Late spring and summer patterns of euphausiid reproduction in Southeast Alaska fjord waters

Citation	Szabo, A. R., & Batchelder, H. P. (2014). Late spring and summer patterns of euphausiid reproduction in Southeast Alaska fjord waters. Marine Ecology Progress Series, 516, 153-161. doi:10.3354/meps11003
DOI	10.3354/meps11003
Publisher	Inter-Research
Version	Accepted Manuscript
Terms of Use	http://cdss.library.oregonstate.edu/sa-termsofuse

LATE SPRING AND SUMMER PATTERNS OF EUPHAUSIID REPRODUCTION IN SOUTHEAST ALASKA FJORD WATERS

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Running Head: Southeast Alaska euphausiids

Keywords: Euphausiids, Southeast Alaska, Spawning timing, Juvenile, Larva, Fjord

ABSTRACT

Abundance, size and development stage data for furcilia and juvenile euphausiids and data on timing and prevalence of attached spermatophores on adult females are used to infer spawning times by four euphausiid species in Frederick Sound and lower Stephens Passage, Southeast Alaska. Results from net tows conducted between late May and September 2008 and a single, opportunistic dip-net sample on 21 April indicate that *Thysanoessa raschii* and *T. longipes* spawned in association with the spring phytoplankton bloom and continued spawning until June, with juveniles first appearing in mid-late June. Presence of female *T. spinifera* carrying spermatophores in mid-April indicate that *T. spinifera* spawns in association with the spring bloom as well; however, absence of larval *T. spinifera* suggest that spawning in the inshore waters is comparatively rare. In contrast, observations of female *Euphausia pacifica* carrying spermatophores from late May-August and the first appearance of early furcilia in August indicate that spawning occurs, at least to some extent, after the primary bloom. However, the appearance of juvenile *E. pacifica* in late June suggests that spawning occurred earlier as well and in discrete bouts. We argue that the absence of *E. pacifica* furcilia that were likely to have originated from an early spawning event may indicate that *E. pacifica* juveniles observed in late June were advected into the study region from the Gulf of Alaska. Overall, phenology of seasonal reproduction in this Alaskan fjord is similar to that observed in coastal waters in arctic and temperate ecosystems.

INTRODUCTION

Southeast (SE) Alaska shares the distinction with Norway, Chile and Greenland as one of the planet's great fjord systems. Inshore waters of SE Alaska are foraging habitats for numerous marine mammal species (Dahlheim et al. 2009, Womble et al. 2009), including one of the largest feeding aggregations of humpback whales (*Megaptera novaeangliae*) in the Northern Hemisphere (Calambokidis et al. 2008). The region also supports a diverse array of marine fishes, including several that are commercially important like *Oncorhynchus* spp (Johnson et al. 2005), and the highest diversity of seaweeds in the state (Lindstrom 2009). Nevertheless, little is known about the biological patterns and processes that characterize the region's inshore waters. As noted recently: "we remain profoundly ignorant of the oceanography, marine biogeography and marine biology of SE Alaska" (Weingartner et al. 2009), an idea echoed by others (Dahlheim et al. 2009, Lindstrom 2009).

This paucity of information extends to euphausiids in SE Alaska fjords, which have received relatively little attention. In coastal regions of Alaska and the Bering Sea where euphausiids have been studied more extensively they have been conceptualized as a relevant trophic link in the transfer of primary production to higher trophic levels (Pinchuk & Hopcroft 2006, Falk-Petersen et al. 2000), and are key prey for several species of cetaceans (Croll et al. 2005, Friedlaender et al. 2006, Laidre et al. 2010), seabirds (Hunt et al. 1996, Abraham & Sydeman 2004, Jahncke et al. 2005), and many commercially valuable fish (Tanasichuk et al. 1991, Wilson et al. 2006, Weitkamp & Sturdevant 2008). The recruitment of immature euphausiids, in particular, can represent a significant resource pulse for predators, such as walleye pollock (*Theragra chalcogramma*), juvenile rockfish (*Sebastes* spp.) and capelin (*Mallotus villosus*) (Reilly & Echeverria 1975, Wilson et al. 2006, Coyle et al. 2008). Information on the spawning schedules of adults and abundance patterns of immature euphausiids can assist in resolving distribution and abundance patterns of these planktivores and others in the region. More generally, it is important towards understanding trophic interactions and energy flow through the marine community.

The objective of this study was to investigate late spring and summer patterns of reproduction by euphausiids in Frederick Sound and lower Stephens Passage, SE Alaska. Net sampling of euphausiids was part of a larger research project examining the foraging ecology of humpback whales in the region and was constrained by the use of a small inflatable vessel to daytime sampling. Because of this logistical limitation, the sampling strategy was insufficient to characterize adult euphausiid abundance given their strong escape reactions (Wiebe et al. 1982, Hovekamp 1989, Simard & Sourisseau 2009). We present abundance, size and development stage data for late larval (furcilia) and juvenile euphausiids (hereafter, we refer to combined furcilia and juveniles as “immatures”) sampled during the late spring and summer. We use these data together with data on the timing and prevalence of attached spermatophores on adult females to infer times of euphausiid spawning.

METHODS

Biological samples and environmental information were collected between 21 April and 9 September 2008 in Frederick Sound and lower Stephens Passage, SE Alaska (56°-57° N, 133°-134° W; Figure 1). These bodies of water are part of a system of fjords and channels that comprise the inside waters of the region. Average sea bottom depth of the study area was estimated from hydroacoustic surveys to be 208 m, with median and maximum depths of 197 m and 491 m, respectively (Szabo, unpublished data).

Euphausiids were sampled from a 6.4 m rigid-hull inflatable boat during a series of daytime hydroacoustic surveys initiated at approximately 20-d intervals between 22 May and 9 September. For each survey, the study region was partitioned into 18 strata, each 4.6 km-wide and oriented perpendicular to the long axis of the Sound. A single transect was randomly placed within each stratum (additional survey details are provided in Szabo 2012). Each day, two single oblique net tows were conducted. Net tow sites were selected before setting out using a random number generator to identify two locations along the transects to be surveyed that day. Random tows were used to provide an unbiased estimate of immature euphausiid abundance and life stage patterns; however, because they might under-sample the presumably patchy distribution of adult euphausiids for the spermatophore analysis, oblique tows were also conducted in areas where the 120 kHz (Simrad EK60) echosounder showed a strong scattering layer. Non-random tows were conducted in all six 20-d surveys; however, random tows were only conducted after 8 June (*i.e.*, starting in the second 20-d survey). Due to variation in day length, transect length and weather conditions, the number of samples per survey varied.

Net tow samples were collected by vertically lowering a black-dyed, 0.75 m diameter General Oceanics ring net with a 3:1 length-to-mouth ratio having 1 mm mesh to 100 m (or within 5 m of the bottom where shallower). The cod-end was weighted to ensure that the net back-flushed during its descent. Maximum net depth, limited by the sampling winch, was verified using pressure data from a ReefNet Sensus Ultra dive recorder (accuracy of ±0.3 m) attached to the net ring. The 100 m maximum was generally sufficient to ensure that the depth of the maximum scatter of the acoustically-observed daytime scattering layer was within the net sampled depth range during summer 2008 (Szabo 2012). Echograms associated with each tow revealed that the net tow failed to capture the peak backscatter layer in only 3% (n=5) of net deployments.

We retrieved the net using a combination of vessel movement and wire retrieval in order to obtain a net speed sufficient to capture immature euphausiids during the day. Estimated densities are presumed to be biased low due to net avoidance and tow geometry, but the relative abundance of euphausiids should be consistent from sample to sample. To avoid fouling the boat propeller, the deployment fulcrum was mid-ship on the port side of the vessel, and the course for retrieval was a gradually curving counterclockwise trajectory. A General Oceanics flow-meter was attached to the net to estimate sampled volume. The dive recorder recorded water temperature (accuracy of ±0.8 °C) at 10 s intervals during net tows after 5 July. Temperatures recorded at the maximum depth are reliable, but temperatures on the up and down deployments are less reflective of the temperature at depth because of the relatively long time constant of the temperature sensor.

Additionally, we opportunistically sampled a dense aggregation of euphausiids observed within several meters of shore using a dip-net (~1 mm mesh) on 21 April at Petersburg Harbor at the confluence of Wrangell Narrows and the eastern arm of Frederick Sound approximately 60 km east of the main study area. A random subsample of 100 individuals from this sample is included in the analysis**.**

Contents from the net tow were preserved at-sea in a buffered 4% formalin solution for later analysis. Samples were split using a Folsom plankton splitter to yield approximately 100 individuals of the most numerous euphausiid species in the smallest subsample. All euphausiids within successively larger sub-samples were counted and identified to species until at least 100 individuals had been examined. Euphausiid length, from the base of the eye stalk to the end of the telson, was recorded to the nearest 0.1 mm, and the number of terminal and postero-lateral spines on the telson, and presence or absence of a petasma and/or attached spermatophore were noted. Individuals having 2 or more postero-lateral spines and a telson that was not fully developed were considered to be larvae and those with only 2 spines and a completely developed telson were considered to be juveniles (Brinton et al. 2000). To simplify analysis, larvae were further classified into broad categories (that slightly change among species): early furcilia (>5 terminal spines), mid furcilia (5 terminal spines) and late furcilia (3 terminal spines). Calyptopis larvae were comparatively rare relative to the abundant early furcilia. We assumed this resulted from sampling bias due to them passing through the 1mm mesh, so we do not include pre-furcilia life stages in the analysis to infer hatching periods as an approximation of the interspecific spawning period. Individuals were considered adults if they had reproductive organs or were clearly larger than the juvenile cohort. Females with spermatophore attached to the thelycum was considered as a qualitative criterion that the species was mating and reproducing during the date of sampling. The density of immature euphausiids was calculated by dividing the count estimates of each sample by the estimated filtered volume of water sampled and expressed as individuals per 1000 m^{-3}. ANOVA was used for temporal and interspecific euphausiid abundance comparisons.

RESULTS

44 random and 110 non-random net samples collected during six different surveys together with a single, opportunistic dip-net sample were analyzed (Figure 1, Table 1). Considering the bottom depth distribution of sampling effort, 12% of the samples were collected from sites where the bottom depth was <100m, 46% from 100m – 200m, 25% from 200m – 300m, 14% from 300m-400m and 1% from locations with depths of 400-500m. Surface temperatures from 5 July onwards ranged from 8.5°C – 15.5°C, with the warmest temperatures in early August (average = 12.4°C; F = 23.488, $p < 0.001$). Temperatures deeper than 50 m measured with the ReefNet Sensus Ultra sensor ranged from 5.3°C – 8.2°C, but did not vary significantly by survey period (F = 0.501, p = 0.683).

Four euphausiid species were observed in the study region: *Thysanoessa raschii*, *T. longipes*, *T. spinifera*, and *Euphausia pacifica*. With the exception of survey 2 (S2) for *T. longipes*, immature *T. raschii* and *T. longipes* were initially present in a high proportion of samples and in high abundances within those samples, but become less prevalent in later surveys (Fig. 2 and 3). Prior to mid-July, close to 100% of *T. raschii* were early furcilia; juvenile *T. raschii* first appear in late June, increasing to ~70% a month later, with the remainder split nearly equally among the three fucilia groups (Fig. 4). Juvenile *T. longipes* (4.2 – 14.9 mm) were first observed in mid-June, but furcilia predominated; by the final survey, nearly 100% of immature *T. longipes* were juveniles (Fig. 4). The size distribution of both species shifted to larger lengths in successive surveys (Fig. 4). However, the size at which *T. longipes* transitioned from furcilia to juveniles was smaller later in the season than it was in earlier surveys (8.1 mm in S2 versus 4.2 mm in S6).

Unlike *T. rashii* and *T. longipes*, *E. pacifica* were initially rare, but become increasingly common in later surveys (Fig. 2). Juvenile *E. pacifica* (5.8 – 14.1 mm) were observed from late-June (S3) onwards; however, with few exceptions *E. pacifica* furcilia (all early) were observed only in the final survey (S6). Immature *T. spinifera* were rarely observed, being found in only 3 samples collected between mid-July and mid-August and in comparably low abundances within those samples. No larval *T. spinifera* were observed; juveniles (6.6 – 14.6 mm) were observed between mid-July and mid-August (Fig. 4).

There was a tendency for the abundance of all four species to decline in later surveys so that abundances were lowest in the final survey (Fig. 3a); however, this was only significant for *T. raschii* (F=36.147, p<0.001) and *T. longipes* (F=7.122, p=0.013).

Only *T. raschii*, *T. spinifera* and *E. pacifica* were observed with attached spermatophores (Table 2). There were notable differences in timing and prevalence of attached spermatophores between the two *Thysanoessa* species and *Euphasia pacifica* (Fig. 3b). Female *T. raschii* and *T. spinifera* dominated the single mid-April sample and approximately one third of the individuals had attached spermatophores; overall, about 30% of *T. raschii* females carried spermatophores prior to late-June, while later in the season, few had spermatophores. In contrast, nearly half of *E. pacifica* females were carrying spermatophores after 22 May (Fig. 3b).

DISCUSSION

Thysanoessa raschii was the most numerous euphausiid in the summer of 2008, which is consistent with previous reports from the inshore waters of SE Alaska (Krieger & Wing 1986, Dolphin 1987, Paul et al. 1990). Immature *T. longipes* were nearly as widespread but were considerably less abundant. *Thysanoessa longipes* is typically found in oceanic waters >200m

(Brinton et al. 2000, Iguchi & Ikeda 2004, Pinchuk & Coyle 2008) so it is possible that net samples collected from depths greater than the 100m limit in this study would have yielded higher abundances. However, where the vertical distribution of larvae and small juvenile *T. longipes* has been studied (*i.e.*, central Japan Sea) they are largely confined to the surface layer (Iguchi & Ikeda 2004). As well, lower abundances of *T. longipes* relative to *T. raschii* are consistent with previous sampling in the region (Bryant et al. 1981, Krieger & Wing 1986, Dolphin 1987).

Juvenile *T. raschii* first appeared in late June and increased in abundance relative to furcilia thereafter. Combining development time estimates derived for *T. raschii* from SE Alaska of 2-3 weeks from egg to calyptopis III (Paul et al. 1990) and six weeks from early furcilia to juvenile (Dehalt 1986) suggests that individuals develop from egg to early juvenile in approximately two months. A similar development time has been reported for *T. raschii* in the North Atlantic (Mauchline 1965). At this rate, the appearance of juveniles in late June suggests that *T. raschii* began spawning around mid to late April, which corresponds well with our 21 April observation that ~30% of *T. raschii* females had attached spermatophores, and with previous reports of high concentrations of *T. raschii* eggs in the region in early spring (Paul et al. 1990). Although juvenile *T. longipes* were observed in early June, the temporal progression from furcilia to juveniles in *T. longipes* was similar to that observed in *T. raschi*, suggesting these species have similar spawning schedules.

The spawning period for *T. raschii* varies considerably among different locations (Berkes 1976, Falk-Petersen & Hopkins 1981, Smith 1991, Hunt et al. 1996). Regional variation in the spawning period corresponds with variation in the onset and duration of the spring phytoplankton bloom (Berkes 1976, Falk-Petersen & Hopkins 1981), which *T. raschii* uses as the major source of energy to support egg production (Mauchline & Fischer 1969, Paul et al. 1990, Dalpadado & Skjoldal 1991). While we have no direct *in situ* measures of early spring 2008 phytoplankton concentrations in Frederick Sound, our estimate of mid-late April for *T. raschii* spawning corresponds with the time of the spring bloom in Auke Bay to the north of the study region (Ziemann et al. 1991, B. Wing, Auke Bay Laboratory, personal communication). Females were rarely observed carrying spermatophores after mid-June and furcilia became proportionally less abundant as the summer progressed. This indicates that the main spawning season for *T. raschii* ended in June, shortly after the spring phytoplankton bloom terminates

(Ziemann et al. 1991). However, observations of early-stage furcilia and a single female with an attached spermatophore at the end of August indicate that breeding may continue through the summer, but at a reduced level as observed for this species in the southeastern Bering Sea (Pinchuk & Coyle 2008). Protracted spawning by *T. raschii* into summer in SE Alaska may be supported by intermittent phytoplankton blooms resulting from wind-driven resupply of nutrients (Iverson et al. 1974, Ziemann et al. 1991).

Thysanoessa longipes females were rarely captured and the few that were lacked spermatophores**.** In other ocean regions, *T. longipes* females with spermatophores are typically found at depths greater than 150 m during the day (Iguchi & Ikeda 2004), so absence from our samples may reflect the comparatively shallow sampling depth. Similar to *T. raschii*, breeding by *T. longipes* is coincident with the spring bloom in other regions (Chiba & Saino 2002, Kasai et al. 2001). A substantial proportion (~30%) of immature *T. longipes* in early June had already developed to the mid-furcilia stage and by late August furcilia were nearly absent from the study region. This suggests a shorter spring spawning period and/or more rapid development through the larval stages than *T. raschii*. In the western North Pacific, spawning of *T. longipes* is confined to April-May (central Japan Sea; Iguchi & Ikeda 2004) and March-May (Oyashio region; Kim et al. 2009). Kim et al. (2009) noted a short period of dominance of *T. longipes* furcilia, which is consistent with our observation that larvae become juveniles at smaller sizes in later surveys.

Immature *T. raschii* and *T. longipes* were found in a lower proportion of samples after late July, when the majority of individuals were juveniles. Their absence from a larger proportion of samples in the last two surveys may reflect the ability of larger juveniles to aggregate in fewer, higher quality habitats. However, the abundance of immature individuals declined within patches as well. Declines in zooplankton abundance from spring to autumn have been reported previously for SE Alaska (Park et al. 2004, Sturdevant et al. 2007) and other regions in the North Pacific (Smith 1991). In the Bering Sea, predation is believed responsible for seasonal declines of immature euphausiids (Smith 1991). In our sampling, progressive declines in abundance might also be the result of methodological limitations (net avoidance of nets with slow wire retrieval and daytime only sampling) that enabled larger, better swimming stages later in the summer to avoid capture.

Thysanoessa spinifera was the rarest euphausiid in the study area, which is consistent with previous sampling in SE Alaska (Bryant et al. 1981, Krieger & Wing 1986). Because of the rarity of both immature and adult *T. spinifera*, it was not possible to identify the breeding pattern. The presence of females carrying spermatophores in mid-April suggests that *T. spinifera* spawns in spring in association with higher phytoplankton concentrations, which is similar to the other *Thysanoessa* species and is consistent with the breeding behavior of this species elsewhere (Pinchuk et al. 2008, Feinberg et al. 2010). However, the complete absence of larval *T. spinifera* in the fjords during our sampling suggests that advection from the Gulf of Alaska may be important in supporting inshore populations.

Euphausia pacifica immature abundance patterns and the timing and prevalence of attached spermatophores on adult females differed from the *Thysanoessa* species. Direct observations of *E. pacifica* females carrying spermatophores from late May through early August and the first appearance of early furcilia in August indicate that *E. pacifia* spawning in SE Alaska occurs, to some extent, after the spring bloom in April. Timing of spawning in *E. pacifica* varies widely over the species range (Feinberg et al. 2013, and references therein), and post spring-bloom spawning of *E. pacifica* is found in other regions as well (Pinchuk & Hopcroft 2006, Kim et al. 2009). Both temperature and food appear to be important in regulating spawning in this species (Feinberg et al. 2006, Pinchuk & Hopcroft 2006, Pinchuk et al. 2008). *Euphausia pacifica* is able to uncouple its breeding activity from peaks in phytoplankton blooms by feeding on microzooplankton (Bollens et al. 1992) and small copepods (Kim et al. 2009). Whether this occurs in SE Alaska is unclear, as delayed spawning in SE Alaska may be supported by secondary, summer phytoplankton blooms (Iverson et al. 1974, Ziemann et al. 1991).

The first appearance of larval *E. pacifica* in late August is consistent with a delayed, summer spawning event; however, the appearance of juvenile *E. pacifica* in late June is not. Development time estimates from egg to juvenile for *E. pacifica* range from 58 days at 10.5°C (Feinberg et al. 2006) to 68 days at 8°C (Ross 1981). At these rates, juveniles observed in June were likely spawned in mid to late April, coincident with the primary plankton bloom. Furthermore, the size distribution of immature *E. pacifica* with non-overlapping modes for larvae and juveniles, and the absence of mid to late furcilia in late August, suggest that spawning was not continuous, but occurred in discrete bouts as reported for *E. pacifica* in the western North Pacific (Kim et al. 2009). No *E. pacifica* furcilia were found that might have originated from an early spawning event associated with the spring bloom. Perhaps spring bloom associated spawning of *E. pacifica* was so brief that the entire larval population had progressed to the juvenile stage by June. Alternatively, the *E. pacifica* juveniles in late June may be offspring produced by offshore *E. pacifica* spawners that are subsequently advected into the inshore fjords. Flow patterns into and throughout the inshore waters of SE Alaska are poorly known; however, spring shelf circulation may carry zooplankton from the Gulf of Alaska into the region through Chatham Strait (Eckert et al. 2007, Weingartner et al. 2009). The narrow shelf at the entrance to Chatham Strait, and the depth of the Strait itself, allow offshore waters of the Gulf – where *E. pacifica* is abundant (Pinchuk et al. 2008) - to communicate with the inshore waters of SE Alaska (Weingartner et al. 2009). The spring bloom appears to occur earlier (March) in the Gulf (Weingartner et al. 2009); therefore, individuals spawned in association with the bloom could potentially transition through the larval stages sooner than those in the inshore waters so that, by late June, the cohort was dominated by juveniles.

This study provides evidence that the three *Thysanoessa* species have similar spawning schedules that are coincident with the spring bloom in SE Alaska, whereas *E. pacifica* differs by spawning primarily after the bloom. As well, the results suggest that *T. spinifera* and *E. pacifica* populations in the inshore waters of SE Alaska may be supported by advection from the Gulf. The role, if any, that advection plays in supporting inshore euphausiid populations in these relatively narrow channels that dissect SE Alaska warrants further investigation. Overall, phenology of seasonal reproduction in this Alaskan fjord is similar to that observed in coastal waters in arctic and temperate ecosystems.

ACKNOWLEDGEMENTS

We thank B. Mate, T. Shaw, and W. Peterson for helpful comments on an earlier version of this manuscript. We are also grateful to the numerous volunteers that assisted us in the field. Alaska Whale Foundation and the Marine Mammal Institute at Oregon State University provided logistical support. Finally, we would like to thank the three anonymous reviewers that provided valuable comments.

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Table 1. Survey dates (2008) and number of associated random and non-random net samples used in the analyses of furcilia and juvenile euphausiids (random samples only) and occurrence of adult females carrying spermatophores (random and non-random samples combined) in Frederick Sound/Stephens Passage, Southeast Alaska. A single, opportunistic dip-net sample collected in Petersburg harbor, Southeast Alaska is included.

Survey	Date	Random (N)	Non-random (N)	Combined
Opportunistic	21 April	0	1	1
1	22 May – 1 June	0	10	10
2	8 June - 17 June	5	18	23
3	27 June - 12 July	9	23	32
4	15 July - 25 July	10	21	31
5	5 August - 15 August	10	18	28
6	27 August - 9 September	10	20	30
Total		44	110	155

Table 2. Lengths of adult female euphausiids and proportion of adult females carrying spermatophores from all surveys and 21 April opportunistic sampling.

	Length (mm)		Surveys 1 - 6			21 April		
Species	Mean	Range	N	Proportion (%)	Adj. Wald 95% CI (%)	N	Proportion (%)	Adj. Wald 95% CI (%)
T. raschii	20.4	14.7 - 25.3	38	7.9	2 - 22	60	30.0	20 - 43
T. spinifera	21.9	15.1 - 26.2	15	6.7	0 - 32	13	38.4	18 – 65
T. longipes	18	11.7 - 24.8	14	0	0 - 19	0	---	---
E. pacifica	19.3	11.0 - 24.8	60	43.9	33 - 56	1	0.0	0 – 41

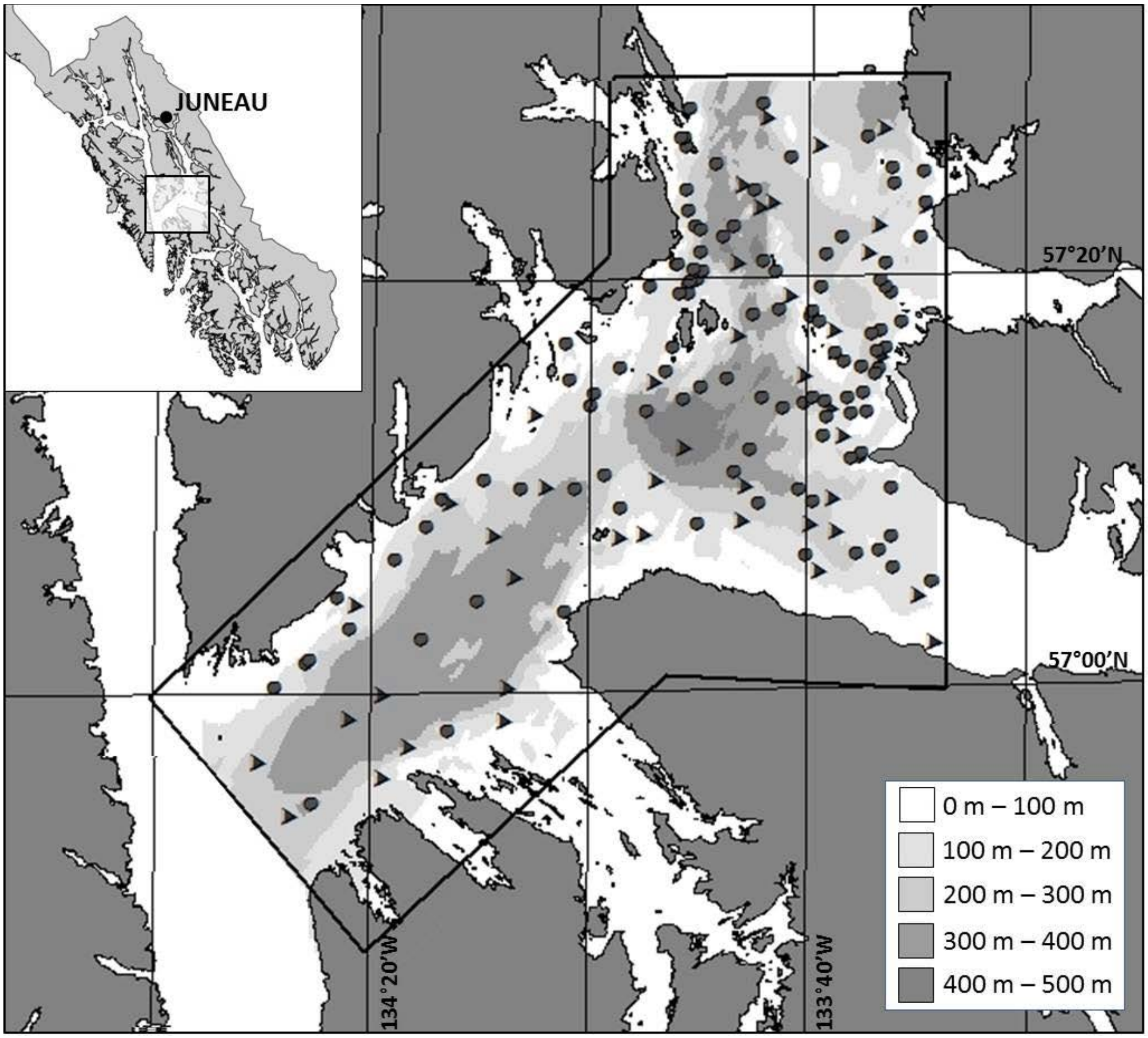

Figure 1. Study area in Frederick Sound and lower Stephens Passage with location of random (triangles) and non-random (circles) net tow sites. Shading indicates sonar-generated bathymetry profile in 100 m depth intervals. The inset shows the location of the study area in Southeast Alaska.

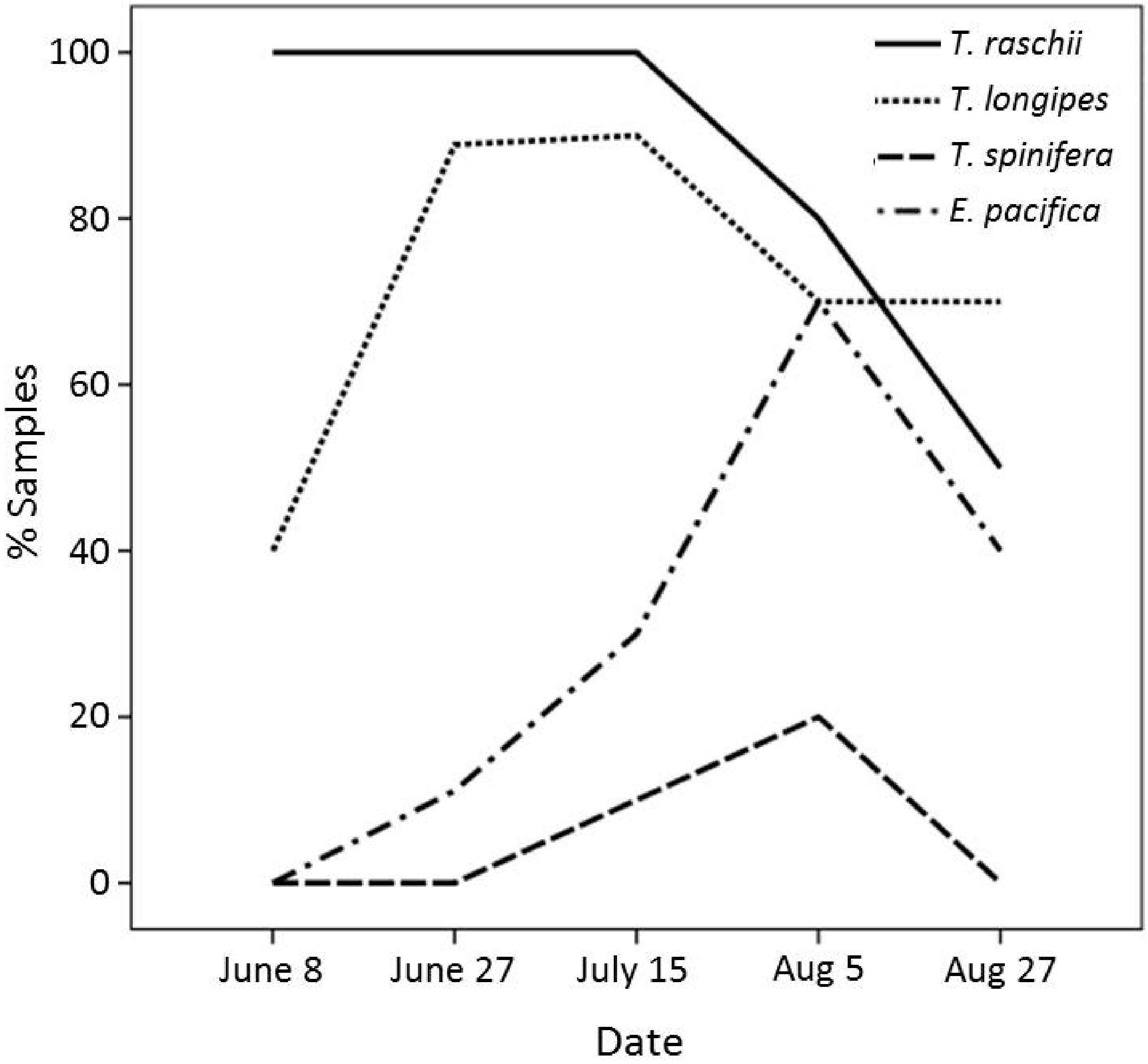

Figure 2. Proportion of random samples collected in Frederick Sound and lower Stephens Passage, Southeast Alaska containing furcilia and juvenile euphausiids from each of four species across the field season. Dates reflect the start of each 20-day sampling block from survey 2 through 6.

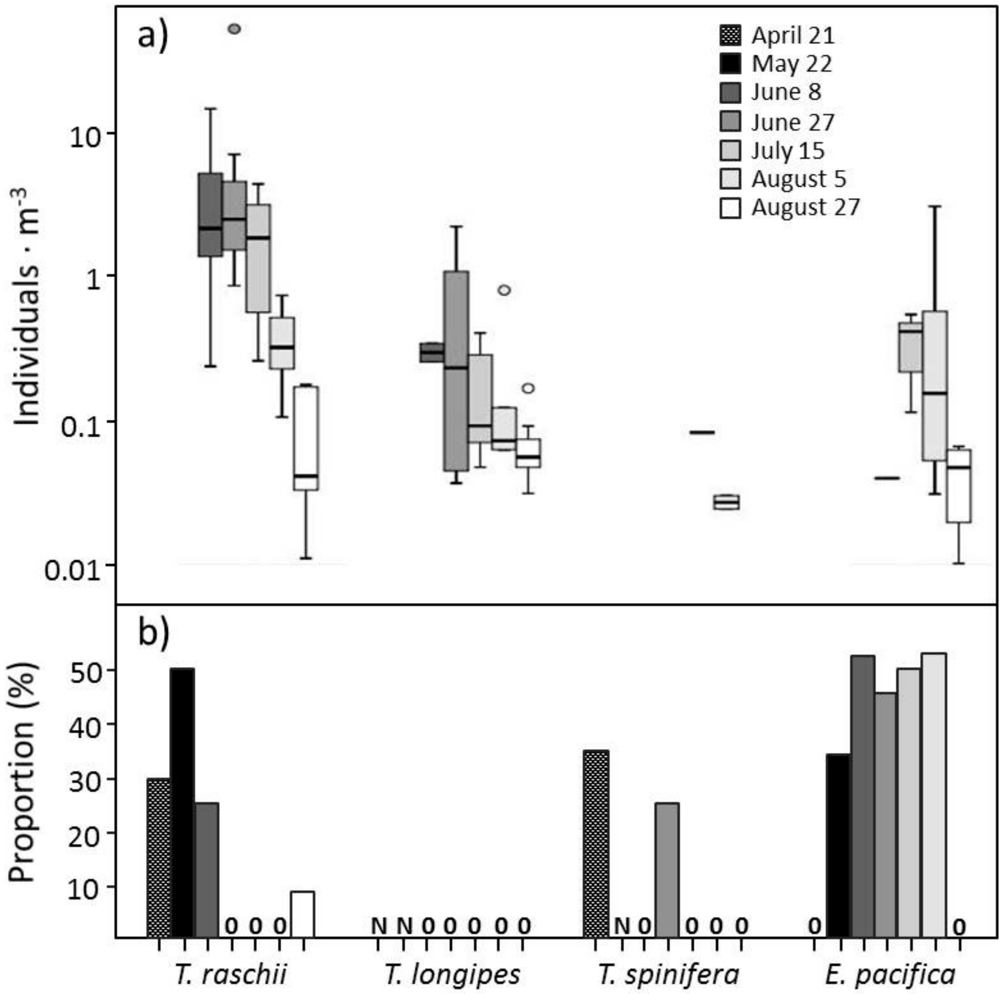

Figure 3. a) Abundance of immature (furcilia and juvenile combined) euphausiids from randomly-located samples where individuals were present in net tows from Frederick Sound and lower Stephens Passage. Boxes represent interquartile range with median indicated by the horizontal line; whiskers represent data range, excluding statistical outliers (circles). b) Percentage of adult female euphausiids carrying spermatophores. N indicates that no females of that species were present, whereas 0 indicates females were present but none were carrying spermatophores. Box and bar colors reflect the first day of each 20-day sampling block (*i.e.*, surveys 1 through 6), with the exception of April 21 when a single opportunistic sample was collected from a surface swarm near Petersburg AK east of the study region.

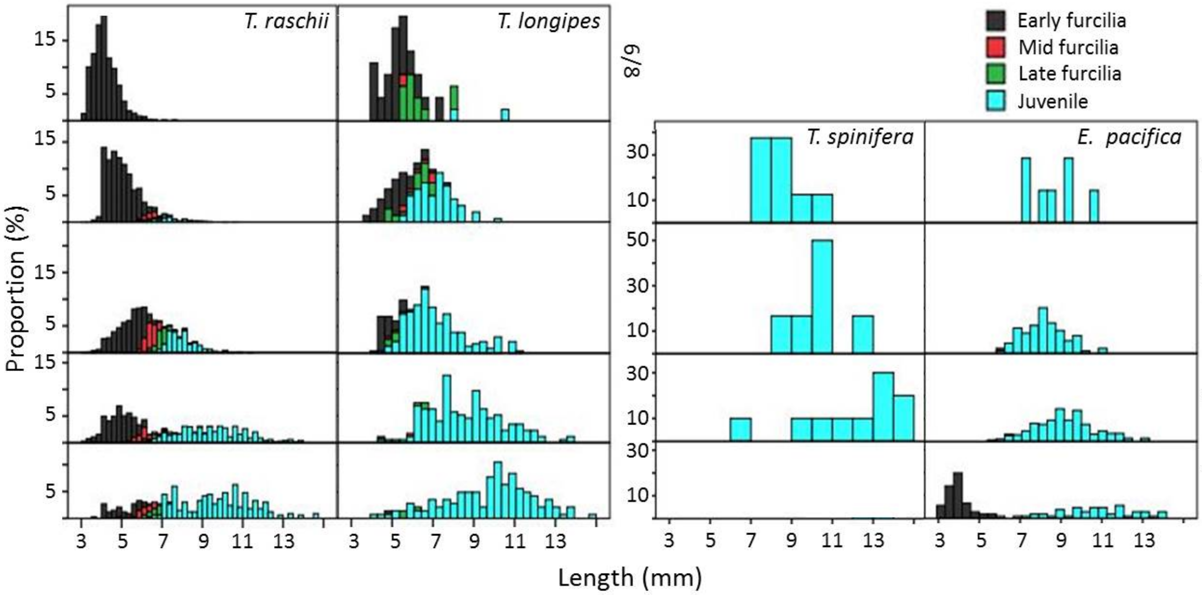

Figure 4. Length distributions of the four species (columns) of euphausiids found in Frederick Sound and lower Stephens Passage, Southeast Alaska. Bar colors indicate immature development stage. Dates (rows) reflect the start of each 20-day sampling block for surveys 2 through 6.