Inverse modelling of developmental parameters in Euphausia pacifica: The relative importance of spawning history and environmental forcing to larval stage-frequency distributions

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Factors potentially influencing zooplankton larval population dynamics and recruitment include advection, larval processes, biotic interactions (predation, competition, etc.), and spatial-temporal variability in the magnitude of egg release (Fig. 1). Research has shown that oceanographic conditions can impact larval developmental pathways and demography in *Euphausia pacifica*, thus contributing to variability in recruitment (Brinton, 1976; Knight, 1984). The focus of this paper is to evaluate variability in *E. pacifica* larval stage-frequency distributions observed during two cruises in the Southern California Bight. Relative comparisons of back-calculated (inverse modelled) stage-specific vital parameters (stage duration and specific mortality) and histories of egg input were conducted. The results of the model, in the context of the sampled oceanographic environment and observed larval developmental pathways, were evaluated to determine the relative importance of variability in developmental and specific mortality rates vs. egg-input variability at different scales (within cruises and between cruises).

Within-Cruise Comparisons

Within-year, among-station, differences in stage-frequency structure are more likely associated with developmental loss (variability in stage duration or specific mortality) than with variability in egg input. Although the larval demography for cruise S9602 generally reflects sampling during the crescendo of a spawning pulse, and that for J9701 suggests sampling toward the end of a pulse (Fig. 2A and 3A, respectively), it is unlikely that differences among stations were forced by *spatial* variability in spawning histories. Back-calculated solutions of S9602 relative egg-input indicate that if station differences in larval stage-frequencies was driven by egg-input alone, as much as a 2000% fluctuation in egg-input among stations is required (Fig. 2B). Variability to such an extent exceeds that observed by Brinton (1976) even between peak-spawning and background-spawning winter months (approximately $<500\%$). The differences in relative egg input calculated for J9701 (Fig. 3B) is considerably less than the S9602 solutions, but egg inputs for the "warm" stations would have to have been more than twice those of the cool stations for stages CI-FII (a period representing about a month and approximately 50% of the total larval developmental time at ambient temperatures; Ross, 1981). Such extreme differences in the magnitude of egg release during a spawning peak, persisting over 1 km spatial scales (station spacing for S9602) and month time scales, is unlikely.

Due to the exponential nature of larval mortality in the model, the difference in stage duration or specific mortality necessary to explain observed station larval demographics is considerably less than that for egg inputs. The back-calculated solutions of relative developmental loss (stage duration and specific mortality) for the "blue" S9602 stations were more positive than those for the higher chlorophyll "green" stations (Fig. 2C).

The necessary differences in back-calculated stage duration or specific mortality necessary to explain among-station differences in larval stage-frequencies was considerably less than the egg input solutions for the J9701 station groups as well (Fig. 3C). The back-calculated developmental parameters for the "cool" J9701

stations were more positive than the "warm" station solutions for stages CI-FII. The elevated mortality (approximately 10-50%) for these stages at the cool stations is consistent with prolonged developmental times associated with the 1-3°C cooler temperatures.

Between-Cruise Comparisons

A peak in winter spawning activity in the Southern California Bight typically occurs during the months of January-February (Brinton, 1976), however, between-cruise comparison of back-calculated egg inputs (Fig. 4B) suggests that the cruise stage-frequencies (Fig. 4A) reflect sampling at different times during a spawning pulse. Cruise S9602 appears to have sampled toward the peak of a "normal" January-February spawning pulse, while J9701 indicates sampling when the magnitude of spawning activity had diminished. Alternatively, the predominance of younger larvae in the stage-structures of the S9602 stage-frequencies could be the result of elevated mortality in the later larval stages relative to J9701 (Fig. 4C). Such an increase in mortality might be attributable to increased stage durations or specific mortalities, however, an elevated developmental loss during S9602 contradicts observed temperature-chlorophyll conditions and larval developmental pathways. It is more likely that between-cruise differences in larval age-structure were driven by different histories of egg input than by differences in developmental parameters.

Application of a simple inverse model, and some significant assumptions, has allowed me to evaluate the impact of variability in developmental and specific mortality rates in relation to variability in spawning histories in forcing observed differences in larval stage-frequency distributions. A more rigorous comparison of these factors would require an abundance of shiptime and ancillary larval rearing data at prohibitive cost and effort. Ideally one would obtain a time series of egg release prior to the Lagrangian sampling of the larval population, requiring approximately 145 days of ship time (i.e. twice the duration of larval development). Additionally, shipboard observations of stage durations and specific-mortalities at ambient temperature/food conditions, in concert with a time series of stage-frequency curves, would afford the application of more quantitative techniques of estimating stage-specific mortality rates. The inverse method used, the set of assumptions applied, and the relative comparisons of parameters conducted has afforded the opportunity to address hypotheses that otherwise could only be considered by a large-scale research program.

References

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Ross, R. M., 1981. Laboratory culture and development of *Euphausia pacifica*. Limnology and Oceanography 26(2): 235-246.

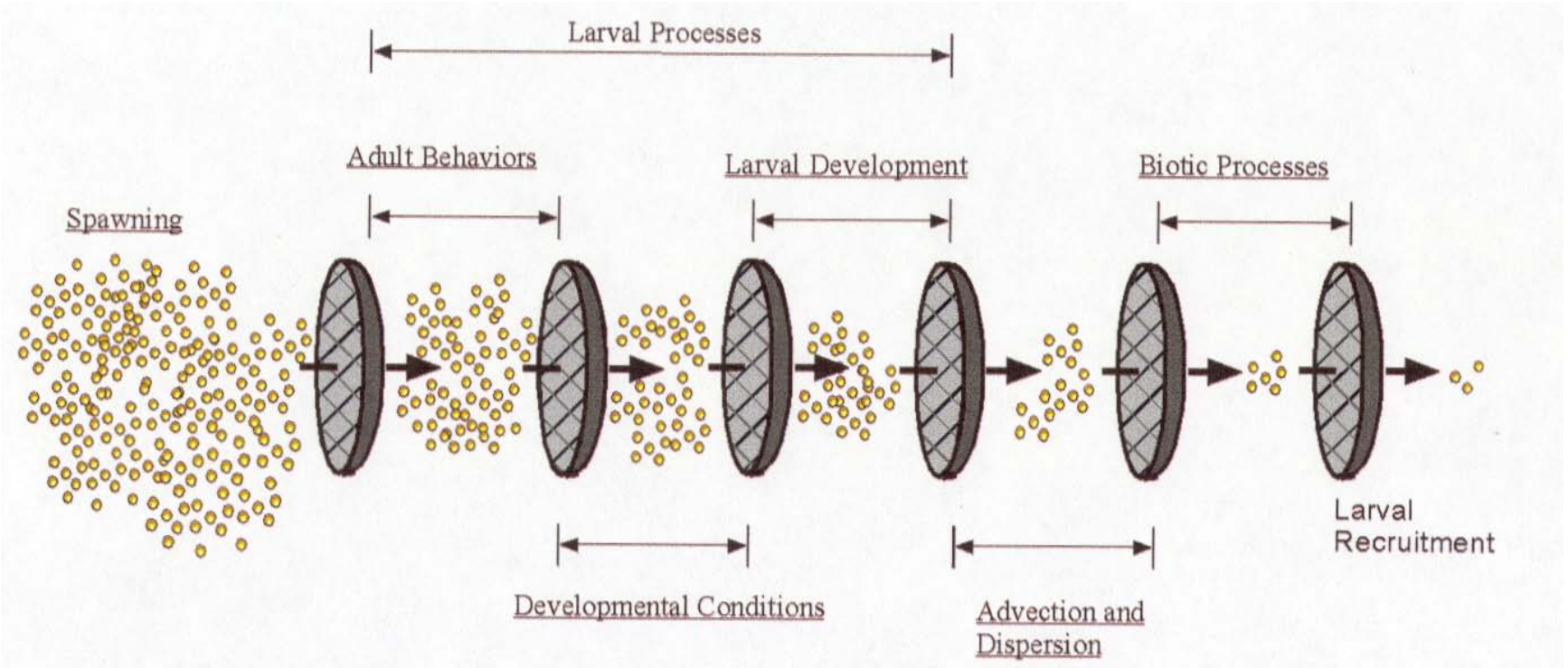

Fig. 1 Schematic representation of processes and behaviours which affect zooplankton recruitment dynamics in general, and *Euphausia pacifica* in particular. The focus of this dissertation includes items grouped under "larval processes".

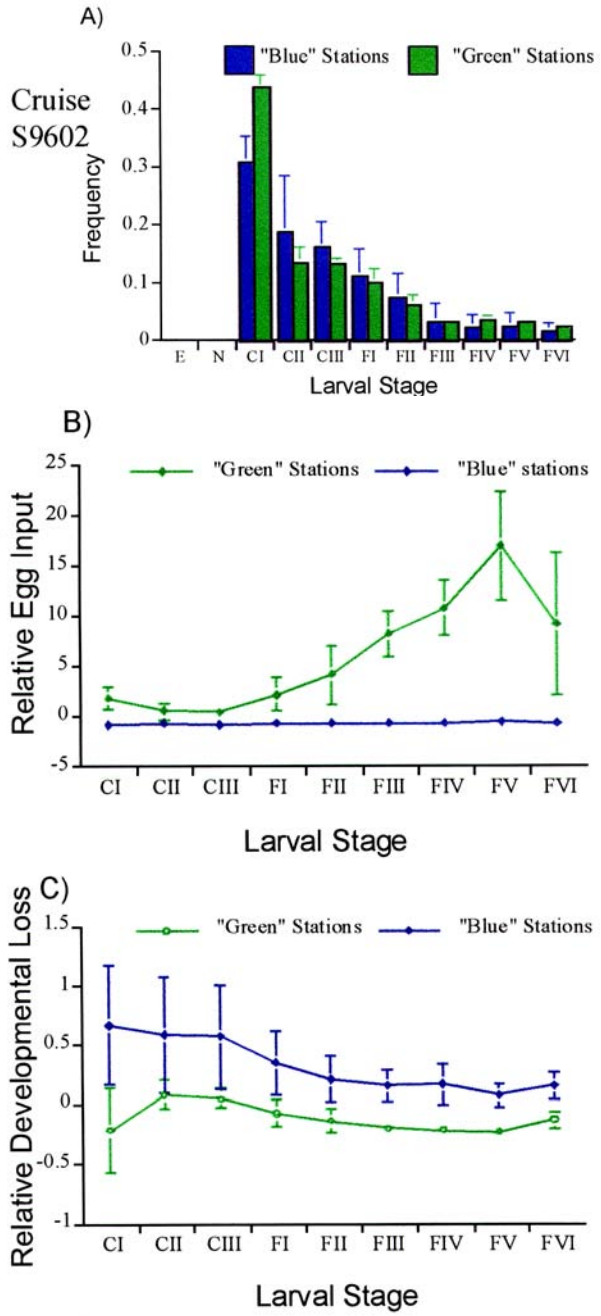

Fig. 2 A) Larval *Euphausia pacifica* stage-frequency distributions for high-and low-chlorphyll station groups during the February 1996 cruise. B) Back-calculated values of relative egg input. C) Back-calculated values of relative developmental loss.

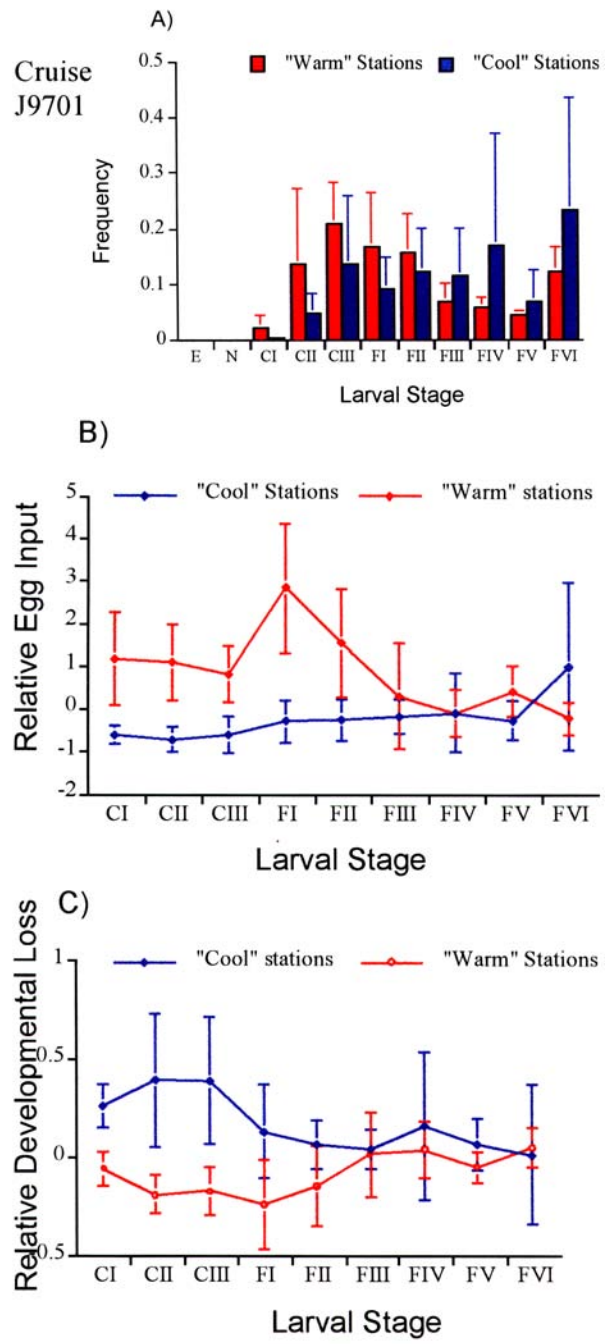

Fig. 3 A) Larval *Euphausia pacifica* stage-frequency distributions for warm- and cool-temperature station groups during the January 1997 cruise. B) Back-calculated values of relative egg input. C) Back-calculated values of relative developmental loss.

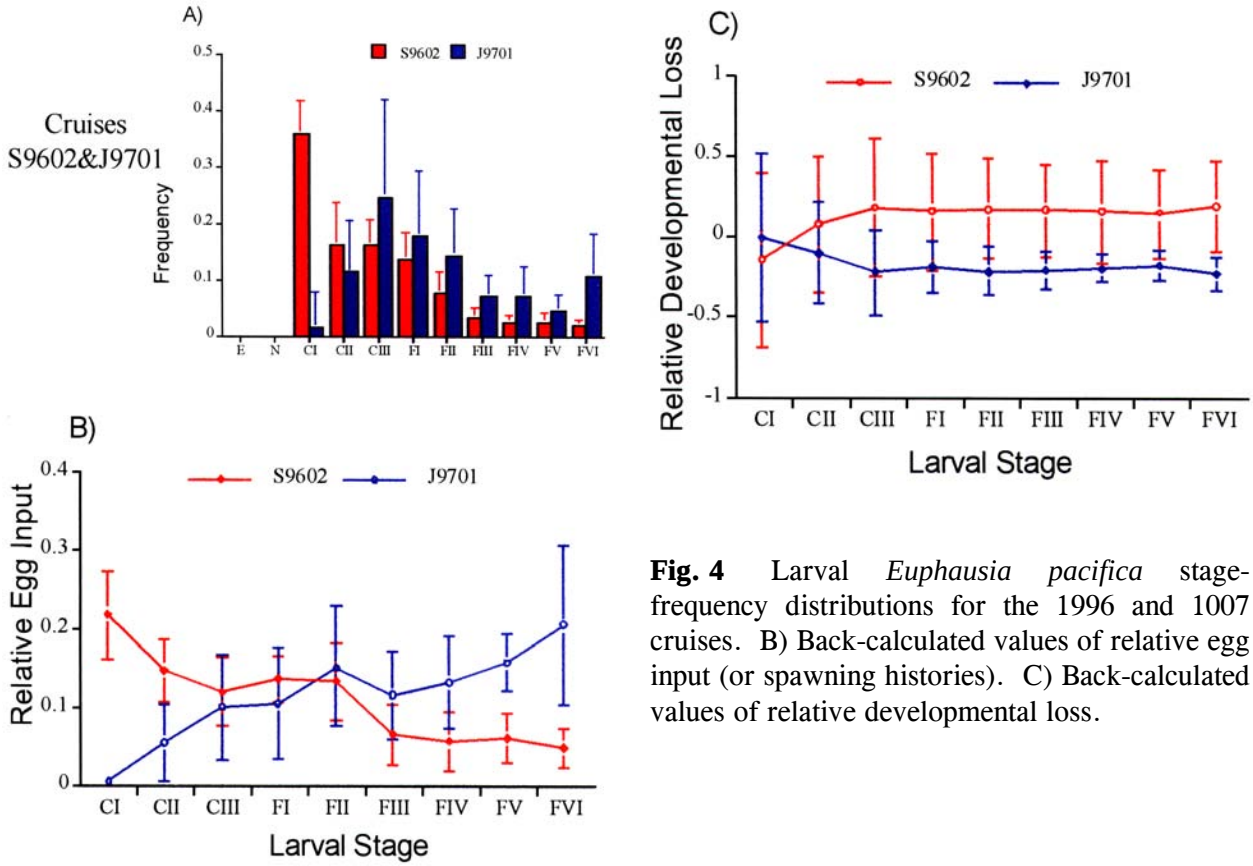

Fig. 4 Larval *Euphausia pacifica* stage-frequency distributions for the 1996 and 1007 cruises. B) Back-calculated values of relative egg input (or spawning histories). C) Back-calculated values of relative developmental loss.

An ecosystem model with zooplankton vertical migration focused on Oyashio region

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An ecosystem model with eight compartments (Fig. 1) was developed in order to describe a Northern Pacific primary and secondary production. This model was made by the request of PICES GLOBEC CCCC Program. Model equations describe the interactions of nitrate, ammonium, two phytoplankton size fractions (tentatively, these are diatom and dinoflagellate), two zooplankton size fractions (tentatively, copepod and microzooplankton), PON, and DON. Formulations for the biological processes are based primarily upon KKYS(Kawamiya et al., 1996, 1997). One dimensional physical-biological coupled model including mixed layer closure model is used to simulate time dependent features of ecosystem off Sanriku district(Fig. 2). Time series of nutrient and plankton distributions obtained from Hokkaido National Institute of Fisheries provide verification of model results. The simulated results were well reproduced the seasonal and interannual change of ecosystems there. Model simulations indicate that vertical migration of copepod is a potentially important factor in determining the trophic structure in the change of phytoplankton species during spring bloom.