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Discovery of a large offshore population of the northeast Pacific burrowing shrimp *Neotrypaea* sp. (Decapoda: Axiidea)

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Data Availability

The datasets analyzed during the current study are available from the corresponding author on request.

Abstract

The burrowing ghost shrimp *Neotrypaea californiensis* and *Neotrypaea gigas*, are recognized primarily from soft-sediment intertidal mudflats of estuaries and coastal lagoons in the northeastern Pacific from southern Alaska to Baja California. Individual records, however, are also known from occasional deep-water offshore collections. In previous offshore grab samples from California to Washington, USA, *Neotrypaea* spp. were present in about 14% of stations between 20 and 130 m depth. We assumed these usually low density (1 – 2 per core) small individuals were errant settlers from estuarine sources until summer 2019 when we found the first known large multi-year class population in an area 58 to 77 m deep 12 km offshore of Newport, Oregon, USA. The newly discovered *Neotrypaea* population, that we tentatively identify as, occurred at 35 of 52 stations (67%) in densities up to 26 individuals per 0.1 m² box core and included multiple size classes. Plan view camera samples indicate burrow densities of over 400 openings m⁻². This is the first report of a major burrowing shrimp population on the continental northeast Pacific coastal ocean.

Key Words: box core, burrows, continental shelf, distribution, ghost shrimp, SPI camera, subtidal

1. Introduction

Burrowing shrimp are important ecosystem engineers through modification of the sediment itself and increasing nutrient fluxes (Dumbauld et al., 2001; Dumbauld and Wyllie-Echeverria, 2003; Webb and Eyre, 2004; D'Andrea and DeWitt 2009; Pillay and Branch, 2011; Castorani et al., 2014). The two recognized eastern Pacific ghost shrimp on the shelf north of Morro Bay, California, are *Neotrypaea californiensis* (Dana, 1854) and *Neotrypaea gigas* (Dana, 1852). Both species are known primarily from intertidal, and occasionally, subtidal, soft mud and sand sediments of coastal habitats of the northeastern Pacific and range from southern Alaska to Baja California (Griffis & Chavez 1988; Campos et al., 2009; Jensen 2014). Previous subtidal depth records were to 26 m for *N. californiensis* and 88 m for *N. gigas* (Jensen 2014). *N. californiensis* are abundant while *N. gigas* are relatively rare in sandy mud intertidal and sublittoral of Oregon and Washington estuaries with *N. gigas* reported to be more common south

of Point Conception (Kuris et al., 2007). Wicksten (2011) reported “abundant callianassids” taken in benthic offshore surveys conducted in the Southern California Bight in the late 1970s but noted that whether the intertidal estuary and offshore *Neotrypaea* were the same or different species has not been determined, nor have species from California and Oregon been compared with specimens from Mexico. In deeper waters, *Callianopsis goniophthalma* (Rathbun 1902) is known from Alaska to Mexico in 483–1920 m (Hendrickx 1995; Wicksten 2011; Poore et al., 2019).

Like most burrowing shrimp, *N. californiensis* alter sediment topography and increase solute exchange via burrow digging and irrigation (D’Andrea and DeWitt 2009). Amensalistic sediment dependent interactions of burrowing shrimp and bivalves are well documented (Dumbauld et al., 2001; Pillay et al., 2007; Takeuchi et al., 2013, 2015), and shellfish farmers actively control *N. californiensis* populations due to their negative effects on Pacific oyster aquaculture (Feldman et al., 2000; Dumbauld et al., 2006). *N. californiensis* are important prey of fish, sturgeon (Dumbauld et al., 2008), and whales (Weitkamp et al., 1992; Darling et al., 1998; Dunham and Duffus 2001) and may be key consumers of phytoplankton and bacteria (Bosley et al., 2017) which, potentially, could make them vectors for domoic acid transfer to higher trophic levels (Kvitek et al., 2008).

Both north Pacific *Neotrypaea* species have pelagic larvae that enter the coastal ocean from estuaries on ebb tides as they hatch between May and late September. Pacific Northwest *N. californiensis* larvae develop within 20 km of shore (Johnson and Gonor 1982; Breckenridge and Bollens 2010) and return to estuaries as post-larvae June through November (Dumbauld et al., 1996; Dumbauld and Bosley 2018). *Neotrypaea* larvae are frequent members of coastal zooplankton communities (Morgan et al., 2009; Fisher et al., 2014; Hameed et al., 2018), but *Neotrypaea* larvae cannot be identified to species; therefore, the fractions of *Neotrypaea* larval species leaving and returning to estuaries and the *Neotrypaea* species composition in coastal ocean waters are unknown. *Neotrypaea* larvae distributions in offshore waters suggest that they moderate swimming behavior to remain in coastal waters (Morgan et al., 2009). The seasonal production of *Neotrypaea* larvae results in discontinuous recruitment to the benthos and discrete annual size modes within populations (Dumbauld and Bosley 2018, Bosley et al. 2019) that can be used for estimating age from size (McDonauld and Pitchard 1979).

As *Neotrypaea* larvae can be one of the most abundant crustaceans in the nearshore meroplankton (Fisher et al., 2014; Hameed et al., 2018), occasional settlers in the offshore benthos were expected. In previous shelf surveys, however, we recovered *Neotrypaea* spp. in 12% (64 of 540) of van Veen grab samples collected from 20 to 130 m depths in 2003 between the Mexican and Canadian borders (Henkel and Nelson 2018) and in 15% (128 of 850) of box cores collected from 20 to 130 m depths between 2010 and 2016 from northern California to central Washington (Henkel and Politano 2017; Henkel and Gilbane 2020). We assumed however, that these were errant settlers, not likely to persist, as few of those 0.1 m² samples contained more than 1-2 small shrimp (typically too small to distinguish between *N. californiensis* and *N. gigas*). We report herein a population of multiple age classes of *Neotrypaea* sampled in approximately 70 m water depth, 12 km offshore central Oregon, USA, during the summer recruitment season. Our analyses were performed to assess whether this apparently new, large offshore population challenges previous conceptions of the distributions and ecological significance of *Neotrypaea* outside of estuaries.

2. Methods

2.1 Sample/Image Collections

We used Sediment Profile Imaging and Plan View (SPI-PV) technology ground-truthed with box core grabs to characterize benthic physical and biological conditions within a 6 km² area with an average depth of 70 m, 13 km southwest of the entrance to Yaquina Bay, Oregon, USA (124° 13' 30" W, 44° 33' 15" N) at a site we call PacWave-South (PWS from here on). This site, offshore central Oregon, was identified as sand-dominated continental shelf habitat and was surveyed to demonstrate the performance of the SPI-PV technology in that sand habitat as compared to muddy seafloors where it has primarily been used. The SPI-PV system used (owned and operated by Integral Consulting Olympia, WA) is an Ocean Imaging System (OIS; Pocasset, Massachusetts) full ocean depth (4,000-m depth rating) Model 3731-D Sediment Profiling System camera that features OIS DSC 24,000 digital still cameras (within their respective watertight housings) and an attached OIS remote head strobe Model 3831. The SPI camera obtains a cross-sectional image of surface sediments in profile (to a maximum depth of 21 cm below the sediment–water interface [SWI]; Fig. 1). The plan view (PV) camera of this system obtains an image of the seabed from above immediately in front of where the SPI image is taken.

The SPI-PV image survey was conducted on 26 and 28 June 2019; three replicate SPI and plan view images were taken at each of 49 stations (not shown).

Ground truth box core samples were taken on 1 July 2019 at approximately half ($n = 26$) of the SPI-PV stations (Fig. 2; green dots). We aimed for penetration depth of at least 5 cm and no evidence of disturbance to be accepted for processing. An aliquot - approximately 80 milliliters (mL) - of sediment was removed from the surface of each acceptable core sample for median grain size (medianGS) analyses using a Beckman Coulter Laser Diffraction Particle Size Analyzer (LD-PSA). The remaining contents of the sample were then washed onboard on a 1 mm mesh sieve. Organisms retained on the sieve were collected and fixed in 5% formalin/seawater. After collecting unexpected numbers of *Neotrypaea* in the July 2019 box cores, we collected box cores opportunistically on other research cruises to more clearly define the *Neotrypaea* bed area and edges. In September 2019 we collected sixteen box cores (Fig. 2; blue dots) (ghost shrimp from the September 2019 collections were immediately frozen upon recovery from the box core to save for later genetic analysis), and on 7 October 2019 we collected an additional ten box cores (Fig. 2; orange dots). We had box cored the area around the PWS site more broadly between 2013 and 2018 (Fig. 2; black shapes).



Fig. 1. The SPI system (inset) and example Plan View (left; showing burrow openings on the sediment surface) and SPI (right; showing one intersected burrow segment) photographs.

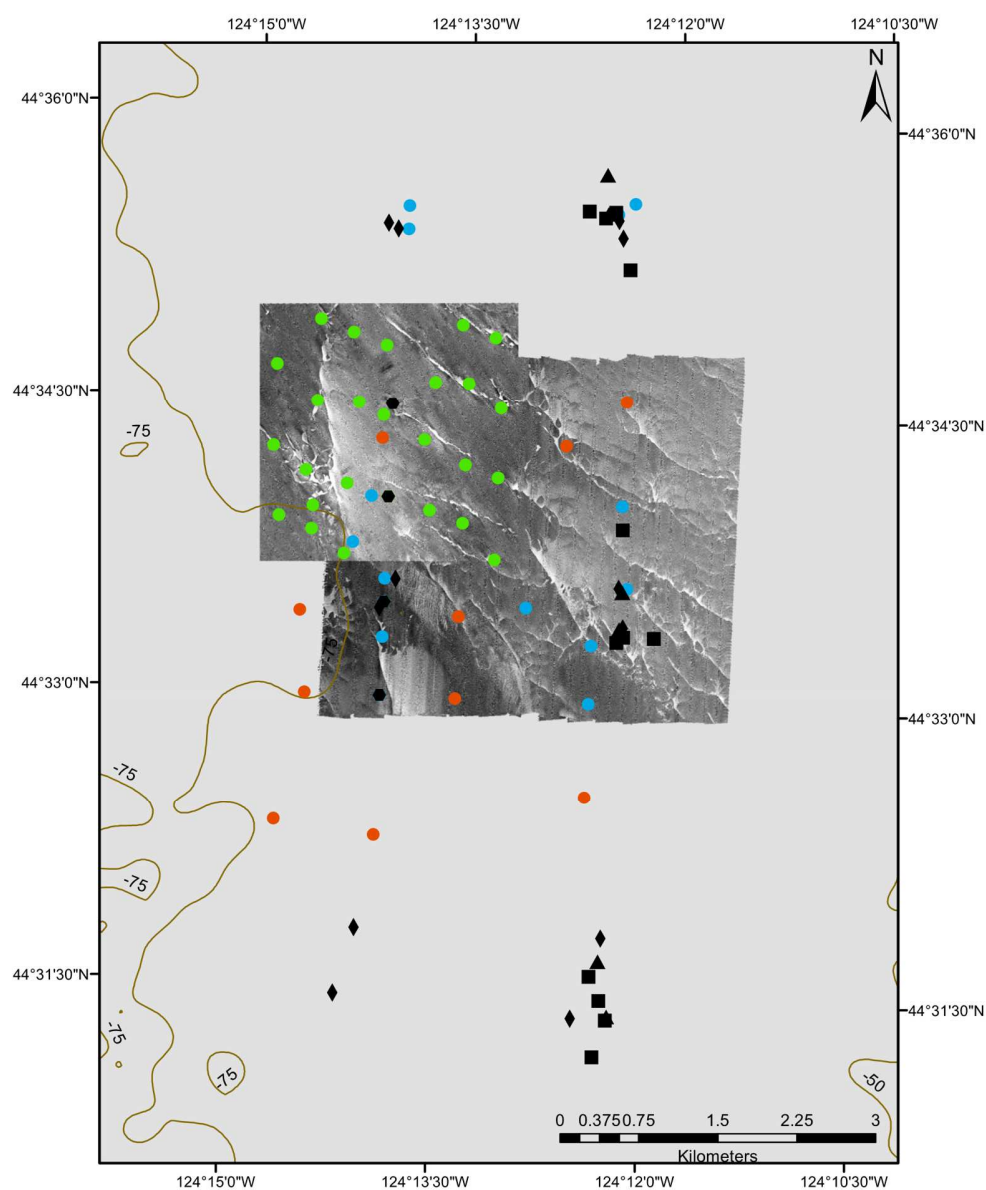


Fig. 2. Current and past box core sampling in the PacWave-South area. Colored dots represent 2019 sampling (green – 1 July; blue – 12-15 September; orange – 7 October). Black shapes represent sampling by Henkel in previous years (hexagons – 2018; diamonds – 2015, squares – 2014; triangles – 2013). Background imagery is acoustic backscatter (pixel resolution 4 m) showing roughness and relative sediment grain size of the surface. The 50 m and 75 m isobaths are shown.

2.2 Image/Sample Processing

Burrow openings were evident in many of the PV images collected (Figure 1). SPI images were also inspected for transected burrows; however, only two images showed transected burrows (e.g., Figure 1), so no further analyses using SPI images were conducted for this ghost shrimp population evaluation. The plan view images provide a much larger view of surface sediment conditions and, when present, shrimp burrows were clearly visible; scale information provided by the underwater lasers allowed density counts of burrow openings m^{-2} .

Formalin preserved shrimp were transferred to 70% ethanol before processing. We sexed the shrimp when possible, using the presence or absence of a gonopore and pleopod, and measured their lengths from the distal end of the eye stalk to the back edge of the carapace (to be comparable with measurements taken by Dumbauld et al. (2021) of estuarine *N. californiensis*). Larger shrimp were measured to the nearest 0.1 mm using calipers; smaller shrimp ($\sim < 5$ mm carapace lengths) were measured using a calibrated ocular micrometer under 6X magnification to the nearest 0.01 mm. Of the 246 *Neotrypaea* recovered from 1 July to 7 October 2019, 236 were suitable for measuring carapace length and 227 were sufficiently undamaged to determine sex.

2.3 Population analyses

We inferred cohort age frequencies and growth in the PWS *Neotrypaea* populations from comparisons of predicted and observed *Neotrypaea* carapace length frequencies to interpret general age groups using methods outlined by MacDonauld and Pritcher (1979). Bosley et al. (2019) corroborated increasing ages among increasing size frequency modes from the correspondence of increasing lipofuscin concentrations with size among Yaquina Bay *N. californiensis*. We therefore assumed for our analyses: that age in the offshore PWS *Neotrypaea* also increases with size, a correspondence of major size modes created by seasonal annual settlement, normally distributed cohort sizes, and cumulative mortality with age. We also assumed mathematically simple relations of cohort growth and size for our analyses but also that heterogeneous spatial remixing and variable recruitment of cohorts among years in these populations increases variation in relative cohort abundances among sample locations. We assumed thus that cohort sizes and size frequencies are more readily measured than absolute or relative cohort abundances.

We used “mixdist” package in R (MacDonald 2015, R Core Development Team 2015) for graphical and statistical estimates of carapace length (CL) frequency modes. We defined length frequencies and standard deviations (SD) for initial analyses in 1 mm length bins. Carapace length frequency modes were similar for > 10 mm CL males and females and thus separate size analyses by sex were unnecessary.

We assumed that sizes within cohorts are normally distributed and that mortality is cumulative with age. We estimated age structures, growth and mortality from changes in carapace length modes over time. We estimated growth by comparing predicted and observed *Neotrypaea* carapace length frequencies. We assumed for these estimates that growth and mortality vary in simple relations with age and that heterogeneous spatial remixing of cohorts in these populations can contribute to variation in relative cohort abundances among surveys and samples.

We determined a wet weight (wWt) to CL relationship across the range of carapace lengths of the PWS population using 33 blotted dry shrimp (previously preserved in EtOH) weighed the nearest 0.01 gram. We used the estimate of PWS shrimp weight per length ($wWt = aCL^b$) for estimates of biomass and production. We estimated *Neotrypaea* wet biomass m^{-2} (B) from by summation of population wet weights per carapace length times frequency per 1 mm carapace length interval (F) divided by sample area (A):

$$B = \sum_{i=1}^n \frac{(F_{1,i}(wWt))}{A} \quad (1).$$

Resolution of cohort ages (even in samples collected in time invariant states) permitted estimates of average annual production, P , by cohort summations (Wildish and Peer 1981, Crisp 1984) where:

$$P = \frac{1}{n} \sum_{i=1}^n S \left(\sum_{i=1}^n \left(\frac{(N_{1,i} + N_{2,i})}{2} \times (W_{2,i} - W_{1,i}) \right) \right) \quad (2)$$

in which, $N_{1,i}$ and $N_{2,i}$ are the number of shrimp m^{-2} in sequential cohorts and $W_{2,i}$ and $W_{1,i}$ are the respective estimated weights of those sequential cohorts averaged over the n surveys, S .

3. Results

3.1 Collections

SPI camera penetration averaged 6.8 cm (range 2 – 13 cm) and all images from all 49 stations were usable, indicating suitable performance of the SPI camera in this substrate type (although those images are not used further in these analyses). At least one plan view (PV) image was also useable from each of the 49 stations. Plan view images averaged 0.86 m² (range 0.2 – 1.2 m²). Box core penetration averaged 8.2 cm (range 4 – 12 cm) in the area of the SPI survey during the July collection. Box cores collected in September and October averaged 10.2 cm (5 – 18 cm) penetration. Median sediment grain sizes ranged from 228.8 to 805.1 μm .

We identified our specimens as *Neotrypaea gigas* based on the predominantly concave lateral edges, divergent medial edges and acute anterior of the eye stalks, and the parallel lateral edges of the male carpus and propodus (Pernet et al., 2010). However, we recognize the potential for cryptic species in this habitat distal to known populations and therefore refer to the PWS shrimp generally from here on as *Neotrypaea*.

We collected *Neotrypaea* in sixteen of twenty-six 0.1 m² box core samples in July 2019 (61.5% occurrence) with an average of 7.5 (\pm 3.0) shrimp per sample in which they were recovered. We recovered *Neotrypaea* in eleven of our sixteen 0.1 m² box cores in September (69%) with an average of 5.6 (\pm 4.1) shrimp per sample in which they occurred. We recovered *Neotrypaea* in eight of our ten October box cores (80%) with an average of 8.6 (\pm 9.2) shrimp per sample in which they occurred. Counts ranged from 1 to 26 shrimp (average = 7.2) per box corer at the stations where they occurred for an overall density of 4.73 shrimp per box core (Fig. 3) or 47.3 shrimp per m² over the three sampling dates.

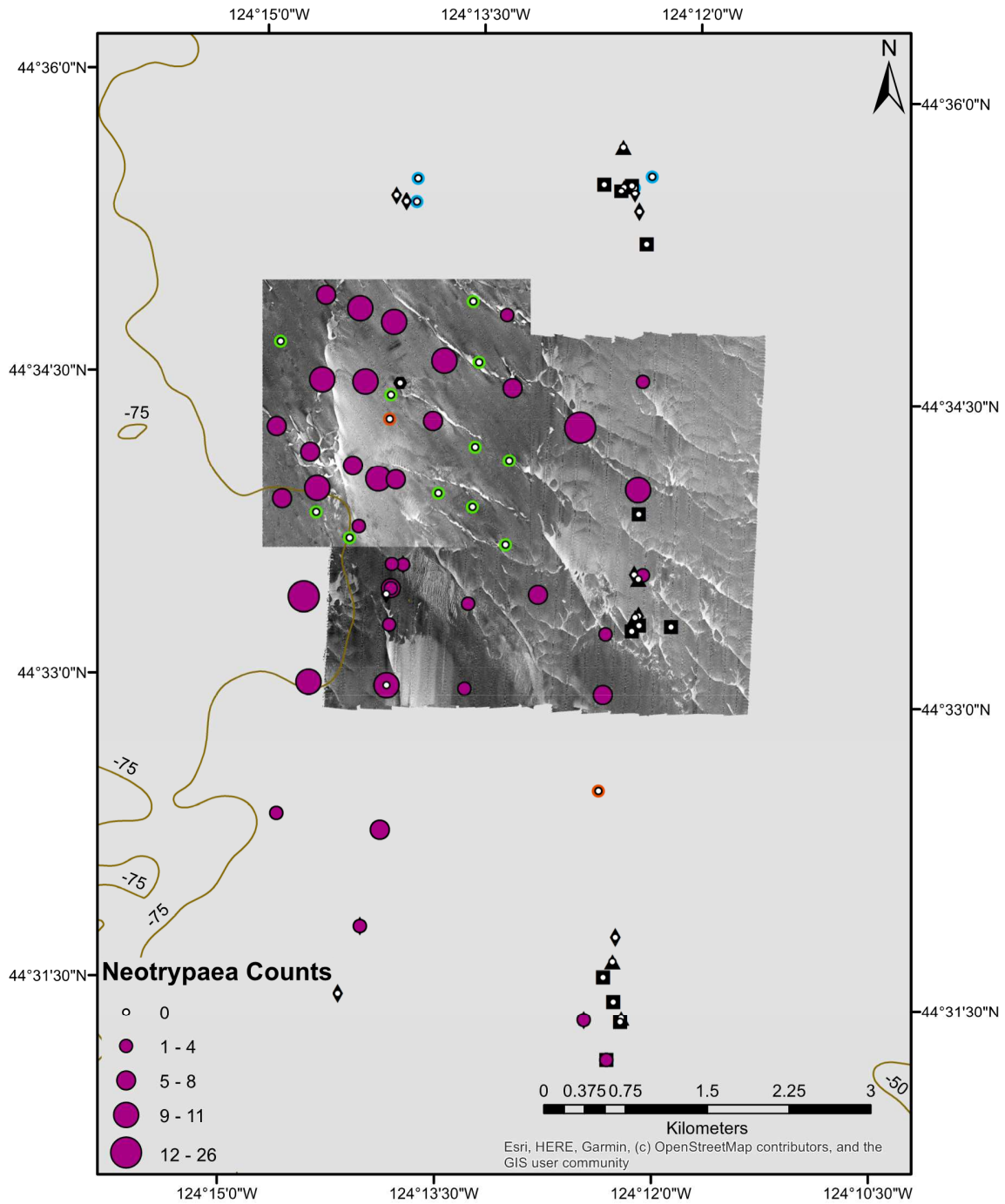


Fig. 3. The number of *Neotrypaea* per 0.1 m² box core (purple) collected from ~ 70 m depths

near Newport, OR, with hollow dots where no shrimp were recovered and halos indicating month/year of collection (green - July 2019; blue - September 2019; orange – October 2019; black - previous years). Background imagery is acoustic backscatter (pixel resolution 4 m) showing roughness and relative sediment grain size of the surface. The 50 m and 75 m isobaths are shown.

Burrow openings averaged $112 (\pm 124.5)$ per m^2 in the plan view images; all but one of the images from within the 6 km^2 primary survey area captured at least one burrow opening (even where no *Neotrypaea* were collected) up to a maximum of 413 burrow openings per image. The number of burrows observed per plan view image were closely correlated with the number of *Neotrypaea* collected in box cores ($r = 0.845$, $p < 0.001$; Fig. 4) with approximately two to three burrow openings per shrimp ($y_{\text{burrows}} = 2.13x_{\text{shrimp}} + 29.1$). Shrimp occurrences appeared to vary with seafloor topography, but this was an artifact of the July 2019 sampling grid corresponding to the direction of sand waves at the site. Neither the penetration of the sampling devices (Fig. 5a,b) or shrimp burrow densities (Fig. 5c,d) were correlated with the median grain sizes of sediments. However, SPI camera penetration, a measure of sediment bearing strength, and burrow hole density as observed by the plan view camera were correlated ($r = 0.943$, $p < 0.001$; Fig. 6a) as were box core penetration depths and shrimp per box core ($r = 0.549$, $p < 0.001$; Fig. 6b). Box core and SPI camera penetration depths may thus have depended on shrimp burrow density with deeper penetration among higher shrimp densities. Captured *Neotrypaea* size nevertheless, did not vary with penetration depth (Fig. 7a). Collection of *Neotrypaea* in the 2019 sampling also did not appear to depend on deeper box core penetration depths as the average penetration depths in 2019 were not different from 2013, 2014, 2015 or 2018 sampling (one-way ANOVA, factor = year; $p = 0.203$; Fig. 7b) while the densities of *Neotrypaea* were more than 10-fold higher (4.73 per core in the 2019 sampling versus 0.3 per core in the 2013-2015 sampling).

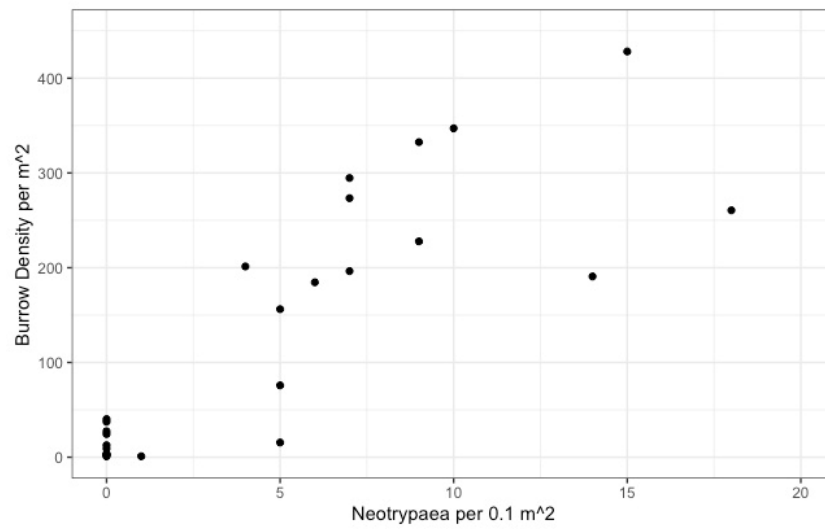


Fig. 4. Number of burrows observed per m² in plan view images (June 2019) versus number of *Neotrypaea* collected per 0.1 m² at each nearest box core station (n = 26; July 2019).

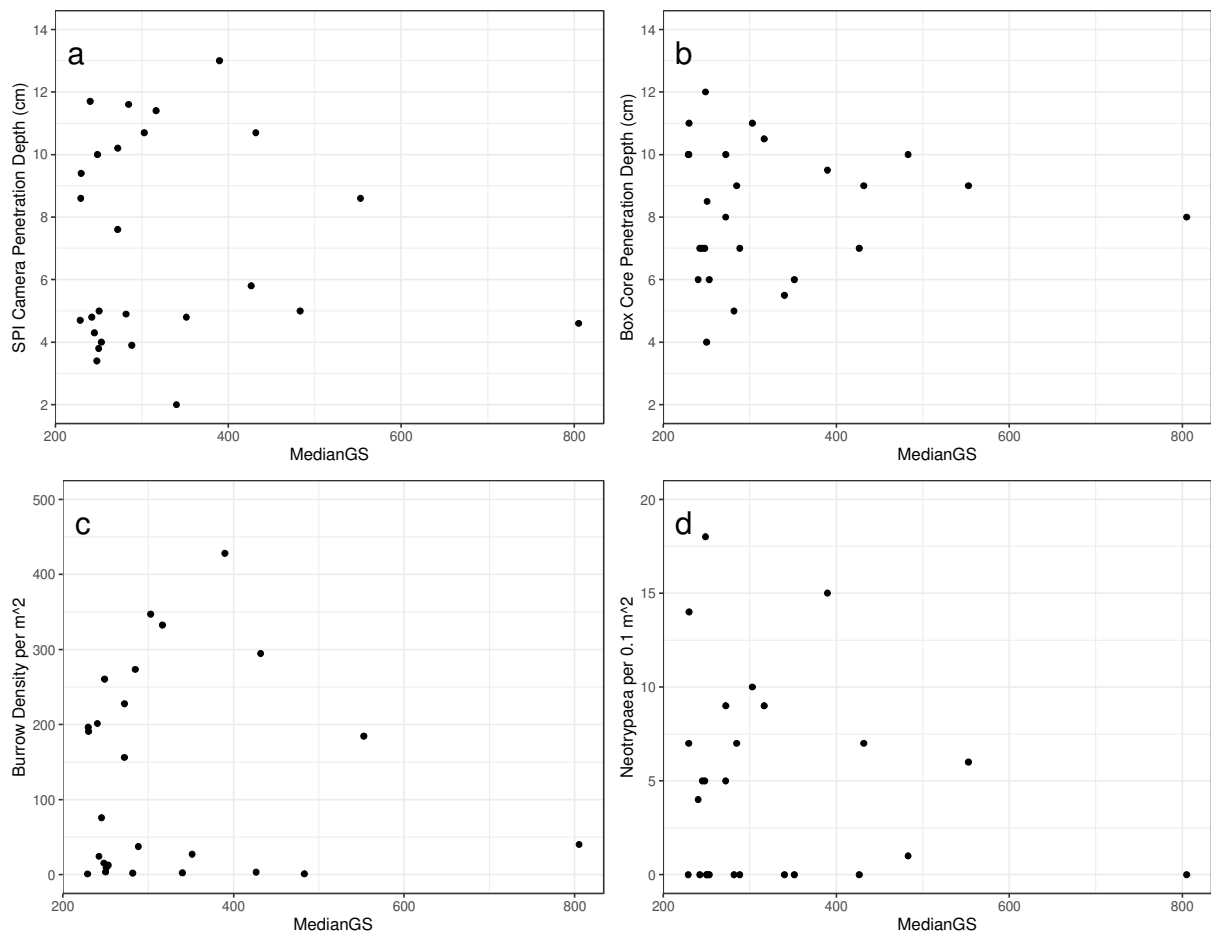


Fig. 5. A) SPI camera penetration depth (cm) versus median grain size (μm). b) Box core penetration depth (cm) versus median grain size (μm). c) Burrow density per m^2 as observed in plan view camera images versus median grain size (μm). d) Number of *Neotrypaea* collected per 0.1 m^2 box core versus median grain size (μm). All plotted data are from stations ($n = 26$) sampled in June (SPI/PV) & July (box core) 2019.

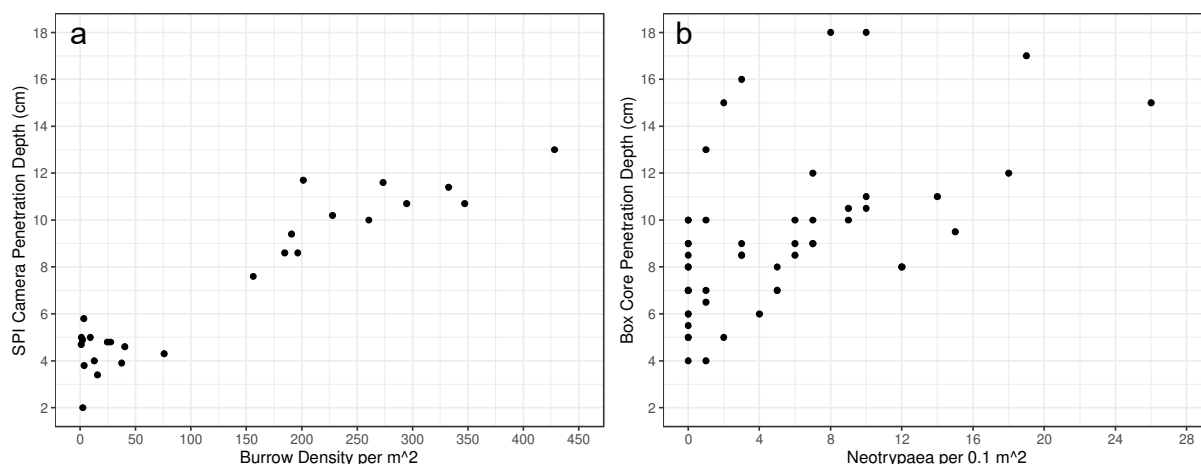


Fig. 6. A) SPI camera penetration depth (cm) versus number of burrows m^{-2} observed in plan view images in June 2019. B) Box core penetration depth (cm) versus number of *Neotrypaea* in each $0.1 m^2$ box core among all 2019 collections.

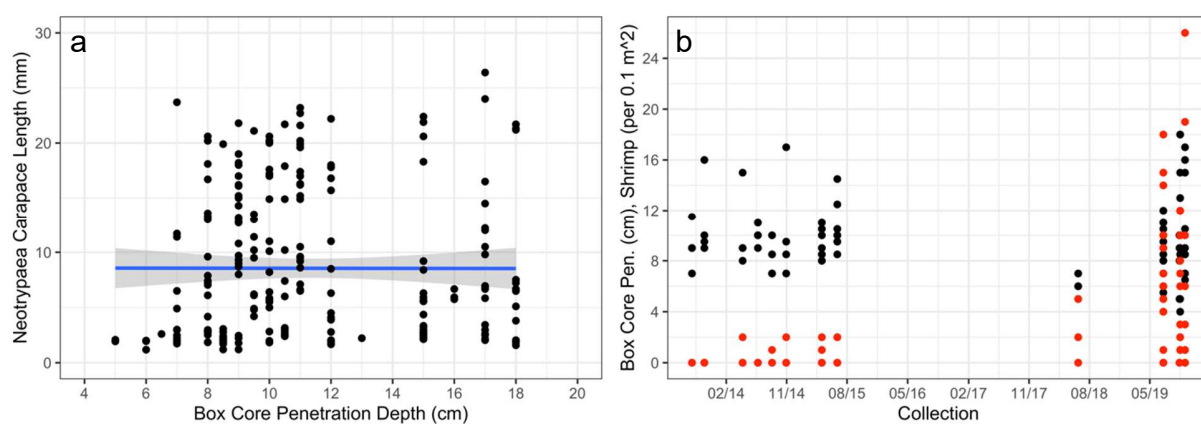


Fig. 7. A) *Neotrypaea* carapace length (mm) with box core penetration depth in 2019. B) Box core penetration depth (black) with *Neotrypaea* $0.1 m^2$ (red) by sampling period 2013-2019. In 2013-2015 in the PWS area, just 12 shrimp total were collected from 40 box cores.

3.2 Age structure, growth, biomass, and survival

Carapace lengths among the 236 measured specimens ranged from 1.2 to 26.4 mm. Of the shrimp large enough to sex, 45% were females, and 13 females were ovigerous, ranging from 16 to 26.4 mm CL. Larger *Neotrypaea* were collected primarily from the NW corner of the sampled area (in July) with smaller *Neotrypaea* collected from further south and east (in September and

October) (Fig. 8). The occasional small *Neotrypaea* recovered in the 2013-2015 surveys (Fig. 3) were consistent with either sampling in population perimeters or with initial settlement events.

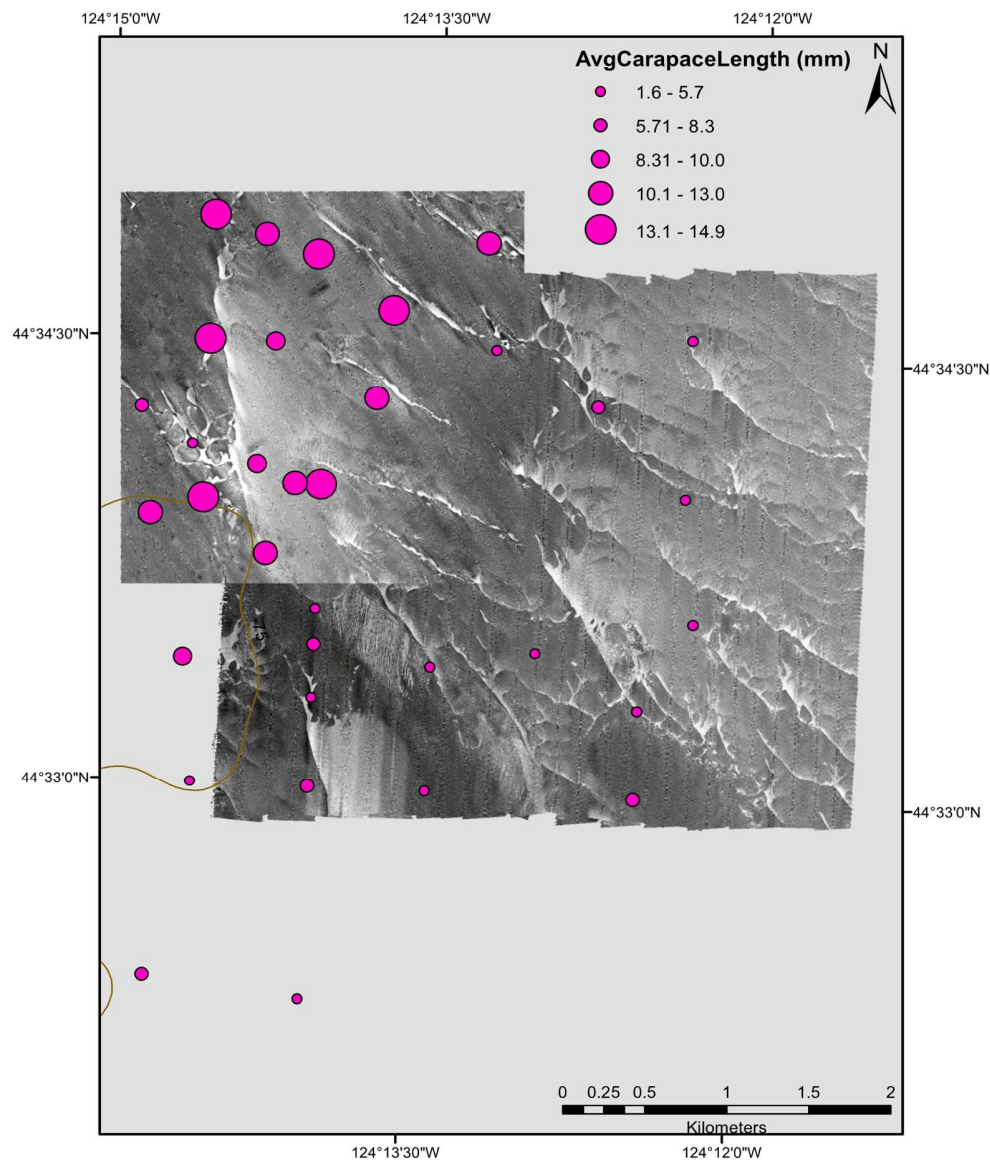


Fig. 8. Average *Neotrypaea* carapace length (mm) from each station where they were collected. The brown line indicates the 75 m isobath.

We detected 6 cohorts of *Neotrypaea* in the summer (July; Fig. 9a) and fall (Sept/October; Fig. 9b) populations. Whether the estimated fall and summer growth rates (4.9 and 3.7 mm yr⁻¹) (Fig. 9c) were significantly different is uncertain due to the lower numbers of observations in the largest size modes in the fall sampling (Fig. 9b). The regularly increasing standard deviations

among increasingly older cohorts (Fig. 9d) are consistent with regular growth within and among cohorts over time.

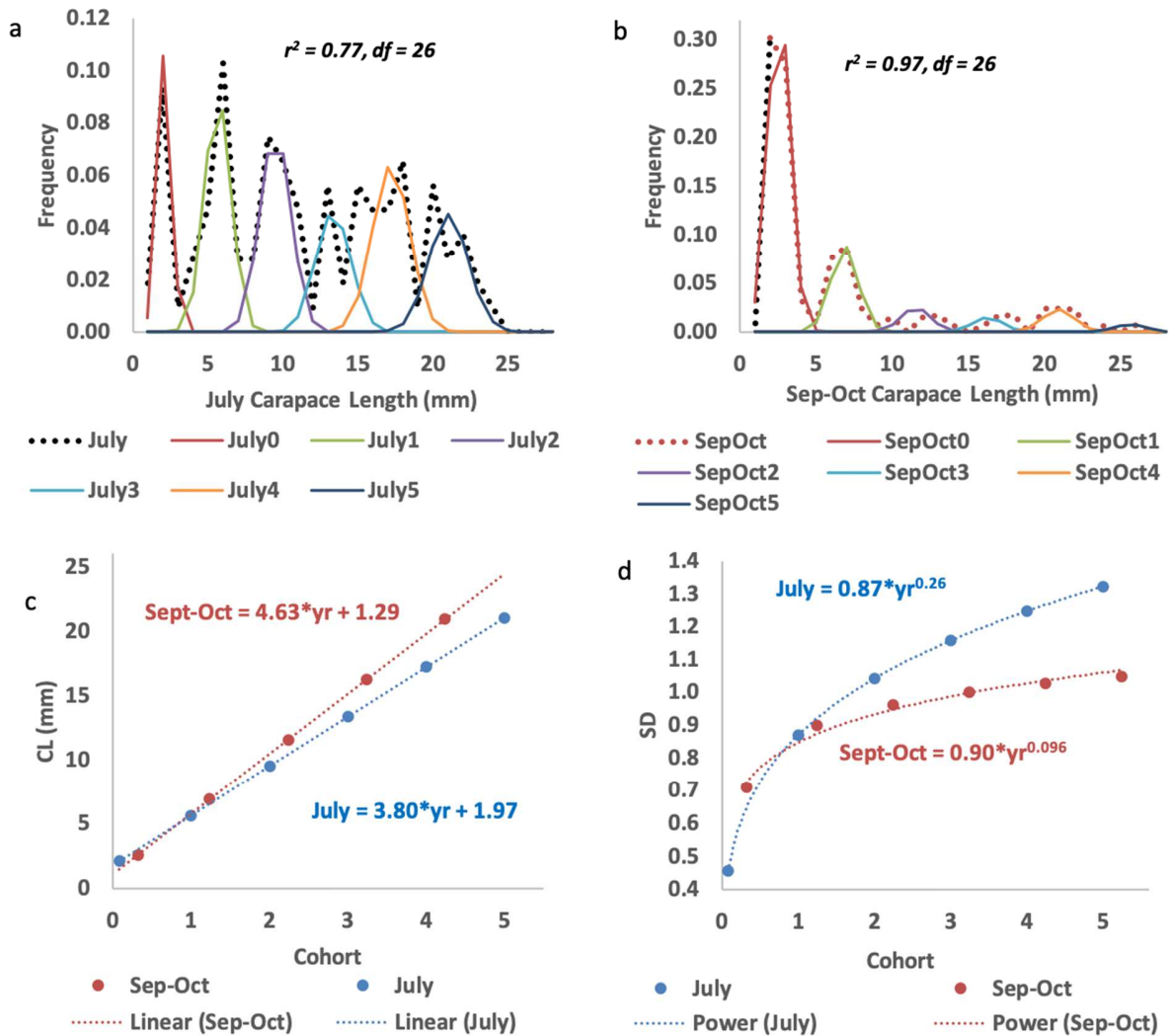


Fig. 9. Observed (dotted lines) and estimated (solid lines) *Neotrypaea* cohort lengths based on carapace length frequencies of the (a) July survey alone and (b) the combined September and October surveys, (c) estimated July and September-October carapace lengths among cohorts and (d) estimated standard deviations (SD) among cohort length frequencies.

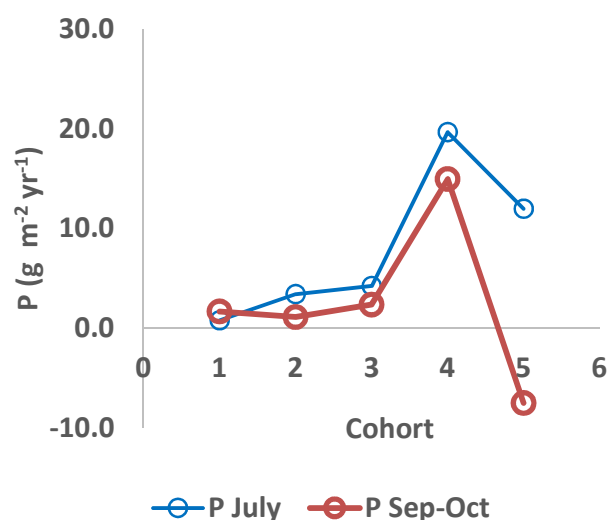


Fig. 10. Estimated production of July and combined September and October sample populations.

Wet weights of 33 randomly selected shrimp were varied closely with carapace length by the relations: wet weight (g) = $4E^{-4} * CL^{3.1826}$; $r = 0.935$ Wet weight biomass estimates (Equation 1) were 82.2 g/m^2 in the July 6 km^2 area sampled and 46.2 g/m^2 across the 16 km^2 area sampled in the fall (Table 1). Production (Fig. 10; Equation 2) was greater among cohorts 3-4 than among younger cohorts (Fig. 10b) due to their exponentially increasing biomass; reduced production of later cohorts was due to rarer occurrence (Fig. 10), consistent with mortality effects. From our biomass/CL estimates relative cohort abundances, productivity appears to have been about three times higher in the interior of the bed (July) than in the periphery (sampled Sept/Oct) (Table 1).

Table 1. *Neotrypaea* density (**N**) and biomass (**B**) per meters squared, total biomass in the survey areas (**M**) (tonnes^{-area}), and productivity (**P**) ($\text{g m}^{-2} \text{ yr}^{-1}$) in the July and in the September-October offshore survey areas.

Survey (area)	July (6 km^2)	Sept-oct ($\sim 16 \text{ km}^2$)
N (m^{-2})	41.2	53.4
B (g m^{-2})	82.2	46.2
M ($\text{t}^{-\text{Area}}$)	493	740
P ($\text{g m}^{-2} \text{ yr}^{-1}$)	40.2	12.7

4. Discussion

The *Neotrypaea* that we tentatively identify as *N. gigas* at the PacWave-South (PWS) site are far more abundant than estuary *N. gigas*. The low (less than 1 m⁻²) densities of *N. gigas* in Oregon and Washington estuaries (JWC personal observations) preclude precise quantitative estimates of their abundances or population dynamics and thus a lack of literature on *N. gigas*. Their extreme low densities place *N. gigas* as minor members of Oregon and Washington estuary ecosystems and, relative to *N. californiensis* in particular, ecologically unimportant. The biology of coastal offshore *Neotrypaea* has, understandably, remained unexamined due to their previously rare occurrences in benthic samples.

The widespread offshore shrimp bed with multiple cohorts and brooding females described herein challenges previous tacit assumptions have been that: 1) burrowing shrimp of the northeastern Pacific are significant as ecosystem engineers only in estuaries, 2) coastal *Neotrypaea* larvae are predominantly of estuary origin and 3) the dynamics of estuary burrowing shrimp populations are controlled predominantly by growth, survival and reproduction of those estuary populations. A possible emergence of substantial offshore *Neotrypaea* populations also poses a potential significant disruption of the benthic community offshore.

The density of 47.3 *Neotrypaea* m⁻² we collected offshore in 2019 is comparable to that estimated for *N. californiensis* in nearby Yaquina Bay, OR, in 2014 (68.1 m⁻²; Bosley et al., 2019 Table 1). However, our collections spanned a total of 18.2 km² that included an estimated 8.6 million offshore *Neotrypaea* while Bosley et al. (2019) sampled a 5.8 km² *N. californiensis* bed. The largest recent known extent of that bed was in 2013 at 9.2 km² for a maximum population size of 7.1 million estuary *N. californiensis* (Bosley et al., 2019), a substantial decline from an estimated 110 million estuary *N. californiensis* in 2002 (Dumbauld et al., 2021). Thus, the offshore population of *Neotrypaea* appears to rival or exceed the present estuarine population of *N. californiensis* and greatly exceed the estuarine population of the much less abundant *N. gigas*.

Little has been published regarding habitat preferences of *N. gigas* in Yaquina Bay, Oregon; however, *N. gigas* are typically found lower in the intertidal than *N. californiensis* (SKH and JWC personal observations). In Bahia de San Quintin, Baja California, Mexico, where both species exist in high densities, the same spatial separation has been reported with *C. gigas* typically inhabiting mid- and low- intertidal muddy sites as compared to higher intertidal sandy

sites for *N. californiensis* (Griffis & Chavez 1988). Thus, while it may be reasonable to expect the PWS *Neotrypaea* to be *N. gigas* based on previous reports of *N. gigas* from deeper depths on the shelf (Jensen 2014), the clean coarse sand at PWS (MSG 228.8 to 805.1 μm) did not match their apparent preference for muddy sites where it occurs predominantly in Yaquina Bay.

Polymodality can be a misleading guide to underlying age-groups (Bosley et al. 2019, McDonauld and Pitcher 1979) however, the widely separated size frequency modes of the PWS *Neotrypaea* are consistent with seasonal settlement and approximately 3 mm annual growth increments and may be due to a shorter settling season and longer overall lifespan for these offshore *Neotrypaea* than other species. Our observations differ starkly from the nearly unimodal to occasionally bimodal size frequency distributions observed in local estuarine *N. californiensis* (Bosley et al., 2019) and estuarine *F. filholi* (in New Zealand; Berkenbusch and Rowden 2000) and complete lack of consistent cohorts observed for *Callianassa subterranea* (North Sea; Witbaard and Duineveld 1989). In common with estuary *N. californiensis* (Bosley et al., 2019), relative survival among the PWS 0-year cohort *Neotrypaea* is likely to be low. The large difference between the July and Sept/Oct 0-year cohort frequencies may have resulted from settlement between August and September and/or October (either as one long recruitment event or multiple events). The 0-year cohort difference also could have been a result of sampling primarily in the $\sim 6 \text{ km}^2$ interior bed in July and the perimeter areas in September and October. Both scenarios are consistent with broad but seasonal *N. californiensis* settlement observed in the Yaquina, OR, and Willapa Bay, WA, estuaries (Dumbauld and Bosley 2018).

The one year and older PWS shrimp appear to have equal or greater annual survival than previously observed Willapa Bay (Dumbauld et al. 1996) or Yaquina Bay (Bosley et al. 2019) populations. Assuming that our resolved size modes (Figure 9a and 9b) are annual cohorts, mortality among 1-5 cohorts appeared to be low (-0.06 to -0.01 compared to the average -0.71 mortality estimated among 4-7 year for Yaquina *N. californiensis*; Bosley et al., 2019). Unlike the Yaquina Bay *Neotrypaea*, that reached up to 7 years in age, older than five year PWS shrimp were not apparent. Whether the PWS population reached a stable age distribution by 2019 is thus unclear. The apparently low PWS mortality, if it occurs, may be temporary due to its recent origins or artifacts of sampling bias. Increasingly smaller cohorts, for example, could be under-sampled or highly variable age-dependent mortality could also occur among in the PWS age

cohorts. We lack direct production estimates for Yaquina Bay or Willapa Bay *Neotrypaea* and are unaware of previous estimates of eastern Pacific *Neotrypaea* production. The likely 3.8 to 4.6 mm yr⁻¹ increases in carapace lengths of PWS *Neotrypaea* are greater than among *N. californiensis* in Yaquina Bay (21 mm CL in ~7 years; Bosley et al., 2019) or Willapa Bay (18 mm in ~7 years; Dumbauld et al. 1996). While many studies have indicated that both food quality and temperature influence growth in crustaceans (e.g. Stoner et al. 2013 and references therein), Bosley's 2016 laboratory investigations of temperature on estuarine *N. californiensis* growth rates indicated temperature to be less important in controlling growth than food availability: there was no difference in mean change in carapace length among temperature treatments (10° C, 13° C and 16° C which represent lower, average and upper temperatures commonly experienced by burrowing shrimp populations in Yaquina Bay, Oregon). There was a significant effect of temperature growing degree-days for field-raised *N. californiensis* (Bosley 2016). Temperatures at the PWS site have ranged from 7.3 to 9.3° C in our collections from 2013 to 2019, indicating a temperature regime with little overlap compared to the estuary.

The concentrated PWS *Neotrypaea* are a potential food source for fish and marine mammals. Gray whales forage for *N. californiensis* in the Salish Sea (Weitkamp et al., 1992) and have been observed engaging in benthic feeding at depths up to 100 m offshore Kodiak, AK (Moore et al., 2007); thus, *Neotrypaea* are a favorable food for gray whales and this newly discovered population is within observed feeding depths of gray whales. The PWS *Neotrypaea* standing biomass in the 6 km² July surveyed area was 82.2 g m⁻² or 493 tonnes (*t*) biomass. PWS *Neotrypaea* production yr⁻¹ thus, could be 241 *t* yr⁻¹ (from Table 1: 40.2 g m⁻² yr⁻¹ production x 6E6 m²). Nerini (1984) estimated that mature gray whales require approximately 61.4 tonnes of the Bering Sea amphipod crustacean *Ampelisca macrocephala* per year, obtained in their approximate 5 month breeding season. Assuming *Ampelisca* and *Neotrypaea* caloric contents and extraction efficiencies are similar, and 20% disturbance for feeding (as observed by Weitkamp et al., 1992 on *N. californiensis* in the Salish Sea), gray whales could harvest (0.2 x 241 *t*) = 48.2 *t* from the interior (July sampled) area each year, a biomass that is sufficient for the sustainable annual food requirements of nearly one gray whale per year according to Nerini's estimates.

Reproduction and fecundity

Brooding *Neotrypaea* females collected offshore comprised 24% of >1 year females recovered in

the survey and averaged 19 mm CL compared to Dumbauld et al.'s (1996; Willapa, WA) 14 mm and Bosley et al.'s (2019; Yaquina, OR) 10 mm average carapace lengths of brooding *N. californiensis* females. The larger offshore females might be expected if they are *N. gigas*. Brooding seasons of estuary *N. gigas* coincide approximately with *N. californiensis* (Chapman, personal observation). Brooding *N. californiensis* are most frequent in Oregon and Washington estuaries between July and October (Dumbauld et al., 1996; Bosley et al., 2019) but can occur as late as January and as early as March (Dumbauld and Bosley 2018; Bosley et al., 2019). MacGinitie (1934) found brooding *N. californiensis* in Elkhorn Slough, California, year-round, with greatest egg production in July and August. Bird (1982) concluded that Oregon estuary *N. californiensis* produce multiple broods per year. The high proportion of brooding females in our July – October PWS *Neotrypaea* collections is therefore consistent with bay and estuary *Neotrypaea* reproductive periods. The *Neotrypaea* brooding period is 5-6 weeks (as described by Bird 1982) and the planktonic residence period is 6-8 weeks (McCrow 1972; Johnson and Gonor 1982; Pimentel 1983). Dumbauld and Bosley (2018) found settlement in Yaquina Bay, OR, between June and November while Dumbauld et al. (1996) found *Neotrypaea* spp. settlement in Willapa Bay, WA, from August through October. The two small size classes we observed in July possibly were the result of an earlier reproductive season than in Yaquina Bay and possibly late summer settlement also. In mid-September, recruits comprised 54% percent of the recovered PWS shrimp. This apparent increase could have been due, in part, to our September-October sampling on the periphery of the July sample area. The greater frequencies of *Neotrypaea* recruits in September and October when we sampled outside of the main bed is consistent with Dumbauld & Bosley's (2018) observations of greater densities of new *N. californiensis* at the interface of the adult *N. californiensis* bed and in the open sand habitat.

The PWS *Neotrypaea* sex ratio was nearly 1:1 overall in contrast to an observed female:male ratio of 2:1 for *N. californiensis* observed in both Willapa Bay (Dumbauld et al., 1996) and Yaquina Bay (Bosley et al., 2019) and the nearly 2:1 male bias observed for *Callinassa subterranea* in the North Sea (Rowden and Jones 2009). The unbiased sex ratio is more similar to that documented by Berkenbusch and Rowden (2000) in intertidal *Filhollianassa* (*Callinassa*) *filholi* populations in New Zealand; however, previous surveys found female dominance in that species as well (Berkenbusch and Rowden 1998), supporting that the sex-ratios of burrowing shrimp may vary not only among species and populations but also over time

(Tunberg 1986; de Vaugelas et al., 1986; Tamaki et al., 1996).

The broad spatial and temporal settlement of the newly recruiting juveniles, brooding and ovigerous females, and broad size and age ranges of the PWS *Neotrypaea* are consistent with long term persistence maintained by self-recruitment. The likely 5 year or more offshore *Neotrypaea* life spans are similar to the 5 – 10 year life spans suggested by Dumbauld et al. (1996), Bosley and Dumbauld (2011) and Dumbauld and Bosley (2018) for *N. californiensis*. The offshore bed is located where sparse sampling was concluded in June 2015 and thus whether it appeared since 2015 or was present before we discovered it in July 2019 is unclear.

Ecosystem effects

The occurrence of sustained offshore *Neotrypaea* populations could change interpretations of estuary population recruitment dynamics and inferred oxygen and nutrient cycling mechanisms on the shelf. *Neotrypaea* are primary architects of sediment structure and burrow to greater depths than other common offshore bioturbating species. Burrowing shrimp irrigation increases oxygen penetration to the ~80 cm depths of their burrows (MacGinitie 1934; Thompson and Pritchard 1969) whereas natural molecular diffusion penetrates only a few millimeters (Ziebis et al., 1996a,b; Revsbech et al., 1980; Li et al., 2020). The increased diffusive area and bio-irrigation potential of burrow opening counts of up to 400 m⁻² in this area are significant in this part of the shelf challenged by increasing frequencies and intensities of hypoxic events (Grantham et al., 2004; Chan et al., 2008). While potentially contributing to increased oxygen penetration, these large, abundant, and active shrimp also could be significant competitors for the limited oxygen on the benthos. In New Zealand, benthic oxygen consumption was three times greater in incubation chambers containing the deep-sea burrowing shrimp, *Eucalastacus torbeni*, than in chambers without these shrimp (Leduc and Pilditch 2017), and annual uptake of O₂ by *Callianassa subterranea* in the North Sea is estimated to be 17% of the total O₂ consumption by the local community (Witbaard and Duineveld 1989).

Burrow walls of *N. californiensis* (MacGinitie 1934; Griffis and Suchanek 1991) as well as *Callianassa subterranea* (Laverock et al., 2010) are a rich and stable substrate for production of microbes responsible for N₂ fixation. Bertics et al. (2010) demonstrated greatly increased nitrogenase activity in coastal sediments bioturbated by the *N. californiensis* that is potentially

due to sulfate reducing-bacteria. Much like other coastal regions, sediments on the Oregon shelf are a net sink of water column fixed N (Berelson et al., 2013). The offshore bed of deep-burrowing shrimp described herein could produce significant positive impacts on local benthic productivity that is normally limited by available nitrogen.

The offshore *Neotrypaea* could also be disrupting the resident macrofauna of the area. Shrimp burrows affect community composition (Brenchley 1981; Posey 1986; Posey et al. 1991; Dumbauld et al., 2001) and ecological structure and processes in estuarine and nearshore benthic habitats (Berkenbusch and Rowden 2003). In addition to the disruptive structural effects of their burrows (as demonstrated in our study by the impromptu penetrometer in the form of the SPI camera), Bird (1982) experimentally demonstrated that organic content decreased significantly faster in the presence of *N. californiensis* than where shrimp were absent. Bird (1982) therefore hypothesized that fewer deposit feeding polychaetes and tanaids could be supported with greater shrimp biomass. The degree to which this offshore bed affects the mid-shelf benthic community composition or abundance remains to be determined.

The massive newly discovered offshore population thus challenges previous assumptions that northeastern Pacific burrowing shrimp are ecosystem engineers only in estuaries, that coastal *Neotrypaea* larvae are predominantly of estuary origin, and that the dynamics of estuary burrowing shrimp populations are controlled predominantly by growth, survival and reproduction in those estuary populations. Overall, how increased presence of offshore *Neotrypaea* (that are highly adapted for low oxygen conditions; Thompson and Pritchard 1969) will change communities at the sediment-water interface remains to be tested. Genetic investigations along with detailed morphological analyses are underway to test whether the PWS *Neotrypaea* are a native species shifting its distribution and/or abundance in response to climate change or other environmental alterations on this coast or an unrecognized foreign species introduction. Either possibility could alter Oregon and Washington estuaries by seeding intertidal *Neotrypaea* populations with a new genotype or species.

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