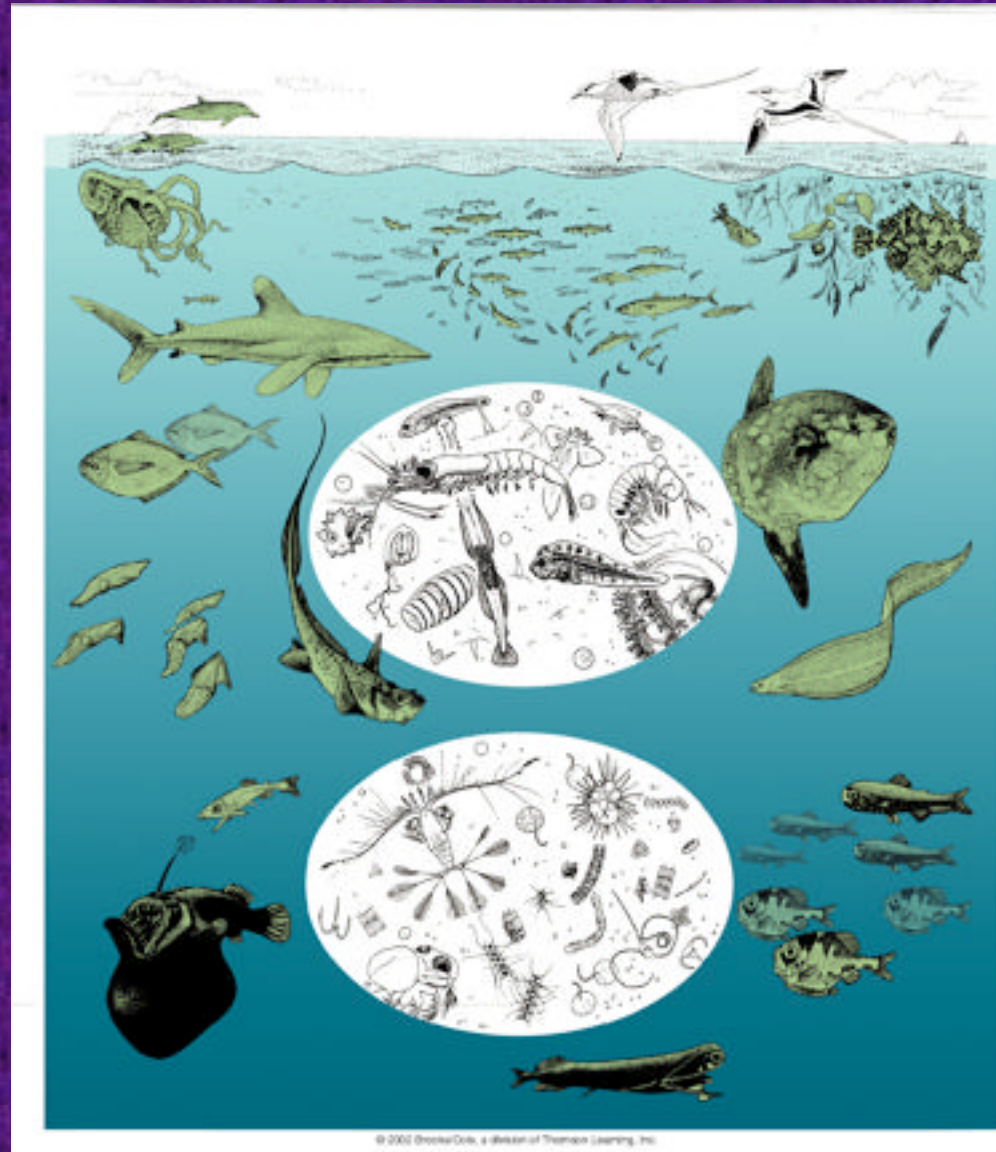


# Food Webs



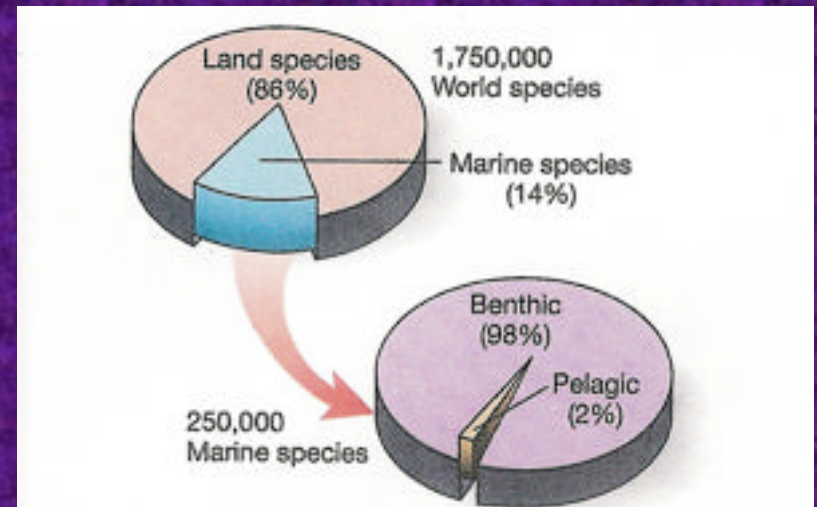
K.Selph, OCN 621 Spring 2010

## Relatively few species

*(discounting the controversy over the number of microbes)*

Yet:

- 1) High diversity in terms of trophic mode, e.g., herbivory, carnivory, mixotrophy, omnivory
- 2) Trophic level changes with developmental phase (egg to adult) within a species
- 3) Prey selection based on size, but not necessarily at a ratio of 1:10, especially for raptorial/direct interception consumers
- 4) Behaviors lead to niche partitioning, even though environment relatively uniform, e.g., diel vertical migration



**Figure 13-6 Distribution of species on Earth.**

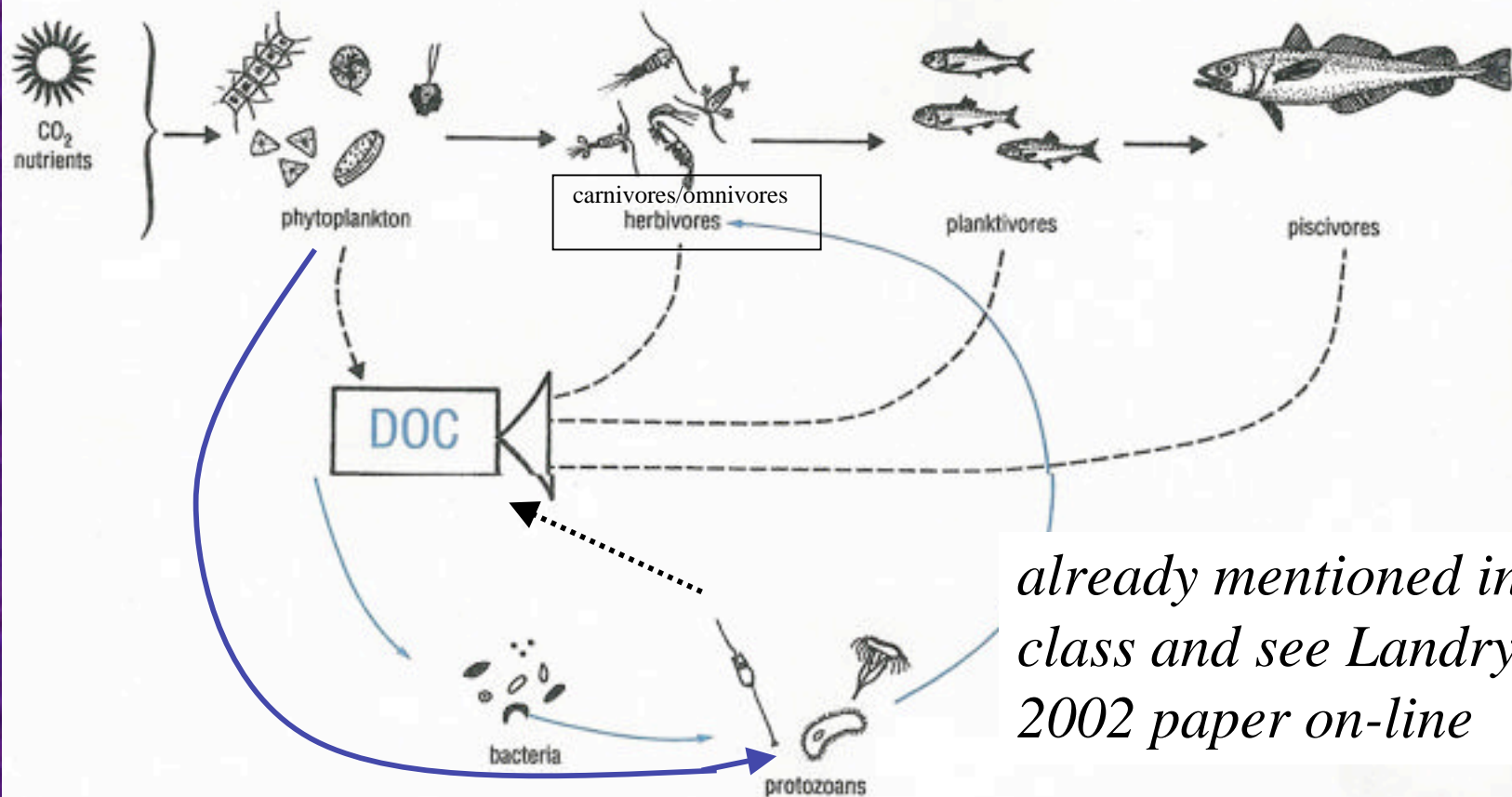
Of the 1,750,000 known species on Earth, 86% inhabit land environments and 14% inhabit the ocean. Of the 250,000 known marine species, 98% inhabit the benthic environment and live in or on the ocean floor, while only 2% inhabit the pelagic environment and live within the water column as either plankton or nekton.

Given this background, how would we expect food webs to look?



# Integrating Classical and Microbial Loop Food Webs

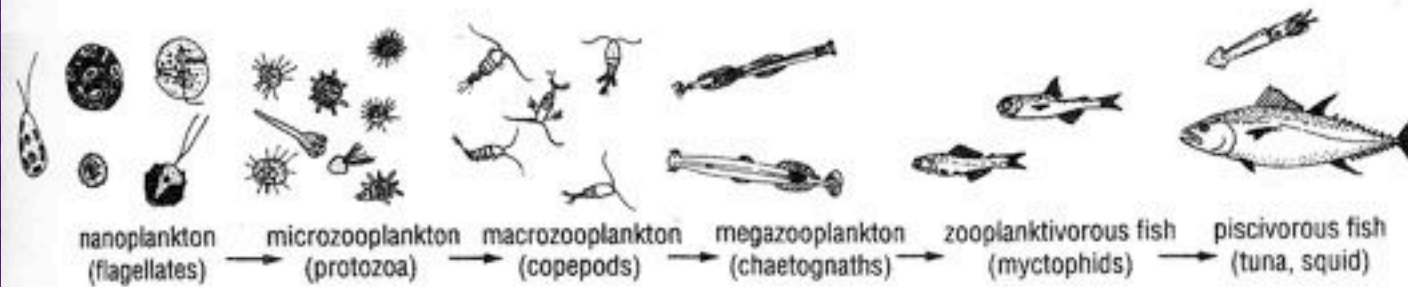
Figure 5.7 A schematic illustration showing the coupling of the pelagic grazing food chain (phytoplankton to piscivorous fish) and the microbial loop (bacteria and protozoans). Dashed arrows indicate the release of dissolved organic material (DOC) as metabolic by-products. The DOC is utilized as a source of carbon by heterotrophic bacteria. The bacteria are consumed by protozoans, which in turn are eaten by larger zooplankton.



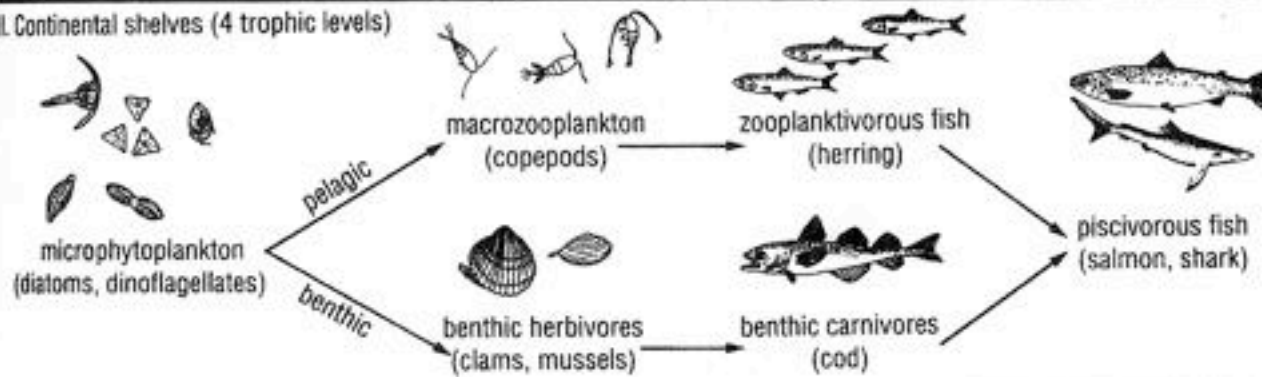
*already mentioned in  
class and see Landry  
2002 paper on-line*

# Comparison of food web structures

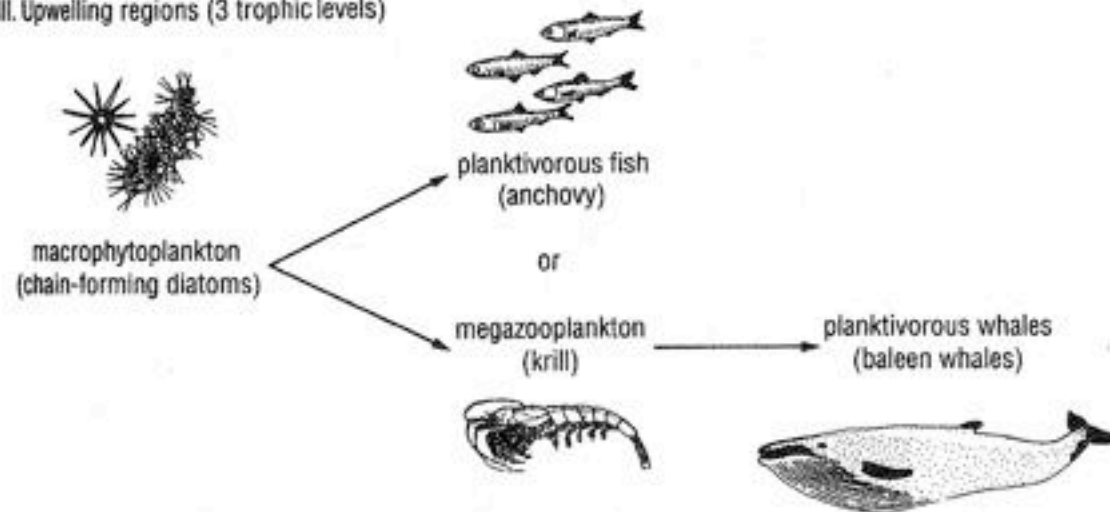
## I. Open ocean (6 trophic levels)



## II. Continental shelves (4 trophic levels)



## III. Upwelling regions (3 trophic levels)



oligotrophic



eutrophic

Lalli & Parsons 1997



# NW Atlantic Food Web

Humans (7 - 10)

Whales/porpoises/  
birds (6 - 9)

Squid (5 - 8)

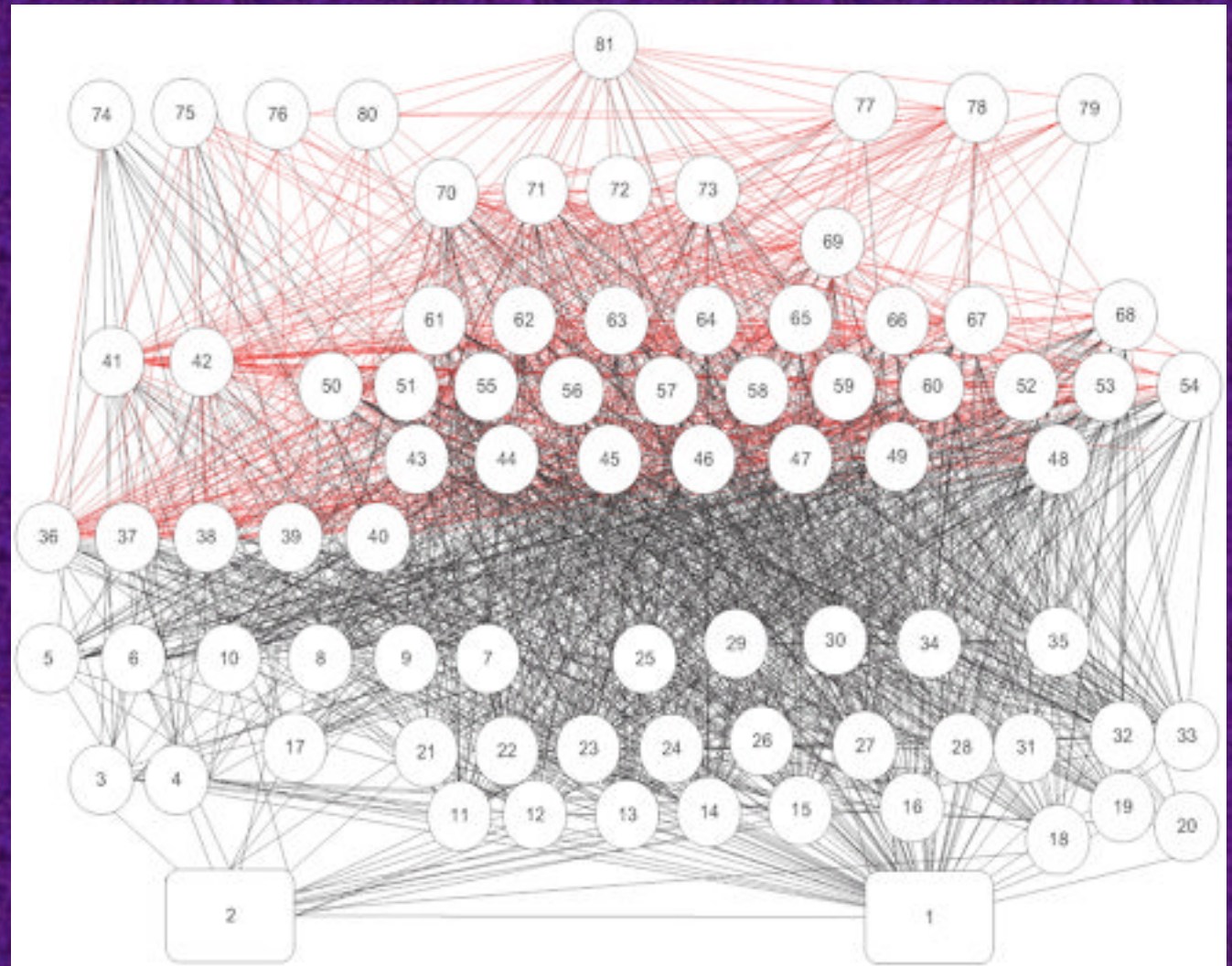
Bigger fish (4 - 7)

Small fish (4 - 6)

Ctenophores/  
Chaetognaths (3 - 5)

Copepods (2 - 4\*)

Phytoplankton (1)



# Trophic Transfer Efficiency

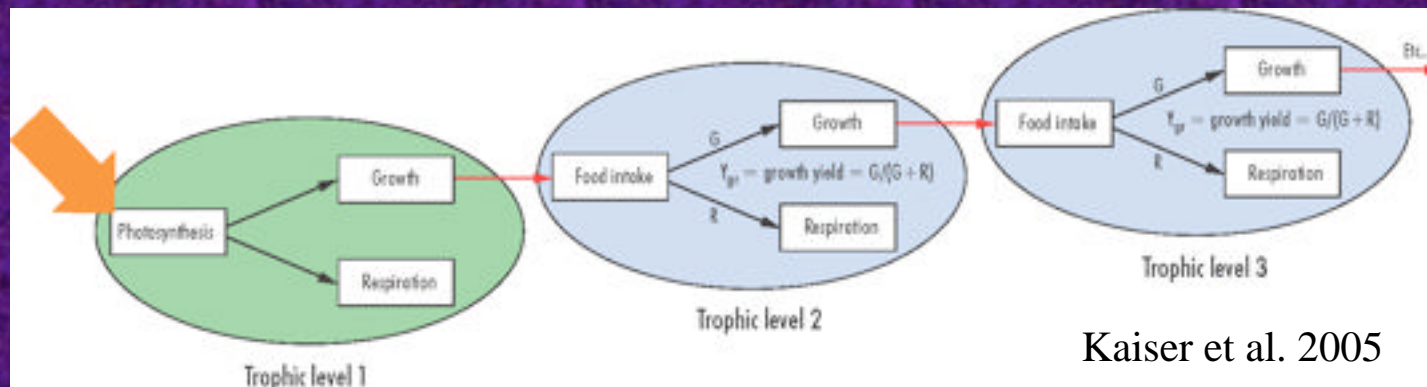
TTE (or Trophic Yield) = *Amount of production at trophic level (X+1)  
relative to production at trophic level X*

-- *Usually thought to be lower than GGE, because of other modes of death  
(e.g., viral lysis, natural death...)*

-- *Because of losses to metabolism/egestion at each step, longer food chains  
result in less yield to the top predator*

How to apply to actual food chain?

Overall Food Chain Efficiency =  $TTE(2) * TTE(3) * TTE(4) * TTE(n)$



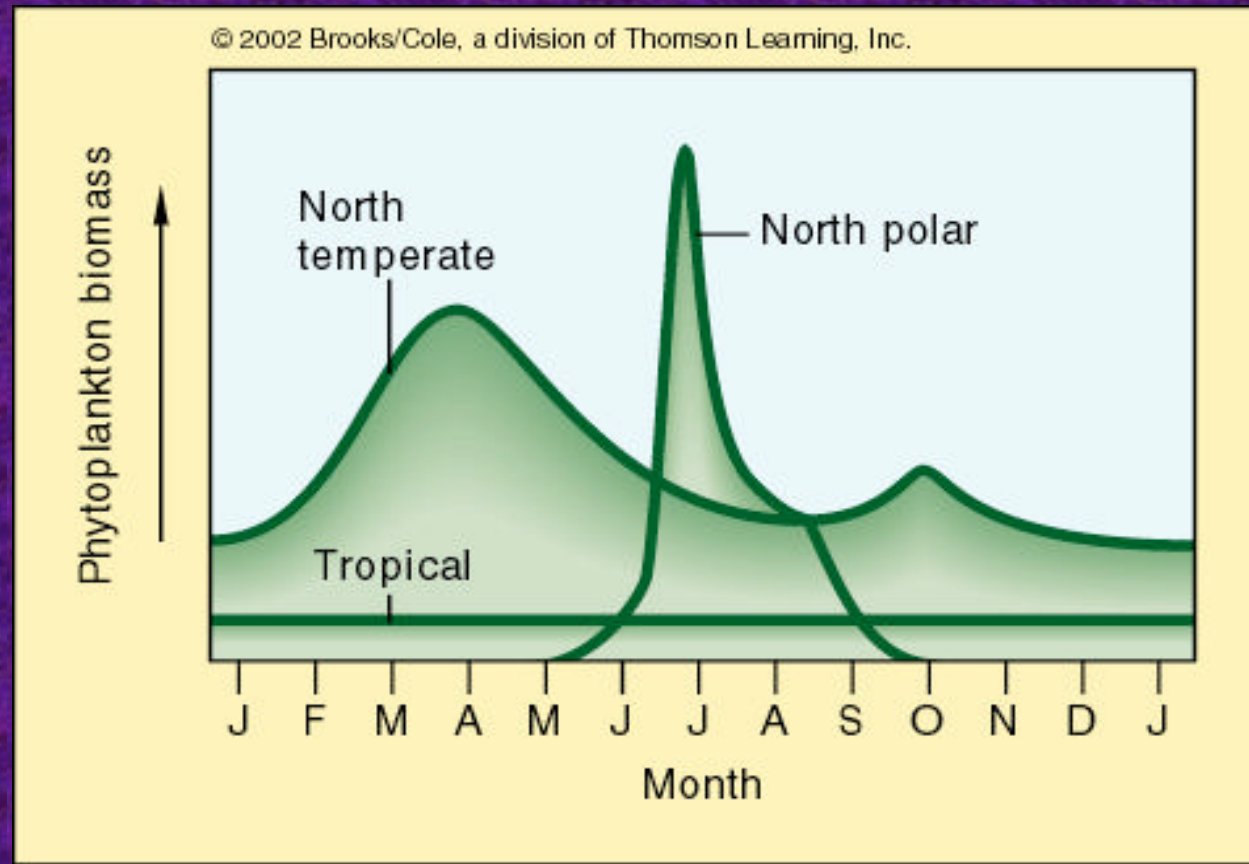


How does  
biomass  
change over  
a seasonal  
cycle and  
what does it  
mean?



# Spring blooms

biomass, not production



This is the general view of three of the ocean ecosystems on the planet...



# Historical Observations of Seasonal Cycles

- Using net tows, catch diatoms, large dinoflagellates and zooplankton
- From these catches, infer food web relations and seasonal cycles
- Did use *in situ* chlorophyll measurements around the world's seas to generate maps  
(note: didn't have large scale, synoptic maps such as we have today with satellites)

## North Atlantic Bloom

- 1) Phytoplankton low through the winter:  
light limited, nutrients sufficient  
deep winter mixing
- 2) Spring Bloom  
reduced winds, stratification near  
surface  
increased light, nutrients sufficient
- 3) Summer: Low phyto biomass  
grazers consume the  
phytoplankton  
nutrients depleted and not  
renewed

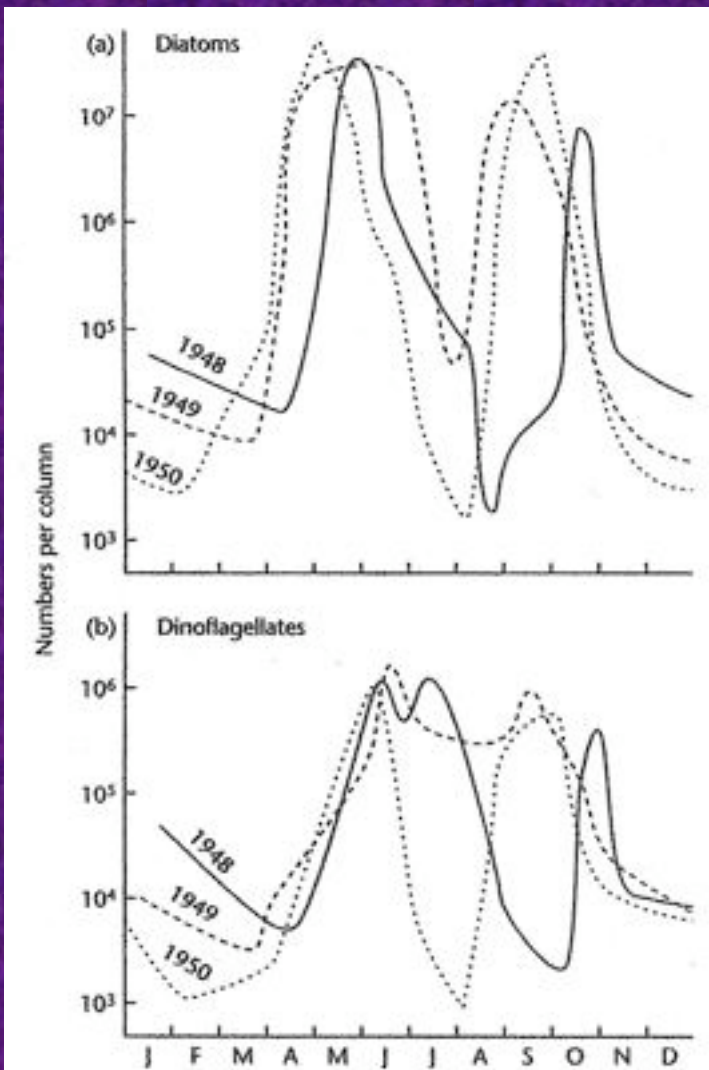


Fig. 1.12 Seasonal cycles of (a) diatoms and (b) dinoflagellates at Station "I" (60°N, 20°W) in the North Atlantic. Diatoms bloom, and then are replaced by dinoflagellates. Bloom timing varies among years by a month or more. Cells were counted with a microscope. (After Corlett 1953.)



## End of North Atlantic Bloom

- 4) Fall: Second bloom
  - Fewer grazers: non-feeding stage
  - Intermittent storms
  - Inject nutrients, but still stratified
  - Light sufficient
- 5) Early winter:
  - Storm mixing
  - Re-supply of nutrients to surface
  - Set for next Spring Bloom

### The "Classic" Temperate Bloom Cycle:

#### Spring Bloom

water-column stability  
compensation depth exceeds mixing  
P grows at expense of N  
Z lags P

#### The "Crash"

N exhausted; Z grazing overshoots P growth

#### Summer equil.

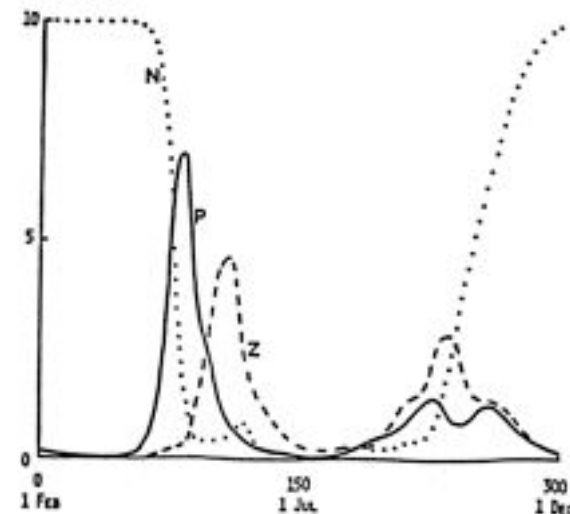
P, N, & Z at low, stable levels; balanced processes

#### Fall Bloom

early storm mixing followed by stability

#### Winter decline

light limitation; mixing of N into surface water



*In places where phytoplankton cycles are strongly different (most of the rest of the world's oceans!), they are usually discussed in contrast to the spring bloom cycle.*

# An ecosystem change?

## Jellyfish in the North Atlantic

Hot topic -- *Hydrobiologia* special issue in 2009

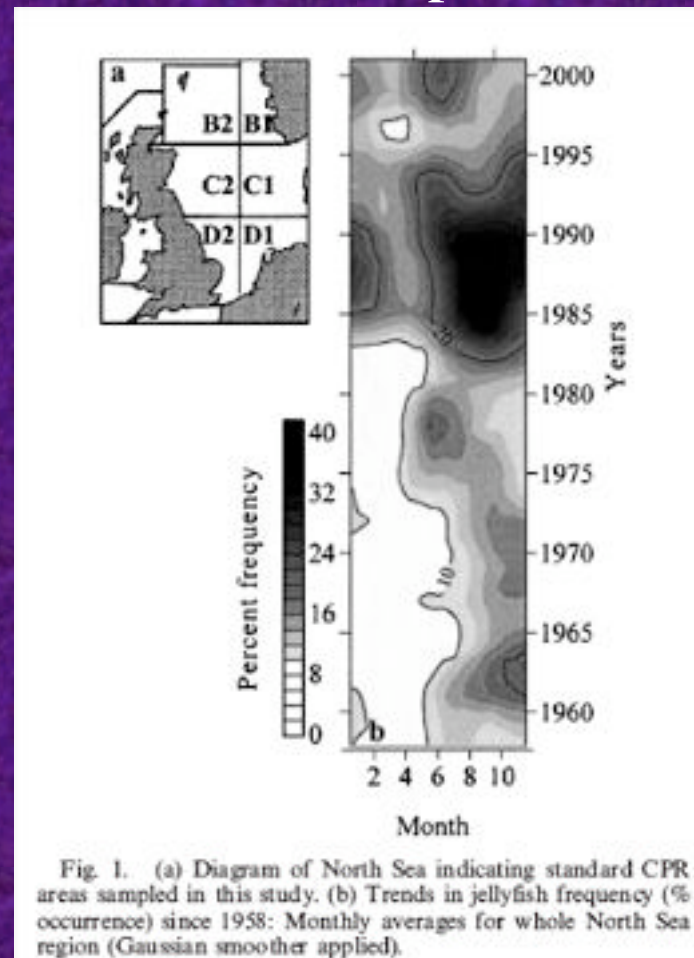
Usual top predator: Cod or other fish species

Observation:

Jellyfish increasing  
in frequency in  
North Sea

*Data from  
Continuous  
Plankton Recorder*

(towed monthly behind  
merchant ships at 6.5 m --  
records presence/absence  
of nematocysts)



Attrill et al. 2007

Hydrobiologia	
Volume 616, Number 1 / January, 2009	
Jellyfish Blooms: Causes, Consequences, and Recent Advances: Proceedings of the Second International Jellyfish Blooms Symposium held at the Gold Coast, Queensland, Australia, 24-27 June, 2007 / Guest Editors: K. A. Mills & J. E. Ruesink	
Journal	Hydrobiologia
Publisher	Springer Netherlands
ISSN	0013-8558 (Print) 1573-5117 (Online)
Pages	1-189
Subject Collection	Biomedical and Life Sciences
SpringerLink Date	Tuesday, December 23, 2008
Editorial View Condensed List View Expanded List View	
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The growth of jellyfishes	11-21
Extension of methods for jellyfish and dinoflagellate trophic ecology to large-scale research	23-50
Patterns of jellyfish abundance in the North Atlantic	51-65
Jellyfish in ecosystems, online databases, and ecosystem models	67-85
Quantifying movement of the tropical Australian cubozoan <i>Chiropsylla</i> <i>flaccida</i> using acoustic telemetry	87-97
Acoustic survey of a jellyfish-dominated ecosystem (Milet Island, Croatia)	99-111
Stock enhancement of the edible jellyfish ( <i>Rhopilema esculentum</i> Kishinouye) in Laodong Bay, China: a review	113-118



# Bad years for herring = good years for jellyfish?

Data set from a 15 year survey (1971-1986), with jellyfish as by-catch

herring recruitment

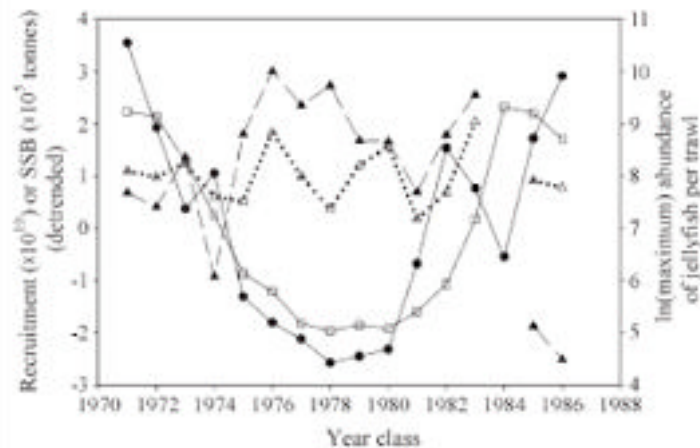


Fig. 4. *Clupea harengus*, *Aurelia aurita* and *Cyanea capillata* in the North Sea. Detrended time series of herring recruitment (solid line, ●), SSB (solid line, □) and the abundance of *A. aurita* (dashed line, ▲) and *C. capillata* (dotted line, △). For ease of comparison, the *C. lamarckii* data are all +5. Correlation coefficient between herring recruitment and SSB,  $r = 0.79$ ; between herring recruitment and medusa abundances: *A. aurita*  $r = -0.67$  and *C. capillata*  $r = -0.68$  (all  $p < 0.01$ )

jellyfish abundance

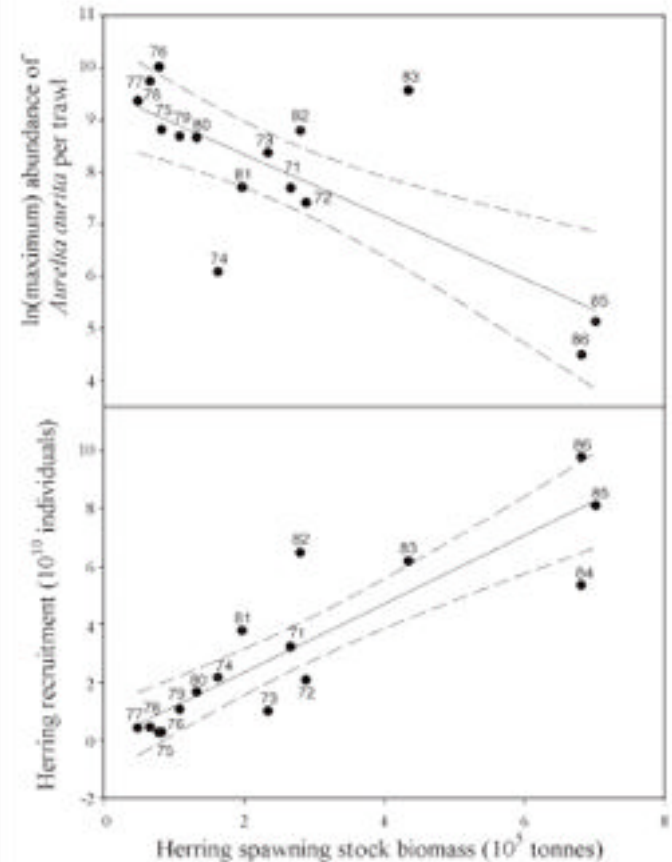


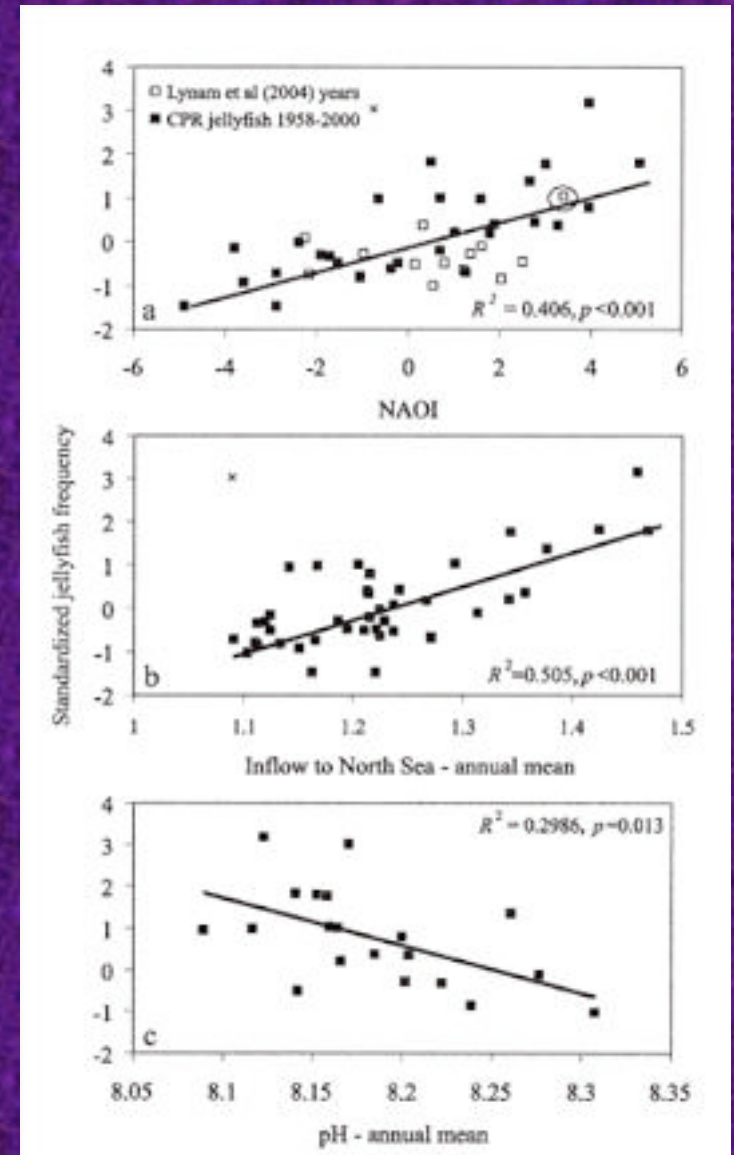
Fig. 2. *Clupea harengus* and *Aurelia aurita* in the North Sea. Correlations between the raw herring SSB (spawning stock biomass) and recruitment ( $r = 0.89$ ,  $p < 0.01$ , bottom panel) and between SSB and the ln(maximum) abundance of *A. aurita* ( $r = 0.75$ ,  $p < 0.01$ , top panel)

# Why? Natural Environmental Variability (NAO) *and/or* effect of overfishing

Jellyfish (medusoid Scyphozoa) eat larval herring and also compete with them for their zooplankton prey

Adult finfish and jellyfish also compete for prey

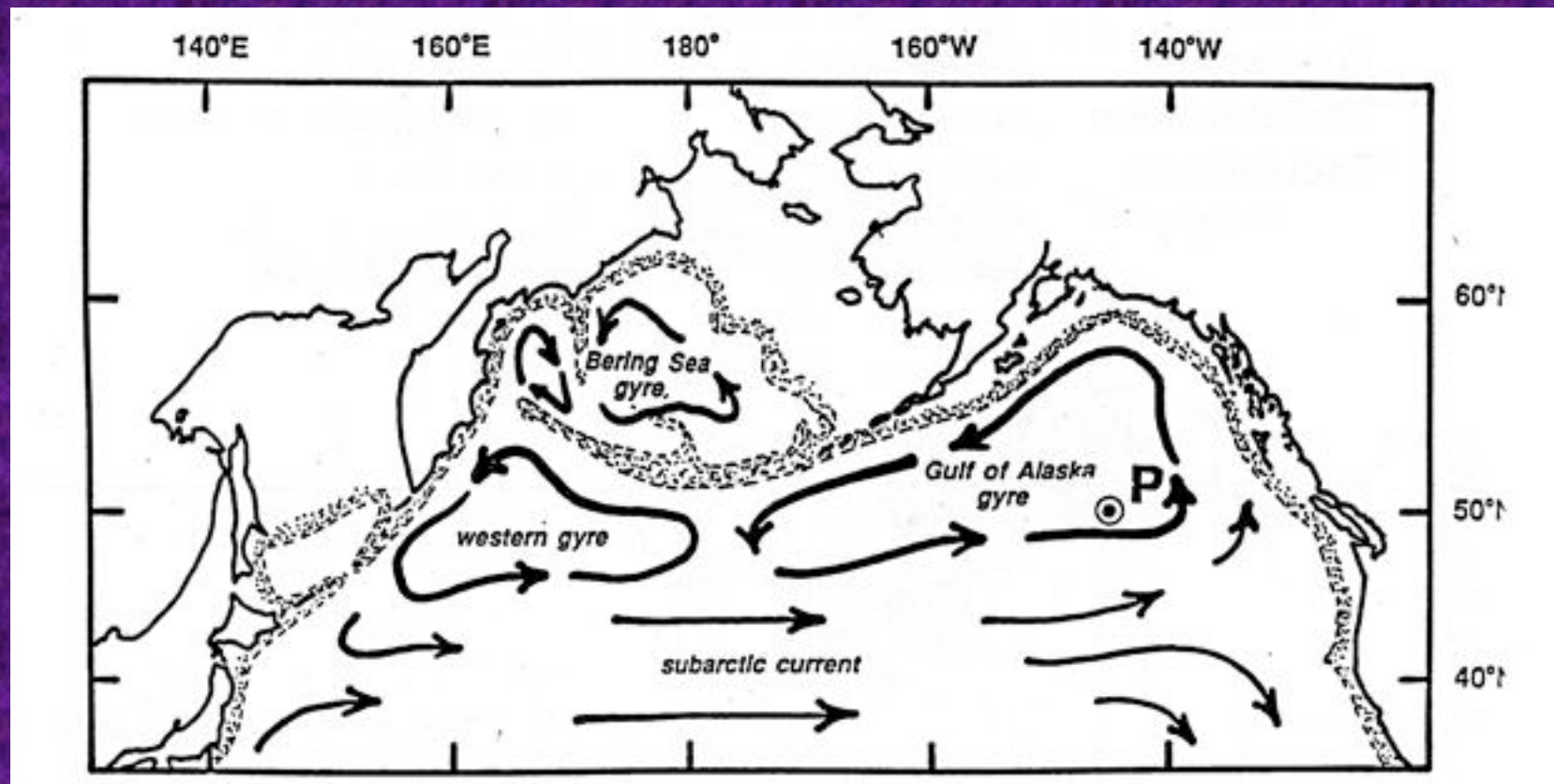
Reduced larval herring stocks, and therefore adult herring, further allow jellyfish to outcompete them





## Subarctic Pacific - HNLC region

- Objective: to test the “Major Grazer” Hypothesis (1980)
- Experimental goal: Can mesozooplankton grazers control phytoplankton stocks?



# Observations

- Seasonal blooms do not occur -- Canadian weathership at Station P (50°N, 145°W)
- Occupied station from 1950s until mid-1981

*This is in contrast to the  
North Atlantic --  
chlorophyll levels  
>1 mg/m<sup>3</sup> every year*

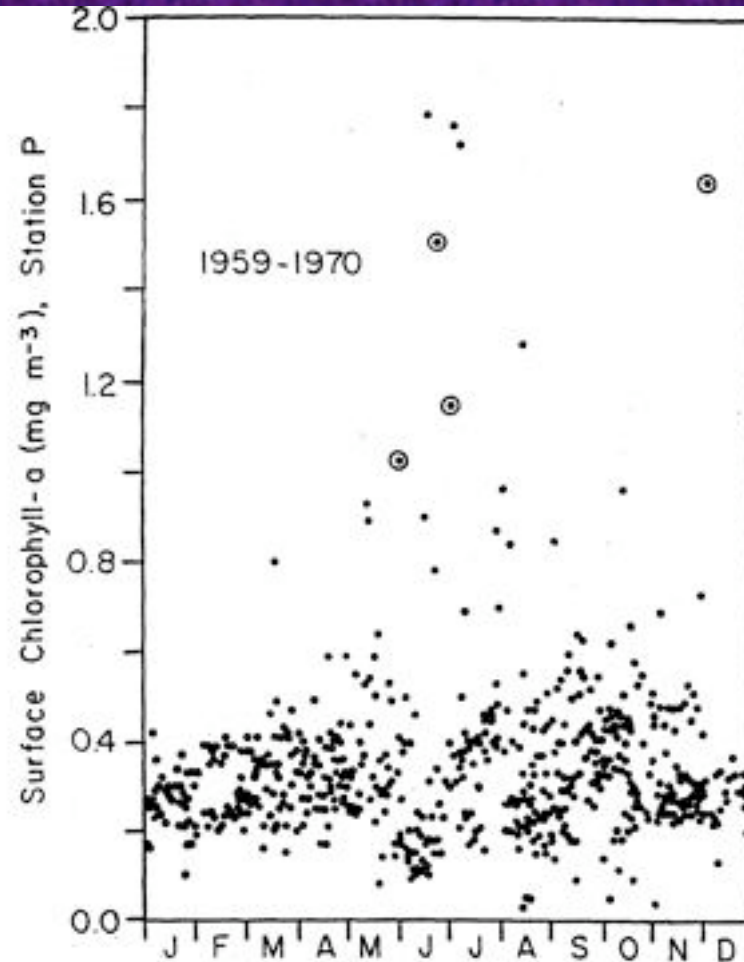
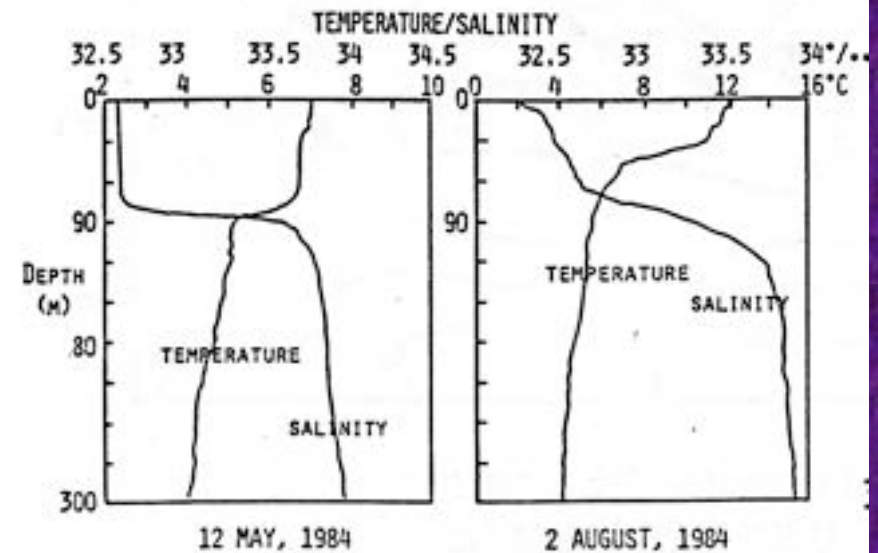
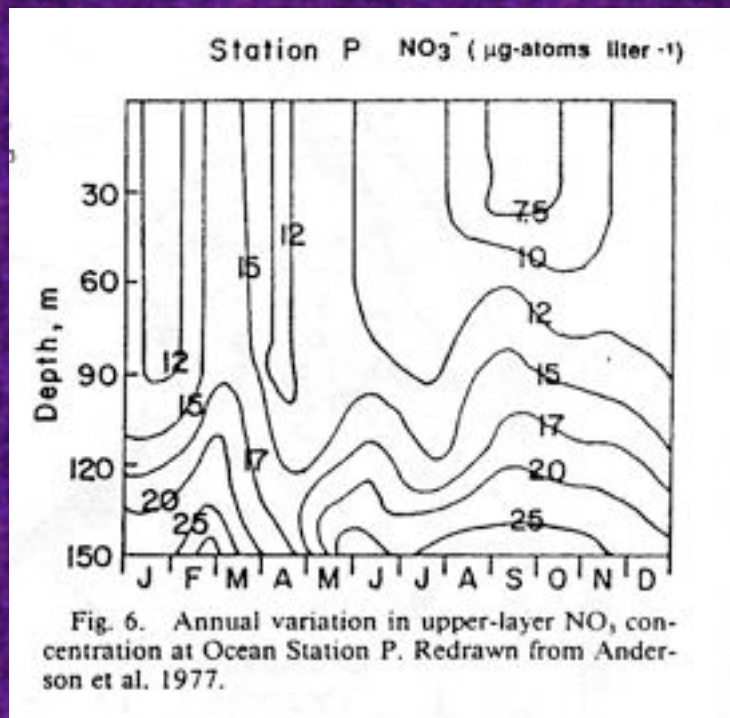


Fig. 1. Cumulative chlorophyll-*a* data from Ocean Stn. P over 10 years. Note that scale extends only to 2.0 mg/m<sup>3</sup>. Circled points are all additional values over 1.0 mg/m<sup>3</sup> during 1976-76. From Anderson et al. (1977).

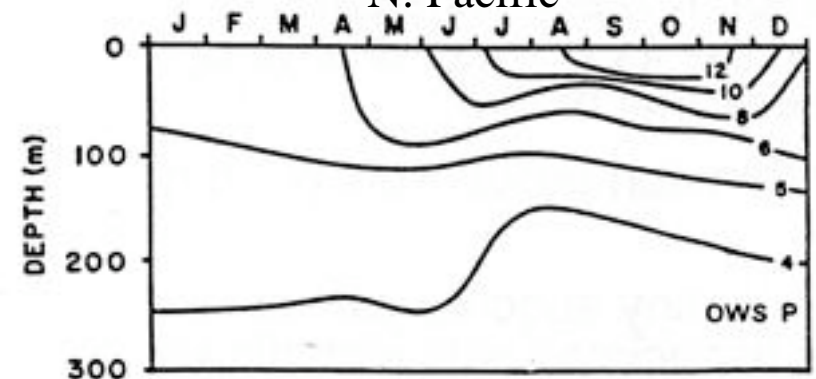


# Characteristics of Subarctic Ecosystems

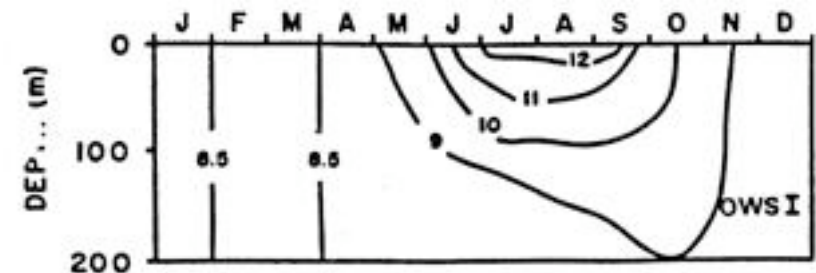
- deep winter mixing in Atlantic, but a permanent halocline in the Pacific
- low summer nitrate in Atlantic, but still high in summer in Pacific



N. Pacific

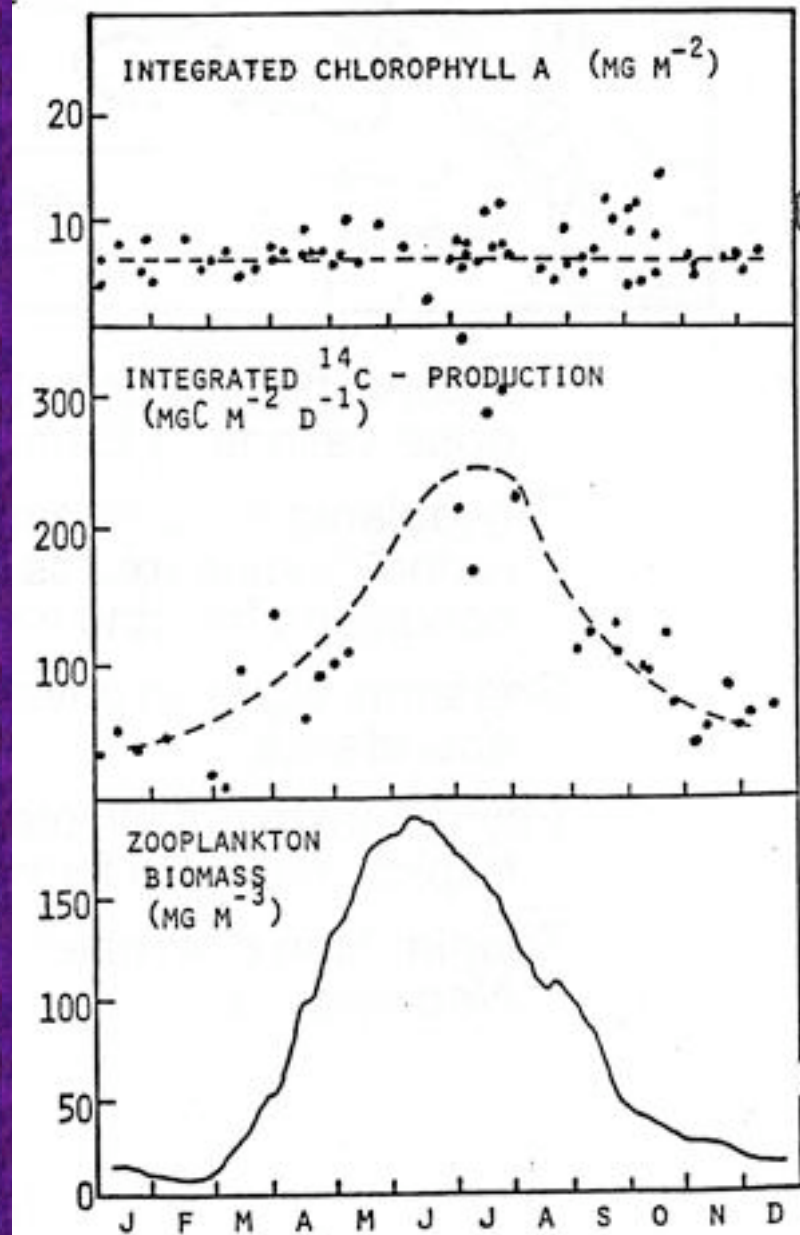


N. Atlantic



# Plankton

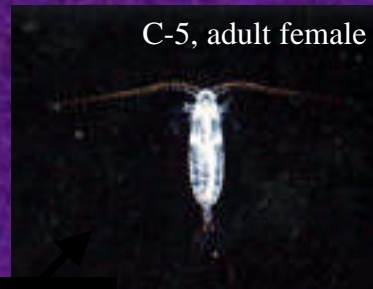
- Phytoplankton concentration low & nearly constant year round despite excess nutrients (nitrate) & physical conditions favoring a seasonal bloom.
- Seasonal signal in phytoplankton production, but not abundance
- Phytoplankton dominated by tiny species, similar to tropics, not large forms associated with high nitrate





# Seasonal migration of *Neocalanus plumchrus*

- Zooplankton dominated by large species, *Neocalanus* (4-5 mm)



C-2, C-3, C-4

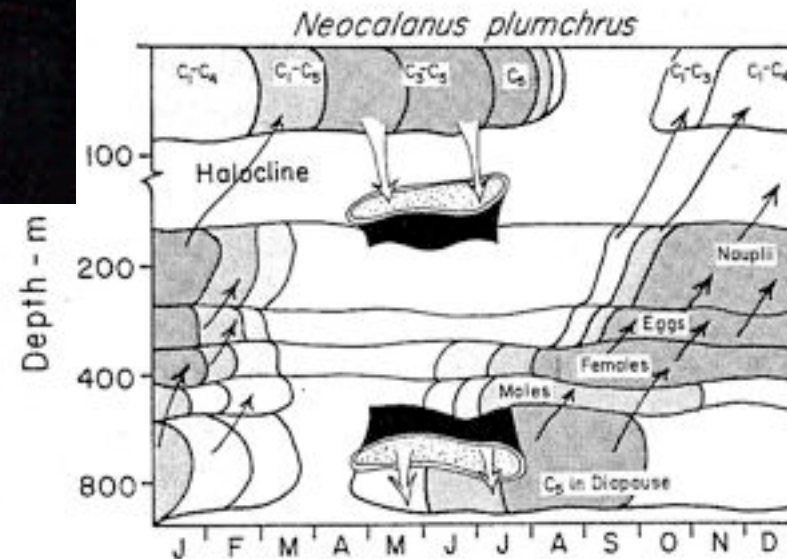


FIG. 28. Schematic diagram showing the distribution of the life cycle stages of *Neocalanus plumchrus* with respect to season (abscissa) and depth (ordinate). A rough indication of abundance is given by shading: darker implies greater abundance. Drawn in the format of Fig. 5 of FULTON (1973) for comparison to the Strait of Georgia situation.

Miller et al. 1984

- Zooplankton biomass peaks in summer: leads to historical hypothesis that phytoplankton controlled by grazing by large copepods.

# Control Capabilities of *Neocalanus*

- Could consume cells 2-30  $\mu\text{m}$ , but *food limited* at ambient concentrations

- Could keep phytoplankton in check at an abundance of 1 copepod/Liter

- Without them present, phytoplankton did bloom

*But: not present in sufficient density to control blooms (only ~0.2/L)*

- Another role: to consume smaller grazers...

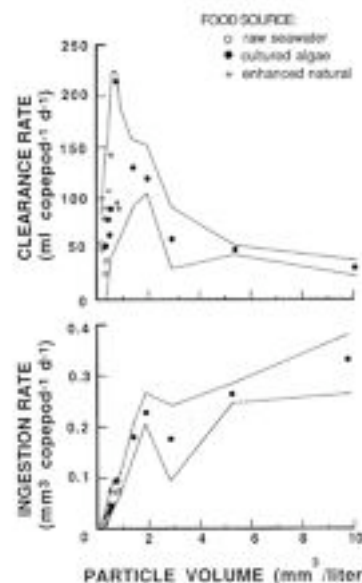


Fig. 3. Effect of food concentration (total particle volume 2–40  $\mu\text{m}$  ESD) on clearance and ingestion rates of *Neocalanus plumchrus*. The figure summarizes the results of feeding experiments with natural particulates from the subarctic Pacific, natural particulates grown to higher abundance levels in shipboard incubations, and mixed phytoplankton cultures (*Isocryptis galbana* and *Thalassiosira weissflogii*). Each point represents the mean of 3–5 rate measurements. The upper and lower lines bound the complete range of variability observed in individual replicate bottles.

Left: Rate estimates from bottle expts.

Right: Experiments in 60-L microcosms

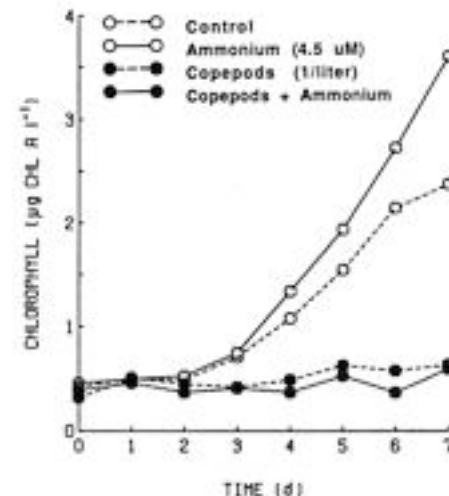
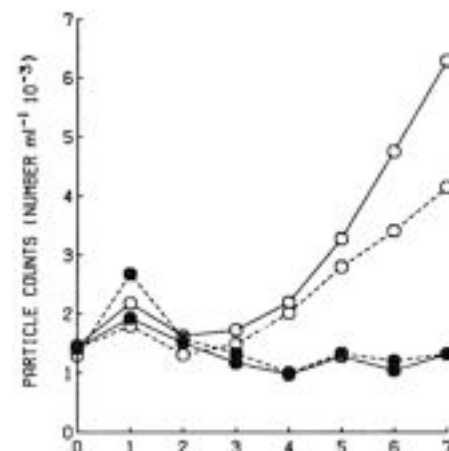


Fig. 4. Observed temporal changes in the abundance of phytoplankton, measured as particle densities (top) and chlorophyll (bottom), when natural seawater from the subarctic Pacific was incubated in microcosms with added ammonium (5  $\mu\text{M}$ ), copepods (*Neocalanus plumchrus* CSs = 1 copepod/liter), or ammonium and copepods.

Landry & Lehner-Fournier 1988



# Role of Protists

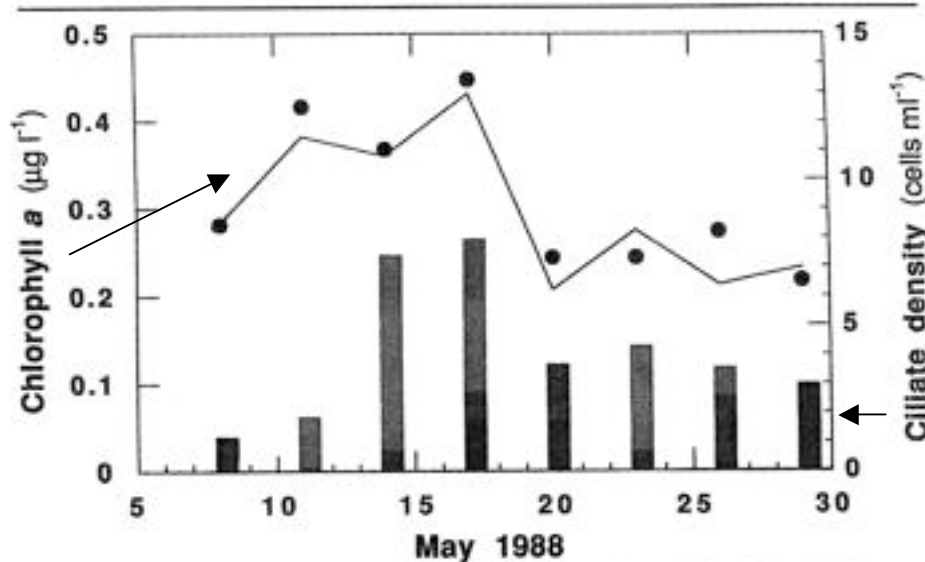


Fig.4. Temporal relationships among predicted and observed values of chlorophyll and ciliate density at Station P in May 1988. Filled circles are observed chlorophyll concentrations in the mixed layer from the measurements made at the start of dilution experiments (Table 1). Line represents the predicted chlorophyll concentration based on net growth rate (mean of  $r_{24}$  and  $r_{48}$ ) determined in dilution experiments. Histogram shows the density of ciliates from water collected at the start of each experiment (Table 1).

**Abstract** – Dilution experiments were conducted on SUPER Program cruises in June 1987 and May and August 1988 to assess the role of microzooplankton in controlling phytoplankton stocks in the subarctic Pacific. Net growth rates of chlorophyll *a* varied in individual experiments from  $-0.4$  to  $+0.7 \text{ d}^{-1}$ . Experiments incubated for 48h gave higher net estimates than 24h incubations ( $0.01$  to  $0.22 \text{ d}^{-1}$  for different cruises), exaggerating the imbalance between growth and grazing. Specific growth rates ( $\mu$ ) and grazing mortality ( $m$ ) for 24h incubations were approximately balanced for the June and May cruises, and net growth estimates from the dilution experiments predicted changes in chlorophyll concentrations for May that closely matched those observed in the field. A major decline in phytoplankton abundance in the middle of May coincided with a high abundance of ciliates. Cell counts indicated that *Synechococcus* and small autotrophic nonflagellates were always kept in check by microzooplankton grazing, even when chlorophyll indicated uncontrolled phytoplankton growth in August 1988 experiments. Diatoms showed high growth potential in most incubations and dominated among the cells that bloomed in August. Our results support the hypotheses that micrograzers are major consumers of phytoplankton in the subarctic Pacific and that their grazing can control some elements of the phytoplankton community. However, growth limitation, presumably from iron deficiency, remains essential to the explanation of phytoplankton control in mid to late summer.

Landry et al. 1993

# Subarctic Pacific Ecosystem

- 1) Major grazers were not eating enough phytoplankton to provide for their own growth -- omnivores, eating phagotrophic protists
- 2) Too few mesozooplankton to keep phytoplankton in check
- 3) Microzooplankton grazing provides the top-down control on the system
- 4) First project to start to explore Fe-limitation to phytoplankton growth -- we know from subsequent studies that Fe-limitation alone is not sufficient to explain the system, need grazing regulation, too



# Upwelling Zones

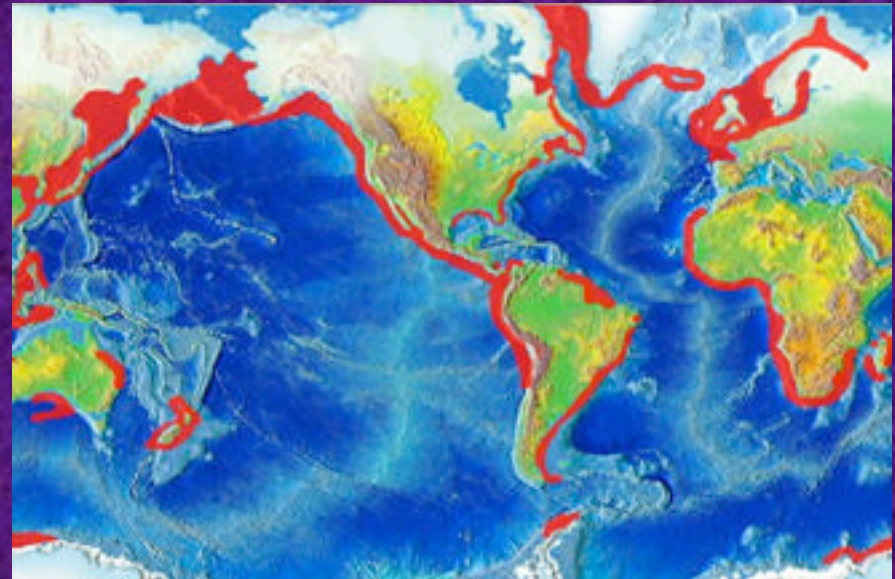
## Continental Shelf Ecosystem

“Classical” coastal upwelling regions of eastern boundary currents and other coasts.

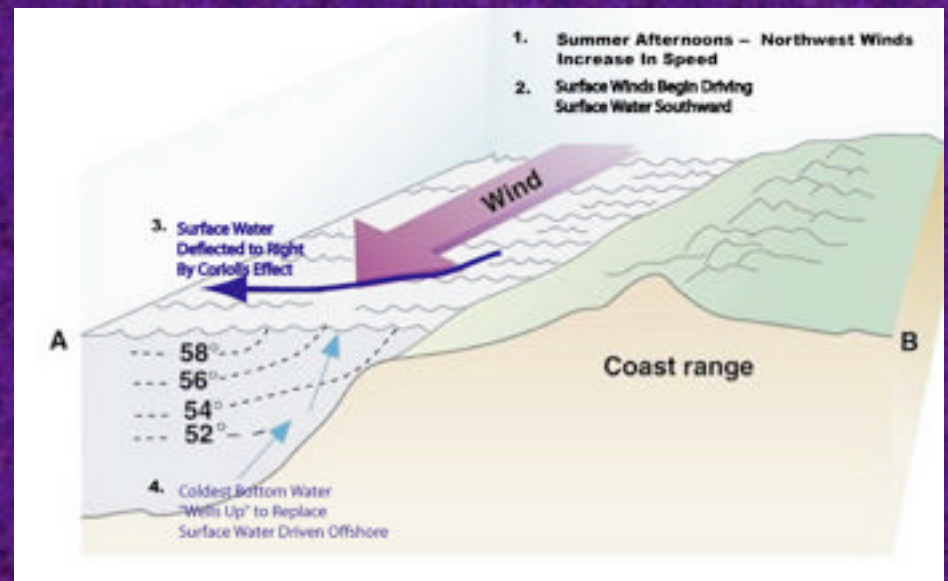
Narrow shelf, river effluent influences minor.

Primary producers: diatoms

Primary herbivores: copepods, anchovies and/or sardines



<http://oceanservice.noaa.gov>



# Small (<5 $\mu\text{m}$ ) Phytoplankton in Upwelling Zones

Despite dominance of diatoms in upwelling zones -- smaller phytoplankton are present, too

Table 3

Abundances ( $10^4 \text{ cells ml}^{-1}$ ) of coccoid cyanobacteria and of photosynthetic eukaryotes in the euphotic zone of upwelling ecosystems

Upwelling region	Coccoid cyanobacteria $10^4 \text{ cells ml}^{-1}$	Photosynthetic eukaryotes $10^4 \text{ cells ml}^{-1}$	Reference
Banc D'Arguin, Mauritania	0.01–6	0.06–0.62	Bak and Nieuwland (1993)
Mauritanian upwelling	up to 40	—	Partensky et al. (1996)
Arabian Sea, Monsoons	1.2–18	0.07–1.6	Brown et al. (1999)
Arabian coast	45	—	Burkill et al. (1993)
Costa Rican Dome	up to 150	—	Li et al. (1983)
New Zealand coastal upwelling	0.3–2	0.15–1.2	Hall and Vincent (1990)
Santa Barbara Channel, California Current system	$12.3 \pm 2.4$	—	Putt and Prezelin (1985)
Northern Gulf of Alaska, SE Bering Sea	6–8	4	Liu et al. (2002)
Upwelling front, Oregon coast	2–29	0.08–0.39	Hood et al. (1992)
Oregon upwelling system	0.05–58	0.01–8.6	This study



# Distribution of Small vs. Large Phytoplankton in Oregon Upwelling System

onshore → offshore

Near Shore, relatively few small ( $<5\ \mu\text{m}$ ) phytoplankton -- mostly diatoms

Offshore, phytoplankton biomass dominated by small cells

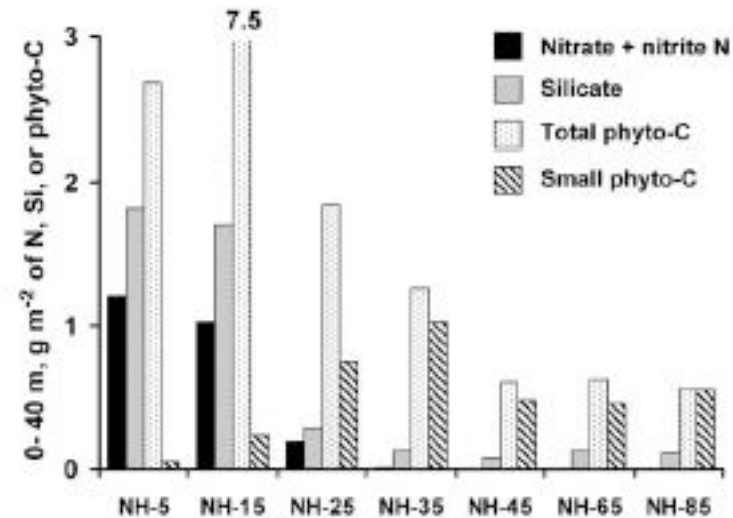
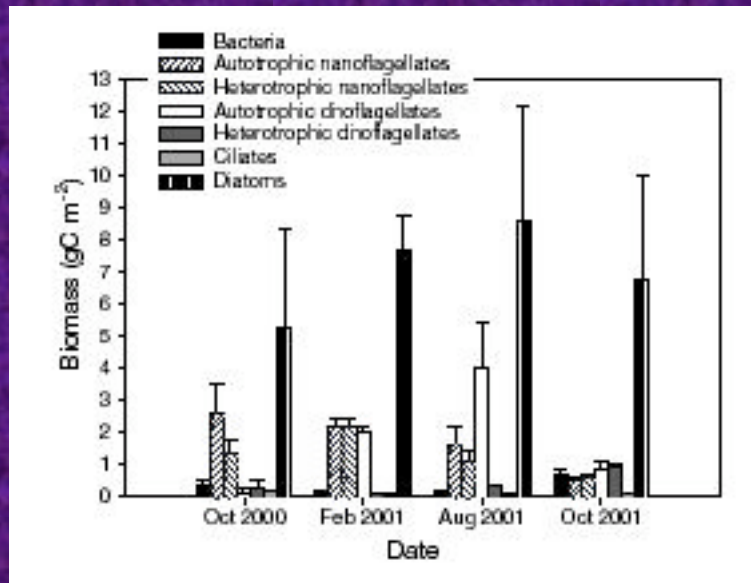


Fig. 4. Comparison of integrated 0–40 m stocks of nitrate + nitrite ( $\text{g N m}^{-2}$ ) and of silicate ( $\text{g Si m}^{-2}$ ) with biomass ( $\text{g C m}^{-2}$ ) of total phytoplankton based on chlorophyll-*a* concentration and of small phytoplankton (SYN + small PEK) based on flow cytometric analysis across the Newport Hydroline in July 2001.

Sherr et al. 2005

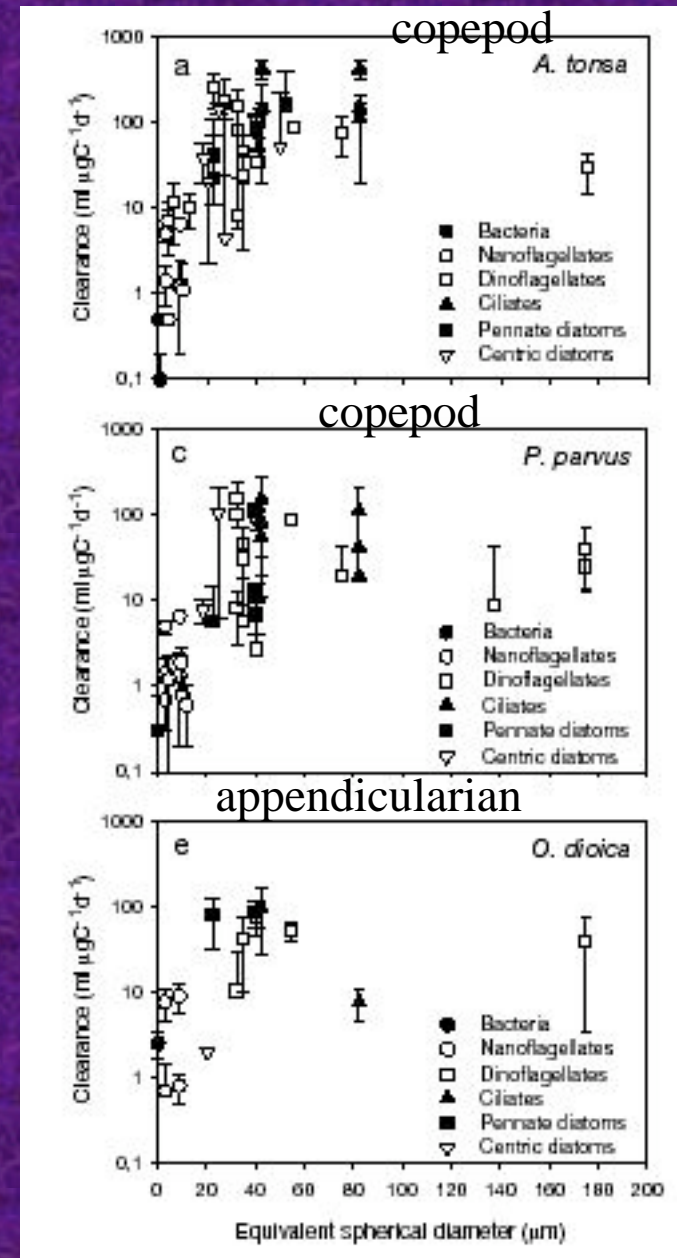
# Food Webs in Chilean Upwelling System



Biomass dominated by diatoms

Copepods and appendicularians  
have high clearance rates on  
microzooplankton, too --  
omnivory

K.Selph, OCN 621 Spring 2010



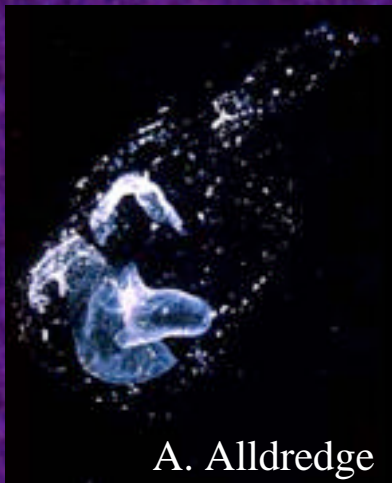
Vargas & Gonzalez 2004



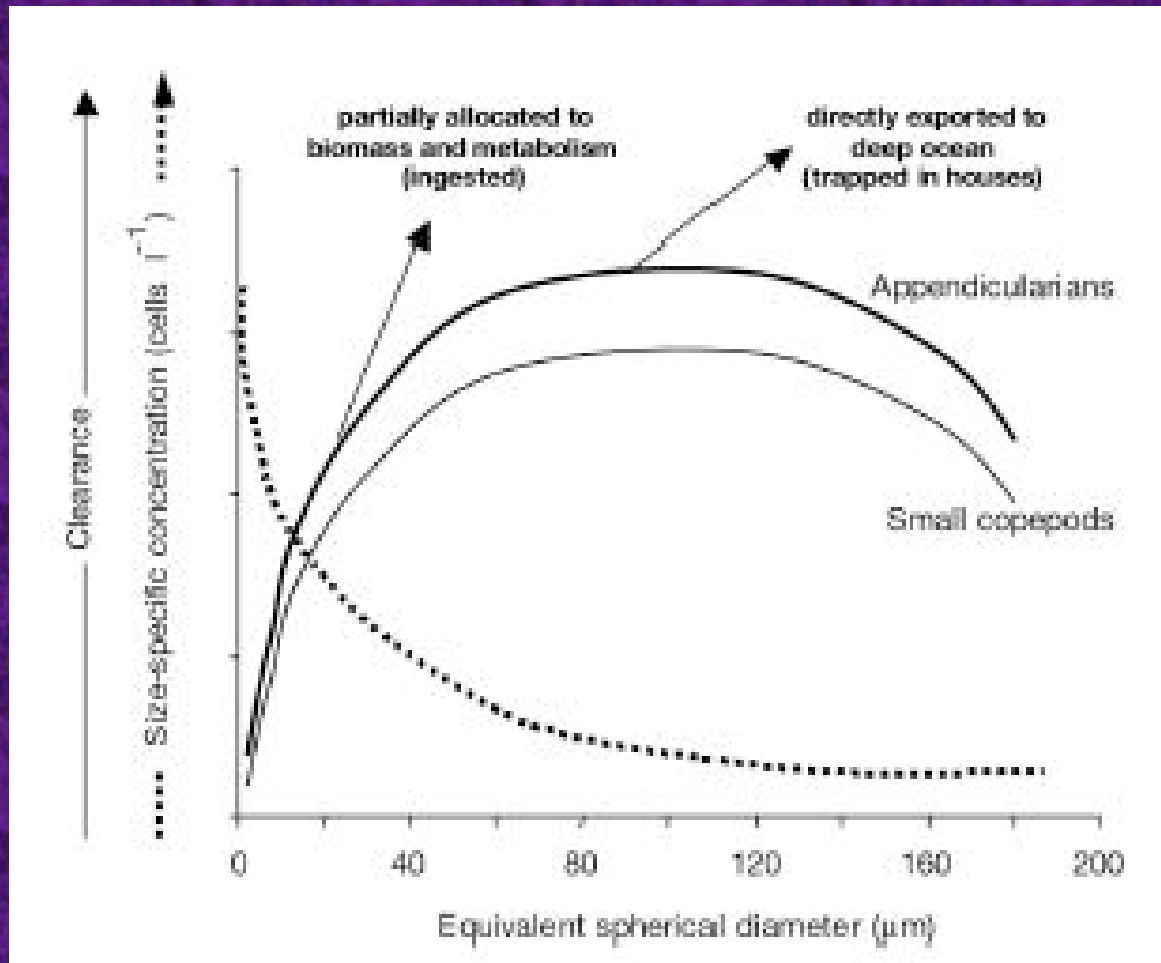
# More than one pathway for export flux...

Clearance rates show optimum prey size

Appendicularians -- consumers and responsible for passive particle scavenging



A. Alldredge

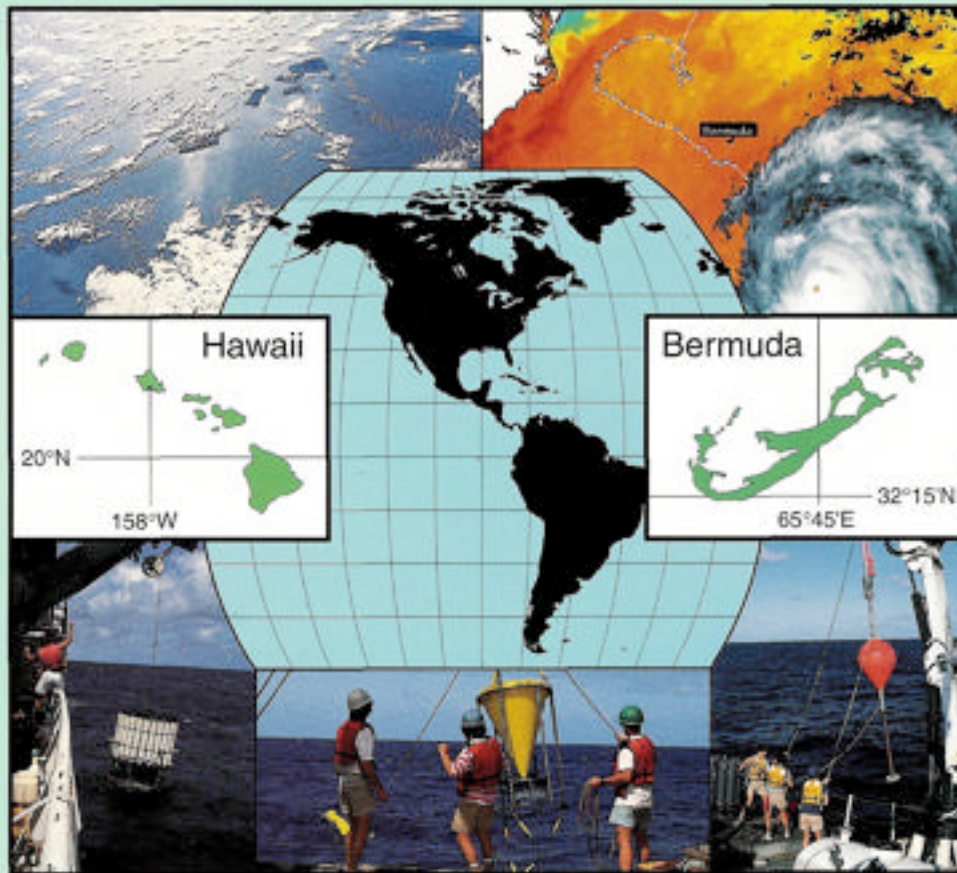


Vargas & Gonzalez 2004

# SubTropical Ecosystems

## OCEAN TIME-SERIES: RESULTS FROM THE HAWAII AND BERMUDA RESEARCH PROGRAMS

*Guest Editors: D. M. Karl and A. F. Michaels*



DSR II 1996 Vol 43

DSR II 2001 Vol 48

DSR II 2006 Brix et al.  
Vol 53:698-717

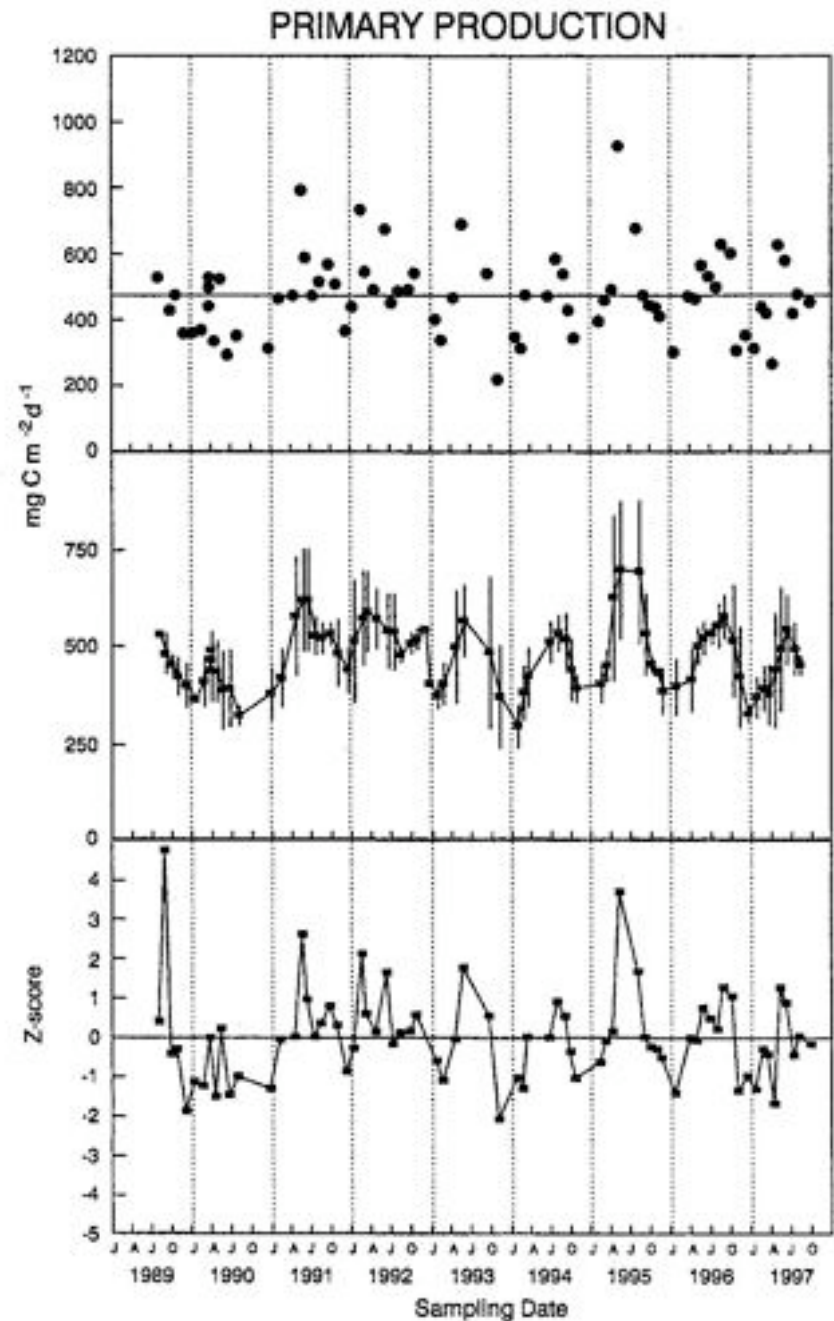
HOT Site: 22°45'N, 158°W  
BATS Site: 31°40'N, 64°10'W  
1988 to present



# HOT -- Primary Production

Figure 7. Temporal variability in depth-integrated (0–200 m) primary production measured at Sta. ALOHA over the first 9 y of the HOT program. **Top** Total euphotic-zone primary production ( $\text{mg C m}^{-2} \text{d}^{-1}$ ) measured during in situ  $^{14}\text{C}$  incubation experiments approximately monthly. The solid line is the mean value ( $473 \text{ mg C m}^{-2} \text{d}^{-1}$ ) for the full data set ( $n = 74$ ). **Center** Three-point running mean ( $\pm 1 \text{ SD}$ ) for the data presented in the top panel. **Bottom** Standard deviate (Z-scores;  $Z = [\text{value} - \text{mean}] / \text{SD}$ ) for the primary production data set showing evidence for both seasonal and interannual variability.

summer usually sees the highest phytoplankton biomass/production



# BATS -- Primary Production

Spring bloom  
(not summer like  
HOTS)

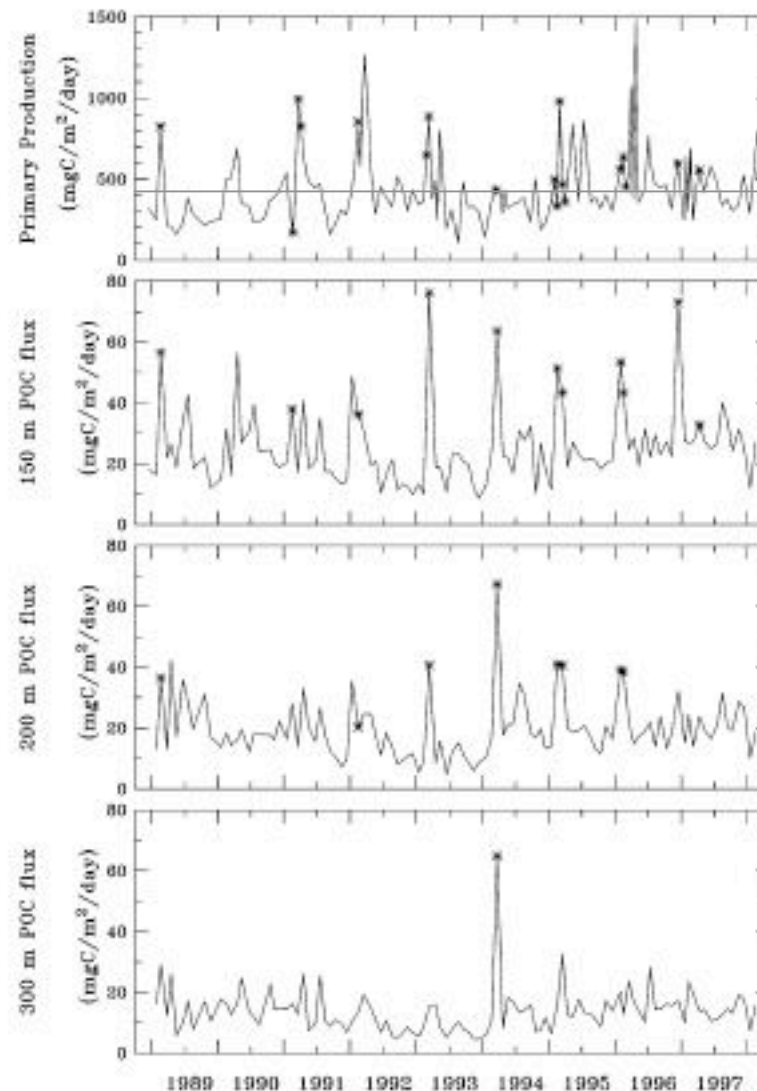


Fig. 10. Time series of integrated primary production (0–140 m) compared to the particulate organic carbon flux measured with a sediment trap at 150, 200, and 300 m. Stars indicate times of the year when physical mixing was deeper than the depth of the measurement (e.g. mixing was deeper than 150 m for integrated primary production and 150-m trap flux, and deeper than 200 m for 200-m trap flux).

Steinberg et al. 2001 DSR II, 48, 1405-1447



# Data Comparison

Table 2

Variability in primary production ( $^{14}\text{C}$  method), particulate carbon export (measured at 150 m using sediment traps) and the export ratio (e-ratio) for the 11-year BATS and HOT data sets

Parameter	BATS	HOT
Primary Production ( $\text{mg C m}^{-2} \text{ d}^{-1}$ )		
Mean $\pm$ SD	$416 \pm 178$	$480 \pm 129$
Range	111 to 1039	184 to 923
Number of observations	125	94
Particulate Carbon Flux ( $\text{mg m}^{-2} \text{ d}^{-1}$ )		
Mean $\pm$ SD	$27.2 \pm 13.9$	$28.3 \pm 9.91$
Range	8.7 to 76.1	10.7 to 57.0
Number of observations	125	98
Export Ratio		
Mean $\pm$ SD	$0.072 \pm 0.038$	$0.062 \pm 0.026$
Range	0.016 to 0.214	0.020 to 0.149
Number of observations	125	89

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# Ecosystem Structure in Gyres

Multi-level, start out with small primary producers (picoplankton)...



how many trophic levels?



# Trophic Cascades

- Microbial loop organisms the most important (recycling system)
- Size fractionation experiments suggest several trophic levels smaller than 20  $\mu\text{m}$

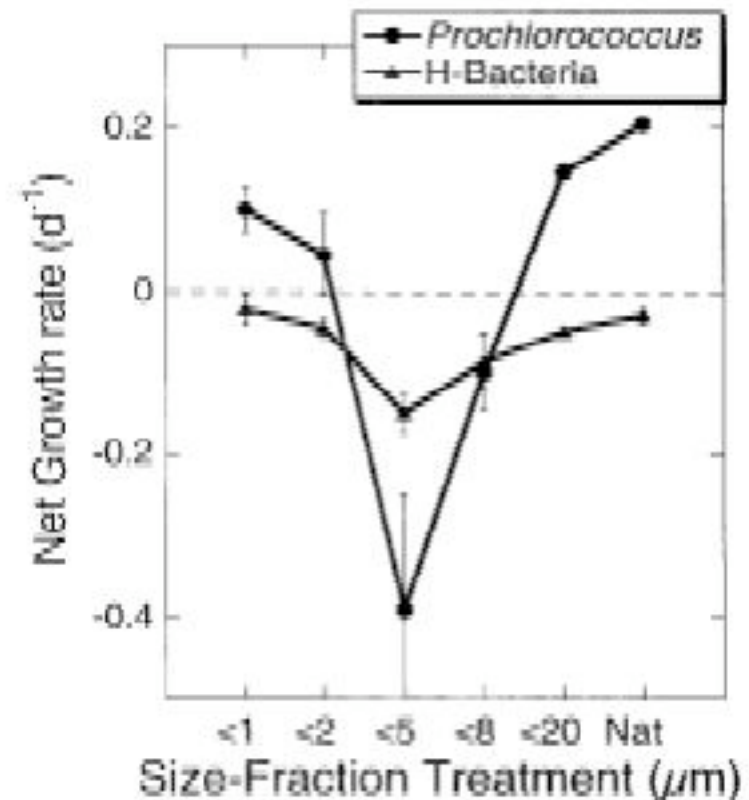


Figure 2. Effects of size-fraction removal of protistan consumers on the net growth rate of heterotrophic bacteria and *Prochlorococcus*. Seawater was collected from 110 m in the subtropical Pacific (Stn. ALOHA). Net population changes were determined from flow cytometric analyses on initial and final samples incubated at 1% surface light for 24 h after filtration through polycarbonate membrane filters of 1–20  $\mu\text{m}$  pore size (Nat=natural sample control with no filtration). Vertical bars show standard errors of 4 replicates (modified from Calbet & Landry, 1999).

# Mesozooplankton Biomass, HOT site

Timing of maximum is the most puzzling:

In the summer, when the water column is the most stratified (as opposed to the spring, after winter mixing)

Coincides with blooms of  $N_2$  fixers, such as *Trichodesmium*

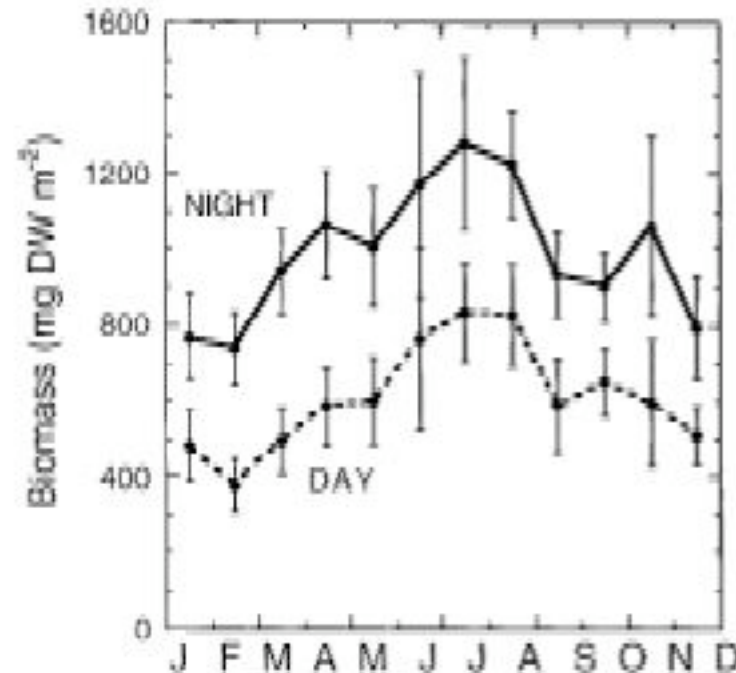
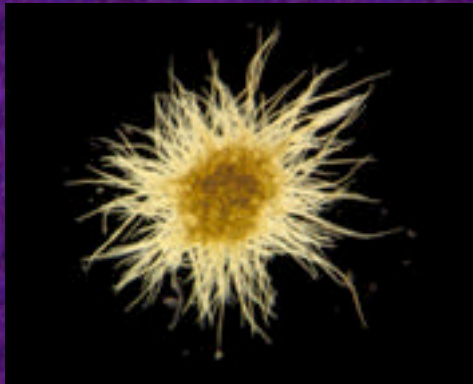


Figure 5. Seasonal variation of mesozooplankton biomass in day-time (1000–1400) and nighttime (2200–0200) net collections at Stn. ALOHA, subtropical North Pacific. Dry weight samples were taken from integrated oblique hauls over the euphotic zone (mean tow depth=155 m) with a 1-m<sup>2</sup> net and 200- $\mu$ m mesh (Landry et al., 2001). Error bars are 95% confidence intervals for the means of all samples collected within each month from 1994 through 2000.



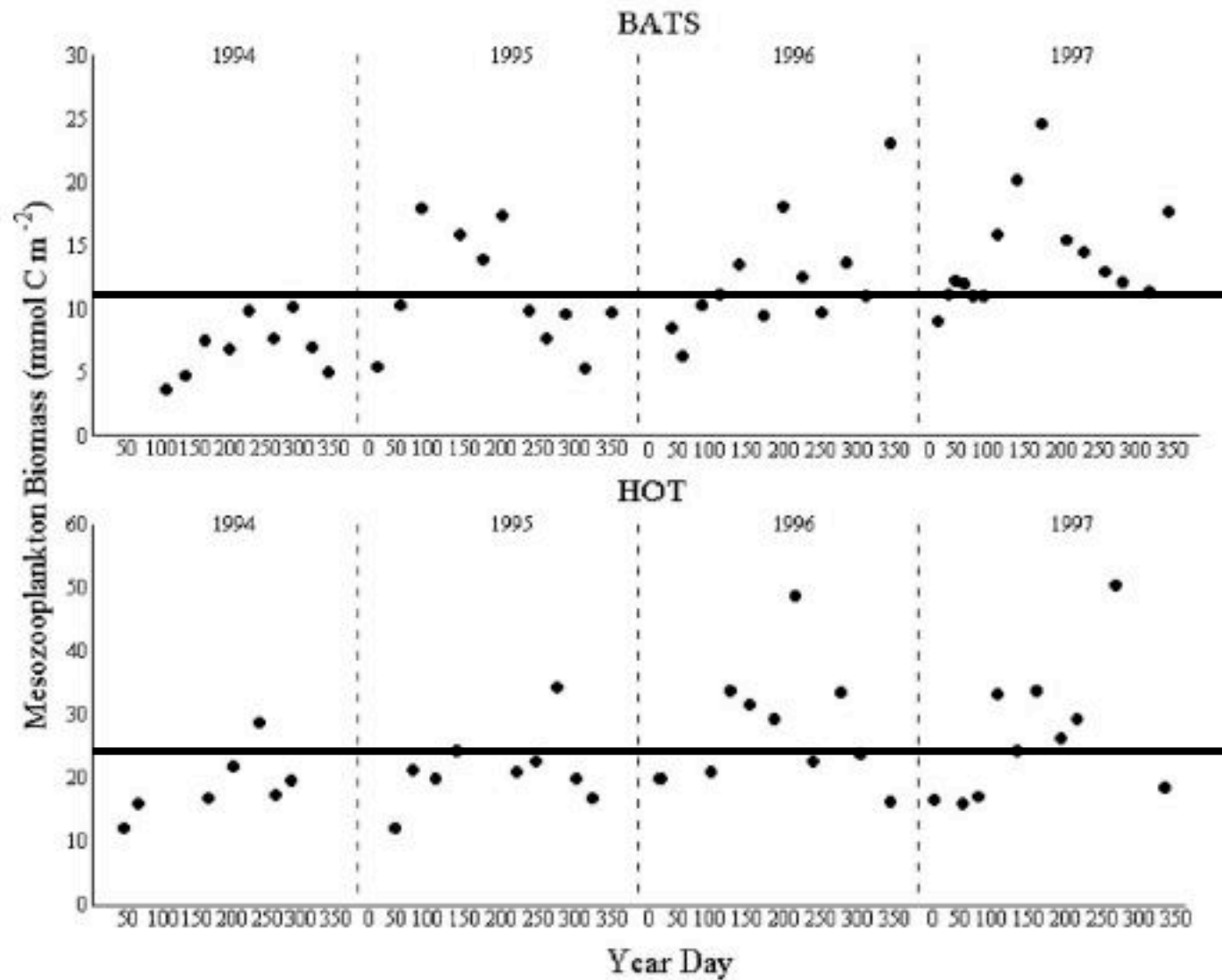


Fig. 1. Mesozooplankton biomass (mmol C m<sup>-2</sup>) in the surface 150 m at BATS and HOT for 1994–1997.

# HOT/BATS MesoZP comparison

Table 1

Hawaii ocean time series and Bermuda Atlantic time series 1994–1997<sup>a</sup>

	Mean <sup>HOT</sup>	SD <sup>HOT</sup>	N <sup>HOT</sup>	Mean <sup>BATS</sup>	SD <sup>BATS</sup>	N <sup>BATS</sup>
0.2–0.5 mm zooplankton mmol C m <sup>-2</sup> (% total)	4.33 (18.16)	1.42	36	2.46 (21.62)	0.98	47
0.5–1 mm zooplankton mmol C m <sup>-2</sup> (% total)	5.66 (23.74)	2.49	36	3.01 (26.45)	1.24	47
1–2 mm zooplankton mmol C m <sup>-2</sup> (% total)	6.69 (28.06)	3.26	36	2.54 (22.32)	1.09	47
2–5 mm zooplankton mmol C m <sup>-2</sup> (% total)	5.64 (23.66)	2.80	36	2.46 (21.64)	1.26	47
> 5 mm zooplankton mmol C m <sup>-2</sup> (% total)	1.52 (6.38)	1.17	36	0.91 (8.00)	0.62	47
Total zooplankton mmol C m <sup>-2</sup>	23.84	8.85	36	11.38	4.61	47
Zoopl production and egestion mmol C m <sup>-2</sup> d <sup>-1</sup>	2.25	0.73	35	0.95	0.30	46
Zooplankton ingestion mmol C m <sup>-2</sup> d <sup>-1</sup>	7.49	2.42	35	3.17	1.00	46
Zooplankton mortality mmol C m <sup>-2</sup> d <sup>-1</sup>	2.20	0.80	35	0.93	0.34	46
Temperature (C°)	24.32	1.05	36	21.50	1.53	47
Sinking flux mmol C m <sup>-2</sup> d <sup>-1</sup>	2.14	0.49	31	2.26	0.74	43
Primary production mmol C m <sup>-2</sup> d <sup>-1</sup>	41.08	9.84	34	35.31	8.05	46

<sup>a</sup>Values integrated from surface to 150 m.

Roman et al. 2002, DSR II, 49: 175-192



Table 3

Integrated annual values ( $\text{mol C m}^{-2} \text{yr}^{-1}$ )

	Primary production	Zoopl prod and egestion	Zoopl./prim prod ratio	Sinking flux	Eges/sinking ratio
<i>BATS</i>					
1994	13.00	0.20	0.02	1.03	0.20
1995	14.01	0.34	0.02	0.73	0.46
1996	14.92	0.37	0.02	0.91	0.41
1997	11.79	0.42	0.04	0.85	0.49
Mean <sub>SD</sub>	13.43 <sub>1.17</sub>	0.33 <sub>0.08</sub>	0.02 <sub>0.01</sub>	0.88 <sub>0.11</sub>	0.39 <sub>0.11</sub>
<i>HOT</i>					
1994	13.66	0.62	0.05	0.68	0.91
1995	18.61	0.70	0.04	0.67	1.05
1996	14.14	0.92	0.07	0.77	1.20
1997	13.25	0.90	0.07	0.92	0.98
Mean <sub>SD</sub>	14.92 <sub>2.16</sub>	0.79 <sub>0.13</sub>	0.05 <sub>0.01</sub>	0.76 <sub>0.10</sub>	1.03 <sub>0.11</sub>

Why the difference? Don't know for sure,  
but...

- Salps and sarcodines at BATS -- not quantified well with net tows (grazers and mixotrophs)
- Mesoscale eddies at BATS leading to episodic nutrient enrichments -- uncoupling of 1° producers and consumers

[www.pbs.org](http://www.pbs.org)



L. Madin, WHOI





**On the relationships between primary, net community, and export production in subtropical gyres, 2006, Deep-Sea Res. II, 53:698-717,**  
Holger Brix, Nicolas Gruber, David M. Karl and Nicholas R. Bates

- Export POC/Net Primary Production
  - If ratio high, then “export pathway” ecosystem  
(larger phytoplankton)
  - If ratio low, then “regeneration” ecosystem  
(microbial loop organisms dominate)
- Switch between these states by addition of increased nutrients
- 10 year data set at HOTS and BATS:
  - BATS: Export pathway in Spring, Regeneration Pathway in Summer, Fall
  - HOTS: Regeneration pathway all year round

## Aside: Modern Primary Production Measurements vs. Historical

Subtropical Gyres: 111 - 1039 mg C/m<sup>2</sup>/d

(~40 - 380 g C/m<sup>2</sup>/y)

historical: <100 g C/m<sup>2</sup>/y

Note that fisheries oceanographers still use the lower numbers, along with lower estimates of trophic levels leading to fish -- the combined effect of these opposing trends may luckily end up with fisheries yields that aren't too far off...

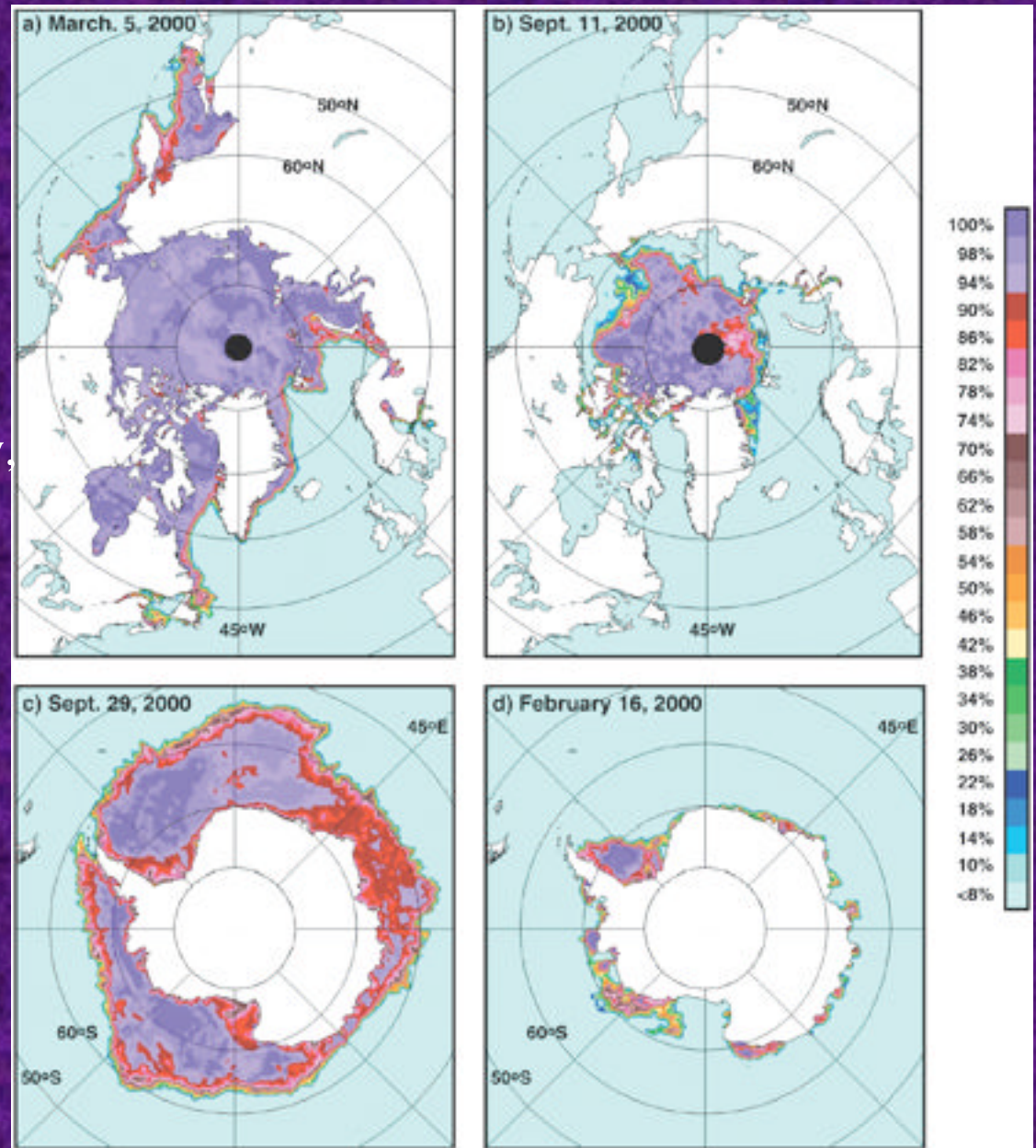


# Polar Ecosystems: Arctic vs. Antarctic

- Size (15 mill km<sup>2</sup> vs. 36 mill km<sup>2</sup>)
- Arctic Sea Ice only 2-fold annually, whereas it is 5-fold lower in the Southern Ocean over that period
- Sea surrounded by Land vs. Land surrounded by Sea, so ability to exchange with other regions very different

Max (end of winter)

Min (~Fall)



## Arctic vs. Southern Ocean -- very different

- 1/3 of Arctic Ocean is shelf seas ( $\leq 100$  m), mean depth 1800 m
- Continental shelves of Antarctica very narrow, with pack ice zone over deep ocean basins (4000 - 6500 m deep)
- Arctic affected by freshwater flows from surrounding rivers and their contents (high productivity in coastal/upwelling areas, but short-lived)
- Southern Ocean fairly isolated from land (HNLC area)  
-- high productivity in areas affected by shelf sediments, otherwise Fe-limited and fairly low



# Arctic Ocean

## *Ice effect on Bloom Timing*

e.g., bloom relatively late in year as ice needs to melt

- Results in short growing season (tied to light)
- Zooplankton: grow slowly, have short feeding season, rest at depth over winter
- May take two-three years to complete growth cycle e.g., *Calanus glacialis* & *C. hyperboreus*

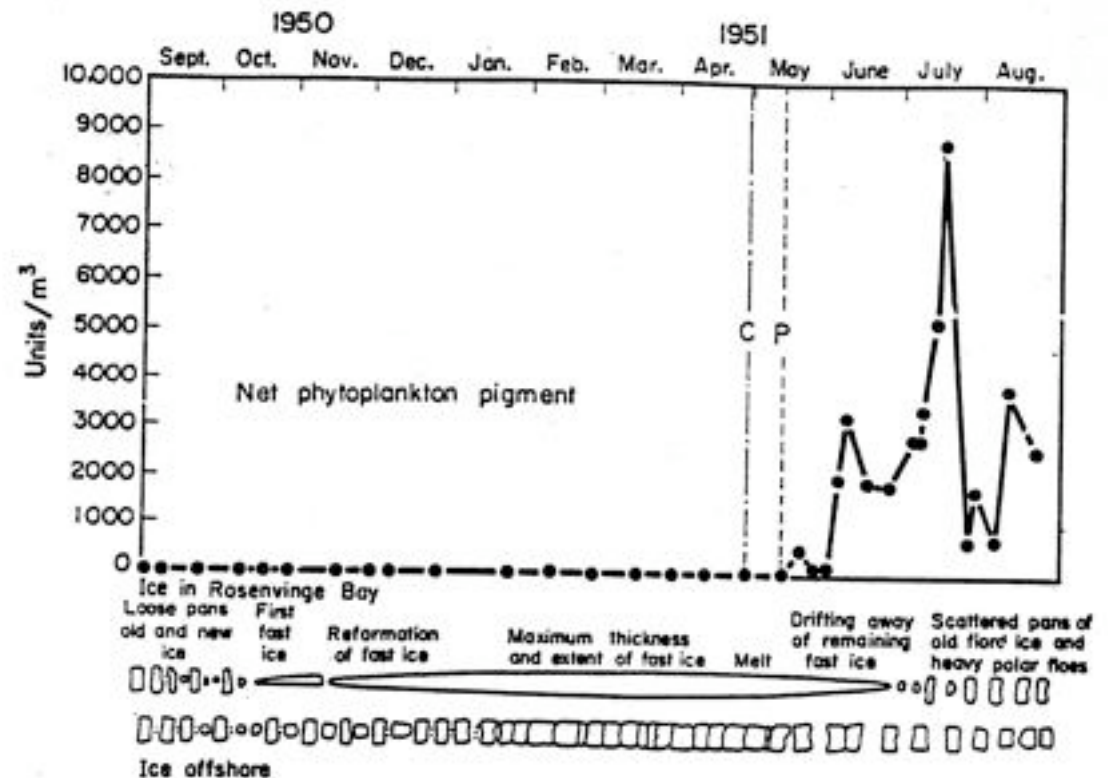
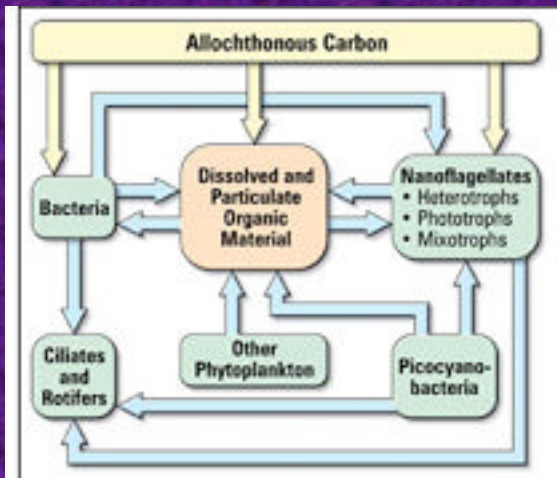
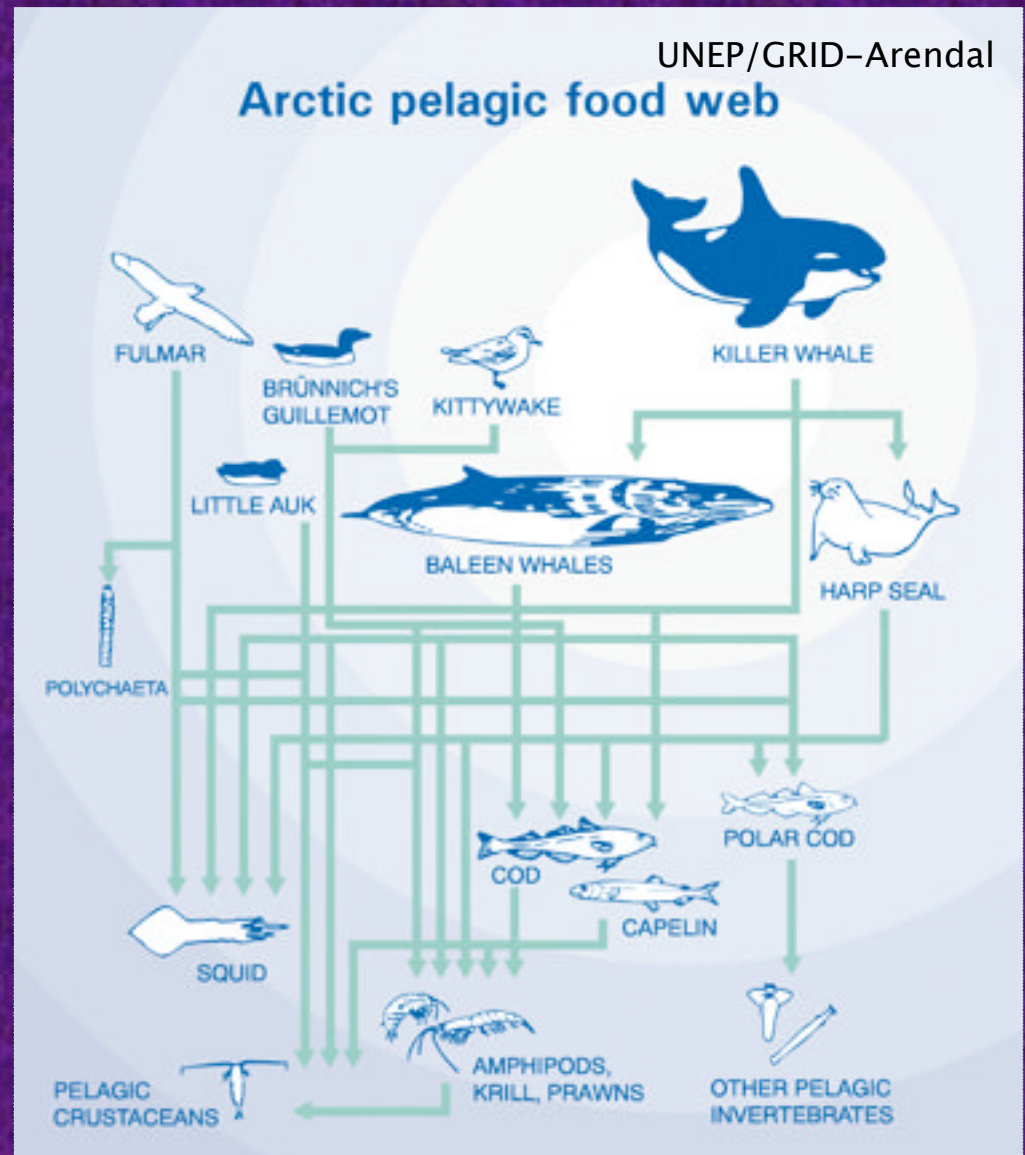


FIG. 8.2 Seasonal changes in growth of phytoplankton and in ice conditions in Scoresby Sound, Greenland.  
C = date of onset of phytoplankton growth as seen by cell counts.  
P = date by which phytoplankton growth was indicated by net pigment (after Digby, 1953).

# Arctic Pelagic Food Web



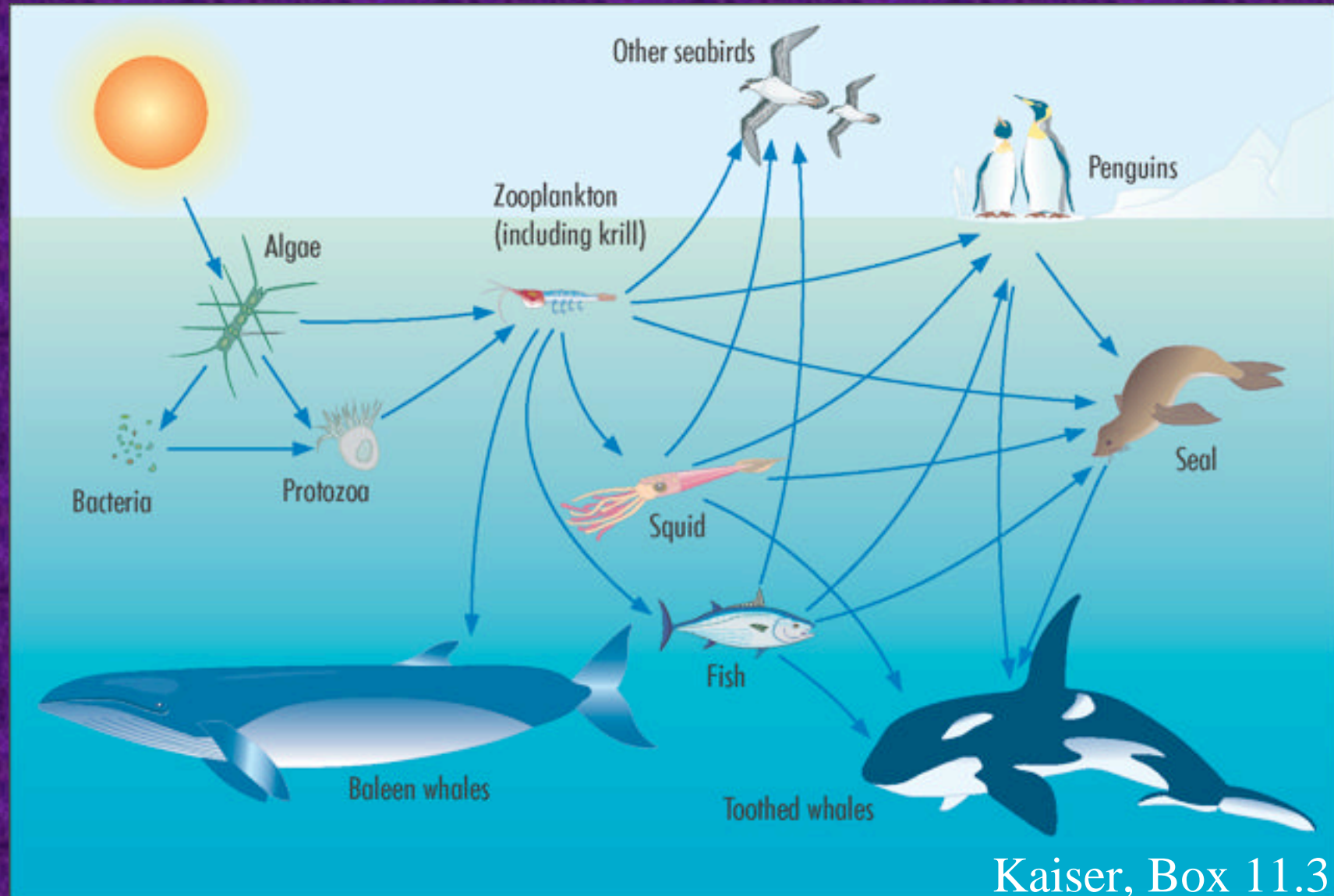
<http://www.cen.ulaval.ca/merge/index.php?url=11214>



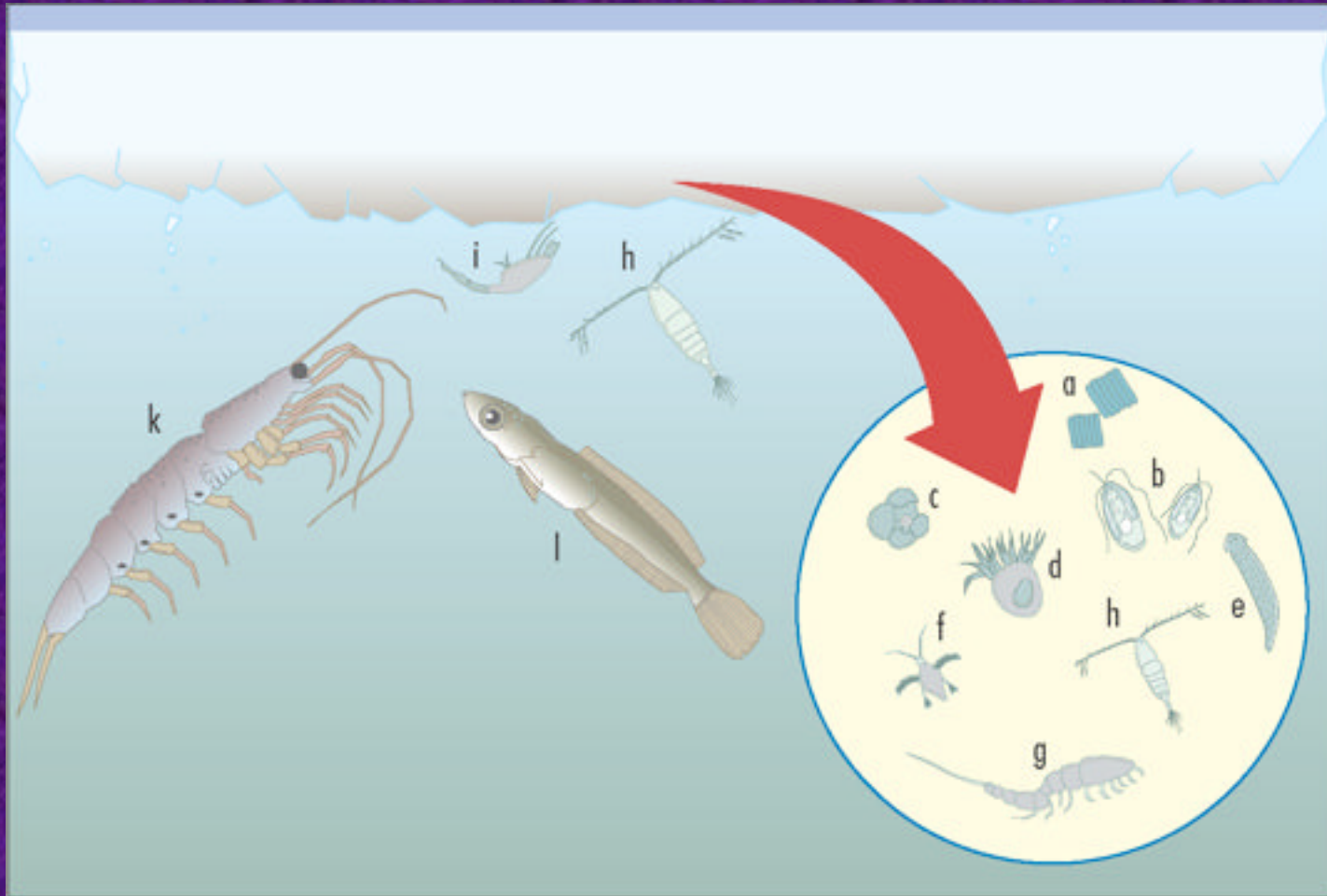
<http://maps.grida.no/go/graphic/arctic-pelagic-food-web>



# Antarctic: Southern Ocean Krill as a Keystone Species



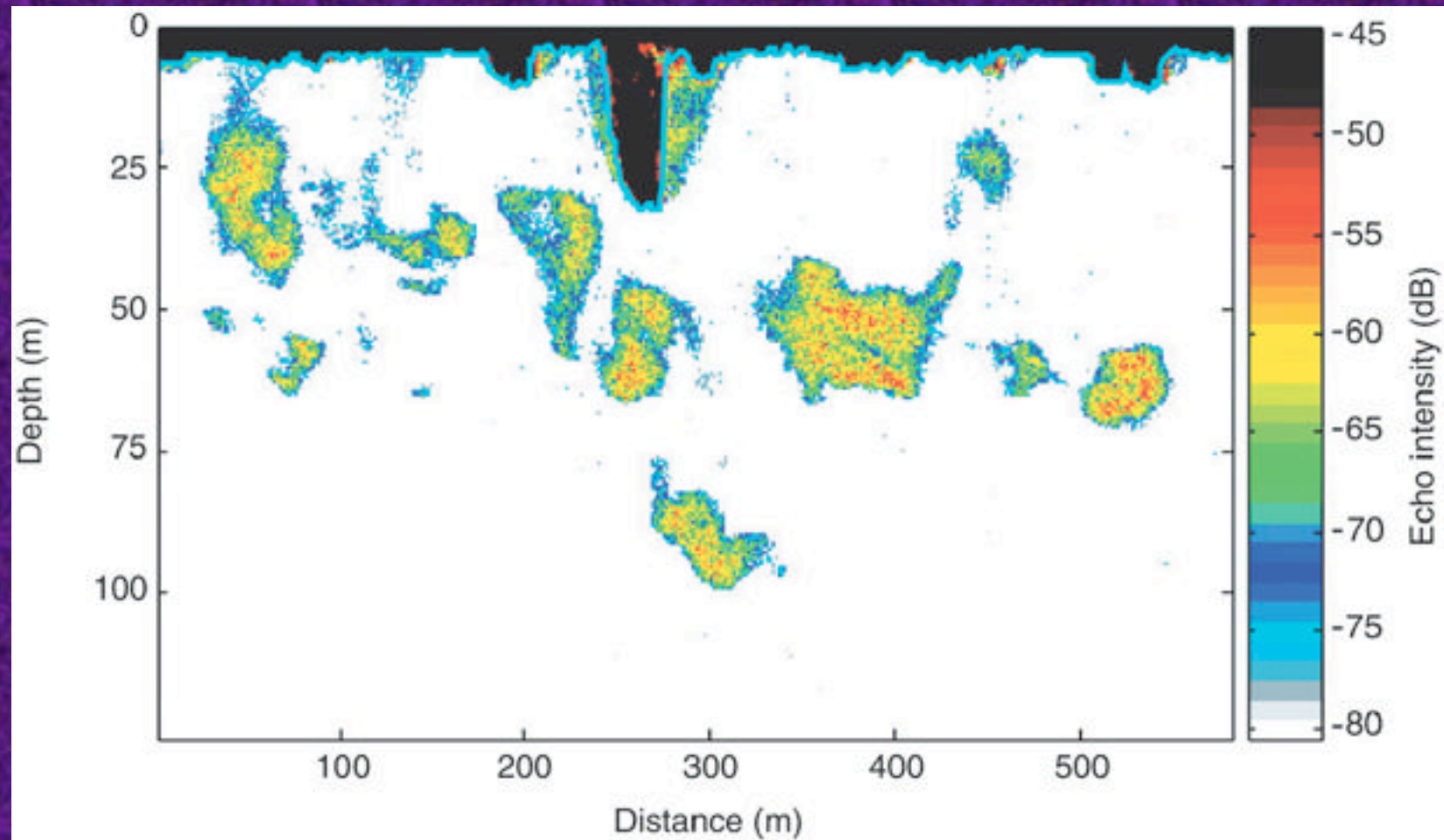
# Antarctic Sea Ice Community



Kaiser, Fig. 11.8



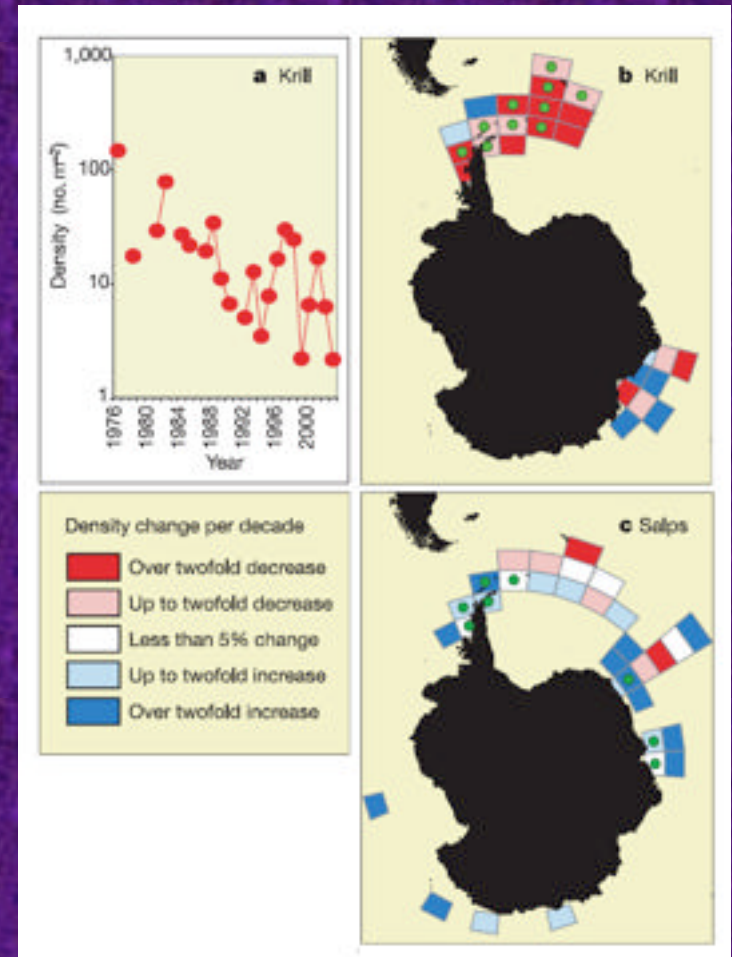
# Krill Swarms under the Sea Ice



Kaiser, Box 11.3

# Krill vs. Salps

- Changing Ecosystem -- may be due to decline in sea ice
  - Since 1926, decline in krill populations (38 - 75%) and an increase in salps (>66%)
  - krill need sea ice algae nutrition prior to spawning & for juvenile stages in winter and feed on Spring bloom phytoplankton
  - salps can survive in warmer water and at lower phytoplankton concentrations and do not feed on sea ice



Atkinson et al. 2004



# Summary:

## Why are marine ecosystems so different?

Why does the North Atlantic bloom so dramatically?

Why doesn't the North Pacific?

Why aren't there ever blooms in the vast open ocean regions?

### *Extraordinarily Simplistic Answer*

All systems have microbial organisms, as well as the larger phytoplankton and consumers, but physical processes force the system towards dominance of one ecosystem over another.

# Dominant Pathways are determined by physical processes

- Small cells are more efficient in competing for low N (high surface area:volume)
- General size hierarchy of consumers based on energetic considerations, i.e., for like organisms, reduced size and biomass of prey makes the environment more suitable for smaller consumers
- Energetic reasons why small primary consumers are favored in oligotrophic open ocean systems (subtropical gyres):
  - reduced [phyto]  $\longrightarrow$  I declines for given  $F_{\max}$
  - decreased phyto size  $\longrightarrow$   $F_{\max}$  declines for consumer of given size
  - increased  $T^{\circ}\text{C}$   $\longrightarrow$  higher I is required for maintenance or to sustain a given level of growth



# Diatoms : “dynamic” component in the food web

Diatoms are responsive to high nutrient conditions and can escape “control” of grazers.

In the absence of “external energy” to stimulate diatom blooms, a eutrophic system shifts to oligotrophic system

-seasonally, e.g., spring to summer in temperate systems

-spatially, e.g., distance from upwelling source

100  $\mu$ m

Diatoms decrease in relative abundance from:

–Eutrophic Systems	→	Oligotrophic Systems
–High Latitude	→	Low Latitude
–Spring Season	→	Summer Season
–Upwelling Source	→	Distance from Upwelling



# Low Energy Stable Systems

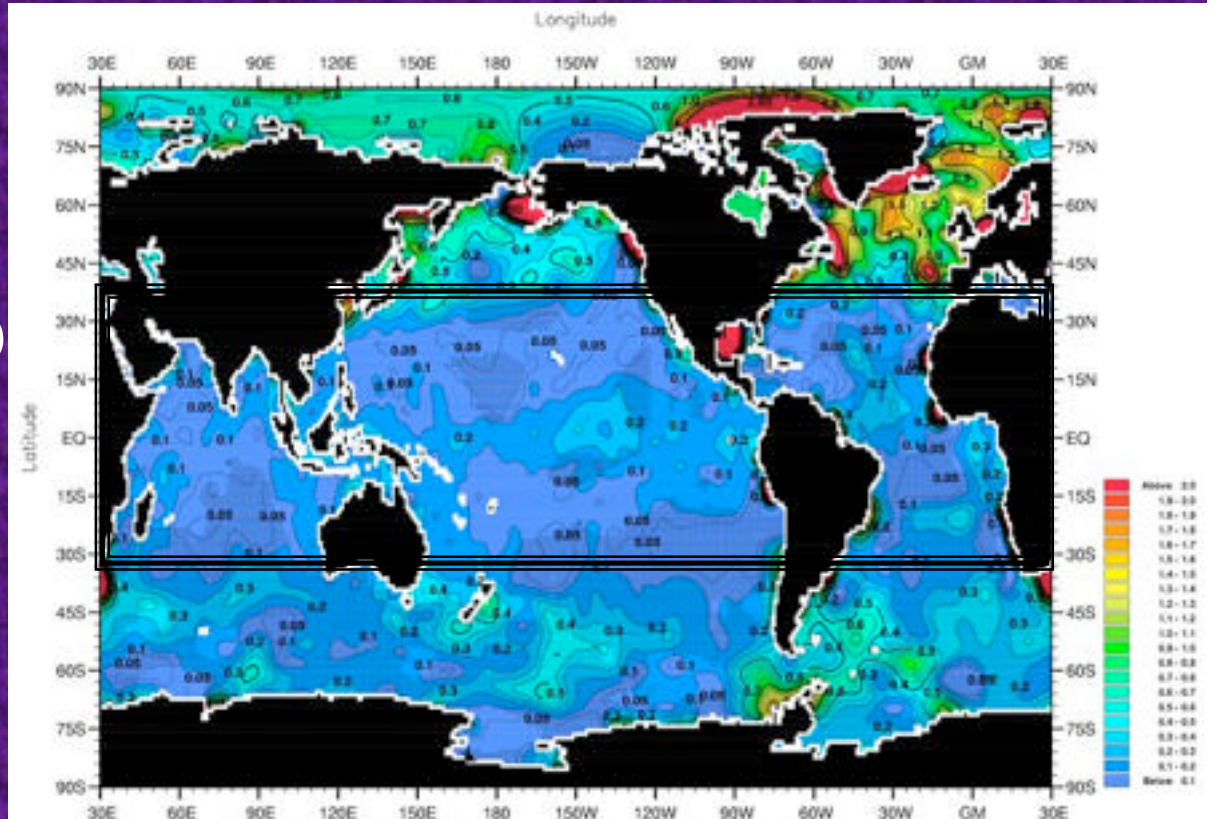
Low energy → Lack of nutrient re-supply

↓  
Low nutrients  
(oligotrophic)

↓  
Small Phytoplankton  
(high surface:volume ratio)

↓  
Long food chains  
(small consumers at base)

↓  
Relatively stable  
system (high recycling)





# High Energy Unstable Systems

High energy  
(storm activity, eddy  
action, upwelling, etc.)



High nutrients  
(eutrophic)



Large Phytoplankton  
(small, too)



Short food chain (dynamic)  
(superimposed on stable long food chain)



Unstable (dynamic)  
system  
(High “new” production)

