MOVEMENT AND HABITAT UTILIZATION BY GOLDEN KING CRAB

*Lithodes aequispinus* BENEDICT 1895 IN FREDERICK SOUND, ALASKA

By

Zachary N. Hoyt

RECOMMENDED:

ADVISING COMMITTEE CHAIR

Director, Fisheries Division

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

Date
MOVEMENT AND HABITAT UTILIZATION BY GOLDEN KING CRAB
LITHODES AEQUISPINUS BENEDICT 1895 IN SOUTHEASTERN ALASKA

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

MASTERS OF SCIENCE

By
Zachary N. Hoyt, B.S.

Fairbanks, Alaska

December 2003
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Abstract

Movements and habitat use of golden king crabs (GKC), Lithodes aequispinus, were investigated with a manned submersible and ultrasonic telemetry in Frederick Sound, Alaska. Crabs were collected with commercial crab pots and ultrasonic transmitters were attached to the carapaces of 26 crabs; movements and depth distribution of male and female crabs were monitored bi-monthly from May 11, 2000 to April 12, 2001. Crabs preferred steep, complex habitat with hard substrate; few were on flat, soft substrate. Male and female GKC were not segregated by depth in mid-May. Seventeen pairs of courting crabs were observed during dives; 14 of these pairs were associated with either intermittent or continuous boulder fields and 3 with wall substrates. Crabs did not have seasonal site fidelity. Crabs had seasonal changes in depth distribution, moving to deeper water during late fall and winter and returning to shallower depths during spring. Crabs moved as far as 39 km over one year. No evidence of spatial fidelity was observed; golden king crabs may be moving greater distances or site fidelity maybe on a longer temporal scale than our study, or golden king crabs may be nomadic in nature.
# TABLE OF CONTENTS

Title Page..........................................................................................................i
Signature Page...................................................................................................ii
Thesis Abstract..................................................................................................iii
Table of Contents..............................................................................................iv
List of Figures...................................................................................................vi
List of Tables.....................................................................................................x
List of Appendices............................................................................................xii
Acknowledgements...........................................................................................xv

CHAPTER 1. A REVIEW OF GOLDEN KING CRAB BIOLOGY..............1
Literature cited..................................................................................................9

CHAPTER 2. MOVEMENTS BY GOLDEN KING CRAB IN
SOUTHEASTERN ALASKA....................................................15
Abstract............................................................................................................16
Introduction .....................................................................................................16
Material and Methods.......................................................................................18
Results.............................................................................. 28
Discussion........................................................................................................38
Literature cited.................................................................................................43
List of Figures

CHAPTER 1. A REVIEW OF GOLDEN KING CRAB BIOLOGY .............1

Figure 1.1 Distribution of GKC in the North Pacific Ocean ..........3
Figure 1.2 Historic harvest record of GKC in Alaska ...............5

CHAPTER 2. MOVEMENTS BY GOLDEN KING CRAB IN
SOUTHEASTERN ALASKA .............................................15

Figure 2.1 Study site in Frederick Sound, Alaska .....................19
Figure 2.2 Study site including bathymetry, locations of capture and release sites for acoustically tagged GKC .....................22
Figure 2.3 Search grid used to standardize effort of tracking GKC ....25
Figure 2.4 Relocation points and movement vectors of GKC relocated during May and July 2000 .................30
Figure 2.5 Relocation points and movement vectors of GKC relocated during September and November 2000 ........31
Figure 2.6 Relocation points and movement vectors of GKC relocated during February and April 2001 ............32
Figure 2.7 Relocation points and movement vectors of GKC relocated in the 2001 and 2002 southeast GKC fishery ........33
Figure 2.8 Average depth distributions of sonically tagged golden king crabs in Frederick Sound, Alaska ...........37
CHAPTER 3. HABITAT UTILIZATION BY GOLDEN KING CRAB IN SOUTHEASTERN ALASKA

Figure 3.1 Study site in Frederick Sound, Alaska

Figure 3.2 Tracks of submersible dives conducted at six sites in Frederick Sound, Alaska

Figure 3.3 Dive tracks conducted at dive sites 1 and 2

Figure 3.4 Dive tracks conducted at dive site 3

Figure 3.5 Dive tracks conducted at dive site 4

Figure 3.6 Dive tracks conducted at dive site 5

Figure 3.7 Dive tracks conducted at dive site 6

Figure 3.8 Depth distribution of distance traveled (meters) by the submersible DELTA in Frederick Sound

Figure 3.9 Sightings of courting and solitary GKC per kilometers traveled by the DELTA submersible in May 2000

Figure 3.10 Substrate electivity index for courting and non-courting GKC

Figure 3.11 Slope electivity index for courting and non-courting GKC

Figure 3.12 Average slope (± standard error) for each substrate type for submersible surveys in Frederick Sound, Alaska

Figure 3.13 Frequency of substrate type encountered for all dives
APPENDICES ......................................................................................................84

Figure A1. Temperature profile of the water column at selected dive sites........85

Figure A2. Conductivity profile of the water column at selected dive sites.......86

Figure A3. Acidity profile of the water column at selected dive sites............87

Figure A4. Dissolved oxygen profile of the water column at
selected dive sites .........................................................................................88

Figure A5. Percent O₂ saturation profile of the water column at
selected dive sites .........................................................................................89

Figure A6. Salinity profile of the water column at selected dive sites ..........90

Figure A7. Depth of each thirty second interval plotted by habitat type.........91

Figure A8. Positions of solitary and courting GKC observed from the
submersible DELTA; 12-19 May 2000 at dive sites 1 and 2......................92

Figure A9. Positions of solitary and courting GKC observed from the
submersible DELTA; 12-19 May 2000 at dive site 3.................................93

Figure A10. Positions of solitary and courting GKC observed from the
submersible DELTA; 12-19 May 2000 at dive site 4.................................94

Figure A11. Positions of solitary and courting GKC observed from the
submersible DELTA; 12-19 May 2000 at dive site 5.................................95

Figure A12. Positions of solitary and courting GKC observed from the
submersible DELTA; 12-19 May 2000 at dive site 6.................................96
Figure A13. Proportional distribution of macro invertebrates on soft sediment substrate.................................97

Figure A14. Proportional distribution of macro invertebrates on pebble substrate.........................................................98

Figure A15. Proportional distribution of macro invertebrates on cobble substrate.........................................................99

Figure A16. Proportional distribution of macro invertebrates on intermittent cobble..............................................101

Figure A17. Proportional distribution of macro invertebrates on boulder substrate......................................................102

Figure A18. Proportional distribution of macro invertebrates on intermittent boulder substrate...............................103

Figure A19. Proportional distribution of macro invertebrates on walls........104

Figure A20. Proportional distribution of fish on soft sediment substrate.........105

Figure A21. Proportional distribution of fish on pebble substrate..................106

Figure A22. Proportional distribution of fish on cobble substrate......................107

Figure A23. Proportional distribution of fish on intermittent cobble substrate.........................................................108

Figure A24. Proportional distribution of fish on boulder substrate...............109

Figure A25. Proportional distribution of fish on intermittent boulder.................110

Figure A26. Proportional distribution of fish on wall substrate.........................111
List of Tables

CHAPTER 2. MOVEMENTS BY GOLDEN KING CRAB IN

SOUTHEASTERN ALASKA.................................15

Table 2.1 Chronology of crab relocations completed in 2000.................20

Table 2.2 Tag number carapace length, capture site, date of capture and
release for 26 golden king crabs with ultrasonic transmitters.... 23

Table 2.3 Habitat characteristics at the six release sites, and the
number of crabs released at each of these sites.....................24

Table 2.4 Summary statistics from surface and submarine relocations
of depth (m), vertical movement (m) and
daily vertical movement rate (m/d) .............................................35

Table 2.5 Summary statistics of minimum distance moved (m)
and horizontal movement rate (m/d) traveled
by adult male and female golden king crab.........................36

CHAPTER 3. HABITAT UTILIZATION BY GOLDEN KING CRAB

IN SOUTHEASTERN ALASKA.................................47

Table 3.1 Matrix of habitat rankings of a compositional
analysis performed on solitary crab .................................. 70

Table 3.2 Matrix of habitat rankings of a compositional
analysis performed on courting crab ................................... 77
APPENDICES..................................................................................................................84

Table A1. Growth statistics for seven isthmus tagged GKC
caught in the 2001 and 2002......................................................................................84

Table A2. Correlation matrix of habitat variables and presence
of solitary and courting GKC.....................................................................................92
List of Appendices


Appendix 2. Temperature profile of the water column at selected dive sites in Frederick sound in May 2000........85

Appendix 3. Conductivity profile of the water column at selected dive sites in Frederick sound in May 2000........86

Appendix 4. pH profile of the water column at selected dive sites in Frederick sound in May 2000........87

Appendix 5. Dissolved oxygen profile of the water column at selected dive sites in Frederick sound in May 2000........88

Appendix 6. Percent O\textsubscript{2} saturation profile of the water column at selected dive sites in Frederick sound in May 2000........89

Appendix 7. Salinity profile of the water column at selected dive sites in Frederick sound in May 2000........90

Appendix 8. Depth of each thirty-second interval plotted by habitat type.........................................................91

Appendix 9. Correlation matrix of habitat variables and presence of solitary and courting GKC.........................92
Appendix 10. Positions of solitary and courting GKC observed at dive sites 1 and 2. .................................93
Appendix 11. Positions of solitary and courting GKC observed at dive site 3. ..............................................94
Appendix 12. Positions of solitary and courting GKC observed at dive site 4. ..............................................95
Appendix 13. Positions of solitary and courting GKC observed at dive site 5. ..............................................96
Appendix 14. Positions of solitary and courting GKC observed at dive site 6..............................................97
Appendix 15. Distribution of macro invertebrates on soft sediment substrate ..............................................98
Appendix 16. Distribution of macro invertebrates on pebble substrate ......................................................99
Appendix 17. Distribution of macro invertebrates on cobble substrate .......................................................100
Appendix 18. Distribution of macro invertebrates on intermittent cobble substrate ................................101
Appendix 19. Distribution of macro invertebrates on boulder substrate ......................................................102
Appendix 20. Distribution of macro invertebrates on intermittent boulder substrate ................................103
Appendix 21. Distribution of macro invertebrates on walls.................104
Appendix 22. Distribution of fish on soft sediment substrate .............105
Appendix 23. Distribution of fish on pebble substrate .....................106
Appendix 24. Distribution of fish on cobble substrate .....................107
Appendix 25. Distribution of fish on intermittent cobble substrate ........108
Appendix 26. Distribution of fish on boulder substrate .....................109
Appendix 27. Distribution of fish on intermittent boulder substrate ....110
Appendix 28. Distribution of fish on walls ......................................111
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Chapter 1

A REVIEW OF GOLDEN KING CRAB, *LITHODES AEQUISPINUS*, BIOLOGY

The thesis is prepared for submission to journals, except for chapter 1, which is an overview chapter.
The golden king crab (GKC), *Lithodes aequispinus* Benedict (1895), is a widely distributed and commercially important crustacean in the North Pacific Ocean. Golden king crab are anomuran decapods and are not true crabs but more closely related to the hermit crabs. Golden king crab are in the family Lithodidae which includes approximately 105 known species of stone crabs and king crabs worldwide (Zaklan 2002). Key characteristics of the family include a well-developed rostrum and a triangular carapace (Dawson and Yaldwyn 1985).

Three commercially important species of king crab occur in Alaskan waters, the red king crab, *Paralithodes camtschaticus* (RKC), the blue king crab, *Paralithodes platypus*, and the golden king crab, *Lithodes aequispinus*. At times the golden king crab fishery has been the most important commercial king crab species in Alaska (Shirley and Zhou 1997).


Commercial exploitation of king crab from southeastern Alaska waters was first documented in 1960 (Koeneman and Buchanan 1985). Following the decline of the RKC fishery in the early 1980's fishing effort increased for GKC in southeastern Alaska (Otto 1989, ADF&G 2003). The increase in fishing effort led to an increase in life history
Figure 1.1 Distribution of GKC in the North Pacific Ocean. Circles denote approximate catch locations for golden king crab.
studies (Blau and Pengilly 1994, Blau et al. 1996, Jewett et al. 1985, Koeneman and Buchanan 1985, Love and Shirley 1993, Otto and Cummiskey 1985, Shirley and Zhou 1997, Sloan 1985, Somerton and Otto 1986). In southeastern Alaska the GKC catch has been sporadic, peaking in the late 1980’s, decreasing in the early 1990’s and rebounding in the late 1990’s (Figure 1.2). Golden king crab harvest in other regions of the state has had the same historic trends as southeast Alaska (ADF&G 2003). These large variations in catch, which could be the result of cyclic populations or lack of biological data for managers to make decisions, are a concern. Golden king crab fisheries may have the same precarious future as other crab stocks in Alaska. Knowledge of bathymetric and spatial movement patterns and information on the reproductive biology of GKC would help implement a stock assessment program and management plan, as is the case for RKC in southeastern Alaska (Hebert and Bishop 2002. Introduction to shellfish fisheries. Juneau, AK, Regional Information Report; IJ02-45:1-7). Further, areas used by GKC at sensitive times of their life history could be closed to fishing to protect vulnerable life history stages.

Many marine decapods undertake migrations, which are temporally and spatially linked to basic biological functions, especially feeding and reproduction (Allen 1966). Furthermore, most crustaceans exhibit consistent daily locomotor activities, including feeding excursions, exploratory movements, courtship behavior, and escape responses. These patterns are generally not random, but organized with respect to cues from their environment. Migrations of intertidal and subtidal crustaceans are common and generally
Figure 1.2. Historic harvest record of GKC in Alaska (top panel), and GKC and RKC in southeastern Alaska and Frederick Sound (bottom panel). King crab catch prior to 1972 was a combined harvest of RKC and GKC.
involve seasonal inshore/offshore movements associated with physiological changes (Bainbridge 1961, Allen 1966). Many crustaceans undertake breeding migrations, but the underlying mechanisms are unclear (Stone 1991). Red king crab undertake a seasonal migration associated with their reproductive cycle, but proximate factors involved in the migrational movements are poorly understood (Stone et al. 1992). Both mature male blue crab (Callinectes sapidus) in Chesapeake Bay, Maryland, and mature spider crab (Maja squinado) in Ria de Arousa, Spain, exhibit seasonal migrations from shallow summer habitats to deeper over wintering habitats. Female blue crabs migrate to areas of high salinity rather than deep waters to brood their clutch (Hines et al. 1995).

The maximum distance female RKC moved in Auke Bay and surrounding waters, ranged from 4.2-8.6 km; primiparous females moved significantly further than multiparous females in 11 to 12 months post release (Stone 1991). Further, Simpson and Shippen (1968) reported a maximum annual movement of a male RKC in the Bering Sea to be 426 km. Ninety percent of the crabs that were recaptured moved less than 185 km and 50 percent were captured within 93 km of their release up to seven years post release. Dungeness crab, Cancer magister, annual movements have been measured between 1.5 and 7.2 km in Fritz Cove, Alaska with females moving shorter distances than males (Stone and O'Clair 2001). Diamond and Hankin (1985) studied the movements of adult female Dungeness crabs in northern California using mark-recapture methods and reported 40 percent of relocated crabs moved less than 5 km, however a few moved over 60 km. Movement of 85% of relocated American lobsters, Homarus americanus, near
Cape Cod, MA moved from >10 km to 40 km with four individuals moving more than 100 km (Estrella and Morrissey 1997).

Golden king crab become sexually mature at a carapace width ranging from 92.0 to 120.8 mm for females and from 97.7 to 113.2 mm for males. These sizes are thought to be of a seven to eight year old crab (Loher et al. 2001; Pers. Comm., Tom Shirley, UAF), however there are inconsistencies, particularly in older publications (Otto and Cummiskey 1985, Jewett et al. 1985). Mating occurs over a protracted period extending from at least February to August on the Aleutian fishing grounds and a considerable lag time occurs between hatching and extrusion of the subsequent clutch (Otto and Cummiskey 1985). In Prince William Sound female GKC have extruded eggs in every month of the year (Paul and Paul 2000).

The distribution of GKC larvae in the water column is not known. Golden king crab larvae are lecithotrophic and were demersal, or distributed near the bottom, in laboratory cultures (Shirley and Zhou 1997). However, some researchers have suggested larvae are near the surface in situ, as they are positively phototactic in lab studies (Adams and Paul 1999). No GKC larvae have been reported from plankton studies, supporting the notion that larvae are demersal (Pers. Comm., Tom Shirley, UAF). Shirley and Zhou (1997) reported four zoeal stages and a single glaucothoea stage before a molt to the first crab stage, however all individuals skipped a larval stage, either the 3rd or 4th zoeal stage. Paul and Paul (2001) likewise reported only three zoeal stages and a single glaucothoe stage. The intermolt length of each larval stage is temperature dependent (Paul and Paul 2001). Zoeal 1, Zoeal 2, Zoeal 3 and glaucothoe stages took 12.8-6.2 days, 15.8-6.9 days,
27-10 days, 93–52 days with temperature ranging from 3° to 9° C, respectively (Paul and Paul 2001). Due to the relatively low fecundity compared to other king crab species and large volume of yolk filled eggs (2.39 mm) (Jewett et al. 1985) the reproductive potential for GKC may be considerably less than Paralithodes spp., especially if the reproductive cycle is greater than one year (Paul and Paul 2001). It is not known if GKC reproduce annually or if they exhibit migratory behavior associated with reproduction or other biological needs.

Several parasites have been reported in GKC including rhizocephalan barnacles, notably Briarosaccus callosus which sterilize crab (Meyers et al. 1990) and may have negative effects on the GKC fisheries. The parasite’s sausage-shaped externae reside under the abdominal flap while the internae invade the abdominal cavity of the crab and resemble green root-like structures (Meyer et al. 1990). In addition, eggs of several species of liparid fish are brooded in the gill chambers of GKC and affect survival of the parasitized individual (Love and Shirley 1993, Somerton and Donaldson 1998).

The purpose of the present study was to increase the knowledge of GKC life history through in situ observations of crabs and the monitoring of acoustically tagged individuals over several seasons. Chapter two will focus on movements of acoustically tagged individuals, while habitat associations will be examined in chapter three.
Literature Cited


juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*.


Chapter 2

MOVEMENT OF GOLDEN KING CRAB IN SOUTHEASTERN ALASKA

Prepared for the Marine Ecological Progress Series
Abstract

Golden king crabs (GKC) were collected with commercial crab pots and ultrasonic transmitters were attached to the carapaces of 26 crabs. Movements and depth distribution of male and female crabs were monitored bi-monthly from May 11, 2000 to April 12, 2001 using hydrophones from a surface vessel. A search grid of 709 km² was established to standardize search effort. Male and female GKC were not segregated by depth in mid-May 2000 or in April 2001, but were segregated by depth in July, September, November and February. Crabs did not have site fidelity; initial movements of both translocated (r=0.22, Z=0.46, P=0.64 Rayleigh test) and relocated crabs (r=0.33, Z=0.98, P=0.38) were random. Crabs had seasonal changes in depth distribution, moving to deeper water during late fall and winter and returning to shallower depths during spring. Crabs moved as far as 39 km over one year. Our data suggests if site fidelity exists in this population it is on a scale larger than our study site. Golden king crab may be moving greater distances than could be recorded in our study site or migrational movements may be happening on a longer temporal scale than our study examined.

Introduction

The golden king crab (GKC), Lithodes aequispinus Benedict (1895), is a commercially important crustacean in the North Pacific Ocean. Changes in depth distribution with ontogeny may occur with GKC, but reported depth ranges occupied by particular life stages are inconsistent. Male crabs inhabited shallower depths than
females during July and August along the continental slope of the eastern Bering Sea (Somerton and Donaldson 1998). Catches per unit of effort were higher in August for juvenile males and females at relatively deep depths (550-1005 m) than catch per unit effort for adult females at shallower depths (91-457 m), whereas mature males were most common at intermediate depths (275-350 m) (Blau et al. 1996, Blau et al. 1998). In a deep fjord in northern British Columbia, juvenile male and female crabs were most common at shallow depths (50-150 m) (Sloan 1985a). Little is known of GKC movements in southeastern Alaska. Knowledge of movement patterns in relation to habitat characteristics and seasons for GKC, as is available for red king crab (RKC) (Stone et al. 1992), could enhance the management of the fishery. With knowledge of movement patterns both bathymetrically and spatially and additional information on the reproductive biology of GKC, a stock assessment program and management plan could be established as is the case for RKC in southeastern Alaska (Hebert and Bishop 2002. Introduction to shellfish fisheries. Juneau, AK, Regional Information Report; IJ02-45:1-7). Further, areas used by GKC at sensitive times of their life histories might be closed to fishing to protect vulnerable life history stages.

Information on movement of GKC is limited (Blau and Pengilly 1994, Blau et al. 1998) and only includes release and recapture positions for isthmus-tagged crabs off the Aleutian Islands. Isthmus or spaghetti tags are tags attached around the arthral muscle of a crab and are typically retained through molts, allowing tagged crabs to be recaptured in a commercial fishery.
The purpose of our study was to increase the knowledge of GKC life history through the monitoring of acoustically tagged individuals over several seasons. Specifically, the objectives of the study were to: 1) determine differences in male and female GKC depth distribution in spring, summer, fall and winter; 2) test for site fidelity where site fidelity is defined as the faithfulness of an individual to a measurable area; if site fidelity was present, home ranges of individuals would be calculated; 3) determine if translocated (crabs moved to new location) GKC returned to areas of capture; and, 4) calculate daily movement rates of GKC.

**Materials and Methods**

The study was conducted in Frederick Sound, southeastern Alaska (Figure 2.1), within a commercially fished area for GKC. Fieldwork was conducted between May 11, 2000 and April 12, 2001 (Table 2.1). Adult GKC were captured using baited conical pots with escape hatches closed. The location of each crab collected was measured with a Global Positioning System (GPS) and the crabs were temporarily tagged with color-coded cable ties. In total, 94 crabs were captured from an area of 2.1 km² inside the study site (Figure 2.2). Capture depths ranged between 238 and 444 meters. Crabs were held aboard ship in tanks with flowing seawater until they were measured and tagged. Carapace length and width were recorded to the nearest millimeter with vernier calipers.

Twenty-six crabs were tagged with Sonotronic CHP-87-L/ PRG94HP-L ultrasonic transmitters. The transmitters are 105mm x 6mm, weigh 13g in water (generally less than 2% of the total body weight of the crab), have a range of 3000 m, and
Figure 2.1 Study site in Frederick Sound, Alaska (N57° 22', W134° 20').
Table 2.1 Chronology of crab relocations completed in 2000 to 2002. All surface vessel work was conducted with a high gain hydrophone attached to the vessel and all submersible work was with a low gain hydrophone attached to the vessel.

<table>
<thead>
<tr>
<th>Date of field work</th>
<th>Surface vessel days</th>
<th>Submersible / visually observed Tagged</th>
<th>Surface vessel Tagged</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 11-19, 2000</td>
<td>8</td>
<td>8</td>
<td>84</td>
</tr>
<tr>
<td>July 5-8, 2000</td>
<td>4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sept. 29-Oct. 1, 2000</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nov. 7-11, 2000</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Feb. 1-3, 2001</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 2001 (Fishery)</td>
<td>N/A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>April 11-12, 2001</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March 2002 (Fishery)</td>
<td>N/A</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
an 18-month life expectancy. The crabs selected to be tagged with sonic transmitters were new-shelled, minimally damaged and with few missing appendages. Six females (the only six collected) and 20 males, with carapace lengths ranging from 125-150 mm and 125-180 mm, respectively, received transmitters (Table 2.2). The tags were glued to the carapace of crabs using the methods of Stone et al. (1992). The remaining 68 crabs captured were tagged with isthmus tags (Floy spaghetti tags) and released overboard using the method of Simpson and Shippen (1968). Isthmus tags are typically retained through a molt (Koeneman and Buchanan 1985).

A manned submersible was used to release the 26 sonically tagged crabs between depths of 237 and 309 meters at six different sites on May 13-14, 2000. The submersible was used to obtain exact release positions and minimize stress and injury to the crabs; crabs did not have to fall through the water column. Crabs were released at either their original capture site (relocated, 17 crabs), or at different locations (translocated, nine crabs) (Figure 2.2, Table 2.2). Unique habitat features characterized each release site and tagged crabs were chosen at random to be translocated or relocated at each site.

The habitats, number and sex of crab at the release sites are reported in Table 2.3 and mapped in Figure 2.2. The 26 crabs were tracked over the ensuing seven days using low-gain hydrophones attached to the DELTA submersible and high-gain hydrophones attached to a surface vessel in conjunction with a receiver (Sonotronic model USR-5W). The acoustically tagged crabs which remained in a designated search grid (709 km²) over the entire length of the study (Figure 2.3), were relocated using two high gain hydrophones attached to a surface vessel in 2000 from July 5-8, September 29-October 1,
Figure 2.2. Study site including bathymetry, locations of capture and release sites for the 26 acoustically tagged golden king crab. Location of study area is in Frederick Sound; see Figure 2.1.
Table 2.2. Tag number carapace length, capture site, date of capture and release for 26 golden king crabs with ultrasonic transmitters.

<table>
<thead>
<tr>
<th>Tag No.</th>
<th>Carapace Length (mm)</th>
<th>Capture site*</th>
<th>Date of capture</th>
<th>Date of release</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Translocated Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-5-5</td>
<td>166</td>
<td>4</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>3-4-8</td>
<td>170</td>
<td>4</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>11-5</td>
<td>131</td>
<td>4</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>9-7</td>
<td>130</td>
<td>5</td>
<td>5/12/00</td>
<td>5/14/00</td>
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<tr>
<td>2-6-7</td>
<td>182</td>
<td>5</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>4-6-5</td>
<td>149</td>
<td>5</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>10-6</td>
<td>154</td>
<td>5</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>2-2-2-8</td>
<td>170</td>
<td>5</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>2-9-4</td>
<td>156</td>
<td>6</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>2-2-5-5</td>
<td>172</td>
<td>6</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>3-6-6</td>
<td>180</td>
<td>6</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td>3-7-5</td>
<td>125</td>
<td>6</td>
<td>5/12/00</td>
<td>5/14/00</td>
</tr>
<tr>
<td><strong>Translocated Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2-8-5 (2-7-6)</td>
<td>136</td>
<td>3</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>8-8</td>
<td>125</td>
<td>3</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>15-15B</td>
<td>131</td>
<td>3</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
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<td>3-8-4</td>
<td>125</td>
<td>3</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>3-3-9</td>
<td>150</td>
<td>3</td>
<td>5/12/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td><strong>Relocated Males</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>2-7-6</td>
<td>171</td>
<td>1</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>4-4-7</td>
<td>142</td>
<td>1</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>2-4-5-3</td>
<td>160</td>
<td>1</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>2-4-9</td>
<td>182</td>
<td>1</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>2-5-8</td>
<td>177</td>
<td>1</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>2-2-4-6</td>
<td>171</td>
<td>2</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>3-5-7</td>
<td>165</td>
<td>2</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td>4-5-6</td>
<td>168</td>
<td>2</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
<tr>
<td><strong>Relocated Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15-15A</td>
<td>140</td>
<td>2</td>
<td>5/11/00</td>
<td>5/13/00</td>
</tr>
</tbody>
</table>

* Refer to Figure 1.2 for location of capture sites.
Table 2.3. Habitat characteristics at the six release sites, and the number of crabs released at each of these sites. Sites are mapped in Figure 2.2.

<table>
<thead>
<tr>
<th>Site</th>
<th>Slope</th>
<th>Habitat characteristics</th>
<th>Depth (m)</th>
<th>GKC released</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>20° to 30°</td>
<td>boulder field adjacent to steep wall with ledges</td>
<td>-237 m</td>
<td>Relocated 5 males</td>
</tr>
<tr>
<td>2</td>
<td>0° to 10°</td>
<td>sediment-laden cobbles</td>
<td>-309 m</td>
<td>Relocated 3 males</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Relocated 1 female</td>
</tr>
<tr>
<td>3</td>
<td>75° to 90°</td>
<td>sloped wall with ledges and sediment floor below the wall</td>
<td>-274 m</td>
<td>Relocated 3 females</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Translocated 2 females</td>
</tr>
<tr>
<td>4</td>
<td>10° to 20°</td>
<td>sloped cobble and boulder field on bedrock</td>
<td>-252 m</td>
<td>Translocated 3 males</td>
</tr>
<tr>
<td>5</td>
<td>30°</td>
<td>complex cobbles and shell debris</td>
<td>-237 m</td>
<td>Relocated 5 males</td>
</tr>
<tr>
<td>6</td>
<td>0°</td>
<td>silt and sediment</td>
<td>-283 m</td>
<td>Translocated 4 males</td>
</tr>
<tr>
<td></td>
<td></td>
<td>seafloor; no hard substrate present</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.3. Search grid used to standardize effort of tracking GKC. Each station is no more than 2.15 km from another. The transmitter range is 3000m. The search area was 709 km². Location of study area is in Frederick Sound; see Figure 2.1.
November 7-11, and in 2001 from Feb. 1-3, March (during the commercial fishery), and April 11-12 (Table 2.1). A search grid was established to standardize effort during all relocation trips and to incorporate negative data (absence of crabs) into the analysis. The grid was designed so all suitable habitats were surveyed at 0.75 times the distance of the transmitters range. Signals are transmitted 3000 m by tags; survey stations were a maximum of 2.15 km apart (Figure 2.3). Position, depth and time were recorded for each relocated crab using a Differential Global Positioning System and boat-mounted depth sounder.

Fishermen participating in the commercial fishery, which begins on February 15 and typically extends for 2.5 weeks or until the guideline harvest level is met, were informed of the study by personal contact and posters located at all major ports and processors. Fishermen were asked to record position, time and depth of any tagged crabs caught. Two sonically tagged crabs were caught in the 2001 fishery and their positions were included in the movement statistics. One additional crab was caught in the 2002 fishery and was not included in any analysis but is reported. One of the crabs in the 2001 fishery was a female (not a legal catch by the fishery) and was re-released. Seven isthmus tagged crabs were also caught in the fishery in 2001 and 2002 and positions are reported.

Data were incorporated into a Geographic Information System (GIS) ArcView database. Spatial movement and depth distribution trends were explored with ArcView (ESRI 1999). Circular statistics were used to determine if there was any directional movement of either translocated or relocated crabs using the relocation data from the
May 2000 sampling and a Raleigh Z-test (Zar 1999). This technique has been used to determine directional movement of other crustaceans (Boles and Lohmann 2003).

A Monte Carlo random walk site fidelity test (Spencer and Cameron 1990) was conducted. The Animal Movement Extension to ArcView (AMAE) was used to conduct the test (Hooge et al. 1999, ESRI 1999). The AMAE program modifies the method by Spencer and Cameron (1990) by using the order of distances in the original movement path rather than the bootstrapped movement distances; the modification controls for sequentially dependent movement patterns. AMAE also allows for constraining the random walks to areas actually occupied by the animal (animals will not walk over islands or unsuitable habitat). Typically 25 relocations points per individual are needed to test for site fidelity (Hooge et al. 1999). Our study had substantially fewer points for each tagged crab and results from the site fidelity analysis should be viewed with caution (Table 2.1). For each crab 100 random walks were generated and the null hypothesis was tested; observed movement was random. Depth distributions of the tagged female and male crabs were tested for difference from sampling period to sampling period (approximately bimonthly) with a one-way ANOVA (Stone et al. 1992, Zar 1999).

The accuracy of positions of tagged crabs was determined by blindly estimating the position of a transmitter lowered to the sea floor between depth of 107 and 198 meters using hydrophones from a surface vessel. Estimated positions were then compared with the known positions. The procedure was repeated and an average percent deviation was found to be 0.07. Error increased with the depth of transmitter and proximity to hard substrate where echoes were observed. Stone (1991) estimated the error associated with
location as ± 30.3 m with similarly designed receiving equipment. Stone’s (1991) error is less than our calculated error but he was working in shallower water and did not have GPS; his position determinations were made via triangulation. Differential GPS has an accuracy of 5.4 m and the error was assumed to be insignificant in determining positions of sonically tagged GKC.

Results

One in particular of the 26 tagged crabs was relocated during every sampling period and on average crabs were only located on two out of five sampling trips. Five crabs were assumed to be unsuccessfully tagged, because the tags remained stationary or signals were never received. Explanations could be molting, death, tag loss or tag failure. Two sonically tagged crabs were caught in the 2001 fishery and a third was caught in the 2002 fishery with an apparent scar from a sonic transmitter. The latter crab was identified from a secondary tag (colored cable tie) inadvertently left on the crab. Data from the two crabs caught in the 2001 fishery were included in the depth distribution analysis but not in any movement analysis because of the lack of precision of the fisherman’s positions. Five other crabs were only located once. Since a designated search grid was established and acoustic searches were thorough in all trips except September 2000 (due to weather conditions), unlocated crabs were assumed to have moved out of the designated study site or transmitter failure was assumed. Our study was the first to use Sonotronic transmitters at depths greater than 300 meters.
Movements of many sonically tagged GKC were greater than the search grid. Seven isthmus tagged crabs caught by commercial fisherman led to interesting insights of GKC movements. Several crabs were relocated early in the study and were not located again until the end of the study. Crabs were assumed to have moved out of the study grid and then returned. The assumption was supported by the catch of one sonically tagged and four isthmus tagged crabs in the commercial fishery outside of the search grid, one to two years post release. Three additional isthmus tagged crabs were caught within the search grid in the 2002 fishery. The positions of all commercially caught crabs are in Figure 2.7. The furthest movement from release was an isthmus tagged crab, which was caught 25 km outside of the designated search area. Of the crabs retained in the commercial fishery in 2001 none had molted; all crabs retained in the commercial fishery in 2002 had molted (Appendix 1).

No evidence of site fidelity was found. The null hypothesis could not be rejected for any crab movement path. Site fidelity is a precursor and must exist prior to being able to test for home ranges, thus, home ranges were also indeterminable.

Crabs dispersed randomly with time from their original release sites without directionality (Figures 2.4-2.7). Minimum straight-line distance traveled varied from 1.5 km to 18.6 km, averaging 11.5 km for sonically relocated crabs in the 11 months post release. Four isthmus tagged crabs were caught outside of the search area, with one moving 39 km from its release site and 25 km out of the search grid (Figure 2.7). No movement patterns were detected. Bi-monthly locations and distance from release vectors are in Figures (2.4–2.7) for the seven relocations.
Figure 2.4. Relocation points and movement vectors of GKC relocated during May and July 2000. Location of study area is in Frederick Sound; see Figure 2.1.
Figure 2.5. Relocation points and movement vectors of GKC relocated during September and November 2000. Location of study area is in Frederick Sound; see Figure 2.1.
Figure 2.6. Relocation points and movement vectors of GKC relocated during February and April 2001. Location of study area is in Frederick Sound; see Figure 2.1.
Figure 2.7. Relocation points and movement vectors of GKC relocated in the 2001 and 2002 southeast GKC fishery. Location of study area is in Frederick Sound; see Figure 2.1.
Eight sonically tagged crabs were relocated during the submersible research in May, 2000 (Table 2.1) when high-resolution movements were measured over eight days. Crabs were confirmed to move a maximum distance of 1174 m on a horizontal axis and increase 21.8 m in depth from 12-19 May 2000 from positions obtained at a minimum of every other day (n=12 crabs). The average horizontal movement was 560 m and a mean rate of daily movement of 112 m per day was calculated for eight days in May 2000. The initial movements (May 2000) of both relocated and translocated crabs were random (r=0.22, Z=0.46, P=0.64 for relocated and r=0.33, Z=0.98, P= 0.38 for translocated, Raleigh z-test, respectively). Movement of translocated crabs did not differ from those of crabs returned to their original collection site (ANOVA, P=0.47).

Crabs continued to disperse from their original locations throughout the study. The mean distance from release sites increased from May until November 2000, excluding September when the entire search grid could not be sampled due to an early winter storm. February and April 2001 sampling also had average distances from release site being greater than 6 km and distance from the previous location were greater than in any other months (Table 2.4).

Average distance from release site, mean distance moved from previous location, and a daily rate of movement are reported for female and male crabs and all crabs combined (Table 2.4). Crabs moved distances and rates that would allow them to move away from and return to the study site on a regular basis (Table 2.5).

No trends in changes in depth of tagged crabs were observed during the initial sampling period from May 11-19, 2000 (Table 2.4). However, a downward trend
Table 2.4. Summary statistics from surface and submarine relocations of depth (m), vertical movement (m) and daily vertical movement rate (m/d) of golden king crab from May 2000 to April 2001 in Frederick Sound. Depths are reported as means of all crabs, female, male, translocated and relocated crabs. Sample size (repositioned crabs) is noted in parenthesis. Note: *Five crabs were unsuccessfully tagged. **Translocation or relocation was assumed to be of no affect in 2001.

<table>
<thead>
<tr>
<th></th>
<th>May</th>
<th>July</th>
<th>Sept.</th>
<th>Nov.</th>
<th>Feb.</th>
<th>Fish</th>
<th>April</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Average depth (m)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All crabs tagged (26 crabs)</td>
<td>-264 (21)*</td>
<td>-264 (8)</td>
<td>-333 (4)</td>
<td>-344 (13)</td>
<td>-375.3 (6)</td>
<td>-314 (3)</td>
<td>-227 (5)</td>
</tr>
<tr>
<td>Females (6 crabs)</td>
<td>-281 (5)</td>
<td>-287 (2)</td>
<td>-416 (2)</td>
<td>-407 (2)</td>
<td>-403 (2)</td>
<td>-364 (1)</td>
<td>-232 (3)</td>
</tr>
<tr>
<td>Males (20 crabs)</td>
<td>-258 (17)*</td>
<td>-257 (6)</td>
<td>-278 (2)</td>
<td>-334 (11)</td>
<td>-364 (4)</td>
<td>-289 (2)</td>
<td>-224 (2)</td>
</tr>
<tr>
<td>Translocated (9 crabs)</td>
<td>-263 (7)</td>
<td>-268 (4)</td>
<td>-382 (3)</td>
<td>-326 (9)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Relocated (17 crabs)</td>
<td>-266 (14)</td>
<td>-236 (3)</td>
<td>-261 (2)</td>
<td>-305 (7)</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td><strong>Mean vertical movement (m)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>All crabs</td>
<td>1.1 (20)</td>
<td>-3.9 (7)</td>
<td>-80.0 (1)</td>
<td>-41.0 (3)</td>
<td>-15.4 (5)</td>
<td>+55.4(1)</td>
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<tr>
<td><strong>Mean rate (m/day) of vertical movement</strong></td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>All crabs</td>
<td>0.52 (20)</td>
<td>-0.08 (7)</td>
<td>-0.95 (1)</td>
<td>-0.33 (3)</td>
<td>-0.19</td>
<td>+1.85 (1)</td>
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Table 2.5. Summary statistics of minimum distance moved (m) and horizontal movement rate (m/d) traveled by adult male and female golden king crab from May to November in Frederick Sound. Distances are reported as means. Sample size (number of crabs repositioned) is noted in parenthesis.

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Mean distance (m) from</td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>release</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>497(15)</td>
<td>3988(6)</td>
<td>1495(2)</td>
<td>7558 (11)</td>
<td>1054 (3)</td>
<td>9395 (2)</td>
</tr>
<tr>
<td>Female</td>
<td>443 (5)</td>
<td>2485(2)</td>
<td>1660(2)</td>
<td>9090 (2)</td>
<td>3590 (3)</td>
<td>4423 (3)</td>
</tr>
<tr>
<td>All Crab</td>
<td>489(20)</td>
<td>3613(8)</td>
<td>1578(4)</td>
<td>10248(13)</td>
<td>7065 (6)</td>
<td>6412 (5)</td>
</tr>
<tr>
<td>Mean distance (m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>location</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>3791(6)</td>
<td>(0)</td>
<td>3340(2)</td>
<td>10575(3)</td>
<td>4704 (2)</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>1726(2)</td>
<td>1285(1)</td>
<td>13743(1)</td>
<td>11047(2)</td>
<td>6457(2)</td>
<td></td>
</tr>
<tr>
<td>All Crab</td>
<td>3275(8)</td>
<td>1285(1)</td>
<td>6807 (3)</td>
<td>10764 (5)</td>
<td>5580 (4)</td>
<td></td>
</tr>
<tr>
<td>Daily rate of movement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(m/day) since previous</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>relocation</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>85.5 (6)</td>
<td>(0)</td>
<td>65.4(2)</td>
<td>36.0 (3)</td>
<td>14.1 (2)</td>
<td></td>
</tr>
<tr>
<td>Female</td>
<td>53.2 (2)</td>
<td>40.7 (1)</td>
<td>58.3 (1)</td>
<td>38.6 (2)</td>
<td>19.4 (2)</td>
<td></td>
</tr>
<tr>
<td>All Crab</td>
<td>76.3 (8)</td>
<td>30.9 (1)</td>
<td>64.1(3)</td>
<td>26.8 (5)</td>
<td>19.3 (4)</td>
<td></td>
</tr>
</tbody>
</table>
Figure 2.8. Average depth distributions of sonically tagged golden king crabs in Frederick Sound, Alaska. Depths of crabs that were relocated multiple times were averaged for the May sampling period. Numbers adjacent to symbols represent numbers of crabs relocated.
occurred as the summer and fall progressed. Crabs were found at deeper depths throughout the winter before they returned to relatively shallower waters in spring (Figure 2.8, Table 2.4). Neither sex inhabited a significantly different depth in May than in July (P=0.95 and P=0.94, for females and males, respectively) or in the September to November relocations (P=0.97, P=0.94, respectively) when tested for mean depth by sexes. However, when females and males where pooled between months (May, July= spring/summer) and (September, November = fall) females inhabited significantly deeper depths (P=0.001) and males did not (P=0.307). The pooling approach was conducted due to a low numbers of relocations in July and September (Table 2.1). Males inhabited significantly deeper depths in February than November, however females did not (P=0.047 and P=0.97 respectively). Both male and female crabs did not inhabit significantly shallower depths between the February and April sampling (P=0.152, 0.117, respectively), however both female and male crabs inhabited shallower depths and relatively the same average depth. The mean depth for females was greater than the mean depth for males in all months, but was not significant (P=0.21).

Discussion

Male and female crabs were not segregated by depth in May, and many mating pairs were observed from the submersible (Chapter 3). In July, September and November tagged female crabs inhabited deeper depths than tagged males. However, during February they were found at deeper depths before both sexes returned to shallower depths in April. Our results are consistent with reports of segregation by depth between sexes
(Sloan 1985a), at least for a portion of the year. However, our numbers must be viewed with caution, as the number of crabs relocated in September, February and April was low (n=4, n=6 and n=5, respectively). Crabs observed mating in May could have ceased mating in July and September and returned to the depths inhabited when not mating. The upward movement of crabs between the February and April sampling might be explained by crabs moving from brooding and feeding grounds at depth to shallower areas preferred for mating.

There was no evidence of site-fidelity or home ranges. The infrequency of relocations over the sampling trips may confound these results; however, if GKC have home ranges, they are larger than the designed search grid (709 km²). There may be some degree of site fidelity in the Frederick Sound population; however, the small number of relocations precluded statistical rigor. Alternate explanations are that GKC are nomadic in nature without home ranges, or that migration cycles are temporally longer than this study.

For the time period sampled, a clear trend existed of increasing distance moved from the release site and crabs did not appear to be returning to sites where they were captured (for translocated crabs). Possibly depth and not location is an important factor for GKC reproductive biology. Segregation by depth of different life history stages in populations of GKC has been reported in British Columbia and the Bering Sea, however the reports are inconsistent (Sloan 1985b, Somerton and Donaldson 1998).

Habitat preferred for mating may be located at depths other than those used typically for feeding and brooding (Sloan 1985a), or crabs may move to a reproductive
refuge to mate to avoid predation or cannibalism of the soft-shelled females. Our results suggest crabs may be seeking out complex rocky habitats to mate during late spring, and once at these steep, complex habitats, movement is decreased compared with the times GKC are at deeper depths (Chapter 3). Other crab species have been reported to seek out refuges for molting (Stone 1999), the mating time for female GKC. Once mating activity ceases the crabs may return to deeper habitats in late summer, which may be more suitable for feeding or egg development. An alternate explanation is that mating pairs occur throughout the year.

Dispersal patterns seem to be bimodal in the Frederick Sound population of GKC, with many individuals moving short distances and some moving long distances. An explanation may be a limited availability of optimum habitat. Once the resources of a habitat become limiting, crabs may be dispersing to find other preferred habitats. Both the distributions of patches of suitable habitat and the frequency of change in a habitat may affect the need or advantages of long-distance dispersal for adults, which may not be obtainable in the larval life history of GKC. Some tagged crabs dispersed widely from the region of release; the large movements suggest GKC in southeastern Alaska may constitute a single population.

The tagging procedure and carrying of tags were assumed to not affect crab behavior; sonic tags similar to the ones used in this study did not affect female red king crab behavior in the laboratory (Stone et al. 1992). However, crab movements may not have represented natural movements because of the stress incurred by crabs during capture, tagging, and release.
Seasonal bathymetric movements have been documented in snow crab, *Chionoecetes opilio*, in a Newfoundland fjord (Taylor et al. 1985). In RKC a "spawning migration" typically begins in November, when male crabs followed by female crabs move from deeper to shallower depths, where they reside for several months (November to May) in shallow (20-30 meters) bays. During time at shallow depths females hatch eggs (first week of March to April), molt, court, and mate (within 9 days of molting) before returning to intermediate depths in June and July where egg extrusion occurs (Stone et al. 1992, Shirley and Shirley 1989, Z. Hoyt personal observations). The scenario concluded for RKC is speculative for GKC based on the limited data; further study is needed to confirm the possible life cycle.

The commercial crab fishery inadvertently translocates sublegal-sized male and female crabs some distance by returning them to sea while vessels are underway. Some concerns have existed about the effects of translocation of sublegal and female crabs to unsuitable habitats. Spiny lobsters in the Florida Keys use magnetic maps to migrate to their original location if translocated to new sites (Boles and Lohmann 2003). The translocation of crabs over short distances in the experiments in May resulted in random crab movements. Movements of translocated crabs did not differ from movements of crabs returned to their original release site.

Golden king crab may not have a home range, or may be unable to navigate back to a familiar area once they are some distance away from this area. We could not test if home ranges were present in the Frederick Sound population because 25 to 100 location
points are needed to estimate a home range for a single animal depending on the type of test being conducted (Spencer and Cameron 1990, Worton 1987).

Stocks of GKC may not be vulnerable to serial depletion like other crustacean stocks due to the random nature of their movements and sufficiently large degree of movement (Orensanz et al. 1998). Golden king crab in this study moved distances comparable to red king crab in the Bering Sea (Simpson and Shippen 1968) but to a much lesser degree than American lobsters in New England (Estrella and Morrissey 1997) and Dungeness crab on the west coast (Stone and O’Clair 2001, Gotshall 1978) all of which are vulnerable to serial depletion (Orensanz et al. 1998, Estrella and Morrissey 1997). In contrast, these other studies documented seasonal movement with the ability of the individual to navigate, while our findings found that GKC do not have seasonal movements. For other species which move longer distances, serial depletion may have a negative impact on the fishery if the intensity and geographic scale of the fishery are similar in scale to the movements of the species, e.g., Red king crab in the Bering Sea (Orensanz et al. 1998).
Literature Cited


Loher, T., D.A. Armstrong, and B.G. Stevens. 2001. Growth of juvenile red king crab (*Paralithodes camtschaticus*) in Bristol Bay (Alaska) elucidated from field


Chapter 3

HABITAT UTILIZATION BY GOLDEN KING CRAB IN SOUTHEASTERN ALASKA

Prepared for the Journal of Crustacean Biology
Abstract

The distribution of golden king crabs (GKC), *Lithodes aequispinus*, on different habitat types were recorded with video from a manned submersible during May, 2000 in Frederick Sound, Alaska. Thirty-seven dives were made at six locations in Frederick Sound, sampling 18 km at depths between 191 and 354 m. A habitat affinity index (HAI) and compositional analysis were used to determine selection of habitat for both solitary and courting GKC. Crabs selected steep, complex habitat with a hard substrate; few were on flat, soft substrate. Seventeen pairs of courting crabs were observed during dives; 13 were on or underneath intermittent boulders, 3 were on vertical walls and 1 was associated with a continuous boulder field. The habitats selection rankings were calculated using compositional analysis as follows: 6) intermittent cobble, 5) intermittent boulder, 4) wall, 3) pebble, 2) boulder, 1) cobble and 0) soft sediment for solitary GKC; and 2) wall, 1) intermittent boulder, and 0) boulder for courting pairs. No mating pairs were observed on soft sediment, pebble, cobble, or intermittent cobble and only seven solitary crabs where associated with a soft substrate. Golden king crab were more common at shallower depth than at deeper depths during mid-May.

Introduction

The fishery for GKC is larger than the red king crab fishery in southeastern Alaska, accounting for an average annual catch of 0.24 million kg, and an average of 2.97 million kg statewide in the last 10 years (Alaska Department of Fish and Game 2003). Paradoxically, there is an absence of information on GKC biology, particularly regarding
larval distribution and reproductive biology. Further, there is little information concerning habitat affinities and the physical and biological characteristics of habitats utilized by GKC. The lack of basic knowledge is surprising considering GKC have been commercially exploited since the early 1960's in southeastern Alaska (Koeneman and Buchanan 1985). The life history of GKC is more poorly understood than the life history of other crab species because perhaps GKC inhabit greater depths and rocky substrate, which preclude trawl sampling (Blau and Pengilly 1994). Though GKC are known to inhabit rocky substrate and depths greater than red king crab (RKC), specific habitat associations have not been reported. Further, little is known of the habitat types used by different life history stages, no studies have addressed the distribution of larvae and juveniles, nor are there any in situ observational studies of GKC.

Knowledge of distribution, abundance and habitat characteristics of deep-water, benthic crabs in southeastern Alaska is critical for wise management. Of particular importance is the identification and protection of areas for critical life history stages, such as reproductive activities. If the depth distribution and timing of reproduction for GKC or the habitats in which mating occurs was determined, the information could be used to protect the species during the GKC fishery in southeastern Alaska and other GKC fisheries in the North Pacific.

A method to quantify the use of resources in relation to their availability was developed by Ivlev (1961). Preference or electivity indices seek to compare frequency of the use of a resource with the availability of the resource in an animal’s environment by representing the data as a single index value. Many indices have received attention,
especially with regards to analysis of food habits of terrestrial vertebrates and marine fish (Morrison 1982, Strauss 1979). These indices have also been applied to vegetation and physical measures of the environment (Morrison et al. 1998). Ivlev's index of electivity has been used to assess preference of habitat types by estuarine fish (Monaco et al. 1998), and small mammals (Choromanski-Norris et al. 1989), and has been termed Habitat Affinity Index (HAI). While the HAI graphically represents the use of a resource, it does not rank or present statistical validity. Therefore compositional analysis was used to rank habitat preference for solitary and courting GKC in Frederick Sound.

Habitat quality, and the abundance of preferable habitat types may be significant environmental determinants of distribution and abundance of GKC. Characterizing and quantifying elements of suitable habitat, such as depth distribution, substrate type, slope, and the presence or absence of GKC are important considerations for evaluating the effectiveness of spatial and temporal fishery refuges as marine reserves. The purpose of this study was to characterize GKC habitat in southeastern Alaska, with the following specific objectives: 1) observe GKC reproductive behavior and habitat use in situ with a manned submersible during mid-May; 2) determine what habitat types are most important for solitary and courting crabs and search for evidence of aggregations; and 3) quantify physical or biological characteristics of GKC habitat.

**Materials and Methods**

A two-person research submersible, *DELTA* (Delta Oceanographics Inc.), was used to assess GKC assemblages and associated habitats in Frederick Sound, in May
2000 (Figure 3.1). Frederick Sound is the largest protected body of water in southeastern Alaska with depths greater than 600 meters (Figure 3.1), and is an important area for the southeast GKC commercial fishery (Pers. comm. Ladd Norheim, GKC commercial fisherman, F/V Frigland, Petersburg, Alaska). The site was selected due to the relatively high abundance of GKC coincident with depths in which the manned submersible DELTA could be safely operated. Within the study area, six sites were chosen with appropriate depths for operation of the submersible. Each site was unique (Table 2.3).

The six sites chosen to conduct dives were the same as the release sites in chapter 2 (Figure 3.2). In total, 37 dives were made, with at least two dives conducted at each site. Forty-six hours were logged at depths between 191 and 353 meters from May 12-19, 2000. Eight dives were made to release crabs; 26 dives were made to locate and observe behavior of tagged and untagged crabs; and three dives were made along transects in habitats suitable for GKC.

DELTA houses a pilot and observer and has a working depth limit of 360 meters. Search patterns (referred to as transects) were conducted and adapted onboard as the dives were underway. Some dives were near straight line transects while others focused on specific habitat types or observations (Figures 3.3-3.7), however, some dives or portions of dives were not linear because the topography precluded a straight line; more commonly either the scientist or pilot onboard pursued observations of habitats or sonically tagged crabs. The R/V Medeia, a 34-meter vessel chartered from the Alaska Department of Fish and Game, was the support ship.

Habitat and associated fauna were videotaped continuously with a self-focusing
Figure 3.1 Study site in Frederick Sound, Alaska. (N57° 22', W134° 20').
Figure 3.2. Tracks of submersible dives conducted at six sites in Frederick Sound, Alaska.
Figure 3.3. Dive tracks conducted at dive sites 1 and 2. A DELTA dive number accompanies each track.
Figure 3.4. Dive tracks conducted at dive site 3. A DELTA dive number accompanies each track.
Figure 3.5. Dive tracks conducted at dive site 4. A DELTA dive number accompanies each track.
Figure 3.6. Dive tracks conducted at dive site 5. A DELTA dive number accompanies each track.
Figure 3.7. Dive tracks conducted at dive site 6. A DELTA dive number accompanies each track.
video camera attached to the starboard side of the submersible facing perpendicular to the bow of the vessel. Photographs were taken from a 35mm camera mounted aft of the video camera and operated by the observer. All video footage was recorded onto "Hi-8" video onboard the submersible and an audio recording of the observer was recorded on the videotape. Two parallel lasers were mounted on either side of the external video camera at the fixed distance of 20 cm apart. The laser spots projected onto the seafloor or encountered organisms and were visible to the observer and were recorded onto the videotape. The lasers were critical in accurately estimating substrate, visibility, and slope. Other physical variables were recorded on the tape either continually (depth, height off bottom, and time) or at some interval (temperature, pH, conductivity, salinity, dissolved O$_2$, depth) and are reported (Appendix 2-7).

An acoustic track-point system and a differential global positioning system (DGPS) were used on board the support vessel to record the underwater location of the submersible. Positions were recorded at 30 second intervals during all dives and imported into a geographic information system (GIS) database in which each transect was mapped (Figures 3.3-3.7). The time of the position recorded was used to correlate the position of the submersible to the video observations.

The observer immediately interpreted video after each dive on board the support vessel. The video was interpreted in the lab in more detail at a later date. Substrate type, slope, silt load, depth and biological data were recorded. The habitat information was included in the GIS databases of each dive as attributes. Visibility was estimated and each track point was linked to the visibility value to provide an area surveyed. Substrate
type was determined by estimation of particle size, which followed the Wentworth scale when applicable, at each 30-second interval. These included soft substrate (including sand, silt, possibly clay and granules, <4 mm particle size), pebble (4-64 mm), cobble (64-264 mm), boulder (>264 mm), and wall (near or vertical bedrock). Two other types of substrate were classified as intermittent cobble and intermittent boulder. The last two substrates were defined as cobble or boulder in sparse proximity to one another with soft sediment lying between. Slope was classified into 8 categories including flat (0°), 1°-10° slope, 11°-20° slope, 21°-30° slope, 31°-40° slope, 41°-50° slope, 50°-75° slope, and walls (>75°). Slope was estimated by determining the distance of the 20 cm laser separation on the video screen and the distance off the bottom of the submersible. All species observed from the video were identified to the lowest possible taxon or placed in broad categories when identification was not possible. The presence or absence of a species was recorded for each 30-second record (counts of individuals other than crabs were not made). Finally, the presence or absence of GKC was recorded for each record, including sex and reproductive state when distinguishable. The database was sorted to remove records of no visibility, records with errors in the track point location, or records when the submersible was stationary.

The data from all dives were then combined and the following equation was used to determine selectivity of one habitat type over another for noncourting and courting GKC:
\[ HAI = \frac{(C - S)}{(C + S)} \]

where,

\( HAI \) = Habitat Affinity (electivity) Index,

\( C \) = Relative number of crab on a substrate type,

\( S \) = Relative substrate type available.

The HAI technique is commonly used to determine prey selectivity in ecological studies as Ivlev's electivity index (Ivlev 1961) and is also useful in determining preference of habitat type which may directly relate to prey selection for benthic species (Baxter and Hauer 2000, Monaco et al. 1998, Morrison et al. 1998, Gilroy et al. 1992, Jacobs 1974, Choromanski-Norris et al. 1989). If the animal's relative use of that habitat type and the relative availability of that item in the environment are equal for all items, then the animal is choosing the items randomly. If the relative availability of that item in the environment and the relative use of that item differ, the animal is assumed to be either avoiding (a negative index value) or selecting (positive value) an item (Morrison et al. 1998). The HAI technique was used to determine slope selectivity of non-courting and courting king crabs by replacing substrate type with slope type in the HAI equation.

The notion of “preference” of a habitat type is useful as long as habitat types are ranked from least to most preferred. To rank the habitat types in order of selective importance a compositional analysis technique developed by Aebischer et al. (1993) was conducted. This technique was conducted using the program Resource Selection © 1999 developed by Leban (1999). Further, it was determined whether slope, substrate and the
presence of courting and solitary GKC were correlated using Pearson's correlation coefficient's to test one variable against another. Differences in habitat preference of courting and solitary crabs were explored using a Chi-square (goodness of fit) test to determine if there was a difference between solitary and courting crab habitat distribution (Zar 1996).

Distances traveled of the submersible during each dive were calculated using GIS. The distances were grouped into depth intervals of 10 meters and a sighting per meter traveled via submersible at each depth interval was calculated and is reported.

Other relevant observations included observations of GKC coincident with other taxa and are reported. The results of the study are discussed in the context of GKC life history and fisheries management.

Results

Ninety-two GKC were observed from the submersible in May, 2000. Of the ninety-two crabs, eighty-four were untagged. Crabs were tagged to conduct simultaneous experiments presented in Chapter 2. Untagged crabs were observed during submersible dives between 211 m and 342 m depth; not all depths were sampled equally. The average depth surveyed was 274 m and the greatest distance traveled by the submersible during a single dive was 2877 m at a depth of 290 to 300 m (Figure 3.8). Thirty-seven dives were made with 18,457 m traveled at depth. The depth limit of the DELTA submersible is 360 m.

Seventeen courting pairs were documented from 12-19 May 2000. Male GKC attend females prior to their molting in a hand-holding behavior, but may also hold
Figure 3.8. Depth distribution of distance traveled (meters) by the submersible \textit{DELTA} in Frederick Sound. The average depth of the submersible was 274 meters. The depth limit of the submarine is 360 meters (Entire distance traveled = 18,457 meters).
females under their abdomen to carry them. These premating activities are collectively referred to as courting. During mating the female is held by the male, abdomen to abdomen; discerning courting from mating is difficult. Usually the male is considerably larger than the female. In many cases, a female carried by a male was not noticed by the submersible observer but was later detected from videotape reviews. Mating pairs represented 40% of all observations of untagged crabs during submersible dives in May. Of the 17 pairs observed, 13 were on or underneath boulders, 3 were on vertical walls and 1 was associated with a cobble substrate. No mating pairs were observed on soft flat bottom absent of rocks and only seven individual crabs where associated with a soft substrate.

No segregations of sexes or reproductive stages were observed with respect to depth (Figure 3.9) during May 2000. Courting pairs and solitary crabs were more commonly encountered in shallower depths than deeper depths. Due to the submersible depth limit of 360 m, our observations were limited to a maximum depth of 353 m. The depth of the different substrate types were similar to one another (Appendix 8). Crabs were observed on slopes from 0 to 90 degrees, with the highest abundance associated with vertical walls and moderately-sloped boulder fields (Figures 3.10, 3.11). Crabs were commonly observed in crevasses in boulders and walls.

Courting crabs selected boulder or steep wall habitats and non-mating crabs had an affinity for all habitat types encountered excluding soft sediment seafloors (Figures 3.10, 3.11). Substrate and slope where significantly correlated (Pearson correlation coefficient) as was slope and the presence of courting GKC; slope and solitary GKC were
Figure 3.9. Sightings of courting and solitary GKC per kilometers traveled by the *DELTA* submersible in May 2000.
Figure 3.10. Substrate electivity index for courting and non-courting GKC. A value of one suggests substrate preference; a value of negative one suggests substrate avoidance; a value of zero suggests the crab is choosing the substrate at random.
Figure 3.11. Slope electivity index for courting and non-courting GKC. A value of one suggests slope preference; a value of negative one suggest slope avoidance; a value of zero suggests the crab is choosing the slope at random.
not correlated, habitat type was correlated with courting GKC but was not with solitary GKC (Appendix 9). The mean slopes of each substrate type were significantly different from one another, $P < 0.004$ ANOVA – Tukey (Figure 3.12).

Compositional analysis ranked habitat types in order of importance with soft substrate types being the least important for solitary crab while wall, intermittent boulder and intermittent cobble were the habitat type most selected (Table 3.1). Since courting GKC were only observed on 3 of the 7 habitat types surveyed, the ranking analysis was simpler, with wall type being the most selected, followed by intermittent boulder and then boulder (Table 3.2).

Dives were mostly conducted on gradients of sloped, rock to steep, walled habitats (73% of the dive time) with fewer dives (27% of dive time) on soft sediment substrates with little or no slope (Figure 3.13). Crabs were associated with steep, complex habitats, therefore diving was concentrated on these types of areas. Only 7 (8%) of the 84 observed crabs were associated with the soft, level substrate. The data from submersible observations revealed no substrate-depth relationship, as all habitat types were found at all depths surveyed. Boulders were rarely seen on slopes greater than thirty degrees. The two variables slope and substrate were significantly correlated (Pearson correlation coefficient = 0.72, $P<0.000$) (Figure 3.12, Appendix 9).

The proportions of courting crabs on different habitat types were different from the proportions of solitary crab crabs (chi-square statistic<22.458, DF=6, $P<.001$). Crabs were concentrated within habitats in Frederick Sound, however, no aggregations were
Figure 3.12. Average slope (± standard error) for each substrate type for submersible surveys in Frederick Sound, Alaska.
Table 3.1 Matrix of habitat rankings of a compositional analysis performed on solitary crab in Frederick Sound, Alaska. A (+) represents a selection, a (−) represents avoidance and, (+++) and (---) represent significant results, respectively. Ranking of habitat types are from (0) least selected to (6) most selected.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Soft</th>
<th>Pebble</th>
<th>Cobble</th>
<th>Boulder</th>
<th>Inter. Cobble</th>
<th>Inter. Boulder</th>
<th>Wall</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soft</td>
<td>−−−</td>
<td>−</td>
<td>−−−</td>
<td>−−−</td>
<td>−−−</td>
<td>−−−</td>
<td>−−−</td>
<td>(0)</td>
</tr>
<tr>
<td>Pebble</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>(3)</td>
</tr>
<tr>
<td>Cobble</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−−−</td>
<td>−</td>
<td>−</td>
<td>(1)</td>
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<tr>
<td>Boulder</td>
<td>+++</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>(2)</td>
</tr>
<tr>
<td>Inter.</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>(6)</td>
</tr>
<tr>
<td>Cobble</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inter.</td>
<td>+++</td>
<td>+</td>
<td>+++</td>
<td>+</td>
<td>−</td>
<td></td>
<td>+</td>
<td>(5)</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Wall</td>
<td>+++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>(4)</td>
</tr>
</tbody>
</table>
Table 3.2. Matrix of habitat rankings of a compositional analysis performed on courting crab in Frederick Sound, Alaska. A (+) represents a selection, a (−) represents avoidance and, (+++) and (−−−) represent significant results, respectively. Ranking of habitat types are from (0) least selected to (2) most selected. Courting GKC were only observed on 3 of the 7 habitat types.

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Boulder</th>
<th>Intermittent</th>
<th>Wall</th>
<th>Rank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boulder</td>
<td></td>
<td>0</td>
<td></td>
<td>(0)</td>
</tr>
<tr>
<td>Intermittent</td>
<td>+</td>
<td></td>
<td>-</td>
<td>(1)</td>
</tr>
<tr>
<td>Boulder</td>
<td></td>
<td></td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Wall</td>
<td>+++</td>
<td>+++</td>
<td></td>
<td>(3)</td>
</tr>
</tbody>
</table>
Figure 3.13. Frequency of substrate type encountered for all dives (Distance surveyed = 18,457 meters).
encountered. Some dives produced 0 or few crab observations while others had multiple observations. The maximum number of crabs observed in one dive was 14 (Dive 5107, Appendix 10-14). Females were observed in several stages of reproduction, including ovigerous, nonovigerous, courting, crabs with eyed eggs and crabs releasing eggs, at depths of 152-336 m. The observations were made either from the submersible or from crabs caught in pot gear onboard the fishing vessel used to originally capture crabs for tagging on May 11-12 (Chapter 2).

An interesting observation was the virtual absence of large crabs of any species other than GKC within the study area. One large male red king crab was observed at 299 meters, and two large Tanner crabs, *Chionoecetes bairdi*, were observed at 263 and 288 m. Biological relationships were not examined as a characteristic of habitat but are reported by substrate type for both macro invertebrate (Appendix 15-21) and fish (Appendix 22-28).

**Discussion**

Perhaps the most notable observation made with the submersible was the observation of courting pairs of GKC. Many lithodid species have been reported to have seasonally asynchronous reproduction (Lovrich and Vinuesa 1993). Female GKC in the Bering Sea can be collected at any stage of the reproductive cycle (with or without eggs, and eggs containing embryos in different stages of development) during mid-summer (Otto and Cumminskey 1985). Golden king crab eggs from Prince William Sound can hatch in all months of the year in laboratory culture (Adam and Paul 1999). Many researchers have suggested the reproductive cycle of mature female GKC is not seasonal
or annual as in RKC (Paul and Paul 2001, Shirley and Zhou 1997); GKC may reproduce every other year or even less frequently depending on environmental conditions (Paul and Paul 2001). Our documentation of 17 mating pairs, i.e., 34 crabs, from a total of 84 (40%) observed crabs, indicate May is a time of high reproductive activity in the Frederick Sound population of GKC.

Sexes were not segregated by depth in late spring and summer and then were segregated by depth during the fall and winter suggesting mating/courting occurs during late spring and early summer (Chapter 2). The reproductive cycle of female GKC was 590 days in laboratory experiments (Paul and Paul 2001). Further, Otto and Cumminskey (1985) reported a substantial lag time between hatching and extrusion of the next clutch. With 40% of observed crabs courting in May and segregation by depth in fall and winter (Chapter 2), GKC may have a two-year reproductive cycle that is not entirely synchronous. Northwest Pacific populations of GKC had a seasonal spawning in late spring and summer (Hiramoto and Sato 1970, Rodin 1970). With a further review of his data, Hiramoto (1985) concluded asynchronous mating occurred with an “indistinct” seasonal cycle, citing “prominent periods” of mating. The lack of synchronicity may be a result of GKC larval life history, which is not dependent on the spring plankton bloom (Shirley and Zhou 1997, Paul and Paul 2001, Adams and Paul 1999) as are species in the genus *Paralithodes* (Shirley and Shirley 1989). From Chatham Strait, an area near our study site (Figure 3.1), fourteen ovigerous females collected in earlier studies released their embryos in the lab from 2 April - 3 August in 1992 (most of the females released embryos over a 3 week period in late April and early May (Love and Shirley 1993,
Shirley and Zhou 1997). The results of Love and Shirley (1993) and Shirley and Zhou (1997) provide additional evidence that female molting and mating may occur during late spring and summer in southeastern Alaska.

The spatial distribution of eighty-four GKC appeared to be random in suitable habitat types within Frederick Sound (Appendix 10-14). Although the locations of transects were not randomly selected, four of our six dive sites were chosen randomly, suggesting GKC are not aggregating, at least during May. Studies conducted on RKC by Stone (1991) and Jewett (1999) sighted 13 (by submersible) and 19 crabs (by SCUBA and ROV over three years), respectively, on randomly chosen transects, implying crabs were not randomly distributed and likely aggregated. Aggregations of ovigerous RKC have been reported in southeastern Alaska (Stone et al. 1993). No aggregations of GKC were observed during our study.

No juvenile crabs were observed in our study. However, in another submersible research project using the DELTA immediately subsequent to our study, a concentration of approximately 200 juvenile GKC (of approximately 25 mm carapace width) was observed near Cape Ommaney, in southeastern Alaska (Figure 3.1) (Pers. comm., L. Freese, NMFS, NOAA). The observation site had similar fauna and substrate to our study area. The juvenile GKC were on a 40-degree slope at 216 m depth.

Courting GKC selected only steep walled habitat or boulders on moderate slopes while non-courting crabs were distributed among other substrates. Females ready to mate may seek out steep, rocky habitats for protection during molting, or habitats where males are common. Fishermen typically set their gear on ledges or as near as possible to steep
seafloors to catch male GKC (Pers. comm. Ladd Norheim, Bruce Meriforom, GKC commercial fishermen). Males inhabited shallower depths than females other than late spring in our study (Chapter 2); females inhabited deeper depths than males when they were not hatching eggs (Sloan, 1985). Seasonal changes in depth distribution may be a result of females avoiding antagonistic interactions with males, competition with larger males for food, cannibalism, avoidance of predators, or for other ecological or physiological reasons.

Golden king crab were found to avoid soft sediment habitats. The avoidance of soft sediments and the absence of other large crabs suggest other crab species, specifically Tanner crab, *Chionoecetes bairdi*, and RKC do not have competitive interactions with GKC in deep, complex habitats. Golden king crab are scarce in shallow, productive environments where RKC are more common. Tanner crab, which commonly inhabit similar depths as GKC within our study area prefer soft substrate (silt and sand) (Slizkin 1982, Personal observations). Golden king crab have lecithotrophic larvae which are rarely found in the plankton and may be demersal in nature, whereas RKC and Tanner crab have planktonic larvae and are common in plankton tows within their respective ranges (Shirley and Shirley 1989, Slizkin 1989).

The patchy distribution of both resources and consumers has a variety of ecological consequences. Aggregative responses of predators to patches of high prey abundance may be one explanation for GKC selection of complex habitats which act as a refuges. Large fish predators that prey upon mature king crab may have difficulties feeding in boulder fields and walls which act as a refuges for GKC. Golden king crab
were often observed in crevasses between rock and walls when approached by the submersible. As GKC move about their environment, they may remain to feed in areas where prey items occur in high densities. Since patches may differ in productivity, individual crabs may select more productive areas. Both an active choice of habitat and a simple response to resource availability can bring about such habitat selection. While the occurrence of the predominate habitat types did not differ by depth in the study site, only a small area of the study site was traversed with the submersible (Appendix 8). In addition, this area of Frederick Sound has never been mapped with multi-beam or side scan sonar technology. A major caveat is that dives were conducted only in May and the submersible had a depth limit of 360 meters; the greatest depth of the study site is approximately 612 m.

Crabs associated with vertical structures were commonly found in the same area as a large barnacle species, similar in size to Balanus nubilus. Valves of deceased barnacles were abundant at the base of slopes. Echinoderms (especially crinoids, but also ophiuroids, asteroids and holothuroids) were often abundant on boulders where crabs were observed. The proximity of the crabs and the suspension feeding barnacles and echinoderms may have been related to the presence of boulders. Golden king crab may be selecting these species or areas as food resources or breeding grounds. The giant Pacific octopus, Octopus dofleini, a known predator of RKC (Stone 1991, Z. Hoyt personal observation), typically live in steep, complex habitat and crevasses between boulders; they were observed on 12 dives during our study. Octopus readily prey upon decapods (Vincent et al. 1998) and are likely the only significant predator of adult male GKC,
however, large bottom fish such as halibut and Pacific cod have also been reported to prey upon adult Tanner crab (Loher et al. 1998).

A consequence of the heterogeneous nature of substrate inhabited by GKC is the inability to accurately estimate crab abundance with conventional trawl surveys. In addition, pot surveys are biased for assessing GKC abundance (Sergey and Bukin 2002), especially in areas of steep, rocky substrates, requiring development of new techniques to determine GKC abundance. Further, if sexes are segregated by depth, and areas of high reproductive behavior are documented, then specific areas might be protected from fishing of GKC.

Additional research is needed to elucidate GKC life history, especially larval and juvenile distribution, reproductive behavior and movements. With increased knowledge of life history, innovative approaches in crab management might help prevent the depletion of GKC stocks. A reproductive refuge established by regulation may be an example of an innovative approach, much like the Bristol Bay red king crab savings area, which protects reproducing crabs (Witherell 1998). The Habitat Affinity Index (HAI) and Habitat Suitability Modeling (Boyce et al. 2002) are tools which have been used in terrestrial wildlife management and may be useful in refining knowledge of benthic habitats and association with commercially important benthic species.
Literature Cited


Appendices

Appendix 1. Table A1. Growth statistics for seven isthmus tagged GKC caught in the 2001 and 2002 commercial fisheries. * Crab11410 was not recognized as a tagged crab until it reached the processor.

<table>
<thead>
<tr>
<th>Crab #</th>
<th>Date released</th>
<th>Carapace length at release</th>
<th>Date caught</th>
<th>Days post release</th>
<th>Carapace length at capture</th>
<th>Molted?</th>
<th>Growth (mm)</th>
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<tr>
<td>11410</td>
<td>5/12/00</td>
<td>167 mm</td>
<td>2/15-3/01*</td>
<td>~300</td>
<td>Not measured</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>11406</td>
<td>5/12/00</td>
<td>147 mm</td>
<td>2/27/01</td>
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<td>149 mm</td>
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<tr>
<td>11416</td>
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<td>3/4/01</td>
<td>297</td>
<td>135 mm</td>
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<td>0 mm</td>
</tr>
<tr>
<td>11431</td>
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<tr>
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<td>15 mm</td>
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<tr>
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<td>694</td>
<td>169 mm</td>
<td>yes</td>
<td>14 mm</td>
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</tbody>
</table>
Appendix 2. Figure A1. Temperature profile of the water column at selected dive sites in Frederick Sound in May 2000.
Appendix 3. Figure A2. Conductivity profile of the water column at selected dive sites in Frederick sound in May 2000.
Appendix 4. Figure A3. Acidity profile of the water column at selected dive sites in Frederick sound in May 2000.
Appendix 5. Figure A4. Dissolved oxygen profile of the water column at selected dive sites in Frederick sound in May 2000
Appendix 6. Figure A5. Percent O₂ saturation profile of the water column at selected dive sites in Frederick sound in May 2000.
Appendix 7. Figure A6. Salinity profile of the water column at selected dive sites in Frederick sound in May 2000.
Appendix 8. Figure A7. Depth of each thirty second interval plotted by habitat type. The mean depth of each habitat type is represented by a white circle.
Appendix 9. Table A2. Correlation matrix of habitat variables and presence of solitary and courting GKC. Values given are Pearson’s correlation (Top) coefficients and P values (bottom).

<table>
<thead>
<tr>
<th></th>
<th>Slope</th>
<th>Substrate</th>
<th>Courting GKC</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Slope</strong></td>
<td></td>
<td></td>
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<tr>
<td><strong>Substrate</strong></td>
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<td><strong>Courting GKC</strong></td>
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<td><strong>Solitary GKC</strong></td>
<td>0.138</td>
<td>0.208</td>
<td>0.468</td>
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</table>
Appendix 10. Figure A8. Positions of solitary and courting GKC observed from the submersible DELTA; 12-19 May 2000 at dive sites 1 and 2. Dive tracks and associated DELTA dive numbers.
Appendix 11. Figure A9. Positions of solitary and courting GKC observed from the submersible DELTA; 12-19 May 2000 at dive site 3.
Appendix 12. Figure A10. Positions of solitary and courting GKC observed from the submersible DELTA; 12-19 May 2000 at dive site 4.
Appendix 13. Figure A11. Positions of solitary and courting GKC observed from the submersible DELTA; 12-19 May 2000 at dive site 5.
Appendix 14. Figure A12. Positions of solitary and courting GKC observed from the submersible DELTA; 12-19 May 2000 at dive site 6.
Appendix 15. Figure A13. Proportional distribution of macro invertebrates on soft sediment substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 16. Figure A14. Proportional distribution of macro invertebrates on pebble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 17. Figure A15. Proportional distribution of macro invertebrates on cobble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 18. Figure A16. Proportional distribution of macro invertebrates on intermittent cobble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 19. Figure A17. Proportional distribution of macro invertebrates on boulder substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 20. Figure A18. Proportional distribution of macro invertebrates on intermittent boulder substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 21. Figure A19. Proportional distribution of macro invertebrates on walls surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 22. Figure A20. Proportional distribution of fish on soft sediment substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 23. Figure A21. Proportional distribution of fish on pebble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 24. Figure A22. Proportional distribution of fish on cobble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 25. Figure A23. Proportional distribution of fish on intermittent cobble substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 26. Figure A24. Proportional distribution of fish on boulder substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 27. Figure A25. Proportional distribution of fish on intermittent boulder substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.
Appendix 28. Figure A26. Proportional distribution of fish on wall substrate surveyed using a manned submersible in Frederick Sound, Alaska. Organisms were identified to lowest possible taxa and grouped when applicable.