Life history characteristics of fjord-dwelling golden king crabs *Lithodes aequispina*

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ABSTRACT: In an interconnecting system of silled, narrow, steep-walled fjords in northern British Columbia (Canada) 3800 golden king crab *Lithodes aequispina* Benedict and 184 red king crab *Paralithodes camtschatica* (Tilesius) were taken between 51 to 569 m in 3 samples over a 10 mo period. Larval retention within the most isolated fjords is suggested as an explanation for the relatively high numbers of *L. aequispina* and the relatively high (41.0 %) infection level of the crabs by the castrating rhizocephalan barnacle parasite *Briarosaccul callosus* Boschma. Life history characteristics of king crab species in fjords are related to depth. The normally continental shelf- and slope-dwelling *L. aequispina* were found significantly deeper than the characteristically intertidal to continental shelf-dwelling *P. camtschatica*. Depth stratification of *L. aequispina* was related to reproductive state among unparasitized crabs and parasitism by *B. callosus* of the others. Reproduction of unparasitized *L. aequispina* was continuous and aseasonal. Coexisting female *P. camtschatica* displayed strong synchronous reproduction characteristic of the species elsewhere. I propose that juvenile female *L. aequispina* recruit in the shallows (usually <100 m). Females mate and extrude eggs at usually <150 m and incubate eggs slightly deeper (≈150 to 250 m). Spawned out (matted setae) females dominate the unparasitized female population at >200 m and comprise the largest proportion of unparasitized females overall. This last phase may exceed a year in length and is probably followed by upward migration to the level (50 to 150 m) at which the less migratory unparasitized adult males are most abundant. Parasitized male and female *L. aequispina* behave like matted setae females and are the largest component of the total crab population from 200 to 400 m.

INTRODUCTION

The golden king crab *Lithodes aequispina* Benedict is a little known, deep-water North Pacific anomuran crab. A fishery for *L. aequispina* has recently developed in fjords and trenches off southeast Alaska (T. Koeneman pers. comm.) and along continental slopes of the eastern Bering Sea and Aleutian Islands (Otto et al. 1983). This development has been stimulated by marked stock declines of the comparatively shallow-water red king crab *Paralithodes camtschatica* (Tilesius) (Armsong 1983). *L. aequispina* also occurs off the west coast of Vancouver Island north of 49°N (Butler & Hart 1962), on Gulf of Alaska seamounts (Hughes 1981), on the continental shelf and slope of the Okhotsk Sea, west of Kamchatka (Rodin 1970) and in deep bays off the central east coast of Honshu (Hiramoto & Sato 1970, Suzuki & Sawada 1978), although apparently not in commercial quantities at any of these localities.

I report here on some life history characteristics of fjord-dwelling golden king crab *Lithodes aequispina* from 51 to 569 m in fjords within the Portland Inlet system of northern British Columbia. Emphasis is placed on reproduction and vertical distribution of *L. aequispina* in the narrow, steep-sided fjords. These characteristics are compared with those of other *Lithodes* spp. Comparative data on coexisting red king crab *Paralithodes camtschatica* are also provided and discussed.

STUDY SITE

The Portland Inlet system is a group of deep, interconnected fjords at the extreme northern end of the British Columbia coast (Fig. 1A). The steep-sided basins of the fjords are partially isolated by sills as minimum sill depths range from 25 m for Alice Arm, 55 m for Hastings Arm, 46 m for Observatory Inlet at its south end and 21 m for Work Channel (Fig. 1B). Port-
Portland Inlet has a deep (180 m) sill outside the Inlet proper at the eastern end of Dixon Entrance (Pickard 1961, D. J. Stucchi pers. comm.). Observatory Inlet thus has sills at both its ends. The level bottoms of all fjords are characterized by soft sediment, similar to other deep N. E. Pacific fjords (Cimberg 1982, Levings et al. 1983).

MATERIALS AND METHODS

A total of 390 single king crab pot sets and 45 Tanner crab pot sets (35 of these being paired pots) were made throughout the deep troughs of 5 fjords in the Portland Inlet system over 3 sampling periods (Oct/Nov 1983; Feb/Mar 1984; Jul 1984). The depth and soak time of each pot were recorded. Approximately 68.0 % of the sampling effort occurred in Alice Arm (see Table 1 for details).

Alaskan side-entry king crab pots measuring 1.8 × 1.8 × 0.9 m and covered with 9.0 × 12.0 cm mesh were used. Pots had 2 tunnels each with 88.0 × 19.0 cm openings or ‘tunnel eyes’. Each pot was baited with two 2 l, perforated jars of chopped frozen herring. The tapered, rectangular Tanner crab pots measured 1.1 × 1.1 m at the base, 0.7 m high and 0.7 × 0.7 m at the top and were covered with 5.0 × 5.0 cm mesh. There was a single top opening with a fibreglass tunnel of 33.0 × 33.0 cm that tapered to 18.0 × 18.0 cm. Each Tanner pot was baited with one 2 l jar of chopped frozen herring.

Captured Lithodes aequispina were measured for carapace length and right cheliped height (subsample of males only) to the nearest mm (Wallace et al. 1949) and weighed to the nearest 0.05 kg (1983 sample only). Crabs were noted for missing or regenerating limbs and individuals with those conditions were not weighted. Shell class was noted as either: (1) for crabs that had moulted recently, i.e. clean, light-colored exoskeleton showing little abrasion, or (2) for other crabs, discolored, abraded exoskeletons with epizoites. Sex and carapace length of Paralithodes camtschatica were also recorded.

Crabs were examined for the presence of the rhizocephalan barnacle parasite Briarosaccus callosus Boschma, externae or their remaining scars, especially callosus on the ventral abdomen surface. A random subsample of externae was examined to establish whether parasites differed from hosts in reproductive synchronization. Externae were slit open and observed, using a microscope, for condition of eggs or larvae in the mantle cavity. Development stages were: 0, if the mantle cavity was empty; 1, if eggs were present but unhatched; 2, if fewer than half the eggs had hatched (into nauplii); 3, if more than half the eggs had hatched (Bower & Sloan 1985).

Sexual maturities of unparasitized female Lithodes aequispina and Paralithodes camtschatica were classified as juvenile (no eggs nor their remnants on pleopod setae), egg-bearing (eggs attached to pleopods) or matted setae (post-spawned condition in which pleopods have long entangled setae sometimes bearing egg remnants). For unparasitized males, size at sexual maturity was calculated with Somerton’s (1980) method (Jewett et al. 1985) using the relation between carapace length and right cheliped height. All males ≤ 114 mm carapace length were classified as juvenile.

RESULTS

Sampling effort and catch

Sampling effort, depths and catches are listed according to cruise date and fjord in Table 1. A total of 470 pots were deployed in 51 to 569 m (\( \bar{x} = 230 \) m) for soak times ranging between 5.5 and 96.8 h (\( \bar{x} = 31.5 \) h). Sampling was deepest in Observatory Inlet with a mean pot depth of 409 m. The total catch was 3800 Lithodes aequispina, 184 Paralithodes...
Table 1. *Lithodes aequispina*. Sampling effort, depths, catch, and catch per unit effort of king crabs in fjords within the Portland Inlet system

<table>
<thead>
<tr>
<th>Cruise dates</th>
<th>Fjord</th>
<th>No. of pot sets</th>
<th>Sampling effort (hours of soak time)</th>
<th>Pot depths (m)</th>
<th>Catch (CPUE(^2))</th>
<th>L. aequispina</th>
<th>P. camtschatica</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oct 27–Nov 6, 1983</td>
<td>Alice Arm</td>
<td>44</td>
<td>1434</td>
<td>261</td>
<td>93–382</td>
<td>1032 (0.72)</td>
<td>65 (0.05)</td>
</tr>
<tr>
<td></td>
<td>Hastings Arm</td>
<td>44</td>
<td>1465</td>
<td>253</td>
<td>82–315</td>
<td>258 (0.18)</td>
<td>7 (&lt;0.01)</td>
</tr>
<tr>
<td></td>
<td>Observatory Inlet</td>
<td>31</td>
<td>1076</td>
<td>409</td>
<td>110–569</td>
<td>104 (0.10)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Portland Inlet</td>
<td>31</td>
<td>732</td>
<td>335</td>
<td>205–439</td>
<td>2 (&lt;0.01)</td>
<td>0</td>
</tr>
<tr>
<td>Feb 24–Mar 5, 1984</td>
<td>Alice Arm</td>
<td>98</td>
<td>4675</td>
<td>109</td>
<td>51–402</td>
<td>1484 (0.32)</td>
<td>17 (&lt;0.01)</td>
</tr>
<tr>
<td></td>
<td>Hastings Arm</td>
<td>34</td>
<td>1000</td>
<td>291</td>
<td>165–318</td>
<td>165 (0.17)</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Work Channel</td>
<td>19</td>
<td>460</td>
<td>233</td>
<td>53–318</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Jul 20–30, 1984</td>
<td>Alice Arm</td>
<td>134(^3)</td>
<td>3956</td>
<td>221</td>
<td>59–399</td>
<td>755 (0.19)</td>
<td>95 (0.02)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>435(^3)</td>
<td>14799</td>
<td>230</td>
<td>51–569</td>
<td>3800 (0.26)</td>
<td>184 (0.01)</td>
</tr>
</tbody>
</table>

1 Single king crab pot sets unless otherwise specified
2 CPUE = catch per unit effort (crabs h\(^{-1}\) soak time)
3 Includes 45 Tanner crab pot sets, of which 35 sets were paired pots

*camtschatica*, and 2721 brachyuran Tanner crabs *Chionoecetes bairdi* Rathbun. Tanner crabs occurred in > 80% of the pots in all fjords and at all depths. On the first cruise sampling effort was similar in Alice Arm and Hastings Arm although the catch of *L. aequispina* in Alice Arm was 4 times greater. Catch per unit effort

in Observatory Inlet was even less than in Hastings Arm, extremely low in Portland Inlet and no *L. aequispina* were taken in Work Channel. By-catch of halibut *Hippoglossus stenolepis* (Schmidt) was highest in Portland Inlet (in 62% of pots), lower in Observatory Inlet (in 35% of pots) and lowest in Alice and Hastings Arms (in < 5% of pots). *P. camtschatica* were caught only in Alice and Hastings Arms where the catch was < 5.0% of the *L. aequispina* catch.

Sex ratios

Males comprised 48.8% (*n = 1854*) of *Lithodes aequispina*, whereas 35.8% (*n = 66*) of *Paralithodes camtschatica* captured were males. Fig. 2 illustrates the frequency distribution of the proportion of male *L. aequispina* per pot for the 158 pots which yielded ≥ 10 golden king crabs. Proportions of males ranged widely (0.09 to 0.90) but were normally distributed (Shapiro-Wilk test; *p < 0.01*) about the mean of 0.49. Among just the unparasitized adult *L. aequispina*, however, a depth-related trend in sex ratio is described below.

Parasites and associates

Infection by the rhizocephalan parasite *Briarosaccus callosus* occurred in 41.0% (*n = 1558*) of the *Lithodes aequispina* among which 49.1% (*n = 756*) of the hosts were males. Only one *Paralithodes camtschatica* (a female) was parasitized. None of the 803 parasitized female crabs bore eggs. *B. callosus* probably sterilizes the crabs it infects (Bower & Sloan 1985) and certainly retards growth of male, although not female, hosts (Sloan 1985).

Adults, and deposited cocoons, of the sanguivorous fish leech *Notostomum cyclostroma* (Johansson) were commonly found on all crab species, especially *L. aequispina*, but caused them no harm (Sloan et al. 1984).
Depth preferences

In Alice and Hastings Arms, where the 2 king crab species were found together, the mean depth at which the 3694 *Lithodes aequispina* were caught was 272 m (range 51 to 402 m), that for the 184 *Paralithodes camtschatica* 114 m (59-384 m). Only 6 *P. camtschatica* were taken deeper than 150 m: a female at 159 m and 5 males between 183 and 384 m.

The distribution of juvenile, adult and parasitized *Lithodes aequispina* according to depth in all fjords (to 400 m) is shown in Fig. 3. The deeper pots (401 to 569 m) are excluded here because only one (yield of 16 crabs at 402 m) occurred outside Observatory Inlet whose *L. aequispina* had a very low infection rate (2.9% of *Briarosaccus callosus* (Sloan 1985). Proportions of juvenile *L. aequispina* were maximum at 50 to 100 m, adult males at 101 to 150 m, adult females at 151 to 250 m and parasitized crabs at 251 to 400 m. Approximately 68.4% of all unparasitized *L. aequispina* between 50 and 150 m were males, whereas females comprised 57.4% of all unparasitized crabs between 301 and 400 m.

Crab sizes

Table 2 lists the means and ranges of carapace lengths of unparasitized *Lithodes aequispina* and *Paralithodes camtschatica*. The females of both species were similar in size, although smaller than male conspecifics. Male *L. aequispina* were larger than male *P. camtschatica*. The largest male and female *L. aequispina* weighed 5.15 kg and 3.05 kg respectively. Both were unparasitized and both came from 476 m in Observatory Inlet. The carapace length-body weight relations for unparasitized *L. aequispina* from the 1983 cruise were estimated by fitting lines to log-transformed data (illustrated in Sloan 1985) and characterized by the power curve formulae:

*Male body weight* = $2.8 \times 10^{-7}$ carapace length$^{3.17}$ ($r^2 = .97; n = 326$)

*Female body weight* = $19.4 \times 10^{-7}$ carapace length$^{2.73}$ ($r^2 = .95; n = 396$).

There were some between-fjord differences in body size of *Lithodes aequispina* listed in Table 3. The carapace lengths of both male and female unparasitized *L. aequispina* from Observatory Inlet in the first cruise were significantly larger (Student's t-tests; $0.01 < p < 0.001$) than those of males or females from either Alice Arm or Hastings Arm. The carapace lengths of unparasitized *L. aequispina* from Alice and Hastings Arms, combined from the first 2 cruises, revealed that the males from Hastings Arm were slightly larger than males from Alice Arm (Student's t-test; $p < 0.05$). Female *L. aequispina* from Hastings Arm were no different in size than females from Alice Arm (Student's t-test; $p > 0.05$).

The mean carapace lengths of unparasitized adult *Lithodes aequispina* varied little (142.3 to 144.9 mm) according to depth at 50 m intervals between 50 and 400 m. If, however, the sizes of juveniles were included, the mean sizes at the 50 to 100 m and 101 to 150 m depth levels were significantly smaller (Student's t-tests; $p < 0.01$) than those of just the adult samples because of the relatively large proportion of juveniles at 50 to 150 m, illustrated in Fig. 3.

Histograms of carapace lengths according to different reproductive stages of unparasitized female *Lithodes aequispina* are illustrated in Fig. 4. Juveniles...
Table 3. *Lithodes aequispina*. Carapace lengths of unparasitized males and females according to fjord in the Portland Inlet system. Cruise I = Oct/Nov, 1983; Cruise II = Feb/Mar, 1984

<table>
<thead>
<tr>
<th>Fjord</th>
<th>Cruise number</th>
<th>Male <em>L. aequispina</em> Carapace length (mm)</th>
<th>Female <em>L. aequispina</em> Carapace length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>n</td>
<td>± SD</td>
</tr>
<tr>
<td>Observatory Inlet</td>
<td>1</td>
<td>61</td>
<td>154.7 ± 18.7</td>
</tr>
<tr>
<td>Hastings Arm</td>
<td>I &amp; II</td>
<td>125</td>
<td>143.8 ± 26.1</td>
</tr>
<tr>
<td>Alice Arm</td>
<td>I &amp; II</td>
<td>541</td>
<td>140.5 ± 16.7</td>
</tr>
</tbody>
</table>

Juvenile

- n = 101
- \( \bar{x} = 97.8 \)
- SD = ± 14.9

New eggs

- n = 164
- \( \bar{x} = 126.6 \)
- SD = ± 10.0

Eyed eggs

- n = 154
- \( \bar{x} = 126.9 \)
- SD = ± 10.6

Matted setae

- n = 503
- \( \bar{x} = 128.0 \)
- SD = ± 11.2

were significantly smaller (Student’s t-test; p < 0.001) than egg-bearing or matted setae females. No size differences occurred among the 3 classes of adult females (Student’s t-tests; p > 0.05).

**Shell class and moulting**

New shelled (recently moulted) crabs represented 34.6% (n = 1276) of the *Lithodes aequispina* sampled to 400 m (Table 4). The highest frequency of new-shelled (i.e. recently moulted) crabs occurred at < 150 m, with the majority between 101 and 150 m. The trend of increasing proportions of old-shelled crabs with depth was most marked among unparasitized females, although it also occurred among unparasitized males and parasitized crabs. Among unparasitized females, all those with new eggs were shell class 1 whereas all those in the matted setae were shell class 2.

**Reproduction and vertical migration**

Fig. 5 illustrates that female *Lithodes aequispina* from Alice and Hastings Arms spawn continuously with similar proportions at each stage of female maturity throughout the year. Most of the unparasitized females (50.0 to 66.4%) were in the matted setae con-

Table 4. *Lithodes aequispina*. Percentage of shell class 1 (new shelled) individuals among 3687 crabs according to depth (to 400 m) in the Portland Inlet system.
Lithodes aequispina is a continental shelf- and slope-dwelling species (Otto et al. 1983) whose life history characteristics are discussed here for relatively confined, fjord-dwelling populations. These characteristics are related to the deep-water preferences of *L. aequispina* and may be accentuated by confinement in the narrow, steep-walled British Columbia fjords. Life history data on less confined continental slope-dwelling *L. aequispina* from the eastern Bering Sea are forthcoming (D. A. Somerton pers. comm.). *Paralithodes camtschatica* is an intertidal to continental shelf-dwelling species (see review in Hayes 1983) which, when confined in British Columbia fjords, occupied shallower depths, displayed different reproductive characteristics and had different colouration than coexisting *L. aequispina*. *L. aequispina* was usually a light orange colour overall (similar to the overall bright red characteristic of another deep-water king crab *L. couesi* (Benedict); Somerton 1981, and in contrast to the dorsal dark burgundy and ventral white colouration of coexisting *P. camtschatica*).

**DISCUSSION**

Among fjords in the Portland Inlet system, *Lithodes aequispina* occurred as isolated populations. The most isolated, innermost fjords in the system, Alice Arm and Hastings Arm, yielded the most crabs per unit fishing effort although density in the former was appreciably greater than in the latter. Catches were lower in Observatory Inlet and extremely low to nonexistent in the outermost fjords of Portland Inlet and Work Channel. These differing densities of *L. aequispina* may be due to retention of oceanographically confined pelagic larvae.

In a multiple fjord system, Gade & Edwards (1980) suggested that higher vertical water exchange in the outer basins increases the likelihood of deep water renewal. The similar sill depths (25 to 55 m) of the 2 innermost fjords and their expected decrease in tidal currents, with increasing isolation causes less energetic flushing, i.e. lower coefficient of turbulent diffusivity (D. J. Stucchi pers. comm.). Observatory Inlet is tidally energetic (Stacey 1984) and experiences more flushing than the innermost fjords.
Retention of *Lithodes aequispina* larvae is enhanced by their hatching at depth (Sloan 1985 and discussed below). Larvae occurring at depth may be moved inland as predicted by the 2-layer model of fjord (estuarine) oceanography. Reliance on this simple model should, however, be cautious when discussing specific fjords as their exchange processes are ‘generally unsteady and can embrace a wide range of timescales’ (Farmer & Freeland 1983). Both Alice Arm (D. J. Stucchi pers. comm. and unpubl.) and Observatory Inlet (Stacey 1984) have characteristics which confound 2-layer flow. The Portland Inlet system as a whole, therefore, possesses complex oceanographic characteristics difficult to predict.

Despite the fairly shallow sills in most of the fjords, all probably experience complete deep-water (> sill depth) renewal annually, with considerable interannual variations, in different seasons according to fjord (D. J. Stucchi pers. comm.). These renewals may not be important to overall larval retention of *Lithodes aequispina* or *Briarosaccus callosus* as both breed continuously, as will be discussed later.

Further evidence for fjordic isolation is provided by the relatively high infection levels of *Briarosaccus callosus* among *Lithodes aequispina* from the innermost fjords, where the parasite larvae are broadcast at depth and thus retained similarly to their hosts’ larvae (Sloan 1985). Thus, ‘larval confinement’ sensu Pearson (1980) may have given rise to relatively high numbers of, and parasite infection among, *L. aequispina* in the innermost fjords.

Relatively high *Lithodes aequispina* numbers in the innermost fjords may also relate to exclusion by the sills of predators of planktonic larvae and/or post-metamorphosed crabs. For example, halibut *Hippoglossus stenolepis*, which can eat adult king crab (Gray 1964), decreased significantly as pot by-catch going inland from Portland Inlet, through Observatory Inlet to Alice and Hastings Arms.

The comparatively large size of Observatory Inlet *Lithodes aequispina* may indicate less food limitation in its deeps compared to those of the 2 Arms, whose populations are probably denser. Similarly, males from the less dense Hastings Arm population were larger than males from the more dense Alice Arm population.

**Reproduction and migration in fjord-dwelling *Lithodes aequispina***

Female *Lithodes aequispina* are continuous, aseasonal spawners with similar proportions of egg-bearing individuals found at all times of year. Coexisting female *Paralithodes camtschatica*, on the other hand, displayed strongly synchronized, seasonal reproduction which is characteristic of the species (Hayes 1983). *Briarosaccus callosus* infecting *L. aequispina* were continuous spawners. It would be interesting to establish whether *B. callosus* infecting *P. camtschatica* would be influenced by their hosts’ more seasonally-cued life history.

The relatively low proportion of egg-bearing females compared to matted setae females at all times suggests that the post-spawned phase may be rela-
tively long. Somerton & MacIntosh (1982) found relatively large proportions (33 to 52% of the female population) of 'barren' (matted setae) females to be a persistent feature of an Alaskan blue king crab Paralithodes platypus (Brandt) population. They suggested 'active' (egg-bearing) and 'inactive' (matted setae) phases during the mature life of females. In the western Bering Sea, Sasakawa (1973) proposed that P. platypus had a biennial spawning cycle with, however, an egg-bearing stage of 19 mo compared to a much shorter matted setae stage.

There was a marked vertical stratification of Lithodes aequispina in the fjords through migration which I suggest is controlled by sexual maturation among unparasitized crabs and parasitism in the remainder. This migration is likely aseasonal and, therefore, continuous. The entire L. aequispina population demonstrated a 1:1 sex ratio although segregation among unparasitized crabs occurred according to depth. The greatest proportion of juvenile L. aequispina occurred in the shallows (50 to 100 m), adult males were slightly deeper, adult females were deeper still and parasitized crabs dominated at > 200 m (Fig. 3). Relatively shallow distribution of juveniles compared to adults has been reported for some Paralithodes spp. (Somerton 1981) and Lithodes spp. (Stuardo & Solis 1963, Rodin 1970). I should qualify, however, that numbers of juveniles caught were probably underestimated due to escapement through the pot mesh as also suggested by Somerton (1981) for pot fishing of L. couesi. Among unparasitized crabs and females showed similar shallow-water preferences. I suggest that egg-bearing females may migrate downward as incubation progresses through the eyed egg stage to hatching which occurs mostly > 200 m (Fig. 6). This is opposite to ovigerous females of the deep-water brachyuran Geryon quinquedens Smith which migrate upward to shallower, warmer waters to 'enhance egg development and hatching' (Haefner 1978).

Female Lithodes aequispina may eventually migrate upwards to moult, mate and extrude eggs in the upper levels (< 150 m). The relatively high proportions of parasitized adult male and new-egg females L. aequispina at < 150 m suggests this is the depth level at which mating takes place. New-egg females were all shell class 1 (new-shelled) which suggests that mating and egg extrusion probably occur soon after moultling as among other lithodid species (Stuardo & Solis 1963, Somerton & MacIntosh 1982, Hayes 1983). The relatively high proportion of new-shelled males at < 150 m may mean that males moult before mating, as do Paralithodes camtschatica (Hayes 1983), which is in contrast to L. antarcticus Jacquinot (Stuardo & Solis 1963) where males apparently delay moultling until after mating. Moultling and mating in relatively shallow water is known for other Lithodes spp. (Stuardo & Solis 1963, Hiramoto & Sato 1970, Arnaud et al. 1976). Otto et al. (1983) also reported higher proportions of large male L. aequispina at shallower shelf depths than females in the Pribilov district of the eastern Bering Sea. The majority of the unparasitized adult male L. aequispina population may reside continually in the upper fjordic depths and not be as migratory as the unparasitized female population.

In summary, the life history pattern for unparasitized Lithodes aequispina in fjords is aseasonal and suggested to include (1) recruitment in the shallows; (2) moultling, mating and egg extrusion slightly deeper, although still relatively shallow; (3) downward migration among incubating females while males tend to remain in the shallows; (4) hatching and larval release at depth; (5) post-spawning recovery in deep water; (6) eventual upward migration by females to mating grounds in shallower fjordic depths. This aseasonal cycle is probably longer than 1 yr. Parasitized male and female L. aequispina generally behaved like post-spawned females (Sloan 1985) and congregate in deep water; possibly for longer periods as the parasites may remain with their hosts, permanently sterilizing them (Bower & Sloan 1985).

Reproduction and migration in Lithodes spp.

Reproductive and migratory characteristics reported for 5 Lithodes spp. differ considerably, even among L. aequispina from different areas as summarized in Table 5. Although Rodin (1970) suggested L. aequispina was a seasonal (summer) spawner, he proposed that no depth-related migration occurred among L. aequispina due to what he considered as an unvarying 'hydrological regime' of their continental slope habitat. Somerton (1981) suggested aseasonal spawning in Lithodes couesi (to 850 m) which I suggest is controlled by sexual maturation.

In fjords the unparasitized female population may reside continually at shallower shelf depths. There was a marked vertical stratification of Lithodes aequispina in the fjords through migration which I suggest is controlled by sexual maturation among unparasitized crabs and parasitism in the remainder. This migration is likely aseasonal and, therefore, continuous. The entire L. aequispina population demonstrated a 1:1 sex ratio although segregation among unparasitized crabs occurred according to depth. The greatest proportion of juvenile L. aequispina occurred in the shallows (50 to 100 m), adult males were slightly deeper, adult females were deeper still and parasitized crabs dominated at > 200 m (Fig. 3). Relatively shallow distribution of juveniles compared to adults has been reported for some Paralithodes spp. (Somerton 1981) and Lithodes spp. (Stuardo & Solis 1963, Rodin 1970). I should qualify, however, that numbers of juveniles caught were probably underestimated due to escapement through the pot mesh as also suggested by Somerton (1981) for pot fishing of L. couesi. Among unparasitized crabs and females showed similar shallow-water preferences. I suggest that egg-bearing females may migrate downward as incubation progresses through the eyed egg stage to hatching which occurs mostly > 200 m (Fig. 6). This is opposite to ovigerous females of the deep-water brachyuran Geryon quinquedens Smith which migrate upward to shallower, warmer waters to 'enhance egg development and hatching' (Haefner 1978).

Female Lithodes aequispina may eventually migrate upwards to moult, mate and extrude eggs in the upper levels (< 150 m). The relatively high proportions of parasitized adult male and new-egg females L. aequispina at < 150 m suggests this is the depth level at which mating takes place. New-egg females were all shell class 1 (new-shelled) which suggests that mating and egg extrusion probably occur soon after moultling as among other lithodid species (Stuardo & Solis 1963, Somerton & MacIntosh 1982, Hayes 1983). The relatively high proportion of new-shelled males at < 150 m may mean that males moult before mating, as do Paralithodes camtschatica (Hayes 1983), which is in contrast to L. antarcticus Jacquinot (Stuardo & Solis 1963) where males apparently delay moultling until after mating. Moultling and mating in relatively shallow water is known for other Lithodes spp. (Stuardo & Solis 1963, Hiramoto & Sato 1970, Arnaud et al. 1976). Otto et al. (1983) also reported higher proportions of large male L. aequispina at shallower shelf depths than females in the Pribilov district of the eastern Bering Sea. The majority of the unparasitized adult male L. aequispina population may reside continually in the upper fjordic depths and not be as migratory as the unparasitized female population.

In summary, the life history pattern for unparasitized Lithodes aequispina in fjords is aseasonal and suggested to include (1) recruitment in the shallows; (2) moultling, mating and egg extrusion slightly deeper, although still relatively shallow; (3) downward migration among incubating females while males tend to remain in the shallows; (4) hatching and larval release at depth; (5) post-spawning recovery in deep water; (6) eventual upward migration by females to mating grounds in shallower fjordic depths. This aseasonal cycle is probably longer than 1 yr. Parasitized male and female L. aequispina generally behaved like post-spawned females (Sloan 1985) and congregate in deep water; possibly for longer periods as the parasites may remain with their hosts, permanently sterilizing them (Bower & Sloan 1985).

Reproduction and migration in Lithodes spp.

Reproductive and migratory characteristics reported for 5 Lithodes spp. differ considerably, even among L. aequispina from different areas as summarized in Table 5. Although Rodin (1970) suggested L. aequispina was a seasonal (summer) spawner, he proposed that no depth-related migration occurred among L. aequispina due to what he considered as an unvarying 'hydrological regime' of their continental slope habitat. Somerton (1981) suggested aseasonal spawning in Lithodes couesi (to 850 m) which I suggest is controlled by sexual maturation. Firstly, seasonal fluctuations of environmental conditions could be less detectable by crabs in deep water. Secondly, and more likely according to Somerton, L. couesi larvae may not rise to the euphotic zone and thus not be cues to seasonal shallow water production cycles. On the other hand, both L. aequispina and L. longispina (to 900 m) in the N. W. Pacific Ocean were claimed to be seasonal, warm month spawners (Table 5). The most shallow-water species, the Centolla, L. antarcticus from southern Chile, appears to fill a niche similar to that of Paralithodes camtschatica in the northern hemisphere (Table 5). Male L. antarcticus precede females into the shallows (< 10 m) in the warm season (Nov–Dec), incoming females then moult, copulate, extrude eggs and disperse with males off-
shore to deeper water. Indeed, a major problem with the Centolla fishery in Southern Chile is that the fishing season coincides with the species' shallow-water reproductive activities (Campodónico 1981). As with P. camtschatica, juvenile L. antarcticus recruit and spend the first few years of life in very shallow (2 to 3 m) water (Stuardo & Solis 1963). The proposed seasonal upward migration and reproduction of L. murrayi Henderson from various subantarctic sites are strictly anecdotal and should be considered tentative (Table 5).

The reported reproductive differences among Lithodes spp. requires further verification for, despite these differences, the 5 Lithodes spp. in Table 5 show the same important characteristics of relatively fewer (<40,000), large (mean or median egg size ≥ 2.2 mm) eggs (Jewett et al. 1985). On the other hand, the 2 unequivocally seasonal Paralithodes spp. produce many (maxima of 285,000 and 390,000), small (<1.2 mm) eggs (Haynes 1968, Sasakawa 1975). Tyler et al. (1982) have shown that among coexisting deep-sea (>2200 m) echinoderm species both seasonal and aseasonal reproductive strategies occurred. All the seasonal species, produced many small eggs. Their larval abundance was suggested to be cued to pulses of organic particles originating from springtime phytoplankton production in overlying waters. The aseasonal species all produced fewer, but approximately 10 times larger, (more yolky) eggs for 'increased efficiency of reproduction' and 'minimal wastage' before recruitment. The small number and large size (<28,000; x = 2.4 mm; S. C. Jewett et al. 1985) of eggs produced by the fjord-dwelling L. aequispina further supports my proposal of its continuous reproduction independent of the seasons.

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LITERATURE CITED


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