

### 3. Summer Distribution and Feeding of Spiny Dogfish off the Washington and Oregon Coasts

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**Abstract.**—Our understanding of the spiny dogfish *Squalus acanthias* of the northeastern Pacific is based almost exclusively on nearshore populations from enclosed regions (e.g., Strait of Georgia, Hecate Strait, and Puget Sound), with little attention given to more offshore populations along the open coast. Our purpose here was to characterize the summer distribution and diet of dogfish off the Washington and Oregon coasts by means of two fishery surveys: the National Marine Fisheries Service (NMFS) triennial shelf groundfish survey, 1977–2004, and the NMFS/Oregon State University juvenile salmon survey, 1998–2002. Dogfish catches were patchy throughout the entire period and showed a broad distributional range along the Washington and Oregon coasts. The highest abundances occurred in shallow waters (55–184 m) off the northern Washington and central Oregon coasts. Around the Columbia River plume, dogfish catch per unit of effort was significantly related to salinity and surface temperature patterns, but not to chlorophyll concentrations. Dogfish consumed a variety of prey, including both pelagic and benthic taxa, and with increasing size exhibited a shift in their diet to more fish and larger prey overall.

#### Introduction

The distribution and dynamics of marine fish populations are shaped directly and indirectly by physical environmental conditions that vary spatially and temporally. Understanding how and at what scale these conditions vary to affect fish populations is

central to sustainable management. For many marine fishes our understanding remains rudimentary, and the spiny dogfish *Squalus acanthias* is no exception. This small squaloid shark is among the world's most abundant sharks and is widely distributed in temperate waters. It has been subject to intense fishing pressure from both targeted and bycatch fisheries, resulting in concerns about the species' sustainability and cascading effects on the structure of the ecosys-

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tem due to the removal of an important predator (e.g., Musick et al. 2000; Stevens et al. 2000). These concerns are compounded by the species' exceptionally slow growth, late age at maturation, and low fecundity, all of which make it especially prone to rapid over-exploitation and slow recovery.

Our understanding of northeastern Pacific spiny dogfish is based almost exclusively on research of inshore populations from enclosed regions (e.g., Strait of Georgia, Hecate Strait, and Puget Sound). Yet, the species is also common in open coastal waters of the northeastern Pacific from Baja California to Alaska (Alverson and Stansby 1963; Nakano and Nagasawa 1996; McFarlane and King 2003). Moreover, these offshore populations are thought to be distinct from the less migratory inshore populations (Saunders et al. 1984; Ketchen 1986; Holts 1988; Bonfil 1999; McFarlane and King 2003).

Tagging studies have indicated that the offshore population of spiny dogfish is highly migratory (Alverson and Stansby 1963; McFarlane and King 2003; Taylor et al. 2009, this volume) and that migration appears to be seasonal, with the fish moving north in spring and summer and south during fall and winter (Bonham et al. 1949; Holland 1957; Ketchen 1986; Bonfil 1999; McFarlane and King 2003), a pattern also observed in the Atlantic (McMillan and Morse 1999; Campana et al. 2009, this volume). Observations from other regions suggest that dogfish shoal according to size and sex, with mature individuals tending to remain more inshore than immature individuals (Hickling 1930; Nammack et al. 1985; McMillan and Morse 1999; Shepherd et al. 2002). Among mature dogfish, females are usually found in shallower bottom waters than males, with sexes intermingling mainly during the breeding season (Shepherd et al. 2002).

In addition to depth, water temperature has been hypothesized to play an important role in spiny dogfish distribution through seasonal, annual, or even decadal fluctuations (Hickling 1930; McMillan and Morse 1999; Shepherd et al. 2002). In the northeastern Pacific, the species' distribution appears to reflect its temperature preference, with the highest concentrations occurring in waters with surface temperatures ranging between 7°C and 15°C (Brodeur and Pearcy 1986; Holts 1988; see also Shepherd et al. 2002). This surface temperature range is most consistently found in waters from northern Oregon to southeast Alaska, where dogfish are abundant (McFarlane and King 2003; Conrath and Foy, this volume).

The plume of freshwater flowing from the Columbia River may also be significant in influencing spiny dogfish distribution patterns along the Oregon and Washington coasts. This plume contains three distinct zones: the plume zone, the transition zone (frontal zone), and the oceanic zone (Hickey and Landry 1989). The plume zone is where low-salinity freshwater, flowing from the Columbia River, lies on top of high salinity oceanic water; this zone has been specified as those waters contiguous to the Columbia River mouth having salinities of less than 32.5‰ (Stefansson and Richards 1963; Barnes et al. 1972). The transition zone, or frontal zone, is where freshwater starts to mix with oceanic water. The oceanic zone lies beyond the frontal zone and is characterized by high salinity oceanic water. In summer, the Columbia River plume lies offshore and to the south of the river (Landry et al. 1989) and contains a relatively high amount of nutrients, which can generate and sustain plankton blooms.

The presence and extent of such blooms can be estimated remotely by quantifying the amount of chlorophyll, which is indicative of the amount of plankton present or primary productivity. Increased primary productivity provides the food base for larger organisms (e.g., zooplankton and fish) and may indirectly affect the distribution of dogfish.

Spiny dogfish are thought to be opportunistic feeders (Bonham 1954; Jones and Geen 1977), and may have significant impact on prey populations (Beamish et al. 1992). Although dogfish are top predators in many communities and have very high potential densities, their dietary habits are generally inadequately studied and poorly understood (Cortés 1999).

The objective of this study thus was to analyze the distribution of northeastern Pacific spiny dogfish along the Oregon and Washington coasts based on two different sampling programs that collected this species as bycatch during regular sampling. We also predicted that the distribution of dogfish would show a latitudinal pattern (see Vega et al. 2009, this volume), reflecting surface temperature and bottom depth, and that features such as the Columbia River plume might also influence distribution. Stomach contents from recent dogfish collections were examined to determine general feeding habits and look for dietary shifts that might be associated with the body size of these top predators.

## Methods

Data analyzed in the present study were derived from the National Marine Fisheries Service (NMFS) triennial shelf groundfish survey and the NMFS/Oregon State University (OSU) juvenile salmon survey.

### Field sampling

Every three years between 1977 and 2004, NMFS has conducted a survey of the continental shelf from the coast of Vancouver Island, B.C., to southern California to evaluate the distribution, abundance, and biology of groundfish species (Shaw et al. 2000). Each triennial survey was conducted from approximately June 1 to August 9. A high-opening Poly Nor'Eastern bottom trawl with bobbin roller gear (headrope 27.2 m, footrope 37.4 m) was deployed and towed for 30 min. The depths surveyed ranged from 55 to 500 m (Shaw et al. 2000).

The NMFS/OSU juvenile salmon study has been conducted since 1998, with cruises in June and September of each year. Transects were located from La Push, Washington (47°90'N) to Newport, Oregon (44°70'N), and were perpendicular to shore (Brodeur et al. 2005). At each station, a CTD (conductivity, temperature, and depth meter) cast was made, surface chlorophyll samples were taken, and a Nordic 264 otter trawl (width 30 m, depth 18 m) was deployed, with the headrope at the surface. The net contained graded mesh sizes ranging from 162.6 cm at the mouth of the net to 8.9 cm at the cod end, with a 0.8 cm knotless liner in the cod-end section (Brodeur et al. 2003). The trawl was hauled for 30 min parallel to the shore at each predetermined station; most sampling was conducted during daylight hours.

The processing procedure was the same in both surveys: spiny dogfish were measured for total length, sexed, and assessed for maturity.

### Distribution analysis

Data on all hauls in the NMFS triennial shelf groundfish survey containing spiny dogfish were extracted from the Resource Assessment and Conservation Engineering (RACE) database. Hauls occurring between 47°50'N and 48°20'N and between 42°00'N and 43°00'N were extracted to create a Washington and Oregon database. Each haul from this survey was sorted by month, year, and International North Pacific Fisheries Commission (INPFC) statistical area (Brodeur et al. 2003). Haul data were then

averaged by depth (shallow = 55–183 m, medium = 184–366 m, and deep = 367–500 m) according to INPFC specifications. Catch per unit effort (CPUE) was calculated using the following equation:  $CPUE = \text{catch weight (kg)} / \text{distance fished (km)} * (\text{net mouth width (m)} / 1,000)$ . The CPUEs were plotted by year for the Washington and Oregon coasts for both surveys, and CPUE plots by depth were constructed for three INPFC designated regions: U.S. Vancouver (47°50'N–48°20'N), Columbia (47°40'N–43°00'N), and Eureka (42°00'N–42°59'N).

Since weights were not available for all hauls in the NMFS/OSU survey, CPUEs were calculated as number per volume filtered ( $10^6 \text{ m}^3$ ). The environmental data corresponding to each NMFS/OSU station sampled were compared with the calculated CPUEs by means of a generalized additive model (GAM). GAMs are nonparametric generalizations of multiple linear regressions and are less restrictive in assumptions about the underlying statistical distribution of the data (Hastie and Tibshirani 1990). Since GAMs do not assume functional relationships between the predictor and response variables, they allow the relationship between environmental variables and catch rates to be explored, particularly when they are nonlinear (Bigelow et al. 1999; see also Swartzman et al. 1992, 1995; Welch et al. 1995) as in the current study. GAMs were used to analyze the effect on spiny dogfish distribution of salinity, chlorophyll, and surface temperature patterns associated with the Columbia River plume. Models were compared by means of a stepwise approach that removed covariates with  $P$  values  $> 0.05$  and minimized the model generalized cross-validation measure (GCV), which takes into account both fit and degrees of freedom. A Gaussian distribution was assumed with an identity link function, and all models were implemented with the R statistical package (Wood 2001).

Length-frequency information for males and females captured during the two surveys was also analyzed for sex differences.

### Diet analysis

During the NMFS/OSU surveys, spiny dogfish stomachs were removed at sea and placed in a 10% formalin mixture until dissected. Stomachs were collected during each year of the surveys (1998–2004), predominantly in June, over a broad size range of dogfish. A limited number of stomachs were frozen in order to preserve bones and otoliths. In the laboratory, fullness and digestive state of the stomachs were

qualitatively evaluated. Prey items were removed from the stomach and identified to the lowest taxonomic category possible under a dissection microscope. To assist in identification of well-digested prey, voucher collections were constructed for fish vertebrae and squid beaks. The number of each prey type was recorded, and each item was measured to the nearest millimeter. Excess moisture was removed with paper towels, and prey items were weighed to the nearest 0.01 g with an analytical balance. The data collected from stomach contents were used to calculate percent number (%N), percent weight (%W), and frequency of occurrence (%O) of prey.

## Results

While the surveys covered a broad latitudinal range, most large spiny dogfish catches occurred off the northern Washington and central Oregon coasts (Figures 1–2). Both surveys showed that the highest catches were at the northern end of the survey area, generally off the northern coast of Washington. The NMFS/OSU juvenile salmon survey displayed consistently large catches of dogfish off Willapa Bay and Grays Harbor on the Washington coast, and catches were generally lower off Oregon (Figure 2). Few juveniles were caught, all off the Washington coast in June. Dogfish catches were patchy throughout this period (Figures 1–2). When spatial distribution was examined in reference to average depth and INPFC areas for the NMFS surveys, the largest catches occurred in shallow waters (55–184 m) (Figure 3). The largest deepwater catches (367–500 m) occurred in the Eureka region (Figure 3).

Analyzing spiny dogfish catches in the NMFS/OSU surveys with respect to influence of the Columbia River plume showed that all three environmental variables examined (i.e., surface temperature, salinity, and chlorophyll) were significantly nonlinearly related to each other ( $\chi^2$  tests:  $P < 0.01$ ). Surface temperature and salinity explained the most about dogfish distribution, providing the largest reduction in residual deviation (overall  $P < 0.0001$ ,  $R^2 = 0.43$ ). The best fit model form in terms of lowest GCV was  $\ln(\text{CPUE}) \sim s(3 \text{ m temperature}) + s(3 \text{ m salinity})$ , where  $s$  is the spline smoother term. The nominal CPUE was positively associated with both salinity ( $P = 0.004$ ) and surface temperature ( $P = 0.003$ ), and the effects were most pronounced at the higher values of each factor (Figure 4).

The length-frequency distributions of spiny

dogfish from the NMFS and NMFS/OSU salmon surveys were similar in terms of the range of fish sizes captured and the domination of females among the largest length classes and males in the 70.0–89.9 cm length classes (Figure 5). Although the sampling gears and periods were different for the two surveys, we compared the summed length-frequency distributions for 1998 and 2001, the two years during which both surveys collected dogfish and found no significant differences in length distributions (Kolmogorov-Smirnov 2 sample test;  $Z = 0.08$ ,  $P > 0.05$ ). Females matured at larger sizes than males, the smallest mature female sampled being 85 cm. Over 50% of the females reached maturity in the 85.0–89.9 cm length class. The smallest mature male sampled was 64 cm, 50% of the males reaching maturity at 75 cm.

A total of 152 stomachs were examined, of which 140 contained some food. Results indicated that the spiny dogfish diet consisted primarily of Osteichthyes (%N = 68.2; %W = 92.1%), with other prey categories contributing very little in combined stomachs (Table 1). A total of nine species of Osteichthyes were identified from dogfish stomachs. The most frequently occurring fish were whitebait smelt *Allosmerus elongatus*, northern anchovy *Engraulis mordax*, Pacific sardine *Sardinops sagax*, and Pacific herring *Clupea pallasii*. By weight, Clupeidae accounted for 62.8% of the dogfish diet, although unidentified Osteichthyes were most important in terms of occurrence in the stomachs (%O = 33.6). Both Dungeness crab *Cancer magister* adults (%W = 3.9) and megalopae were found, and euphausiids occurred in a few stomachs (%O = 7.9). *Histioteuthis heteropsis* beaks were found (%O = 1.3), but squid flesh was found only in one stomach, along with the beak. Moon snails (Gastropoda, subfamily Pollicinae), Pacific lamprey *Lampetra tridentata*, and salps (Thaliacea) were present in stomachs, but were limited contributors to the overall diet.

There was substantial size-related variability in food habits (Figure 6). Stomachs from spiny dogfish in smaller size classes often contained plankton in the form of euphausiids, *Cancer magister* megalopae, or gelatinous zooplankton, whereas larger size classes consumed mostly fishes and adult crabs. There was a significant positive relationship between the body length of dogfish and the length of prey consumed, although the spread increased, suggesting that dogfish continue to feed on smaller prey as they mature (Figure 7).

Summer Distribution and Feeding of Spiny Dogfish off the Washington and Oregon Coasts

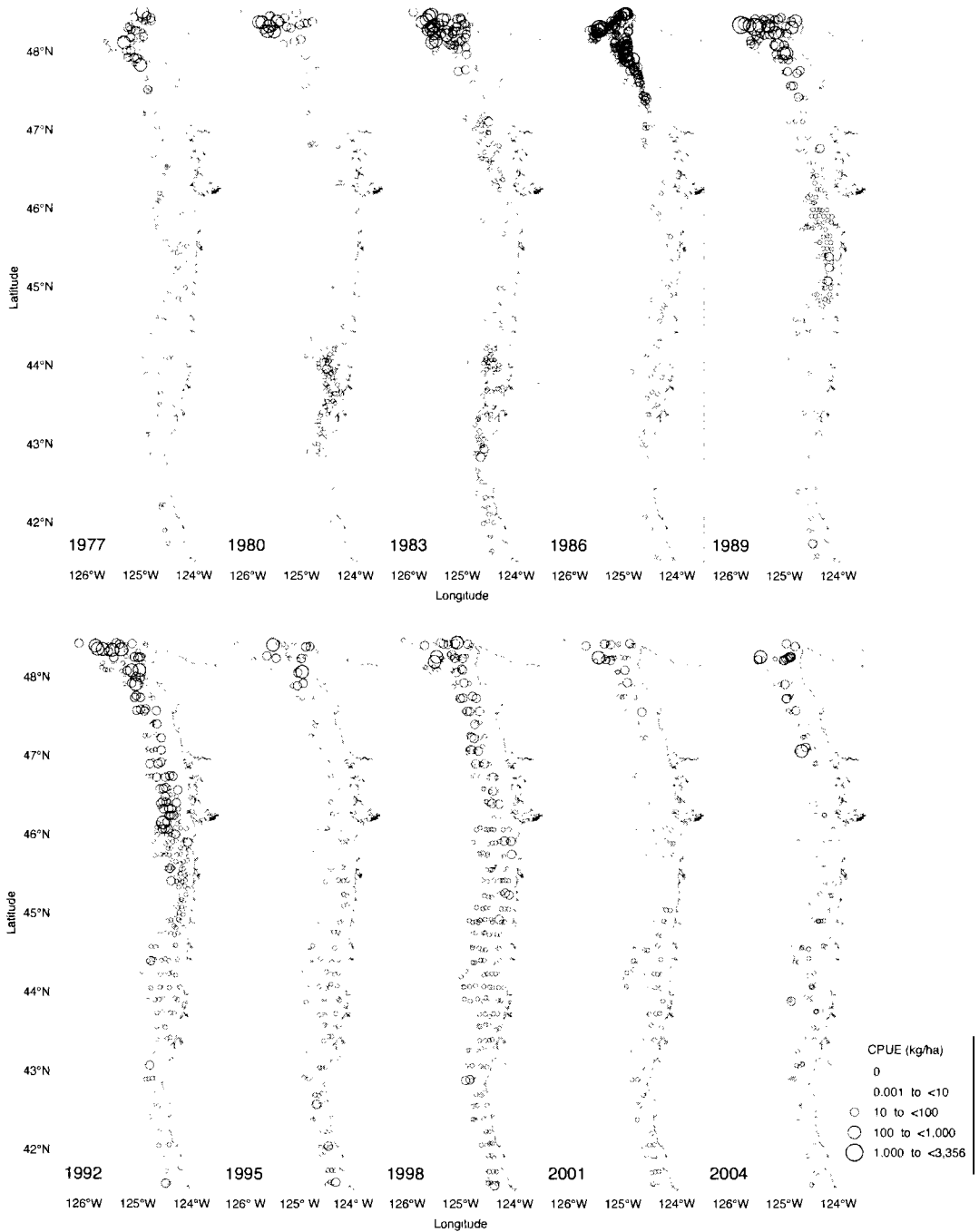


Figure 1. Sample sites and average catch per unit effort (CPUE) for the National Marine Fisheries Service (NMFS) West Coast triennial shelf groundfish survey from 1977 to 2004. + = successful trawls conducted for each year; light gray lines = 100- and 200-m isobaths.

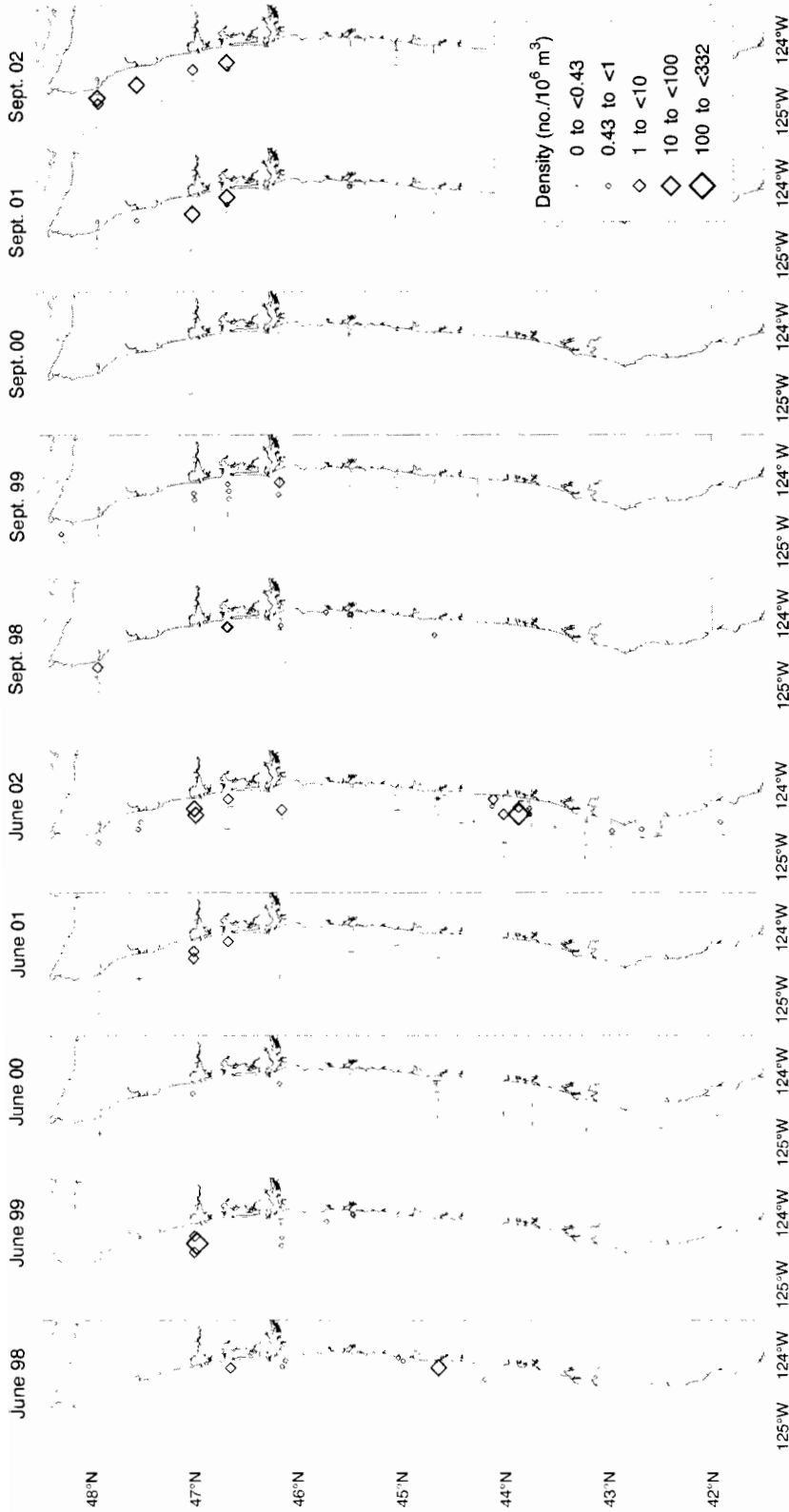


Figure 2. Average CPUE for the NMFS/Oregon State University (OSU) juvenile salmon survey from 1998 to 1902. Light gray lines = 200-m isobath.

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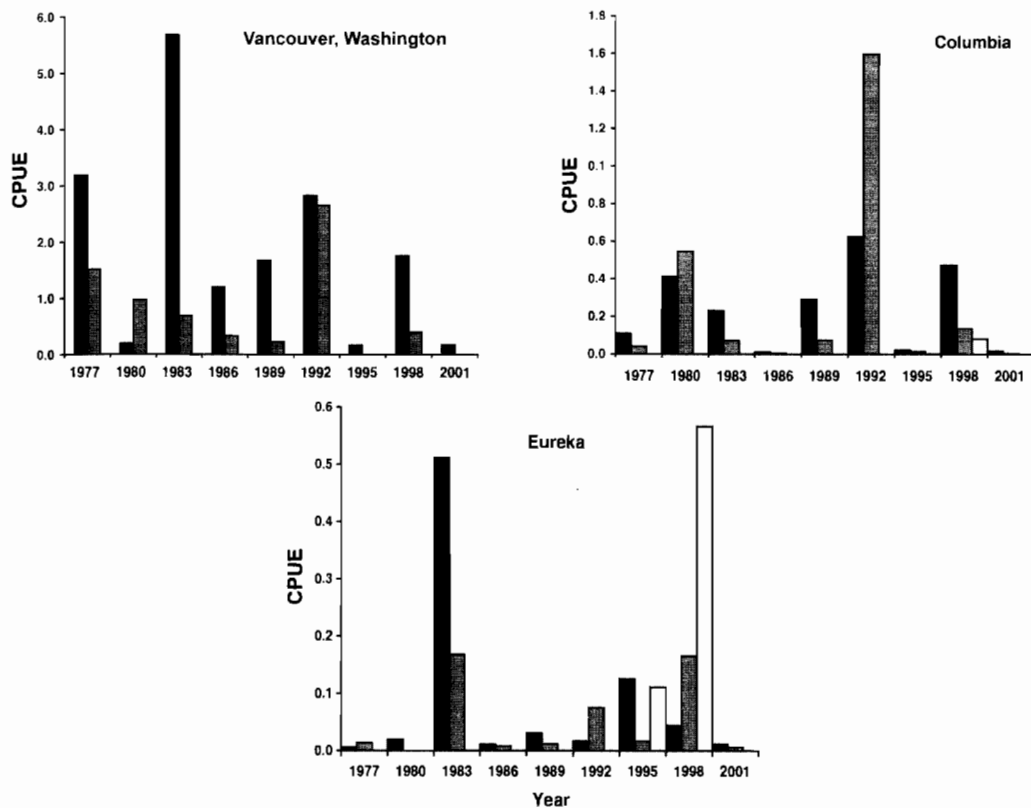


Figure 3. Average CPUE for the National Marine Fisheries Service NMFS triennial shelf groundfish survey by bottom depth for the three International North Pacific Fisheries Commission (INPFC) regions: Vancouver (USA), Columbia, and Eureka. The three depth strata are as follows: shallow (black bars) = 55–183 m, medium (gray bars) = 184–366 m, and deep (white bars) = 367–500 m.

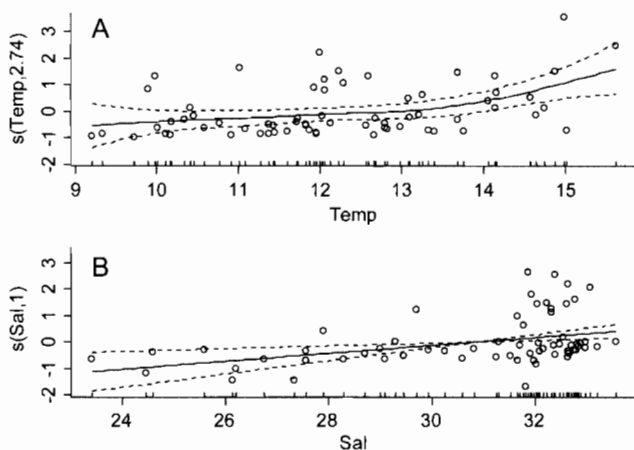


Figure 4. Partial additive effects on spiny dogfish abundance for a model that includes (A) temperature at 3 m and (B) salinity at 3 m for each collection site in a Generalized Additive Model. Predicted result at a specified level of an environmental variable is given by the sum of partial effects of each variable plus a model constant. ---- = Bayesian 95% confidence interval around the mean prediction (—). Whiskers on x-axis indicate locations of variables for that covariate. The values on the y-axis are on a log scale and values less than 0 indicate a negative effect of that variable on dogfish density whereas values greater than 0 indicate a positive effect.

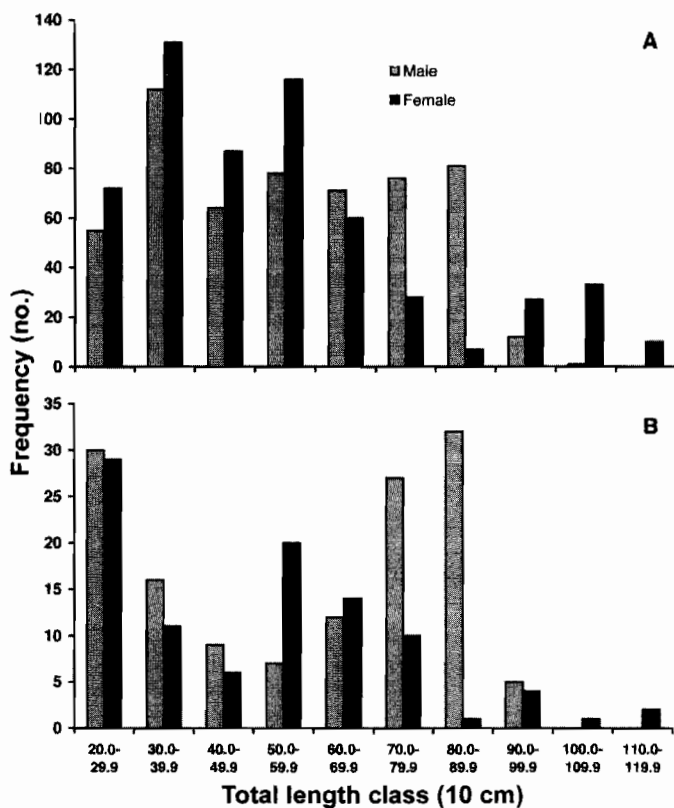


Figure 5. Length-frequency distribution of male and female spiny dogfish from (A) the 23-year NMFS triennial shelf groundfish survey and (B) the 5-year NMFS/OSU juvenile salmon survey.

## Discussion

Spiny dogfish have a broad range along the coasts of Washington and Oregon, and throughout the surveys the largest and most frequent catches occurred off the northern coast of Washington. However, during some years high catches were also recorded off the central Oregon coast. These findings were similar to those of previous studies (Alverson and Stansby 1963; McFarlane and King 2003). The northern area between Washington and Vancouver Island, British Columbia, may be a transition zone between the coastal and offshore populations, allowing mixing and overflow. Dogfish may prefer this region for the abundance of food (which may be concentrated by topographic upwelling and eddies) flowing from Puget Sound and the Strait of Georgia, (Robinson and Ware 1994; Hickey and Banas 2003).

The occasional high catches recorded off the central Oregon coast may reflect the Columbia

River plume's effect on prey availability for predatory fishes, such as dogfish, around the transitional zone (Hickey and Landry 1989). While the plume zone itself may be avoided to some extent by spiny dogfish, as discussed below, the surrounding transition zone, with its abundance of prey items, may attract them. These increased catches could also be due to increased upwelling that occurs during the summer months, where cold, nutrient-rich water moves up from the depths to replace the warmer surface waters that northwest winds have forced away from shore. Such areas of high nutrient concentration generate high productivity that can maintain large fish populations (Bowden 1983). It has been noted that this region off the Oregon coast has some of the strongest occurrences of upwelling along the coast of the northeastern Pacific Ocean (Xie and Hsieh 1995).

Alternatively, the distribution patterns of spiny



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Table 1. Spiny dogfish diet composition by taxon for all years. Included are calculated indices of percent number (%N), percent weight (%W), and frequency of occurrence (%O). \* = value was incalculable.

Prey items	%N	%W	%O
Policinae	0.8	< 0.1	0.7
<i>Histioteuthis heteropsis</i>	1.2	0.1	1.3
Unidentified euphausiids	*	0.4	7.9
<i>Euphausia pacifica</i>	0.4	< 0.1	0.7
<i>Thysanoessa spinifera</i>	0.4	< 0.1	0.7
<i>Cancer magister</i> adults	1.3	3.9	2.0
<i>Cancer magister</i> megalopae	0.4	< 0.1	0.7
Thaliacea	0.8	< 0.1	1.3
Gelatinous material	10.0	1.1	15.8
<i>Lampetra tridentata</i>	0.4	1.0	0.7
<i>Merluccius productus</i>	1.3	2.3	2.0
<i>Clupea pallasii</i>	7.1	18.3	5.9
Unidentified Clupeidae	17.2	36.6	11.2
<i>Sardinops sagax</i>	3.4	7.9	3.3
<i>Engraulis mordax</i>	7.5	5.4	5.3
Unidentified Clupeiformes	2.9	5.2	4.6
<i>Allosmerus elongatus</i>	1.7	0.5	2.0
<i>Hypomesus pretiosus</i>	0.4	0.1	0.7
Unidentified Osmeridae	0.4	0.2	0.7
<i>Ammodytes hexapterus</i>	0.4	< 0.1	0.7
<i>Hemilepidotus spinosus</i>	0.4	< 0.1	0.7
<i>Leptocottus armatus</i>	0.4	0.4	0.7
Pleuronectiformes	0.8	0.8	0.7
Unidentified Osteichthyes	25.1	15.2	33.6
Unidentified material	*	0.4	12.5

Total no. stomachs examined	152
Total stomachs with food	140
Mean length of predators (cm)	62.5
Length range of predators (cm)	22.7–131.2

- Unidentified Osteichthyes
- Clupeidae
- Clupea pallasii*
- Sardinops sagax*
- Engraulis mordax*
- Merluccius productus*
- Allosmerus elongatus*
- Leptocottus armatus*
- Lampetra tridentata*
- Cancer magister* (adults)
- Euphausiids
- Gelatinous Zooplankton
- Other

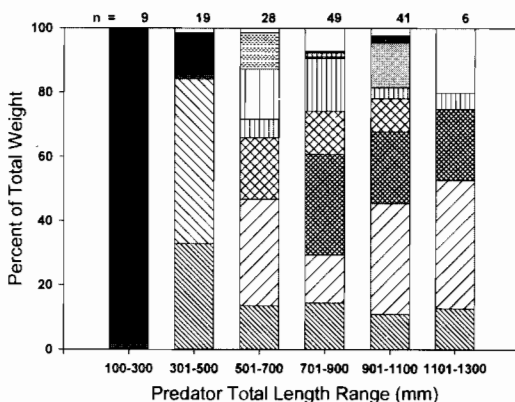


Figure 6. Spiny dogfish diet (% weight) from NMFS/OSU cruises for all years combined as a function of predator size-class. Fish prey are shown as white bar with patterns and invertebrate prey are shown as shaded bars. Sample size of fish in each size category is shown above each bar.

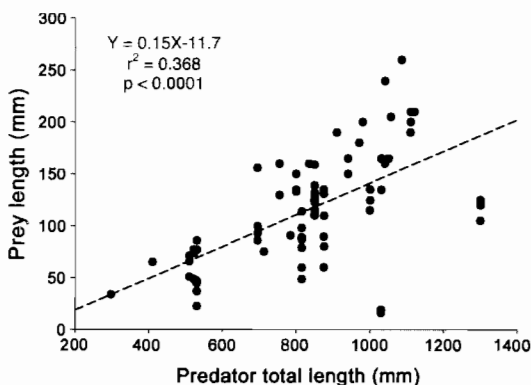


Figure 7. Relationship between dogfish predator size and prey size for all measurable prey from NMFS/OSU cruises for all years. The best-fit linear regression is shown as a dashed line.

dogfish may reflect temperature or physical habitat preferences. It has been noted that dogfish catches decreased off the West Coast about the time of the 1983 El Niño event (Brodeur et al. 2003). Whether this was due to coastal warming, which may have a negative effect on survival, or to a migration north to cooler water is unknown. Unfortunately, there are no data available to differentiate among these potential alternatives. The trend of high abundance in the north with declining abundance southward has also been documented in the northeastern Atlantic dogfish population (Rago et al. 1998; Garrison 2001; Link et al. 2002; Rago and Sosebee 2009, this volume). As in the case of northeast Pacific dogfish, this southward decline may reflect temperature preference, latitudinal clines in prey abundance, or both, with Georges Bank being a northern area of high productivity (Rago et al. 1998).

Spiny dogfish in the present study were caught mostly at shallow depths (55–184 m) possibly because of shoreward migration of males and females for the pupping (late summer and early fall) and breeding (late fall) seasons (Hickling 1930; Saunders et al. 1984; Ketchen 1986; McFarlane and King 2003). If surveys had been conducted during the winter season, we may have found more mature females at greater depths (Hickling 1930).

Spiny dogfish appear to avoid the Columbia River plume, or at least congregate more outside than within the plume, as indicated by the decrease in catches in areas of decreasing surface temperature and salinity. The relationship between the plume and surface temperature was not straightforward, and neither was its effect on dogfish distribution. The plume is generally warmer than other coastal waters of the same distance offshore, but oceanic waters generally get much warmer farther offshore (Hickey and Landry 1989): for example, along the inshore to offshore transects of the NMFS/OSU juvenile salmon cruises. This is also true for the transect running through the core of the plume (Emmett et al. 2006). So the warmer habitats that dogfish were found in were probably indicative of catches far offshore rather than within the plume region. Moreover, salinity is more indicative of the plume, with various salinity thresholds differentiating inside versus outside the plume (Stefansson and Richards 1963). A possible caveat with this analysis was the limited data for each variable throughout the entire range, making fits somewhat tenuous. Despite this, the GAM indicated significant influences of temperature and salinity, indicating that dogfish prefer

the region outside rather than inside the Columbia River plume.

Despite temporal and spatial differences between the two surveys (e.g., the 27-year survey period for NMFS versus only 5-years for NMFS/OSU), common patterns were evident in the length-frequency distributions of captured spiny dogfish. Not surprisingly, more immature (i.e., fish less than 70 cm total length; Figure 5) than mature females were caught in both surveys. Juveniles in this population are estimated to experience a mortality rate of 0.94 per year (Wood et al. 1979). The surveys also demonstrated that males dominated the 70.0–89.9 cm length classes (Figure 5). This dominance probably reflects the maturation of males at this size and the subsequent decrease in growth that accompanies the diversion of energy and resources to reproduction, a pattern found commonly in fishes (Roff 1982). Male dogfish rarely exceed 100 cm in length (Saunders et al. 1984; Vega et al. 2009). The largest fish in both surveys were female, which reflects their larger size and age size at maturity compared to males (see also Ketchen 1972; Jones and Geen 1977; Saunders and McFarlane 1993).

Spiny dogfish stomachs collected during the NMFS/OSU survey contained a wide variety of prey, including benthic invertebrates, demersal fishes, and epipelagic plankton, supporting the concept that dogfish are relatively unselective predators that forage throughout the water column (Brodeur et al. 1987). Stomach contents from this study corresponded well with contents collected in other coastal diet studies of spiny dogfish in the northeastern Pacific (Jones and Geen 1977; Brodeur et al. 1987; Tanasichuk et al. 1991).

Bony fishes were the most common category of prey, being found in nearly all stomachs and providing the greatest component of diet by mass. A substantial portion of the stomach contents consisted of unidentifiable bony fish remains. Dogfish are known to eat infrequently and have a long gastric evacuation period (Jones and Geen 1977; Hannan 2009, this volume). Overall, they tend to be opportunistic feeders, and individuals of the same size-class demonstrated a wide range of feeding habits. Clear shifts in diet, associated with ontogeny, were apparent from this study. Young dogfish are pelagic planktivores that later shift to feeding on schooling fishes before ultimately, as adults, subsisting on demersal and benthic organisms. Large females consumed the most benthic invertebrates and also consumed flatfish.

In conclusion, the northeastern Pacific spiny

dogfish population in U.S. waters shows its greatest abundance off the northern Washington and central Oregon coasts, the largest catches occurring during spring and summer months in shallow waters. This population seems to prefer the waters outside the Columbia River plume, instead using more of the transition and oceanic zones. Spiny dogfish consumed a variety of prey, including both pelagic and benthic taxa, and showed a shift in their diet with increasing size. While the surveys used in this study did not specifically target spiny dogfish, which could create difficulties in assessing population abundance, they were probably indicative of the range of habitats occupied by this species.

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