

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 *Briarosaccus 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 (\approx 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) (Armstrong 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-

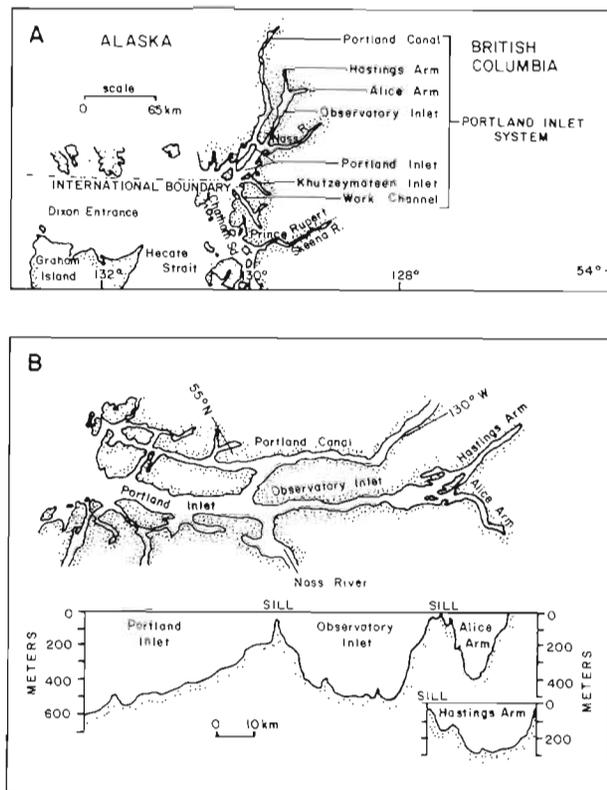


Fig. 1. (A) Portland Inlet system, northern British Columbia. Component fjords; (B) longitudinal depth profile showing position and depth of sills in Observatory Inlet, Hastings Arm and Alice Arm (after D. J. Stucchi)

land 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 $1.8 \times 1.8 \times 0.9$ 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 epizooites. 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 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

Cruise dates	Fjord	No. of pot sets ¹	Sampling effort (hours of soak time)	Pot depths (m)		Catch (CPUE ²)	
				\bar{x}	Range	<i>L. aequispina</i>	<i>P. camtschatica</i>
Oct 27–Nov 6, 1983	Alice Arm	44	1434	261	93–382	1032 (0.72)	65 (0.05)
	Hastings Arm	44	1465	253	82–315	258 (0.18)	7 (<0.01)
	Observatory Inlet	31	1076	409	110–569	104 (0.10)	0
	Portland Inlet	31	732	335	205–439	2 (<0.01)	0
Feb 24–Mar 5, 1984	Alice Arm	98	4675	109	51–402	1484 (0.32)	17 (<0.01)
	Hastings Arm	34	1000	291	165–318	165 (0.17)	0
	Work Channel	19	460	233	53–318	0	0
Jul 20–30, 1984	Alice Arm	134 ³	3956	221	59–399	755 (0.19)	95 (0.02)
	Total	435 ³	14799	230	51–569	3800 (0.26)	184 (0.01)

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

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 cyclostoma* (Johansson) were commonly found on all crab species, especially *L. aequispina*, but caused them no harm (Sloan et al. 1984).

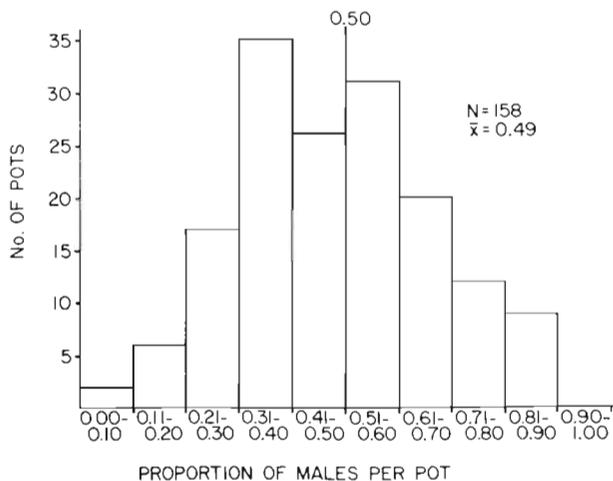


Fig. 2. *Lithodes aequispina*. Histogram illustrating frequency of proportions of males per pot in pots with ≥ 10 crabs in the Portland Inlet system

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

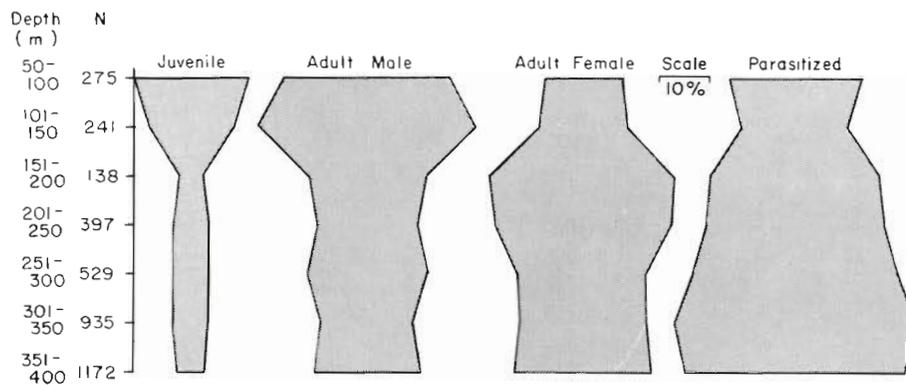


Fig. 3. *Lithodes aequispina*. Distribution of proportions of juveniles, adult males, adult females, and parasitized crabs ($n = 3687$) according to depths (50 to 400 m) in the Portland Inlet system. Scale bar: 10% of population

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

Table 2. *Lithodes aequispina* and *Paralithodes camtschatica*. Carapace lengths of unparasitized king crabs from Alice and Hastings Arms in the Portland Inlet system

Species	Sex	n	Carapace length (mm)	
			\bar{x}	Range
<i>Lithodes aequispina</i>	Male	1089	140.8	62–192
	Female	1153	124.5	59–174
<i>Paralithodes camtschatica</i>	Male	66	128.6	74–164
	Female	117	124.9	82–170

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:

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

$$\text{Female body weight} = 19.4 (\times 10^{-7}) \text{ carapace length}^{2.75} \quad (r^2 = .95; n = 396).$$

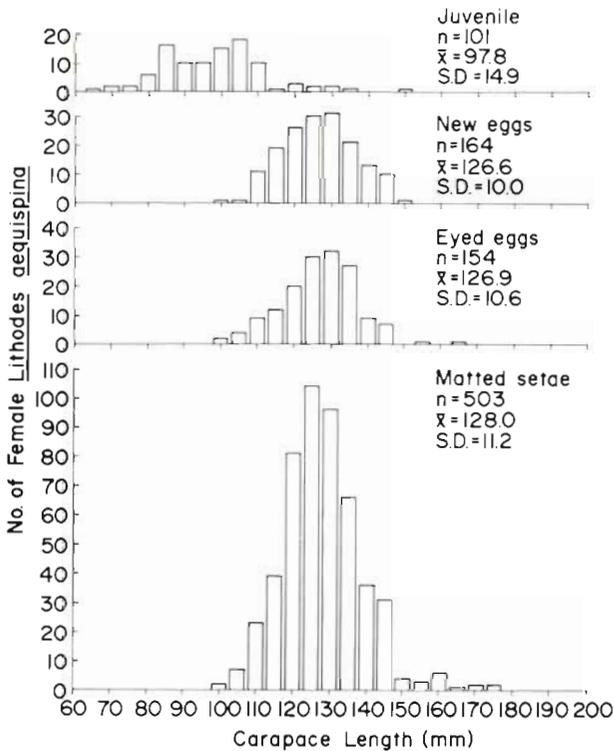
There were some between-fjord differences in body size of *Lithodes aequispina* listed in Table 3. The carapace lengths of both male and female unparasitized *L. aequispina* from Observatory Inlet in the first cruise were significantly larger (Student's t-tests; $0.01 < p < 0.001$) than those of males 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

Fjord	Cruise number	Male <i>L. aequispina</i>		Female <i>L. aequispina</i>	
		n	$\bar{x} \pm SD$	n	$\bar{x} \pm SD$
Observatory Inlet	I	61	154.7 \pm 18.7	40	141.6 \pm 19.2
Hastings Arm	I & II	125	143.8 \pm 26.1	126	122.3 \pm 18.4
Alice Arm	I & II	541	140.5 \pm 16.7	684	124.4 \pm 11.9

Fig. 4. *Lithodes aequispina*. Histograms of carapace-length size classes of 922 unparasitized females according to different maturity stages from juvenile to matted setae

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

Depth (m)	Total number of crabs	Number of shell class 1 crabs	All crabs	% of shell class 1 crabs		
				Unparasitized males	Unparasitized females	Parasitized males & females
50-100	275	133	48.4	38.2	58.2	58.4
101-150	241	152	63.1	62.3	72.1	54.0
151-200	138	52	37.7	35.1	37.0	40.4
201-250	397	137	34.5	40.6	20.5	45.1
251-300	529	154	29.1	26.7	22.1	35.4
301-350	935	276	29.5	27.8	16.4	37.8
351-400	1172	372	31.7	29.4	15.0	44.0
Totals	3687	1276	34.6	35.3	23.7	42.0

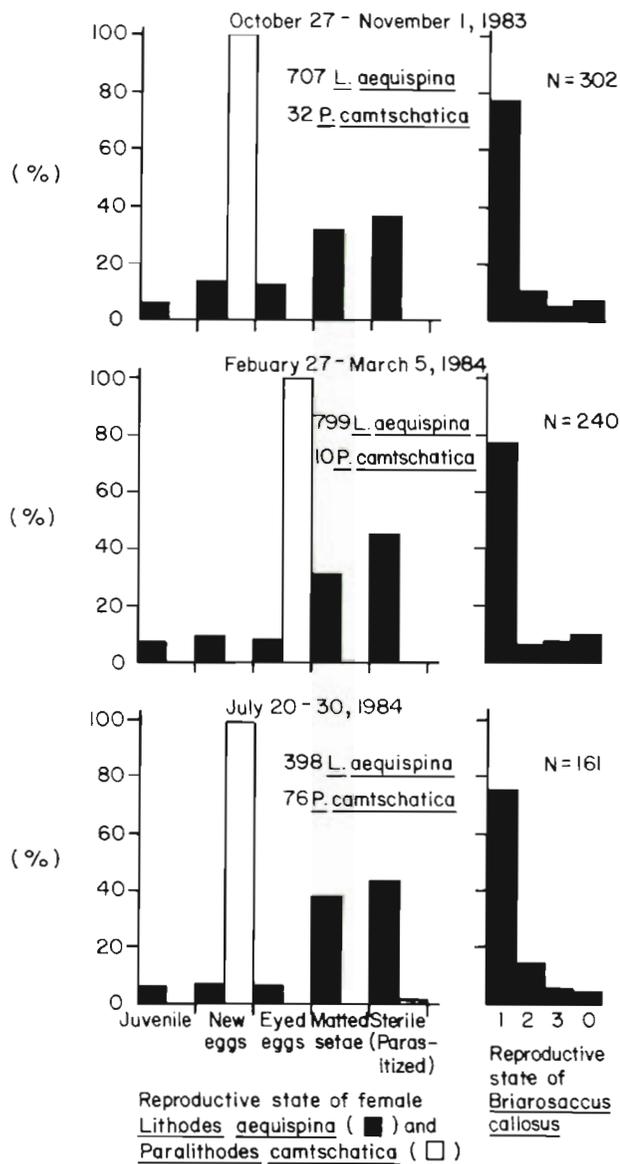


Fig. 5. Reproductive states of 1904 female *Lithodes aequispina* and 118 female *Paralithodes camtschatica*, according to the 3 sample periods. Reproductive states of 703 *Briarosaccus callosus* infecting *L. aequispina* from the 3 sample periods are also illustrated

dition. *Briarosaccus callosus*, infecting both male and female hosts, also was an asynchronous, continuous spawner as the majority (>75.0% in all samples) of the externae had packed mantle cavities of unhatched eggs at all times of year. Coexisting female *Paralithodes camtschatica* demonstrated marked peaks in reproductive activity. Within each sample all unparasitized females were in the same maturity stage with probable spring-time (after March) larval release.

The depth distributions (to 400 m) of different maturity stages of unparasitized *Lithodes aequispina* are illustrated in Fig. 6. The highest proportion of juvenile

males occurred at 50 to 100 m and juvenile females at 50 to 150 m. The highest proportion of new-egged females occurred from 101 to 150 m and eyed egg females from 151 to 200 m. Matted setae females dominated the unparasitized female samples at depths >200 m.

DISCUSSION

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*).

Confinement in fjords

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.

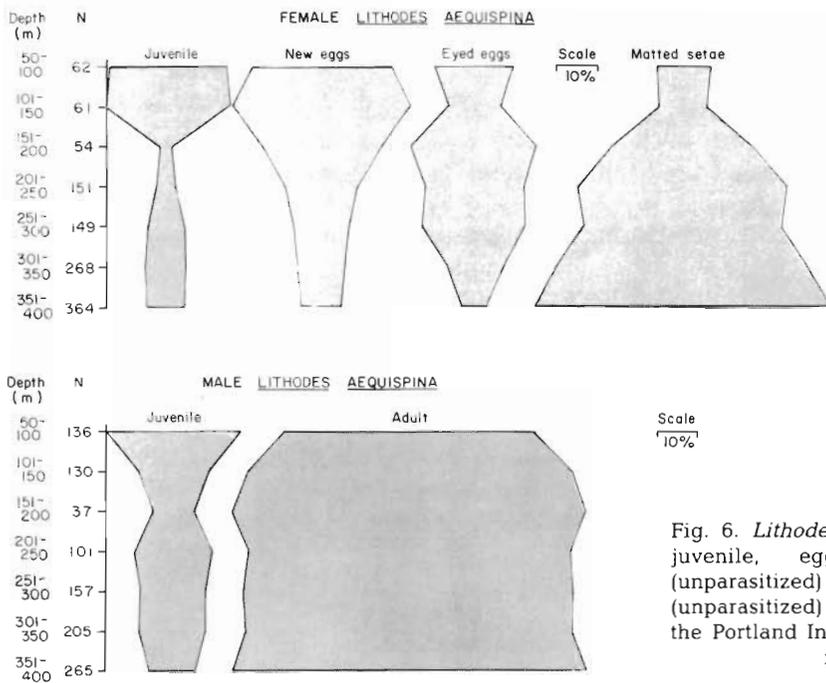


Fig. 6. *Lithodes aequispina*. Distribution of proportions of juvenile, egg-bearing and matted-setae females (unparasitized) ($n = 1109$), and of juvenile and adult males (unparasitized) ($n = 1031$) according to depth (50 to 400 m) in the Portland Inlet system. Scale bar: 10% of the female or male unparasitized population

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 time scales' (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 only unparasitized *L. aequispina*, juvenile males 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 unparasitized adult male and new-egged female *L. aequispina* at <150 m suggests this is the depth level at which mating takes place. New-egged females were all shell class 1 (new shelled) which suggests that mating and egg extrusion probably occur soon after moulting 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 moulting until

after mating. Moulting 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 Pribilof 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) moulting, 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 long 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) was related to depth. 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 cued 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-

Table 5. Published records of spawning and migration among *Lithodes* species

Species	Author(s)	Locality; latitude; habitat; depth (m)	Notes on spawning and migration
<i>L. aequispina</i>	Hiramoto & Sato (1970)	E. coast of central Honshu; 35°N; deep bay; 400–900	Seasonal spawner: spawning occurs from mid Jun to Oct during which the proportion of adults was relatively high in shallow water (400 to 500 m); adults then disperse to the depths
<i>L. aequispina</i>	Rodin (1970)	Okhotsk Sea; 53°–57°N; continental shelf and slope; 250–850	Seasonal spawner: between Aug to mid Sept crabs moult, mate, and spawn; assumed no seasonal migrations because of suggested uniformity of oceanographic conditions on the continental slope
<i>L. aequispina</i>	This paper	N. British Columbia; 55°N; fjords; 51–569	Aseasonal spawner: unparasitized females spawn continuously with 13 to 26 % females egg-bearing at any one time. Incubating females migrate downwards prior to larval release
<i>L. antarcticus</i>	Stuardo & Solis (1963)	Strait of Magellan; 53°S; deep bay; 10–200	Seasonal spawner: after moulting, mating and spawning in shallows during the warm months (Dec to Jan); incubating females and adult males then disperse to the depths in Feb
<i>L. couesi</i>	Somerton (1981)	Gulf of Alaska; 55°–57°N; tops of seamounts; 384–850	Aseasonal spawner: migration unlikely on the relatively level seamount tops
<i>L. longispina</i>	Hiramoto (1974)	E. coast of central Honshu; 35°N; deep bay; 400–900	Seasonal spawner: spawn between mid Aug to mid Oct, no data on migrations
<i>L. murrayi</i>	*Arnaud (1971); *Arnaud et al. (1976); Arnaud & Do-Chi (1977)	S. W. Indian Ocean; 45°S; continental shelf of oceanic islets; 75–187	Seasonal spawner: implied from anecdotal observations that migration to shallows (to spawn?) occurs in warm months (Dec to Apr)

* Included anecdotal observations from other subantarctic areas to 600 m

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 few (<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 phyto-

plankton 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; $\bar{x} = 2.4$ 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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