

The infestation and dispersion patterns of *Carcinonemertes* spp. (Nemertea) on their crab hosts

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Abstract

Seasonal changes in the infestation and dispersion patterns of egg predatory nemerteans on their crab hosts were analyzed. Marked differences in the seasonal patterns of infestation were noted between worm species, yet, common patterns in the aggregation of the worms were found. Worm aggregation increased at the onset of the reproductive seasons of the hosts, and at the nadirs of the reproductive seasons for those hosts with year round breeding. The aggregation patterns of two worm species fluctuated with the physical environment of their estuarine hosts. Salinity changes as a result of seasonal rains may have caused changes in the underlying dispersion patterns of *Carcinonemertes epialti* on *Hemigrapsus oregonensis*, and *C. mitsukurii* on *Portunus pelagicus*. Lastly, the embryogenic cycle of the host species was significant in shaping the infestation and aggregation patterns of *C. epialti* on *Cancer anthonyi* and *C. regicides* on *Paralithodes camtschaticus*. Worm immigration and emigration were linked to crab embryogenesis and directly influenced the dispersion patterns of the worms.

Introduction

The dispersion of parasite populations among their host populations is typically aggregated. Such dispersion patterns are characterized by many hosts possessing few parasites and few hosts possessing many parasites. Several different theoretical frequency distributions (*i.e.*, negative binomial, log normal, log series, Neyman type A, Polya-Aeppli) may describe aggregated populations (Anscombe, 1950; Evans, 1953; Williams, 1964), but the negative binomial frequency distribution has received the most attention in

parasite-host systems (e.g., Crofton, 1971; Pennycuik, 1971; Anderson & May, 1978; Hirsch, 1980; Kitron, 1980; Scott, 1987).

The forces that generate aggregated dispersion patterns are varied, and are broadly classified as either demographic or environmental in nature (May, 1975; Anderson & Gordon, 1982). Demographic factors such as immigration and death rates, or host and parasite genetic variability may have different effects on the dispersion of parasites (May, 1975; Anderson & Gordon, 1982; McCallum & Anderson, 1984). Demographic factors are, however, greatly affected by environ-

mental factors, e.g., temporal or spatial changes in the environment.

The underlying mechanisms that lead to aggregation can be examined by an analysis of the infestation and dispersion patterns of parasites (Crofton, 1971; Iwao & Kuno, 1972; Kitron, 1980). For example, changes in parasite prevalence and mean intensity in the host population appear to reflect changes in the degree of aggregation of the parasite population (Kitron, 1980; Kitron & Higashi, 1985; Scott, 1987). Fluctuations in both parameters can, however, obscure their contributions to the degree of aggregation in the population.

Worms in the genus *Carcinonemertes* von K  lliker are specialized egg predators of decapod crustaceans. The distinctive patterns of prevalence and intensity of the different species suggest that their infestation dynamics may provide insight into the causal mechanisms that lead to their observed aggregation patterns. For example, *Carcinonemertes epialti* on the yellow crab, *Cancer anthonyi*, has a high prevalence (mode 100%) and low mean intensity (Shields *et al.*, 1990), whereas *Carcinonemertes epialti* on the shore crab, *Hemigrapsus oregonensis*, has a markedly variable prevalence and mean intensity (Kuris, 1978; Roe, 1979; Shields & Kuris, 1988). Different infestation patterns have been observed for species of *Carcinonemertes* on the Dungeness crab, *Cancer magister*, the red king crab, *Paralithodes camtschaticus*, and the sand crab, *Portunus pelagicus* (Wickham, 1986; Kuris *et al.*, 1991; Shields & Wood, 1993). The patterns of infestation appear well tuned to the seasonal production of host eggs and their embryogenesis.

The objectives of the present study were: (1) to compare the seasonal changes in abundance and aggregation of *Carcinonemertes epialti* on two of its hosts, *Cancer anthonyi*, and *H. oregonensis*, that of *Carcinonemertes regicides* on *Paralithodes camtschaticus*, and that of *C. mitsukurii* on *Portunus pelagicus*; (2) to investigate the influence of the infestation parameters, prevalence and intensity, on the underlying dispersion patterns; and (3) to determine what demographic processes lead to these patterns of aggregation.

Material and methods

The methods of collection and examination of the crabs and nemerteans have been previously described. *Cancer anthonyi* with *Carcinonemertes epialti* were collected from the Santa Barbara Channel, California (1981–1983) (Shields *et al.*, 1990); *Hemigrapsus oregonensis* with *C. epialti*, from Bodega Harbor, California (1982–1985) (Shields & Kuris, 1988); *Paralithodes camtschaticus* with *C. regicides*, from Kachemak Bay, Alaska (1983–1985) (Kuris *et al.*, 1991); and *Portunus pelagicus* with *C. mitsukurii* from Moreton Bay, Australia (1990) (Shields & Wood, 1993). Ovigerous crabs were used in the analysis, except in the case of *Portunus pelagicus*, where mature, non-ovigerous and ovigerous crabs were used. Only data that had seasonal or monthly samples of hosts and symbionts were used in the analysis.

The dispersion of the nemertean populations was determined to be either random or aggregated. The variance (s^2):mean abundance (\bar{x}) ratio (hereafter the variance:mean ratio, also known as the index of dispersion), Lloyd's mean crowding ($\bar{\bar{x}}$), and the related patchiness ($\bar{\bar{x}}/\bar{x}$) indices were used to measure overdispersion and for comparisons between aggregated distributions (Lloyd, 1967; Elliott, 1977). The variance:mean ratio, while calculated, has serious flaws which limit its usefulness as an index of dispersion (e.g., the ratio is not independent of mean abundance; distributions that are clearly not Poisson may be indicated as such by the ratio, etc. – see Hurlbert, 1990). The mean crowding index is defined as the mean number of individuals per individual on the same host. It is estimated using the equation $\bar{\bar{x}} = \bar{x} + (s^2/\bar{x}) - 1$, where $\bar{\bar{x}} = \bar{x}$ for a random distribution, $\bar{\bar{x}} < \bar{x}$ for a regular or uniform distribution, and $\bar{\bar{x}} > \bar{x}$ for an aggregated distribution, such as the negative binomial distribution. Patchiness represents the mean crowding of an individual if the population it is drawn from has a random distribution (Lloyd, 1967). The χ^2 -test of David & Moore (1954) was employed to examine differences between variance:mean ratios; the usefulness of this test was, however, limited by unequal sample sizes.

Two other indices of dispersion were used to examine changes in aggregation patterns. The regression of mean crowding on mean abundance, $\bar{x} = a + b \bar{x}$, provided information on dispersion and contagion (Iwao, 1968, 1970; Iwao & Kuno, 1971). The Y-intercept, a , represents the index of basic contagion, and the slope, b , represents the density-contagiousness coefficient. The index of basic contagion (a) estimates the numbers of parasites that arrive as a simultaneous unit on the host. It may consist of a single individual or a group of individuals. When $a = 0$, then single individuals compose the basic unit of contagion; when $a > 0$, then more than one individual represents the basic unit of contagion; $a < 0$ represents evidence of negative density dependence or repulsion. The density-contagiousness coefficient (b) presents the dispersion pattern of the symbionts. When $b = 1$, then a random distribution is indicated; when $b < 1$, a regular or uniform distribution; and when $b > 1$, an aggregated distribution is indicated.

In addition, τ , the mortality index of Iwao & Kuno (1971) was used to examine differences in the population dynamics during the course of host embryogenesis for *Carcinonemertes epialti* on *Cancer anthonyi*. $\tau = \text{Patchiness}_1 / \text{Patchiness}_0$, where Patchiness_0 represents the initial patchiness, and Patchiness_1 represents patchiness after the operation of mortality. τ represents recruitment if the mean intensity increases from Patchiness_0 to Patchiness_1 . When $\tau = 1$, mortality/recruitment is independent of parasite density; when $\tau < 1$, mortality/recruitment is density-dependent; and when $\tau > 1$, mortality/recruitment is either inversely density-dependent or it resembles an all-or-none type of response.

Standard statistical tests are from Sokal & Rohlf (1981). The terms prevalence, abundance, mean density, and mean intensity are defined in Margolis *et al.* (1982). However, mean abundance was used in lieu of mean density since density has been used to describe the number of worms per 1000 crab eggs (Wickham, 1979). The terms dispersion and distribution are defined in Pielou (1977) and Anderson & Gordon (1982).

Results

Seasonal patterns

Carcinonemertes epialti exhibited two seasonal peaks in abundance on *Cancer anthonyi* (Fig. 1). The late summer peaks in worm abundance were associated with a highly aggregated dispersion of worms among hosts, but the winter peaks in worm abundance were not as highly aggregated. Prevalence was 100% in every month but August when prevalence was over 80% (1982 & 1983). Late summer peaks in the variance:mean ratio were significantly greater than other periods (χ^2 of David & Moore, $P < 0.05$). Patchiness showed an increase in relative aggregation only in the late summer months (Fig. 1B). In every case, the distribution of worms on *C. anthonyi* was highly overdispersed. The variance:mean ratio was never consistent with the expected ratio of the Poisson distribution ($\chi^2 > 200$, d.f. = 9–27).

Carcinonemertes epialti on *Hemigrapsus oregonensis* experienced a seasonal peak in worm intensity in the fall season (Fig. 2). The peak in worm abundance was paralleled by an increase in the variance:mean ratio but not by the patchiness index. The variance:mean ratios did not agree with the expected ratios of the Poisson distribution ($\chi^2 > 100$, $P < 0.05$, d.f. = 8–54), with the exception of the winter sample of 1983, ($\chi^2 = 30$, $P > 0.05$, d.f. = 29). In March, 1983, the dispersion pattern fit a Poisson distribution because both prevalence and intensity were extremely low. In other months, the dispersion of the worm was highly overdispersed.

Carcinonemertes regicides from *Paralithodes camtschaticus* experienced a long summer plateau in worm abundance (Fig. 3A). The summer increase in worm abundance coincided with an increase in patchiness (Fig. 3B), but the decline in abundance in the fall did not. The variance:mean ratios never agreed with the expected values of the Poisson distribution ($\chi^2 > 1000$, $P < 0.05$, d.f. = 8–29). Patchiness was highest during the nadir in crab reproduction and worm abundance (April).

Carcinonemertes mitsukurii from non-ovigerous

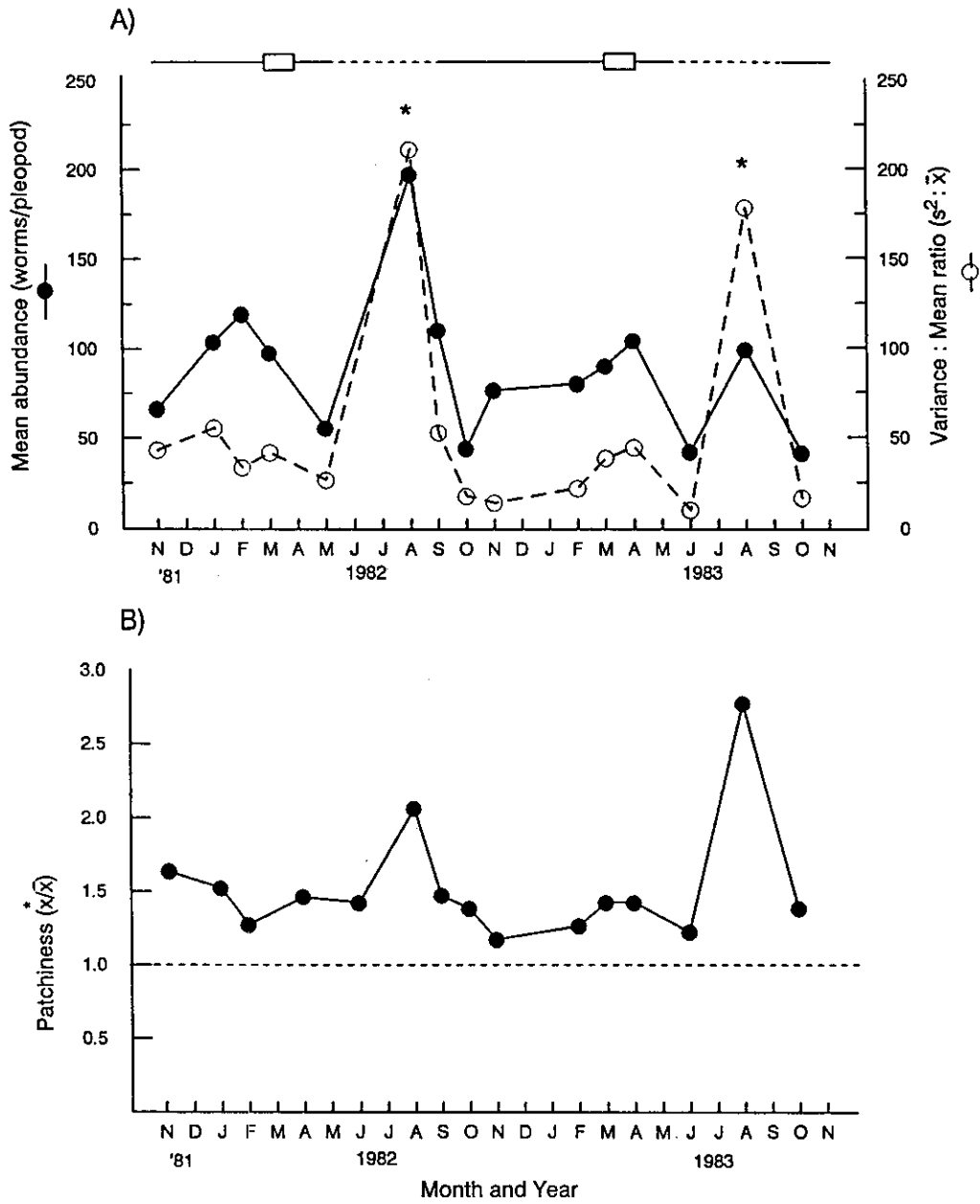


Fig. 1. Changes in abundance and relative aggregation of *Carcinonemertes epialti* on *Cancer anthonyi* from 1981-1983. A) Mean abundance and the variance:mean ratio. Data on crab reproduction are presented as a bar (peak in numbers of ovigerous females), line (moderate numbers of ovig. females), and dotted line (few ovig. females) [Data from Reilly (1987) and Shields *et al.* (1991)]. *Variance:mean ratio significantly greater than other ratios (David & Moore, 1954). B) Patchiness; the reference line indicates distributions approaching random dispersion ($\bar{x} = \bar{x}$).

and ovigerous *Portunus pelagicus* exhibited a summer peak in abundance (Figs 4A & 4C). For worms on non-ovigerous hosts, the variance:

mean ratio paralleled the fluctuations in worm abundance but patchiness showed a strong increase in aggregation in the late fall and early

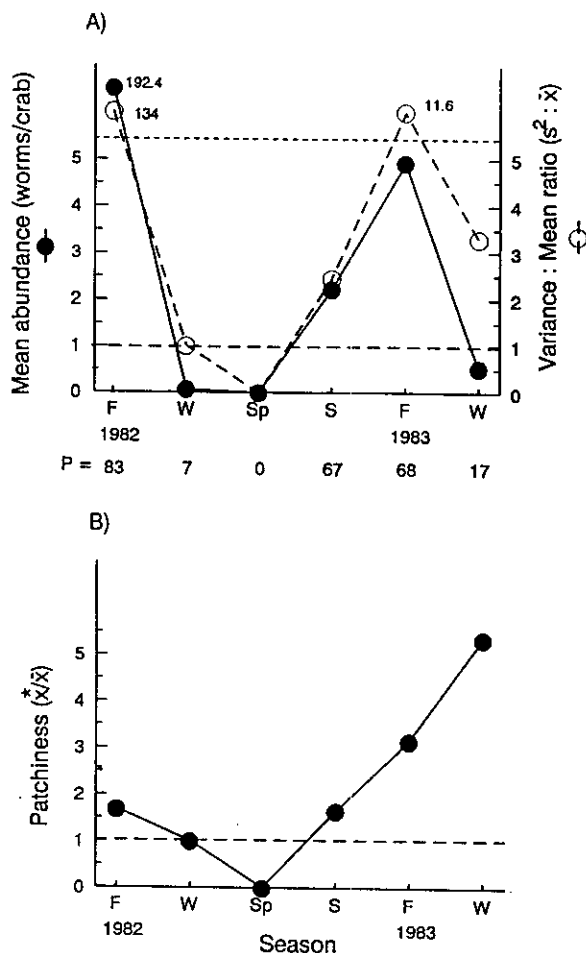


Fig. 2. Changes in abundance and relative aggregation of *Carcinonemertes epialti* on *Hemigrapsus oregonensis* over one year. A) Mean abundance and the variance:mean ratio; P = prevalence (%). B) Patchiness; the reference line indicates random dispersion ($\bar{x}^* = \bar{x}$); dotted line indicates small size of host population.

winter months (Fig. 4B). The underlying aggregation pattern was different for worms from ovigerous crabs (Fig. 4D). In August, patchiness declined for worms on non-ovigerous hosts but increased sharply for worms on ovigerous hosts; these changes occurred at the onset of crab reproduction (Figs 4B & 4D).

The regression of mean crowding (\bar{x}^*) on mean abundance (\bar{x}) was calculated for each worm species (Table 1). The correlation coefficient was high in every relationship ($R > 0.700$, $P < 0.05$). The regression coefficient (b), termed the density con-

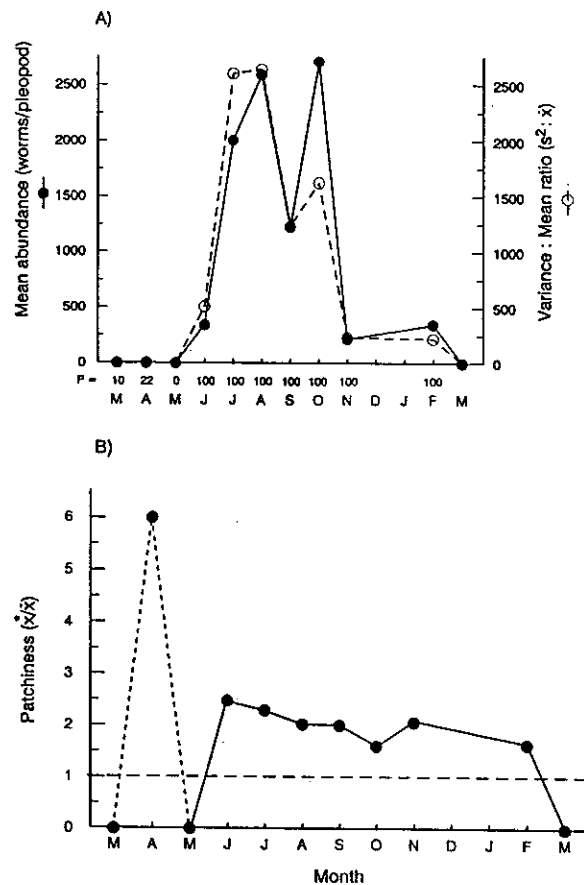


Fig. 3. Changes in abundance and degree of aggregation of *Carcinonemertes regicides* on *Paralithodes camtschaticus* with season (figure represents composite data of 3 years after Kuris *et al.*, 1991). A) Mean abundance and the variance:mean ratio; P = prevalence (%). B) Patchiness; the reference line indicates random dispersion ($\bar{x}^* = \bar{x}$); dotted line indicates small size of host population.

tagiousness coefficient, was significantly greater than one for the dispersion of each worm species ($t_s > 2.42$, $P < 0.05$) (Table 1). The Y-intercept, a , the index of basic contagion, was not significantly different from zero for any of the worm species ($t_s < 1.604$, $P > 0.05$).

Patterns with host embryogenesis

The dispersion pattern of *C. epialti* on *Cancer anthonyi* changed over the course of host embryogenesis. From early to late embryogenesis, the

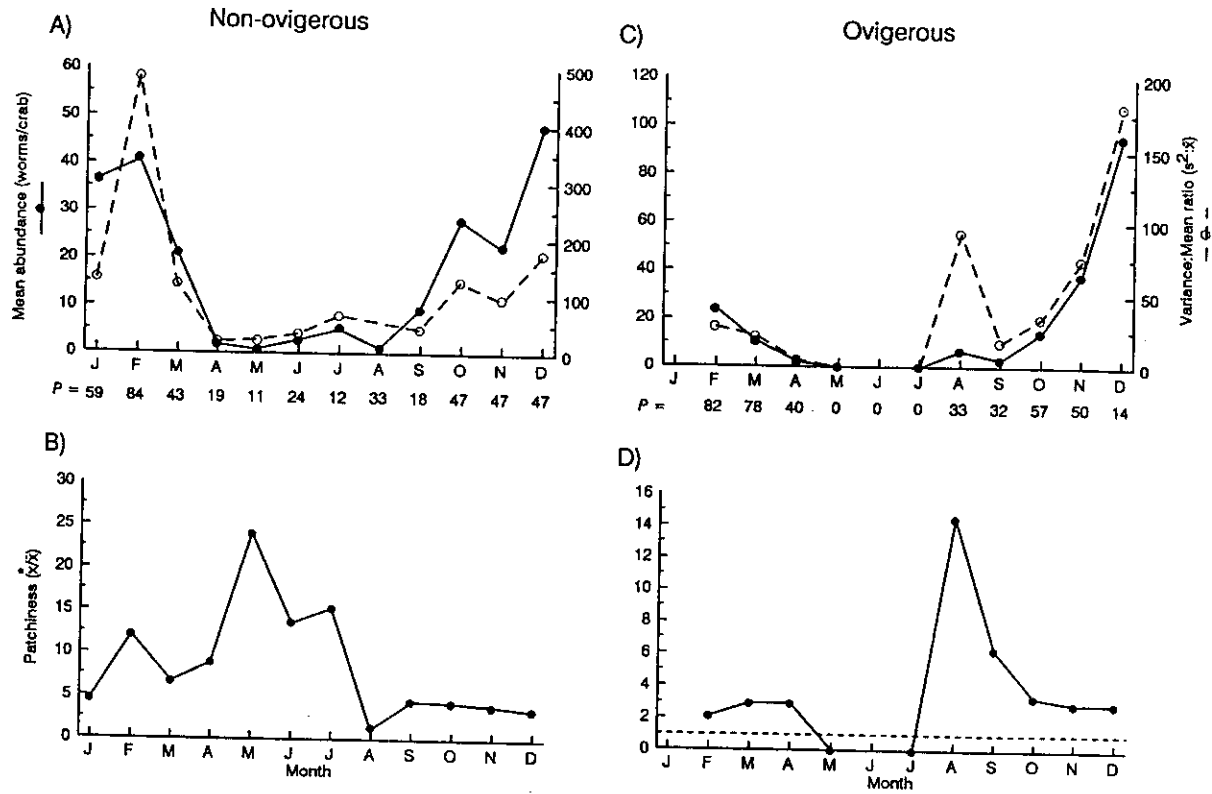


Fig. 4. Changes in abundance and degree of aggregation of *Carcinonemertes mitsukurii* on *Portunus pelagicus* with season; non-ovigerous and ovigerous hosts (A and B), ovigerous hosts (C and D). A) Mean abundance and the variance:mean ratio; P = prevalence (%). B) Patchiness; the reference line indicates random dispersion ($\bar{x} = \bar{x}$). C) Mean abundance and the variance:mean ratio; P = prevalence (%). D) Patchiness; the reference line indicates random dispersion ($\bar{x} = \bar{x}$).

underlying distributions became more highly aggregated, possibly even polymodal, until host

eclosion when the population was most highly overdispersed (Fig. 5, EDS VIII). The χ^2 -test (for

Table 1. Regression statistics for mean crowding (\bar{x}) on mean abundance (\bar{x}). All correlation coefficients were significantly greater than zero ($P < 0.05$). All regression coefficients were significantly greater than one. Data for *Cancer magister* are from Wickham (1986).

Host	Nemertean	r	a	b	n
<i>Cancer anthonyi</i>	<i>C. epialti</i>	0.908	-47.34	2.128	15
<i>Hemigrapsus oregonensis</i>	<i>C. epialti</i>	0.988	12.89	1.666	7
<i>Cancer magister</i>	<i>C. errans</i>	0.979	53.48	1.533	8
<i>Paralithodes camtschaticus</i>	<i>C. regicides</i>	0.982	67.03	1.887	10
<i>Portunus pelagicus</i>	<i>C. mitsukurii</i> ^b	0.700	40.20	4.486	12
<i>Portunus pelagicus</i>	<i>C. mitsukurii</i> ^o	0.947	15.59	2.637	8
<i>Portunus pelagicus</i>	<i>C. mitsukurii</i> ⁿ	0.749	9.21	6.081	12

^b Worms from non-ovigerous and ovigerous hosts.

^o Worms from ovigerous hosts only.

ⁿ Worms from non-ovigerous hosts only.

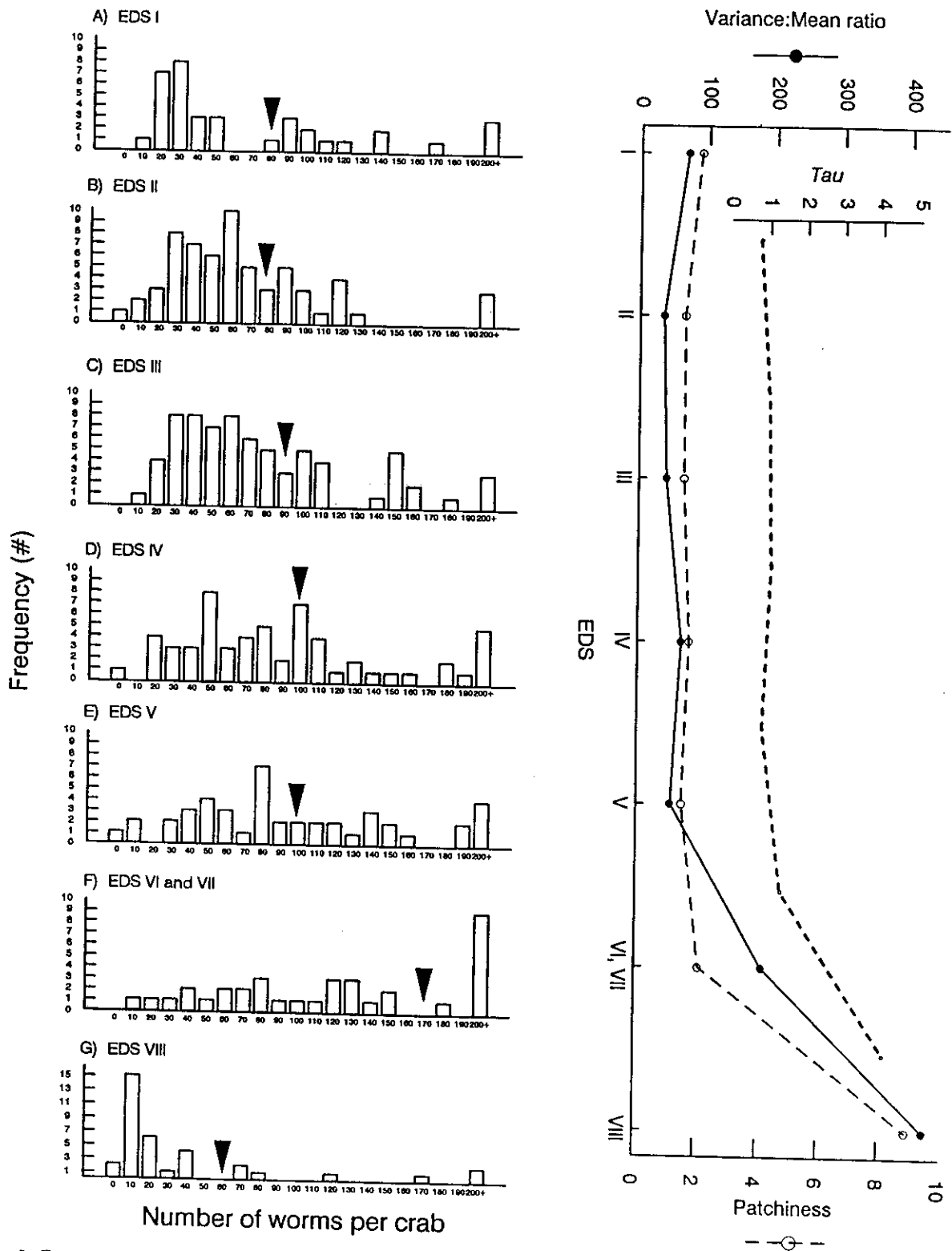


Fig. 5. Frequency distributions, mean abundance (arrow), variance:mean ratio, patchiness, and τ for *Carcinonemertes epialti* on *Cancer anthonyi* in relation to crab embryogenesis. Developmental stages of the crab eggs (EDS) are detailed in Shields *et al.* (1990).

the variance:mean ratio) was significantly different from the Poisson distribution for the dispersion of worms at every developmental stage of embryogenesis ($\chi^2 > 1591$, $P > 0.05$, d.f. = 8-61). In every case, the distributions of the worms were highly overdispersed.

The index of mortality/recruitment (τ) for *Carcinonemertes epialti* on *Cancer anthonyi* changed little during the early and middle periods of host embryogenesis (Fig. 5). Worm recruitment during this time was most likely independent of worm intensity. Later, near host eclosion, mortality operated in what may have been a many-or-few type of response (e.g., either most of the worms died on a host or relatively few died).

Discussion

Several models of infection dynamics may give rise to the aggregated dispersion patterns of parasites on their hosts (e.g., Bliss & Fisher, 1953; Crofton, 1971; Pennycuik, 1971). These are: (1) A heterogeneous host or parasite population

(e.g., genetic variability); (2) constant birth-immigration-death rates of parasites through time; (3) infection by random clumps of individuals *versus* single individuals; (4) true contagion, wherein the presence of a parasite increases or decreases the probability of the host acquiring more parasites; and (5) superimposed or heterogeneous exposures of a parasite, in which the probability of infection is random (heterogeneous Poisson transmission) (see Elliott, 1977). Few tests have been devised to evaluate the mechanisms of aggregation, but the relationships between mean abundance, mean crowding, and patchiness may provide some insight (Iwao & Kuno, 1972; Kitron, 1980).

Four common patterns in the aggregation of the worms emerged and these were related to the timing and synchrony of reproduction of the host species (Table 2). (1) For worms on *Cancer anthonyi* and non-ovigerous *Portunus pelagicus*, aggregation increased at the nadir of the reproductive season of the host. For example, the patchiness of *C. epialti* on *Cancer anthonyi* increased with worm abundance only during the

Table 2. General patterns in the infestation and dispersion dynamics of *Carcinonemertes* spp., and related patterns in the reproductive ecology of their hosts.

Symbiont	<i>C. epialti</i>	<i>C. epialti</i>	<i>C. regicides</i>	<i>C. mitsukurii</i>
Prevalence	high	intermediate	high	intermediate
Intensity	low	low	high	intermediate
# seasonal peaks	2	1	1	1
Season of peak	summer, winter	fall	summer-fall	summer
Peak in $(\bar{x})/\bar{x}$	summer	winter	spring-summer	summer, winter
Peak in s^2/\bar{x}	summer	fall	early summer	summer
Host	<i>Cancer anthonyi</i>	<i>H. oregonensis</i>	<i>P. camtschaticus</i>	<i>P. pelagicus</i>
Broods/year	multiple	multiple	single	multiple
Seasonal peak in reproduction	winter	winter	summer-fall	late winter, summer
Seasonal nadir in reproduction	summer	spring	spring	fall
Duration of embryogenesis	intermediate	intermediate	long	short
Aggregation pattern	1, 4	1, 3	1, 2, 4	1, 2, 3

Key to aggregation pattern - worm dispersion changes in relation to:

- 1 - Nadir in host reproduction.
- 2 - Onset of host reproduction.
- 3 - Physical/environmental change.
- 4 - Embryogenic cycle of host.

late summer. The worm population reached its maximum abundance and was most highly aggregated in association with the reproductive nadir of the crab population (Shields *et al.*, 1990). Worm aggregation (and abundance) is relatively lower in the winter than in the summer because more hosts are available for completion of the life cycle of the worm and because heavy infestations (outliers) have a greater impact on smaller populations (summer months).

(2) For worms on ovigerous *P. pelagicus* and *Paralithodes camtschaticus*, aggregation (as measured by patchiness) increased at the onset of the reproductive season of the host. For example, the abundance and aggregation of *Carcinonemertes regicides* on the red king crab, *Paralithodes camtschaticus*, followed a distinctive pattern that may be related to both season and crab embryogenesis. Female red king crabs oviposit in March–May, and embryos hatch in February–March (Marukawa, 1934; Kuris *et al.*, 1991). Reproduction is synchronized in the crab population and this synchronization reduces the heterogeneity of the population to transmission by the worms. The degree of aggregation changed most notably with host oviposition and eclosion, *i.e.*, events which respectively increase opportunities for worm transmission and mortality (see #4 below). In general, as intensity increased, the degree of aggregation of *C. regicides* on *P. camtschaticus* decreased. This phenomenon was not observed in the *Cancer anthonyi*-*C. epialti* relationship, perhaps as a result of the seasonal fluctuations in the proportion of ovigerous hosts in the population.

(3) For worms on *P. pelagicus* and *H. oregonensis*, aggregation may have changed with fluctuations in the physical environment of the estuarine hosts. Changes in salinity are known to limit the abundance of *C. errans* on estuarine *Cancer magister* (McCabe *et al.*, 1987). For *C. mitsukurii*, abundance decreased while aggregation increased with decreased salinity during the rainy season (February–June; Shields & Wood, 1993). In addition, the aggregation pattern shifted in July and August (late winter) prior to and during the onset of crab reproduction. This was reflected in the

differences between aggregation patterns of worms from ovigerous and non-ovigerous hosts. For *C. epialti* on *H. oregonensis*, worm dispersion was less aggregated at low densities (spring), than that at high densities (fall). The spring nadir in worm abundance and aggregation coincided with a sharp decline in the salinity of Bodega Bay (the El Niño storms of Spring 1983; Shields, pers. obs.) and with the nadir in crab reproduction (Kuris, 1978). Seasonality and the pattern of host reproduction could not be separated in the *C. epialti* – *H. oregonensis* association.

Changes in the dispersion patterns and related changes in parasite densities show the dynamic nature of the underlying factors that shape animal distributions. At low densities, many parasitic insects are distributed randomly among their host plants; while at higher densities, their underlying distribution is over-dispersed (Finney, 1941; Harcourt, 1961; Forsythe & Gyrisco, 1963). Further increases in density may shift the distribution back to an under-dispersed form (Waters, 1959; Dybas & Davis, 1962). Similarly, at low densities, worms on *H. oregonensis* were less aggregated than those at high densities, and occasionally were randomly distributed on the host population. Worms on *P. camtschaticus* were highly aggregated early in the reproductive season, but the degree of aggregation declined with increasing worm abundance and prevalence.

(4) Changes in the abundance and aggregation pattern of *Carcinonemertes epialti* over the developmental period of *Cancer anthonyi* documented two important forces acting on the dispersion of the worms. Firstly, the dramatic changes in the relationship between mean crowding and mean abundance with host embryogenesis provided evidence for heterogeneous waves of infestation (immigration, Fig. 6). Immigration into the egg mass had, however, two quite different effects on aggregation. After host eclosion, planktonic larvae colonized their new hosts. The effect of colonization was to reduce the degree of aggregation. Later in the course of embryogenesis, immigration caused an increase in the degree of aggregation. The sharp increase in abundance, mean crowding, and patchiness in the late stages

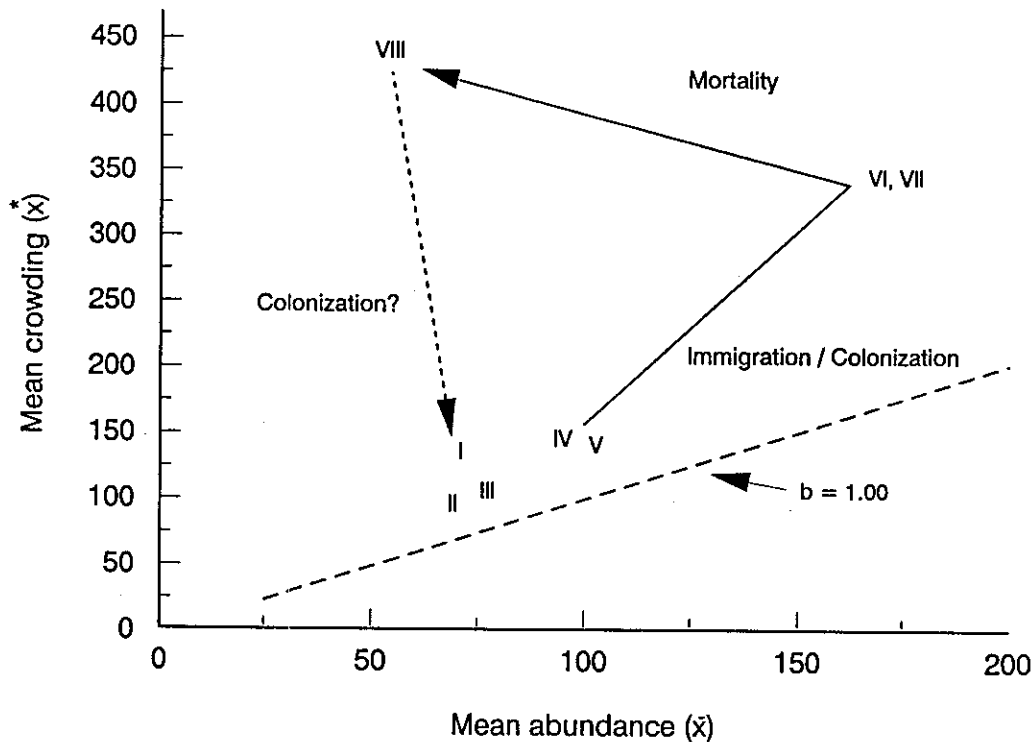


Fig. 6. Changes in the aggregation pattern of *Carcinonemertes epialti* on *Cancer anthonyi* in relation to embryogenesis of the host. Developmental stages of the crab eggs are detailed in Shields *et al.* (1990). The effect of colonization/immigration and worm mortality on aggregation are evident.

of host embryogenesis suggests that the immigration rates are not constant among hosts.

Secondly, death rates varied with the embryogenesis of the host. Species of *Carcinonemertes* either die or emigrate out of the egg masses of their hosts immediately prior to or during host eclosion (for review see Wickham & Kuris, 1985; Shields & Kuris, 1990; Kuris, 1993). Worm mortality/emigration increased just prior to host eclosion and acted to increase the degree of aggregation (Fig. 6). Worm immigration, emigration and mortality strongly shaped the observed aggregation patterns.

The life histories of the nemertean worms revolve closely around the duration of the embryogenic cycle of their respective hosts (Shields & Kuris, 1990). In an analogous manner, the infestation and dispersion patterns of each worm species was tightly linked to the reproductive ecology of their

hosts, even though details of the life histories of the host species and the worms vary considerably.

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