

## INFESTATION OF AN INTRODUCED HOST, THE EUROPEAN GREEN CRAB, *CARCINUS MAENAS*, BY A SYMBIOTIC NEMERTEAN EGG PREDATOR, *CARCINONEMERTES EPIALTI*

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**ABSTRACT:** The recent introduction of the European green crab, *Carcinus maenas*, to the west coast of the U.S. has provided an opportunity for host transfer of the symbiotic nemertean egg predator, *Carcinonemertes epialti*, from its native shore crab host, *Hemigrapsus oregonensis* to the exotic *C. maenas*. Two surveys of *C. maenas* in Bodega Harbor, California, revealed that, in March 1995 prevalence of *C. epialti* on *C. maenas* was significantly lower than on *H. oregonensis* (11% versus 74%), but in November 1995 there was no significant difference between the 2 species (79% versus 98%). Only juvenile *C. epialti* were recovered from *C. maenas* in March 1995. However, in November 1995, ovigerous *C. maenas* were harboring actively feeding adult worms. Prevalence in both crab species significantly differed from March to November. Laboratory studies revealed that *C. epialti* fed and reproduced on eggs of *C. maenas*. The feeding rate of *C. epialti* on *C. maenas* eggs (2.5 eggs/trial) was not significantly different from that on *H. oregonensis* eggs (3.6 eggs/trial). Our findings suggest that this nemertean may have less host specificity than was previously thought. If *C. epialti* causes brood mortality of *C. maenas* in nature, it could potentially impact populations of this exotic crab.

Host specificity is determined by the number of host species to which a symbiont can successfully recruit and on which it can grow and reproduce. Ecological and behavioral constraints may limit recruitment and the potential host range of a symbiont. When a symbiont can recruit to a new host species, physiological specificity governs the success of establishment. Cospeciation analyses offer several examples of host transfer in groups thought to be generally host specific (Clayton, 1990; Brooks and McLennan, 1993). Such host transfers should be most likely where ecologically similar hosts are syntopic.

Introductions of exotic species are "natural" experiments that provide opportunities to study host specificity and host transfer. In marine systems, introduced species are often free of natural parasites because they usually enter a new system as uninfected larvae (Lafferty and Kuris, 1994). Examining parasite accumulation on introduced species provides information on parasite colonization, which is otherwise difficult to study. Here, we document the novel host transfer of a symbiotic nemertean egg predator from a native crab to an introduced species of crab. (We use "symbiotic" in the original sense of de Bary [1879] as an overall term for all intimate interspecific interactions including parasitism, mutualism, and commensalism.) We also investigate the ability of the worm to feed and reproduce on this exotic crab. We use this information to predict the role of this new host in the population dynamics of the nemertean egg predator and the potential impact of the worm on population control of the introduced crab.

Nemerteans in the genus *Carcinonemertes* are obligate symbiotic egg predators of decapod crustaceans. Their ecological impact is that of a predator, as they kill individual embryos; however, their life cycle, intimacy, and use of chemically mediated cues from their hosts are such that their biology is effectively akin to parasitism (Kuris, 1993). Planktonic larvae settle on juvenile or adult crabs (Wickham, 1980). Juvenile worms acquire nutrients by absorbing dissolved organic material leaked

from their host (Crowe et al., 1982). When female crabs oviposit, the worms migrate to the egg mass, feed on embryos, mature, and lay their egg masses among the host eggs.

*Carcinonemertes epialti* was first described by Coe (1902) from the kelp crab, *Pugettia producta*. The host list of this nemertean now includes 10 other species (Humes, 1942; Kuris, 1971; Wickham, 1978; Roe, 1979). Although worms in the genus *Carcinonemertes* were considered to exhibit little host specificity (Humes, 1942), minor differences exist among the worms infesting some of these different hosts, suggesting that *C. epialti* may represent a species complex (Wickham and Kuris, 1988).

In Bodega Harbor, California, *C. epialti* commonly infests the yellow shore crab, *Hemigrapsus oregonensis*, occasionally occurs on the purple shore crab, *Hemigrapsus nudus*, rarely infests *P. producta*, and is absent on the striped shore crab, *Pachygrapsus crassipes* (Kuris, 1978). Roe (1979) recorded it from *P. crassipes* at Elkhorn Slough, 200 km south of Bodega Harbor. Based on the absence of *C. epialti* from *P. crassipes*, a confamilial crab that considerably overlaps in habitat with *H. oregonensis*, host specificity may limit the distribution of *C. epialti* on its crab hosts (Kuris, 1978). *Carcinonemertes errans* Wickham, 1978, found in the same geographic region as *C. epialti*, is specific to the Dungeness crab, *Cancer magister* (Wickham, 1978). Wickham and Roe (1987) experimentally showed that host selectivity may control settlement of *C. epialti* in nature. They demonstrated that *C. epialti* larvae differentially settled on 3 crab species, preferring *H. oregonensis* and *H. nudus* over *C. magister*. Further, worms settled on *H. oregonensis* at a rate approximately twice that of *H. nudus*. Roe (1984), however, found that adult *C. epialti* exhibits no strong feeding preference for eggs of their own host. Thus, host specificity appears to be determined more by larval recruitment than by the suitability of the host for juvenile maintenance or adult maturation, growth, and reproduction.

The European green crab, *Carcinus maenas* was first reported from San Francisco Bay, California, in 1989-1990 (Cohen et al., 1995). It has since successfully spread south to Elkhorn Slough, Monterey, and north to Humboldt Bay (E. Grosholz and T. Miller, pers. comm.). In Bodega Harbor, *C. maenas* and *H. oregonensis* are largely syntopic species.

TABLE I. Season, sample size (n), prevalence, intensity, relative abundance, and variance of relative abundance ( $s^2$ ) of *Carcinonemertes epialti* on *Carcinus maenas* and *Hemigrapsus oregonensis* at Bodega Harbor (spring, 27–30 March 1995 and Fall, 3–4 November 1995). Nonovigerous female *H. oregonensis* were not examined in the spring.

	Season	n	Prevalence	Mean intensity	Relative abundance	$s^2$
<i>C. maenas</i>						
Males	Spring	32	16	8	1.3	15.4
	Fall	28	93	41.6	38.7	3,360
Females						
Non-ovigerous	Spring	19	11	2.5	0.3	0.8
	Fall	12	50	22	11	551
Ovigerous	Spring	11	0	0	0	0
	Fall	3	67	7.5	5	61
Total crabs	Spring	62	11	6.4	0.7	8.5
	Fall	43	79	36.2	28.6	2,503
<i>H. oregonensis</i>						
Males	Spring	20	65	5.3	3.5	29.6
	Fall	24	96	72	68.7	2,274
Females						
Non-ovigerous	Spring	—	—	—	—	—
	Fall	26	100	23.2	23.2	218
Ovigerous	Spring	14	86	15.9	13.6	276
	Fall	2	100	50	50	338
Total crabs	Spring	34	74	10.4	7.6	156
	Fall	52	98	40.1	45.2	1,647

In western Europe, where *C. maenas* is native, it is commonly infested with *Carcinonemertes carcinophila* (Crothers, 1968). Following the introduction of green crabs to the western Atlantic over 100 yr ago, the green crab became very abundant in New England and the Canadian Maritime Provinces (Glude, 1955). However, despite the common occurrence of a very similar worm, currently given the subspecific status, *Carcinonemertes carcinophila immunita* on the lady crab, *Ovalipes ocellatus* (Sumner et al., 1913; Humes, 1942), no nemerteans have been recorded from the abundant northwest Atlantic populations of the green crab.

To address the ability of *C. epialti* to infest a new host, we documented the successful recruitment of *C. epialti* to *C. maenas* in nature and experimentally determined that the nemertean can eat the eggs of and reproduce on *C. maenas* in the laboratory.

## MATERIALS AND METHODS

We collected *C. maenas* in Bodega Harbor, California, by hand on mudflats at low tide and with minnow traps (Gee MT2). We modified the traps by increasing the diameter of the opening, baited them with anchovies, and set them overnight. All crabs encountered were collected and taken to Bodega Marine Laboratory for immediate examination. We recorded crab size (carapace width), sex, female reproductive condition, and abdomen width. We sampled crabs in March 1995 and November 1995. In March, we examined all ovigerous females (n = 11) and the first 51 other crabs collected for nemerteans using a stereomicroscope. In November, we examined all crabs encountered (3 ovigerous and 40 other crabs).

We collected *H. oregonensis* from an adjacent site in Bodega Harbor by overturning rocks. In March, the first 20 males and all ovigerous females (n = 14) encountered were collected. In November, we examined 52 crabs, 2 of which were ovigerous. These crabs were examined for nemerteans as described above. We compared worm prevalence on both crab species using chi-square analyses. Prevalence was defined as the percentage of crabs infested, mean intensity as the average number of worms per infested crab, and relative abundance as the average number of worms per infested and uninfested crabs (Margolis et al., 1982).

In feeding experiments, we removed fascicles of setae with 40–50 entwined eggs from the pleopods of ovigerous crabs of either *H. oregonensis* or *C. maenas*. Each fascicle was placed in a 35 × 10-mm petri dish with 3 ml of filtered seawater. To increase consistency among replicates, we used eggs in the same developmental stage, i.e., early-middle (Kuris, 1978). Eggs used in the experiment were taken from uninfested crabs to ensure that nemertean feeding behavior was not influenced by prior exposure of eggs to predation. We monitored the eggs during the experiment to ensure they were not fouled by epibiotic organisms.

We removed adult *C. epialti* from *H. oregonensis* egg masses and placed them into the petri dishes. The experiment included 2 treatments (*C. maenas* eggs with worms and *H. oregonensis* eggs with worms) and 2 controls (*C. maenas* eggs without worms and *H. oregonensis* eggs without worms), each replicated 10 times. We placed the petri dishes in laminated steel trays (30 × 45 mm) and covered them with nylon mesh. The trays were kept in running seawater at 15 C to maintain constant temperature.

Worms fed for 5 days, after which we counted the number of dead or damaged eggs. We based egg mortality on the presence of remnant egg membranes without yolk or pierced eggs exuding yolk (Wickham, 1979; Kuris et al., 1991). We accounted for all eggs by comparing our initial and final egg counts. The seawater in each dish was replaced once midway through the trial. We tested the resulting data for normality and analyzed it by ANOVA.

Following the in vitro experiments, we infested 1 ovigerous female *C. maenas* with 12 *C. epialti* by placing them on her egg mass. Prior to infestation, we clipped 1 pleopod and examined its egg mass with the aid of a stereomicroscope to assess initial egg mortality. The crab was isolated in aerated seawater. After 6 days, we removed all remaining eggs and examined them under a stereomicroscope. We haphazardly selected 15 fascicles with 40–60 eggs each and counted all of the dead eggs.

## RESULTS

Of the 159 *C. maenas* collected in March, we carefully examined all ovigerous females (n = 11) and a haphazardly selected sample of 51 other crabs for *C. epialti*. In March, both male and nonovigerous female *C. maenas* were infested at low prevalences with low intensities of juvenile *C. epialti* (Table I). The juvenile worms were encased in a mucous sheath either near the limb axillae or in the abdominal furrows of the crabs. No *C. epialti* were found on any of the 11 ovigerous females (including the egg mass). Both male and ovigerous female *H. oregonensis* were infested with juvenile worms and the ovigerous females also were infested with actively feeding adult worms. *Carcinonemertes epialti* prevalences on male and ovigerous female crabs were significantly higher on *H. oregonensis* (65%, 86%) than on *C. maenas* (16%, 0%),  $\chi^2 = 12.9$ ,  $P < 0.01$  and  $\chi^2 = 16.4$ ,  $P < 0.01$ , respectively for male and ovigerous female crabs.

In November, male and nonovigerous *C. maenas* were infested at significantly higher prevalences of juvenile *C. epialti* than in March (93% versus 16% for males,  $\chi^2 = 35.7$ ,  $P < 0.001$  and 50% versus 11% for nonovigerous females,  $\chi^2 = 5.98$ ,  $P < 0.05$ ). Further, 2 of the 3 ovigerous female *C. maenas* collected were infested with actively feeding adult worms. Male *H. ore-*

*gonensis* were also infested at significantly higher prevalences of juvenile worms (96% versus 65%,  $\chi^2 = 6.97$ ,  $P < 0.01$ ). The 2 ovigerous *H. oregonensis* also harbored actively feeding adult worms. *Carcinonemertes epialti* prevalences on male crabs of both species were not significantly different (*H. oregonensis*, 96%; *C. maenas*, 93%;  $\chi^2 = 0.21$ ,  $P > 0.05$ ). With our fall sample we were able to compare worm prevalence on nonovigerous female crabs. This was significantly higher for *H. oregonensis* (100%) than for *C. maenas* (50%),  $\chi^2 = 15.4$ ,  $P < 0.001$ . We did not compare the prevalences on ovigerous crabs due to the small sample sizes. The high variance-to-mean ratio for relative abundance (Table I) was similar for worms on both crab species. This indicates that worms were overdispersed (aggregated) on their crab hosts.

Egg counts in the feeding experiments revealed that after 5 days there was substantial mortality in both treatments relative to the respective controls (in which we observed no egg mortality),  $F = 44.71$ ,  $P < 0.0001$ . On average, *C. epialti* ate 2.5 *C. maenas* eggs and 3.6 *H. oregonensis* eggs over the 5-day experiment (Fig. 1). These feeding rates were not significantly different ( $F = 1.45$ ,  $P > 0.05$ ).

Samples from the egg mass before the in vivo feeding experiment revealed no egg mortality. Six days after infestation, we recovered 6 worms moving actively in the egg mass (the others may have been lost in handling). The remaining pleopods were clipped off and the fascicles were carefully stripped. By counting dead eggs, we estimated an average mortality of 1.3 eggs per fascicle (each fascicle contained an average of 52 eggs). Although the worms were not measured before the experiment, an increase in worm size was apparent after 6 days. We also observed an orange substance in the guts of the worms, suggesting they had fed on crab egg yolk. In addition, several nemertean egg masses were attached to the setae of the crab.

## DISCUSSION

*Carcinonemertes epialti* is able to infest *C. maenas* in nature, despite its otherwise restricted host range (Kuris, 1978; Wickham, 1978; Roe, 1979; Wickham and Roe, 1987). Worm prevalence was much lower on the introduced green crab than on the native *H. oregonensis* in March. In November, worm prevalence was similar between male crabs of the 2 species but was still much lower for nonovigerous female *C. maenas*. One might expect that prevalence on a new host would increase over time. This is consistent with observations of parasitoid assemblages on introduced insects (Cornell and Hawkins, 1994) and for herbivorous insects on introduced plants (Kuris et al., 1980; Blaustein et al., 1983). It is also possible that the differences in prevalence and intensity between the 2 samples may merely reflect the autumn peak in abundance of *C. epialti* on *H. oregonensis* at Bodega Harbor and elsewhere (Kuris, 1978; Roe, 1979; Shields and Kuris, 1988).

The recovery of a native nemertean symbiotic egg predator on an introduced host is a novel discovery. There are no other reports of such transfers despite the frequent introduction of crab species in San Francisco Bay and elsewhere (Carlton, 1987, 1989; Zibrowius, 1991). This record is particularly notable because *C. maenas* is a well-studied and abundant component of the intertidal and shallow water fauna of the northeastern coast of North America where a nemertean egg predator, *C. carci-*

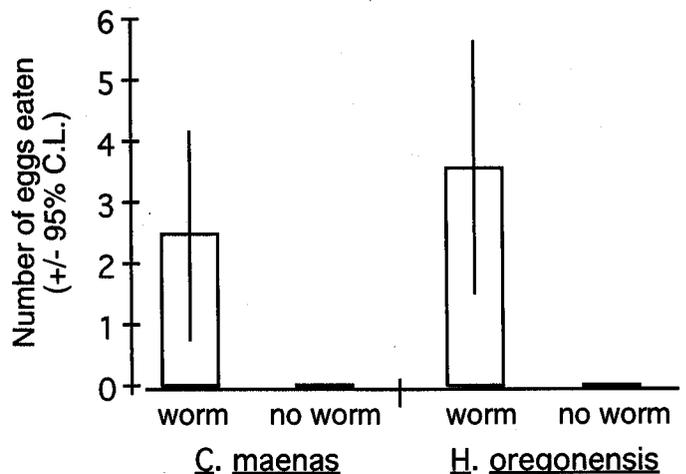


FIGURE 1. The number of *Carcinus maenas* and *Hemigrapsus oregonensis* eggs eaten in vitro by *Carcinonemertes epialti*. Error bars represent 95% confidence intervals.

*nophila immunita*, closely related to the nemertean on the green crab in Europe, *Carcinonemertes carcinophila carcinophila*, is present. Yet, there are no published records of host transfer and our investigations of green crab parasites in southern New England yielded only negative records for any nemerteans, including *C. carcinophila immunita*, which infests the lady crab, *O. ocellatus*.

Interestingly, juveniles of *C. epialti* were only recovered from the limb axillae and abdominal furrows of their crab hosts. These are the normal sites for *C. epialti* on *H. oregonensis* (Kuris, 1978, 1993). Also, male as well as female crabs were infested. Juveniles of *C. carcinophila* infesting *C. maenas* and of *Carcinonemertes mitsukurii* Humes, 1942, infesting other portunid crabs, are generally found in the branchial chambers, usually on the gill lamellae, and are rarely recorded from male crabs. These sites reflect important differences in the life cycles and epizootiology of the *C. epialti* and *C. carcinophila* groups (Kuris, 1993). It will be of considerable interest to discover if *C. epialti* infesting *C. maenas* will be able to detect the cues that trigger transfer from the exuvia to the postmolt crab and from males to females that typify the life cycles of *C. epialti* and its relatives in contrast to *C. carcinophila* (Kuris, 1978, 1993; Wickham et al., 1984). Preliminary evidence suggests that predation on infested *H. oregonensis* by *C. maenas* may also facilitate transmission (M. E. Torchin, unpubl. obs.). This may provide an unrecognized transmission mechanism for symbiotic nemertean egg predators.

Our laboratory results show that *C. epialti* eats *C. maenas* and *H. oregonensis* eggs at similar rates in vitro. This similarity is consistent with the lack of feeding specificity that Roe (1984) found in her laboratory experiments. Our field observations, however, suggest that *C. epialti* displays broader host specificity in nature than was previously thought.

The introduction of marine invertebrates to new geographic locations has often had deleterious consequences (Carlton, 1987, 1989; Zibrowius, 1991). In their native range, green crabs are voracious predators of many benthic invertebrates (Scherer and Reise, 1981; Klein Breteler, 1983; Sanchez-Salazar et al., 1987).

It is probable that the introduction of these crabs and the absence of their natural enemies (Lafferty and Kuris, 1996) have already altered the distribution and abundance of the intertidal and subtidal fauna of west coast estuaries (Grosholz and Ruiz, 1995), as had previously occurred on the northwest Atlantic coast (MacPhail et al., 1955).

Brood mortality caused by nemertean infestations can be severe (Wickham, 1986; Shields and Kuris, 1988; Shields et al., 1990; Kuris et al., 1991). However, there are no available studies of brood mortality caused by the European nemertean egg predator, *C. carcinophila* on *C. maenas*. It will be of considerable interest to track the spread of *C. epialti* on the recently introduced crab. It might be suggested that the high potential for damage caused by *C. maenas* may be reduced by *C. epialti* if the nemertean can complete its life cycle on this invader and establish high prevalences and intensities in nature. However, the geographic distribution of *C. epialti* on its native host is quite patchy (Kuris, 1978; Roe, 1979). These egg predators have only been detected in abundance at a few locations (including Bodega Harbor). Unless *C. maenas* enables the worms to become more widely dispersed, or if recruitment of *C. maenas* is highly localized, the impact of nemertean egg predation will be unlikely to significantly reduce the abundance of the introduced green crab. (See Kuris and Lafferty [1992] for a discussion of marine host and parasite recruitment scales.) The present findings call for studies of brood mortality of infested and uninfested crabs to determine the impact of *C. epialti* on the reproductive output of the introduced host, as well as the potential effects of the exotic crab on the population dynamics of the nemertean egg predator.

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