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Zooplankton Community Patterns in Puget Sound:

Description of a 20-year qualitative dataset

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Introduction

The Salish Sea Marine Survival Project (SSMSP; http://marinesurvivalproject.com/) is a trans-boundary collaboration created to identify the primary factors responsible for low marine survival of salmonids in the Salish Sea, the inland sea composed of the Strait of Georgia (Canada), Juan de Fuca (U.S./Canada), and Puget Sound (U.S.). The SSMSP is intended to evaluate factors that directly or indirectly influence salmonid survival, e.g., disease, predation, contaminants, and prey supply, and to investigate how these factors have changed since the 1970s-1980s.

Zooplankton are a primary prey source for juvenile salmon during early marine life. Species composition, distribution, and abundance of the zooplankton community are therefore key to understanding juvenile salmon growth potential, and declines in the abundance or quality of zooplankton prey may contribute to declines in salmon survival. This report describes changes in zooplankton composition in Puget Sound indicated by a qualitative zooplankton dataset collected over the period 1974-1994 as part of herring spawning surveys by the Washington Department of Fish and Wildlife (WDFW).

Background – Zooplankton as Indicators of Fish Prey and Ecosystem Health

Zooplankton serve an important role in marine food webs as the link between primary producers and vertebrate consumers. Population fluctuations in the zooplankton community track seasonal and annual changes in the environment; zooplankton can be useful indicators of ecosystem health and food web function. Zooplankton time series around the globe indicate changes in abundance, species composition, and lifecycle timing linked to climate cycles (e.g., the Pacific Decadal Oscillation (PDO), El Niño/La Niña, and the North Atlantic Oscillation (NAO)). Plankton responses to climatic events can include shifts in biomass and/or timing of seasonal cycles (Mackas et al. 1998, Edwards and Richardson 2004), which can have ecosystem-wide implications, such as trophic mismatches and alteration of food web structure (Bertram et al. 2001, Hunt Jr. et al. 2002, Beaugrand and Reid 2003, Keister and Peterson 2003, McGowan et al. 2003).

Zooplankton communities respond to fluctuations in the physical environment on both long and short timescales. Low-frequency (e.g., decadal) variation in overall abundance and timing of peak abundance can occur due to decadal climatic forcing (Brodeur and Ware 1992, Roemmich and McGowan 1995, Francis et al. 1998, Hare and Mantua 2000, Bond and Adams 2002, Chiba et al. 2006), while multi-decadal and interannual variation can result from El Niño/La Niña ocean conditions and local water mass properties (Miller et al. 1985, Mackas et al. 2001, Mackas and Galbraith 2002). Zooplankton communities also vary intra-annually in response to climate conditions and local water mass properties; for example, Oregon coast copepod species richness is significantly correlated with monthly PDO values and monthly averaged sea surface temperatures (Hooff and Peterson 2006), and short-term localized zooplankton community composition in the Mediterranean Sea indicates the presence of low-salinity water mass intrusions (Raybaud et al. 2008).

Zooplankton community indices can be useful indicators of marine fish population condition and survival. In the northeast Pacific Ocean, the zooplankton community undergoes a state-shift from warm/El Niño years to cool/La Niña years (Peterson et al. 2002, Keister et al. 2005, Hooff and Peterson 2006, Mackas et al. 2006). In warm years, the community has high species diversity and is dominated by subtropical, lipid-poor taxa. In contrast, during cool years, lipid-rich boreal taxa are abundant and species diversity decreases. This shift in the zooplankton community may catalyze a trophic cascade, causing multi-species population fluctuations. Statistical relationships between zooplankton community indices and fish populations have been developed for some species: copepod species richness and northern copepod biomass are correlated with coho salmon survival, an observation which is now commonly used in predictive models for salmon returns (Peterson and Schwing 2003, Peterson 2009).

Zooplankton and the Salish Sea Marine Survival Project

Significant changes throughout the Salish Sea ecosystem have been observed since the 1970s, such as herring stock age structure depression and population declines (Landis and Bryant 2010), groundfish declines and distributional shifts (Essington et al. 2013), altered abundance and distribution of forage fishes (Penttila 2007, Greene et al. 2015), and declining marine survival of salmonid species (Moore et al. 2010, Miller et al. 2014, Zimmerman et al. 2015). One leading hypothesis is that these observed changes reflect reduced capacity of the Salish Sea to support mid- and upper-trophic level species as a result of climate impacts, altered nutrient loading, and habitat alteration (Feely et al. 2010, Greene et al. 2015). Because zooplankton community indices can be good indicators of ecosystem conditions, food web structure, and fish survival, there is increasing desire for research and monitoring of Puget Sound zooplankton communities (PSEMP 2013). Short-term, localized studies suggest the Puget Sound zooplankton community is spatially and seasonally variable (Hebard 1956, Cooney 1971, Aron unpub); however, the lack of consistently sampled time series has precluded documentation of long-term trends.

Recently, a 20-year qualitative (presence/absence and ranked numeric abundance) dataset of zooplankton collected from across Puget Sound was made available for analysis by the WDFW. This qualitative dataset allows the first look into the zooplankton community across two decades of Puget Sound's changing ecosystem. The objectives of this report are to 1) document the existence and potential utility of this dataset and 2) use this dataset to qualitatively describe changes in zooplankton community patterns between 1974 and 1994 in three regions of Puget Sound.

Methods

Study Sites and Sample Collection

Zooplankton sampling sites were adjacent to Washington Department of Fish and Wildlife (WDFW) study sites for herring spawn surveys (Stick et al. 2014). Puget Sound herring stocks spawn across Puget Sound from the Canadian border and the San Juan Islands to the southern end of Puget Sound (Fig. 1) on intertidal and shallow subtidal vegetation between early January and mid-June. Spawning sites and spawn timing are stock-specific. Plankton sampling sites were located offshore of marine vegetation beds with herring spawn and sampling dates varied in accordance with spawn timing for each site (Table A1).

Plankton samples were collected by WDFW staff (Penttila, *unpub*), 1974-1994, using a 0.5 m diameter, 500 µm mesh single-ring net towed horizontally at approximately 1 m/s at 2 m water depth. Contact with the bottom was avoided and any samples contaminated with benthic material were discarded without processing. Catches were preserved in formalin and processed within a few weeks of each survey. Tow data and ranked numeric abundance data were recorded on paper datasheets, which were compiled into notebooks and placed in storage. In 2012, WDFW provided these notebooks to the authors, who made electronic copies of all datasheets and translated data by hand into an electronic workbook. Digitized data were reviewed post-entry for translation errors.

Data Analysis

Because this dataset represents the only zooplankton data available for many regions of Puget Sound across this time period, a description of the full dataset is presented. However, collection efforts were not consistent for all regions across time. For example, North Puget Sound was sampled 2,563 times total over 26 weeks in 20 years, while Whidbey Basin was sampled only 228 times total over 23 weeks in 18 years. Three regions of Puget Sound with the highest quality sampling records over time were selected for further analysis: Cherry Point (North), Central Puget Sound (a combination of Port Orchard/Madison and Quartermaster Harbor spawning sectors), and Squaxin (South).

The full dataset consists of 5770 total samples (Table 1). Time of day, minutes spent towing, and depth of tow were recorded for 63%, 58%, and 68% of samples respectively. Of the samples with recorded data, virtually all were taken during daylight hours between 6:00 and 18:00 (43% morning, 56% afternoon). Most tows (89%) were five minutes long, and most (79%) at tow depths of 0-2 m.

Geolocation data were not included in the dataset; however, site identifiers (e.g., “south of Wildcat Cove”, “Hale Pass”) were recorded for 99% of tows (Table A2). Approximate site locations were determined by cross-referencing identifiers with nautical charts (NOAA 2009: Nautical Charts 18421, 18440, 18500, and additional site-specific charts as needed). There were 71 samples for which site was not identifiable (either no site recorded or an unclear site record, e.g., “orange marker”). Based on recorded sampling dates and times, 32 of those samples were identifiable to herring spawning sector (e.g., Cherry Point) and 54 were identifiable to general region (e.g., North Puget Sound).

Sampling dates were standardized using International Organization for Standardization weeks (ordinal weeks of the year; hereafter referred to as ISO weeks) for analysis. Each taxon was assigned a qualitative abundance ranking based on the numerical abundance of that taxon within a sample (see full list of taxa in Table 2; abundance rankings in Table A3). Taxa which were absent (i.e., not encountered within a sample) were not assigned a ranking. The most common ranking category was a checkmark indicating presence (75% of assigned rankings), followed by “common” (12% of assigned rankings) and “uncommon” (4% of assigned rankings). Ranking assignments were specific to each sample, i.e., the numerical abundance of a specific taxon in a sample was assessed relative to the abundance of other taxa in that sample, and categories were not consistent across years. To account for inconsistencies, qualitative abundance data for all taxa were transformed into a binary (presence-absence only) dataset.

Logistic regressions of presence-absence data were used to evaluate trends in taxa presence in a region over time, and non-metric multidimensional scaling (NMDS) ordinations with the R package vegan (Oksanen et al. 2013) allowed visualization of spatial and temporal variation in the zooplankton community (Legendre and Legendre 2012). Because the total number of sampling events within a week varied from site-to-site and week-to-week, weekly encounter rates were calculated for use in ordinations as:

$$E_{ywT} = \frac{P_{ywT}}{N_{yw}}$$

where E is encounter rate of taxon T, P is the number of samples in which taxon T was present, N is total number of samples, y is year and w is ISO week.

NMDS is a flexible ordination method, since it has few underlying data assumptions (e.g., linearity is not assumed) and uses rank order rather than absolute distance. Pairwise distances among samples were calculated using Bray-Curtis dissimilarity index. Relationships between ordination stress (a measure of goodness-of-fit; lower stress indicates better fit) and dimensionality were examined. For all ordinations, two dimensions were sufficient to explain a high proportion of total variation in the dataset; monte carlo permutation tests indicated that the final stress statistic in each ordination was significant, i.e., the probability that the dataset had no real correlation structure is low. Ordination solutions were oriented such that Axis 1 (representing the first dimension) reflected the highest dispersion of points. Estimations of variance reflected in each axis were calculated by correlating the distance matrix derived from the data with ordination distance using scores from each ordination axis. Results from Ward’s hierarchical agglomerative clustering (Legendre and Legendre 2012) conducted with R package pvclust (Suzuki and Shimodaira 2011) suggested appropriate year-groupings (Table 3) for analyses of communities over time. All analyses were performed in R version 3.1.1 (R Core Team 2014).

Cherry Point, April-June, 1975-1993

The Cherry Point sector in the northern region (Fig. 1) was sampled in ISO weeks 15-22 from 1975-1993 and was the most consistently sampled region throughout the full study. From 1975-1988, sampling effort was highly consistent; effort declined post-1988. This dataset consists of 1198 samples (Fig 2a).

Central Sound (Port Orchard/Madison and Quartermaster Harbor), January-March, 1976-1994

Two sectors in Central Puget Sound were sampled: Port Orchard/Madison and Quartermaster Harbor (Fig. 1). Samples from these sectors were aggregated into one "Central Sound" region to increase sample size for comparisons among Puget Sound regions. Sampling was most consistent in ISO weeks 5-13 from 1978-1985; the region was sampled at a lower rate in 1976-1977, 1986-1987, and 1992-1994, and was not sampled at all in 1988-1991. The Central Sound dataset consists of 699 total samples: 341 from Quartermaster Harbor and 358 from Port Orchard/Madison (Fig. 2b).

Squaxin, January-April, 1975-1994

The Squaxin sector in South Puget Sound (Fig. 1) was sampled at approximately five-year intervals (1975-1979, 1984-1986, 1990-1994) over January-April (ISO weeks 5-15). Sampling effort declined over time (i.e., good sampling effort in the 1970s, poor in the 1990s). This dataset consists of 932 total samples, 75% of which were taken in the 1970s (Fig. 2c).

Comparison across regions

Data from the Cherry Point (North), Central Sound, and Squaxin (South) datasets described above were combined to assess regional and temporal variation across Puget Sound.

Results

Community Patterns and Trends in Taxa

Cherry Point, April-June, 1975-1993

Correlating the original distance matrix with ordination distance indicated that a two-dimensional NMDS ordination (stress = 0.22) explained an estimated 77% variance in the Cherry Point zooplankton community dataset. The ordination showed a seasonal shift (April-May-June) in the community (Fig. 3a) and longer-term temporal variation across the dataset (Fig. 3b), where zooplankton communities in 1975-1977 were separated to some degree from communities in 1978-1985 and communities in 1986-1993. Relationships between the ordination axis scores (Table 4) with each taxon indicated that Axis 1 (Figs. 7a, 8a) was most highly correlated with cladocerans (positive correlation, $R^2 = 0.68$), barnacle nauplii (positive, $R^2 = 0.42$), mollusc veligers/eggs (positive, $R^2 = 0.41$), and ctenophores (positive, $R^2 = 0.35$). Axis 2 (Figs. 9a, 10a) was most highly correlated with barnacle cyprids (negative, $R^2 = 0.35$), larvaceans (negative, $R^2 = 0.31$), and ctenophores (positive, $R^2 = 0.28$).

Logistic regression on presence-absence data for each taxon in the Cherry Point dataset indicated significant trends over time in the presence of several taxa (Table 5). Notable trends were an increase in presence of ctenophores (Fig. 11a) and decreases in presence of chaetognaths, crab megalopae, and barnacle cyprids (Fig. 12a).

Central Sound, January-March, 1976-1994

A two-dimensional NMDS ordination (stress = 0.22) explained an estimated 78% variance in the Central Sound zooplankton community dataset. A seasonal shift (January-February-March) in the community was apparent (Fig. 4a). Temporal groups consisting of 1976-1981, 1982-1987, and 1992-1994 separated to some degree in ordination space (Fig. 4b). Axis 1 (Figs. 7b, 8b) was most highly correlated with siphonophores (negative, $R^2 = 0.52$) and ctenophores (negative, $R^2 = 0.29$), while Axis 2 (Figs. 9b, 10b) was most highly correlated with barnacle nauplii (positive, $R^2 = 0.64$), and small medusae (positive, $R^2 = 0.34$) (Table 4).

Of the three regions, Central Sound had the fewest taxa that showed significant trends over time (Table 5). Presence of ctenophores and siphonophores decreased (Fig. 11b), while amphipods increased (Fig. 12b).

Squaxin, January-April, 1975-1994

A two-dimensional NMDS ordination (stress = 0.19) explained an estimated 85% variance in the Central Sound zooplankton community dataset. There was clear separation of the January and April zooplankton communities in ordination space, with February and March communities intermediate (Fig. 5a). Year groupings as determined by cluster analysis were more complex in Squaxin than in other regions; while some years were separated in ordination space (e.g., 1975-1976 versus 1993-1994), most years overlapped (Fig. 5b). Axis 1 (Figs. 7c, 8c) was most highly correlated with barnacle nauplii (positive, $R^2 = 0.71$); Axis 2 (Figs. 9c, 10c) was most highly correlated with annelids (positive, $R^2 = 0.36$) (Table 4).

The Squaxin region was characterized throughout the dataset by high presences of siphonophores, ctenophores, and small medusae. Presence of other gelatinous organisms (larvaceans, large medusae) increased significantly over the time period sampled (Table 5, Fig. 11c), while presence of some non-gelatinous taxa decreased (crab zoeae, amphipods, chaetognaths; Fig. 12c). Based on recorded genera of medusae, small medusae were < 2 cm bell diameter (genera *Clytia*, *Obelia*, *Sarsia*). Large medusae exceeded 2 cm in bell diameter (genera *Aequorea*, *Aurelia*, *Cyanea*). The genus *Halistaura* was recorded in both small and large medusae categories, possibly reflecting catches of juvenile and more mature specimens. Based on sampling gear and technique (0.5 m diameter net towed horizontally in the upper water column), medusae larger than 0.3 m bell diameter were likely not sampled representatively. These data therefore may not reflect the full size range of medusae found within Puget Sound.

Comparison across regions

A two-dimensional NMDS ordination (stress = 0.19) explained an estimated 83% variance in the Puget Sound zooplankton community. The three regions (Cherry Point, Central Sound, Squaxin) formed distinct groups in ordination space (Fig. 6c) and displayed a similar seasonal progression (January-February-March-April-May-June) in the zooplankton community as was observed for each region separately (Fig. 6a). These results are confounded due to sampling time: the Central Sound and Squaxin zooplankton communities were concurrently sampled (January-March and January-April, respectively), whereas Cherry Point was sampled later in the season (April-June). The concurrently sampled Central Sound and Squaxin communities did show evidence of spatial grouping. Additionally, the April samples from the Squaxin community were separated in ordination space from the Cherry Point April samples; each grouped with their respective region. No temporal trend across years was observed; year groupings overlapped highly in ordination space (Fig. 6b). Axis 1 (Fig. A4a) was most highly correlated with mollusc veligers/eggs (negative, $R^2 = 0.71$), barnacle nauplii (negative, $R^2 = 0.59$), cladocerans (negative, $R^2 = 0.58$), and barnacle cyprids (negative, $R^2 = 0.36$). Axis 2 (Fig. A4b) was most highly correlated with siphonophores (positive, $R^2 = 0.55$), and ctenophores (positive, $R^2 = 0.49$) (Table 4).

Discussion

Given the qualitative nature of this dataset, small-scale community composition and abundance fluctuations were not detectable, but broad-scale patterns were apparent. Our results indicate spatially explicit seasonal and interannual patterns in the Puget Sound zooplankton community, and significant, region-specific trends in the presence of some taxa over a multi-decadal scale. These findings are generally consistent with the hypothesis that the Puget Sound ecosystem has changed from its “historical” state in the 1970s to present-day, and the apparent increase in gelatinous organism presence at Squaxin is in accordance with surface townetting catches that show increased jellyfish catches in South Puget Sound since the 1970s (Greene et al. 2015).

Region-specific groupings across Puget Sound may be influenced by two factors: 1) sampling timing and 2) location. Central Sound and Squaxin zooplankton communities were sampled in the winter (January-March/April), whereas Cherry Point was sampled in the spring (April-June). Given the seasonal distinctions observed in all ordinations and the sample timing of each sector, regional groupings likely reflect a temporal signal. Both Squaxin and Cherry Point sectors were sampled during the first week of April and the April Squaxin community was separate in ordination space from the April Cherry Point community. Although based on limited data, this suggests that, in addition to the temporal signal, there is a geographic signal – i.e., the Cherry Point zooplankton community differs from the Squaxin community due to their geographic locations in Puget Sound.

Presence-absence surveys are often used to indirectly infer species abundance and distribution patterns (Fangliang et al. 2002, Stauffer et al. 2002). Presence-absence studies can generally detect large population fluctuations; however, the power to detect small-to-modest changes is often limited, especially in cases with few sites, low encounter rates, spatially variable populations, and variable detectability of the taxon in question (Strayer 1999, Joseph et al. 2006); statistically, a low number of events per variable causes low power to detect trends in standard logistic regression (Morris 1994, Rhodes et al. 2006). We assumed perfect detection: if a taxon was present at a site, it was present in the sample. However, non-detection does not necessarily imply a genuine absence of that taxon from the sampling site. A taxon may be present at a site but go undetected due to sampling design, life history characteristics specific to that taxon, or simply random chance. In addition, detectability of a taxon is unlikely to remain constant over space and time, given the dynamic nature of ecosystems (Mackenzie 2005). For example, Puget Sound experiences localized periodic high freshwater input and mixing forces which may affect zooplankton presence in the upper water column. In the case of this dataset, the power to detect abundance trends is limited. Several taxa (e.g., tectibranchs, euphausiids) were rarely encountered in the dataset, but are unlikely to be truly absent from the Puget Sound zooplankton community. These taxa were likely not representatively sampled with the methods used in this study. Other taxa were ubiquitous (e.g., copepods, see Table 3A) but may have changed in undetected ways such as shifts in copepod species composition or abundance. Significant trends in taxa which were regularly encountered using the sampling methods described (e.g., barnacle larvae, ctenophores) are more likely to reflect real changes in community composition, abundance, and/or distribution.

Increases in gelatinous organisms (jellyfish, ctenophores, siphonophores) at Cherry Point and Squaxin and concurrent declines in forage fish abundances in these regions (Penttila 2007, Greene et al. 2015) may be indicative of altered food web structure and a transition towards a truncated foodweb. Inverse relationships between gelatinous zooplankton and planktivorous fishes over time have been suggested in other regions. Parsons and Lalli (2002) postulate a framework based on the dual food chain hypothesis (Greve and Parsons 1977) wherein two types of pelagic food chains co-exist: high-energy (large diatoms-large zooplankton-fish) and low-energy (small flagellates-small zooplankton-cnidarians/ctenophores). In this framework, factors such as climate change, nutrient input (pollution, eutrophication), and overfishing act alone or synergistically to produce ecosystem conditions favoring low-energy food chains and increases in cnidarian and ctenophore populations (Parsons and Lalli 2002, Richardson et al. 2009).

Oceanographic properties such as temperature and dissolved oxygen levels in Puget Sound basins influence community structure; basins with higher relative abundances of jellyfish also have lower relative abundances of forage fishes (Rice et al. 2012). This pattern may also reflect food web dynamics. For example, gelatinous zooplankton are important predators on smaller crustacean zooplankton (Mackas et al. 2001); jellyfish and planktivorous fishes may compete for zooplankton prey (Purcell and Arai 2001, Purcell and Sturdevant 2001). Furthermore, the life history and ecology of jellyfishes may enable them to outcompete fishes. Jellyfish are typically generalist predators which feed continuously without satiation, can compensate for periodic food limitations, can reproduce sexually or asexually, and have fairly short generation times (Purcell et al. 1999). Some jellyfish may also prey directly upon fish eggs and larval or juvenile fishes (Lebour 1922, Purcell and Arai 2001). An increase in presence of gelatinous zooplankton in Puget Sound could therefore have important implications for the quantity and quality of the forage base available to fish.

Our results suggest significant trends over time in regional presence of gelatinous taxa and other zooplankton taxa such as chaetognaths, amphipods, crab larvae, and barnacle larvae. The latter taxa are common prey items for several fish species in Puget Sound (e.g., chinook salmon, coho salmon, pink salmon, and herring; Duffy et al. 2010, Kemp 2014). Small gelatinous zooplankton (larvaceans, ctenophores) also serve as fish prey in Puget Sound (e.g., chum, smelt; Kemp 2014, Greene *unpub data*). At Cherry Point, nearly half the estimated variance in the community was reflected in the first ordination axis, which was associated most strongly with increasing cladoceran presence over time ($p = 0.001$). In Central Puget Sound, the first axis also reflected nearly half the variance, and was negatively associated with siphonophore presence, which decreased over time ($p < 0.001$). This axis appeared to be associated with year groupings, reflecting community change across time. At Squaxin, the first axis reflected 61% of the community variance, and was highly correlated with barnacle nauplii presence. This axis appeared to be associated with seasonal progression of the community to a greater extent than in Central Sound or Cherry Point. In all three individual regions, barnacle larvae and larvaceans were identified in the four highest correlations of axis scores with taxa. Altered abundance and distribution of these zooplankton prey sources and potential jellyfish competitors among basins of Puget Sound may influence fish community dynamics and contribute to the patterns observed by Rice et al. (2012).

Recommendations for Future Work

Validation of this methodology against a quantitative dataset is strongly recommended. Transforming a methodically-collected time series of zooplankton data (e.g., comparable surface tows collected by Greene et al. 2012) to presence-absence data and performing analogous analyses would verify the ability of qualitative datasets to characterize and track zooplankton communities over time and space. Additionally, validation of the qualitative methodology would enable comparison of the patterns observed in this dataset to zooplankton data from other regions and link to ongoing sampling in Puget Sound.

Additional metadata on samples within this dataset may exist. WDFW herring spawn survey vegetation sample field data sheets, which have recently been digitized (Tessa Francis, *pers comm*), may include data on zooplankton sampling locations, tow durations, and time of tows. Flowmeters were deployed on select plankton tows in later years of the dataset (Dan Penttila, *pers comm*). Flowmeter data were recorded on vegetation sample data sheets and field report notebooks and were not available for inclusion in the current analysis. A small amount of larval fish length data included in this dataset remains unanalyzed. These data alone are not of sufficient quality to justify further analysis at this time, but may be useful as a supplement to other ichthyoplankton datasets to document larval fish catch timing and length from the 1970s to present at specific sites in Puget Sound.

Although there are many caveats associated with qualitative datasets, these analyses summarize a unique long-term zooplankton collection effort in Puget Sound and, when assessed in comparison with current Puget Sound zooplankton sampling program data collected through the Salish Sea Marine Survival Project (US Salish Sea Technical Team 2014), have the potential to provide information on ecosystem shifts within the Salish Sea over several decades.

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Tables

Table 1. Metadata for the full dataset across Puget Sound (5770 samples total): number, depth in meters, and duration in minutes of tows each year.

Year	Total Number of Tows	Number of Tow Depth Records	Tow Depth (m) (Mean ± 1 Std)	Number of Tow Duration Records	Tow Duration (minutes) (Mean ± 1 Std)
1974	5	5	0.9 ± 0	0	
1975	333	333	0.1 ± 0.3	318	7 ± 2
1976	437	437	1.7 ± 1.9	419	6 ± 2
1977	515	515	2.9 ± 1.7	510	5 ± 1
1978	377	377	2.3 ± 1.2	377	5 ± 0
1979	323	242	3.1 ± 1.4	281	5 ± 0
1980	307	296	1.7 ± 0.3	302	5 ± 0
1981	300	296	1.8 ± 0.1	296	5 ± 0
1982	408	359	1.8 ± 0	374	5 ± 1
1983	452	2	1.8 ± 0	14	5 ± 1
1984	450	20	3.5 ± 1.2	57	8 ± 2
1985	365	0		99	6 ± 2
1986	329	329	0.9 ± 0.2	53	5 ± 0
1987	277	277	0.9 ± 0.1	24	5 ± 0
1988	214	214	0.9 ± 0.1	10	7 ± 3
1989	111	40	1.8 ± 0	46	5 ± 0
1990	93	18	1.8 ± 0	18	9 ± 2
1991	142	60	1.1 ± 0.4	55	6 ± 2
1992	146	25	1 ± 0.3	28	5 ± 0
1993	121	40	0.9 ± 0	40	5 ± 0
1994	41	0		0	
1997	6	6	0.9 ± 0	0	
1998	10	10	0.9 ± 0	2	4 ± 1
1999	8	8	0.9 ± 0	4	5 ± 0

Table 2. Number of times each taxon was observed over the full dataset, proportion of tows in which each taxon was present, and recorded comments by the sampler for each taxon (e.g., size, genus). Note that sampler comments were opportunistically recorded and do not provide consistent information across samples or years.

Taxon	# Times Observed	% Tows Present	Comments
Copepods	5597	97.0	Size (tiny, very small, small, medium, large, very large, mixed sizes) was recorded for 319 tows. Additional comments recorded for 214 tows. Recorded comments were calanoid, caligids, copepodids (juvenile copepods), fish lice, predaceous.
Miscellaneous fish larvae	5477	94.9	Eulachon and longfin smelt larvae (osmerids) were not confidently distinguished; however, both may have been encountered in the Cherry Point region. Numeric data and limited length data were recorded for herring larvae (3111 tows), sand lance larvae (2351 tows), and osmerid larvae (1051 tows). Comments on larval taxonomy recorded for 108 tows. Comments included anchovy, Cottidae, flatfish, Pholidae, eulachon, Hexagrammidae, single species, mixed species, "short gut".
Crab zoeae	5338	92.5	Size (tiny, small, very small, large, very large, mixed) recorded for 159 tows.
Mysid larvae	5166	89.5	"Mysid" was a catch-all taxon, intended to include all shrimp-like crustacean larvae, presumably of true shrimps, mysid shrimps, and possibly juvenile euphausiids. Comments (*Callianassa*, ghost shrimp, mud shrimp) recorded for 129 tows.
Small medusae	4789	83.0	Comments (*Aequorea*, *Clytia*, *Halistaura*, hydroid, *Obelia*, mixed, *Sarsia*) recorded for 193 tows.
Pelagic fish eggs	4645	80.5	Numeric data recorded for 25 tows; anchovy eggs recorded separately for 37 tows. It is unclear whether anchovy eggs were always recorded separately when they occurred in samples.
Oikopleura larvaceans	4600	79.7	
Chaetognaths	4506	78.1	Numeric data recorded for adult chaetognaths for 348 tows. Lifestage (adult, juvenile, mixed) noted for 328 tows.
Amphipods	3609	62.5	Comments (benthic, ectoparasite, epibenthic, gammarid, hyperiid, mixed) recorded for 78 tows.
Ctenophores	3146	54.5	Numeric data recorded for 271 tows.
Barnacle nauplii	2817	48.8	
Siphonophores	2683	46.5	
Mollusc veligers/eggs	2095	36.3	Comments (*Littorina*, clam, gastropod, veliger) recorded for 118 tows.
Annelids	1368	23.7	Comments (polychaete, syllid, tentacled worm, *Tomopteris*, trochophore (larval stage), worm) recorded for 38 tows.

Cladocerans	1190	20.6	
Pteropods	935	16.2	Comments (*Clione*, *Limacina*, *helicina*, *Corolla*) recorded for 589 tows.
Crab megalopae	625	10.8	
Echinoderm larvae	580	10.1	
Mysids	554	9.6	
Barnacle cyprids	423	7.3	
Large medusae	302	5.2	Numeric data recorded for 263 tows. Comments (*Aequorea*, *Aurelia*, *Cyanea*, *Halistaura*, *Clytia*) recorded for 205 tows.
Ostracods	265	4.6	
Euphausiids	258	4.5	Numeric data recorded for 130 tows.
Bryozoan larvae	187	3.2	
Cumaceans	140	2.4	
Tectibranchs	23	0.4	

Table 3. Year groupings produced by Ward's hierarchical cluster analysis on yearly encounters by region. Groupings were simplified for use in NMDS ordinations.

Region	Year groupings produced by cluster analysis	Year groupings used in ordination
Cherry Pt	1975-1977, 1990, 1992	1975-1977
	1978-1979, 1981, 1983-1985, 1988	1978-1985
	1980, 1982, 1986-1987, 1989, 1991, 1993	1986-1993
Central Sound	1976-1981, 1986	1976-1981
	1982-1985, 1987, 1993	1982-1987
	1992, 1994	1992-1994
Squaxin	1975-1976, 1984, 1990, 1992	1975-1976
	1977-1979, 1985-1986, 1991	1977-1979
	1993-1994	1984-1986
		1990-1992
		1993-1994
Multi-region	1975-1986, 1991, 1994	1975-1986
	1987-1990, 1992-1993	1987-1990
		1991-1994

Table 4. Top four taxa correlations with NMDS axis scores for each region. Direction of correlation and R^2 value in parentheses.

Axis 1 scores	**Cherry Point**	**Central Sound**	**Squaxin**	**Multi-region**
	Cladocerans (+, 0.68)	Siphonophores (–, 0.52)	Barnacle nauplii (+, 0.71)	Mollusc veligers/eggs (–, 0.71)
	Barnacle nauplii (+, 0.42)	Ctenophores (–, 0.29)	Echinoderm larvae (+, 0.23)	Barnacle nauplii (–, 0.59)
	Mollusc veligers/eggs (+, 0.41)	Mysids (–, 0.23)	Annelids (+, 0.19)	Cladocerans (–, 0.58)
	Ctenophores (+, 0.35)	Crab zoeae (+, 0.21)	Crab zoeae (+, 0.17)	Barnacle cyprids (–, 0.36)
Axis 2 scores				
	Barnacle cyprids (–, 0.35)	Barnacle nauplii (+, 0.64)	Annelids (+, 0.36)	Siphonophores (+, 0.55)
	Larvaceans (–, 0.31)	Small medusae (+, 0.34)	Small medusae (+, 0.32)	Ctenophores (+, 0.49)
	Ctenophores (+, 0.28)	Larvaceans (+, 0.21)	Mysids (+, 0.28)	Annelids (+, 0.19)
	Echinoderm larvae (–, 0.22)	Chaetognaths (+, 0.12)	Larvaceans/Ostracods (both +, 0.18)	Mysids (+, 0.17)

Table 5. Trends observed by logistic regressions of taxa presence/absence in each region over time. Formula: glm(Taxon~Year, family=binomial(link=”logit”). The year coefficient estimate is provided, indicating direction and magnitude of trend over time. * indicates p-value <0.05, ** indicates p-value <0.01, and *** indicates p-value <0.001. Note that sampling effort was not consistent over time (see Fig. 2).

Taxon	**Cherry Point**	**Central Sound**	**Squaxin**
Mysids	-0.21***	-0.3***	0.05**
Ctenophores	0.09***	-0.17***	0.01
Larvaceans	-0.07***	0.01	0.13***
Pelagic fish eggs	-0.1***	-0.13	-0.06***
Fish larvae (misc)	0.22***	-0.01	0.63**
Chaetognaths	-0.04**	-0.05	-0.07***
Echinoderm larvae	-0.05**	-0.14**	-0.01
Crab zoeae	-0.43**	-0.06	-0.07*
Annelids	-0.01	-0.11*	0.03*
Siphonophores	0.02	-0.23***	-0.02
Large medusae	0.11	0.02	0.14***
Barnacle cyprids	-0.12***	0	-0.04
Ostracods	-0.01	0.05	0.08***
Crab megalopae	-0.06***	-0.18	-0.04
Cladocerans	0.04***	0.12	0.01
Small medusae	-0.07**	-0.01	0.05
Amphipods	-0.01	0.04	-0.06**
Copepods	0.02	0.3**	0.21
Euphausiids	-0.04	0	-0.2*
Pteropods	-0.01	0.17*	0.02
Mysid larvae	0.05	0.09*	0
Mollusc veligers/eggs	0.01	0.08*	0.01
Bryozoan larvae	0.05*	0	0
Barnacle nauplii	0.01	0	0
Tectibranchs	0.19	0	0.17
Cumaceans	0.1	-0.04	0.03

Figures

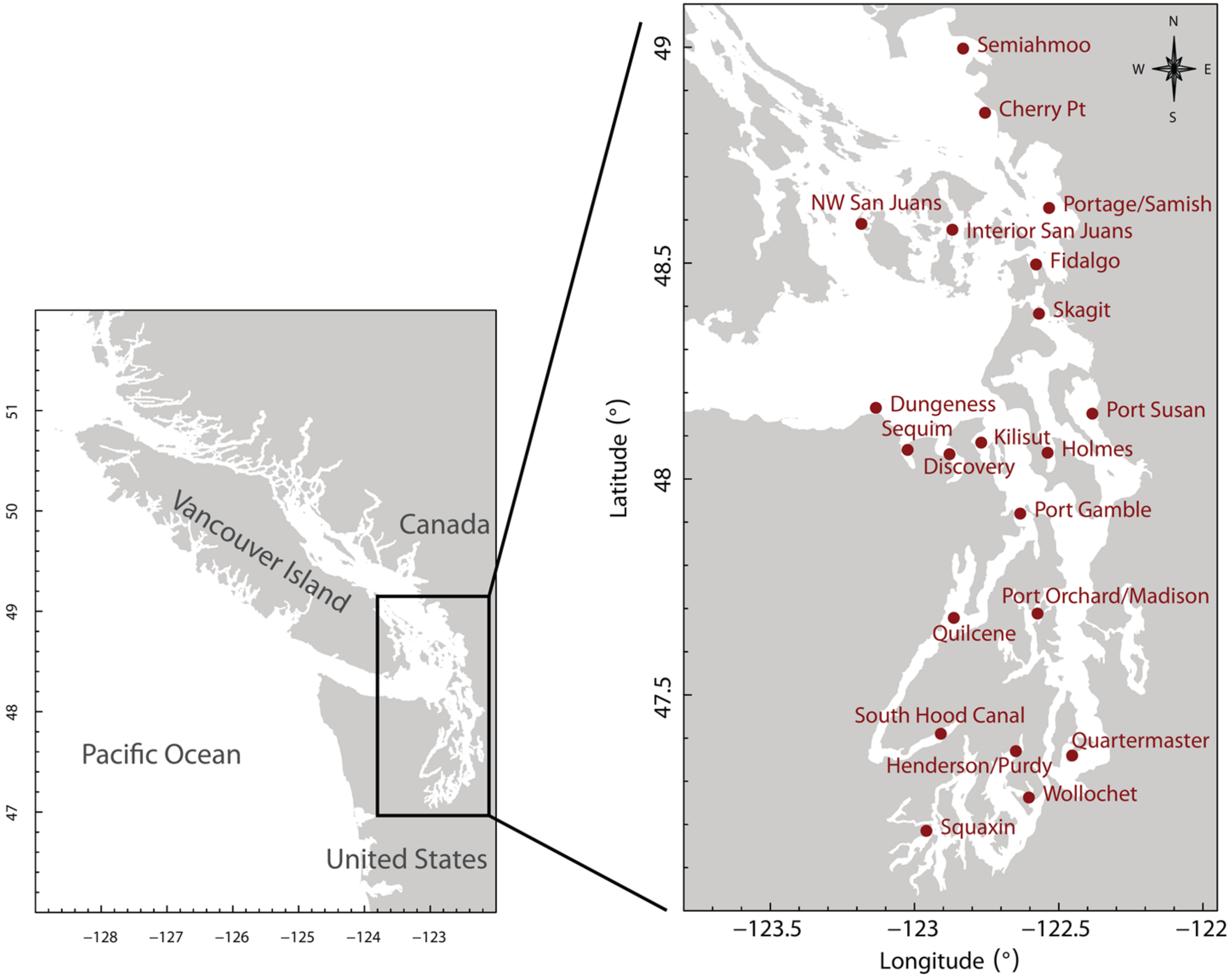


Figure 1.Approximate locations of zooplankton sampling near documented herring spawning grounds in Puget Sound.

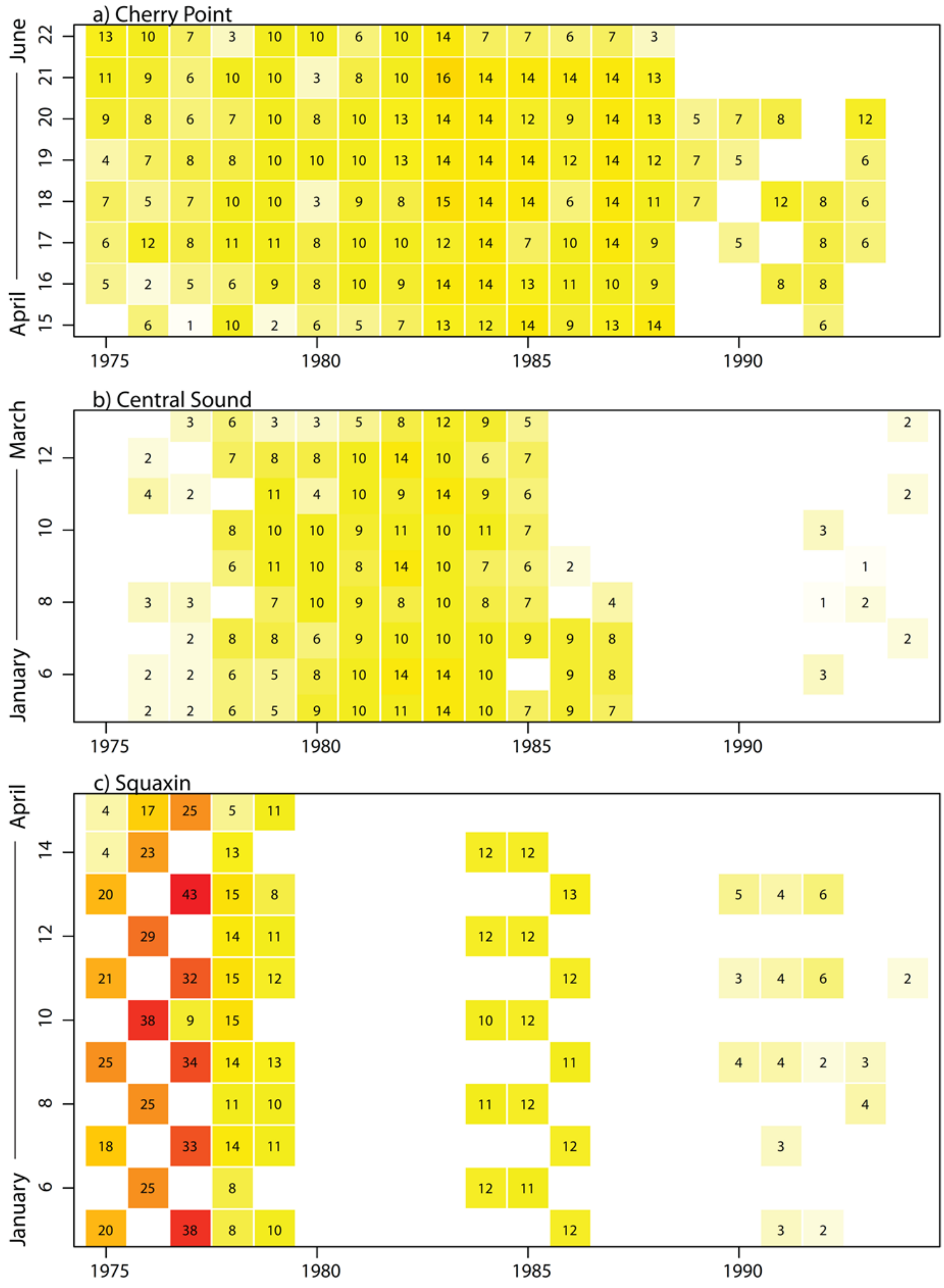


Figure 2. Number of samples taken in Cherry Point (a), Central Sound (b), and Squaxin (c) by year (x-axis, aligned across regions) and ISO week (y-axis). Colors are scaled across regions and indicate sampling effort, from no sampling (white) to high-frequency sampling (red).

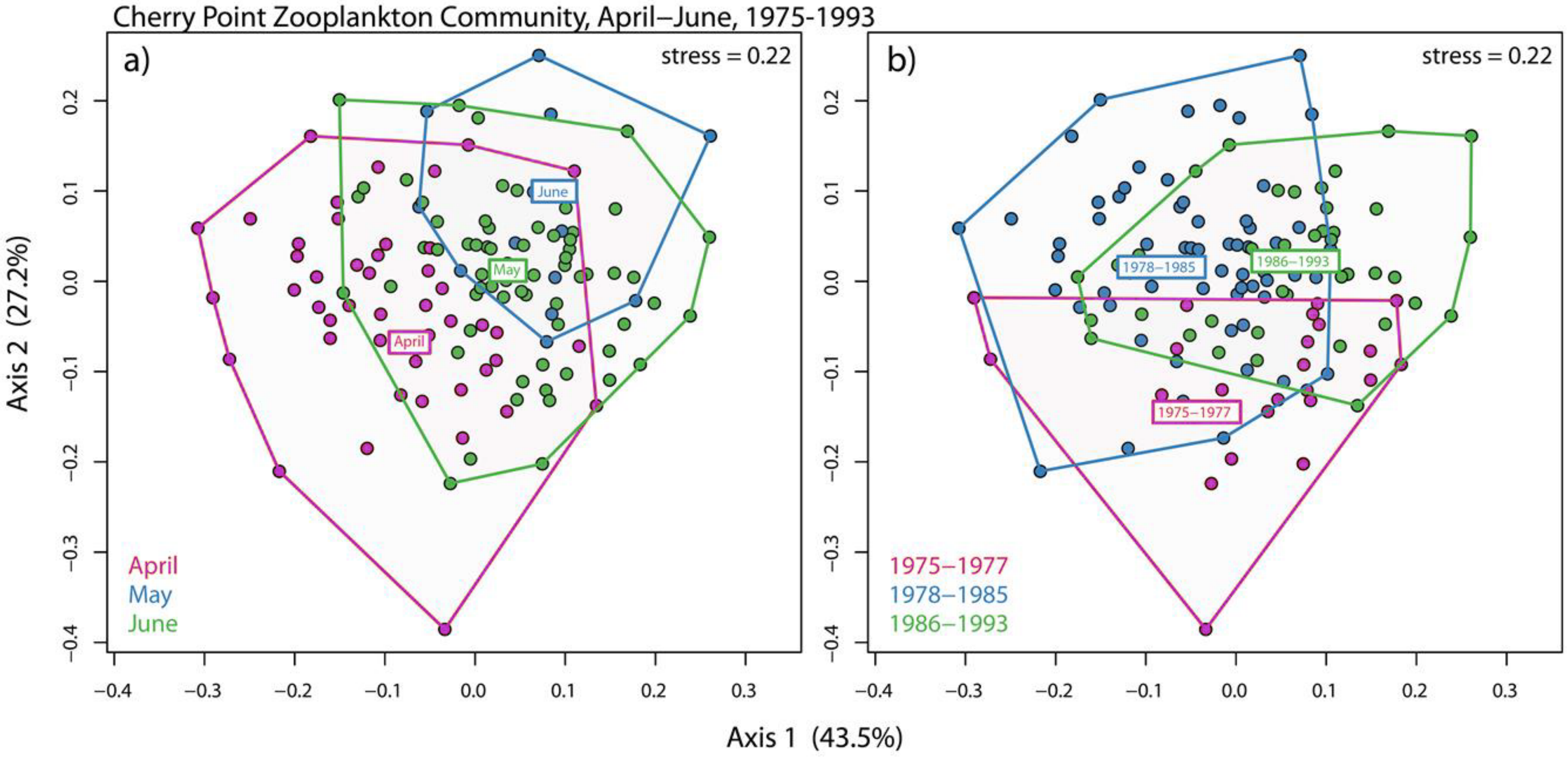


Figure 3. NMDS ordination (2 dimensions, stress = 0.22) of the Cherry Point zooplankton community, April-June, 1975-1993, suggesting seasonal patterns (a) and patterns across time (b). Estimated axis variance (correlation of original distance matrix with ordination distance of each axis) is provided.

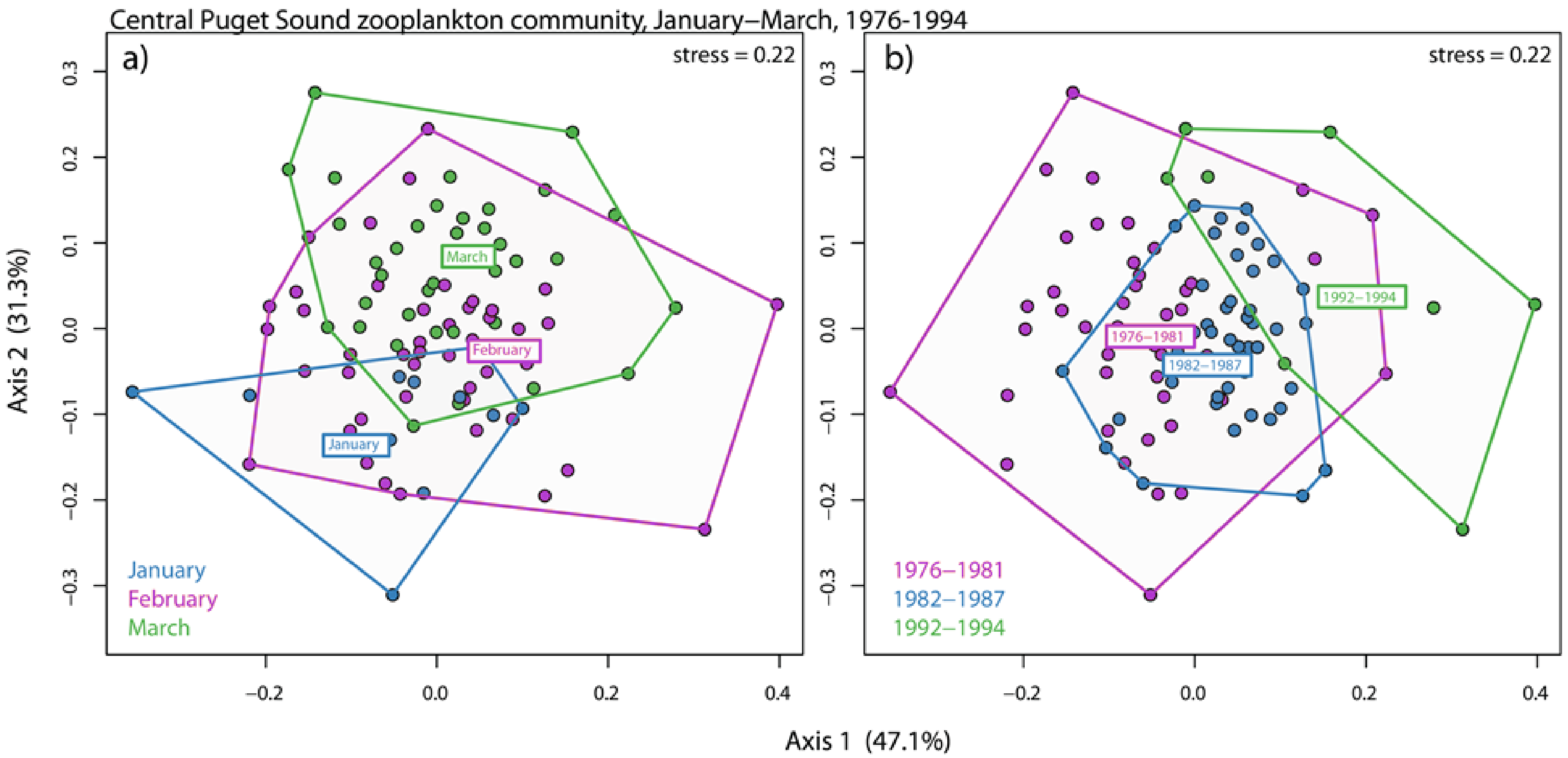


Figure 4. NMDS ordination (2 dimensions, stress = 0.22) of the Central Sound zooplankton community, January-March, 1976-1994, suggesting seasonal patterns (a) and patterns across time (b). An estimate of variance for each axis (correlation of original distance matrix with ordination distance of each axis) is provided. Note that Central Sound was not sampled in 1988-1991.

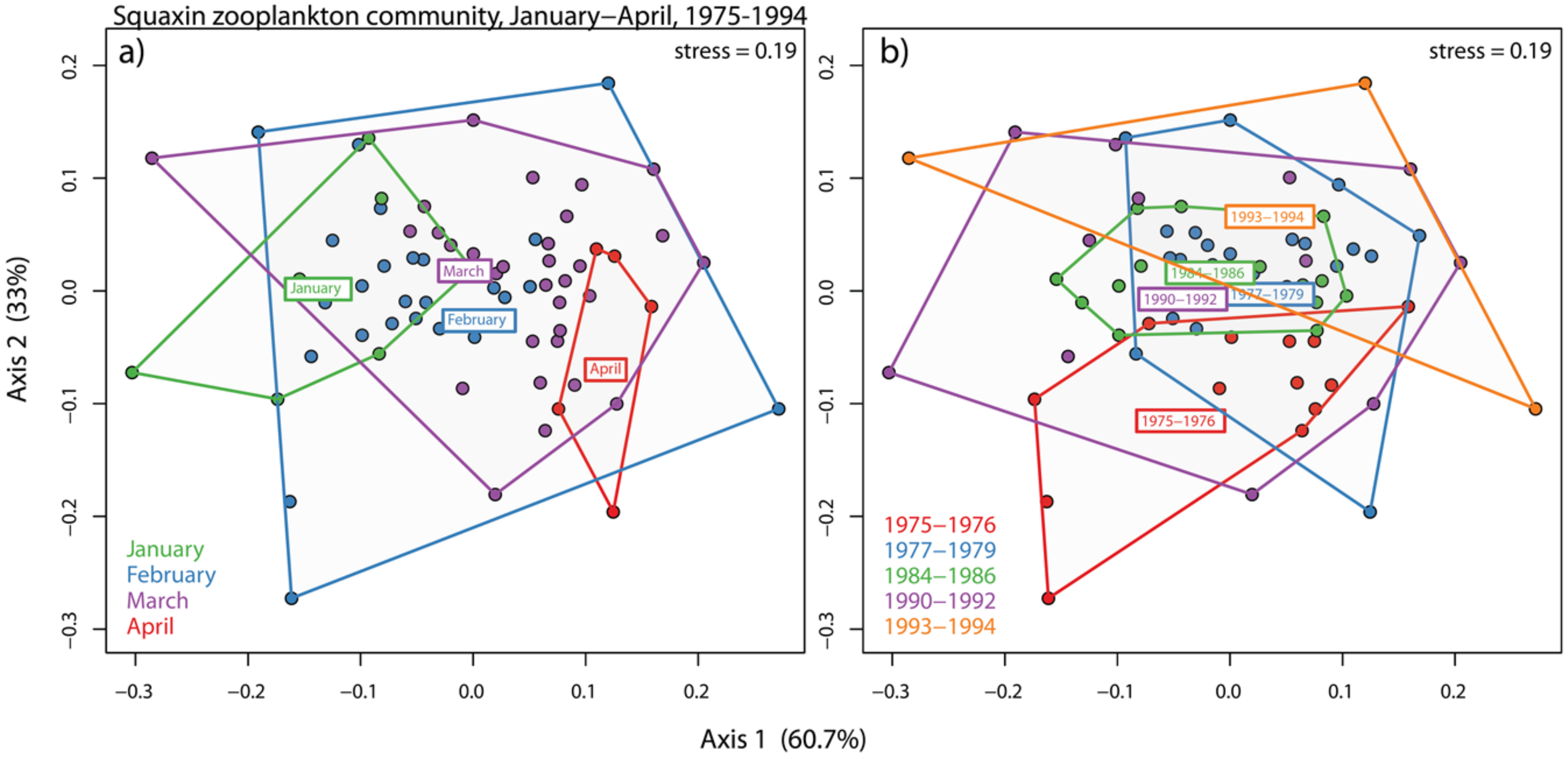


Figure 5. NMDS ordination (2 dimensions, stress = 0.19) of the Squaxin zooplankton community, January-April, 1975-1994, suggesting seasonal patterns (a) and patterns across time (b). An estimate of variance for each axis (correlation of original distance matrix with ordination distance of each axis) is provided. Note that Squaxin was not sampled in 1980-1983 or 1987-1989.

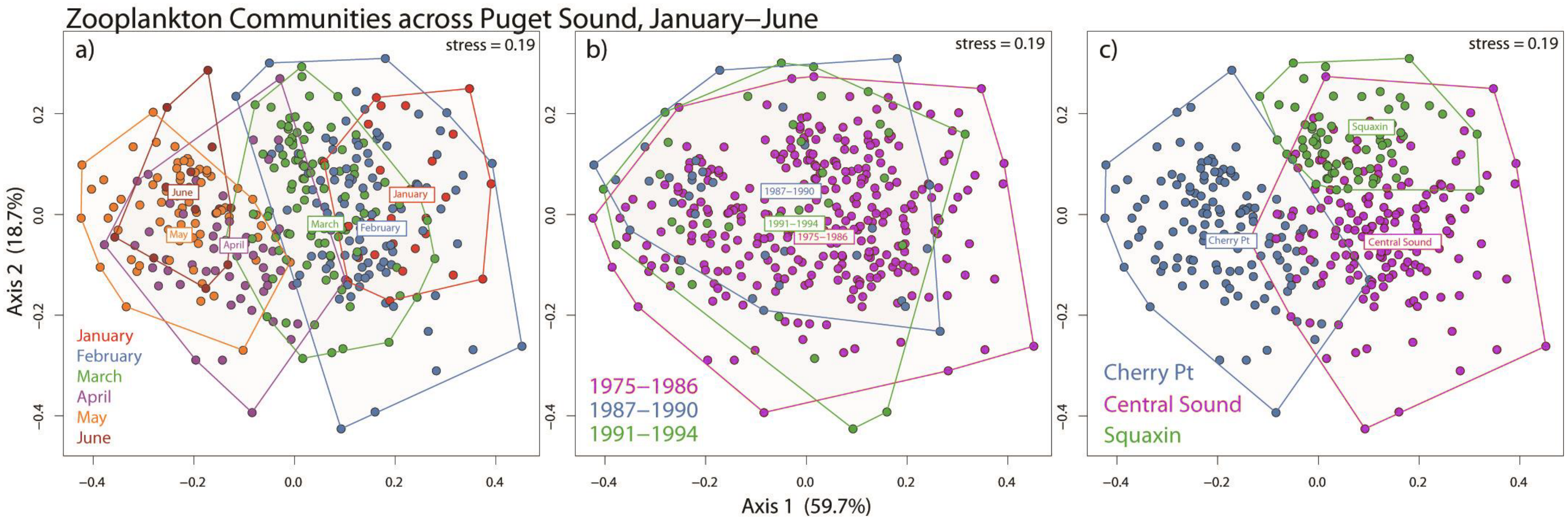


Figure 6. NMDS ordination (2 dimensions, stress = 0.19) of the zooplankton community across Puget Sound, including Cherry Point, Central Sound, and Squaxin datasets. Seasonal patterns (a) and spatial patterns (c) are apparent, but multi-year temporal patterns (b) are not supported by these data. Note that seasonal and spatial factors are confounded, since sampling times in each region were not identical (see Fig. 2). Central Sound and Squaxin were sampled in winter (January-March/April) whereas Cherry Point was sampled in spring (April-June). An estimate of variance for each axis (correlation of original distance matrix with ordination distance of each axis) is provided.

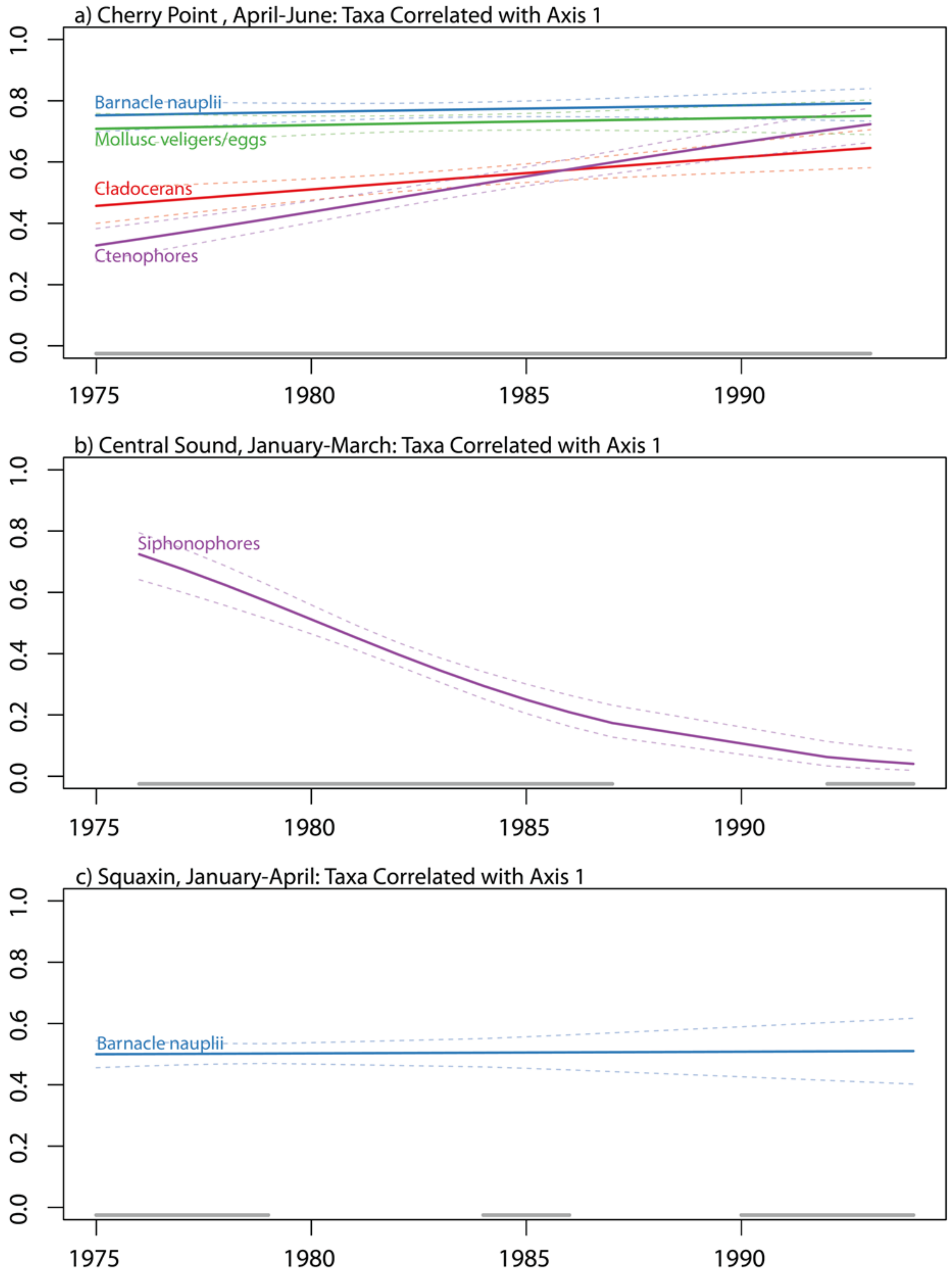


Figure 7. Interannual patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in presence over two decades of a) Cherry Point, b) Central Sound, and c) Squaxin taxa most strongly correlated with NMDS axis 1 ($R^2 > 0.30$). Gray lines at the base of each plot denote years sampled in each region.

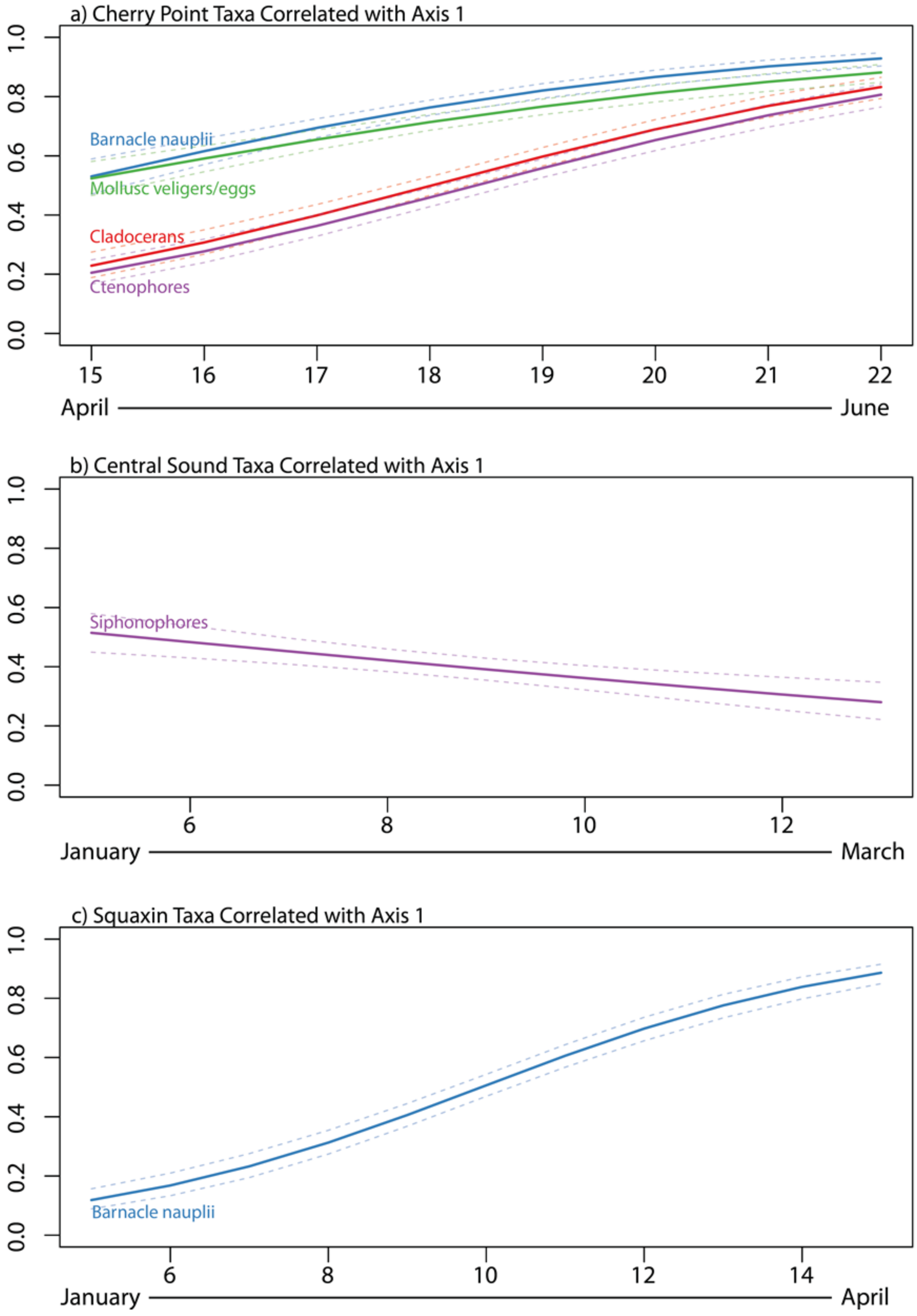


Figure 8. Seasonal patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in seasonal presence of a) Cherry Point, b) Central Sound, and c) Squaxin taxa most strongly correlated with NMDS axis 1 ($R^2 > 0.30$).

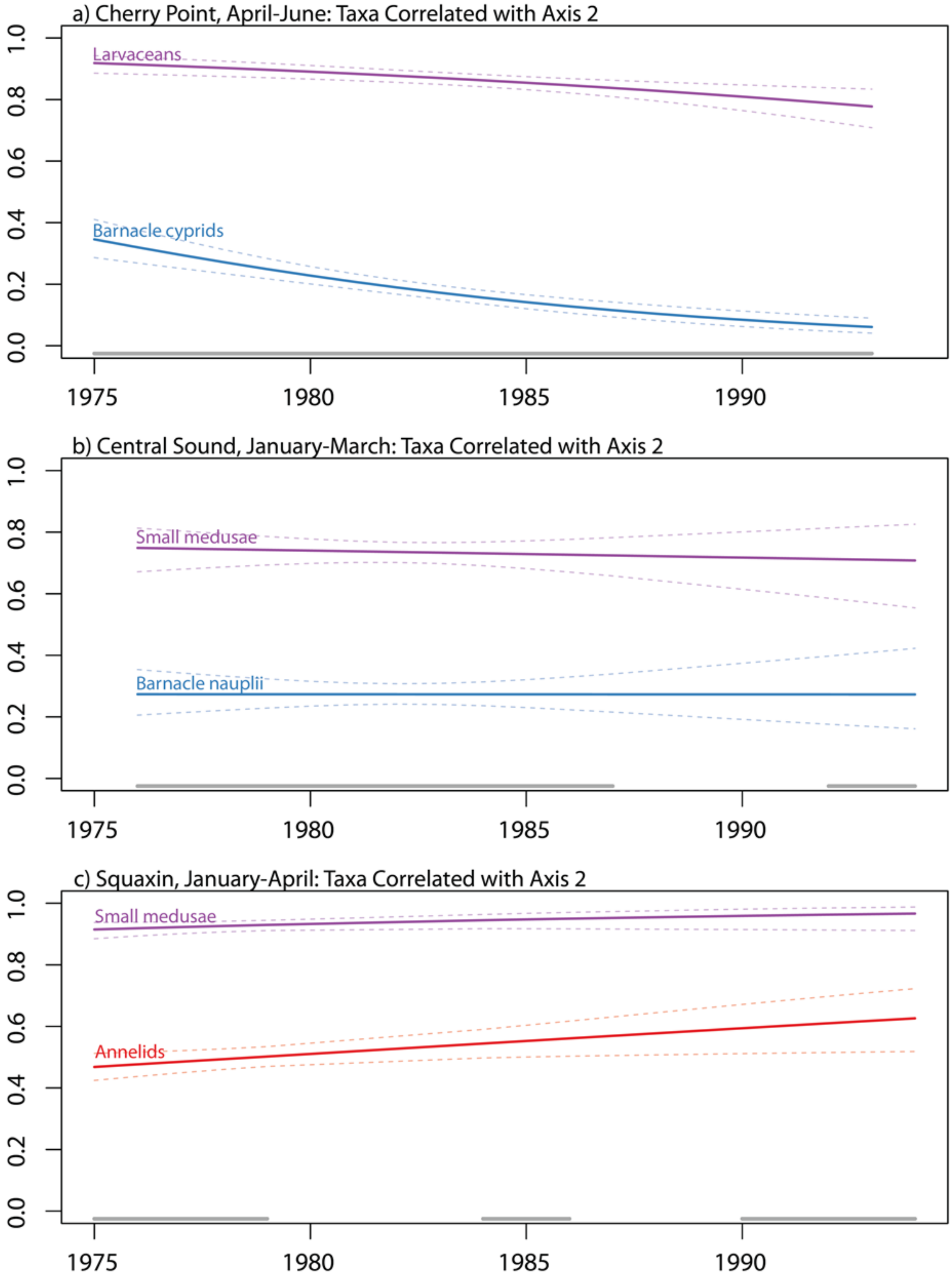


Figure 9. Interannual patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in presence over two decades of a) Cherry Point, b) Central Sound, and c) Squaxin taxa most strongly correlated with NMDS axis 2 ($R^2 > 0.30$). Gray lines at the base of each plot denote years sampled in each region.

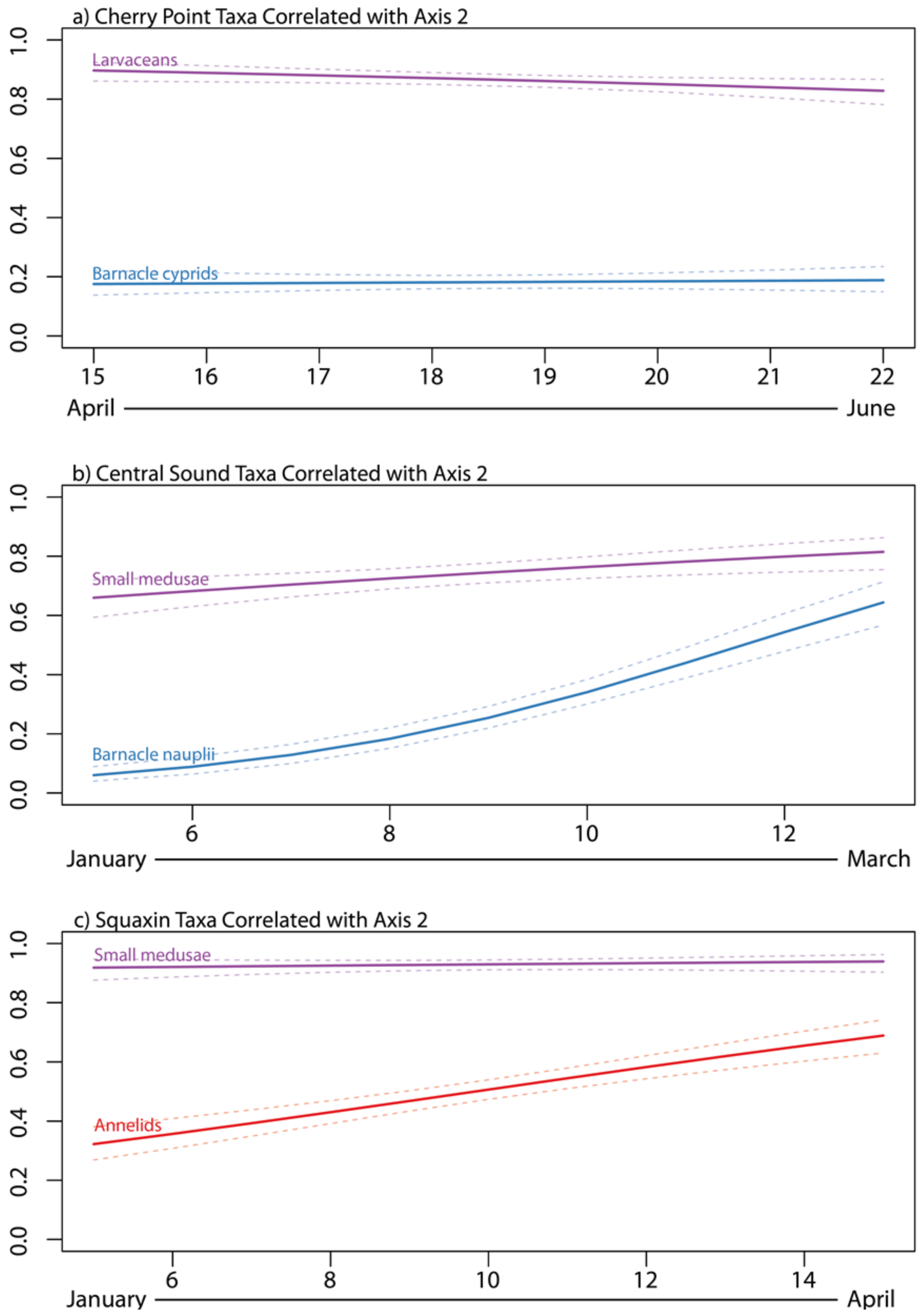


Figure 10. Seasonal patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in seasonal presence of a) Cherry Point, b) Central Sound, and c) Squaxin taxa most strongly correlated with NMDS axis 2 ($R^2 > 0.30$).

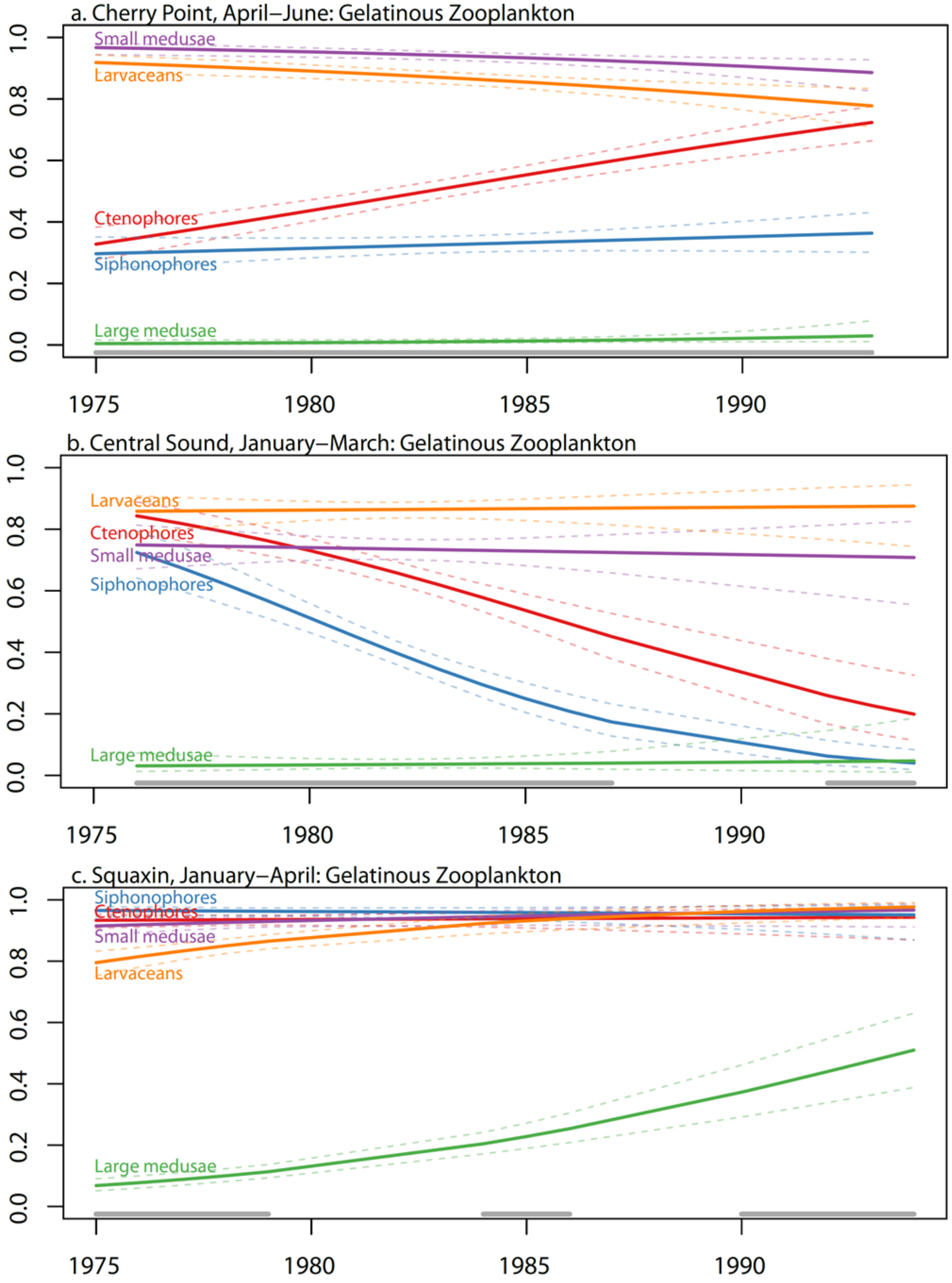
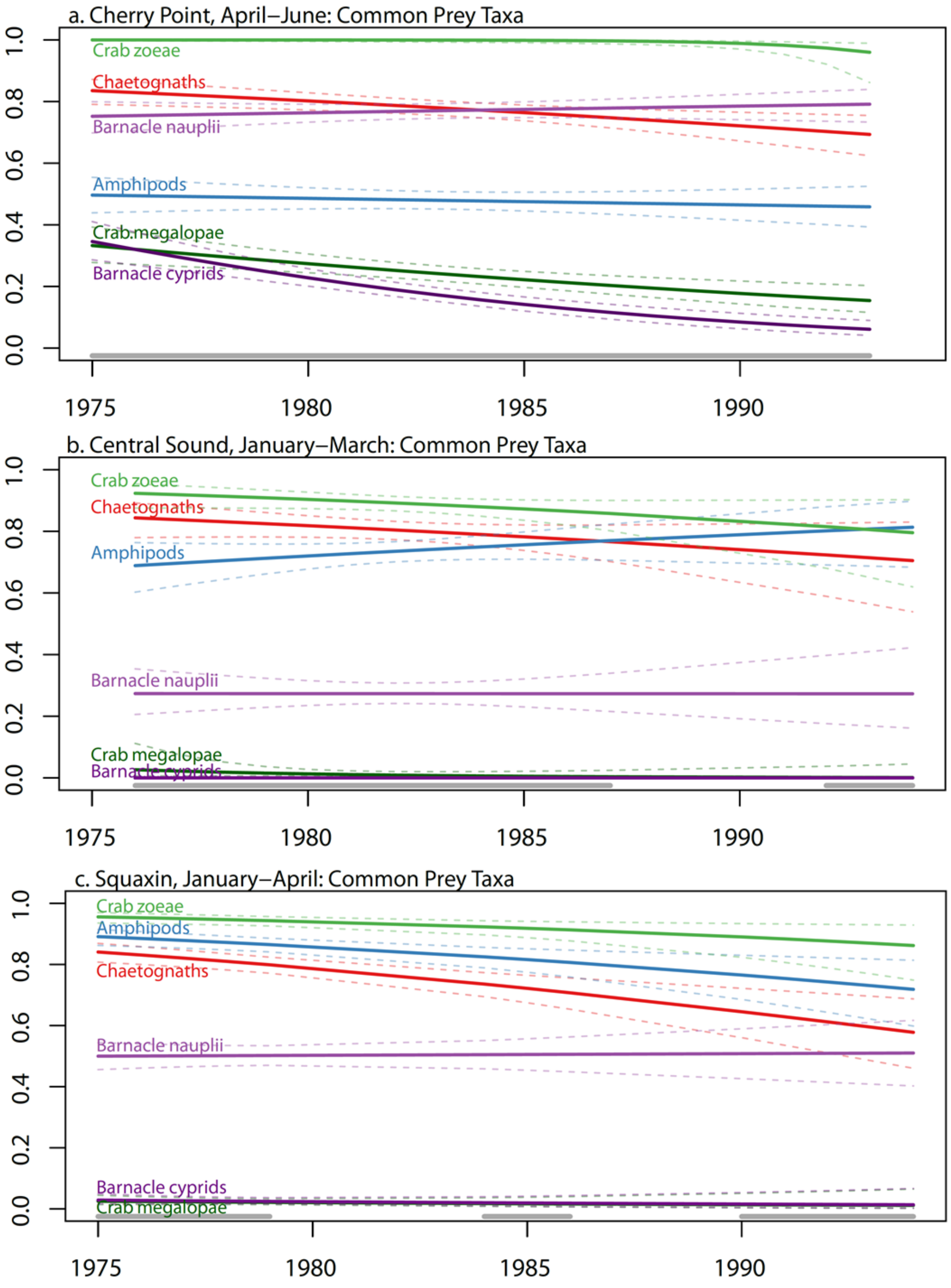


Figure 11. Interannual patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in yearly presence of gelatinous zooplankton at a) Cherry Point, b) Central Sound, and c) Squaxin. Gray lines at the base of each plot represent years sampled in each region.


a. Cherry Point, April–June: Common Prey Taxa

b. Central Sound, January–March: Common Prey Taxa

c. Squaxin, January–April: Common Prey Taxa

Figure 12. Interannual patterns in zooplankton taxa: logistic regression predictions (solid lines) and 95% confidence intervals (dotted lines) in yearly presence of zooplankton taxa commonly found in salmon and forage fish diets at a) Cherry Point, b) Central Sound, and c) Squaxin. Gray lines at the base of each plot represent years sampled in each region.

Appendix

Table A1. Approximate herring spawn timing and zooplankton sample timing for each sector, and total number of zooplankton samples from each sector.

Stock/Sector	Herring spawn timing	Zooplankton sampling timing (years sampled)	Total number samples
Semiahmoo	mid-Jan to mid-April	April-May (19)	721
Cherry Pt	mid-March to June	April-June (19)	1429
Portage/Samish	Feb to mid-April	April-June (11)	113
Interior San Juans	mid-Jan to April	*inconsistent* (9)	82
NW San Juans	mid-Jan to mid-April	*inconsistent* (6)	15
Fidalgo	mid-Jan to mid-April	Feb-March (16)	200
Skagit	Feb to mid-April	*inconsistent* (10)	69
Port Susan	mid-Jan to mid-April	Feb-March (10)	114
Holmes Harbor	Feb to April	*inconsistent* (12)	45
Dungeness/Sequim	mid-Jan to March	Feb-March (14)	95
Discovery	Feb to mid-April	Feb-March (16)	199
Kilisut	Feb to mid-April	Feb-March (10)	95
Port Gamble	mid-Jan to mid-April	Jan-March (15)	203
Quilcene	mid-Jan to mid-April	*inconsistent* (9)	69
South Hood Canal	Jan to mid-March	*inconsistent* (7)	37
Port Orchard/Madison	Jan to mid-April	Jan-April (16)	442
Quartermaster	Jan to mid-April	Jan-March (16)	392
Henderson/Purdy	mid-March to late-March	*inconsistent* (9)	59
Wollochet	Jan to mid-March	*inconsistent* (7)	160
Squaxin	mid-Jan to mid-March	Jan-April (13)	1118
Grays Harbor	Feb to March	Feb-March (3)	16
Willapa Bay	Feb to mid-March	Feb-March (4)	48

Table A2. Complete list of all recorded sites sampled within each sector, within each region. Sites and sectors are alphabetized. Regions are arranged roughly north to south within Puget Sound, with coastal sites at the end of the table. Number of times a site was recorded is in parentheses after the site indicator. Sites that were sampled >100 times are italicized.

Region	**Herring Spawning Sector**	**Site Indicator**
North Puget Sound	Cherry Pt	Alden Bank (6)
		Arco Dock (32)
		Birch Bay (401)
		BP Dock (5)
		Cherry Pt (142)
		Hale Pass (40)
		Infalco Dock (4)
		Lummi Bay (66)
		Pt Migley (40)
		Mobil Dock (149)
		Neptune Beach (6)
		Sandy Pt (181)
		Viewpoint (145)
		Village Pt (34)
		Pt Whitehorn (171)
	Fidalgo	Crandall Spit (15)
		Fidalgo Bay (61)
		Hat Island (2)
		March Pt (98)
		Padilla Bay (20)
		Cap Sante (4)
	Interior San Juans	Blind Bay (8)
		Brigantine Bay (2)
		Clark Island (4)
		Deer Harbor (4)
		Pt Doughty (3)
		Echo Bay (1)
		Hunter Bay (6)
		Pt Lawrence (2)
		Lopez Island (1)
		Matia Island (4)
		Mud Bay (5)
		Orcas Island (8)

		Parker Reef (1)
		Patos Island (4)
		Rosario (2)
		Shoal Bay (3)
		Sinclair Island (7)
		Sucia Island (5)
		Pt Thompson (4)
		Vendovi Island (2)
		Waldron Island (1)
		West Sound (6)
	NW San Juans	Mitchell Bay (1)
		Mosquito Pass (2)
		Roche Harbor (4)
		Westcott Bay (6)
	Portage/Samish	Chuckanut Bay (3)
		Pt Francis (44)
		Portage Bay (40)
		Samish Bay (26)
	Semiahmoo	*Blaine Harbor (130)*
		Boundary Bay (1)
		False Pt (1)
		Pt Roberts (172)
		Semiahmoo Bay (411)
		Tongue Pt (4)
Admiralty Inlet	Discovery	Adelma (8)
		Beckett Pt (16)
		Discovery Bay (145)
		Gardiner (4)
		Tukey (26)
	Dungeness	Dungeness Bay/Harbor (32)
	Kilisut	Kala Pt (4)
		Kilisut Harbor (59)
		Pt Townsend Bay (31)
	Sequim	Sequim Bay (63)
Whidbey Basin	Holmes	Camano State Park (1)
		Dines Pt (1)
		Freeland (1)
		Holmes Harbor (35)
		Onamac Pt (1)
		Penn Cove (3)

		Rocky Pt (2)
	Port Susan	Camano Island (2)
		Cavelero Beach (1)
		Herman Pt (1)
		Kayak Pt (32)
		Langley (1)
		McKees Beach (1)
		Sandy Pt (1)
		Spee-bi-dah (19)
		Port Susan (19)
		Tillikum Beach (1)
		Triangle Cove (1)
		Tulalip Bay (30)
	Skagit	Cornet Bay (1)
		Crescent Harbor (1)
		Deception Pass (2)
		Dugualla Bay (23)
		Hope Island (1)
		Oak Harbor (1)
		Coupeville (1)
		Rocky Pt (1)
		Similk Bay (15)
		Skagit Bay (7)
		Snee-oosh (11)
		Utsalady Bay (4)
Hood Canal	Port Gamble	Byurnden Bay (2)
		Coon Bay (2)
		Port Gamble (153)
		Hood Head (4)
		Hood (14)
		Lofall (4)
		Port Ludlow (1)
		North Hood Canal (3)
		Salsbury (21)
		Twin Spits (1)
	Quilcene	Brinnan Flats (1)
		Central Hood Canal (1)
		Dabob Bay (23)
		Dosewallips (2)
		Duckabush Flats (4)

		Hazel Pt (1)
		Hood Pt (1)
		Misery Pt (1)
		Pleasant Harbor (2)
		Quilcene Bay (21)
		Seabeck Bay (8)
		Stavis Bay (1)
		Tekiv Pt (2)
	South Hood Canal	Alderbrook Inn Dock (1)
		Dewatto (3)
		Happy Hollow (2)
		Hoodsport (1)
		Lynch Cove (4)
		North Shore (1)
		Shady Beach (1)
		South Hood Canal (14)
		Sisters Pt (2)
		Smadings Beach (1)
		Sunset Boh (2)
		Turavoh (2)
		Twanoh State Park (2)
		Union (1)
Central Puget Sound	Port Orchard/Madison	Agate Pass (26)
		Alki (1)
		Arrow Pt (23)
		Battle Pt (12)
		Blaine (1)
		Blakeley Harbor (3)
		Pt Bolin (4)
		Dolphin Pt (1)
		Dyes Inlet (20)
		Eagle Harbor (6)
		Fletcher Bay (1)
		Hidden Cove (56)
		Illahee (1)
		Keyport (56)
		Liberty Bay (20)
		Port Madison (66)
		Miller Bay (14)
		Pt Monroe (5)

		Port Orchard (25)
		Manzanita Bay (22)
		Sinclair Inlet (23)
		University Pt (46)
	Quartermaster	Pt Defiance (1)
		Dumas Bay (1)
		Gig Harbor (5)
		Neill Pt (2)
		Manzanita (8)
		Quartermaster Harbor (370)
		Three Tree Pt (1)
South Puget Sound	Henderson/Purdy	Burley Lagoon (1)
		Cutts Island (18)
		Glen Cove (4)
		Henderson Bay (1)
		Horsehead Bay (4)
		Mayo Cove (2)
		Minter Cr (14)
		Penrose Pt (1)
		Purdy (15)
		Raft Island (1)
	Squaxin	Allyn (2)
		Arcadia (2)
		Boston Harbor (2)
		Briscoe Pt (57)
		Budd Inlet (76)
		Buffington’s Lagoon (11)
		Burns Pt/Cove (37)
		Burro Cove (1)
		Case Inlet (3)
		Cape Cod (2)
		Cooper Pt (4)
		Dana Pass (14)
		Deepwater Pt (4)
		Devil’s Head (20)
		Dougall Pt (6)
		Dutcher Cove (10)
		Eld Inlet (6)
		Flapjack Pt (19)
		Gallagher Cove (3)

	Hammersley Inlet (3)
	Hartstone Island (5)
	Henderson Inlet (22)
	Herron Island (14)
	Hope Island (5)
	Hungerford Pt (61)
	Hunter Pt (80)
	Jarrell Cove (6)
	Johnson Pt (9)
	Kamilche Pt (88)
	Libby Pt (4)
	McMicken Island (5)
	Munson Pt (1)
	Oakland Bay (1)
	Oyster Bay (1)
	Peale Pass (42)
	Pickering Pass (44)
	Reach Island (10)
	Rocky Pt (3)
	Sanderson Harbor (31)
	Skookum Inlet (7)
	Squaxin Island (2)
	Steamboat Island (3)
	Stretch Island (5)
	Taylor Bay (7)
	Totten Inlet (284)
	Whiteman Cove (6)
	Wildcat Harbor (1)
	Windy Pt (70)
	Young’s Cove (19)
Wollochet	Amsterdam Bay (1)
	Balch Pass (2)
	Carr Inlet (2)
	Cole Pt (15)
	Day Island (8)
	Drayton Pass (20)
	Pt Evans (2)
	Filucy Bay (3)
	Fox Island (4)
	Gertrude Island (14)

		Green Pt (15)
		Hale Pass (8)
		Ketron Island (16)
		Nisqually Reach (17)
		Oro Bay (1)
		South Head (12)
		Steilacoom (1)
		Toliva Shoal (13)
		Wollochet Bay (7)
Coastal WA	Grays Harbor	Bay City (2)
		Elk Channel (1)
		Neds Rk (1)
		South Bay (12)
	Willapa	Bay Center (8)
		Bruceport (7)
		Jensen Pt (1)
		Nahcotta (11)
		Nemah (7)
		Oysterville (9)
		Stackpole Harbor (3)
		Willapa Bay (2)

Table A3. Qualitative abundance rankings applied to up to 26 taxa in each sample. Italics denote ranking used >50 times within one year; bold denotes ranking used >1000 times within one year.

Year	Total # Samples	# Ranking Categories	Ranking Categories (ordered from least to most abundant)
1974	5	9	rare, uncommon, checkmark/present, fairly common, common, very common, abundant, super-abundant
1975	333	17	rare, very uncommon, *uncommon*, few, *checkmark/present*, several, *fairly common*, *common*, many, quite common, *very common*, numerous, *abundant*, very abundant, codominant, dominant
1976	437	18	trace, ***uncommon***, occasional, few, some, *checkmark/present*, relatively common, several, *fairly common*, **common**, *very common*, very very common, numerous, *abundant*, very abundant, codominant, dominant
1977	515	10	***checkmark***/present, fairly common, *common*, very many, *very common*, *abundant*, very abundant, extremely abundant, dominant
1978	377	7	***checkmark***, *common*, *very common*, abundant, very abundant, extremely abundant, dominant
1979	323	10	uncommon, ***checkmark***, fairly common, *common*, many, very common, abundant, very abundant, most common, dominant
1980	307	7	***checkmark***, *common*, *very common*, *abundant*, very abundant, extremely abundant, dominant
1981	300	7	***checkmark***, *common*, *very common*, *abundant*, very abundant, extremely abundant, dominant
1982	408	9	few, ***checkmark***, fairly common, *common*, *very common*, *abundant*, very abundant, extremely abundant, dominant
1983	452	7	***checkmark***, *common*, *very common*, abundant, very abundant, extremely abundant, dominant
1984	450	8	***checkmark***, fairly common, *common*, *very common*, *abundant*, very abundant, extremely abundant, dominant
1985	365	6	***checkmark***/present, *common*, *very common*, abundant, very abundant
1986	329	8	***checkmark***, present, *common*, *very common*, *abundant*, very abundant, extremely abundant, dominant
1987	277	6	***checkmark***, *common*, very common, *abundant*, very abundant, extremely abundant
1988	214	6	***checkmark***, fairly common, *common*, very common, abundant, very abundant
1989	111	5	*checkmark*, *common*, very common, abundant, very abundant
1990	93	6	*checkmark*, relatively common, *common*, very common, abundant, very abundant
1991	142	9	***checkmark***, relatively common, fairly common, *common*, very common, abundant, very abundant, codominant, dominant
1992	146	5	***checkmark***, *common*, very common, abundant, very abundant
1993	121	6	*checkmark*, *common*, very common, abundant, very abundant, dominant
1994	41	5	*checkmark*, common, very common, abundant, very abundant
1997	6	2	checkmark, common
1998	10	4	checkmark, common, very common, abundant
1999	8	2	*checkmark*, common

Table A4. The five most frequently observed taxa in terms of percent occurrence in samples and the five taxa most often recorded numerically dominant/co-dominant in each region of Puget Sound. Note that dominant/co-dominant taxa were not recorded consistently across samples.

	Most Frequently Occurring Taxa (% times observed in samples)	**Numerically Dominant or Co-dominant Taxa (# times recorded as dominant or co-dominant)**
North Sound 2563 samples 181 records of dominance	1. Crab zoeae (98%) 2. Copepods (96%) 3. Miscellaneous fish larvae (96%) 4. "Mysid" larvae (92%) 5. Small medusae (89%)	1. Copepods (50) 2. Barnacle nauplii (35) 3. Crab zoeae (28) 4. Miscellaneous fish larvae (13) 5. Pelagic fish eggs (10)
Whidbey Basin 228 samples 21 records of dominance	1. Copepods (96%) 2. Miscellaneous fish larvae (91%) 3. Crab zoeae (88%) 4. "Mysid" larvae (75%) 5. Chaetognaths (64%)	1. Miscellaneous fish larvae (8) 2. Copepods (5) 3. Crab zoeae (3) 4. Barnacle nauplii (2) 5. Appendicularians (1)
Admiralty Inlet 389 samples 35 records of dominance	1. Copepods (99%) 2. Chaetognaths (95%) 3. Miscellaneous fish larvae (94%) 4. Crab zoeae (90%) 5. Pelagic fish eggs (87%)	1. Copepods (12) 2. Chaetognaths (6) 3. Miscellaneous fish larvae (5) 4. Appendicularians (4) 5. Small medusae (3)
Hood Canal 313 samples 46 records of dominance	1. Copepods (98%) 2. Miscellaneous fish larvae (89%) 3. Crab zoeae (85%) 4. Chaetognaths (82%) 5. Pelagic fish eggs (78%)	1. Barnacle nauplii (14) 2. Copepods (8) 3. Miscellaneous fish larvae (5) 4. Crab zoeae (5) 5. Chaetognaths (4)
Central Sound 837 samples 43 records of dominance	1. Copepods (97%) 2. Pelagic fish eggs (95%) 3. Miscellaneous fish larvae (93%) 4. Crab zoeae (88%) 5. "Mysid" larvae (86%)	1. Ctenophores (13) 2. Copepods (9) 3. Pelagic fish eggs (8) 4. Crab zoeae (4) 5. Miscellaneous fish larvae (3)
South Sound 1358 samples 615 records of dominance	1. Copepods (98%) 2. Miscellaneous fish larvae (97%) 3. "Mysid" larvae (96%) 4. Siphonophores (95%) 5. Crab zoeae (93%)	1. Copepods (190) 2. Barnacle nauplii (110) 3. Siphonophores (78) 4. Ctenophores (68) 5. Crab zoeae (58)