Overview of Artificial Cohort Method for Estimating Zooplankton Production in the Ocean

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Outline

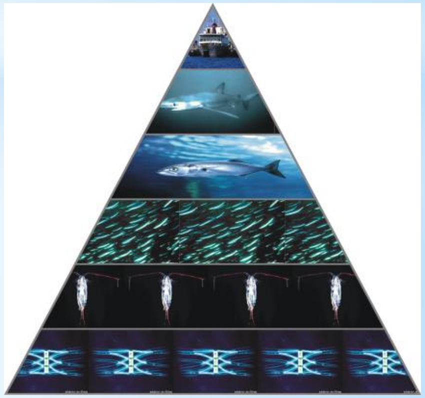
- Classical methods for measuring zooplankton production
- Artificial Cohort (AC) methods and Caveats
- Utility and practicality of AC methods
- Status of AC research in the USA

Zooplankton Production

- Limited spatial-temporal resolution of zooplankton production
- A bottleneck for estimating zooplankton production

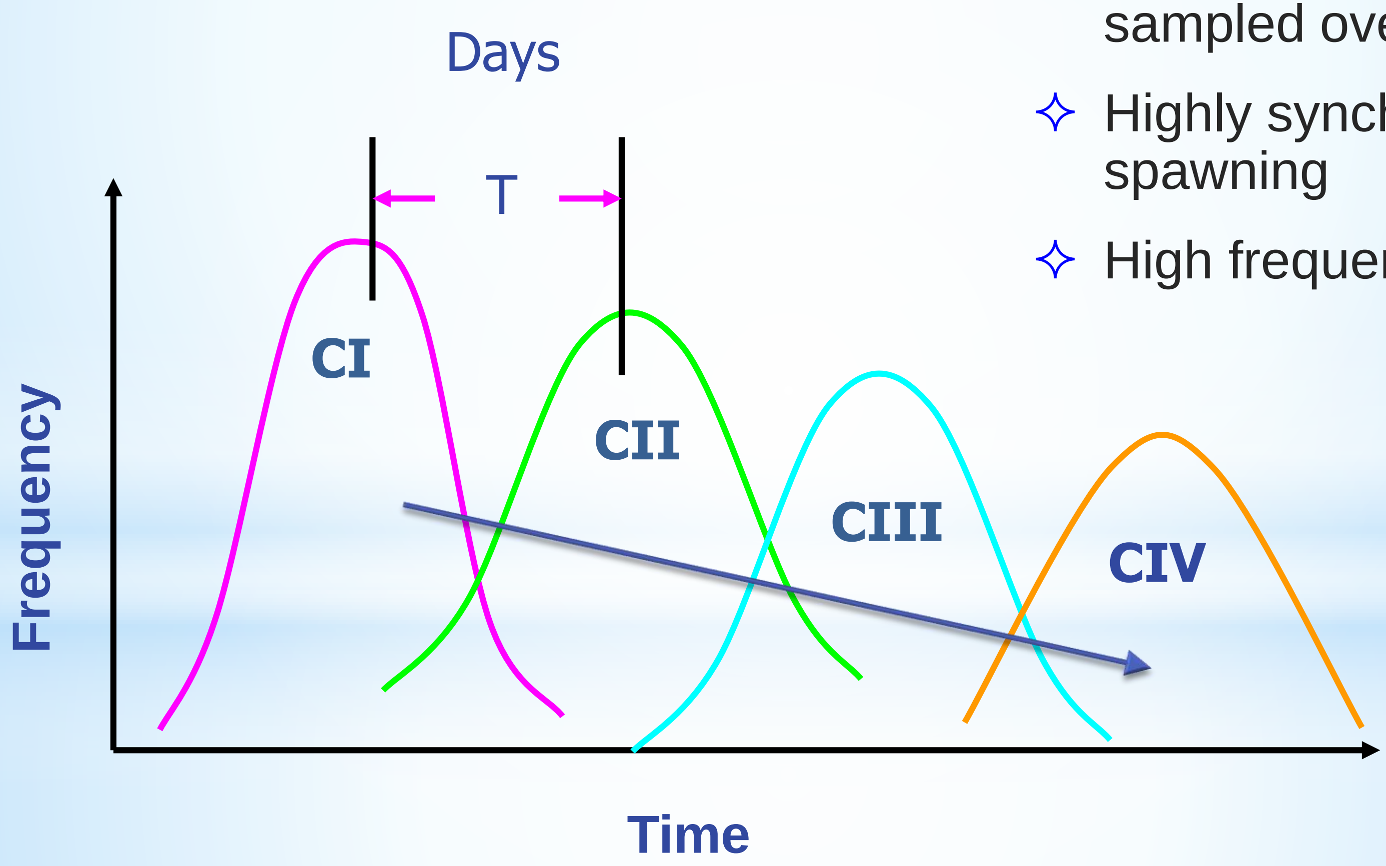
$$P_{2nd} = \sum_{i=1}^{n} G_i \times B_i$$

- Lack of consensus on practical methods for measuring zooplankton growth (Hirst et al. 2005, Kimmerer et al. 2007, Liu et al. 2013)



Methodological Challenge

Natural cohort method

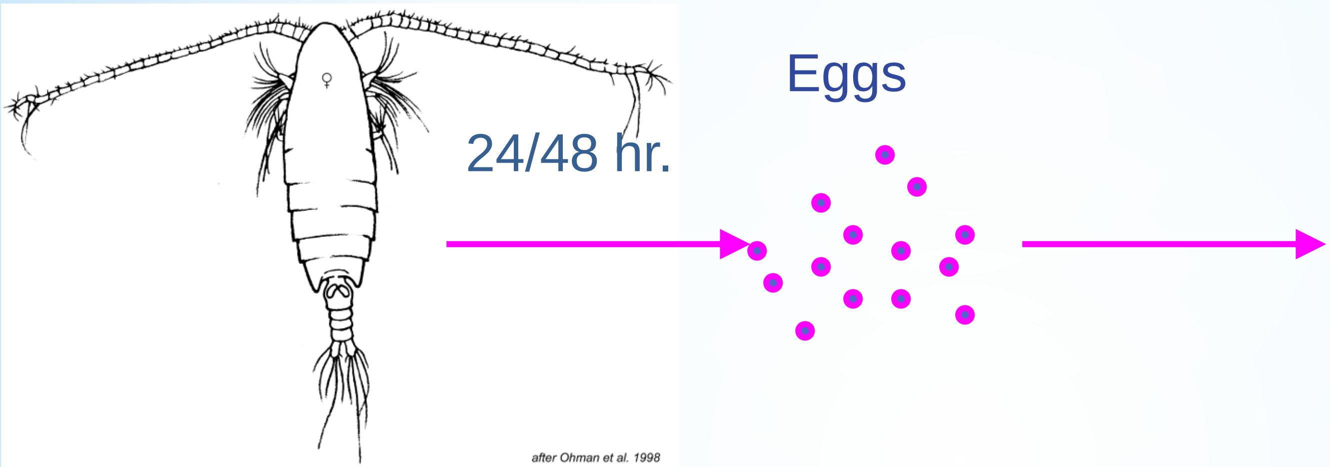


Assumptions:

- Same population to be sampled over time
- Highly synchronized spawning
- High frequency sampling

Egg production rate

Female



Specific Egg Production (SEP) (% of female weight produced as eggs per day)

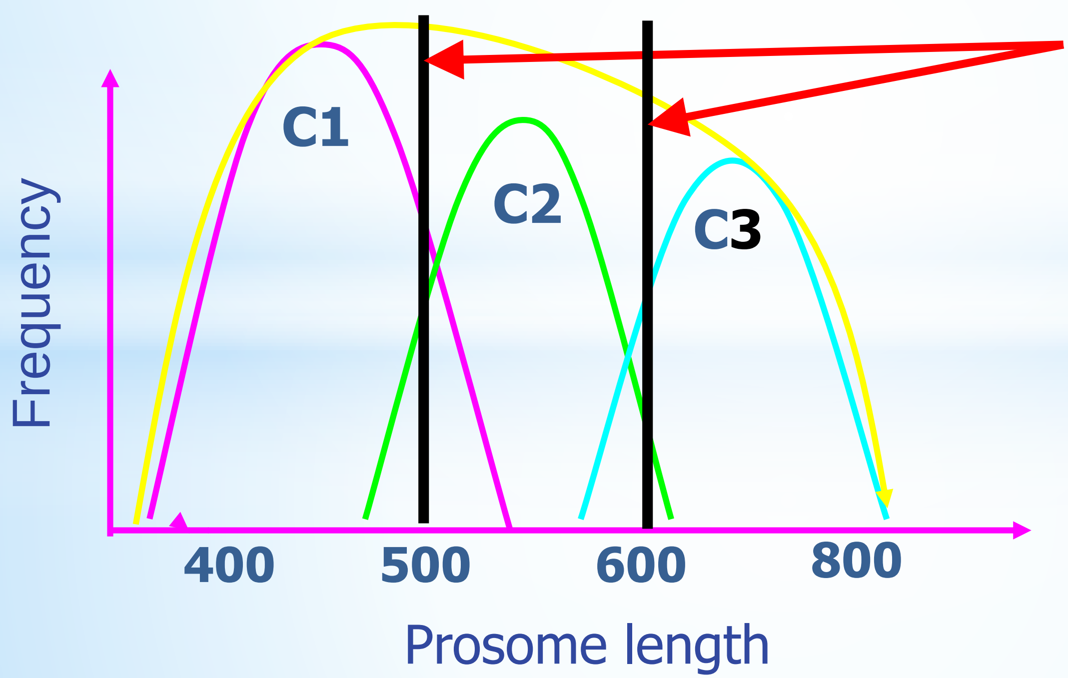
Courtesy of Ohman et al. 1998

Assumptions

- SEP not influenced by incubation
- Somatic growth of all preceding stages is equivalent to female SEP
- Female remains in steady-state

Artificial Cohort Method (Kimmerer & McKinnon 1987)

- uses sieves of varying mesh sizes to separate the copepod community into different size classes (size-fractioned cohorts)
- also can be done by manually picking specific stages (cleaned and sorted cohorts)



Screens restrict sizes/stages into 3 classes more easily followed over time

Caveats of AC methods

Assumptions

- Close coupling between moulting and growth (Hart 1990, Peterson et al. 1991)
- Handing does not stimulate moulting, “moulting burst” (Miller et al. 1991)

Limitations

- No control over number and kinds of species
- Differential growth among stages and species
- Different developmental stage isolated for different species. Incubation times to be appropriate for species and stages of interest

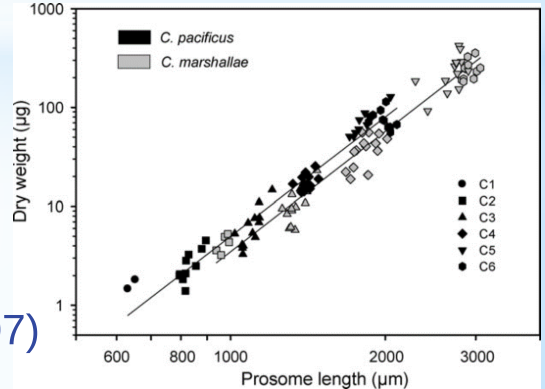
Methodological considerations of AC

- Age structure within stages

Ideally uniform age structure within stages assumed (Hirst et al. 2005). In practice growth often labeled by stage, not age

- Biomass increment of growth

Direct measurement of biomass (Kimmerer et al. 2007), or using a length-weight relationship (Liu & Hopcroft 2006a&b,&07&08)



Liu & Hopcroft (2007)

Applications of AC

Table 1. Applications of the Kimmerer & McKinnon (1987) artificial cohort method. Temp.: ambient mean temperature or range; MR: experiments that measured molting rates alone and not growth; C: copepodite stages; N: naupliar stages

Location Species	Temp. (°C)	Weight method	Growth rate (d^{-1})	Incubation period (h)	Source
Australia					
Acartia fancetti	11–22	Mean weight of stage	0.025–0.26	26–50	Kimmerer & McKinnon (1987)
Skagerrak					
Centropages typicus	16–17	Length–weight regression	0.24–0.77	24	Peterson et al. (1991)
Temora longicornis			0.15–0.56		
Paracalanus parvus			0.16–0.48		
Pseudocalanus spp.			0.12–0.35		
Calanus finmarchicus			0.01–0.14		
Acartia longiremis			0.15–0.24		
Norway					
Temora longicornis	18	Length–weight regression	0.00–0.32	1 sample $(24\ h)^{-1}$	Hernández-León et al. (1995)
Canary Islands					
Oncaea sp.	29				
Jamaica					
Oikopleura dioica		Length–weight regression	1.38–3.12	120	Hopcroft & Roff (1995)
Parvocalanus crassirostris			0.24–0.79	1 sample $(24\ h)^{-1}$	
Jamaica					
Acartia spp.	28	Length–weight regression	0.25–1.43	120	Hopcroft et al. (1998b)
Centropages velificatus			0.70–1.00	1 sample $(24\ h)^{-1}$	Hopcroft & Roff (1998b,c)
Paracalanus aculeatus			0.25–1.26		
Parvocalanus crassirostris			0.44–1.08		
Temora turbinata			0.34–1.23		
Corycaeus spp.			0.10–0.36		
Oithona nana			0.40–0.91		
Oithona simplex			0.17–0.53		
France					
Acartia bifilosa		Length–weight regression	0.03–0.14	72	Irigoien & Castel (1995)
Agulhas Bank					
Calanus agulhensis	17–18	Length–weight regression	0.19–0.46	24	Peterson & Hutchings (1995)
North Sea					
Temora longicornis	6–16	–	MR	24	Klein Breteler et al. (1998)
Pseudocalanus elongatus			MR		
Plymouth					
Calanus helgolandicus	15	–	MR	48	Shreeve et al. (1998)
Alboran Sea					
Centropages typicus	17	Volume–weight relationship	<0.01–0.27	24–26	Calbet et al. (2000)
Georges Bank					
Calanus finmarchicus		Volume–weight relationship	C: –0.09 to 0.31 N: –0.07 to 0.20	48	Campbell et al. (2001a)
Indian Ocean					
Mixed calanoid guild	21–31	Volume–weight relationship	C: 0.38 N: 0.43	48 24	McKinnon & Duggan (2003)
Mixed cyclopoid guild			C: 0.28 N: 0.38	48 24	
Great Barrier Reef					
Mixed calanoid guild	22–30	Volume–weight relationship	C: 0.12–0.53	48 (2 expts sampled also after 24 h)	McKinnon et al. (2005)
Mixed cyclopoid guild			C: 0.16–0.48		
Gulf of Alaska					
Neocalanus flemingeri/ plumchrus	5–9	Length–weight regression	0.01–0.28	120	Liu & Hopcroft (2006a)
Gulf of Alaska					
Metridia pacifica	5–14	length–weight regression	0.01–0.28	96 or 120	Liu & Hopcroft (2006b)
Gulf of Alaska					
Calanus marshallae, C. pacificus	5–14	Length–weight regression	0.03–0.30	96 or 120	H. Liu & R. R. Hopcroft (unpubl.)

By 2008,

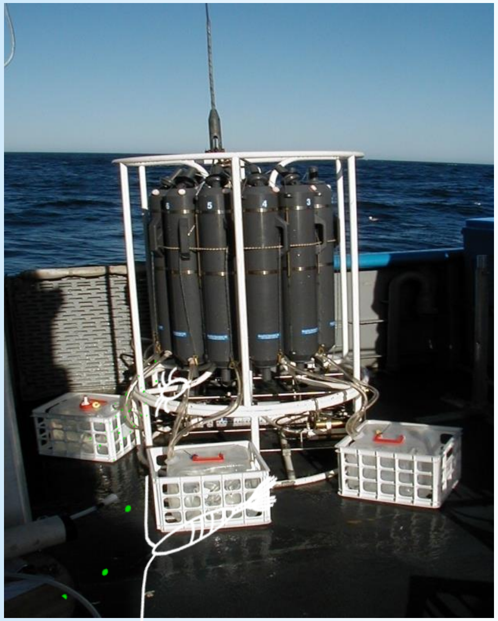
18 studies,

14 regions,

31 species and 4 copepod guilds

Kimmerer et al. (2007)

Deployment of the AC experiments



Size-fractionated vs. manually picked cohorts

Comparison of Two Methods

Single-Stage Method
Pros:
1: known development stages for given species
2: exact stage-specific growth data available
Cons:
1: apt for few large species
2: labor intensive and requires suitable working condition at sea

Screen-Filter Method
Pros:
1: routinely deployed at sea
2: simultaneously applicable to whole copepod community
Cons:
1: mixed development stages
2: exact stage-specific growth data unavailable

Stage Error in Screen-Filter Data
Forcing numerical values calculated from mixed stages to represent the single stage to facilitate comparison to the single-stage method

Liu et al. (2013)

Photos Courtesy of Russ Hopcroft

Size-fractionated vs. manually picked cohorts

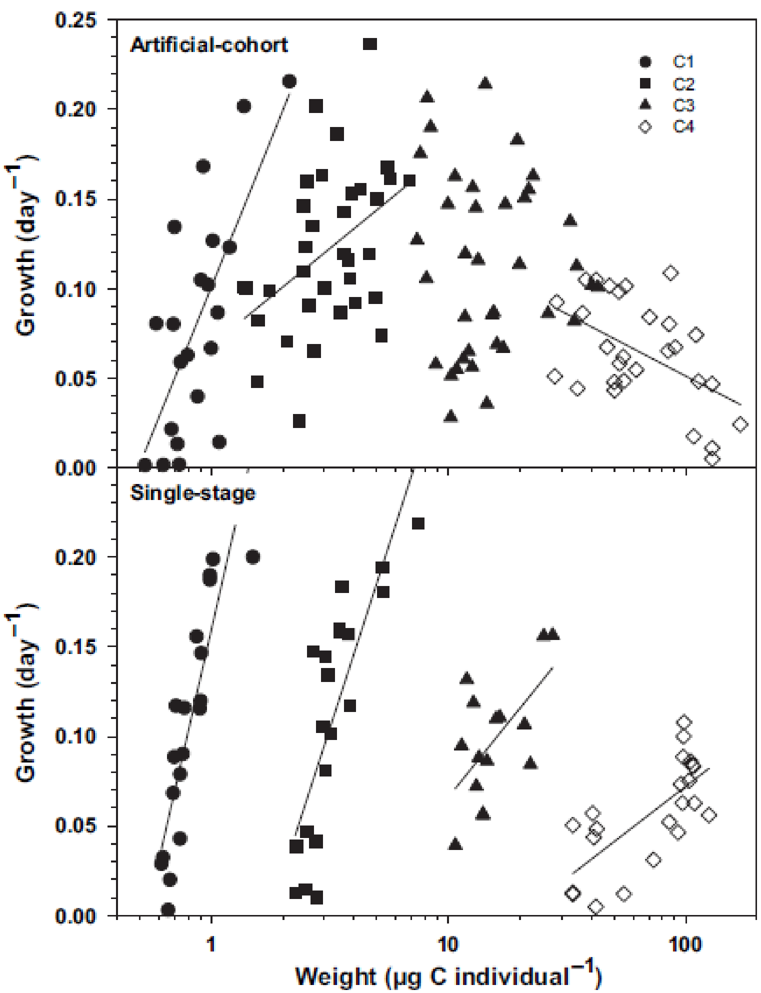
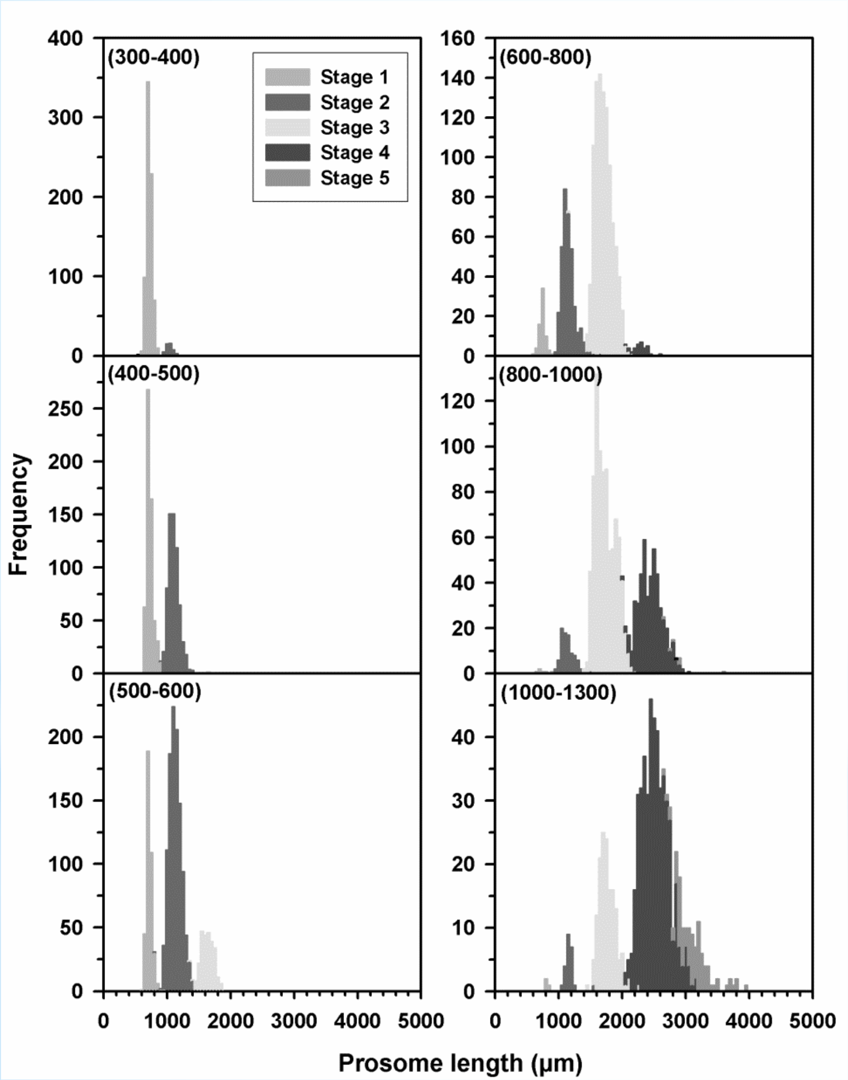


Fig. 6. Relationship between growth rate of *Neocalanus flemingeri/plumchrus* and the body weight (µg C individual^{-1}) within early copepodite stages estimated by artificial-cohort and single-stage methods in the northern Gulf of Alaska.

Liu & Hopcroft (2006)

Mixed stages in size-fractionated cohorts



$$\overline{C} = \sum_{i=1}^{5} (fc)_i / N$$

C: stage (1,2,3,4,5)

f: stage frequency

N: total observations of target species at each mesh size

Liu et al. (2013)

Quantifying the stage error in size-based cohorts

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Statistical modeling of copepod growth rates: Comparisons for data collections using the artificial cohort (AC) method

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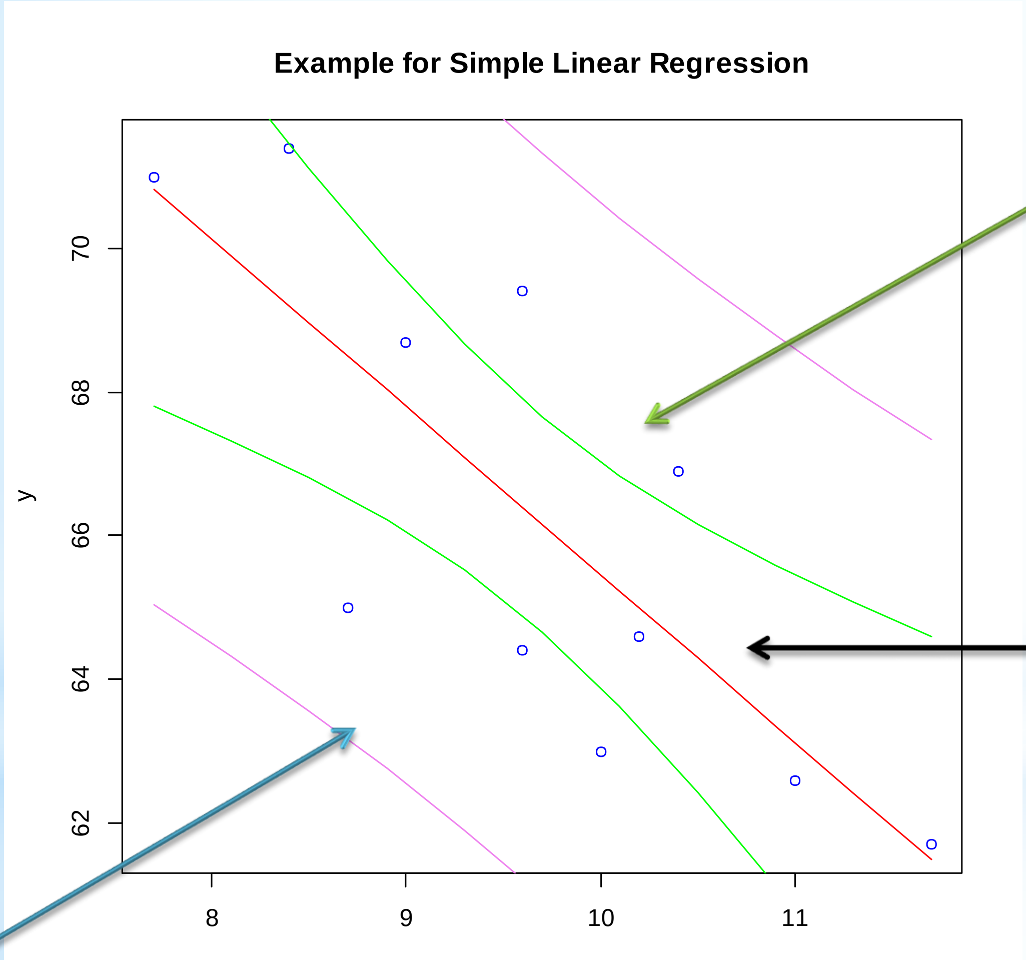
$S_i(\cdot)$: univariate smoothing function for $i = 1,2$ ε_i ~ iid $N(0, \sigma^2)$		
Model 2 $Y_i = \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + \beta_4 X_{i4} + \beta_5 \log_{10}(X_{i5}) + \beta_6 X_{i6}/(X_{i6} + \beta_7) + \varepsilon_i$ The X_{ij} is the same as in Model 1 ($j = 1,\ldots,6$), and, as before, the ε_i ~ iid $N(0, \sigma^2)$	1. Nonlinear Model 2. Parametric approach 3. Prediction	Same as Model 1
Model 3 Y_i ~ normal (μ, σ^2) $\mu_i = (\beta_1 + \Delta_1 \times \text{ind})X_{i1} + (\beta_2 + \Delta_2 \times \text{ind})X_{i2} + (\beta_3 + \Delta_3 \times \text{ind})X_{i3} + (\beta_4 + \Delta_4 \times \text{ind})X_{i4} + \beta_5 \log_{10}(X_{i5}) + \beta_6 X_{i6}/(X_{i6} + \beta_7)$ The X_{ij} is the same as Model 1 ($j = 1,\ldots,6$) Δ_i ($i = 1,2,3,4$) the stage errors for stage 1 to stage 4	1. Bayesian model 2. Parameters considered as random variables 3. Posterior estimation for parameters based on data available	Modeling growth rates and discerning the stage errors in the screen-filter data

- Stage errors estimated not significantly different from zero
- The stages labeled with the practical technique in the screen-filter method not statistically different from that identified by manually picking

Uncertainty for using the L-W equations



$$a+bx^* \pm t_{n-2,\alpha}\sqrt{S^2_{a+bx^*}}$$

$$S_{a+\beta x^*} = S_e\sqrt{\frac{1}{n}+\frac{(x^*-\bar{x})^2}{S_{xx}}}$$

$$\hat{y} = a+bx$$

$$a+bx^* \pm t_{n-2,\alpha}\sqrt{S^2_e + S^2_{a+bx^*}}$$

Inferences of a prediction value a+ βx* using the L-W equations

- The estimated standard deviation of the statistic a+ βx* is

$$S_{a+\beta x^*} = S_e\sqrt{\frac{1}{n} + \frac{(x^* - \overline{x})^2}{S_{xx}}}$$

- When the assumptions are met, the probability distribution of is t-distribution with df=(n-2)

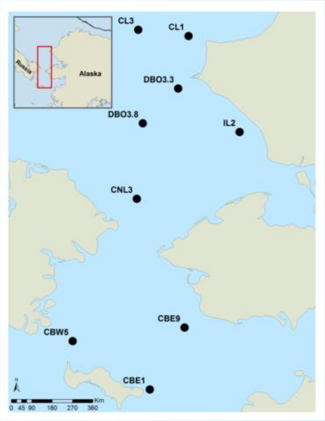
$$t = \frac{a + bx^* - (\alpha + \beta x^*)}{S_{a+\beta x^*}}$$

- Confidence interval for a+ βx* has form:

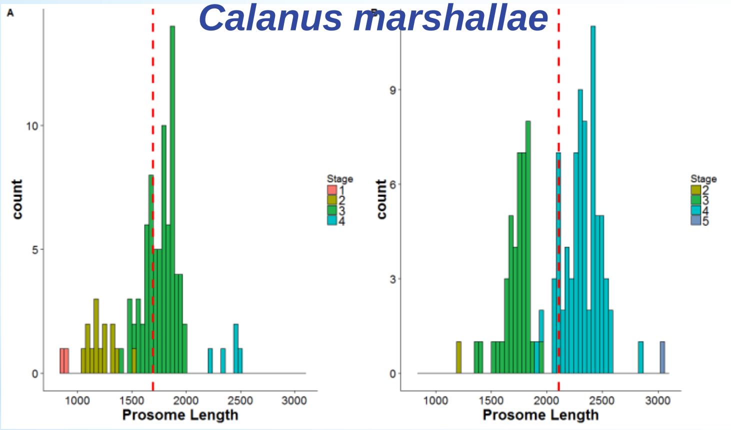
$$a + bx^* \pm t_{n-2,\alpha} S_{a+bx^*}$$

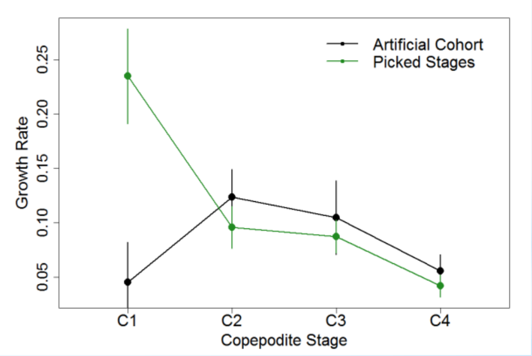
Current AC research in the USA

- Field AC work ongoing in the Bering Sea and Chukchi Sea on *Calanus marshallae* and *Pseudocalanus spp*. (Hopcroft)



Calanus marshallae





- Modeling research on AC (Liu)
- Others

Recap

- Size-based AC method is mostly practical for measuring growth rates of zooplankton with caveats
- Sized-based method can be a substitute of the manually picked methods for measuring stage-specific growth rates
- A potential way to tackle the uncertainty using L-W relationship for measuring biomass
- Methods of theoretically perfect and practically operational

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Thank You