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MANAGEMENT APPLICATIONS

Recruitment Ecology of Burrowing Shrimps in US Pacific Coast Estuaries

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Abstract

Recruitment is a strong determinant of year class strength and adult population density especially for sessile benthic invertebrates where post-settlement mortality and competition are low or relatively stable over time. A series of surveys were undertaken to characterize recruitment and post-settlement processes for two species of burrowing shrimps, *Neotrypaea californiensis* and *Upogebia pugettensis* in order to determine how they influenced broader adult populations in US west coast estuaries. On average, *U. pugettensis* decapodids settled earlier (April–July), recruited almost exclusively to areas with conspecific adults, and grew more rapidly during their first summer than *N. californiensis*. *Neotrypaea californiensis* decapodids settled and recruited over a longer period (June–November) and were distributed across the tidal flat. While initially more abundant in areas with conspecific adults, they also either survived better or redistributed as small juvenile shrimp to areas where adults were absent. Linear relationships were found between abundance of newly recruited (0+ age class) shrimp and that of older 1+ shrimp a year later. Positive slopes were close to one for *N. californiensis* but less than one for *U. pugettensis,* suggesting lower survival. Annual recruitment varied dramatically but was more consistent for both species in Yaquina Bay. Patterns in strong recruitment years amongst estuaries, particularly for *U. pugettensis*, suggest the presence of multi-estuary metapopulations linked via larval dispersal. These results have important implications for shrimp population management including control for shellfish aquaculture, but also conservation of estuarine habitats due to the strong influence of these ecosystem engineers on the benthic community.

Keywords Ecosystem engineers · Estuary · *Neotrypaea californiensis* · Mortality · Recruitment limitation · Settlement · *Upogebia pugettensis*

Introduction

Several species of burrowing shrimp inhabit estuaries along the US Pacific coast including two species of ghost shrimp *Neotrypaea californiensis* and *N. gigas* (Decapoda: Axiidea: Callianassidae) and the blue mud shrimp *Upogebia pugettensis* (Decapoda: Gebiidea: Upogebiidae). These shrimp are considered to be ecosystem engineers because they make and maintain extensive galleries in intertidal and subtidal sediments and influence not only sediment biogeochemistry (Webb and Eyre 2004; D'Andrea and DeWitt 2009), but also benthic community composition and the presence of other engineers like seagrass via bioturbation and burrow irrigation (Dumbauld et al. 2001; Dumbauld and Wyllie-Echeverria 2003; Pillay and Branch 2011; Castorani et al. 2014). They play a key role in estuarine food webs not only as consumers of phytoplankton and bacteria (Shimoda et al. 2007; Bosley et al. 2017), but also as prey for other consumers from whales to sturgeon and smaller fish (Feldman et al. 2000; Harada and Tamaki 2004; Dumbauld et al. 2008). From a management perspective, these shrimp have been shown to influence the abundance of important suspension feeding bivalves in estuaries worldwide (Pillay et al. 2007; Takeuchi et al. 2013) and have been actively controlled in US Pacific coast estuaries by shellfish farmers due to the negative effects they have on bivalve, particularly Pacific oyster

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(*Crassostrea gigas*) aquaculture (Feldman et al. 2000; Dumbauld et al. 2004; Dumbauld et al. 2006).

Neotrypaea californiensis and *U. pugettensis* have pelagic larvae that hatch in the estuary, leave as early stage larvae by moving to the surface on ebb tides, and develop in the nearshore coastal ocean (Johnson and Gonor 1982; Breckenridge and Bollens 2010; Shanks et al. 2014). Post-larval or decapodid stages recruit back to estuaries along this coast during two mostly separate periods (April–July for *U. pugettensis* and August–December for *N. californiensis*; Dumbauld et al., 1996). Like some of their counterparts elsewhere in the world (Wooldridge and Loubser 1996; Yannicelli et al. 2006b; Pineda et al. 2010; Tamaki et al. 2010; Hernaez et al. 2012; de Oliveira et al. 2016), the pelagic larval durations vary by species (PLD of 3 weeks for *U. pugettensis* (Hart 1937) and up to 8 weeks for *N. californiensis* (Bosley and Fritz, unpublished data) and their larvae are generally found within 10 nautical miles of the coastline where they can be one of the most abundant crustaceans in the meroplankton (513 m^{-3}, Fisher et al. 2014; Hameed et al. 2018; T. D'Andrea, unpublished data). Unlike several other US west coast benthic invertebrates with broader distributions and more researched larval recruitment patterns like Dungeness crab and barnacles (Broitman et al. 2008; Shanks et al. 2010; Menge et al. 2011; Woodson et al. 2012) or species with larvae that are mostly retained in estuaries like native oysters (Peteiro and Shanks 2015; Wasson et al. 2016), populations of these shrimp largely depend on larval and post-larval behavior to facilitate their return to small estuaries located at relatively large distances from one another along this open coastline.

Shrimp population density and recruitment to one of these estuaries, Willapa Bay, Washington, have been monitored for several decades and changes in population abundance over this time period previously hypothesized to be a result of fluctuations in larval recruitment (Dumbauld et al. 2004; Dumbauld et al. 2006; Dumbauld et al. 2011). Recruitment to a population is a process that involves decapodid settlement to the benthos, subsequent survival, and potential movement thereafter. Although these shrimp are thought to be sedentary as adults, juveniles of some species have been shown to move and relocate their burrows (Tamaki and Ingole 1993; Feldman 2001). Previous work has shown recruitment to be a strong determinant of adult population density especially for species where both interspecific and intraspecifc competition are low. This has been exhibited in several species of sessile invertebrates that inhabit hard substratum (e.g., barnacles and mussels; Gaines and Roughgarden 1985), but the pattern is less clear for marine soft sediment systems where disturbance and interspecific interactions are important (Woodin 1976; Woodin et al. 1995; Thrush et al. 2012). Evidence from relatively small-scale removal experiments suggested an inverse relationship between recruitment and adult density for *N. californiensis* (Feldman et al. 2000), yet Tamaki and Ingole (1993) found that a related species, *Neotrypaea harmandi*, settled broadly and juvenile survival was higher where adults were present.

We examined long-term time series of burrowing shrimp recruitment and adult population density in two estuaries along the US Pacific northwest coast with the goal of determining whether successful recruitment is related to overall population trends in these estuaries. For the purpose of this study, we define recruitment somewhat generally as the abundance of surviving settlers that recruit to the benthos and are quantified during the first year (age 0+). Our primary objectives were to (1) determine if trends in long-term recruitment data at single locations reflected overall population trends within and amongst estuaries and (2) further characterize the recruitment process and broader spatial distribution of burrowing shrimp recruitment within estuaries, taking advantage of 2 years with strong recruitment events. We were also interested in whether recruitment to these two estuaries was temporally synchronous amongst years and therefore might reflect overall trends in a larger coastwide metapopulation. Spatiotemporal trends in recruitment could suggest potential links to oceanographic variables that might eventually be used to evaluate and potentially forecast population size. Our overall goal was not only to inform continued burrowing shrimp population monitoring and management for shellfish aquaculture, but also to inform conservation efforts for these shrimp and other estuarine resources in recognition of the broader role that these deep-dwelling burrowing shrimp play as engineers in these coastal systems.

Methods and Materials

Study Locations

This study was conducted in Yaquina Bay, Oregon (44° N, 124° W), and Willapa Bay, Washington (46° N, 124° W; Fig. 1), drowned river valley estuaries located along the Pacific northwest coast of the continental USA. Forty-eight percent (8.2 km^2) of the Yaquina estuary and 68% (227 km^2) of Willapa Bay consists of intertidal sand and mudflats that are regularly exposed on semidiurnal low tides. Both *U. pugettensis* and *N. californiensis* occur at low density in subtidal areas (< 50 m^{-2}; T.H. DeWitt, unpublished data), but their distribution is thought to be limited mostly to intertidal areas by predation (Posey 1986). *Upogebia pugettensis* densities are highest in the low to mid intertidal zone and *N. californiensis* are most abundant in the mid to upper intertidal and densities of both species can exceed 400 shrimp m^{-2} (Bird 1982; DeWitt et al. 2004; Dumbauld et al. 2011).

Long-Term Population Monitoring

Population structure and local shrimp density were quantified by collecting sediment cores annually within dense shrimp

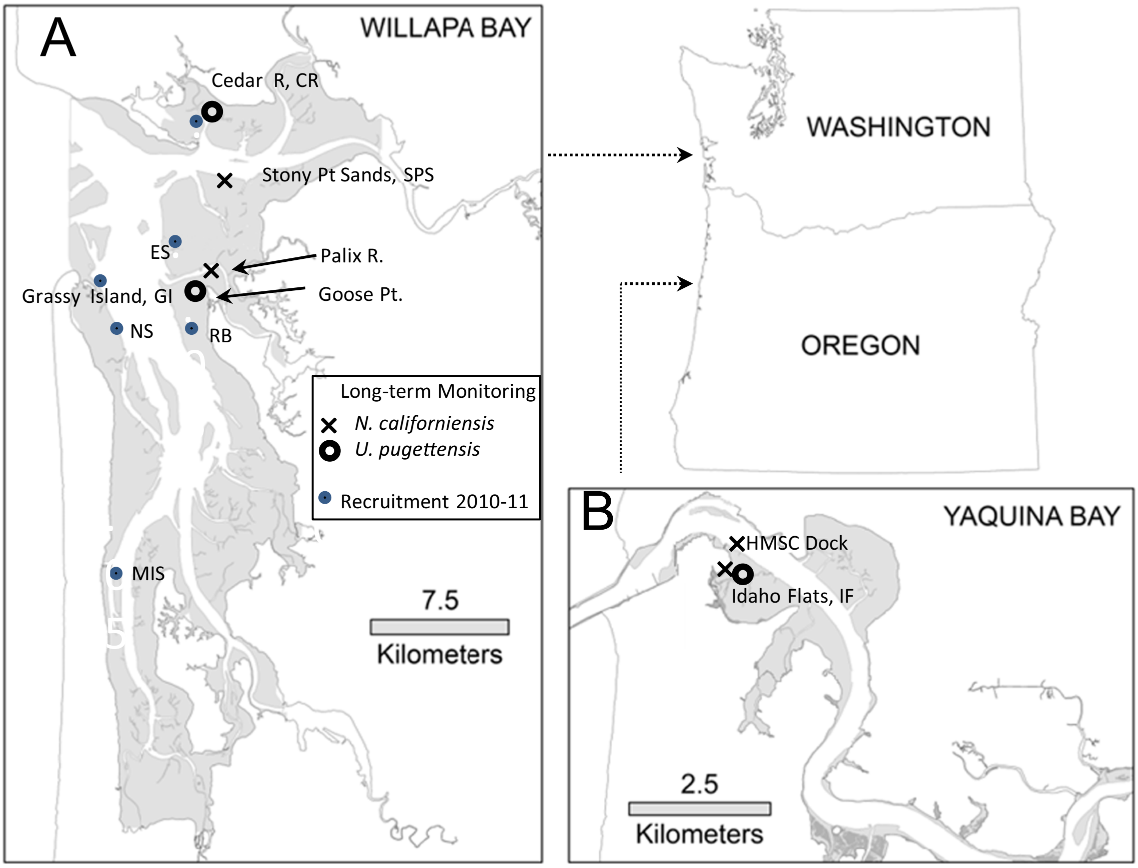


Fig. 1 Map showing long term monitoring locations for both species of burrowing shrimp in Willapa Bay, Washington and Yaquina Bay, Oregon, USA. Also shown are broad area locations surveyed in 2010–11 (CR Cedar River, ES Ellen Sands, SPS Stony Point Sands, GI Grassy Island, MIS Middle Island Sands, NS N. Stackpole, RB Rhodesia Beach in Willapa Bay, IF Idaho Flats in Yaquina Bay)

colonies. *Neotrypaea californiensis* were collected from two locations in Willapa Bay: near the Palix River (1988–2009) and near Stony Point (2009–2016), as well as from one location on Idaho Flats in Yaquina Bay (2005–2016; Fig. 1). These samples were typically taken in September or October. Due to sampling constraints and effort required, cores were initially haphazardly located within a dense shrimp colony at each location. Subsequent sampling efforts from population assessments conducted at a broader spatial scale and utilizing burrow counts have shown that the records obtained from these haphazard sampling protocols adequately track trends in the larger shrimp populations (see the "Discussion" section). Nonetheless, a randomized sample design utilizing a fixed area within the shrimp colony at each location was adopted in 2014 to better reflect the fine-scale variability in shrimp density. *Upogebia pugettensis* were collected from two locations in Willapa Bay: near the Cedar River (1988 to 2004 and 2007) and near Goose Pt. (2003–2009), as well as from one location on Idaho Flats in Yaquina Bay (2005–2016; Fig. 1). Samples for *U. pugettensis* were also taken in September and October from 1988 to 2004 and then in June or July from 2005 to present. Ten core samples were taken at each location for both species by inserting a large core (60 cm depth × 40 cm diameter) in the substrate, excavating the contents with a shovel and sieving sediments (3-mm mesh) to collect all shrimps. Species, gender, and size (carapace length, CL in mm) were recorded for all shrimp collected.

The abundance of small juvenile < 1-year-old shrimp that were presumed to have recently recruited to the sediment was quantified using smaller cores (20 cm depth × 26.5 cm diameter; 1998–2012 and 20 cm depth × 12.3 cm diameter; 2013–2016) at the same locations and in the same months described above (except samples for *U. pugettensis* recruitment were continued at Goose Pt. in Willapa Bay through 2016). Sediment was excavated from 10 cores (three 12.3-cm diameter cores were combined to represent each of 10 samples from 2013 to 2016) and sieved (1 mm mesh) to retain juvenile shrimp. Small shrimp were placed under a dissecting scope where the size (CL in mm) was measured and recorded for all shrimp collected. These recruit surveys were generally conducted once annually alongside large cores made for each species.

Recruitment Surveys

Several additional surveys were conducted to take advantage of recruitment events that occurred in Yaquina Bay in 2010 and 2011 and in Willapa Bay from 2012 to 2015 to gain further understanding of shrimp recruitment patterns. First, the temporal pattern of shrimp recruitment was assessed by taking 10 samples (20 cm depth × 26.5 cm diameter core, contents sieved on 1 mm mesh) approximately every 2 weeks from June to December 2010 at the established monitoring locations (described above) for *N. californiensis* and from April to October 2011 for *U. pugettensis*. In addition, the depth distribution of small shrimp was measured either by excavating samples within 26.5 cm diameter cores to progressive depth intervals (0–5, 5–10, 10–15, and 15–20 cm) or sampling with smaller 12.5 cm diameter cores, extruding contents and then partitioning contents by depth interval (0–20, 20–30, and 30–60 cm).

Second, we characterized the spatial distribution of shrimp recruitment across one large tidal flat known as Idaho Flat in Yaquina Bay (Fig. 1) in October 2010 and July 2011. We used data collected in a broader estuary-wide survey conducted in 2010 to select 50 sampling locations that were classified as being dominated by *U. pugettensis* (15 locations), *N. californiensis* (16 locations), or neither species (open habitat, 19 locations). A single 26.5-cm diameter core was excavated to 10 cm depth at each location and contents sieved (1 mm mesh) to retain juvenile shrimp. A follow-up survey was conducted in April 2011 at a subset of locations where *N. californiensis* recruits had been sampled the previous fall (October 2010, except not at locations where *U. pugettensis* adults were present) using larger cores (40 cm diameter × 60 cm depth sieved with 1 mm mesh) in order to examine survival rate and quantify the relationship between *N. californiensis* recruit density and the abundance of older shrimp. The fine-scale distribution of newly recruited shrimp inside and outside of an established *N. californiensis* colony in Yaquina Bay was also characterized by taking cores (26.5 cm diameter to 20 cm depth) at five locations along four transects located 10 m outside the shrimp colony, along the outside edge of the colony, along the inside edge of the colony, and 10 m within the colony in November 2010.

Finally, to examine recruitment more broadly, we conducted an along estuary survey of *N. californiensis* recruitment in spring 2012 at 7 locations adjacent to shellfish growing areas in Willapa Bay, but with relatively high adult *N. californiensis* density (10 samples, each consisting of three 12.3 cm diameter cores to 20 cm depth at each location). Core samples were also taken along a transect across the intertidal gradient at one of these locations in Willapa Bay (Grassy Island,10 samples) in spring 2013 and at three tidal elevations at a location in Yaquina Bay (OSU Dock, 12 samples in spring 2013 and 9 samples in 2014).

Data Analyses

All data from the long-term monitoring locations were entered into an MS Access database and imported into R (R Core Development Team 2015) for the graphical and statistical analyses. The mean density of shrimps per unit area sampled (m^2) was calculated for each location and year. Frequency histograms of carapace length were then examined to discern the presence and size of newly recruited (within a year of settlement, 0+) shrimp during years when relatively large recruitment events took place in Yaquina Bay (*N. californiensis*, 2010 and *U. pugettensis*, 2011) and the subsequent year to discern 1-year-old (1+) shrimp. We combined shrimp length measurements from small cores with those from large cores and used the "mixdist" package in R (MacDonald 2015) to fit a mixture of lognormal distributions to the resulting combined length frequency distributions and establish breaks between size classes. A bin size of 0.5 mm was used for these analyses because it gave the greatest resolution of modes, and initial starting values were selected based on visual inspection of the modes within the overall length frequency distribution. Visual knife-edge breaks seemed adequate for separating age 0+ shrimp from age 1+ shrimp for both species, so we did not use the mixdist program and/or the resulting distributions to reclassify data from all years but instead used it to establish these visual breaks between presumed age classes. We encountered the most difficulty in establishing the break between 1+ and > 1+ shrimp (adults) but used size class definitions to estimate the density of shrimp collected within three size/age classes (0+, 1+, and > 1+) for all years and estuaries. In several cases, historical collections from Willapa Bay were not made at the same time of year, so size breaks were adjusted slightly for these cases based on ancillary data collected during both periods.

The relationship between the average density of new recruits (0+ age class) and that of older 1+ and > 1+ shrimp for each estuary was quantified with a series of regression models. Initially, simple linear regression was used to relate average 0+ shrimp density lagged 1 year to average 1+ density to examine the relationship of shrimp recruitment in each year to age 1+ shrimp collected the following year. Simple linear models were applied using least squares regression and resulting slopes compared to a 1:1 relationship. Next, we identified relationships between 1+ shrimp abundance estimated from the cohort analysis and older > 1+ shrimp abundance by exploring several lag periods (1–4 years) for these older shrimp to determine whether strong recruitment events resulted in large shrimp populations and over what timescale this increase occurred. Simple linear and quadratic models were applied to each lag period using least squares regression. Best fitting models were selected by visual inspection of model residuals and evaluation of model fit with adjusted r^2. Both 0+ and 1+ shrimp numbers were 1 + log-transformed prior to analysis to reduce heteroscedasticity and skewness in the data. All regression analyses were conducted in R (R core development team 2015). Data from 2010 to 2011 recruitment surveys were analyzed using analysis of variance (ANOVA) in a general linear model with fixed factors (e.g., location and habitat; NCSS® statistical software).

Results

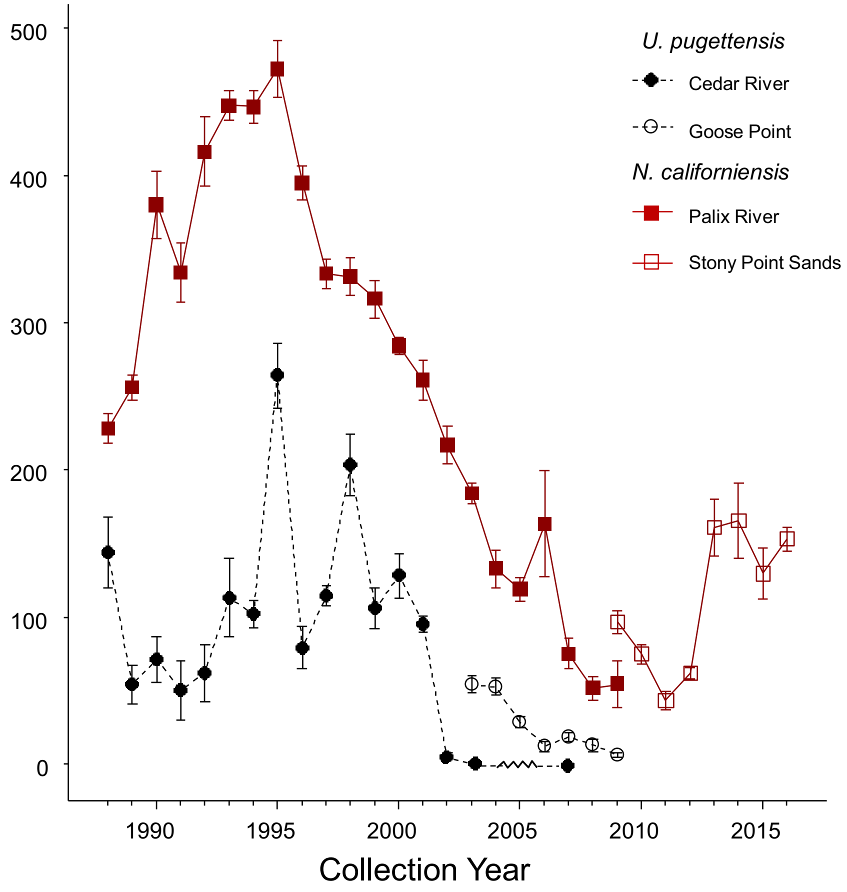
Long-Term Population Monitoring

Neotrypaea californiensis density at the Palix River location in Willapa Bay, Washington (Fig. 1) increased between 1988 and 1995 to a high of 472 shrimp m^{-2} and then declined to 54 shrimp m^{-2} in 2009 (Fig. 2). Shrimp disappeared from our standard monitoring area and became increasingly patchy at the scale of several hundred meters at this location making coring impractical. In response, we moved our monitoring location to Stony Point Sands (Fig. 1) in 2009, where mean *N. californiensis* density was comparable, but where the distribution of shrimp was more homogenous and extensive so that cores could still be made. *Neotrypaea californiensis* density at Stony Point Sands declined from 97 shrimp m^{-2} in 2009 to 43 shrimp m^{-2} in 2011 and then increased to 153 shrimp m^{-2} by 2016. The majority of small (0–3.5 mm CL) newly recruited shrimp likely passed through our 3 mm mesh sieves, but these shrimp were present in separate samples taken with smaller cores and a finer 1-mm mesh sieve (Fig. 3). Strong *N. californiensis* recruitment events occurred in 1989 and 1993 (88 and 102 shrimp m^{-2} respectively; no data for 1990–1992) followed by little to no recruitment from 1995 to 2012 and then some moderate events in 2012, 2013, 2015, and 2016 (9–36 shrimp m^{-2}).

Upogebia pugettensis density at the Cedar River location in Willapa Bay exhibited broad fluctuations around an average of 100 shrimp m^{-2} between 1988 and 2001 but declined to zero in 2003 and remained at zero in 2004 and 2007. In 2003, we moved our sampling location for *U. pugettensis* to a location near Goose Point where the density was 54 shrimp m^{-2}, but by 2006, this population declined to near zero as well (Fig. 2). *Upogebia pugettensis* recruitment events also regularly occurred through 2000 (up to 88 shrimp m^{-2}) and then declined to low levels for the remainder of the period monitored with the exception of 2010 (13 shrimp m^{-2}; Fig. 3).

The density of *N. californiensis* on Idaho Flat in Yaquina Bay, Oregon declined from 414 shrimp m^{-2} in 2004 to 151 shrimp m^{-2} in 2014 and then increased to 280 shrimp m^{-2} in 2016 (Fig. 4). *Upogebia pugettensis* density fluctuated around an average of 200 shrimp m^{-2} increasing from 157 shrimp m^{-2} in 2005 to 368 shrimp m^{-2} in 2007 and declining to 145 shrimp m^{-2} in 2016. Small peaks in *U. pugettensis* density observed in 2007 and 2012 and *N. californiensis* density in 2011 followed similar

Fig. 2 Long-term record of mean adult densities of *N. californiensis* and *U. pugettensis* in Willapa Bay, Washington (bars represent SE)



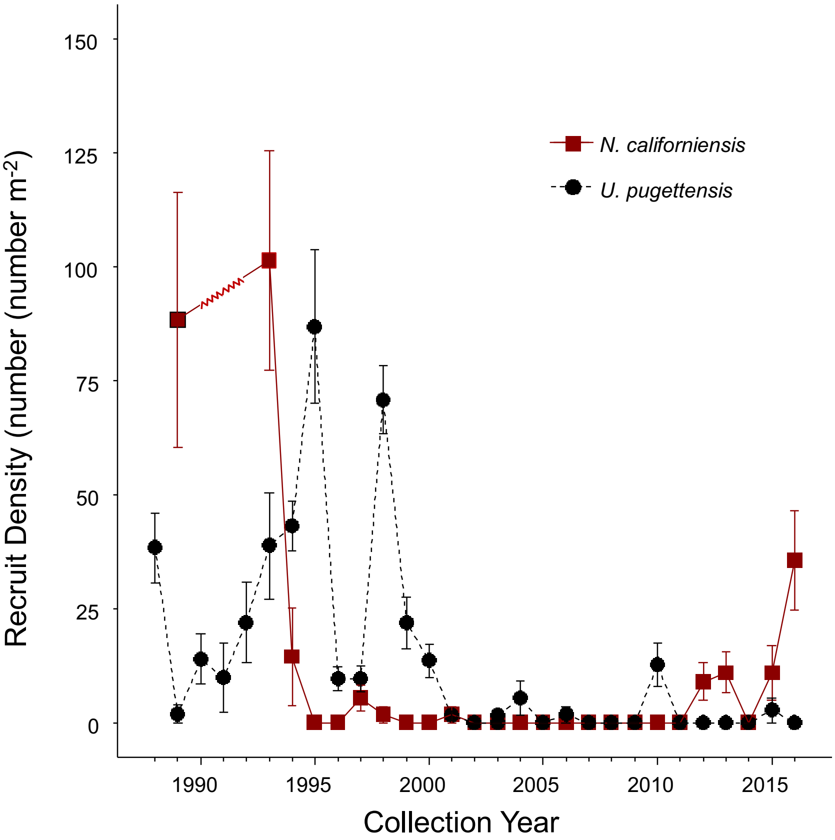


Fig. 3 Long-term record of recruitment for *N. californiensis* and *U. pugettensis* in Willapa Bay, Washington. Values represent the mean density of small shrimp taken in 20 cm deep cores (bars represent SE). No data collected for *N. californiensis* from 1990 to 1992

peaks in the density of small shrimp sampled in separate recruitment samples the previous year (250 and 136 *U. pugettensis* recruits m^{-2}, and 41 *N. californiensis* recruits m^{-2}, respectively; Fig. 5).

Recruitment Surveys

Significant recruitment events in 2010 and 2011 provided the opportunity to better characterize and understand the recruitment process. Newly recruited *N. californiensis* (two instars with mean CL of 1.1–1.5 and 2.3–2.7 mm CL, respectively) were noted in Yaquina Bay in late June 2010 and present in samples thereafter through December (Online resource Fig. S1). Though it was difficult to distinguish growth of these small shrimp, two cohorts were found in late September of 2010 and they were primarily found in the top 20 cm of sediment (Fig. 6). The smallest individuals (1–2 mm CL) were found exclusively in the top 10 cm. Newly recruited *U. pugettensis* (instar with mean CL of 1.9 mm; Online resource Fig. S2) were first present in Yaquina Bay in mid-May 2011. These small recruits were also primarily found in the top 5 cm, and all were found in the top 20 cm in June 2011. While a second cohort recruited in July, this first cohort grew to a mean size of 6.9 mm CL and remained near the surface (top 20 cm) through September of that year (Fig. 7). A broad area survey conducted across Idaho Flat in Yaquina Bay during October 2010 revealed a significantly higher density of *N. californiensis* recruits in habitat where adult *N. californiensis* were present than in open habitat where no shrimp were present, and no *N. californiensis* recruits were found in areas where *U. pugettensis* dominated (ANOVA, habitat, $F = 6.23$, $df = 2$, $p = 0.004$; Fig. 8a). *Upogebia pugettensis* recruits were much larger ($\bar{x} = 8.2$ mm CL, SE = 0.46) and only found in habitat where adult *U. pugettensis* were present. Results of a follow-up survey conducted in April 2011 for *N. californiensis* using a larger core (but sieving to 1 mm) showed no difference in the abundance of surviving recruits ($\bar{x} = 4.19 \pm 0.1$ mm CL) in open habitat and areas where older *N. californiensis* were present (Fig. 8b). *Neotrypaea californiensis* also recruited to Willapa Bay in 2010, but they were not found at our long-term monitoring location at Stony Point Sands (Fig. 3). After a report from another researcher confirmed that recruits were present in the estuary (Jacob Moore, pers. comm.), we re-surveyed our long-term monitoring location and several other locations in April 2011. While recruits were still not found at our Stony Point Sands monitoring location or a nearby location, we documented low but variable abundance at several other locations along an estuarine gradient with statistically higher abundance at a location near Grassy Island ($\bar{x} = 14.5$ shrimp m^{-2}, ANOVA on log transformed density, $F = 2.51$, $df = 6$, $p = 0.033$) and similar density at our Yaquina Bay location (7.25 shrimp m^{-2}; Fig. 8c).

Fig. 4 Density of adult *N. californiensis* and *U. pugettensis* at long-term monitoring locations on Idaho Flat in Yaquina Bay, Oregon (bars represent SE)

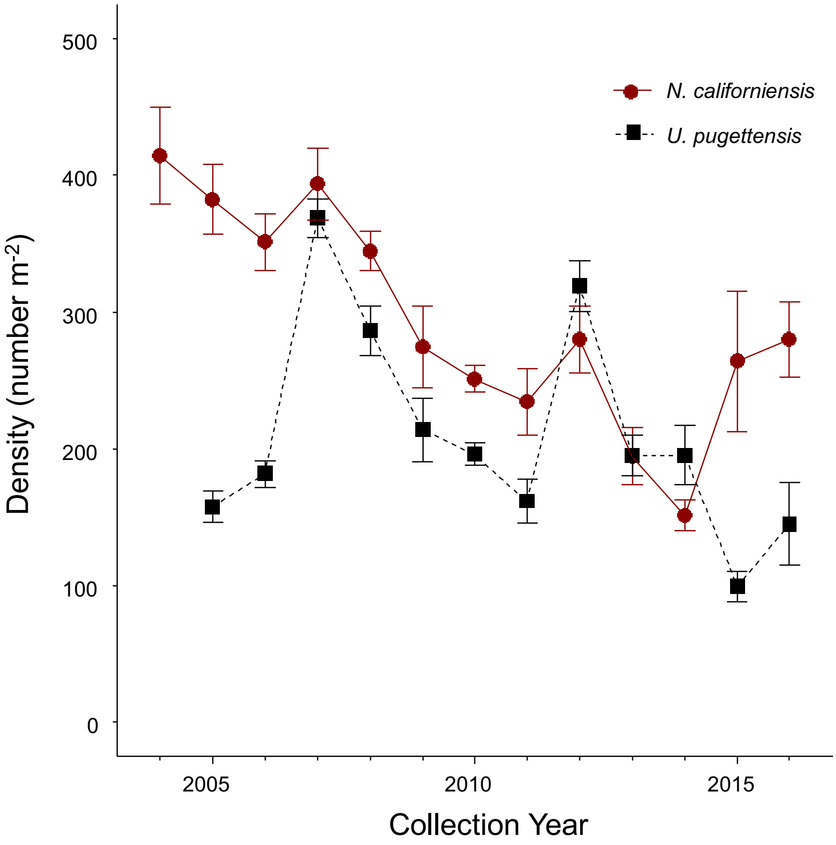
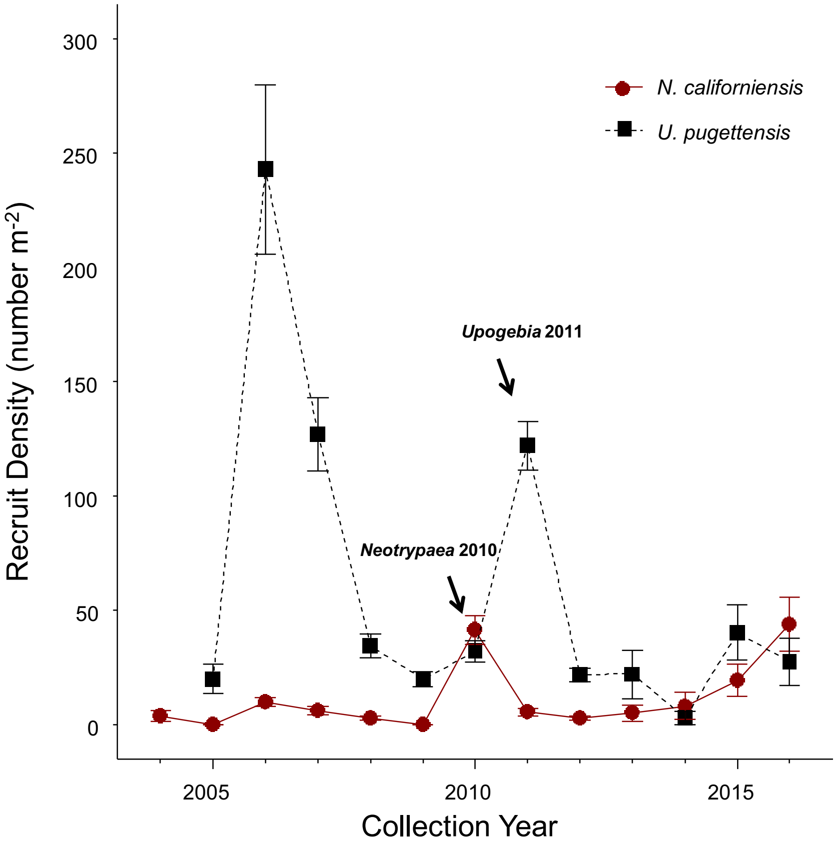


Fig. 5 Recruitment of *N. californiensis* and *U. pugettensis* in Yaquina Bay, Oregon. Values represent the mean density of small shrimp taken in 20 cm deep cores (bars represent SE). Note recruitment events for *N. californiensis* in 2010 and *U. pugettensis* in 2011, years that we conducted broader surveys across tidal flat



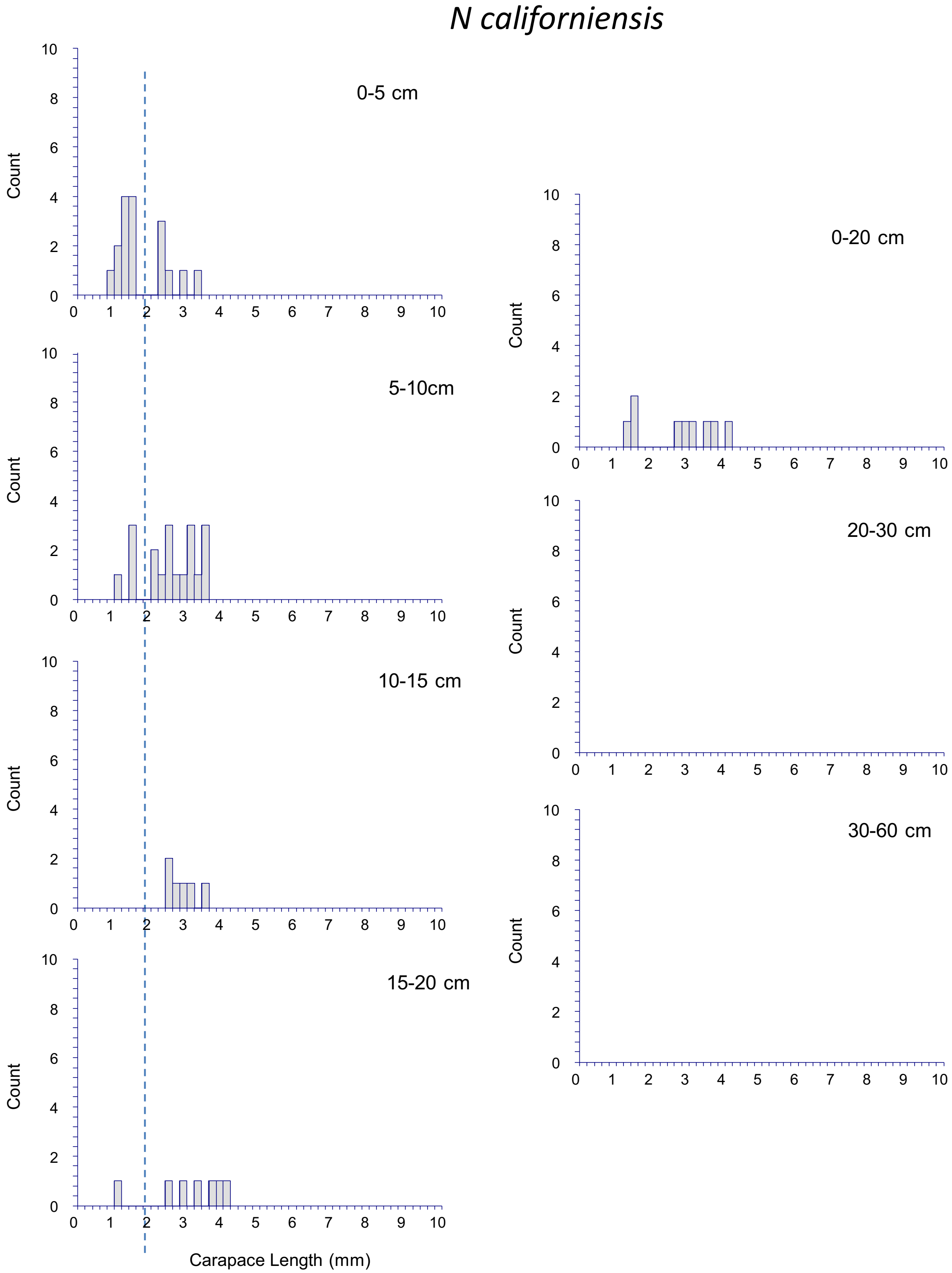


Fig. 6 Size frequency (carapace length, CL in mm) of *N. californiensis* sampled on Idaho Flats in Yaquina Bay Oregon (September 28–30, 2010) separated by sediment depth (cm). Dashed line represents break for small < 2 mm CL presumably first instar shrimp

In a second survey conducted in Yaquina Bay in July 2011, small *N. californiensis* recruits (CL < 3.5 mm) were found in all three habitats including the area with adult *U. pugettensis* (no significant difference in abundance, ANOVA, habitat, $F =$ 0.33, df = 2, $p = 0.72$; Fig. 8d). *Upogebia pugettensis* recruits ($\bar{x}$ = 4.0 ± 0.08 mm CL) were again most abundant where adults were present, though a few were also found in open habitat (ANOVA, habitat, $F = 10.70$, df = 2, $p < 0.001$;

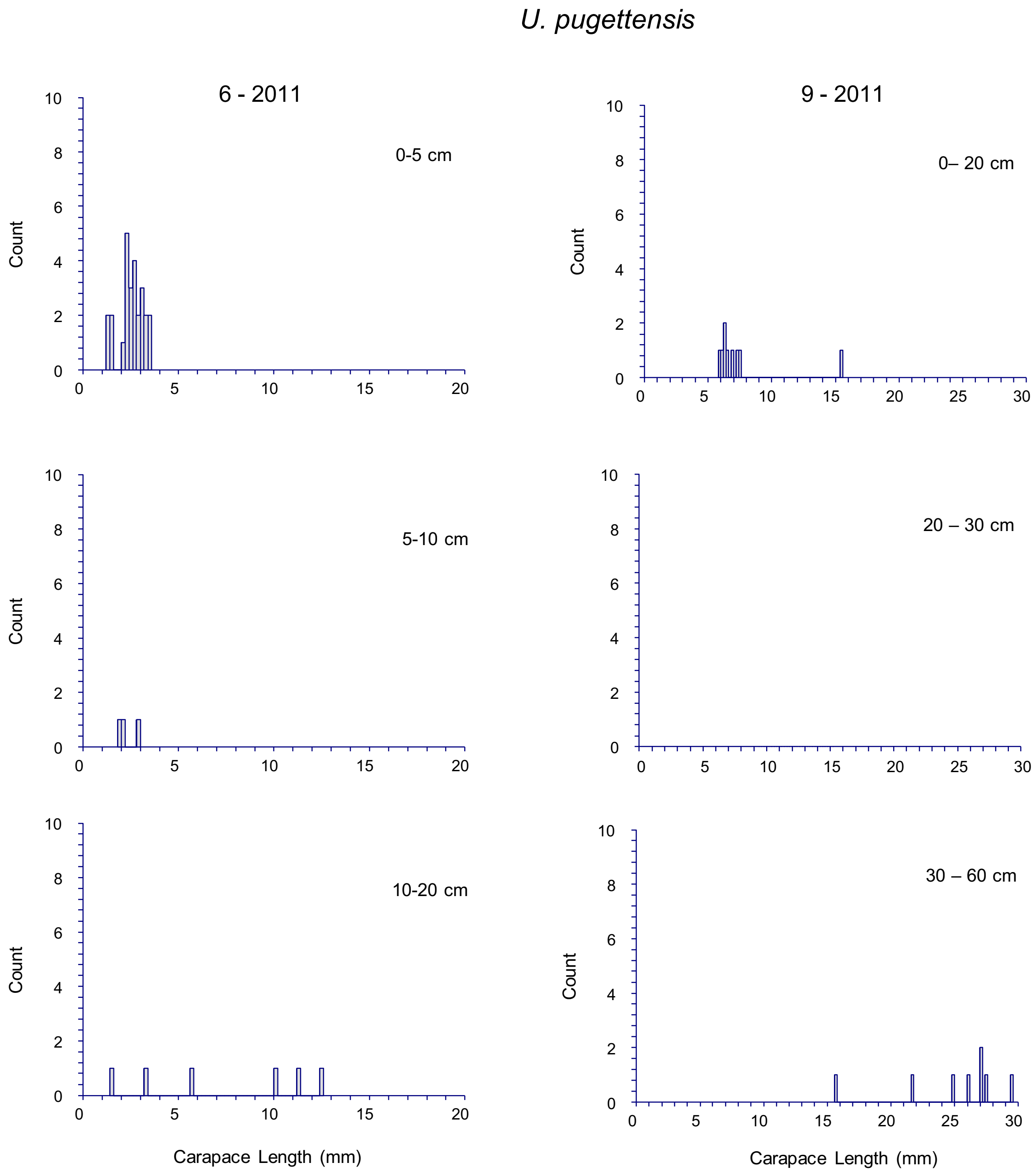


Fig. 7 Size frequency (carapace length, CL in mm) of *U. pugettensis* sampled on Idaho Flats in Yaquina Bay Oregon in June and September 2011 separated by sediment depth (cm)

Fig. 8d). We found significantly more *N. californiensis* recruits along the edge in both open habitat and within a dense shrimp colony in Yaquina Bay, but no significant difference between habitats themselves in November 2011 (ANOVA, habitat, $F = 0.20$, df = 1, $p = 0.023$, Edge/Interior F = 6.35, df = 1, $p = 0.662$, Online resource Fig. S3A). This difference was not significant when only small < 2 mm CL shrimp were selected, but the power to detect a difference was low. Density of *N. californiensis* recruits and the subsequent year class of 1 year old shrimp varied with tidal elevation or at least distance to channel but was highest near the middle of the tidal flat at locations where this gradient was easily measured in Yaquina Bay (ANOVA, location, $F = 5.88$, df = 2, $p = 0.012$ for 0+ shrimp and location, $F = 15.19$, df = 2, $p < 0.001$ for 1+ shrimp; Online resource Fig. S3B) and a similar trend was observed in Willapa Bay (Online resource Fig. S3C).

Size Cohort Analyses 2010–2012

A closer examination of size cohorts of shrimp sampled in Yaquina Bay during significant recruitment events and subsequent years (2010–2012) suggests that there are

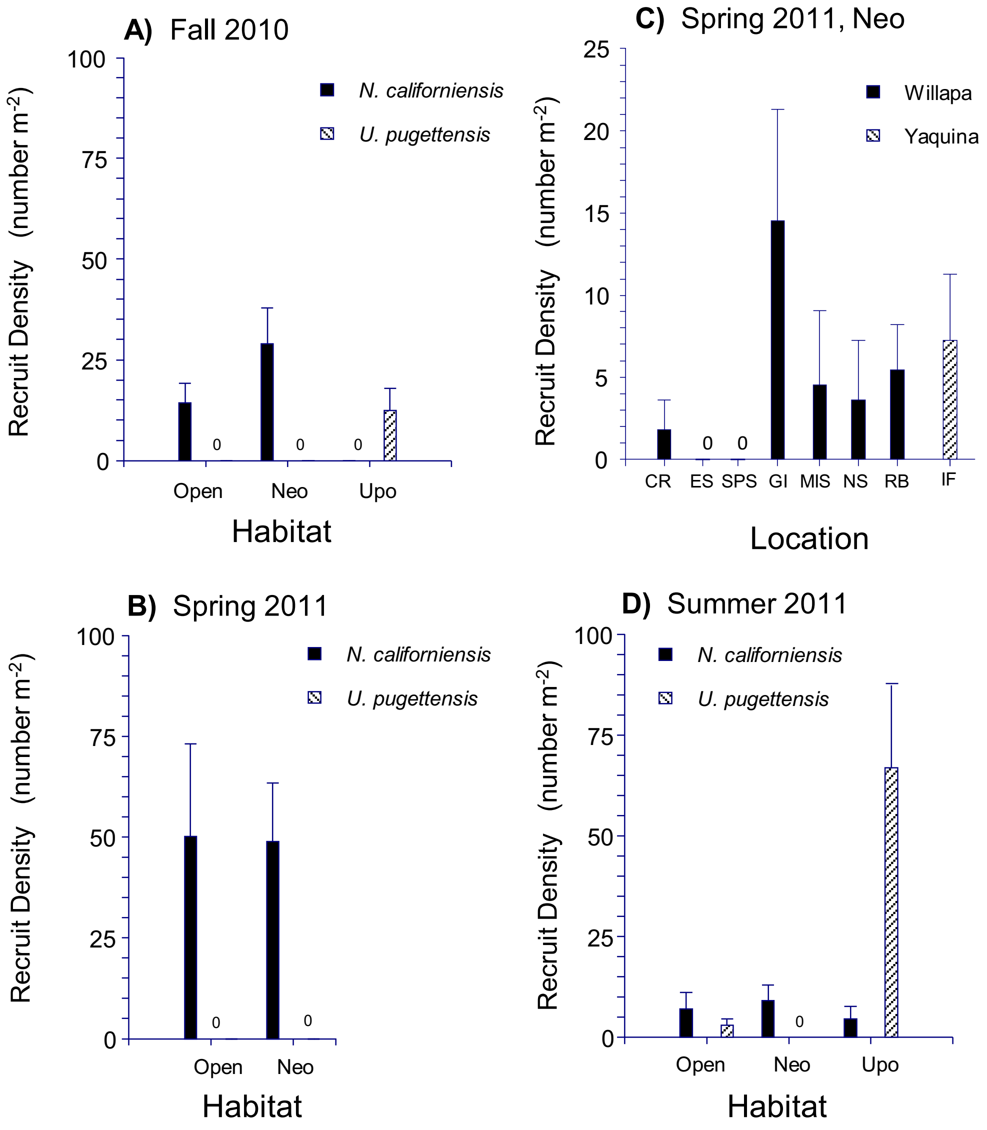


Fig. 8 Average density of **a** small recruits (both species) from open habitat (no adult shrimp) and that with each species of adults present in a wide area tidal flat survey in Yaquina Bay during fall 2010, **b** older 1+ shrimp from same locations in Spring 2011 (only in open habitat and that dominated by *N. californiensis* adults, **c** *N. californiensis* recruits from a broader area survey in Willapa Bay during spring 2011 (CR Cedar River, ES Ellen Sands, SPS Stony Point Sands, GI Grassy island, MIS Middle island Sands, NS N Stackpole, RB Rhodesia Beach; see Fig. 1, also shown is Idaho flats from Yaquina Bay = IF), and **d** shrimp density from Yaquina Bay tidal flat surveys in summer 2011, small recruits (both species) from open habitat (no adult shrimp) and that with each species of adults present in broad tidal flat survey

often at least two cohorts of new 0+ shrimp recruits (both species) present in a given year. The cohort analysis also illustrates the difficulty in discerning a size range for older 1+ animals, particularly the break between these and potentially older animals (Table 1; Fig. 9). Juvenile *U. pugettensis* recruits grew much faster than *N. californiensis* with juvenile shrimp reaching a mean size of 9.6 to 12.1 mm CL 1 year post-settlement, whereas 1-year-old *N. californiensis* were smaller at 4.6 to 6.6 mm CL (note that the 1+ age class of shrimp in the recruitment event year (2010) were mostly absent and thus their estimated mean size (8.4 mm CL) is misleading). These discrete recruitment events, however, enabled us to use these size breakdowns to establish visual size breaks between 0+, 1+, and > 1+ shrimp in order to estimate densities and examine recruitment relationships for the long-term database (Table 2).

Table 1 Results of size frequency analysis ("mixdist" algorithm in R) on shrimp collected in Yaquina Bay in 2010–2012 during and following substantial recruitment events. Shown are mean carapace lengths in millimeters (SE) for each species of shrimp. In most cases, two peaks were assigned for 0+ recruits as these cohorts were evident in size frequency distributions (Fig.9)

Shrimp	Yr	0+	1+	> 1+
U. pugettensis	2011	1.91 (0.11) 3.46 (0.09)	12.08 (0.42)	18.36 (0.74) 23.05 (0.69) 26.91 (0.34)
	2012	1.99 (0.05) 3.69 (0.12)	9.65 (0.61)	16.53 (1.41) 24.09 (0.48) 27.43 (0.35)
N. californiensis	2010	1.09 (0.08) 2.34 (0.08)	8.38 (1.82)	10.98 (0.07)
	2011	1.44 (0.08) 2.75 (0.09)	4.55 (0.43) 6.58 (2.06)	11.42 (0.14)

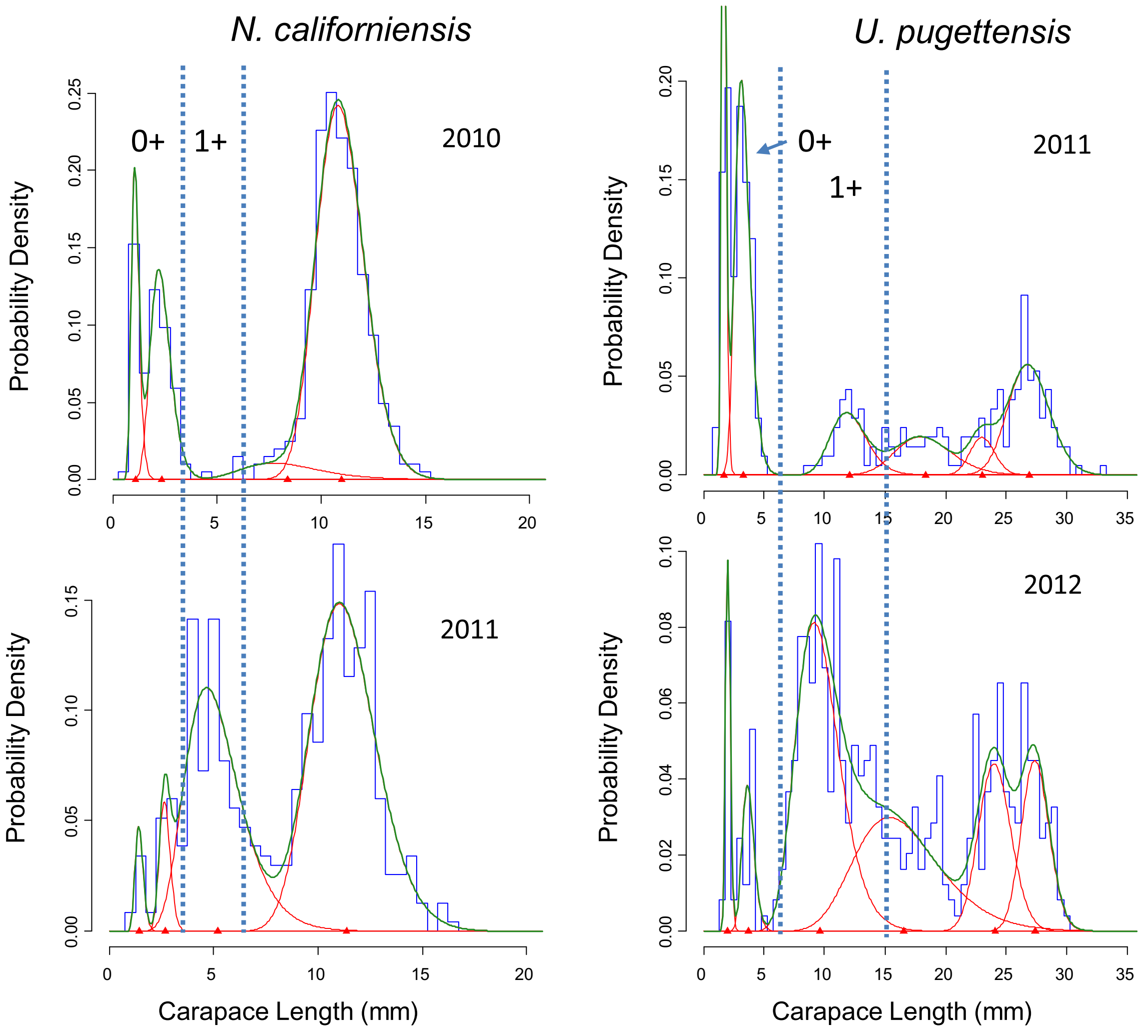


Fig. 9 Results of cohort analyses on combined data for recruits from small cores and older shrimp from large cores using the "mixdist" package in R to fit a mixture of log normal distributions to combined length frequency distributions. Dashed lines represent cutoffs for 0+ and 1+ shrimp (see also Table 1). Data are shown for years when significant recruitment occurred and the subsequent year (2010, 2011 for *N. californiensis*, left and 2011, 2012 for *U. pugettenis*, right)

Correlation of Recruitment with Juvenile and Adult Density

Linear relationships between newly recruited (0+ age class) shrimp lagged 1 year with that of older 1+ shrimp were significant with positive slopes and best fit using a multiplicative model (Fig. 10; Table 3). Slopes of these relationships for *N. californiensis* were very close to 1 (Willapa Bay, 0.92 ± 0.22; Yaquina Bay, 0.83 ± 0.28), while those for *U. pugettensis* were less (Willapa Bay, 0.76 ± 0.39; Yaquina Bay, 0.63 ± 0.09), suggesting lower first-year survival for *U. pugettensis* in both Willapa Bay and Yaquina Bay. There were also obvious outliers in these relationships where recruitment was either not observed at all or was relatively low, yet the older 1+ age class of shrimp was found at higher density the following year. This was particularly the case for *N. californiensis* in Willapa Bay, suggesting either sampling error or post-recruitment movement/immigration of these small shrimp. Explorations of relationships between the 1+ year class and older > 1+ shrimp (grouped together as one "adult" age group) revealed significant relationships for both species in

Table 2 Size breaks (CL in mm) used to calculate density by year class and analyze recruitment relationships. Note that differences between estuaries and years are a result of adjustments made for sampling time frame

Species	Location	Year	0+	1+	>1+
U. pugettensis	Yaquina	≥ 2005	$x \leq 7.0$	$7 < x < 15$	$x \geq 15$
	Willapa	< 2005	$x \leq 12$	$12 < x < 20$	$x \geq 20$
	Willapa	≥ 2005	$x \leq 7.0$	$7 < x < 15$	$x \geq 15$
N. californiensis	Yaquina	All	$x < 3.5$	$3.5 \leq x < 8$	$x \geq 8$
	Willapa	All	$x < 3.5$	$3.5 \leq x < 6.5$	$x \geq 6.5$

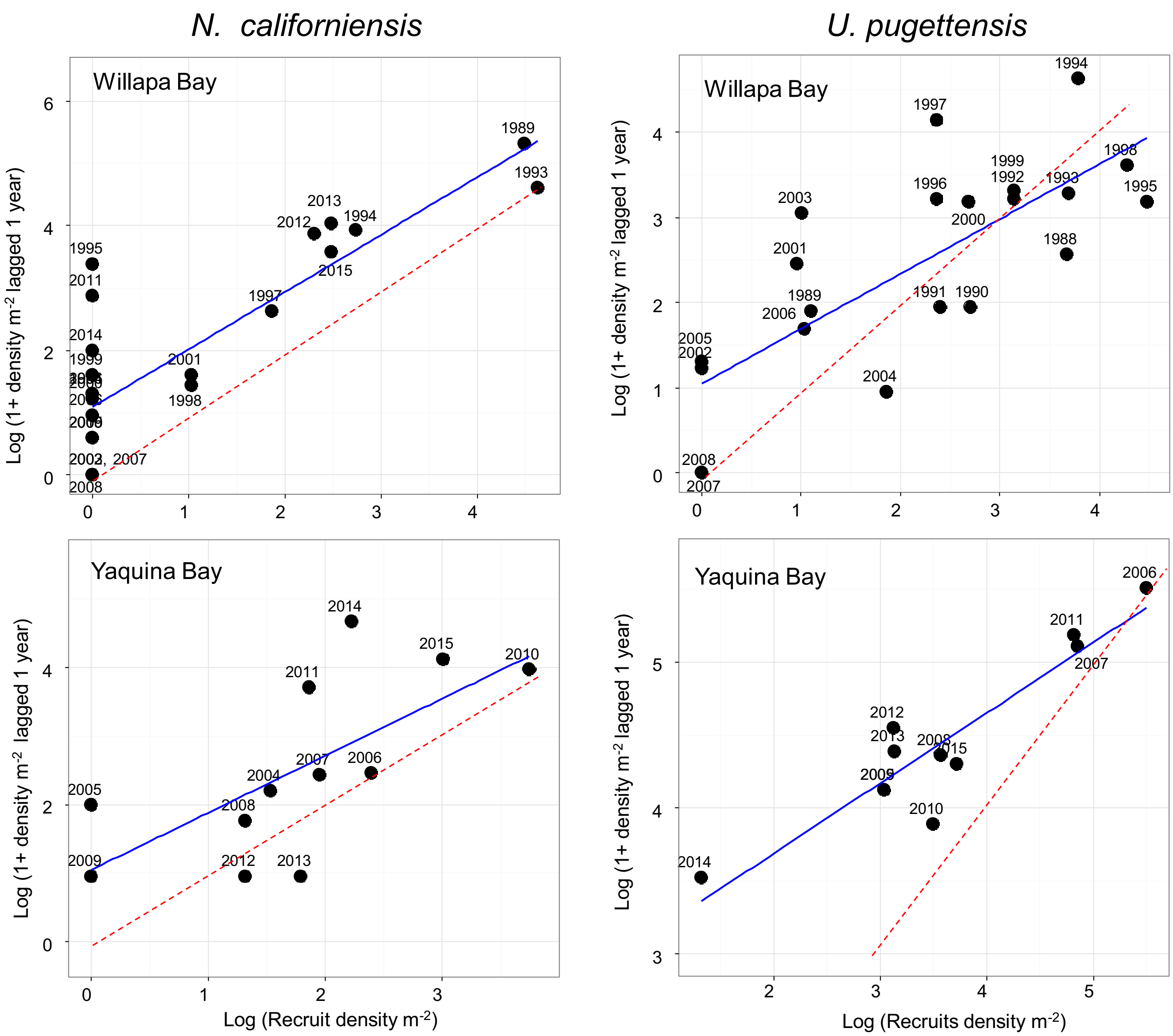


Fig. 10 Multiplicative relationships between recruitment estimates (0+) and subsequent 1-year-old (1+) cohorts of shrimp estimated using a 1-year lag for both species of shrimp in each estuary. Also shown are dashed lines with slopes of 1 and intercept of 0. Labels represent the recruitment year

Willapa Bay with the best relationship achieved using a 2-year lag for *U. pugettensis* and longer 4-year lag for *N. californiensis* (Fig. 11; Table 4; see also Online resource Figs. S4 and S6). Linear relationships were not significant for either species of shrimp in Yaquina Bay, although a quadratic relationship with a 2-year lag of adults fit the *N. californiensis* numbers reasonably well ($r^2 = 0.57$, $p = 0.017$) and there was a slight positive linear trend with a 2-year lag for *U. pugettensis*. (Fig. 11; Table 4; see also Online resource Figs. S5 and S6).

Discussion

Our results confirm that recruitment of two species of burrowing shrimps, *N. californiensis* and *U. pugettensis*, is highly variable from year to year but is directly related to subsequent abundance of larger shrimp and therefore directly influences population size of these important ecosystem engineers in US west coast estuaries. We found interspecific differences in seasonal timing of the return of decapodids from the ocean to these coastal estuaries, spatial patterns of recruitment to the benthos within the estuary, and growth of these small recruits and therefore the depth of their burrows in the sediment. These results have significant management implications, particularly for shellfish aquaculture operations where they are considered to be pests, but also for broader ecosystem management goals and conservation efforts in these estuaries.

The number of burrowing shrimp recruiting to the benthos at our long-term monitoring locations in two estuaries was highly variable from year to year and annual patterns clearly differed

Table 3 Results of regression analysis of 0+ vs 1+ shrimp densities for both estuaries. Graphical representations of these relationships are given in Fig. 10

Coeff	Estimate	SE	*p* value
N. californiensis			
Willapa Bay			
($r^2 = 0.70$, $F = 54.08$ on 1 and 22 df, $p < 0.001$)			
Intercept	1.09	0.22	<0.001
Log(0+)	0.92	0.13	<0.001
Yaquina Bay			
($r^2 = 0.44$, $F = 8.757$ on 1 and 10 df, $p = 0.014$)			
Intercept	1.05	0.58	0.10
Log(0+)	0.83	0.28	0.01
U. pugettensis			
Willapa Bay			
($r^2 = 0.54$, $F = 24.37.08$ on 1 and 19 df, $p < 0.001$)			
Intercept	0.63	0.39	0.13
Log(0+)	0.76	0.15	<0.001
Yaquina Bay			
($r^2 = 0.83$, $F = 48.87$ on 1 and 9 df, $p < 0.001$)			
Intercept	1.50	0.34	0.002
Log(0+)	0.63	0.09	<0.001

between the two shrimp species. Variable recruitment and lack of a significant adult spawner–juvenile recruitment relationship displayed by marine invertebrates and fish have intrigued ecologists and fishery managers for over a century (Houde 2008) but are hallmark features of these organisms with pelagic planktotrophic larvae that are subject to broad dispersal by currents, variable feeding conditions, and high predation in the ocean. While there has been extensive research on larval development and behaviors of individual invertebrate species including seminal original work by Thorson (1950, 1966), relatively few long-term recruitment records exist. This is particularly true for the US west coast where most of these records are for commercially fished or important managed species (Hannah 2011; Shanks 2013; Wasson et al. 2016), for those that inhabit hard substrates along the open coast (Broitman et al. 2008; Menge et al. 2011), or in another case, the introduced European green crab, *Carcinus maenas* (Yamada and Kosro 2010).

Recruitment limitation has been the established paradigm, especially for benthic invertebrates in regions like the US west coast, where strong seasonal upwelling dominates nearshore oceanography resulting in Eckman transport of surface waters equatorward and away from the shore (Connolly and Roughgarden 1998; Leslie et al. 2005; Shanks and Shearman 2009; Pineda et al. 2010). Until recently, it was expected that episodic recruitment was the result of storms and/or relaxation events where these currents reverse (Dudas et al. 2009; Garcia-Reyes and Largier 2012). Many estuarine invertebrate larvae exhibit behavior which allows them to be retained in estuaries (Strathmann 1982; Sulkin and Van Heukelem 1982; Ogburn et al. 2009; Kunze et al. 2013; Peteiro and Shanks 2015); however, recent evidence suggests that larvae of some marine invertebrates and fish also have behavioral adaptations that allow them to remain in the nearshore zone along the coast and recruit to the shore despite the influence of these predominant currents (Morgan et al. 2009; Morgan et al. 2012; Shanks et al. 2014). The estuarine populations of both burrowing shrimp species we studied have early-stage larvae that are exported from the estuary and then return to the relatively small entrances to these estuaries after development in coastal ocean waters. Research examining larvae from other species of burrowing shrimp along the upwelling coasts of South Africa and South America (Wooldridge and Loubser 1996; Yannicelli et al. 2006a; Teske et al. 2008), as well as *N. californiensis* (Morgan and Fisher 2010; Morgan et al. 2014; Hameed et al. 2018), suggests that shrimp larvae are either always present in deeper water or have diel vertical migration patterns which keep them both close to shore and in deeper water where they avoid dominant surface transport patterns. Though not in regular upwelling systems, similar behavior has been noted for late-stage larvae and decapodids of *Lepidophthalmus siriboia* and *Upogebia vasquezi* in South America and *Nihonotrypaea harmandi* in Japan where they take advantage of rapid flood tide transport to return to shore (Tamaki et al. 2010; de Oliveira et al. 2012; Tamaki et al. 2013). We have yet to directly relate our annual recruitment data to long-term records for these physical transport mechanisms in the coastal ocean, but marked interannual differences in shrimp recruitment were observed in both estuaries clearly suggesting that recruitment limitation occurs in some locations and years. Recruitment of both species was more consistent to Yaquina Bay, and there were a few coherent patterns amongst these two estuaries which are 250 km apart (Fig. 12). These patterns may indicate links between these populations and to nearshore coastal oceanography. For example, most of the highest *N. californiensis* recruitment occurred after 2010 in both estuaries and the only strong recruitment years for *U. pugettensis* in Willapa Bay, where an adult spawning population is virtually absent, ocurred in 2006, 2010, and 2015 which were also strong recruitment years in Yaquina Bay. While not conclusive, this suggests that shrimp from individual estuaries might contribute larvae and subsequent recruits to a larger multi-estuary metapopulation (Camus and Lima 2002; Kritzer and Sale 2004; Lipcius et al. 2008; Watson et al. 2012), but the number of larvae returning to individual estuaries is still subject to variable ocean conditions along this coast.

Despite variable recruitment from year to year, we show that the number of 0+ recruits of both shrimp species was directly related to the density of 1+ and older shrimp present

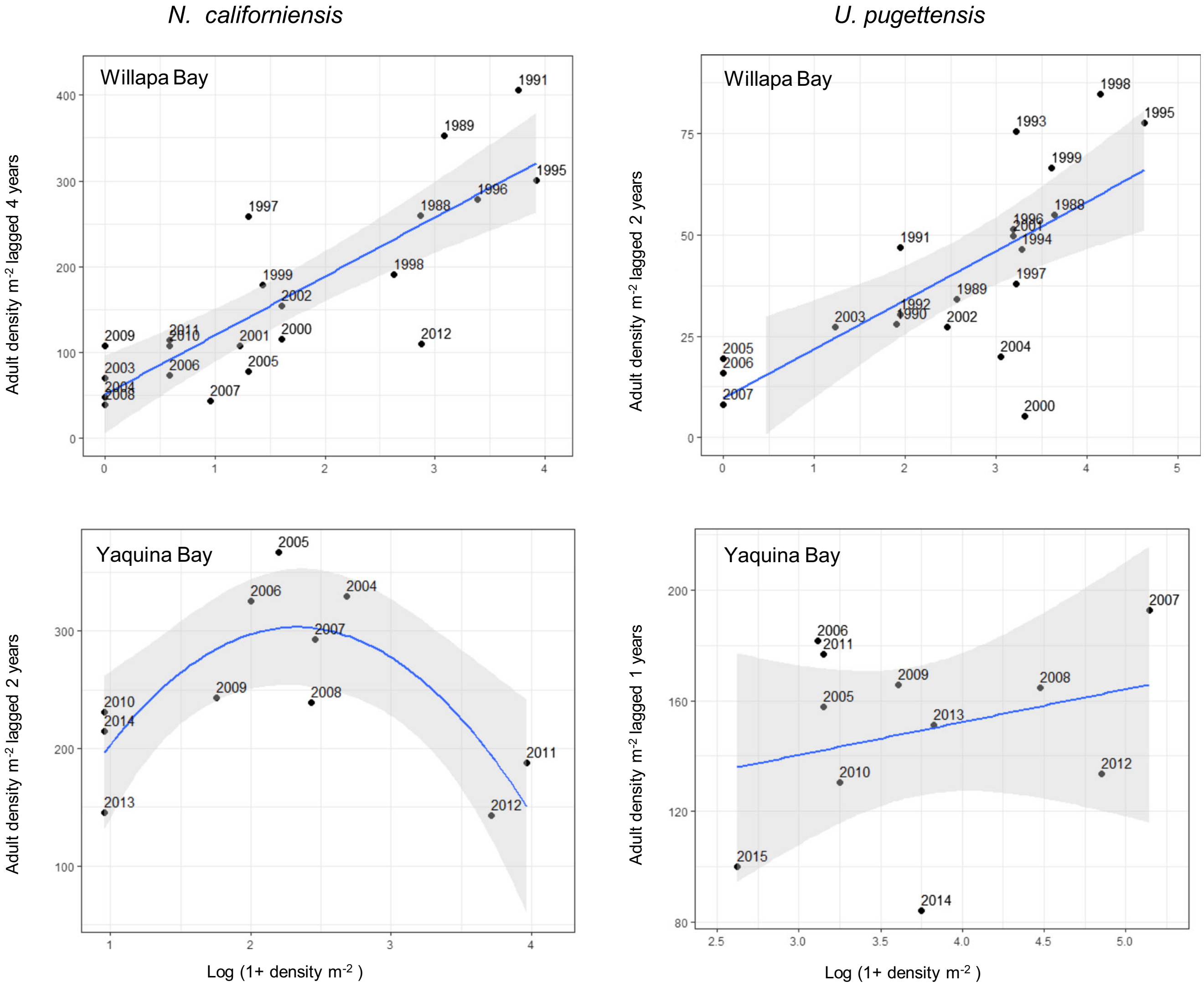


Fig. 11 Relationships between 1+ shrimp density and older age classes (> 1+) for both species and estuaries. Labels represent the recruitment year. Coefficients and model statistics are presented in Table 4

at the same locations in subsequent years. This is not surprising because recruitment rate is a necessary parameter that appears in all population dynamics models and the expectation for most benthic marine invertebrates is that mortality decreases exponentially with age (i.e., Type III survivorship). Unfortunately, it is also difficult to determine age for these shrimp especially using size alone, though efforts have been made to independently assess this using the pigment lipofuscin (Bosley and Dumbauld 2011; Bosley 2016). Simple linear models suggest that mortality is higher for *U. pugettensis* than for *N. californiensis* during this first year. We speculate that this is, in part, a result of seasonal timing as *U. pugettensis* recruit to intertidal locations during the summer months when known predators such as Pacific staghorn sculpin (*Leptocottus armatus*) and juvenile Dungeness crab (*Carcinus magister*; Armstrong et al. 1995; Feldman et al. 1994; Feldman 2001) are most abundant and active.

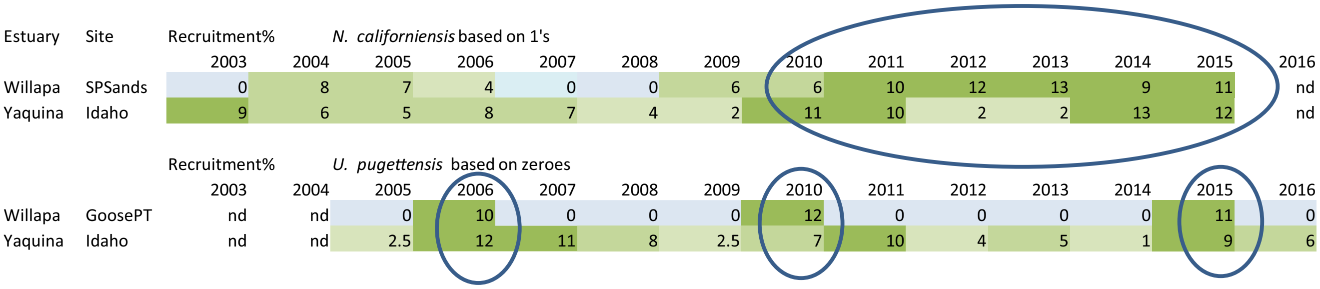
We also found significant differences between these two shrimp species with respect to seasonal timing and patterns of settlement and post-settlement mortality that corroborate their previously documented life histories (Bird 1982; Dumbauld et al. 1996; Feldman et al. 1997; Feldman 2001), but this work further clarifies observed recruitment patterns across broader estuarine intertidal areas. *Neotrypaea californiensis* have been documented to reproduce and extrude eggs in the spring and summer (March–July) which results in larvae developing in the nearshore coastal ocean during summer and decapodids returning during late summer and fall (Dumbauld et al. 1996). Conversely, *U. pugettensis* extrude eggs in the fall (Oct–Dec), larvae develop in the ocean earlier in the spring, and decapodids return to estuaries in late spring and early summer (April–July). We demonstrated that two cohorts of each species recruited to Yaquina Bay in 2010 and 2011, but numbers differed markedly by species and year.

Table 4 Results of best fitting models from correlation analysis of 1+ to > 1+ shrimp for each species and estuary. Graphical representations of these relationships are given in Fig. 11

Coeff	Estimate	SE	*p* value
N. californiensis			
Willapa Bay			
($r^2 = 0.76$, $F = 74.65$ on 1 and 23 df, $p < 0.001$)			
Intercept	59.70	18.91	0.004
Log(1+)	61.07	7.07	< 0.001
Yaquina Bay			
($r^2 = 0.57$, $F = 7.024$ on 2 and 8 df, $p = 0.017$)			
Intercept	− 3.54	78.43	0.96
Log(1+)	263.70	73.13	0.007
Log(1+)^2	− 56.70	15.15	0.01
U. pugettensis			
Willapa Bay			
($r^2 = 0.48$, $F = 18.28$ on 1 and 18 df, $p < 0.001$)			
Intercept	9.71	8.08	0.25
Log(1+)	12.14	2.84	< 0.001
Yaquina Bay			
($r^2 = -0.025$, $F = 0.756$ on 1 and 9 df, ns)			
Intercept	104.66	51.97	ns
Log(1+)	11.89	13.68	ns

These patterns were preceded by similar peaks in abundance of decapodids sampled in plankton tows from a dock near the mouth of the estuary (J. Chapman et al., unpublished data). *Upogebia pugettensis* recruits grew rapidly over the summer reaching a mean size of 9.6 to 12.1 mm CL in 1 year compared to *N. californiensis* which recruited later and grew slower reaching only 4.6 to 6.6 mm CL by the following summer. While mud shrimp grew faster, both species built relatively shallow burrows at first and were still present primarily in the top 20 cm by September. Faster growth also resulted in these two separate *U. pugettensis* cohorts remaining distinguishable the following year. It was more difficult, however, to track *N. californiensis* cohorts and distinguish this 0+ age class from larger/older shrimp due to their slower and highly variable growth and our inability to use other aging techniques on these small shrimp (Bosley 2016; Bosley et al., submitted).

While settlement and early post-settlement mortality or movement are separate processes and often decoupled (Olafsson et al. 1994; Etherington and Eggleston 2000; Pineda et al. 2010), we could not distinguish these processes for shrimp decapodids in our field collections (but see Tamaki et al. 2013 for methods to make such distinctions). Our broader sampling efforts across the tidal flat in Yaquina Bay revealed that *N. californiensis* decapodids and small juveniles were present across habitats, but the numbers were higher where *N. californiensis* adults were present in 2011 (a strong recruitment year). We could not detect a difference, however, in abundance of older 1+ juveniles across habitats the following spring. *Neotrypaea californiensis* recruits were again found in both habitats including locations where adult *U. pugettensis* were present later in 2012 (a moderate recruitment year). In contrast, *U. pugettensis* either appeared to be more selective and did not settle to or perhaps failed to survive in open areas where adult shrimp were absent or in areas where adult *N. californiensis* were present. Results of relatively small-scale field and laboratory experiments conducted by Feldman et al. (1997) demonstrated that *N. californiensis* preferentially settled in mud/sand substrate versus habitat with mollusk shells present and that post-settlement mortality was higher in shell substrates where they were exposed to predation by juvenile Dungeness crabs, *C. magister*. Posey (1986) also documented recruitment of *N. californiensis* outside established adult colonies and subsequent mortality, especially at seaward ends of the adult beds due to predation by both crab and sculpins which resulted in higher juvenile abundance in established colonies. Similarly, Tamaki and Ingole (1993) found that decapodids of a sister species, *Nihonotrypaea harmandi,* settled broadly but appeared to survive better in areas where adult shrimp were present. Though Tamaki et al. (1992) documented the use of adult burrows by juveniles of *N. harmandi*, no settlement cues aside from the presence of suitable sand substrate have been identified for



Recruitment% *N. californiensis* based on 1's

Estuary	Site	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Willapa	SPSands	0	8	7	4	0	0	6	6	10	12	13	9	11	nd
Yaquina	Idaho	9	6	5	8	7	4	2	11	10	2	2	13	12	nd

Recruitment% *U. pugettensis* based on zeroes

Estuary	Site	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016
Willapa	GoosePT	nd	nd	0	10	0	0	0	12	0	0	0	0	11	0
Yaquina	Idaho	nd	nd	2.5	12	11	8	2.5	7	10	4	5	1	9	6

Fig. 12 Annual recruitment estimates for *N. californiensis* (top) and *U. pugettensis* (bottom) ranked from highest to lowest within each estuary shaded with colors representing four groups (0 = light blue, low (1–4) = light green, moderate (5–8) = medium green, high (> 8) = dark green (nd= no data). Both species displayed more consistent recruitment to Yaquina Bay and strong recruitment years differed by species. Circled are years with highest recruitment and some coherence between estuaries (color figure online)

these axiid shrimp. Whether or not this result is due to facilitation by adult shrimp is not clear because competition for food resources may also occur. We found a trend of higher abundance of *N. californiensis* recruits at the edge of the established colony in Yaquina Bay suggesting that at least some initial settlement cue may be present. Feldman (2001) also conducted settlement experiments with *U. pugettensis,* which revealed active settlement choice of habitats with epibenthic shell present versus open mud in the field, but a laboratory experiment suggested that they did not appear to actively cue in on larger conspecifics. In contrast with her results for *N. californiensis*, she found that juvenile Dungeness crabs were not a significant source of post-settlement mortality for this species. Thus, it seems that distribution and recruitment of both species are ultimately linked to post-settlement processes that not only include mortality due to predation but may also involve post-settlement dispersal of juvenile shrimp after metamorphosis, a process often overlooked for many benthic invertebrates (Pilditch et al. 2015). Feldman (2001) observed small-scale movement of both 0+ and even older 1+ *U. pugettensis* into experimental settlement trays and larger shell plots but did not directly observe this movement for *N. californiensis.* The patterns we observed in Willapa Bay where the 1+ age class of *N. californiensis* appeared at our long-term monitoring location without documented settlement the previous year suggest that post-settlement movement might occur for this species as well and there is evidence that it occurs for other congeners (Tamaki and Ingole 1993; de Oliveira et al. 2012; Tamaki et al. 2013). Variable but consistently higher numbers of *N. californiensis* recruits at locations close to the estuary mouth and at middle tidal elevations in both estuaries agree with results from previous studies and other recent surveys (Bird 1982; Patten and Norelius 2016).

Conservation and Management Implications

Upogebia pugettensis populations have recently declined dramatically to very low levels in many US west coast estuaries where they were once abundant raising conservation concerns for the shrimp themselves (Chapman et al. 2012). This decline has been linked to very high prevalence of an introduced bopyrid isopod, *Orthione griffenis*, that directly affects recruitment by rendering adult female shrimp incapable of producing eggs (Dumbauld et al. 2011; Repetto and Griffen 2012; Asson et al. 2017). As a result, this species is no longer ecologically important in Washington state coastal estuaries including Willapa Bay where the population at our Goose Pt. monitoring location was reduced to a level after 2010 where we could no longer use cores to quantitatively sample adults. *Upogebia pugettensis* are still present at relatively high density in Yaquina Bay, but this decline has also occurred in Oregon estuaries and the spatial extent of their populations has decreased in Yaquina Bay (Bosley 2016; Dumbauld et al. unpublished manuscript). The data we present here suggest that recruitment to Willapa Bay has been less since the mid-1990s and that while there is a positive relationship between the number of 0+ shrimp and older 1+ shrimp, the slope of this relationship is less than one and these new recruits may experience relatively high mortality. Furthermore, they appear to only settle and recruit to areas where conspecific adults are present which would enhance declines and restrict population expansions. It is not yet clear why *U. pugettensis* populations near the center of their coastwide distribution in Oregon estuaries have persisted, while those further north and south near the ends of that distribution have declined even though *O. griffenis* continues to be recorded at high prevalence in all extant populations (Chapman et al. 2012; Chapman and Carter 2014, B. Dumbauld unpublished data). The data we collected here show that higher recruitment years for *U. pugettensis* in Willapa Bay were also strong recruitment years in Yaquina Bay (though not necessarily vice versa). This suggests that these populations are part of a larger metapopulation, so the proximity of nearby estuaries and potential for larval return could be one factor sustaining them.

Population density of *N. californiensis* also declined dramatically in both of the estuaries we studied beginning in the mid-1990s in Willapa Bay and from the outset of our monitoring program in Yaquina Bay in 2004, and these trends are reflected in the spatial extent of these populations as well (Dumbauld et al. unpublished manuscript). *Neotrypaea californiensis* population trajectories reversed from 2012 to 2014 in both estuaries, and we show that this is directly correlated to strong recruitment events beginning in 2010/2011. The slope of the relationship between 0+ shrimp density and that of older age classes was close to one suggesting that either mortality of these new recruits is low or that it is more difficult to track them as they have a broader recruitment window and post-settlement movement of juveniles occurs. It is not known whether there are other diseases or parasites that affect *N. californiensis*, but their population dynamics are not likely to be influenced by their native bopyrid isopod parasite *Ione cornuta,* which has always been observed at low prevalence (< 10%). *Neotrypaea californiensis* are longer lived than *U. pugettensis* (Dumbauld et al. 2011; Bosley 2016) which is likely linked to the longer, 4-year lag period and the lack of a linear relationship between 1+ and older shrimp in Yaquina Bay. *Neotrypaea californiensis* decapodids may also be initially attracted to settle where adults are present, but they appear to ultimately recruit more broadly across the estuarine landscape and the period over which this occurs is temporally variable.

As estuarine ecosystem engineers, these burrowing shrimp have clearly been shown to influence sediment biogeochemistry, benthic community composition, the presence of other suspension feeders, and even other engineers like seagrass via their bioturbation and burrow irrigation (Feldman et al. 2000; Pillay and Branch 2011; Takeuchi et al. 2013). They are also recognized for their role in estuarine food webs as both consumers and as prey. While some of these consumers with threatened populations like green sturgeon have raised recent concern (Dumbauld et al. 2008; Borin et al. 2017), only the shrimp's effect on shellfish aquaculture operations has received direct management attention in the US west coast estuaries we studied.

Both species of shrimp have caused a significant problem for oyster culture operations that occur in these estuaries because oysters are often seeded directly on the sediment surface. As sessile organisms, they succumb readily to bioturbation and sediment turnover caused by the shrimp (Dumbauld et al. 2004; Dumbauld et al. 2006). Oyster growers in Washington State applied a pesticide (carbaryl, n-methyl carbamate) at low tide to treat shellfish beds in coastal estuaries and remove these shrimp beginning in the early 1960s (Feldman et al. 2000). The growers signed an agreement to pursue integrated pest management (IPM) in 2000 and participated in an out-of-court settlement in 2002 where they agreed to stop using this pesticide by 2013. Research on alternative treatments resulted in continued studies and a recent evaluation of a less toxic pesticide, Imidacloprid (Washington State Dept. Ecology 2015, 2018). The tenets of IPM include knowledge of the pest's life history in order to target treatment at the most opportune point in time for control as well as knowledge of pest population dynamics in order to treat and control them when the level of pest abundance reaches a threshold (Kogan 1998; Lefebvre et al. 2015). These concepts have been little applied for aquaculture pests (see Rae 2002), and the threshold model has also proven difficult to apply for shellfish aquaculture in the case of these shrimp (Dumbauld et al. 2006). This is because the shrimp have a complex life cycle, and shellfish are also a perennial crop, grown in a spatially and temporally variable estuarine environment, and subject to economic market volatility.

Monitoring pest abundance is an essential component of IPM and the ability to predict shrimp abundance, even 1 year or one season before treatment would be valuable, especially for grow-out or fattening beds where shellfish are only present for a short period of time (Dumbauld et al. 2006). Here we document annual monitoring that has occurred in Willapa Bay for over two decades and show that annual recruitment patterns clearly influence resulting shrimp populations in areas with dense shrimp adjacent to shellfish beds. While shrimp density is lower on most culture beds, it is clearly useful to maintain such a monitoring program and understand shrimp recruitment ecology, regardless of the ultimate fate and nature of a control program. Several results from our research are insightful in this regard:

1) The only practical way to assess the abundance of larger shrimp across culture beds is via counts of burrow openings on the surface. Due to their small size, burrow openings of new recruits are only recognizable at a minimum of 1 year of age and it is likely that only 1+ *U. pugettensis* are counted in most surveys. For *N. californiensis*, burrow openings are smaller and more easily disturbed so this species may be 2 years old before they are counted in population assessments. Continuing to monitor the abundance of 0+ shrimp (and perhaps 1+ *N. californiensis* because small 0+ shrimp settle over a longer period and move to new areas after settlement) at long-term monitoring locations outside the culture beds will provide a window of opportunity for growers to anticipate and seek control.
2) Differences in recruitment behavior amongst species suggest that *N. californiensis* decapodids and small juveniles are more likely to recruit to shellfish beds even where previous treatment has recently removed adults. They distribute broadly and do not appear to be as selective in their behavior as *U. pugettensis* (but see Feldman 2001 who found that *U. pugettensis* also select areas where shell is present).
3) Due to their greatly reduced populations, *U. pugettensis* are currently less of an issue for shellfish growers, but they also appear to experience higher natural mortality during their first year of benthic life than *N. californiensis*. Juvenile *N. californiensis* grow more slowly and thus remain in relatively shallow burrows over the summer and fall (July–November) when they too are potentially more susceptible to control methods which could include enhanced biocontrol via predation and alternative physical control measures.

Our results thus provide important insight for managers that seek not only to maintain shrimp populations as native bioengineers that shape the ecology of the predominantly soft sediment ecosystems in these US Pacific coast estuaries, but also to control them and grow shellfish which play an equally important role in that ecology (D'Andrea and DeWitt 2009; Dumbauld et al. 2009; Ferraro and Cole 2010; Ferraro and Cole 2011; Volkenborn et al. 2012; Dumbauld and McCoy 2015).

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