Fecampia erythrocephala rediscovered: prevalence and distribution of a parasitoid of the European shore crab, Carcinus maenas

Armand M. Kuris*‡, Mark E. Torchin* and Kevin D. Lafferty†

*Department of Ecology, Evolution and Marine Biology and Marine Science Institute, University of California, Santa Barbara, CA 93106, USA. †US Geological Survey, Western Ecological Research Center c/o Marine Science Institute, University of California, Santa Barbara, CA 93106, USA. ‡Corresponding author, e-mail: kuris@lifesci.ucsb.edu

An ecological assessment of *Fecampia erythrocephala*, reporting its habitat distribution, abundance, host specificity, size-specific prevalence, frequency distribution among hosts, effect on host growth, and its site specificity within these hosts is presented. At the Isle of Man and near Plymouth, *Fecampia erythrocephala* cocoons were generally abundant on the undersides of rocks in the *Ascophyllum* and *Fucus serratus* zones. Infected crabs were also most common in these habitats. Both *Carcinus maenas* and *Cancer pagurus* were parasitized at similar prevalences, although the former species was relatively much more common in the habitats where the worm cocoons were abundant. *Fecampia erythrocephala* did not infect crabs larger than 11 mm carapace width, and prevalence decreased significantly with crab size. Prevalences reached 11% in areas where cocoons were abundant. Together with the large size of these worms relative to the size of the host crabs and the observations on worm emergence, these life history features indicate that *F. erythrocephala* is a parasitoid of young shore crabs. *Fecampia erythrocephala* cocoon abundance is often high in localized areas and size-prevalence information suggests that worms mature rapidly in these crabs. This suggests that *F. erythrocephala* is an important contributor to crab mortality and to the ecology of shore crabs at these sites.

INTRODUCTION

In 1950, Alan Southward wrote that the cocoons of the parasitic worm, *Fecampia erythrocephala*, were, 'probably familiar by appearance, if not by name, to all shore collectors' (Southward, 1950). And with his brief note (and a morphological study) and new host and geographic records (Brun, 1967; Bellon-Humbert, 1983), information about this unique, interesting, common, and perhaps ecologically important worm effectively ceased.

Our interest in this worm was kindled by an extensive parasitological examination of shore crabs in Europe (N > 2000 crabs, all > 20 mm, Torchin et al., 2002) to detect and evaluate potential natural enemies of the shore crab for possible use as biological control agents where this crab is an introduced pest (Lafferty & Kuris, 1996). *Fecampia erythrocephala* was the one reported parasite of shore crabs we did not find in our surveys. A review of the early literature indicated that the reason for its absence in our samples was its occurrence in very small crabs (we had only sampled large crabs because, over time, larger crabs accumulate parasites). To rectify this oversight, we undertook a search for *F. erythrocephala* where it was reported to be common according to the faunal lists of the Isle of Man (Bruce et al., 1963) and Plymouth, England (Marine Biological Association, 1957). Here, we synthesize the past literature (most from the original French) and report new information on the habitat, abundance, host specificity, site specificity, size-specific prevalences, frequency distribution among hosts and effects on host growth of this fascinating

parasite. Questions are also raised concerning its ecological importance and to provide some guidance for future research.

Giard (1886) discovered *F. erythocephala* and recognized the major features of its biology. Additional details were provided by Caullery & Mesnil (1903), Southward (1950), Brun (1967) and Bellon-Humbert (1983). Worms commonly
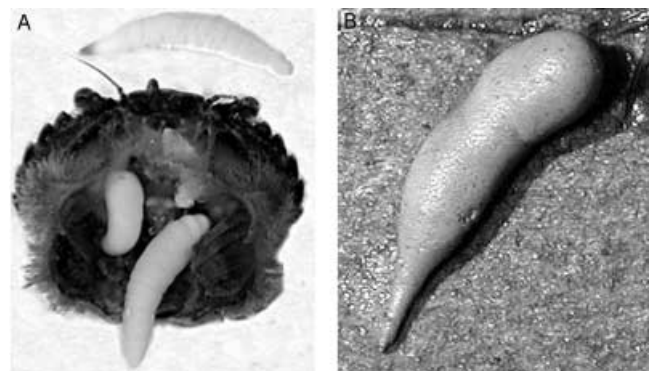

Figure 1. (A) *Fecampia erythrocephala* infecting a small shore crab, *Carcinus maenas*, from Port St Mary, Isle of Man. Worms are crawling out of the haemocoel of a 10 mm wide crab dissected in our study. (B) *Fecampia erythrocephala* cocoon attached to the underside of a rock. Cocoon length is approximately 8 mm in length. Note that eggs were expelled from aperture of cocoon as a result of pressure applied to side of cocoon.

develop in the shore crab *Carcinus maenas* and the rock crab, *Cancer pagurus*. Infected crabs are very small (4–11 mm carapace width, Caullery & Mesnil, 1903). The worm is quite large compared with the host; mature worms of 8–12 mm length can emerge from these small crabs (Figure 1A). Hosts with fully developed worms have very reduced digestive glands, and the host dies after emergence of the parasite (Southward, 1950). The free-living worms then secrete white, parchment-like cocoons, 6–10 mm long (Figure 1B), that Giard (1886) described as being shaped like a *larme batavique* ('Rupert's drop', a simile that is obscure to us). From our perspective, the shape of the cocoon is similar to an amphora with a sharply tapered spout. Inside its cocoon, the worm releases eggs in a gelatinous mass and eventually dies (Caullery & Mesnil, 1903; Bellon-Humbert, 1983). The eggs develop over several months before being released as ciliated larvae through the spout of the cocoon. Presumably, the larvae settle on and penetrate young crabs, perhaps most often in early autumn (Giard, 1886).

Morphologically, the worms are distinctive. They lack a gut, have a hermaphroditic reproductive system (morphologically unlike other Platyhelminthes), and a very substantial glandular nidamental organ that secretes the cocoon. They are rose-salmon in colour with a striking crimson head. Only one worm can be found in a cocoon, suggesting that they are self fertilizing (Caullery & Mesnil, 1903). Although originally considered turbellarians highly modified for a parasitic life style (Giard, 1886; Caullery & Mesnil, 1903), they are now recognized as a separate class, Fecampiida, along with the related dioecious genus *Kronborgia* (Rohde et al., 1994).

The worms (or at least their cocoons) have been found throughout the Irish Sea and along both coasts of the English Channel (Giard, 1886; Caullery & Mesnil, 1903; Southern, 1936; Southward, 1950; Williams, 1954). Brun (1967) reported worms, differing in colour from these Atlantic forms, in *Carcinus estuarii* in the Mediterranean Sea.

Morphologically similar worms assigned to *F. erythocephala* have also been reported from hermit crabs (*Eupagurus bernhardus*, *Anapagurus hyndmani*) and shrimp (*Paleamon serratus* (Giard, 1886; Mouchet, 1931; Bellon-Humbert, 1983) without evaluation of the conspecific nature of the worms from these different hosts (other than Brun's observations on differences in colour and size). A related species, *F. xanthocephala*, has been described from isopods and amphipods (Caullery & Mesnil, 1903; Toulmond & Truchot, 1964; Brun, 1967). Reports of this parasite from hermit crabs and prawns suggest a different pathology from that seen in crabs. The worm infects larger, sexually mature hosts, causes parasitic castration; and sometimes these hosts may, at least briefly, survive emergence of the worm from the gill chamber (Mouchet, 1931; Bellon-Humbert, 1983). In prawns, worms exit through the gill chamber (Bellon-Humbert, 1983).

MATERIALS AND METHODS

Five rocky shore sites were surveyed in the British Isles from 2–7 May 2001. These were Castletown (54°4.53N 4°38.54W), Port St Mary (54°4.48N 4°44.25W) and Pooyll Vaaish (54°4.54N 4°41.11W) located on the southeast corner of the Isle of Man in the Irish Sea. We also

surveyed Rum Bay in Plymouth Sound, England (50°21.31N 4°7.52W) and Blackstone Rocks at Wembury, England (coordinates not recorded). All these sites were protected rocky coast with a mix of bedrock, boulder and sandy habitats. Algae on larger rocks typically reached 100% cover below the *Fucus vesiculosus* zone.

Cocoon distribution was quantified in the intertidal zone at Pooyll Vaaish and, to a lesser extent, at Port St Mary. The shore was divided into zones according to the dominant species of alga (as per Southward, 1965). These were, from high to low: *Fucus vesiculosus*, *Ascophyllum nodosum*, *Fucus serratus* and laminarians (*Laminaria digitata* and other laminarians). Due to the habitat specificity of cocoons (underside of rocks) and the uneven distribution and accessibility of such habitat, we did not employ a random sampling design. Instead, starting in the laminarian zone and working up, 0.25 m² quadrats were placed over potentially suitable and easily sampled habitat (10–25 cm long rocks that could be turned over by hand). For each quadrat, we identified the algal zone, turned over rocks and carefully inspected them. The number of cocoons under each rock was counted, their colour noted, and whether the cocoons expressed eggs when touched was noted. To determine the actual amount of habitat searched, we used the quadrat to estimate, by eye, the surface area of the undersides of the rocks that we inspected for cocoons. At Pooyll Vaaish, we removed the cocoons from the rock, measured them in the laboratory and calculated a size–frequency distribution. At Castletown, Rum Bay and Blackstone Rocks, cocoons and crabs were sampled (see below) from the *Fucus serratus* zone.

Small (3–20 mm) *C. maenas*, as well as other crab species we encountered (*Cancer pagurus*, *Pilumnus hirtellus*, *Necora puber*, *Porcellana platycheles*), were hand collected by turning rocks in pools and on the exposed shore. Sampling in the *Fucus serratus* zone was increased enabling a comparison among sites and species (this zone was common at all sites, had a relatively high density of cocoons and was an area of overlap between *Carcinus maenas* and *Cancer pagurus*). Small crabs were difficult to sample quantitatively but, sufficient sample sizes of these crabs were obtained for parasitological examination.

A total of 626 crabs was dissected under a stereo microscope. The carapace of the crab was removed and the haemocoel and included organs examined for parasites. For each crab, sex, size and moult stage (dividing crabs into active (postmoult, late premoult) and inactive (intermoult and early-premoult, C_4–D_1) were recorded using the presence of the membranous layer (onset of C_4) and the presence of the new cuticle of the general body surface (onset of D_2) (for details, see Drach, 1939; Poinar & Kuris, 1975). The number of *Fecampia erythrocephala* was counted and the presence of trematode metacercariae in the digestive gland was also recorded. Crabs were examined for cuticular scars indicating the emergence of worms. Statistics are reported for *Carcinus maenas* unless otherwise stated.

RESULTS

At all locations, small shore crabs were found under rocks, especially in the *Ascophyllum* and *Fucus serratus* zones. *Fecampia erythrocephala* cocoons were present under rocks in various sizes and stages of development ranging from recently secreted to vacant. Cocoon colour ranged from
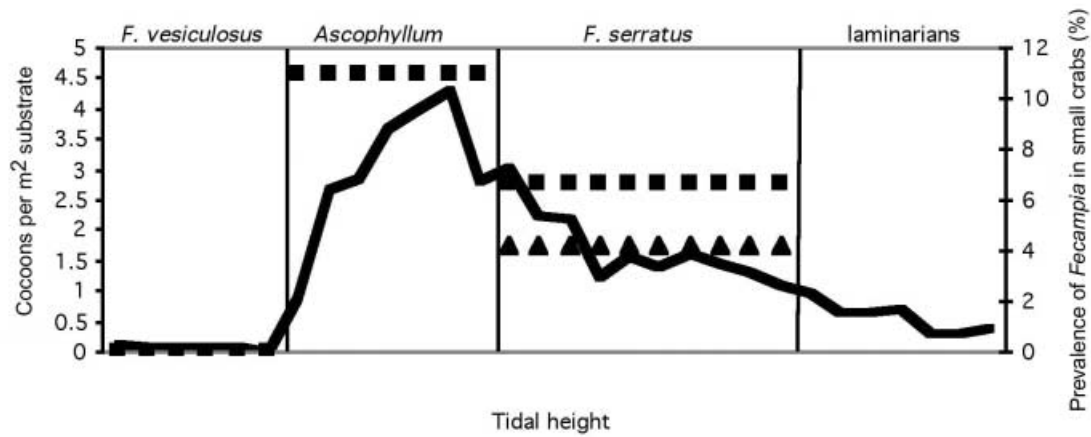
Figure 2. Cocoons per m² substrate and prevalence of *Fecampia erythrocephala* in small crabs. ? indicates cocoon density, ?? is *F. erythrocephala* prevalence in *Carcinus maenas* and ??? is *F. erythrocephala* prevalence in *Cancer pagurus*.
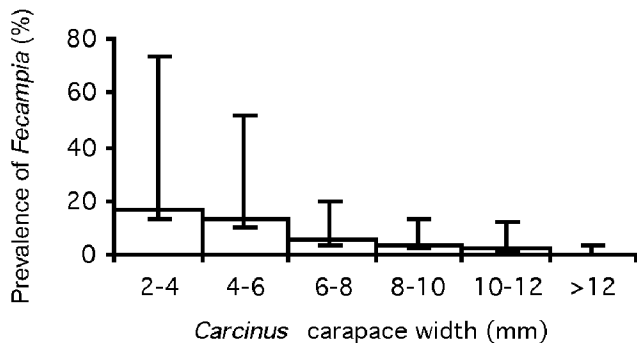

Figure 3. Prevalence (% infected) of *Fecampia erythrocephala* in *Carcinus maenas*. Data are given for 2 mm size-classes. Error bars are 95% confidence intervals (calculated according to Rohlf & Sokal, 1981).
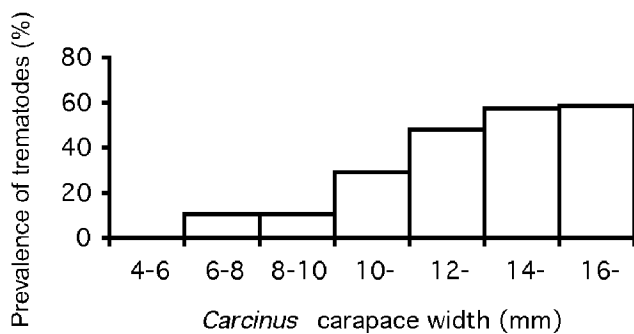

Figure 4. Prevalence of trematodes in *Carcinus maenas*. Data are given for 2 mm size-classes.

white (55%) to beige (45%). The white cocoons contained a higher proportion of live worms. A third of the cocoons were filled with orange eggs that were extruded when pressure was applied to the firm but pliable parchment-like cocoon with a finger-nail. The remaining cocoons were empty and several of these were flattened as if their contents had been expressed.

Cocoons tended to be on rocks greater than 10 cm in length whose undersides supported spirorbid polychaetes, sponges and encrusting coralline algae. Cocoons and other fouling organisms were not found on rocks with only green

algae on the upper surface, nor under rocks set firmly in soft sediment.

Cocoon density varied among algal zones, being rare up in the *Fucus vesiculosus* zone, most abundant in the *Ascophyllum* zone, common in the *Fucus serratus* zone and nearly absent down in the laminarian zone (see Figure 2). Cocoons occurred on 17% of the approximately 500 rocks quantitatively examined. Cocoon density also varied among the sample sites. Although most cocoons were isolated, as many as ten cocoons were present per rock and cocoons were often closely clustered with their neighbours. Cocoons were significantly more aggregated on rocks than expected based on a comparison with a Poisson distribution (Chi-square, $P < 0.001$). Mean cocoon length was 6 mm (SE=0.17) and ranged from 3–10 mm.

As with the distribution of cocoons, the distribution of crabs varied with the algal zone, although, this was not explicitly quantified. In particular, shore crabs were relatively more abundant in the upper zones compared with the other crab species.

Fecampia erythrocephala was never recovered from crabs larger than 11 mm carapace width. The prevalence of *F. erythrocephala* in parasitized crabs 3–11 mm varied among algal zones. Infected crabs of any size or species were not found in the *Fucus vesiculosus* zone or laminarian zone. *Fecampia erythrocephala* was present in the *Ascophyllum* zone (e.g. 11%, 2/18 of small shore crabs at Pooyll Vaish) and *Fucus serratus* zone (e.g. 7%, 4/60 of small shore crabs at Pooyll Vaish), a difference that was not significant (2×2 Chi-square=0.39, $P=0.54$). Prevalence did not vary statistically among sites (crabs from Castletown were not dissected as cocoon density was very low and comparison of prevalence across site had little power given the small number of infected crabs found). Prevalence decreased significantly with shore crab size (Figure 3, R-square= -0.90, $P < 0.01$). In marked contrast, the prevalence of trematode metacercariae in shore crabs, sharply increased with crab size (Figure 4, R-square=0.95, $P < 0.001$). The intensity of *F. erythrocephala* in shore crabs ranged from one to four worms per crab. Although most worms were in single infections, the worms were significantly aggregated within the host population (Chi-square, $P < 0.001$). The prevalence of *F. erythrocephala* in small *Cancer pagurus*

(N=41) in the *Fucus serratus* zone was 4.2% (not significantly different from the 6.7% in shore crabs (N=511)). *Fecampia erythrocephala* was not found in small *Necora puber* (N=10), *Porcellana platycheles* (N=22) nor *Pilumnus hirtellus* (N=35). Crabs in late premoult/early postmoult stages (N=298) were as likely to be parasitized by *F. erythrocephala* as were crabs in intermoult/early premoult moult cycle stages (N=311), suggesting that there was no association between growth rate and infection.

All but two worms were at least 8 mm long and the largest measured 12 mm (live length). Most worms were found folded over in the anterolateral regions of the carapace or bent in a U-shape ventral to the gut in the posterior part of the thoracic haemocoel. None were recovered from the abdomen. In the smallest crabs, a single worm could extend from the anterolateral angle of the carapace to the posterior part of the thorax. The two smallest worms (3.5 and 4.5 mm) were white with a crimson head and were in a multiple infection with two large, rose-coloured, crimson-headed worms. The two large worms were both in the anterolateral part of the carapace, while the two small worms were in the posterior of the thoracic region and one was partially embedded in the musculature at the base of the last periopod. In a dying crab with three large worms, one worm was seen emerging, head first, from the ventral region between the first and second thoracic sternites. This worm and another large specimen were in the anterior carapace while a third, smaller worm was alongside the intestine in the thoracic haemocoel. Although the emerging worm seemed to kill the host crab, we did not see the start of the process and the worm simply may have been exiting from a wound caused by handling.

DISCUSSION

The existence of *Fecampia erythrocephala*, locally common, and brightly coloured was almost lost to science; probably because very young, small crabs are almost never examined by parasitologists. Ironically, the abundance of cocoons in some parts of the intertidal zone makes their local presence easier to determine than almost any crab parasite. The key to their detection lies in the ability of field ecologists to recognize the cocoons as a free-living life-history stage of a crab parasite (Figure 1B).

The presence of recently secreted white cocoons together with beige, weathered living cocoons on the rocks indicates that the *F. erythrocephala* life cycle is not tightly synchronized in time. This supports the observations of Caullery & Mesnil (1903) that brooded embryos had not been synchronously oviposited because a wide range of developmental stages were present within a cocoon. The frequent occurrence of empty cocoons suggests that the adult worm often dies long before its secreted tough parchment cocoon erodes away.

In the crab, the worm's location, and the displacement (or replacement by the parasites) of much of the digestive gland tissue is remarkably similar to that of juvenile entoniscid isopods in their hosts (Veillet, 1945; Kuris et al., 1980). Also like the entoniscids (and other parasitic castrators and parasitoids), the relative size of *F. erythrocephala* is very large (>10% weight of the host), falling well above the maximum size of a typical parasite (∼1% weight of the host if not trophically transmitted, Kuris & Lafferty, 2000). Development of larval *F. erythrocephala* in *Carcinus maenas*

appears rapid. When the parasite is mature, its surface colour changes from white to rose (Giard, 1886; Caullery & Mesnil, 1903; Bellon-Humbert, 1983). All but two parasites recovered were large (8–12 mm) and rose-coloured, even those from crabs only 3 mm carapace width (a few weeks old, Brockhuysen, 1936), suggesting that these parasites may mature in just a few weeks.

Declining prevalence with host size is consistent with Southward (1950) and the present study and suggests that host death follows emergence of the parasites. Since it is in the haemocoel, dead parasites cannot be evacuated and, if present, would be readily detected by a melanized mass (Kuris et al., 1980). Hence, parasites in the haemocoel (even dead ones) tend to accumulate with host size, as was readily apparent for the microphallid metacercariae in the crabs. No crabs were observed with cuticular scars indicating survival after worm emergence.

For these reasons, *Fecampia erythrocephala* appears to be a parasitoid of brachyuran crabs. A parasitoid is a consumer that attacks only one host and always kills that host (Doutt, 1959; Kuris, 1974; Kuris & Lafferty, 2000). *Fecampia erythrocephala* shares other important life-history features with terrestrial parasitoid insects. Both tend to infect young hosts (often first instars of insects Clausen, 1972). Parasitoids can have important effects on host population density, even at low prevalence (Clarke et al., 1967, p. 141), because they remove hosts from the population before other mortality factors can act (Begon et al., 1999). Age-structured models indicate that a parasitoid that attacks early life-history stages and to which later stages are invulnerable (such as *F. erythrocephala*) can be a very effective biological control agent (Murdoch et al., 1987; Briggs et al., 1999).

Although the overall prevalence of *F. erythrocephala* was rather low (4–7%), it may still be an important source of mortality for shore crabs. Given a 6.7% prevalence in shore crabs from 2–10 mm carapace width, a prevalence of at least 15% in 2–4 mm crabs can be extrapolated from the size–prevalence regression. Hence, *F. erythrocephala* appears to be responsible for killing a greater proportion of young shore crabs than its mere overall prevalence would suggest.

Fecampia erythrocephala did not appear to reduce the moulting frequency of small crabs since the same proportion of infected crabs were in the active portion of the moult cycle (A–C_3, D_{2-4}), as were infected crabs. Studies of growth of small shore crabs indicate that it takes 20 to 50 days for a crab to grow from 2.5 to 4 mm and 1 to 5 months to reach 10 mm carapace width (Klein Breteler, 1975a,b). Hence, mature worms in a 4 mm carapace-width crab appear to have become fully developed 2 to 7 weeks (assuming the first infectable postlarval instar crab is 2.5 mm, the smallest crabs in our sample). Assuming a comparable rate of worm development in the larger crabs, this strongly suggests that these crabs were exposed repeatedly to *F. erythrocephala* over the available host size range (up to 11 mm). Thus, the overall mortality of crabs before they reach 11 mm was considerably greater than the mean prevalence or even the higher prevalence seen in the smallest (2–4 mm) crabs.

The effect of *F. erythrocephala* appears to be restricted to a subset of suitable *C. maenas* habitats. *Carcinus maenas* is also found in estuarine habitats and along rocky shores where

the rocks are well-buried in fine sediment. Two estuarine sites (Plym River Estuary and Tamar River Estuary) with high abundances of small (<11 mm) shore crabs were surveyed and cocoons were not found. The general presence of cocoons with other fouling organisms, and their absence on rocks covered with green algae, suggested that the rocks with cocoons had not been recently flipped over. Successful establishment of cocoons may require an infrequently disturbed substrate and perhaps higher salinity for settlement. The lack of cocoons under rocks set firmly in soft sediment indicated that some space was necessary for cocoons to attach. For this reason, it is unlikely that *F. erythrocephala* can have an impact on the crabs in estuarine habitats. While *F. erythrocephala* has the potential to locally reduce the abundance of *C. maenas* in semi-protected rocky intertidal zone habitats, its ability to influence the abundance of *C. maenas* at larger scales will depend on the relative importance of these different habitats as sources of larval supply.

The aggregated distribution of cocoons among algal zones and among rocks within an intertidal zone should make some rocks riskier places for crabs to shelter than others. This may explain the aggregated distribution of worms among crabs. It also suggests that when worms emerged from crabs, they rapidly made cocoons, perhaps under the same rock where their host found shelter. Preferred cocoon sites may account for host specificity of *F. erythrocephala*. The shore crab is by far the most common crab in the habitat where cocoons are most abundant.

The aggregated distribution of *F. erythrocephala* among both *C. maenas* and *Cancer pagurus* is atypical for parasitoids which are usually relatively uniformly dispersed among hosts. However, aggregation of parasitoids should occur if foci of transmission are highly localized (as seems likely based on the comparison of distributions of cocoons and infected crabs), or if the searching larval worms do not avoid previously infected hosts, or worms cannot competitively exclude or suppress growth of other worms (a common characteristic of parasitoid and parasitic castrator life histories—Salt, 1961; Kuris, 1974).

The host specificity of *F. erythrocephala* is biologically interesting and important for its potential as a biological control agent where *Carcinus maenas* is an introduced pest. This needs to be examined experimentally and the genetics of isolates from the several reported hosts need to be compared. *Fecampia erythrocephala* has a castrating effect (infecting adults, not juveniles) on hermit crabs and caridean shrimp (Mouchet, 1931; Bellon-Humbert, 1983). Are cryptic species involved, or does *F. erythrocephala* have a remarkably plastic host utilization physiology?

Fecampia erythrocephala is able to infect two of the crab species dissected. No gross differences in the morphology of the worms from *Cancer pagurus* vs *Carcinus maenas* was observed, though further morphological investigations and host specificity experiments are needed to determine the host specificity of these worms. Assuming that the worms in *Cancer pagurus* and *Carcinus maenas* form a single population, it appears that *F. erythrocephala* has less of an impact on the *Cancer pagurus* population than on the *Carcinus maenas* population. The distribution of *F. erythrocephala* within the intertidal zone overlaps with the range and abundance of *C. maenas* more than it does with *Cancer pagurus* which tends to be lower in the intertidal zone. The prevalence of

F. erythrocephala is similar in *C. pagurus* and shore crabs within the *Fucus serratus* zone, suggesting that their intrinsic susceptibility to these parasites is similar. However, the proportion of the crab population that lives in this zone is lower for *C. pagurus* than it is for *Carcinus maenas*, resulting in a lower risk of exposure for *Cancer pagurus* even if its individual susceptibility is similar to that of *Carcinus maenas*. The abundance of juvenile *Cancer pagurus* in lower intertidal and subtidal zones suggests that these crabs have a considerable habitat refuge from *F. erythrocephala*.

It seems probable that Fecampias may be present in other regions and in other crabs. Searches for cocoons and parasitological investigations of young crustaceans might reveal the more extensive presence of these interesting mortality agents. Several features of the life history and ecology of *F. erythrocephala* suggest that this is an ecologically important and biologically fascinating species warranting further study. Because it is locally common, it may be readily cultured (suggested by the ready secretion of cocoons in glass dishes in the laboratory, (Caullery & Mesnil, 1903; Southward, 1950; Bellon-Humbert, 1983)), studies of its biology should be tractable and fruitful.

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