LABORATORY REFERENCE DOCUMENT NUMBER 83-26

PARAMETER ESTIMATION MODEL OF MARINE COPEPOD POPULATION DYNAMICS

by

Rosalind E. Cohen

☑ APPROVED FOR DISTRIBUTION

A C Lawrence
(APPROVING OFFICIAL)

9/22/83
(DATE)

National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole Laboratory
Woods Hole, Massachusetts 02543

September 1983

Introduction

The Northeast Fisheries Center in Woods Hole, Massachusetts has been conducting intensive, fine-scale studies on Georges Bank since 1981 in order to investigate the major factors controlling larval cod and haddock survival. Predation is probably the most important direct biological source of larval mortality; food quantity and quality may act indirectly by affecting larval growth rates and general condition which could ultimately affect their vulnerability to predation. It would be valuable to be able to predict the size-specific abundances of dominant larval fish prey (developmental stages and adult copepods) over the spawning season in order to assess the feeding environment of the larvae.

One approach to this problem is the use of simulation and predictive models (Argentesi et al., 1974; Sonntag and Greve, 1977; Parslow et al., 1979; Seitz, 1979; Bossicart, 1980; Davis, 1982; Myers and Runge, 1983). These models often have stringent requirements for the input data: population must have a stable-age or stage distribution; data must be collected from a single population or cohort; data must represent a long time series of samples collected at closely spaced intervals with fine mesh nets. It is not often practical or possible to meet any of these requirements in an open marine ecosystem.

The major aim of this study was to derive a parameter estimation model with less strict assumptions which could calculate survival of each copepod life stage and predict the

stage structure of the species population over defined spatial and temporal scales using standard survey-type data. The rationale and use of a Leslie-type matrix model for prediction of population structure is described by Caswell (1982a and 1982b). Several data sets were used to test and evaluate the parameter estimation model. One data set was taken from Marshall (1949), and the results of these trials were previously described by Cohen (1982, MS) and will not be repeated here. The other two sets of data were selected from NMFS data files, and required two slightly different versions of the basic model.

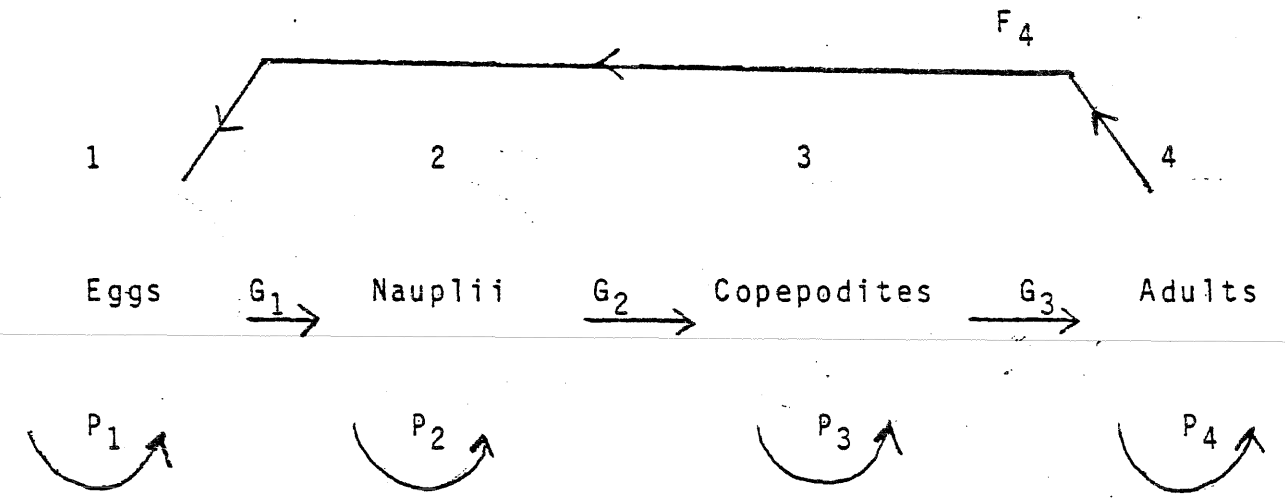
Methods

A. The model

1. Pump data

The first data set was derived from plankton pump collections on eastern Georges Bank within a dense aggregation of larval haddock during May 1981. All 13 developmental stages of the copepods were counted in subsamples at 4 different depths. The numbers per m^3 for all depths were combined at each station, and the stages were combined into eggs, nauplii, copepodites and adults of each species. No corrections were made for sampling errors (avoidance, patchiness, etc.) at this time.

a. Life cycle graph



Definitions:

σ_i = probability of survival of stage i

$\alpha_i = 1/D_i$ = rate of passage from stage i to i+1

D_i = duration of stage i in terms of t

t = sampling interval (in days here)

$P_i = \sigma_i(1-\alpha_i)$ = survival probability of animals remaining in stage i during time t

$G_i = \sigma_i \alpha_i$ = survival probability of animals growing from stage i to i+1 during time t

i = stage

n_i = number of individuals in stage i.

Assume for all species that 50% of the adults are females, and that 50% of the females have clutches at any one time.

$$F_4 = [(\text{number of eggs}/♀/t) \times .5 \times t/D_1 \times n_4(t)/2]$$

If females retain eggs in sacs, the σ_i really represents $\sigma_{egg} \times \sigma_4$.

b. Linear equations

$$n_1\ (t+1) = F_4 + \sigma_1(1-\alpha_1)n_1(t)$$

$$n_2\ (t+1) = \sigma_1\alpha_1 n_1(t) + \sigma_2\ (1-\alpha_2)\ n_2(t)$$

$$n_3\ (t+1) = \sigma_2\alpha_2 n_2(t) + \sigma_3(1-\alpha_3)\ n_3(t)$$

$$n_4\ (t+1) = \sigma_3\alpha_3 n_3(t) + \sigma_4(1-\alpha_4)\ n_4\ (t)$$

c. Matrix equation

$$\begin{bmatrix} (1-{}^{1}/D_1)n_1(t) & ({}^{1}/D_1)n_1(t) & 0 & F_4 \\ 0 & (1-{}^{1}/D_2)n_2(t) & ({}^{1}/D_2)n_2(t) & 0 \\ 0 & 0 & (1-{}^{1}/D_3)n_3(t) & ({}^{1}/D_3)n_3(t) \\ 0 & 0 & 0 & (1-{}^{1}/D_4)n_4(t) \end{bmatrix} \times \begin{bmatrix} \sigma_1 \\ \sigma_2 \\ \sigma_3 \\ \sigma_4 \end{bmatrix} = \begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \\ n_4(t+1) \end{bmatrix}$$

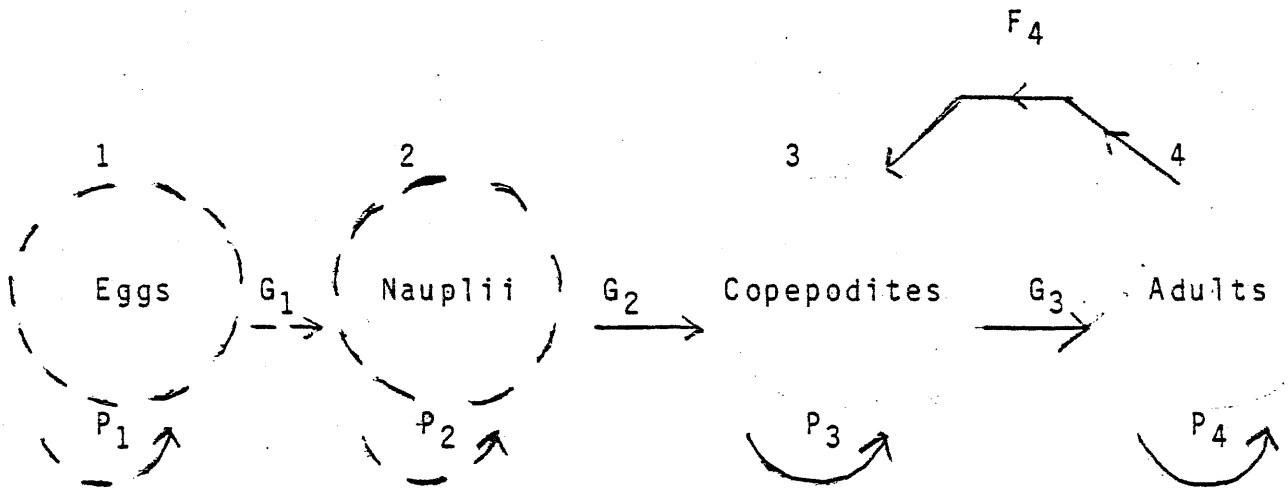
Solve for the σ_i's.

2. Bongo data

These data were derived from samples collected using 20-cm bongo nets (.165 mm mesh) towed obliquely at stations within a larval herring patch on Nantucket Shoals, Cape Cod during autumn 1978. This mesh size quantitatively samples copepodites and adults of the copepod species considered, but does not collect their eggs and nauplii (Davis, 1980). The life cycle was therefore reduced to only 2 stages, copepodites and adults. The actual census counts for each stage are the mean value of 2 stations located in the larval patch center for each patch mapping (11/4, 11/6, 11/7, 11/8). The assumption was that

the patch center represented the same water mass over time. No corrections were made for sampling errors (patchiness, avoidance, extrusion, clogging, etc.).

a. Life cycle graph



Same definitions as in part "1", except

$$F_4 = [(\text{number of eggs}/♀/t) \times .5 \times t/(D_1+D_2) \times n_4(t)/2] \times \sigma_1\sigma_2$$

b. Liner equations

$$n_3\ (t+1) = F_4 + \sigma_3(1-\alpha_3)n_3(t)$$

$$n_4\ (t+1) = \sigma_3\alpha_3(t) + \sigma_4(1-\alpha_4)n_4(t)_4$$

c. Matrix equation

$$\begin{bmatrix} (1-{}^{1}/D_3)n_3(t) & (1/D_3)n_3(t) \\ 0 & (1-1/D_4)n_4(t) \end{bmatrix} + \begin{bmatrix} F_4 \\ 0 \end{bmatrix} \times \begin{bmatrix} \sigma_3 \\ \sigma_4 \end{bmatrix} = \begin{bmatrix} n_3\ (t+1) \\ n_4\ (t+1) \end{bmatrix}$$

B. Life History Information - assumes isochronal development

1. Pump samples - temperature approx. 7°C

a. <u>Pseudocalanus</u> sp. (Corkett and McLaren, 1978)

D_1 = 5 days
D_2 = 20 days
D_3 = 20 days
D_4 40 days

10 eggs/♀/week

b. <u>Oithona</u> sp. (Eaton, 1971)

D_1 = 7 days
D_2 = 30 days
D_3 = 30 days
D_4 60 days

10 eggs/♀/week

2. Bongo samples - temperature approx. 11°C

a. <u>Centropages typicus</u> (Lawson, 1969)

D_1 = 3 days
D_2 = 15 days
D_3 = 15 days
D_4 30 days

10 eggs/♀/week

b. <u>Pseudocalanus</u> sp. (Corkett and McLaren, 1978)

D_1 = 3 days
D_2 = 15 days
D_3 = 15 days
D_4 30 days

10 eggs/♀/week

C. Census Counts

1. Pump samples

a. *Pseudocalanus* sp. (no./m^3)

Stage	5/25/81	5/26/81	5/25/81	5/26/81	5/25/81	5/26/81
Eggs	209	2036	265	1100	873	1205
Nauplii	8909	6422	2785	5684	9665	4282
Copepodites	2277	5968	1289	3144	2107	1777
Adults	79	725	120	157	78	112

b. *Oithona* spp.

Stage	5/25/81	5/26/81	5/25/81	5/26/81	5/25/81	5/26/81
Eggs	336	1022	532	490	462	691
Nauplii	11409	14765	3907	1315	8220	7107
Copepodites	2734	4452	1082	2469	2450	2473
Adults	1105	2216	465	805	1156	514

2. Bongo samples

a. *Centropages typicus* (no./m^3)

Stage	11/4/78	11/6/78	11/7/78	11/8/78
Copepodites	1518.9	1165.6	2885.7	1654.4
Adults	453.5	950.6	516.4	1090.2

b. *Pseudocalanus* sp.

Stage	11/4/78	11/6/78	11/7/78	11/8/78
Copepodites	3602.5	1947.8	1697.1	2435.3
Adults	716.8	1013.6	496.6	1007.8

Results

The time series analyzed here were selected to reflect population dynamics over small temporal and spatial scales in order to reduce some of the variability in the abundance estimates. The results of the model runs are presented in Tables 1 and 2. The combined stage durations and the adult stage durations are much longer than the sampling intervals of 1 to 4 days. It was therefore expected that the values of the probability of surviving at the same stage over the sampling interval (P_i) would be very close to 1.0 and the values of surviving over the sampling interval and growing into the next stage (G_1) would be close to 0. The values of G_4 should have all been equal to 0 because the adults do not molt.

All the values of G_1, except 2, were in the range of 0 to 1.0, and 32 out of 40 were less than 0.20 as expected. Unfortunately, 22 out of 40 values of P_i were greater than 1.0, and one half of these values were greater than 2.0. All the G_4 values were greater than 0, but only 1 exceeded 1.0.

There are many possible sources of error which could account for these discrepencies:

1. Sample collection errors (net clogging, extrusion, avoidance, patchiness, etc). (See UNESCO manual on Zooplankton Sampling, 1968).
2. Sample counting errors due to subsampling errors (for example see Frolander, 1968 and McEwen et al., 1954-55).

3. Physical processes disrupting the integrity of the water mass sampled and its populations of organisms (diffusion, advection, vertical and horizontal shear, currents, etc.).
4. Biological processes not accounted for in the model (immigration, emigration, predation, vertical migration, aggregation).
5. Incorrect estimates of growth and fecundity.
6. Non-isochronal development by some copepod species.
7. Too much compression of stages (13 into 2).
8. Basic problem in the model formulation.

Perhaps the model could be upgraded to include variable functions for stage durations dependent on temperature (McLaren, 1978), and for fecundity dependent on body size (McLaren, 1965). Confidence limits for the abundance estimates might also be incorporated.

The assumptions and requirements of this parameter estimation model are not yet fully defined. The overall survival of a stage during a specified time interval (σ_i) probably really represents an index of the sum total of all the biological and physical processes acting on the sampled population, plus the sampling error involved in calculating the stage abundances under a given set of conditions and temporal and spatial scales. Over very small temporal and spatial scales, σ_i may be a measure of sampling variability alone. It might therefore be useful to run the model with different data sets reflecting various levels of

biological and physical complexity and temporal and spatial scales in order to quantify the components of σ_i. Some suggested data sets are time series collected from:

1. Laboratory-reared single species populations of copepods whose life history information is known under controlled conditions.
2. Enclosure and large tank studies (CEPEX and MERL).
3. Warm- and cold-core rings.
4. Plankton patches.
5. Meso-, coarse, and fine-scale survey data. Various combinations of stations, geographic areas, and temporal scales could be considered.

Once σ_i is defined and the model assumptions clarified, the results might be used in the Leslie-type population projection matrix models described by Caswell (1982a and 1982b). Several different matrices might be required to represent the population changes of a species over a yearly cycle. Eventually it might be possible to calculate and predict secondary production in this manner.

REFERENCES

Argentesi, F., R. D. Bernardi, and G. D. Cola. 1974. Mathematical models for the analysis of population dynamics in species with continuous recruitment. Mem. Ist. Ital. Idrobiol. 31: 245-275.

Bossicart, M. 1980. Use of a multicohort model to derive biological parameters. ICES C.M. 1980/L:24.

Caswell, H. 1982a. Stable population structure and reproductive value for populations with complex life cycles. Ecology 63: 1223-1231.

_____. 1982b. Optimal life histories and the maximization of reproductive value: a general theorum for complex life cycles. Ecoloy 63: 1218-1222.

Cohen, R. E. MS 1982. Population dynamics of two species of marine copepods. Class project report.

Corkett, J. C. and I. A. McLaren. 1978. The biology of Pseudocalanus. Adv. mar. Biol. 15: 1-231.

Davis, C. S. 1980. Preliminary estimates of extrusion from .333-mm and .165-mm mesh plankton nets. NAFO SCR 80/IX/132.

_____ 1982. Processes controlling zooplankton abundance on Georges Bank. Ph.D. Thesis, Boston University Marine Program, Woods Hole, MA.

Eaton, J. M. 1971. Studies on the feeding and reproductive biology of the marine cyclopoid copepod, Oithona similis, Claus. Ph.D. Thesis, Dalhousie University.

Frolander, H. F. 1968. Statistical variations in zooplankton numbers from subsampling with a Stempel pipette. J. Water Pol. Control Fed. 40: 82-88.

Lawson, T. J. 1969. Centropages typicus Krøyer, 1847 (Copepoda: Calanoida), its developmental stages and factors affecting its distribution. M.A. Thesis, University of North Carolina at Chapel Hill.

Marshall, S. M. 1949. On the biology of the small copepods in Loch Striven. J. Mar. Biol. Ass. U.K. 28: 45-122.

McEwen, G. F., M. W. Johnson, Th. R. Folsom. 1954-55. A statistical analysis of the performance of the Folsom plankton sample splitter, based on test observations. Arch. Meteoral. Geophys. Ser. A-B 7: 502-527.

McLaren, I. A. 1965. Some relationships between temperature and egg size, body size, development rate, and fecundity, of the copepod Pseudocalanus. Limnol. Oceanogr. 10: 528-538.

McLaren, I. A. 1978. Generation lengths of some temperate marine copepods: esstimation, prediction and implications. J. Fish. Res. Board Canada 35: 1330-1342.

Myers, R. A. and J. A. Runge. 1983. Predictions of seasonal natural mortality rates in a copepod population using life-history theory. Mar. Ecol. Prog. Ser. 11: 189-194.

Parslow, J., C. Sonntag, J. B. L. Matthews. 1979. Techniques of systems identification applied to estimating copepod population parameters. J. Plank. Res. 1: 137-151.

Seitz, A. 1979. On the calculation of birth rates and death rates in fluctuating populations with continuous recruitment Oecologia (Berl.) 41: 343-360.

Sonntag, N. C. and W. Greve. 1977. Investigation of the impact of mercury on enclosed water columns using a zooplankton simulation model. J. Fish. Res. Board Can. 34: 2295-2307.

UNESCO Press. 1968. Zooplankton sampling. UNESCO Press, Paris, 174 pp.

Table 1. Results of model runs using pump samples.

Species and Stage	t	σ_i	P_i	G_i
Pseudocalanus sp.	1 day			
Eggs		9.79	7.83	1.96
Nauplii		0.64	0.61	0.03
Copepodites		2.26	2.15	0.11
Adults		9.42	9.18	0.24
	1 day			
Eggs		4.30	3.44	0.86
Nauplii		2.02	1.92	0.10
Copepodites		2.50	2.38	0.13
Adults		1.34	1.31	0.03
	1 day			
Eggs		1.54	1.23	0.31
Nauplii		0.42	0.40	0.02
Copepodites		0.81	0.77	0.04
Adults		1.47	1.43	0.04
Oithona sp.	1 day			
Eggs		0.59	0.51	0.08
Nauplii		1.28	1.24	0.04
Copepodites		1.62	1.57	0.05
Adults		2.05	2.01	0.04
	1 day			
Eggs		0.40	0.34	0.06
Nauplii		0.28	0.27	0.08
Copepodites		2.30	2.23	0.07
Adults		1.77	1.73	0.04
	1 day			
Eggs		1.14	0.98	0.16
Nauplii		0.86	0.83	0.03
Copepodites		1.02	0.99	0.03
Adults		0.65	0.64	0.01

Table 2. Results of model runs using bongo samples.

Species and Stage	t	σ_i	P_i	G_i
*Centropages typicus	1 day			
σ_2 = 30%				
Copepodites		0.45	0.42	0.03
Adults		2.18	2.11	0.07
σ_2 = 50%				
Copepodites		0.44	0.41	0.03
Adults		2.18	2.11	0.07
σ_2 = 70%				
Copepodites		0.44	0.41	0.03
Adults		2.18	2.11	0.07
	2 days			
σ_2 = 30%				
Copepodites		0.52	0.45	0.07
Adults		2.25	2.09	0.16
σ_2 = 50%				
Copepodites		0.50	0.44	0.07
Adults		2.25	2.09	0.16
σ_2 = 70%				
Copepodites		0.49	0.43	0.06
Adults		2.25	2.09	0.16

Table 2. Continued

Species and Stage	t	σ_i	P_i	G_i
	3 days			
σ_2 = 30%				
Copepodites		2.02	1.62	0.40
Adults		1.27	1.14	0.13
σ_2 = 50%				
Copepodites		1.99	1.59	0.40
Adults		1.27	1.14	0.13
σ_2 = 70%				
Copepodites		1.84	1.47	0.37
Adults		1.27	1.14	0.13
	4 days			
σ_2 = 30%				
Copepodites		0.41	0.30	0.11
Adults		2.76	2.40	0.36
σ_2 = 50%				
Copepodites		0.37	0.27	0.10
Adults		2.76	2.40	0.36
σ_2 = 70%				
Copepodites		0.33	0.24	0.09
Adults		2.76	2.40	0.36

Table 2. Continued

Species and Stage	t	σ_i	P_i	G_i
	1 day			
Pseudocalanus sp.				
σ_2 = 30%				
Copepodites		1.37	1.27	0.10
Adults		2.09	2.03	0.06
σ_2 = 50%				
Copepodites		1.37	1.27	0.10
Adults		2.09	2.03	0.06
σ_2 = 70%				
Copepodites		1.36	1.26	0.10
Adults		2.09	2.03	0.06
	2 days			
σ_2 = 30%				
Copepodites		0.38	0.33	0.05
Adults		1.52	0.11	1.41
σ_2 = 50%				
Copepodites		0.37	0.32	0.05
Adults		1.52	0.11	1.41
σ_2 = 70%				
Copepodites		0.35	0.30	0.05
Adults		1.52	0.11	1.41

Table 2. Continued

Species and Stage	t	$\dot{\sigma}_i$	P_i	G_i
	3 days			
σ_2 = 30%				
Copepodites		0.37	0.30	0.07
Adults		0.77	0.69	0.08
σ_2 = 50%				
Copepodites		0.35	0.28	0.07
Adults		0.77	0.69	0.08
σ_2 = 70%				
Copepodites		0.33	0.26	0.07
Adults		0.77	0.69	0.08
	4 days			
σ_2 = 30%				
Copepodites		0.29	0.21	0.08
Adults		1.62	1.41	0.21
σ_2 = 50%				
Copepodites		0.26	0.19	0.07
Adults		1.62	1.41	0.21
σ_2 = 70%				
Copepodites		0.23	0.17	0.06
Adults		1.62	1.41	0.21

*Assume σ_1 = 90%; σ_2 tested at 30%, 50% and 70%.