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Environmentally forced variability in larval development and stage-structure: Implications for the recruitment of Euphausia pacifica (Hansen) in the Southern California Bight

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Summary

The intent of this field work was to provide empirical evidence in observed larval distributions, stage-structure, and inferred developmental pathways of whether the developmental regime affects the development and abundance of particularly elastic larval stages. Armed with the insights from life-history modelling and demographic analyses (Rumsey and Franks, 1999), I sought to address particular aspects of the *Euphausia pacifica* life-history. First, how are the larval stages distributed vertically in the field with respect to each other and the developmental environment? Second, as indicated by the vertical distribution of calyptopis I stage larvae, is there evidence that females restrict the depth-range of spawning to enhance the profitability of the initial developmental environment? Third, I investigated whether there was variability in furcilia I-II developmental pathways over short (mesoscale) spatial scales, and if found, with what oceanographic conditions particular pathways are associated. Fourth, I described the spatial variability of larval stage-frequency distributions, and the environmental conditions and/or developmental processes with which such variability was associated.

Oceanographic and Demographic Data

Two cruises were conducted in the Southern California Bight, south of the Santa Barbara Channel and Channel Islands, in the winters of 1996 (cruise S9602) and 1997 (J9701). Samples of *Euphausia pacifica* larvae were obtained by MOCNESS transects across mesoscale oceanographic features (Fig. 1). CTD-fluorometer profiles accompanied each station (Fig. 2). *E. pacifica* larvae were identified to stage using morphological criteria (Boden, 1955). The developmental instar of pleopod development was noted for furcilia I-II stage larvae, and the dominant furcilia I-II pleopod developmental pathways determined for each station (after Knight, 1984; Lavaniegos-Espejo, 1994).

Spawning Distribution

Despite differences in the vertical distribution of *E.* pacifica larval stages between cruises, the majority ($>95\%$) of larval stages were found in the upper 100 m (Fig. 3). Eggs were not sampled during either cruise, nonetheless, the presence/absence of the initial larval stages (being weakly swimming, e.g. calyptopis I) with depth is indicative of the depth range of spawning by gravid females. Although the vertical distribution of post-larvae in the night-time samples of both cruises was predominantly in the upper 150 m, their daily ambit spanned 0-300 m depth

(observed in J9701 day samples; Mauchline and Fisher, 1969; Brinton, 1976). The distribution of CI larvae is evidence that the depth range of egg release by *E. pacifica* is restricted relative to that of gravid females. Restricting the depth range of egg release to < 100 m would ensure warmer temperatures (and thus shorter developmental times) as well as enhanced availability of phytoplankton-food for first-feeding larvae.

Furcilia I-II Developmental Pathways

Prolonged developmental times, associated with indirect furcilia I-II pleopod developmental pathways, represent morphogenic plasticity that is likely an adaptive trait in neritic euphausiids inhabiting inherently variable environments. A predominance of indirect pleopod developmental pathways was associated only with the "cool" stations of cruise J9701 (Fig. 4). The proximate developmental temperatures for these larvae were 1-3 °C cooler (0-100 m) relative to temperature profiles for the other J9701 stations and the S9602 stations (Fig. 2). Furcilia I-II developmental pathways were predominantly direct at all S9602 stations (Fig. 4), and the cyclonic eddy with which they were associated was a persistent feature, comparable to the time scale of *E. pacifica* larval development. It is surprising, given the comparatively low chlorophyll conditions for cruise S9602 (Fig. 2), that furcilia development was so direct. Despite > 4-fold difference in chlorophyll fluorescence between cruises (Fig. 2) the proportion of S9602 indirect developmental pathways was indistinguishable from the J9701 "warm" stations, suggesting that temperature regime has a greater impact on early furcilia development than does ambient chlorophyll.

Winter and spring euphausiid abundances (*E. pacifica* included) have increased over the last 40 years in the Southern California Bight (Brinton, 1996), concurrent with a 1.5°C increase in surface temperatures and an 80% decrease in overall macrozooplankton biomass (Roemmich and McGowan, 1995). In contrast to overall macrozooplankton, one might expect diminished euphausiid recruitment success and indirect developmental pathways to be correlated with cooler developmental temperatures. The results of elasticity analyses (Rumsey and Franks, 1999) and the association of indirect furcilia I-II developmental pathways with cooler temperatures during cruise J9701 are in accordance with this notion. Observations of direct furcilia development associated with locally cooler temperatures over a broad geographic range (Puget Sound, Ross et al., 1982; Baja California, Lavaniegos, 1994; Southern California Bight, Knight, 1984), however, are difficult to reconcile with the observations of cruise J9701 and Brinton (1996). Furthermore, it is difficult to reconcile the impaired development observed in association with 10-12 °C conditions given that viable populations farther north in *E. pacifica*'s range certainly endure much colder developmental temperatures yet are not necessarily characterized by indirect furcilia development and diminished recruitment success. The response and tolerance of larval development to temperature heterogeneity may be determined by the temperature conditions during oogenesis and/or at egg release. Thus, variability in *E. pacifica* larval development may be in response to temperature anomalies rather than absolute conditions. Alternatively, the inconsistent relationship between development and temperature among regional populations could result from different physiological "races", each adapted to a distinct temperature range.

Larval Stage-Frequency Distributions

The high proportion of calyptopis I (CI) larvae in the stage-frequency distributions of cruise S9602 (Fig. 5A), suggest that spawning was ongoing or had only recently ceased. The greater proportion of CI larvae at the "green" stations may reflect differences in recent egg release or differences in egg through CI mortality among stations. Although small-scale (~ 1 km) differences in egg-inputs remains a possible contributing factor, associated differences among stations in chlorophyll conditions suggest the importance of differences in CI mortality. The CI stage is the first-feeding euphausiid larval stage. Several investigators have asserted that mortality during the CI stage is especially sensitive to environmental conditions (Brinton, 1976; Ross et

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al., 1988; Paul et al., 1990), in particularly conditions of food-availability (Hofmann et al., 1992). The greater proportion of CI larvae at the green stations, with significantly greater chlorophyll (0-25 m), may reflect lower mortality at these stations due to more favorable food conditions. Additionally, the proportion of post-larvae (predominantly juveniles and non-mature adults) present at the green stations was greater than at those stations with lower surface chlorophyll. The proportion of post-larvae at a given station provides a rough index of local recruitment success (as most of the post-larvae sampled were juveniles, presumably having recently completed larval development). Although the chlorophyll regime appeared to have little impact on observed furcilia development (previous section), food availability during early larval development in *E. pacifica* may affect CI survivorship and subsequent larval recruitment. Lavaniegos-Espejo (1992) found that laboratory survivorship of *N. simplex* larvae was most affected by state of calyptopis development at the time of collection. The increased survivorship of larvae that started out as CIII vs. CII larvae in her experiments suggests that the food history of calyptopis phase larvae can impact the survivorship of later stages.

Differences in larval stage-frequencies during cruise J9701 (Fig. 5B) were driven mostly by variability in the proportion of the later furcilia stages (furcilia III-VI). FIII-FVI larvae at the "warm" stations exhibited direct pathways of pleopod development, relative to the cooler stations. Accelerated FIII-FVI developmental times associated with warmer temperatures could result in earlier recruitment and result in fewer larvae of these stages sampled. The higher proportion of post-larvae associated with the warm stations further supports this notion of earlier recruitment.

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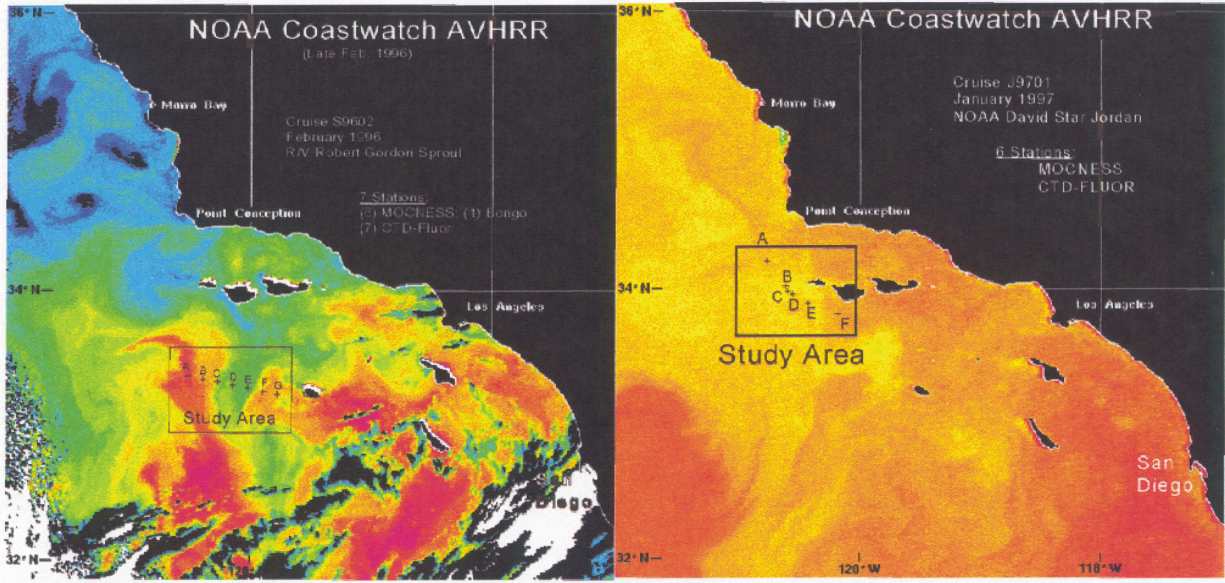
Fig. 1 AVHRR images of sea surface temperature illustrating the study region and station locations for the February 1996 (S9602) and January 1997 (J9701).
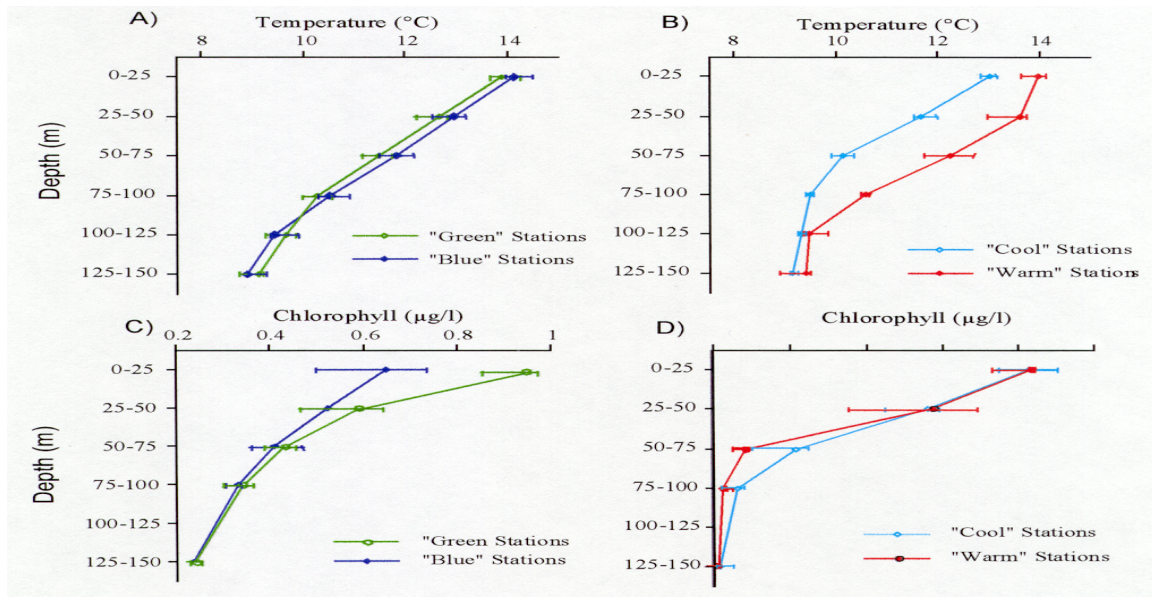

Fig. 2 Temperature and chlorophyll profiles S9602 (A and C) and J9701 (B and D). To facilitate discussion and presentation, high- and low-chlorophyll stations, and warm- and cool-temperature stations are grouped together for the S9602 and the J9701 cruises, respectively.
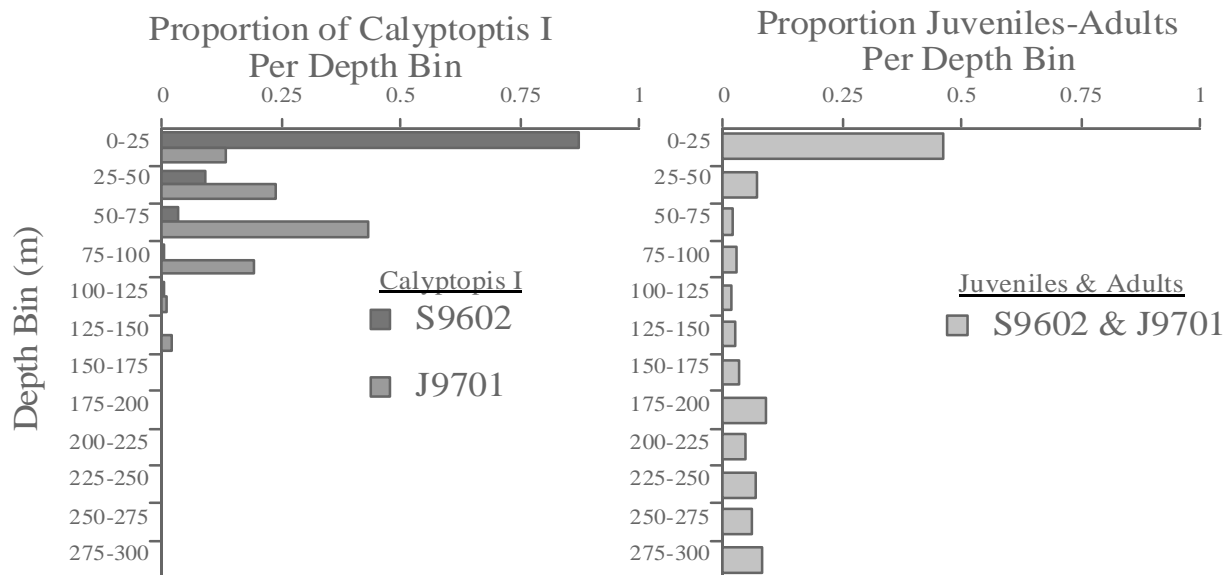
Fig. 3 Inferred depth range of egg release for *Euphausia pacifica* females from the depth distribution of calyptopis I stage larvae. The proportion of calyptopis I stage larvae sampled per 25 m depth bin is presented.
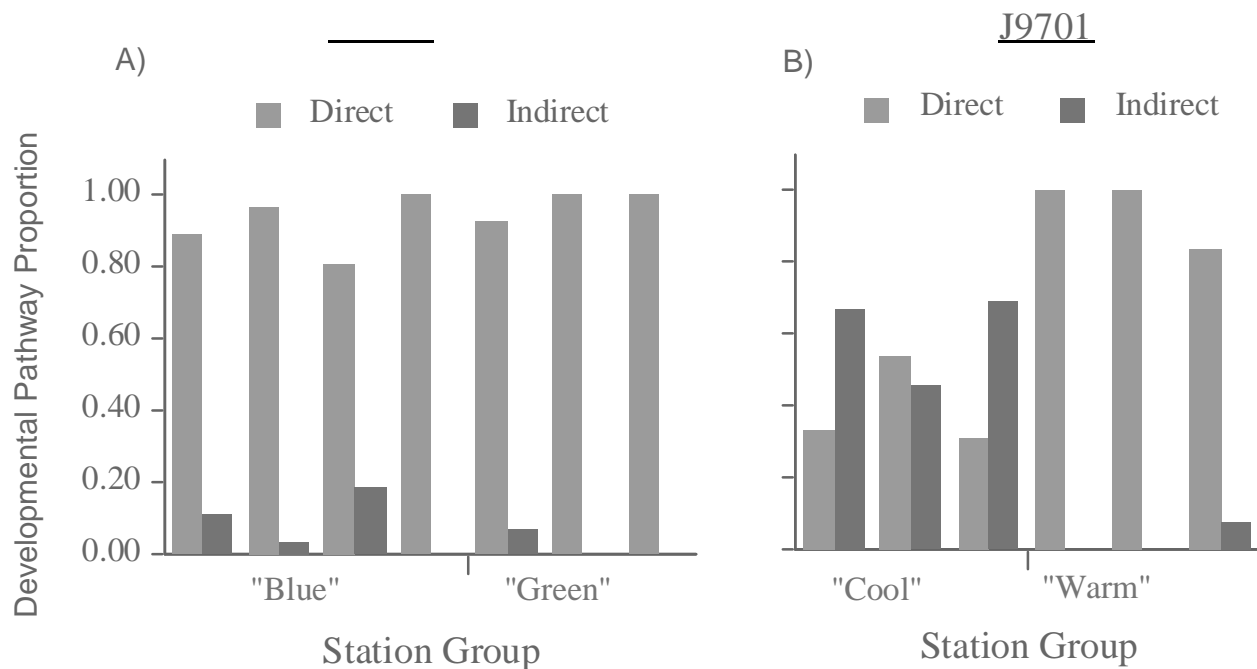

Fig. 4 The proportion of direct vs. indirect developmental pathways, of furcilia I-II stage *Euphausia pacifica* larvae. Data are presented for stations grouped according to chlorophyll regime for cruise S9602 (A), and temperature regime for cruise J9701 (B). ** (p<0.001); * (p<0.025); ns (not significant).