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Prevalence of parasitic larval trematodes in *Batillaria attramentaria* throughout Elkhorn Slough

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ABOUT THIS DOCUMENT

P. P. Lin prepared this document as a part of a field methods course at Moss Landing Marine Laboratories, CA.

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ABSTRACT: Parasites are an important, though often under-appreciated, part of any functioning ecosystem. They have the potential to influence host ecology and population dynamics by altering survival, abundance, distribution, reproductive capacity, and behavior. *Batillaria attramentaria* (= *Batillaria cumingi*), an introduced species in North America, reaches its highest recorded densities in Elkhorn Slough, CA. *Cercaria batillariae* (Heterophyidae, Digenea) is a parasitic trematode whose larval form uses *B. attramentaria* as its first intermediate host and causes parasitic castration in the snail host by consuming gonadal tissue. It is believed that a possible mechanism for the success of invasive species is through the release from natural enemies, including parasites. This study evaluated differing prevalence of the trematode in *Batillaria* populations at various sites throughout Elkhorn Slough, in an attempt to clarify the role of the parasite in mediating the success of the exotic snail. Prevalence was shown to increase exponentially with host shell size. Results indicate that snail size at 95% infection rate varied by site, and ranged between 26.8 and 34.5 mm. The proposed reason behind this finding is that the definitive host (fish-eating birds) account for most of the spatial heterogeneity in recruitment of larval trematodes to the host snail population. Despite high rates of parasitization, *Batillaria* numbers do not seem to be adversely affected in this system. Future studies should investigate the potential of differing degrees of parasitic castration to decrease *Batillaria* densities, and corroborate the extent to which habitat use by definitive hosts define spatial variability in *C. batillariae* distribution in Elkhorn Slough.

KEY WORDS: *Batillaria attramentaria* · *Cercaria batillariae* · parasites · larval trematodes · Elkhorn Slough · prevalence · parasitic castration · invasive species · spatial heterogeneity · infection rate

INTRODUCTION

Parasites are a pervasive, if too often overlooked, part of any functioning ecosystem (Lafferty 2005). In addition to their role in increasing connectivity of a food web (Lafferty 2005), they influence host population dynamics by altering host behavior, growth, survival, distribution, abundance, and reproductive capacity (Lafferty 1993, Lafferty 2005, McDermott 1996, Hall 2004, Torchin et al. 2002). For example, *Euhaplorchis*, a confamilial trematode to the subject in this study, is one of the fluke species known to parasitize *Cerithidea californica*, the native estuarine snail on the West Coast of North America. Its second larval stage forms cysts on the brains of killifish, and causes the fish to perform attractive behaviors that increase the chances of the host being eaten by a bird (Lafferty 2005). Once in the bird's digestive tract, the fluke completes its life cycle. Thus, the parasite not only exploits the existing food web, but also acts to strengthen a trophic link in the system (Lafferty 2005).

The subject of this study is the trematode *Cercaria batillariae* (Heterophyidae, Digenea) (Miura et al. 2005). It was first documented by Shimura and Ito (1980) and so named for the stage observed (cercariae) and its host (*Batillaria cumingi*, in its native range; *Batillaria attramentaria*, where it is introduced), the Asian estuarine mud snail. Miura et al. (2005) determined, with genetic studies, that this species name encompasses at least eight cryptic species of trematodes in *B. cumingi*. As these species are virtually indistinguishable morphologically, this study will refer to them collectively as *C. batillariae*.

While the complete life cycle of this parasites is undescribed and the adult form has not been observed (Torchin et al. 2002, Hall 2004), *C. batillariae* belongs to a taxa which uses shorebirds as definitive hosts and fishes as second intermediate hosts (Miura et al. 2005). The terms “definitive host” and “intermediate host” refers to organisms which harbor the adult and larval forms, respectively. Passage from second intermediate to final hosts is via trophic transmission (Miura et al 2005), whereby the fish carrying the larval stage must be eaten by a bird in order for the trematode to complete its life cycle. Inside the bird's digestive tract, the trematode matures into its adult form and produces eggs which are passed with the bird's excreta (Hall 2004). These eggs are then either ingested by the first intermediate host (*B. attramentaria*) in the course of its feeding or hatch into miracidia which burrow into the snail's tissues (Smith 2001). All trematodes within an individual snail are presumed to be genetically identical products of asexual reproduction (Miura et al. 2005).

In addition to the gaps in understanding of *C. batillariae*'s life cycle, virtually nothing is known of its impacts on its hosts. In particular, the ability of the trematode to regulate *Batillaria attramentaria* (hereon referred to as “*Batillaria*”) populations is of interest. The parasitic trematodes most often infect mature snails and subsequently feed on host gonadal tissue

(Lafferty 2005, Torchin et al. 2002). The process is known as "parasitic castration," as the host is deprived of its reproductive capacity and is relegated, instead, to producing more larval trematodes (Lafferty 2005). A knowledge of the affect of parasites on *Batillaria* populations is vital in light of the success of the invasive snail over its native ecological counterpart, *Cerithidea californica* (hereon referred to as "*Cerithidea*"). One of the proposed mechanisms behind the success of exotic species is a release from natural enemies, including parasites (Torchin et al. 2002). By exerting effects on host community structure, parasites may also mediate success of introduced species (Torchin et al. 2002).

Batillaria is an estuarine snail native to Japan that was accidentally introduced to the Pacific coast of North America with the importation of oysters during the last century (Byers 1999). It shares many life history and ecological characteristics with *Cerithidea*, in that both are direct developers (rather than producing planktonic larvae with high dispersive ability, their crawl-away young hatch from demersal egg strings), both are long-lived (may live up to 10 years) and iteroparous, and both are deposit feeders which mainly extract benthic diatoms from the mud (McDermott 1996, Byers 1999). Following the establishment of *Batillaria*, there have been significant declines in the native *Cerithidea* populations. Where *Batillaria* co-exists with *Cerithidea*, the native species has been declining in number, or already extirpated (McDermott 1996, Byers 1999). Elkhorn Slough, the southernmost point in *Batillaria*'s introduced range, has the highest densities of the snail observed, reaching as high as 8,000 to 10,000 individuals per m^2 (Byers 1999). This study may be seen, therefore, as a first step into investigation of the role of its parasites in the tremendous success of *Batillaria* in Elkhorn Slough.

C. batillariae was most likely introduced with *Batillaria* because host specificity at the first intermediate host stage is greater than that for either second intermediate or definitive hosts

(Miura et al. 2005, Torchin et al. 2002). Indeed, a researcher from UC Santa Barbara has been able to infect a broad range of native fishes with *C. batillariae* and has found the parasite in field surveys of fishes in Elkhorn Slough (R.F. Hechinger, personal communication). As mentioned, which birds host the adult stage is still unknown. Other studies, however, have found that spatial distribution of larval trematodes in snails is correlated with microhabitat use by definitive bird hosts (Lafferty et al. 2005, Smith 2001). The high dispersive capability of the birds and low mobility of *Batillaria*, combined with a short life span and limited swimming abilities of miracidia mean that trematodes must infect snails in close proximity to where their eggs were deposited (Smith 2001). Thus, percentage of infection in *Batillaria* should vary by site in Elkhorn Slough.

As stated, very little is known of the effects of parasitic trematodes on *Batillaria* populations. Much more is known of the parasites' effects on *Cerithidea*. Sousa (1983) found parasite prevalence (= percentage of hosts that are infected) to increase exponentially with snail size. Lafferty (1993) presumed that infection is most likely a function of age. McDermott (1996) concurred Lafferty's theory when he found that larger snails were not more susceptible to infection by free-swimming miracidia than smaller conspecifics. Therefore, higher prevalence at larger snail size is probably the result of chronic exposure (McDermott 1996). Based on that finding, prevalence of parasites in Elkhorn Slough *Batillaria* should also increase with shell length.

To refine the first hypothesis of differing infection rate by site, and given the expectation that prevalence of parasite is related to exposure time, areas with fewer trematode eggs should have lower rates of infection, and translate into greater size at 95% prevalence.

METHODS

Seven sites were sampled in Elkhorn Slough (Fig. 1). They were, from nearest to the Monterey Bay to farthest, the Harbor Mouth near Elkhorn Yacht Club, the West Bank of the Old Salinas River Channel, the East Bank of the Old Salinas River Channel, Long Valley in the Elkhorn Slough National Estuarine Reserve, Hummingbird Island, Kirby Park, and Hudson's Landing. Both sides of the Old Salinas River were sampled to establish whether microgeographic differences existed in parasite prevalence, as these sites were separated by only a few meters. At each of these sites, at least 50 snails were collected randomly and opportunistically, in an attempt to represent size classes present.

A total of 404 snails, ranging in size from 12.6 to 46.2 mm shell length, were examined for parasites. Most were over 17 mm, as previous work indicated that *Batillaria* matures at 18 mm (McDermott 1996). In the lab, longest shell length was measured with calipers to nearest 0.1 mm. The shell was cracked with a hammer, and soft tissue extracted with forceps. Digestive and reproductive tissue (found near the apex of the shell) were pressed onto a microscope slide with a cover slip and examined under a dissecting microscope. Presence or absence of parasites was recorded. Data were organized and analyzed using Excel 2003 for Windows. Logistic regression was performed on size and presence or absence of parasites, and quantile analysis was done to find size at 95% infection rate. The latter two mathematical functions were peformed on Systat 10.

RESULTS

Of the 404 snails examined, 186 (46.0%) were infected. Table 1 shows infection rate by site and size class, as well as overall, for which all data were compiled. For all figures and tables, size class "< 17 mm" includes all snails that measured 16.9 mm or less, "17-18 mm" includes all snails 17.0 to 18.9 mm (and so on), and "> 37 mm" includes all snails 37.0 mm or greater. Prevalence increases exponentially with size for each site (Fig. 2 and 4) as well as for Elkhorn Slough overall (Fig. 3), mirroring Sousa's (1983) findings. Therefore, logistic regression was the best way to model the relationship between size and prevalence of parasites. Size at 95% infection rate, predicted by logistic regression, varies by site (Table 2), with accuracy of prediction ranging from 68.9 to 95.4% at the individual sites, and 82.7% for all data compiled. The 95% confidence intervals are included as an estimate of variability, but most likely are the relic of sampling (as all size classes were not represented equally, and some were not represented at all, at each site).

Overall, in Elkhorn Slough, *Batillaria* can be expected to be 95% infected by larval trematodes at a size of 30.3 mm. The small 95% confidence interval about this figure (29.2 to 32.0 mm) is probably the result of greater precision afforded by greater replication when data for all sites were compiled.

DISCUSSION

Sousa's field results (1983) from native *Cerithidea* populations in Bolinas Lagoon found all snails above 33 mm in length to be infected. Indeed, examination of *Batillaria* from Elkhorn Slough overall showed that 100% of snails were infected above around 35 mm (Fig. 3), with that figure varying from 27 to 35 mm for individual sites (Fig. 4). Examination by eye shows that size at predicted 95% parasite prevalence in *Batillaria* decreases with increasing distance from the ocean (Table 2). This implies that higher availability of trematodes results in snails becoming infected at smaller sizes (hence, younger age) in the upper slough. Indeed, the author readily observed large fish-eating birds (e.g. herons, egrets, kingfishers) in the upper slough sites (Hummingbird Island, Kirby Park, and Hudson's Landing) and not at the other sites (P. Lin, personal observation). While this observation supports previous findings that indicate microhabitat use by the most mobile hosts (e.g. shorebirds) defines spatial heterogeneity in larval trematode recruitment to first intermediate hosts, future studies should directly address this issue by corroborating bird survey data to varying parasite prevalence throughout the Slough. This author suspects that more shorebird use (resulting in greater abundance of bird droppings, and hence, trematode eggs) at a site should result in smaller size at 95% infection rate of *Batillaria*.

Small-scale differences in parasite prevalence, as evidenced by the different size at predicted 95% infection rate at West and East Banks of the Old Salinas River Channel, suggests that *Batillaria* subpopulations are relatively closed due to limited dispersal ability of snails. As a result of the absence of a planktonic larval stage, young snails recruit to their parents' subpopulation. In addition, adult snails do not move more than 9-10 cm in a day (Byers 2000c) or 3 meters in a month (Lafferty 1993). On the other hand, recruitment of larval trematodes is open, due to the migratory and otherwise highly mobile habits of the birds carrying the adults and eggs. Movement by intermediate hosts may act to either homogenize or increase patchiness of trematode distribution (Smith 2001). How much *Batillaria* disperse in Elkhorn Slough is unknown, as is the relative effect of second intermediate fish hosts on parasite distribution. Both would be worthy of future investigation.

In addition to habitat use by definitive hosts, other studies have found abiotic factors (such as temperature, water currents, oxygen concentration, and light) to play a role in the transmission of parasites (Latham and Poulin 2003). How much any of these factors may be in effect in this system is open to future work.

Despite the high rates of parasitization observed in this study, *Batillaria* populations in Elkhorn Slough do not seem to be adversely affected. In fact, given that this area contains the highest known densities of the snail (Byers 1999), the opposite seems to be the case. Lafferty (1993) found a negative correlation between snail density and parasite prevalence, which is to be expected if parasitized populations reproduce at a lower rate. Indeed, the same study found that parasitized *Cerithidea* populations experienced reduced egg production and greater mortality, both of which would result in lower snail density (Lafferty 1993). The mechanisms behind *Batillaria*'s extraordinary success in this system, despite its high parasite loads, would, therefore, be a worthwhile pursuit. In particular, the potential for differing degrees of parasitic castration in the adult population to exert density control in introduced *Batillaria* populations should be investigated. The author suspects that because the snail is iteroparous, and its maturity is hastened in the presence of parasites (Lafferty 1993, as cited by McDermott 1996), that *Batillaria* is able to produce enough young in its smaller size classes to overcome the population's reduction in reproductive capacity due to parasitic castration.

While parasitic trematodes are not transmitted from snail to snail (the complex life cycle of the parasite precludes this), high host densities increase the chances of establishing a parasite population (Lafferty 2005). As with other pathological organisms, including agents of disease, greater host abundance results in higher parasite number and diversity (Lafferty 2005). However, due to various biological 'filter' mechanisms and founder effects that hinder the migration of parasites with an invasive species, average prevalence of parasites may be as much as two times greater in a species' native range than where it is introduced (Torchin et al. 2002). How prevalence of *Cercaria batillariae* in introduced versus native populations of *Batillaria* differ is unknown, but would be of interest in determining the mechanisms behind the snail's success as an invader.

Miura et al. (2005) suspect that the assemblage of trematodes in *Batillaria* on this coast is a subsample of the species they found in Japanese snails. The parasites very likely experienced population bottlenecks of their first intermediate hosts in the process of the snail's introduction, such that probability of all *C. batillariae* species reaching North America is unlikely. Just which species are present in *Batillaria*'s introduced range are, again, unknown. Determining which genetic lineages exist here is significant because, while the cryptic species appear identical externally, they differ phylogenetically and evolutionarily (Miura et al. 2005). This means that their respective impacts on host-parasite ecologies (including invasion biology) will also differ (Miura et al. 2005).

Because *Cerithidea* and *Batillaria* do not share parasitic trematodes (R.F. Hechinger, personal communication), the reduction in the native snail was not due to the recruitment of exotic parasites to the native snail species. Therefore, *Cerithidea* declines were more likely the direct result of competitive exclusionary effects of *Batillaria*. In particular, *Batillaria*'s resistance to hypoxia (Byers 2000b), greater conversion efficiency of food resources (Byers 2000c), and the apparent absence of intraspecific competition even at high densities (Byers 2000a), makes it a better competitor than the *Cerithidea* in this age of ubiquitous anthropogenic disturbance in coastal habitats.

Despite their important ecological ramifications, parasites are often mentioned only briefly in most textbooks (Lafferty 2005). Perhaps this is because they are small and less visible (especially in the case of endoparasites), so their energetic contributions seem insignificant

(Lafferty 2005). In Elkhorn Slough, at least, their effects on the flow of energy in this system can hardly be considered unimportant. Parasites serve as indicators of healthy systems composed of complex ecological links, and pristine areas have been shown to exhibit greater parasite diversity than do degraded sites (Lafferty 2005). That *Batillaria* replaces *Cerithidea* means that with the introduced snail's lower diversity of parasites, entire estuarine ecosystems may suffer. The loss of *Cerithidea* and its parasites may result in weaker trophic links and less complex energy webs (assuming that *C. batillariae* does not cause any behavioral changes in second intermediate hosts), ultimately leading to reductions in charismatic megafauna populations.

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Figure 1. Sampling sites around Elkhorn Slough. 1 = Harbor Mouth, near Elkhorn Yacht Club. 2 = West Bank, Old Salinas River Channel. 3 = East Bank, Old Salinas River Channel. 4 = Long Valley, Elkhorn Slough National Estuarine Research Reserve. 5 = Hummingbird Island, Elkhorn Slough National Estuarine Research Reserve. 6 = Kirby Park. 7 = Hudson's Landing.

(map from http://www.elkhornslough.org/map.htm, modified)

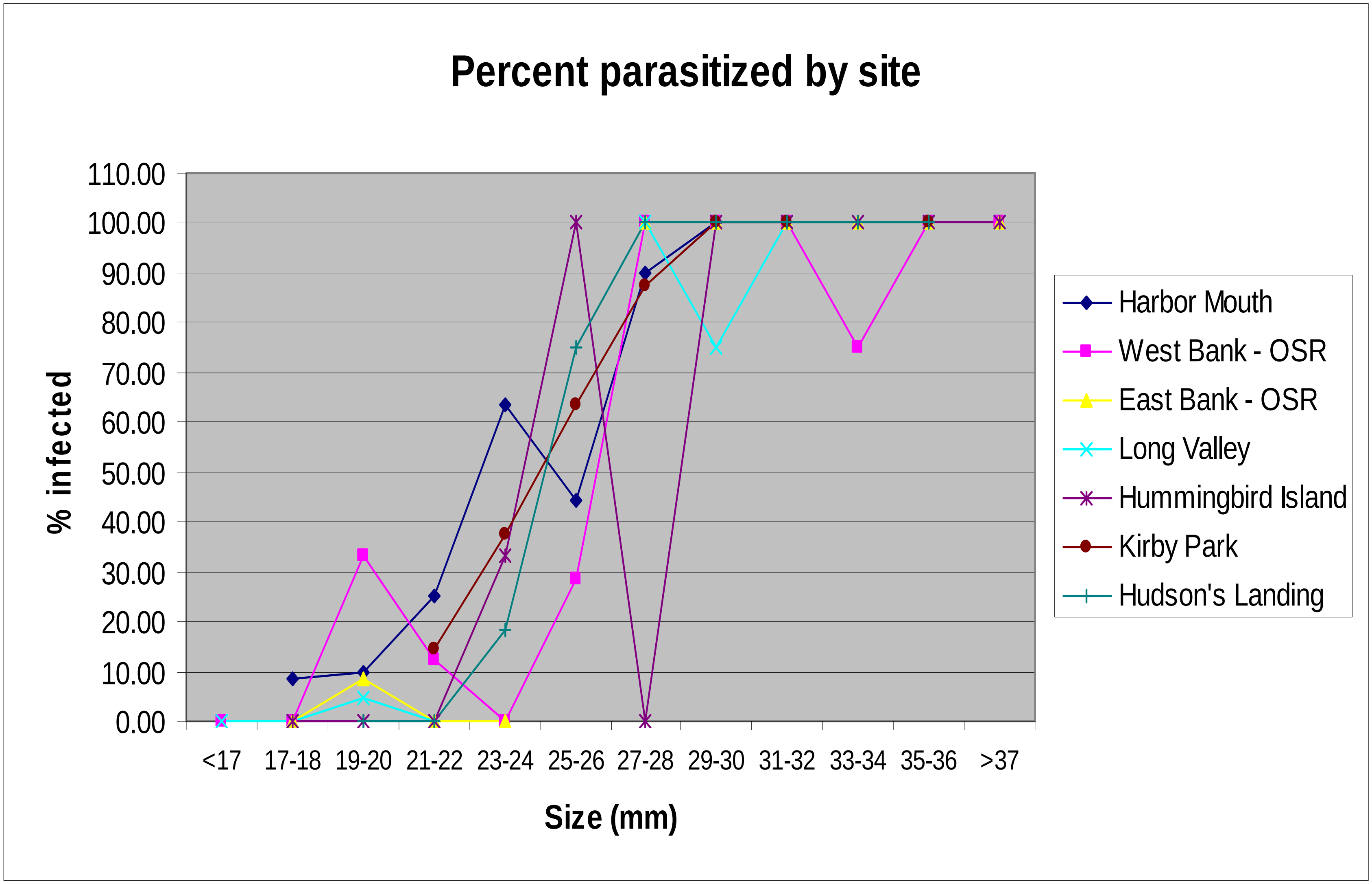

Figure 2. Percentage of Batillaria infected by trematode parasites in various sites around Elkhorn Slough.
Note on size classes: 17-18 mm includes all snails whose shell lengths measured 17.0 to 18.9 mm, and so on.
<17 size class includes all snails that measured 16.9 mm or less.

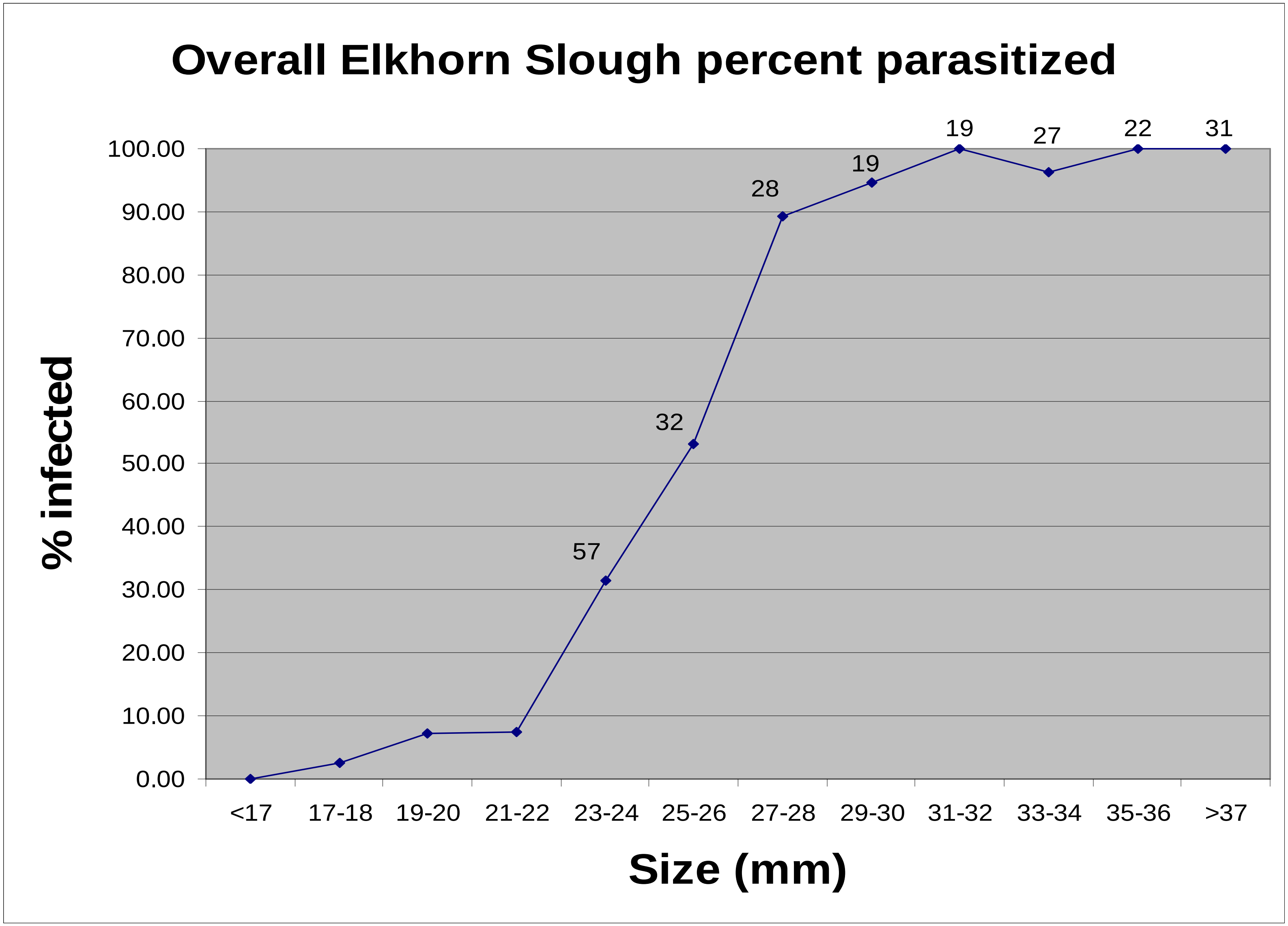

Figure 3. Percentage of Batillaria infected by trematode parasites by size. Data from individual sites were compiled to get parasite prevalence for all of Elkhorn Slough. Again, <17 size class includes all snails that measured 16.9 mm or less, 19-20 size class includes snails with shell lengths from 19.0 to 20.9 mm, and so on. Numbers above data points indicate sample size within each size class.

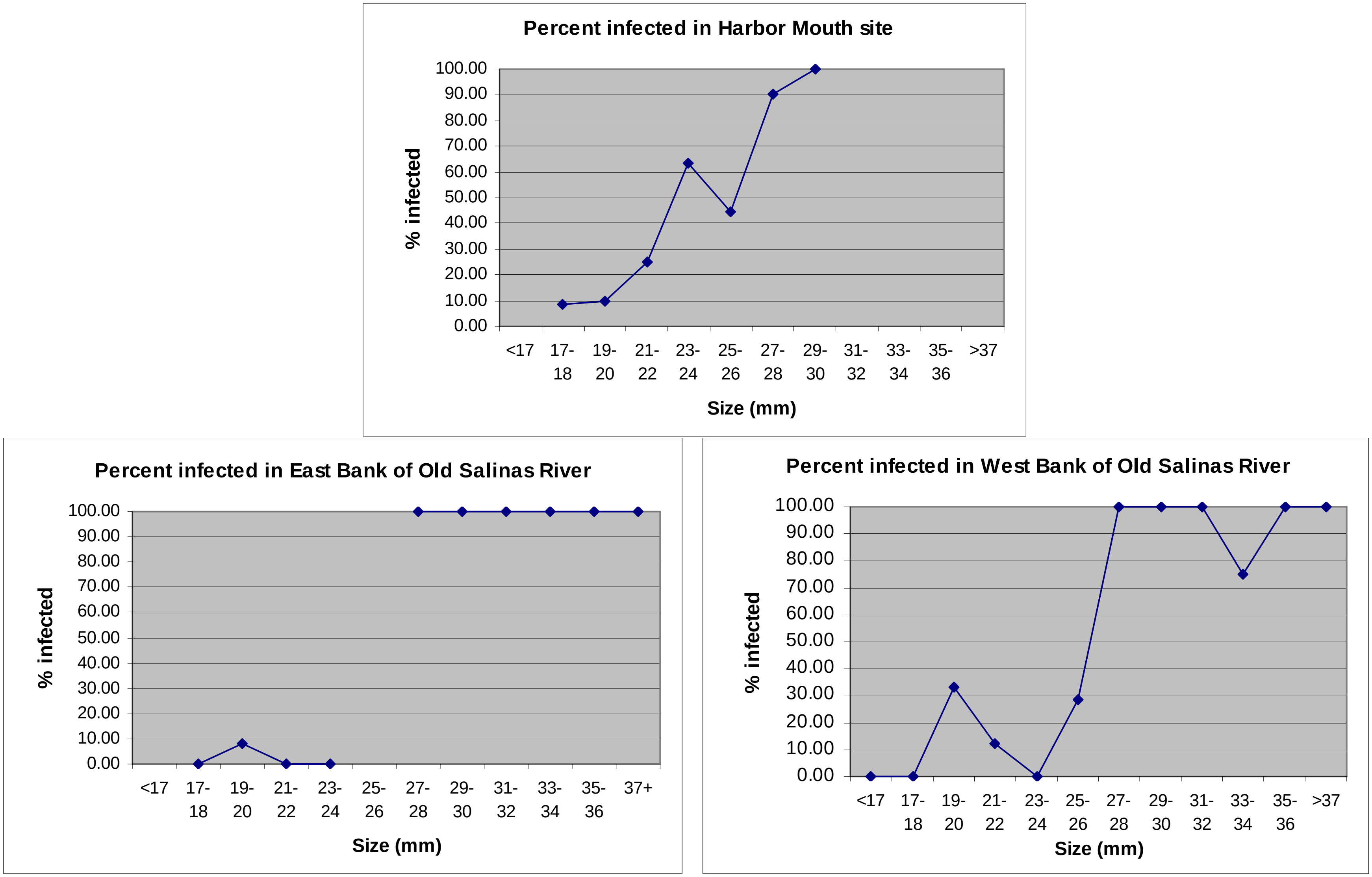

Figure 4. Percentage of Batillaria of each size class infected by trematode parasites, at each site. Size classes not represented by data points indicate no snails of that size were collected from that site.

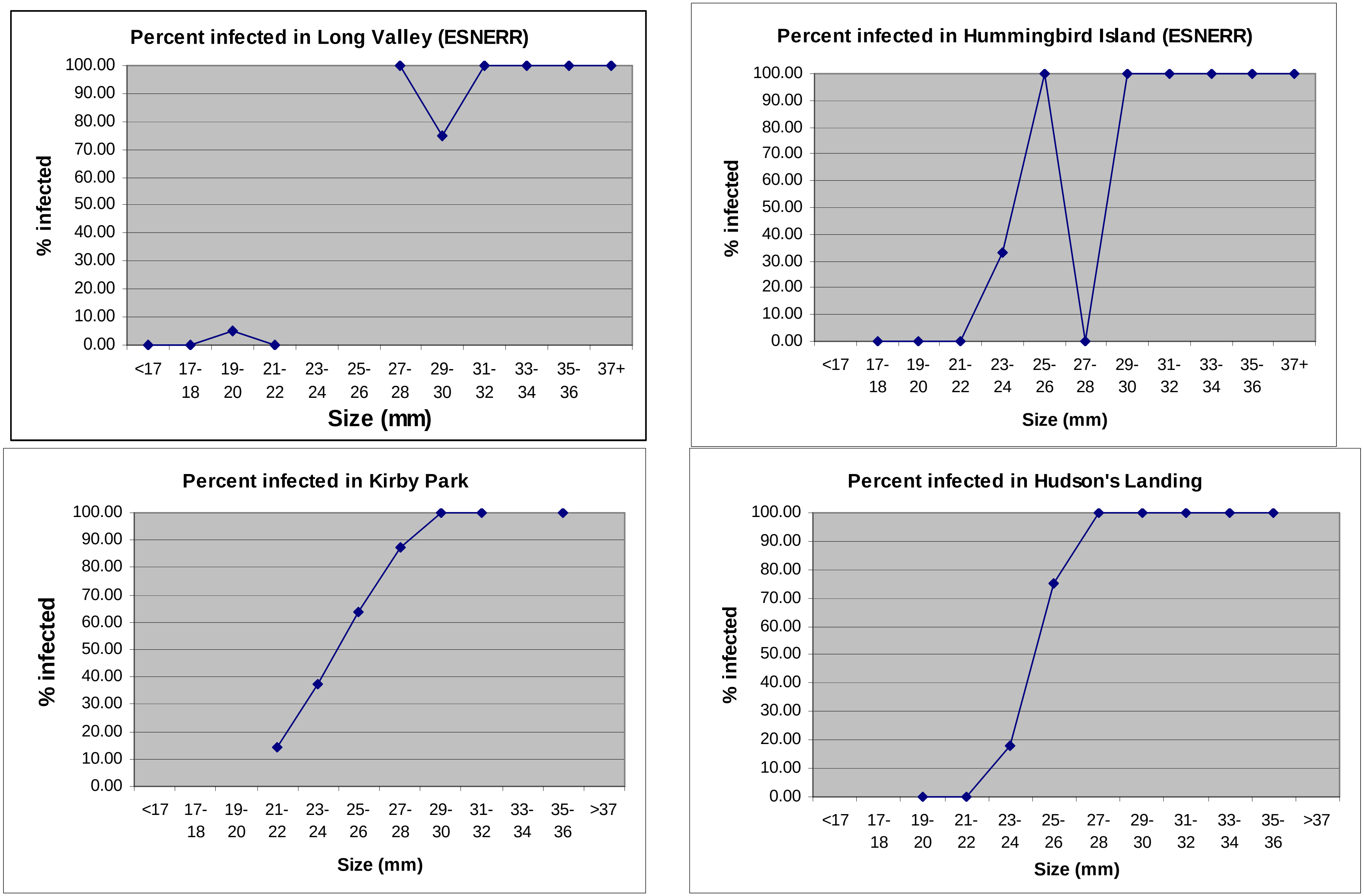

Figure 4 (continued). Percentage of Batillaria of each size class infected by trematode parasites, at each site. Size classes not represented by data points indicate no snails of that size were collected from that site.

Site	% infected	Size	n		Site	% infected	Size	n
Harbor Mouth		<17			Hummingbird Island		<17	
	8.33	17-18	12			0.00	17-18	1
	10.00	19-20	10			0.00	19-20	4
	25.00	21-22	12			0.00	21-22	11
	63.64	23-24	11			33.33	23-24	9
	44.44	25-26	9			100.00	25-26	1
	90.00	27-28	10			0.00	27-28	1
	100.00	29-30	5			100.00	29-30	1
		31-32				100.00	31-32	2
		33-34				100.00	33-34	6
		35-36				100.00	35-36	7
		>37				100.00	37+	9
West Bank -	0.00	<17	2		Kirby Park		<17	
Old Salinas River	0.00	17-18	2				17-18	
	33.33	19-20	3				19-20	
	12.50	21-22	8			14.29	21-22	7
	0.00	23-24	9			37.50	23-24	16
	28.57	25-26	7			63.64	25-26	11
	100.00	27-28	1			87.50	27-28	8
	100.00	29-30	3			100.00	29-30	3
	100.00	31-32	2			100.00	31-32	4
	75.00	33-34	4				33-34	
	100.00	35-36	6			100.00	35-36	1
	100.00	>37	4				>37	
East Bank -		<17			Hudson's Landing		<17	
Old Salinas River	0.00	17-18	3				17-18	
	8.33	19-20	12			0.00	19-20	5
	0.00	21-22	10			0.00	21-22	14
	0.00	23-24	1			18.18	23-24	11
		25-26				75.00	25-26	4
	100.00	27-28	1			100.00	27-28	5
	100.00	29-30	1			100.00	29-30	2
	100.00	31-32	4			100.00	31-32	2
	100.00	33-34	6			100.00	33-34	6
	100.00	35-36	2			100.00	35-36	2
	100.00	37+	15				>37	
Long Valley	0.00	<17	4		**Overall**	**0.00**	**<17**	**6**
	0.00	17-18	22			**2.50**	**17-18**	**40**
	4.76	19-20	21			**7.27**	**19-20**	**40**
	0.00	21-22	6			**7.35**	**21-22**	**68**
		23-24				**31.58**	**23-24**	**57**
		25-26				**53.13**	**25-26**	**32**
	100.00	27-28	2			**89.29**	**27-28**	**28**
	75.00	29-30	4			**94.74**	**29-30**	**19**
	100.00	31-32	5			**100.00**	**31-32**	**19**
	100.00	33-34	5			**96.30**	**33-34**	**27**
	100.00	35-36	4			**100.00**	**35-36**	**22**
	100.00	37+	3			**100.00**	**>37**	**31**

Table 1. Summary of data showing sample sizes of Batillaria collected at each site within each size range, and percentage of those infected by trematode parasites. Blank spaces indicate no snails of that size range were examined from that site.

Site	Size at 95% prevalence (mm)	Overall correct prediction by logistic regression
Harbor Mouth	30.7 (28.2 - 37.2)	68.9%
East Bank - OSR	30.2 (26.7 - 46.8)	95.4%
West Bank - OSR	34.5 (31.2 - 44.4)	79.5%
Long Valley	31.0 (28.2 - 37.7)	94.6%
Hummingbird Island	29.2 (26.4 - 69.0)	89.0%
Kirby Park	28.8 (27.2 - 34.6)	70.1%
Hudson's Landing	26.8 (25.4 - 34.2)	92.3%
Overall	30.3 (29.2 - 32.0)	82.7%

Table 2. Size at 95% infection rate predicted by logistic regression, at each site and for Elkhorn Slough overall (all data compiled). Size at 95% prevalence is followed by the 95% confidence intervals, and overall accuracy in prediction by Systat.