RHIZOCEPHALAN INFECTION IN BLUE KING CRABS, *PARALITHODES PLATYPUS*, FROM OLGA BAY, KODIAK ISLAND, ALASKA

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ABSTRACT

An isolated population of blue king crabs, *Paralithodes platypus*, in Olga Bay, Kodiak Island, was sampled quarterly during 1980-81. It was found to contain abnormal mature females with degenerate ovaries and/or no sign of having extruded ova following molt. Histological studies of these females and of males and females collected subsequently in April 1982 showed that rhizocephalan internas (roots) were present in up to 50% of the population. Both males and females were infected, but male gonads and secondary sexual characteristics were apparently unaffected. Presence of the rhizocephalan was strongly related to ovarian abnormalities. Evidence suggests that infected females can molt, but do not extrude or retain embryos. The Olga Bay rhizocephalan is not related to *Briarosaccus callosus*, which parasitizes several species of Alaskan king crabs, including the blue king crab. Externas of the Olga Bay parasite were not found. The possible relationship of this rhizocephalan to the genus *Thompsonia*, which has minute multiple externa that might be missed during gross examination, and the possibility that the blue king crab is an abnormal host that does not allow development of externas are discussed.

Molting, mating, and extrusion of ova occur annually in red king crabs, *Paralithodes camtschatica*, and biennially in blue king crabs, *P. platypus*. Because embryos of both species hatch within about 1 yr, empty embryo cases are carried on blue king crabs in the second year (Powell and Nickerson 1965; Sasakawa 1973, 1975; Somerton and MacIntosh in press). Somerton and MacIntosh (1982)[4] studied an isolated population of blue king crabs in Olga Bay (Kodiak Island, AK) and found abnormal females that were of mature size but lacked external evidence of having extruded eggs or that had apparently degenerate ovaries. This paper reports results of gross and histological examination of blue king crabs from the aberrant Olga Bay population and from three apparently normal eastern Bering Sea populations. A rhizocephalan, which was found only in the Olga Bay crabs, appears to be responsible for the abnormal reproductive pattern.

MATERIALS AND METHODS

Blue king crabs in Olga Bay were sampled quarterly: spring (March-April 1980), summer (June 1980), autumn (October 1980), and winter (January 1981). Seasonal sample sizes ranged from 155 to 229 crabs, and a total of 422 males and 337 females was examined. Both sexes were measured to the nearest millimeter in carapace length (see Wallace et al. 1949, for measurement). Carapace lengths ranged from 12 to 162 mm for males and 16 to 143 mm for females. Data were taken on external egg clutches of females by relative volume, color of embryos, and presence or absence of eyespots on embryos. Presence or absence of empty embryo cases on nonovigerous females was also noted.

For the purposes of this paper, "oogonia" are stem cells; "oocytes" are developing cells before full maturity; and "ova" are cells that have completed vitellogenesis, have a thick chorion, and are ready for fertilization. "Embryo" refers to an external, fertilized, and developing egg or ovum.

The entire ovary and a pleopod with attached embryos or empty embryo cases (if present) were removed from each female considered to be mature or in the prepubertal stadium (>68 mm carapace length (CL)). These were preserved in 10% freshwater (river water) Formalin[5] solution buffered with sodium

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[4]Somerton, D. A., and R. A. MacIntosh. 1982. Aspects of the life history of the blue king crab (*Paralithodes platypus*) in Alaska. Document submitted to the annual meeting of the International North Pacific Fisheries Commission, Tokyo, Japan, October 1982.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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borate (10 g/L solution). The wet weight of preserved ovaries was recorded to the nearest g and diameters of a sample of oocytes/ova were recorded to the nearest 0.1 mm using a stereomicroscope.

Because many of the ovaries appeared abnormal and could not be classified easily by oogenetic stage, histological examination was undertaken of ovaries and pleopods from the largest sample, collected in January 1981 (Table 1). To provide material for a more detailed examination, the Olga Bay population was sampled again in April 1982, and three apparently normal Bering Sea populations of blue king crabs were also sampled (Table 1). Except as indicated, tissues taken in these collections included portions of the central nervous system, gut, hepatopancreas, gills, eyestalks, epidermis, heart, antennal gland, bladder, ovary, female pleopods, anterior vas deferens, and, in some cases, testis and hemopoietic tissue.

Except for the January samples from Olga Bay (fixed in borate Formalin), all tissues were fixed in Helly's solution (containing zinc chloride rather than mercuric chloride) for 3-4 d, washed 1-2 h in 50% ethyl alcohol, and stored in 70% ethyl alcohol until being processed by standard histological methods.

To provide a basis for comparison, ovaries and pleopods of 11 female red king crabs collected at Olga Bay, January 1981, and fixed in borate Formalin, and tissues from two blue king crabs collected at Glacier Bay, AK, infected with the rhizocephalan *Briarosaccus callosus*, and fixed in Helly's solution, were also prepared for histological examination.

RESULTS

Prevalence of the Rhizocephalan

The roots (internas) of a rhizocephalan were associated with either or both the ovary and the pleopod in 52% of the 104 blue king crab females taken from Olga Bay in January 1981, and with various tissues in 40% of the 15 females and 33% of the 15 males taken from Olga Bay in April 1982 (Table 2). The rhizocephalan was also found in 1 of the 11 red king

TABLE 1.—Origins of blue king crabs examined histologically.

Location	Date	Number of specimens	Carapace length (mm)
Olga Bay	8-14 Jan. 1981	104 females (ovaries and pleopods)	69-136
Olga Bay	5-9 Apr. 1982	15 males	88-151
		15 females	90-128
Pribilof Is.	25 June-3 July 1982	10 males	83-155
		10 females (plus ovaries and pleopods from an additional 10 females)	96-145
Pribilof Is.	21 Feb. 1983	10 females	113-137
St. Matthew I.	10-13 July 1983	17 males	68-158
		9 females	61-129
St. Lawrence I.	5-11 Sept. 1982	5 males	85-106
		5 females	79-104

TABLE 2.—Rhizocephalans in individual male and female blue king crabs, Olga Bay, Kodiak Island, AK, April 1982.

			Major areas parasitized (in tissue sections)					
Sex	Intensity of infection	Degenerate roots	Nerve cord, assoc. bladder	Bladder in other areas	Gut	Gonad	Antennal gland	Hepato-pancreas
Female	±[1]		+[2]					
	+		+	+	+	+	+	+
	+	+[3]	+	+	+			
	++	+	+			+		
	++	+	+	+	+	+		+
	+++	+	+	+		+	+	+
Male	±			+				
	+		+		+			+
	+	+	+	+	+			+
	++	+	+	+	+		+	+
	++	+	+	+	+	+	+	+

[1] ± = light infection; + to +++ = medium to very heavy infection.
[2] + = parasite present.
[3] + = present.

crab females taken from Olga Bay in January 1981. Rhizocephalan externas were never detected. Rhizocephalan tissue was not found in any of the 76 blue king crabs collected from the Bering Sea and examined by us.

Data on females collected from Olga Bay in January 1981 and April 1982 were combined and then separated into various categories of reproductive condition, based on both histological condition and reproductive features of the ovary and on external reproductive features. Females in all categories were further classified by the presence or absence of rhizocephalan infection, as determined histologically (Table 3).

The effect of the rhizocephalan on female reproduction was examined by testing the independence of probable future reproductive success and rhizocephalan presence. Based on ovarian categories (Table 3), probable future reproductive success was judged as either successful (no degenerating gonadal cells) or unsuccessful (ovary empty or ovary with degenerate gonadal cells). Independence of probable future success and rhizocephalan presence was rejected for both measures, implying that rhizocephalan infestation significantly reduces the probability of future reproductive success ($\chi^2 = 16.81$, df = 1, $P < 0.001$ for empty ovary; $\chi^2 = 20.41$, df = 1, $P < 0.001$ for ovary with degenerate gonadal cells).

Three of the external categories of females (Table 3) represent crabs at different times after extrusion of ova. Embryos begin to develop eyes about 4 mo after extrusion. Hatching occurs slightly more than 12 mo after extrusion. Following hatching, empty embryo cases persist on the pleopod setae until the crab molts again, usually slightly <12 mo later (Somerton and MacIntosh in press). Therefore, the generalized time since extrusion for the uneyed, eyed, and empty-embryo-case categories is 0-4 mo, 4-14 mo, and 14-24 mo, respectively. If parasitic attacks are random and prevent successful extrusion and embryo attachment, then prevalence of the parasite should be low for females with uneyed embryos and should increase with time. Independence between prevalence and time since extrusion (using uneyed and empty-embryo-case categories) was rejected ($\chi^2 = 7.79$, df = 1, $P < 0.01$).

TABLE 3.—Prevalence of rhizocephalan infection in female blue king crabs (>68 mm CL) collected in Olga Bay, Kodiak Island, AK, January 1981 and April 1982.

	Parasitized		Not parasitized
	n	%	
Ovarian categories			
Ovary empty	15	71	6
Ovary with gonadal cells[1]			
With some degenerate cells	38	64	21
No degenerate cells	7	18	32
External categories			
Clean pleopod setae	19	51	18
Ovigerous			
Uneyed embryos	1	10	9
Eyed embryos	12	48	13
Previously ovigerous (embryo cases)	27	59	19

[1]Oocytes and/or ova.

Females are grasped by males and held in a "precopulatory embrace" before molting and mating. Of the 10 grasped females collected January 1981, 5 showed no evidence of previous reproductive activity, and 5 had empty embryo cases. None were infected with the rhizocephalan, although three of the females with empty embryo cases had some degenerate gonadal cells.

Based on the April 1982 sample, which includes males, independence between sex and rhizocephalan presence was not rejected ($\chi^2 = 0.14$, df = 1, $P = 0.75$). The rhizocephalan, therefore, does not appear to discriminate by host sex.

Presence of the rhizocephalan apparently did not affect the gonads of males. Both infected and noninfected males had numerous spermatophores in the anterior vas deferens. Spermatocytes, some of them dividing, and developing and mature sperm were present in the four crabs whose testes were sampled (one parasitized and three nonparasitized). In the field, we saw no males exhibiting female secondary sexual characteristics.

Histological Observations

Rhizocephalan roots occupied the hemal spaces of the pleopods, were associated with the exterior of the ovary, and occasionally lay within internal hemal spaces of the ovary of infected females collected in January 1981. Roots were associated with various tissues of males and females collected from Olga Bay in April 1982 (Table 2). Hemal sinuses of the ovary and those abutting the gut, the bladder, and the thoracic ganglia were the most frequently invaded sites. Roots lay within the glia of the thoracic ganglia of one crab, but otherwise were confined to hemal spaces and did not invade tissues.

Roots were cylindrical and surrounded by a PAS-positive cuticle of variable thickness (Figs. 1, 3). Cells within the roots usually had large vesicular nuclei, and refractile spherules were sometimes present in the cytoplasm. Usually the roots were tubular, with a defined lumen, and those with large, empty lumens often had a flattened epithelium. Loosely anasto-

FIGURE 1.—Olga Bay rhizocephalan: Cross sections of roots with occluded lumens. PAS. C, cuticle; S, refractile cytoplasmic spherules. Bar = 10 μm.

FIGURE 2.—Olga Bay rhizocephalan: Normal roots, lying in an area invaded by hemocytes. Note variable size of the lumen and one tubule with a group of small, central nuclei and another with anastomosing cells in the lumen (arrows). PAS. H, hemocytes; T, tubular roots. Bar = 20 μm.

mosing cells filled the lumen of some tubules, and a defined epithelium was not present in these (Fig. 2). Roots with narrow or occluded lumens often had smaller, denser nuclei in the epithelium, or an additional interior layer or group of cells with small, dense, or condensed nuclei (Fig. 2). The occluded roots may represent the distal, growing portions of the organism.

Intensity of infection varied (Table 3). In all of the heavier infections and most of the medium ones, portions of the roots were degenerate or necrotic (Fig. 3). Host hemocytes had aggregated in such areas and often had encapsulated the degenerate roots. In heavy infections with many degenerating and necrotic roots, blackened areas, probably due to melanin deposition in the roots, were visible with the naked eye in the tissues. Sometimes hemocytes had invaded the lumens of degenerate and necrotic roots, and other roots had been reduced to amorphous material surrounded by hemocytes (Fig. 3). In all cases, roots of normal appearance were also present in the same areas. In only one instance were normal roots surrounded by hemocytes (Fig. 2). Probably the section had been cut just peripherally to a large area of degenerating roots.

Ovaries of 88% (53/60) of parasitized females as opposed to 46% (27/59) of normal females either contained no oocytes or had some or all degenerate oocytes (Fig. 4). Figure 5 shows a normal ovary with previtellogenic oocytes. Grasped females all had normal oocytes that were in late vitellogenesis and enclosed by a thick chorion. Of the 10 grasped females, 9 were in the premolt condition, and the 10th, a precocious juvenile 77 mm CL, was in the intermolt.

None of the parasitized crabs were in advanced premolt, although some were judged to be in early premolt because the pleopod epidermis was thickened, and occasionally a developing epicuticle was present.

Excepting the ovary, tissues and organs appeared normal in the parasitized crabs. Whether or not there was reduced lipid storage in the hepatopancreas was not evident by histological examination of the present series.

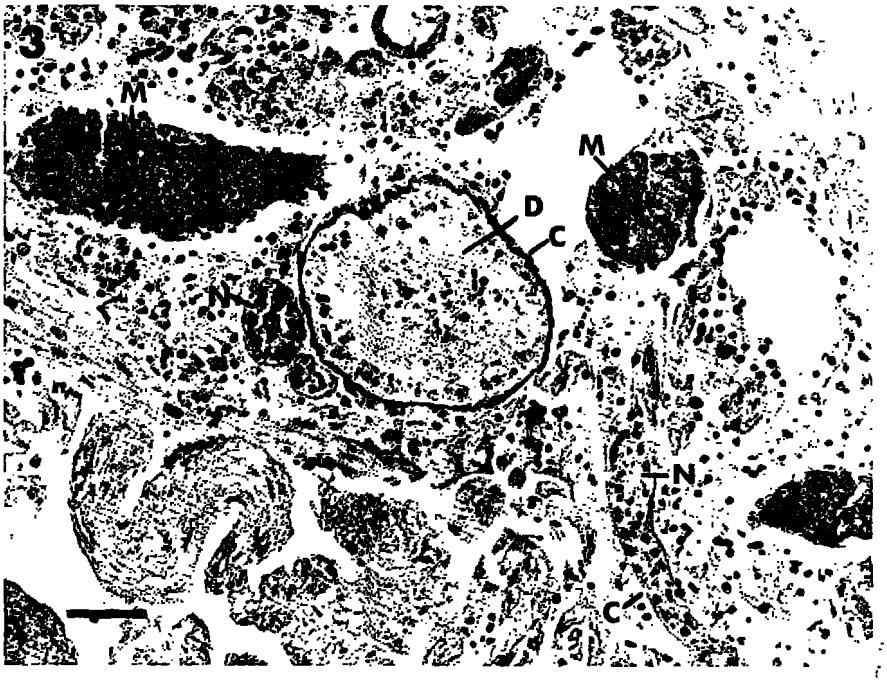

FIGURE 3.—Olga Bay rhizocephalan: Degenerating and normal roots. PAS. N, normal tubule; C, cuticle; D, tubules with sloughing epithelium; M, completely necrotic tubule; H. hemocytes. Bar = 0.05 mm.

FIGURE 4.—Olga Bay rhizocephalan: Empty ovary of an infected crab. Arrows point to roots of the parasite. PAS. Bar = 0.2 mm.

DISCUSSION

The presence of the rhizocephalan in female blue king crabs appears to impair reproductive function. Most parasitized crabs have empty ovaries or ovaries that contain degenerate gonadal cells. We assume that these traits are linked to reproductive failure, although there are also unparasitized crabs within each category. It is not unusual to find a few retained ova—destined to be resorbed—in a normal postextrusion ovary. Therefore, these crabs are also a source of degenerate gonadal cells. The 2-yr reproductive cycle of the blue king crab might also lead to presence of degenerate gonadal cells that had been produced early in the cycle and had become senescent. This speculation remains to be investigated.

The increase in the incidence of infection over time in postextrusion crabs also suggests reproductive impairment. Not only is the prevalence very low (10%) among females that had recently extruded (with uneyed embryos), it is zero among grasped premolt females that were presumably about to molt, mate,

FIGURE 5.—Normal ovary with oogonia and previtellogenic oocytes. PAS. Same scale as Fig. 4.

and extrude. These facts suggest that the rhizocephalan might preclude mating and subsequent extrusion and attachment of fertilized ova.

The external category of reproductive condition we term "clean pleopod setae" would normally be associated with immature crabs. In this study, it contained both small females and females of mature size (total size range 69-133 mm CL). The average size at maturity of females in Alaskan populations lacking the rhizocephalan ranges from 80 to 96 mm (Somerton and MacIntosh 1983). Crabs larger than 114 mm could reasonably be expected to be carrying embryos or empty embryo cases, but 10 crabs in the combined January-April sample (9 of which had the rhizocephalan) were not. Two of the parasitized females were soft-shelled, suggesting that molting can occur in parasitized females.

Presence of the rhizocephalan in male crabs from Olga Bay apparently did not interfere with normal gonadal function. Species of *Sacculina* and many other rhizocephalans cause a varying degree of external feminization and gonadal dysfunction of their male hosts (Reinhard 1956). For example, *Thompsonia mediterranea* causes external appendages of males of *Callianassa truncata* to approach the female condition (Caroli 1931), but a species of *Thompsonia* parasitizing *Portunus pelagicus* does not affect males (Phang 1975). *Briarosaccus callosus* parasitizes the blue, red, golden (*Lithodes aequispina*), and deep-sea (*Lithodes couesi*) king crabs in the Gulf of Alaska (McMullen and Yoshihara 1970; Somerton 1981; Hawkes et al. 1985). Meyers[6] found testicular regression and broadening of the abdomen in *Briarosaccus*-infected male blue king crabs from Glacier Bay.

High prevalences of infection with rhizocephalans have been reported previously in other decapod species, so the high prevalence in blue king crabs of Olga Bay is not surprising. McMullen and Yoshihara (1970) found 14 of 21 golden king crabs, captured near Kodiak Island, infected with *B. callosus*, and Hawkes et al. (1985) reported 76% prevalence of the same species in blue king crabs from Glacier Bay; Phang (1975) reported prevalences between 24% and 68% of *Thompsonia* sp. in groups of *Portunus pelagicus* captured near Singapore; and Perry (1984) said that sometimes over 50% of blue crabs sampled from a single population in the Gulf of Mexico were infected with *Loxothylacus texanus*.

Although nearly 800 blue king crabs were sampled from Olga Bay at quarterly intervals, no rhizocephalan externas were observed, and the one red king crab female found infected with what appeared to be the same rhizocephalan also lacked an externa. Due to the absence of externas, the Olga Bay rhizocephalan cannot be indentified with certainty. Its roots are similar histologically to those of other rhizocephalans [*Thompsonia* (Potts 1915); *Sacculina* (Fischer 1927; Dornesco and Fischer-Piette 1931); and *Peltogaster* and *Gemmosaccus* (Nielsen 1970)], corresponding best with the roots of *Thompsonia*, which have a thinner cuticle than the others (Potts 1915). Roots of the Olga Bay parasite differ histologically in several ways from those of *Briarosaccus callosus*. They are of lesser diameter, have a thinner cuticle, lack large peripheral nuclei, often have a large lumen and flattened epithelium, and seldom have the cytoplasmic vacuoles (probably representing lipid storage) that are common in the *B. callosus* roots. (Compare Figures 1, 2, and 3 with Figure 6.) The Olga Bay parasite and *B. callosus* also differ in that the roots of *B. callosus* are a bright green when fresh (Hawkes et al. 1985) and blue-green when fixed in Helly's solution, whereas the roots of the Olga Bay parasite are colorless.

[6]T. Meyers, Assistant Professor of Fisheries, School of Fisheries and Science, University of Alaska, 11120 Glacier Highway, Juneau, AK 99801, pers. commun. October 1984.

The lack of obvious externas on the parasitized crabs is puzzling. One possibility is that externas are produced but are inconspicuous and/or evanescent. Most rhizocephalans produce easily detected externas that emerge from the venter of the abdomen. Species of *Thompsonia*, however, produce multiple small externas 1-4.5 mm long and no more than 1.1 mm in diameter. These externas occur on the appendages and venters of the thorax and abdomen, depending on the species, and those of at least one of the species are easily dislodged (Häfele 1911; Potts 1915; Phang 1975). If few and scattered externas of the *Thompsonia* type were present, they could have escaped notice on animals as large as the blue king crabs investigated. The second possibility is that externas are not developed in the blue king crab. Host ranges of rhizocephalans are often broad, but some of the host/parasite associations may be accidental or not fully evolved. *Sacculina carcini* is known to react differently in different species of crabs. In *Carcinus maenas* multiple broods of larvae are produced by *S. carcini*, but if the host is *Portunus holsatus*, it breeds but once and then is shed, which suggests that *C. maenas* is a natural host but *P. holsatus* is an adventitious and not entirely competent one (Baer 1951). Perhaps the Olga Bay parasite is not a usual parasite of the blue king crab, and although the interna develops extensively and causes severe damage to female gonads, externas cannot be produced in this species. The fact that some roots of the parasite were degenerating or necrotic in most infected crabs suggests that parasites do die within the blue king crab, and that infections might be lost before externas are formed.

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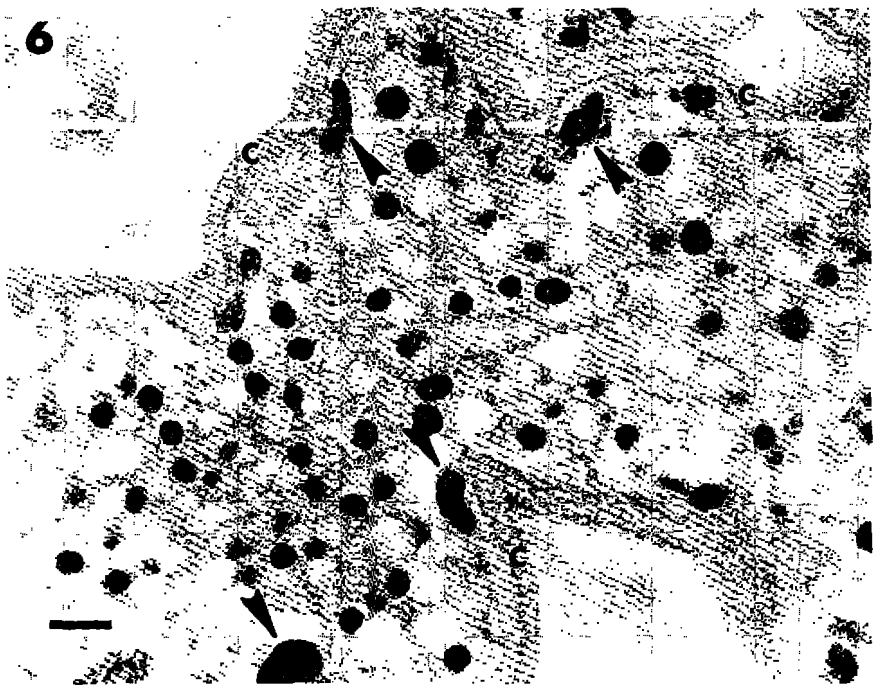

FIGURE 6.—*Briarosaccus callosus*: Roots. Note lack of a central lumen and the very large, peripheral nuclei (arrows). Feulgen. C, cuticle. Bar = 10 μm.

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