# Recent biological invasion may hasten invasional meltdown by accelerating historical introductions

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**Biological invasions are rapidly producing planet-wide changes in biodiversity and ecosystem function. In coastal waters of the U.S., >500 invaders have become established, and new introductions continue at an increasing rate. Although most species have little impact on native communities, some initially benign introductions may occasionally turn into damaging invasions, although such introductions are rarely documented. Here, I demonstrate that a recently introduced crab has resulted in the rapid spread and increase of an introduced bivalve that had been rare in the system for nearly 50 yr. This increase has occurred through the positive indirect effects of predation by the introduced crab on native bivalves. I used field and laboratory experiments to show that the mechanism is size-specific predation interacting with the different reproductive life histories of the native (protandrous hermaphrodite) and the introduced (dioecious) bivalves. These results suggest that positive interactions among the hundreds of introduced species that are accumulating in coastal systems could result in the rapid transformation of previously benign introductions into aggressively expanding invasions. Even if future management efforts reduce the number of new introductions, given the large number of species already present, there is a high potential for positive interactions to produce many future management problems. Given that invasional meltdown is now being documented in natural systems, I suggest that coastal systems may be closer to this threshold than currently believed.**

nonindigenous | predation | indirect effects | green crabs

The impacts of biological invasions now rank among the most pervasive threats to native ecosystems and human economies (1–5). Nonnative introduced species are accumulating in coastal systems worldwide at an increasing rate, and >500 species have become established in the coastal waters of the U.S (6–9). The majority of these introduced species are believed to have minimal impact on native species and ecosystem processes (10); however, some species may change from a low-impact introduction to an acute management threat. The rates at which these transformations occur and how they take place have been almost entirely unknown for any system until now. In this study, I demonstrate that transformation from a benign introduction to an expanding invasion can result from positive interactions among invaders. Given the large number of introduced species in coastal systems, there is an increasing likelihood that such transformations due to positive interactions among invaders could produce a positive feedback cycle similar to the invasional meltdown scenario now being documented in other natural systems (11–13).

Unlike early models of biological invasions that emphasized the deterrent effects of species diversity on subsequent invasions (14), modern views of invasion now include positive interactions as a force influencing invasion success (11–13, 15). This view parallels the increasing recognition of the importance of positive interactions, particularly in marine habitats, where the emphasis had been on negative interactions such as predation and competition (16, 17). Most models that discuss positive interactions among introduced species typically fall into one of three categories (12, 15). The first category suggests that, as the number of introduced species increases, this disturbance destabilizes native populations and makes the system more easily invaded. A second category, which is the most widely discussed, posits that early invaders produce a qualitative change in the system that facilitates the establishment and spread of subsequent invaders. A third category contends that more recent invaders can produce changes in the system that can result in the acceleration and expansion of an earlier invasion. This third category typically focuses on the direct effects of a new introduction, such as the introduction of a new specialist pollinator, but rarely have the direct effects of recent introductions on older introductions been investigated at the population level. What has not been seriously discussed is the potential for the indirect effects of positive interactions among invaders. The increasing number of new invaders and the large number of older introductions strongly suggest that positive indirect interactions among invaders are likely to become increasingly common.

Here, I demonstrate at the population level that a recent invader has rapidly turned a historically benign introduction into a quickly expanding invasion. This transformation has resulted from the positive indirect effects of predation mediated through the presence of a third prey species. A recently introduced crab, by preferentially consuming native clams, has rapidly accelerated the invasion of a clam that was introduced nearly 50 yr earlier and had for decades maintained a very restricted and nearly static distribution. These results demonstrate an important mechanism by which recent introductions can rapidly transform older, benign introductions into aggressive invaders.

## Methods

**Site and Invasion History.** I have documented a dramatic increase in the distribution and abundance of introduced eastern gem clams *Gemma gemma*, which are native to the eastern U.S., in Bodega Harbor, CA (38° 19′ N, 123° 04′ W), where they have been established since at least the 1960s and likely earlier (18–20). Bodega Harbor is a largely marine embayment with mostly coarse, sandy mud substrate and limited, seasonal freshwater input that influences salinity only during winter storm events. Estimated flushing times are on the order of days (J. Largier, personal communication), and water temperatures within the bay are typically within 5–10° of ocean surface waters. *G. gemma* was first introduced to the western U.S. in the late 1800s by means of the oyster trade and is now established at several sites between Humboldt Bay and Monterey Bay in central California, including the current study site (20). I show that the rapid increase in *G. gemma* is the result of the introduction of the European green crab (*Carcinus maenas*), which was first introduced to the western U.S. in San Francisco Bay around 1989. It became established outside of San Francisco Bay in nearby estuaries including Bodega Harbor in 1994 and is now common

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in bays and estuaries from Monterey Bay, CA, to Gray's Harbor, WA (21).

**Long-Term Patterns.** At this site, *G. gemma* cooccurs intertidally with two small native bivalves, *Nutricola tantilla* and *Nutricola confusa* (henceforth *Nutricola* spp. for both species), which are common in western U.S. bays and estuaries. The abundance and distribution of the ecologically similar native *Nutricola* spp. and the introduced *G. gemma*, as well as >25 species of infauna and epifauna, have been tracked over a 20-yr period starting in 1982, excluding a 5-yr period from 1988–1993 (21, 22). Detailed data on the distribution of infaunal species are also available for several years during the early 1970s (23). Densities of clams and other infaunal species were estimated at each of five sites in Bodega Harbor from replicated infaunal cores (10-cm diameter $\times$ 5-cm depth) collected from four tidal heights (five cores per tidal height) at each site. Relative densities of green crabs and five other native crabs were estimated from annually replicated pitfall traps collected from the same four tidal heights (three traps per tidal height) at two of the five sites. Tests of association among green crabs and clam populations used Spearman nonparametric correlation.

**Predation Experiments.** I tested for the differential effects of green crab predation on both native and introduced clams in laboratory trials. Crabs were offered equal numbers (25 each) of *G. gemma* and *N. confusa* in small containers (25-cm diameter) filled with 2 cm of defaunated sediment. Clams were placed in containers several hours before adding crabs to allow them to bury and position themselves in the sediment. Crabs were allowed to feed for 6 hr and were then removed from containers and the remaining clams were counted. Survival was analyzed by using the square-root transformed number of clams per treatment, with treatment as a fixed factor (clam species, two levels).

**Competition Experiments.** To measure the competitive effects of the native clam on the invasive, I conducted two field experiments in which native and introduced clams were transplanted into the sediment in containers [7.5-cm diameter poly(vinyl chloride) pipe with 1-mm mesh sides and tops] in the following treatments. For experiment one, I used eight replicate containers for each of five low- to medium-density treatments: (*i*) 10 *G. gemma*, (*ii*) 10 *G. gemma* plus 10 *N. confusa*, (*iii*) 20 *G. gemma*, (*iv*) 20 *G. gemma* plus 20 *N. confusa*, and (*v*) 40 *G. gemma* (40 per container equals $\approx$4,000 per $m^2$). Clams were allowed to grow in field enclosures under these treatment conditions for 5 mo and then harvested. For experiment two, I used eight replicate containers for each of the three medium- to high-density treatments: (*i*) 40 *G. gemma*, (*ii*) 40 *G. gemma* plus 40 *N. confusa*, and (*iii*) 80 *G. gemma*. Clams in this second experiment were harvested after 4 mo in the field. Note that treatment *v* in the first experiment and treatment *i* in the second experiment are the same, which permitted comparisons between experiments. For both experiments, replicates were randomly assigned a location in a rectangular field array with containers 1 m apart. Clams for both experiments were labeled with calcein before placement in the field, so new shell growth was visualized under an epifluorescence microscope and quantified for individual clams by using METAMORPH image analysis software. Also, for both experiments, I analyzed growth data with a nested univariate ANOVA, with treatment (five levels for experiment one, three levels for experiment two) as a fixed factor and field enclosures (eight replicates in both experiments) as a random factor nested within treatment. Mean growth values were used as the dependent variable and were calculated for each enclosure from log-transformed growth increments measured for individual clams. I also analyzed survival data with univariate ANOVA with treatments (five levels for experiment one, three levels for experiment two) as a fixed factor and the square-root transformed number of clams surviving per container as the independent variable. ANOVA was conducted with the General Linear Module procedure (PROC GLM) in SAS 8.02 (SAS Institute, Cary, NC).

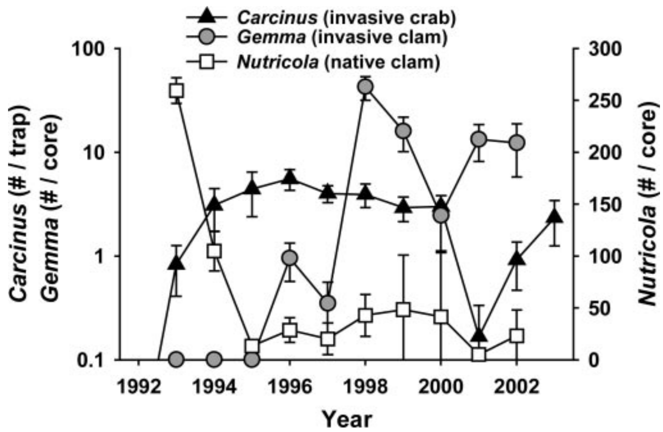


**Fig. 1.** Plot of the abundance of native clams (*Nutricola* spp.), invasive clams (*G. gemma*), and invasive European green crabs (*Carcinus maenas*) showing changes in abundance of the clams after the invasion of green crabs during 1993–1994. Each point represents the total for all transects for one site for that year, and error bars represent 1 SEM.

**Extrinsic Factors.** I investigated other factors that might explain the rapid acceleration of the *G. gemma* in Bodega Harbor after nearly 50 yr of stasis. The site in Bodega Harbor that was historically occupied by *G. gemma* was also the location of the only significant freshwater input, and *G. gemma* is more resistant to variable salinity than *Nutricola* spp. Thus, interannual cycles in rainfall, water, and air temperature might have contributed to changing environmental conditions that could have triggered the *G. gemma* expansion. Bodega Marine Laboratory is a National Weather Service reporting station, with rainfall records extending back to 1968 and air temperature records back to 1970. Sea surface temperatures, which are now part of the National Data Buoy Center network, extend back to 1988. I tested for patterns of association between native and introduced clam abundance and minimum, maximum, and mean monthly sea surface temperatures, mean and minimum monthly low air temperatures, mean and maximum monthly high air temperatures, and mean and maximum monthly rainfall, as well as total annual rainfall.

## Results

**Long-Term Patterns.** Based on data sets that span nearly 30 yr at Bodega Harbor (21–23), *G. gemma* occurred at only one site in Bodega Harbor, since their introduction nearly a half-century earlier. By contrast, *Nutricola* spp. were widely distributed throughout Bodega Harbor and historically represented a large portion of the infaunal biomass, with densities exceeding 10,000 per $m^2$ (22–24). Given that these small bivalves generally live only 1–1.5 yr (25–28), this distribution has been maintained for $\approx$30–40 generations.

I found a remarkable and rapid increase in the abundance of *G. gemma* associated with the dramatic decline in the relative dominance of *Nutricola* spp. (Fig. 1). Previous work had documented that the decline in *Nutricola* spp. was the result of green crab predation (21). Not only has the abundance of *G. gemma* increased, but, since the declines of *Nutricola* spp. in 1996, *G. gemma* has rapidly expanded its distribution in Bodega Harbor. *G. gemma* now is found at all five long-term sampling sites and

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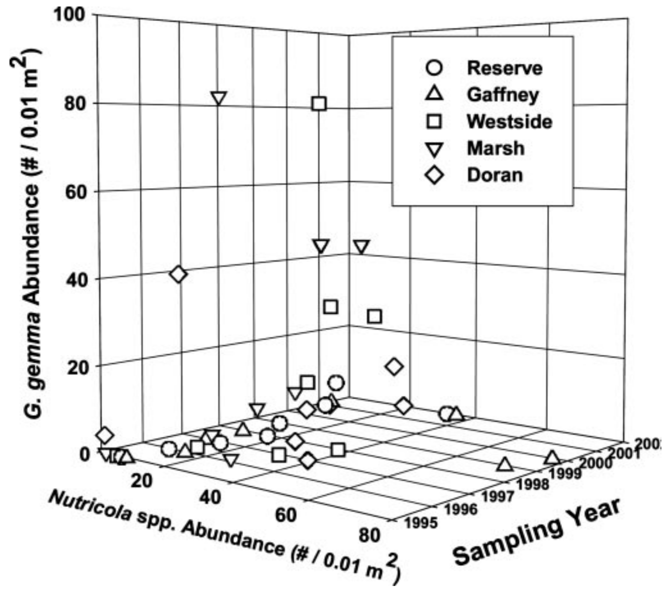


**Fig. 2.** Plot of the abundance of *Nutricola* spp. (*N. confusa* and *N. tantilla*) vs. *G. gemma* vs. sample year (1995–2002) for all study sites. Each point represents the mean clam abundance for each site and year measured at the upper tidal height where the highest densities of both natives and invaders cooccurred. Circle, Reserve; triangle, Gaffney; square, Westside; inverted triangle, Marsh; diamond, Doran).

at higher densities at sites where *Nutricola* spp. densities are lower (Fig. 2). Sites that are farthest from the Marsh Site (Gaffney and Reserve; see Fig. 2) have been colonized by *G. gemma* more recently, so densities there are lower for both *Nutricola* spp. and *G. gemma*. There is also unexplained variation in the time series (including significant declines in 2001 for both *Nutricola* spp. and *C. maenas* that are currently unaccounted for). These declines were unrelated to weather or other measured variables; however, the consequences of this atypical year were apparently short-lived.

**Predation Experiments.** In laboratory trials, I verified that green crabs strongly prefer to consume *Nutricola* spp. Green crabs ate *Nutricola* spp. (mean survival = 25.6 ± 6.5% SE) at more than twice the rate they consumed introduced *G. gemma* (mean survival 60 ± 6.6% SE), and this difference was highly significant ($F = 14.1$, df = 1, $P < 0.002$). This preference for *G. gemma* was largely driven by size differences, as demonstrated in other lab trials. Green crabs consumed larger adult *Nutricola* spp. at roughly three times the rate they consumed smaller juvenile *Nutricola* spp. that were the same size as adult *G. gemma* ($P < 0.01$).

**Competition Experiments.** The results from the first field competition experiment demonstrated that currently reduced densities of *Nutricola* spp. (typically now 1,000 per m$^2$) due to bay-wide predation by introduced green crabs no longer provide a competitive obstacle to expansion by *G. gemma*. At these lower densities, I found no evidence of interspecific competitive effects of *N. confusa* on *G. gemma* growth ($F = 0.78$, df = 4,35, $P > 0.54$) or *G. gemma* survival ($F = 1.17$, df = 4,34, $P > 0.33$) (Fig. 3*A*). *N. confusa* had much greater growth rates than *G. gemma* in all treatment combinations.

The results of the second field competition experiment, which included high densities equivalent to those before the green crab invasion, showed strong interspecific competitive effects of native *N. confusa* on growth of the introduced *G. gemma*. Growth of *G. gemma* was 52% less in the high interspecific

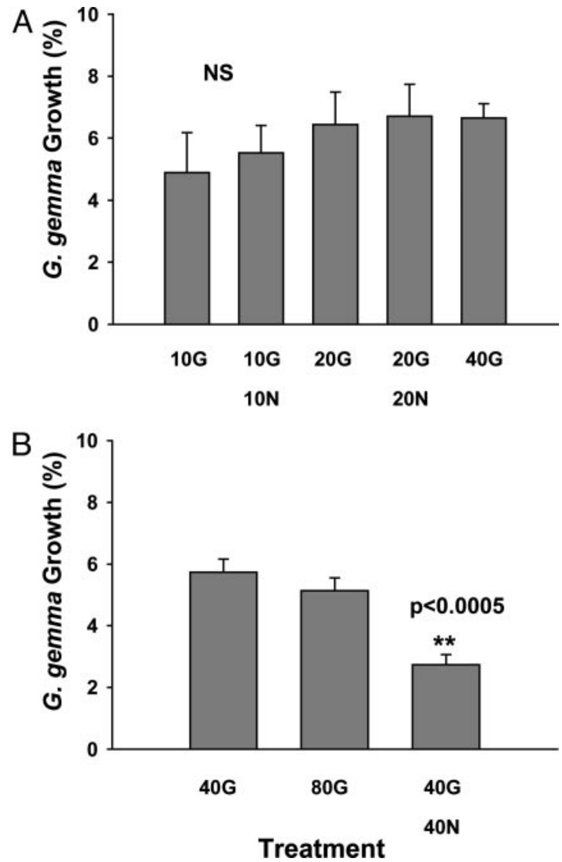


**Fig. 3.** The results of field experiments measuring interspecific competitive effects of *N. confusa* on growth and survival of *G. gemma*. (*A*) Plot of first field experiment examining interspecific competitive effects of *N. confusa* on *G. gemma* (see *Methods*) at low and medium densities. There were no significant differences in the growth of *G. gemma* when comparing low-density treatments with 20 *G. gemma* (20G) vs. 10 *G. gemma* and 10 *N. confusa* (10G plus 10N) or medium-density treatments with 40 *G. gemma* (40G) vs. 20 *G. gemma* and 20 *N. confusa* (20G plus 20N) (see *Competition Experiments* for statistical results). (*B*) Plot of second field experiment examining interspecific competitive effects of *N. confusa* on *G. gemma* (see *Methods*) at medium and higher densities. There was a significant decline (52%) in the growth of *G. gemma* at the high-density treatment with 40 *G. gemma* together with 40 *N. confusa* (40G plus 40N) relative to medium-density treatment with 40 *G. gemma* (40G) or high conspecific densities 80 *G. gemma* (80G) (see *Competition Experiments* for statistical results).

competition treatments with *N. confusa*, compared with the medium density or high density conspecific treatments ($F = 11.55$, df = 2,21, $P < 0.0005$) (Fig. 3*B*). Survival was also slightly lower in the high-density treatment, but not significantly so ($P > 0.50$).

**Extrinsic Factors.** I found no significant relationship between the distribution of *G. gemma* or *Nutricola* spp. and ocean and atmospheric variables including minimum, maximum, and mean sea surface temperatures, mean and minimum daily low air temperature, mean and maximum daily high air temperatures, and annual total, monthly mean, and monthly maximum rainfall. Of these variables, only mean ($P = 0.026$) and minimum ($P = 0.029$) daily low air temperatures showed any association with *G. gemma* density, and paradoxically high clam densities were associated with low temperatures, making this an unlikely mechanism.

## Discussion

The results presented here are among the first to demonstrate the population level consequences of a new invader rapidly transforming a historically benign introduction into an aggressively expanding invasion. This study shows that this transformation can be the result of positive indirect interactions among invaders. Examples of positive interactions among invaders have been known or suspected in several other systems. For example, the introduction of new specialist pollinators can greatly increase seed production through direct effects on previously introduced plants (15). In coastal systems, a recent study has shown positive indirect interactions among two new invaders, an introduced alga (*Codium fragile* ssp. *tomentosoides*) and a bryozoan (*Membranipora membranacea*), that are simultaneously invading the Gulf of Maine (29). However, the population level consequences of either direct or indirect effects of new invaders on older invasions have not been demonstrated for most systems.

The disproportionately greater impact of green crab predation on the native clams is the result of differences in both adult size and life history between the native and introduced species. The experiments described above show that green crabs strongly prefer larger clams; and native *Nutricola* spp. are significantly larger (means of 5–6 mm, maximum >7 mm) than the introduced *G. gemma* (means of 3–4 mm, maximum <5 mm). Also, both *Nutricola* species are protandrous hermaphrodites; thus, all individuals >4 mm are reproductive females (24, 26). Therefore, as the green crabs selectively prey on larger *Nutricola* spp., they disproportionately consume large, reproductive females. The introduced *G. gemma* is dioecious with no external sexual dimorphism (27, 28), so green crabs consume approximately equal numbers of males and females. Consequently, the per capita impact of green crab predation on population growth is much greater for the native clams. It might be expected that, as the number of *Nutricola* spp. eventually declined, green crabs would have rapidly increased their consumption of *G. gemma*. Although this switch may have occurred to some degree, the observed increase in *G. gemma* abundance suggests that the generalist green crabs switched to other prey including polychaetes and small crustaceans, which they readily consume in the native range (30).

In the competition experiments, the results from the lower density treatments demonstrate the absence of competition at current densities and support the idea that *Nutricola* spp. are not now an obstacle to the spread of *G. gemma*. However, the results from higher density treatments suggest that the historically high densities of native *Nutricola* spp. likely competitively suppressed *G. gemma* by substantially reducing growth and, as a consequence, also reducing size-dependent reproduction. This result suggests that the distribution of *G. gemma* was restricted for many decades until the release from competition with *Nutricola* spp. after the green crab invasion.

In conclusion, the data presented suggest that it is possible for a new invader to transform an older invader into a serious new management problem by means of positive indirect interactions that may produce an invasional meltdown. In areas that have already been heavily invaded, simply reducing the numbers of new introductions may not be a sufficient strategy for management. Rather, in addition to preventing future introductions, it may be necessary to mitigate the impacts of exotic species that have already become established, while realizing that such mitigations may, themselves, have unexpected impacts because of indirect interactions.

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