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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 4(1) : 117-128

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2012.680403

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 4:117–128, 2012

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2012.680403

ARTICLE

Geographic Patterns of Fishes and Jellyfish in Puget Sound Surface Waters

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Abstract
We explored patterns of small pelagic fish assemblages and biomass of gelatinous zooplankton (jellyfish) in surface waters across four oceanographic subbasins of greater Puget Sound. Our study is the first to collect data documenting biomass of small pelagic fishes and jellyfish throughout Puget Sound; sampling was conducted opportunistically as part of a juvenile salmon survey of daytime monthly surface trawls at 52 sites during May–August 2003. Biomass composition differed spatially and temporally, but spatial differences were more distinct. Fish dominated in the two northern basins of Puget Sound, whereas jellyfish dominated in the two southern basins. Absolute and relative abundance of jellyfish, hatchery Chinook salmon *Oncorhynchus tshawytscha*, and chum salmon *O. keta* decreased with increasing latitude, whereas the absolute and relative abundance of most fish species and the average fish species richness increased with latitude. The abiotic factors with the strongest relationship to biomass composition were latitude, water clarity, and sampling date. Further study is needed to understand the spatial and temporal heterogeneity in the taxonomic composition we observed in Puget Sound surface waters, especially as they relate to natural and anthropogenic influences.

Small pelagic fishes and gelatinous zooplankton (pelagic cnidarians and ctenophores; hereafter referred to as jellyfish) are major components of pelagic food webs as consumers of phytoplankton and zooplankton and as prey for many species (Alaska Sea Grant 1997; Cury et al. 2000; Purcell and Arai 2001; Arai 2005). Larger, more frequent jellyfish blooms have been observed throughout the world (CIESM 2001; Pitt and Purcell 2009; Richardson et al. 2009; Brotz et al. in press). Anthropogenic disturbances such as overfishing, eutrophication, species introductions, and increases in hard substrates in estuarine and marine environments may be factors influencing these blooms (Mills 1995, 2001; Arai 2001; Kideys 2002;

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Received March 24, 2010; accepted December 23, 2011

Lynam et al. 2006; Purcell et al. 2007), although uncertainty about the magnitude of the problem and causal mechanisms remains (Mills 2001; Pauly et al. 2009; Condon et al. 2012). Interactions between fishes and jellyfish are complex and can include competition for food, predation by jellyfish on fishes (including eggs and larvae), predation by some fish (e.g., chum salmon *Oncorhynchus keta*) on jellyfish, and commensalism (Purcell and Arai 2001; Lynam and Brierley 2007; Brodeur et al. 2008). Inverse relationships between the abundances of fishes and jellyfish have been hypothesized (e.g., Parsons and Lalli 2002; Pauly et al. 2009) but rarely documented (e.g., Lynam et al. 2006).

Because jellyfish have fewer predators than fishes, they are considered an important trophic node that may prevent the flow of energy to higher trophic levels that are occupied by predatory fishes, birds, and mammals (Greve and Parsons 1977; Parsons and Lalli 2002; Ruzicka et al. 2007; Condon et al. 2011). Several attributes of jellyfish biology, such as short life span, sexual and asexual reproduction, broad diets, passive feeding, and low metabolic requirements, enable them to reproduce rapidly when resources become available and also to tolerate some environmental stressors better than fishes. For example, tolerance of hypoxic conditions can favor jellyfish over fishes in direct predator–prey interactions (Breitburg et al. 1997). Jellyfish are also quite conspicuous in the environment, often dominating the catch in some commercial fisheries and research surveys. These characteristics and the apparent worldwide increase in jellyfish blooms suggest a role for jellyfish as indicators of ecosystem condition (Brodeur et al. 2002; Hay 2006; Attrill et al. 2007; Purcell et al. 2007; Pauly et al. 2009; Richardson et al. 2009; Samhouri et al. 2009). Unfortunately, research and monitoring of small pelagic fishes and jellyfish are lacking in most coastal ecosystems, including Puget Sound, an urbanized, fjord–estuary complex on the Pacific coast of North America.

Historical changes in Puget Sound biota include declines in fishes, birds, and mammals (West 1997; PSP 2010) that use the pelagic zone and are presumably affected by mid-level consumers, such as small pelagic fishes and jellyfish. However, little effort has focused on these relationships or on the natural and anthropogenic factors that affect them (Rice 2007). Recent declines of some south Puget Sound recreational fisheries and poor survival in yearling coho salmon *O. kisutch* and Chinook salmon *O. tshawytscha* have raised concerns about the ecological health of Puget Sound's pelagic zone (Preikshot and Beattie 2001). Modeling efforts to explore these and other perceived problems in Puget Sound identified a major insufficiency in data for many taxa, including jellyfish and small pelagic fishes (Preikshot and Beattie 2001; Harvey et al. 2010). While some limited information on the spatial and temporal distributions of jellyfish in Puget Sound does exist (e.g., Mills 1981; Reum et al. 2010), the data are restricted in space or time and do not include fishes.

We explored patterns of pelagic macrofaunal community composition in Puget Sound using data collected opportunistically as part of a study of juvenile Chinook salmon (Rice et al. 2011). Although information on nontarget species such as jellyfish is often discarded as "bycatch" in biological field surveys, such data can provide valuable insights into the ecology and health of ecosystems (e.g., Brodeur et al. 1999). Our goals were to (1) describe broad spatial and temporal abundance patterns of small pelagic fishes and jellyfish in pelagic surface waters of Puget Sound; (2) determine whether specific taxa contribute to spatial and temporal patterns; and (3) assess whether easily measured environmental variables are useful in describing patterns of biomass composition.

METHODS

Study sites and data collection.—As this study formed part of a natural history survey of juvenile Chinook salmon in estuarine habitats (Rice et al. 2011), most sites were located in river mouth estuaries, but marine areas in between river systems were also sampled. River mouth sites were selected to sample the approximate center of the delta front and the two adjacent shorelines. Fifty-two sites were sampled from Nisqually Reach to Bellingham Bay (a distance of 185 km); the study area included six river mouth estuaries and several areas in between (Figure 1). Sites within Puget Sound proper (bounded by Admiralty Inlet, Deception Pass, and Swinomish Channel) were assigned to three oceanographic regions of Puget Sound: Whidbey Basin (north), Main Basin (central), and South Sound (Burns 1985). Northern areas outside of Puget Sound proper (Padilla and Bellingham bays) were assigned to a fourth basin, referred to as "Rosario Basin" because of its proximity to Rosario Strait. Sampling was conducted during neap tides to reduce tidal influence on the spatial distribution of the biota. Consequently, during each month, the northern and southern study sites were sampled 2 weeks apart.

Sampling occurred monthly during May–August 2003 using a 3.1-m-high × 6.1-m-wide Kodiak surface trawl (townet) deployed between two boats, each with a 50-m towline connected to a bridle on the net. Mesh sizes in the net were 76-mm stretch in the forward section, 38 and 19 mm in the middle sections, and 6 mm in the cod end. The net was towed at the surface for 10 min at a typical towing speed of 3.70–5.56 km/h (2–3 knots). Distance through the water was recorded with a mechanical flowmeter (General Oceanics Model 2030) deployed by the smaller vessel. Area swept was calculated as the distance traveled through the water multiplied by the width of the net opening (average $\pm$ SD $= 0.377 \pm 0.047$ ha; range $= 0.145$–0.682 ha). Two tows in opposite directions were made per site for a total of 410 samples. Water depth at sampling sites ranged from 4.7 to 46.7 m, with an overall mean of 11.9 m.

At the end of each tow, the entire catch was placed in tanks supplied with flowing water from the site, and the fish were identified, counted, and weighed by species. Jellyfish were weighed together without counting and were not further identified due to the project's primary emphasis on fishes and due to time and staffing limitations. Surface water temperature

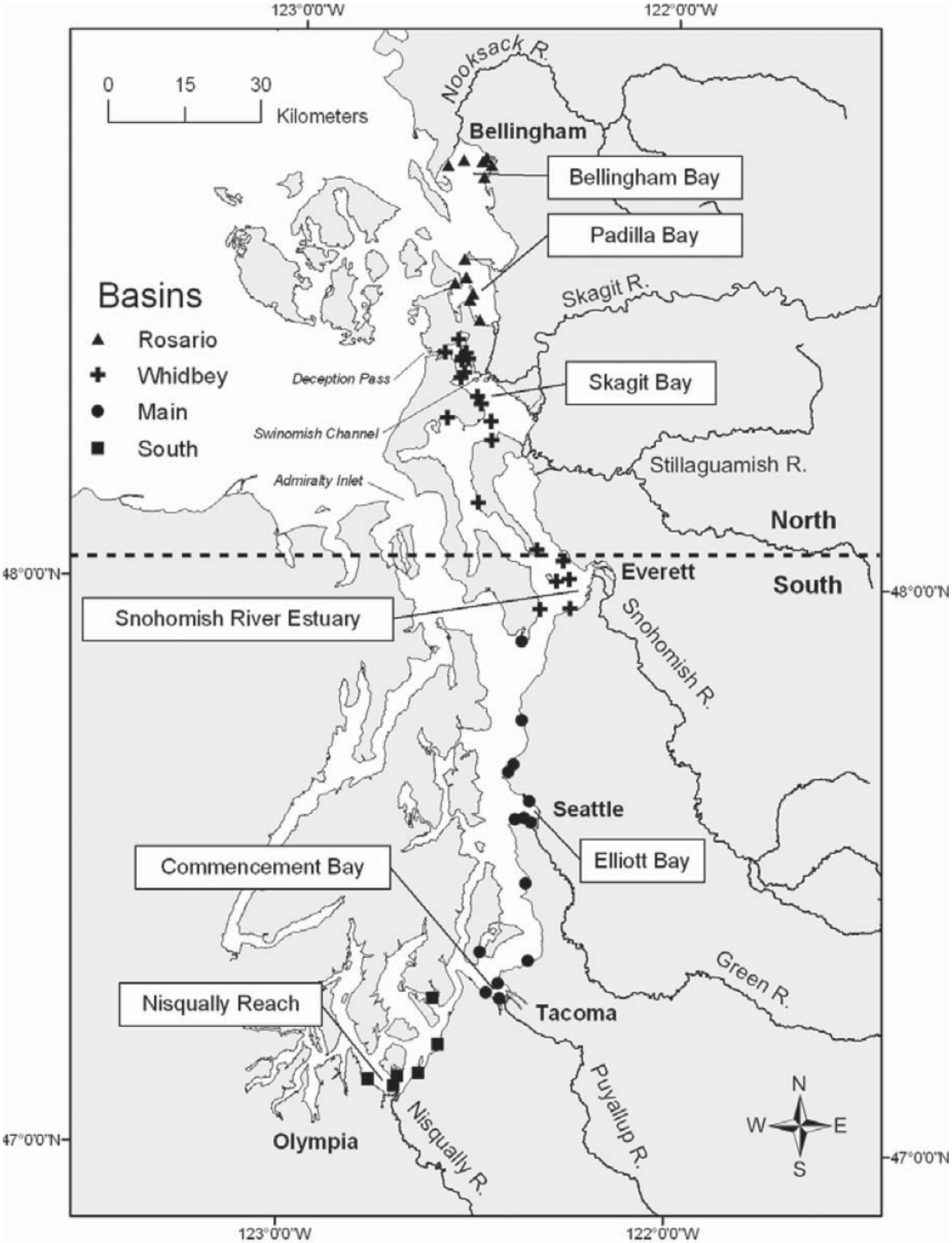

FIGURE 1. Map of Puget Sound, Washington, indicating sites that were sampled monthly during May–August 2003. Sites within basins are indicated by symbols; embayments are marked by labels. Northern and southern areas (separated by the dashed line) were sampled 2 weeks apart on alternating neap tide series.

and salinity measurements were taken during each tow, and Secchi depth was recorded once at each site visit using a 20-cm black-and-white disk.

Statistical analyses.—Statistical analyses focused primarily on influences of oceanographic basin and month on patterns of biomass composition. The first part of the analysis combined fish biomass into a single group to treat them with the same level of taxonomic discrimination as the combined jellyfish biomass (i.e., comparison of two biomass categories; hereafter, "fish–jellyfish biomass analysis"). A second, separate analysis used only fish biomass at the species level for a more detailed examination of fish assemblage structure (hereafter, "fish-only biomass analysis"). Finally, relationships between biomass composition and latitude, salinity, temperature, water depth, and Secchi depth were also evaluated. Biomass (kg wet weight/ha) was the primary abundance measure because it was the only information collected for both jellyfish and fishes. Marked Chinook salmon (those with adipose fin clips or coded wire tags indicating hatchery origin) and unmarked Chinook salmon (the majority of which were naturally spawned) were treated as separate species in the analysis in order to evaluate similarities and differences between hatchery and wild fish. Other salmonids either were not distinguishable as hatchery fish (no detectable marks) or were rarely caught.

Relationships between biomass composition and the categorical abiotic variables of basin and month were evaluated with nonparametric multivariate analyses (Clarke 1993; Clarke and Warwick 2001) using PRIMER-E software (Clarke and Gorley 2006). Biomass was averaged for each site × month combination (two tows), and the data matrices were square-root transformed to downweight the effects of abundant taxa. Resemblance matrices of all pairwise similarities between sites (based upon the taxa present and their biomass) were calculated for each month by using the Bray–Curtis distance measure. These steps were followed for the fish–jellyfish biomass analysis and the fish-only biomass analysis.

A two-way analysis of similarities (ANOSIM) procedure was applied to the resemblance matrices to evaluate differences in the composition of biomass related to basin and month. The ANOSIM procedure calculates an R-statistic based upon the difference between average within-group rank similarities and average among-group rank similarities. Values of R usually range between 1 (all replicates within areas or months are more similar to each other than to any replicates from different areas or months) and 0 (rank similarities between and within areas or months are the same, on average) but can be slightly negative. An exact P-value was computed using permutation (999 iterations). Next, a two-way similarity percentage procedure was applied to the same resemblance matrices to evaluate the contribution of various taxa to similarities in the biomass composition by month and basin.

To further evaluate relationships between biomass composition and abiotic variables, distance-based linear modeling and distance-based redundancy analysis (dbRDA) routines were applied using the PERMANOVA module of PRIMER-E (Anderson et al. 2008; based on Legendre and Anderson 1999 and McArdle and Anderson 2001). These techniques allowed regression modeling of relationships between multivariate biological resemblance matrices and several continuous, abiotic predictor variables as well as the selection and visualization of the most parsimonious models. Spatial and temporal variables (latitude and calendar date) and temperature, salinity, and water depth were averaged for each site × date combination. Secchi depth (1 measurement per site × date combination) was also included, and water depth data were log transformed to remove high skew. Distance-based linear modeling procedures were used to generate linear regression models for taxonomic resemblance matrices and abiotic variables alone and in all additive combinations; the most parsimonious models were identified using Akaike's information criterion (AIC; Burnham and Anderson 2002). Ordinations of the fitted values of the most parsimonious models for fish–jellyfish biomass and fish-only biomass were plotted using dbRDA.

RESULTS

Fish–jellyfish biomass composition varied by basin and month (Table 1). Jellyfish comprised more than 60% of the

TABLE 1. Mean (SD in parentheses) biomass (kg wet weight/ha) of fish and jellyfish captured by surface trawls in four Puget Sound basins during May–August 2003.

Basin	Group	May	Jun	Jul	Aug
Rosario	Fish	1.85 (3.88)	24.48 (24.01)	8.76 (9.77)	8.16 (11.40)
	Jellyfish	0.32 (0.46)	30.30 (36.24)	1.02 (1.56)	0.86 (0.88)
Whidbey	Fish	1.01 (1.61)	7.60 (13.55)	4.41 (5.03)	3.63 (4.82)
	Jellyfish	0.79 (1.40)	1.39 (3.80)	6.17 (12.07)	1.45 (4.41)
Main	Fish	2.07 (5.70)	4.60 (7.75)	1.33 (1.70)	0.63 (2.17)
	Jellyfish	22.68 (35.47)	18.96 (20.14)	25.89 (41.52)	3.08 (5.29)
South Sound	Fish	4.58 (14.73)	4.30 (3.48)	2.57 (6.16)	0.18 (0.32)
	Jellyfish	25.24 (14.77)	14.97 (28.26)	30.89 (33.35)	3.83 (2.75)

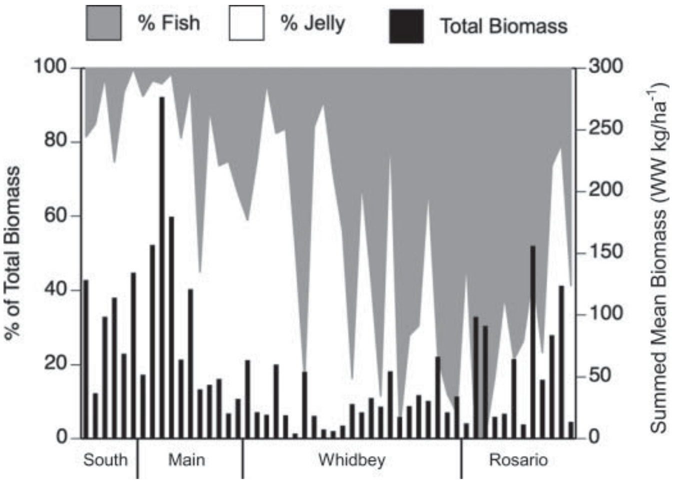

FIGURE 2. Percentage fish (% Fish; gray) and jellyfish (% Jelly; white) in the total biomass (kg wet weight [WW]/ha; black bars) for sites within four Puget Sound basins. Each bar is the sum of the four monthly means (May–August) for each site. Sites are arranged from south (left) to north (right).

total wet biomass for all sites and months combined. The jellyfish biomass percentage decreased with increasing latitude (Figure 2): jellyfish constituted nearly 90% of the total biomass in the Main Basin and South Sound but contributed less than 45% of the biomass in Rosario and Whidbey basins. Detailed taxonomic identification of jellyfish was not recorded for each sample, but catches usually consisted of several scyphomedusa species, including *Cyanea capillata*, *Phacellophora camtschatica*, occasionally *Aurelia* sp., the hydromedusae *Aequorea* sp. and *Mitrocoma cellularia*, and ctenophores (primarily *Pleurobrachia bachei*). We caught 33 fish species (Table 2). Fish species richness was similar in May across all basins, with the northern basins having higher species richness than the southern basins (Figure 3). Fish assemblages at each site were typically composed of fewer than 10 species/tow; the average species richness was 4–7 species/tow in Rosario and Whidbey basins and 1–4 species/tow in the Main Basin and South Sound. The Pacific herring, surf smelt, Pacific sand lance, threespine stickleback, and juvenile salmonids *Oncorhynchus* spp. were the most common fish taxa encountered. The most obvious differences in the fish assemblage among basins were the higher percentages of chum salmon and marked (known hatchery-origin) Chinook salmon and the lower percentage of Pacific herring and other species in South Sound compared with the other three basins (Figure 4).

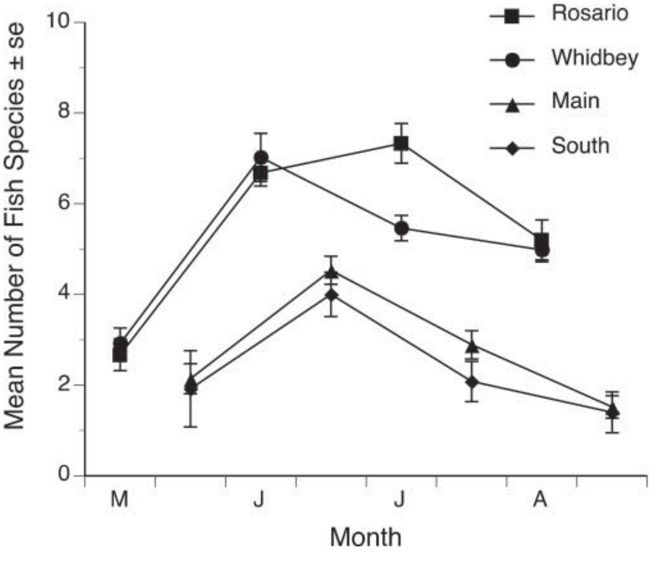

FIGURE 3. Mean (± SE) fish species richness per tow at four Puget Sound basins by month.

TABLE 2. Fish taxa captured by surface trawls at 52 sites in greater Puget Sound during May–August 2003; taxa are ranked in order based on highest to lowest frequency of occurrence.

Taxon	Percent frequency
Chinook salmon *Oncorhynchus tshawytscha*	65.6
Pacific herring *Clupea pallasii*	57.6
Threespine stickleback *Gasterosteus aculeatus*	51.5
Surf smelt *Hypomesus pretiosus*	50.0
Chum salmon *O. keta*	35.4
River lamprey *Lampetra ayresii*	25.4
Pacific sand lance *Ammodytes hexapterus*	22.4
Coho salmon *O. kisutch*	11.7
Bay pipefish *Syngnathus leptorhynchus*	11.2
Pacific sandfish *Trichodon trichodon*	9.0
Starry flounder *Platichthys stellatus*	8.8
Shiner perch *Cymatogaster aggregata*	6.1
Steelhead *O. mykiss*	3.7
Northern anchovy *Engraulis mordax*	3.4
Pink salmon *O. gorbuscha*	2.4
Tubesnout *Aulorhynchus flavidus*	2.2
Sockeye salmon *O. nerka*	1.7
Soft sculpin *Psychrolutes sigalutes*	1.7
Striped seaperch *Embiotoca lateralis*	1.5
Cods (Gadidae)	1.2
Snake prickleback *Lumpenus sagitta*	1.2
Gunnels *Pholis* spp.	1.0
Cutthroat trout *O. clarkii*	0.7
Greenlings *Hexagrammos* spp.	0.7
Pacific staghorn sculpin *Leptocottus armatus*	0.7
American shad *Alosa sapidissima*	0.5
English sole *Parophrys vetulus*	0.5
Pile perch *Rhacochilus vacca*	0.5
Plainfin midshipman *Porichthys notatus*	0.5
Pacific spiny lumpsucker *Eumicrotremus orbis*	0.5
Pacific pompano *Peprilus simillimus*	0.2
Saddleback gunnel *Pholis ornata*	0.2
Sculpins (Cottidae)	0.2

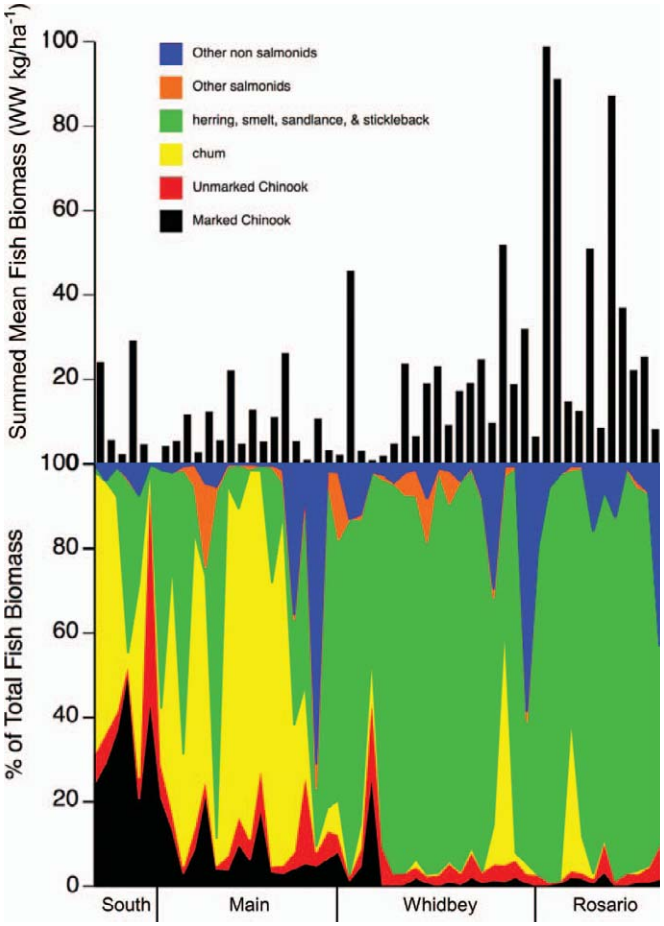

FIGURE 4. Summed mean fish biomass (kg wet weight [WW]/ha) at each of the 52 sites (upper panel) and percentage of selected fish groups in the total biomass (lower panel; see Table 2 for full species names) sampled within four Puget Sound basins. Each bar is the sum of the four monthly means (May–August) for each site. Sites are arranged from south (left) to north (right).

The ANOSIM tests for differences in biomass composition among our a priori groupings by basin (Table 3) and month (Table 4) both produced clear differences, but basin patterns had higher *R*-values than month patterns. The greatest pairwise differences generally corresponded to geographic distance between basins, although the ranks based on fish–jellyfish biomass and fish-only biomass differed slightly (Table 3). Between-basin comparisons of biomass composition indicated significant differences based on both fish–jellyfish and fish-only measures, except in the Main Basin and South Sound (Table 3). All between-month comparisons revealed significant differences in fish–jellyfish biomass and fish-only biomass measures (Table 4).

Similarity percentage tests across basins and months also showed clear differences, with spatial patterns being more distinct than temporal ones. Consistent with the patterns in Table 1, jellyfish biomass accounted for considerable statistical within-group similarity across basins and months but was most dominant in the Main Basin and South Sound (74% and 85% of statistical similarity, respectively). In contrast, jellyfish were less dominant in Rosario and Whidbey basins (30% and 20%, respectively). When fish-only biomass was analyzed in detail, eight fish species (surf smelt, Pacific herring, threespine stickleback, juvenile Chinook salmon, chum salmon, Pacific sand lance, shiner perch, and river lamprey) contributed 90% of the statistical similarity (Tables 5, 6). Juvenile chum salmon and hatchery Chinook salmon dominated in the Main Basin and South Sound, whereas Pacific herring, surf smelt, and threespine stickleback dominated in the Rosario and Whidbey basins. Surf smelt and Pacific herring tended to dominate across months.

Abiotic Variables

Water temperature showed clear seasonal patterns, with the two northern basins generally 1°C warmer than the two southern basins (Figure 5). Mean water temperature ranged from 11.7°C to 17.3°C, demonstrating an increase from May to a summer peak in July, followed by a decline in August. Salinity varied temporally and among basins (Figure 5). Due to the high freshwater input they receive from large rivers, Rosario and Whidbey basins had lower overall salinity than the Main Basin and South Sound and had a wider range of salinities (from 16‰ in April to over 20‰ in August). The salinity of the Main Basin and South Sound always averaged between 25‰ and 30‰.

TABLE 3. Results of two-way analysis of similarities (*R*-statistics) for between-basin comparisons of total biomass composition (two biomass categories: fish and jellyfish) and fish-only biomass composition (biomass for individual fish species) across all months (999 permutations). Ranks are in bold italics (1 = greatest difference; 6 = least difference).

Between-basin comparison	Fish and jellyfish ($R^a = 0.26$; $P = 0.001$)	Fish only ($R^a = 0.35$; $P = 0.001$)
Rosario vs. South Sound	0.58 ($P = 0.001$) ***1***	0.63 ($P = 0.001$) ***2***
Rosario vs. Main	0.39 ($P = 0.001$) ***2***	0.37 ($P = 0.001$) ***4***
Whidbey vs. South Sound	0.37 ($P = 0.001$) ***3***	0.66 ($P = 0.001$) ***1***
Whidbey vs. Main	0.30 ($P = 0.001$) ***4***	0.40 ($P = 0.001$) ***3***
Rosario vs. Whidbey	0.11 ($P = 0.002$) ***5***	0.13 ($P = 0.002$) ***6***
Main vs. South Sound	−0.07 ($P = 0.89$) ***6***	0.15 ($P = 0.02$) ***5***

[a] Global *R*-statistic for overall differences.

TABLE 4. Results of two-way analysis of similarities (*R*-statistics) for between-month comparisons of total biomass composition (two biomass categories: fish and jellyfish) and fish-only biomass composition (biomass for individual fish species) across all Puget Sound basins (999 permutations). Ranks are in bold italics (1 = greatest difference; 6 = least difference).

Between-month comparison	Fish and jellyfish ($R^a = 0.21$; $P = 0.001$)	Fish only ($R^a = 0.16$; $P = 0.001$)
Jun vs. Aug	0.21 ($P = 0.001$) ***1***	0.18 ($P = 0.001$) ***4***
May vs. Jun	0.18 ($P = 0.001$) ***2***	0.19 ($P = 0.001$) ***3***
May vs. Aug	0.15 ($P = 0.001$) ***3***	0.21 ($P = 0.001$) ***2***
Jul vs. Aug	0.12 ($P = 0.001$) ***4***	0.05 ($P = 0.02$) ***6***
May vs. Jul	0.10 ($P = 0.003$) ***5***	0.22 ($P = 0.001$) ***1***
Jun vs. Jul	0.10 ($P = 0.006$) ***6***	0.08 ($P = 0.005$) ***5***

[a] Global *R*-statistic for overall differences.

TABLE 5. Average similarity of fish biomass composition among sites within each Puget Sound basin and ranked similarity percentages for species that contributed 90% to the similarity within each basin (two-way similarity percentage analysis adjusted for month effect, where 100 = perfect similarity and 0 = a complete lack of similarity; UM = unmarked; M = marked).

Rosario Basin (average similarity = 37)		Whidbey Basin (average similarity = 38)		Main Basin (average similarity = 31)		South Sound (average similarity = 21)	
Species	Contribution (%)	Species	Contribution (%)	Species	Contribution (%)	Species	Contribution (%)
Pacific herring	28	Surf smelt	37	Chum salmon	40	M Chinook salmon	44
Threespine stickleback	26	Pacific herring	23	M Chinook salmon	23	Chum salmon	27
Surf smelt	17	UM Chinook salmon	14	Pacific herring	14	UM Chinook salmon	18
UM Chinook salmon	11	Threespine stickleback	7	UM Chinook salmon	12	Shiner perch	8
M Chinook salmon	7	M Chinook salmon	6	Surf smelt	4		
Pacific sand lance	4	River lamprey	4				

TABLE 6. Average similarity of fish biomass composition among Puget Sound sites within each month and ranked similarity percentages for species that contributed 90% of the similarity within each month (two-way similarity percentage analysis adjusted for basin effect, where 100 = perfect similarity and 0 = a complete lack of similarity; UM = unmarked; M = marked).

May (average similarity = 18)		Jun (average similarity = 43)		Jul (average similarity = 43)		Aug (average similarity = 37)	
Species	Contribution (%)	Species	Contribution (%)	Species	Contribution (%)	Species	Contribution (%)
Surf smelt	20	Surf smelt	24	Surf smelt	24	Surf smelt	30
Chum salmon	20	Pacific herring	22	Pacific herring	20	Pacific herring	24
Threespine stickleback	17	Chum salmon	17	UM Chinook salmon	14	UM Chinook salmon	20
Pacific herring	15	M Chinook salmon	12	M Chinook salmon	13	Threespine stickleback	12
Pacific sand lance	8	UM Chinook salmon	9	Chum salmon	12	M Chinook salmon	8
M Chinook salmon	7	Threespine stickleback	5	Threespine stickleback	8		
UM Chinook salmon	5	Coho salmon	4				

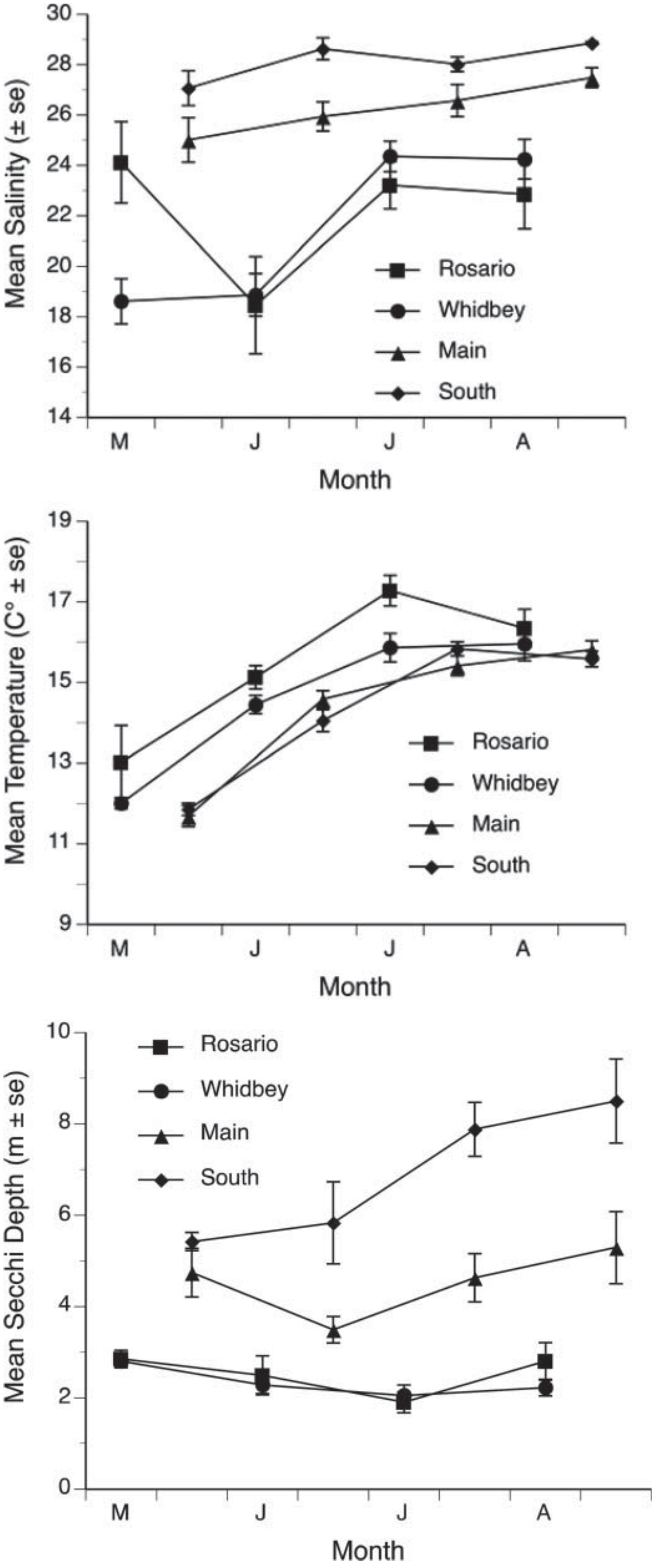

FIGURE 5. Mean (± SE) salinity (‰; upper panel), temperature (°C; middle panel), and Secchi depth (m; lower panel) measured in the four Puget Sound basins during the study period.

Secchi depth varied between months, but the largest differences were spatial (Figure 5). Secchi depth ranged from over 10 m (maximum line length of the instrument) in South Sound to less than 1 m at the mouth of the Puyallup River (Main Basin); this minimum value was due to high levels of glacial sediment in the water during a summer sampling event. Secchi depths in the Main Basin and South Sound were typically around 6 m, whereas sites in the Whidbey and Rosario basins typically had Secchi depths near 3 m. As the season progressed into summer, Secchi depth at the central and southern sites increased, whereas Secchi depth at sites in the northern basins decreased.

Statistical relationships between biomass composition and abiotic variables were not very strong, but some clear patterns emerged. Fish–jellyfish biomass composition was most closely related to latitude and Secchi depth. Latitude and Secchi depth were also the variables that were most closely related to the fish-only biomass composition, but sampling date was equally important. Graphical patterns from the dbRDA ordinations (Figure 6) illustrate these relationships, showing that the basic attribute of fish–jellyfish biomass composition was consistent over the months we sampled, whereas the taxonomic composition based on fish species biomass had a strong temporal pattern. In addition, biomass composition at sites from the South Sound was most strongly related to Secchi depth, whereas biomass composition at other sites was primarily related to latitude.

DISCUSSION

Our findings are the first to reveal spatial differences in the relative abundance of fish and jellyfish in Puget Sound—that is, the dominance of fish in the northern basins (Whidbey and Rosario basins) and the dominance of jellyfish in the Main Basin and South Sound. These results have significant management implications. At a minimum, the differences we observed in pelagic macrofauna among basins suggest that target conditions and vulnerability to anthropogenic stressors (critical considerations in ecosystem management) are not uniform across Puget Sound.

Pelagic communities are structured by complex interactions among many physical and biological components (Miller 2004; Mann and Lazier 2006), few of which have been well characterized in Puget Sound. The basins of Puget Sound are different in terms of bathymetry, connectivity to ocean water, freshwater input, and tidal regime (Burns 1985), all of which should influence pelagic ecology (Strickland 1983). The consequences of these differences for physical oceanography include water circulation and residence times (Babson et al. 2006; Moore et al. 2008), and the greatest contrasts in these attributes do loosely correspond to the areas exhibiting the greatest difference in biomass composition during our study (e.g., South Sound versus Whidbey Basin), but further study is needed to identify causal relationships. The statistical association of biomass composition with latitude and

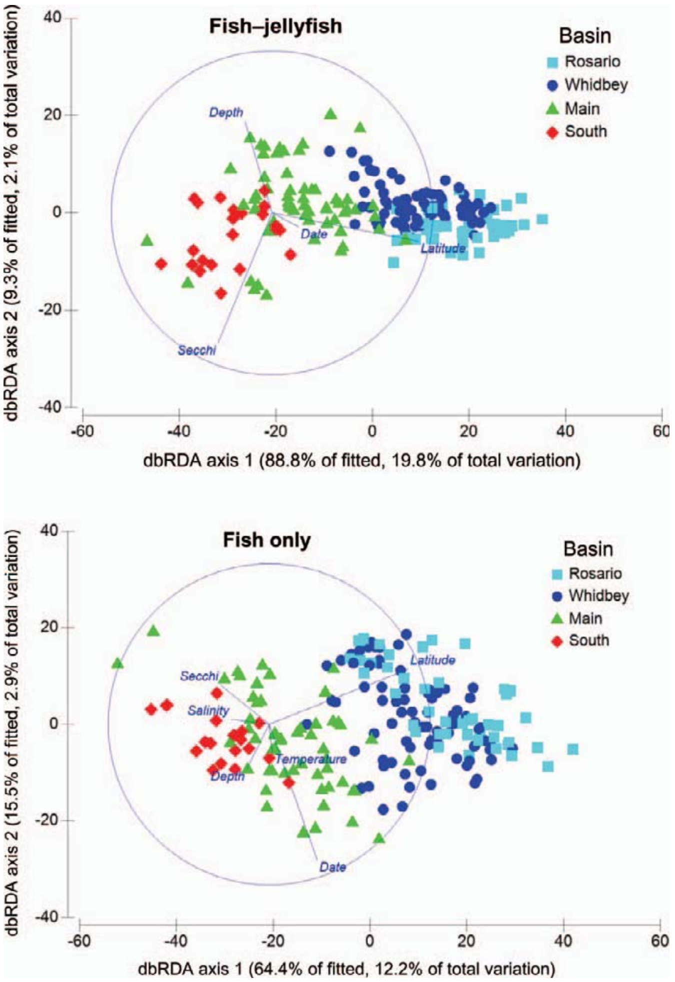

FIGURE 6. Ordination plots of fitted values from distance-based redundancy analysis (dbRDA) of the most parsimonious models relating biomass composition to abiotic variables in four Puget Sound basins (Secchi = Secchi depth). The top panel shows fish–jellyfish analysis (i.e., two biomass categories: fish and jellyfish) while the bottom panel shows fish-only analysis (biomass for individual fish species, with jellyfish biomass excluded).

water clarity indicates that the strong spatial patterns were likely caused by characteristics that were not measured in this study (e.g., phytoplankton and zooplankton abundance, water column structure, and oxygen and nutrient levels) and that result from environmental features (e.g., bathymetry, connectivity, and wind and wave exposure) or other factors, including human activity. We suspect that differences in the relative abundance of jellyfish are not simply a matter of aggregation by physical forcing since such phenomena have been documented at local scales rather than landscape scales and because jellyfish can maintain local residence by horizontal and vertical movements into favorable current patterns (Graham et al. 2001).

The distinct spatial and temporal differences in pelagic macrofauna across the study area, including inverse relationships between jellyfish biomass and both fish biomass and fish species richness, are consistent with hypotheses regarding alternative or bifurcated pelagic food webs (Greve and Parsons 1977; Parsons and Lalli 2002; Richardson et al. 2009; but see Mills 2001). These hypotheses state that simple autotrophs (cyanobacteria, flagellates, and dinoflagellates) may be favored when water quality conditions worsen, leading to a predominance of jellyfish over fish at middle trophic levels and consequently resulting in a trophic "dead end," where little energy is transferred to upper trophic levels (e.g., predatory fishes, mammals, and birds). A bifurcated food web may result because simple autotrophs constitute prey for smaller types of zooplankton and early stages of jellyfish—prey types that fish prefer less than the larger zooplankton that consume larger diatoms. While these patterns have experimental support (Parsons et al. 1981), they have not been tested in the field. Anthropogenic factors surely interact with natural influences (e.g., turbulence; Lauria et al. 1999) on the base of pelagic food webs and presumably affect upper trophic levels. Studies that more thoroughly characterize the taxonomic composition of lower to middle trophic levels across natural and anthropogenic gradients would be an informative avenue for future research.

Puget Sound's basins differ in the nature and magnitude of human activities that may affect pelagic ecology, but the contrasting pelagic fauna in the different basins are not simply a matter of local urbanization. Skagit Bay (northern) and Nisqually Reach (southern) are two of the most biologically different areas but are among the least urbanized estuaries in Puget Sound. However, human activity may play a role in several interacting ways: (1) locally, such as through nutrient loading, shoreline (Shipman et al. 2010) and substrate hardening, and manipulation of the pelagic fish fauna by hatchery supplementation (Mobrand et al. 2005) and fishery harvests (sport, commercial, and subsistence); and (2) globally, such as through species introductions (Cohen 1998; Mills et al. 2000; Cohen et al. 2001) or influences on climate that affect physical forcing and nutrient delivery from the Pacific Ocean or surrounding watersheds (Snover et al. 2005; Moore et al. 2008). Efforts to understand the myriad effects of human activity and their interactions on the pelagic ecosystem in Puget Sound have been negligible.

Interpretation of our results is complicated by low taxonomic resolution of the jellyfish samples. Our lumping of gelatinous zooplankton into a single jellyfish biomass category does not imply that the different species of jellyfish are full equivalents in their ecology. We recognize that the lack of jellyfish taxonomic resolution limits our ability to make more detailed inferences, but we also believe that the simple distinction of fish biomass versus jellyfish biomass is an ecologically meaningful one (CIESM 2001; Purcell and Arai 2001; Parsons and Lalli 2002; Hay 2006; Boero and Bonsdorff 2007; Richardson et al. 2009) and that the clear differences we documented in the basic character of pelagic biota are compelling. In reporting these preliminary results, we hope that future studies not only include more detailed taxonomic treatment of jellyfish but also include a focus on the natural and anthropogenic influences on fish and jellyfish abundance in Puget Sound. Better cooperation between jellyfish ecologists and fisheries ecologists (e.g., Pauly et al. 2009) and greater attention to jellyfish ecology (Hay 2006; Richardson et al. 2009) are warranted because for too long, jellyfish have either been discarded as bycatch or ignored in fisheries studies.

Although no historical data on jellyfish are available for our sites, seasonal patterns in our fish assemblage data from Padilla and Skagit bays are similar to those recorded in the 1960s and 1970s (Stober and Salo 1973; Fresh 1979). The contributions of different salmon species to within-month similarity are consistent with life history patterns and juvenile salmon use of estuaries (Simenstad et al. 1982; Groot and Margolis 1991). The statistical importance of chum salmon in May; chum salmon, Chinook salmon, and coho salmon in June; and only Chinook salmon in July and August corresponds to the typical out-migration timing and degree of estuarine use by these species. The difference between marked and unmarked Chinook salmon demonstrates the contrasting seasonal abundance distributions of hatchery and wild Chinook salmon, despite the fact that incomplete marking of hatchery fish results in an underestimation of hatchery fish abundance (Rice et al. 2011). Wild fish tend to have a more protracted seasonal presence (Burke 2004; Rice et al. 2011) and longer individual residence times (Levings et al. 1986) than hatchery fish. Our fish data do suggest potentially different food web structure across basins and consequent differences in the suitability of various areas as juvenile salmon rearing habitat. In the South Sound, for example, the vast majority of the fauna were jellyfish, hatchery subyearling Chinook salmon, and chum salmon, and the latter species is among the few fish predators of jellyfish (Black and Low 1983; Welch and Parsons 1993; Welch 1997; Arai 2005; Romanuk and Levings 2005; Sweeting et al. 2007).

By revealing significant differences in pelagic biota across Puget Sound, our results raise fundamental questions about the ecological character and health of this system. What structures the pelagic communities across basins? Are current patterns different from historical patterns? Is human activity a significant factor in generating the current patterns? Considering the biological significance of Puget Sound's pelagic zone and its vulnerability to human stressors, monitoring and assessment should focus more attention on pelagic ecology. Most pressing is the need to characterize spatial and temporal patterns of biotic character and to identify natural and human influences on those patterns. Based on that knowledge, pelagic attributes that are most effective at detecting and diagnosing problems should be monitored to guide management actions. The results presented here are a small step in that direction.

ACKNOWLEDGMENTS

We thank the Environmental Conservation Division of the Northwest Fisheries Science Center (National Oceanic and Atmospheric Administration, Seattle) for providing research vessels and field staff, and we also thank the Western Fisheries Research Center (U.S. Geological Survey, Seattle) for providing field staff. Seattle City Light and the U.S. Army Corps of Engineers provided supplemental funding. J. Purcell and T. Parsons gave helpful comments on an early draft of the manuscript; R. Brodeur, B. Feist, P. Hershberger, P. Roni, T. Collier, C. Mills, F. Boero, A. Overton, and three anonymous reviewers provided thorough and constructive reviews. K. Kloehn helped create the map, and C. Stehr and W. Reichert assisted with the review process. The use of trade, firm, or corporation names does not constitute endorsement by the U.S. government.

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