative teleosts (species means) collected from the Eastern Gulf of Shark Bay. Ranges of $\delta^{13}C$ for seagrasses, macroalgae, and plankton (based on $\delta^{13}C$ of filter feeders) are given along the $\delta^{13}C$ axis (see Burkholder et al. 2011). Only individuals of species included in analyses are given for the large predator groups

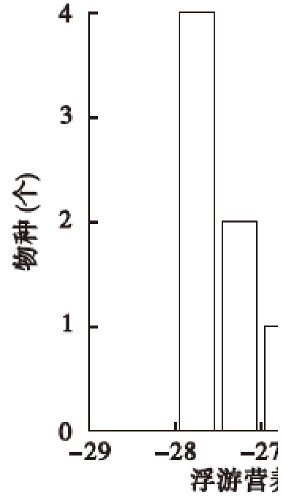



图 2　东太湖主要物种

Fig. 2　$\delta^{13}$C freque

Lake Taihu

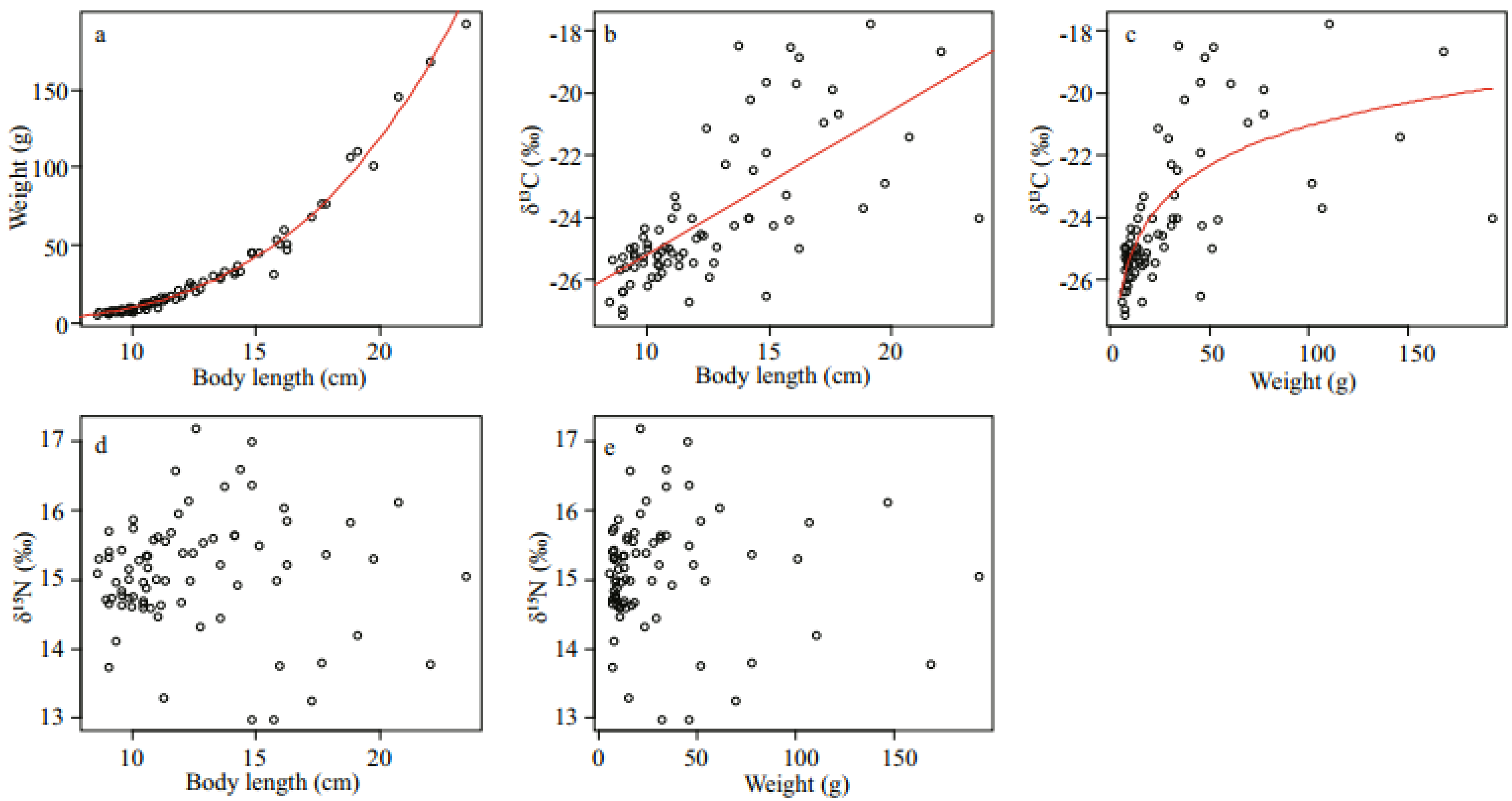



**Fig.2 Relationship between *Cultrichthys erythropterus* weight and standard length (a), muscle $\delta^{13}$C and standard length and weight (b, c), and muscle $\delta^{15}$N and body length and weight (d, e) in East Lake Taihu**

Red lines represented the significant relationships.

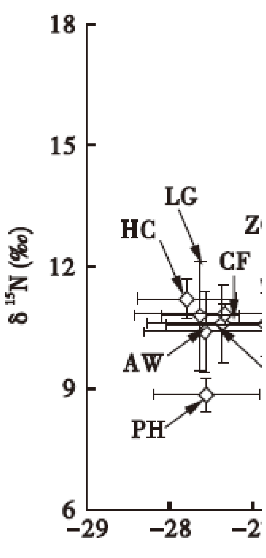



图 3　东太湖食物网结构

**Fig. 3　Food web structure of the East Lake Taihu**

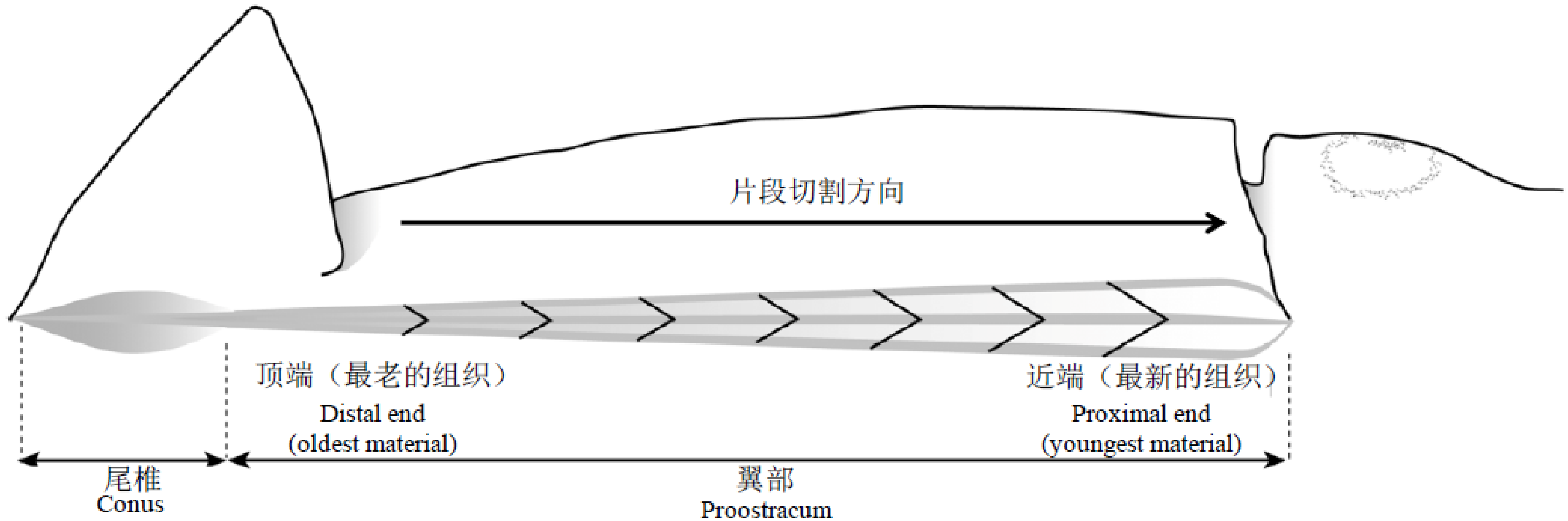
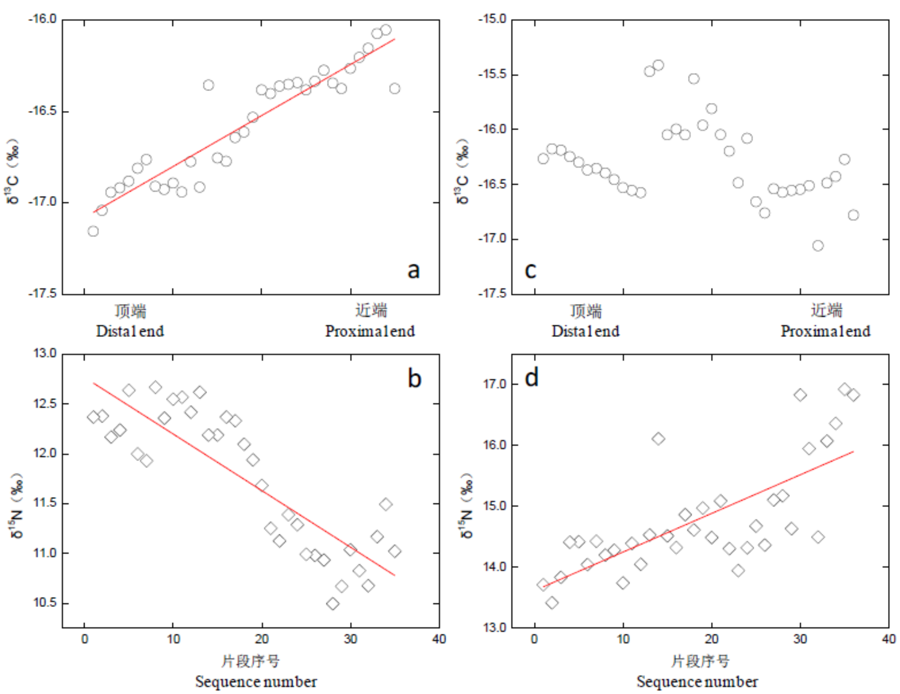



图 1.茎柔鱼内壳横截图

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

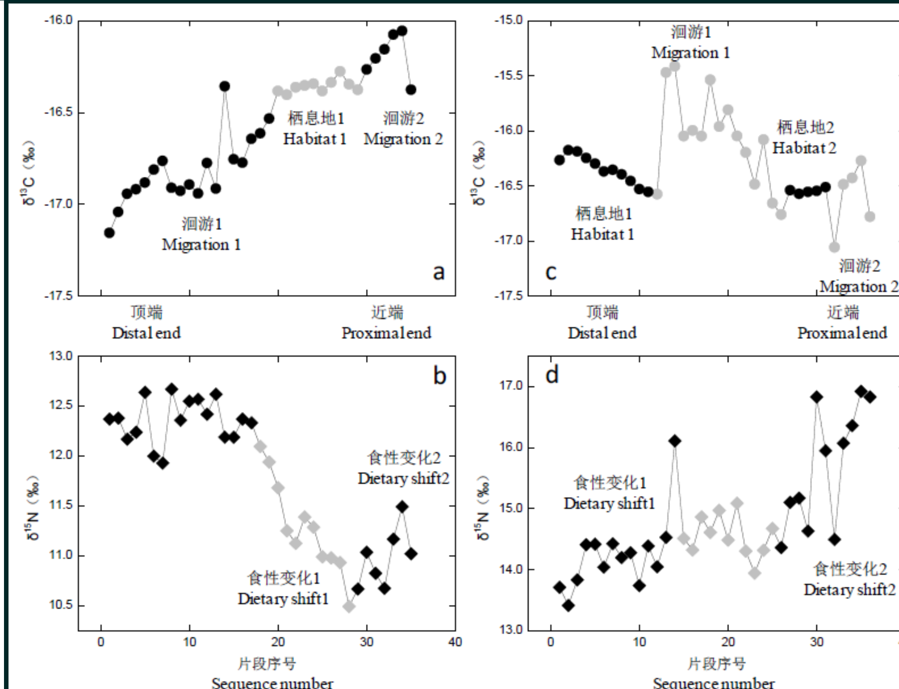
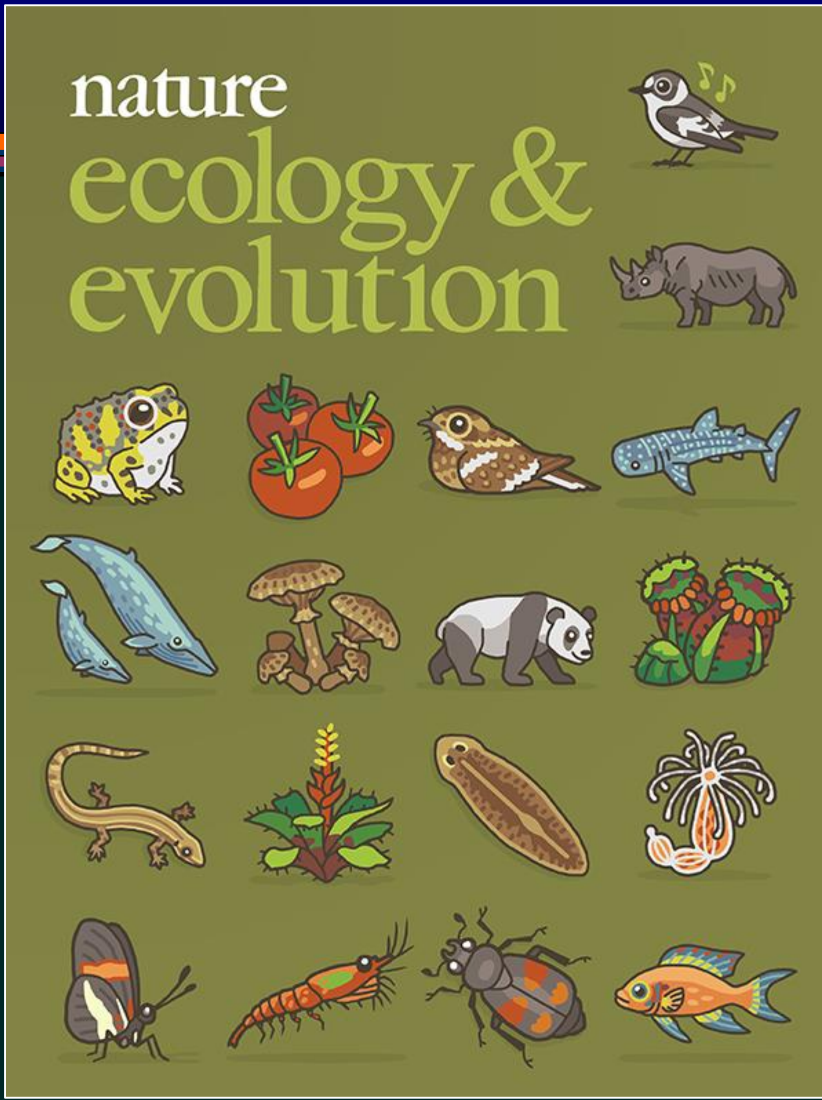



图 3 茎柔鱼 A（图 a, b）茎柔鱼 B (图 c, d) 生活史中的洄游和栖息地变化






nature
ecology & evolution



Article

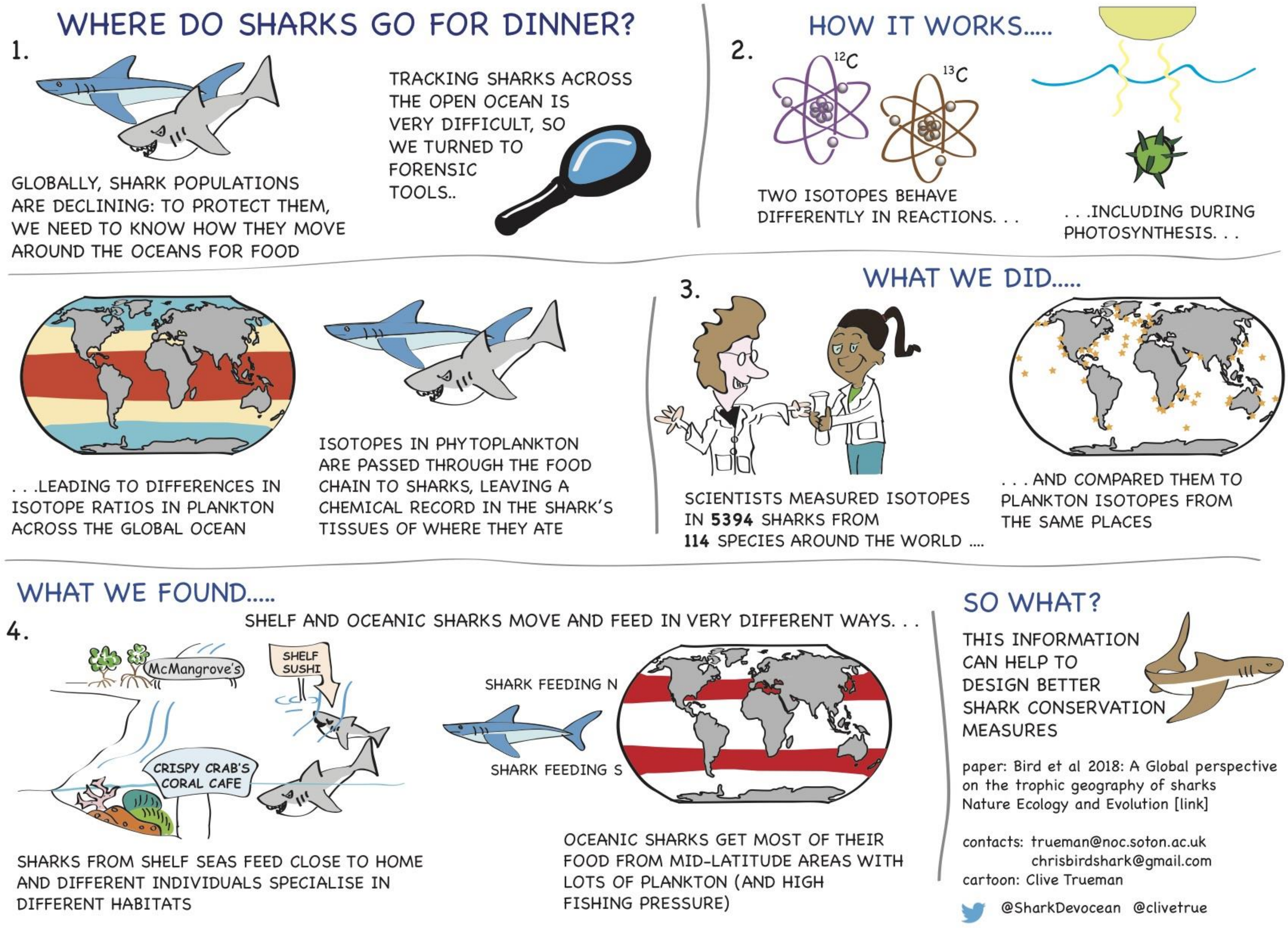
# A global perspective on the trophic geography of sharks

Christopher S. Bird, Ana Veríssimo, Sarah Magozzi, Kátya G. Abrantes, Alex Aguilar, Hassan Al-Reasi, Adam Barnett, Dana M. Bethea, Gérard Biais, Asuncion Borrell, Marc Bouchoucha, Mariah Boyle, Edward J. Brooks, Juerg Brunnschweiler, Paco Bustamante, Aaron Carlisle, Diana Catarino, Stéphane Caut, Yves Cherel, Tiphaine Chouvelon, Diana Churchill, Javier Ciancio, Julien Claes, Ana Colaço, Dean L. Courtney, Pierre Cresson, Ryan Daly, Leigh de Necker, Tetsuya Endo, Ivone Figueiredo, Ashley J. Frisch, Joan Holst Hansen, Michael Heithaus, Nigel E. Hussey, Johannes Iitembu, Francis Juanes, Michael J. Kinney, Jeremy J. Kiszka, Sebastian A. Klarian, Dorothée Kopp, Robert Leaf, Yunkai Li, Anne Lorrain, Daniel J. Madigan, Aleksandra Maljković, Luis Malpica-Cruz, Philip Matich, Mark G. Meekan, Frédéric Ménard, Gui M. Menezes, Samantha E. M. Munroe, Michael C. Newman, Yannis P. Papastamatiou, Heidi Pethybridge, Jeffrey D. Plumlee, Carlos Polo-Silva, Katie Quaeck-Davies, Vincent Raoult, Jonathan Reum, Yassir Eden Torres-Rojas, David S. Shiffman, Oliver N. Shipley, Conrad W. Speed, Michelle D. Staudinger, Amy K. Teffer, Alexander Tilley, Maria Valls, Jeremy J. Vaudo, Tak-Cheung Wai, R. J. David Wells, Alex S. J. Wyatt, Andrew Yool & Clive N. Trueman - Show fewer authors

*Nature Ecology & Evolution* **2**, 299–305 (2018)
doi:10.1038/s41559-017-0432-z
Download Citation

Ecosystem ecology Marine biology
Stable isotope analysis

Received: 11 April 2017
Accepted: 28 November 2017
Published online: 18 January 2018


WHERE DO SHARKS GO FOR DINNER?
1.
GLOBALLY, SHARK POPULATIONS ARE DECLINING: TO PROTECT THEM, WE NEED TO KNOW HOW THEY MOVE AROUND THE OCEANS FOR FOOD
TRACKING SHARKS ACROSS THE OPEN OCEAN IS VERY DIFFICULT, SO WE TURNED TO FORENSIC TOOLS..
HOW IT WORKS.....
2.
12C
13C
TWO ISOTOPES BEHAVE DIFFERENTLY IN REACTIONS. . .
. . .INCLUDING DURING PHOTOSYNTHESIS. . .
. . .LEADING TO DIFFERENCES IN ISOTOPE RATIOS IN PLANKTON ACROSS THE GLOBAL OCEAN
ISOTOPES IN PHYTOPLANKTON ARE PASSED THROUGH THE FOOD CHAIN TO SHARKS, LEAVING A CHEMICAL RECORD IN THE SHARK'S TISSUES OF WHERE THEY ATE
WHAT WE DID.....
3.
SCIENTISTS MEASURED ISOTOPES IN 5394 SHARKS FROM 114 SPECIES AROUND THE WORLD ....
. . . AND COMPARED THEM TO PLANKTON ISOTOPES FROM THE SAME PLACES
WHAT WE FOUND.....
4.
SHELF AND OCEANIC SHARKS MOVE AND FEED IN VERY DIFFERENT WAYS. . .
McMangrove's
SHELF SUSHI
CRISPY CRAB'S CORAL CAFE
SHARKS FROM SHELF SEAS FEED CLOSE TO HOME AND DIFFERENT INDIVIDUALS SPECIALISE IN DIFFERENT HABITATS
SHARK FEEDING N
SHARK FEEDING S
OCEANIC SHARKS GET MOST OF THEIR FOOD FROM MID-LATITUDE AREAS WITH LOTS OF PLANKTON (AND HIGH FISHING PRESSURE)
SO WHAT?
THIS INFORMATION CAN HELP TO DESIGN BETTER SHARK CONSERVATION MEASURES
paper: Bird et al 2018: A Global perspective on the trophic geography of sharks Nature Ecology and Evolution [link]
contacts: trueman@noc.soton.ac.uk
chrisbirdshark@gmail.com
cartoon: Clive Trueman
@SharkDevocean @clivetrue

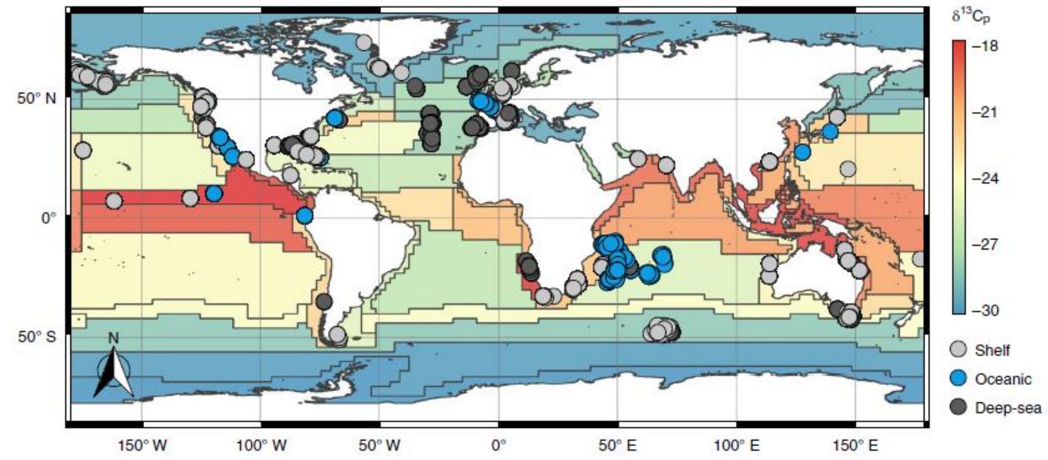



**Fig. 1 | Distribution of compiled shark data overlaid on a spatial model of annual average biomass weighted $\delta^{13}C_P$ within Longhurst biogeographic provinces from the median sampling year (2009).** The coloured points signify the habitat classification of those samples. Most studies provided one location for multiple samples.

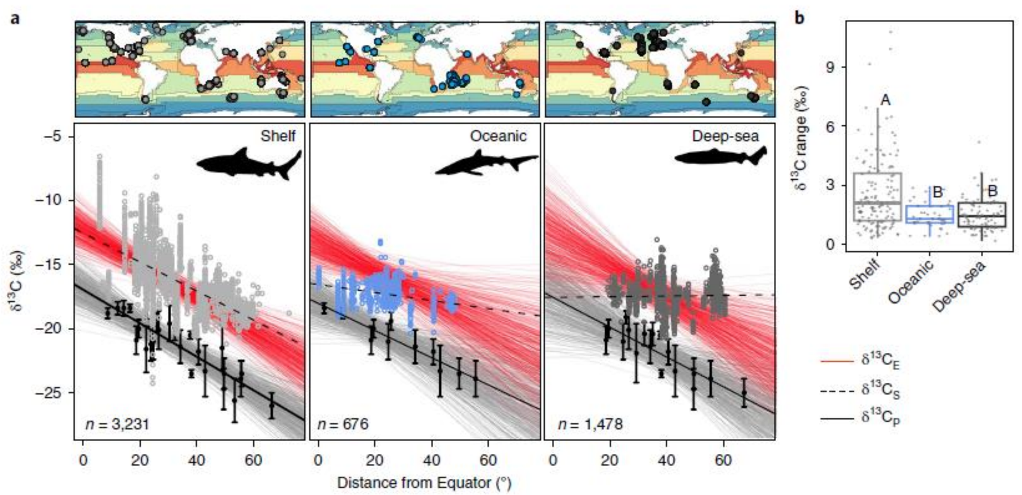



**Fig. 2 | Carbon isotope data. a**, The relationship between $\delta^{13}C_P$ from Longhurst biogeographic provinces associated with shark capture locations (solid black line) and $\delta^{13}C_S$ values (dashed black line and open circles) and latitude (bottom row). The confidence envelopes reflect 500 Monte Carlo iterations considering the variance in $\delta^{13}C_P$ values within each Longhurst biogeographic province (grey lines) and the same latitudinal trends predicted for $\delta^{13}C_S$ with an offset of 4.6‰ added corresponding to the mean offset between $\delta^{13}C_P$ and $\delta^{13}C_S$ (red lines) and to the trophic effects on $\delta^{13}C$ values. The maps provide the individual shark sample locations overlaid with the $\delta^{13}C_P$ isoscape from Fig. 1. **b**, Distribution of the observed $\delta^{13}C_S$ ranges of species-specific shark populations in each habitat. The horizontal line is the mean $\delta^{13}C_S$ range across shark populations within that habitat. Boxes contain 50% of the data and lines correspond to the 95% confidence interval. The letters signify analysis of variance, Tukey HSD results for significant difference, with the same letters representing mean values that are not significantly different from each other.

Journal of Experimental Marine Biology and Ecology 483 (2016) 97–103

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

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

Yunkai Li [a,b], Yuying Zhang [b], Xiaojie Dai [a,*]

[a] College of Marine Sciences, Shanghai Ocean University, 999 Huchenghuan Rd, Shanghai 201306, China
[b] Marine Sciences Program, School of Environment, Arts and Society, Florida International University, 3000 NE 151st St., North Miami, Florida 33181, USA

ARTICLE INFO

*Article history:*
Received 23 November 2015
Received in revised form 26 April 2016
Accepted 27 April 2016
Available online xxxx

*Keywords:*
Pelagic sharks
Stable isotope
Trophic roles
Trophic overlap
Central Pacific

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,

* Corresponding author.
*E-mail address:* xjdai@shou.edu.cn (X. Dai).

http://dx.doi.org/10.1016/j.jembe.2016.04.013

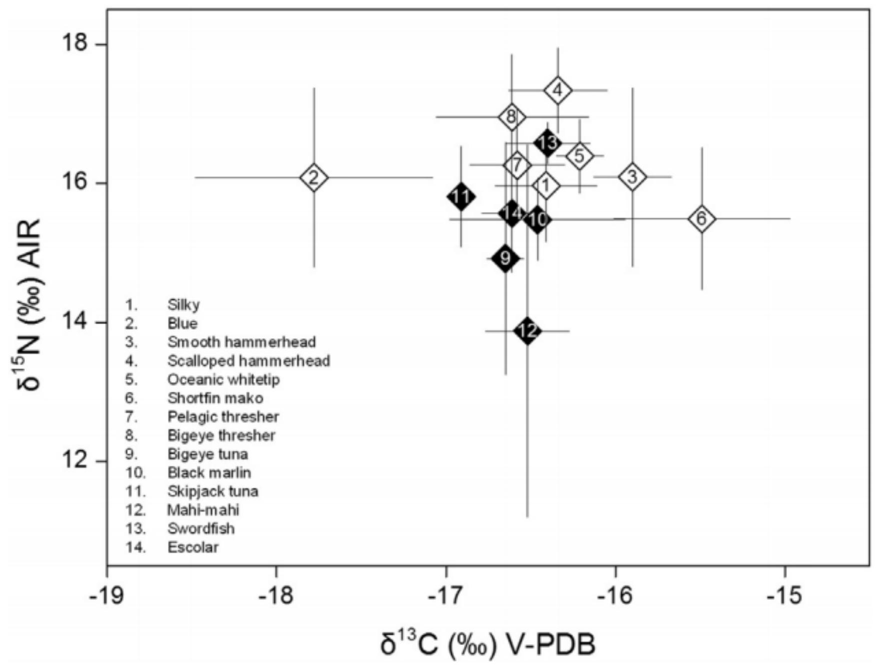




**Fig. 2.** A biplot of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± SD) for pelagic sharks (open diamonds) the large predatory teleosts (black diamonds) of the northeast central Pacific pelagic community.

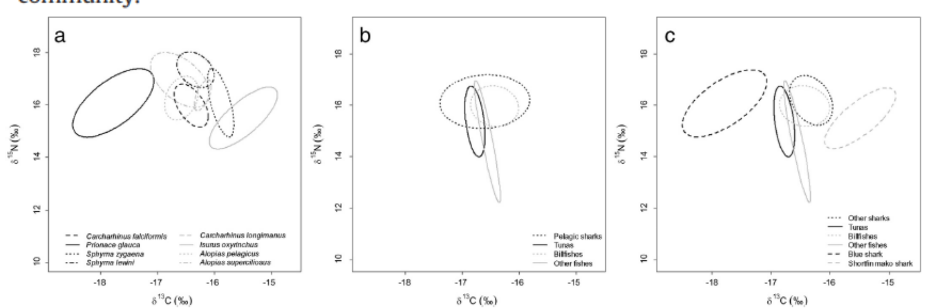
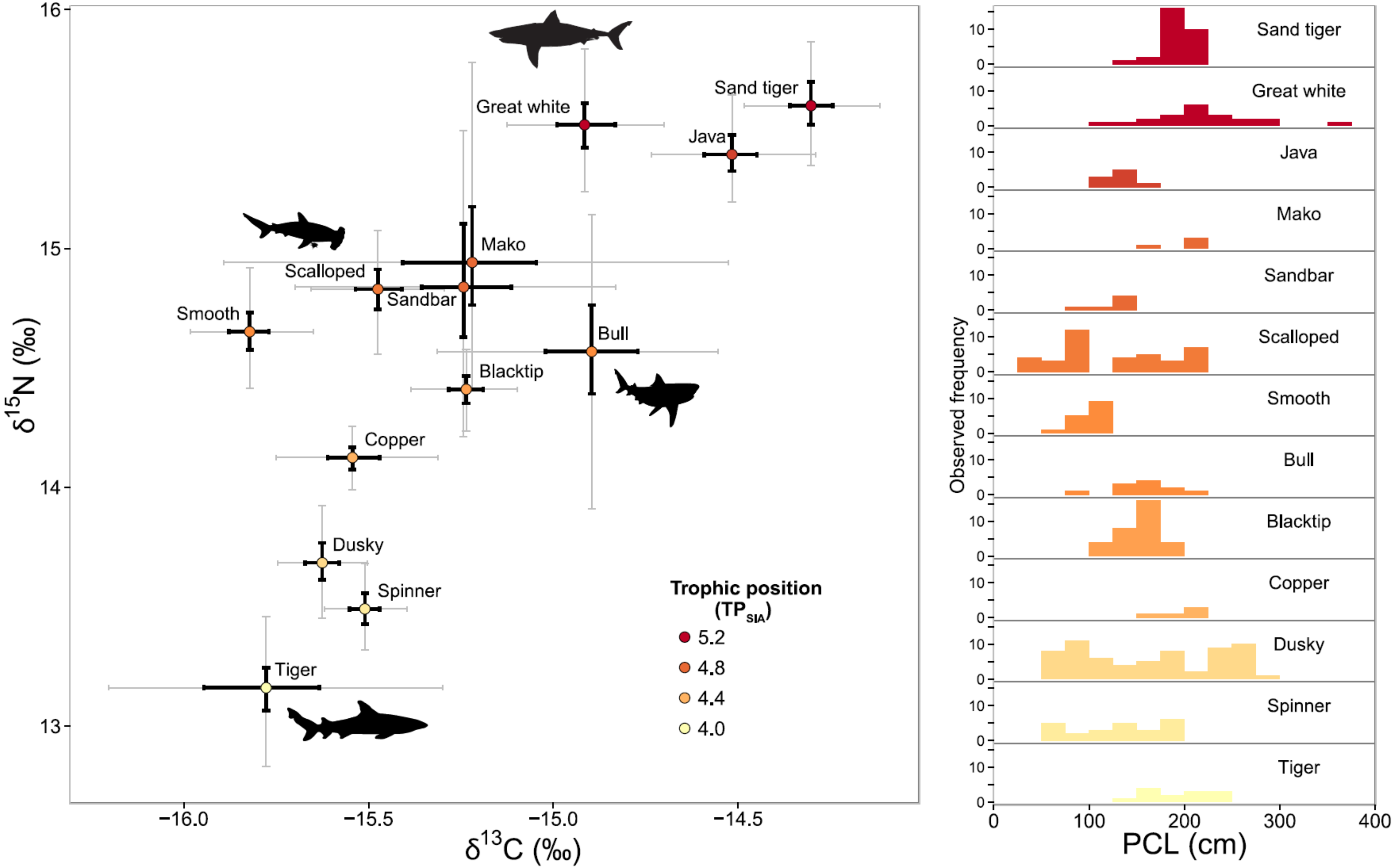
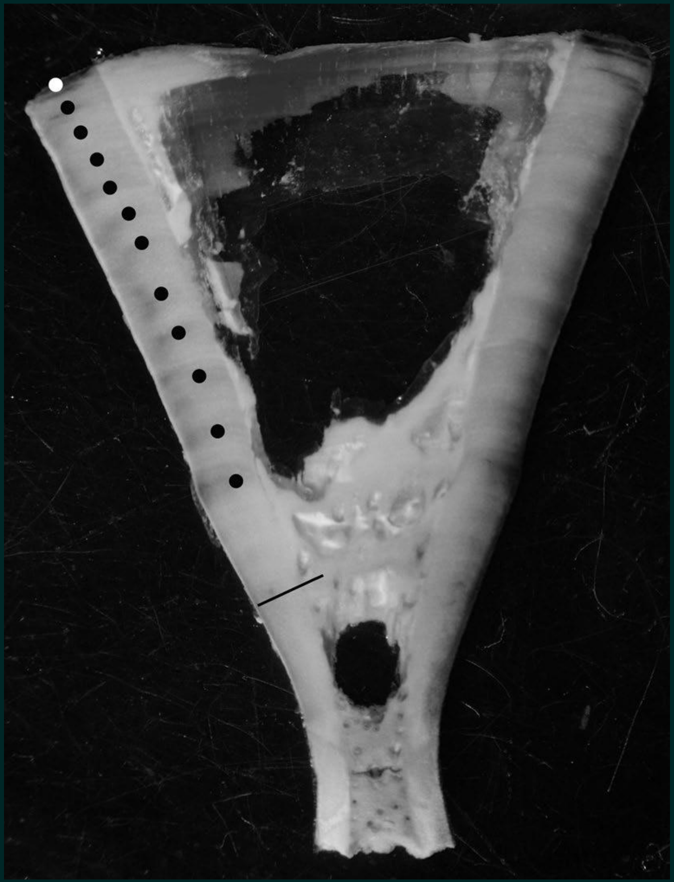


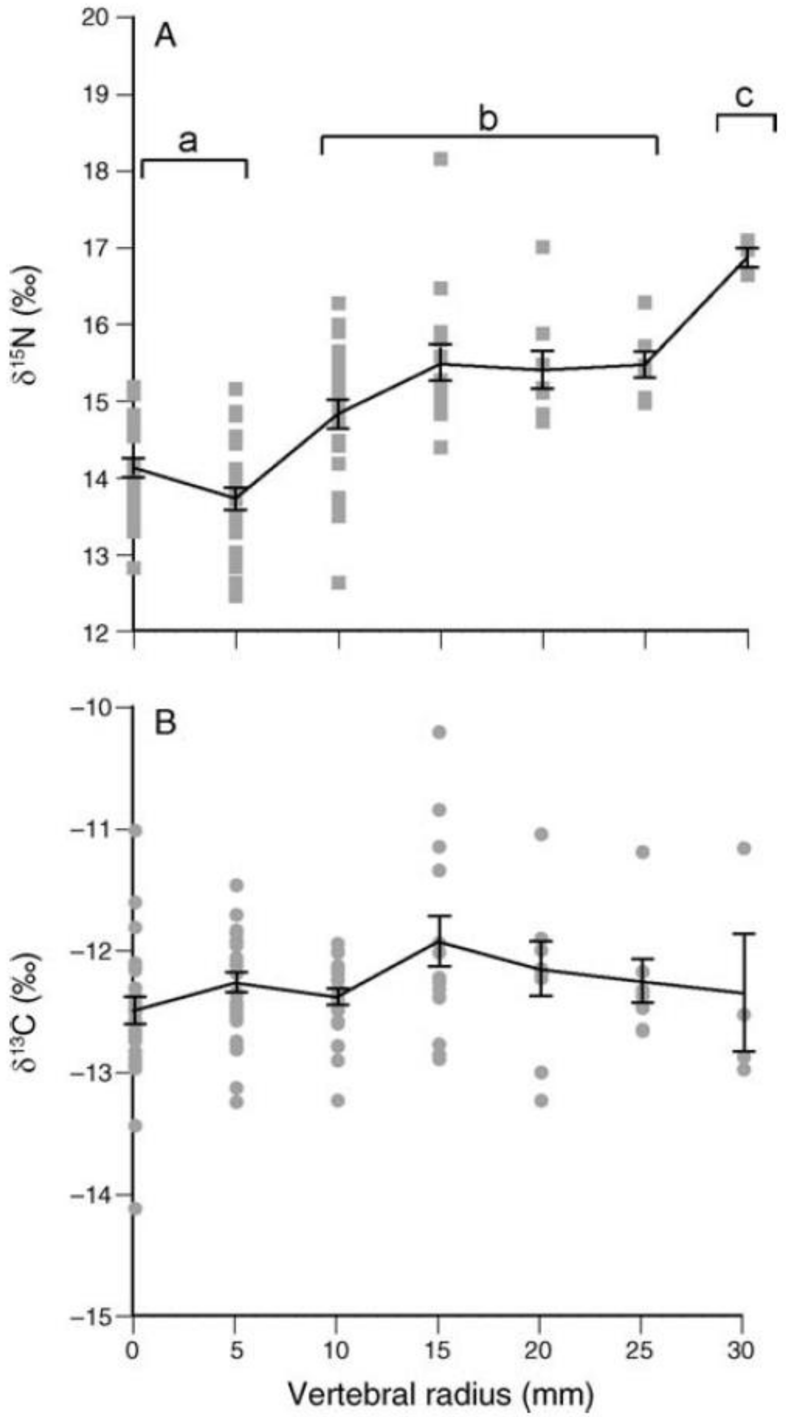

**Fig. 3.** Stand ellipse areas corrected for sample size (SEAc) of pelagic sharks (a), pelagic guilds (b), and pelagic guilds with blue sharks and shortfin mako sharks separated from the pelagic shark guild (c).



δ15N (‰)
δ13C (‰)
16
15
14
13
−16.0
−15.5
−15.0
−14.5
Great white
Sand tiger
Java
Mako
Scalloped
Sandbar
Smooth
Bull
Blacktip
Copper
Dusky
Spinner
Tiger
Trophic position (TPSIA)
5.2
4.8
4.4
4.0
Sand tiger
Great white
Java
Mako
Sandbar
Scalloped
Smooth
Bull
Blacktip
Copper
Dusky
Spinner
Tiger
Observed frequency
10
0
PCL (cm)
0
100
200
300
400

# Shark vertebrae sampli





# Example

- The upside-down jellyfish depends on algae in its body for certain nutrients. The algae are protected by the jellyfish and supplied with nutrients. This relationship would be an example of

A. Mutualism
B. Commensalism
C. Parasitism

- According to the ten percent rule, how many kilograms of phytoplankton would be needed to produce 10 kilograms of fish that were second-order consumers?

A. 1 kilogram
B. 10 kilograms
C. 100 kilograms
D. 1000 kilograms
E. 10000kilograms

- The ultimate source of energy for most life in the ocean is

A. Photosynthesis
B. The sun
C. Thermal vents
D. Predation
E. Phytoplankton

- The most important primary producers in marine ecosystems are

A. Seaweeds
B. Plants
C. Phytoplankton
D. Detritivores
E. Filter feeders

- Oysters and other broadcast spawners produce large numbers of offspring, of which very few survive. However, those that do survive usually exhibit a low mortality rate as adults. The type of survivorship curve that best fits this life cycle would be

A. A type I curve
B. A type II curve
C. A type III curve

- The dispersion pattern that frequently results when there is competition among species is

A. Clumping
B. Uniform
C. Random

- A sample of 50 tuna is captured, tagged, and released back into the population. Four weeks later, another sample 50 tuna is taken and 10 of them have tags. Based on this information, we would estimate the size of the tuna population in this range to be

A. 100 tuna
B. 200 tuna
C. 250 tuna
D. 500 tuna
E. 1000 tuna

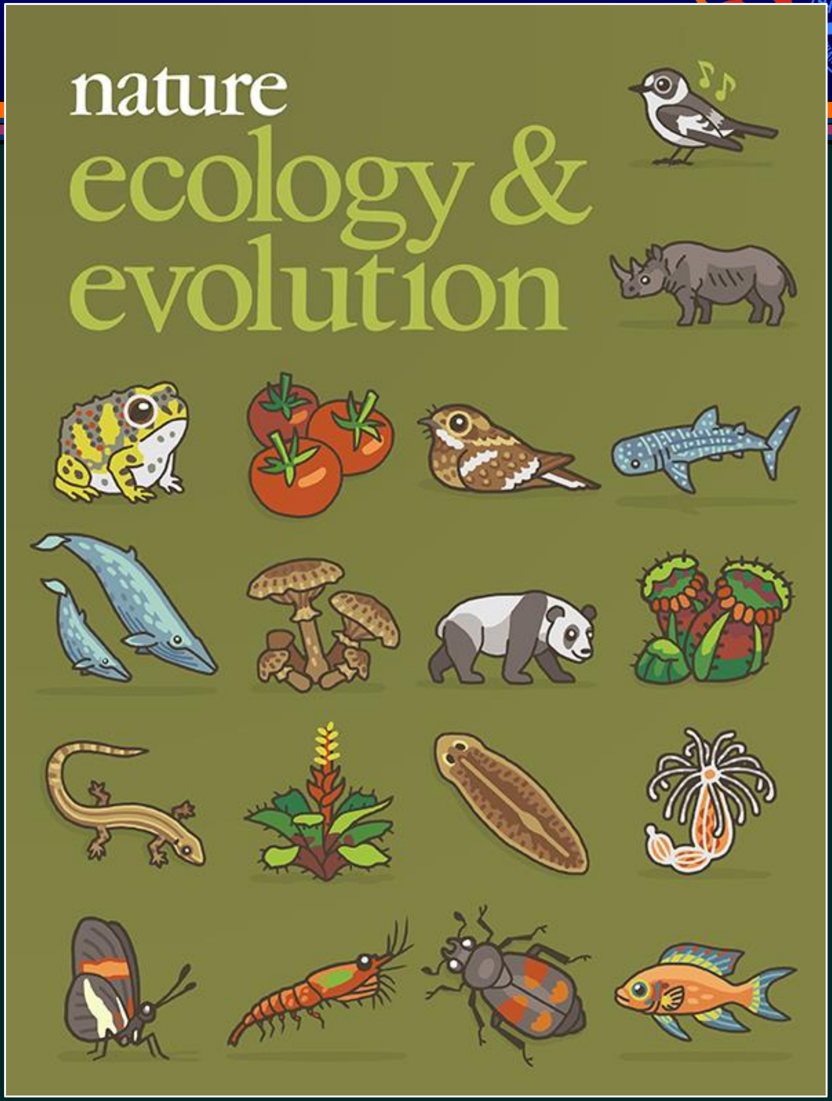
# Key Terms

- 1. abiotic environment
- 2. autotroph
- 3. biotic environment
- 4. community
- 5. detritus
- 6. homeostasis
- 7. niche
- 8. osmosis
- 9. population
- 10. primary productivity
- 11. symbiosis
- 12. trophic level
- 13. food web

# Further Reading


- Paine, R. T. 1974. Intertidal Community Structure: Experimental Studies on the Relationship between a Dominant Competitor and Its Principal Predator, *Oecologica* 15: 93-120.
- McClintock, J. B., and B. J. Baker. 1998. Chemical Ecology in Antarctic Seas: Chemical Interactions Can Lead to Unusual Arrangements between Species, *American Scientist* 86(3).


nature
ecology & evolution


nature
ecology & evolution