Severe introduced predator impacts despite attempted functional eradication

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ABSTRACT

24   Established non-native species can have significant impacts on native biodiversity without any possibility of complete eradication. In such cases, one management approach is

26   functional eradication, the reduction of introduced species density below levels that cause unacceptable effects on the native community. Functional eradication may be particularly

28   effective for species with limited dispersal ability, which may limit rates of reinvasion from distant populations. Here, we evaluate the potential for functional eradication of introduced

30   predatory oyster drills (*Urosalpinx cinerea*) using a community science approach in San Francisco Bay. We combined observational surveys, targeted removals, and a caging experiment

32   to evaluate the effectiveness of this approach in mitigating the mortality of prey Olympia oysters (*Ostrea lurida*), a conservation and restoration priority species. Despite the efforts of over 300

34   volunteers that removed over 30,000 oyster drills, we report limited success and discuss several possible mechanisms for this result with broad relevance to management for this and other

36   introduced species. We also found a strong negative relationship between oyster drills and oysters, showing virtually no coexistence across eight sites. At two removal sites, there was no

38   effect of oyster drill removal on oyster survival, which was only observed by caging treatment (0 and 1.6% survival in open and partial cage treatments, as compared to 89.1% in predator

40   exclusion treatments). We conclude that functional eradication of this species requires significantly greater effort and may not be a viable management strategy. Oyster restoration

42   efforts should not be undertaken where *Urosalpinx* is established or is likely to invade.

   Keywords: Atlantic oyster drill, community science, functional eradication, Olympia oyster,

44   *Ostrea lurida*, *Urosalpinx cinerea*

46 **INTRODUCTION**

Despite widespread efforts to reduce the invasion of non-native species, the rate of

48 introductions appears to be increasing for many taxa (Seebens et al. 2017). The prevention of

non-native species introduction is crucial to maintaining and conserving native biodiversity.

50 However, established introduced species can have ongoing negative impacts on native species

(Grosholz 2002), and these consequences may be intensified by changing environmental

52 conditions such as climate change (Dukes and Mooney 1999, Sorte et al. 2013). One means of

mitigating the impacts of non-native species is managed suppression or "functional eradication"

54 (Hulme 2006, Green et al. 2014), especially when complete eradication may not be achievable.

Functional eradication reduces non-native species density below levels that cause unacceptable

56 effects on recipient communities (Green and Grosholz 2021). This approach has been likened to

the provisioning of a spatial refuge for native species, such as is the case with protected areas in

58 the context of hunting and extraction (Green et al. 2017).

Functional eradication may be a particularly effective strategy in freshwater and marine

60 habitats where reinvasion rates are high because most taxa produce planktonic dispersive larvae

that are cast into the currents (Wray and Raff 1991). The dispersal of these propagules can be

62 several orders of magnitude greater than on land (Kinlan and Gaines 2003), which complicates

complete eradication efforts because population rescue can occur via distant populations.

64 However, the potential use of this approach with taxa that have limited dispersal potential and

direct development remains less explored. Such species may be good targets for functional

66 eradication, especially when their geographic extent is limited and the probability of reinvasion

is low (Liebhold et al. 2016).

68   In highly invaded San Francisco Bay, the introduced Atlantic oyster drill (*Urosalpinx*

cinerea; hereafter *Urosalpinx*) is a direct developing species that is patchily distributed and may

70   be a good candidate for functional eradication for several reasons, including its potential for

ecological and economic harm and the potential for success in limiting its abundance and extent.

72   Atlantic oyster drills are predatory snails native to the Atlantic coast of the United States that

were introduced to the Pacific and Gulf coasts, as well as parts of Europe beginning in the late

74   1800s (Fofonoff et al. 2020). *Urosalpinx* is a generalist consumer that can have significant

negative impacts on native communities as well as commercial oyster fisheries and aquaculture

76   (Buhle and Ruesink 2009, Kimbro et al. 2009, Koeppel 2011, Cheng and Grosholz 2016).

Furthermore, climate change is expected to intensify the impacts of *Urosalpinx* by increasing

78   growth and consumption rates under warming scenarios (Cheng et al. 2017).

Urosalpinx has limited dispersal because it lays benthic egg capsules from which fully-

80   formed young emerge (i.e., it does not broadcast spawn its larvae; Carriker 1955). Thus, attempts

at removal or managed suppression may not be overwhelmed by reinvasion or recruitment from

82   distant populations (Simberloff 2003). Oyster drills also appear to have limited mobility as

adults. In a pilot mark-recapture study of over 500 oyster drills, snails moved a maximum of 4 m

84   from their origin over the course of eight months (A.L. Chang, *unpublished data*). Drills also

tend to prefer hard substrate upon which they find prey species and lay egg capsules (Carriker

86   1955). This can be advantageous in regions where hard substratum is patchy; such is the case in

San Francisco Bay, where rocky shores are often isolated by mudflats, which may limit

88   recolonization (immigration) from adjacent habitat patches.

There is also some evidence that key native species may coexist with *Urosalpinx*,

90   including the foundational Olympia oyster (*Ostrea lurida*), a preferred prey species, provided

that oyster drill densities remain low (Kimbro and Grosholz 2006, Buhle and Ruesink 2009,

92   Cheng and Grosholz 2016). Bioeconomic models also suggest that the removal of the

functionally similar Japanese oyster drill (*Ocinebrellus inornatus*) can be an effective and

94   economical control strategy (Buhle et al. 2005). Moreover, functional eradication may be the

only option for controlling introduced species such as *Urosalpinx* in a management landscape

96   with limited resources. Taken together, the biology and management of this system suggests that

functional eradication may be a viable option that could have the potential for long lasting and

98   positive effects for native biodiversity.

Community science approaches have garnered much attention as a means of non-native

100   species detection and management (Delaney et al. 2008, Dickinson et al. 2010, Gallo and Waitt

2011). Volunteer-based efforts can vastly increase the spatial and temporal scale of management

102   efforts while reducing financial resources used for control programs (Simberloff 2003). The

integration of community members into invasion science also represents an important "social

104   pillar" of sustainable invasive species management (sensu Larson et al. 2011) that can increase

social and political capital for such initiatives (Overdevest et al. 2004, Novoa et al. 2018).

106   Community science approaches may also have broader impacts, such as increasing science

literacy and the likelihood that participants engage in pro-environmental activities (Crall et al.

108   2013). At the practical level, community science approaches are a useful management strategy

that can have species identification accuracy rates that compare favorably to those of

110   professional scientists (Crall et al. 2011). Volunteer-based hand removal methods can also have

high precision and limited environmental impact, as compared to alternatives such as the use of

112   chemical control measures and may be the only feasible approach for mitigating invasive species

impacts where such chemicals may not be desirable.

114   Here, we describe a community science-based approach to attempt the functional

eradication of Atlantic oyster drills in Richardson Bay (a sub-embayment of central San

116   Francisco Bay, California USA). San Francisco Bay harbors an overlapping distribution of non-

native oyster drills and their prey, the native Olympia oyster. This native oyster is a restoration

118   and conservation priority along the west coast of the U.S. (McGraw 2009, Wasson et al. 2014)

that appears to be functionally extinct in many estuaries throughout its range (Zu Ermgassen et

120   al. 2012). San Francisco Bay supports one of the largest remnant Olympia oyster populations

throughout its entire range (Polson and Zacherl 2009, Cheng et al. 2016) and invasive oyster

122   drills are thought to be a primary impediment to their restoration and persistence in California

(Wasson et al. 2014). Our goals were to (1) quantify the relationship in abundance between non-

124   native oyster drills and native oysters, (2) assess the potential for community science-based

removals to reduce oyster drill density, and (3) quantify the effect of removal efforts on oyster

126   survival and growth.

MATERIALS & METHODS

128   *Site selection*

We focused on Richardson Bay, CA (Fig. 1) because of strong stakeholder interest in the

130   potential long-term observation and maintenance of restoration sites in this region. In addition,

the predatory impact of oyster drills had not been quantified anywhere within San Francisco Bay,

132   which supports high native oyster abundance at some sites, primarily where freshwater input

may limit drill populations because they are intolerant of low salinity conditions (Cheng et al.

134   2015, 2017). To broadly quantify the relationship between oyster drills and native oysters, we

established eight intertidal field sites. Of these sites, we further focused on a subset of four sites,

136   establishing two sites for community science-based oyster drill removals and two sites as paired

controls. One of our removal sites, Lani's Beach (hereafter Lani's) was selected because of easy

138 access, high public use, and because it is valuable to the community due to its use in outdoor

educational programs at the immediately adjacent Richardson Bay Audubon Center & Sanctuary.

140 If non-native control efforts were successful, this site could be the focus of ongoing community-

based invasive species management. Lani's was paired with a control area that was separated by

142 50 m along shore (Fig. 1; S1), which greatly exceeds estimated maximum adult movement rates

of 4 m over 8 months (A.L. Chang *unpublished data*). Second, we used two sites located on

144 Aramburu Island because of extensive habitat restoration activities that were completed by the

Audubon Society in 2010 (Wetlands and Water Resources, Inc. 2010). The Aramburu removal

146 and control sites were separated by ~140 m along shore (Fig 1, Fig S1). In contrast to Lani's,

Aramburu can only be accessed by boat, making it less frequently visited by the public. Local

148 scale habitat features differ between the sites in that Lani's is characterized by larger boulders

interspersed with mud and cobble, whereas Aramburu is largely characterized by high cover of

150 smaller cobbles with mud located at lower tidal elevations only. Sites also differ in their

shoreline orientation which could affect physical characteristics of the environment (e.g., wind

152 exposure, wave energy; Blumenthal 2019).

Observational sampling

154   To quantify the abundance of *Urosalpinx* and its relationship to native oysters, we

conducted quadrat surveys at each of the eight field sites. At each site, we established a

156 permanent 30 m transect at +0.5 m above mean lower low water (MLLW; see Supplementary

Information S1 for additional site details). This intertidal elevation typically contains dense

158 native oyster populations in San Francisco Bay and other estuaries (Wasson et al. 2014), and it

has hard substrate suitable for oyster recruitment and persistence at our field sites. Along each

160   transect, we censused all oyster drills and oysters at the surface and by overturning all stones

within 10 randomly distributed 0.5 x 0.5 m quadrats. Quadrats were randomly stratified such that

162   five were conducted between 0-15 m of the transect and the remaining five occurred between 15-

30 m. For each site, surveys occurred two to five times (20-50 quadrats, mean = 40.5 quadrats)

164   during the low tides of summer, fall, and winter of 2017 and spring and summer of 2018. We

then conducted an analysis on a subset of these quadrat data to standardize sampling effort and

166   establish the relationship between drills and oysters prior to any eradication attempts (see

Statistics).

168   ***Functional eradication of drills***

At each removal site, we established a 60 m swath of shoreline (along shore) from the

170   lower mud zone to the upper barnacle zone (approximately 15 m across shore) to serve as the

focal area for removals (see Supplementary Information S1 for maps). For the removal sites, the

172   60 m total swath included the 30 m fixed transect with additional 15 m buffer zones on each side

(along shore). Paired with each eradication site, we established a similar swath of shoreline to

174   serve as a control area except snails were not removed from these areas. Control and removal

zones were also separated by stretches of shoreline that did not have hard substrate, potentially

176   limiting the movement of oyster drills. All areas were marked with stakes for the duration of the

experiment.

178   Removals were carried out in the spring with the intent of removing drills before they had

laid eggs. We organized drill-removal events, inviting members of the public to assist us in

180   finding and removing drills. To increase community participation, we scheduled drill removals

on weekends and only during daylight low tides. In 2017, we organized four removal days at

182   Lani's and three at Aramburu; in 2018, we held three removal days at each location. Between 20

and 35 people participated at each event and were provided project background and training prior

184   to removal efforts. Teams then worked for 1-2 hours, removing snails by hand. Teams also

searched for snails on the surface of the mud, but these were rarely found. To ensure complete

186   spatial coverage of the removal area, we divided removal and buffer areas into ~2 m wide swaths

running perpendicular to shore and assigned volunteers to these zones. For each team, we

188   recorded the number of personnel, their time spent removing drills (h), and the number of snails

removed. Collected snails were taken to the Smithsonian Environmental Research Center's

190   Tiburon, CA laboratory (housed at the Estuary & Ocean Science Center, San Francisco State

University) and frozen.

192   To quantify whether removal efforts were effective at reducing snail densities, we used

two approaches. First, we quantified oyster drill densities using quadrats along a fixed transect as

194   in the observational sampling described above. Prior observational data from Tomales Bay

suggests that oyster drill and oyster coexistence is possible at an oyster drill density of 5 m^{-2}.

196   Experimental data also supports this finding, indicating that the survival of experimentally

deployed oyster prey was greater than 50% over 6 months at sites with < 5 drills m^{-2} (Cheng and

198   Grosholz 2016), which we set as our "removal density target". In 2017, we surveyed before and

after each removal event; in 2018 we surveyed immediately before removal events and several

200   days before the oyster outplant experiment described below. In addition to transect surveys, we

conducted supplementary surveys at Lani's where drills aggregate in high densities on several

202   large boulders. Here, we counted drills within 9 haphazardly placed 0.25 m^2 quadrats placed

vertically around the base of each boulder (where drills tended to aggregate). Second, we

204   calculated catch per unit effort (CPUE; number of collected snails per person per hour) from the

removal events. We hypothesized that CPUE should decrease over time if functional eradication

206   efforts were successful in depleting the target population.

Oyster outplant experiment

208   To determine whether snail removal efforts were sufficient to increase oyster survival, we

conducted a field caging experiment in July 2018. This experiment also allowed us to determine

210   whether the physical conditions at each site were able to support oyster survival and growth in

the absence of oyster drills. We used the experimental approach from our past efforts to quantify

212   predation intensity in nearby Tomales Bay (Cheng and Grosholz 2016) with a few modifications.

First, we constructed experimental units by attaching 8-10 hatchery reared Olympia oysters

214   (Puget Sound Restoration Fund, CA DFW Permit #2018-5211, mean oyster count = 9.8, SD =

0.42) with cyanoacrylate glue to ceramic wall tiles (Daltile model RE1544HD1P4, 10.6 x 10.6

216   cm). Tiles were individually numbered and held in flow-through seawater tables for two days to

verify secure attachment between oysters and tiles. The tiles were also photographed prior to

218   deployment to evaluate potential differences in oyster size, but there was no difference in size

across cage treatments (linear mixed model, Wald χ^2 = 1.1, Df = 3, P = 0.83). We then randomly

220   assigned tiles to one of three treatments: 1) uncaged, fully exposed to predators; 2) caged, no

exposure to predators; 3) cage controls. Cages were made of polyethylene aquaculture netting

222   (Memphis Net & Twine PN3, 62.5 mm mesh), wrapped with plastic window screening (Phifer

BetterVue Screen, 1 mm mesh), which improved the exclusion of oyster drills in pilot

224   experiments. The cage controls were designed to evaluate cage artifacts, such as shading and

reduction of water flow. Cage controls which were identical to the caged treatment except for

226   openings (2.5 x 5 cm) that were cut into each cage, which allowed drills access to oysters. Tiles

and cages were installed facing horizontally, attached with plastic cable ties to bricks, which

228   were in turn attached to metal rebar driven into the substrate. The bricks were used to keep the

       experimental units upright and secured to the rebar. Experimental units were randomly stratified

230   by caging treatment type along the +0.5 m MLLW tidal elevation within each removal and

       control zone at our two field sites (8 replicates x 3 cage treatments x 2 eradication treatments x 2

232   sites = 96 experimental units). Tiles and cages were checked one day after deployment (after

       exposure to two periods of submergence by high tide) to confirm cage integrity.

234   After 30 days of exposure to field conditions, we recovered 95 of 96 experimental tiles

       (one uncaged tile was lost) and returned them to the laboratory where each was photographed

236   and examined under a dissecting microscope. Of the 32 caged tiles, we excluded 4 from analysis

       and graphing because predator exclusion cages were compromised, allowing entry by oyster

238   drills. Oysters were recorded as falling into one of four categories: alive, dead, drilled, or

       missing. Oysters were scored as alive if the valves retracted upon tapping with a probe. Oysters

240   were classified as dead if no body tissue was found in valves or if the upper valve was removed

       entirely but the basal valve remained. Oysters were scored as drilled if a bore hole was evident in

242   one of the oyster valves and no body tissue remained. We also quantified oyster growth for

       surviving oysters from the caged treatment by measuring shell area using image analysis

244   software (ImageJ ver 1.51j8; Schneider et al. 2012). Quantifying oyster growth in the caged

       treatment allowed us to determine whether the sites were suitable in the absence of oyster drills.

246   Growth was quantified as the final shell area minus the initial shell area for individual surviving

       oysters.

248   ***Statistics***

           To quantify the relationship between the abundances of oyster drills and prey oysters, we

250   used a permutation approach to calculate the Spearman rank correlation between their

abundances in the quadrat survey data prior to eradication efforts. We used this approach

252   because there was very little coexistence between predator and prey in observational data (i.e.

drills and oysters were rarely found in the same quadrat; Fig. 2). This had the effect of generating

254   non-parametric data and many ties in rank that precluded calculation of a p-value for correlation

tests. Thus, we randomized (permuted) the data 10,000 times and generated a distribution of

256   Spearman rank correlations and compared it to our original rank correlation to calculate a p-

value.

258   To evaluate the efficacy of oyster drill eradication efforts, we used two approaches. First,

we formulated a removal density target based on prior work from nearby Tomales Bay (Cheng

260   and Grosholz 2016), which demonstrated the potential for oyster drill and oyster coexistence at

average drill densities of 5 m^{-2}. We then evaluated oyster drill densities at the eradication and

262   control sites with respect to this density removal target using quadrat data after the initiation of

removal efforts. Second, we modeled CPUE over time with the expectation that decreased yield

264   would occur once removal efforts began having negative impacts on oyster drill populations. We

used generalized linear mixed models to evaluate the fixed effect of time (day of year), site, and

266   their interaction on CPUE (number of drills captured per person). For these models we used a

random year effect with a negative binomial error distribution, and an offset term to account for

268   the number of persons and the length of time (person hours) as an index of effort.

To quantify the effect of the removals and cage treatments, we initially used generalized

270   linear mixed models to measure oyster survival. However, the data exhibited complete

separation, which occurs when the response data is perfectly predicted by the independent

272   variables (i.e. there is zero variation in a predictor level). Therefore, we used Firth's bias reduced

logistic regression (Heinze and Schemper 2002), which uses a penalized maximum-likelihood

274   estimation procedure. For this analysis, we modeled the effects of experimental manipulation

(snail removal vs. control), caging treatment (caged, open, partial), and their interaction as

276   predictors of oyster survival. We modeled surviving and dead oysters at the level of replicate tile

(i.e. binomial regression) and assumed that missing oysters were dead. To explore the potential

278   for site-specific differences in environmental conditions to influence oyster performance in the

absence of predator effects, we quantified the growth of living oysters within the caged plots

280   (predator exclusion) across all sites. Here we used a linear mixed model with Gaussian error

distribution to evaluate the fixed effect of site and the random effect of tile on oyster growth. All

282   analyses and plots were produced in R (ver. 4.0.3; R Core Team 2020), using the packages

'brglm', 'tidyverse', and 'glmmTMB' (Brooks et al. 2017, Wickham et al. 2019, Kosmidis and

284   Firth 2020).

RESULTS

286   *Observational sampling*

Quadrat surveys revealed a strong inverse relationship between oyster drills and oysters

288   across the eight monitoring sites (Fig. 2). At 7 of 8 sites, quadrats revealed the presence of

oysters or oyster drills but never both. In fact, only 2 out of 324 quadrats contained at least one

290   live oyster and one live drill (both quadrats at Aramburu control). The randomization test

revealed strong evidence for a negative relationship between oysters and drills (ρ = -0.55, P

292   <0.001).

Functional eradication of drills

294   Over 6 events in 2017 and 2018 at the Aramburu removal site, we recruited 115

participants who worked 183 hours to remove 12,261 oyster drills. Over 7 events in 2017 and

296   2018 at Lani's, we recruited 202 participants who worked 284 hours to remove 19,297 oyster

drills. Success in achieving the density removal target was limited. The target of 5 oyster drills

298   m^{-2} was only achieved at 1 of 6 possible time points (excluding the survey prior to removal

efforts) at Aramburu (Fig. 3). At Lani's the target removal density was achieved at 3 of 7

300   possible time points in cobble habitat and at 0 of 7 time points in boulder habitat (Fig. 3). In

addition, drill densities were well above the target density prior to the July 2018 oyster outplant

302   experiment, averaging 16.4 drills m^{-2} at Aramburu and 15.2 and 207.1 drills m^{-2} at Lani's cobble

and boulder habitat, respectively. There was no evidence that oyster drill CPUE changed over

304   time at either site (Table 1, Fig. 4).

Oyster outplant experiment

306   Oyster drill removal efforts did not appear to affect oyster survival. Survival in the oyster

outplant experiment was highly dependent on caging treatment but not the removal treatment,

308   nor their interaction (Table 1, Fig. 5-6). In the caged plots, overall survival was 89.1% (246 of

276 oysters), whereas survival was 0% (0 of 305 oysters) and 1.6% (5 of 315 oysters) in the open

310   and partial caged plots, respectively (Fig. 6). The number of drilled oysters also differed based

on cage treatment. We found 0 drilled oysters in caged plots, as opposed to 148 (48.5%) and 127

312   (40.3%) in open and cage control plots, respectively (Supplementary Information S2). Oysters

from the caged plots not only survived well across sites but also exhibited high growth that

314   ranged from 1.8-2.3 cm^2 (378-456%) over the 30-day experiment (Fig. 7). There was some

marginal evidence for differences in growth across sites (Wald $\chi^2 = 6.9$, df = 3, P = 0.075) but

316   differences were small and all locations supported positive and high levels of growth.

DISCUSSION

318   Even though oyster drills have life history traits that appear ideal for functional

eradication, our efforts to manage this species resulted in limited success. Removals of over

320   30,000 oyster drills from Aramburu and Lani's partly reduced oyster drill abundances but were

insufficient to reach target oyster drill densities, only achieving this goal for 4 of 13 total survey

322   time points in cobble habitat. We also saw no evidence for declining CPUE, which would have

been expected if oyster drill populations were undergoing significant depletion. Consequently,

324   the survival of Olympia oysters in our outplant experiment was extremely low and unaffected by

the removal treatment. In contrast, survival was highly dependent on the caging treatment (high

326   survival only in predator exclusion treatments) where up to 48.5% of oysters had drill holes,

highlighting the role of predator-induced mortality by drills. There was also no evidence that

328   environmental site-specific differences could have driven oyster mortality. Oysters in the

predator exclusion treatment exhibited high survivorship and high growth across all sites. Taken

330   together with our observational surveys which revealed a strong negative relationship between

oysters and predatory oyster drills, these data suggest large negative effects of non-native

332   *Urosalpinx* on Olympia oysters in Richardson Bay and likely other regions of San Francisco Bay

(Wasson et al. 2014).

334   Future functional eradication efforts are likely to be most successful if the mechanisms

underlying population persistence of the introduced species are well understood. Efforts to

336   control other introduced marine species have been successful at low population sizes and early

stages of invasion. For example, successful control efforts for non-native mussels in Spain used

338   community science approaches to remove approximately 800 mussels in one event at 1-2 years

after initial detection (Miralles et al. 2016). Likewise, community science-based control efforts

340   with lionfish "derbies" have been successful in areas with annual removals on the order of 1,000

fish (Green et al. 2017). By contrast, our efforts over 3-4 removal events yielded 5,000 -10,000

342   oyster drills per year at each site but without lasting impact on local densities, suggesting a much

greater total population size for these established *Urosalpinx* populations. Such results highlight

344 the importance of focused high-intensity control efforts soon after introduction when abundance and population persistence may be low (Simberloff et al. 2013). The above discussed removal

346 efforts may also have been aided by the lack of a temporal or spatial refuge (e.g., sessile or tropical species). In contrast, our removal efforts may have been further compounded by the

348 overwintering of oyster drills. During colder winter months, drills reduce their activity and may burrow within sediments which could provide a spatial and temporal refuge from removal efforts

350 not seen with sessile species such as mussels (Carriker 1955). We aimed for spring removals, prior to initiation of egg clutch laying to prevent the recruitment of young drills, but it was also

352 possible that not all drills were active in earlier removal events, reducing the efficacy of these efforts. Another possible mechanism limiting our success may have been reinvasion of oyster

354 drills from neighboring habitat via emigration, as opposed to larval dispersal. This could have occurred if drills were located at intertidal heights below our focal removal area or adjacent to

356 our focal removal areas in the alongshore direction. Given the limited movement of oyster drills observed in pilot mark-recapture experiments, this mechanism would seem possible but less

358 likely. We also observed an initial decrease in oyster drill density at Aramburu concomitant with the removal events, followed by an increase (Fig. 3A). The mechanism for this pattern is unclear

360 but could have been linked to "overcompensation" or the "hydra effect", which occurs when removals counterintuitively result in population increases (Roos et al. 2007, Abrams 2009). Such

362 a phenomenon can arise if removal reduces the strength of negative intraspecific interactions (e.g. competition or cannibalism) driving greater population growth, as seen in fish harvesting

364 efforts in lakes (Zipkin et al. 2008) and the removal of invasive European green crabs (Grosholz et al. 2021).

366   Instead of functional eradication, greater success with oyster drill control might be

achieved via species interactions with native species (i.e., biotic resistance; Kimbro et al. 2009).

368   Native rock crabs (*Romaleon antennarius* and *Cancer productus*) are generalist consumers that

prey upon oyster drills in laboratory and field experiments and appear to set the local range limit

370   of oyster drills (*Urosalpinx* and *Ocinebrellus inornatus*) in Tomales Bay (Cheng and Grosholz

2016). Although we did not quantify native crab densities in this study, we rarely observed these

372   crab species at our sites and observed extremely high oyster drill densities as compared to other

estuaries, suggesting that oyster drills experience low predator-induced mortality. Given the

374   coastal distribution of these crabs and evidence for lower thermal preferences (Sulkin and

McKeen 1994, Padilla-Ramírez et al. 2015), one possibility is that rock crabs are thermally

376   limited in Richardson Bay. These sites are located adjacent to broad intertidal mudflats which

may limit the movements of crabs and the accessibility of thermal refugia (e.g. deep, cooler

378   waters). In addition, crabs themselves may be subject to predator-induced mortality from birds,

sharks, and rays (Gray et al. 1997, Ebert and Ebert 2005). Future oyster restoration efforts may

380   benefit from a greater mechanistic understanding of the forces limiting crab abundance to take

advantage of the trophic cascades that these predators can generate (Kimbro et al. 2009, Cheng

382   and Grosholz 2016).

        Oyster drills have widespread predatory effects on native oysters throughout many

384   estuaries in California, including Tomales Bay (Kimbro et al. 2009, Cheng and Grosholz 2016),

Humboldt Bay (Koeppel 2011), and San Francisco Bay (this study). Oyster drills have are also

386   established in Willapa Bay, WA although they appear to have a smaller role in driving oyster

mortality there (Buhle and Ruesink 2009). *Urosalpinx* impacts include lethal, as well as non-

388   lethal effects, such as induced shell thickening in the presence of oyster drills (Bible et al. 2017).

Evidence from this study and others suggests oyster restoration at sites with established

390   populations of oyster drills are unlikely to be successful. Oyster populations at central San

Francisco Bay sites, which experience more frequent low salinity periods, appear to have refuge

392   from predators because the salinity tolerance of drills is lower than that of oysters (Cheng et al.

2017). However, such sites can also experience both extreme low-salinity events that can drive

394   oyster mass-mortality events (Cheng et al. 2016) and extreme variation in oyster recruitment

(Chang et al. 2018). Alternatively, lower estuary sites may be suitable if they can support crab

396   populations that can suppress oyster drill abundance. However, these sites may have diminished

recruitment of oyster larvae driven by greater coastal influence and reduced residence time of

398   water masses (Wasson et al. 2016, Chang et al. 2018). Given the dynamic variation of physical

and abiotic conditions within estuaries, the impacts of oyster drills, and therefore success of

400   oyster restoration efforts will be highly dependent on within estuary siting.

One largely successful aspect of this project was the engagement with community

402   members. This project recruited over 300 volunteers in our outreach and research activities,

highlighting the significant interest in non-native species control and shoreline restoration, and a

404   small group of volunteers enthusiastically continued to remove snails from Lani's, removing

another ~13,000 snails in 2019. Such a partnership is critical for building science knowledge

406   among the public and garnering public support for environmental science issues (Larson et al.

2011, Novoa et al. 2018). Community science partnerships have grown considerably in the last

408   several decades , and this project serves as a regional model for interacting with the community

in a science-based context.

410   Overall, our study highlights the difficulties of managing established and highly abundant

introduced species that have negative effects on native communities. For well-established and

412   successful species, functional eradication may be a viable option for suppressing introduced

species, but there should be careful consideration of the species' life history and environmental

414   conditions in determining project success. In situations where functional eradication may not be

feasible, promoting biotic resistance by native enemies and focusing on containment may be

416   more desirable uses of the limited time and resources available to manage highly successful

invaders whose impacts may intensify under radically changing environmental conditions.

418   **ACKNOWLEDGEMENTS**

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596

598 **Table 1.** Statistical results from multiple surveys and experiments. A) Catch per unit effort

modeling, testing for a change in CPUE over time (day of year) across sites. CPUE is modeled as

600 number of drills caught standardized by effort with a person-hour offset. B) Results from bias

reduced logistic regression for the oyster caging experiment. The caged plots at control sites are

602 the intercept and all parameter estimates are in relation to this group. The model estimates

survival, so a negative estimate indicates that survival declines in relation to the caged treatment

604 (i.e. for open and partial cage treatments). Only caged treatments had an effect on oyster

survival, whereas oyster drill eradication had no effect.

	Parameters	Estimate	SE	z-value	P
606					
	A) Catch per unit effort				
608	Aramburu (intercept)	4.17	0.49	8.5	<0.001
	Day of year	0.00	0.01	0.12	0.90
610	Lani's	0.62	0.57	1.11	0.27
	Day of year * Lani's	-0.01	0.01	-0.89	0.38
612					
	B) Oyster caging experiment				
614	Caged (intercept)	2.14	0.30	7.14	<0.001
	Open	-7.84	1.45	-5.40	<0.001
616	Partial cage	-5.67	0.57	-10.02	<0.001
	Eradication	-0.11	0.39	-0.30	0.77
618	Open x Eradication	0.07	2.05	0.03	0.97
	Partial cage x Eradication	-1.01	1.03	-0.98	0.33

620

Figure 1. Map of study sites within Richardson Bay, California. Green circles represent sites

622   selected as monitoring locations. Blue triangles represent experimental eradication treatment and

control sites. Inset map: the red rectangle depicts location of Richardson Bay within greater San

624   Francisco Bay.

626

628
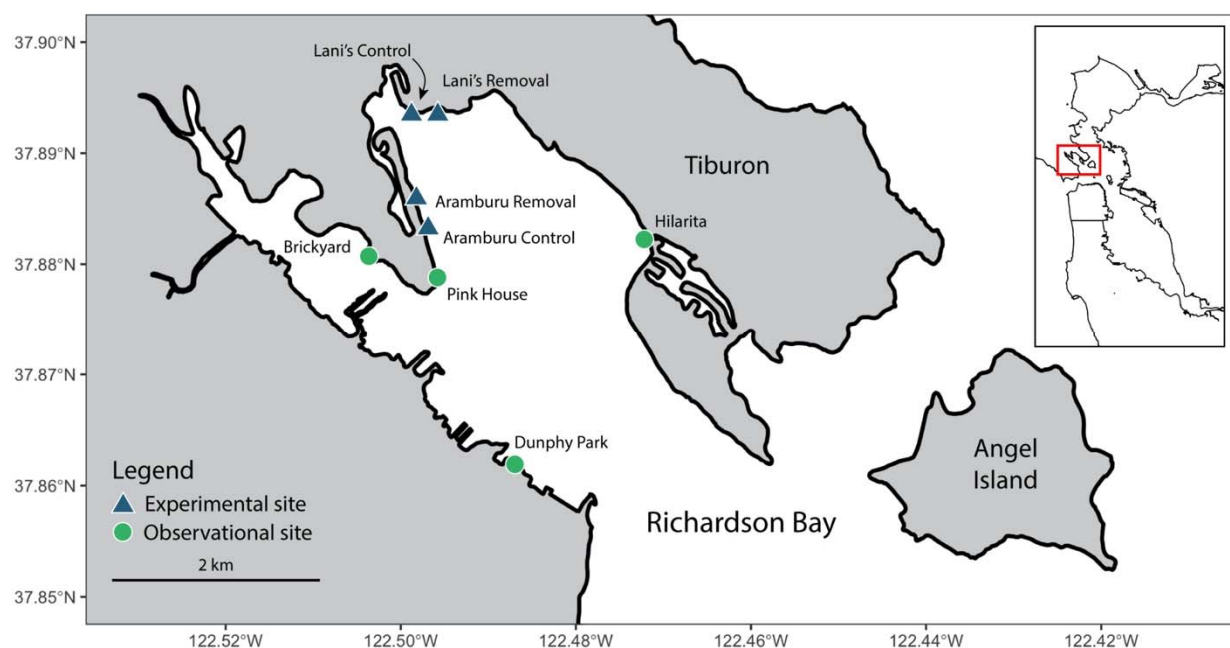
Figure 2. Relationship in abundance between non-native oyster drills and native oysters. There

630   is a strong inverse relationship between the two species where they are rarely found in the same

quadrat. Points represent mean counts at each site from quadrat data. Error bars represent

632   standard errors of mean and are calculated for both oysters and drills as double error bars

(vertical and horizontal). Most points do not have visible double error bars because of the strong

634   inverse correlation between species. Vector images courtesy of Tracy Saxby and the Integration

& Application Network at the University of Maryland Center for Environmental Science.


636
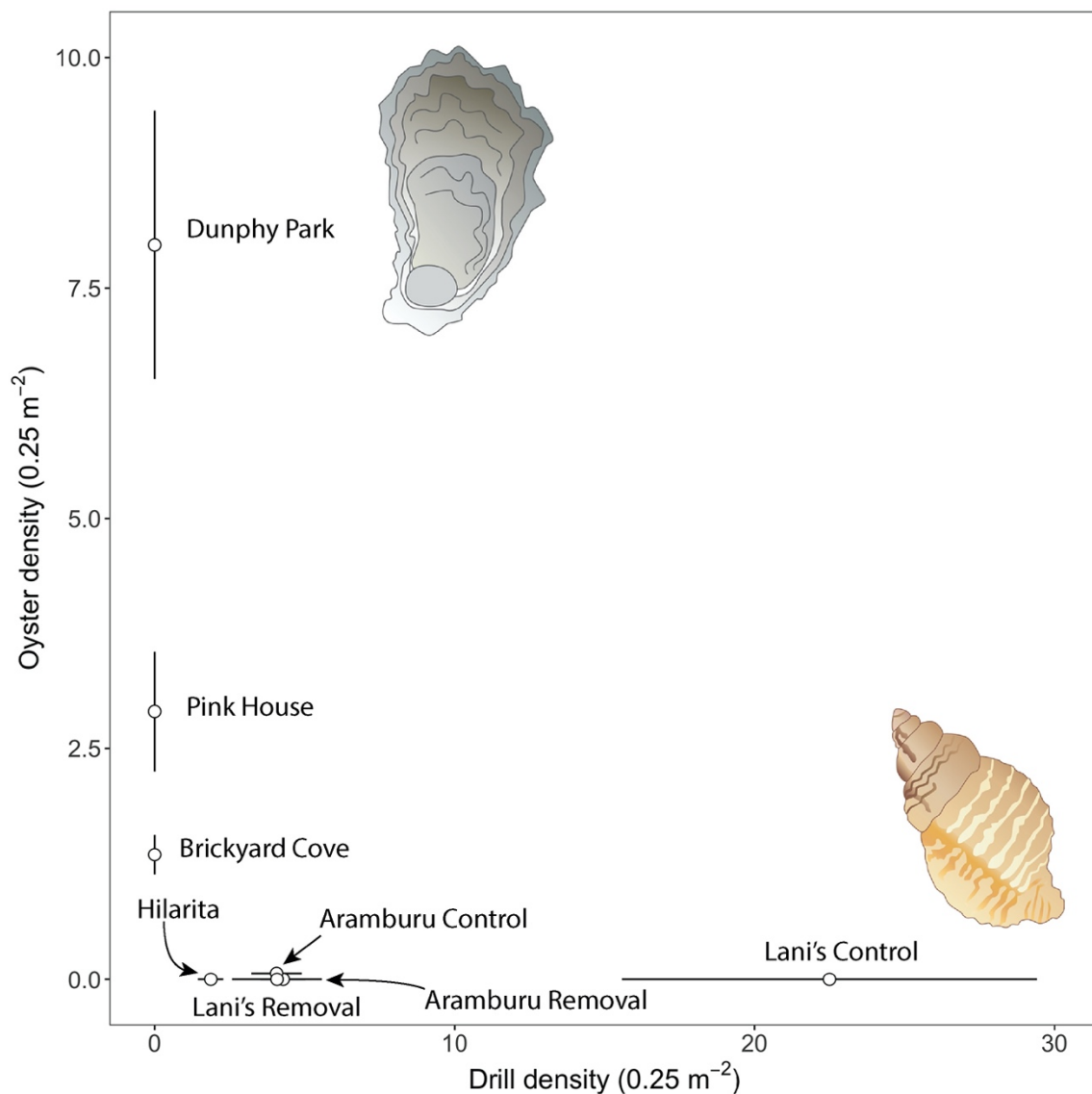
Figure 3. Oyster drill densities across control and removal sites at A) Aramburu and B) Lani's.

638   Point and error estimates refer to mean $\pm$ SEM. Dashed line represents the density target based

on coexistence of oyster drills and oysters in nearby Tomales Bay. Note the different y-axis

640   scales on each panel.

642
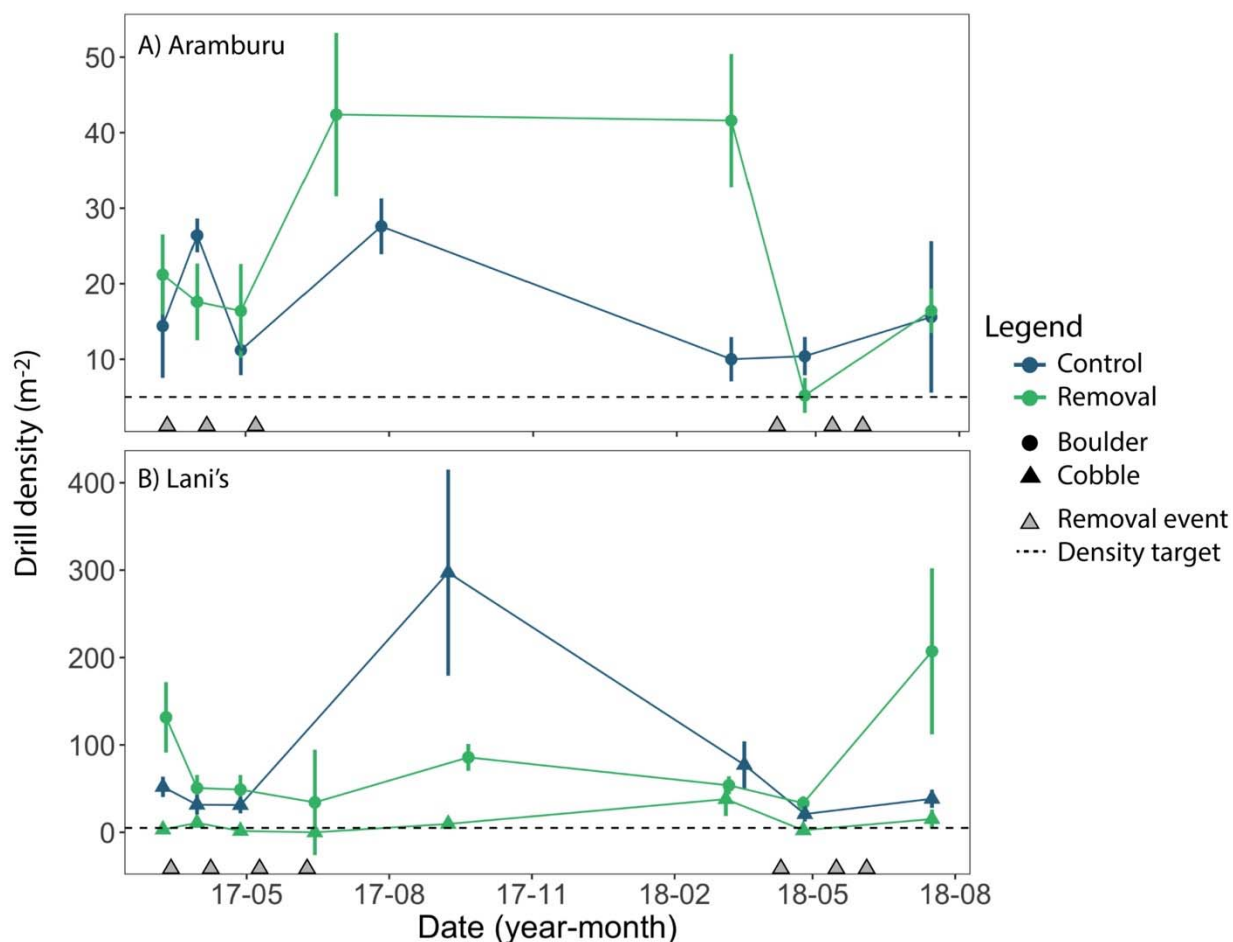
Figure 4. Catch per unit effort (CPUE) across day of year at each eradication site in 2017 and

2018. CPUE is calculated as number of drills captured per person-hour. Each point refers to a

CPUE estimate for individual volunteer groups. Bolded point and error bar refers to mean CPUE

and standard error of the mean for that eradication day. We hypothesized that CPUE would show

a downward trend over time if removals were causing declines in population abundance.
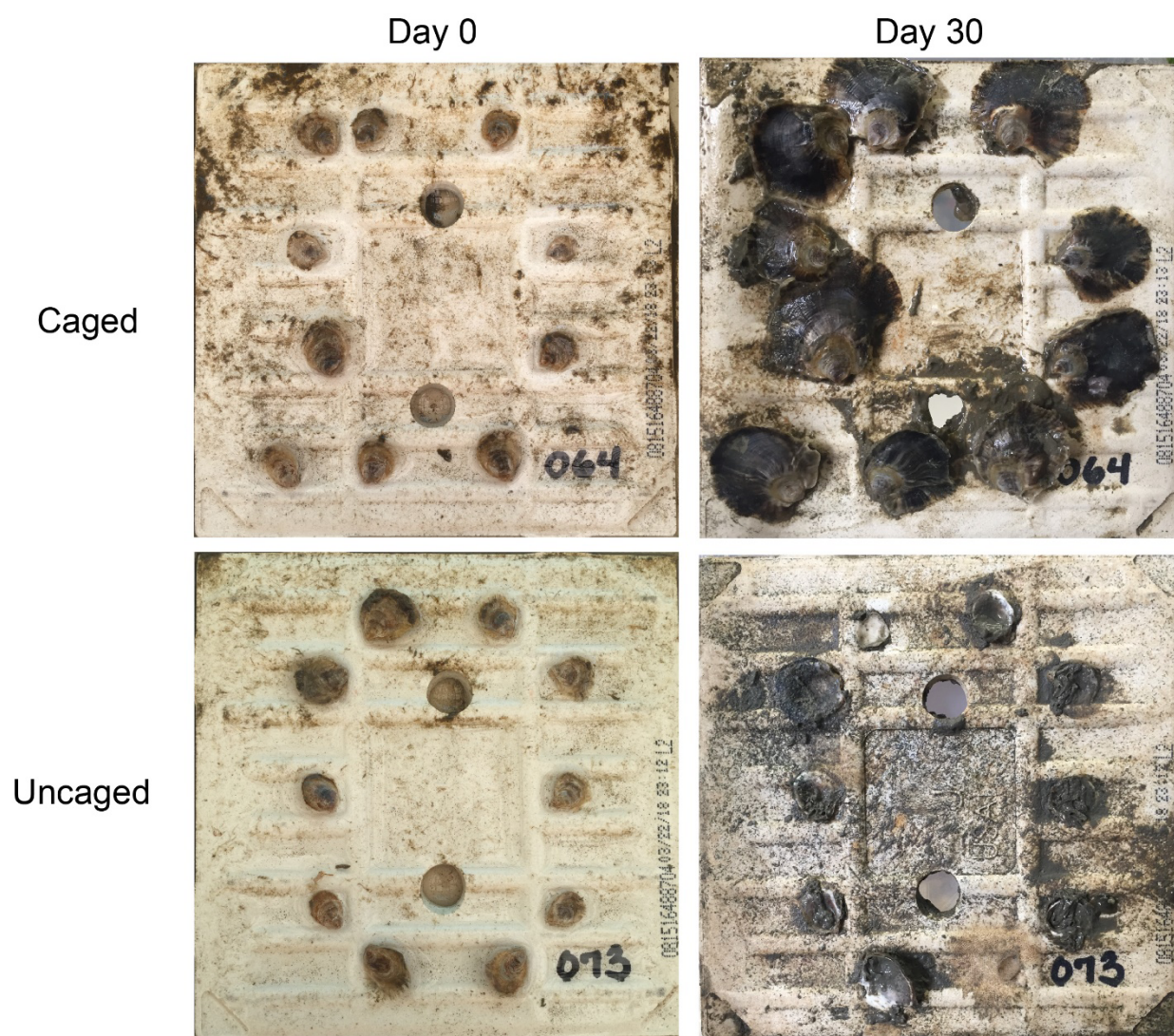

648
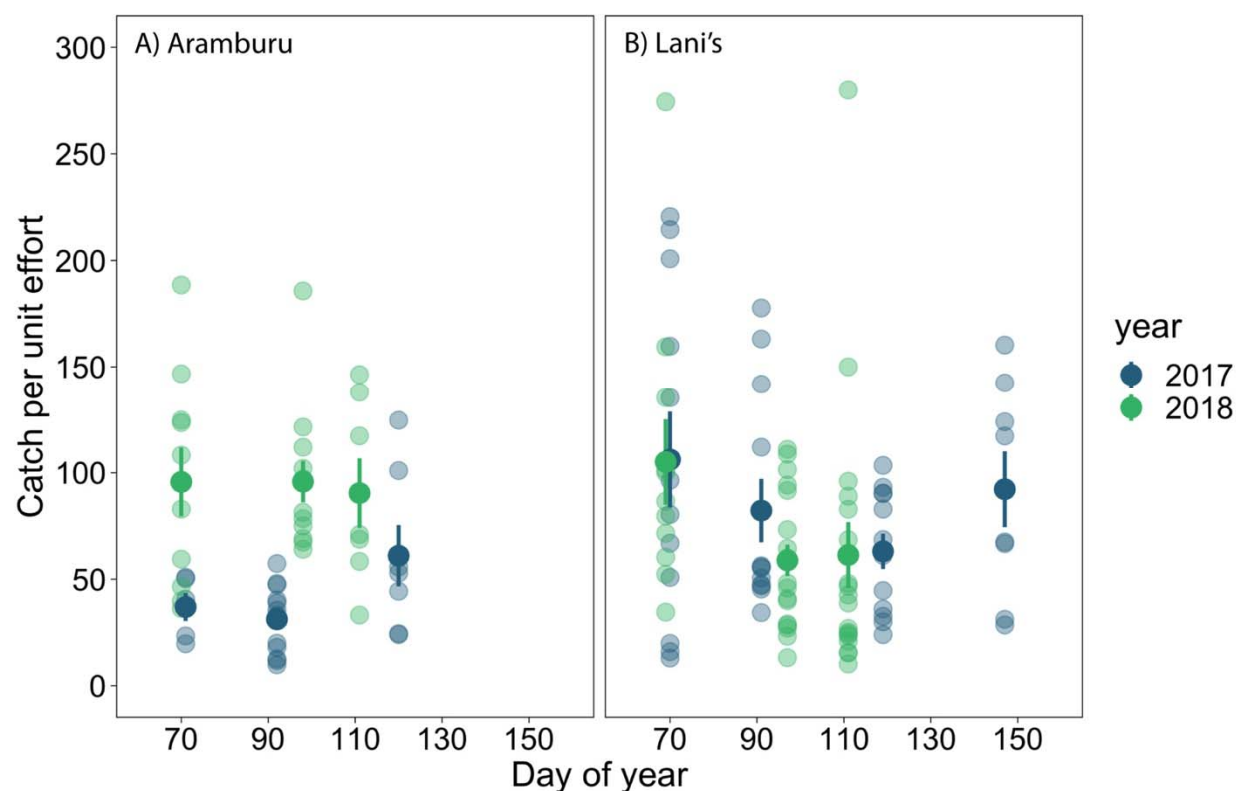
650   **Figure 5.** Sample photographs of oyster tiles before (day 0) and after field deployment (day 30).

The caged tile was protected from predators whereas the uncaged tile was exposed. The center

652   bore holes were used to affix the tile to the cage and/or rebar stake.


654

656

Figure 6. Oyster survival across caging treatments at A) Aramburu and B) Lani's at control and

658   removal sites. Survival is plotted with boxplots and overlaid jittered points. Proportional survival

was calculated at the tile level (N = 5-8 tiles per treatment). Boxplots collapse to a solid line

660   because of zero variation (and zero survival) in most open and partial cage plots.

662
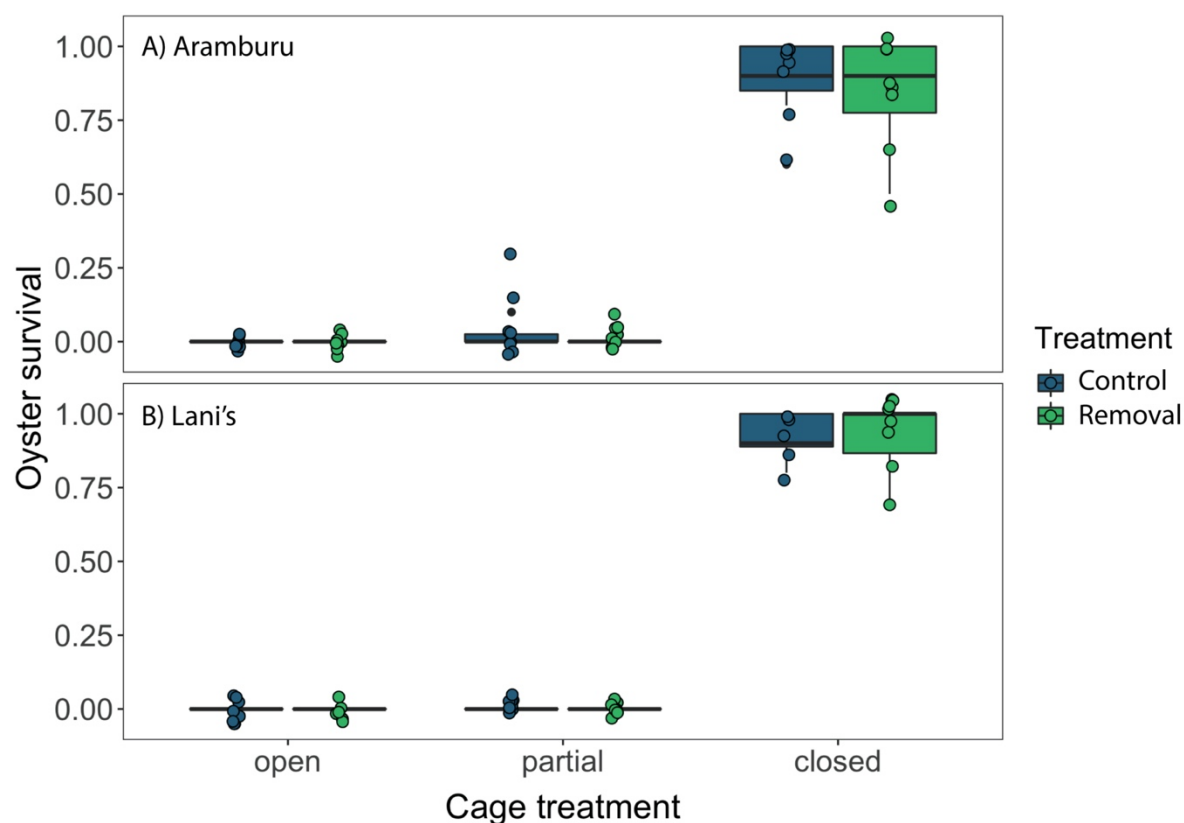
Figure 7. Violin plots of oyster growth from caged (predator exclusion) tiles across sites at A)

664   Aramburu and B) Lani's. Point and error estimates within each violin refer to the mean $\pm$SD. N =

68 and 67 oysters at Aramburu control and removal, respectively. N = 43 and 74 oysters at

666   Lani's control and removal, respectively.

![Violin plots of oyster growth (cm²) by treatment (Control, Removal) for A) Aramburu and B) Lani's.](image)

668
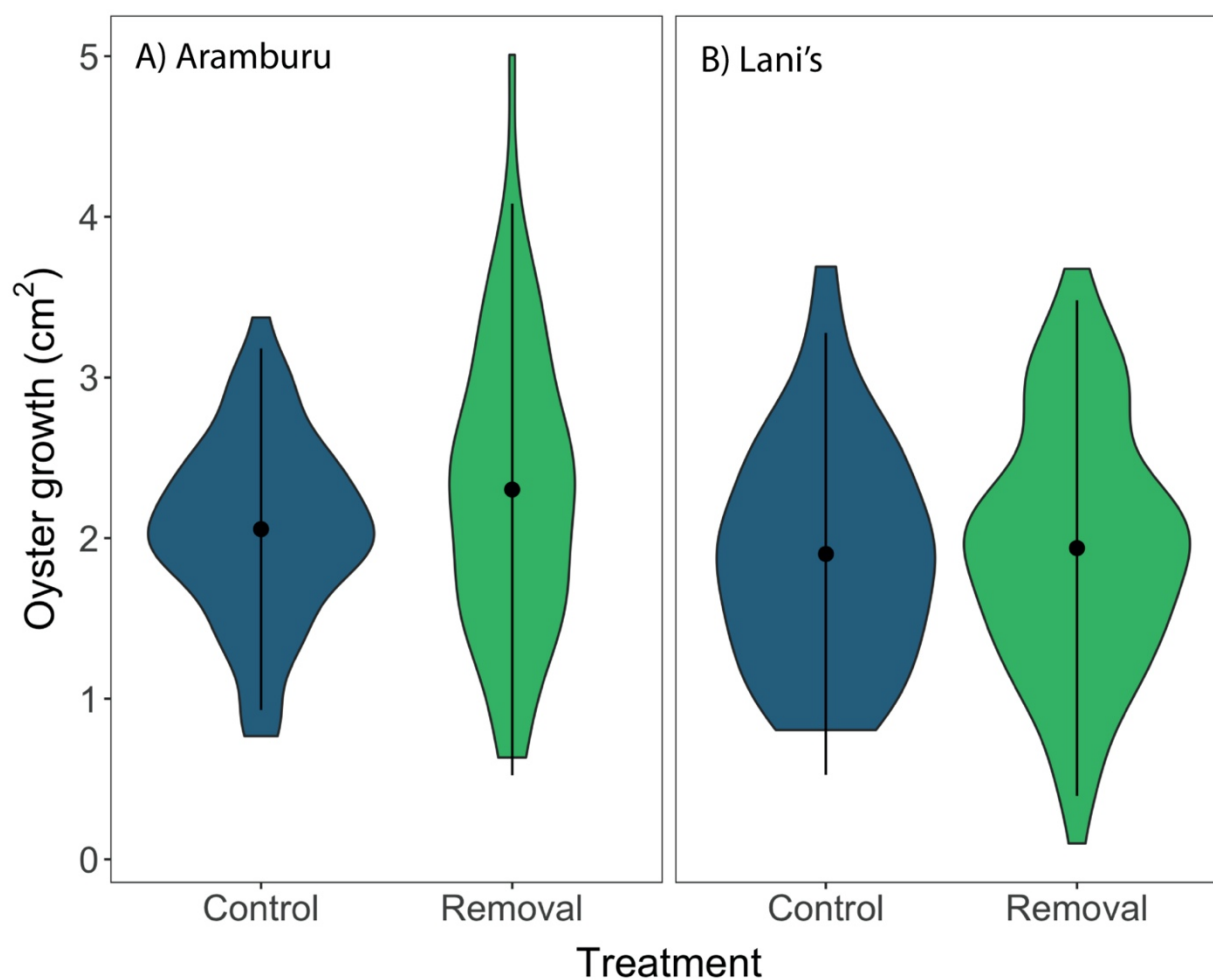
Supplementary Information S1. Specific location of observational transects (dashed lines, 30

670   m length) and eradication zones (solid rectangles, 60 x 15 m) at **A)** Aramburu Control, **B)**

Aramburu Removal, and **C)** Lani's Control and Removal. Lines and rectangles are

672   approximately drawn. *Google Earth*, earth.google.com/web (June 10, 2019). Eye altitude 550

feet.

674

676   **Supplementary Information S2.** Drilled oysters across caging treatments at A) Aramburu and

B) Lani's at control and removal sites. Drilled oysters are plotted with boxplots and overlaid

678   jittered points. Drilled oysters were calculated as a proportion (number of oysters possessing at

least one drill hole divided by the initial number of oysters at the tile level). N = 5-8 tiles per

680   treatment. Boxplots collapse to a solid line because of zero variation (and zero survival) in all

closed plots.

682