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Temporal variation in abundance of the egg predator *Carcinonemertes epialti* (Nemertea) and its effect on egg mortality of its host, the shore crab, *Hemigrapsus oregonensis*

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Abstract

An outbreak of the nemertean, *Carcinonemertes epialti*, was observed on *Hemigrapsus oregonensis* during October, 1982 at Campbell Cove, Bodega Harbor, California. Mean worm intensity (296 worms/crab) was the highest recorded for this nemertean egg predator on *H. oregonensis*. During the outbreak, male crabs were found to harbor more worms than both non-ovigerous and ovigerous females. Crab egg mortality was substantial; 83% of the ovigerous females experienced 75–100% brood mortality. The seasonal peak in worm abundance coincided with the seasonal low in crab reproduction at this locality. A method for estimating the impact of *C. epialti* on *H. oregonensis* natality was developed using crab size and fecundity, and worm prevalence and intensity. For a non-outbreak sampling period, a mean of 5.6% egg mortality was experienced by infested crabs for the period selected. Thus, brood mortality during the outbreak was much greater than that experienced at non-outbreak periods. Heavy fishing pressure on some commercially important crab species has been suggested as a possible factor inducing worm outbreaks and facilitating their continued persistence. These observations suggest that fisheries are not necessarily responsible for the outbreaks of nemerteans on commercially important crab species. However, fishing pressure may still be a sufficient condition to promote nemertean outbreaks.

Introduction

Nemerteans of the genus *Carcinonemertes* have been recognized as specialized symbionts on decapod crustaceans for some time (*e.g.* von Kölliker, 1845). Humes (1942) noted that *C. carcinophila* was an egg predator, and work by Wickham (1979a, 1979b, 1980), Roe (1984), and Kuris & Wickham (1987) established feeding rates of *C. errans* and *C. epialti* on the eggs of their respective crab hosts. Recently it has been established that these worms are widespread and may cause substantial egg mortality on several commercially important species, including the blue crab, *Callinectes sapidus*, the Dungeness crab, *Cancer magister*, the American lobster, *Homarus americanus*, and the red king crab, *Paralithodes camtschatica* (Humes, 1942; Wickham, 1979a, 1979b; Aiken *et al.*, 1985; Wickham *et al.*, 1985; Kuris & Wickham, 1987). Outbreaks of *Carcinonemertes errans* on the Dungeness crab reach densities of 46000 worms per crab with 100% of the crabs being infested. An undescribed nemertean on the red king crab reaches densities of 600 000 worms per crab with infestation levels of 100%. The resultant egg mortality to the crab host ranges from 40–100% of the brood (Wickham 1979a, 1979b, 1980; Wickham *et al.*, 1985).

Nemertean egg predation has attracted attention as a potentially important component of Dungeness and red king crab fisheries. Brood mortality caused by *C. errans* has been suggested as a contributory cause of the collapse or non-recovery of the historically important central California Dungeness crab fishery (Botsford & Wickham, 1978; Wickham, 1979a, 1979b, 1980). Clearly, in crab populations where over 50% of the eggs are eaten, egg mortality caused by nemertean worms represent the largest mortality factor in the life cycle of these crabs.

Infestations of an egg predator, *Carcinonemertes epialti*, have been noted on the shore crab, *Hemigrapsus oregonensis* (Kuris, 1971, 1978; Roe, 1979). Worms are found on both sexes of crab but maturation of the worms occurs only on ovigerous female crabs. The geographic range, seasonal pattern of abundance, and worm location on the host have been described for worms from Bodega Harbor, Sonoma County, California (Kuris, 1971, 1978; Kuris & Wickham, 1987). Seasonal abundance, feeding rates, and the contribution of the worms to crab egg mortality have also been studied at Elkhorn Slough, Monterey County, California (Roe, 1979).

Here we report an outbreak of *C. epialti* on an unfished or lightly fished population of the shore crab, *H. oregonensis*, and compare this episode with non-outbreak periods for crab egg mortality, worm prevalence, intensity, and seasonal abundance. A method for estimating the impact of nemertean egg predators on the natality of their hosts is also presented. Further, we propose the use of the *H. oregonensis – C. epialti* interaction as a model system for the study of nemertean outbreaks on commercially important hosts.

Material and methods

Hemigrapsus oregonensis were collected by hand, under rocks, during low tides, at Campbell Cove, Bodega Harbor, Sonoma County, California. Eight collections of *H. oregonensis*, consisting of 498 crabs, were examined from Campbell Cove. In February, 1985, four additional collections of 196 crabs were made at other locations around the harbor (Fig. 1): Campbell Cove (CC), Westshore Park (WP), the turning basin (TB), the eastern shore (EA), and Coast Guard Cove (CG). The carapace width of each crab was measured at its width length. The limb axillae, the abdomen and the sternal-abdominal furrow of male and non-ovigerous female crabs were carefully examined; the crabs were then released. Ovigerous female crabs were examined as above; and, their egg-bearing pleopods were removed for further examination. Worms were counted with the aid of a dissecting microscope. The developmental stages of the eggs from all of the crabs were analyzed according to Kuris (1971, 1978).

Fecundity estimates and egg mortality data were collected by counting a random subsample of approximately one thousand eggs and noting the number of dead eggs. The subsample and the remaining eggs (after having been carefully stripped from the pleopods) were dried at 60 °C, allowed to cool to room temperature, and weighed on a Cahn microbalance. Fecundity was then estimated using the proportional weight of the random subsample to the weight of the entire egg mass. The size-fecundity relationship of *H. oregonensis* was examined in order to estimate size-specific egg mortality rates. Size of *H. oregonensis* was highly correlated with the total number of eggs present ($Y = 469 + 1.4 X^3$, $r = 0.841$, $P < 0.01$, $n = 16$). Egg mortality data were expressed as the percentage of dead eggs in the subsample. Where appropriate, worm abundance, measured as the number of worms per crab was transformed to the number of worms per 1 000 crab eggs as in Wickham (1979a, 1979b, 1980).

Prevalence is the number of infected hosts per total number of hosts ($\times$ 100), and mean intensity is the mean number of parasites per infected host (Margolis *et al.*, 1982). All statistical analyses are from Sokal & Rohlf (1982). The arcsin transformation was used for tests of proportional data. A heterogeneity G-test (G_H) with an *a posteriori* simultaneous test procedure was used to analyze differences in prevalence between collection sites for the February, 1985 sample. Pearson's product-moment correlation coefficient is given as r. A value of $P < 0.05$ was accepted as significant.

Data from Kuris (1978) and the present study were combined for further analysis as there were no significant differences in worm prevalence and mean intensity (U-test, $P > 0.05$, $n = 15$). Prevalence and in-

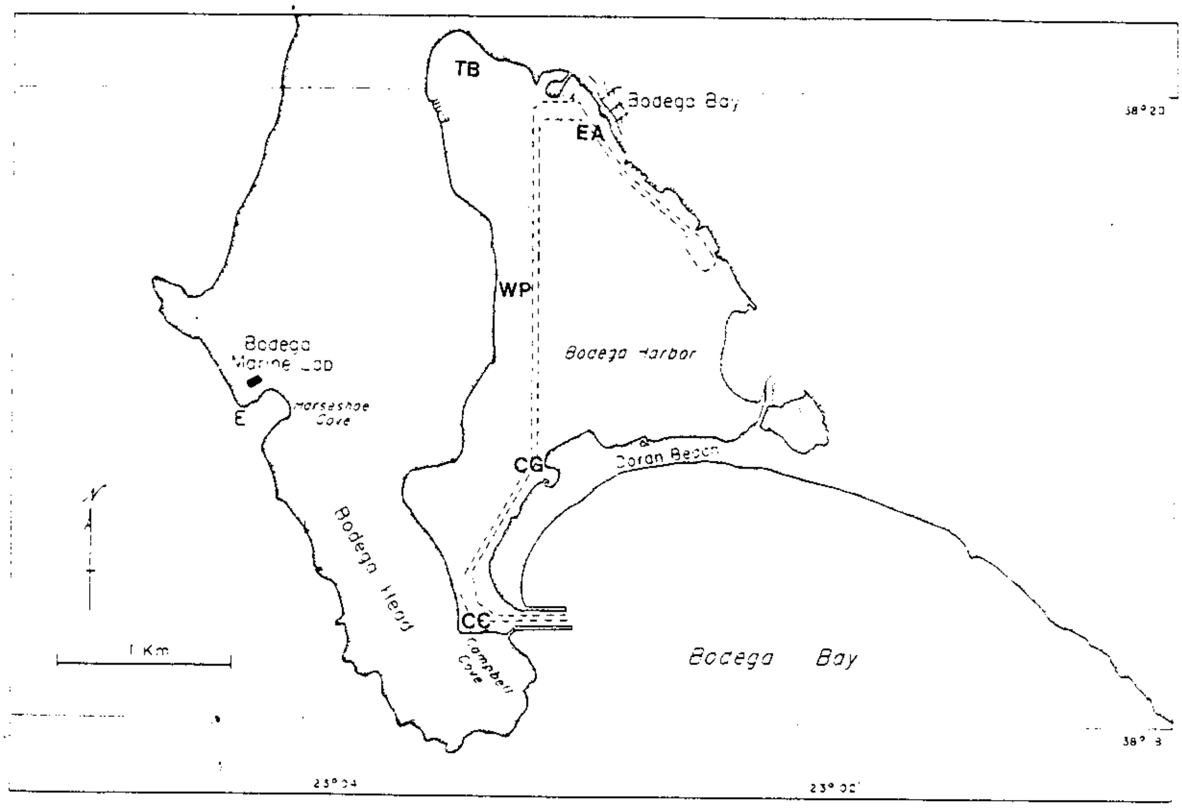

Fig. 1. Bodega Harbor. Collection sites for *Hemigrapsus oregonensis* are as follows: CC = Campbell Cove; CG = Coast Guard Cove; WP = Westshore Park; EA = the eastern shore; and TB = the turning basin.

tensity were higher at Elkhorn Slough (Roe, 1979) when compared to Bodega Harbor (U-test, $P < 0.05$, $n = 26$). Hence, the data for Bodega Harbor and Elkhorn Slough were analyzed separately.

Results

Carcinonemertes epialti exhibited a marked seasonal pattern in worm abundance (Fig. 2). A peak in worm prevalence and mean intensity occurred in five out of six autumn samples.

In October, 1982, we observed an outbreak of *Carcinonemertes epialti* on *Hemigrapsus oregonensis* (Table 1). The mean intensity of worms was highest on male crabs and lowest on non-ovigerous female crabs. The mean intensity of 296 worms/crab was much higher than the fall mean of 15 worms/crab found at Bodega Harbor (Kuris, 1971, 1978). During the outbreak, prevalence reached 97% of the adult crabs, compared to the fall mean of 48% of the adult crabs in other years at Bodega Harbor. The October, 1982, outbreak was ephemeral. By March, 1983, worm prevalence and intensity had returned to baseline levels (Fig. 2).

Brood loss was substantial during the outbreak. Nearly complete brood loss (75 – 100% of the eggs) was observed on 83% of the ovigerous crabs. The remaining ovigerous female crabs had lost between 20 – 50% of their eggs. Most ovigerous crabs exhibiting complete or nearly complete brood loss retained a few eggs; the presence of a few living embryos in the egg masses provided a record of the developmental stage of the eggs, and enabled us to distinguish these clutches from recently hatched broods. If remnant eggs were in very late developmental stages they were excluded from the analysis to avoid confusion with hatching broods. The numerous worms reco-

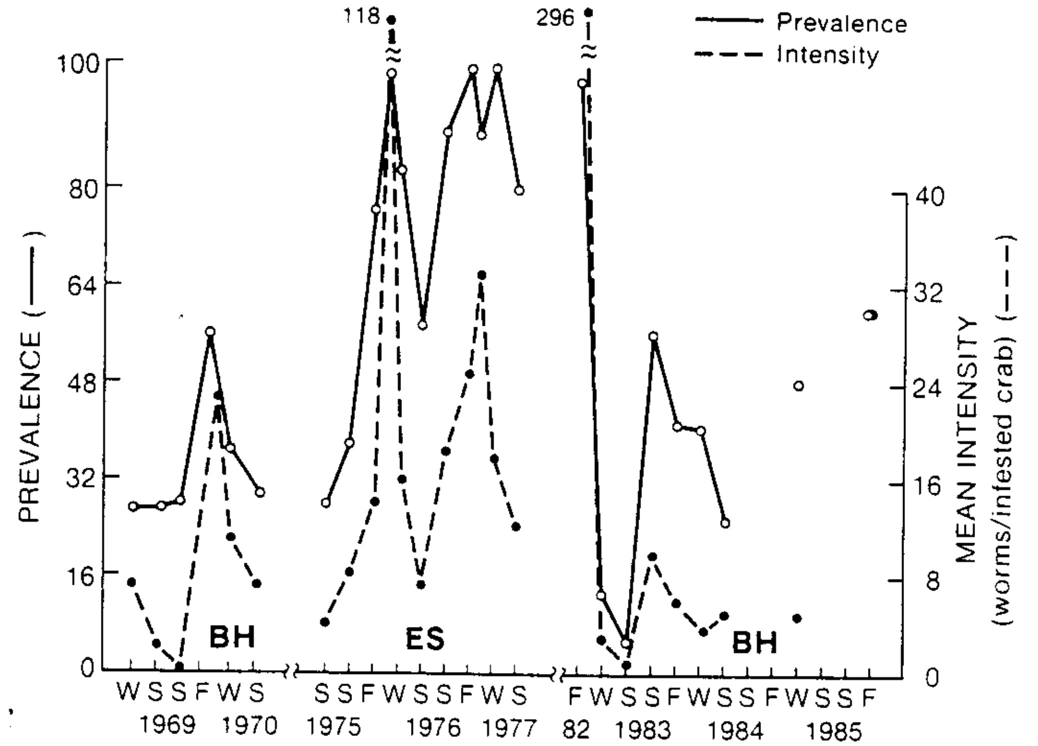

Fig. 2. Prevalence and mean intensity of *Carcinonemertes epialti* on *Hemigrapsus oregonensis*. Data for 1969–1970 are from Kuris (1978), for 1975–1977 from Roe (1979), for 1982–1985 from the present study. BH = Bodega Harbor; ES = Elkhorn Slough, Monterey.

Table 1. Distribution and abundance of *Carcinonemertes epialti* on *Hemigrapsus oregonensis* during the outbreak of October, 1982 in Campbell Cove, Bodega Harbor, California.

	Males	Non-ovigerous females	Ovigerous females	Total
Prevalence (%)	100	100	83	97
Mean intensity ± s.d.	570 ± 521	149 ± 180	231 ± 147	296 ± 280
Range	5 – 1680	14 – 700	12 – 1000	5 – 1680
n	15	15	12	42

Table 2. Abundance of *Carcinonemertes epialti* and egg mortality estimates from *Hemigrapsus oregonensis* at five locations within Bodega Harbor, February, 1985.

	CC	CG	TB	WP	EA	Total
Prevalence (%)	49	58	29	55	40	48
Mean intensity	6.6 ± 12.4	4.9 ± 5.3	3.0 ± 3.5	4.6 ± 5.9	6.0 ± 7.4	5.3 ± 8.3
Mean mortality	5.2 ± 4.8	8.9 ± 5.5	–	0.2 ± 0.03	6.1 ± 4.2	4.8 ± 4.2
Prevalence of egg mortality (%)	82	80	–	15*	90	73
Ovigerous crabs	48	20	0	13	20	101
Total crabs	76	52	31	58	55	272

CC = Campbell Cove; CG = Coast Guard Cove; TB = the turning basin; WP = Westshore Park; EA = the eastern shore.
*$P < 0.05$; $G_H = 25.88$, d.f. = 3.

vered from heavily infested crabs (>90 worms/crab) were smaller than worms from lightly infested ovigerous crabs (<13 worms/crab) bearing eggs at a similar stage of embryogenesis. The relatively small worms on the heavily infested crabs were similar to the worms found on crabs whose clutches had hatched or were in a very late stage of egg development (see Kuris, 1971, 1978; Roe, 1984).

The February, 1985, data typify the baseline data collected during non-outbreak years (Fig. 2). At this time, 49% of the crabs were infested and the mean intensity was 6.6 worms per crab (Table 2). In February, 1985, crabs were sampled from four additional sites inside Bodega Harbor. Few differences were found between sites for prevalence, mean intensity, and mean egg mortality (Table 2). The TB sample had a lower prevalence of worms, and a lower mean worm intensity than the other sites but the differences were not significant because the variance in the samples was large (prevalence, GH=9.35, $0.10>P>0.05$, d.f.=4). No ovigerous females were found at the TB site. Four sites contained ovigerous females. West Shore Park (WP) had a significantly lower prevalence of egg mortality (GH=25.88, $P<0.05$, d.f.=3) and lower mean egg mortality ($P>0.05$, n.s.). Campbell Cove (CC), CG, and EA had similar mean egg mortalities and similar prevalences of egg mortality (Table 2).

Egg mortality varied with embryonic development of the host (Table 3). Clutches with eggs in early stages of development experienced negligible egg mortality; 94% of those clutches had less than 1.0% egg mortality. Of the 37 crabs whose egg clutches were in mid- to late developmental stages, 75.6% experienced greater than 1.0% egg loss. Further, 54.0% of the mid- to late stage egg clutches experienced greater than 10.0% egg mortality. The low egg mortality suffered by crabs with eggs in early embryogenesis was significantly less than the higher egg mortality observed on crabs with eggs in later stages of development (GH=45.4, $P<0.01$, d.f.=6).

Table 3. Egg mortality in relation to egg development stage.

EDS	Egg mortality (%)				
	<1%	1.0–10%	10–20%	>20%	Total
I (early)	30	2	0	0	32
II (middle)	6	5	4	4	19
III (late)	3	3	6	6	18
Total	39	10	10	10	69

Data are from CC, CG, EA, and WP for February, 1985. EDS = egg developmental stage (see Kuris, 1971, 1978).

Egg mortality increased in relation to worm abundance for the February, 1985, sample. Egg mortality varied from 0.0% to 52%, and worm abundance varied from 0.1 to 30.3 worms per thousand eggs. Egg mortality was significantly correlated with the number of worms per thousand eggs (r=0.557, $P<0.05$, d.f.=14). Egg mortality was also highly correlated with worm intensity (r=0.367, $P<0.01$, d.f.=48).

Discussion

Our findings have an important consequence. The discovery of high intensity *Carcinonemertes* infestations on heavily fished commercial crabs led to the suggestion that the fishery itself contributed to the epidemic outbreak observed in these systems (Botsford & Wickham, 1978; Wickham, 1979a, 1979b, 1980). Outbreaks of nemertean egg predators on unfished populations of shore crabs, such as is reported here, demonstrate that there is no *necessary* connection between heavy fishing pressure and nemertean abundance. However, fishing pressure may still be a *sufficient* condition to promote a nemertean outbreak.

Prevalence and mean intensity serve as indicators of parasite abundance and the dispersion of the parasites among their hosts (Kitron, 1980; Margolis *et al.*, 1982; Kitron & Higashi, 1985). Prevalence indicates the extent of the infested population, while mean intensity and its variance measure the dispersion of the parasite population on infested hosts. Parasite populations are typically overdistributed or aggregated in the host population (Crofton, 1971; Kitron, 1980); thus, mean intensity is frequently characterized by a large variance. Changes in mean intensity may not necessarily reflect changes in prevalence, and *vice versa* (Kitron, 1980; Kitron & Higashi, 1985). When all hosts are infected, prevalence no longer contributes to parasite aggregation. The prevalence of *Carcinonemertes* spp. on their respective decapod hosts often reaches levels where 70–100% of the hosts are infested (Wickham, 1979a; Brattey *et al.*, 1985). However, the mean intensity of the worms on their respective hosts may vary from extremely low levels to extremely high levels even when prevalence is high (Table 1). This pattern is also seen for nemerteans on red king crabs, American lobster, *Cancer magister*, and *Cancer* spp. (Wickham, 1979a; Brattey *et al.*, 1985; Wickham *et al.*, 1985). Thus, mean intensity is generally a more useful indicator of the dispersion of *Carcinonemertes* spp. among their hosts than is prevalence.

The October, 1982, outbreak coincided with the seasonal peak in worm abundance, and represented the highest mean intensity observed for *C. epialti* on *H. oregonensis*. In a two year study of 755 crabs at Bodega Harbor, the maximum intensity recorded for any monthly sample was 26 worms per crab, with a prevalence of 47% (Kuris, 1978). In a two year study of the *H. oregonensis*–*C. epialti* association at Elkhorn Slough, California, Roe (1979) recorded a maximum mean intensity of 118 worms per crab with a prevalence of 97% in November, 1975. In any case, the intensity of worms in October, 1982, represented a peak in worm abundance much greater than expected based on the other samples for this locality and, thus, satisfied the definition of a population outbreak (Carpenter, 1940; Kendeigh, 1961).

At Bodega Harbor, *Hemigrapsus oregonensis* bred 3–5 times per year with a seasonal peak in abundance of ovigerous crabs beginning in December or January (Kuris, 1971, 1978). While worms were found on crabs throughout the year, worm prevalence and intensity were highest in autumn. This is consistent with experimental studies of worm transmission in the field (Bauman, 1983). Interestingly, the frequency of brooding females was lowest in autumn (Kuris, 1971). Thus, the autumn peaks in worm intensity, including the October, 1982, outbreak, affected relatively few brooding crabs. Consequently, the seasonal impact of high worm abundance on annual brood production is minimized.

A realistic estimate of the impact of nemertean egg predators on crab natality during non-outbreak periods must consider the following factors: crab fecundity, worm prevalence, and worm intensity. These factors are all size dependent but to varying degrees. Hence, the size structure of the ovigerous crabs must be included in any analysis. Using the size-fecundity relationship of $Y = 469 + 1.4\ X^3$, the feeding rate estimate of 57 eggs per worm (Roe, 1984; Kuris & Wickham, 1987), and the February, 1985, data on worm intensity summarized in Table 2, we can project brood loss through the embryogenic period (Table 4). When all of the relationships are considered, 5.6% of the eggs produced would ultimately be consumed by *C. epialti* (Table 4). The ratio of the number of worms infesting a size class of crabs to the number of eggs oviposited by that size class

Table 4. Projected egg mortality in relation to crab fecundity and worm intensity.

	Size class (CW mm)			
	10	14	18	Total
(Infested crabs/Total # of crabs) = Prevalence (Np/N) = P	10/21	44/64	12/16	66/101
Estimated fecundity/crab (F)	1869	4310	8634	-
Estimated total # of eggs oviposited (N × F) = E	3.9×10^4	27.5×10^4	13.8×10^4	45.3×10^4
Estimated # of eggs on infested crabs (Np × F) = EI	1.8×10^4	18.9×10^4	10.3×10^4	31.1×10^4
Total # of worms on infested crabs (W)	33	292	117	442
Mean intensity of worms (W/Np) = I	3.3	6.6	9.8	6.7
Estimated # of eggs consumed (W × 57) = EC	1881	16644	6669	2.5×10^4
Percentage of eggs eaten on infested crabs (EC/EI)	10.1	8.8	6.4	8.1
Percentage of eggs eaten on all crabs (EC/E)	4.8	6.0	4.8	5.6
Worms/1000 eggs ((I/F) × 1000)	1.8	1.5	1.1	1.4

Crab fecundity estimated by $Y = 469 + 1.4\ X^3$. Worm feeding rate was based on an estimate of 57 eggs consumed per worm over a 43 day development period (Roe, 1979). The February, 1985 samples from Bodega Harbor were used for the mortality projections.

is similar for all three size classes. Thus, each size class loses a similar 4.8% to 6.0% of its eggs to nemertean predation.

However, infested crabs in the smallest size class (8.0–11.9 mm) lost a large proportion of their eggs (10.1%). In contrast, infested crabs in the largest size class (16.0–20.0 mm) lost only 6.4% of their eggs. This is a consequence of crab fecundity being a power function with respect to crab size, and fecundity increases at a greater rate with crab size than does worm intensity. Thus although both size classes lost a similar 4.8% of their eggs to worm predation, the risk of egg predation on an infested crab is greatest for the smallest size class.

Further, the *H. oregonensis – C. epialti* interaction may now provide an excellent system for the study of nemertean population dynamics. The commercially important species are relatively inaccessible, hard to sample, and experimental manipulations on stock are difficult to imagine. In contrast, *H. oregonensis* is readily accessible and abundant, amenable to careful quantitative sampling and experimental manipulation, and individuals may be marked and recaptured with a high rate of return (Kuris, 1971).

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