

AN ABSTRACT OF THE THESIS OF

Jaclyn M. Richards for the degree of Master of Science in Fisheries Science presented on May 24, 2004.

Title: Distribution and Life History of the Spiny Dogfish (*Squalus acanthias*) off the Oregon and Washington Coasts.

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Ian A. Fleming

This study examines the spatial and temporal distribution and life history of the "offshore" component of the Northeastern Pacific spiny dogfish (*Squalus acanthias*) population. Distribution was examined in relation to latitude, depth, the Columbia River plume and large-scale climate changes. Fishery and survey data indicate that the Northeastern Pacific spiny dogfish population has a broad range along the Washington and Oregon coasts, with the highest abundance occurring off the northern Washington and central Oregon coasts. Catches, however, were patchy throughout the 37-year period of available survey data. In terms of depth, the greatest abundances of spiny dogfish were captured in shallow waters (55 – 184 m). An examination of the influence of the Columbia River plume using a generalized additive model (GAM) indicated that the fish were influenced significantly by the salinity, chlorophyll and surface temperature patterns associated with the plume, preferring the oceanic zone to the plume zone. In contrast, there was no indication that the catch-per-unit-effort of spiny dogfish was influenced by the Pacific Decadal Oscillation (PDO) or the El-Niño (ENSO) over 24-year period of the National Marine Fisheries (NMFS) triennial shelf groundfish survey

(1977 – 2001). The multi-cohort age structure of the population, due to the spiny dogfish's late age at maturity and long lifespan, as well as the low fecundity make it difficult to detect the loss of a single cohort or two when examining abundance trends. Moreover, effects on abundance may be time-lagged, especially if, as is likely, the youngest cohort(s) is the most vulnerable life stage. Their absence would not become evident until they were large enough to have been captured by the survey gear. Sensitive abundance data and/or age-structured data would be needed to identify a pattern.

I quantified the age, maturation and fecundity of the spiny dogfish and use these data to develop an age-structured matrix model to examine the sensitivity of the population's growth rate to changes in mortality (i.e. fishing). Female spiny dogfish in this population have an average age at 50% maturity of 28 years and males 20 years. Average length at 50% maturity was 85.0 cm for females and 71.5 cm for males. Female fecundity was extremely low, averaging eight pups per clutch biennially and ranging from four to 14. The number of pups increased with length, but not age. Using these data, a deterministic, female-based model was developed. Asymptotic population growth rate (λ) was determined to be very low, 1.01, and comparable to population growth rates calculated for "coastal" populations. When fishing mortality was incorporated into the model, the fishery was only sustainable when exploitation was low and strict size limits enforced. When fecundity was doubled, the population growth rate increased from 1% to 3% per year. This 33% increase in population growth was equivalent to the effect of a decrease

in the age at first maturity of three years. Given that responses to changes in population demographics through shifts in fecundity or spawning frequency are likely constrained, responses would then seem likely to involve changes in age at maturity. These life history traits translate into a low potential population growth and as a consequence high susceptibility to overfishing.

My findings indicate that the Northeastern Pacific spiny dogfish are relatively slow growing, late to mature, and have low fecundity and a patchy distribution, with large catches occurring off the northern Washington and central Oregon coasts in shallow waters (55 – 184 m). These life history traits and distributional patterns are useful in the development of population models to predict responses to environmental fluctuations or increased mortality and thus the management of the population. It is evident from my findings that periodic monitoring is necessary to track possible catch declines off the northern Washington and central Oregon coasts and prevent collapse of the population should it be targeted by a fishery and overfishing occur.

**Distribution and Life History of the Spiny Dogfish (*Squalus acanthias*) off the
Oregon and Washington Coasts.**

**by
Jaclyn M. Richards**

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APPROVED
Redacted for Privacy

Major Professor, representing Fisheries Science

Redacted for Privacy

Head of the Department of Fisheries and Wildlife

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Dean of the Graduate School

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**Distribution and Life History of the Spiny Dogfish (*Squalus acanthias*) off the
Oregon and Washington Coasts**

Chapter 1

INTRODUCTION

Jaclyn M. Richards

**Oregon State University
Department of Fisheries & Wildlife
Nash 104
Corvallis, Oregon 97331-3803**

“Life history” refers to broad features of a life cycle - organism growth, maturation, reproduction, number of offspring produced, offspring size and longevity (Beverton, 1992; Stearns, 1992). A species' life history pattern directly influences its reproduction and survival and is bound together by numerous trade-offs among life history traits. As such, the evolution of life history patterns and their plasticities determine population dynamics and are thus critical to our understanding of the functioning of species.

Three basic assumptions underlie life history theory: 1) there is some measure of fitness that is maximized, 2) constraints and trade-offs limit the set of possible life histories and 3) there is sufficient genetic variation to permit the attainment of the optimal combination (Roff, 1992). An organism's measure of fitness can be either global or local. Global measures involve the interaction of all life history components, while local measures assume that maximization of a fitness component will also maximize the overall fitness of the organism (Roff, 1992). An example of a global measure is Fisher's Malthusian parameter r (the instantaneous rate of increase). This parameter is used because it can be associated with genotypes that favor particular life histories with the highest value of r (Roff, 1992). Examples of local measures of fitness include growth rate and net rate of energy intake, which assume that maximizing these rates do not detrimentally affect the components of fitness. Optimality modeling is a tool used for measuring both global and local of an

organism's fitness. It assumes that evolution is maximizing the fitness of the organism (Roff, 1992).

The parameter r can be associated with lambda (λ), which is the population growth rate from matrix models. λ is the finite rate of population increase or the rate of population growth in one year (or one time period) and thus is a discrete measure, whereas r is the instantaneous rate of population increases. $\lambda = N_1/N_0$ or the ratio of population sizes from one year versus the next (or one time period versus the next). The mathematical relation between these two population growth variables is $\ln(\lambda) = r$, the intrinsic rate of increase representing the fraction by which a population would grow during a very short period of time and is calculated from a life table (Caswell, 2001; Heppell *et al.*, 1999). In the analysis of deterministic life cycle models for management and conservation, λ is used as an index of population health or status (Heppell *et al.*, 2000a).

An organism can maximize its fitness by optimizing trade-offs among traits. These trade-offs occur because organisms have finite amounts of energy and resources. An organism has to optimize allocation of a lifetime energy budget into select traits. When looking at the trade-offs among different traits, there is an examination of the fitness gained by an organism from investing in one trait over another. When limited resources are allocated to improve one aspect of an organism's fitness there will be a cost incurred elsewhere by that organism (Jennings *et al.*, 2001).

An example of trait trade-offs is the choice by a mother to have many small young or few larger young (e.g. Rickman *et al.*, 2000). The survival rate is low for small young, but due to their abundance some may survive. For marine organisms, the survival of small young is usually dependent on oceanic conditions, which can be highly stochastic. Large young, on the other hand, may have a higher survival rate, but they come at a cost to the mother in terms of the number that can be produced. Another example of a trade-off is whether an organism uses its energy resources to mature early and have fewer or smaller offspring, or utilizes its energy resources to grow large and mature later, producing either more and/or larger offspring. Most organisms have an optimal size and age at maturity (Roff, 1992). Short-lived species must reach maturity at a young age to ensure reproductive success (Beverton, 1963). Whereas, a long-lived species can utilize energy resources early in life to attain a larger size, increasing fecundity before maturing. Both of these examples are displayed among the marine organisms.

The diversity of life history strategies within fish communities is extraordinary. Life history patterns have been categorized as "slow" and "fast" for a wide variety of taxa, including fish (Heppell *et al.*, 1999; Cortes, 2002). A "slow" life history pattern often involves long life, slow development, delayed maturity, high parental investment and low reproductive rates. An organism with a "fast" life history pattern has a short life span, develops quickly, early to mature, very little parental investment and high reproductive rates. This

method should be used with the knowledge that not all fish are either "slow" or "fast", but somewhere in between. Most teleosts tend towards "fast" life history patterns, relying on specific events or ocean conditions and high fecundity to yield high recruitment, while chondrichthyans tend towards "slow" life history patterns, relying on long gestation periods (in the live-bearing forms), high survival at all stages, and longevity after maturity (Frisk *et al.*, 2001). Chondrichthyans are a long-lived marine group exhibiting "slow" life history patterns.

Chondrichthyans display traits such as slow growth, late maturity, iteroparity and low fecundity (Musick, 1999). These traits translate into low rates of reproduction and low potential rates of population increase, making it difficult for sharks to maintain or increase their population. Despite these apparently restrictive life history traits, sharks have remained successful components of the marine ecosystem, as evidenced by their ecological diversity and abundance (Compagno, 1990). There are over 750 species of sharks throughout the world's oceans, both large and small. As a rule, larger sharks display slower growth rates and later age at maturity than smaller sharks. An exception to this rule is the spiny dogfish, *Squalus acanthias*, which are found throughout the northern Atlantic and Pacific oceans.

Spiny Dogfish Life History:

The Northeastern Pacific spiny dogfish (*Squalus acanthias*) are long-lived, small sharks, with late age at maturity and low fecundity, and are

distributed from Baja California to Alaska (Ketchen, 1972; Nakano and Nagasawa, 1996, McFarlane and King, 2003). Most of the studies conducted on this species have examined the Straits of Georgia, Hecate Strait or the Puget Sound subpopulations (Bonham *et al.*, 1949; Ketchen, 1972, 1975; Jones and Geen, 1977 a-c; Saunders and McFarlane, 1993). The spiny dogfish population inhabiting the above mentioned waters has been designated as the "coastal" population, with the "offshore" population considered to inhabit the more open oceanic waters (Saunders *et al.*, 1984; Ketchen, 1986; Holts, 1988; Bonfil, 1999; McFarlane and King, 2003).

The life history pattern of the "offshore" population should be similar to that of the "coastal" population (i.e., a late age at maturity, low fecundity, produce large, well-formed young and are long lived). The most current reported age at maturity is 35 years for females, which average eight pups every two years and have been reported to live up to 100 years (Saunders and McFarlane, 1993; Cortes, 2000). This life history pattern of the "coastal" population will be contrasted with that of the "offshore" population to determine the extent of differences, if any.

The purpose of this study is to characterize the distribution, habitat and life history pattern of the spiny dogfish population off the Washington and Oregon coasts. This study is the first in many years that is directed specifically at the spiny dogfish population inhabiting the shores off the Washington and Oregon coasts, i.e. since Bonham *et al.* (1949). Bonham *et*

al. (1949), however, used selective ageing methods, which included only the relatively young portion of the population, and thus may not have been representative of the population as a whole. Moreover, specimens from the “offshore” and “coastal” populations were not examined independently, potentially confounding life history and distributional patterns of the two populations. The specific purposes of this study were to: 1) describe the spatial and temporal distribution of spiny dogfish off the Oregon and Washington coasts; 2) quantify age composition and age at maturity; and 3) develop an age structured model to examine the effects of age at maturity, fishing mortality and fecundity on population growth. These characteristics are important in understanding the population dynamics of the spiny dogfish and their sustainability in the face of environmental and human impacts.

Chapter 2

Spatial and Temporal Distribution of Spiny Dogfish
(*Squalus acanthias*) off the Washington and Oregon Coasts.

Jaclyn M. Richards

Oregon State University
Department of Fisheries & Wildlife
Nash 104
Corvallis, Oregon 97331-3803

Abstract:

Our understanding of the spiny dogfish (*Squalus acanthias*) of the Northeastern Pacific has been based almost exclusively on research of nearshore populations from enclosed regions such as the Straits of Georgia, Hecate Strait or the Puget Sound. Much less attention has been given to more offshore populations along the open coast of the Pacific Northwest of North America. Our purpose here was to characterize the spatial and temporal distribution of spiny dogfish off the Washington and Oregon coasts using fishery surveys dating back to 1965. These surveys included (1) the Soviet Union bottom trawl survey, 1965 – 1978, (2) the National Marine Fisheries Service (NMFS) triennial shelf groundfish survey, 1977 – 2002, and (3) the National Marine Fisheries Service (NMFS)/Oregon State University (OSU) juvenile salmon survey, 1998 – 2002. The Northeastern Pacific spiny dogfish were found to occupy a broad distributional range along the Washington and Oregon coasts, with the highest abundances occurring off the northern Washington and central Oregon coasts. Catches, however, were patchy throughout the 37-year period. In terms of depth, the greatest abundances of spiny dogfish were captured in shallow waters (55 – 184 m). An examination of the influence of the Columbia River plume using a generalized additive model (GAM) indicated that the fish were influenced significantly by the salinity, chlorophyll and surface temperature patterns associated with the plume, preferring the oceanic zone to the plume zone. In

contrast, there was no indication that the catch-per-unit-effort of spiny dogfish was influenced by the Pacific Decadal Oscillation (PDO) or the El-Niño Southern Oscillation (ENSO) over 24 – year period of the National Marine Fisheries (NMFS) triennial shelf groundfish survey (1977 – 2001). The multi-cohort age structure of the population, due to the spiny dogfish's late age at maturity and long lifespan, as well as the low fecundity make it difficult to detect the loss of a single cohort or two when examining abundance trends. Moreover, effects on abundance may be time-lagged, especially if, as is likely, the youngest cohort(s) is the most vulnerable life stage. Their absence would not become evident until they were large enough to have been captured by the survey gear. Sensitive abundance data and/or age-structured data would be needed to identify a pattern.

Introduction:

Spiny dogfish, *Squalus acanthias*, is an abundant elasmobranch species distributed throughout the world's oceans. In the Pacific Ocean, spiny dogfish inhabit temperate coastal waters ranging from Baja California to Alaska in the eastern Pacific, and from the Kamchatka Peninsula to Japan in the western Pacific (Kaganovskaia, 1960; Alverson and Stansby, 1963; Ketchen, 1972; Nakano and Nagasawa, 1996; McFarlane and King, 2003). This distribution appears to reflect the temperature preferences of the spiny dogfish (Shepherd *et al.*, 2001). The greatest concentrations occur in waters with surface temperatures ranging between 7 and 15°C (Brodeur and Pearcy,

1986; Holts, 1988; Shepherd *et al.*, 2001). In the eastern Pacific, this surface temperature range is most consistently found in waters located from northern Washington to southeast Alaska, where spiny dogfish are most abundant (McFarlane and King, 2003). Although this habitat appears to be the preferred by spiny dogfish, these elasmobranches migrate south on a seasonal basis and can be found as far south as California.

Spiny dogfish in the northeastern Pacific Ocean have been classified into two populations: a "coastal" population, inhabiting the protected waters of Hecate Strait, Strait of Georgia and Puget Sound, and an "offshore" population inhabiting the more open ocean waters (Saunders *et al.*, 1984; Ketchen, 1986; Holts, 1988; Bonfil, 1999; McFarlane and King, 2003). The "coastal" population has short seasonal migrations and usually stays within inland waterways.

Tagging studies have indicated that the "offshore" spiny dogfish population is highly migratory (Alverson and Stansby, 1963; McFarlane and King, 2003). Migration is seasonal, moving north in spring and summer, and south in fall and winter (Bonham *et al.*, 1949; Holland, 1957; Ketchen, 1986; Bonfil, 1999; McFarlane and King, 2003). Some of the migrations are trans-oceanic, where the spiny dogfish are believed to migrate along the Aleutian Island chain to the western Pacific. One fish, tagged in Willapa Bay, WA, was recovered off the northeast corner of Honshu Island, Japan (McFarlane and King, 2003). However, spiny dogfish are frequently caught in high seas gill

nets (Ketchen, 1986; Nakano and Nagasawa, 1996) far from the coast and many may travel straight across the Pacific.

Spiny dogfish appear to shoal according to size and sex (Ford, 1921; Hickling, 1930; McMillan and Morse, 1999). This behavior results in the segregation of immature spiny dogfish from mature individuals, which has been suggested to decrease intercohort predation (Ford, 1921; Hickling, 1930; McMillan and Morse, 1999). While both sexes shoal together as juveniles, they segregate into single sex aggregations upon reaching maturity, which has been suggested to decrease competition between the sexes (Hickling, 1930). Mature females are usually found in deeper bottom waters, whereas mature males inhabit shallower bottom waters (Hickling, 1930; McMillan and Morse, 1999). The only time during the year when mature males and females intermingle is the breeding season. The females migrate to shallower waters (15 – 20 m) to bear their young in late summer, early fall (Hickling, 1930). After pupping, females breed with males that migrate to the breeding grounds in the late fall. Migrations are cued by environmental changes in ocean conditions, such as temperature changes and daylight fluctuations (McMillan and Morse, 1999; McFarlane and King, 2003).

The oceanic environment not only cues the breeding season, but also may influence the survival of young spiny dogfish. The young appear to inhabit productive waters that are within their surface temperature preference range. Environmental changes in ocean conditions strongly affect fishery

resources, influencing their distribution and recruitment, and as such are important factors in fisheries management models (Sharp *et al.*, 1983; Bigelow *et al.*, 1999). Examining the changes in distribution of spiny dogfish catches over time gives us a picture of how this species might be affected by fishing effort.

Temperature is an environmental factor that can play an important role in spiny dogfish distribution, through annual or even decadal fluctuations in oceanic temperatures (Shepherd *et al.*, 2001). Two environmental processes influencing temperatures in the North Pacific Ocean are the Pacific Decadal Oscillation (PDO) and the El Niño-Southern Oscillation (ENSO). The PDO is related to basin-scale changes in atmospheric pressure, particularly the intensification and position of the Aleutian Low Pressure System (Mantua *et al.*, 1997). There is a 20 - 30 year cycle of alternating cool and warm ocean regimes. The northeastern Pacific Ocean was anomalously cool in 1900-1924, warm in 1925-1946, cool in 1947-1976, and warm from 1977-1999 (Mantua *et al.*, 1997). Recent evidence suggests that the west coast of North America has entered a cool phase since 1999, with corresponding changes in biological productivity (Peterson and Schwing, 2003). ENSO produces a series of alternating warm (El Niño) and cold (La Nina) episodes in the equatorial Pacific with durations of two to seven years (Huyer *et al.*, 2002). When these equatorial events are particularly intense and persistent, they may

affect temperature and other aspects of the ocean environment as far north as the Bering Sea.

In addition to depth and surface temperature, another environmental factor analyzed was the plume of fresh water flowing out from the Columbia River. This plume may be important in affecting the distribution of spiny dogfish. The Columbia River plume is a tongue of low salinity surface water, which lies offshore and to the south of the river in the summer (Landry *et al.*, 1989). This freshwater tongue contains a relatively high amount of nutrients, which can cause 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). This increase in predators and prey items can usually be found around the transitional zone of the Columbia River plume (Kaartved *et al.*, 1996). The plume region can be divided into three distinct zones: the plume zone, the transitional zone (frontal zone) and the oceanic zone (Hickey and Landry, 1989). The plume zone is where low salinity fresh water, flowing out from the Columbia River, lies on top of the high salinity oceanic water and, for convenience, has been specified as those waters contiguous to the Columbia River mouth having salinities of less than 32.5‰ (Stefansson and Richards, 1963). 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.

The objectives of this study were to analyze the distribution of Northeastern Pacific spiny dogfish along the Oregon and Washington coasts based upon three different sampling programs, which collected this species as by-catch during regular sampling. Specifically, we examined latitudinal patterns and the association of spiny dogfish catches with surface temperature and bottom depth. The effect of the Columbia River plume, as measured by its effects on sea surface temperature, chlorophyll and salinity, was also examined. Finally, we tested for effects of PDO and ENSO events on spiny dogfish abundance, as estimated by catch, off the Washington and Oregon coasts over a 23-year survey period.

Methods:

Distributional patterns were analyzed using data from three different surveys: (1) the Soviet Union bottom trawl survey, (2) the National Marine Fisheries Service (NMFS) triennial shelf groundfish survey and (3) the National Marine Fisheries Service (NMFS)/Oregon State University (OSU) juvenile salmon survey.

Soviet Union Survey:

The Soviet Union bottom trawl survey was conducted from 1965 to 1978, prior to initiation of the U.S. Exclusive Economic Zone (EEZ). This survey was conducted three times a year using a flare trawl with a mouth

opening of 27 x 8 m and 20-mm mesh in the codend (Ermakov and Stepanenko, 1996). Hauls occurring between 48°20' - 42°00' N in the months from July to September were extracted from the overall database to allow comparison with the NMFS triennial shelf groundfish survey described below. Catch-per-unit-effort (CPUE) was then calculated to standardize the hauls. The nominal CPUE was used as a fishery performance index to investigate trends in resource abundance (Bigelow *et al.*, 1999).

CPUE was calculated using the following equation: $CPUE = \text{catch weight (kg)} / (\text{distance fished (km)} * (\text{net mouth width (m)} / 1000))$. Each haul was separated by month, year and International North Pacific Fisheries Commission (INPFC) statistical area (Figure 1). These were then averaged together by depth, shallow = 55 – 183 m, medium = 184 – 366 m and deep = 367 – 500 m, according to INPFC specifications (Figure 1).

The CPUEs were plotted by year and surface temperature for the Washington and Oregon coasts. Charts comparing CPUE, year and depth were constructed for the three INPFC designated regions, U.S. Vancouver portion (47°50' - 48°20'N), Columbia (47°40' - 43°00'N) and Eureka (42°00' - 42°99'N).

NMFS Triennial Shelf Groundfish Survey:

Over the last 23 years, National Marine Fisheries Service (NMFS) has conducted a triennial continental shelf groundfish survey to evaluate the distribution, abundance and biology of groundfish species (Shaw *et al.*, 2000).

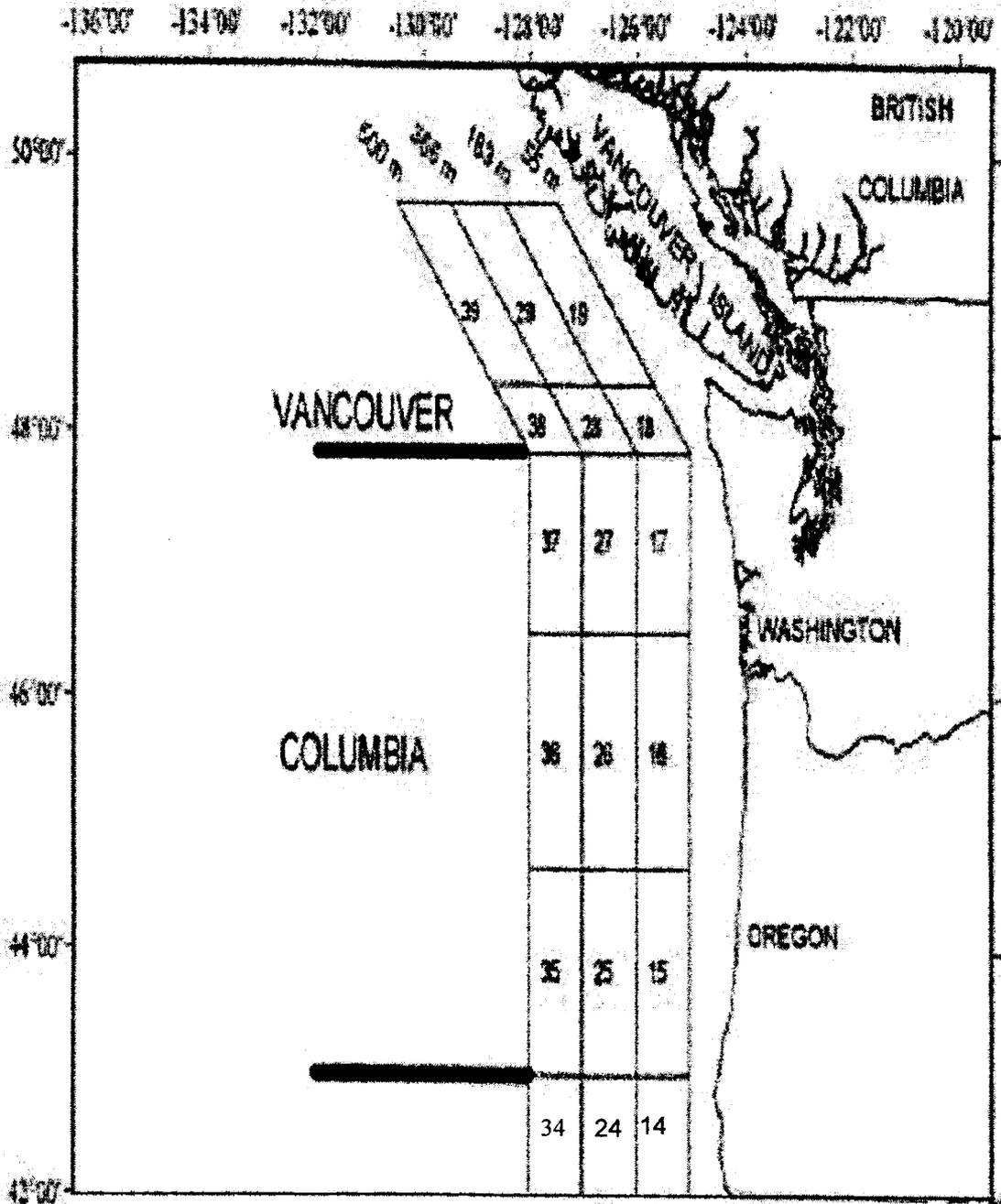


Figure 1: International North Pacific Fisheries Commission (INPFC) statistical areas for the west coast triennial shelf groundfish survey.

This study originated in 1977, collecting biological data on all groundfish, including spiny dogfish. Each triennial survey encompassed the area from the coast of Vancouver Island, BC, down to southern California and began ca. 1 June and ended ca. 9 August. A high-opening Poly Nor'Eastern bottom trawl with bobbin roller gear (headrope 27.2 m, foot rope 37.4 m) was deployed and towed for 30 minutes. The depths surveyed ranged from 55 to 500 m (Shaw *et al.*, 2000). At each sampling site, a bucket thermometer was used to measure sea surface temperature (Shaw *et al.*, 2000).

Data on all hauls containing spiny dogfish were extracted from the Resource Assessment and Conservation Engineering (RACE) database. Hauls occurring between 47°50' - 48°20' N and 42°00' - 43°00' N were extracted to create an Oregon and Washington database. CPUE was calculated as described above for the Soviet Union survey. Then a length-frequency chart of male and female spiny dogfish was developed from the available data.

Pacific Decadal Oscillation (PDO) monthly anomaly data were obtained from <http://www.cdc.noaa.gov/coads/> and the monthly anomaly data for El Niño -Southern Oscillation (ENSO) events were extracted from <http://www.cpc.ncep.noaa.gov/data/indices/index.html>. These environmental data corresponded to the survey years when spiny dogfish were collected and compared against the calculated averaged CPUEs using a generalized additive model (GAM).

Since generalized additive models (GAMs, Hastie and Tibshirani, 1990) do not assume functional relationships between the predictor and response variables, they allow the relationship between environmental variables and catch rates to be explored (Bigelow *et al.*, 1999). 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).

Loess smoothers replace the least-squares fits in the regression (Bigelow *et al.*, 1999). Loess smoothing calculates the local average such that there is no long run mean and the span designates the total number of observations to use in the analysis.

GAMs have been used in fisheries research to detect trends in abundance of groundfish in the Bering Sea and of walleye pollock in relation to depth and temperature (Swartzman *et al.*, 1992; Swartzman *et al.*, 1995) and to detect the upper thermal limits of high seas fish distribution (Welch *et al.*, 1995). A GAM was used for this analysis because the functional relationships between fishing performance and environmental conditions are likely nonlinear (Bigelow *et al.*, 1999). Model comparison was performed using the Akaike Information Criterion (AIC, Akaike, 1974) and a stepwise method with the S-plus statistical package (Stat Sci Inc., 1700 Westlake Ave. N., Suite 500, Seattle, WA 98109, USA). A poisson distribution was assumed with a log link function.

NMFS/OSU Juvenile Salmon and Predator Surveys:

The National Marine Fisheries Service (NMFS)/Oregon State University (OSU) juvenile salmon study has been conducted since 1998, with three cruises a year, one each in May, June and September (no May cruise in 1998). Transects were located from La Push, WA (47°90' N) to Newport, OR (44°70' N) and were perpendicular to shore (Figure 2). At each station, a CTD (conductivity, temperature and depth meter) cast was made and then a Nordic 264 otter trawl (width 30 m, depth 15-18 m) was deployed and hauled for 30 min parallel to the shore at each station. Most of the sampling was conducted during daylight hours.

In addition, a series of NMFS/OSU juvenile salmon predator cruises have been conducted since 1998, with sampling occurring every two weeks from April to the end of July and done entirely at night (Emmett *et al.*, 2001). There were two transects, Willapa Bay (46°66') and Columbia River (46°16'), with six stations each, oriented perpendicular to shore. At each station, a CTD cast was made and then a Nordic 264 otter trawl was towed for 15 minutes parallel to shore.

The processing procedure for spiny dogfish was the same for both BPA surveys. Spiny dogfish were measured for total length, sexed and maturity assessed. CPUE was calculated for each haul (as described earlier) and then the hauls were averaged together by year, month and site.

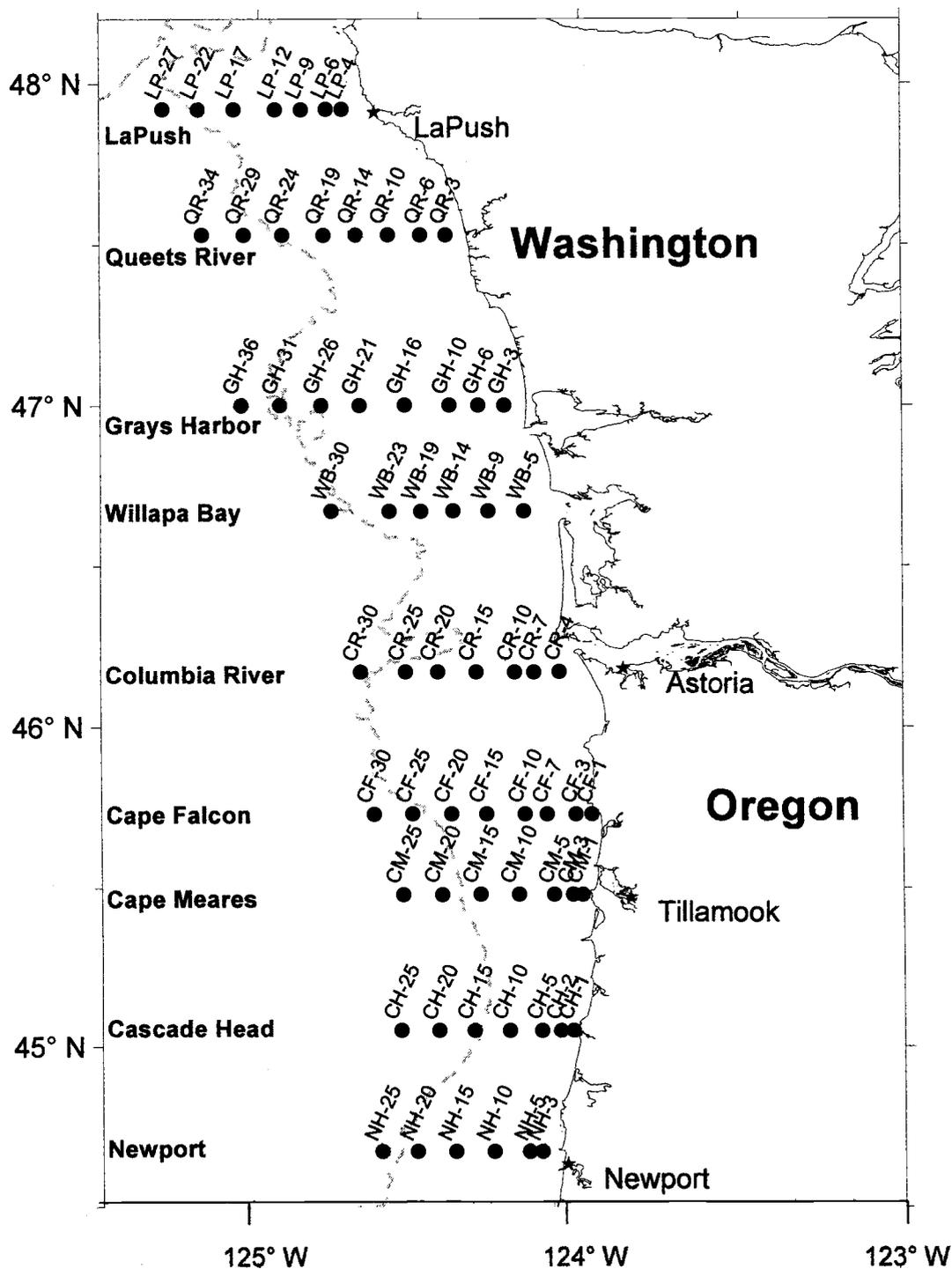


Figure 2: Sample sites for the NMFS/OSU juvenile salmon survey. The letter codes and the numbers signify the transect name and distance from shore in nautical miles.

CPUEs for the Soviet Union, NMFS triennial shelf groundfish and NMFS/OSU juvenile salmon surveys were plotted for the Oregon and Washington coasts.

GAMs were used to analyze the effect of salinity, chlorophyll and surface temperature patterns associated with the Columbia River plume on spiny dogfish distribution, with station depth and distance from shore incorporated as covariates. Model fitting procedures used are the same as mentioned for the PDO and ENSO analyses.

Length-frequency differences between males and females captured during the NMFS/OSU juvenile salmon and juvenile salmon predator surveys, as well as the NMFS triennial shelf groundfish survey were also analyzed.

Results:

All three surveys covered a broad latitudinal range of sites, with most of the large catches of spiny dogfish occurring off of the northern Washington and central Oregon coasts (Figures 3 – 12). Spiny dogfish catches declined by orders of magnitude from the Soviet Union survey (conducted from 1965 to 1978; Figures 3 – 7) to the NMFS triennial shelf groundfish survey (conducted from 1977 to 2002; Figures 8 - 10). The NMFS/OSU juvenile salmon survey displayed consistently large catches of spiny dogfish off of Willapa Bay and Grays Harbor (Figures 11 – 12). Spiny dogfish catches were patchy throughout this 37-year period (Figures 3 – 12).

When spatial distribution was examined in reference to average depth and INPFC areas for the Soviet Union and NMFS surveys, the largest catches

occurred in shallow waters (55 – 184 m) (Figures 13 and 14). There were, however, proportionately more mid-water (185 – 366 m) catches in the NMFS than the Soviet Union survey (Figures 13 and 14). The largest deep water catches (367 – 500 m) occurred in the Eureka region (Figures 13 and 14).

Analyzing the NMFS/OSU surveys with respect to the potential influence of the Columbia River plume on spiny dogfish distribution, the best fit model form was: $\ln(\text{CPUE}) \sim \ln(\text{Salinity}) + \ln(\text{Chlorophyll}) + \ln(\text{Surface Temperature})$, which suggested that all three variables significantly affected the abundance of spiny dogfish catches (all variables $p < 0.001$, d.f. = 48; Figure 15). All relationships between the predictor variables and the spiny dogfish CPUE were significantly non-linear (three χ^2 – tests: all $P < 0.001$; Figure 15). Chlorophyll and surface temperature were the most significant explanatory variables, providing the largest reduction in residual deviation. Both chlorophyll and surface temperature explained 37% of the cumulative variance and salinity explained 11% of the cumulative variance found in $\ln(\text{CPUE})$. The nominal CPUE was positively associated with both salinity and surface temperature, and somewhat negatively with chlorophyll. Neither station depth nor distance from shore showed significant relationships to spiny dogfish catches.

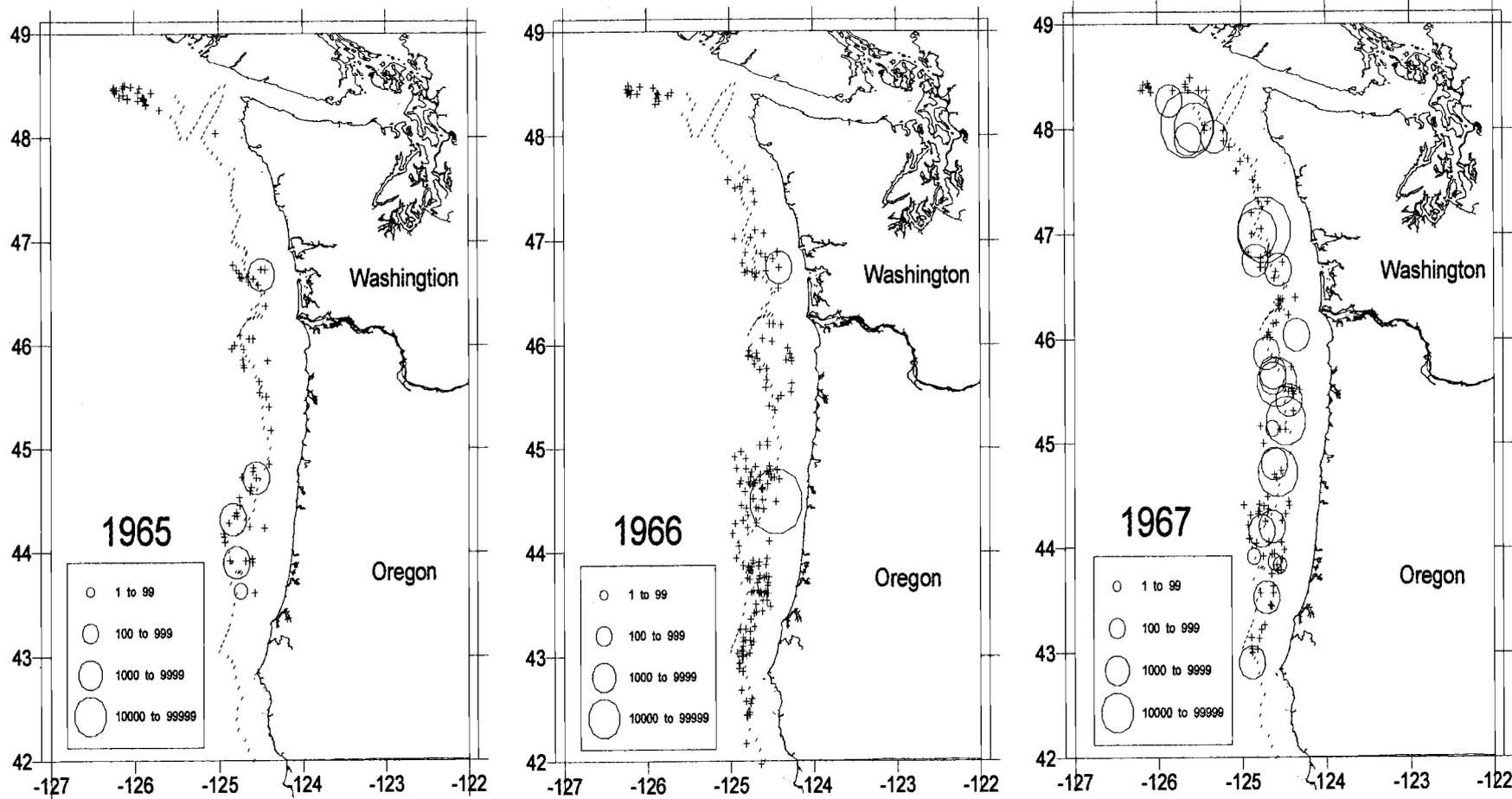


Figure 3: The sample sites and averaged CPUE for the Soviet Union bottom trawl survey from 1965 to 1967. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

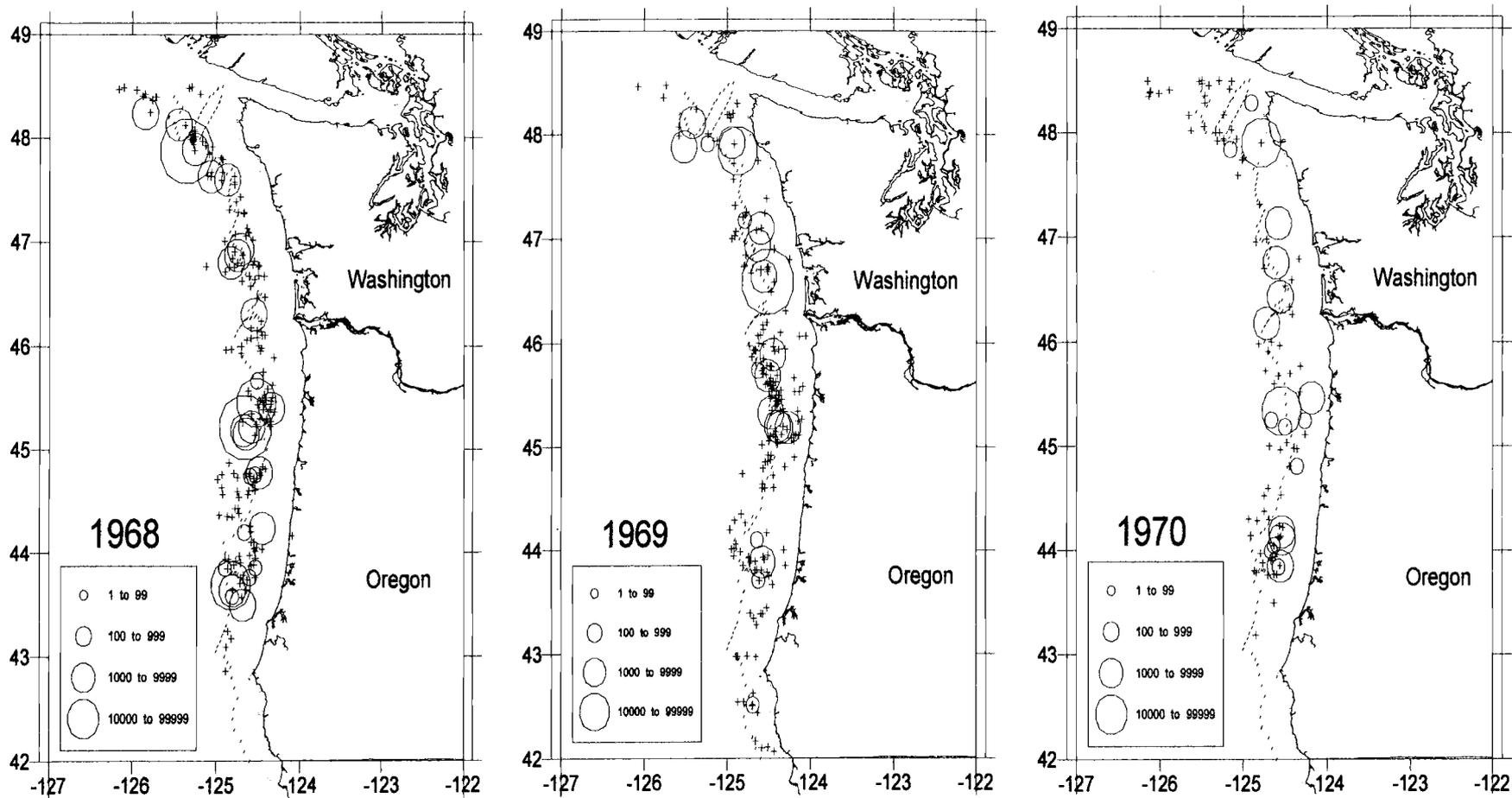


Figure 4: The sample sites and averaged CPUE for the Soviet Union bottom trawl survey from 1968 to 1970. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

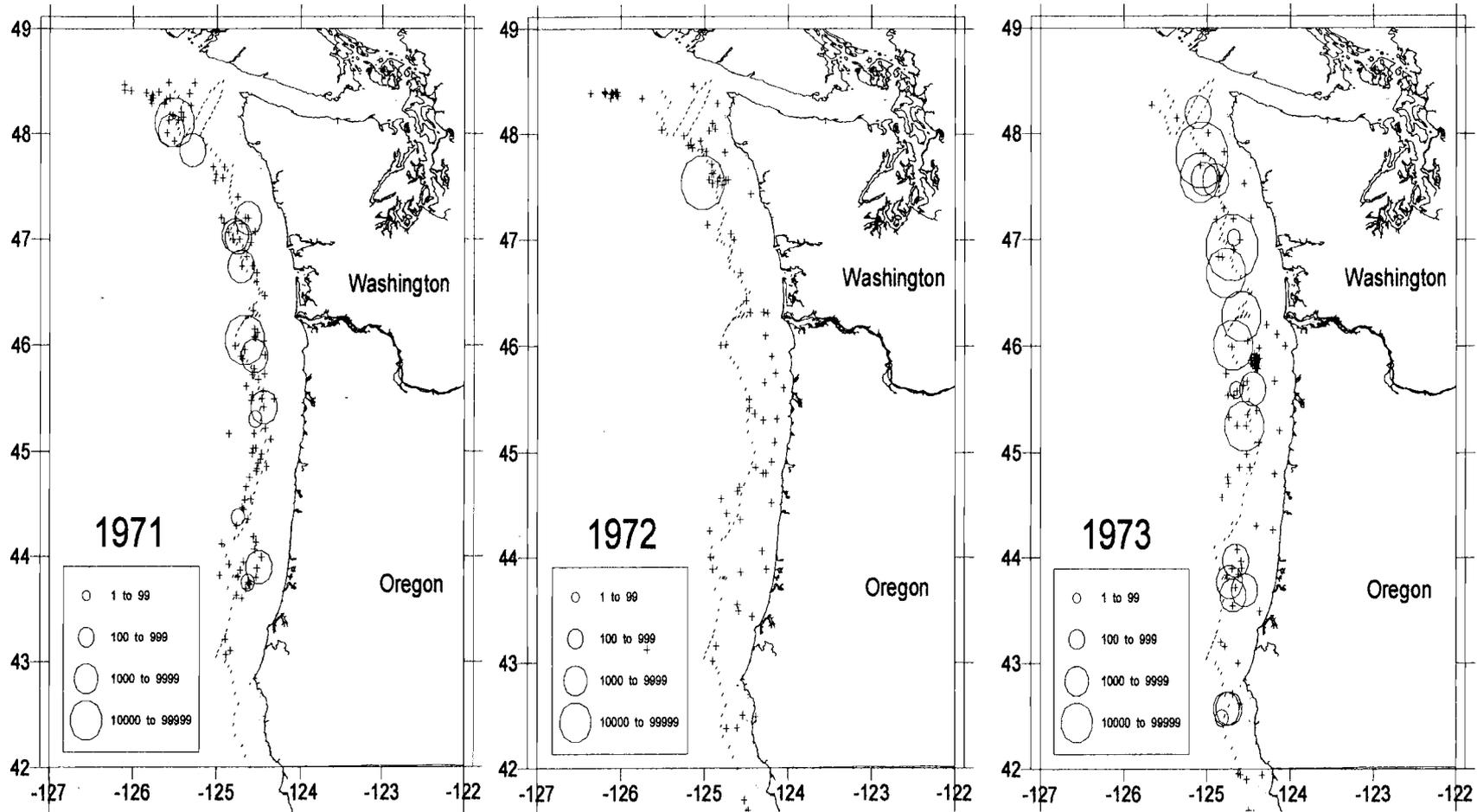


Figure 5: The sample sites and averaged CPUE for the Soviet Union bottom trawl survey from 1971 to 1973. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

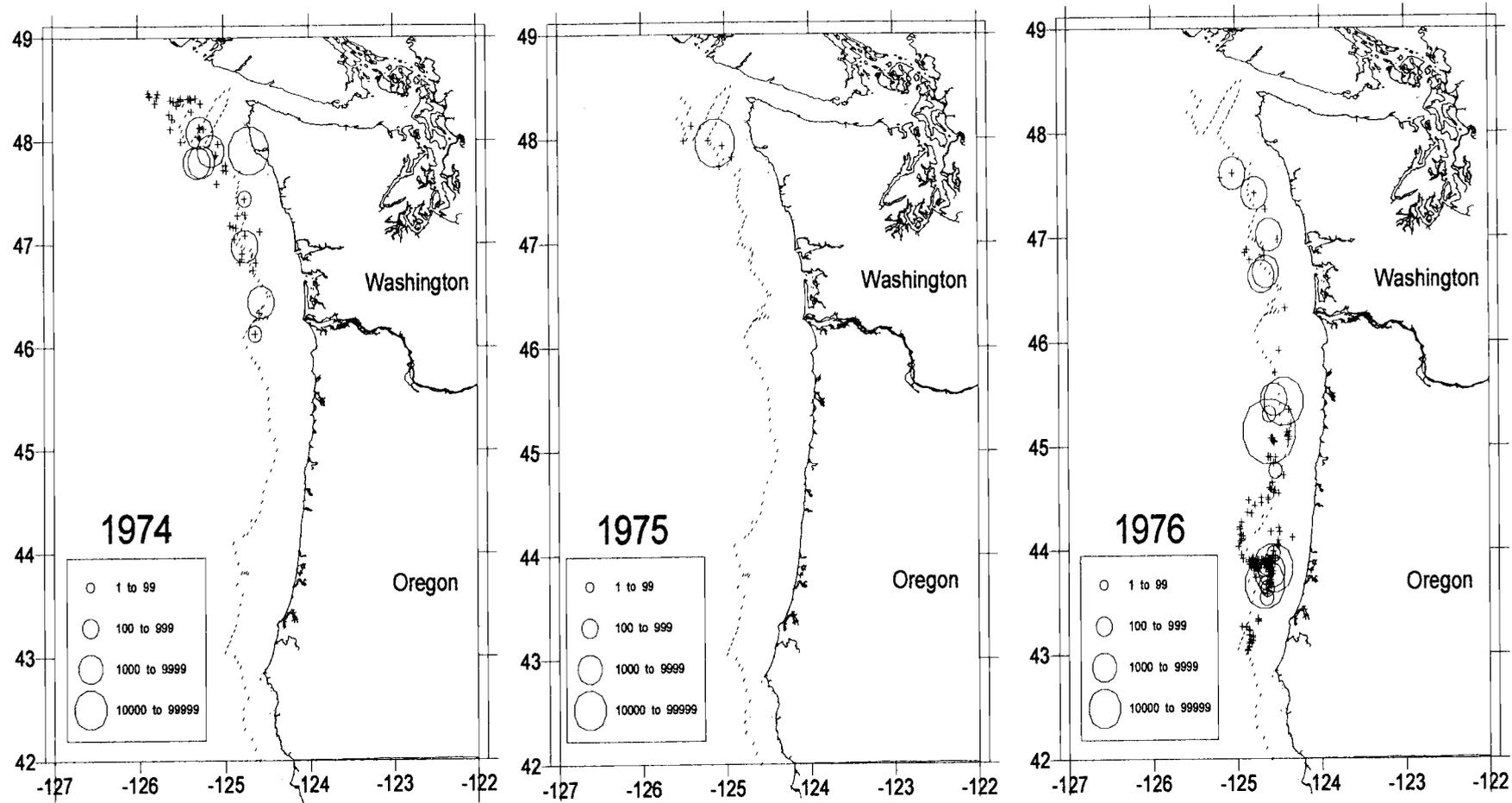


Figure 6: The sample sites and averaged CPUE for the Soviet Union bottom trawl survey from 1974 to 1976. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

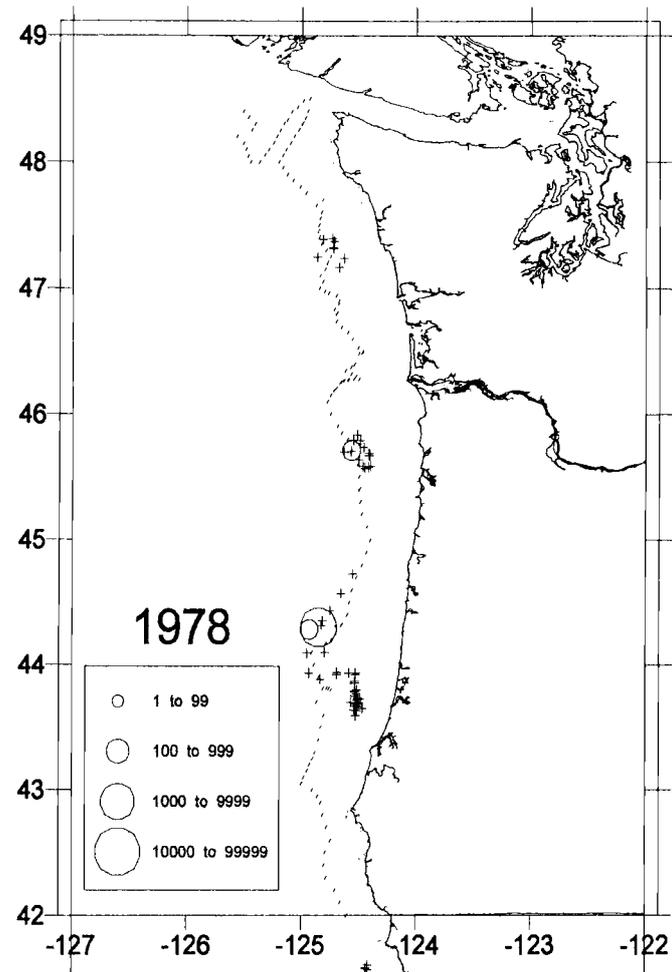
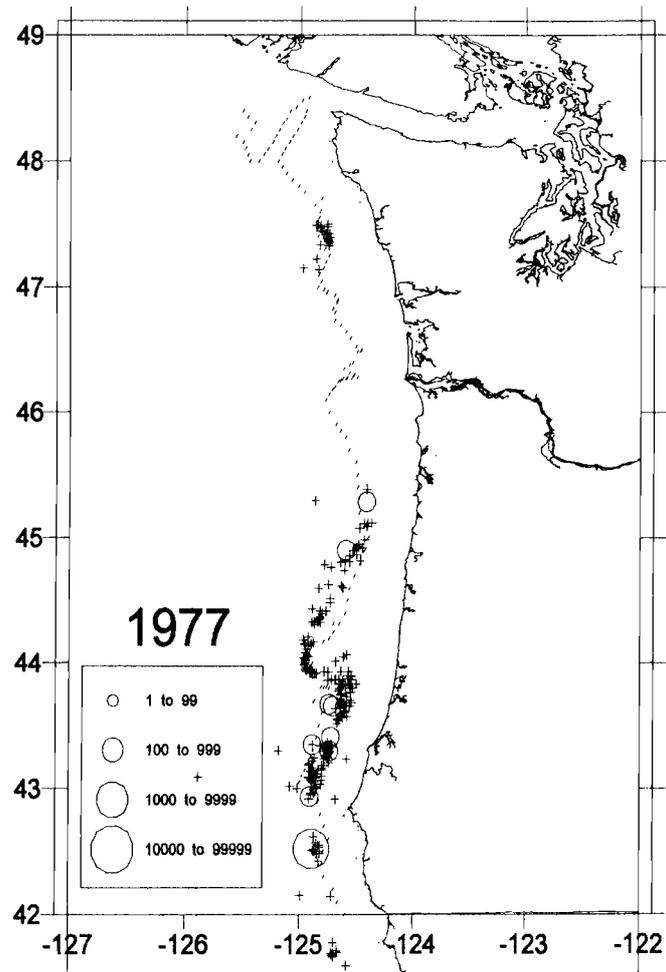


Figure 7: The sample sites and averaged CPUE for the Soviet Union bottom trawl survey from 1977 to 1978. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

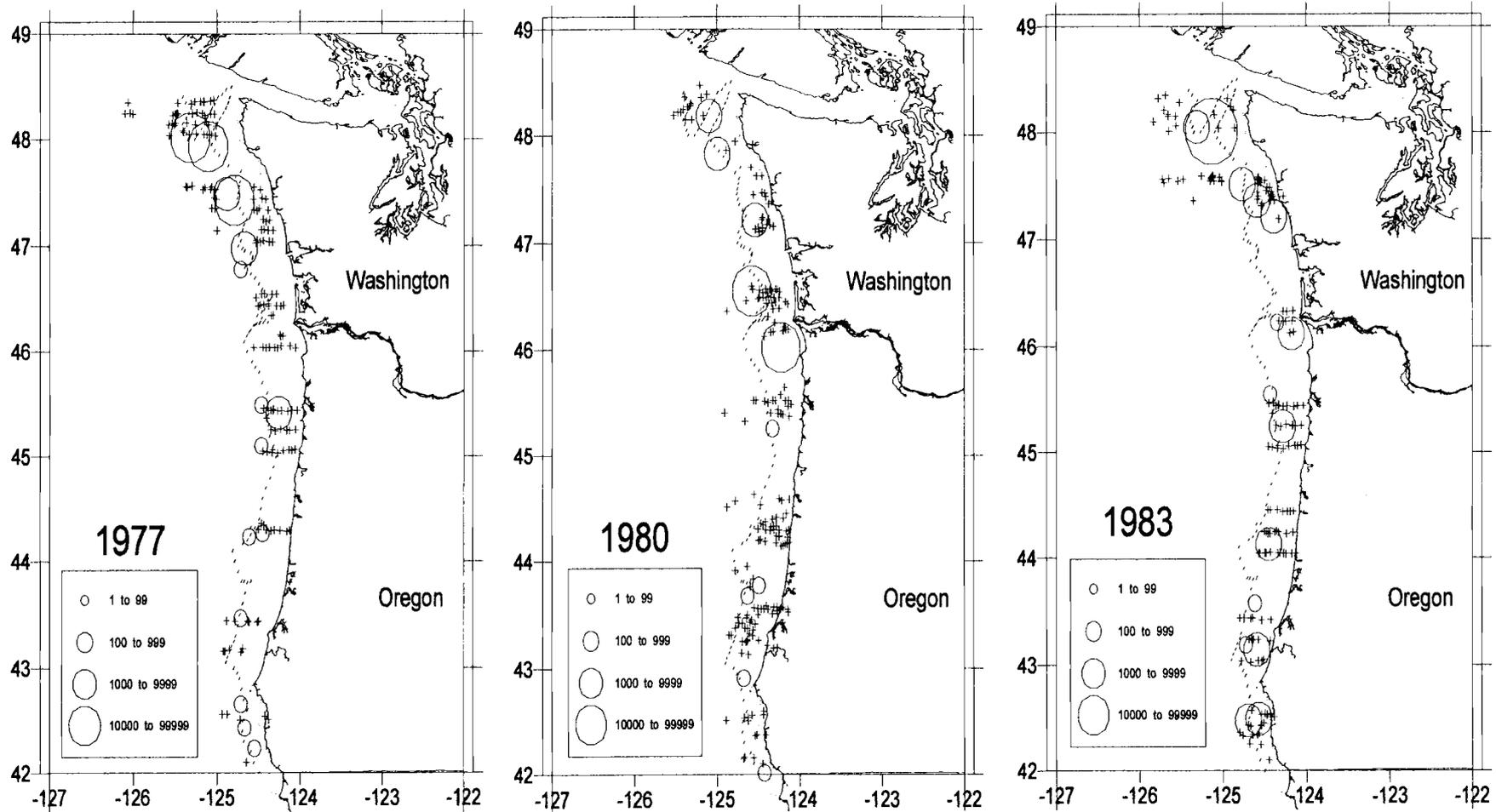


Figure 8: The sample sites and averaged CPUE for the National Marine Fisheries Service west coast triennial shelf groundfish survey from 1977 to 1983. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

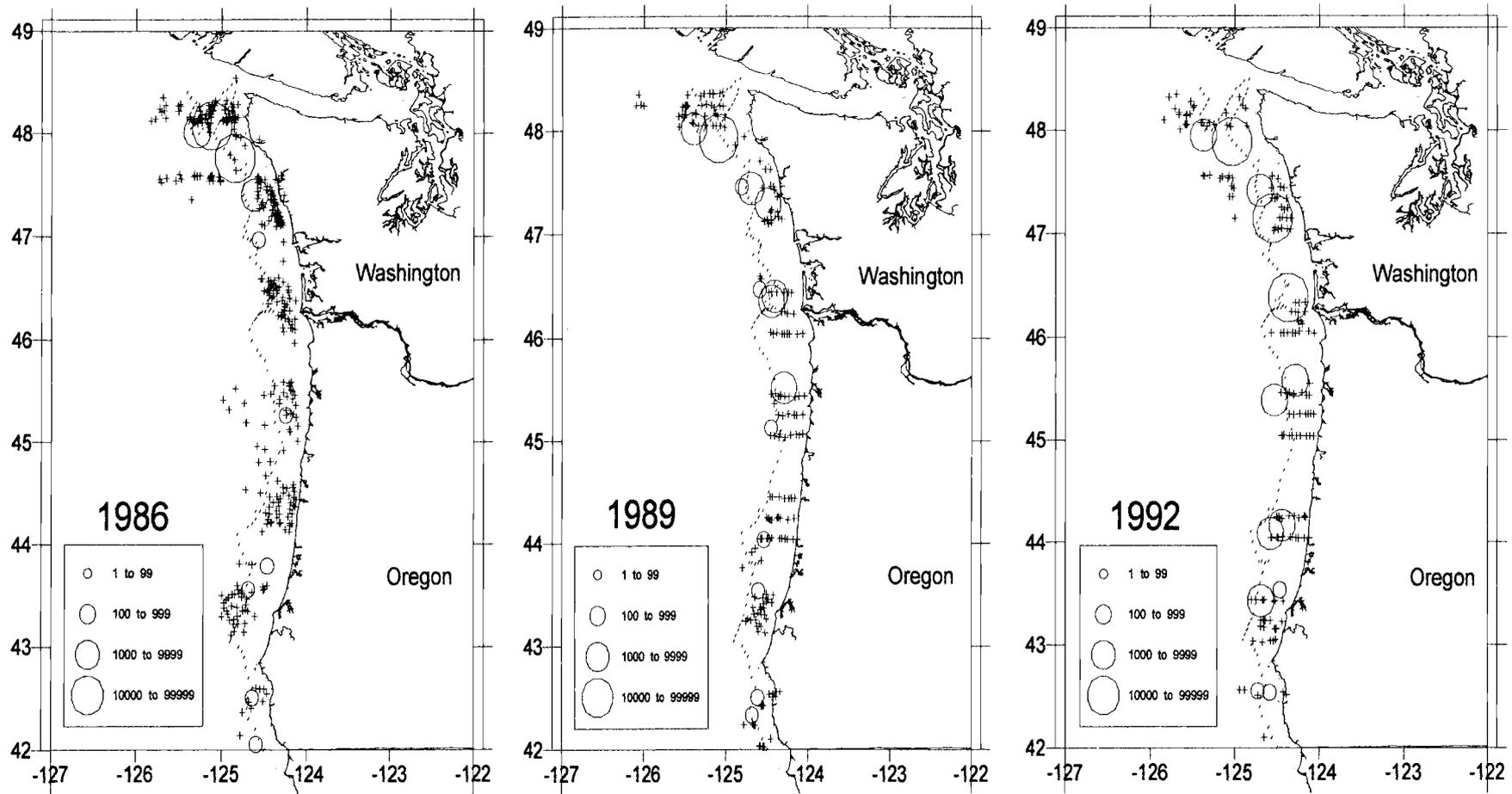


Figure 9: The sample sites and averaged CPUE for the National Marine Fisheries Service west coast triennial shelf groundfish survey from 1986 to 1992. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

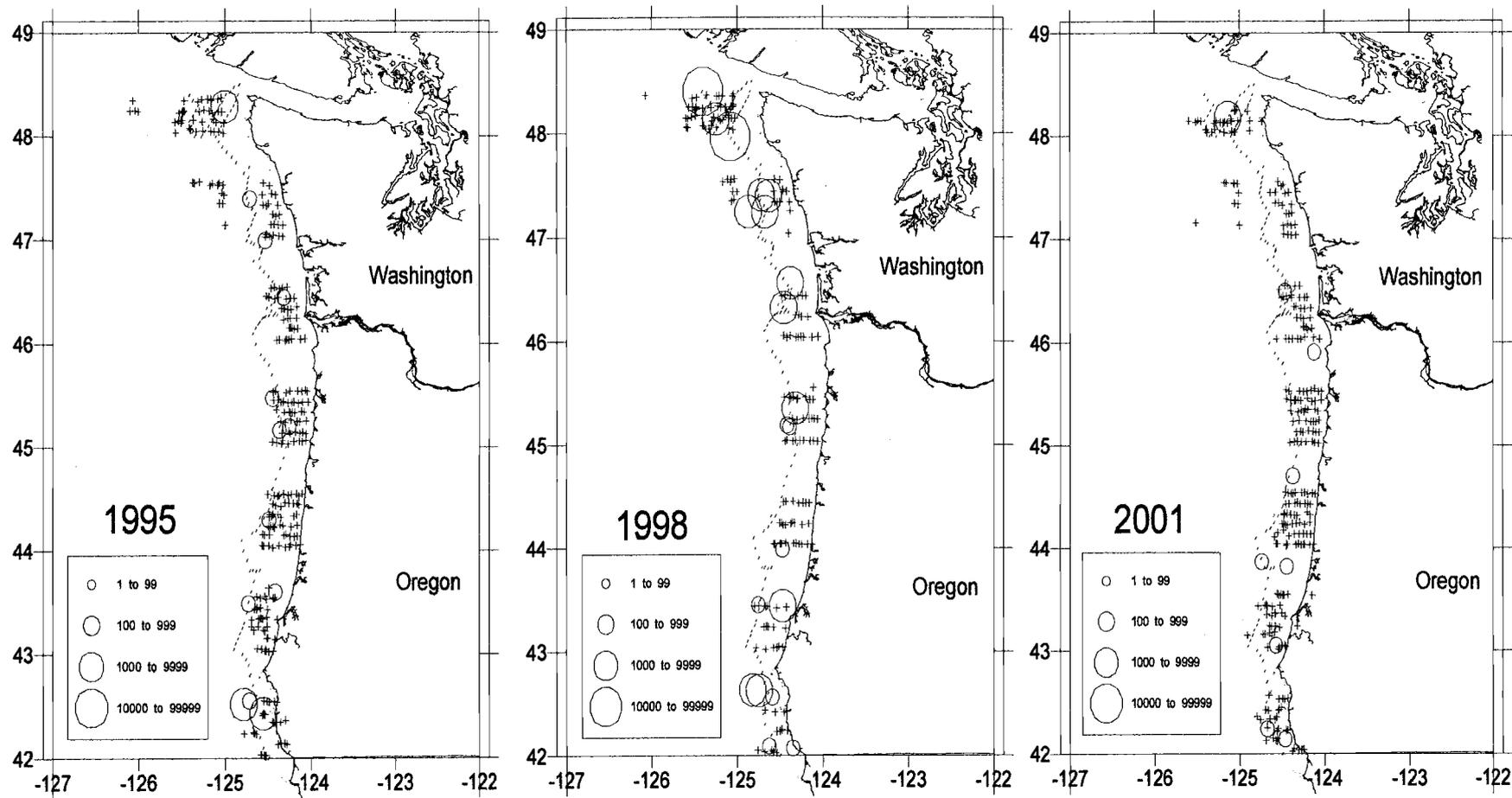


Figure 10: The sample sites and averaged CPUE for the National Marine Fisheries Service west coast triennial shelf groundfish survey from 1995 to 2001. The + symbol indicates the successful trawls conducted for each year. The dashed line indicates where the continental shelf is located.

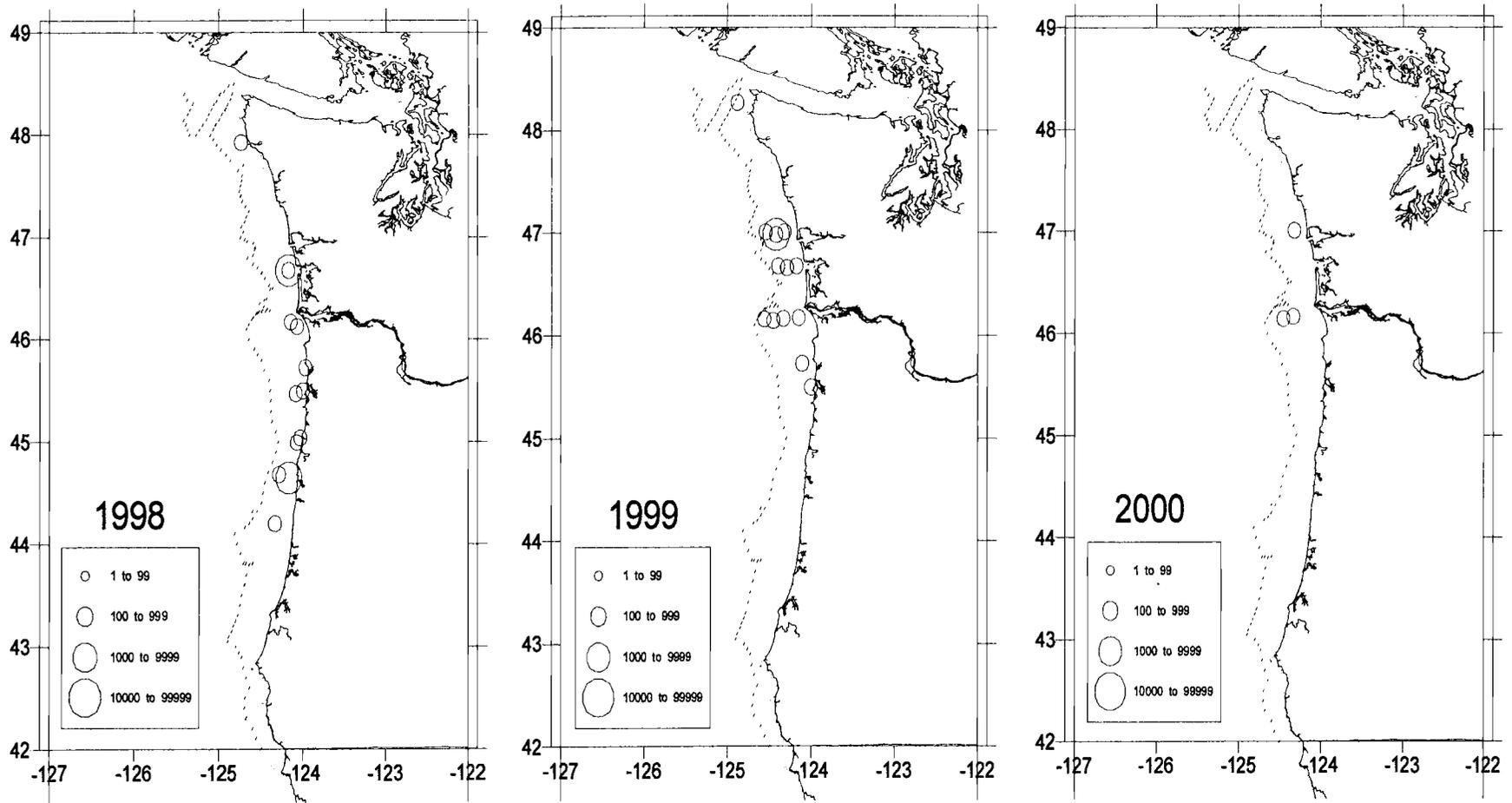


Figure 11: The averaged CPUE for the NMFS/OSU juvenile salmon survey from 1998 to 2000. The dashed line indicates where the continental shelf is located.

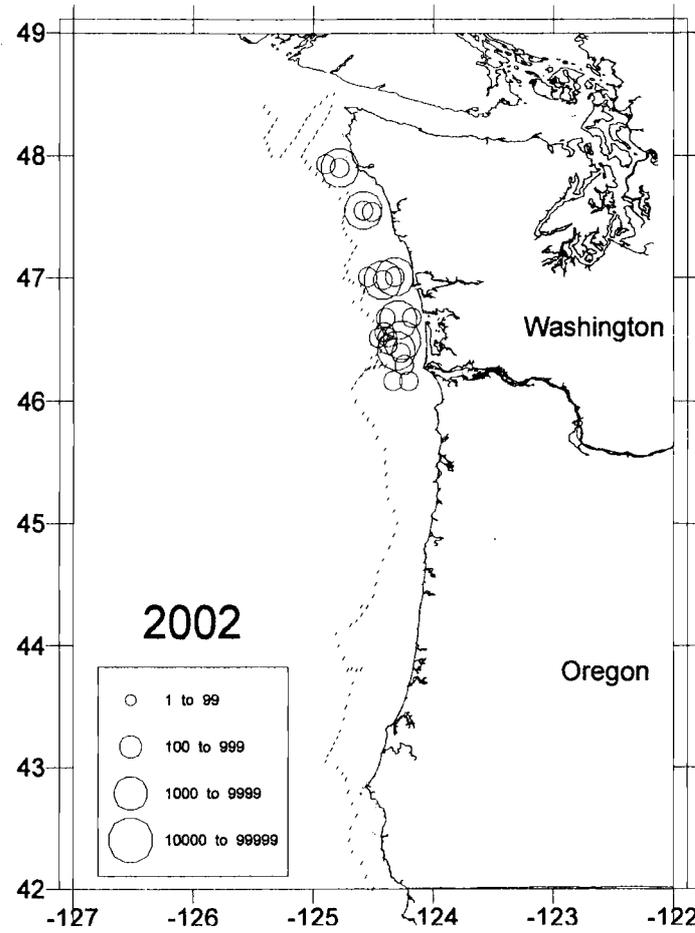
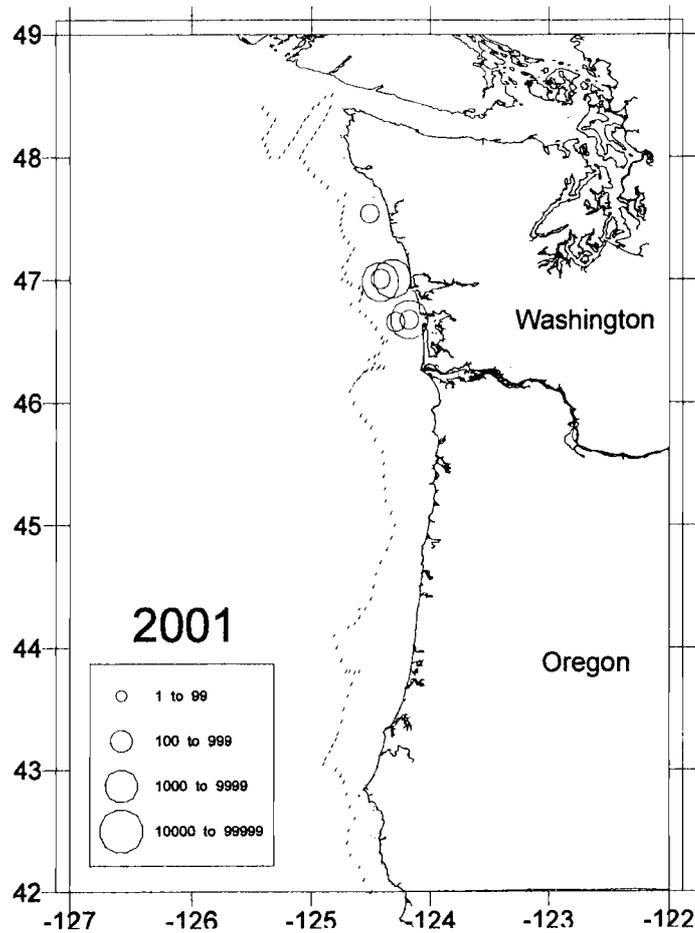


Figure 12: The averaged CPUE for the NMFS/OSU juvenile salmon survey from 2001 to 2002. The dashed line indicates where the continental shelf is located.

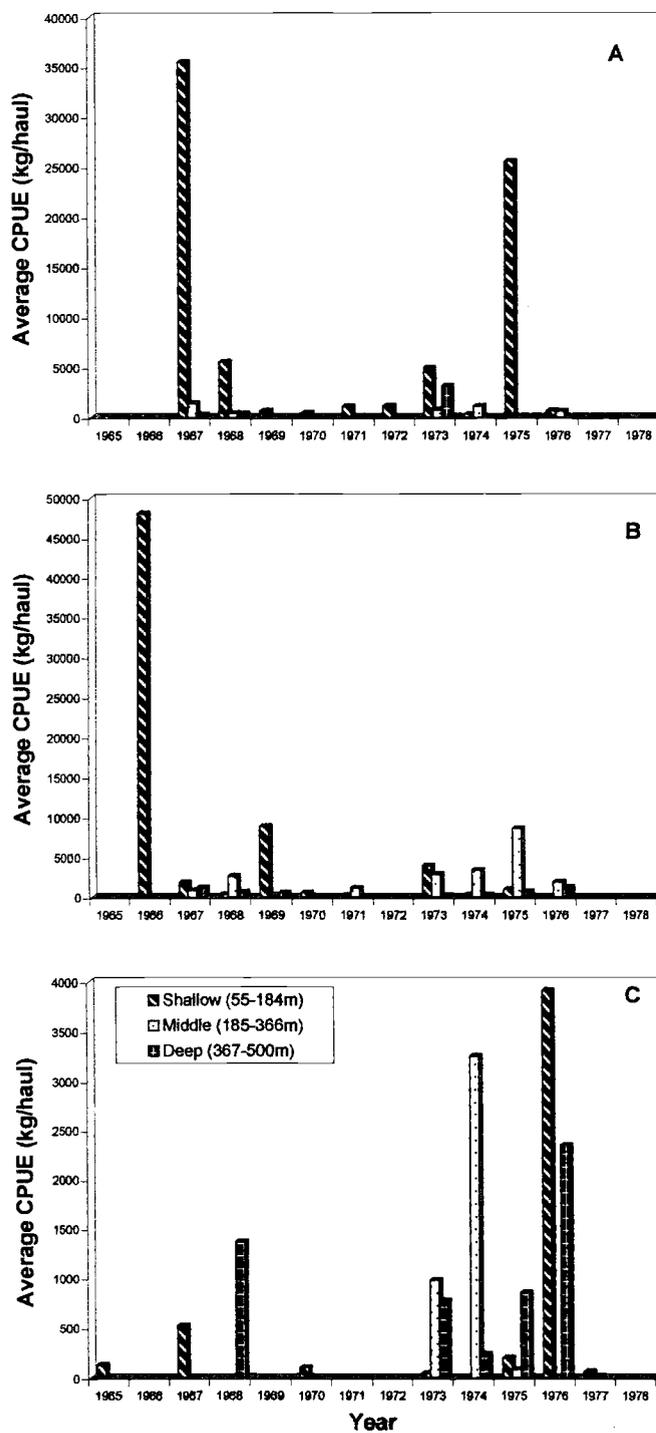


Figure 13: Averaged CPUE for the Soviet Union bottom trawl survey by year and bottom depth for all three regions: (A) U.S. Vancouver, (B) Columbia and (C) Eureka.

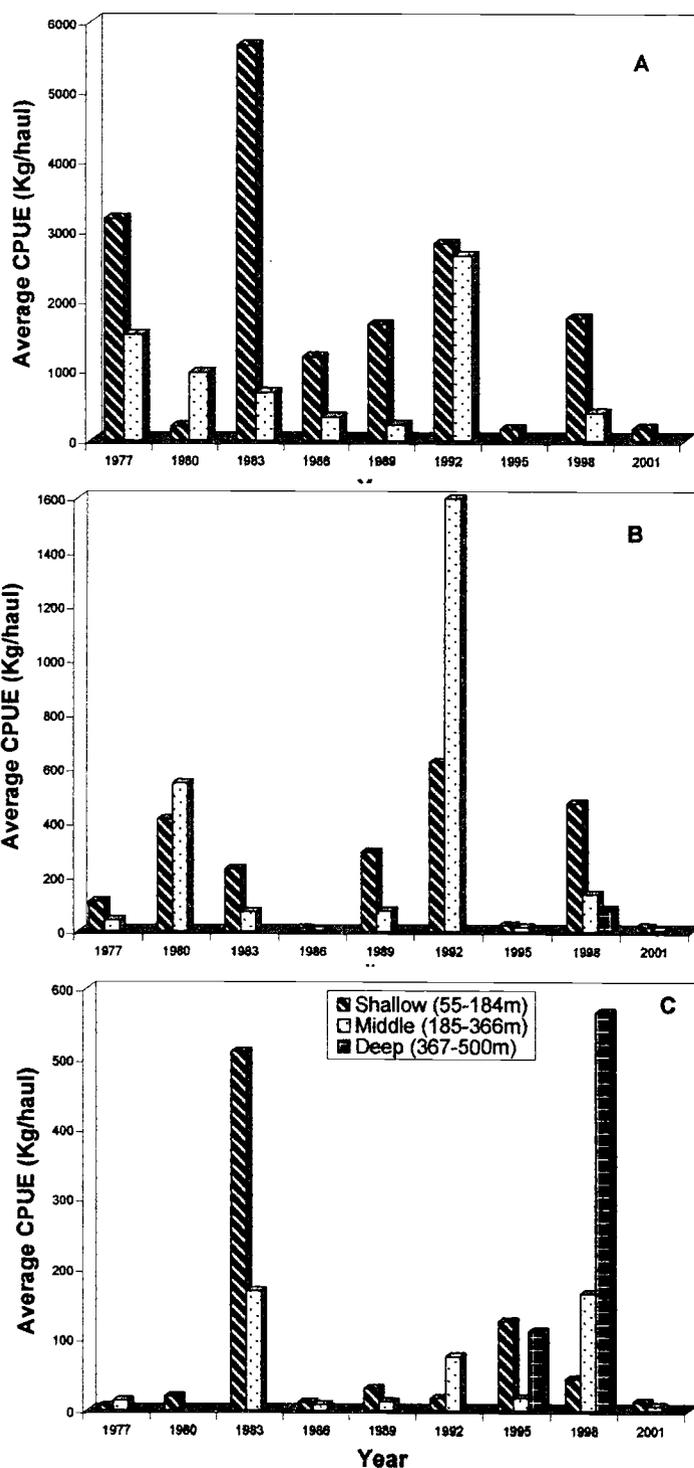


Figure 14: Averaged CPUE for the NMFS triennial shelf groundfish survey by year and bottom depth for the three regions: (A) U.S. Vancouver, (B) Columbia and (C) Eureka.

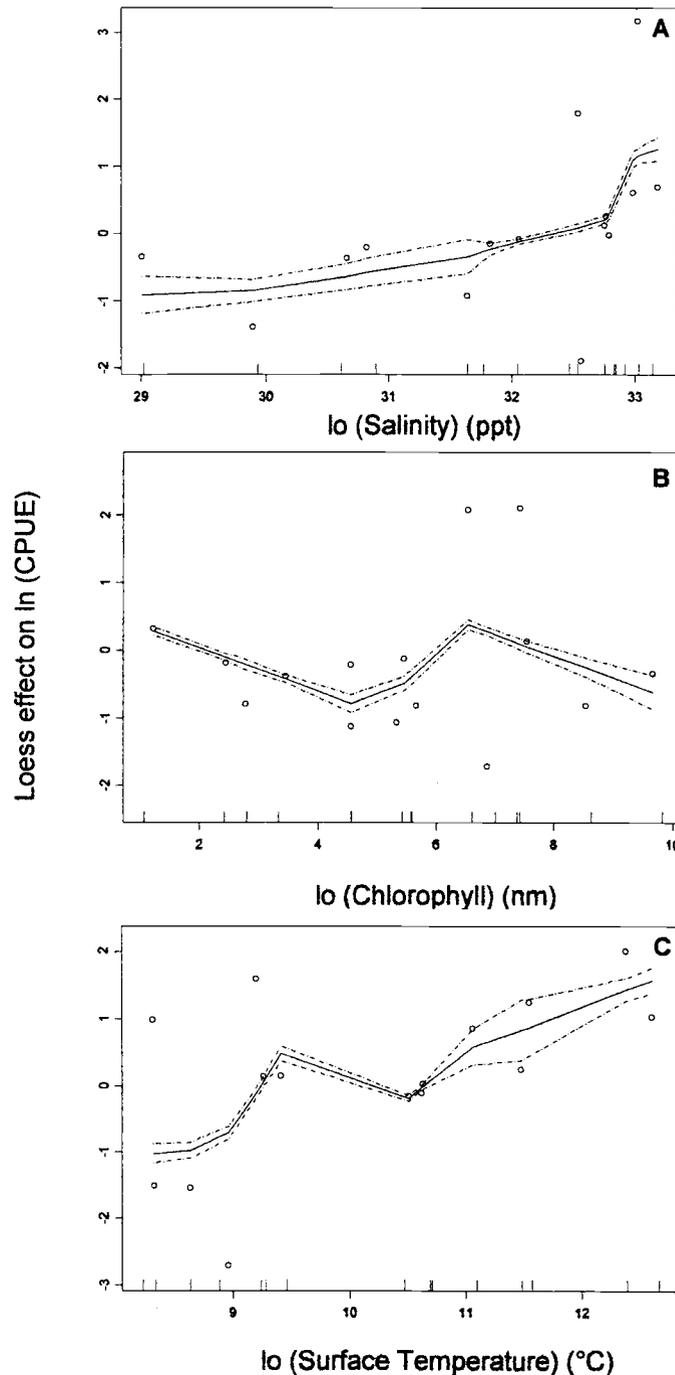


Figure 15: Generalized additive model (GAM) derived effects of salinity, chlorophyll and surface temperature on spiny dogfish nominal CPUE deviances (log transformed). (A) Salinity; d.f. = 5.2, chi square = 282.214, $p < 0.001$, (B) Chlorophyll; d.f. = 4.6, chi square = 398.1784, $p < 0.001$, and (C) Surface Temperature; d.f. = 4.9, chi square = 358.7050, $p < 0.001$. Dashed lines indicated 95% confidence bands. The relative density of data points is shown by the "rug" on the x-axis (i.e. the interior ticks indicating the x values).

In terms of temporal patterns of abundance (i.e. CPUE from the NMFS triennial shelf groundfish surveys) in response to temperature anomalies (i.e. PDO and ENSO monthly anomalies), the best fit form of a GAM was: $\ln(\text{CPUE}) \sim \text{lo}(\text{PDO}, 0.3, 1) + \text{lo}(\text{ENSO}, 0.3, 1)$. However, it was not significant, as CPUE showed no relationship with either the PDO or ENSO monthly anomalies (Chi square = 7.795, d.f. = 8.5, P = 0.504).

The length frequency distributions of spiny dogfish from the NMFS triennial and the NMFS/OSU salmon surveys were similar only in terms of the domination of males in the 70.0 to 89.9 length classes (Figures 16 and 17). These were the length classes in which males typically become mature. In the NMFS triennial survey, females dominated all other length classes, whereas in the NMFS/OSU salmon surveys, females only dominated the 50.0 – 59.9 and 100.0 to 119.9 length classes (Figure 17).

Discussion:

Spiny dogfish have a broad range along the coasts of Washington and Oregon, with the largest and most frequent catches occurring off the northern coast of Washington throughout the surveys. However, during some years high catches were also recorded off of 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, B.C. may be a transitional zone between the “coastal” and “offshore” populations, allowing mixing and overflow.

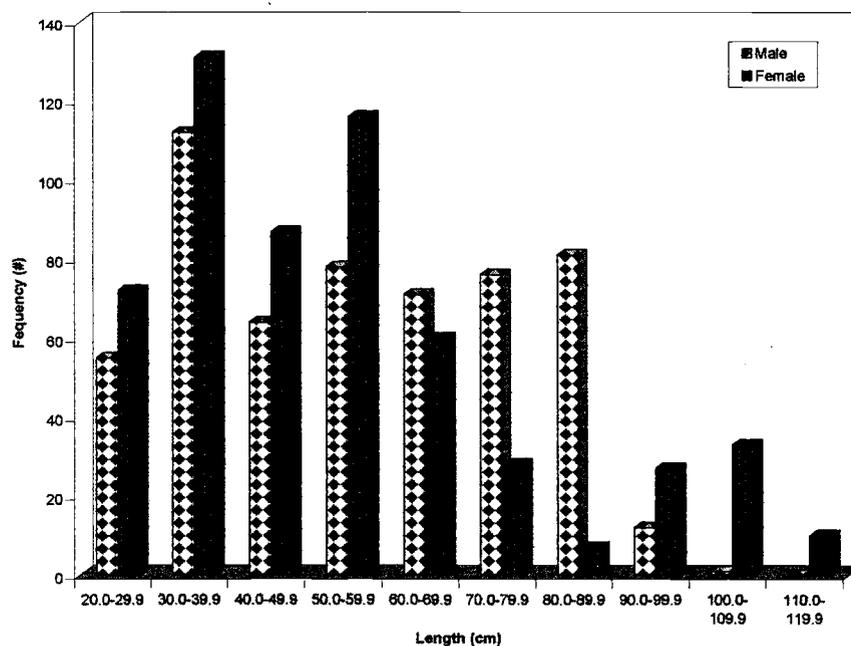


Figure 16: Length-frequency chart of male and female spiny dogfish from the 23-year NMFS triennial shelf groundfish survey.

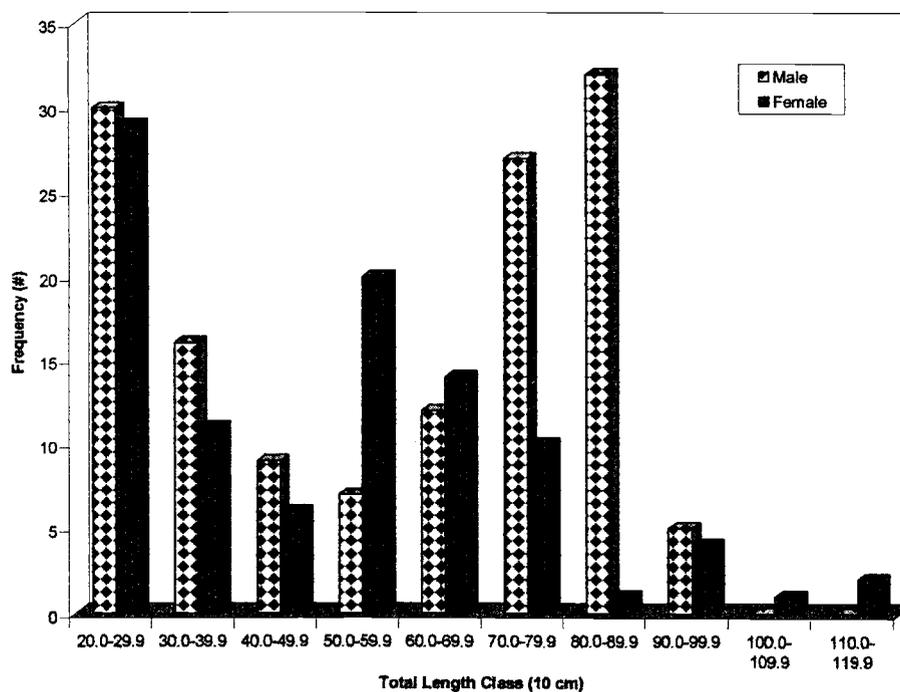


Figure 17: Length-frequency chart of male and female spiny dogfish from the NMFS/OSU juvenile salmon and juvenile salmon predator studies.

Spiny dogfish may prefer this region for the abundance of food flowing out from Puget Sound and the Strait of Georgia, which may be concentrated by topographic upwelling and eddies (Robinson and Ware, 1994; Hickey and Banas, 2003). The occasional high catches recorded off the central Oregon coast may reflect the effect of the outflow of the Columbia River plume on prey availability for predatory fishes, such as spiny 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 transitional zone, with its abundance of prey items, may attract them. These increased catches could also be due to the increased upwelling that occurs during the summer months. Upwelling regions consist of cold, nutrient rich water moving up from the depths to replace the warmer surface waters that the northwest wind has pulled away from the shore (Mann and Lazier, 1991). Such areas of high nutrient concentration generate high productivity that can maintain large fish populations (Bowden, 1983). It has been noted that this region has some of the strongest occurrences of upwelling along the coasts of the northeastern Pacific Ocean (Xie and Hsieh, 1995; Wong *et al.*, 2003).

Alternatively, the distribution patterns of spiny dogfish may reflect physical habitat or temperature preferences. It has been noted previously that spiny dogfish catches decreased off the west coast about the time of the 1983 ENSO event (Brodeur *et al.*, 2003). Whether this is due to coastal warming which may have a negative effect on survival or whether there was a migration

north to cooler water is unknown. Unfortunately, there are no studies/data available by which to differentiate among these potential alternatives. The trend of high abundance in the north, declining southward has also been documented in the Northeastern Atlantic spiny dogfish population (Rago *et al.*, 1998; Garrison, 2001; Link *et al.*, 2002). The southward decline could be due to temperature preferences or possibly the abundance of prey items located on and around Georges Bank (Rago *et al.*, 1998).

Spiny dogfish were caught mostly at shallow depths (55 – 184 m). This could be due to shoreward migration of males and females for the pupping and breeding seasons, which occur in late summer-early fall and late fall, respectively (Hickling, 1930; Saunders *et al.*, 1984; Ketchen, 1986; McFarlane and King, 2003). If the surveys had been conducted during the winter season, it seems likely that more mature females would have been caught at greater depths (Hickling, 1930).

Spiny dogfish appear to avoid the plume zone of the Columbia River plume, or at least congregate more outside than within the plume as indicated by the decrease in catches with increasing chlorophyll, and decreasing surface temperature and salinity. The Columbia River plume expands and contracts depending on the season (Barnes *et al.*, 1972). This low salinity, low density, higher temperature water creates a transition zone, which is inhabited by many different species (Hickey and Landry, 1989). Spiny dogfish were found to prefer lower amounts of chlorophyll, which is indicative of phytoplankton.

Large amounts of chlorophyll can decrease visibility and make it more difficult for visual predators, (Ryer *et al.*, 2002), such as spiny dogfish. In reference to spiny dogfish preference for higher temperature, the relationship between the plume and surface temperature was not straightforward. The plume is generally warmer than other coastal waters at the same distance offshore, but oceanic waters generally get much warmer as you go offshore 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.*, 2001). With this in mind, the higher temperature habitats that spiny dogfish were found in is probably indicative of catches far offshore rather than within the plume zone. Moreover, salinity is more indicative of the plume with various thresholds differentiating inside versus outside the plume, particularly the 31 or 32.5 ppt (Stefansson and Richards, 1963). A possible caveat with this analysis is that there was not a lot of data throughout the entire range of each variable, making fits somewhat tenuous. Despite this, the GAM indicated significant influences of the three variables, which were indicative of spiny dogfish inhabiting preferentially the region outside rather than inside the Columbia River plume.

Many salmonid and baitfish studies have shown that the abundances of these fish populations fluctuate with large-scale regime shifts (Beamish, 1993; Mantua *et al.*, 1997; Hare *et al.*, 1999; Emmett and Brodeur, 2000; Brodeur *et al.*, 2003). The abundance of spiny dogfish over the 23 – year survey period

used in this study showed no correlation with PDO or ENSO events. These results differ from the Brodner *et al.* (2003) study, which found a decrease in spiny dogfish catches during the 1983 ENSO event. This may be a result of the coarser scale of temporal sampling of the shelf groundfish survey data used in the present study (i.e. sampling triennially) in comparison to the annual sampling data used by Brodner *et al.* (2003). A possible factor no climatic effect on spiny dogfish distribution was displayed is that multiple cohorts may buffer the population against such events, where an age class is lost but there are many other age classes by which to compensate for this loss (Jacobson and Cadrin, 2002). The youngest age-class(es) of spiny dogfish may be the most sensitive life stage to environmental change, as seen in other long-lived fishes (Clark and Hare, 2001; Lehodey *et al.*, 2003). If this were the case, then particular cohorts associated with the PDO/ENSO anomaly years would be expected to be absent. However, the present data were limited to abundance measures and not age-sensitive. The loss of a single cohort or two would not be very evident in terms of its affect on abundance in part because of the large number of other cohorts present (i.e. due to species' long lifespan). Moreover, each cohort represents a relatively small proportion of the total population because of the species' low annual fecundity (i.e. four pups per year). Effects on abundance are also likely to be time-lagged, because the absence of the youngest cohort(s) would not become evident until they were large enough to have been captured by the survey gear. If instead, the mature or older portion

of the population was affected by PDO or ENSO events, then the effect might be expected to be more dramatic because it would not only involve the loss of individuals to the population, but also a loss of reproductive potential (i.e. breeders) and thus recruitment to the next generation. As there was no evidence of a depression in adult abundance, let alone recruitment, this suggests that if there was an effect of the PDO or ENSO on the population it involved the youngest age classes, which would be difficult to detect with the present data. To detect the latter effect would require extensive age-sensitive data.

More immature than mature females were caught in the NMFS triennial shelf groundfish survey and the NMFS/OSU surveys (Figures 16 and 17). This likely reflected the high mortality that juvenile spiny dogfish experience. The calculated mortality rate for a juvenile in this population is 0.94/yr (Wood *et al.*, 1979). These surveys also demonstrate that males dominate in the 70.0 to 89.9 cm length classes (Figures 16 and 17). This dominance likely reflects the maturation of males at this size and a subsequent decrease in growth that accompanies the diversion of energy and resources to reproduction, a pattern found commonly in fishes (Roff, 1982). Male spiny dogfish rarely exceed 100 cm in length (Saunders *et al.*, 1984). These two surveys display differences in their respective length frequency distributions likely because the length data collected for the NMFS triennial survey was from a 23-year survey period (nine years of actual data), whereas the length data collected for the NMFS/OSU

juvenile salmon survey was from a 5-year survey period. When CPUEs are compared between the Soviet Union and the NMFS triennial groundfish survey, we see that Soviet Union CPUEs are at least a magnitude greater than those of the NMFS triennial groundfish survey (Figures 13 and 14). This may indicate a decline in the spiny dogfish population starting in 1977.

Alternatively, differences in gear and sampling design could account for some of these differences between the two time periods (Broder *et al.*, 2003).

However, there are indications that many juvenile spiny dogfish were caught as by-catch in an intense fishery during the 1970s (Ahlgren, 1960; Bailey *et al.*, 1982), which could have led to a long-term decline in abundance.

In conclusion, the Northeastern Pacific spiny dogfish population shows its greatest abundance off the northern Washington and central Oregon coasts, with the largest catches occurring in shallow waters during the spring and summer months. The population seems to prefer the waters outside the Columbia River plume, utilizing more of the transitional and oceanic zones. There was no evidence of large-scale climatic changes, the PDO and the ENSO, affecting population abundance, however, an extensive age-sensitive study on spiny dogfish is needed to fully assess this. While the surveys used in this study did not specifically target spiny dogfish, which can create difficulties in assessing population abundance, they were likely indicative of the range of habitats occupied by this species. Decreases in catch abundance off the Washington and Oregon coasts in association with the surveys are thus

likely to be indicative of a true decline in the population. If more in-depth knowledge and time-sensitive data are desired, a survey specifically targeting spiny dogfish would then be necessary.

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Chapter 3

Aspects of the Life History and Population Dynamics of Northeastern Pacific
Spiny Dogfish (*Squalus acanthias*) off the Oregon and Washington Coasts

Jaclyn M. Richards

Oregon State University
Department of Fisheries and Wildlife
Nash 104
Corvallis, Oregon 97331-3803

Abstract:

We quantify the age, growth, maturation and fecundity of the Northeastern Pacific spiny dogfish (*Squalus acanthias*) off the Washington and Oregon coasts, and used these data to develop an age-structured matrix model to examine the sensitivity of the population's growth rate to changes in mortality (e.g., fishing). Between April and October 2002, 393 spiny dogfish were collected during two surveys conducted jointly by the National Marine Fisheries Service (NMFS) and Oregon State University (OSU). Analysis of age and growth using dorsal spines revealed that 50% of females matured at 28 years of age and 50% of males at 20 years. Average length at 50% maturity was 85.0 cm for females and 71.5 cm for males. Female fecundity was extremely low, averaging eight pups per clutch biennially and ranging from four to 14. The number of pups per female increased with length, but not age. Using these data, a deterministic, female-based model was developed. Asymptotic population growth rate (λ) was determined to be very low, 1.01, and comparable to population growth rates calculated for "coastal" populations. When fishing mortality was incorporated into the model, the fishery was only sustainable when exploitation was low and strict size limits enforced. When fecundity was doubled, the population growth rate increased from 1% to 3% per year. This 33% increase in population growth was equivalent to the effect of a decrease in the age at first maturity of three years. Given that responses to changes in population demographics through shifts in

fecundity or spawning frequency are likely constrained, responses would then seem likely to involve changes in age at maturity. The life history traits of the Northeastern Pacific spiny dogfish thus translate into a low potential for population growth and as a consequence a high susceptibility to overfishing.

Introduction:

Life history studies allow scientists and managers to characterize the responses of fish populations to changes in the environment, fishing mortality, or population size. Knowledge of a particular species' life history has the potential to improve management practices by allowing managers and scientists to model how a population fluctuates under different scenarios (Kokko *et al.*, 2002). Projections of responses under these scenarios can be developed using life tables or matrix models. Such models enable scientists to examine the capability of populations to withstand anthropogenic changes in survival rates (Adams, 1980; Roff, 1984; Jennings *et al.*, 1999).

Life history research addresses the tremendous variability that exists in characteristics among species and, perhaps more importantly from an ecological and management perspective, among populations within species and among individuals within the same population (Hutchings, 2002). There have been a number of life history studies conducted over the years which have examined relationships between the responses of populations to exploitation and age at maturity, fecundity, lifespan, etc., for many commercially important teleosts. These species include the American plaice,

Hippoglossoides platessoides (Roff, 1982); North Sea sole, *Solea solea* (De Veen, 1976); Atlantic salmon, *Salmo salar* (Klemetsen *et al.*, 2003; Letcher, 2003) and Pacific salmon species, *Onchorhynchus spp.* (Cass and Riddell, 1999; Crespi and Teo, 2002). These analyses demonstrate that fish life histories help to determine exploitation responses of different fish species (De Veen, 1976; Roff 1982; Cass and Riddell, 1999; Letcher, 2003).

Life history patterns have been categorized as "slow" and "fast" for a wide variety of taxa, including fishes (Roff, 1992; Dulvy *et al.*, 2002, Heppell *et al.*, 1999, Cortes, 2002). In the Northeastern Pacific Ocean, teleosts show a variety of life history patterns, ranging from fast growth, early maturity, short lifespan, and batch spawning (e.g. anchovy or sardines) to slow growth, late maturity, long lifespan and batch spawning (e.g. Pacific rockfish). In contrast, elasmobranchs show limited diversity in life history patterns and can be generally characterized by a pattern of slow growth, late maturity, long lifespan and low fecundity. Even within the "slow" life history pattern of elasmobranchs, however, there are many variations throughout this group. Smaller sharks, such as the small-spotted catshark (*Scyliorhinus canicula*) and the brown smooth-hound shark (*Mustelus henlei*) usually mature within the first five years of life, have relatively fast growth (compared to the larger sharks) and shorter lifespans, living about 13 years (Cortes, 2002). Larger sharks, such as the copper shark (*Carcharhinus brachyurus*) and the bull shark (*Carcharhinus leucas*), grow slowly and mature around age 20, but have

a long lifespan, living to about 30 years (maximum empirical age; Cortes, 2002).

The Northeastern Pacific spiny dogfish (*Squalus acanthias*) is a small shark (<1.7 m) that displays the life history characteristics of larger sharks. Spiny dogfish are an abundant species that inhabits shelf and inland waters of Oregon and Washington coasts (Bonham *et al.*, 1949; Alverson and Stansby, 1963; Ketchen, 1972; Brodeur and Pearcy, 1986; Nakano and Nagasawa, 1996; McFarlane and King, 2003). These sharks are divided into two populations in the northeastern Pacific Ocean: an "offshore" population found on the continental shelf from southeastern Alaska to northern California and a "coastal" population, which inhabits the waters of Hecate Strait, Strait of Georgia and Puget Sound (Saunders *et al.*, 1984; Ketchen, 1986; Holts, 1988; McFarlane and King, 2003).

Much of what is known about the life history of the Northeastern Pacific spiny dogfish is derived from the "coastal" population, including age at maturity (Table 1). Earlier studies reported age at maturity to be from 20 to 23 for females and from 11 – 14 for males of the "coastal" population (Table 1; Bonham *et al.*, 1949; Ketchen, 1975). Bonham *et al.*'s (1949) estimates were based solely on the examination of growth marks on unworn dorsal spines; older, worn spines were excluded from age analysis. Ketchen (1975) estimated 17 years to maturity for males and 34 years to maturity for females caught in Hecate Strait, based on growth mark estimations on worn and

unworn spines, but argued that his own results were “preposterous” and instead averaged his estimates of age at maturity with those of Bonham *et al.* (1949) (Table 1). It seemed impossible for a small shark to take such a long time to reach reproductive age.

Delayed maturity allows female sharks to grow to a size where there is enough energy storage to provide suitable nutrition for their large and well-formed young (Garrick, 1982; Roff, 1992; Saunders and McFarlane, 1993; Cortes, 2000; Jennings *et al.*, 2001). This delayed maturity relates to greater reproductive returns for larger females, due to their ability to produce and provision more pups. By producing large, well-developed young, spiny dogfish are increasing the odds of pup survival. However, this increase comes at a price; the extended gestation period of 22 months means that a female can only reproduce every other year and has low fecundity, averaging eight pups every two years (Ketchen, 1972, 1975; Jones and Geen, 1977 a – c; Saunders and McFarlane, 1993). On the plus side, reproductive senescence in female spiny dogfish has never been reported (Pratt and Casey, 1990; Cortes, 2000). Once a female becomes sexually mature, she will produce a litter of pups every other year until death (Pratt and Casey, 1990; Cortes, 2000).

Spiny dogfish life history traits translate into long generation times and slow population growth rates. Like other long-lived marine species, spiny dogfish may not be able to respond rapidly to compensate for reductions in

survival rates (Musick, 1999; Sminkey and Musick, 1996; Heppell *et al.*, in press). A directed fishery or large increase in by-catch of spiny dogfish could cause an extreme decrease in population size and population recovery could take many decades. Low fecundity and slow growth rates also suggest that density-dependent increases in these variables are unlikely to compensate for decreased adult survival (Heppell *et al.*, 1999; Cortes, 2002). The relative effects of a range of fishing mortality rates on a population of spiny dogfish can be compared with an age-structured model that accounts for the long generation time in this species.

Age-structured models or Leslie matrix models can be used to address conservation issues and help display the relationships between life history traits and population growth rates (Benton and Grant, 1999). These models have allowed scientists and managers to examine extinction risk, population growth rates, population size, harvest rates and potential impacts of management options on shark populations (Sminkey and Musick, 1996; Heppell *et al.*, 1999; Cortes, 2002). Age-structured matrix models are a class of dynamic population models that incorporate age-specific survival and reproductive parameters (Wood *et al.*, 1979; Caswell, 2001). Matrix population models are particularly well suited for populations of long-lived species, such as sharks, where experiments to examine changes in a population over several generations are impossible. Age-structured models make full use of available biological information on age, growth, fecundity and

natural mortality (Cortes, 1998). Thus, an age-structured model can increase our understanding of spiny dogfish population dynamics and allow us to examine the effects of different fishing scenarios, compare the different female ages at maturity from past and present studies, and investigate the effects of changes in fecundity on the asymptotic growth rate (λ).

Elasticity analysis of a deterministic matrix model examines the effects of proportional changes in demographic rates (survival, growth and reproductive parameters) on the asymptotic population growth rate, λ (Stearns, 1992; Heppell *et al.*, 2000a). λ is the proportional growth rate given by the dominant eigenvalue of the transition matrix, and is related to the intrinsic rate of increase of a population, r ($r = \ln(\lambda)$). Scientists use λ as an index of population health (Heppell *et al.*, 2000a), a measure of fitness (Caswell, 2001), and as a response variable to compare management strategies that invoke changes in different life history parameters. Elasticity analysis is an example of prospective analysis. It addresses the question: if a vital rate (survival, growth or reproduction) changes by a small proportion, while all other parameters remain constant by what proportion will λ change (Benton and Grant, 1999)? Elasticity analyses have two important applications: to make preliminary management proposals for data-poor populations with known life history characteristics and to categorize species or populations according to their elasticity patterns (Heppell *et al.*, 2000b). Sea turtles and sharks with late age at maturity and adult annual survival rates

around 0.9 display the highest elasticity values for juvenile survival, primarily because most individuals are in the juvenile stage and a change in their annual survival rate affects a large proportion of the population (Heppell *et al.*, 1999).

The purpose of this study was to quantify age at maturity, length at maturity, and fecundity for spiny dogfish caught in surveys off the Washington and Oregon coasts, and to use these data to develop an age-structured matrix model for the “offshore” population. Our objective was to use the model to examine how population growth rate is affected by changes in survival rates, e.g., increased fishing or by-catch mortality. We also compared population growth rates and stage-specific survival elasticities from models representing the “coastal” population with those representing the “offshore” population. Finally, the model was used to examine the effect of changes in fecundity on population growth rate, as increased litter size could be a response to decreased population density in a harvested population.

Methods:

Collection:

Spiny dogfish used in this analysis were obtained from two sources: (1) the National Marine Fisheries Service (NMFS)/Oregon State University (OSU) juvenile salmon study; and (2) the NMFS/OSU juvenile salmon predator study. The juvenile salmon study has been conducted since 1998, with three cruises a year, one each in May, June and September (no

May cruise for 1998). At each station, a CTD (conductivity, temperature and depth meter) was cast and then a Nordic 264 otter trawl (width 30 m, depth 15-18m) deployed and hauled for 30 minutes parallel to the shore (Figure 1).

The juvenile salmon predator study has also been conducted since 1998, with nocturnal sampling (beginning each evening at dusk) occurring every two weeks from April to the end of July (Emmett *et al.*, 2001). Like the juvenile salmon study, a CTD was cast and then a Nordic 264 otter trawl was towed parallel to shore for 15 minutes (Figure 2). In 2002, 393 spiny dogfish were captured during these two NMFS/OSU surveys. Their distribution ranged from La Push, WA (47°90') down to Newport, OR (44°60') (Figure 1). Dorsal spines were removed and frozen and sex and maturity were assessed for each fish. Males were considered mature if their seminal vesicles contained a visible amount of sperm and claspers were well developed and firm (Ketchen, 1972, 1975; Jones and Geen, 1977 a – c). Females were considered mature if uterine eggs greater than 20 mm in diameter were present in the ovaries or the uterus contained pups (Saunders *et al.*, 1984; Saunders and McFarlane, 1993). The number and development of the pups and eggs found in a female were recorded.

Pups were categorized into two stages: first year and second year embryos. First year embryos were less than 100 mm and had large yolk sacs. Second year embryos, or near-term embryos, were greater than 100 mm and had almost absorbed the yolk sac (Ketchen, 1975).

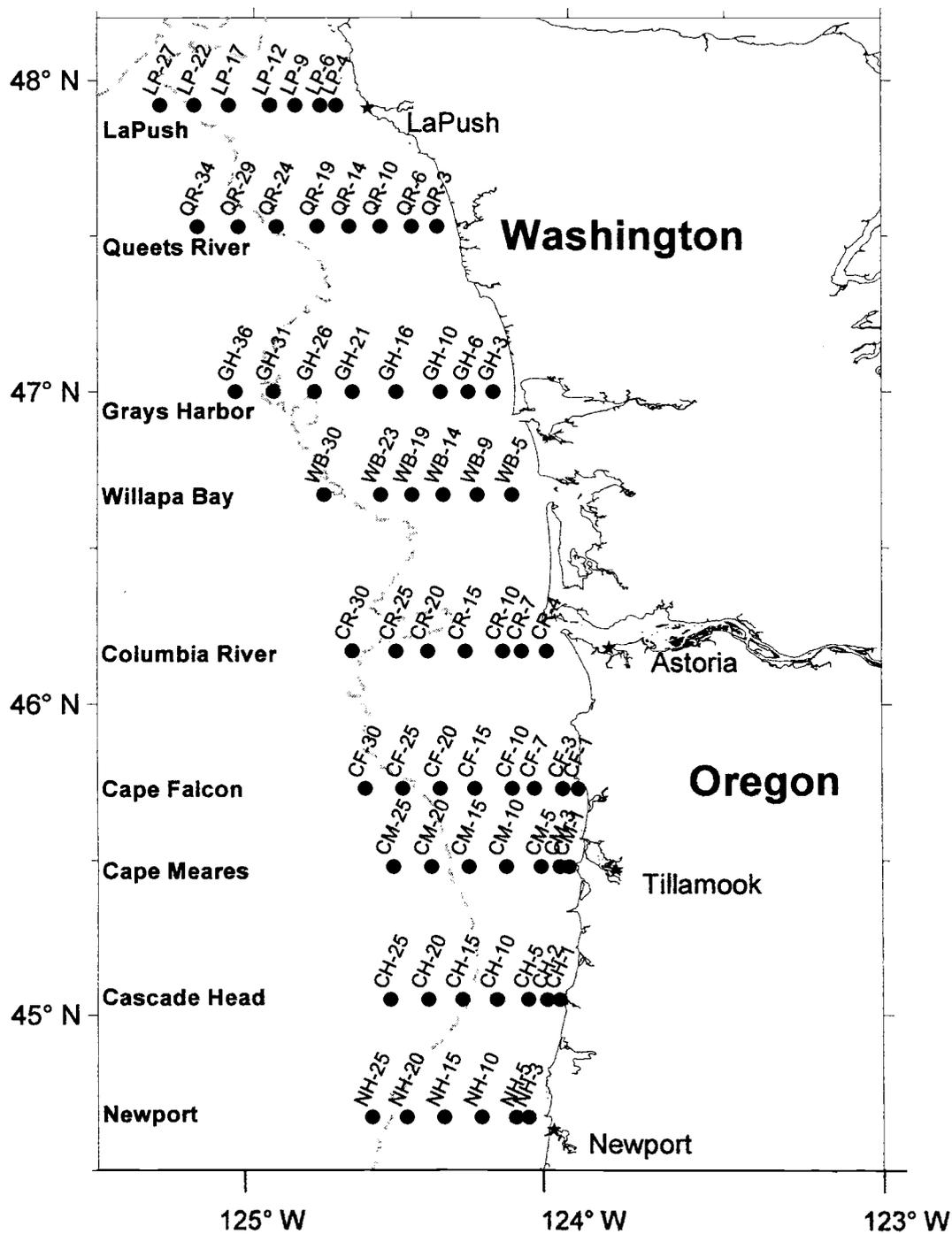


Figure 1: Sample sites for the NMFS/OSU juvenile salmon surveys. The letter and numbers signify the transect name and distance from shore in nautical miles.

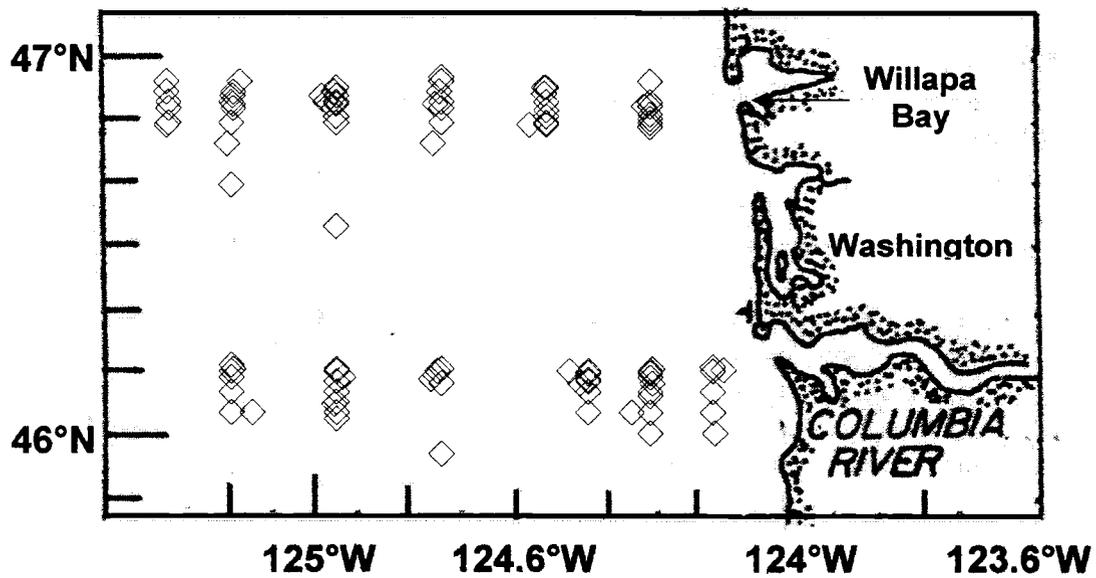


Figure 2: Sample sites for the NMFS/OSU juvenile salmon predator survey. Diamonds represent trawling locations.

Spine preparation and ageing:

Age determination in elasmobranches is difficult because of the lack of cycloid or ctenoid scales, otoliths or other calcified body parts (Ketchen, 1975; Harvey, 1979). Ageing animals by a count of annual rings found on vertebra centra, which can be impregnated with silver nitrate to make them more conspicuous, was not found to be a verifiable method for spiny dogfish (Cailliet *et al.*, 1983). However, McFarlane and Beamish (1987) used oxytetracycline (OTC) injections and disc tags to verify that the rings found on the second dorsal spine are laid down annually and can be used to age spiny dogfish. Age determination using the second dorsal spine is a cost effective and less time consuming than other fish ageing methods, such as x-ray chromatography.

In the laboratory, all flesh was removed from the second dorsal spine and dried for 24 hours. Spines were rubbed briskly with a commercial wiping cloth to expose annuli clearly (Figure 3; Chilton and Beamish, 1982). Annuli may form in a series of small tight bands and must be counted individually, not as groups or a series of groups (Figure 4; Chilton and Beamish, 1982; McFarlane and Beamish, 1987). The opaque bands are deposited from September through April (winter bands), whereas the translucent bands are deposited from February to October (summer bands) (Chilton and Beamish, 1982; Tucker, 1985; McFarlane and Beamish, 1987).

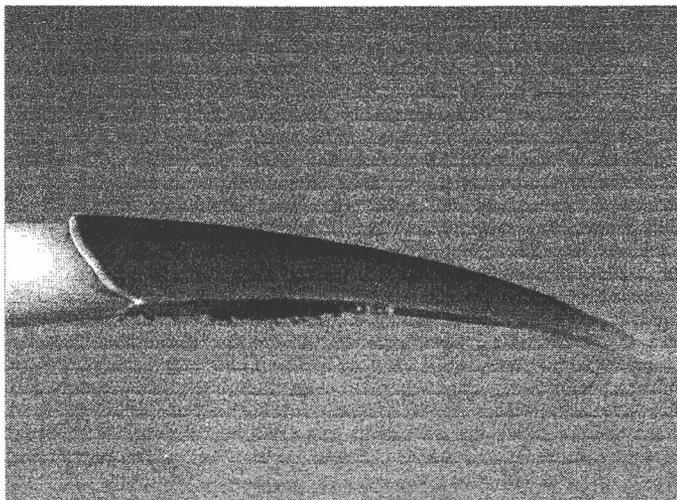


Figure 3: Zero age spine, no dark bands are visible.

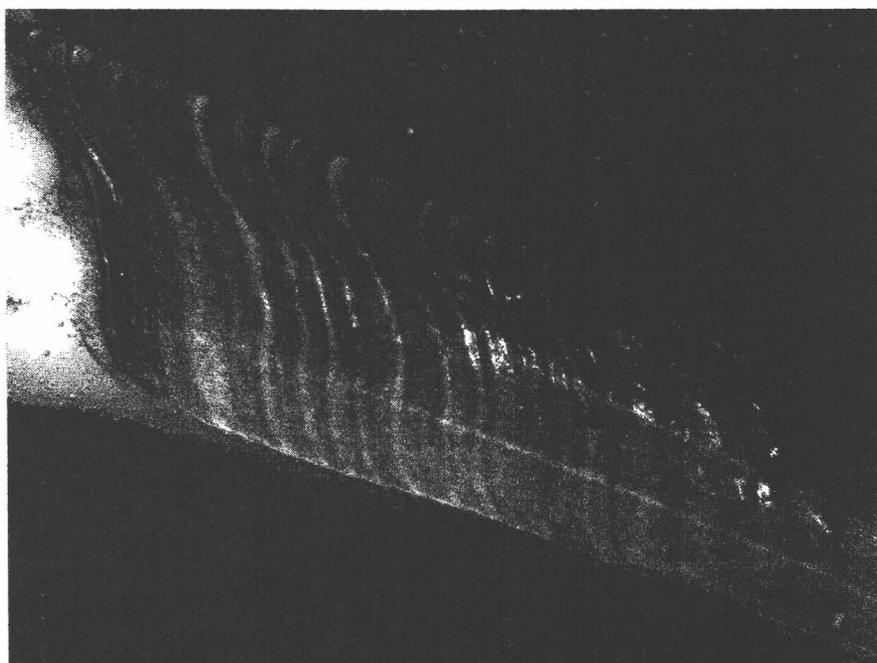


Figure 4: Older worn spine, displaying dark and opaque bands.

The least distinct bands (broad and faintly colored) were usually those marking the first 5 – 7 years of growth; these bands are located at the tip of the spine (Chilton and Beamish, 1982). The bands for older ages tend to be closely arrayed, yet quite sharp and distinct, and located at the base of the spine (Figure 4; Ketchen, 1975). The posterior or second dorsal spine is used for ageing the fish because it is larger and subject to less wearing (Chilton and Beamish, 1982).

The dorsal spines used for spiny dogfish ageing display seasonal ring deposition, consisting of dark and light bands demarking one year of growth. These bands are created by an outer mantle made up of hard polished enamel, with the inner layer being made up of soft glandular tissue (Holden and Meadows, 1962; McFarlane and Beamish, 1987). The translucent and opaque bands are deposited from the enamel gland located at the base of the spine (Chilton and Beamish, 1982; Cailliet *et al.*, 1986; McFarlane and Beamish, 1987). As spiny dogfish dorsal spines grow, the enamel at the top of the spines is worn down or away, removing the older annual rings.

Following the “no wear point” (NWP) method developed by Ketchen (1975), I estimated the ages of all spiny dogfish in my samples (Figure 5; see also McFarlane and Beamish, 1987). The first step for this method was to count the rings on spines that had not been worn-down; these were considered unworn spines (Figure 3). Next, the base diameter of all unworn spines was taken with Vernier calipers (precision 0.05 mm) (X_1 - X_2).

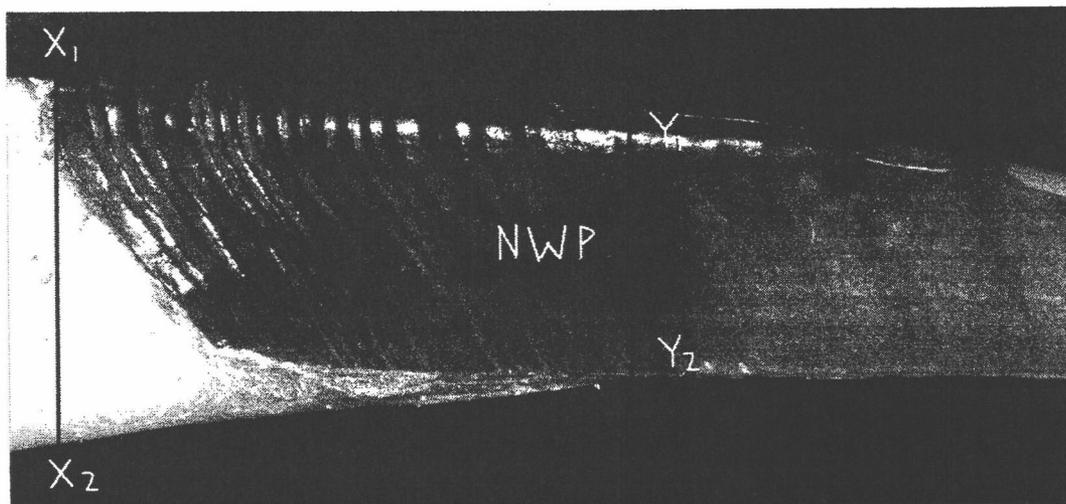


Figure 5: Photo of a spiny dogfish spine showing the location of Vernier caliper measurements for development of the regression equation to estimate age of worn spines. $X_1 - X_2$ is the spine base diameter measurement. NWP (No Wear Point) is the last ring before the wear on the spine begins. $Y_1 - Y_2$, is the width of the spine at the NWP, used in the analysis to determine how many more years should be added to the count.

For this study, the unworn spine data were pooled for males and females because there was no statistical difference between the sexes ($F_{1,121} = 1.1707$, $P = 0.2134$). Base diameter was plotted against spine age for unworn spines to create a functional regression to estimate the number of annuli lost to wear for worn spines. Next, all dark rings were counted up to the first complete annulus below the worn portion of the spine. This last ring was considered the no wear point (NWP; Ketchen, 1975); a mark was placed on this ring so the repeated counts stopped at the same NWP ($Y_1 - Y_2$) (Figure 5). Then, Venier calipers were used to measure the diameter of the NWP, so the number of lost rings could be estimated from a functional regression of the number of rings counted by the base diameter of the unworn spines. All spines were examined under a Leica dissecting microscope at 120x power with direct lighting from above. Annuli were identified as ridges, dark bands or both, which were identifiable under the microscope and counted for each spine (Ketchen, 1975; Chilton and Beamish, 1982; Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). Annuli from prepared spines were counted three times. If two counts agreed, then that annuli count was used for final analysis. If the three estimates differed by one or two annuli, then the average was taken for the estimated age. If the estimates differed by three or more annuli then the spine was rejected as unreadable (Ketchen, 1975). Three of the spines collected for this study fell into the unreadable category; two were male and one was female. All of the annuli were enumerated if they could be

seen under a microscope even if there was irregular spacing between opaque bands (G.A. McFarlane, Pacific Biological Station, personal communication, 2003). A quantitative measure of ageing accuracy was calculated using the coefficient of variation (CV) as per Chang (1982). The coefficient variation was calculated two times: one time comparing my counts with Mike Smith's counts (retired Pacific Biological Station Ageing Lab employee, who had calculated spiny dogfish ages for Saunders and McFarlane [1993]). The second CV was calculated using three series of counts used for this study. Age and length at 50% maturity were determined for both females and males from a logistic curve fitted to the proportion of mature individuals in each 2 year age class and 5 cm length class (Roa *et al.*, 1999). We estimated the age-length relationship with a von Bertalanffy growth equation from the age-length data using least-squares nonlinear regression in an Excel spreadsheet (Carlson *et al.*, 2003).

Model:

An age-structured, Leslie matrix model was created using MathCAD (Mathsoft Engineering and Education, Inc.) and focused on female spiny dogfish traits. This model was a pre-breeding census because the data used were collected before pupping occurred, so pups were not included in the model explicitly and:

fertility = female pups per female per year*survival rate of pups to age 1.

Pup survival to age one for this population was an unknown, and was set to that of leopard sharks as reported by Cailliet (1992; Appendix 1). The leopard shark parameter was used because the pups are birthed in similar habitats as spiny dogfish pups. Average fecundity for the model was calculated from the study population, and it was assumed that half of the pups were female (Bonham *et al.*, 1949). Northeastern spiny dogfish have a two-year gestation period (Bonham *et al.*, 1949; Ketchen, 1975). A rate of instantaneous natural mortality of 0.094, determined for "coastal" dogfish in British Columbia waters (Wood *et al.*, 1979), was applied to calculate the average annual survival rate ($S = e^{-0.094}$) for all age classes greater than 1.0. The Wood *et al.* (1979) instantaneous natural mortality was used for this model because it is the best representation we have of a natural (i.e. unfished) rate (M). Age at maturity was calculated from the ageing data and was modeled as a "knife-edge", with all females maturing at a constant age, and the maximum age was set at 100 years (Ketchen, 1986).

An elasticity analysis was performed to examine the difference in proportional change of the asymptotic population growth rate (λ) following a proportional change in the annual survival rate of the juvenile and adult life history stages. The matrix was then modified to estimate the effects of different rates of fishing mortality (0.05, 0.10, 0.15, 0.20, 0.25, 0.30 and 0.35) and minimum size limits for the catch of spiny dogfish (total lengths of 50, 60, 70, 80, 90, 100 and 110 cm) on λ . The von Bertalanffy growth curve

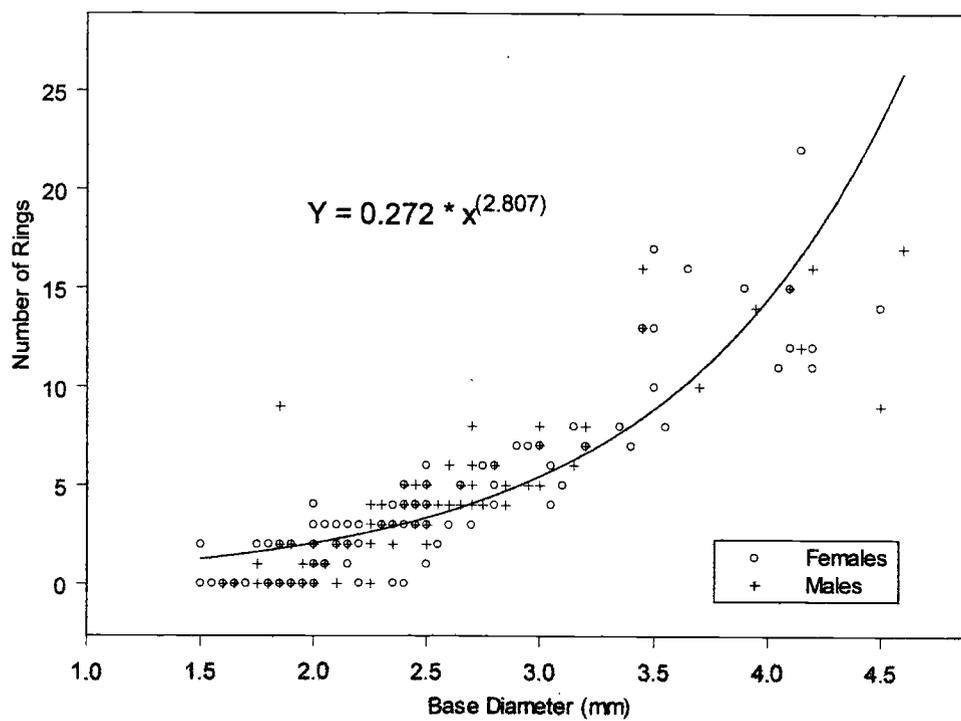
estimated from our data was used to relate lengths of harvested fish to age classes in the model. For each model scenario, we applied various fishing mortality rates (F) to age classes determined by a minimum size limit, assuming that fishing mortality was additive (annual survival = $e^{-(M+F)}$) (Heppell *et al.*, 1999).

Finally, we compared the population growth rate from this model to those calculated for other populations, where age at maturity ranged from 20 to 36 years. Finally, the effect of fecundity on the asymptotic population growth rate and elasticities was examined by halving, doubling or quadrupling the value (i.e. within the natural range of spiny dogfish fecundity for this study population), and comparing the results with those obtained using the empirically-derived data.

Results:

Ageing and maturation curve estimation:

The relation between spine base diameter (D) and number of annuli (A) of unworn spines was highly significant $A = 0.272 * D^{(2.807)}$ ($n = 221$, $R^2 = 0.829$, $P < 0.001$; Figure 6). However, the strength of the relationship deteriorated somewhat above a base diameter of 3.5 mm, suggesting that estimates of the number of rings (age) from spines above this diameter are less reliable. The coefficient of variation (CV) estimate was 3.8% for ageing accuracy, suggesting the ages are highly reproducible (Chang, 1982).



From 200 readable spines and gross examination of the gonads, the age at 50% maturity for females was determined to be 28 years (95% confidence interval = 27.801 to 28.199 years, $R^2 = 0.795$; Figure 7). From 179 readable spines, the age at 50% maturity for males was determined to be 19.5 years (95% confidence interval = 19.078 to 19.922 years, $R^2 = 0.823$; Figure 8). There is thus an eight year difference in the age at 50% maturity between male and female spiny dogfish, with females having to survive longer before reproducing than males.

The frequency of age classes of both female and male spiny dogfish decreased rapidly during their first five years of life and then remained relatively stable until a second decline between 12 – 16 years of age.

Thereafter, the frequency of female age classes remained relatively constant, while that of males showed a slight increase between 20 – 25 years of age and then dropped off again (Figure 9).

Growth and Fecundity:

The parameters for the female spiny dogfish growth curve developed from this sample were: k (growth constant) = 0.0201, L_{∞} (theoretical average maximum length) = 163.63 and t_0 (x intercept or hypothetical age at length zero if such a point existed) = -9.5056 (Figure 10; $R^2 = 0.937$). Males had relatively rapid growth until about age 25, then the growth rate leveled out (Figure 11; $R^2 = 0.920$).

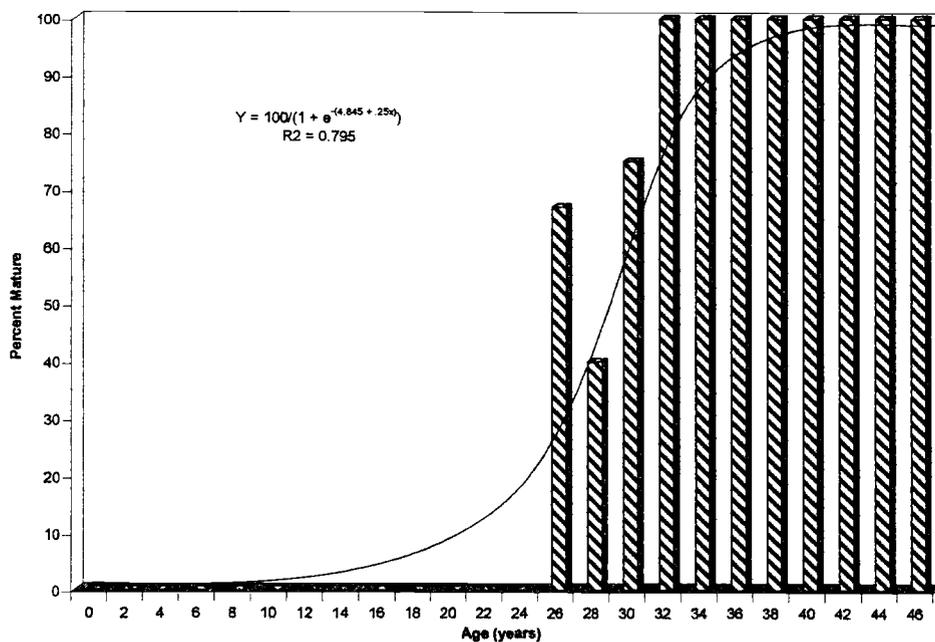


Figure 7: Relationship between the age of female spiny dogfish (*Squalus acanthias*) and percent mature. A two year binning was used for this graph.

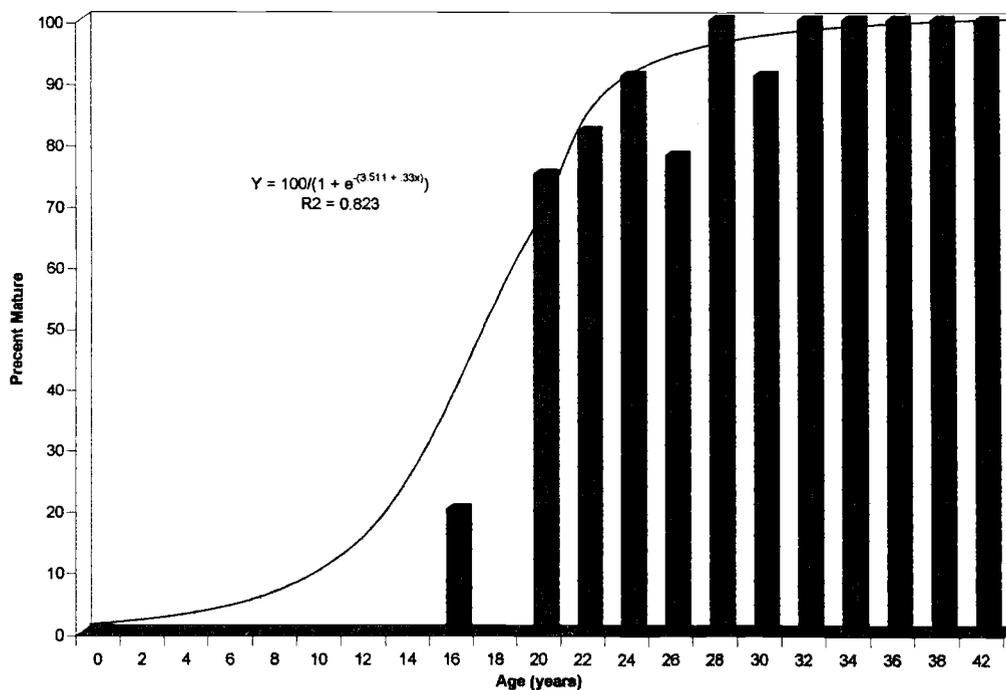


Figure 8: Relationship between the age of male spiny dogfish (*Squalus acanthias*) and percent mature. A two year binning was used for this graph.

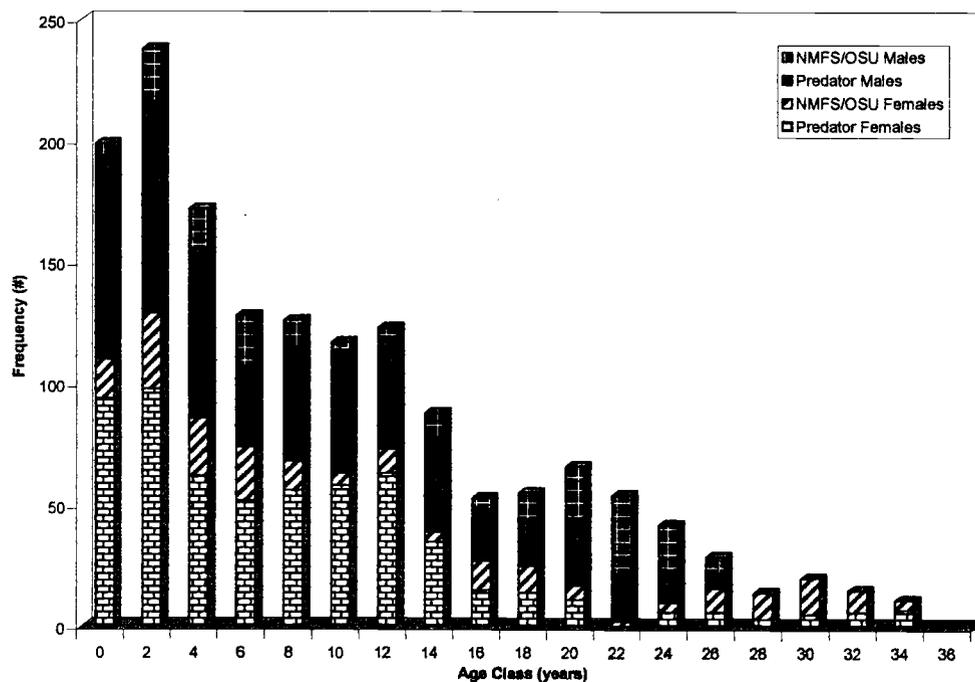


Figure 9: Female and male spiny dogfish (*Squalus acanthias*) age frequency.

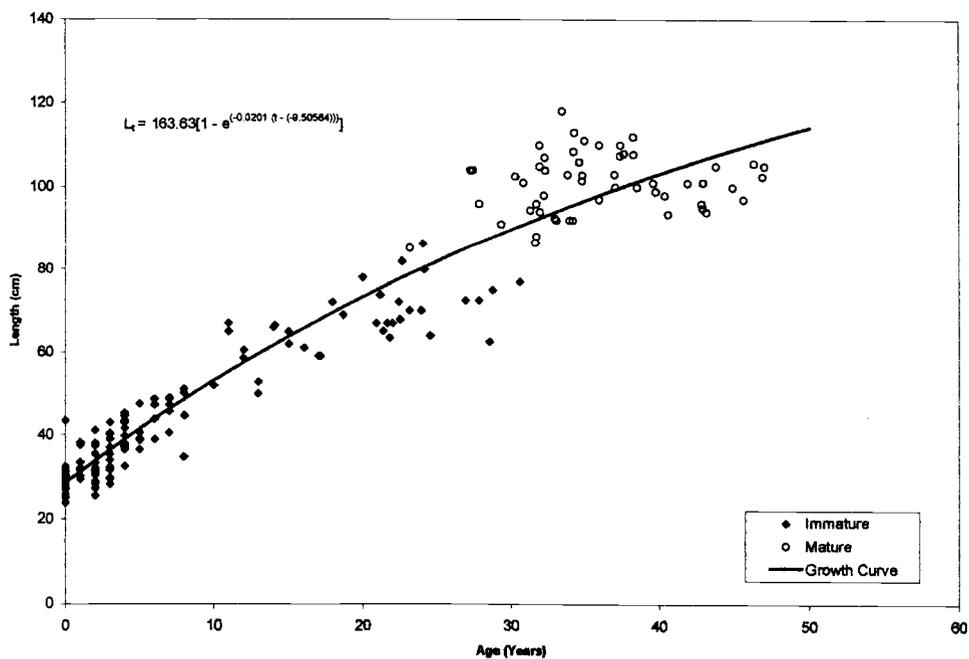


Figure 10: Relationship between age and body length for female spiny dogfish (*Squalus acanthias*).

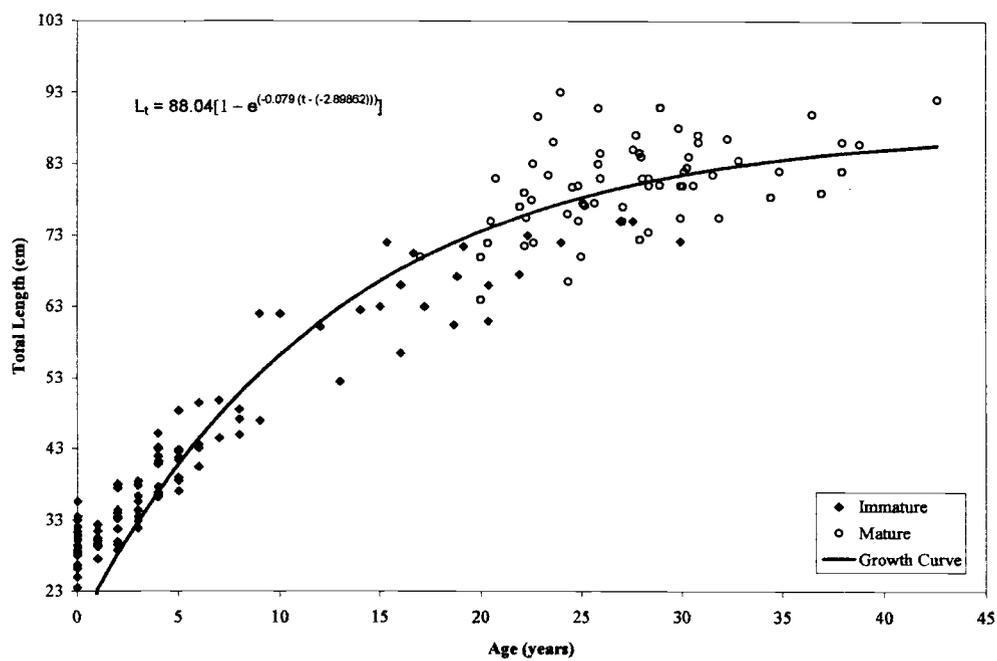


Figure 11: Relationship between age and body length for male spiny dogfish (*Squalus acanthias*).

The growth rates of the sexes were similar, except females did not show the same degree of leveling off in growth with age as shown by the males (Figures 10 and 11). For both sexes, there appeared to be no change, or even a slight jump in growth associated with maturity, which is somewhat counterintuitive given that organisms transfer somatic energy from growth to reproductive investments at maturity.

The minimum size of a mature female from the sample population was 85.0 cm. A curve fitted to the percent mature by length shows an abrupt change, with 50% of the females reaching maturity at 85.0 cm (95% confidence interval = 84.574 to 85.426 cm, $R^2 = 0.699$; Figure 12). Minimum size of a mature male from the sample population was 64.0 cm, with 50% of the males reaching maturity at 75 cm (95% confidence interval = 71.113 to 71.887 cm, $R^2 = 0.752$; Figure 13).

A significant relationship was found between female size and number of embryos ($F = 7.56$, d.f. = 53, $P < 0.001$, $R^2 = 0.3199$; Figure 14). However, no significant relationship was found between female age and number of embryos ($F = 3.15$, d.f. = 53, $P = 0.08$, $R^2 = 0.057$; Figure 15).

Model:

Age at 50% maturity was set at 28 years, and annual fecundity was held constant at 2.125 pups per year, as clutch size did not increase with age in our sample. Thus, the resulting growth rate for this population was determined to be approximately 1% per year ($\lambda = 1.009$).

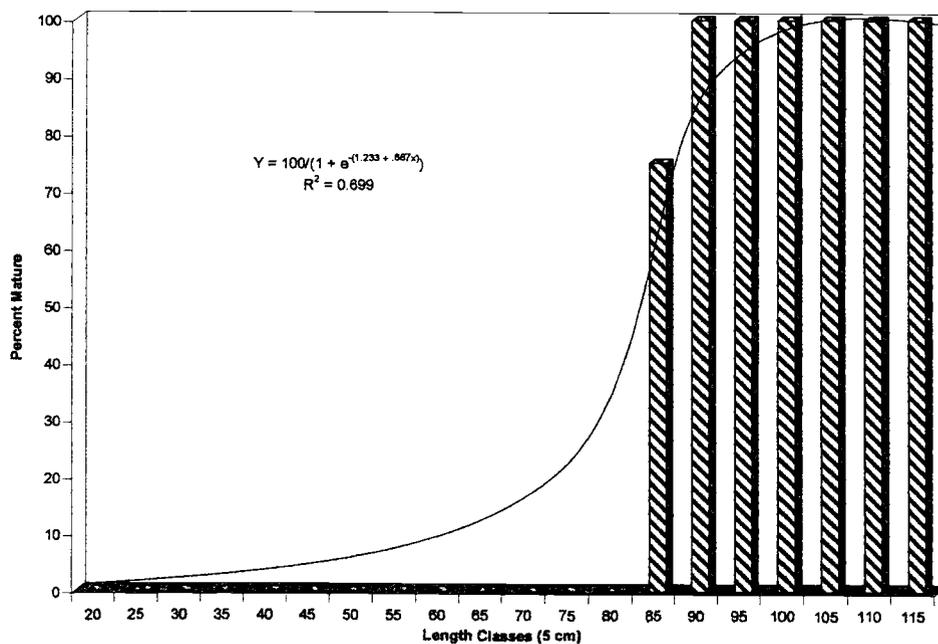


Figure 12: Relationship between the length of female spiny dogfish (*Squalus acanthias*) and percent maturity. A 5 cm binning was used for this graph.

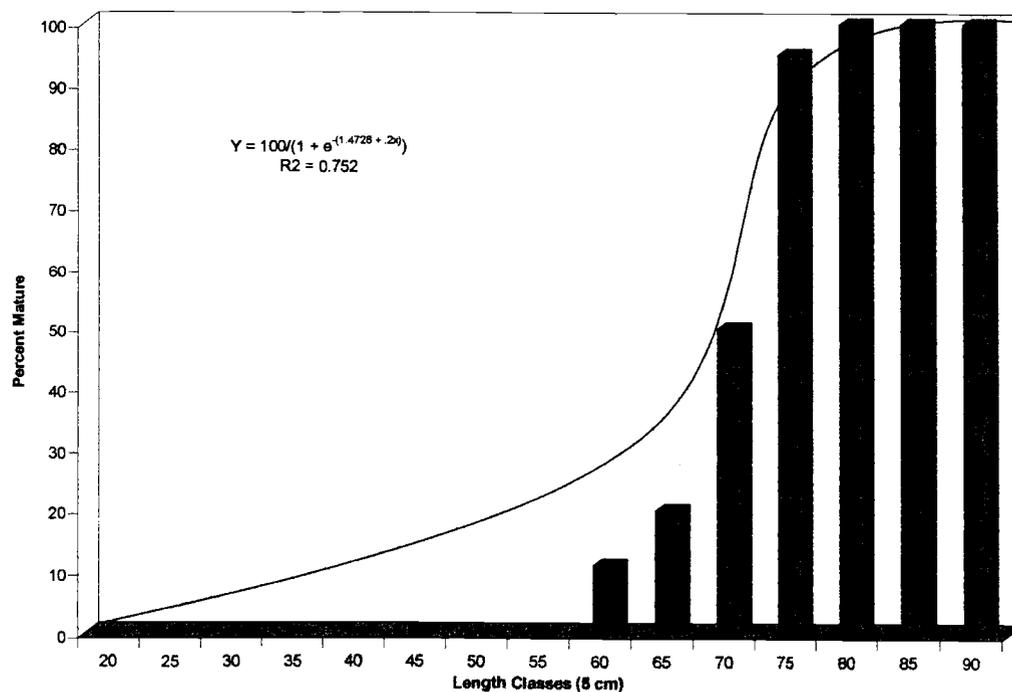


Figure 13: Relationship between the length of male spiny dogfish (*Squalus acanthias*) and percent mature. A 5 cm binning was used for this graph.

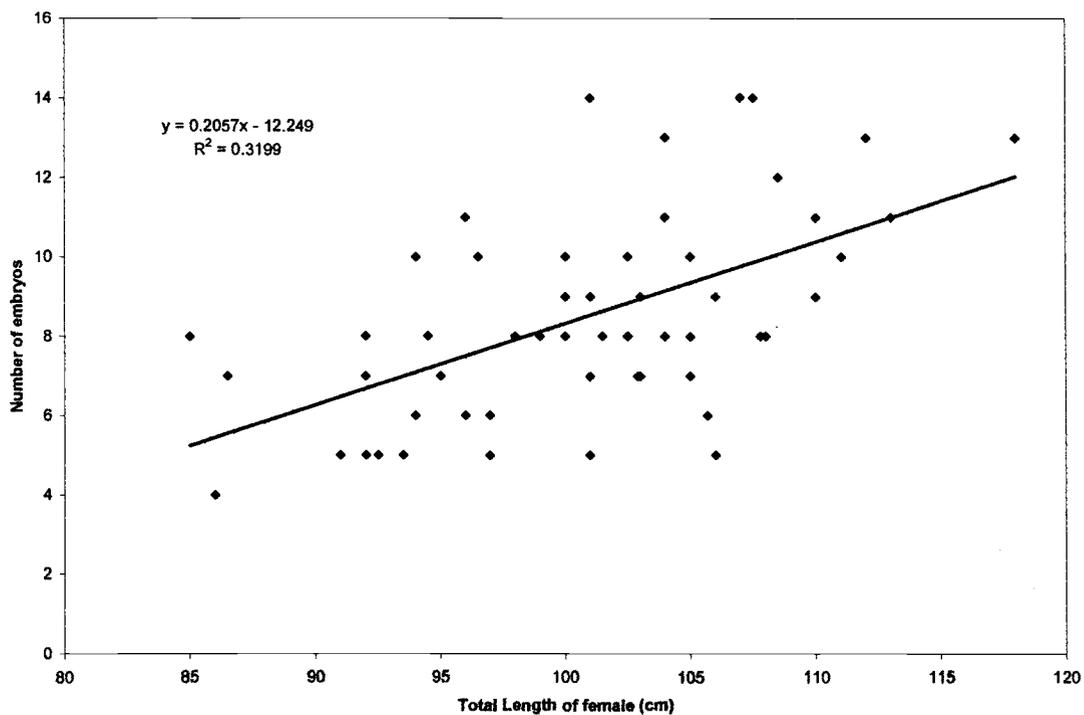


Figure 14: Relationship between female body length and fecundity.

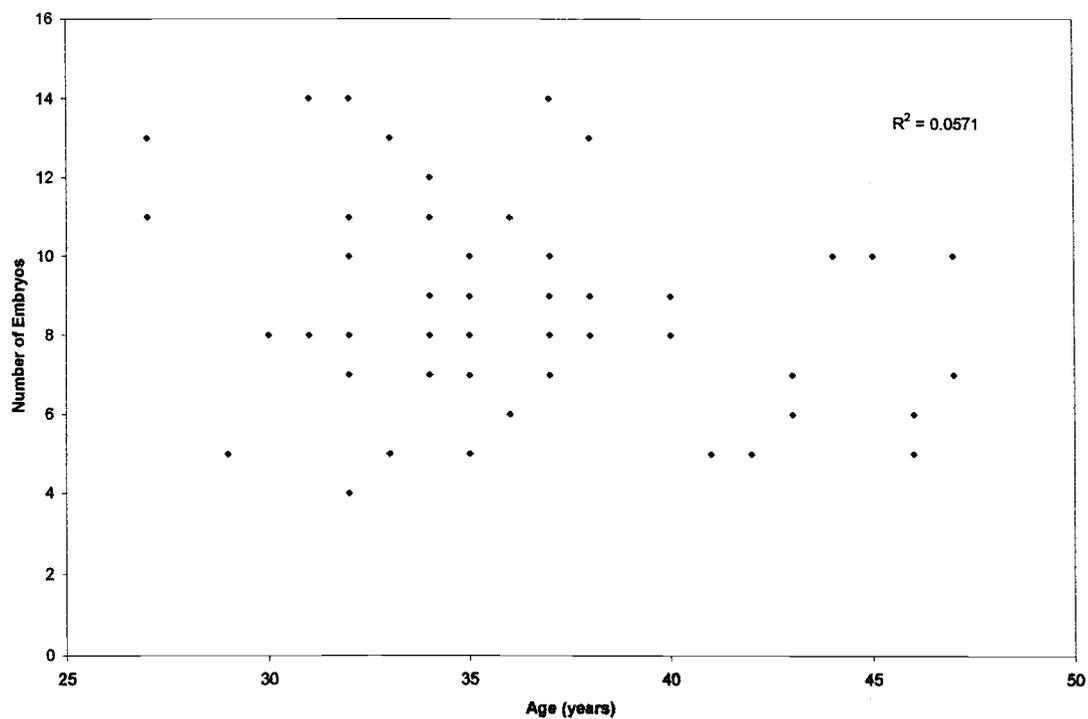


Figure 15: Relationship between female age and fecundity.

The elasticity (= proportional sensitivity) analysis performed on this population demonstrated that the proportional contribution λ of juveniles (i.e. the effect on λ of a proportional change in annual survival for all age classes within a stage) was 0.729 and 0.247 for adults. The fecundity elasticities, which include the contribution of age zero fish survival, summed to 0.0262 for all adult age classes and thus had little effect relative to that of survival (i.e. it was an order of magnitude smaller). The elasticity analysis demonstrated that the survival rate of the juvenile group had a relatively greater proportional contribution to population growth rate than that of the adults. Thus, a proportional change in the annual survival rate of juveniles will have a larger effect on λ than the same proportional change in adult annual survival.

The population growth rate of this population naturally decreased when fishing mortality was added to the model because the model did not include density-dependent changes in vital rates. When a 0.05 fishing mortality was added, λ decreased from about 1% (1.009) to -1.4% (0.986) per year (Figure 16). The effect of fishing mortality depended on the minimum size of the fish at entry into the fishery. The population growth rate decreased faster with higher fishing mortality rates and smaller minimum entry sizes (Figure 16). Smaller minimum entry sizes expose more of the population to fishing exploitation, meaning that fishing pressure on the population as a whole has increased (i.e. more spiny dogfish are being removed as the minimum size limit is decreased).

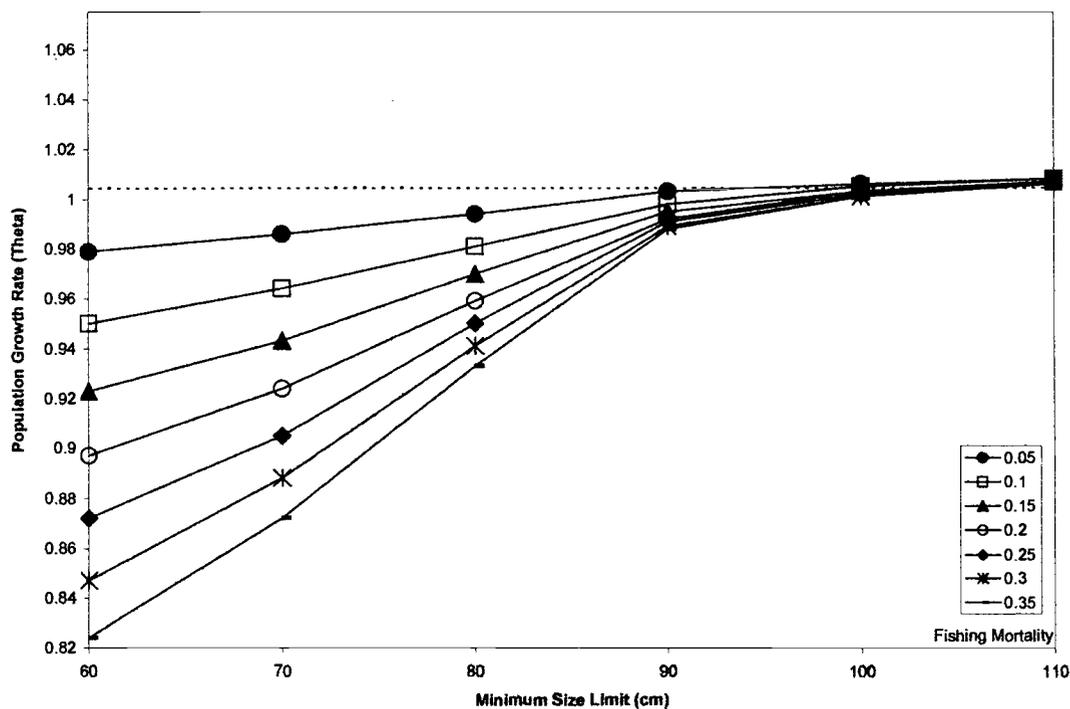


Figure 16: Population growth rate predictions for spiny dogfish (*Squalus acanthias*) under different scenarios of fishing mortality. The horizontal dashed line represents one-half the rate of increase calculated for the preharvested population.

When the annual survival rates and annual fecundity were held constant, the lower ages at maturity reported for other spiny dogfish populations resulted in an increase in the population growth rate (Table 1, Figures 17 and 18). Reduced age at maturity meant that females not only began reproducing at an earlier age, but also produced more offspring throughout their lifetimes.

Fecundity had a low proportional effect on population growth rate (λ). When fecundity is doubled, the population growth rate increases from 1% per year to 3% per year (Table 2). This is a 33% increase, but the same type of increase could occur if the age at first maturity is reduced by three years (Table 1).

Discussion:

This study provided insights into the life history and population dynamics of the "offshore" Northeastern Pacific spiny dogfish. Age at maturity was lower than that reported for the "coastal" population, female and male growth continues to level off after maturity and this population has low fecundity, similar to that reported from previous studies. The incorporation of these life history data into an age structured model allowed us to examine the asymptotic population growth rate for the "offshore" spiny dogfish, which was calculated to be only 1% per year.

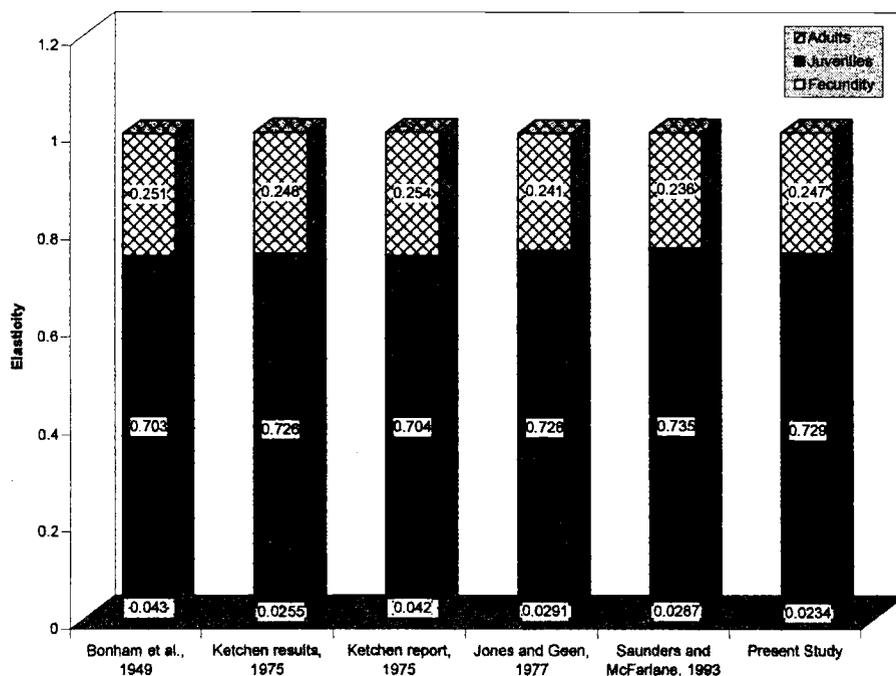


Figure 17: Sensitivity (=elasticity) of the Northeastern Pacific spiny dogfish population from previous studies and the present study.

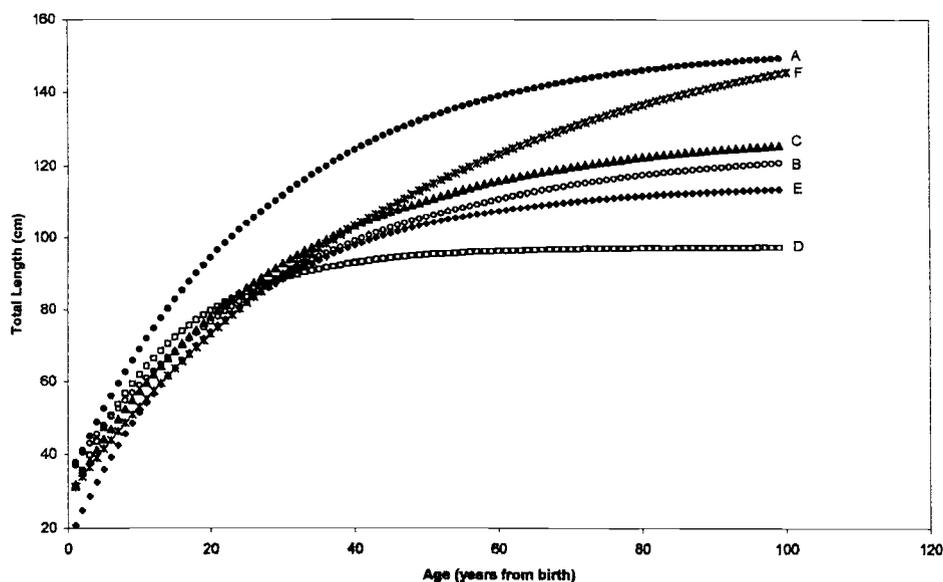


Figure 18: Comparison of the von Bertalanffy growth curves for female spiny dogfish from the northeastern Pacific. (A) Bonham *et al.*, 1949; (B) Ketchen Hecate Strait, 1975; (C) Ketchen Strait of Georgia, 1975; (D) Jones and Geen, 1977c; (E) Saunders and McFarlane, 1993; (F) present study.

Table 1: Age at 50% maturity for female and male spiny dogfish (*Squalus acanthis*) from the previous studies conducted in the Northeastern Pacific Ocean. Ketchen (1975) reported unadjusted and adjusted estimates of age at maturity.

	Bonham <i>et al.</i> , 1949 (Puget Sound)	Ketchen, 1975 Unadjusted Adjusted (Hecate Strait and Strait of Georgia)		Jones and Geen, 1977, a - c (Hecate Strait and Strait of Georgia)	Saunders and McFarland, 1993 (Hecate Strait and Strait of Georgia)
Female	20	34	23	29	35.5
Male	11	17	14	16	
Population Growth rate, λ	3% (1.033)	<0% (0.989)	2% (1.018)	0% (1.002)	<0% (0.986)
Average Fecundity	1.817	1.65	1.65	1.8	1.65
Sample size (N)	215	410	410	14,150	3068

Table 2: Changes in asymptotic growth rate (λ) when female spiny dogfish fecundity was altered.

	Half (0.5)	Doubled (2)	Quadruple (4)	Normal
Growth rate (λ)	0.991 = <0%	1.029 = 3%	1.049 = 5%	1.009 = 1%

Age estimates based on spine increment counts suggested that the females of the "offshore" population of spiny dogfish reach 50% maturity about seven to eight years earlier than that most recently reported for the "coastal" population (Saunders and McFarlane, 1993; see also Ketchen, 1975 unadjusted). However, our estimate was similar to that reported for the "coastal" population by Jones and Geen (1977, a, b, c) and about five to eight years greater than that reported by Bonham *et al.* (1949) and Ketchen (1975; adjusted). The age at maturity calculated by Bonham *et al.* (1949) is likely an underestimate, because it was based on unworn spines only and thus older fish were excluded frequently from the analysis. Ketchen's (1975) adjusted calculation of age at maturity is likely flawed similarly, because it was based on averaging with that of Bonham *et al.* (1949). Jones and Geen (1977 a, b, c) used a different method to determine age that involved vertebral counts (number of rings) from the X-ray spectrometry. Cailliet *et al.* (1983), however, found this method to have low repeatability. Our calculated age at 50% maturity should also be taken with some caution because the relation between spine base diameter and number of rings used to calculate ages from worn spines became weaker at base diameters greater than 3.5 mm (Figure 6). Saunders and McFarlane (1993) used Ketchen's (1975) functional regression for ageing worn spines, which was stronger for spines with base diameters greater than 3.5 mm ($Y = 0.6907 * X^{(2.2115)}$). Of the 221 unworn spines we used to formulate our relation, only 21 were counted to be 10 years or more

(measured at or above the 3.5 mm spine base diameter). Moreover, counting the number of rings on older spines was difficult because of the small distance between the older rings (Figure 5). It should also be noted that our calculation of age at 50% maturity was based on 200 readable spines, whereas those calculated for the "coastal" population by Ketchen (1975; unadjusted) and Saunders and McFarlane (1993) were based on 410 and 3068 spines, respectively. Thus, although the present study demonstrates a lower age at 50% maturity for females in relation to that most recently reported for the "coastal" population (Saunders and McFarlane, 1993), it is still within the previously reported ranges (Jones and Genn, 1977 a, b, c).

Assuming model survival and fecundity rates are similar, the eight year older age at first maturity reported by Saunders and McFarlane (1993) than that of the present study (cf. Jones and Geen, 1977 a, b, c) translates into a decrease in the asymptotic population growth rate to -1.4% per year. The different asymptotic population growth rates derived from the previous studies indicate how increasing female ages at maturity influence negatively the potential growth rate of a population (Table 1). Female age at maturity, thus, is a critical parameter to be carefully considered in fisheries management plans for spiny dogfish, particularly given the late age at which it occurs.

The growth of female and male spiny dogfish in this study did not follow the predicted decline associated with maturity and thus did not fit a von Bertalanffy growth curve well. This may have been due partly to the decline

in strength of the relation used to predict annuli number for worn spines above a spine base diameter of 3.5 mm (i.e. older aged fish) as discussed above.

While the sample size of unworn spines greater than 3.5 mm used to establish the relation is small (21 of 221), the problem is more likely one of increasing inaccuracies with the ageing of larger spines.

Currently in the inshore waters of Puget Sound, the spiny dogfish fishery is second only to that on Pacific salmon (V. Gallucci, Washington State University, personal communication, 2004). The ageing data combined with the population model can aid in the management of this species. Such long-lived and late maturing animals can be affected strongly by intense fisheries. In the Northwestern Atlantic, for example, where spiny dogfish mature at younger ages (females ca. 10 years and males ca. 6 years), a commercial fishery on the species only lasted for five years. Large females were rapidly exploited, decimating the reproductive capacity of the population (Walsh, 1993; Nammack *et al.*, 1985; Kondyurin and Myagkov, 1984; Soldat, 1982). This occurred despite a 10% expected annual population growth rate, in the absence of fishing mortality. A model would have allowed the fishery managers to get a picture of how this population was likely to respond to such an intensive fishery and the possible loss of the larger females. Life history models are thus useful tools in fishery management, allowing managers and scientists the ability to place populations in hypothetical situations and observe the possible responses. They are particularly valuable for evaluating potential

population changes under various conditions of fishing mortality (Hoenig and Gruber, 1990; Sminkey and Musick, 1996).

The present model provides insight into the susceptibility of the Northeastern Pacific population to overexploitation, suggesting that it will be dependent not only on the intensity of fishing mortality, but also on the minimum-size of the fish at entry into the fishery. While the model presented in this study depends on a number of assumptions and is oversimplified, it does provide important insight into the sensitivity of the spiny dogfish life history to changes in annual survival rates. The Puget Sound fishery, for example, might want to consider setting a minimum size, a specific fishing rate and/or a limit on the number of permits to thus allow for some population growth under exploitation. Even so, there does not appear to be much room for a sustainable, directed fishery for spiny dogfish. The model revealed that as fishing mortality increased, the asymptotic population growth rate decreased more rapidly (Figure 12). The Northeastern Pacific spiny dogfish fishery could easily face the same or more severe problems than those faced by that in the Atlantic if the fishery targets larger individuals or fishing mortality rates are even moderately too high for population replacement.

Fecundity can be an important factor influencing population growth and responses to environmental change (Roff, 1992). However, our life history model suggested that changes in fecundity in the spiny dogfish of the Northeast Pacific would have little influence on population growth rate

because of its low value and the rather constrained level of among female variation (range 4 – 14 pups biennially). This low fecundity is a result of the large size of the young produced and the long gestation period. Late age at maturity also contributes to the limited influence of fecundity on population growth rate because of the lag in effects and the decrease in probability of surviving to maturity with increasing age at maturity. Population level changes in fecundity can increase or decrease population growth rate, however, the ability of the fish to do so is likely constrained (e.g. physiologically and/or morphologically). While changes in fecundity are important to consider in the dynamics of populations, in the case of the spiny dogfish, management strategies to protect juveniles (e.g., bycatch reduction) will likely have the most direct impact on potential population growth and be amongst the most important conservation tools.

This Northeastern Pacific spiny dogfish population has been heavily exploited in the past. In the 1940's, there was a major commercial fishery out of Canada for spiny dogfish for liver oil as a source of vitamin A (Ketchen, 1986). This intense fishery devastated the population and Barraclough (1948) suggested that the stock had declined by over 60%. Even with this extreme decline, ten years later the commercial fishers were reporting high catches of spiny dogfish on the fishing grounds (Ketchen, 1986). This relatively fast rebound may be due to the age at maturity lag, where older juveniles, left alone by the fishery because of their small size, mature within 10 years and

move into available habitat. Juveniles (age-classes 1-27), particularly older ones, may be an important resource that needs to be protected if this population experiences heavy exploitation. The elasticity analysis demonstrated that this age class has the greatest proportional affect on the asymptotic growth rate (λ).

In conclusion, our findings indicate that females reach 50% maturity at 28 years and males at 19.5 years for this "offshore" Northeastern Pacific spiny dogfish population. Moreover, average biennial female fecundity was 8.48, with a range of 4 – 14 pups. The elasticity analysis of the age-structured, matrix model suggested that the population was most vulnerable to changes in juvenile survival. Moreover, the model indicated that this "offshore" population could sustain only a low level of exploitation. Beyond the knowledge of the life history provided by this study, an incorporation of a population-specific, natural mortality rate would allow further development of the model and more detailed insight into possible population responses to environmental and anthropogenic driven changes. In the meantime, periodic monitoring should be encouraged to track possible population declines off the northern Washington and central Oregon coasts and prevent potential collapse should the population be targeted by a fishery.

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Distribution and Life History of the Spiny Dogfish (*Squalus acanthias*) off the

Oregon and Washington Coasts

Chapter 4

CONCLUSION

Jaclyn M. Richards

Oregon State University

Department of Fisheries & Wildlife

Nash 104

Corvallis, Oregon 97331-3803

The Northeastern Pacific spiny dogfish (*Squalus acanthais*) population has a broad distribution along the Oregon and Washington coasts. The latitudinal distribution demonstrates high abundances off of the northern Washington and central Oregon coasts. In relation to depth, spiny dogfish were found to have the greatest abundance in shallow waters (55 – 184 m) during the spring and summer months. This study found spiny dogfish distribution to be affected by salinity, chlorophyll, and surface temperature in relation to the Columbia River plume, but unaffected by either the Pacific Decadal Oscillation (PDO) or El Niño-Southern Oscillation (ENSO). Keep in mind that the data used for these analyses may not have been sufficient to draw a definitive conclusion.

Distributional range and migration patterns of long lived fishes, such as chondrichthyes, could be key factors in determining susceptibility of populations to anthropogenic or environmental. Worldwide, most chondrichthyes (55% of the species) occur on the continental shelves from the intertidal zone to 200 m depth (Compagno, 1990). The continental shelves are also the areas where most of the world's fisheries occur. A possible method to reduce shark by-catch would be for fisheries managers to restrict fishing in shallow waters (55 – 184 m) found along the continental shelves during the spring and summer months because this is when and where spiny dogfish were caught in the highest abundance.

This study demonstrated that freshwater intrusions have some effect on shark distribution, although the strength of the effect was uncertain. If most of the shark species inhabiting waters of the Northwest Pacific avoid freshwater intrusions, then during the spring and summer months, when more runoff occurs, these areas could allow fisheries to occur without high shark by-catch issues. This reduction in shark by-catch would be good for both the fishers and the shark populations because usually fishers are not targeting the sharks. This issue of where and when sharks in these waters are caught in high numbers needs to be addressed for all commercially important species in these waters.

When climatic issues were examined, no significant change in the spiny dogfish population was found, but other shark populations along these coasts could be effected by the PDO or ENSO. Changes in shark population due to the climatic changes can be an important factor when using models to examine how a population might respond to different mortality pressures. The model used for this study was oversimplified, but it was able to demonstrate how this spiny dogfish population might respond to increased fishing pressure and that having an accurate age at first maturity is extremely important for model input.

Matrix models can be very useful in helping managers and scientists to determine sustainable fishing mortality rates for sharks throughout the world's oceans (Caswell, 2001). They can be used to compare previously exploited

populations with populations, which have experienced no directed fishery, such as the Northwestern Atlantic spiny dogfish versus the Northeastern Pacific spiny dogfish (Nammack *et al.*, 1985). These models could be used to examine the different life history characteristics occurring in conspecific shark populations, which inhabit different oceans.

This study demonstrated that examining distributional patterns and life history characteristics of long lived fish is important to analyzing how a population will respond to anthropogenic or environmental changes. Matrix models are also shown to be helpful tools in fisheries management, but need to be used with caution. These models are developed from life history characteristics calculated from sample populations. Life history studies of long lived fishes can demonstrate how these fish could be effected by changes in their environment.

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APPENDIX

Appendix 1: Age-structured matrix model

ORIGIN = 1

asm := 28

maxage := 100

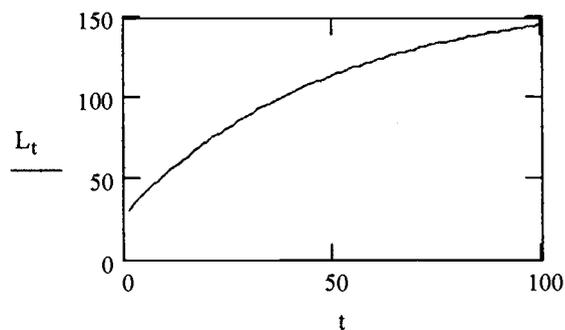
t := 1..maxage

adult := asm..maxage

Growth curve (in cm - translate to inches):

Linf := 163.632, k := 0.02013, tzero := -9.5056

$$L_t := \text{Linf} \left[1 - e^{-k[t - (\text{tzero})]} \right]$$



$$\text{minsize} := \frac{28}{.3937}$$

round(x) := if(x - floor(x) < 0.5, floor(x), ceil(x))

$$\text{minage} := \text{round} \left[\frac{-\ln \left[\frac{-(\text{minsize} - \text{Linf})}{\text{Linf}} \right] - k \cdot \text{tzero}}{k} \right]$$

minsize = 71.12

minage = 19

7	46.27
8	46.81
9	50.903
10	53.15
11	55.352
12	57.511
13	59.626
14	61.7
15	63.732
16	65.723
17	67.675
18	69.588
19	71.463
20	73.3
21	75.101
22	76.866
23	78.595
24	80.29
25	81.952
26	83.58
27	85.176
28	86.74
29	88.273
30	89.775
31	91.247
32	92.69
33	94.105
34	95.491
35	96.849
36	98.18
37	99.485
38	100.764
39	102.017
40	103.245
41	104.449
42	105.629
43	106.785
44	107.918
45	109.029
46	110.116
47	111.184
48	112.23
49	113.255
50	114.259
51	115.243
52	116.208
53	117.153
54	118.08
55	118.988
56	119.878
57	120.75
58	121.605
59	122.443
60	123.264
61	124.069
62	124.857
63	125.63
64	126.388
65	127.13
66	127.858
67	128.571
68	129.27
69	129.955
70	130.626
71	131.284
72	131.929
73	132.561
74	133.181
75	133.788
76	134.383
77	134.966
78	135.537
79	136.097
80	136.646
81	137.184
82	137.711
83	138.228
84	138.734
85	139.231
86	139.717
87	140.194
88	140.661
89	141.119
90	141.568
91	142.008
92	142.438
93	142.861
94	143.275
95	143.681
96	144.079
97	144.469
98	144.851
99	145.225
100	145.592

L =

(Appendix 1 – continued)

$$F := 0.00 \quad M := 0.094 \quad \text{fsurv} := e^{-(M+F)}$$

$$\text{ufsurv} := e^{-M}$$

survival rate: fished age classes

unfished age classes

$$\text{ufsurv} = 0.91$$

$$\text{fage} := \text{minage}.. \text{maxage} - 1$$

$$\text{ufage} := 1.. \text{minage}$$

Fecundity is age dependent

$$\text{juv} := 1.. \text{asm} - 1$$

$$q := 1.. 73$$

$$\text{neosurv} := 0.750$$

$$\text{fec}_{\text{juv}} := 0$$

$$f_q := 2.124$$

$$\text{fec}_{q+\text{asm}-1} := f_q \cdot \text{neosurv}$$

Construct the matrix

$$M_{1, \text{adult}} := \text{fec}_{\text{adult}}$$

$$M_{\text{ufage}+1, \text{ufage}} := \text{ufsurv}$$

$$M_{\text{fage}+1, \text{fage}} := \text{fsurv}$$

$$\text{rows}(M) = 100$$

$$\text{cols}(M) = 100$$

$$\lambda := \max(\text{Re}(\text{eigenvals}(M)))$$

$$\lambda = 1.009$$

$$\ln(\lambda) = 0.009$$

The image displays a large, dense grid of small tables, likely a statistical or reference table. The grid is composed of many small, individual tables arranged in a regular pattern. Each small table appears to have multiple columns and rows, but the text within them is too small to be legible. The overall layout is a large rectangular area filled with this grid structure.

$$w_2 := \frac{\text{eigenvec}(M_2, \lambda)}{\sum \text{eigenvec}(M_2, \lambda)} \quad v_2 := \frac{\text{eigenvec}(M_2^T, \lambda)}{\text{eigenvec}(M_2^T, \lambda)_1}$$

1	1
2	1.109
3	1.229
4	1.363
5	1.511
6	1.675
7	1.857
8	2.059
9	2.283
10	2.532
11	2.807
12	3.112
13	3.45
14	3.825
15	4.241
16	4.702
17	5.214
18	5.78
19	6.409
20	7.106
21	7.879
22	8.735
23	9.684
24	10.737
25	11.904
26	13.199
27	14.634
28	16.224
29	16.224
30	16.222
31	16.221
32	16.22
33	16.219
34	16.217
35	16.215
36	16.213
37	16.211
38	16.209
39	16.206
40	16.203
41	16.2
42	16.198
43	16.192
44	16.188
45	16.183
46	16.178
47	16.171
48	16.165
49	16.157
50	16.149
51	16.14
52	16.13
53	16.119
54	16.106
55	16.092
56	16.077
57	16.06
58	16.041
59	16.02
60	15.997
61	15.972
62	15.943
63	15.912
64	15.877
65	15.838
66	15.795
67	15.747
68	15.694
69	15.636
70	15.571
71	15.499
72	15.419
73	15.331
74	15.233
75	15.124
76	15.003
77	14.87
78	14.721
79	14.557
80	14.375
81	14.173
82	13.949
83	13.7
84	13.425
85	13.12
86	12.781
87	12.406
88	11.99
89	11.528
90	11.017
91	10.45
92	9.821
93	9.124
94	8.361
95	7.494
96	6.544
97	5.49
98	4.322
99	3.027
100	1.592

0.098
0.088
0.08
0.072
0.065
0.059
0.053
0.048
0.043
0.039
0.035
0.032
0.028
0.026
0.023
0.021
0.019
0.017
0.015
0.014
0.012
0.011
0.01
0.009
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0.001
9.431-10 ⁻⁴
8.506-10 ⁻⁴
7.972-10 ⁻⁴
6.92-10 ⁻⁴
6.241-10 ⁻⁴
5.629-10 ⁻⁴
5.077-10 ⁻⁴
4.579-10 ⁻⁴
4.13-10 ⁻⁴
3.725-10 ⁻⁴
3.36-10 ⁻⁴
3.03-10 ⁻⁴
2.733-10 ⁻⁴
2.465-10 ⁻⁴
2.224-10 ⁻⁴
2.006-10 ⁻⁴
1.809-10 ⁻⁴
1.631-10 ⁻⁴
1.472-10 ⁻⁴
1.327-10 ⁻⁴
1.197-10 ⁻⁴
1.08-10 ⁻⁴
9.739-10 ⁻⁵
8.783-10 ⁻⁵
7.922-10 ⁻⁵
7.145-10 ⁻⁵
6.445-10 ⁻⁵
5.813-10 ⁻⁵
5.243-10 ⁻⁵
4.729-10 ⁻⁵
4.265-10 ⁻⁵
3.847-10 ⁻⁵
3.47-10 ⁻⁵
3.129-10 ⁻⁵
2.822-10 ⁻⁵
2.546-10 ⁻⁵
2.298-10 ⁻⁵
2.071-10 ⁻⁵
1.868-10 ⁻⁵
1.685-10 ⁻⁵
1.519-10 ⁻⁵
1.37-10 ⁻⁵
1.236-10 ⁻⁵
1.115-10 ⁻⁵
1.006-10 ⁻⁵
9.07-10 ⁻⁶
8.19-10 ⁻⁶
7.378-10 ⁻⁶
6.655-10 ⁻⁶
6.002-10 ⁻⁶
5.414-10 ⁻⁶
4.883-10 ⁻⁶
4.404-10 ⁻⁶
3.972-10 ⁻⁶
3.593-10 ⁻⁶

(Appendix 1 – continued)

$i := 1..100 \quad j := 1..100$

$$E2_{i,j} := \frac{v2_i \cdot w2_j \cdot M2_{i,j}}{v2 \cdot w2 \cdot \lambda}$$

$$E2_{2,1} = 0.033$$

The table consists of a dense grid of data points on graph paper. The grid is approximately 30 columns wide and 100 rows high. The data is organized into several distinct sections:

- Top Section:** Contains numerical values, likely representing coordinates or measurements, arranged in a regular grid.
- Middle Section:** Features larger text labels, possibly identifying specific data points or groups of data. These labels include terms like "POINT", "LINE", and "AREA", followed by alphanumeric identifiers.
- Bottom Section:** Continues the grid of numerical data, mirroring the structure of the top section.

The overall layout suggests a detailed technical drawing or a data table for a specific project, with the grid providing a precise reference for the data points.