

Differential parasitism of native and introduced snails: replacement of a parasite fauna

Mark E. Torchin^{1,2,*}, James E. Byers^{1,3} & Todd C. Huspeni¹

¹Marine Science Institute and Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA; ²Present Address: Smithsonian Tropical Research Institute, Apartado Postal 2072, Balboa, Ancon, Republic of Panama; ³Present Address: University of New Hampshire, Department of Zoology, 46 College Road, Durham, NH 03824-2617, USA; *Author for correspondence (e-mail: torchinm@si.edu)

Received 8 July 2003; accepted in revised form 5 February 2004

Key words: *Batillaria attramentaria*, *Batillaria cumingi*, *Cerithidea californica*, fish parasites, invasion ecology, local extinctions, non-indigenous species, trematodes

Abstract

The role of parasites in a marine invasion was assessed by first examining regional patterns of trematode parasitism in the introduced Japanese mud snail, *Batillaria cumingi* (= *B. attramentaria*), in nearly all of its introduced range along the Pacific Coast of North America. Only one parasite species, which was itself a non-native species, *Cercaria batillariae* was recovered. Its prevalence ranged from 3 to 86%. Trematode diversity and prevalence in *B. cumingi* and a native sympatric mud snail, *Cerithidea californica*, were also compared in Bolinas Lagoon, California. Prevalence of larval trematodes infecting snails as first intermediate hosts was not significantly different (14% in *B. cumingi* vs 15% in *C. californica*). However, while the non-native snail was parasitized only by one introduced trematode species, the native snail was parasitized by 10 native trematode species. Furthermore, only the native, *C. californica*, was infected as a second intermediate host, by *Acanthoparyphium spinulosum* (78% prevalence). Given the high host specificity of trematodes for first intermediate hosts, in marshes where *B. cumingi* is competitively excluding *C. californica*, 10 or more native trematodes will also become locally extinct.

Introduction

Although invasions often exert significant ecological impacts on native species and systems, the effects of most invasions remain unknown (e.g., Ruiz et al. 1999), especially for introduced parasites (Torchin et al. 2002). Parasites can influence invasion processes in three distinct ways. First, introduced species often escape the parasites that infect them in their native range, and colonization by new parasites does not make up for that loss (Torchin et al. 2003). This reduction of parasites may be associated with an increase in ecological performance (i.e., density, body size, biomass) in

introduced populations (Torchin et al. 2001). And, because the impacts of an invader correlate with its performance (e.g., Crivelli 1983), a reduction in parasites will ultimately enhance an invader's impacts (Torchin et al. 2002). For example, lack of parasites may confer an advantage to an invader competing with heavily parasitized native species because parasites can affect the viability and competitiveness of their hosts (Park 1948; Freeland 1983; Holt 1984; Price et al. 1988; Lafferty 1991; Minchella and Scott 1991; Schall 1992; Holt and Lawton 1994). Second, parasites that are transferred with non-indigenous species may themselves threaten native species. If infected

hosts invade a new locale, non-indigenous parasites may switch hosts and infect phylogenetically or ecologically similar native species with potentially devastating consequences (Osmanov 1971; Andrews 1980; Font and Tate 1994; Holmes and Minchin 1995; Secord and Kareiva 1996; Barse and Secor 1999; Mitchell et al. 2000; Hayward et al. 2001). A rarely considered third scenario through which parasites influence invasion impacts, and one we consider in more detail here, occurs when native parasites themselves are locally extirpated during an invasion. This may produce cascading effects in the trophic interactions throughout the native community, especially if predator-prey interactions are influenced by parasites or symbionts (Holmes and Bethel 1972; Lafferty and Morris 1996; Augustine and Muller-Parker 1998; Lafferty 1999). In sum, the ubiquity of parasites and the extent of their effects demands increased attention to their role in the success and impacts of exotic species.

Study system

The Japanese mud snail, *Batillaria cumingi* (= *B. attramentaria*), was first introduced in the west coast of North America in the early 1900s. This snail, originally misidentified in North America as *B. zonalis* (Morris et al. 1980), was transplanted from Japan, with Pacific oysters (*Crassostrea gigas*) imported into California for aquaculture (Bonnot 1935; Barrett 1963). Although the name *B. attramentaria* (Sowerby, 1855) has been used for this species in North America, we are following nomenclature that is suggested by McLean (in preparation) and used by authors where this species is native (Ozawa 1996; Adachi and Wada 1998). *Batillaria cumingi* now occurs, in discontinuous populations, from Boundary Bay, British Columbia to Elkhorn Slough, Monterey, California (Byers 1999). In northern California, its distribution overlaps with a native mud snail, *Cerithidea californica*. Both snails feed on epipellic diatoms and experimental evidence indicates that they compete with one another for food (Whitlatch and Obrebski 1980; Byers 2000a). In areas where the two snails are sympatric, *C. californica* populations are being excluded and in areas where the introduced snail is abundant, the native snail appears to have

entirely disappeared (Carlton 1975; Byers 1999; Byers and Goldwasser 2001).

Cerithidea californica serves as a first intermediate host to at least 18 native trematode species throughout its range in California (Martin 1972). All but one of these trematodes are trophically transmitted to the final host and infect multiple hosts during their life cycle (Figure 1). Snails serving as first intermediate hosts contain asexually reproducing trematode larval stages (rediae or sporocysts), and all infected snails are castrated, preventing any future reproduction. Trematodes often also reduce the infected snail's growth rate (Sousa 1983; Lafferty 1993). Depending on the trematode species, molluscs, crustaceans, or fishes may serve as second intermediate hosts for the metacercarial cysts. The life cycle is completed when a second intermediate host is eaten by the final host, typically a shorebird (Figure 1).

We distinguish between snails parasitized as first and second intermediate hosts and separate them in our analyses, because the fitness consequences of parasitism are different for each. The first intermediate snail hosts are permanently castrated by a single infection (Kuris 1974, 1997). The effects on second intermediate hosts generally depend on the number of infections. Second intermediate hosts often experience a decrease in growth rate and survivorship (Lim and Heyneman 1972; Heyneman et al. 1972; Kuris and Warren 1980) and often suffer increased susceptibility to predation (Holmes and Bethel 1972; Lafferty and Morris 1996; Lafferty 1999). One trematode species, *Acanthoparyphium spinulosum*, infects *C. californica*, by using it as both a first and second intermediate hosts. It frequently encysts in the buccal mass of *C. californica* (Martin and Adams 1961; Martin 1972). However, its effect on the fitness of *C. californica* individuals is unexplored.

In this study, we examined patterns of trematode parasitism in introduced populations of *B. cumingi*. Parasitism in *B. cumingi* and its native competitor, *C. californica* were compared in Bolinas Lagoon, where the two species co-occur. First we quantified the species richness, prevalence, intensity and mean abundance (*sensu* Bush et al. 1997) of larval trematodes in allopatric populations of *B. cumingi* and in sympatric populations of *C. californica* and *B. cumingi*. Second, to determine whether *B. cumingi* was resistant to infection

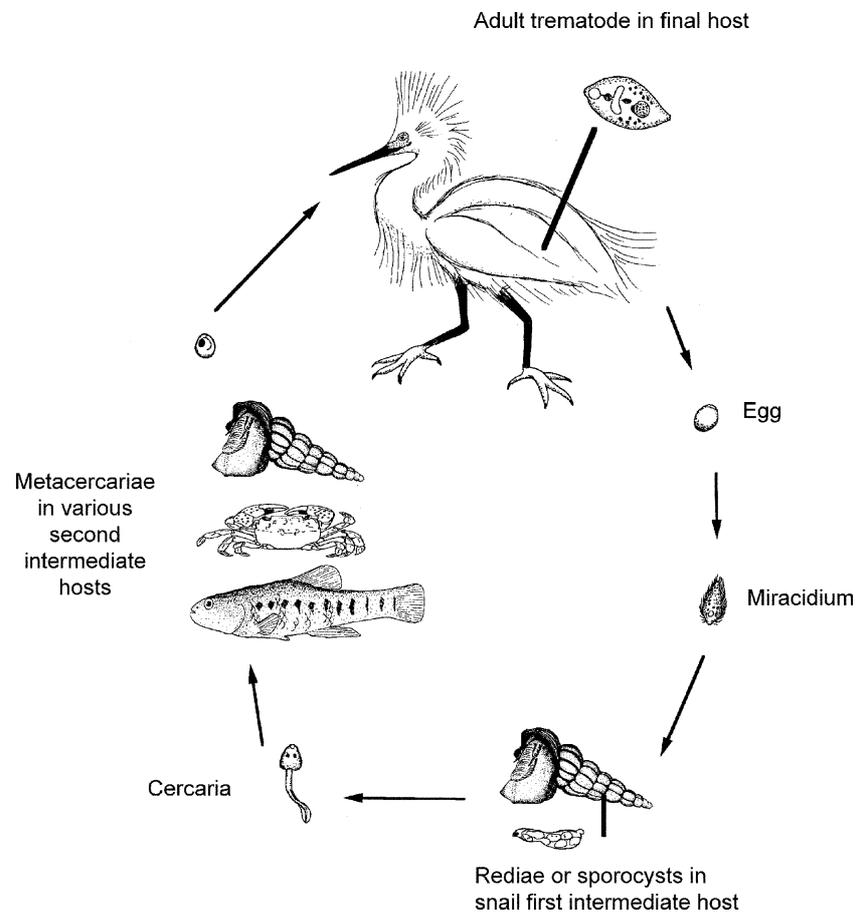


Figure 1. Generalized life cycle for trematode species using *Cerithidea californica* as first intermediate host. The particular type of second intermediate host used (e.g., a fish or a crustacean) is dependent upon trematode species, and not all second intermediate hosts used by trematodes in *C. californica* are depicted here. Figure adapted from Huspeni and Lafferty (2004).

by parasites that infect *C. californica*, the susceptibility of the two snail species to infective *A. spinulosum* cercariae was experimentally tested. Based on these results, we speculate on some likely, yet potentially cryptic, impacts of the invasive snail due to differences in parasitism between *C. californica* and *B. cumingi*. This is a necessary step in the evaluation of how parasites influence the success and impact of this invasive species.

Materials and methods

Local and regional-scale parasite surveys

To examine the parasites of *Batillaria cumingi* and *Cerithidea californica*, snails of each species

from sympatric populations at five marsh pannes in the south marsh of Bolinas Lagoon, California were collected in September 1998. Marsh pannes are elevated areas devoid of macro-vegetation, where snails typically achieve their highest population densities within a marsh (Sousa 1990; Byers 2000a). Furthermore, because both snail species exhibit direct development (Whitlatch 1972; Behrens Yamada and Sankurathri 1977) and limited dispersal as adults (Sousa 1990), these pannes comprise relatively closed populations of snails. This low snail mobility and potential genetic variation in susceptibility between populations may result in differences in snail infection across relatively small spatial scales. We also collected *B. cumingi* from three locations within Elkhorn Slough, Monterey,

California (May and September 1998, July 1999 and October 2001) and two locations in Tomales Bay, California (February 2000) and one location in Padilla Bay, Washington (June 2000) (Table 1).

Snails were measured from the apex of the spire to the vertical margin of the aperture with vernier calipers. Snails were dissected by gently cracking the shell with a hammer and then teasing shell fragments and tissue apart in a few milliliters of filtered seawater in a Syracuse watch glass. Snail gonads, digestive glands and mantle tissues were examined for trematode sporocysts, rediae or cercariae. Trematode species were identified according to Martin (1972). We compared parasite prevalence in snails serving as first intermediate hosts using a χ^2 test and a logistic regression model, with host species, host size, and site within the marsh as independent variables. The effect of latitude and snail size on prevalence was examined using a general linear model for *B. cumingi* across all of the sites we sampled.

To determine the extent to which snails were infected as second intermediate hosts, we examined the muscles associated with the buccal mass of a sub-sample comprising 50 individuals of each snail species from each of the five sites within Bolinas Lagoon. This tissue was examined with the aid of a compound microscope at 40 \times . We quantified the percentage of infected hosts (prevalence), the mean number of cysts in infected hosts (intensity), and the mean number of cysts in infected and uninfected snails (mean abundance). We examined the buccal masses of both snail species for cysts of *A. spinulosum*. Mean abundance of this parasite in the two snails was compared using the Kruskal–Wallis test because the data were not normally distributed.

Infection experiment

To determine if *B. cumingi* was refractory to infection as a second intermediate host, we exposed it to high concentrations of infective *A. spinulosum* cercariae. From a source population of *C. californica* known to be infected with *A. spinulosum* as first intermediate hosts (Point Mugu, California), we collected cercariae by inducing them to shed from infected snails. Snails were isolated in individual plastic containers with a few milliliters of seawater and exposed to light (6 h light at 28–30 °C). This technique enables non-destructive collection of trematode cercariae (Lafferty 1991). Approximately 4000 cercariae were obtained, and placed in a rectangular plastic aquarium (29 \times 18 cm) along with 25 *C. californica* and 25 *B. cumingi* from Bolinas Lagoon in one liter of filtered seawater. A 3.2 mm plastic mesh (Vexar™) cover was placed over the surface to prevent the snails from crawling out of the water. The snails were exposed for 40 h, removed from the container and rinsed with filtered seawater. We measured shell length, then dissected and processed them as above. New metacercarial infections (existing prior to exposure) were distinguished from old ones by having incompletely developed cyst walls. We analyzed the mean number of new infections of *A. spinulosum* in *B. cumingi* and *C. californica* using a Kruskal–Wallis test as above.

Second intermediate host survey

A single trematode species, which was itself a non-native species, was found to parasitize *B. cumingi* as a first intermediate host. A dichotomous key and published descriptions of native trematode

Table 1. Trematode prevalence in *Batillaria attramentaria* at our collection sites (listed north to south) n = sample size.

Location	Site	Latitude (°N)	Shell length (mm)			Trematode prevalence (%)
			n	Mean	Variance	
Padilla Bay, Washington	Bay View State Park	48.31	275	25.8	25.2	86.2
Tomales Bay, California	Hog Island Oyster Co.	38.15	80	23.1	5.3	8.8
	Millerton	38.15	102	24.3	10.4	10.8
Bolinas Lagoon, California	South Marsh	37.09	499	23.1	9.4	14.0
Elkhorn Slough, California	Hummingbird Island	36.41	102	21.4	4.7	3.9
	Jetty Road	36.41	75	19.9	3.8	2.7
	Kirby Park	36.41	50	19.8	22.4	4.0

species in California enabled identification down to the family level (Martin 1972; Yamaguti 1971, 1975). Using descriptions and parasitological evidence of trematodes in snails from Japan, we identified this trematode as *Cercaria batillariae*, described from *Batillaria cumingi* from Japan (Shimura and Ito 1980; Ito 1988) (Figure 2). To determine which fish species served as the second intermediate host for this non-native trematode species, we collected fishes from Elkhorn Slough (an estuary where *C. californica* does not presently occur (Byers 1999)) in October 2001. Using a beach seine (5 m long, 3 mm mesh width) the fishes were caught at an average depth of 1 m. All fishes caught (*Atherinops affinis*, *Clevelandia ios*, *Gillichthys mirabilis* and *Leptocottus armatus*) were examined for exotic trematode metacercariae. We compared the morphology of larval worms in the metacercarial cysts to those in *B. cumingi* to confirm their identification.

Results

Local scale parasite survey

We examined 499 *Batillaria cumingi* and 396 *Cerithidea californica* from Bolinas Lagoon, where the two snail species are sympatric. Ten trematode species infected *C. californica*, and only one species, *Cercaria batillariae*, infected *B. cumingi*. When all snails were pooled, we found no significant difference in overall prevalence of trematodes



Figure 2. Cercaria of the non-indigenous trematode (*Cercaria batillariae*) infecting non-indigenous *Batillaria cumingi* in Bolinas Lagoon. Total length of cercaria is approximately 0.5 mm.

infecting *B. cumingi* (14%) and *C. californica* (15%) as first intermediate hosts in Bolinas Lagoon ($\chi^2 = 0.03$, $df = 1$, $P > 0.05$). When we examined trematode prevalence in more detail using a full factorial logistic regression model (JMP, SAS Institute Inc.) accounting for snail species, snail size, and collection site, again, no significant difference in prevalence between snail species was found ($\chi^2 = 0.11$, $df = 1$, $P > 0.05$). Site ($\chi^2 = 29.8$, $df = 4$, $P < 0.0001$) and snail size ($\chi^2 = 75.5$, $df = 1$, $P < 0.0001$) had a significant effect on infection status, with larger snails exhibiting higher prevalences than smaller snails. There was also a significant interaction effect of site and species ($\chi^2 = 31.1$, $df = 4$, $P < 0.0001$), and species and size ($\chi^2 = 19.6$, $df = 1$, $P < 0.0001$) on infection status. When each snail species was examined separately, there was a significant effect of size on prevalence for both snail species ($\chi^2 = 7.9$, $df = 1$, $P < 0.01$ for *C. californica* and $\chi^2 = 70$, $df = 1$, $P < 0.0001$ for *B. cumingi*).

The size-dependent infection prevalence was more extreme for *B. cumingi* than for *C. californica* (Figure 3a), with a very steep increase in infected *B. cumingi* at 27 mm. The size frequency distributions of the two snails were also different (Figure 3b), with the mean size of *C. californica* (25 mm) larger than that of *B. cumingi* (23 mm) ($t = -12.4$, $df = 893$, $P < 0.0001$).

Of the 250 *C. californica* examined for the metacercariae of *Acanthoparyphium spinulosum* from Bolinas Lagoon, California, 78% were infected as second intermediate hosts compared to 0% of the 252 *B. cumingi* examined ($\chi^2 = 295$, $df = 1$, $P < 0.0001$). The mean abundance of metacercariae in *C. californica* was five. There was a positive association between size of snail and the prevalence of cysts in *C. californica* ($r^2 = 0.89$, $P < 0.0001$, Figure 4a). However, there was no association between snail size and the intensity of cysts in infected *C. californica* ($r^2 = 0.003$, $P > 0.05$, Figure 4b).

Regional scale parasite survey

Throughout its introduced range, *Batillaria cumingi* was infected with only a single trematode species, the non-native, *Cercaria batillariae* ($n = 4$ estuaries, $n = 7$ sites, $n = 1183$ *B. cumingi*). Prevalences of this trematode varied greatly among

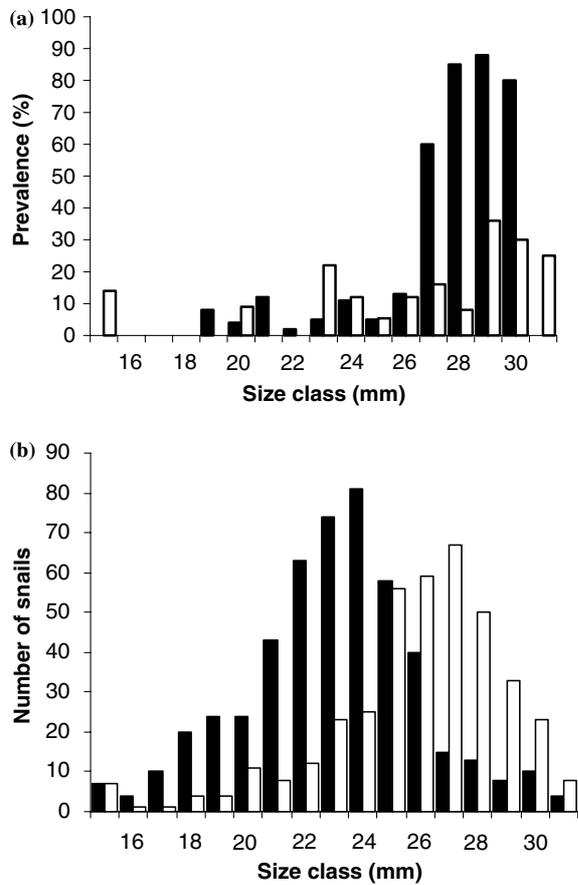


Figure 3. (a) Size – prevalence distribution of larval trematodes (using snails as first intermediate hosts) in *Batillaria cumingi* (solid bars represent prevalence of the exotic *Cercaria batillariae*) and *Cerithidea californica* (open bars represent overall prevalence of 10 trematode species combined) in Bolinas Lagoon, California; (b) Size – frequency distribution of *Batillaria cumingi* (solid bars) and *Cerithidea californica* (open bars) in Bolinas Lagoon, California. Data are for all panes combined.

the locations (Table I). Latitude was positively associated with infection status ($R^2 = 0.98$, $F = 270$, $df = 1, 6$, $P < 0.0001$), however, this association was heavily influenced by the northern-most site, Padilla Bay, Washington. Here nearly 9 out of 10 adult snails were infected.

Infection experiment

In the 40 h of exposure to infective cercariae, none of the 25 *B. cumingi* experimentally exposed to *A. spinulosum* metacercariae became infected,

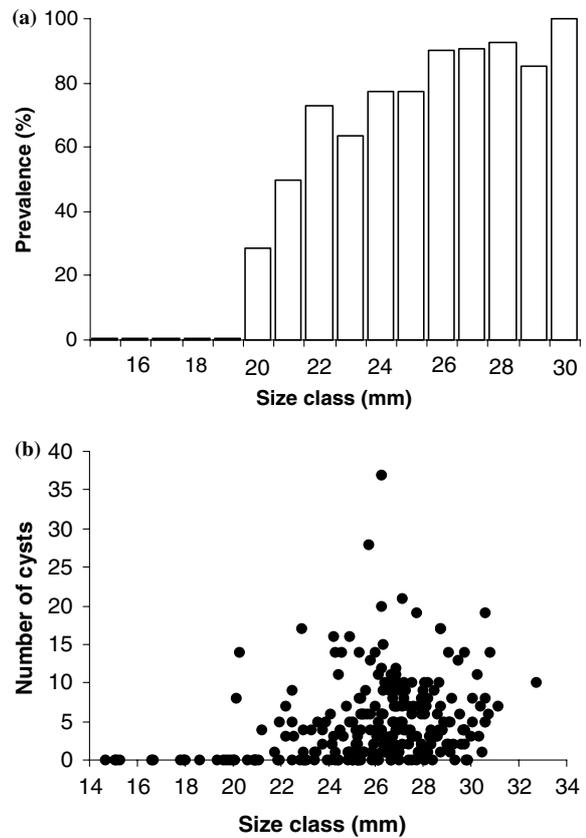


Figure 4. (a) Size – prevalence distribution of *Acanthoparyphium spinulosum* metacercariae (i.e., using the snail as a second intermediate host) in *Cerithidea californica* in Bolinas Lagoon, California; (b) Association between intensity of *A. spinulosum* metacercariae and snail size.

while 13 of the 25 *C. californica* from Bolinas Lagoon became infected with an average of one new infection per snail (Kruskal–Wallis $\chi^2 = 16.8$, $df = 1$, $P < 0.0001$).

Fish survey

All of the fishes we caught in our collections from Elkhorn Slough were infected as second intermediate hosts with metacercariae of the non-native trematode, with the exception of two small (4 and 5 cm), juvenile topsmelt (*Atherinops affinis*). The fishes infected with the exotic parasite included: the arrow goby (*Clevelandia ios*, $n = 16$, mean cyst intensity = 21), the longjaw mudsucker (*Gillichthys mirabilis*, $n = 3$, mean cyst intensity ~500) and the staghorn sculpin (*Leptocottus armatus*,

$n=2$, mean cyst intensity ~ 250). We found metacercariae of the exotic *Cercaria batillariae* throughout the body cavity of the fishes. These were primarily concentrated in the connective tissue lining the pericardium, coelom, the dorsal surface of the mouth, and pharynx (Figure 5).

Discussion

Batillaria cumingi and *Cerithidea californica* differ markedly in the assemblage of parasites utilizing each as a first intermediate host. We found 10 native trematode species infecting *C. californica* as a first intermediate host, while only one species infected *B. cumingi*. *Batillaria cumingi* was transplanted from Japan with imported oysters (*Crassostrea gigas*), and adult snails infected with trematodes were probably introduced. Alternatively, but much less likely, the movement of avian hosts from Japan to the West Coast of North America may have also provided an avenue by which *Cercaria batillariae* could invade. In either case, *Cercaria batillariae* could not have established until its obligate first intermediate host (*B. cumingi*) was itself introduced. Because trematodes are typically less host-specific for second intermediate and final hosts (Llewellyn 1965;

Shoop 1988), *Cercaria batillariae* was able to complete its life cycle in North American hosts such as fishes and birds. This non-indigenous parasite has presumably been present, impacting multiple native species for more than 50 years, in many estuaries on the Pacific Coast of North America. In the literature, trematodes were first reported parasitizing populations of *Batillaria cumingi* in North America by Whitlatch (1974) and by Ching (1991), although they did not recognize the trematode as an introduced parasite species.

Regardless of the vector by which *Cercaria batillariae* was introduced, it appears that only one of the several (six reported and two undescribed) trematode species which infect *Batillaria cumingi* in its native range (Shimura and Ito 1980; Rybakov and Lukomskaya 1988; Harada and Suguri 1989; M. Torchin and A. Kuris, in preparation) invaded along with the snail host. This release from parasites is consistent with other examples of invasive marine species (Torchin et al. 2001, 2002, 2003). Interestingly, in Japanese populations of *B. cumingii* *Cercaria batillariae* is more widespread and prevalent than other trematode species and it is also common in areas of shellfish aquaculture (M. Torchin and A. Kuris, in preparation). Thus, *Cercaria batillariae* may have had an increased chance of being introduced with *B. cumingii* compared to the other trematode species.

In Bolinas Lagoon, the overall proportion of snails infected as first intermediate hosts (and thus castrated) did not differ between *B. cumingi* and *C. californica*. This suggests that in Bolinas Lagoon, *B. cumingi* may not experience an advantage over *C. californica* because of reduced parasitism as a first intermediate host. However, the positive association between size and prevalence was more extreme for *B. cumingi* than for *C. californica*. While trematode prevalence increased dramatically at 27 mm for *B. cumingi* (Figure 3a), there were relatively few snails greater than 26 mm in our study (Figure 3b). Conversely, even though the increase in prevalence was not as great in larger *C. californica*, there were more *C. californica* in the larger size classes compared to *B. cumingi*. Thus, to fully evaluate the differential impacts of trematodes on these snails, information on size-specific

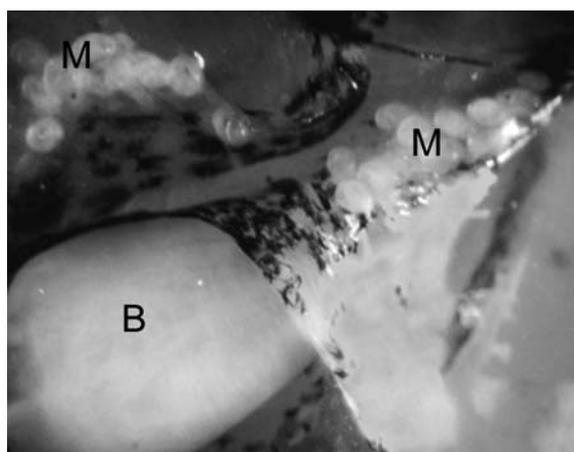


Figure 5. Metacercariae of the exotic *Cercaria batillariae* infecting a native goby (*Gillichthys mirabilis*). These metacercarial cysts were concentrated in the connective tissue lining the pericardium. M indicates metacercarial cysts and B indicates the bulbus arteriosus of the fish. Diameter of metacercaria is approximately 0.3 mm.

fecundity, size-specific infection rates and snail growth rates, will be required.

Since larval trematodes generally display less host specificity for second intermediate hosts than for first intermediate hosts (Llewellyn 1965; Shoop 1988), we hypothesized that *B. cumingi* and *C. californica* may share parasites that utilize both of them as second intermediate hosts. Metacercarial cysts of *A. spinulosum* often occur in high intensities in the musculature of the buccal mass of *C. californica* (Martin and Adams 1961; T. Huspeni and M. Torchin, unpublished data). However, while none of the *B. cumingi* examined were parasitized by *A. spinulosum*, nearly 80% of the *C. californica* were infected by this trematode species. Our infection experiment demonstrated *B. cumingi* was not a compatible host for *A. spinulosum*. Studies examining the impact of *A. spinulosum* on *C. californica* are needed to adequately determine the potential for *A. spinulosum* to mediate interactions between the two snail species.

The direct effects of the invasion of *B. cumingi* have been well documented, particularly with respect to its negative effects on *C. californica* (Whitlatch and Obrebski 1980; Byers 2000a, b; Byers and Goldwasser 2001). We submit that there are also probable community level impacts resulting from the exclusion of *C. californica*, and its associated parasites. Heterophyid trematodes use fishes as their second intermediate hosts, and fish-eating birds and mammals as final hosts. In Elkhorn Slough, we found metacercariae of the heterophyid, *Cercaria batillariae* in all of the three fish species for which we examined adult individuals. In two of the species, we found hundreds of metacercariae per individual host, suggesting that high intensities are common in these native hosts. Further studies examining the full range of second intermediate host use and the impact of this parasite on the growth, behavior and survival of infected fishes are necessary to elucidate the extent of the impact of this invasion.

Perhaps equally as important, should *C. californica* become extirpated at Bolinas Lagoon, its parasites will also become locally extinct. None use alternative first intermediate hosts, including *B. cumingi*. Although the precise manifestations of these local extinctions on the marsh community remain unclear, the removal of 10 or more native trematode species will ultimately result in the

local elimination of infections in molluscs, crustaceans and potentially several fishes that serve as second intermediate hosts for *C. californica*'s parasites (Martin 1972; Figure 1). This may alter host population dynamics (Lafferty 1992) and potentially alter the foraging and abundances of shorebirds as well (Lafferty and Morris 1996). The loss of *C. californica* and the concomitant loss of its dependent larval trematode species may have far-reaching effects on the community structure of this native marsh system. This study highlights the importance of thoroughly examining parasites when considering the success and impacts of non-indigenous species.

Acknowledgements

We thank A. Kuris, K. Lafferty and R. Hechinger for comments and suggestions, John Meyer and the Conservation Biology Class (Summer 2000) at Friday Harbor Laboratories for field and laboratory assistance. We acknowledge J. and C. O'Connor for hospitality at the Bolinas Lagoon field site. This work was supported, in part, by funds from NSF through the NIH/NSF Ecology of Infectious Diseases Program (DEB 0224565) and by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration (NOAA), US Department of Commerce under Grant Number [NA06RG0142], project number [R/CZ-162] through the California Sea Grant College System, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The US government is authorized to reproduce and distribute this paper for governmental purposes.

References

- Adachi N and Wada K (1998) Distribution of two gastropods, *Batillaria multiformis* and *B. cumingi* (Batillariidae) at a co-occurring area. *Venus (Japanese Journal of Malacology)* 57: 115–120
- Andrews JD (1980) A review of introductions of exotic oysters and biological planning for new importations. *Marine Fisheries Review* 42: 1–11

- Augustine L and Muller-Parker G (1998) Selective predation by the mosshead sculpin *Clinocottus globiceps* on the sea anemone *Anthopleura elegantissima* and its two algal symbionts. *Limnology and Oceanography* 43: 711–715
- Barrett EM (1963) The California oyster industry. California Department Fish and Game, Fish Bulletin 123: 2–103
- Barse AM and Secor DH (1999) An exotic nematode parasite of the American eel. *Fisheries* 24: 6–11
- Behrens Yamada S and Sankurathri CS (1977) Direct development in the intertidal gastropod *B. zonalis*. *Veliger* 20: 179
- Bonnot P (1935) The California oyster industry. California Fish and Game 21: 65–80
- Bush AO, Lafferty KD, Font JM and Shostak AW (1997) Parasitology meets ecology: definitions, clarifications, examples and Margolis et al. revisited. *Journal Parasitology* 83: 575–583
- Byers JE (1999) The distribution of an introduced mollusc and its role in the long-term demise of a native congeneric species. *Biological Invasions* 1: 339–352
- Byers JE (2000a) Competition between two estuarine snails: implications for invasions of exotic species. *Ecology* 81: 1225–1239
- Byers JE (2000b) Differential susceptibility to hypoxia aids estuarine invasion. *Marine Ecology Progress Series* 203: 123–132
- Byers JE and Goldwasser L (2001) Exposing the mechanism and timing of impact of non-indigenous species on native species. *Ecology* 82: 1330–1343
- Carlton JT (1975) Extinct and endangered populations of the endemic mud snail *Cerithidea californica* in Northern California. *Bulletin of the American Malacological Union* 41: 65–66
- Ching HL (1991) Lists of larval worms from marine invertebrates of the Pacific Coast of North America. *Journal of Helminthological Society Washington* 58: 57–68
- Crivelli AJ (1983) The destruction of aquatic vegetation by carp. *Hydrobiologia* 106: 37–42
- Font WF and Tate DC (1994) Helminth parasites of native Hawaiian freshwater fishes: an example of extreme ecological isolation. *Journal of Parasitology* 80: 682–688
- Freeland WJ (1983) Parasites and the coexistence of animal host species. *American Naturalist* 121: 223–236
- Harada M and Suguri S (1989) Surveys on cercariae in brackish water snails in Kagawa Prefecture, Shikoku, Japan. *Japanese Journal of Parasitology* 38: 388–391
- Hayward CJ, Iwashita M, Crane JS and Ogawa K (2001) First report of the invasive eel pest *Pseudodactylogyrus bini* in North America and in wild American eels. *Diseases of Aquatic Organisms* 44: 53–60
- Heyneman DH, Lim K and Jeyarasasingam U (1972) Antagonism of *Echinostoma liei* (Trematoda: Echinostomatidae) against the trematodes *Paryphostomum segregatum* and *Schistosoma mansoni*. *Parasitology* 65: 223–233
- Holmes JC and Bethel WM (1972) Modification of intermediate host behavior by parasites. In: Canning EU, Wright CA (eds) *Behavioral Aspects of Parasite Transmission*, pp 123–149. Academic Press, London
- Holmes JC and Minchin D (1995) Two exotic copepods imported into Ireland with Pacific oyster *Crassostrea gigas* (Thunberg). *Irish Naturalist's Journal* 25: 17–20
- Holt RD (1984) Spatial Heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124: 377–406
- Holt RD and Lawton JH (1994) The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25: 495–520
- Huspeni TC and Lafferty KD (2004) Using larval trematodes that parasitize snails to evaluate a salt-marsh restoration project. *Ecological Applications* 14: 795–804
- Ito J (1988) A subsequent monograph of cercariae in Japan. *Japanese Journal of Parasitology* 37: 269–322
- Kuris AM (1974) Trophic interactions: similarity of parasitic castrators to parasitoids. *Quarterly Review of Biology* 49: 129–148
- Kuris AM (1997) Host behavior modification: an evolutionary perspective. In: Beckage NE (ed) *Parasites and Pathogens: Effects on Host Hormones and Behavior*, pp 293–315. Chapman Hall, New York
- Kuris AM and Warren J (1980) Echinostome cercarial penetration and metacercarial encystment as mortality factors for a second intermediate host, *Biomphalaria glabrata*. *Journal of Parasitology* 66: 630–635
- Lafferty KD (1991) Effects of parasitic castration on the salt marsh snail, *Cerithidea californica*. PhD dissertation. University of California, Santa Barbara
- Lafferty KD (1992) Foraging on prey that are modified by parasites. *American Naturalist* 140: 854–867
- Lafferty KD (1993) Effects of parasitic castration on growth, reproduction and population dynamics of the marine snail *Cerithidea californica*. *Marine Ecology Progress Series* 96: 229–237
- Lafferty KD (1999) The evolution of trophic transmission. *Parasitology Today* 15: 111–115
- Lafferty KD and Morris AM (1996) Altered behavior of parasitized killifish increases susceptibility to predation by final bird hosts. *Ecology* 77: 1390–1397
- Lim HK and Heyneman D (1972) Intramolluscan intertrematode antagonism: a review of factors influencing the host-parasite system and its possible role in biological control. *Advances in Parasitology* 10: 191–268
- Llewellyn J (1965) The evolution of parasitic platyhelminths. In: Taylor AER (ed) *Evolution of Parasites*, pp 47–78. Blackwell Scientific Publications, Oxford
- Martin WE (1972) An annotated key to the cercariae that develop in the snail *Cerithidea californica*. *Bulletin of Southern California Academy of Science* 71: 39–43
- Martin WE and Adams JE (1961) Life cycle of *Acanthoparyphium spinulosum* Johnston, 1917 (Echinostomatidae: Trematoda). *Journal of Parasitology* 47: 777–782
- Minchella DJ and Scott ME (1991) Parasitism: a cryptic determinant of animal community structure. *Trends in Ecology and Evolution* 6: 250–254
- Mitchell AJ, Salmon MJ, Huffman DG, Goodwin AE and Brant TM (2000) Prevalence and pathogenicity of a heterophyid trematode infecting the gills of an endangered fish, the fountain darter, in two central Texas spring-fed rivers. *Journal of Aquatic Animal Health* 12: 283–289
- Morris RH, Abbott DP and Haderlie EC (1980) *Intertidal Invertebrates of California*. Stanford University Press, Stanford, California
- Osmanov SO (1971) Parasites of fishes of Uzbekistan. Tashkent: FAN (in Russian)

- Ozawa T (1996) A new species of *Batillaria* (Gastropoda: Batillariidae) from Japan. *Venus (Japanese Journal of Malacology)* 55: 189–197
- Park T (1948) Experimental studies of interspecific competition. I. Competition between populations of flour beetles *Tribolium confusum* Duval and *T. castaneum* Herbst. *Ecological Monographs* 18: 265–307
- Price PW, Westoby M and Rice B (1988) Parasite-mediated competition: some predictions and tests. *American Naturalist* 131: 544–555
- Ruiz GM, Fofonoff P, Hines AH and Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnology and Oceanography* 44: 950–972
- Rybakov AV and Lukomskaya OG (1988) On the life cycle of *Acanthoparyphium macracanthum* sp.n. (Trematoda, Echinostomatidae). *Parazitologiya* 22: 224–229
- Schall JJ (1992) Parasite-mediated competition in *Anolis* lizards. *Oecologia* 92: 58–64
- Secord D and Kareiva P (1996) Perils and pitfalls in the host specificity paradigm. *BioScience* 46: 448–453
- Shimura S and Ito J (1980) Two new species of marine cercariae from the Japanese intertidal gastropod, *Batillaria cumingi* (Crosse). *Japanese Journal of Parasitology* 29: 369–375
- Shoop WL (1988) Trematode transmission patterns. *Journal of Parasitology* 74: 46–59
- Sousa WP (1983) Host life history and the effect of parasitic castration on growth: a field study of *Cerithidea californica* Haldeman (Gastropoda: Prosobranchia) and its trematode parasites. *Journal of Experimental Marine Biology and Ecology* 73: 273–296
- Sousa WP (1990) Spatial scale and the processes structuring a guild of larval trematode parasites. In: Esch GW, Bush AO and Aho JM (eds) *Parasite Communities: Patterns and Processes*, pp 41–67. Chapman and Hall, New York
- Torchin ME, Lafferty KD and Kuris AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. *Biological Invasions* 3: 333–345
- Torchin ME, Lafferty KD and Kuris AM (2002) Parasites and marine invasions. *Parasitology* 124: 137–151
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ and Kuris AM (2003) Introduced species and their missing parasites. *Nature* 421: 628–630
- Whitlatch RB (1972) The ecology, life history and feeding biology of *Batillaria zonalis*. Masters thesis, University of the Pacific
- Whitlatch RB (1974) Studies on the population ecology of the salt marsh gastropod *Batillaria zonalis*. *Veliger* 17: 47–55
- Whitlatch RB and Obrebski S (1980) Feeding selectivity and coexistence in two deposit feeding gastropods. *Marine Biology* 58: 219–225
- Yamaguti S (1971) Synopsis of digenetic trematodes of vertebrates (Vol. 1 and 2). Keigaku Publishing Company, Tokyo, Japan
- Yamaguti S (1975) A synoptical review of life histories of digenetic trematodes of vertebrates with special reference to the morphology of their larval forms. Keigaku Publishing Company, Tokyo, Japan