Cohort analysis of *Euphausia pacifica* from the Northeast Pacific population using a Gaussian mixture model

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ABSTRACT
Euphausia pacifica cohorts were identified from biweekly zooplankton samples collected on the Newport Hydrographic Line (Newport, Oregon, USA) from 2001-2011. Cohorts were identified using a Gaussian mixture model and tracked over time from the juvenile stage through adulthood. Initial size mode at the juvenile stage was typically 4-5mm and final size modes ranged from 12-18mm. In total, 28 cohorts were identified, of which 22 appear to be complete cohorts that were tracked from start to finish during the 11-year study period. Of these 22 cohorts, 19 were tracked for ≤1.5 years. The three cohorts tracked for >2 years grew more slowly than other cohorts, though their final size modes were similar. These three cohorts were associated with delayed upwelling and moderate chlorophyll concentrations, suggesting that their extended duration and slower growth were related to suboptimal environmental conditions. Growth rates calculated from cohort size modes decreased overall as animals reached adult size. Cohort analysis captured some instances of negative growth, particularly after animals reached a total length of 10mm, similar to instantaneous growth rates (IGR) measured in a previous study. Survivorship curves were created from eggs and larvae for each year from 2001-2005.

Survivorship was similar among years except in 2005 when upwelling and subsequent spawning were delayed by one month. Based on the survivorship curves, the *E. pacifica* juvenile stage lasts an average of six months and the total life span in the study area is approximately two years. Successful identification and tracking of cohorts suggests that euphausiids at station NH25 are representative of the overall population dynamics of *Euphausia pacifica* in the shelf-break region off the Oregon Coast.

KEYWORDS
Euphausia pacifica; Northeast Pacific; cohort analysis; growth rate; survivorship, Gaussian mixture model

1. INTRODUCTION

Euphausia pacifica is the most abundant species of euphausiid in the North Pacific (Brinton 1962, Mauchline and Fisher 1969) and is present off the Oregon Coast year-round (Shaw et al. (this volume)). *E. pacifica* may spawn as early as February and as late as October but there is typically an intense period of spawning activity during the summer months of July and August (Smiles and Pearcy 1971, Brinton 1976, Feinberg and Peterson 2003) in association with phytoplankton blooms that are driven by coastal upwelling. The intense spawning activity during the summer when large numbers of eggs are produced over a short time period may serve to establish cohorts that can be tracked over time. *E. pacifica* in this area develop from egg to juvenile in an average of 60 days (Feinberg et al. 2006), therefore juveniles collected approximately two months after a spawning event could be attributed to those eggs. The Newport Hydrographic Line time series has sampled for juvenile and adult euphausiids approximately every two weeks since 2001. Here we apply a Gaussian mixture model to length frequency data from these samples to determine whether we can identify cohorts of *E. pacifica* and track their growth and development.

Cohort analysis relies on sampling the same population over time. It is difficult to define what constitutes a population in a dynamic upwelling habitat like the Oregon Coast, let alone ascertain whether the same population is being sampled, even when samples are collected at the same location. For this study we hypothesized (as did Smiles & Pearcy 1971), that our samples were either of the same population or of populations with similar age structure and growth rates.

As in other crustaceans, molting is an integral part of euphausiid development and occurs frequently from the first calyptopis stage to adulthood (Mauchline 1980, Feinberg et al. 2006). Unlike many other crustaceans, euphausiids continue to molt regularly as adults, and their length may increase, decrease, or stay the same after each molt (Mauchline and Fisher 1969, Marinovic and Mangel 1999, Pinchuk and Hopcroft 2006). Euphausiid growth is commonly measured either by following cohorts using modal progression of length frequencies in preserved samples (Smiles and Pearcy 1971, Brinton 1976, Bollens et al. 1992), or conducting instantaneous growth rate (IGR) experiments on live animals (Ikeda and Dixon 1982, Buchholz 1991, Quetin and Ross 1991, Nicol et al. 1992, Virtue et al. 1996, Marinovic and Mangel 1999, Cuzin-Roudy 2000, Pinchuk and Hopcroft 2006, Shaw et al. 2010). Growth rates from cohort analysis reflect overall population trends and are calculated from the change in length of size modes between samples, yielding one growth rate for each size mode present in sequential samples. IGR experiments measure growth rates of individual live euphausiids during short-term laboratory incubations

(Quetin and Ross 1991, Nicol et al. 1992). They yield one growth rate per euphausiid that molts during the experiment and reflect the range of individual variability. Previous cohort studies of *Euphausia pacifica* growth used simple visualization, identifying size modes in length frequency graphs and attempting to track them over time using modal progression (Smiles and Pearcy 1971, Brinton 1976, Bollens et al. 1992, Yoon et al. 2000, Kim et al. 2009). The simple visualization method can be somewhat subjective and cannot distinguish occasions when size modes overlap. The mixed normal distribution method employed in the present study increases the accuracy of growth rates from cohort analysis by identifying overlapping size modes.

The Newport Hydrographic Line time series is uniquely suited to apply the cohort analysis method to tracking *Euphausia pacifica* growth and development in the Northeast Pacific and to assess these results within a larger context. The data are from an 11-year time series that encompassed a wide range of environmental conditions. *E. pacifica* growth rates from live animal (IGR) experiments provide context for cohort growth rates. Here we identify cohorts, track them over time, calculate growth rates from cohort size modes, and create survivorship curves to estimate the lifespan of *E. pacifica* in our study area.

2. METHODS

2.1. Sampling

Samples were collected as part of an ongoing long-term sampling program on the Newport Hydrographic (NH) line off the coast of Newport, Oregon, USA (44°39.1'N) (Fig. 1). Data for this study are from January 2001 – December 2011. Cruises took place approximately every two weeks but sampling intervals were sometimes longer due to weather conditions, particularly during winter months. Sampling intervals ranged from 2-72 days, with a median of 16 days. Out of a total of 197 samples, only 21 had a sampling interval >40 days. Cruises were generally aboard the 54' RV *Elakha* but some sampling was from larger vessels during longer research cruises. The same gear and towing protocol were used regardless of sampling platform. Juvenile and adult euphausiids were collected at station NH25, located 25 nautical miles (40km) from shore (water depth 296m), just beyond the continental shelf break (Fig. 1), in oblique tows to 25m using a 60cm bongo with 333µm black mesh nets. Tows were conducted at night (between one hour after sunset and one hour before sunrise) since *E. pacifica* are diel vertical migrators. The tow depth of 25m targeted vertically migrating euphausiids (Brinton 1967, Bollens et al. 1992). Data for euphausiid eggs and larvae are from vertical net tows (50cm ring net, 202µm mesh, 100m max tow depth) at stations NH05, NH15, and NH25 (Fig. 1). Surface chlorophyll-*a* samples were collected with a bucket, making them true surface values rather than ~1m depth as with many chlorophyll samples collected from the "surface" bottle on a CTD rosette. Zooplankton samples were preserved at sea in 4% buffered formalin and sorted in the laboratory at Hatfield Marine Science Center. All juvenile and adult euphausiids were identified, staged, and measured by one author (CTS) to minimize

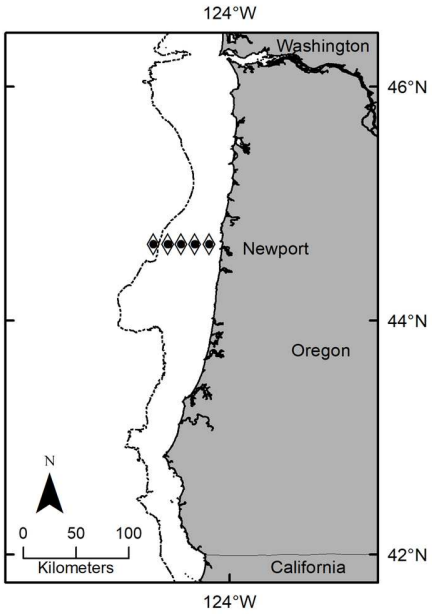

Figure 1 Newport Hydrographic (NH) line off Newport, Oregon, on the west coast of the USA. Station names from inshore to offshore: NH05, NH10, NH15, NH20, NH25. Station number represents the distance offshore (nm).

observer bias. Egg counts were by WTP and LRF, euphausiid larvae were identified, staged, and measured by LRF.

2.2. Environmental Conditions

Euphausia pacifica off the Oregon Coast are most strongly influenced by temperature and upwelling (Shaw et al. (this volume)). The phase of the Pacific Decadal Oscillation (PDO) serves as a proxy for temperature, although temperatures in the study area may lag changes in the PDO by several months. The PDO was in cool phase 2000-2002, warm phase 2003-2006, and cool phase 2007-2011. The spring and fall transition dates mark the start and end of the upwelling season and are calculated from cumulative wind stress data measured at the jetty in Newport, OR (http://damp.coas.oregonstate.edu/windstress/allyears.html). Typically the spring transition occurred in April and the fall transition was in September or October, with the upwelling season lasting 4-6 months. *Euphausia pacifica* spawning activity is fueled by phytoplankton blooms so the timing and duration of the upwelling season serve as a proxy for when ocean conditions should be favorable for blooms. During three years of this study the spring transition was delayed by approximately one month - 2000 (12-June), 2005 (22-May), and 2010 (10-June) - resulting in a corresponding one-month delay in the formation of phytoplankton blooms and subsequent spawning activity by *E. pacifica*.

2.2.1. Chlorophyll

Surface chlorophyll-*a* was measured using the acidification protocol (Welschmeyer 1994). There is a clear pattern of higher chlorophyll concentrations from July-September (Fig. 2, Table 1), consistent with the timing of intense *Euphausia pacifica* spawning activity. A subsurface chlorophyll-max was often present during summer months so chlorophyll concentrations available to euphausiids may have been higher than what is represented by surface samples collected with a bucket.

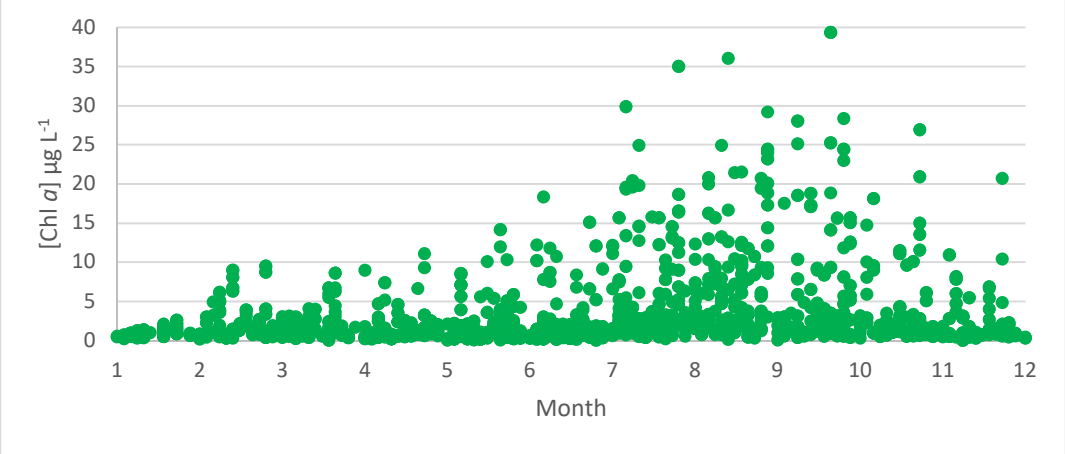

Figure 2. All individual surface chlorophyll-*a* measurements at stations NH05, NH10, NH15, NH20, NH25 for the years 2000-2011.

Table 1. Average surface chlorophyll (µg L^{-1}) from stations NH05, NH10, NH15, NH20, NH25 by month and year. Blank squares = no samples.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec

2000	0.48	0.53	1.82	1.80	0.45	0.43	6.36	4.61	1.71	1.54	0.91	0.34
2001	0.47	1.45	1.19	0.46	0.87	2.44	5.03	1.76	3.08	6.12	2.71	
2002	0.74	3.06	1.55	1.75	3.80	1.26	10.96	7.38	2.12	7.73	5.54	1.42
2003	0.73	2.43	1.64	1.94	0.49	3.82	5.51	8.61	7.54	0.90	1.48	
2004	0.80	0.52	1.54	0.36	0.74	1.42	6.74	4.62	2.16	1.51	1.26	1.27
2005	1.01	3.70	2.74	2.51	0.67	1.06	0.91	9.58	9.53	1.41	0.78	1.25
2006		1.72	0.54	1.17	1.96	0.83	4.57	4.46	3.71	4.24	0.71	1.15
2007	1.24	2.91	2.71	1.10	2.68	2.56	4.93	7.39	3.86	2.28	3.08	0.84
2008		1.04	4.31	1.60	2.65	1.74	3.63	3.41	10.88	2.65	1.11	0.79
2009	1.40	1.79	0.86	3.10	2.43	2.72	5.68	3.31	3.79	10.05	5.92	0.99
2010		3.07	0.43	1.94	1.83	1.85	13.35	6.13	7.32	2.12	1.27	1.20
2011	0.76	1.33	1.68	1.48	0.85	1.67	2.37	17.93	5.83	0.94	0.81	1.98
Avg	**0.85**	**1.96**	**1.75**	**1.60**	**1.62**	**1.82**	**5.84**	**6.60**	**5.13**	**3.46**	**2.13**	**1.12**

2.3. Euphausiid Data

2.3.1. Euphausiid eggs and larvae

Data for euphausiid eggs and larvae are from vertical net samples from stations NH05, NH15, and NH25 (Fig. 1). The euphausiids *Euphausia pacifica* and *Thysanoessa spinifera* both spawn in this area but their eggs can be identified to species since *T. spinifera* eggs are very sticky and were often covered in adhered debris (Summers 1993, Gomez-Gutierrez et al. 2007, Feinberg et al. 2010) while *E. pacifica* eggs were clean and did not stick to sorting dishes, forceps, each other, etc. Egg data are from 2000-2011 to include eggs from the 2000 spawning season that would give rise to cohorts in 2001. High densities of eggs (>200 eggs m^{-3}, referred to as "egg peaks") indicate the period of intense summer spawning by *E. pacifica*. Survivorship curves for *E. pacifica* were created for 2001-2005 from eggs and larvae (nauplii, calyptopis, furcilia).

2.3.2. Adult and juvenile euphausiids

Euphausia pacifica from the nighttime bongo tows at NH25 were counted and measured to generate length frequencies for each sample. Details of length measurements are in Shaw et al. (this volume). Cohorts are based on juveniles and adults since the bongo net mesh size was too large to sample larvae quantitatively. Sample sizes of juveniles and adults were not large enough to separate cohorts by life stage.

2.4. Gaussian Mixture Models for Cohort Analysis

Size modes for each sample were identified using Gaussian mixture models in Matlab (R7, Mathworks). A Gaussian mixture model is a probabilistic model for representing different cohorts in the population at a given time where each cohort is approximated by a normal distribution (Titterington et al. 1985), a more rigorous (and less subjective) method than identifying cohorts by simple visualization of length frequencies. By placing each observed individual in a specific cohort, the Gaussian mixture model allows us to infer the statistical properties associated with each cohort. In other words, the Gaussian model can work with a mixture of normal distributions with overlap, where two size modes overlap within a similar size range (Fig. 3). This is essential to accurate interpretation of the data and is very difficult to do using simple visualization.

To identify size modes, we constructed a length frequency histogram for each sample. A mixture of multiple normal distributions was fitted to each length histogram to identify overlapping size modes. The underlying assumptions are that if the histogram followed a mixture of multiple normal distributions, individuals within the same normal distribution were likely to have originated from the same cohort whereas individuals from different distributions were likely from different cohorts. If the histogram followed a single normal distribution, individuals were considered to be members of the same cohort. The probability distribution of length frequency x can be written as $f(x) = \sum_{i=1}^{n} w_i \times g(x|i, \theta_i)$, where $f(x)$ is the mixed normal distribution, x_i is the length frequency from the ith normal distribution or cohort, $g(x|i, \theta_i)$ is the probability density function of the ith normal distribution with parameter θ_i , and w_i is the mixing coefficient, i.e., the percentage of the ith cohort.

Estimates of each parameter required a mixing coefficient w_i and a parameter for each normal distribution $\theta_i = \{\mu_i, \sigma_i\}$, where μ_i is the mean length and σ_i is the variance of ith cohort. The standard log-likelihood for $X = \{x_1, x_2, \dots, x_i\}$ can be expressed as $E = -lnL(\gamma) = -\sum_{i=1}^{n} \ln g(x|i, \gamma)$, where $\gamma = \{w_1, w_2, \dots, w_i, \theta_1, \theta_2, \dots, \theta_i\}$. The mixing coefficient, mean length, and variance for each normal distribution were estimated by maximizing the log-likelihood. The distributions were visualized over time and cohorts were tracked between samples based on size mode and the length of the sampling interval (Fig. S1). Euphausiid distribution is notoriously patchy, which could explain the occasional disappearance and reappearance of size modes.

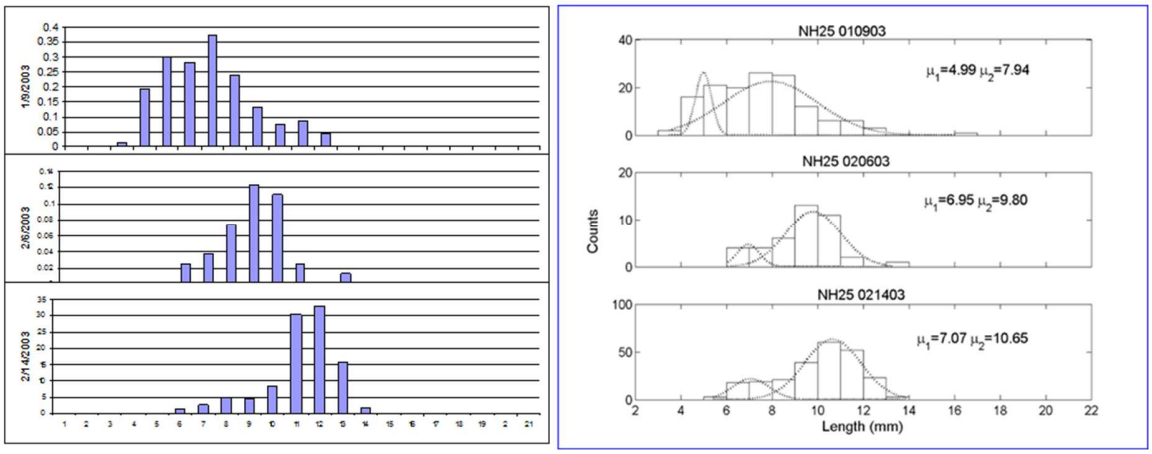

Figure 3. Example length frequency data from the same three samples shown using simple visualization (left panels) and Gaussian mixture model with overlapping size modes (right panels). μ_x = mean of each size mode. All Gaussian graphs are in Figure S1.

2.5. Growth Rates

2.5.1. Cohort growth rates

Mean size modes identified from the Gaussian mixture models are designated as μ_1, μ_2 etc. for each size mode in a sample (ex. Fig. 3, Fig. S1). Cohort growth rate was calculated as $growth = (\mu_{i,t2} - \mu_{i,t1})/(t2 - t1)$. The μ values are the means of size modes in sequential samples and *t* values are the sampling dates. Hence this subtracts the earlier size mode from the more recent one and divides by the number of days between samples, yielding a growth rate in mm d^{-1} (ex Fig. 3, Fig. S1). There is one growth rate for each size mode comparison, e.g., if

there are two size modes in a sample there is a separate growth rate for the change in size of each mode. Sampling intervals of two weeks or more might span two or more intermolt periods. As such, euphausiids could have molted two or three times during the sampling interval, and might grow, shrink, or remain the same size at each molt. Different size modes in the same sample cannot belong to the same cohort.

2.5.2. Instantaneous Growth Rates (IGR)

Instantaneous growth rate (IGR) experiments were conducted 2001-2009 using live *Euphausia pacifica* collected at station NH25 in the same bongo net tows as the preserved samples used for cohort analysis. See Shaw et al. (2010) for details of IGR experiments. Growth rates from IGR experiments are compared with growth rates from cohort analysis reported in the present study. Growth rates from both methods are expressed in units of mm d^{-1} even though euphausiid growth occurs incrementally at the time of each molt (every 7-10d) rather than as a continuous process.

3. RESULTS

3.1. Cohort Identification

Cohorts of *Euphausia pacifica* were successfully identified and tracked over time based on size modes determined from length frequency data using a Gaussian mixture model (Fig. 4). The "detection date" of a cohort is the sampling date when a size mode was first identified, as distinct from the "start date," which is the predicted hatching date of the eggs that initiated the cohort (Table 2). Given the sampling interval of approximately twice per month, the detection date may vary by up to a month from when the size mode was first present in the ocean.

Cohorts were detected during most months, with 2-3 cohorts detected in most years, and 4 detected in 2011 (Table 2). Every year except 2006 included cohorts tracked over shorter (<1yr) and longer (>1yr) durations starting from detection date. Cohorts detected during the typically downwelling months of November-February were always tracked for <1yr. All cohorts tracked for >1yr were detected from March-October but three of the cohorts tracked for <1yr were also detected during these months. There are partial cohorts at the start (Cohort 1) and end (Cohorts 25-28) of the study where the full cohort progression did not fall within the study period (Fig. 4). Cohort 1 began in 2000, prior to the start of sampling for juvenile and adult euphausiids, so this cohort was detected at a larger size mode of ~11mm. Cohort 2 could have been present earlier than its January 2001 detection date, as this was the first month of sampling for juvenile and adult euphausiids. Cohorts 3-24 appear to be complete cohorts that were tracked from start to finish (detection to disappearance) during the study period. Cohorts 7 and 8 likely merged as the animals developed over time, as indicated by the reduced power (lower R^2) to distinguish these cohorts (Fig. 4). Cohorts 25-28 were detected May-December of 2011 and likely continued into 2012, which was not analyzed for cohorts. Cohort start date is estimated from the date progression trendline (Fig. 4). The similar slopes of the trendlines (Fig. 4) suggest that growth rates were similar overall throughout the study period (one-way ANOVA $p<0.05$).

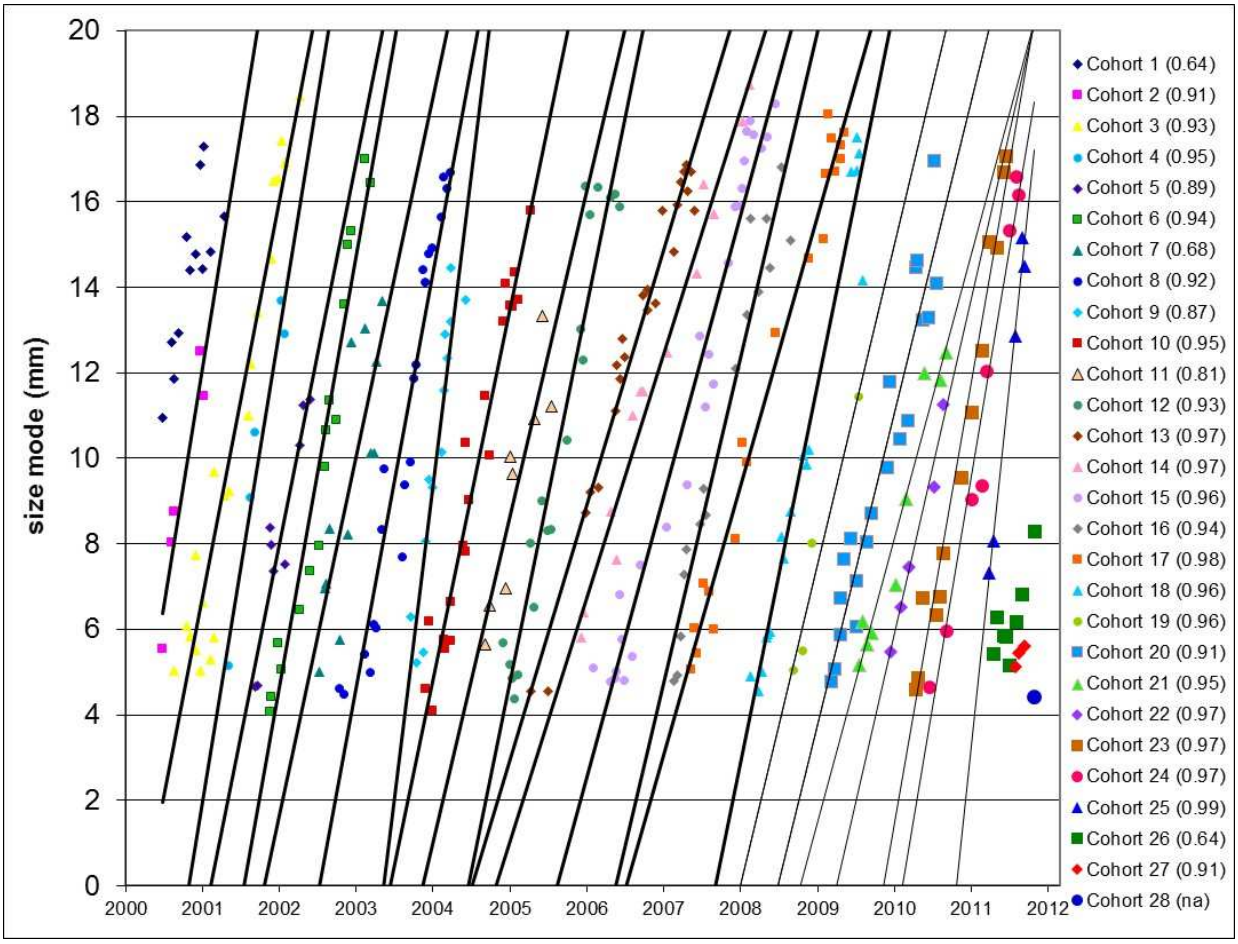

Figure 4. Date progression of all cohorts from 2001-2011. The full progressions of Cohort 1 and Cohorts 25-28 were not encompassed by the sampling period. Figure legend includes R^2 values of trendlines (in parentheses). See Table 2 for predicted cohort start dates.

3.2. Cohorts by Cumulative Days

To compare progression patterns, the complete cohorts (Cohorts 3-24, detected 2001-2010) are shown by cumulative days from detection date (Fig. 5). Size mode at detection was 4-6mm and final size modes were typically 12-18mm (Table 2). Note that this does not represent the largest *Euphausia pacifica* individuals since a size mode comprises both smaller and larger animals (Figure S1). The largest *E. pacifica* were ~26mm but the average length was ~17mm (Shaw et al. (this volume)), similar to maximum cohort size modes. Many cohorts followed a similar pattern of size mode progression from ~5mm to ~17mm within ~500d (Fig. 5). Cohorts 13, 14, and 15 deviate from this pattern, increasing in size more slowly and persisting for closer to 800d. Since these three cohorts were the only ones tracked for over two years, they are the only cohorts represented after day 600 (Fig. 5). Throughout their progression, size modes of Cohorts 13 and 14 are often slightly smaller than other cohorts, and Cohort 15 is noticeably smaller than any other cohort until after day 600 (Fig. 5, purple circles).

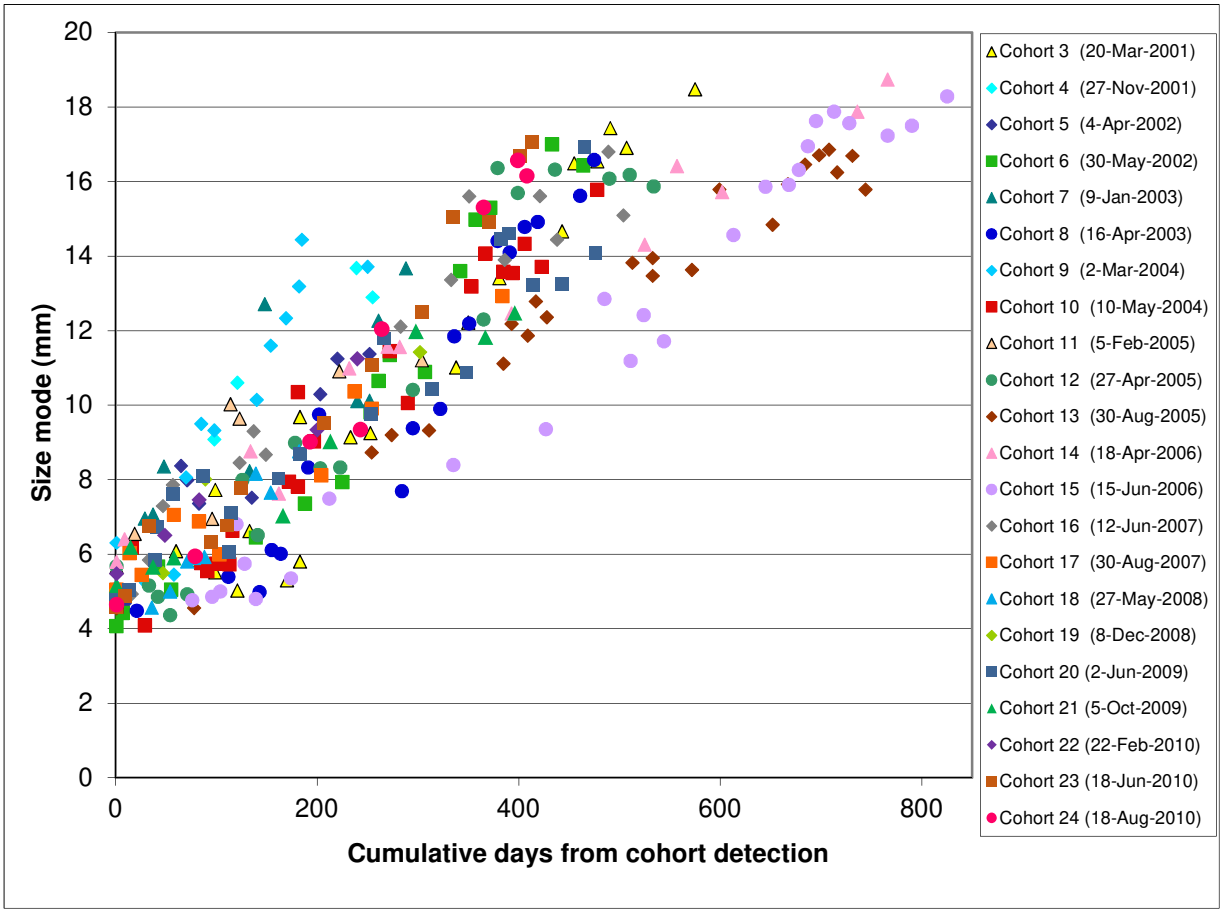

Figure 5. Size modes of probable complete cohorts (3-24) shown by cumulative days from cohort detection to compare progression patterns. Cohort detection dates are shown in the figure legend. All cohorts combined R^2=0.8347, all cohorts excluding 13-15 R^2=0.8631, cohorts 13-15 R^2=0.9297.

3.3. Projected Cohort Start Dates

The projected start date is the estimated hatching date of eggs that initiated the cohort. Projected start dates were estimated using two methods: date progression (Fig. 4) and cumulative days (Fig. 5). There is good agreement overall between the start dates predicted by these two methods (Table 2, R^2=0.9988), and about half of the predictions were within a few days of each other. However, predicting the exact date of hatching is too precise for this data set given the inherent uncertainty from sampling intervals and overlapping size modes so further date comparisons are by month.

Table 2. Cohort details. Detection date and end date are the first and last dates the cohort size modes were tracked in samples. Size mode start and end are the first and last size modes attributed to that cohort. Projected start dates are predicted hatching dates derived from date progression (d) (Fig. 4) and cumulative days from cohort detection (c) (Fig. 5). There are no values for duration or projected start date from cumulative days for Cohort 1 as it was initiated in 2000, prior to the start of sampling for juvenile and adult euphausiids. Cohorts 25-27 are likely

incomplete but start dates have been calculated from the available size modes. Cohort 28 only has one size mode as it was detected during the last month of the study.

Cohort #	Detection date	End date	Cohort duration (years)	Size mode - start (mm)	Size mode - end (mm)	Projected cohort start date from date progression (d)	Projected cohort start date from cumulative days (c)
1	*27-Jan-01*	7-Nov-01	na	*10.96*	15.66	22-Mar-99	na
2	27-Jan-01	18-Jul-01	0.47	5.54	11.46	5-Jul-00	10-Jul-00
3	20-Mar-01	15-Oct-02	1.57	5.04	18.48	17-Sep-00	15-Nov-00
4	27-Nov-01	8-Aug-02	0.70	5.13	12.89	20-Jul-01	27-May-01
5	4-Apr-02	3-Dec-02	0.67	4.66	11.37	14-Jul-01	12-Sep-01
6	30-May-02	5-Sep-03	1.27	4.07	16.43	25-Mar-02	2-Feb-02
7	9-Jan-03	23-Oct-03	0.79	4.99	13.67	4-May-02	22-Apr-02
8	16-Apr-03	30-Aug-04	1.38	4.60	16.67	23-Mar-03	10-Jan-03
9	2-Mar-04	6-Nov-04	0.68	6.30	13.71	7-Oct-03	29-Oct-03
10	10-May-04	30-Aug-05	1.31	4.59	15.78	6-Jan-04	29-Nov-03
11	5-Feb-05	5-Dec-05	0.83	5.66	11.21	19-Feb-04	6-Mar-04
12	27-Apr-05	12-Oct-06	1.46	5.67	15.87	1-Oct-04	19-Nov-04
13	30-Aug-05	12-Sep-07	2.04	4.55	15.79	19-Mar-05	7-Dec-04
14	18-Apr-06	22-May-08	2.10	5.80	18.74	26-Feb-05	25-Mar-05
15	15-Jun-06	16-Sep-08	2.26	5.07	18.29	9-Nov-05	28-Dec-05
16	12-Jun-07	27-Oct-08	1.38	4.80	15.09	18-Sep-06	30-Sep-06
17	30-Aug-07	16-Sep-08	1.05	5.05	12.93	15-Sep-06	7-Dec-06
18	27-May-08	24-Nov-08	0.50	4.91	17.13	11-Oct-07	13-Dec-07
19	8-Dec-08	5-Oct-09	0.82	5.04	11.42	10-Apr-08	11-Apr-08
20	2-Jun-09	20-Sep-10	1.30	4.77	14.09	28-Sep-08	29-Sep-08
21	5-Oct-09	4-Nov-10	1.08	5.16	12.48	8-Jan-09	9-Jan-09
22	22-Feb-10	19-Oct-10	0.65	5.48	11.25	23-Jun-09	24-Jun-09
23	18-Jun-10	4-Aug-11	1.13	4.58	17.07	23-Jan-10	24-Jan-10
24	18-Aug-10	29-Sep-11	1.12	4.65	16.15	19-Apr-10	16-Apr-10
25	18-May-11	26-Oct-11	0.44	7.32	*14.50*	20-Dec-10	21-Dec-10
26	8-Jun-11	10-Dec-11	0.51	5.43	*8.30*	21-Apr-10	22-Apr-10
27	13-Sep-11			5.13	*5.62*	26-May-10	26-May-10
28	10-Dec-11			4.39			

3.4. Cohorts and Egg Densities

Estimated cohort start dates were compared to monthly egg densities to investigate the relationship between timing of egg peaks and cohort detection date. Use of a monthly timescale is based on a previous study that followed *Euphausia pacifica* development from egg to juvenile (Feinberg et al. 2006). This study found that the amount of time individual animals spent at each developmental stage increased with successive stages and varied among individuals such that development time to juvenile for individuals spawned within a few days of each other varied by as much as three weeks (Feinberg et al. 2006). This suggests that age estimates for animals collected in the field are only accurate to within approximately one month. The mean hatching time for euphausiid eggs in our study area is ~40 h (Gómez-Gutiérrez 2002, Feinberg et al. 2006) so eggs are present in the water column for <2 days. Our median sampling interval of 16 days will not detect every small individual spawning event but is sufficient to identify the timing of intense spawning activity during the summer. Egg densities are shown as monthly totals for stations NH05, 15, and 25 combined (Table 3). Total eggs is a more informative measure than

the monthly average due to occasional elevated egg densities outside of the peak spawning season.

Chlorophyll and egg densities are often high in the same month (Table 3) since *Euphausia pacifica* spawning events are fueled by phytoplankton blooms (Smiles and Pearcy 1971, Brinton 1976) and the euphausiids spawn rapidly in response to an increase in chlorophyll, even if it is only a relative increase from the previous month (Table 1). The highest densities of *E. pacifica* eggs were typically during the upwelling months of July and August (Fig. 6, Table 3), coincident with the periods of highest chlorophyll (Table 1). Egg densities dropped after August in most years but in 2005 and 2010 the highest values were in September (Fig. 6, Table 3) as the one-month delay in the onset of upwelling in these years led to a corresponding delay in elevated egg densities. There were February egg peaks in 2005 and 2007 (Table 3), possibly in response to brief periods of upwelling-favorable winds that resulted in an increase in chlorophyll (Table 1).

Projected cohort start dates calculated from both cumulative days (c) and date progression (d) (Table 2) were matched to monthly egg densities (Table 3). Predictions from date progression matched better overall than those from cumulative days, but date progression also sometimes matched the start dates of two different cohorts to the same egg peak (Jul-01, Sep-06). Some predicted start dates match beautifully with high egg densities (e.g. July 2000, July 2001, February 2005), others do not, particularly when cohorts were detected during the winter months of November – January. Months with high egg densities often do not match a projected cohort start date. There is less data for October – January due to reduced sampling opportunities during winter months, though existing data and low chlorophyll concentrations (Table 1), which are not conducive to *E. pacifica* spawning, suggest that egg densities are likely to be low at this time of year. Cohorts with predicted start dates during these months are thus unlikely to result from a high density of eggs.

Table 3. Egg density (eggs m^{-3}) by month and year matched to predicted cohort start dates. Egg densities are monthly totals for stations NH05+NH15+NH25. Empty squares=no samples. Gray shading shows predicted cohort start dates by cohort number and prediction method (c=cumulative days, d=date progression). Red squares indicate cohort start dates that correspond with egg densities >200 eggs m^{-3}.

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
2000			27.93	317.71		24.08	3257.47 (2c,d)	1543.91	238.68 (3d)		7.62 (3c)	22.42
2001	20.00	160.66	4.86	109.46	84.84 (4c)	15.13	3111.68 (4d, 5d)	323.61	74.24 (5c)			
2002	1.67	36.59 (6c,d)	50.47	46.57 (7c)	878.16 (7d)	137.15	1488.57	965.05	57.17	22.77	137.43	
2003	(8c)	6.22	(8d)	2.95	55.90	10.04	1150.91	58.54	76.89	(9c,d)	(10c)	
2004	(10d)	(11d)	190.14 (11c)	14.09	2.74	96.96	61.04	1448.49	87.59	(12d)	1.37 (12c)	(13c)
2005		1392.56 (14d)	(13d, 14c)		7.51	11.08	195.59	359.41	425.86		(15d)	(15c)
2006		1.60		6.96	43.18		1465.38	2795.64	642.06 (16c,d; 17d)	74.24		(17c)

2007	2.71	941.66	93.97	6.33	256.67	122.19	93.51	896.13 (18d)	152.67	1.40	10.56	(18c)
2008			324.79	789.12	253.18 (19c,d)	5.36	866.26	212.91	200.14 (20c,d)	3.88	1.53	
2009	(21c,d)	6.48	36.91	343.52	835.54	80.41 (22c,d)	1413.45	244.80	103.79	19.53	7.79	
2010	(23c,d)	18.41		3.91 (24c,d)	103.69	278.08	450.37	957.83	1761.19	3.93	1.26	(25c,d)
2011		9.58		125.59		124.15	25.05	1464.08	241.95			

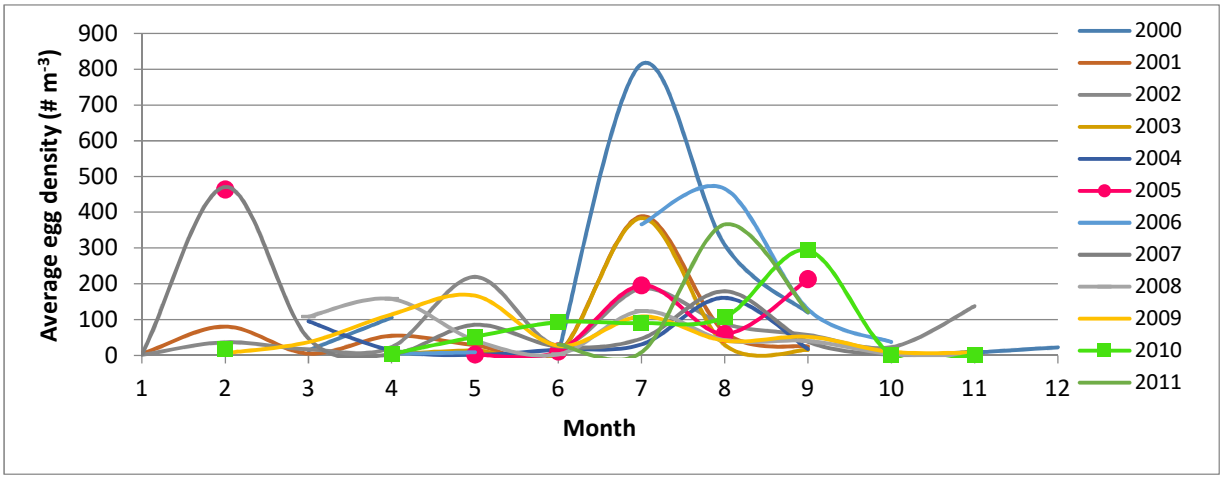

Figure 6. Average monthly egg densities 2000-2011 for stations NH05, NH15, and NH25 combined. High egg density in February 2005 is due to an early phytoplankton bloom. Late onset of upwelling delayed highest summer egg densities until September in 2005 (pink circles) and 2010 (green squares).

3.5. Growth Rates

3.5.1. Growth rates among cohorts

Average cohort growth rates were in the range of 0.05-0.1 mm d^{-1} with some cohorts more variable than others (Fig. 7). There was no noticeable pattern between growth rates and cohort duration. The longest-duration cohorts (Cohorts 13-15) took longer to reach the maximum size mode and were clearly smaller than other cohorts at similar points in their progression (Fig. 5) but had fairly narrow ranges of growth rates, similar to the shortest duration cohorts and also to some that were tracked for just over one year.

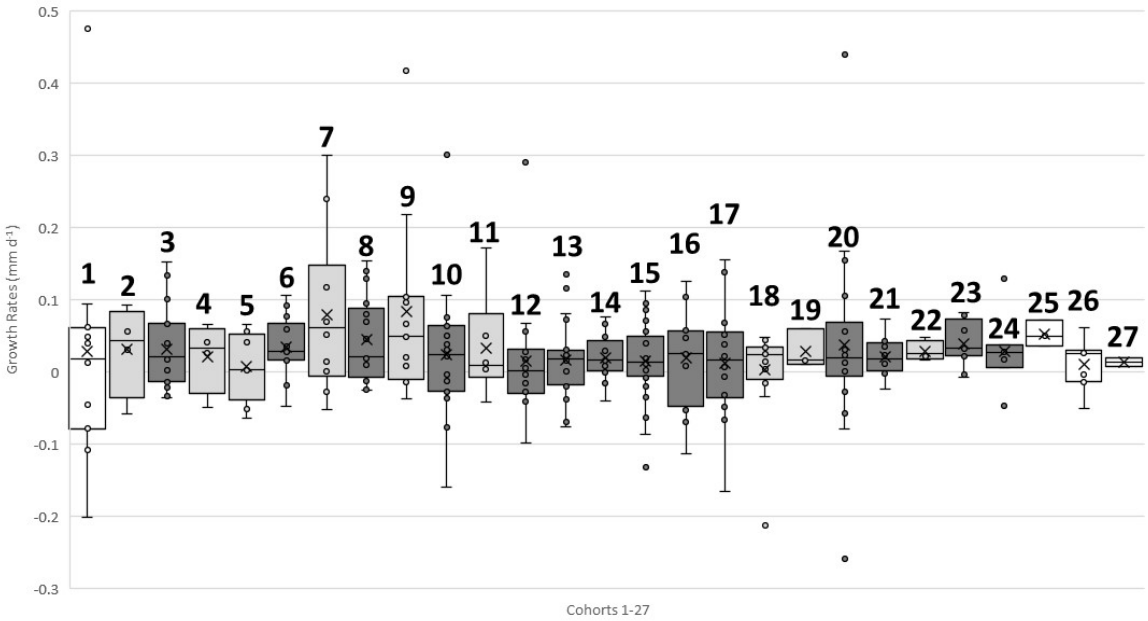

Figure 7. Box & whisker plot showing the median and first and third quartiles of growth rates (mm d^{-1}) for Cohorts 1-27. White = partial cohorts, light gray = cohorts tracked <1 yr, dark gray = cohorts tracked >1 yr. See Table 2 for cohort durations. Cohort 28 is not shown since it consists of a single size mode.

3.5.2. Comparison of cohort and IGR growth rates

A comparison of cohort growth rates from the present study with instantaneous growth rates (IGR) from a previous study (Shaw et al. 2010) shows that results from both methods may be highly variable (Fig. 8). Cohort growth rates were usually positive and in the range of 0.01-0.2mm d^{-1}. Growth rates were positive for animals <5mm and higher overall for smaller size modes. Several of the higher negative growth rates for animals <10mm were from 2006, when Cohort 15 was notably smaller than all other cohorts for the period from ~350-~550 days (Fig. 5). Growth rates >0.2mm d^{-1} were uncommon but occurred occasionally in 2001, 2002, 2004, 2006, 2008, and 2011 (Fig. 8). Negative growth rates were usually <0.05mm d^{-1} for all size modes, which may reflect slight variations between sampling dates rather than actual negative growth in the population. The fact that negative growth of individuals was frequently observed in IGR experiments once animals reached a length of 10mm (Shaw et al. 2010) suggests that negative growth in cohort size modes ≥10mm is more likely to reflect the actual growth rate in the population. Negative growth was more common in 2005 and 2010 (delayed upwelling), 2006 and 2007 (slow growing cohorts), and 2011 (chlorophyll low until August (Table 1)). The range of growth rates is similar among years, with minimal interannual variability.

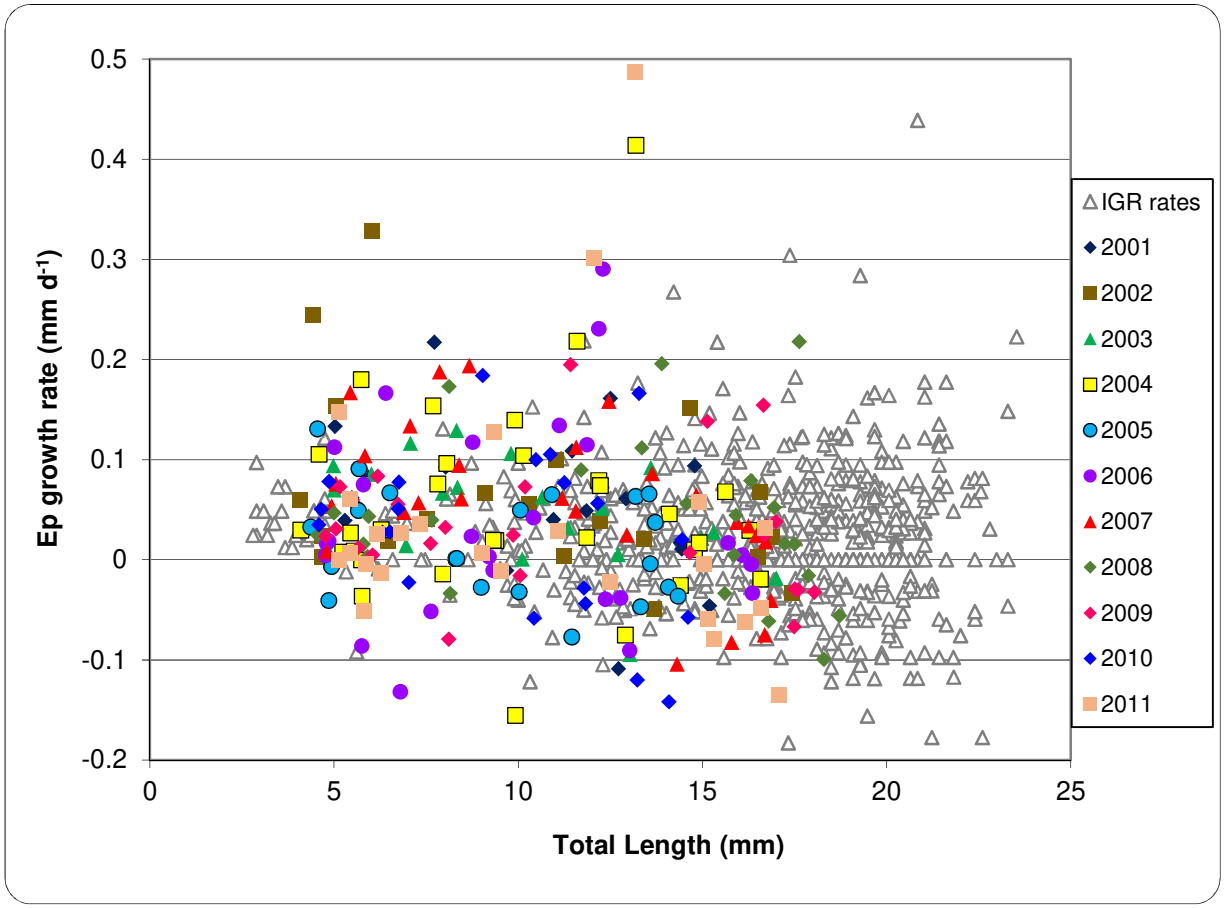

Figure 8. Growth rates of *E. pacifica* by total length. Note that the axes do not intersect at zero. To examine interannual variability, colors designate the year the growth rate was measured rather than the cohort to which it belongs. IGR growth rates from 2001-2009 (gray Δ) are shown for comparison. There are no cohort rates for animals >18 mm since that is the maximum cohort size mode.

3.5.3. Monthly average growth rates

Monthly average cohort growth rates were always positive (Fig. 9) even though negative cohort growth rates were not uncommon (Fig. 8). Average growth rates from IGR experiments are positive March-October, but negative in November, December, and January, and only slightly positive in February. IGR growth rates are similar to cohort growth rates in March and September but lower in all other months. Negative growth has more influence on IGR rates since there are more measurements of negative growth for individuals than for cohorts.

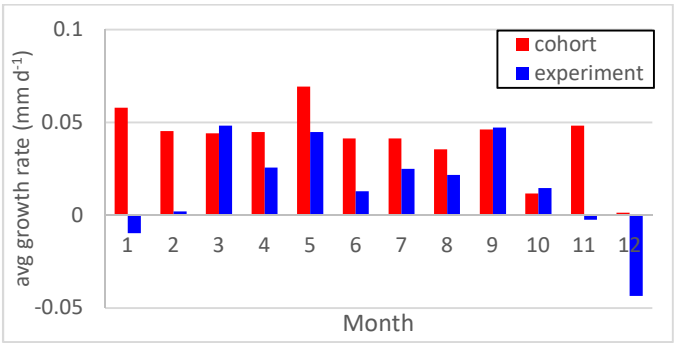

Figure 9. Monthly average growth rates for cohort and IGR experiments.

3.6. Survivorship Curves

Survivorship curves for each year from 2001-2005 (Fig. 10) are based on counts of eggs and larvae in vertical net samples. Values for eggs, nauplii, calyptopis, and furcilia were determined by dividing annual averages by stage duration (Feinberg et al. 2006). Survivorship followed an exponential decline for all years, with similar fit during 2001-2004 ($R^2 \approx 0.90$ for all years), but egg density was much higher in 2005 and this, coupled with low survivorship, resulted in a weaker fit ($R^2 = 0.68$) (Fig. 10). Juveniles and adults were fitted to the curves since we do not have measured durations for these stages. Estimated stage durations for juveniles and adults are 180d and 270d, respectively, suggesting a total lifespan of ~2 years.

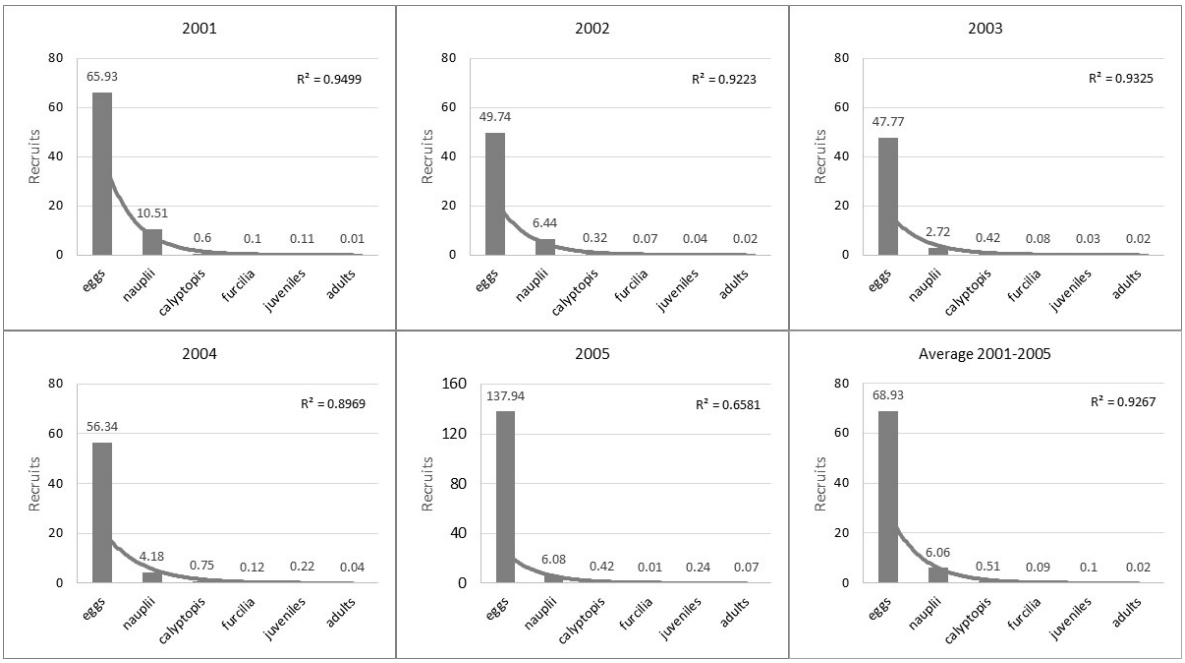

Figure 10. Survivorship curves 2001-2005 and average of all five years. Note the different scale for 2005 due to extremely high egg densities.

4. DISCUSSION

The cohort analysis technique is predicated on sampling the same population on an appropriate timescale for the target species. The present study successfully identified cohorts and tracked

them over time, suggesting that biweekly samples from station NH25 satisfied these criteria for *Euphausia pacifica*. Although sampling intervals sometimes exceeded two weeks, particularly during winter months, cohorts were successfully tracked over these longer periods. Longer sampling intervals in winter may be mitigated to some extent by the fact that food resources are typically low during these months and thus euphausiid growth is likely to be minimal. *E. pacifica* are also known to shrink during winter when food availability is reduced (Mauchline and Fisher 1969, Marinovic and Mangel 1999, Pinchuk and Hopcroft 2006). Although it is complicated to define what constitutes a "population" in a dynamic upwelling region like the Oregon Coast, the success of the present study at tracking cohorts suggests that euphausiids at station NH25 are representative of the overall population dynamics of *E. pacifica* in the shelf-break region off the Oregon Coast.

4.1. Seasonality of Cohorts

Complete cohorts were tracked for periods of 6-27 months. There was a tendency for cohorts with longer durations to be detected during upwelling and those with shorter durations during downwelling but there were exceptions in both cases. Other studies have also found seasonal differences in *Euphausia pacifica* cohort duration. Off of southern California, cohorts detected from June-December were tracked for 10-13mo while those detected from February-May were tracked for 5-8mo (Brinton 1976). In the Oyashio region of Japan, cohorts initiated in May had a duration of 17mo, compared to 26mo for those initiated in August (Kim et al. 2009). Cohort duration off of Oregon did not have clear seasonal relationships. All cohorts tracked for >12mo (n=14) were detected from March-October. However, three of the eight cohorts tracked for <12mo were detected from March-May. Cohorts detected from December-February were all tracked <12mo. The relationship with upwelling was also unclear, as cohorts detected during upwelling conditions were tracked from 6-27mo and those detected during downwelling from 8-19mo. The study period spanned cool and warm phases of the PDO but cohort durations were similarly variable during both phases, suggesting that these large-scale temperature differences were not strongly affecting *E. pacifica* spawning or development.

4.2. Growth

Cohort growth rate is a measurement at the population (or subpopulation) level and represents average growth during the sampling interval (~16d in the present study). IGR growth rates are for individual euphausiids and integrate the conditions they experienced during the previous intermolt period (usually 7-10d off the Oregon Coast) (Shaw et al. 2010). Both methods provide useful information about euphausiid growth when conducted rigorously, but the different methodologies mean that the data are not interchangeable. Growth rates from cohort analysis reflect an overall population trend while IGR rates show the range of individual variability (Fig. 8). Cohort growth rates declined with increasing length, indicating that population growth as a whole decreases as animals reach adulthood, while IGR growth rates show that individual variability remains high (Fig. 8). The most common growth rate measured in IGR experiments was zero, meaning the animal molted with no change in length (Shaw et al. 2010). The cohort analysis method would be unlikely to measure a growth rate of zero, though it did capture some very low growth rates and even some negative ones. Cohorts 13-15 progressed much more slowly to adult size than other cohorts but the range of their growth rates was similar (Fig. 7). The fact that these three cohorts took two years to grow to the same size that other cohorts achieved in ≤1 year suggests that growth rates for these cohorts were often close to zero.

Interestingly, average monthly growth rates from both cohort and IGR methods were similarly high in March and September (~0.045mm d^{-1}) (Fig. 9), coinciding with the typical timing of seasonal transitions in spring (March/April) and fall (September/October). This may reflect increased food availability at the start of the upwelling season, and an increase in smaller animals from the summer spawning season growing at higher rates in the fall prior to the onset of downwelling conditions.

4.3. Maximum Size Mode

Most cohorts attained their maximum size mode of ~17mm after ≤1yr. Cohorts 13, 14, and 15 grew more slowly but attained maximum size modes of 15.8mm, 18.7mm, and 18.3mm, respectively, similar to those of other cohorts (Table 2). The >17mm size range may be advantageous for reproduction. A synthesis of *Euphausia pacifica* brood sizes at various locations in the North Pacific found that females of all sizes (13-25mm) produced broods of up to 200 eggs but only females ≥16mm produced broods >200 eggs (up to 700 eggs per brood) (Feinberg et al. 2013). Although overall size ranges of adult *E. pacifica* were similar among years during this study, smaller adults comprised a larger percentage of the population during the period when Cohorts 13-15 were present (Shaw et al. (this volume)). The percentage of adults >20mm was already low in 2004 (7.5%), suggesting that adults in the population were smaller overall going into 2005. In 2005 only 3.3% of adults were >20mm. In 2006 almost 13% of adults were >20mm but this was still low compared to an average of 28% during the study period and >60% in 2008 and 2009. Egg densities were high in the summer of 2006, indicating that reproductive effort was high even though the spawning population had a high percentage of smaller females.

4.4. Cohorts and Environmental Conditions

A longer lifespan may seem like a positive outcome, but the slower growth rates and longer durations of Cohorts 13, 14, and 15 may have resulted from unfavorable environmental conditions rather than optimal ones. Growth of oceanic zooplankton such as euphausiids is driven primarily by temperature and food (Huntley and Boyd 1984, Clark and Peck 1991, Hirst et al. 2003) and growth rates of these three cohorts may have been slower based on the food resources available. Cohort 13 was initiated in 2005, a year when the PDO was in warm phase, the onset of upwelling was delayed by a month, and the upwelling season was very short (Shaw et al. (this volume)). Chlorophyll values were relatively high in August and September of 2005 but low during the fall and winter into 2006, with chlorophyll values in summer 2006 being the lowest overall during the study period (Table 1). Cohorts 14 and 15 were detected in 2006, probably formed from euphausiids that overwintered as juveniles after the late spawning in 2005. Timing and duration of upwelling were more typical in 2006 but the PDO was still in warm phase and summer chlorophyll concentrations peaked at 4.5µg L^{-1} while in other years they were typically >7µg L^{-1} during at least one summer month (Table 1). The anomalously small size modes in Cohort 15 correspond to the period from May-December 2007 when chlorophyll was relatively low, except for a moderately high value in August (Table 1). Chlorophyll is a useful proxy for food availability but does not represent all potential prey and euphausiid diets may vary seasonally in the study area (Du and Peterson 2014, Fisher et al. (this volume)). Phytoplankton community composition is affected by changes in water temperature (Iriarte and González 2004, Kudela et al. 2006, Du et al. 2015), with warmer water shifting the community from larger species to smaller ones, resulting in reduced energy transfer from primary production

to larger animals (Cavole et al. 2016). The slower growth of these cohorts may be related to lower quality and/or abundance of food resources, which increased the time it took for them to grow to large adult size. The ability of this analysis to capture the effect of environmental conditions on euphausiid growth makes it a potentially useful tool to apply to similar data sets to assess responses to environmental variability.

4.5. Relationship between Egg Peaks and Cohort Start Dates

The impetus for this study was to investigate the relationship between egg peaks and cohort start dates. Timing of spawning informs the survival and development of larvae based on the environmental conditions they experienced as they grew up. For example, larvae hatched in July and August are likely to encounter two months of elevated phytoplankton concentrations, which should favor maturation to the juvenile stage prior to the onset of downwelling conditions. As seen in this study, the later onset of upwelling in 2005 and 2010 delayed the timing of highest egg densities (Table 3, Fig. 6). Larvae spawned later in the season are less likely to encounter a prolonged period of favorable feeding conditions as they develop, which may reduce overall survival or increase development time to juvenile. As a result, they may not develop to juvenile prior to winter, or if they do they may be smaller and in poorer condition, reducing overwintering survival. However, matching egg peaks with cohort start dates met with limited success (Table 3). Timing of egg peaks may not be the most useful predictor of cohort initiation as biweekly sampling is likely too long an interval to accurately predict cohorts based on egg peaks, particularly due to the short residence time of eggs in the water column. However, even if egg data were collected with finer temporal resolution, relating the projected start date of a cohort to a specific egg peak would still be imprecise due to the inherent uncertainty from variability in developmental rates from egg to juvenile.

Intense summer spawning activity may not be the only way to establish a cohort. The composition of *Euphausia pacifica* life stages in preserved samples from late fall to early spring suggests that they regularly overwinter in the juvenile stage (Brinton 1976, Shaw et al. (this volume)). Euphausiids from late summer and fall spawning events may develop at different rates and coalesce into cohorts during the late fall or winter, resulting in cohorts that are not descended from an egg peak. After overwintering, juveniles that comprise one size mode may be the product of several spawning events and span an age range of a month or more. This variability is another confounding factor when trying to match a cohort start date to a period of high egg density.

4.6. Other Predictive Relationships

Given that the spring transition (ST) initiates conditions favorable for phytoplankton blooms, and *Euphausia pacifica* spawn in response to elevated chlorophyll concentrations, we investigated whether any relationships among these events could predict the appearance of cohorts. The ST is inherently less variable than other parameters since it is determined using land-based instrumentation and thus not dependent on at-sea sampling intervals. Chlorophyll concentrations might have better predictive value than egg densities since phytoplankton blooms are longer-duration events and more likely to coincide with at-sea sampling than the short periods when eggs are present in relation to a spawning event. Comparisons use the first month that chlorophyll concentration and egg density are notably higher than in previous months since these relative increases will trigger a response. This comparison investigates response to ST so

spawning events that occur prior to ST are not included. The interval between ST and increased chlorophyll was 2.3 months on average, similar to the ~2.5 month interval between ST and elevated egg density (Table 4). Elevated chlorophyll and egg density often occur in the same month since *E. pacifica* spawn rapidly in response to increases in chlorophyll concentrations. The relationship between egg density and cohort detection (Table 4) is the most variable due to short residence time of eggs in the water column and variability in euphausiid development times, resulting in two sources of potential mismatch between egg density and cohort detection. The timing between ST and cohort detection averaged ~6 months, but ranged from ~2-9 months. This interval was shorter in 2005 and 2010 when delayed onset reduced the length of the upwelling season. The relationship between ST and chlorophyll is fairly consistent and varies predictably in relation to the timing of upwelling, in spite of potential variability due to sampling intervals. ST has the advantage of being measured without going to sea and its consistent relationship with elevated chlorophyll may make it a useful proxy for the timing of increased spawning activity. This can provide an estimate for the timing of summer and fall cohorts based on *E. pacifica* development times. Chlorophyll concentrations measured at finer temporal scales using autonomous gliders or satellites have potential predictive value for euphausiid spawning and growth as these measurements provide more detailed environmental conditions than can be obtained from shipboard sampling.

Table 4. Timing of spring transition, elevated chlorophyll (chl) and egg densities, and cohort detection dates. Chl and Eggs are the first month of elevated values (Tables 1 & 3). Columns 5-9 are the number of months between the two events in the column header. Shaded values do not make biological sense and are excluded from averages. Size mode could have appeared any time between the previous sampling date and the collection date.

Spring Transition (ST)	Chl	Eggs	Cohort Detection Date	ST to Chl (mo)	ST to Eggs (mo)	ST to Cohort (mo)	Chl to Cohort (mo)	Eggs to Cohort (mo)	Cohort #
1-May-01	Jul-01	Jul-01	27-Nov-01	2.03	2.03	7.00	4.97	4.97	4
17-Apr-02	Jul-02	Jul-02	09-Jan-03	2.50	2.50	8.90	6.40	6.40	7
20-Apr-03	Jul-03	Jul-03	02-Mar-04	2.40	2.40	10.57	8.17	8.17	9
21-Apr-04	Jul-04	Aug-04	05-Feb-05	2.37	3.40	9.67	7.30	6.27	11
22-May-05	Aug-05	Sep-05	30-Aug-05	2.37	3.40	3.33	0.97	-0.07	13
20-Apr-06	Jul-06	Jul-06	12-Jun-07	2.40	2.40	13.93	11.53	11.53	16
27-Apr-07	Aug-07	Aug-07	30-Aug-07	3.20	3.20	4.17	0.97	0.97	17
29-Apr-08	Sep-08	Jul-08	08-Dec-08	4.17	2.10	7.43	3.27	5.33	19
14-May-09	Jul-09	Jul-09	05-Oct-09	1.60	1.60	4.80	3.20	3.20	21
10-Jun-10	Jul-10	Sep-10	18-Aug-10	0.70	2.77	2.30	1.60	-0.47	24
			Average	**2.37**	**2.58**	**5.95**	**4.60**	**5.72**	

4.7. Survivorship

Survivorship of *Euphausia pacifica* is rarely reported as it is time consuming to determine and requires frequent sampling with a small enough mesh size to collect all larval stages quantitatively. Survivorship in our study declined exponentially from egg to juvenile, though high egg density and low survivorship in 2005 resulted in a weaker relationship. Off southern California, Brinton (1976) found a similar survivorship pattern, with a roughly exponential rapid decline during the larval phase. Low survivorship from egg to juvenile in 2005 was clearly

related to environmental conditions. The onset of upwelling was delayed by one month in 2005, with a corresponding delay in the phytoplankton blooms (Table 1) that fuel *Euphausia pacifica* spawning. Although spawning effort was high once it began, the delay meant that egg densities were highest in September, a month or more later than the typical pattern of highest egg densities in July-August (Fig. 6). Although conditions were good for spawning, they probably were not good for survival of larvae produced so late in the season, as this likely resulted in a mismatch between when larvae need to feed and when sufficient food resources were available. Based on the average development time of 60 days, (Feinberg et al. 2006) juveniles spawned in September would likely recruit in November when chlorophyll concentrations are typically low (Table 1), resulting in an unfavorable food environment and increased mortality.

4.8. Lifespan of *Euphausia pacifica* off the Oregon Coast

Reported lifespans for *Euphausia pacifica* range from ~10 months to 2 years, with longer lifespans at higher latitudes (Lasker 1966, Brinton 1976, Ross 1981, Iguchi et al. 1993, Kim et al. 2009). Since lifespan appears to vary with geographic location and environmental conditions, estimates from one region are likely not applicable to other areas. It is difficult to determine the lifespan of euphausiids. It can be estimated by raising euphausiids from eggs in the laboratory, but this is time-consuming and may not represent survival in the wild due to animals being raised in small containers, differences in diet, and the absence of predation (Ross 1981, Feinberg et al. 2006). The age of individual euphausiids can be estimated using pigment analysis but this is labor-intensive, highly technical, and can be costly (Harvey et al. 2010). It would be a laborious, and most likely inconclusive, long-term project to measure stage durations of juveniles and adults in the laboratory, especially with a species as highly variable as *E. pacifica*. The estimated stage durations of 180d for juveniles and 270d for adults obtained from survivorship curves suggest that, in our study area, the juvenile stage lasts an average of 6 months, and *E. pacifica* have a potential total lifespan of two years (if they avoid being eaten by one of the myriad predators). This potential for *E. pacifica* to grow to adulthood and comprise part of the adult population for over a year could confound the process of distinguishing their original cohort. However, we found only one occasion where it seems likely that two cohorts merged (Cohorts 7 and 8) (Table 2). The actual duration of the juvenile stage will vary based on timing of spawning, food resources, development time, and environmental conditions. The estimate of a two-year lifespan for *E. pacifica* is consistent with previous studies (Lasker 1966, Iguchi et al. 1993, Kim et al. 2009), ageing studies of *E. pacifica* from the Oregon Coast using lipofuscin (Harvey et al. 2010), and laboratory observations (*E. pacifica* collected as adults lived for 2+ years in the lab in Oregon, Shaw & Feinberg, pers. obs.). An estimated lifespan for *E. pacifica* in this region may be useful for modeling and stock assessment purposes.

5. CONCLUSIONS

Cohort analysis using a Gaussian mixture model successfully identified cohorts of *Euphausia pacifica* and tracked them for up to two years off the Oregon Coast. The use of mixed normal distribution methods improves the ability to track size modes over time by identifying overlapping size modes. A sampling interval of approximately two weeks was sufficient in this study area, though appropriate sampling intervals for this species will differ in other areas since their spawning patterns, growth, development, and lifespan differ geographically. Sampling intervals longer than two months are likely not biologically relevant for tracking cohort progression or calculating growth rates. Growth rates from cohort analysis represent general

668 population trends, in contrast with growth rates from IGR experiments that encompass the wide
669 range of individual variability. Population growth rates may be more useful for modeling and
670 stock assessment applications than the highly variable individual rates.
671
672 An unexpected but potentially significant finding is that this analysis detected an effect of
673 environmental conditions on cohort growth. The cohorts detected in August 2005 and April and
674 June 2006 were the only cohorts tracked for over two years, had noticeably smaller size modes
675 than other cohorts at similar days from detection, and progressed more slowly to adult size.
676 These cohorts were associated with delayed upwelling and moderate chlorophyll concentrations,
677 suggesting that their slow growth was a result of suboptimal environmental conditions. The
678 abundance of smaller adults from these cohorts resulted in a higher percentage of smaller adults
679 (<20mm) for a period of two years. The Gaussian mixture model method may be useful to
680 analyze other data sets for environmental effects, particularly for retrospective analyses of data
681 from other long-term sampling programs.
682
683 The slower growth and longer duration of these cohorts is an example of the inherent plasticity
684 of *Euphausia pacifica* that allows them to respond to changes in their environment. The range of
685 environmental variability during the study period was apparently within the tolerance range for
686 this species, but the reduced survivorship, slower growth, and higher percentage of small adults
687 in response to delayed upwelling indicate that these conditions were not optimal and raise
688 concerns for the future. Continued warming will affect the ecosystem off of Oregon in ways yet
689 unknown, but some predictions suggest that the timing and duration of upwelling will be
690 affected. If later onset of upwelling becomes more common, *E. pacifica* spawning is likely to
691 occur later in the year, resulting in reduced survivorship and slower growth to large adult size.
692 This would shift the population to a higher percentage of small adults, which has consequences
693 for the many higher trophic level predators that prey on euphausiids. Smaller adults would be a
694 lower-quality food resource and also produce smaller broods of eggs. Consequently, a higher
695 percentage of small adults may lead to reduced reproductive success and an overall decrease in
696 abundance. Later spawning could also result in a mismatch in the phenology of euphausiid prey
697 availability, particularly for migratory predators and nesting seabirds.
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