Food habit variability of arrowtooth flounder (*Atheresthes stomias*) along the U.S. west coast

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Abstract

A diet study of arrowtooth flounder (*Atheresthes stomias*) was undertaken to provide current information on their food habits and predator-prey relationships in the California Current Ecosystem. Arrowtooth flounder stomachs (n=573) were collected between 2013 and 2018 from 397 trawls during the Northwest Fisheries Science Center's west coast groundfish bottom trawl survey. A total of 357 stomachs (62.3%) contained prey, which revealed a highly piscivorous diet across all lengths examined (14 – 77 cm) and described a regionalized and opportunistic feeding behavior. Increased predator length correlated both with an increase in percentage of fish prey consumed and an increase in depth of capture. Smaller (< 43 cm) and shallower (≤ 183 m) arrowtooth flounder consumed a relatively high percentage of euphausiids and shrimp, while larger arrowtooth flounder (≥ 43 cm) captured at greater depths (> 183 m) consumed more fish and fewer shrimp and euphausiids. Arrowtooth flounder diet varied by geographic area, likely resulting from regional differences in prey availability. North of the mean latitude of capture (44.45°N), Pacific hake (*Merluccius productus*) and Pacific herring (*Clupea pallasii*) were the predominant fish in arrowtooth flounder diets, while arrowtooth flounder caught south of the mean latitude consumed mostly Pacific hake and rockfishes (Scorpaenidae). Unidentified teleost fish contributed much to the diet across all size, depth, and latitude ranges.

Keywords: *Atheresthes stomias*, diet analysis, food habits, California Current Ecosystem, multivariate analysis

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1. Introduction

Identifying trophic relationships is fundamental to understanding ecosystem dynamics, and directives for movement towards ecosystem-based fisheries management (EBFM) have elevated the need for food web analyses (Field and Francis, 2006; Gaichas et al., 2010; Heymans et al., 2016). Increasingly, EBFM tools such as ecosystem models and management strategy methods are implemented to complement stock assessments and to better manage commercially important groundfish species (Gaichas et al., 2010; Kaplan et al., 2013; Collie et al., 2016). Important components of an effective EBFM approach include detailed knowledge of predator-prey relationships and integrated trophic-inclusive or food-web models (Kaplan et al., 2013; Koehn, 2016; Livingston, et al., 2017; Tam et al., 2017). This management approach has led to a critical need for diet information that provides high resolution of prey taxa (Pacific Fisheries Management Council (PFMC), 2018). However, the diets of many of the groundfish species managed under the PFMC's Groundfish Fishery Management Plan (FMP) remain largely understudied and lack substantive data.

The primary goal of this study was to provide detailed and updated information on the feeding habits of arrowtooth flounder (*Atheresthes stomias*; hereafter ATF) throughout its latitudinal and depth ranges within the California Current Ecosystem (CCE). ATF is an abundant predatory groundfish reported to be opportunistic and piscivorous, but is also known to feed on invertebrates, particularly euphausiids and shrimps (Yang et al., 2006; Knoth and Foy, 2008; Love, 2011). Since ATF have a wide geographic range, with increasing abundance from central California north to the Bering Sea (Love, 2011; Keller et al., 2013; Sampson et al., 2017), they experience varying degrees of dietary overlap and competition for prey with other top consumers in their habitats (Yang, 1995; Buckley et al., 1999; Barnes et al., 2018). Previous research provided information on the diet of ATF from multiple regions in the northeastern Pacific Ocean (Gotshall, 1969; Yang and Livingston, 1986; Yang, 1995; Buckley et al., 1999; Lang et al., 2000; Yang et al., 2006), although recent studies were primarily in Alaskan waters. In the northern extent of their range, they are noted for feeding on commercially important walleye pollock (*Gadus chalcogrammus*) (Yang and Livingston, 1986; Lang et al., 2000), while further south along the west coast of North America their main prey consisted of Pacific hake (*Merluccius productus*; hereafter hake) and clupeids, namely Pacific herring (*Clupea pallasii*; hereafter herring) (Gotshall, 1969; Buckley et al., 1999). Since historical data for ATF diet within the CCE date from 1992 or earlier, there is a gap in our understanding of how the variability in diet of ATF might have changed over the last several decades. In an effort to fill this knowledge gap, detailed diet composition and multivariate statistics using recent (2013-2018) data from the National Oceanic and Atmospheric Administration (NOAA) Northwest Fisheries Science Center's (NWFSC) west coast groundfish bottom trawl survey is presented here.

Describing groundfish diets and trophic relationships has become increasingly important for EBFM, particularly against a background of a changing climate. Along the U.S. west coast, these changes include the recent appearance of anomalous warm water episodes such as 'the Blob' (Bond et al., 2015; Cavole et al., 2016), as well as natural oceanographic fluctuations linked to the El Niño-Southern Oscillation (ENSO), the North Pacific Gyre Oscillation (NPGO), and the Pacific Decadal Oscillation (PDO) (Mantua et al., 1997; Chavez et al., 2003; Di Lorenzo et al., 2008; Wolter and Timlin, 2011; Santora et al., 2017a). Trophic interactions can also vary in response to anthropogenic activities, such as fishing pressure and ocean acidification (Santora et al., 2017a; Doyle et al., 2018). These combined environmental and anthropogenic effects can influence and alter local and regional ecosystems, impacting key prey species for groundfishes (Chavez et al., 2003; Santora et al., 2017b). Changes in primary productivity or shifts in the distribution and abundance of higher trophic-level predators also have consequences on the location, abundance, and mortality of important prey items (euphausiids, shrimp, and forage fishes) for groundfishes in the northeast Pacific Ocean (Dufault et al., 2009; Kaplan et al., 2013).

Updating trophic information for ATF with current data for species-specific food habits, and regional prey variability, will potentially provide new insight into this species' adaptability, help identify potential threats to their local, regional and coast-wide populations, and improve our understanding of predator-prey interactions in the CCE food web to support future EBFM efforts.

2. Materials and Methods

2.1. Trawl survey and study area

The NWFSC has conducted annual bottom trawl surveys of the continental shelf and slope waters from the U.S.-Canada (48.5°N) to the U.S.-Mexico (32.5°N) borders since 2003. The survey samples depths from 55-1280 m, divided into three depth strata (55-183 m, 184-549 m, and 550-1280 m), using a stratified-random sampling design (Keller et al., 2012, 2017). Four chartered, commercial trawlers (20-28m length) annually sample between mid-May and mid-October, conducting 15 min tows at a target speed of 4.07 (±0.93) km hr^{-1} (2.2 ±0.5 knots) during daylight hours from sunrise to sunset. The trawl survey utilizes an Aberdeen-style trawl net with a 3.8-cm mesh codend liner, 25.9 m headrope, and 31.7 m footrope, designed to operate in strict compliance with protocols established for NMFS bottom trawl surveys (Stauffer, 2004). All fish captured during the survey hauls are sorted and identified to species, or the lowest taxonomic category possible. Randomly selected subsamples of fish are counted and measured for total length. Invertebrates are also sorted and identified to the lowest possible taxonomic level. At a minimum, all contents of each haul are weighed and counted. A more detailed description of all trawl survey protocols appears in Keller et al. (2017).

2.2. Biological samples

ATF stomachs were collected from May through October in 2013, 2014, 2016, and 2018 during annual bottom trawl surveys conducted by the NWFSC (Fig. 1). Stomachs were collected from subsamples randomly selected to measure length and determine sex. All fish with signs of net feeding (partially or recently ingested prey with no detected level of digestion) or regurgitation (i.e., extruding stomach, or prey in the gills, mouth, or throat) were excluded from stomach collections. Length-based size bins and a limited collection of two stomachs per haul were used to optimize the size range and maximize spatial coverage. Although rare, opportunistic samples were occasionally collected to fill gaps in size, spatial, and temporal ranges. Total length, weight, and sex for each fish selected for stomach removal were recorded at sea, along with trawl station information, including capture location and depth.

Stomachs were excised, placed into individual cloth bags, and preserved in 10% buffered formalin at sea. Samples were subsequently rinsed with fresh water and stored in 70% ethanol when returned to the laboratory at the conclusion of each survey pass. In the laboratory, stomach contents were removed, blotted dry, and identified to the lowest possible taxonomic classification using a Leica MZ75 dissecting stereo microscope. Ohaus Scout Pro portable precision electronic balance scales with 200 g and 400 g capacities were used to weigh individual prey items to the nearest hundredth gram (0.01 g) damp weight. Due to advanced levels of digestion, prey were often difficult to enumerate, therefore prey counts were not included in analyses.

Prey items were aggregated by individual species (e.g., hake) or family (e.g., clupeids, rockfish, euphausiids, and pandalids) for abundant prey (≥ 3% frequency of occurrence (FO)), grouped into higher taxonomic categories (other shrimp, flatfish, and other fish) for less frequent prey taxa (< 3% FO), or excluded if < 3% FO and prey could not be further consolidated into larger groups (cephalopods, other prey, and miscellaneous). Unidentified teleosts, mainly fish bones, scales, and/or fish too digested to be accurately identified to higher taxa, were an important portion of the overall diet and therefore included as a separate prey group. Empty stomachs were quantified, but omitted from any further analyses. Lengths were measured and recorded for intact prey, although were not used in this study, as were metrics for stomach fullness, level of digestion, and parasite load.

2.3. Statistical analyses

Diet data for each fish were summarized by the following gravimetric and occurrence indices (Hyslop, 1980): percent by weight,

$$\%\ W_i = [W_i \ / \sum_{i=1}^{n} W_i] \times 100 \quad (1)$$

where n is the total number of prey taxa observed (individual or grouped), W_i is weight in grams for prey taxa i, divided by the summed weight for all prey taxa included in the study; and percent frequency of occurrence,

$$\%\ FO = (N_i / N_s) \times 100 \quad (2)$$

where N_i is the number of stomachs containing an individual prey taxa i, and N_s is the total number of stomachs with contents examined. To determine if sample size was sufficiently large, species accumulation curves (Ferry and Cailliet, 1996) were generated for both individual prey at the lowest taxa and higher taxonomic groups, using sample-based rarefaction of randomly selected stomach samples with 999 permutations (Fig. S1). The slope (b) of the linear regression through the final five sample points of the curve was used to assess if an acceptable asymptote was reached ($b \leq 0.05$; Bizzarro et al., 2007).

The final diet matrix for statistical analysis consisted of nine major prey groups: clupeids, euphausiids, hake, other fish, pandalid shrimp, other shrimp (including unidentified shrimp which could include pandalids), flatfish, rockfish, and unidentified teleosts (which could include other listed fish groups). An environmental matrix, composed of continuous and categorical variables (year, depth, latitude, longitude, and fish length and weight), and *a priori*-specified binned groupings (<30, 30-39, 40-49, 50-59, and >60 cm length bins; <100, 100-199, 200-299, 300-399, and >400 m depth bins; and <39, 39-41, 41-43, 43-45, 45-47, and >47 °N latitude bins) based upon historical groundfish bottom trawl survey catch data, were generated to measure prey differences along spatial and ontogenetic boundaries. Sexes were pooled for analyses since fish gender was not parameterized in the sample collection design.

Multivariate analyses were conducted using relativized weight of stomach contents whereby each value was proportioned by the total weight. Permutational analysis of variance (PERMANOVA; Anderson, 2001, 2017) utilizing a Bray-Curtis distance matrix was used with 999 permutations to determine whether significant prey differences existed with regard to year and the *a priori* binned variables. Year was excluded as a variable from this analysis due to inconsistency in the stomach collections between years.

A non-metric multidimensional scaling (NMDS; Kruskal, 1964; McCune and Grace, 2002) ordination also using a Bray-Curtis distance matrix (Bray and Curtis, 1957; McCune and Grace, 2002) was conducted to visually represent diet variability within different spatial and ontogenetic bounds (Bosley et al., 2014). 95% confidence ellipses were additionally plotted to convey diet differences in multivariate space between the categorical groups.

An indicator species analysis (ISA; Dufrêne and Legendre, 1997) was employed using 9,999 iterations to distinguish if any prey items were significantly associated with a particular *a priori* group. Mean length (43 cm), mean latitude (44.45 °N), depth strata (modified from Keller et al., 2017) to include only two depth strata: ≤ 183 m and > 183 m), and latitude and depth strata combined were also compared. All analyses were conducted using R programming software, version 3.5.1 (R Core Team, 2018), with *vegan* (NMDS, PERMANOVA; Oksanen et al., 2018), and *labdsv* (ISA; Roberts, 2019) packages.

3. Results

Stomachs from 573 ATF were analyzed for this study, 357 (62%) of which contained prey. Ranging in size from 14.0 cm to 77.0 cm and depths from 61 m to 541 m, the shallower fish tended to be smaller while the deeper fish were larger (Table S1). Prey accumulation curves showed sample numbers were sufficient for both the lowest identified taxon and at the higher taxonomic groups (Fig. S1).

ATF primarily consumed teleost fish across the size range collected, in all areas and depths encompassed by this study. Fishes and unidentified fish remains occurred in nearly 75% of stomachs with contents, and accounted for over 97% of the overall total diet weight (Table 1). Among the fish prey identified to species, hake (44% W), clupeids (18%), and flatfish (15%) made up the most significant portion of ATF diet. Rockfishes (10%) also contributed a considerable amount to the total diet, with only greenstriped rockfish (*Sebastes elongatus*) and shortbelly rockfish (*S. jordani*) identifiable to species. Other fish prey represented only a small percentage (2%) of the total diet. Unidentified teleost fish comprised a substantial proportion of the total diet by frequency of occurrence (28%), but not by weight (7%) due to frequent occurrences of only bones and/or scales in stomachs. Where possible, otoliths and scales were used to identify fish remains to taxonomic family or species.

Shrimp and euphausiids occurred in stomachs with high frequency (17% FO and 19% FO respectively), but because of their small sizes each only accounted for minimal weight (Table 1).

Cephalopods were included in initial % W and % FO calculations for diet composition, but with low % W and % FO were excluded from subsequent analyses, as were other prey and miscellaneous unidentifiable, highly digested, and inorganic materials (e.g. pebbles, sand) present at very low percent weight (Table 1). Collectively, invertebrates only accounted for a small part of the total overall diet of arrowtooth flounder, but a significant portion by frequency.

Variability in diet composition was observed among the discrete size classes (Fig. 2). Despite piscivory throughout the size classes examined here, a noticeable ontogenetic shift from a diet with frequent euphausiid and shrimp predation to one of almost exclusive piscivory occurred around the mean predator length (43 cm). The diet of the smallest size class of ATF comprised the largest proportion of invertebrates (euphausiids and shrimp) by weight and frequency. Euphausiids and shrimp accounted for less than one percent by weight of the total diet for the two largest size bins combined, but still had a relatively high rate of occurrence. For fish prey, clupeids remained the largest prey group by weight for each of the smallest three size classes, while hake was the dominant prey of the two largest size bins. The distribution and frequency of ATF prey groups by predator length is shown in Fig. S2. Of note were the occurrences of engraulids and osmerids identified only from stomach contents of ATF < 35 cm. There were also several instances of young-of-the-year (YOY) hake found in stomachs collected from smaller ATF in shallower depths. This suggests the smaller and shallower predators fully utilized these small forage fishes where available. However, as high numbers of fish prey were necessarily described as unidentified teleost fish due to advanced levels of digestion, they could potentially be under-represented in the overall diets of both small and large ATF.

Diet proportions by weight and frequency of occurrence showed similar patterns when analyzed using 100-m depth intervals (Fig. 2). Clupeids, flatfish, other fish (mostly anchovy and smelt), euphausiids, and shrimp comprised a larger proportion of ATF diet at shallower depths, whereas hake and rockfish were a proportionately larger part of their diet at greater depths. Shallower ATF were typically smaller in size, and more than twice as likely to feed upon shrimp and euphausiids. The higher number of larger ATF present in the deeper stratum tended to prey on fish considerably more than those in the shallower stratum. Flatfishes were a major prey component of ATF diet along the west coast, and were the dominant prey in the shallowest depth bin, accounting for well over half of the total diet weight. Large and small ATF, both shallow and deep, had substantial proportions of flatfish in their diet, which indicated flatfishes form an integral portion ATF diet composition throughout their size and spatial ranges. In mid-depths, clupeids and flatfish each made up about one-third of the diet by weight, but euphausiids and shrimp prey comprised over half of all prey occurrences. For those ATF found at deeper depths, rockfish, and hake especially, contributed the highest proportions to the diet. The distribution and frequency of ATF prey groups by depth is shown in Fig. S3.

A clear pattern of prey variability also emerged based on analysis of latitudinal differences (Fig. 2). Clupeids were predominant in the northernmost latitude bin but decreased in the southern latitude bins. The high incidence of clupeids, namely herring, in stomachs collected in the northern part of the survey area, both in shallow and deep waters, indicated potential greater availability of herring as prey in more northern latitudes. Herring decreased in diet frequency farther south, likely becoming less available compared to other prey. Hake, most predominant in the middle latitudes, also accounted for over one-third of the diet by weight in the northernmost latitude bin, while no hake were found in stomachs collected from the southernmost area. Rockfish were rare in the northernmost latitude bin, but predominant in the southernmost bins. Shrimp, mainly pandalids, were most prevalent in the 41-43°N bin and the 45-47°N bin. No pandalids occurred in ATF stomach contents collected south of 41.5°N. However, crangon and other shrimp species still occurred, although not to the extent as further north. Euphausiids were consumed throughout the latitudinal range examined in this study, but their presence in stomach contents notably decreased from north to south. Rockfishes and flatfishes were more important components of ATF diets, by both % W and % FO, in the south compared to the north, while clupeids, and to a lesser extent euphausiids, had greater importance further north. The distribution and frequency of ATF prey groups by latitude is shown in Fig. S4. Spatial distributions of ATF prey group densities, based upon haul-specific frequency of occurrence, are shown in Fig. S5.

With respect to inter-annual variability among prey groups, the preponderance of hake prey, by weight, was observed in all collection years except 2014, when clupeids contributed the most weight (Fig. 2). Notable was the absence of clupeid prey in 2013, as well as minimal flatfish and rockfish occurrences the same year, which might be attributed to the limited sample numbers that year, or identification constraints due to advanced digestion levels. The highest % FO of euphausiids occurred in 2013, although the total number of stomachs containing euphausiid prey was slightly higher in 2014, again likely due to higher overall sample numbers that year. Other fish and shrimp were fairly consistent diet contributors in most sampled years.

PERMANOVA results confirmed statistically significant associations between prey and the binned variables, despite low R^2 values (Table 2). The highest variance explained among the singular variables was with respect to latitude ($R^2 = 0.0504$), while among the interactive variables the variance explained was highest when latitude, depth, and length were all considered ($R^2 = 0.0783$).

NMDS ordination resulted in a 2-dimensional solution (stress = 0.067) after 20 iterations that correlated to ontogenetic and environmental vectors (Table S2). The wide distribution of points reinforced the generalist diet habits of ATF, and confidence ellipses of each predator group visually compared dietary trends with respect to the ontogenetic and spatial variables, supporting the PERMANOVA results (Fig. 3). While considerable diet overlap among different groups was apparent, there were significant differences as diets generally transitioned in ordination space from euphausiids and shrimp to stronger associations with fish prey, namely hake and rockfish, as predator length and depth increased. Flatfish prey were an exception with respect to depth; the majority were found in stomachs collected from the shallower depths. Latitude also showed a significant change in diet; stomachs collected from more southern ATF had a higher degree of rockfish association while hake was predominant in the mid-latitudes. Contour plots further illustrated these dietary differences and patterns of association with respect to length, latitude, and depth (Fig. 4).

ISA results indicated several prey groups had significant associations with the ontogenetic and spatial grouping variables (Table 3). For example, using mean length as the grouping variable, euphausiids and pandalids were highly significant ($p < 0.005$) indicator prey for smaller ATF, while hake and rockfish were highly significant indicators for larger ATF. Euphausiids and hake were strong indicators for 2013. Latitude also exhibited a high association with certain prey, especially concerning clupeid consumption in the north, and rockfish consumption in the south. Clupeids were significant prey for ATF found north of the mean latitude of capture, while rockfish were significant for the southern group. Additionally, several prey groups were strongly associated with depth strata; however, no highly significant prey indicators were found with respect to binned depths.

4. Discussion

ATF food habits as described here were consistent with their characterization as opportunistic predators feeding predominantly upon schooling fishes, some euphausiids and shrimp (Buckley et al., 1999; Lang et al., 2005; Yang et al., 2006; Knoth and Foy, 2008). The majority of their diet consisted of pelagic or semi-pelagic prey, supporting prior research indicating ATF along the west coast are mainly pelagic predators and trend towards increased piscivory with increasing size (Yang and Livingston, 1986; Yang, 1995; Buckley et al., 1999; Lang et al., 2005; Yang et al., 2006; Knoth and Foy, 2008).

Diets of predators are largely dependent upon the geographic availability and size of prey (Mittelbach and Persson, 1998; Brodeur et al., 2014), and as predators of different lengths may inhabit the same habitat at any given time, significant differences in diet composition can be attributed to their size and the accessibility of certain prey (Portner et al., 2020). Since a larger mouth-gape size occurs with increasing predator size, allowing for the ingestion of increasingly larger prey to meet the higher energy needs of larger predators (Mittelbach and Persson, 1998; Doyle et al., 2018), it follows that larger ATF, with their larger mouths, were able to feed upon larger prey.

Although results presented here were limited to mainly during summer months, they could provide some insight into the availability and abundance of prey (Ng et al., 2021), especially as spatial and temporal variation in diets often mimic changes in prey density (Buckley et al., 2016; Buckley and Whitehouse, 2017). Since an increase in herring abundance with an increase in latitude has previously been described (Thompson et al., 2017), and the highest contributions of herring to diet composition were shown here in the higher latitudes, it appears indicative of the greater availability of herring as prey in more northern latitudes, and underscores the characterization of ATF as opportunistic feeders.

Euphausiids had a significant diet presence in 2013, possibly attributed to a higher abundance of euphausiids during that year (Wells, et al., 2013; Leising, et al., 2014; Brodeur et al., 2019). Euphausiids are abundant during nutrient-rich upwelling conditions normally associated with cooler water (PFMC, 2008), and 2013 was the last cold water period recorded with moderate to strong upwelling among the years of this study (https://www.ncdc.noaa.gov/teleconnections/pdo/; http://www.o3d.org/npgo/). These cooler conditions preceded an anomalous marine heat wave that began in the winter of 2013-2014 (Leising, et al., 2014, 2015; Bond et al., 2015; Cavole et al., 2016; Gentemann et al., 2017; Peterson et al., 2017).

The prevalence of rockfish prey in ATF stomachs collected at the southern extent of their survey range further demonstrates the opportunistic food habits of these upper trophic-level flatfish. Notably, the highest concentration of rockfish prey found in the ATF stomachs collected during the study period occurred in and around the Greater Farallones and the Cordell Bank National Marine Sanctuaries (https://farallones.noaa.gov; https://cordellbank.noaa.gov). Combined, these marine areas extend from around Pt. Arena down to San Francisco Bay, and are known to be highly productive marine environments with an abundance of rockfish species (Marks, et al., 2015; Graiff and Lipski, 2020).

The majority of shrimp prey were found in stomachs collected in the mid- to northern latitudes of the survey range (Fig. 4). This is approximately where pandalid abundance, especially that of *Pandalus jordani*, decreases from its maximum density off central Oregon (Dahlstrom, 1970), and just north of where ATF abundance begins to decline (Bradburn et al, 2011; Keller et al, 2013). This decline in abundance could potentially be linked to prominent topographical features along the U.S. west coast, such as Cape Mendocino (40.4°N), Point Arena (39.0°N), and Point Reyes (38.0°N), which influence ocean currents and wind patterns (Magnell et al., 1990; Largier et al., 1993), potentially influencing many forage species (Friedman et al. 2018). Pandalid distribution and abundance may also be affected by changes in seasonal environmental events south of Cape Mendocino (Hannah, 2011), potentially pushing pandalids slightly more northward in recent years, and decreasing their availability to ATF as a food resource in the southernmost part of their range.

Walleye pollock is an abundant fish species found in Alaskan waters and the predominant prey by weight of arrowtooth flounder inhabiting that region (Yang and Livingston, 1986; Yang and Nelson, 2000; Yang et al., 2006; Knoth and Foy, 2008). Similarly, hake is the most abundant groundfish along the U.S. west coast (Hamel et al., 2015; Berger et al., 2019), and was the predominant prey by weight of ATF found in this study. Hake then, at least with respect to ATF predation, could be considered the trophic counterpart to walleye pollock in lower latitudes of the northeast Pacific Ocean. Also, as Hollowed et al. (2000) described the importance of ATF predation to the natural mortality of walleye pollock in the Gulf of Alaska (GOA) ecosystem, it is probable that ATF fill a similar niche with respect to hake in the CCE, and perhaps ATF predation plays a key role in influencing gadid population dynamics in the CCE as was shown in the GOA (Gaichas et al., 2011). Recent work has linked higher recruitment of age-0 hake in the CCE to periods with high arrowtooth flounder biomass, which likely results from increased arrowtooth flounder predation on older (age-2+) hake and reduced mortality due to cannibalism on age-0 and age-1 juvenile fish (Vestfals, unpublished data).

It has been suggested that ATF move to deeper water as they grow and mature (Zimmerman and Goddard, 1996; Blood et al., 2007), and hake are also known to display diurnal vertical migration and tend to aggregate further northward and deeper offshore as they mature (Ressler et al., 2007; Hamel et al., 2015). Results here illustrated a high prevalence of hake in stomachs collected from both larger ATF and those from greater depths, which indicated a potential correlation between ATF ontogeny and hake life history. Since hake have been shown to prey considerably upon euphausiids (Buckley and Livingston, 1997; Buckley et al., 1999; Hamel et al., 2015), and could show increased growth as euphausiid density increases with upwelling (Hamel et al., 2015), the significance of hake prey found in ATF stomachs in 2013 could be associated with the significance of euphausiid prey that same year. Additionally, the highest % W and % FO of hake prey and the highest % FO of euphausiid prey both occurred in stomachs collected in 2013, underscoring the opportunistic behavior and adaptive feeding capability of ATF as a high-level predator and the important functional role it plays in the CCE.

ATF are considered among the highest trophic level flatfish in the CCE, along with Pacific halibut (*Hippoglossus stenolepis*) and petrale sole (*Eopsetta jordani*; Sampson et al., 2017), thus their trophic influence on the ecosystem as a high-level predator is likely significant (Gaichas et al., 2011). By incorporating this diet and predator-prey information into estimates of natural mortality, an important parameter used in stock assessments, estimates of distribution and abundance, as well as harvest level projections, become more precautionary and sustainable (Pikitch et al., 2012). Evaluating these predator-prey relationships not only enhances management decisions of commercially important groundfish by improving population estimates, but also allows for a better accounting of forage species populations and their influences on overall ecosystem health. (Gaichas et al., 2010).

5. Conclusion

This study provided comprehensive stomach contents and multivariate analysis of ATF diet along the U.S. West Coast, and confirmed previous research suggesting that ATF is an opportunistic and highly piscivorous feeder. However, variability in arrowtooth flounder diet during the winter months could be a worthwhile inclusion in future studies, as diets may vary seasonally (Reum and Essington, 2008), and an underlying limitation of this study was the survey duration being confined to mostly the summer months, from mid-May to mid-October, each year. Also, analyzing prey composition through stomach contents alone necessitates numerous collections over long periods of time to obtain a more complete description of diet, but space and time constraints might lead to inadequate sample numbers, potentially underestimating the importance of prey low in abundance but high in nutritional value. Therefore comparisons of different time series of diet data, such as results here with that of Buckley et al. (1999), while challenging across various measurement indices, would improve understanding of long-term changes in populations and enhance sustainable ecosystem management strategies.

Identifying carbon and nitrogen stable-isotope (S-I) ratios of consumers and prey will also provide additional trophic information (Peterson and Fry, 1987), while combining stomach contents analyses with analyses of these S-I ratios would provide an effective and more comprehensive method to evaluate diets, predation mortality, and the trophic relationships among species which overlap spatially and temporally. Studies focused on comparing food-web interactions, dietary overlap, and competition, while incorporating S-I analyses to produce time-integrated descriptions of diet and food sources, are warranted for further consideration.

This research provided updated quantitative diet information of a high trophic level predator in the CCE. Dietary influences of size, as well as of depth and latitude, were reflected in the variability of prey found in ATF stomach contents. The high percentage weight of fish such as herring, and particularly of Pacific hake and rockfish in the larger fish, indicated a shift to higher energy resources as ATF grew larger. Spatio-temporal variability of prey resources also had a direct impact on arrowtooth food habits, as oceanographic fluctuations and geographic boundaries continue to influence prey composition and availability. These additional, and perhaps indirect, influences on diets and trophic interactions may be shown through correlating environmental effects (Brodeur and Pearcy, 1992), and should be included in further research. Diets of many demersal fish managed under the PFMC's FMP are poorly studied and most current assessments list diet studies as an area of critical research needed for future assessments (Bizzarro et al., 2017; PFMC, 2018), with significant influence of predation metrics on natural mortality estimation. Examining diets of predators would also provide essential information on forage species and prey abundance (Brodeur et al., 2014; Ng et al., 2021). Future research encompassing food habits and prey composition of fishes, S-I, the extent of spatial and temporal prey variability, linking local and basin-scale climate indices (PDO, NPGO, Multivariate ENSO Index (MEI)) characterizing environmental variability (temperature, dissolved oxygen, chlorophyll, salinity, etc.), will support fully-developed ecosystem-based management strategies, and lead to a better understanding of the ecological role of groundfish in the CCE.

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Tables

Prey categories	Weight	% W	% FO
***Merluccius productus* (Pacific hake)**	**3662.89**	**44.48**	**10.08**
Clupeid	**1500.72**	**18.24**	**11.20**
Clupea pallasii (Pacific herring)	1446.27	17.56	9.52
Clupeidae (unidentified clupeid)	54.45	0.66	1.68
Flatfish	**1246.3**	**15.13**	**12.89**
Citharichthys sordidus (Pacific sanddab)	338.04	4.11	1.96
Citharichthys sp. (unidentified sanddab)	1.95	0.02	0.28
Glyptocephalus zachirus (rex sole)	246.93	3.00	1.40
Lysopsetta exilis (slender sole)	389.05	4.72	4.76
Microstomus pacificus (Dover sole)	179.88	2.18	0.56
Pleuronectiformes (unidentified flatfish)	90.45	1.10	3.92
Rockfish	**866.14**	**10.52**	**9.52**
Sebastes elongatus (greenstriped rockfish)	88.51	1.07	0.28
Sebastes jordani (shortbelly rockfish)	78.31	0.95	1.12
Sebastes sp. (unidentified rockfish)	699.32	8.49	8.12
Other Fish	**151.14**	**1.84**	**3.08**
Allosmerus elongates (whitebait smelt)	5.27	0.06	0.28
Engraulis mordax (northern anchovy)	67.65	0.82	0.84
Osmeridae (unidentified osmerid)	4.49	0.05	0.28
Radulinus asprellus (slim sculpin)	1.92	0.02	0.28
Squalus suckleyi (Pacific spiny dogfish)	14.56	0.18	0.28
Thaleichthys pacificus (eulachon)	20.89	0.25	0.28
Zoarcidae (unidentified eelpout)	36.36	0.44	0.84
Teleost (unidentified fish)	**602.9**	**7.32**	**28.01**
Euphausiid	**85.63**	**1.04**	**18.77**
Euphausia pacifica (North Pacific krill)	33.49	0.41	5.04
Euphausiacea (unidentified euphausiid)	33.64	0.41	8.68
Thysanoessa spinifera	18.5	0.22	5.04

Table 1. Weight (g), percent weight (% W), and percent frequency of occurrence (% FO) of prey items found in arrowtooth flounder stomachs (n=357) collected during the west coast groundfish bottom trawl survey. Totals by prey category appear in bold. Asterisks indicate values < 0.01. Cephalopod, Other prey, and Miscellaneous groups were excluded from any further analyses.

Prey categories	Weight	% W	% FO
Pandalid	**78.74**	**0.96**	**8.40**
Pandalidae (unidentified pandalid shrimp)	3.44	0.04	1.40
Pandalus jordani (ocean shrimp)	75.3	0.91	7.00
Other Shrimp	**20.42**	**0.25**	**8.40**
Crangonidae (unidentified crangon)	0.07	*	0.28
Dendrobrachiata (unidentified shrimp)	11.49	0.14	5.04
Lissocrangon stylirostris (smooth crangon)	0.38	*	0.28
Neocrangon communis (twospine crangon)	1.09	0.01	0.56
Neognathophausia ingens (giant red mysid)	0.73	0.01	0.28
Pasiphaea pacifica (Pacific glass shrimp)	5.75	0.07	1.40
Spirontocaris holmesi (slender bladed shrimp)	0.81	0.01	0.28
Spirontocaris sica (offshore blade shrimp)	0.1	*	0.28
Cephalopod	**5.39**	**0.07**	**0.84**
Abraliopsis felis	0.98	0.01	0.28
Doryteuthis opalescens (California market squid)	4.4	0.05	0.28
Teuthida (unidentified squid)	0.01	*	0.28
Other prey	**12.14**	**0.15**	**2.24**
Echinacea (unidentified sea urchin)	4.48	0.05	0.56
Isopoda (unidentified isopod)	0.11	*	0.56
Luidia foliolata (flat mud star)	0.93	0.01	0.28
Strongylocentrotus fragilis (fragile sea urchin)	6.62	0.08	0.84
Miscellaneous	**2.28**	**0.03**	**4.20**
Gelatinous digested material	0.67	0.01	2.24
Miscellaneous (unidentified material)	1.1	0.01	0.56
Mud/Sand/Pebble/Rock	0.47	0.01	0.56
Unidentified digested organic material	0.04	*	0.84

Table 1 continued. Weight (g), percent weight (% W), and percent frequency of occurrence (% FO) of prey items found in arrowtooth flounder stomachs (n=357) collected during the west coast groundfish bottom trawl survey. Totals by prey category appear in bold. Asterisks indicate values < 0.01. Cephalopod, Other prey, and Miscellaneous groups were excluded from any further analyses.

Grouping variable	**Df**	**SSqs**	**R^2**	**Pseudo-*F***	***P* (999 permutations)**
Latitude	5	7.278	0.0504	3.8852	0.001*
Depth	4	5.697	0.0394	3.8010	0.001*
Length	4	3.245	0.0225	2.1655	0.001*
Latitude x Depth	19	9.056	0.0627	1.2721	0.015*
Latitude x Length	18	6.854	0.0474	1.0163	0.429
Depth x Length	14	5.881	0.0407	1.1211	0.188
Latitude x Depth x Length	22	11.318	0.0783	1.3730	0.004*
Residuals	254	95.167	0.6586		
Total	340	144.497	1.0000		

Table 2. Results of PERMANOVA analysis of Bray-Curtis dissimilarities in prey for categorical binned groupings of arrowtooth flounder; Df = degrees of freedom; SSqs = sum of squares; R^2 = explained variance; Pseudo-F = F value; P = significance value by permutation. Values with an asterisk indicate statistical significance at $P \leq 0.05$.

Figure captions

Figure 1 Trawl locations during the west coast groundfish bottom trawl surveys from which arrowtooth flounder (*Atheresthes stomias*) stomach samples (n=573) were collected. Colors represent different collection years and symbol size represents the number of samples collected at each trawl station. Isobaths of the minimum (55 m) and maximum (1280 m) depth extent of the groundfish bottom trawl survey (Keller et al., 2017) are also shown.

Figure 2 Stacked barplots of diet proportions by weight (top) and frequency of occurrence (bottom) of arrowtooth flounder (*Atheresthes stomias*) prey categories by collection year (left), size (middle-left), latitude (middle-right), and depth (right). Stomach sample size (n) is shown above each bin.

Figure 3 NMDS ordinations of diet data (stress = 0.067, R^2 = 0.987) with 95% confidence ellipses showing diet variability and ordination spread of prey categories; (**A**) multivariate spread of individual sample points with overlay of environmental vectors; (**B**) variability by predator length, (**C**) variability by depth, and (**D**) variability by latitude.

Figure 4 NMDS ordination plots with individual sample points and overlay of the multivariate spread of prey categories showing diet variability with respect to environmental vectors and contours of (**A**) depth, (**B**) latitude, and (**C**) length.

Fig 1

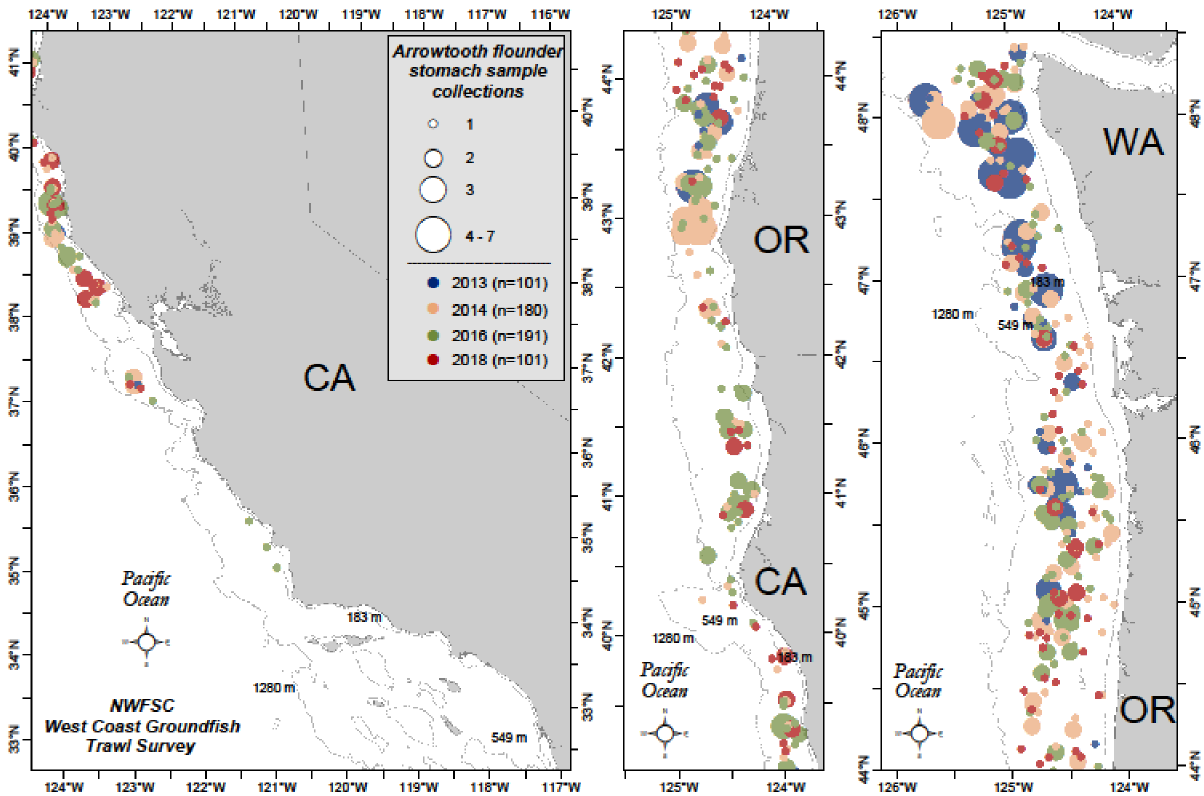

Arrowtooth flounder stomach sample collections
1
2
3
4 - 7
2013 (n=101)
2014 (n=180)
2016 (n=191)
2018 (n=101)
CA
OR
WA
Pacific Ocean
NWFSC
West Coast Groundfish
Trawl Survey
183 m
549 m
1280 m

Fig 2

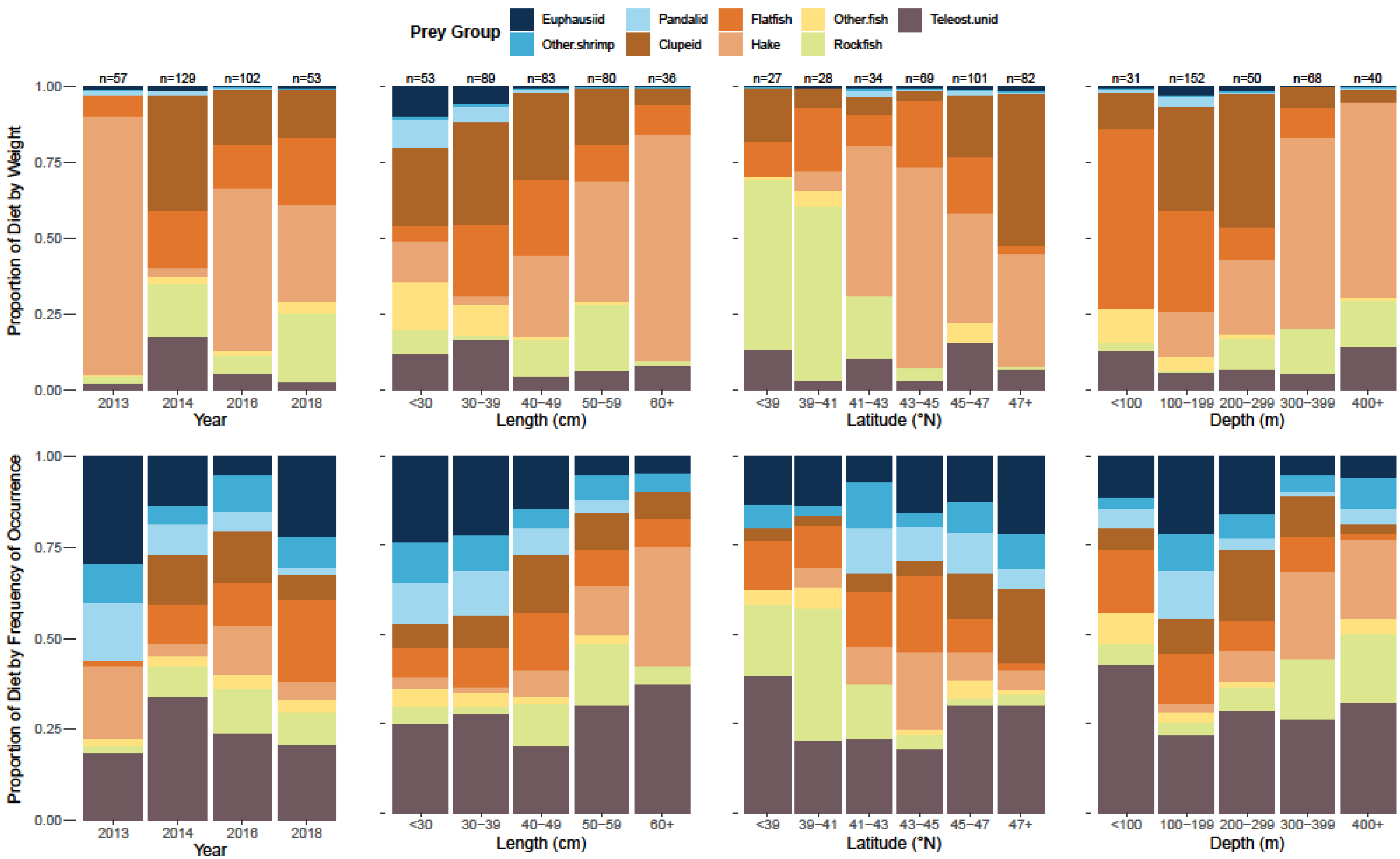

Prey Group
Euphausiid
Other.shrimp
Pandalid
Clupeid
Flatfish
Hake
Other.fish
Rockfish
Teleost.unid
Proportion of Diet by Weight
Proportion of Diet by Frequency of Occurrence
n=57
n=129
n=102
n=53
n=53
n=89
n=83
n=80
n=36
n=27
n=28
n=34
n=69
n=101
n=82
n=31
n=152
n=50
n=68
n=40
0.00
0.25
0.50
0.75
1.00
2013
2014
2016
2018
Year
<30
30-39
40-49
50-59
60+
Length (cm)
<39
39-41
41-43
43-45
45-47
47+
Latitude (°N)
<100
100-199
200-299
300-399
400+
Depth (m)

Fig 3

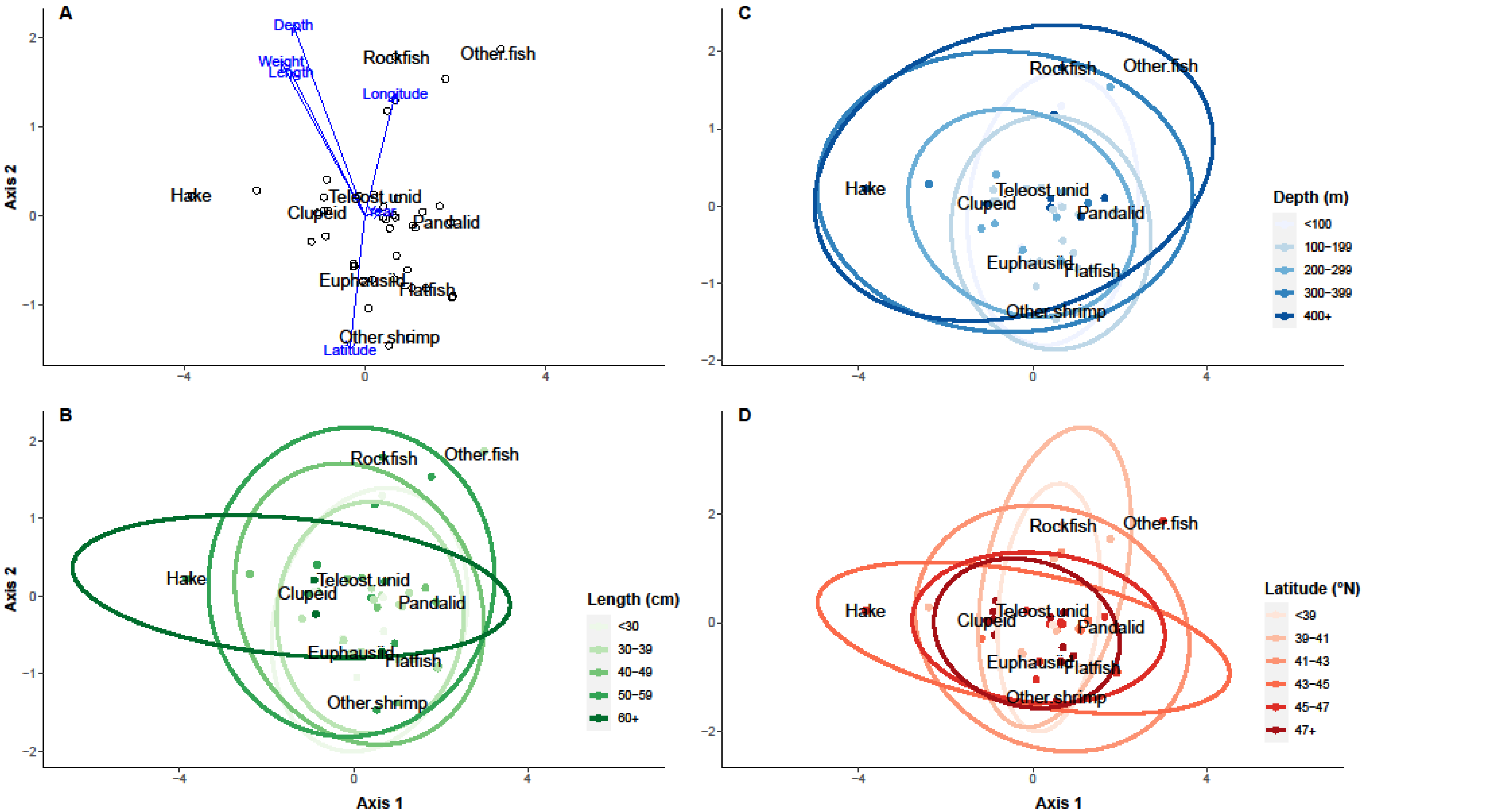
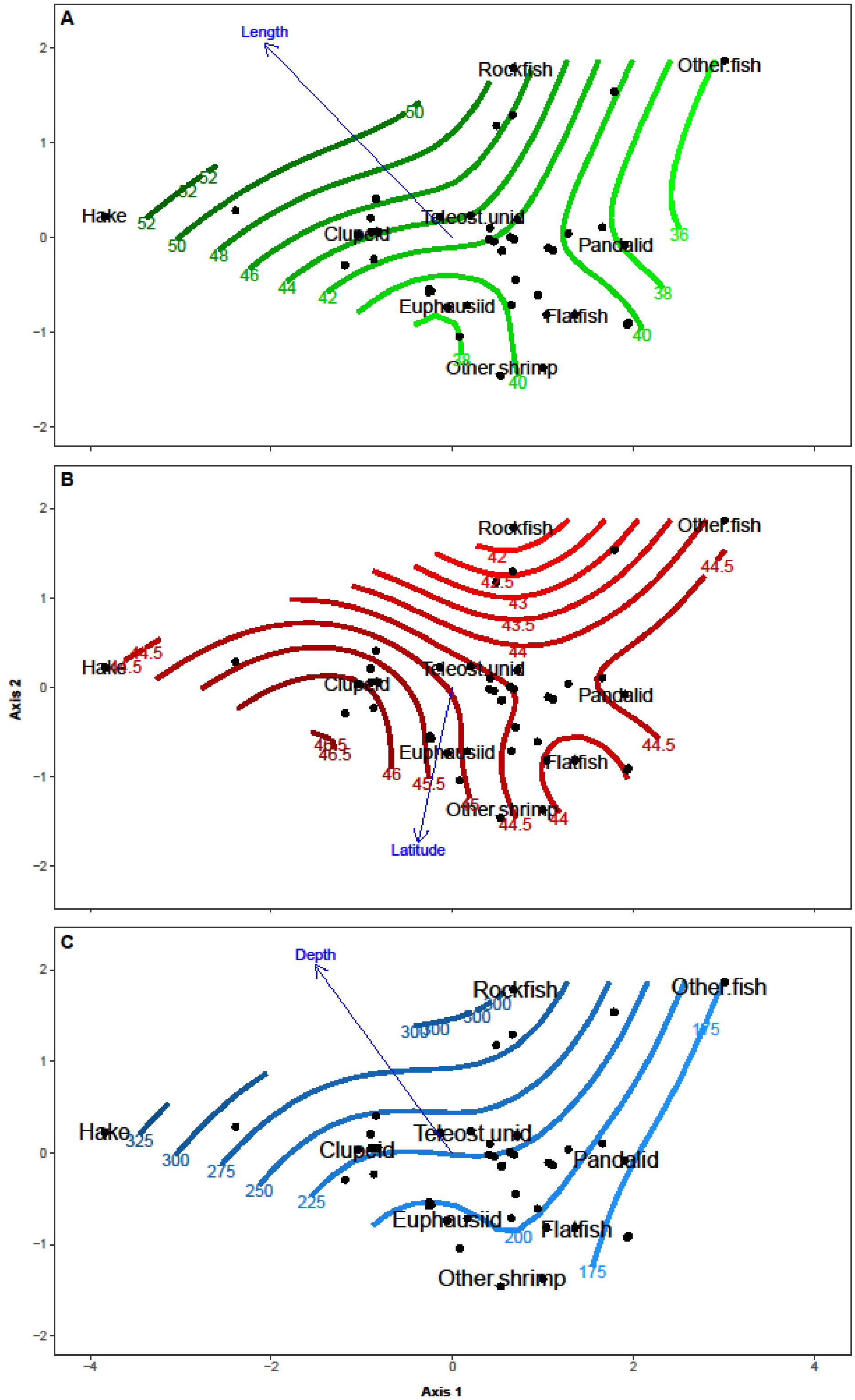

A
Depth
Weight
Length
Longitude
Latitude
Rockfish
Other.fish
Hake
Teleost.unid
Clupeid
Pandalid
Euphausiid
Flatfish
Other.shrimp
Axis 2
B
Length (cm)
<30
30-39
40-49
50-59
60+
Axis 1
C
Depth (m)
<100
100-199
200-299
300-399
400+
D
Latitude (°N)
<39
39-41
41-43
43-45
45-47
47+

Fig 4



A
Length
Rockfish
Other.fish
Hake
Teleost.unid
Clupeid
Pandalid
Euphausiid
Flatfish
Other.shrimp
B
Latitude
C
Depth
Axis 1
Axis 2

Supplemental tables and figures

Year	Size (cm)	Depth strata		% Non-empty	
		Stratum 1	Stratum 2	Stratum 1	Stratum 2
2013	< 30	18	1	33.0	0.0
(n=101)	30-39	9	8	88.9	25.0
	40-49	9	15	66.7	73.3
	50-59	5	15	60.0	73.3
	≥ 60	1	20	0.0	75.0
2014	< 30	40	2	82.5	100.0
(n=180)	30-39	22	19	68.2	78.9
	40-49	15	19	93.3	68.4
	50-59	7	36	71.4	72.2
	≥ 60	2	18	50.0	44.4
2016	< 30	10	4	60.0	0.0
(n=191)	30-39	38	20	60.5	60.0
	40-49	21	29	52.4	58.6
	50-59	14	33	50.0	57.6
	≥ 60	2	20	50.0	45.0
2018	< 30	6	1	83.3	100.0
(n=101)	30-39	23	6	60.7	33.3
	40-49	14	13	57.1	53.8
	50-59	6	17	66.7	52.9
	≥ 60	3	12	66.7	50.0

Table S1. Arrowtooth flounder (*Atheresthes stomias*) stomach collections by year, size class (< 30 cm, 30-39 cm, 40-49 cm, 50-59 cm, and ≥ 60 cm), and depth strata (Stratum 1 is 55-183 m, Stratum 2 is > 183 m). The percentage of non-empty stomachs is also shown for each collection category.

	Axis 1	**Axis 2**	**R^2**	***P***
Year	0.80021	0.59971	0.0063	0.332
Depth	-0.59304	0.80517	0.1521	0.001*
Length	-0.71056	0.70364	0.1132	0.001*
Weight	-0.73026	0.68317	0.1379	0.001*
Latitude	-0.21316	-0.97702	0.0509	0.001*
Longitude	0.44138	0.89732	0.0496	0.002*

Table S2. Correlation of environmental and ontogenetic variables to non-metric multidimensional scaling (NMDS) ordination axes of arrowtooth flounder (*Atheresthes stomias*) diet data (999 permutations); R^2 = explained variance; P = significance value by permutation. Values with an asterisk indicate statistical significance at $P \leq 0.05$.

Supplemental figure captions

Figure S1 Species accumulation curves (solid line) of arrowtooth flounder (*Atheresthes stomias)* prey groups; the upper panel shows all individual prey taxa (*b* = 0.0485), the lower panel shows all aggregated prey groups including cephalopod, other prey, and miscellaneous categories (*b* = 0.0033); shaded areas represent 95% confidence intervals.

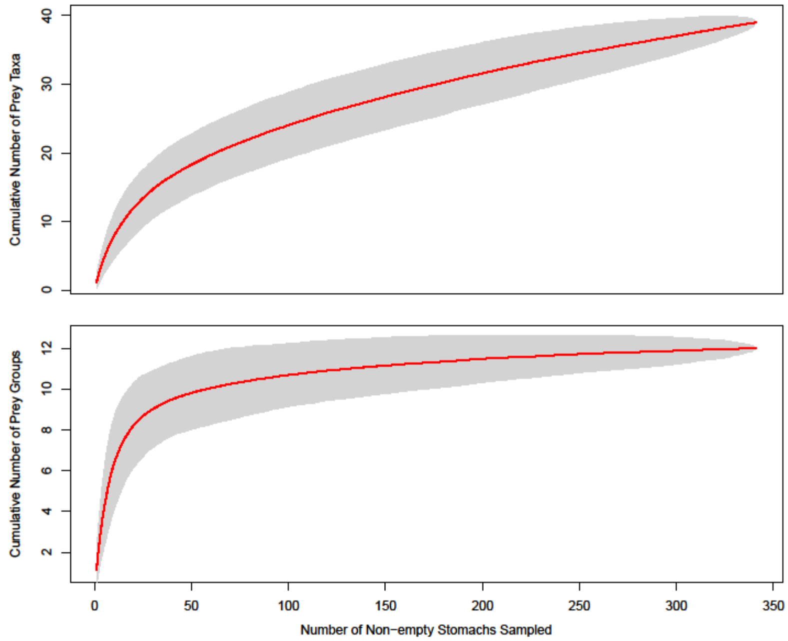
Figure S2 Distribution of arrowtooth flounder (*Atheresthes stomias*) prey groups by predator length, ordered by increasing predator mean size. The vertical dashed line denotes the mean length of arrowtooth flounder from which stomachs were collected and containing specific prey group.

Figure S3 Distribution of arrowtooth flounder (*Atheresthes stomias*) prey groups by predator depth, ordered by increasing mean depth. The vertical dashed line denotes the mean depth of arrowtooth flounder from which stomachs were collected and containing specific prey group.

Figure S4 Distribution of arrowtooth flounder (*Atheresthes stomias*) prey groups by predator latitude, ordered by decreasing mean latitude. The vertical dashed line denotes the mean latitude of arrowtooth flounder from which stomachs were collected and containing specific prey group.

Figure S5 Prey density distribution map of location-specific frequency of occurrence (%FO) for arrowtooth flounder (*Atheresthes stomias*) stomach samples for all collection years combined.

Fig S1



Cumulative Number of Prey Taxa
0
10
20
30
40
Cumulative Number of Prey Groups
2
4
6
8
10
12
0
50
100
150
200
250
300
350
Number of Non−empty Stomachs Sampled

Fig S2

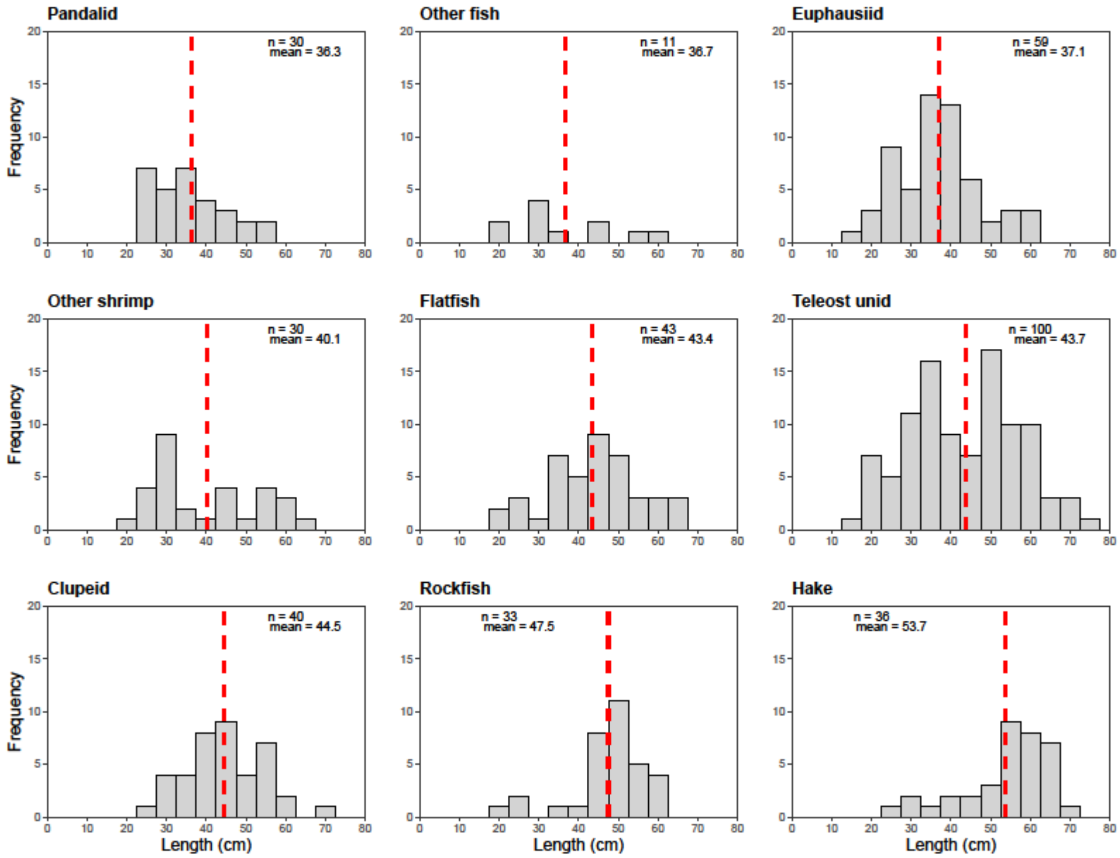

Pandalid
n = 30
mean = 36.3
Other fish
n = 11
mean = 36.7
Euphausiid
n = 59
mean = 37.1
Other shrimp
n = 30
mean = 40.1
Flatfish
n = 43
mean = 43.4
Teleost unid
n = 100
mean = 43.7
Clupeid
n = 40
mean = 44.5
Rockfish
n = 33
mean = 47.5
Hake
n = 36
mean = 53.7
Frequency
Length (cm)

Fig S3

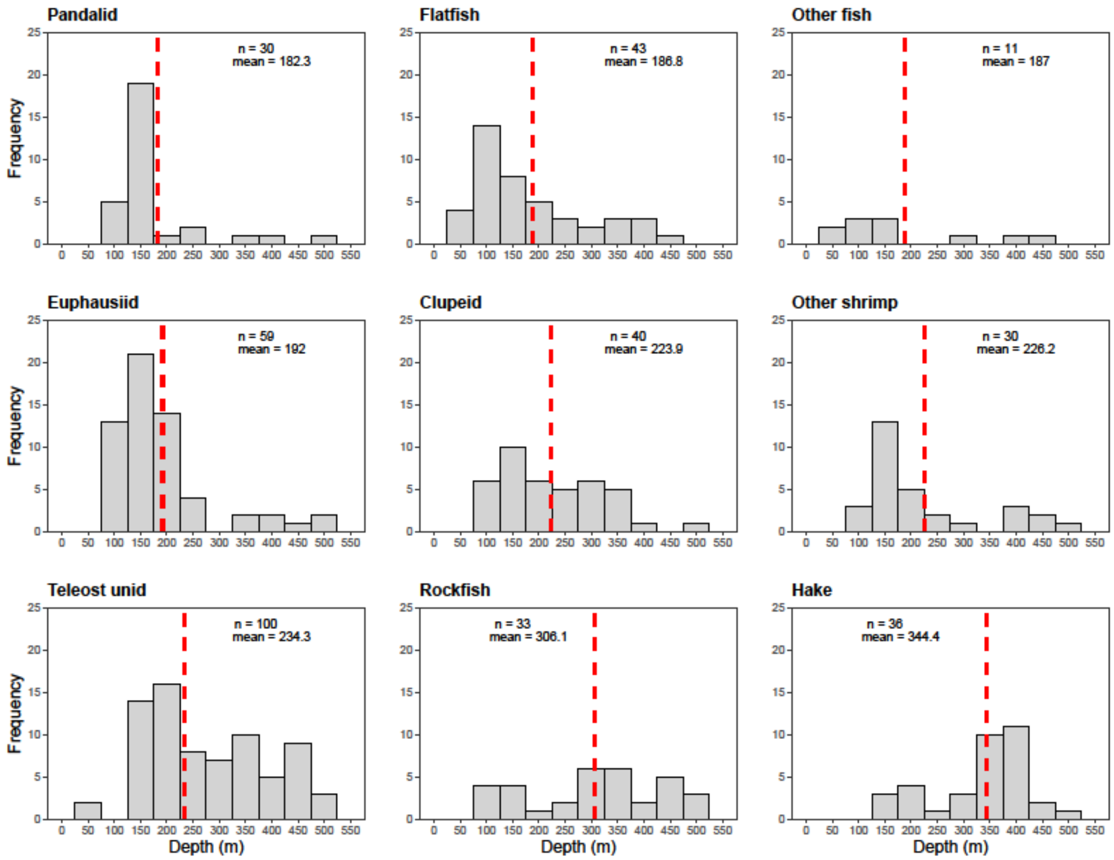
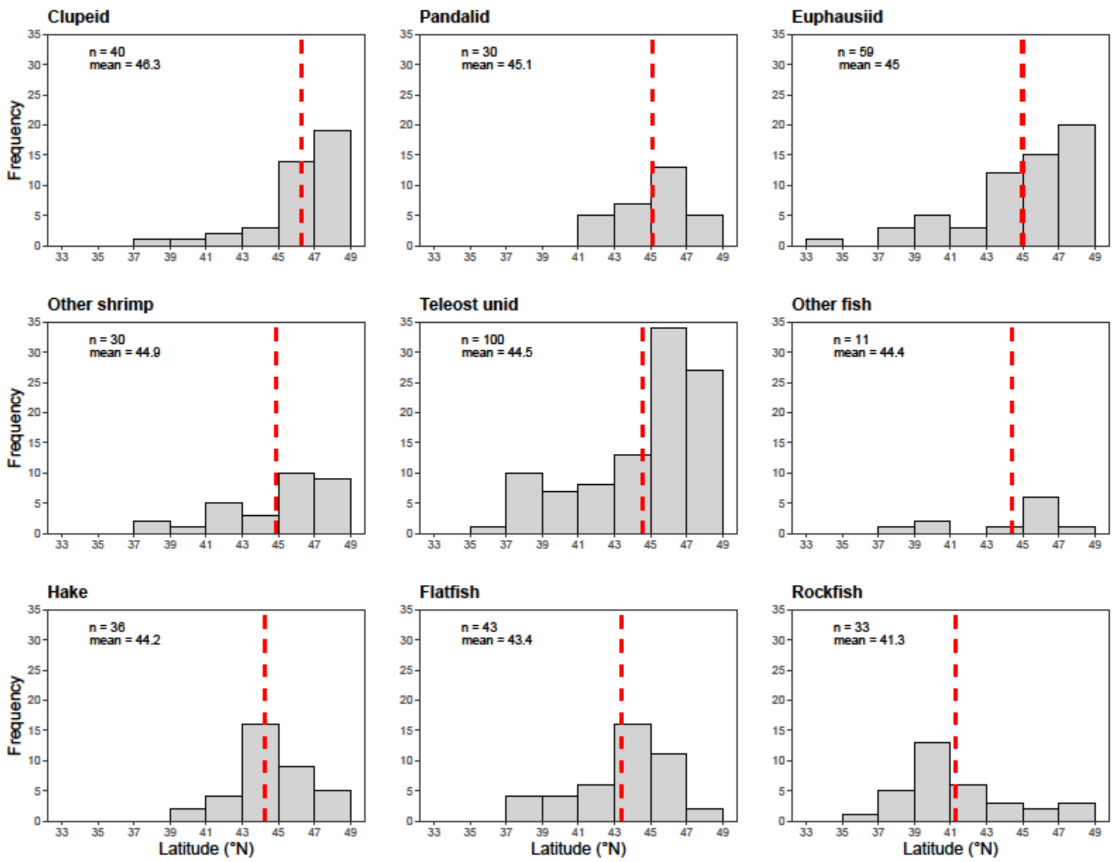
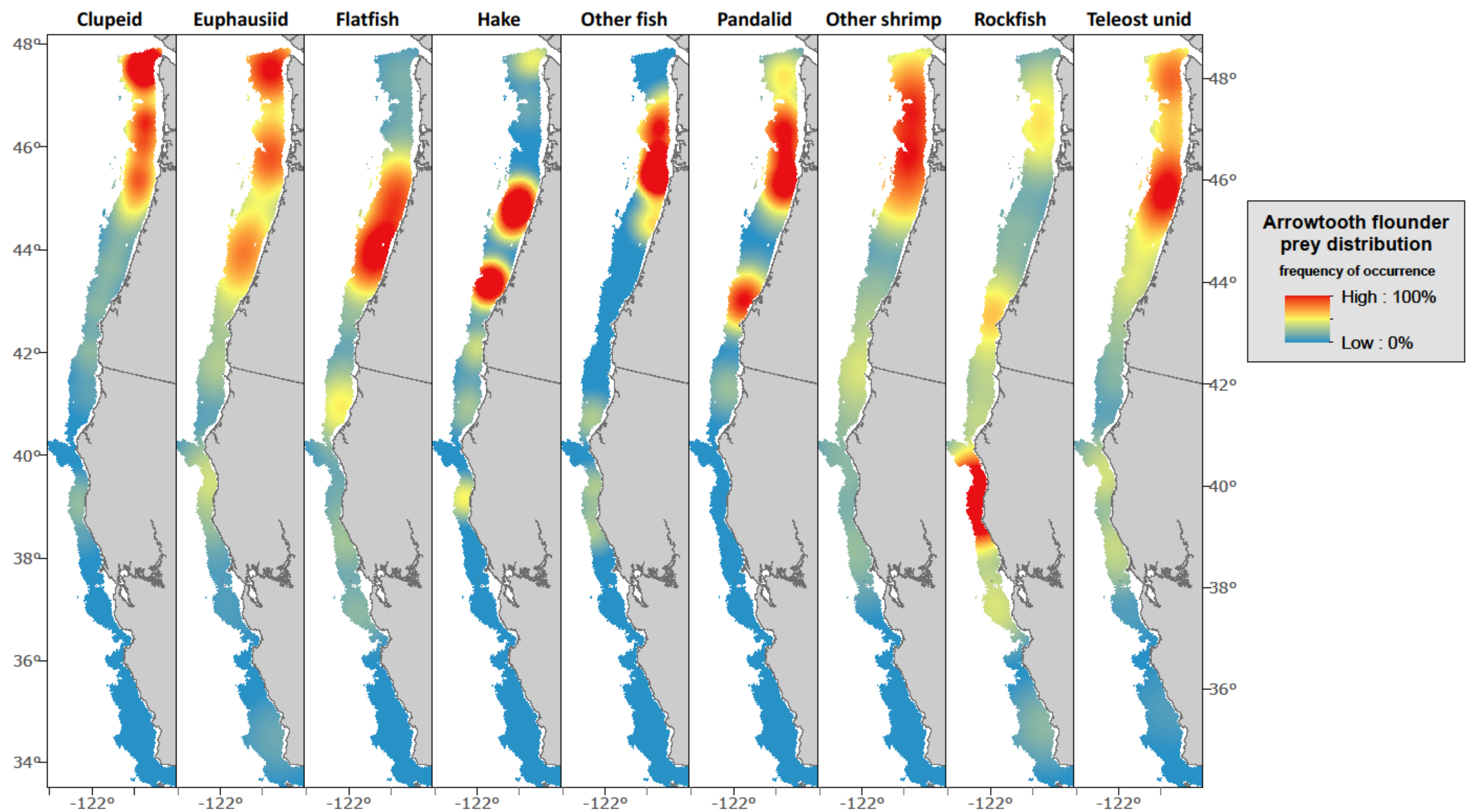

Pandalid
n = 30
mean = 182.3
Flatfish
n = 43
mean = 186.8
Other fish
n = 11
mean = 187
Euphausiid
n = 59
mean = 192
Clupeid
n = 40
mean = 223.9
Other shrimp
n = 30
mean = 226.2
Teleost unid
n = 100
mean = 234.3
Rockfish
n = 33
mean = 306.1
Hake
n = 36
mean = 344.4
Frequency
Depth (m)

Fig S4


Clupeid
n = 40
mean = 46.3
Pandalid
n = 30
mean = 45.1
Euphausiid
n = 59
mean = 45
Other shrimp
n = 30
mean = 44.9
Teleost unid
n = 100
mean = 44.5
Other fish
n = 11
mean = 44.4
Hake
n = 36
mean = 44.2
Flatfish
n = 43
mean = 43.4
Rockfish
n = 33
mean = 41.3
Frequency
Latitude (°N)

898 Fig S5



899

900