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### Authors

Nickels, Catherine F  
Ohman, Mark D

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# CCEIII: Persistent functional relationships between copepod egg production rates and food concentration through anomalously warm conditions in the California Current Ecosystem

Catherine F. Nickels\*, Mark D. Ohman

Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093-0218, USA

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## ABSTRACT

We hypothesized that copepod egg production rates would be suppressed relative to their normal functional relationships with food availability during the NE Pacific warm anomalies of 2014–2015 and the El Niño event of 2015–2016. We also hypothesized that copepods would show increased rates of egg production and recruitment in association with ocean fronts. Three species of copepods (*Calanus pacificus*, *Metridia pacifica*, and *Eucalanus californicus*) were incubated at sea in simulated *in situ* conditions to ascertain egg production rates and egg hatching success during a sequence of 3–5 California Current Ecosystem-Long Term Ecological Research (CCE-LTER) cruises across diverse ocean conditions. Several indices of food availability were measured. The warm events had no significant effect on egg production rates measured in the experiments conducted here. Egg production and net naupliar production rates varied markedly among copepod species and across spatial gradients, but relationships with food concentration during warm events did not consistently diverge from functional relationships during El Niño-neutral conditions. Egg production was most commonly elevated inshore compared to offshore, but was not elevated within fronts. The egg production of *C. pacificus* was best explained by total Chl-*a*, while *E. californicus* was best explained by the > 20 size fraction of Chl-*a*. *M. pacifica* showed no relationship between egg production and any food metric tested. *C. pacificus* showed higher EPR than the other two species in virtually all conditions encountered, which may contribute to its numerical dominance throughout the region.

## 1. Introduction

In 2014–2016, the California Current Ecosystem (CCE) experienced anomalous conditions, first due to strong warm anomalies of 2013–15 (Bond et al., 2015; Zaba and Rudnick, 2016) and then due to El Niño originating in the equatorial Pacific (Jacox et al., 2016). El Niño in the CCE is characterized by positive water temperature anomalies, enhanced poleward flow, and a deepening of the nutricline (Bograd and Lynn, 2001). This large scale climate forcing can influence the favorability of conditions for planktonic copepods (Rebstock, 2001). In the winters and springs of the more moderate 1992–1993 El Niño, the abundance of the copepod *Calanus pacificus* was reduced, and daily egg production rate (EPR) was lower in winter compared to El Niño-neutral conditions (Mullin, 1997). El Niño can also shift composition of the copepod assemblage to dominance by warmer water species (Peterson et al., 2002).

Because copepods exhibit determinate growth, ceasing molting and

development upon reaching the adult stage, EPR can approximate adult copepod growth and production when potential body mass changes are accounted for (Hirst and McKinnon, 2001). EPR can serve as a proxy for secondary production when multiplied by the biomass of females, and as a proxy for recruitment when further multiplied by hatching success (Poulet et al., 1995). As copepod nauplii are frequently an important food source for many species of fish larvae, the sensitivity of the vital rates of these copepod species to food concentrations could determine whether they link phytoplankton variability to planktivorous fishes (Runge, 1988).

Oceanic fronts are common in the CCE domain and are increasing in frequency offshore of southern California and northern Mexico (Kahru et al., 2012), but frequency of occurrence diminished during the recent warm anomalies (Kahru et al., this volume). These fronts are defined by their physical properties, but are often also zones of steep gradients of biotic properties (Powell and Ohman, 2015b). While investigating a CCE frontal feature denoted the A-Front in 2008, Ohman et al. (2012)

\* Corresponding author.

E-mail addresses: [cnickels@ucsd.edu](mailto:cnickels@ucsd.edu) (C.F. Nickels), [mohman@ucsd.edu](mailto:mohman@ucsd.edu) (M.D. Ohman).<https://doi.org/10.1016/j.dsr.2018.07.001>Received 16 January 2018; Received in revised form 2 May 2018; Accepted 2 July 2018  
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observed an increased density of copepods and inferred an increase in recruitment rate of nauplii female<sup>-1</sup> within the frontal region. These maxima corresponded to an area of enhanced diatom biomass that, like copepod and nauplii concentrations, dropped off abruptly on either side of the front (Taylor et al., 2012). The investigators hypothesized that a local increase in EPR, egg hatching, and/or early naupliar survivorship caused the increased naupliar abundance. Smith and Lane (1991) found reproductively active *Eucalanus californicus* within and south of a jet and filament off Point Arena, California, with abundance related to ambient food concentration.

Here we focus on three prominent suspension-feeding copepod species in the California Current Ecosystem: *Calanus pacificus* Brodsky, *Metridia pacifica* Brodsky, and *Eucalanus californicus* Johnson. In terms of relative abundance of calanoid copepods in this region, the average ranks of these species are 1, 2, and 4, respectively (Rebstock, 2001). (We did not conduct experiments with the third ranked species, *Pleuramma borealis* Dahl.) All three are broadcast spawners, releasing their eggs directly into the water column. In the Southern California sector of the CCE, *C. pacificus* and *M. pacifica* spawn year round (Mullin, 1991; Ohman et al., 1998) while *E. californicus* ceases egg production in the winter but retains the ability to emerge rapidly if conditions change (Ohman et al., 1998). Behaviorally, *M. pacifica* is the most active species, followed by *C. pacificus*. In contrast, *E. californicus* employs an ambush feeding behavior (pers. obs.). *M. pacifica* and *C. pacificus* display some degree of omnivory (Halsband-Lenk, 2005; Landry, 1981), but diet composition has not been studied in detail for *E. californicus*. *E. californicus* has a higher average water content (93%) and lower protein to wet mass (2%) than *C. pacificus* and *M. pacifica* (Ohman et al., 1998). *E. californicus* also uses triacylglycerols as storage lipids, while *C. pacificus* and *M. pacifica* use wax esters (Ohman et al., 1998). This range of physical and behavioral characteristics may cause the processes controlling EPR and hatching success to vary among co-occurring species.

We investigated the functional relationships between copepod EPR and food availability (as represented by size-fractionated Chl-*a*, particulate organic C, and particulate organic N) to determine whether these relationships were altered during the warm anomalies of 2014 and El Niño of 2015–16. We also investigated interspecific differences in spatial patterns of EPR in relation to smaller-scale frontal gradients and larger-scale crossshore gradients. We hypothesized that enrichment within fronts, as previously observed, would be a repeated phenomenon and that inshore waters would show higher EPR than offshore. We hypothesized that the EPR of the more herbivorous *C. pacificus* and *E. californicus* would be more closely correlated with measures of chlorophyll-*a*, while the more omnivorous *M. pacifica* would be better explained by particulate organic carbon or nitrogen.

## 2. Materials and methods

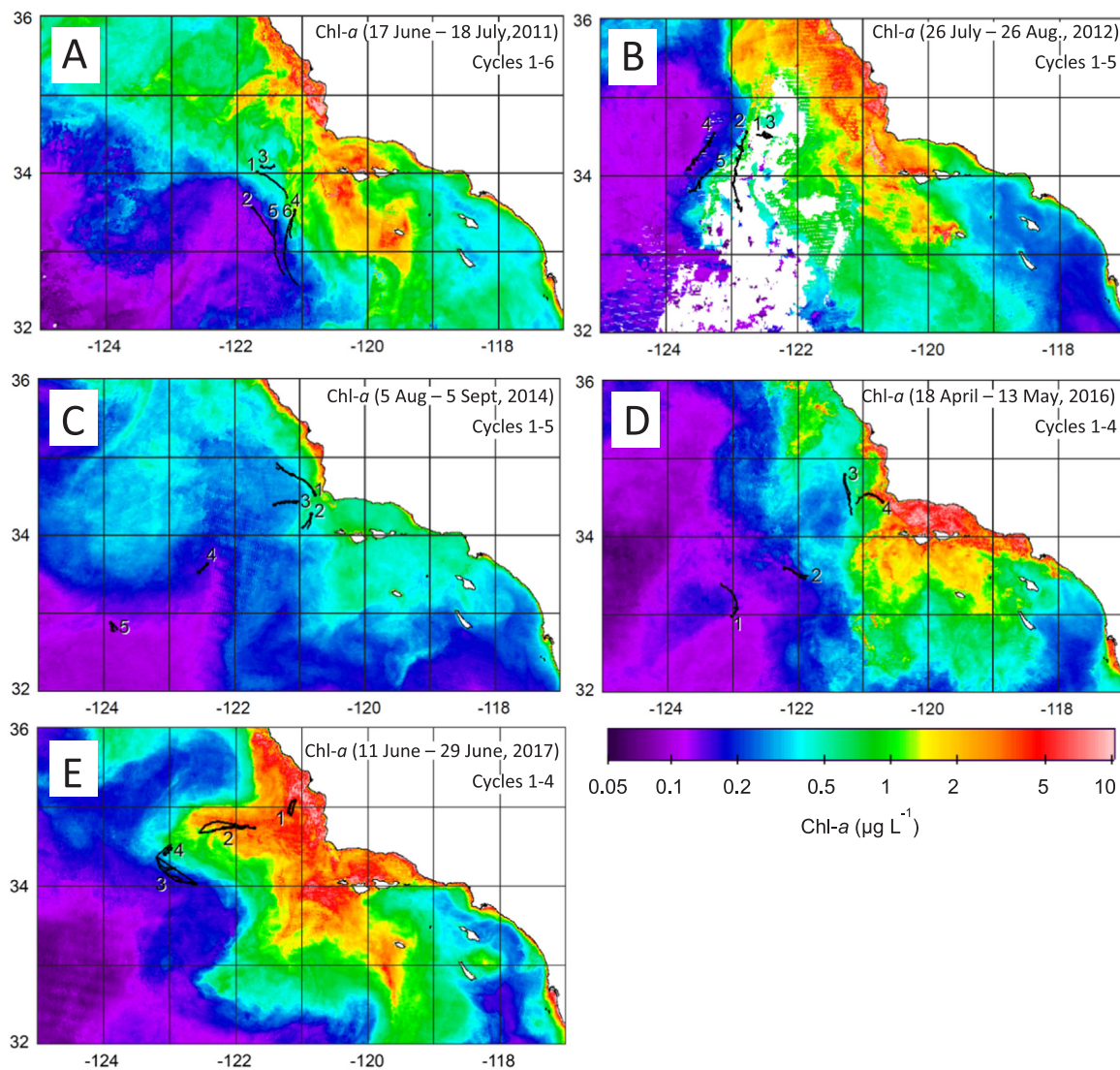
Shipboard egg production experiments were conducted on five cruises, four in summer (18 June–17 July 2011, 28 July–26 August 2012, 6 August–4 September 2014, and 1 June–2 July 2017) and one in spring (19 April–12 May 2016). Incubations were conducted west or southwest of Point Conception, California as part of the California Current Ecosystem - Long Term Ecological Research (CCE-LTER) program (Fig. 1). The cruises were organized into quasi-Lagrangian experimental “Cycles” comprised of replicated measurements conducted within a water parcel followed with a modified holey sock drifter drogued at 15 m (Landry et al., 2009; Niiler et al., 1995) and tracked by satellite. Frontal systems were first identified using satellite derived Chl-*a*, sea surface temperature, and sea surface height (M. Kahru, pers. commun.), then their subsurface structure resolved with *Spray* ocean gliders (Zaba and Rudnick, 2016) or towed SeaSoar surveys (Ohman et al., 2013), and finally localized with underway Moving Vessel Profiler vertical profiles (Ohman et al., 2012, 2013). Two of the cruises sampled major frontal systems, designated the C-Front (California Current Front, June 2011, Fig. 1A) and the E-Front (Eddy Front, August

2012, Fig. 1B), with experimental cycles conducted within and on either side of each front. On the third cruise, during the anomalously warm conditions in the CCE region in August 2014 (Zaba and Rudnick, 2016), we sampled spatial subregions but detected no pronounced frontal regions (Fig. 1C). The fourth cruise was conducted in April 2016 to test the effects of El Niño on copepod reproductive responses in hydrographically distinct water parcels extending from nearshore to offshore (Fig. 1D). On the fifth cruise, in June 2017 we performed an experimental series along the axis of an offshore-flowing coastal filament (Fig. 1E).

Live copepods were collected with a 333- $\mu$ m mesh, 71-cm diameter bongo net with non-filtering cod ends during 1–3 tows per Cycle. Tows were conducted at approximately 0830 PDT with the exception of the collections during Cycle 1 in 2011, which took place at 1700. The bongo net was lowered at 50 m min<sup>-1</sup> to approximately 210 m, held at depth for 3 min, and then recovered at 20 m min<sup>-1</sup> while the ship moved at 0.5–1 m s<sup>-1</sup>. The contents were immediately diluted with seawater that was collected below the thermocline the preceding night and placed in a cooler. Adult females were promptly sorted individually into 20 mL Petri dishes using a dissecting microscope and a fiber optic light source.

Egg production rates (EPRs) were assessed following Runge (1985) and Runge and Roff (2000). Experiments in 2011–2016 included *C. pacificus* and *E. californicus*. Where sufficient specimens were collected, *M. pacifica* was added in 2012, 2014, and 2016. 2017 experiments were performed with only *C. pacificus*. Up to 30 adult females of each species were incubated at sea, and only tows in which two or more females of a species were sorted were included in subsequent analysis. While most stations had higher sample sizes, 1 station for *C. pacificus*, 0 for *M. pacifica*, and 2 for *E. californicus* included only 2 females. Each female was placed in an individual Petri dish containing seawater collected from the chlorophyll maximum layer the preceding night, which was checked by microscope to ensure that no existing eggs were present in the dishes at the start of the experiment. The dishes were placed in a dark incubator at 13.5 °C, which was chosen to approximate the temperature at the chlorophyll maximum layer averaged over all cycles (median: 13.6 °C, range 12.4–15.4 °C; individual temperature profiles are available at: <http://oceaninformatics.ucsd.edu/datazoo/data/ccelter/datasets>). It was not feasible to conduct experiments across a range of temperatures at sea, so a single temperature was selected to approximate typical subsurface conditions experienced in this region and to remove temperature as a variable.

Dishes were checked for eggs by microscope and the chlorophyll maximum water replaced every 12 h. The females and eggs remained together in 2011, but in 2012 any eggs were removed from the dish and combined by species into a single dish at each time point for egg hatching success assessment. In 2014 and 2016, females were moved to a new dish with fresh chlorophyll maximum water if any eggs were present, leaving the eggs to mature in their original dish. After 24 h, *C. pacificus* and *M. pacifica* were removed from their dishes and preserved in scintillation vials filled with seawater and several drops of 37% formaldehyde. *E. californicus* was incubated for 24 h for Cycles 1 and 2 in 2011, but laid almost no eggs. Ohman et al. (1998) also observed *E. californicus* females to not lay eggs during the first 24 h of incubation but began to release eggs after 2.5 days. Beginning with Cycle 3 of that year, *E. californicus* was incubated for 72 h before preservation, with egg checks and seawater changes continuing every 12 h. Observation continued to 72 h even if a *E. californicus* female laid eggs before an earlier check. The total number of *E. californicus* eggs laid during the experiment was then divided by the 3 days of incubation to obtain average eggs female<sup>-1</sup> d<sup>-1</sup>. EPR for all species was expressed as eggs female<sup>-1</sup> d<sup>-1</sup>. Clutch sizes were defined as the number of eggs laid by a single female in excess of 5 eggs within a single 12 h check period, although smaller clutches were included in EPR, spawning frequency, and hatching success calculations (Melle et al., 2014). Spawning frequency denotes the percentage of females that spawned at any time



**Fig. 1.** Study locations at numbered Lagrangian Cycles overlaid on satellite images of Chl-*a*. Curved black lines illustrate the trajectories of satellite-tracked drift arrays (solid circles indicate deployment locations). Studies were conducted in (A) June–July 2011 (P1106), C-Front; (B) July–Aug. 2012 (P1208), E-Front; (C) Aug.–Sept. 2014 (P1408), warm anomaly, (D) April–May 2016 (P1604), El Niño, and (E) June–July 2017 (P1706). White patches in images indicate cloud cover. Satellite images courtesy of M. Kahru, SIO.

during the incubation. Copepods that died before preservation, and any eggs they produced before they died, were not included in calculations. All eggs were incubated an additional 36 h after their discovery to allow them to hatch. Several drops of acetic acid were added to the dish to stain the nauplii and unhatched eggs to facilitate identification for assessment of hatching success (J. Runge, pers. commun.).

Following each cruise, prosome lengths of preserved females were measured under a microscope using an ocular micrometer. Vertically integrated and maximum concentrations of chlorophyll-*a* (Chl-*a*), particulate organic nitrogen (PON), and particulate organic carbon (POC) were measured in vertical profiles from CTD-rosette bottle casts at 0200 on the day of the bongo tow (<http://oceaninformatics.ucsd.edu/datazoo/data/ccelter/datasets>; R. Goericke, pers. commun.) and used as food metrics. Methods for chlorophyll (<http://cce.lternet.edu/data/methods-manual/augmented-cruises/chlorophyll-a-size-fractionation>) and PON/POC analysis (<http://cce.lternet.edu/data/methods-manual/augmented-cruises/particulate-organic-carbon-nitrogen>) are available online. Integrated euphotic zone values of Chl-*a*, PON, and POC were calculated using the trapezoidal rule. Total chlorophyll-*a* (Chl-*a* retained on a GFF filter) and Chl-*a* in different size fractions (1–3, 3–8, 3–20, 8–20  $\mu\text{m}$ , as well as all Chl-*a* > 3 or > 20  $\mu\text{m}$ ), was measured at

the depth of the Chl-*a* maximum layer. Nonlinear regressions of an Ivlev fit between EPR and the food metrics were calculated in SigmaPlot vers. 13.0 (Systat Software, San Jose, CA). Kruskal Wallis and Wilcoxon Rank-Sum post hoc tests for differences in EPR and food concentrations between stations and interspecifically were calculated in R vers. 3.1.2 (R Core Team, 2014).

Runge (1984) found an effect of female body size on clutch size for *C. pacificus*, thus we constructed generalized additive models (GAMs) to investigate the effect that inclusion of prosome length has on the *C. pacificus* EPR. GAMs of *C. pacificus* EPR as a function of prosome length and different food metrics were created with the mixed GAM computational vehicle (mgcv) package in R software (Hastie and Tibshirani, 1990; Wood, 2006). EPR was modeled assuming a Poisson distribution with a log link function and a relationship of the form

$$\begin{aligned}\log(\text{EPR}) &= f(\text{prosome length}) \\ \log(\text{EPR}) &= f(\text{food metric}) \text{ or} \\ \log(\text{EPR}) &= f(\text{prosome length}) + f(\text{food metric}).\end{aligned}$$

Only one food metric was included in any model run to avoid collinearity. Model selection criteria included un-biased risk estimator

(UBRE), Akaike's Information Criterion (AIC), significance of the explanatory variables,  $r^2$ , percent deviance explained, and the pattern of residuals between the data and the smoothed fit.

We calculated the C-specific production of *C. pacificus* from each tow as mean egg C mean female  $C^{-1} \text{ day}^{-1}$ . Egg  $C \text{ day}^{-1}$  was estimated from an assumed egg diameter of 160  $\mu\text{m}$  (Runge, 1984) using the equation (Kiørboe and Sabatini, 1995)

$$\mu\text{g egg C} = 1.4 \times 10^{-7} \times (\text{egg volume, } \mu\text{m}^3)$$

and then multiplied by EPR. For female C, we calculated dry mass as (Runge, 1980)

$$\ln(\text{mean dry mass}) = 2.5 \times \ln(\text{mean prosome length}) + 2.99$$

and (Ohman, 1988)

$$C = 0.45 \times \text{dry mass}$$

We calculated a nonlinear regression of an Ivlev fit between *C. pacificus* C-specific production and the best fit food metric from the EPR regressions in SigmaPlot vers. 13.0 (Systat Software, San Jose, CA).

To assess whether there was a difference in the functional response of EPR to food availability during the warm anomaly and El Niño, we used graphical analysis of relationships of average per capita EPR, EPR of the most fecund female, and carbon-specific EPR to maximum chlorophyll concentration in the euphotic zone, together with other reproductive variables. We employed sign tests for analysis of residuals. We analyzed results in relation to spatial gradients defined by frontal regions in 2011 and 2012, and across broader inshore vs. offshore contrasts in all years.

### 3. Results and discussion

#### 3.1. Relationship between egg production and food metrics

There was no clear single strongest predictor variable applicable to egg production rate (EPR) of all three species. The maximum Chl-*a* concentration and vertically integrated Chl-*a* were significant predictors only for EPR of *C. pacificus*. Best fit relationships by species are presented in Fig. 2A-C. The concentration of total Chl-*a* within the Chl-*a* maximum layer was among the best fits with *C. pacificus* EPR ( $r^2 = 0.55$ , Fig. 2A), although not statistically different from the fit with the  $> 3 \mu\text{m}$  or  $> 20 \mu\text{m}$  Chl-*a* fractions ( $r^2 = 0.55$ ,  $r^2 = 0.54$ , respectively). Chl-*a* in the  $> 20 \mu\text{m}$  fraction was the best predictor for *E. californicus* EPR, although the  $r^2$  value was low ( $r^2 = 0.29$ , Fig. 2C). *M. pacifica* showed no significant relationships with any of the food metrics tested, and is here plotted against total Chl-*a* concentration ( $p > 0.05$ , Fig. 2B). A Holling Type II fit for these three best relationships did not provide a significant improvement over an Ivlev fit with threshold. Particularly notable in these results was the ability of *C. pacificus* to sustain moderately high EPR (15–25 eggs female $^{-1} \text{ day}^{-1}$ ) and clutch sizes (20–45 eggs) even at low food concentrations, as measured by Chl-*a* (Fig. 2A,G). For comparison with published literature, EPR and the other reproductive indicators are also plotted against vertically integrated euphotic zone Chl-*a* in Fig. S1.

None of the three species showed consistently lower EPR during the warm years than expected from the relationship developed during neutral conditions. When pooled together, the residuals from the warm years were not consistently positive or negative for either *C. pacificus* or *E. californicus* EPR ( $p > 0.10$ , Fig. 2A,C). Only the 2016 values from *E. californicus* were significantly negative when tested separately ( $p < 0.05$ , Fig. 2C). Although statistically significant, the difference was small (median difference =  $-0.25$ ) and is therefore not readily visible in the figure.

The relationships between chlorophyll concentration and EPR of the most productive individual female from each cycle (Fig. 2D-F) provide an estimate of the maximum potential fecundity of each species in these conditions. Average EPRs were substantially lower than the EPRs of just

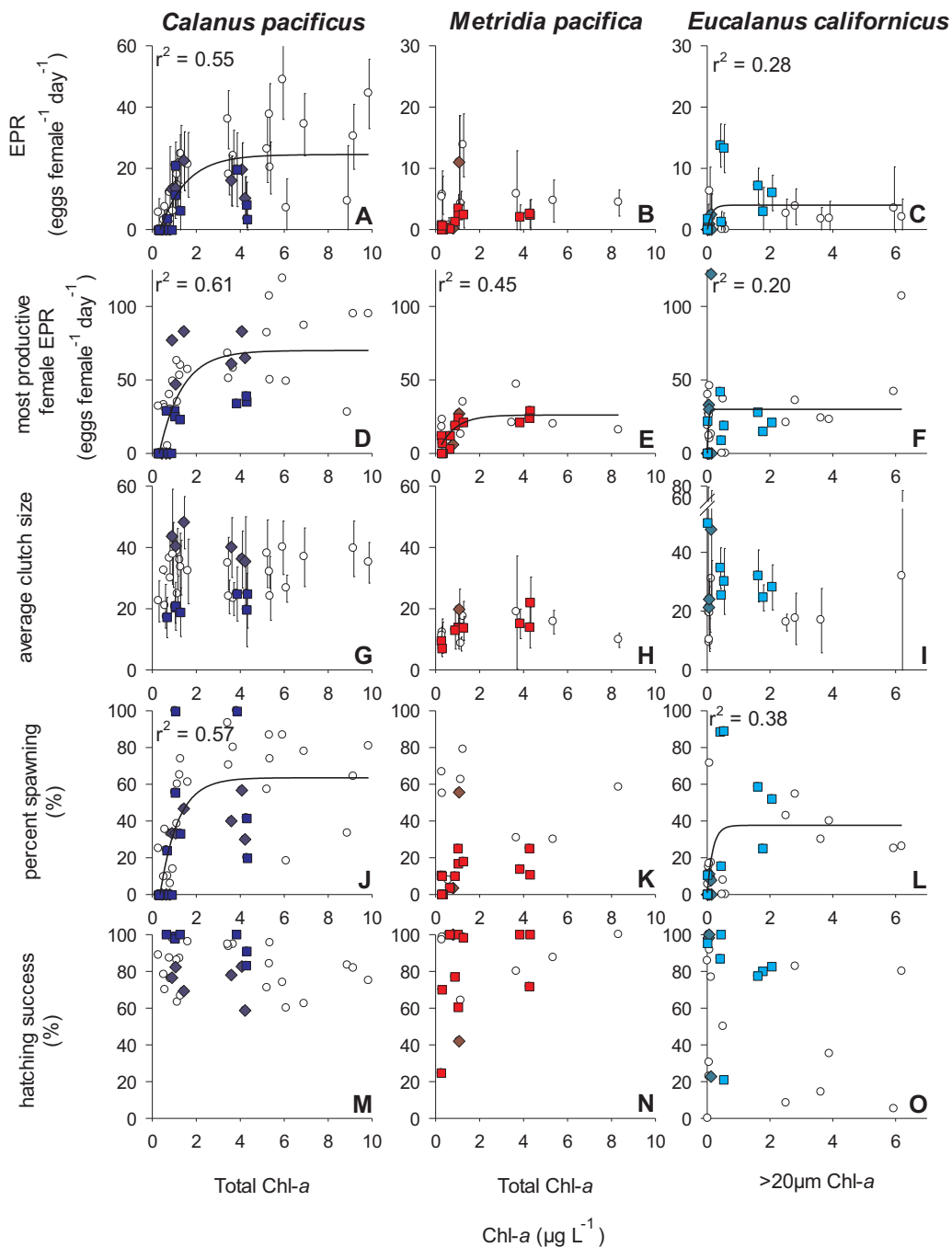
the most productive individual of each species. All three species showed significant Ivlev fits between most productive female EPR and the best fit food metric for total EPR. Only *C. pacificus* in the warm anomaly years of 2014 differed consistently from the fitted curve, with negative residuals ( $p < 0.05$ ). Average clutch size was independent of chlorophyll (Fig. 2G-I,  $p > 0.05$ ). Like the EPR for the most productive female, the *C. pacificus* average clutch size was significantly smaller in 2014 than the median of all years, but the 2016 average clutch size was significantly larger ( $p < 0.05$ ). These differences cannot be explained by seasonal variation in prosome length, because the average prosome length was no larger during the spring sampling in 2016 than the other years studied ( $p > 0.05$ ). The average prosome length of *C. pacificus* was lower in 2014 than all other years ( $p \leq 0.05$ ), however, which may explain the significantly lower clutch sizes in that year. The average clutch size of *E. californicus* was significantly higher during the 2014 warm anomaly than the other years ( $p < 0.05$ ). The percent of *M. pacifica* females spawning (Fig. 2K), was independent of food concentration ( $p > 0.05$ ), but *C. pacificus* and *E. californicus* showed significant Ivlev fits with the best food metric from EPR ( $p < 0.01$ , Fig. 2, J,L). The percent of females spawning for both *C. pacificus* and *E. californicus* was significantly lower during 2016 than the other years ( $p < 0.05$ ). The egg hatching success of *M. pacifica* and *E. californicus* (Fig. 2N,O) did not show significantly positive or negative residuals from the all year median during the warm years ( $p > 0.05$ ), but *C. pacificus* showed significantly positive residuals in 2014 and negative residuals in 2016 ( $p < 0.05$ ). We did not detect evidence of a “diatom effect” of decreased EPR or egg hatching success at high Chl-*a* concentrations. We did not analyze the species composition of phytoplankton in our study, but instead analyzed the hatching success patterns compared to concentrations of total and size fractionated Chl-*a*.

Interestingly, *C. pacificus* demonstrated an opposing pattern of response of average clutch size and hatching success in the warm anomaly and El Niño. While clutch size was significantly depressed in 2014 and enhanced in 2016, hatching success was significantly enhanced in 2014 and depressed in 2016. When naupliar production rate (nauplii female $^{-1} \text{ d}^{-1}$ ) was calculated by multiplying the EPR (Fig. 2A-C) by the hatching success rate (Fig. 2M-O), the shape of the relationship did not differ substantially from EPR alone (Fig. 3). The differences between average clutch size and hatching success between years for *C. pacificus* cancelled one another, resulting in no net effect on reproductive success as defined by naupliar production rate (Fig. 3A).

Female prosome length has been shown to be related to clutch size for *C. pacificus* (Runge, 1984) and *C. finmarchicus* (Head et al., 2013). In the best fit GAM for *C. pacificus*, total Chl-*a* was still the best predictor variable (73.2% of deviance explained,) while the inclusion of prosome length increased the explained deviance to 80.7% (UBRE 2.5181, AIC 368.6,  $r^2 = 0.80$ , Table S1). Both Chl-*a* and prosome length were significant in the model ( $p < 0.001$ ), but non-linear (Fig. S2). EPR increased steeply with increasing total Chl-*a* up to about  $75 \mu\text{g m}^{-2}$ , where the response flattened out. Prosome length and integrated Chl-*a* were uncorrelated with one another ( $P > 0.05$ ). However, the two are not independent factors, because food availability over the course of ontogeny also affects copepod adult body size (Campbell et al., 2001; Vidal, 1980), albeit on a relatively longer time scale than the direct effects on female egg production.

We also investigated the carbon-specific production of *C. pacificus* as egg C female  $C^{-1}$  in relation to the concentrations of C, N, and Chl-*a*. C-specific production was significantly explained by both integrated euphotic zone C ( $r^2 = 0.32$ ) and total Chl-*a* ( $r^2 = 0.58$ , Fig. 4). Although there was considerable variability, as for EPR, the residuals from the anomalously warm years (2014 = filled squares, 2016 = filled diamonds, Fig. 3) were not consistently positive or negative ( $p > 0.10$ ).

Similar to findings for *C. finmarchicus*, food availability has an effect on EPR, but the high degree of variability makes prediction imprecise (Melle et al., 2014). *C. pacificus* has been shown to display dietary plasticity, switching from herbivorous to carnivorous behavior based on



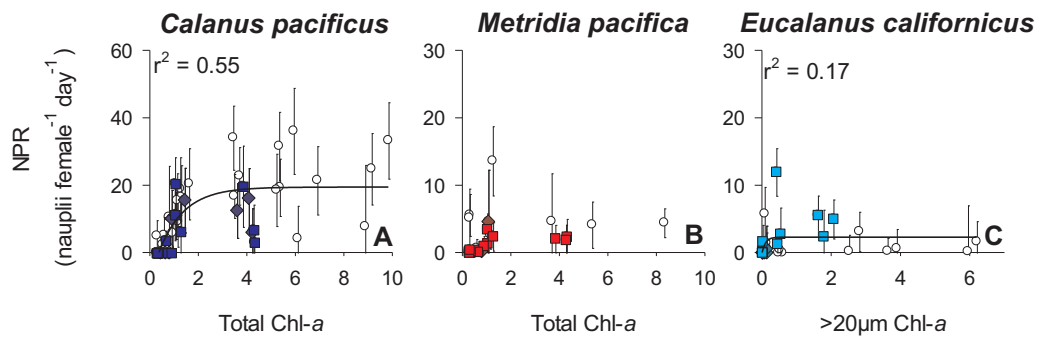
**Fig. 2.** Relationship between copepod reproductive variables and food concentration as either total Chl-a or the > 20 µm size fraction, both at the depth of the Chl-a maximum. (Upper row): average Egg Production Rate (EPR,  $\bar{x} \pm 95\%$ ), (Second row): EPR of the most fecund female, (Third row): average clutch size ( $\bar{x} \pm 95\%$ ), (Fourth row): percent spawning, and (Bottom row): egg hatching success. (A, D, G, J, M) *C. pacificus*, (B, E, H, K, N) *M. pacifica*, and (C, F, I, L, O) *E. californicus*. Filled squares indicate measurements from the warm anomaly in 2014, filled diamonds indicate El Niño experiments in 2016. Significant Ivlev fits in top row: *C. pacificus*:  $y = 24.51 * (1 - \exp(-0.85 * (x - 0.36)))$ ,  $p < 0.01$  and *E. californicus*:  $y = 3.10 * (1 - \exp(-7.45 * (x - 0.01)))$ ,  $p < 0.01$ . Significant Ivlev fits in second row: *C. pacificus*:  $y = 70.03 * (1 - \exp(-0.97 * (x - 0.31)))$ ,  $p < 0.01$ , *M. pacifica*:  $y = 26.14 * (1 - \exp(-1.34 * (x - 0.07)))$ ,  $p < 0.01$ , and *E. californicus*:  $y = 30.08 * (1 - \exp(-27.97 * (x - 0.01)))$ ,  $p = 0.01$ . Significant Ivlev fits in fourth row: *C. pacificus*:  $y = 63.49 * (1 - \exp(-1.21 * (x - 0.35)))$ ,  $p < 0.01$  and *E. californicus*:  $y = 37.62 * (1 - \exp(-5.66 * (x - 0.0002)))$ ,  $p < 0.01$ .

the relative abundance of food types (Landry, 1981) and *C. finmarchicus* utilize microzooplankton prey (Ohman and Runge, 1994). *C. pacificus* has also been shown to reject certain species of dinoflagellate (Huntley et al., 1986) and diatom (Leising et al., 2005) prey that can contain harmful chemical compounds. This weakens their link to any one specific measure of food availability as food types can compensate for one another.

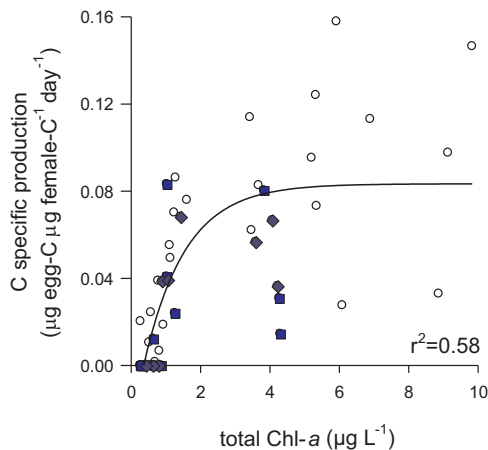
We expected *M. pacifica* to show a closer relationship to particulate

organic carbon or nitrogen than Chl-a due to their omnivorous diets (Halsband-Lenk, 2005). However, *M. pacifica* EPR did not have a significant relationship with any of the food metrics tested. We used measurements of particulate organic carbon and nitrogen as metrics inclusive of non-photosynthetic prey, but direct consideration of key microzooplankton taxa as potential prey could lead to different conclusions.

The fit of the > 20 µm size fraction for *E. californicus* in this study



**Fig. 3.** Relationship between copepod naupliar production rate (NPR,  $\bar{x} \pm 95\%$ ) and food concentration as either total Chl-*a* or the  $> 20 \mu\text{m}$  size fraction, both at the depth of the Chl-*a* maximum. (A) *C. pacificus*, (B) *M. pacifica*, and (C) *E. californicus*. Filled squares indicate measurements from the warm anomaly in 2014, filled diamonds indicate El Niño experiments in 2016. Significant Ivlev fits: *C. pacificus*:  $y = 19.456 * (1 - \exp(-0.97 * (x - 0.37)))$ ,  $p < 0.01$  and *E. californicus*:  $y = 2.30 * (1 - \exp(-9.50 * (x - 0.01)))$ ,  $p < 0.05$ .



**Fig. 4.** Carbon-specific production of *Calanus pacificus* plotted against total Chl-*a* at the Chl-*a* maximum layer. Filled squares indicate measurements from the warm anomaly in 2014, filled diamonds indicate El Niño experiments in 2016. Significant Ivlev fit is shown:  $y = 0.08 * (1 - \exp(-0.84 * (x - 0.36)))$ ,  $p < 0.01$ .

may have to do with a threshold of total Chl-*a*. The  $> 20 \mu\text{m}$  size fraction has very low biomass in the CCE below a total Chl-*a* concentration of  $0.5 \mu\text{g L}^{-1}$ , but shows a dramatically increased contribution above this concentration (Goericke, 2011). Another possibility for the relationship with *E. californicus* is that this large, ambush feeder may have higher encounter rates with large cells. For all three copepod species, the relationship with larger cells may be attributable to more efficient detection and clearance of large cells (Frost, 1977).

The feeding history of the copepods may alter their response to changes in food conditions. Head and Ringuelet (2017) determined a “seasonality coefficient” for *C. finmarchicus* by grouping sampling stations into regions and half-month time periods, that improved predictions of EPR by including the local feeding and temperature climatologies. Hirche et al. (1997) found that *C. finmarchicus* spawning took 2–3 days to respond to changes in food concentration, but showed higher EPR in pre-fed individuals compared to pre-starved. *E. californicus* EPR also begins to respond to changes in food concentration after 2 days, even when in winter dormancy (Ohman et al., 1998). We observed considerable variability between individuals under the same conditions, including a high number of mature but unreproductive females. An additional confounding factor is that some copepods, such as *C. finmarchicus*, can use body reserves to produce oocytes even at low food concentrations (Niehoff, 2004).

The adult females and their eggs were not separated until termination of the experiment in 2011, and only approximately every 12 h afterward. In the time between checks, cannibalism or other female-mediated effects may have taken place. These effects may be of

differing importance for the different species studied, as *Metridia longa* clutch sizes increase when egg separation is employed, while *C. finmarchicus* clutch sizes are unaffected (Plourde and Joly, 2008). For *M. pacifica*, eggs can begin to disappear within the first hours after laying (Halsband-Lenk, 2005). Cannibalism may be more pronounced at lower food concentrations (Plourde and Joly, 2008). In addition to cannibalism, eggs may disintegrate as a result of an absent or compromised membrane (Hopcroft et al., 2005). Loss of these disintegrating eggs would have diminished our estimate of EPR and increased our estimate of hatching success if they were present during the experiment. Egg separators may damage freshly laid eggs, however, so it is unclear whether separation would have led to a more or less accurate estimate of hatching success (Plourde and Joly, 2008). Our egg check interval of 12 h probably increased our likelihood of discovering fragile eggs before cannibalism or disintegration over that from of 24 h interval, but the increase may not be as great as for the 6 h check intervals employed by Head and Ringuelet (2017).

The El Niño event of 2015–2016, which we sampled in spring 2016, did not appear to cause a departure from the functional relationships observed in other years in this study, although we do not have data from another, neutral spring for comparison. However Mullin (1991) found that *C. pacificus* in our study region can achieve an EPR in excess of 30 eggs female $^{-1}$  day $^{-1}$  year round, although these rates are more widespread geographically in winter and spring than summer and fall. Additionally, the warm event of 2014 was sampled in summer and also did not result in a consistent departure from the functional curve. Mullin (1997) found no depression of reproductive potential in *C. pacificus* coincident with the El Niño conditions of 1992–1993 and concluded that winter egg production was likely food limited but spring egg production recovered along with chlorophyll biomass. Our results agree that any effects of El Niño on copepod EPR compared to spring in other years would likely be caused by changes in phytoplankton concentration, without another mechanism disrupting the normal functional relationship. All of our incubations were conducted at a constant temperature, so the established relationship of temperature with laboratory EPR for several species (Head et al., 2013; Hirche et al., 1997; Runge, 1984; Smith and Lane, 1991) is outside the scope of this study. Melle et al. (2014) found a highly variable relationship between changes in temperature and EPR *in situ* for *C. finmarchicus*. Like Head et al. (2013), we suspect that the concurrent changes in temperature and the food metrics considered are representative of different source water masses and that food effects will be of more direct consequence *in situ*. EPR increase in response to renewed food resources following a warm event would support the population recovery of *C. pacificus* and *M. pacifica* after short term warm anomalies shown by Lilly and Ohman (this issue).

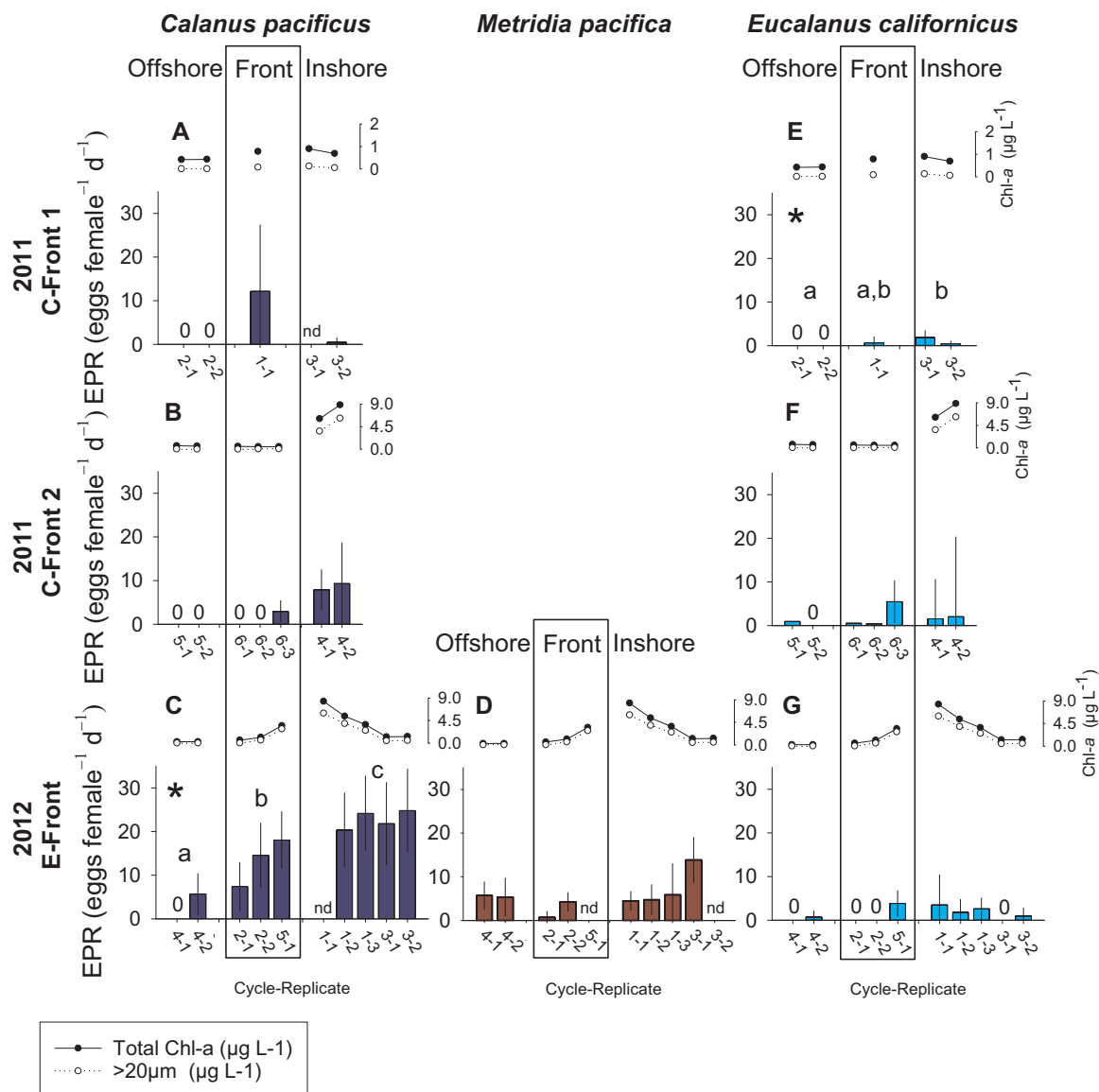


Fig. 5. Egg Production Rates (EPR,  $\bar{x} \pm 95\%$ ) of (A, B, C) *C. pacificus*, (D) *M. pacifica*, and (E, F, G) *E. californicus* in relation to frontal features (outlined in rectangles). Upper row: measurements across the C-Front in 2011 (comparison 1); Middle row: C-Front (comparison 2); Bottom row: E-front in 2012. Numbers below bars indicate Cycle number-replicate number; 0 = no eggs produced; nd = no data; \* =  $p < 0.05$  with lower case a, b, c denoting significant groups. Concentration of total Chl-a in the Chl-a maximum layer (filled circles) and in the  $> 20 \mu\text{m}$  size fraction (open circles) at corresponding stations illustrated above each plot.

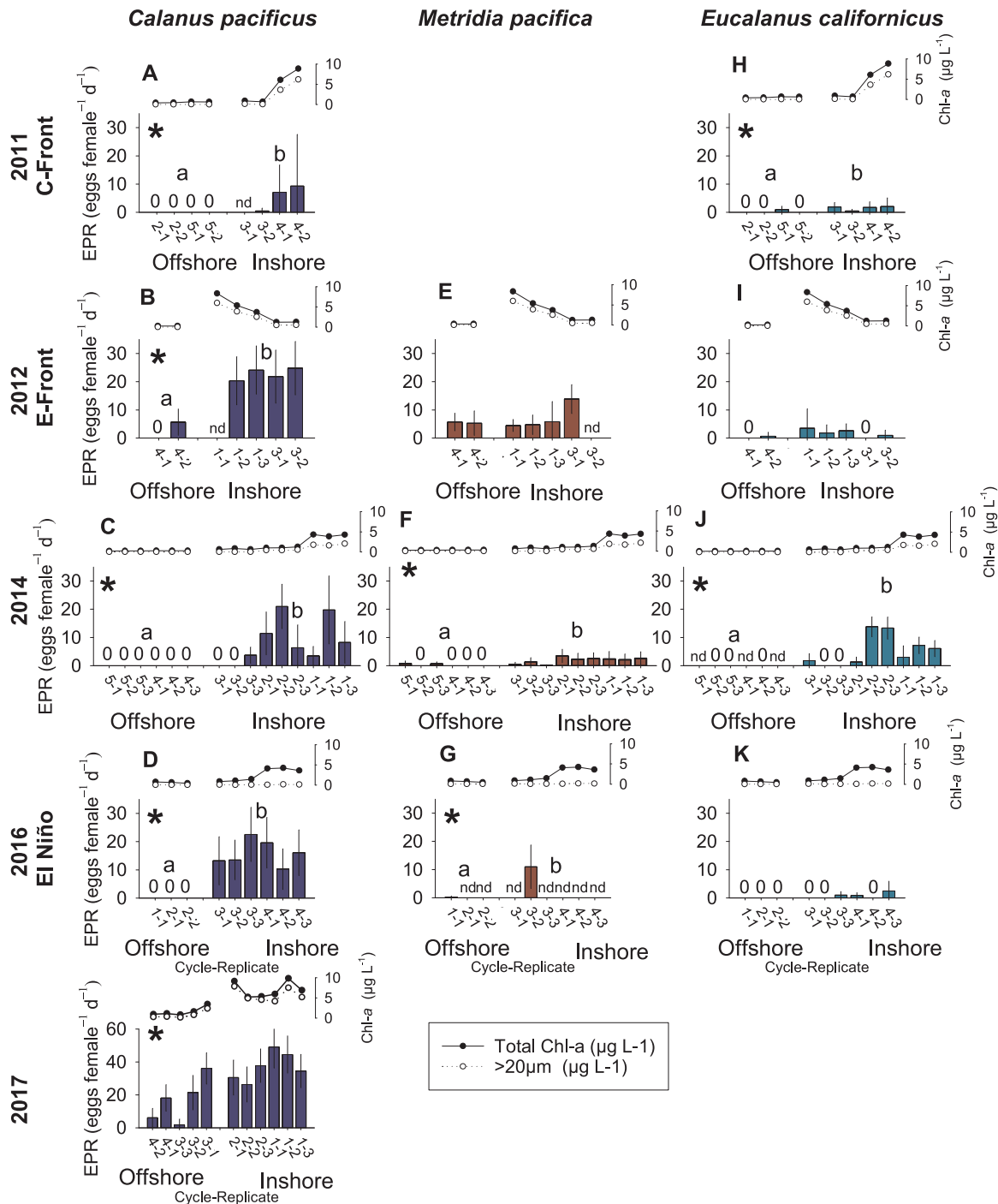
### 3.2. Spatial patterns

In notable contrast to naupliar recruitment inferred in the study of the A-Front (Ohman et al., 2012), we did not find evidence of front-related elevation of copepod egg production rates (EPR) or naupliar production rates. The C-Front (2011) was sampled twice in different locations (Fig. 5). Although there was some spatial heterogeneity in daily EPRs across the C-Front ( $p < 0.05$ , Fig. 5A-F, Kruskal-Wallis), in neither instance were copepod EPRs significantly enhanced at the front itself. On the first C-Front crossing *E. californicus* had higher EPR inshore of the front than offshore ( $p < 0.01$ , Fig. 5E), but EPR at the front did not differ from either inshore or offshore. On the second C-Front crossing neither species showed significant differences. The E-Front (2012) was crossed only once. Only *C. pacificus* showed significant spatial heterogeneity, with all three regions differing ( $p < 0.05$ , Fig. 5C), but EPR was highest on the inshore side of the front and decreased with increasing distance offshore. EPR of *M. pacifica* and *E. californicus* did not differ significantly among regions across the E-Front ( $p > 0.05$ , Fig. 5D, G). There were no significant differences in food

concentrations across the C-front for any of the food metrics measured ( $p > 0.05$ ). Across the E-front the vertical maximum total Chl-a concentration as well as the Chl-a in 3–20  $\mu\text{m}$  and 8–20  $\mu\text{m}$  size fractions were significantly higher inshore of the front compared to offshore ( $p < 0.05$ ), but the other food metrics did not show significant differences in concentration across the front. This is not surprising as fronts can arise due to a variety of processes, including convergent or divergent flows, horizontal shear, local changes in plankton growth rates, and behavioral aggregations (Franks, 1992; Powell and Ohman, 2015a).

We hypothesized that EPR would be elevated within fronts based upon the findings of Ohman et al. (2012) at the A-Front. The A-Front previously studied was the site of elevated nutrient fluxes (Li et al., 2012) and diatom biomass (Taylor et al., 2012), and was a stable, persistent structure. However, Ohman et al. (2012) did not distinguish species of copepods and enumerated nauplii in situ but did not measure EPR, making it difficult to directly compare that study with the present results. The C-Front was a more dynamic feature under formation at the time of our study, with evidence for low Si:N ratios and iron-stressed





**Fig. 6.** Contrasting offshore and inshore Egg Production Rate (EPR,  $\bar{x} \pm 95\%$ ) of (A, B, C, D) *C. pacificus*, (E, F, G) *M. pacifica*, and (H, I, J, K) *E. californicus*, in 2011, 2012, 2014, 2016, and 2017. Where differences were significant, EPR was higher inshore than offshore for all three species ( $p < 0.05$ ). Numbers below bars indicate Cycle number-replicate number; 0 = no eggs produced; nd = no data; \* =  $p < 0.05$  with lower case a, b denoting significant groups. Concentration of total Chl-*a* in the Chl-*a* maximum layer (filled circles) and in the  $> 20 \mu\text{m}$  size fraction (open circles) at corresponding stations illustrated above each plot.

diatoms (Brzezinski et al., 2015). The early stage of development and low iron and silica of the C-Front make it unlikely to support the same elevated naupliar recruitment inferred for the more stable and productive A-Front. The E-Front was a persistent eddy-related front and a site of elevated mesozooplankton grazing and particle export (Stukel et al., 2017), but the present results show that it was not a site of elevated naupliar production. In order for front-related processes to result in persistent increases in copepod recruitment, it appears that a suite of conditions must obtain that result in elevated prey concentrations and ingestion, physical retention of spawned embryos, and low mortality

over an extended time period.

We compare inshore and offshore domains of the study area in Fig. 6. In all five years, *C. pacificus* showed significantly higher EPR inshore than offshore ( $p < 0.05$ , Kruskal-Wallis, Fig. 6A-D). *M. pacifica* did not exhibit a significant difference between areas in 2012 ( $p > 0.05$ , Fig. 6E) but showed significantly higher EPR inshore than offshore in 2014 ( $p < 0.05$ , Kruskal-Wallis, Fig. 6F) and 2016, although in the latter year *M. pacifica* was only collected at one offshore and one inshore location. EPR of *E. californicus* did not differ between regions in 2012 or 2016 ( $p > 0.05$ , Fig. 6I, K). *E. californicus* had significantly

higher EPR inshore than offshore in 2011 and 2014 ( $p \leq 0.05$ , Kruskal-Wallis, Fig. 6,J). In the warm anomaly summer of 2014 and El Niño spring of 2016, all three species showed very low (zero or near-zero) rates of egg production in the offshore domain. EPR of *C. pacificus* and *M. pacifica* increased significantly in the inshore domain both years, but the increase for *E. californicus* was not significant in 2016 due to high variability inshore and low sample size offshore ( $P > 0.05$ , Fig. 6K). In all years, when there were significant differences, food metrics were elevated inshore compared to offshore ( $p \leq 0.05$ , Kruskal-Wallis).

The consistent enrichment of EPR inshore is not surprising, as it was associated with regionally increased food resources and is supported by the functional relationships determined above. This finding complements that of Powell and Ohman (2015a), who found increased acoustic backscatter and Chl-*a* fluorescence inshore of fronts compared to offshore when averaging all the glider-resolved sections in their study. Niehoff and Hirche (2000) also found higher EPRs in *C. finmarchicus* on the shelf in the Norwegian Sea, associated with an early spring phytoplankton bloom and higher Chl-*a* concentration, compared to the open sea Atlantic.

The 2014 experiments occurred during anomalously warm conditions (Bond et al., 2015) and exhibited the same spatial pattern as the 2016 El Niño spring. This similarity suggests that the spatial contrast is robust to seasonal and climatic differences in forcing. Higher EPR inshore may compensate for the increase in predation-related mortality for *C. pacificus* inshore in the CCE (Ohman and Hsieh, 2008). Inshore egg production may also serve as seed populations for offshore oligotrophic areas, as suggested for *E. californicus* north of the study domain in the Point Arena jet by Smith and Lane (1991).

Locations where no or very few individuals of a particular species were incubated could have been caused by those species residing at deeper depths, rather than being absent from the area. Smith and Lane (1991) noted unpublished data from D. Mackas that female *E. californicus* were caught in a MOCNESS tow to 500 m, even when none were present in their 200 m tows. Powell and Ohman (2015a) and Ohman and Romagnan (2016) documented an increase in the amplitude of diel vertical migration offshore of fronts compared to inshore, with some layers of animals migrating 200–300 m deeper.

### 3.3. Interspecific differences

We observed considerable differences in reproductive responses among the three copepod species incubated in the same experimental conditions (Table 1). *C. pacificus* had the highest average EPR ( $p < 0.01$ ), both for all females in the study and considering only actively spawning females. *M. pacifica* had a significantly lower average clutch size than the other two species ( $p < 0.01$ ). Clutch sizes here could be overestimates, as it is possible that some females released two clutches during the 12 h check interval. However, the observed maximum clutch sizes do not appear unreasonable (Runge, 1984).

*Calanus pacificus* has consistently the highest and *Eucalanus californicus* typically the lowest rates of per capita egg and naupliar production, with *Metridia pacifica* showing intermediate values. Whether coincidentally or not, this sequence also corresponds to the average rank order of adult abundance of these three species in this region (Rebstock, 2001). Abundances are the resultant of many subsequent life

history events that must follow naupliar production, notably including survivorship across all developmental stages (Hirst and Kiorboe, 2002; Ohman et al., 2004), therefore egg production alone cannot predict recruitment. However, successful recruitment of the next generation necessarily begins with production of viable offspring, and our results suggest that the reproductive advantage of *C. pacificus* can have longer-term consequences. We note that while the potential fecundity of *Eucalanus californicus* is actually the highest of the three species (Ohman et al., 1998; Smith and Lane, 1991), this potential fecundity is rarely realized in our study site. The ability of *C. pacificus* to sustain moderately high EPR (15–25 eggs  $\text{♀}^{-1} \text{d}^{-1}$ ) and clutch sizes (20–45 eggs), even at low food concentrations (as measured by Chl-*a*) and even during anomalously warm conditions, may confer a substantial advantage upon this species.

Our EPR measurements are comparable to *in situ* rates from the literature. We observed a range of means of 0–49 eggs  $\text{female}^{-1} \text{day}^{-1}$  for *C. pacificus*. This was similar to the range of 0–48 eggs  $\text{female}^{-1} \text{day}^{-1}$  measured by Runge (1985), 0–68 eggs  $\text{female}^{-1} \text{day}^{-1}$  by Mullin (1991), 8–30 eggs  $\text{female}^{-1} \text{day}^{-1}$  by Ohman et al. (1998), 28–52 eggs  $\text{female}^{-1} \text{day}^{-1}$  by Gomez-Gutierrez and Peterson (1999), and 0–45.3 eggs  $\text{female}^{-1} \text{day}^{-1}$  by Pierson et al. (2005). (For a more extensive comparison with published values, see Table 4 in Pierson et al., 2005.) Our maximum measured clutch size of *C. pacificus* (109 eggs  $\text{female}^{-1}$ ) is higher than those of both Runge (1984), and Pierson et al. (2005). The mean EPR of *M. pacifica* ranged from 0 to 21 eggs  $\text{female}^{-1} \text{day}^{-1}$ . This value is comparable to the 3–30 eggs  $\text{female}^{-1} \text{day}^{-1}$  measured by Hopcroft et al. (2005) and 0–19.4 eggs  $\text{female}^{-1} \text{day}^{-1}$  measured Halsband-Lenk et al. (2005). The range of mean EPR of *E. californicus* was 0–19.7 eggs  $\text{female}^{-1} \text{day}^{-1}$ . This value is much lower than that measured by Smith and Lane (1991), who observed a range of 0–190 eggs  $\text{female}^{-1} \text{day}^{-1}$ , or Ohman et al. (1998) who measured 0–100 eggs  $\text{female}^{-1} \text{day}^{-1}$ . Our measured range is much closer to that measured by Gomez-Gutierrez and Peterson (1999) for *E. californicus* of 12–38 eggs  $\text{female}^{-1} \text{day}^{-1}$ . The lower value for *E. californicus* is likely the result of the smaller body size of these species in our study site.

## 4. Conclusions

Three co-occurring copepods (*C. pacificus*, *M. pacifica*, and *E. californicus*) showed marked differences in reproductive responses, with *C. pacificus* consistently showing elevated rates of production of eggs and nauplii in comparison to the other two species. Among the best predictor variables for *C. pacificus* egg production rate (EPR) was the total Chl-*a* concentration, while the  $> 20 \mu\text{m}$  Chl-*a* size fraction was among the best for *E. californicus*. The 2014–2015 Warm Anomaly and 2015–2016 El Niño did not result in a consistent departure from the EPR functional relationships developed during El Niño-neutral conditions. Similarly, most other reproductive characteristics (clutch size, percent spawning, egg hatching success) did not differ during the warm conditions, but where they did for *C. pacificus*, compensatory changes in clutch size and hatching success resulted in no net change in naupliar production rate. We did not find elevated copepod EPR or altered hatching success for any of the three species at the two frontal systems analyzed. Over a regional scale we documented increased EPR inshore as compared to offshore wherever crossshore differences were

**Table 1**

Summary data for all three species. Overall EPR includes all females in the experiment, while spawning females includes only those individuals that laid eggs.

Species	$\bar{x} \pm 95\% \text{ CI}$				maximum
	Prosome length (mm)	Overall EPR (eggs $\text{female}^{-1} \text{d}^{-1}$ )	Spawning Females EPR (eggs $\text{female}^{-1} \text{d}^{-1}$ )	Clutch Size (eggs $\text{female}^{-1}$ )	Clutch Size (eggs $\text{female}^{-1}$ )
<i>Calanus pacificus</i>	2.50 $\pm$ 0.01	13.44 $\pm$ 1.34	37.98 $\pm$ 2.24	33.87 $\pm$ 1.77	109
<i>Metridia pacifica</i>	1.61 $\pm$ 0.01	2.48 $\pm$ 0.50	12.39 $\pm$ 1.47	14.10 $\pm$ 1.37	47
<i>Eucalanus californicus</i>	5.59 $\pm$ 0.03	2.19 $\pm$ 0.44	11.56 $\pm$ 1.36	28.32 $\pm$ 0.82	116

significant, a consistent spatial pattern over the five years. The ability of *C. pacificus* to sustain moderately high reproductive rates, even in low concentrations of autotrophic prey, may contribute to its numerical dominance across the region and may relate to the ubiquity of the genus *Calanus* elsewhere..

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2018.07.001.

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