

Spatial differences in mortality of *Calanus pacificus* within the California Current System

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Received November 15, 2007; accepted in principle December 28, 2007; accepted for publication December 29, 2007; published online January 28, 2008

Corresponding editor: Roger Harris

A vertical life table method was used to estimate patterns of mortality of late developmental stages of Calanus pacificus in the southern sector of the California Current System from seven California Cooperative Oceanic Fisheries Investigations (CalCOFI) cruises (three spring, four late autumn–early winter). Copepodid stage durations were described as a continuous function of both food concentration and temperature from reanalysis. This function was combined with vertical profiles of temperature and Chl a to estimate stage durations in the field and solve for instantaneous mortality rates of two stage pairs: C5/adult females and C5/adult males. Male mortality rates averaged two to three times higher than the corresponding female mortality rates. There was no significant difference between seasons (spring versus winter) in either male or female mortality rates. There was a consistent spatial pattern of higher mortality rates of both males and females in the inshore region relative to the offshore region. This inshore increase in mortality rates is the opposite of that expected from the effects of food limitation, but is correlated with an index of abundance of zooplanktivorous fishes obtained from the CalCOFI ichthyoplankton series (a fishery-independent data source). Elevated predation risk may mitigate the inferred benefits to zooplankton of increased food supply.

INTRODUCTION

Coastal upwelling zones have traditionally been considered regions of elevated primary production, with relatively simple food webs permitting mesozooplankton to benefit from high concentrations of large, readily edible food particles. Consequently, secondary production by mesozooplankton is usually thought to be elevated in such regions because of enhanced rates of somatic growth and egg production (e.g. Mullin, 1991; Smith and Lane, 1991; Irigoien *et al.*, 2005). However, better foraging opportunities also may be accompanied by increased risks, for example, predation. Increasingly, zooplankton behavior and life-history traits are considered to represent trade-offs between feeding opportunities and associated risks rather than responses to single factors in the surrounding environment (Aksnes and Giske, 1990; Ohman *et al.*, 2002).

Models of zooplankton population dynamics rarely incorporate spatial differences in zooplankton risks, in large part because of the paucity of empirical information that would help constrain rates in nature. Hence, the most common assumption is that at a given stage of the life history, mortality rates are spatially uniform (e.g. Lynch *et al.*, 1998; Batchelder *et al.*, 2002). Although evidence is emerging that there may be geographic regions of elevated mortality (e.g. Eiane *et al.*, 2002; Ohman *et al.*, 2004; Li *et al.*, 2006; Ohman *et al.*, 2008), such spatial contrasts are yet to be incorporated into forward models of zooplankton dynamics.

Here, we test the spatial uniformity of zooplankton mortality in the southern sector of the California Current System, a region characterized by elevated phytoplankton biomass and primary production in the vicinity of Pt. Conception (Kahru and Mitchell, 2000, 2002).

We base our analysis on juvenile (copepodid stage 5) and adult *Calanus pacificus* Brodsky because, as the largest developmental stages, these individuals are responsible for a disproportionate fraction of copepod secondary production. In addition, they are quantitatively sampled by the CalCOFI (California Cooperative Oceanic Fisheries Investigations) sampling protocol.

METHODS

We described the durations of copepodid stages 2 (D_2) through 5 (D_5) as a function of both food concentration and temperature from Vidal’s (1980a, b) experimental work with *C. pacificus*. Food concentration (in volumetric units of parts per million) was converted to C units (P' , $\mu\text{g C/L}$) using the average value of $61.6 \mu\text{g C/L/ppm}$ from experimental sets 1 through 4 in Vidal (1980a). The minimum stage duration (D_{min}) as a function of temperature (T ; 8° , 12° , 15.5°C) was taken from Table I in Vidal (1980b), expressed as the difference between the cumulative times between successive stage pairs. We used a Bělehrádek function (McLaren *et al.*, 1989) to describe stage duration as a continuous function of temperature (see Table I for parameter values):

$$D_{\text{min}} = a(T - k)^{-2.05} \tag{1}$$

Vidal (1980b) reported the parameter ε , which describes the slope of the hyperbolic relation between stage duration and food concentration. We converted values of ε in Vidal’s Table I to units of $\mu\text{g C/L}$ ($\beta = \varepsilon/61.6$) and described β as a continuous function

of temperature ($r^2 = 0.939$):

$$\beta = qT^s \tag{2}$$

Equations (1) and (2) above were substituted into equation (1) in Vidal (1980b), to describe stage duration (D) as a joint function of temperature ($^\circ\text{C}$) and food concentration (P' , $\mu\text{g C/L}$):

$$D = \frac{a(T - k)^{-2.05}}{1 - e^{-(qT^s)P'}} \tag{3}$$

Equation (3) is a preferred expression over the values reported in Table 3 of Vidal (1980b) because the latter tend to underestimate D at low food concentrations, at intermediate and higher temperatures. Parameter values for equation (3) may be found in Table I and the resulting values of stage durations in Fig. 1. We use only the function for C5 in the present study, but include parameter values for additional stages for use by others.

Equation (3) was combined with *in situ* vertical profiles of temperature and phytoplankton carbon derived from Chl *a* concentration, defined from conductivity-temperature-depth (CTD) profiles plus hydrocasts at 20 depths at each station, to estimate stage durations in the field. We assumed that the average temperature and food concentration experienced by copepods were those at the depth of the chlorophyll maximum layer. Vertically integrated Chl *a* is highly correlated with maximum Chl *a* in this region (Mullin, 1991). Chl *a* was converted to organic C assuming a C:Chl *a* ratio of 50. We solved for the instantaneous mortality rates of two stage pairs from equation (4): C5/adult females ($m_{5/F}$) and C5/adult males ($m_{5/M}$), where $r_{5/A}$ is the ratio of either C5/adult females or C5/adult males, assuming a 1:1 primary sex ratio:

$$m_{5/A} = \frac{\ln(r_{5/A}) + 1}{D_5} \tag{4}$$

Table I: Parameter values describing stage durations of Calanus pacificus as a function of temperature and food concentration, for copepodid stages 2 (C2) through 5 (C5), based on a reanalysis of the results in Vidal (1980b)

Developmental stage	<i>a</i>	<i>k</i>	r^2	<i>q</i>	<i>s</i>	r^2
C5	3124	-9.101	0.960	0.0581	-0.5174	0.939
C4	2120	-9.101	0.936	0.1789	-0.8796	0.989
C3	1773	-9.101	0.982	0.9160	-1.4806	0.999
C2	1582	-9.101	0.921	0.8629	-1.3991	0.935

Parameters *a*, *k* from text equation (1); parameters *q*, *s* from text equation (2); r^2 denotes percentage of variance explained by the fitted relation.

The stage-specific copepod enumerations utilized in this study were published by the late M.M. Mullin or by G.A. Rebstock, based on samples taken from seven CalCOFI cruises. Three cruises were conducted in spring (7804, 9304, 9504, where the first two digits indicate the year and the second two the month) and four in late autumn–early winter (8810, 8911, 9011, 9301). These cruises were selected because copepod stage structure (Mullin, 1997; Rebstock, 2001), Chl *a*, and temperature (see <http://calcofi.org/newhome/data/>) were all measured. Zooplankton samples were taken with 71-cm diameter, 505- μm mesh, metered double-oblique

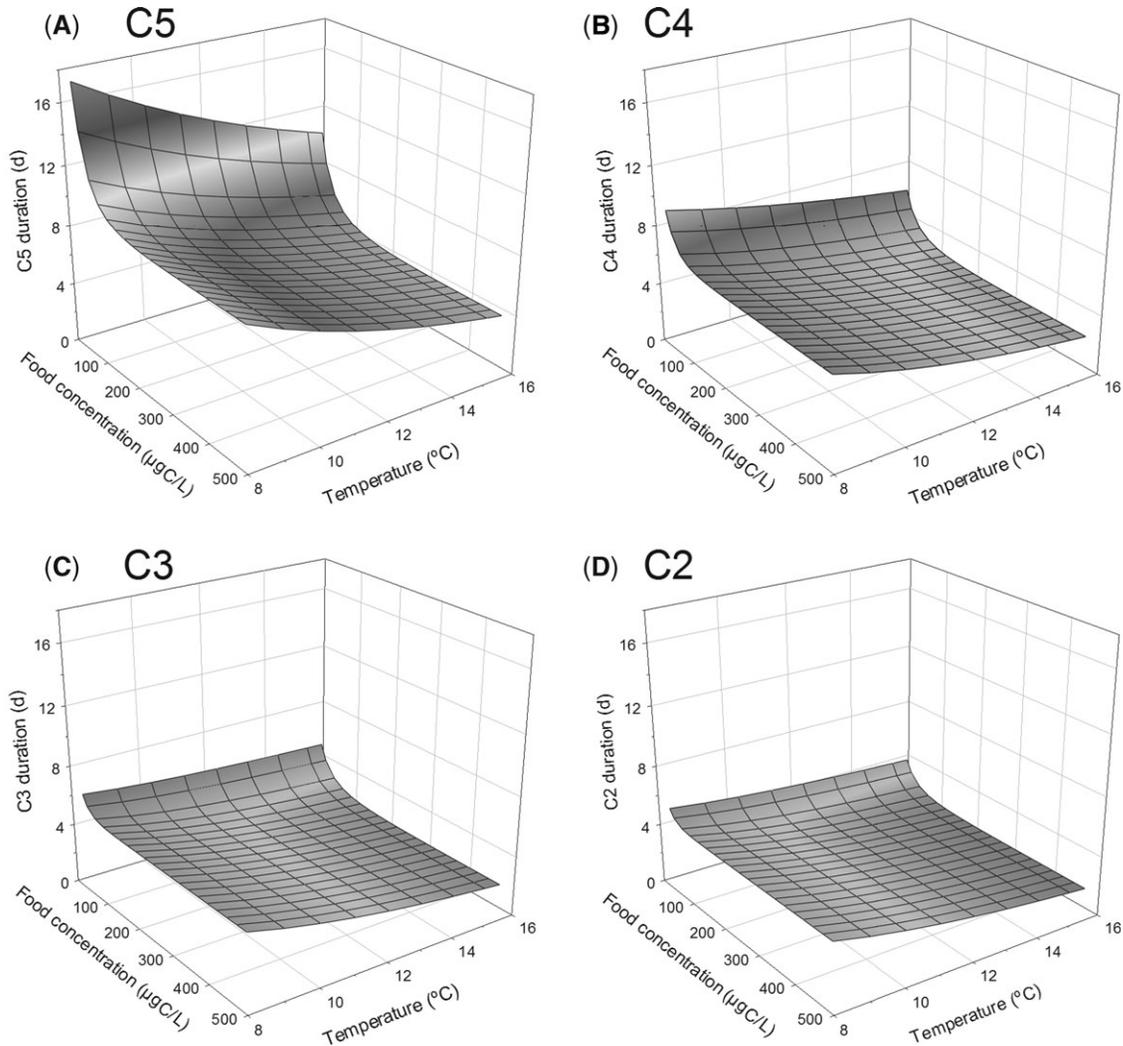


Fig. 1. Dependence of the duration of *Calanus pacificus* copepodid stages (A) C5, (B) C4, (C) C3 and (D) C2 on temperature and food concentration, based on a reanalysis of the results in Vidal (1980).

bongo tows from 210–0 m, or to within 10 m of the bottom if restricted by bathymetry. Previous results show that dormant stages of *C. pacificus* occur well below 210 m (Ohman *et al.*, 1998; Johnson, 2004, 2007). Epipelagic *C. pacificus* females show virtually continuous, year-round reproduction in this region (Mullin and Brooks, 1967; Mullin, 1991, 1993). Thus, there is no well-defined cohort structure that would restrict application of vertical life table methods. Copepod stage ratios and mortality estimates were calculated from 9 to 52 stations per cruise. Simulations previously showed that approximately eight replicate stage ratio estimates are needed to obtain stable estimates of mortality (Aksnes and Ohman, 1996).

An index of abundance of epipelagic zooplanktivorous fishes was developed from the extensive CalCOFI

ichthyoplankton database (Southwest Fisheries Science Center, National Marine Fisheries Service; Hsieh *et al.*, 2005). Based on the feeding ecology data from FishBase (Froese and Pauly, 2005), we identified 22 fish taxa in the CalCOFI database as zooplanktivorous (Fig. 3). From these sources, we calculated the average abundances of larval stages of 21 taxa considered, as adults, those most likely to represent predation pressure on calanoid copepods.

RESULTS

Average values of phytoplankton-derived organic carbon and temperature show the classical spring upwelling conditions of reduced temperatures and

elevated phytoplankton biomass along the California coast in the vicinity of Pt. Conception (34.4°N, 120.5°W) near the northeast edge of the sampling pattern (Fig. 2a, c). In contrast, the same region shows markedly higher and more uniform temperatures, combined with reduced average phytoplankton biomass, in the late autumn–early winter period (Fig. 2b, d), although phytoplankton concentrations remain higher nearshore than in the offshore zone. All three developmental stages of *C. pacificus* considered (C5, adult males, adult females) show elevated abundances in the nearshore zone (Fig. 2e–j). In winter there is a suggestion of reduced concentrations of *C. pacificus* in the southeast sector nearshore, a region which typically experiences strong inflow from the south in the Inshore Countercurrent at this time of year (e.g. Lynn and Simpson, 1987). Densities of *C. pacificus* (sum of the three stages) were positively correlated with phytoplankton carbon biomass (for either individual cruises or all cruises combined; $P < 0.05$, Spearman's rho).

Average instantaneous mortality rates of both C5/adult male and C5/adult female *C. pacificus* showed a consistent spatial pattern of elevated mortality in the nearshore zone (defined as inshore of the dashed red line in Fig. 3a), in both spring and autumn–winter (Fig. 3a–d). Individual cruises nearly always showed elevated copepod mortality in the inshore zone, with the sole exception of C5/Males on cruise 7804 (Fig. 4a, b). For inshore/offshore comparisons, the offshore zone was defined as extending from the dashed line out to and including sta. 100, because the abundance of both copepods and fish are so low beyond this point. Using all data would show the same result, but inflate the contrast. Both C5/Female ($P < 0.01$, Mann–Whitney U test) and C5/Male ($P < 0.05$) mortality rates were significantly higher inshore than offshore. Fish larvae also showed consistently elevated abundances in the nearshore zone relative to the offshore (Fig. 4c, $P < 0.05$).

C5/Male mortality rates averaged two to three times higher than corresponding C5/adult female rates ($P < 0.001$, Wilcoxon-matched pairs signed rank test; note the scale differences between Fig. 3a, b and Fig. 3c, d). In addition, the disparity between inshore and offshore mortality rates was somewhat greater in the case of females than males. The mean inshore:offshore ratio for C5/adult female mortality rates was 3.40, while that for C5/adult males was 1.63 ($P = 0.06$, Wilcoxon-matched pairs signed rank test). Mortality rates of both C5/Female ($P < 0.001$, Spearman's rho) and C5/Male ($P < 0.01$) *C. pacificus* were correlated with abundances of fish.

DISCUSSION

Both the average spatial pattern of copepod mortality as well as estimates for seven individual cruises show consistently elevated mortality in the nearshore zone relative to the offshore domain of the California Current System. This result is not consistent with the hypothesis of spatial uniformity of zooplankton mortality rates. It implies that the probability of successful development from the copepodid V to the adult stage, and therefore initiation of copepod reproduction, varies substantially depending on the geographic subregion in which the copepods reside.

It is not feasible to analyse specific locations of elevated or diminished mortality on a cruise-by-cruise basis because of the need for multiple estimates to obtain a robust mortality value (Aksnes and Ohman, 1996). Averages by season suggest that a limited number of locations in the inshore region could be sites of especially elevated mortality, although the broader areal means over the entire nearshore region are more reliable because of the larger number of stations included in such averages.

We suggest that increased predation pressure in the nearshore region, especially by zooplanktivorous fish, may be responsible for elevated copepod mortality. While our surrogate estimate of fish abundance is strongly correlated with copepod mortality rates, there is not a close spatial match on a station-by-station basis. In spring, in particular, maximum abundance of larval fishes is displaced to the south of the apparent maximum in mortality. However, as noted, areally averaged mortality is more robust than a single location. Also, we have grouped many putatively zooplanktivorous fish species together, while it is not clear which of them is a predator of juvenile and adult *Calanus*. Some certainly are (cf. Koslow, 1981). Larval fish are imperfect surrogates of predation pressure by adults, because adults may feed in different locations than they spawn. However, the relationship between abundance of larvae and the adults that spawned them has been established previously in this region (Hsieh *et al.*, 2005, 2006). Moreover, the use of fish larvae as an index of abundance of contemporaneous adults has the distinct advantage that it is a fishery-independent index of abundance, based on equal sampling effort throughout the geographic range occupied and encompasses unexploited as well as commercially exploited species.

The predation hypothesis is also consistent with the larger inshore/offshore contrast in mortality rates for C5/adult females than for C5/adult males. *Calanus* males typically have higher mortality rates than females (Ohman *et al.*, 2002; Hirst *et al.*, 2007). This may be

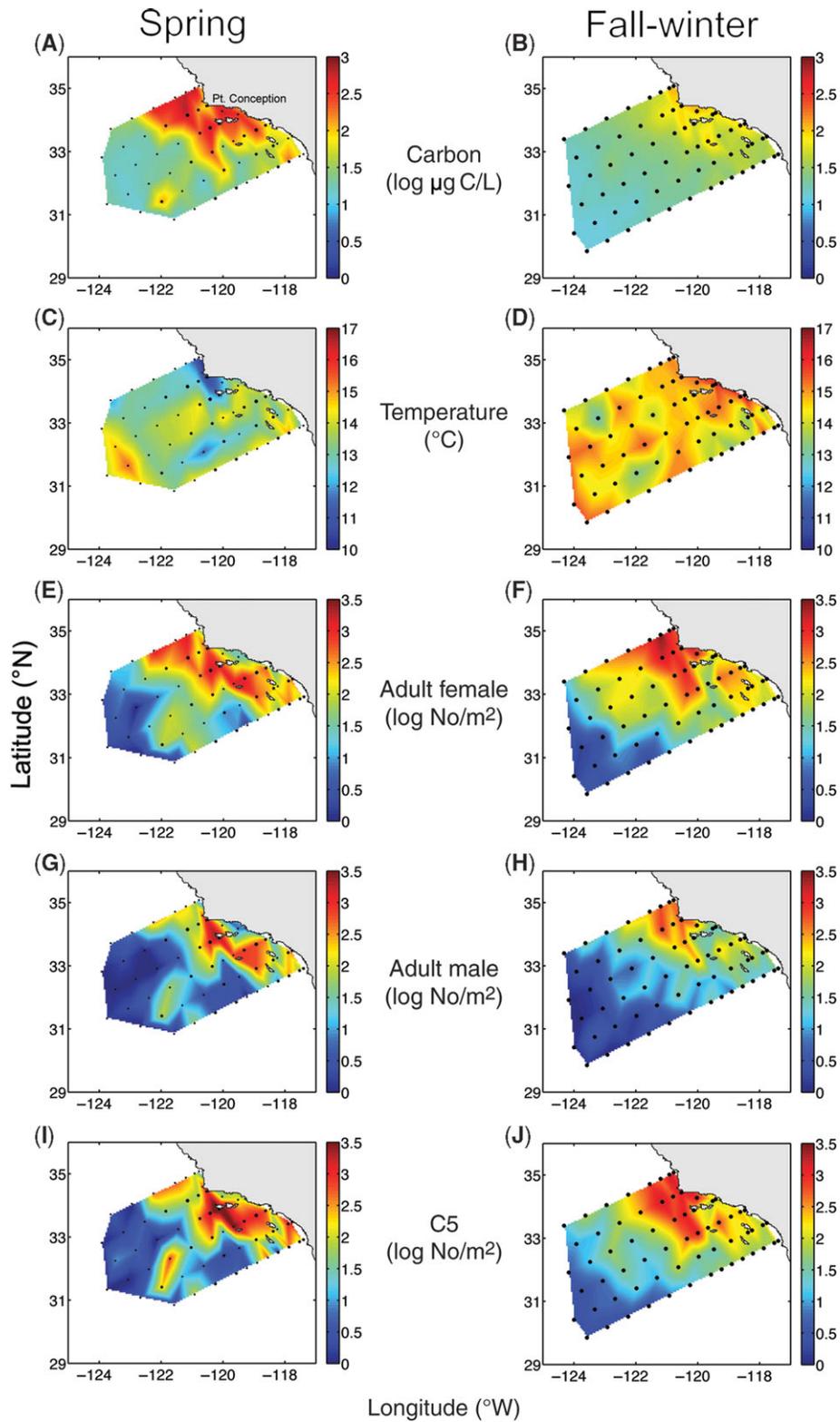


Fig. 2. Average spatial patterns from three spring cruises and four autumn–winter cruises of (A, B) phytoplankton-derived organic carbon concentration (Log $\mu\text{g C/L}$) at the chlorophyll maximum (C, D) corresponding temperature (°C) and abundance of three developmental stages of *Calanus pacificus* (log No./m²): (E, F) adult females, (G, H) adult males and (I, J) copepodid stage 5's. Grey shading indicates the land mass of southern California.

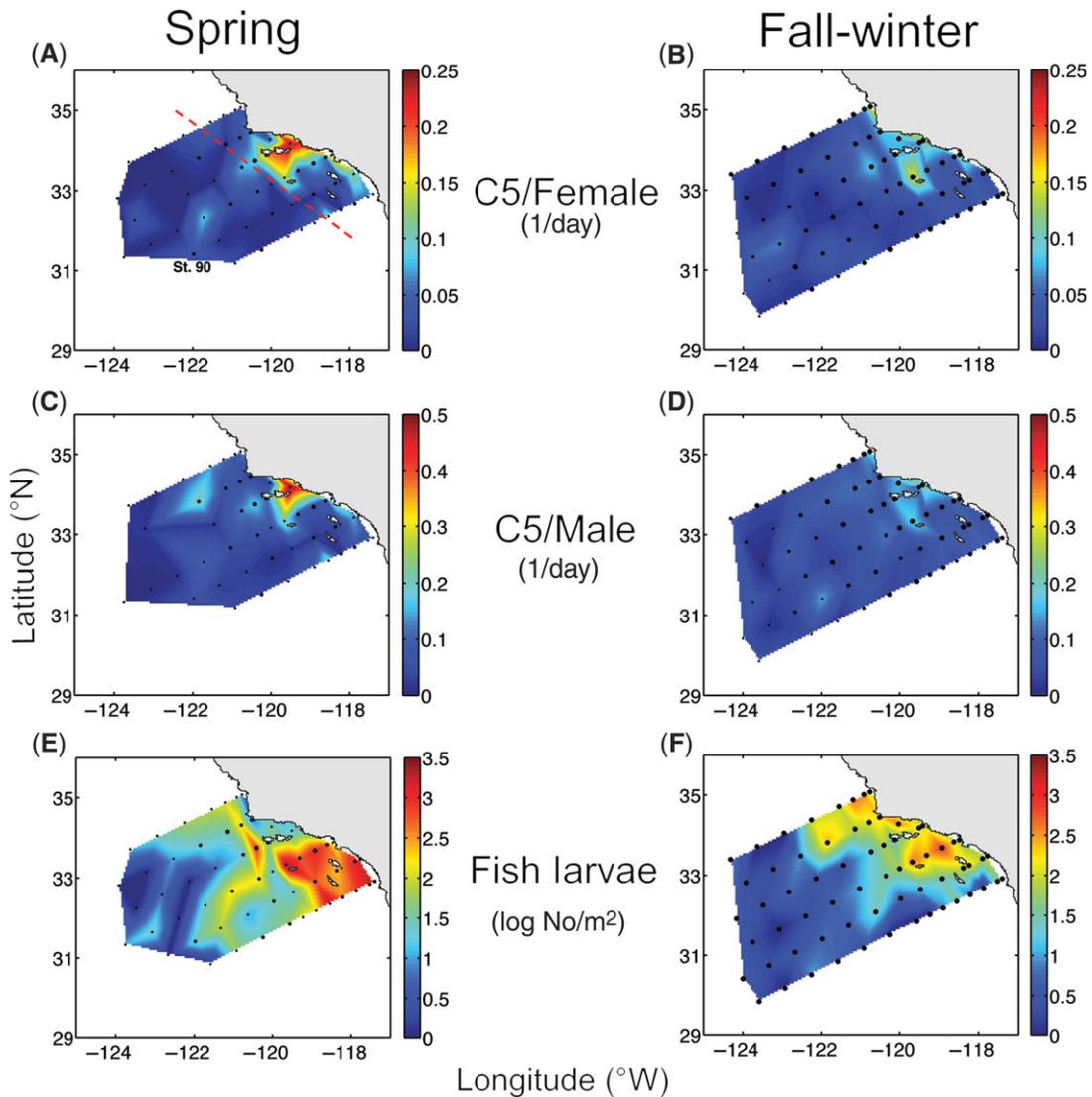


Fig. 3. Average spatial patterns from three spring cruises and four autumn–winter cruises of (A, B) mortality rate of C5/adult female *Calanus pacificus* (1/d), (C, D) mortality rate of C5/adult male *C. pacificus* (1/d) and (E, F) abundance of larvae of potentially zooplanktivorous fishes, from CalCOFI cruises. Average abundance of the following species of fish larvae combined: *Engraulis mordax*, *Ichthyops lockingtoni*, *Leuoglossus stilbius*, *Merluccius productus*, *Sardinops sagax*, *Scomber japonicus*, *Tetragonurus cuvieri*, *Trachipteridae*, *Trachipterus altivelis*, *Trachurus symmetricus*, *Argentina sialis*, *Atherinops affinis*, *Atractoscion nobilis*, *Aulorhynchus flavidus*, *Etrumeus teres*, *Lepidopus fitchi*, *Sarda chiliensis*, *Sebastes goodei*, *Sebastes jordani*, *Sebastes paucispinis*, *Seriola lalandi*. All abundances are \log_{10} transformed. Red line in panel (A) separates inshore from offshore stations. Offshore averages described in the text extended to Sta. 100, whose location is shown by the upper left-most station in the right hand panels.

because of reduced ability to escape predators or because they have reduced, poorly functional mouthparts and thus a limited lifespan in which to fertilize females. Much of the mortality of males may be unrelated to predation, but rather to exhaustion of storage reserves. Adult female *C. pacificus*, in contrast, feed actively to produce eggs (Runge, 1985; Mullin, 1991) and have considerably longer potential life spans. The elevated mortality rates of adult females in the inshore, phytoplankton-enriched zone relative to the offshore is

the opposite pattern from that expected if females were experiencing the effects of food limitation. Carnivorous zooplankton (especially ctenophores, hydromedusae, scyphomedusae, chaetognaths and predatory copepods) are also likely to significantly impact *C. pacificus* juveniles and adults in the region. However, while we have measures of temporal variations in abundance of carnivorous zooplankton in the region (Lavaniegos and Ohman, 2007), we do not have corresponding measures of their spatial variations for these cruises.

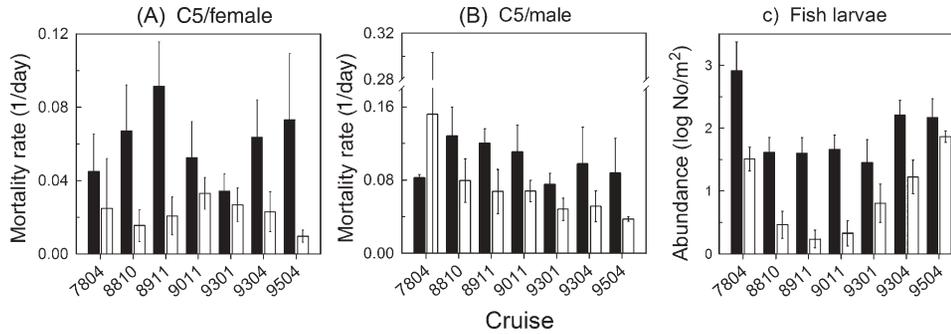


Fig. 4. Contrast between inshore (solid bars) and offshore (open bars) values of (A) mortality rate of C5/adult female *Calanus pacificus* (1/d), (B) mortality rate of C5/adult male *C. pacificus* (1/d) and (C) abundance of larvae of potentially zooplanktivorous fishes (log No/m²). Mean \pm 95% CI for each of the seven cruises.

Two potential sources of error in stage ratios, upon which the mortality rates depend, are the presence of dormant developmental stages and departures from a 1:1 primary sex ratio of C5s. In the southern California region in spring, *C. pacificus* are in the upper 100 m and there is no evidence of dormancy (Smith *et al.*, 1989; Johnson, 2004; Johnson and Checkley, 2004). The onset of dormancy appears to begin in mid-summer (Johnson, 2004). Later in the year, a biphasic life history is apparent, with an active surface population overlying a dormant deep population (Ohman *et al.*, 1998). In the late autumn–early winter period both ecdysteroid levels and jaw phase analysis suggest that near-surface C5s are not entering dormancy (Johnson, 2004). Moreover, adult female *C. pacificus* in the epipelagic layer actively feed and produce eggs in winter (Ohman *et al.*, 1998). Deeper individuals remain continuously in deeper strata and nearly all are in a dormant state (Ohman *et al.*, 1998; Johnson and Checkley, 2004). Only a very small subset of the deep C5s is likely to molt to adults in winter and enter the surface layer (Johnson, 2004), and thus bias the stage ratios utilized here for mortality estimation. To the very limited extent this occurs, it would result in a slight underestimate of winter mortality rates, but no onshore/offshore bias. Concerning sex ratios, Fleminger (1985) suggested that the quadrithek morph of presumptive C5 male *C. pacificus* may change sex and mature as adult females, particularly in late winter. If this occurred in the present study, our winter estimates of male mortality would be somewhat high and female mortality estimates correspondingly low. We do not have enumerations of trithek/quadrithek C5s that would enable us to assess a possible deviation from a 1:1 primary sex ratio, but based on Fleminger’s results the magnitude of the bias in stage ratios would appear to be no more than 12–18% departure from 1:1. This would contribute a corresponding, relatively small error to mortality estimates. Irigoien *et al.* (2000) also

suggested that there can be environmental modification of primary sex ratios.

Abundances of late developmental stages of *C. pacificus* are higher in the nearshore zone, despite the increased mortality rates in that region (Figs 2 and 3). Thus, population growth and/or net influx remain positive in the nearshore zone, which is reflected in the elevated rates of egg production in that region (Mullin, 1991, 1993). However, the implication of the present result is that both abundances and production rates of *C. pacificus* are lower there than would occur under the assumption of spatially uniform mortality.

Our results suggest a trade-off between elevated feeding rates and concurrently elevated mortality rates in the productive nearshore zone. While the nearshore zone downstream of this major upwelling center may exhibit favorable conditions of elevated phytoplankton and other microplankton prey resources for copepods, this nutritionally rich environment may carry compensatory risks. As Bakun (2006) stated, ‘in the ocean, for planktonic organisms . . . food heaven almost invariably equates to predation hell.’

ACKNOWLEDGEMENTS

We thank Ginger Rebstock and the late Michael M. Mullin for furnishing copepod data used in these analyses and the highly skilled CalCOFI technical group for their work at sea. A contribution of the Pelagic Invertebrates Collection of the Scripps Institution of Oceanography.

FUNDING

Supported by the California Current Ecosystem Long-Term Ecological Research program (NSF OCE-0417616).

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