THE DISTRIBUTION OF TWO MARINE CLADOCERANS DURING UPWELLING AND RELAXATION EVENTS OFF THE OREGON COAST

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Offshore surface currents that appear during upwelling events have the potential to carry nearshore coastal zooplankton offshore. I tested the hypothesis that the marine cladocerans *Podon leuckarti* and *Evadne nordmanni* are pushed offshore during summer upwelling. Additionally, stratified horizontal currents during upwelling, with surface regions moving offshore and deeper layers moving onshore, could differentially distribute reproductive stages or sizes that have different vertical distributions. I tested the hypothesis that reproductive stages and sizes of cladocerans would be distributed differentially from one another during upwelling and relaxation events. The fecundity of marine cladocerans off Oregon was also investigated. A vertically stratified transect of 7 stations located from 0.5 to 28 km offshore near Coos Bay, Oregon was sampled for zooplankton on four days in the summer of 2007. Two of the sample dates (27 June and

14 August) were characterized by upwelling conditions, and two (3 and 18 July) were characterized by relaxation or weak downwelling conditions. Preserved cladocerans were counted, measured, and assigned a reproductive stage. In females the number of embryos was counted. Neither cladoceran species showed evidence of offshore surface transport during upwelling, and both showed densest concentrations nearshore, although a deeper offshore concentration of *E. nordmanni* may have been affected by deep onshore upwelling currents. Parthenogenic *P. leuckarti* with early embryos were distributed similarly to those with advanced embryos, and males tended to stay near the bottom or surface nearshore. All stages of *E. nordmanni* stayed primarily near the bottom or surface nearshore. Smaller cladocerans and parthenogenic females with early embryos were found in larger proportions closer to shore, while larger cladocerans and parthenogenic females with advanced embryos were found farther offshore. Cladoceran fecundity in Oregon was high, with a mean and 95% confidence interval of 5.42±0.37 embryos per parthenogenic *P. leuckarti* and 10.21±0.247 embryos per parthenogenic *E. nordmanni*. Complex interactions between physical oceanography and cladoceran behavior may account for observed cladoceran distributions off the Oregon coast.

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TABLE OF CONTENTS

INTRODUCTION

Physical oceanography

The Oregon coast is characterized by the oceanographic phenomenon of seasonal upwelling. Upwelling occurs in Oregon and California when winds blow from the north, pushing surface water south alongshore. This is known as Ekman transport. The surface water is then deflected to the right of its path of travel (offshore) by the Coriolis force, which is a result of the Earth's rotation. Thus, the net Ekman transport of surface water is away from the shoreline. This causes a dip in sea level at the shoreline that is replaced by deeper water "upwelling" nearshore to replace lost surface water. The amount of water that is upwelled from the depths is equal to the amount of water that is moved offshore through Ekman transport (Huyer 1983).

Upwelling in Oregon is seasonal, generally starting in April or May and continuing intermittently through September (Huyer et al. 1974, Smith 1974). This seasonality results from changes in atmospheric pressure systems north and south of Oregon that create winds that are primarily southward in the summer, causing upwelling, and primarily northward in the winter, causing downwelling. Downwelling is the opposite of upwelling. When the wind is blowing northward, Ekman transport of surface water is toward the shore, where water builds up and must move downward. Seasonal upwelling and downwelling are net effects, and conditions can vary from day to day, depending on wind characteristics. Downwelling can occur for periods in the summer and upwelling in the winter (Huyer 1983). Summers in Oregon generally exhibit cycles of upwelling and relaxation or downwelling that are roughly 8 days long (Peterson et al. 1979).

Upwelling and downwelling events have both horizontal and vertical components. Horizontal currents are the cross-shelf currents created in the axis of nearshore to offshore. The relatively strong offshore current during upwelling can transport water up to several kilometers per day in Oregon (Peterson et al. 1979). Vertical currents are the currents that move up or down within the water column. During upwelling there is a relatively weak current moving from deep water, generally deeper than 30 m, up toward the surface nearshore (Huyer 1983). Transitory horizontal and vertical currents created during upwelling and downwelling events have the potential to greatly affect the small planktonic organisms living in the coastal ocean.

Upwelling can be identified by several physical trends. Water in the ocean is not homogenous, and distinct water masses can be identified on the basis of temperature, salinity, and ultimately density. Warm water is less dense than cooler water and will therefore float on top of cold water, forming discrete layers of increasing water temperature from deep water to shallow water. In these layers, there is a region of rapidly changing temperature with depth known as the thermocline. Additionally, water with high salinity is denser than water with low salinity. High salinity water will sink to the bottom, while low salinity water will float on top. Like the thermocline, there is a region where salinity rapidly changes with depth known as the halocline. Both the thermocline and the halocline are created because of differences in the density of water layers. The area where water density changes rapidly with depth is known as the pycnocline. These clines are interrelated and their locations are important indications of upwelling and downwelling.

During upwelling, warm surface waters along the coast are pushed offshore through Ekman transport and colder deep water is upwelled to the surface near the coastline. This results in a band of cold water along the shore and a mass of warmer water offshore that can be identified through temperature satellite imaging. Additionally, vertically sampling the water column shows that the thermocline, or lines of constant temperature, is bent upward and contacts the surface nearshore (Huyer 1977). Likewise, upward bends in the halocline and pycnocline appear during upwelling. This surface contact area is known as the upwelling front, because it indicates where the warm surface water that previously contacted the coastline ends and the cold, upwelled water begins (Peterson et al. 1979).

During downwelling, an opposite trend is observed. Since Ekman transport is toward shore, warm surface water contacts the coastline and there is no cold water band visible in a temperature satellite photo. Vertical sampling of the water column shows that the thermocline bends downward and contacts the bottom nearshore, because warm surface water is being pushed downward. Likewise the halocline and pycnocline bend downward and contact the bottom. This contact point is called the downwelling front, since it represents the boundary between previously surface water that has been moved deeper and originally deep colder water (Huyer 1983). During relaxation from upwelling, a downwelling front is not observed, but the warm surface water returns to contact the coastline and the thermocline, halocline, and pycnocline return to a position relatively parallel with the surface.

Wind-driven upwelling is a coastal process that primarily influences the region within 10 to 25 km of the shoreline (Huyer 1983). In Oregon, the continental shelf

generally extends about 30 km from the shore and ranges between 50 and 200 m in depth offshore. The surface layer affected by Ekman transport is shallower nearshore and increases in magnitude offshore. Within 10 km of the shore the Ekman layer is usually about 5 m deep, while farther offshore it can be 10 to 30 m deep (Peterson et al. 1979, Huyer 1983). The surface water mass pushed offshore during upwelling does not continuously move offshore and become lost in the open ocean, but rather moves about 20 to 40 km offshore and then returns to the coast during relaxation and downwelling events (Peterson et al. 1979). This is important for the communities of zooplankton that reside in coastal systems and may be affected by upwelling currents.

Biological oceanography: An ongoing dispute about Ekman transport

Seasonal coastal upwelling occurs along the entire west coast of the United States, although it is much stronger in California than in Oregon (Huyer 1983, Connolly et al. 2001). Upwelling events have long been assumed to influence zooplankton exactly as they affect surface water masses, pushing zooplankton offshore during upwelling events and back onshore during relaxation and downwelling (e.g. Roughgarden et al. 1988), but more recent studies have shown that this is not always the case (e.g. Shanks and Shearman 2009).

This theory was formed to explain why recruitment events, when pelagic larvae rejoin adult populations, are sporadic and variable in upwelling systems. Roughgarden et al. (1988) looked at stage VI naupliar larvae of the barnacle *Balanus glandula* in California and found that the distance offshore of the larvae increased with stronger upwelling conditions and decreased during times of relaxation. They justified looking at

only one stage of the larvae because at this age, if the larvae do not settle soon they die at sea. Roughgarden et al. (1988) suggested that their results with *B. glandula* could be considered representative of intertidal invertebrate larvae, and that they had demonstrated that upwelling events inhibit recruitment. They further suggested that their data supported a broad ecological model in which upwelling determines the community structure in areas where larval supply, rather than competition for space, is a limiting factor.

Farrell et al. (1991) continued this work in California by measuring recruitment in the intertidal barnacles *B. glandula* and *Chthamalus* spp. and found that recruitment was highly variable but occurred in four large pulses during relaxation periods. They also sampled zooplankton from the first 1 m of the water column, within the Ekman layer, and their data indicated that many benthic invertebrate larvae were being swept offshore during upwelling. However, since they sampled only within the Ekman layer, they did not consider larvae that may have remained below the Ekman layer and outside the effects of Ekman transport. This is an important factor in the counter-argument to the theory of upwelling as a determinant of larval recruitment.

This theory not only attempted to explain highly variable recruitment events in upwelling systems, but also the difference between intertidal communities in Oregon and California. In Oregon, upwelling is relatively weak and larval recruitment high, and the main limiting factor for organisms is competition for space. In California, upwelling is relatively strong and larval recruitment is low, and the main factor determining species composition is larval supply (Roughgarden et al. 1988, Connolly et al. 2001).

Connolly et al. (2001) measured recruitment of the intertidal barnacles *Balanus* and *Chthamalus* and the mussel *Mytilus* (*M. trossulus* and *M. californianus* combined in analysis) along the coast from northern Oregon to central California and found that recruitment was up to two orders of magnitude higher in northern and central Oregon than in northern and central California. Upwelling is much weaker to the north of Cape Blanco, Oregon than to the south, and Connolly et al. (2001) hypothesized that in the north larvae were not carried as far offshore, thereby allowing them a higher chance of settlement.

The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) has been operating since 1999 and consists of marine researchers from Oregon State University, Stanford, University of California Santa Cruz, and University of California Santa Barbara. PISCO contains many of the original researchers of the model proposed by Roughgarden et al. (1988) and is a strong proponent of this hypothesis. PISCO research on the effect of upwelling on recruitment primarily focuses on relating oceanographic conditions to settlement rates, but does not typically measure larval supply onshore through oceanographic larval sampling (e.g. Connolly et al. 2001, Broitman et al. 2005, 2008, Dudas et al. 2009). For example, Dudas et al. (2009) measured barnacle recruitment in Oregon and found that recruitment increased with frequency of relaxation events over the season.

The theory that upwelling events limit larval recruitment has the potential to explain highly variable settlement patterns in upwelling systems. However, in recent years oceanographers have repeatedly found that this is not the case for all species of larvae.

Shanks et al. (2003) tested the theory by sampling larval benthic invertebrates during upwelling off North Carolina. They found that many larvae remained within 5 km of the shore during upwelling, while some larvae acted more like passive particles and were swept offshore. Additionally, both groups of larvae became concentrated in areas of vertical upwelling currents, likely by swimming downward against these currents. Shanks et al. (2002) sampled the same site during a downwelling event. Again, some species of larvae did not behave as passive particles tied to the movements of a water mass, and became concentrated in areas with vertical currents. Other species of larvae did act as passive particles. Species that were more intertidally restricted were found closer to shore than those that had a wider subtidal range, indicating that the larval distribution was not random, but rather specific to life-history traits. This complements the work of Grosberg (1982), who found that the vertical distribution of *Balanus* larvae matched the vertical distribution of adults.

Shanks and Brink (2005) sampled the North Carolina site yet again during a cycle that shifted from upwelling to downwelling to upwelling again and looked specifically at clam larvae, which are small, ciliated slow-swimmers and would be the least capable of swimming against a current. Some larvae remained within 5 km of shore regardless of upwelling or downwelling conditions. Others stayed below the thermocline, which caused them to be pushed offshore during downwelling and brought back to shore during upwelling, opposite what the hypothesis predicts. Poulin et al. (2002) found that gastropod larvae remained nearshore regardless of upwelling or downwelling.

Ample evidence of larval retention during upwelling events has also been documented on the west coast. Shanks and Shearman (2009) examined larvae from a wide variety of taxa including barnacles, crabs, and mussels and found that upwelling and downwelling events did not affect the average distance offshore. Most larvae remained within 5 km of the shore consistently. Only *Balanus nubilus* cyprids, the latest larval stage of a subtidal barnacle, were found farther offshore during upwelling. Due to the distribution of adult *B. nubilus*, this would not inhibit the recruitment of the species (Shanks and Shearman 2009).

In a similar study at Bodega Bay and Point Reyes, one of the strongest upwelling areas in California, Morgan et al. (2009*b*) showed that 45 species of nearshore crustacean larvae remained consistently within 6 km of the shore, regardless of upwelling or downwelling. Most larvae remained nearshore throughout development, but some species exhibited different distributions with larval stage. This age stratification indicates that larvae can regulate their horizontal position over time.

Morgan et al. (2009*a*) tested the theory that upwelling inhibits larval settlement by comparing 5 years of recruitment data to upwelling data and found that in most species, upwelling was not a good predictor of recruitment patterns. Finally, if upwelling limits recruitment then protected embayments with lighter winds should have more larvae than open coasts that experience strong upwelling events. Morgan and Fisher (2010) found that this is not the case, and that the larvae of 19 out of 20 nearshore crustacean species were equally abundant on open coasts, if not more so.

These studies show that while upwelling can push larvae offshore and limit recruitment, this effect varies among species and the effect cannot be assumed for any

species that has not been explicitly studied. Roughgarden et al. (1988) generalized about all intertidal benthic invertebrate larvae from one species and one larval stage. Additionally, as Shanks and Brink (2005) noted, the samples for the Roughgarden et al. study were no closer than 8 km from shore, whereas the studies just discussed found highest larval concentrations within 5 to 6 km of shore. It is clear that some larvae avoid being pushed offshore by upwelling, and there is evidence that they may do so by regulating their vertical position in the water column.

In two studies, larvae became concentrated in areas with vertical currents (Shanks et al. 2002, 2003). This indicates that the larvae were likely swimming against those currents, causing a gradual buildup of organisms in the area. Additionally, larvae avoided the nearshore surface region, thereby avoiding the shallow area of Ekman transport (Shanks and Brink 2005, Morgan et al. 2009*b*, Shanks and Shearman 2009, Morgan and Fisher 2010). Thus, by regulating their vertical position in the water column, larvae are able to avoid being swept offshore. The larvae of many benthic intertidal invertebrates are known to regulate their vertical position and even undergo vertical migrations (Mileikovsky 1973). Additionally, while horizontal currents produced by upwelling are far too rapid for larvae to swim against, the slow-moving vertical currents are slower than most larval swimming speeds (Mileikovsky 1973, Huyer 1983). A schematic of larvae maintaining a preferred depth in the face of upwelling and downwelling is illustrated by Shanks and Brink (2005).

This model of larval distribution during upwelling and downwelling accounts for both physical and biological factors and can explain the distributions of all the taxa studied. The vertical position of larvae and other zooplankton during upwelling events

ultimately determines their horizontal position due to layered currents. Differential vertical distribution at different larval stages can account for horizontal differences in larval stages (Morgan and Fisher 2010), and given that nearshore species tend to have more nearshore larval retention than offshore species (Shanks and Eckert 2005), vertical positioning may be an evolved trait that helps coastal species to maintain their adult populations.

While the larvae of benthic invertebrates, or meroplankton, have been studied because of the importance of larval retention for recruitment, holoplankton, or organisms that carry out their entire life cycle in the plankton, have also been shown to have interesting distributions during upwelling and downwelling events. Peterson et al. (1979) found that the five species of copepods that make up most of the summer zooplankton biomass in Oregon have vertical distributions that counteract the effects of upwelling currents. Most meroplankton and holoplankton avoided the upper 5 m of the water column nearshore and were not swept offshore during upwelling events. Additionally, different copepods had specific horizontal distributions depending on their stage of development and reproduction. Peterson et al. (1979) suggested that copepods use vertical position to ride different horizontal currents onshore and offshore at the appropriate times in their life cycles, but noted that since the species have such wide geographical distributions it would be presumptous to assume that this is a special evolutionary adaptation to Oregon seasonal upwelling conditions.

The consequences of upwelling and downwelling for zooplankton are a current and ongoing subject of research in biological oceanography and marine ecology. Less is known about the effects of upwelling and downwelling on holoplanktonic organisms

such as cladocerans. The purpose of the present study was to examine the distribution of marine cladocerans during upwelling and downwelling or relaxation events off Oregon.

Marine Cladocera

Cladocerans are small aquatic crustaceans. While there are about 600 extant species of cladocerans, most inhabit fresh or brackish waters and only eight are categorized as marine species (Egloff et al. 1997, Durbin et al. 2008). Of these eight species, seven are in the order Onchopoda and family Podonidae. The two cladocerans identified off the Oregon coast were the podonids *Podon leuckarti* Sars, 1862 and *Evadne nordmanni* Lovén, 1836.

Marine Cladocera are cosmopolitan organisms, meaning that a single species is found all over the world rather than localized to a particular region (Baker 1938). *Evadne nordmanni* and *Podon leuckarti* are morphologically similar around the world, although genetic studies have revealed geographically distinct genetic differences that indicate that populations have been present around the globe for millions of years (Gieskes 1971, Durbin et al. 2008).

Both *Evadne* and *Podon* are omnivorous predators that use their thoracic appendages for prey capture and feed on other planktonic organisms such as microalgae (dinoflagellates and diatoms) and invertebrates (tintinnid ciliates, copepods, naupliar larvae, and rotifers) (Bainbridge 1958, Egloff et al. 1997, Rivier 1998). *Evadne* can consume larger particles than *Podon*, but is a slower swimmer due to smaller second

antennae (the locomotory structures) and may be restricted to less mobile prey (Katechakis and Stibor 2004).

Evadne nordmanni is primarily neritic worldwide, meaning it lives in the coastal area over the continental shelf, but the species is also found in bays and other mixed waters (Frolander et al. 1973, Egloff et al. 1997). *Evadne nordmanni* also occurs in the open ocean in some areas, and other species of *Evadne* have been found more than 1500 km offshore (Bainbridge 1958, Gieskes 1971, Longhurst and Seibert 1972). In Monterey, California *E. nordmanni* was found most abundantly in temperatures between 12 and 14°C, but it can withstand wide ranges of temperatures and salinities (Baker 1938, Gieskes 1971). *Podon leuckarti* is in many areas exclusively neritic, but occurs in bays in Oregon (Gieskes 1971, Frolander et al. 1973, Viñas et al. 2007). In the Atlantic Ocean, it is most abundant at 12 to 13°C, but has been observed at temperatures of 6.5°C (Gieskes 1971).

In temperate regions, such as Oregon, podonids tend to appear in the spring, peak in abundance during the summer, and then disappear in the fall (Frolander et al. 1973, Rivier 1998). However, seasonality varies in different regions and sometimes cladocerans can be present during different seasons or year-round (Baker 1938, Komazawa and Endo 2002, Buyukates and Inanmaz 2009). Marine cladocerans overwinter as resting eggs, and Komazawa and Endo (2002) found that while *E. nordmanni* resting eggs are capable of hatching year-round and in a wide variety of temperature and salinity conditions, colder temperatures cause them to have longer incubation periods.

Cladocerans have a complex life cycle that alternates between asexual parthenogenic and sexual gamogenic reproduction. Parthenogenic females are generally produced during rising population abundance and throughout the season, while males and gamogenic females appear primarily when populations decline and conditions become unfavorable for growth. In the freshwater cladoceran *Daphnia magna*, decreased daylight, a decrease in food availability, and chemically mediated crowding all interacted to cue sexual reproduction (Kleiven et al. 1992). The environmental cues that cause sexual individuals to be produced in marine podonids are not known (Egloff et al. 1997). Parthenogenic podonids are reported to be able to switch to gamogenesis, but this has not been specifically verified for *E. nordmanni* or *P. leuckarti* (Rivier 1998).

Parthenogenesis occurs when parthenogenic females release diploid eggs into their brood pouches that develop directly into embryos, and is the fastest form of reproduction (Rivier 1998). Gamogenic reproduction occurs when a gamogenic female mates with a male, fertilizing her haploid eggs. These embryos halt in early development and form resting eggs that can withstand harsh conditions (Egloff et al. 1997). After the production of benthic resting eggs, the female generally dies. The resting eggs sink to the bottom and eventually hatch into parthenogenic females that can rapidly start a new population (Gieskes 1971, Egloff et al. 1997). Additionally, the highly durable resting eggs can pass through the digestive systems of predators unharmed, allowing podonids to be dispersed by organisms that consume them (Rivier 1998).

Podonids undergo direct development within the maternal brood pouch, which means that they are released from their mother with an adult morphology and do not have larval stages (Egloff et al. 1997, Rivier 1998). Additionally, they exhibit paedogenesis, in which embryos start developing in parthenogenic females before the females are released from their own mothers brood pouch (Egloff et al. 1997, Komazawa and Endo 2002). Embryonic development takes longer in cooler environments; *E. nordmanni* embryos take more than six days to develop at 4°C but only 3.4 days at 18°C (Rivier 1998). The young of parthenogenic podonids are released only during molting because the brood pouch is completely closed to the external world (Bryan 1979, Rivier 1998).

Morphological distinctions can be identified to classify podonids as parthenogenic female, gamogenic female, or male. Males tend to be less voluminous than females. They have reduced exoskeletal valves with no brood pouch inside, a pair of compact testes that are visible through the exoskeleton on either side of the intestine, and a pair of penes posterior to the last thoracic appendages. Males also have a hook on each of the first thoracic limbs, likely for gripping the female during copulation (Egloff et al. 1997, Rivier 1998). Females have paired ovaries that are also located on either side of the intestine, but are oblong (Rivier 1998). Parthenogenic females have large brood pouches that are completely closed to the external environment, while gamogenic females have a vagina that connects the brood pouch to the external world and is used in copulation (Egloff et al. 1997).

Because gender and reproductive stage affect the size and morphology of podonids, they can result in different regulatory behaviors. *Evadne nordmanni* and other

related species have been observed to release young only during the night, likely to avoid visual predation, as the mature young have large, darkly pigmented eyes that would be easily visible to predators when concentrated in a brood pouch (Bryan 1979, Onbé 2002). Parthenogenic *Evadne tergestina* do not carry embryos with pigmented eyes except at night when they are released, which is also likely a defense against visual predation (Mullin and Onbé 1992). Newly released young are thought to remain at the surface during the day, while older individuals sink deeper (Rivier 1998).

Podonids are known to exhibit vertical migrations, meaning that they rise up toward the surface and descend into the depths alternately. Many come to the surface at night and descend during the day (Rivier 1998). Saito and Hattori (2000) found that *P. leuckarti* females with advanced resting eggs stayed exclusively near the bottom during the day, while all other reproductive stages were found in layers both near the bottom and near the surface. During night, females with advanced resting eggs dispersed throughout the water column. This is hypothesized to be a defensive behavior because resting eggs are darkly pigmented and may be easy for predators to see in illuminated surface regions (Saito and Hattori 2000). Females of the freshwater cladoceran *Daphnia* are consumed by predators more when they have a darkly pigmented resting egg than when they have a lighter one or none at all (Mellors 1975). These are examples of how reproductive stage can impact selective pressures and behavior, particularly vertical distribution.

As previously discussed, the vertical distribution of zooplankton is important for determining eventual cross-shelf distribution in upwelling systems. Cladocerans are generally found to be most concentrated in the upper 20 m of the water column,

although they can be found down to depths of 100 m (Gieskes 1971, Longhurst and Seibert 1972, Egloff et al. 1997, Rivier 1998). Bosh and Taylor (1973*b*) found that the estuarine cladoceran *Podon polyphemoides* exhibits a diurnal vertical migration in which it is found near the surface where net non-tidal flow is out of the estuary during the day, and sinks deeper where net non-tidal flow is into the estuary at night. This vertical pattern causes it to remain within the estuary, since the net flows balance one another.

Peterson et al. (1979) identified and counted *Evadne nordmanni* and *Podon leuckarti* off the coast near Newport, Oregon and found that they generally stayed within 5 km of the shore regardless of upwelling or downwelling events. Cladoceran data was not included in the paper, as the study was focused on copepod distribution, but their findings indicate that cladocerans may exhibit distribution patterns that differ from those expected from passive particles. Meyers (1975) noted the presence of *E. nordmanni* and *P. leuckarti* in samples off the Oregon coast during upwelling events, but abundances were low and their distribution was not discussed. The present study was conducted to determine the distribution of *E. nordmanni* and *P. leuckarti* during upwelling events off the Oregon coast and to see if different reproductive stages are distributed differently. Additionally, cladoceran reproductive characteristics in Oregon were investigated.

I hypothesized that marine cladocerans would remain nearshore regardless of upwelling or downwelling events off the central Oregon coast because this has been the tendency for meroplankton and copepods, and for cladocerans north of Newport, Oregon (Peterson et al. 1979, Shanks and Shearman 2009). I also hypothesized that

different reproductive stages would be distributed differently, as different stages can have different vertical migration patterns, and vertical position determines susceptibility to stratified horizontal currents (Bryan 1979, Saito and Hattori 2000, Onbé 2002).

I predicted that parthenogenic females with more advanced embryos would be larger than those with less developed embryos, since the release of young is accompanied by molting and young embryos require less space (Rivier 1998, Onbé 2002). If different stages distribute differently and there is a correlation between size and stage, then different sizes should distribute differently as well. Finally, I examined the fecundity of parthenogenic females, hypothesizing that it would be similar to fecundity in other temperate regions.

METHODS

Sampling

Oceanographic sampling was conducted by Alan Shanks (Shanks and Shearman 2009) on four dates in the summer of 2007. They used satellite images of sea surface temperature that were taken from NOAA Polar Orbiting satellites and enhanced with 1 km high resolution by Terrafin (www.terrafin.com) to select sampling dates during upwelling and downwelling or relaxation events. Upwelling was occurring on 27 June and 14 August 2007 and relaxation or weak downwelling was occurring on 3 and 18 July 2007. A transect starting 6 km north of the entrance to Coos Bay, Oregon and running roughly perpendicular to the shore was sampled on each date. The transect consisted of seven stations that started 0.5 to 0.7 km offshore and ended about 28 km offshore. Station locations and depths of zooplankton tows are given in Table 1.

Station depth intervals were selected based on the depth of the thermocline at each station so that sampling on the four dates was consistent with respect to vertical strata of the water column. At the most shallow nearshore stations three to four depth intervals were sampled, representing always the neuston (the surface region, defined here as 0.2 m deep) and above and below the thermocline, and additionally within the thermocline at slightly deeper stations. At stations with a bottom depth >70 m, five depth intervals were sampled, representing the neuston, mixed layer above the thermocline, inside the thermocline, and two samples below the thermocline. Sampling was also consistent in the time each transect was done in relationship to sunrise. The most offshore station was always sampled first, at least an hour after sunrise, to keep the relative time of station samples consistent across dates, and the transect was completed

during daylight. This ensured that the effects of diel vertical migration, in which organisms alter their position in the water column during day and night, were not a variable among sample dates. This was important for the study of marine cladocerans, which have been shown to exhibit diel vertical migration (Saito and Hattori 2000).

Zooplankton sampling was done from a 13-m research boat using a Manta net with 330-µm mesh for the neuston samples and a Tucker Trawl with a 205-µm net for all other samples. Messenger-activated releases on the Tucker trawl were used to control the depth interval at which the net opened, and flow meters in the nets provided data on the volume of seawater filtered for each sample. Samples were preserved with buffered formalin in the field. At each station, a SeaBird Model 19 CTD was deployed to gather data on the conductivity, temperature, and depth of water. These physical data were used to support the classification of each date as an upwelling or relaxation event.

Shanks and Shearman (2009) analyzed the oceanographic data collected by the CTD and the available satellite images. These data demonstrated that conditions on 27 June and 14 August 2007 were characteristic of upwelling events, and conditions on 3 and 18 July 2007 were characteristic of relaxation or weak downwelling events.

Lab work

Samples were rinsed thoroughly with freshwater in a 149-µm sieve, added to a beaker, and diluted with approximately 150-200 mL freshwater. Each sample was weighed on a digital scale to determine the total volume of the sample, using the following approximation: 1g=1mL. Subsamples were taken by stirring vigorously to ensure homogeneity and using a 5 mL Stemple pipette twice to transfer a 10 mL

subsample to a counting tray. Cladocerans in subsamples were counted on an inverted compound scope with 40× magnification, and 100× magnification was used for counting embryos and verifying sex and stage. The inverted scope provided a very clear image of cladoceran morphological details. Some of the samples from farther offshore were counted under a dissecting microscope in order to get a better view of some larger veligers I was also counting, and it was more difficult to count cladoceran embryos in these samples.

Podon leuckarti and *Evadne nordmanni* were identified using the exopodite setae formulae and other morphological and distributional characteristics found in Baker (1938), Rivier (1998), and Durbin et al. (2008), as well as a personal correspondence with Bill Peterson (NOAA at Hatfield Marine Science Center, OR), who has experience with cladoceran identification. Both species of cladocerans were observed in a lateral position and measured in two perpendicular body axes under 40× magnification using an ocular micrometer (one ocular unit=11.6μm) (Figure 1). Sex was determined and females were assigned a reproductive stage based on the developmental state of the embryos (Table 2). The number of embryos present in the brood pouch was also counted. If any of these measurements could not be performed on an individual due to damage or lack of clarity, a "U" for undetermined was written in that measurement category for that individual, and it was not considered in the final data analysis. After counting all samples for two of the sample dates (14 August and 3 July 2007), I decided to further distinguish the female reproductive stages for the remaining two sample dates (27 June and 18 July 2007), as indicated in Table 2. In *E. nordmanni*, the percentage of the valve space occupied by the brood pouch was

estimated (0-25%, 25-50%, 50-75%, 75-100%). This approximation was made because brood pouches and valves were variable in shape, and no consistent form of precise measurement could be recorded. The percentage assigned was the upper limit of the range it fell into (for example, if the valves appeared to be about 35% filled, the number recorded would be 50%). This was not done in *P. leuckarti* because in this species the brood pouch generally filled the valves completely, while in *E. nordmanni* the pouch initially filled very little of the valves but grew to fill them completely.

In each sample, I attempted to collect data on these classifications and measurements for 50 individuals of each species, and continue counting subsamples of 10 mL until I had observed 100 of each species. In some samples, cladocerans were too sparse to reach this goal.

Data analysis

Percentage of the sample counted, flow meter readings, and counting data were used to calculate the concentration of organisms per cubic meter of seawater at each station and depth interval. Contour plots of cladoceran concentration for each date were generated with the software IGOR Pro 6.1 (Figures 2 and 4). The average distance offshore for each species was calculated by multiplying the concentration at each depth interval by the magnitude of the interval and summing these at each station along the transect to isolate the horizontal component of concentration. These numbers were used to find the mean distance offshore on each sample date. Daily upwelling indices were acquired from the Pacific Fisheries Environmental Laboratory website (www.pfeg.noaa.gov) and the indices five days prior to each sampling date were

summed by Shanks and Shearman (2009). The five-day sum of the upwelling indices was plotted against average distance offshore to determine whether upwelling strength affected distribution (Figure 3). To examine differences in the spatial distribution of reproductive stages, contour plots of distribution were generated for each reproductive stage (Figures 5-6, 10-11). Sex frequency diagrams (Figures 7-9, 12-14) and size frequency diagrams (Figures 15-20) were constructed to examine the reproductive composition and size composition at each station and depth interval. Frequency diagrams were only constructed for stations 1 to 3 where cladocerans were abundant, and at depth intervals with ten or more individuals counted ($n \geq 10$).

Individual measurements of cladoceran size and reproductive data were then compiled from all of the stations and sample dates. The average size of each reproductive stage was plotted for each species (Figures 21-22), and the number of embryos (Figure 23) and percentage of the valves filled by the brood pouch (Figure 24) for each parthenogenic stage were plotted for *E. nordmanni.* The average numbers of embryos for parthenogenic females of both *P. leuckarti* and *E. nordmanni* were calculated.

All statistical analyses were done in Systat ver. 10. Only stations 1 through 3, where the greatest concentrations of cladocerans were found, were used because at more offshore stations cladoceran counts were too low to analyze statistically. I did 4-way nested ANOVAs (dates nested within oceanographic condition and depths nested within stations) to analyze the effects of oceanographic condition (upwelling or relaxation), sampling date, station, and depth on species and stage distributions. I used Likelihood

Ratio G-tests to analyze the differences in reproductive stages and size classes by date, depth, oceanographic condition, and station, respectively.

RESULTS

Horizontal and vertical distribution

Podon leuckarti

Contour plots of *Podon leuckarti* distribution depicted both a nearshore concentration center and a sparse offshore concentration center, and indicated that the nearshore center of concentration remains within 12 km of shore regardless of upwelling or relaxation. During upwelling (Figure 2), *P. leuckarti* did not exhibit signs of being pushed offshore with Ekman surface transport. On 27 June 2007 *P. leuckarti* was most concentrated 5 to 15 m deep and within 5 km of shore and was not found beyond 10 km offshore. On 14 August 2007, *P. leuckarti* concentrations were very low ($<10/m^3$), but were greatest from just below the surface to 10 m deep and 5 km offshore, and this nearshore group was constrained within 12 km of shore (Figure 2). Low concentrations were also found 25 to 28 km from shore at 30 to 40 m depth and this concentration center on the contour plot was from individuals ($2/m^3$) caught at a single station, about 28 km offshore and 25 to 45 m deep. Low concentrations ($0.52/m^3$) were also caught 24 km offshore at 60 to 70 m deep, but this does not appear on the contour plot because the graph depth was truncated for consistency between dates.

The nearshore concentration of *Podon leuckarti* was not found closer to shore during relaxation events than upwelling events. On 3 July, *P. leuckarti* was most concentrated 10 to 30 m deep and within 5 km of shore although low numbers ($\leq 3/m^3$) were found out to 12 km offshore. Nearshore, *P. leuckarti* occurred in high concentration as deep as 50 m, which was deeper than any of the other sampling dates. Additionally, very low ($\leq 3.1/m^3$) concentrations appeared 30 to 40 m deep over 25 km

offshore. This offshore concentration center came from two samples ranging 15 to 40 m deep at the most offshore station. On 18 July, *P. leuckarti* was most concentrated 10 to 25 m deep and within 5 km of shore, but was found in low densities out to 10 km offshore. At station 6 (25 km offshore) extremely low abundances ($<0.01/m^3$) were detected.

The nearshore concentration of *P. leuckarti* occurred in the same horizontal region on all four dates, and the offshore center of concentration occurred on one upwelling and one relaxation date. A plot of *P. leuckarti* average distance offshore against the 5-day sum of the upwelling indices prior to sampling (Figure 3) indicates that *P. leuckarti* generally averaged within 3 km of shore regardless of upwelling or relaxation. However, on 14 August 2007, the weaker of the two upwelling dates, *P. leuckarti* averaged 7.36 km offshore.

Podon leuckarti concentrations were transformed prior to statistical analysis, using the following transformation: ln(x+0.1). Then I did a 4-way nested ANOVA (dates nested within oceanographic conditions and depths nested within stations) and found that oceanographic conditions, date, station, and depth moderately accounted for the variance in *P. leuckarti* concentration ($R^2=0.678$). Oceanographic condition was not significant ($F=1.692$, $df=1$, $p=0.203$), but date ($F=5.433$, $df= 2$, $p=0.009$) and depth ($F=3.311$, $df=9$, $p=0.006$) were highly significant and station ($F=10.592$, $df=2$, $p<0.001$) was very highly significant.

Evadne nordmanni

Contour plots of *Evadne nordmanni* distribution depicted a nearshore concentration that was clustered near the surface or the bottom, and a deeper offshore concentration center, and did not appear to be affected by offshore surface transport during upwelling events. On 27 June 2007 (Figure 4), *E. nordmanni* was most concentrated within 5 km of shore and around 10 to 20 m deep. Low concentrations ($\leq 4/m^3$) were detected 15 to 25 km offshore at the deepest sampling depths (40 to 50 m), and a small portion ($1/m^3$) of this concentration center pushed upward and toward shore, as deep upwelling currents do. On 14 August 2007, *E. nordmanni* concentrations were extremely low ($\leq 3/m^3$). Highest concentrations were observed about 5 km offshore from 10 to 20 m deep and over 25 km offshore between 30 and 40 m deep. The offshore center of concentration resulted from one sample from the farthest offshore station (25-45 m deep) with a concentration of $3/m^3$.

During relaxation, the nearshore concentration of *E. nordmanni* was not pushed closer to shore. On 3 July, *E. nordmanni* was most concentrated within 5 km of shore and 10 to 20 m deep. There was also a less dense center of concentration ($<8/m^3$) 15 to 20 km offshore, 30 to 40 m deep. This more offshore concentration was the result of data from several samples. On 18 July, *E. nordmanni* was concentrated less than 5 km offshore and 10 to 20 m deep, but also had high concentrations 5 to 10 km offshore at the surface. No offshore concentration center was detected.

The average distance offshore of *Evadne nordmanni* was different during upwelling and relaxation events. A plot of *E. nordmanni* average distance offshore against the 5-day sum of the upwelling indices prior to sampling (Figure 3) indicates

that *E. nordmanni* occurred closer to shore during relaxation events and farther offshore during upwelling events.

Evadne nordmanni concentrations were transformed prior to analysis, using the following transformation: ln(x+0.1). Then I did a 4-way nested ANOVA (dates nested within oceanographic conditions and depths nested within stations) and found that oceanographic condition, date, station, and depth moderately accounted for the variance (R^2=0.636). Oceanographic condition was not significant (F=0.510, df=1, p=0.480), but depth (F=2.705, df=9, p=0.019) was significant, and station (F=6.419, df=2, p=0.005) and date (F=7.330, df=2, p=0.002) were highly significant.

Interestingly, *E. nordmanni* and *P. leuckarti* had similar spatial distribution patterns that included a nearshore concentration center and an offshore center, although for *E. nordmanni* the offshore center was more variable and larger. Additionally, the highest concentrations of both species occurred early in the summer on 27 June 2007, and on each subsequent date the total abundance decreased, until on 14 August 2007 both species had minimal concentrations. This appears to be a seasonal trend, but since only four dates throughout the summer were sampled no conclusions can be drawn about this pattern.

Sex and stage differences

Podon leuckarti

Parthenogenic *Podon leuckarti* in various stages of advancement did not show consistent differences in spatial distribution, although males tended to stay near the surface or the bottom nearshore, while parthenogenic females were more spread through

the water column. Gamogenic females were not analyzed due to the paucity of data. On 27 June 2007 (Figure 5), an upwelling date, PE and PA distributions closely resembled one another, and PAJ was similar but constrained slightly closer to shore. Males occurred in low concentrations ($<1/m^3$) and were found only in the upper 5 m of the water column within 5 km of the shore. On 14 August 2007 (Figure 5), an upwelling date, individual PEs were most concentrated about 5 km offshore between 0 and 15 m deep. PAs were most concentrated ($\leq 2/m^3$) less than 5 km offshore and 5 to 20 m deep, but some ($0.2/m^3$) were also found over 35 km offshore in the deepest samples (50 to 60 m). PAJ was not categorized on 14 August 2007 (this category was added after 3 July and 14 August had been counted). Males were found < 5 km from shore near the bottom in very low concentrations ($0.8/m^3$).

On 3 July 2007 (Figure 6), a relaxation date, PE and PA distributions closely resembled one another, with the center of concentration nearshore near the bottom but low concentrations extending out to 12 km. The PE center of concentration, however, was more nearshore and shallower (10 m deep) than that of PA (20 m deep). PAJs were not categorized on 3 July. Males occurred closer to the shore and near the bottom in much lower concentrations than females. Males were also found at low concentrations near the surface between 0 and 5 km offshore. Gamogenic *P. leuckarti* females were only caught on 3 July, and these were found at station 1, 0 to 6 m deep (n=2) and station 5, 40 to 70 m deep (n=1). On 18 July 2007 (Figure 6), a relaxation date, PE, PA, and PAJ distributions closely resembled one another, with highest concentrations around 20 m deep and very close to shore. Males, however, were concentrated nearshore at 30 m deep near the bottom, with a second center of concentration 0 to 10 m deep a few km

offshore. On both relaxation dates males had two centers of distribution, one at the surface, and another deeper against the bottom.

Podon leuckarti male, PE, and PA (including PAJ) concentrations were transformed prior to statistical analysis, using the following transformation: ln(x+0.1). Then I did 4-way nested ANOVAs (dates nested within oceanographic conditions and depths nested within stations). I found that oceanographic condition, date, station, and depth moderately accounted for the variance in male concentration (R^2=0.518). Oceanographic condition (F=1.037, df=1, p=0.311) and date (F=0.196, df=2, p=0.822) were not significant for male concentration, but depth (F=1.66, df=25, p=0.043) was significant and station (F=6.590, df=6, p<0.001) was very highly significant. The four factors accounted for much of the variance in PE concentrations (R^2=0.788). Oceanographic condition (F=2.376, df=1, p=0.127) was not significant for PE concentration, but date (F=4.898, df=2, p=0.010) was significant and station (F=42.669, df=6, p<0.001) and depth (F=3.032, df=25, p<0.001) were very highly significant. The four factors accounted for much of the variance in PA concentrations (R^2=0.722). Oceanographic condition (F=0.243, df=1, p=0.623) was not significant for PA concentrations, but date (F=4.295, df=2, p=0.017) was significant, depth (F=2.117, df=25, p=0.005) was highly significant, and station (F=29.907, df=6, p<0.001) was very highly significant.

Sex frequency diagrams for stations 1 to 3 at depths with n≥10 revealed a trend for parthenogenic females with early embryos to comprise larger proportions of the population nearshore, and those with advanced embryos to comprise larger proportions offshore. This trend, however, was not consistent across all sample dates. On 27 June

2007 (Figure 7), PE tended to make up the largest proportions of the more nearshore stations and the neuston samples, while PA tended to dominate farther offshore and in deeper samples, but this was by no means an absolute trend. This was also the only date that had a distinct male presence (n=12, 46.15%) compared to females at one station, but despite this no gamogenic females were detected. Males were found only in the neuston at stations 1 and 2. On 14 August 2007 *P. leuckarti* counts were very low (n=46), and reproductive stage frequency diagrams were not constructed.

On 3 July 2007 (Figure 8), PE and PA were the dominant stages in all samples, but did not have distinct vertical or horizontal trends that encompassed all samples. At station 1, PEs were dominant at all depth intervals, and decreased in proportion deeper in the water column. At stations 2 and 3, PE dominated at all depth intervals except the deepest. No males were found, but a gamogenic female (n=1) was caught at station 5, 40 to 60 m deep. On 18 July 2007 (Figure 9), PEs dominated at station 1 and PAs at stations 2 and 3. Males were caught at station 2 but nowhere else. On all four sampling dates, parthenogenic females dominated the population (n=1115, 96.04%); males (n=44, 3.79%) and gamogenic females (n=2, 0.002%) were rare.

A series of Likelihood Ratio G-tests indicated that the proportions of PE and PA at stations 1 to 3 varied significantly at different depths ($G=11.812$, $df=4$, $p=0.019$) and very highly significantly with different oceanographic conditions ($G=16.038$, $df=1$, $p<0.001$), dates ($G=59.416$, $df=3$, $p<0.001$), and stations ($G=63.552$, $df=2$, $p<0.001$).

Evadne nordmanni

Parthenogenic *Evadne nordmanni* in various stages of advancement did not show consistent differences in spatial distribution, and males and gamogenic females were not analyzed due to lack of data. All stages of parthenogenic females tended to stay near the surface or the bottom nearshore, often with a center of concentration at each. On 27 June 2007, an upwelling date, PERs occurred within 5 km of shore at less than 30 m deep (Figure 10). PEs were most concentrated nearshore near the bottom at about 10 m deep, and there were additional individuals 20 to 25 km offshore and 40 to 50 m deep. The distribution of PAs resembled that of PEs, but there was an additional dense concentration of PAs around 2.5 km offshore at the surface. PAJs were most abundant about 2.5 km offshore and 0 to 5 m from the surface. On 14 August 2007, an upwelling date, there was not sufficient *E. nordmanni* present to compare the distribution of reproductive stages (n=15).

On 3 July 2007 (Figure 11), a relaxation date, PEs and PAs had similar distributions, but the surface of the water column was occupied only by PEs. PEs were more concentrated than PAs. On 18 July, (Figure 11), a relaxation date, PERs, PEs, PAs, and PAJs all had similar distributions. Overall, there were only slight differences among the distribution of females with embryos at different stages of advancement, but there were no overall trends suggesting consistent spatial distributional differences in *E. nordmanni*.

Evadne nordmanni PE (with PER included) and PA (with PAJ included) were transformed prior to statistical analysis, using the following transformation: $\ln(x+0.1)$. Then I did a 4-way nested ANOVA (dates nested within oceanographic conditions and

depths nested within stations). I found that oceanographic condition, date, station, and depth accounted for much of the variance in PE concentrations (R^2=0.791). Oceanographic condition (F=3.481, df=1, p=0.067) was not significant for PE concentrations, but date (F=4.649, df=1, p=0.035) was significant and both station (F=24.267, df=6, p<0.001) and depth (F=3.306, df=25, p<0.001) were very highly significant. The four factors accounted for much of the variance in PA concentrations (R^2=0.736). Date (F=0.022, df=1, p=0.883) was not significant for PA concentrations, but oceanographic condition (F=7.049, df=1, p=0.010) and depth (F=2.046, df=25, p=0.012) were significant, and station (F=18.909, df=1, p<0.001) was very highly significant.

Sex frequency diagrams for stations 1 to 3 at depths with n≥10 revealed a trend for parthenogenic *E. nordmanni* with early embryos to comprise larger proportions of the population nearshore, and those with advanced embryos to comprise larger proportions offshore. This trend, however, was not consistent across all sample dates. On 27 June 2007 (Figure 12), PERs represented a small percentage (<13%) of the individuals at the stations where they were present, and PEs, PAs, and PAJs constituted large proportions of the population at many of the stations. PERs and PEs dominated the composition at station 1, while PAs and PAJs dominated at stations 2 and 3. No males or gamogenic females were caught. On 14 August 2007, there were insufficient individuals caught (n=15) to construct sex frequency diagrams.

On 3 July 2007 (Figure 13), PEs were the dominant stage at stations 1 and 2, while PAs were more dominant at station 3 below the neuston. Males and gamogenic females were not caught. On 18 July 2007 (Figure 14), PEs were the most dominant

stage at station 1, while PAs and PAJs were dominant at stations 2 and 3. Males were extremely rare, and found only at station 3 in the neuston (n=1, 2.27%).

Only 3 gamogenic females were caught: on 27 June 2007 at station 1 in the neuston (n=1) and on 18 July 2007 at station 2 in the neuston (n=2). On all four sampling dates, parthenogenic females (n=768, 99.48%) dominated the *E. nordmanni* population; gamogenic females (n=3, 0.39%) and males (n=1, 0.13%) were rare.

A series of Likelihood Ratio G-tests indicated that the proportions of PE (including PER) and PA (including PAJ) varied significantly with different depths ($G=11.231$, $df=4$, $p=0.024$) and oceanographic conditions ($G=11.942$, $df=1$, $p=0.001$), and very highly significantly with different sample dates ($G=77.911$, $df=3$, $p<0.001$) and stations ($G=68.433$, $df=2$, $p<0.001$).

Size frequency distribution

Podon leuckarti

Size frequency distributions at stations 1 to 3 at depths where $n\geq10$ displayed trends similar to sex frequency distribution. Although intermediate sizes were generally dominant, small individuals tended to occur in larger proportions closer to shore, just as parthenogenic females with early embryos did, and large individuals occurred in larger proportions offshore, as parthenogenic females with advanced embryos did. Size frequency distributions for *P. leuckarti* on 27 June 2007 (Figure 15) indicate that small individuals were found in higher proportions nearshore at station 1, and large individuals offshore at stations 2 to 3. At all stations individuals of intermediate size were most common. On 14 August 2007, not enough individuals (n=46) were caught to

make stage frequency diagrams. On 3 July 2007 (Figure 16), small individuals were found closer to shore in the neuston, in similar proportions at all three stations at the shallowest depth interval, and in higher proportions farther offshore in the second depth interval from the surface. Large individuals were uncommon at all stations (<15%). On 18 July 2007 (Figure 17), intermediate sizes dominated the samples, but the smallest individuals were found nearshore and the largest offshore.

A series of Likelihood Ratio G-tests indicated that the frequency of different size classes differed very highly significantly on different dates ($G=64.453$, $df=6$, $p<0.001$), depths ($G=49.600$, $df=8$, $p<0.001$), oceanographic conditions ($G=46.075$, $df=2.00$, $p<0.001$), and stations ($G=25.852$, $df=4$, $p<0.001$).

Evadne nordmanni

Size frequency distributions at stations 1 to 3 at depths where $n\geq10$ displayed trends similar to sex frequency distribution. Small individuals tended to comprise larger proportions close to shore, just as parthenogenic females with early embryos did. On 27 June 2007 (Figure 18), small individuals were found in high proportions nearshore. At station 1, small individuals constituted large proportions of all three depth intervals. At station 2 small individuals were found mostly in the deepest sample, and at station 3 in the neuston. Large individuals were not present at station 1 and were found in low proportions at stations 2 and 3. The low number of *E. nordmanni* caught (n=15) on 14 August 2007 prevented an analysis of size distributions. On 3 July 2007 (Figure 19), small individuals appeared in proportions roughly equal to or greater than those of intermediate individuals at all stations and depths. In the neuston, the proportion of

small individuals was comparable to that of intermediate individuals at all 3 stations, but at deeper intervals smaller individuals were found in higher proportions nearshore. Large individuals did not appear at any stations. On 18 July 2007 (Figure 20), small individuals were found in greater proportions nearshore, and large individuals were rare.

A series of Likelihood Ratio G-tests indicated that the frequency of different size classes varied highly significantly at different depths ($G=21.083$, $df=8$, $p=0.007$), and very highly significantly during different oceanographic conditions ($G=20.946$, $df=2$, $p<0.001$) and at different stations ($G=32.979$, $df=2$, $p<0.001$).

Reproductive stages and fecundity

Podon leuckarti

Female *P. leuckarti* with more advanced embryos tended to be larger than females with less developed embryos (Figure 21). Unidentified individuals (U) and PEs were the smallest stages. Males were the next smallest. Very few gamogenic females were encountered and the 95% confidence interval spanned the entire range of *P. leuckarti* sizes. PAs were the next largest stage, and PAJs were the largest. Many of the individuals with unidentified stages were very small and it was difficult to see details like penes or embryos, and accordingly it is the category with the smallest mean area. It is possible that some of these individuals with unidentified stages were males. The average size of the individuals identified only as parthenogenic (P) were close in size to the PAs.

Counting embryos in *P. leuckarti* proved to be very difficult because the brood pouch became very thick and therefore dark as the embryos developed. Additionally, the brood pouch was semi-spherical in shape, so that any viewpoint resulted in overlapping embryos, making them difficult to distinguish from one another. Embryos were only distinguishable in the earliest stages, so early parthenogenic females provided most of the data collected on embryos. Parthenogenic *P. leuckarti* had between 3 and 12 embryos although a brood of 12 was found in only one individual, and the next highest count was 9. The mean number of embryos with a 95% confidence interval was 5.42±0.37 (n=83). Only two gamogenic females were found in all of the samples, but these appeared to have a single resting egg.

Evadne nordmanni

The mean area of parthenogenic *E. nordmanni* increased with the advancement of the embryos (Figure 22). PERs and PEs were similar in size and were the smallest stages. Gamogenic females (G) were the next smallest stage, but had a large confidence interval because few (n=3) were encountered. PAs were the next largest, and PAJs had the largest mean area. P and U appear to be closest in size to the earlier parthenogenic stages, so many of the unclassifiable individuals may have belonged to these groupings.

Because *E. nordmanni* are relatively planar and embryos in the brood pouch rarely overlapped, counting embryos in *E. nordmanni* was simpler than *P. leuckarti*. Parthenogenic *E. nordmanni* had 3 to 21 embryos. The mean number of embryos with a 95% confidence interval was 10.21±0.247 (n=459). Only 3 gamogenic females were found, of which one individual had a single resting egg and the other two had two

resting eggs each. One of the resting eggs was measured and found to be 139.2 μm in diameter.

The number of embryos in parthenogenic *E. nordmanni* decreased slightly with embryonic advancement (Figure 23). The percentage of the valve space occupied by the brood pouch increased with embryo advancement, with PER embryos occupying the smallest portion of the valves and PAJ embryos occupying most of the valve space (Figure 24). This indicates that the embryos grow to fill the valve space completely before being released.

In *E. nordmanni*, the fully developed embryos that are ready to be released are moved into the valve space and a new brood of embryos appears in the brood pouch before the advanced embryos are released. The younger brood always consisted of small, perfectly round early embryos when two broods were present. The younger brood generally had more embryos than the advanced brood. One mother had 6 mature embryos and at least 6 young embryos. Another had 7 mature embryos and 17 young embryos. Yet another had 9 mature embryos and 11 young embryos. Additionally, one of this mother's mature embryos had 8 embryos of its own.

It was often difficult to count the number of embryos in the brood pouch of an advanced embryo nearing release because they were very small and at times they were covered by other advanced embryos. However, on 27 June 2007 three advanced embryos were positioned so that their own broods could be definitively counted. One embryo from a brood of 9 had 8 of its own offspring. Two embryos from the same brood of 7 each had 5 of their own offspring. In another brood of 15 advanced embryos, two had 5 of their own offspring and one had 8. These data indicate that that the number

of embryos in a new juvenile is variable, and not all members of the same brood have the same number of embryos.

Male *E. nordmanni* were very rare on the four dates sampled (n=1). Most *E. nordmanni* were readily identified as parthenogenic females by the presence of embryos. However, when no embryos or resting egg were present, defining male characteristics like the penis were extremely difficult to identify because the thoracic appendages were densely clustered together and the penis is extremely small. The testes were visible and were the main indicator for males. However, it is possible that some of the "unclassified" *E. nordmanni* were males.

DISCUSSION

Cladoceran distribution during upwelling and relaxation

The Oregon coast experiences seasonal upwelling that brings nutrients to surface waters and fuels the growth of a diverse zooplankton community. Upwelling also transports surface waters offshore and has the potential to affect the distribution of coastal zooplankton (Peterson et al. 1979, Huyer 1983, Roughgarden et al. 1988, Farrell et al. 1991, Connolly et al. 2001). The distribution of the marine cladocerans *Podon leuckarti* and *Evadne nordmanni* was examined to determine whether they show signs of being pushed offshore by surface currents generated during upwelling events.

Physical data collected on 27 June and 14 August 2007 clearly indicated that upwelling was occurring on these days. The thermocline and halocline were bent upward to the surface nearshore, a band of cold water appeared near the coast in satellite images, and five-day sums of the upwelling indices were positive (Shanks and Shearman 2009). On 27 June 2007, the upwelling front was about 7 km offshore, and on 14 August 2007 about 10 km offshore. Physical data from 3 and 18 July 2007 indicated that these were relaxation or weak downwelling events. The thermocline and pycnocline were flattened out and more parallel to the surface, warm surface water was in contact with the coastline, and five-day sums of the upwelling indices were near zero. One of the sample dates representing relaxation (3 July) was only six days after a sample date representing upwelling (27 June), but physical characteristics of each date clearly distinguished them from one another oceanographically. Since the thermocline did not bend down and contact the bottom, there was no downwelling front (Shanks and Shearman 2009).

I tested the hypothesis that Ekman surface transport carries cladocerans offshore during upwelling and found no evidence to support this. Oceanographic condition, representing upwelling and relaxation in a 4-way ANOVA, was not significant in explaining variance in *P. leuckarti* concentrations ($p=0.203$) or *E. nordmanni* concentrations ($p=0.480$) nearshore at stations 1 to 3. Nearshore concentrations of *Podon leuckarti* were not pushed offshore during upwelling events (Figure 2). A nearshore group of *P. leuckarti* distributed within 12 km of shore and densest within 5 km of shore occurred on all four dates. This was primarily on the shoreward side of the upwelling fronts on the upwelling dates. The nearshore center of concentration was always deeper than 5 m, and thus below the Ekman layer within 10 km of shore (Peterson et al. 1979). However, *P. leuckarti* did not avoid the upper 5 m entirely and was often collected from the neuston, so an avoidance of the Ekman layer cannot entirely explain nearshore retention in this case, as it has been used to explain similar larval retention (e.g. Shanks and Shearman 2009).

The nearshore concentration center of *P. leuckarti* appeared slightly deeper on relaxation days than on upwelling days, and may have been shifted by vertical upwelling and downwelling currents. A sparse offshore (>25 km) center of concentration occurred on one upwelling (14 August 2007) and one relaxation (3 July 2007) date. Concentrations offshore were so low ($\leq 2/m^3$) that they may have been present on all four dates, but too sparse to be detected via our sampling techniques. Since the offshore concentration appeared in the same region during both upwelling and relaxation, it was not likely result of these conditions.

A plot of average distance offshore, calculated by determining the total density at each station and finding the mean distance offshore, against the five-day sum of the upwelling indices (Figure 3) indicates that *P. leuckarti* averaged within 3 km of shore during both relaxation events and the stronger upwelling event, when populations were relatively high. However, on 14 August 2007, the weaker upwelling event, *P. leuckarti* averaged 7.36 km offshore. This could be interpreted as *P. leuckarti* being pushed offshore by upwelling currents, but the contour plot of concentration (Figure 2) shows that they were not found in the surface region of Ekman transport as they would have been if upwelling currents were driving them offshore, but rather had a deep offshore center of concentration that was likely altering the average distance offshore. On 3 July 2007, one of the two dates with an offshore (>25 km) concentration of *P. leuckarti*, concentrations nearshore were three orders of magnitude greater than those offshore. Since *P. leuckarti* concentrations were low on 14 August 2007 and the nearshore concentration was the same order of magnitude as the offshore concentration, the average distance offshore was more impacted by the offshore concentration on 14 August 2007 than on 3 July 2007. Additionally, if upwelling were pushing *P. leuckarti* offshore we would expect to see a higher average distance offshore during the stronger upwelling event. Thus, considering all evidence, *P. leuckarti* does not appear to be pushed offshore by Ekman surface transport.

Evadne nordmanni distribution (Figure 4) was not pushed offshore by Ekman surface transport. During upwelling, *E. nordmanni* was concentrated primarily nearshore of the upwelling front within 10 km of shore except for a deep center of concentration that occurred farther than 20 km offshore on both dates. During

relaxation, the nearshore concentration of *E. nordmanni* was found out to 10 km on 3 July 2007 and 15 km on 18 July 2007, the farthest expansion of the nearshore group. This is opposite the trend we would expect if surface currents were pushing organisms offshore during upwelling and onshore during relaxation. Although it maintained a nearshore concentration during upwelling, *E. nordmanni* was not consistently found below the upper 5 m where of Ekman transport is strongest. During upwelling, densest concentrations were below the region of Ekman transport, but *E. nordmanni* still appeared in the neuston and surface region in low concentration, particularly on 27 June 2007.

A plot of average distance offshore against the five-day sum of the upwelling indices (Figure 3) indicates that *E. nordmanni* was found farther offshore during upwelling events than relaxation events. This alone could be interpreted as *E. nordmanni* being pulled offshore by upwelling currents and pushed back onshore during relaxation. If this were the case, we would expect the strongest upwelling event to yield the farthest average distance offshore. However, the distance offshore was greatest on 14 August 2007, the weaker of the upwelling dates. Additionally, the contour plots of concentration (Figure 4) show that the nearshore concentration of *E. nordmanni* did not move offshore during upwelling, but rather a deep offshore center of concentration appeared. This offshore group, not Ekman surface transport, is what is increasing the average distance offshore on upwelling dates.

The offshore group may be a concentration of offshore *E. nordmanni* that was pulled toward shore and into the sampling region by the deep upwelling currents (Huyer 1983). If this were the case, upwelling would be affecting the cross-shelf distribution of

E. nordmanni, but a deep offshore population rather than the nearshore population. Evidence of this is particularly strong on 27 June 2007, when a deep offshore concentration is slanted upward toward the shore (Figure 4). Deeper portions of the nearshore population may break away and move offshore during relaxation and downwelling, as may be represented on 3 July 2007. *Podon leuckarti* was also present in deeper waters offshore, but appeared in the same region on upwelling and relaxation dates. More sampling needs to be done farther offshore and deeper in the water column to examine the potential for an offshore population of *E. nordmanni* or *P. leuckarti* and to assess the effects of upwelling and relaxation offshore.

Peterson et al. (1979) noted that abundant zooplankton was found within 5 km of shore in Oregon during the upwelling season, and attributed this to a thin Ekman layer and slow water exchange combined with vertical distribution. Additionally, studies from various upwelling regions have shown that meroplankton and holoplankton have the capability to remain nearshore during upwelling events, likely through vertical regulation (Peterson et al. 1979, Poulin et al. 2002, Shanks et al. 2002, 2003, Shanks and Brink 2005, Shanks and Shearman 2009, Morgan et al 2009*a, b,* Morgan and Fisher 2010). Cladocerans off the Oregon coast appear to fit into a model in which zooplankton can be retained nearshore even during upwelling conditions. This is consistent with cladoceran observations made by Peterson et al. (1979).

Distribution by sex and reproductive stage

Saito and Hattori (2000) found that the cladoceran *P. leuckarti* in Japan tends to stay near the surface or the bottom during the day and disperse throughout the water

column at night, and that females with advanced resting eggs stay only at the bottom during daylight. *Podon leuckarti* off Oregon showed no major differences in the spatial distribution of parthenogenic females in various stages of advancement (Figures 5 and 6) although during upwelling the center of concentration for females with advanced embryos (PA) was slightly deeper than that of females with early embryos (PE). This may have been because females with advanced embryos are larger and have darker, more visible brood pouches, but this trend was not observed during relaxation. Males were always located nearshore at the surface or along the bottom, which is consistent with the observations of Saito and Hattori (2000), but females were often found mid-water column during daylight nearshore. Unfortunately, few gamogenic females were caught and their behavior in Oregon remains unknown.

Evadne nordmanni showed no consistent difference in the distribution of parthenogenic females carrying embryos in various stages of development (Figures 10 and 11). Males and gamogenic females were not abundant enough to analyze. The shape of concentration contours indicate some tendency for all stages to stay near the bottom or surface nearshore, but females were also found mid-water column. Staying near the surface likely provides greater feeding opportunities but a higher risk of predation, while staying near the bottom provides less food but more safety (Saito and Hattori 2000). These factors may be interacting to determine vertical distribution.

Podon leuckarti sex frequency diagrams (Figures 7-9) indicated that parthenogenic females with early embryos (PE) tended to be more dominant nearshore, while parthenogenic females with advanced embryos (PA) were more dominant offshore, but this was not a consistent trend. Males and gamogenic females were rare.

Evadne nordmanni sex frequency diagrams (Figures 12-14) indicated that higher proportions of parthenogenic females with early embryos (PE) occurred nearshore, while higher proportions of parthenogenic females with advanced embryos (PA) occurred offshore. Males and gamogenic females were extremely rare. This is not surprising, as *Evadne* males are known to occur much less frequently than females and are restricted to a shorter part of the season (Baker 1938, Gieskes 1971, Longhurst and Seibert 1972).

Evadne releases young only at night, and this is likely because the large pigmented eyes of mature embryos are highly visible to predators (Bryan 1979, Onbé 2002). Parthenogenic mothers with the most advanced embryos (PAJ) in the current study were not distributed differently than those with less developed embryos, but due to preservation the eye pigmentation was largely lost and it is unknown whether these mothers carried embryos with darkly pigmented eyes.

The proportions of early and advanced parthenogenic females varied significantly across stations and depths for both *P. leuckarti* ($p<0.001$ and $p=0.019$) and *E. nordmanni* ($p<0.001$ and $p=0.024$). However, if different vertical positionings of cladoceran reproductive stages were causing them to be swept onshore or offshore differentially, we would expect to see spatial differences in their distributions that changed with oceanographic conditions, which was not observed. The distribution of various parthenogenic stages of both *P. leuckarti* and *E. nordmanni* were not consistently spatially different, and they do not appear to be riding horizontal currents on and offshore based reproductive stage, as copepods do (Peterson et al. 1979).

Size frequency distribution

Size frequencies for both *P. leuckarti* (Figures 15-17) and *E. nordmanni* (Figures 18-20) exhibited trends in which smaller individuals were found in larger proportion closer to shore and larger individuals more offshore, and size frequency differed very highly significantly ($p<0.001$) across stations for both species. This matches with sex frequency data, as females earlier in development were found dominating nearshore and also tended to be smaller. In the Clyde Sea on the west coast of Scotland, samples down to a depth of 50 m contained smaller *Evadne* only during daylight, indicating that different sizes may differentially regulate vertical position, although this may also be a relic of the fact that young are released just before daylight (Bainbridge 1958, Onbé 2002). However, *P. leuckarti* does not have different diel vertical migrations based on size (Saito and Hattori 2000). Since samples in the present study were taken consistently with respect to sunrise, these effects should not cause variation among the sample dates but may cause variation with depth. Size structure may also be a result of sample date, as larger cladocerans tend to be found earlier in the season when populations are on the rise (Jorgensen 1933, Bainbridge 1958). The frequency of different size classes varied very highly significantly ($p<0.001$) by date for both *P. leuckarti* and *E. nordmanni.* Size structure can additionally be modified by predation. The freshwater cladoceran *Daphnia* was found to be smaller on average and have a younger age structure when it is under higher predation pressure and higher food availability (Gliwicz et al. 1981). Thus, it is possible that nearshore dense plankton concentrations provide high food availability but also high predation, resulting in a smaller size structure of cladocerans.

Temporal changes

Concentrations of both *P. leuckarti* and *E. nordmanni* decreased drastically from June to August. With only four sample dates, conclusions cannot be drawn about seasonality, but a great abundance in June and declining abundance mid-August is a feasible temperate season for these cladocerans (Gieskes 1971, Frolander et al. 1973, Rivier 1998, Viñas et al. 2007). However, seasonality is variable by region, so we cannot be sure that the sample dates followed a seasonal trend (Baker 1938, Bainbridge 1958, Gieskes 1971, Buyukates and Inanmaz 2009). Many species of meroplankton collected in the same samples followed the same seasonal trend, with high abundances in June and low concentrations in August (Shanks and Shearman 2009). A common factor, such as primary productivity, may have been affecting the summer zooplankton community during the sample dates, but we cannot know for sure.

The lack of males and gamogenic females on 14 August 2007 was surprising, as the populations of both cladocerans were drastically reduced, and this is when sexual reproduction is supposed to become prominent (Egloff et al. 1997). *Podon leuckarti* males were present in very low concentrations ($<1/m^3$) on all sample dates, and *E. nordmanni* males were rarely found. Only a few gamogenic females were encountered during the study. Either males and gamogenic females were not a significant part of cladoceran populations on the sample dates, or they were distributed outside the sampling area. The latter is unlikely, as an entire nearshore group of cladocerans was observed, from surface to bottom, and other studies have documented parthenogenic and sexual individuals in the same horizontal region (e.g. Bainbridge 1958, Saito and Hattori 2000). Additionally, resting eggs may be more successful closer to shore

because the hatched young do not have to swim up from extreme depths to find food (Egloff et al. 1997). However, it is possible that sexual individuals move offshore or deeper than sampling depths beyond the scope of this study. Peterson et al. (1979) observed copepods moving offshore by sexual stage by riding upwelling and downwelling currents, and it is possible sexual cladocerans are doing so as well. However, it is more likely that they were simply not present on the sampling dates.

Cladocerans have been known to sustain populations through late fall in many regions, and sexual individuals do not appear in great abundance until the end of the breeding season, so sexual reproduction may not have been occurring by the last sample date (Bainbridge 1958, Gieskes 1971, Frolander et al. 1973, Rivier 1998, Viñas et al. 2007). Sexual individuals may have been absent due to a lack of environmental cues during the population crash. Conversely, the nearshore population may have remained intact but been transported to another site by alongshore currents (Smith 1974).

Cladoceran reproductive traits in Oregon

In *Podon leuckarti* (Figure 21) and *Evadne nordmanni* (Figure 22), the area of parthenogenic females increased with the developmental advancement of their embryos, as predicted. This is consistent with observations of *E. nordmanni* in the Clyde Sea, where females with advanced embryos are significantly larger than those with the earliest embryos (Bainbridge 1958). *Podon leuckarti* males were slightly larger than parthenogenic females with early embryos. Gamogenic *E. nordmanni* were smaller than parthenogenic with advanced embryos on average, which differs from observations in the Clyde Sea, where gamogenic *E. nordmanni* specimens are much larger than

parthenogenic individuals (Bainbridge 1958). However, very few gamogenic females were observed in the present study.

Parthenogenic *P. leuckarti* had a mean of 5.42 (CI=0.37, n=83) embryos, with a range of 3 to 12. Those counted were mostly early embryos, because as embryos advanced they overlapped and became difficult to distinguish. The mean number of embryos observed off Oregon is different from reports of *P. leuckarti* in Japan, where the species has just one embryo per parthenogenic female, and the Clyde Sea, where the species has a mean of 2.6 embryos and a range of 1 to 6 (Cheng 1947, Saito and Hattori 2000). Gamogenic *P. leuckarti* had 1 resting egg. This matches with other descriptions of *P. leuckarti* (Jorgensen 1933, Saito and Hattori 2000).

Parthenogenic *E. nordmanni* had a mean of 10.21 (CI=0.247, n=459) embryos, with a range of 3 to 21. This is a much higher fecundity than was reported for *E. nordmanni* in the Clyde Sea, where it had a mean of 4.4 embryos and a range of 1 to 10 (Cheng 1947). Parthenogenic *E. nordmanni* females are reported to have more embryos earlier in the season than later when populations start to decline and sexual reproduction becomes common (Gieskes 1971). Gamogenic *E. nordmanni* females had 1 to 2 resting eggs. This matches previous observations (Jorgensen 1933, Bainbridge 1958).

In a study by Durbin et al. (2008) *Evadne nordmanni* was collected from four sites in the NE Atlantic, a site in the NW Atlantic, two sites in the NE Pacific, and a site in the SW Pacific, and *Podon leuckarti* was collected from three sites in the NE Atlantic, a site in the NW Atlantic, and three sites in the NE Pacific including the Oregon Coast. Mitochondrial DNA analysis indicated that both species had geographic differences in phylogenetic structure that were comparable to levels distinguishing

separate species, so it is possible that regional differences in fecundity are the result of speciation processes.

My observations of parthenogenic *E. nordmanni* indicated that they release a new brood of young embryos into the brood pouch before their fully developed embryos are released from the valve space. This has previously been observed in *Evadne tergestina* (Bryan 1979).

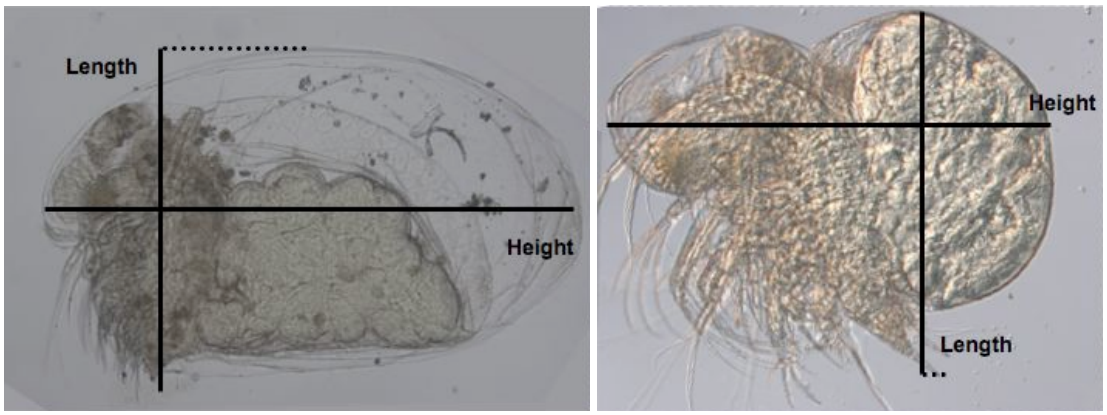
In parthenogenic *E. nordmanni*, the brood pouch grew with embryonic development to fill the valve space of the mother. More of the valve space was filled in mothers with more advanced embryos (Figure 24). Additionally, the mean number of embryos per parthenogenic female decreased with embryonic advancement (Figure 23). This trend was also found by Bainbridge (1958) in the Clyde Sea. Embryos may be resorbed or crowded out, resulting in fewer hatching embryos than initial embryos. Since offspring start developing their own embryos before they are released from their own mother, it is possible that some embryos have a longer development than others. The small brood pouches of advanced embryos do not likely hold up to 21 embryos, as was observed in adults. Thus, more embryos may be released as the cladoceran grows. This is simply a hypothesis based on the observed trends, and would require further observation to test.

Advanced embryos with their own broods generally had fewer embryos in their brood pouch than their mother. The number of young embryos in an advanced embryo varied, even among advanced embryos in the same brood. This may further indicate that some embryos are more advanced than others within the same brood, as more embryos may be released after young cladocerans separate from their mothers.

The mean number of embryos in parthenogenic females is dependent on cladoceran age and the season (Rivier 1998). Gieskes (1971) suggested that the fecundity of marine cladocerans is an ecological indicator for the region in which they are found. High cladoceran fecundity may indicate that Oregon is a supportive environment for cladocerans.

Table 1. Sample dates, station distances offshore, and the stratified sample depths at each station for a transect off Coos Bay, Oregon in 2007. N=neuston, ML=mixed layer, AT=above thermocline, T=thermocline, BT=below the thermocline.

	27 June			3 July		18 July		14 August	
Station	Distance offshore (km)	Depth category	Depth intervals (m)	Distance offshore (km)	Depth intervals (m)	Distance offshore (km)	Depth intervals (m)	Distance offshore (km)	Depth intervals (m)
1	0.7	N	0.2	0.7	0.2	0.7	0.2	0.5	0.2
		AT	0-5		0-6		0-12		0-5
		BT	5-10		6-13		12-25		5-9
2	2.9	N	0.2	2.8	0.2	1.8	0.2	2.0	0.2
		AT	0-8		0-12		0-10		0-10
		T	8-16		12-18		Tow fail		10-18
		BT	16-25		18-28		20-28		
3	4.7	N	0.2	5.6	0.2	6.8	0.2	5.0	0.2
		ML	0-12		0-16		0-15		0-8
		T	12-18		16-30		15-30		8-20
		BT	18-28		30-40		30-45		20-40
		BT	18-40		40-70		45-70		40-50
4	9.6	N	0.2	11.1	0.2	13.8	0.2	11.9	0.2
		ML	0-15		0-15		0-15		0-10
		T	15-30		15-30		15-30		10-20
		BT	30-40		30-40		30-40		20-50
		BT	40-70		40-70		40-70		50-70
5	16.6	N	0.2	16.7	0.2	18.4	0.2	17.2	0.2
		ML	0-15		0-15		0-15		0-7
		T	15-25		15-30		15-25		7-25
		BT	25-40		30-40		25-40		25-50
		BT	40-60		40-70		40-70		50-70
6	22.3	N	0.2	22.2	0.2	25.0	0.2	23.8	0.2
		ML	0-10		0-15		0-15		0-15
		T	10-30		15-30		15-25		15-30
		BT	30-40		30-45		25-45		30-60
		BT	40-60		45-60		45-70		60-70
7	27.6	N	0.2	27.8	0.2	28.0	0.2	27.7	0.2
		ML	0-10		0-15		0-15		0-5
		T	10-15		15-30		15-25		5-25
		BT	15-40		30-40		25-45		25-45
		BT	40-60		40-70		45-70		45-70



(A) (B)

Figure 1. Examples of the length and height axes measured on (A) *Evadne nordmanni* and (B) *Podon leuckarti*. The brood pouch of *Evadne nordmanni* fills approximately 50% of the valve space of this individual.

Table 2. The stages assigned to the marine cladocerans (A) *Podon leuckarti* and (B) *Evadne nordmanni* in this study.

(A) *Podon leuckarti*

Abbreviation	Stage	Distinguishing features
PE	Parthenogenic female with early embryos	Embryos are light in color, no thoracic segments distinguishable, no distinct appendages, eye is undeveloped
PA	Parthenogenic female with advanced embryos	Thoracic segments becoming distinct, eye forming
PAJ (used only on 27 June and 18 July, subcategory of PA)	Parthenogenic female with juveniles nearing release	Brood pouch very dark due to density of embryos, embryos have full adult morphology including developed eyes, antennae, thoracic appendages, and their own broods of embryos
P	Parthenogenic female (stage not determined)	Identified as parthenogenic but brood pouch may be damaged or embryo stage unclear
G	Gamogenic female	A dark resting egg is present in the brood pouch. Vagina is present
M	Male	Penis present just anterior to cauda, valves small compared to head, interior of valves irregular shaped and lumpy, testes present just above cauda
U	Unidentifiable individual	Sex not determined. Individual may be badly damaged or ambiguous in characteristics

(B) *Evadne nordmanni*

Abbreviation	Stage	Distinguishing features
PER (used only on 27 June and 18 July, subcategory of PE)	Parthenogenic female with youngest embryos	Embryos are small and perfectly round
PE	Parthenogenic female with early embryos	Embryos starting to elongate, no thoracic segments distinguishable, no eye organ
PA	Parthenogenic female with advanced embryos	Thoracic segments becoming distinct, eye organ forming
PAJ (used only on 27 June and 18 July, subcategory of PA)	Parthenogenic female with juveniles nearing release	Embryos have full adult morphology, including developed eyes, antennae, thoracic appendages, and their own broods of embryos
P	Parthenogenic female (stage not determined)	Identified as parthenogenic but brood pouch may be damaged or embryo stage unclear
G	Gamogenic female	A dark resting egg is present in the brood pouch
M	Male	Small penis present (very hard to observe), testes protruding into valve space, valves elongate and more pointed at posterior
U	Unidentifiable individual	Sex not determined. Individual may be badly damaged or ambiguous in characteristics

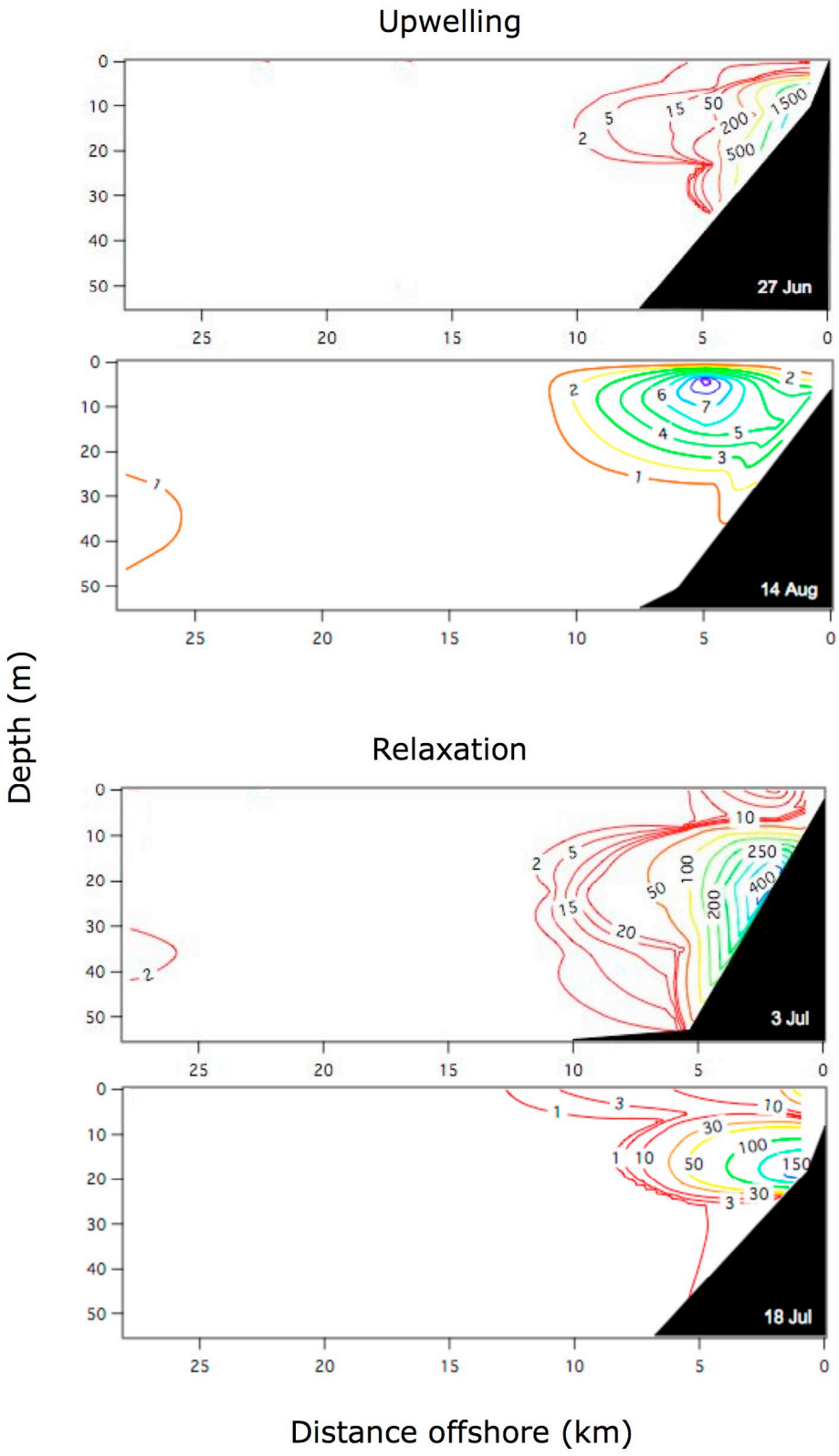


Figure 2. Contour plots of *Podon leuckarti* distributions off Coos Bay, Oregon in the summer of 2007. Contour lines represent concentrations in #/m^3.

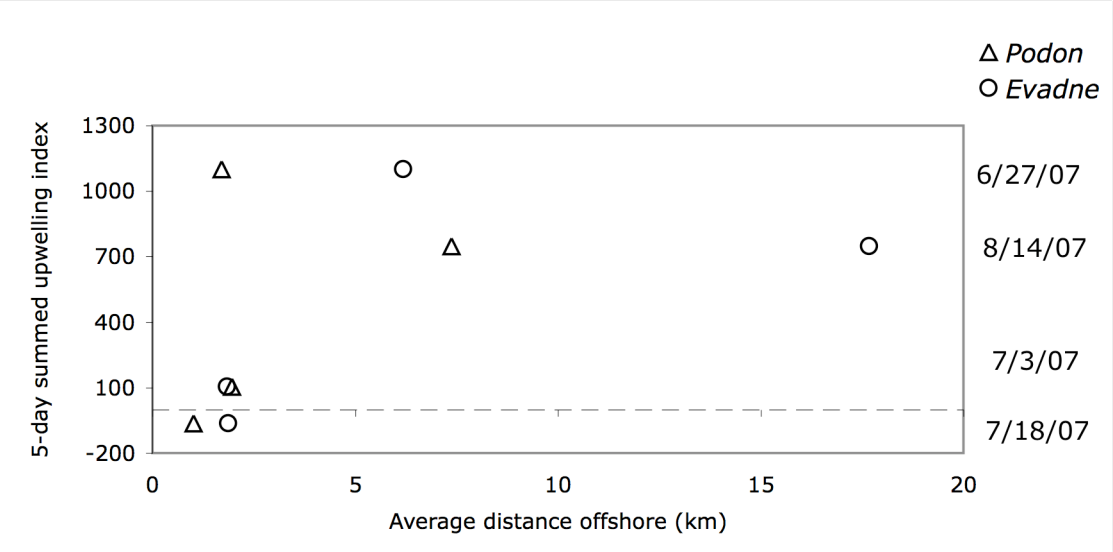


Figure 3. The average distance offshore of *Podon leuckarti* and *Evadne nordmanni* plotted against the five-day sum of the upwelling indices prior to the sampling date in the summer of 2007 off Coos Bay, Oregon. Positive indices indicate upwelling conditions, and a dashed line indicates an index of 0. Sample dates are displayed on the right along the y-axis; 27 June and 14 August were upwelling dates and July 3 and 18 were relaxation or weak downwelling dates.

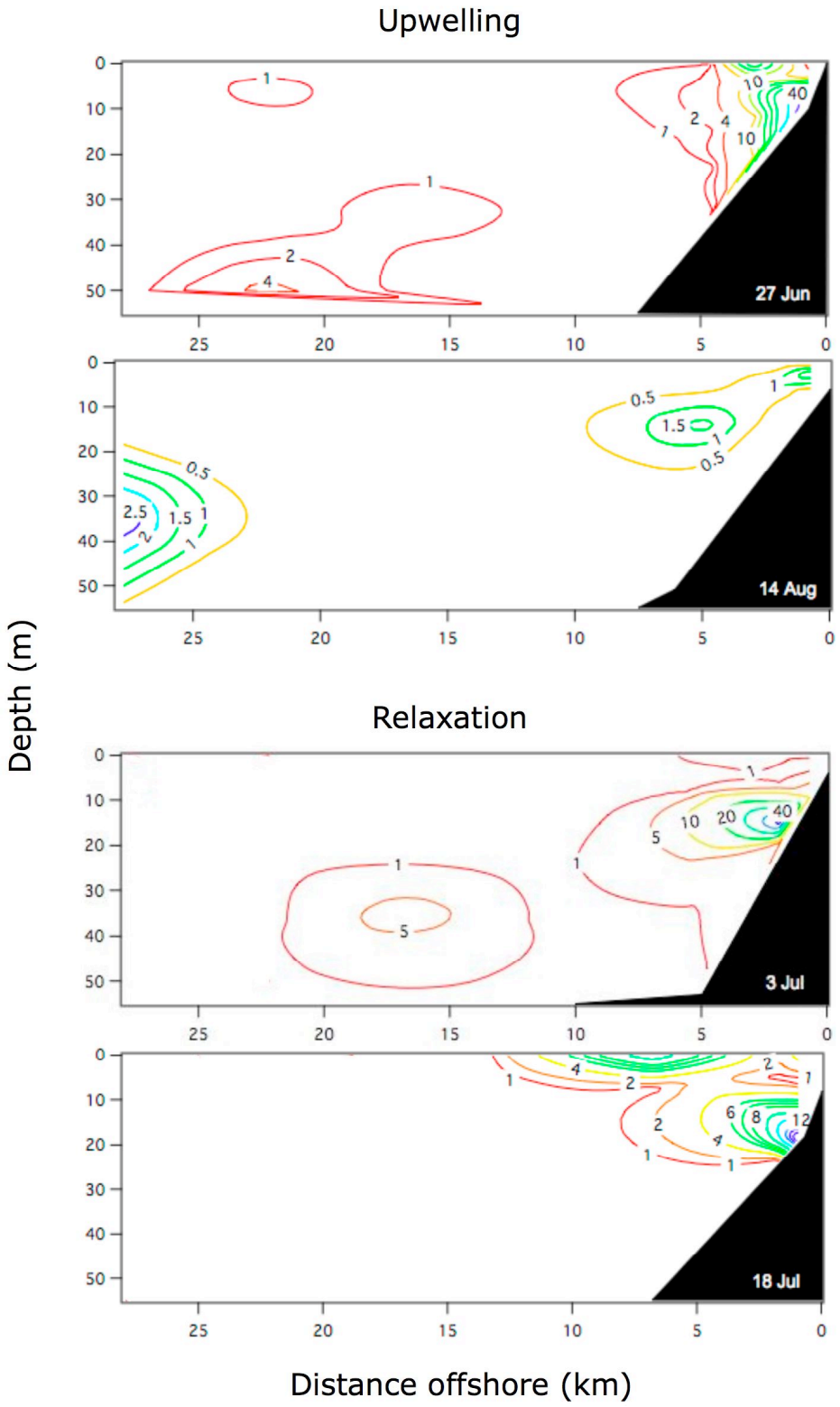


Figure 4. Contour plots of *Evadne nordmanni* distributions off Coos Bay, Oregon in the summer of 2007. Contour lines represent concentrations in #/m^3.

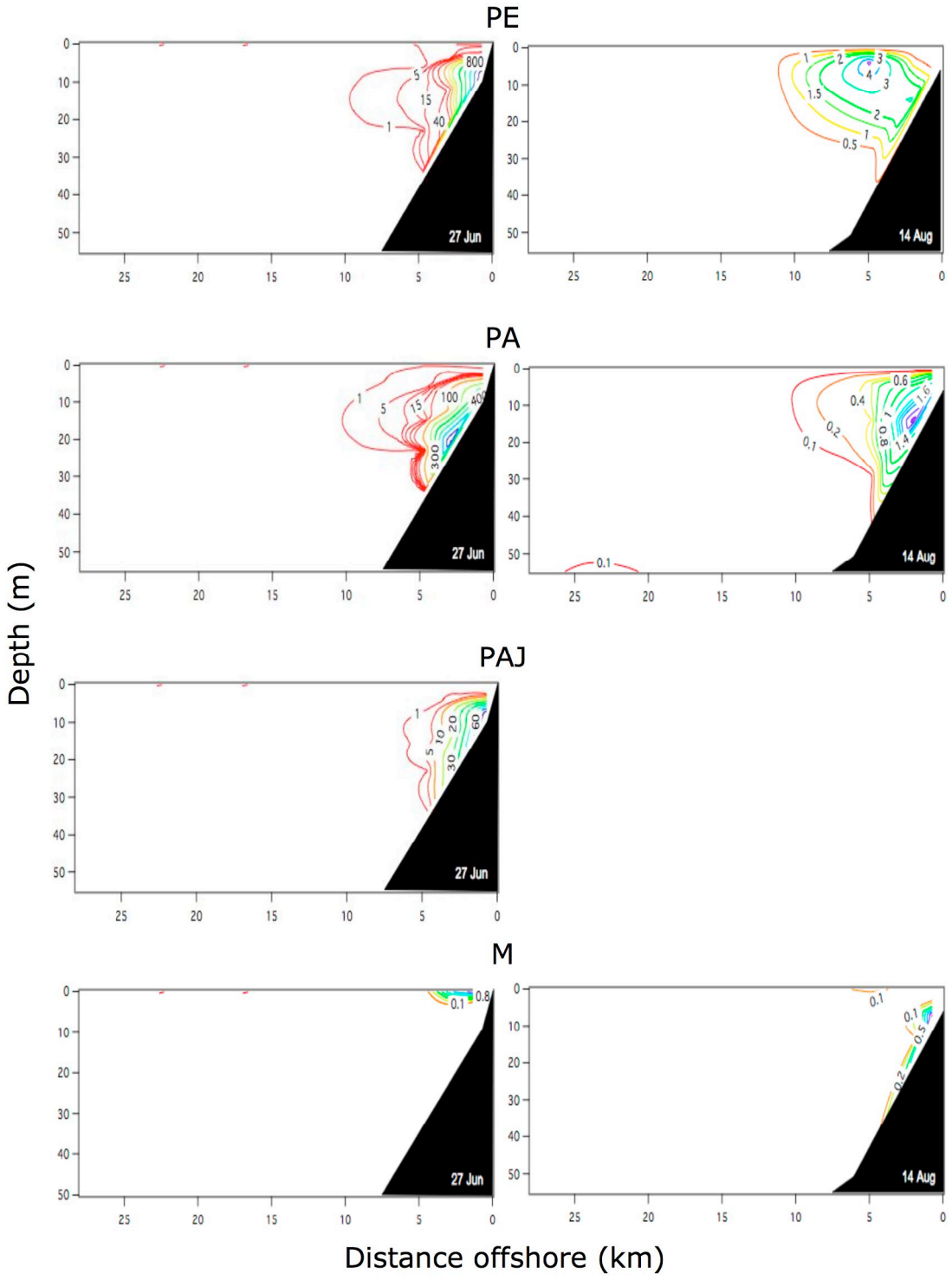


Figure 5. Contour plots of the distribution of *Podon leuckarti* by sex and reproductive stage during upwelling events off Coos Bay, Oregon in summer 2007. Contour lines represent concentration in #/m^3. PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release (not distinguished from PA on 14 August), M=male.

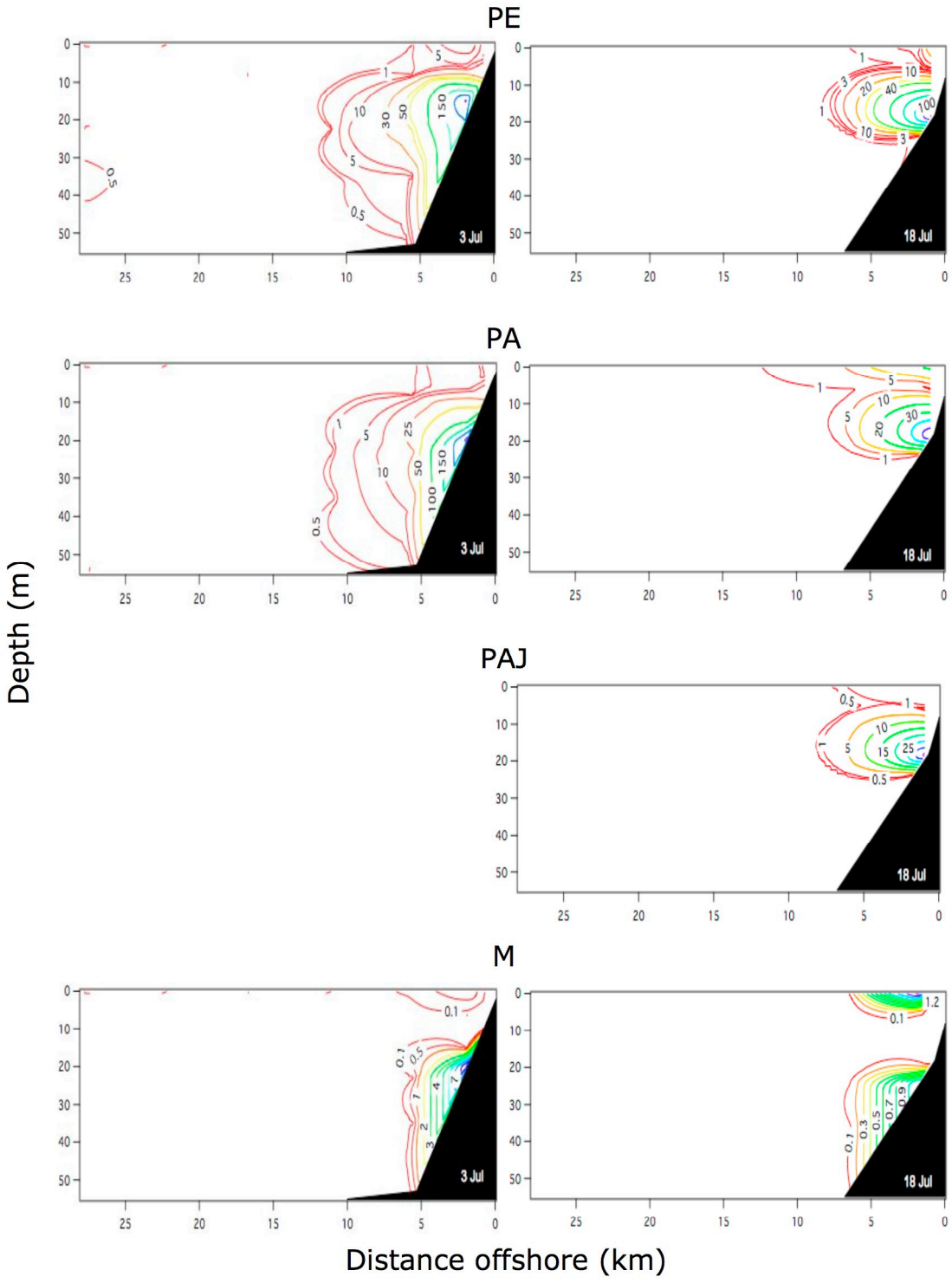


Figure 6. Contour plots of the distribution of *Podon leuckarti* by sex and reproductive stage during relaxation events off Coos Bay, Oregon in summer 2007. Contour lines represent concentration in #/m^3. PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release (not distinguished from PA on 3 July), M=male.

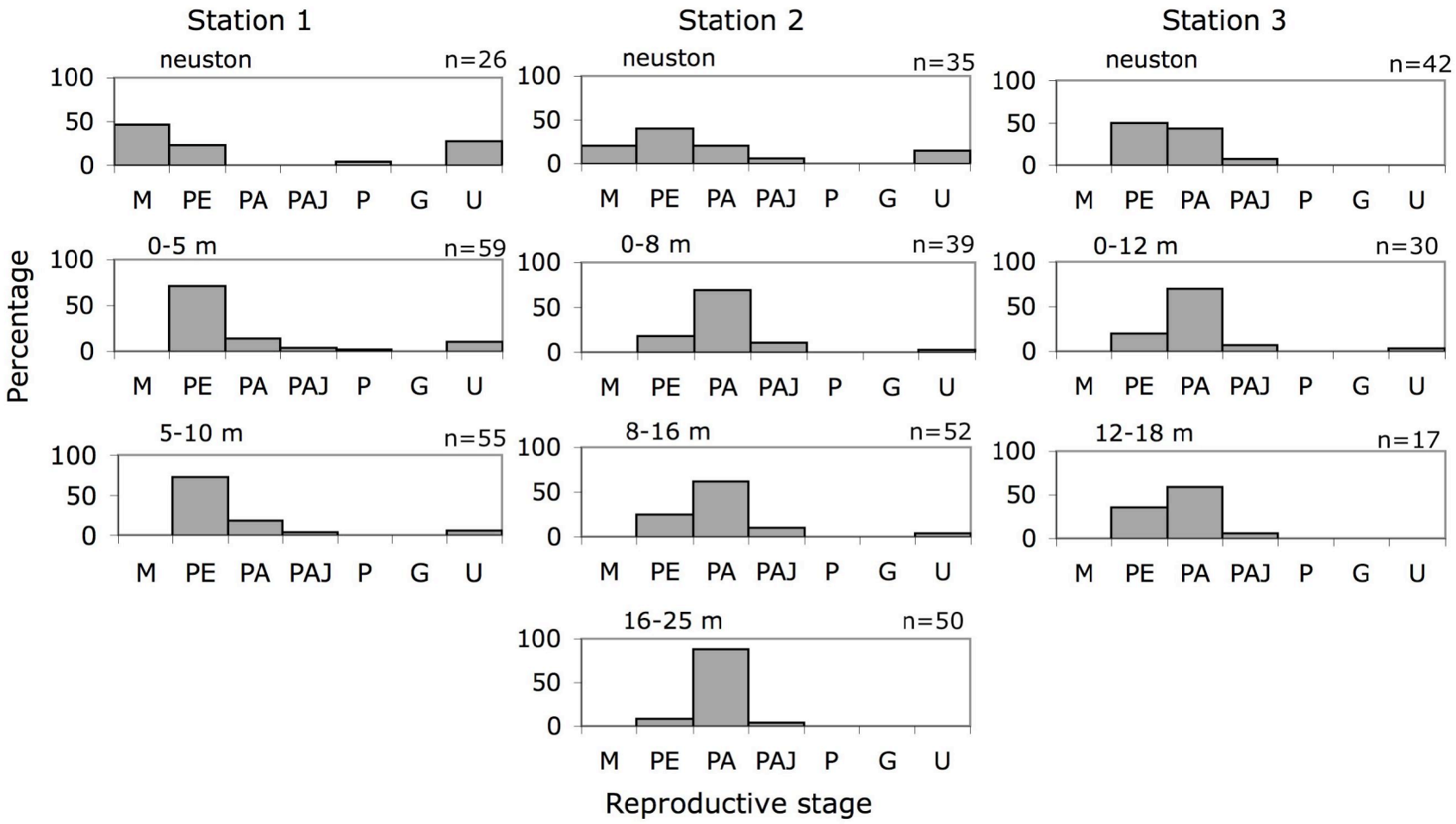


Figure 7. Sex frequency distribution of *Podon leuckarti* off Coos Bay, Oregon on 27 June 2007 (upwelling) for stations 1-3. Depth intervals with n<10 were excluded. M=male, PE=parthenogenic with early embryos, PA= parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

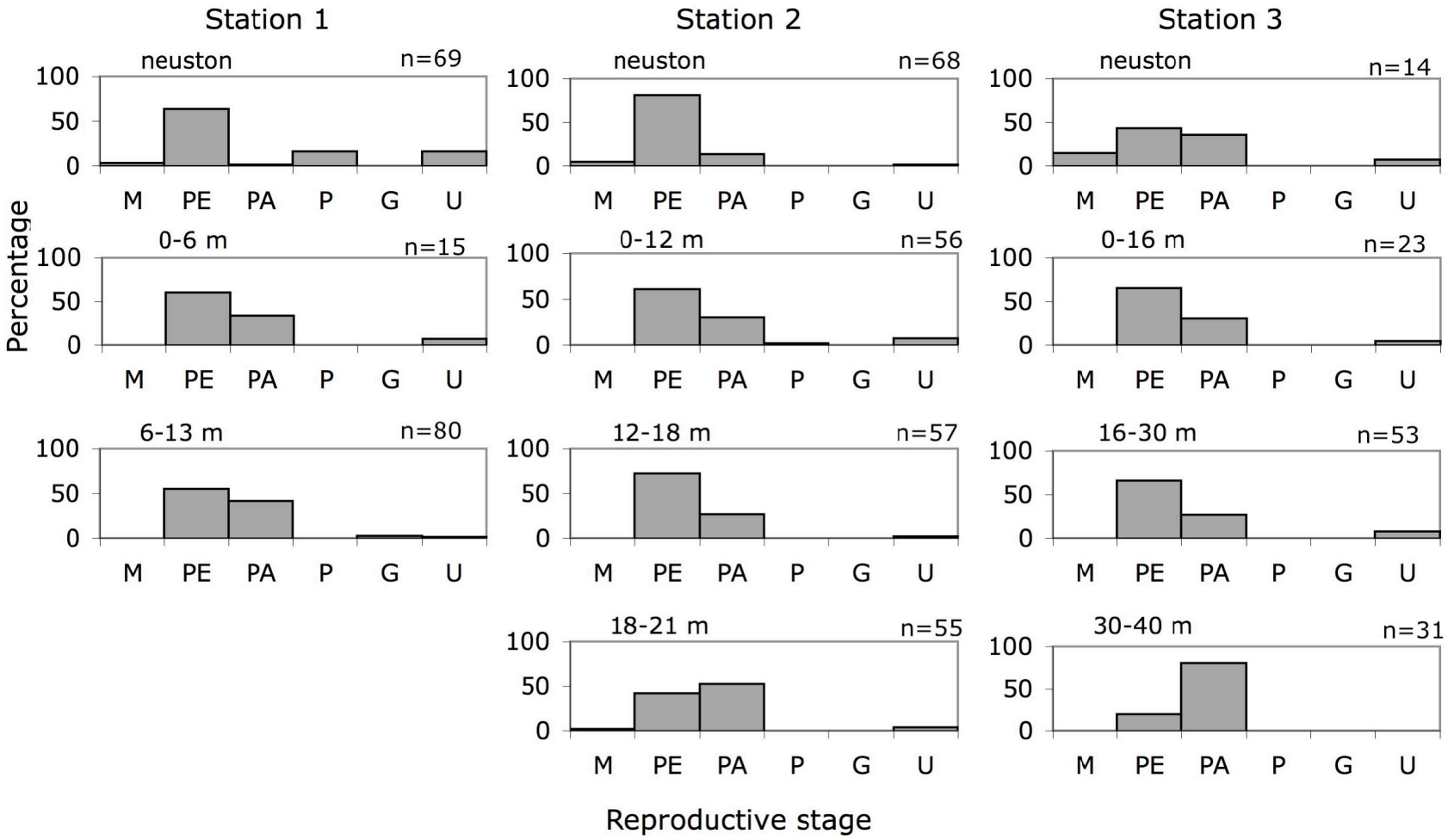


Figure 8. Sex frequency distribution of *Podon leuckarti* on 3 July 2007 (relaxation) off Coos Bay, Oregon at stations 1-3. Depth intervals with n<10 were excluded. M=male, PE=parthenogenic with early embryos, PA= parthenogenic with advanced embryos, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

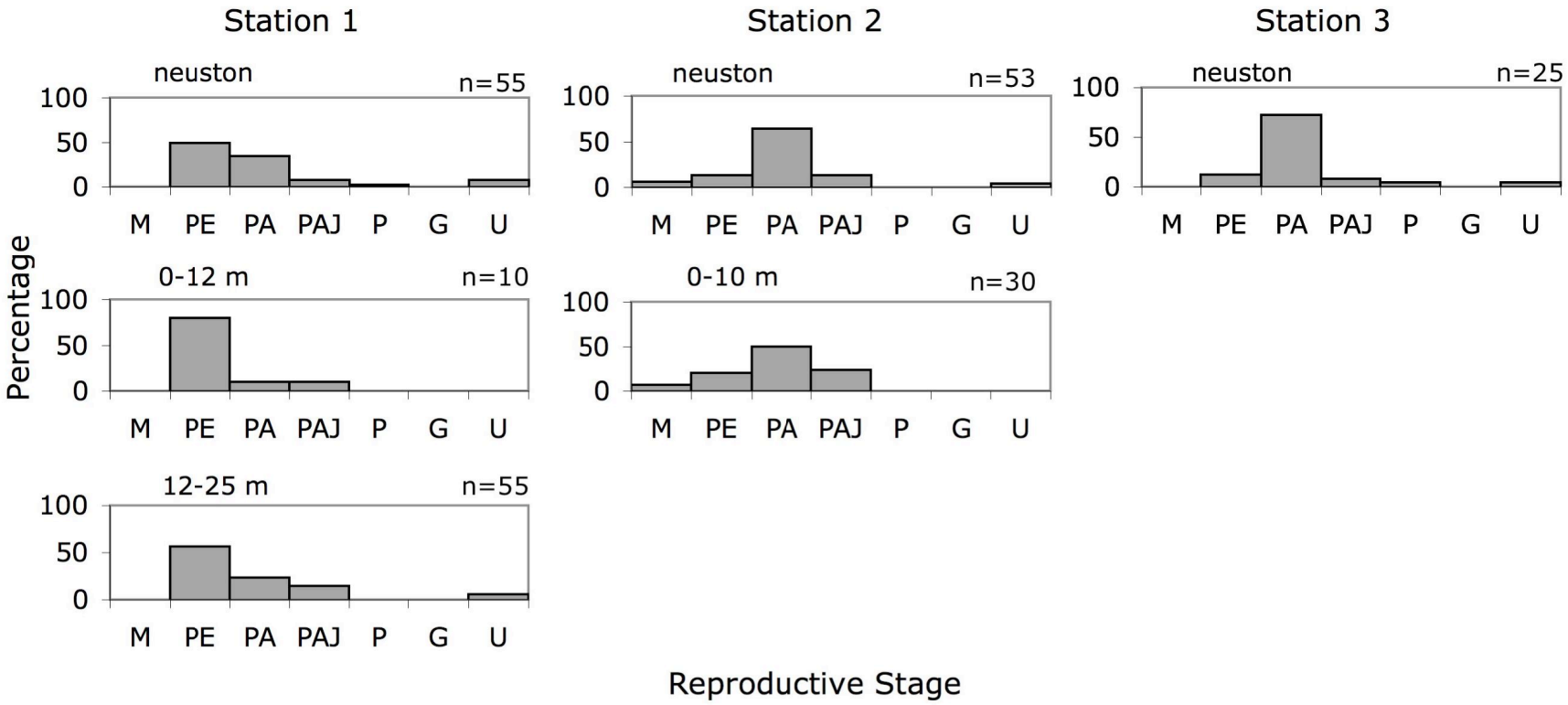


Figure 9. Sex frequency distribution of *Podon leuckarti* on 18 July 2007 (relaxation) off Coos Bay, Oregon. Depth intervals with n<10 were excluded. M=male, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

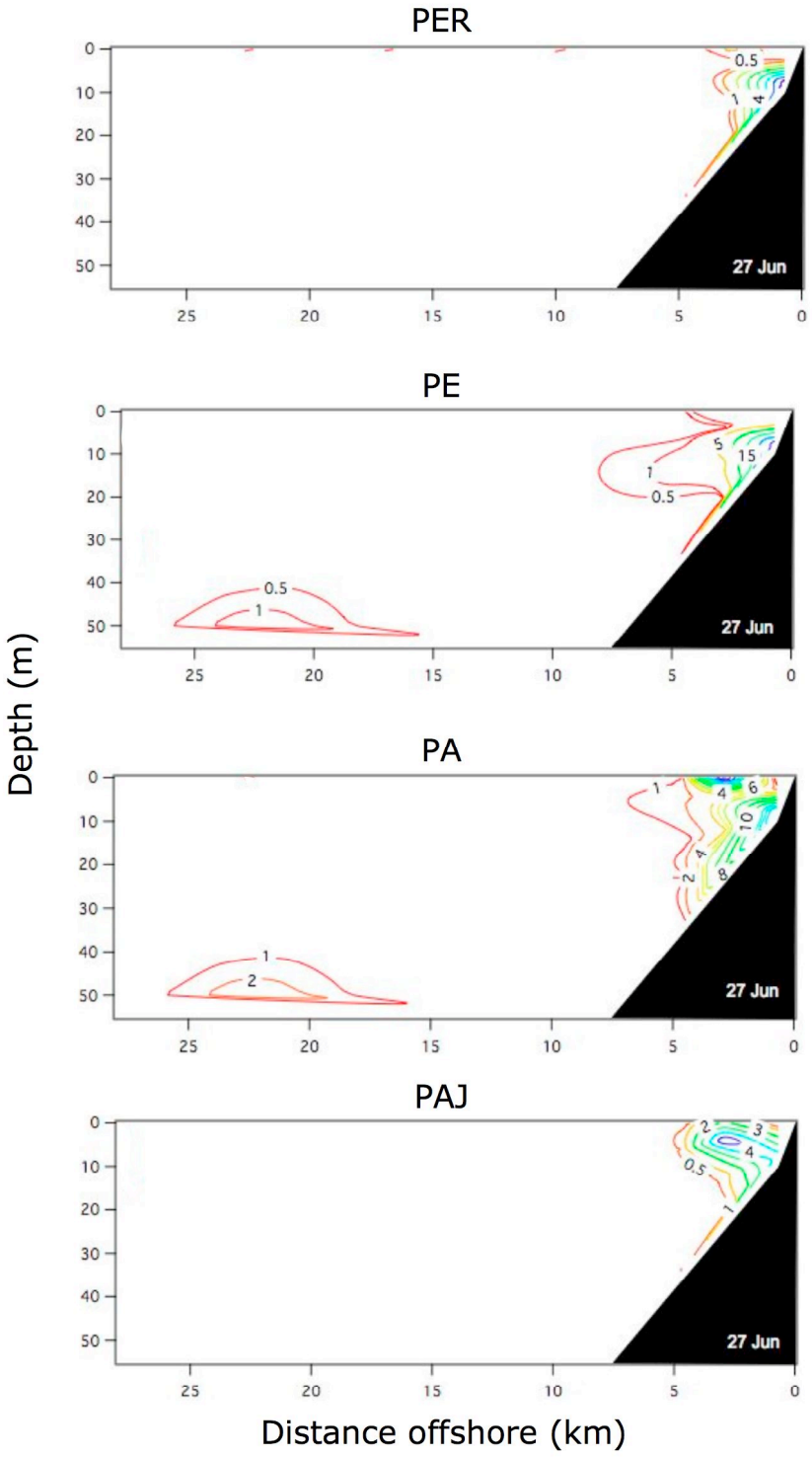


Figure 10. Contour plots of the distribution of *Evadne nordmanni* by sex and reproductive stage during upwelling events off Coos Bay, Oregon in summer 2007. Contour lines represent concentration in #/m^3. Concentrations on 14 August were negligible. PER=parthenogenic with earliest embryos, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release.

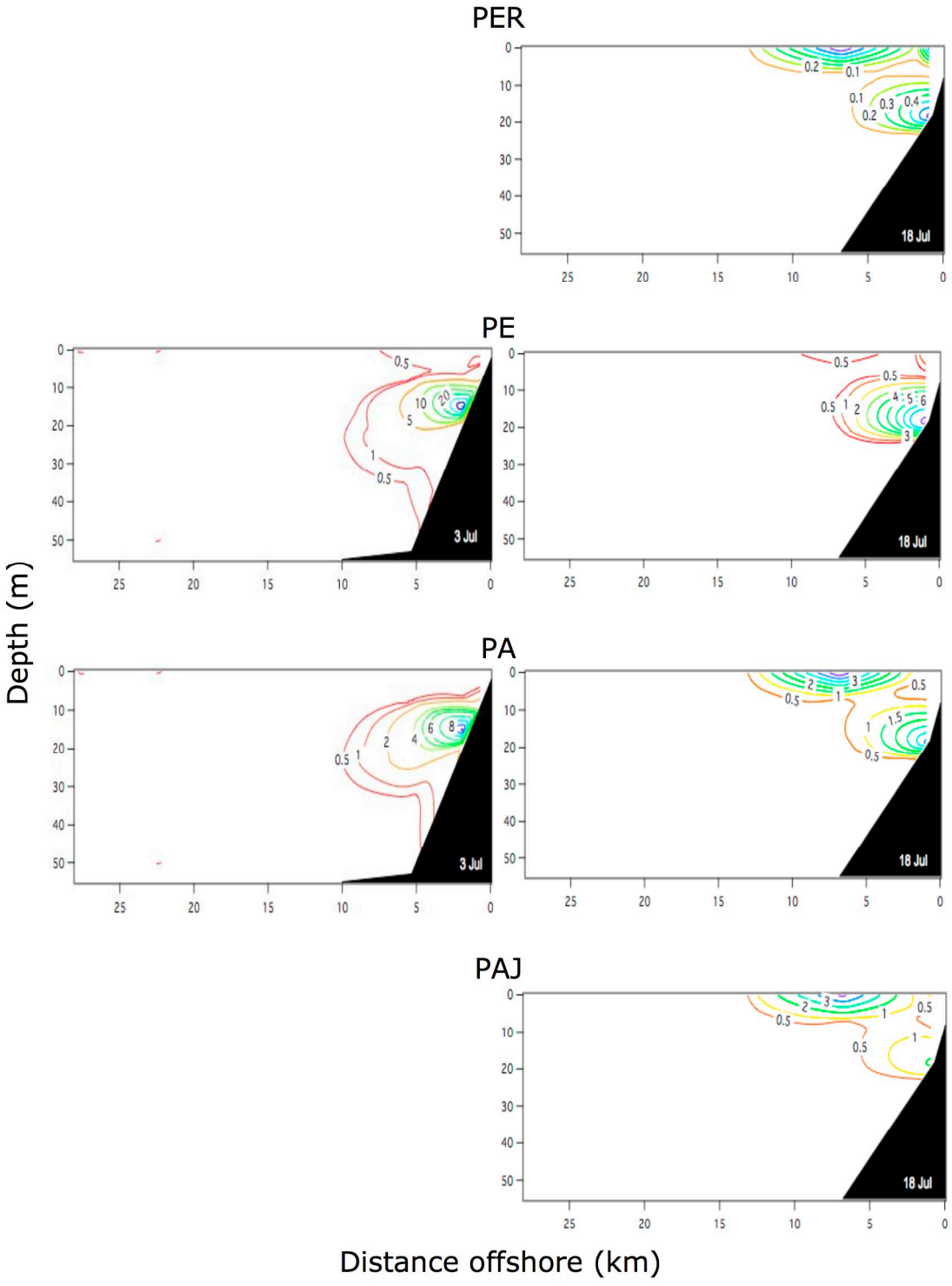


Figure 11. Contour plots of the distribution of *Evadne nordmanni* by sex and reproductive stage during relaxation events off Coos Bay, Oregon in summer 2007. Contour lines represent concentration in #/m^3. PER=parthenogenic with earliest embryos (not distinguished from PE on 3 July), PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release (not distinguished from PA on 3 July).

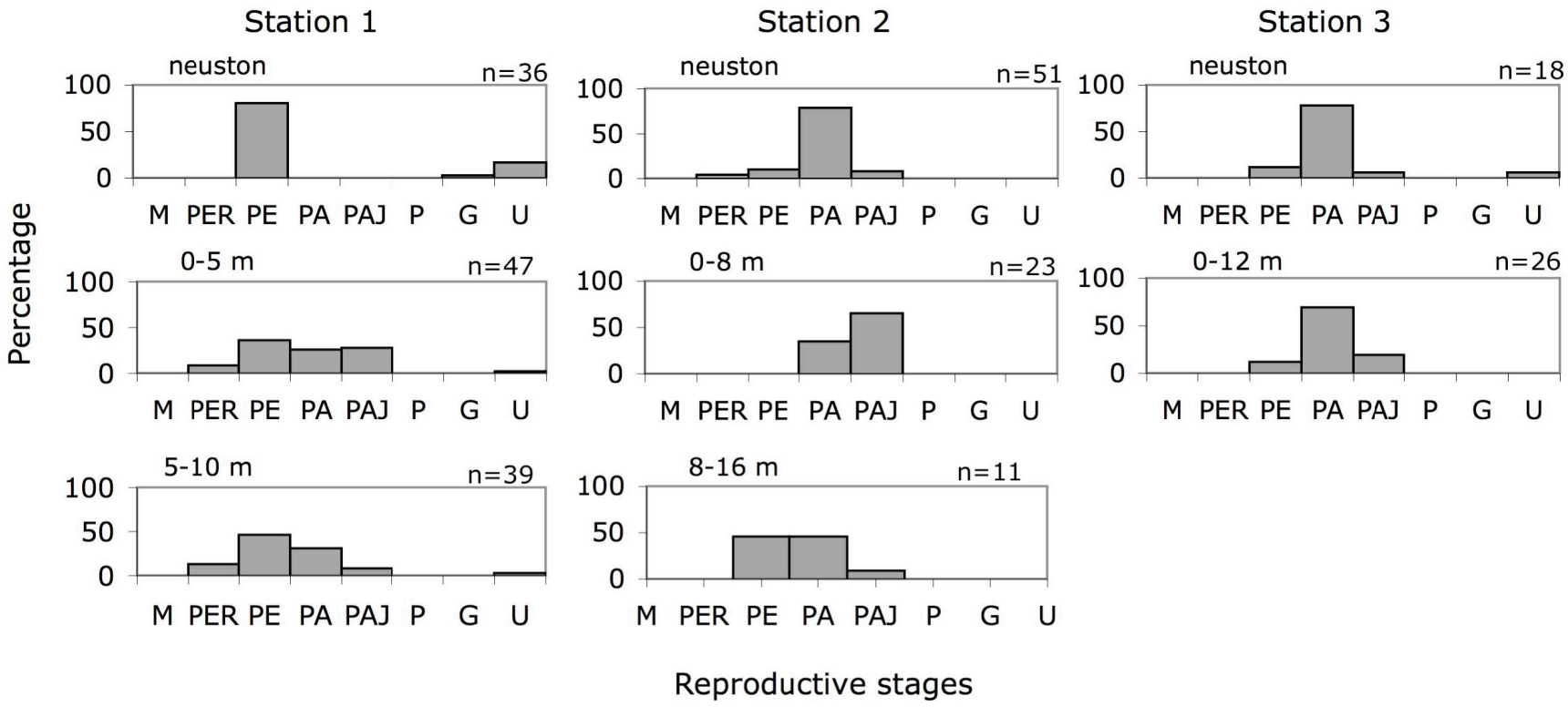


Figure 12. Sex frequency distributions of *Evadne nordmanni* on 27 June 2007 (upwelling) off Coos Bay, Oregon at stations 1-3. Depth intervals with n<10 were excluded. M=male, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

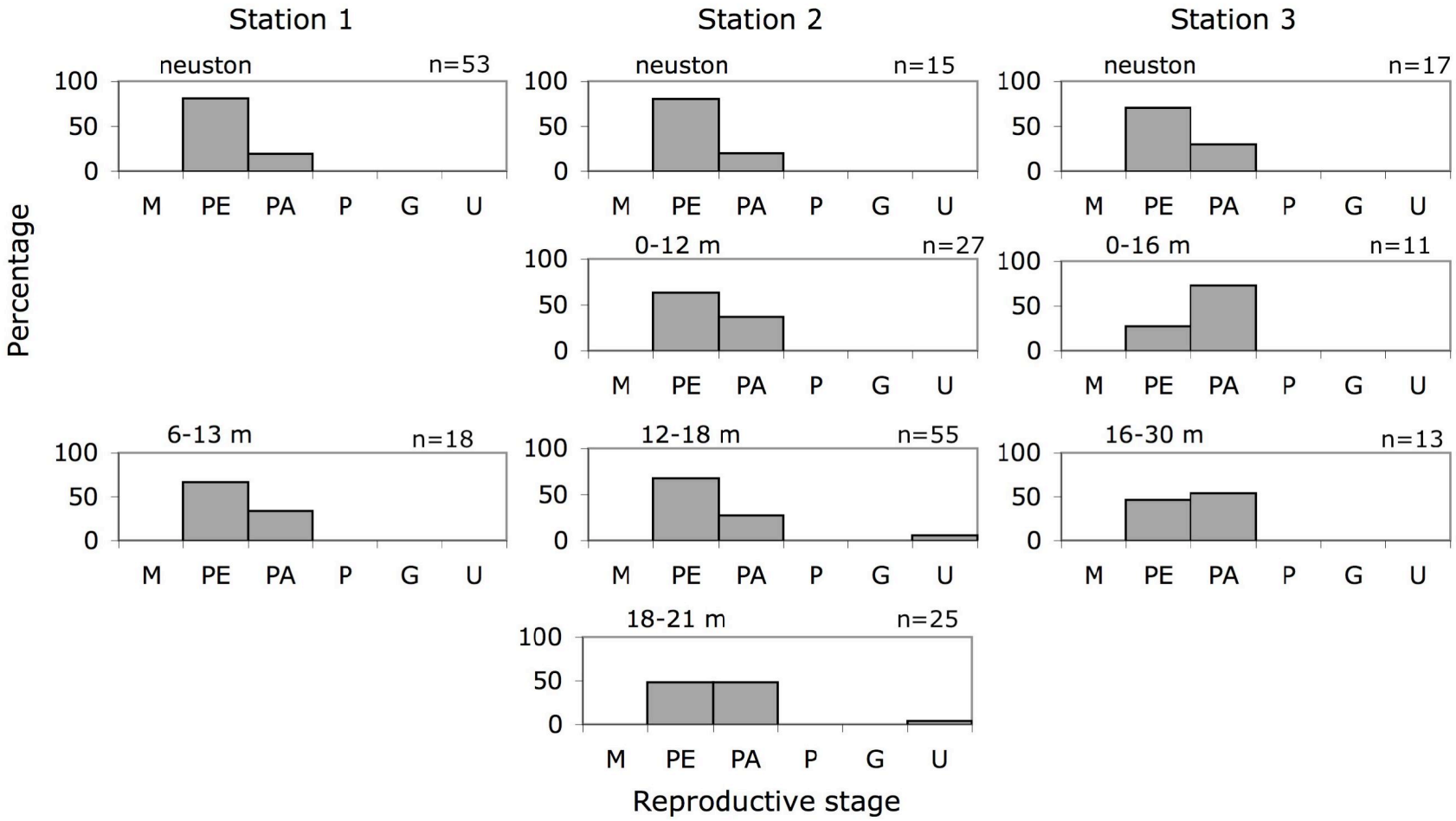


Figure 13. Sex frequency distribution of *Evadne nordmanni* on 3 July 2007 (relaxation) off Coos Bay, Oregon at stations 1-3. Depth intervals with n<10 were excluded. M=male, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

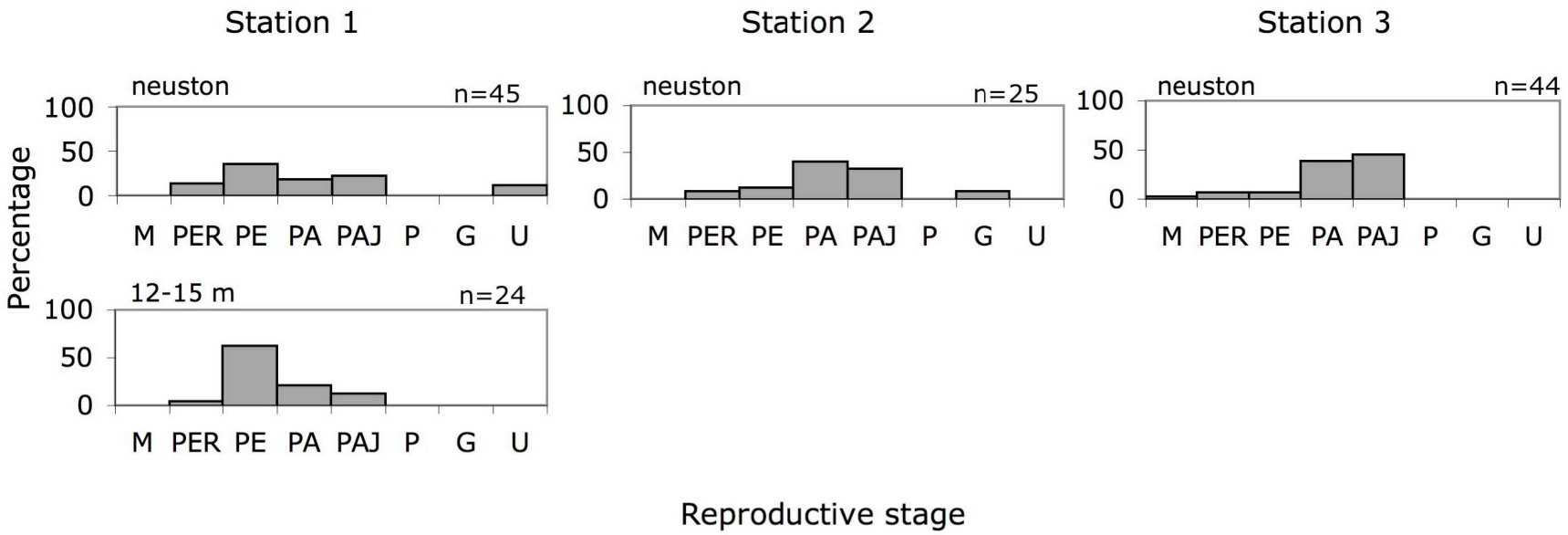


Figure 14. Sex frequency distribution for *Evadne nordmanni* on 18 July 2007 (relaxation) off Coos Bay, Oregon at stations 1-3. Depth intervals with n<10 were excluded. M=male, PER=parthenogenic with earliest embryos, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release, P=parthenogenic with stage unknown, G=gamogenic female, U=unidentified sex/stage.

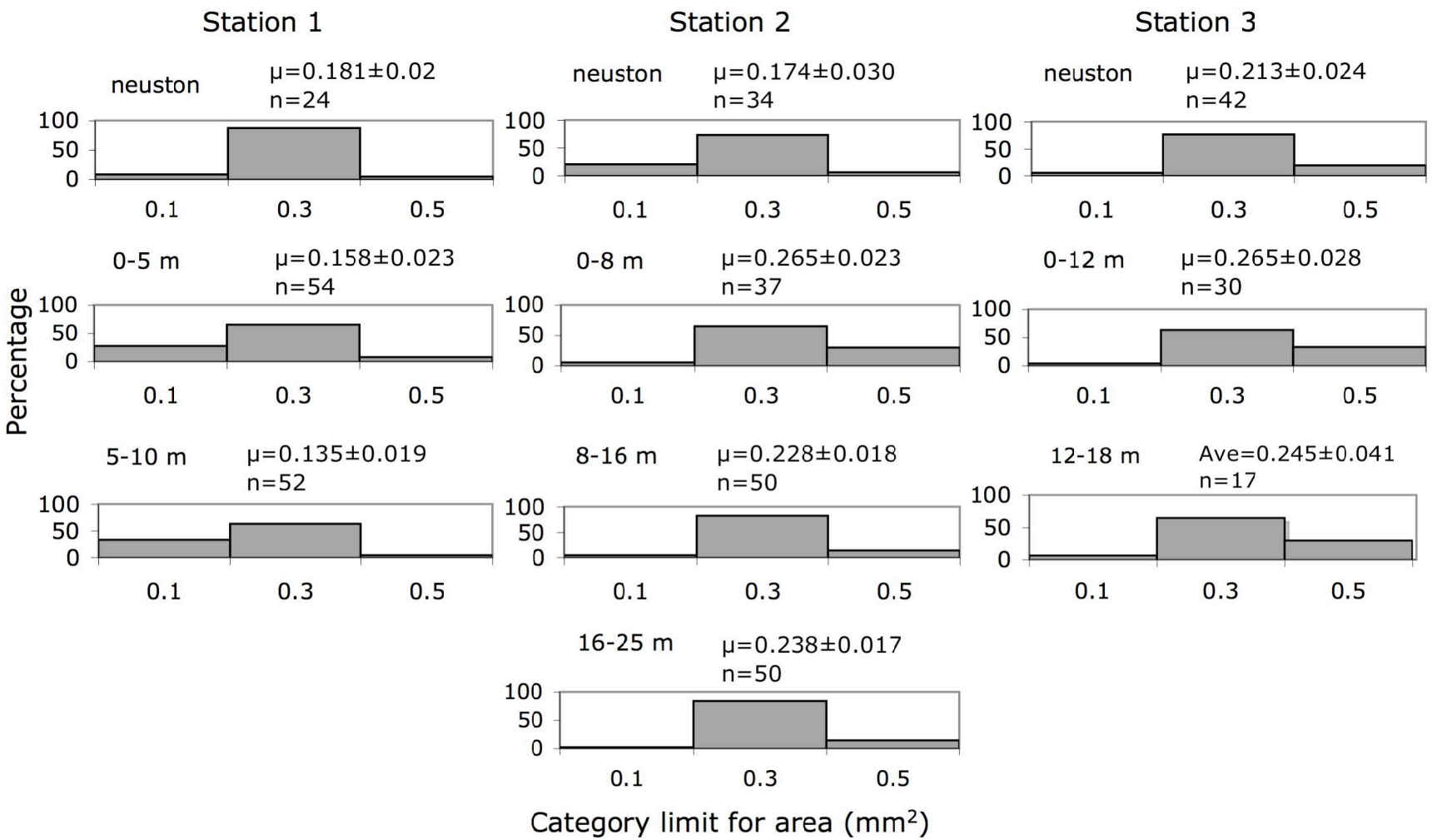


Figure 15. Size frequency distributions for *Podon leuckarti* on 27 June 2007 (upwelling) at stations 1-3 off Coos Bay, Oregon. Depth interval, number of individuals measured (n), mean area, and a 95% confidence interval are listed on each chart. Depth intervals with n<10 were excluded.

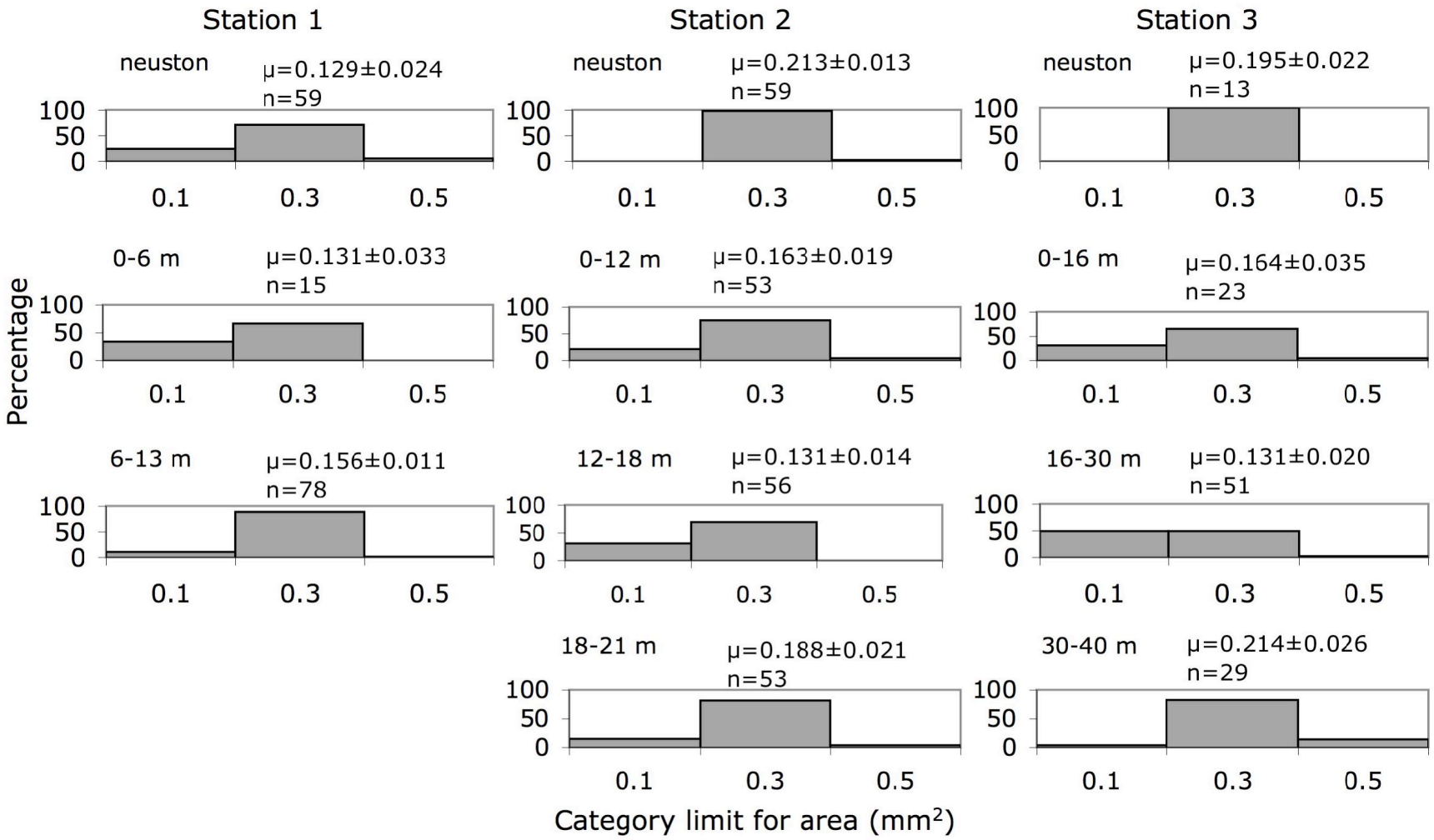


Figure 16. Size frequency distributions for *Podon leuckarti* on 3 July 2007 (relaxation) at stations 1-3 off Coos Bay, Oregon. Depth interval, number of individuals measured (n), mean area, and a 95% confidence interval are listed on each chart. Depth intervals with n<10 were excluded.

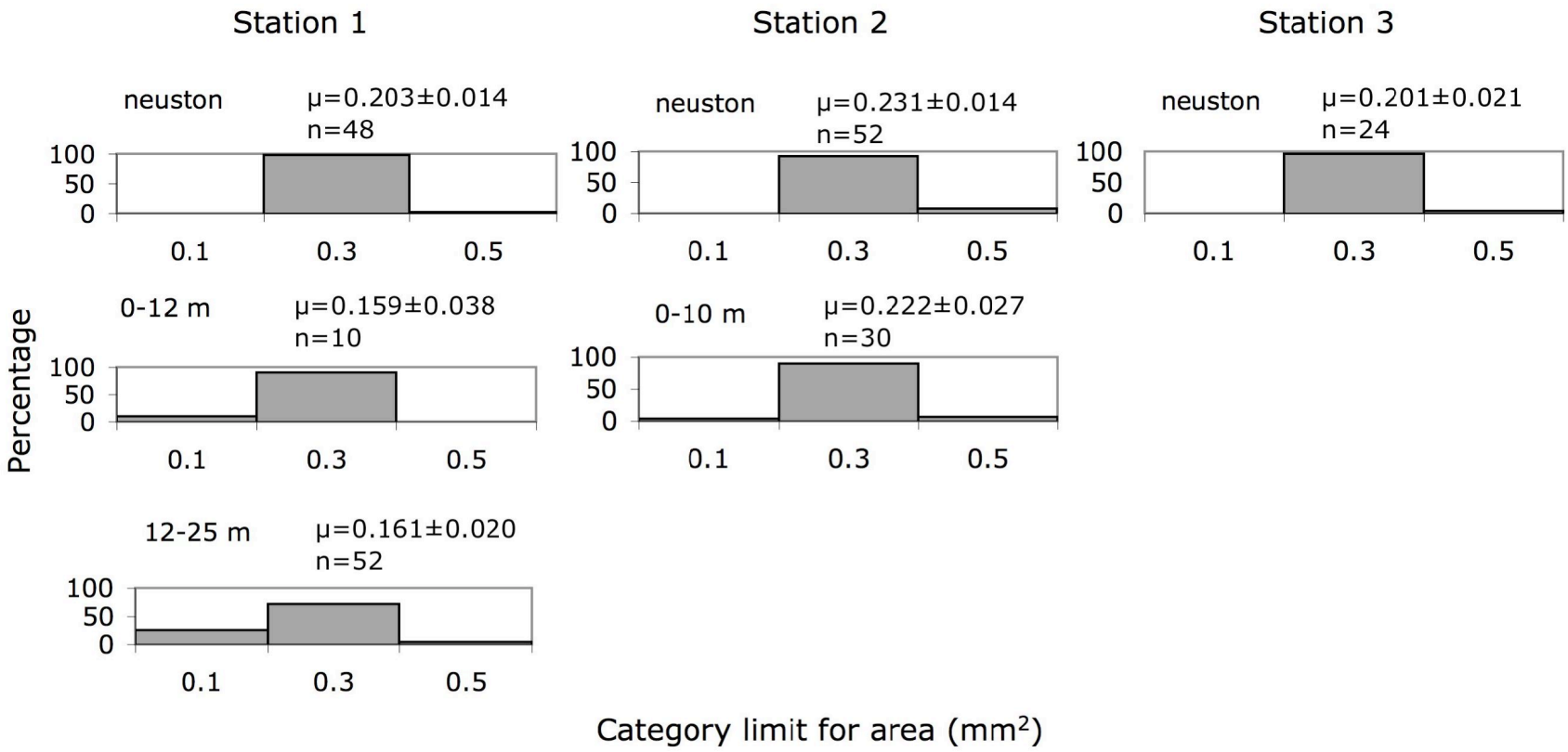


Figure 17. Size frequency distributions for *Podon leuckarti* on 18 July 2007 (relaxation) at stations 1-3 off Coos Bay, Oregon. Depth interval, number of individuals measured (n), mean area, and a 95% confidence interval are listed on each chart. Depth intervals with n<10 were excluded.

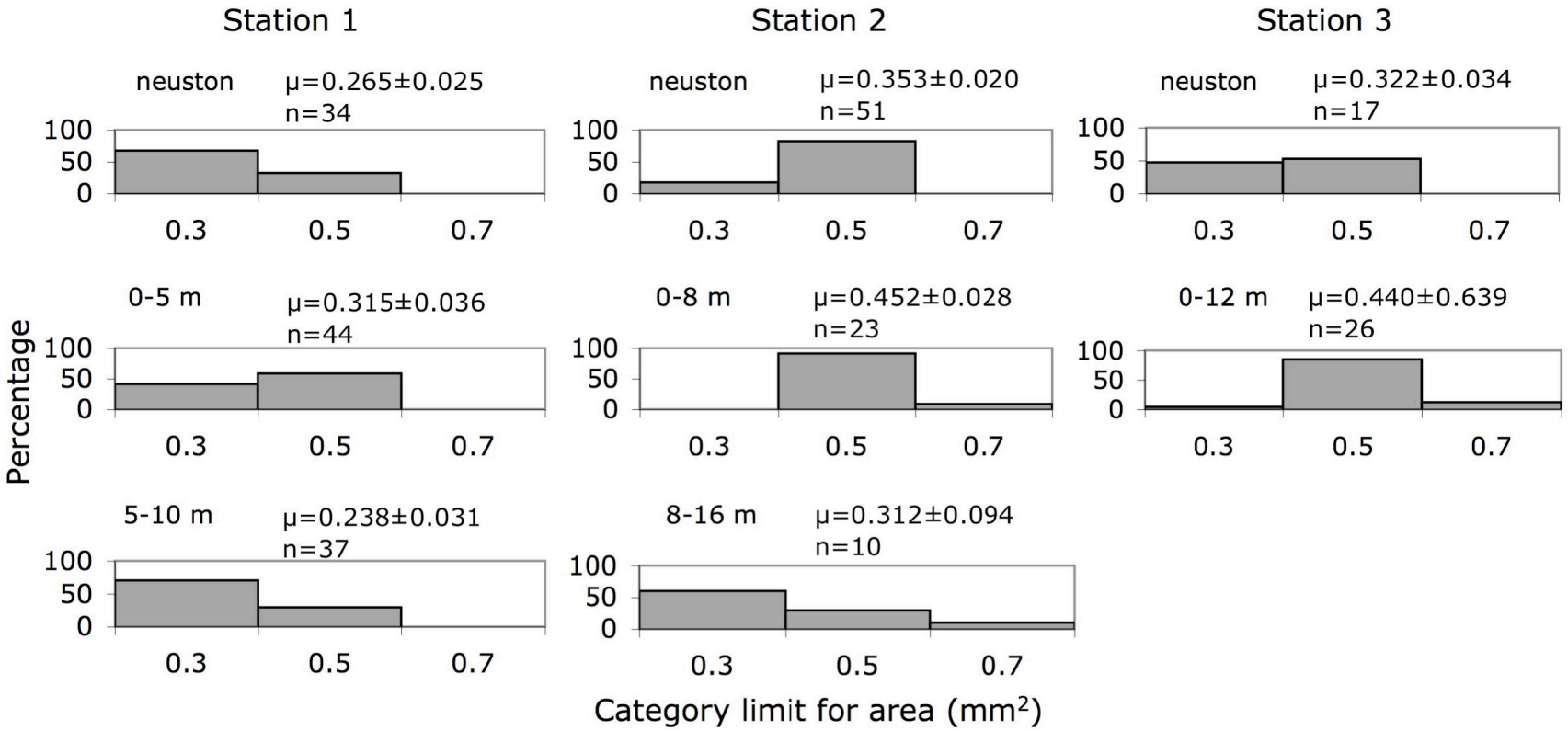


Figure 18. Size frequency distributions for *Evadne nordmanni* on 27 June 2007 (upwelling) at stations 1-3 off Coos Bay, Oregon. The depth interval, number of individuals sampled (n), mean area, and a 95% confidence interval are listed on each chart. Depth intervals with n<10 were excluded.

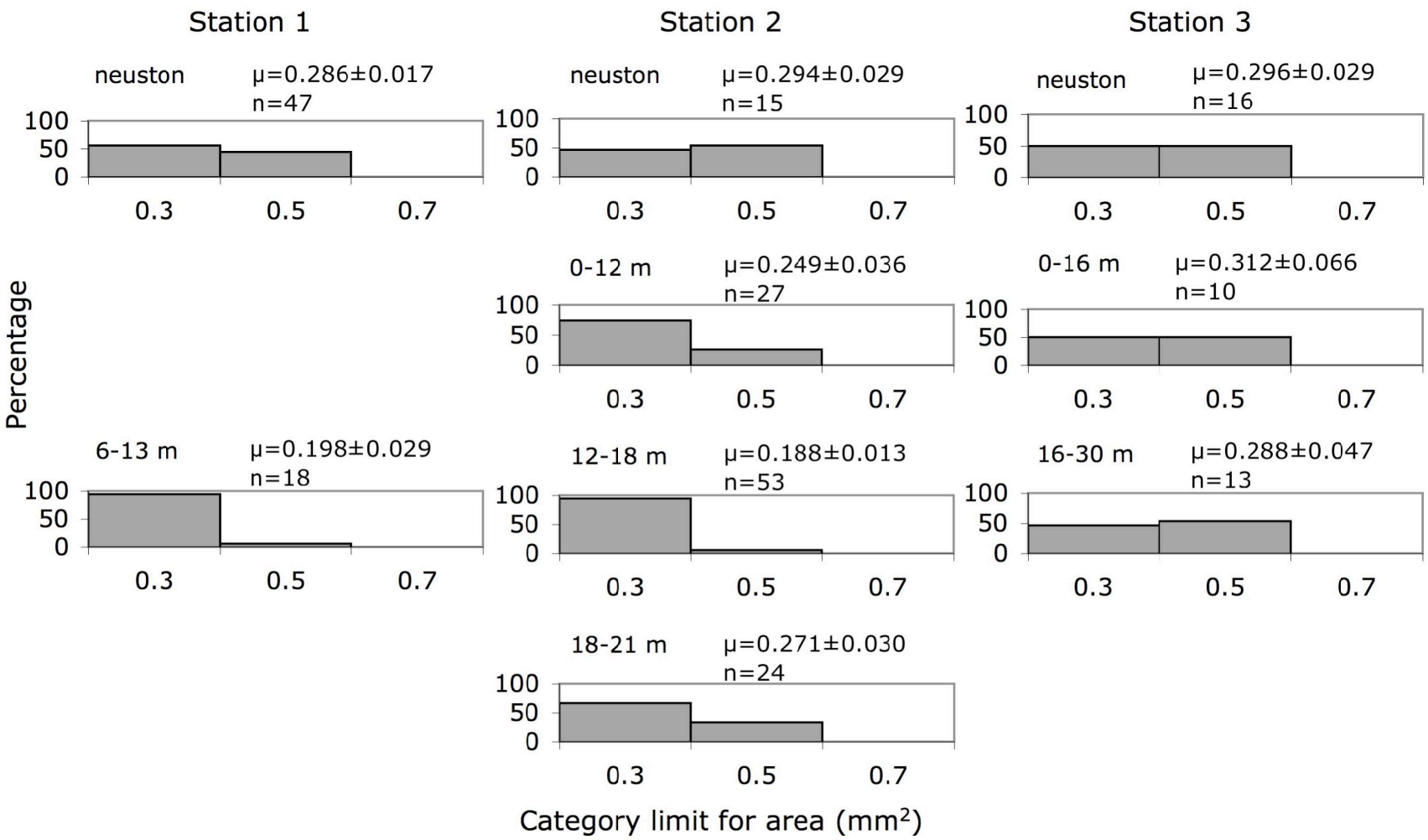


Figure 19. Size frequency distributions of *Evadne nordmanni* on 3 July 2007 (relaxation) at stations 1-3 off Coos Bay, Oregon. Depth interval, number of individuals measured (n), mean area, and a 95% confidence interval are indicated on each chart. Depth intervals with n<10 were excluded.

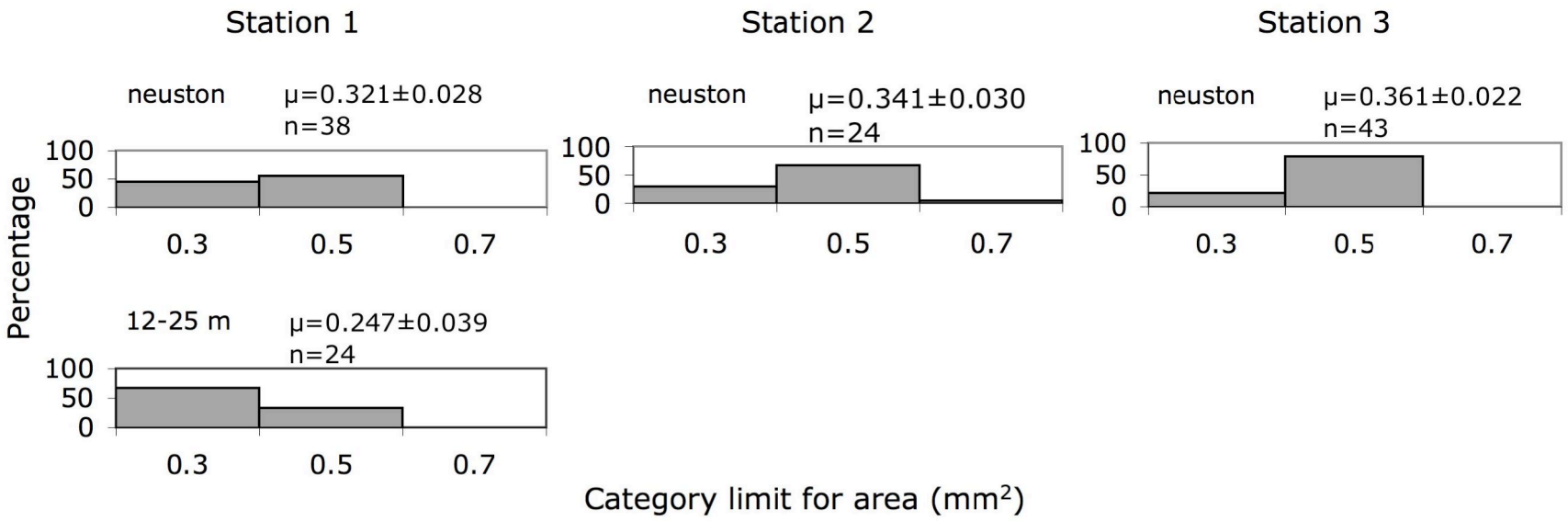


Figure 20. Size frequency distributions for *Evadne nordmanni* on 18 July 2007 (relaxation) at stations 1-3 off Coos Bay, Oregon. Depth interval, number of individuals measured (n), mean area, and a 95% confidence interval are indicated on each chart. Depth intervals with n<10 were excluded.

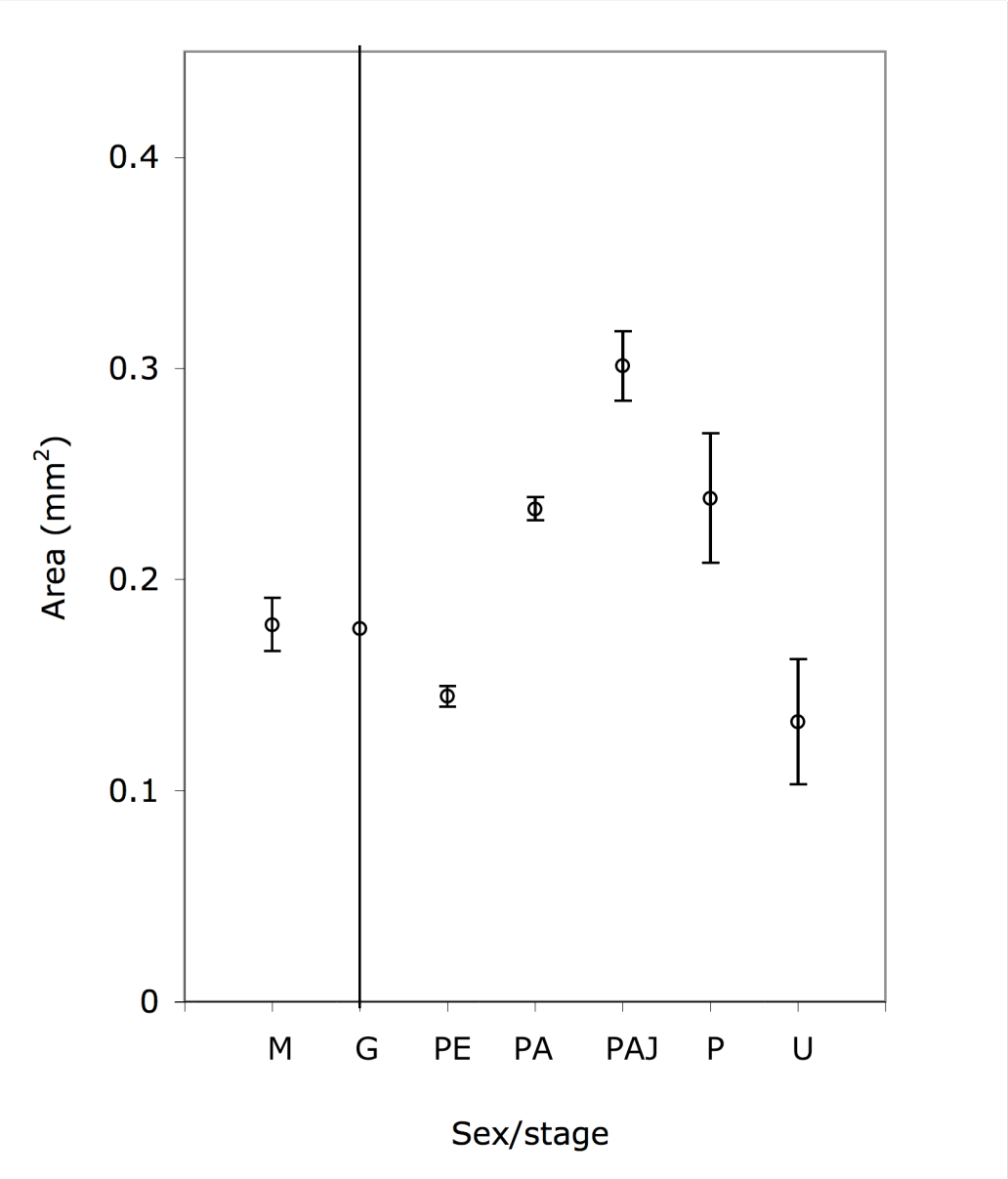


Figure 21. The mean area with an error bar representing the 95% confidence interval for each sex and stage of *Podon leuckarti* measured from the summer of 2007 off Coos Bay, Oregon. M=male (n=44), G=gamogenic female (n=2), PE=parthenogenic with early embryos (n=577), PA=parthenogenic with advanced embryos (n=469), PAJ=parthenogenic with juveniles nearing release (n=54), P=parthenogenic female with stage unidentified (n=15), U=unidentifiable sex/stage (n=29).

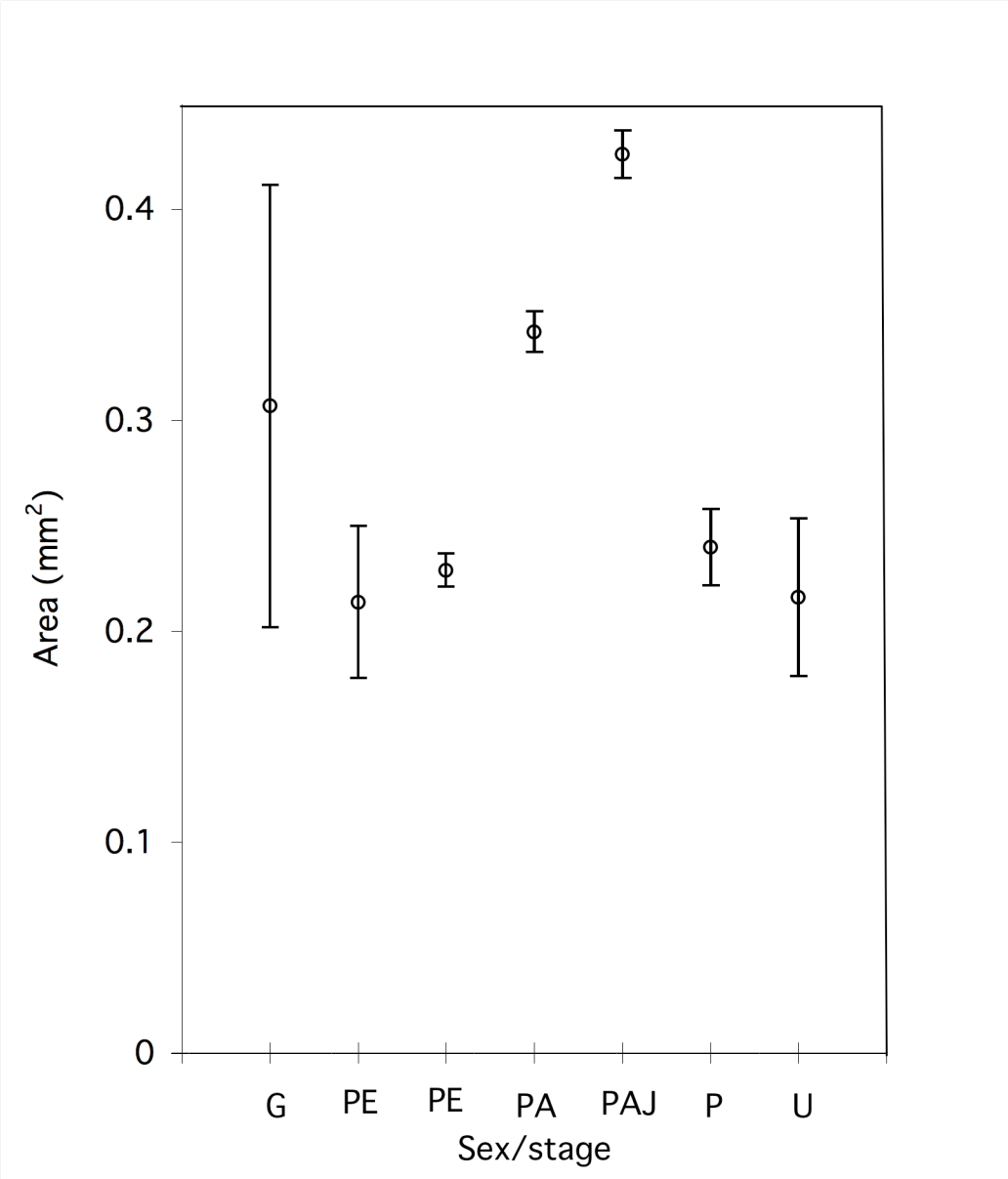


Figure 22. The mean area with an error bar representing the 95% confidence interval for each sex and stage of *Evadne nordmanni* measured from the summer of 2007 off Coos Bay, Oregon. G=gamogenic female (n=3), PER=parthenogenic with earliest embryos (n=22), PE=parthenogenic with early embryos (n=311), PA=parthenogenic with advanced embryos (n=256), PAJ=parthenogenic with juveniles nearing release (n=98), P=parthenogenic female with stage unidentified (n=81), U=unidentifiable sex/stage (n=20).

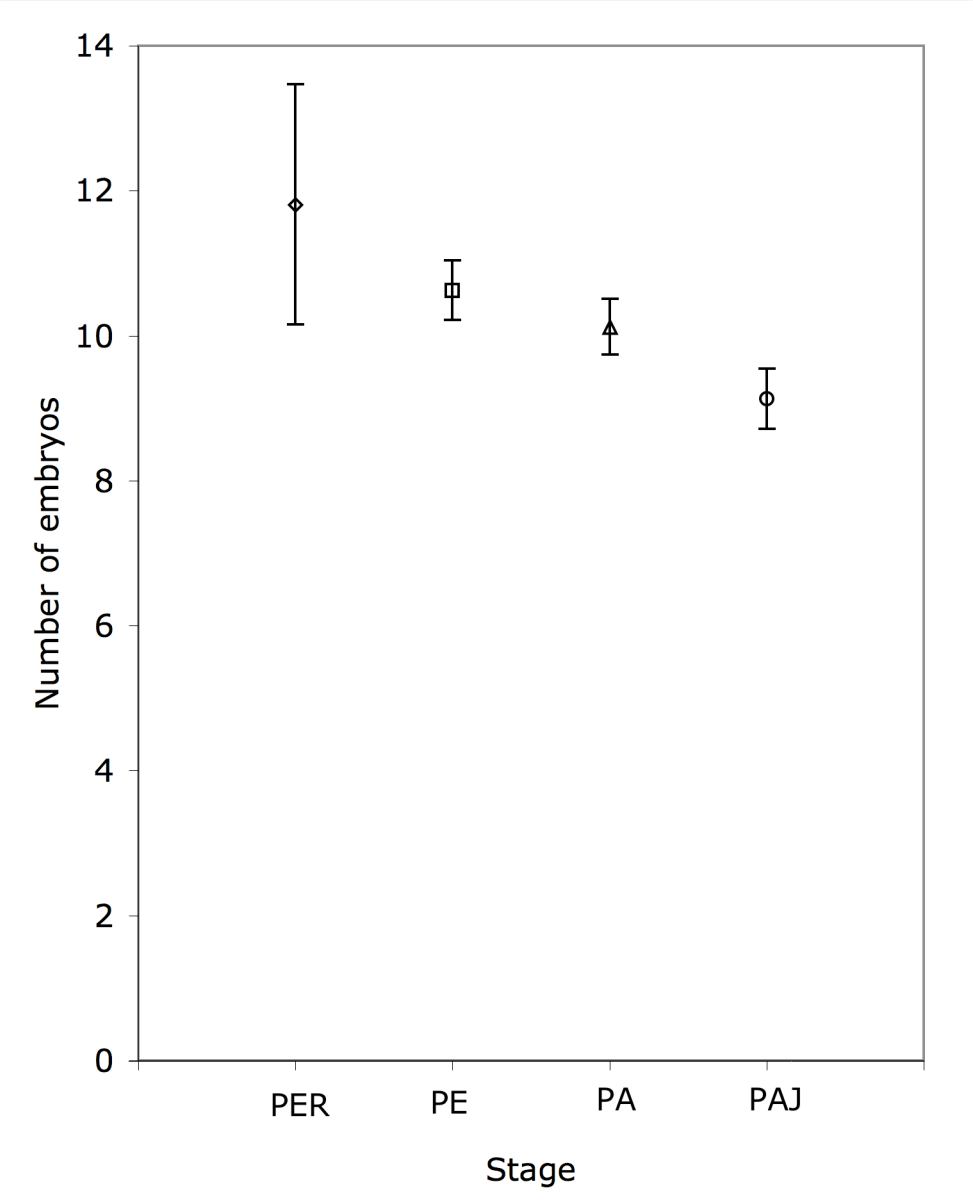


Figure 23. The mean number of embryos counted in each stage of parthenogenic *Evadne nordmanni* from the summer of 2007 off Coos Bay, Oregon. Error bars represent the 95% confidence intervals. PER=parthenogenic with earliest embryos (n=21), PE=parthenogenic with early embryos (n=196), PA=parthenogenic with advanced embryos (n=148), PAJ=parthenogenic with juveniles nearing release (n=94).

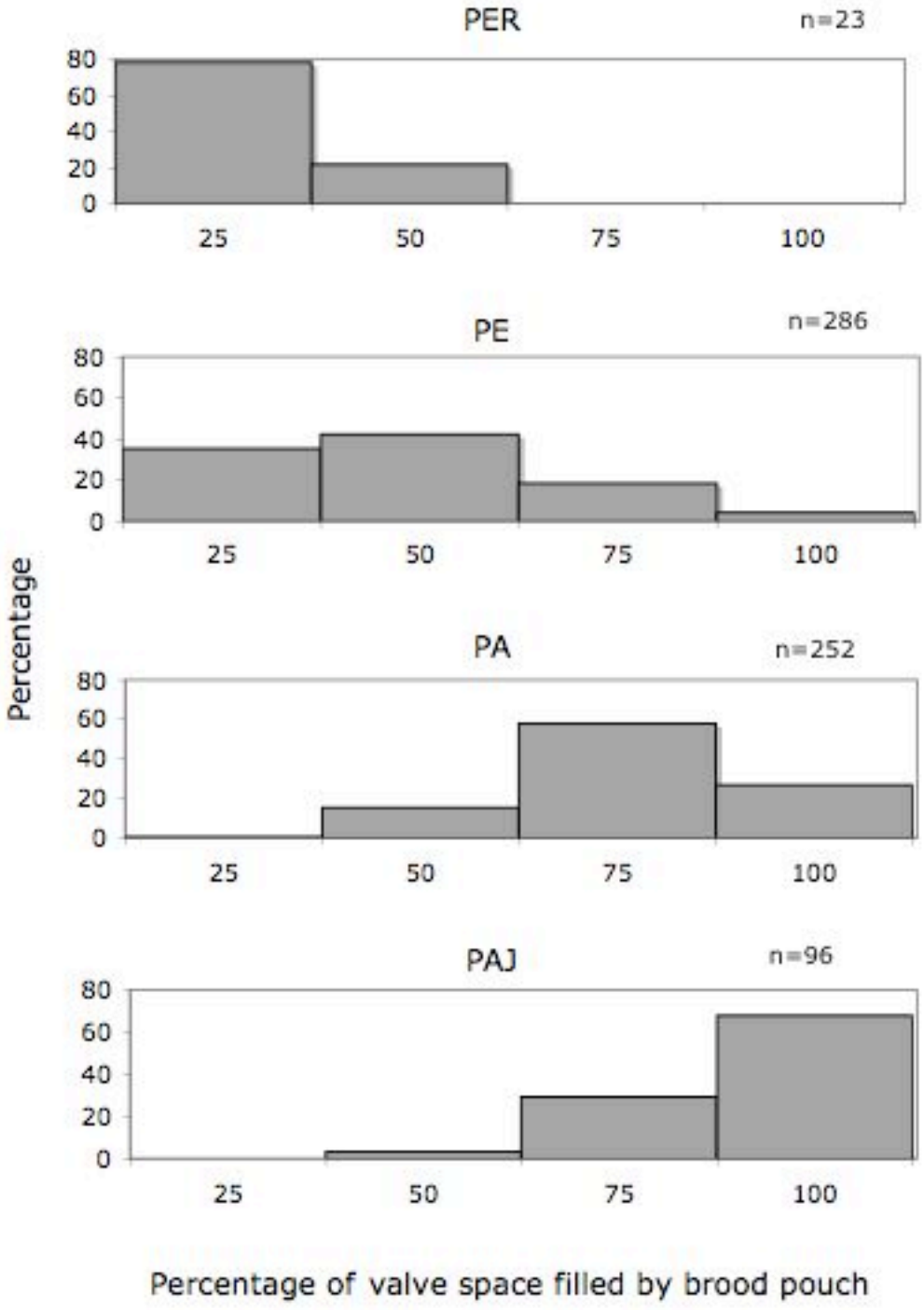


Figure 24. A frequency distribution of the approximate percentage of the valve space filled by the brood pouch in parthenogenic *Evadne nordmanni* with embryos in various stages of advancement. PER=parthenogenic with earliest embryos, PE=parthenogenic with early embryos, PA=parthenogenic with advanced embryos, PAJ=parthenogenic with juveniles nearing release.

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