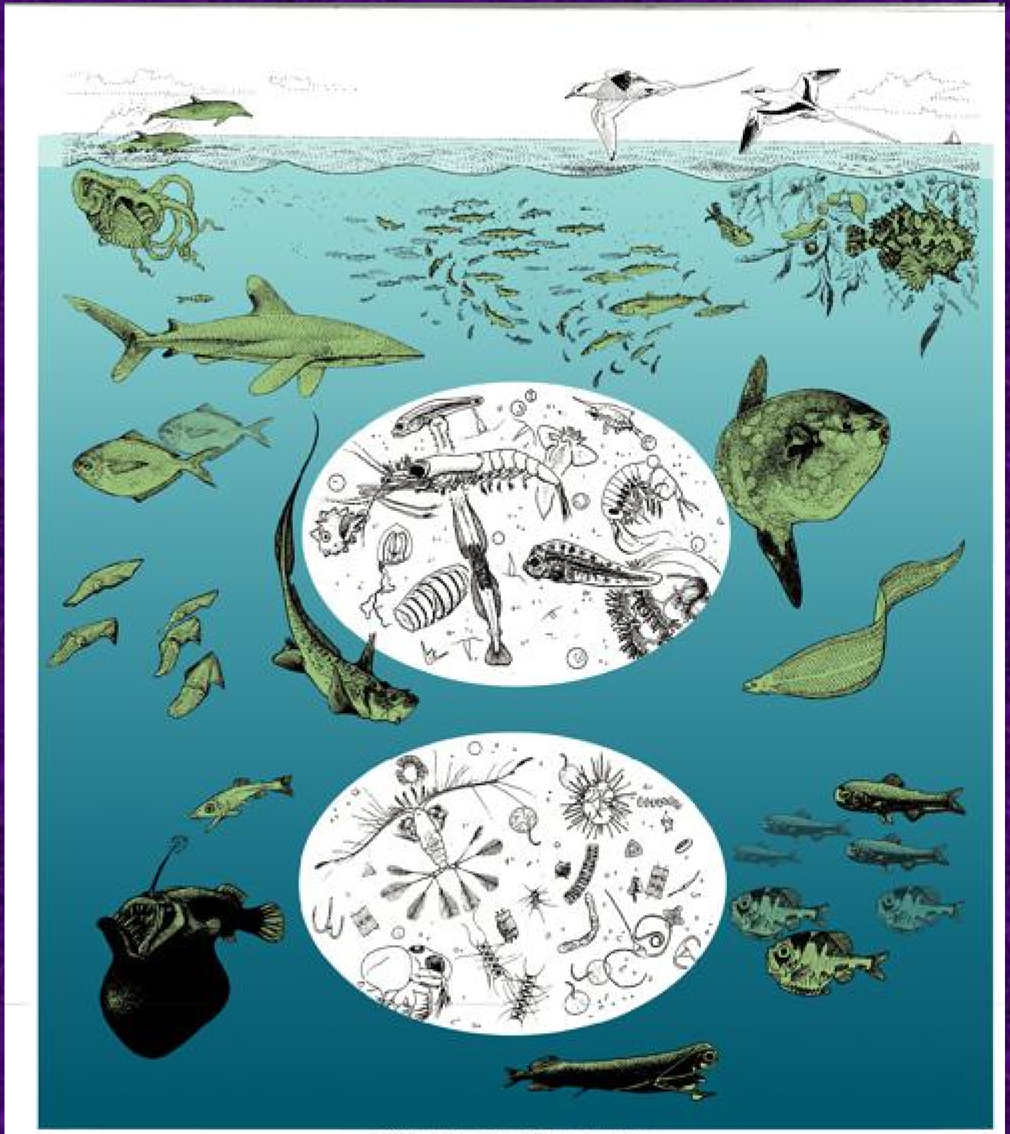
Food Webs



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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

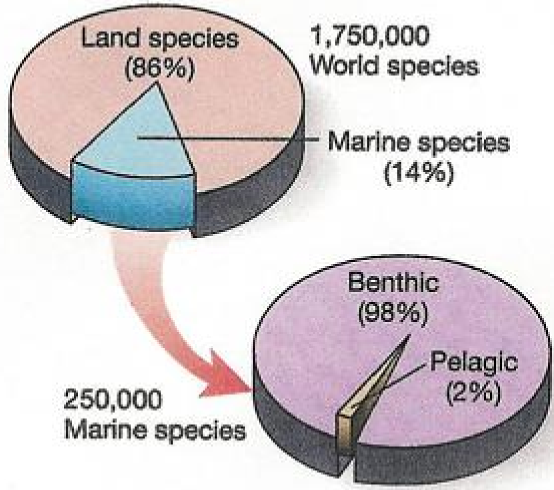


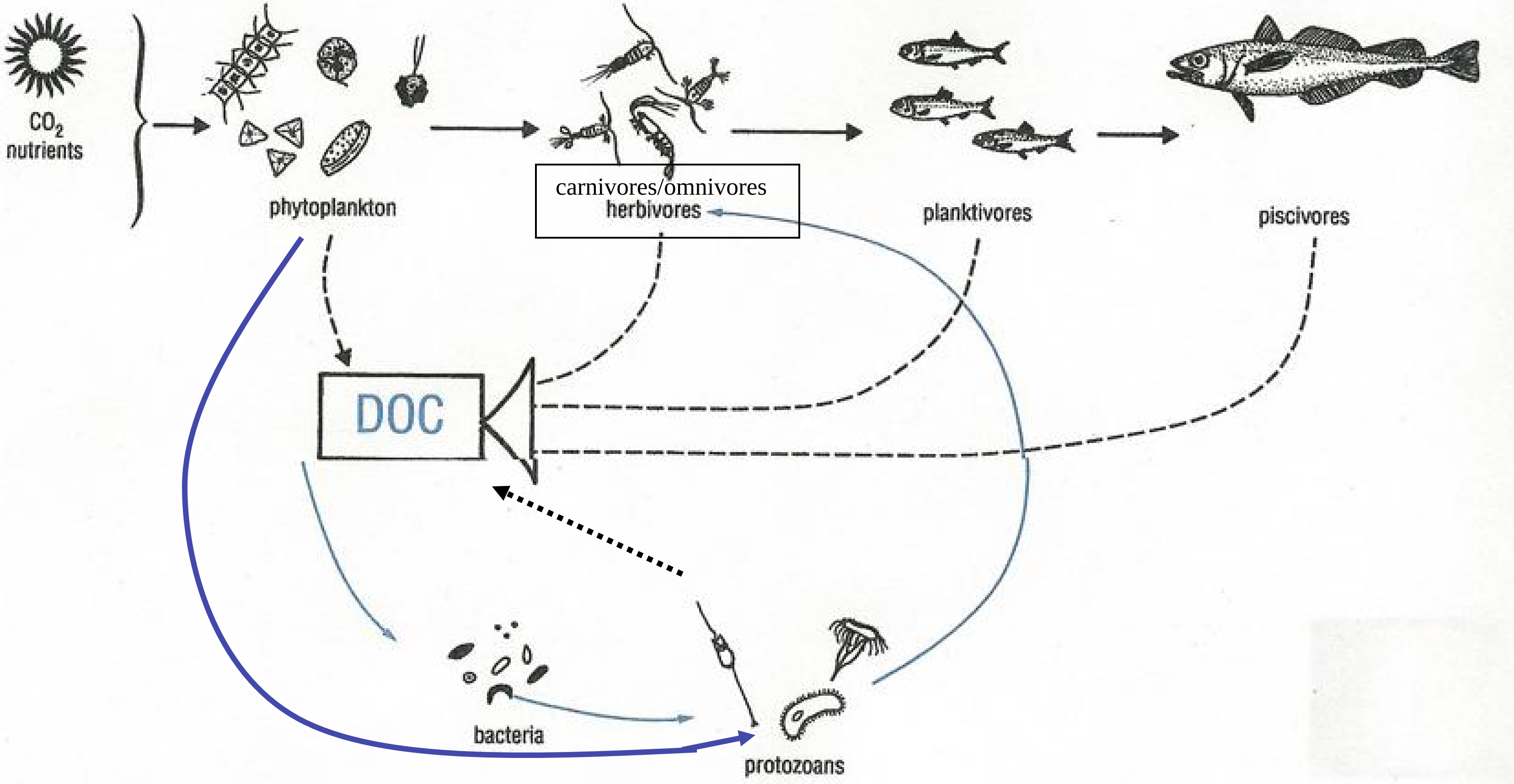
Figure 13–6 **Distribution of species on Earth.**

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?

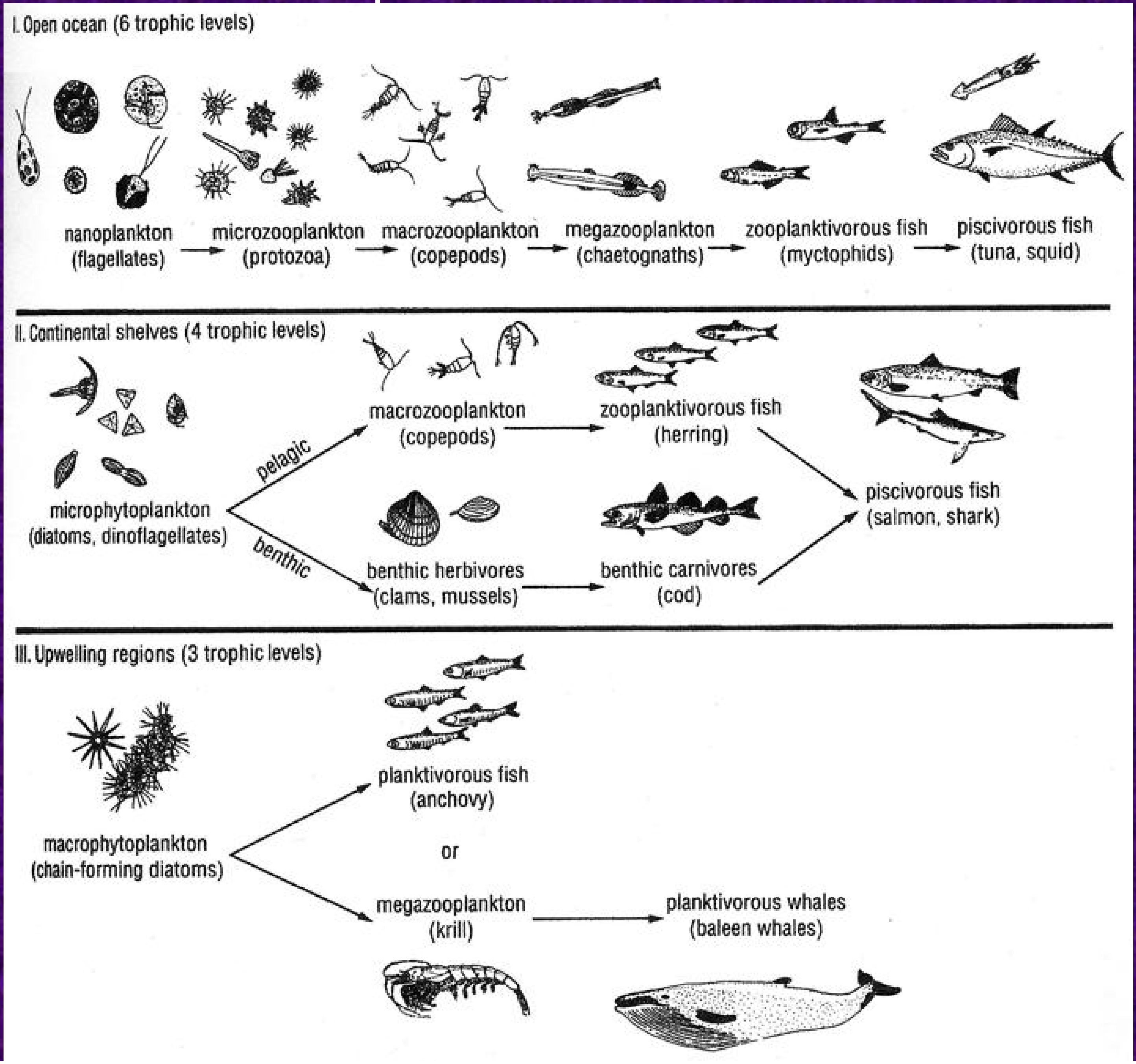
Integrating Classical and Microbial Loop Food Webs

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.



modified from Lalli & Parsons 1997

Comparison of food web structures



oligotrophic

↓

eutrophic

Lalli & Parsons 1997

NW Atlantic Food Web

Humans (7 - 10)

Whales/porpoises/ birds (6 - 9)

Squid (5 - 8)

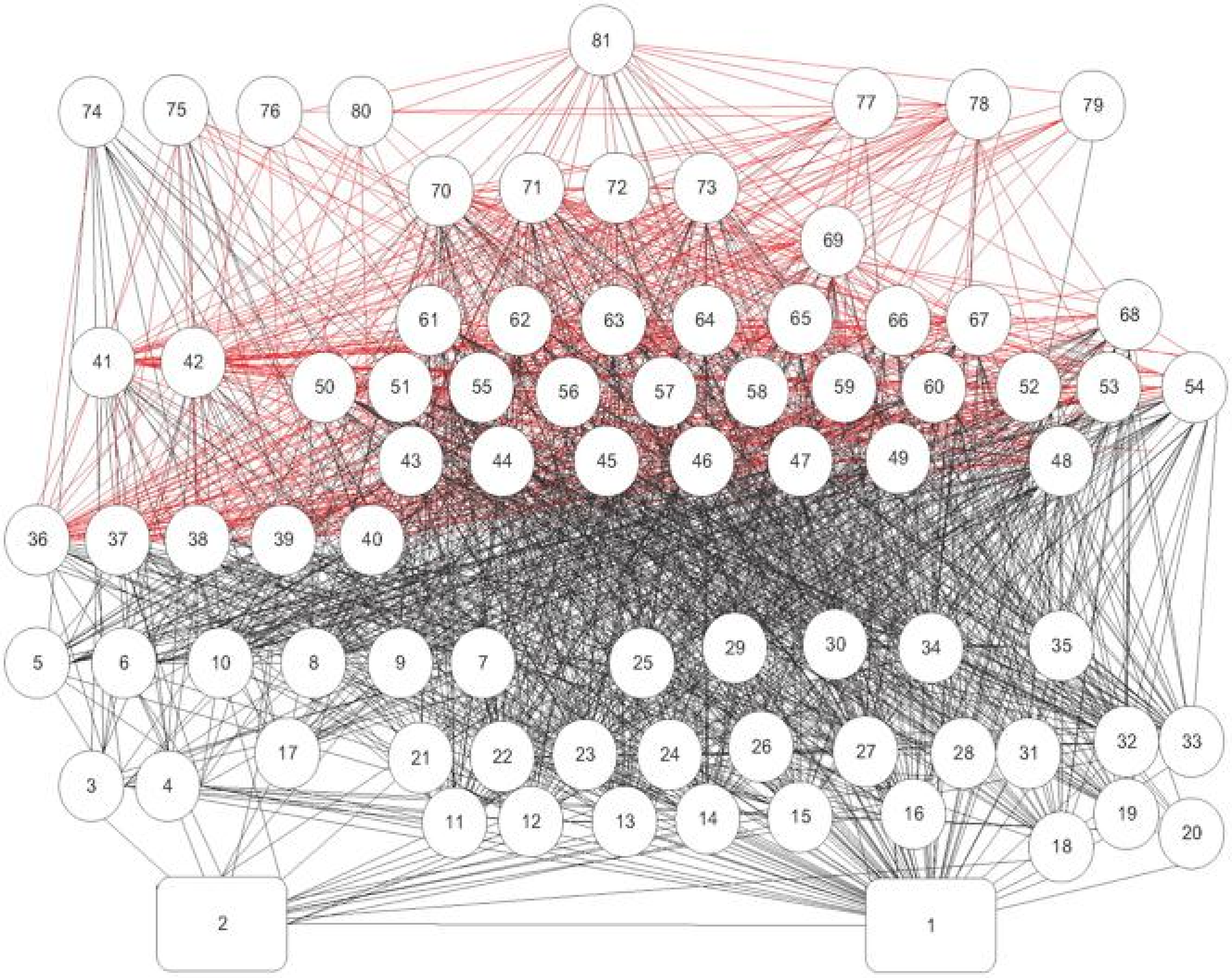
Bigger fish (4 - 7)

Small fish (4 - 6)

Ctenophores/ Chaetognaths (3 - 5)

Copepods (2 - 4*)

Phytoplankton (1)



Link, 2002

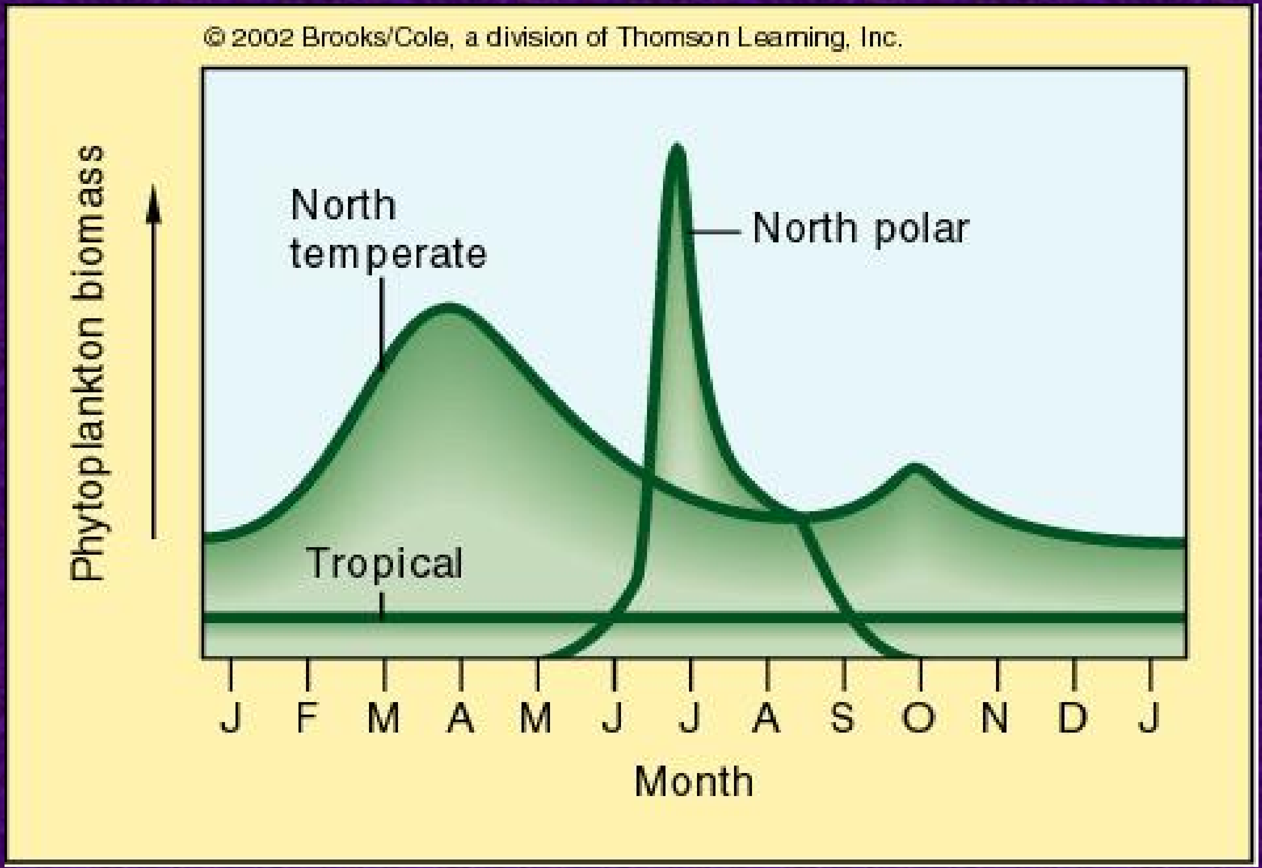
Historical Observations of Seasonal Cycles

- 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)

Spring blooms

biomass, not production



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

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

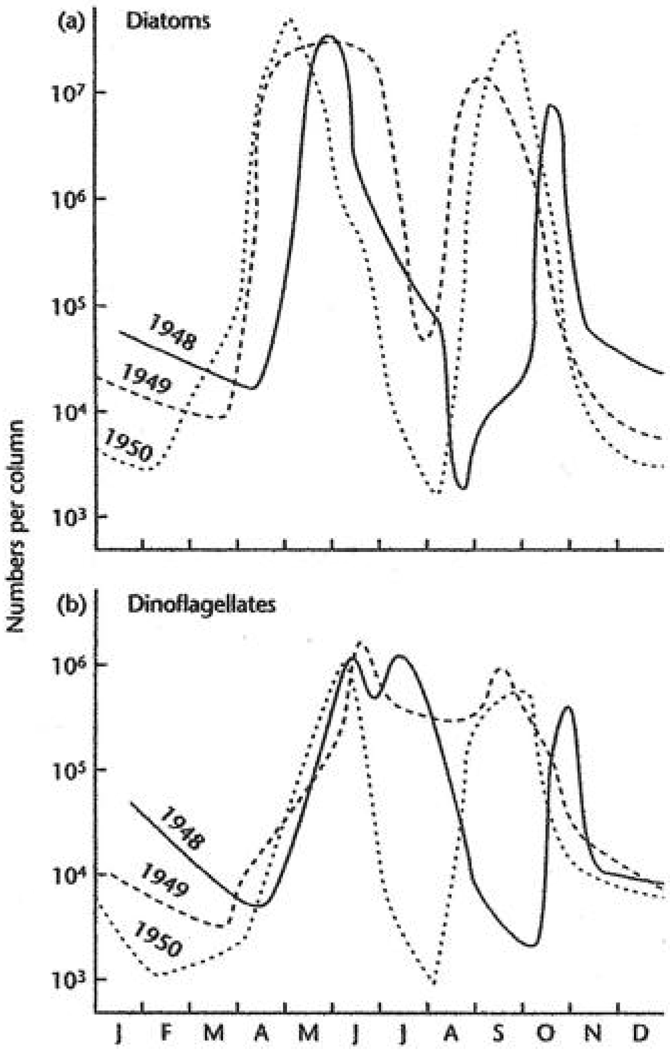
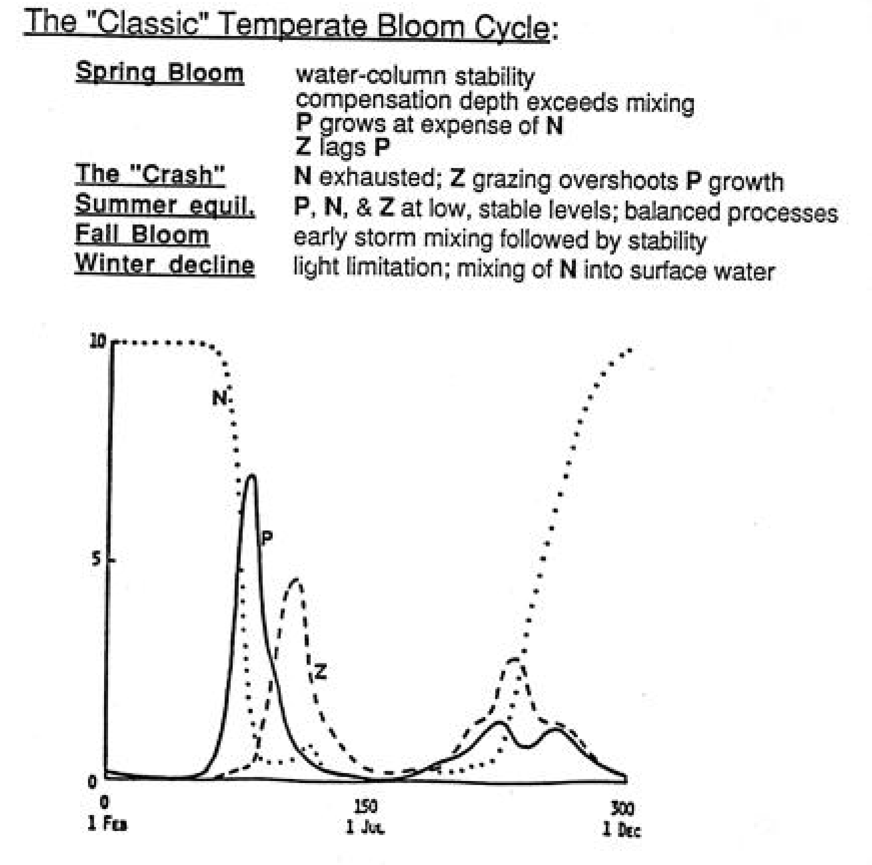


Fig. 1.12 Seasonal cycles of (a) diatoms and (b) dinoflagellates at Station "I" (60°N, 20°W) in the North Atlantic. Diatoms bloom, and then are replaced by dinoflagellates. Bloom timing varies among years by a month or more. Cells were counted with a microscope. (After Corlett 1953.)

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)

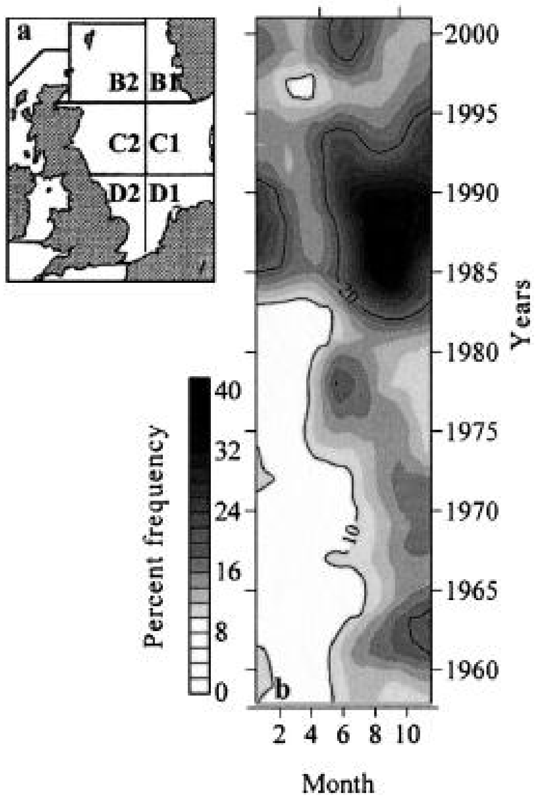


Fig. 1. (a) Diagram of North Sea indicating standard CPR areas sampled in this study. (b) Trends in jellyfish frequency (% occurrence) since 1958: Monthly averages for whole North Sea region (Gaussian smoother applied).

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. Pitt & J. E. Purcell

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Pages	1-289
Subject Collection	Biomedical and Life Sciences
SpringerLink Date	Tuesday, December 02, 2008

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Stock enhancement of the edible jellyfish (*Rhopilema esculentum* Kishinouye) in Liaodong Bay, China: a review Jing Dong, Lian-xin Jiang, Ke-fei Tan, Hai-ying Liu, Jennifer E. Purcell, Pei-jun Li and Chang-chen Ye PDF (264.7 KB) HTML	113-118

Attrill et al. 2007

Bad years for herring = good years for jellyfish?

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

herring recruitment

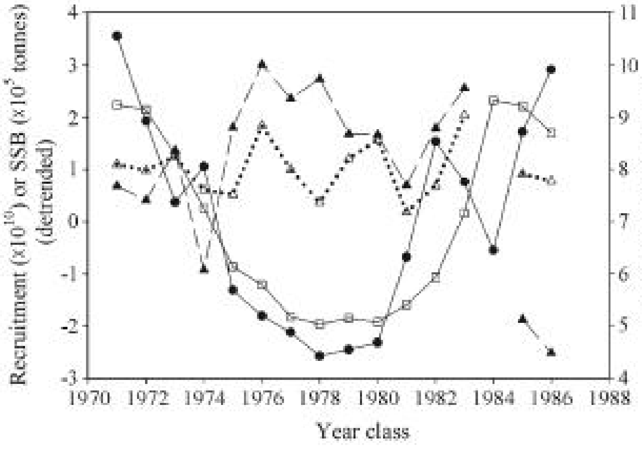


Fig. 4. *Clupea harengus*, *Aurelia aurita* and *Cyanea capillata* in the North Sea. Detrended time series of herring recruitment (solid line, ●), SSB (solid line, □) and the abundance of *A. aurita* (dashed line, ▲) and *C. capillata* (dotted line, Δ). For ease of comparison, the *C. lamarckii* data 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

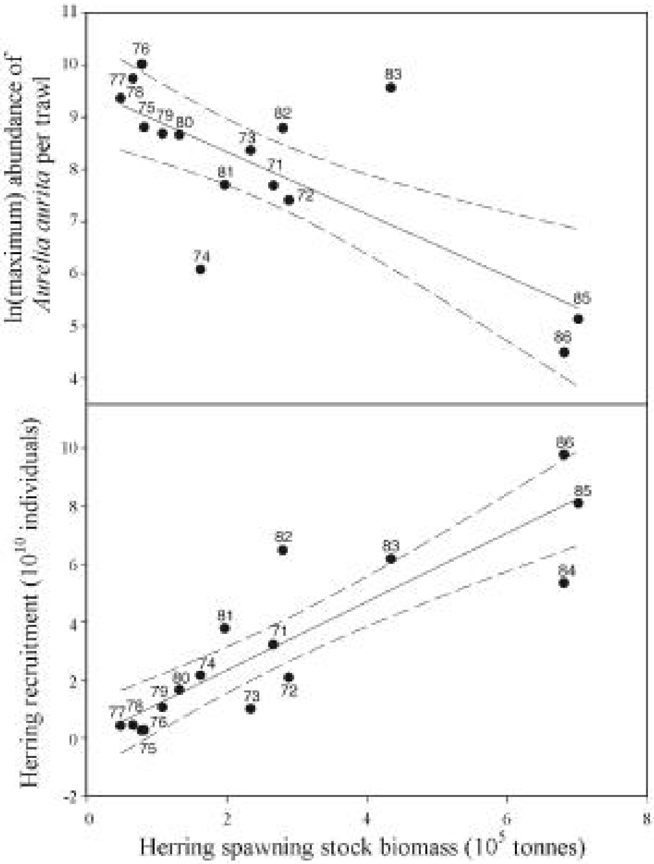


Fig. 2. *Clupea harengus* and *Aurelia aurita* in the North Sea. Correlations between the raw herring SSB (spawning stock biomass) and recruitment ($r = 0.89$, $p < 0.01$, bottom panel) and between SSB and the ln(maximum) abundance of *A. aurita* ($r = 0.75$, $p < 0.01$, top panel)

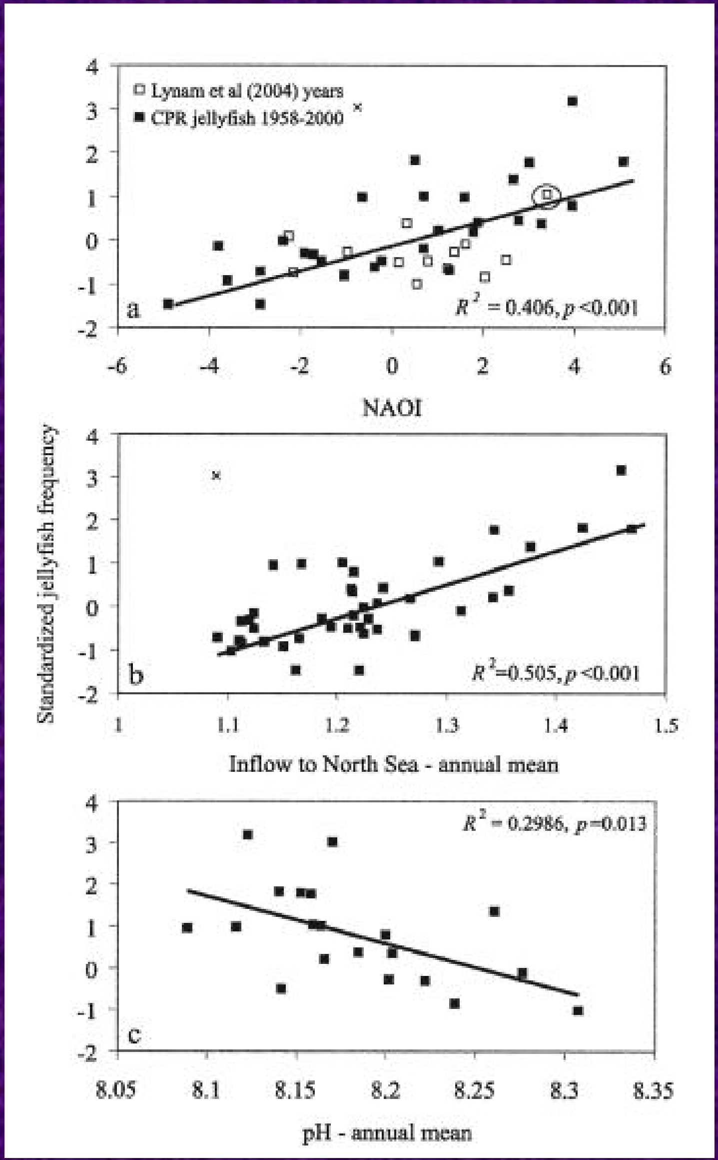
Lynam et al. 2005

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

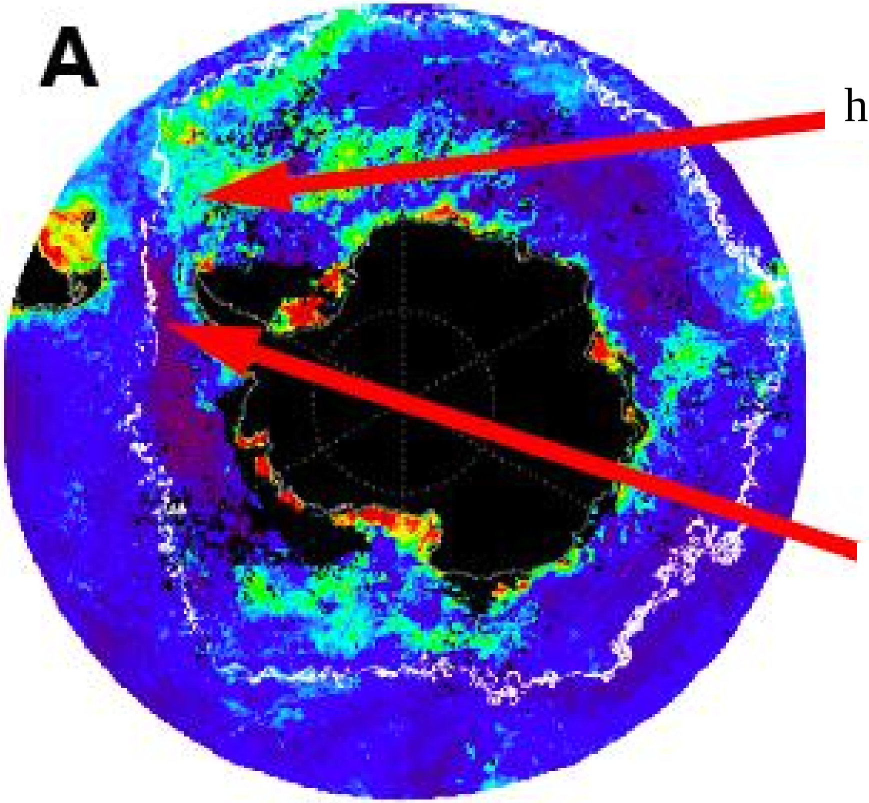
Reduced larval herring stocks, and therefore adult herring, further allow jellyfish to outcompete them



Attrill et al. 2007

Southern Ocean Phytoplankton Blooms

Mean Chl a composite, SeaWIFS, January 1998/1999

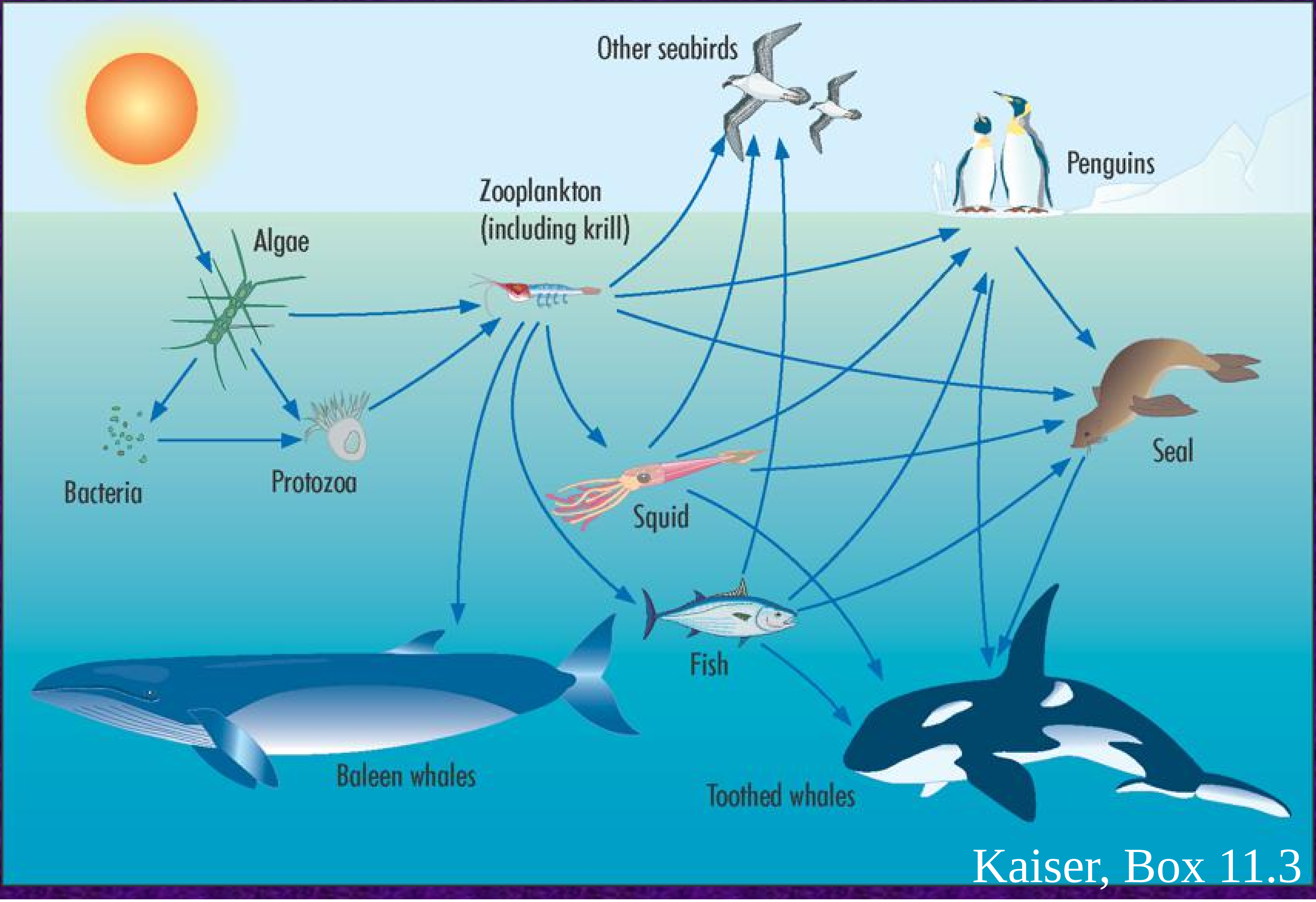


high chlorophyll

low chlorophyll

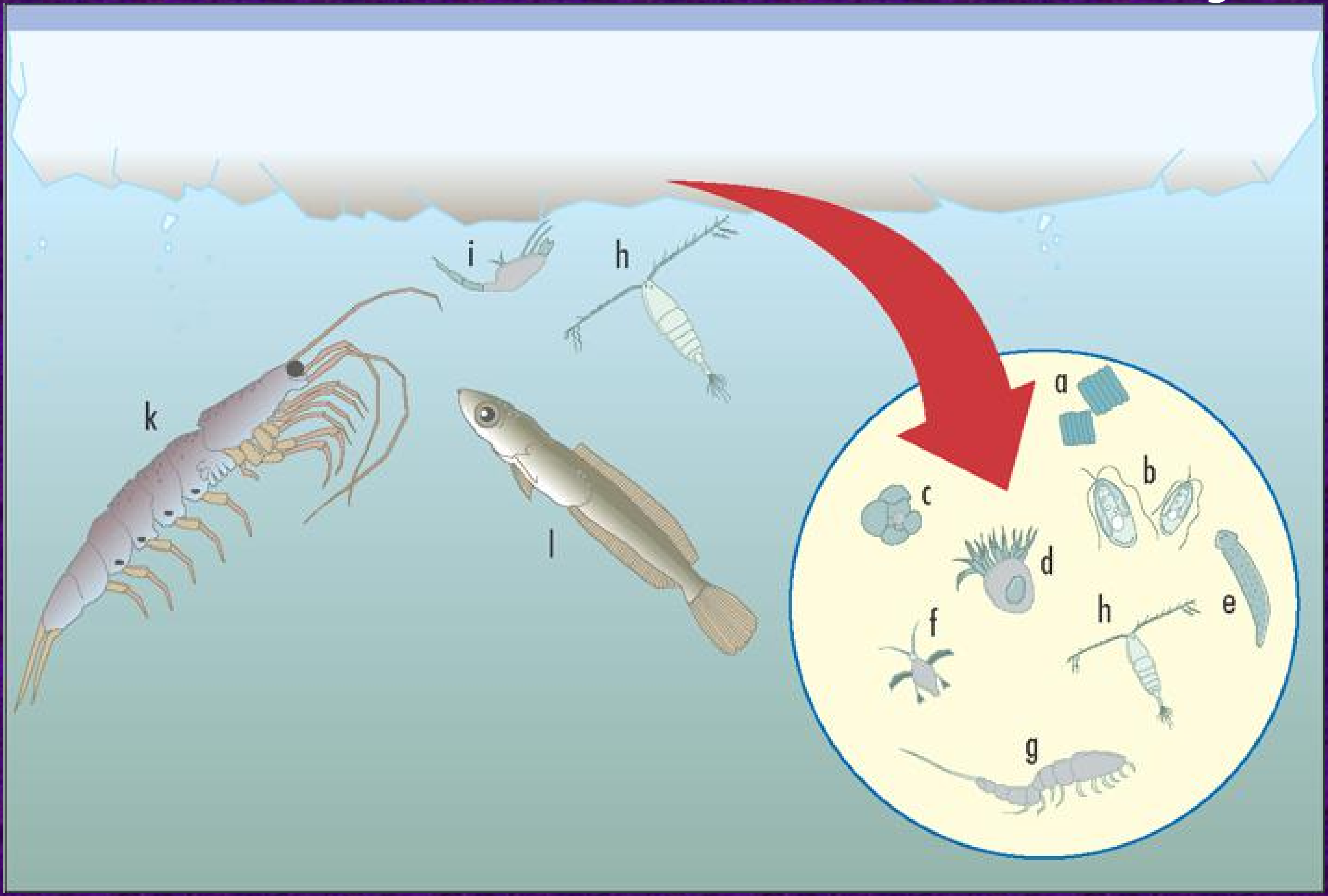
Mitchell et al., SIO

Antarctic: Southern Ocean
Krill as a Keystone Species



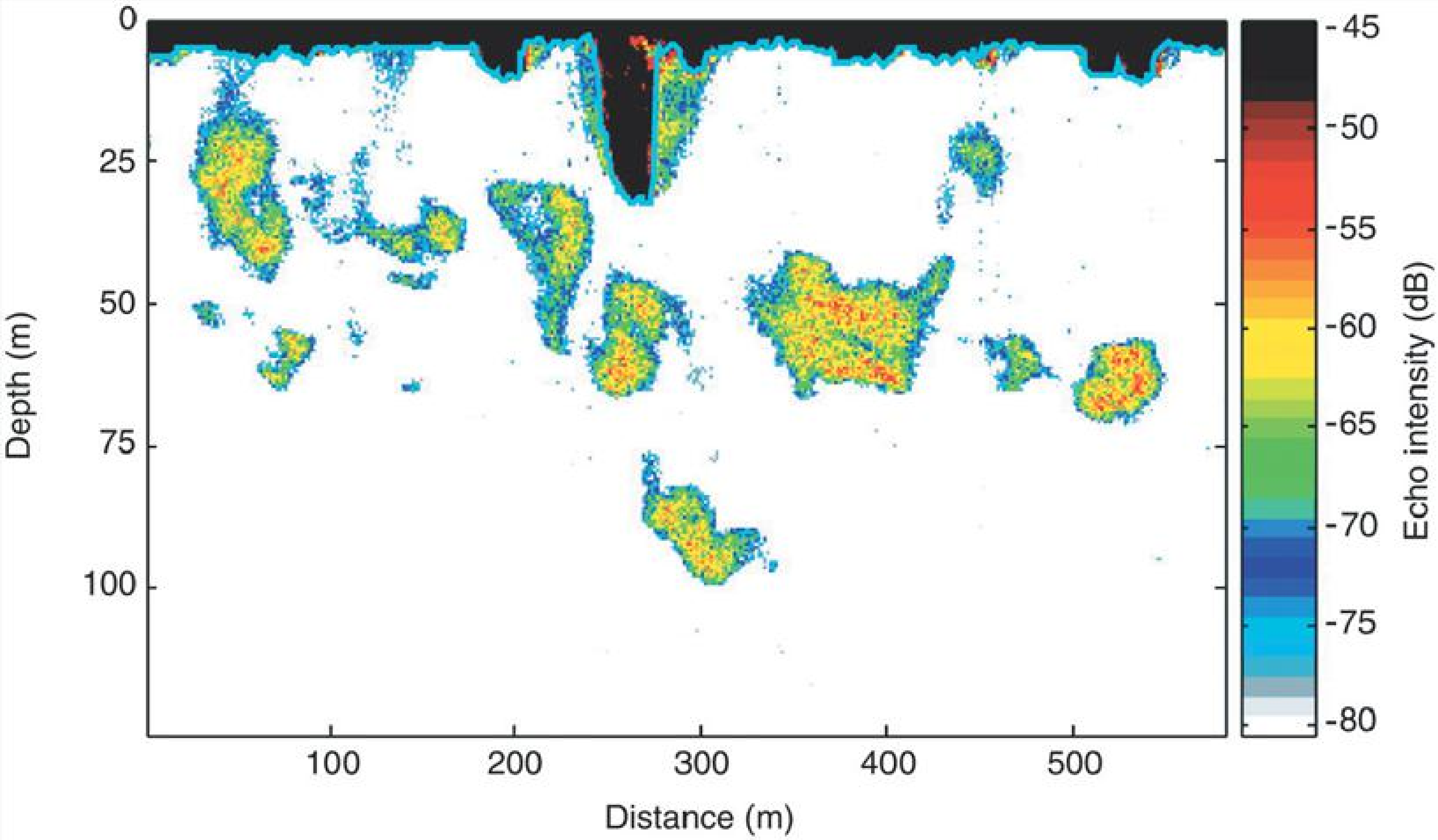
Kaiser, Box 11.3

Antarctic Sea Ice Community



Kaiser, Fig. 11.8

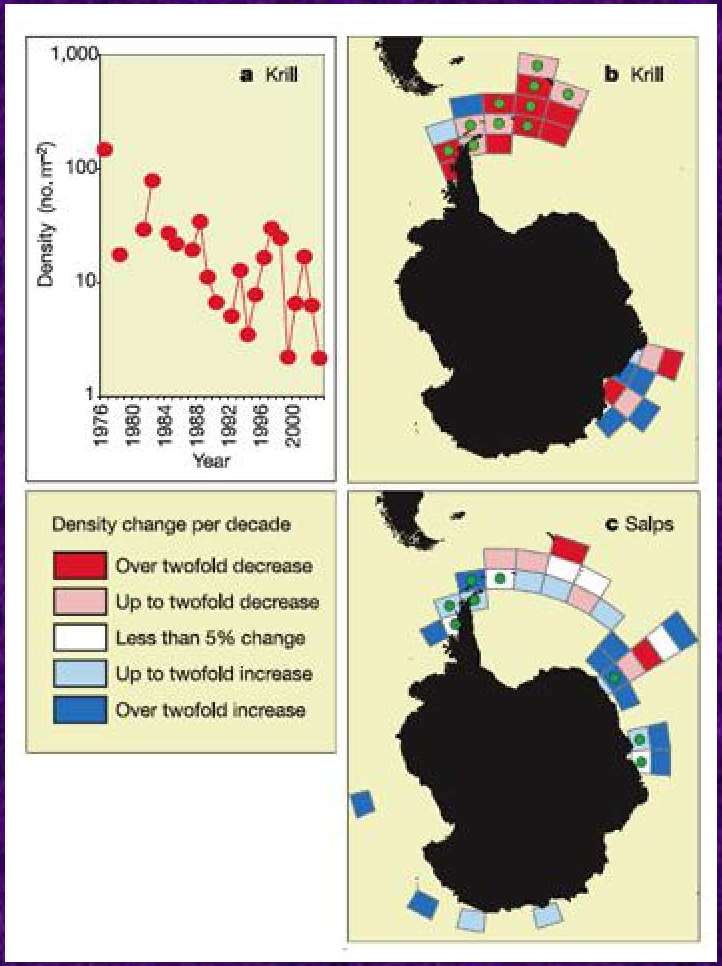
Krill Swarms under the Sea Ice



Kaiser, Box 11.3

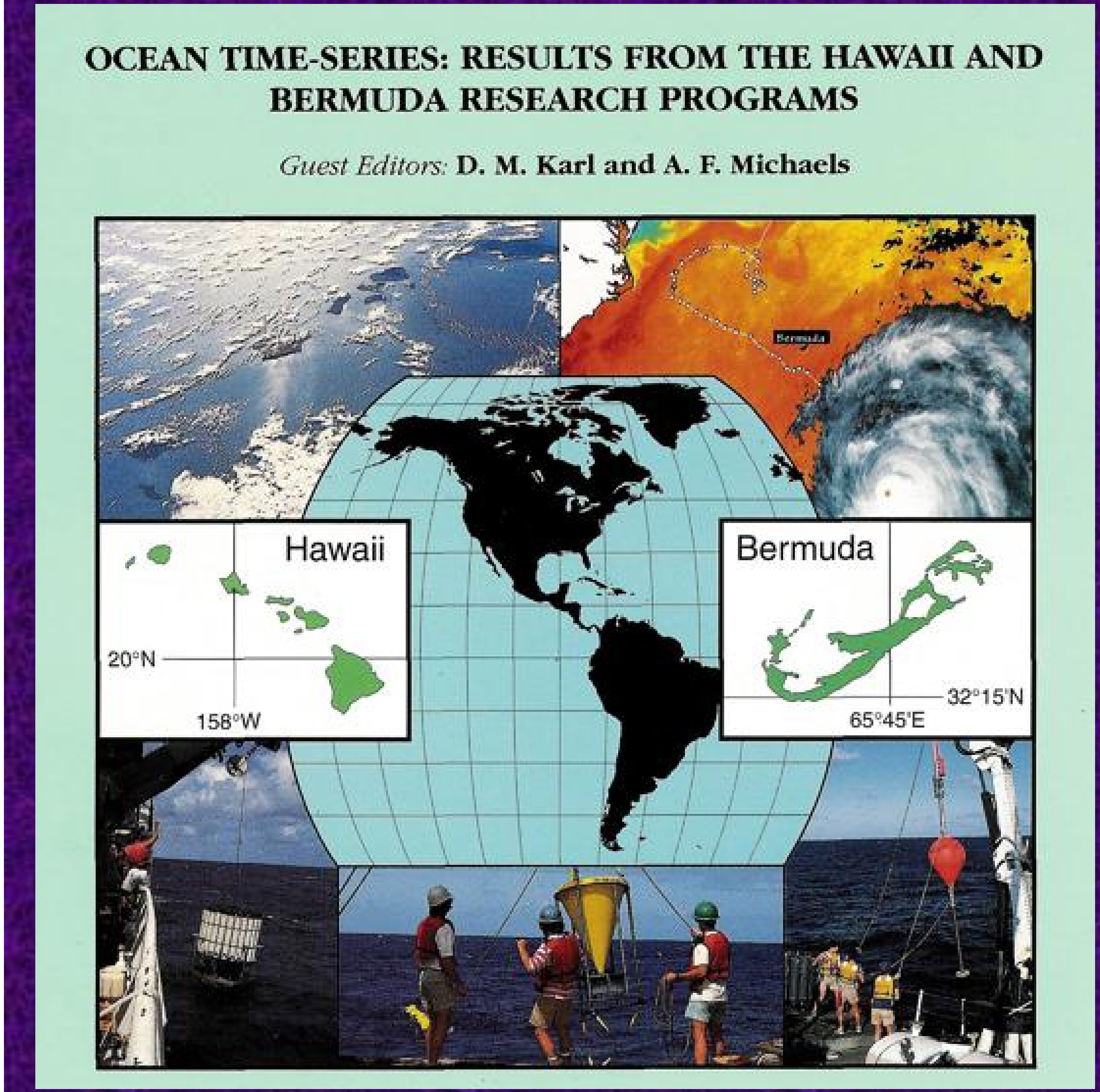
Krill vs. Salps

- 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

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

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

Ecosystem Structure in Gyres

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

how many trophic levels?

HOTS -- Primary Production

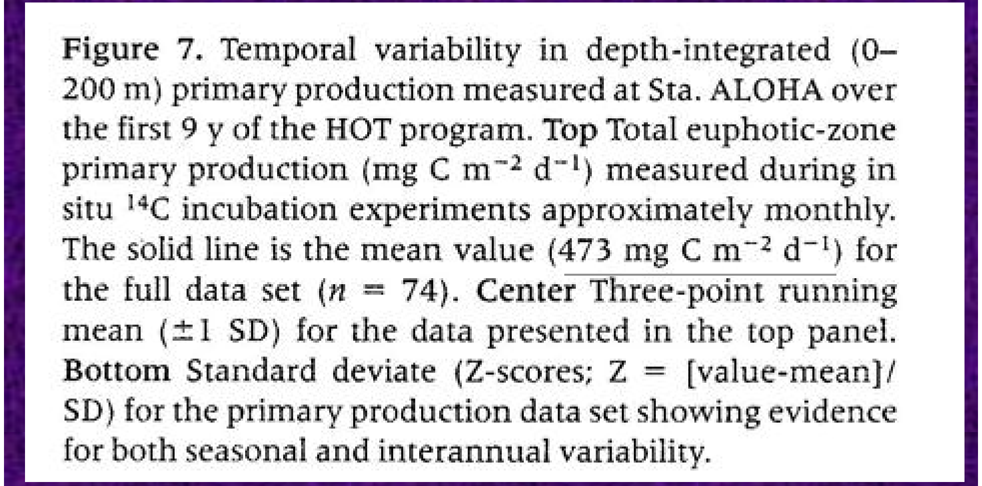
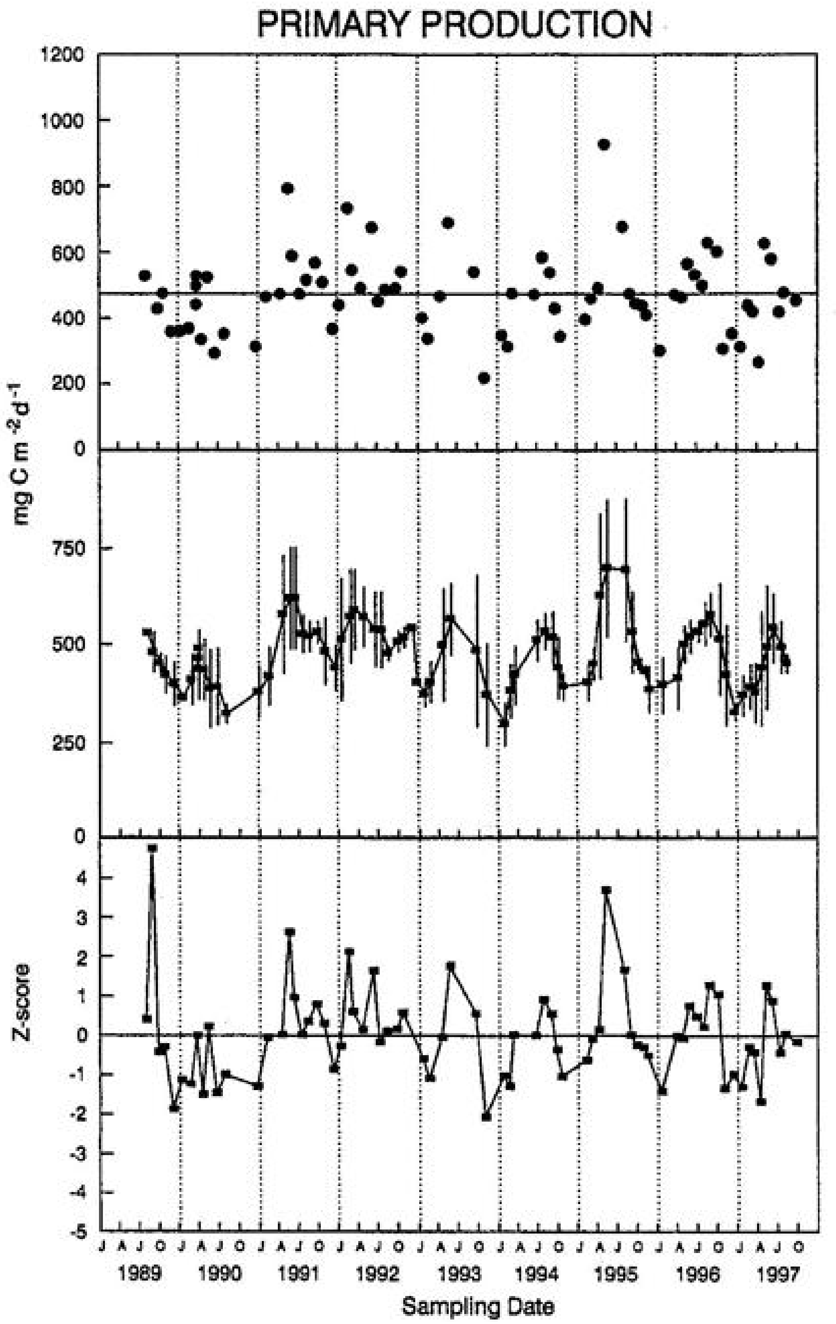


Figure 7. Temporal variability in depth-integrated (0–200 m) primary production measured at Sta. ALOHA over the first 9 y of the HOT program. **Top** Total euphotic-zone primary production (mg C m^{-2} d^{-1}) measured during in situ ^{14}C incubation experiments approximately monthly. The solid line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



D. Karl 1999 Ecosystems 2:181-214

summer usually sees the highest phytoplankton biomass/production

BATS -- Primary Production

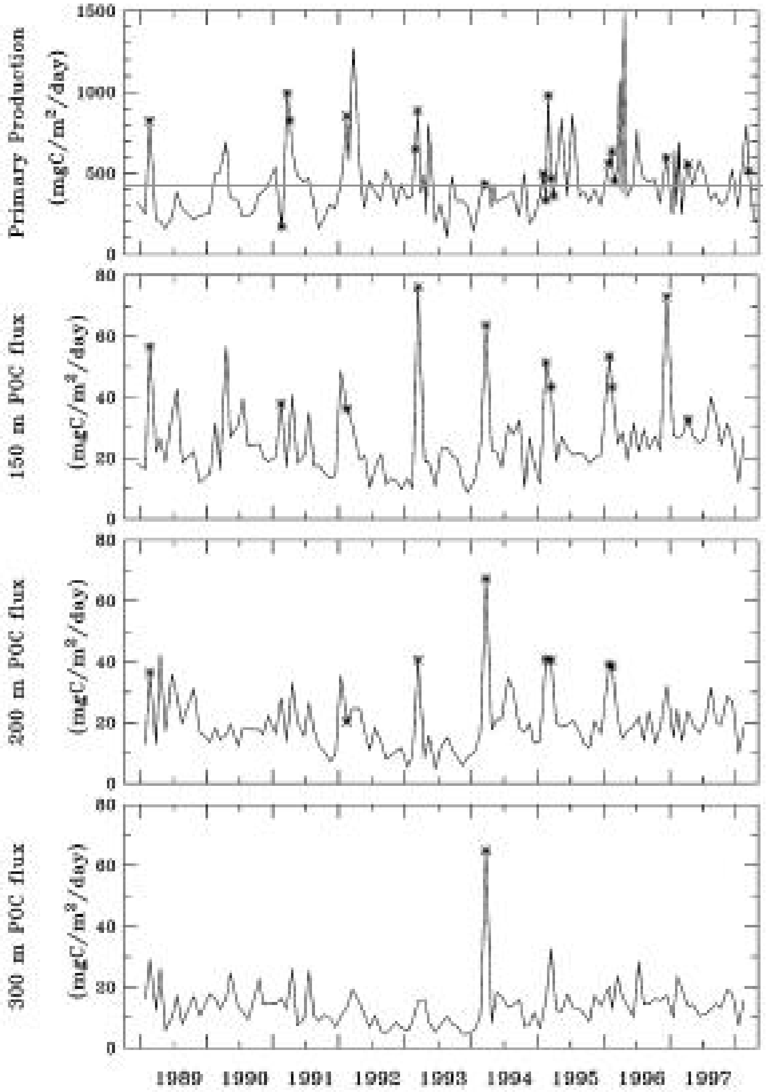


Fig. 10. Time series of integrated primary production (0–140 m) compared to the particulate organic carbon flux measured with a sediment trap at 150, 200, and 300 m. Stars indicate times of the year when physical mixing was deeper than the depth of the measurement (e.g. mixing was deeper than 150 m for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

Spring bloom
(not summer like
HOTS)

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

Data Comparison

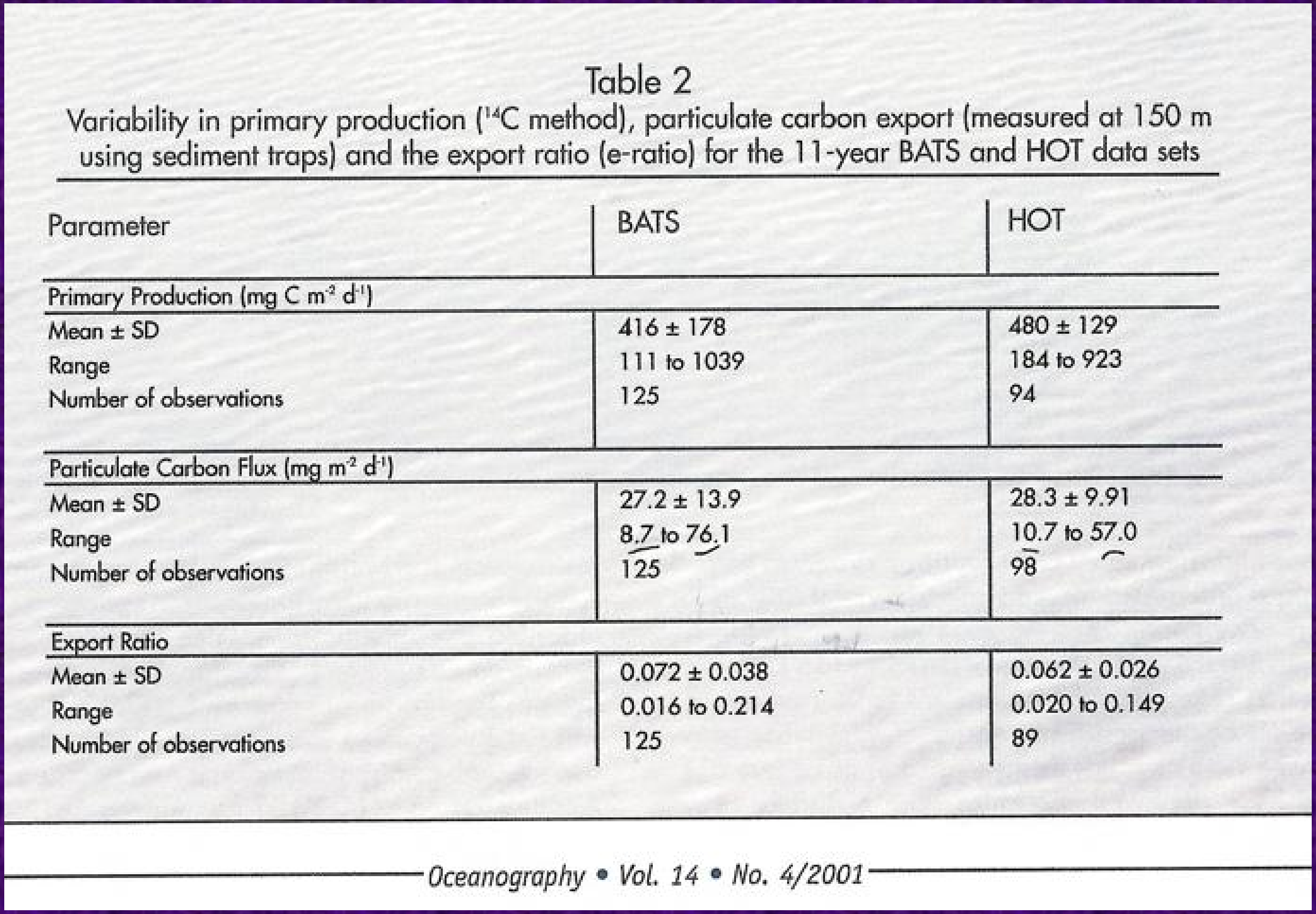


Table 2

Variability in primary production (^{14}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

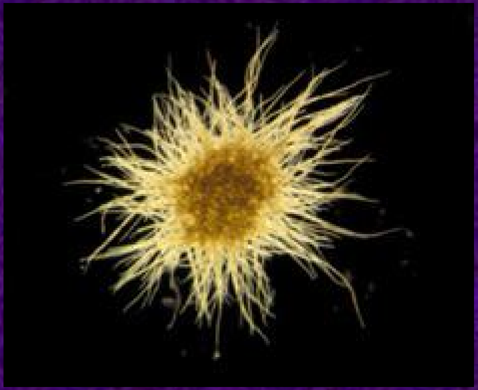
Parameter	BATS	HOT
Primary Production (mg C m^{-2} d^{-1})		
Mean ± SD	416 ± 178	480 ± 129
Range	111 to 1039	184 to 923
Number of observations	125	94
Particulate Carbon Flux (mg m^{-2} d^{-1})		
Mean ± SD	27.2 ± 13.9	28.3 ± 9.91
Range	8.7 to 76.1	10.7 to 57.0
Number of observations	125	98
Export Ratio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

Oceanography • Vol. 14 • No. 4/2001

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*



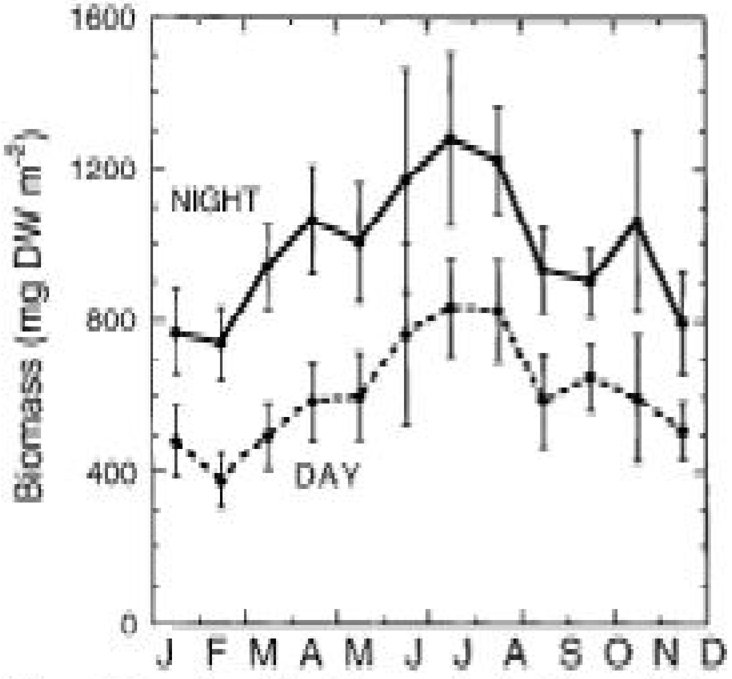
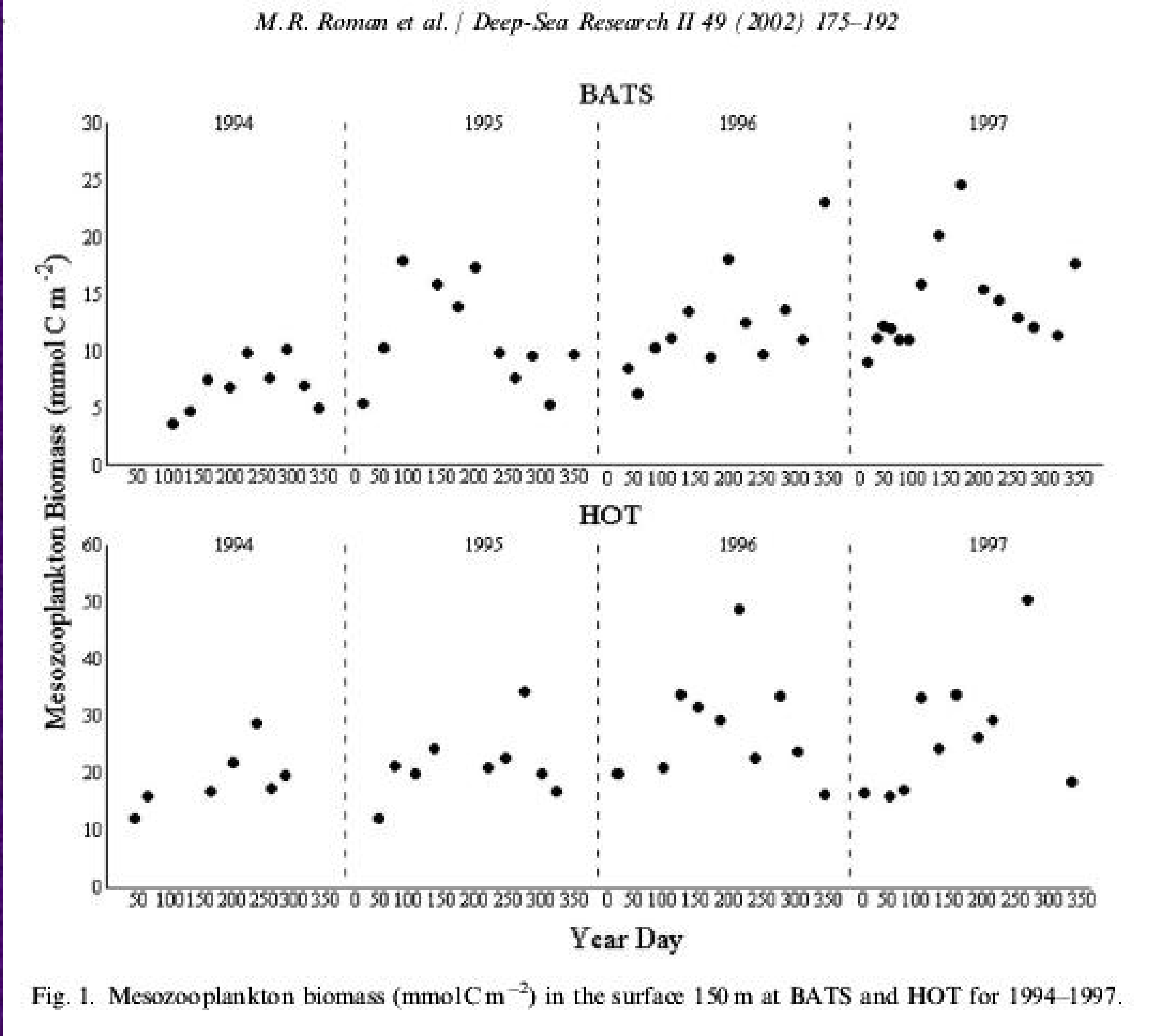


Figure 5. Seasonal variation of mesozooplankton biomass in daytime (1000–1400) and nighttime (2200–0200) net collections at Stn. ALOHA, subtropical North Pacific. Dry weight samples were taken from integrated oblique hauls over the euphotic zone (mean tow depth=155 m) with a 1-m^2 net and 200-μm mesh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



M.R. Roman et al. / Deep-Sea Research II 49 (2002) 175–192

Fig. 1. Mesozooplankton biomass (mmol C m^{-2}) in the surface 150 m at BATS and HOT for 1994–1997.

HOT/BATS MesoZP comparison

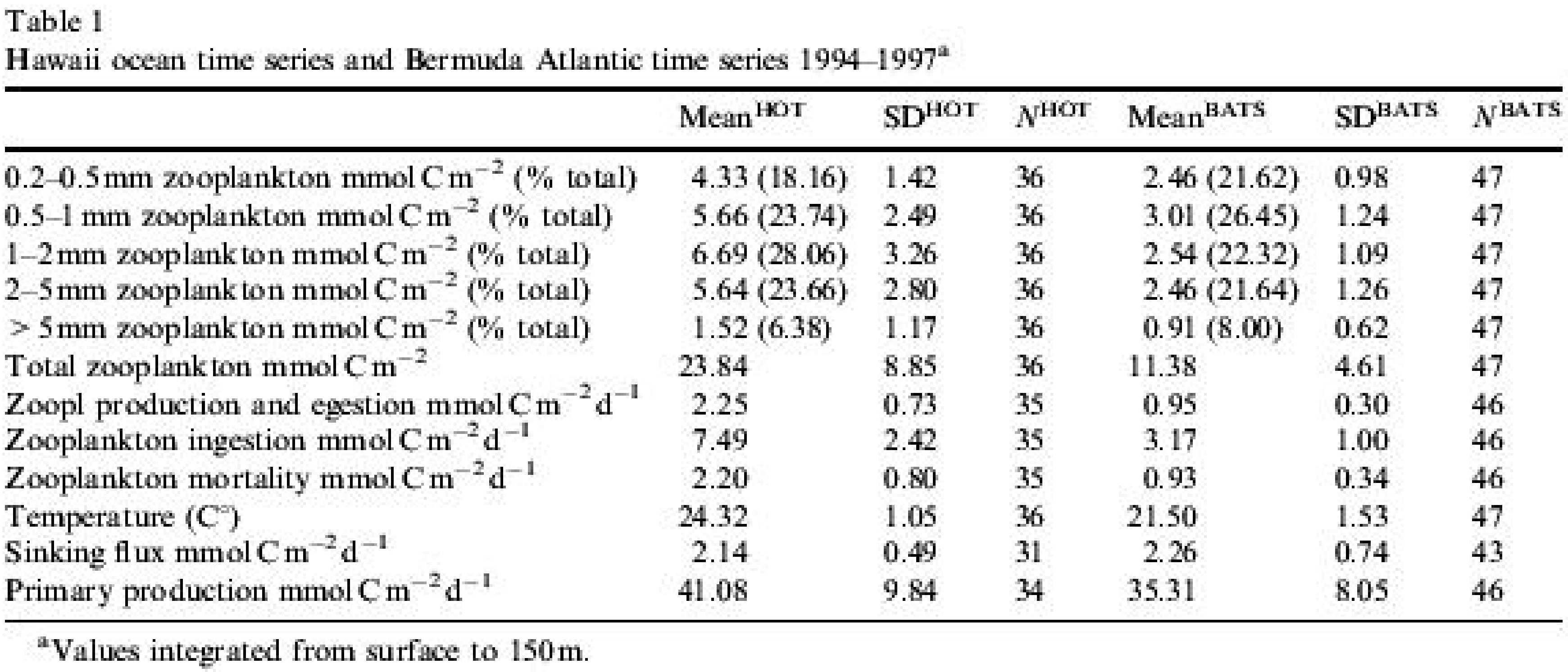


Table 1

Hawaii ocean time series and Bermuda Atlantic time series 1994–1997[a]

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

[a] Values integrated from surface to 150 m.

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

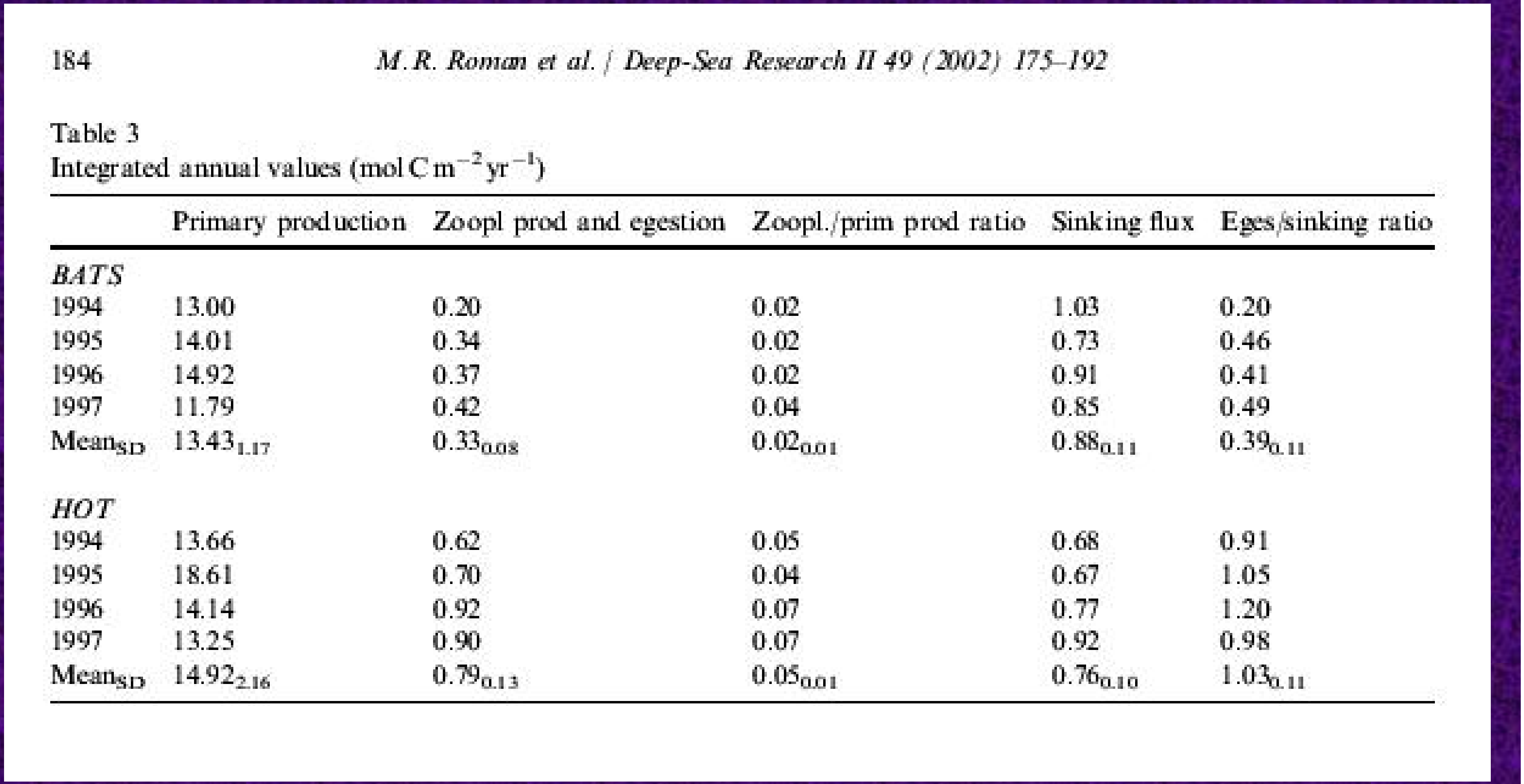


Table 3
Integrated annual values (mol C m^{-2} yr^{-1})

	Primary production	Zoopl prod and egestion	Zoopl./prim prod ratio	Sinking flux	Eges/sinking ratio
BATS					
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$_{SD}$	13.43$_{1.17}$	0.33$_{0.08}$	0.02$_{0.01}$	0.88$_{0.11}$	0.39$_{0.11}$
HOT					
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$_{SD}$	14.92$_{2.16}$	0.79$_{0.13}$	0.05$_{0.01}$	0.76$_{0.10}$	1.03$_{0.11}$

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

L. Madin, WHOI

www.pbs.org

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^2/d

(~40 - 380 g C/m^2/y)

historical: <100 g C/m^2/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...

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] → **I** declines for given $\mathbf{F}_{\mathbf{max}}$
  - decreased phyto size → $\mathbf{F}_{\mathbf{max}}$ declines for consumer of given size
  - increased T°C → 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.

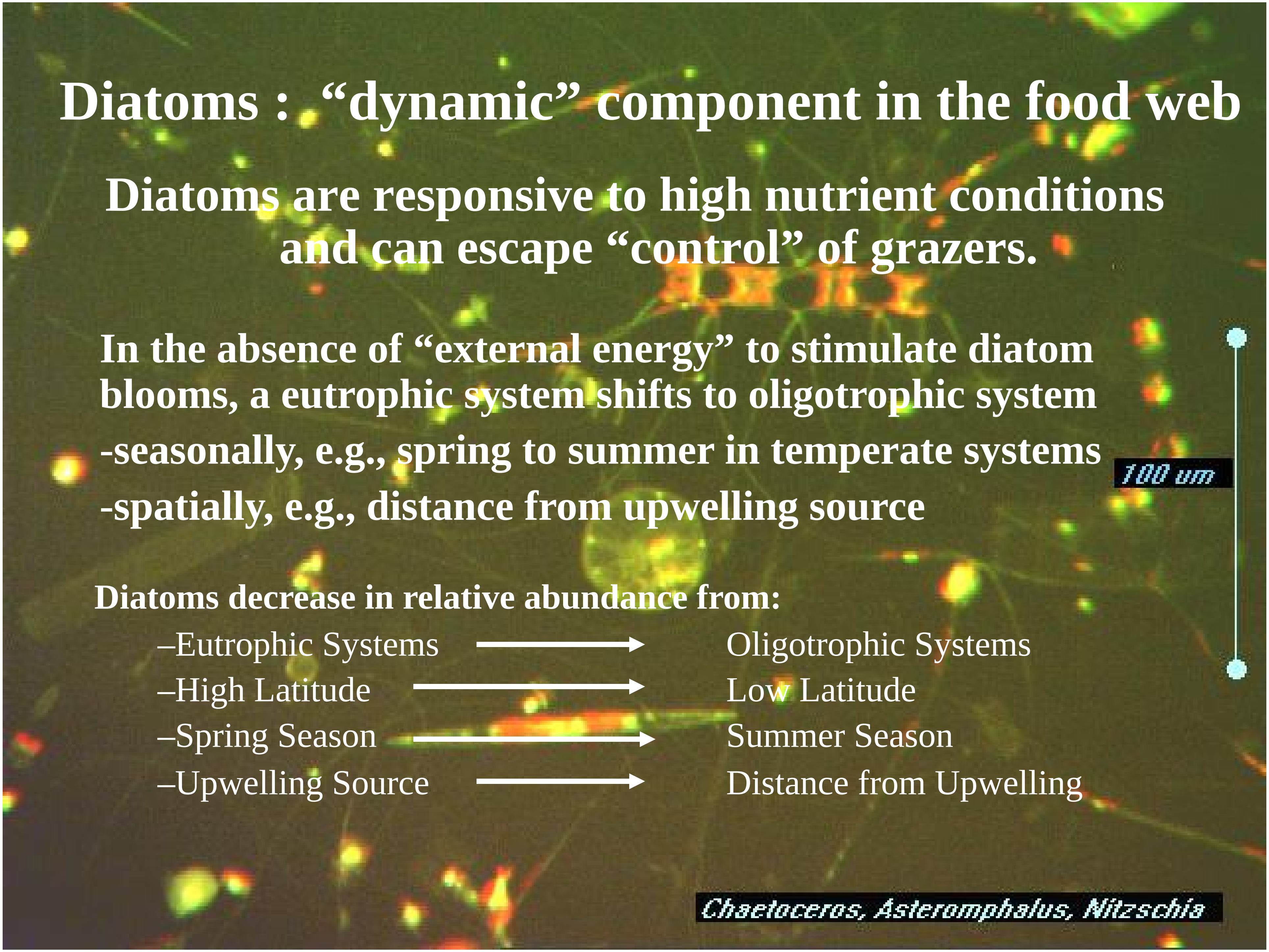
In the absence of “external energy” to stimulate diatom blooms, a eutrophic system shifts to oligotrophic system

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

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

Diatoms decrease in relative abundance from:

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



Chaetoceros, Asteromphalus, Nitzschia

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)

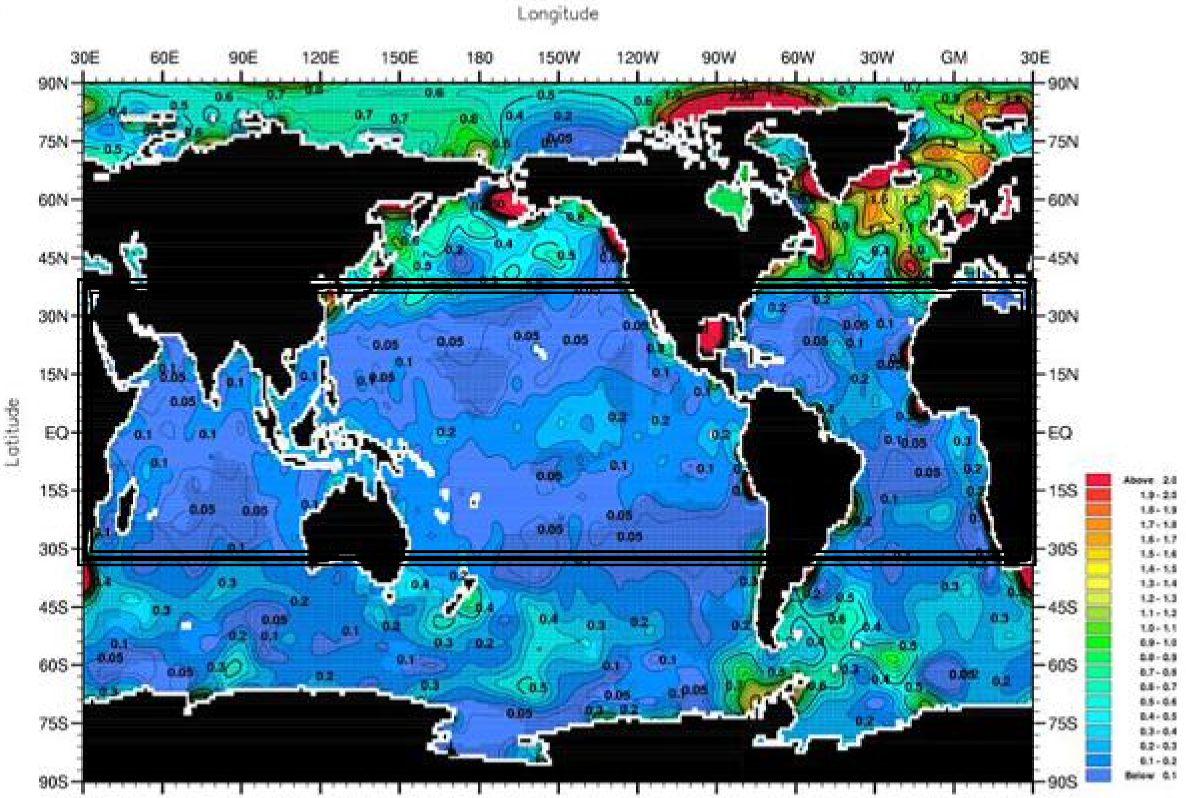


Fig. C2-1. Spring (Apr.-Jun.) mean chlorophyll (µg/l) at the surface.

Minimum Value= 0.00 Maximum Value= 13.42 Contour Interval: 0.10

World Ocean Atlas 2001
Ocean Climate Laboratory/NODC

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)

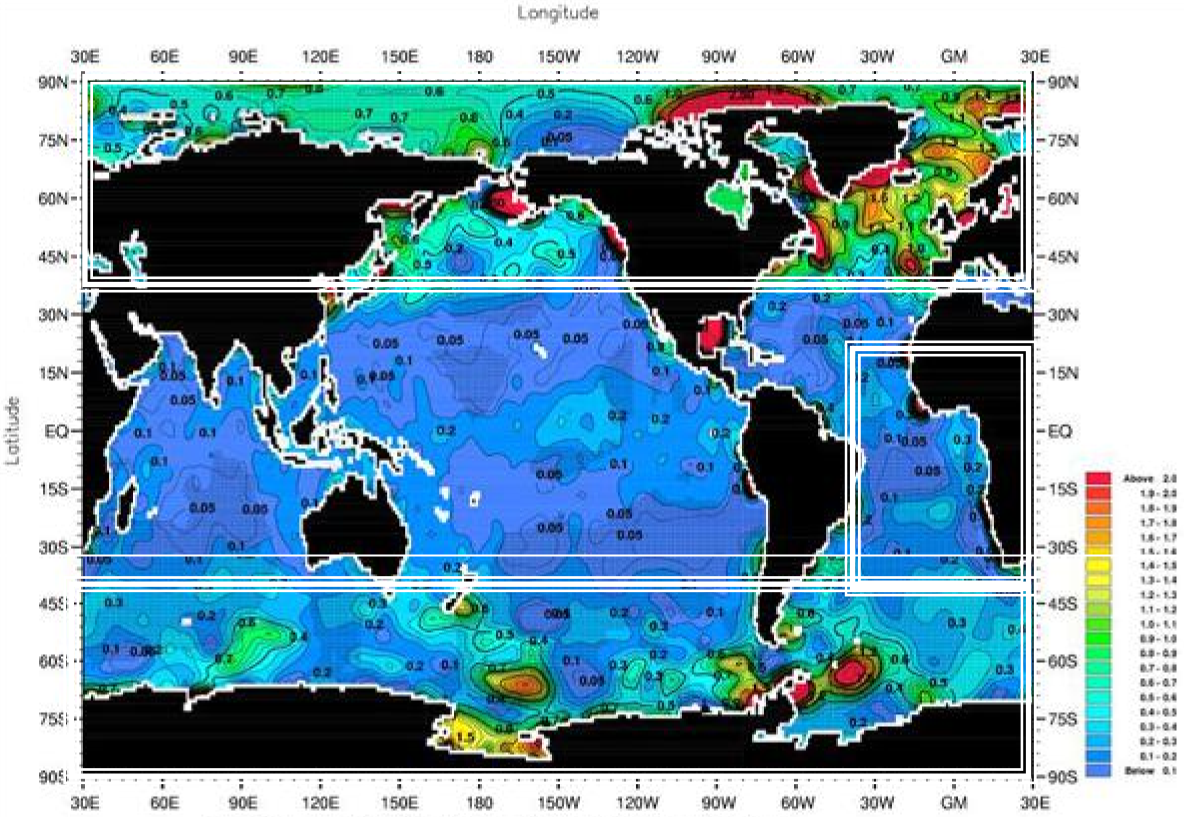


Fig. E2-1. Fall (Oct.-Dec.) mean chlorophyll (µg/l) at the surface.

Minimum Value= 0.00 Maximum Value= 8.68 Contour Interval: 0.10

World Ocean Atlas 2001
Ocean Climate Laboratory/NODC

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.