PELAGIC AND DEMERSAL FISH PREDATORS ON JUVENILE AND ADULT FORAGE FISHES IN THE NORTHERN CALIFORNIA CURRENT: SPATIAL AND TEMPORAL VARIATIONS

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ABSTRACT

A requisite for reliable food web models and ecosystem-based management in regions such as the California Current is the availability of diet information on key predators. In upwelling ecosystems, much of the lower trophic level energy may be transferred through a relatively small set of very abundant pelagic forage fish taxa, such as anchovies, sardines, smelts, and herring. In addition the pelagic juvenile stages of some important midwater and demersal fishes (Pacific hake and rockfishes) may act as forage fishes during a more limited time period each year. In this paper, we review what is known about the utilization of these forage species by larger fish predators and elasmobranchs in the Northern California Current (NCC) from northern Washington to northern California (Cape Mendocino) to examine spatial and temporal variations in the kinds and sizes of forage fishes consumed. We found that predation on forage fishes was highly variable in space and time, and was often dependent on the size of the prey available as well as the predator. Pacific hake and spiny dogfish have the potential to be dominant forage fish predators due to their high biomass but other species such as arrowtooth flounder and Pacific halibut can be important due to their high proportion of forage fish in the diet. We also highlight where diet information is limited or lacking, and areas where regular fish diet monitoring could be useful for ecosystem-based management.

INTRODUCTION

Variability in the spatial and temporal magnitude of predation has important implications for the population structure of prey species (Livingston 1993; Bakun et al. 2009). As a group, small pelagic fish species (and juvenile stages of larger pelagic and demersal species) often form the bulk of fish predator diets, particularly in highly productive upwelling ecosystems. These prey species, collectively called forage fishes, are generally short-lived but highly abundant, and form dense aggregations or schools as an anti-predator strategy in near-surface waters. Forage fish act as an intermediate trophic level and conduit of energy from a large number of primary consumer species up to highly diverse upper trophic levels, but in upwelling systems are generally limited to a few key species, thus giving rise to the term "wasp-waist" ecosystems (Rice 1995; Cury et al. 2000). Although recent studies in the California Current (Ware and Thomson 2005; Miller et al. 2010; Madigan et al. 2012) and other pelagic systems (Hunt and McKinnell 2006; Fréon et al. 2009) suggest this is not always the situation, the importance of these small pelagic fishes is unequivocal for some predators. Recent modeling studies suggest that depleting forage fishes can have detrimental effects on upper trophic levels (Field et al. 2010; Smith et al. 2011; Ruzicka et al. 2012; Kaplan et al. 2013). Having an overabundant species of forage fish can also negatively affect predatory fish populations (Bakun et al. 2009). Direct harvesting of this trophic level has precipitated recommendations to leave aside a specific percentage of the forage fish biomass for higher trophic levels dependent upon them as a precautionary approach (Cury et al. 2011; Pikitch et al. 2012, 2014). Conversely, fisheries on predator species can lead to higher biomasses of forage fishes in an ecosystem (Houle et al. 2013).

Forage fishes occupy a prominent role in the pelagic ecosystem of the Northern California Current (NCC), and often dominate catches during pelagic surveys (Brodeur et al. 2005; Emmett et al. 2005; Litz et al. 2014). Some forage species are NCC residents throughout the year (northern anchovy *Engraulis mordax*; Pacific herring *Clupea pallasii*, several smelt species including whitebait smelt *Allosmerus elongatus,* surf smelt *Hyposmesus pretiosus*, and eulachon *Thaleichthes pacificus*), but others are transients, spawning in other regions and migrating into the NCC seasonally (Pacific sardines *Sardinops sagax*), and a few species are of suitable size to be consumed by fish predators only when they are age-0 or age-1 juveniles (juvenile rockfish *Sebastes* spp., and juvenile Pacific hake *Merluccius productus*). However, this occurs only in certain years when their distributions make them available to NCC predators (Phillips et al. 2007, 2009; Brodeur et al. 2011).

Although a substantial body of literature exists on what individual fish predators and even assemblages of fishes consume in the NCC (Brodeur et al. 1987; Buckley et al. 1999; Miller and Brodeur 2007; Dufault et al. 2009), few studies (see Emmett et al. 2006) have examined this from the perspective of the prey (i.e., what are the important predators on a particular prey species?). In this paper, we review what is known about the utilization of these forage species by larger fish predators and elasmobranchs in the Northern California Current from northern Washington to northern California (Cape Mendocino) to examine spatial and temporal variations in the kinds and sizes of forage fishes consumed. As many fish predator diets change as they increase in size, we attempt to examine ontogenetic or size-based changes as well. We also discuss factors (seasonal occurrence, aggregation patterns, energetic quality) that make these forage fishes attractive prey for these nektonic predators. We also highlight where diet information is limited or lacking and areas where regular fish diet monitoring could be useful for ecosystem-based management.

METHODS

The geographic area considered in this study is primarily the continental shelf waters off the coast of Washington, Oregon, and northern California down to Cape Mendocino (fig. 1), which encompasses the majority of the NCC domain. This domain can extend northward to off the west coast of Canada in many years and some diets studies have been done in the northern region of the NCC for the predators considered in this study (e.g., Tanasichuk et al. 1991; Ware and McFarlane 1995; Tanasichuk 1997), but we chose to narrow our focus to the NCC in US waters where the bulk of the studies have been undertaken.

We conducted a review of primary and unpublished (theses and technical reports) diet studies for all potential fish predators on forage fishes. Although a large number of studies exist on elasmobranch and fish predators from this geographic area (many summarized by Dufault et al. 2009), we restricted our analysis to those species that had at least 25% by weight of their diet made up of forage fish, to focus on the main predators. To make the available data comparative among the different predators, we summarized diet information based on the percent by weight of the total diet made up by the following forage fishes: northern anchovy, Pacific herring, true smelts (Family Osmeridae, several species combined as often not differentiated in the diet studies), Pacific sardine, juvenile rockfish, and juvenile Pacific hake. Other forage fishes were found occasionally (Pacific saury *Cololabis saira*, Pacific sand lance *Ammodytes hexapterus*, juvenile salmon *Oncorhynchus* spp., and American shad *Alosa sapidissima*) but their occurrence was highly sporadic (i.e., often just one predator preyed upon them or they were consumed only in one or two studies), so for the purposes of this study we grouped these into a category called "other fishes", which may include some prey fishes not listed above (juvenile flatfishes, mesopelagic species, sculpins, etc.). This category also includes all fishes not identified to family due to poor state of digestion and may in fact include some proportion of our target forage fish taxa but were not identifiable to one of our forage groupings. Other important prey not considered forage fish such as euphausiids, other crustaceans, squids (mostly the market squid *Doryteuthis opalescens*), and jellyfish (gelatinous zooplankton) were included when consumed, but these alternative prey were not emphasized in the diet comparisons. Fish predators were grouped into pelagic fishes and demersal fishes depending on the primary habitat of the adult population. When available, data were summarized from tables provided in the source literature or from unpublished data from the original author(s). The reader is referred to the original publication for detailed information on sampling and stomach analysis methodologies. We could not provide graphs for all the studies examined as in some cases the sample size was insufficient or the data were not provided in a form that we could use (e.g., diets given in percent by number or frequency of occurrence), but in these cases we refer to these studies in the text.

We also incorporated some unpublished data for certain predators or time periods where a sufficient body of literature was unavailable. The main source for this additional diet data is a food habits database from West Coast groundfish surveys undertaken within the past decade (Keller et al. 2012). Yellowtail *Sebastes flavidus*, yelloweye *Sebastes ruberrimus*, rougheye *Sebastes aleutianus*, and bocaccio rockfish *Sebastes paucispinis* stomachs were collected from May through September of 2005–13 as part of an ongoing diet study conducted during the annual Northwest Fisheries Science Center (NWFSC) West Coast Groundfish Bottom Trawl (WCGBT) surveys. Sablefish *Anoplopoma fimbria* stomachs were collected as well in 2005 and 2008 on this survey. The WCGBT survey uses an Aberdeen 85–104 bottom trawl, and the fishing stations are selected by stratified random sampling design. This survey operates annually from May–October from the Mexico/US border (32.5°N) to Cape Flattery, WA. (48.2°N) but we used only samples obtained from the area north of Cape Mendocino, CA (fig. 1) (40.26°N) for this study. WCGBT sampling is conducted during daylight hours and target depths from 55 to 1280 m. Stomachs are randomly selected from each haul, but any sampled fish with signs of regurgitation or extruding stomach are excluded from collection. Samples are preserved in individual bags and length, weight, and sex of each fish are recorded at sea, along with trawl station information, including location and depth. In the laboratory, stomach contents are identified under a dissecting microscope down to species when possible and weighed. Several items in the stomach were subsequently discarded as they were likely offal from bait fisheries.

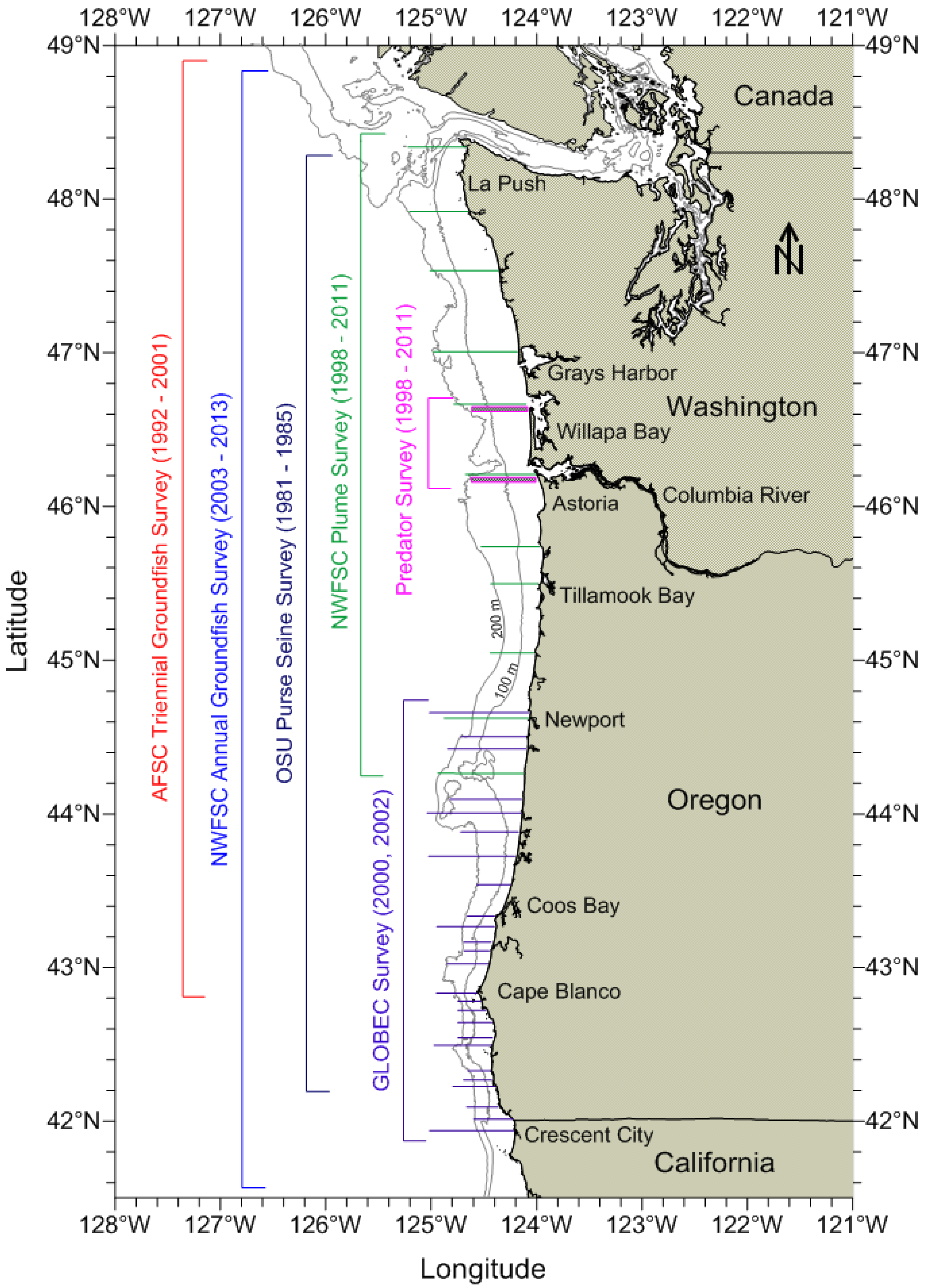

Figure 1. Location of major sampling programs off the coasts of Washington, Oregon and Northern California. Transect lines regularly sampled during NWFSC Plume surveys, predator surveys, and GLOBEC survey are indicated and the other surveys occupied a more irregular sampling pattern.

We also examined the prey size composition of two predators (Pacific hake and adult Chinook salmon *Oncorhynchus tshawytscha*) for which we had substantial prey length information (Emmett and Krutzikowsky 2008; Daly et al. 2009) and compared these to what were available from pelagic trawl surveys done at night in the same region (Emmett et al. 2005; Litz et al. 2014).

To estimate the relative impact of the various forage fish predators in the NCC, we derived estimates of the summer biomass along the shelf and slope waters off Washington, Oregon, and Northern California based

TABLE 1
List of Northern California Current fishes that have the potential to have forage fish in their diets and that were included in this study.

Scientific Name	Common Name	Included	Diet Information
Lamna ditropis	Salmon shark		Not available for N. California Current
Alopias vulpinus	Thresher shark		Not available for N. California Current
Galeorhinus zyopterus	Soupfin shark	x	
Prionace glauca	Blue shark	x	
Squalus suckleyi	Spiny dogfish	x	
Torpedinidae	Electric (torpedo) rays		Not available for N. California Current
Oncorhynchus kisutch	Coho salmon	x	
Oncorhynchus tshawytscha	Chinook Salmon	x	
Oncorhynchus clarki	Cutthroat trout		Limited information
Oncorhynchus mykiss	Steelhead		Limited information
Gadus macrocephalus	Pacific cod		Not available for N. California Current
Merluccius productus	Pacific hake	x	
Sebastes spp.	Rockfishes	x	
Ophiodon elongatus	Lingcod	x	
Anoplopoma fimbria	Sablefish	x	
Scopaenichthys marmoratus	Cabezon		Limited information
Trachurus symmetricus	Jack mackerel	x	
Thunnus alalunga	Albacore	x	
Trichodon trichodon	Pacific sandfish		Not available for N. California Current
Anarrhichthys ocellatus	Wolf-eel		Not available for N. California Current
Hippoglossus stenolepis	Pacific halibut	x	
Atheresthes stomias	Arrowtooth flounder	x	

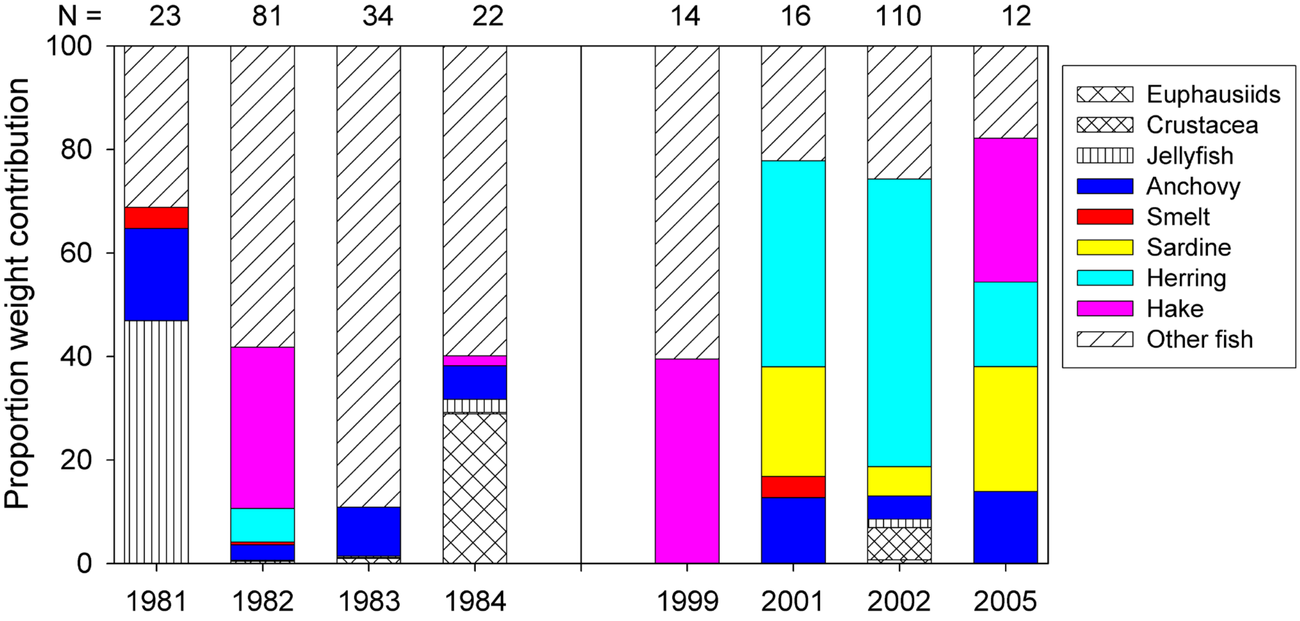

Figure 2. Diet composition of spiny dogfish (*Squalus suckleyi*) collected off Oregon and Washington during the OSU Purse Seine Survey (left panel) and the NWFSC Plume Survey (right panel) from May through September during different years. Number of stomachs with food is indicated at the top of each bar.

on stock assessments available from the Pacific Fisheries Management Council or the International Pacific Halibut Commisision. For unassessed species we used biomass estimates from the WCGBT surveys for demersal species (see Keller et al. 2012 for sampling details) and from scaled biomass estimates derived for ecosystem modeling (Ruzicka et al. 2012) for pelagic species. As the population size and age structure changes through time, we attempted to confine our biomass estimates to the decade of 2000–09 where possible, although in some cases only a limited number of years were available.

RESULTS AND DISCUSSION

Overall, the number of fishes or elasmobranchs that have large proportions of their diet composed of forage fish is relatively small (table 1). Unfortunately there are

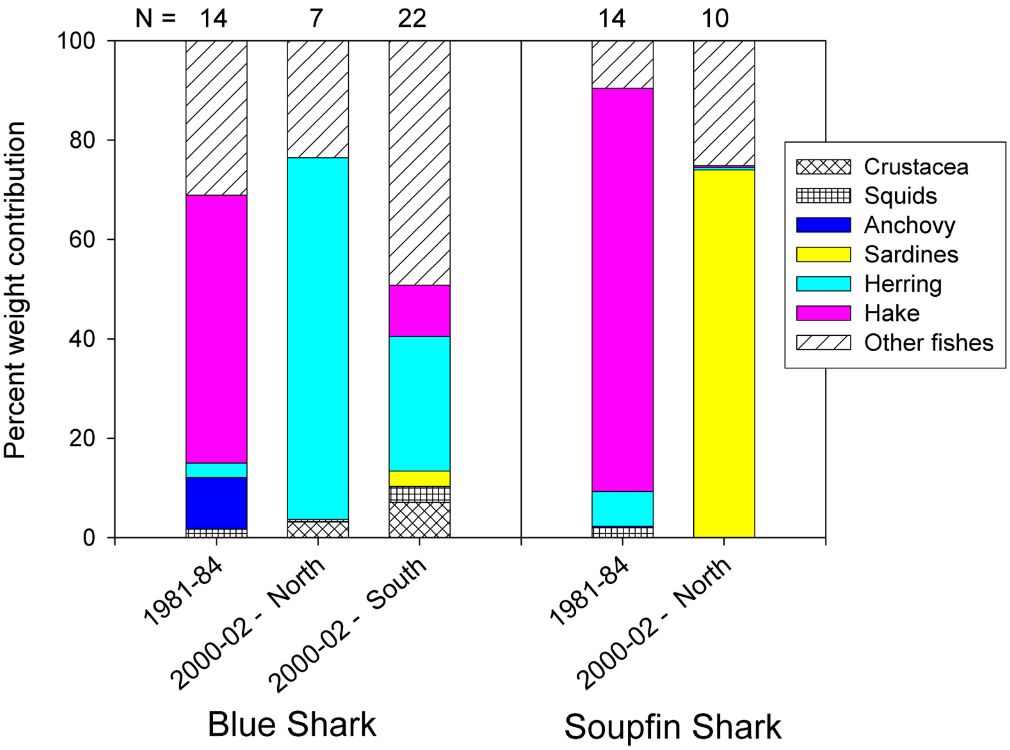

Figure 3. Diet composition of blue sharks (*Prionace glauca*, left) and soupfin sharks (*Galeorhinus zyopterus*, right) collected off Oregon and Washington during different time periods and regions. Number of stomachs with food is indicated at the top of each bar. Data from the 1980s were presented in Brodeur et al. 1987. North and South designate shelf areas north (Brodeur unpub. data) and south (Miller and Brodeur 2007) of Newport, OR (44˚ 40').

gaps in our knowledge regarding the diets of some large sharks (e.g., Preti et al. 2012) and other elasmobranch such as skates (Bizzaro et al. 2007) in the NCC. However, given the relatively small biomass of these species (Keller et al. 2012), they probably have relatively small effects on forage fish populations. Many rockfish species inhabit the Northern California Current but most tend to consume primarily crustaceans, gelatinous zooplankton, or other small fishes (Brodeur and Pearcy 1984; York 2005; Lee and Sampson 2009) and only a few rockfishes included here can be considered major consumers of forage fishes. Similarly, there are several flatfishes that are very important in terms of NCC biomass, but other than Pacific halibut (*Hippoglossus stenolepis*) and arrowtooth flounder (*Atheresthes stomius*), these species feed mainly on crustaceans and other benthic animals (Pearcy and Hancock 1978; Wakefield 1984).

Spiny Dogfish. The spiny dogfish (*Squalus suckleyi*) is a relative small shark species that is widely distributed in the Northern California Current. It is commonly caught in both pelagic and demersal trawl surveys on the shelf extending offshore (Brodeur et al. 2009). Dominant forage fishes consumed in the 1980s from purse seine caught dogfish (length from 320–1190 mm) included juvenile Pacific hake, northern anchovy, and Pacific herring, although flatfish juveniles were most important in the "other fish" category (Brodeur et al. 1987; fig. 2). In more recent trawl sampling, these same three forage taxa contributed to the diet with the addition of Pacific sardine and smelt in some years (Brodeur et al. 2009; fig. 2). Studies off British Columbia north of our study area documented Pacific herring and Pacific hake as important prey as well (Jones and Geen 1977; Tanisichuk et al. 1991). Dogfish have been shown to transition from a mostly invertebrate diet (euphausiids and gelatinous zooplankton) to a predominantly fish diet as they increase in size (Tanisichuk et al. 1991; Brodeur et al. 2009).

Blue Shark. The diet composition (fig. 3) of blue sharks (*Prionace glauca*) consists primarily of fishes, including Pacific hake and northern anchovy in the 1980s (Brodeur et al. 1987) but also Pacific hake and small proportions of Pacific sardine and Pacific herring in more recent periods (Miller and Brodeur 2007). Studies of this species in Monterey Bay, California, indicated that it consumes large amounts of pelagic nekton (northern anchovy, spiny dogfish, and Pacific hake) by percent volume, although euphausiids can also be important (Harvey 1989). Studies off Baja California, Mexico and elsewhere indicate that cephalopods are often dominant prey in the diets of these sharks (Markaida and Sosa-Nishizaki 2010).

Soupfin Shark. Soupfin sharks (*Galeorhinus zyopterus*) in the NCC fed primarily on Pacific hake in the 1980s (Brodeur et al. 1987; fig. 3), however, the majority (74%

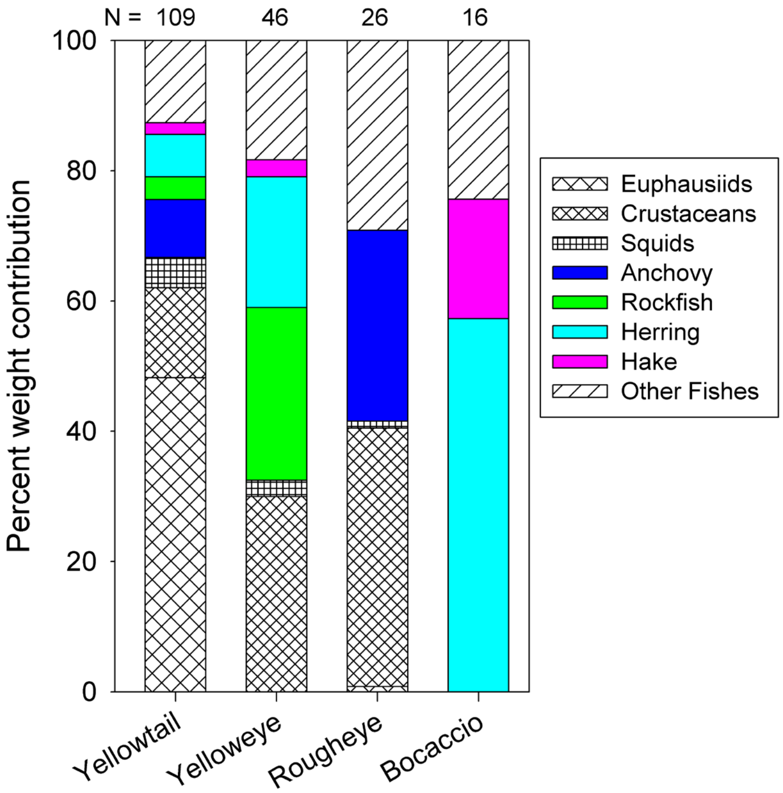

Figure 4. Diets of four species of adult rockfishes (*Sebastes* spp.) collected from Northwest Fisheries Science Center Groundfish Surveys off Washington, Oregon and Northern California from May–September, from 2005–13 (Buchanan, unpub.). Number of stomachs with food is indicated at the top of each bar.

by weight) of the prey in the early 2000s were Pacific sardine (Brodeur, unpub. data), but it is noteworthy that other fish prey consumed included unidentified juvenile salmon (*Oncorhynchus* sp.) and hagfish (*Eptatretus* sp.; fig. 3).

Yellowtail Rockfish. Forage fish made up 28.5% of the overall diet weight in yellowtail rockfish (*Sebastes flavidus*) stomachs collected during the 2006 and 2008 WCGBT surveys (fig. 4). Pacific hake, Pacific herring, northern anchovy, Pacific viperfish (*Chauliodus macouni*), as well as lanternfish, rockfish, and flatfish species, were also found. The remainder of prey were euphausiids (*E. pacifica* and *T. spinifera*), shrimp (species of *Pandalus*, *Sergestes*, and *Crangon*), and squids. Fish came in second to euphausiids in yellowtail rockfish diets. Although fish were found in the stomachs of small individuals ranging from 20–55 cm, the majority of fish prey was consumed by larger yellowtail rockfish (>40 cm fork length (FL)). The fish prey taxa were primarily adult northern anchovy (14 cm FL), juvenile Pacific herring (8–10 cm FL), adult and juvenile Pacific hake and juvenile rockfishes. Euphausiids dominated the juvenile (<30 cm) size-classes food composition by weight, whereas fishes and squids became increasingly important prey as rockfish grew in size. Fishes (mostly age-0 Pacific hake) were the dominant prey of yellowtail rockfish during the summer of 1998, although quarterly samples during other times of the year showed that salps and euphausiids were equally important by weight proportions (Lee and Sampson 2009).

Yelloweye Rockfish. Yelloweye rockfish (*Sebastes ruberrimus*) stomachs were collected in 2008 to 2013 on WCGBT surveys. Stomachs were obtained from fish ranging from 18–68 cm FL, however, few <40 cm FL fish were obtained. Fish made up 68.2% of the overall weight in yelloweye rockfish diets (fig. 4). Pacific herring (20–25 cm), Pacific hake, and juvenile and smaller adult rockfishes (5–25 cm) were the primary forage fish consumed; but rex sole (*Gylptocephalus zachirus*), slender sole (*Lyopsetta exilis*), and arrowtooth flounder were found in the stomachs in lesser proportions. The remaining prey types consisted of shrimp (*Pandalus jordani* and *Pandalus platyceros*), crab (Galatheidae and *Lopholithodes*), and cephalopod species (fig. 4). York (2005) found Pacific herring made up over half of the diet of yelloweye rockfish (n = 9) collected in the NCC in summer and fall of 2003 and 2004.

Rougheye Rockfish. Rougheye rockfish (*Sebastes aleutianus*) stomachs were collected in 2008 and 2013 during the NWFSC WCGBT survey. Stomachs were obtained from fish ranging from 11–55 cm FL, however,

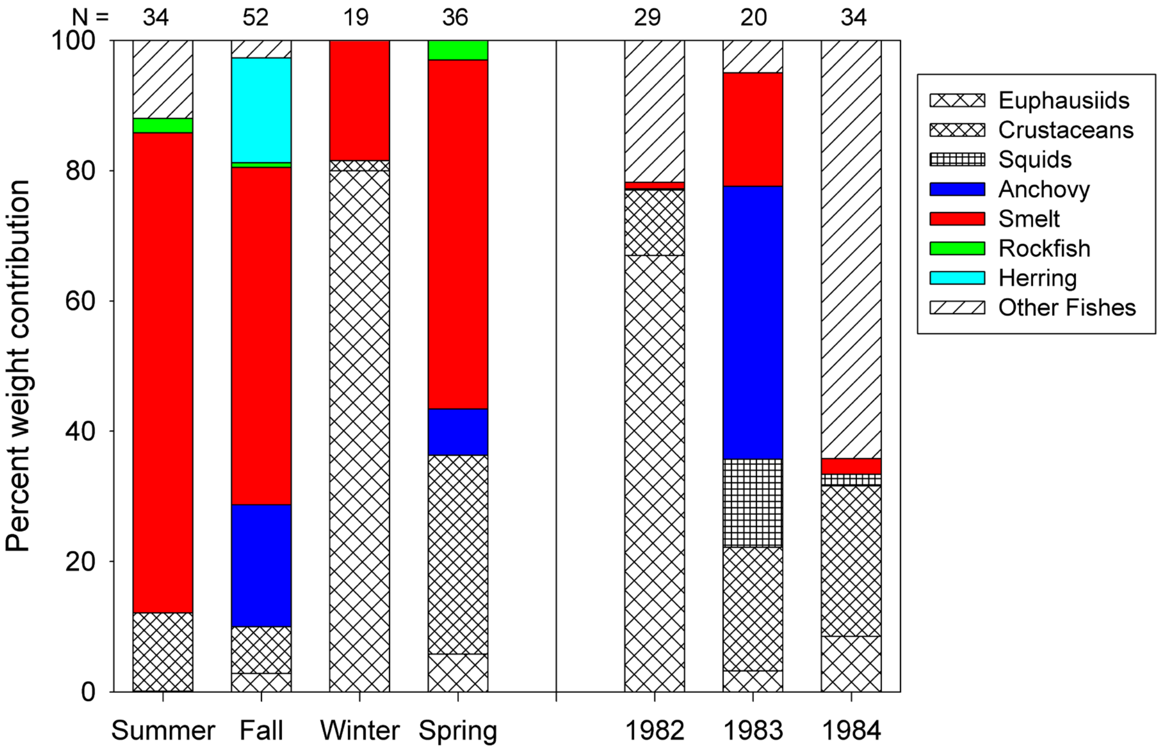

Figure 5. Diet composition of black rockfish (*Sebastes melanops*) collected seasonally from sport fishing vessels off central Oregon from 1976–77 (left, Steiner 1979) and collected during the summers of 1982–84 from OSU purse seine surveys off Oregon and Washington (right, Brodeur et al. 1987). Number of stomachs with food is indicated at the top of each bar.

few juveniles or large adults were collected. Fish made up 57.1% of the overall weight in the rougheye rockfish diet (fig. 4), with most of the weight coming from one sample containing northern anchovy. The remaining prey types were shrimp (species of *Pasiphaea*, *Pandalus* and *Crangon*), amphipods, and euphausiids.

Bocaccio. Bocaccio rockfish (*Sebastes paucispinis*) stomachs were collected from 2005–12 on the NWFSC WCGBT surveys. Sampled fishes ranged from 13–82 cm FL, but most were taken from 50+ cm FL fish. Fish made up 100% of the diet in the NCC samples (fig. 4). Age-1 and -2 Pacific hake and adult Pacific herring were the dominant fish prey. Other bocaccio samples taken from off southern California during the same survey revealed the addition of market squid as a prey item, as well northern anchovy, and Pacific sardine (J. Buchanan, unpub. data).

Black Rockfish. Black rockfish (*Sebastes melanops*) is one of the dominant coastal reef fishes in the NCC although they can often be caught close to the surface. Seasonal sampling from charter fishing boats on a reef just north of Newport, Oregon, showed that the diet was dominated by smelt all year, but northern anchovy and Pacific herring were also seasonally important (Steiner 1979; fig. 5). The proportion of fish eaten declined to less than 20% of the prey total in winter due to a high consumption of gelatinous zooplankton. Stomach data from pelagic purse seine catches showed that black rockfish diets were very variable. In 1982, diet consisted mainly of crustaceans, whereas forage fishes (northern anchovy and Pacific herring) were dominant in the El Niño year of 1983 (Brodeur et al. 1987; fig. 5). A recent study of sport-caught black rockfish caught off Newport, OR from May to August of 2010 and 2011 showed a lower percent of fish biomass consumed compared to crustaceans, with smelt being the dominant forage species consumed (Gladics et al. 2014).

Lingcod. Lingcod (*Ophiodon elongatus*) are an important nearshore demersal predator known to consume a variety of fishes. Seasonal studies off central Oregon (Steiner 1979), revealed that Pacific hake were a dominant prey in all but winter when hake Pacific hake have largely migrated to the Southern California Current, and were replaced by smelt and rockfishes (fig. 6). Other fishes such as flatfishes and sculpins were the most important prey, but less so in the summer. In a study of sport-caught lingcod at two sites off central Oregon from May through October of 2003–05 (Tinus 2012) found that Pacific herring was the most important forage fish consumed, with juvenile rockfishes of secondary importance (fig. 6).

Sablefish. Sablefish (*Anoplopoma fimbria*), also known as black cod, is one of the dominant groundfish species in outer shelf and slope waters in the NCC. Early stud-

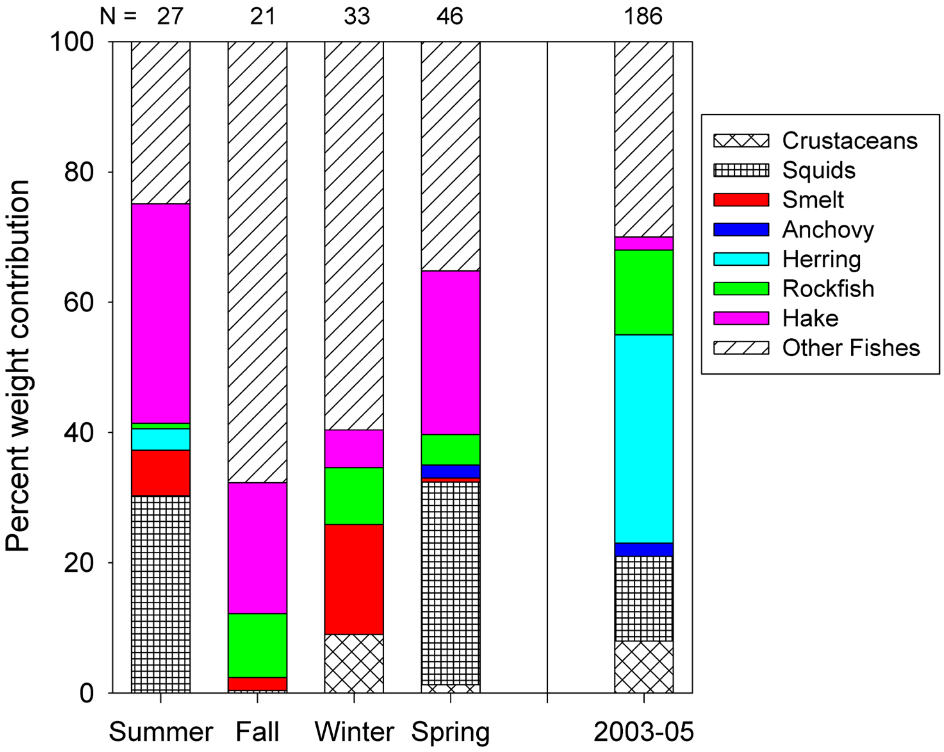

Figure 6. Diet composition of lingcod (*Ophiodon elongatus*) collected seasonally from sport fishing vessels off central Oregon from 1976 to 1977 (left, Steiner 1979) and collected over a three year period from surveys off central and southern Oregon (right, Tinus 2012). Number of stomachs with food is indicated at the top of each bar.

ies conducted during the West Coast Alaska Fisheries Science Center (AFSC) Triennial Groundfish surveys and Upper Continental Slope surveys (fig. 1) indicated substantial diet variability, with Pacific herring being the dominant forage fish in summer 1989, and rockfish and Pacific hake important in autumn 1992 (fig. 7). More recently, sablefish stomachs were collected during the 2005 and 2008 summer–fall WCGBT surveys from depths ranging from 62–1242 m. Diet results from these two years were remarkably similar, with fish making up 83.1% (2005) and 81.1% (2008) of the overall diet by weight in these samples. Pacific herring and northern anchovy were found in both years. Other fish prey identified were Pacific hake, longspine thornyhead (*Sebastolobus altivelis*), Dover sole (*Microsotmus pacificus*), slender sole (*L. exilis*), Pacific viperfish (*C. macouni*), and miscellaneous lanternfish, rockfish, and flatfish species. The remaining important prey types encountered were euphausiids (*E. pacifica* and *T. spinifera*) and several squid species. In contrast to the NCC fish, sablefish stomachs collected from off of California during the 2005 and 2008 WCGBT surveys showed decreased consumption of euphausiids, but increased crab predation, and the addition of Pacific sardines to the diet. The species composition of sablefish diet from these two years was analogous except for the absence of rockfish as a prey item in 2008. A breakdown of diet composition into size classes for both years showed that the euphausiid diet of smaller sablefish (<50 cm FL) was replaced by increased consumption of fish and cephalopods as the sablefish grew. In the region just north of our study area (southwest Vancouver Island), Tanasichuk (1997) found euphausiids to be the main prey of sablefish but Pacific herring were the most important fish prey consumed. In the most complete analysis of sablefish diets to date, Laidig et al. (1997) examined 1868 stomachs from NCC (Oregon and California north of Cape Mendocino) and southern California Current (south of San Francisco Bay to Point Conception) and found that fishes represented >76% of the diet by volume, with rockfishes comprising 35% and Pacific hake 11% of the total diet. These authors also found the volume of fish consumed increased as the sablefish size increased.

Jack Mackerel. Adult jack mackerel (*Trachurus symmetricus*) migrate up from California spawning grounds during the summer and are important predators in the NCC (Emmett and Krutzikowsky 2008). Based on jack mackerel caught during summer in purse seine in the 1980s, Brodeur et al. (1987) found that mackerel diets varied interannually, from a high reliance on northern anchovy during the strong upwelling year of 1982, to a diet dominated by crustaceans the following two years (fig. 8). Euphausiids were the dominant prey consumed during two of the three years examined. In

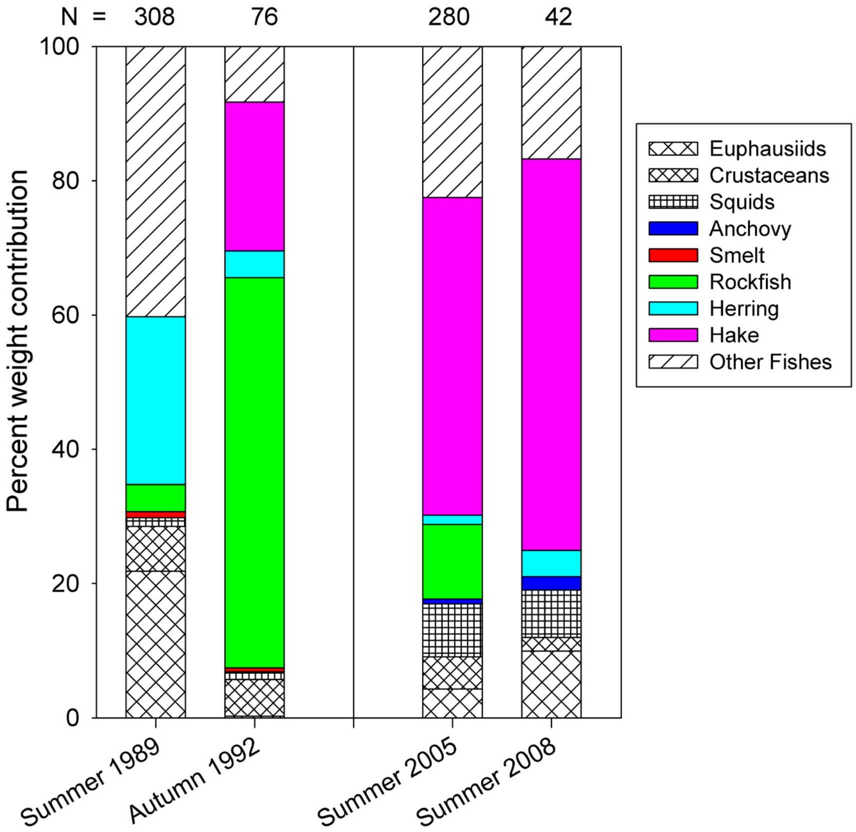

Figure 7. Diet composition of sablefish (*Anoplopoma fimbria*) collected from West Coast trawl surveys conducted by the Alaska Fisheries Science Center in 1989 and 1992 (left, Buckley et al. 1999) and more recent NWFSC (2005 and 2008) annual surveys off Washington to northern California (right, Buchanan unpub.). Number of stomachs with food is indicated at the top of each bar.

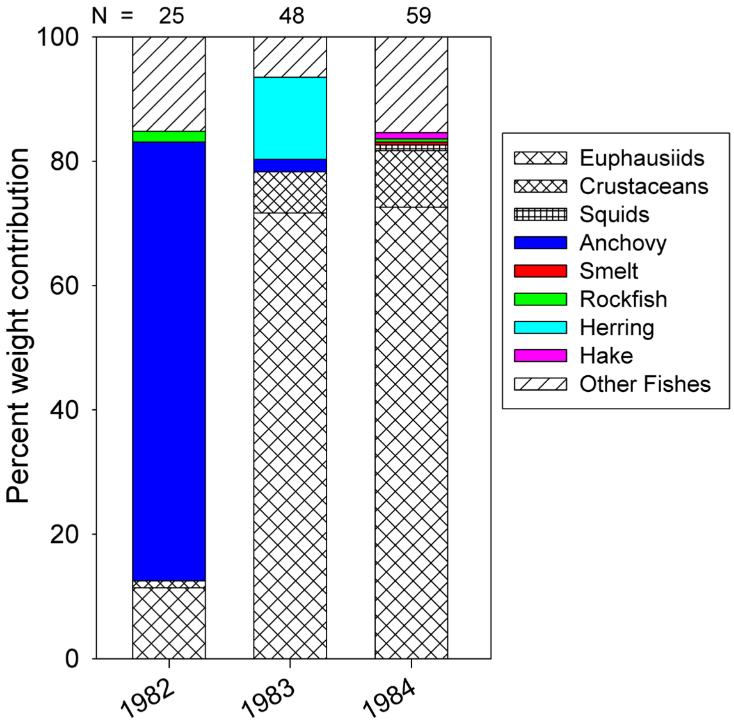

Figure 8. Diet composition of jack mackerel (*Trachurus symmetricus*) collected annually (1982–84) from purse seine surveys off Oregon and Washington (Brodeur et al. 1987). Number of stomachs with food is indicated at the top of each bar.

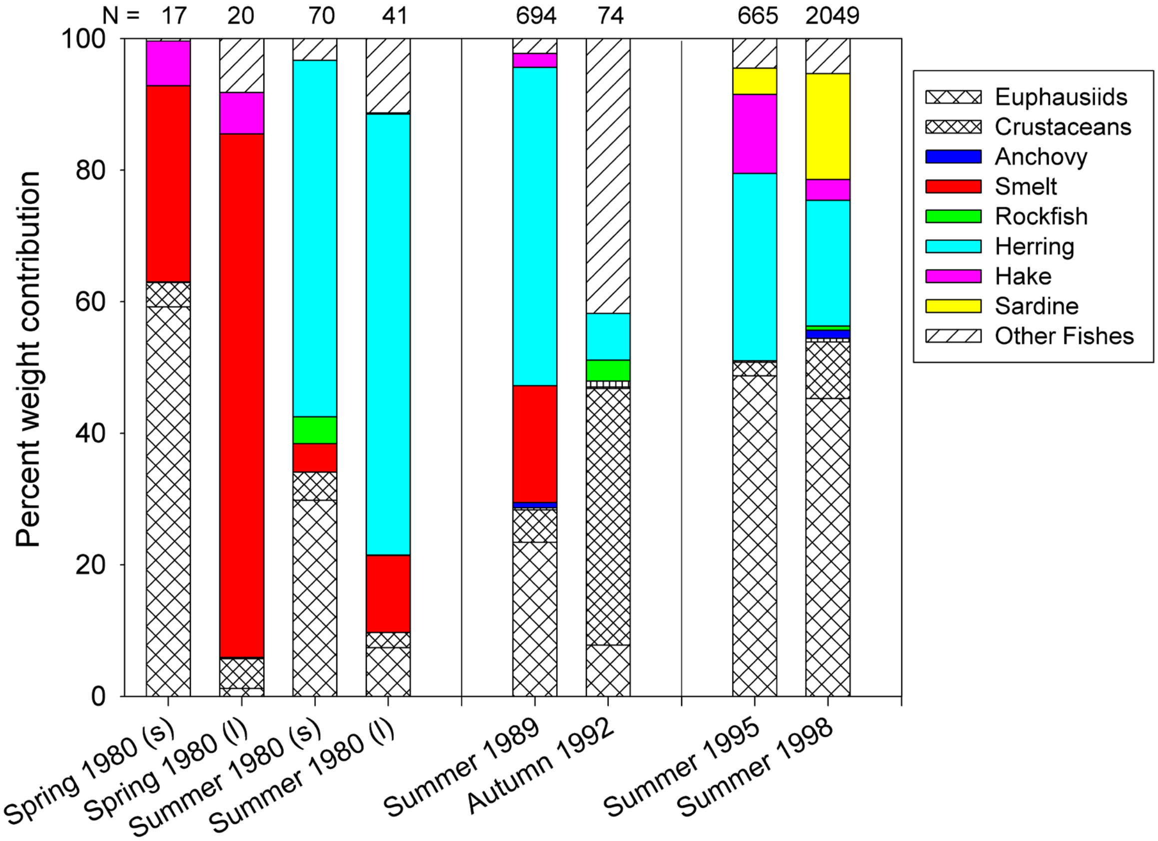

Figure 9. Diet composition of Pacific hake (*Merluccius productus*) collected from West Coast trawl surveys conducted by the Alaska Fisheries Science Center in spring and summer of 1980 for two size classes (s = 450–549 mm and l = >550 mm) (left, Livingston 1983), in summer of 1989 and autumn of 1992 (center, Buckley et al. 1999) and in 1995 and 1998 at onshore (< 200 m depth) locations (right, Nelson 2004). Number of stomachs with food is indicated at the top of each bar.

more recent studies, Miller and Brodeur (2007) found that jack mackerel predominantly fed on euphausiids in most years, with relatively small (<5% by weight) contributions by forage fish. In a seven year (1998–2004) study off the mouth of the Columbia River, Emmett and Krutzikowsky (2008) found forage fishes to occur frequently (no weight data available) in the diet in some years and not others. They found that northern anchovy, and to a lesser extent Pacific herring and whitebait smelt, were consumed by jack mackerel in higher proportions than their abundance would indicate from trawl catches (Emmett and Krutzikowsky 2008).

Pacific Hake. Pacific hake (*Merluccius productus*), play a major trophic role in the NCC ecosystem due to their high biomass. They migrate into the NCC in summer and back to California waters in the fall and winter (Ressler et al. 2007). Numerous studies have examined the diets of Pacific hake in different months, years, and geographic areas (Livingston and Bailey 1985; Ressler et al. 2007) and we summarize only a few representative studies here. Livingston (1983) examined dietary variability in Pacific hake caught in the NCC during spring and summer of 1980. This study showed that Pacific hake exhibited substantial changes in diet between the seasons, shifting from mostly smelt (primarily eulachon, *Thaleichthys pacificus*) in spring, to mainly Pacific herring in the summer. This was especially true for larger Pacific hake (fig. 9). However, neither smelt nor Pacific herring were common in the diet of Pacific hake in the summer of 1967 (Livingston 1983). Buckley et al. (1999) examined hake diets from the summer of 1989 and found a high proportion of fish (primarily northern anchovy and smelt) but a relatively small proportion in autumn (fig. 9). Nelson (2004) examined Pacific hake diet from the same area in 1995 (non-El Niño year) and 1998 (El Niño year) collected on and off the shelf. He found Pacific herring to be the dominant forage fish consumed in 1995 but were largely supplemented by Pacific sardine in 1998. The differences by year and location were relative minor, with more forage fishes consumed in 1995 (fig 9).

The ontogenetic shift in diet to more piscivory can be clearly seen in Figure 10, with smaller size classes of Pacific hake consuming mostly euphausiids, whereas the larger size classes (>45 cm FL) consuming mostly fish (Rexstad and Pikitch 1986). The largest size class consumed almost entirely smaller Pacific hake (fig. 10).

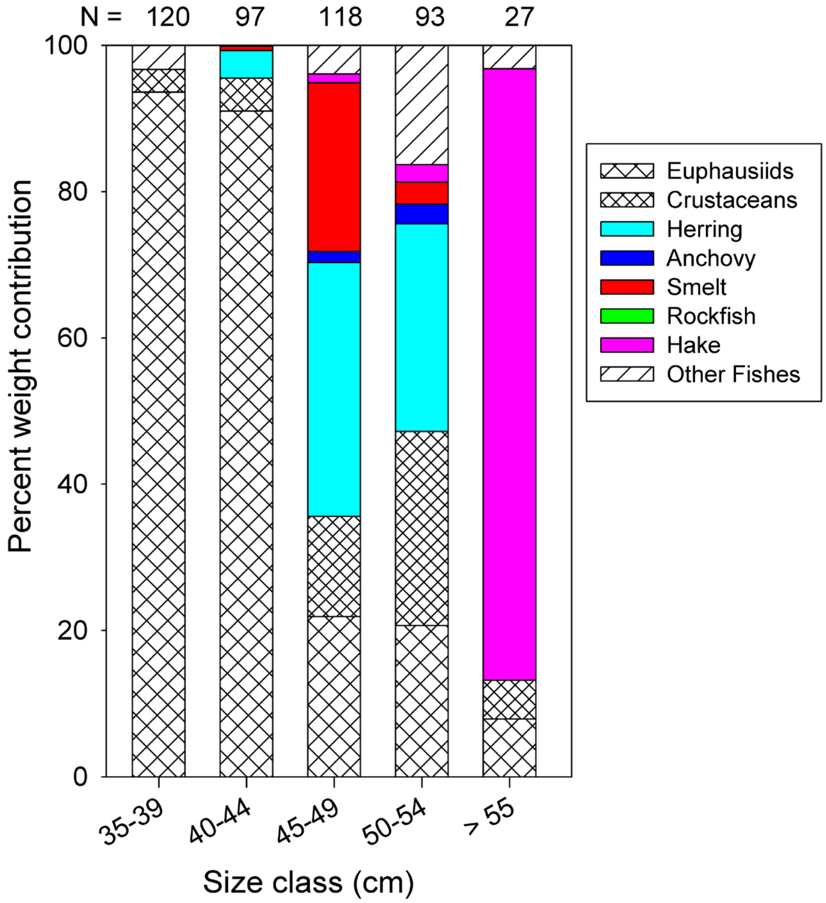

Figure 10. Diet composition of Pacific hake (*Merluccius productus*) collected from the 1983 West Coast trawl surveys conducted by the Alaska Fisheries Science Center off Washington and Oregon for five size classes (in cm) from Rexstad and Pikitch 1986. Number of stomachs with food is indicated at the top of each bar.

This cannibalistic behavior (primarily on age-0 and age-1 individuals) has been noted in other studies on this species (e.g., Buckley and Livingston 1997), and is an important aspect of their population biology.

Coho Salmon. Coho salmon (*Oncorhynchus kisutch*) are anadromous and spend their juvenile and adult lives in coastal or offshore waters before returning to freshwater to spawn. Juveniles consume a mixed diet of crustaceans and fishes when they first enter the ocean but soon become mostly piscivorous, although they are able to consume only larval and juvenile fishes until they become adults (Daly et al. 2009). Therefore, we restrict our analysis to adults in coastal waters prior to return to freshwater. Despite their importance as a commercial and recreational species, there have been relatively few studies directed at their feeding ecology as adults. The diet of coho salmon adults collected from 1948 to 1950 in the commercial fisheries off Oregon showed that they were feeding mostly on fish, mainly northern anchovy in the early summer, and then switched to eating more Pacific herring in late summer, and a combination of Pacific herring and Pacific hake in the fall (Heg and van Hyning 1951; fig. 11a). Coho salmon adults caught in purse seines from 1981 through 1984 showed a remarkable consistency in the diet from year to year, with Pacific herring and northern anchovy being the primary forage prey overall (fig. 11b). Juvenile rockfishes were also eaten during all years including 1979 and 1980, years that showed higher predation on smelt (Brodeur et al. 1987). Silliman (1941) also found Pacific sardine to be an important food of adult coho salmon caught off Washington in 1938. Recent studies have confirmed that adult coho salmon have fed on Pacific sardine since the resurgence of this important resource in the NCC in the late 1990s (Emmett et al. 2006).

Chinook Salmon. Similar to coho salmon, adult Chinook salmon (*Oncorhynchus tshawytscha*) are large-bodied piscivores known to feed on forage fishes during their marine life (Daly et al. 2009). Numerous studies have examined juvenile Chinook salmon diets in the NCC (e.g., Brodeur and Pearcy 1992; Daly et al. 2009) but there have been relatively few which have examined adult stomachs prior to their entry into fresh water. Although northern anchovy were the dominant

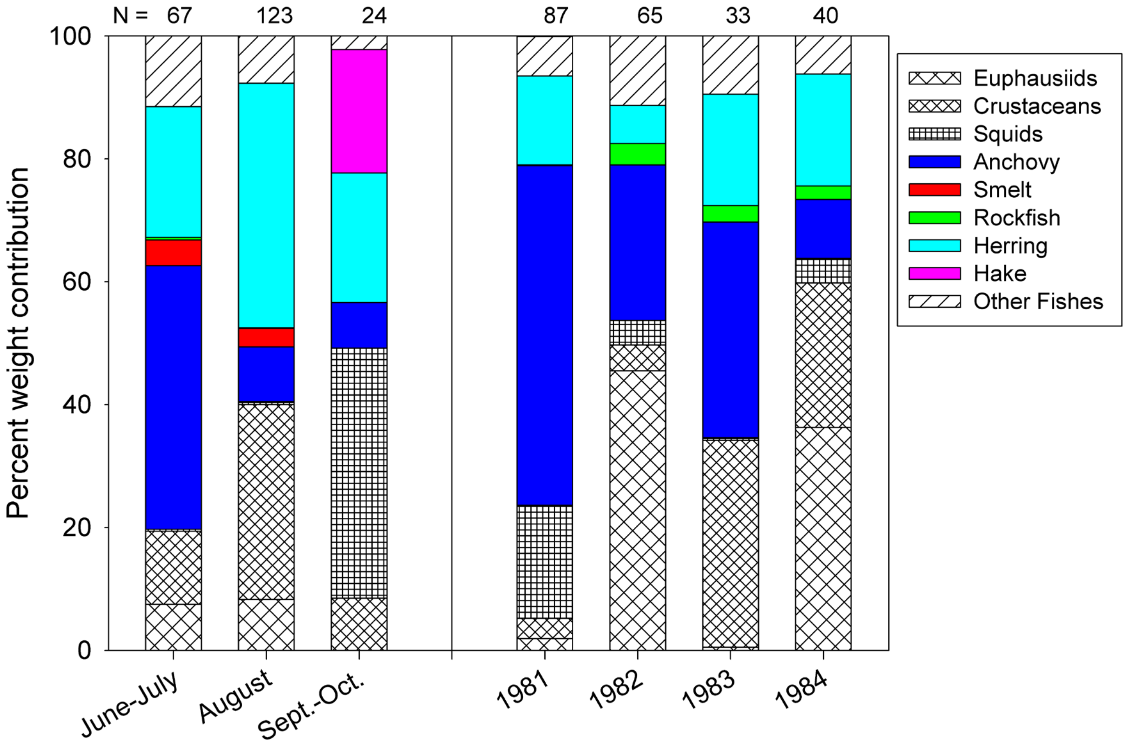

Figure 11. Diet composition of adult coho salmon (*Oncorhynchus kisutch*) collected from 1948–50 commercial fisheries off Oregon from Heg and van Hyning 1951 (left) and from purse seine surveys from 1981–84 from Brodeur et al. 1987 (right). Number of stomachs with food is indicated at the top of each bar.

forage prey of Chinook salmon in four years of summer sampling off Washington and Oregon in the early 1980s (Brodeur et al. 1987), other prey such as Pacific hake, Pacific herring, and rockfish were important in some years (fig. 12). Chinook salmon adult diets tend to be more piscivorous in recent (since 1999) summer trawl sampling with Pacific herring and smelt supplanting northern anchovy as important prey during different time periods (fig. 12). In a diet study of multiple predators off southern Oregon and northern California during 2000 and 2002, Miller and Brodeur (2007) found that Pacific herring and Pacific sardine were important prey of adult Chinook salmon, especially in late summer. In a study of sport caught adult Chinook salmon along the California coast north of Cape Mendocino, Hunt et al. (1999) found in the summers of 1994 and 1995 that Pacific herring and various smelt species were the dominant forage fish prey consumed during one summer, whereas northern anchovy, Pacific herring, and Pacific saury were important in the following year. Thayer et al. (2014) found that central California coast Chinook salmon diets declined in diversity since 1955, with recent diets dominated by northern anchovy, euphausiids, and Pacific sardine. This study showed substantial seasonality in Chinook salmon diets with juvenile rockfish important mainly in the summer, northern anchovy in the summer and fall, and Pacific herring only in the winter months (Thayer et al. 2014). All these studies taken collectively suggest substantial plasticity in the forage fish feeding of adult Chinook salmon in the ocean.

Albacore. In the eastern North Pacific, albacore (*Thunnus alalunga*) are the dominant non-tropical tuna species that migrate into the offshore waters of the California Current to feed as juveniles during the summer and fall, before undergoing transoceanic migrations to their spawning grounds in the Western North Pacific. Albacore collected from commercial fisheries in 1968 (July–November) and 1969 (July–August) (Pinkas et al. 1971) north of Cape Blanco fed predominantly (>50% by weight) on northern anchovy. In contrast, more recent work done in 2005–06, they consumed a high proportion of northern anchovy, but juvenile Pacific hake rockfishes and Pacific sardine were also represented in the diets (Glaser 2010; Glaser et al. 2014; fig. 13). Earlier work by Pearcy (1973) found that fish (primarily Pacific saury and rockfishes) were the dominant prey of albacore caught in the Columbia River plume off Oregon, but their diet was dominated by squid and crustaceans offshore in more oceanic waters.

Pacific Halibut. Pacific halibut (*Hippoglossus stenolepis*) are known to be important piscivores throughout their distribution and capable of eating fairly large fish (see review by Best and St. Pierre, 1986). Surprisingly little diet information is available on Pacific halibut caught in the NCC. Pacific halibut collected in recreational fish-

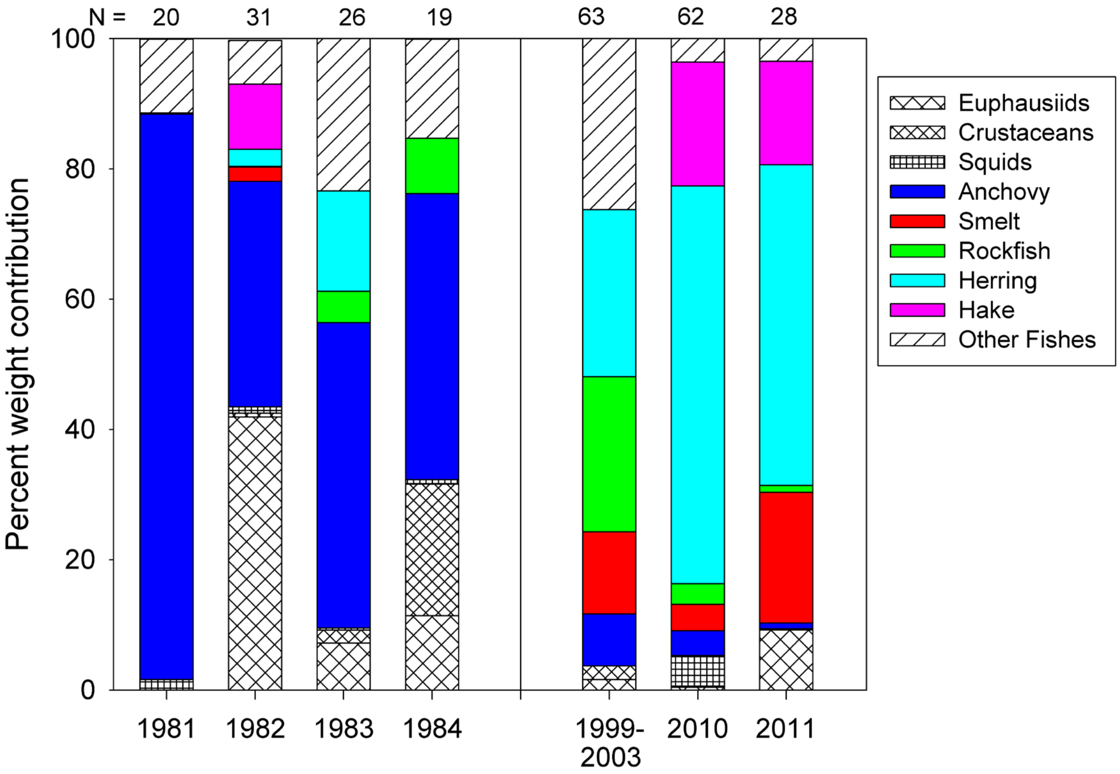

Figure 12. Diet composition of adult Chinook salmon (*Oncorhynchus tshawytscha*) collected from summer purse seine surveys from 1981–84 (Brodeur et al. 1987, left) and from summer surface trawl collections from 1999–2011 (Daly and Brodeur, unpub., right). Number of stomachs with food is indicated at the top of each bar.

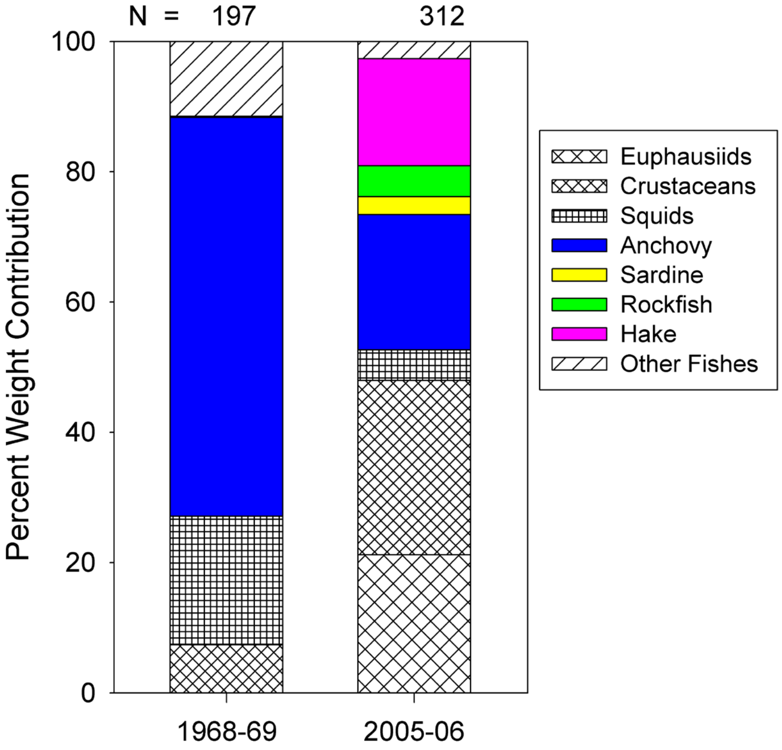

Figure 13. Diet composition of albacore (*Thunnus alalunga*) collected from commercial fisheries from 1968–69 (Pinkas et al. 1971) and from 2005–06 (Glaser 2010) north of Cape Blanco, Oregon. Data were originally presented as percent energetic values by Glaser 2010 but are given here as percent by weight based on unpublished data (Glaser unpub.). Number of stomachs with food is indicated at the top of each bar.

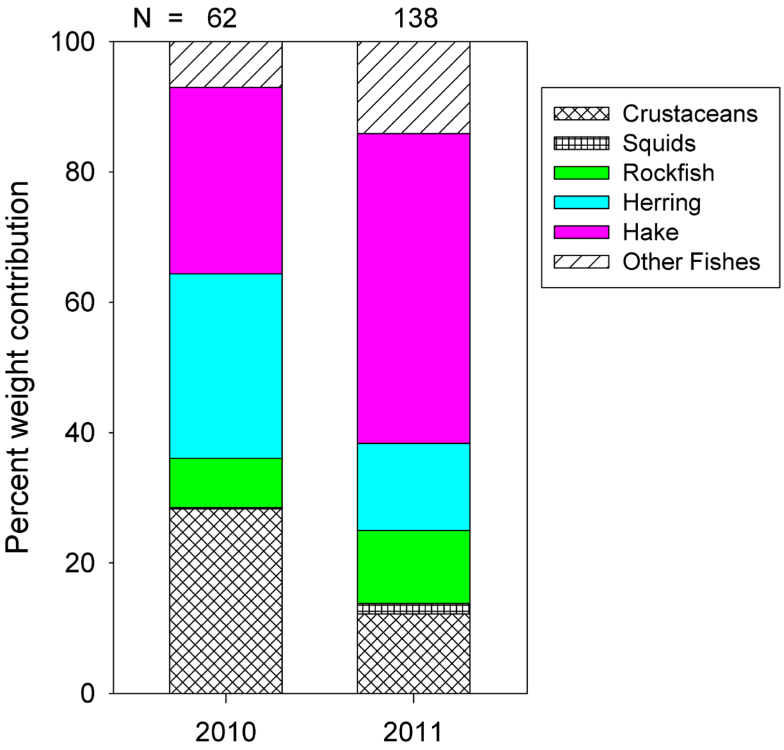

Figure 14. Diet composition of Pacific halibut (*Hippoglossus stenolepis*) collected in May–August from recreational fisheries from 2010–11 off central Oregon (Gladics et al. 2014). Number of stomachs with food is indicated at the top of each bar.

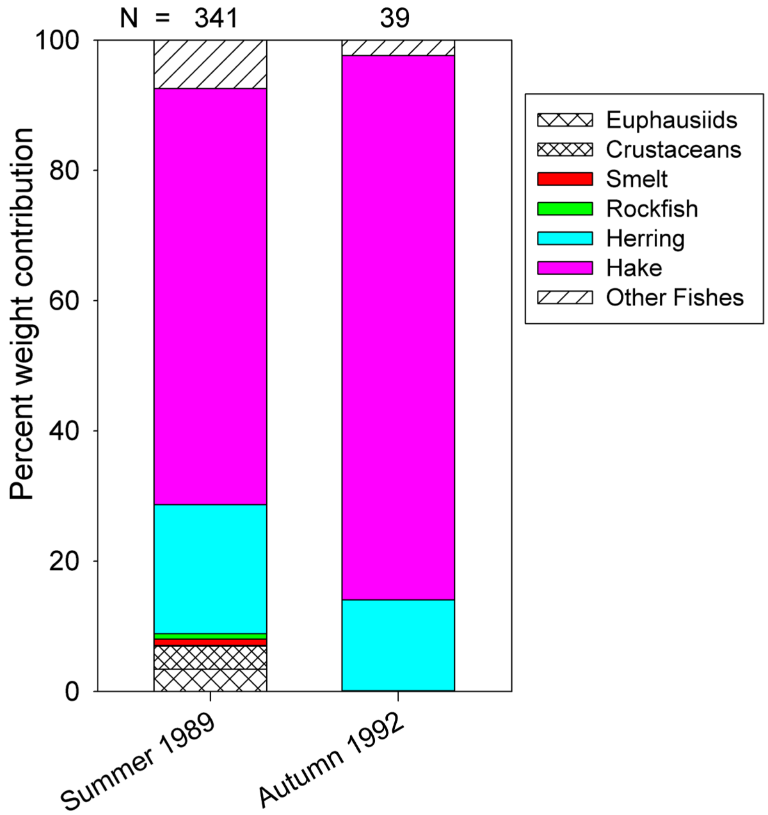

Figure 15. Diet composition of arrowtooth flounder (*Atheresthes stomius*) collected from West Coast trawl surveys conducted by the Alaska Fisheries Science Center in 1989 and 1992 (Buckley et al. 1999). Number of stomachs with food is indicated at the top of each bar.

eries from May through August of 2010–11 off central Oregon (Gladics et al. 2014) found Pacific hake, Pacific herring, and juvenile rockfishes to be the dominant prey in these two contrasting years in terms of oceanography (fig. 14).

Arrowtooth Flounder. Arrowtooth flounder (*Atheresthes stomius*) are a large-bodied, semipelagic flatfish known to be an important fish predator throughout their range, which is mainly north of our study area. Fish were the dominant prey in arrowtooth flounder collected from the AFSC West Coast trawl surveys conducted in the summer of 1989 and autumn of 1992 (Buckley et al. 1999; fig. 15). The majority of the fish diet was Pacific hake, with herring also being of secondary importance (Buckley et al. 1999). Gotshall (1969) found fish to be of less importance than shrimp in terms of volume for arrowtooth flounder collected off northern California.

Size Composition of Prey and Available Prey

The size and availability of various forage fish species plays an important role in the determining the diets of forage fish predators. Predators are generally limited as to the largest prey they can consume because of their mouth size and their swimming speeds (Juanes et al. 2002). For example, adult Pacific sardine averaged about 200 mm FL (fig. 16a) off Oregon from 1998–2011 and therefore only large predators such as sharks, adult Chinook salmon, and large Pacific hake are able to feed on fish of this size. While capturing a large forage fish (i.e., Pacific sardine) provides a large amount of calories, it requires the expenditure of time and energy that would not be necessary if other smaller prey are available, particularly if the latter are very abundant. Predators commonly switch to eating prey that is highly abundant even if this prey is on the lower range of their size spectrum (Murdock et al. 1975; Rindorf et al. 2006).

Small forage fish such as smelt and northern anchovy mature at relatively small sizes and are thus available as prey for many predator species (fig. 16a). Pacific herring, in contrast, can reach relatively large size as they mature, but their juvenile stages (0 and 1-age) are often abundant in the NCC and thus a primary food for predators during some years (Tanasichuk et al. 1991).

Annual and decadal oceanographic conditions directly affect forage fish abundance (Chavez et al. 2001; Emmett et al. 2006; Litz et al. 2008, 2014). Off Oregon, large annual fluctuations in the abundance of forage fish can alter the size structure of available fish prey community (fig. 16b) and thus directly affect the diets of predators. For example, during 1998 and 1999 the forage prey size spectrum was weighted heavily towards large prey (i.e., older Pacific herring and Pacific sardine) and not towards smaller forage fishes such as northern anchovy (fig 16a). In 2003, Pacific herring had two abundant year classes (one small and one large) (fig. 16a) and thus were available as prey for many different sizes of predators. Other years (2010, 2011) had predominantly northern anchovy and whitebait smelt, the smaller forage fishes generally available (fig. 16a). As such, the suite of forage fish species/sizes that is available any given year varies significantly (fig 16b), which may impact the relative foraging success of piscivores.

Most fish predators have a preferred prey size range (Juanes et al. 2002). Pacific hake (size range 338–731 mm, n = 581) off Oregon for example, appear to eat fish prey of a mean size of 120 mm (fig. 17), which would substantiate why we found that northern anchovy, smelt, and Pacific herring are their most common fish prey. Adult Chinook salmon (252–506 mm, n = 114), in contrast, do not appear to have a preferred prey size (fig. 17), but appear instead to eat a wide size range of prey. Chinook salmon can grow relatively large, enabling them to eat the larger forage fish prey. Chinook salmon are very active and mobile predators that can quickly switch to the most abundant forage fish prey available.

Ranking of Important Fish Predators on Forage Fishes

The overall ecological effect of any fish predator on an ecosystem and forage fish population can be estimated by considering the biomass of the predator and the percent of forage fish in its diet (fig. 18). From this analysis it is evident that Pacific hake has a very large effect on the forage fish community, primarily because of its very large population biomass. Other predators that have a large effect on forage fish include spiny dogfish, albacore tuna, and jack mackerel. Albacore may have a disproportionally large overall effect on forage fish because their substantial biomass in the NCC in summer coupled with a high metabolic rate (Sharp and Dizon 1979), which allows them to digest prey relatively quickly. Glaser (2010) calculated that albacore can have substantial impacts on northern anchovy populations in the California Current, but these consumption estimates are sensitive to predator abundance estimates.

Many predators appear to have similar predation effects on forage fish populations. This is because they have similar population biomass (approximately 1,000 mt) and composition of forage fish in their diet, 40–60% (fig. 18). Two large shark predators, blue shark and soupfin shark, probably do not have a large effect on forage fish abundance because their population biomasses are relatively small. Our estimates of the relative importance of the forage fish predators are only meant to be approximate and are based on the limited diet studies reported here and estimates of biomass from various methodologies, each of which has considerable variability on both a seasonal and interannual basis.

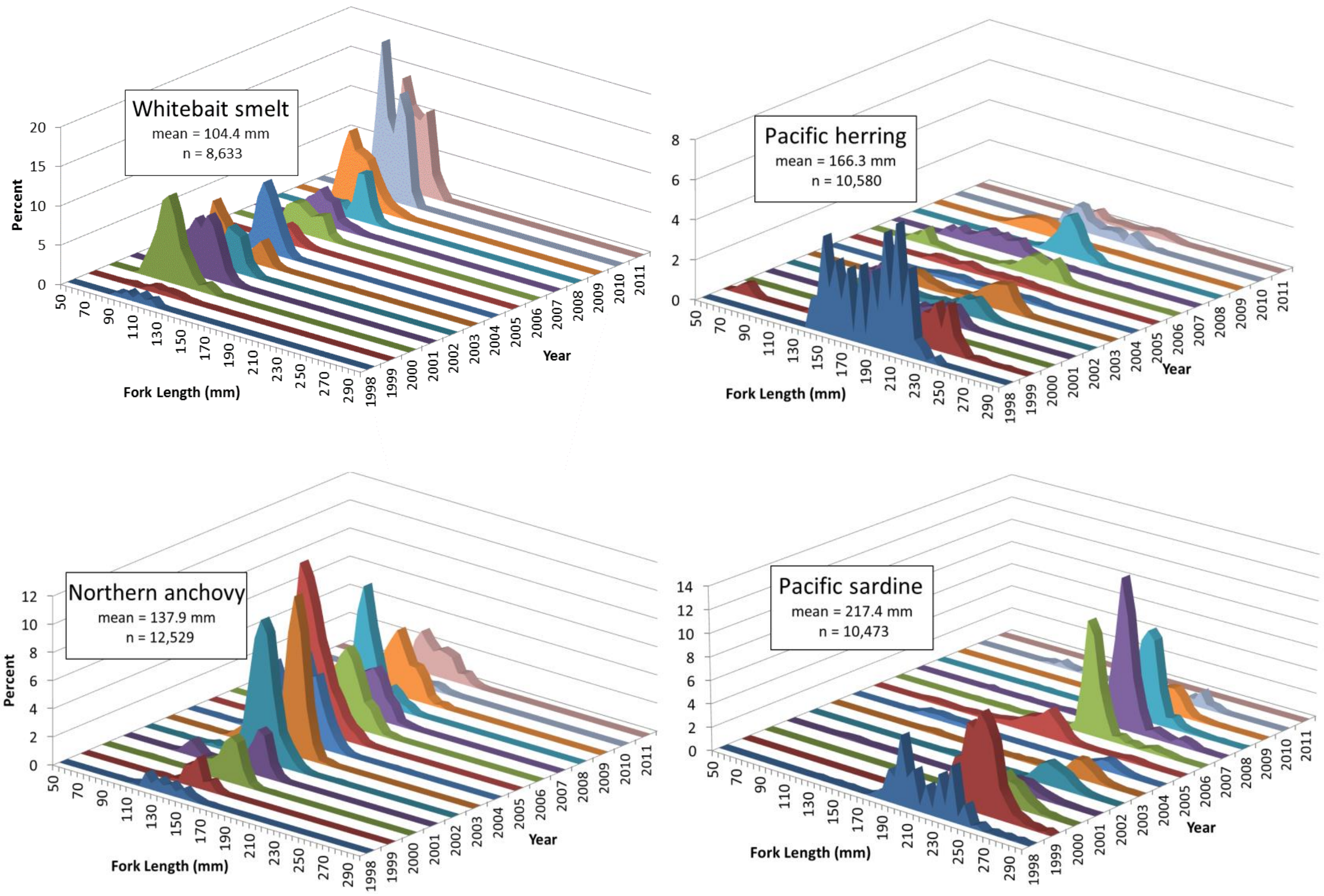

Figure 16a. Available forage fish fork length distributions from spring–summer trawl surveys off the mouth of the Columbia River from 1998–2011 (Emmett unpub. data). These four species represent greater than 90% of all forage fish collected in these pelagic trawl surveys done at night. Data are represented as a percent of the catch made up of that length (mm) within a given year.

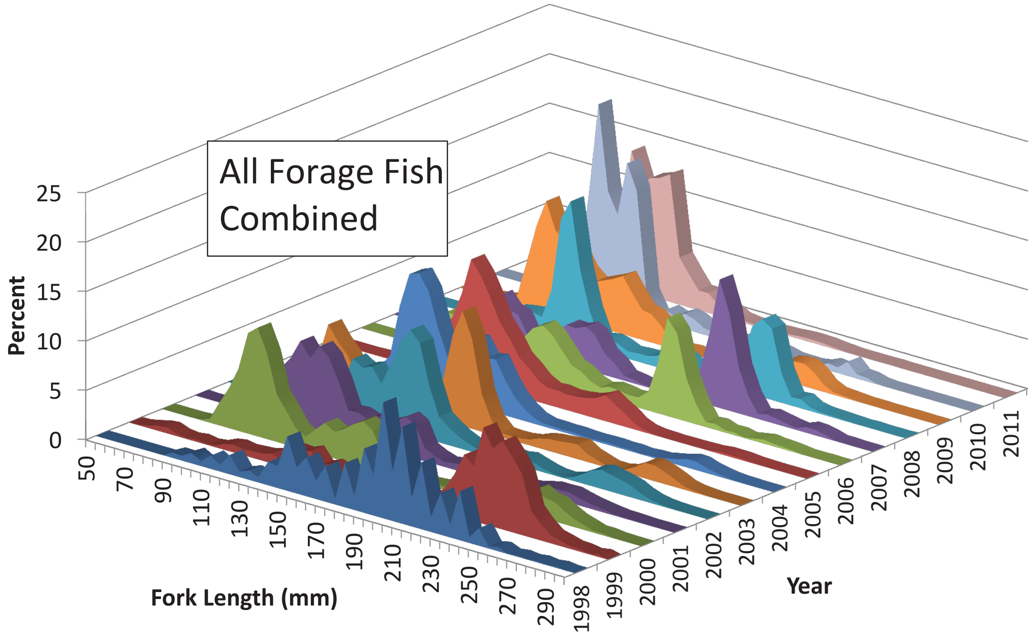

Figure 16b. Summed availability of the four forage fish fork length distributions from spring–summer trawl surveys off the mouth of the Columbia River from 1998–2011 by year (Emmett unpub. data). Data are represented as a percent of the catch made up of that length (mm) within a given year.

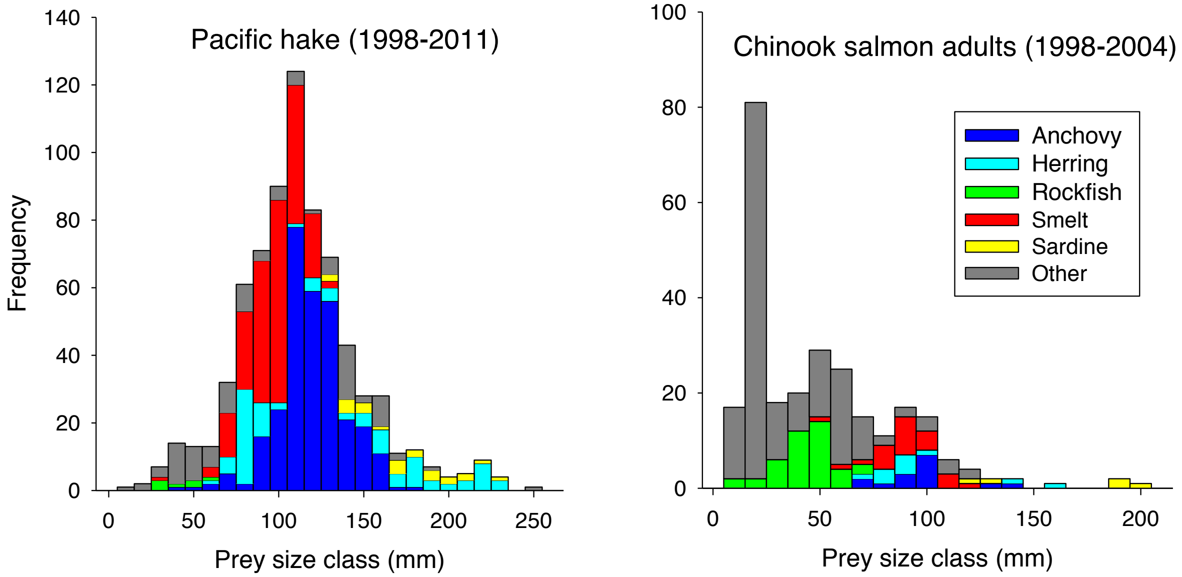

Figure 17. Size (total length) frequencies of the dominant forage fishes found in Pacific hake (left) and Chinook salmon adult (right) stomachs collected in summer (May through August) of the years indicated on each graph.

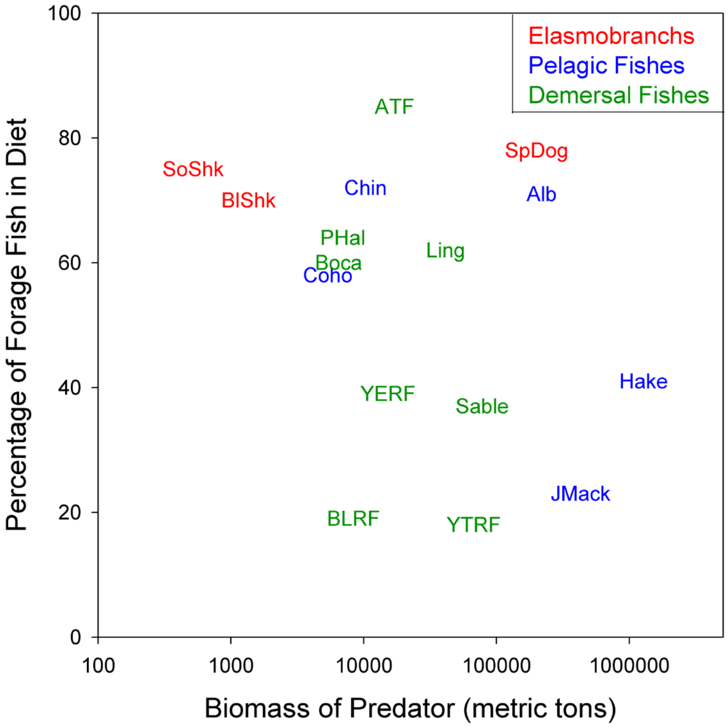

Figure 18. Comparison of usage of forage fish by the dominant predators examined in this study, based on the estimated predator biomass from 2000–09 (*x* axis) and the percentage of forage fish in the diets (*y* axis). The predators are color coded by type (red = elasmobranchs, blue = pelagic fishes, green = demersal fishes). ATF = arrowtooth flounder, SpDog = spiny dogfish, PHal = Pacific halibut, Alb = albacore, BLRF = black rockfish, BlShk = blue shark, Boca = bocaccio, Sable = sablefish, Chin = Chinook salmon, Coho = coho salmon, SoShk = soupfin shark, YERF = yelloweye rockfish, Hake = Pacific hake, Ling = lingcod, JMack = jack mackerel, YTRF = yellowtail rockfish.

Spatial and Temporal Variability

The coastal waters of the NCC are affected by several large-scale and local environmental variables with seasonal, annual, and even decadal variability (Checkley and Barth 2009). These variations may have been enhanced by climate changes over the past several decades (Sydeman et al. 2013). Primary drivers of these changes at the large scale include the Pacific Decadal Oscillation (PDO, Mantua et al. 1997) and El Niño/Southern Oscillation (ENSO) cycles (Chavez 1992) while at a more regional scale, upwelling and riverine plumes may have more spatially-localized effects. The PDO is likely to affect the spatial distribution and recruitment of the forage fishes and their predators (Chavez et al. 2001), whereas ENSO may have direct effects on the food web leading up to the top predators (Brodeur and Pearcy 1992; Francis et al. 2012).

Changes in ocean conditions can affect the spatial distribution of the predators and prey, creating novel forage communities and predator ensembles during some years. Examples of this are the northward shift of Pacific hake spawning in some warm years which results in age-0 and age-1 fish occurring in the NCC (Phillips et al. 2007), where they may be preyed upon by piscivores. On longer time scales, increases in abundance of forage species such as Pacific sardine along with changes in ocean conditions allowed this species to spread to the NCC in recent years where they were absent for decades (Emmett et al. 2006). Thus, Pacific sardine was evident in the diet of several species (spiny dogfish, sharks, Pacific hake, albacore) in recent sampling but not in the 1970s and 1980s, when it rarely occurred north of Southern California. Changing ocean conditions may also allow for the invasion of new predators into the region, which can directly affect the biomass of forage fish and their predators. The recent influx of the voracious cephalopod predator, Humboldt squid (*Dosidicus gigas*) into the NCC from southern latitudes (Field et al. 2007; Litz et al. 2011) is a striking example of this.

Changes in the food web structure associated with El Niño conditions can have major impacts on higher trophic level predators in the NCC (Brodeur et al. 1987; Brodeur and Pearcy 1992; Nelson 2004; Lee and Sampson 2009). However, not all El Niños are alike and during a particular El Niño, not all predators are similarly affected (Gladics et al. 2014). Other years, such as 2005, which was not an El Niño year, had extremely delayed spring upwelling resulting in El Niño-like conditions in the NCC (Brodeur et al. 2006). In addition to changing the availability of these forage species, changes in the base of the food web in these years of poor ocean conditions in the NCC can lead to differences in the quality (lipid content, fatty acid composition) of the forage fish prey (Daly et al. 2010; Litz et al. 2010), further diminishing their utility as prey to top predators.

The relative consumption calculations of the various predators on forage fishes are only meant to be first-order approximations for comparative purposes and encompass many assumptions and unknowns. Our abundance estimates used in were derived mainly for the summer months (May–October; Keller et al. 2012) when the most predator sampling and diet information are available. Although some migratory species that exhibit high biomass (Pacific hake, jack mackerel, and albacore) are only present in the NCC during the productive summer months, a number of lower biomass but resident species (rockfishes, lingcod, sablefish) may have potentially greater cumulative impacts throughout the year that were not accounted for in our analysis. Our biomass estimates include all age/length categories of the predators and does not account for ontogenetic changes in diet composition (Rexstad and Pikitch 1986; Daly et al. 2009). We have considered that consumption rates per capita are equal for all the fish and years we examined and this assumption is not likely as temperature and hence metabolism levels are likely to differ particularly between highly-migratory pelagic species (albacore, jack mackerel) and more sedentary demersal species (rockfish, sablefish).

Finally, the NCC is not homogeneous in terms of its productivity or standing stocks of fish prey (Checkley and Barth 2009). Areas such as the Columbia River Plume may act as important hotspots of forage fish biomass and predator abundance (Emmett et al. 2006; Litz et al. 2014). Cross-shelf differences tend to be more pronounced than along shelf differences and certain predators may be found mainly inshore (e.g., black rockfish) whereas others are restricted to more offshore waters (e.g., albacore, blue sharks), thus limiting the suite of forage fish prey available to them. Spatially explicit mapping of where predation is occurring on the important forage species (e.g., Buckley et al. 1999; Glaser 2009) should be considered in future studies and would be critical to differentiating where the important predation hotspots are located. More spatial information of this kind is needed to assess the predator-prey interactions which may happen on localized scales that may not be detected in large-scale surveys.

CONCLUSIONS

Forage fish species, size, and availability vary substantially in the NCC on seasonal, annual, and decadal scales (Brodeur et al. 2003; Emmett et al. 2006; Litz et al. 2014). These fluctuations affect the feeding, growth, migration, and movements of predatory fishes such as Pacific hake, tuna, sharks, and adult salmon. As Field et al. (2006) found, Pacific hake/forage fish interactions have a very large influence in the fish trophic community in the California Current. When analyzed by specific forage fish taxa, Pacific hake may significantly influence populations of northern anchovy, Pacific sardine, Pacific herring, smelt, and its own population abundance (cannibalism) (Buckley and Livingston 1997). Unfortunately there is limited information indicating whether predation by Pacific hake or other predators is directly influencing forage fish abundance (i.e., top-down) or if bottom-up processes are determining forage fish populations abundance. Bottom-up processes appear to be have important effects on Pacific sardine and northern anchovy populations (Rykaczewski and Checkley 2008), and perhaps most forage fish populations in the NCC (Ware and Thompson 2005; Hill et al. 2014). Top-down processes may be most important for Pacific herring (Ware and McFarlane 1995) and northern anchovy during some years (Glaser 2011; Glaser et al. 2014).

The abundance and size of available forage fish influences the diets of predators. The typical length of adult northern anchovy is a suitable prey size for a large number of predators and thus of primary importance to many predatory fishes in the California Current (Glaser 2011). Young Pacific herring and Pacific sardine may also fulfill the same role, although the size of these forage fish can often exceed the gape limitations of many of the smaller fish piscivores. Rockfish and Pacific hake populations make up a large biomass within the northern California Current system and these species serve as predators upon juvenile and adult forage fish as well as being prey during their juvenile pelagic stage for other midwater and demersal elasmobranchs and fishes. Analysis of stomachs of apex predators indicated that they feed on a wide range of prey and have the capacity to exploit what is readily available (Brodeur and Pearcy 1984, 1992; Emmett and Krutzikowsky 2008), making them an important nexus in shelf food webs (Field et al. 2006; Ruzicka et al. 2012).

Despite the abundance of information on some key predators species such as Pacific hake and adult salmon, there is a paucity of information on some key species which are important in terms of biomass (albacore, jack mackerel, sablefish) or consumption of forage fishes (elasmobranchs, Pacific halibut, arrowtooth flounder). Monitoring the diets of these and other top predators can provide valuable information on the recruitment success and abundance of forage species (Anderson et al. 1980; Mills et al. 2007; Thayer et al. 2008; Brodeur et al. 2011; Gladics et al. 2014). Although new information is provided in our study, many of the studies of demersal species in this region were conducted during past decades when environmental and biological conditions were vastly different. Therefore a critical need exists to continue and expand the sampling to include all potential forage fish predators. Much of the information presented herein is based upon collections made primarily in late spring through early fall, when most surveys of fish abundance (and diet studies) are routinely conducted, and a critical data gap exists on what predators are important during other times of the year (e.g., Thayer et al. 2014). Fisheries for many of the forage fish examined here are under federal (hake, rockfish, sardine, and anchovy) or state (herring) management at the present time and the role these fishes play in the ecosystem is being considered. However, other taxa not directly fished (e.g., smelts, lanternfishes) presently lack protection although measures are under consideration would include the trophic importance of these species in the food web of the West Coast (http://www.pcouncil.org/ecosystem-based-management/protection-for-unfished-forage-fish-initiative/). Consumption by fish and elasmobranch predators may be substantial but in estimating impact on the forage fishes themselves, the competing needs of other predators not examined here (seabirds, marine mammals, large squid, and humans) need to be evaluated (e.g., Cury et al. 2011; Kaplan et al. 2013; Ainley et al. 2014; Pikitch et al. 2014). Examining the spatial and temporal complexities of predator-prey relationships involving forage fishes is essential when moving towards Ecosystem Based Fisheries Management in the California Current in the future (Field and Francis 2006; Pacific Fishery Management Council 2013; Ainley et al. 2014).

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