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Seasonal variation of zooplankton abundance and community structure in Prince William Sound, Alaska, 2009–2016

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A B S T R A C T

Large calanoid copepods and other zooplankters comprise the prey field for ecologically and economically important predators such as juvenile pink salmon, herring, and seabirds in Prince William Sound (PWS). From 2009–2016, the Gulf Watch Alaska program collected zooplankton 5–10 times each year at 12 stations in PWS to establish annual patterns. Surveys collected 188 species of zooplankton with *Oithona similis*, *Limacina helicina*, *Pseudocalanus* spp., and *Acartia longiremis* as the most common species present in 519 samples. Generalized additive models assessed seasonal abundance and showed peak abundance in July (mean: 9826 no. m^{-3} [95% CI: 7990–12,084]) and lowest abundance in January (503 no. m^{-3} [373 to 678]). Significantly higher zooplankton abundance occurred in 2010 (542 no. m^{-3} ± 55 SE) and lowest in 2013 (149 no. m^{-3} ± 13). The species composition of communities, determined via hierarchical cluster analysis and indicator species analysis, produced six distinct communities based on season and location. The winter community, characterized by warm-water indicator species including *Mesocalanus tenuicornis, Calanus pacificus,* and *Corycaeus anglicus*, diverged into four communities throughout the spring and summer. The first spring community, characterized by copepods with affinities for lower salinities, occurred sound-wide. The second spring community, comprised of planktonic larvae, appeared sporadically in PWS bays in 2011–2013. Spring and summer open water stations were defined by the presence of large calanoid copepods. A summer community including the most abundant taxa was common in 2010 and 2011, absent in 2013, then sporadically appeared in 2014 and 2015 suggesting interannual variability of zooplankton assemblages. The zooplankton community shifted to a uniform assemblage characterized by cnidarians in the early autumn. Community assemblages showed significant correlations to a set of environmental variables including SST, mixed layer depth, location, depth of chlorophyll-*a* max, mixed layer average salinity, chlorophyll-*a* maximum, and bottom depth ($\rho = 0.24$, $p < 0.05$). The disappearance of the summer community coincided with the appearance of the Gulf of Alaska warm water anomaly known as "The Blob". A shift in zooplankton community composition during critical grazing periods for predators such as juvenile Pacific herring (*Clupea pallasi*) could have energetic consequences for overwintering success.

1. Introduction

Located at the northernmost part of the Gulf of Alaska (GOA), Prince William Sound (PWS) is a large estuary defined by numerous marginal fjords, containing approximately 3300 km of shoreline (Grant and Higgins, 1910). This small inland sea, approximately the size of Massachusetts (17,700 km^2), has experienced drastic oceanic and atmosphere changes over the past 30 yrs including several ENSO cycles, the recent marine heat wave known as "The Blob" (Hermann et al., 2016; Bond et al., 2015), and the Exxon Valdez oil spill, which still has measurable impacts (Boufadel et al., 2016). However, little is known about the structure of the PWS zooplankton community and overall zooplankton abundance during such environmental changes.

In the northern GOA and PWS, large lipid-rich copepods, mainly *Calanus marshallae*, *Neocalanus plumchrus*, *Neocalanus flemingeri*, *Eucalanus bungii*, and *Neocalanus cristatus*, constitute the majority of zooplankton biomass during the critical grazing period of the spring phytoplankton bloom and are thus the most thoroughly described species in this region in regards to life histories and abundance (Cooney, 1986; Cooney et al., 2001b; Coyle and Pinchuk, 2003, 2005; Coyle et al., 2013; Sousa et al., 2017). These species and other zooplankters comprise the prey field for ecologically and economically important predators such as juvenile pink salmon (Willette, 2001), herring (Foy and Norcross, 1999), juvenile walleye pollock, gelatinous carnivores (Purcell and Sturdevant, 2001), and other fishes, seabirds, and marine mammals.

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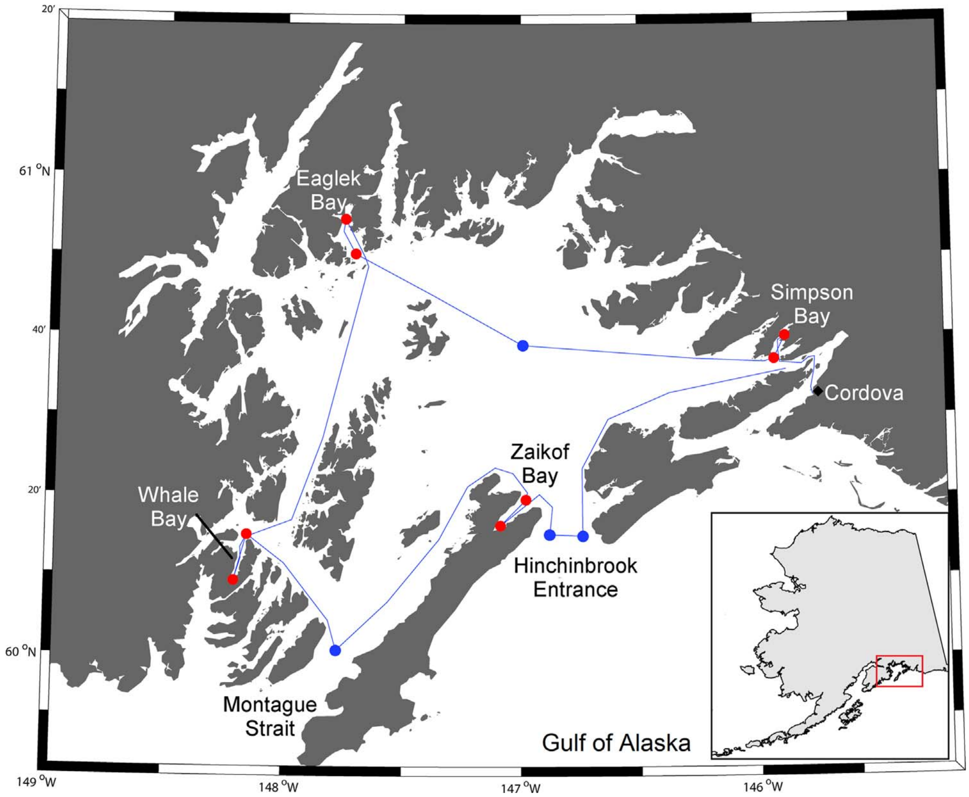

Fig. 1. Gulf Watch Alaska sampling stations within Prince William Sound, AK encompassing four bays (red dots), the two main entrances of PWS, and a central sound location. Blue dots signify stations considered here as "open water". The blue line indicates the travel path during each monthly cruise. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In the years following the oil spill, the Sound Ecosystem Assessment (SEA) program (1994–1997) examined the causes of PWS herring and pink salmon declines including the role zooplankton stocks played in the ecology of these planktivores. Cooney et al., 2001b described the cyclical abundance and biomass of the major zooplankton taxa found in PWS during SEA. A total of 88 zooplankton species were reported, but no multivariate analysis of the overall community structure of zooplankton assemblages or correlations to environmental variables was included.

On the northern GOA continental shelf (the Seward, or GAK line) the Northeast Pacific GLOBEC Program (1997–2004) investigated the effects of climate change and atmospheric anomalies on coastal phytoplankton and zooplankton productivity and included some western PWS stations. These results showed clear differences in species abundance based on atmospheric forcing between the open waters of the continental shelf and the protected inner waters of PWS (Coyle et al., 2013; Coyle and Pinchuk, 2005; Doubleday and Hopcroft, 2015). For example, *Neocalanus plumchrus* and *Neocalanus flemingeri* peak in abundance earlier in the spring in PWS than on the shelf (Coyle and Pinchuk, 2005). Also, pteropod abundance (*Limacina helicina*) on the continental shelf exhibited strong relationships with large scale climate patterns including the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO), although these relationships did not occur with *Limacina helicina* from PWS (Doubleday and Hopcroft, 2015).

Indicator species can reflect environmental conditions and community shifts resulting from those environmental conditions that may otherwise go unnoticed if the focus resides on only the most abundant taxa. First, a thorough description of community taxa is required for such an analysis (Dufrene and Legendre, 1997; Keister et al., 2009; Keister and Peterson, 2003; Morgan et al., 2003; Peterson and Keister, 2003). Zooplankton are often indicators of particular water masses based on correlations with water mass physical properties such as temperature, salinity, and stability of the mixed layer. Off the coast of Oregon, on-shelf zooplankton community structure characterized by three northern cold-water associated copepods supported the hypothesis that the source of the water mass was from the GOA (Morgan et al., 2003). Examination of southern warm-water associated species as indicators also described how ENSO shifts the zooplankton community to a more subtropical structure (Keister and Peterson, 2003; Peterson and Keister, 2003). Zooplankton community structure (along with abiotic variables) gave further evidence of changes in mesoscale circulation patterns in this region (Keister et al., 2009). In PWS, community structure and an examination of indicator species has not been thoroughly investigated.

The environmental drivers component of the Gulf Watch Alaska (GWA) program has collected zooplankton and oceanographic data in PWS approximately monthly during the annual production cycle since late 2009. In this study, our primary objective was to explore the characteristics of PWS zooplankton assemblages based on seasonal abundance, species composition, and the underlying environmental variables driving these communities. To do this, we used ANOVA to evaluate among-year zooplankton abundance differences, and multivariate techniques to describe patterns in the zooplankton community including indicator species analysis (ISA), non-metric multidimensional scaling (NMDS), and the BIO-ENV "Best" procedure to assess correlations between environmental variables and zooplankton community structure. A clear knowledge of how abundance and composition of zooplankton communities vary seasonally and interannually is an essential prerequisite to assess how they may be impacted by anthropogenic factors such as future oil spills or climate change.

2. Methods

2.1. Field collection

A total of 12 stations were selected for the GWA monitoring program based on prior sites occupied during the SEA program (Fig. 1). These sites included four bays around the periphery of PWS, the primary entrances, and a central sound station (PWS). For the purposes of