Infestation by Brood Symbionts and Their Impact on Egg Mortality of the Red King Crab, *Paralithodes camtschatica*, in Alaska: Geographic and Temporal Variation

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Egg masses of 772 red king crab, *Paralithodes camtschatica*, were sampled to determine the prevalence, intensity, and patterns of cooccurrence of brood symbionts from 28 Alaskan localities. *Carcinonemertes regicides* and three other undescribed nemertean egg predators were recovered from many localities, as were an undescribed turbellarian and an amphipod, *Ischyrocerus* sp. A widespread outbreak of nemerteans occurred in the 1983–84 and 1984–85 red king crab brooding seasons. At some locations, nearly all of the eggs were consumed in the 1983–84 brood season. Feeding of *C. regicides* on eggs was documented in vitro and these worms caused substantial egg mortality at many locations. The amphipod was also an egg predator and may have had a significant impact at three locations. The turbellarian did not kill eggs. From the seasonal pattern of *C. regicides* infestation at Kachemak Bay, we postulate an abbreviated life cycle and autoinfection for *C. regicides*. Such life history features may have contributed to the peak intensities observed late in the 1983–84 and 1984–85 brooding seasons. At some localities, heavy brood mortality may reduce or eliminate recruitment of some year classes to the fishery.

Les masses d'oeufs de 772 crabes royaux rouges *Paralithodes camtschatica* ont été échantillonnées afin de déterminer la fréquence, le degré d'infestation et les régimes de coexistence de symbiotes à 28 endroits de l'Alaska. *Carcinonemertes regicides* et trois autres némertiens inconnus, prédateurs des oeufs de crabe, ont été découverts à de nombreux endroits, ainsi qu'un turbellarié inconnu et un amphipode du genre *Ischyrocerus*. Une flambée générale de némertiens s'est produite au cours des saisons de reproduction du crabe royal rouge en 1983–1984 et 1984–1985. À certains endroits, presque tous les oeufs ont été dévorés au cours de la saison 1983–1984. La prédation des oeufs de crabe par *C. regicides* a été étudiée *in vitro*; ces vers sont la cause d'un taux élevé de mortalité des oeufs à de nombreux endroits. L'amphipode *Ischyrocerus* sp. est aussi un prédateur des oeufs et peut avoir eu un important impact à trois endroits. Le turbellarié n'a pas dévoré les oeufs. D'après le régime saisonnier d'infestation de *C. regicides* dans la baie Kachemak, les auteurs formulent l'hypothèse que le cycle vital de *C. regicides* est raccourci et qu'il y a auto-infection. Ces caractéristiques du cycle vital peuvent avoir contribué aux degrés d'infestation élevés observés vers la fin des saisons de reproduction de 1983–1984 et 1984–1985. À certains endroits, un taux de mortalité élevé des oeufs de crabe peut réduire ou éliminer le recrutement de certaines classes d'âge à la pêche.

O ver the last three decades the red king crab, *Paralithodes camtschatica*, from Alaska has provided one of the most valuable crab fisheries in the world (Otto 1981). In the 1980–81 season, 81 200 t of red king crab was harvested, the third highest yield in the history of the fishery. Three years later (1983–84) the harvest declined precipitously to 1000 t, the lowest catch in over 30 yr. Six of 11 Alaska Department of Fish and Game (ADF&G) management areas were completely closed to commercial crab fishing in 1983.

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Near-term recovery of these stocks cannot presently be predicted (Blau 1986).

Fishery biologists from the ADF&G and the U.S. National Marine Fisheries Service (NMFS) have monitored aspects of red king crab biology using annual surveys in various management areas for 15 yr. Visual observations on the size (reported as percentage full clutch) and state of crab egg clutches have been a regular component of these surveys (Blau 1986). Fertilized eggs (embryos) are usually oviposited in the spring (March to May) and are brooded on pleopods under the abdomen of the female crab for 11–12 mo. Hatching precedes the annual molt of the female in the following March or April (Powell and Nickerson 1965). The ADF&G biologists from Homer noted that the egg clutches of red king crabs from Kachemak Bay, in the Cook Inlet Management Area, were much smaller in November 1982 and January 1983 than were clutches examined in July 1982. Of 143 females collected in November 1982 and January 1983, the clutches of 66% were rated less than 30% full clutch (G. C. Powell, unpubl. obs.). Although some living embryos were still present in these clutches and appeared to be developing normally, many embryos were dead; often only their empty egg membranes remained attached to the pleopods. Further examination revealed that nemertean and turbellarian worms were abundant in these egg masses (Wickham et al. 1985; Blau 1986). The nemerteans included several undescribed species of *Carcinonemertes* and related undescribed genera (Wickham and Kuris 1988; Gibson et al. 1990). A new species, *C. regicides*, was the most abundant of these (Shields et al. 1989). All of the known species in this genus are symbionts of decapod crustaceans and feed on the eggs of their host (Wickham and Kuris 1985). One species, *C. errans*, has caused substantial egg mortality and has been implicated in the prolonged nonrecovery of the Dungeness crab, *Cancer magister*, fishery in central California (Wickham 1979, 1986; Kuris and Wickham 1987).

A sampling program was begun in 1983, over a large portion of the geographic range of *P. camtschatica*, to investigate the decline observed in some red king crab stocks, coincident with reports of massive egg mortalities and high-intensity infestations of nemerteans. Our goal was to determine the role of *Carcinonemertes* with respect to crab egg losses and evaluate its occurrence and impact over the range of the red king crab in Alaska. Firstly, clutch samples were collected over as broad a geographic range of the red king crab in Alaska as feasible. Egg mortality was quantified, and clutch symbionts were identified and enumerated. Relative contributions of the several symbionts to egg mortality were assessed. To study the seasonality of egg mortality, progressive embryo losses were documented for the red king crab through the brooding season in Kachemak Bay. Lastly, the role of *C. regicides* as an egg predator was established by laboratory observations including an experimental study of egg mortality in captive female crabs.

Materials and Methods

Adult female red king crabs were captured during 1983–85 over a broad geographic range in eight ADF&G king crab management areas: Southeastern Alaska, Cook Inlet (Kachemak and Kamishak bays), Kodiak Island, Alaska Peninsula, Dutch Harbor, Adak, Bristol Bay, and Norton Sound (Fig. 1). Females were caught either in baited king crab pots or in 400 eastern otter trawls primarily on ADF&G or NMFS surveys, which were generally conducted in the summer. Females were occasionally obtained from fishermen during various commercial seasons. Eighteen male and 12 nonovigerous female crabs were examined for nemerteans at Seward and Juneau.

To provide a sample to quantify egg mortality and the abundance of nemertean worms and other symbionts, the fourth pleopod of each female crab was excised at its base and preserved immediately in a vital containing 5% formalin in seawater (FSW). Of the six pleopods present, the fourth was chosen because it is located near the center of the clutch. The second to fifth pleopods carry most of the eggs (Marukawa 1933). A comparison of worm intensity among pleopods of the yellow rock crab, *Cancer anthonyi*, found that a sample of a single pleopod was a good representation of overall intensity and also of crab fecundity (Shields et al. 1990a). Carapace length, estimate of percent clutch size, depth, and location of capture were recorded for each female sampled. Percent clutch is a visual estimate of the percentage of the maximum volume of eggs that a female of such a size could carry (Blau 1986). It provides a rough estimate of fecundity (Shields et al. 1990b). Collections generally consisted of 5–30 pleopods from each management area surveyed during the summer. Replicate samples of 10 pleopods per month for several months each year were taken in Kachemak Bay, in the Cook Inlet Management Area. Seasonal sampling also occurred around Kodiak Island as additional nonsummer surveys became available. After January 1985, sampling at Kachemak Bay was randomized so that every tenth crab collected was sampled. The individual collection sites within the ADF&G king crab management areas sampled are listed in Tables 1 and 2 and are shown in Fig. 1 and 2.

To quantify nemertean infestation intensity and egg mortality on individual crabs, the symbionts present in a pleopod sample were extracted by agitation of the pleopod, identified, counted, and preserved in FSW. Manual separation of the eggs from six of these pleopods showed that over 99% of the worms were obtained by the agitation method. If the number of extracted worms exceeded about 2000, a subsampling procedure was used to estimate the number of worms per pleopod sample. The worms were poured into a petri dish with a 1-cm^2 grid. Worms were counted in six squares. The mean number of worms per square centimetre was then multiplied by the area of the dish (square centimetres) for the estimated total number of worms per pleopod. After the worms were separated from the eggs, all of the egg-bearing setae of each sampled plepod were carefully removed from the pleopod and a subsample of approximately 1000 eggs was counted and assessed for egg mortality as in Wickham (1979). Crabs whose clutches were in the process of hatching, or had already hatched, were excluded from this analysis, as egg mortality could not be distinguished from hatched eggs. Intact eggs containing normally developing embryos were counted as live, while eggs containing abnormal embryos, or eggs partially or completely devoid of their contents, were counted as dead. Abnormal eggs included opaque eggs, presumably infected with fungi, and eggs whose developmental stage was markedly retarded compared with the rest of the brood. In four samples from the Kodiak Management Area, frayed or broken funiculi, indicating detachment of eggs, were numerous (see Table 2). In these samples the mortality estimate included the count of such funiculi. Egg mortality was expressed as a percentage of the number of dead eggs per total number of counted eggs. Samples from 765 red king crabs (*Lithodes aequispina*) were analyzed in this manner.
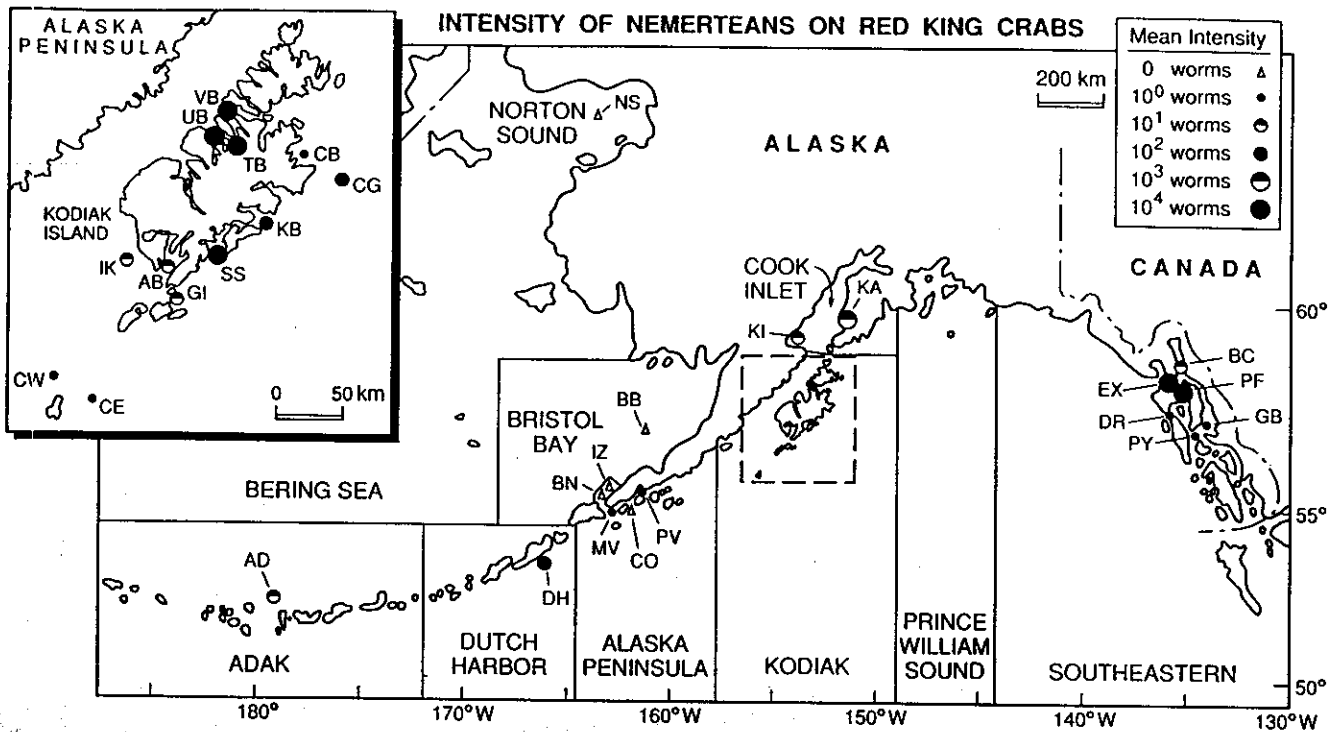
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FIG. 1. Geographic distribution and intensity of *Carcinonemertes regicides* in the egg masses of red king crabs, *P. camtschatica*, in Alaska. Management areas are labelled and their boundaries are demarcated. Collecting site abbreviations are coded as in Table 1. Intensity ranges over five orders of magnitude as coded in the upper right-hand corner. Samples collected early in the brooding season (April to May) when few worms were present and egg mortality was low were omitted (see Table 1). Inset enlarges collecting sites in the Kodiak Island Management Area (broken box).
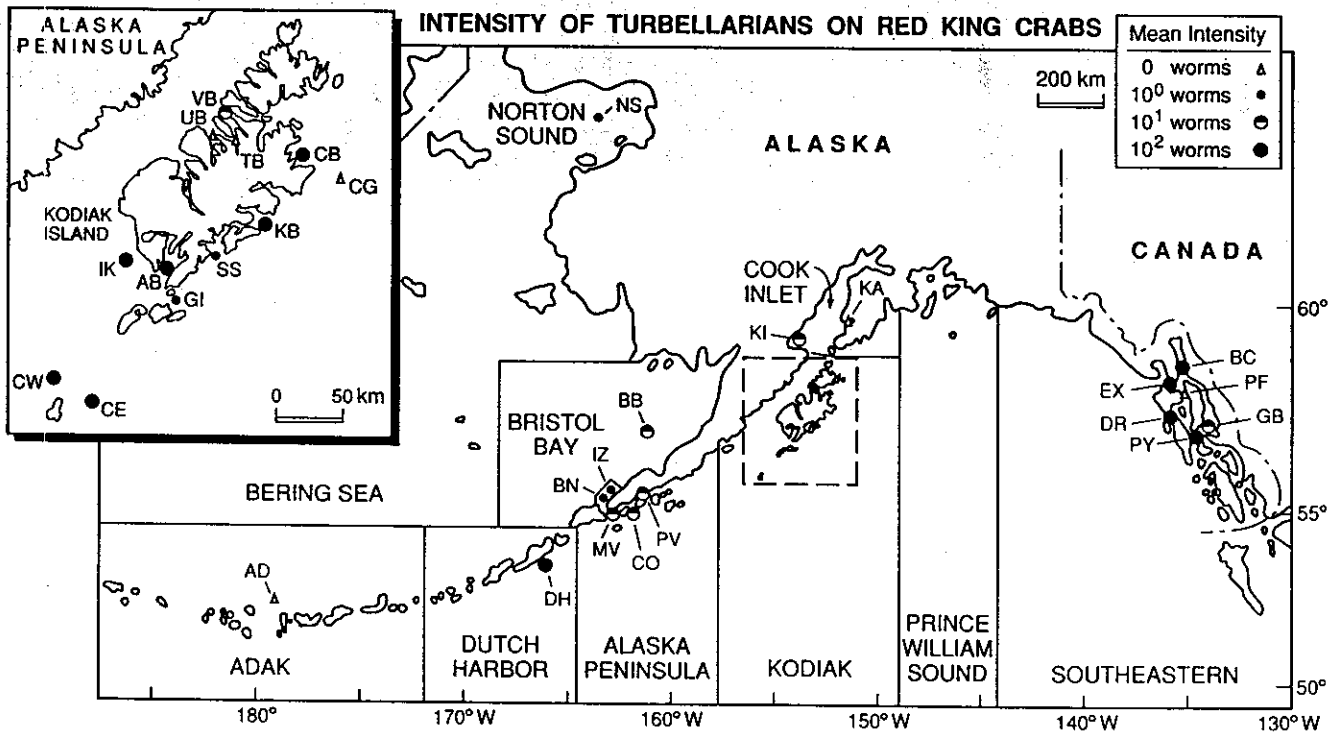

FIG. 2. Geographic distribution and intensity of turbellarians in the egg masses of red king crabs, *P. camtschatica*, in Alaska. Intensity ranges over three orders of magnitude as coded in the upper right-hand corner. See Table 1 for locality codes and Fig. 1 for other details.

In the laboratory of the Seward Marine Center, an experimental study of egg mortality compared egg losses on infested ovigerous female crabs from Kiliuda Bay and Uganik Bay (Kodiak Island) with egg losses on uninfested crabs from Kam- ishak Bay (Cook Inlet). All of these crabs were collected in the spring and summer of 1984. Sample sizes were 7, 22, and 20 crabs, respectively. Crabs from each location were maintained separately in flowing seawater at 6–11°C with a salinity of 31–

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33 ppt. Every 30 d for 120 d, a random sample of eggs was removed from the pleopods and 300 eggs were counted. The proportion of dead eggs (empty shells or opaque embryos) and the number of nemerteans present were recorded. Additional observations on worm behavior and feeding were made in vitro.

The terms prevalence and mean intensity are defined in Margolis et al. (1982). Briefly, prevalence is the proportion of infested individuals in the host population, and mean intensity is the mean number of symbionts per infested host.

Statistical analyses were computed with the aid of SAS Institute, Inc. (1982) as per Sokal and Rohlf (1981). Correlation

analyses were run on data with and without log transformation. A value of $P < 0.05$ was accepted as significant.

Results

Geographic Variation of Brood Mortality

Egg mortality increased during the brooding season (see below); thus, geographical comparisons were best made in the middle of or late in the brooding season (after July). Brood mortality exhibited considerable geographic variation (Tables

TABLE 1. Mortality of eggs of the red king crab, *P. camtschatica*, and prevalence (percentage of crabs infested) and mean intensity (number of symbionts per pleopod) ($\bar{X} \pm$ SD) of symbiotic nemerteans, turbellarians, and amphipods from various Alaskan locations (see Table 2 for details in the Kodiak Island Management Area). *N* is sample size.

Management areas and collection sites	Date (mo/yr)	N	Crab egg mortality (%)	C. regicides Prevalence (%)	C. regicides Intensity ($\bar{X} \pm$ SD)	Nemertean form 4 Prevalence (%)	Nemertean form 4 Intensity ($\bar{X} \pm$ SD)	Nemertean form 5 Prevalence (%)	Nemertean form 5 Intensity ($\bar{X} \pm$ SD)	Turbellaria spp. Prevalence (%)	Turbellaria spp. Intensity ($\bar{X} \pm$ SD)	Ischyrocerus sp. Prevalence (%)	Ischyrocerus sp. Intensity ($\bar{X} \pm$ SD)
Southeastern Alaska													
Barlow Cove (BC)	6/83	5	0.4 ± 0.3	100	48 ± 15	60	36 ± 14	40	32 ± 42	100	167 ± 145	40	2 ± 1
Deadman's Reach (DR)	6/83	5	0.4 ± 0.4	100	11 ± 5	0	—	100	11 ± 5	100	392 ± 327	0	—
Excursion Inlet (EX)	6/83	3	78.3 ± 15.3	100	10 248 ± 5950	100	6041 ± 5372	0	—	33	433	33	1
Gambier Cove (GB)	6/83	5	0.5 ± 0.6	60	4 ± 3	0	—	60	4 ± 2	100	56 ± 51	0	—
Port Frederick (PF)	6/83	7	72.9 ± 35.5	100	18 522 ± 15 006	57	6693 ± 2186	0	—	0	—	0	—
Pybus Cove (PY)	6/83	5	0.0 ± 0.0	60	7 ± 7	0	—	60	7 ± 5	100	237 ± 268	0	—
Cook Inlet													
Kachemak Bay (KA)	2/83	9	54.1 ± 33.3	100	347 ± 276	0	—	0	—	22	178 ± 189	33	19 ± 6
	7/83	10	47.5 ± 40.4	100	2008 ± 2286	0	—	0	—	0	—	0	—
	8/83	11	87.3 ± 24.6	100	2591 ± 2616	0	—	0	—	0	—	0	—
	10/83	15	95.6 ± 16.8	100	2712 ± 2100	0	—	0	—	0	—	13	8 ± 3
	3/84	10	0.1 ± 0.2	10	1	0	—	0	—	0	—	0	—
	4/84	10	0.1 ± 0.2	20	3 ± 3	0	—	0	—	0	—	0	—
	5/84	5	0.1 ± 0.3	0	—	0	—	0	—	0	—	0	—
	6/84	20	1.0 ± 1.1	100	345 ± 419	0	—	0	—	0	—	0	—
	9/84	19	59.2 ± 20.7	100	1229 ± 1232	0	—	0	—	0	—	10	1 ± 0
	11/84	20	45.4 ± 18.8	100	217 ± 224	0	—	0	—	0	—	10	5 ± 1
	4/85	20	—[a]	0	—	0	—	0	—	0	—	45	6
	7/85	30	0.4 ± 0.4	100	17 ± 21	0	—	0	—	0	—	0	—
	11/85	14	6.7 ± 13.7	100	28 ± 15	0	—	0	—	0	—	21	1 ± 0
Kamishak Bay (KI)	6/83	25	2.1 ± 6.5	88	23 ± 34	0	—	0	—	0	—	0	—
	6/84	29	0.4 ± 0.7	31	6 ± 5	0	—	0	—	55	12 ± 15	0	—
Alaska Peninsula													
Bechevin Bay (BN)	9/83	5	0.4 ± 0.8	0	—	0	—	0	—	60	7 ± 10	0	—
Cold Bay (CO)	8/84	5	1.6 ± 2.5	0	—	0	—	0	—	80	58 ± 73		
Izembek Lagoon (IZ)	9/83	10	0.2 ± 0.4	0	—	0	—	0	—	75	8 ± 11	0	—
Morshovoi Bay (MV)	7/84	10	0.6 ± 0.4	0	—	70	1 ± 1	0	—	100	37 ± 35	0	—
Pavlof Bay (PV)	9/83	10	0.8 ± 1.2	0	—	30	1 ± 0	0	—	100	21 ± 14	0	—
	8/84	10	0.2 ± 0.1	0	—	30	5 ± 3	0	—	100	25 ± 23	0	—
Dutch Harbor (DH)	10/83	10	13.3 ± 24.0	80	20 ± 21	40	14 ± 15	30	2 ± 2	100	142 ± 137	10	4
	8/84	22	37.1 ± 39.7	96	1976 ± 3968	5	10	23	29 ± 35	46	311 ± 417	9	4 ± 4
	8/85	14	30.3 ± 30.8	100	1053 ± 2047	77	1509 ± 2268	0	—	43	369 ± 800	7	4
Adak (AD)	12/83[b]	8	6.1 ± 7.5	0	—	25	2 ± 1	50	62 ± 35	75	41 ± 67	0	—
Bristol Bay (BB)	6/84	11	1.9 ± 1.3	0	—	0	—	0	—	0	—	0	—
	8/84	9	1.3 ± 1.9	0	—	0	—	0	—	0	—	0	—
	9/84	19	0.3 ± 0.3	0	—	0	—	0	—	79	33 ± 33	0	—
	6/85	28	0.0 ± 0.0	0	—	0	—	0	—	10	11 ± 12	7	1 ± 0
Norton Sound (NS)	8/83[c]	28	0.0 ± 0.0	0	—	0	—	0	—	0	—	0	—
	8/84	30	0.2 ± 0.3	7	1 ± 0	0	—	0	—	3	11	0	—
	7/85	19	0.0 ± 0.0	0	—	0	—	0	—	0	—	0	—

[a]Egg mortality could not be quantified because eggs were hatching in this sample.
[b]Includes samples from 11/83.
[c]Includes samples from 6/83.

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Table 2. Mortality of eggs of the red king crab, *P. camtschatica*, and prevalence (percentage of crabs infested) and mean intensity (number of symbionts per pleopod) ($\bar{X} \pm$ SD) of symbiotic nemerteans, turbellarians, and amphipods from various sites in the Kodiak Island Management area. *N* is sample size.

Management areas and collection sites	Date (mo/yr)	N	Crab egg mortality (%)	C. regicides		Nemertean form 4		Nemertean form 5		Turbellaria spp.		Ischyrocerus sp.	
				Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)	Prevalence (%)	Intensity ($\bar{X} \pm$ SD)
Alitak Bay (AB)	2/84	15	4.4 ± 3.3	80	9 ± 5	67	16 ± 19	7	2	80	61 ± 133	47	1 ± 1
	8/84	7	1.9 ± 1.9	100	23 ± 40	71	5 ± 7	14	1	100	356 ± 407	29	2 ± 1
	2/85	13	23.7 ± 27.6	85	50 ± 28	0	—	0	—	62	46 ± 49	38	4 ± 5
	4/85[a]	15	—[b]	62	16 ± 19	40	19 ± 16	0	—	53	674 ± 954	27	7 ± 9
	4/85[a]	3	1.9 ± 3.1	0	—	0	—	0	—	33	54	0	—
Chiniak Bay (CB)	9/83	4	0.7 ± 1.3	100	5 ± 3	100	2 ± 1	25	1	100	458 ± 266	25	1
	1/84	6	0.3 ± 0.7[c,d]	33	1 ± 0	17	2	0	—	100	493 ± 371	100	2 ± 1
	8/84	5	0.3 ± 0.2	80	4 ± 4	20	2	0	—	100	166 ± 84	0	—
Chiniak Gully (CG)	8/83	10	7.9 ± 19.1	100	529 ± 550	0	—	0	—	0	—	0	—
	4/84	3	—[b]	100	41 ± 32	0	—	0	—	0	—	0	—
East of Chirikof I. (CE)	7/84	9	0.1 ± 0.1	22	2 ± 1	22	2 ± 1	0	—	100	469 ± 431	44	2 ± 1
West of Chirikof I. (CW)	7/83	3	0.0 ± 0.0	33	1	10	1	0	—	100	259 ± 237	67	2
Geese Island (GI)	2/85	8	52.6 ± 37.6[c]	75	87 ± 102	0	—	0	—	12	9	50	8 ± 6
Cape Ikolik (IK)	2/84	17	2.5 ± 1.4[c]	65	11 ± 8	82	8 ± 4	47	10 ± 7	82	469 ± 515	100	2 ± 1
	8/84	10	3.5 ± 4.4	100	5 ± 7	50	5 ± 3	0	—	100	152 ± 155	50	1 ± 0
Kiliuda Bay (KB)	2–3/83	10	—[b]	30	385 ± 288	70	48 ± 55	0	—	0	—	10	9
	2/84	12	29.5 ± 28.7[c]	92	10 ± 6	83	17 ± 9	17	2 ± 1	83	567 ± 1044	100	12 ± 17
	7/84	10	17.0 ± 14.8	100	632 ± 570	100	723 ± 871	10	2	50	169 ± 218	0	—
Sitkalidak Strait (SS)	8/83	1	70.2	100	2 024	0	—	0	—	100	5	0	—
	2/84	8	34.8 ± 32.3[c]	62	4 ± 4	50	9 ± 8	12	1	25	4 ± 3	88	18 ± 25
	6/84	10	11.3 ± 28.6	100	8098 ± 16 352	60	357 ± 350	60	2 ± 2	0	—	0	—
Terror Bay (TB)	6/84	13	72.5 ± 24.0	100	85 244 ± 22 918	100	24 672 ± 28 325	0	—	0	—	0	—
	2/85	1	100.0	100	28	0	—	0	—	0	—	0	—
Uganik Bay (UB)	9/83	5	70.7 ± 44.3	100	379 ± 309	0	—	0	—	0	—	40	1
	6/84	12	41.0 ± 19.9	100	24 935 ± 7456	100	17 654 ± 10 160	0	—	0	—	0	—
	8/84	13	84.5 ± 21.9	100	28 759 ± 29 817	100	21 952 ± 12 061	0	—	0	—	46	1 ± 1
Viekoda Bay (VB)	9/83	2	34.4 ± 48.6	100	19 ± 12	100	222 ± 37	0	—	100	93 ± 130	100	6 ± 1
	6/84	10	5.8 ± 6.9	100	1758 ± 963	100	1684 ± 978	0	—	0	—	40	1 ± 0
	8/84	5	68.4 ± 26.3	100	1415 ± 1221	100	8545 ± 8700	0	—	0	—	40	1 ± 0

[a]At AB in 4/85, 15 crabs had very late embryos from the 1983–84 brooding season and three crabs had recently oviposited early embryos from the 1985–86 brooding season.
[b]Egg mortality could not be quantified because eggs had begun to hatch in these samples.
[c]Eggs of some or all of the samples had numerous frayed funiculi consistent with heavy predation by *Ischyrocerus*.
[d]Does not include one sample with 100% egg loss and many frayed funiculi.

1 and 2). Losses were considerable (>30%) or severe (>70%) in some samples from Kachemak Bay in the Cook Inlet Management Area, Excursion Inlet and Port Frederick in the Southeastern Alaska Management Area, and at Dutch Harbor. In the Kodiak Archipelago, considerable or severe egg mortality was seen at Geese Island, Sitkalidak Strait, Terror Bay, Uganik Bay, and Viekoda Bay. Other locations exhibited little egg mortality (<5%), for example Barlow Cove in Southeastern Alaska, Kamishak Bay in Cook Inlet, and Chiniak Bay on Kodiak Island, Brood mortality was also negligible in samples from Bristol Bay and Norton Sound. In the Adak Management Area, 6.1% egg mortality was recorded.

Presence of Symbionts

Several kinds of symbionts were associated with the eggs of red king crabs. At least five species of nemerteans, one species of turbellarian, and one species of amphipod, *Ischyrocerus* sp., some of which were similar to *I. anguipes*, Sars 1895, were recognized. One species of nemertean, *C. regicides*, Shields et al. 1989, was most abundant and widespread. It is a small (1–3 mm) two-eyed nemertean and was formerly designated from No. 1 by Wickham and Kuris (1988). Four other species of symbiotic nemerteans found in these samples have been partially described (Wickham and Kuris 1988; Gibson et al. 1990). These undescribed nemertean species have been designated form Nos. 2–5 (Wickham and Kuris 1988). Form 4 is also abundant and widespread.

Carcinonemertes regicides was not present on the male and nonovigerous crabs examined. Two of these crabs were infested with juvenile worms of form 4.

Geographic Range and Abundance of Symbionts

Carcinonemertes regicides was recorded from all management areas sampled except the Alaska Peninsula, Bristol Bay,

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and Adak (Tables 1 and 2). It reached very high mean intensities (>10³ worms per pleopod) in Kachemak Bay (Cook Inlet), in the vicinity of Kodiak Island near Dutch Harbor, and in Southeastern Alaska (Fig. 1). It was recovered as far north as Norton Sound and as far west as Dutch Harbor. In the Kodiak Island area, where sufficient samples are available for a finer scale geographic analysis, C. regicides reached peak mean intensities of >10³ worms per pleopod along the northwest coast of Kodiak Island and in Sitkalidak Strait.

From 4 of Wickham and Kuris (1988), a small, eyeless species, was recovered from 10 of the 12 localities in the Kodiak Archipelago, in Southeastern Alaska, along the southern coast of the Alaska Peninsula, near Dutch Harbor, and Adak (Tables 1 and 2). It was also observed in unquantified samples from Resurrection Bay, Cook Inlet Management Area. Form 4 was recovered in relatively low numbers except at Kiliuda Bay, Sitkalidak Strait, Uganik Bay, and Viekoda Bay near Kodiak Island, at some Southeastern Alaska localities, and near Dutch Harbor. At these localities, intensity was high, ranging from 10² to 10⁴ worms per pleopod (Table 2).

Form 5 of Wickham and Kuris (1988) was also eyeless but long and robust. It was found at 5 of the 12 localities in the Kodiak Island Management Area but was never common (Table 2). Prevalence did not exceed 60% and intensity was never more than 10 worms per pleopod. It was present in Southeastern Alaska, ranged as far west as the Adak Management Area, and was found near Dutch Harbor (Table 1). However, it was absent from the several localities sampled along the Alaskan Peninsula. It was also absent from Cook Inlet, Bristol Bay, and Norton Sound. In the Kodiak Island Management Area it always cooccurred with form 4. However, in Southeastern Alaska and Adak it was generally present at localities where form 4 was absent or rare. Intensity of these worms was highest at Adak where it reached an intensity of 62 worms per pleopod (Table 1).

Form 2 of Wickham and Kuris (1988) could be recognized in fresh samples on the basis of proboscis armature measurements and the type of sheath produced by adult males. In preserved samples it was distinguished from C. regicides on the basis of its larger size. Examination of the size distribution of worms in our preserved samples suggests that it was not abundant at any locality. Form 2 probably includes the newly described species of symbiotic nemertean, Alaxinus oclairi, collected near Juneau in Southeastern Alaska (Gibson et al. 1990).

The remaining species, form 3 of Wickham and Kuris (1988), had two eyes and an expanded head. Only a single specimen was recognized in a fresh sample from Kiliuda Bay, east of Kodiak Island.

Turbellarians were widespread, ranging from Dutch Harbor in the south and west to Norton Sound in the north and Southeastern Alaska in the east (Table 1; Fig. 2). At many localities, prevalance was 100%. They reached high levels of intensity (>10² per pleopod) near Dutch Harbor, at several sites in Southeastern Alaska, and in 1 of 13 samples from Kachemak Bay. Turbellarians were recovered from 9 of the 12 localities in the Kodiak Archipelago (Table 2; Fig. 2). They reached high intensities (>10² per pleopod) at Alitak Bay, Chiniak Bay, Chirikof Island, Cape Ikolik, and Kiliuda Bay. In contrast, turbellarians were not recovered from Chiniak Gully, Terror Bay, and Uganik Bay.

Both presence and abundance of the amphipod Ischyrocerus sp. were undoubtedly underestimated, as these may become

dislodged during collection and preservation of the samples. It was recorded as present in samples from Southeastern Alaska, west to Dutch Harbor, and north to Bristol Bay and Cook Inlet (Table 1). These amphipods were collected from 10 of 12 locations in the Kodiak Management Area (Table 2). It was absent in samples from the Alaska Peninsula and Norton Sound. When present, prevalence was generally low (often about 10%) (Tables 1 and 2). The highest mean intensities were observed in the 2/83 sample from Kachemak Bay (19 amphipods per pleopod) and the 2/84 sample from Sitkalidak Strait (18 amphipods per pleopod).

Seasonal and Annual Patterns

Our most extensive series of observations at one locality was for Kachemak Bay, south of Homer on the Kenai Peninsula. Virtually all nemerteans recovered from this area were C. regicides (Table 1). Shortly after oviposition in March or April, few female red king crabs were infested with nemerteans and worm intensity was very low. By June, all of the crabs examined were infested but intensity remained low. Little egg mortality was observed. Intensity rose sharply in July and August, reaching a mean approaching 2600 worms per pleopod in August 1983. Worms were readily visible in the egg mass of such heavily infested crabs. Brood mortality was appreciable in 1983 and 1984 (45–85%). In September and October, worm prevalence and intensity remained high and clutch losses rose from 59 to near 100% in those years. In the late fall and winter, nemertean intensity declined, although prevalence remained high. Egg mortality did not increase further through the remainder of the brooding period.

In Kachemak Bay, samples from the 1983–84 and 1984–85 brooding seasons exhibited mean intensities of nemerteans of 2700 and 1200 worms per pleopod, and mortality peaked at 96 and 59%, respectively. In the 1983–84 brooding season, clutch mortality was virtually total. Intensity of the infestation and the associated egg mortality subsided in the 1985–86 brooding season.

Comparable longitudinal data for the turbellarians at Kachemak Bay are lacking because only a few turbellarians were collected in but a single sample. To develop a picture of seasonal dynamics of the turbellarian, all collections from the Kodiak region were combined. Only 5 mo were represented. No consistent seasonal or annual patterns were evident.

At Kachemak Bay, the amphipod Ischyrocerus sp. appeared to have a seasonal pattern of abundance (Table 1). It was not recovered in any of the samples taken in the first half of the brooding season (April to August) but was present in seven of eight samples from the latter part of the brooding season (September to April). It reached its peak in both prevalence and intensity in February. These sparse observations are supported by data from other locations. From various sites in the Kodiak Archipelago, presence of the amphipod increased from 7 of the 13 samples taken early in the brooding season to 11 of 13 samples from late in the brooding season. Both prevalence and intensity were generally higher in the later samples.

Egg Loss in Captive Crabs

We compared changes in egg survival and nemertean density on crabs held in flowing seawater. At capture, the uninfested control crabs (from Kamishak Bay) had experienced negligible egg mortality (2.4%) which did not increase during the 120 d of captivity (Fig. 3). In contrast, crabs from Kiliuda Bay had
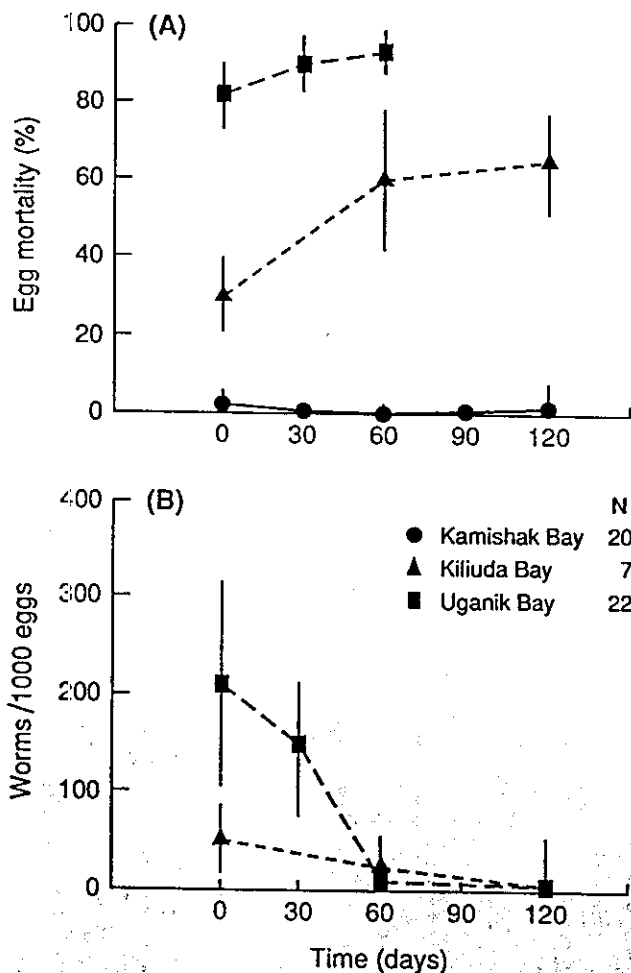
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FIG. 3. Changes in (A) egg mortality and (B) nemertean density (worms per 1000 crab eggs) of *C. regicides* on red king crabs held in captivity for 120 d at the Seward Marine Center. Clutches were from the 1985–86 brooding season. Uninfested control crabs were collected from Kamishak Bay, Cook Inlet. Infested crabs were collected from Uganik and Kiliuda bays, Kodiak Island, Alaska. Error bars represent standard deviations.

an initial mortality of 30% and a mean density of 48 nemerteans per 1000 crab eggs. Mortality rose to 68% over the 120-d observation period. Nemertean abundance decreased substantially over the observation period. Crabs from Uganik Bay had already suffered 86% egg mortality upon capture. Over 60 d, mortality increased to 94%. Nemertean abundance of these crabs was 204 per 1000 crab eggs at the start and declined to 3 per 1000 crab eggs at the end of the observation period. A comparable loss of nemerteans in situ under captive conditions has also been observed for *Carcinonemertes epialti* on *Hemigrapsus oregonensis* (Kuris 1978).

Feeding Behavior of Symbionts

Examination of living worms from captive crabs revealed that most worms were *C. regicides*. Some of the small eyeless nemerteans (form 4) were present. Both species of nemerteans were observed feeding on crab eggs in vitro. These nemerteans were seen to pierce intact egg membranes and feed on the contents using the sucking action of their pharynx as reported for other species of *Carcinonemertes* (Wickham 1978; Roe 1984). In addition, crab egg yolk and eye placodes were frequently

TABLE 3. Pearson product-moment correlation (*r*) for egg mortality (%) in relation to intensity of various symbionts inhabiting the clutch of *P. camtschatica*. Data from crabs collected in the Kodiak Island Management Area from June to August 1984 ($N = 80$). *$0.01 < P < 0.05$, **$P < 0.01$, correlation coefficients significantly different from zero.

Symbiont	*r*
Carcinonemertes regicides	0.552**
Nemertean form 4	0.458**
Both nemerteans[a]	0.657**
Turbellarians	−0.326*
Ischyrocerus sp.	0.010

[a]*C. regicides* and nemertean form 4 combined for analysis.

TABLE 4. Correlation (*r*) matrix for the various symbionts found in the clutches of *P. camtschatica*. ND indicates comparison was not made. Data are from crabs collected in the Kodiak Island Management Area from June to August 1984 ($N = 80$). *$P < 0.05$, correlation coefficient significantly different from zero.

	C. regicides	Nemertean form 4	Turbellaria
C. regicides	—		
Nemertean form 4	0.138	—	
Both nemerteans[a]	ND	ND	−0.264*
Turbellaria	−0.180	−0.218*	—
Ischyrocerus sp.	−0.031	0.025	0.115

[a]*C. regicides* and nemertean form 4 combined for analysis.

observed in the gut of both species of nemertean worms removed from crab egg masses.

Turbellarians, although sometimes quite numerous, were not observed to feed on intact eggs. However, in vitro observations indicated that they did move in the direction of a ruptured egg and fed on the contents.

Dissections of the amphipod *Ischyrocerus* sp. revealed numerous crab egg membranes packed in the gut. When feeding, these amphipods apparently detached the eggs from the funiculi. In a few samples from the Kodiak Archipelago, frayed funiculi, indicating detachment of eggs, were often observed and could be counted (Table 2). Three of these four sites had substantial egg mortality (29–53%) and had the three highest intensities of amphipods reported from the Kodiak Island Management Area (8–18 amphipods per pleopod).

Association of Egg Mortality with Symbionts

Collections from the Kodiak Island Management Area during June to August 1984 ($N = 80$) were used to analyze the relationship between egg mortality and symbiont infestation. In these samples, most of the symbionts were found at relatively high intensities and sufficient time had elapsed for brood mortality to be evident. Egg mortality was strongly correlated ($P < 0.01$) with the intensity of *C. regicides* infestations, the intensity of nemertean form 4 infestations, and the intensity of both nemertean infestations combined (Table 3). The intensity of the turbellarian infestations was negatively correlated with egg mortality, while that of amphipod infestations was not correlated with egg mortality.

The intensity of the turbellarian infestations was significantly negatively correlated with intensity of both *C. regicides* and form 4 combined (Table 4). Intensity of *C. regicides* was not correlated with intensity of form 4, and intensity of neither the

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nemerteans nor turbellarians was correlated with the amphipod (Table 4). Similar trends were noted from other collection sites and when all of the samples were combined for analysis.

Seasonal variation in the correlation of egg mortality of *P. camtschatica* with intensity of *C. regicides* infestations was examined at Kachemak Bay, as other symbionts were rare or absent at this location. Here, infestation by *C. regicides* was strongly correlated with egg mortality during July ($r = 0.814$, $P < 0.01$) and February ($r = 0.906$, $P < 0.001$). Egg mortality was also highly correlated with intensity of *C. regicides* when all the monthly samples were combined ($r = 0.548$, $P < 0.001$).

Discussion

This survey documents high mortality of red king crab embryos from 1983 to 1985 at certain locations in Alaska. Several consistent features were associated with egg mortality. Sites exhibiting high mortality were geographically clustered, notably in the Kodiak Archipelago and Southeastern Alaska. Further, impacted areas were usually affected in all of the brooding seasons for which data were available. Two features are consistently associated with substantial brood losses. Firstly, high egg mortality usually occurred when high-intensity infestations of symbiotic nemerteans were recorded in the egg mass. Secondly, mortality, where it occurred, was strongly seasonal.

Certain broad geographic regions experienced negligible (<5%) egg mortality. These included the Alaska Peninsula, Bristol Bay, and Norton Sound. Some locations were uninfested although they were within the same management area as were locations experiencing severe egg mortality. For example, Kachemak Bay was severely impacted, while across Cook Inlet, Kamishak Bay was unaffected. Variation in the extent of egg mortality was also considerable in the Kodiak Archipelago.

Generally, locations that were in close proximity had similar patterns of egg mortality, nemertean species composition, and intensities. For example, Excursion Inlet and Port Frederick in Southeastern Alaska face each other across the 25-km-wide Icy Strait. At both sites, mortality was substantial and infestation patterns were similar, with intensities of $>10^4$ *C. regicides*, $>10^3$ form 4, and no form 5. In contrast, Gambier and Pybus coves, whose entrances are separated by 20 km, had low egg mortality, had few *C. regicides*, lacked form 4, and had similar low intensity infestations of form 5. Similarly, in the Kodiak Archipelago, Uganik, Viekoda, and Terror bays are in close proximity and had very high egg mortality and comparable high-intensity nemertean infestations ($>10^4$). Locations east and west of Chirikof Island had low egg mortality and comparable low-intensity infestations of nemerteans.

In situ and in vitro laboratory observations and the presence of crab embryo fragments in the gut of the nemerteans demonstrated that egg predation by the symbionts was the cause of most of the observed egg mortality. This was supported by the data on distribution and abundance of the worms. Either *C. regicides* or form 4 were absent or rare in almost all samples when egg mortality was less than 5% and were present in abundance in almost all samples having more than 10% egg mortality.

Our study probably underestimated egg mortality of red king crabs, since mortality estimates were based on the proportional loss of eggs from samples mostly obtained 3–6 mo into an 11-mo brooding season. Thus, we do not consider the likely continued loss of eggs to brood predators during the remainder

of the season. To project these losses for an estimate of total mortality through the entire brooding season, as has been calculated for the shore crab *Hemigrapsus oregonensis* (Shields and Kuris 1988a), estimates of feeding rates and the duration of the feeding period would be necessary. This information is not available for the egg predators of red king crab. Both direct in vitro observations on individual worms (Roe 1984; Okazaki 1986; Shields and Kuris 1988b) and indirect methods (Kuris and Wickham 1987) are available for estimation of nemertean feeding rates.

The cause of the outbreak of symbionts to epidemic levels is unknown, as is the reason for its apparent subsidence. It is also difficult to place this in a historic perspective, as detailed examinations of red king crab egg clutches for symbionts have not been a regular feature of stock monitoring policy. Presumably, *C. regicides* and the other nemertean symbionts have coexisted with king crabs. What appears to be unusual, perhaps unique, is the outbreak from low endemic levels to the epidemic levels documented here. One might expect that the high-intensity infestations would have been observed and reported from relatively accessible and well-studied stocks such as those near Kodiak Island and Cook Inlet. However, Haynes (1986 *in litt.*) recalled that "*Carcinonemertes* were not uncommon" in Kachimak Bay in the 1960's. This suggests that at certain locations, annual nemertean outbreaks, resulting in significant brood losses, may often occur but have been unrecognized or unreported.

Substantial reduction in clutch sizes and complete loss of clutches have been noted to affect specific stocks in the past (Powell and Lebida 1968; McMullen 1968). In the 1960's, adult female red king crabs from several stocks in the Kodiak Island Management Area did not carry eggs or sloughed their eggs in the first half of the brooding season. Affected females were infertile, as they either never oviposited (resorbing their ova), or their extruded eggs never embryonated (McMullen and Yoshihara 1969). Overfishing of male crabs was suggested as the cause of the insufficient fertilization rate (McMullen 1968). Our observations indicate that egg predation by symbiotic nemerteans can also be an important source of brood failure. Infertility and egg predation can be distinguished by the timing of brood loss as well as by direct observations on the egg mass and ovary. It would be useful to examine whether stocks with heavy infestations of nemertean egg predators experienced greater fishing pressure than did similar stocks with low-intensity infestations.

Blau (1986) observed that poor recruitment of juvenile red king crab began as early as 1978 in the Kodiak Island Management Area. We cannot, at present, evaluate whether nemertean egg predation contributed to the onset of poor area-wide recruitment, but it may impact recruitment in some local areas. It is probable that the epidemic levels of nemertean egg predators will exacerbate recovery of certain stocks. As there is an 8- to 10-yr lag between spawning and recruitment to legal size (Blau 1986), the effects of the 1983-85 episode of brood failure should be most evident in 1991-93. The importance of these effects will be strongly dependent on transport patterns of larvae and resultant patterns of early recruitment. The geographic variation in productivity, seen in the episodes of brood failure in both the 1960's and 1980's, supports the need for further studies of larval transport and settlement (Incze 1985; Jamieson 1986).

Our survey recovered and quantified an unsuspected diversity of symbionts in the egg masses of the red king crab. In the

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samples from the Kodiak Archipelago, *C. regicides* often cooccurred with nemerteans forms 4 and 5 (Table 2). Elsewhere, however, this pattern of cooccurrence was not evident (Table 1). Most notably, at Kachemak Bay, *C. regicides* was very abundant and was the only nemertean present in the numerous samples available at this locality. Adak appeared to be the only locality where a nemertean other than *C. regicides* or form 4 was the principal cause of egg mortality.

The turbellarians appear to be harmless commensals. Their primary source of food is unknown. They may obtain some nutrition by feeding on the remnants of eggs after nemertean predation. This could be an important food source, as small nemerteans consume only a small portion of the egg contents (Roe 1984). Also, the negative association of the turbellarians with the nemerteans suggests the possibility that the turbellarians may be predators on the nemerteans.

Species of *Ischyrocerus* have not previously been reported as crustacean egg predators. These amphipods are probably not sufficiently abundant to often have a significant impact on productivity of the red king crab. However, the association of high amphipod intensities with numerous frayed funiculi and substantially reduced clutch sizes at a few locations near Kodiak Island suggests that these symbiotic amphipods may occasionally have a significant negative effect on egg output.

The locations where nemerteans were most abundant are all narrow fjords, inlets, or passages, often with shallow sills. For example, Terror Bay has two sills as does the head of Uganik Bay. Locations with a low mean intensity of nemerteans include a variety of oceanographic and topographic conditions such as oceanic banks, open coasts, embayments, and fjords. The distribution of these nemerteans elsewhere in Alaska is consistent with this pattern. In Southeastern Alaska, high mean intensities of nemerteans were recorded from fjords and inlets such as Excursion Inlet and Port Frederick (Table 1) which have sills at their entrance. In Cook Inlet, Kamishak Bay, where crabs were lightly infested, is a shallow, open embayment whereas Kachemak Bay, where heavy infestations were documented in all years, is partially enclosed by a spit at Homer and a low sill.

Sloan (1984) has proposed that fjords, particularly those with shallow sills, may entrap rhizocephalan larvae and that retention of larval parasites may contribute to their persistent high prevalence and intensity at such locations. This sort of environment may also contribute to the establishment of nemertean outbreaks and their persistence at high intensities.

In contrast, high intensities of turbellarians were generally found at locations other than narrow fjords, inlets, and passages. In the Kodiak Archipelago, mean turbellarian intensities $>10^2$ worms per pleopod were recorded from very open sites such as Cape Ikolik, the east and west coasts of Chirikof Island, and from open embayments or fjords such as Chiniak, Alitak, and Kiliuda bays. Elsewhere in Alaska, high intensities of turbellarians were noted in collections from some of the fjords and passages of Southeastern Alaska and the open coast near Dutch Harbor. In contrast with the nemerteans, turbellarians were commonly recovered from the Bering Sea localities. These observations suggest that the mechanisms of recruitment for the nemertean and turbellarian symbionts are quite different.

At Adak and four of the six Southeastern Alaska locations, the species composition of the nemertean guild differed from the remaining areas. At these sites, a large nemertean, form 5, was either the most abundant nemertean or matched the order of magnitude of *C. regicides* infestations. Further efforts

devoted to the systematics of these nemerteans should be focused on Adak and Southeastern Alaska.

The natural history of *C. regicides* on *P. camtschatica* reveals some of the epidemiological features of this host–symbiont system that may have contributed to the outbreak. Very low prevalence and intensity early in the brooding season (March to May) suggests that few worms are retained on females during the brief interbrood period; nor are worms transmitted from males to females during copulation, as experimentally shown for *C. errans* on Dungeness crabs (Wickham et al. 1984). In June, the worms spread through the entire host population and intensity begins to rise. Through June there is little egg mortality and worm intensity and egg mortality are not correlated. In July and August, worm intensity surges to high levels of over 2000 worms per pleopod and intensity and egg mortality are highly correlated. As high worm numbers persist through September and October, most of the eggs are eaten. Worm intensity decreases markedly late in the brooding season (November to February), but all crabs remain infested.

This temporal pattern suggests that the duration of the transmissive larval stage for *C. regicides* is brief and that crabs are rapidly and continually reinfested by larvae that have dispersed but a short distance in the plankton. An abbreviated life cycle, perhaps incorporating autoinfection, would account for the very rapid increase in nemertean intensity, over three orders of magnitude, seen over a few months in samples from Kachemak Bay (Table 1). Such a life cycle would be particularly damaging to host populations in the enclosed fjords and passages where *C. regicides* reached peak intensities. Direct development, with an ephemeral nonplanktonic larva, has been described for *Pseudocarcinonemertes homari* in the American lobster, *Homarus americanus* (Aiken et al. 1985). Indeed, autoinfection has been documented for *P. homari* on lobsters (Aiken et al. 1985).

The rapid increases in intensity seen for *C. regicides* during a brooding period have not been observed in other nemertean–host associations. Instead, small but significant changes in nemertean intensity during a brooding period have been noted in these systems (Kuris 1978; Brattey et al. 1985; Shields et al. 1990a).

In contrast with *C. regicides* on *P. camtschatica*, juvenile *C. epialti*, *C. errans*, and form 4 are regularly found in abundance on the exoskeletons of male and nonovigerous female hosts (Kuris 1978; Wickham et al. 1984; A. M. Kuris and D. E. Wickham, unpubl. obs.). In these other systems, effective transmission between instars at molt, and from males to females at copulation, delivers large numbers of worms to the ovipositing female (Wickham et al. 1984).

For other nemertean egg predators, increased rates of egg mortality during the brooding season are attributed primarily to increased growth and feeding of the adult worms (Kuris 1978; Kuris and Wickham 1987; Shields and Kuris 1988a; Shields et al. 1990a). In contrast, *C. regicides*, the smallest known adult nemertean egg predator, produces increased egg mortality by a numerical response rather than by a developmental (growth) response.

For *C. errans* on *C. magister*, prevalence of nemerteans was 80–100% even in lightly infested populations (Wickham 1986). Efficiency of transmission of juvenile worms may have stabilized population levels and decreased the degree of aggregation of worms on hosts. Where outbreaks occurred, such as for *Carcinonemertes epialti* on *H. oregonensis*, even male and nonovigerous female crabs exhibited high-intensity infestations (Shields and Kuris 1988a). Delivery of these worms to the ovi-

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gerous females may have contributed to the high-intensity infestations seen on females with recently oviposited broods. In contrast, *C. regicides* appears able to undergo a population explosion on ovigerous red king crabs, relying on transmission solely between ovigerous females. Reliance on larval transmission, perhaps involving competent larvae that settle on crabs after a very brief planktonic existence, may be an important adaptation facilitating the localized outbreaks of epidemic proportions seen on the red king crabs in Alaska.

The spatial and temporal patterns of nemertean abundance documented here do not implicate the fishery as a contributor to the pervasive brood failure seen in some stocks of red king crab. However, the reproductive output of several localized areas has been greatly reduced due to nemertean egg predation. Additional monitoring of crab reproduction would facilitate retrospective studies of crab fecundity, expand our knowledge of the systematics and ecology of clutch symbionts, and may permit development of more precise fishery closure standards. A baseline for assessment of future reproductive crashes would provide continued perspective on the past and might guide management decisions in the future.

Acknowledgements

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