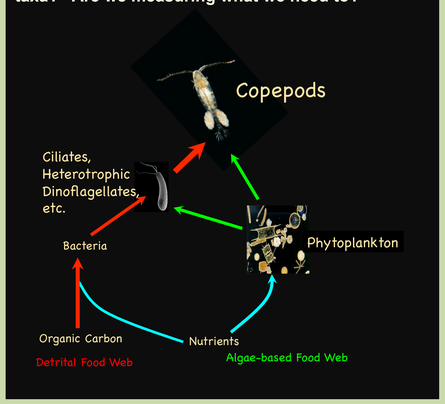
How well do we understand the reproductive consequences of copepod diet in the San Francisco Estuary? A survey of the direct evidence

Diana L. Engle, Larry Walker Associates, 2151 Alessandro Dr., Suite 100, Ventura, CA 93001, DianaE@lwa.com

1. Introduction

Purpose: What are the reproductive consequences of different diets for SFE copepod taxa? Are we measuring what we need to?



Context Over the last three decades, a shift in phytoplankton composition has been observed in the upper San Francisco Estuary (SFE) characterized by a decline in the relative abundance of diatoms, especially centric diatoms in the order *Thalassiosirales*, and an increase in other taxa including flagellates, green algae, and cyanobacteria. It is widely assumed that these changes signal a deterioration in the quality of food for estuarine copepods, and calanoid copepods in particular, that may have repercussions for organisms at higher trophic levels. Although it is frequently asserted that diatoms are an important direct food source for SFE copepods, local investigations using natural seston indicate that *motile* food sources (including heterotrophic ciliates and *non-diatom* phytoplankton) are the dominant prey for SFE copepods, including the calanoid species that are important prey for pelagic fish (Bouley & Kimmerer 2006, Gifford et al. 2007, Gould & Kimmerer 2010). Although local investigations have addressed prey choice, the reproductive consequences of consuming various prey spectra are less well understood. A literature survey was conducted to evaluate the extent to which reproductive outcomes are measured in feeding experiments using copepod taxa which are pertinent to the SFE (resident SFE species and their cofamilials).

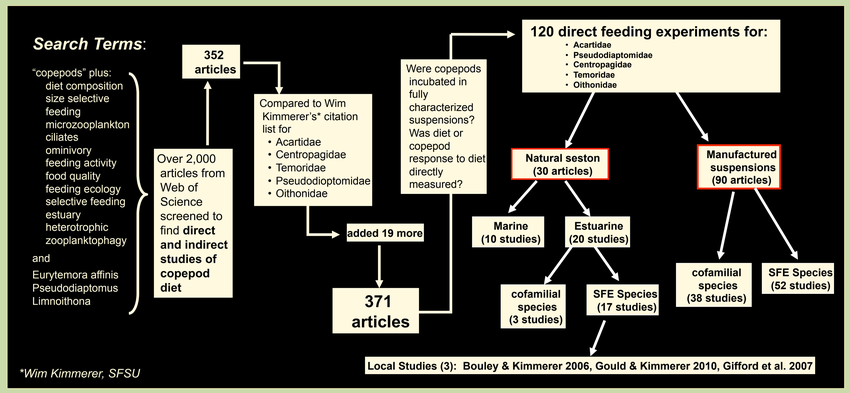
Methods The academic literature was surveyed for experiments in which copepod feeding behavior – and the consequences of feeding choices - were measured by incubating copepods in well-characterized suspensions of prey (direct feeding experiments). Literature was screened for studies using taxa in the principal SFE copepod families (*Acartidae, Pseudodiaptomidae, Centropagidae, Temoridae, and Oithonidae*). Experimental designs were evaluated to determine which taxa of copepods and prey were used and which types of measurements were made to characterize feeding behavior and the energetic or reproductive outcomes observed for copepods.

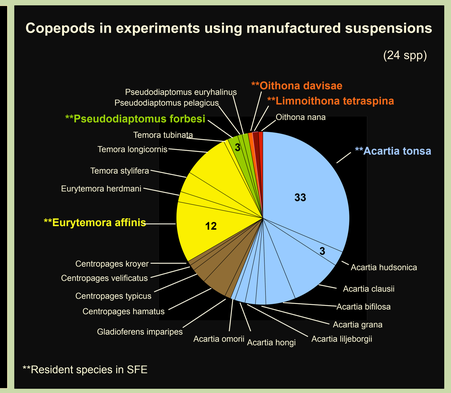
Taxonomy of principal SFE copepods:

- Calanoid
  - Acartidae (*Acartia tonsa, A. californiensis, A. hudsonica, A. sinensis*)
  - Centropagidae (*Sinocalanus doerrii*)
  - Pseudodiaptomidae (*Pseudodiaptomus forbesi*)
  - Temoridae (*Eurytemora affinis*)
- Cyclopoid — Oithonidae (*Oithona davisae, Limnoithona tetraspina*)

2. Results of Literature Search

The literature included over 370 studies of diet for species of copepods that are resident to the SFE or their cofamilials. 120 studies utilized direct feeding trials (in which taxon-specific ingestion rates, egg production, or other direct measurements of copepod diet and copepod response to diet, were made during incubations in well-characterized suspensions). 30 of the direct feeding trials utilized natural seston; 90 trials utilized manufactured suspensions of selected prey taxa. 24 species of copepods from SFE families were represented in studies using manufactured suspensions.





3. Selected Results for Experiments using Manufactured Suspensions of Prey

Although ciliates and dinoflagellates are important prey for SFE copepods, they have not been used in feeding experiments with several of the resident copepod species.

Number of experiments combining SFE copepods and prey types in artificial suspensions

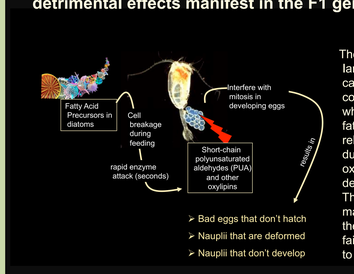
Prey Categories	SFE Copepod Species: *Acartia tonsa*	*Eurytemora affinis*	*Acartia hudsonica*	*Pseudodiaptomus spp.*	*Oithona davisae*	*Limnoithona tetraspina*
Ciliates	19					
Diatoms	25	2	2	1	2	1
Chlorophytes	5	6		2		
Cryptophytes	13	2	1	1		1
Cyanobacteria		3		2		
Dinoflagellates	22 (12*)				1	
Haptophytes	15	4	2	3		

* toxic red tide dinoflagellates

We rarely track consequences of diet through the next generation. Very few studies using SFE-pertinent copepod taxa have measured hatching success or naupliar development.

What is reported in feeding trials?		Number of exp. designs
feeding rates	prey-specific ingestion or clearance rates	39
	fecal pellet production	3
	ingestion of carbon	1
survival or reproduction	survival, mortality	11
	secondary production (population C, #/Liter)	2
	egg production rate (incl. egg efficiency)	19
	hatching success	9
	naupliar development (stage reached, stage duration)	3
efficiency indices	individual growth efficiency (C or N based)	3
	population growth efficiency	2
diet chemistry	fatty acid profiles	8
	diet C:N	5
	other (proteins, amino acids, carbohydrate)	4

Direct feeding on diatoms can cause reproductive failure in copepods. This effect is not measured in studies that rely on egg-counts to evaluate food quality because the detrimental effects manifest in the F1 generation.



The toxicity (reviewed in Ianora & Miralto 2010) is caused by organic compounds (oxylipins) which are produced from fatty acid precursors released from diatom cells during feeding. These oxylipins induce genetic defects in copepod eggs. The genetic defects are manifested by a failure of the eggs to hatch or a failure of hatched offspring to develop normally.

Reproductive outcomes of diatom grazing for SFE copepods or their co-familials

Copepod	Diatom	Egg Prod	Hatching Success	Normal Nauplii	Complete Develop.
Acartia tonsa	*Thalassiosira weissflogii*	-			-
	Thalassiosira pseudo nana	-			-
	Thalassiosira weissflogii	+	+		
	Chaetoceros affinis	-			
	Phaeodactylum tricornutum	-	-		
Acartia hudsonica	*Skeletonema costatum*	+			
Acartia clausi	*Thalassiosira rotula*	+	-		
Centropages typicus	*Thalassiosira rotula*	-			
Temora stylifera	*Thalassiosira rotula*			-	-
	Skeletonema costatum			-	-
	Phaeodactylum tricornutum			-	-
	Thalassiosira rotula	+	-		
	Thalassiosira weissflogii	+	-		
	Phaeodactylum tricornutum	-	-		
	Skeletonema costatum	-	-		
	Thalassiosira rotula	+	-		
Temora longicornis	*Thalassiosira rotula*				+
	Thalassiosira weissflogii				+
	Leptocylindricus danicus				+
	Skeletonema costatum				+
	Chaetoceros affinis				-
	Chaetoceros decipiens				-
	Chaetoceros socialis				-
	Thalassiosira rotula				-
	Thalassiosira pseudo nana				-
	Thalassiosira rotula	+	-		
	Thalassiosira weissflogii	+	-		
	Chaetoceros affinis	+	-		
	Leptocylindricus danicus	-	-		
	Skeletonema costatum	-	-		

negative result | positive result

Fatty acid composition of prey is rarely paired with measurements of reproductive success in feeding experiments. We don't really know whether fatty acid content affects reproductive success for SFE copepods.

Fatty Acid Content determined for:	Measure of reproductive success* Egg Prod	Hatching Success	F1 development
Diatom	3	1	
Green			
Cryptophyte	4	1	
Haptophyte	2		
Dinoflagellate	4	1	
Ciliate	2		

*All available studies for SFE-pertinent copepods used either A. tonsa or A. hudsonica.

Selectivity for diatoms (vs non-diatoms) has only been evaluated for SFE-pertinent copepod taxa in 10 studies. In half of those studies, the alternate non-diatom prey do not occur the SFE.

Diatoms presented one at a time…….. 13 studies

Diatoms presented in mixtures with non-diatoms……..10 studies

alternate non-diatom prey were:

toxic (red tide) dinoflagellates…….. 3 studies
haptophyte algae that don't occur in the upper SFE……3 studies
non-toxic dinoflagellates……..3 studies
ciliates*……..2 studies

not pertinent

*Strombidium, Balanion

4. Conclusions

- Parameters that measure reproductive success (e.g., hatching success and development of F1 generation) are rarely measured in copepod diet studies. The ultimate reproductive outcomes of different diets is essentially unknown for SFE copepod species.
- Artificial suspensions used in diet studies for most of the SFE copepod species have not included their primary heterotrophic and motile prey.
- Only one study involving an SFE-relevant copepod paired a chemical determination of food quality (e.g., fatty acid content) with a measurement of hatching success.
- Comparisons between feeding rates on diatoms and other taxa have rarely included non-diatom taxa that are pertinent to the SFE.
- In at least 17 experiments, diatoms had deleterious effects on reproductive success of copepods from pertinent families.
- Toxic effects of diatoms are unrecognized in lab or field studies from the SFE that rely on gut contents, clearance rates, or egg counts to determine the nutritional status of copepods, or to infer the nutritional value of suspended matter. This is because the detrimental effects of diatoms are manifested after egg laying.

5. Acknowledgements:

- Special thanks to Dr. Wim Kimmerer (Romburg Tiburon Center, San Francisco State University) for sharing his citation list for SFE copepod families.
- Funding was provided by Sacramento Regional County Sanitation District

6. References cited

- Bouley, P., and W.J. Kimmerer. 2006. Ecology of a highly abundant, introduced cyclopoid copepod in a temperate estuary. Mar. Ecol. Prog. Ser. 324: 219-228.
- Gould, A.L., and W.J. Kimmerer. 2010. Development, growth, and reproduction of the cyclopoid copepod *Limnoithona tetraspina* in the upper San Francisco Estuary. Mar. Ecol. Prog. Ser. 412: 163-177.
- Gifford, S.M., G. Rollwagen-Bollens, and S.M. Bollens. 2007. Mesozooplankton omnivory in the upper San Francisco Estuary. Mar. Ecol. Prog. Ser. 348: 33-46.
- Ianora, A., and A. Miralto. 2010. Toxigenic effects of diatoms on grazers, phytoplankton and other microbes: a review. Ecotoxicology 19: 493-511.