 

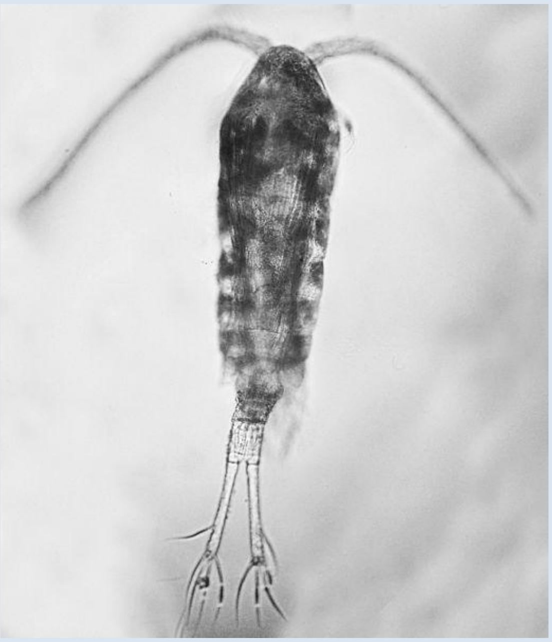 

DRERIP Delta Conceptual Model

Delta Aquatic Foodweb

Prepared by: John Durand, University of California, Davis

October 2008

Delta Aquatic Foodweb – DRERIP Delta Conceptual Model

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For further inquiries on the DRERIP Delta Conceptual Models, please contact Hildie Spautz at hspautz@dfg.ca.gov or Mike Hoover at Michael_Hoover@fws.gov.

Photo of Liberty Island by Patrick Kelly
Photo of delta smelt by Dale Kolke, DWR.
Photo of Eurytemora affinis: http://commons.wikimedia.org/wiki/File:Eurytemora_affinis1.jpg
Photo of the Sacramento National Wildlife Refuge from USFWS and photographer Justine Belson. Date**:** 19 October 2010. Item ID: 5413580126_129fa0b455_b. Website: http://digitalmedia.fws.gov/cdm4/item_viewer.php?CISOROOT=/natdiglib&CISOPTR=12089&CISOBOX=1&REC=1

PREFACE

This Conceptual Model is part of a suite of conceptual models which collectively articulate the current scientific understanding of important aspects of the Sacramento-San Joaquin River Delta ecosystem. The conceptual models are designed to aid in the identification and evaluation of ecosystem restoration actions in the Delta and to structure scientific information such that it can be used to inform public policy decisions.

The DRERIP Delta Conceptual Models include both ecosystem element models (including process, habitat, and stressor models) and species life history models. The models were prepared by teams of experts using common guidance documents developed to promote consistency in the format and terminology of the models at http://www.dfg.ca.gov/ERP/drerip_conceptual_models.asp.

The DRERIP Delta Conceptual Models are qualitative models which describe current understanding of how the system works. They are designed and intended to be used by experts to identify and evaluate potential restoration actions. They are not quantitative, numeric computer models that can be "run" to determine the effects of actions. Rather they are designed to facilitate informed discussions regarding expected outcomes resulting from restoration actions and the scientific basis for those expectations. The structure of many of the DRERIP Delta Conceptual Models can serve as the basis for future development of quantitative models.

Each of the DRERIP Delta Conceptual Models has been subject to a rigorous scientific peer review process, as described on the DFG-DRERIP website and as chronicled on the title page of the model. The scientific peer review was overseen by Dr. Jim Anderson, at University of Washington for all species models and by Dr. Denise Reed, University of New Orleans, for all ecosystem models.

The DRERIP Delta Conceptual models will be updated and refined over time as new information is developed, and/or as the models are used and the need for further refinements or clarifications are identified.

Introduction.

This model is a stylization of the actual food web dynamics of the Sacramento-San Joaquin Delta, which are highly dynamic. The region itself comprises a variety of habitats, determined by salinity regimes, residence time, hydrology, benthos and physical structure. These physical parameters, or drivers, determine species composition and trophic relationships. The Delta is a tidal system which is subject to varying water inflow. Because inflow and outflow vary as the result of anthropogenic alterations and water management needs, habitats are not static. Rather they are subject to hourly, daily, seasonal and inter-annual variation, and different organisms respond in different ways to these time scales, depending upon their own life histories.

Thus salinity and temperature regimes may create different outcomes from food web interactions, based upon how species distributional and recruitment patterns overlap. In general, food web linkages are not static or linear. Organisms switch feeding strategies opportunistically, and these patterns of variability in feeding strategy tend to increase with trophic level. Many organisms, particularly plankton, undergo many generations in the course of a year, and selective forces may allow for rapid evolution which can alter habitat preferences or other life history characteristics.

The Delta food web is further dynamic in that new species are regularly introduced into the Estuary, competing with, replacing, or preying upon other organisms. For example, the overbite clam, *Corbula amurensis*, was introduced in 1986, precipitating a cascade of changes that are still not wholly understood. Zebra and quagga mussels are expected to invade the Delta within the next few years, and will bring further changes.

The topology of a food web model will be necessarily complex given these factors. Even without such variability, the potential linkages create a spider web of relationships that is difficult if not impossible to disentangle. In order to create a working model of the Delta food web that is useful for education, for hypothesis-generation, and for management decision-making, it is necessary to create limits to what linkages will be examined.

In order to do this, this Delta food web model focuses on organisms that supply food for fish. This is particularly important given the recent concern for pelagic organism decline, which is described mostly for fishes, some of which are listed as endangered or threatened. A key assumption is that fish are integrators of ecosystem function.

Also included in the model are invasive organisms that have a large impact on food web dynamics (such as *C. amurensis*), as are organisms that are particularly abundant (such as the copepod *Limnoithona tetraspina*), whether or not they are used directly by fish.

Finally, organisms from the microbial web are also included, although relatively little is known about their overall role in the Delta. It appears that a significant amount of production is microbial, utilizing energy from the ample supply of detrital carbon. The scale of microbial production may dwarf the amount of primary production, so it is important to include in the model.

Thus, most benthic organisms are not included, because there is not good evidence that they are particularly important to pelagic fish, or that they have any major impact on the pelagic foodweb. However, the invasive clams *C. amurensis* and *Corbicula fluminea* are included because of their known impact on plankton populations. Macrocrustaceans (including mysids, amphipods, isopods and insects) are included because they may be useful for fish, and because there is some evidence that introduced amphipods have taken over a place in the foodweb formerly occupied by mysids. Meiofauna, in contrast, are not discussed because they are poorly represented in the literature, and not important in fish diets.

No discrimination was made in terms of invasive or native organisms. Organisms have been introduced at least since the early 1800s, including the copepod *Eurytemora affinis*, once considered native. Many of these organisms have become naturalized to the system. In certain habitats of the San Francisco Estuary and Delta, exotics make up 40-100% of species, 97% of the total number of organisms, and up to 99% of the biomass. While it is sometimes useful to distinguish between native and non-native species, this model focuses on the state of the food web at the turn of the 21st Century (1998-2008), in an effort to describe which organisms support trophic functioning and which do not. Because non-native organisms are both ubiquitous and abundant, they dominate the ecology of the Delta. Having established, the possibilities of removal are quite small. This model assumes that they are fully integrated into the food web, although adjustments may occur with certain invasions that take years or decades to complete.

Trophic research on the Delta relies on a variety of methods that vary with trophic level. Phytoplankton nutrient uptake research uses labeled isotopes of C and N. Ciliate and rotifer grazing rates are calculated using fluorescently marked bacteria. Zooplankton and clam diets are determined largely through prey removal experiments. Fish diets are investigated using gut analyses.

Missing from much of the research are stable isotope analyses, which apparently have limited utility in open water organisms, largely from the muddying influence of marine, riverine, and terrestrial inputs, which prevent a clear signal in the data. Perhaps for this reason, also missing are studies of the ecology of a number of newly introduced copepods, mysids, isopods and shrimp. These species may have replaced native mysids and shrimp, but little is known about their trophic positions.

Because of the complexity of the model, it has been broken down into sections that follow rough "trophic levels". Each diagram emphasizes different relationships using the same template, to facilitate understanding. Drivers show abiotic parameters and emphasize their relative importance, intermediate outcomes show primary and secondary trophic relationships, and the final outcome emphasizes predators, in this case fish (as well as clams and hydrozoans). Each of the linkages between organisms and trophic levels are described in detail, along with a relevant bibliography to facilitate further investigation.

Confusion about the significance of the linkage arrows often occurs with food web models. The arrows in this model represent ecological relationships and the state of our knowledge of those relationships. The opposing arrows represent the influences on each of the populations, influences that may be asymmetrical. Positive arrows reflect positive population effects, carbon/nutrient flows, or bottom-up effects. Negative arrows reflect negative population effects, predation, or top-down effects.

Note that arrows do not reflect the importance of linkages relative to the ecosystem of the entire Delta. Rather, they only reflect importance to the organisms to which the arrow is directed. Each arrow refers to the immediate relationship between the organisms it links, without reference to the larger system, or its importance to management and restoration goals.

To summarize briefly, the model is not intended to be a static resource. Rather it is intended to guide individuals seeking further knowledge about the Delta, to generate discussion, and to assist in the development of new hypotheses about trophic relationships. Additionally, it is hoped that it will provide a useful tool to support decision-making around restoration actions for the Delta. Because the model is modular, it may be easily re-formulated to accommodate changes as new understandings become available. The model should be understood as a snap-shot representation of the dynamic Delta food web.

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Cohen AN, Carlton, JT. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279: 555-558.

Kimmerer WJ. 2004. Open water processes of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2 (1).

Mueller-Solger A, Hall C, Jassby A, Goldman, C. May 2006. Food resources for zooplankton in the Sacramento-San Joaquin River Delta. Final Report, Calfed Project ERP-01-N50/2001-K221.

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Orsi JJ, Ohtsuka S (1999) Introduction of the Asian copepods Acartiella sinensis, Tortanus dextrilobatus (Copepoda:Calanoida), and Limnoithona tetraspina (Copepoda:Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biol Ecol 46:128–131

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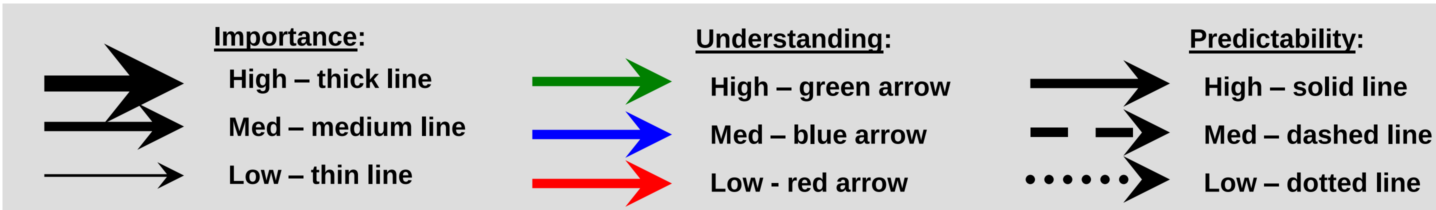
User Notes.



- All numbered links are click-able. Text descriptions with references are linked. Page headings are also linked to descriptive text for overviews.
- Linkage arrows reflect importance, predictability and understanding relative to the organism, guild or trophic level indicated by the direction of the arrow.
- Negative arrows reflect negative population effects, or top-down effects.
- Positive arrows reflect positive population effects, carbon/nutrient flows, or bottom-up effects.
- Note that arrows do not reflect the importance of linkages relative to the ecosystem of the entire Delta. Rather, they only reflect the importance to the organisms to which the arrow is directed. Each arrow refers to the immediate relationship between the organisms it links, without reference to the larger system.

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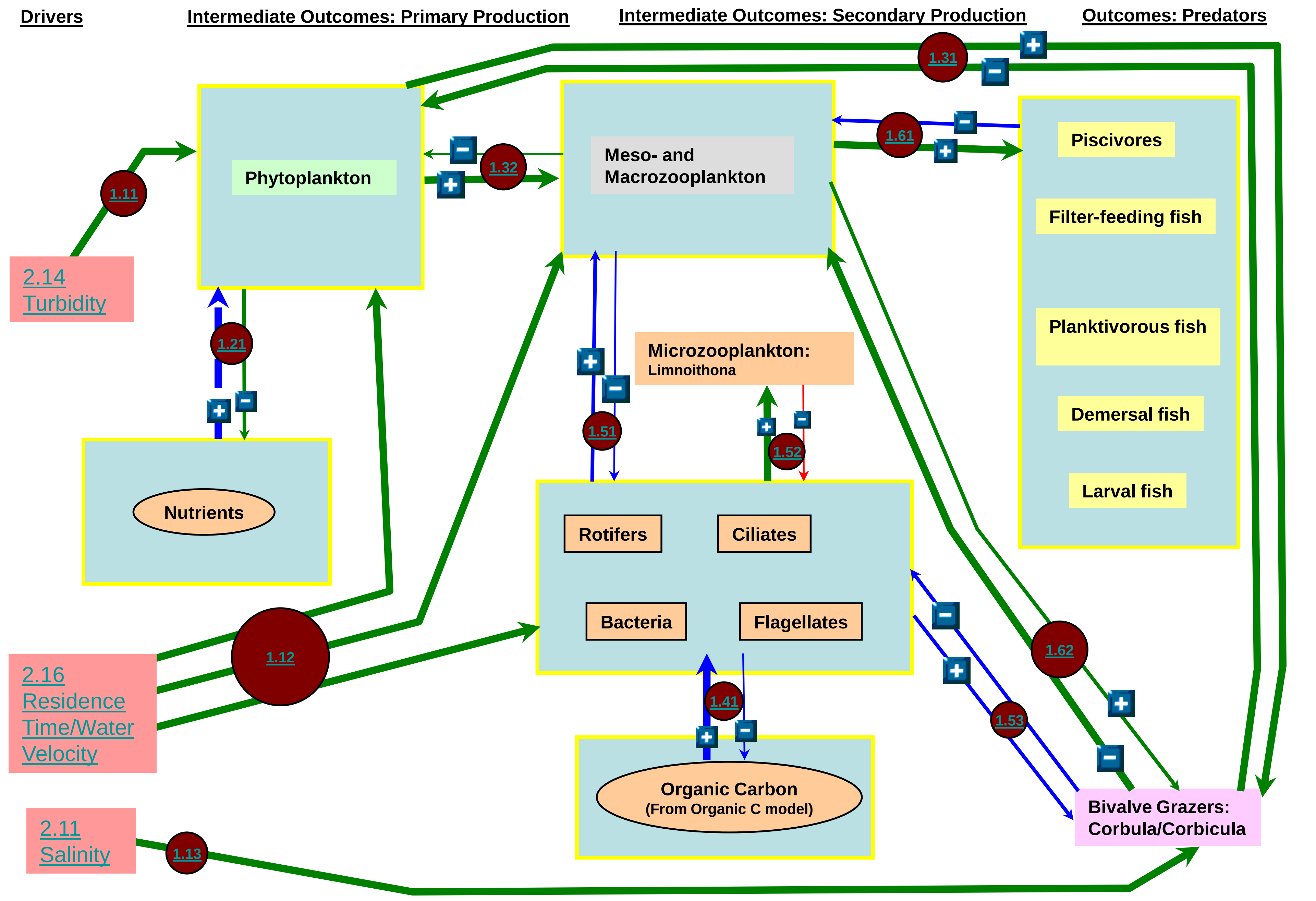
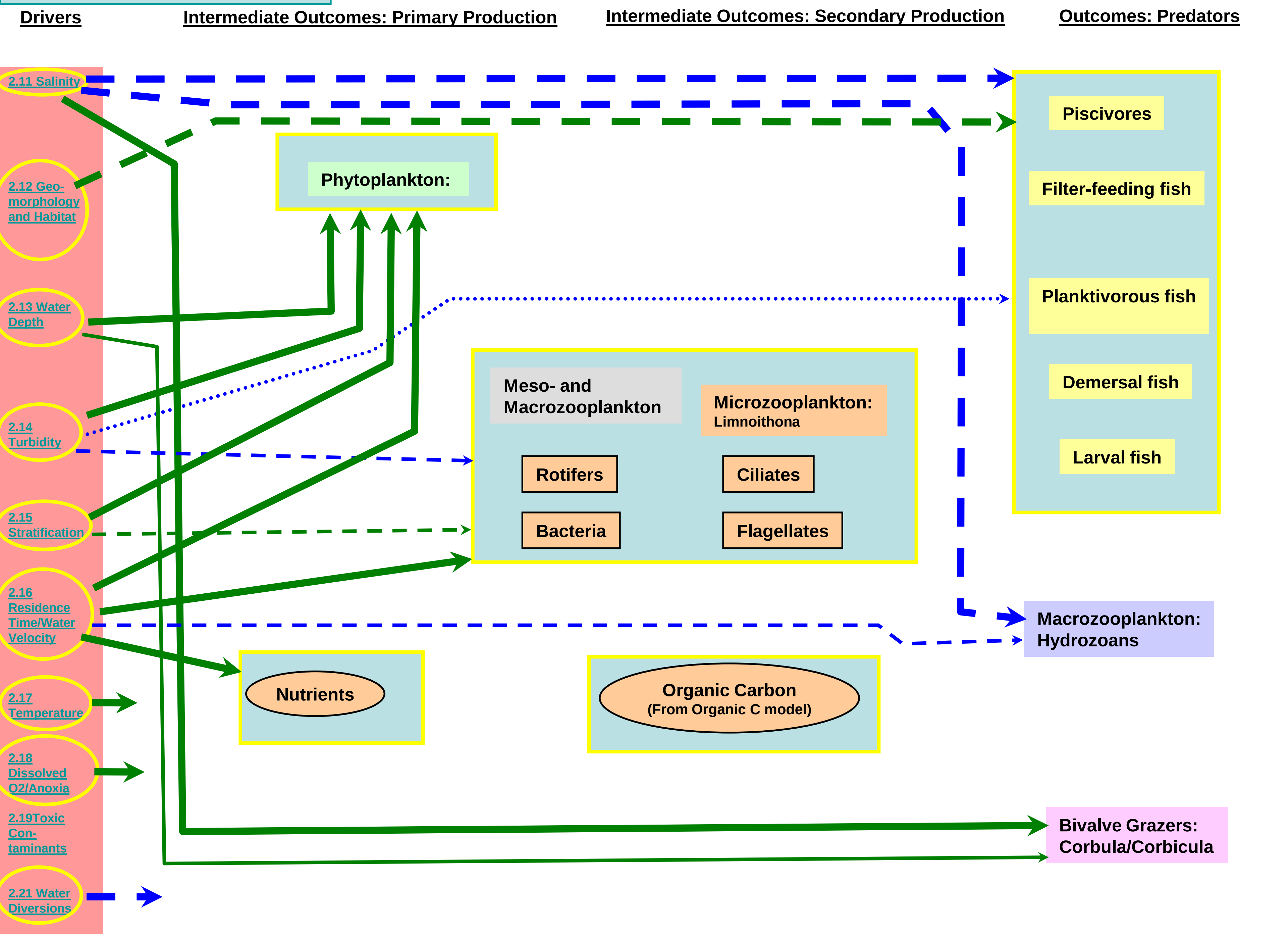
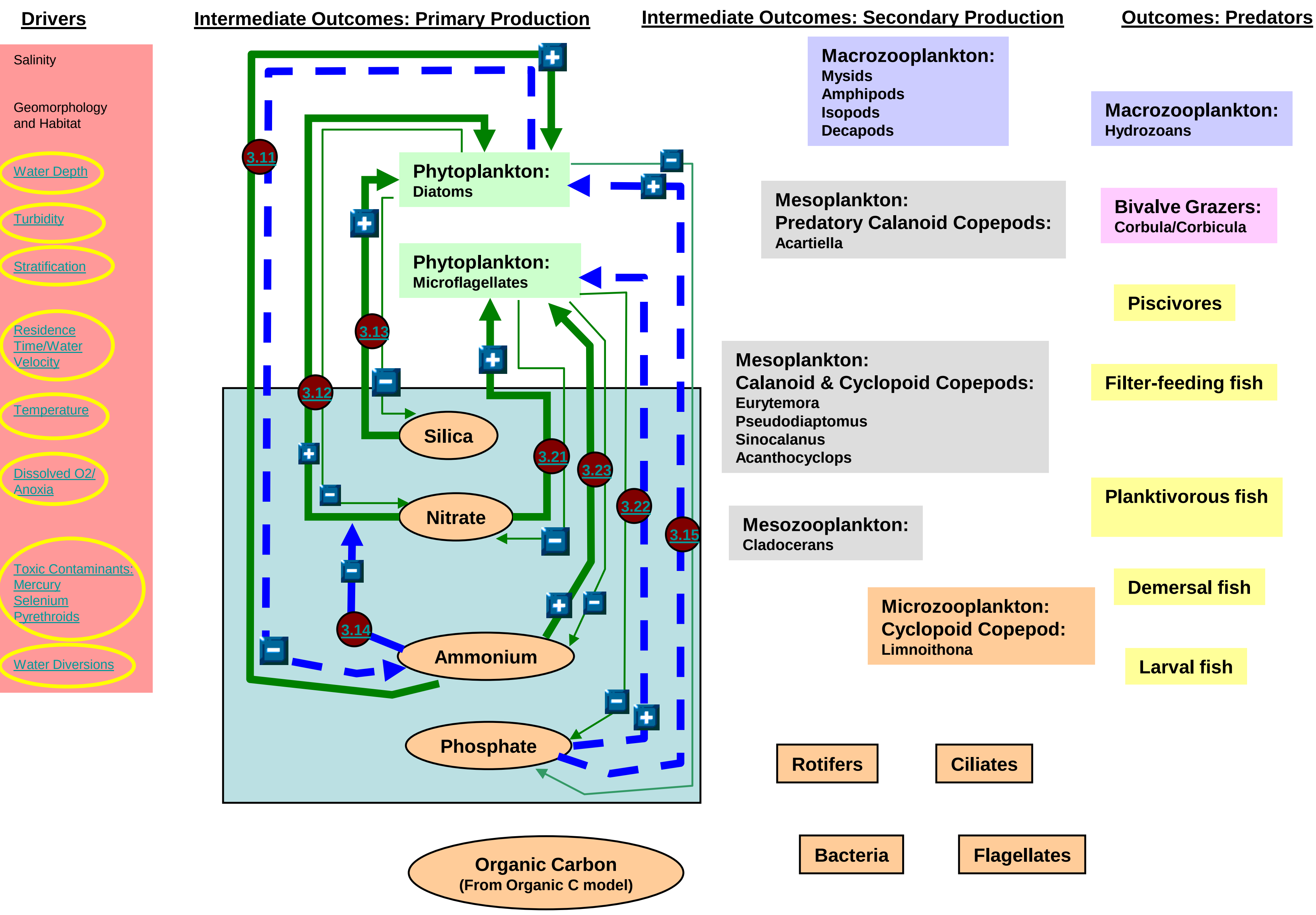


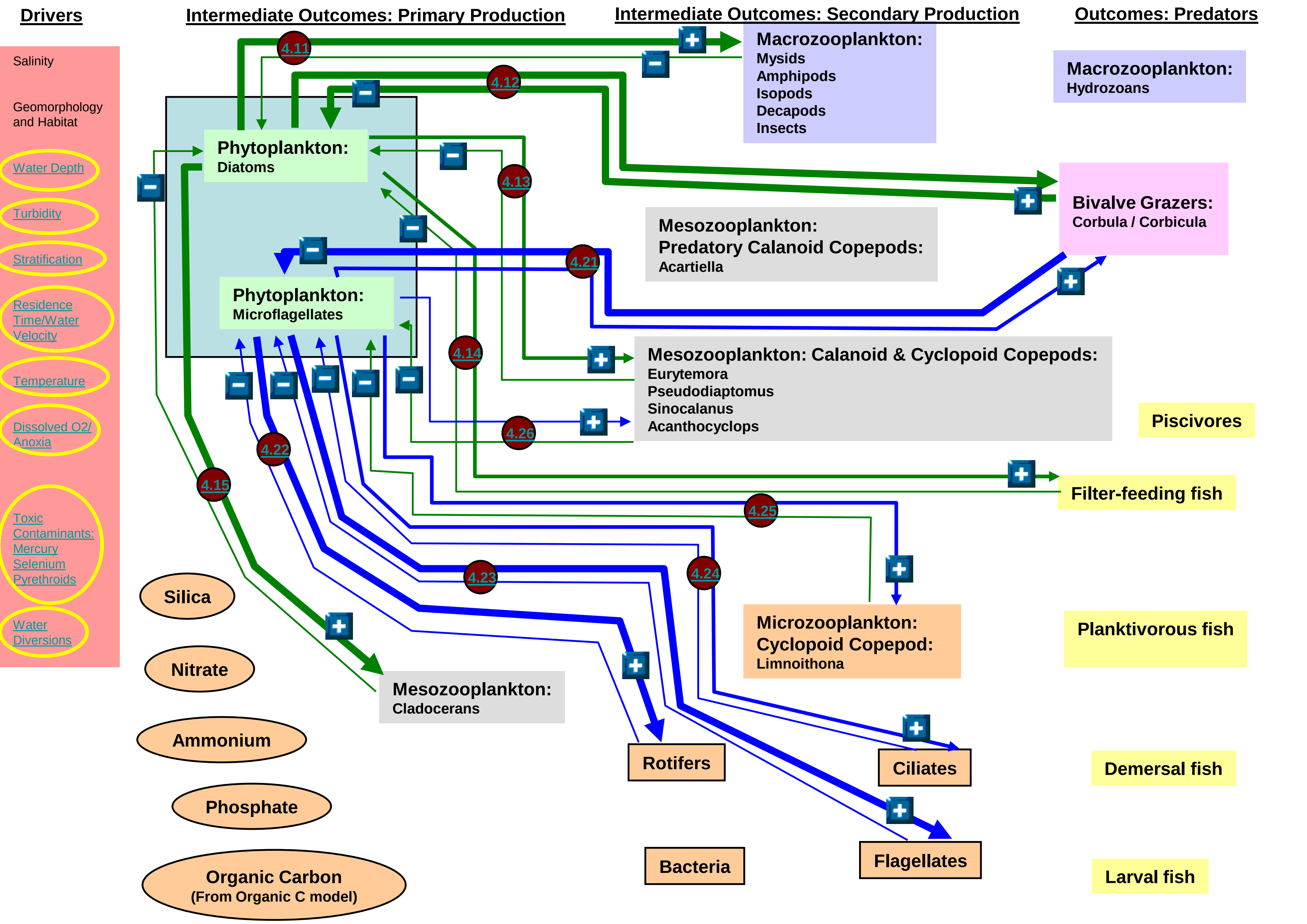
2. Delta Foodweb Overview: Drivers



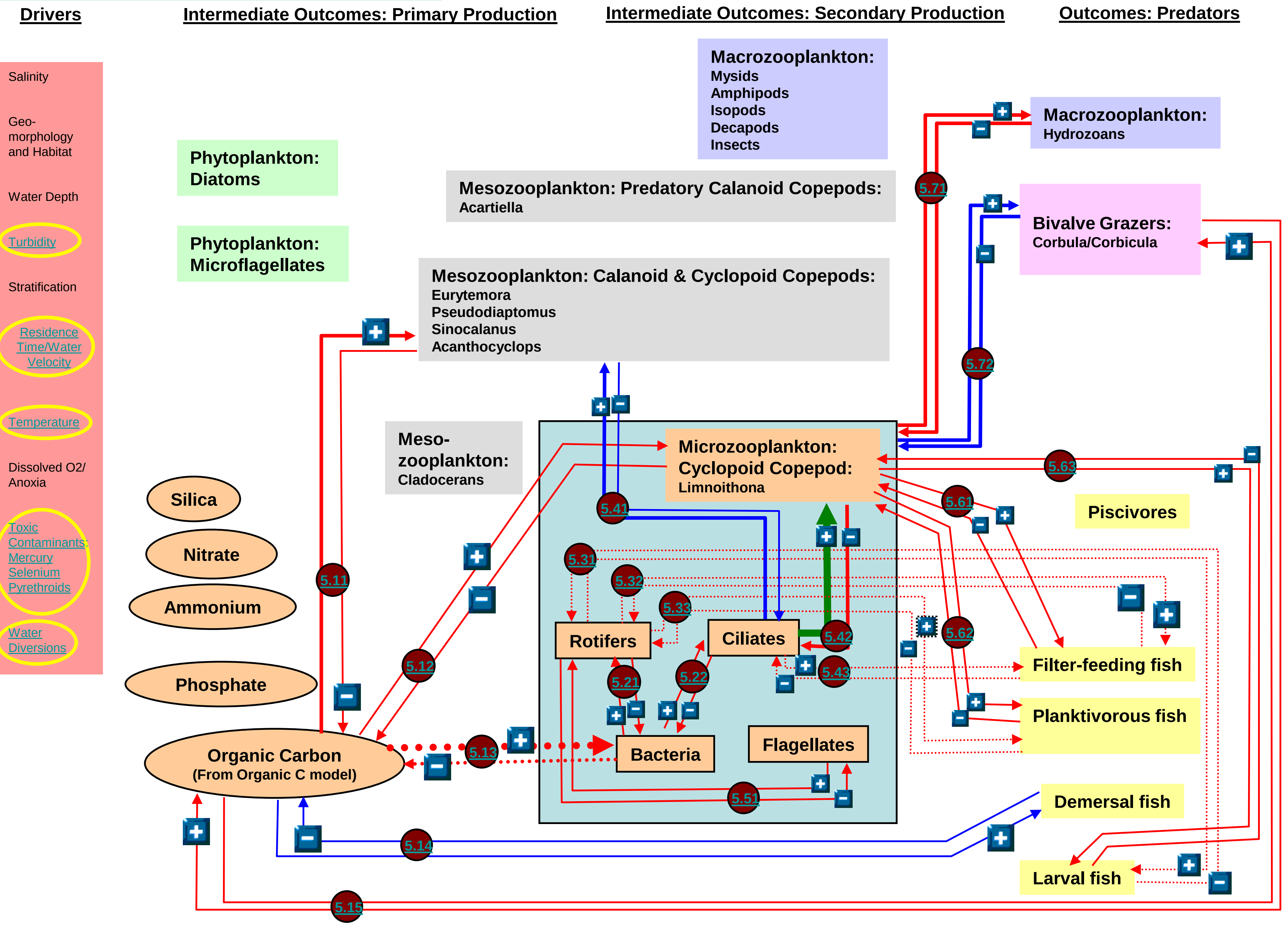
3. Nutrient Supply



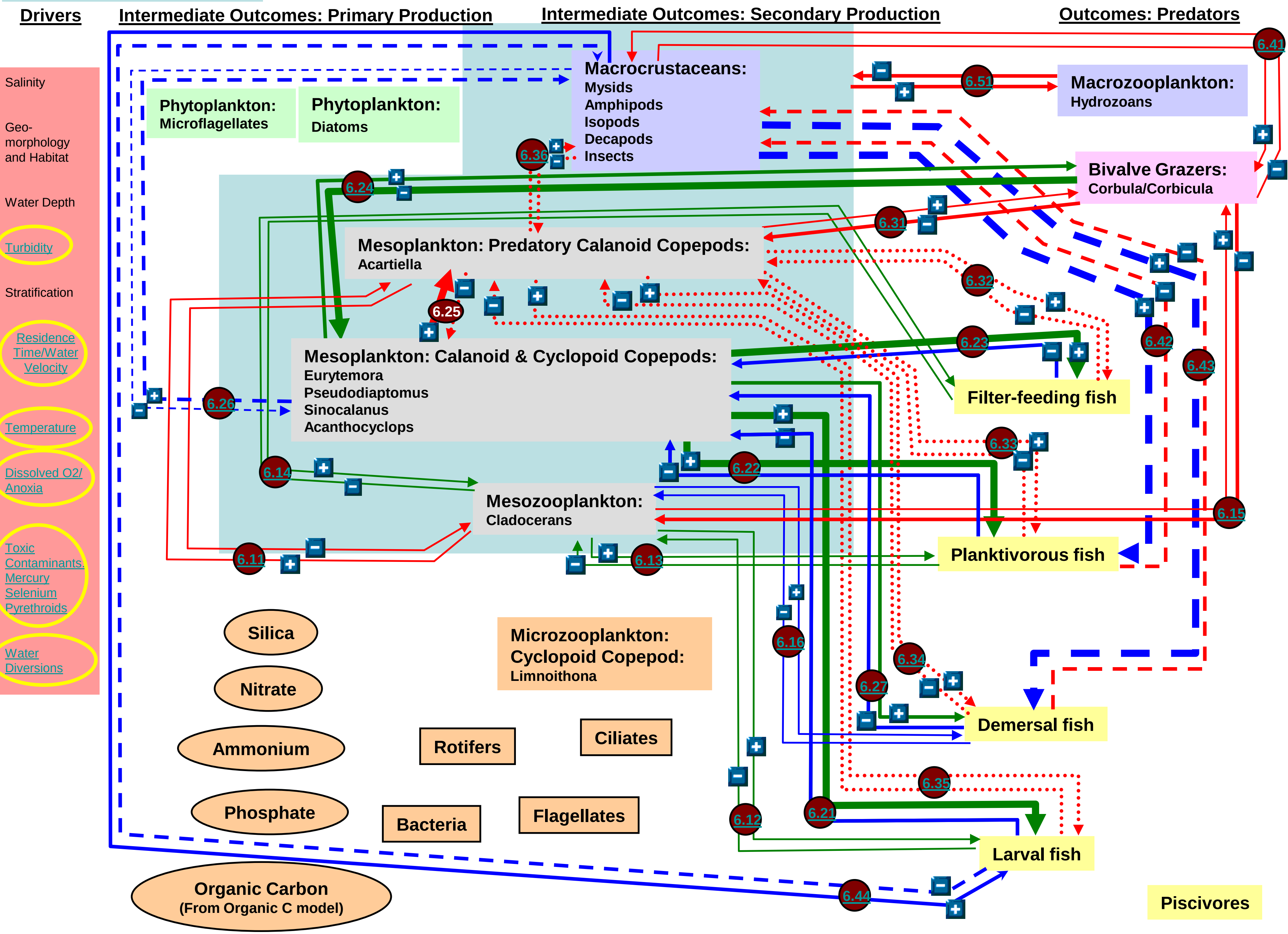
4. Primary Production

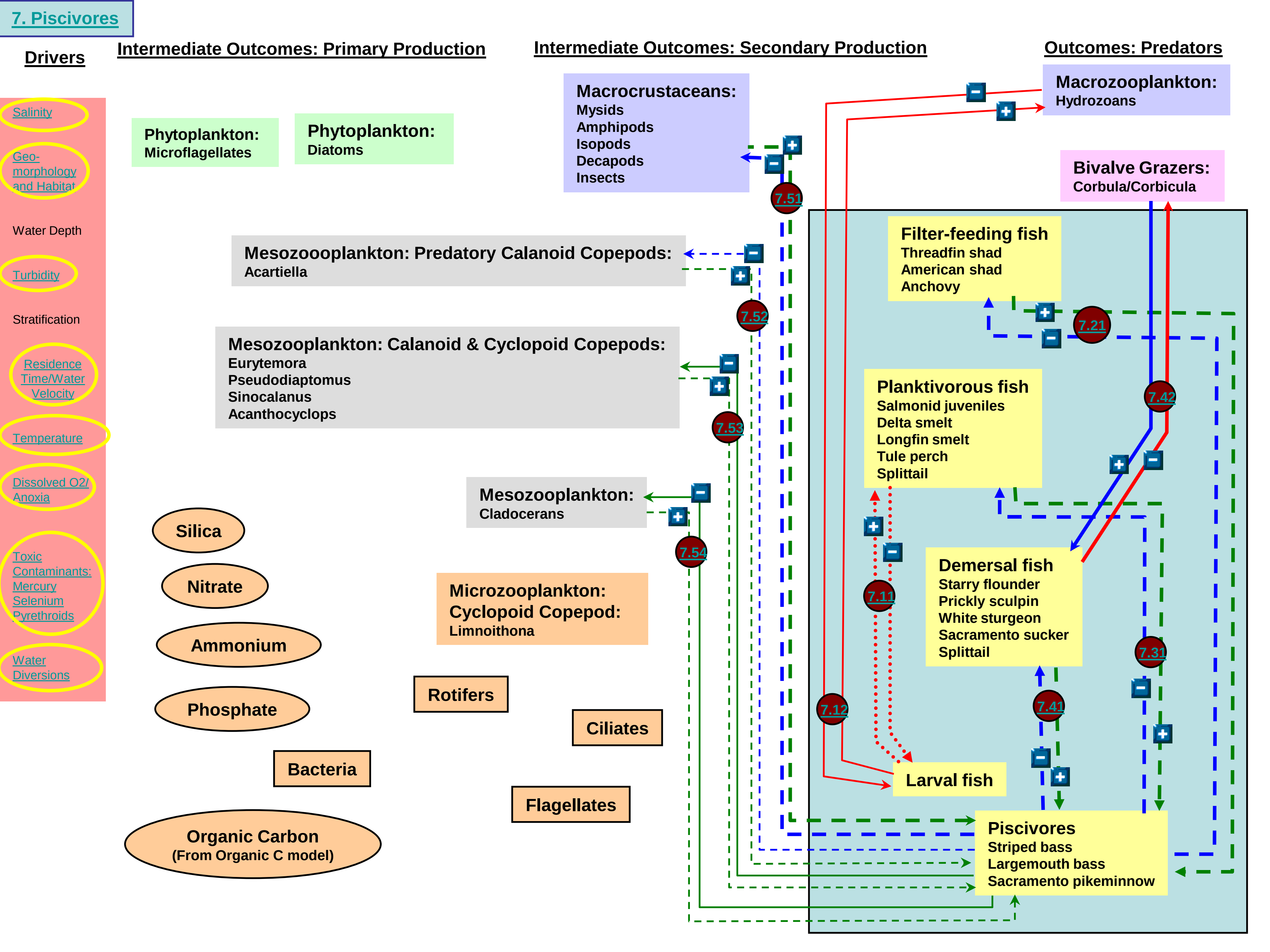


5. Organic Carbon and Microzooplankton Supply



6. Mesozooplankton Supply





7. Piscivores
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Intermediate Outcomes: Primary Production
Intermediate Outcomes: Secondary Production
Outcomes: Predators
Salinity
Geo-morphology and Habitat
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Stratification
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Phytoplankton: Diatoms
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Mesozooplankton: Calanoid & Cyclopoid Copepods: Eurytemora Pseudodiaptomus Sinocalanus Acanthocyclops
Mesozooplankton: Cladocerans
Microzooplankton: Cyclopoid Copepod: Limnoithona
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Nitrate
Ammonium
Phosphate
Organic Carbon (From Organic C model)
Rotifers
Ciliates
Bacteria
Flagellates
Filter-feeding fish Threadfin shad American shad Anchovy
Planktivorous fish Salmonid juveniles Delta smelt Longfin smelt Tule perch Splittail
Demersal fish Starry flounder Prickly sculpin White sturgeon Sacramento sucker Splittail
Larval fish
Piscivores Striped bass Largemouth bass Sacramento pikeminnow
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Acknowledgements.

- Wim Kimmerer, Chuck Hanson, Jon Burau, and Chris Enright contributed important conceptual frameworks for the foodweb at the outset of the modeling process.

- Alex Parker patiently explained the nuances of phytoplankton dynamics while providing key background and resources.

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- Stuart Siegel, Bruce Herbold, Anke Müller-Solger and Michael Johnson were extremely helpful in their comments, reviews, and general assistance.

- John Melack, Peter Moyle and two anonymous reviewers greatly improved the manuscript through their suggestions.

- Because of the broad scope of a foodweb model, by design or accident it will have omissions, generalizations and inconsistencies. Any factual or conceptual errors are mine and mine alone.

John Durand
UC Davis
December 20, 2007

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1.0 Delta Foodweb Overview: Critical Drivers and Linkages

Phytoplankton production is largely limited by the twin drivers of turbidity and residence time. Limited primary production in turn limits secondary production, although omnivorous zooplankton may be able to supplement diets with inputs from the microbial loop, which tends to be driven by organic carbon inputs in the form of riverine, sewage and agriculturally derived detritus (as well as phaeophyton from endogenous phytoplankton production).

Both phytoplankton and some zooplankton are limited by grazing pressure from the two bivalves *Corbicula amurensis* and *Corbicula fluminea.* The ecological impact of these organisms is due to their high abundance and filtration rates, which are estimated to allow them to filter the entire water column on a timescale on the order of days (for phytoplankton) to weeks (for bacterioplankton). Those zooplankton not subject to direct predation may be affected indirectly by competition with clams for phytoplankton.

The Delta foodweb is dominated by benthic filter feeding bivalves, curtailing the production of plankton and the availability of food for most fish. Instead, carbon is directed into the benthos where it is either sequestered, advected out of the system, recycled into the microbial loop, or made available to a limited set of benthic feeding fish and birds.

Key uncertainties:

1. The role of benthic feeders in recycling organic carbon.
2. The dynamics of the microbial loop and how it supports secondary production and fish populations.
3. The role of fish populations in structuring the zooplankton community.
4. Mortality from piscivorous fish on young native fishes.
5. The fate of carbon being directed through *Limnoithona tetraspina, Corbula amurensis,* and *Corbicula fluminea.*
6. The role of nutrients in limiting phytoplankton production.

View Slide: Critical Drivers & Linkages

PREVIOUS VIEW

1.1

Turbidity to Phytoplankton

Importance: High
Understanding: High
Predictability: High

The high turbidity levels in the Delta are well documented to have an inhibitory effect on phytoplankton bloom formation by reducing photic zone depth. Whenever mixing occurs below the critical depth, photorespiration exceeds carbon fixation by photosynthesis, reducing the amount of primary production available for consumption by higher trophic levels. This has a negative feedback on bloom formation, since it tends to inhibit sufficiently high biomass to cause a bloom.

Bloom conditions rarely occur in the northern San Francisco Estuary and Delta. The required conditions are:

1. Vertical salinity stratification allowing for improved light conditions, reducing mixing below the photic zone, and separating phytoplankton from benthic grazers
2. High levels of photosynthetically active radiation (ie, no cloud cover)
3. Short enough residence times to allow pulses of nutrients to enter the water column from upriver, with long enough residence times to allow for bloom formation
4. Low concentrations of NH_4, which can otherwise interfere with nitrate uptake and rapid growth rates in diatoms.

Cole BE, Cloern JE. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. Marine Ecology Progress Series 17:15-24

Dugdale RC, Wilkerson FP, Hogue, VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science 73:17-19.

Lehman, PW. 1992. Environmental factors associated with long-term changes in chlorophyll concentration in the San Joaquin Delta and Suisun Bay, California. Estuaries 15(3): 335-348

1.12
Residence Time/Water Velocity to Phytoplankton, Microzooplankton, and Mesozooplankton
Importance: High
Understanding: High
Predictability: High

Residence time is the amount of time a fixed particle remains within a given physiographic region. Increased residence time allows for nutrient retention, biomass accumulation (critical for a bloom to occur), and temperature increase. Decreased residence time allows for nutrient and organism advection to other portions of the Estuary, and for nutrient recharge within a given physiographic region. Production appears to be a function of four conditions related to “mixed” residence times.
These conditions are:

1. Nutrient recharge, necessary to fuel primary productivity. This necessitates a residence time short enough to allow new inputs of nutrients. If residence time is too high, nutrients will draw down, limiting production.

2. Biomass accumulation and advection. Biomass accumulation is required to reach high densities of organisms. Because primary and secondary production are rates, they increase or decrease biomass logarithmically. Biomass accumulates faster at higher densities, bounded asymptotically by nutrient or food availability. Advection allows production from productive regions of the Delta to subsidize less productive habitats. Dispersal also prevents conditions from becoming eutrophic, which reduces dissolved oxygen and inhibits production.

3. Warm water temperatures can increase production.

4. Sufficient trophic response time to phytoplankton blooms ensures that primary production is retained in the system long enough to promote secondary production, which may also be dispersed.

Ball MD, Arthur JF. 1979. Planktonic chlorophyll dynamics in the northern San Francisco Bay and Delta. In: Conomos TJ, editor. San Francisco Bay: the urbanized estuary. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 265-285.

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PREVIOUS VIEW

1.13
Salinity to Bivalve Predators: Corbula/Corbicula
Importance: High
Understanding: High
Predictability: High

Salinity has a strong controlling effect on benthic organisms with low mobility, including the clams *Corbula amurensis* in the brackish Delta and *Corbicula fluminea* in the fresh water. These clams have compromised the ability of the foodweb to deliver carbon to higher trophic levels. They bypass a series of trophic steps, delivering energy to top predators without supporting diversity, hence their important role in the current ecology and restoration efforts of the Delta.

Both clams are bounded by different salinity gradients, which explains their non-overlapping distributions. *C. fluminea* is unable to tolerate brackish or marine water for extended periods, while *C. amurensis* does not tolerate fresh water well. The distributional area of the clams follows shifts in salinity over protracted times. During extended periods of low outflows, *C. amurensis* follows the increasing salinity gradient upriver, primarily through larval dispersion. Alternatively, during years of high outflow, *C. amurensis* may have high mortality at upstream, fresh water areas and *C. fluminea* will establish down stream. Populations may be controlled by altering salinity regimes on a time scale shorter than the lifespan of the clams (about 2-3 years), effectively removing some of the effects of benthic grazing around low salinity and fresh water boundaries in the Delta.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. Marine Ecology Progress Series 66:95-101.

PREVIOUS VIEW

1.21

(+) Nutrients to Phytoplankton

Importance: High
Understanding: Moderate
Predictability: Moderate

Phytoplankton in the Delta are limited more by turbidity and photosynthetically available radiation (PAR) than by nutrients. However, key nutrients or nutrient ratios may have an important impact on primary production rates and selection of phytoplankton types.

Ammonium at concentrations above 1 µmol L^{-1} may be used preferentially by phytoplankton, inhibiting uptake of nitrate. However, some diatoms have higher rates of primary production using nitrate rather than ammonium. As a result, bloom formation for these diatoms tends to occur only when ammonium levels have been drawn down below the threshold at which they can successfully utilize nitrate.

(-) Phytoplankton to Nutrients

Importance: Moderate
Understanding: High
Predictability: High

The Delta is seldom if ever limited by nutrient availability. It receives inputs from sewage treatment facilities, agricultural areas and urban runoff. Phytoplankton tend not to draw down nutrients because of the rarity of bloom formation in the Estuary. Occasionally conditions occur (low wind, high stratification, low turbidity, high residence time) which permit the drawdown of ammonium by phytoplankton below the 1 µmol L^{-1} threshold, allowing increased nitrate uptake by certain diatoms. Under such conditions, diatom growth can be linear (or biphasic), allowing a bloom to occur as a result of increased primary production. This has happened only rarely since 2000.

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Lancelot C, Billen G. (1985). Carbon-nitrogen relationships in nutrient metabolism of coastal marine ecosystems. Advances in Aquatic Microbiology **3**: 263-321.

Serra JL, Llama MJ, Cardenas E. (1978). Nitrate utilization by the diatom *Skeletonema costatum*. Plant Physiology **62**: 991-994.

Wilkerson, FP, Dugdale RC, Hogue V, Marchi A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. Estuaries and Coasts **29**(3): 401-416.

PREVIOUS VIEW

1.31

(+) Phytoplankton to Bivalve Grazers: Corbula/Corbicula

Importance: High
Understanding: High
Predictability: High

Corbula amurensis and *Corbicula fluminea* can occur at extremely high densities (>1000 $(m^2)^{-1}$) throughout the Delta, with a correspondingly large grazing effect. They both rely heavily on phytoplankton, although *C. amurensis* has been well documented to graze ciliates, microflagellates, bacteria, particulate matter, and zooplankton.

(-) Bivalve Predators: Corbula/Corbicula to Phytoplankton

Importance: High
Understanding: High
Predictability: High

Since *C. amurensis* appeared in 1986, phytoplankton densities have undergone a stepwise and dramatic decline. The effect on zooplankton is equally severe, but is a function both of direct grazing on larval stages (ie, copepod nauplii) and the indirect effects of competition for phytoplankton. The result has been a decline in zooplankton that has paralleled the loss of phytoplankton in the system. Both clams may be food limited at least some of the time, which suggest that few other factors limit their populations. The implication of this is that the clams may be able to graze down plankton production so efficiently that bloom conditions are effectively suppressed during the spring, summer and fall, when clam abundance is highest. This results in a "short-circuited" food web, in which primary and secondary production is re-directed from the multi-dimensional pelagic foodweb to the benthos. There, energy from primary production is essentially locked up, and available to only a few benthic grazers, such as white sturgeon and some diving birds. It is not known if pseudofeces from these bivalves recycles dissolved organic carbon (DOC) into the water column, fueling an increase in microbial activity and the microbial loop. If so, the clams would be promoting an alternate foodweb, based more upon organic carbon, detritus, and the microbial loop, rather than a more energetically efficient web based upon primary and secondary production.

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

Cole BE, Thompson JK, Cloern JE. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. Journal of Marine Research 113:219–225.

Jassby, Alan. 2008. Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes and Their Trophic Significance. San Francisco Estuary and Watershed Science, Vol. 6, Issue 1 (February), Article 2.

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. Marine Ecology Progress Series 66:95-101.

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis* - Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnology and Oceanography 38:949-964.

PREVIOUS VIEW

1.32

(+) Phytoplankton to Meso- and Macrozooplankton

Importance: High
Understanding: High
Predictability: High

Phytoplankton is important to most secondary producers. In particular, diatoms produce a rich, accessible foodweb, because of their large size and accessibility for consumption. Larger organisms result in fewer trophic links and a more direct, energetically efficient pathway to consumers. Copepods like *Pseudodiaptomus forbesi* use phytoplankton nearly exclusively. *Eurytemora affinis* and *Sinocalanus doerri* use it in conjunction with detritally derived food sources. Mysids rely heavily on phytoplankton especially during early stages in their life history, moving to omnivory as they approach adulthood. Phytoplankton supply has been greatly reduced in the San Francisco Estuary following the introduction of *Corbula amurensis* in the mid-1980's, leading to similar step-wise declines in zooplankton.

(-) Meso- and Macrozooplankton to Phytoplankton

Importance: Low
Understanding: High
Predictability: High

While phytoplankton is critical for many zooplankton species, phytoplankton abundance in the Delta is not strongly limited by zooplankton. Rather, it is limited by abiotic factors relating to turbidity and residence time, and biotic factors relating to grazing by the bivalves *Corbula amurensis* and *Corbicula fluminea*. These factors have resulted in low abundances of phytoplankton, with a notable absence of the spring blooms that once characterized the Estuary. Zooplankton in turn are food limited, while exerting only a small influence on primary production.

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

Kost ALB, Knight AW. 1975. The food of *Neomysis mercedis* Holmes in the Sacramento-San Joaquin Estuary. California Fish and Game 61:35-46.

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1.41

(+) Organic Carbon to Microzooplankton: Bacteria and Protists

Importance: High
Understanding: Moderate
Predictability: High

Particulate and dissolved organic carbon are responsible for five times the amount of bioavailable carbon derived from autotrophic sources. While phytoplankton-derived carbon fuels the most energetically efficient and useful trophic pathway, organic carbon by virtue of its abundance may be more important to foodweb dynamics. Organic carbon is typically derived from upstream sources, endogenous production from phytoplankton and phaeophyton, and from rainwater and tidal runoff adjacent to the Delta. It feeds directly into the microbial loop, a many-tiered sub-foodweb that may ultimately support some secondary production. Bacteria may utilize organic carbon directly, either as bacterioplankton or attached to detrital particles. Detritally borne bacteria may support the microbial loop and may also be grazed upon directly by *C. amurensis.* Bacterioplankton feeds into the microbial loop, being used directly by rotifers and ciliates. Rotifers are large enough to support zooplankton as well as a number of larval, filter-feeding and planktivorous fish. Ciliates may be eaten by rotifers, mesozooplankton and even some filter-feeding fish. Ciliates may also be the primary energetic pathway to the invasive cyclopoid copepod *Limnoithona sinensis*, suggesting that, in contrast to other zooplankton, it receives most of its energetic carbon from the organic carbon based foodweb, rather than the autotrophic foodweb.

(-) Microzooplankton: Bacteria and Protists to Organic Carbon

Importance: Low
Understanding: Moderate
Predictability: High

The Delta appears to have a large supply of organic carbon derived from a variety of sources: riverine inputs, agricultural and floodplain runoff, sewage treatment facility outfall, and endogenous phaeophyton production. Bacteria are unlikely to limit accumulation of high organic carbon loads. Likely, it is controlled more by physical forcing due to residence time, advection and dispersal.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. MEPS 324:219-228.

Hollibaugh JT, Wong PS. 1996. Distribution and activity of bacterioplankton in San Francisco Bay. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 263-288.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis* - Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnology and Oceanography 38:949-964.

PREVIOUS VIEW

1.51

(+) Microzooplankton: Bacteria and Protists to Meso- and Macrozooplankton
Importance: Moderate
Understanding: Moderate
Predictability: High

Many zooplankton species are omnivorous, relying on particulate organic matter, bacteria and protists to supplement a diet of phytoplankton. In the case of the Delta, the copepods *Eurytemora affinis* and *Sinocalanus doerri* appear to utilize detritally-borne microbial food sources. Mysids, isopods and amphipods likewise are omnivorous and may rely at times on microbial sources of food, particularly in the Delta where primary production is typically depressed.

(-) Meso- and Macrozooplankton to Microzooplankton: Bacteria and Protists
Importance: Low
Understanding: Moderate
Predictability: High

It is not clear what role zooplankton may have in regulating the microbial loop. Because the energy source that supports the loop is large and because microbial doubling time is on the order of hours, while mesozooplankton doubling time is on the order of days or weeks, it seems unlikely that zooplankton have much regulatory or limiting capacity. In addition, omnivorous zooplankton populations are depleted by phytoplankton declines and in at least some cases, direct predation by *C. amurensis*, further limiting the grazing impact of these populations on microzooplankton.

The primary driver for detrital production and the microbial loop is advection of organic carbon into the Delta system. The main controls on production are probably downstream advection and dispersal. The other controlling agent may be grazing effects from *C. amurensis*, although filtration efficiencies are somewhat less for bacterioplankton than for diatoms.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. MEPS 348:33-46.

Islam MS and Tanaka M. 2006. Spatial variability in nursery functions along a temperate estuarine gradient: role of detrital versus algal trophic pathways Can. J. Fish. Aquat. Sci. 63: 1848–1864

Mueller-Solger A, Hall C, Jassby A, Goldman, C. May 2006. Food resources for zooplankton in the Sacramento-San Joaquin River Delta. Final Report, Calfed Project ERP-01-N50/2001-K221.

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1.52

(+) Microzooplankton: Bacteria and Protists to Microzooplankton: Limnoithona

Importance: High
Understanding: High
Predictability: High

Limnoithona tetraspina relies primarily on microbial zooplankton, particularly ciliates, for its dietary needs. It may also use autotrophic microflagellates and detritally borne bacteria as secondary sources. *L. tetraspina* is an invasive cyclopoid copepod that became established in the San Francisco Estuary in 1993. It has since become the numerical and biomass dominant zooplankter in the low salinity zone of the San Francisco Estuary. Its small size may allow it to utilize ciliates that are unavailable to larger calanoid copepods, while at the same time avoiding heavy predation pressure from piscivorous and filter-feeding fish. It appears that *L. tetraspina* is largely an energetic dead end, utilizing detrital energy without passing it on to higher trophic levels. The fate of this energy is unknown, but may be directed to the benthos with senescence, or downstream and out of the system through advection.

(-) Microzooplankton: Limnoithona to Microzooplankton: Bacteria and Protists

Importance: Low
Understanding: Moderate
Predictability: High

Although *L. tetraspina* is abundant, there is no information on its effect on the ciliate population. Because ciliates are largely driven by the availability of organic carbon and bacteria, and because organic carbon is abundant in the Delta, while the doubling time for bacteria (hours) is far less than the doubling time for *L. tetraspina* (days to weeks), it seems unlikely that microzooplankton would be limited by copepods. Ciliates are more likely to be limited by advection out of the system, rather than by predation.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. MEPS 324:219-228.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. MEPS 348:33-46.

1.53

(+) Microzooplankton: Bacteria and Protists to Bivalve Grazers: Corbula/Corbicula
Importance: Moderate
Understanding: Moderate
Predictability: High

C. amurensis has been shown to rely upon bacterioplankton and detritally borne bacteria as a supplement to phytoplankton. However, filtration efficiencies are somewhat less than for phytoplankton, and perhaps because of this, *C. amurensis* has been found to be food limited at times. Nonetheless, it does appear that *C. amurensis* has some ability to "short circuit" both the autotrophic and detrital foodwebs. *C. fluminea* appears to graze mostly on phytoplankton.

(-) Bivalve Grazers: Corbula/Corbicula to Microzooplankton: Bacteria and Protists
Importance: Moderate
Understanding: Moderate
Predictability: High

At measured densities and feeding rates, *C. amurensis* has been calculated to have high enough grazing rates to clear the water column faster than the rate of production of bacteria (and phytoplankton), even at the lower rate of assimilation that it demonstrates for bacterioplankton. Given this and the fact that *C. amurensis* appears food limited at times, it appears that the clam is effectively able to graze down detritally based microbial production. However, short residence times may cause import of detrital material that allows sustained production from the microbial loop.

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis* - Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnology and Oceanography 38:949-964.

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1.61

(+) Meso- and Macrozooplankton to Fish
Importance: High
Understanding: High
Predictability: High

Most Delta fish feed on zooplankton at some point in their life cycle. Even adult piscivorous fish occasionally feed on large copepods and certainly use mysids, amphipods and isopods to at least supplement their diet. Typically, larval stages of most fish are planktivorous, with dietary shifts occurring in the post larval stage. Estuarine fish in general tend to be less specialized in their feeding requirements, in large part due to the dynamic nature of estuaries: fluxes in temperature, salinity, tide, fresh versus marine inputs and animal migrations require that species have a wide tolerance for a variety of conditions, including food sources.

(-) Fish to Meso- and Macrozooplankton
Importance: Moderate
Understanding: Moderate
Predictability: High

Because of the generalist nature of estuarine fish, they tend to be opportunistic. As such they may not structure zooplankton populations as much as is commonly seen in lakes. The exception to this may be the small introduced cyclopoid copepod, *Limnoithona tetraspina*, which appears to be largely immune to predation and is currently the most abundant copepod in the Delta.

Meso- and macrozooplankton seem to be primarily structured by predation from the benthic bivalve *Corbula amurensis*, through both resource competition and direct predation on nauplii. This intensive grazing pressure has depressed zooplankton populations since 1986 (when the clam was introduced) and may have resulted in food limitation for planktivorous fishes as well. Thus fish are being limited by top down control from another competitive predator.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

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Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Moyle PB, Cech JJ. 2000. Fishes: An introduction to ichthyology. 4th ed. Prentice-Hall, New Jersey. Pp 443-441.

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1.62

(+) Meso- and Macrozooplankton to Bivalve Grazers: Corbula/Corbicula

Importance: Moderate
Understanding: High
Predictability: High

Corbula amurensis grazes upon the nauplii of calanoid copepods like *Eurytemora affinis* and *Pseudodiaptomus forbesi* in addition to feeding on phytoplankton, bacterioplankton and detritus. It may feed on other larval zooplankton as well, but to what extent is largely unknown. *Corbicula fluminea* appears to rely primarily on phytoplankton.

(-) Bivalve Grazers: Corbula/Corbicula to Meso- and Macrozooplankton

Importance: High
Understanding: High
Predictability: High

Because of its high abundance and high rates of filtration, *Corbula amurensis* can directly structure population recruitment in both *E. affinis* and *P. forbesi*. In addition to direct predation, it has been demonstrated that *C. amurensis* also competes directly with zooplankton for food resources, indirectly controlling populations of meso- and macrozooplankton as well. A step change in phytoplankton and zooplankton that occurred after 1986 is attributed to the establishment of *C. amurensis* in that year.

Although *Corbicula fluminea* tends not to prey directly upon zooplankton, it too has high rates of filtration that allow it to compete for phytoplankton, thus suppressing populations of zooplankton. An efficient competitor, it can have a large impact in certain regions of the Delta where it is abundant.

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

2.0 Delta Foodweb Overview: Drivers

The key physical drivers of the foodweb are listed on the left and are clickable for explanations. Primary effects are shown by the color coded arrows. To summarize, the key drivers of primary production are related to the development of a critical depth that will promote phytoplankton growth. Currently, production is often limited by turbidity, mixing, and low residence times. Zooplankton growth is limited by phytoplankton growth, but may also be affected by turbidity both for capturing prey and for being preyed upon.

Salinity also has a controlling effect on the foodweb. The position of X2 determines the extent of tidal freshwater habitat throughout the Estuary. The fluctuation of salinity on different timescales exerts effects that influence fish habitat, and the extent of the ranges of the benthic bivalves, *Corbula amurensis* and *Corbicula fluminea.*

Key uncertainties:

1. The affect of salinity and its variability on fish populations.
2. The affect of turbidity on zooplankton and fish predation.
3. The affect of salinity on jelly blooms
4. The direct impact of diversions on nutrients, and plankton, and the resulting indirect impact on fishes.

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2.11 Salinity

Affects: Fish, Hydrozoan Jellies, Bivalves
Importance: High
Understanding: Moderate to High
Predictability: Moderate to High

Salinity primarily affects organisms that have a fixed relationship to the benthos or physical structure. Vertebrates seeking refuge or invertebrates incapable of locomotion are more exposed to shifts in salinity.

Demersal fishes may be more vulnerable to salinity changes, as are fishes that prefer to establish within stands of submerged aquatic vegetation. Ultimately however, these animals can move when salinity shifts become too great to tolerate, even at the risk of increased vulnerability to predation or starvation. For fishes, salinity gradients may be viewed as a shift in habitat extent. In seasons (or years) of high Delta outflow, when salinity drops, freshwater "habitat" is functionally increased. The opposite may occur in periods of high salinities, during which the range of freshwater habitat may be reduced.

In general, many native fishes are tolerant of salinity shifts, having evolved in a dynamic estuarine environment. Many of the recent estuarine invaders, both vertebrate and invertebrate, appear to have more limited ranges of salinity tolerance.

In contrast, planktonic organisms are not particularly vulnerable to salinity changes. Rather they tend to drift in the water. As water of a given salinity shifts, they move with the shift.

Invertebrates that attach to a fixed surface are more vulnerable to direct mortality from salinity shifts. Hydrozoan jelly life cycles include a sedentary benthic polyp that is critical to asexual reproduction. Jelly blooms occur when salinity conditions favor strobilation by these polyps. Adult medusae move with salinity gradients as do other planktonic organisms, rendering this stage of their life cycle less vulnerable to salinity.

Benthic organisms such as the adult clams of *Corbula amurensis* and *Corbicula fluminea* are also vulnerable. Broad shifts in salinity effectively determine the complementary ranges of these two bivalves, with *C. amurensis* residing primarily in marine to brackish water, and *Corbicula fluminea* in fresh water. Adult mortality and annual larval recruitment determines the population extent of these organisms. Large salinity shifts (outside the range of their physiological tolerance) that occur on timescales smaller than their lifespan (2-3 years) but longer than their ability to tolerate unfavorable conditions will result in high mortality. Shifts that occur over long timescales or very short timescales (ie, less than their ability to tolerate unfavorable conditions) result in large, dense populations becoming established.

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2.12 Geomorphology and Habitat

Affects: Fish (also affects many other Drivers, including Salinity, Turbidity, Stratification, Residence Time, Temperature, and Dissolved O_2.)
Importance: High
Understanding: High
Predictability: Moderate

Certain demersal and predatory fish are considered most fixed to specific habitats or benthic environments. Pelagic fish like Delta smelt or anchovy are probably less influenced by physical structure, but do need to be able to navigate through sloughs, channels, straits and salinity gates to be able to follow salinity gradients, food or migratory patterns.

While planktonic organisms are not strictly considered to be influenced by physical structure, they show indirect responses to certain aspects of structure as it influences salinity shifts, turbidity, stratification, residence time, temperature and dissolved oxygen. Certain fixed geographic regions tend to show high productivity because of the interaction of these drivers with geomorphology. For instance, the lower channel of the Sacramento River before the Confluence tends to show low productivity, because it is a deep, partially mixed channel with high turbidity. As a result, the critical depth for phytoplankton production is typically quite shallow, making this channel heterotrophic. In contrast, certain shallow sloughs with high residence time demonstrate high productivity, presumably because the water column is shallow enough to keep phytoplankton above the critical depth, and temperature and nutrient loads are conducive to high production, which fuels secondary production.

Finally, geomorphology and substratum also play some role in determining the distribution of benthic clams. *Corbicula fluminea* has a patchy distribution that is not well explained, but may be a function of water velocity, depth and predation rates from birds and fish. *Corbicula amurensis* seems to be more ubiquitous in brackish water, and while it is restricted to sandy or soft bottom substrata, this is widely available throughout the Delta.

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2.13 Water Depth

Affects: Primary production; indirectly secondary production; connectivity between benthos and water column
Importance: High
Understanding: High
Predictability: Medium; production and predation also subject to: T, stratification, turbidity (PAR), nutrients, species composition

Under mixed conditions water depth may influence the availability of Photosynthetically Available Radiation (PAR) by moving phytoplankton below the critical depth. Net production under mixed conditions tends to be higher in shallow portions of the Delta, where phytoplankton cannot be mixed below the critical depth (or photic zone). Deep channels tend to be net heterotrophic as zooplankton and benthic grazers assimilate productivity exported from shoals.

Water depth only indirectly influences secondary production by influencing phytoplankton production. The most important copepod species tend to be mixed throughout the water column by stage and gender; thus in shallow net autotrophic areas with high primary productivity, secondary production tends also to be high.

Water depth may also influence connectivity between the water column and the benthos. Stratification typically occurs only at some depth; in shallow regions (ie, less than the photic zone), primary and secondary production may be highly susceptible to predation by benthic grazers such as *Corbula amurensis* and *Corbicula fluminea*.

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

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2.14 Turbidity

Affects: PAR, and indirectly, primary production; also predation rates for visual predators
Importance: High
Understanding: High (for primary production) to Low (for predation effects)
Predictability: Medium to Low; primary production and predation also subject to T, stratification, nutrients, species composition

Turbidity decreases the amount of Photosynthetically Active Radiation (PAR) available to primary producers. It also decreases the critical depth in the water column. Turbidity may also have an effect on the ability of predators to capture prey. At high plankton densities this may be less important, but at low densities, particle density and size may negatively impact visual or tactile predators, as in certain copepods and planktivorous fish. Alternatively, Delta smelt larvae may rely upon high light intensity and turbidity to assist with visual discrimination of prey during feeding.

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Cole BE, Cloern JE. 1987. An empirical model for estimating phytoplankton productivity in estuaries. Marine Ecology Progress Series 36:299-305

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2.15 Stratification

Affects: Temperature, critical depth, benthic grazing rates, and indirectly, primary production
Importance: High
Understanding: High
Predictability: Medium; stratification depends on wind and thermal conditions; primary production also subject to turbidity, nutrients, species composition

Thermal or haline stratification tends to increase primary production by maintaining phytoplankton assemblages in the photic zone, and removed from benthic grazers. Wind, current or tidally generated mixing reduces stratification and production rate by moving phytoplankters below the critical depth at which the rate of photosynthesis exceeds the rate of respiration. Thus, deeper channels tend to be heterotrophic when the water column is unstratified.

Zooplankton nauplii tend to be well mixed throughout the water column unless stratification occurs. Thus predation by benthic grazers such as *Corbula amurensis* or *Corbicula fluminea* may be temporarily reduced through stratification, although nauplii may continue to be vulnerable for a longer period than most stratification events.

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2.16 Residence time/Water Velocity

Affects: Temperature, nutrients, primary production
Importance: High
Understanding: High
Predictability: Medium; primary and secondary production subject to a range of thermal conditions, as well as nutrient and dissolved oxygen concentrations

Residence time (=duration that a neutrally buoyant particle remains in a geographically defined area) affects the accumulation of plankton such that biomass accumulation is inversely related to flow. High residence times can indirectly influence growth rate by increasing water temperature, resulting in higher rates of production. Blooms occur when thermal stratification occurs in conjunction with high residence time. Extended residence time may also lead to a drawdown in nutrients associated with phytoplankton blooms. Shorter residence times may promote the export of organisms and nutrients to other regions of the Estuary through advection. Generally a pattern of mixed residence times allows for nutrient exchange, moderate temperatures and the export of organisms from high density to low density regions of the Delta.

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<u>2.17 Water Temperature</u>

Affects: Primary production; secondary production; predators
Importance: High
Understanding: High
Predictability: High; but primary production also subject to turbidity (PAR), stratification, nutrients, species composition; secondary producers and predators also subject to food availability

Phytoplankton growth varies directly as a function of temperature. Temperatures in the Delta range from 12 C in winter to 22 in summer, with a corresponding change in productivity by season, as phytoplankton are limited by temperature and light availability (see Turbidity) more than by nutrient availability.

Secondary producers and predators are also influenced physiologically by temperature, but increases in growth rates due to temperature are subject to food availability. Because most calanoid copepods appear to be limited by phytoplankton production, and fish by reduced copepod abundance; increased productivity due to temperature increase may be negated by metabolic demands that cannot be accommodated by food supply.

There is some evidence that mysids, particularly the native *Neomysis mercedis* and the shrimp *Crangon franciscorum* have upper temperature limits of about 22 C; thus they may be indirectly limited by low flow/high residence time conditions that promote higher temperatures in the summer. Mysids reproduce in the spring, leaving juveniles especially vulnerable to high summer temperatures, when water export demands are typically high.

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<u>2.18 Dissolved O_2/Anoxia</u>

Affects: Primary production (via photorespiration); secondary production; predators
Importance: High (but limited extent of impact in Delta)
Understanding: High
Predictability: High; but anoxic conditions are subject to T, stratification, nutrients, plant biomass, organic carbon

Anoxia may result from eutrophic conditions that promote high plant production and subsequent bacterial growth, a typical problem in many estuaries. Nutrient loads in the Delta are derived from waste water treatment facilities, urban runoff, and agriculture. Changes in waste water treatment throughout the SF Estuary have led to a reduction in nutrient and organic loads in the 1960s and 1970s, eliminating anoxic conditions in most regions of the Delta. An exception is the Stockton Ship Channel, which regularly has depressed levels of dissolved oxygen. Current primary production is light limited in the estuary (see turbidity), generally preventing eutrophication even with high levels of nutrient inputs.

Nichols F, Cloern J, Luoma S, Peterson D. 1986. The modification of an estuary. Science 231:567-573.

Cole BE, Cloern JE. 1984. Significance of biomass and light availability to phytoplankton productivity in San Francisco Bay. Marine Ecology Progress Series 17:15-24.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

2.19 Toxic Contaminants. Link to Chemical Stressors Model

Werner I, Anderson S, Larsen K, and Oram J. 2008. Chemical stressors conceptual model. Sacramento (CA): Delta Regional Ecosystem Restoration Implementation Plan.

Drivers

Nutrient Supply

Primary Production

Organic Carbon

Mesozooplankton Supply

Piscivores

Drivers
Nutrient Supply
Primary Production
Organic Carbon
Mesozooplankton Supply
Piscivores

<u>2.21 Water Diversions</u>.
Affects: Phytoplankton biomass
Importance: Potentially high
Understanding: Low
Predictability: Low; phytoplankton biomass subject to primary production (biomass x growth rate), a function of T, turbidity (PAR), stratification, nutrients, and mortality, integrated over residence time and diversion rates.

The principal water diversions are the state and federal pumping facilities in the south Delta, and agricultural pumps situated throughout the region. These facilities may remove nutrients, primary and secondary production, and fish directly out of the ecosystem, and as such act as non-selective grazers to any organism entrained in the flow. While export of production may be countered by growth rates, total biomass may be affected.

Jassby AD, Powell TM. 1994. Hydrodynamic influences on interannual chlorophyll variability in an estuary: upper San Francisco Bay-Delta (California, U.S.A.). Estuarine, Coastal, and Shelf Science 39:595-618.

Jassby AD, Cloern JE. 2000. Organic matter sources and rehabilitation of the Sacramento-San Joaquin Delta (California, USA). Aquatic Conservation: Marine and Freshwater Ecosystems 10:323-352.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

3.0 Nutrient Supply

Slide overview.

The phytoplankton of the Delta is dominated by diatoms and microflagellates. Diatom growth rates are subject to the availability of silicates, ammonium and nitrate, and phosphate. Microflagellates are driven primarily by nitrates. The Delta and most of the San Francisco Estuary tend to have high nitrogen loads largely due to anthropogenic inputs. In spite of this, the Delta and the rest of the Estuary have relatively low levels of primary production. This is probably due to the high level of turbidity in the Delta, which limits the photic zone and suppresses phytoplankton growth. Additional research suggests that high levels of ammonium may lead to preferential uptake of ammonium over nitrate, resulting in a less efficient metabolic pathway and lower growth rates for diatoms.

Key uncertainties:

1. The influence of ammonium on diatom production

2. The effect of nutrients and nutrient ratios on phytoplankton blooms and species composition.

View Slide: Nutrient Supply

PREVIOUS VIEW

3.11

(+) Ammonium to Diatoms

Importance: High
Understanding: High
Predictability: High

Ammonium at concentrations above 1 µmol L^{-1} may be used preferentially by phytoplankton, inhibiting uptake of nitrate. However, some diatoms have higher rates of primary production using nitrate rather than ammonium. As a result, bloom formation for these diatoms tends to occur only when ammonium levels have been drawn down below the threshold at which they can successfully utilize nitrate.

Ammonium may have increased in the estuary since the Clean Water Act with the introduction of secondary treatment at waste water treatment facilities.

(-) Diatoms to Ammonium

Importance: Medium
Understanding: Medium
Predictability: Medium

Diatoms occasionally deplete the available NH_4 in embayments or sloughs or when thermal stratification occurs, preventing nutrient exchange from proximate water masses. Under these conditions, phytoplankton may draw down ammonium below the 1 µmol L^{-1} threshold, allowing increased nitrate uptake by certain diatoms. Blooms may then occur as a result of increased primary production, until conditions shift back to normally high ammonium concentrations. This has happened only rarely since 2000.

Collos Y, Vaquer A, Souchu P. 2005. Acclimation of nitrate uptake by phytoplankton to high substrate levels. Journal of Phycology **41**(3): 466-479.

Dugdale RC, Wilkerson FP, Hogue, VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science 73:17-19.

Dugdale RC, Wilkerson FP, Hogue V, Marchi A. 2006. Nutrient controls on new production in the Bodega Bay, California, coastal upwelling plume. Deep Sea Research Part II: Topical Studies in Oceanography. 53(25-26): 3049-3062.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Lancelot C, Billen G. (1985). Carbon-nitrogen relationships in nutrient metabolism of coastal marine ecosystems. Advances in Aquatic Microbiology **3**: 263-321.

Schemel LE, Hager SW. 1986. Chemical variability in the Sacramento River and in northern San Francisco Bay. Estuaries 9:270-283.

Wilkerson, FP, Dugdale RC, Hogue V, Marchi A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. Estuaries and Coasts **29**(3): 401-416.

PREVIOUS VIEW

3.12
(+) Nitrate to Diatoms
Importance: High
Understanding: High
Predictability: High

The high nutrient conditions that exist in the Delta are largely derived from anthropogenic inputs, including waste water treatment plants, non-point source urban and agricultural runoff. Diatom blooms are not typically limited by nitrate, however, but rather by light limitation (turbidity), temperature and ammonium. When these conditions are lifted, blooms may occur.

(-) Diatoms to Nitrate
Importance: Low
Understanding: High
Predictability: High

Nitrate is non-limiting except during the conditions required to produce a bloom. Under such conditions, usually created by warm temperature, thermal stratification, and the drawdown of ammonium, blooms occur, which have the ability to temporarily deplete nitrate. Once the bloom is ended and conditions change, nitrate levels are quickly replenished, due to large inputs of NO_3 from a variety of sources.

Dugdale RC, Wilkerson FP, Hogue, VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science 73:17-19.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Jassby AD, Koseff JR, Monismith SG. 1996. Processes underlying phytoplankton variability in San Francisco Bay. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 325-349.

PREVIOUS VIEW

3.13
(+) Silica to Diatoms
Importance: High
Understanding: High
Predictability: High

In the euphotic zone, diatom growth may be a function of silicate abundance, since diatoms require silicates for the production of tests. Because of high turbidity, ammonium concentration, and mixing, silicates are not limiting in the Delta.

(-) Diatoms to Silica
Importance: Low
Understanding: High
Predictability: High

Silicate concentrations may be significantly reduced only under rare conditions following a diatom bloom in the Delta.

Peterson DH, Festa JF, Conomos TJ. 1978. Numerical simulation of dissolved silica in the San Francisco Bay. Estuarine and Coastal Marine Science 7:99-116.

Peterson DH, Smith RE, Hager SW, Harmon DD, Herndon RE, Schemel LE. 1985. Interannual variability in dissolved inorganic nutrients in Northern San Francisco Bay Estuary. Hydrobiologia 129:37-58.

3.14
(-) Ammonium to Nitrate Uptake
Importance: High
Understanding: Medium
Predictability: High

The presence of ammonium appears to inhibit phytoplankton nitrate uptake. The threshold value for nitrate (NO_3) inhibition in the Estuary occurs at ammonium (NH_4) concentrations greater than 1 µmol L^{-1}, with complete NO_3 inhibition above NH_4 concentrations of 4 µmol L^{-1}.

However, diatoms exhibit higher N uptake and primary production (carbon fixation) rates when they are able to use nitrate rather than ammonium. For certain phytoplankton species, particularly some diatom species, nitrate uptake may be linear (or biphasic), while ammonium uptake shows classical Michaelis-Menten kinetics, saturating at concentrations above 5 µmol L^{-1} NH_4. Thus, when light conditions are favorable, phytoplankton may still contend with high NH_4 concentrations, which inhibit access to NO_3, and the capacity to achieve maximal N uptake and biosynthesis, suppressing blooms. Optimal conditions for diatom production may occur only when thermal stratification occurs, maintaining diatoms in the euphotic zone. Since stratification isolates the water body, phytoplankton ammonium draw-down can occur, relieving inhibition of NO_3 uptake, allowing bloom formation as a result of high primary production rates.

Ambient ammonium concentrations in the Delta may be increasing due to secondary treatment in waste water treatment facilities in the region.

Collos Y, Vaquer A, Souchu P. 2005. Acclimation of nitrate uptake by phytoplankton to high substrate levels. Journal of Phycology **41**(3): 466-479.

Dugdale RC, Wilkerson FP, Hogue V, and Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science. 73: 17-29

Dugdale RC, Wilkerson FP, Hogue V, Marchi A. 2006. Nutrient controls on new production in the Bodega Bay, California, coastal upwelling plume. Deep Sea Research Part II: Topical Studies in Oceanography. 53(25-26): 3049-3062.

Huntsman S, Barber RT. 1977. Primary production off northwest Africa: the relationship to wind and nutrient conditions. Deep Sea Research **24**(1): 25-33.

Lancelot C, Billen G. (1985). Carbon-nitrogen relationships in nutrient metabolism of coastal marine ecosystems. Advances in Aquatic Microbiology **3**: 263-321.

Serra JL, Llama MJ, Cardenas E. (1978). Nitrate utilization by the diatom *Skeletonema costatum*. Plant Physiology **62**: 991-994.

Wilkerson, FP, Dugdale RC, Hogue V, Marchi A. 2006. Phytoplankton blooms and nitrogen productivity in San Francisco Bay. Estuaries and Coasts **29**(3): 401-416.

PREVIOUS VIEW

3.15

(+) Phosphorus to Diatoms

Importance: High
Understanding: Medium
Predictability: Medium

Phosphorus is unlikely to be limiting in the brackish parts of the Delta. However, some research suggests that high N:P ratios found in freshwater regions may be limiting to primary production, including diatoms. Low phosphorus ratios may be due to the increase in secondary treatment in wastewater treatment facilities since the 1970s and 1980s.

(-) Diatoms to Phosphorus

Importance: Low
Understanding: High
Predictability: High

Diatoms are unlikely to have an impact on phosphorus levels, due to limitation at the source by waste water treatment facilities. Since diatoms are typically limited by other factors (benthic grazing, nitrogen, ammonium, turbidity (PAR), temperature) in the brackish and freshwater delta, and limited by phosphorus inputs in the freshwater delta, blooms are rare and unlikely to be the source of phosphorus depletion.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal estuary. Limnology and Oceanography 47:698-712.

Lehman, PW. 1992. Environmental factors associated with long-term changes in chlorophyll concentration in the San Joaquin Delta and Suisun Bay, California. Estuaries 15(3): 335-348.

Van Nieuwenhuyse, EE. 2007. Response of summer chlorophyll concentration to reduced total phosphorus concentration in the Rhine River (Netherlands) and the Sacramento – San Joaquin Delta (California, USA). Canadian Journal of Fisheries and Aquatic Science 64(11):1529–1542.

PREVIOUS VIEW

3.21

(+) Nitrate to Microflagellates
Importance: High
Understanding: High
Predictability: High

The high nutrient conditions that exist in the Delta are largely derived from anthropogenic inputs, including waste water treatment plants, non-point source urban and agricultural runoff. Microflagellate blooms are not typically limited by nitrate, however, but rather by light limitation (turbidity), temperature and benthic grazing. When these conditions are lifted, blooms may occur.

(-) Microflagellates to Nitrate
Importance: Low
Understanding: High
Predictability: High

Nitrate is non-limiting except during the conditions required to produce a bloom. Under such conditions, usually created by warm temperature, thermal stratification, and low turbidity, blooms may occur, which have the ability to temporarily deplete nitrate. Once the bloom peaks and conditions change, nitrate levels are quickly replenished, due to large inputs of NO_3 from a variety of sources, primarily waste water treatment facilities and non-point agricultural and urban sources.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Jassby AD, Koseff JR, Monismith SG. 1996. Processes underlying phytoplankton variability in San Francisco Bay. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 325-349.

3.22

(+) Phosphorus to Microflagellates

Importance: High
Understanding: Medium
Predictability: Medium

Phosphorus is unlikely to be limiting in the brackish parts of the Delta. However, recent research suggests that high N:P ratios found in freshwater regions may be limiting to primary production, including microflagellates. Low phosphorus ratios may be due to the increase in secondary treatment in wastewater treatment facilities since the 1970s and 1980s.

(-) Microflagellates to Phosphorus

Importance: Low
Understanding: High
Predictability: High

Microflagellates are unlikely to have an impact on phosphorus levels, due to limitation at the source by waste water treatment facilities. Since microflagellates are typically limited by other factors (benthic grazing, nitrogen, turbidity (PAR), temperature) in the brackish and freshwater delta, and limited by phosphorus inputs in the freshwater delta, blooms are rare and unlikely to be the source of phosphorus depletion.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal estuary. Limnology and Oceanography 47:698-712.

Lehman, PW. 1992. Environmental factors associated with long-term changes in chlorophyll concentration in the San Joaquin Delta and Suisun Bay, California. Estuaries 15(3): 335-348.

Van Nieuwenhuyse, EE. 2007. Response of summer chlorophyll concentration to reduced total phosphorus concentration in the Rhine River (Netherlands) and the Sacramento – San Joaquin Delta (California, USA). Canadian Journal of Fisheries and Aquatic Sciences 64(11):1529–1542.

PREVIOUS VIEW

3.23

(+) Ammonium to Microflagellates

Importance: High
Understanding: High
Predictability: High

The high nutrient conditions that exist in the Delta are largely derived from anthropogenic inputs, including waste water treatment plants, non-point source urban and agricultural runoff. Microflagellate blooms are not typically limited by ammonium, however, but rather by light (turbidity) and temperature. When these conditions are lifted, blooms may occur.

(-) Microflagellates to Ammonium

Importance: Low
Understanding: High
Predictability: High

Ammonium is non-limiting except during the conditions required to produce a bloom. Under such conditions, usually created by warm temperature, and thermal stratification, blooms may occur, which have the ability to temporarily deplete ammonium (and nitrate). Once the bloom is ended and conditions change, nitrate levels are quickly replenished, due to large inputs of NH_3 (and nitrate) from a variety of sources.

Dugdale RC, Wilkerson FP, Hogue, VE, Marchi A. 2007. The role of ammonium and nitrate in spring bloom development in San Francisco Bay. Estuarine, Coastal and Shelf Science 73:17-19.

Hager SW, Schemel LE. 1992. Sources of nitrogen and phosphorus to northern San-Francisco Bay. Estuaries 15:40-52.

Jassby AD, Koseff JR, Monismith SG. 1996. Processes underlying phytoplankton variability in San Francisco Bay. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 325-349.

4.0 Primary Production

Slide Overview:

Because primary production is limited by turbidity and ammonium levels in the brackish Delta, there is limited support for secondary production. This standing stock of biomass appears to be further susceptible to high levels of benthic grazing by the invasive overbite clam, *Corbula amurensis*, which was became abundant in 1987. It is likely that competition for primary production is responsible for food limitation in the copepod *Eurytemora affinis* and the native mysid *Neomysis mercedis.* Blooms of phytoplankton tend to occur rarely because the necessary conditions for biomass accumulation can only occur when stratification occurs, isolating a potential bloom from the benthos. Under typical conditions, energy from primary production is largely routed from the water column directly to the benthos (via the clams), where it becomes less available to key constituents of the Delta foodweb.

Key uncertainties:

1. The role of microflagellates in the microbial loop.
2. The role of microflagellates in zooplankton and clam diets.
3. The formation of nuisance blooms and their effect on the foodweb and human health.

View Slide: Primary Production

PREVIOUS VIEW

4.11
(+) Diatoms to Macrozooplankton
Importance: Medium
Understanding: High
Predictability: High

Diatoms are an important food source for mysids, particularly juvenile stages. Adults are omnivorous filter feeders that are also capable of raptorial feeding. The decline of phytoplankton since 1987 corresponds to a similar decline in mysids, suggesting that the benthic grazer *Corbula amurensis* is an effective competitor.

The amphipod *Gammarus daiberi* became more abundant as mysids declined, suggesting *G. daiberi* may utilize a wider variety of foods, possibly including detritus as well as diatoms and zooplankton, allowing it exploit a developing niche in the Estuary.

(-) Macrozooplankton to Diatoms
Importance: Low
Understanding: High
Predictability: High

It is unlikely that the macrozooplankton of the Delta have a large grazing effect on diatoms, in large part because of reduced populations of crustacean zooplankton, and because diatoms are largely controlled by the efficient benthic grazers *Corbula amurensis* and *Corbicula fluminea.*

Interagency Ecological Program Estuarine Ecology Team. 1995. Working conceptual model for the food web of the San Francisco Bay/Delta Estuary. IEP Technical Report 42. August.

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

Kost ALB, Knight AW. 1975. The food of *Neomysis mercedis* Holmes in the Sacramento-San Joaquin Estuary. California Fish and Game 61:35-46.

Orsi JJ, Mecum WL. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 375-401.

Siegfried CA, Kopache ME, Knight AW. 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento-San Joaquin Delta. Transactions of the American Fisheries Society 108:262-268.

PREVIOUS VIEW

4.12

(+) Diatoms to Corbula

Importance: High
Understanding: High
Predictability: High

Diatoms are heavily grazed by *Corbula amurensis*. It is likely a key food source for the clams, although it is probably supplemented by bacteria, other phytoplankton, microzooplankton, and mesozooplankton nauplii. Thus, when phytoplankton production is limited by temperature, turbidity, ammonium, or nutrients; *C. amurensis* populations may be only slightly limited because it is able to rely substantially on bacteria or alternate sources of food.

(-) Corbula to Diatoms

Importance: High
Understanding: High
Predictability: High

C. amurensis is the primary controlling factor on diatom abundance in much of the brackish delta. While bloom conditions may also be constrained by other, abiotic factors (as listed above), abundance of phytoplankton has declined since the introduction of the clam in 1986. Thus, deep, rarely stratified areas tend to be net heterotrophic because of clam grazing, while shallow areas without clams are often net autotrophic exporters of primary production.

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

Cole BE, Thompson JK, Cloern JE. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. Journal of Marine Research 113:219–225.

Jassby, Alan. 2008. Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes and Their Trophic Significance. San Francisco Estuary and Watershed Science, Vol. 6, Issue 1 (February), Article 2.

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. Marine Ecology Progress Series 66:95-101.

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis* - Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnology and Oceanography 38:949-964.

PREVIOUS VIEW

4.13

(+) Diatoms to Mesozooplankton Calanoid and Cyclopoid Copepods
Importance: Medium
Understanding: High
Predictability: High

Copepods may rely on a variety of sources of food, including diatoms, microflagellates, ciliates, particulate organic carbon and other zooplankton. Different species may have different requirements, but in the Delta, diatoms are generally of moderate importance to the most important species, particularly *Pseudodiaptomus forbesi*, which relies upon diatoms as a primary food source. Other species, such as *Sinocalanus doerri* and *Eurytemora affinis* tend to not use diatoms exclusively, supplementing their diets substantially with particulate organic matter or ciliates.

(-) Mesozooplankton Calanoid and Cyclopoid Copepods to Diatoms
Importance: Low
Understanding: High
Predictability: High

Historically in the San Francisco Estuary, and in many other ecosystems, copepods may have a strong top-down effect on phytoplankton blooms. However, the effect is muted in the Estuary, because of strong limitations on copepod populations from predation, primarily benthic grazing by clams, and because diatoms are mostly limited by abiotic factors and by *Corbula amurensis* grazing.

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

Mueller-Solger A, Hall C, Jassby A, Goldman, C. May 2006. Food resources for zooplankton in the Sacramento-San Joaquin River Delta. Final Report, Calfed Project ERP-01-N50/2001-K221.

PREVIOUS VIEW

4.14
(+) Diatoms to Filter-feeding Fish
Importance: Medium
Understanding: High
Predictability: High

Threadfin shad, American shad and anchovy rely on large phytoplankton such as diatoms as well as calanoid copepods for diet. Anchovy have appear to have declined in the brackish Delta due to depressed phytoplankton levels, presumably from competitive grazing by the clam *Corbula amurensis.*

(-) Filter-feeding Fish to Diatoms
Importance: Low
Understanding: High
Predictability: High

Traditionally, anchovy probably had a moderate impact on phytoplankton abundance. The behavioral shift that led to the departure of anchovy from the Delta due to competition with *C. amurensis* helped to minimize some of the foodweb effects of the invasive clam.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. MEPS 324:207-218.

PREVIOUS VIEW

4.15
(+) Diatoms to Cladocerans
Importance: High
Understanding: High
Predictability: High

Cladocerans are found primarily in the freshwater Estuary, especially in the spring. They feed non-selectively on particles, but their abundance is strongly correlated with chlorophyll a in the Delta, suggesting that they rely heavily on diatoms, tracking blooms as they develop.

(-) Cladocerans to Diatoms
Importance: Low
Understanding: High
Predictability: High

While cladocerans have been well demonstrated to control the progression of phytoplankton blooms in freshwater lakes, this effect is largely muted in the Delta due to the competitive effects of both *Corbula amurensis* and *Corbicula fluminea.* This competition leaves most zooplankton populations that rely on phytoplankton fairly food-limited.

Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

Obrebski S, Orsi J, Kimmerer W. 1992. Long-term trends in zooplankton abundance in the Sacramento-San Joaquin Estuary. Sacramento (CA): Interagency Ecological Program for the San Francisco Bay-Delta Estuary. Technical Report 32.

Sommer U, Maciej Gliwicz Z, Lampert W, Duncan A. 1986 The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106(4):433-471.

PREVIOUS VIEW

4.21

(+) Microflagellates to Corbula

Importance: Medium
Understanding: Medium
Predictability: High

Microflagellates are heavily grazed by *Corbula amurensis.* It is likely a secondary food source for the clams, after diatoms, which tend to be most abundant in the Delta. When phytoplankton production is limited by temperature, turbidity, or nutrients; *C. amurensis* populations may be slightly food limited because it is able to rely substantially on bacteria or alternate sources of food.

(-) Corbula to Microflagellates

Importance: High
Understanding: Medium
Predictability: High

C. amurensis is one of the primary controlling factors on microflagellate abundance in much of the brackish delta. While bloom conditions may also be constrained by other, abiotic factors (as listed above), overall abundance of phytoplankton has seriously declined since the introduction of the clam in 1986. Thus, deep, rarely stratified areas tend to be net heterotrophic because of clam grazing, while shallow areas without clams are often net autotrophic exporters of primary production.

Alpine AE, Cloern JE. 1992. Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. Limnology and Oceanography 37:946-955.

Cole BE, Thompson JK, Cloern JE. 1992. Measurement of filtration rates by infaunal bivalves in a recirculating flume. Journal of Marine Research 113:219–225.

Jassby, Alan. 2008. Phytoplankton in the Upper San Francisco Estuary: Recent Biomass Trends, Their Causes and Their Trophic Significance. San Francisco Estuary and Watershed Science, Vol. 6, Issue 1 (February), Article 2.

Nichols FH, Thompson JK, Schemel LE. 1990. Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam *Potamocorbula amurensis*. 2. Displacement of a former community. Marine Ecology Progress Series 66:95-101.

Werner I, Hollibaugh JT. 1993. *Potamocorbula amurensis* - Comparison of clearance rates and assimilation efficiencies for phytoplankton and bacterioplankton. Limnology and Oceanography 38:949-964.

4.22

(+) Microflagellates to Rotifers

Importance: High
Understanding: Medium
Predictability: High

Microflagellates are an important source of prey for rotifers, supplemented by bacteria and possibly ciliates.

(-) Rotifers to Microflagellates

Importance: Low
Understanding: Medium
Predictability: High

Rotifer grazing is probably not a significant source of limitation for microflagellates.

Arndt H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255:231-246

Holst H, Zimmermann H, Kausch H, Koste W (1998) Temporal and spatial dynamics of planktonic rotifers in the Elbe estuary during spring. Estuary and Coast Shelf Science 47(3):261-273

PREVIOUS VIEW

4.23

(+) Microflagellates to Flagellates

Importance: High
Understanding: Medium
Predictability: High

Phytoplankton is an important food source for flagellates and ciliates in marine systems, but little is known from direct experimentation about the ecology of micro- and nanozooplankton in the Delta.

(-) Flagellates to Microflagellates

Importance: Low
Understanding: Medium
Predictability: High

Flagellates may be important grazers on microflagellates, but it is unlikely that they limit or control production, based upon the limited understanding of their role in the Delta.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. MEPS 348:33-46.

Landry MR, Calbet A (2004) Microzooplankton production in the oceans. ICES Journal of Marine Sciences 61:501–507

PREVIOUS VIEW

4.24

(+) Microflagellates to Ciliates

Importance: Medium
Understanding: Medium
Predictability: High

Phytoplankton is an important food source for flagellates and ciliates in marine systems, but little is known from direct experimentation about the ecology of micro- and nanozooplankton in the Delta.

(-) Ciliates to Microflagellates

Importance: Low
Understanding: Medium
Predictability: High

Ciliates may be important grazers on microflagellates, but it is unlikely that they limit or control production, based upon the limited understanding of their role in the Delta.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. Marine Ecology Progress Series 348:33-46

Landry MR, Calbet A (2004) Microzooplankton production in the oceans. ICES Journal of Marine Science 61:501–507

PREVIOUS VIEW

4.25

(+) Microflagellates to Limnoithona

Importance: Medium
Understanding: Medium
Predictability: High

Limnoithona tetraspina appears to be a raptorial predator that utilizes only motile prey. While it may be primary carnivorous, there is evidence that it will consume flagellated phytoplankton.

(-) Limnoithona to Microflagellates

Importance: Low
Understanding: High
Predictability: High

There is no evidence that consumption by *L. tetraspina* has a controlling influence on microflagellate abundance.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. Marine Ecology Progress Series 348:33-46.

PREVIOUS VIEW

4.26

(+) Microflagellates to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Small
Understanding: Medium
Predictability: High

Copepods may rely on a variety of sources of food, including diatoms, microflagellates, ciliates, particulate organic carbon and other zooplankton. Different species may have different requirements; in the Delta, microflagellates are generally of less importance than diatoms, which supply the majority of production. However, there is evidence from other estuaries that species like *Eurytemora affinis* tend not to use diatoms exclusively, supplementing their diets substantially with nanophytoplankton, particulate organic matter or ciliates.

(-) Mesozooplankton Calanoid and Cyclopoid Copepods to Microflagellates

Importance: Small
Understanding: High
Predictability: High

Historically in the San Francisco Estuary, and in many other ecosystems, copepods may have a strong top-down effect on phytoplankton blooms. However, the effect is muted in the Estuary, because of strong limitations on copepod populations from predation, primarily benthic grazing by clams, and because phytoplankton growth is limited primarily by abiotic factors and by *Corbula amurensis* grazing.

Gasparini S, Castel J (1997) Autotrophic and heterotrophic nanoplankton in the diet of the estuarine copepods *Eurytemora affinis* and *Acartia bifilosa*. Journal of Plankton Research 19:877–890

Gifford DJ, Dagg MJ (1988) Feeding of the estuarine copepod *Acartia tonsa* Dana: carnivory vs herbivory in natural microplankton assemblages. Bulletin of Marine Science 43:458–468

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93

Rollwagen-Bollens GC, Penry DL. 2003. Feeding dynamics of *Acartia* spp. copepods in a large, temperate estuary (San Francisco Bay, CA). Marine Ecology Progress Series 257:139-158

5.0 Organic Carbon and Microzooplankton Supply

Slide Overview:

Nearly five times as much carbon is imported into the Delta from exogenous sources than originates internally via phytoplankton growth. Although a less efficient energetic pathway, organic carbon supports a complex and active microbial loop. How this loop supports higher trophic levels, or is recycled into the benthos is largely unknown. The relationships between flagellates, rotifers and ciliates can be complex and species specific, but the size of the organisms creates the need for many more trophic steps before carbon becomes available to top level trophic organisms like fish.

Key uncertainties:

1. The extent to which benthic grazers recycle or sequester organic carbon in the system.
2. The availability of organisms from the microbial loop to other zooplankton.
3. The availability of *Limnoithona tetraspina* as a food source to other organisms.

View Slide: Organic Carbon & Microzooplankton Supply

PREVIOUS VIEW

5.11

(+) Organic Carbon to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Medium
Understanding: Low
Predictability: High

Copepods may rely on a variety of sources of food, including diatoms, microflagellates, ciliates, particulate organic carbon and other zooplankton. Different species may have different requirements. While phytoplankton tends to be the most important source of carbon to Delta copepods, it is often limited by abiotic factors or competitive grazing from introduced bivalves. *Eurytemora affinis* and *Sinocalanus doerri* tend not to use phytoplankton exclusively, supplementing their diets substantially with particulate organic matter or ciliates.

(-)Mesozooplankton Calanoid and Cyclopoid Copepods to Organic Carbon

Importance: Low
Understanding: Low
Predictability: High

The Delta is typically turbid due to high levels of particulate organic carbon, and it is unlikely that copepods have a significant effect in consuming carbon relative to the magnitude of the inputs from rivers, agriculture and sewage treatment facilities.

Islam MS, Tanaka M. 2006. Spatial variability in nursery functions along a temperature estuarine gradient: role of Detrital versus algal pathways. Canadian Journal of Fisheries and Aquatic Science 63:1848-1864.

Mueller-Solger A, Hall C, Jassby A, Goldman, C. May 2006. Food resources for zooplankton in the Sacramento-San Joaquin River Delta. Final Report, Calfed Project ERP-01-N50/2001-K221.

Sobczak W, Cloern JE, Jassby AD, Müller-Solger AB. 2002. Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources. Proceedings of the National Academy of Sciences 99:8101-8110

PREVIOUS VIEW

5.12

(+) Organic Carbon to Limnoithona

Importance: Low
Understanding: Low
Predictability: High

Limnoithona tetraspina appears to be an omnivorous raptorial predator that utilizes primarily motile prey. Based upon limited studies of its ecology, it appears to not graze on particulate organic matter.

(-) Limnoithona to Organic Carbon

Importance: Low
Understanding: Low
Predictability: High

L. tetraspina has a minor impact on organic carbon in the Delta.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. Marine Ecology Progress Series 348:33-46.

PREVIOUS VIEW

5.13

(+) Organic Carbon to Bacteria

Importance: High
Understanding: Low
Predictability: Low

Bacterioplankton production is high relative to primary production in the northern San Francisco Estuary and Delta. Much of the carbon to supply bacterial production must come from riverine and terrigenous sources of dissolved or particulate organic carbon rather than phytoplankton. While phytoplankton provides a more energetically efficient transfer of carbon up the food chain, low primary productivity means that microbial production from organic carbon sources provides a significant proportion of energy to the Delta.

Additionally, bacteria are the main consumers of dissolved organic carbon, which is inaccessible to most organisms in the Delta. By using DOC, bacteria make carbon available in a particulate form which can be ingested and utilized by other organisms in the foodweb, such as ciliates, rotifers, and even *Corbula amurensis.*

(-) Bacteria to Organic Carbon

Importance: Medium
Understanding: Low
Predictability: Low

Bacteria are the primary consumers of dissolved organic carbon, although particulate organic carbon is consumed by a number of other organisms, including protists, bivalves, and fish. It is unclear however, whether bacterial production is ever limited by organic carbon availability. It is likely that carbon inputs vary by season, inflow, rainfall, and temperature, as well as phytoplankton production rate. It is further difficult to parse the source of inputs of DOC, DIC, and POC and how they may be utilized by the foodweb. See Organic Carbon Model for more information.

Hollibaugh JT. 1999. Bacteria and the microbial loop in northern San Francisco Bay and the Sacramento-San Joaquin Delta. IEP Newsletter 12(2):8-11. Available at: http://www.iep.water.ca.gov/report/newsletter.

Hollibaugh JT, Wong PS. 1996. Distribution and activity of bacterioplankton in San Francisco Bay. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 263-288.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

PREVIOUS VIEW

5.14

(+) Organic Carbon to Demersal Fish

Importance: Low
Understanding: Medium
Predictability: High

Suckers and catfish consume some benthic detritus either intentionally or incidentally while bottom feeding for other organisms.

(-) Demersal Fish to Organic Carbon

Importance: Low
Understanding: Medium
Predictability: High

Demersal fish have a low impact on organic carbon loads in the Delta, since primary production and exogenous inputs have a far great magnitude of influence.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405

Feyrer FV. 1999. Food habits of common Suisun Marsh fishes in the Sacramento-San Joaquin estuary, California. M.S. thesis, Calif. State Univ., Sacramento. 53 pp.

Ganssle D. 1966. Fishes and decapods of San Pablo and Suisun Bay. Pages 64-94 *in* DW Kelley, ed. Ecological studies of the Sacramento –San Joaquin Estuary. Part 1. CDFG Fish Bulletin 33:64-94

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

McCall JN. 1992. Source of harpactacoid copepods in the diet of juvenile starry flounder. Marine Ecology Progress Series 86:41-50

Muir WD, Emmett RL, McConnell RJ. 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. California Department of Fish and Game Bulletin 74:49-54

Orcutt HG. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). California Fish and Game Fish Bulletin 78:1-64.

Radtke LD. 1966. Distribution of smelt, juvenile sturgeon and starry flounder in the Sacramento-San Joaquin Delta. *In* SL Turner and DW Kelley, eds. Ecological studies of the Sacramento-San Joaquin Delta, Part II. California Department of Fish and Game Bulletin 136:115-119

Sobczak W, Cloern JE, Jassby AD, Müller-Solger AB. 2002. Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources. Proceedings of the National Academy of Sciences 99:8101-8110

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 126:961–976

Villa NA. 1985. Life history of the Sacramento sucker, *Catostomus occidentalis*, in Thomes Creek, Tehama county, California. Calif. Fish Game 71:88-106

PREVIOUS VIEW

5.15

(+) Organic Carbon to Corbula/Corbicula

Importance: Low
Understanding: Low
Predictability: High

Both bivalves are relatively undiscriminating in the types of particles they consume, so it may be expected that some organic material in the form of detritus is consumed. It is unknown whether they are able to use dissolved organic carbon, as some marine invertebrates are known to do, but unlikely.

(+) Corbula/Corbicula to Organic Carbon

Importance: Low
Understanding: Low
Predictability: High

Although these clams may use organic carbon sources directly, they consume much more through bacterial production. Thus direct effects are likely to be small. It is unknown however, if *C. amurensis* contributes significantly to increased dissolved organic carbon loads through elimination of digested products.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Manahan DT. 1990. Adaptations by invertebrate larvae for nutrient acquisition from seawater. American Zoologist 30:147-160.

PREVIOUS VIEW

5.21

(+) Bacteria to Rotifers

Importance: Low
Understanding: Low
Predictability: High

Rotifers have been shown to use bacteria, ciliates and flagellates as food sources, but little work has been done on this aspect of the microbial loop in the Delta.

(-) Rotifers to Bacteria

Importance: Low
Understanding: Low
Predictability: High

It is largely unknown to what extent rotifers and ciliates use bacteria in the Delta.

Arndt H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255:231-246

Holst H, Zimmermann H, Kausch H, Koste W. 1998. Temporal and spatial dynamics of planktonic rotifers in the Elbe estuary during spring. Estuary Coast and Shelf Science 47(3):261–273

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

Orsi J, Mecum W. 1986. Zooplankton distribution and abundance in the Sacramento-San Joaquin Delta in relation to certain environmental factors. Estuaries 9:326-339.

PREVIOUS VIEW

5.22

(+) Bacteria to Ciliates

Importance: Low
Understanding: Low
Predictability: High

Bacteria may provide a substantial subsidy to ciliates based upon a few studies from other estuaries and marine systems. Little has been done to elucidate this in the San Francisco Estuary.

(-) Ciliates to Bacteria

Importance: Low
Understanding: Low
Predictability: High

It is unlikely that ciliates could drawdown available bacteria, but one study in the Hudson River Estuary (Vacqué 1992) showed that all predators (including ciliates) removed only 3-21% of bacterial standing stock per day. Others have shown ciliates to account for nearly 100% of bacterial consumption, but no research has been conducted in the Delta.

Rollwagen-Bollens GC, Bollens SM, Penry DL. 2006. Vertical distribution of micro- and nanoplankton in the San Francisco Estuary in relation to hydrography and predators. Aquatic Microbial Ecology 44:143-163.

Sherr, EB, Sherr BF. 1987. High rates of consumption of bacteria by pelagic ciliates. Nature 325:710-711.

Vacqué D, Pace ML, Findlay S, Lints D. 1992. Fate of bacterial production in a heterotrophic ecosystem: grazing by protists and metazoans in the Hudson Estuary. Marine Ecology Progress Series 89:155-163.

PREVIOUS VIEW

5.31

(+) Rotifers to Larval Fish

Importance: Low
Understanding: Low
Predictability: Low

Rotifers may be a source of food for larval fish, as they are large enough to be used by planktivores, but there are few studies of this available in the San Francisco Estuary, in part because they are difficult to identify in gut content analyses. Rotifers have been used to raise Delta smelt larvae, and presumably other fish rely upon them as well.

(-) Larval Fish to Rotifers

Importance: Low
Understanding: Low
Predictability: Low

Rotifer populations are likely controlled by bottom up dynamics rather than top down from planktivory, although this is not well examined in the Delta.

Foss SF, Miller LW. 2004. Growth and growth rate variability of larval striped bass in the San Francisco Estuary, California. American Fisheries Society Symposium 39:203-217.

Kurth R, Nobriga M. 2001. Food habits of larval splittail. Interagency Ecological Program Newsletter 14(2):40-42. Available at: http://www.iep.ca.gov/report/newsletter/

Mager RC, Doroshov SI, Van Eenennaam JP, Brown RL. 2004. Early life stages of Delta smelt. American Fisheries Society Symposium 39:169-180.

PREVIOUS VIEW

5.32

(+) Rotifers to Filter-feeding fish

Importance: Low
Understanding: Low
Predictability: Low

Rotifers may supplement the diet of filter feeders, but larger copepods and cladocerans are preferred. Most Delta filter-feeders supplement by planktivorous picking, but low light levels due to turbidity inhibit their ability to do so, resulting in large amounts of detritus, phytoplankton and microzooplankton in the stomachs of species like threadfin shad.

(-) Filter-feeding Fish to Rotifers

Importance: Low
Understanding: Low
Predictability: Low

It is unlikely that filter-feeders have much impact on rotifer abundance.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Halonov SH, Tash JC. 1978. Particulate and filter feeding in threadfin shad, *Dorosoma petenense* at different light intensities. Journal of Fish Biology 13:619-625

Kjelson MA. 1971. Selective predation by a freshwater planktivore, the threadfin shad, *Dorsoma petenense.* PhD dissertation, Univ. Calif. Davis.123 pp

Levesque RC, Reed RJ. 1972. Food availability and consumption by young Connecticut River shad, *Alosa sapidisima.* Journal of the Fisheries Research Board Canada 29:1495-1499

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

O’Connell CP. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). Journal of the Fisheries Resources Board Canada 29:285-293.

Ziebell CD, Tash JC, Barefield RL. 1986. Impact of threadfin shad on macrocrustacean zooplankton in two Arizona lakes. Journal of Freshwater Ecology 3:399-406.

PREVIOUS VIEW

5.33
(+) Rotifers to Planktivorous Fish
Importance: Low
Understanding: Low
Predictability: Low

Because of the large size of rotifers relative to other microzooplankton, they are probably used by certain planktivores, particularly small fish and juveniles. However, copepods, cladocerans and aquatic insects are probably more important to planktivore diets.

(-) Planktivorous Fish to Rotifers
Importance: Low
Understanding: Low
Predictability: Low

It is unlikely that planktivores have much impact on rotifer abundance.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter.

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. MEPS 324:207-218.

Lott J. 1998. Feeding habits of juvenile and adult Delta smelt from the Sacramento-San Joaquin river estuary. Interagency Ecological Program for the San Francisco Estuary Newsletter 11(1):14-19. Available at: http://www.iep.water.ca.gov/report/newsletter.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of the delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.

Nobriga, ML 2002. Larval Delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. California Department of Fish and Game Bulletin 88:149-164.

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 126:961–976

PREVIOUS VIEW

5.41
(+) Ciliates to Mesozooplankton Calanoid and Cyclopoid Copepods
Importance: Medium
Understanding: Medium
Predictability: High

Eurytemora affinis and *Sinocalanus doerri* appear to exploit ciliates or detritus (or both) in addition to using phytoplankton as a nutrient source. In this regard they differ from *Pseudodiaptomus forbesi*, which selectively grazes more exclusively on phytoplankton. Little information exists on *Acanthocyclops vernalis.*

(-) Mesozooplankton Calanoid and Cyclopoid Copepods to Ciliates
Importance: Low
Understanding: Medium
Predictability: High

E. affinis is highly limited by direct predation from *C. amurensis*. It is unlikely that it would have a large direct effect on ciliates. *S. doerri* is likewise not sufficiently abundant to be limiting to prey.

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. Marine Ecology Progress Series 348:33-46.

Islam MS and Tanaka M. 2006. Spatial variability in nursery functions along a temperate estuarine gradient: role of detrital versus algal trophic pathways Canadian Journal of Fisheries and Aquatic Sciences 63: 1848–1864

Islam MS, Ueda H, Tanaka M. 2005. Spatial distribution and ecology of dominant copepods associated with turbidity maximum along the salinity gradient in a highly embayed estuarine system in Ariake Sea, Japan. Journal of Experimental Marine Biology and Ecology 316:101-115.

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. In: Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

Mueller-Solger A, Hall C, Jassby A, Goldman, C. May 2006. Food resources for zooplankton in the Sacramento-San Joaquin River Delta. Final Report, Calfed Project ERP-01-N50/2001-K221.

Rollwagen-Bollens GC, Penry DL (2003) Feeding dynamics of Acartia spp. copepods in a large, temperate estuary (San Francisco Bay, CA). Marine Ecology Progress Series 257:139–158

PREVIOUS VIEW

5.42

(+) Ciliates to Limnoithona

Importance: High
Understanding: High
Predictability: High

Ciliates are important to *Limnoithona. tetraspina*, linking it to the detrital foodweb, rather than the autotrophic (phytoplankton-based) foodweb. This may give it an apparent advantage as an invader to the San Francisco Estuary, since detritally derived carbon is about five times more abundant than photosynthetically derived carbon. It may also feed upon autotrophic microflagellates and other microbial organisms, including detritally-borne bacteria.

(-) Limnoithona to Ciliates

Importance: Medium
Understanding: Low
Predictability: High

The effect of *L. tetraspina* on ciliates is unknown. It is the numerically dominant copepod in the northern San Francisco Estuary, with a biomass equivalent to that of the formerly dominant calanoid copepods (*Eurytemora affinis* and *Pseudodiaptomus forbesi*) Because of this it is conceivable that it could have some ability to graze down ciliate populations, but this is unknown.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228

Gifford SM, Rollwagen-Bollens G, Bollens SM. 2007. Mesoplankton omnivory in the upper San Francisco Estuary. Marine Ecology Progress Series 348:33-46

Sobczak W, Cloern JE, Jassby AD, Müller-Solger AB. 2002. Bioavailability of organic matter in a highly disturbed estuary: The role of detrital and algal resources. Proceedings of the National Academy of Sciences 99:8101-8110

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zoological Studies 43:255–266

PREVIOUS VIEW

5.43

(+) Ciliates to Filter-feeding Fish

Importance: Low
Understanding: Low
Predictability: Low

Ciliates are likely supplements to filter-feeders' diets, but only incidentally. Likely, the larger rotifers are more available than ciliates. Gut contents of anchovy and shad indicate the presence of phytoplankton, detritus and rotifers as well. It is likely an unimportant constituent of their diet.

(-) Filter-feeding Fish to Ciliates

Importance: Low
Understanding: Low
Predictability: Low

It is unlikely that filter-feeders have a controlling influence on ciliate abundance.

Halonov SH, Tash JC. 1978. Particulate and filter feeding in threadfin shad, *Dorosoma petenense* at different light intensities. Journal of Fish Biology 13:619-625.

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324:207-218.

Kjelson MA. 1971. Selective predation by a freshwater planktivore, the threadfin shad, *Dorsoma petenense.* PhD dissertation, Univ. Calif. Davis.123 pp.

Levesque RC, Reed RJ. 1972. Food availability and consumption by young Connecticut River shad, *Alosa sapidisima.* Journal of the Fisheries Research Board Canada 29:1495-1499

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

O'Connell CP. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). Journal of the Fisheries Resources Board Canada 29:285-293.

Ziebell CD, Tash JC, Barefield RL. 1986. Impact of threadfin shad on macrocrustacean zooplankton in two Arizona lakes. Journal of Freshwater Ecology 3:399-406.

PREVIOUS VIEW

5.51

(+) Flagellates to Rotifers
Importance: Low
Understanding: Low
Predictability: High

Rotifers are able to utilize flagellates in their diet, although bacteria and phytoplankton are probably more important sources.

(-) Rotifers to Flagellates
Importance: Low
Understanding: Low
Predictability: High

It is unlikely that rotifers have much impact on the abundance of flagellates.

Arndt H. 1993. Rotifers as predators on components of the microbial web (bacteria, heterotrophic flagellates, ciliates) – a review. Hydrobiologia 255:231-246.

Holst H, Zimmermann H, Kausch H, Koste W (1998) Temporal and spatial dynamics of planktonic rotifers in the Elbe estuary during spring. Estuary and Coast Shelf Science 47(3):261–273

PREVIOUS VIEW

5.61
(+) Limnoithona to Filter-feeding Fish
Importance: Low
Understanding: Low
Predictability: High

Although it is the numerically dominant copepod in the Delta, *Limnoithona tetraspina* does not occur frequently in gut content analyses of any fish, although presumably it would be available to filter feeders based upon size alone. Possibly its abundance has increased in areas to the west of the Delta due to a decline in filter-feeders, particularly anchovy.

(-) Filter-feeding Fish to Limnoithona
Importance: Low
Understanding: Low
Predictability: High

L. tetraspina appears not to be limited by a biotic parameter, although little is known about its life history.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228.

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324:207-218.

PREVIOUS VIEW

5.62

(+) Limnoithona to Planktivorous Fish
Importance: Low
Understanding: Low
Predictability: High

Although it is the numerically dominant copepod in the Delta, *L. tetraspina* does not occur frequently in gut content analyses of any fish. It may be that it is too small to be readily available to planktivores.

(-) Planktivorous Fish to Limnoithona
Importance: Low
Understanding: Low
Predictability: High

L. tetraspina appears not to be limited by a biotic parameter, although little is known about its life history.

Bennett WA. 2005. Critical assessment of the Delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3(2):Art 1.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228

PREVIOUS VIEW

5.63
(+) Limnoithona to Larval Fish
Importance: Low
Understanding: Low
Predictability: High

Although it is the numerically dominant copepod in the Delta, *L. tetraspina* does not occur frequently in gut content analyses of any fish. It may be that it is too small to be readily available to planktivores.

(-) Larval Fish to Limnoithona
Importance: Low
Understanding: Low
Predictability: High

L. tetraspina appears not to be limited by a biotic parameter, although little is known about its life history.

Bennett WA. 2005. Critical assessment of the Delta smelt population in the San Francisco Estuary, California. San Francisco Estuary and Watershed Science 3(2):Art 1.

Bouley P, Kimmerer WJ. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Marine Ecology Progress Series 324:219-228.

PREVIOUS VIEW

5.71

(+) Microzooplankton to Scyphozoans

Importance: Medium
Understanding: Low
Predictability: High

Microzooplankton may be eaten or incidentally killed by blooms of invasive jellies that occur throughout late summer in the Delta.

(-) Scyphozoans to Microzooplankton

Importance: Medium
Understanding: Low
Predictability: High

Jelly invasions have been documented worldwide that have large disruptive impacts on planktonic foodwebs. Little research has been done on the effects of these invasions, although anecdotal reports and new data suggest that they may have strong regional effects on zooplankton populations.

Mills CE, Rees JT. 2000. New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (=*M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary. Scientia Marina 64(suppl 1):151-155**.**

Mills CE, Sommer F. 1995. Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexpectata* and *Blackfordia virginica*, invade San Francisco Bay. Marine Biology 122:279-288.

Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:145-176.

Rees J. 1999. Non-indigenous jellyfish in the upper San Francisco Estuary: potential impacts on zooplankton and fish. IEP Newsletter 12(3):46-50.

Schroeter RE. Unpublished data.

PREVIOUS VIEW

5.72

(+) Microzooplankton to Corbula

Importance: Medium
Understanding: Moderate
Predictability: High

C. amurensis supplements its diet from a wide variety of available particles, making it a formidable grazer. Because of these supplements, depletion of one source, such as phytoplankton, may not be limiting for clam populations. As a result of their omnivorous disposition, these clams are able to maintain high abundance between years and conditions, and exert consistent control over phytoplankton (and other) production.

(-) Corbula to Microzooplankton

Importance: Medium
Understanding: Moderate
Predictability: High

C. amurensis is capable of efficiently filtering microzooplankton, and to a lesser degree nanoplankton. Filtration rates suggest that it suppresses the abundance of bacteria, given the availability of carbon. Likewise, these bivalves may also be able to utilize ciliates, rotifers, and copepod nauplii of some species. Other potential prey, such as *Limnoithona tetraspina*, seem to be unaffected, possibly because of a well developed escape response to entrainment by a siphon.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

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6.0 Mesozooplankton Supply

Slide overview:

Mesozooplankton form a critical link between production and consumption at higher trophic levels. The decline in abundance of a number of key species, such as *Eurytemora affinis, Pseudodiaptomus forbesi* and the native mysid *Neomysis mercedis* has been indicated as one possible stressor on fish populations, in the form of lost food supply. Much of the decline is due to declines in phytoplankton abundance, competition for food with benthic grazers, and direct predation by benthic grazers. Species composition of plankton has also shifted, such that new residents such as *Limnoithona tetraspina* may not be as available to fish populations, but may still be the primary conduit for much of the organic carbon introduced into the Delta.

Key uncertainties:

1. The success of copepods over cladocerans in the system.
2. The ecology of *Acartiella sinensis.*
3. The role of amphipods in filling the niche once inhabited by the native mysid *Neomysis mercedis.*
4. The impact of invasive jellies on zooplankton populations.
5. The role of insects and isopods in the foodweb.

View Slide: Mesozooplankton Supply

6.11
(+) Cladocerans to Acartiella
Importance: Low
Understanding: Low
Predictability: High

Little work has been done on *A. sinensis*, but it is probably omnivorous, feeding opportunistically on other zooplankton and detritus of appropriate size.

(-) Acartiella to Cladocerans
Importance: Low
Understanding: Low
Predictability: High

A. sinensis tends to occur in more brackish water than do cladocerans, which occur at high densities in fresh water. Thus *A. sinensis* feeds only on cladocerans occasionally if at all.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

6.12

(+) Cladocerans to Larval Fish

Importance: Low
Understanding: High
Predictability: High

Cladocerans may provide a minor source of food for larval fishes in the fresh water Delta, but cladocerans tend not to be as abundant there as copepods, which form the main source of secondary production.

(-) Larval Fish to Cladocerans

Importance: Low
Understanding: High
Predictability: High

The impact of fish on cladocerans is unknown, but is probably not large. Cladoceran abundance is primarily limited by phytoplankton availability. *C. fluminea* grazing in the freshwater Delta and *C. amurensis* in brackish water control phytoplankton abundance.

Meng L, Orsi JJ. 1991. Selective predation by larval striped bass on native and introduced copepods. Transactions of the American Fisheries Society 124(4):538-549

Foss SF, Miller LW. 2004. Growth and growth rate variability of larval striped bass in the San Francisco Estuary, California. American Fisheries Society Symposium 39:203-217.

Kurth R, Nobriga M. 2001. Food habits of larval splittail. Interagency Ecological Program Newsletter 14(2):40-42. Available at: http://www.iep.ca.gov/report/newsletter/

Mager RC, Doroshov SI, Van Eenennaam JP, Brown RL. 2004. Early life stages of Delta smelt. American Fisheries Society Symposium 39:169-180.

Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

PREVIOUS VIEW

6.13

(+) Cladocerans to Planktivorous Fish

Importance: Low
Understanding: High
Predictability: High

Cladocerans may provide a minor source of food for planktivores in the freshwater Delta, but cladocerans tend not to be as abundant there as copepods, which form the main source of secondary production.

(-) Planktivorous Fish to Cladocerans

Importance: Low
Understanding: High
Predictability: High

The impact of fish on cladocerans is unknown, but is probably not large. Cladoceran abundance is primarily limited by phytoplankton availability. *C. fluminea* grazing in the freshwater Delta and *C. amurensis* in brackish water control phytoplankton abundance.

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter.

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324:207-218.

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Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of the delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.

Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

Nobriga, ML 2002. Larval Delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. California Fish and Game 88:149-164

Sommer T, Baxter R, Herbold B. 1997. Resilience of splittail in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 126:961–976

PREVIOUS VIEW

6.14
(+) Cladocerans to Filter-feeding Fish
Importance: Low
Understanding: High
Predictability: High

Cladocerans may provide a minor source of food for filter-feeders in the freshwater Delta, but cladocerans tend not to be as abundant there as copepods, which form the main source of secondary production.

(-) Filter-feeding Fish to Cladocerans
Importance: Low
Understanding: High
Predictability: High

The impact of fish on cladocerans is unknown, but is probably not large. Cladoceran abundance is primarily limited by phytoplankton availability. *C. fluminea* grazing in the freshwater Delta and *C. amurensis* in brackish water control phytoplankton abundance.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Halonov SH, Tash JC. 1978. Particulate and filter feeding in threadfin shad, *Dorosoma petenense* at different light intensities. Journal of Fish Biology 13:619-625

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Kjelson MA. 1971. Selective predation by a freshwater planktivore, the threadfin shad, *Dorsoma petenense.* PhD dissertation, Univ. Calif. Davis.123 pp

Levesque RC, Reed RJ. 1972. Food availability and consumption by young Connecticut River shad, *Alosa sapidisima.* Journal of the Fisheries Resources Board Canada 29:1495-1499.

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O'Connell CP. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). Journal of the Fisheries Resources Board Canada 29:285-293.

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PREVIOUS VIEW

6.15

(+) Cladocerans to Corbula/Corbicula

Importance: Low
Understanding: Low
Predictability: High

It is not known whether *C. amurensis* or *C. fluminea* are able to directly feed upon cladoceran adults or juveniles.

(-) Corbula/Corbicula to Cladocerans

Importance: Medium
Understanding: Low
Predictability: High

Cladocerans are likely limited in the Delta less from direct predation than by food limitation due to competition with these bivalves.

Cohen RRH, Dresler PV, Phillips EJP, Cory RL. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnology and Oceanography 29:170-180.

Foe C, Knight A. 1985. The effect of phytoplankton and suspended sediment on the growth of Corbicula fluminea (Bivalvia). Hydrobiologia 127:105-115.

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Jassby AD, Cloern JE, Cole BE. 2002. Annual primary production: patterns and mechanisms of change in a nutrient-rich tidal estuary. Limnology and Oceanography 47:698-712.

Lucas LV, Cloern JE, Thompson JK, Monsen NE. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: restoration implications. Ecological Applications 12:1528-1547.

Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

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PREVIOUS VIEW

6.16
(+) Cladocerans to Demersal Fish
Importance: Low
Understanding: Medium
Predictability: High

Some demersal fish undoubtedly use cladocerans opportunistically or incidentally, but it is unlikely that they are an important source of food. Juvenile stages of splittail, starry flounder or sturgeon may use cladocerans incidentally, but copepods are much more abundant in the Delta.

(-) Demersal Fish to Cladocerans
Importance: Low
Understanding: Medium
Predictability: High

Demersal fish are unlikely to have a consistently large impact on cladocerans, which are largely limited by grazing from benthic bivalves.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405

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Ganssle D. 1966. Fishes and decapods of San Pablo and Suisun Bay. Pages 64-94 *in* DW Kelley, ed. Ecological studies of the Sacramento –San Joaquin Estuary. Part 1. California Department of Fish and Game Fish Bulletin 33:64-94

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McCall JN. 1992. Source of harpactacoid copepods in the diet of juvenile starry flounder. Marine Ecology Progress Series 86:41-50

Muir WD, Emmett RL, McConnell RJ. 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. California Department of Fish and Game Fish Bulletin 74:49-54

Orcutt HG. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). California Department of Fish and Game Fish Bulletin Bulletin 78:1-64.

Radtke LD. 1966. Distribution of smelt, juvenile sturgeon and starry flounder in the Sacramento-San Joaquin Delta. Pages 115-119 *in* SL Turner and DW Kelley, eds. Ecological studies of the Sacramento-San Joaquin Delta, Part II. CDFG fish Bull. 136

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 126:961–976

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6.21

(+) Mesozooplankton Calanoid and Cyclopoid Copepods to Larval Fish

Importance: High
Understanding: High
Predictability: High

The larval fish of a number of species are highly dependent upon copepod adults and nauplii, including striped bass, delta smelt, and splittail. Nearly every fish in the Delta relies upon copepod zooplankton as a food source at some point in its life cycle. Larval fish are possibly food limited because of an overall decline in phyto- and zooplankton as a result of benthic grazing from invasive bivalves.

(-)Larval Fish to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Medium
Understanding: Medium
Predictability: High

Although it is probable that larval fish historically had some control over copepod abundance following spring blooms, it is unlikely that this occurs now. One reason is that fish populations are at an historic low in the Estuary; as a result predation pressure on zooplankton is likely to be released. Secondly, copepod populations are primarily controlled by competition with *C. amurensis* and *C. fluminea*, which competes directly with zooplankton for phytoplankton and also grazes directly on nauplii. Third, as a result of the clams, anchovies left the Suisun region, relieving some competitive pressure for phytoplankton and zooplankton on larval fish of other species.

Meng L, Orsi JJ. 1991. Selective predation by larval striped bass on native and introduced copepods. Transactions of the American Fisheries Society 124(4):538-549.

Nobriga, ML 2002. Larval Delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. California Department of Fish and Game Fish Bulletin 88:149-164.

Foss SF, Miller LW. 2004. Growth and growth rate variability of larval striped bass in the San Francisco Estuary, California. American Fisheries Society Symposium 39:203-217.

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PREVIOUS VIEW

6.22
(+) Mesozooplankton Calanoid and Cyclopoid Copepods to Planktivorous Fish
Importance: High
Understanding: High
Predictability: High

Copepods are a key food source for most planktivorous fishes. Because of declines in zooplankton abundance due to clam grazing, many planktivores may be food limited in the Delta.

(-) Planktivorous Fish to Mesozooplankton Calanoid and Cyclopoid Copepods
Importance: Medium
Understanding: Medium
Predictability: High

Although it is probable that planktivores historically had some control over copepod abundance following spring blooms, it is unlikely that this occurs now. One reason is that fish populations are at an historic low in the Estuary; as a result predation pressure on zooplankton is likely to be released. Secondly, copepod populations are primarily controlled by competition with *C. amurensis* and *C. fluminea*, which competes directly with zooplankton for phytoplankton and also grazes directly on nauplii. Third, as a result of the clams, anchovies left the Suisun region, relieving some competitive pressure for phytoplankton and zooplankton on planktivores of other species.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD.

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405.

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter.

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324:207-218.

Kimmerer WJ, Orsi JJ. 1996. Causes of long-term declines in zooplankton in the San Francisco Bay estuary since 1987. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 403-424.

Lott J. 1998. Feeding habits of juvenile and adult Delta smelt from the Sacramento-San Joaquin river estuary. Interagency Ecological Program for the San Francisco Estuary Newsletter 11(1):14-19

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Moyle PB, Herbold B, Stevens DE, Miller LW. 1992. Life history and status of the delta smelt in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 121:67-77.

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Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 126:961–976

PREVIOUS VIEW

6.23

(+)Mesozooplankton Calanoid and Cyclopoid Copepods to Filter-feeding Fish

Importance: High
Understanding: High
Predictability: High

Copepods are a key food source for filter-feeding fishes. Because of declines in zooplankton abundance due to clam grazing, many filter-feeders may be food limited in the Delta.

(-) Filter-feeding fish to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Medium
Understanding: Medium
Predictability: High

Although it is probable that filter-feeders historically had some control over copepod abundance following spring blooms, it is unlikely that this occurs now. One reason is that fish populations are at an historic low in the Estuary; as a result predation pressure on zooplankton is likely to be released. Secondly, copepod populations are primarily controlled by competition with *C. amurensis* and *C. fluminea*, which competes directly with zooplankton for phytoplankton and also grazes directly on nauplii. Third, as a result of competition from clams, anchovies left the Suisun region, relieving some competitive pressure for phytoplankton and zooplankton on filter-feeders of other species.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Halonov SH, Tash JC. 1978. Particulate and filter feeding in threadfin shad, *Dorosoma petenense* at different light intensities. Journal of Fish Biology 13:619-625

Kimmerer WJ. 2006. Response of anchovies dampens effects of the invasive bivalve *Corbula amurensis* on the San Francisco Estuary foodweb. Marine Ecology Progress Series 324:207-218.

Kjelson MA. 1971. Selective predation by a freshwater planktivore, the threadfin shad, *Dorsoma petenense.* PhD dissertation, Univ. Calif. Davis.123 pp

Levesque RC, Reed RJ. 1972. Food availability and consumption by young Connecticut River shad, *Alosa sapidisima.* Journal of the Fisheries Resources Board Canada 29:1495-1499

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O'Connell CP. 1972. The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). Journal of the Fisheries Resources Board Canada 29:285-293.

Ziebell CD, Tash JC, Barefield RL. 1986. Impact of threadfin shad on macrocrustacean zooplankton in two Arizona lakes. Journal of Freshwater Ecology 3:399-406.

6.24

(+)Mesozooplankton Calanoid and Cyclopoid Copepods to Corbula/Corbicula

Importance: Moderate
Understanding: High
Predictability: High

In addition to feeding upon phytoplankton and bacteria, *Corbula amurensis* is able to graze directly upon the nauplii of at least some species of copepods. Thus, *C. amurensis* is able to maintain high abundance by capitalizing on a varied suite of food sources. Abundances of *C. amurensis* can range up to thousands per square meter in the brackish Delta.

Corbicula fluminea appears to be limited to mostly phytoplankton as a primary food source. It can be quite abundant, but its distribution, limited to the freshwater Delta, is patchier than that of *C. amurensis.*

(-) Corbula/Corbicula to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: High
Understanding: High
Predictability: High

High abundances of *C. amurensis* result in a large controlling effect on copepods, both through competition for food resources, and through direct predation upon nauplii. Populations of zooplankton in the brackish Delta have been significantly reduced since the appearance of *C. amurensis* in 1986. Although *C. amurensis* is largely restricted to brackish water, it apparently depletes zooplankton abundance well into the eastern Delta, due to mixing from tidal action.

C. fluminea has a more patchy distribution than *C. amurensis* and therefore has a more isolated impact on phytoplankton abundance, which varies with habitat conditions and connectivity between shallow shoals and deepwater channels. It does not appear to graze directly on zooplankton, so its impact is limited due to indirect competitive effects, rather than direct predation. It is restricted primarily to freshwater habitats in the Delta.

Cohen RRH, Dresler PV, Phillips EJP, Cory RL. 1984. The effect of the Asiatic clam, *Corbicula fluminea*, on phytoplankton of the Potomac River, Maryland. Limnology and Oceanography 29:170-180.

Foe C, Knight A. 1985. The effect of phytoplankton and suspended sediment on the growth of Corbicula fluminea (Bivalvia). Hydrobiologia 127:105-115.

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PREVIOUS VIEW

6.25

(+)Mesozooplankton Calanoid and Cyclopoid Copepods to Acartiella

Importance: High
Understanding: Low
Predictability: High

Acartiella sinensis is probably omnivorous, based upon it morphology. There is some anecdotal evidence that it has a preys upon other copepods and their nauplii. However, there is a lack of solid evidence as to what role *A. sinensis* actually does play in the foodweb.

(-) Acartiella to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Moderate
Understanding: Low
Predictability: High

There is some evidence suggesting that *A. sinensis* can have an impact on other copepod populations, based upon abundance shifts of other species during *A. sinensis* blooms. However, very little work has been done with this species and its feeding ecology.

Kimmerer, W. 2004. Open water process of the San Francisco Estuary: from physical forcing to biological responses. San Francisco Estuary and Watershed Science 2(1).

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

6.26

(+) Mesozooplankton Calanoid and Cyclopoid Copepods to Macrozooplankton Arthropods

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

There is little data about these organisms, except for mysids, which rely upon a variety of food sources, including phytoplankton, detritus and copepods. Amphipods and isopods may have eclipsed mysids in importance for much of the Delta, but little is known about their diets and ecology. Little is known about the role of aquatic insects in the Delta.

(-) Macrozooplankton Arthropods to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Low
Understanding: Moderate
Predictability: Moderate

Mysids may have at one time had an impact upon copepod populations, but mysid populations are currently food limited due to competition with *C. amurensis.* Isopods, amphipods, decapods and insects may have a slight impact on copepods, but it is unlikely that is significant.

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter.

Siegfried CA, Kopache ME, Knight AW. 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento-San Joaquin Delta. Transactions of the American Fisheries Society 108:262-268.

Wahle RA. 1985. The feeding ecology of *Crangon franciscorum* and *Crangon nigricauda* in San Francisco Bay, California. Journal of Crustacean Biology 5:311–326

PREVIOUS VIEW

6.27

(+)Mesozooplankton Calanoid and Cyclopoid Copepods to Demersal Fish

Importance: Moderate
Understanding: High
Predictability: High

Copepods may contribute to the diet of a number of demersal fish species, but it is difficult to predict to predict the relative contribution, since fish diets are largely opportunistic, and therefore a function of temperature, season, benthos, geography, and prey availability.

(-) Demersal Fish to Mesozooplankton Calanoid and Cyclopoid Copepods

Importance: Moderate
Understanding: Moderate
Predictability: High

Demersal fish probably have some controlling influence on copepod populations, but their influence is diminished due to the major impact of bivalve grazing.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Feyrer F, Sommer T, Hobbs J. 2007. Living in a dynamic environment: variability in life history traits of age-0 splittail in tributaries of San Francisco Bay. Transactions of the American Fisheries Society 136:1393-1405

Feyrer FV. 1999. Food habits of common Suisun Marsh fishes in the Sacramento-San Joaquin estuary, California. M.S. thesis, Calif. State Univ., Sacramento. 53 pp.

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Müller-Solger AB, Jassby AD, Müller-Navarra D. 2002. Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento-San Joaquin River Delta). Limnology and Oceanography 47:1468-1476.

McCall JN. 1992. Source of harpactacoid copepods in the diet of juvenile starry flounder. Mar. Ecol. Prog. Ser. 86:41-50

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Orcutt HG. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). California Fish and Game Fish Bulletin 78. p 1-64.

Radtke LD. 1966. Distribution of smelt, juvenile sturgeon and starry flounder in the Sacramento-San Joaquin Delta. Pages 115-119 *in* SL Turner and DW Kelley, eds. Ecological studies of the Sacramento-San Joaquin Delta, Part II. CDFG fish Bull. 136

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 126:961–976

Villa NA. 1985. Life history of the Sacramento sucker, *Catostomus occidentalis*, in Thomes Creek, Tehama county, California. Calif. Fish Game 71:88-106

PREVIOUS VIEW

6.31

(+) Acartiella to Corbula/Corbicula

Importance: Low
Understanding: Low
Predictability: High

Little is known of the biology of *Acartiella sinensis*, specifically if it is subject to predation by *Corbula amurensis*. If it is, it would provide only a small contribution to the overall diet of the clam.

(-) Corbula to Acartiella

Importance: Moderate
Understanding: Low
Predictability: High

If *C. amurensis* preys upon *A. sinensis,* it could have a large impact on its population, especially if it grazes upon nauplii and interferes with recruitment, as it does with the copepod *Eurytemora affinis*. However, no work has been done on this relationship as of the present time.

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

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PREVIOUS VIEW

6.32

(+) Acartiella to Filter-feeding Fish

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella sinensis may provide an important, if occasional, supplement to filter-feeders, particularly if it is able to maintain abundance in spite of competition or predation from *C. amurensis.*

(-) Filter-feeding Fish to Acartiella

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella sinensis is probably an omnivore, based on the functional morphology of its mouthparts. As such, is may be less severely limited than other copepod species by the competition with *Corbula amurensis.* If so, it may be more susceptible to control by predatory fishes.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

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Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

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Ziebell CD, Tash JC, Barefield RL. 1986. Impact of threadfin shad on macrocrustacean zooplankton in two Arizona lakes. J. Freshw. Ecol. 3:399-406.

PREVIOUS VIEW

6.33

(+) Acartiella to Planktivorous Fish

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella sinensis may provide an important, if occasional, supplement to planktivores, particularly if it is able to maintain abundance in spite of competition or predation from *C. amurensis.*

(-) Planktivorous Fish to Acartiella

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella is probably an omnivore, based on the functional morphology of its mouthparts. As such, is may be less severely limited than other copepod species by the competition with *Corbula amurensis.* If so, it may be more susceptible to control by predatory fishes.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

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Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

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Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 126:961–976

PREVIOUS VIEW

6.34

(+) Acartiella to Demersal Fish

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella sinensis may provide an important, if occasional, supplement to demersal fish, particularly if it is able to maintain abundance in spite of competition or predation from *C. amurensis.*

(-) Demersal Fish to Acartiella

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella is probably an omnivore, based on the functional morphology of its mouthparts. As such, is may be less severely limited than other copepod species by the competition with *Corbula amurensis*. If so, it may be more susceptible to control by predatory fishes.

Emmett RL, Stone SL, Hinton SA, Monaco ME (1991) Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

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Feyrer FV. 1999. Food habits of common Suisun Marsh fishes in the Sacramento-San Joaquin estuary, California. M.S. thesis, Calif. State Univ., Sacramento. 53 pp.

Ganssle D. 1966. Fishes and decapods of San Pablo and Suisun Bay. Pages 64-94 *in* DW Kelley, ed. Ecological studies of the Sacramento –San Joaquin Estuary. Part 1. CDFG Fish Bull. 33:64-94

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McCall JN. 1992. Source of harpactacoid copepods in the diet of juvenile starry flounder. Mar. Ecol. Prog. Ser. 86:41-50

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Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

Orcutt HG. 1950. The life history of the starry flounder *Platichthys stellatus* (Pallas). California Fish and Game Fish Bulletin 78. p 1-64.

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Sommer T, Baxter R, Herbold B (1997) Resilience of splittail in the Sacramento-San Joaquin Estuary. Trans Am Fish Soc 126:961–976

Villa NA. 1985. Life history of the Sacramento sucker, *Catostomus occidentalis*, in Thomes Creek, Tehama county, California. Calif. Fish Game 71:88-106

6.35

(+) Acartiella to Larval Fish

Importance: Moderate
Understanding: Low
Predictability: Low

Acartiella sinensis may provide an important, if occasional, supplement to larval fish, particularly if it is able to maintain abundance in spite of competition or predation from *C. amurensis.*

(-) Larval Fish to Acartiella

Importance: Moderate
Understanding: Low
Predictability: Low

Although larval fish may have a moderate impact, it is currently unclear what controls blooms of *Acartiella sinensis.*

Foss SF, Miller LW. 2004. Growth and growth rate variability of larval striped bass in the San Francisco Estuary, California. American Fisheries Society Symposium 39:203-217.

Kurth R, Nobriga M. 2001. Food habits of larval splittail. Interagency Ecological Program Newsletter 14(2):40-42. Available at: http://www.iep.ca.gov/report/newsletter/

Mager RC, Doroshov SI, Van Eenennaam JP, Brown RL. 2004. Early life stages of Delta smelt. American Fisheries Society Symposium 39:169-180.

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

PREVIOUS VIEW

6.36

(+) Acartiella to Macrozooplankton Arthropods

Importance: Moderate
Understanding: Low
Predictability: Low

There is little data about these organisms, except for mysids, which rely upon a variety of food sources, including phytoplankton, detritus and copepods. Amphipods and isopods may have eclipsed mysids in importance for much of the Delta, but little is known about their diets and ecology. Little is known about the role of aquatic insects in the Delta. Likewise, the ecology of *A. sinensis* is poorly understood, but it may be an important source of zooplankton during occasional blooms which occur each year in the Delta.

(-) Macrozooplankton Arthropods to Acartiella

Importance: Moderate
Understanding: Low
Predictability: Low

Mysids may have at one time had an impact upon copepod populations, but mysid populations are currently highly food limited due to competition with *C. amurensis.* Ispods, amphipods, decapods and insects may have a slight impact on copepods, but it is unlikely that is significant.

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter

Orsi JJ, Ohtsuka S. 1999. Introduction of the Asian copepods *Acartiella sinensis*, *Tortanus dextrilobatus* (Copepoda: Calanoida), and *Limnoithona tetraspina* (Copepoda: Cyclopoida) to the San Francisco Estuary, California, USA. Plankton Biology and Ecology 46:128-131.

Siegfried CA, Kopache ME, Knight AW. 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento-San Joaquin Delta. Transactions of the American Fisheries Society 108:262-268.

Wahle RA (1985) The feeding ecology of *Crangon franciscorum* and *Crangon nigricauda* in San Francisco Bay, California. J Crustac Biol 5:311–326

6.41
(+) Macrocrustaceans to Corbula/Corbicula
Importance: Low
Understanding: Low
Predictability: High

Most adult macrocrustaceans are too large to supply *Corbicula amurensis* with a food source. However, larval stages might be available, although little research has been done on this topic. In addition, the freshwater macrocrustaceans, such as crayfish (decapoda) or insects would be outside of the usual brackish salinity preferred by *C. amurensis. Corbicula fluminea* feeds primarily upon phytoplankton.

(-) Corbula/Corbicula to Macrocrustaceans
Importance: Low
Understanding: Low
Predictability: High

The direct impact of *C. amurensis* and *C. fluminea* on macrocrustaceans is largely unknown, although they are probably responsible for food limitation in juvenile mysids (through competition for phytoplankton).

Kimmerer WJ, Gartside E, Orsi JJ. 1994. Predation by an introduced clam as the probable cause of substantial declines in zooplankton in San Francisco Bay. Marine Ecology Progress Series 113:81-93.

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6.42

(+) Macrocrustaceans to Planktivorous Fish

Importance: High
Understanding: Moderate
Predictability: Moderate

Macrocrustaceans have historically been quite important to planktivores, and this is probably still true, although abundance of the native mysid has declined since 1986. Possibly, planktivores have responded to this decline by switching to an invasive amphipod, *Gammarus daiberi*, which have become abundant in the wake of mysid declines.

(-) Planktivorous Fish to Macrocrustaceans

Importance: High
Understanding: Moderate
Predictability: Moderate

It is not known what impact planktivores have on macrocrustaceans. While mysids are largely food limited by *Corbula amurensis*, other crustaceans have widely variable life histories. Because predation by fish tends to be opportunistic, it is difficult to know what impact they have on macroinvertebrates. Little research has been done on the impact on prey populations of fish predation in the Delta.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

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Nobriga, ML 2002. Larval Delta smelt diet composition and feeding incidence: environmental and ontogenetic influences. California Department of Fish and Game Fish Bulletin 88:149-164

Sommer T, Baxter R, Herbold B. 1997. Resilience of splittail in the Sacramento-San Joaquin Estuary. Transactions of the American Fisheries Society 126:961–976

PREVIOUS VIEW

6.43

(+) Macrocrustaceans to Demersal fish

Importance: High
Understanding: Moderate
Predictability: Moderate

Macrocrustaceans have historically been quite important to demersal fish, and this is probably still true, although abundance of the native mysid has declined since 1986. Possibly, demersal fish have responded to this decline by switching to an invasive amphipod, *Gammarus daiberi*, which have become abundant in the wake of mysid declines.

(-) Demersal Fish to Macrocrustaceans

Importance: Moderate
Understanding: Low
Predictability: Moderate

It is not known what impact demersal fish have on macrocrustaceans. While mysids are largely food limited by *Corbula amurensis*, other crustaceans have widely variable life histories. Because predation by fish tends to be opportunistic, it is difficult to know what impact they have on macroinvertebrates. Little research has been done on the impact on prey populations of fish predation in the Delta.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD.

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Villa NA. 1985. Life history of the Sacramento sucker, *Catostomus occidentalis*, in Thomes Creek, Tehama county, California. California Department of Fish and Game Fish Bulletin 71:88-106.

PREVIOUS VIEW

6.44

(+) Macrozooplankton to Larval Fish

Importance: Moderate
Understanding: Moderate
Predictability: High

Macrocrustaceans have been historically quite important to larval fish, particularly mysids and early life stages of the larger organisms. This is probably still true, although abundance of the native mysid has declined since 1986. Possibly, larval fish have responded to this decline by switching to an invasive amphipod, *Gammarus daiberi*, which has become abundant in the wake of mysid declines.

(-) Larval Fish to Macrozooplankton

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

It is not known what impact larval fish have on macrocrustaceans. While mysids are largely food limited by *Corbula amurensis*, other crustaceans have widely variable life histories. Larval fish tend to utilize smaller organisms, possibly early life stages, rather than adults, and so may influence invertebrate recruitment. Little research has been done on the impact on prey populations of fish predation in the Delta.

Gartz R. 1999. Density dependent growth and diet changes in young-of-the-year striped bass (*Morone saxatilis*) in the Sacramento-San Joaquin Delta. IEP Newsletter 12(1):22-24. Available at: http://www.iep.water.ca.gov/report/newsletter.

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PREVIOUS VIEW

6.51

(+) Crustacean Zooplankton to Hydrozoans

Importance: Moderate
Understanding: Low
Predictability: High

Crustaceans probably provide a moderately important food source to the suite of invasive hydrozoans that have appeared in the Delta. To date, little research has been done with these jellies, although it is likely that they utilize copepods adults and possibly nauplii. Jellies may also rely upon other resources, but this is unknown.

(-) Hydrozoans to Crustacean Zooplankton

Importance: Moderate
Understanding: Low
Predictability: High

It is unknown how jellies impact zooplankton populations. Jellies can form dense blooms during the summer months, and in addition to consumed prey, they tend to kill any small organisms (ie, copepods) that come into contact with their tentacles. Thus, the impacts could be severe, although little research has been completed that addresses the impact of jellies on copepod populations.

Mills CE, Rees JT. 2000. New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (=*M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary. Scientia Marina 64(suppl 1):151-155**.**

Mills CE, Sommer F. 1995. Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexpectata* and *Blackfordia virginica*, invade San Francisco Bay. Marine Biology 122:279-288.

Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:145-176.

Rees J. 1999. Non-indigenous jellyfish in the upper San Francisco Estuary: potential impacts on zooplankton and fish. IEP Newsletter 12(3):46-50.

Schroeter RE. Unpublished data.

7.0 Piscivores

Slide Overview:

Fish tend to be opportunistic. Feeding strategies are often Type III functional responses to prey availability. Ontogenetic development also influences the kinds of food sources utilized, as well as size relationships. Often prey types have been well established for many fishes, but it is difficult to be predictive about which sources fish will be exploiting at a given time or place. It is also difficult to establish the ecological role fish have in structuring prey populations. The functional response to abundance suggests that fish capitalize on highly abundant organisms and therefore then not to limit annual recruitment. But because of this, the role of piscivores in controlling native and other fish populations is not well established.

Key uncertainties:

1. The effect of fish on prey populations.
2. The impact of piscivorous fish on native fishes.
3. The impact of planktivory on larval fishes and recruitment to adulthood.
4. The ecology of jellies and their effect on larval fish survival.
5. The availability of *Corbula amurensis* and *Corbicula fluminea* to fish predators.

View Slide: Piscivores

7.11

(+) Larval Fish to Planktivorous Fish

Importance: Moderate
Understanding: Low
Predictability: Low

No information is available on the contribution of larval fish to planktivorous fish.

(-) Planktivorous Fish to Larval Fish

Importance: Moderate
Understanding: Low
Predictability: Low

No information is available on the impact of predation on larval fish in the Delta.

Foss SF, Miller LW. 2004. Growth and growth rate variability of larval striped bass in the San Francisco Estuary, California. American Fisheries Society Symposium 39:203-217.

Kurth R, Nobriga M. 2001. Food habits of larval splittail. Interagency Ecological Program Newsletter 14(2):40-42. Available at: http://www.iep.ca.gov/report/newsletter/

Mager RC, Doroshov SI, Van Eenennaam JP, Brown RL. 2004. Early life stages of Delta smelt. American Fisheries Society Symposium 39:169-180.

7.12

(+) Larval Fish to Hydrozoans
Importance: Low
Understanding: Low
Predictability: High

Jellies are typically undiscriminating in their diets. Larval fish may be sufficiently small to be vulnerable to at least one of the invasive jellies in the Delta, *Maeotias marginita.*

(-) Hydrozoans to Larval Fish
Importance: Low
Understanding: Low
Predictability: High

Invasive jellies have been demonstrated to have large impacts on ichthyoplankton in other estuaries; however, the effect has not been investigated in the Delta.

Cowan JH, Houde ED. 1993. Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. Marine Ecology Progress Series 95:55-65.

Mills CE, Rees JT. 2000. New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (=*M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary. Scientia Marina 64(suppl 1):151-155

Mills CE, Sommer F. 1995. Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexpectata* and *Blackfordia virginica*, invade San Francisco Bay. Marine Biology 122:279-288.

Purcell JE, Arai MN. 2001. Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451:145-176.

Rees J. 1999. Non-indigenous jellyfish in the upper San Francisco Estuary: potential impacts on zooplankton and fish. IEP Newsletter 12(3):46-50.

PREVIOUS VIEW

7.21

(+) Planktivorous Fish to Piscivores

Importance: Moderate
Understanding: High
Predictability: Moderate

Piscivores are known to feed upon planktivorous fish, based upon gut contents and co-occurrence data. Most piscivores behave opportunistically to food availability, so it is difficult to predict what food source they are using, except that they tend to follow prey items of high abundance.

(-) Piscivores to Planktivorous Fish

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

Piscivory in Delta fishes is a function of density dependence of prey species. Piscivores tend to track abundance either because of Type III functional response (prey-switching) or because of increased probability of encounter with prey organisms at abundance. While predation may have some effect on prey abundance, it is likely that abiotic factors have greater control on planktivore populations in the Delta.

Lindley ST, Mohr MS. 2003. Modeling the effect of striped bass (*Morone saxatilis*) on the population viability of Sacramento River winter-run chinook salmon (*Oncorhynchus tshawytscha*). Fishery Bulletin 101:321B331.

Brown LR. 2003. will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary and Watershed Science 1: Article 2.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. Vol 5(2): Article 4.

7.31

(+) Filter-feeding fish to Piscivores

Importance: Moderate
Understanding: High
Predictability: Moderate

Piscivores are known to feed upon filter-feeding fish, based upon gut contents and co-occurrence data. Most piscivores behave opportunistically to food availability, so it is difficult to predict what food source they are using, except that they tend to follow prey items of high abundance.

(-) Piscivores to Filter-feeding Fish

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

Piscivory in Delta fishes is a function of density dependence of prey species. Piscivores tend to track abundance either because of Type III functional response (prey-switching) or because of increased probability of encounter with prey organisms at abuncdance. While predation may have some effect on prey abundance, it is likely that abiotic factors have greater control on filter-feeding fish populations in the Delta.

Brown LR. 2003. will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary and Watershed Science 1: Article 2.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. Vol 5(2): Article 4.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

7.41

(+) Demersal Fish to Piscivores

Importance: Moderate
Understanding: High
Predictability: Moderate

Piscivores are known to feed upon demersal fish, based upon gut contents and co-occurrence data. Most piscivores behave opportunistically to food availability, so it is difficult to predict what food source they are using, except that they tend to follow prey items of high abundance.

(-) Piscivores to Demersal Fish

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

Piscivory in Delta fishes is a function of density dependence of prey species. Piscivores tend to track abundance either because of Type III functional response (prey-switching) or because of increased probability of encounter with prey organisms at abuncdance. While predation may have some effect on prey abundance, it is likely that abiotic factors have greater control on demersal fish populations in the Delta.

Brown LR. 2003. will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary and Watershed Science 1: Article 2.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 5(2): Article 4.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

PREVIOUS VIEW

7.42
(+) Corbula/Corbicula to Demersal Fish
Importance: Moderate
Understanding: Moderate
Predictability: High

Corbula amurensis has been found in the guts of white sturgeon, suggesting that demersal fish are able to utilize these clams as a prey item.

(-) Demersal Fish to Corbula/Corbicula
Importance: Moderate
Understanding: Low
Predictability: High

Demersal fish may have some control over clam abundance. Other organisms, such as diving ducks, have been suggested as controlling agents of *C. amurensis* on shoals, but little research has been done to date on other sources of predation. Because of the life history attributes of *C. amurensis*—yearly spawning, planktonic larvae, and multi-year life span, it seems unlikely that fish or bird populations will be able to exert much control over *C. amurensis.*

Corbicula fluminea demonstrates a patchy abundance that has yet to be thoroughly explained, although it has shown to be food limited at times. It may be that predation upon the clam from piscivores (or diving birds) could be exerting control in certain areas, but this has yet to be demonstrated.

Foe C, Knight A. 1985. The effect of phytoplankton and suspended sediment on the growth of Corbicula fluminea (Bivalvia). Hydrobiologia 127:105-115.

Lopez CB, Cloern JE, Schraga TS, Little AJ, Lucas LV, Thompson JK, Burau JR. Ecological values of shallow-water habitats: Implications for the restoration of disturbed ecosystems. 2006. Ecosystems 9:422-440.

Peterson H. 1997. Clam-stuffed sturgeon. IEP Newsletter 10(1):21. Available at: http://www.iep.water.ca.gov/report/newsletter.

Poulton VK, Lovvorn JR, Takekawa JY. 2002. Clam density and scaup feeding behavior in San Pablo Bay, California. Condor 104:518-527.

7.51

(+) Macrocrustaceans to Piscivores

Importance: Moderate
Understanding: High
Predictability: Moderate

Macrocrustaceans have historically been quite important to piscivorous fish, and this is probably still true, although abundance of the native mysid has declined dramatically since 1986. Piscivorous fish may have responded to this decline by switching to an invasive amphipod, *Gammarus daiberi*, which have become abundant in the wake of mysid declines.

(-) Piscivores to Macrocrustaceans

Importance: Moderate
Understanding: Moderate
Predictability: Moderate

It is not known what impact piscivorous fish have on macrocrustaceans. While mysids are largely food limited by *Corbula amurensis*, other crustaceans have widely variable life histories. Because predation by fish tends to be opportunistic, it is difficult to know what impact they have on macroinvertebrates. Little research has been done on the impact on prey populations of fish predation in the Delta.

Brown LR. 2003. Will tidal wetland restoration enhance populations of native fishes? San Francisco Estuary and Watershed Science 1: Article 2.

Emmett RL, Stone SL, Hinton SA, Monaco ME. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries, Vol II. Species life history summaries. ELMR Report No. 8, National Oceanic and Atmospheric Administration/National Ocean Survey Strategic Environmental Assessments Division, Rockville, MD

Feyrer FV. 1999. Food habits of common Suisun Marsh fishes in the Sacramento-San Joaquin estuary, California. M.S. thesis, Calif. State Univ., Sacramento. 53 pp.

Ganssle D. 1966. Fishes and decapods of San Pablo and Suisun Bay. Pages 64-94 *in* DW Kelley, ed. Ecological studies of the Sacramento –San Joaquin Estuary. Part 1. California Department of Fish and Game Fish Bulletin 33:64-94

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer F, Baxter RD, Chotkowski M. 2005. Fish community ecology in an altered river delta: spatial patterns in species composition, life history strategies, and biomass. Estuaries 28:776-785.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California’s Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. Vol 5(2): Article 4.

Orsi JJ, Mecum WL. 1996. Food limitation as the probable cause of a long-term decline in the abundance of *Neomysis mercedis* the opossum shrimp in the Sacramento-San Joaquin estuary. *In* Hollibaugh JT, editor. San Francisco Bay: the ecosystem. San Francisco (CA): Pacific Division, American Association for the Advancement of Science. p 375-401.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

7.52
(+) Mesozooplankton: Acartiella to Piscivores
Importance: Low
Understanding: High
Predictability: Moderate

Acartiella is a large copepod that can be quite abundant during blooms in fresh water. As such, it is probably opportunistically exploited by piscivorous fish when abundant.

(-) Piscivores to Acartiella
Importance: Low
Understanding: Moderate
Predictability: Moderate

Acartiella is probably an omnivore, based on the functional morphology of its mouthparts. As such, is may be less severely limited than other copepod species by the competition with *Corbula amurensis.* If so, it may be more susceptible to control by predatory fishes.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. Vol 5(2): Article 4.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Soceity 114:12–30.

7.53

(+) Calanoid and Cyclopoid Copepods to Piscivores
Importance: Low
Understanding: High
Predictability: Moderate

Copepods may contribute to the diet of a number of piscivorous fish species, but it is difficult to predict to predict the relative contribution, since fish diets are largely opportunistic, and therefore a function of temperature, season, benthos, geography, and prey availability. Piscivorous fish are more likely to use copepods at earlier life stages and smaller sizes. As they get larger, they tend to switch to larger prey.

(-) Piscivores to Calanoid and Cyclopoid Copepods
Importance: Low
Understanding: High
Predictability: High

Demersal fish probably have some controlling influence on copepod populations, but their influence is greatly diminished due to the major impact of bivalve grazing.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science. Vol 5(2): Article 4.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.

7.54

(+) Cladocerans to Piscivores
Importance: Low
Understanding: High
Predictability: Moderate

Some piscivorous fish undoubtedly use cladocerans opportunistically or incidentally, but it is unlikely that they are an important source of food. Juvenile stages of piscivores may use cladocerans incidentally, but copepods are greatly more abundant in the Delta.

(-) Piscivores to Cladocerans
Importance: Low
Understanding: High
Predictability: High

Piscivorous fish are unlikely to have a consistently large impact on cladocerans, which are largely limited by grazing from benthic bivalves.

Moyle PB. 2002. Inland Fishes of California. University of California Press. Berkeley, Los Angeles, London.

Nobriga ML, Feyrer, F. 2007. Shallow-water piscivore-prey dynamics in California's Sacramento-San Joaquin Delta. San Francisco Estuary and Watershed Science 5(2): Article 4.

Stevens DE, Kohlhorst DW, Miller LW, Kelley DW. 1985. The decline of striped bass in the Sacramento-San Joaquin Estuary, California. Transactions of the American Fisheries Society 114:12–30.