Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*

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Abstract.—Along the continental slope of the eastern Bering Sea, two species of *Careproctus* snailfishes deposit eggs within the branchial chambers of the commercially important golden king crab (*Lithodes aequispinus*). The larger of the two species is the pink snailfish (*C. furcellus*); the smaller species is an undescribed species referred to as the red snailfish. According to 1982 trawl survey data, incidence of snailfish eggs and larvae within crab branchial chambers increases with carapace length (CL) and is greater for male than female crabs. A logistic model fitted to the incidence data predicts that a 140-mm-CL male will have an incidence of 0.52, approximately 1.9 times greater than the incidence for a 100-mm male. Incidence for a 100-mm-CL male is approximately 1.9 times greater than that for a female of equal size. On the basis of developmental stages of embryos carried by female golden king crab and the developmental stages of snailfish embryos within a female's branchial chambers, snailfish appear to deposit eggs preferentially in crabs that are early in their molt cycle. The presence of the egg masses results in gill compression, localized necrosis of gill tissue and, in extreme cases, total loss of gill tissue on one side of the body. For crabs of commercial size, the presence of eggs and larvae increases mortality within the holds of fishing vessels by 35%. The current incidence of eggs and larvae in commercial sized males, however, is so low that the effect on the commercial fishery is considered to be small.

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Liparid snailfish in the genus *Careproctus* extrude eggs through an anteriorly positioned ovipositor into the branchial chambers of large lithodid crabs. This relationship was first described, independently, by Rass (1950) and Vinogradov (1950) for *C. sinensis* and *Paralithodes camtschatica* in the northwest Pacific. Subsequent studies, however, have shown that additional species both within *Paralithodes* as well as within three other lithodid genera (*Lithodes, Lopholithodes* and *Paralomis*), also serve as hosts to various *Careproctus* species and that the association appears to be widespread according to reports from the North and South Pacific and South Atlantic (Hunter, 1969; Parrish, 1972; Peden and Corbett, 1973; Anderson and Cailliet, 1974; Balbontin et al., 1979; Melville-Smith and Louw, 1987; and Love and Shirley, 1993).

The advantages that snailfish gain by placing their eggs within an enclosed, constantly aerated space have been recognized since the association between *Careproctus* and lithodid crabs was discovered (Rass, 1950). The disadvantages to the crab, however, remain equivocal, with reports of no obvious damage (Hunter, 1969; Parrish, 1972), minor gill compression by the egg mass (Anderson and Cailliet, 1974; Melville-Smith and Louw 1987), and gill bleeding (Love and Shirley, 1993). Knowledge of the disadvantages is important because most affected lithodid species support commercial fisheries.

In this paper, we report on the deposition of egg masses by two species of *Careproctus* into the branchial chambers of the golden king crab (*Lithodes aequispinus*), a large, commercially harvested lithodid occurring along the continental slope of the North Pacific (Somerton and Otto, 1986). The identity of the two *Careproctus* species is uncertain because the taxonomy of the family Liparididae is problematic and incomplete (Allen and Smith, 1988). The larger species (Fig. 1), henceforth called the pink snailfish, is certainly within the *C. melanurus* group of morphologically similar species (Allen and Smith, 1988) and is likely to be *C. furcellus* which has been observed throughout the Bering Sea and Aleutian Islands (Kido, 1988). The smaller species (Fig. 1), henceforth called the red snailfish, is tentatively identified as a member of the *C. mederi* group described by Kido (1988), who re-

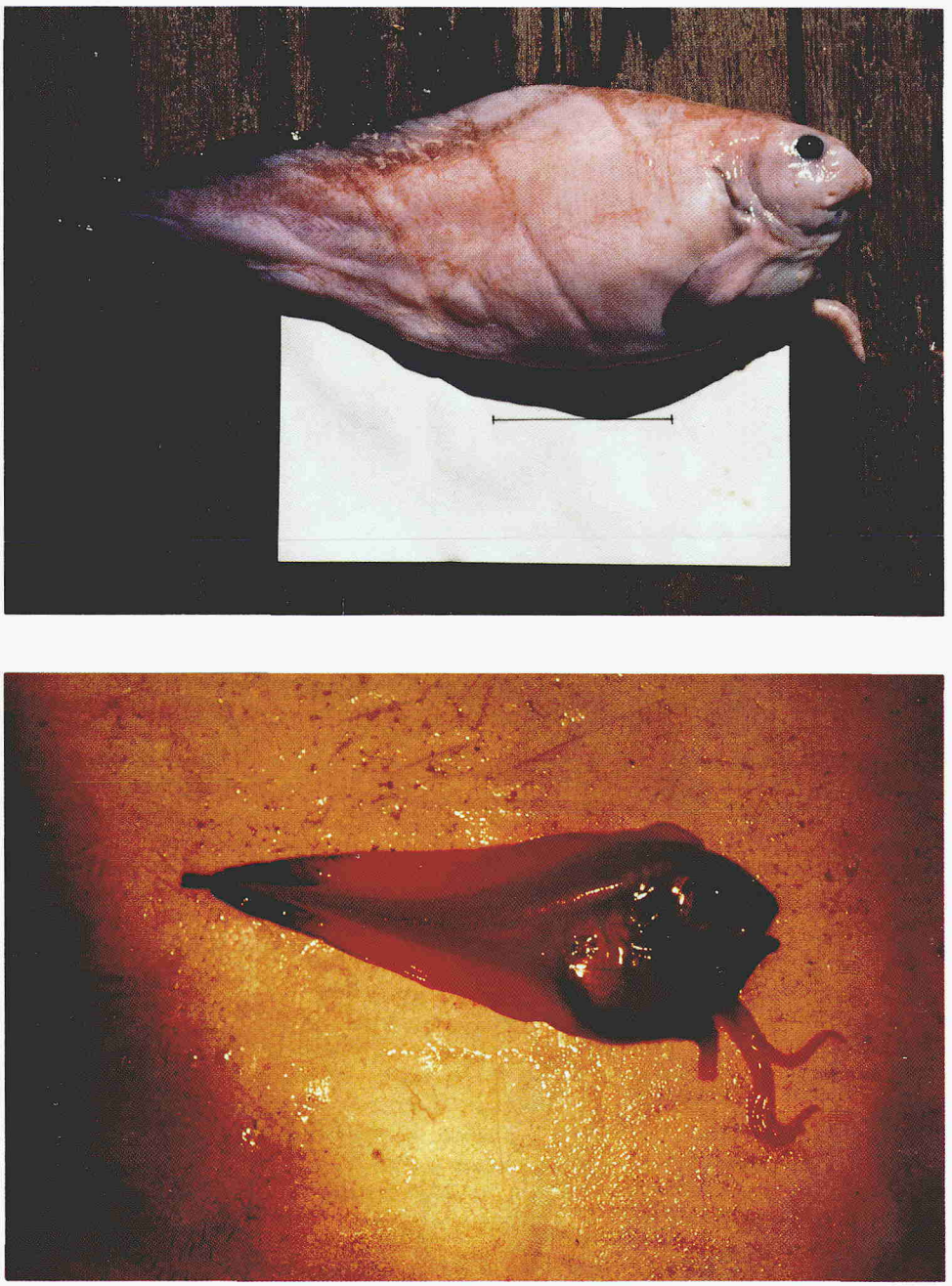

Figure 1

(Upper) pink snailfish (*Careproctus furcellus*); (lower) red snailfish (*C.* species). Both specimens are ripe females with their ovipositors extended. Note that the red snailfish has extremely long lobes on the pectoral fins that, in the picture, have been positioned in front of the body for clarity.

ferred to it as *Careproctus* species B.[1] Here we first examine the characteristics of this association, then consider how *Careproctus* snailfish choose their host crabs and what the consequences may be to the crabs.

[1] Stein, D. 1996. National Marine Fisheries Service, 1315 East-West Hwy., Silver Springs, MD, 20910. Personal commun.

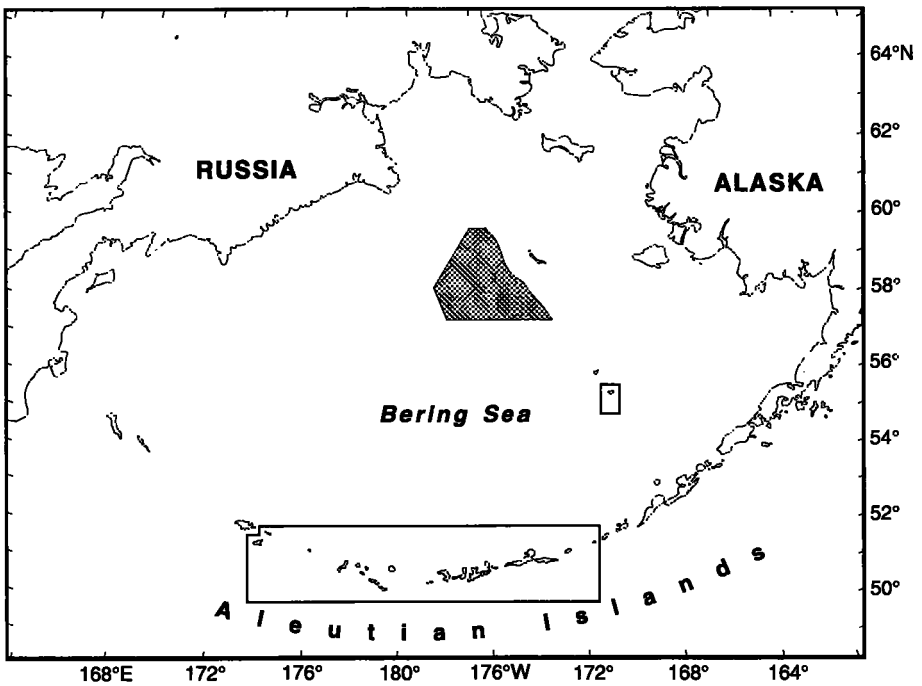

Figure 2

Collecting sites for the 1982 trawl survey (shaded area) and the 1996 commercial catch sampling areas in the Bering Sea and Aleutian Islands (unshaded areas).

Materials and methods

Golden king crab were sampled 11 July–25 August 1982 aboard the FV *Rujin Maru no. 8* while it was conducting a bottom trawl survey of the benthic resources along the continental slope of the eastern Bering Sea (Fig. 2). All golden king crab were first sorted to sex, then measured for carapace length (CL) from the base of the eye to the posterior midline of the carapace. Females were evaluated for maturity, on the basis of relative width of their abdomens, and if mature, their pleopods were examined to determine whether they were carrying uneyed embryos, eyed embryos, or remnants of recently hatched embryos (egg cases and funiculi), or whether they were bare.

During this sampling, the senior author discovered that many of the crabs contained *Careproctus*-like egg masses or larvae within their branchial chambers. Further inspection of the egg masses and larvae revealed that there appeared to be two distinct types, one with egg diameters or larvae lengths considerably larger than the other. Several species of *Careproctus* were also captured in the trawls but two species, pink and red snailfish, predominated. Gentle pressure applied to the abdomens of some individuals of both species resulted in eggs being extruded through the ovipositor (Fig. 1) or milt being extruded out the genital papilla (Stein, 1980). The eggs of pink snailfish were visibly larger than those of red snailfish and the egg sizes of both species clearly matched the egg sizes found within the crabs. Consequently, starting on 27 July, 48 consecutive trawl hauls were sampled as follows for *Careproctus* spp. and their eggs and larvae.

All golden king crabs were examined for the presence of *Careproctus* egg masses or larvae clusters by removing their carapaces. Each mass was evaluated to type (uneyed embryos, eyed embryos, or larvae) and species (large eggs and larvae were assigned to pink snailfish; small eggs and larvae were assigned to red snailfish), and for location (i.e. which side of the crab it was obtained). Snailfish were first sorted to species, then externally sexed, if possible, by the presence of either an ovipositor or a genital papilla. Snailfish were then gently squeezed about the abdomen and classified as ripe if either eggs or milt were extruded. Thus, the sex could be either known or unknown and, if known, the individual could be either ripe or unripe.

The 1996 incidence of snailfish eggs and larvae within golden king crab were assessed by Alaska Department of Fish and Game at-sea observers and port samplers during the golden king crab fishing season in the Aleutian Islands and eastern Bering Sea. Female and small (<135 mm-CL) male golden

king crab, which are not retained by the fishery, were sampled aboard commercial vessels by occasionally collecting all individuals from one randomly chosen trap. Sampled crabs were first measured for carapace length, then examined for the presence of snailfish eggs and larvae, without regard to species, by removing their carapaces. Legal-size male crab were sampled from the commercial catches when they were landed at the processing plant. Catches were first separated into groups of live and dead crabs, then counted and subsampled by examining up to 100 individuals from each group for the presence of snailfish eggs. Port samples were collected for crabs caught either in the Bering Sea (three landings) or the Aleutian Islands (six landings; Fig. 2), but at-sea samples were collected only in the Aleutian Islands.

Thirteen golden king crabs found, during commercial sampling, to contain snailfish eggs or larvae were frozen whole, with the eggs or larvae left in place for later processing. Eighteen of 23 egg and larvae samples were nonhatched egg masses that were placed in water overnight to fully rehydrate, then weighed to the nearest 1 mg. Displacement volume of the egg masses (mL) was measured in a graduated cylinder. Egg masses were then teased apart and the total number of eggs counted. Diameters of approximately 200 eggs randomly chosen from each egg mass were measured to the nearest 0.03 mm with an optical micrometer. Volumes of the gills on both the affected and unaffected side of the crab were measured by displacement after they were excised with a scalpel at their bases. Volume of the empty branchial chamber on one side of the crab was then measured by securing the carapace in its proper place on the crab and then injecting Polycel insulating foam into the branchial cavity through a small hole. After any excess was removed, the volumes of the foam casts were then measured by displacement to the nearest milliliter. The 23 egg and larvae samples were then subjected to restriction fragment length polymorphism (RFLP) analysis (Dowling et al., 1996) by using six restriction enzymes to determine species identity.[2] Species identification patterns were established by using the RFLP analysis on six *Careproctus rastrinus*, eight *C. furcellus*, and one *C. cypselurus* collected in crab pots during commercial sampling.

The incidence (e.g. probability of occurrence) of snailfish eggs and larvae as a function of several predictor variables was described with a generalized linear model, with a logit link function and a binomial variance function (Venables and Ripley, 1994). For each crab, model inputs included a binary response variable (presence or absence of eggs or larvae). For the 1982 survey data, predictors included two continuous variables (carapace length and depth) and a discrete variable (sex). For the 1996 port sampling data, predictors included two discrete variables (area and whether the crab was alive or dead). Model selection was accomplished iteratively by first testing the significance of each interaction term with a likelihood ratio test, then by discarding the least significant term. This process was then repeated on each main effect and any associated interaction terms.

Differences in the depth distributions of male and female crab and of spawning and nonspawning snailfish were tested by first calculating a Cramer-von Mises statistic from catch-per-tow and depth data, then by determining the significance of the statistic with randomization (Syrjala, 1996).

Association between the developmental stage of eggs carried by a female golden king crab and the developmental stage of snailfish eggs within a crab's branchial chambers was tested with a Spearman's rank order correlation coefficient. Because king crabs extrude eggs onto their pleopods soon after molting (Powell and Nickerson, 1965; Sloan, 1985), the stage of embryonic development is a crude measure of the relative time since molting. Positive correlation between the developmental stages of crab and snailfish embryos would indicate that snailfish preferentially choose newly molted crabs as hosts. To simplify interpretation, 3 of 26 females were not used because they contained more than a single egg mass or larvae cluster. Embryonic developmental stages for snailfish (uneyed, eyed, and larval) and crabs (uneyed, eyed, and hatched) were considered as ordered variables and were assigned numeric codes (i.e. 1, 2, 3). Mature female crabs without any obvious egg remnants attached to the pleopods were grouped with females carrying hatched eggs because egg remnants may have been missed in the macroscopic examination performed at-sea.

The mortality rate of male crabs in the holding tanks of commercial vessels was estimated separately for crabs with and without snailfish eggs and larvae on the basis of 1996 port sampling data for commercial crab landings. For each landing, the total number of live crabs that were infested was estimated by multiplying the number of live crabs landed by the infested proportion in the catch subsample. The total number of infested dead crabs was estimated similarly. The mortality rate of infested and uninfested crabs was then estimated as the number dying divided by the total in each category. Average mortality rate was then estimated as the mean over all landings.

[2] Lopez, A. 1996. Marine Molecular Biological Laboratory, University of Washington, Seattle, WA. Personal commun.

Results

Depth distributions of golden king crabs and snailfish

The 48 hauls sampled on the 1982 survey were randomly distributed between 192 and 900 m. Over this range, golden king crab catch-per-tow (Fig. 3) and carapace length (Fig. 4) declined with increasing depth. Male and female crab occurred at significantly different depths (randomization test, P=0.005), with the median depth of males (203 m) being less than that of females (336 m).

Pink snailfish abundance declined with depth; most of the population occurred at depths <450 m (Fig. 5). Conversely, red snailfish abundance increased with depth; most of the population occurred at depths >450 m. (Fig. 5). Red snailfish was approximately six times more abundant, averaged over the entire survey area, than pink snailfish (mean catch per haul: red snailfish=4.57, pink snailfish=0.75, total number of both species=226). As a result, red snailfish were predominate at depths as shallow as 350 m. The proportion of the individuals that were ripe (both sexes combined) did not differ significantly between species (chi-square test, df=1, P=0.341). Ripe pink snailfish (both sexes combined) were found at significantly shallower depths than unripe individuals (randomization test, P<0.001), but ripe and unripe red snailfish did not differ in depth (P=0.255).

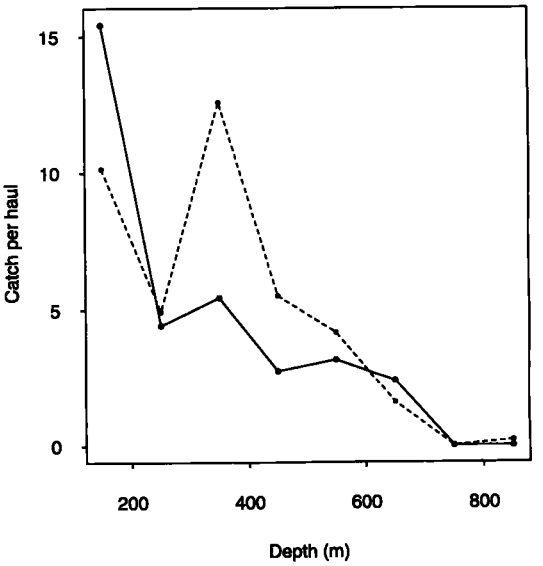

Figure 3

Catch per haul by 100-m depth intervals for male (solid) and female (dotted) golden king crab.

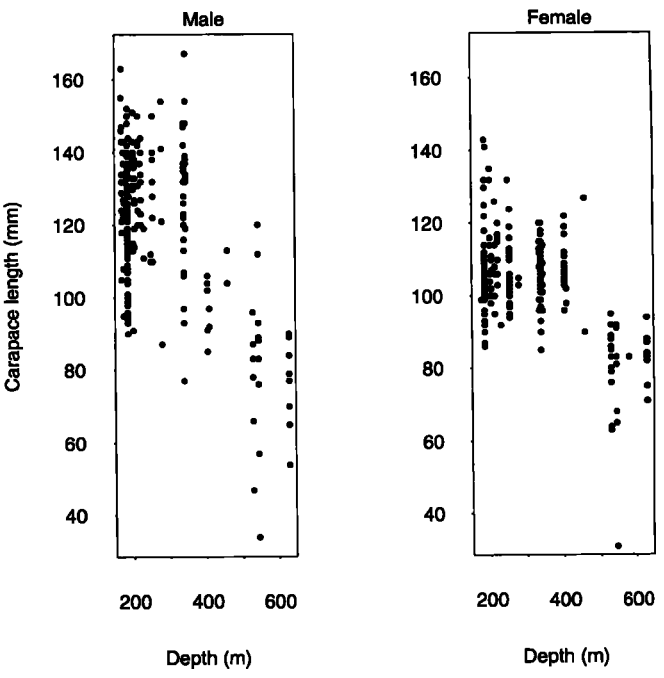

Figure 4

Carapace length of all crabs captured as a function of depth for male (left) and female (right) golden king crab.

Careproctus eggs and larvae

Snailfish eggs are self adhesive and form compact masses that are often shaped like casts of the interior of the branchial chambers (Fig. 6). After hatching, larvae remain grouped together within the crab, thus allowing multiple batches of larvae to be easily distinguished. Of the 515 golden king crab examined on the 1982 survey, 97 contained 128 egg masses or larvae clusters. Twenty-three of the crabs had more than one egg mass or larval cluster (16 had 2, 6 had 3, and 1 had 4 egg masses or larvae clusters). The abundance of multiple occurrences relative to single occurrences did not differ between snailfish species (chi-square test, df=1, P= 0.111), indicating that the two species were equally likely to deposit eggs in previously infested crabs. Combined over both species, the number of egg masses found within infested crabs increased with carapace length (linear regression, n=94, P=0.049), indicating that large crabs tended to have more multiple occurrences. In three cases of multiple occurrences, eggs or larvae of both snailfish species were present. The relative abun-

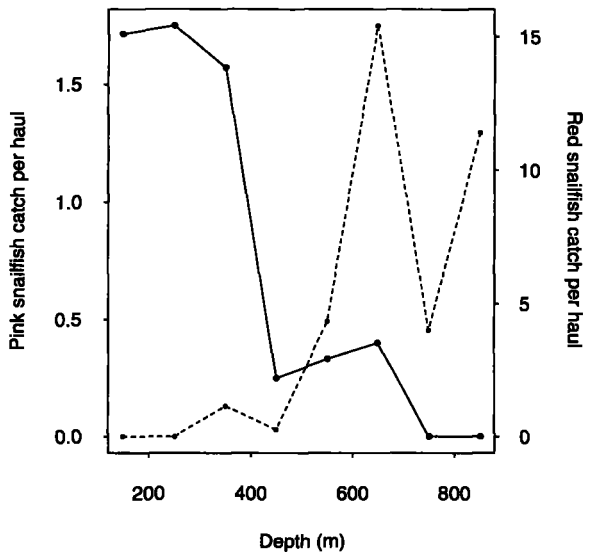

Figure 5

Catch per haul by 100-m depth intervals for pink snailfish (solid) and red snailfish (dotted).

dance of the three developmental stages (uneyed eggs, eyed eggs, and larvae) did not differ between snailfish species (chi square test, P=0.163), indicating that the timing of the egg deposition events and subsequent embryonic and larval developmental rates were about the same for both species. Summed over both species, the relative abundance of uneyed and eyed embryos was about equal, whereas the abundance of larvae was less than 20% that of either embryonic stage (Table 1).

Mean egg diameter was 4.83 mm (SD=0.29, eggs=4207, egg masses=18) and mean egg number was 688 (SD=84.0, egg masses=15). By comparison, the mean diameter of eggs taken from the ovarian lumen of a single pink snailfish was 4.9 mm (SD=0.124, n=208) and the total number of eggs was 790 with a displacement volume of 48.2 mL. Based on this specimen, mean egg volume was 0.061 mL (SD=0.017) and mean egg mass was 0.064 gm (SD=0.020).

Volume of single egg masses increased asymptotically with branchial volume (Fig. 7), indicating that up to some crab sizes, egg mass volume is limited by the available space in the branchial chambers. Up to 65% of the available volume within the branchial chambers (i.e. branchial volume – gill volume) was filled by a single egg mass.

Table 1

Incidence of *Careproctus* egg masses and larval clusters by species and stage of development.

	Uneyed embryos	Eyed embryos	Larvae	Total
Red snailfish	36	45	6	87
Pink snailfish	24	14	3	41
Total	60	59	9	128

Incidence of snailfish eggs and larvae in golden king crab

Before developing a statistical model describing the 1982 incidence of snailfish eggs and larvae as a function of crab sex, carapace length, and sampling depth, we performed statistical tests to determine whether the two snailfish species could be combined in the analysis. Incidence of pink and red snailfish eggs did not differ by sex of host (chi-square test, df=1, P=0.28), nor by size of host (t-test, df=128, P=0.58), but incidence did differ by depth. Pink snailfish occurrences declined with increasing depth until none were encountered at depths >400 m (Fig. 8). In contrast to this, red snailfish masses increased in abundance with depth until reaching a peak at between 300–400 m, then declined until none were encountered at depths >600 m. Despite the difference in depth distribution for each species, the species were combined to simplify analysis. Because the combined incidence of eggs and larvae increased with depth to a peak at 250 m, then subsequently declined (Fig. 8), the depth effect in the model included a quadratic term. The best fit of a logistic model to the combined incidence data indicated that sex (P<0.001), length (P=0.003), and depth (P<0.001) were all highly significant (Table 2). The fitted model predicts 1) incidence increases with size (Fig. 9), 2) incidence is greater for males than females (Fig. 9), and 3) incidence is greater at middepth (i.e. significant quadratic depth effect, Table 2).

The best fit of a logistic model to the 1996 incidence in commercial males indicated that area (P<0.001) and whether the crabs were landed dead or alive (P=0.046) were both significant (Table 2). Incidence in the Bering Sea was over three times greater than in the Aleutian Islands. Incidence in dead crabs was 1.9 times greater than in live crabs in the Bering Sea and 1.6 times greater in the Aleutian Islands (Table 3). Incidences in live commercial males from the Aleutian Islands were 2.5 times greater than in sublegal males and 12.5 times greater than in females (Table 3). Incidence in 1996 of live commercial males in the Bering Sea was less than 20% of the incidence in 1982 commercial size males

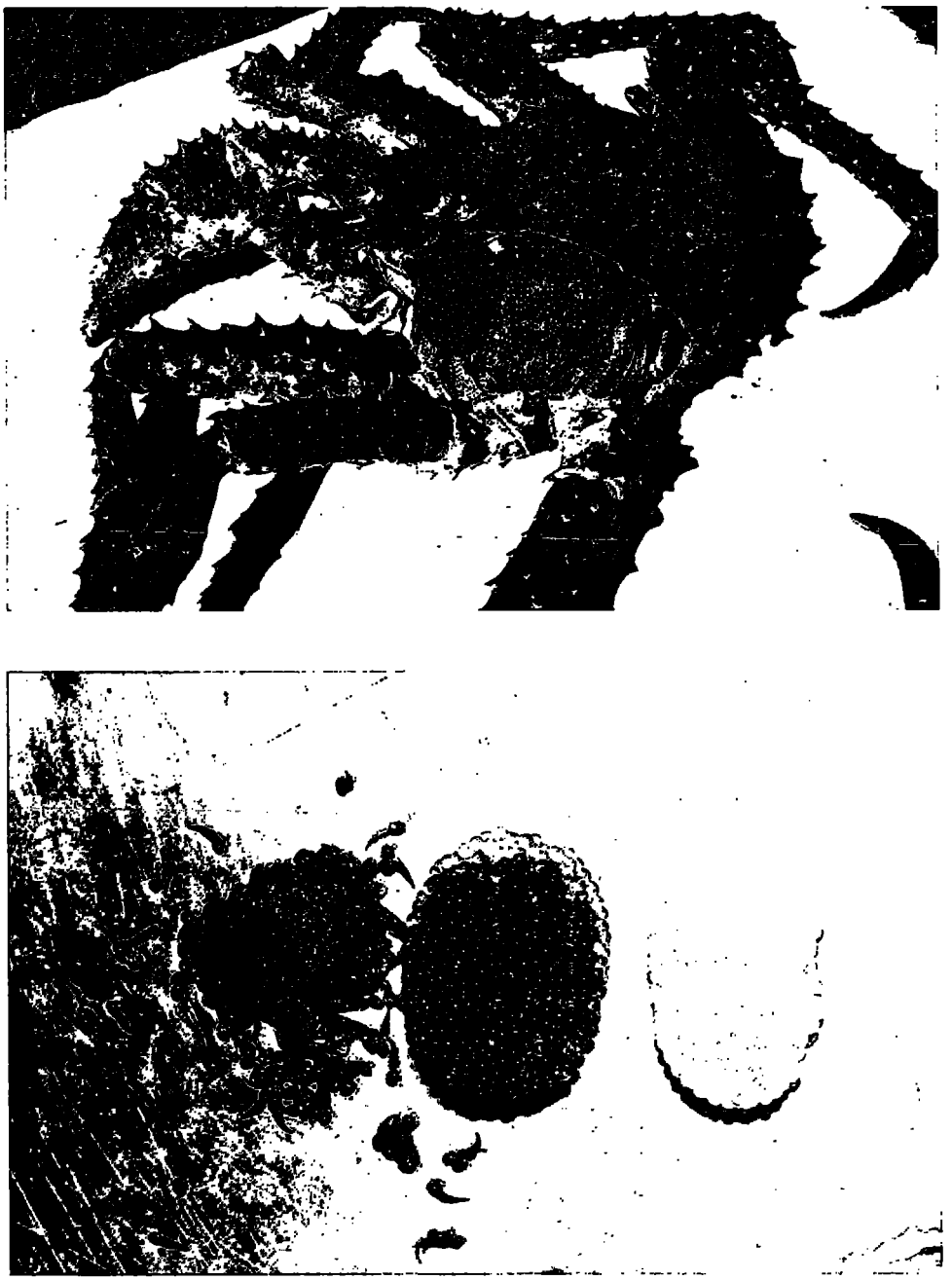

Figure 6

(Upper) A male golden king crab with part of the carapace cut away to show two *Careproctus* egg masses in different stages of development. (Lower) An early uneyed egg mass (right), a late uneyed egg mass (center), and a larvae cluster (left) taken from a single golden king crab.

(CL>135 mm; Table 3). The probability of a male dying in the holding tank of a commercial vessel was 0.035 if the crab contained snailfish eggs and larvae and 0.025 if the branchial chambers were empty, indicating that snailfish infestion increases the holding mortality of crabs.

Association between crab and snailfish embryonic development stages

Mature female golden king crab carried snailfish embryos in all three stages of development (uneyed, eyed, and larval) only when they themselves were

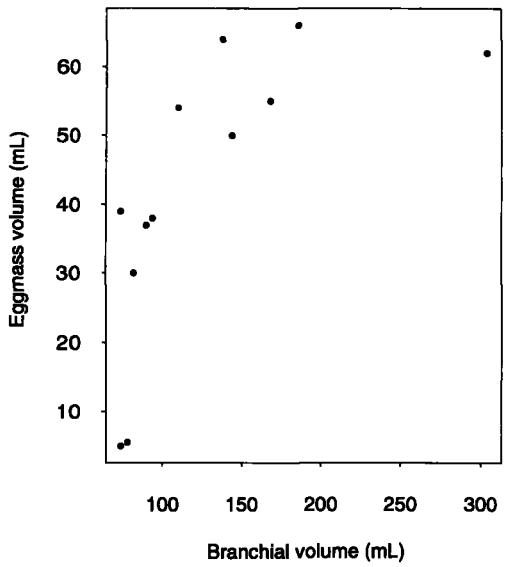

Figure 7

Volume of single egg masses as a function of the volume of the branchial chambers of the host crab.

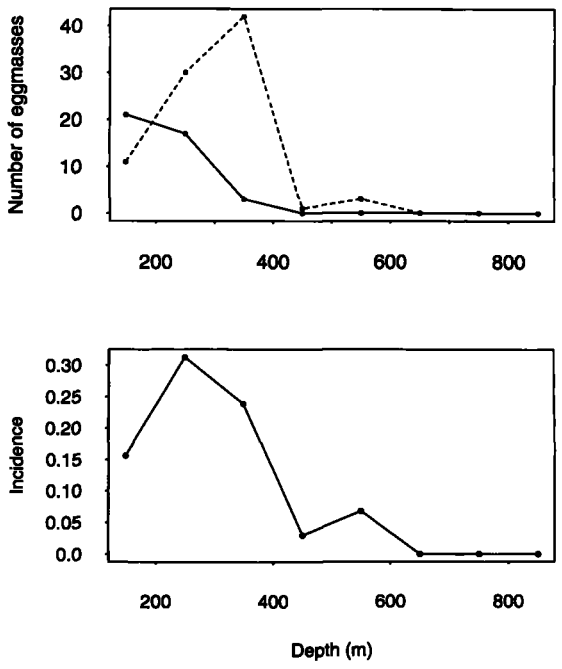

Figure 8

Number of egg masses by 100-m depth intervals for pink snailfish (solid line) and red snailfish (dotted line, upper). Incidence, or proportion of all crabs having snailfish eggs or larvae of either species, by 100-m depth interval (lower).

Table 2

Summary statistics of the fitted logistic models.

Model 1 (1982 survey data)

logit(incidence) = intercept + sex + length + depth + depth^2 + sex*depth + sex × depth^2

Coefficient	Value
Intercept	–8.6724639
Sex	–2.2823274
Length	0.0261672
Depth	0.0310400
Depth^2	–0.0000432
Sex × depth	0.0187658
Sex × depth^2	–0.0000512

Significance tests of main effects

Effect	Likelihood ratio	df	Probability
Length	8.87	1	0.003
Sex	25.02	3	<0.001
Depth	20.92	4	<0.001

Model 2 (1996 port sampling of commercial catch)

logit(incidence) = intercept + area + dead or alive

Coefficient	Value
Intercept	–2.744489
Area	–0.667367
Dead or alive	–0.300833

Significance tests of main effects

Effect	Likelihood ratio	df	Probability
Area	22.39	1	<0.001
Dead or alive	3.96	1	0.046

carrying uneyed embryos (Table 4). As crab embryos became more developed, so too did the snailfish embryos. Thus, crabs with eyed embryos were not found with uneyed snailfish embryos, and crabs with hatched embryos were not found with uneyed or eyed snailfish embryos. Considering the three development stages of both species as an ordered random variable, the crab developmental stages were highly correlated (rho=0.68, P=0.005) with the snailfish developmental stages.

Genetic determination of species identity

All 14 of the fish samples, but only 10 of the 23 egg and larvae samples, collected by commercial fishery observers were sufficiently well preserved to allow

Table 3

Incidence of snailfish (*Careproctus* spp.) egg clusters within golden king crab (*Lithodes aequispinus*). Included are the total landed catch in numbers of live and dead crab, number of crab in each category examined, and the number with egg masses.

Sampling type	Area	Condition	Catch	Crabs examined	Crabs with fish eggs	Percent infested
Incidence in male crabs >135 mm CL						
1996 port	Bering Sea	live	12788	302	25	8.3
		dead	351	44	7	15.9
	Aleutian Is.	live	46206	603	15	2.5
		dead	1508	343	14	4.1
1982 survey	Bering Sea	live		55	24	43.6
Incidence in female crabs and male crabs ≤135 mm CL						
1996 at-sea	Aleutian Is.	male		1641	12	0.7
		female		1631	4	0.2
1982 survey	Bering Sea	male		183	44	24.0
		female		274	26	9.5

DNA amplification. *Careproctus furcellus*, *C. rastrinus*, and *C. cypselurus* fish samples could be readily distinguished in the RFLP analysis. Of the 10 usable egg and larvae samples, two were identified as *C. furcellus* and eight clearly differed from all of the fish samples.

Effect of the egg masses on gill function

The presence of egg masses within the branchial chamber of a crab was associated with three distinct pathological conditions of the gills. First, egg masses compressed the gills so strongly that a distinct impression of the egg mass was left on the gill surface (Fig. 10, upper, p. 880). Second, gills on the infested side of a golden king crab were often darker in color than those on the opposing side (Fig 10, lower, p. 880). Third, gills on the infested side often had areas of blackened, necrotic tissue (Fig. 10, p. 881). Several gills with necrotic tissue were examined microscopically after standard histological preparation.[3] A stage-wise progression of tissue damage was evident, beginning as small lesions with hemocyte encapsulations. As the lesions increased in size, they were more likely to be melanized, indicating a chronic condition, and often occluded one or more gill lamellae. Small (occluding one or more lamellae) to medium size (occluding the gill stem) lesions typically possessed new cuticle and normal respiratory epithelium underneath the affected area, indicating that the gill tissue would be regenerated during the next molt. In extreme cases, all of the gills on the affected side of the body were reduced to blackened stubs (Fig. 10, p. 881).

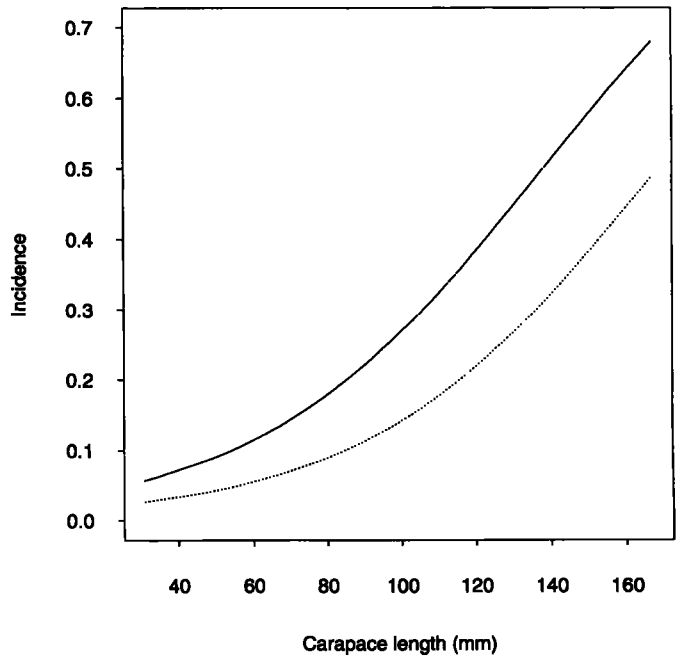

Figure 9

Incidence of *Careproctus* eggs and larvae, predicted by the generalized linear model, for male (solid line) and female (dotted line) golden king crab as a function of carapace length.

[3] Morado, F. 1996. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA. Personal commun.

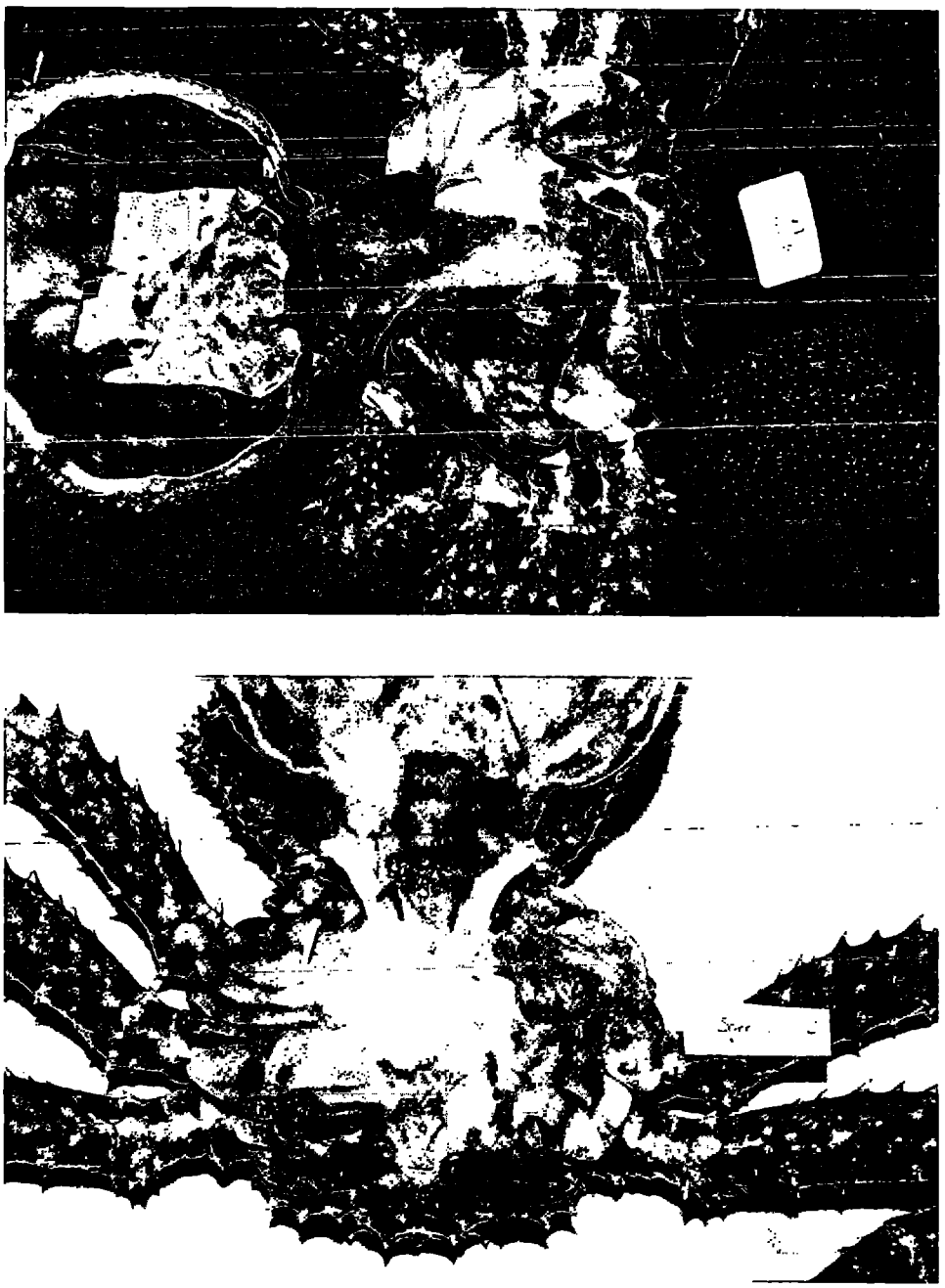

Figure 10

Pathological conditions associated with the presence of a snailfish egg mass in the branchial chamber of a golden king crab. Compression of the left gills and impression of individual eggs on the gill surface (upper). Blackened necrotic tissue on the right gills (lower). Complete loss of left gills (facing page). The fifth pereiopods, which act as gill cleaning appendages, are shown in their folded state at the posterior junction of the carapace and abdomen (lower).

Discussion

The branchial chambers of golden king crab provide *Careproctus* embryos and larvae with a well aerated environment and protection from predators. This advantage would be jeopardized if they were ejected prematurely by crab molting. To minimize the risk of this happening, snailfish must either have the

Figure 10 (continued)

ability to choose host crabs that are early in their molt cycle or that have embryonic and larval residence times that are short in relation to the intermolt period of the crab. Evidence that snailfish have both attributes is provided by the association that we found between the embryonic developmental stages of crabs and those of the snailfish found within the crabs.

Preference for newly molted crabs is indicated by the observed presence of young (uneyed) snailfish embryos in female golden king crab carrying uneyed embryos but not in those carrying eyed embryos or remnants of hatched larvae (Table 4), because king crabs deposit their eggs soon after molting. Snailfish may locate newly molted crabs olfactorally, by detecting minute traces of molting hormones in the same way that some male crabs locate premolt females (Ryan, 1966).

A relatively short embryonic and larval residence time, compared with the intermolt period of the crab, is indicated by the presence of late snailfish developmental stages (eyed embryos and larvae) in newly molted (uneyed) female golden king crab (Table 4). The length of the embryonic periods for pink and red snailfish are unknown, but the large size of the eggs and low temperatures of the water in which they incubate (average bottom temperature on the 1982 survey was 3.8°C) indicate that the embryonic periods are probably quite long. Incubation times are greater in colder water and for fish with larger eggs (Pauley and Pullin, 1988), but there are no studies applicable to a large egg-producing deep slope species such as *Careproctus*. If chinook salmon (*Oncorhynchus tshawytscha*) are used as an approximate model for a relatively large egg, cold water species, then 4.5 months would be required for hatching at 3.8°C. (Alderdice and Velsen, 1978). Although this rate of embryonic development may be long for a fish, it is considerably shorter than that of golden king crab which perhaps exceeds 1 year (Somerton and Otto, 1986).

If snailfish can preferentially choose newly molted crabs as hosts, then their spawning season must occur at the same time as the molting season of the

Table 4

Number of female golden king crab observed categorized by the development stage of their own embryos and the snailfish embryos within their branchial chambers.

	Snailfish stages		
Crab stages	Uneyed	Eyed	Larvae
Uneyed	9	4	1
Eyed	0	1	0
Hatched	0	0	3

crab. However, the variety of snailfish embryonic stages that occurred during the 1982 sampling (Table 1), coupled with the probable slow developmental rate, indicates that pink and red snailfish have either a protracted spawning season, or perhaps lack spawning seasonality. Previous studies of snailfish reproduction have reported that aseasonal spawning was typical of abyssal and slope snailfishes, although *C. malanurus*, a close relative to pink snailfish, has a seasonal peak in spawning off Oregon (Stein, 1980). The likelihood for preferential selection of early molt-stage crabs is not necessarily diminished by aseasonal spawning in red and pink snailfish because golden king crab also have aseasonal reproduction and molting (Somerton and Otto, 1986).

The incidence of snailfish eggs and larvae was greater in male than in female crabs and increased with crab size in both the 1982 survey (Table 2; Fig. 9) and the 1996 commercial sampling (Table 3). The preference for male crabs as hosts over females is quite pronounced. For example, at the median 1982 sampling depth, a 100-mm male is 1.9 times more likely to contain eggs and larvae than an equal-size female (Fig. 9). As in our study, male *Lithodes tropicalis* had a higher incidence of snailfish eggs than females (Melville-Smith and Louw, 1986), but the apparent sex selection was attributed to size selection and to a large sexual dimorphism in crab size. In our case, we believe sex itself is important in host choice because sex was a significant predictor of incidence even when size and depth effects were included in the model. Such sex selection may not be universal, however, because a previous study of *L. aequispinus* reported that incidence was higher in females (Love and Shirley, 1993). Why a preference for males should occur is not obvious. One possible explanation, based on aquarium observations (Love and Shirley, 1993), is that female golden king crab aggressively defend the embryos attached to their pleopods. Perhaps this aggressiveness can discourage the attempts of a snailfish to extrude her eggs into the branchial chambers of the crab.

The apparent preference for large crabs is also quite pronounced. For example, at the median 1982 sampling depth, a 140-mm-CL male is 1.9 times more likely to contain snailfish eggs or larvae than a 100-mm-CL male (Fig. 9). The apparent preference of snailfish for large crabs is likely due to two distinct attributes associated with size in lithodid crabs. First, large king crabs molt less frequently than small king crabs. Although the molting frequency of golden king crabs is unknown, for male red king crabs (*Paralithodes camtschaticus*), molting frequency diminishes continuously with increasing age (McCaughran and Powell, 1977). Since a lower molt frequency would result in a lower probability of premature release of eggs and larvae, it is an advantageous feature for a perspective host to have. Second, larger crabs have larger branchial chambers to contain snailfish eggs. In our case, egg mass volume increased with branchial volume (Fig. 10), indicating that the size of an egg mass is limited by the size of the branchial chamber. This increase, however, diminished with crab size, indicating that in large crabs the size of an egg mass may be determined more by snailfish fecundity than by the availability of space. It is not clear what effect the space limitation would have on the searching behavior of snailfish. If a female snailfish is capable of partitioning a batch of ripe eggs among several spawning events, then she might be able to reduce the problem of space limitation by depositing eggs in several crabs. If instead female snailfish must deposit their entire batch in one spawning event, then considerably more searching would be required to find a crab with sufficient volume. To help provide some indication of whether a female partitions a batch of eggs, we measured egg batch volume for a single 40-cm pink snailfish, considering only eggs that were free in the ovarian lumen. Because the measured volume (48 mL) is about equal to the median volume of the egg masses found in crabs (Fig. 7), it is possible that a female spawns an entire batch in one event. If this is true, then a female would have to determine, perhaps by probing with her ovipositor, whether a prospective host has sufficient branchial volume for her batch of eggs.

Besides size and sex, other aspects of crab host choice by snailfish have been postulated. Melville-Smith and Louw (1987) suggested that *Careproctus* might preferentially choose only one side of host *L. tropicalus* to deposit egg masses. In our case, neither pink snailfish nor red snailfish chose one side of the crab over the other (binomial test, red snailfish, P=0.39, pink snailfish, P=0.76). Love and Shirley (1993) and Melville-Smith and Louw (1987) suggested, after finding no crabs with egg and larvae masses in both branchial chambers, that snailfish are inhibited from depositing egg masses in the unaffected branchial chamber of previously infested crabs, presumably to reduce host mortality. In our case, this feature was not true because of 23 crabs that had at least two egg or larvae masses, 13 had masses on both sides.

Because large crabs occur in shallower waters than small crabs and males occur in shallower waters than females, the preferred hosts of both snailfish species occur in the shallower portion of the 1982 depth range. Pink snailfish occur at approximately the same depths as their preferred hosts, but red

snailfish live in deeper waters and must migrate into shallower water to find suitable hosts. For red snailfish, a spawning migration is apparent by the shallower peak in the depth distribution of its egg masses (350 m; Fig. 8) compared with the depth distribution of the fish themselves (650 m; Fig. 5). For pink snailfish, by comparison, the depth distributions of the egg masses and fish nearly coincide. If the spawning migration is undertaken only by ripe fish, then a difference in depth distribution between ripe and unripe fish would be expected for red snailfish but not for pink snailfish. We are unable to account for our observation that the expected shift in depth distribution was found for pink snailfish but not red snailfish.

One shortcoming of the 1982 sampling of snailfish eggs and larvae is that the species identification was based on an apparent species difference in egg and larvae size. Although larvae were collected in an attempt to establish identification by linking larval characteristics to adult fish, the larvae were poorly ossified and their identities could not be determined.[1] In a second attempt at species identification, we subjected the eggs and larvae collected in the 1996 sampling to RFLP analysis. On this basis, it was possible to establish that pink snailfish do deposit eggs in golden king crab. Unfortunately, we had no red snailfish tissue available to establish an identification pattern for the RFLP analysis because red snailfish were not captured during the 1996 sampling (the commercial crab fishery does not extend into sufficiently deep water). Therefore, it was not possible to determine if the 8 of 10 specimens not matching any of the three sampled *Careproctus* species were, as we suspect, red snailfish.

Damage to the gills from the presence of egg masses may result from two causes. First, gill compression could be strong enough to restrict blood flow, resulting in localized necrosis. Second, egg masses could interfere with the functioning of the fifth pereiopod (Fig. 10), which is covered with setae and functions as a gill-cleaning appendage (Pohle, 1989). Experiments with other lithodid crabs have demonstrated that gill fouling similar to the discoloration observed in golden king crab could be experimentally produced either by restricting the movement of the fifth pereiopod or removing the setae from this appendage. The fouling is due not only to the accumulation of detritus on the gill surface, but also the accumulation of a host of organisms that feed on the detritus or directly on the gill tissue itself (Pohle, 1989). In golden king crabs, the degeneration of the gill tissue can proceed to the point that all of the gill tissue on the infested side is missing (Fig 10). In cases of small to medium lesions, it was clear from histological examinations that gill regeneration would occur at the next molt, but crabs with extreme cases of gill degeneration were not examined histologically and it is not known whether gill regeneration would occur. However, in at least one case, a newly molted golden king crab was encountered with no gills on one side of the body. Perhaps, this crab was an extreme case of gill damage which did not regenerate. Gill damage not only influences a crab's respiration but also its capability for ion exchange. Lithodid crabs that died as the result of the restriction of their cleaning appendages displayed considerable abdominal swelling which is indicative of ion imbalance (Pohle, 1989).

The 35% higher mortality of infested male crabs, compared with uninfested crabs, within the live tanks of commercial vessels (Table 4) indicates that the presence of egg masses hinders the ability of crabs to withstand the stress of capture and confinement. The impact on the fishery, however, depends on the incidence of snailfish eggs and larvae as well as the additional mortality they induce. In the case of the 1996 incidence in the Bering Sea (8.5%, Table 3, corrected for deadloss), for example, live-tank mortality increased by only 0.08%. Even at the higher incidence found in 1982 (44%), additional live-tank mortality would have been only 0.40%. Although the mortality that is induced on wild crabs is unknown, it appears that the impact of snailfish parasitism on the golden king crab fishery is small.

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Literature cited

Alderdice, D. F., and F. P. J. Velsen.
1978. Relation between temperature and incubation time for eggs of chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 35:69–75.

Allen J. M., and G. B. Smith.
1988. Atlas and zoography of common fishes in the Bering Sea and northeastern Pacific. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 66, 151 p.

Anderson, E. M., and G. M. Cailliet.
1974. Crab and snailfish commensalism in Monterey Bay. Underwater Nat. 8:29–31.

Balbontín, F., I. G. Campodónico, and L. M. Guzmán.
1979. Descripción de huevos y larvae de especies de

Careproctus (Pisces: Liparidae) comensales de *Paralomis granulosa* y *Lithodes antarctica* (Crustacea: Lithodidae). An. Inst. Patagonia 10:235–243.

Dowling, T. E., C. Moritz, J. D. Palmer, and L. H. Rieseberg.
1996. Nucleic acids III: analysis of fragments and restriction sites. *In* D. M. Hillis, C. Moritz, and B. K. Mable (eds.), Molecular systematics, 2nd ed., p. 249–320. Sinauer, MA.

Hunter, C. J.
1969. Confirmation of symbiotic relationship between liparid fishes (*Careproctus* spp.) and male king crab (*Paralithodes camtschatica*). Pac. Sci. 23:546–547.

Kido, K.
1988. Phylogeny of the family Liparididae, with the taxonomy of the species found around Japan. Mem. Fac. Fish. Hokkaido Univ. 35:125–256.

Love, D. C., and T. C. Shirley.
1993. Parasitism of the golden king crab, *Lithodes aequispinus* Benedict, 1895 (Decapoda, Anomura, Lithodidae) by a liparid fish. Crustaceana 65:97–104.

McCaughran, D. A., and G. C. Powell.
1977. Growth model for Alaskan king crab (*Paralithodes camtschatica*). J. Fish. Res. Board Can. 34:989–995.

Melville-Smith R., and E. Louw.
1987. An association between a liparid fish species and the stone crab *Lithodes tropicalis* (Decapoda, Anomura). S.-Afr. Tydskr. Dierk. 22:140–142.

Parrish, R.
1972. Symbiosis in the blacktail snailfish, *Careproctus melanurus*, and the box crab *Lopholithodes foraminatus*. Calif. Fish Game 68:239–240.

Pauly, D., and R. S. V. Pullin.
1988. Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes 22:261–271.

Peden, A. E., and C. A. Corbett.
1973. Commensalism between a liparid fish, *Careproctus* sp., and the lithodid box crab *Lopholithodes foraminatus*. Can. J. Zool. 51:555–556.

Pohle, G.
1989. Gill and embryo grooming in lithodid crabs: comparative functional morphology based on *Lithodes maja*. *In* B. E. Felgenhauer, L. Watling, and A. B. Thistle (eds.), Functional morphology of feeding and grooming in crustacea, p 75–94. A. A. Balkema, Rotterdam.

Powell, G. C., and R. B. Nickerson.
1965. Reproduction of king crabs, *Paralithodes camtschatica* (Tilesius). J. Fish. Res. Board Can. 22:101–111.

Rass, T. S.
1950. Zamechatel'nyi sluchai biologicheskoi svyazi ryby i kraba [An unusual instance of a biological relation between fish and crabs]. Priroda 39(7):68–69. In Russian. Translated by Paul Macy, U. S. Fish and Wildlife Service, Translation Series No. 41. [Available from the Northwest Fisheries Science Center, 2725 Montlake Blvd. E. Seattle, WA 98102.]

Ryan, E. P.
1966. Pheromone: evidence in a decapod crustacean. Science 151:340–341.

Sloan, N. A.
1985. Life history characteristics of fjord-dwelling golden king crab *Lithodes aequispina*. Mar. Ecol. Prog. Ser. 22:219–228.

Somerton, D. A., and R. S. Otto.
1986. Distribution and reproductive biology of the golden king crab, *Lithodes aequispina*, in the eastern Bering Sea. Fish. Bull. 84:571–584.

Stein, D. L.
1980. Aspects of reproduction of liparid fishes from the continental slope and abyssal plain off Oregon, with notes on growth. Copeia 1980:687–699.

Syrjala, S. E.
1996. A statistical test for a difference between the spatial distributions of two populations. Ecology 77:75–80.

Venables, W. N., and B. D. Ripley.
1994. Modern applied statistics with S-plus. Springer-Verlag , New York, NY, 462 p.

Vinogradov, K. A.
1950. K biologii Tikhookeanskogo pinagora v Kamchatskikh vodakh [Biology of the Pacific lumpfishes in Kamchatka waters]. Priroda (Leningrad) 39(7):69–70.