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Diet variability of forage fishes in the Northern California Current System

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ABSTRACT

As fisheries management shifts to an ecosystem-based approach, understanding energy pathways and trophic relationships in the Northern California Current (NCC) will become increasingly important for predictive modeling and understanding ecosystem response to changing ocean conditions. In the NCC, pelagic forage fishes are a critical link between seasonal and interannual variation in primary production and upper trophic groups. We compared diets among dominant forage fish (sardines, anchovies, herring, and smelts) in the NCC collected in May and June of 2011 and June 2012, and found high diet variability between and within species on seasonal and annual time scales, and also on decadal scales when compared to results of past studies conducted in the early 2000s. Copepoda were a large proportion by weight of several forage fish diets in 2011 and 2012, which differed from a preponderance of Euphausiidae found in previous studies, even though all years exhibited cool ocean conditions. We also examined diet overlap among these species and with co-occurring subyearling Chinook salmon and found that surf smelt diets overlapped more with subyearling Chinook diets than any other forage fish. Herring and sardine diets overlapped the most with each other in our interdecadal comparisons and some prey items were common to all forage fish diets. Forage fish that show plasticity in diet may be more adapted to ocean conditions of low productivity or anomalous prey fields. These findings highlight the variable and not well-understood connections between ocean conditions and energy pathways within the NCC.

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1. Introduction

Driven by both short-term and long-term abiotic forcing, the Northern California Current (NCC) is characterized by substantial seasonal and interannual variability of primary and secondary production (Checkley and Barth, 2009; Ware and Thomson, 2005). The California Current is one of only four eastern boundary current upwelling ecosystems in the world which collectively yield a high percentage of the annual fisheries catches, mostly in the form of small pelagic forage fishes (Alder et al., 2008; Pikitch et al., 2012), although the NCC catch is substantially lower than the rest of the upwelling regions (Conti and Scardi, 2010). Pelagic forage fishes are a critical link between variable and seasonally abundant primary production and upper trophic groups since a substantial portion of the forage fish biomass is represented by only a few species feeding at or near the secondary consumer level (Cury et al., 2000) and there are few alternative energy pathways to higher trophic levels in upwelling regions (Ruzicka et al., 2012).

Though underlying mechanisms for the high variability in forage fish abundance in the California Current are unclear, bottom-up (upwelling, El Niño Southern Oscillation, Pacific Decadal Oscillation, North Pacific Gyre Oscillation) and top-down forcing (catch rates and predation) are substantial pressures (Bjorkstedt et al., 2011; Brodeur et al., 1987; Chavez et al., 2003; Emmett et al., 2006; Ware and Thomson, 2005). In a recent analysis of global forage fish management, Pikitch et al. (2012) recommend a dramatic reduction of catch rates since conventional management models do not adequately address the variability and pressures on population abundance and fail to recognize the pivotal role that forage fish play in sustaining upper trophic levels. Using ecosystem simulation modeling, Kaplan et al. (2013) found that fishing forage fish down negatively affected numerous higher trophic level consumers (e.g., predatory fishes, birds, marine mammals) in the California Current. As management of marine resources shifts to an ecosystem-based approach (Field and Francis, 2006; Peck et al., 2014; Pikitch et al., 2004) and in light of altering ocean environments relating to climate change, understanding pelagic energy pathways and trophic relationships in the NCC and other upwelling regions will become increasingly important for predictive fisheries modeling (Brodeur et al., 2007a; Miller and Brodeur, 2007; Ruzicka et al., 2007, 2012).

The purpose of this study was to analyze diets of five dominant forage fish in the NCC, namely surf smelt (*Hypomesus pretiosus*), Pacific herring (*Clupea pallasi*), Pacific sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and whitebait smelt (*Allosmerus elongates*), in seasonal and annual comparisons to examine diet composition, divergence, and overlap. We compare our results to studies done a decade earlier (Miller and Brodeur, 2007) to explore connections between interdecadal variations in ocean conditions and diet composition. We also compared the diets of forage fish with co-occurring subyearling

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Chinook salmon (*Oncorhynchus tshawytscha*) for 2011 to examine the potential for diet overlap and competition. Subyearling Chinook salmon are approximately the same size and often occupy similar horizontal and vertical habitats in coastal waters as forage fish, albeit at much lower abundances (Brodeur et al., 2005; Emmett et al., 2006; Litz et al., 2013).

We hypothesized that there will be a high level of diet variability between forage fish within seasons and years, and that the diet composition of different pelagic forage fish will diverge in times of reduced prey availability to minimize predator competition. Conversely, in times of increased primary production and higher prey abundance such as seen in the summer months during some years, diets will converge as predators capitalize on these superabundant prey resources (Brodeur and Pearcy, 1992). Monitoring the trophic responses of pelagic forage fish may identify trends in energy pathways inherently related to a changing ocean environment.

2. Methods

2.1. Sampling area

The NCC is the northern region of the California Current ecosystem, which extends approximately from 41°N to 49° N along the continental shelf and shelf break between northern California and northern Washington (Fig. 1). This region provides seasonally productive feeding

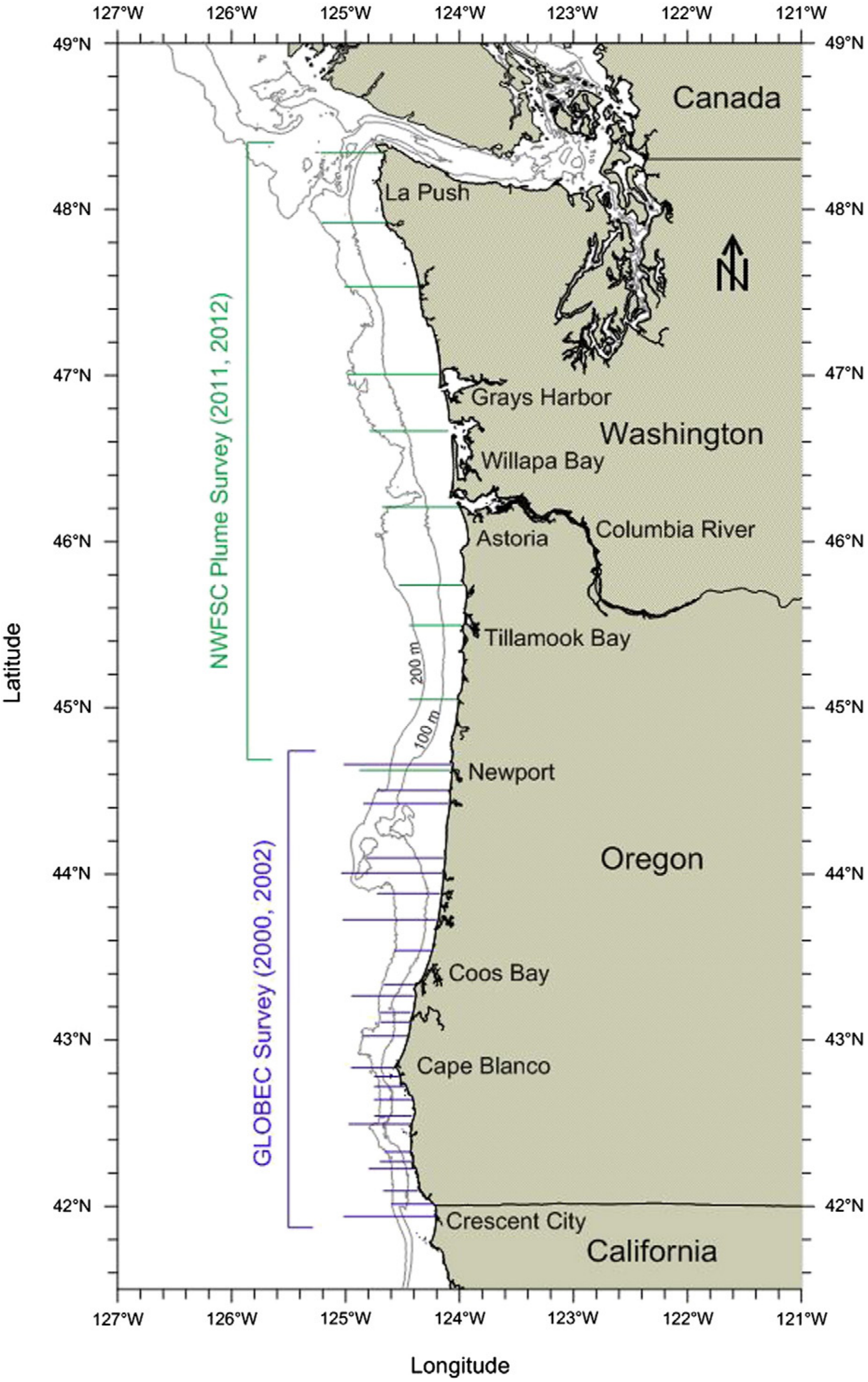

Fig. 1. Location of sampling effort along the shown transects for BPA plume (2011, 2012) and GLOBEC (2000, 2002) sampling.

grounds for a diverse community of pelagic forage fish of both transient and localized populations (Brodeur and Pearcy, 1992; Brodeur et al., 2005; Emmett et al., 2006). The summer physics is dominated by the southward-flowing leg of the North Pacific Current bringing productive waters from higher latitudes to this region (Checkley and Barth, 2009). It is modulated by wind-driven upwelling events bringing cold, nutrient-laden waters to the surface during the spring through fall months (Huyer, 1983). The duration and intensity of upwelling events vary substantially from year to year, leading to variability in zooplankton (Peterson and Keister, 2003) and micronekton (Brodeur et al., 2003) abundances on an interannual scale. Although some climate models predict increasing temperatures and phytoplankton production resulting in higher fish biomass in the California Current (Woodworth-Jefcoats et al., 2013), recent studies suggest that strengthening of upwelling has been observed in recent years due to warming air temperatures, leading to a cooling of California Current and other eastern boundary currents (Sydeman et al., 2014 a,b).

2.2. Fish collections

Nekton samples were collected during May and June of 2011 and June 2012 through the Bonneville Power Administration (BPA) Plume Survey. Samples were collected along a series of transects of multiple stations that extended from Newport, OR (44° 39′ N) to Cape Flattery, WA (48° 23′ N; Fig. 1). Samples were collected with a Nordic-264 Rope Trawl (Nor'Eastern Trawl Systems, Bainbridge Island, WA) that was towed for 30 min during daylight hours (30 m wide by 18 m deep). Sampling details for the BPA Plume Survey are described in Emmett et al. (2004,2005). Latitudes sampled are represented in Fig. 1. At randomly selected stations, up to 10 individuals of each species of nekton were retained, identified, and frozen at sea (−20°). Physical and biological data were collected at the same locations as the fish collections. A CTD (conductivity, temperature, and depth) meter was cast from the surface to 100 m and we used the 3-m depth values for temperature (SST). Pacific Decadal Oscillation (PDO), Northern Pacific Gyre Oscillation (NPGO), El Niño Southern Oscillation (ENSO), and upwelling indices were collected for survey years from http://www.nwfsc.noaa.gov and http://www.pacoos.org and averaged using the sample month and two preceding monthly values to account for developing prey fields.

All fish were thawed, then weighed (±0.01 g) and measured (±0.1 mm) in the laboratory before the stomachs were excised and preserved in formalin for content analysis. The stomachs were removed from the formalin after two weeks of preservation, rinsed in de-ionized water, and stored in 70% ethanol. Diet analysis was performed under a dissecting microscope, and stomach fullness, prey condition, and prey life history stage were quantified to the lowest discernable taxa. The damp weight of prey items was measured using an analytical balance (±0.001 g) after the excess moisture had been absorbed by blotting paper.

Table 1
Total number of stomachs examined by species from the Plume Survey (this study; 2010s) and total number of stomachs analyzed from the GLOBEC (2000s) survey.

Survey	GLOBEC Survey		Plume Survey		
Year	2000	2002	2011		2012
Month	June	June	May	June	June
Pacific herring	117	75	31	10	9
Northern anchovy	–	24	4	4	19
Whitebait smelt	37	23	20	5	–
Surf smelt	155	46	18	16	9
Pacific sardine	6	46	3	8	10
Chinook salmon	–	–	7	31	–
Total	315	214	83	74	47

2.3. Diet analysis

Stomach content analysis was performed individually on 249 stomachs of the six species of nekton but 45 were excluded from analysis, due to emptiness or diets solely comprised of unidentifiable material (Table 1). Prey items of unidentified material, crustacean tissue, or plant material were excluded from the statistical analyses. Weight data was transformed to percent composition per stomach and prey items were grouped into higher taxonomic groups similar to those outlined in Brodeur and Pearcy (1992) for all statistical analyses (App. Table A1). Weight data was further modified for multivariate analysis by removing prey categories that represented less than 3% of the diet for any nekton species within any year. Diet overlap by species was estimated using the Schoener Index of Overlap, which is also known as the Percent Similarity Index (PSI; Schoener, 1974). The PSI is computed as:

$$\mathrm{PSI} = \left[1 - 0.5\sum_{i=1}^{n}\left|p_{ik} - p_{jk}\right|\right] \times 100$$

where p is the proportion of biomass (wet weight) of the kth prey species consumed by predator species i and j. Diet overlap values ≥60% were considered biologically significant (Wallace and Ramsay, 1983). The lowest available taxonomic grouping was used to generate a Percent Similarity Index (PSI).

All multivariate statistics were conducted with the *Vegan*, *MASS*, and *labdsv* packages in R v. 2.15.1 (www.r-project.org, Oksanen et al., 2012; Wood, 2012). Community diet relationships were visually represented with a Nonmetric Multidimensional Scaling (NMDS) ordination of 2 dimensions and tested for significant differences using a Multi-response Permutation Procedure (MRPP) in conjunction with the PSI. For the NMDS, a random starting location was used with all runs with up to 200 iterations per run. The NMDS included environmental data for grouping purposes including: predator length, predator weight, month of sample, year of sample, sample location, ENSO, PDO, SST, and NPGO. Community diet data is difficult to visualize clearly, and a dispersion ellipse was used to visually simplify the diet data using the standard deviation of the average spatial scores (http://www.r-project.org, Oksanen et al., 2012). Significant tests for similarity between groups were examined globally and pair-wise using a MRPP on the percent weight data. The MRPP tests for the null hypothesis of no difference between groups. We used a Bray–Curtis distance measure appropriate for community analyses (McCune and Grace, 2002) and weighting for these tests was determined using functions called *meandist* and *vegdist* in R (R. Development Core Team, 2012). MRPP generates a test statistic (significance level of $p < 0.05$) and an A value that represents the effect size and ranges from 0 to 1, with 1 representing complete within-group agreement and 0 representing within group heterogeneity being equal to chance (McCune and Grace, 2002). For the purposes of this study, we defined an A-value equal or greater to 0.3 as strong differences between grouping (McCune and Grace, 2002), between 0.2 and 0.3 as moderate to moderately strong differences, between 0.1 and 0.2 as weak to moderate differences, while less than 0.1 is no difference to a weak difference. MRPP and NMDS multivariate statistical tests are appropriate for non-normal community data (McCune and Grace, 2002).

Comparisons for diet similarity were constrained by the available dataset. No seasonal comparisons were made within 2012 because fish samples were not available from May 2012. Interannual comparisons were not made for whitebait smelt or subyearling Chinook salmon because they were not collected in 2012. Diets of a single species were compared by season within a year (May to June) only within 2011 and between years (2011–2012) only within a single month (June). Diets of all species were compared within the months of May 2011, June 2011, and June 2012. The diets of all forage fish collected in both June 2011 and June 2012 were compared to the same species collected from the June GLOBEC surveys of 2000 and 2002 (Miller and Brodeur, 2007, Miller et al., 2010) for the interdecadal comparisons. While both studies occurred in June and occurred in what is geographically considered part of the Northern California Current system, the BPA plume study was between 44 and 48° of latitude and the GLOBEC study was between 44 and 42° of latitude, with only one transect in common between the two studies (Fig. 1).

3. Results

3.1. Seasonal and interannual comparisons

In May of 2011 all fish diets were weakly different (global MRPP: A = 0.08, P = 0.002; not shown in tables). There were few significant pair-wise diet comparisons in May of 2011 (Table 2). The highest A-statistic, which measures the strength of the differences, was between surf smelt and Chinook subyearling salmon (A = 0.12) with a 14% diet similarity (PSI; Table 2). Overall, in May 2011, there was relatively high overlap in diets between the forage fish, and the PSI values clarified the non-significant MRPP results. For example, since anchovies had an average PSI of 47% with all the other forage fish and sardines had a 43% PSI with the other forage fish, we would expect to see non-significant MRPP results for these comparisons. Whitebait smelt had the highest average PSI with any other forage fish at 56%. Subyearling Chinook salmon had the lowest diet overlap with any forage fish driving much of the differences in diet in the global MRPP, with maximum percent similarity values of 14% with surf smelt and 13% with whitebait smelt. Surf smelt had the most diet similarity with the other forage fish.

In May 2011 many forage fish diets were not statistically different except the subyearling Chinook salmon though the NMDS ordination (Fig. 2) indicated some specialization. Subyearling Chinook salmon specialized in Teleost (fish) prey, Pacific herring specialized in Anomura prey, particularly Paguridae (hermit crab) larvae, and approximately 20% of surf smelt diets were Hyperiidae (amphipod) prey according to the NMDS ordination and the diet composition chart (Fig. 5). The other predators consumed little of these prey in May 2011. Copepoda and Pteropoda were consumed by all forage fish and represented a large component of the percent weight data (Figs. 2 and 5). Teleost and Euphausiidae prey items were common to almost all fish diets though they represent a small weight percentage (sardine did not consume Teleost prey).

In the global MRPP comparisons of June of 2011, all fish had moderately strong differences in diets (A = 0.27, P = 0.001). Most of the pair-wise MRPP results for June 2011 (Table 3) were significant and many indicated strong differences (A > 0.3) in diets. Anchovy had the strongest differences in diet (avg. A = 0.3) and low PSI values. Herring had moderately strong differences in diets (avg. A = 0.27), the highest PSI value being 26% similar with surf smelt. Surf smelt had the most similarity in diet comparisons with other fish as reflected in the highest observed PSI values (avg. PSI = 13%) and some of the lowest MRPP results (avg. A = 0.13) within June 2011.

For June 2011, all species relied heavily upon a single prey type (Fig. 5). There was no central prey item for all species, as can be seen in May 2011 (Fig. 2), though there was some overlap between diets (Fig. 3). Copepoda was commonly present in forage fish diets, but only anchovy had a weight percent composition above 12%. Herring, subyearling Chinook salmon, and surf smelt consumed Brachyura. Caridea was unique to the diets of surf smelt and subyearling Chinook salmon. Anomura was a shared prey item for herring and subyearling Chinook salmon. Herring and surf smelt were the only predators to consume pteropods. Surf smelt were the only fish to consume Crangonidae (mud shrimp; seen as a component of Caridea in the diet composition chart). Sardine was mostly isolated in the ordination and relied heavily upon phytoplankton (91% of diet).

Surf smelt samples in June 2011 were caught at two sampling sites; diet composition formed two distinct clusters in the prey species space (Fig. 3) and clusters likely reflect distinct prey fields at each site. The dispersion ellipse is centrally located even though the two diet groupings occupy two distinct regions of species space. The MRPP indicated that surf smelt had significantly different diets from all of the other fish and all of the effect sizes indicate weak to moderate differences (0.09 < A < 0.18).

Global MRPP results for June 2012 indicated moderate differences in diets (A = 0.19, P = 0.001) primarily driven by diet differences between herring and all other forage fish (Table 4 and Fig. 4). The differences in diets between surf smelt and sardine were weak (A = 0.06). PSI values (Table 4) showed significant and large similarities (PSI > 69%) in diets between anchovy, surf smelt, and sardine. Diets in June 2012 were similar between forage fish except for herring diets, which had strong and moderate differences in diet with the other forage fish.

In June 2012 Copepoda was a large diet component for anchovy, sardine, and surf smelt (Fig. 5). Herring had a much more diverse diet than any of the other forage fish, which consisted of Copepoda, Euphausiidae, Amphipoda, and Teleost. Anchovy also had a large component of Teleost prey and a unique prey component of Thallassinidae. Surf smelt had a unique prey component of Cnidarian. Copepoda, Brachyura, and Amphipoda were common prey items for most forage fish, though only Copepoda represents a large component of the diets. Amphipoda, Caridea, and Teleosts were shared prey but they represent a small proportion of the diets. Most of the overlap in diet was due to a shared reliance upon Copepoda.

All species-specific pair-wise seasonal MRPP comparisons between May and June of 2011 (not shown in tables), showed weak to moderate differences in diets. Sardine had the greatest difference in diet (A = 0.14, P = 0.044) primarily driven by a seasonal shift in

Table 2
Percent Similarity Index and Multi-response Permutation Procedure results for comparisons among species pairs for predators collected in the May 2011 Plume Survey.

Predator species	N. anchovy	Surf smelt	P. herring	P. sardine	Whitebait smelt
Surf smelt	59% A = −0.01 P = 0.575				
Pacific herring	39% A = −0.01 P = 0.645	45% **A = 0.05** **P = 0.018**			
Pacific sardine	34% A = −0.03 P = 0.38	39% A = 0.01 P = 0.333	41% A = 0.01 P = 0.281		
Whitebait smelt	54% A = 0.10 P = 0.743	64% **A = 0.03** **P = 0.048**	50% A = 0.03 P = 0.066	57% A = −0.01 P = 0.612	
Chinook salmon	7% A = 0.10 P = 0.099	14% **A = 0.12** **P = 0.006**	8% **A = 0.09** **P = 0.001**	9% A = 0.08 P = 0.206	13% **A = 0.10** **P = 0.006**

MRPP results include A statistic and probability value. Significant (P < 0.05) MRPP comparisons are shown in bold text.

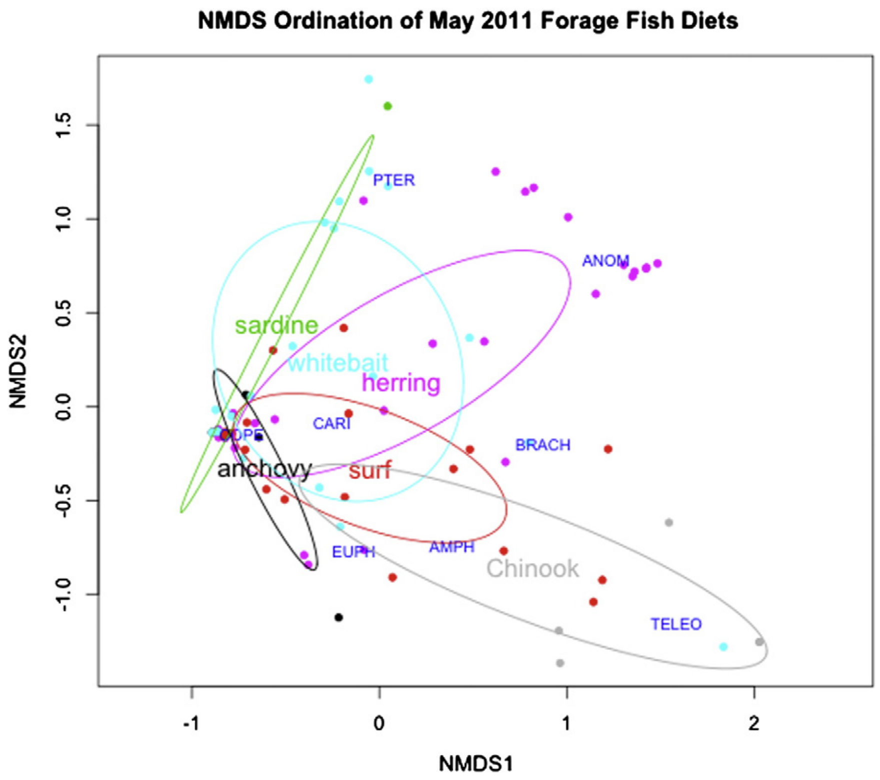

Fig. 2. Nonmetric Multidimensional Scaling (NMDS) plot of the first two axes for the five forage species and Chinook salmon subyearlings in May 2011. Shown are the individual stomachs (color coded by species), ellipses encompassing the major and minor axes of each species, and the location of prey species (blue text) that are most associated with each axis. Stress is 15.5.

consumption from larvaceans to phytoplankton. Whitebait smelt had the next strongest difference in diet (A = 0.1, P = 0.002), the diet shifted from Pteropoda and Teleost to Euphausiidae and Amphipoda. The herring diets (A = 0.09, P = 0.002) shifted away from Euphausiidae, Pteropoda and Copepoda to rely more heavily on Paguridae and Cancer. Anchovy diets (A = 0.09, P = 0.029) shifted from relying largely on Copepoda in May to almost entirely on Copepoda in June. Surf smelt diets had weak differences (A = 0.07, P = 0.004), relying on many prey species in both months, characterized by a reduced reliance on Copepoda, Euphausiidae, Amphipoda, Teleost, and Pteropoda and an increased reliance on Cancer, Paguridae, Pandalidae, and Crangonidae. Generally diets shifted away from Copepoda towards Brachyura, Caridae, and Amphipoda between May and June.

Sardine had a strong difference in diet (A = 0.43, P = 0.001) and herring had a moderately strong (A = 0.2, P = 0.001) difference in diet in the annual pair-wise MRPP comparison between June of 2011 and June of 2012 (not shown in tables). Sardine diets shifted from a diet based upon Phytoplankton to one primarily composed of Copepoda. Herring diets shifted from Paguridae, Brachyura, and Copepoda to a diet composed of Euphausiidae, Teleost, and Amphipoda, with a reduction in Copepoda. There is a moderate diet difference for surf smelt (A = 0.13, P = 0.008) and a non-significant result for anchovy. Surf smelt relied on many prey types in June of 2011 but only on a few of prey types, primarily Copepoda, in June 2012. Generally diets shifted from Brachyura and Anomura in 2011 towards Copepoda in 2012.

3.2. Interdecadal comparisons

There were moderate differences in diets between all species (A = 0.13, P = 0.001) and moderately weak differences between all years (A = 0.08, P = 0.001) in the interdecadal global MRPP comparisons for June 2000, 2002, 2011, and 2012. All species but herring

Table 3
Percent Similarity Index and Multi-response Permutation Procedure results for comparisons among species pairs for predators collected in the June 2011 Plume Survey.

Predator species	N. anchovy	Surf smelt	P. herring	P. sardine	Whitebait smelt
Surf smelt	12% **A = 0.10** **P = 0.027**				
Pacific herring	9% **A = 0.48** **P = 0.003**	26% **A = 0.18** **P = 0.001**			
Pacific sardine	4% **A = 0.36 P = 0.006**	4% **A = 0.14** **P = 0.002**	4% **A = 0.32** **P = 0.001**		
Whitebait smelt	10% **A = 0.36** **P = 0.046**	10% **A = 0.09** **P = 0.009**	10% **A = 0.28** **P = 0.001**	9% A = 0.10 P = 0.081	
Chinook salmon	0% **A = 0.18** **P = 0.001**	13% **A = 0.13** **P = 0.001**	2% **A = 0.10** **P = 0.002**	0% **A = 0.16** **P = 0.001**	0% **A = 0.10** **P = 0.001**

MRPP results include A value and probability value. Significant ($P < 0.05$) MRPP comparisons are shown in bold text.

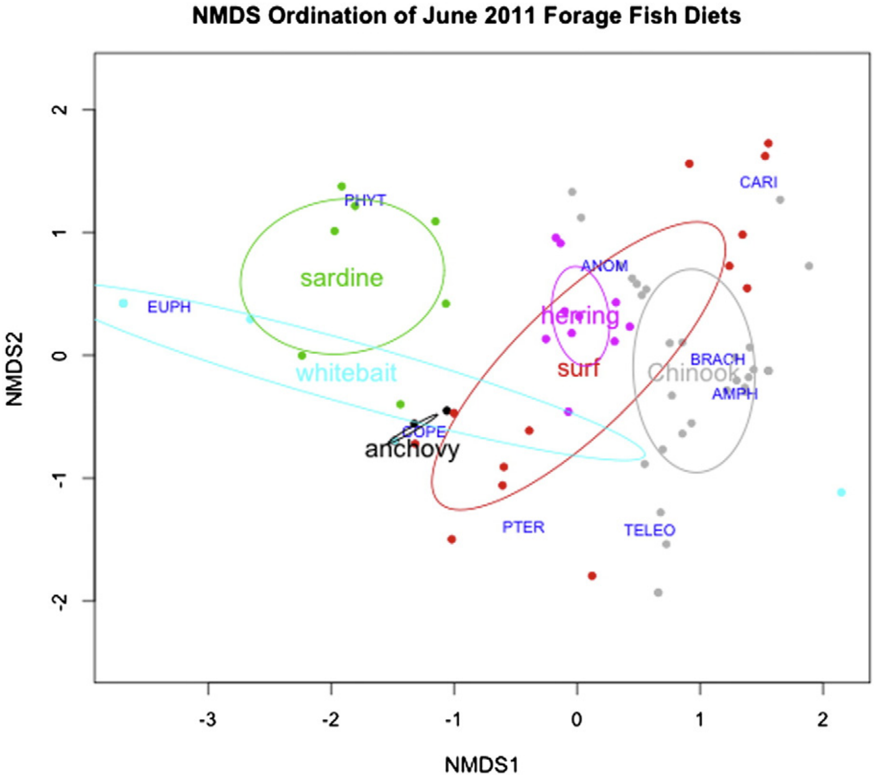

Fig. 3. Nonmetric Multidimensional Scaling (NMDS) plot of the first two axes for the five forage species and subyearling Chinook salmon in June 2011. Shown are the individual stomachs (color coded by species), ellipses encompassing the major and minor axes of each species, and the location of prey species (blue text) that are most associated with each axis. Stress is 13.2.

and anchovy showed some overlap of ellipses and all species showed specialization in the interdecadal NMDS ordination by species (Fig. 6a). Sardine showed the largest overlap with herring and to a lesser degree anchovy. Surf smelt was the most isolated in terms of its prey composition. Based upon the interdecadal NMDS ordination (Fig. 6b), the yearly centroid of all forage fish diets shifted in a linear fashion away from the Euphausiidae, Decapoda, and Amphipoda regions of species space towards the Copepoda and Pteropoda regions with the 2000 centroid at one extreme and the 2012 centroid at the other. The ordination shows this shift occurring inversely to the direction of the PDO and NPGO (Fig. 6b). Pteropoda, Anomura, and Caridae were important prey for 2011 and 2012, whereas Decapoda and Amphipoda were more important for 2000 and 2002.

4. Discussion

The variability of ocean productivity and subsequent prey availability supports the expectation that forage fish diets will be variable on a seasonal and an annual basis (Brodeur et al., 1987; Miller and Brodeur, 2007; Miller et al., 2010). It also follows that forage fish diets will track or at least reflect long-term changes in ocean conditions, adapting to fluctuations in abundance or scarcity of prey (Brodeur and Pearcy, 1992). Other concepts of diet theory suggest a convergence of diets when common prey items become abundant, such as in the summer months or productive years, and specialization in diet in times of scarcity or competition. Diets will be more similar when collected from a single location in time. In this study we expected to find variable diets for all forage fish, with a general convergence of diets when ocean conditions favor higher productivity or prey abundances are high.

Table 4
Percent Similarity Index and Multi-response Permutation Procedure results for comparisons among species pairs for predators collected in the June 2012 Plume Survey.

Predator Species	N. anchovy	P. herring	P. sardine
Pacific herring	28% **A = 0.16** **P = 0.002**		
Pacific sardine	69% A = 0.03 P = 0.069	8% **A = 0.28** **P = 0.001**	
Surf smelt	69% A = 0.03 P = 0.108	8% **A = 0.18** **P = 0.006**	90% **A = 0.06** **P = 0.025**

MRPP results include A value and probability value. Significant ($P < 0.05$) MRPP comparisons are shown in bold text.

4.1. Seasonal and interannual comparisons

The ocean environment of 2011 had a negative but moderate MEI, a negative and moderately strong PDO value, and a moderately positive NPGO value along with a high value for the Northern Copepod Anomaly (Wells et al., 2013). Due in part to the high values for the Northern Copepod Anomaly, we expected to see diet convergence and overlap in 2011 and 2012 however, our results from June 2011 support more specialization and divergence than those for the June 2012 diets. Though our results appear to support a diet divergence from May to June of 2011, forage fish diets may vary on a timescale more closely aligned to population dynamics and intermittence of prey fields than seasonal shifts of ocean conditions. A general shift in diets was seen on a decadal time scale supporting diet specialization for anchovy, surf smelt, and herring, while sardine had dietary overlap with all other forage fish as it was centrally located in the species space (Fig. 6a).

The pair-wise comparisons between species in May indicated diet overlap for all forage fish with no clear indication of specialization due to a shared consumption of Copepoda. Given the high values for the Northern Copepod Anomaly in 2011, these are not unexpected results for May but the June diets had less overlap and counter-intuitively showed evidence of diet specialization with generally much less reliance on Copepoda. Though there is a seasonal diet shift as expected,

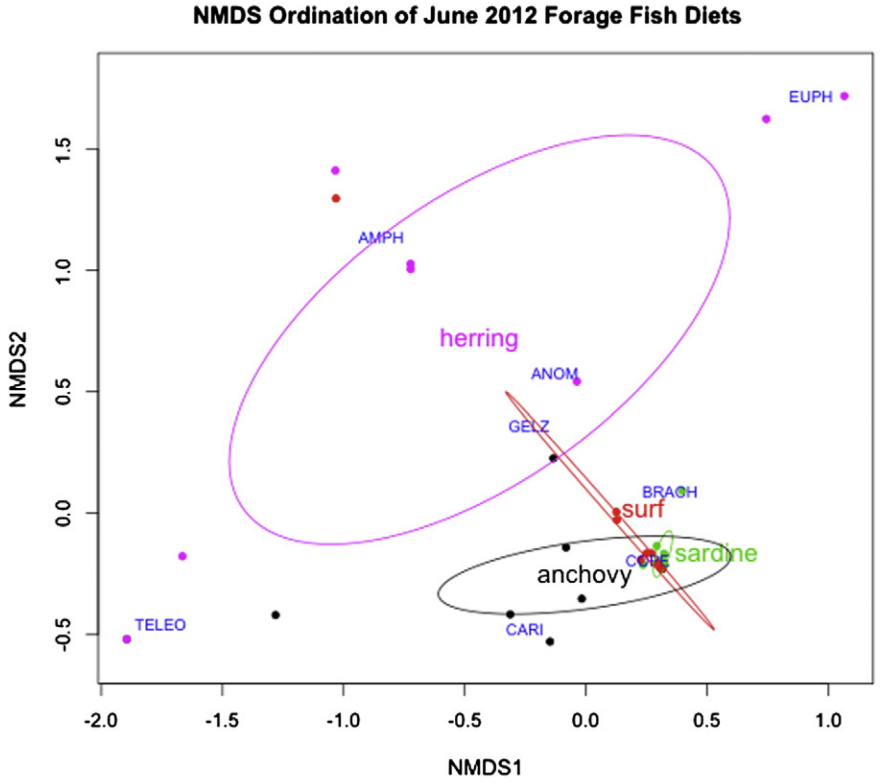

Fig. 4. Nonmetric Multidimensional Scaling (NMDS) plot of the first two axes for the four forage species in June 2012. Shown are the individual stomachs (color coded by species), ellipses encompassing the major and minor axes of each species, and the location of prey species (blue text) that are most associated with each axis. Stress is 6.1.

there are strong differences in diet only for surf smelt, sardine, and whitebait smelt.

The Copepoda biomass data from the Newport Hydrographic Line (44° 40′ N), located at the southern end of our sampling region, was similarly high in both sampling years, although 2012 had the highest values recorded for the entire time series (Wells et al., 2013) and may reflect anomalously strong southward transport of Subarctic waters (Keister et al., 2011). Forage fish diets had a higher degree of overlap in 2012 than in 2011, which seems appropriate given the Copepoda data. However, the diet specialization and lack of diet overlap seen in June of 2011 is unexpected given that the Copepoda biomass was high in both years.

Among the species examined, sardines exhibited the greatest between-cruise variability with the diets dominated by Pteropoda, Phytoplankton, and Copepoda in the three months examined. This is consistent with previous diet studies of sardines in the NCC (Emmett et al., 2005; McFarlane et al., 2005) which showed substantial seasonal and interannual variability. Studies on this species in other similar upwelling regions (e.g., southern Benguela Current) suggest that this species is a non-selective filter feeder and its diet generally reflects the prey type and size of the plankton community in which they were collected (van der Lingen, 2002). This plasticity in sardine diets and dependence upon prey fields more closely linked to primary production may make them more sensitive to changing ocean conditions than other forage fish in the NCC and other eastern boundary upwelling ecosystems (Garrido et al., 2008; McFarlane et al., 2002).

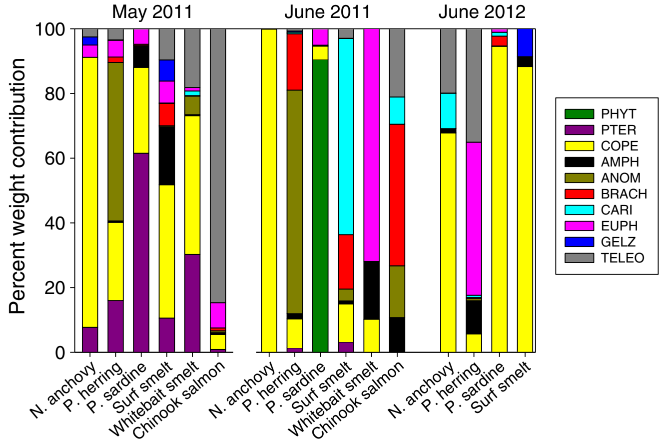

Fig. 5. Stacked bar plots of the dominant prey taxa for each predator species for the different years and months examined.

4.2. Interdecadal comparisons

Our interdecadal comparisons confirm a general forage fish diet shift in prey reliance that may be related to ocean conditions and subsequent prey availability. We expected some species to express more specialization while others show more dietary overlap. In general, our study years (2011, 2012) and the Miller and Brodeur study years (2000, 2002) had mixed but similar values for PDO, NPGO, and MEI, with none of the years particularly outstanding in terms of ocean conditions (Wells et al., 2013). Similarly, upwelling strength was normal prior to and during the sampling period in both time periods (Bjorkstedt et al., 2011). However, the Northern Copepod Anomaly did show that 2011 and 2012 had higher values than 2000 and 2002 during the periods of sampling (Wells et al., 2013). Interannual variability in the Copepoda composition in the NCC appears to be driven by large-scale changes in advection in the North Pacific Ocean, linked to the PDO (Keister et al., 2011). In past surveys (Brodeur et al., 1987; Miller and Brodeur, 2007), Euphausiidae was a more important dietary component than Copepoda for these forage species.

While both studies for the interdecadal comparisons occurred in June and in the Northern California Current, the overlap in sampling stations

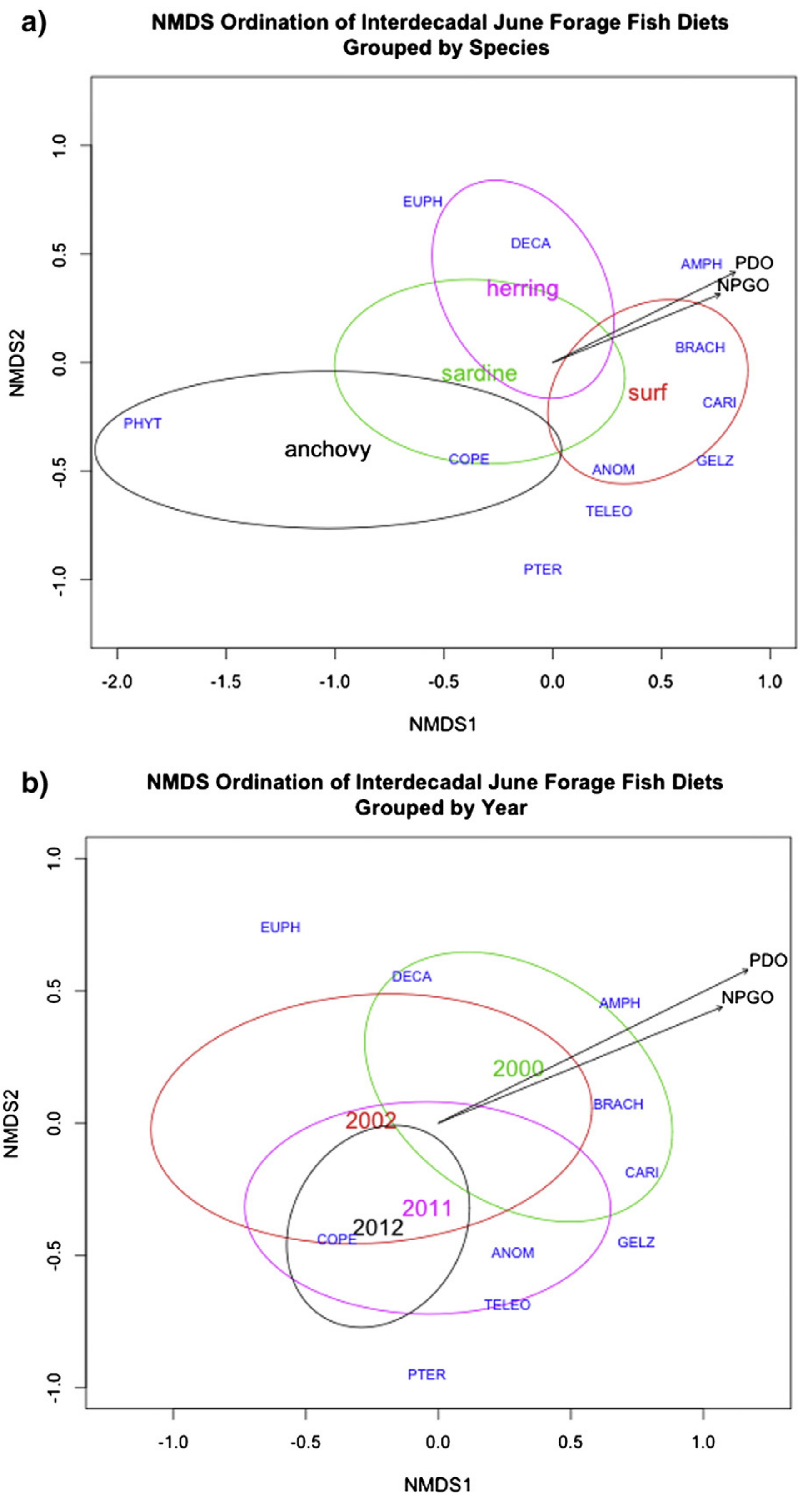

Fig. 6. Nonmetric Multidimensional Scaling (NMDS) plot of the first two axes for the four dominant forage species for all June cruises. Shown are the ellipses encompassing the standard deviation major and minor axes (colored coded by species (a) and year (b)), and the location of prey species (blue text) that are most associated with each axis. Shown as vectors are the relationships with the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO). Stress is 18.7 for both ordinations.

occurred only along the Newport Hydrographic line. When juvenile salmon diets were compared in 2000 and 2002 between different sampling locations (BPA and GLOBEC) similar to this study's interdecadal comparison, the diets were found to be 75% similar (Brodeur et al., 2007b). Lamb (2011) found few significant differences between the copepod biomass and composition between samples taken along the Newport Hydrographic line and off northern Oregon and Washington. Similarly, the densities and community composition of copepods were indistinguishable between off Washington, Oregon and off northern California (C. Morgan, Oregon State University, Newport OR, unpubl.). However, Euphausiidae distributions are known to be spatially non-homogeneous in the California Current (Ressler et al., 2005), and some of the variability between the decades could be attributed differing prey concentrations in the two sampling areas we compared.

Although the PDO and NPGO values do not completely describe the path of combined forage fish diets, we do see a strong link. A change in ocean productivity may shift the combined forage fish diets towards a specific prey benefiting some forage fish species more than others. This shift also has implications for the efficiency of energy pathways and food web structure for economically important species such as salmon and hake in the NCC (Ruzicka et al., 2012). Ocean conditions like those occurring in 2011 and 2012 may benefit sardine and anchovy more than herring or surf smelt because they share Copepoda prey more than the other forage fish. The NMDS ordinations (Fig. 6a/b) show diet specialization for each species, with sardine exhibiting the least specialization. In contrast, ocean conditions similar to those found in the early 2000s may benefit surf smelt or herring more than anchovy or sardine. A continuation of this study in years with ocean conditions contrasting with those found in this study (e.g., Brodeur and Pearcy, 1992) will likely provide more insight as to prey suitability, diet plasticity, and adaptability of forage fish.

4.3. Summary and conclusions

The conclusions of this study will be constrained by the sample sizes of forage fish that we had available, but given the limited information on community diet relationships for these species, our results shed some light on feeding ecology of these important fishes and how they potentially interact with salmon. Forage fish diets in this study supported our expectations of diet variability on seasonal, interannual, and interdecadal bases and comparisons between species indicated differing degrees of diet similarity. Our comparisons show groupings of forage fish: herring and sardine diets had the most similarity, whereas surf smelt and whitebait smelt showed similarity to a lesser degree. This latter grouping may have implications for competition with subyearling Chinook salmon as these forage fishes have the most dietary overlap with subyearling Chinook salmon. Previous work (Brodeur et al., 2008) for the GLOBEC sampling region had also shown that juvenile salmon (mostly yearling salmon in this situation) had relatively dissimilar diets to the forage fish examined here. However, given the higher biomass of the forage fish compared to salmon (Brodeur et al., 2005; Emmett et al., 2006; Litz et al., 2013), the changing diets of forage fish in relation to ocean conditions may have a variable influence on limiting the availability of suitable prey for subyearling Chinook salmon when they first enter the ocean.

Seasonal comparisons showed diet convergence in May of 2011 and June of 2012, when the Northern Copepod Anomaly indicated high values for Copepoda, but even though June 2011 also had a high value, Copepoda were a small component of forage fish diets, which does not support our understanding of diet convergence. In addition to the amount of food available in a given year, the quality of food in terms of energy density, total lipid content, or fatty acid composition can vary interannually which may have important ramifications for forage fish survival and the nutritive content available for higher trophic levels (Litz et al., 2010; Litzow et al., 2006; Spitz and Jouma'a, 2013).

Though the ocean conditions examined in this study are similar to past studies, they highlighted the variability of forage fish diets and their unpredictable response to ocean conditions and prey fields. Diet analyses of forage fish during El Niño and/or warm ocean conditions are lacking in the NCC, and further studies are necessary for a better understanding of the relationship between ocean conditions and trophic responses. Continuing to monitor diet compositions of forage fish in relation to ocean conditions over time may provide indications of which forage fish are most susceptible or well adapted to changing ocean environments (Espinoza et al., 2009; van der Lingen et al., 2009), and provide critical information for the management of other eastern boundary upwelling ecosystems experiencing more top-down pressure in the form of commercial fisheries on forage fish than the NCC. As fisheries management transitions from a species-specific management to an ecosystem-based management (Ainley et al., 2014), understanding the trophic interactions between forage fish, primary production, and upper trophic levels may better inform management decisions and predictive ecosystem models in a time of changing ocean environments in eastern boundary current upwelling ecosystems in the world.

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Appendix A

Table A1
Taxonomic groups found in the stomachs of forage fishes and salmon showing the abbreviations used on multivariate plots and the lower taxonomic groupings used for the Percent Similarity Index calculations. Also shown are an 'Excluded taxa' group of taxa that occurred in less than 3% of the total taxa and were removed prior to the multivariate analysis.

Taxon	Multivariate abbreviation	PSI grouping
Phytoplankton	PHYT	Algae, Phytoplankton
Pteropoda	PTER	Pteropoda, Gastropoda
Copepoda	COPE	*Calanus marshallae*, *Epilabidocera amphitrites*, *Eucalanus* sp., *Pseudocalanus* sp., *Acartia* sp., *Oithona* sp.
Amphipoda	AMPH	*Atylus tridens*, *Jassa* sp., Gammaridae, Caprellidae, *Hyperia medusarum*, *Hyperoche* spp., *Themisto pacifica*, *Vibillia* sp., *Lycaea pulex*, Hyperiidae
Anomura	ANOM	Paguridae
Brachyura	BRACH	*Cancer* sp., *Fabia subquadrata*, *Pachycheles* sp., *Petrolisthes* sp., *Pinnixia* sp., Pinnotheridae, Porcellanidae
Caridea	CARI	Hippolytidae, *Pandalus* sp., *Crangon* sp., *Neotrypaea californiensis*, Thallassinidae
Decapoda	DECA	Other decapods not included above
Euphausiidae	EUPH	*Euphausia pacifica*, *Thysanoessa spinifera*
Gelatinous Zoop.	GELZ	*Oikopleura* sp., Appendicularia, Thecosomata, Salpidae, *Sagitta elegans*
Teleost	TELEO	*Ammodytes hexapterus*, *Hemilepidotus* sp., *Leptocottus armatus*, Cottidae,Osmeridae, Pleuronectidae, *Sebastes* sp., Osteichthyes
Excluded taxa		Cirripedia, Ctenophora, Cumacea, Diptera, Mysidacea, *Neomysis kadiakensis*, Polychaeta

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