Reality and the estimation of mortality for copepod eggs

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The star of the show, *Calanus finmarchicus*, egg producer (and egg eater?) “extraordinaire”.

In situ egg mortality estimated using three “vertical” methods from the literature (Gentleman et al. in prep.)

Method 1 The basic method

$$\frac{N_{egg}}{(EPR.N_{fem})} = \frac{(1 - \exp(-M_{egg}.D_{egg}))}{M_{egg}}$$

- solved iteratively.

Method 2 The ratio (VLT) method

$$\frac{N_{egg}}{N_{N1}} = \frac{(\exp(M_{eN1}.D_{egg})-1)}{(1-\exp(-M_{eN1}.D_{N1}))}$$

- solved iteratively.

Method 3 The alternative method

$$M_{egg} = \frac{(EPR.N_{fem})}{N_{egg}} - \frac{1}{D_{egg}}$$

- solved directly.

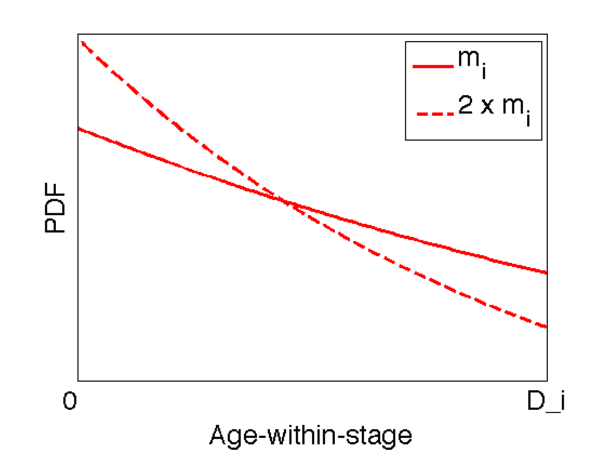
(N_{egg} = Abundance of eggs (eggs m^{-2}), N_{fem} = Abundance of females (f m^{-2}), EPR = Average egg production rate (eggs f^{-1} d^{-1}), D_{egg} = Development time for eggs (d), D_{N1} = Development time for N1 nauplii (d), M_{egg} = Egg mortality (d^{-1}), M_{eN1} = Average mortality for the egg/N1 stage pair(d^{-1}))

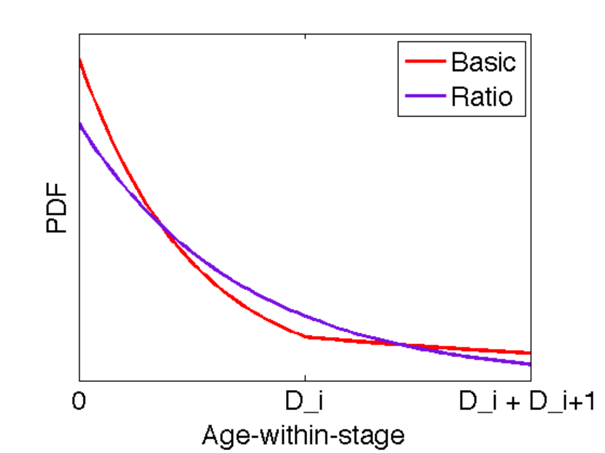
Age-within-stage distributions for eggs (and N1 nauplii) for the three methods of calculating egg (or egg/N1) mortality

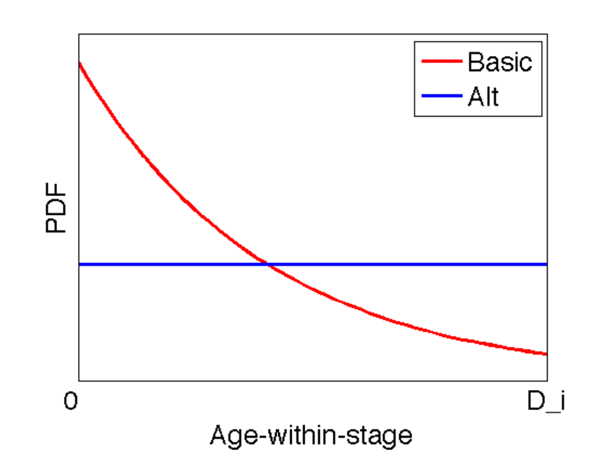
Method 1 (Basic method)
Eggs "die" during development to N1.

Method 2 (Ratio method)
Eggs "die" during development to N1 and N1s "die", at the same rate, during development to N2.

Method 3 (Alternative method)
There is a uniform age-within-stage distribution for eggs.







In theory Method 1 should provide the "best" estimate of egg mortality because –

- Method 2 gives an average value for the mortality of egg/N1 pair.
- Method 3 assumes that mortality occurs during transition to N1.

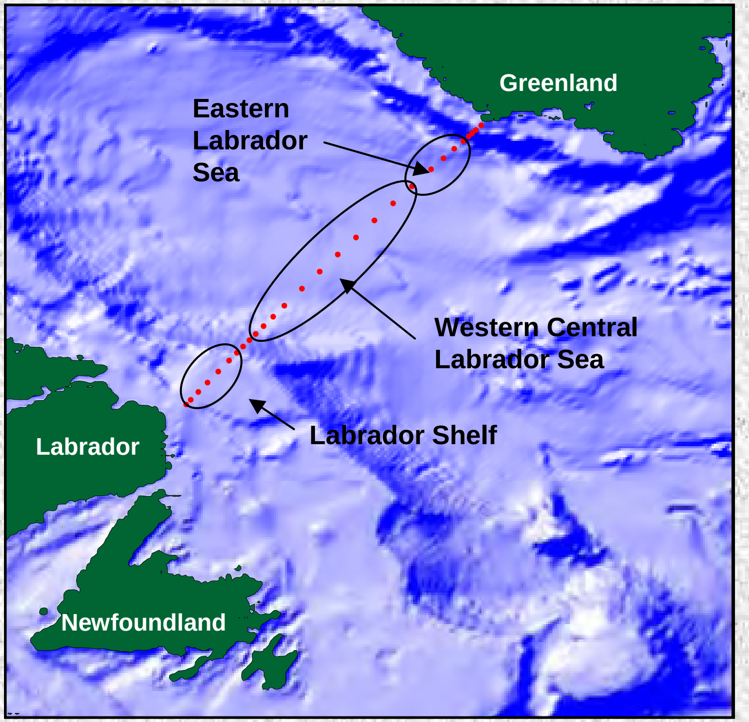
BUT all methods involve a series of assumptions. In the real world does Method 1 give the "best" results?

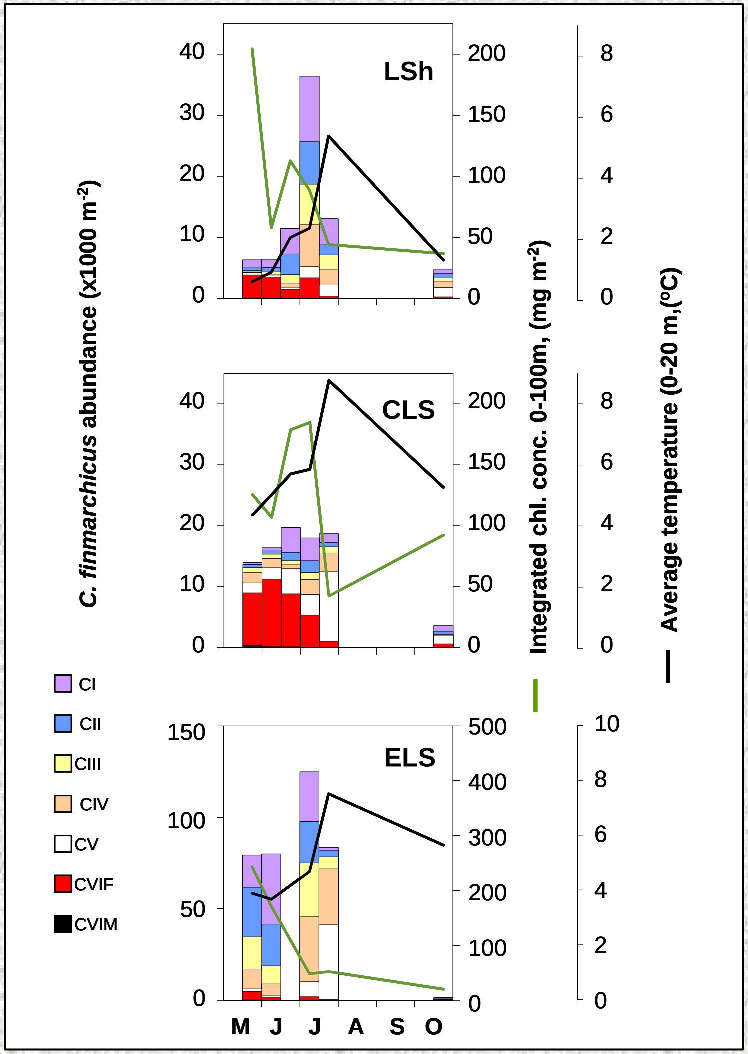
Study area and *Calanus finmarchicus* stage/abundance distributions

There are annual DFO cruises in the Labrador Sea, usually in late May (since 1995).

Calanus finmarchicus is the most abundant large copepod.

In late May females dominate *C. finmarchicus* populations on the Labrador Shelf (LSh) and in the western Central Labrador Sea (CLS); young stages dominate in the Eastern Labrador Sea (ELS).





The data

N_{fem} measured with 202 μm mesh nets at all stations in all years (> 300 stations).
(needed for **Method 1** and **Method 3**)

N_{egg} measured with 76 μm mesh nets at 82 stations since 2002.
(needed for **Method 1** and **Method 3**)

N_{N1} measured with 76 μm mesh nets at 18 stations in 2010.
(needed for **Method 2)**

EPRs were measured at 95 stations (1997-2010). BUT all three (**EPRs**, **N_{egg}** and **N_{fem}**) were measured at only 35 stations. In order to include all 82 stations, EPR was estimated, from an Ivlev function with chlorophyll concentration.
(needed for **Method 1** and **Method 3**)

D_{egg} and **D_{N1}** were estimated based on Campbell et al. 2001 using 5 m temperatures.
(needed for **Method 1**, **Method 2** and **Method 3**)

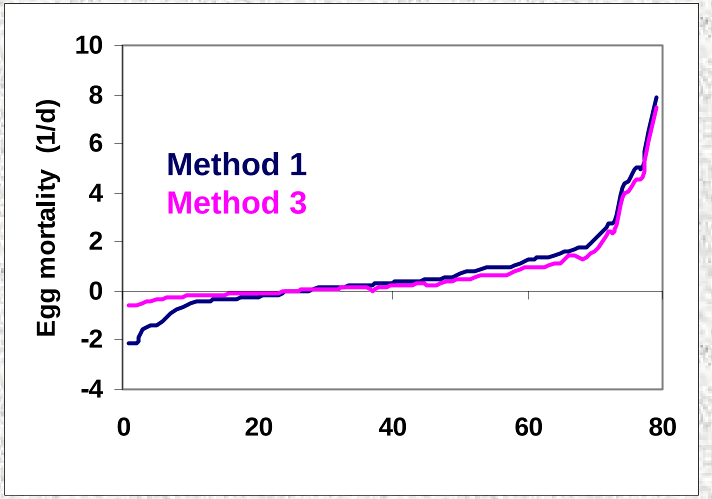
Profiles of **T** and chlorophyll concentration were collected at all stations.
(both needed for **Method 1** and **Method 3**, **T** needed for **Method 2**)

Results of calculations of M_{egg} using Method 1 and Method 3 for the 82 stations where N_{egg} and N_{fem} were measured, and D_{egg} and EPR were calculated

M_{egg} should always be between 0 and ~3 d^{-1}, but was frequently outside this range.

	M < 0	0 < M < 3	M > 3
Method 1	24	49	8
Method 3	24	49	8

Both methods gave the same number of values within and outside the "acceptable" range.



The magnitude of M_{egg} was higher with Method 1 than with Method 3, regardless of the sign.

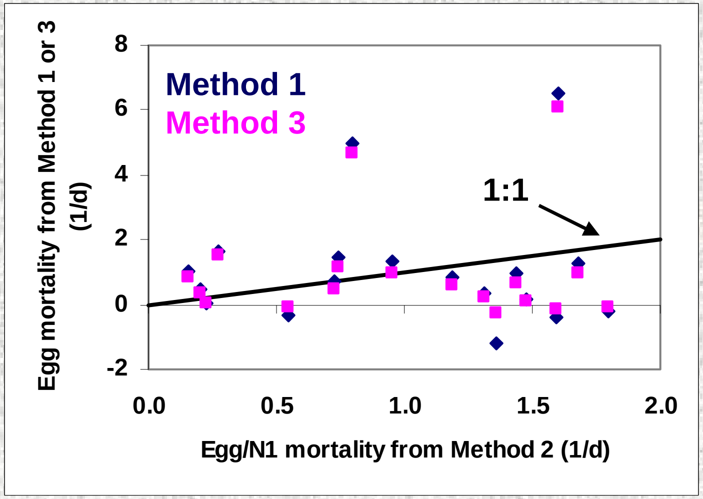
Note that two outliers with M_{egg} values of 21 and 257 d^{-1} were omitted from the lower graph.

Results of calculations of M_{egg} or M_{eN1} for the 18 stations occupied in 2010, where N_{egg}, N_{N1} and N_{fem} were measured and D_{egg}, D_{N1} and EPR were calculated

	M < 0	0 < M < 3	M > 3
Method 1	**4**	**12**	**2**
Method 2	**0**	**18**	**0**
Method 3	**4**	**12**	**2**

Method 2 gave no negative values and all values were <3 d^{-1}, i.e. 100% of values were within the acceptable range.

Method 1 and **Method 3** gave similar results with 67% of values in the 0-3 d^{-1} range.



Method 1 and **Method 3** should give higher values than **Method 2**, since **Method 2** gives the average value for the Egg/N1 stage pair, and egg mortality is likely higher than N1 mortality.

In fact, however, **Method 2** gave higher values in 11 out of 18 cases.

So – it looks as if **Method 2** may give the “best” results.

What could lead to errors in the estimation of M_{egg} or M_{eN1}**?**

Problems with:

1. values of EPRs calculated using the empirically obtained Ivlev equation parameters? (**Method 1** and **Method 3**)

2. estimates of relative abundances of eggs, N1 nauplii and/or females? (**Method 1** and **Method 3** use two net tows; **Method 2** uses one tow)

3. values of D_{egg} or D_{N1} from the Campbell et al. equations? - (All methods)

4. the steady state assumption? - (All methods)

5. eggs not hatching? - (All methods)

6. eggs sinking out? – (All methods)

7. advection? - (All methods)

Potential errors in estimating female egg production rates (EPRs)

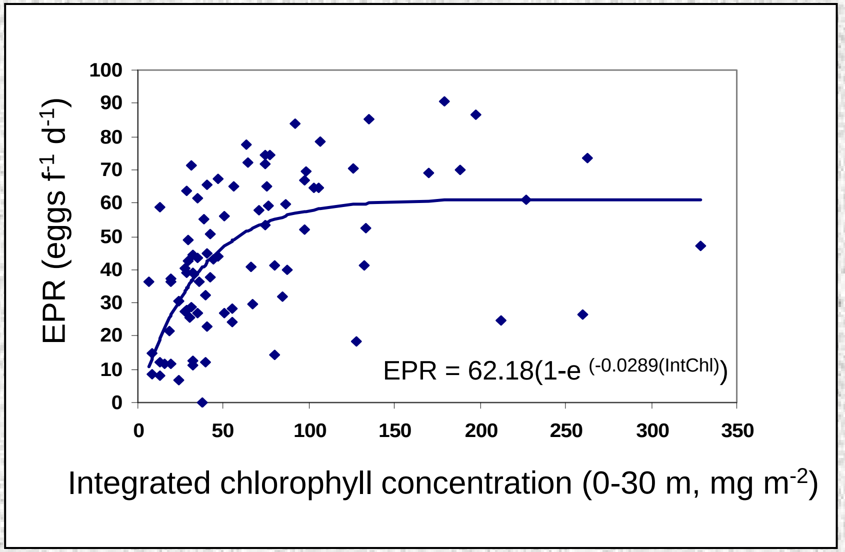
Method 1 and **Method 3** include the term

$$\frac{N_{egg}}{(EPR.N_{fem})}$$

This ratio could be in error if the equation used to calculate EPRs was not always valid.

EPRs are strongly dependent on food concentration, but
- female size
- female age
- food composition
- temperature

probably have some influence.



M_{egg} values were re-calculated using **Method 3** for stations where EPRs were actually measured.

Better? - No!

Method 3	M < 0	0 < M < 3	M > 3
Modelled EPRs (No. of stns)	24	49	6
Modelled EPRs (% of stns)	30	62	8
Measured EPRs (No. of stns)	13	20	2
Measured EPRs (% of stns)	37	57	6

The two outliers (M_{egg} >20 d^{-1}) were omitted.

Potential errors in estimating abundances of N_{fem} and N_{egg}

Method 1 and **Method 3** both include the term $\frac{N_{egg}}{(EPR.N_{fem})}$

Values of this ratio could be in error if estimates of N_{egg} or N_{fem} were incorrect.

"Impossible" and "unlikely" M_{egg} values were re-calculated using **Method 3**, changing the N_{fem}/N_{egg} ratio.

Method 3	M < 0	0 < M < 3	M > 3
Nf/Ne - no change	24	49	6
Nf/Ne - x 2 or x 0.5	13	65	1
Nf/Ne - x 2 or 5 and x 0.5 or 0.2	5	74	0

The two outliers (M_{egg} >20 d^{-1}) were omitted

1st line - original calculations

2nd line - N_{fem}/N_{egg} ratios were increased or decreased by a factor of 2 for stations where the original calculations gave values for M_{egg} of <0 or >3, respectively

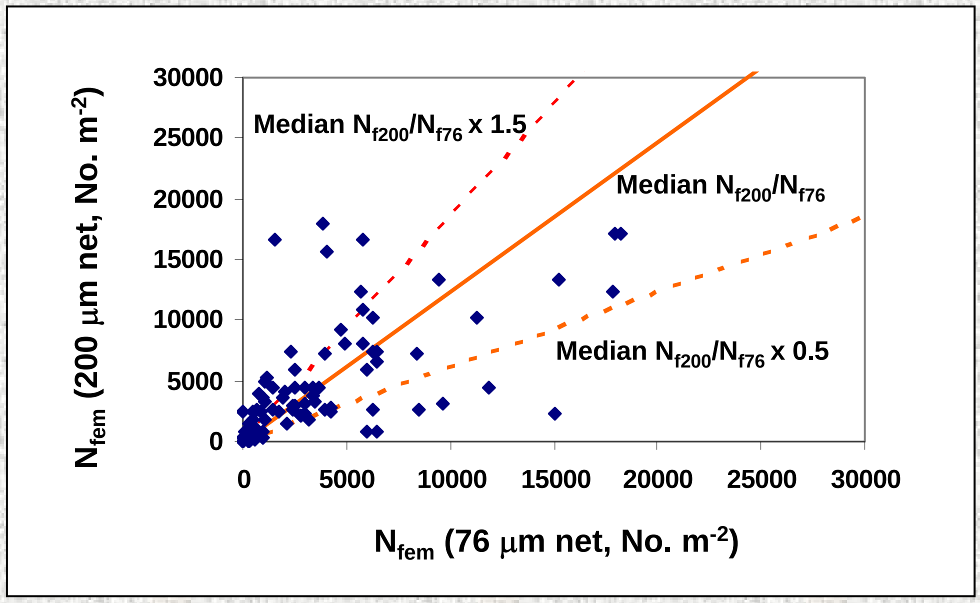
3rd line - for stations where 2nd line values of M_{egg} were still <0 or >3, N_{fem}/N_{egg} original ratios were increased or decreased by a factor of 5, respectively

Better? - Maybe!

Potential errors in Methods 1 and 3 – Why should N_{egg}/N_{fem} ratios be wrong?

- differences in capture efficiencies by different nets (202 *versus* 76 μm)
- patchiness in plankton distributions

Females abundances in the 200 μm nets are generally higher than those in the 76 μm nets.



Large differences from the median ratio might indicate "problems".

M_{egg} was re-calculated, using **Method 3**, for stations where N_{fem200}/N_{fem76} fell between the dashed lines.

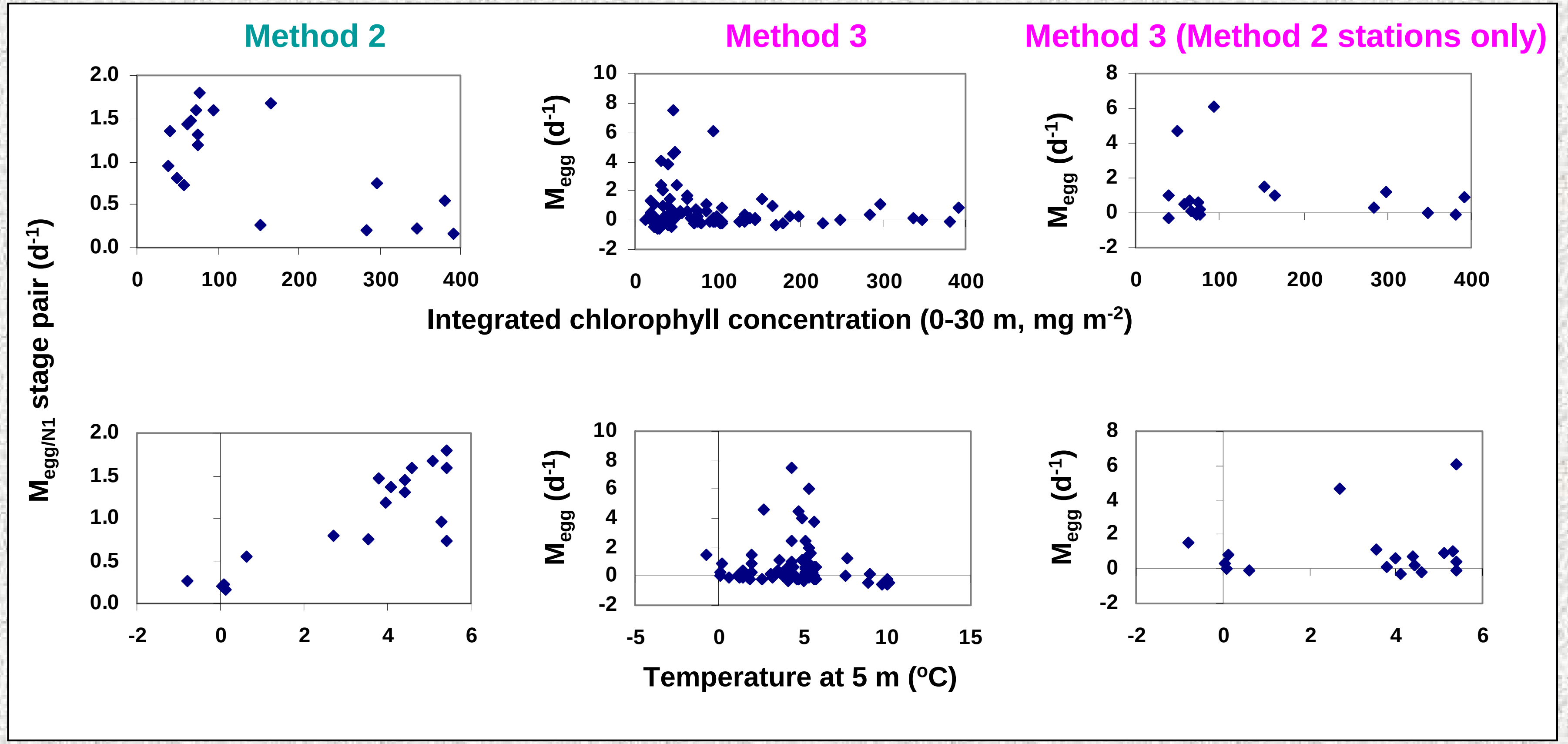
Method 3	M < 0	0 < M < 3	M > 3
All stations (No. stns)	24	49	6
All stations (% stns)	30	62	8
Stns where Nfs are "good" (No.)	12	24	2
Stns where Nfs are "good" (%)	32	63	5

The two outliers (M_{egg} = >20 d^{-1}) were omitted.

Better? - No!

Further support for Method 2? - Relationships between M_{egg}, or the $M_{egg/N1}$ average, and environmental variables

Method 2 gave values that varied systematically with food and temperature; **Method 3** did not. Does this mean **Method 2** gives "better" results?



Other potential sources of error in estimating egg mortality – applicable to all methods

Uncertainty in D_{egg} or D_{N1}? – Probably not important

Environment (T, food, N_{fem}) not constant??? – Probably not important for T or food

N_{egg} not in steady state??? – M too high (if N_{egg} is increasing) or M too low (if N_{egg} is decreasing)

Eggs not hatching? – M too low

Eggs sinking? – M too high, but probably not important

Advection ??? - M too high or too low, depending on upstream sources and flow rates for females, eggs and N1s

Summary

Method 1 and **Method 3**

- gave similar results, but **Method 3** is easier to use. Both gave large proportions of values that are theoretically impossible (M_{egg} <0 d^{-1}) or unlikely (M_{egg}>3 d^{-1}).

- use abundance data from different nets.

- use EPR values, which are highly variable.

- can give realistic mortality estimates if the ratio of $N_{egg}/(EPR.N_{fem})$ is adjusted.

- did not give better results when the dataset was restricted to reduce identifiable sources of error.

- do not appear to give reliable mortality estimates.

Method 2

- gave realistic (0< M <3 d^{-1}) mortality estimates for the egg/N1 stage pair at all stations.

- gave mortality estimates that varied systematically with environmental variables.

- uses abundances of eggs and N1s from the same net haul.

- probably underestimates egg mortality, since it gives average values for egg/N1.