SPATIAL VARIABILITY IN SIZE AT MATURITY AND REPRODUCTIVE TIMING OF GOLDEN KING CRAB (*LITHODES AEQUISPINUS*) IN SOUTHEAST ALASKA

By

Andrew P. Olson, B.S.

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APPROVED:

Dr. Ginny L. Eckert, Committee Chair
Dr. Gordon H. Kruse, Committee Member
Dr. Christopher E. Siddon, Committee Member
Dr. Franz Mueter, Chair
Graduate Program in Fisheries
Dr. S. Bradley Moran, Dean
School of Fisheries and Ocean Sciences
Dr. Michael Castellini, *Dean of the Graduate School*

Abstract

Many crab fisheries around the world are managed by size, sex and season regulations, where male crabs are given at least one opportunity to reproduce before being harvested. Therefore, to set minimum legal size and fishing season for harvest, information on size at maturity and reproductive timing is needed. *Lithodes aequispinus* has supported a commercial fishery in Southeast Alaska since 1972, with an average annual harvest of 207 t. The current legal size and season for harvest are based *L. aequispinus* growth and maturity information from other parts of the range and limited information on reproduction. Additionally, evidence suggests that these life history parameters can vary spatially. Therefore, I investigated size at maturity, reproductive timing, and variation in harvest from the commercial fishery for *L. aequispinus.* I compared size at maturity estimates (males and females), mean spine contribution to legal size male crabs, and depth and bottom temperature among seven management areas in Southeast Alaska (Lynn Canal, Icy Strait, North Stephens Passage, Frederick Sound, Mid-Chatham Strait, Lower Chatham Strait, and Clarence Strait) and investigated reproductive timing of mature females in Frederick Sound. Male size of maturity estimates varied spatially, with an increasing trend with latitude and significant differences occurred among the majority of management areas. Female maturity estimates varied significantly among all areas, but showed no latitudinal pattern. The latitudinal pattern for size at male maturity in Southeast Alaska differed from published values in other parts of the range (Japan, Russia, the Bering Sea and from the Aleutian Islands to Canada), where size at maturity decreased with increasing latitude. When I investigated the ability of environmental factors to explain the patterns in Southeast Alaska, depth and temperature were not found to influence the spatial variation in male maturity estimates. Depth varied by management area, and males and females were distributed at similar depths. Temperature varied less than 1.0 °C among management areas, and monthly temperature measured at a mooring in the Gulf of Alaska also varied by less than 1.0 °C throughout the year at depths where *L. aequispinus* are found (250 m). Mean spine contribution to legal size varied spatially but did not influence calculated legal size. Reproductive timing was determined for eyed embryos, with projected hatching of embryos occurring from April to November, indicating that a distinct reproductive season does not exist. Management implications from this research are that the current legal size (177.8 mm/7.0 in carapace width (CW)) does not allow male crab to reproduce at least once before being harvested for all management areas. If legal size is increased to 196.5 mm/7.7 in CW, a higher proportion of male crab could reproduce at least once before being harvested. This size change could have negative economic impact to the commercial fishery with potential harvest lost in areas with smaller sizes at maturity. This study shows the importance of re-examining legal size and season based on an improved understanding of how life history characteristics change over space and the resulting implications for improved fisheries management.

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Introduction

Crab fisheries in the North Pacific are male-only, size-selective fisheries that are regulated by a minimum legal size limit based on life history parameters, including size at maturity and growth increment per molt. A minimum size limit is intended to allow crabs the ability to reproduce at least once before being harvested (Jewett *et al.*, 1985; Donaldson and Donaldson, 1992) and designed to prevent recruitment overfishing. However, size at maturity can vary within or between geographic areas leading to differences in life history parameters, such as growth and molting frequency. Spatial variability in size at maturity has been observed in high latitude crab species such as *Paralithodes camtschaticus* (red king crab) (Pengilly and Schmidt, 1995), *Paralithodes platypus* (blue king crab) (Somerton and Macintosh, 1983), *Lithodes aequispinus* (golden king crab) (Somerton and Otto, 1986; Nizyaev, 2005), *Chionoecetes bairdi* (Tanner crab) (Somerton, 1981), and *Chionoecetes opilio* (snow crab) (Orensanz *et al.*, 2007). Size at maturity estimates were generally found to decrease with latitude, except for *C. bairdi*, which varied by longitude (Somerton, 1981; Hines, 1989; Blackburn *et al.*, 1999; Meiri, 2011). Furthermore, spatial variability in maturity estimates in other commercially important crustacean species, including *Lithodes santolla* (southern king crab)*, Paralomis granulosa* (false king crab)*, Callinectes sapidus* (blue crab)*, and Homarus americanus* (American lobster), have been incorporated into fisheries management to reflect the viability and sustainability of the species that are being harvested (Guillory *et al.*, 2001; Watson *et al.*, 2013; Lovrich and Tapella, 2014). Causes of variability in size at maturity for these species have been attributed to environmental temperature and its effect on growth and molting frequency (Guillory *et al.*, 2001; Webb, 2014), distribution of larvae from coastal currents (Watson *et al.*, 2013), food availability, and habitat quality (Webb, 2014). Interestingly, the latitudinal pattern of decreased size at maturity is contrary to Bergmann's rule, which states that animals living in lower latitudes and warmer climates are generally smaller than animals living in higher latitudes and colder climates (Meiri, 2011). While spatial variation in size at maturity for crab species in the North Pacific has been hypothesized to be dependent on 1) temperature, which is associated with metabolic rate, growth rate, molt timing, and molt increment, 2) size-selective historical fishing pressure (Somerton, 1981; Hines, 1989; Paul and Paul, 2000; Burmeister and Sainte-Marie, 2010), and 3) genetic variation (Orensanz *et al.*, 2007).

Temperature and food availability are key environmental variables that can influence size at maturity in many different species. In ectotherms, cooler temperatures retard growth and delay maturity, causing individuals to mature at a larger size compared to species in warmer environments (Angilleta *et al.*, 2004). Growth rate and size at maturity are also influenced by food availability, in which increased food can result in earlier maturation due to increased amounts of reserved energy (Jonsson *et al.*, 2013). Whether temperature, food availability, or their interaction is most influential on size at maturity continues to be debated among scientists and is commonly known as the Berrigan-Charnov puzzle (Berrigan and Charnov, 1994; Jonsson *et al.*, 2013).

Size-selective fishing pressure can influence size and age at maturity, with resultant evolutionary effects (Fenberg and Roy, 2008). Size selectivity of fishing gear may remove faster maturing and growing individuals, while allowing late maturing and slow growing individuals to avoid harvest and reproduce, causing an overall decline in size and age at maturity (Ricker, 1981; Fenberg and Roy, 2008). If growth rate is heritable, this resultant evolutionary effect can decrease population growth, greatly impeding recovery in an overfished population and lead to fishery closures (Hutchings, 2005). Evidence of this effect exists for many species, including Pacific salmon (*Salmonidae*) (Ricker, 1981) and gastropods in Southern California (Roy *et al.*, 2003).

For decapod crustaceans size at maturity has been defined in three ways: 1) physiological, referring to the ability of an individual's gonads to produce gametes; 2) morphometric, referring to the full development of an individual's secondary sexual characteristics, where male claw size increases; and 3) functional, referring to the observed size of individuals in mating pairs that have successfully mated and reproduced in nature (Kruse, 1997; Waddy and Aiken, 2005; Pardo *et al.*, 2009). Size at 50% morphometric maturity (SMM) is commonly used to set minimum legal size in male-only crab fisheries, because it is simple to measure, and aging techniques have not been developed for crustaceans as in fish species. Male SMM can be defined by looking at the breakpoint in the ratio between male chela height (CH) and carapace length (CL), because claw size in males is one of the secondary sexual characteristics that changes at the onset of morphological maturity (Somerton, 1980; Goshima *et al.*, 2000; Corgos and Freire, 2006; Zheng, 2008). Males that are physiologically mature, but morphometrically immature, are unlikely to mate successfully due to male-male competition and the ability to properly grasp and hold females during copulation (Corgos and Freire, 2006; Filina, 2011). Male crabs guard and defend females by grasping in a premating embrace until the female is ready to molt. Once a female has molted, the male re-grasps the soft-shelled female for copulation (Christy, 1987; Donaldson and Byersdorfer, 2005; Filina, 2011; Rasmuson, 2013). Observations of grasping pairs of *P. camtschaticus* off Kodiak Island, Alaska, revealed that functionally mature males were often much larger than females and that physiologically mature, small males mate only in the absence of large males or with a female-skewed sex ratio (Powell *et al.*, 2002). In addition, mating studies on *P. camtschaticus*, *C. bairdi*, and *C. opilio* suggest that small-clawed males may have limited ability to grasp and hold the female during courtship (Conan and Comeau, 1986; Paul and Paul, 1989; Paul, 1992). Information on maturity and reproduction has been applied to harvest strategies in Alaska king crab fisheries by first using functional maturity, if mating studies are available, to determine legal size of harvest; otherwise morphometric maturity is used to determine legal size for males, in order to protect a stock's reproductive potential and contribute to future populations (Powell *et al.*, 2002). In the remainder of the thesis the term 'maturity' will be used in reference to size at 50% morphometric maturity (SMM) when disscussing male *L. aequispinus* and size at 50% maturity (SAM) for female *L. aequispinus.*

Lithodes aequispinus is a long-lived commercially important species that has the following life history attributes: morphometrically mature at 8 years, 20 month reproductive cycle, lecithotrophic larvae that remain at depth, mature females molt approximately every 1.5 to 2 yr, and mature males molt every 10 to 33 mo (Sloan, 1985; Paul and Paul, 2001b; Donaldson and Byersdorfer, 2005; Olson *et al.*, 2014). Slow growth and late maturation make *L. aequispinus* vulnerable to overfishing. *Lithodes aequispinus* occupy a broad depth range (100-1,000 m) (Jewett *et al.*, 1985; Somerton and Otto, 1986; Blau *et al.*, 1996). Depth distribution of *L. aequispinus* has been observed using submersible research conducted in Frederick Sound in Southeast Alaska in the spring and fall of 2000 providing some evidence of reproductive behavior (Hoyt *et al.*, 2002). Males and females were observed together in spring, including 17 mating pairs, and were found at the highest frequency between 151 and 342 m. In November males and females were segregated by depth, and no mating pairs were observed (Hoyt *et al.*, 2002). These submersible observations suggest that spring may be the time of year for high reproductive activity in Frederick Sound (Hoyt *et al.*, 2002). Depth segregation by sex, with seasonal vertical migrations and reproduction, has been observed in other deep water *Lithodes* species, including *Lithodes ferox* (Abello and Macpherson, 1991) and *Lithodes murrayi* (Miquel *et al.*, 1985). These species showed similar patterns, in which adult males led the vertical migration to shallower depths, followed by females and then juvenile males (Miquel *et al.*, 1985). Ovigerous females may migrate to shallower depths in relation to embryo development, hatching, and mating with adult males (Miquel *et al.*, 1985; Abello and Macpherson, 1991). Further research on depth distribution by sex for *L. aequispinus* may provide insight on reproductive patterns and vertical migration for this poorly studied species.

Lithodes aequispinus supports commercially important, male-only fisheries in the Aleutian Islands, eastern Bering Sea, and Southeast Alaska that emerged after the collapse of *P. camtschaticus* and *P. platypus* commercial fisheries in Alaska in the early 1980s (Jewett *et al.*, 1985; Koeneman and Buchanan, 1985; Otto and Cummiskey, 1985; Somerton and Otto, 1986). The Aleutian Islands fishery is managed with an individual fishing quota program where participants are assigned shares out of the total allowable catch. The fishery is divided into two separate management areas, east and west of 174°W longitude. The total allowable catch in 2012, as designated by the Alaska Board of Fisheries, was 1,501 t east of 174°W longitude and 1,352 t west of 174°W longitude and can be reduced if the previous season's catch exceeds the prescribed total allowable catch (Fitch *et al.*, 2014). The legal size limit for the Aleutian Islands fishery is 152.4 mm (6.0 in) CW, based on size at maturity estimates by Somerton and Otto (1986). The commercial fishing season spans August 15 to May 15 (Somerton and Otto, 1986; Donaldson and Donaldson, 1992). In the eastern Bering Sea the fishery occurs around St. Matthew and the Pribilof Islands. The St. Matthew Island fishery is managed using a catch quota of 5 to 9 t, with a year-round season to allow for exploratory fishing and data collection. Pot limits per vessel range from 60 – 75 pots based on vessel length. Observer coverage is mandatory to collect biological information to inform management the fishery (Fitch *et al.*, 2014). In the Pribilof Islands the fishery is managed using a catch quota based on long-term average harvest. The fishery is open year round and biological data are collected by onboard observers and from catch landed at the processors (Fitch *et al.*, 2014). Participation is limited in the St. Matthew and Pribilof Islands fisheries and can only be conducted under a commissioner's permit issued by the Alaska Department of Fish Game (ADF&G), which allows for flexibility in establishing specific regulations in a given season (Fitch *et al.*, 2014). For the St. Matthews and Pribilof Islands fisheries the legal size limit for male *L. aequispinus* is 139.7 mm (5.5 in) CW and is based on a SMM study conducted by Somerton and Otto (1986) in the eastern Bering Sea and economic considerations to allow for a commercial fishery to occur where the previously the legal size was 165.1 mm (6.5 in) CW (Somerton and Otto, 1986; Donaldson and Donaldson, 1992). In Southeast Alaska this fishery is managed with entry limited to 57 permits, with each permit having a 100 pot limit. In 2014 the fishery had a total harvest of 107 t and a total ex-vessel value of $1,541,877 (J. Stratman, ADF&G, Petersburg, Alaska personal communication, 2015). Management of the Southeast Alaska

L. aequispinus commercial fishery is conducted based on a 3-S (sex, size, and season) management system and has further developed by limiting the number participants, establishing a catch quota per management area, and allowing management to close areas if there are stock health concerns. Male-only harvest is allowed using a minimum legal size of 177.8 mm (7.0 in) CW, intended to allow crab to mature and reproduce at least once before harvest, with a fishing season typically occurring from February to May or until each management area's catch quota is obtained (Olson *et al.*, 2014). The current management areas for the Southeast Alaska commercial *L. aequispinus* fishery consist of Lynn Canal, Icy Strait, North Stephens Passage, Frederick Sound, Mid-Chatham Strait, Lower Chatham Strait, and Clarence Strait (Figure 1).

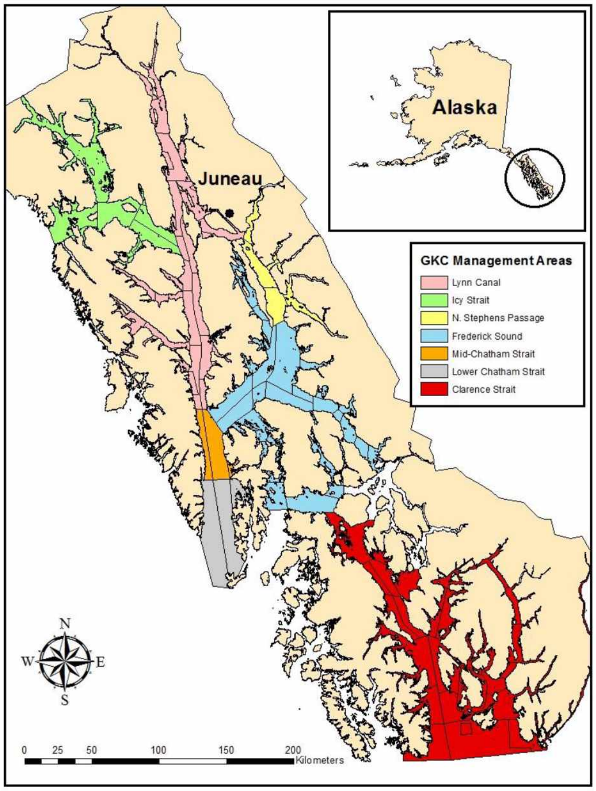

Figure 1. Commercial fishery management areas of *L. aequispinus* in Southeast Alaska.
The Northern, East Central, and Southern management areas are referred to as Lynn Canal, Frederick Sound, and Clarence Strait, respectively, to reflect locations of *L. aequispinus* populations geographically.

The historical process on setting the minimum harvest size limit in Southeast Alaska is not very clear; however, information on a variety sources was considered. The minimum size limit for male *L. aequispinus* was originally based on growth and maturity information for *P. camtschaticus* from the Gulf of Alaska (Weber and Miyahara, 1962; Powell and Nickerson, 1965), due to the lack of biological information on *L. aequispinus*. This size limit was later justified using biological data on *L. aequispinus* life history (Olson *et al.*, 2014) as it became available, which consisted of growth information primarily from Frederick Sound and Lynn Canal in Southeast Alaska using a tagging study (Koeneman and Buchanan, 1985) and SMM estimates from British Columbia, Canada (114.0 mm CL) (Jewett *et al.*, 1985); Prince William Sound, Alaska (110 mm CL) (Paul and Paul, 2001c); and the southeastern Bering Sea (130.0 mm CL) (Somerton and Otto, 1986). Spine length is included in harvest size limits, and thus variability in spine length could influence the impact of size limits on the fished population. Many invertebrate species, such as *Strongylocentrotus franciscanus* (red sea urchin) (Rogers-Bennett *et al.*, 1995), *Rhithropanopeus harrisii* (mud crab) (Morgan, 1989), and *C. sapidus* (Davis *et al.*, 2005), have increased survival attributed to spine morphology that reduces predation risk (Morgan, 1987). Potential predators avoid prey with longer spines due to their unpalatability, and spine length is plastic and can respond to predation pressure (Morgan, 1987; Rogers-Bennett *et al.*, 1995; Davis *et al.*, 2005). How spine length varies in *L. aequispinus* remains unknown.

In Southeast Alaska the *L. aequispinus* fishery first developed in the 1960s when fishermen explored gear types, depth ranges, and geographic areas to find adequate harvests of *L. aequispinus.* The fishery then further developed in the early 1970s and was managed using catch quotas, gear type and size limits. Fish tickets were used to record landings in a management area, and dockside sampling was used to acquire information on recruit classes of crab and average weights of crab harvested in-season. The fishery continued to develop in the 1980s, and harvest rapidly peaked in 1987, with a harvest of 461 t from three management areas (Figure 2). In the 1990s, the fishery harvest declined to

1 t and was considered collapsed in 1996 due to a lack of recruitment and overexploitation (Olson *et al.*, 2014). In response, catch quotas were greatly reduced and Southeast Alaska was divided into five management areas in 1993 in an attempt to disperse fishing effort across the region and allow populations of *L. aequispinus* to rebuild. In 2000 logbook data were collected on crab catch per pot (CPUE) and used to detect declines and manage the fishery in-season. In addition, a voluntary observer program was implemented to collect information on discarded *L. aequispinus* (females and sub-legal males). The sub-legal male discards was compared to legal male harvest to quantify stock health based on the number sub-legal males that would be recruiting into the fishery in the next few seasons. Observers also recorded clutch fullness of mature egg bearing females to assess reproductive success. Management areas were then further sub-divided in 2005 into the current seven separate management areas (Figure 1). In the late 2000s harvest rapidly increased, peaking in 2010 with a harvest of 332 t (Olson *et al.*, 2014). From 2011 to 2014 harvest declined to levels previously observed in the 1990s, with a harvest of 107 t in 2014 (Figure 2).

Currently, there is no fishery-independent stock assessment survey for *L. aequispinus* in Southeast Alaska, and the setting of harvest quotas for each management area prior to the start of a fishing season is based on trends in fishery-dependent data, with each management area having a maximum harvest threshold (quota). Fishery dependent data include: fish tickets (landings), logbooks (CPUE), dockside sampling (size, weight, and recruitment proportions), and onboard observations of discards (female and sub-legal male *L. aequispinus*) during the commercial fishery (Olson *et al.*, 2014). Fish tickets are used to track in-season harvest so that it does not exceed the catch quota in each management area, and logbooks are used to track in-season harvest trends in CPUE.

In Southeast Alaska, *L. aequispinus* size at maturity has not been estimated and information on basic life history parameters specific to Southeast Alaska is needed to ensure that fisheries management reflects the regionally-specific biology of *L. aequispinus* in Southeast Alaska. In this thesis, I estimate spatial variability in SMM and SAM, the influence of temperature, depth and harvest on spatial variation in SMM estimates, and mean spine contribution to legal sized males. In addition, I investigate reproductive timing for *L. aequispinus* in Southeast Alaska. My overall goal is to inform sustainable fishery management.

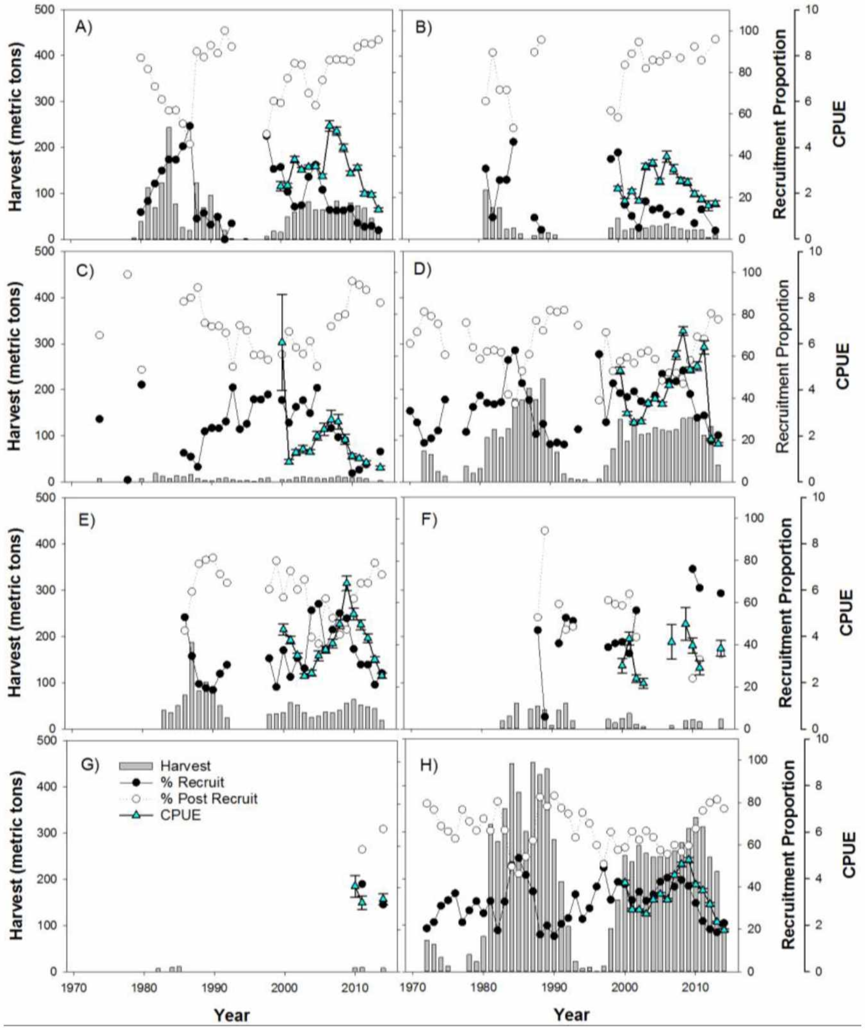

Figure 2. *Lithodes aequispinus* harvest, recruitment proportion, and CPUE for Southeast Alaska. Years with no data indicate either no harvest occurred or less than 3 permit holders participated so that information is confidential. Bars represent the total harvest (t), black circles represent the proportion of recruit crabs harvested, open circles represent the proportion of post recruit crabs harvested and the blue triangles represent CPUE, or the catch per pot based on logbook data. A) Lynn Canal, B) Icy Strait, C) North Stephens Passage, D) Frederick Sound, E) Mid-Chatham Strait, F) Lower Chatham Strait, G) Clarence Strait, H) all management areas.

Methods

Size at Maturity

Lithodes aequispinus were measured during the commercial fishery (February-May) in Southeast Alaska for maturity and reproductive timing by ADF&G observers. Crabs were sampled for morphometric maturity by ADF&G observers during 2007-2014 for males (n=9,786) and for maturity during 1998-2015 for females (n=14,242). Crabs that were visually infected with *Briarosaccus callosus* (n=448) were excluded from the analysis, because they are known to suppress growth, potentially hindering maturity (Sloan, 1984; Hawkes *et al.*, 1987). Observer coverage included at least one trip in one of the seven management areas in Southeast Alaska each year (Figure 1). Male *L. aequispinus* CL and CH were measured to the nearest 1 mm. Male SMM was estimated by fitting a piece-wise linear regression model to the relationship between CL (independent variable) and CH (dependent variable) by least squares. Male SMM was estimated as the breakpoint of the following model:

$$y = \beta_0 + \beta_1(X) + \beta_2(X - C)^+ + \varepsilon, \tag{1}$$

where y=CH (mm), β_0, β_1 and β_2 are estimated regression parameters, X=CL (mm), C represents the breakpoint and ε is the error term. Parameters were estimated using the statistical program R 3.1.3 (R Core Team, 2015) and the extension package SiZer: Significant Zero Crossings (Sonderegger, 2011) and 95% confidence intervals for the breakpoint and the slope parameters were obtained using a bootstrap procedure. One thousand bootstrap samples were taken by resampling the raw data points and refitting the piece-wise linear regression model to calculate SMM for each of the 1,000 estimates (Schwarz, 2013). I compared SMM among management areas using the Fisher-Behrens statistic:

$$z = \frac{|\widehat{C_1} - \widehat{C_2}|}{\sqrt{s_1^2 + s_2^2}}, \tag{2}$$

where C_1 and C_2 are size at morphometric maturity estimates from different areas and s_1 and s_2 are standard errors associated with these estimates. The Fisher-Behrens statistic was then compared to the critical value of a normal distribution, $z_{1-\alpha/2}$, adjusted for multiple tests using a Bonferroni correction, which replaces α with $\frac{\alpha}{n}$, where α = 0.05 and n = total number of hypotheses to be tested (21) (Day and Quinn, 1989; Quinn and Deriso, 1999).

Female SAM was determined based on the presence of embryos or empty embryo cases attached to the pleopods (Jewett *et al.*, 1985; Somerton and Otto, 1986). Maturity was estimated by fitting a logistic regression model to the proportion of mature females at a given CL (mm):

$$P = \frac{1}{1+e^{-a(CL-b)}}, \tag{3}$$

where *P* is the predicted proportion of mature females at a given CL (mm), and *a* and *b* are estimated parameters. Parameter *a* represents the shape of the curve and parameter *b* is the SAM CL (mm). The negative log-likelihood was estimated at each maturity proportion as:

$$-log_e CL = -[Mlog_e(P + 0.0001) + \{Ilog_e[P + 0.0001)]\}, \tag{4}$$

where *M* = number of mature crab and *I* = number of immature crab at a given CL (mm). The Excel SOLVER feature was used to find the values of parameters *a* and *b* that minimize the sum of the negative log-likelihoods (McCullagh and Nelder, 1989). The fitted logistic model was then evaluated to determine the CL that corresponds with SAM (Somerton, 1980), and 95% confidence intervals were determined using bootstrapping with 1,000 replicates, implemented in the statistical program R 3.1.3 (Somerton, 1980; R Core Team, 2015). To determine if SAM differed significantly among areas, a log-likelihood ratio test was used (Quinn and Deriso, 1999; Stahl and Kruse, 2008):

$$X^2 = 2[(-log_e CL_R) - (-log_e CL_F)], \tag{5}$$

where CL_R is the reduced model with a SAM estimate from a given area and CL_F is the full model that estimates maturity for the combined data and is compared to the reduced model.

Male SMM estimates and female SAM estimates from their geographic distribution from published literature (Japan, eastern Russia, eastern Bering Sea, Aleutian Islands, and British Columbia, Canada) as well as from the seven management areas in Southeast Alaska were analyzed together and separately (only Southeast Alaska management areas) as a function of latitude using a linear regression model:

$$y = \beta_0 + \beta_1 x + \varepsilon, \tag{6}$$

where *y* = size at maturity estimates (male SMM or female SAM), β_0 and β_1 are estimated regression parameters, *x* = mean latitude (degrees), and ε = error terms. Size at morphometric maturity for male *L. aequispinus* in Prince William Sound, Alaska (Paul and Paul, 2001c) was estimated using a method that differed from those used in the rest of the literature and, because of this, were excluded from this analysis.

Because removals of males in the fishery could result in variation in SMM estimates, I examined variation in harvest from the commercial fishery using ADF&G fish tickets (J. Stratman, ADF&G, Petersburg, Alaska, personal communication, 2015) among management areas and if harvest pressure was related to variation observed in SMM estimates. Effects of harvest pressure on male SMM estimates from Southeast Alaska were analyzed using linear regression models by comparing the total harvest for each management area from two different time periods, 1972-2014 or 2005-2014, to maturity estimates:

$$y = \beta_0 + \beta_1 x + \varepsilon, \tag{7}$$

where *y* = size at maturity estimates for male crab from seven management areas, β_0 and β_1 are estimated regression parameters, *x*=total harvest (t) from 1972-2014 or 2005-2014 for each management area, and ε=error terms.

Environmental Variability

Depth and temperature, which may vary across management areas and influence variation in SMM for *L. aequispinus,* were measured from February to May during commercial fishing seasons.

ADF&G observers recorded crab pot depth from 1998-2014 from fishing vessel sonar measurements, which ranged from 40-750 m (n=6,804) (Table 1).

Table 1. Sample size and years of pot depth for *L. aequispinus* habitat in Southeast Alaska.

Location	Year	N_D
Lynn Canal (LyC)	2001-2002, 2004, & 2007-2014	1,480
Icy Strait (IS)	2001, 2007-2012, & 2014	615
North Stephens Passage (NSP)	2002, 2004, 2007-2012, & 2014	607
Frederick Sound (FS)	2000-2004, 2007-2008, 2010-2011, & 2013-2014	1,445
Mid-Chatham Strait (MC)	2000-2003 & 2007-2014	1,329
Lower Chatham Strait (LC)	2000-2001 & 2008-2011	761
Clarence Strait (CS)	1998-2000 & 2014	567

To determine if pot depth varied significantly among management areas and could help explain differences in SMM, mean pot depths were determined for each management area. Mean pot depth was then evaluated by fitting a one-way analysis of variance (ANOVA) and compared among management areas using Tukey's honestly significantly different (HSD) test for pairwise comparisons ($\alpha<0.05$) using JMP 11.0.0 statistical software (JMP, 2013):

$$y = \beta_0 + \beta_1 x + \varepsilon, \tag{8}$$

where y = SMM, β_0 and β_1 are estimated regression parameters, x = mean depth, and ε = error terms.

Depth distribution of male and female *L. aequispinus* was investigated to determine if segregation occurs during the commercial fishery between male and female crabs. The proportion of females per pot at depth for each management area (arcsine square root transformed) was fitted using a linear regression model to determine if proportion of females changed as a function of depth ($\alpha<0.05$) using JMP 11.0.0 statistical software (JMP, 2013):

$$y = \beta_0 + \beta_1 x + \varepsilon, \tag{9}$$

where y = the transformed female proportions, β_0 and β_1 are estimated regression parameters, x = depth (m) for each pot, and ε = error terms.

During 2008-2014 temperature was measured to the nearest 0.2°C every hour (n=5,796) using temperature sensors (HOBO TidbiTs Data Loggers, Onset Computer Co.) attached to crab pots (n=40) (Table 2). Temperature sensor deployment ranged from days to several weeks, dependent upon the length of an observer trip.

Table 2. Sample size and timing of temperature data recorded hourly at depth in Southeast Alaska. Temperature samples (N_T) at depth were filtered based on set and haul times of pots during the commercial fishery. Location abbreviations defined in Table 1.

Location	Year	Months	N_T	Mean Depth (m)	Std Dev
LyC	2008, 2010, & 2012	February-April	1,080	344.4	144.1
IS	2008, 2010, & 2012	February	305	282.4	124.5
NSP	2010 & 2014	March-May	1,346	258.3	70.9
FS	2010 & 2013-2014	February-March	894	352.6	55.6
MC	2008-2011 & 2014	March & May	1,090	488.8	109.4
LC	2010 & 2011	April	265	560.2	20.1
CS	2014	March-April	816	345.6	23.3

To determine if temperature varied significantly among management areas, mean temperatures determined for each management area were compared using standard deviations. Pot depth and temperature were then used to determine if they may be related to SMM for male *L. aequispinus* for all management areas by fitting a linear regression model for depth and temperature using month as a covariate for the temperature analysis:

$$y = \beta_0 + \beta_1 x + \varepsilon, \tag{10}$$

where y = size at morphometric maturity, β_0 and β_1 are estimated regression parameters, x = mean depth, and ε=error terms and,

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \varepsilon, \tag{11}$$

where y = size at morphometric maturity, β_0, β_1, and β_2 are estimated regression parameters, x_1 = mean temperature, x_2=month and ε=error terms.

Because temperature data were opportunistically collected by fishery observers and varied by which months and years were sampled across management areas, I examined seasonal and yearly variation in near-bottom temperature at 250 m, a depth representative of *L. aequispinus* habitat, using a long-term time series from a mooring station in the northern Gulf of Alaska. The temperature data were retrieved from a publicly available database maintained by the University of Alaska Fairbanks School of Fisheries and Ocean Sciences (http://www.ims.uaf.edu/gak1/). The Gulf of Alaska (GAK1) mooring station is located adjacent to the coast near Seward (59° 50.7' N, 149°28.0'W) at a depth of 250 m. Temperature measurements at 250 m, recorded every quarter hour (n=200,299), were averaged by month during 2008-2013 (January-December, n=72). Mean monthly temperatures from GAK1 (n=72) were evaluated by fitting a one-way repeated measures ANOVA and compared using Tukey's HSD pairwise comparisons ($\alpha<0.05$). Then monthly mean temperatures for GAK1 and Southeast Alaska (GAK1: February n=6, March n=6, April n=6, May n=6 and Southeast Alaska: February n=7, March n=9, April n=5, and May n=2) were evaluated by fitting a two-way repeated measures ANOVA and compared using Tukey's HSD pairwise comparisons ($\alpha<0.05$). These analyses were used to determine 1) consistency in temperature at depth across months and 2) whether opportunistic intermittent sampling by fisheries observers (February-May from 2008-2014) are representative of those measured consistently in the northern Gulf of Alaska.

Crab Size and Spine Contribution

I investigated the CW, CL and spine contribution to size of legal male *L. aequispinus* to determine variation among and to develop growth equations for management areas of Southeast Alaska. ADF&G observers and port samplers sampled legal sized males during 2013-2014 (n=1,592) and measured CL and CW to the nearest 1 mm with and without spines at the widest point of the carapace. Additionally, port samplers measured CL of legal size males (n=93,075) during 1972-2014 to quantify the size of crab harvested during the commercial fishery. Spine contribution was calculated as the difference in CW with and without spines and includes contribution of spines on both sides of the carapace. Estimates of spine contribution, CW and CL were compared across management areas using an ANOVA and Tukey's HSD pairwise comparisons ($\alpha<0.05$) using JMP 11.0.0 statistical software (JMP, 2013).

Legal Size

To reassess the appropriateness of the current legal size in Southeast Alaska, estimates of mean spine contribution, SMM, and an area wide growth increment (16.3 mm CL, SD=3.0, n=45 from Lynn Canal, Icy Strait, and Frederick Sound) (Koeneman and Buchanan, 1985) were used to recalculate legal size. These metrics were then used in conjunction with CL and CW measurements to develop a CL-CW model in all 7 management areas to determine if *L. aequispinus* males have at least one opportunity to reproduce before being harvested under the current fishery legal size of 177.8 mm/7.0 in CW. The relationship between CL and CW was used in order to convert CL measurements (morphometric maturity and molt increment) into CW because the commercial fishery uses CW for legal size determinations:

$$CW = mCL - b, \qquad (12)$$

where CW is given carapace width (mm), CL is a given carapace length (mm), m is the slope, and b is the CW intercept. Equation 13 was then modified to incorporate SMM estimates, a molt increment, and mean spine contribution:

$$CW = (m(SMM_a + molt\ increment) - b) + mean\ spine\ contribution_a\ , \tag{13}$$

where SMM is the size at 50% morphometric maturity estimate, a is the area of interest, and b is the CW intercept from Eq. 12, and mean spine contribution.

Reproduction

To examine if seasonality exists for the *L. aequispinus* reproductive cycle in Southeast Alaska, 50 mature females were collected from Frederick Sound in March of 2014 during the commercial fishing season and approximately 150 embryos were taken from each female and frozen in vials filled with seawater to determine embryo development stages and to estimate when hatching would occur. Embryo development was used as a proxy for seasonality in reproductive timing by analyzing the projected hatching timing and whether not this timing would span over a specific time frame. Embryos were thawed under room temperature, viewed under a compound microscope and then staged based on published descriptions of embryo development (Table 3) (Stevens, 2006; Long and Van Sant, 2016). All uneyed embryo cell structures were either ruptured or bloated due the freezing process; therefore, staging of uneyed embryos was not possible (n=25 samples). Of the 25 eyed embryo samples, 23 could be staged and hatch timing predicted based on published timing of embryo development (Stevens, 2006; Long and Van Sant, 2016), assuming that each embryo stage (8-12) was at the beginning of its respective stage.

Table 3. Mean duration of embryo development stages for *L. aequispinus* (Long and Van Sant, 2016).

Embryo Development Stage	Description	Mean Duration of Embryo Development Stage (Days)
0	Precleavage	10.00
1	Cleavage and blastula	49.47
2	Gastrula	32.02
3	V-shaped embryo	23.53
4	Prenauplius	27.18
5	Nauplius	17.75
6	Maxilliped formation	14.58
7	Metanauplius	38.18
8	Eye formation	33.32
9	Chromatophore formation	53.79
10	Rapid growth	40.96
11	Prehatching	95.25
12	Hatching	25.67

Results

Size at Maturity

Male SMM estimates varied significantly across management areas, with the largest difference of 40.1 mm (1.6 in) occurring between Icy Strait and Lower Chatham Strait. Fisher-Behrens statistics showed significant differences among many of the management areas (Figure 3). Icy Strait crabs had the largest SMM estimate (158.0 mm CL), followed by Lynn Canal (147.3 mm CL), Clarence Strait (138.5 mm CL), Frederick Sound (137.6 mm CL), North Stephens Passage (131.9 mm CL), Mid-Chatham Strait (127.3 mm CL), and Lower Chatham Strait (117.9 mm CL) (Figure 3 and Table 4). These differences were significant with the exception of North Stephens Passage compared to Frederick Sound, Mid-Chatham Strait, Lower Chatham Strait, and Clarence Strait and Frederick Sound compared to Clarence Strait. Female *L. aequispinus* SAM estimates among Southeast Alaska management areas were all found to be highly significantly different from another ($p<0.001$) using the log-likelihood ratio test, and did not follow the same spatial variability pattern as observed in males (Figure 3). Clarence Strait female crabs had the largest maturity estimate (119.0 mm) followed by Mid-Chatham Strait (108.6 mm), Lynn Canal (106.2 mm), Icy Strait (104.8 mm), Frederick Sound (104.0 mm), North Stephens Passage (103.2 mm), and Lower Chatham Strait (100.4 mm) (Figure 3).

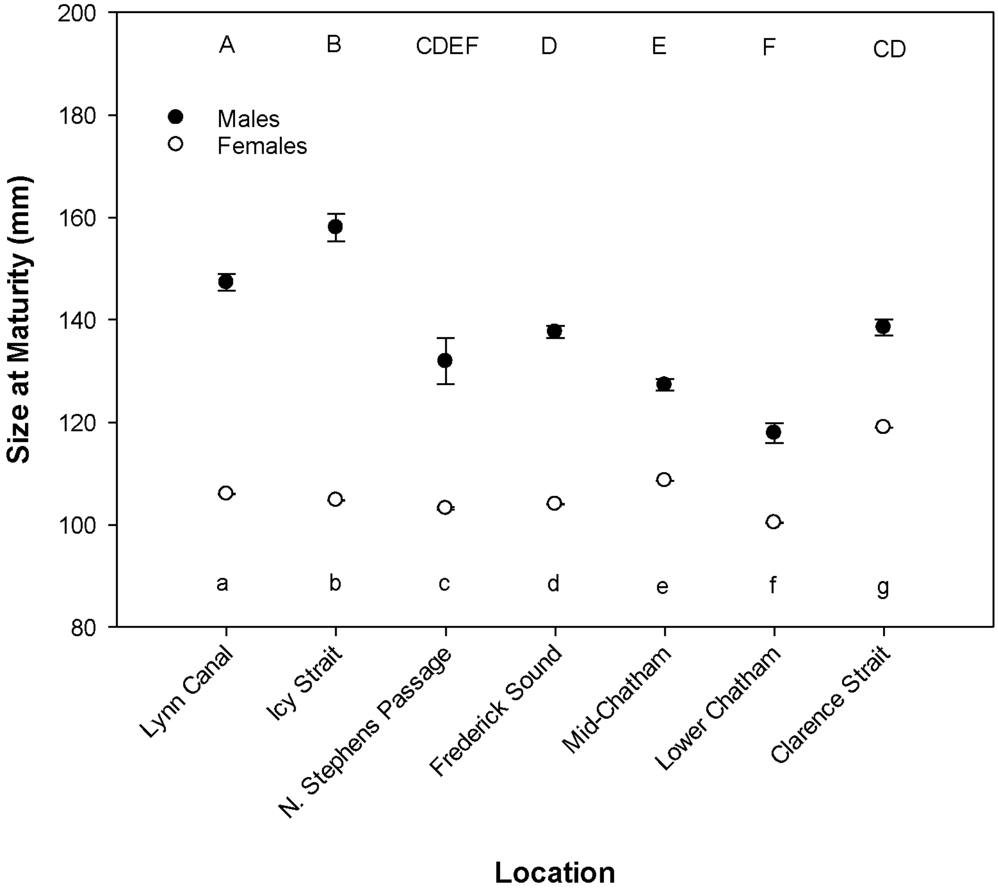

Figure 3. Maturity estimates for male and female *L. aequispinus* from 2007-2014 in Southeast Alaska. Male maturity estimates (solid circles) were compared among management areas using the Fisher-Behrens statistic with significant Bonferroni corrected p-values (< 0.002) and female maturity estimates (open circles) were compared using a log-likelihood ratio test with the associated standard error for all maturity estimates (bars). Significant differences among areas are represented by capital letters (males) at the top and lower case letters (females) at the bottom.

Table 4. Maturity estimates for male (N_M) and for female (N_F) *L. aequispinus* in Southeast Alaska with 95% confidence intervals and mean latitude (decimal degrees) where crab were captured. Location abbreviations defined in Table 1.

					Males				Females	
Location	**Mean Latitude (Decimal Degrees)**	**Std Err**	**Years**	**N_M**	**SMM (mm)**	**95% CI**	**Years**	**N_F**	**SAM (mm)**	**95% CI**
LyC	58.22968	0.009	2007, 2009-2013	1,859	147.3	134.0-150.7	2001, 2004, 2007-2015	1,742	106.2	103.7-108.3
IS	58.15367	0.004	2007-2012, 2014	668	158.0	149.9-162.7	2001, 2003, 2007-2009, 2011-12, 2014	929	104.8	102.2-106.3
NSP	57.90109	0.008	2007-2012, 2014	398	131.9	120.3-181.0	2002, 2004, 2007-2012, 2014	1,192	103.2	102.2-104.2
FS	57.17877	0.003	2007-2008, 2010-2011, 2013-2014	2,294	137.6	131.0-141.0	2000-2004, 2007-2008, 2010-2011, 2013-2014	4,370	104.0	103.4-104.6
MC	56.82732	0.003	2007-2013	2,183	127.3	121.4-131.4	2000-2003, 2007-2014	3,681	108.6	107.8-109.4
LC	56.30801	0.005	2008-2011	1,630	117.9	115.4-121.6	2000-2001, 2008-2011	1,048	100.4	98.4-102.2
CS	55.83010	0.009	2011-2013	754	138.5	130.0-143.0	1998-2000, 2011-2014	1,280	119.0	117.6-120.5

Maturity estimates of *L. aequispinus* decreased with increasing latitude over their geographic distribution when excluding Southeast Alaska, for both males (F=16.75, p-value=0.003, R^2=0.677) and females (F=48.22, p-value=0.0001, R^2=0.858) (Figure 4). Male SMM in Southeast Alaska was not related to latitude when the most southerly area, Clarence Strait, was included in the analysis (F=3.092, p-value=0.139, R^2=0.382) (Figure 5A). However, when Clarence Strait was removed from the analysis there was strong a relationship between latitude and the estimated SMM, such that SMM increased with increasing latitude (F=10.94, p-value=0.0297, R^2=0.665) (Figure 5B). For females latitude was not related to SAM (F=1.64, p-value=0.256, R^2=0.247) (Figure 5A). When crabs from Clarence Strait were removed from the analysis, the relationship between latitude and SAM became non-significant (F=0.310, p-value=0.586, R^2=0.080) (Figure 5B).

Harvest pressure varied among management areas, but was not related to variation in SMM. Total harvest during 1972-2014 was highest in Frederick Sound (3,671 t) and Lynn Canal (2,054 t), followed by Mid-Chatham Strait (1,499 t), Icy Strait (741 t), North Stephens Passage (306 t), Lower Chatham Strait (304 t), and Clarence Strait (161 t). Harvest pressure, using total harvest from the commercial fishery from 1972-2014, did not explain the variation observed in male *L. aequispinus* SMM estimates for Southeast Alaska (F=0.1624, p-value=0.704, R^2=0.032). Additionally, harvest from a more recent time period (2005-2014) did not explain the variation observed in SMM estimates (F=0.205, p-value=0.670, R^2=0.039). Total harvest from 2005-2014 was highest in Frederick Sound (1,131 t) and Lynn Canal (639 t) followed by Mid-Chatham Strait (427 t), Icy Strait (211 t), North Stephens Passage (79 t), Clarence Strait (76 t), and Lower Chatham Strait (65 t).

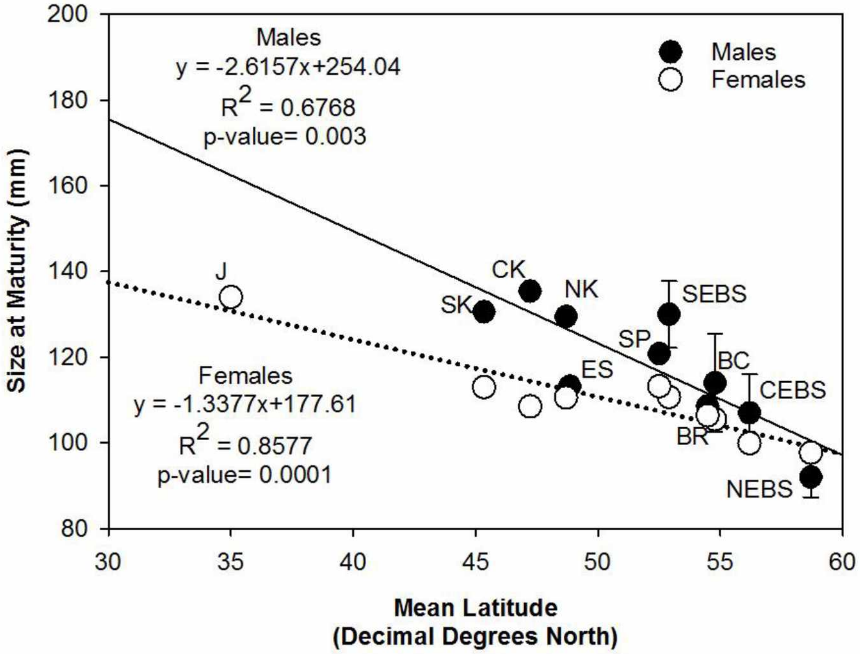

Figure 4. Latitudinal variation in SMM and SAM for *L. aequispinus* from the published literature. Male maturity estimates were determined using SMM and female maturity estimates were determined using SAM. Maturity estimates from the published literature include: Japan (J) (Hiramoto, 1985; Jewett *et al.*, 1985); the southern, central, and northern Kuril Islands (SK, CK, and NK) (Nizyaev, 2005) and eastern Sakhalin Island (ES) (Zhivoglyadova, 2004), Russia; Seguam Pass (SP), Bowers Ridge (BR) (Otto and Cummiskey, 1985); south, central, and northeastern Bering Sea (SEBS, CEBS, and NEBS) with 95% confidence intervals for males (Somerton and Otto, 1986) Alaska; and Canada (BC) with 95% confidence intervals (Jewett *et al.*, 1985). Note that the Japanese estimated SAM for females reflects the estimated size at which 60% of the females were found to be mature (Hiramoto, 1985; Jewett *et al.*, 1985). A linear regression line for male (solid) and female (dotted) *L. aequispinus* is plotted to represent the strength in the latitudinal cline across Japan, eastern Russia, the Bering Sea, Aleutian Islands, and Canada. Both male (R^2=0.677) and female (R^2=0.858) *L. aequispinus* exhibited strong patterns in latitudinal variation with SMM and SAM estimates decreasing as latitude increased.

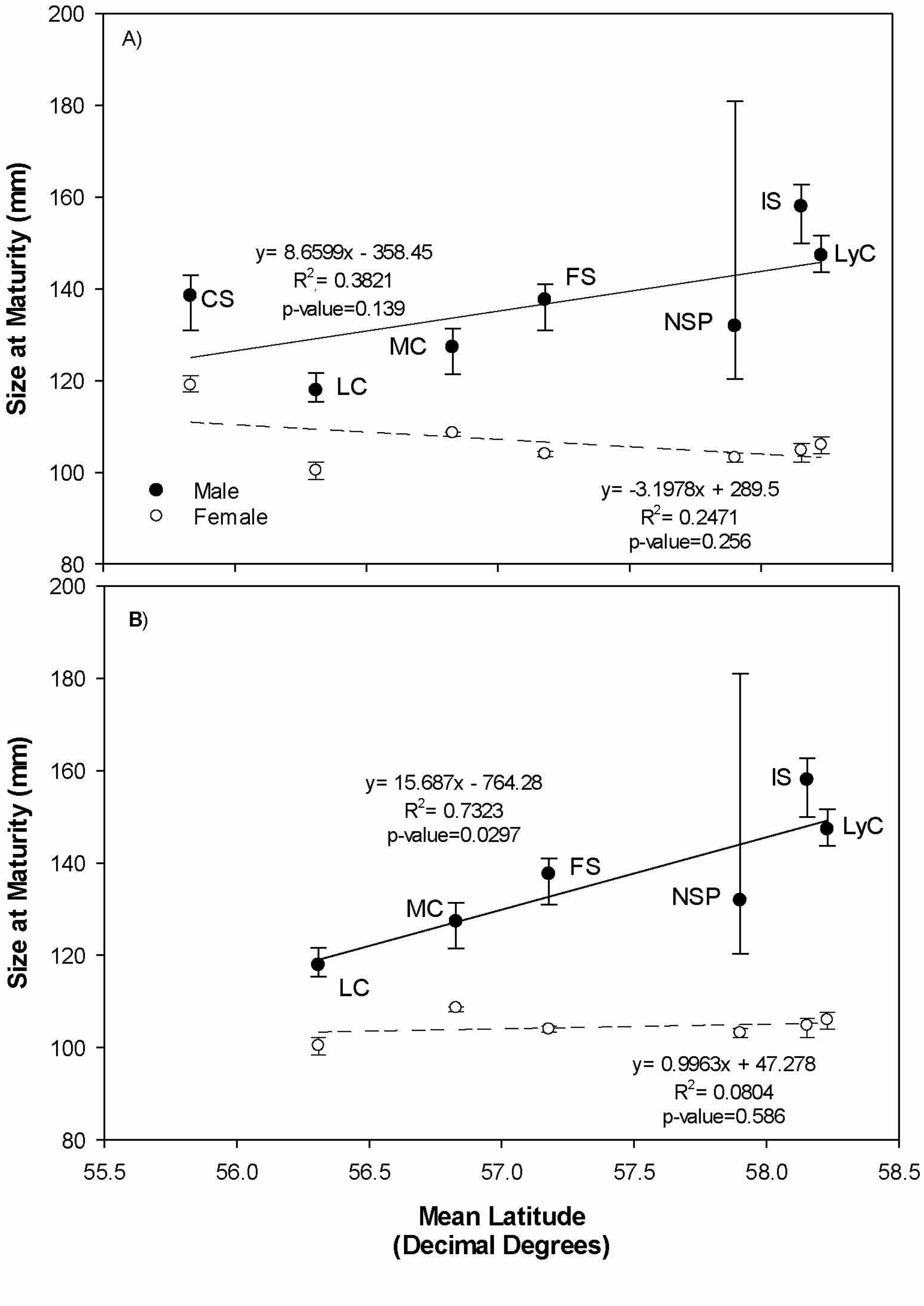

Figure 5. Latitudinal variation in SMM and SAM *L. aequispinus* in Southeast Alaska. Estimates have 95% confidence intervals (bars) for male (solid circles) and female (open circles) *L. aequispinus* in Southeast Alaska. Estimates include: LyC, IS, NSP, FS, MC, LC, and CS with a linear regression A) including all areas and B) with CS removed. Location abbreviations defined in Table 1.

Environmental Variability

The mean depth of pots sampled during the commercial fishery varied significantly among management areas with five groupings (Table 5). Pots sampled in Mid-Chatham Strait and Lower Chatham Strait were the deepest with mean depths below 500 m, followed by Lynn Canal and Clarence Strait with depths ~350 m. Depth of pots in Frederick Sound, Icy Strait, and North Stephens Passage were on average between 240 to 305 m (Table 5).

Table 5. Mean depth of *L. aequispinus* habitat in Southeast Alaska where crabs were harvested. During the commercial *L. aequispinus* fishery depth of pots (m) was recorded and a Tukey's HSD was used to determine if mean depth (m) was significantly different among areas (α=0.05). Location abbreviations defined in Table 1.

Location	Mean Depth (m)	Std Dev	Tukey's HSD
LyC	346.0	101.3	B
IS	277.2	70.3	D
NSP	246.2	41.1	E
FS	305.5	86.1	C
MC	504.1	118.9	A
LC	514.0	72.1	A
CS	357.0	83.7	B

The mean depth distribution overlapped for male and female *L. aequispinus* caught during the Southeast Alaska commercial fishery (February-May), with the proportion of females per pot explaining little of the variation observed across depths (Lynn Canal (F=4.09, p-value=0.0433, R^2=0.00322), Icy Strait (F=47.099, p-value<0.001, R^2=0.0894), North Stephens Passage (F=85.634, p-value<0.0001, R^2=0.154), Frederick Sound (F=46.776, p-value<0.0001, R^2=0.0333), Mid-Chatham Strait (F=14.795, p-value<0.0001, R^2=0.0122), Lower Chatham Strait (F=12.22, p-value=0.0005, R^2=0.0182), and Clarence Strait (F=4.31, p-value=0.0384, R^2=0.00819) (Figure 6 and 7). Additionally, SMM was not related to variation in depth across management areas (F=1.778, p-value=0.240, and R^2=0.262).

The mean monthly temperature sampled during the *L. aequispinus* commercial fishery (February-May) varied within a range of 5.1-6.0°C among management areas and GAK1 mooring station (Figure 8). Monthly mean temperatures for GAK1 throughout the year ranged from 5.3°C in May, June, August, and September to 6.1°C in January (Figure 9 and Table 6). When GAK1 and pooled Southeast Alaska temperatures were analyzed for monthly variation between locations during the timing of the *L. aequispinus* commercial fishery, there was a significant difference found between location and month (F=5.28, p-value=0.006). During the month of February, temperatures measured in Southeast Alaska were significantly cooler than temperatures at 250 m depth at GAK1 (p-value=0.0013), but these differences did not occur in March, April, or May (Figure 9 and Table 6). Additionally, SMM did not relate to variation in mean monthly temperature by management area from Southeast Alaska (F=0.492, p-value=0.5, R^2=0.0394) and month was found to be a non-significant covariate (p-value=0.979).

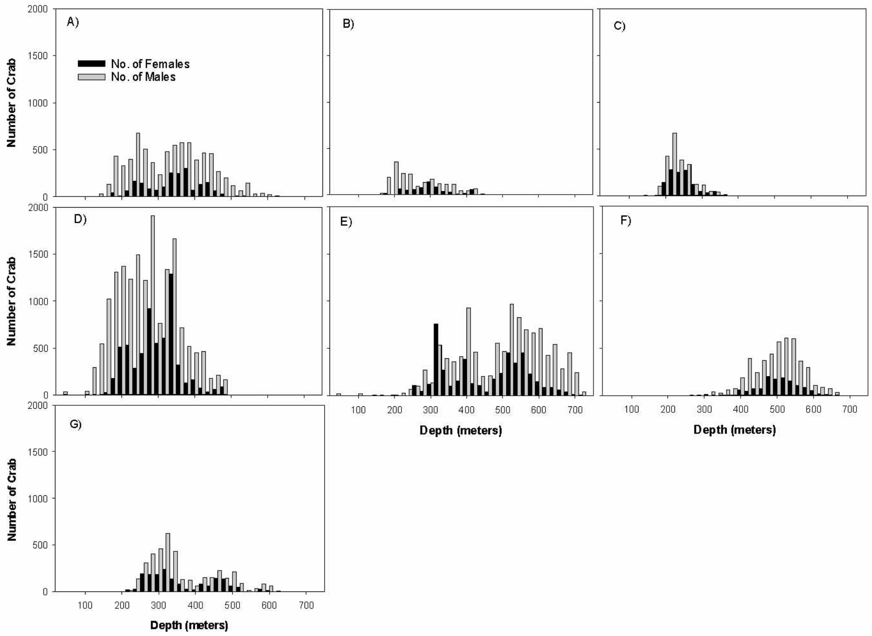

Figure 6. Depth distributions of male and female *L. aequispinus* in Southeast Alaska during 1998-2014. Depth (m) was grouped into 20-m intervals. A) LyC, B) IS, C) NSP, D) FS, E) MC, F) LC, and G) CS. Location abbreviations defined in Table 1.

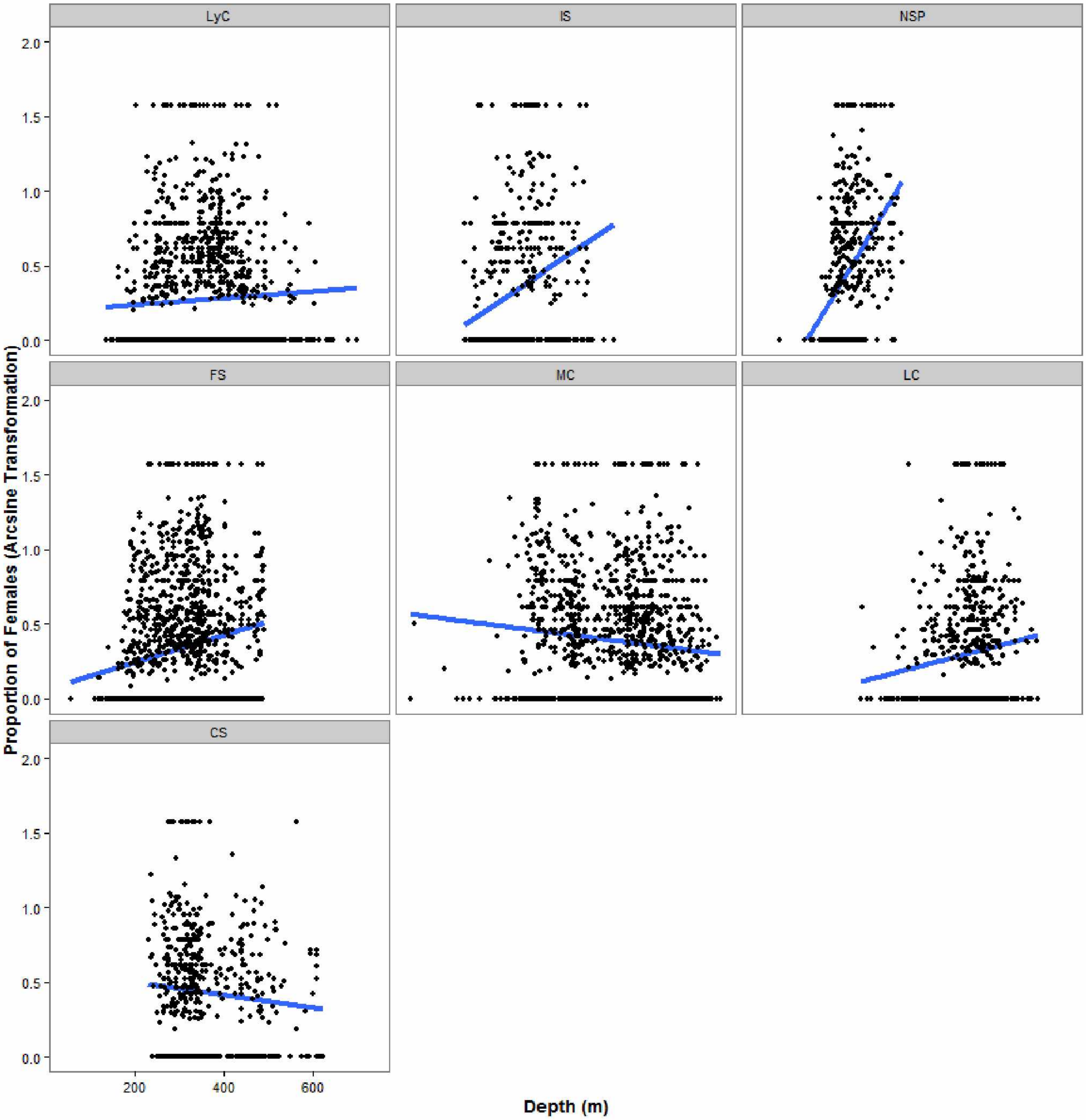

Figure 7. Proportion female *L. aequispinus* per pot at depth (m) observed in Southeast Alaska. Proportion data were transformed using the Arcsine transformation so data could be normalized and analyzed using a linear regression (blue lines). Location abbreviations defined in Table 1.

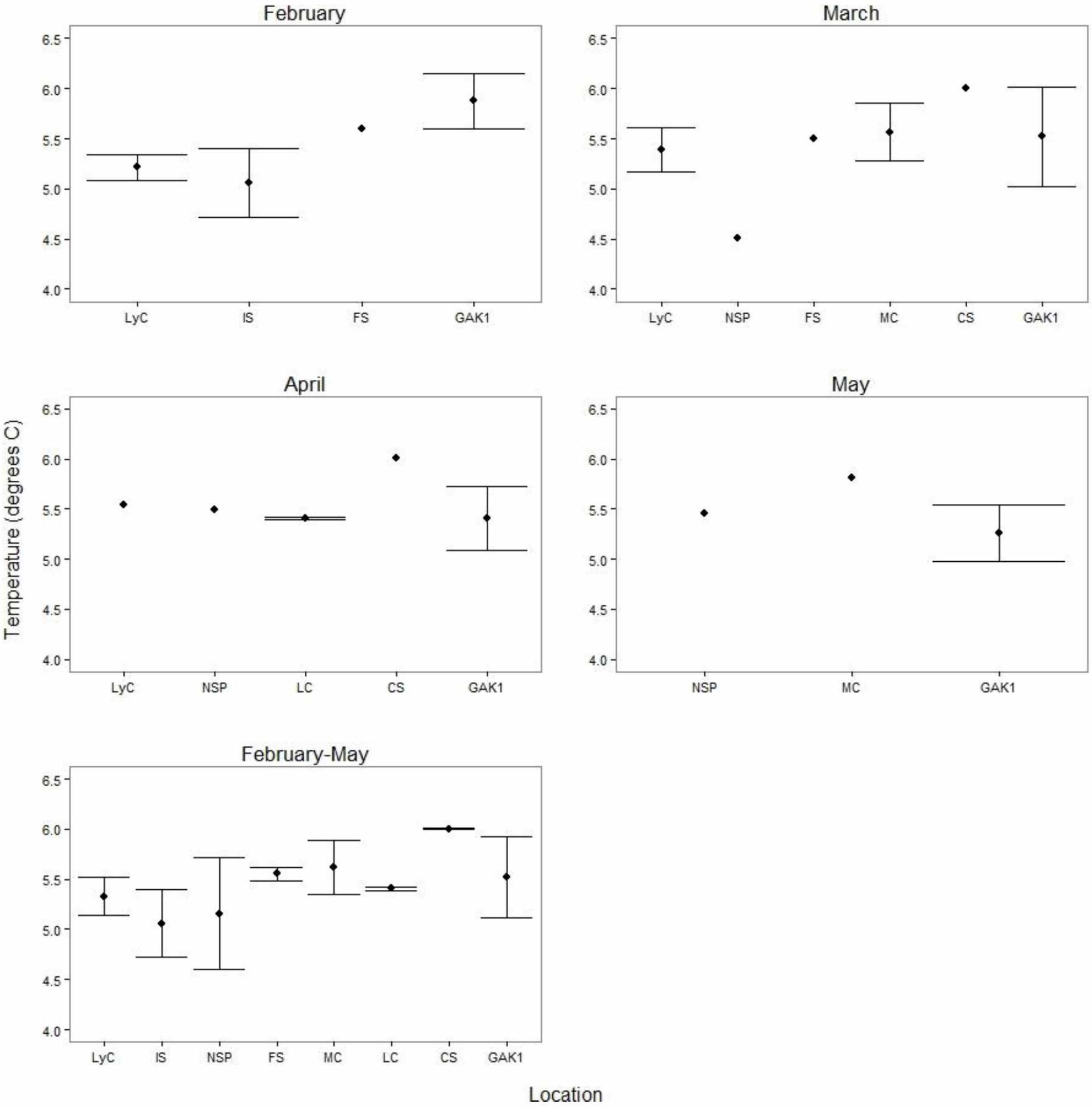

Figure 8. Mean ±SD monthly temperatures at depth among Southeast Alaska management areas and the Gulf of Alaska mooring station (GAK1) (February-May). Location abbreviations defined in Table 1.

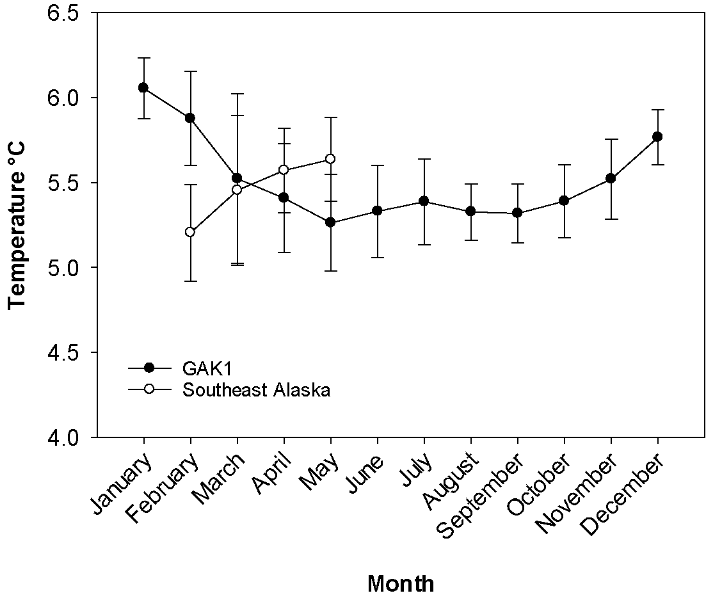

Figure 9. Mean ±SD monthly temperature from GAK1 and Southeast Alaska management areas by month. Temperature sampled at 250 m depth at GAK1 and from 246 to 514 m depth in Southeast Alaska.

Table 6. Mean ±SD monthly temperature from GAK1 and Southeast Alaska compared across months. Temperature sampled at 250 m depth at GAK1 and from 246 to 514 m depth in Southeast Alaska.

	GAK1			Southeast Alaska		
Month	**N**	**Mean Temp**	**Std Dev**	**N**	**Mean Temp (°C)**	**Std Dev**
January	6	6.1	0.2			
February	6	5.9	0.3	7	5.2	0.3
March	6	5.5	0.5	9	5.5	0.4
April	6	5.4	0.3	5	5.6	0.2
May	6	5.3	0.3	2	5.6	0.3
June	6	5.3	0.3			
July	6	5.4	0.3			
August	6	5.3	0.2			
September	6	5.3	0.2			
October	6	5.4	0.2			
November	6	5.5	0.2			
December	6	5.8	0.2			

Crab Size and Spine Contribution

Mean spine contribution (mm) to legal size measurements varied among areas, but the magnitude of the differences was very small and not likely biologically relevant (~1 mm). Clarence Strait had the largest spine contribution (10.1 mm) followed by North Stephens Passage (10.0 mm), Lower Chatham Strait (9.6 mm), Lynn Canal (9.2 mm), Mid-Chatham Strait (9.0 mm), Frederick Sound (8.9 mm), and Icy Strait (8.9 mm). Clarence Strait mean spine contribution to legal size was larger than Lynn Canal, Mid-Chatham Strait, Frederick Sound and Icy Strait (Table 7). North Stephens Passage and Lower Chatham Strait mean spine contribution to legal size was found to be significantly different from Mid-Chatham Strait, Frederick Sound, and Icy Strait (Table 7).

Table 7. Mean spine contribution (mm) to legal sized male *L. aequispinus* in Southeast Alaska. Tukey's HSD was used to determine if mean spine contribution to legal sized males was significantly ($p<0.05$) different among areas. Location abbreviations defined in Table 1.

Location	N	Mean CW (mm)	Std Err	Mean Spine Contribution to Legal Size (mm)	Std Err	Tukey's HSD
LyC	187	200.9	0.9	9.2	0.2	BC
IS	121	200.0	1.2	8.9	0.2	C
NSP	152	196.2	1.4	10.0	0.2	AB
FS	623	181.6	0.5	8.9	0.2	C
MC	268	184.1	0.7	9.0	0.2	C
LC	70	176.6	0.9	9.6	0.4	AB
CS	171	183.4	0.9	10.1	0.2	A

Legal Size

Using the CL-CW relationship for each area and incorporating SMM estimates, growth increment from Southeast Alaska (16.3 mm CL), and mean spine contribution to legal size and assuming that reproduction occurs after molting, I calculated that crab are capable of reproducing at least once before being harvested and reaching the current legal size (177.8 mm CW) in three out of seven areas (Table 8).

Projected area specific legal size estimates (CW) for Icy Strait (196.5 mm) and Lynn Canal (186.0 mm) substantially exceeded current legal size (177.8 mm); Clarence Strait (177.6 mm) and Frederick Sound (173.4 mm) are close. Projected area-specific legal size estimates (CW) for North Stephens Passage (168.8 mm), Mid-Chatham Strait (163.2 mm), and Lower Chatham Strait (159.8 mm) remain under the current legal size. Area specific CL-CW models, which were used to convert SMM in CL to CW, were significant for all areas (p-value<0.001). North Stephens Passage had the strongest relationship (n= 152, F=1,803, R^2=0.92), followed by Frederick Sound (n=623, F=4,362, R^2=0.88), Icy Strait (n=121, F=818.5, R^2=0.87), Clarence Strait (n=171, F=995.6, R^2=0.85), Lynn Canal (n=187, F=1,064, R^2=0.85), Mid-Chatham Strait (n=268, F=1,306, R^2=0.83), and Lower Chatham Strait (n=70, F=136.4, R^2=0.67).

Table 8. Area specific legal size (CW) of male *L. aequispinus* in Southeast Alaska. Incorporating SMM, growth increment per molt (CL 16.3 mm) (Koeneman and Buchanan, 1985) and mean spine contribution for each area (Table 3) (Eq. 7 and 8) resulted in a projected area specific legal size CW (mm) for comparison to current legal size (177.8 mm CW). Location abbreviations defined in Table 1.

Location	Size at Morphometric Maturity (SMM) CL (mm)	Mean Spine Contribution to Legal Size (mm)	Area Specific Legal Size Carapace Width (mm)	Area Specific Legal Size Carapace Width (in)
LyC	147.3	9.2	186.0	7.3
IS	158.0	8.9	196.5	7.7
NSP	131.9	10.0	168.8	6.6
FS	137.6	8.9	173.4	6.8
MC	127.3	9.0	163.2	6.4
LC	117.9	9.6	159.8	6.3
CS	138.5	10.1	177.6	7.0

Reproduction

Development of eyed embryos from 23 mature *L. aequispinus* females varied over stages 8-12, with projection of hatch timing from April to November, based on duration of embryo development from the published literature (Table 8) (Long and Van Sant, 2016). The earliest hatch time is estimated to occur in April for embryo stage 12 (n=6) followed by stage 11 (n=5) in May, stage 10 (n=6) and stage 9 (n=5) in September, and stage 8 (n=1) in November. This would lead to the projection of hatch timing of eyed embryos during April through November.

Discussion

Spatial variation in size of maturity estimates for male and female *L. aequispinus* varied across management areas in Southeast Alaska, with resultant implications for fishery management to allow crabs to reproduce at least once and thus prevent overharvest. The explanation for spatial variation in SMM estimates of male *L. aequispinus* in Southeast Alaska is not immediately apparent, as SMM was unrelated to depth, temperature, harvest pressure, and spine length. Estimates of male SMM generally increased with latitude within Southeast Alaska, but the relationship was not significant, while estimates of female SAM did not vary with latitude. This intriguing pattern, which is the opposite of what is observed over a broad geographic area (Figure 3) and Bergmann's rule, may result from the glacial fjord system and unique habitats for populations of *L. aequispinus* in Southeast Alaska. Female SAM in Southeast Alaska was smaller than male SMM, and estimates varied less among management areas for females than for males. The small differences across management areas for females may indicate that female *L. aequispinus* become sexually mature over a narrow size range. Interestingly, Aleutian Islands female *L. aequispinus* populations sampled in 1981-1984 have a smaller SAM range (106.4 mm-110.7 mm) (Otto and Cummiskey, 1985; Somerton and Otto, 1986) than those in Southeast Alaska (100.4 mm-119.0 mm). Embryo development was asynchronous in this study, but further studies are needed to elucidate the complete picture of reproductive timing.

Estimates of male *L. aequispinus* location-specific mature CWs which incorporated SMM, growth increment, and mean spine contribution to legal size in Southeast Alaska revealed that the current legal size of 177.8 mm/7.0 in CW may not allow crab to reproduce at least once before being harvested in four management areas: Frederick Sound, Icy Strait, Lynn Canal, and Clarence Strait. This indicates that the current legal size for the *L. aequispinus* commercial fishery in Southeast Alaska is not appropriate and needs to be re-evaluated to incorporate area-specific maturity. A review of historical harvest (1972-

2014) under the current legal size (177.8 mm/7.0 in CW) revealed a proportion of the crab that were harvested were sub-legal, indicating there is a lack of enforcement of fishery regulations (Table 9). To resolve this issue and reduce harvest of immature crab, a change in legal size is warranted. Adoption of area-specific legal sizes for each management area would be ideal, but this is not practical because fishermen harvest from multiple management areas at the same time. Another option would be to increase the legal size throughout the region to exceed the largest area specific legal size CW (Icy Strait (196.5 mm/7.7 in CW)), so that no single area is potentially overexploited while allowing for a higher likelihood of crab being able to reproduce at least once before being harvested throughout Southeast Alaska. Potential harvest loss based on historical harvest from 1972-2014 if the legal size was increased to 196.5 mm/7.7 in CW would range across management areas with Lower Chatham having the most impact (84%) to Lynn Canal with the least impact (38%) (Table 9). To alleviate the high potential loss of harvest in Lower Chatham Strait, which has the smallest SMM estimate (117.9 mm CL) and area-specific legal size (159.8 mm CW), an alternative management strategy could be applied by opening this area to a reduced legal size when all other management areas are closed. I did not attempt to calculate long-term harvest loss owing to a reduction in reproductive output associated with harvest of males before they had a chance to reproduce. This issue and the recent decline in harvest and large size at morphometric maturities, especially in Frederick Sound, Icy Strait, Lynn Canal, and Clarence Strait, are worthy of future study.

Male SMM estimates in Southeast Alaska varied spatially among contiguous waterways, including Frederick Sound, Mid-Chatham Strait, and Lower Chatham Strait. This variation may indicate that crabs may segregate by size or could be spatially separate populations. In contrast, areas that were spatially separated had crabs with similar SMM; crabs from Clarence Strait were surprisingly not significantly different in SMM from Frederick Sound and North Stephens Passage. Low power resulting from a small sample size and lack of immature crabs may explain this result for North Stephens Passage and more samples may reveal a difference. I initially planned to examine SMM estimates over time for each management area to reveal temporal variability and elucidate mechanisms for variability in size at morphometric maturity. However, this could not be addressed due to variable sampling effort across management areas and years by fishery observers (Appendix) and due to declines in population levels over the past few years.

Table 9. Potential harvest loss in the *L. aequispinus* fishery with a change to legal size. Area-specific legal size (CW) incorporates SMM, growth increment, and mean spine contribution to legal size. Maximum legal size (7.7 in CW) is the largest size it would need to be so no single area is overexploited. These legal sizes provide a range of potential historical harvest loss from 1972-2014. Location abbreviations defined in Table 1.

				% Harvest Sub-Legal			Total Harvest Loss (t)		
Location	No. of Crab Sampled	Total Harvest (t)	Area Legal Size (in)	Less than 7.0 in	Less than Area Specific Legal Size	Less than 7.7 in	Less than 7.0 in Illegal Harvest	Less than Area Legal Size	Less than 7.7 in
LyC	16,701	2,054	7.3	3	14	38	62	288	781
IS	4,473	741	7.7	5	47	47	37	348	348
NSP	7,580	306	6.6	5	0	51	15	0	156
FS	46,883	3,674	6.8	9	2	74	331	73	2,719
MC	12,653	1,499	6.4	7	0	66	105	0	989
LC	3,354	304	6.3	7	0	84	21	0	255
CS	1,431	161	7.0	2	0	56	3	0	801

I could not detect an influence of depth or temperature on SMM for male *L. aequispinus.* Mean depth varied among management areas and ranged from 246 m to 514 m. The sex ratio of crabs caught in the commercial fishery (February – May) did not vary across depth, indicating a lack of depth segregation for males and females at this time. Mean temperature varied among management areas and GAK1 from February-May within 1.0 °C, while significant differences in mean temperature occurred only in February between Southeast Alaska and GAK1. Monthly temperature data is lacking for June-January in Southeast Alaska and needs to be further investigated to learn the magnitude in temperature differences throughout the year. This indicates that due to the large depths *L. aequispinus* inhabit that temperature is relatively constant by varying less than 1.0 °C at a depth of at least 250 m regardless of location and timing throughout the year. Thus, depth and temperature may not be influential factors on the variability in male maturity estimates observed for *L. aequispinus* in Southeast Alaska.

I found no relationship between total harvest of *L. aequispinus* from 1972-2014 or 2005-2014 and SMM estimates across management areas. This result could arise because I could not resolve shorter-term patterns due to lack of maturity data in a given year. The relationship between maturity and harvest pressure could be further investigated to determine if temporal variability in harvest pressure may have an effect on size at maturity for *L. aequispinus* and to better inform current maturity estimates. The influence of harvest pressure on SMM can have important implications for fisheries management (Ricker, 1981; Zheng, 2008). Due to gear selectivity removing larger and more reproductively viable individuals an adjustment to harvest strategy is needed to maintain harvest rates and spawning biomass when size at maturity has decreased (Zheng, 2008). Reductions in size at maturity can exacerbate population declines leading to a collapse if fisheries management does not adapt by adjusting minimum legal size and gear selectivity in order maintain fishery sustainability (Hutchings, 2005). Because the *L. aequispinus* fishery has collapsed multiple times, it will be important to continue to monitor SMM to detect possible temporal changes. If a larger legal size is adopted, future studies could investigate how this may affect spatial variation of SMM among management areas.

A similar study was conducted in Southeast Alaska looking at influences of latitude, temperature, depth, and harvest pressure on size at maturity estimates for male and female *C. bairdi* (Siddon and Bednarski, 2010). Variability in maturity estimates was observed across Southeast Alaska, but did not follow a latitudinal cline as I observed for populations of *L. aequispinus.* Interestingly, neither temperature, depth, nor harvest pressure explained the variability observed in *C. bairdi* maturity estimates, similar to my results. Siddon and Bednarski (2010) attributed the lack of a relationship between these factors and maturity estimates to temperature influences on growth and the limiting effects of food availability. As temperature increases it was found that molting frequency and overall growth increases in the lab for *C. bairdi* and *Callinectes sapidus* (Cadman and Weinstein, 1988; Paul and Paul, 2001a). When food availability is limited, less energy is available for growth and reproduction, which can cause delays in size at maturation (MacDonald and Thompson, 1986; Yoneda and Wright, 2005). Temperature for *L. aequispinus* habitat at depth varied by location, but by less than 1.0°C, indicating temperature effects on growth and food availability may be minimal. However, competition for prey resources and predator influences on *L. aequispinus* could cause variation in food availability and potentially spatial variation in size at maturity, but this hypothesis needs to be further investigated.

Predation may be influential in determining size at maturity through direct and indirect effects. High levels of predation can increase the rate of growth and speed at which a prey species reaches maturity in order to contribute to future populations with the trade-off of having a higher mortality rate (Abrams and Rowe, 1996; Walsh and Reznick, 2007). On the other hand predators can indirectly influence prey foraging behavior and through reduced foraging opportunity limit food availability, with the result of reduced growth rate and ultimately delaying the onset of maturity (Buskirk and Yurewicz, 1998). A variety of predators consume *L. aequispinus*, such as *Hippoglossus stenolepis* (Pacific halibut), *Gadus macrocephalus* (Pacific cod), and *Anoplopoma fimbria* (sablefish), based on anecdotal reports from the fishing community and observations of stomach contents in processed fish (L. Norheim, fisherman, Petersburg, AK, personal communication, 2015). Published information on groundfish predation rates on king crab is limited; however, an analysis of stomach contents conducted by Livingston (1989) from 1981-1984 looked at trends in *G. macrocephalus* predation on three commercially important crab species in the eastern Bering Sea: *P. camtschaticus, C. opilio* and *C. bairdi.* Female *P. camtschaticus* only made up a small portion of the *G. macrocephalus* diet (1.4%-3.8%), while *C. opilio* and *C. bairdi* at age 1 made up a large proportion of their diet (84%-95% and 27%-57%, respectively) (Livingston, 1989). Similar studies conducted in Kodiak Alaska from 1973-1975 looked at groundfish stomachs of *G. macrocephalus* (n=4,000), *Myoxocephalus spp.* (sculpins, n=320), and *Hemilepidotus jordani* (Yellow Irish lord, n=535) and found that less than 2% of the stomach contents contained *P. camtschaticus,* while *C. bairdi* was the dominant prey crab species (Stevens and Jewett, 2014). This indicates that these groundfish species are not major predators on *P. camtschaticus*, which is similar in size and morphology to *L. aequispinus.*

Mean spine contribution (mm) to legal sized male *L. aequispinus* ranged from 8.9-10.1 mm and varied across management areas, but whether this variation is biologically meaningful is not clear. The 1.2 mm difference between the largest and smallest estimates does not have any resulting management implications. Studies of hatchery-raised and wild juvenile *P. camtschaticus* in Southeast Alaska (Westphal *et al.*, 2014) and *C. sapidus* in Maryland (Davis *et al.*, 2004) suggest that crab spine length can be plastic and become larger in the presence of predators. Future studies could investigate the influence of predators on spine lengths for *L. aequispinus* in Southeast Alaska. It is interesting that even though spine length for *L. aequispinus* varied slightly among management areas, the pattern was different from the spatial pattern in SMM variation.

Variable growth rates could influence *L. aequispinus* size at maturity. In Southeast Alaska historical data on mean growth increment per molt lacked sufficient spatial resolution to determine if variability exists across management areas, as data are available from limited areas, primarily from Frederick Sound and Lynn Canal (Koeneman and Buchanan, 1985). Growth increment per molt for male *L. aequispinus* in the eastern Aleutian Islands (Amukta, Chagulak, and Yunaska) was 14.5 mm CL (n=517, SD=2.95) (Lovrich *et al.*, 2002; Watson *et al.*, 2002). Unfortunately, data on growth in the Aleutian Islands were not spatially identified, so spatial resolution to determine variability in growth rates was not available (Watson *et al.*, 2002). Growth of *L. aequispinus* greater than 90 mm CL from the Aleutians was relatively constant, indicating that growth rates may stabilize once a certain size is reached (Watson *et al.*, 2002). In the Beagle Channel, Argentina *L. santolla* growth increment per molt was 11.4 mm CL (n=66, SD=1.7) (Lovrich *et al.*, 2002). However, other growth studies have been conducted in the Strait of Magellan and Beagle Channel where it was found that crab >70 mm CL on average had a growth increment of 11.1 mm and 9.3 mm CL, respectively, indicating spatial variability in growth (Geaghan, 1973; Boschi *et al.*, 1984). To determine if growth is spatially variable for *L. aequispinus* across Southeast Alaska, mark-recapture studies could be conducted in different management areas.

Another possible explanation that may be influencing *L. aequispinus* growth is the parasite *B. callosus*, a parasitic barnacle that suppresses growth, feminizes and castrates male crab and sterilizes female crab. This parasite has a root system (interna) that runs through the inside of its host taking over their body and produces multiple egg sacs (externa) under the abdominal flap (Sloan, 1984). Because *B. callosus* suppresses growth, it could potentially hinder the size at which crabs become mature, resulting in very few infected crab that would recruit to the fishery and be removed to prevent further infections (Sloan, 1984; Hawkes *et al.*, 1985; Hawkes *et al.*, 1986). In Southeast Alaska, from 1998-2014 observers documented the highest incidence rate of infection in Clarence Strait (3.7%, n=6,011), while the remaining management areas combined from 2000-2014 had a much lower infection rate (0.3%, n=65,043) (personal observation). In the most recent years, from 2011 to 2014, fishery observers documented 176 infected crabs in Clarence Strait, while in contrast, only 27 crabs from the remaining management areas combined were infected.

Research on *L. aequispinus* genetics could reveal stock structure and provide management information to create biologically representative management areas to better manage the fishery. Genetic studies of *P. camtschaticus* in the North Pacific revealed three distinct genetic groupings: 1) Adak Island, 2) Bering Sea-Gulf of Alaska, and 3) Southeast Alaska, with Southeast Alaska having the lowest levels of genetic diversity and mtDNA, but significant genetic heterogeneity among populations over a small geographic scale (Vulstek *et al.*, 2013; Grant *et al.*, 2014). This result suggests that the glacial fjord system and enclosed bays of Southeast Alaska may result in decreased connectivity among king crab populations, with potentially limited larval dispersal and limited gene flow resulting in self-recruiting populations (Grant and Cheng, 2012; Vulstek *et al.*, 2013; Grant *et al.*, 2014). The current management areas in Southeast Alaska are based on historical harvest patterns and are derived from statistical areas that are entirely used for salmon management. Thus, the spatial arrangement of these statistical areas dictates possible boundaries for management areas for *L. aequispinus* and may not be representative of biologically distinct stocks. Future genetic studies of *L. aequispinus* could determine if heterogeneity among management areas exists and inform if the current management areas in Southeast Alaska truly represent separate stocks.

Sampling bias in size at maturity in this study is possible because crab were caught using pots, which are known to capture a disproportionately greater number of larger mature crab than small immature crab (Smith *et al.*, 2004). Sampling bias from pot sampling could result in size at maturity estimates that are biased towards mature individuals due to the size bias of the pot. One of the management areas in this study, North Stephens Passage, contained few small crabs. This maturity estimate may be biased because the likelihood of obtaining smaller crab in the resampling procedure of the bootstrap procedure was low and resulted in a large upper bound confidence interval. Because all crabs in this study were captured with pots, this sampling bias applies throughout and therefore does not simply explain the spatial variability in maturity estimates observed. An alternative sampling method, such as trawling, could potentially sample both small and large crab; but trawling is not feasible due to the narrow channels and rocky shores of the fjord system in Southeast Alaska.

The observations of eyed embryo development in female *L. aequispinus* in Southeast Alaska indicates that hatching would occur from April to November and discrete seasonal trends in reproduction may not exist. Further investigation into uneyed embryo development is needed to confirm if variability is observed throughout all development stages and provide additional support for lack of seasonal trends observed. The lack of segregation by depth of males and females from February through May indicates that reproduction is in theory possible during this time frame. These results based on eyed embryos indicate that *L. aequispinus* does not have a single synchronous time for hatching; however, further research should be conducted on the remainder of the year (June-January) to determine if asynchrony is consistent throughout the year and among management areas. As a result, there is no clear time when a fishery would dramatically impact reproduction. In contrast, other king crab in Alaska, including *P. camtschaticus* and *P. platypus,* have synchronous reproductive cycles and a specific season when the fishery is opened and closed to not interrupt reproduction. A novel technique I used to freeze embryos in sea water retained the embryo structure, making staging fairly simple for eyed embryos. This method did not work for uneyed embryos because the embryos did not retain their shape and the developmental embryo stage was indiscernible. Further investigations on the effects of freezing crab embryos is needed, because this method could be used to collect large sample sizes and avoid limitations of staging only live embryos. Information on life history is a critical to the successful long-term sustainability and management of a fishery. Parameters such as maturity, growth, and reproduction provide a basis for defining fishing seasons, legal size, and harvest levels without adversely affecting the reproductive potential of a fished stock. In Southeast Alaska, *L. aequispinus* is a prime example of the effect of gaps in our understanding of life history on a fishery. Incorporating life history parameters into management and increasing legal size will improve sustainability of the *L. aequispinus* fishery and hopefully allow recovery of a collapsed fishery.

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Appendix

Table A1. Year and sample sizes of male (N_M) and female (N_F) *L. aequispinus* for maturity estimates.

Location	Years	N_M	Years	N_F	Location	Years	N_M	Years	N_F
Lynn Canal	2007	624	2001	281	Icy Strait	2007	440	2001	233
	2009	129	2004	10		2008	5	2003	251
	2010	584	2007	163		2010	31	2007	92
	2011	51	2008	58		2011	25	2008	24
	2012	295	2009	256		2012	69	2009	42
	2013	176	2010	381		2014	98	2011	73
			2011	62				2012	74
			2012	229				2014	140
			2013	134					
			2014	106					
			2015	62					
North Stephens Passage	2007	47	2002	82	Frederick Sound	2007	1,263	2000	547
	2008	24	2004	112		2008	150	2001	93
	2009	34	2007	81		2010	130	2002	785
								2003	388
	2010	42	2008	64		2011	106	2004	1,030
	2011	71	2009	98		2013	551	2007	630
	2012	105	2010	210		2014	94	2008	207
	2014	75	2011	209				2010	126
			2012	243				2011	8
			2014	93				2013	308
								2014	248
Mid-Chatham Strait	2007	438	2000	175	Lower Chatham Strait	2008	414	2000	81
	2008	600	2001	10		2009	682	2001	141
	2009	186	2002	196		2010	421	2008	92
	2010	624	2003	176		2011	113	2009	237
	2011	94	2007	559				2010	252
	2012	198	2008	1,183				2011	245
	2013	43	2009	322					
			2010	161					
			2011	172					
			2012	297					
			2013	62					
			2014	368					
Clarence Strait	2011	349	1998	216					
	2012	238	1999	32					
	2013	167	2000	48					
			2011	313					
			2012	292					
			2013	266					
			2014	113					