The distribution of an introduced mollusc and its role in the long-term demise of a native confamilial species

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Abstract

The estuarine mud snail, *Batillaria attramentaria*, was transported to the Pacific coast of North America with the Pacific oyster, *Crassostrea gigas* (*C. gigas*), imported from Japan in the early part of this century, and has proliferated in several bays where the oyster was introduced. Since the arrival of *Batillaria* there have been declines in populations of its native ecological equivalent, *Cerithidea californica*. This study documents the distribution of the exotic *Batillaria* throughout its entire introduced range, concentrating on the few bays in northern California where both snails exist sympatrically. Using dates of initial importation of *C. gigas* and dates of first documentation of *Batillaria* within a bay, I established the earliest possible date for the introduction of *Batillaria* in a particular area. In cases where *Cerithidea* also was, or had been, present within a bay, I calculated a range of time for either the continued coexistence of the two species or the time until local exclusion of the native. Density measurements of *Cerithidea* within these bays where the species co-occurred allowed comparison of present *Cerithidea* numbers to historical accounts. Results indicated that *Batillaria* is replacing *Cerithidea* in the northern marshes of California. This replacement of the northernmost *Cerithidea* populations is not only reducing *Cerithidea*'s overall range, but also eliminating a race recently shown to be a genetically distinct from southern *Cerithidea* populations. Other studies that have demonstrated superior exploitative competitive ability by *Batillaria* provide a potential mechanism for this displacement pattern. Regardless, the results presented here indicate that the displacement process is slow, taking on average > 50 years to complete. This study illustrates a gradual, but predictable process of exotic replacement of native species, and argues strongly against complacency toward invaders that may currently seem innocuous.

Introduction

As invasions of exotic species become an increasingly widespread problem for native ecosystems, a need exists to expand studies from focusing just on processes of invasion in particular areas to documenting patterns and processes occurring at large spatial and temporal scales. Such broad scale studies are useful in describing overall patterns of invasion, and in potentially gleaning inferences about processes that may be acting on levels not discernable at the scale of a single reserve or typical 2–3 year study. To this end, the invasion of the Pacific coast of North America by the estuarine mud snail, *Batillaria attramentaria*, and its consequent interaction with the native ecological equivalent, *Cerithidea californica*, provides a relatively tractable system to address invasions on larger scales.

Batillaria attramentaria, a potamidid Japanese mud snail, has been documented for decades in salt marshes of northern California and parts of the Pacific Northwest (e.g., Hanna 1966). This species was inadvertently introduced with shipments of Pacific oysters,

Crassostrea gigas (*C. gigas*), imported from Japan for aquaculture production in the early part of this century (Bonnot 1935). *Batillaria*'s ability for dispersal is relatively limited because it produces non-planktonic young in demersal egg pouches (Whitlatch 1972, 1974; Yamada and Sankurathri 1977). Thus, the snail is seemingly found only in bays in which it was introduced with *C. gigas* plantings. Its present distribution on the Pacific coast of North America ranges from Elkhorn Slough in

Monterey Bay, CA (36°49′ N, 121°45′ W) to Boundary Bay, British Columbia (49° N, 122°55′ W) (Figure 1) (Hanna 1966; Carlton 1979; J.E. Byers, pers. obs.).

The native confamilial mudsnail, *Cerithidea californica*, is an abundant epifaunal grazer in many salt marshes and mud flats ranging from San Ignacio Bay, Mexico to Tomales Bay, CA (McLean 1978; Abbott and Haderlie 1980), 50 km north of San Francisco Bay. *Cerithidea*, like *Batillaria*, is limited in dispersal
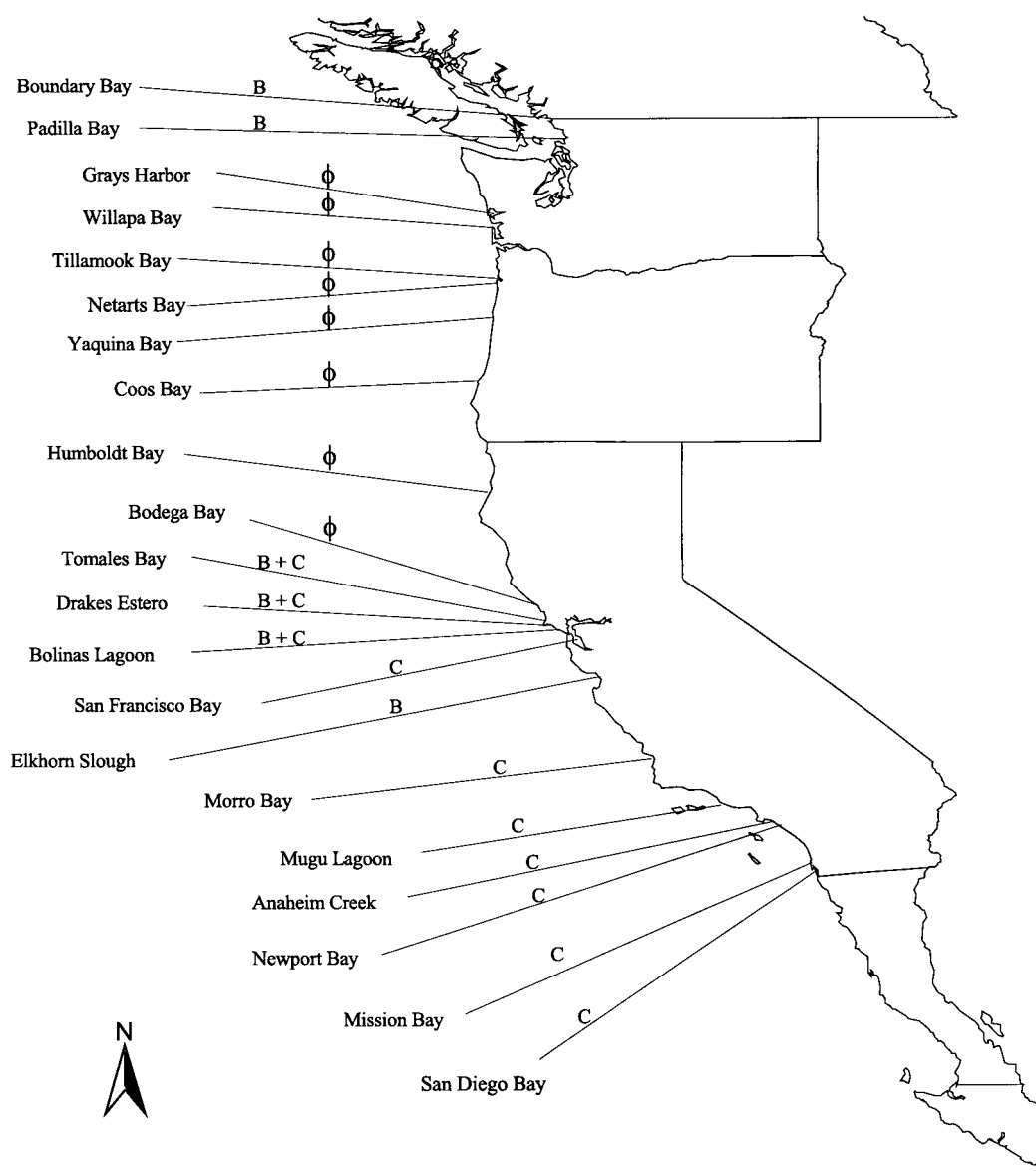

Figure 1. Sample sites along Pacific coast of North America. These bays were selected as they had historically received *Crassostrea gigas* plantings and were therefore most likely to contain *Batillaria attramentaria*. Symbols on lines relate which, if any, species were found in that bay: B = *Batillaria attramentaria*; C = *Cerithidea californica*; and φ = neither species.

ability as it produces egg strands that attach to the mud surface and produce crawl-away larvae (Race 1981; Lafferty 1991). Both snail species utilize the same shared, preferred food resource – epipelic diatoms (Whitlatch and Obrebski 1980; Byers 2000). Populations of *Cerithidea* in northern California, where they overlap with *Batillaria*, have been declining in recent years (Carlton 1976; McDermott 1996). Several authors have noted the potential for interaction between *Cerithidea* and *Batillaria* and suggested that *Batillaria* may be displacing *Cerithidea* in the marshes where they co-occur (MacDonald 1969; Driscoll 1972; Whitlatch and Obrebski 1980; McDermott 1996; Byers 2000). Herein, I (1) document the distribution of the non-native invader, *Batillaria*, (2) document the replacement of *Cerithidea* by *Batillaria* after many years of co-habitation in several marshes of northern California, and (3) calculate the average time this replacement process takes. Additionally, I discuss the potential mechanisms enabling the invasion, and consequences and implications of these findings for conservation of populations of *Cerithidea*.

Methods

In order to ascertain the presence/absence of *Batillaria* in bays along the Pacific coast of North America from southern British Columbia to southern California, I searched all bays which had received reported introductions of *C. gigas* (Figure 1). I chose not to rely solely on published accounts of *Batillaria* population locations in case some populations had not been reported, or the distribution of *Batillaria* had changed. I examined in particular detail the marshes of central/northern California, which represent both the southernmost extent of *Batillaria*'s introduction and the northernmost extent of *Cerithidea*'s native range. I conducted all searches of bays in 1997 (and some additional measurements in 1996 and 1998) during summer months when snails are most active and least covered by sediment. I scoured each area, intensely focusing on tidal creek banks and open mud habitat within the marsh vegetation. In a couple of locations (Tomales Bay and Drakes Estero) I gained access to several sites within a bay via kayak. In locations where either or both snail species were present, I used a 529 cm^2 quadrat to measure population densities ($N = 3$–12 quadrats per site, dependent upon the available area covered by the snail population). When possible, I also interviewed local oysterfishers and biologists about the presence of *Batillaria* as well as the history of *C. gigas* farming within a bay.

To detect potential declines and replacement of *Cerithidea* by *Batillaria* in California bays, I compared my population distribution and density data with published reports of the snails. To calculate an average coexistence time of the species in bays where they co-occur, I determined a range of years for the initial introduction of *Batillaria* into a bay. Since *Batillaria* was introduced to the Pacific coast of North America in shipments of *C. gigas* from Japan (e.g., Bonnot 1935), the earliest possible arrival date for *Batillaria* to a bay was established by determining the first reported importation of *C. gigas*. For a few bays the determination of the introduction of *C. gigas* pinpointed *Batillaria*'s introduction because the period of oyster introduction was very short. In most bays where *C. gigas* was imported over longer periods, the window of time for the introduction of *Batillaria* was also much longer. Prolonged oyster introductions resulted because *C. gigas* generally fails to reproduce in California waters, requiring new oysters to be repeatedly introduced to maintain an oyster fishery in the state (Galtsoff 1932). To narrow the introduction date of *Batillaria* in such cases I searched the literature for the first cited documentation of *Batillaria* in those sites. Using this date of definitive confirmation, I calculated a range of potential dates for the initial introduction of *Batillaria* to a bay – from the first introduction of Pacific oysters to the first documentation of *Batillaria*.

Several assumptions are involved in making the above calculations. Given the potential for an unknown number of rogue or unacknowledged oyster introductions, the recorded dates for first introduction of *C. gigas* are only the best available estimate of the oyster's first introduction. Secondly, a potentially confounding factor is that the introduction of *Batillaria* to a bay does not imply a ubiquitous inoculation within that bay. A given introduction may vary by several years within different areas of the same lagoon, particularly in large bays where the snail may need many years to reach all parts of the bay. Therefore, when I discuss patterns in the larger bays I specify exact places or sections of the bays where introductions and species interactions occur. Additionally, I assumed that *Batillaria*, with its non-planktonic, direct development (Whitlatch 1972; Yamada and Sankurathri 1977), does not disperse from bay to bay on its own, at least within the ecologically short time span it has been in North America (< 70 years) and with its relatively few established source

populations. Finally, for these calculations I assumed that published documentation of *Batillaria* did not refer to ephemeral individuals, but rather represented actual established invader populations.

For Bolinas Lagoon in the southern marsh where densities of both snails are comparable, I sampled snail densities during summer in eight distinct marsh pannes and on one channel bank from 1996 to 1998. Snail populations within marsh pannes, elevated and isolated areas of exposed mud surrounded by vegetation, are likely mostly closed, i.e. independent, populations since both species produce attached benthic eggs and exhibit limited movement as adults (J.E. Byers, unpublished data). Additionally, I sampled the densities of the resident sympatric populations in four of these same marsh pannes in 1994 and 1995 in order to help quantify potential declines in *Cerithidea*. For each species I calculated the percentage change in density within each of the four pannes by averaging the density of each species from 1994 to 1995 and comparing it to the average of measurements from 1997 to 1998. The change for each species within each of these four interacting populations was then averaged to compute a marsh-wide change in snail density weighted by the area covered by each of the four monitored sympatric populations. For purposes of relating changes in *Cerithidea*'s density in the presence of *Batillaria* to natural fluctuations of *Cerithidea* in the absence of the invader, I compared *Cerithidea* population changes in Bolinas to changes in *Cerithidea* where it occurs alone. From the literature I identified two studies detailed enough to serve as baseline measurements for calculating variations in allopatric *Cerithidea* populations over a four year or greater period. In 1998 I measured *Cerithidea* densities in Carpinteria salt marsh to compare to density measurements by Lafferty (1991), and in San Diego Bay to compare with data taken by McCloy (1979) in 1976. While MacDonald (1969) surveyed bays with allopatric *Cerithidea* populations (e.g., Mugu Lagoon and Mission Bay), he did not specify his exact sampling microsites within these marshes to enable adequate habitat matching for meaningful resampling.

In the case of Carpinteria I was able to locate and sample 6 of 8 specific microsites Lafferty had sampled. In San Diego Bay the marsh had changed enough in 22 years to make locating the exact sample spot used by McCloy difficult; however, I was able to match the general habitat type very closely. I conducted density measurements along 12 vertical transects running from the vegetation atop the channel bank down to mean low tide level of two adjacent tidal creeks. I then averaged these measurements and compared them to an average of McCloy's four identically measured transects. The percentage change in *Cerithidea* density from these two exclusive *Cerithidea* sites and the four *Cerithidea* populations coexisting with *Batillaria* in Bolinas Lagoon were compared with a two-tailed *t*-test assuming unequal variances.

Results and discussion

Bays with sympatric populations

As of 1998, only three bays on the Pacific coast of North America, and all within northern California, contained both *Batillaria* and *Cerithidea* – Bolinas Lagoon, Drakes Estero, and Tomales Bay (Figure 2, Tables 1 and 2, Appendix 1). Of these, only Bolinas had relatively equal densities of the two species. The largest congregation of snail populations in Bolinas Lagoon was within the southern salt marsh area. All marsh pannes in this area contained both species except two which were very anoxic and contained only *Batillaria*. Of the nine populations sampled over three summers from 1996 to 1998, snail densities ranged from 120 to 316/m^2 for *Cerithidea* and 110 to 440/m^2 for *Batillaria*. Small areas still exist in other parts of Bolinas Lagoon with entirely allopatric *Cerithidea* populations, notably Kent Island with three or four small pannes with densities from 380 to 1300/m^2, Pine Gultch Creek where *Cerithidea* fill a small tidal channel with densities of 586–1100/m^2, and Audobon Canyon Ranch with densities of 400–500/m^2. In 1997, however, I found eight *Batillaria* at this latter site after two years of thorough examination had revealed only *Cerithidea*. Likewise, in 1999 I found three *Batillaria* at the southeastern edge of Kent Island.

Cerithidea declined an average of 27.2% from 1994/1995 to 1997/1998 in the four sympatric populations I monitored over a longer period in Bolinas Lagoon; over this same time period *Batillaria* declined only 1.7%. A sustained 27% decline in *Cerithidea* every three years would result in less than 10 individuals/m^2 within 32 years. Such a calculation, however, is tenuous due to the high standard deviation in the measurement of this rate of decline ($\pm$14%). Nonetheless, this decline in *Cerithidea* population density in the four sympatric Bolinas populations was significantly greater than the change in *Cerithidea* densities where it occurred alone ($T = 3.4$, $P < 0.03$) (Figure 3). *Cerithidea* from Carpinteria salt marsh, for
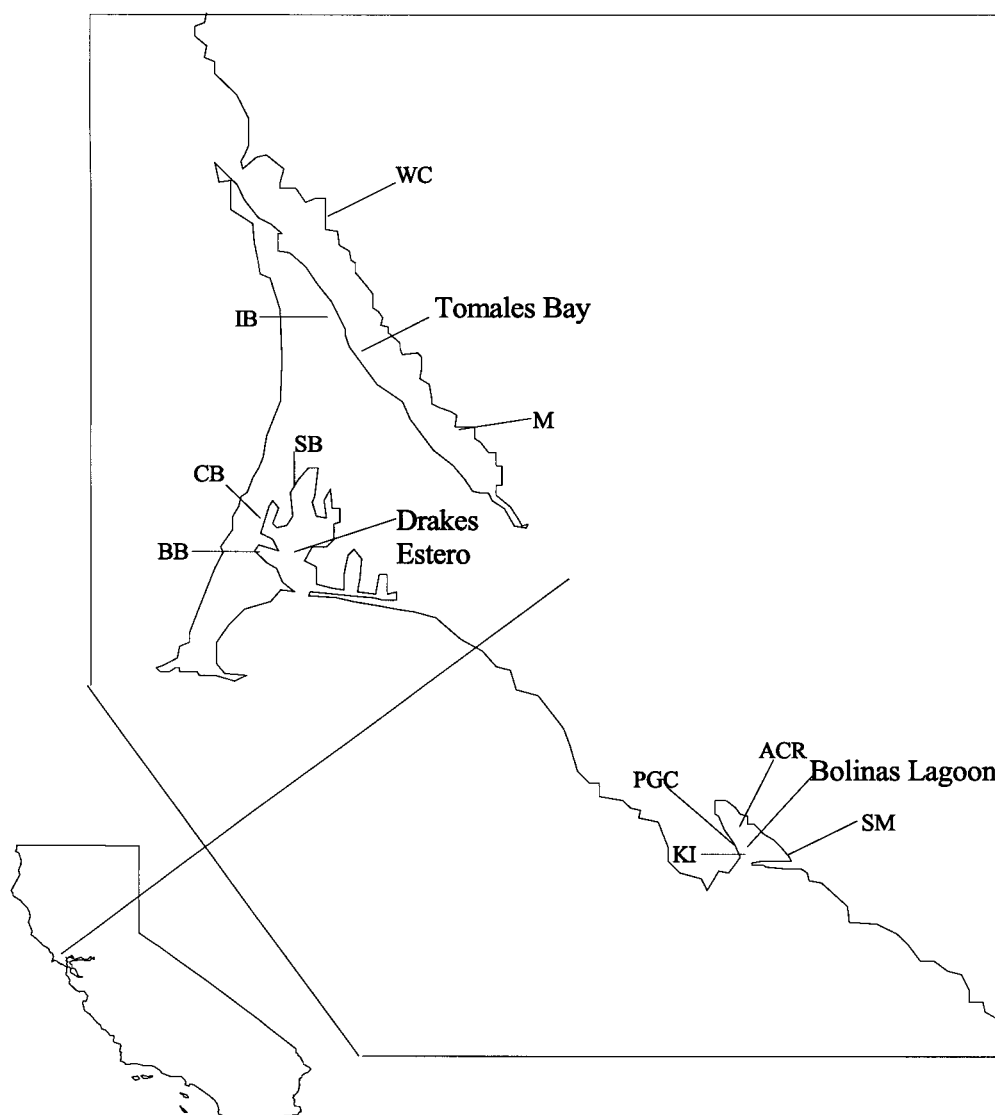
Figure 2. Close-up of northern California marshes where *Batillaria* and *Cerithidea* are sympatric. Specific sites within bays that are mentioned in text are marked: WC = Walker Creek, M = Millerton, IB = Indian Bay, SB = Schooner Bay, CB = Creamery Bay, BB = Barries Bay, KI = Kent Island, PGC = Pine Gultch Creek, ACR = Audobon Canyon Ranch, SM = Southern Marsh.

example, exhibited an average *increase* of 2.7% over the period from 1991 to 1998. San Diego Bay populations of *Cerithidea* decreased 4.3% from 1976 to 1998. These data provide the only quantitative measurements of allopatric *Cerithidea* population fluctuations available. This trend of relative stability in *Cerithidea* populations coupled with the moderate to high densities of *Cerithidea* at other allopatric sites, sharply contrasts the declines measured in *Cerithidea* where it occurs with *Batillaria*.

Drakes Estero contains predominantly *Cerithidea*, but a few populations of *Batillaria* exist in Schooner's Bay on the bank of the primary channel near Johnson's Oyster Farm and in the few marsh pannes immediately to the northwest of the facility. In this area of Schooner's Bay I found two pannes with densities of small individuals of both species greater than $3000/m^2$. Two other pannes contained sympatric populations, but these were composed predominantly of *Cerithidea*. In all, the total area of sympatry was approximately $80\,m^2$.

Table 1. Summary of *Crassostrea gigas* plantings for Pacific coast of North America (Washington and Oregon listings are not exhaustive) and the status of both *Cerithidea californica* and *Batillaria attramentaria*. Sites are listed in order from north to south.

Site	Location within site	Date *C. gigas* introduced	*Batillaria* present? If yes, date confirmed	*Batillaria* densities	*Cerithidea* ever present?	*Cerithidea* still present?	Notes
Puget Sound		1902 (Galtsoff 1932)					
	Boundary Bay		1962 (Carlton 1979)	Med	No	No	I sampled southeastern end of bay at Drayton's Harbor
	Samish Bay (Bellingham)	1905* (Galtsoff 1932)	1924 (Kincaid 1947)	Med–high	No	No	*First commercial planting in the US, however earlier experimental and rogue trials occurred as early as 1875 (Barrett 1963)
	Padilla Bay	1932 (Galtsoff 1932)	1960 (Duggan 1963)	Med–high	No	No	All 3 Puget Sound areas, esp. Padilla and Samish are contiguous and could be considered the same, however I have kept the distinction here as it often appears in the literature
Grays Harbor		1932 (Galtsoff 1932)	No		No	No	MacDonald 1969 also found no *Batillaria*
Willapa Bay		1928–29 (Galtsoff 1932)	No		No	No	Carlton 1992 also reports no *Batillaria*
Tillamook Bay		~1934 (C. Harris, pers. comm.; Robinson 1997)	No		No	No	Spat imported from Japan only until mid 40s when began using Washington stocks
Netarts Bay		~1934 (Robinson 1997)	No		No	No	
Yaquina Bay		1934 (Robinson 1997)	No		No	No	
Coos Bay		1934 (Carlton 1995)	No		No	No	Carlton 1995 and MacDonald 1969 support that no *Batillaria* present
Humboldt Bay		1953 (Barrett 1963)	No		No	No	Active decision to exclude Pacific oysters (at least initially); MacDonald 1969 also found no *Batillaria*

Location	Sub-location	C. gigas	Batillaria	Tidal	Native oysters	Snail	Notes
Bodega Harbor		1932 (Bonnot 1935)	No		Yes	No*	*Extinct by 1963 (Carlton 1976)
Tomales Bay			1941 (Carlton 1992)				W side of Tomales had been all native oyster cultivation (CA Department Public Health 1951)
	Walker Crk.	1939 (Barrett 1963)	1964 (MacDonald 1969)	Med–high	?	No	
	Millerton	1928 (Barrett 1963)	1964 (MacDonald 1969)	Low–med	Yes	Rare	
	West Bank-N of Inverness	Never (CA Department of Public Health 1951)	1996 (pers. obs.)	Low–very high	Yes	Rare	
	West Bank-S of Inverness	Never (CA Department of Public Health 1951)	1996 (pers. obs.)*		No (Dickson 1936)	No	*Only a small handful of *Batillaria* seen in this entire area
Drakes Estero		1932 (Bonnot 1935)					The other two bays of Drakes – Limantour and Home Bays – were planted with oysters by at least 1951, but it is uncertain if they were *C. gigas* (CA Department of Public Health 1951); I did not search these bays for logistical reasons
	Schooner Bay		1996 (pers. obs.)	Low–med	Yes	Yes	
	Creamery Bay		No		Yes	Yes	
	Barries Bay		No		?	No	
Bolinas Lagoon		1955 (Barrett 1963; B. Johnson, pers. comm.)	1955 – only year *C. gigas* imported (B. Johnson, pers. comm.)	Med–high	Yes	Yes	
San Francisco Bay		1932–33* (Barrett 1963)	No**		Yes	Yes	*C. gigas* used little because Eastern oyster failure convinced fishermen bay was poor habitat; **Reference by McClean to *Batillaria* in SF is apparently incorrect – see text and Carlton 1979

Table 1. Continued.

Site	Location within site	Date *C. gigas* introduced	*Batillaria* present? If yes, date confirmed	*Batillaria* densities	*Cerithidea* ever present?	*Cerithidea* still present?	Notes
Elkhorn Slough		1929 (Bonnot 1935)	1951 (Carlton 1992)	Very high	Yes?	No	In 1930 Bonnot (1935) found *Batillaria* here in imported seed oyster while screening for pests
Morro Bay		1932 (Bonnot 1935)	No*		Yes	Yes	*CAS has specimens from 1965 but likely from interception of incoming oysters not field
Mugu Lagoon		1932 (Barrett 1963)	No		Yes	Yes	
Anahiem Bay		1932 (Barrett 1963)	No		Yes	Yes (Lafferty 1991)	
Newport Bay		1932 (Barrett 1963)	No		Yes	Yes	
Catalina Is.		Early 60s (Barrett 1963)	No		No	No (Lafferty, pers. comm.)	These last 2 sites extremely experimental; planted in very small numbers only once
Pt. Loma		Early 60s (Barrett 1963)	No		Yes*	Yes*	*Difficult to determine the exact site of 'Pt. Loma' to which Barrett refers, but both Mission Bay to the N and San Diego Bay to the S have *Cerithidea*

Key to *Batillaria* densities: Low = <100/m^2; Med = 100–500/m^2; High = 501–5000/m^2; Very high = 5000+/m^2.

Bays in bold represent experimental southern CA oyster plantings. These bays mostly were either considered too polluted, or oysters exhibited unsatisfactory growth for extensive plantings.

Note: While British Columbia (with the exception of Boundary Bay) is not included on this chart, *C. gigas* has been planted there in the Strait of Georgia and *Batillaria* has been documented (Hanna 1966; Carlton 1979).

Notably, experiments were run with snails from populations at Montague Harbor, Galiano Island (Yamada 1982).

Table 2. Summary of snail species found in surveyed bays along Pacific coast of North America. Bays used are listed as 'sites' in Table 1, with the addition of Carpinteria salt marsh. Specific subbays of Puget Sound were counted as separate sites for this synopsis. Also, both Mission and San Diego Bays were surveyed for the listing that corresponds to Point Loma in Table 1.

Species found	No. of sites
Both	3
Only *Batillaria*	4
Only *Cerithidea*	8
Neither	9
Total	24
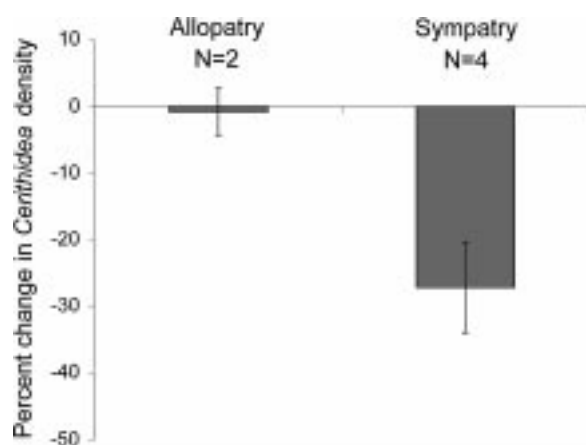
Figure 3. Average change in *Cerithidea* densities (± 1 standard error) in four sympatric populations in Bolinas Lagoon and the two allopatric *Cerithidea* populations (Carpinteria salt marsh and San Diego Bay) that could be quantitatively tracked through time. The difference between the groups is significant ($P < 0.03$).

Allopatric *Cerithidea* populations were found throughout the rest of the northern end of Schooner's Bay with densities up to 1900/m^2. Two of the other bays comprising Drakes Estero were searched and yielded no further sympatric populations. In Creamery Bay *Cerithidea* ranged from < 1/m^2 in open areas on the west bank to 1900/m^2 in some of the higher marsh pannes on the east side. Lower *Cerithidea* densities on the west side of Creamery Bay may be attributable to habitat degradation from cow trampling and excrement. The other bay of Drakes Estero searched, Barries Bay, did not have either snail species despite some small, yet visibly suitable marsh habitat.

In Tomales Bay *Batillaria* is far more abundant than *Cerithidea*, which is currently found at only two small sites. On the west bank, Indian Bay had approximately six marsh pannes comprising a total area of 50 m^2 that contained comparable numbers of both species. One panne at this site contained only *Batillaria* at a density greater that 8000/m^2. Historically, *Cerithidea* had been reported from other sites along the west bank of Tomales (Dickson 1936; Carlton 1976). In fact, Dickson (1936) reports that in the marsh at and north of Inverness, '*Cerithidea* can be seen by the thousands'. With the exception of Indian Bay the west bank now contains only *Batillaria* in isolated populations. The only other Tomales Bay site with any *Cerithidea* was Millerton salt marsh on the east bank, where *Cerithidea* co-occurred in small numbers in an extremely restricted area with larger numbers of *Batillaria*. On a small point here, only three small pannes, the largest of which is < 4 m^2, contained both species (Table 3). A few *Cerithidea* were also found underneath and on pickleweed, *Salicornia virginica*, directly adjacent to these pannes. Given the densities of these sympatric *Cerithidea* and *Batillaria* populations and approximate area of the pannes, I estimate the total number of *Cerithidea* in the pannes and in the underlying vegetation at Millerton Marsh currently to be no greater than 500 individuals. As recently as 1971–1972 Whitlatch and Obrebski (1980) had utilized two sympatric populations of *Batillaria* and *Cerithidea* at Millerton for experiments. They even discuss the presence of at least one allopatric *Cerithidea* population in a marsh panne. The marsh area to the east of the point (behind the dike), which includes the two previously sympatric population sites used by Whitlatch and Obrebski (1980), currently contain only *Batillaria*. The final site intensively sampled within Tomales Bay was Walker Creek, where only *Batillaria* was found in densities ranging from 314/m^2 on the mud flats along the edge of the main bay, to 905/m^2 on banks of small creek channels higher in the marsh.

Bays with only allopatric populations

The majority of marshes in California contain only allopatric populations of snails, including the largest,

Table 3. Densities per square meter (and standard error) of both snail species in sympatric populations in three small marsh pannes at Millerton Marsh, Tomales Bay, California. Marsh pannes are listed from smallest to largest.

	Cerithidea	*Batillaria*
Panne 1 $N = 3$	88 (22.7)	113 (54.6)
Panne 2 $N = 7$	16 (7.6)	143 (18.4)
Panne 3 $N = 11$	7 (2.9)	88 (8.9)

San Francisco Bay, which has no *Batillaria*. Although McLean (1960) made reference to a single *Batillaria* specimen from Sausalito, this specimen seems to have been an anomaly (Carlton 1979) and no others have since been found (Carlton 1979; J.E. Byers, pers. obs.). Pacific oysters were rarely cultivated in San Francisco Bay, primarily due to a consensus among fishermen that the prior failure of aquaculture with the Atlantic oyster, *Crassostrea virginica*, indicated the bay was not suited for raising oysters (Barrett 1963). San Francisco Bay, however, has very few *Cerithidea* populations. *Cerithidea* is extinct in all northern areas of the bay (Carlton 1993; J.E. Byers, pers. obs.), and is scarce in central and south bay areas, in part due to competition with another exotic snail invader, the Atlantic American *Ilyanassa obsoleta*, introduced with importation of *Crassostrea virginica* (Race 1982). In small, elevated marsh pannes at Hayward Shoreline Park in the southeast bay, one of the only sites I was able to find *Cerithidea* in the bay, I measured *Cerithidea* at densities of 830/m^2.

Bays with only allopatric populations of *Batillaria* were found both to the north and south of bays with sympatric populations. Notably, Elkhorn Slough, an exclusive site for *Batillaria*, is the southernmost limit of *Batillaria*'s North American distribution. Elkhorn contains the highest population densities observed for *Batillaria*, ranging from 8000–10,000/m^2 in certain areas of the slough. Although the historical presence of *Cerithidea* in Elkhorn has not been definitively ascertained, evidence seems to indicate it once lived there (Appendix 2).

Areas of snail absence

Areas north of Tomales Bay, California were devoid of both species for hundreds of kilometers. Bodega Harbor (see Figure 1) was the historical northern range limit for *Cerithidea*, but the population of that bay was apparently entirely extinguished around 1963 due to extensive road construction (Carlton 1976). My observations in 1997 confirmed that this extinction appears absolute, i.e. a small number of snails did not survive the disturbance, evade detection, and subsequently repopulate the bay.

Sizable populations of *Batillaria* were found in northern Puget Sound (Washington), specifically Padilla and Boundary Bays (Figure 1). Several bays between Tomales Bay and Puget Sound, however, including, Humboldt Bay, CA, Coos Bay, OR, Yaquina Bay, OR, Tillamook Bay, OR, Grays Harbor,

WA, and Willapa Bay, WA, lacked *Batillaria* despite moderate to high importation of Pacific oysters. MacDonald (1969) and Carlton (1979, 1995) also sampled some of these bays and did not find *Batillaria*. Why *Batillaria* has failed to yet become established in these bays is an issue ripe for further research.

Average coexistence time of Batillaria *and* Cerithidea

C. gigas was first introduced to Millerton Point in Tomales Bay in 1928 (Table 1), thus establishing the earliest possible date for *Batillaria*'s inoculation in Tomales Bay. Museum specimens at the California Academy of Sciences (CAS) verify the exotic within Tomales by 1941 (Carlton 1979). Thus, with the exception of Indian Beach noted above and the essentially negligible *Cerithidea* numbers at Millerton Marsh in 1996, the range of coexistence time for the two species in the majority of Tomales Bay was 55–68 years. The persistence of *Cerithidea* at Indian Beach on the West bank may be attributable to a later arrival of *Batillaria* to that side of the bay, as only native oysters were historically planted on the west bank (California Department of Public Health 1951).

The introduction of *Batillaria* to Bolinas Lagoon appears to be definitive, as *C. gigas* was only planted one year – 1955 (Barrett 1963; B. Johnson of Johnson's Oyster Farm, pers. comm.). Thus, *Batillaria* and *Cerithidea* have coexisted in Bolinas for 44 years now.

My detection of *Batillaria* in Drakes Estero in 1996 represents the first documentation of its presence there. *C. gigas* was introduced to Drakes Estero in 1932 (Table 1), thus the maximum time for the existence of *Batillaria* in this bay is now 67 years. *Batillaria* were probably present in Drakes Estero before 1955 because oysters used to seed Bolinas Lagoon, which presumably introduced *Batillaria* there, came from the oyster farm in Drakes Estero (Barrett 1963; B. Johnson, pers. comm.). The population of *Batillaria* in Drakes, however, remains very restricted – likely a major reason for its apparent absence from previous surveys. Driscoll (1972) while looking for both *Batillaria* and *Cerithidea*, sampled Drakes Estero in what appears to be the exact spot where I report they are presently found, yet he reported only *Cerithidea*. Likewise, Lafferty (1991) sampled Drakes Estero near the oyster farm and reported only *Cerithidea*.

A dozen of the *Batillaria* I found in Drakes were > 50 mm in length, including the largest one ever

recorded in its native or introduced range – 54 mm. A snail of this size surpasses the theoretical maximum size predicted by Whitlatch (1974) for Tomales Bay *Batillaria*, and far surpasses that of Yamada (1982) for British Columbia populations. Additionally, based on size–age relationship produced by Whitlatch (1974), *Batillaria* of this size are > 10 years old. Since *Batillaria* is introduced with oyster imports into bays as eggs or extremely small snails lodged in sediment, the presence of snails of this size in Drakes suggests their presence for at least 10 years before their discovery three years ago. Thus the estimated time of coexistence of *Cerithidea* and *Batillaria* in the extremely limited area of Schooner Bay in Drakes Estero is at minimum 13 years, and most likely 44–67 years. The reason for *Batillaria*'s limited distribution in Drakes Estero, however, is unknown.

The presence of *Cerithidea* in some samples of Elkhorn Slough (Cooper 1850; Carpenter 1857) and its absence in others (MacGinitie 1935; McDonald 1969) suggest that *Cerithidea* may have originally occurred there in low densities or in isolated areas. *Cerithidea* in Elkhorn Slough was likely absent by MacDonald's sampling in 1964; however, its absence in his samples is not absolute proof of its absence in Elkhorn given the substantial size of the estuary and the small area actually sampled (Moss Landing area only). Nevertheless, given the introduction of *C. gigas* in 1929, and assuming *Cerithidea* did reside in Elkhorn and went extinct the year MacDonald sampled the area, the maximum coexistence time for *Batillaria* and *Cerithidea* is 35 years. If, as mentioned above, *Cerithidea* inhabited Elkhorn in low densities or restricted areas, its extinction would likely have been more rapid, possibly leading to this lower value of maximum coexistence time compared to other lagoons. Additionally, *Cerithidea*'s extirpation may have been accelerated due to massive hydrographic and habitat changes in Elkhorn Slough during this time (Elkhorn Slough Wetland Management Plan 1989).

In sum, in the four marshes *Batillaria* has invaded where *Cerithidea* is found (or is thought to have been found) *Cerithidea* is extinct, or nearly extinct, in two; has declined > 25% in the past four years in the third; and has not been impacted measurably in the fourth, perhaps due to small numbers of *Batillaria* that do not substantially impact local *Cerithidea* populations (Table 4). Qualitatively, the trends in these *Cerithidea* populations are very different from allopatric *Cerithidea* populations where densities are moderate to high. Certainly none of

Table 4. Contingency table summarizing the status of *Cerithidea* in bays where it does or did exist as a function of the presence or absence of *Batillaria*. Allopatric *Cerithidea* populations were considered healthy with densities > 300/m^2. Two bays with allopatric *Cerithidea* populations (Carpinteria marsh and San Diego Bay), also had adequate baseline data to determine that populations appear stable (i.e., < 0.2% annual decline) – see text for more information.

	Batillaria	
	Present	Absent
Cerithidea		
Declining or extinct	3	2[a]
Healthy (stable)	1	7[b]

[a]In both of these cases an extinction agent has been identified. In Bodega Harbor the extinction of *Cerithidea* was directly attributable to a major disturbance – road construction (Carlton 1976). In San Francisco Bay although *Cerithidea* density is moderate in certain areas, its overall distribution has been dramatically reduced. The decline of *Cerithidea* in San Francisco Bay has been mostly attributed to another introduced species, the East coast mud snail, *Ilyanassa obsoleta* (Race 1982), but bayshore development has likely played a role as well (J.T. Carlton, pers. comm.).

[b]This number conservatively reflects only the areas documented in this study; many other sites exist where *Batillaria* is absent and *Cerithidea* populations appear healthy.

these allopatric *Cerithidea* populations have experienced density reductions as extreme as those of sympatric *Cerithidea* populations in Elkhorn and Tomales. The two quantitative measurements that were feasible in marshes with only *Cerithidea* also reflect greater stability by *Cerithidea* populations in the absence of *Batillaria*.

Understanding and implications of Batillaria–Cerithidea *interactions*

Previous studies suggest that *Batillaria* and *Cerithidea* compete exploitatively for shared diatom food resources (Whitlatch 1974; Whitlatch and Obrebski 1980; McDermott 1996). Recent experimental work performed in sympatric areas of Bolinas Lagoon has shown that exploitative competition occurs between the species, and provides a sufficient explanation for the displacement of *Cerithidea* populations (Byers 2000). Specifically, *Batillaria* achieves superiority in competitive interactions by converting shared, yet often limiting, diatom resources more efficiently than *Cerithidea*. Furthermore, *Batillaria* exhibits no trade-offs in its

ability to compete at any level of resource availability – an advantage it maintained consistently through three years of competition studies (Byers 2000). The nearly complete overlap of microhabitat and resource use by *Batillaria* and *Cerithidea* (Byers, in press) also suggests that spatial refuges for *Cerithidea* may not exist to ameliorate *Batillaria*'s competitive impact. Competition therefore may help to explain the seeming lack of persistent coexistence between the snails in Elkhorn, Bolinas, and Tomales Bays.

The extinction and endangerment of all the remaining vestiges of *Cerithidea* in northern California (possibly excepting Drakes Estero) is of particular concern in light of recent work that provides evidence of subspecies distinctions (Taylor 1981; Petryk 1998). Taylor (1981) cites subspecies distinctions between northern (San Francisco Bay and north) and southern (Morro Bay and south) *Cerithidea* and claimed to be able to distinguish them on morphological grounds (J.T. Carlton, pers. comm.). More recently, Petryk (1998) using cytochrome oxidase I sequences analyzed mitochondrial 12S rRNA from northern (Tomales Bay and San Francisco Bay) and southern (San Diego Bay) populations of *C. californica*. She reveals that gene flow from south to north appears absent (or extremely restricted), providing evidence that snail populations in the two regions are isolated and likely distinct. Given the loss of some northern *Cerithidea* populations and the likely endangerment of others, it seems probable that a distinct race may be lost.

Southern populations of *Cerithidea* do not appear endangered by *Batillaria* both because of the large number of marshes with *Cerithidea* and because *Batillaria* is not present in any marsh south of Elkhorn Slough. Several introductions of *C. gigas* have been made to these areas (Table 1), however, with the exception of Morro Bay, most oyster plantings were experimental, and therefore small and short lived (typically just one year) (Barrett 1963). (I located specimens of *Batillaria* at the California Academy of Sciences collected in Morro Bay in 1965, but these few specimens were likely intercepted from an incoming oyster shipment and not field collections (J. Wilkins collector 1/17/65, no cataloguing number given with specimens).)

Batillaria's absence in southern habitats in North America is not likely due to cold temperature preferences as water temperatures in marsh pannes in northern California reach $> 40\,^\circ$C on hot summer days. Furthermore, *Batillaria* is found at least as far south as Hong Kong (22° N) in its native Asian range (Wells 1983). The lack of *Batillaria* in these southern California marshes, therefore, seems due to either the lack of sufficient (or any) propagule pressure of short-lived experimentation with non-indigenous oyster plantings, or to an increased resistance to invasion through increased competitive abilities in *Cerithidea* in areas more central to its distribution.

In sum, this study documents the decrease of a native species in the presence of an ecologically similar exotic species. When combined with knowledge of explicit interactions between the exotic and native species (Byers 2000), this documentation provides a rare example of a decline in a native species *mechanistically* attributed to an exotic species (see also Race 1982; Brenchley and Carlton 1983; Settle and Wilson 1990; Petren and Case 1996). The long duration of *Batillaria*'s exclusion of *Cerithidea*, e.g. 55–70 years in most of Tomales Bay, however, underscores that time to local extinction may not be rapid. Time lags in the proliferation of non-indigenous species have often been noted (Cousens and Mortimer 1995; Hobbs and Humphries 1995; Kowarik 1995; Hengeveld 1988; Crooks and Soulé 1999). Thus, the value of examining impacts on native fauna by exotic species over short time periods, as is common in most risk assessment and species removal prioritizations, is questionable. Instead, for successful mitigation of non-indigenous species we may need to act in anticipation of the exotic species' potential interactions with native analogues and not wait until impact becomes detectable to intervene.

Appendix 1: Specific locations of sympatric populations of *Cerithidea* and *Batillaria*

Drakes Estero

Follow Sir Francis Drake Highway north and then west toward Point Reyes lighthouse. Just over 2.5 miles past Pierce Point junction turn left down dirt road to Johnson's oyster farm. Go 2/3 mile and park at buildings. Walk out into bay along the edge of the marsh vegetation, heading due west about 200 m. Sympatric populations are in pannes just to the north in pickleweed.

Tomales Bay

A. *Indian Bay*
Follow Sir Francis Drake Highway north along the west bank of Tomales Bay. Continue north on Pierce Point Road at junction 2 miles north of Inverness. One mile later take road on right to Hearts Desire Beach (State Park). Take nature trail north 1 mile to arrive at Indian Beach (currently marked with a teepee in the sand). A small creek feeds a larger brackish water pool west of the marsh area. Toward this pool and to the northern edge of the marsh are 5–6 sympatric populations.

B. *Millerton Marsh*
Follow Highway 1 north of Point Reyes station along the east side of Tomales Bay for 4 miles. Take dirt parking lot on left for Millerton Point. Walk down to water and head south along edge of small embayment to the next small point sticking out slightly into the bay. An earthen dike partly divides the salt marsh to the east. A tidal creek feeds back into the marsh behind the dike just to the south of this point. Sympatric populations are found on this point in three pannes on the bay side of the dike. One is out near tip of point, a second more central, and the third is north and closer to the dike. Figure 2 in Whitlatch (1972) is a good reference schematic of this area.

Bolinas Lagoon (South Marsh)

Travel approximately 1 mile north of Stinson Beach on Highway 1 to dirt pullout at mile marker 13.32. This pullout is right at the northern edge of the marsh. Just below pullout walk into marsh via the primary channel that runs into it. About 30 m into the marsh one sympatric panne population is on the left, 10 m back from top of channel. Several more on the right.

Appendix 2: Evidence for the previous existence of *Cerithidea* in Elkhorn Slough, Monterey County, California

Four lines of evidence suggest *Cerithidea* may have previously resided in Elkhorn. First from the literature, Carpenter (1857) referenced *Cerithidea* specimens collected by T. Nuttall in 1834–1835 in his species list for the Monterey area. Cooper (1870) seemingly repeats reference to these specimens by noting *Cerithidea* from the Nuttall collection from the Salinas River (Monterey Co.) Secondly, several museum specimens of Elkhorn *Cerithidea* exist, although I was unable to independently confirm the exact collection locations of the specimens. Specifically, I examined four *Cerithidea* specimens at the California Academy of Sciences (CAS) that were collected at the Southern Pacific 'sinking area North of Elkhorn Slough' (C.N. Beard, Fresno State College #38530). No sampling date was included with these specimens, however, the shells are thought to have been collected in the 1940s (J.T. Carlton, pers. comm.). I also examined two *Cerithidea* specimens at CAS (#29320) of more nebulous origin marked only 'Monterey Bay (Hopkins Marine Station)'. Thirdly, possible archaeological records exist in Indian shell midden at Elkhorn Slough (J.T. Carlton, pers. comm. referencing Don Howard at Monterey Archaeological Society). Finally, initial results from enclosure experiments indicate that *Cerithidea* (from Bolinas Lagoon) is able to grow and reproduce in Elkhorn Slough when *Batillaria* densities are greatly or totally reduced (Byers, unpublished data). (These data are drawn from *Cerithidea* reintroduced only for caged experiments, I have not reestablished natural populations.) Since Elkhorn appears currently suitable for *Cerithidea*, the species seems to have had at least the potential to exist there historically.

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