

Brood Mortality and Egg Predation by the Nemertean, *Carcinonemertes epialti*, on the Yellow Rock Crab, *Cancer anthonyi*, in Southern California

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Carcinonemertes epialti had a minimal impact on the egg mortality of a lightly infested population of a commercially important crab host, *Cancer anthonyi*. The nemertean had a high prevalence (>97%) but was found at low intensities (mean intensity = 86.5 worms/pleopod, mean density = 0.3 worms/1000 eggs). Egg mortality varied from 0.0–30.5%, and was highly correlated with both worm intensity, and the timing of crab embryogenesis (mean mortality = 5.7%). Separate sites within the pleopod experienced different causal mechanisms of mortality. Mortality at the base of the pleopod was correlated with the presence, abundance, and immigration of *C. epialti*. Mortality at the tip of the pleopod was less correlated with worm abundance and was most likely a result of abrasion to the eggs or egg mass. Infestations of *C. epialti* varied between seasons and between host species. The worm was more abundant on host species that bred year-round (*Cancer anthonyi* and *Hemigrapsus oregonensis*); hence, infestation dynamics varied markedly between host species. In southern California, *Cancer anthonyi* was virtually always infested with *C. epialti* and is the most important host for the worm in this area.

Carcinonemertes epialti avait peu d'effet sur la mortalité des oeufs d'une population peu infestée d'un crabe hôte à grande valeur commerciale *Cancer anthonyi*. Ce némerterien avait une forte prévalence (97%) mais il a été trouvé à de faibles intensités (intensité moyenne = 86,5 vers par pléopode, densité moyenne = 0,3 vers par 1000 oeufs). La mortalité des oeufs variait de 0,0 à 30,5%, et elle était fortement corrélée à l'intensité des vers et au moment de l'embryogenèse du crabe (mortalité moyenne = 5,7%). Des sites distincts à l'intérieur du pléopode présentaient différents mécanismes responsables de la mort. La mortalité à la base du pléopode était corrélée à la présence, à l'abondance et à l'immigration de *C. epialti*. La mortalité à l'extrémité du pléopode était moins corrélée à l'abondance du ver et elle était très probablement le résultat de l'abrasion des oeufs ou de la masse d'oeufs. Les infestations de *C. epialti* variaient d'une saison à l'autre et d'une espèce hôte à l'autre. Les vers étaient plus abondants chez les espèces hôtes qui se reproduisaient à l'année (*Cancer anthonyi* et *Hemigrapsus oregonensis*); donc, la dynamique de l'infestation variait de façon marquée d'une espèce à l'autre. Dans le sud de la Californie, *Cancer anthonyi* était presque toujours infesté par *C. epialti* et il s'agit de l'hôte le plus important du vers dans ce cas-ci.

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Species of the nemertean genus *Carcinonemertes* are egg predators that may cause substantial brood mortality on their decapod crustacean hosts (Wickham 1979a; Wickham et al. 1985; Kuris and Wickham 1987; Shields and Kuris 1988a). The impact of these nemerteans on the broods of their hosts can be heavy with complete brood loss occurring in many instances (Wickham 1979a; Kuris and Wickham 1987; Shields and Kuris 1988a). Outbreaks of *Carcinonemertes* spp. on the Dungeness crab, *Cancer magister*, and the red king crab, *Paralithodes camtschatica*, may have contributed to the recent decline of certain stocks of these crabs (Wickham 1979a; Wickham et al. 1985). A related nemertean, *Pseudocarcino-*

nemertes homari, has been found at high intensities on the broods of *Homarus americanus*, and may be responsible for much egg mortality on that host (Aiken et al. 1985; Campbell and Bratley 1985).

Infestations of *Carcinonemertes epialti* occur on several crab species: *Cancer antennarius*, *Cancer anthonyi*, *Hemigrapsus oregonensis*, *Pachygrapsus crassipes*, and *Pugettia producta* (Kuris 1971, 1978; Roe 1979, 1984; Shields and Kuris 1988a). Past studies of *C. epialti* have focused on the relationship of the nemertean with its grapsid hosts; little work has been done on the impact of *C. epialti* on *Cancer anthonyi*.

The yellow rock crab, *Cancer anthonyi*, is a commercially harvested crab that is abundant at nearshore depths (≤ 100 m) in the Santa Barbara Channel, California. Annual landings of rock crabs (*C. antennarius*, *C. anthonyi*, and *C. productus*) along the California coast were valued at over 2.0 million dollars in 1985, (Preliminary Notes of Commercial Fish Landings

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by Region; Resource Agency of California, California Fish and Game, 245 Broadway, Suite 350, Long Beach, CA). The Santa Barbara fishery represents between 24–67% of the total landings (1981–86), and *C. anthonyi* is the largest contributor to this fishery in southern California (Carroll and Winn 1988).

Studies of *Carcinonemertes* spp. on other commercially harvested hosts have examined the effects of outbreaks of high worm abundance on crab egg mortality. Since it has been suggested that such outbreaks may be associated with the fishery (Wickham 1979a; Kuris and Wickham 1987; but see Shields

and Kuris 1988a), we undertook the examination of a lightly infested population of commercially harvested crabs.

We develop refinements in sampling procedures to account for spatial variation in mortality within the crab egg mass. The infestation parameters examined include prevalence, worm intensity, and worm density. Egg mortality and the effects of predation on egg natality were analyzed in relation to crab embryogenesis, seasonality, and worm abundance. We compare the dynamics of *Carcinonemertes epialti* infestations on *Cancer anthonyi* with infestations on other crab species.

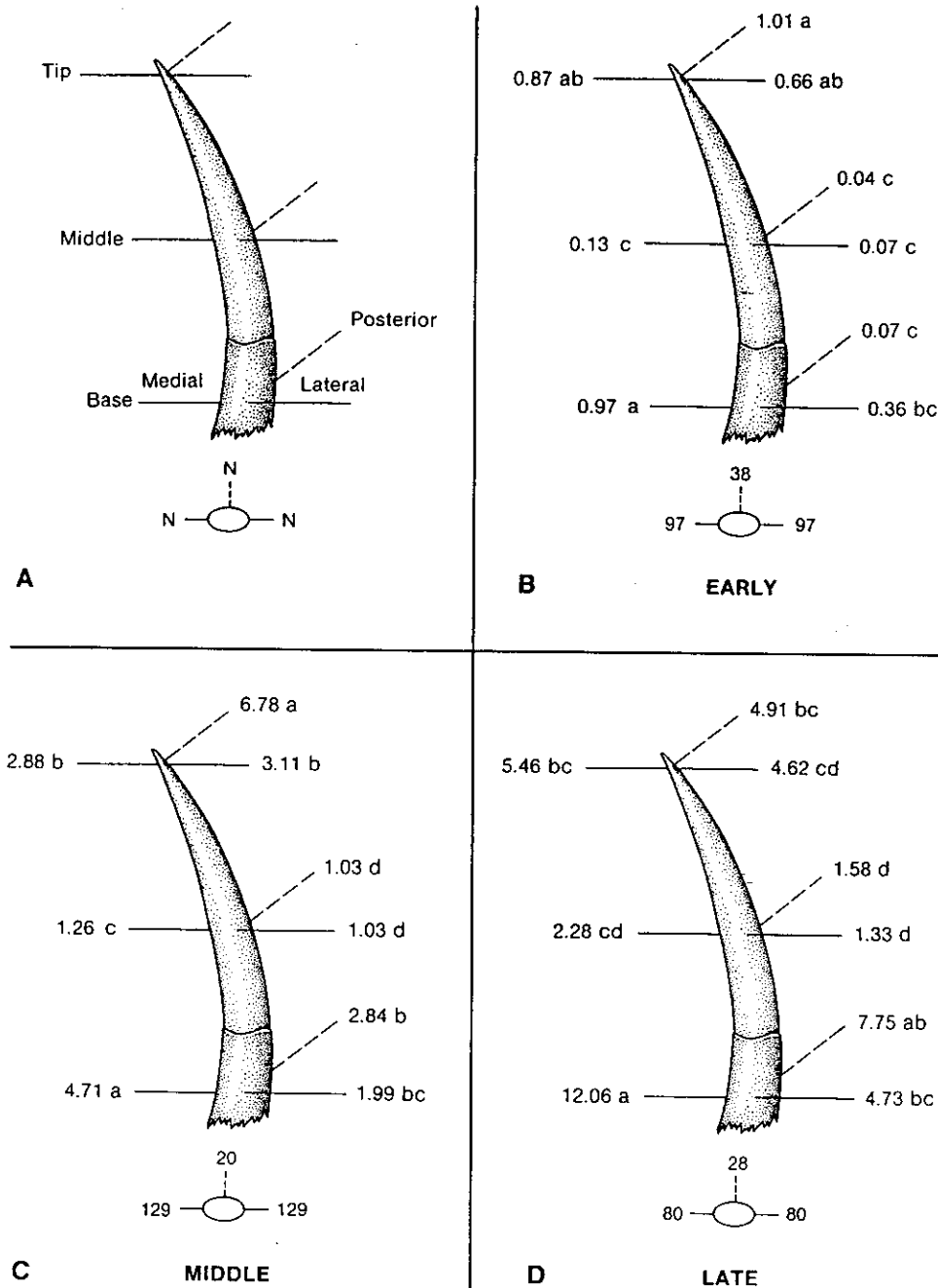


FIG. 1. Mean egg mortality (%) by site in the egg mass of the left second pleopod of *Cancer anthonyi* over the course of embryogenesis. *N* is the number of crabs sampled at the respective locations within the egg mass. Pleopods are illustrated schematically as seen from their anterior surface (which, in situ, is appressed against the thoracic sternites). Ovals at the base of each figure represent cross sections of the pleopods with summed sample sizes (*N*). Means with different letters are significantly different from each other, within the pleopod (ANOVA, Bonferroni's inequality, $P < 0.05$). (A) Key to locations; (B) early EDS I–II; (C) middle EDS III–IV; (D) late EDS V–VII.

Materials and Methods

Ovigerous crabs were collected by commercial fishermen from the Santa Barbara Channel, between Summerland Gaviota, California (approximately 34°23'–34°25', 119°34'–120°12'). Crabs were obtained at nearshore depths of 10–100 m. Random samples of 20 to 25 crabs were obtained at monthly or bimonthly intervals for 2 yr (November 1981–November 1983). A total of 345 *Cancer anthonyi* were sampled with the clutches of 311 crabs fully processed. The entire second left pleopod was excised and stored in 5% formalin in seawater (5% FSW) for further analyses. Crabs were either released or maintained in flowing seawater aquaria.

Egg mortality was estimated by sub-sampling different locations on the ovigerous pleopod. The sub-samples (setae with intertwined eggs) were taken from the following sites on the pleopod (Fig. 1A): medial, lateral, and posterior surfaces at the tip of the pleopod; medial, lateral, and posterior surfaces at the middle of the pleopod; and medial, lateral, and posterior surfaces at the base of the pleopod. A preliminary analysis showed that the middle region of the egg mass had a relatively low and uniform degree of egg mortality in the middle and late developmental stages (developmental stages of embryogenesis — EDS classes), thus, we ceased to sample the middle region after August 1982. In 1982–83, the base sites were replicated, and the three middle sites and all of the posterior sites were no longer sampled. At least 100 eggs were counted from each site and the number of live and dead eggs were recorded. Dead eggs persisting as empty egg membranes were attributed to worm predation as in Wickham (1979a); and this was further substantiated by personal observations (Shields and Kuris 1988b). The numbers of worms and worm egg strings found on these sub-samples were also recorded.

To determine the extent of egg mortality along the length of the pleopod and to correct for bias in our sub-sampling, 12 pleopods were divided into 10 equal length pieces and the medial sites were examined. Egg mortality, worm number, and the number of brooded eggs were analyzed along the lengths of each of these pleopods. Since these data compared favorably with those from the site-specific sub-sampling routine, the data were grouped according to region (base, middle, and tip) for statistical analyses.

To correct for variation within the egg mass, the overall mean percentage of egg mortality for each crab was estimated by summing the dead eggs from each sub-sample and dividing by the sum of the total number of eggs in each sub-sample. Egg mortality was then expressed as the percentage of eggs that were dead. A constant mortality estimate was factored into total egg mortality values for each crab sampled after August 1982, since the middle sites were no longer sampled after that date. Egg mortality could not be reliably estimated when hatching was imminent (approximately 40 d post-oviposition) because hatched eggs could not be distinguished from dead eggs. Thus, clutches at or near hatching (EDS stage VIII, see below) were excluded from the statistical analyses.

Crab embryogenesis was quantified as the number of days since oviposition and was based on the mean cumulative time to reach the midpoint of the developmental stage of the eggs (EDS, see Fig. 4). These times were based on daily observations of crabs observed throughout the brood period. Embryogenesis was split into three periods (early development, I–II; middle development, III–V; and late development, VI–VII) for some statistical analyses.

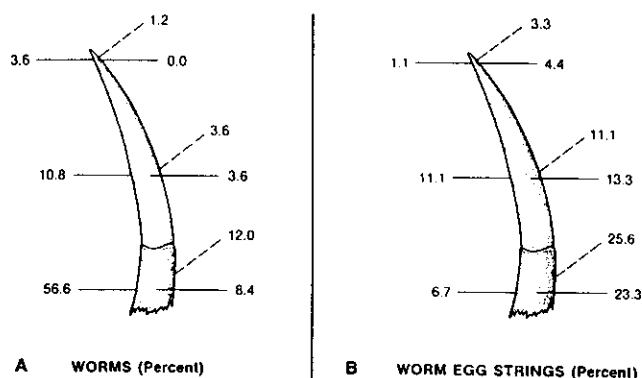


FIG. 2. Distribution of *Carcinonemertes epialti* found at different sites in sub-samples of crab eggs: (A) Worms ($N=83$ sub-samples); (B) worm egg strings ($N=90$ sub-samples).

Egg mortality was projected through the developmental period using mortality estimates from clutches in early and middle stages of development (Stages I–IV). Projections were estimated by dividing the proportion of dead eggs in a sub-sample by the cumulative time to the midpoint of the EDS, then multiplying the result by 40, the average number of days in the embryogenic period.

Nemerteans were collected by agitating the complete pleopod (minus the sub-samples) in 400–500 mL of seawater for a minimum of three 1-min washes. After decanting, the worms were transferred to a petri dish and counted under a dissecting microscope. The worms were then stored in 5% FSW.

Nemertean abundance was measured in terms of prevalence, the proportion of infected hosts, and mean intensity, the mean number of worms per infested host (Margolis et al. 1982). Worm intensity was split into four classes (1–30, 31–60, 61–120, and 121+ worms/pleopod) for statistical analyses. Where appropriate, worm intensity was transformed into worm density, defined as the number of worms per 1000 eggs after Wickham (1979a,b; Margolis et al. 1982).

The number of eggs per pleopod was assessed as per Shields and Kuris (1988a). In addition, the total number of eggs per crab was determined for 12 crabs (96 pleopods). The proportion of eggs on each pleopod and the number of worms on each pleopod were also assessed for these crabs.

Results

Site-Specific Mortality

Mortality varied between sites on the pleopod throughout embryogenesis. The base and tip regions exhibited significantly greater egg mortality than the middle region (Fig. 1B–D; ANOVA, Bonferroni's inequality, $P<0.05$).

The distributions of the worms and worm egg strings within the pleopod showed distinctive patterns. Worms were found throughout the pleopod but they were more frequently found in the base sites, especially the medial base site (Fig. 2A). The prevalence and intensity of worms on the individual lengths of the pleopod were significantly lower in the tip region than in the middle and base regions (Table 1). The base region also contained significantly more worm egg strings than the other region (Fig. 2). The egg strings were not, however, markedly abundant at the medial base site where worm numbers and egg mortality were relatively high.

The distribution of the worms was related to the distribution of eggs in the brood (Table 2). Significantly more worms were

TABLE 1. Distribution of *Carcinonemertes epialti* within regions of the pleopod and associated crab egg mortality. The proportion of eggs in each region of the pleopod is also shown, $N=12$ crabs.

	Mean proportion of eggs on pleopod	Prevalence of worms in separate lengths(%)	Worm number by region	Proportion of worms in regions	Mean intensity	Mean mortality (%)
Tip	0.295	22/48 ^a (45.8)	50	0.107	4.2 ± 3.3	1.0
Middle	0.424	31/36 (86.1)	127	0.273	10.6 ± 7.7	0.7
Base	0.281	34/36 (94.4)	290	0.620	24.2 ± 19.4 ^b	3.2
Total	1.000	87/120 (72.5)	467	1.000	38.9 ± 27.6	1.6

^a $P < 0.05$, $G_H = 30.6$, $d.f. = 2$, significantly different from other regions.

^b $P < 0.05$, ANOVA, Bonferroni's inequality, significantly different from other regions.

TABLE 2. Distribution of *Carcinonemertes epialti* and crab eggs on individual pleopods of *Cancer anthonyi*. The mean total fecundity was approximately 2 608 000 eggs per crab (Shields, Okazaki, and Kuris, unpubl. data). Means with different letters are significantly different from each other (ANOVA, Bonferroni's inequality, $P < 0.05$). $N=12$ crabs, 2858 worms, 96 pleopods. Fecundity and worm data were arcsin-square root transformed for the analysis.

Pleopod pair	Percentage of total fecundity (± SE)	Percentage of total worm abundance (± SE)	Worm density (worms/1000 eggs) mean (± SE)
One	27.4AB (0.3)	34.2A (1.6)	0.111 (0.024)
Two	31.5A (0.4)	29.4A (2.7)	0.093 (0.029)
Three	24.6B (0.7)	20.1B (1.1)	0.085 (0.019)
Four	16.4C (0.5)	16.1C (0.8)	0.087 (0.019)
Total	100.0	100.0	0.093 (0.010)

TABLE 3. Correlation statistics for egg mortality at the tip and base of the pleopod in relation to worm intensity during different developmental periods. Mortality data were arcsin-square root transformed for the analysis. R represents the Pearson product-moment correlation coefficient, N , number of pleopods.

Site	Developmental period	Worm intensity	
		R	N
Tip	Early	0.079	85
	Middle	0.271 ^a	120
	Late	0.218	76
Base	Early	0.142	85
	Middle	0.281 ^a	120
	Late	0.641 ^b	76

^a $P < 0.025$, correlation coefficient significantly different from zero.

^b $P < 0.0001$, correlation coefficient significantly different from zero.

found on the first and second pairs of pleopods (those adjacent and closest to the thoracic sternites) than on the other pleopods.

Mortality at the base of the pleopod was highly correlated with worm intensity during the middle and late embryonic periods (Table 3). Mortalities at the base and tip sites were not correlated with worm intensity during early embryonic stages, as nemerteans would, as yet, have had little time to effect egg mortality. Projections of egg mortality from crabs having low intensity infestations (1–30 worms/pleopod) indicate that the tip region may experience a relatively constant egg mortality of approximately 4.0–6.0% (for projections see

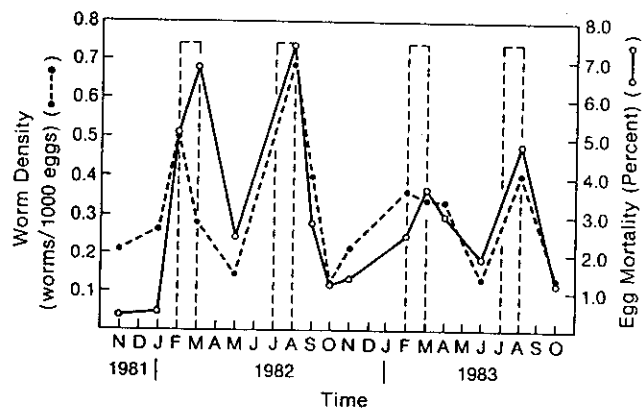


FIG. 3. Density of *Carcinonemertes epialti* (worms/1000 eggs) and egg mortality of *Cancer anthonyi* through time. Winter and summer values (reference bar) were significantly greater than spring and fall values for both density and mortality.

TABLE 4. Relationship between worm intensity and egg mortality. N is the number of pleopods sampled. Means (and standard deviations) with different letters represent significantly different groups (ANOVA, Bonferroni's inequality $P < 0.05$), after arcsin-square root transformation of egg mortality data. Egg mortality is the number of dead eggs per total number of eggs in sub-samples.

Worms/pleopod	N	Egg mortality (%)
0	3	0.7 ± 0.3A
1–30	55	1.1 ± 1.5A
31–60	72	1.7 ± 2.0A
61–120	95	3.2 ± 3.5B
121+	63	5.2 ± 5.9B

Shields 1987). Since worms were infrequently recovered from the tip sites (Fig. 2), other mortality factors appear to have operated there. Further, a significant correlation was found between mortality at the tip of the pleopod and worm intensity only for clutches in the middle of embryogenesis (Table 3).

Overall Mean Egg Mortality

Carcinonemertes epialti exhibited seasonal variation in mean density on *Cancer anthonyi*, with winter and summer peaks in both years (Fig. 3). The winter and summer peaks in both worm density and total egg mortality were significantly greater than the spring and fall values (ANOVA, Bonferroni's inequality, $P < 0.05$). In both years, the total percentage of egg mortality coincided with the July–August peak in worm density, but lagged slightly behind the February–March peaks. The seasonal

pattern for mean intensity (not shown) was similar to that for mean density since prevalence was 100% for 13 of the 15 months sampled.

Egg mortality ranged from 0.0–30.5% of the clutch. On individual crabs, egg mortality varied with worm intensity (Table 4), being significantly greater at 61–120 and 121+ worms than at lower intensities (ANOVA, Bonferroni's inequality, $P < 0.05$). Two-way ANOVA between egg mortality, and the class variables, intensity, and EDS, showed significant variation in egg mortality with intensity and with EDS ($F = 23.67$, $d.f. = 9$ and 287 , $P < 0.0001$), but no significant interaction was found between intensity and EDS ($F = 0.79$, $d.f. = 3$ and 6 , $P < 0.715$).

Time since oviposition, as indicated by EDS, was highly correlated with egg mortality ($R = 0.603$, $P < 0.0001$, $d.f. = 283$, $Y = 0.040 + 0.006 X$). Egg mortality rose from a mean of less than 0.2% (2.5 d post-oviposition) to over 6.0% (37.5 d post-oviposition) over the duration of embryogenesis (Fig. 4a).

Worm density was highly correlated with EDS ($R = 0.407$, $P < 0.0001$, $d.f. = 283$, $Y = 0.327 + 0.010 X$). Worm density varied from 0.01–2.83 worms/1000 eggs or 1–765 worms per pleopod (Fig. 4b). Significant increases in worm density were detected at 21.5 d after oviposition and at 34 d after oviposition when compared with 2.5 and 7.5 d after oviposition (ANOVA, Bonferroni's inequality, $P < 0.05$).

Discussion

Carcinonemertes epialti had little effect on the broods of *Cancer anthonyi*. The nemertean never reached the high intensities observed on other decapod species and egg mortality resulting from *C. epialti* rarely exceeded 10% of the clutch. Since rock crab landings have steadily increased over the past 6 yr (Carroll and Winn 1988; Preliminary Notes of Commercial Fish Landings by Region; Resource Agency of California, California Fish and Game, 245 Broadway, Suite 350, Long Beach, CA, 1981–86, unpubl. data) and the intensities of *C. epialti* have remained low, *C. epialti* has at present a minimal impact on the rock crab fishery in southern California.

This analysis documents two causes of site-specific egg mortality in *Cancer anthonyi*. Firstly, egg mortality at the base of the pleopod was strongly associated with the abundance of *C. epialti*, and may result primarily from egg predation. Mechanical damage to the egg mass is unlikely at the base sites of the pleopod and cannot account for the relatively high mortality observed there (see below). Relatively high egg mortality in the basal portion of the clutch may be caused by the continued immigration and feeding of these worms at this site from oviposition to eclosion.

Secondly, egg mortality may be produced by abiotic means. A relatively constant egg mortality of 4.0–6.0% was projected for the tip of the pleopod when worm intensity was low. The mortality at the tip site may be due to exposure resulting in mechanical damage; the abdomen of *Cancer anthonyi* does not completely enclose the distal portion of the egg clutch. Abrasion to the egg mass may occur when female crabs bury and rebury themselves (Wild 1983).

Worm egg strings were located in sites adjacent to the most heavily infested medial base site. Wickham (1979b; 1980) found that the egg strings of *C. errans* were distributed evenly within the egg mass of *Cancer magister* in relation to the distribution of the mature worms (>40 d post-host oviposition in a 90-d embryogenic period). Since an increase in egg mortality may

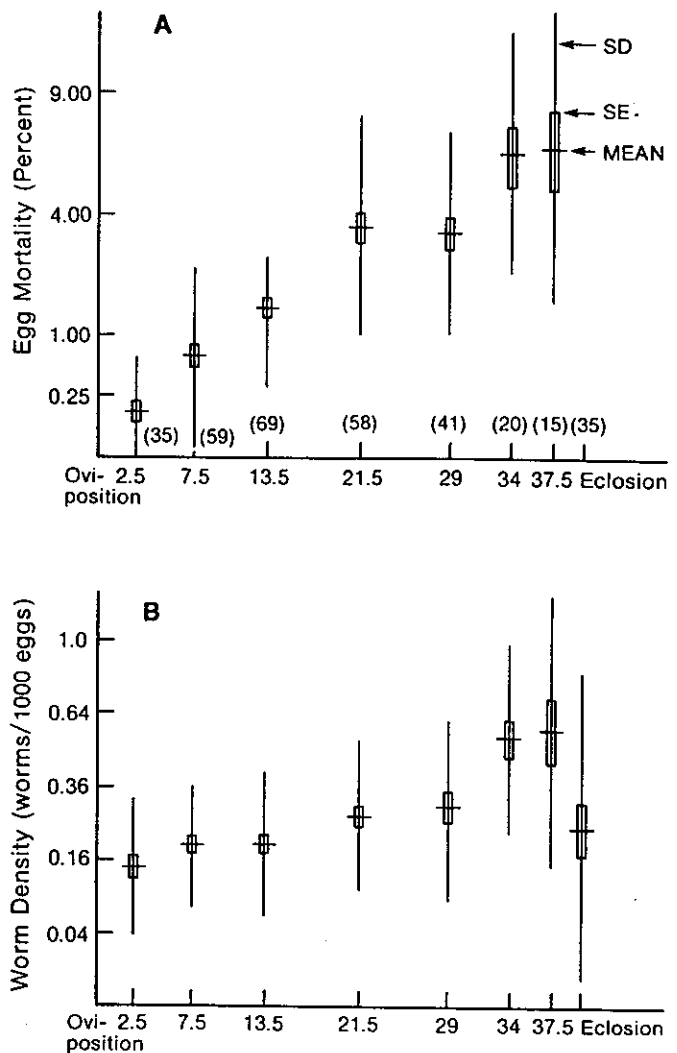


FIG. 4. Mean egg mortality of *Cancer anthonyi*, and mean worm density of *Carcinonemertes epialti* over the course of crab egg embryogenesis. N is the number of crabs sampled. Key to egg development stages (cumulative time to midpoint of developmental stage, in days): I, one-cell stage through blastulation (2.5); II, gastrulation through development of tagmata (7.5); III, limb buds evident through buds well developed (13.5); IV, development of eye placodes and eyes, faint heartbeat in live eggs (21.5); V, completed eyes, yolk in four distinct lobes, strong heartbeat in live eggs (29.0); VI, yolk reduced to a band or two lobes (34.0); VII, yolk reduced to two small masses (37.5); VIII, hatching (40). (A) Mean egg mortality of *Cancer anthonyi* through embryogenesis. Egg mortality data were arcsin-square root transformed for the analysis. (B) Mean worm density of *C. epialti* through crab embryogenesis. Density data were square root transformed for the analysis.

increase the abundance of fouling micro-organisms (Fisher and Wickham 1976), eggs oviposited away from the most heavily affected sites would not be adversely affected by the fouling community.

Carcinonemertes epialti was most abundant on the first and second pairs of pleopods. These pleopods contain the largest proportion of the clutch, and may also be more protected than the other pleopods. They are closest to the thoracic sternites, and worms may move to the sternites prior to host oviposition (Kuris 1978). *Pseudocarcinonemertes homari* behaves in an analogous manner. That is, it avoids the more exposed pleopods (inner and outer pairs) of its lobster host (Campbell and Bratney

TABLE 5. Mean worm densities (worms/1000 eggs) of various species of *Carcinonemertes* on their decapod hosts and projected host egg mortalities.

Host species	Worm species	Mean density	Projected mortality (%)	Reference
<i>Cancer anthonyi</i>	<i>C. epialti</i>	0.3	5.7	Present study
<i>Hemigrapsus oregonensis</i>	<i>C. epialti</i>	1.4	8.1	Shields and Kuris 1987
		≈40.0	100.0	
<i>H. oregonensis</i>	<i>C. epialti</i>	0.5	6.9–7.5	Kuris and Wickham 1987
		1.0–3.1	17.4–19.0	
<i>Cancer magister</i>	<i>C. errans</i>	1.8	10.6	Wickham 1979b; 1980
		4.0	30.0	
		8.6	50.3	
		14.6	63.3	
<i>Paralithodes camtschatica</i>	<i>C. regicides</i> ^a	39.7	65.4	Wickham et al. 1985
		140.2	96.9	
<i>Homarus americanus</i>	<i>P. homari</i>	2.4	34.0–39.0	Campbell and Bratney 1986

^aDescribed as *Carcinonemertes regicides* Shields, Wickham, and Kuris 1989.

1985). *Pseudocarcinonemertes homari* is centrally located within the lobster egg mass, residing primarily on those pleopods in the middle of the clutch.

The increase in worm density with increasing EDS showed that worms immigrated into the crab egg clutch throughout the embryogenic period. In contrast, Kuris (1978) found that the prevalence and intensity of *C. epialti* on ovigerous *Hemigrapsus oregonensis* increased through the early and middle stages of crab embryogenesis, but decreased during the late stages of embryogenesis. Campbell and Bratney (1985) found that the prevalence of *Pseudocarcinonemertes homari* declined with EDS but worm intensity was not correlated with EDS. Since *P. homari* undergoes direct development on its host, *Homarus americanus* (Uhazy et al. 1985), it is surprising that prevalence and intensity were not positively correlated with EDS. However, lobsters clean their egg masses of dead eggs and thus, reduce the number of worms found in the clutch (Aiken et al. 1985). For crabs, selective larval settlement (Bauman 1984; Wickham and Roe 1987), or contact transmission of juvenile worms to the ovigerous crabs (Kuris 1978) may account for the increase in worm density late in the embryogenic period.

Carcinonemertes epialti may be found on its hosts throughout the year, but the seasonal pattern of infestation varies with each host species. The yellow rock crab, *Cancer anthonyi*, experiences two seasonal peaks in the abundance of *C. epialti*. The shore crabs, *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*, experience a single fall peak in the abundance of *C. epialti* (Kuris 1978; Roe 1979; Shields and Kuris 1988a). Both *Cancer anthonyi* and *H. oregonensis* produce multiple broods per year (Kuris 1971; 1978; J. D. Shields, R. K. Okazaki, and A. M. Kuris, unpubl. data), whereas *P. crassipes* generally produces a single brood per year with few females producing eggs during other seasons (Hiatt 1948; Roe 1979). Seasonal peaks in worm abundance precede the onset of the winter reproductive period of *H. oregonensis* (Roe 1979; Shields and Kuris 1988a) but are unrelated to the spring–summer reproductive period of *P. crassipes* (Roe 1979).

Carcinonemertes epialti is frequently found on *Hemigrapsus oregonensis* and *Pachygrapsus crassipes* in northern and central California (Kuris 1978; Roe 1979), but it is rarely found on these species in southern California (Kuris 1971; A. M. Kuris unpubl. data). Ovigerous *Cancer anthonyi* may be found year-round in southern California (Reilly 1987), and thus, may sup-

ply a suitably large, continuous resource of eggs for these predatory nemertean. *Cancer anthonyi* is virtually always infested with *C. epialti*, hence it is the most important host for *C. epialti* in southern California.

Infestations of *C. epialti* on *Cancer anthonyi* did not reach the outbreak levels observed for other carcinonemertids on the more heavily fished populations of Dungeness and red king crabs (Table 5). Outbreaks of *C. errans* on *Cancer magister* in central California have resulted in nearly complete brood loss in this stock for several years (Wickham 1986). Episodic outbreaks of a new species, *C. regicides* (Shields et al. 1989) and an unidentified form (nemertean form #4, Wickham and Kuris 1988) on the red king crab, *Paralithodes camtschatica*, have caused complete brood loss in localized nidi in several geographically distinct areas of Alaska (Wickham et al. 1985; A. M. Kuris et al. unpubl. data). Outbreaks of *Pseudocarcinonemertes homari* on *Homarus americanus* can attain high levels, and may result in a moderate degree of egg mortality on this host (Aiken et al. 1985; Campbell and Bratney 1985). While nemertean have been implicated in causing massive declines in fishery stocks, their role has yet to be determined.

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