Stage-specific overcompensation, the hydra effect, and the failure to eradicate an invasive predator

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As biological invasions continue to increase globally, eradication programs have been undertaken at significant cost, often without consideration of relevant ecological theory. Theoretical fisheries models have shown that harvest can actually increase the equilibrium size of a population, and uncontrolled studies and anecdotal reports have documented population increases in response to invasive species removal (akin to fisheries harvest). Both findings may be driven by high levels of juvenile survival associated with low adult abundance, often referred to as overcompensation. Here we show that in a coastal marine ecosystem, an eradication program resulted in stage-specific overcompensation and a 30-fold, single-year increase in the population of an introduced predator. Data collected concurrently from four adjacent regional bays without eradication efforts showed no similar population increase, indicating a local and not a regional increase. Specifically, the eradication program had inadvertently reduced the control of recruitment by adults via cannibalism, thereby facilitating the population explosion. Mesocosm experiments confirmed that adult cannibalism of recruits was size-dependent and could control recruitment. Genomic data show substantial isolation of this population and implicate internal population dynamics for the increase, rather than recruitment from other locations. More broadly, this controlled experimental demonstration of stage-specific overcompensation in an aquatic system provides an important cautionary message for eradication efforts of species with limited connectivity and similar life histories.

hydra effect | biological invasions | overcompensation | eradication | predator mortality

Theoretical population models can produce counterintuitive predictions regarding the consequences of harvest or removal of predatory species. These models show that for simple predator-prey systems, there can be positive population responses to predator mortality resulting from harvest for fisheries or population management, which can create an increased equilibrium level of that predator species (1–5). Among these mortality processes is the "hydra effect," named after the mythical multi-headed serpent that grew two new heads for each one that was removed (6, 7). This counterintuitive outcome can be driven by a density-dependent process known as overcompensation. The hydra effect typically refers to higher equilibrium or time-averaged densities in response to increased mortality, typically involving consumer populations undergoing population cycles. Population increases in response to mortality can be the result of stage-specific overcompensation, which involves an increase in a specific life history stage or a size class following increased mortality. The first analysis of overcompensatory responses to mortality did not depend on stage specificity and was applied initially to fisheries harvests (1). Subsequent models have included stage specificity and have been applied to a broad range of systems in which species have been harvested for consumption or removed for population control of non-native species (4, 5, 8–15).

Theory suggests that overcompensation in response to harvest or removal can occur for a variety of reasons, including 1) reduced competition for resources and increased adult reproduction rates, 2) faster rates of juvenile maturation or greater success in reaching the adult stage, and 3) increased juvenile or adult survival rates (1–7). An increase in reproductive output in response to reduced adult density can be the result of a reduction in resource competition (*SI Appendix*, Fig. S1).

While there is substantial evidence that conditions that could produce density-dependent overcompensation occur frequently, evidence for overcompensation in natural populations is rare. For only a few populations do we have the long-term demographic data collected over a sufficiently long duration and for population densities over a wide enough range to detect this effect. Unfortunately, recent reviews of population increases in response to increased mortality do not include field studies with explicit controls for removals (13–17).

There are examples of density-dependent overcompensation from field populations (4, 13–15), as well as a larger number of studies from the laboratory and greenhouse typically involving plant and insect populations (18–22). Among the field examples is a population control program for smallmouth bass in a lake in upstate New York, which paradoxically resulted in greater bass

Significance

Theoretical models of population dynamics have shown the counterintuitive conclusion that harvest can increase the equilibrium size of a population. These models of increases in response to mortality have been considered for fisheries harvest and removal of non-native species and can be driven by density-dependent overcompensation. This is the first controlled experimental field demonstration showing that harvest-driven overcompensation produced a 30-fold, single-year increase in the abundance of the invasive European green crab (*Carcinus maenas*), one of the world's most invasive predators. Using multiple lines of evidence, we provide both a robust demonstration of a fundamental prediction of population models in a field population and an important cautionary message for future eradication efforts for similar invasive species.

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abundance, primarily of juveniles, after 7 y of removal efforts (23, 24). Another field study in the United Kingdom showed that perch populations responded similarly when an unidentified pathogen decimated adults (25). Other programs that attempted to remove invasive fishes, including pikeperch in England (26), brook trout in Idaho (27), and *Tilapia* in Australia (28), showed similar results. However, although many of these examples involved well-executed studies with substantial field data, none had explicit controls for removal, such as comparable populations without harvest (or disease). Thus, despite the support of current theory in these studies, the contribution of external factors to observed population responses to harvest remains uncertain. To date, we are unaware of any experimental studies with comparable controls in a field population that demonstrates overcompensation in a single species (13–15).

Results and Discussion

Beginning in 2009, we undertook an intensive effort to eradicate the invasive European green crab (*Carcinus maenas*) in a small estuary in central California (Seadrift Lagoon, Stinson Beach; latitude 37.906, longitude −122.658; *SI Appendix*, Fig. S2). European green crabs have successfully colonized five continents (29), negatively impacted benthic communities in California (30), produced $20 million in losses of commercial shellfish annually in the US (31), and are listed as one of the world's 100 worst invaders (32). This eradication program reduced the entire population of green crabs in Seadrift Lagoon by >90%, from 125,000 crabs in 2009 to <10,000 crabs by 2013. Population estimates based on trapping data were validated in most years with extensive mark-recapture studies involving 5,000 to 10,000 marked crabs (Fig. 1*A*). After 5 y of steady reductions in population abundance due to trapping, we documented a population explosion due to a massive recruitment event. By August 2014, there were ∼300,000 green crabs in Seadrift Lagoon, representing a >30-fold increase over 2013 levels and nearly triple the original population size from 2009, when removal efforts began (Fig. 1*A*).

Our data are consistent with density-dependent stage-specific overcompensation, where there is a negative, nonlinear relationship between adult abundance in one year (t) and the abundance of juveniles (recruitment) (y) in the following year ($t + 1$) (Fig. 1*B*; $y = \exp[a * x + b]$, $a = -0.00015145$, $b = 6.52$). Because of the enormous effort required for mark-recapture estimates, we used trapping data (catch per unit effort [CPUE]) to compare the Seadrift Lagoon population with other control bays where green crabs were not removed. In contrast with Seadrift Lagoon, we found no significant relationship between adult and juvenile abundances in Bodega Harbor or in other control bays (*SI Appendix*, Fig. S3). We note that although CPUE provides an excellent comparative measure of population levels, the very highest population levels are not reflected in the CPUE data for Seadrift Lagoon in 2014. This is because CPUE estimates are limited by the trap capacity (saturation) at these extremely high densities, causing these 2014 estimates to appear relatively lower than expected from the mark-recapture estimates. We also note that CPUE estimates in 2014 are somewhat lower than the 2009 level due to the secondary influence of juveniles' greater unwillingness than adults to enter extremely crowded traps. Our data also show that in the 4 y after the 2014 recruitment event (2015 to 2018), ongoing removal efforts decreased the population from its peak and maintained a population size ∼30% of the maximal size (30,000 to 50,000), and have not resulted in any similar reproductive irruptions.

Our results show a large change in the size structure of the populations, which provides evidence for stage-specific overcompensation, a result predicted by population models (2–5). Importantly, we witnessed this rapid shift in stage structure for Seadrift Lagoon within a single year from 2013 to 2014 in terms of both abundance (Fig. 2*A*) and biomass (Fig. 2*B*) as the population rapidly transitioned from one dominated by adults in 2013 to one

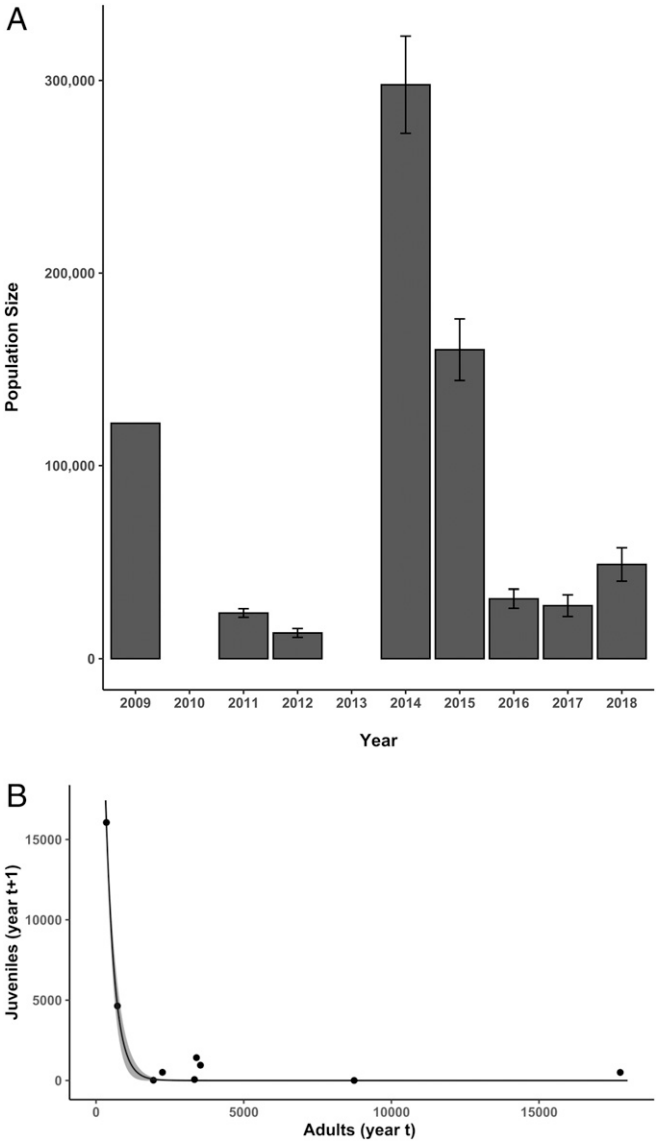

Fig. 1. Relationship between adult population size and recruitment in the Seadrift Lagoon population explosion. (*A*) Estimated population size for most years from 2009 to 2018 based on mark-recapture experiments using Lincoln–Petersen estimation methods. Note that CPUE estimates were calculated for all years (Fig. 2 *A* and *B*). Bar heights represent estimated population size, and error bars represent 95% confidence intervals (CIs). (*B*) Plot of the relationship between adult abundance in one year (t) and juvenile abundance (recruitment) in the following year ($t + 1$) based on equal annual trapping effort (720 trap days) at Seadrift Lagoon between 2009 and 2010, with envelope representing 95% CIs. The negative exponential curve (*Methods*) highlights the nonlinear relationship predicted by overcompensation (*SI Appendix*, Fig. S1).

dominated by juveniles in 2014. We observed these changes in stage structure only in Seadrift Lagoon and not in control populations, such as nearby Bolinas Lagoon (*SI Appendix*, Fig. S4 *A* and *B*).

We have several lines of evidence supporting the hypothesis that this unusual recruitment event was the result of local population dynamics caused by overcompensatory juvenile survival in response to our intensive eradication efforts in this relatively closed lagoon, and not due to any external environmental or demographic influences. The first line of evidence comes from time series data collected as part of a contemporary study of European green crab populations in four adjacent bays in the

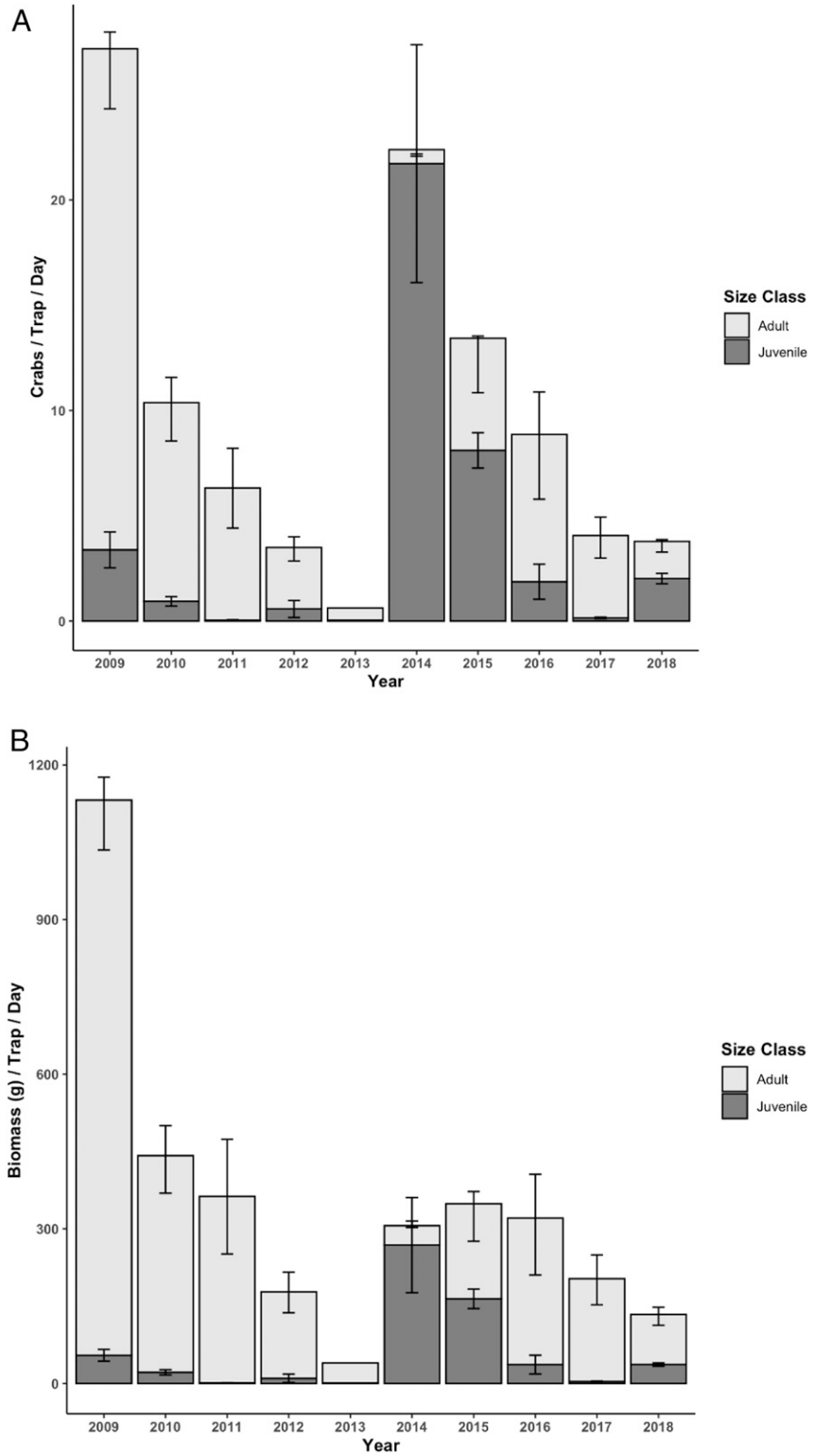

Fig. 2. Annual abundance and biomass of green crabs at Seadrift Lagoon. (*A*) Annual estimates of population abundance CPUE (crabs/trap/day) for Seadrift Lagoon. Values for adults and juveniles for each year are shown separately, with bar heights representing mean abundance and error bars representing ±1 SE. (*B*) Annual estimates of population biomass for Seadrift Lagoon. Values for adults and juveniles for each year are shown separately, with bar heights representing mean biomass and error bars representing ±1 SE. Biomass estimates are calculated from the size-biomass equation (see text).

region sampled in most years over an 8-y period from 2009 to 2016 (*SI Appendix*, Fig. S2). These four bays were not harvested and hence serve as control populations for comparisons with Seadrift Lagoon. When we compared the population increase witnessed in Seadrift Lagoon in 2014 with data from these other bays, we found no significant increases in these other sites (Fig. 3; $P < 0.01$). This suggests that regional atmospheric or oceanographic processes were not responsible for the reproductive event in Seadrift, since

regional processes likely would have produced similar population increases in these other bays, including the adjacent Bolinas Lagoon. Population increases in these control bays would have been readily detected with our trapping protocol that involved 120 trap-days per year at each site. Based on several studies of green crab distribution in the western US, if there were high densities of green crabs at these other sites, these densities would not have been dissipated by juvenile or adult dispersal out of the bays. Unlike Europe and the eastern US, postlarval green crab populations in this region are restricted to shallow intertidal and subtidal zones of bays and estuaries and are not found in outer coasts areas, likely due to predation by much larger, predatory cancrid crabs (33, 34). We also note that the Seadrift Lagoon had consistently higher abundances than unharvested bays for several years before the harvest began in 2009, for reasons that may be related to larval retention (see below). This population explosion also is not likely the result of "reactivity" as discussed in predator-prey models (35). Most of the common near-surface infaunal invertebrates that would be prey for green crabs, including small venerid clams (<6 mm maximum adult size), corophiid and aorid amphipods, and cirratulid and spionid polychaetes, have generation times of several months to <2 y (36–38). Therefore, the population explosion in 2014 is very unlikely to have been driven by a delayed response of prey populations to 5 y of removal.

Our second line of evidence is based on experimental tests of predictions from population models that describe the conditions in which overcompensation would be most likely for invasive species removal programs. Populations with strong negative adult–juvenile interactions (e.g., cannibalism), when coupled with removal programs that focus on adult stages, would be among the most likely to experience overcompensation (4). Our trapping program, like many similar programs, targeted adult crabs due to the constraints on minimum crab size determined by the mesh size of the traps. Green crabs reach nearly full adult size and maturity within the first year. We used 50 mm as an approximate cutoff for juvenile vs. adult crabs, but adults (age >1 y) are very easy to distinguish in the field from juveniles (age <1 y) of similar size, because adult carapaces are much more calcified and darker. Because strong adult–juvenile interactions, and cannibalism in particular, are common in decapod crustacea (39), we first predicted that adults would readily cannibalize small recruiting juveniles. Cannibalism by larger adults on smaller juvenile recruits would be necessary for adults to exert strong direct control of recruitment. We then predicted that cannibalism would be much less likely to occur among equivalently sized crabs, such as among recruits of the same age, as noted in other studies (40). Otherwise, the recruitment cohort would have rapidly consumed itself, thus erasing the results of overcompensatory recruitment, which we did not observe. Instead, we witnessed the persistence of the recruitment

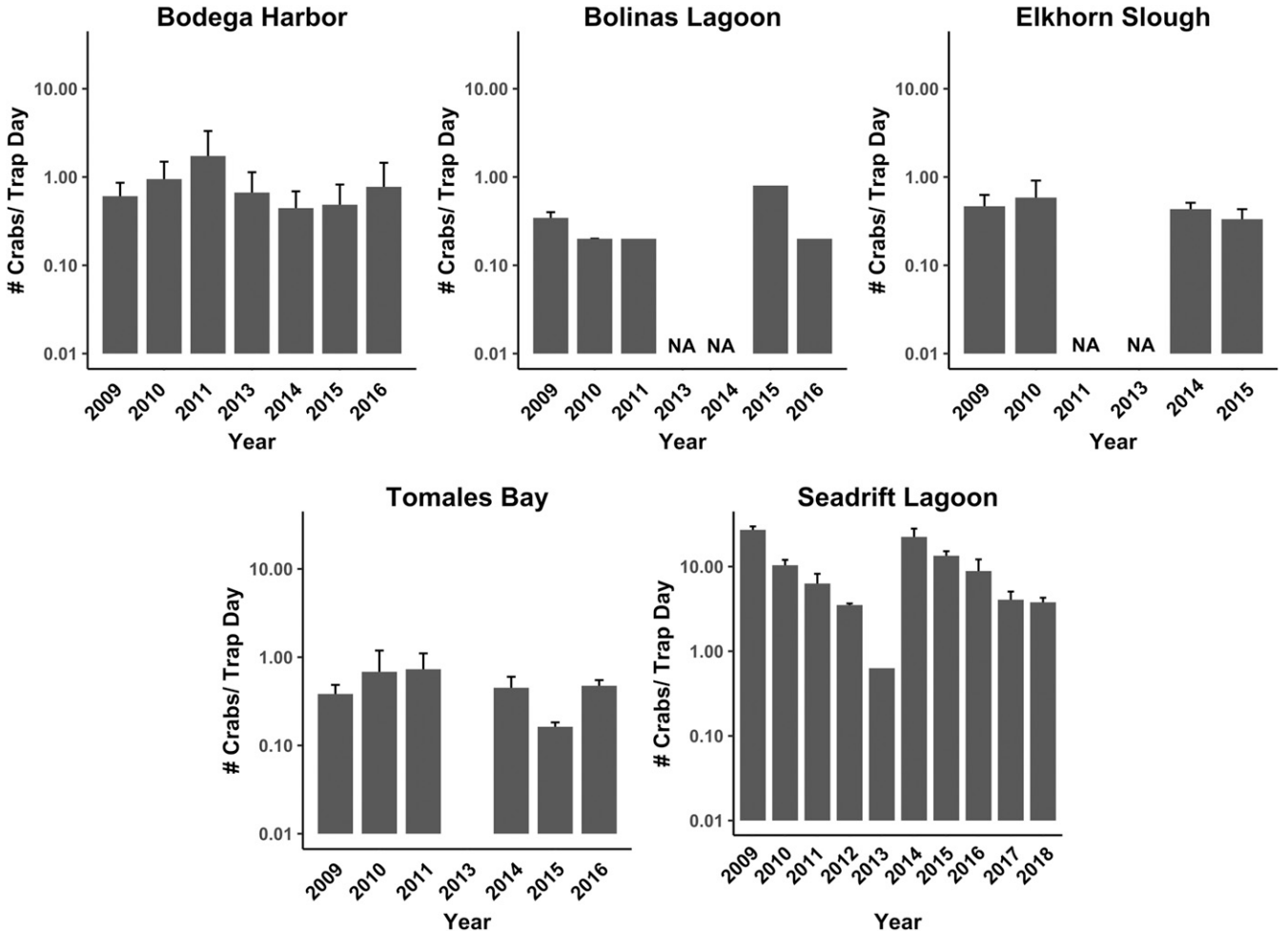

Fig. 3. Comparison of annual variation of abundance in Seadrift Lagoon with surrounding bays. Shown are plots of CPUE comparing Seadrift Lagoon and four other regional bays (*SI Appendix*, Fig. S2) based on annual estimates (*Methods*). Except for Seadrift Lagoon, no other bays show evidence of elevated recruitment in 2014 (note log scale on the *y*-axis). Bar heights represent the mean of 10 baited traps in each of four locations within each bay ($n = 40$ per bay) over a 3 d period, and error bars represent 1 SE.

boom in the population structure, resulting in a highly skewed size distribution (Fig. 2 *A* and *B*)

We tested these two predictions with a single set of experiments involving predation trials with crabs of different sizes (i.e., carapace widths) in outdoor mesocosms. We ran trials simultaneously over 48 h in nine mesocosms with one adult crab and five juvenile crabs in each, to evaluate the effect of size asymmetry on cannibalism (*Methods*). We repeated these trials in nine mesocosms run nine times over several weeks, yielding 405 encounters between individual adult and juvenile crabs within 81 independent mesocosm trials. Our analysis using summary values for each of the independent mesocosm trials showed that the frequency of cannibalism per mesocosm was significantly and positively related to the mean size ratio of the adult crab to each of the juvenile crabs ($P < 0.0005$, iteratively reweighted least squares regression; logistic equation, $y = 0.0593x$ (± 0.0153) + 0.0639 (± 0.0737); df = 79; $R^2 = 0.1596$). In short, as the size difference between the adult and juvenile crabs increased, the likelihood of cannibalism also significantly increased, as illustrated by the logistic regression for all pairwise interactions shown in Fig. 4. The results indicate that a ratio of adult size to juvenile size (mm) of 4.75 would result in cannibalism with a 50% probability, and a size ratio of 8.25 would result in cannibalism with a 90% probability. The data also showed that when crabs were of a similar size, particularly young recruits, cannibalism was very rare. These results are consistent with other studies of *C. maenas* showing that intracohort cannibalism was rare among new recruits (40).

We also conducted experiments comparing cannibalism rates at Seadrift Lagoon with one of our control sites, Bolinas Lagoon. Using replicate juvenile green crabs attached to tethers at the same field locations that we used for trapping, we measured rates of consumption of tethered crabs, which, given the rarity of heterospecific predators in Seadrift Lagoon, we could reasonably assume was largely due to cannibalism by adult green crabs. We found that rates of consumption were much higher at Seadrift Lagoon in 2009 and 2014, when densities of adult green crabs were relatively high, in comparison with low rates of consumption at Bolinas Lagoon, which had much lower adult green crab densities (*SI Appendix*, Fig. S5 and Fig. 3). This finding provides additional field experimental support that cannibalism by adult green crabs was high at Seadrift Lagoon and resulted in high mortality of juvenile green crabs.

In addition to cannibalism being supported by results from both mesocosm and field experiments, our data also suggest that high levels of reproduction, potentially the result of greater resources available to adults at low density, also may have contributed to the stage-specific overcompensation. As a proxy for reproductive output (and indirectly for resource availability), we examined the percentage of reproductive age females that were ovigerous in each year. Our data show a relatively high percentage of gravid females in 2013 just prior to the population explosion in 2014 (*SI Appendix*, Fig. S6). However, we hasten to point out that this higher fecundity was not a sufficient condition for overcompensation, since there was a nearly equally high percentage of gravid females in 2011, which did not result in any population increase in 2012. We also note that although the percentage of gravid females was higher in these years of low adult abundance, the total production of larvae (and overall reproductive output) actually would have been greater during years of high adult abundance (i.e., fecundity multiplied by high numbers of adult females). Therefore, although increased reproductive output may have contributed somewhat to the stage-specific overcompensation in 2014, we conclude that the very low number of adults in 2013 and associated low level of cannibalism was the necessary condition for the population explosion in 2014.

A third line of evidence also supports the hypothesis that overcompensation was due to internal population dynamics. We analyzed 5,118 independent, putatively neutral transcriptome-derived single nucleotide polymorphisms (SNPs) from Seadrift Lagoon and five other sites spanning the species' range along the North American Pacific coast (Fig. 5*A*). Twelve individuals per site were sampled during 2015 and 2016, and previously published data from 2011 at two sites (including Seadrift Lagoon) were reanalyzed to assess temporal stability (41). Pairwise F_{ST} (Table 1) showed that Seadrift Lagoon was significantly differentiated from all other tested sites ($P < 0.001$), while no other sites were significantly differentiated from each other ($P > 0.05$); these other sites include two of the four reference populations for long-term dynamics. Temporal samples spanning two to three crab generations demonstrated that Seadrift's differentiation was stable over time (Fig. 5*B*; pairwise F_{ST} within sites across years, $P > 0.05$). There was no evidence that Seadrift's distinctive genetic signature was caused either by an introduction of novel alleles to the site or by selection; instead, the significantly lower allelic richness in Seadrift appeared to be driving the observed pattern (Fig. 5*C*; $P < 0.005$), suggesting that Seadrift is an isolated and bottlenecked population relative to the rest of the west coast. These results support the idea that the recruitment event was due to internal population dynamics within Seadrift Lagoon and not due to larval input from other local populations.

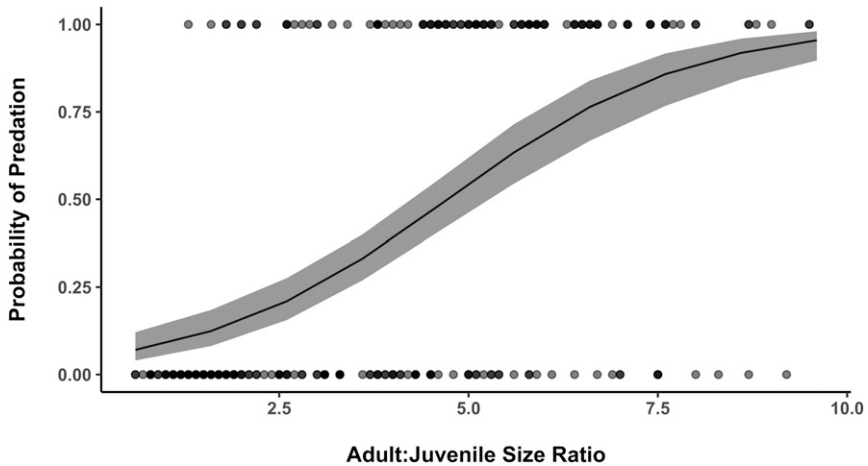

Fig. 4. Effect of crab size ratio on the probability of cannibalism. Logistic regression shows the probability of cannibalism as a function of the difference in size between green crabs in mesocosm experiment encounters, with envelope representing 95% CIs (see text for equation). The adult-to-juvenile size ratio (*x*-axis) is the ratio of carapace width of the larger crab to the smaller crab for each data point. The probability of cannibalism is the binomial outcome of the experiment (cannibalism = 1, no cannibalism = 0).

In summary, these multiple lines of evidence provide consistent and robust support for the hypothesis that the population explosion seen at Seadrift Lagoon in 2014 was due to stage-specific density-dependent overcompensation driven by eradication efforts that removed adult control of recruitment. This controlled field experiment demonstrates stage-specific overcompensation as the result of mortality, in this case active removal of adults, resulting in a large increase in juvenile survivorship. These results support several theoretical predictions from fundamental models of positive population responses to mortality, which apply to both fisheries management and invasive species control, where population increases have been shown to occur in response to mortality. One prediction of these models is that stage-specific overcompensation can result in shifts in stage-specific biomass and abundance of a population (2, 3). Within a single year, we found that the harvested population shifted from one dominated by adults to one dominated by juveniles, which is consistent with predictions. These changes were observed only in Seadrift Lagoon, associated with eradication efforts, and were not seen in several nearby control populations.

A second prediction is that populations that experience cannibalism would be more likely to demonstrate stage-specific overcompensation (3). Our results show that cannibalism was likely the primary driver of the stage-specific overcompensatory response, although increased reproductive output also may have been a minor contributor. Overall, our data suggest that the harvest of adults and subsequent reduction of cannibalism of recruits led to the overcompensatory recruitment.

As a result, we now have a convincing controlled field-based demonstration of this fundamental population phenomenon that continues to be a focus of debate (13–15). This overcompensatory event lasted only a single year, since the large recruitment class became adults the next year, thus reestablishing relatively high adult cannibalism of the recruits in the following year. We believe that these results point to interesting directions for future theoretical investigation.

Finally, the results of this study provide an urgent warning to those involved in the management of invasive species. Programs aimed at eradicating invasive species are currently being undertaken worldwide, often at substantial cost (42), including eradication of the European green crab. Invasive species with limited connectivity, highly fecund adults, and strong adult control of juvenile abundance have the potential for overcompensation and thus pose a substantial challenge for eradication programs (43, 44). It is critical to improve our predictive abilities in this area and to more fully understand how and why expensive and time-consuming invasive management programs can fail or, even worse, potentially exacerbate the current impacts of invasive species.

Table 1. Pairwise F_{ST} values between Seadrift and other sites for samples collected in 2015 to 2016

	BB 2015	ES 2015	BC 2016	OR 2016	SF 2016	SL 2016
BB 2015	—	0.6	0.1	0.06	0.2	**<0.00001**
ES 2015	−0.00699	—	0.2	0.9	0.7	**<0.00001**
BC 2016	−0.00432	−0.00438	—	0.2	0.2	**<0.00001**
OR 2016	−0.00397	−0.00822	−0.00483	—	0.5	**0.0001**
SF 2016	−0.00498	−0.00683	−0.00409	−0.00592	—	**<0.00001**
SL 2016	0.00481	0.0072	0.00602	0.00315	0.00411	—

F_{ST} values are below the diagonal, and the significance of those values after Benjamini–Hochberg multiple test correction are above the diagonal. BC, Barkley Sound, British Columbia, Canada; OR, Tillamook Bay, Oregon; BB, Bodega Bay, California; SFB, San Francisco Bay, California; ES, Elkhorn Slough, California; SL, Seadrift Lagoon, California. *P* values shown in bold are statistically significant ($P \leq 0.05$) based on analysis of 5,118 independent, putatively neutral SNPs. Seadrift is significantly different from all other tested embayments; no other population pairs were significantly differentiated.

Methods

Study Sites. We conducted parallel studies of green crab populations in Seadrift Lagoon and four other regional estuaries: Bolinas Lagoon, Bodega Harbor, Tomales Bay, and Elkhorn Slough. The European green crab (*C. maenas*) has been present continuously at all of these sites since the mid-1990s following its initial North American Pacific coast introduction in San Francisco Bay (29, 30). Seadrift Lagoon is a marine lagoon in Stinson Beach, CA (latitude 37.906, longitude −122.658). It is a small, semi-enclosed embayment ∼2 km long with limited, seasonal hydrological connection to the outer Bolinas Lagoon via a tide gate. The larger Bolinas Lagoon (37.918, −122.669) is a strongly tidally mixed estuary with seasonally variable salinity and a primary connection to the Pacific Ocean at Bolinas, CA. Bodega Harbor (38.317, −123.057) is strongly tidally mixed but is a largely marine embayment with limited freshwater inflow and primary connection to the Pacific Ocean in Bodega Bay, CA. Tomales Bay (38.150, −122.889) is a linear drowned river estuary with seasonally variable salinity and high residence times in the upper bay and primary connection to the Pacific Ocean by Dillion Beach, CA. Elkhorn Slough (36.841, −121.746) is a strongly tidally mixed estuary with seasonally variable salinity and areas with muted tidal exchange with primary connection to the Pacific Ocean at Moss Landing, CA.

Trap-Based Population Estimates. In Seadrift Lagoon, we conducted a targeted eradication program over a 10-y period from 2009 to 2018 aimed at testing the success of eradication given a continued removal effort. In each year at least three times between June and August, we deployed 15 traps at each of six locations within the lagoon over a 4-d period. In most years, we had >1,000 trap-days per year (*SI Appendix*, Table S1). All traps were Fukui crab traps (60 × 45 × 20 cm, 1.25-cm mesh) baited with herring or anchovy in bait containers and were deployed at similar intertidal to shallow subtidal depths in equivalent mud/sand flat habitats without cobbles or other structure at all sites. All traps were retrieved and rebaited approximately every 24 h. We

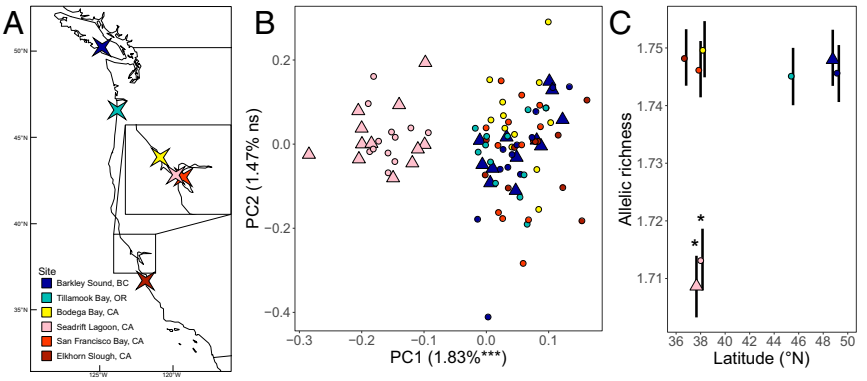

Fig. 5. Genetic differentiation of the Seadrift Lagoon population. (*A*) Map of genetic sampling sites across western North America including Seadrift Lagoon (in pink in the map inset). The vertical plane of the diagram runs directly north to south, with longitude and latitude shown in 5° intervals. (*B*) Principal components analysis of population structure for 2011 (triangles) and 2015 to 2016 (circles) for the sites listed in *A*. (*C*) Allelic richness using the same sites and time points shown in *B* (*Methods*). Asterisks indicate significantly lower allelic richness ($P < 0.005$) in Seadrift compared with all other populations in all years.

estimated relative population sizes across time points using CPUE, which represents the number of European green crabs caught per trap per day.

Trapping was also conducted annually in all five bays in most years from 2009 to 2016 as part of a project that began independently of the Seadrift Lagoon eradication project. At each of these sites, we deployed 10 baited traps, five of each of two sizes, the same collapsible traps as well as minnow traps (40 cm × 23 cm with 0.65 cm mesh and a 5-cm opening), at four locations ($n = 40$ traps) per bay. Traps were sampled at ∼24-h intervals for three consecutive days. At each sampling, data were collected for all crabs regarding size, sex, species, parasites, eggs, and related variables. To compare relative population sizes among sites and time points, we used the same CPUE metric as above using only the large traps. We used these CPUE population estimates to test the difference between the large population size in Seadrift Lagoon in 2014 vs. the other bays in that year. We also calculated population abundance (CPUE) as well as biomass using biomass estimated from an equation relating biomass (mass in grams) to size (carapace width) generated from Seadrift Lagoon crabs ($y = -0.071x + 0.003x^2 + 0.0002x^3$). We found significantly higher abundance values in Seadrift Lagoon for 2014 to 2015 than in any of the four other bays (*Results*) using a Wilcoxon one-sample test with the wilcox.test function in R 3.6.1.

Mark-Recapture Population Size Estimates. To more accurately estimate the size of the European green crab population in Seadrift Lagoon, we conducted an extensive capture-mark-recapture program in most years. Prior to crab removal for eradication, we deployed 15 baited Fukui crab traps in June at each of six locations within the lagoon. Over the succeeding 3 d, we marked all crabs caught by clipping two spines on the carapace, recording their size and sex, and releasing them back to their original location. Within successive weeks, as part of the eradication efforts, we recorded the number of marked crabs that were recaptured, along with their size and sex. We used the resulting mark and recapture data, which represented 5 to 10% of the total population, to estimate crab population sizes for the lagoon. Because of the isolated nature of the population and the short time scale of each annual mark-recapture study (no significant death, tag loss, or immigration/emigration) we used the Lincoln–Petersen model for closed populations including estimated confidence intervals for each year (45).

Cannibalism Experiments. In 2015, to investigate the relationship between the size ratio of adult and juvenile crabs vs. the likelihood of cannibalism, we conducted mesocosm experiments in 10-gallon closed aquaria at the Estuary and Ocean Science Center of San Francisco State University, Tiburon, CA. Between June 15 and August 7, 2015, we ran nine separate trials, each involving nine mesocosms, over a 48-h period. In general, green crabs grow to nearly adult size and mature within the first year (29). We use 50 mm as the approximate cut off for juveniles in our sampling and experiments; in practice, juveniles (age <1 y) are very easy to distinguish from adults (age >1 y). Adults are much more calcified and darker in color than juveniles, and the reproductive morphology of mature females is very distinctive. For this experiment, five juvenile crabs were added to each of nine mesocosms, together with one larger crab from one of three size classes as available (larger crabs ranged from 30 to 82 mm). The size of the juveniles increased over the course of the trials, from 10 to 15 mm carapace width in early trials to 25 to 35 mm in the latest trials. One trial also explicitly included crabs of similar sizes in which all six crabs were juveniles as a control to examine cannibalism among recruits. All crabs were measured at the start of the trial, and alternate prey were provided by including five live small clams (3 to 9 mm) in each tank with the crabs. At the end of the experiment, all crabs were retrieved, and those that were no longer present were assumed to have been consumed (often remains were present). We tested the functional relationship between the frequency of cannibalism in these trials and the size ratio of adult to juvenile carapace width (mm). We conducted this analysis by first calculating the frequency of cannibalism for each of the 81 mesocosms (nine concurrent mesocosm trials repeated nine times) by summing the results (cannibalism = 1, no cannibalism = 0) across the five juveniles in each mesocosm trial. We then calculated the adult to juvenile size ratio for that mesocosm using the adult carapace width divided by the mean value for the carapace width of the five juvenile crabs. Our analysis showed that the frequency of cannibalism per mesocosm was significantly and positively related to the mean size ratio of the adult crab to each of the juvenile crabs based on a least squares regression (*Results*) using the lm function in R 3.6.1. To better illustrate the data from all adult-juvenile encounters, we plotted these values as a logistic regression with values for each juvenile crab (either 1 or 0) plotted against the size ratio of the adult vs. that crab using the ggplot2 package in R 3.6.1.

Population Genomics. We sequenced mRNA extracted from cardiac tissue from crabs collected at each of six sites in 2015 to 2016: Barkley Sound, British Columbia, Canada; Tillamook Bay, OR; Bodega Bay, CA; Seadrift Lagoon, CA; San Francisco Bay, CA; and Elkhorn Slough, CA. These sites span most of the current range of *C. maenas* along the Pacific coast of North America, from its southern extent in Elkhorn Slough to near its northern extent in Barkley Sound (Fig. 5*A*). In addition, we reanalyzed previously published data collected in 2011 from two of these sites, Seadrift Lagoon and Barkley Sound (41). Individually indexed cDNA libraries were prepared from 12 crabs per site × year using the Illumina TruSeq Stranded mRNA Kit and sequenced at 18 samples per lane on an Illumina HiSeq 4000 to generate 50-bp single-end reads. The resulting reads were cleaned and aligned to an existing North American *C. maenas* cardiac transcriptome (46). Single nucleotide polymorphisms (SNPs) were identified and individually genotyped with the Genome Analysis Toolkit v4.1.4.1 (47). Biallelic SNPs with high-quality (phred ≥20), high-coverage (five or more reads) genotypes for nine or more crabs per site × year group were tested for linkage disequilibrium (LD) using the R package LDna v0.60 (48), and all but one SNP in each group in LD >0.8 were removed from further analysis. Remaining unlinked SNPs were screened for potential outlier loci using BayPass v2.1 (49) and removed if they were potential outliers at a false discovery rate of ≤0.1. This resulted in a set of 5,118 high-quality, putatively neutral, unlinked SNP loci for population genomics. Principal components analysis was conducted with these markers using the smartpca function in Eigensoft v7.2.1 (50). Pairwise F_{ST} was calculated using the Weir and Cockerham approach (51) in Arlequin v3.5.2 (52), using 100,000 permutations to calculate *P* values. *P* values were adjusted for multiple tests according to the Benjamini–Hochberg method (53). Allelic richness was calculated using ADZE v1.0 (54). All plotting was done using the R package ggplot2 (55) with additional details available.

Data Availability. The ecological data are available through the NSF's Biological and Chemical Oceanography Data Management Office at https://www.bco-dmo.org/person/699768. Raw transcriptome reads from new sequencing for this project have been deposited in GenBank's Sequence Read Archive (SRA) under BioProject ID PRJNA690934 and BioSample IDs SAMN17267686 to SAMN17267781. These new raw data have been embargoed and will be released publicly on the publication of a companion paper focused on genomics in this region. The cleaned transcriptome and high-quality individual SNP genotypes used in this paper have been deposited in Figshare at doi:10.6084/m9.figshare.13564694 and 10.6084/m9.figshare.13564676 and will be made available on the publication of this paper. Raw sequence reads from 2011, reanalyzed in this project, are available in the SRA under BioProject ID PRJNA283611 and BioSample IDs SAMN03653390 to SAMN03653413. Custom scripts used in this bioinformatics pipeline are available in a Figshare archive at doi: 10.6084/m9.figshare.c.5182427.v1.

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