A comparison of four techniques for stage-specific mortality rates of copepods

Hongsheng Bi[1], Mark Benfield[2],
Kenneth Rose[2], Bill Peterson[3]
[1]Oregon State University, Newport, OR 97365
[2]Louisiana State University, Baton Rouge, LA 70803
[3]NOAA Fisheries, Newport, OR 97365

"There were two bears yesterday and there are three bears today. Does this mean that one bear has been born or that 101 bears have been born and 100 have died?"

Wood (1994)

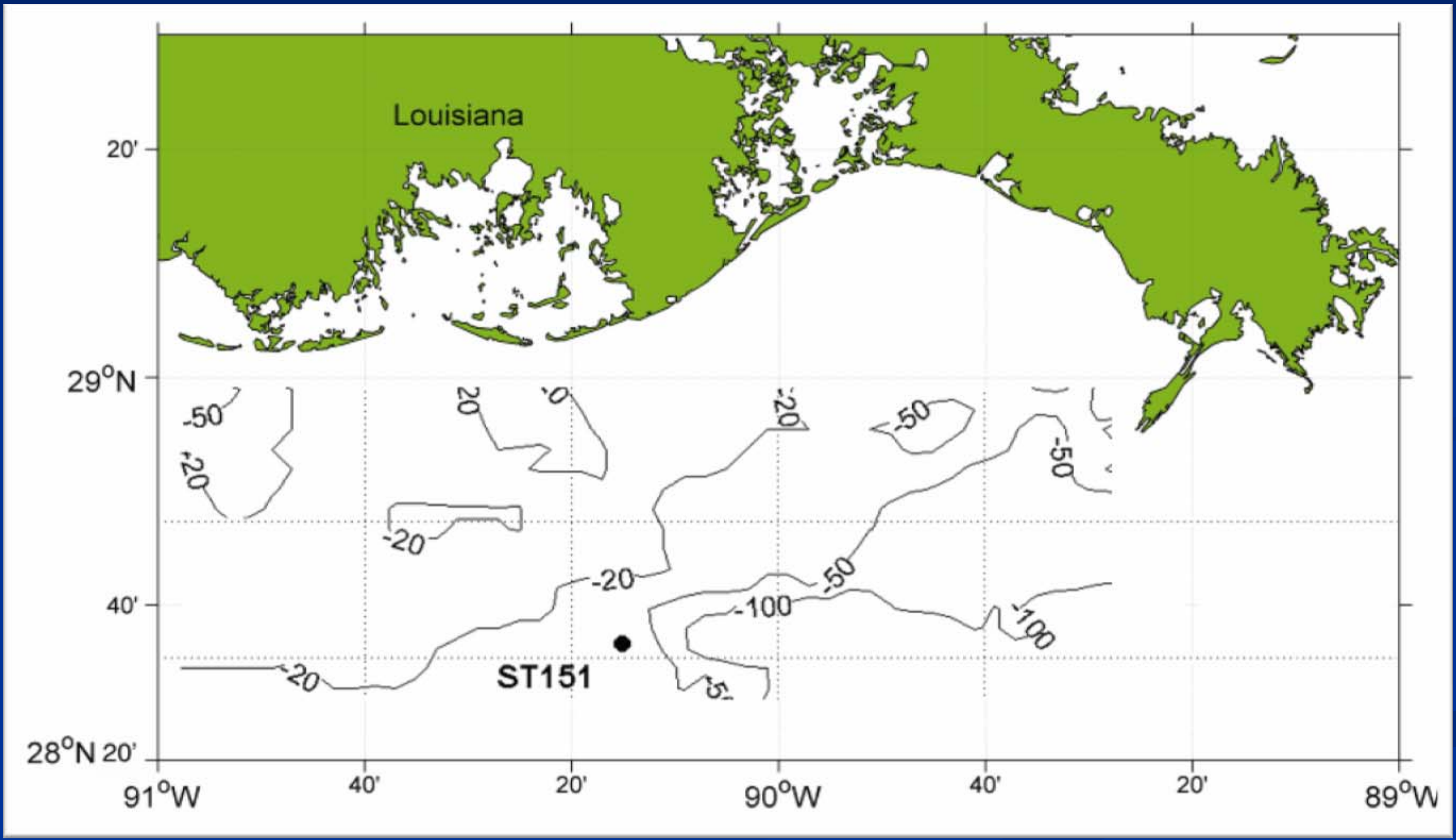
Introduction

- Very few papers on mortality (12 after 1996), while >100 on egg production and growth
- Difficulties in copepod stage-specific mortality estimation
  - Short sampling interval necessary
  - Temporal coverage, at least one generation
  - Bias caused by gear selection
  - Not feasible to track the same copepod population by Eulerian or Lagrangian measurements
  - Mathematical problems: Recruitment – Death = ΔN
    - Existence of solution
    - Uniqueness of solution
    - Stability

Study location

Study location

Study location



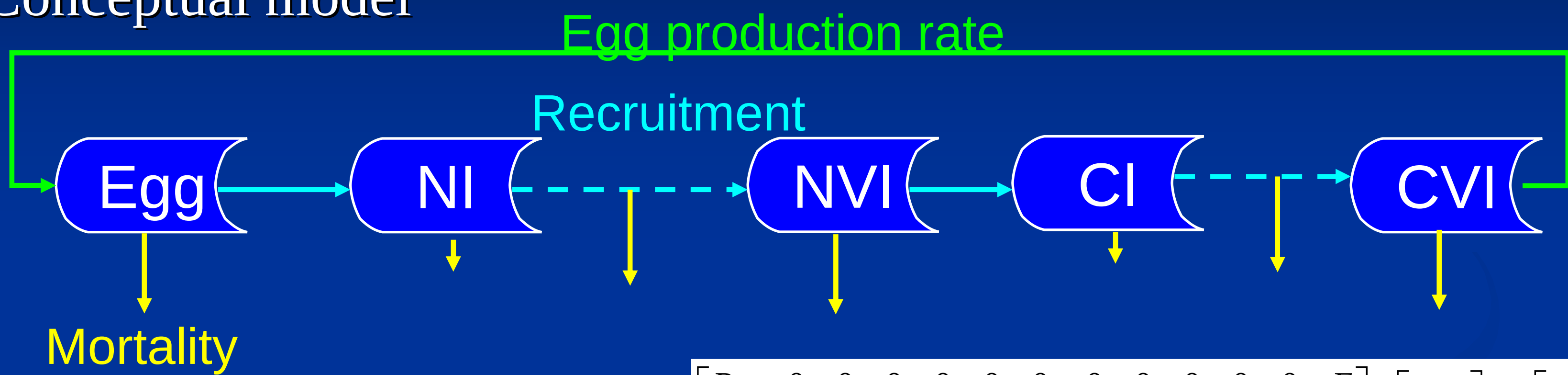
Sampling

- Target species: *Clausocalanus furcatus*
- March 18 - April 6
  May 15 - June 9, 2003
- Samples taken every 12 hours

- 153-µm zooplankton net samples (0 - 15m) with 3 replicates: enumerate to species and developmental stages
- 30-L Niskin water bottle (5, 15, 25m) with 3 replicates

Matrix projection population model

- Conceptual model



- Mathematical model
  $N_t - N_{t-1} = R - D - M$
  E is egg production rate
  P*ii*: Probability of surviving and staying in the same stage
  Gij: Probability of surviving and entering the next stage

$$
\begin{bmatrix}
P_{11} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & E \\
G_{21} & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & &
\end{bmatrix}
\times
\begin{bmatrix} N1 \\ \\ \vdots \\ \\ N13 \end{bmatrix}_t
=
\begin{bmatrix} N1 \\ \\ \vdots \\ \\ N13 \end{bmatrix}_{t+1}
$$

Matrix elements

- Egg production rates estimated from egg ratio method: 3.40 eggs female^{-1} day^{-1} in March-April and 0.5 eggs female^{-1} day^{-1} in May-June
- Stage-specific developmental times estimated from incubation experiments: 13-19 days
- $P_{ii}=(1-m_i)*(1-\Delta t/D)$
- $G_{ji}=(1-m_i)*\Delta t/D$
- $[N_1\ N_2\ N_3\ N_4 \cdots\cdots N_{12}\ N_{13}]_t{}'$: stage specific abundance at time *t* from field samples
- $[N_1\ N_2\ N_3\ N_4 \cdots\cdots N_{12}\ N_{13}]_{t+1}{}'$: stage specific abundance at time *t+1* from field samples

$$
\begin{bmatrix}
P_{11} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & E \\
G_{21} & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & & & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & &
\end{bmatrix}
\times
\begin{bmatrix} N1 \\ \vdots \\ N13 \end{bmatrix}_t
=
\begin{bmatrix} N1 \\ \vdots \\ N13 \end{bmatrix}_{t+1}
$$

Overview on assumptions

- Mortality estimation techniques:
  - Horizontal life table method (HLT)
    - Time series of stage-specific abundances (cohort)
  - Vertical life table method (VLT)
    - Stable population
  - Surface smooth method (SSM)
    - Time series of stage-specific abundances
    - Mortality rates change smoothly between consecutive stages
  - Inverse matrix method with quadratic programming algorithm (IMM-Q) and nonlinear algorithm (IMM-N)
    - Time series of stage-specific abundances
    - Information on egg production rate and stage duration
- SSM and VLT are currently commonly used

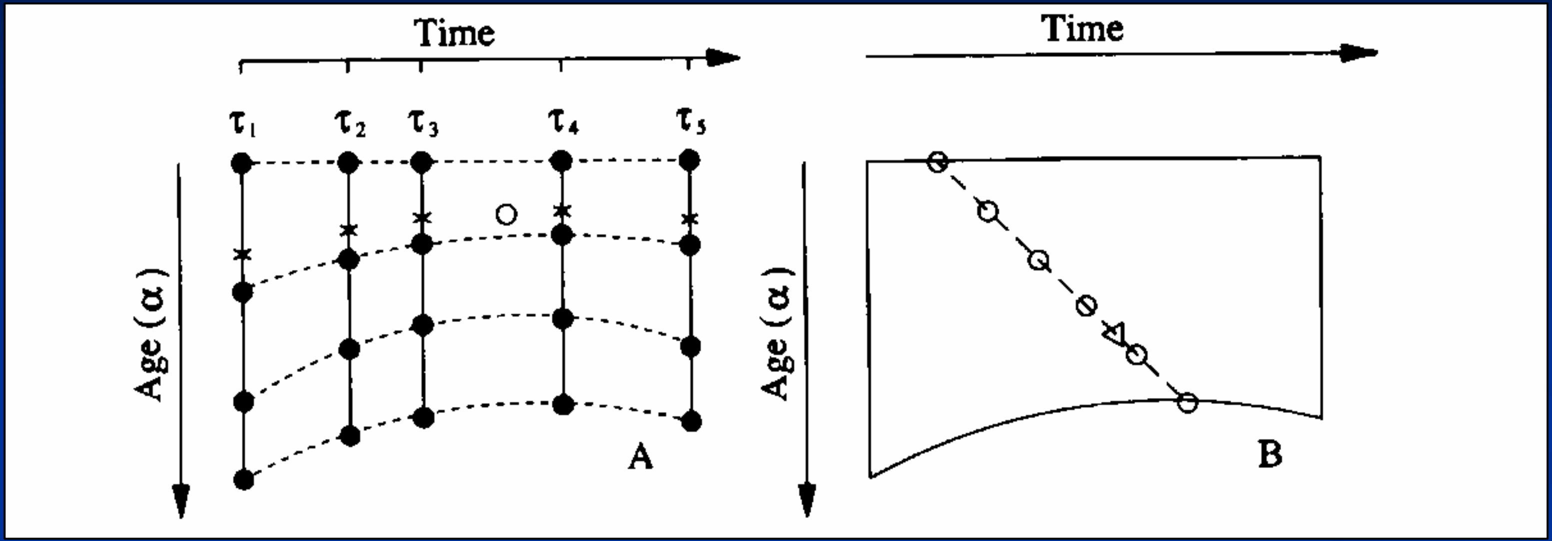
Methods 1 & 2: HLT & VLT

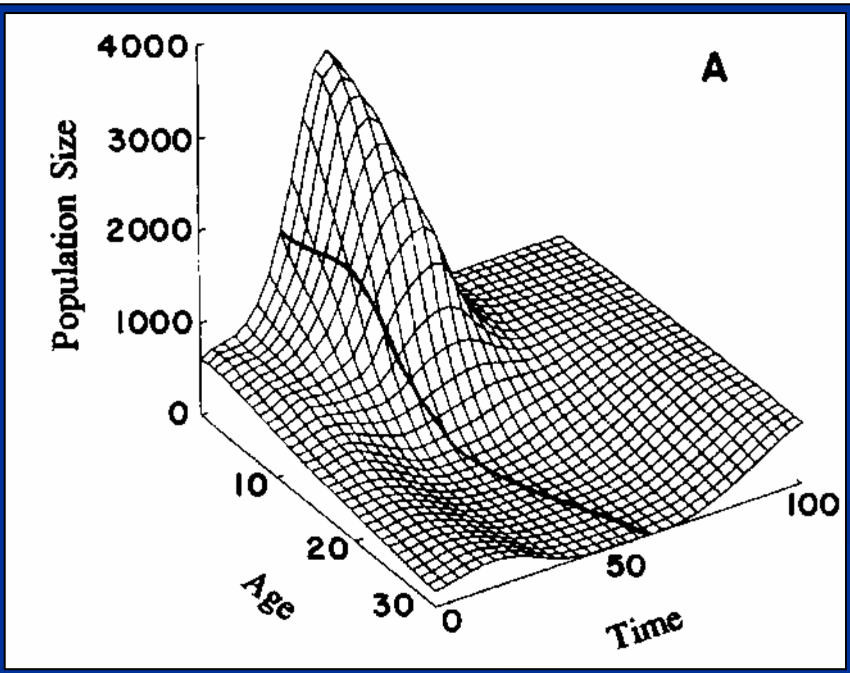
Time (days)	NI	NII	NIII	NIV	NV		Total (n m^{-3})
77.88	111	89	111	67	67	…	1841
78.38	22	266	244	89	244	…	3994
78.88	152	44	44	33	30	…	2711
Mean	76	110	114	54	114	…	3014

- Horizontal life table method

  Mortality for NIII at 78.38 = (244-33)/244=0.86
  Notice the negative estimates
- Vertical life table method
  Mortality for NIII=0.48

Method 3: SSM





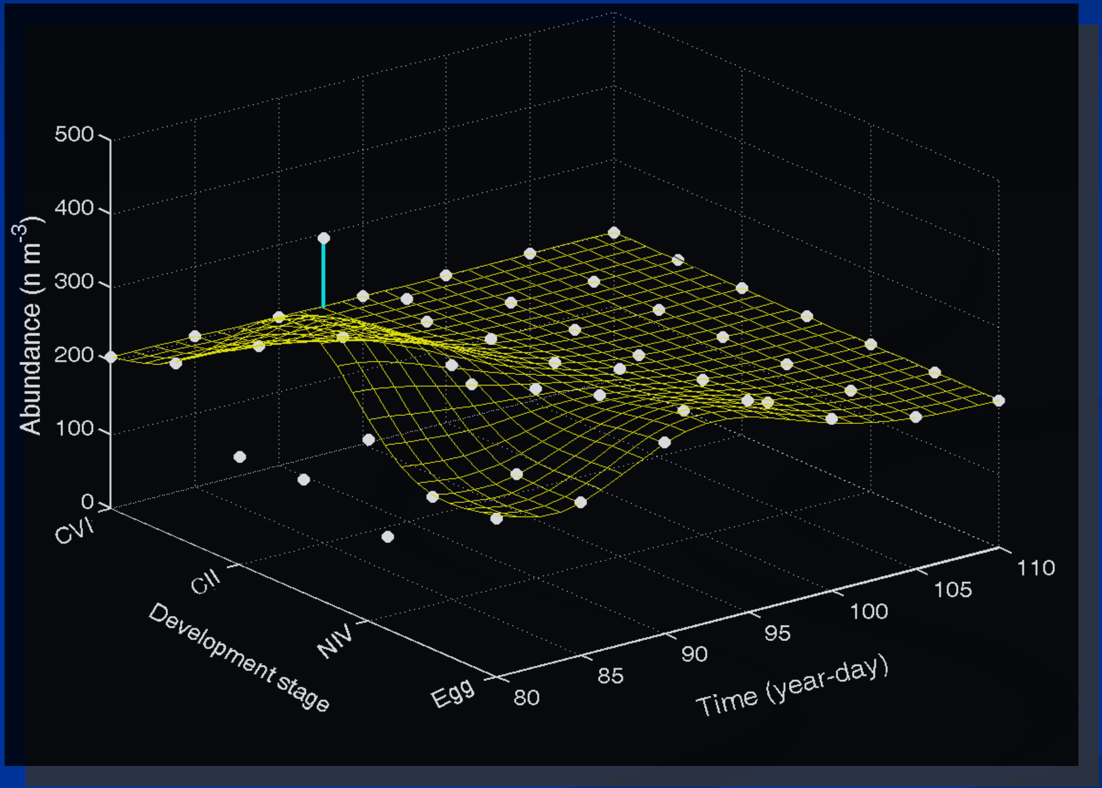
$$\frac{\partial \eta}{\partial t} + \frac{\partial \eta}{\partial \alpha} + \mu\eta = 0,$$

$$\tilde{\mu}\tilde{\eta} = -\frac{\partial \tilde{\eta}}{\partial t} - \frac{\partial \tilde{\eta}}{\partial \alpha}$$

Wood (1994)

Method 4 & 5: IMM-Q and IMM-N

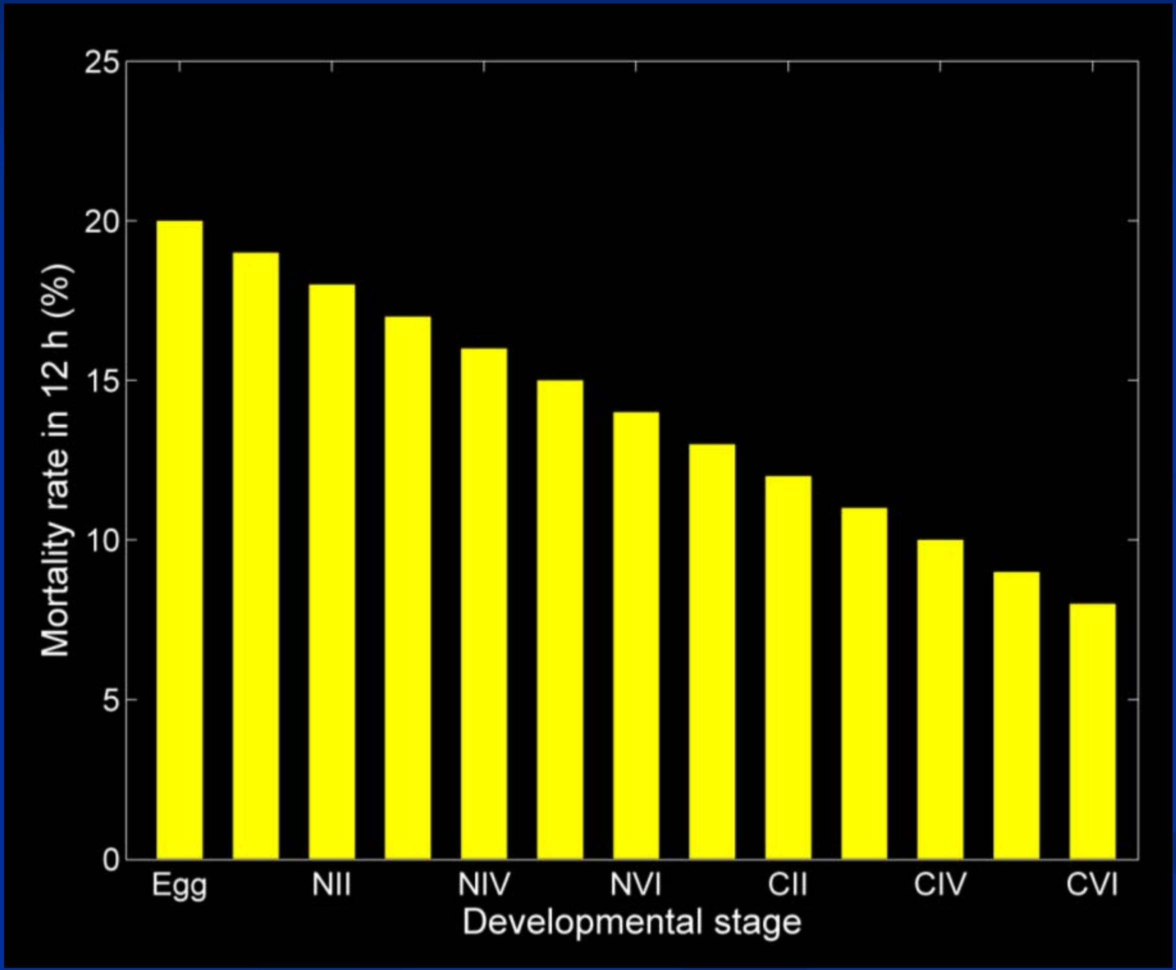
- Project population using stage-structured population model: $A_{t+1} = \beta \times A_t$
- IMM-Q: Find the best fit surface through quadratic programming algorithm



- IMM-N: Find the mortality rates best fit for observation data using Gauss-Levenberg-Marquardt algorithm (PEST)

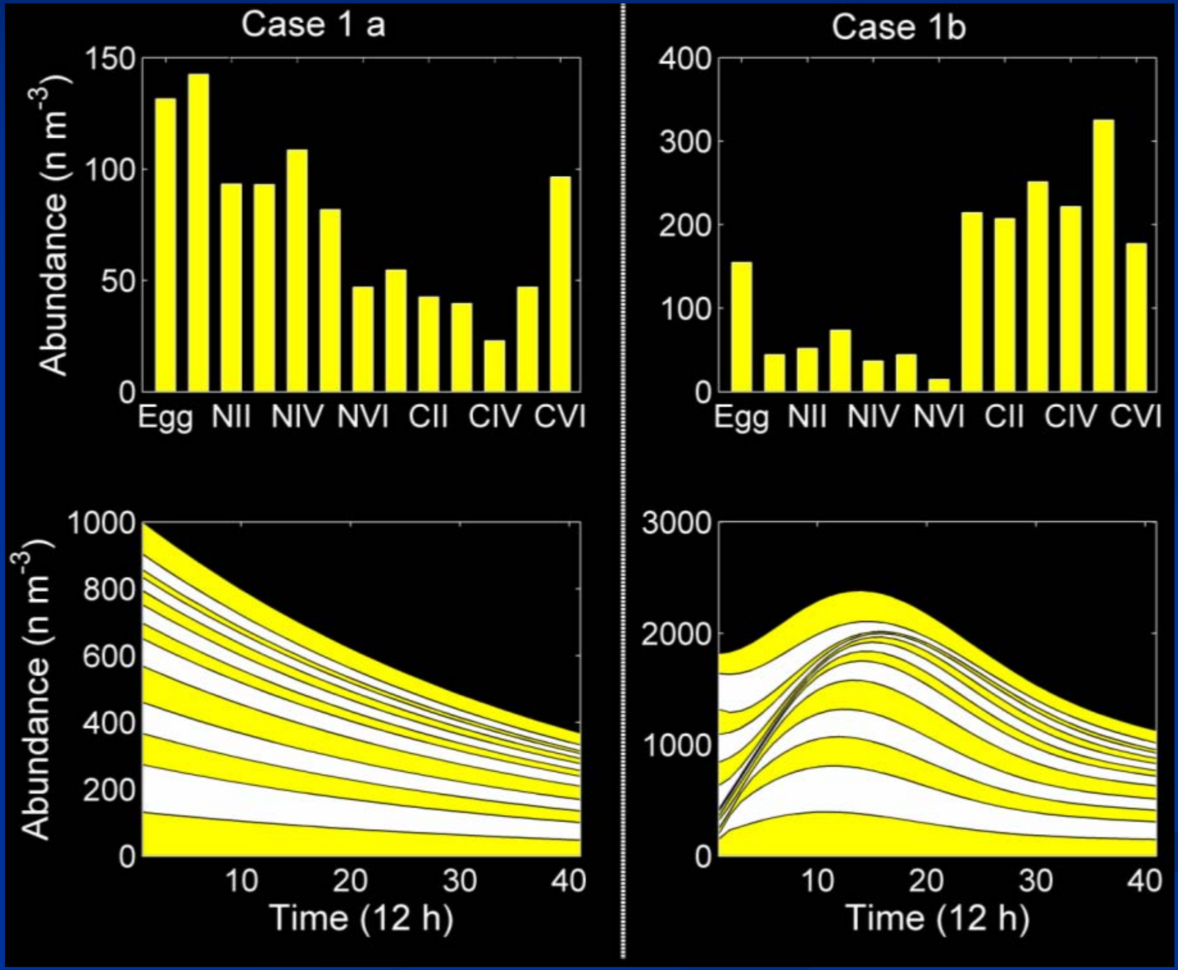
Simulated case 1a & 1b

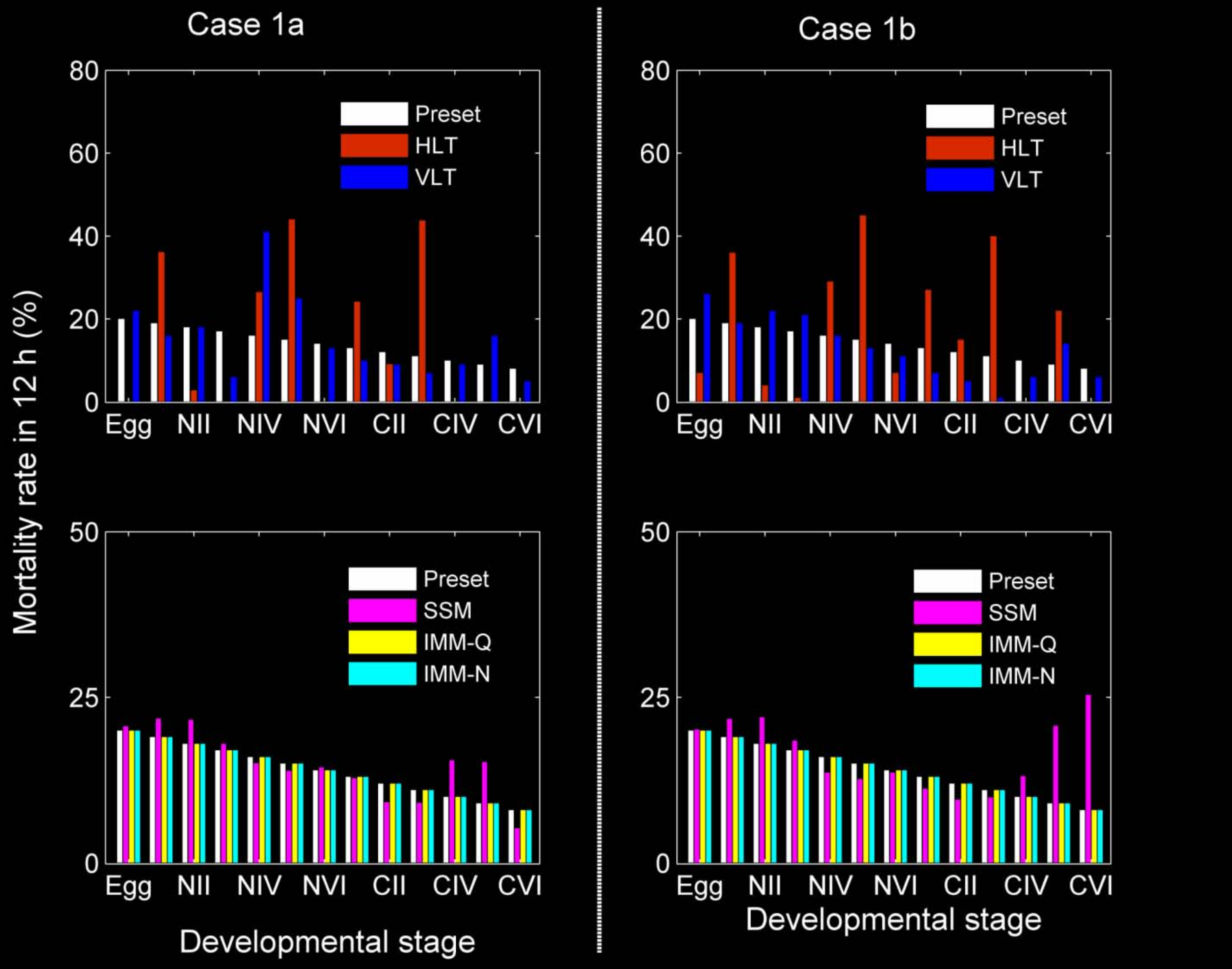
- Mortality rates change smoothly between two consecutive stages (SSM)
- Population 1a was initialized with stable-age distribution (VLT)
- Population 1b was initialized with field abundances



Simulated case 1a & 1b

- Mortality rates change smoothly between two consecutive stages (SSM)
- Population 1a was initialized with stable-age distribution (VLT)
- Population 1b was initialized with field abundances

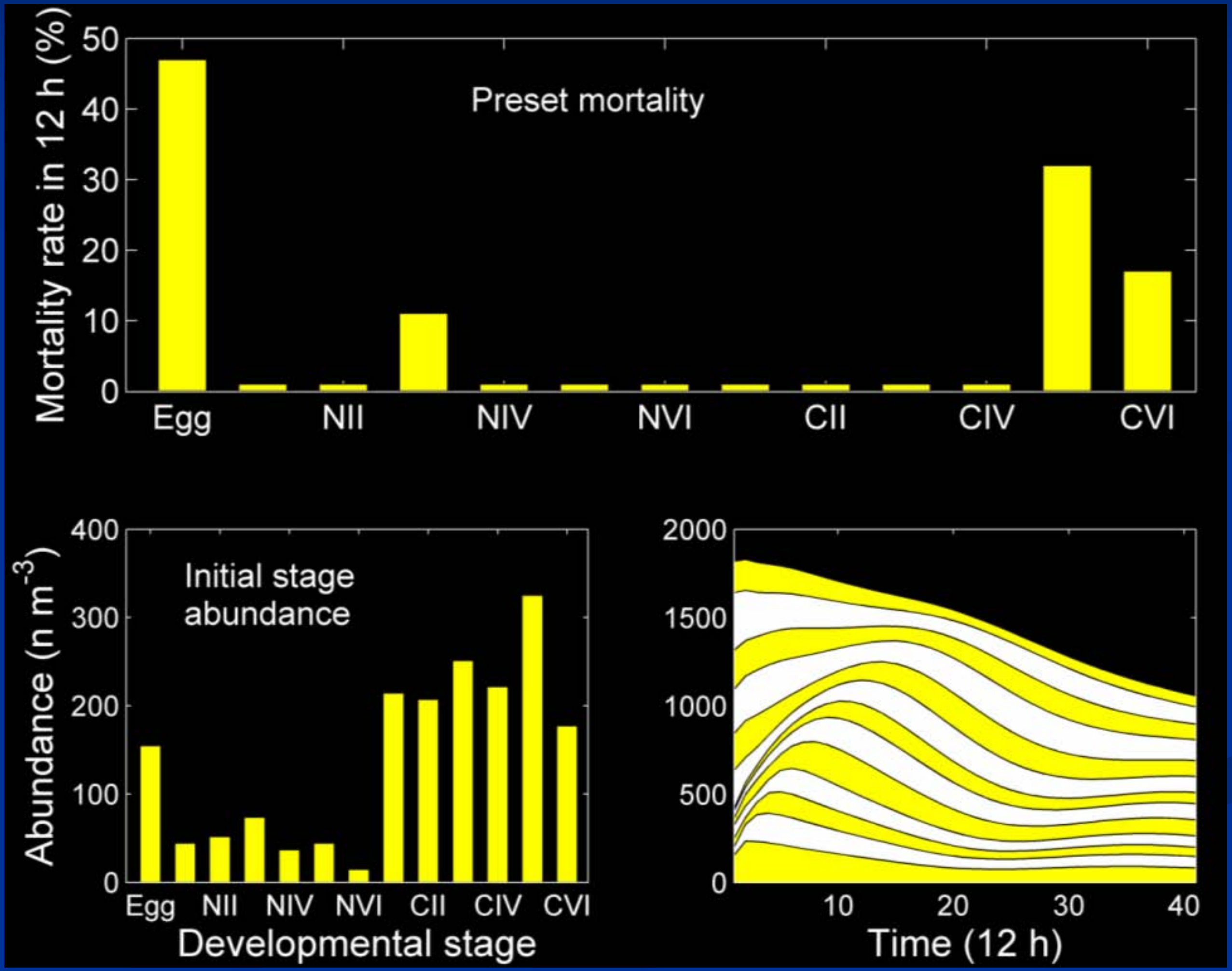




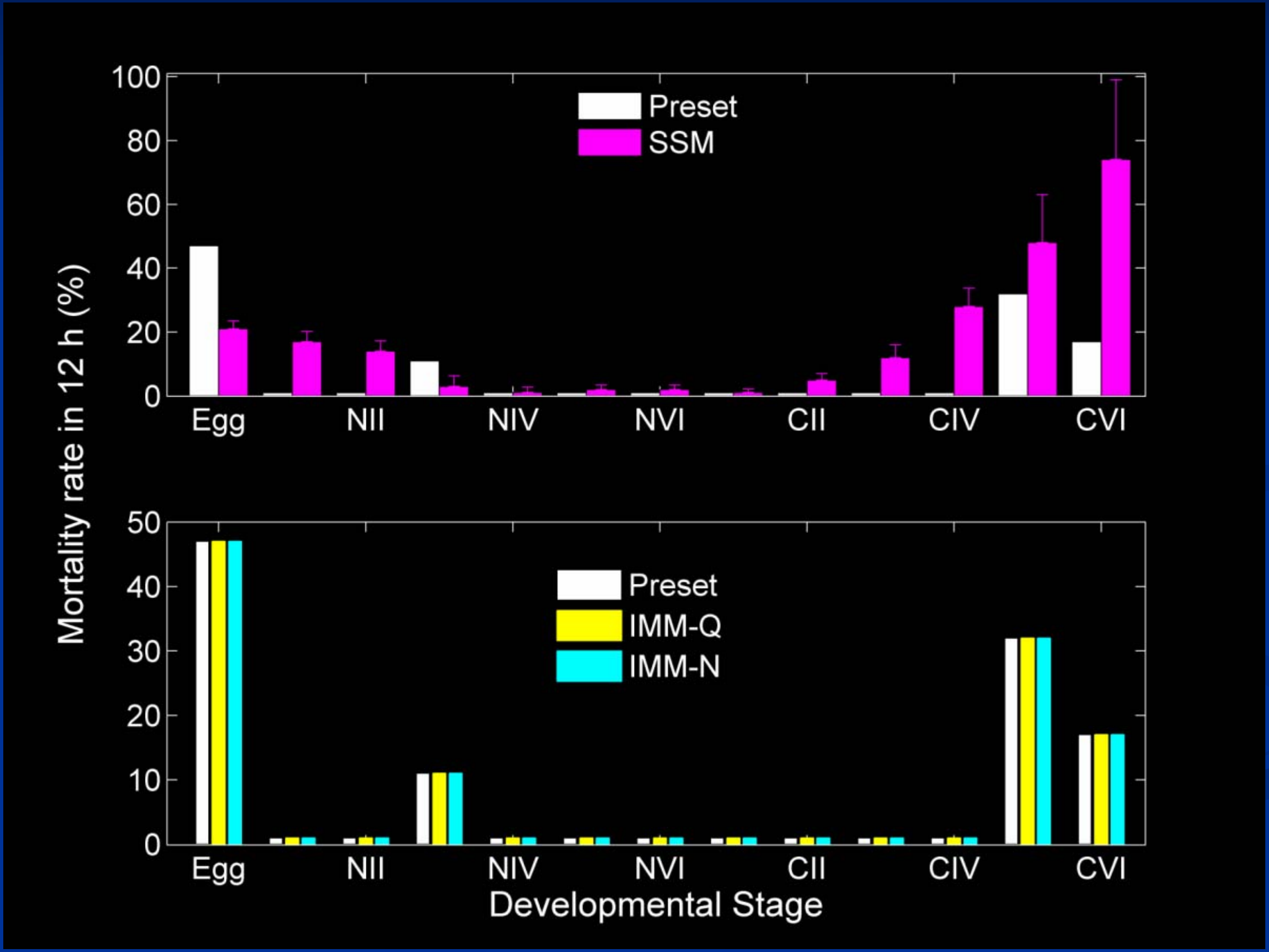
Case 1a
Case 1b
Mortality rate in 12 h (%)
Preset
HLT
VLT
SSM
IMM-Q
IMM-N
0
20
40
60
80
0
25
50
Egg
NII
NIV
NVI
CII
CIV
CVI
Developmental stage

Simulated case 2

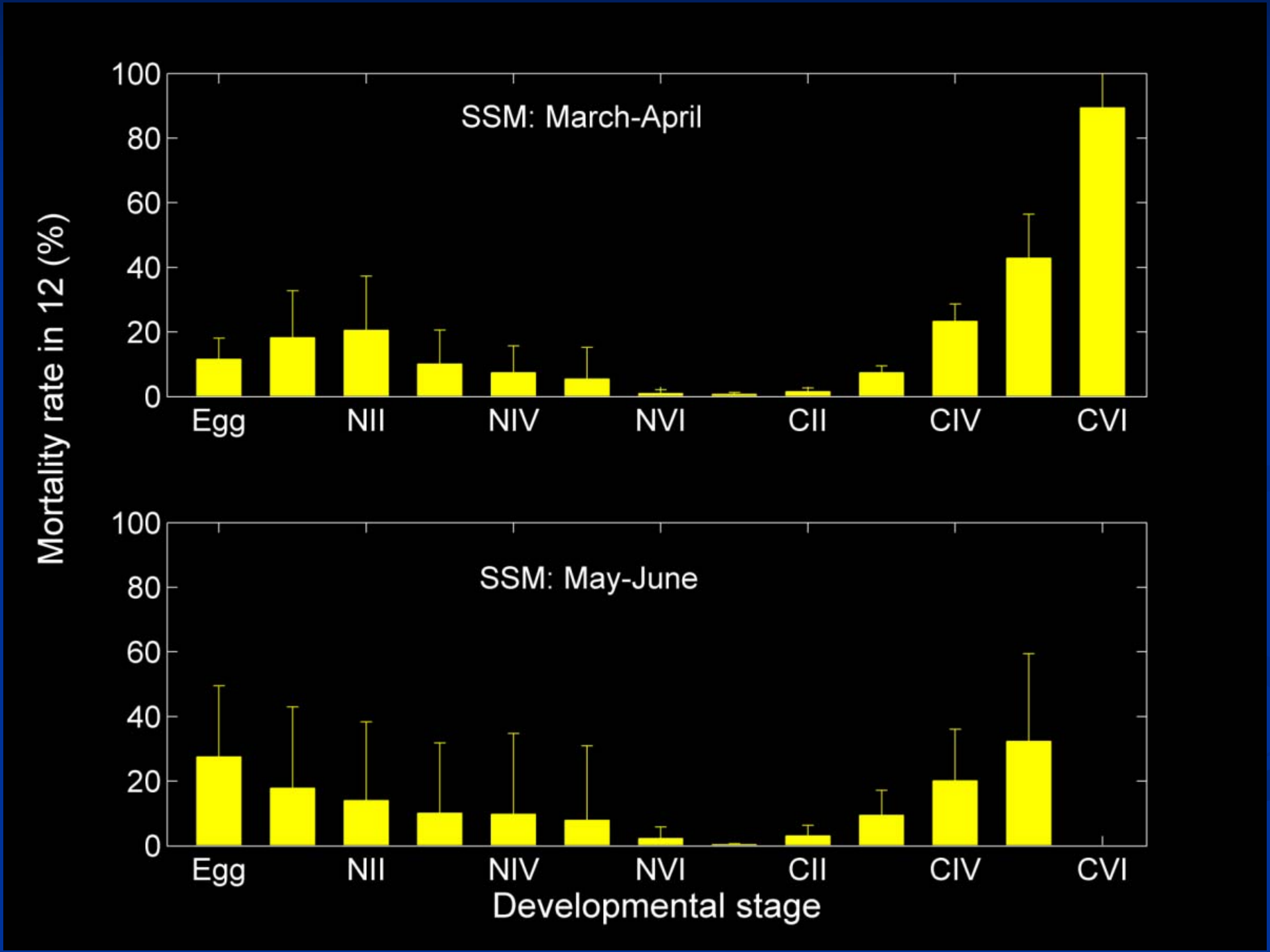
- From case 1:
  - HLT & VLT fail
  - SSM deviation in later stages
- Case 2:
  - Mortality rates change relatively large



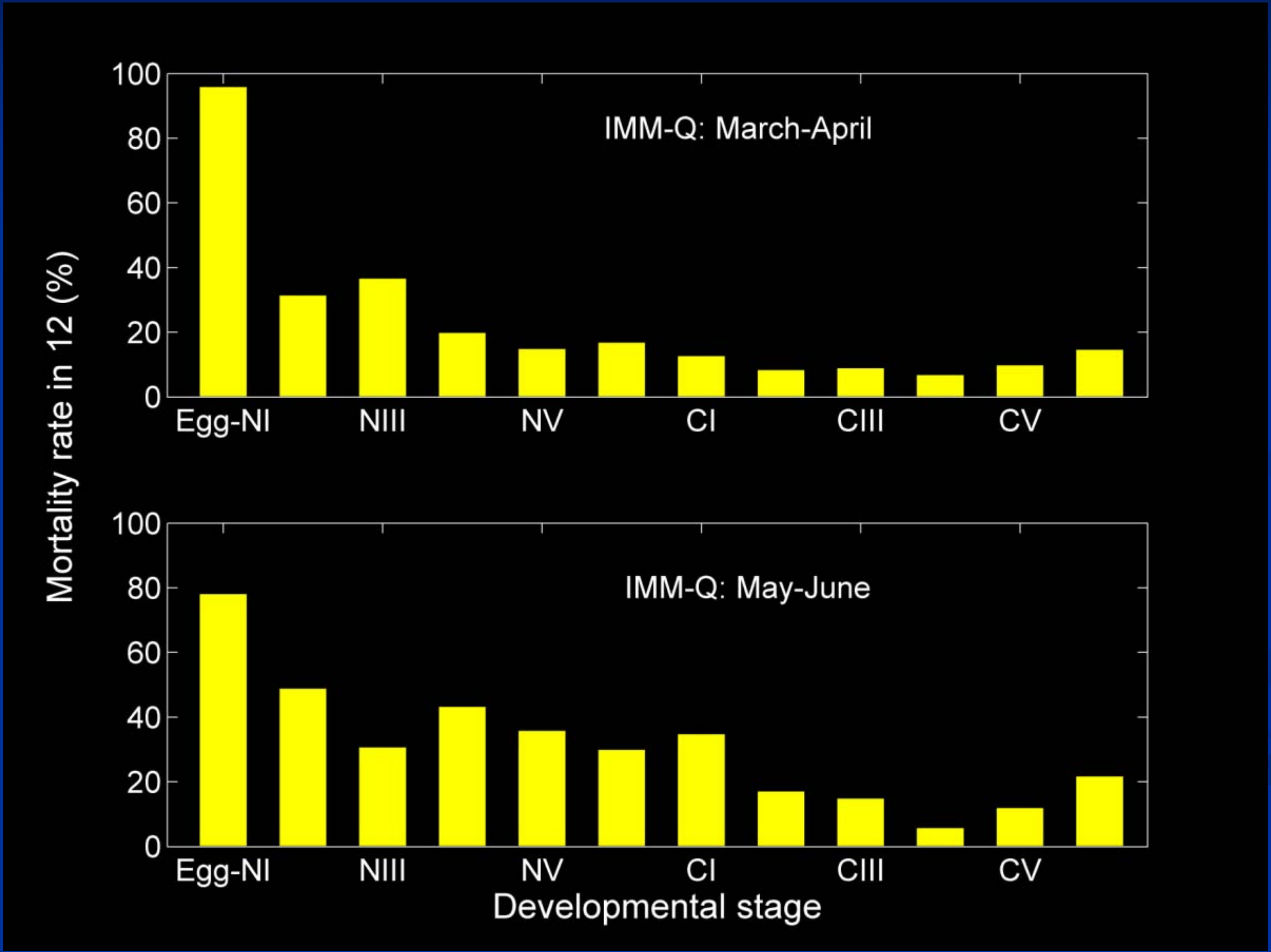
Simulated case 2



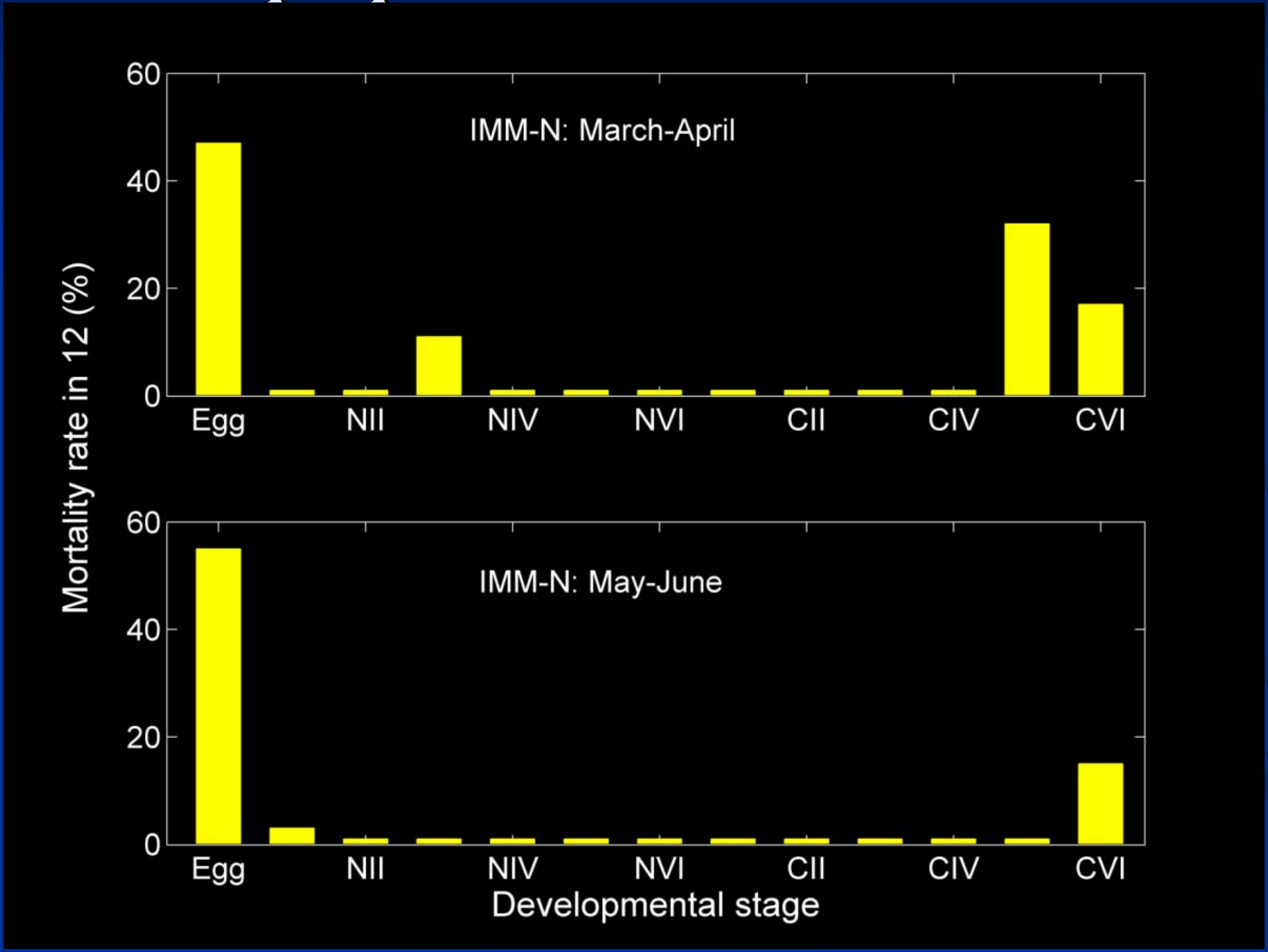
Field population: SSM

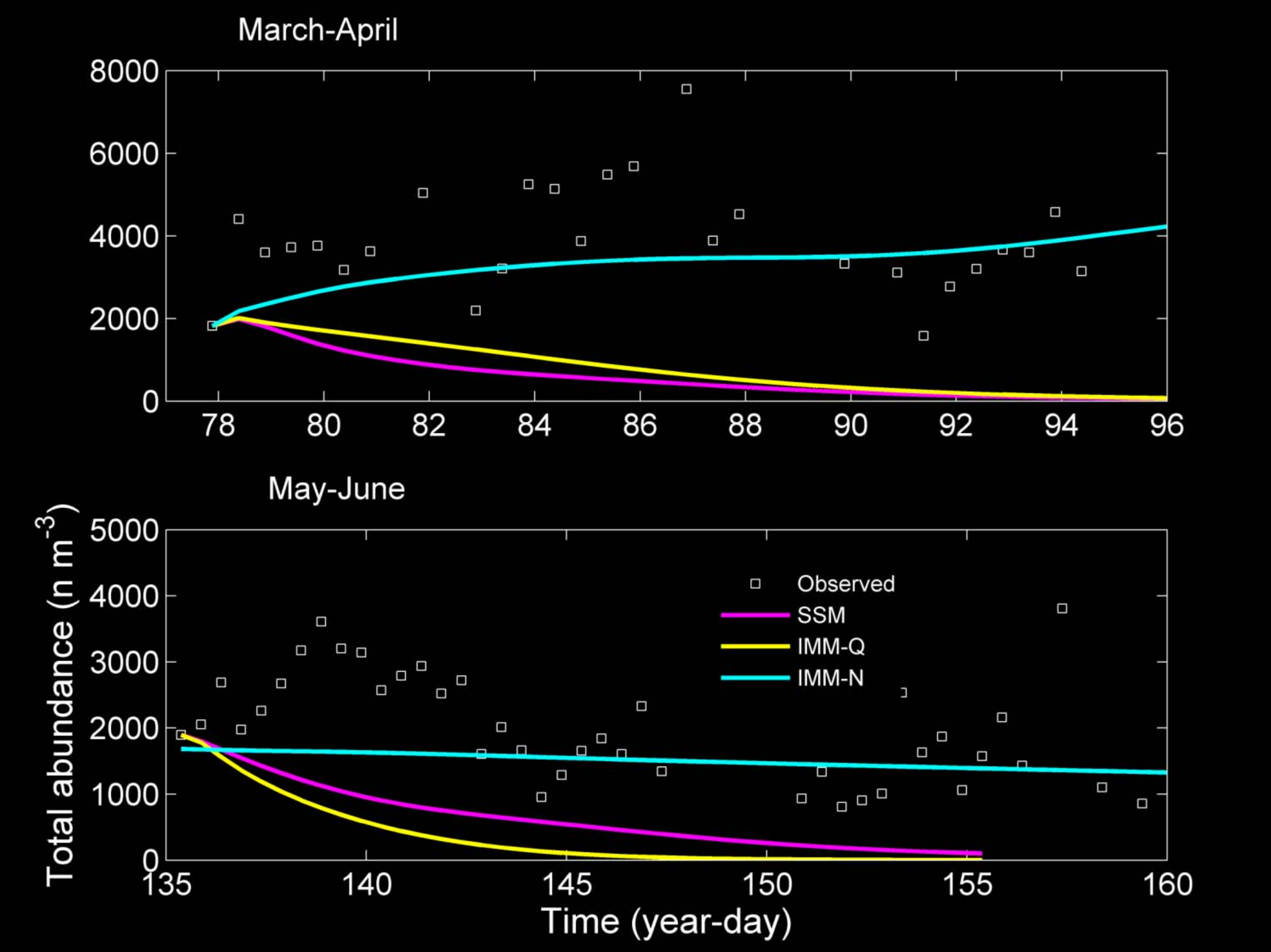


Field population: IMM-Q



Field population: IMM-N




March-April
8000
6000
4000
2000
0
78
80
82
84
86
88
90
92
94
96
May-June
Total abundance (n m-3)
5000
4000
3000
2000
1000
0
135
140
145
150
155
160
Time (year-day)
Observed
SSM
IMM-Q
IMM-N

Conclusions

- Stage-specific mortality estimation is problematic
- Different results from different methods reflect the uncertainty in copepod stage-specific mortality estimation
- IMM-N performed the best
- Eggs experienced high mortality rates in both March-April and May-June
- The adult stage had high mortality rate in both March-April and May-June
- Copepodite V had high mortality in March-April

Acknowledgements

- ChevronTexaco
- Michael Dagg, Robert Downer, Richard Shaw, and Dandina Rao
- Crew on South Timbalier 151
- Zooplankton lab at LSU: Sean Keenan, Harmon Brown and Malinda Sutor
- Zooplankton group at Hatfield Marine Science Center, Oregon State University: Jay Peterson, Linda O'Higgins, Leah Feinberg, Tracy Shaw, Cheryl Morgan, Jesse Lamb, Julie Keister, and Jennifer Menkel