LIFE HISTORY, DEMOGRAPHY, AND ECOLOGY OF THE SPINY DOGFISH (*SQUALUS ACANTHIAS*) IN THE GULF OF ALASKA

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A

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Abstract

The spiny dogfish (*Squalus acanthias*) is a small, cosmopolitan shark species, common in sub-tropical and sub-arctic waters. The species is often targeted commercially in most areas of the world throughout it's range, and in some cases it is overfished or the subject of conservation concern. In the Gulf of Alaska, spiny dogfish are not targeted and not generally retained, but incidental catches can be high for this schooling species. Previously, biological parameters for spiny dogfish in the Gulf of Alaska were assumed from estimates for this specie's neighboring areas, including British Columbia and Washington State. The purpose of this study was to examine spiny dogfish in the Gulf of Alaska and estimate important parameters for stock assessment in four stages: (1) general biology, distribution, and life history; (2) modeling age and growth; (3) population demographic modeling; and (4) ecological interactions revealed by diet analysis. Spiny dogfish are similar in length in the Gulf of Alaska to neighboring regions, but mature at larger sizes and have a greater fecundity than reported elsewhere. There is high natural variability in estimated ages for the species, which is reflected in the poor fit of the growth models, possibly owing to measurement error from using the dorsal fin spine as the aging structure. A two-phase growth model provided the statistical best fit. However, questions were raised about the biological interpretation of the model and whether more traditional models (e.g., von Bertalanffy and Gompertz) may be more appropriate. Using the life-history and growth data, Leslie matrix type age- and stage-based demographic models were created to estimate sustainable fishing mortality rates and to examine the risk of harvest scenarios. Female Gulf of Alaska spiny dogfish can

support up to a 3% annual harvest rate; fisheries that target juveniles have the greatest risk of population decline below threshold levels. Spiny dogfish are generalist opportunistic feeders that feed on whichever prey is available, however shrimp are the most important prey type, followed by cephalopods. Results of this study will be used in future ecosystem modeling and stock assessments for this species. Taking into account the history of targeted fisheries for the species on the U.S. east coast and in British Columbia and Washington, as well as the susceptibility of the species to overfishing, fishery managers will need to take a cautious approach should a target fishery develop in the Gulf of Alaska.

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Chapter 1: Introduction

The spiny dogfish (*Squalus acanthias*) is a small species of shark, common to sub-tropical waters around the globe. This species is also commercially harvested in most of the regions it inhabits, except the Gulf of Alaska (GOA). In the eastern North Pacific Ocean, spiny dogfish have been harvested for over a century in British Columbia (BC, Canada) and Puget Sound (WA), while in the western North Atlantic Ocean, spiny dogfish have only been harvested since the mid 1980s. In both examples, the commercial harvest followed a classic "boom and bust" pattern where harvest increased rapidly, followed by steep declines due to overharvesting, catch limitations, or market changes. In the U.S., western North Atlantic spiny dogfish stocks were determined to be overfished in 1998 (Rago et al. 1998), with strict catch restrictions put in place shortly thereafter. The fishery targeted the largest females, which have the highest fecundity and greatest offspring survival (Rago et al. 1998, Sosesbee 2002), resulting in recruitement overfishing and a strongly male-biased population. In the case of the BC and WA fisheries, the "boom" was largely driven by market changes for oil and vitamin A, meaning that the "bust" phase was a result of reduced demand (Ketchen 1986). In the most recent phase beginning in the mid 1970s, the fishery supplied meat for human consumption, catches peaked in the 1990s, and began to decline while the market demand was still present. Stock assessments do not exists for spiny dogfish in BC or WA, but survey indices in BC showed a decline in recruitment and the average size of landed

spiny dogfish declined by 13 cm (King and McFarlane 2009), suggesting that that population may be overfished.

Spiny dogfish are a long-lived, slow growing, and late maturing species, all characteristics indicative of a species that is vulnerable to overfishing. This conclusion based on life-history theory is supported by the history of spiny dogfish fishing that shows that the species is susceptible unless harvest is managed at relatively low sustainable levels. In the GOA, spiny dogfish are not commercially harvested, but frequently occurs as bycatch (Tribuzio et al. 2009). Given catch restrictions elsewhere and continued market demand, there is growing interest to harvest spiny dogfish in the GOA. Currently, observed catches of spiny dogfish in the GOA average about 700 t annually, which does not include catches from unobserved fisheries such as the halibut and salmon fisheries. Similar to BC and WA, a stock-assessment model does not exist for GOA spiny dogfish, but survey biomass indices and catch estimates are updated and monitored annually (Tribuzio et al. 2009).

There were a number of motivating factors for this study. First was the need for regionally specific research because all biological knowledge of the species is borrowed from areas outside of the GOA and using those parameters as a proxy for GOA spiny dogfish may not be appropriate. Second, with the reauthorization of the Magnuson-Stevens Fishery Conservation and Management Act, the practice of setting catch specifications for sharks in aggregate with the "other species" will be discontinued in favor of establishing total allowable catches for individual shark species, necessitating the need for improved stock assessments of each species. Lastly, if catches increase due to

market development or other reasons, managers will need to know sustainable harvest rates as well as the risk of the population falling below threshold levels (i.e., biomass of maximum sustainable yield, B_{MSY}) is.

The study reported in this dissertation was funded by the North Pacific Research Board to investigate the spiny dogfish in the Gulf of Alaska. All sample collections were conducted in compliance with University of Alaska Fairbanks Institutional Animal Care and Use Committee guidelines (protocol number 04-36). This dissertation consists of four chapters, each building on the results of the others. The first chapter is a general overview of the biology of the spiny dogfish in the GOA, examining reproduction, size distributions, maturity, and natural mortality. Dorsal fin spines were used to age and model the growth of spiny dogfish in the second chapter. The age data, fecundity, and natural mortality estimates were incorporated into age- and stage-based Leslie matrix models to estimate sustainable fishing mortality rates and a risk analysis in the third chapter. The last chapter is an examination of the diet of spiny dogfish and its trophic position in the GOA.

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Chapter 2: Life history of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska[1]

2.1 Abstract

The spiny dogfish (*Squalus acanthias*) is a small shark species common in coastal temperate to sub-arctic waters. Spiny dogfish have been and are harvested in most regions throughout their range. However, spiny dogfish have not been subjected to targeted commercial exploitation in the Gulf of Alaska. The purpose of this study was to examine the basic life history and distribution of spiny dogfish in the Gulf of Alaska to establish a baseline for future comparison and to provide critical information for demographic modeling and stock assessments. Average total length of females (87.7 cm) was significantly larger than males (80.3 cm); size at 50% maturity (74.5 cm and 97.3 cm, males and females, respectively) and age at 50% maturity (21 and 36 years, respectively) were also significantly different between the sexes. Average fecundity was 8.5 pups per female, and individual fecundity was a linear function of either length or whole weight. The best estimate of instantaneous natural mortality was 0.097. The delayed age of maturity, low natural mortality, and low rates of reproduction imply that only low rates of fishing mortality are sustainable. We provide first-time evidence that a small portion of the adult female population may undergo an extended resting period between pregnancies of one year or more.

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[1] Tribuzio, C. A. and G. H. Kruse. (in prep). Life history of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Prepared for submission to Marine and Coastal Fisheries.

2.2 Introduction

Spiny dogfish (*Squalus acanthias*) are a small, cosmopolitan species of shark. They inhabit sub-tropical and temperate waters in all ocean basins, generally over the continental shelf (Compagno 1984). Spiny dogfish tend to form large schools, often segregated by size, sex, or reproductive state (Compagno 1984; Ketchen 1986; Tribuzio et al. 2009a). They are opportunistic and highly active feeders (Jones and Geen 1977; Bowman et al. 2000; Tribuzio et al. in prep). As a result they are often caught in a variety of commercial and sport-fishing activities. Owing to their small size and high survival in captivity, this species is popular for public aquaria, as teaching tools, and for laboratory research. However, field research on wild populations is more limited and geographic plasticity in life-history attributes drives the need for regionally specific studies are necessary. As there is a lack of spiny dogfish studies in the Gulf of Alaska (GOA) all knowledge of the species in the Northeast Pacific Ocean is based on studies conducted in British Columbia (BC) and Washington (WA) State (Ketchen 1972; Saunders and McFarlane 1993; Tribuzio et al. 2009a).

Regionally specific research is important for appropriate fisheries management, particularly in the case of spiny dogfish. Life-history characteristics can vary substantially between populations (or stocks or management areas) especially if migration rates between those groups is low (Conover 1998; Guinand et al. 2004). Latitudinal changes in spiny dogfish growth rates exist in the North Pacific between southern California and the Strait of Juan de Fuca (Vega et al. 2009). On this basis, Vega et al. (2009) proposed a northern and southern demographic subunit along the coast, but

they only proposed a dividing line between the two clades and not limit boundaries. It is unknown if the GOA spiny dogfish are part of this northern clade or a separate clade. Tagging studies conducted in both WA and BC suggest two different demographic groups, coastal and inside waters, with the coastal (those inhabiting the west coast of Vancouver Island and WA) spiny dogfish being more likely to undertake large-scale migrations and the inside waters (those inhabiting the Puget Sound, PS, or Strait of Georgia) spiny dogfish more likely to remain in the general area they were tagged (McFarlane and King 2003; Taylor et al. 2009).

Spiny dogfish are commercially targeted in both United States (US) and Canadian (CA) waters of the North Pacific. This transboundary fishery is centered in the Puget Sound (US), and the Strait of Georgia and the west coast of Vancouver Island (CA) (Bargmann 2009; Wallace et al. 2009). This area is also viewed as the center of abundance for the species in the eastern North Pacific (Ketchen 1986). Spiny dogfish are not targeted in the GOA, but on average about 700 metric tons (t) of catch is reported annually, which does not include bycatch in unobserved fisheries such as the halibut and state-managed (e.g., salmon) fisheries where substantial bycatch sometimes occurs (Tribuzio et al. 2009b). While GOA spiny dogfish cannot be considered as a virgin population, the level of harvest is sufficiently low that current population parameters can be used as a lightly exploited population baseline for future comparisons to spiny dogfish population under commercial harvest.

The primary goal of this study was to examine the GOA population of spiny dogfish for life-history parameters before a targeted fishery on this species might develop

and potentially change those measures. Specifically, the objectives of this study were to define reproductive parameters of spiny dogfish, such as length and age at maturity, to estimate demographic parameters, such as natural mortality, and to investigate seasonal and local differences in size and spatial distributions in the GOA. There are important gaps in the understanding of spiny dogfish life-history in this region. Results of this study will be incorporated into demographic analyses and used in stock assessments of this species for fisheries management.

2.3 Methods

Spiny dogfish were sampled from July 2004 and April 2007 by a variety of platforms: targeted rod and reel sport fishing, longline and trawl assessment surveys, and commercial trawl and gill-net fisheries. Samples were collected widely across the GOA during targeted research cruises, National Marine Fisheries Service and Alaska Department of Fish and Game research surveys, and from commercial fishery bycatch (Figure 2.1). All sample collections were conducted in compliance with University of Alaska Fairbanks Institutional Animal Care and Use Committee guidelines (protocol number 04-36). All spiny dogfish were sexed and length was measured to the nearest 0.1 cm (total length extended = TL_{ext}; total length natural = TL_{nat}; fork length = FL; and precaudal length = PCL; Tribuzio et al. 2009a); in addition, whole and eviscerated weight was recorded. Maturity, reproductive state, and fecundity (where applicable) were assessed following the criteria of Tribuzio et al. (2009a). Male clasper inner length (CIL), from the anterior margin of the cloaca to the posterior tip of the left clasper, was

recorded to the nearest 0.1 cm. For pregnant females, the TL_{ext} and sex of embryos were recorded. Spiny dogfish may abort pups during the catching process, either prior to capture or on the deck of the boat. When pups were aborted on the deck, they were recorded, but not assigned to any female. Ages for some analyses were ascertained in a companion study (Tribuzio et al. 2010).

Data were categorized by sex (male or female), region of capture (Cook Inlet-CI, Prince William Sound-PWS, Yakutat Bay-YAK, and Gulf of Alaska-GOA), gear type (longline-LL, set net-SET, sport-SPT and trawl-TWL), and season (spring, summer and autumn). Table 2.1 summarizes the sample size for each data grouping. Average and standard deviation of TL_{ext} were calculated for each category. A students t-test (Zar 1999) was used to determine if the means and medians were significantly different between categories at α=0.05 (H_0=means are equal). There is no standard for length measurements in sharks, and different lengths are reported in different studies. Here, linear length-at-length and eviscerated weight-at-whole weight conversion equations and exponential weight-at-length curves were created to convert between the different length and weight measurements, and to allow comparison of the results of this study to others.

To determine maturity, we followed the maturity scales described in Tribuzio et al. (2009a) and (Stehmann 2002; Taylor et al. 2009). However, assessing maturity in spiny dogfish is not always unambiguous. Three researchers participated in field collections at different sampling events, each with different levels of experience in maturity identification. If maturity was questionable or the sampler was not confident in their assessment of maturity, that sample was removed from age and length at 50%

maturity calculations. Male and female age and TL_{ext} and male *CIL* at 50% maturity were estimated using the following equations (da Silva and Ross 1993):

$$P = \frac{e^{f+gTL_{ext}}}{1+e^{f+gTL_{ext}}}, \qquad \text{(Eq. 2.1)}$$

where P is the proportion mature and f and g are estimated parameters. An alternate model for males using *CIL* at TL_{ext} can also be used to estimate size at 50% maturity using the following equation (da Silva and Ross 1993):

$$CIL = h + \frac{i * e^{j+kTL_{ext}}}{1+e^{j+kTL_{ext}}}, \qquad \text{(Eq. 2.2)}$$

where h, i, j, and k are estimated parameters. The estimate for TL_{ext} at 50% maturity using this equation is the point of inflection along the curve, $TL_{ext} = -j/k$. Models were run using R statistical software (R, vers 2.10.0, www.r-project.org) and 95% confidence intervals were estimated by bootstrapping the residuals and re-estimating the parameters 5,000 times. Confidence intervals were the 97.5th and 2.5th percentile of the results.

For spiny dogfish, individual fecundity is generally reported as a linear function of maternal length. Here, we examined fecundity as a linear function of length, age, and weight (both whole and eviscerated). Average fecundity was calculated in two ways: (1) average of the pup count of pregnant females (hereafter termed "individual average"); and (2) total number of pups divided by the number of pregnant females (hereafter termed "total average"). The individual average is what is generally reported in literature, but may underestimate the actual fecundity. The latter estimation procedure accounts for pups that were aborted on deck and therefore unable to be assigned to a particular female. To facilitate comparisons with other studies we also estimated

fecundity as a quadratic function of length using least squares regression. A t-test of the average fecundity and ANOVAs of the fecundity regressions by gear types were conducted to indicate if gear type differentially affected the rate of pup abortion. To explore possible maternal effects, we graphed the length of the pups against female size. Similarly, we also plotted pup sex ratio against pup size to determine how measurement error might change as the pup size increased and sex determination became more certain. Lastly, embryo lengths were categorized by season and binned by 1-cm size classes to examine the trend in pup size classes by season of capture to try to determine at what time of year pupping might occur.

Instantaneous natural mortality rate (M) for spiny dogfish in the GOA was estimated with a variety of life-history-based methods (Table 2.1). A total of 12 estimates were calculated based on gonadosomatic index (GSI), maximum age, age at 50% maturity, and von Bertalanffy growth parameters: k, t_0, L_∞, and W_∞, (Alverson and Carney 1975; Pauly 1980; Hoenig 1983; Gunderson and Dygert 1988; Chen and Watanabe 1989; Jensen 1996; Frisk et al. 2001). In this study, we used four GSIs: ovary weight/eviscerated weight, ovary weight/whole weight, standardized ovary weight/eviscerated weight, and standardized ovary weight/whole weight. Ranges for M estimates were calculated using the upper and lower 95% confidence intervals of the input parameters if available. The von Bertalanffy growth parameters were obtained from a companion study (Tribuzio et al. 2010). We utilized two estimates of maximum age, 80 years (Saunders and McFarlane 1993) and 107 years (G. McFarlane, pers. comm.). For the Pauly (1980) models, temperature was estimated as the long-term

average surface temperature at the GAK1 station (http://www.ims.uaf.edu/gak1/) in the northern GOA. For the Frisk et al. (2001), model we chose the Requiem shark model over the Rajidae model because spiny dogfish have life histories more similar to the former.

2.4 Results

A total of 2,151 spiny dogfish were sampled for this study (650 males and 1,501 females). The average size of males was 80.3 cm TL_{ext} (53.0 – 98.7 cm, minimum and maximum) and the average size of females was 87.7 cm (50.0 – 122.6 cm) (Figure 2.2). The mean and median lengths for males were significantly smaller than females ($p < 0.01$). Cook Inlet and PWS males were significantly larger than those from all other regions ($p < 0.01$) and YAK males were significantly larger than GOA males ($p < 0.01$) and smaller than CI and PWS males (Figure 2.3A, $p < 0.01$). Longline-caught males were significantly smaller than all other gear types ($p < 0.02$); SET, SPT, and TWL were not significantly different from each other (Figure 2.3B, $p > 0.1$). Mean and median male sizes differed in each of the three seasons with autumn being largest and summer the smallest (Figure 2.3C, $p < 0.01$). Females caught in CI were significantly larger than those caught in all other regions ($p < 0.01$), PWS and YAK females were not significantly different from each other ($p = 0.43$) and both were significantly larger than GOA females (Figure 2.3D, $p < 0.01$). Mean and median female sizes caught on SPT or SET gear were not significantly different from each other ($p = 0.66$) and both were significantly larger than LL and TWL caught dogfish ($p < 0.01$). Longline and TWL caught females were not significantly different in length (Figure 2.3E, $p = 0.63$). Similar

to males, mean and median female size differed among all three seasons with autumn being the largest and summer the smallest (Figure 2.3F, $p < 0.01$).

Male and female length-at-length, length-at-weight, and weight-at-weight data were pooled for estimated conversions because there was no significant difference among the sexes (t-test, $p < 0.001$). All length-at-length conversion model fits had $R^2 \geq 0.98$, R^2 for converting whole weight to eviscerated weight was 0.96 and for the weight-at-length conversions were 0.87 for males and 0.94 for females (Table 2.3). All subsequent length analyses were conducted with TL_{ext} measurements.

Maturity of the sampled spiny dogfish varied depending on sex and sampling categories. Overall, 79% of males were mature compared to 43% of the females. The lowest proportion of mature males (59%) was in PWS and the greatest (97%) was in the autumn. For females, the proportion mature was low (16%) in YAK and high (73%) in SET.

A number of large females were observed that appeared to be mature that were neither pregnant (maturity stage A-H, Tribuzio et al. 2009a) nor preparing for pregnancy (as in stage I, Tribuzio et al. 2009a). These females did not have obvious signs of developing eggs for the next pregnancy as would be expected in non-pregnant mature females; however, the oviducal gland appeared developed, supporting the classification of "mature". Further, pregnant females were encountered that did not show signs of developing ova for the next pregnancy (Figure 2.4).

The minimum/maximum size of immature animals sampled was 53.9/98.7 cm for males and 60/122.6 cm for females. Male length at 50% maturity was estimated at 74.5

cm (73.1 – 75.4 cm, 95% CI) and female length at 50% maturity was 97.3 cm (96.0 – 98.4 cm) and male *CIL* at 50% maturity was estimated by equation 1 was 7.5 cm (7.3-7.7 cm) (Figure 2.5A-C). Male age at 50% maturity was 20.9 years (19.9 – 22.0 years) and female age at 50% maturity was 36.1 years (34.0 – 38.9 years) (Figure 2.5D-E). Male *CIL* and TL_{ext} at 50% maturity estimated by equation 2 were 6.2 cm (6.1 - 6.4 cm) and 72.0 cm (71.5-72.3 cm), respectively (Figure 2.5F). All estimated parameters are reported in Table 2.4.

Fecundity was significantly influenced by length, weight, and eviscerated weight (all $p < 0.01$) but not age ($p = 0.28$). Individual average fecundity (1) was 7.98 (0.5-15.4 95% CI, 3.81 standard deviation), and total average fecundity (2) was 8.46 pups/female and ranged between 1-23 pups. The individual fecundity (which does not include aborted pups) increased 0.25 pups for every cm of growth in length and 0.42 pups for every kg increase in weight (Figure 2.6). The quadratic regression of fecundity with length resulted in the equation: fecundity=$0.0065TL_{ext}^2$-$1.1TL_{ext}$+52.123, which was not significantly different from the linear regression ($p = 0.75$). The t-test of the average fecundities between gear types found no significant differences at $\alpha = 0.05$, similarly the ANOVA tests of the linear regressions also found no significant differences at $\alpha = 0.05$ between the fecundities for each gear type.

No trend in embryo size due to maternal size was evident; however, the sample sizes at each reproductive stage may be too small to detect differences. There was a strong positive correlation between the male:female pup sex ratio and the TL_{ext} of the pups (correlation coefficient = 0.69, $R^2 = 0.48$, Figure 2.7). Smaller pups (< 15 cm) tend

to be identified more often as females while those > 15 cm tend to be identified more often as males, suggesting that males are more difficult to identify in smaller pups and sex ratios should only be estimated from near-term pups (fully absorbed yolk sacs, stage H, Tribuzio et al. 2009a).

During each of the three seasons sampled, there were two clear size classes of pups, supporting the published estimates of 18-22 months for gestation (Figure 2.8). Pups in the smaller size class were about 3 cm TL_{ext} and showed little progression in size into the summer, while the larger size class was about 14 cm TL_{ext} and progressed to about 20 cm TL_{ext} in the summer. In autumn, the small size class progressed to about 7 cm and the large size class progressed to about 23 cm. The smallest pups (minimum of 2.6 cm) were encountered in the spring and summer, while the largest pups (up to 26.6 cm) were encountered in the autumn. Seven females were sampled that had near-term pups, two of which were sampled in the summer and five were sampled in the autumn. Stage H is estimated to last about 1-2 months (Tribuzio et al. 2009a) so those females could potentially give birth from August through November.

Point estimates of M ranged from 0.035 (Gunderson and Dygert 1988 (4)) to 0.151 (Frisk et al. 2001). Eliminating the models that did not incorporate any elasmobranch species in their derivation leaves seven methods: Frisk et al. (2001), Gunderson and Dygert (1988) (1-4) and Pauly (1980) (1 and 2). The Frisk et al. (2001) and Pauly (1980) weight-based (2) methods both result in estimates of M that seem unreasonably high. Of the Gunderson and Dygert (1988) methods, model (1) is likely the best of the four, as the GSI is the same format as that used in the original model

derivation. Further, Gunderson and Dygert (1988) used Puget Sound spiny dogfish in the model derivation, whereas Pauly (1980) used two species of Lamnidae sharks from the Northwest Atlantic. Therefore, we conclude that the best estimate of M for GOA spiny dogfish is 0.097 (Gunderson and Dygert 1988).

2.5 Discussion

Spiny dogfish in the GOA, while not significantly different in overall size, have significantly different reproductive characteristics from those sampled in studies conducted in neighboring regions. Maximum and average lengths observed in this study were similar to those reported in BC and Puget Sound; however, both male and female length at 50% maturity was significantly larger for GOA spiny dogfish than for Puget Sound (Tribuzio et al. 2009a) and BC (Ketchen 1972; Saunders and McFarlane 1993) spiny dogfish. Further, individual average fecundity and the maximum number of pups observed per female were larger in GOA spiny dogfish than in other studies. Moreover, we provide first time evidence that there may be an extended non-pregnant period between pregnancies.

While differences in characteristics between spiny dogfish inhabiting different ocean basins are expected (i.e., North Atlantic versus North Pacific spiny dogfish), dramatic differences between spiny dogfish inhabiting the same coastline of the eastern North Pacific Ocean is more surprising. A mark-recapture study may help explain some of these differences. Much of the reproductive and life-history research from the Northeast Pacific was based on spiny dogfish caught in inside waters (Ketchen 1972;

Tribuzio et al. 2009a). The migration rate between the inside waters and coastal dogfish is low (e.g. only 3% of fish tagged in inside waters of the Strait of Georgia were collected in coastal waters of WA or BC, McFarlane and King 2003), enough that different characteristics develop over time. The spiny dogfish collected for this study were more likely of the coastal type because GOA spiny dogfish are migratory similar to the coastal type (Tribuzio, unpublished data). However, it is unknown if the GOA spiny dogfish are part of a continuous distribution with the coastal type in WA and BC.

Other potential sources of the disparity between studies could be measurement error. With regards to fecundity, pregnant female spiny dogfish, especially those in the latter half of the pregnancy, tend to abort pups during the catching process. It is possible that pups had been aborted prior to landing; however, the probability of this having a significant impact on the estimates of fecundity may be small. We used four gear types in this study, some more invasive (trawling) than others (sport fishing) and there was no significant difference in the fecundity at size and average fecundity among the different gear types. These results suggest that gear type is not a factor in the potential for pups to be aborted during the catching process. At the same time, these results cannot address the question if pups are aborted at all. Pup abortion on deck is not uncommon, especially for near-term pups, but those pups were counted in this study.

Another source of measurement error could be misidentification of maturity. In this study, we noticed difficulties in identifying mature females, particularly when samplers had less experience. With spiny dogfish, the sampler is more likely to falsely identify a mature animal as immature than to identify an immature animal as mature. In

our case, when maturity was questionable or the sampler was uncertain, that sample was removed from the analysis. Removing the questionable samples from the analysis could have the same effect as falsely identifying a mature animal as immature and result in an artificially high estimated size or age at 50% maturity but this effect is likely minimal because only about 3% of female samples were removed. In this study, it is unlikely that misidentification of maturity had a significant impact on the model results. Examination of the female length at 50% maturity model results (Figure 2.5B) shows that the model fit was good and the data points, with a few exceptions, were clustered near the model. In particular, only two data points appear to have a suspiciously low percent maturity at size. Nevertheless, it is something that should not be forgotten when interpreting the results, and conducting a blind assessment of sampler's ability to identify maturity may provide means to account for some of the measurement error.

Generally speaking, sexually mature female spiny dogfish have some evidence of either pregnancy or developing ovarian follicles providing easy criteria for maturity classification. However, large females (> 110 cm) were encountered in this study that were neither pregnant, nor did the ovaries contain developing eggs large enough for ovulation (~40 mm diameter, Tribuzio et al. 2009a). It is possible that some of these females were sterile, not yet mature, or senescent. Senescence has not been confirmed in elasmobranchs, but a few studies have reported individuals that exhibited those characteristics. The most striking example is in the Aleutian skate (*Bathyraja aleutica*), where the number of oocytes (and thus fecundity) peaked and then declined towards the largest sizes and some large individuals appeared to have atrophied ovaries (Ebert 2005).

Two other studies (Atlantic angel sharks, *Squatina dumeril*, Baremore 2010; and school shark, *Galeorhinus galeus*, Peres and Vooren 1990) reported one (each) large individual that appeared to have atrophied ovaries. Fecundity did not appear to decrease at the largest sizes, but ovaries were not examined in detail in this study so senescence cannot be ruled out. However, it is also possible that some were in an extended resting period between pregnancies. Evidence to support this theory is based on what appeared to be developed oviducal glands in these females. Oviducal glands must enlarge prior to the first ovulation for the ova to be able to pass through, in mature spiny dogfish a developed oviducal gland is generally at least 15 mm in diameter (Tribuzio 2004). Spiny dogfish in most regions have about a 22-month gestation, followed by a brief "resting" period of about two months and then begin another pregnancy, with no evidence of extended resting periods (Ketchen 1972; Campana et al. 2009; Tribuzio et al. 2009a). Samples collected in this study suggest that in the GOA, a small portion of the mature female population may take an extended resting period between pregnancies. Extended resting periods between pregnancies have not specifically been studied in sharks, but observations of salmon sharks also suggest a possible extended resting period between pregnancies (Goldman and Musick 2006; Tribuzio 2004). Some high latitude or deep-water sharks have been reported to have extended gestations of a year or longer (i.e., Tanaka et al. 1990), but none have reported on the extent of a non-pregnant phase in mature females. More detailed physiological analysis is necessary to determine: 1) if those females are in fact mature; 2) if they are mature, the extent to which regression may

occur; and 3) how long this resting period may last; and 4) what conditions may trigger such a resting period.

Pregnant females were most often caught in the late summer and autumn sampling events, sometimes in large aggregations. For example, at one sampling event in Yakutat Bay, 75 of 76 females sampled were pregnant. The sizes of the pups from all pregnant females within a sampling time frame (spring, summer, autumn) was clearly bimodal (Figure 2.8), agreeing with other reports of an extended gestation of up to two years. Few females were encountered with stage H pups, those which have fully absorbed the yolk sac and are ready for parturition. Those that were encountered suggest that pupping occurs late in the autumn and possibly into the winter. It is likely that the autumn pupping would be the earlier end of the pupping season because no other near-term females were encountered earlier in the year. The presence of candled embryos (stage A and B, Tribuzio et al. 2009a) during the spring and summer sampling also suggests that fertilization occurs and that pregnancies begin in the spring and may extend into the summer. We did not address the question of mating season in this study, but it is believed that female spiny dogfish do not store sperm for significant lengths of time (Gauld 1979; Demirhan and Seyhan 2006) and mating likely precedes ovulation by about a few weeks.

As with other slow growing, late maturing, and long-lived species, spiny dogfish have low natural mortality. Sharks in generally have a low natural mortality, due in part to the fact that they are born as miniature adults and fully predatory (Carrier et al. 2004). Having precocial young with high survival at younger ages allows sharks to have lower

fecundity, but also results in a low ability for the populations to rebound from or tolerate fishing pressure (Cortes 1998). Spiny dogfish have been targeted in other areas with mixed results. On the U.S. east coast, spiny dogfish were fished heavily for 10 years then determined to be overfished (Cortes 1998). Similarly, in WA and BC the long history of spiny dogfish fishing is a characteristic boom and bust fishery with periods of heavy exploitation followed by periods of limited fishing (Ketchen 1986). In the WA and BC examples, the populations always rebounded fairly rapidly because the fishery only targeted the largest females, leaving the juveniles untouched. In the most recent boom phase of the fishery, the average size of landed spiny dogfish decreased and more fishing pressure was being placed on juveniles (King and McFarlane 2009). The U.S. east coast, WA and BC cases are examples of recruitment overfishing, reducing the spawning stock to the point where it can no longer replenish itself. These examples clearly show that a targeted fishery on spiny dogfish is difficult to maintain and always bears the risk of overfishing.

In the GOA, spiny dogfish are not yet targeted, but significant levels of bycatch can occur (Tribuzio et al. 2009b). Further, the low productivity and natural mortality further reduce rebound potential and the population's ability to recover from fishing pressure (Tribuzio and Kruse in review). Spiny dogfish are currently managed as part of the "shark complex" as a Tier 6 species (North Pacific Fishery Management Council 2009), where overfishing levels and acceptable biological catches are determined by the average catch from 1997-2007 (Tribuzio et al. 2009b). The Magnuson-Stevens Fishery Conservation and Management Act was recertified in 2006 (NMFS 2007), and new

requirements are being developed to improve management plans for all species, including sharks. If spiny dogfish move from a Tier 6 species to a Tier 5 species, where Acceptable Biological Catch and Over Fishing Limits are based on average biomass and natural mortality, life-history parameters, such as those estimated in this study, will become even more critical for fisheries management.

2.6 Acknowledgements

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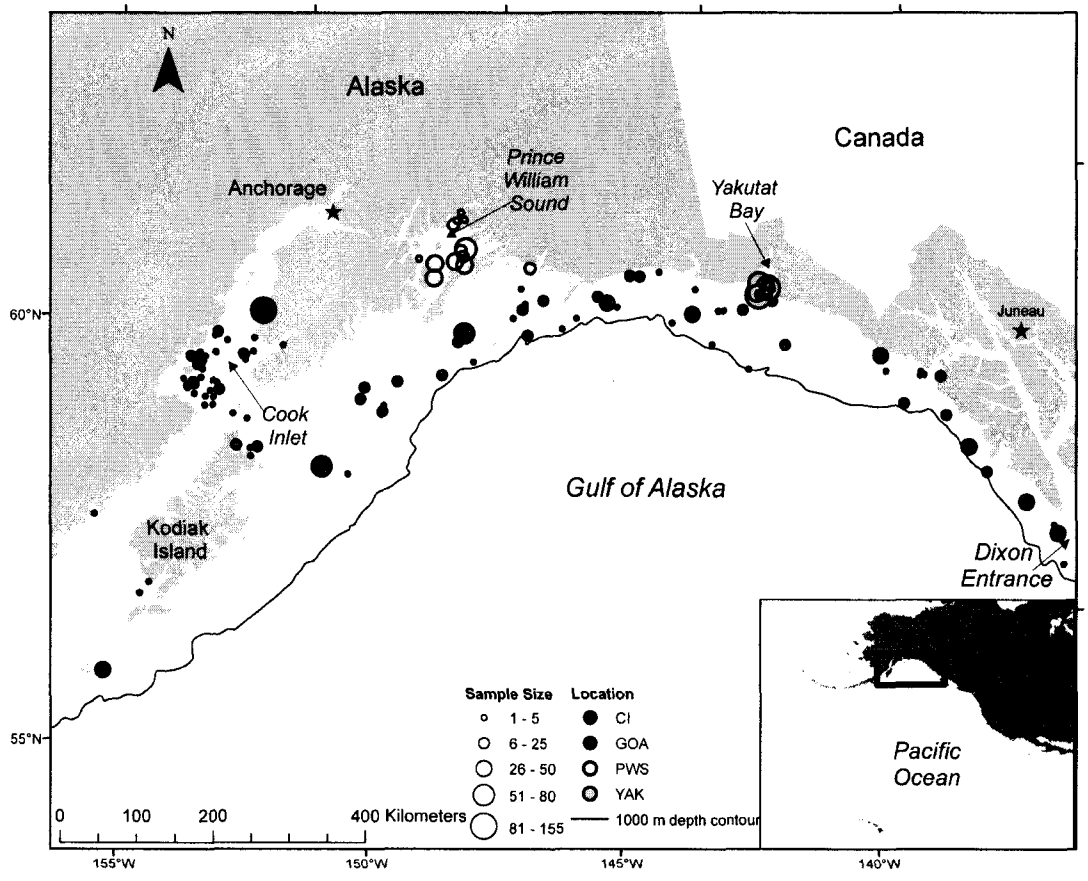

Figure 2.1 Map of sampling locations within the Gulf of Alaska. Circle size represents the sample size at each sampling station. The four regions used in this study are identified, Cook Inlet (black circles), Prince William Sound (open circles), Yakutat Bay (grey open circles), and Gulf of Alaska (grey circles).

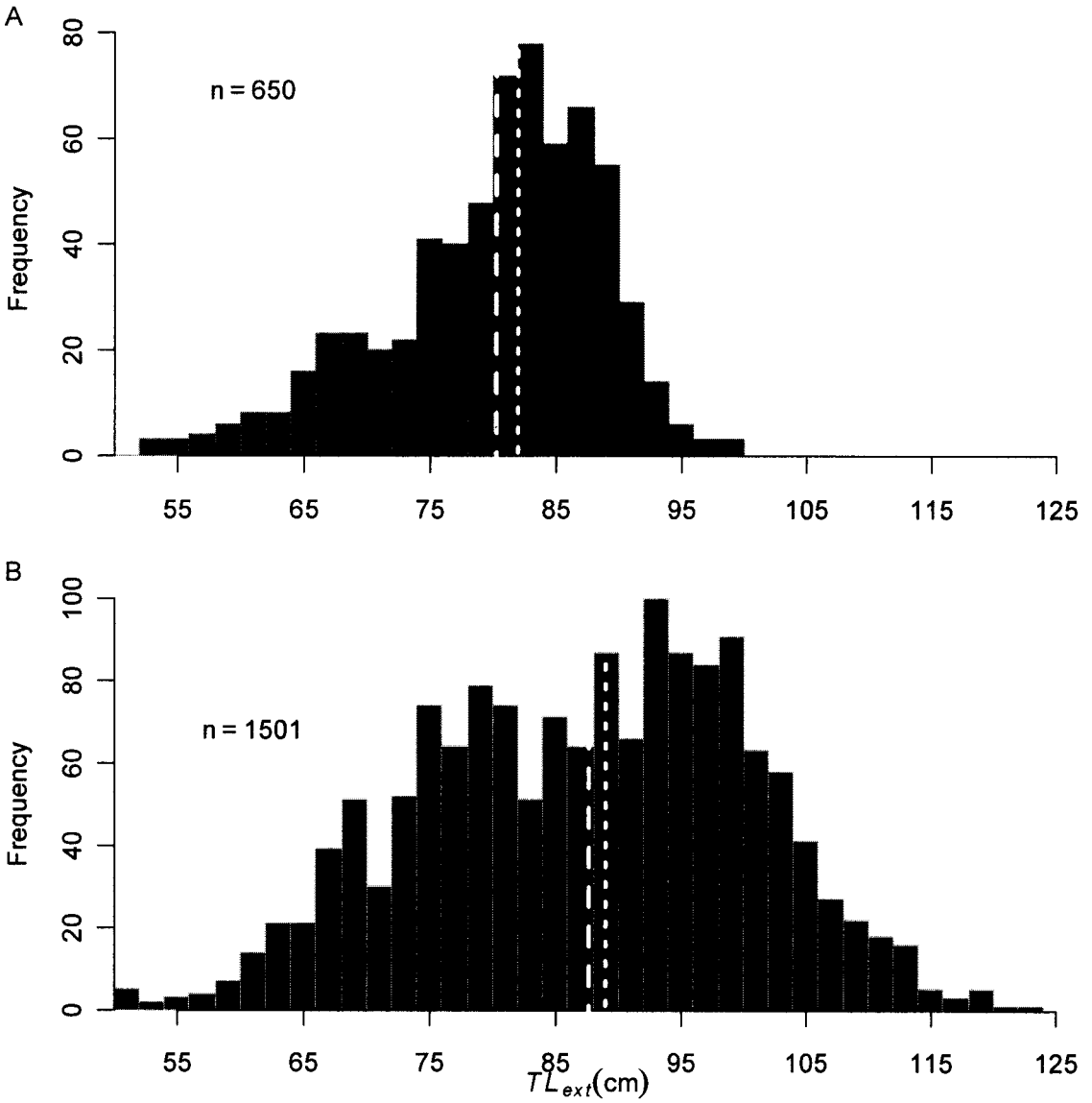

Figure 2.2 Size-frequency distributions. Size-frequency distribution of males (A) and females (B) sampled in this study. The solid line is the sample mean and the dashed line is the sample median.

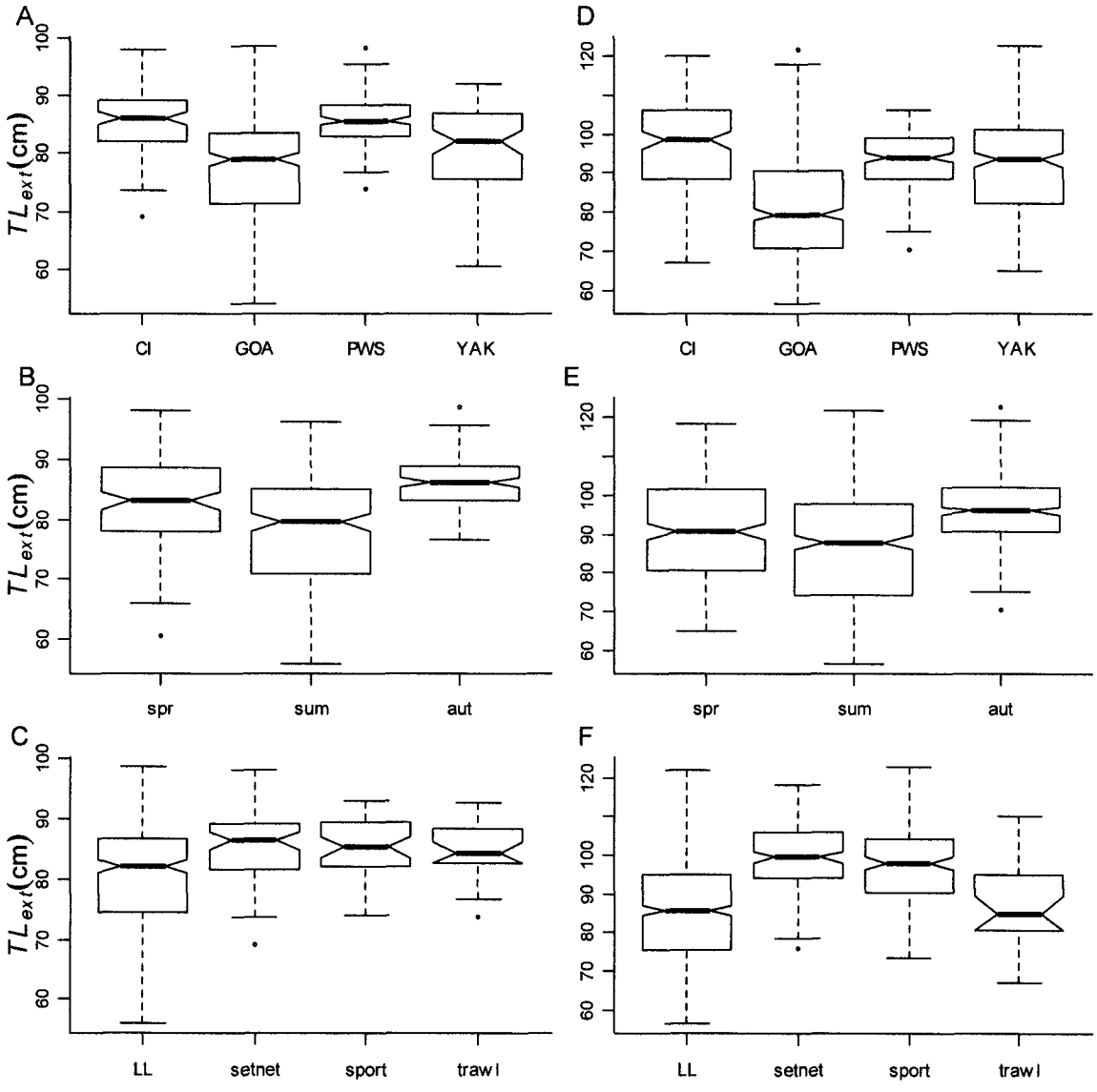

Figure 2.3 Box plots of size distribution by sampling category. Box plots of the size data for males (A-C) and females (D-F), and each sex by region (A and D), season (B and E), and gear type (C and F). Boxes represent the median and interquartile range, with whiskers representing the minimum and maximum. Notches show the 95% confidence interval around the median, therefore overlapping notches indicate no significant differences between medians.

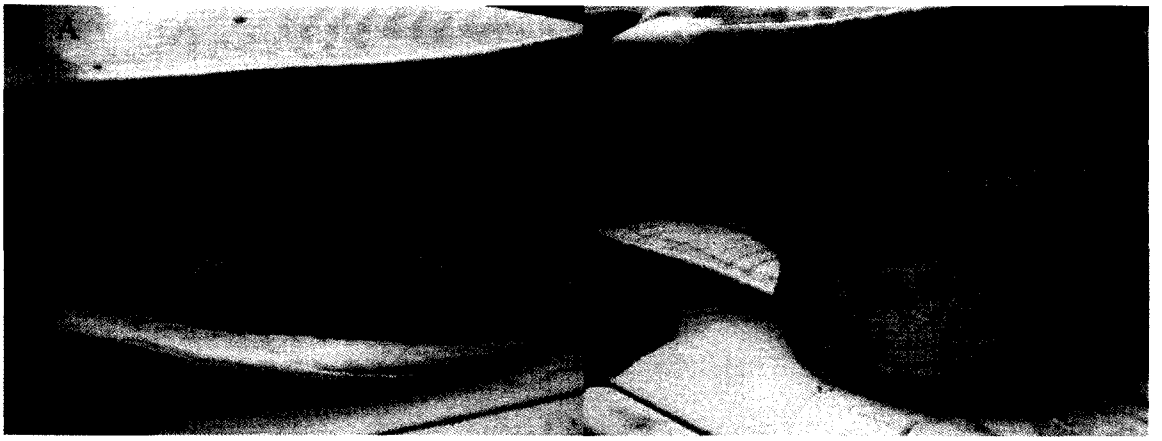

Figure 2.4 Examples of pregnant females. Both females were caught on the same day at the same location and are at about the same stage of gestation based on embryo size. Note that ovary in female A has large yolky ova developing, while female B shows no sign of developing eggs for the next pregnancy.

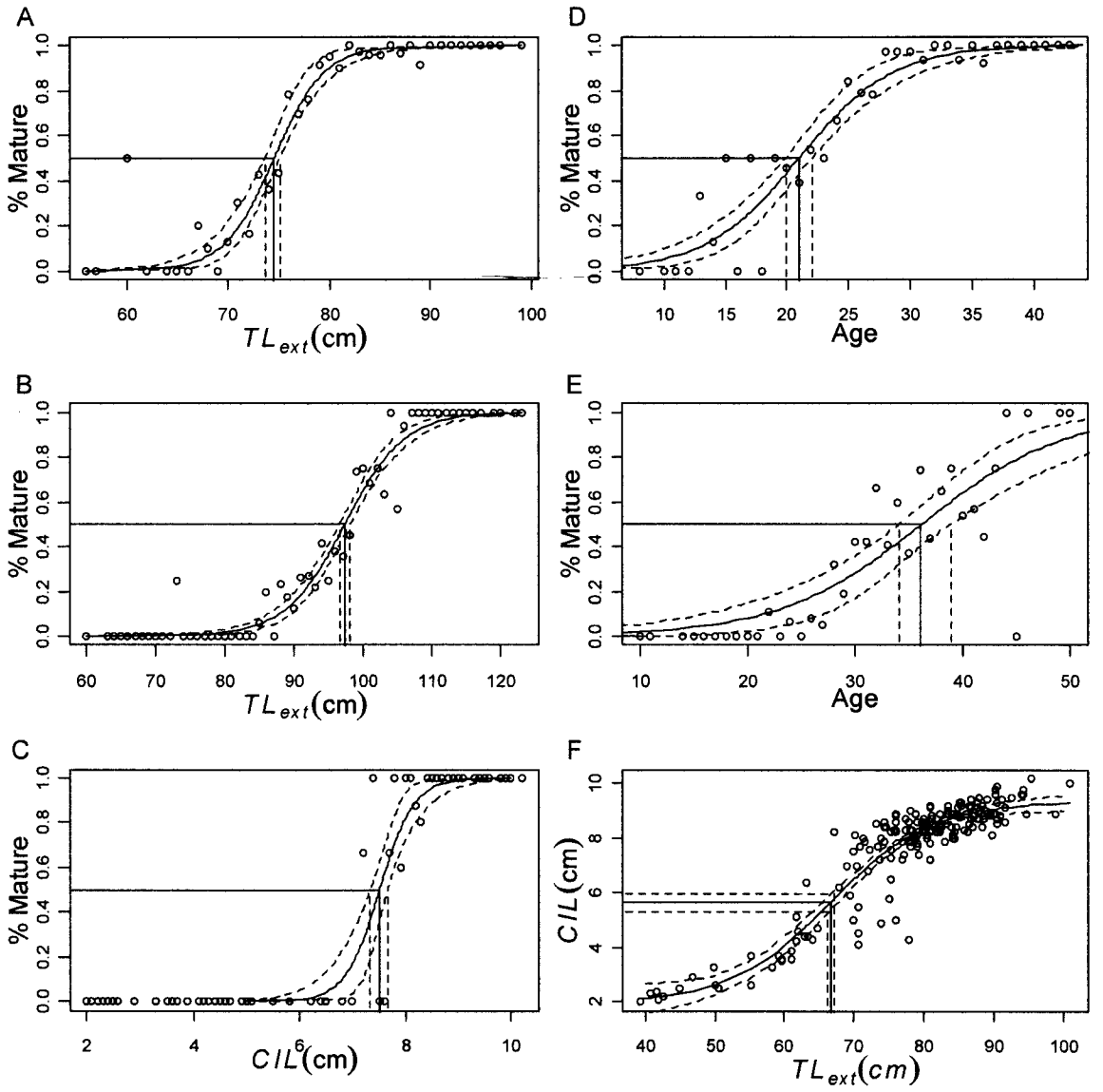

Figure 2.5 Size and age at 50% maturity. Total length (TLext) at 50% maturity for males (A), females (B), and male clasper inner length (CIL) (C). Age at 50% maturity for males (D) and females (E). Male CIL at TLext can also be used to estimate size at 50% maturity (F). Solid curve is the model estimates and dashed lines are the upper and lower 95% confidence interval. Horizontal and vertical lines are to help indicate the length or age at 50% maturity and the confidence intervals.

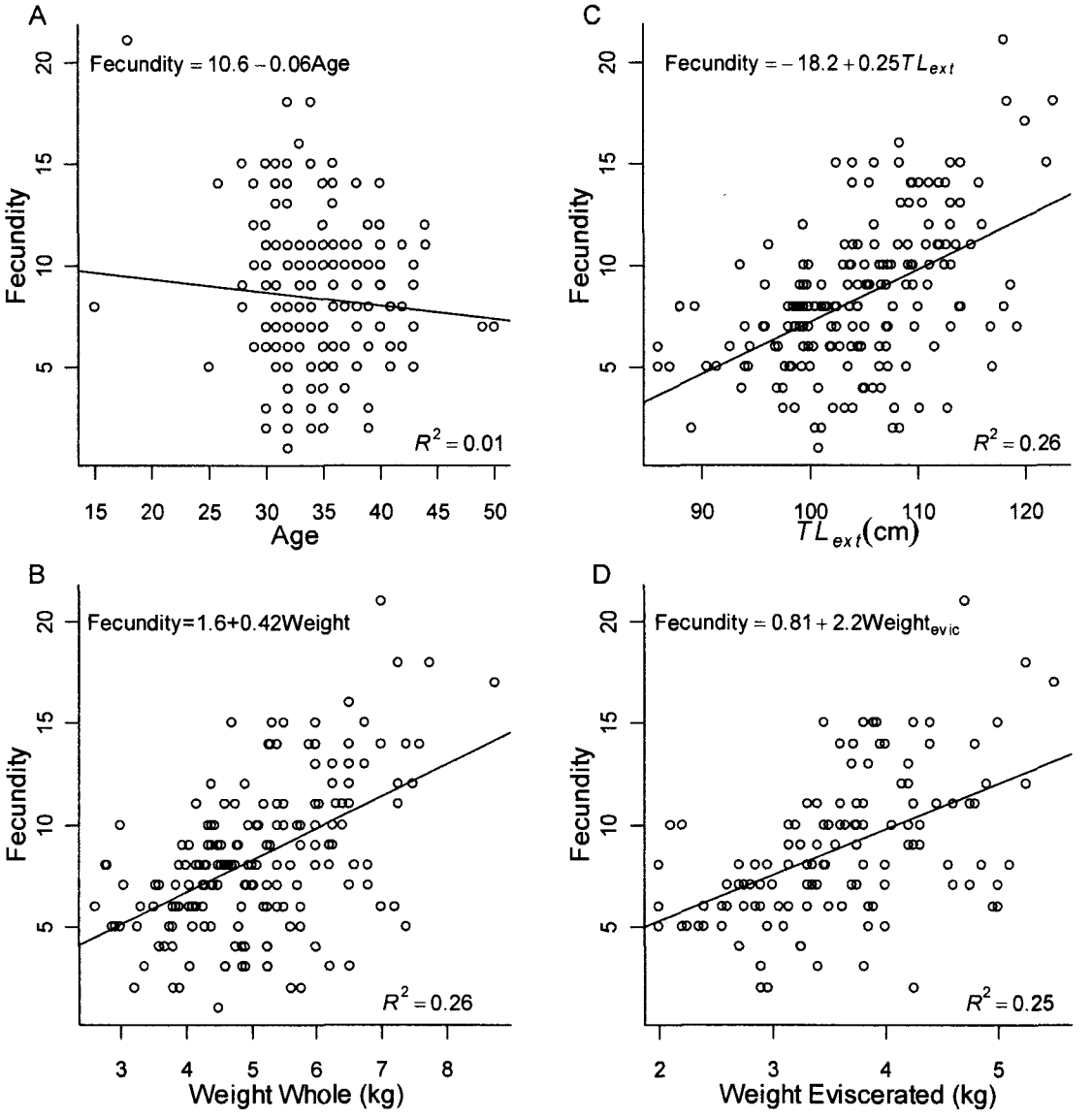

Figure 2.6 Relationships between fecundity, size, and age. Linear relationships between fecundity and age (A), fecundity and whole weight (B), fecundity and length (C), and fecundity and eviscerated weight (D). Linear models are provided with the model fit (R^2).

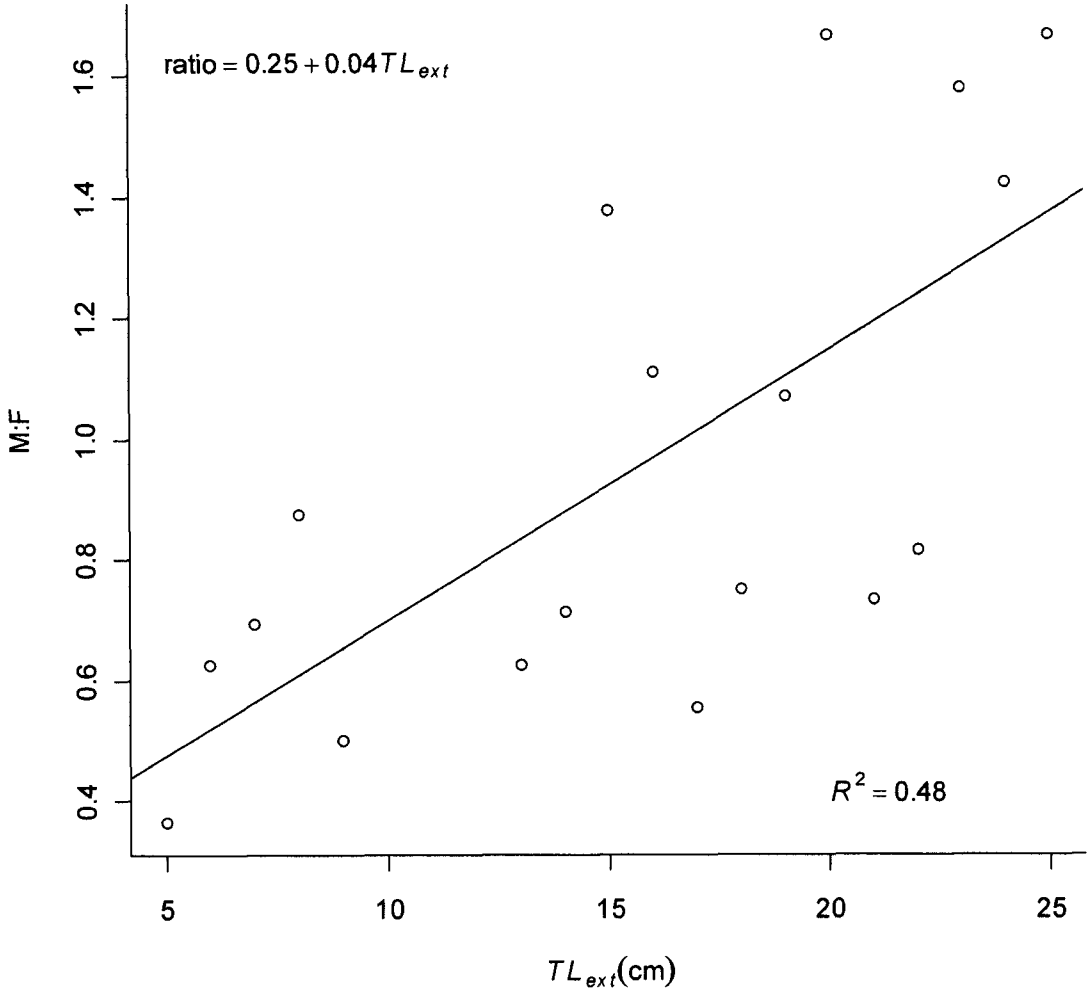

Figure 2.7 Relationship between sex ratio and embryo size. The relationship between the ratio of male to female embryos and the size of the total length (TLext) of the embryos. The linear regression and model fit are provided.

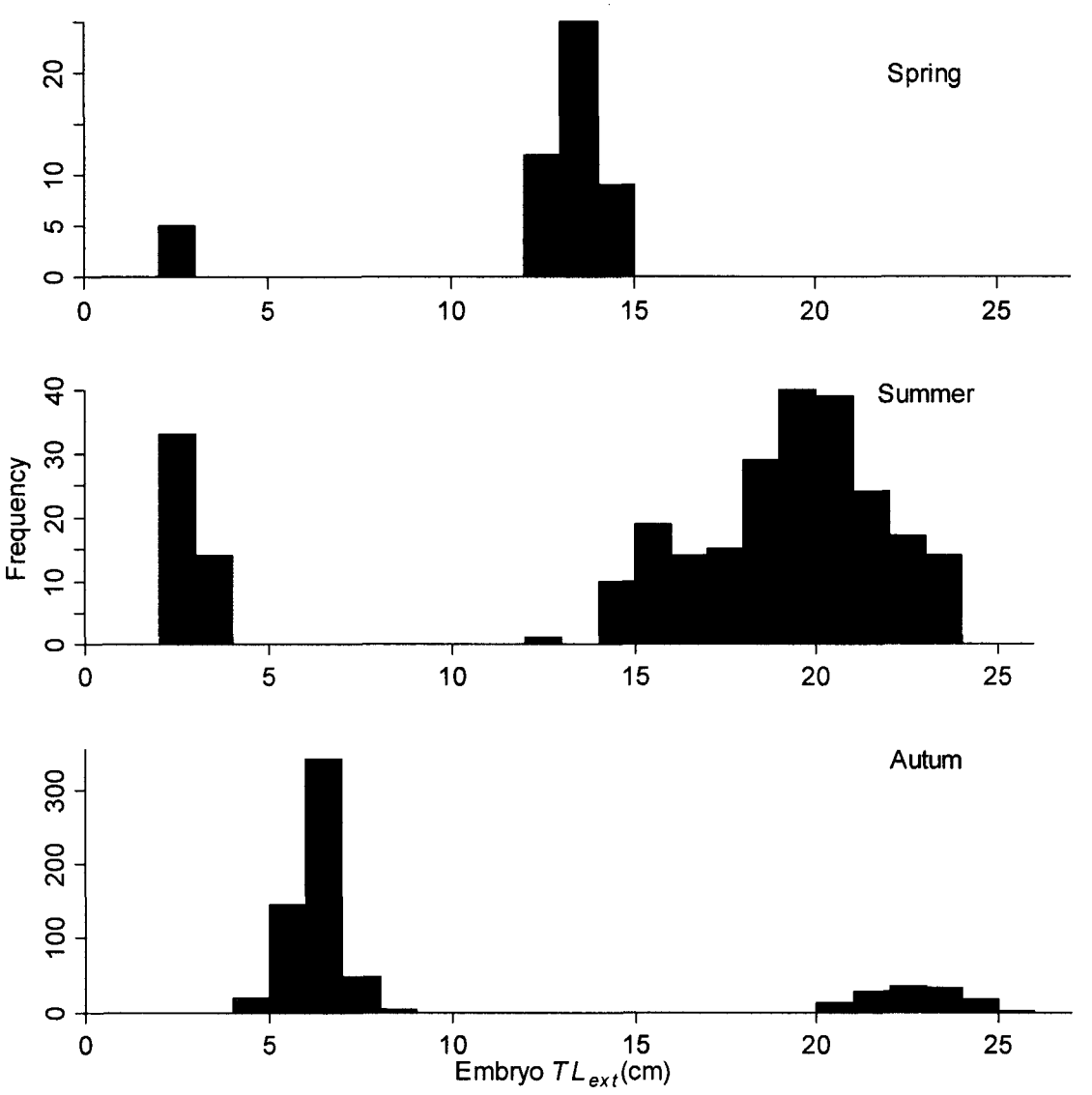

Figure 2.8 Frequency of embryo sizes by season. The data show a clear bimodal size distribution and the growth of cohorts throughout the seasons.

Table 2.1 Summary statistics of spiny dogfish size. Summary of spiny dogfish (*Squalus acanthias*) size, caught by sex, region, gear type and season. Includes sample size (n), minimum and maximum observed, mean, and standard deviation (SD). The percentage of mature individuals in each sampling category is also included.

		Male						Female					
		n	Min	Max	Mean	SD	% mature	n	Min	Max	Mean	SD	% mature
		650	53.0	98.7	80.3	8.5	80%	1501	50.0	122.6	87.7	13.1	45%
Region	CI	90	69.1	98.1	85.6	5.4	89%	151	67.1	120.0	97.4	11.2	53%
	GOA	195	53.0	97.0	74.7	9.8	59%	164	50.0	122.0	80.6	14.2	27%
	PWS	145	72.3	98.5	85.0	4.5	96%	311	63.3	109.5	91.1	9.0	24%
	YAK	79	60.5	92.2	80.9	7.4	78%	370	65.0	122.6	93.3	10.5	59%
Gear	LL	431	53.0	98.5	79.0	8.9	77%	525	50.0	122.0	83.5	12.5	23%
	SET	66	69.1	98.1	85.4	5.5	89%	152	75.8	118.3	98.2	7.6	76%
	SPT	37	76.4	93.0	85.9	4.3	95%	154	76.0	122.6	97.3	9.0	56%
	TWL	24	73.6	92.6	84.4	4.7	79%	26	67.1	110.2	86.7	10.9	30%
Season	SPR	135	60.5	98.1	82.8	7.3	82%	286	65.0	118.3	91.1	13.0	41%
	SUM	238	53.0	97.0	76.5	9.9	65%	340	50.0	122.0	86.2	13.8	46%
	AUTUM	136	72.3	98.5	85.1	4.5	97%	231	63.3	122.6	94.5	10.2	48%

Table 2.2 Estimates of natural mortality. The source and equation are based on the original publication of the model, the M estimates are the average or best estimate (95% confidence intervals in parentheses). In the case of Hoenig (1983), the range of M estimates is presented because the input parameter t_{max} had two possible values and no confidence intervals exist for those values. The comments refer to relevancy of the model to spiny dogfish.

Source	Equation	M estimates	Comments
Alverson & Carney 1975	$M=3\kappa/(e^{0.38\kappa t_{max}}-1)$	0.07(0.059-0.074)	Two estimates of maximum age available
Chen & Watanabe 1989	$M(t,t<t_m)=\kappa/(1-e^{-\kappa(t-t0)})$, $M(t,t\geq t_m)=\kappa/(a_0+a_1(t-t_m)+a_2(t-t_m)^2)$ $a_0=1-e^{-\kappa(tm-t0)}, a_1=\kappa e^{-\kappa(tm-t0)}, a_2=-0.5\kappa^2 e^{-\kappa(tm-t0)}$,	0.041(0.038-0.05)	No shark species used in model derivation
Frisk et al. 2001	$\ln M=1.10\ln\kappa-0.8$	0.151(0.14-0.159)	Based on Requiem sharks
Gunderson & Dygert 1988 (1)	$M=0.03+1.68GSI$, $GSI=$ovary weight/eviscerated weight	0.097(0.05-0.176)	Used Puget Sound spiny dogfish in model derivation, may be most biologically meaningful method
Gunderson & Dygert 1988 (2)	$M=0.03+1.68GSI$, $GSI=$ovary weight/whole weight	0.081(0.044-0.13)	
Gunderson & Dygert 1988 (3)	$M=0.03+1.68GSI$, $GSI=$standardized ovary weight/eviscerated weight	0.037(0.032-0.046)	
Gunderson & Dygert 1988 (4)	$M=0.03+1.68GSI$, $GSI=$standardized ovary weight/whole weight	0.035(0.031-0.041)	
Hoenig 1983	$M=e^{1.44-0.982\ln(tmax)}$	0.043-0.057	Two estimates of maximum age available
Jensen 1996 (1)	$M=1.65/t_{50\%mature}$	0.046(0.045-0.05)	May be overly simplified
Jensen 1996 (2)	$M=1.5\kappa$	0.051(0.035-0.068)	
Jensen 1996 (3)	$M=1.6\kappa$	0.054(0.037-0.072)	
Pauly 1980 (1), length	$\ln M=-0.0152-0.279\ln(TL_{ext\infty})+0.6543\ln\kappa+0.4634\ln T$	0.068(0.054-0.079)	Two lamnid species used in derivation
Pauly 1980 (2) weight	$\ln M=-0.4852-0.0824\ln(W_\infty)+0.6757\ln\kappa+0.4627\ln T$	0.19(0.167-0.218)	

Table 2.3 Length and weight conversions. Factors for converting between different length and weight measurements. All length to length and weight to weight conversions are linear of the form: $y=a+bx$, weight to length conversions are of the form: $y=cL^d$. 95% confidence intervals for estimated parameters and the model fit (R^2) are provided.

	n	*a*	95% CI	*b*	95% CI	R^2
PCL to TL_{ext}	1483	3.49	(2.94-4)	1.20	(1.2-1.2)	0.98
FL to TL_{ext}	876	2.17	(1.35-2.98)	1.10	(1.09-1.11)	0.98
Tl_{nat} to TL_{ext}	953	1.64	(0.97-2.31)	1.02	(1.01-1.03)	0.98
PCL to Tl_{nat}	954	2.54	(1.76-3.32)	1.17	(1.16-1.18)	0.98
FL to Tl_{nat}	877	1.22	(0.38-2.07)	1.07	(1.06-1.08)	0.98
PCL to *FL*	879	1.78	(1.18-2.39)	1.09	(1.08-1.09)	0.99
whole wt to evic wt	1483	0.20	(0.17-0.2)	0.65	(0.64-0.7)	0.96
	n	*c*	95% CI	*d*	95% CI	R^2
male						
whole wt to TL_{ext}	536	$4.98*10^{-6}$	$(3.05*10^{-6}$-$8.08*10^{-6})$	2.94	(2.83-3.05)	0.87
evic wt to TL_{ext}	536	$9.38*10^{-6}$	$(6.04*10^{-6}$-$1.45*10^{-6})$	2.73	(2.63-2.83)	0.87
female						
whole wt to TL_{ext}	993	$1.75*10^{-6}$	$(1.34*10^{-6}$-$2.29*10^{-6})$	3.20	(3.14-3.26)	0.94
evic wt to TL_{ext}	993	$3.53*10^{-6}$	$(2.80*10^{-6}$-$4.46*10^{-6})$	2.97	(2.92-3.02)	0.94

Table 2.4 Length and age at 50% maturity. Length and age at 50% maturity and model parameters with 95% confidence intervals. Lengths are in cm.

		50% maturity	(95% CI)	*f*	(95% CI)	*g*	(95% CI)
length	male	74.5	(73.1-75.4)	-30.4	(-41.6--23.5)	0.406	(0.317-0.560)
	female	97.3	(96.0-98.4)	-22.8	(-26.9--19.5)	0.235	(0.200-0.276)
	CIL	7.1	(7.0-7.72)	-12.9	(-16.4--10.4)	1.816	(1.463-2.307)
age	male	20.9	(19.9-22.0)	-5.6	(-7.3--4.3)	0.269	(0.207-0.353)
	female	36.1	(34.0-38.9)	-5.4	(-7.7--3.9)	0.152	(0.107-0.215)

CIL at TL_{ext}									
50% maturity	(95% CI)	*h*	(95% CI)	*i*	(95% CI)	*j*	(95% CI)	*k*	(95% CI)
CIL	6.2	(6.1-6.4)	-18.9	(-20.1--17.4)	0.263	(0.244-0.278)	3.2	(2.6-3.7)	6.0	(5.7-6.5)
TL_{ext}	72.0	(71.5-72.3)								

Chapter 3: Age and growth of spiny dogfish *(Squalus acanthias)* in the Gulf of Alaska: analysis of alternative growth models[1]

3.1 Abstract

Ten growth models were fitted to age data and growth data for spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Previous studies of spiny dogfish growth have all fitted the t_0 formulation of the von Bertalanffy model without examination of alternative models. Among the alternatives, we present a new two-phase von Bertalanffy growth model formulation with a logistically scaled k parameter and which estimates L_0. A total of 1,602 dogfish were aged from opportunistic collections with longline, rod and reel, set net, and trawling gear in the eastern and central Gulf of Alaska between 2004 and 2007. Ages were estimated from the median band count of three independent readings of the second dorsal spine plus the estimated number of worn-bands for worn spines. Owing to a lack of small dogfish in the samples, lengths at age of small individuals were back-calculated from a subsample of 153 dogfish with unworn spines. The von Bertalanffy, two-parameter von Bertalanffy, two-phase von Bertalanffy, Gompertz, two-parameter Gompertz, and logistic models were fitted to length-at-age data for each sex separately, both with and without back-calculated lengths at age. The two-phase von Bertalanffy growth model produced the statistically best fit for both sexes of

[1] Tribuzio, C. A., G. H. Kruse and J. T. Fujioka. 2010. Age and growth of spiny dogfish *(Squalus acanthias)* in the Gulf of Alaska: analysis of alternative growth models. Fishery Bulletin. 108:119-135.

Gulf of Alaska spiny dogfish, resulting in L_{∞}=87.2 and 102.5 cm and k=0.106 and 0.058 for males and females, respectively.

3.2 Introduction

The spiny dogfish (*Squalus acanthias*) is a small, long-lived shark common among temperate coastal areas in the Atlantic and Pacific oceans (Compagno, 1984). This species has been the target of commercial fisheries over much of its range, in some cases for over a century (Ketchen, 1986). In some areas, severe declines in population abundance and stock structure have occurred (e.g., Rago et al., 1998). Many elasmobranchs, including spiny dogfish, are "equilibrium strategists" that are highly susceptible to overfishing because of their slow growth rates, low fecundity, and late maturation (King and McFarlane, 2003), all of which are directly related to recruitment and parental stock sizes (Holden, 1974; 1977). Off the west coast of North America, spiny dogfish were depleted by intense fisheries in the 1940s, owing to the quantity and quality of vitamin A in their livers (Ketchen, 1986). However, the fishery demand decreased by 1950 with the development of synthetic vitamin A (Ketchen et al., 1983). Since the 1970s, spiny dogfish have continued to be targeted by commercial fisheries in British Columbia and the state of Washington for human consumption.

While not targeted, spiny dogfish is a common bycatch species in many fisheries in both state and federal waters off the coast of Alaska. In the Gulf of Alaska (GOA), spiny dogfish are taken in Pacific salmon (*Oncorhynchus* spp.) gill-net fisheries, sablefish (*Anoplopoma fimbria*) fisheries, Pacific halibut (*Hippoglossus stenolepis*) longline fisheries, and groundfish trawl fisheries (Boldt, 2003). Although an estimated average of 482.1 metric tons (t) of spiny dogfish was taken annually from 1997 to 2007 in observed fisheries (Tribuzio et al., 2008), the bycatch in state waters is unknown and the bycatch

rates in federally managed fisheries are likely underestimated because of unobserved fisheries (e.g., the halibut individual fishing quota, IFQ). Nearly all of this unintended bycatch was and still is discarded at sea. Even though estimated catch is <1% of estimated spiny dogfish biomass (Courtney et al., 2006), the potential development of a commercial fishery demands further investigation of the effect of total fishing mortality on biomass and an investigation of spiny dogfish life-history characteristics in Alaska.

Biological reference points (e.g., biomass at maximum sustainable yield, B_{MSY}, fishing rate which reduces spawning biomass per recruit to 35% of unfished, $F_{35\%}$) are benchmarks against which stock abundance or fishing mortality rates can be compared to determine stock status. Most commonly used reference points are functions of stock productivity, such as growth, recruitment, and natural mortality (Bonfil, 2005), thus accurate estimates of age and growth are important. For instance, estimates of age and the growth coefficient (k) are critical for estimating natural mortality (M), where a lack of data prevent direct estimation of M, abundance, and appropriate harvest rates. In the GOA, biological reference points, such as those from age and growth models, have yet to be determined for spiny dogfish.

Extension of life-history parameters from other regions to Alaska may be inappropriate because age and growth characteristics of spiny dogfish vary widely over its geographic range. For example, maximum age in the northwest Atlantic Ocean is 35–40 years (Nammack et al., 1985), but in the eastern North Pacific, spiny dogfish have been aged to over 80 years (Saunders and McFarlane, 1993). Growth characteristics also vary widely throughout the North Pacific and North Atlantic oceans (Ketchen, 1975;

Nammack et al., 1985). Even within the North Pacific basin, biological parameters, such as k, can vary with latitude (Vega, 2006).

The selection of an appropriate growth model is important when estimating regionally specific parameters. Elasmobranch age and growth studies have generally focused on fitting length-at-age data to the von Bertalanffy (vB) growth equation, irrespective of goodness-of-fit or alternative growth models (Carlson and Baremore, 2005). Despite its common use, the vB growth equation may not be the best-fit growth model for all elasmobranch species. For example, the logistic model fitted best among four models tested for the spinner shark (*Carcharhinus brevipinna,* Carlson and Baremore, 2005), and a two-phase vB model fitted best among five models for the piked spurdog (*Squalus megalops*, Braccini et al., 2007). A model that is not the best descriptor of a species' growth could have compounding effects on demographic analyses, stock assessment, and fishery management.

Typical growth models involve parameters of asymptotic length (L_∞), k, and t_0 (Cailliet et al., 2006). The t_0 parameter is biologically difficult to interpret because it is not measurable and testable in wild animals (Beverton and Holt, 1957). This parameter is the age at which the animal is of zero length and is based on an assumption of a fixed growth curve from fertilization through life (Beverton and Holt, 1957). It is generally interpreted to represent the period of gestation in teleost fish species, but this assumption is violated for elasmobranchs (Driggers et al., 2004). For instance, when considering males and females separately, models will estimate different t_0 values. If t_0 is truly representative of gestation time, then it leads to the incorrect inference that male and

female pups have different gestation periods. For these reasons, growth models that use size at birth (L_0) instead of t_0 may be more appropriate for elasmobranchs (Cailliet and Goldman, 2004).

The purpose of this study was to estimate best-fit growth models for male and female spiny dogfish in the GOA. Resultant growth equations provide critical parameters for a better understanding of spiny dogfish biology, estimation of biological reference points including indirect estimates of M (see chapter 2) and population growth rates (see Chapter 4). These results will by used by fishery managers to improve stock assessments, which had previously been based on little data or information from other regions, and to develop sound fishery management plans for this species in waters off Alaska.

3.3 Materials and methods

3.3.1 Sample collection

Spiny dogfish were collected by targeted sampling cruises, state and federal assessment surveys, and opportunistic fishery bycatch samples between July 2004 and April 2007 across the GOA (Figure 3.1, Table 3.1). All spiny dogfish were sexed and length was measured to the nearest centimeter (total length extended=TL_{ext}; total length natural=TL_{nat}; precaudal length=PCL; and fork length=FL; Tribuzio et al., 2009). Here, length measurements are reported as total length extended (TL_{ext}). The posterior dorsal spine was removed and stored frozen for laboratory analyses. In the laboratory, spines

were cleaned by thawing, by boiling briefly, and the loose tissue was scraped free. Spines were allowed to dry overnight and then stored in individual paper envelopes for subsequent age reading.

Sampling bias was examined because we sampled with multiple gear types in different locations. To test for potential bias, a chi-squared (χ^2) test was conducted to test for statistically significant ($P<0.05$) differences in the mean length at age by sex for each gear (trawl, set net, longline, rod and reel) and region (Cook Inlet, Prince William Sound, Yakutat Bay, and Gulf of Alaska). Statistically significant differences among different gears would provide evidence of sampling bias. However, statistically significant differences among different geographic areas would provide equivocal evidence of bias because the possibility of true underlying differences in size distributions by area could not be dismissed.

3.3.2 Age determinations

The posterior dorsal spines were read in the laboratory according to the methods of Ketchen (1975) and Beamish and McFarlane (1985). Each band pair (hereafter termed "band"), consisting of one dark and one light band, was counted as one year or annulus (Cailliet et al., 2006). Aging was conducted by two scientists at the Washington Department of Fish and Wildlife's age laboratory and by the lead author at the University of Alaska Fairbanks. Ease of age reading was categorized from 1 (easiest) to 3 (most difficult). Spines were photographed on a 1×1 mm grid to standardize measurements. All measurements were rounded to the nearest 0.01 mm by using Bersoft Image Measurement vers 5.0 software (Bersoft, Inc., http://bersoft.com). Measurements

included spine base diameter (*SBD*), enamel base diameter (*EBD*), last readable point (*LRP*, also called the no-wear point); and, for nonworn spines, base length (*BL*), and spine total length (*TL*, Figure 3.2) were also measured to the nearest 0.01 mm. Nonworn spines were those spines with a *LRP*<2.45 mm (McFarlane and King, 2009), which is the *EBD* at birth.

Aging bias and precision were evaluated for all three readers. Pair-wise age-bias plots were used to compare each reader against the other two (Campana et al., 1995) and a χ^2 test for symmetry was used to test for statistically significant systematic bias among the three readers (Hoenig et al., 1995). Readers were considered to be in agreement when ages were within 10% of each other rather than within some fixed 1- or 2-year age interval. For instance, if reader X counted 10 bands, then reader Y's count would have to have been between 9–11 bands to be in agreement, but if reader X counted 40 bands, then reader Y's count would have to be between 36–44 to be in agreement. We contend that the use of a percentage to define the interval size is more appropriate for this long-lived species. Finally, the coefficient of variation (CV) between readers was calculated according to Campana's methods (2001).

Spiny dogfish ages are not always equal to the number of counted bands for two reasons: 1) bands are deposited during embryonic development; and 2) because the external spines can become worn or can break off. This problem was addressed by a correction method for estimating the number of missing bands that was based on a regression of band counts on the *SBD* of unworn spines (Ketchen, 1975). This method was subsequently re-examined and accepted as the best available method for the original

samples plus additional samples from the same geographic region (McFarlane and King, 2009).

Various regression approaches were compared to determine which method resulted in the best model for estimating the number of worn-bands in spiny dogfish collected from the GOA, including: nonlinear least squares regression (NLS, Eq. 3.1), and ordinary least squares (OLS, Eq. 3.2):

$$\text{Band Count} = b_0 EBD^{b_1} \qquad \text{(Eq. 3.1)}$$

$$\ln(\text{Band count}) = \ln(b_0) + \ln(EBD)b_1\,, \qquad \text{(Eq. 3.2)}$$

where b_0 and b_1 are estimated parameters (based on Ketchen 1975, McFarlane and King 2009). Also, we fitted parameters for Equations. 3.1 and 3.2 with weighted nonlinear least squares (WNLS) and weighted ordinary least squares (WOLS), where weights were applied to the residuals as follows: spines in readability category 1 were given a weight of 1, those in category 2 were weighted by 0.5, and those in category 3 by 0.3. These values were chosen to discount the contribution of individual length at-age data points to the estimation process based on the degree of uncertainty in the age estimates for difficult-to-read spines. As an alternative to this weighting scheme, we explored the weighting process by using the inverse of the variance in assigned ages for each readability category. Ages of worn spines were then estimated by equating the *LRP* to the *EBD* in the best-fit model from Equations 3.1-3.2 and by adding the resultant number of bands to the median band count from the three readings and by subtracting two years (for bands deposited during gestation) to obtain the final estimated age of the animal (Ketchen, 1975). In the case of nonworn spines, age was estimated by the median band

count minus two years. Data for males and females were combined for these worn-band models.

3.3.3 Fitting of growth models

A total of 10 growth model variations were fitted separately to the length-at-age data for males and females (Table 3.2). The growth models included 1) the vB growth model for estimating t_0; 2) the two-parameter vB with fixed L_0; 3) the two-phase vB with L_0 (used in the present study); 4) the Gompertz; 5) the two-parameter Gompertz; and 6) the logistic. For comparison with previous studies, L_0 is estimated for model 1 by setting t=0. An estimate of L_0 (i.e., the size at birth) for GOA spiny dogfish was not available; therefore, model 2 was run with L_0 fixed at 26.2 cm (size at birth for spiny dogfish from British Columbia; Ketchen, 1972). Models 3 and 5 were run in three different ways: 1) L_0 was estimated by the model; 2) with L_0 set at the value estimated from model 1; and 3) with L_0 set at 26.2 cm. Model 3 is an adaptation of the two-phase vB model (Soriano et al., 1992). Standard fitting procedures with the two-phase model resulted in the A_t parameter from Soriano et al. (1992) changing for a brief time period and then returning to its original value. To correct this, we reformulated the A_t parameter from Soriano et al. (1992); this treatment changes k, depending on the age of the dogfish, so that A_t would follow a logistic pattern and remain in the second phase. Another problem we encountered fitting the two-phase model was that using the typical differential form of the vB equation can result in a suggested decrease in length at the transition between phases. To prevent this unlikely result, the difference equation form of the vB equation (Gulland 1969) is used in this analysis.

Model parameters for equations describing the number of worn-bands or growth were fitted by nonlinear least-squares regression or ordinary least-squares regression, and confidence intervals were estimated by a bootstrap procedure with 5,000 replicates by using R statistical software (R, vers. 2.10.0, www.r-project.org). Confidence intervals (95%) for parameter estimates were based on the lower and upper 2.5^{th} percentile of the bootstrap replications. Parameters were considered significantly different if the 95% confidence intervals did not overlap. To evaluate best model fit for the male and female datasets, Akaike information criteria (AIC) and model summary statistics were calculated (Quinn and Deriso, 1999; Burnham and Anderson, 2004).

3.3.4 Back-calculation methods

Owing to a paucity of specimens with *EBD*<3.5 mm, back-calculation methods were used to fill in the size range missing from samples. The spine diameter at each band along the spine (hereafter called "band diameters") was measured from a random subsample of 153 unworn spines for use in the estimation of worn-bands (Eqs. 1–4); spiny dogfish with unworn spines tend to be smaller and younger than those with worn spines. We examined the Dahl-Lea, linear Dahl-Lea, and size at birth modified Fraser-Lee back-calculation methods (Francis, 1990; Campana, 1990; Goldman et al., 2006). The Fraser-Lee method produced results that on an individual level could be quite unreasonable (large negative ages), but on average were more biologically reasonable than either of the Dahl-Lea methods. Further, growth model results with either of the Dahl-Lea methods were unreasonable (Linf of >150cm TLext), therefore, we used the

Fraser-Lee method for our data. Thus, the following equation was used to estimate back-calculated length-at-age data:

$$TL_i = TL_c + \frac{(EBD_i - EBD_c)(TL_c - TL_{birth})}{EBD_c - EBD_{birth}}, \qquad \text{(Eq. 3.3)}$$

where, TL_i = the back calculated length;

TL_c = the length at capture;

TL_{birth} = the length at birth;

EBD_i = the enamel base diameter at band I;

EBD_c = the enamel base diameter at capture; and

EBD_{birth} = the enamel base diameter at birth.

3.4 Results

3.4.1 Sample collection

A total of 1,608 spiny dogfish were sampled over the four years of the study (539 males, 1,069 females,). Lengths ranged from 56 to 99 cm TL_{ext} for males, and 56 to 123 cm TL_{ext} for females. The χ^2 test revealed no significant differences between the mean length at age of any of the data groupings ($P>0.99$, $0.019<\chi^2<4.525$). Thus, we failed to find evidence of sampling bias or geographic differences in average size at age.

3.4.2 Age determinations

Sampled dogfish ranged in age from 8 to 50 years old. The χ^2 test and the age-bias plots indicated no significant systematic bias between the three readers (χ^2=241, 206, and

259 for reader 2 versus 1, reader 2 versus 3, and reader 3 versus 1, respectively; all $P>0.05$; Figure 3.3A–C). The percent agreement between reader 2 versus 1 (Figure 3.3D) and reader 3 versus 1 (Figure 3.3E) was high for band counts less than 30 but was more variable or decreased for band counts greater than 30 (Figure 3.3D–F). For reader 2 versus 3, the percent agreement was more variable for band counts less than 20 (Figure 3.3F). The CV between all three readers was generally low (<30%) for band counts less than 30, and there was a notable increase in the variability and CV for band counts greater than 30.

Spiny dogfish spines grow in a predictable pattern with age (Figure 3.4). The brownish-black banded enameled portion of the spine grows in length at a faster rate than the white base portion. However, larger dogfish tend to have worn or broken spines, therefore while the enameled portion of the spine grows at a faster rate than the base portion, it is more likely to be broken or worn resulting in a shorter spine.

Inclusion of the back-calculated band diameter data dramatically changed the worn-band estimation models (Figure 3.5), and therefore further worn-band estimations were made with both the observed and back-calculated band diameter data. There were no significant differences between the worn-band estimation model parameters, but the WOLS model had the lowest AIC value and therefore was chosen as the best-fit model (Table 3.3). Alternative fits to the WOLS and WLNS models, based on weightings by using the inverse variance in assigned ages for each readability category, yielded very similar parameter values and nominally poorer fits indicated by slightly larger AIC values (not shown). A high degree of natural variation resulted in wide 95% confidence

intervals for all parameters. Moreover, parameter confidence intervals for the WOLS GOA model widely overlapped the parameter confidence intervals for the Hecate Strait and Strait of Georgia models (McFarlane and King, 2009). Although the parameters were not statistically significantly different, the GOA, Hecate Strait, and Strait of Georgia models appear to represent biologically meaningful differences in growth (Figure 3.5). The Hecate Strait and Strait of Georgia models tend to overestimate the band count for larger spines and underestimate for smaller spines of spiny dogfish collected from the GOA.

3.4.3 Fitting of growth models

The two-phase vB models fitted the observed data best for males and females based on AIC values (Figure 3.6, A and D, Table 3.4 and Table 3.5). For males, the two-phase model using L_0 from model 1 (model 3B) was the best fit and for females it was the model which used L_0 estimated from model 1 (model 3B). Estimated (and 95% confidence limits) asymptotic lengths (L_∞) were 87.2 cm (range 85.7–89.5 cm) and 102.5 cm (range 99.9–106.3 cm) and growth coefficients (k) were 0.106 (range 0.097–0.117) and 0.058 (range 0.052–0.063) for males and females, respectively. After including the back-calculated data and the mean back-calculated data, the two-phase models were no longer the best-fit for males. The best-fit model with inclusion of back-calculated data was model 2, and model 1 fitted best for the data including the mean back-calculated data. Similarly, for females the two-phase models were not the best-fit based on AIC values after the inclusion of back-calculated and mean back-calculated data: model 6 was the best-fit with inclusion of back-calculated data, and model 5c (with L_0 from model 1)

was the best fit for the data including the mean back-calculated data (Table 3.4 and Table 3.5, Figure 3.6B, C, E, F).

Predicted length-at-age was similar for males and females for the observed data, up to about age 15, when a transition between growth phases occurred (Figure 3.6). After the transition, females continued to grow at a faster rate and to larger sizes than males (Figure 3.6A and D). At the point of transition in the two-phase models, growth increased for about five years before slowing for both sexes.

3.5 Discussion

The model fits for all 10 examined growth models were similar with very small differences in AIC, but the estimated parameters differed substantially. For example, the growth coefficient (k) was significantly different between some models, which could impact estimates of natural mortality and subsequent demographic analyses. The values of k tended to fall into two groupings (in both data sets), and those models that estimated the higher k were also those that estimated lower estimates for L_{∞}. Interestingly, even with the significantly different estimates of k, these estimates were still at the lower range of reported growth rates for different types of shark species (Cailliet and Goldman, 2004).

Cailliet et al. (2006) recommended considering more than one form of evaluation of model performance and considering biological interpretations along with statistical fit when choosing the best model. Mean squared error and the correlation coefficient (r^2) were also calculated for each model, but determinations of best fit by the above criteria

did not differ from those where AIC was used and therefore are not reported. For the observed data models 3a and 3b were the statistical best fit for males and females, respectively. However, the two-phase models tended to be unstable and would converge at different localized minima, depending on the starting value. A further consideration for the two-phase models is that the growth curve suggests a period of rapid growth immediately following the age at transition. The purpose of a two-phase model is to incorporate changes in energy allocation as animals grow: immature fish use surplus energy for growth, whereas mature fish use surplus energy for reproduction (Soriano et al., 1992). Thus, the rate of growth changes after maturation. In our case, the transition between the two growth phases occurred before the age at 50% maturity for both males and females The early age at transition and the period of rapid growth after transition suggest that for female spiny dogfish there is a "growth spurt" about 15 years prior to age at 50% maturity. For males, the pattern was similar, but occurred just prior to age at 50% maturity. This does not follow the theory behind the two-phase model and indicates that a two-phase model may not be most appropriate in this situation.

The two-phase vB model by Soriano et al. (1992) has been examined with data sets from many species of sharks to determine if it is an adequate descriptor of shark growth (Araya and Cubillos, 2006). Whereas the two-phase model was better than the standard vB model in 8 of 11 species for females and 7 of 11 for males, the two-phase model did not perform better than the vB (model 1 here) for spiny dogfish. Because Araya and Cubillos (2006) included only one spiny dogfish population (Black Sea), which appears to have different age and growth characteristics from those in the GOA,

and only examined average length at age data (Avsar, 2001), we feel that it was worth while to investigate the two-phase family of models in this study. Braccini et al. (2007) found that the two-phase model was the best statistical fit for the piked spurdog, which is a similar species to spiny dogfish. However, the resultant models showed some of the same characteristic difficulties that we encountered. Those results also suggested a decrease in length after transition (Figure 3.7, Braccini et al., 2007) and that the A_t parameter appears to only change briefly before returning to it's original value. In that study, they did not address those issues as we have attempted here. A more comprehensive examination, which includes multiple data sets from different regions for each species, and a complete sample of the size range may lead to a more conclusive determination as to which species exhibit two-phase growth.

Disregarding the two-phase models, the best fit model was model 2 for males and model 5c for females. In this example, given the lack of data and difficulties with the two-phase models, it may be more appropriate to select the best model not based on the AIC criteria alone, but to also consider the biological soundness of the models. Model 2 (males) and model 5c (females) are the statistical best fit of the more biologically reasonable models. Both of these best-fit models require L_0 as an input, not as an estimated parameter. The lack of data for spiny dogfish <50 cm TLext likely causes the models that estimate L_0 to have difficulty fitting and as a result estimate L_0 to be larger than would be expected.

The majority of published spiny dogfish age and growth studies use the traditional von Bertalanffy model. To facilitate a broader comparison of our results with growth

parameter estimates for other regions of the geographic distribution of spiny dogfish, we compared parameters estimated from model 1 (Table 3.4 and Table 3.5) with growth curves fitted by using the traditional vB formulation, as reported in published studies (Table 3.6, Figure 3.7). Clear differences in spiny dogfish growth exist between the North Pacific and North Atlantic oceans. For instance, we found that male and female dogfish reach larger asymptotic sizes (87.2 and 112.2 cm TL_{ext}, respectively) in the GOA than off the northeastern United States (82.5 and 100.5 cm TL_{ext}, respectively; Nammack et al., 1985). Indeed, virtually all studies have found large differences in growth of spiny dogfish between the North Pacific and North Atlantic (Table 3.6, Figure 3.7). Fish from the North Atlantic tend to grow more rapidly, achieve smaller asymptotic sizes, and have shorter life spans than those from the Pacific. Differences in growth also exist within the Pacific (Table 3.6, Figure 3.7). For example, our GOA growth estimates are similar to those for spiny dogfish from offshore Washington State waters (Figure 3.7) but greater than those caught in inshore Washington state waters (Puget Sound) and British Columbia (Ketchen, 1975; Jones and Geen, 1977; Saunders and McFarlane, 1993; Vega, 2006). The age and growth studies from British Columbia were conducted on spiny dogfish collected in inshore waters (Strait of Georgia and Hecate Strait); therefore, the possibility cannot be ruled out that spiny dogfish from the British Columbia offshore region would have growth estimates similar to those of Washington offshore and GOA spiny dogfish. The vB growth model parameter estimates (L_∞ and k) for northern California spiny dogfish (defined as spiny dogfish between Point Conception to the

Oregon border; Vega, 2006) were radically different from our results for the GOA, but the fits for California may have been adversely affected by small sample size.

The wide variability in length-at-age contributes to the lack of statistically significant differences among growth models and worn-band estimation models. This variability may be attributable to one or more of the following factors: measurement error in either length or age readings, sampling bias, true underlying variability in growth at age, misidentification of worn and unworn spines. We considered the potential role of each of these factors.

Measurement error in the length measurements alone is insufficient to explain the relatively large variability in the size-at-age data. Aging errors may take two forms: imprecision and bias. We found no bias among the three readers tested, but imprecision of the band counts among readers could contribute to variability in the size-at-age data, especially for older ages. We used the median band count (from the three readers) to account for reduced precision because this measure of central tendency is less sensitive to outliers than the mean for small sample sizes (Dudewicz and Mishra, 1988). A more thorough analysis of the precision of age estimates for spiny dogfish in the Pacific Ocean revealed that the overall coefficient of variation for aging estimates among four laboratories to be 19% (Rice et al., 2009). Systematic bias was found for two of the laboratories (one biased high, the other biased low) in relation to the other two, but relative bias did not always result in statistically different parameters estimated from vB growth curves (Rice et al., 2009).

Age validation is crucial for growth studies to assure that physical structures used for aging are correctly interpreted. For instance, a systematic aging error could result if the periodicity of band formation is not annual. Annual periodicity of band deposition on second dorsal spines was validated for spiny dogfish in British Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987). Moreover, radioactive carbon isotopes absorbed into spiny dogfish spines provided age estimates that agree with previous aging results for the British Columbia spiny dogfish (Campana et al., 2006) and verified that periodicity is annual, even at old ages (Campana, 2001). We assumed that this annual periodicity of band formation in spiny dogfish, which was confirmed for this species in British Columbia, also applies to fish from the GOA. Because spiny dogfish from British Columbia have different age characteristics (e.g., worn-band curves, Figure 3.5) from those of the GOA, it is possible that the pattern of band deposition may also differ.

Sampling bias was considered by examining potential differences in average size at age among gear type and location of capture. Because there were no significant differences among the average size at age with the different gear types used or the areas sampled, we do not believe that sampling bias was a significant factor affecting our results. However, the lack of significant differences in our study should not be misconstrued to rule out considerations of sampling bias in future spiny dogfish studies, because this species may school by size and sex (Nammack et al., 1985; Ketchen, 1986).

In the western North Atlantic Ocean, commercial fisheries target the largest and oldest age classes (Rago et al., 1998). Thus, the size-frequency distributions determined

from commercial catches may not be representative of the full size range of fish in the population. Moreover, depletion of large old fish from the population by heavy exploitation means that subsequent research surveys may not catch a representative sample of the full size and age ranges of the population. In the GOA, spiny dogfish are taken as bycatch in multiple fisheries. In some cases, dogfish bycatch is largely unaccounted for, owing to the lack of observers on small (<60 ft) vessels, such as those vessels with salmon gill nets, as well as longline vessels targeting halibut and small sablefish, resulting in an unknown level of total fishing mortality (Courtney et al., 2006). However, in the GOA, it is unlikely that the fishing mortality has truncated the size distribution of spiny dogfish because spiny dogfish are not targeted and recent (2006) estimates of spiny dogfish biomass are 80–100% of the estimated theoretical population carrying capacity (Rice, 2007). Therefore, it is unlikely that the fishery has created size-selective impacts that would lead to erroneous selection of the two-phase models as the best-fit models (Braccini et al., 2007).

One limitation of our size-frequency distributions is the absence of spiny dogfish smaller than 50 cm TL_{ext}. The lack of samples from smaller spiny dogfish is likely due to fishery-dependent opportunistic sampling which apparently occurs in areas devoid of juvenile spiny dogfish. Examination of NMFS spring and fall trawl surveys along the U.S. east coast revealed that in spring most juveniles were caught in water between 50 and 150 m deep (range: 7–390 m) in offshore waters from North Carolina to the eastern edge of Georges Bank, whereas in fall most were caught between 25 and 75 m (range: 12–366 m) in various locations, such as on Georges Bank, Nantucket Shoals, and

throughout the Gulf of Maine (McMillan and Morse, 1999). Spiny dogfish smaller than 50 cm TL_{ext} have been surveyed in both Puget Sound, Washington (Tribuzio et al., 2009), and in the northern Strait of Georgia (McFarlane et al., 2006) by using bottom trawl gear. In this study, we made numerous unsuccessful attempts to capture juvenile dogfish smaller than 50 cm TL_{ext} in the GOA using sport and longline gear in Yakutat Bay, longline gear with small (10/0 circle) hooks in Southeast Alaska (K. Munk, personal commun.[2]), and commercial bottom trawls off Kodiak Island (J. Gauvin, personal commun.[3]).

A missing size group, such as small dogfish in our case, may cause growth models to overestimate t_0 or L_0, thus decreasing the k estimate. Further, this missing size group may have caused the age of transition, t_h, in the two-phase models to be underestimated. Also, the lack of small animals may have limited our ability to discriminate among competing growth models. We used band-diameter data and back-calculated lengths derived from unworn spines to attempt to address this data gap. The inclusion of the band-diameter data greatly improved the worn-band estimation models, but minimally changed the growth models. Few of the growth-model parameter estimates based on the back-calculated and mean back-calculated data were significantly different from those estimated based on the observed data alone.

Back-calculation methods are designed to be used when sample sizes are small or if sampling hasn't occurred each month (Goldman, 2005), but in this case it was the entire smaller end of the size range that was being estimated. Using the Fraser-Lee size

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[2] Munk, Kristen. 2007. Alaska Department of Fish and Game, Juneau, Alaska, 99801.
[3] Gauvin, John. 2007. Gauvin and Associates, LLC. Burien, WA 98166.

at birth modified method required assuming that average size at birth was known. We use 26.2 cm, which is based on data collected from spiny dogfish inside the Strait of Georgia, British Columbia (Ketchen, 1972). Sizes at birth are reportedly similar for the species across the northern hemisphere, with ranges of 23-30 cm (Ketchen, 1972; Tribuzio et al., 2009). We also assumed that 2.45 mm was the spine diameter at birth, based on studies of British Columbia spiny dogfish (McFarlane and King, 2009). Because this is an average as well, it is likely that some spines are classified as "unworn" when they should be "worn". Spines that are classified as "unworn" can lead to underestimating the age, and in the case of the back-calculation resulted in instances where 20 cm or more of growth was predicted in the first year. Back-calculations may not be appropriate for this species when using dorsal fin spines as aging structures, and may work well if a structure such as vertebrae were used.

The relatively large variability in size at age of spiny dogfish in the GOA could also reflect true underlying variability in growth rates. Individuals experiencing different thermal and feeding histories are expected to have different growth characteristics. It is also conceivable that our samples represent collections of dogfish from multiple, mixed populations. For instance, 4 of 2,940 recoveries (0.14%) of spiny dogfish tagged in British Columbia were recovered in Alaska (McFarlane and King, 2003). Because the movements of spiny dogfish from other areas to and from Alaska are unknown, the degree of mixing is uncertain. However, there is no evidence of genetic differentiation in the Northeast Pacific based on analyses of eight microsatellite loci from dogfish sampled from the Bering Sea, the Gulf of Alaska, Strait of Georgia, Puget Sound, and the coasts of

Washington, Oregon, and California (Hauser, 2009). Mixtures of spiny dogfish from other areas with growth characteristics that are different from those of Alaska resident dogfish could contribute to the variability in size at age that we observed in the GOA. Nevertheless, the existence of a statistically significant difference in growth rates from different areas of the Northeast Pacific (Vega, 2006; Table 3.4 and Table 3.5 this document) indicates that mixing is incomplete.

Our findings have at least two important implications for management of the species. First, for estimation of stock productivity and biological reference points for spiny dogfish in the GOA, it is important to use growth curves that are fitted to size-at-age data from dogfish captured in the GOA. Although alternative growth model parameters were not statistically significantly different from one another in our study, the variation among predicted length may be of biological significance. For instance, the worn-band estimation curves for the GOA and British Columbia, resulted in very different estimates of ages (Figure 3.5); use of growth curves for British Columbia would result in estimated numbers of worn-bands from dogfish spines in the GOA that would be biased high for large spiny dogfish and biased low for small spiny dogfish. For example, for a spiny dogfish with a 1.8 mm *EBD*, the GOA model would estimate an age of seven years, whereas both of the British Columbia models would estimate an age of four years. A fish with a 6 mm *EBD* would be estimated to be age 24 by the GOA model and ages 46 and 37 by the two British Columbia models. Such biases in growth estimates may lead to biases in estimates of biological reference points for fishery management.

Second, as in other portions of their range, the largest spiny dogfish are the oldest females. Because commercial fisheries for spiny dogfish select for the largest individuals, fishing mortality rates are disproportionately higher for this reproductive segment of the population. In the Northwest Atlantic Ocean, a sharp increase in landings during 1987–1993 led to a fivefold increase in fishing mortality rates on fully exploited females from 0.016 to 0.26; and fishing mortality rates exceeding 0.10 on large (≥80-cm) females resulted in negative pup replacement, subsequently leading to stock decline (Rago et al., 1998). Thus, to sustain spiny dogfish in the GOA, fishery management plans should consider not only slow growth rates, low fecundity, and late maturation of this species (King and McFarlane, 2003), but also the potentially disproportionate number of removals of the mature female component of the stock by commercial fishing by estimating size- and sex-specific fishing mortality rates and biological reference points.

Future research should address the many uncertainties remaining about spiny dogfish biology and life-history in Alaska. In particular, results from this study indicate several areas of research needed to improve our understanding of spiny dogfish age and growth. First, although demonstrated for fish captured off British Columbia (Beamish and McFarlane, 1985; McFarlane and Beamish, 1987; Campana et al., 2006), validation of annual band formation, as well as worn-band properties, for spiny dogfish collected from the GOA should be conducted to describe potential sources of bias in the aging estimates for spiny dogfish at this northern portion of their range in the Pacific Ocean. Second, the collection of juvenile dogfish (<50 cm) is needed to provide more precise estimates of growth over their full life-history, as well as to help identify statistically

best-fit growth models. Third, tagging studies, such as those conducted in British Columbia (McFarlane and King, 2003), would help elucidate the degree to which dogfish in Alaska represent mixed stocks with different growth attributes; such tagging results would help to delineate stock boundaries essential for fishery management. Fourth, controlled experiments are necessary to fully examine the selectivity of various fishing gears for spiny dogfish by size and sex. This would be an important preliminary step toward gear standardization, if long-term sampling programs are envisioned for spiny dogfish. Finally, continued sampling of spiny dogfish over small regional scales is necessary to fully evaluate potential geographic differences in growth and resultant parameters (i.e., natural mortality) within the GOA, as well as to more broadly understand the life-history of this species in this portion of its range. Although our study would not have been possible without the diversity of low-cost sampling opportunities afforded to us, including the valuable assistance of state and federal agencies and sport and commercial fishermen, further progress will be accelerated by a full-scale, directed field program, which would be more successful at providing an unbiased sample set of spiny dogfish in the waters off Alaska, and which would aid in efforts to build a more detailed stock assessment, and thus models of population dynamics.

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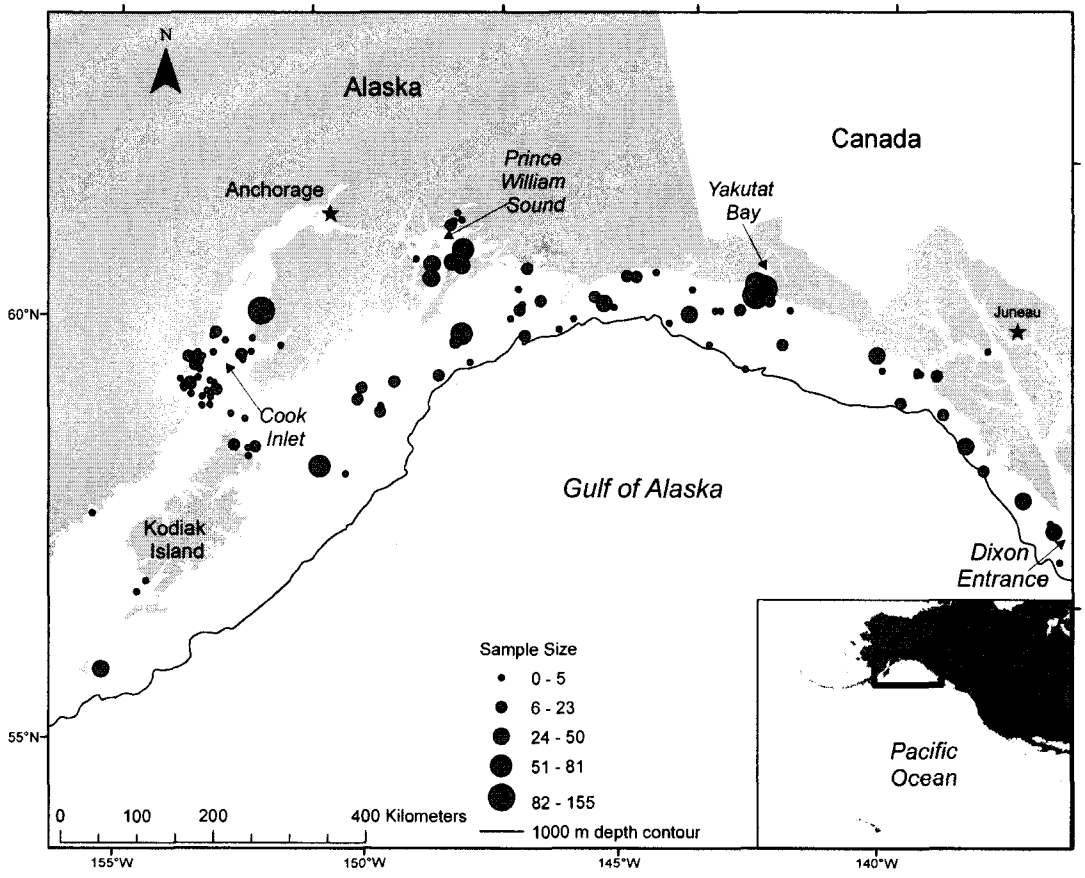

Figure 3.1 Sampling locations. Locations sampled in the Gulf of Alaska in 2004–2007. The size of the circle is proportional to the number of spiny dogfish (*Squalus acanthias*) sampled at each location.

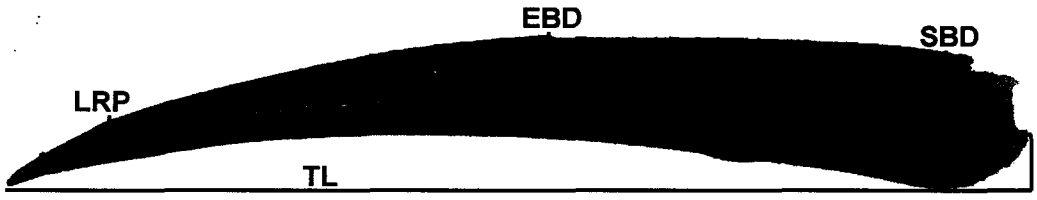

Figure 3.2 Spine measurements. Measurements taken on spiny dogfish (Squalus acanthias) spines. Last readable point (LRP) is the point where the bands are no longer visible on the leading edge of the spine (upper edge in this picture). EBD = enamel base diameter, SBD = spine base diameter, BL = base length, and TL = spine total length, which only applies to spines that are unworn. All measurements were taken in millimeters.

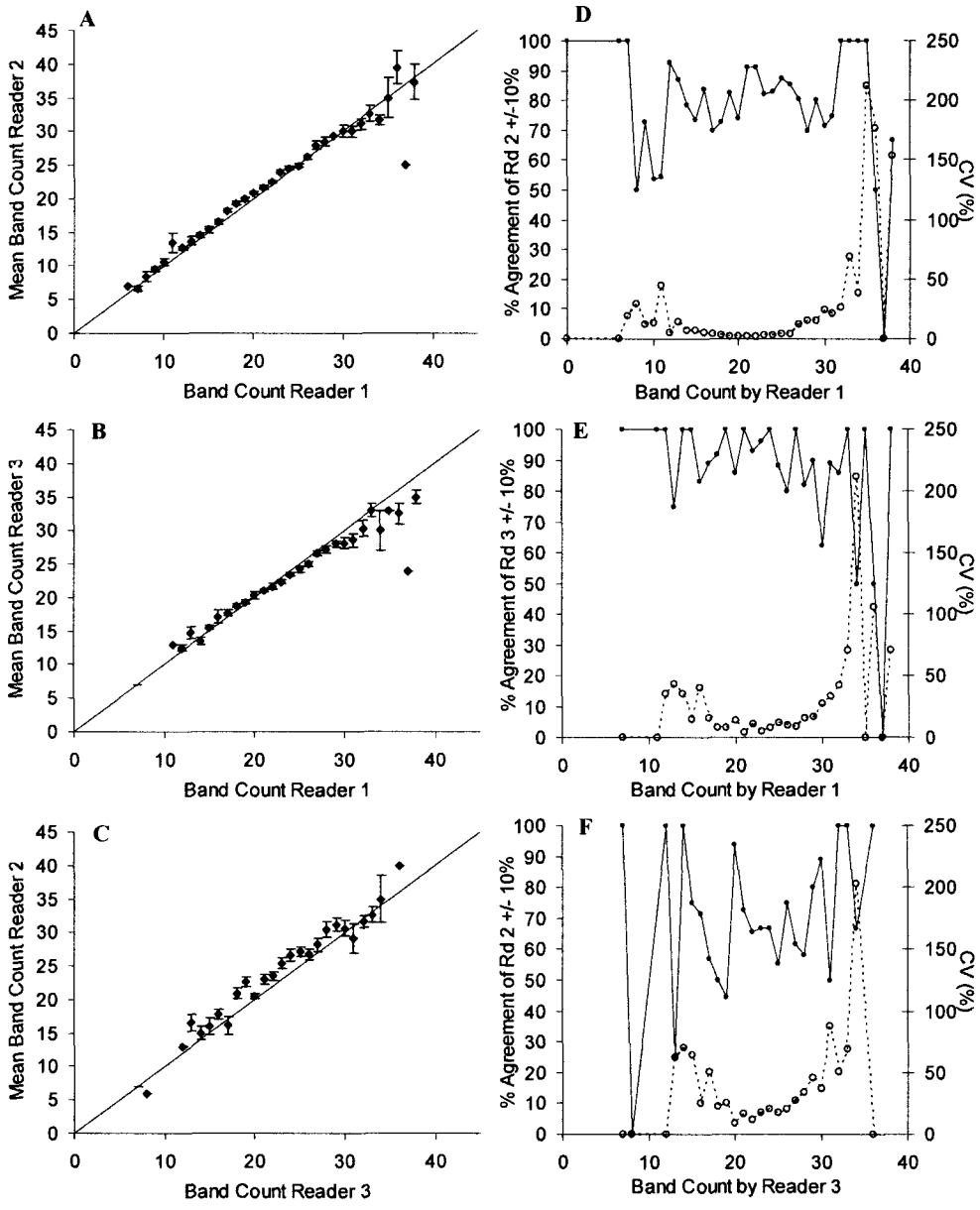

Figure 3.3 Aging precision and bias. A comparison of age counts among readers. (A) Reader 2's mean band counts (y-axis) in relation to the band counts of reader 1; (B) Reader 3's mean band counts in relation to the band counts of reader 1; and (C) Reader 2's mean band counts in relation to the band counts of reader 3. Vertical lines are 95% confidence intervals and the diagonal line is the 1:1 relationship line. (D) Percent agreement and coefficient of variation for reader 2 (Rd 2) compared to reader 1 The percent agreement (±10%) is represented by the solid line and circles and the coefficient of variation (CV) by the dashed line and open circles. (E) Percent agreement and coefficient of variation of reader 3 (Rd 3) compared to reader 1; and (F) Percent agreement and coefficient of variation of reader 2 compared to reader 3.

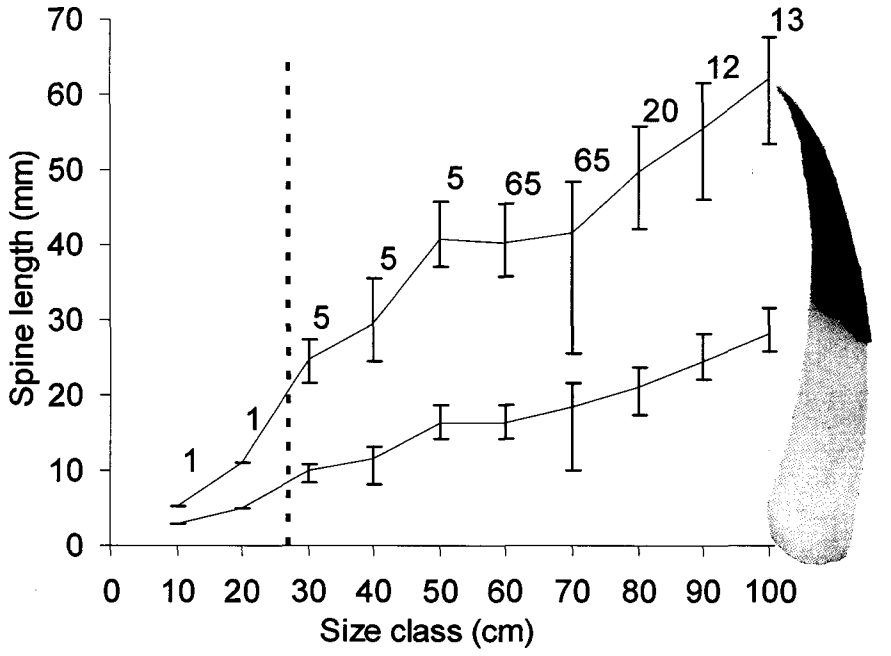

Figure 3.4 Spine growth. Relationship between mean second dorsal spine length and fish size determined from unworn spines from spiny dogfish (Squalus acanthias) collected in the Gulf of Alaska. The top line is spine total length (TL) and bottom line is base length (BL) in millimeters. Numbers above upper line represent the sample size for each 10-cm size class. Solid vertical lines represent 95% confidence intervals. The dashed vertical line represents the approximate size at birth.

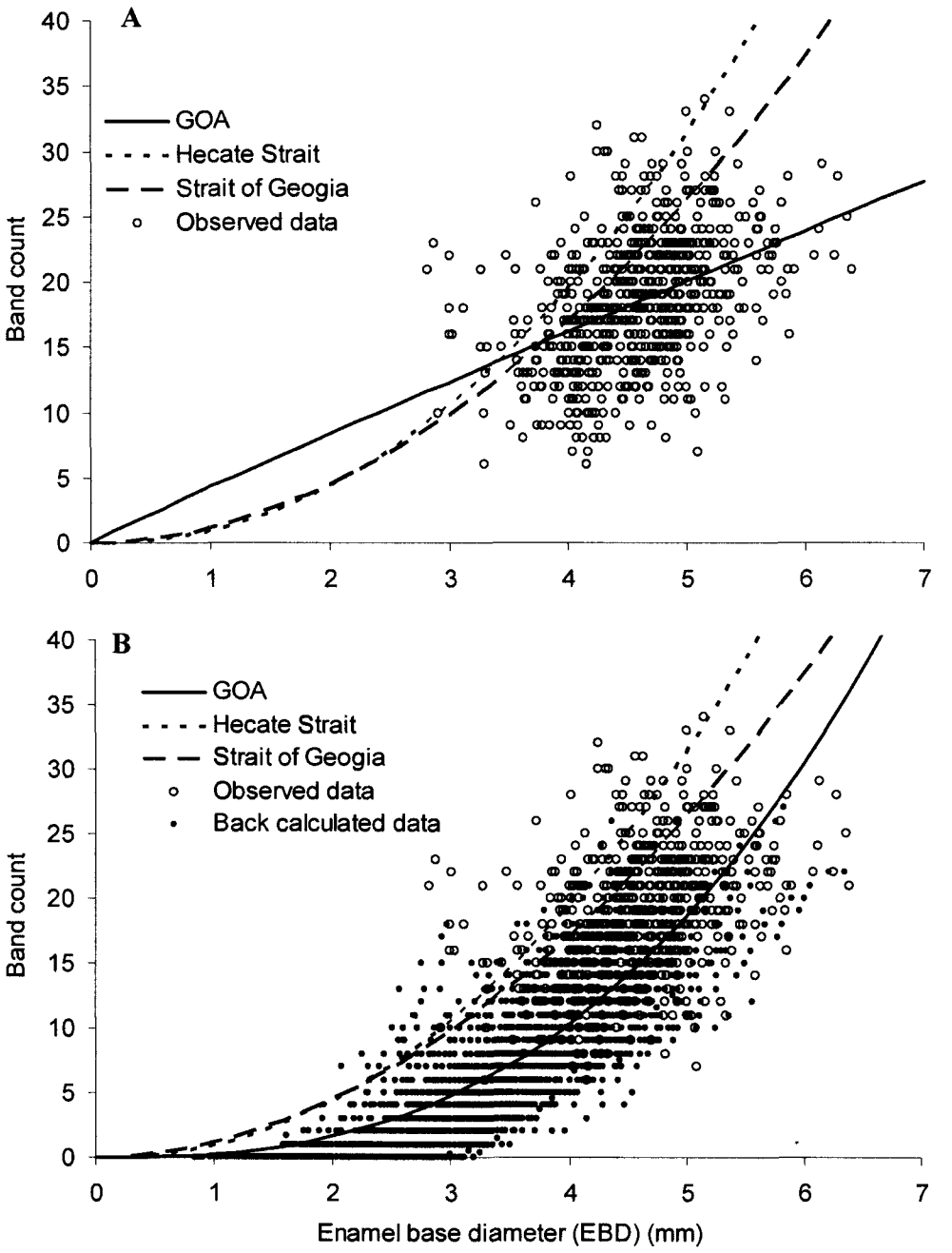

Figure 3.5 Worn-band estimation models. Relationship of band count to enamel base diameter for spiny dogfish (Squalus acanthias) collected in the Gulf of Alaska (GOA) between 2004 and 2007. The best-fit model (WOLS) for (A) the observed data only; and (B) the observed data with the band-diameter data; both sections A and B show the published best-fit relationships for spiny dogfish collected from Hecate Strait and the Strait of Georgia, British Columbia (McFarlane and King, 2009) for comparison.

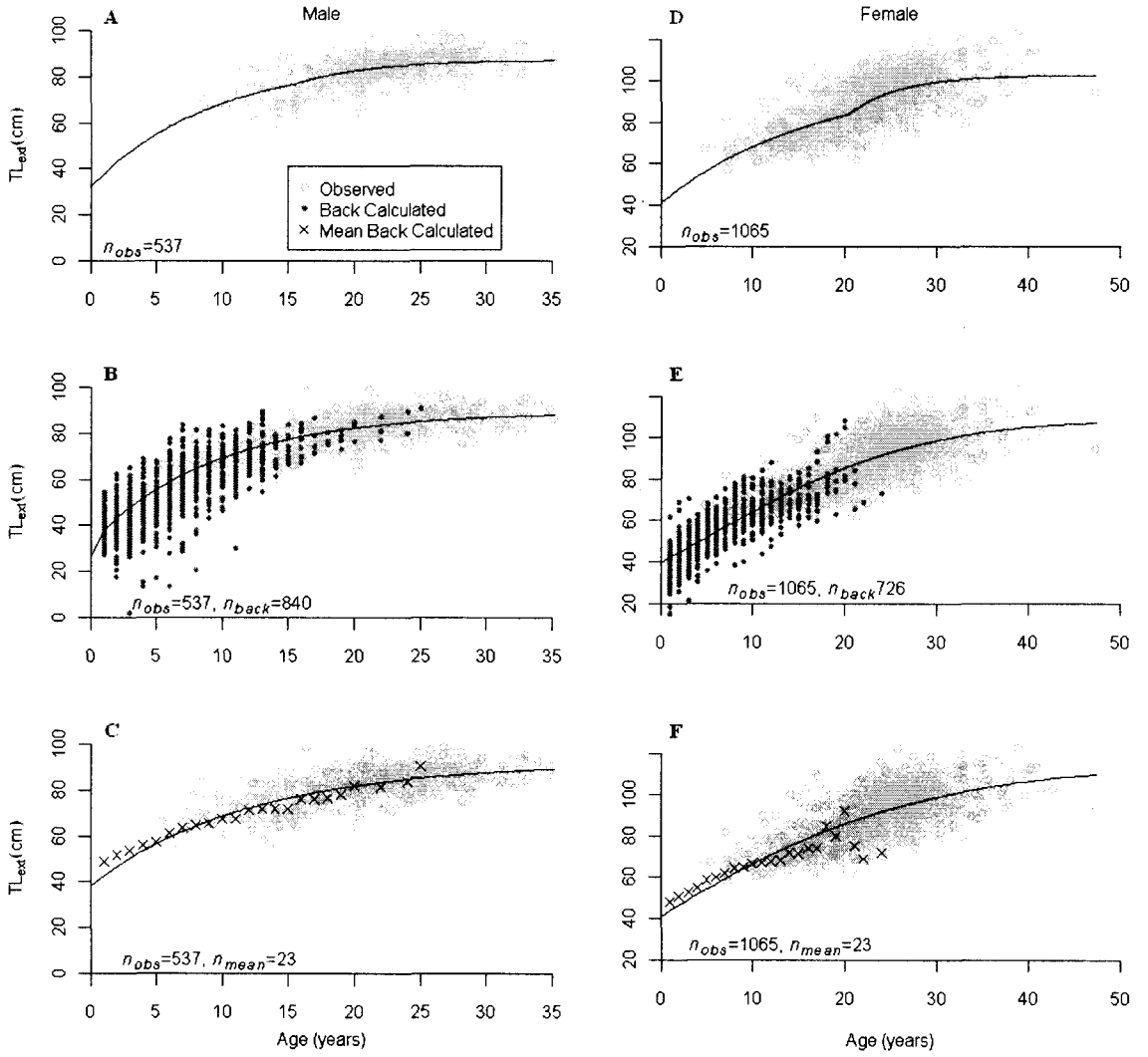

Figure 3.6 Growth model fits. Model fits for male (A–C) and female (D–F) spiny dogfish (Squalus acanthias) length-at-age data. (A and D) Best-fit growth models based on the observed sample data; (B and E) best-fit growth models based on the observed sample data and the back-calculated data; and (D and F) best-fit growth models based on the observed sample data and the mean back-calculated data. nobs is the number of samples and nback is the number of data points created through back calculation of the ages from band-diameter data.

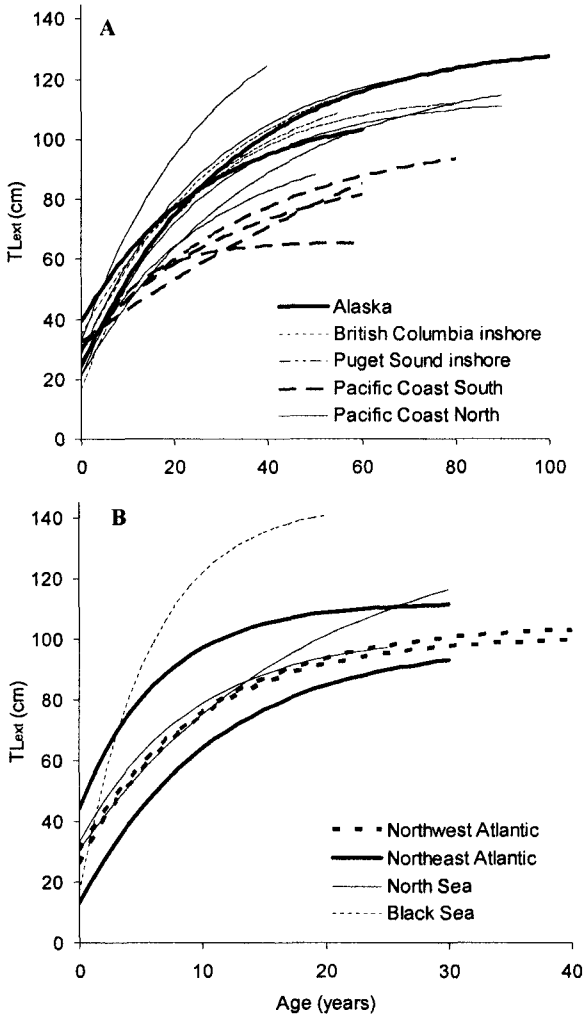

Figure 3.7 von Bertalanffy growth model comparison. Comparison of published spiny dogfish (Squalus acanthias) female growth models from sources listed in Table 4. (A) Growth models published for Pacific Ocean spiny dogfish: "Alaska" includes the Gulf of Alaska (GOA) model from this study and a Prince William Sound (PWS) model (Vega, 2006); "British Columbia inshore" includes three models for dogfish sampled within the Strait of Georgia and Hecate Strait (Ketchen, 1975; Saunders and McFarlane, 1993); "Puget Sound inshore" covers models based on samples collected within the Puget Sound area south off British Columbia and east of the Washington coast (Vega, 2006); "Pacific Coast South" includes four models based on samples collected off Oregon and California (Vega, 2006); "Pacific Coast North" includes models based on samples collected off of Washington and the west coast of Vancouver Island (Ketchen, 1975; Jones and Geen, 1977; Vega, 2006); (B) The growth models from the Atlantic Ocean, North Sea. and Black Sea (Holden and Meadows, 1962; Sosinski 1978; Nammack et al., 1985; Fahy, 1989; Avsar, 2001; Henderson et al., 2002; Soldat, 2002). Note the different x-axis scales.

Table 3.1 Summary of samples. Locations, gear types, and sample sizes for male and female spiny dogfish (*Squalus acanthias*) collected during 2004–07. "Sport" gear refers to hook-and-line fishing with rod and reel, "longline" refers to multiple hooks on a groundline, "trawl" denotes either bottom or pelagic trawls, and "set net" refers to a stationary floating gill net, generally anchored at one end to the shore.

Year	Area	Gear	Males (*n*)	Females (*n*)
2004	Yakutat Bay	Sport	16	35
2004	Gulf of Alaska (GOA)	Longline	50	81
2005	Southeast Alaska (SEAK)	Longline	1	13
2005	Yakutat Bay	Longline	11	23
2005	Yakutat Bay	Sport	0	15
2005	Cook Inlet	Sport	2	28
2005	Yakutat Bay	Longline	41	95
2005	GOA	Longline	108	199
2005	Cook Inlet	Sport	8	12
2005	Yakutat Bay	Sport	1	70
2005	Prince William Sound	Longline	27	62
2005	GOA	Trawl	83	125
2006	Kamishak Bay	Trawl	24	26
2006	Cook Inlet	Set net	50	83
2006	Copper River	Set net	9	5
2006	Yakutat Bay	Set net	4	55
2006	Icy Point (SEAK)	Trawl	0	1
2006	Prince William Sound	Longline	81	87
2006	Cherikoff Island (SW GOA)	Trawl	28	13
2007	Cherikoff Island (SW GOA)	Trawl	20	16

Table 3.2 Growth models. The models fitted to spiny dogfish (*Squalus acanthias*) length-at-age (Lt) data. Parameters are: asymptotic length (L∞), the growth coefficient (k), length at birth (L0), age at size zero (t0), a phase change parameter (At) for the two-phase model, age at transition (th), magnitude of the maximum difference between model 1 and the two-phase model (h), time increment from previous t value (δ), and the inflection point of the logistic curve (a).

Model number	Model name	Model equation	Reference
1	vB 1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	von Bertalanffy (1938)
2	vB 2	$L_t = L_\infty - \left(L_\infty - L_0\right)e^{-kt}$	Fabens (1965)
3a–3c	Two-phase vB with L_0	$L_t = L_{t-\delta} + \left(L_\infty - L_{t-\delta}\right)*\left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right)$, $A_t = 1-\frac{h}{1+e^{slope(t_h-t)}}$	This study
4	Gompertz	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	Ricker (1975)
5a–5c	Two-parameter Gompertz	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}, G = \ln\frac{L_\infty}{L_0}$	Mollet et al. (2002)
6	Logistic	$L_t = \frac{L_\infty}{1+e^{-k(t-a)}}$	Ricker (1979)

Table 3.3 Worn-band estimation models and fits. Summary of the parameters used in the worn-band estimation models and model fits for spiny dogfish (*Squalus acanthias*). The observed data are sample data, the band-diameter data were determined from a subsample of unworn spines where the diameter of each band was measured to simulate size at age for younger animals that were not sampled in this study. Regression models are ordinary least squares (OLS), weighted ordinary least squares (WOLS), nonlinear least squares (NLS) and weighted nonlinear least squares (WNLS). Estimated model parameters (95% confidence intervals in parentheses) and goodness-of-fit indicators: r2, AIC, the Akaike information criteria, and MSE, the mean squared error.

		Observed sample data n=685		Observed band-diameter data n=3877	
Model	Parameter	Estimate	AIC	Estimate	AIC
OLS	b_0	2.690 (1.952–3.708)	6.205	0.211 (0.199–0.223)	3.738
	b_1	1.135(0.949–1.322)		2.867(2.825–2.910)	
WOLS	b_0	2.471 (1.788–3.415)	6.219	0.212 (–0.201–0.224)	3.721
	b_1	1.179 (0.991–1.367)		2.856 (2.814–2.898)	
NLS	b_0	4.325 (3.400–5.444)	4.016	0.539 (0.487–0.594)	3.781
	b_1	0.955 (0.807–1.111)		2.241 (2.178–2.309)	
WNLS	b_0	4.009 (3.106–5.231)	4.018	0.528 (0.475–0.586)	3.763
	b_1	0.998 (0.826–1.164)		2.247 (2.180–2.318)	

Table 3.4 Male growth model results. Summary of male growth model results for spiny dogfish (*Squalus acanthias*). The "Observe data" were the actual age at length data from individual spines, the "With back-calculated data" were the observed data with the estimated back-calculated size at age data and the "With mean back-calculated data" were the observed data with the mean size at age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞ and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age at size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting t_0=0, this allowed for comparison with other studies. The best-fit models are in bold.

			Observed data		with back-calculated data		with mean back-calculated data	
			n=537		n=1377		n=562	
Model #	Model equation	Parameter	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC
1	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	L_∞	88.3(87.0–89.7)	4.545	94.5(92.0–97.6)	4.476	**92.1(89.5–95.6)**	**4.436**
		k	0.095(0.083–0.107)		0.076(0.068–0.085)		**0.082(0.065–0.099)**	
		t_0	–4.8(-6.5–3.4)		–5.6(–6.3—4.9)		**–6.6(–9.4–4.5)**	
		Calculated L_0	32.3(27.4–36.3)		32.7(32.1–33.2)		**38.4(34.4–40.9)**	
2	L_0=*26.2*	L_∞	87.7(86.6–88.8)	4.474	**89.3(87.8–90.9)**	**4.435**	89.2(87.9–90.6)	4.457
	$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$	k	0.105(0.098–0.113)		**0.104(0.098–0.110)**		0.109(0.101–0.117)	
3a	$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta})*\left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right)$	L_∞	87.6(85.7–89.5)	5.58	89.3(86.2–94.9)	4.570	87.5(85.8–90.4)	4.504
		k	0.062(0.034–0.085)		0.087(0.074–0.098)		0.090(0.072–0.104)	
	$A_t = 1 - \frac{h}{1+e^{slope(t_h - t)}}$	h	-2.0(-5.8—1.0)		-0.6(-2.0–0)		-1.0(-2.4—0.3)	
		t_h	15.4(13.5–17.6)		14.3(10.9–18.1)		15.7(13.4–17.5)	
		L_0	54.6(46.0–63.1)		32.5(31.0–34.0)		40.4(34.3–46.7)	
3b	*L_0=from Model 1*	L_∞	**87.2(85.3–90.0)**	**4.472**	89.5(86.4–94.2)	4.565	87.1(85.8–90.1)	4.507
		k	**0.106(0.097–0.117)**		0.086(0.076–0.094)		0.100(0.087–0.108)	
		h	**-0.7(-2.8—0.2)**		-0.6(-2.1–0.0)		-2.3(-6.5—0.4)	

Table 3.4 Continued

		t_h	**15.4(12.2–19.2)**
3c		L_∞	86.9(85.1–88.8)
	L_0=26.2	k	0.116(0.106–0.128)
		h	-0.5(-2.9–-0.1)
		t_h	15.4(12.0–19.7)
4		L_∞	87.5(86.3–88.8)
	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	k	0.115(0.100–0.132)
		t_0	–1.1(–2.7–0.3)
5a		L_∞	87.8(86.3–88.8)
	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}$	L_0	36.3(30.6–41.4)
	$G = \ln \frac{L_\infty}{L_0}$	k	0.116(0.100–0.132)
5b		L_∞	86.3(85.4–87.2)
	L_0=26.2	k	0.144(0.136–0.152)
5c		L_∞	87.0(86.0–87.9)
	L_0=*from model 1*	k	0.126(0.119–0.134)
6		L_∞	87.1(86.0–88.5)
	$L_t = \frac{L_\infty}{1+e^{-k(t-a)}}$	k	0.130(0.111–0.151)
		a	1.2(-0.4–2.6)

	14.3(10.9–18.2)		20.0(19.6–20.9)	
4.490	85.9(83.9–89.1)	5.549	86.3(85.1–90.0)	4.526
	0.114(0.101–0.118)		0.121(0.107–0.128)	
	-1.3(-6.2–-0.1)		-2.6(-4.6–-0.1)	
	16.0(13.3–19.3)		20.0(14.7–20.3)	
4.559	90.6(88.8–92.6)	4.477	90.9(88.7–93.8)	4.458
	0.111(0.102–0.120)		0.099(0.081–0.119)	
	–0.3(–0.6–0.0)		–2.5(-4.5–-1.0)	
4.557	90.6(88.7–92.7)	4.479	90.9(88.7–93.8)	4.458
	34.3(33.0–35.6)		41.8(36.7–46.5)	
	0.111(0.102–0.121)		0.099(0.082–0.119)	
4.570	85.6(84.5–86.7)	4.515	87.1(86.1–88.1)	4.492
	0.163(0.156–0.170)		0.154(0.145–0.163)	
4.556	89.3(87.9–90.8)	4.475	89.8(88.4–91.5)	4.557
	0.121(0.115–0.127)		0.111(0.102–0.120)	
4.571	88.5(87.0–90.1)	4.499	90.0(88.2–92.6)	4.475
	0.146(0.135–0.157)		0.116(0.096–0.137)	
	2.8(2.5–3.1)		0.3(-1.1–1.5)	

Table 3.5 Female growth model results. Summary of results from the female growth models for spiny dogfish (*Squalus acanthias*). The "Observed data" were the actual age at length data from individual spines; the "With back-calcualted data" were the observed data with the estimated back-calculated size at age data;" " and the "With mean back-calculated data" were the observed data with the mean size at age from the back-calculated data. Estimated model parameters with 95% confidence intervals in parentheses and Akaike information criteria, AIC. Asymptotic length (L_∞ and size at birth (L_0) are in centimeters. The growth coefficient (k) and the theoretic age at size length zero (t_0) are not reported with units. In model 1, L_0 was solved for by setting t_0=0, this allowed for comparison with other studies. The best-fit models are in bold.

			Observed data n=1065		With back- calculated data n=1791		With mean back-calculated data n=1090	
Model Number	Model Equations	Parameter	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC	Estimate (95% CI)	AIC
1	1	L_∞	121.4(112.9–137.6)	5.677	128.4(122.3–136.5)	5.365	128.8(118.6–148.7)	5.317
	$L_t = L_\infty\left(1-e^{-k(t-t_0)}\right)$	k	0.034(0.023–0.045)		0.037(0.032–0.043)		0.036(0.024–0.047)	
		t_0	-12.1(-17.9—8.2)		-8.9(-9.9—8.0)		-10.5(-15.0—7.2)	
		Calculated L_0	40.9(38.1–42.5)		36.4(33.2–39.7)		40.3(35.9–42.7)	
2	L_0=*26.2*	L_∞	108.9(106.3–111.9)	5.668	108.0(106.0–110.2)	5.364	114.2(110.8–118.1)	5.314
	$L_t = L_\infty - (L_\infty - L_0)e^{-kt}$	k	0.055(0.051–0.059)		0.067(0.063–0.071)		0.057(0.052–0.062)	
3a		L_∞	102.5(99.9–106.2	5.371	103.8(100.9–107.8)	5.387	101.7(99.4–104.9)	5.374
	$L_t = L_{t-\delta} + (L_\infty - L_{t-\delta}) * \left(1-e^{-A_{t-\delta}k(t-t_{t-\delta})}\right)$	k	0.053(0.040–0.064)		0.057(0.052–0.063)		0.057(0.048–0.065)	
	$A_t = 1 - \frac{h}{1+e^{slope(t_h-t)}}$	h	-2.5(-4.3—1.5)		-1.5(-2.4—0.9)		-2.2(-3.7—1.4)	
		t_h	20.3(19.2–21.8)		19.4(18.1–20.6)		20.0(19.4–20.5)	
		L_0	45.8(37.5–54.3)		35.6(34.3–37.0)		42.2(35.8–48.4)	
3b		L_∞	**102.5(99.9–106.3)**	**5.371**	103.8(101.5–113.1)	5.387	100.76(98.8–103.4)	5.374
	L_0=*from Model 1*	k	**0.058(0.052–0.063)**		0.057(0.046–0.060)		0.061(0.056–0.065)	
		h	**-2.1(-3.7—1.2)**		-1.7(-2.5—0.4)		-2.8(-3.9—1.8)	
		t_h	**20.3(19.2–21.8)**		19.8(15.3–20.6)		20.8(20.5–20.9)	
3c		L_∞	101.8(99.2–105.4)	5.389	98.5(96.5–100.0)	5.395	100.2(98.2–102.7)	5.390

Table 3.5 Continued

	L_0=26.2	k	0.073(0.066–0.078)
		h=a	-1.4(-2.9–-0.7)
		t_h=$P50$	20.3(18.8–22.1)
4		L_∞	115.7(109.2–127.4)
	$L_t = L_\infty e^{-e^{\left(-k(t-t_0)\right)}}$	k	0.048(0.036–0.060)
		t_0	-1.1(-2.7–0.4)
5a		L_∞	115.6(109.3–127.4)
	$L_t = L_0 e^{G\left(1-e^{-kt}\right)}$	L_0	45.0(40.1–49.9)
	$G = \ln \frac{L_\infty}{L_0}$	k	0.048(0.036–0.060)
5b		L_∞	102.4(101.0–104.0)
	L_0=26.2	k	0.090(0.086–0.094)
5c		L_∞	111.2(108.1–114.8)
	L_0=*from Model 1*	k	0.060(0.053–0.061)
6		L_∞	112.3(106.9–120.9)
	$L_t = \frac{L_\infty}{1+e^{-k(t-a)}}$	k	0.062(0.049–0.075)
		a	5.1(3.8–607)

	0.081(0.075–0.083)		0.076(0.070–0.080)	
	-3.0(-5.1—1.5)		-2.0(-3.1—1.1)	
	21.3(20.4–21.9)		20.8(20.5–20.9)	
5.683	115.7(112.2–119.9)	5.355	119.5(112.5–130.5)	5.314
	0.064(0.059–0.069)		0.056(0.043–0.068)	
	1.6(1.2–2.1)		0.3(-0.8–1.5)	
5.681	115.7(112.2–119.8)	5.355	119.5(112.7–130.5)	5.314
	38.2(37.1–39.3)		43.1(38.4–47.6)	
	0.064(0.059–0.070)		0.056(0.043–0.068)	
5.660	100.1(98.8–101.3)	5.412	105.9(103.8–108.0)	5.330
	0.115(0.111–0.120)		0.096(0.091–0.101)	
5.539	112.1(109.7–114.8)	5.410	**116.0(112.2–120.4)**	**5.309**
	0.071(0.068–0.075)		**0.062(0.057–0.067)**	
5.687	**109.8(107.2–112.7)**	**5.352**	114.5(109.3–122.0)	5.310
	0.091(0.085–0.097)		0.075(0.062–0.089)	
	6.3(5.7–6.9)		5.7(4.7–7.0)	

Table 3.6 Comparison to other published studies with von Bertalanffy parameters. Summary of von Bertalanffy parameters (model 1) for growth models for female spiny dogfish (*Squalus acanthias*) from the North Pacific and North Atlantic oceans and the North and Black seas. Parameters are asymptotic length (L_∞) size at birth (L_0), growth coefficient (k), and the theoretic age at size length zero (t_0). Here, L_0 was solved for from the published parameter estimates for the purposes of comparison.

Location	L_∞	k	t_0	L_0	Reference
Alaska, Gulf of Alaska	121.4	0.034	–12.1	40.9	This study
Alaska, Prince William Sound	110.4	0.038	–11.6	39.4	Vega (2006)
British Columbia, Hecate Strait	125.1	0.031	–10.6	35.0	Ketchen (1975)
British Columbia, Strait of Georgia	129.1	0.034	–7.3	28.4	Ketchen (1975)
British Columbia, Strait of Georgia	114.9	0.044	–3.6	16.8	Saunders and McFarlane (1993)
British Columbia, offshore	128.5	0.036	–6.9	28.3	Jones and Geen (1977)
U.S., inshore (WA north)	113.5	0.04	–5.2	21.3	Vega (2006)
U.S., inshore (WA south)	100.4	0.036	–8.4	26.2	Vega (2006)
U.S., offshore (WA)	123.6	0.027	–6.9	21.0	Vega (2006)
U.S., offshore (WA)	152.9	0.036	–6.7	32.8	Ketchen (1975)
U.S., offshore (OR)	101.9	0.027	–12.7	29.6	Vega (2006)
U.S., offshore (OR and CA combined)	90.9	0.031	–13.0	30.2	Vega (2006)
U.S., offshore (CA north)	158.9	0.009	–25.3	32.4	Vega (2006)
U.S., offshore (CA south)	123.6	0.027	–6.9	21.0	Vega (2006)
Northwest Atlantic (U.S.)	100.5	0.106	–2.9	26.6	Nammack et al. (1985)
Northeast Atlantic (Ireland)	98.8	0.090	–1.6	13.3	Fahy (1989)
Northeast Atlantic (Ireland)	112.0	0.150	–3.4	44.7	Henderson et al. (2002)
Northwest Atlantic	104.5	0.095	–3.7	31.0	Soldat [1]
North Sea	137.1	0.054	–4.7	30.7	Sosinski 1978 (as cited in Avsar, 2001)
North Sea	101.4	0.110	–3.6	33.2	Holden and Meadows (1962)
Black Sea	145.0	0.170	–0.7	16.3	Avsar (2001)

[1] Soldat, V. T. 2002. Spiny dogfish (*Squalus acanthias* L.) of the northwest Atlantic Ocean (NWA). NAFO Sci. Counc. Res Doc 02/84, 33 p.

Chapter 4: Demographic and risk analyses of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska using age- and stage-based population models[1]

4.1 Abstract

Age- and stage-based demographic models were developed to examine the intrinsic rebound potential (r) and potential risk of fishing for spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska. Monte Carlo simulations were conducted using an assumed virgin population size and varying harvest levels. For an unfished population, r was estimated to be 0.02-0.03% per year. Fishing mortalities of F=0.03 and 0.04 (stage- and age-based models, respectively), resulted in r=0 indicating that populations fished at these levels and higher are not sustainable. Elasticities showed that r was most sensitive to changes in juvenile and adult survival rates. Harvest strategies targeting juveniles (age-based model) and sub-adults (stage-based model) caused the highest risk of the population falling below a specified population threshold after 20 years. The age- and stage-based models performed similarly regarding the estimation of r and sustainable fishing mortality, suggesting: 1) spiny dogfish can only tolerate low levels of F; and 2) the stage-based model is an appropriate substitute for the age-based model.

[1] Tribuzio, C. A. and G. H. Kruse. (in prep) Demographic analyses of spiny dogfish (Squalus acanthias) in the Gulf of Alaska using Age- and Stage-based population models. Prepared for submission to Marine and Freshwater Research.

4.2 Introduction

Demographic models are used often in lieu of, or to strengthen stock assessments. In the case of elasmobranch studies, demographic models are generally only based on fundamental biological information (i.e., vital rates) about a species, such as natural mortality and fecundity schedules, to estimate population growth rate or growth potential, along with age distributions, reproductive potential, and generation times (Caughly 1977; Krebs 1985; Caswell 2001). These types of models became popular for modeling elasmobranch populations in the 1990's where data to perform more complex population dynamics models was lacking (Cailliet 1992; Cortes 1998; Simpfendorfer et al. 2005). These models can also be used to examine how a population reacts to fishing pressure (Au and Smith 1997; Cortes, 1998; Smith et al. 1998; Simpfendorfer 1999; Beerkircher et al. 2003) and can include distribution and migration parameters (Heifetz and Quinn 1998). While demographic models can be complex, including migration rates and regional abundances (e.g. Heifetz and Quinn 1998), they are also ideal for populations with data limitations, such as fishery-dependent data and are well suited for simulations of hypothetical scenarios when vital rate data are not available (Cortes 2002).

Compared to other approaches, demographic models have a number of advantages and disadvantages. In terms of advantages, modeling results can be compared between models as biological reference points or indicators of a population's status, they allow for examination of constraints imposed by life-history traits, and they permit examination of fishing effects and migration on a species (Cortes 1998; Heifetz and Quinn 1998; Au and Smith 1997; Smith et al. 1998; Simpfendorfer 1999; Gallucci et al.

2006). Unfortunately, most demographic population models provide only a static species-specific assessment, because vital rates are assumed to be constant over time (Cortes 1998). Thus, they do not account for dynamics owing to density dependence, migration or a changing environment (Gedamke et al. 2007). If the effects of density dependence are known, that can be incorporated into the model to correct this drawback (Caswell 2001). Moreover, because these models can be run with minimal data (only requiring fecundity and natural mortality at a minimum), they can overlook the influences of migration when estimating a population's potential for growth or ability to rebound from exploitation. Nonetheless, demographic models can be powerful tools for strategic management advice.

Demographic models have not been previously developed for spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska (GOA), because this species has not been targeted commercially and has only recently become a management concern there. In many other regions where spiny dogfish have been commercially harvested, such as the North Atlantic and Northeast Pacific Oceans, dogfish have either become a management concern (King and McFarlane 2009) or worse, overfished (Rago et al. 1998). The species has characteristics rendering it highly susceptible to overfishing: it is long lived, with late maturity, slow growth and low fecundity (King and McFarlane 2009). If interest in developing a market for GOA spiny dogfish increases, the history of spiny dogfish fisheries in other jurisdictions, as well as the life-history characteristics of this species, indicate that dogfish fisheries in the GOA should be developed in a precautionary manner.

A number of studies have been conducted on Northeast Pacific spiny dogfish in the last few years. These studies focused on migration (McFarlane and King 2003; Taylor 2008), regional life-history (Vega 2006; Tribuzio et al. 2009a; Tribuzio and Kruse *in prep*), age and growth (McFarlane and King 2009; Rice et al. 2009; Tribuzio et al. 2010), bycatch, and abundance estimation (Rice 2007).

The primary goal of this study was to create a demographic model for the GOA spiny dogfish population based on life-history and abundance information from these previous studies. Our secondary goal was to determine if a stage-based demographic model would be an appropriate substitute for a fully age-structured demographic model. Using Monte Carlo simulation we examined the effects of natural variability, variability among published life-history traits, and multiple harvest scenarios for the GOA population (Cortes 2002). Lastly, we conducted a risk analysis for different harvest scenarios (Burgman et al. 1993; Aires-da-Silva and Gallucci 2007).

4.3 Methods

4.3.1 Age-class and stage-class models

Two forms of matrix-population models were used to investigate the population demography of GOA spiny dogfish: age-structured and stage-structured (Figure 4.1; Brewster-Geisz and Miller 2000; Caswell 2001; Frisk et al. 2002). These types of models are convenient and easily implemented because they only require basic life-history information (Simpfendorfer 2005). Both models incorporate female data only: males are

not considered in the context of the population demographics. The basic formulation for both models is:

$$N_{t+1} = \mathbf{M}N_t \qquad \text{(Eq. 4.1)}$$

where N_t is the vector of numbers of animals at each age class at time t and **M** is the transition or projection matrix composed of survival and fecundity for each age (Caswell 2001; Simpfendorfer 2005). It should be noted that the models in this study ignore the impact of density dependence on parameters such as survival, fecundity, and growth. Because knowledge of the mechanisms of density-dependent compensation is largely theoretical for spiny dogfish, we assumed density independence (Walker 1998).

The projection matrix **M** differs for each model. For the age-based model, **M** is a Leslie matrix of the form (Aires-da-Silva and Gallucci 2007):

$$M = \begin{bmatrix} f_0 & f_1 & \cdots & f_{i-1} & f_i \\ l_0 & 0 & \cdots & 0 & 0 \\ 0 & l_1 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & l_{i-1} & 0 \end{bmatrix}, \qquad \text{(Eq. 4.2)}$$

where i is the age class, l is the age-specific survival, and f is age-specific per-captia fecundity rate (fertility). We assumed a birth pulse, post-breeding census, where birth occurs at the end of the year and fertility given by:

$$f_i = l_i m_i, \qquad \text{(Eq. 4.3)}$$

where m_i is the age-specific female fecundity (the number of female pups produced by each female each year). Spiny dogfish have been aged to at least 100 years in the northeastern Pacific Ocean (G. A. McFarlane, Department of Fisheries and Oceans

Canada, pers. comm.), so we included a maximum of 120 age classes depending on the random distribution for longevity (described later).

The stage-based model was developed with five classes (Figure 4.1): neonates, juveniles, sub-adults, adults-pregnant, and adults-resting. Stages and durations were determined by reviewing the species' life-history (Ketchen 1972; Saunders and McFarlane 1993; Tribuzio et al. 2009a; Tribuzio and Kruse *in prep*). Neonates (*N*) are the young of the year and must either die or survive to the next stage in one year. Juveniles (*J*) tend to inhabit shallower, inshore waters, do not mix with the adult schools, and are not susceptible to the fishery. Sub-adults (*S*) move out of the nursery areas and do mix with the schools of larger adults. Mature female dogfish could either be pregnant (*AP*, adult-pregnant) or not (*AR*, adult-resting), and can go back and forth between these two stages. Gestation is 18-22 months for spiny dogfish, which determines the 2-year duration for adult-pregnant. There is some evidence that females may skip a year between pregnancies in the GOA (Tribuzio and Kruse *in prep*); however, this has not been observed in dogfish populations at lower latitudes (Ketchen 1972, Tribuzio et al. 2009a). The resting stage was defined such that a female that proceeded to this stage must return to the pregnant stage after one year, and a pregnant female may either return to the pregnant stage or proceed to the resting stage.

The resulting 5-stage projection matrix is:

$$M = \begin{bmatrix} 0 & 0 & 0 & f_{AP} & 0 \\ G_N & P_J & 0 & 0 & 0 \\ 0 & G_J & P_S & 0 & 0 \\ 0 & 0 & G_S & P_{AP} & G_{AR} \\ 0 & 0 & 0 & G_{AP} & 0 \end{bmatrix}, \qquad \text{(Eq. 4.4)}$$

where G_x is the product of the probability of an individual in stage x surviving (σ) and the probability of shifting to the another stage (γ), such that $G_x=\sigma_x\gamma_x$ and P_x is the probability of an individual surviving and remaining in its current stage, such that ($P_x=\sigma_x(1-\gamma_x)$, (Brewster-Geisz and Miller 2000; Frisk et al. 2002). Estimates of σ_x over a single time step can be written $\sigma_x=e^{-Z}{}_x$ (where Z is the total mortality). Estimates of γ_x are calculated by:

$$\gamma_x = \frac{\left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x} - \left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x-1}}{\left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x} - 1}, \qquad \text{(Eq. 4.5)}$$

where t_x is the duration of stage x, which assumes that all individuals within a stage have equal survival (Caswell 2001). The λ_{init} parameter is determined by iteratively changing it in the static stage model (prior to incorporating the stochastic variables) until it equals the λ from eigen analysis.

Both models were run using Poptools, an add-in for MS Excel (PopTools version 3.1, Hood 2009). Model outputs were the same for both models. The above matrices can be used to solve the Euler-Lotka equation (Caughly 1977) for the instantaneous rate of increase (r), population growth rate ($\lambda=e^r$), net reproductive rate or the total number of

female offspring produced per individual in a single cohort (R_0), generation time or the time for the population to increase by R_0 ($T=lnR_0/ln\lambda$), the mean age of the parents of a cohort ($\mu 1$), and the population doubling time ($t_{x2}=ln(2)/r$). The right eigenvector, **w**, represents the stable age or stable stage distributions (SAD or SSD, respectively) and the left eigenvector, **v**, the reproductive value (RV) which are the proportion at age or stage and the contribution of offspring by each class to future classes for a stable population (r=0), respectively. See Caswell (2001) for a detailed explanation of the matrix algebra and solving for r, R_0, *mu1 SAD/SSD* and *RV*. Elasticities (e_{ij}) were also estimated to examine how the population growth rate is affected by changes in individual age/stage survival and fecundity using the equation (Heppell et al. 1999; Caswell 2001):

$$e_{kj} = \frac{a_{kj}}{\lambda} \frac{v_k w_k}{\langle \mathbf{w}, \mathbf{v} \rangle}, \qquad \text{(Eq. 4.6)}$$

where a_{kj} are the elements of **M**, **v** and **w** are the left and right eigenvectors of **M** and <**w**,**v**> is the scalar product of **v** and **w**. Elasticities are additive and all the elasticities for a population (the sum of the elasticities over all k and j) must sum to 1.

4.3.2 Stochasticity and Input parameters

While many studies of spiny dogfish age, growth, life-history, and movement have been conducted, there remains a great deal of uncertainty in the parameter estimates. Statistical distributions (probability density functions, pdfs, or probability mass functions, pmfs) were defined for the input parameters to account for this uncertainty or natural variability and both models were run using a simulation approach (Cortes 2002). The

Monte Carlo simulations involved randomly drawing each parameter from the defined distributions and recording the output parameters (described above) for that "population". The average of 10,000 replications was taken as the parameter value with 95% confidence intervals being the 2.5^{th} and 97.5^{th} percentile.

Growth-model parameters for GOA female spiny dogfish (Tribuzio et al. 2010) were used to estimate the instantaneous natural mortality (M) using a set of indirect techniques (Cortes 2002; Simpfendorfer et al. 2005; Tribuzio and Kruse *in prep*). Eight models using either the growth coefficient (k), size at 50% maturity, longevity, gonad somatic index, or size at age-0 (t_0), or a combination, were used to estimate M (Alverson and Carney 1975; Pauly 1980; Hoenig 1983; Gunderson and Dygert 1988; Chen and Watanabe 1989; Jenson 1996). A triangular pdf was used to incorporate uncertainty around the M estimate in the models with the median M estimate (0.054) as the most likely value and the minimum (0.011) and maximum (0.101) estimates (Tribuzio and Kruse *in prep*) forming the range . Then, the estimates of M were converted to survivorship ($S=e^{-Z}$, where $Z=F+M$) and incorporated into the model (Figure 4.2A). Longevity was based on the estimates of M (*longevity*=-ln(0.01)/M, Hewitt and Hoenig 2005), and a similar triangular pmf was used with the minimum, median and maximum longevity estimates (Figure 4.2B).

Age at first capture was either fixed at 4 years (the youngest age encountered in GOA dogfish sampling), or allowed to vary uniformly between zero and 60 years or between zero and the age at 50% maturity, depending on the analysis. Stage at first capture was fixed at the sub-adult stage or allowed to vary between neonates and adult-

pregnant. The pmf for age at 50% maturity was a normal distribution with a mean of 34 years and standard deviation of 7 years (Tribuzio et al., *in prep*; Figure 4.2C).

Female fecundity used in the models was the number of female pups per adult female per year, using a 1:1 sex ratio of pups, and a 2 year reproductive cycle (Tribuzio et al. in press). For the stage-based model, female fecundity (m_x) was the overall population average and standard deviation of female pups per female was used (4.9±1.7 female pups/female, Tribuzio and Kruse *in prep*) with a random normal distribution for the pdf (Figure 4.2D). Fecundity was a function of length at age for the age model (no. female pups=$0.251TL_{ext}$-17.631, Tribuzio and Kruse *in prep*). To include uncertainty around the age-specific fecundity, we estimated the standard deviation for each average female fecundity at age and created a random normal distribution pdf for each age class (Figure 4.2E).

The duration of the juvenile and sub-adult classes in the stage model were also allowed to vary because of the uncertainty around the age at 50% maturity and to add uncertainty around the minimum t_c. The age at 50% maturity marked the end of the sub-adult stage and the t_c marked the end of the juvenile stage. Thus, the juvenile stage duration was the randomly selected t_c minus one (for the neonate stage) with a uniform random distribution between one and 10, and the sub-adult stage duration was the random age at 50% maturity minus the juvenile stage duration then minus one (for the neonate stage).

4.3.3 Fishing effects

Both the age- and stage-based models were run without fishing to determine the parameters of an assumed virgin population (i.e, $Z=M$), then fishing mortality (F) was included to examine the effects of different fixed harvest rates on the population ($Z=F+M$). Instantaneous fishing mortality ranged between 0 and 1. We then set t_c and s_c to different ages or stages to examine for which combinations of t_c or s_c and F the r was above 0, thus sustainable. Fishing mortality was applied uniformly across the age or stage classes that were susceptible to fishing (i.e., knife-edge selectivity).

4.3.4 Risk assessment

We conducted a risk assessment to explore the probabilities of a population declining to a threshold value at given levels of F (Burgman et al. 1993). Spiny dogfish are not targeted by commercial fisheries or research surveys in the GOA. This situation creates difficulties when trying to estimate abundance or build a stock assessment model. However, Rice (2007) created a biomass estimate utilizing multiple data sources in the GOA for 2006 ($B_{2006}\approx$1.5 million metric tons (t)) and estimated the maximum sustainable yield (MSY=24,080 t) and biomass at which MSY can occur ($B_{MSY}\approx$0.9 million t). In this case, B_{MSY}=63% of B_{2006} which is $B_{63\%}$. We used B_{2006} and the average fish weight (Tribuzio and Kruse *in prep*) to estimate the abundance in numbers of dogfish for 2006, and then estimated the number of females by assuming a 1:1 sex ratio which we set as our starting population size. Fisheries management in the GOA is based on limit and target reference points, such as B_{MSY} or $B_{35\%}$ and $B_{40\%}$ (biomass that is 35% or 40% of the

virgin biomass, the former of which is used as a proxy for B_{MSY}), respectively, and their associated fishing mortality rates (F_{MSY}, $F_{35\%}$, and $F_{40\%}$), depending on the available information for a given species. However, inflection points ($\sim B_{MSY}$) on population growth curves for sharks tend to occur at biomass values greater than one half of virgin biomass as typically assumed for teleost fish populations (Cortes 2007; Simpfendorfer et al. 2008). Moreover, it has been argued that management should strive to maintain biomass of less productive shark populations, such as spiny dogfish, well above B_{MSY} levels owing to time lags associated with their delayed maturity and high longevity (Musick et al. 2000). Therefore, for this study we chose to evaluate three threshold values, B_{MSY}, $B_{40\%}$, and $B_{50\%}$ (based on B_{2006}).

The assumption of uniform F across all susceptible classes is not realistic, so we allowed F to vary independently for immature and mature spiny dogfish in the age model and for juveniles, sub-adults and both adult stages in the stage model. Harvest scenarios for the age model consisted of two fishing mortalities, one for juveniles and one for adults (e.g. F_J=0, F_A=0.04), while the scenarios for the stage model had three fishing mortalities, one each for juveniles, sub-adults and adults-pregnant/resting (e.g. F_J=0, F_S=0.1, F_A=0.04). Projections were made over a 20-year time period, with 1,000 replications for each harvest scenario. A risk statistic was calculated as the proportion of the simulated populations that fell below the threshold criteria after 20 years. We allowed F to vary uniformly between zero and 0.1, because trial model runs at F>0.1 rapidly took the biomass to zero. We were interested in the sustainable F, so we examined a smaller range of F values.

4.4 Results

4.4.1 Virgin population

For the Gulf of Alaska, in the absence of fishing, age-based model estimates are r=0.034 (0.012-0.06, 95% confidence intervals) and λ=1.035 (1.012-1.064). The stage-based model estimates are r=0.020 (-0.031-0.082) and λ=1.020 (0.969-1.086). The net reproductive rate, R_0, is 4.794 (1.967-8.445) for the age model and 2.438 (0.233-8.192) for the stage model. The mean generation time is 46.3 (33.6-59.5) and 34.9 (23.9-48.9). The doubling time is 20.4 (11.1-56.7) and 35.4 (13.1-43.8), and the mean age of parents is 49.0 (38.0-60.9) and 38.0 (30.2-47.0), for the age and stage models, respectively.

Estimation of the SAD/SSD and RV for the two models had some similarities and some differences. For the age model, the majority of the virgin population is <20 years old with young of the year (or neonates) dogfish being dominant at 9.2% (Figure 4.3A), while the stage model estimates the majority of the population to be sub-adults at 51.9% followed by juveniles at 33% and neonates (Figure 4.3B). However, the neonates in the stage model account for 8.5% of the population, which is similar to the young of the year from the age model. Reproductive value is maximized at 47 years for the age model (0.019, Figure 4.4A) and in the *AP* stage for the stage model (0.463, Figure 4.4B). While the RV for all ages classes is a bell-shaped curve, showing small changes between age classes, the stage model RV is low for the *N*, *J*, and *S* stages and nearly all of the RV is contained in the *AP* and *AR* stages.

Elasticity analysis showed that changes in the survival of *S* stage or <20 year old dogfish have the greatest impact on *r*. In the age model, annual survival at ages <24 years all had a 2.2% elasticity, and the elasticity decreased to near zero by age 54 (Figure 4.5A). The maximum contribution of fecundity to changes in *r* was <1% for an 18 year old dogfish (Figure 4.5B). In the stage model, because there were fewer groupings the impact of one group was larger. Survival of the sub-adult class contributed 38.5% to changes in *r*, and pregnant adult survival contributed 26.8%. Similarly, fecundity in the stage model only contributed 3.7% (Figure 4.5C).

4.4.2 Fishing effects

Both models were dramatically impacted with the inclusion of fishing mortality. The *r* value dropped to negative values at (i.e.$0<\lambda<1$) at $F>0.04$ for the age model and 0.03 for the stage model (Figure 4.6). Both R_0 and t_{x2} decreased to negative values with $F>0.03$ and 0.04, respectively. Likewise, $\mu 1$ also decreased, however *T* only decreased slightly, and for the stage model it increased at $F>0.1$. The SAD/SSD shifted to younger ages, but the overall pattern of age distributions did not change (Figure 4.3A & B). However, the RVs for the two models behaved differently. In the age model, there was very little change in RV at age with changes in *F* (Figure 4.4A). On the other hand, in the stage model, as *F* increased and the RV of *AP* and *AR* decreased the RV of *N* and *J* increased (Figure 4.4B).

Not surprisingly, delaying age of entry into the fishery increases the values of *F* that are sustainable. In the age model, fishing at all levels is sustainable if the $t_c>50$, and

sustainable at t_c=40 for F<0.7 (Figure 4.7A). For the stage model, however, delaying the s_c to the adult stage only increases the sustainable F to 0.1 (Figure 4.7B).

The analysis of impacts of various harvest strategies indicates that targeting the juveniles in the age model and the sub-adults in the stage model has the greatest impact on the proportional risk of a population reaching the threshold criteria. In both models, the populations had a higher risk of decline to B_{msy} than B_{50} and B_{40} under any given harvest scenario. If F_J was held at zero in the age model, only a small increase was seen in the risk as F_A increased, but if F_A was held at zero there was an increase in risk as F_J increased (Figure 4.8). Similarly, for the stage model, the greatest increase in risk was seen as F_S increased, with only slight increases as F_J and F_A increased (Figure 4.9).

4.5 Discussion

4.5.1 Demographic and risk analysis

Our results suggest that the GOA spiny dogfish populations can tolerate only a very low harvest rate (F<0.04). The GOA spiny dogfish population has a very low growth rate, which only decreases with increased fishing pressure, and the rebound potential of the population is among the lowest of all shark species (Smith et al. 1998). This means that the population naturally increases at a very slow rate and its ability to recover from fishing is limited or, at best, a slow process. Our application of these models do not take into account the possibility of density-dependent compensation and assume that all model inputs are static throughout time, both of which could cause the

model to overestimate the population's ability to cope with fishing pressure. Because the nature of demographic models is a snapshot of the population, the only way to address the issue of static input information would be to have a time series of data on vital rates, and to run the demographic models independently for each time step.

The effects of density dependence may be difficult to impossible to completely elucidate (Walker 1998), however a number of studies have tried. First, it is important to consider the point in time when vital-rate data (i.e., fecundity, growth and survival) were collected; that is, whether they were collected early on from a virgin population or later after harvest has been ongoing because density-dependent effects may vary with F (Smith et al. 1998). Second, density-dependent responses may be less dramatic in elasmobranchs than in teleosts because of slow growth, low fecundity and late maturity characteristics (Cortes 1998). The instantaneous population growth rate is related to the population size, such that the intrinsic rebound potential ($r_{intrinsic}$) is the maximum growth rate (which only occurs in the absence of fishing at low population sizes) and the conditional rebound potential ($r_{conditional}$) is the growth rate at given population conditions in the absence of fishing (Gedamke et al. 2007). It may be more appropriate for this study to consider r to be $r_{conditional}$, as opposed to $r_{intrinsic}$, because we are looking at a snap-shot of a population that has not undergone intense fishing pressure and the effects of density-dependence are unknown.

The generally accepted means for compensation is an increase in reproductive output in the form of reduced size at maturity or more/larger offspring which may result in increased young-of-the-year survival and increased pup growth (Cortes and Parsons

1996). These mechanisms have not been seen in harvested populations of spiny dogfish. In the Northwest Atlantic population of spiny dogfish, size at first maturity decreased from 75 to 66 cm (total length; however, it was not described how total length was measured), but fecundity did not change as a result of fishing pressure (Bonham et al. 1949; Sosebee 2002). The average size of females also decreased by 5 cm (Rago et al. 1998), resulting in smaller females producing smaller offspring. Increased juvenile survival, in the form of reduced competition with adults as a result of a fishery that targets the largest fish, was determined to be the mechanism of compensation for a harvested population of spiny dogfish in British Columbia, Canada (Wood et al. 1979).

Sensitivity analysis also suggested that r is most sensitive to juvenile survival. In fact, small changes in M can result in large changes in r, such that a very slight increase in juvenile survival may increase r a great deal (Simpfendorfer 1999). The sensitivity of models to changes in M is very important, especially because of the uncertainty surrounding the indirect estimates of M (Pascual and Irbine 1993). Sensitivities are not consistent across all shark species: large pelagic species tend to be more sensitive to juvenile and adult survival, whereas small coastal species tend to be more sensitive to changes in fertility. This is mostly because small coastal species tend to have higher fecundity, mature earlier and have shorter generation times, whereas pelagic species are older at maturity, have lower fecundity and long generation times. Lower productivity species tend to be more sensitive to changes in juvenile survivals (Heppell et al. 1999). Spiny dogfish, while being a small coastal species, are more similar to the large pelagic species in their life-history traits, and should be managed more similarly to pelagic

species. This type of analysis can be useful to management because specific groups can be identified for protection (de Kroon et al. 2000); for example, size limits to increase survival of earlier ages. This may be difficult for spiny dogfish because of the large size at maturity relative to maximum size and the high degree of natural variability in the population (Tribuzio et al. 2009a; Tribuzio and Kruse *in prep*).

Spiny dogfish are amongst the longest lived, slowest growing, and least productive (e.g. low fecundity and slow rate of population growth) of all shark species (Smith et al. 1998; Cortes 2002). Sharks in general have low productivities (most $r<0.1$) in comparison to teleost species; however, some small or more productive species can have an r value as high as 0.28 and sustain harvest (Simpfendorfer 1999; Stevens 1999; Frisk et al. 2002; Aires-da-Silva and Gallucci 2007). The North Atlantic blue shark (*Prionace glauca*) population is highly productive (for a shark) with $r=0.21$ and has tolerated harvest for many years (Aires-da-Silva and Gallucci 2007). Also, among a dozen shark species examined, it was the only species with a population inflection point less than one half of virgin population size (Simpfendorfer et al. 2008). Further, in the North Atlantic, a demographic analysis of the little (*Leucoraja erinacea*), winter (*Leucoraja ocellata*) and barndoor skates (*Diturus laevis*) showed that the smaller, more productive species have higher r values and were more tolerant to fishing pressure than the larger less productive barndoor skate (Frisk et al. 2002). The Australian school and gummy shark fishery is an example of a fishery where two species are harvested together, and while the school shark (which is less productive and has a lower value of r) declined,

the gummy shark (a more productive species with a higher r value) was more tolerant of the levels of exploitation (Stevens 1999).

Shark harvest strategies are possible that allow fishing under sustainable r values ($r>0$). For instance, because r is most sensitive to late juvenile and adult survival, harvest of neonate or small juvenile Australian sharpnose sharks *(Rhizoprionodon taylori)* may be sustainable at fairly high levels ($F=0.67$), if the large juvenile and adult stages are protected (Simpfendorfer 1999). This may work in fisheries that routinely target or incidentally catch neonates and small juveniles, but in the case of the spiny dogfish, the neonates and small juveniles are not encountered in commercial fisheries and F occurs on large juveniles and adults. In the Northwest Atlantic spiny dogfish fishery, F was >0.1 for females >80 cm total length for many years, which resulted in negative pup replacement, as well as an estimated 50% bycatch mortality for spiny dogfish as small as 50 cm total length (Rago et al. 1998). In the British Columbia spiny dogfish fishery, the largest females have been targeted historically, but the average size of the landed females has decreased by 13 cm over the 30+ years of fishing and larger juveniles are constituting a greater portion of the catch in recent years (King and McFarlane 2009). The British Columbia spiny dogfish population was able to recover from previous periods of heavy exploitation because of increased juvenile survival (Wood et al. 1979), but with the recent trend towards catching more juveniles, the population may not recover as readily as before.

In the GOA, spiny dogfish are not targeted, but do occur (sometimes frequently) as bycatch in many fisheries and it is mostly large juveniles and adults that are caught.

Bycatch mortality has not been investigated in these fisheries, but has been observed by one of us (CAT) to be as high as 100% in some cases. The demographic models presented here assume that the GOA population is essentially in a virgin state because abundance is estimated to be 90% of the theoretical carry capacity (Rice 2007). Although F (as a result of bycatch) is small for GOA spiny dogfish, estimated to be only 1% of the total GOA population (Courtney et al. 2006), the simulations presented here suggest that directed fishing of spiny dogfish would not be sustainable. Fishing mortality would be almost exclusively on large juveniles and adults, and as shown here, this would result in a significant reduction in r.

The rebound potential estimated here does not include potential migration into and out of the GOA. Tagging studies have been conducted on British Columbia (McFarlane and King 2003) and Washington (reviewed in Taylor 2008) spiny dogfish populations, and studies are on-going for GOA populations. Results of these studies may be used to estimate migration rates, which could then be incorporated into these models (following a model structure similar to Heifetz and Quinn 1998).

Management of the spiny dogfish in the GOA falls under the "other species" category of the Fishery Management Plan for Groundfish of the Gulf of Alaska (NPFMC 2008). Under the current management strategy, the other species group can make up to 5% of the total catch taken, and it would be possible for that 5% to be comprised of just one species. A similar situation occurred when a new market developed for skates in 2003, dramatically increasing the catch of skates within the other species group (Gaichas et al. 2003). That species group was subsequently removed and assigned its own total

allowable catch. In 2008, the estimated spiny dogfish catch was 534 t, 18% of the total other species catch (Tribuzio et al. 2009b). If the same scenario as the skates were to occur with dogfish and the allowable catch was maximized (to become 100% of the total other species catch), the catch could be as high as 27,000 t (5% of the groundfish acceptable biological catch for 2008, NPFMC 2007), which would be about 1.7% of the estimated biomass in 2006 (Rice 2007). While the percentage seems low, the British Columbia and Northwest Atlantic spiny dogfish fisheries have seen significant changes in abundance and biological impacts with catches as low as 2,000 t up to 22,000 t, respectively (Rago et al. 1998; King and McFarlane 2009). As shark fisheries in other areas of the globe become overfished, the interest in expanding a market in the GOA may increase and future management strategies will need to take into account the low productivity of the species.

4.5.2 Age class versus stage class models

We examined both a fully age-structured model and a stage-structured model to determine if the less cumbersome stage-based model would produce comparable results for the GOA spiny dogfish. In some cases, the two methods produced comparable results, while in others the results were quite different. For example, the SAD/SSD distributions performed similarly for both models, in both cases as fishing mortality increased the peak of abundance shifted towards young ages or stages, but the overall distribution did not change much. This similarity extended to the RV distributions as well. As F increased, the RV of the older immature dogfish decreased and for the

youngest dogfish it increased. The overall pattern was consistent between both models, but was exaggerated in the stage model, as was expected because of the condensed groupings.

The estimated parameters did not follow the same consistent pattern between models. The rebound potential (r) for both models was low in the absence of fishing and became negative quickly as F increased (>4%); however, r from the age model decreases linearly while the estimated r from the stage-model asymptotes at about -0.3. The important factor here is not that they decrease at different rates, but instead that both models had similar estimates of sustainable F, where r=0. The two age-dependent parameters ($\mu 1$ and T) were quite different between the two models. Unlike the age model, where each age class has a specific age attached to it, the stage model is essentially age independent, in that time is only included in the stage durations, which could lead to the differences in $\mu 1$ and T. The net reproductive rate (R_0) did perform similarly between the two models, with the only difference being that the age model had greater R_0 for a virgin population.

A similar study found that the two modeling approaches resulted in similar demographic outcomes (Mollet and Caillet 2002). However, this was only true if the stage groupings were appropriately specified in the stage-class model. For example, they found that a three-stage model (with stage durations of 1, 1, and 8 years) produced comparable results to the age-class model for the pelagic stingray (*Dasyatis violacea*), but not a two-stage model (with durations of 2 and 8 years). In the case of the sandbar shark, a five-stage model was most appropriate because it was longer lived and had a

more complex life-history (Brewster-Geisz and Miller 2000). We adopted the same five stages here as they seemed most biologically meaningful and logical for spiny dogfish. The five-stage model included a resting stage between pregnancies. Previous studies have cited no evidence that dogfish have a resting period between pregnancies in British Columbia and Puget Sound (Ketchen 1972; Tribuzio et al. 2009a); however, evidence in the GOA suggests that a resting period of a year or more may occur in this northern population (Tribuzio and Kruse *in prep*). Regardless, misspecification of the reproductive cycle may have a small effect on the model outcome as the model is most sensitive to juvenile and adult survival, not reproductive cycle (Secor 2008).

Besides the number of stages, there are other considerations with the stage models. For models with few stages, T may be better represented by μl because correcting for the slow down of juveniles through the stages defeats the purpose of using the stage model (Heppell et al., 2000; Mollet and Caillet 2002). Models with only a few stages may be more appropriate for fast-growing species which reach maturity quickly. Owing to their grouped nature, stage models also have larger dampening ratios and may reach stable populations sooner than age models.

4.5.3 Conclusion

The spiny dogfish is a long lived, slow growing, low fecundity, and very low productivity species, which is highly susceptible to overfishing. Our results suggest that any harvest management strategy of spiny dogfish needs to consider the stock structure (and migration rates between the GOA and neighboring management areas) and be

conservative if a large proportion of the stock is exposed to the harvest. Regardless of which model is used, the conclusions are essentially the same; a spiny dogfish stock can only sustain a very low harvest rate. In the case of the GOA spiny dogfish, the stage model produces comparable results to the age class model, in regards to estimating the rebound potential and sustainable fishing mortality of a population, while being much simpler to implement. Thus, the stage-based model is an appropriate substitute.

4.6 Acknowledgements

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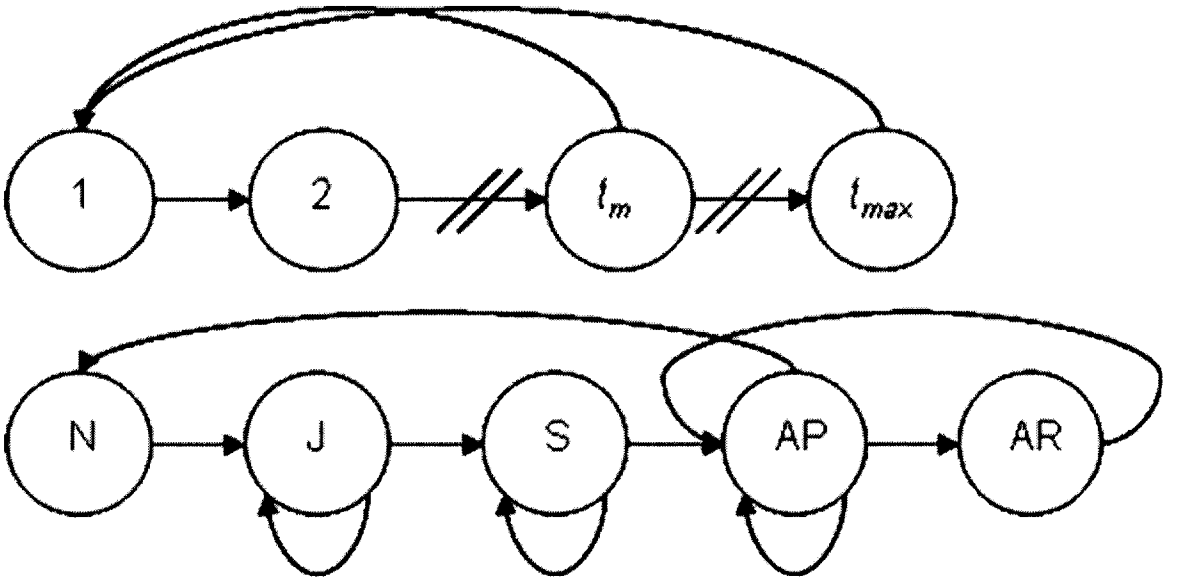

Figure 4.1 Life-cycle diagram. Life-cycle diagrams for age (top) and stage models (bottom) used in this study. Numbers represent ages and capital letters represent stages, N=neonate, J=juvenile, S=sub-adult, AP=adult-pregnant, and AR=adult-resting. The age model has 120 age classes; parallel diagonal lines indicate breaks in the age structure not shown in the diagram (removed for clarity), t_m and t_{max} represent the age at maturity and maximum age. Straight arrows from left to right represent the progression from one age class or stage to the next. Curved arrows above the diagram represent feedback to previous ages or stages and the curved arrows below the diagram indicate a feedback loop to the same stage, indicating that an animal does not progress to the next stage.

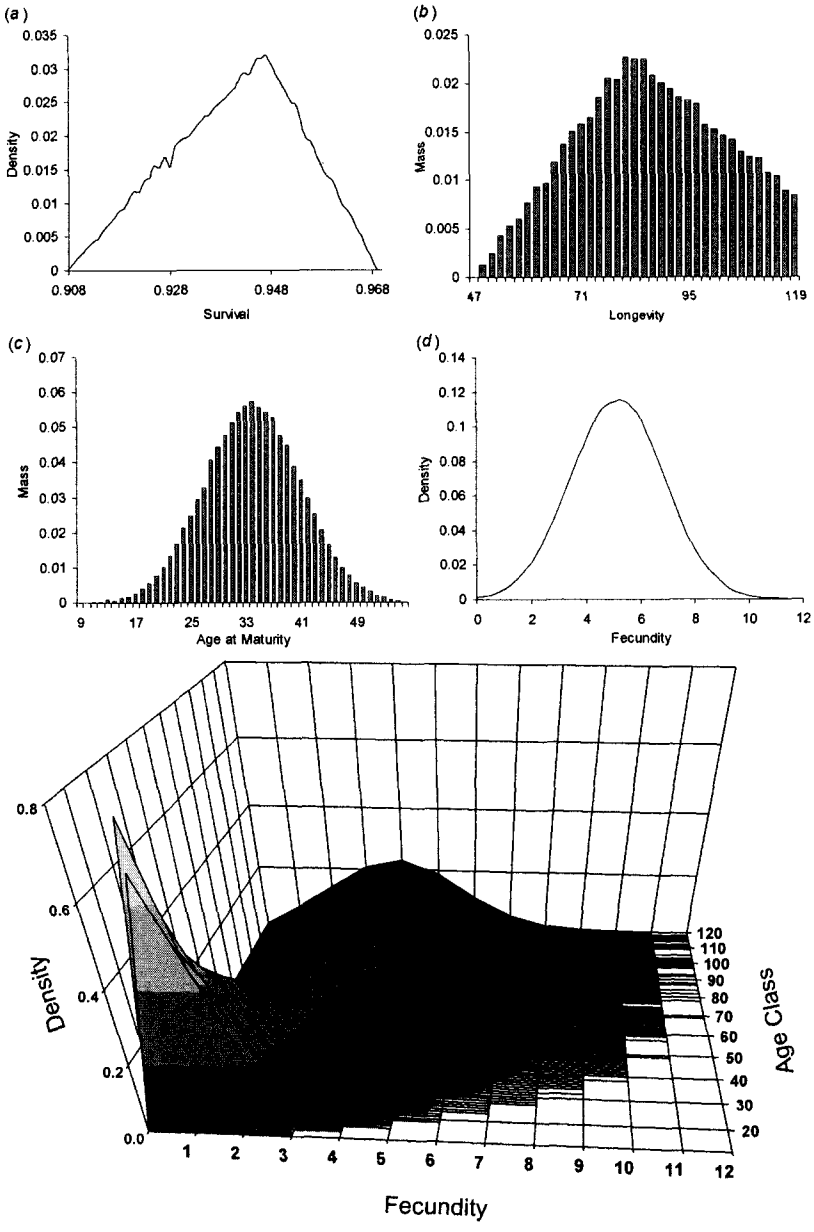

Figure 4.2 Probability functions. Probability density and mass functions of input parameters for the age-based and stage-based models. (a) Survival and (b) longevity were assigned triangular distributions based on the median, minimum and maximum estimates of natural mortality; longevity densities were not estimated for the stage model because that model is not age dependent. (c) Age at maturity was only estimated for the age model, by definition. (d) Female fecundity for the stage model was assigned a random normal distribution with average and standard deviation values based on all dogfish data. Finally, to estimate (e) female fecundity for all age classes, each class was randomly assigned a fecundity value from a normal distribution specific to that age class.

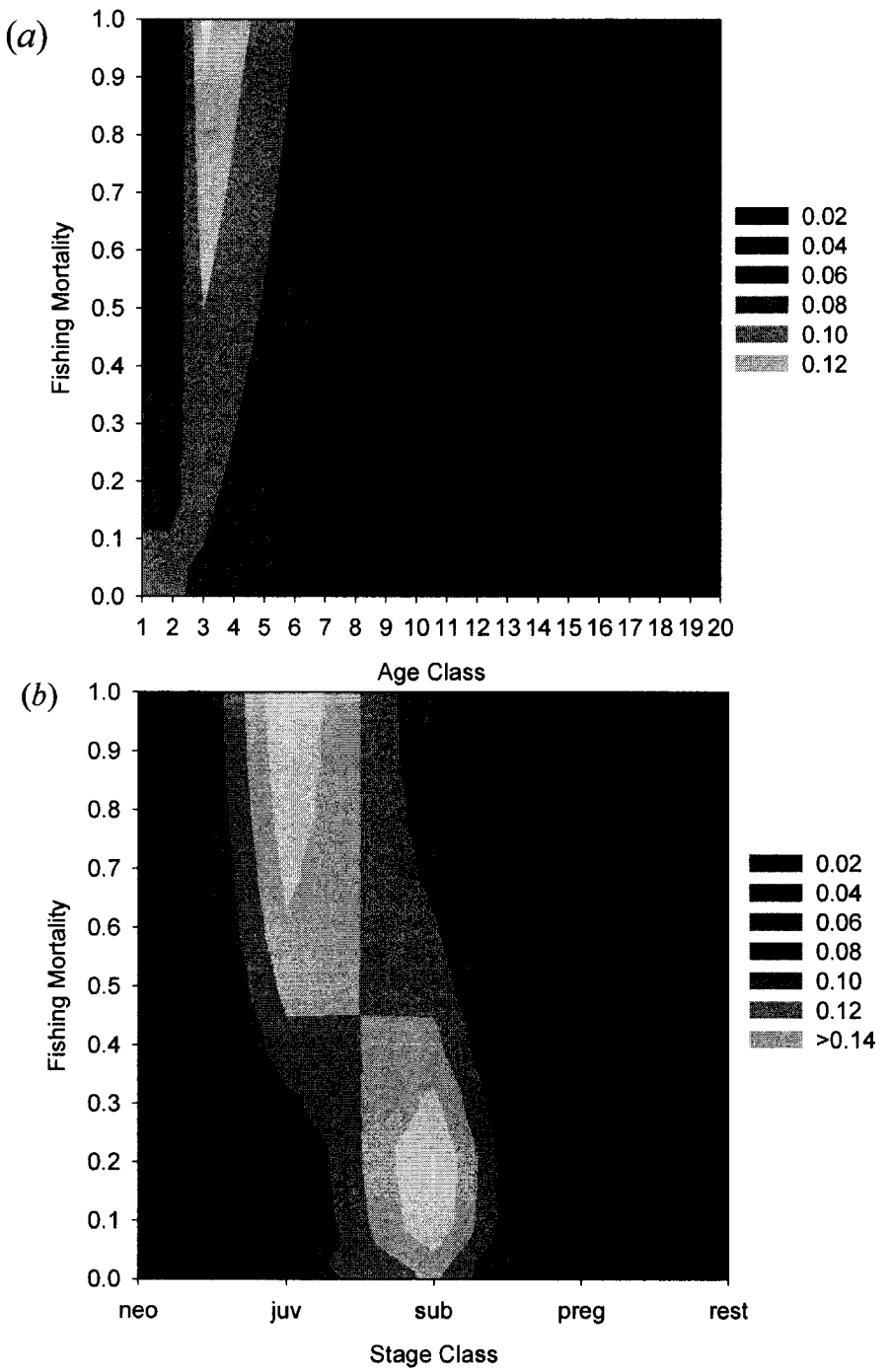

Figure 4.3 Stable-age and stage distributions. (a) Stable-age distribution at varying levels of instantaneous fishing mortality, truncated at 20 years for clarity. (b) Stable-stage distribution. Contours represent the proportions at age for each fishing mortality scenario.

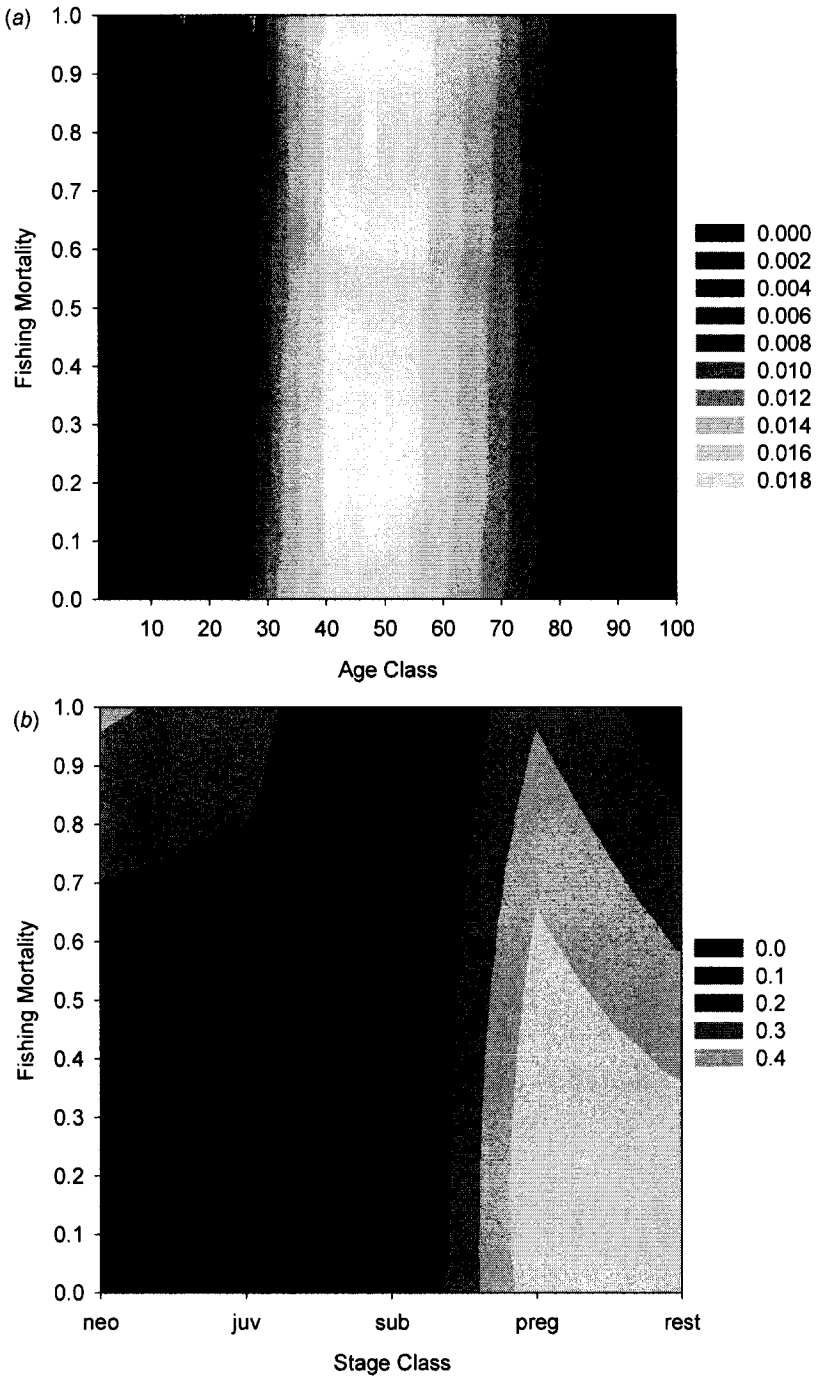

Figure 4.4 Reproductive value. Reproductive value distributions for the (a) age- and (b) stage-based models at different levels of fishing mortality.

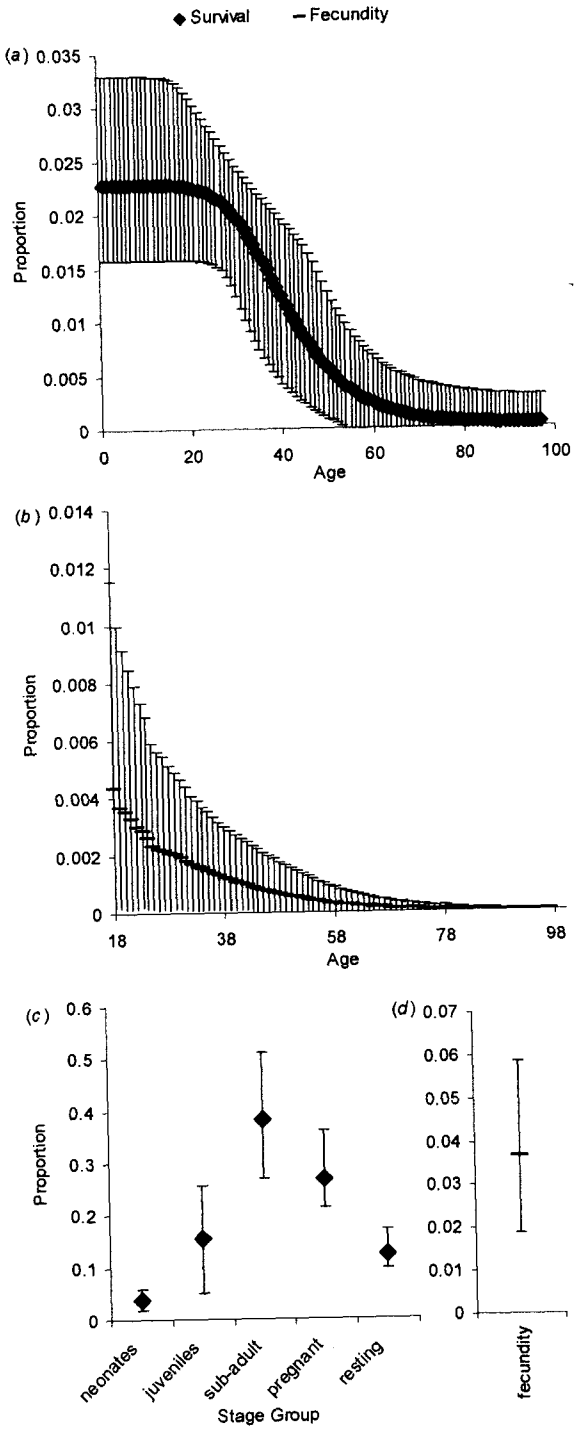

Figure 4.5 Survival and fecundity elasticities. Elasticities of (a) survival and (b) fecundity parameters for the age model; and (c) elasticities of (c) survival and (d) fecundity parameters for the stage model. Error bars are 95% confidence intervals.

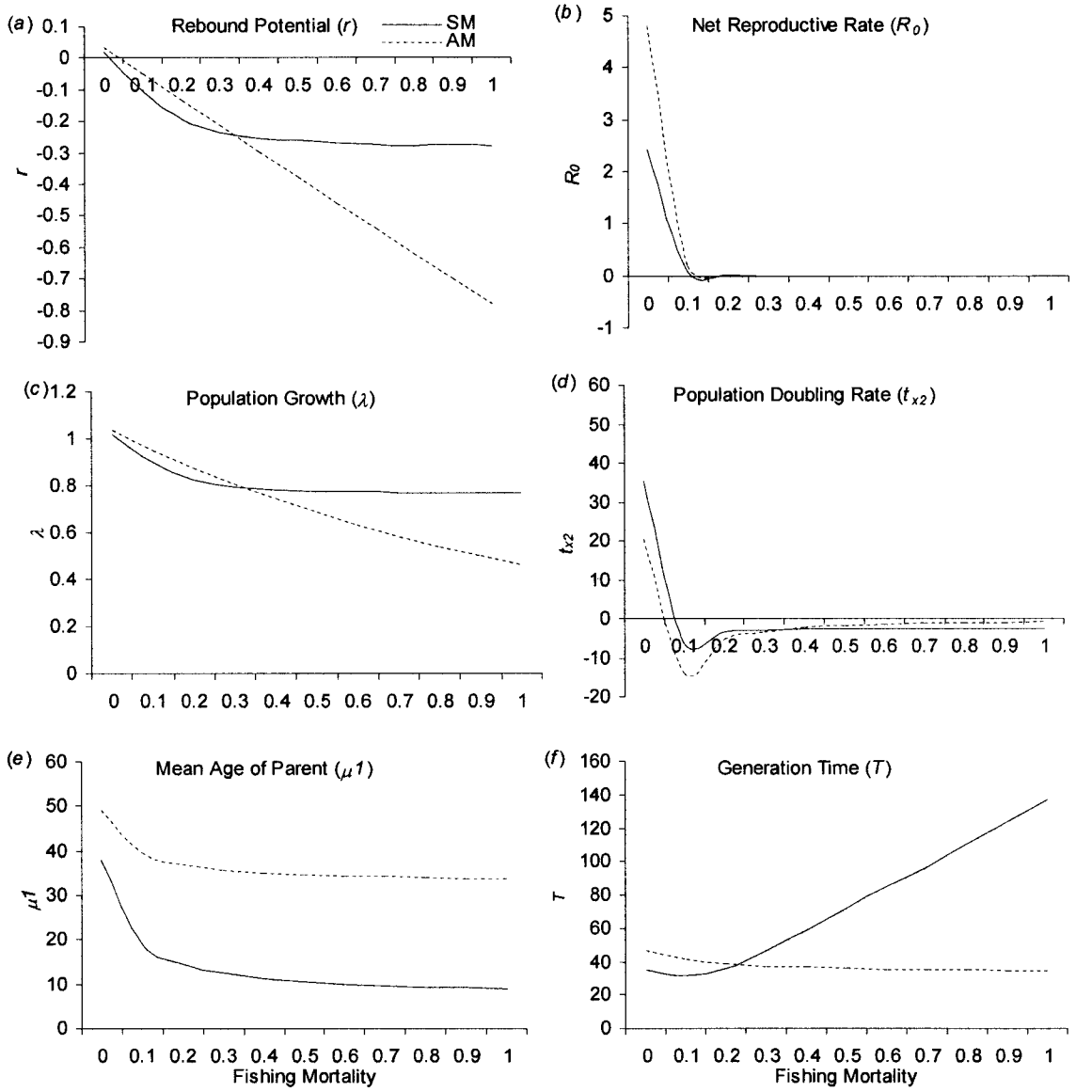

Figure 4.6 Demographic parameter estimates. Estimates of (a) rebound potential, (b) net reproductive rate, (c) population growth, (d) population doubling rate, (e) mean age of parent, and (f) generation time for the age- and stage-based models.

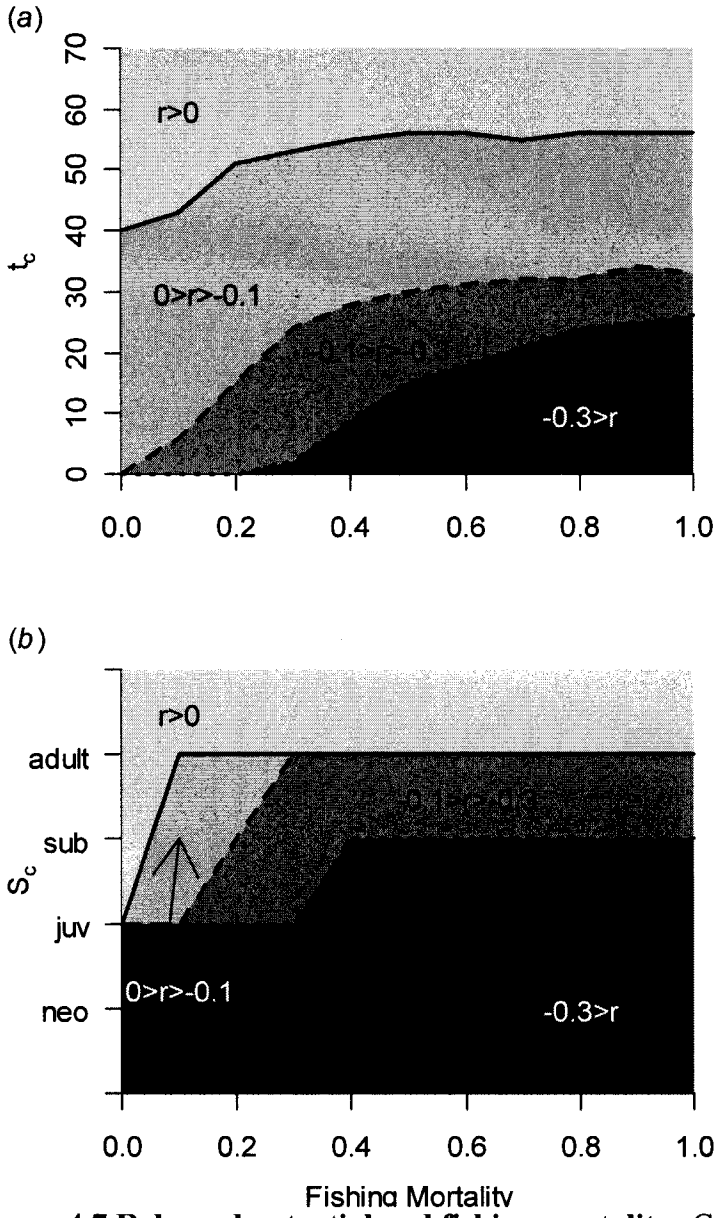

Figure 4.7 Rebound potential and fishing mortality. Contour plots of the rebound potential (r) with changes in fishing mortality (F) and age/stage at first capture (tc or sc). Only the curves for r=0, -0.1 and -0.3 are shown for convenience. Any combination of F and tc or sc which is above the r=0 line is sustainable.

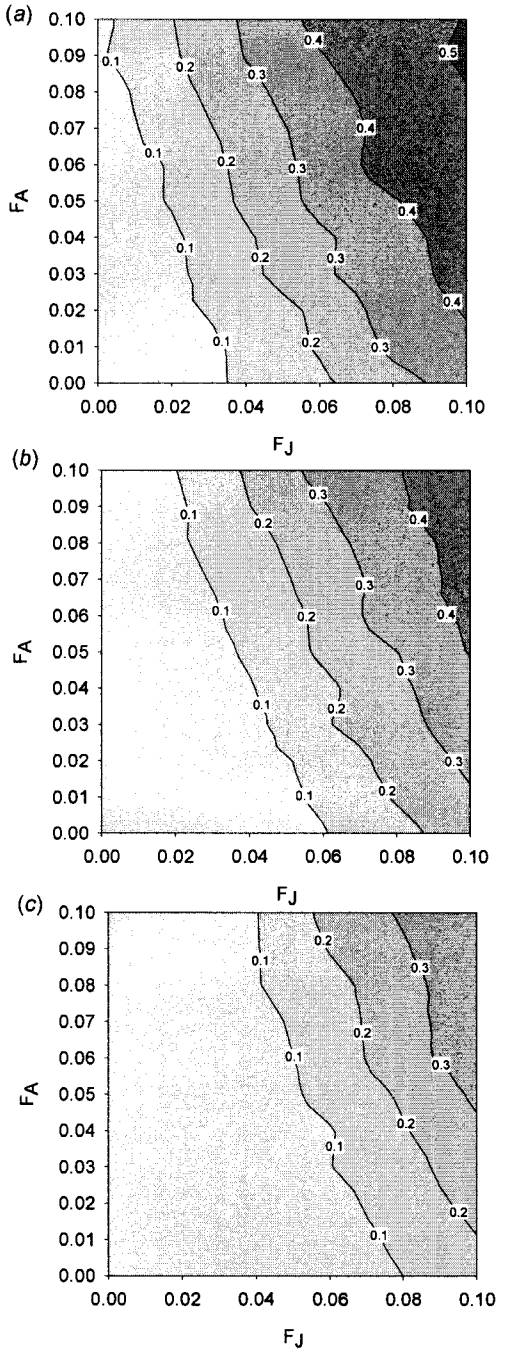

Figure 4.8 Age-based model proportional risk graphs. Proportional risk for populations with different rates of harvest for juveniles and adults in the age model. The proportional risk is the proportion of the simulated populations that declined below a threshold value (BMSY, B50 or B40) after 20 years of constant harvest. Each panel is a different threshold value: (a) BMSY , (b) B50, and (c) B40.The F value for adults (FA) is shown along the y-axis and the F value for juveniles (FJ) is along the x-axis. The contours are the risk statistics with darker shading indicating greater risk.

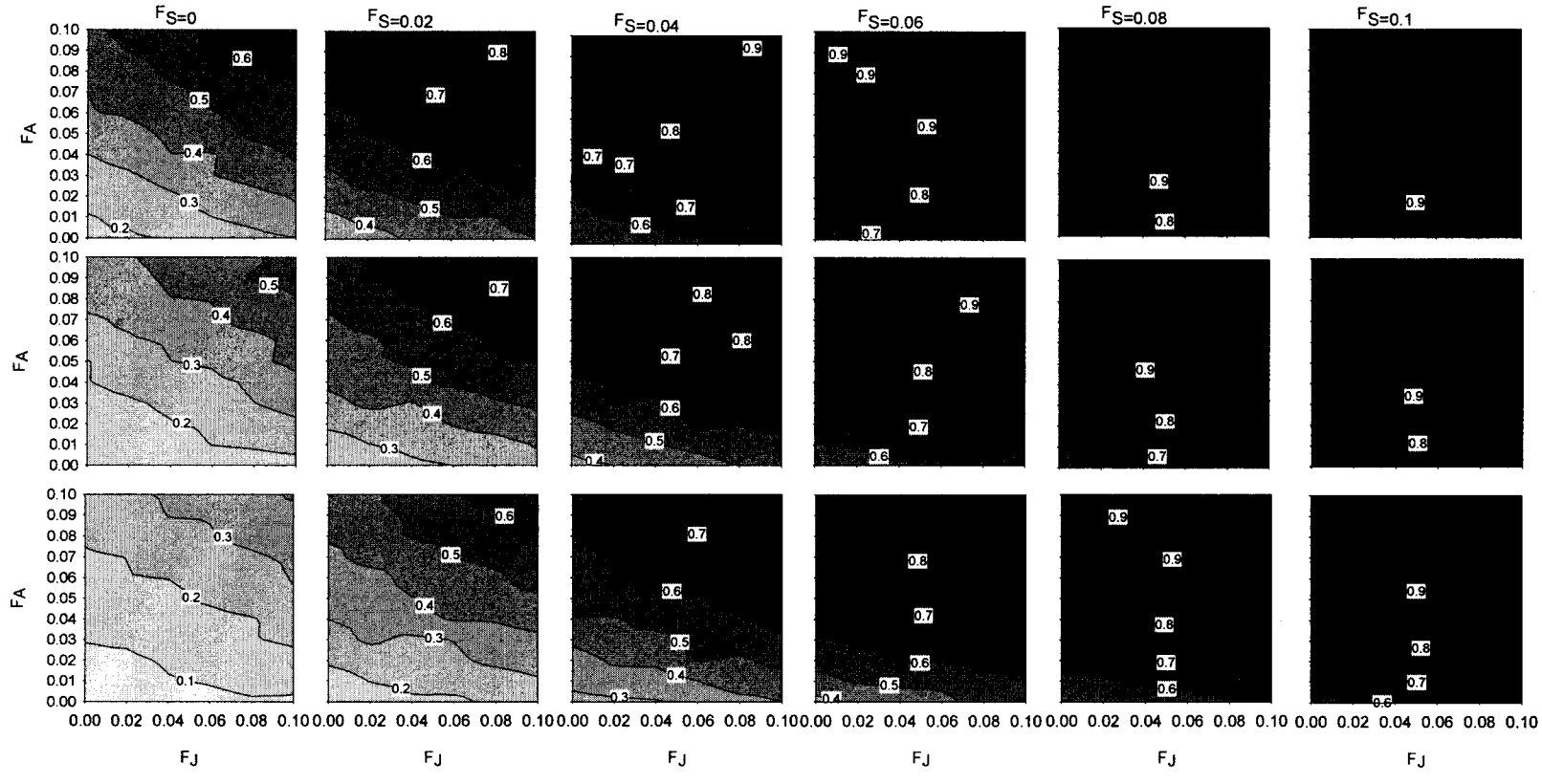

Figure 4.9 Stage-based model proportional risk graphs. Proportional risk for populations with different rates of harvest for juveniles and adults in the stage model. The proportional risk is the proportion of the simulated populations that declined below a threshold value (BMSY, B50 or B40) after 20 years of constant harvest. Each row is a different threshold value: (top) BMSY , (middle) B50, and (bottom) B40. Each column is a different level of F for sub-adults (left to right: F=0, 0.02, 0.04, 0.06, 0.08 and 0.1). The F value for adults (FA) is shown along the y-axis and the F value for juveniles (FJ) is along the y-axis. The contours are the risk statistics with darker shading indicating greater risk.

Chapter 5: The diet of spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska with an examination of seasonal and ontogenetic influences[1]

5.1 Abstract

Stomach contents from 1,221 spiny dogfish (*Squalus acanthias*) in the Gulf of Alaska were collected from 2004-2006 and analyzed to determine predominant prey species. Of the 58% of stomachs with prey contents, shrimp (35.8%IRI, the percentage index of relative importance), cephalopods (24.1%IRI), and forage fish (18.9%IRI) were the most important prey categories. The balance of the diet was variable. Commercially valuable species such as salmon, *Oncorhynchus* spp., (1.2%IRI) and rockfish, *Sebastes* spp., (<1%IRI) constituted small proportions of the spiny dogfish diet. The diet composition was not significantly influenced by spatial, temporal, or ontogenetic factors; however, trophic level of prey and average prey item weight was influenced by ontogenetic and temporal changes. Spiny dogfish in the Gulf of Alaska are generalist feeders with a variable diet. As they grow, they incorporate larger prey items to their diet, and prey selection appears to be driven more by availability and prey size than any other factors.

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5.2 Introduction

Diet analysis of marine fishes is necessary to understand species interactions, such as predation and food competition among species within a marine ecosystem. It also provides critical information for ecosystem modeling, such as Ecopath and Ecosim (Pauly et al. 2000). Marine ecosystem modeling began in the late 1970s and early 1980s (Anderson & Ursin 1977; Polovina 1984), and has been an area of recent rapid development, especially since the 1990s when fisheries managers have been advised to broaden their scope of awareness beyond single-species considerations towards an ecosystem approach for management (FAO 2003).

Diet analysis is also an evolving field. Many older diet studies only considered one or two indices, such as frequency of occurrence, to indicate predominant prey species (Jones & Geen 1977; Hyslop 1980), and those indices were not always consistently applied across studies. Additionally, many studies failed to consider sample size, which was often insufficient to accurately estimate the composition of a species' diet (Ferry & Cailliet 1996). In recent years, methods to both standardize diet analysis and determine adequate sample sizes have been developed (Ferry et al. 1997; Cortes 1999; Bizzarro et al. 2007).

The spiny dogfish (*Squalus acanthias*), a common temperate small coastal shark, is an interesting candidate for both diet analysis and ecosystem modeling. The spiny dogfish occurs throughout temperate regions of the world's oceans, including much of the Gulf of Alaska (GOA). In some regions, this species has been called a voracious predator and blamed for decimating populations of more "desirable", commercially

valuable species (Atkins 1904; Bigelow & Schroeder 1953; Stolpe 2006). Some studies of spiny dogfish have found them to be generalist opportunistic predators (Jones & Geen 1977; Bowman et al. 1984), while others have identified them to target specific prey species at times (Beamish et al. 1992). In some coastal bays in inlets in Alaska, seasonal increases in apparent abundance occur between late spring and early fall, thought to coincide with the spawning migrations of capelin (*Mallotus villosus*, J. Capra, National Park Service, pers. comm.) and sockeye salmon (*Oncorhynchus nerka*, G. Woods, Alaska Department of Fish and Game, pers. comm.), respectively.

The lack of data on spiny dogfish diets in the GOA represents a potentially important gap in understanding of this large marine ecosystem. Recent assessments indicate that spiny dogfish biomass increased between 1990 and 2007 (Beamish et al. 1992) and may have been at 80-100% of carrying capacity in 2006 (Rice 2007). Given their apparent high and increasing biomass and frequent bycatch in commercial and recreational fisheries for other species in Alaska, there is much interest by fishery stakeholders and the scientific community to clarify the potential effects of spiny dogfish in the marine ecosystem and potential effects on commercial species. At present, ecosystem models have provided little insight, owing to the lack of knowledge about the trophic relationships of spiny dogfish in Alaska. With this in mind, the objectives of this study were to: 1) describe the diet of spiny dogfish in the GOA; 2) examine regional and seasonal differences in diet; and 3) investigate ontogenetic shifts in diet composition.

5.3 Methods

Spiny dogfish were collected at various locations across the GOA between July 2004 and September 2006 (Figure 5.1). Multiple platforms were used, including targeted sampling cruises, state and federal assessment surveys, and opportunistic fishery bycatch samples, using longline, rod and reel, set net and trawl gear. Sampling occurred in the spring, summer and fall in areas from the nearshore to the continental shelf break in waters from 0-600 m in depth. All sampled spiny dogfish were humanely dispatched upon landing following approved animal care protocols (University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol number 04-36). Spiny dogfish were sexed and measured for length (total length extended, TLext, to the nearest 1.0 cm) and weight (to the nearest 0.1 kg). Reproductive data and aging structures were also collected as part of three companion studies.

Stomachs were dissected at the anterior end of the esophagus and contents drained into a container for preliminary inspection. At the time of collection, all contents were visually identified to the lowest taxon possible – species or family. Stomachs containing water, bait and those with no contents were recorded as "empty". All stomachs, including those visually assessed to be empty or containing water only, were emptied into fine-mesh bags and the stomachs rinsed to ensure all particles were collected. Contents were preserved initially in 10% buffered formalin seawater solution and then transferred to 70% EtOH for laboratory analysis. In the laboratory, each taxon was counted, weighed wet (to the nearest 0.1 g) and measured by volume displacement (to the nearest

0.1 ml) in the laboratory. Each prey item was given a state of digestion code from least to most digested on a scale of 1-6 (Lang 2004).

Stomach samples were pooled to investigate the potential effects of various biotic and abiotic factors. Abiotic factors were location (Cook Inlet=CI, Prince William Sound=PWS, Yakutat Bay=YAK, and Gulf of Alaska=GOA, Figure 5.1), gear type (longline=LL, set net=SET, sport=SPT, and bottom trawl=TWL), year (2004, 2005, and 2006), season (spring, summer, and fall) and depth (0-99m=DEP0, 100-199m=DEP100, 200-299m=DEP200, and >300m=DEP300); biotic factors were sex (male=M and female=F), length (<80cm TLext=TL70, 80-89cm TLext=TL80, 90-99cm TLext=TL90, and >100cm TLext=TL100) and weight (<2kg=WT0, 2-3.9kg=WT2, and >4kg=WT4).

Prey items were grouped into 11 prey categories. This served two purposes: 1) to create a set of prey categories that were comparable across all data groupings; and 2) to reduce biases introduced by variable prey identification (Cortes 1997). Teleost fish were divided into three categories: "forage fish", which includes Pacific herring *Clupea pallasii*, capelin, eulachon *Thaleichthys pacificus*, and other smelts (Family Osmeridae); "fish", which includes Pacific salmon (*Oncorhynchus* sp.), cod (Family Gadidae), greenling (Family Hexagrammidae), rockfish (*Sebastes* sp.), and flatfish (Family Pleuronectidae); and "other fish", which consists mostly of sculpins (Family Cottidae), Pacific sandlance *Ammodytes hexapterus*, and myctophids (Family Myctophidae). Invertebrates were categorized as "shrimp", "cephalopod", "crab", "bivalve", "amphipod", "worms", "jellyfish/salps" or "other invertebrates". The proportion of empty stomachs and the proportion of stomachs with multiple prey categories were

calculated for each data grouping and chi-square tests were performed to determine if the proportions were independent of the data grouping (i.e. H_0: the proportion of empty stomachs is independent of the location of capture, α=0.05, Zar, 1999)

Cumulative prey curves were used to determine whether sample sizes were adequate for statistical analysis. Stomachs were drawn at random without replacement until the total sample size was sampled, and the cumulative number of distinct prey categories encountered was recorded. This was repeated 500 times and the mean and standard deviation estimated. The mean and standard deviation were plotted against the number of stomachs drawn, and the sample sizes were considered sufficient if the curves reached an asymptote (Ferry & Cailliet 1996). While quantitative methods have been proposed to determine if a given curve has reached asymptote (Bizzarro et al. 2007), those methods resulted in unreasonably small minimum sample sizes (i.e. 39 stomachs for all of the data combined) and were not considered appropriate for use in this study. Instead, coefficients of variation (CV) for the total sample size were calculated.

Five relative measures of prey quantity were utilized: percentage by number (%N), percentage by weight (%W), percentage by frequency of occurrence (%FO), index of relative importance (IRI) and the percentage by IRI (%IRI) (Cortes 1999). The %N is the number of individuals of each species or prey category for all stomachs expressed as a proportion of total number of individuals in all prey categories. Similarly %W is the summed weight of each species or prey category for all stomachs expressed as a proportion of total weight of individuals in all prey categories. The %FO is the number of stomachs containing individuals of each species or prey category for all stomachs

expressed as a percentage of the total number of stomachs containing prey items. Because none of these indices can be considered accurate by themselves (i.e., %W is based on the weight of the digested prey item, not the potential weight of the whole item, or %N can be high for small species such as krill and low for large species such as squid), we include the IRI and %IRI in this study. The IRI was calculated as: IRI=%FO(%W+%N) (Pinkas et al. 1971). The %IRI, is the IRI for each species or prey category expressed as a percentage of summed IRI of all species or prey categories (Barry et al. 1996; Cortes 1997). To consider whether %IRIs were significantly different within a prey category, the %IRI was averaged over all data groupings and upper and lower 95% confidence intervals were calculated.

Trophic level (*TrL*) of spiny dogfish was calculated based on all data combined and for each data grouping separately using the equation (Cortes 1999):

$$TrL = 1 + \sum_{i=1}^{n} \left(P_i * TrL_i \right), \qquad \text{(Eq. 5.1)}$$

where i is the prey category, n is the total number of prey categories, P_i is the proportional index (here %IRI), and TrL_i is the trophic level of the prey category. Trophic levels of prey items were from The Sea Around Us Project (www.seaaroundus.org). Shannon-Wiener diversity indices (H') and evenness (E) scores were also calculated based on all of the data combined and each data grouping using the following equations (Krebs 1999):

$$H' = \sum_{i=1}^{n} (P_i * \ln P_i)$$
$$E = \frac{H'}{H_{max}} \qquad \text{(Eq. 5.2)}$$

where i is the prey category, n is the total number of prey categories, and P_i is the proportional index (here %IRI).

Dietary overlap between data groupings was investigated with the simplified Morisita's similarity index, C_h, (Krebs 1999). The index was calculated with the following equation:

$$C_h = \frac{2 * \sum P_{ij} P_{ik}}{\sum P_{ij}^2 + \sum P_{ik}^2}, \qquad \text{(Eq. 5.3)}$$

where P_{ij} and P_{ik} are the proportions of prey category i in dogfish groupings j and k. Similarity values greater than 0.6 were considered highly overlapped (Langton 1982).

Differences in diets among data groupings were examined with statistical tests (described below), cluster analysis and principal component analysis (PCA). A paired Wilcoxon rank sum test was used to test for statistically significant differences in the diet compositions between data groupings within each factor with α=0.05 (Zar 1999). The simplified Morisita's similarity index was used in a cluster analysis to identify independent trophic guilds within each factor based on the unweighted pairwise group mean average method with Euclidean distance as a measure of dissimilarity. First, all of the data groupings were combined into one cluster to: 1) verify that logically hierarchical sub-clusters resulted; and 2) examine potential associations (i.e., LL being highly similar to fall-caught spiny dogfish) that would not have been revealed by the within factor

clusters. Then, each data factor was clustered to examine the similarity between groups within each data factor. The PCA was conducted to further examine dietary patterns between factors and data groupings. Euclidean bi-plots were created from the principal component scores and vector plots from the eigenvectors. In addition, all data computations were conducted using the *R* statistical software package (R, vers. 2.10.0, www.r-project.org).

Average %W and standard errors of each prey type were calculated for each data grouping and for all data combined. A Spearman's rank correlation test (Zar 1999) was conducted to determine if there was a significant correlation between prey size in weight and predator size in total length (Volger 2009). Prey length was not used because it was difficult to obtain from many prey items owing to advanced stages of digestion. Nevertheless, conclusions from our analysis are tempered by the fact that weights of some prey items are likely underestimated because stage of digestion. The range of prey sizes eaten was examined by converting the prey weight to a ratio scale by dividing by predator weight (Scharf et al. 2000); least-squares linear regression was used to fit a relationship between this ratio and predator weights.

5.4 Results

A total of 1,221 spiny dogfish stomachs were collected and analyzed from locations around the GOA (Figure 5.1). Of these, 921 were subjected to detailed laboratory analysis, and 300 had only field notes taken. The latter samples were not included in the detailed diet analyses, but were used for other comparisons, such as the

proportions of empty stomachs. Overall 42% of stomachs contained no prey items. The proportion of empty stomachs was lowest in PWS and the fall (13% each) and was greatest in 2004 (60%,Table 5.1). The proportion of empty stomachs was significantly influenced by each data factor in all cases ($\chi^2 \geq 5.9$, $p<0.05$), except for spiny dogfish weight ($\chi^2 = 5.2$, $p=0.07$).

One hundred and four (12.1%) of 862 stomachs with field notes taken contained prey items resulting from human activity (i.e., bait, offal/discards, or cannery sludge). Of sport-caught, 31.3% (73 of 233) stomachs contained bait or offal, while 7.1% (44 of 616) of longline-caught spiny dogfish stomachs contained bait or offal. A small portion of set net-caught samples contained salmon (13 of 180, 7.2%); however, our sampling methods did not allow us to discern whether any of these resulted from net feeding. Net feeding or other prey related to human activity was not indicated in any trawl caught samples. Forty-eight percent of all stomachs had items from more than one prey category (Table 5.1); and most of the data groupings ranged between 30-60% of the stomachs containing multiple prey categories. The proportion of stomachs with multiple prey was highest in DEP300 (71%) and lowest in spring (18%). The proportion of stomachs with multiple prey categories was significantly influenced by each data factor in all cases ($\chi^2 \geq 11.6$, $p<0.05$), except for spiny dogfish weight and sex ($\chi^2 = 3.3$ and 3.5 and $p = 0.06$ and 0.19, respectively).

Cumulative prey curves indicated sufficient sample sizes for the majority of the data groupings (Figure 5.2). The cumulative prey curves for the following data groupings did not appear to reach an asymptote, indicating that the sample sizes may be

small: GOA, SET NET, TRAWL, DEP0, DEP300, TL70, and WT0 (Table 5.2); however, CVs for these data groupings were <3%. Further analyses were conducted with all of the data groupings with the understanding that results for these seven groups may not be significant owing to small sample size rather than lack of effect.

Relative importance of prey in the dogfish diet depended somewhat on the choice of index (Table 5.2). Shrimp had the greatest %FO (29.0%) followed by cephalopods (15.6%) and other fish (14.2%). By weight (%W), fish were most important (30.6%) followed by forage fish (26.3%) and cephalopods (25.7%). By total count, shrimp were most important (28.6%), followed by forage fish (14.7%) and other fish (12.8%). Using the %IRI to combine these three measures, shrimp was most important (35.8%), followed by cephalopods (24.1%) and forage fish (18.9%). The %IRI for shrimp was consistent across all data groupings (no proportions were outside the 95% confidence interval of the average %IRI), for cephalopods it was significantly more important in PWS and fall than in any other data grouping, forage fish was greater in trawl, other fish was greater in DEP300, and fish were significantly greater in SET (Table 5.3). Most notably was jellyfish/salps in 2004, which was on average 1.3%IRI, but in 2004 was 14.5%IRI. In 18 of 27 data groupings, shrimp was the most important prey category, followed by forage fish with five data groupings, cephalopods and other fish were each the most important prey category in two data groupings.

Prey items that were identified to at least Order were used to further resolve the composition of the top three prey item categories. Of shrimp, 48.7% were from the family Pandalidae and 30.7% were small shrimps (Euphausidae and Mysidae), 10% were

Pasiphaeoidea, 8.6% were Crangonidae and 1.5% were Oregonidae. Of cephalopods, 53.3% were only able to be identified to the Order Teuthida, 20.2% were specifically identified as *Loligo opalescens*, 14.7% were only able to be identified to the Order Octopoda), and 11.0% were specifically identified as *Rossia pacifica*. Of forage fish, 66.2% were herring, 21.3% were capelin, 7.4% were other smelts (Family: Osmeridae) and 5.1% were eulachon.

The %IRI was used for comparisons among data groupings (Table 5.3, Figure 5.3). Whereas shrimp, cephalopods, and forage fish composed the majority of the overall diet (Table 5.2), the most important prey items varied spatially, temporally, and by sampling gear. Fish and/or "other fish" were relatively more important in CI and YAK. The importance of cephalopods was relatively minor in CI and YAK where fish and/or "other fish" were more important. Cephalopods played a minor role in the diet overall in 2004, when jellyfish and salps (14.5%) were the second ranked prey item. Amphipods were relatively important prey item in one depth range, DEP200. Diet differed among the sexes. Nearly half of the diet of males was shrimp. Shrimp accounted for slightly more than a quarter of the diet of females; females tended to consume more forage fish, fish, and "other fish."

Trophic level was calculated for each data grouping (Table 5.3). The average trophic level for all was 3.99 (±0.02 standard error), ranging from 3.75 in 2004 to 4.17 for relatively large (TL90) spiny dogfish. Mean trophic levels from a majority of the data groupings were at least one standard error different from the average: GOA, PWS, sport, trawl, 2004, all seasons and depths, M, TL70, TL90, TL100, WT0 and WT4. The TrL

for PWS samples was greater than all three other locations, and for 2004 samples it was lower than other years (Figure 5.3). There appeared to be an increasing trend in TrL from spring to fall. Gear type and depth did not appear to influence TrL. Trophic level increased with size (both in length and weight) and females had a higher TrL than males (Figure 5.4).

The Shannon-Wiener diversity index (H') and evenness (E) suggested differences in the diversity of the prey types based on sampling situation (Table 5.3, Figure 5.4). Spiny dogfish caught in PWS had the lowest diet diversity owing to the predominance of cephalopods, while CI and YAK had the greatest. Diet diversity of trawl-caught samples was an order of magnitude lower than that for dogfish caught in other gears due to the preponderance of forage fish in trawl-caught samples. The diversity differences between years was minimal, but within years, summer caught samples had the greatest diversity. The shallowest caught spiny dogfish had the greatest diversity, and those caught between 100-200 m had the lowest diversity. For the biotic factors the diversity and evenness increased with larger animals and females had a greater H' and E than males.

Trends in TrL, H', and E, did not equate to significant changes in the diet compositions. No significant differences in the distribution of prey categories were detected for location of capture, gear type used, year, season or depth of capture; as well as for the three biotic factors (Wilcoxon rank sum test, $P>0.05$).

Morisita's diet similarity among data groupings within categories indicated significant overlap ($C_h>0.6$) among all data groupings with the exception of trawl-caught spiny dogfish (Figure 5.5). Two distinct groups were identified by location: YAK/CI and

PWS/GOA (Figure 5.5A), gear types had three groupings, trawl was a separate group from the other three gear types, and longline was separate from sport/set net (Figure 5.5B). Samples collected in 2005 and 2006 were a distinct group (Figure 5.5C), as were those collected in the fall and summer (Figure 5.5D). The depth factor also had two distinct groups: 100 m/200 m and 0 m/300 m (Figure 5.5E). Cluster analysis identified two major groupings based on either length or weight, in both cases; the smallest spiny dogfish were a separate grouping from all other size groups (Figure 5.5G and Figure 5.5H). However, dogfish of length TL80 and TL100 clustered separately from those of length TL90.

The cluster analysis was deemed an appropriate analysis because data groupings that would be expected to be closely related were clustered near each other, such as WT0 and TL70, WT4 and TL100, and fall and PWS (fall and PWS because most of the samples collected in PWS were caught during the fall, Figure 5.5I). Cross-category associations included YAK/SPR/CI/SET, F/WT2/DEP0, and M/LL/TL80/2006 were closely related.

The PCA shows distinct loadings for the six most prominent prey categories: shrimp, cephalopods, forage fish, fish, other fish, and bivalves (Figure 5.6A). Forage fish were the only prey category that loaded negatively on PC1, and bivalves had only a slight positive loading, the remaining four categories were positive and loaded more heavily on PC1. Cephalopods and shrimp loaded positively on PC2, while fish and other fish loaded negatively and bivalves were strongly negative.

Examination of the Euclidian bi-plots suggests trends within factors. For locations, YAK and CI (Figure 5.6B) and for gear types, SET, SPORT and TRAWL (Figure 5.6C) loading was negative on PC2, while SET loaded positive on PC1. For seasons, fall was positive for both PC1 and PC2 (Figure 5.6D). The loadings for 2006 were positive on PC1 and negative for PC2 for 2005 (Figure 5.6E). All depths 100 m and deeper were negatively loaded on PC2 (Figure 5.6F). For length, only the largest size group, 100 cm, showed a trend of negative loading on PC2 (Figure 5.6G). No trend was apparent for the sex and weight categories.

Significant trends in the average wet weight of prey items were observed between 2004 and 2005 samples and between fall and spring caught samples, but there were no significant differences within the locations, gear types or depths (Figure 5.7). Significant changes in prey size were observed between males and females, between TL80cm and TL90cm/TL100cm, and between WT2kg and WT4kg spiny dogfish. The correlation between prey weight and predator length was positively significant ($r_s=0.478$, $P<0.001$), as was predator weight ($r_s=0.409$, $P<0.001$). Further, there was a significant negative slope for the regression of the prey weight to predator weight ratio ($P<0.05$). Results suggest that as spiny dogfish grow, they add new prey items and larger prey to their diet without abandoning smaller prey items.

5.5 Discussion

Overall, shrimp and cephalopods comprised the majority of the diets (35.84 and 24.08%IRI, respectively), but the most important prey category by data grouping varied

spatially, temporally and by gear type (Table 5.3, Figure 5.3). Shrimp were the most important prey category in 18 of 27 of the data groupings, followed by forage fish in 5 of 27 categories. Spiny dogfish diet is highly variable, indicating an opportunistic feeding behavior. For example, in 2004 jellyfish/salps and invertebrates were significantly more important that in all other data groupings. Although diet compositions were not significantly influenced by any factors, size, and sex significantly influenced the presence of multiple prey categories and stomach emptiness. Trends in prey diversity and trophic level increased with increasing spiny dogfish size, but also increased with some sampling situations (i.e. sport gear or summer sampling).

Of all the data groupings, shrimp have the greatest importance in the smallest length and weight groups and in males. Males tend to be smaller than females (Tribuzio and Kruse, in prep), so it may be likely that the importance of shrimp in the diet of males is attributable mostly to size and not sex-based effects. The importance of shrimp in the diet of dogfish might be construed to indicate a high abundance of shrimp in the GOA. The shrimp group is very diverse, ranging from the larger Pandalidae shrimp to small Euphausiacea and Mysidae shrimp. Unfortunately, regional stock-assessment surveys provide abundance indices of Pandalid shrimps only. In the western GOA, indices of the commercially valuable species (from the family Pandalidae) was low in 2004-2006 (Jackson 2008) and was not correlated with spiny dogfish abundance. About 49% of the shrimp in the spiny dogfish diets were from the family Pandalidae, a family that grows to larger sizes, but tends to be softer bodied and inhabit open areas (Kruse 2007), possibly making them an easier target for spiny dogfish compared to other shrimp species.

Euaphausiids and Mysids comprised 30.7% of the diet combined and these species tend to be more pelagic. There are spatial patterns of these taxa in dogfish diets. Spiny dogfish caught in offshore waters tended to have more Euaphausiids and Mysids in their diet as did smaller spiny dogfish. The remainder of shrimp in the diet tended to be species of intermediate body sizes (compared to Pandalidae and Mysidae), benthic, and commonly associated with nearshore waters. Whereas the availability of shrimp may be a factor in their importance in the diets of spiny dogfish, it is also plausible that they are selected as prey owing to their small size and body type allowing them to be ingested whole by fish with relatively small mouths.

Forage fish were also more prominent in the diets of smaller spiny dogfish with decreasing importance as size increased. Overall, forage fish were the third most important prey category, but were the most important in five of the data groupings. Spring and trawl gear may be interacting factors because most of the trawl sampling occurred in the spring, but the other factors where forage fish were most important are not likely interacting. Most of the trawl samples were collected during a single survey in CI in the spring, and capelin was prominent in the diet of those samples; one of these stomachs contained 29 individuals. Spiny dogfish have also been observed to gorge on capelin during the spawning in Dry Bay (northern Southeast Alaska) to the extent that spiny dogfish were stranded on the beach while feeding (J. Capra, National Park Service). These observations suggest that the spiny dogfish are feeding intensely during a brief time period. Capelin and herring are spring spawners whose spawning aggregations can provide a dense, high-energy food source for predators (Cooney 2007). The

predominance of forage fish in the spring diet could reflect the spiny dogfish taking advantage of a readily and briefly available food source. Without data on winter feeding habits, we can only speculate that this brief period of intense feeding may aid in replenishing energy reserves potentially lost over the winter (Paul 1997).

The importance of cephalopods in the diet is not influenced by spiny dogfish size or sex, but by location and time of year. Cephalopods were significantly more important in PWS and in the fall than any other data grouping; however, PWS was only sampled in the fall, so these factors likely interact. Squid comprised 73% of all cephalopods in dogfish stomachs. Commercial catches of squid increased over 2004-2006 (Ormseth & Gaichas 2009), corresponding to an increasing importance of squid in the spiny dogfish diets over the same period (Table 5.3, Figure 5.3). On the other hand, biomass surveys are conducted in the GOA only in odd years; therefore, biomass estimates only exists for one year (2005) during our study (Ormseth & Gaichas 2009). Much of the octopus portion of the cephalopods in dogfish diets consisted of large chunks of arms observed in late summer and fall caught samples. This is likely the result of opportunistic feeding on post-spawning males which are known to "wander" between mating and senescence and are thus more available than denned octopi (Anderson et al. 2002).

The significant increase in the importance of jellyfish and ctenophores (referred to as "jellies") in 2004 may reflect changes in prey availability or sampling. Ecosystem assessments (Boldt & Zador 2009) and estimated commercial bycatch of jellies (J. Gasper, NMFS, Juneau, pers. comm.) suggest that biomass of jellies did not substantially change over 2000-2009 in the GOA, but data is limited. Alternatively, stomach contents

of a known opportunistic feeder can be used as an indicator of abundance for species that are not well sampled by surveys, such as jellies (Link & Ford 2006). However, this method requires rigorous and long-term sampling. The significant increase in importance of jellies in 2004 may reflect trends in abundance, but it may also be a result of limited sampling. First, sampling methods where consistent across years, but sample size was low in 2004. Further, jellies are likely underrepresented in the diet analysis because they tend to dissolve during the preservation process and they digest rapidly in stomachs, and in a small number of stomachs with field notes taken jellies were identified, but had disappeared in the laboratory analysis. The dramatic increase in jellies in 2004 was not enough to result in a significant difference in the overall diet composition because jellies are a small portion of the overall diet.

Shifts in diet composition as well as prey item size are expected with increasing body size (Lucifora et al. 2000; Skjaeraasen & Bergstad 2000; Braccini & Perez 2005). Larger animals can physically ingest more/larger prey types and sizes owing to an increase in mouth gape. In the case of spiny dogfish, smaller animals ate more invertebrates while larger dogfish tended to eat more teleosts and cephalopods (bearing in mind that "smaller" animals includes most of the males). As spiny dogfish grow in size and new, larger prey items are added to the diet, they still continue to feed to some extent on the same, smaller prey as do smaller spiny dogfish, a phenomenon also been observed in the angular angel shark *Squatina guggenheim* (Volger 2009). Diet diversity and trophic level also increased with body size; larger spiny dogfish are more generalized

feeders and include some prey items at higher trophic levels than do smaller spiny dogfish.

The transition from smaller, lower trophic level prey types to larger, higher trophic level prey types occurs prior to size at 50% maturity for females and may overlap size of maturity for males (Tribuzio & Kruse in prep). The smallest size classes (by length and weight) are a separate trophic guild from all of the larger size classes, suggesting that a shift in diet occurs between 70 and 80 cm total length (or between <2 kg and >2 kg) spiny dogfish. Sample sizes were too small to further subdivide size groups to determine the size of diet transition for males and females separately. This shift in diets and trophic guilds may occur about the size that the spiny dogfish recruit from the schools of small juveniles to the schools of larger juveniles and adults. This study lacked animals between the size at birth (about 26 cm total length) and 50 cm total length. Lacking spiny dogfish in the smallest size ranges could underscore the importance of smaller invertebrates in the diet, as well as dampen the overall diet shift as the animal grows.

Spiny dogfish are upper trophic level feeders, with an average TrL of 3.99 (on a scale of 1-5, with one being phytoplankton and five marine mammals). The trophic levels estimated in this study range from 3.75-4.19 dependent on the data grouping, which is at the lower end of the range from other published studies (TrL=3.9, Cortes 1999, up to TrL=4.5, Bowman et al. 1984; Ebert et al. 1992; Fujita et al. 1995). Trophic levels increase significantly with size for elasmobranchs (Cortes 1999; Ebert & Bizzarro 2007), which is the opposite of marine mammals (Pauly et al. 1998). In this study,

trophic level significantly increased from 3.8 to 4.2 as the animals grew, and the trend would likely be more pronounced if samples from the missing size range were included.

Sampling bias must also be remembered when considering the results of this study as well. Although the diet compositions were not significantly different, suggesting that sampling bias is not a factor, there was a difference in the proportion of empty stomachs in all but the weight data groupings. Longline and sport fishing resulted in percentages of empty stomachs that were similar to other studies of elasmobranchs (Morato et al. 2003; Volger 2009). The proportions of empty stomachs from trawl caught spiny dogfish was low, with only one study of the Patagonian skate being lower (Scenna et al. 2006). Empty stomachs are expected for baited fishing methods, as fish that have fed to satiation are less attracted to bait (Lokkeborg et al. 1995; Morato et al. 2003). Data on regurgitation and stomach flushing were not recorded and it was not possible to verify if the empty stomachs were empty from digestion or from regurgitation or stomach flushing during the catching process. While differences in the proportion of empty stomachs would be expected for different gear types, the significant influences of the other factors were unexpected. Prey availability could play a role in the emptiness of stomachs, such as less prey may be available in some seasons than others, of different depths. There could also be interactions of factors, e.g., most of the fall sampling occurred in PWS and with LL gear.

The possibility of interactions between factors may play a role in this analysis as well. Collinearity between factors can influence the interpretation of results, such as the significant increase in importance of cephalopods in fall and PWS because most of the

samples collected in the fall were in PWS, but also on LL gear, which although not significant did have the greatest importance of cephalopods compared to other gear types. Season and depth have been shown to be related in that diet diversity was high in the shallows in the spring, and at depth in the fall for *S. guggenheim* (Volger 2009). The most likely means for this interaction to manifest itself would be between year variability in prey availability. Besides the high between year variability, the availability of prey can also be influenced by seasons or within year variability (Bowman et al. 1984), such as the availability of forage fish in the spring to larger teleosts and octopus in the fall.

The cumulative prey curves for most data groupings appeared to reach an asymptote, and the CVs were all <3%, indicating that in most data groups a sufficient sample size was collected. However, minimum sample sizes for statistical significance can be low if the between sample diversity is low, and therefore, enough stomachs may be collected for statistical significance, but may not truly represent complete diet composition (Braccini & Perez 2005). Sample size was, at least in part, a deciding factor in the determination of prey categories. Higher level taxonomic groups were used here because using lower level groupings reduced the sample size such that the cumulative prey curves would not reach asymptotes. The inherent problem with using higher level taxonomic groupings is that subtle, and possibly significant, differences in the diet compositions may be hidden (Morato et al. 2003; Ebert & Bizzarro 2007).

Another aspect of the empty stomachs is that a low proportion can indicate a constant feeding strategy (Cortes et al. 1996; Robinson et al. 2007). Gastric evacuation has been estimated at 52 hours based on captive animals and an all herring diet (Hannan

2009) to 111 hours based on wild caught stomach content observations (Jones & Geen 1977) for 90% digestion, suggesting that spiny dogfish with empty stomachs went at least 3 days without feeding. However, most of the stomachs contained more than one prey item (either the same types or from multiple prey categories) in different stages of digestion, suggesting feeding at a faster constant rate (Robinson et al. 2007). In the case of trawl and set net captured spiny dogfish the proportion of empty stomachs was low (<5%). Feeding may also be seasonal, with spiny dogfish feeding constantly throughout the warmer months and less often during the cooler months. In British Columbia, spiny dogfish captured in the summer had only 19% empty stomachs, while in the winter 68% of stomachs were empty (Beamish & Smith 1976).

The impacts of the spiny dogfish population on valuable commercial species have been an issue of concern among fishermen in the GOA and elsewhere (Link et al. 2002). Spiny dogfish have been implicated in either the decline of or the prevention of recovery for Atlantic cod (*Gadus morhua*) and other valuable species on the U.S. east coast (Stolpe 2006); however, even with the highest estimates of predatory removal, model results showed that spiny dogfish predation was not likely detrimental to the spawning stock biomass of cod, haddock (*Melanogrammus aeglefinus*), and other valuable species (Clark 1998). In the western North Atlantic, spiny dogfish feed more on small fish (Atlantic herring, *Clupea harengus*, Atlantic mackerel, *Scomber scombrus*, etc), while ctenophores were the most predominant invertebrate in the diet and shrimp was a small portion (Link et al. 2002), likely having a greater impact on teleosts in that region than spiny dogfish in the GOA have on local stocks of teleosts because of the importance of shrimp and

cephalopods in the GOA diets. In the GOA, some fishermen claim that spiny dogfish have depressed the population of Tanner crab *(Chionoecetes bairdi)*, razor clams (*Siliqua patula*), Dungeness crab (*Cancer magister*) and scallops (family Pectinidae). While these prey items were not commonly found in the diets, in fact no scallops were encountered at all, it is possible that even a small rate of feeding on a particular prey item or heavy, but localized feeding may have a significant impact on prey at small population sizes. In a British Columbia study, spiny dogfish appeared during a hatchery salmon smolt out-migration, and while only a small percentage of spiny dogfish fed on smolts, the smolt mortality was high due to the large abundance of sharks (Beamish et al. 1992). Spiny dogfish are estimated to consume 0.4 - 2.6% of their body weight each day (Wetherbee & Cortes 2004), which, given population abundances, this consumption rate could result in a significant impact on a given prey species. Daily ration estimates may overestimate the actual feeding rate because of the slow gastric evacuation, and methods for estimating daily ration are generally based on satiation feeding studies or bioenergetics models (Holden 1966; Jones & Geen 1977; Brett & Blackburn 1978; Tanasichuk et al. 1991).

Accounting for changes in feeding behavior throughout the growth of a species is important to accurately describe the feeding patters for that species and to better characterize food web dynamics of the ecosystem inhabited by the target species (Jennings 2005); in fact, diets can differ between size classes to the extent that they may be considered separate species in terms of trophic dynamics. Thus, studies that examine the diet compositions of different size classes may be more valuable for determining trophic roles in a system (Ebert & Bizzarro 2007). Diet studies on adult spiny dogfish

have reported them to feed primarily on pelagic and forage fish species and squid, while juveniles tend to feed mostly on euphausiids, ctenophores, and small fish (Beamish & Smith 1976; Bowman et al. 1984; Ebert et al. 1992; Fujita et al. 1995; Ellis et al. 1996; Alonso et al. 2002). This pattern was similar for GOA spiny dogfish; however, the "fish" category was the second most important prey group for the smallest size class of GOA spiny dogfish. The "fish" category contained species that were generally large and/or commercially important, but also included juveniles of these species, on which the smaller spiny dogfish likely feed.

Spiny dogfish are generalized, highly opportunistic predators. The species may have evolved to be generalist feeders to avoid putting too much pressure on any given prey item (Ellis & Musick 2007) and this species likely switches prey depending on the availability, further reducing the impact on less abundant species (Link & Garrison 2002). In an ecosystem context, spiny dogfish are important predators, feeding on many prey types, but primarily on shrimp, cephalopods, and forage fish. In a natural system, without fishing pressure, the presence of a predator such as spiny dogfish would exert a stabilizing influence, by feeding on those species that are "booming" and reducing impact on "crashing" species (natural population fluctuations or fishing induced abundance changes). Fisheries management in the GOA is done by individual species, but each stock assessment includes data relevant to an ecosystem context (i.e. Tribuzio et al. 2009). Along with the single-species management plans produced annually (or biennially), an ecosystem assessment is produced each year as well, which incorporates diet, food webs, feeding rates and abundances (Boldt & Zador 2009). Because spiny

dogfish are top predators in the GOA ecosystem, the flow of energy to this non-commercial species can have important implications on ecosystem modeling and ecosystem approaches to fisheries management of commercially important competitors.

5.6 Acknowledgements

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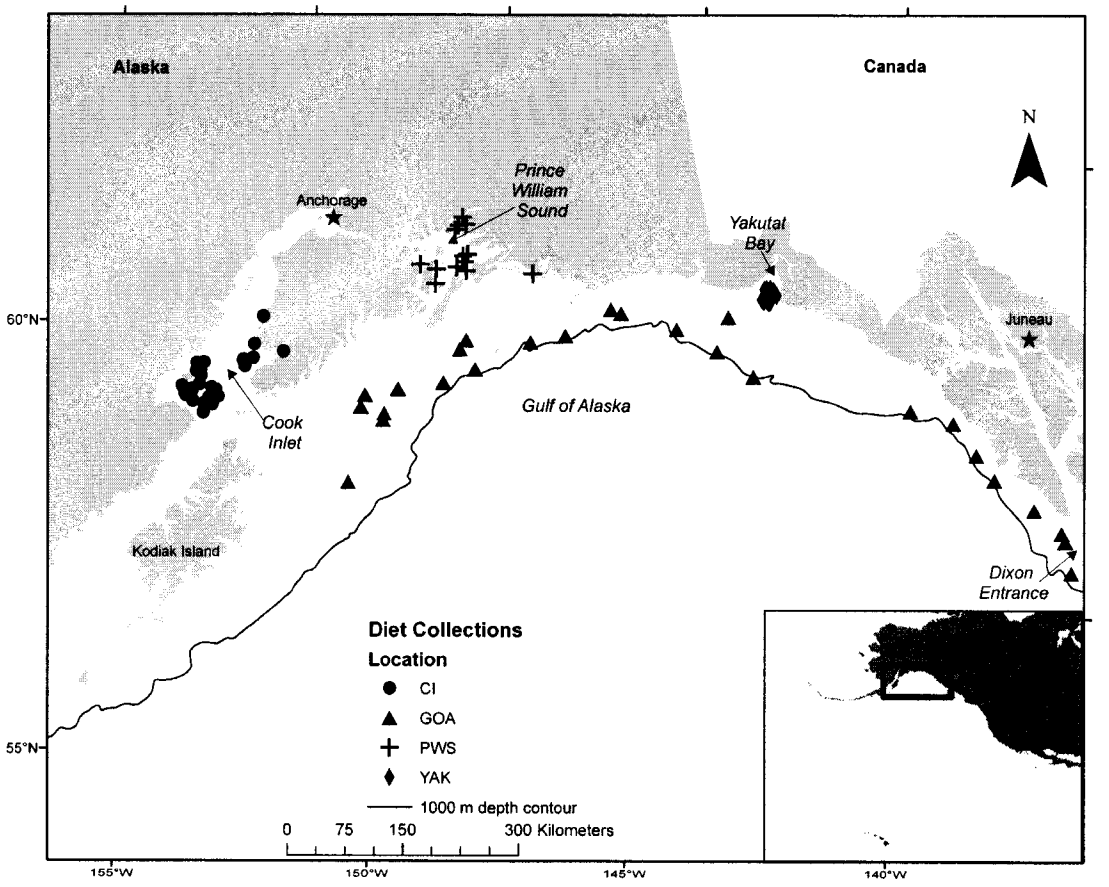

Figure 5.1 Map of sampling locations. Sampling locations of spiny dogfish off Yakutat (YAK), Prince William Sound (PWS), Cook Inlet (CI), and on the continental shelf throughout the Gulf of Alaska (GOA). The cluster of samples at YAK represents 30 sampling locations.

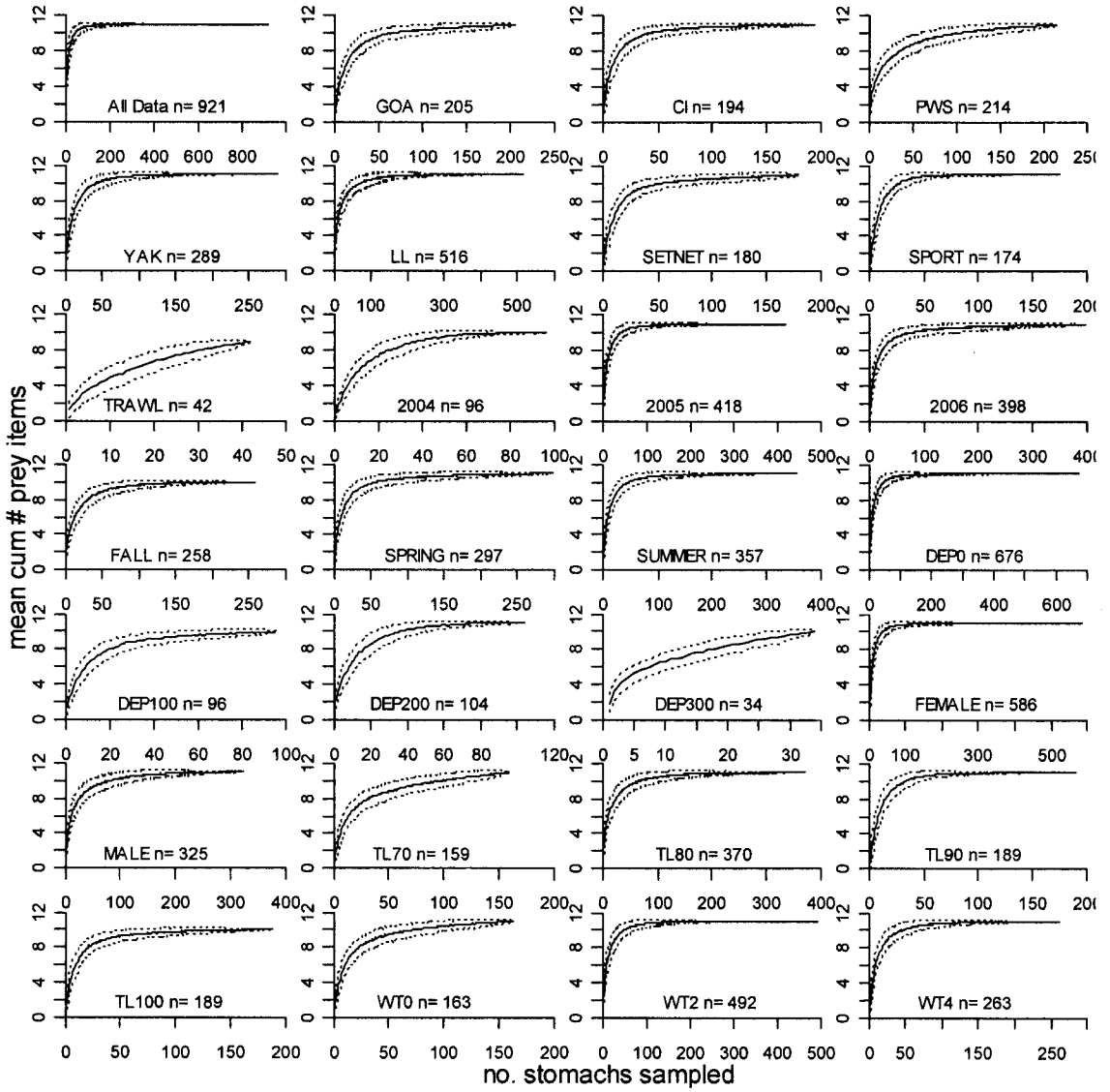

Figure 5.2 Cummulative prey curves. Mean cumulative number of prey taxa by sample size. Solid line is the mean, dashed lines are the standard deviations. Each panel represents a different data grouping and n is the total sample size for that grouping.

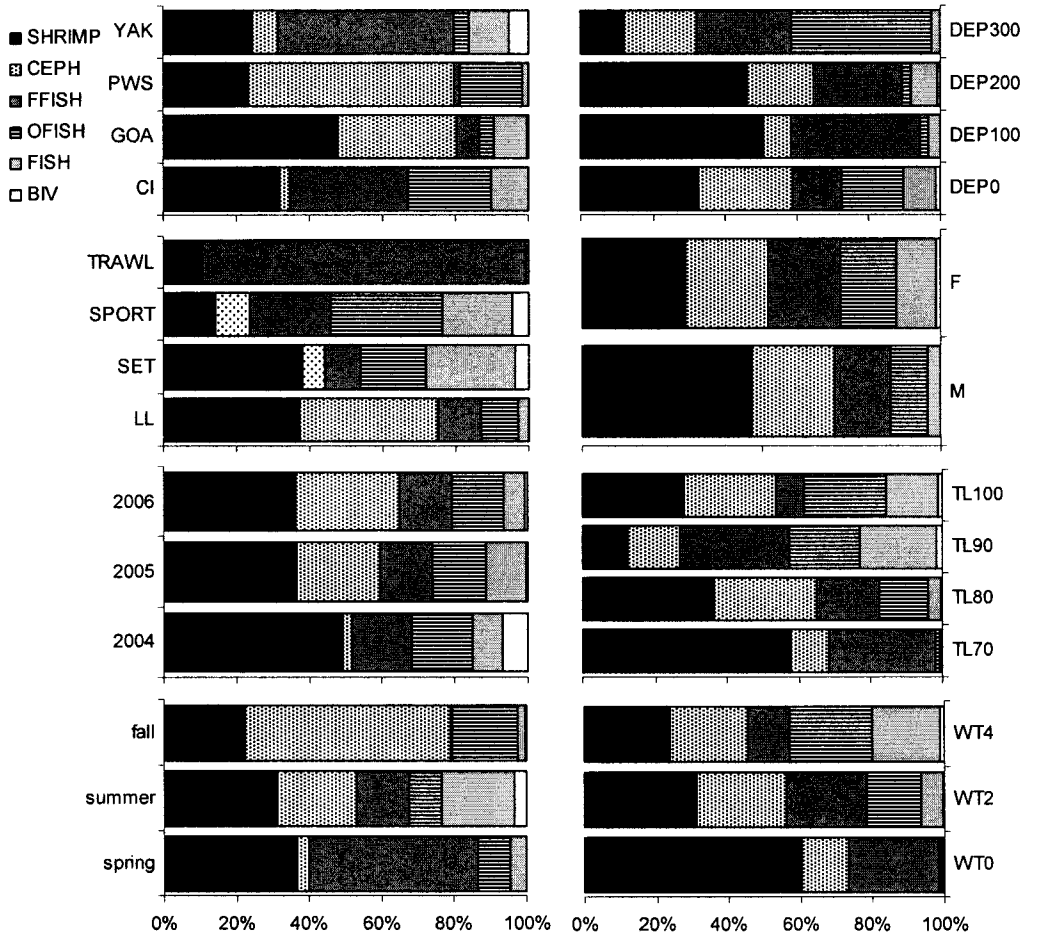

Figure 5.3 Comparative index of relative abundance. Comparison of the index of relative importance (%IRI) for each data grouping. For simplicity, only prey items which compose >5% of the diets are shown. See Table 5.1 for data grouping labels.

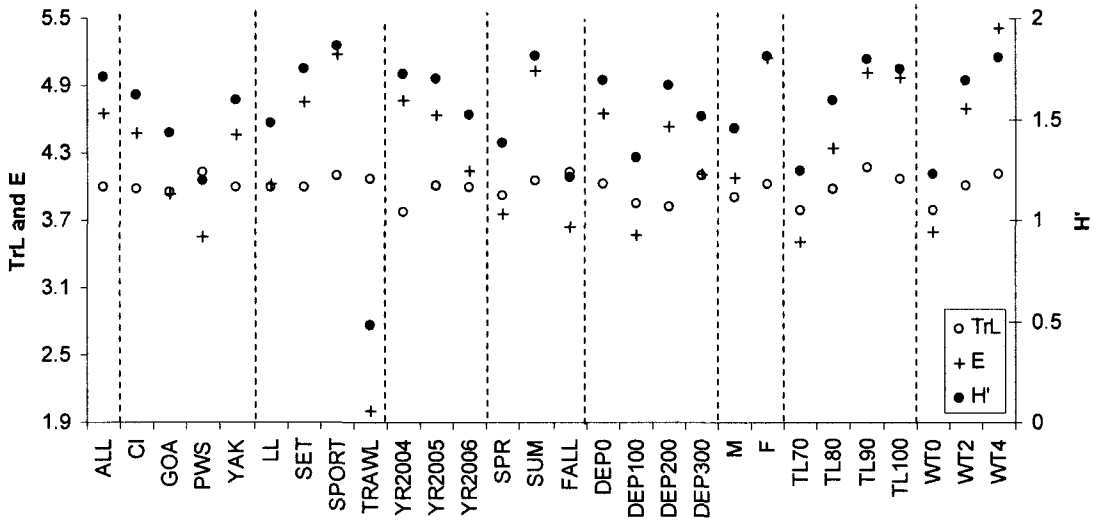

Figure 5.4 Trohpic level, diversity and eveness of diet compositions. Trophic level (TrL, open circles), evenness (E, crosses) and diversity (H', closed circles) for all data groupings. Vertical lines separate data groupings.

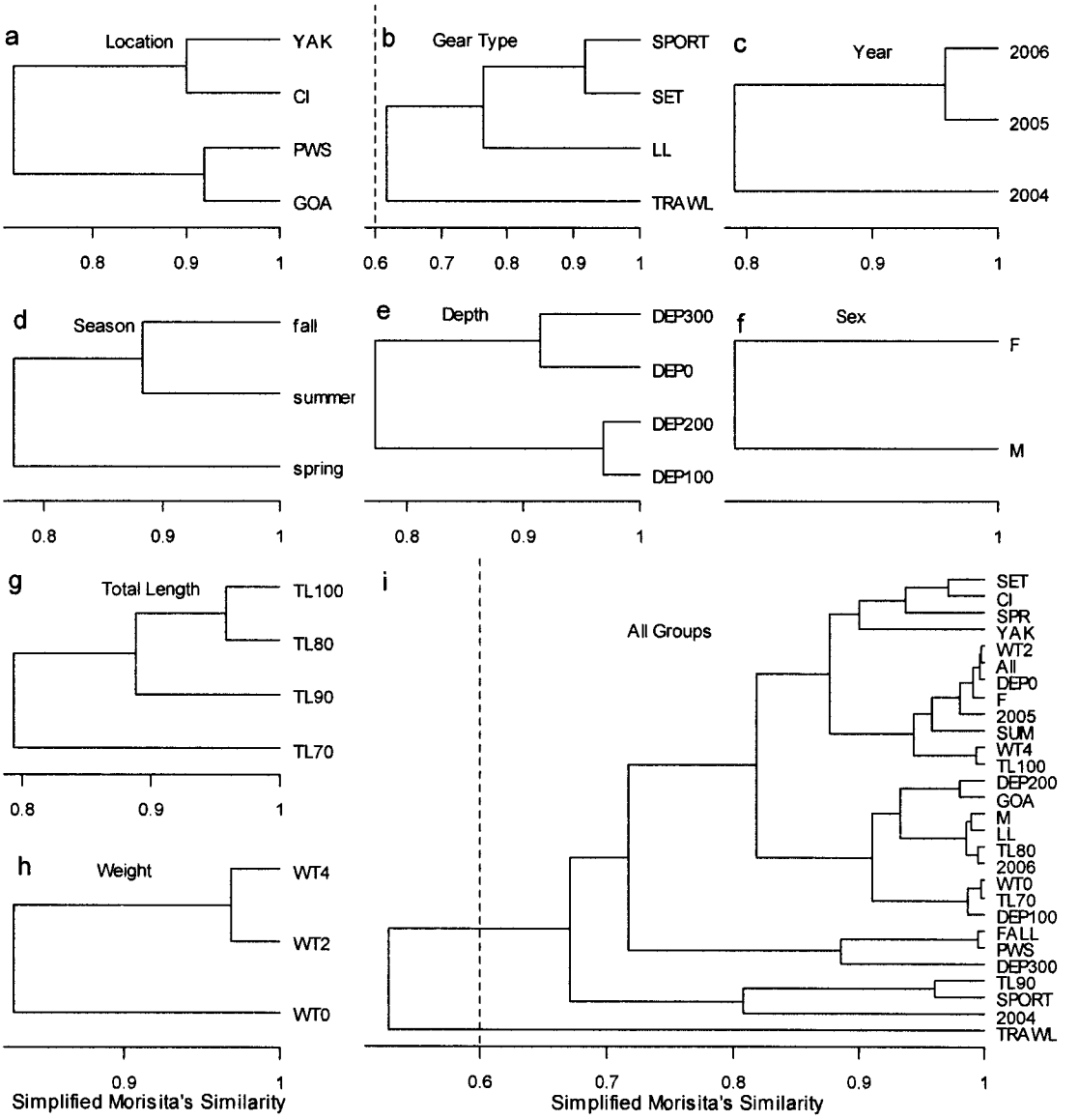

Figure 5.5 Cluster of similarity indices. Cluster analysis using the simplified Morisita's similarity index. The individual data groupings are represented in panels A-H and all of the data groupings combined are in panel I. The vertical dashed line represents the "significant overlap" boundary. Note the scale changes on the axes.

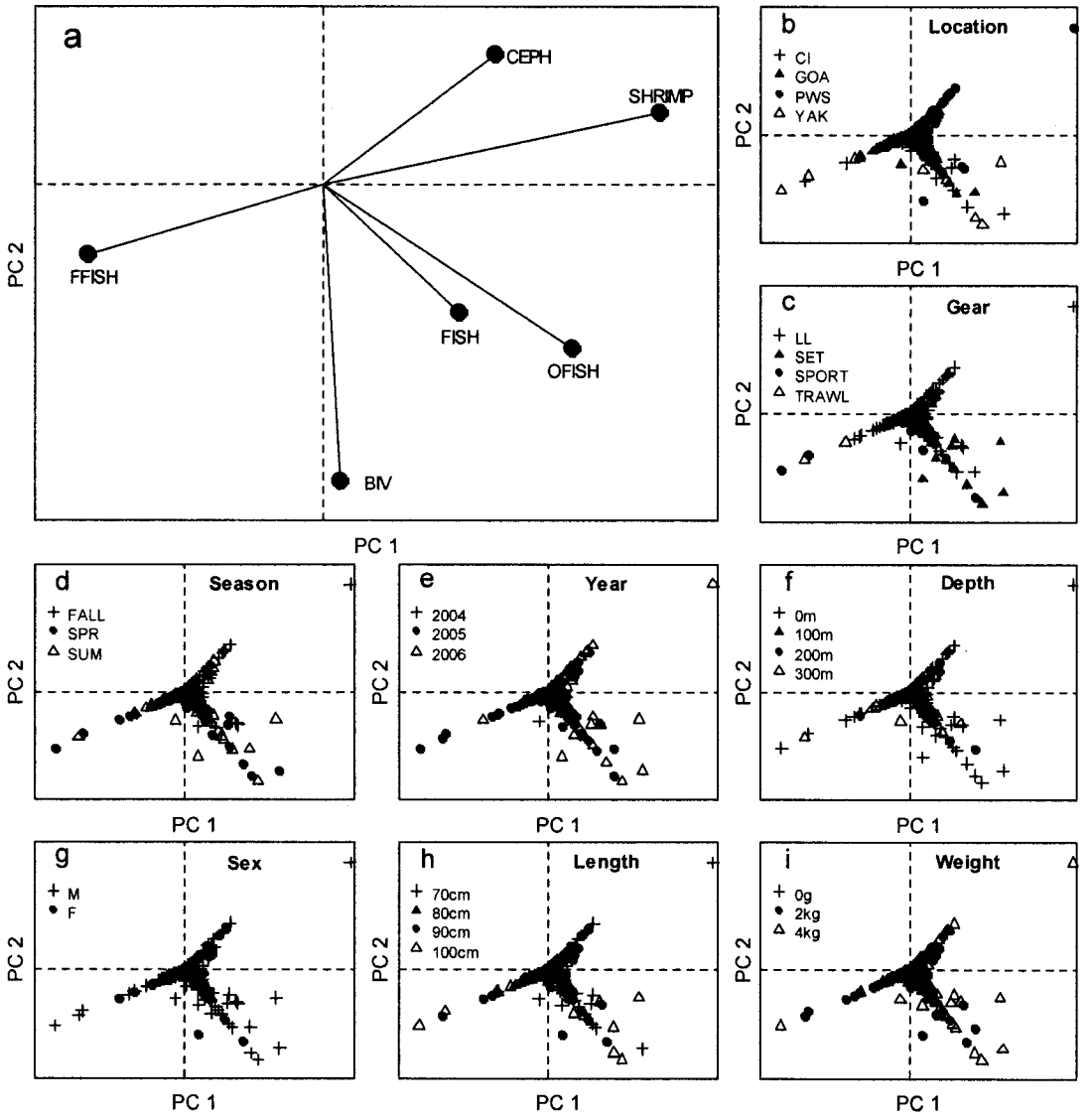

Figure 5.6 Principal component graphs. Principal component analysis vector plot for: (A) all data and (B-I) bi-plots for each data factor.

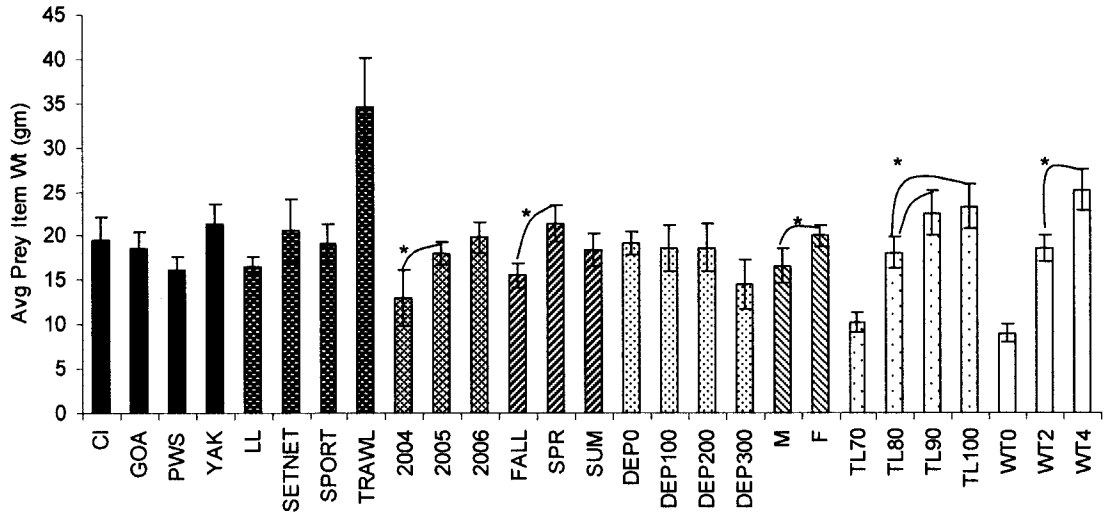

Figure 5.7 Prey size for each data category. Average size of individual prey items by weight (gm) for each data grouping with standard error bars. Significant differences within a data group are represented by curved lines and asterisks.

Table 5.1 Summary data and sample sizes. Summary of mean cumulative prey numbers for each data grouping, including sample size from detailed laboratory analysis (n), the coefficient of variation at the sample size from the cumulative prey curve simulations (CV%), the proportion of empty stomachs and the proportion of stomachs that contained more than one prey category. Data groups are all (ALL), Cook Inlet (CI), Gulf of Alaska (GOA), Prince William Sound (PWS), Yakutat Bay (YAK), longline (LL), set net (SET), sport (SPT), trawl (TWL), year of capture (2004, 2005, 2006), season of capture (spring, summer, fall), depth of capture (DEP0, DEP100, DEP200, DEP300), sex (male, M, or female, F), length (TL70, TL80, TL90, TL100) and weight (WT0, WT2, WT4). NR stands for not recorded.

Factor	Data Group	n	CV%	% empty	% Multiple
	ALL	921	0%	42.0%	47.8%
Location	CI	194	0%	46.0%	59.8%
	GOA	205	0.7%	46.7%	40.3%
	PWS	214	0.9%	13.1%	64.5%
	YAK	289	0%	57.5%	33.0%
Gear Type	LL	516	0%	31.7%	52.1%
	SET	180	0.6%	100.0%	41.1%
	SPORT	174	0%	41.2%	39.7%
	TRAWL	42	2.9%	40.0%	57.1%
Year	2004	96	0%	60.2%	17.7%
	2005	418	0%	29.5%	50.5%
	2006	398	0%	43.9%	52.3%
Season	spring	258	0%	42.1%	59.7%
	summer	297	0%	55.7%	52.2%
	fall	357	0%	13.0%	35.6%
Depth	DEP0	676	0%	41.8%	46.2%
	DEP100	96	1.3%	15.4%	56.8%
	DEP200	104	0%	49.2%	43.8%
	DEP300	34	1.9%	40.3%	70.6%
Sex	M	586	0%	36.5%	45.3%
	F	325	0%	44.8%	54.9%
Length	TL70	159	0.9%	42.6%	38.1%
	TL80	370	0%	33.8%	46.1%
	TL90	189	0%	50.4%	46.6%
	TL100	189	0%	42.8%	50.6%
Weight	WT0	163	0.7	43.2%	43.7%
	WT2	492	0%	38.5%	47.8%
	WT4	263	0%	47.1%	59.8%

Table 5.2 Overall diet composition. Summary of diet composition for all stomachs combined, including the percent of the frequency of occurrence (%FO), percent of total weight (%WT), percent of the total count (%N) and the percent of the index of relative importance (%IRI). The category, "fish", is broken out into salmon, cod, greenling, rockfish and flatfish categories.

	%FO	%W	%N	%IRI
shrimp	29.0%	2.3%	28.6%	35.8%
cephalopod	15.6%	25.7%	12.5%	24.1%
forage fish	11.7%	26.2%	14.7%	18.9%
other fish	14.2%	12.1%	12.8%	14.0%
fish	5.9%	30.6%	3.9%	7.6%
salmon	1.8%	16.2%	1.1%	1.2%
cod	0.8%	3.2%	0.6%	0.0%
greenling	0.3%	1.1%	0.2%	0.0%
rockfish	1.3%	3.6%	0.8%	0.2%
flatfish	1.8%	6.6%	1.2%	0.6%
amphipod	3.9%	0.1%	10.3%	1.6%
crab	6.3%	1.3%	4.3%	1.4%
bivalve	4.6%	1.3%	2.7%	0.7%
worms	2.8%	0.2%	6.5%	0.7%
jelly/salp	4.7%	0.4%	2.7%	0.6%
invertebrates	1.3%	0.1%	1.1%	0.1%

Table 5.3 Percent relative importance (%IRI) for prey items in each data grouping. Included are calculations for the trophic level (TrL), Shannon-Wiener Diversity Index (H') and evenness (E). Bold values are significantly different from the average over the prey category.

	shrimp	ceph	forage	other	fish	amphi	crab	bivalve	worms	jelly/salp	invert	TrL	H'	E
ALL	33.3%	22.9%	17.9%	7.6%	7.6%	1.5%	1.5%	0.7%	0.7%	0.6%	0.1%	4.0	1.7	4.7
CI	30.0%	2.9%	30.2%	21.6%	9.6%	0.6%	2.7%	0.2%	1.9%	0.3%	0.1%	4.0	1.6	4.5
GOA	45.6%	31.2%	5.9%	4.2%	8.6%	1.5%	1.5%	0.2%	0.0%	1.1%	0.2%	4.0	1.4	3.9
PWS	22.7%	**55.4%**	1.5%	16.7%	1.7%	0.8%	0.6%	0.1%	0.5%	0.0%	0.0%	4.1	1.2	3.6
YAK	23.4%	6.3%	46.1%	3.6%	10.4%	1.1%	1.1%	**5.2%**	0.3%	2.4%	0.0%	4.0	1.6	4.5
LL	35.7%	36.4%	11.7%	9.5%	2.8%	2.0%	1.2%	0.1%	0.2%	0.3%	0.0%	4.0	1.5	4.0
SET	35.7%	5.7%	9.1%	16.9%	**23.0%**	0.3%	**3.1%**	3.5%	1.6%	1.0%	0.0%	4.0	1.7	4.8
SPORT	13.6%	8.9%	20.5%	29.1%	18.1%	1.1%	1.2%	4.0%	2.2%	0.7%	0.5%	4.1	1.9	5.2
TRAWL	10.6%	0.0%	**87.2%**	0.6%	0.1%	0.0%	0.4%	0.0%	0.6%	0.5%	0.0%	4.1	0.5	2.0
2004	43.8%	2.1%	4.8%	14.7%	7.5%	1.2%	2.0%	**6.0%**	0.0%	**16.3%**	**1.5%**	3.8	1.7	4.8
2005	25.7%	16.0%	33.9%	10.2%	7.7%	3.5%	1.2%	0.4%	0.9%	0.4%	0.1%	4.0	1.7	4.6
2006	38.1%	30.5%	6.6%	15.3%	6.3%	0.2%	1.7%	0.7%	0.5%	0.3%	0.0%	4.0	1.5	4.1
spring	35.0%	3.1%	44.6%	8.9%	4.1%	1.0%	1.9%	0.1%	0.6%	0.7%	0.0%	3.9	1.4	3.8
summer	29.6%	20.8%	13.8%	8.5%	19.0%	1.1%	1.7%	3.3%	0.1%	1.9%	0.2%	4.1	1.8	5.0
fall	21.8%	**55.3%**	0.5%	17.4%	2.3%	0.7%	0.6%	0.3%	1.0%	0.0%	0.0%	4.1	1.2	3.6
DEP0	31.3%	25.5%	13.1%	16.8%	8.9%	0.4%	1.9%	1.0%	0.5%	0.4%	0.1%	4.0	1.7	4.7
DEP100	48.3%	7.2%	34.2%	2.3%	3.1%	1.4%	1.9%	0.1%	0.0%	1.4%	0.0%	3.8	1.3	3.6
DEP200	39.0%	15.8%	21.0%	2.2%	6.2%	**12.5%**	0.8%	0.6%	0.8%	1.0%	0.1%	3.8	1.7	4.5
DEP300	11.4%	19.4%	24.8%	**37.6%**	2.2%	0.0%	0.0%	0.0%	**4.4%**	0.1%	0.0%	4.1	1.5	4.1
M	45.9%	22.5%	15.3%	10.1%	3.4%	0.4%	1.4%	0.2%	0.0%	0.7%	0.0%	3.9	1.5	4.1
F	26.7%	21.8%	19.2%	14.8%	10.4%	2.4%	1.6%	1.1%	1.4%	0.5%	0.1%	4.0	1.8	5.2
TL70	54.3%	10.2%	27.7%	1.1%	0.4%	2.0%	1.8%	0.5%	0.0%	1.9%	0.0%	3.8	1.2	3.5
TL80	34.9%	27.5%	16.7%	12.9%	3.8%	1.8%	1.7%	0.3%	0.1%	0.3%	0.0%	4.0	1.6	4.3
TL90	11.8%	13.6%	29.1%	18.5%	20.6%	0.8%	1.1%	1.5%	1.7%	1.1%	0.2%	4.2	1.8	5.0
TL100	26.4%	24.0%	7.2%	21.6%	13.7%	0.3%	1.2%	1.1%	**4.4%**	0.1%	0.0%	4.1	1.7	5.0
WT0	56.9%	12.5%	23.6%	0.8%	0.3%	1.5%	2.2%	0.5%	0.0%	1.7%	0.0%	3.8	1.2	3.6
WT2	29.4%	24.2%	21.0%	14.7%	5.8%	2.0%	1.6%	0.5%	0.2%	0.4%	0.1%	4.0	1.7	4.7
WT4	22.0%	20.8%	11.1%	21.4%	18.1%	0.3%	1.0%	1.1%	**3.9%**	0.2%	0.0%	4.1	1.8	5.4

Chapter 6: Conclusions

The results of this study have progressed the state of knowledge for spiny dogfish in the Gulf of Alaska (GOA). Results suggest that the GOA spiny dogfish are amongst the slowest growing of all reported sharks species and mature at larger sizes that spiny dogfish populations elsewhere in the world. Fecundity for GOA spiny dogfish is greater than for other spiny dogfish, but net productivity may be low because the reproductive cycle may take longer than two years, as it is in most other regions. Low productivity, combined with low natural mortality, results in a low estimated sustainable harvest rate. Simulation results reported in the demographic chapter suggest that harvest strategies that target the juveniles or sub-adults have the greatest risk to the overall biomass of the population.

While the results of the diet chapter are not directly related to the other three chapters, they do relate to ecosystem approaches to fishery management of spiny dogfish. In this regard, the results are directly relevant to ecosystem modeling and understanding the impact of the species on other species. A common concern of commercial fishermen is that spiny dogfish are depredating commercially valuable species. However, results of this study show that spiny dogfish feed primarily on non-commercial species. Results also showed that spiny dogfish are highly opportunistic, feeding on whatever food source is available or most abundant at that time.

This study has had a broad and valuable impact in the management of the species and the shark complex as a whole. The results have already been applied to the annual stock assessments for sharks, will be used to set new annual catch limits for spiny dogfish

and the shark complex as a whole (which has previously been managed as part of a complex of "other species") by the North Pacific Fishery Management Council, and have also provided the basis for additional investigations into spiny dogfish in the GOA.