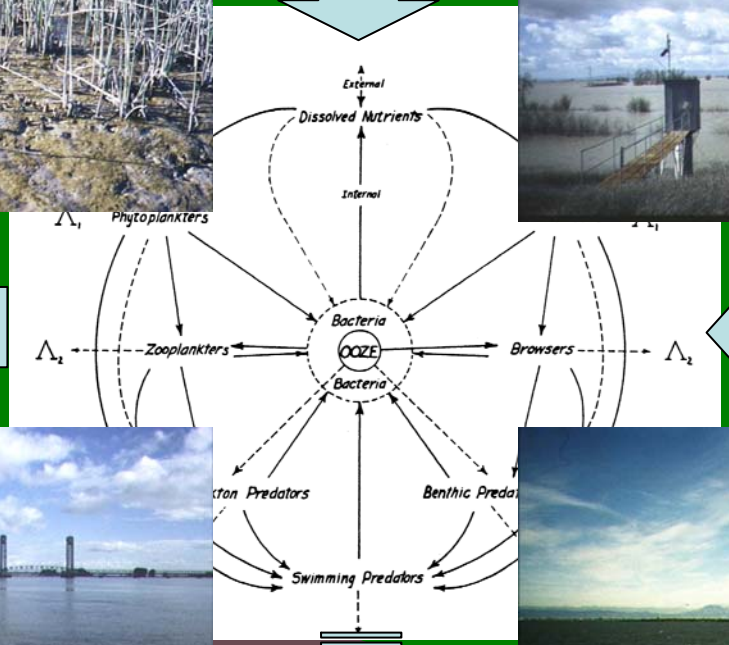
Productivity and the Aquatic Foodweb

Anke Mueller-Solger, DWR

CALFED Science Workshop 5-16-2008



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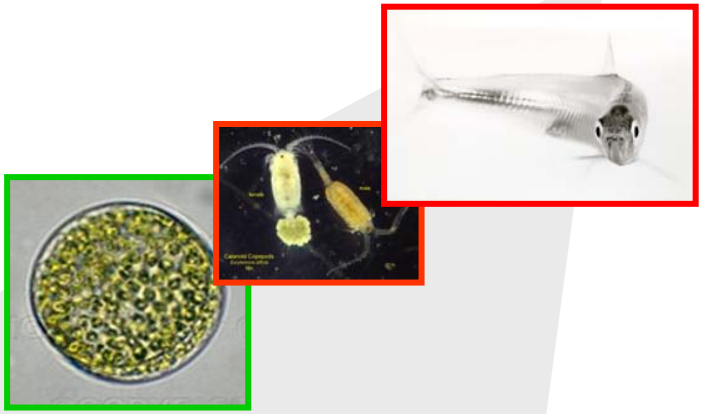
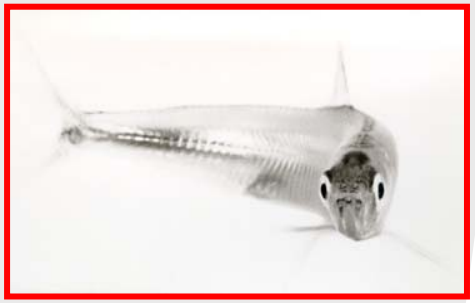
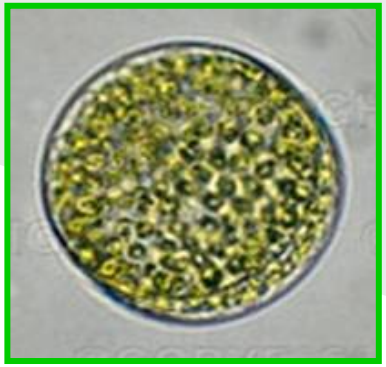


1. What is productivity?
2. Who are the producers?
3. Sources & sinks of (B)OC
4. Bacteria production & biomass
5. Phytoplankton production & biomass
6. Phytoplankton as a food source
7. Restoration & water operations impacts
8. Conclusions

1. What is productivity?





What is “Productivity?”

Economics: “Unit output per unit of input” in time & space

Production Process

Raw Material Input → Product Output

Time & Space

Input and Output Units: Quantity & Quality

(Photoautotrophic)

Gross primary production: making sugar (= org. carbon)

Raw Material Input | Production Process | Product Output

Photosynthesis

Inorganic compounds, light energy

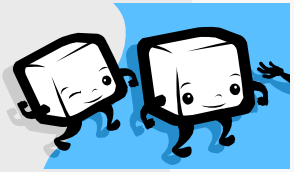
$6CO_2 + 6H_2O$ + *Light* → Organic compounds, chemical energy

$C_6H_{12}O_6 + 6O_2$

Time & Space

The SFE is turbid - primary production is generally light limited!

Glucose isn't an organism, so…



e.g. Cole & Cloern, MEPS 1987; Jassby & Cloern, Aq.Cons 2000; Jassby, Cloern, Cole L&O 2002

Net Primary Production: making live biomass from sugar

Raw Material Input	Production Process	Product Output
Glucose, chemical energy, inorganic compounds (*P, N, Si*…)	→ Metabolism	Heat, CO_2, H_2O, **Biomass** *Complex carbohydrates* *Lipids* *Proteins* *Nucleic acids*

Time & Space

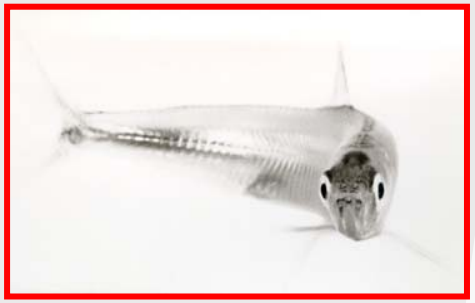
No primary production step 2 without step 1;
Nutrients etc. generally only matter
when there is sufficient light.

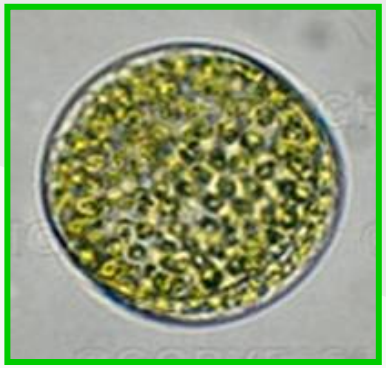
Secondary Production: making new biomass from old biomass

Raw Material Input	Production Process	Product Output
Primary Producer Biomass	→ Consumption, Metabolism	Secondary producer = primary consumer biomass, Heat, CO_2, H_2O,

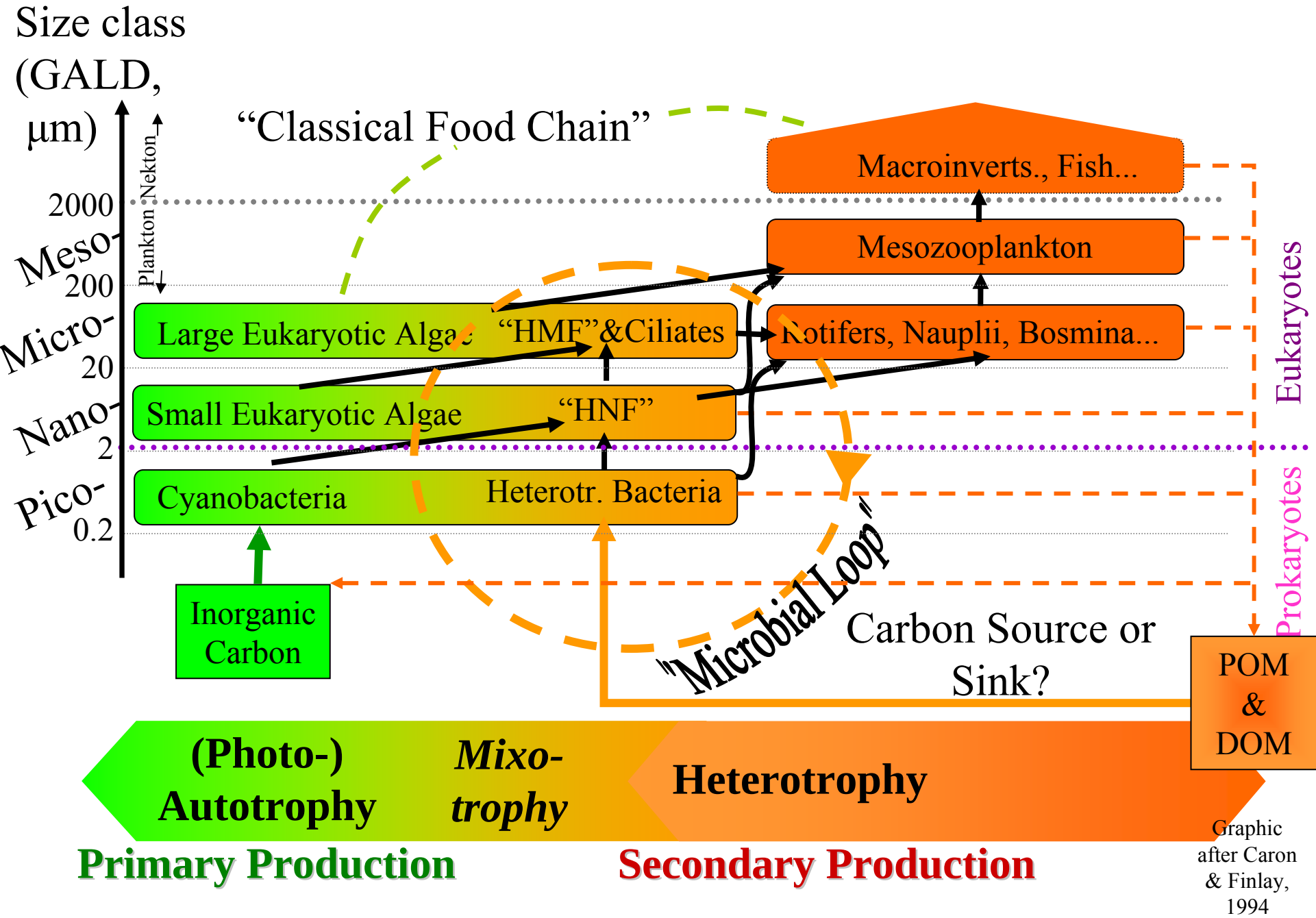
Time & Space

2. Who are the producers?



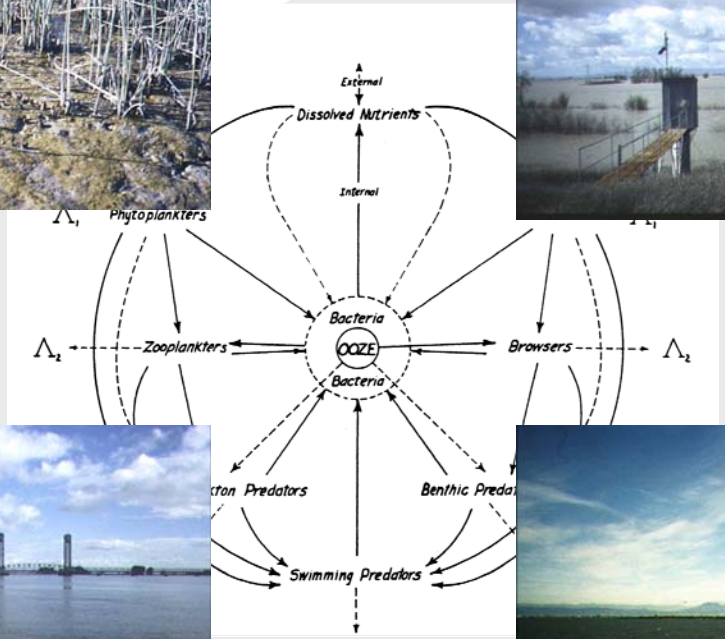


Pelagic food web



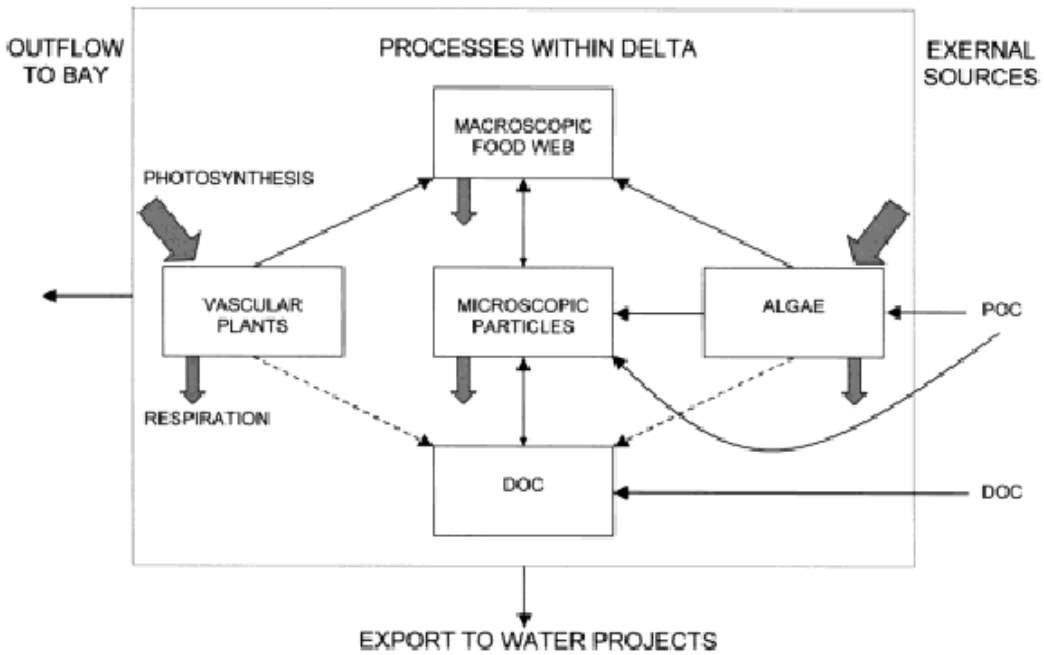
Graphic after Caron & Finlay, 1994

3. Sources & sinks of OC in the upper San Francisco Estuary (Delta & Suisun)



Conceptual Models

OC pools & flows



Delta hydraulics

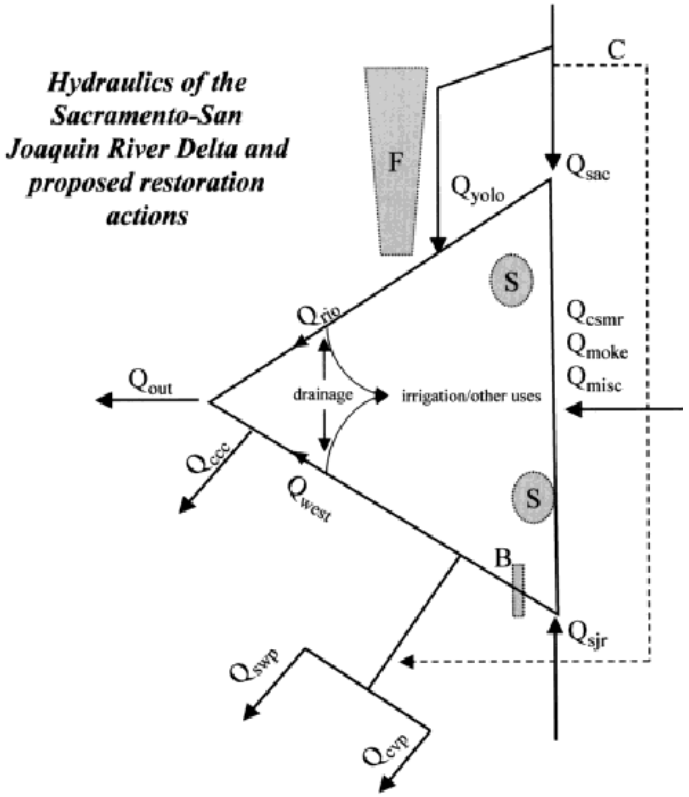
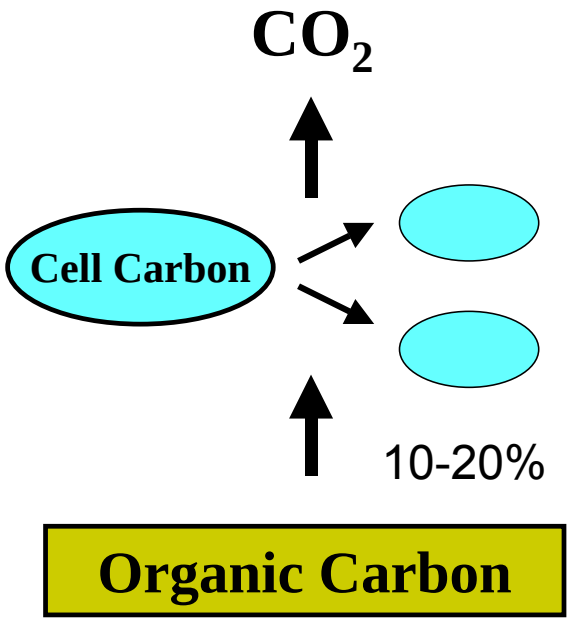


Fig.s from Jassby & Cloern 2000

Conceptual Models

Growth (in)efficiency



OC Bioavailability

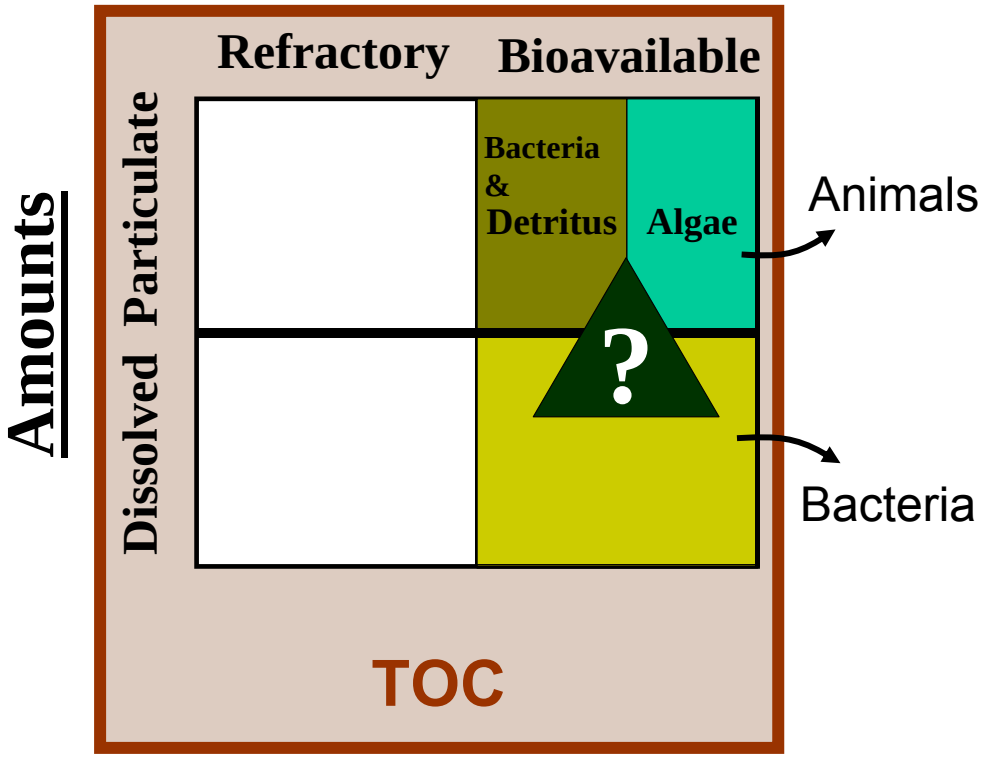


Fig.s from W. Sobczak, pers. com.

Organic matter sources in the upper San Francisco Estuary
Jassby & Cloern 2000

TOC sources to the Delta (1968-1995):

- Tributary-borne loading (270±50 t TOC /day)
- Phytoplankton PPr (47 ± 5 t/d)
- Agricultural drainage (36 t/d)

POC sources to the Delta:

Tributary-borne loading & phytoplankton production

> agricultural drainage

Delta is net producer in very dry years, but production goes south… (not west)

(t POC/day)	Phytoplankton NPP	Tributary load	Agricultural drainage
Wet years ("above normal)			
Autumn	20	51	3.3
Winter	3.9	460	10
Spring	58	110	3.9
Summer	54	74	3.8
Dry years ("below normal")			
Autumn	14	53	3.3
Winter	17	82	10
Spring	81	44	3.9
Summer	50	48	3.8

Fate of carbon in the upper San Francisco estuary

The upper SFE is a carbon sink

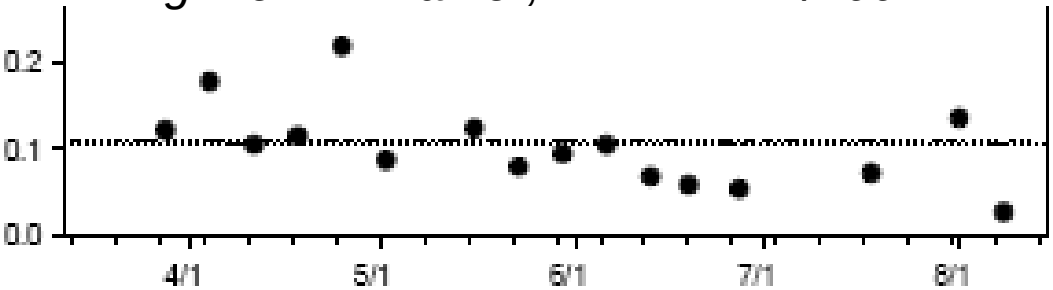
= net heterotrophic, consumes more C than it produces, relies on river C inputs (Rudek & Cloern 1996, Hollibaugh & Wong 1996, Sobczak et al 2002, 2005)

Reasons:

- BDOC > BPOC
- Only bacteria can access BDOC
- Bacteria utilize C inefficiently
- Bacterial production and biomass are lower than phytoplankton production & biomass, but phytoplankton production alone cannot satisfy bacterial carbon demand.

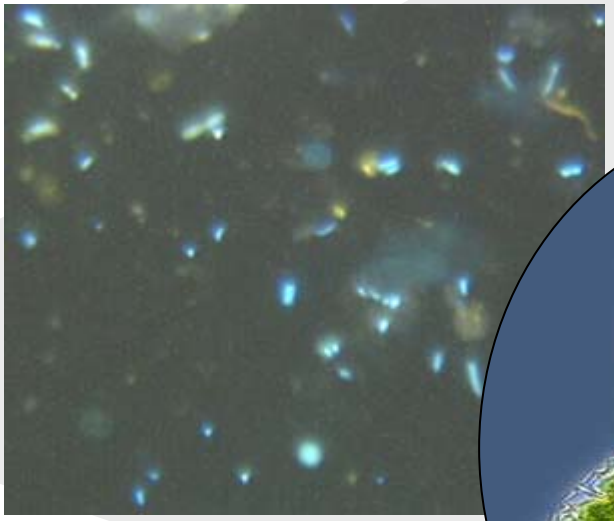
Fig. from A. Parker, IEP EET 12/2007

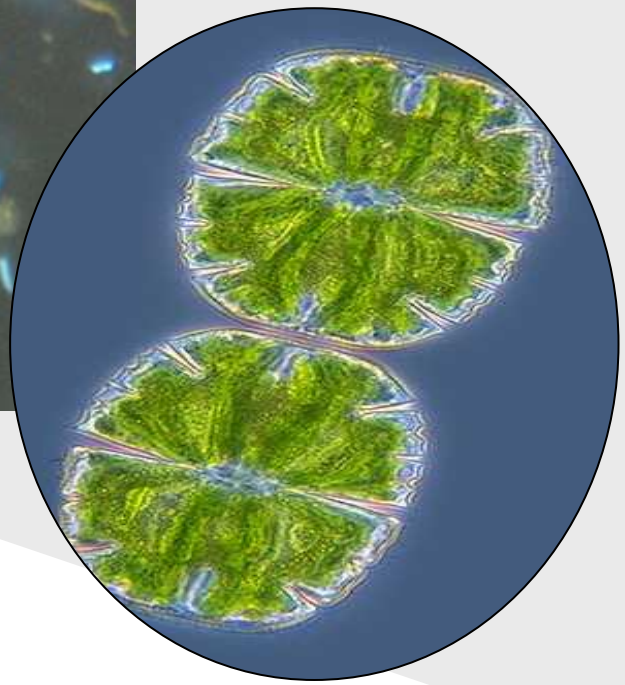
Bacterial Production/ Respiration (2006) ~11%



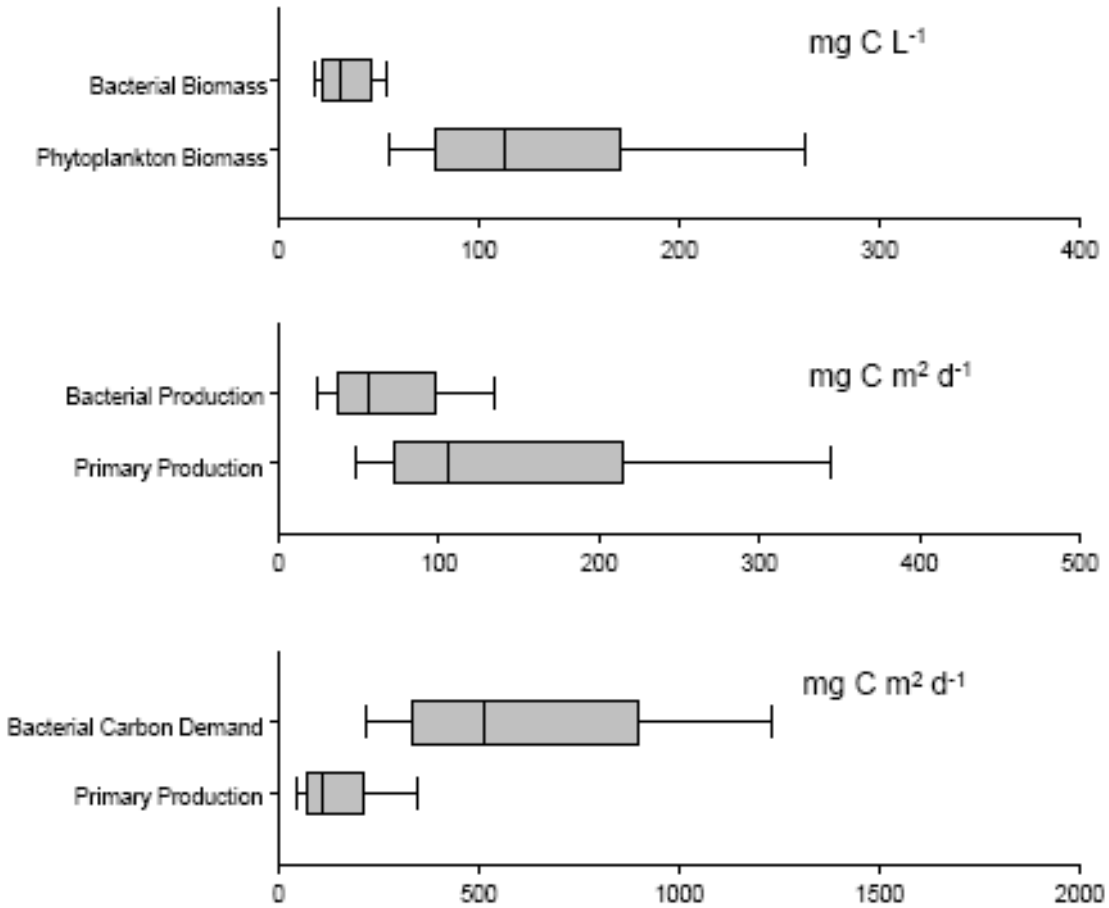
Low compared to other estuarine systems – **“bad”/old DOC**?

4. Bacterial versus phytoplankton production, biomass, and trophic role in the upper SFE





Bacterial Production & Biomass are low compared to phytoplankton, but bacterial C demand is high



"Bad" DOC?

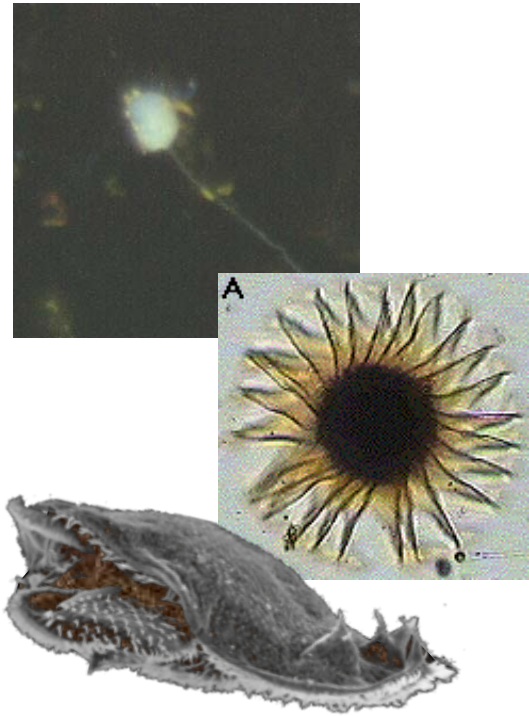
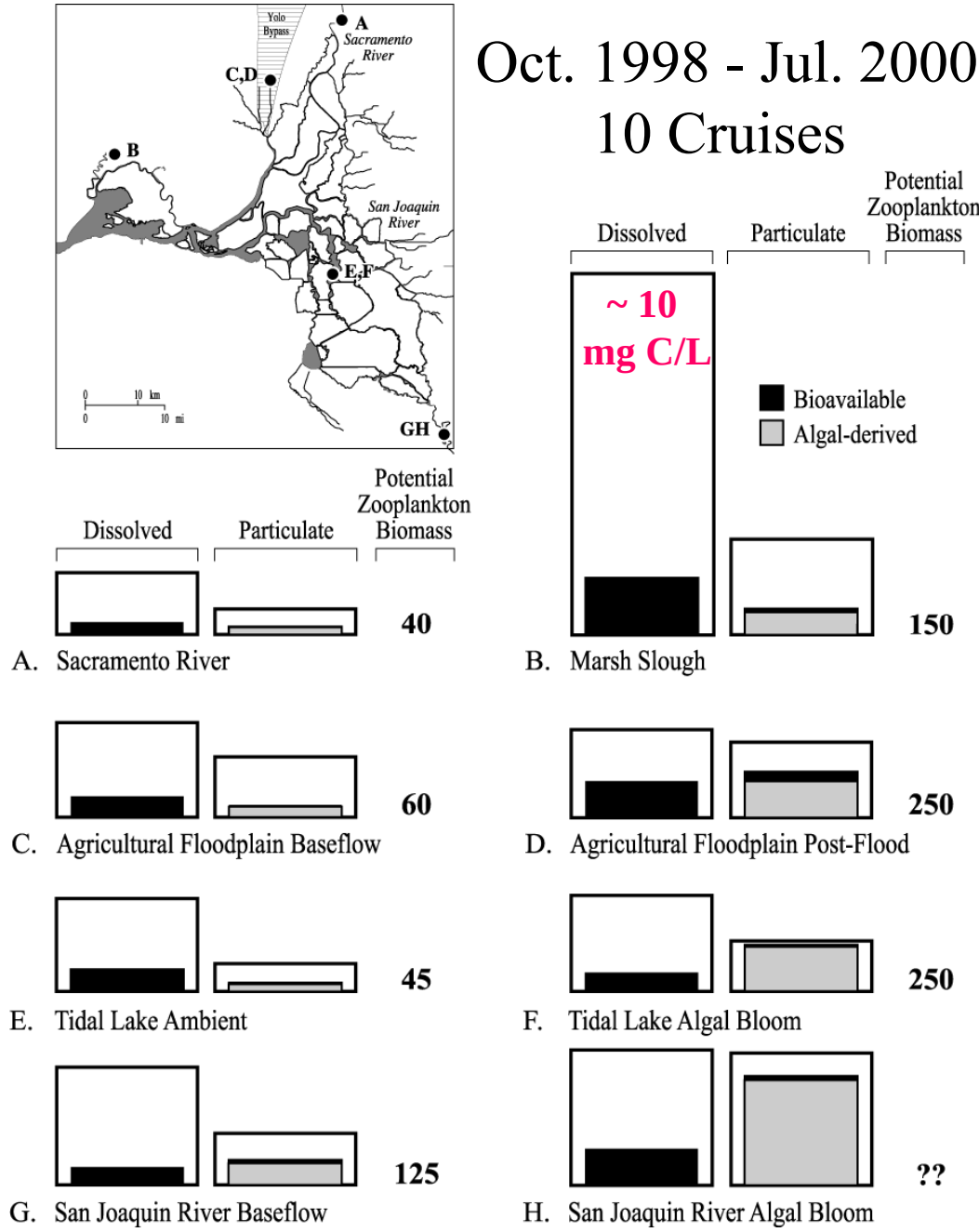


Figure from A. Parker, IEP EET 12/2007

DOC & POC amounts & bioavailability in the Delta & Suisun Marsh

- DOC > POC
- BDOC > BPOC
- But POC is more bioavailable than DOC
- **Most BPOC is from algae, fuels food web**
- Habitat & seasonal differences
- Rivers support less phyto- & zooplankton than wetlands

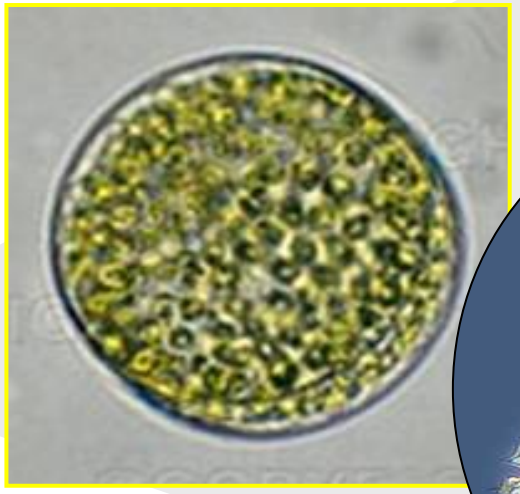
Fig. 10 in Sobczak et al 2005

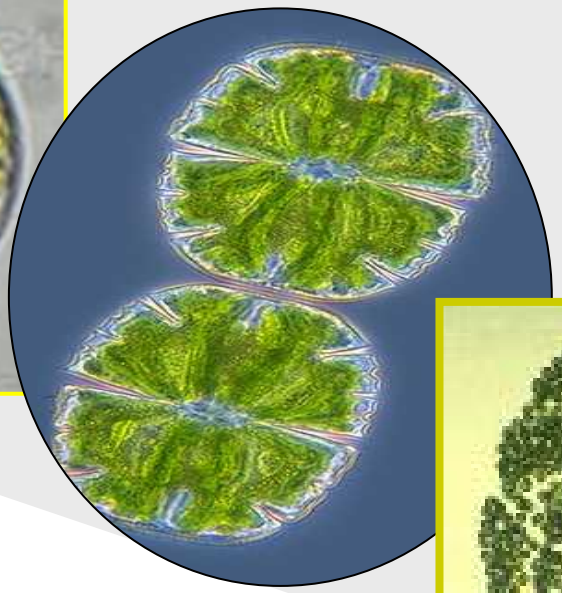


5. Phytoplankton production & biomass in the upper SFE & elsewhere

How much? & Why?

Light, flow, transport, nutrients, species





Phytoplankton C sources & sinks in the upper SFE

Jassby et al 2002

1975-1993

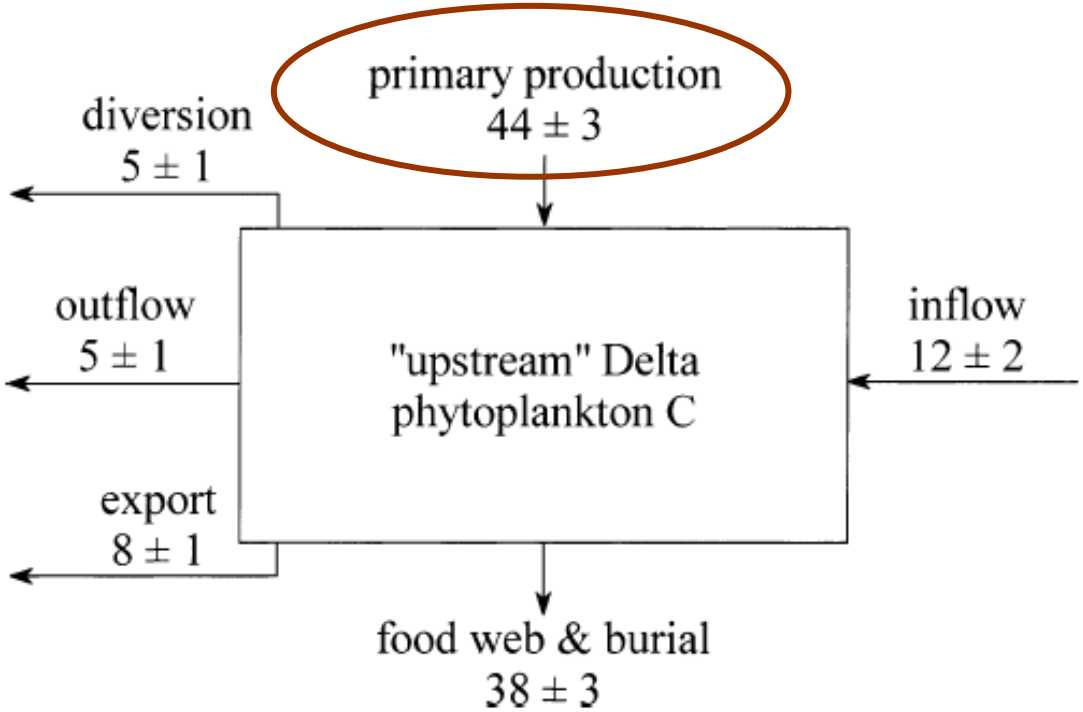


Fig. 9. Phytoplankton C budget (tons d^{-1} ± SE among years) for the upstream Delta, averaged for March–October during 1975–1993. Primary (net) production is estimated as described in this publication. Inflow, outflow, diversion, and export are estimated as described by Jassby and Cloern (2000). Food web and burial is the residual amount required to balance the other flows.

Phytoplankton primary production needs "starting biomass" & light

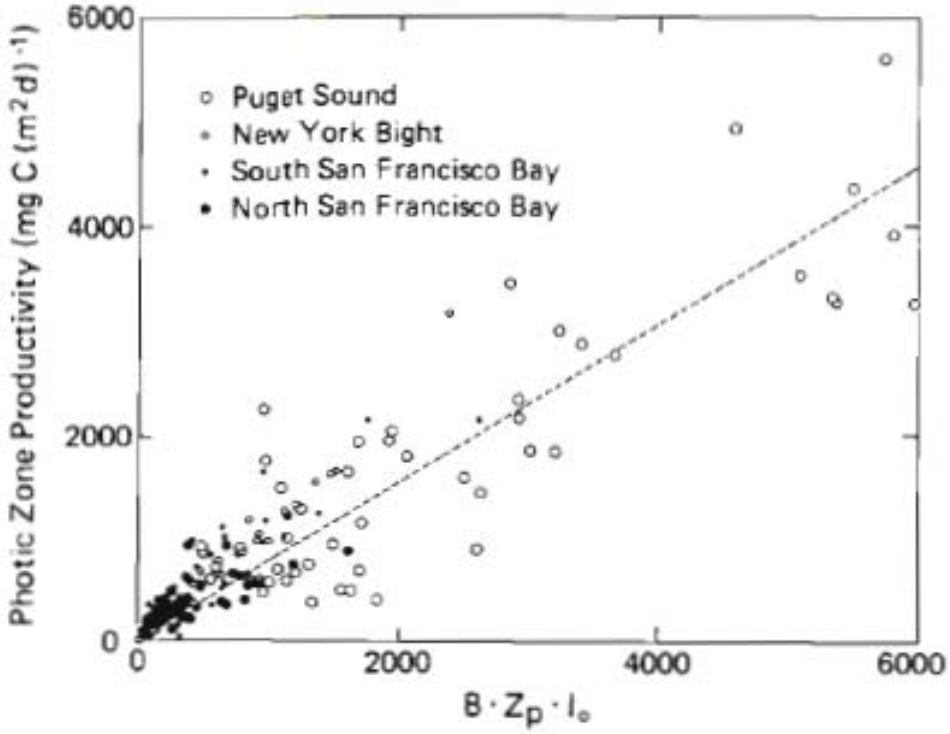


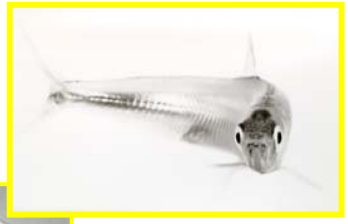
Fig. 2. Regression of photic zone productivity against the composite parameter $B Z_P I_o$ for 211 incubation experiments. $P = 150 + 0.73 (B Z_P I_o)$; $r^2 = 0.82$; S_{yx} (standard error of the estimate) = 410

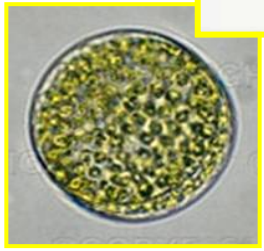
Phytoplankton production in estuaries is highly correlated with phytoplankton biomass, light, and photic zone depth

Fig. 2 in Cole & Cloern 1987

Phytoplankton Primary Production

… is related to Fisheries Yields in many Marine Systems (Nixon 1988)





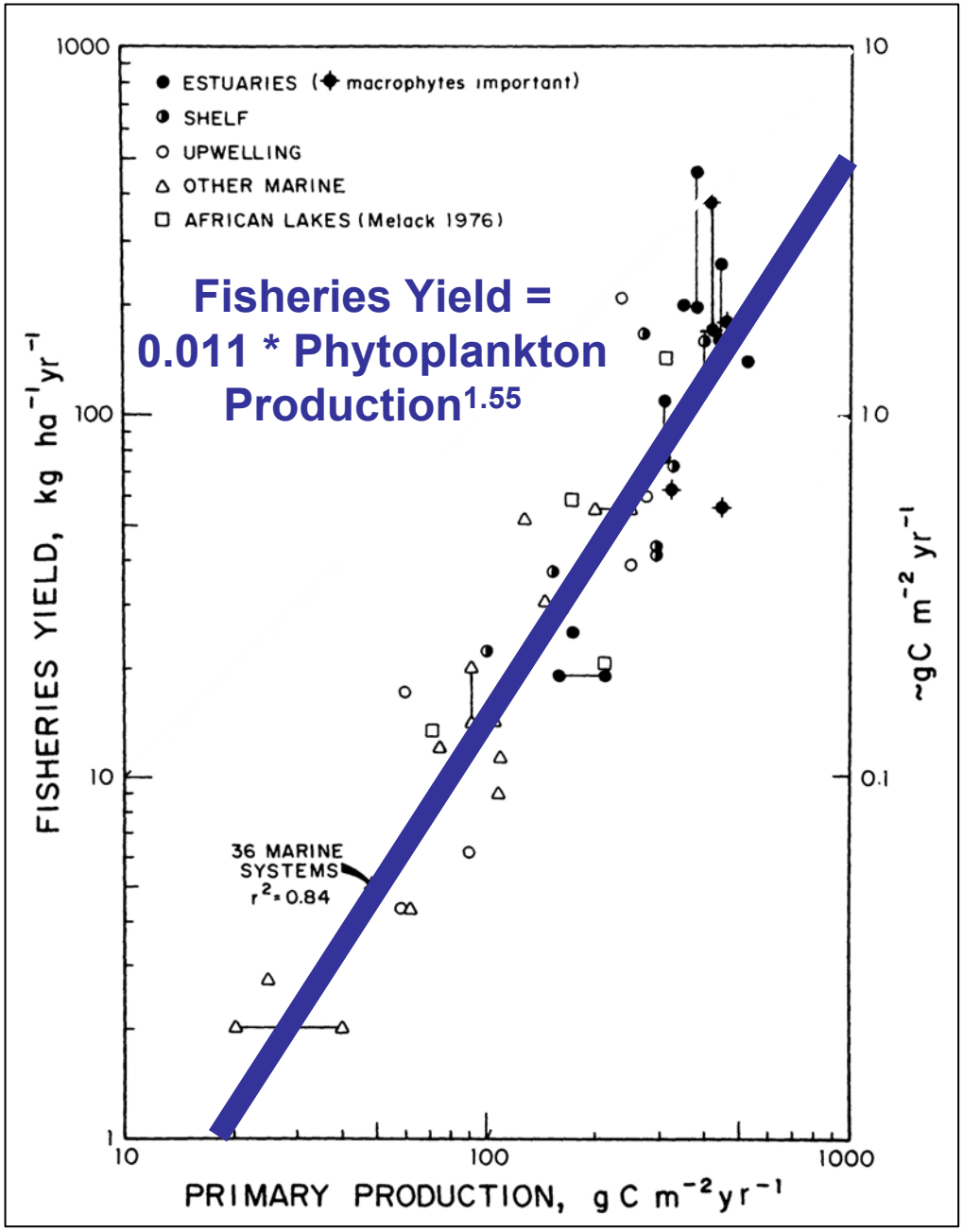
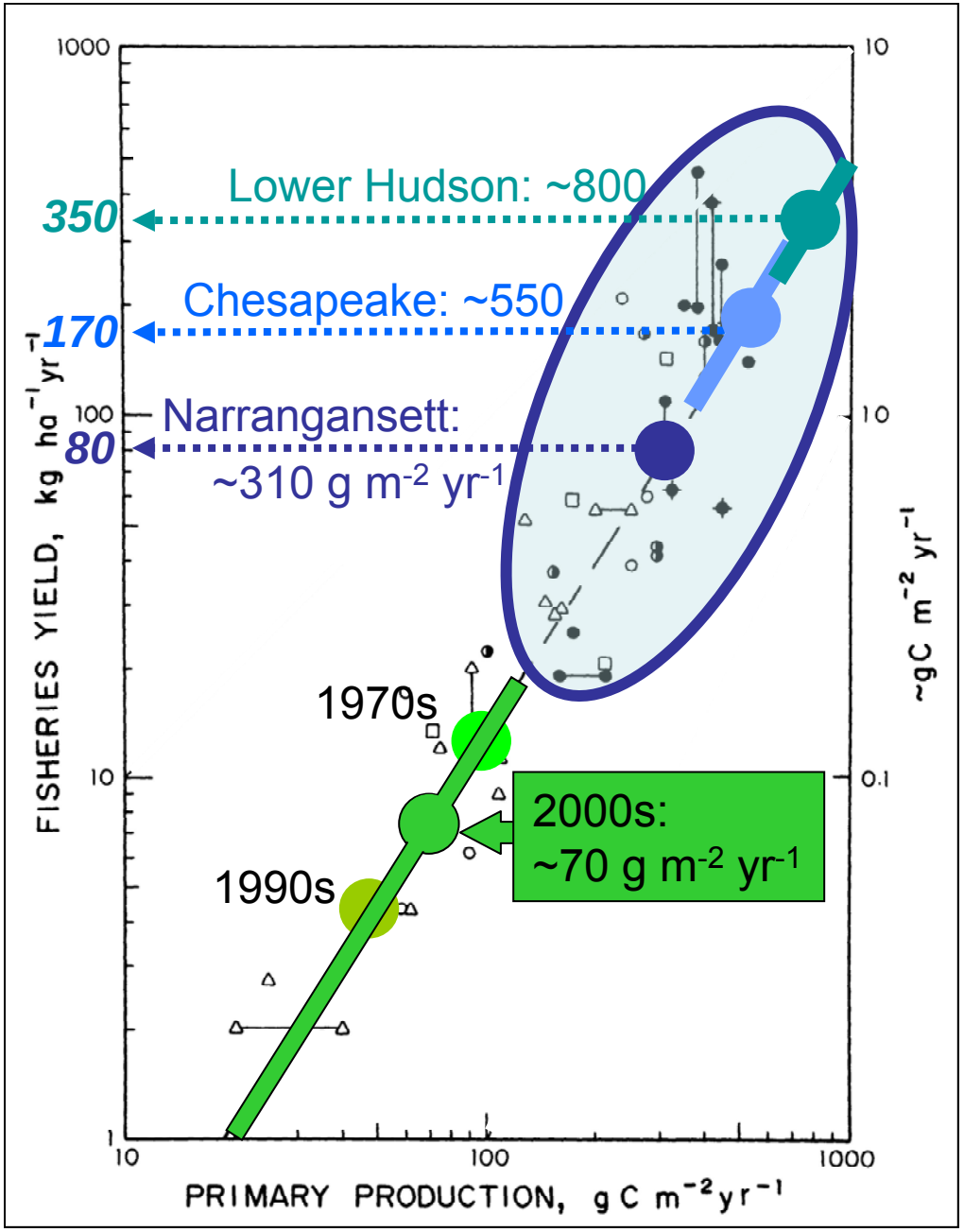


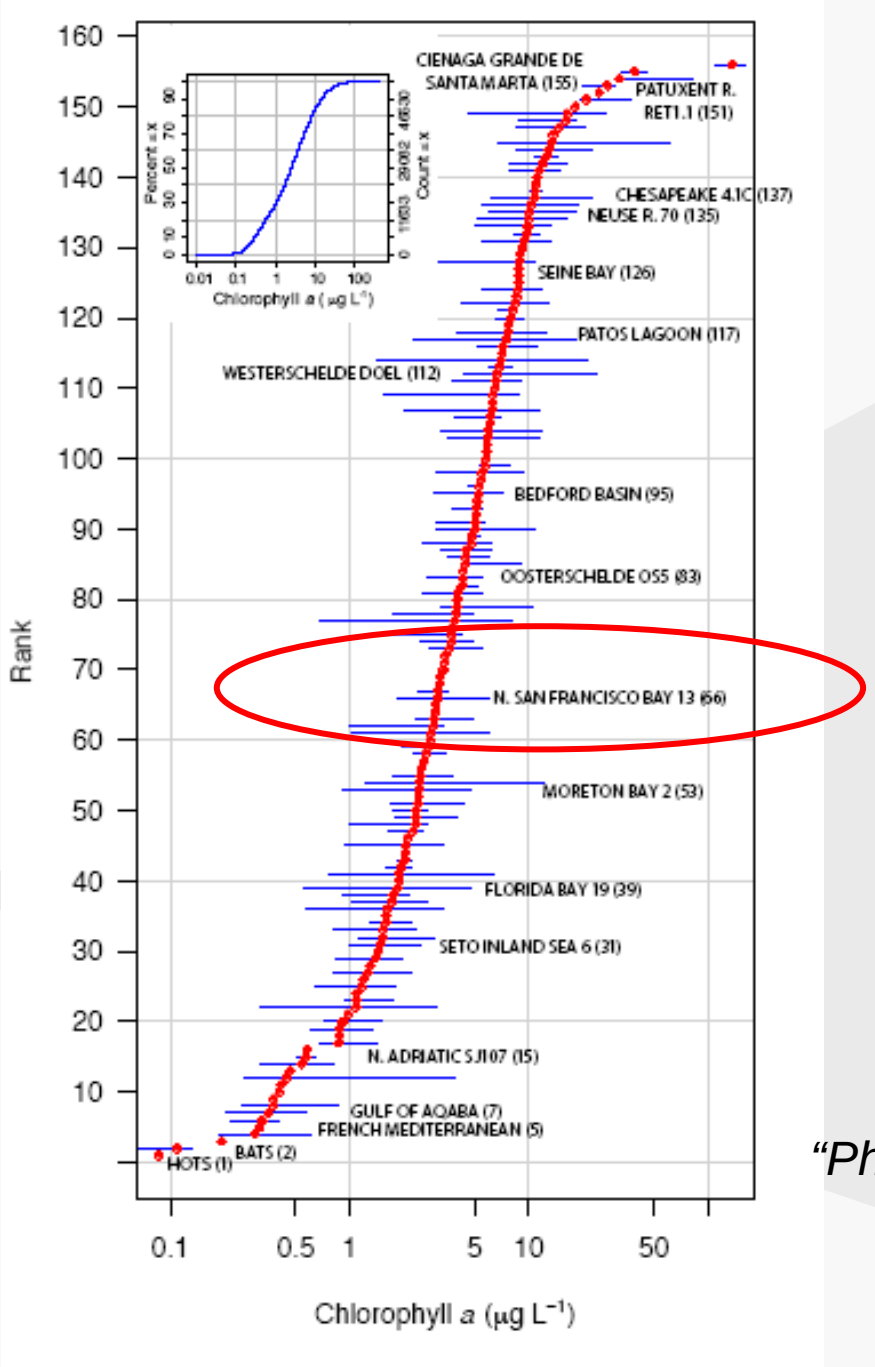
Figure 6 in Nixon 1988

Phytoplankton Primary Production

… in the Delta & Suisun Bay is lower than in other estuaries, and has DECLINED



Sources: A. Jassby (UCD), J. Cloern (USGS), IEP data



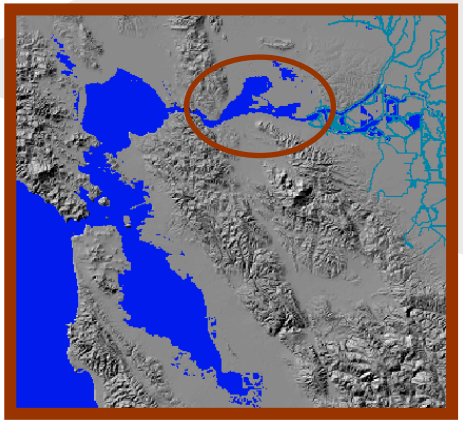
Coastal phytoplankton biomass tends to fall in a narrow & fairly low range (1-10 ug Chl a/L)

SFE is no exception, although there have been long-term DECLINES, esp. in Suisun Bay

Fig. 1 in Cloern & Jassby, "Phytoplankton Seasonal Patterns across the World's Coastal Marine Ecosystems." Submitted to Ecol. Letters (Thanks for letting me show this!)

Phytoplankton Biomass & Primary Production

… CRASHED in Suisun Bay right after the 1987 *Corbula* invasion



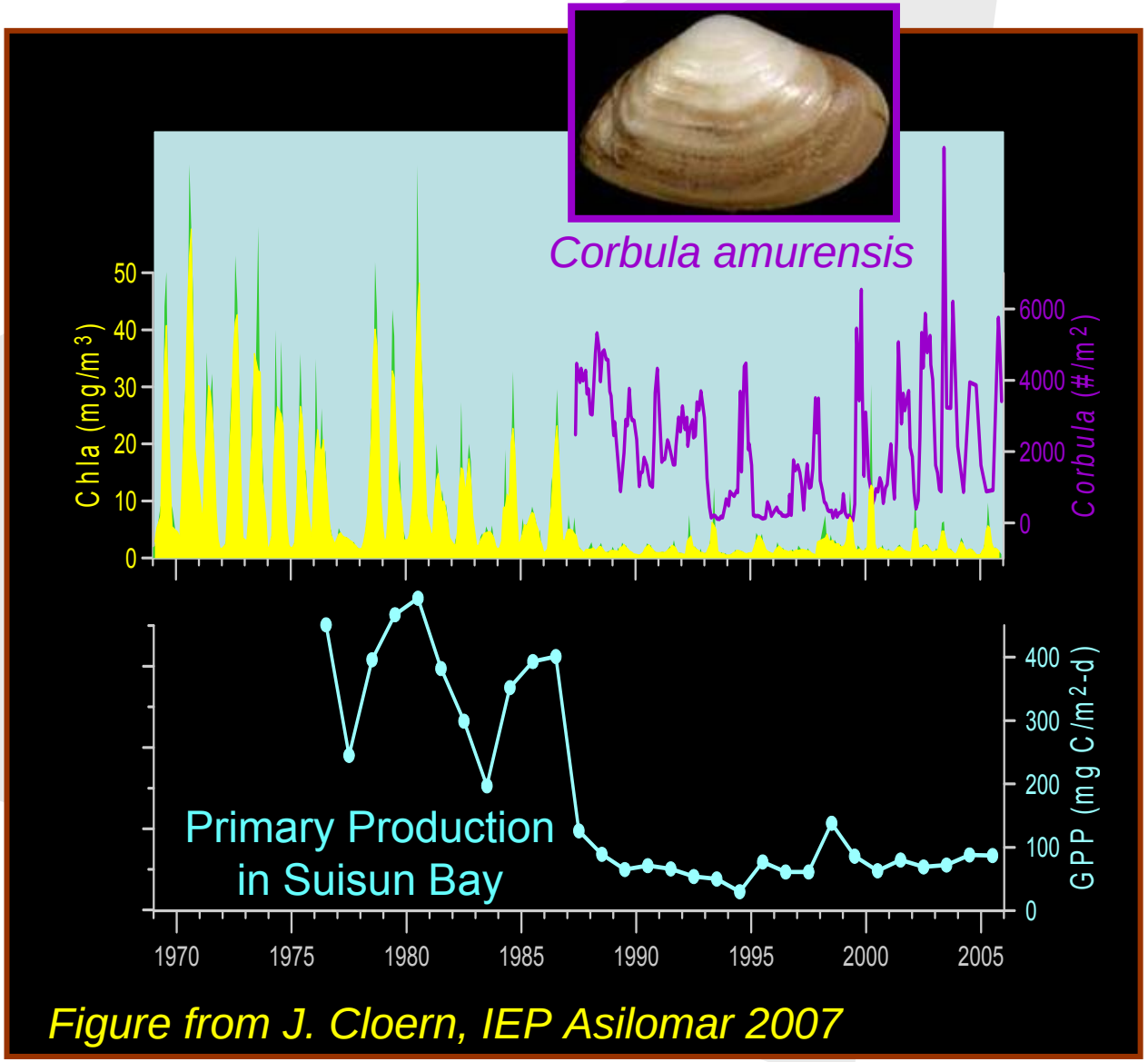


Figure from J. Cloern, IEP Asilomar 2007

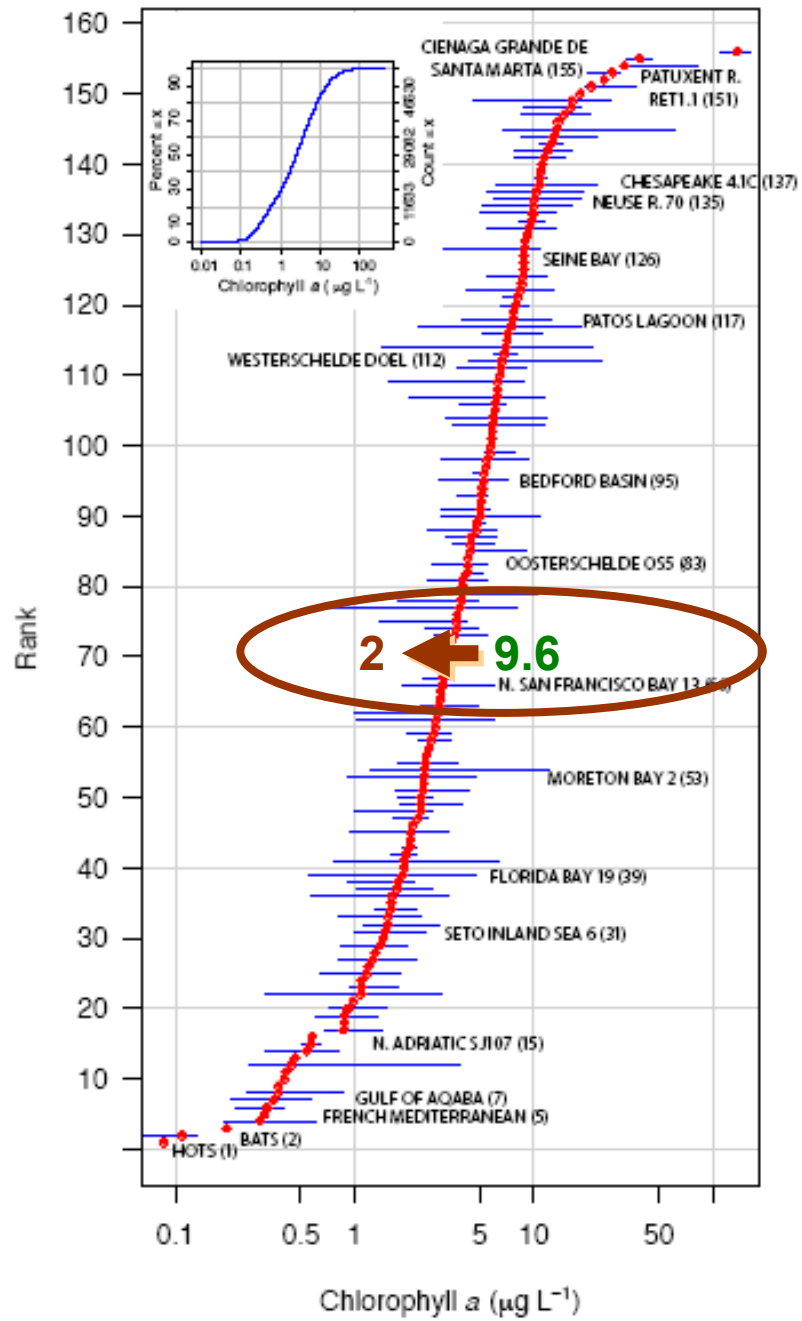


Fig. 1 in Cloern & Jassby, submitted

Coastal phytoplankton biomass: 1-10 µg Chl a/L

Upper SFE:

- Long-term declines
- Recent uptrends in Delta & SF Bay, but not in Suisun Bay
- Typically 2-3 µg Chl a/L (range 0 – 500)
- "High nutrient - Low Chl"

Lehman 2002, 2004
Jassby et al 2002
Cloern et al 2007
Jassby 2008

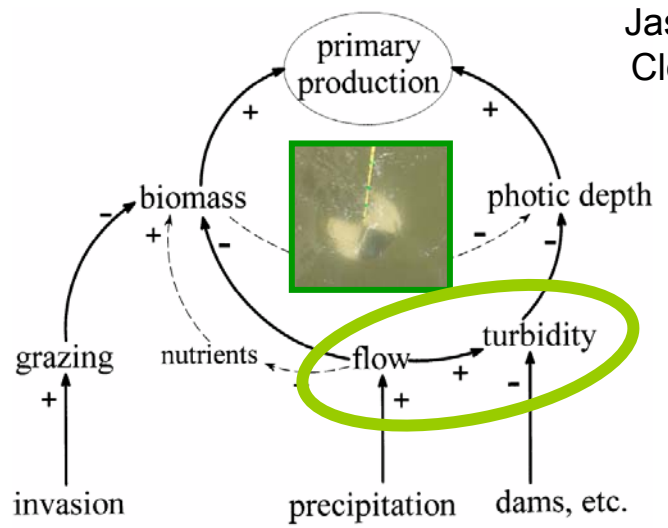


Fig. 12 in Jassby et al 2002

Flow determines much of the variability in Delta & Suisun Phytoplankton Biomass

Less flow, more phytoplankton

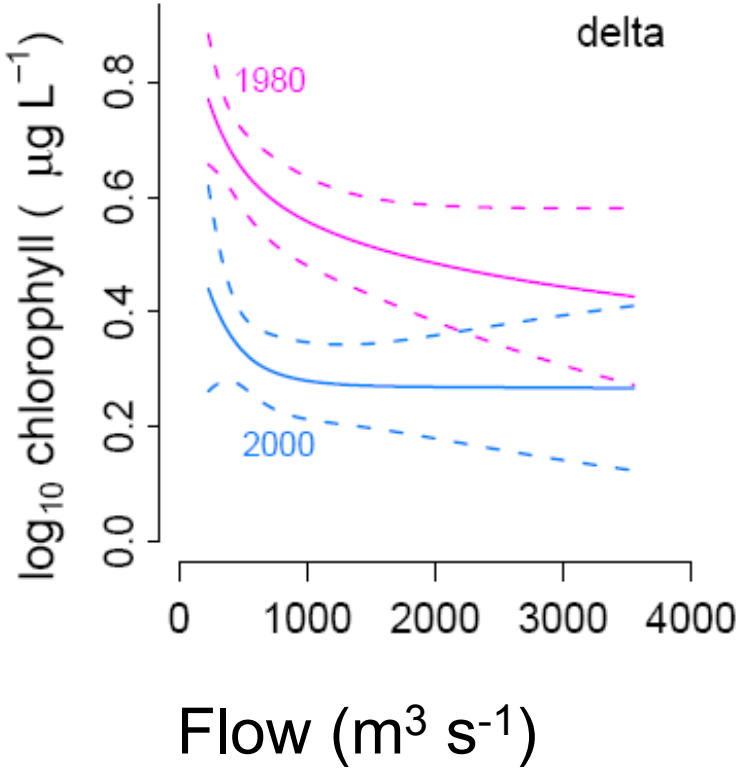


Fig. 10 in Jassby 2008

… & in the San Joaquin River, too

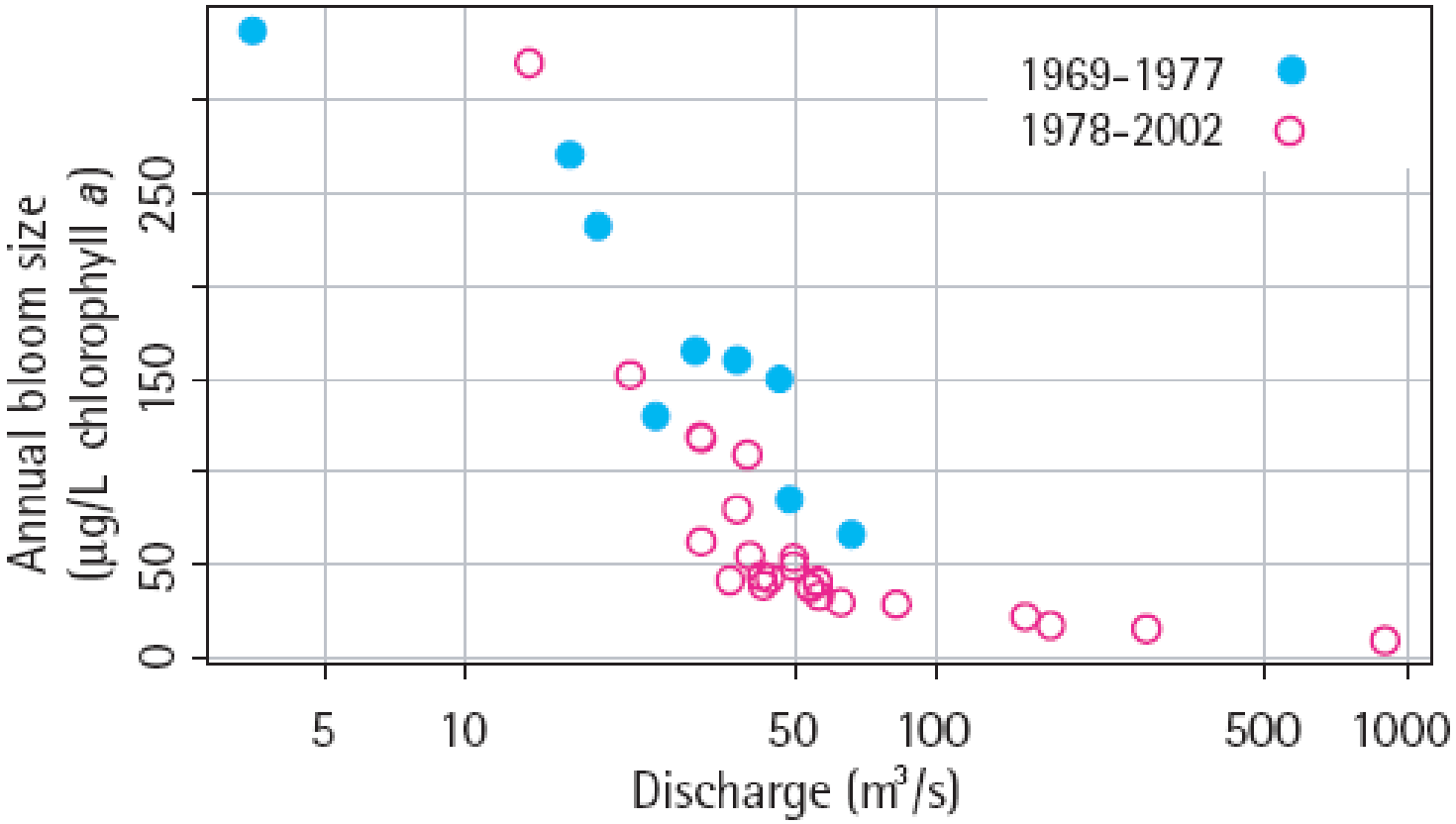


Fig. 8 in Jassby 2005

MUCH more on flow & phytoplankton:
L. Lucas, N. Monsen, W. Kimmerer…

An exception: Suisun Bay in the 2000s
Less flow, LESS phytoplankton

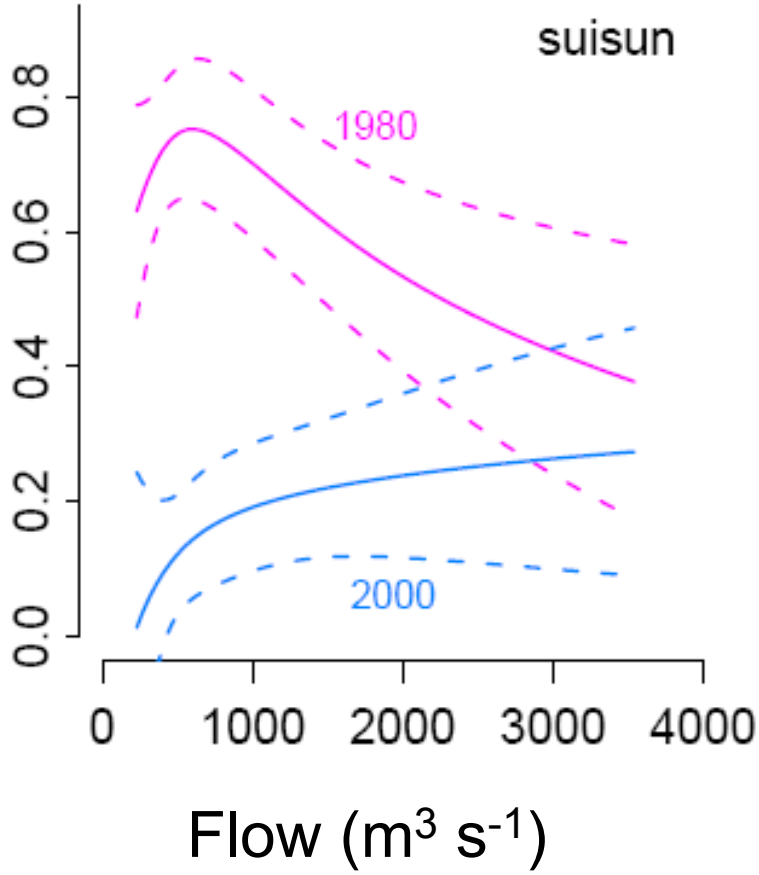


Fig. 10 in Jassby 2008

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Habitat connectivity is also important

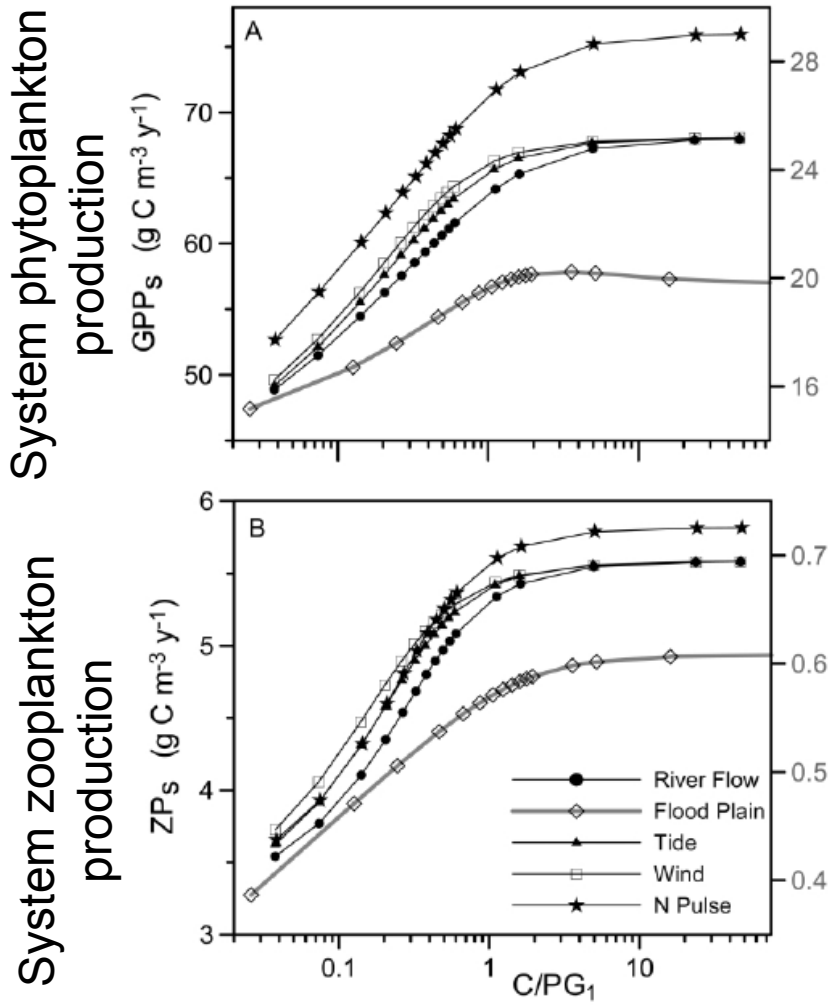
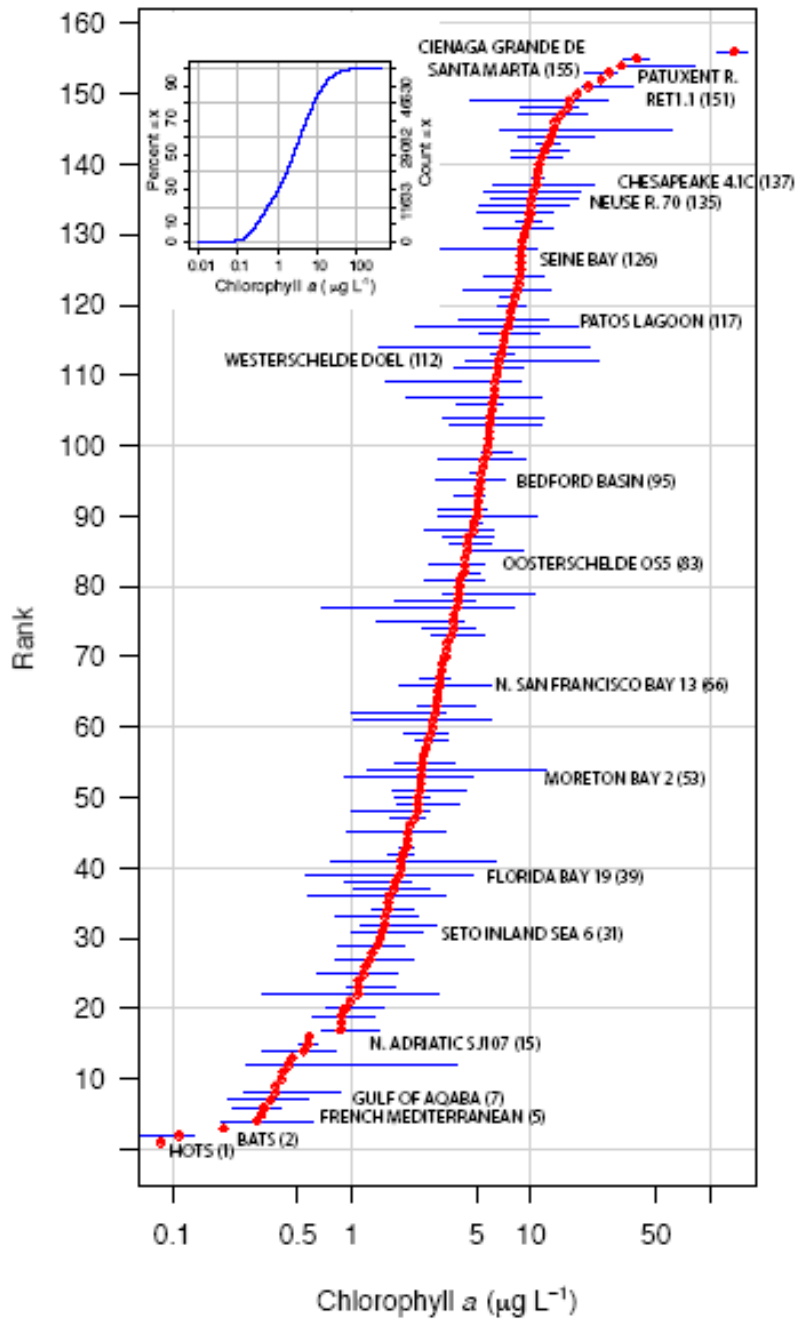


Fig. 5 in Cloern 2007

Transport of nutrients & biomass between heterotrophic to autotrophic habitats sustains higher system primary production; System production is optimized when the transport rate matches the growth rate of primary producers.

MUCH more on flow & phytoplankton:
L. Lucas, N. Monsen, W. Kimmerer, Cosumnes research group…



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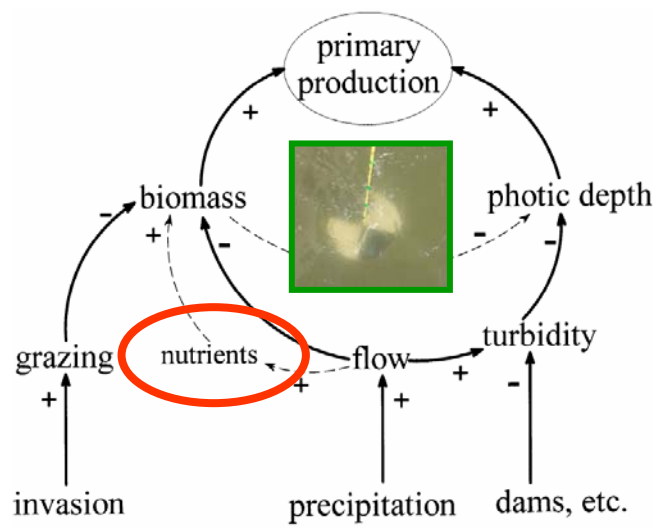
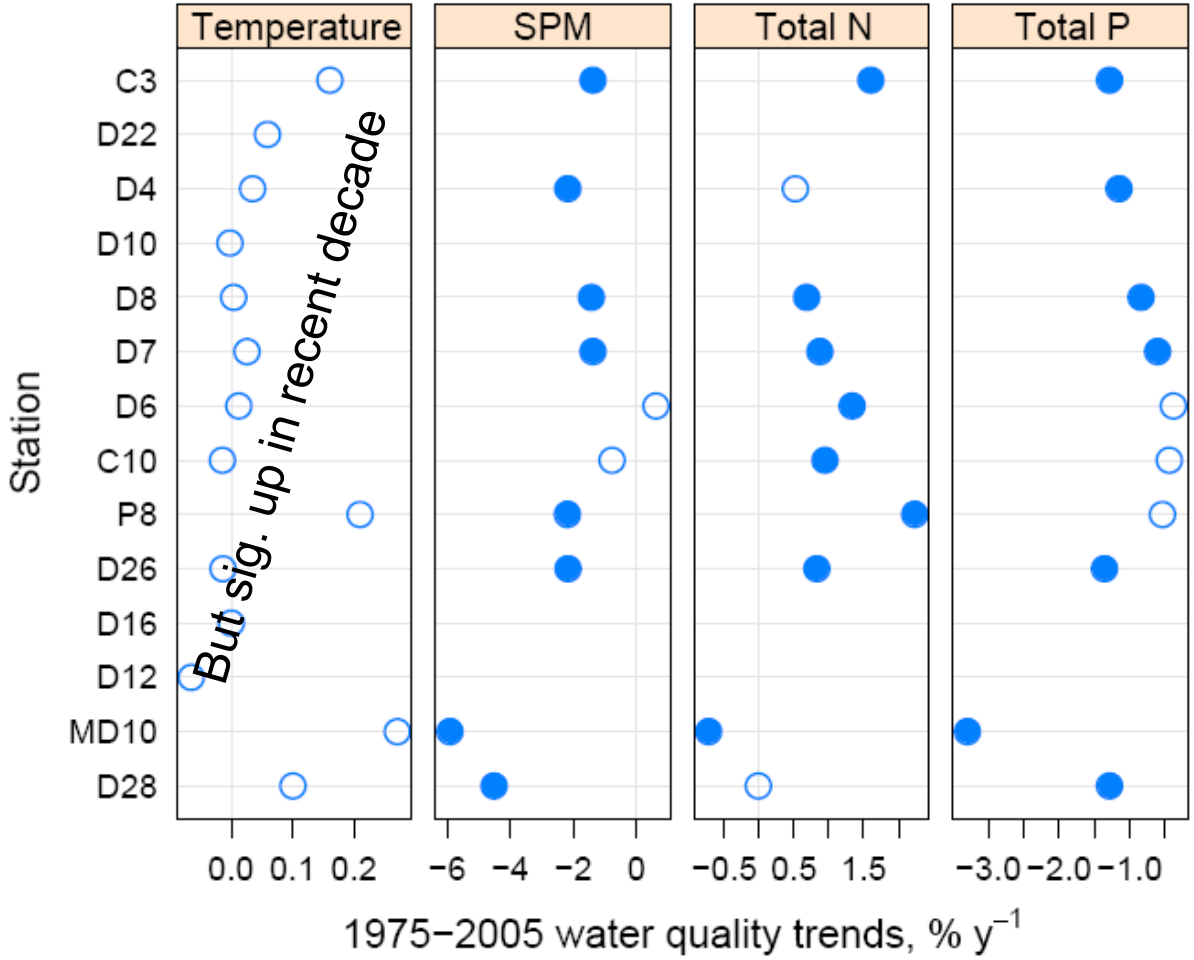


Fig. 12 in Jassby et al 2002

Recent work: nutrients may matter – **when light doesn't**

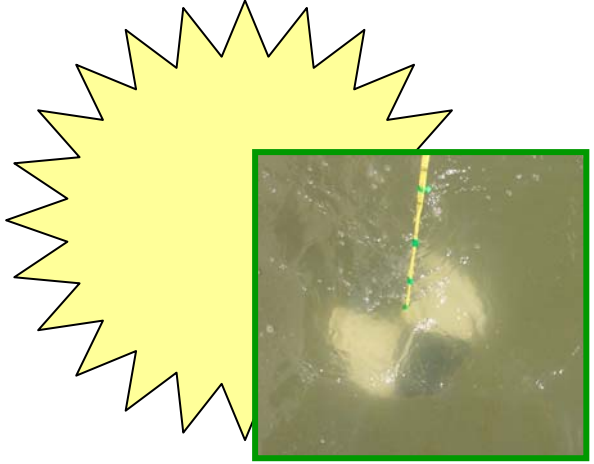
- Dugdale et al 2007, Wilkerson et al 2006: N
- Van Nieuwenhuyse 2007: P
- Cloern 2007: in shallow habitats

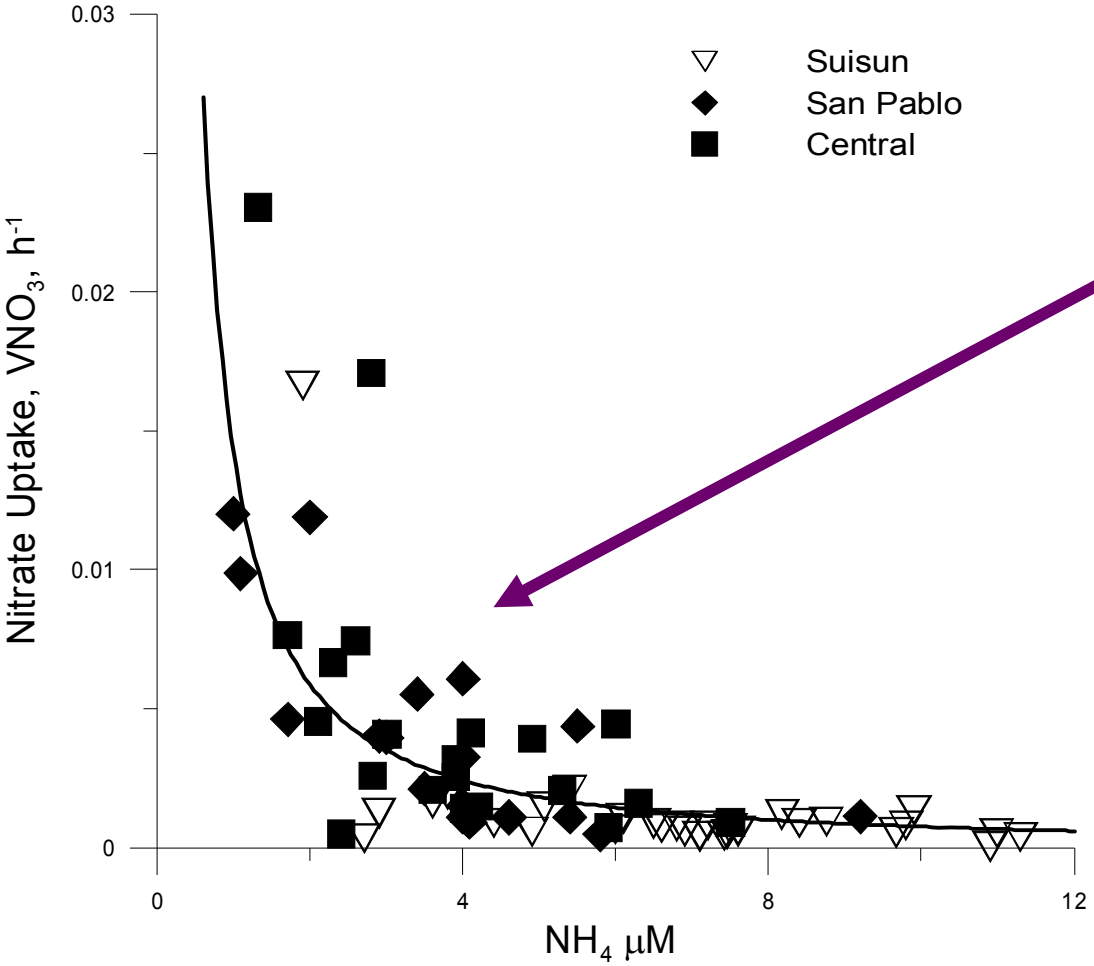


- Turbidity (SPM) has decreased
- N has increased
- P has decreased
- Shallow habitat restoration

Fig. 10 in Jassby 2008

Nitrate uptake inhibition hypothesis:
Ammonium inhibits nitrate uptake/growth





~ 90% inhibition at 4 µmol NH_4-N

(=0.06 mg/L)

Fig. 3 in Dugdale et al 2007

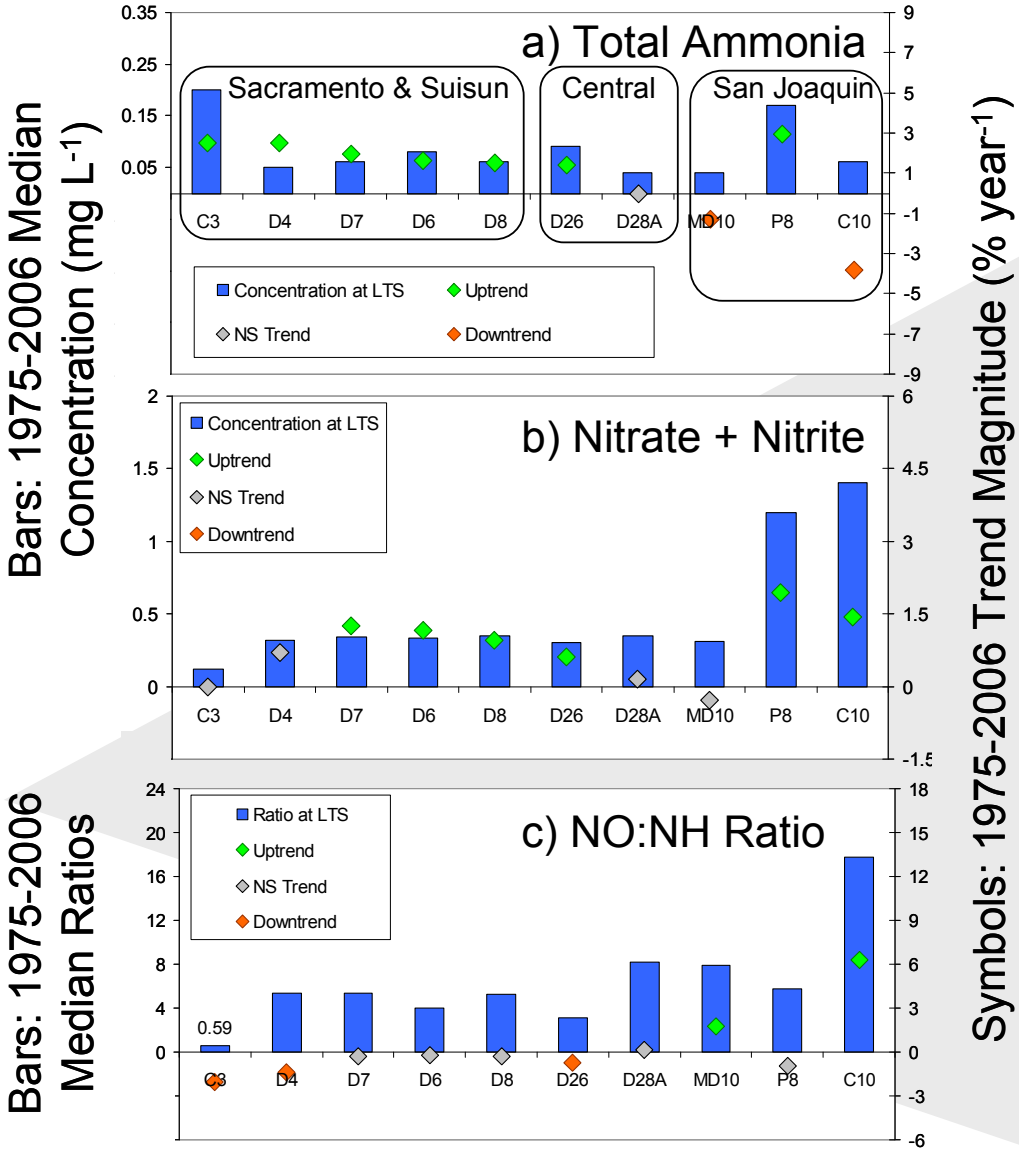


Figure: A. Mueller-Solger, IEP data, unpublished

Ammonium levels in the Delta are on the rise & often > 4 µmol

A big source is urban wastewater discharge

(Jassby 2008)

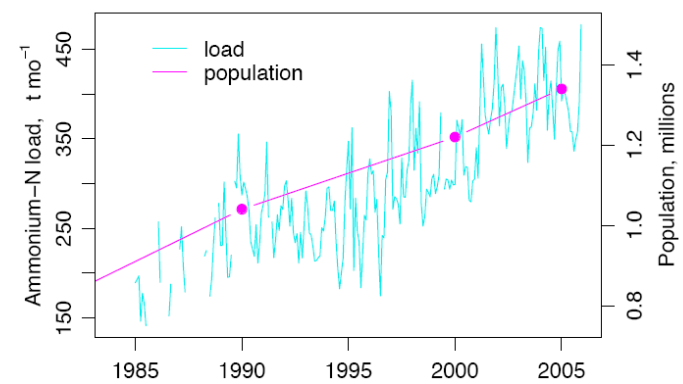


Figure 15. Monthly load of ammonium-N in wastewater from the County of Sacramento Regional Wastewater Treatment Plant. County population is also shown for comparison.

Britto & Kronzucker, J. Plant. Physiol. 2002:

"Ammonium is a paradoxical nutrient ion"

- Major N source
- Easy uptake by plants (no reduction necessary)
- Intermediate in many metabolic reactions

BUT:

- Can inhibit algae production
- Can be toxic to plants
- Can be toxic to animals (NH_3)
- Can be toxic to humans – neurological, insulin, liver disorders

Ammonium toxicity known since at least 1882: Charles Darwin described NH_4+-induced growth inhibition in *Euphorbia peplus* (aka Petty spurge, Cancerweed)

Ammonium affects different groups of algae differently;

Diatoms are especially affected

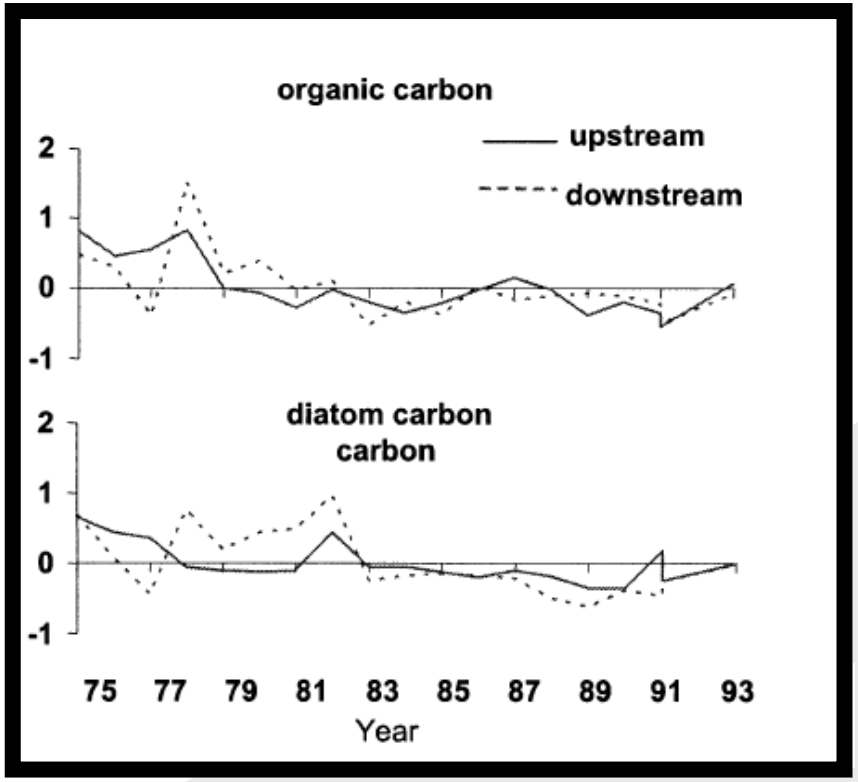
(Dortch, MEPS 1990)

Table 3. Percent of reports[a] of species preference for ammonium[b] compiled from Table 2 and Antia et al. (1975)

Taxon	% Preference NH_4^+	
	V_{max}	μ_{max}
Diatoms	65 (17)	16 (25)
Dinoflagellates	45 (11)	20 (5)
Cyanobacteria	50 (4)	28 (14)
Chlorophytes	50 (4)	57 (7)
Other	100 (6)	26 (19)

[a] Number of reports given in parentheses. Duplicates or conflicting reports for the same species counted seperately since environmental conditions can influence preference

[b] Preference defined as in Table 2



Phytoplankton Community Composition in the Delta & Suisun has changed

P. Lehman, Estuaries 2004

Diatoms DOWN

(climate)

Fig. 4 in Lehman 2004

T. Brown, IEP-Asilomar 2008
(non-par. multivariate ANOVA & Bray-Curtis dissimilarities)

Suisun Bay	1970s	2000s	
Taxon	Ave. Abund	Ave. Abund	Ave. Diss
Thalassiosira	0.90	0.08	15.46
Cyclotella	0.70	0.11	11.50
Skeletonema	0.51	0.08	8.00
Misc Flagellates	0.08	0.42	7.28

Common diatoms DOWN

Misc. Flagellates: UP

This didn't happen in San Francisco Bay (Cloern & Dufford 2005)

On the rise: *Microcystis aeruginosa* blooms

Toxic!

Bad food!

P. Lehman, Hydrobiologia, 2005 and 2008, & pers. com.)

- Seasonal blooms since 1999, June-November
- Blooms peak in the central delta in August and September
- Low **streamflow** strongly associated with high cell density in 2004
- 2007 was the worst bloom year on record (1.4 million cells/ml at Antioch)

Microcystis & temperature

- Grow better at higher temperatures (often above 25°C) than do diatoms and green algae (Paerl 2008, also *Cylindrospermopsis raciborskii*)

Microcystis & light: Float/migrate vertically

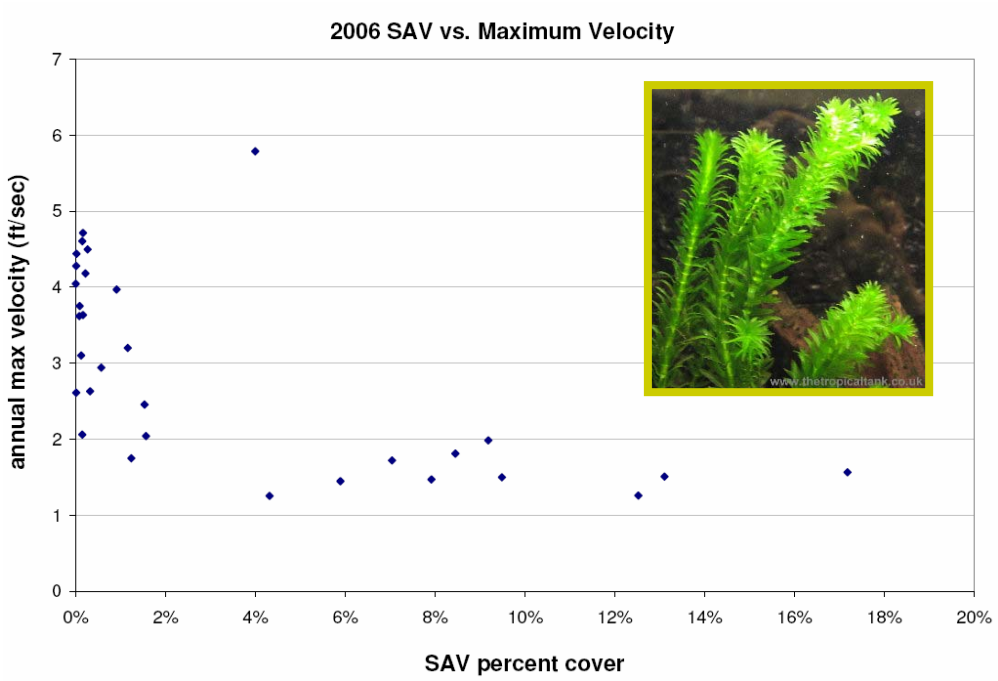
Microcystis & nutrients:

- N-specialist: can grow rapidly on NH_4^+ & NO_3^- (von Rueckert & Giani, Revista Brasil. Bot. 2004)
- P-storage-adapted species: high capacity to absorb & store inorganic phosphorus (Marinho & Feliciano, Aquat. Ecol. 2007)
- Low N/P ratio may be consequence, not cause, of blooms (Marinho & F. Aquat. Ecol. 2007)
- Nutrient uptake not inhibited by high light intensity (Takamura et al, JPR 1987)

Also on the rise: Submerged aquatic vegetation

Schoellhamer & Hestir, IEP Asilomar 2008

- SAV (*Egeria*) areal cover increasing (by 12-13% each year from 2004-2006
- Inversely correlated to **water velocity**
- **"Ecosystem engineers"**



Egeria & nutrients:

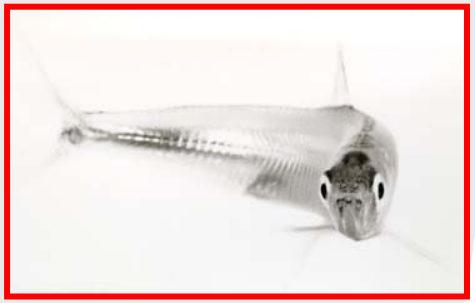
Pennington & Sytsma,
Portland State Univ., 2005:

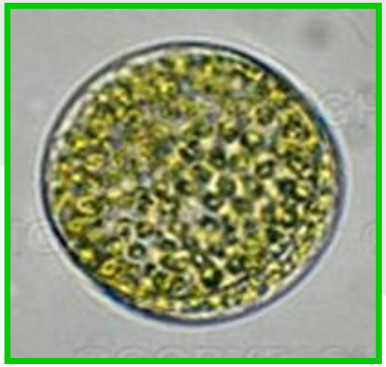
- High nitrogen content increases **photosynthetic efficiency in *Egeria*** in the Delta (need less light with lots of N)

UCD Extension (ANR):

- ***Egeria densa*** biomass increases with increased **ammonium** in stream water and with total nitrogen in sediments.
- Tolerates a wide range of phosphorus.

6. Phytoplankton as a food source in the upper SFE





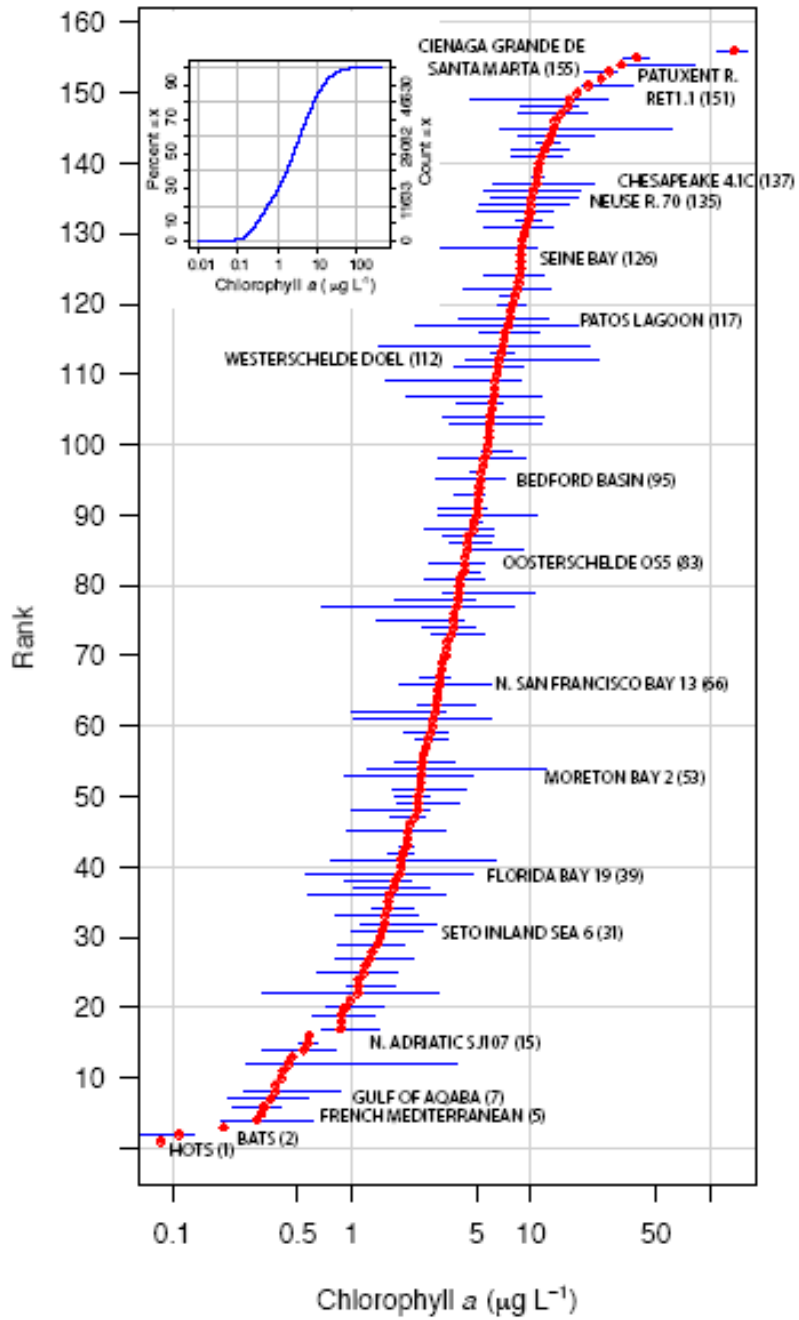


Fig. 1 in Cloern & Jassby, submitted

Coastal phytoplankton biomass: 1-10 µg Chl a/L

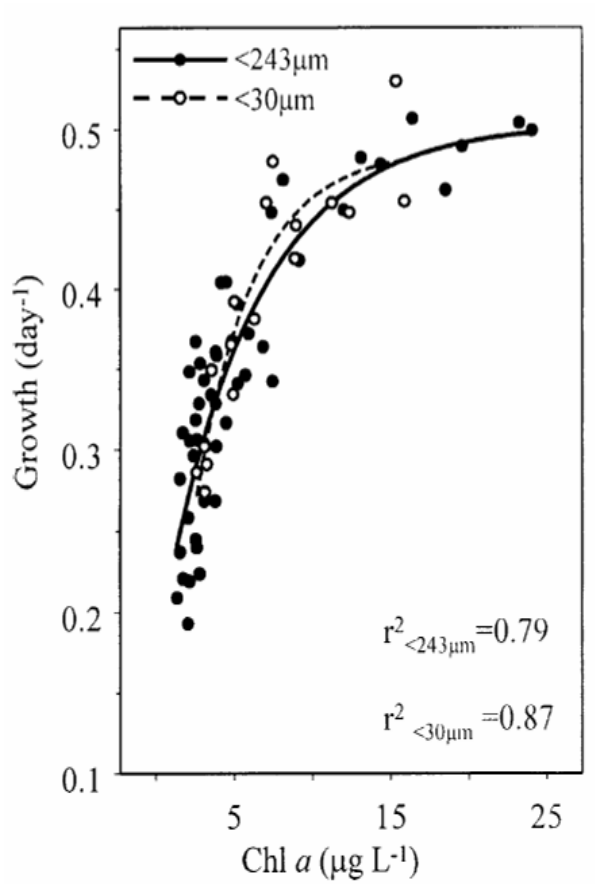
This is exactly the growth limiting range for several SFE zooplankton species!

Are estuarine zooplankton adapted to this (rel. low) phytoplankton biomass?

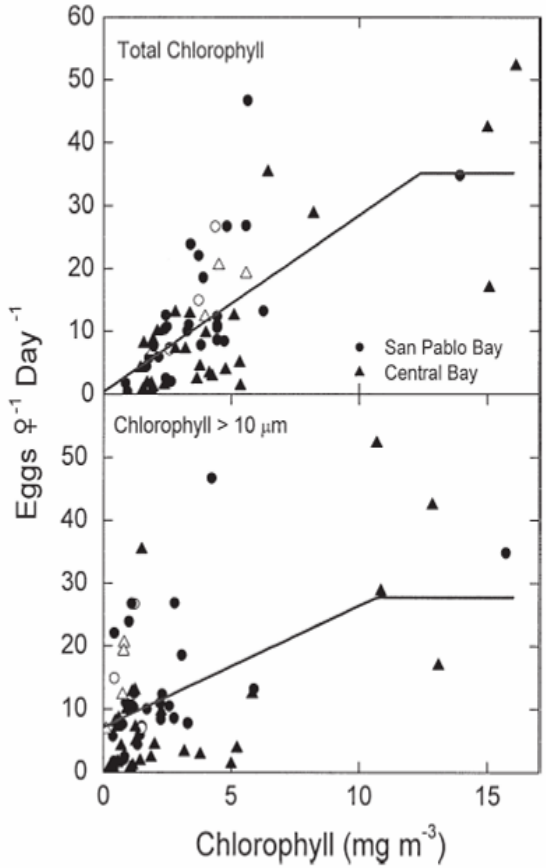
Is estuarine phytoplankton grazed particularly efficiently?

Chl *a* < ~ 10 µg/L limits some Bay-Delta zooplankton species…

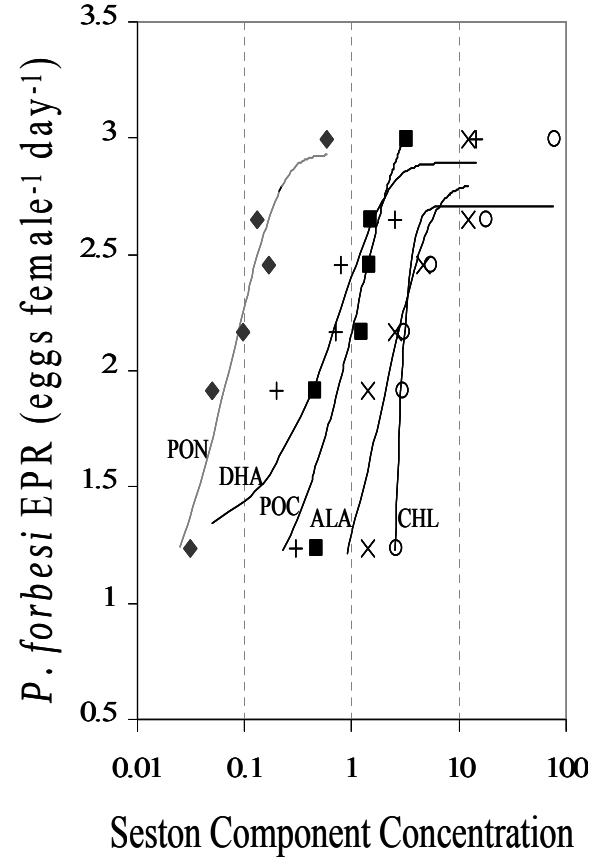
Daphnia magna
Mueller-Solger et al., L&O 2002



***Acartia* spp.**
Kimmerer et al., Estuaries 2005

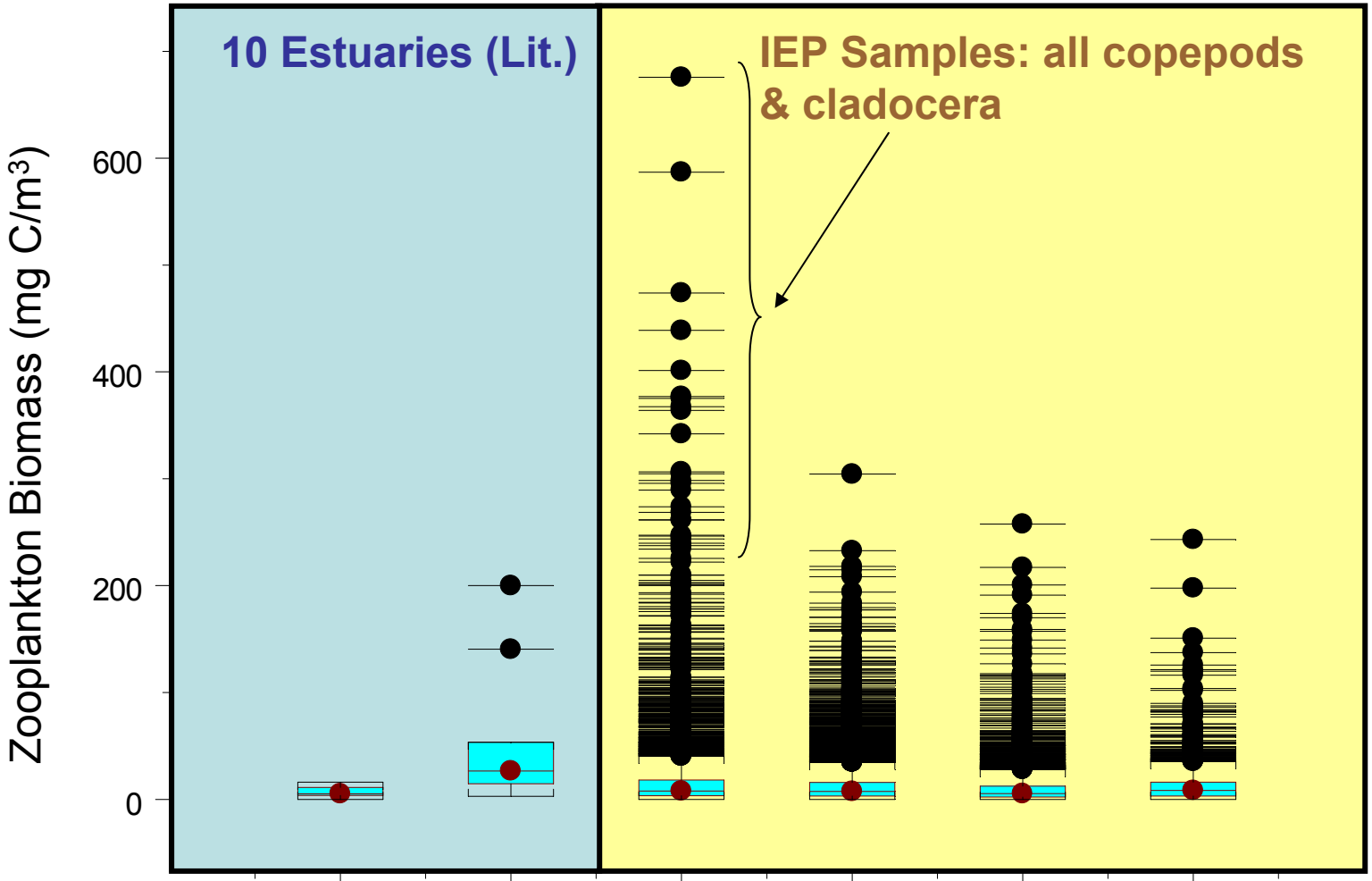


Pseudodiaptomus forbesi
Mueller-Solger et al., CALFED 2006



… but not all: no relationships found for *Limnoithona tetraspina* (Bouley & Kimmerer, MEPS 2006) and *Eurytemora affinis* (Mueller-Solger et al., CALFED 2006)

Total SFE mesozooplankton biomass: ~ “normal” ?



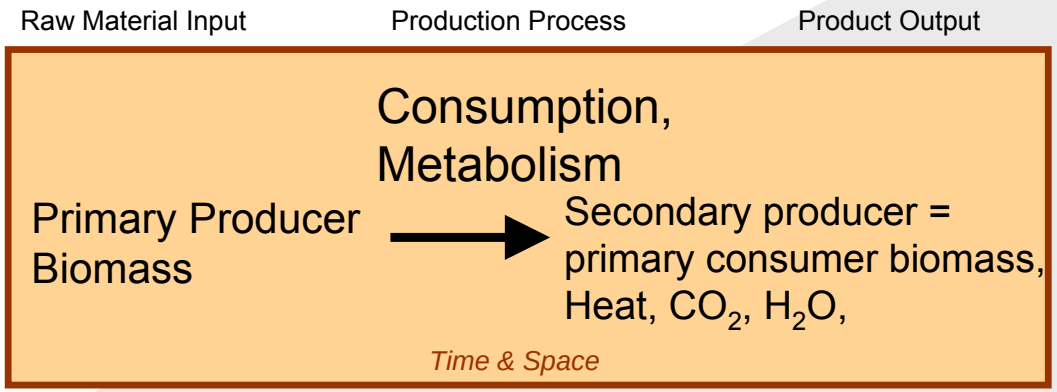
A. Mueller-Solger
IEP EET 2008

	Min	Max	72-76	77-86	87-96	97-06
n	10	10	4016	8776	4938	2118
Mean	7	54	18	13	10	12
Median	5	27	8	7	5	8
Maximum	16	200	676	304	258	243

Is estuarine phytoplankton grazed particularly efficiently?

Secondary Production: making new biomass from old biomass

It's not 100% efficient!!!



Rule of thumb:

Only about 5-20% of old biomass becomes new biomass, rest is "lost" as DOC, POC, CO_2

(output/input = 0.05 – 0.2 biomass units)

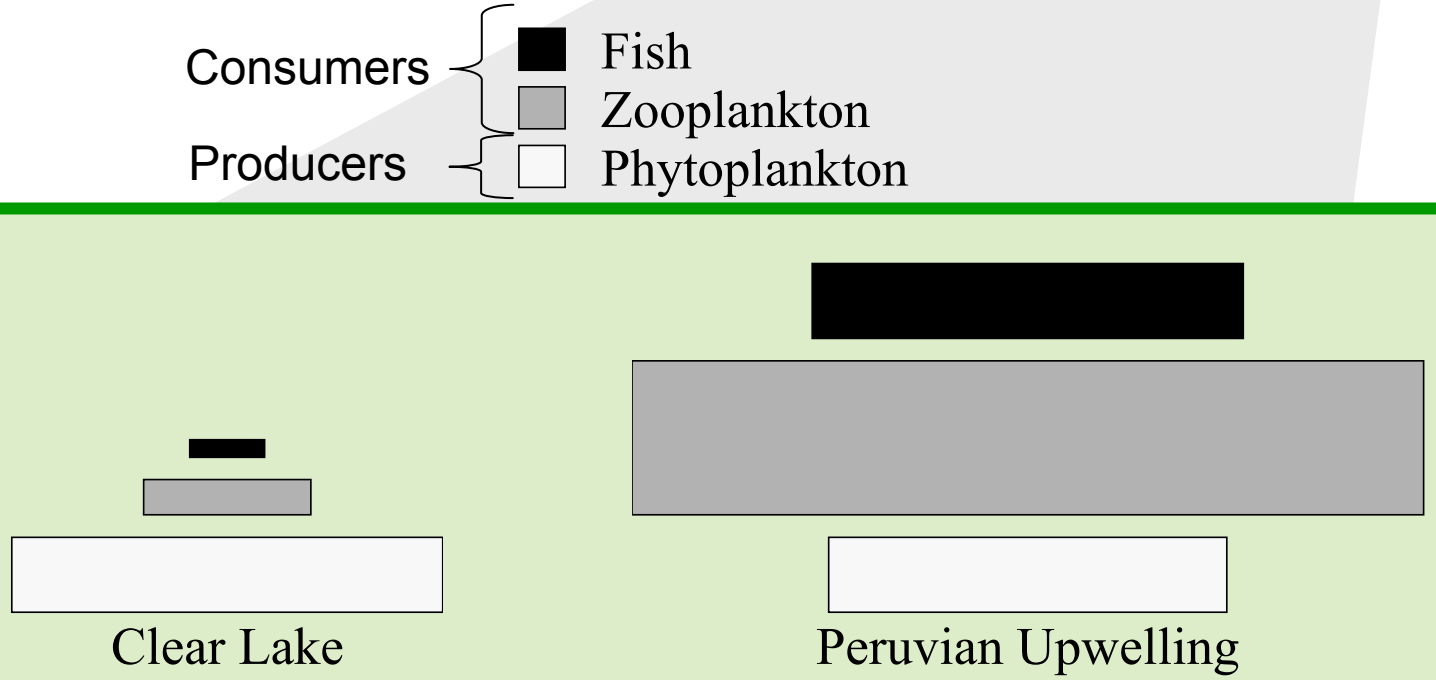
BUT there is a lot of variability

= different trophic efficiencies

Primary Production + TROPHIC EFFICIENCY: Making (lots of?) fish

Example: Relative producer and consumer biomass in a hypereutrophic lake (Clear Lake, CA) and a coastal upwelling system (Peru)

Brett & Müller-Navarra, Freshwater Biol. 1997



INEFFICIENT

EFFICIENT

50 times more fish/phyto than Clear Lake

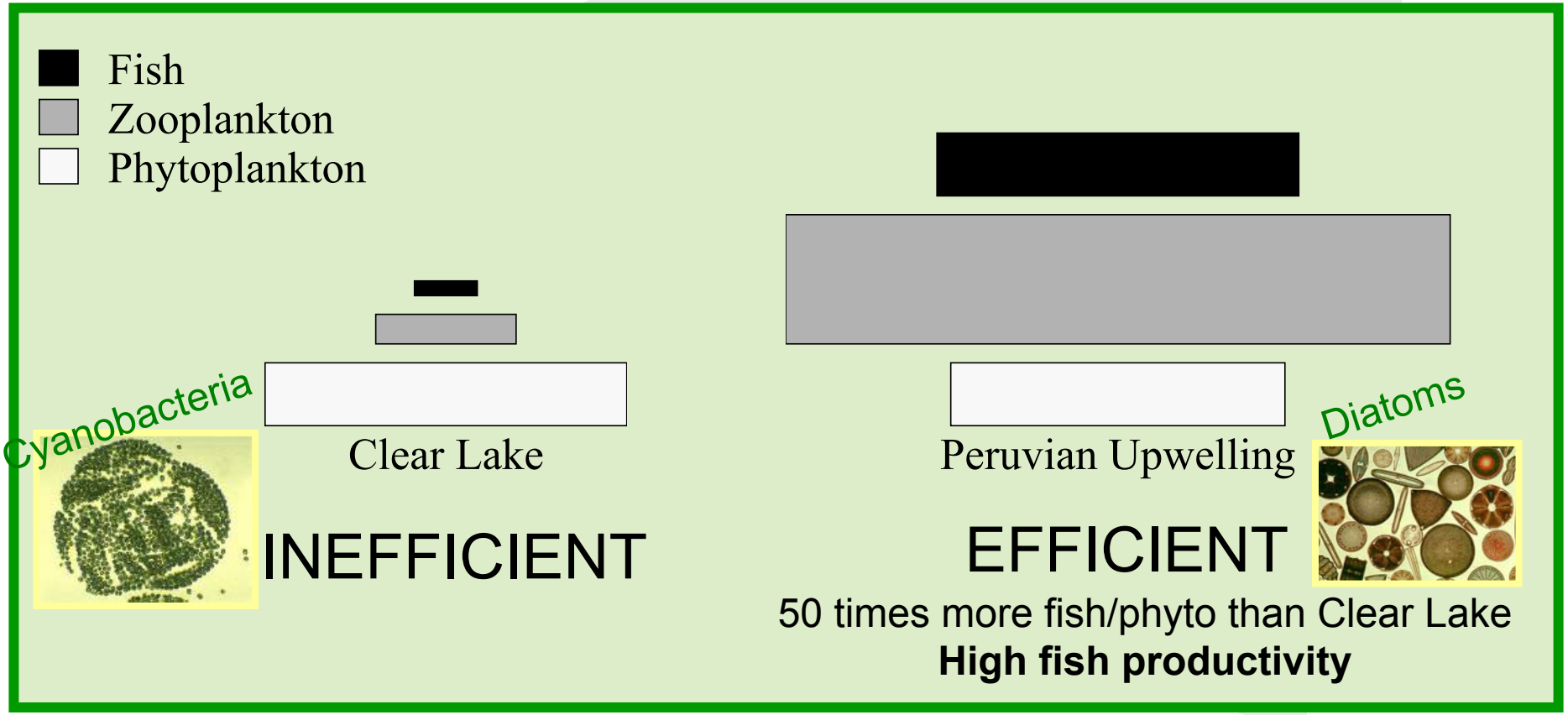
High fish productivity

Coastal/estuarine phytoplankton may be more nutritious than lake phytoplankton

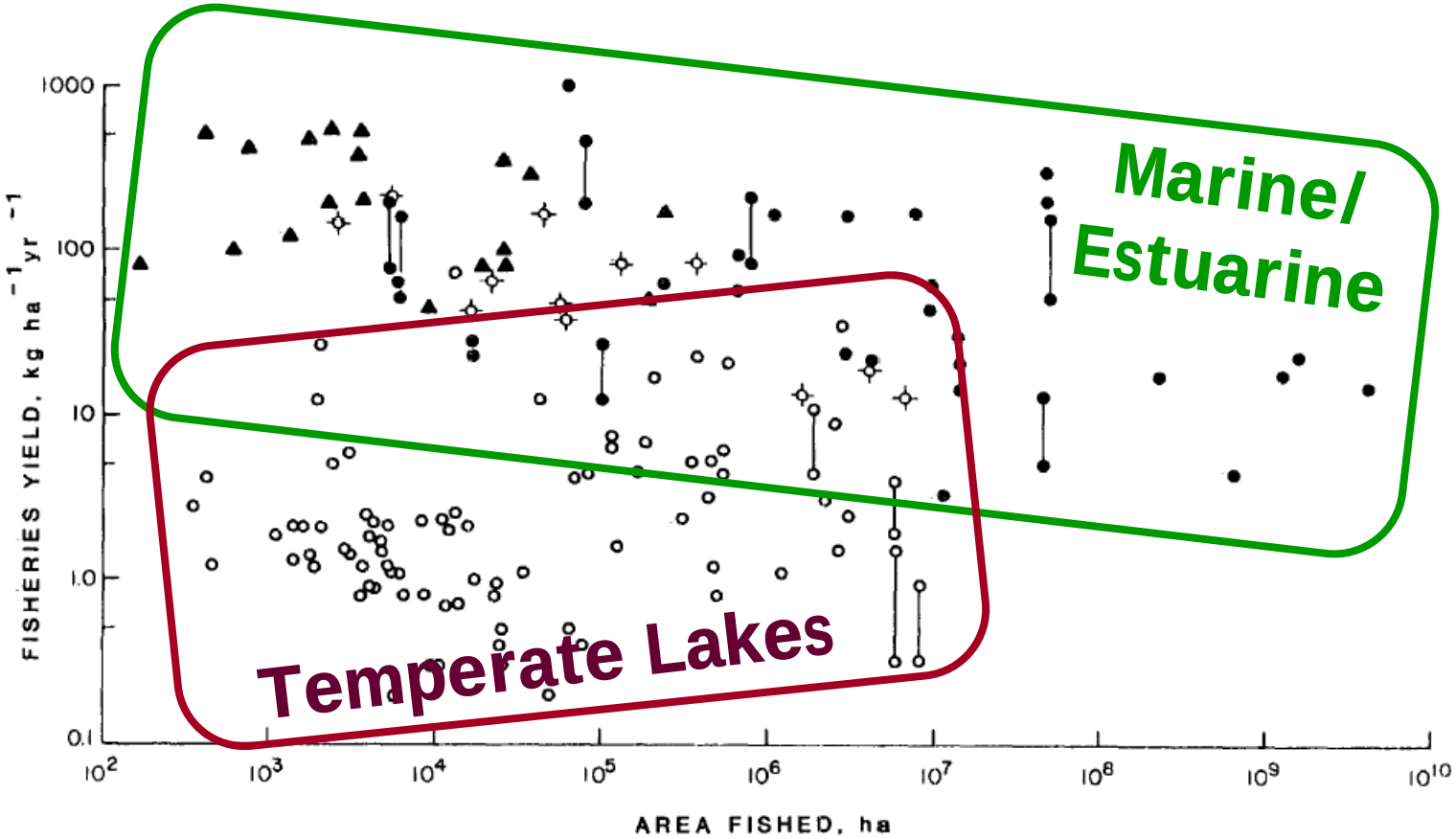
Higher quality algae: higher trophic efficiency

Diatoms, Cryptophytes > Green algae > Cyanobacteria

(Brett & Müller-Navarra, Freshwater Biol. 1997)



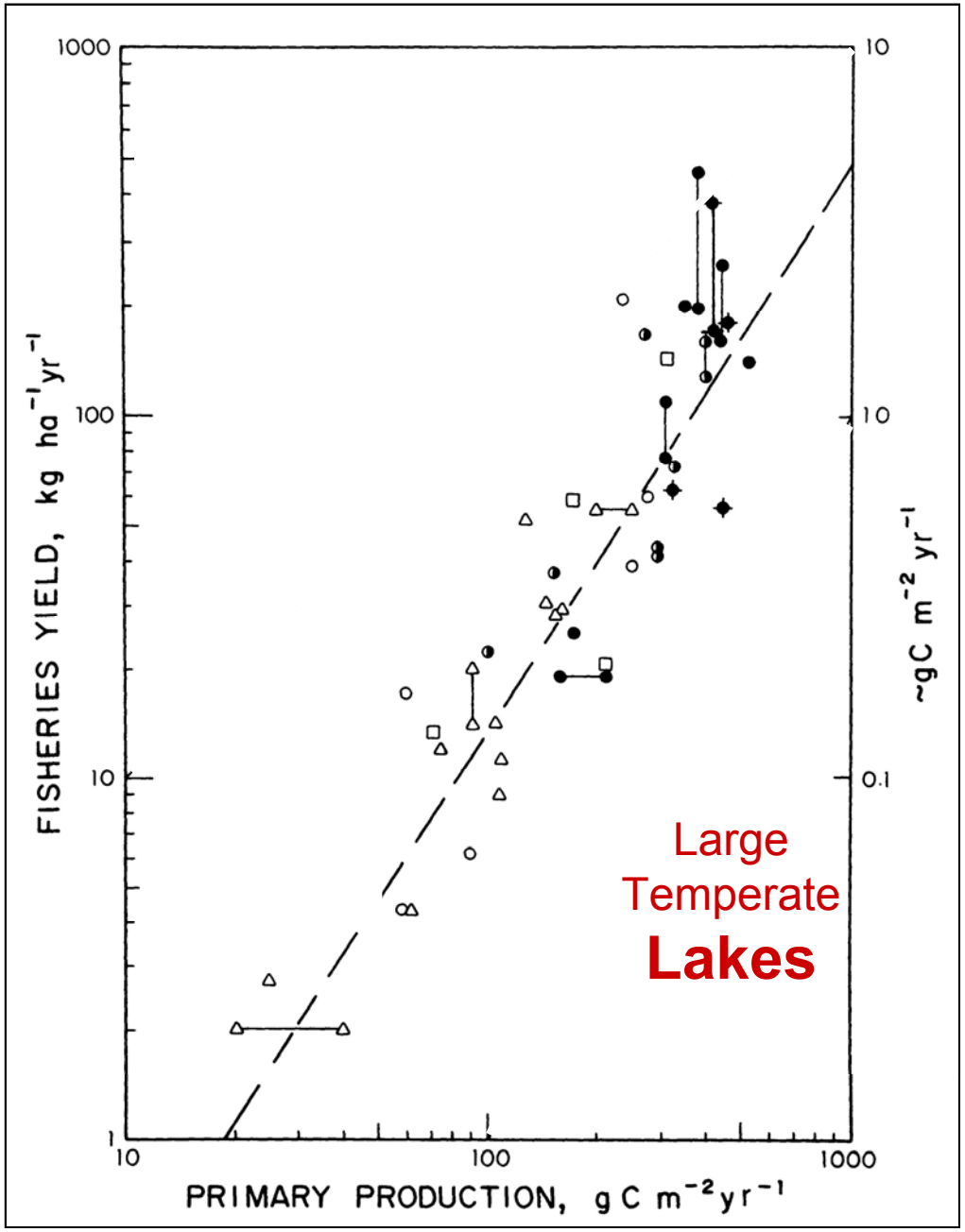
Coastal systems produce more fish than lakes

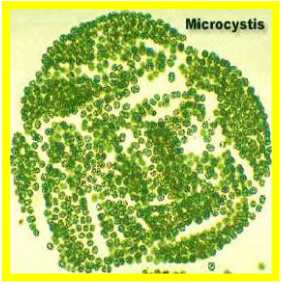


Scott Nixon, L&O 33 (4), 1988, p. 1018

Phytoplankton Primary Production & Fish Yield

… uncovering the hidden line in the Nixon graph



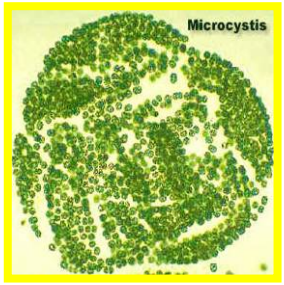


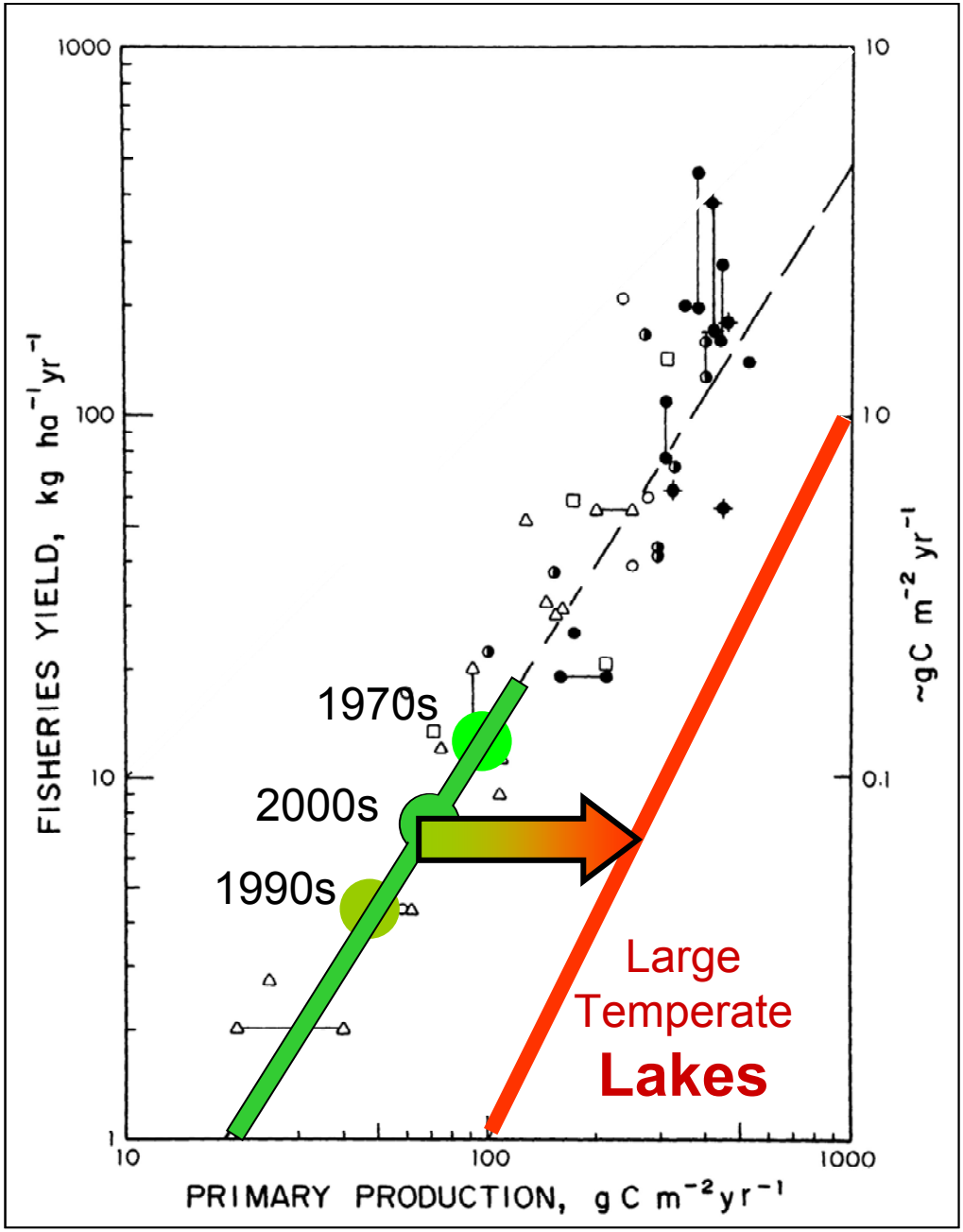
Hypothesis:

Phytoplankton Primary Production in the SFE

… **may** be becoming less nutritious, causing **lower "trophic efficiency"** as found in lakes.

Causes: changes in flows, nutrients, turbidity, temperature…



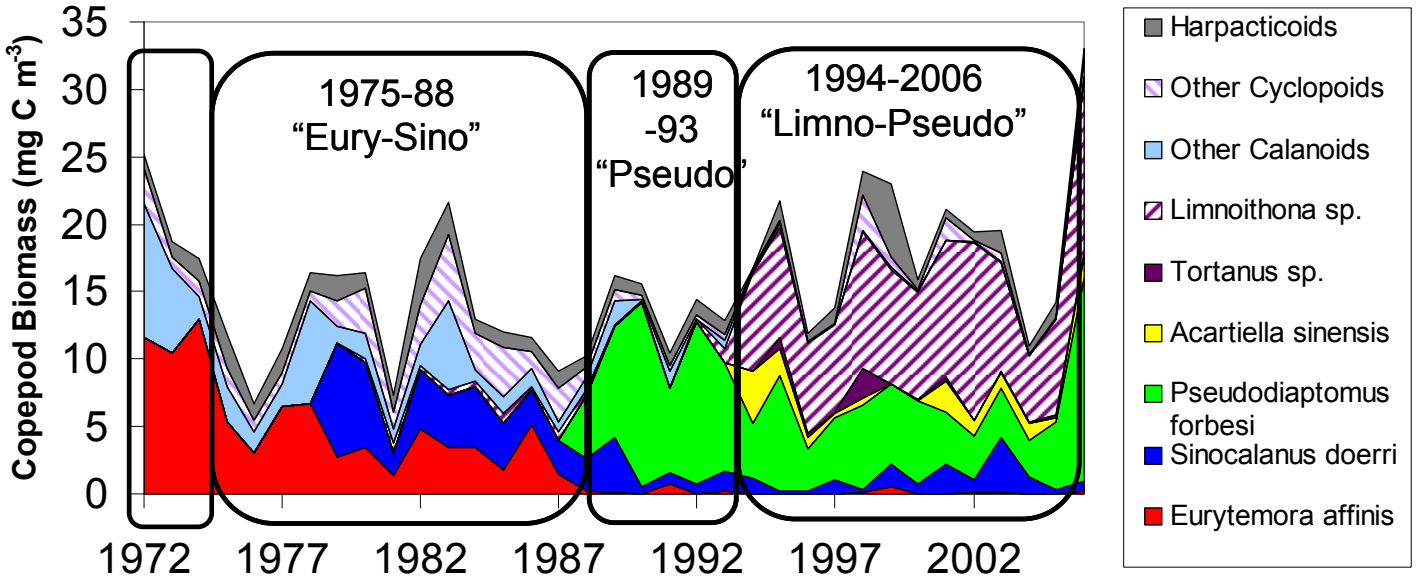


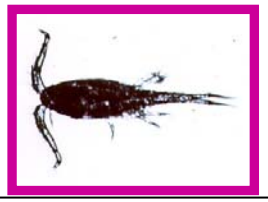
Zooplankton species declines and community shifts

How has biomass of copepods changed since 1972?

Average Annual Summer (June-September) Adult & Juvenile Copepod Biomass in "Delta Smelt Summer Habitat"

Four "Prey Periods"



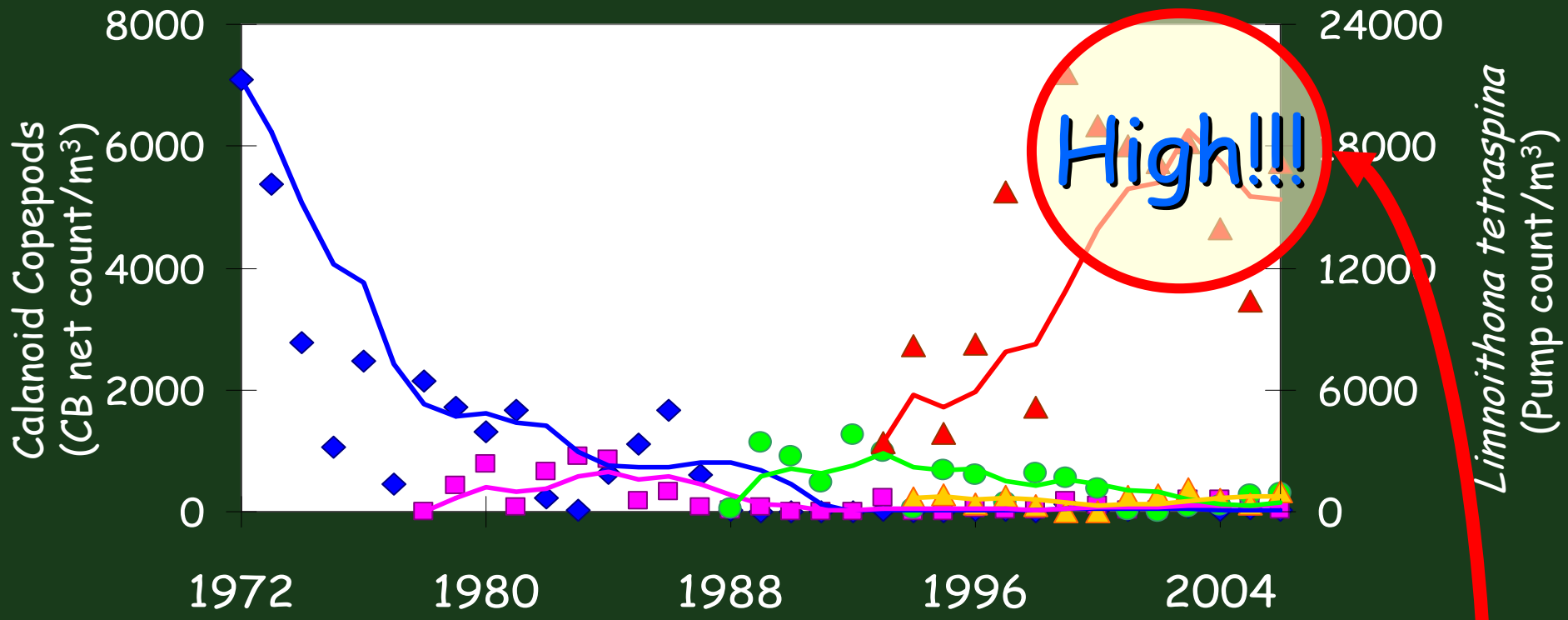


Average Copepod Biomass in delta smelt summer habitat**

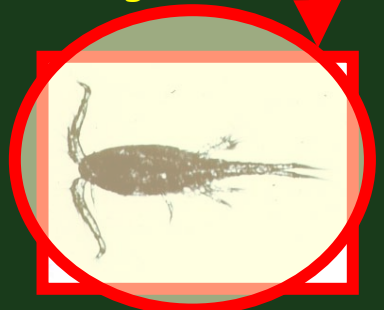
Range ~ 7-30 mg C/m^3

** *Matt N.*

Zooplankton Species Invade in "Waves"

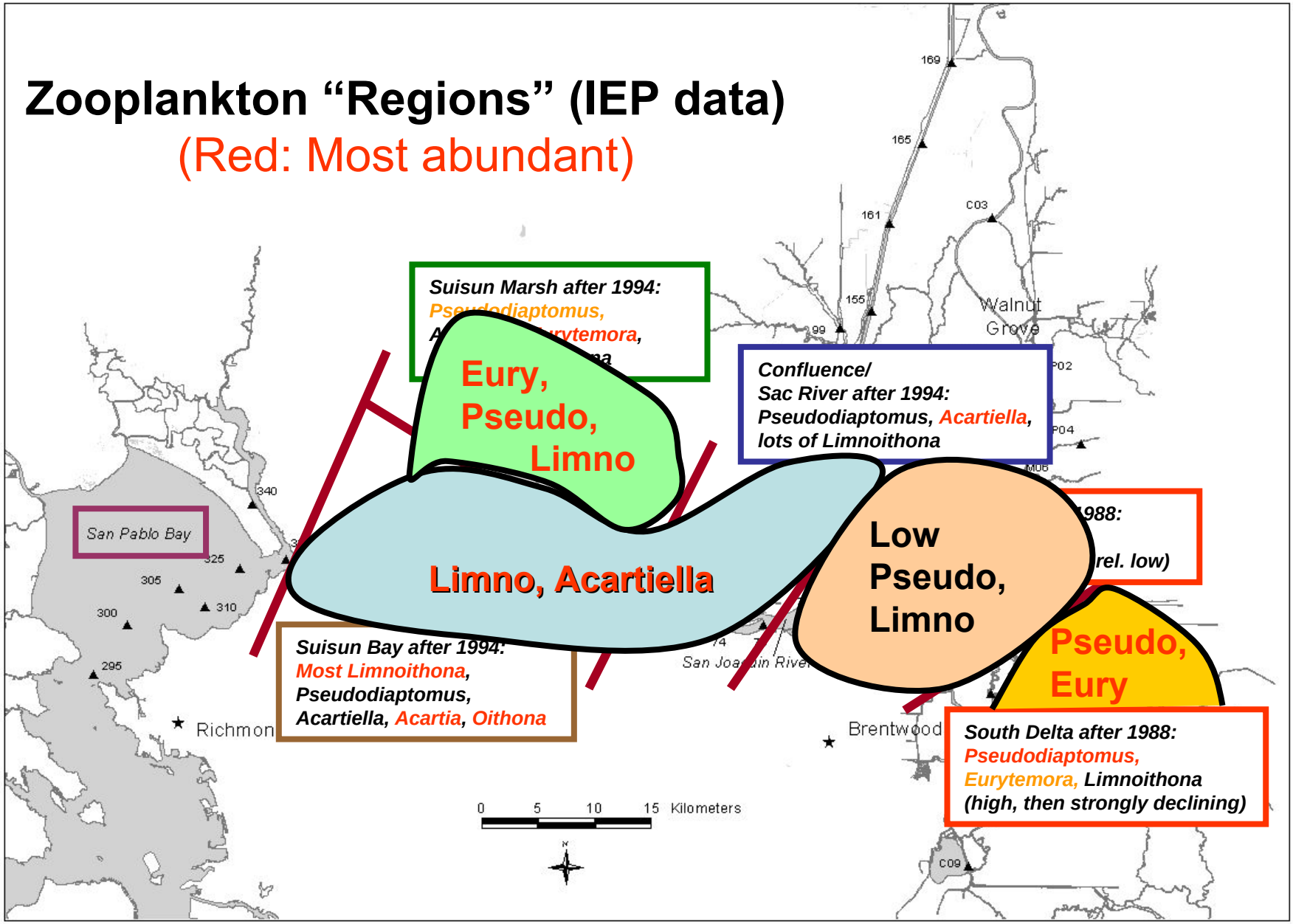


Adult copepods at Chipps Island, yearly averages with 5-year moving average lines

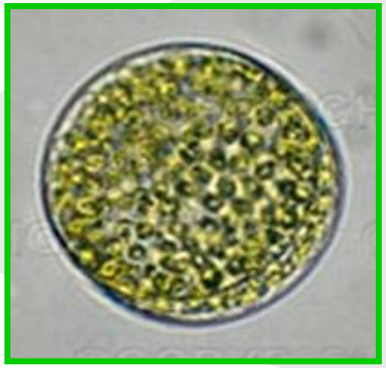


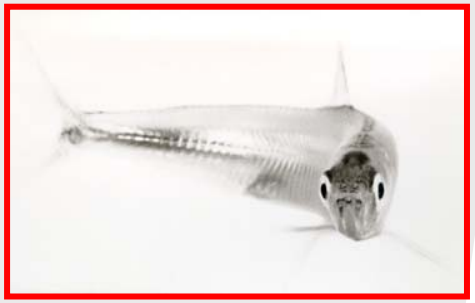
Zooplankton "Regions" (IEP data)

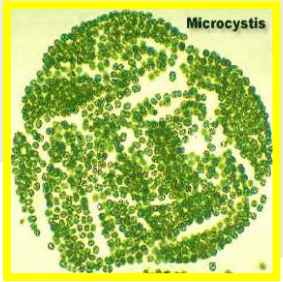
(Red: Most abundant)



7. Restoration & water operations impacts on producers in the upper SFE



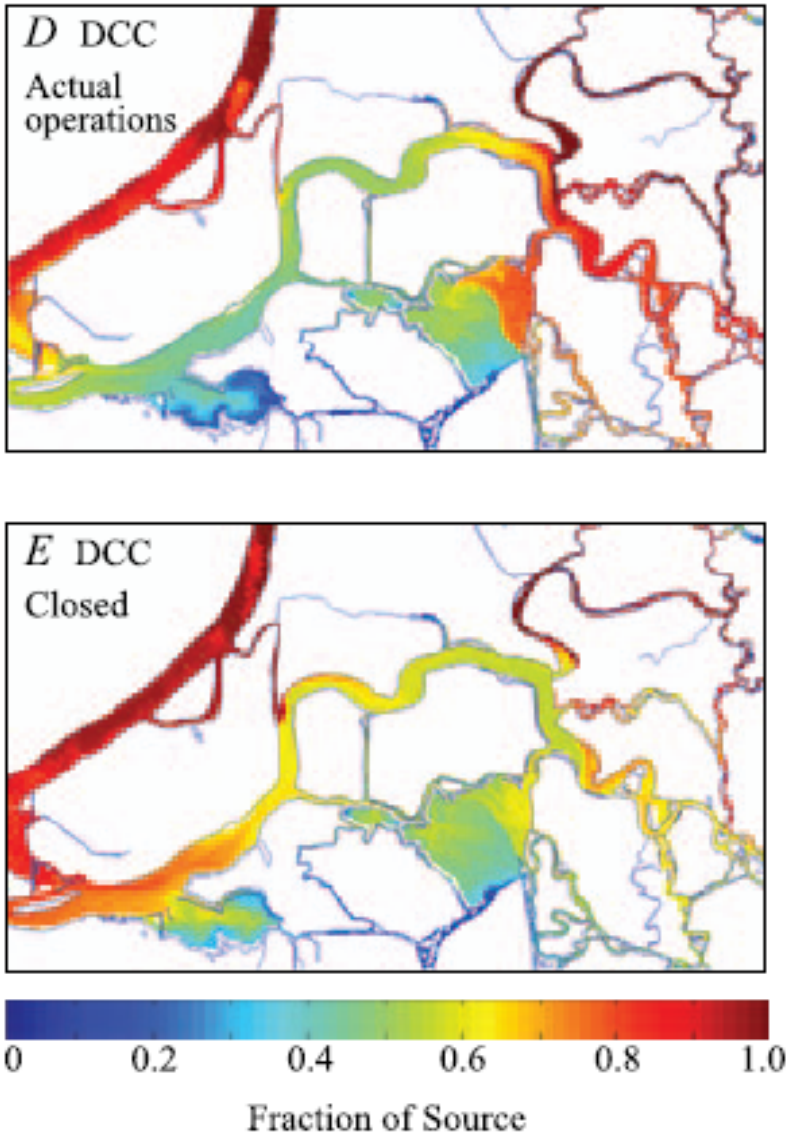




Restoration Impacts on Delta carbon budget

Jassby and Cloern. 2000

- ¤ “Isolated diversion channel (only):” increased C-loadings, esp. in winter & fall
- ¤ Fish and flow barriers: variable impacts, potentially significant
- ¤ Flooded islands: higher PPr
- ¤ Floodplains (Yolo Bypass): large additional phytoplankton habitat



Barriers & diversions impact flows/water routing

Figure 6 in Monsen et al 2007

Flood plains, flooded islands, and tidal marsh support more zooplankton (Daphnia) growth than lower river channels

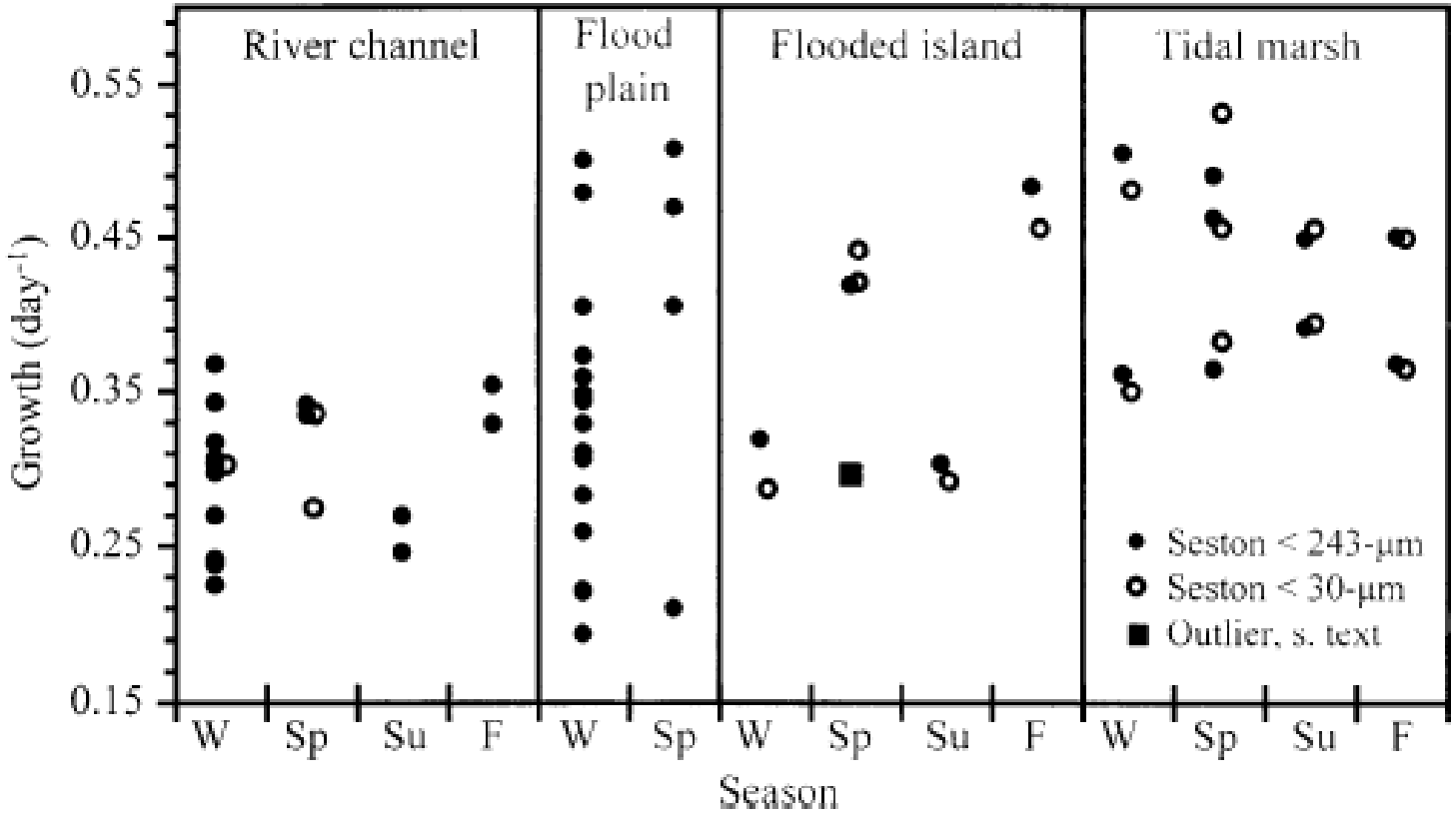
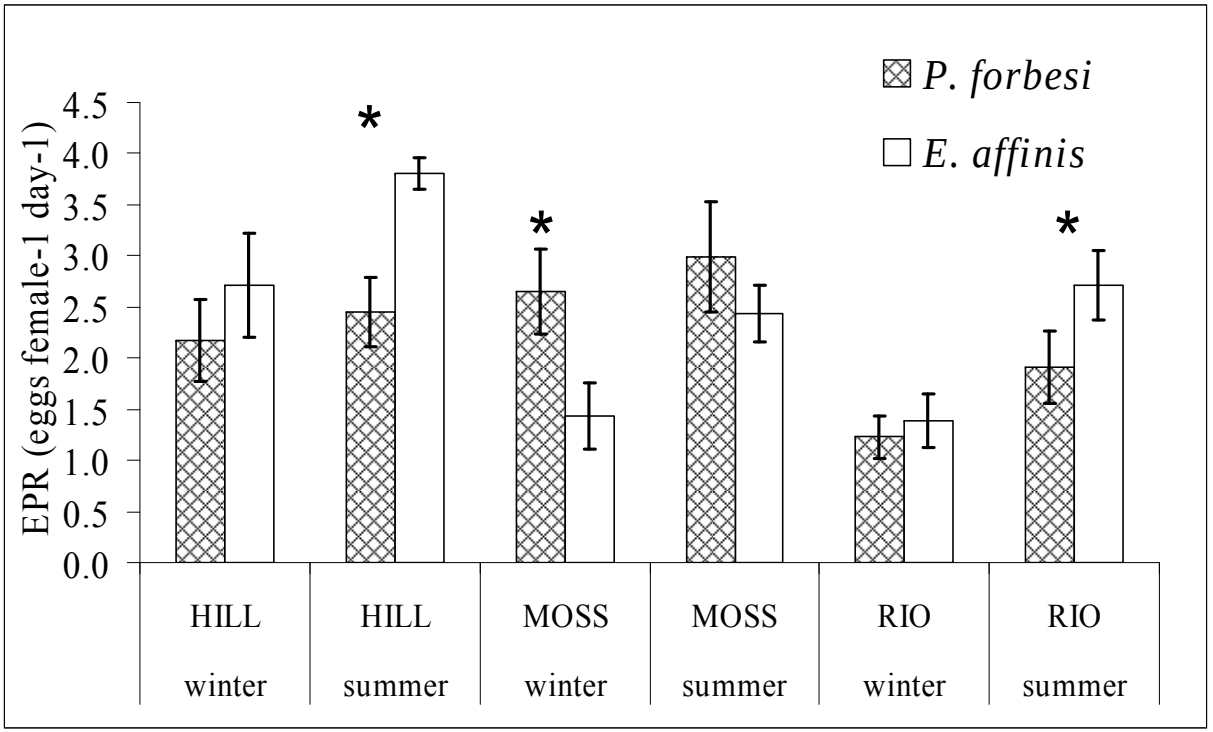


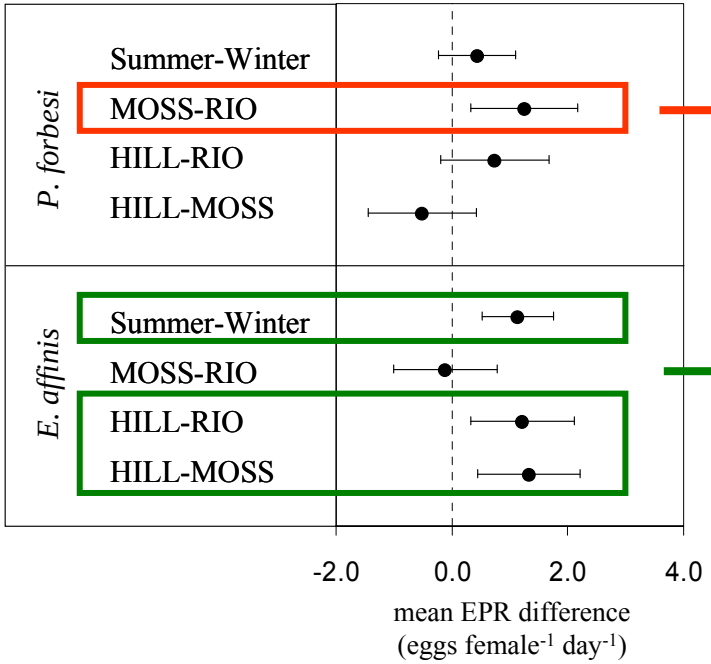
Fig. 2. Seasonal and habitat-related variation in *Daphnia* growth rates under standardized experimental conditions. W, winter; Sp, spring; Su, summer; and F, fall.

Mueller-Solger et al 2002

SJ River & Suisun Marsh slough support higher calanoid growth than Sac River

Eurytemora & Pseudodiaptomus egg production rates: low & fairly similar



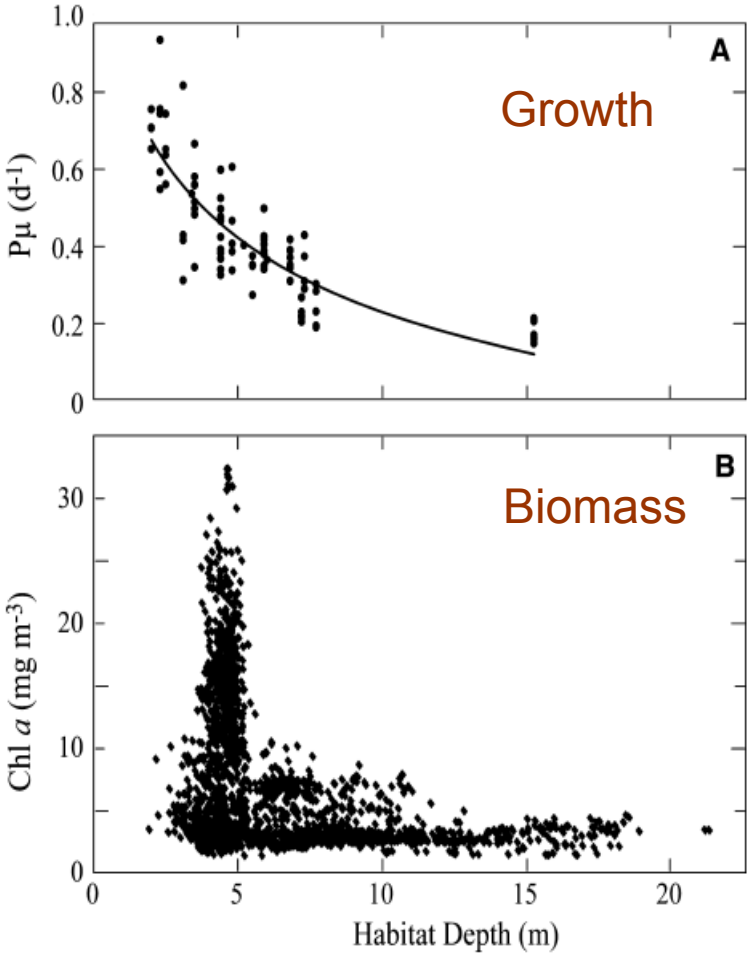


P. forbesi: Sig. higher EPR at MOSS than at RIO; HILL also good

E. affinis: Sig. higher EPR at HILL than at RIO or MOSS & in summer than in winter

Mueller-Solger et al Calfed 2006

Flooded Islands: may support high production (of invasive species)



- Faster growth in shallower habitats
- But not necessarily more phytoplankton production & biomass
- Depends on grazing, transport, mixing
- System impact depends on shallow-deep CONNECTIVITY

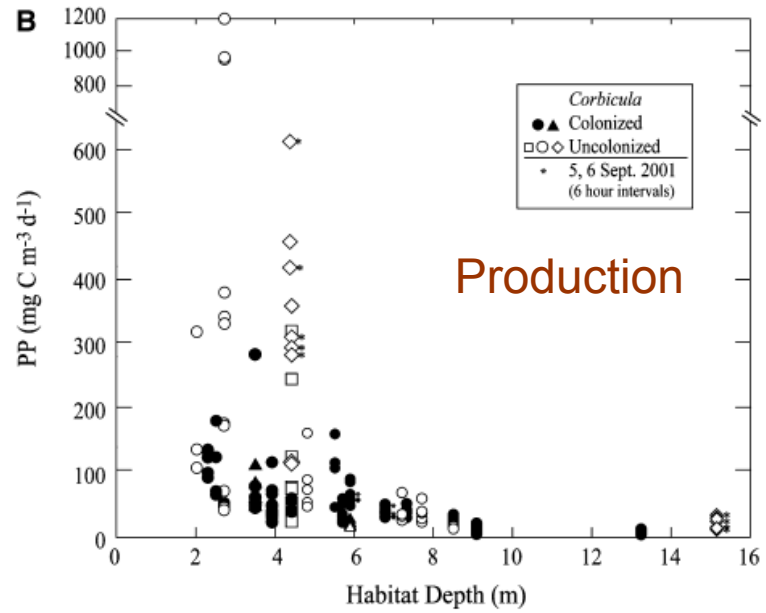
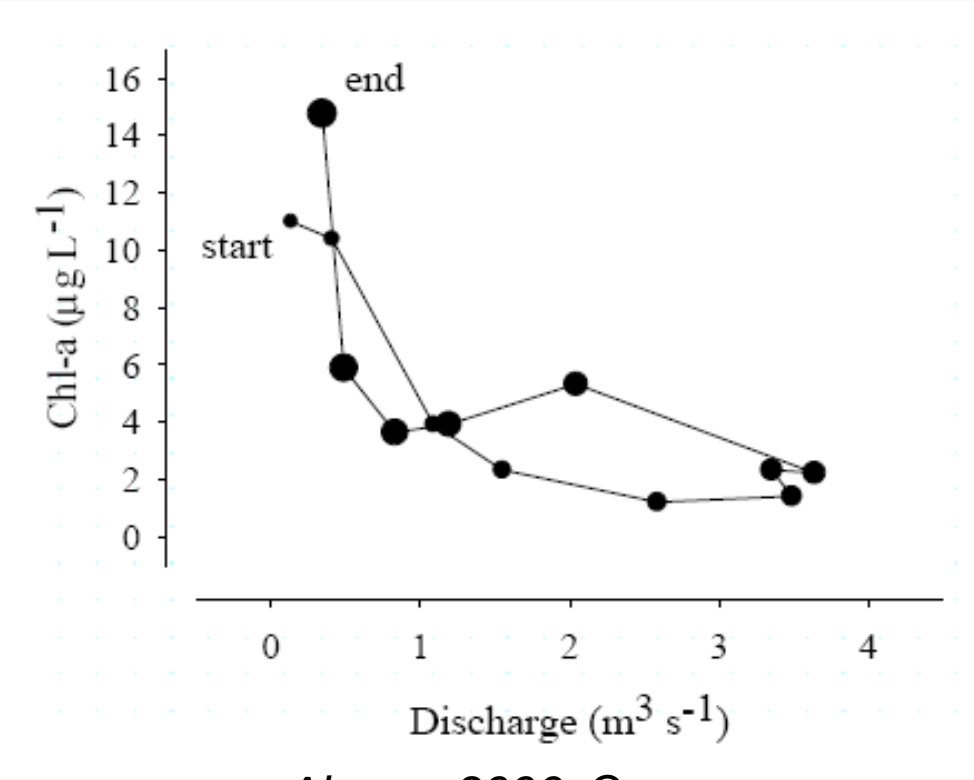


Fig.s 3 & 4 in Lopez et al 2006

Floodplains: Seasonal OC "pumps," Support native invertebrates & fish (Moyle, Grosholz, Sommer) Seasonal flow & connection-disconnection cycles; timing (early for natives)



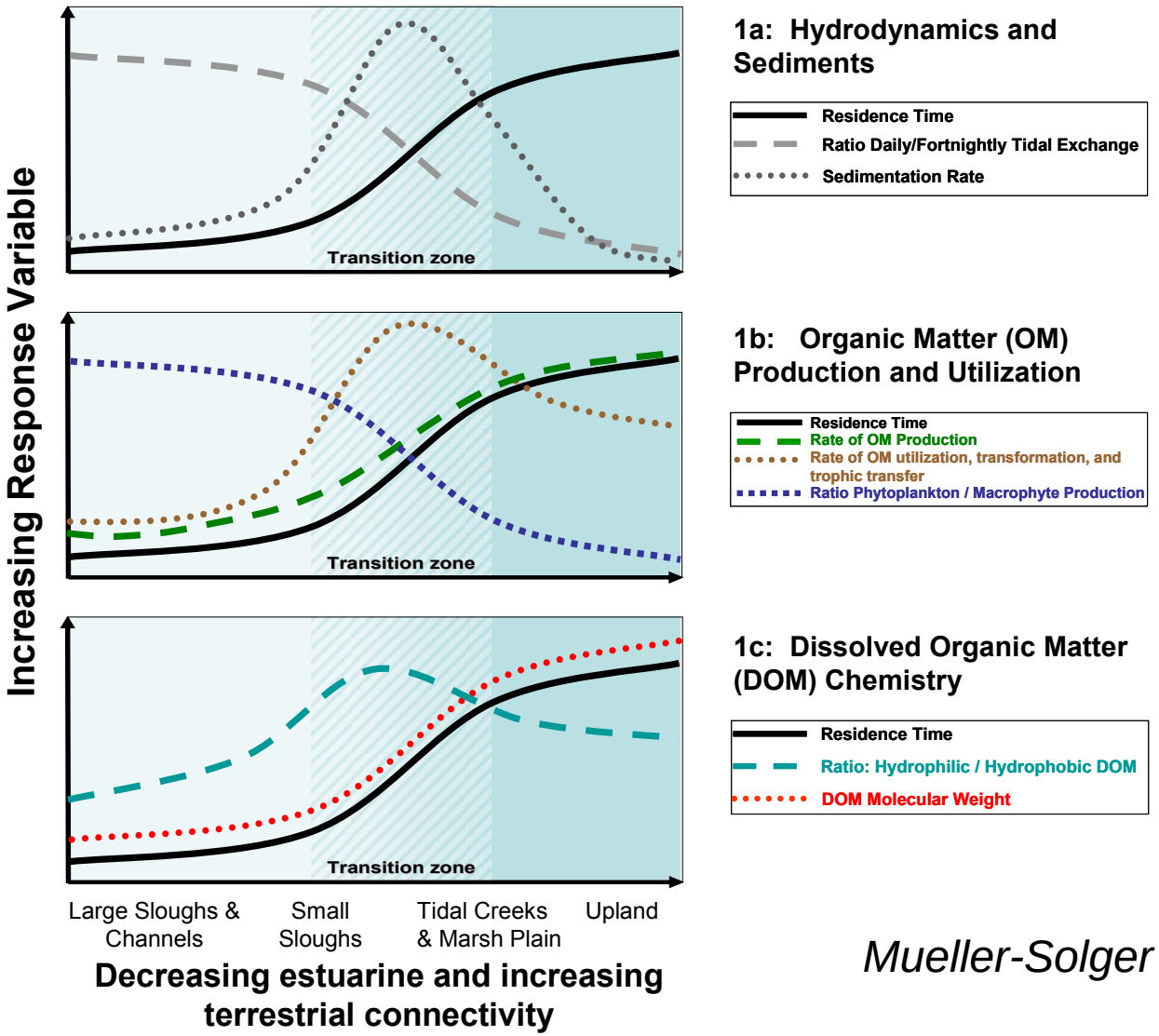
Ahearn 2006, Cosumnes

Also Yolo Bypass work (Lehman, Sommer)

Tidal Marsh: Tidal OC pumps

Supports native invertebrates & fish (Moyle, Schroeter, Herbold)

Tidal flow & connection-disconnection with marsh plain



Mueller-Solger & Bergamaschi 2005

Tidal marsh geometry affects water quality (& ecology?)

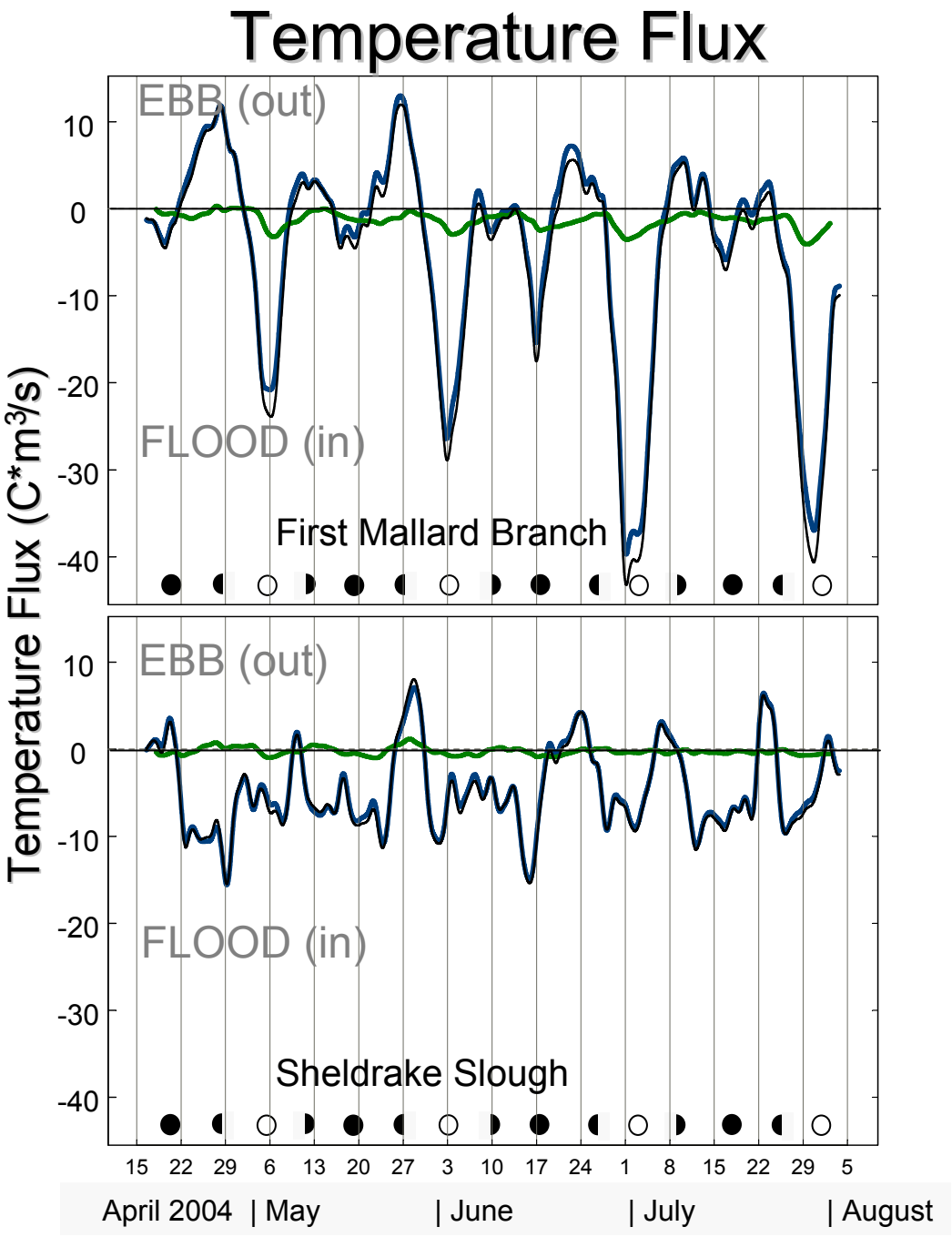
Enright 2008

First Mallard:
unleveed = connected

Greater temp. variability

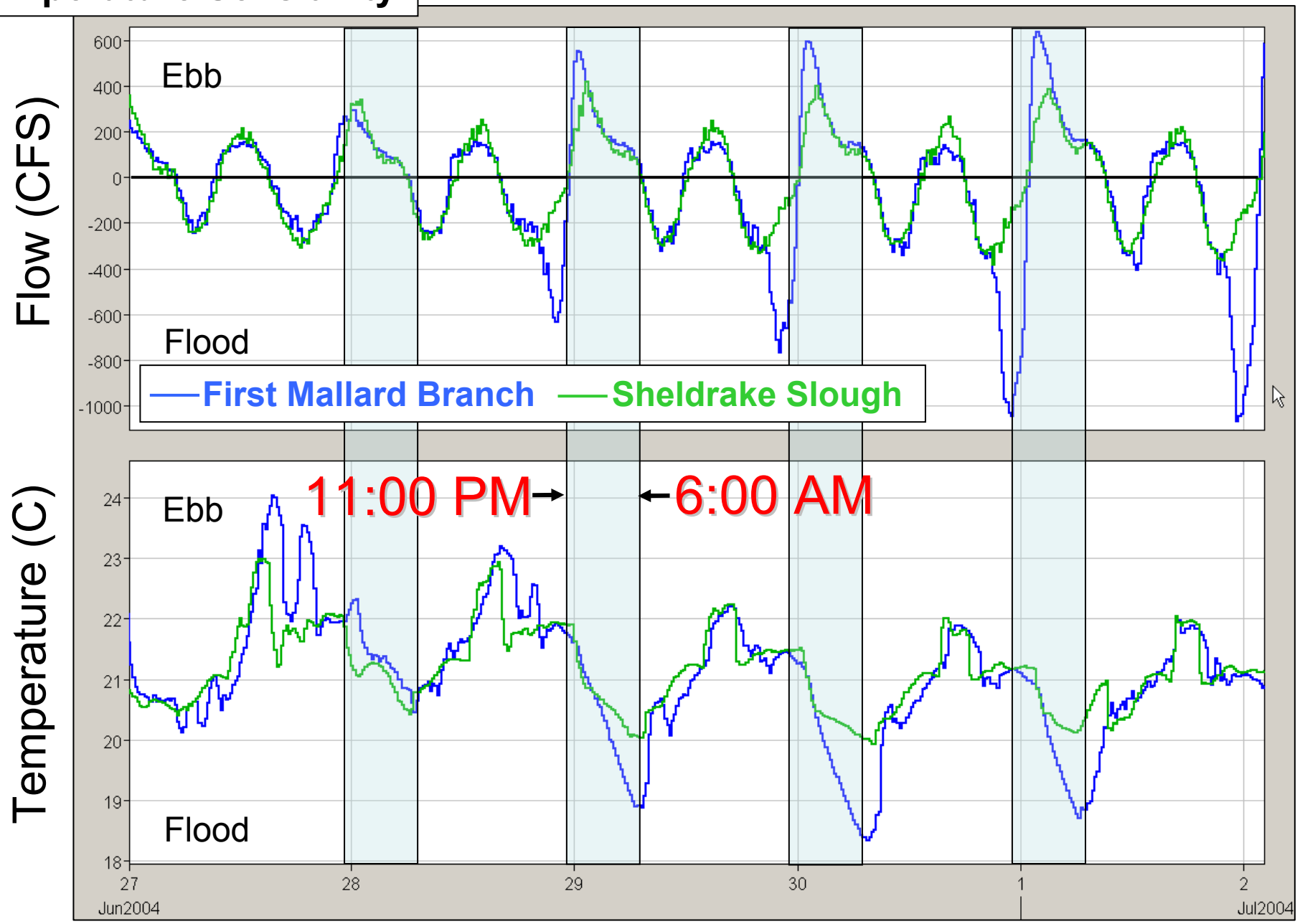
Sheldrake slough:
leveed = disconnected

More stable



Spring Tide Diurnal Temperature Sensitivity

Coolest water out overnight, >5°C change



8. CONCLUSIONS
a) Food sources

- Delta is net heterotrophic
- Bioavailable OC: **phytoplankton** – supports food web
- Typical coastal/estuarine chl a levels: 1-10 ug/L
- SFE is quite typical
- But phytoplankton production has declined, esp. in Suisun Bay
- Phytoplankton & zooplankton community composition has changed; microbial loop?
- Light & flow & connectivity are essential, nutrients at times
- Trophic efficiency may have decreased
- Upper SFE may be becoming more “lake like” (less variability, connectivity, trophic efficiency…)

8. CONCLUSIONS
b) Food Management

- Goal: keep average chl in 1-10 ug/L range; “good food species”
- Sacramento River & Suisun Bay: low phytoplankton
- San Joaquin River: high phytoplankton (eutrophic)
- Shallow habitats: more phytoplankton, need to be connected to increase system productivity
- Flooded islands: variable productivity, invasives, *Microcystis*
- Floodplains & tidal marsh: food pumps, natives
- Peripheral canal: may increase river OC loading, but not with phytoplankton/during growth season
- Barriers etc: variable impacts

VARIABILITY & (VARIABLE) CONNECTIVITY ARE KEY TO SUPPORTING NATIVE ESTUARINE SPECIES

Bacterial Production & Biomass are low & production may be declining

	Hollibaugh & Wong, 1996	2006	2007
Production (µg C L^{-1} d^{-1})	27.7 8-111	6.2 (2-17.7)	4.1 (1.3-8.9)
Abundance (10^9 cells L^{-1})	1.68 0.47-3.77	1.7 (0.4-3.4)	- -
Biomass (µg C L^{-1})	33.6 9.4-75	34.5 (7.7-67.2)	- -

Table from A. Parker, IEP EET 12/2007