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Finding refuge: The estuarine distribution of the nemertean egg predator *Carcinonemertes* errans on the Dungeness crab, *Cancer magister*

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ABSTRACT

Parasites can significantly impact ecosystems by altering the distributions and population sizes of their host organisms. Some hosts are thought to find refuge from parasitism by entering habitats where their parasites cannot survive. The nemertean worm *Carcinonemertes errans* is an egg predator that infects the Dungeness crab, *Cancer magister*, throughout the host's range. To determine if *C. magister* experiences a refuge from *C. errans* within estuarine environments, we examined the distribution of *C. errans* on Dungeness crabs within Oregon's Coos Bay Estuary. Year-round sampling over a three-year period also allowed us to test for temporal variation in the parasite's distribution. We found that parasite prevalence, mean intensity, and parasite density of *C. errans* infecting *C. magister* varied along a clear estuarine gradient, with crabs nearest the ocean carrying the heaviest parasite loads. Larger crabs were more heavily infected with worms, and seasonal infection patterns were observed at some sites within the bay. Crabs sampled from coastal waters near the estuary carried significantly more worms than did crabs from the bay, suggesting that the estuary is acting as a spatiotemporal parasite refuge for this important fishery species.

1. Introduction

Transitions in temperature and salinity along an estuarine gradient are known to affect the ecology and distribution of organisms within the estuary (Kennish, 1986), including some parasites (Barber et al., 1997; Kvach, 2004; Tolley et al., 2006). These parasites can in turn significantly impact the structure of estuarine ecosystems by altering the distributions and population sizes of host organisms (Haskin and Ford, 1982; Kuris et al., 2008). The characteristics of host-parasite populations may also vary with the seasonal changes in temperature and salinity that accompany periods of higher or lower freshwater runoff in estuarine environments (Crosby and Roberts, 1990). Lower instances of parasite infections in some hosts inhabiting estuaries have led several authors to suggest that these host populations are experiencing "salinity refuges" from their parasites (Reisser and Forward, 1991; Tolley et al., 2006).

The best studied example of a functioning salinity refuge is the relationship between the Atlantic oyster *Crassostrea virginica* and its parasites, the sporozoan *Haplosporidium nelsoni* and the apicomplexan protozoan *Perkinsus marinus* (Andrews, 1964; Haskin et al., 1965, 1966; Sprague et al., 1969; Haskin and Ford, 1982; Burreson and Ragone Calvo, 1993; Chu et al., 1996). The data from these studies suggest that *C. virginica* finds refuge from its parasites by living in parts of estuaries where low salinities and high temperatures do not allow its parasites to either infect the oysters or proliferate within them. A second example of a salinity refuge is the relationship between the rhizocephalan barnacle *Loxothylacus panopaei* and the xanthid crab *Panopeus obesus*. The effect of the parasite was reduced upstream during seasonally wet months when salinity gradients were more fully expressed, leading to the conclusion that estuaries may act as spatiotemporal refuges for successful reproduction by potential host crabs (Tolley et al., 2006).

The Dungeness crab, *Cancer magister* Dana 1852, is an important commercial and sport fishery species, occurring along the Pacific coast of North America from Alaska to California (Pauley et al., 1989). Adult Dungeness crabs are known to tolerate salinities ranging from 11 to 35, though juveniles tolerate less saline conditions (Cleaver, 1949; Robinson and Potts, 1979). The majority of Dungeness crabs are found offshore on sandy bottoms, but many

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individuals are known to move into estuaries for part or all of their lives (Armstrong et al., 2003). Could this movement of some crabs into estuaries serve as a refuge from parasitism?

Cancer magister is known to host the nemertean worm *Carcinonemertes errans* Wickham 1978 (Wickham, 1979a). Worms of the genus *Carcinonemertes* (Nemertea: Enopla: Hoplonemertea) are egg predators of decapod crustaceans (Coe, 1902; Humes, 1942; Wickham, 1978; Roe, 1984). The descriptive term "egg predator" has been adopted by some authors instead of "parasite" because the worms feed on many host embryos during their lifetime, mimicking the feeding behavior of a predator more closely than that of a parasite (Kuris, 1997). However, since these worms spend their entire lives on one or a few host individuals and their biology is closely attuned to that of their hosts, they can easily be modeled as parasitic castrators, having an effect on host reproductive output (Kuris and Lafferty, 1992). Although worms require host eggs to mature and complete their life cycle, juvenile worms are able to survive for months on the exoskeletons of their hosts, feeding on nutrients "leaking" from the crabs (Crowe et al., 1982). Worms are also able to transfer to the host's new exoskeleton during molting and from male hosts to females during mating with high efficiency (Wickham et al., 1984), making worms present on juvenile and male crabs just as important in terms of potential negative effect on host reproduction as those found on adult females themselves.

The majority of studies involving the relationship between *Cancer magister* and *Carcinonemertes errans* have been carried out using oceanic populations of adult crabs, where worms can number in the tens of thousands on single host specimens (Wickham, 1979b). The one study that examined the estuarine dynamics of this relationship found that the occurrence of *C. errans* on *C. magister* followed a salinity gradient in the river-dominated Columbia River Estuary (McCabe et al., 1987). Within this estuary, parasite prevalence was 6% compared to 79% in offshore waters. Prevalence at the estuary mouth was intermediate (25%; McCabe et al., 1987). No rigorous studies have tested the salinity tolerance of *C. errans*. Scrocco and Fabianek (1970) found adult specimens of the Atlantic congener *Carcinonemertes carcinophila* to be tolerant to salinities above 10. Below that threshold, however, all worms died within two days. The long-term changes in prevalence or intensity of *C. errans* within or between estuaries has not been studied, although such data would be ideal for understanding these dynamic environments where conditions are highly dependent on both freshwater runoff and tidal influence and vary widely from one estuary to another.

In this study, we conducted a multi-year survey of the distribution of *Carcinonemertes errans* on *Cancer magister* along an estuarine gradient in a Pacific Northwest estuary and assessed the potential of such estuarine habitats to provide salinity refuges for Dungeness crabs.

2. Materials and methods

2.1. Study site

Coos Bay is a drowned river estuary 54 km^2 in area located on the southern coast of Oregon. Input from rivers and streams varies seasonally, from 150 $m^3 s^{-1}$ during the rainy winter to <3 $m^3 s^{-1}$ in the dry summer months (Roegner et al., 2007). The bay can be divided into four distinct salinity regimes: the euhaline regime (>30) which is located near the mouth of the bay, the polyhaline regime (18–30) which stretches from about river mile 5 to river mile 12, the mesohaline regime (5–18) which consists of most of the upper-bay sloughs, and the oligohaline regime (<5) which is riverine (Davidson, 2006). Based on pilot trapping surveys, we chose seven sampling sites that spanned the distribution of adult *Cancer magister* within the estuary and were accessible by shore and boat (Fig. 1). The names and characteristics of each of these sites can be found in Table 1.

2.2. Estuarine distribution of *Carcinonemertes errans*

Dungeness crabs were captured year-round in the Coos Bay Estuary. Sampling occurred monthly between June 2008 and June 2011, and each site was sampled at least once quarterly. All trapping was performed using baited Fukui FT-100 multi-species marine traps (60 cm × 45 cm × 20 cm). The 12 mm mesh size of these traps captured nearly all size classes of crabs. Bait was typically tuna, but squid, herring, and halibut were also used occasionally. To maximize the size range of crabs available for examination, trapping was conducted both intertidally and subtidally. Intertidal traps were set during a low tide, allowed to soak through an entire tidal cycle, and then examined the next day. Subtidal traps were deployed by boat, allowed to soak 2–4 h before and after a slack tide, then collected. Shorter subtidal trapping durations were necessary to avoid substantial drifting (and subsequent loss) of traps left for more than a few hours. Temperature and salinity were measured at each sampling site at the time of trapping using a hand-held YSI meter (YSI Model 30 Salinity, Conductivity, and Temperature System). Crabs taken from offshore waters with the aid of commercial fishermen were also examined, mostly at the time of collection on the fishing vessel. The rest were examined at a fish processing plant, where a subset of crabs was inspected as they were offloaded from fishing vessels.

The carapace width (CW) of each captured crab was measured just anterior to the 10th lateral spine. The sex of the crab was also noted. Infections by *Carcinonemertes errans* were initially determined using two standard parasite metrics: parasite prevalence and parasite intensity (Margolis et al., 1982). To determine parasite prevalence, each crab was carefully examined for the presence of

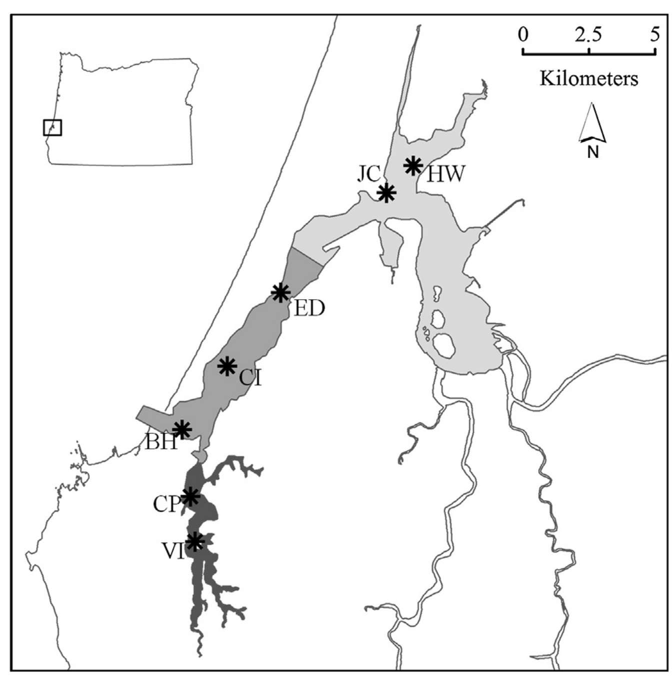

Fig. 1. Sites for trapping survey within the Coos Bay Estuary and the South Slough, Oregon. The three regions of the bay are represented by dark gray (South Slough), gray (Lower Bay), and light gray (Upper Bay). Site abbreviations: BH = OIMB Boathouse, CI = Clam Island, ED = Empire Docks, JC = Jordan Cove, HW = Highway, CP = Collver Point, VI = Valino Island.