

RESEARCH ARTICLE

The survival of hatchery-origin pinto abalone *Haliotis kamtschatkana* released into Washington waters

Henry S. Carson¹  | Dana J. Morin² | Joshua V. Bouma³ | Michael Ulrich¹ | Robert Sizemore¹

¹Washington Department of Fish and Wildlife, Fish Management Division, Olympia, Washington, USA

²Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, Illinois, USA

³Puget Sound Restoration Fund, Bainbridge Island, Washington, USA

Correspondence

Henry S. Carson, Washington Department of Fish and Wildlife, Fish Management Division, 1111 Washington St. SE, Olympia, WA, USA. Email: henry.carson@dfw.wa.gov

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Abstract

1. Wild populations of pinto abalone (*Haliotis kamtschatkana*) in Washington State have declined by 97% since 1992, despite a fishery closure since 1994. No recruitment has been detected recently, indicating probable reproductive failure due to low densities. A pilot programme placed a total of over 11,000 hatchery-origin juveniles, age 18–22 months, at 10 sites in the San Juan Islands.
2. Observed (naive) year 1 survival averaged 10.2% (0–23% range) and was most influenced by site compared with lineage or size-at-outplant. Families survived in the approximate proportions that they were outplanted, and there was little support for an effect of size-at-outplant on survival.
3. Detection was low due to the small chance of sighting individuals on complex substrate. When derived from repeated sampling, an upper bound on naive detection rate averaged 0.38 and increased with size. When derived from a closed capture–recapture model, average detection was estimated at 0.19.
4. Growth was highly variable and confounded with detection, but an average 3.4% of detected outplants across all sites (0–7.5% range) had reached reproductive size in 2017.
5. A state-space model of exponential population growth was modified to account for imperfect detection and yielded an estimated density of abalone for each survey. Seven out of eight sites included in the model remained above a target abalone density of 0.3 m⁻² throughout the project.
6. The majority of tagged abalone made little net movement over weekly and annual timescales, although some emigration likely reduced survival estimates.
7. The restoration programme is transitioning from a pilot phase to a production phase, including optimization of hatchery and outplant processes. Existing well-performing sites will receive additional cohorts every 4–5 years to maintain aggregation densities. New sites will replace poorly performing ones, although this is hampered by a poor understanding of the mechanisms behind site performance.

KEYWORDS

archipelago, benthos, fishing, invertebrates, modelling, recovery, subtidal

1 | INTRODUCTION

Abalone populations have declined in many places worldwide in recent decades while illegal harvest has increased (Cook & Gordon, 2010). The pinto or northern abalone (*Haliotis kamtschatkana kamtschatkana*) is no exception, with population declines documented throughout its range in Alaska (Woodby, Larson, & Rumble, 2000), British Columbia (Campbell, 2000), Washington (Rothaus, Vadopalas, & Friedman, 2008), and California (Rogers-Bennett, 2007). The US National Marine Fisheries Service conducted a comprehensive status review of the species in 2014 for potential listing as threatened or endangered under the Endangered Species Act (National Oceanic and Atmospheric Administration [NOAA], 2014). The panel did not list the species, citing, among other things, insufficient evidence that it is distinct from the threaded abalone (*Haliotis kamtschatkana assimilis*), which if correct would substantially extend the range. Since the Endangered Species Act does not permit listing of distinct population segments for invertebrates, the panel found that 'the pinto abalone is not currently in danger of extinction throughout all or a significant portion of its range'. Given considerable uncertainty about the severity of threats and demographic risks, the panel retained it as a 'species of concern' (NOAA, 2014). It has been listed as an endangered species in Canada since 2009 (Committee on the Status of Endangered Wildlife in Canada, 2009).

Putting the uncertainty about the range-wide status of the species aside, the pinto abalone population in Washington State is clearly in peril. The Washington Department of Fish and Wildlife (WDFW) closed the recreational fishery in 1994 following concerns of population decline. Abalone densities at 10 fixed index sites placed in areas of known abundance in the San Juan Islands declined from 0.18 m⁻² in 1992 to 0.04 m⁻² in 2006 (Rothaus et al., 2008) and further to 0.005 m⁻² in 2017 (WDFW, unpublished data). The sites collectively held 359 abalone in 1992; 12 remain. The earliest estimates of San Juan Island density are from WDFW timed-swim surveys at 30 sites in 1979 and averaged 25.5 individuals encountered by two divers in 20 min of searching (WDFW, unpublished data). During broodstock collection dives for the research described here, divers averaged 1.1 abalone per 20 min search (WDFW, unpublished data). While adult density declined, there was little evidence of recruitment (Bouma, Rothaus, Straus, Vadopalas, & Friedman, 2012) and the remaining individuals increased in average size. Average shell length in 1979 was 97.6 mm. It had increased to 105.3 mm during the first index station survey in 1992 and has increased to 127.3 mm on those sites in 2017 (WDFW, unpublished data).

Recreational harvest prior to the 1994 closure is a likely cause of population decline. Rogers-Bennett, Hubbard, and Juhasz (2013) demonstrated the ability of recreational fishers to quickly and severely impact a previously unfished red abalone (*Haliotis rufescens*) population in California. In Washington, Bargmann (1984) estimated an annual recreational catch of 38,000 individuals based on diver surveys, and a later survey by Gesselbracht (1991) estimated that catch to be 41,000 annually. Palsson, Lippert, and Goff (1991) documented the popularity of dive charters specifically for finfish and shellfish collection, during which abalone were frequently targeted.

The causes of the continued decline after the fishery closure could include disease, changing ocean conditions, illegal harvest, and recruitment failure due to a low adult density (i.e. the Allee effect, reviewed in marine systems by Gascoigne & Lipcius, 2004). Although north-eastern Pacific abalone species are susceptible to a variety of diseases with potential population-scale effects such as withering syndrome (Friedman et al., 2000), the Endangered Species Act review panel found no evidence of disease outbreaks in any wild pinto abalone populations (NOAA, 2014). Changing ocean conditions may have led to severe population declines over a 30-year period at the southern edge of the pinto abalone's range where they are not fished (Rogers-Bennett, 2007). Crim, Sunday, and Harley (2011) showed that pinto abalone larvae are negatively affected by elevated parts per million CO₂, but the treatment level tested, 800 ppm, was meant to simulate conditions in the year 2100. It is unlikely that the thermal tolerances of abalone are being approached in Washington waters (Bouma, 2007; data presented in Section 2.3). High-profile arrests of abalone poachers in the 1990s are testament that at least some harvest continued after the fishery was closed (WDFW, unpublished data). It is difficult to determine the scale of illegal fishing, but the extremely low densities of abalone that occur now probably tip the balance of risk versus reward away from continued illegal harvest at the commercial scale.

Rothaus et al. (2008) reviewed various causes for post-fishery population declines in the pinto abalone, concluding that the most parsimonious explanation was recruitment failure due to the low remaining density of broadcast spawning adults (Allee effect). Since establishment in 1992, San Juan Island index stations have hosted a density of adults well below an estimated fertilization threshold for a congeneric abalone (density of individuals 0.3 m⁻², Babcock & Keesing, 1999; see also Zhang, 2008). The observation that larger individuals are persisting is not consistent with typical patterns of poaching, and the lack of recruit observations (Rogers-Bennett, Allen, & Rothaus, 2011), later confirmed experimentally by Bouma et al. (2012), suggests that juveniles are not being produced.

If the Washington State population of pinto abalone has indeed experienced recruitment failure for several years, it is unlikely to recover without intervention. Accordingly, WDFW and the Puget Sound Restoration Fund partnered with a number of other organizations, including the National Marine Fisheries Service, University of Washington, Western Washington University, American Indian tribes, the SeaDoc Society, and the Skagit County Marine Resources Committee, to begin captive breeding and supplementation efforts for *Haliotis kamtschatkana*. Wild broodstock were collected from the San Juan Islands and used to produce juveniles for outplanting on test plots in the wild. The goal of this paper is to summarize the results of this effort and subsequent monitoring activities to date. Specifically, the feasibility of large-scale pinto abalone population enhancement via the outplant of hatchery-reared juveniles is evaluated by testing the effect of site, family, and size-at-outplant on the survival of outplanted abalone. The potential impacts of abalone movement, tag loss, and the detection rate of abalone during surveys are discussed. Lastly, the data generated by the project are used to recommend changes to the enhancement programme as planning for population-scale recovery begins.

2 | METHODS

2.1 | Species information

'Abalone' refers to the taxonomic assemblage of gastropod molluscs belonging to the Haliotidae family. The 56 currently described species of abalone are strictly marine and worldwide in distribution. The known range of *H. kamtschatkana kamtschatkana* is from Point Conception, California to Sitka, Alaska (Geiger, 2000) where they are patchily distributed in exposed and semi-exposed coasts. The southern subspecies *H. kamtschatkana assimilis* extends the species' range onto the Baja California Peninsula (Geiger, 2000). The nearshore depth distribution of the pinto abalone tends shallower with increasing latitude across its range (Sloan & Breen, 1988). In the area of this study, adult pinto abalone are most often found from -1 to -12 m mean lower low water. Pinto abalone favour hard substrates of bedrock, boulders, and large cobbles. They are herbivores and actively graze epiphytes and drift macroalgae on the benthos.

Pinto abalone, like other abalone species, are dioecious synchronous broadcast spawners. Timed to environmental cues, males and females independently discharge gametes into the water column. Gamete viability is limited, and therefore successful fertilization is necessarily dependent on a close aggregation of spawning adults (Babcock & Keesing, 1999; Zhang, 2008). Following a relatively short planktonic larval period of 7–10 days, settled juveniles can be highly cryptic and shelter into the interstices of the benthic habitat (Sloan & Breen, 1988). At a shell length between 50 and 70 mm pinto abalone become emergent to exposed areas of the benthos and mature to reproductive capability (Campbell, Manley, & Carolsfeld, 1992; Larson & Blakenbeckler, 1980; Paul & Paul, 1981). The average life span of pinto abalone is unknown; however, specimens in captivity have been kept for longer than 20 years (Paul & Paul, 2000).

2.2 | Hatchery rearing

The restoration partners developed a conservation aquaculture programme located at the NOAA Mukilteo Research Station, Mukilteo, WA. The primary goal of the hatchery programme is to produce genetically diverse, disease-free larvae and juveniles for research and supplementation efforts. Captive-bred juveniles reared for outplant have been produced at this hatchery facility since 2007. Wild broodstock were taken from the San Juan Archipelago by WDFW and Puget Sound Restoration Fund divers. Collection objectives included targeting reproductively isolated individuals from a wide geographic range across the archipelago. Considerable effort was made to avoid disturbance of natural aggregations during broodstock collections. Upon encountering a candidate 'singleton' abalone, divers thoroughly searched the benthos in a 5 m radius for additional conspecifics. If one or more were found, the abalone were not collected.

Upon arrival at the hatchery, intake of broodstock abalone included a general health assessment, measurement of shell length, weight, and visual gonad index, marking with a unique vinyl disc tag on the dorsal exterior shell, and passive integrated transponder on the ventral anterior shell according to Hale, Bouma, Vadopalas, and

Friedman (2012). A genetic sample from each animal in the form of several epipodial tentacle clips was taken and preserved. Broodstock were held in flow-through seawater tanks and fed fresh macroalgae ad libitum in preparation for induced spawning attempts. Conservation goals of the restoration collaboration in Washington State dictate that only F1 hatchery populations from wild collected broodstock are used during supplementation efforts, heightening the importance of these broodstock collection, handling, and maintenance protocols.

Feed regimes, modulation of pH, temperature, and light, along with the addition of hydrogen peroxide (Morse, Duncan, Hooker, & Morse, 1977), were used to induce spawning in the hatchery, and the gametes were used to produce single-parent crosses. Distinct families of lecithotrophic larvae were kept separate and reared to competency in flow-through columns for 7 days. The larvae were induced with γ -aminobutyric acid (Searcy-Bernal & Anguiano-Beltran, 1998) to settle into nursery tanks enhanced with fibreglass wavy plates. Following metamorphosis, post-larvae were reared on naturally occurring biofilm and supplemented with two cultured diatom feeds: *Navicula incerta* and *Amphora salina*. At approximately 6 months age, juvenile abalone were weaned from diatoms to a cultured red algae feed: *Palmaria mollis*. From 1 year until outplant age, the juvenile diet was diversified with the addition of bull kelp *Nereocystis luetkeana*.

The term 'family' is used to describe the offspring of each pairing of one female and one male broodstock. Some families share maternal lineage with other families; that is, one female's eggs were separately fertilized with sperm from multiple males, resulting in multiple families of half-siblings. Each family was reared in separate hatchery tanks through all life stages, so their success could be tracked during rearing. When the juveniles grew large enough, the separation of families allowed for tagging prior to outplant to track family success in the field. However, this means that any effects ascribed to family herein cannot be separated from possible impacts that the specific rearing environment ('tank effect') had before or after outplant.

2.3 | Site selection and establishment

Outplant sites were chosen during scouting dives (hereafter, 'dive' is used to denote the use of scuba) throughout the San Juan Islands. Criteria determining quality abalone habitat included depth, substrate type, substrate rugosity, algal cover, and current exposure. Selected sites were between -4 and -8 m mean lower low water, and were dominated by rocky reef habitat with high complexity and ample refugia (Aguirre & McNaught, 2013; Read, Lessard, & Boulding, 2013). Rock covered mainly with crustose coralline algae, as opposed to sessile invertebrates, was preferred, as was nearby bull kelp *N. luetkeana* (Rogers-Bennett et al., 2011; Sloan & Breen, 1988). Another criterion considered was current-swept areas without an accumulation of sediment on surfaces. The presence of existing abalone in the area was used as a signal of appropriate habitat, although wild adults are rare.

Specific site locations will not be fully described here, nor will a map be provided, due to the potential for illegal harvest. Site names, which would include the island name and other location information, have been replaced with code names derived from allied amphibious

assaults during the Second World War. Four sites were established on two San Juan Islands in 2009. Utah and Omaha are both on the south-west shore of the same island, separated by 700 m of linear distance. Gold and Juno are located approximately 1.5 km away on the south-west shore of another island, 200 m apart. Sword and Jubilee were established in 2011, 26 km away from the original four sites. They are located on the north-west (Sword) and east (Jubilee) shores of the same small island, 110 m apart. Husky and Baytown were established on a fourth island in 2015, located 7.5 km away from the original sites. They are on the south and east shores respectively and are 3 km apart. Avalanche and Dragoon were established in 2016 on the south shore of a fifth island, 20 km away from the original sites. Dragoon is located on an offshore reef 300 m from the coastline, and is separated from Avalanche by 1 km. All islands are uninhabited by humans, with the exception of Avalanche and Dragoon, which are located far from sparse island settlements.

Each plot consisted of a rectangle approximately 10 m on the alongshore sides and 8 m on the sides perpendicular to the shoreline. Divers placed four permanent pitons at the corners and attached buoyant polyethylene line to them to improve visibility. To begin each survey, a metre tape was strung through the pitons to define the plot boundary, and lead line was used to define five 2-m-wide lanes to subdivide the plot. Plots were surveyed before any outplant activity occurred, to note the presence of any existing abalone and also the presence/absence of other invertebrates and algae. Metre tapes and lead lines were removed after each survey.

Water temperature at all sites likely remained within the thermal tolerance of Washington pinto abalone throughout the project. HOBO Water Temperature Pro data loggers (Onset Computer Corporation, Bourne, MA) were affixed to one shallow and one deep corner of the plots at three sites, programmed to record the seawater temperature every 15 min. The time series on sites Utah and Juno extends from 2010 to 2015, with the exception of 2013 when data could not be retrieved. The time series on Sword extends from 2014 to 2017. October–March temperatures averaged 8.5–9.0°C for each site/depth, and April–September temperatures averaged 9.9–11.0°C. The all-time minimum temperature of 6.2°C is well above the 2°C threshold for behavioural abnormalities documented in Alaska (Paul & Paul, 1998). The all-time maximum temperature recorded (16.3°C) is well below the thermal tolerance thresholds derived for adult (24°C; Paul & Paul, 1998) and larval pinto abalone (21°C; Bouma, 2007).

2.4 | Juvenile tagging and outplanting

Juvenile abalone raised in the hatchery were outplanted at approximately 20 months after settlement. During tagged outplants, maximum shell length of each individual was measured to the nearest tenth of a millimetre using calipers. Size from various cohorts and families varied considerably (Supporting Information Table S2). Tagging and outplant procedures generally followed that of Hansen and Gosselin (2013), who demonstrated minimal tagging or handling mortality as a result. Abalone were marked with 2 mm circular bee-keeping tags (queen marking kit, The Bee Works, Ontario, Canada).

They were affixed to the shell near the spire using cyanoacrylate adhesive (Zap-A-Gap CA+ medium viscosity, Super Glue Corporation, Ontario, CA, USA). Tags were one of four colours, and each had a two-digit number, the combination of which could be used to identify an individual's family and initial size upon recapture. Whenever possible, families were divided evenly among available sites.

Whether or not the abalone were tagged, individuals were grouped into lots of approximately 50 and loaded into 15 cm diameter, polyvinyl chloride pipes 45 cm in length. Pipes were conditioned in flow-through seawater tanks for at least 1 week before use. Mesh netting was secured over each end using rubber bands to retain individuals while allowing water flow. Pipes were transported to outplant sites in aerated seawater tanks as quickly as possible. Divers placed each pipe on the plot and secured it in place with existing stones. All outplanting occurred during daylight hours, usually during midday slack tides. After an in-situ acclimatization period of 24 hr, divers returned to the plots to remove the netting and allow the abalone to leave the pipe.

2.5 | Outplant site surveys

At varying time intervals after outplant, ranging from 1 month to 7.5 years (Supporting Information Table S1), divers returned to the plots and re-established the plot perimeter and survey lanes (defined as a survey). Divers meticulously searched each lane for abalone, using flashlights and dental mirrors to examine all surfaces and refugia to the extent possible. On average, a diver required ~30 min to complete the search of one 2 m × 8 m lane. Upon encountering an abalone, divers measured the maximum shell length using calipers where possible, or estimated the size where not possible. Divers recorded the location of recapture, size, and presence or absence of a tag, or unknown if the tagged portion of the shell could not be viewed. Tag colour and number were recorded when possible. Divers also qualitatively assessed each abalone's prominence on the substrate, assigning one of three categories: emergent (entirely visible on the outside of boulder or bedrock), semi-emergent (partially visible, located in a crack or under an overhang), or cryptic (would not have been seen if rocks had not been moved). Empty abalone shells encountered were measured, searched for a tag, and then removed from the plot. In 2015, 2016, and 2017, divers also conducted perimeter surveys, examining the 2 m border around the plot for additional individuals or shells. Except in the rare case that a pre-existing, large abalone was found on a site prior to outplant, all tagged or untagged abalone were assumed to have been part of the experiment due to very low levels of natural recruitment in the region (Bouma et al., 2012; Rogers-Bennett et al., 2011).

The majority of outplants and annual surveys were done in the first part of the year, between January and April (Supporting Information Table S1). The earliest outplants (2009) and some early surveys took place during the summer, and some sites received autumn surveys in the year of outplant to collect a six-month status. The winter timing of the bulk of survey effort was partly due to the availability of staff and resources, but also coincides with the lowest density of macroalgae in the region, which was hypothesized to increase

detection. However, it is also possible that aggregating behaviours closer to the summer spawning months would have also aided detection (Seamone & Boulding, 2011).

In five instances, a closed-session capture–recapture methodology was employed (Supporting Information Table S1). Four sites were surveyed multiple times within 1 month, repeating the survey methods noted earlier. Thus, in these instances, the month-long interval comprised a single ‘session’ consisting of four or five repeated sampling ‘occasions’ (there were two sessions for the Gold site in consecutive years, and one session each in Omaha, Husky, and Baytown, for a total of five sessions). The repeated sampling was used to assess the movement and detection rate of tagged abalone. The Gold site was surveyed four times in the summer of 2011 and five times in the summer of 2012. The Omaha site was surveyed five times in the summer of 2012. The Husky and Baytown sites were each surveyed four times in the winter of 2016.

2.6 | Detection rate

Pilot outplants conducted prior to those described here suggest that any given site survey is unlikely to detect the majority of abalone that exist on the plot at the time of the survey; that is, the detection rate of pinto abalone is low. The pilot outplant studies, described by Stevick (2010), were specifically designed to test survival and detection by placing hatchery-reared abalone on suitable habitat (bedrock and boulders) that was surrounded by unsuitable habitat (sand) to eliminate emigration. After 1 year, these four plots were surveyed once as described earlier, then surveyed a second time ‘destructively’—lifting, examining, and discarding each rock to reveal the true abundance of survivors. Fifteen animals were found on the four plots in the first annual survey, but an additional 27 were found during the subsequent destructive surveys, a 0.36 detection rate (± 0.9 SE).

Imperfect detection can bias estimates of parameters of interest, including survival and abundance (Seber, 1965). The term ‘observed’ (naive) is used to describe counts, densities, or rates derived directly from survey data, without accounting for the detection rate. Detection of outplanted animals in this study was evaluated in several ways. First, the repeated sampling occasions within a month-long session were used to empirically assess the observed proportion of surviving animals that would be detected during a typical single survey. With each successive survey occasion, new tag numbers encountered were used to plot cumulative tags detected over time. Theoretically, the number of new recaptures will decrease with each subsequent occasion, until an asymptote can be calculated that estimates the total number of individuals on the plot.

Second, the effect of size (shell length) on detection was assessed using the emergent, semi-emergent, and cryptic categories assigned to all abalone during surveys. Although the size of animals not detected at all is unknown, mean sizes for the existing categories were compared using *t*-tests. The decreasing chance of being assigned to the cryptic category with increasing size was evaluated using logistic regression.

Third, the five instances with repeated sampling occasions within a single month-long session was used to estimate detection (p)

implementing a closed capture–recapture model (M0; Otis, Burnham, White, & Anderson, 1978) in R (R Core Team, 2016) using JAGS (Plummer, 2013) and a wrapper package (jagsUI; Kellner, 2017). Closed capture–recapture detection rates were estimated separately for two seasons. Capture histories for primary sessions were combined by season (summer: four occasions for Gold July 2011, five for Omaha and Gold July–August 2012; winter: four occasions for Husky and Baytown, March–April 2016). Capture histories for all five sessions were then combined for an overall estimate of detection. Three Markov chain Monte Carlo chains with 2,000 adaptations, 5,000 burn-in, and 15,000 iterations (no thinning) were used to fit the models. Detection for winter and summer surveys was estimated separately, and posterior distributions of p were compared to determine whether there was evidence for seasonal differences in detection due to potentially reduced visibility during summer surveys.

2.7 | Survival

Knowing the factors that affect survival of outplanted abalone allows for managers to make decisions about how to allocate resources and prioritize efforts in future implementation. The Cormack–Jolly–Seber (CJS) model produces unbiased estimates of apparent survival ϕ by accounting for imperfect detection over multiple sampling surveys and allows for comparison of factors and covariates affecting apparent survival (Lebreton, Burnham, Clobert, & Anderson, 1992). The goal was to assess whether site, family, and size at outplant had an effect on survival in the first year (the interval when the greatest amount of mortality is suspected to occur). Relative support for each of these factors was assessed using multimodel inference and model selection (Burnham & Anderson, 2003). The R package RMark (Laake, 2013) was used to construct models for program MARK (White & Burnham, 1999) and estimated apparent survival using a CJS framework. Data from only eight of the 10 sites were incorporated into the framework, as the two newest sites (Avalanche and Dragoon) did not have sufficient survey history. Initial outplanting occurred at different times for different sites. Thus, to allow for estimation of site effect, data from different sites were combined based on time since outplant, not survey date. The initial outplant was considered as session 1, the survey 1 year following as session 2, and the survey 2 years following as the final session (required to allow estimation of survival over the first interval, year 1, as survival for the last interval and detection for the last session are confounded in time-dependent CJS models). The limited duration (1 year) considered also reduced potential bias from tag loss, which increased over time. Two sites were surveyed twice within 1 month of the year following release, whereas the remaining sites were surveyed once in the year following. Thus, survey effort was accounted for in the detection component of the model. Preliminary models of detection and previous studies indicated that detection of abalone is strongly affected by size (Zhang, Campbell, & Lessard, 2007), which increases over time. However, the size of outplants not detected during a survey is unknown, resulting in missing values, a common problem for individual covariates (Kéry & Schaub, 2012). As size at outplant was known for all individuals, all models were fitted

with the full or nested subsets of a global detection model p (size at outplant + time + sampling effort).

A time-dependent candidate model set was formulated to compare models of survival, including site, size-at-outplant, and family as grouping factors and covariates. Because survival was only estimable for the first year, the value for survival for the second interval (year 2, confounded with detection for session 3) was fixed equal to 1, and year 2 survival was not estimated. As a result, survival and the effects of covariates on survival were only estimated for the first year—the interval thought to be most important for overall site success and least subject to tag loss over time. For lineage, alternate models were compared using family or maternal lineage for each covariate combination. A total of 2,776 marked abalone were released across sites, including individuals from 46 families. However, there was a broad disparity in the number of individuals outplanted from each family (range = 1–229, median = 42). Because first-year survival was expected to be low, the data were restricted to only include families with at least 100 individuals, as poor survival of families represented by small groups of individuals could very likely be due to stochastic demography, and not necessarily due to family traits. The final data set included 1,531 individuals from 10 families (four maternal lineages) over the eight sites. Models were compared using the corrected Akaike information criterion (AICc) and evidence ratios (Anderson, 2008; Burnham & Anderson, 2003).

There was concern that a residence of up to 2 years in the hatchery would lead to selection for families that survive well in a hatchery environment, which may not be optimal for survival in the wild. This concern was addressed by evaluating whether families that survived well in the hatchery continued to survive well in the wild. Crosstabulation tables were used to compare the proportion of all year 1 tagged survivors from each family with the proportion that would be expected given the relative numbers outplanted. Since site was the most important factor influencing survival, analyses were run separately by site, with only 2011 cohorts at Omaha and Gold, 2015 cohorts at Husky and Baytown, and 2016 cohorts at Avalanche and Dragoon having sufficient sample size. The difference in proportions were evaluated using Pearson's chi square tests. For all six of the analyses, however, low representation in some families created sparseness in many cells of the table, which violated the assumptions of the test. Therefore, an approximative chi-square test was used based on 10,000 Monte Carlo resamplings using the R package coin (Hothorn, Hornik, van de Wiel, Winell, & Zeileis, 2017).

2.8 | Individual growth

Individual growth rates were calculated using the recaptures of tagged abalone that occurred at the approximate 1 year anniversary of outplant ($n = 204$ over all sites) by subtracting the size-at-outplant from the observed sizes and dividing by the number of days since outplant. All recapture lengths ($n = 535$) at age (time since outplant) were fitted with a von Bertalanffy growth curve using the R software packages nlstools (Baty et al., 2015) and FSA (Ogle, 2017). Further statistical analysis of growth (by site, family, or as related to outplanted

size) was confounded by assumption violations related to the fact that detection of abalone is low and heavily influenced by size.

2.9 | Movement

During all outplant surveys, recaptured animals were located in one of the five 2 m wide 'lanes' that comprise the plot. When a tagged animal was recaptured a second or third time, the lane of recapture was compared with previous positions to assess net movement over the survey interval, typically 1 year. The proportion of abalone that moved each of the possible distances that could be detected (zero, one, two, three, or four lanes) was compared with the proportions that would result if movements were random. A Pearson's chi-square test was used to determine if these proportions were significantly different. This same method was used during the five repeated-sampling events to assess movement on a weekly timescale.

2.10 | Tag loss

To estimate the longevity of tags in the field, the proportion of tagged individuals remaining among all recaptures at each survey was calculated for the 2009 and 2011 outplants ($n = 652$). Later outplants at new sites could not be assessed because their greater numbers necessitated that only a portion of the outplanted animals were tagged. For the purposes of this paper, 'tag loss' refers to the point at which a tag no longer is completely legible. Many tags were located still affixed to shells where one or both of the digits could no longer be read, meaning that the specific individual could no longer be identified. Tags in this condition were defined as 'lost'. The proportion still tagged is certain during surveys for which only the tagged cohort is present on the plot (i.e. all recaptured abalone either have a tag or once had a tag). The proportion becomes less certain when subsequent untagged individuals are added, especially given the variability in growth. For these surveys, animals without a tag were assigned to the tagged cohort based on having a shell length within the range of those animals that did have tags. A tag loss rate per day was calculated using a logistic regression on tag status versus days since outplant.

2.11 | Lineage diversity

All or part of the first outplant at a site had tags affixed, with the exception of two sites where only the second outplant was tagged (Supporting Information Table S1). This allowed for the assessment of the diversity of lineages that survived and potentially interbred on a particular plot. In order to calculate the probability that siblings or half-siblings would mate at each site, a number of simplifying assumptions were necessary, including equal sex ratios, no difference in detection rate among families, and equal reproductive output among all individuals regardless of family or size. When not all individuals were tagged, the survival of the tagged individuals was assumed to be representative. Additionally, the most information is available from tags at the year 1 survey, when not all animals had reached reproductive size. Therefore, the calculations assume that proportional survival after the year 1 survey did not change among families.

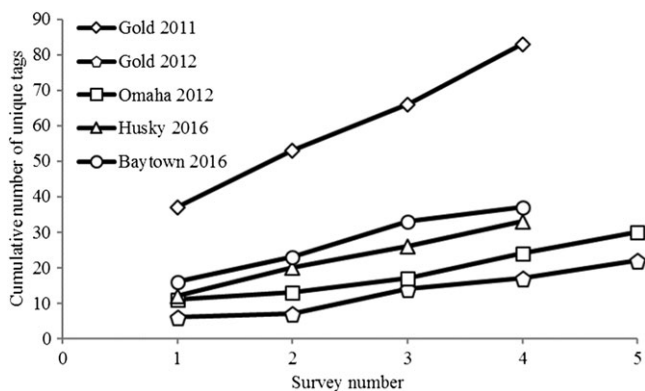


FIGURE 1 Repeated surveys over 1 month of four plots in an attempt to exhaust the number of previously undetected tags placed on hatchery-origin juvenile pinto abalone. The allotted effort of four or five surveys was insufficient to reach exhaustion

A Simpson's dominance index was calculated for each site by summing the squared proportions of each family represented at the year 1 survey. It results in a value between zero and one describing the balance of families represented on the plot; larger values mean that one or more families are highly abundant relative to others. Because multiple families shared the same mother, Simpson's dominance values were also calculated based on mother instead of family. The chance of reproducing with a sibling or half-sibling was calculated by dividing the number of sibling or half-sibling tags found on the plot by the number of all other survivors, averaged across all individuals.

2.12 | Density estimates and predictions

A state-space model (SSM) of exponential growth population dynamics (Kéry & Schaub, 2012) was constructed to assess outplanting success at each site based on plot density D_t at time t , and to predict when additional outplanting would be required to maintain a predefined reproductive density threshold (0.3 m^{-2}). The basic model was modified to allow for unequal intervals between surveys and the addition of outplants following monitoring surveys. As with the CJS model, data from only the eight older sites with sufficient survey history were used.

The SSM is a hierarchical model, meaning there is both a process model that describes the latent (unknown) underlying state of a site (the abundance of individuals and the rate of change) and an observation model that describes how researchers observe the process model imperfectly. In this case, the count, an index of the unknown population size, includes the total number of individuals detected for a survey N_t , the rate individuals are added to or removed from the population between surveys represented by the population growth parameter λ_t and also a known number of outplants $N_{\text{outplants}_t}$ that are added to the site ($N_t \times \lambda_t + N_{\text{outplants}_t} = N_{t+1}$, notation consistent with Kéry and Schaub (2012), chapter 5). Immigration was assumed not to occur due to the complete lack of recruits detected on index or other sites. Using observed counts without accounting for imperfect detection can result in negative bias in abundance estimates. Thus, an ad hoc correction was incorporated in the SSM, adjusting estimates of observed counts by using an informed prior

distribution for detection (details of model construction and fit are provided in Supplementary Information Appendix 1). The SSM models were fitted in R using JAGS (Plummer, 2013) and a wrapper package (jagsUI; Kellner, 2017) for eight sites separately using data collected from 2009 to 2016, and density and observed counts for each site predicted for 2017. Predicted density was used to forecast when the population for each site would decline below an assumed reproductive threshold (0.3 m^{-2}) and provide guidance on when future outplanting would be required for each site.

3 | RESULTS

3.1 | Detection rate

Repeated sampling occasions (four or five surveys in the span of a month) attempted to estimate the observed detection rate on the experimental plots by counting the number of previously undetected tag numbers in each subsequent survey. However, no decrease in the number of new tags per survey was evident after four or five repetitions (Figure 1), and there were insufficient resources to continue the effort. Although additional surveys would have been likely to detect additional unique tags, an upper bound on observed detection can be calculated by dividing the number of tags found in the first survey by the total amount found in all surveys. This 'maximum' observed detection rate averaged 38% ($\pm 3\%$ SE) and ranged from 27% (Site Gold in 2012) to 45% (Gold 2011). Closed capture–recapture population model estimates of detection (mean = 0.19, 95% credible interval [CRI] = 0.15–0.23) were lower than this maximum observed rate. In addition, detection estimates were similar between summer (mean = 0.17, 95% CRI = 0.13–0.22) and winter surveys (mean = 0.18, 95% CRI = 0.13–0.25), suggesting no seasonal trend in detection.

All detected abalone (tagged and untagged) were assigned a designation of cryptic, semi-emergent, or emergent based on their ease of detection during the survey process ($n = 961$). There was no difference in the average sizes of emergent (59 mm shell length) and semi-emergent (62 mm) individuals (t -test, $p = 0.274$), so those two categories were combined for further analysis. Cryptic animals were smaller on average (48 mm) than the emergent or semi-emergent animals (60 mm) in a t -test ($p < 0.001$). A logistic regression ($p < 0.001$) suggests that the chance of being easily observed on the plot increases 2% with each millimetre of growth, (1.4–2.5%; 95% confidence bounds). In the CJS analysis, there was substantial support for all three covariates on detection (size at outplant, time since outplant, and number of occasions within a survey), and increases in each resulted in greater detection rates.

3.2 | Survival

There was overwhelming support for the CJS model including differences in year 1 survival by site (Table 1), and no comparable support for models including maternal lineage ($\Delta\text{AIC}_c = 46.63$), family ($\Delta\text{AIC}_c = 49.59$), or size at outplant ($\Delta\text{AIC}_c = 62.42$). When site is not considered, maternal lineage received greater model support than family, and size at outplant received the least support and was

TABLE 1 Corrected Akaike information criterion (AICc) results for Cormack–Jolly–Seber models for first year survival of outplants. Models in the candidate set included effects of outplant site, lineage (family and maternal lineage), and size at outplant (SAOP) on apparent survival ϕ , while accounting for imperfect detection p as a result of SAOP, time since outplant, and survey effort (one or two surveys). Models were compared using AICc and model weight of evidence (w_i)

Model	K	AICc	Δ AICc	w_i	Deviance
ϕ (site + time) p (time + effort + SAOP)	7	660.22	0	1.00	646.15
ϕ (site + time) p (~effort + SAOP)	6	681.20	20.98	<0.01	669.15
ϕ (site + time) p (~SAOP)	6	681.40	21.18	<0.01	669.34
ϕ (maternal + time) p (~time + effort + SAOP)	9	706.84	46.63	<0.01	688.73
ϕ (family + time) p (time + effort + SAOP)	12	709.80	49.59	<0.01	685.61
ϕ (SAOP + time) p (time + effort + SAOP)	6	722.03	61.81	<0.01	709.97
ϕ (time) p (time + effort + SAOP)	5	723.81	63.59	<0.01	713.77
ϕ (maternal + time) p (SAOP)	7	727.08	66.87	<0.01	713.01
ϕ (maternal + time) p (effort + SAOP)	8	728.60	68.38	<0.01	712.51
ϕ (family + time) p (SAOP)	10	729.07	68.85	<0.01	708.93
ϕ (family + time) p (effort + SAOP)	10	729.41	69.20	<0.01	709.27
ϕ (SAOP + time) p (SAOP)	4	742.01	81.79	<0.01	733.98
ϕ (SAOP + time) p (effort + SAOP)	5	743.43	83.22	<0.01	733.39
ϕ (time) p (SAOP)	3	744.37	84.15	<0.01	738.36
ϕ (time) p (effort+ SAOP)	4	745.62	85.41	<0.01	737.60

K is the number of parameters included in each candidate model.

competing with the simplest time-dependent model with no covariates on survival. Because of the number of sites (seven parameters) and very low detection rate estimates relative to the number of sampling sessions considered for the maximum likelihood analysis, estimates of year 1 survival could only be obtained for three sites (Gold: 0.38, 0.16–0.66 95% confidence interval [CI]; Omaha: 0.32, 0.14–0.56 CI; Utah: 0.79, 0.02–1.00 CI). Observed (naïve) survival estimates are reported acknowledging the probable low bias resulting from ignoring detection (Table 2), but assuming detection bias was constant across sites. The most successful site, Omaha, had an observed year 1 naïve survival of 23%, and an ‘outplant success’ (detected, reproductively sized adults as a percentage of the total

outplanted there) of 7.5%. In contrast, the least successful site, Jubilee, had only seven live abalone in total observed over five surveys—the last of which found none.

Two-way contingency tables demonstrated that there were not significant differences between the proportional representation of families at the time of outplant and 1 year later. Approximate Pearson's tests for six cohorts tested separately had chi-square values ranging from 18.58 to 4.96, with associated p -values of 0.119–0.996. Although none were significant, the cohort with the most difference in proportions was the 2015 outplant to site Baytown. Of 14 families outplanted, three were conspicuously underrepresented. Three individuals from each family might have been expected given 47

TABLE 2 Summary of observed survival of hatchery-origin juvenile pinto abalone at 10 sites in the San Juan Islands, WA, sorted by ‘outplant success’. Outplant success is defined as the percentage of the total number outplanted that were observed on or near the plot in 2017 surveys to have attained a size of likely maturity (>50 mm shell length). Perimeter density was calculated using the search area of a 2 m wide swath outside the plot's boundaries. Confirmed mortalities were empty shells encountered during surveys within the first year. The line separates the six sites that have priority for continued supplementation and the four sites subject to replacement

Site	Total outplanted (all years)	Observed year 1 survival ^a (%)	Year 1 confirmed mortalities ^a	2017 abalone >50 mm	2017 plot observed density (m ⁻²)	2017 perimeter density (m ⁻²)	Observed outplant success (%)
Omaha	1166	23.0	1	65	0.72	0.24	7.5
Baytown	1327	11.4	20	52	1.02	0.13	5.3
Gold	1183	19.7	1	34	0.38	0.27	5.0
Utah	1190	10.2	31	37	0.37	0.21	4.8
Dragoon	619	12.3	5	18	0.82	0.28	4.8
Avalanche	619	9.5	5	14	0.59	0.10	2.7
Juno	1202	4.0	10	8	0.12	0.15	1.7
Husky	1326	8.7	14	11	0.39	0.10	1.4
Sword	1466	3.2	10	4	0.11	0.02	0.4
Jubilee	759	0.0	28	0 ^b	0.00 ^b	0.00 ^b	0.0 ^b

^aA year after the 2011 outplant (Utah, Omaha, Juno, Gold, Sword, Jubilee), after the 2015 outplant (Husky, Baytown), or the 2016 outplant (Avalanche, Dragoon).

^bLast survey at Jubilee was in 2015 and found no live abalone.

recaptures, but none were. Conversely, two other families were over-represented at year 1, with 10 and six individuals sighted when four and two respectively would have been expected given the outplant proportions. These same families, simultaneously outplanted to site Husky, did not exhibit survival out of proportion there.

3.3 | Individual growth

On all 10 sites, 204 tagged abalone survived and were detected at the approximate 1 year survey after outplant. The average size of these individuals was 26 mm (± 0.5 mm SE) shell length at the time of outplant. These abalone grew at an average rate of 0.05 mm shell length per day (± 0.002 mm SE) over their first year to reach an average shell length of 44 mm (± 0.9 mm). For all recaptures, not just those at the 1 year mark, 535 abalone with legible tags were measured. A plot of these measurements shows considerable variability among individuals of the same age (Figure 2).

A von Bertalanffy growth model (see Zhang, Lessard, & Campbell, 2009) was used to fit a line to the growth data (Figure 2) taking the form of:

$L[t] = L_{\infty} [1 - e^{-K(t-t_0)}]$ where L_{∞} is the mean maximum shell length of the population (in this case 147.6 ± 24 mm),

K is the growth rate coefficient (0.00048 ± 0.00014 day $^{-1}$), and t_0 , although devoid of biological meaning, is the time when average shell length was zero (-359 ± 69 days).

The relatively large SEs for these calculated parameters reflect the variability in the underlying data. This growth variability also hampered the ability to assign untagged individuals to an outplant cohort. If growth was less variable, untagged individuals could be assigned to an outplant cohort of origin using the growth trajectory of tagged individuals on that site. However, even when separated by one or more years in age, shell lengths from disparate cohorts likely had substantial overlap.

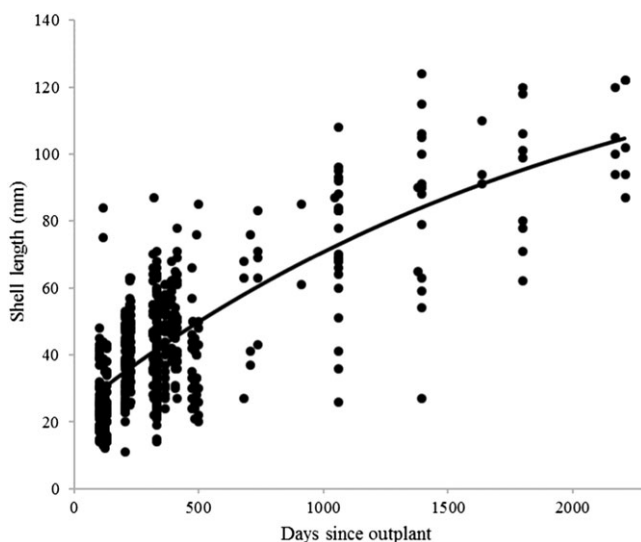


FIGURE 2 Shell lengths (mm) at age (days since outplant) for all tagged abalone recaptures on all sites ($n = 535$). The fit line was calculated using a von Bertalanffy growth model

Available data suggests that abalone grow, on average, about as fast on the outplant sites as they do in the hatchery. The juveniles recaptured at year 1 ($n = 204$) grew at approximately 1.3 mm shell length per month in the hatchery, with an average age of 20 months and average shell length of 26 mm at the time of outplant. These same individuals grew on average 1.6 mm each month in the year following outplant.

3.4 | Movement

Across all sites, 84 tagged abalone were recaptured two or more times after outplant, allowing for the assessment of long-term (annual-scale) net movement at the outplant sites. The proportion of abalone that moved each of the possible distances from first recapture (zero, one, two, three, or four lanes) was significantly different than the proportions expected given random movement (Pearson's chi-square, $p = 0.005$). In the year or more between surveys, 77% of the individuals showed little or no net movement (zero or one lane), whereas this would be expected to have been found 52% of the time under the random expectation (Figure 3). Similarly, net movement across the plot (three or four lanes) occurred 7% of the time, compared with a 24% random expectation.

At four sites, researchers returned approximately weekly and did multiple repeat surveys of a site over the span of a month session. During these surveys, 67 tagged individuals were recaptured more than once. Again, the proportion of abalone that had moved each of the possible lane distances was different than that expected at random (Pearson's chi-square, $p < 0.001$). At this shorter timescale, net movement was even more restricted, with 73% of observations occurring in the same lane, and over 95% moving either zero or one lane (Figure 3).

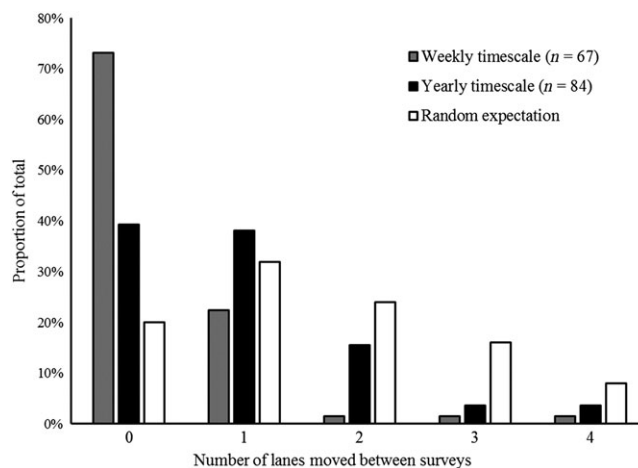


FIGURE 3 Proportion of tagged abalone that moved among portions of the plot ('lanes') in between surveys on the weekly and yearly timescales. Grey bars represent the 67 animals recaptured more than once during repeated sampling surveys at four sites. Black bars represent the 84 animals recaptured more than once during annual surveys at eight sites. White bars represent the proportions that would be expected if abalone moved among lanes randomly

3.5 | Tag loss

Dedicated tag-longevity experiments were not conducted in the laboratory or field. A rate of tag loss was estimated using the proportion of recaptured animals still retaining tags during a series of sessions at a site (Figure 4). A logistic regression on tag status at time since outplant ($p < 0.001$) had an odds ratio of 0.998, suggesting a 0.2% smaller chance of being located with a legible tag for each day that passes since outplant. The last legible tags found at Utah, Juno, and Sword were all at about 5 years after outplant. There were still

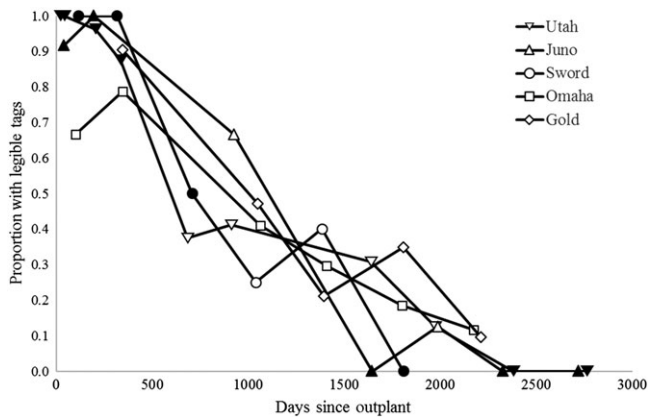


FIGURE 4 Tag loss for hatchery-origin abalone on five sites in the San Juan Islands ($n = 651$). Symbols represent the proportion of animals still retaining a legible tag at the time of the survey. For closed symbols, those proportions are known because no untagged abalone had been placed on a site, so all untagged abalone represented animals that had lost a tag. When the proportion is zero, this is also represented with a closed symbol since this proportion is also certain. Open symbols represent surveys during which individuals from untagged outplants (before or after the tagged outplant) were present on the plot to potentially be mistaken for animals that had lost a tag. Untagged abalone were placed in the 'tag lost' category based on having a similar size to tagged animals; other smaller or larger abalone were assumed to be from another outplant and not included in the calculation

four legible tags left at Omaha and five at Gold during the 2017 surveys, approximately 6 years after outplant.

3.6 | Lineage diversity

Table 3 reports the results of the assessment of lineage diversity, including the Simpson's dominance index of family representation (overall mean = 0.14) and chance that siblings mate (mean = 12.5%). In a given hatchery spawning event, there were often more males than females spawning, meaning that eggs from one female were split into groups to be fertilized by multiple males. Therefore, Simpson's dominance values were also calculated for maternal lineage (mean = 0.35), as were the chances of mating with a half-sibling (mean = 25.3%). These values apply specifically to possible within-in cohort mating and do not account for the addition of new families during subsequent untagged outplants.

3.7 | Density estimation

SSM estimates converged for all sites, although some parameters were unidentifiable for some sites and returned the informed prior distribution. In addition, 95% CRIs were often relatively wide, suggesting the collected data did not provide substantial weight to the posterior distributions, even when parameters were identifiable. In particular, it was not possible to fit a random effect to population growth due to the small number of years since initiation (lack of convergence and nonsensical estimates). Annual population growth was estimable as a stochastic temporal effect, but near or equal to 0.50 (the median of the uniform prior) for most intervals for all sites (mean estimates ranged from 0.47 to 0.54). However, this provides an opportunity to compare estimated and observed counts to evaluate site success across a relatively constant standard ($\lambda_{\text{annual},i} \approx 0.50$). When estimated counts are less than observed counts, the site is performing better than expected. When estimated counts are greater than observed counts, the population is likely declining at a rate greater than 0.50.

TABLE 3 Lineage diversity based on tag recaptures at one year after outplant for tagged outplants only. Subsequent outplants with new families, as well as large numbers of undetected animals from the tagged outplant, make the estimates of dominance or probability of sibling or half-sibling matings conservatively high. Simpson's dominance indices were calculated first by family and then by summing across families that share the same mother. Averages listed at the bottom are weighted by the number of tags detected

Outplant	Families at outplant	Year 1 families detected	Year 1 tags detected	Simpson's dominance index		Chance of mating (%)	
				Family	Mother	With sibling	With half-sibling
Avalanche 2016	14	11	30	0.12	0.30	10.7	18.5
Dragoon 2016	14	10	21	0.13	0.17	11.7	10.7
Husky 2015	14	12	28	0.11	0.17	7.7	12.2
Baytown 2015	14	10	47	0.14	0.19	12.3	15.7
Omaha 2011	17	14	63	0.11	0.43	9.8	35.8
Gold 2011	17	11	62	0.11	0.48	10.0	39.1
Sword 2011	17	6	13	0.23	0.25	16.7	7.7
Jubilee 2011	17	0	0				
Utah 2009	7	4	15	0.49	0.76	45.7	28.6
Juno 2009	7	1	1				
Weighted average				0.14	0.35	12.5	25.3

For example, at Utah, a successful site, observers 'beat the model' predictions on five of nine occasions (four out of five after the second cohort was placed), whereas observer counts at Sword and Jubilee (the least successful sites) were consistently less than predicted counts. It should be noted that predicted counts assume an informed prior on detection that does not explicitly account for an increase in detection over time (due to the larger size and emergent behaviour of older abalone). Therefore, counts for the first few occasions could be expected to be low in comparison with later occasions. The informed prior on detection also allows for assessment of derived density estimates. Mean estimates of density correspond to the mean detection rate (0.19 as estimated by the closed capture–recapture model), whereas the lower 95% CRI for density corresponds to the upper 95% CRI for detection (0.36 as estimated using the destructive sampling method).

4 | DISCUSSION

When placed on suitable habitat, hatchery-origin pinto abalone grew to reproductive size and survived (and did not emigrate) in sufficient numbers to create viable spawning aggregations. Captive rearing and restocking is therefore a viable option to save this species from local extinction. This pilot phase of the operation provided much information to inform a scale-up of the programme with the goal of state-wide restoration.

4.1 | Detection rate

The plots in the present study were chosen specifically for their abundance of refugia with the aim of increasing survival. These hiding spaces, combined with the possibility that abalone move on and off the plot, result in imperfect detection and make estimation of survival difficult. Furthermore, the probability of detecting an individual pinto abalone increases with size. This was apparent in the pilot experiment, where the abalone found only during destructive plot surveys were, on average, smaller than those found in initial surveys (Stevick, 2010). No destructive surveys were conducted on the restoration plots here, but, again, animals labelled as cryptic (those that would not have been seen without moving or turning over a rock) were smaller on average than emergent animals. These results concur with those of Zhang et al. (2007), who showed that the probability of being cryptic increased with decreasing size in wild Canadian pinto abalone populations. These observations could be due to a variety of factors: larger abalone are easier to see, larger abalone can no longer fit in as many obscured spaces, and larger abalone are subject to fewer predators and therefore may spend more time in the open.

4.2 | Survival

Site was by far the most important factor affecting outplanted abalone survival. It is not clear why abalone at some sites remain and survive while at others they either die or emigrate. All sites were selected using the same criteria, and while there are differences among them, there is nothing obvious about the most or least successful sites to

be replicated or avoided. The most puzzling example may be the case of Gold and Juno, which are only 200 m apart on the same island. Observed year 1 survival was almost fivefold greater at Gold, and that has continued over four subsequent outplant cohorts—making Gold three times more successful in terms of observed, reproductively sized adults during the 2017 surveys. More obviously, the two least successful sites, Sword and Jubilee, are on the same small island. Jubilee was abandoned after outplants in 2011 and 2013 had very poor performance, despite the 2011 cohort performing well elsewhere. Sword, however, ended up receiving more abalone than any other site (1,466), from four different years' cohorts, and still had very low success (0.4%). Although it is clear that something about this island does not promote abalone survival or retention, it is not clear what. Both sites happen to be located within view of a marine reserve monitoring station on a nearby adjacent island. Therefore, it is unlikely that illegal harvest has affected these two sites.

Assuming that macroalgal food and refuge habitat are not limiting at any of these sites, as appears to be the case, differential abundance of predators may explain poor performance at some sites. Hansen and Gosselin (2013) demonstrated that almost all early mortality of outplanted pinto abalone in their study could be attributed to predation. Sites for the present study were not periodically surveyed for the abundance of predators such as crab, octopus, sea stars, or fish (Griffiths & Gosselin, 2008). The appearance of the empty shells found on the plot could be a clue to the cause of death (Hofmeister et al., 2018). Missing chips from the edge of the shell, by far the most common damage encountered, may indicate that crabs are the most important predators to juvenile abalone at these sites.

Hofmeister et al. (2018) demonstrated an increase in predator density, particularly octopus, at stocking sites for the red abalone (*H. rufescens*) in California and found a substantial percentage of empty shells with octopus drill holes. Although the octopus species in that study are not found in Washington, similar local species, such as *Octopus rubescens*, could be important predators. They can be densely populated, cryptic, and prey primarily on gastropods (Anderson, Hughes, Mather, & Steele, 1999; Onthank, 2008). Empty shells with drill holes indicating attack from small octopus have not been encountered; however, *O. rubescens* do not eject shells from their burrows to be found (Onthank, 2008). At site Juno, a giant Pacific octopus (*Enteroctopus dofleini*) den was noted during the 1-year site survey, and survival was low. However, it was not clear that the octopus was the cause of any of the mortality (as would be evidenced by abalone shells in or around the den). Additionally, an octopus den is located on the Dragoon site, and retention and survival there has been high.

Another important predator may have been the sunflower star *Pycnopodia helianthoides*. Abalone consistently show an escape response when touched by a sunflower star arm. This response is so consistent that sunflower stars are the preferred method to collect broodstock without the potentially damaging impacts of prying off rock. However, since sunflower stars are now rare throughout the San Juan Islands due to sea star wasting disease (Montecino-Latorre et al., 2016), it cannot explain continued differential mortality at the juvenile outplant sites.

At three of the poorly performing sites, Jubilee, Sword, and Husky, a large recruitment event of acorn barnacles (*Balanus* spp.) took

place after outplanting. These barnacles covered much of the available surface areas, including the surviving abalone shells. Since abalone tend to prefer smooth rock covered in crustose coralline algae (Rogers-Bennett et al., 2011), it is possible that these barnacles restricted movement, reduced the surface area available for diatom grazing, or made it difficult for abalone to maintain a secure foot muscle grip on the substrate. There was no such barnacle recruitment event observed at site Juno, the fourth poorly performing site.

Another possibility is that animals migrate off certain sites more than others and are therefore missing from survey data. It is difficult to distinguish between mortality and migration and may not be important to do so for the purposes of conservation planning. Mortalities can be confirmed when empty shells are found during surveys, but the number found is surprisingly low, and more shells are not necessarily found at sites with poorer survival (Table 2). However, detection of mortalities may also be low. Fragile juvenile pinto abalone shells may be swallowed or crushed by predators, remain obscured in predator dens, or drift away in the currents.

Family origin was not nearly as important as site to pinto abalone survival. There were no signs of hatchery acclimatization impacts on survival in the wild, at least at the inter-family level. Most families were represented approximately equivalently at the time of outplant and 1 year later. When a particular family was over- or underrepresented at year 1 on a given site, it was most likely due to random chance given the large numbers of families and low detection rates. This is supported by the fact that the three cohorts tested were each placed on two sites, and at no time was a family over- or underrepresented at both of the sites. Data are not available to assess if the hatchery environment selected for certain traits *within* families that may or may not promote survival in the wild, such as naïveté to predator cues (Hansen & Gosselin, 2016; Straus & Friedman, 2009). Also, it is possible that acclimatization impacts would show up later than the first year. However, as tag recaptures become more sparse in subsequent years, it becomes more difficult to test the proportional survival of families.

The most recent surveys show an observed on-plot individuals density $>0.3 \text{ m}^{-2}$, a rough estimate of the minimum density needed for successful fertilization during broadcast spawning, on seven of the 10 sites (Table 2). The most successful sites, like Omaha and Gold, have been continuously above this threshold since 2011, and even without further supplementation would likely remain there for several years. Poorer-performing sites, like Juno or Sword, only achieved this density briefly (in the survey a year after outplants) before dipping back below that in subsequent surveys.

4.3 | Growth

Outplanted pinto abalone had highly variable growth rates (Figure 2). An extreme example of this variability can be seen at Gold, where one individual was recaptured on the plot 4 years after outplant, having grown only 2 mm in shell length during that time. In contrast, a second individual recaptured during that same survey had a net growth of 58 mm.

The available data confound the ability to test for the impact of site, family, or size-at-outplant on growth. Since detection is low,

and heavily influenced by size, the assumption of random, independent sampling is violated. However, growth did not seem to vary substantially by site (Table 4), and even the rank-order of sites' average growth did not correspond to survival there. This suggests that site characteristics that contribute to growth, such as food availability, are not the mechanisms behind differential survival at the sites. This is corroborated by qualitative observations of ample macroalgae at all sites.

Our tag and capture–recapture data detected a similar and slightly higher growth rate after outplanting (an increase from 1.3 to 1.6 mm per month), despite the fact that growth rate is expected to slow as the animals age. It is possible that the diversity and quality of natural foods promotes growth more than hatchery feed, or that feeding rates in the hatchery are restricted by the high density of animals in the tanks. We did not hold portions of cohorts in the hatchery past the outplant age to formally compare growth between the hatchery and wild. However, we take the similar growth rate in the wild as evidence that, at the very least, captive abalone are able to transition to wild food sources with relative ease.

4.4 | Movement

Clearly, the majority of tagged abalone that took up residence on the experimental plots stayed close to home, even when subjected to the potential 'harassment' of being illuminated with flashlights and measured with calipers. However, a minority did migrate across spatial scales relevant to restoration. This paradigm is similar to that observed for the pink abalone *Haliotis corrugata* in California (Coates, Hovel, Butler, Klimley, & Morgan, 2013). Another study confirmed the relative site fidelity of pink abalone in California and contrasted it with low fidelity and greater movement in the green abalone *Haliotis fulgens* (Taniguchi, Stein, Lampson, & Rogers-Bennett, 2013). Tagged red abalone *H. rufescens* in California also exhibited greater movement than the pinks, although almost 90% remained in their ~50 m 'zone' of release on annual timescales (Ault & DeMartini, 1987).

TABLE 4 Average year 1 growth, by site, of hatchery-origin, tagged, juvenile pinto abalone outplanted to 10 sites in the San Juan Islands, WA. Growth values are potentially biased by the effect of size on the detection rate of abalone during surveys

Site	Tag recaptures at year 1	Mean growth (mm day ⁻¹)	SD
Utah	7	0.062	0.022
Dragoon	21	0.057	0.027
Baytown	48	0.056	0.024
Husky	32	0.052	0.022
Omaha	22	0.051	0.030
Avalanche	30	0.049	0.033
Sword	9	0.046	0.022
Gold	34	0.034	0.021
Juno	0		
Jubilee	0		

This study only measured *net* movement on the weekly and annual timescales and has no estimate of total movement that may occur. Part of the relatively low detection rate of tagged abalone may stem from potential movement on and off the experimental plots relative to the timing of any given survey. A study on the congeneric *H. corrugata* that used acoustic telemetry showed regular movements around a home range that in most cases was larger than the experimental plots described here (Coates et al., 2013). In other words, it is unclear whether the majority of surviving individuals really are hiding under boulders or in out-of-sight crevices on the plots, or whether a portion are off the plot and may return to be viewed during a future year's survey. The estimates of detection do not distinguish between these two possibilities.

Lastly, there is a potential distinction to be made between individuals that have died and those that are missing because they have migrated a substantial distance away from their site of outplant. It is possible that initial stocking in high densities (dozens per metre squared) may encourage abalone to disperse relatively quickly in order to secure refugia or food. The data presented herein are from individuals that have established themselves on the plot and remain there on an annual basis, and would not reflect these immediate emigrants. Pinto abalone have the ability to move relatively rapidly when they decide to, on the order of metres per minute. On one occasion, divers happened to observe one individual make a net movement as far as is likely to be detected given the survey methods—from outside the plot perimeter on the shallow left corner to outside the plot perimeter on the deep right corner. This 15–20 m movement in the span of 1 week shows that, although it may be rare, successful emigration is likely reducing the estimates of overall survival at least somewhat.

On the other hand, as it concerns restoration goals, it may not be important to distinguish between abalone that have died and those that have emigrated away from the plot. The goal is to create dense aggregations of adults to increase successful local reproduction and subsequent regional recruitment (Rossetto et al., 2013). Although the emigrants certainly have the potential to contribute to future population growth, for the foreseeable future it is unlikely that they will find themselves spawning next to a member of the opposite sex unless they return to the experimental area. Thus, in this context, whether they are actually dead or just reproductively isolated may not be important to determine.

4.5 | Tag loss

The bee tags affixed with adhesive did not appear to impact the animals, although possible effects on growth or mortality from tagging were not assessed. This minimally invasive and inexpensive technique has a cost, in that there is a steady decay in their ability to be read over time. Using the interpolated time of 50% tag loss as a metric, the half-life of tags on the five sites with sufficient tagging history (Figure 4) averaged 2.4 years (± 0.28 years SE). Future research could use 2 years as a rule of thumb for tag longevity when planning studies using this tagging method, and inference about population parameters based on tagged recaptures is not recommended beyond year 1. Since

21% of all tags that remained affixed could not be read, this longevity could be extended with more durable imprint text.

4.6 | Lineage diversity

The estimates presented in Table 3 are likely a 'worst case scenario' for two main reasons. First, given the rapid tag loss and low detection rate of pinto abalone on these sites, many potential family representatives were likely not identified. Second, subsequent outplants add individuals from new families not represented in the original outplant. Given the longevity of the animals and variability in growth rate, the reproductive windows of animals of various ages likely overlap for multiple years. The listed estimates are more applicable to a hypothetical situation in which only one set of families was placed at a site, and not four or five as is typical here. Despite the many caveats, within a particular cohort in isolation, an abalone has an estimated one-in-eight chance of mating with a sibling, and a one-in-four chance of mating with a half-sibling.

There was a notably high chance of half-sibling matings resulting from the 2011 outplants to Omaha and Gold; 58% of the juveniles placed at those sites came from two prolific females with offspring that survived in high numbers in the hatchery. These nine families also apparently did well in the wild, as the proportion of survivors from those matrilineages after 1 year on the plot increased to 80%. This resulted in Simpson's dominance values over 0.40 and probabilities of half-siblings mating over one in three (Table 3). The dominance by a small number of females depends on the number and condition of available broodstock and is not typical of subsequent outplant cohorts. Issues with variance in gamete production among pinto abalone broodstock and the subsequent loss of genetic diversity are discussed by Lemay and Boulding (2009).

Of course, lineage diversity is not the same as genetic diversity. Genetic samples have not been thoroughly analysed to determine the degree of relatedness among individuals collected at various sites and used as broodstock in the hatchery. Owing to the constraints of using tags to identify family membership longer than 2 years, an assessment of the genetic diversity on the plots is planned using tissue samples from survivors and comparing their genotypes with hatchery broodstock. The goal is to produce juveniles with as high genetic diversity as possible to avoid the genetic bottlenecks that may result from this rapidly dwindling wild population. In British Columbia, Canada, loss of genetic diversity from an 80% population reduction had not yet been detected as of 2003 (Withler et al., 2003), although the 2017 Washington State population is likely even more reduced. After reviewing the results of planned genetic analyses, the conservation team may consider importing broodstock from out of state to increase genetic diversity.

As the total number of abalone on a plot decreases, the lineage diversity likely decreases as well. This can be mitigated by adding subsequent outplants from new lineages. However, the data presented here suggest new additions to a particular site are likely to survive just as well (or just as poorly) as previous outplants. This presents a strategic choice for conservation practitioners, as to whether

to devote juveniles to where they are 'needed' on poorly performing plots with low diversity, or to devote them to already-diverse plots where they will survive the best. As discussed in Section 4.8, the team has chosen the latter.

4.7 | Density estimation and prediction

Predicted density for each site was estimated using the SSM model, and CRIs for predicted counts overlapped observed counts for 2017. However, the CRIs for parameter estimates were typically wide. The low precision, although perhaps accurately representing uncertainty in the data, limits the effective use of those estimates in management decisions. The use of an integrated population model framework could improve precision of estimates (Abadi, Gimenez, Arlettaz, & Schaub, 2010; Schaub & Abadi, 2011), but initial attempts to fit this type of model resulted in severely negatively biased estimates, likely due to tag loss and skewed distribution of marked individuals across cohorts. In addition, the low survival rate exacerbated by low detection rates resulted in a very small number of recaptures. These limitations could be reduced and precisions in estimates improved by some changes in study design that would allow for simultaneous unbiased estimation of detection, survival, population growth rate, and density. Typically, entire cohorts of outplants for a site were marked or not marked, with marked cohorts commonly released in the first year of site establishment. Combined with increased detection and survival as outplants increase in size, bias in estimates resulting from tag loss is compounded over time. Stratifying marked individuals across sites and cohorts (providing marks on a proportion of outplants in each cohort) could allow for better estimation of detection and resulting parameters of interest for each cohort. In addition, providing a greater number of, and proportion of, marked individuals relative to unmarked individuals would increase the number of individuals recaptured. Finally, as abalone grow after release and as tag losses accumulate over time, other methods may be required to better estimate parameters for larger abalone established on sites for multiple years. More durable tags, repeated marking over time, or multiple observer methods could alleviate this issue. In general, if mark-recapture methods are continued, a tag loss study would allow for a better understanding of how this assumption violation is biasing estimates and that may be accounted for in the future. Temporary emigration, where individuals are alive but not available to be detected, such as when hiding in crevices, is likely site dependent. Thus, while detection was estimated based on a few sites, site-specific covariates related to the amount of available refugia could improve accuracy of estimates.

4.8 | Changes to the juvenile outplant operation

The Washington State abalone restoration effort is currently in transition from a pilot phase focused on data collection towards an active restoration phase focused on production. As part of the transition, four sites have been identified where documented outplant success is low enough (0–2%) to preclude additional outplants there, and six sites that will continue to receive hatchery animals periodically due to sufficient success rates (2–8%). Documented outplant success only

considers observed adult animals located within or near the plot boundaries. It is likely that many more animals are not observed, with cryptic reproductive adults on the plots contributing to greater 'success'. It is also probable that many animals have left the plots, potentially encountering other emigrants or wild individuals and reproducing. However, the strategy focuses on creating high-density aggregations of animals for reproductive purposes. A hypothetical site where survival is high but animals disperse would be devalued in favour of those where animals remain on or nearby the plot in high density.

The new strategy of 'repeal and replace', whereby sites with low initial success are abandoned and new sites established, began in 2017. The most recent cohort was placed on the six most successful sites (Table 2), and two new ones (Blackstone and Brushwood) not described in this paper. Early in the programme, poorly performing sites continued to receive outplants in later years because of a theory that abalone may remain hidden for a number of years before emerging as adults. Indeed, evidence has been presented here that the detection rate of abalone increases with size. However, 8 years into the programme, sites with low densities detected in initial surveys continued to have poor success throughout (Figure 5). Although nine out of 10 sites consistently achieved estimated densities above the target threshold of 0.3 m^{-2} when accounting for detection, the mortality at sites on the lower end of the spectrum creates an inefficiency compared with better sites. The scale-up in restoration activities is going to require efficient use of hatchery resources to produce the highest number of reproductive adults in the wild.

The repeal and replace strategy would be greatly aided by a better understanding of what makes some existing sites better than others. The criteria outlined here yielded several successful sites, but also produced sites with little or no success over multiple trials. The spatial scale of this variability in survival (in some cases only hundreds of metres) is difficult to explain. If, indeed, predation is the most important factor controlling site success, available evidence suggests that (a) the predators in question do not range among nearby sites, (b) they remain important at a site over successive outplants/years, but also (c) their abundance is not apparent to divers during daytime surveys. Unless additional biological (e.g. key predator density) or physical (e.g. in-situ measurements of current speed) variables that may differentiate sites can be identified, the scale-up of juvenile production in the hatchery will still be subject to inefficient trial-and-error outplants on new sites.

Another efficiency may be gained by outplanting juveniles sooner than the average 20 months after fertilization used in this experiment. Research suggests that this age, and a size close to 23 mm on average (Supporting Information Table S2), may allow pinto abalone to avoid the most significant predation pressure that comes from small crabs (Griffiths & Gosselin, 2008). However, the effect of size-at-outplant on survival was swamped by the site effect in the CJS model, and again by lineage even when site effects were removed. If, indeed, the greater mortality associated with outplanting sooner is minimal, the savings in time and resources in the hatchery could be substantial. For instance, Roberts, Keys, Prendeville, and Pilditch (2007) used a cost-benefit approach balancing greater cost to produce larger juveniles with higher survival. They calculated an 'economically

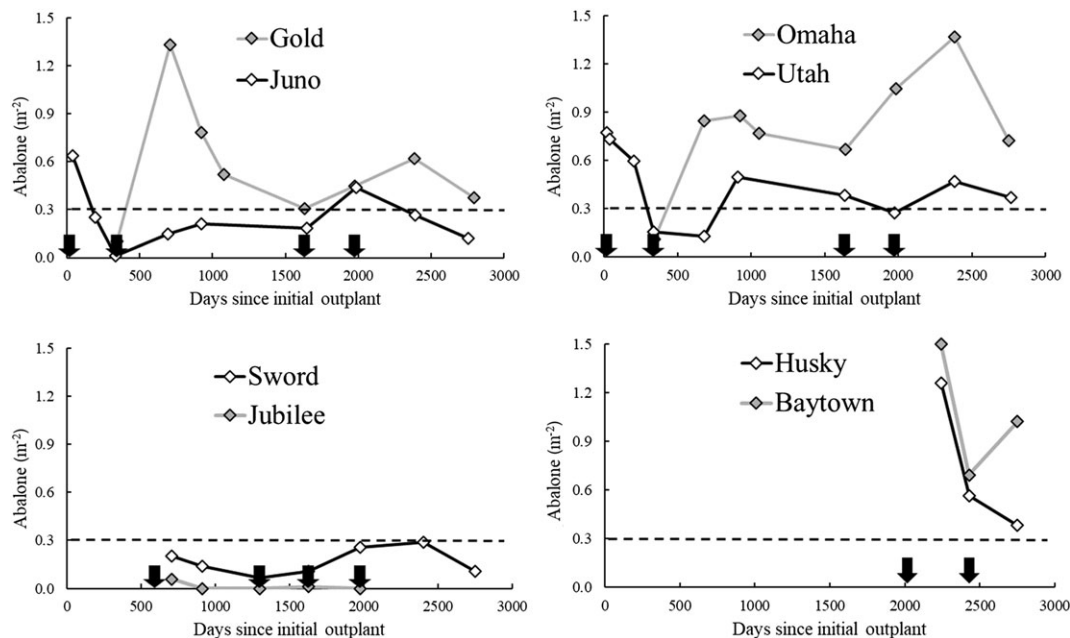


FIGURE 5 Observed (naive) density of hatchery-origin pinto abalone on eight sites in the San Juan Islands. Each plot shows two sites located on the same island. The dashed line represents the target abalone density of 0.3 m^{-2} to promote successful reproduction during broadcast spawning. Arrows show the timing of successive outplants to the sites. Densities were not adjusted to reflect the addition from outplants; only individuals detected in surveys are shown. Site Jubilee did not receive the third and fourth outplants shown

optimal' juvenile size of 10 mm for the rainbow abalone *Haliotis iris*. Available data show that growth is similar or may even increase after outplant, suggesting that outplanting at a younger age is unlikely to increase the time needed to reach reproductive size compared with our current strategy. Experiments are in progress testing the survival and growth of 9-month-old (average 8 mm size) and 14-month-old (average 14 mm size) abalone in the field and laboratory. Additionally, outplanting animals at a younger age may decrease their habituation to movement, shadows, and contact in the hatchery. This habituation is hypothesized to explain why hatchery-origin pinto abalone demonstrate a muted behavioural response to nearby movement, direct contact, or predator cues compared with wild individuals, and why the lack of response is more pronounced in individuals that remain in the hatchery longer (Hansen & Gosselin, 2016).

Previous pilot work took the younger outplant strategy to its logical extreme: deploying competent larvae together with a settlement cue onto the benthos. Despite the success of laboratory controls, no abalone were found at the larval outplant sites in follow-up surveys (WDFW, unpublished data). More methods trials are needed before this strategy is abandoned. The mass deployment of very early stages has had some success with pinto abalone (Read, Lemay, Acheson, & Boulding, 2012), although, given the genetic methodology used to identify hatchery animals, only a small number of adults were confirmed to have resulted. Restocking using very young juveniles or competent larvae has been tried in various other abalone species around the world with variable success (e.g. Hamasaki & Kitada, 2008; Searcy-Bernal, Anguiano-Beltran, Espinoza-Montes, & Carpizo-Ituarte, 2013).

In the early years of the operation, teams would leave outplant tubes containing abalone sealed with mesh for 24 hr to allow the abalone to acclimatize before being exposed to predators. This

required a return trip to all plots to remove the mesh. In response to research that shows little benefit to acclimatization (Hansen & Gosselin, 2013), in later years the mesh was removed immediately at the time of outplant. There was no increase in mortality that could be attributed to this choice, although the new families, different years, and new combinations of sites greatly confounded the ability to assess this decision. Since predation appears to be the greatest contributor to juvenile mortality (Hansen & Gosselin, 2013), it is possible that placing a high concentration of juveniles that attracts predators (Hofmeister et al., 2018), without allowing the juveniles to immediately leave the tubes and find refuge, is actually giving the predators a 24 hr head start. Instead, outplanting in lower concentrations over a larger area may help reduce immediate juvenile mortality (Read et al., 2013). Outplanting in diffuse arrays rather than a concentrated group did not affect juvenile mortality in the black-lipped abalone *Haliotis rubra* (Chick, Worthington, & Kingsford, 2013), but their 'diffuse' arrays were more concentrated than the outplants in the present study. Diffuse outplanting could also lower eventual densities of reproductive adults.

Until signs of natural recruitment are seen on reference index sites, adult densities on outplant sites will likely continue to decline in between outplants. Using the estimated annual population growth rate from the SSM model of 0.5, and an initial outplant of 500 individuals, a successful site might need to receive new cohorts every 4–5 years to remain above the target reproductive density. Sites could receive new cohorts more frequently, but it is unclear at what point the efficiency of repeated outplants at a successful site will be reduced by density-dependent processes. Abalone on overpopulated sites might have reduced growth or reproduction due to food limitation, increased mortality due to the limitations of refuge space, or increase migration behaviour to avoid these impacts. For now, even

the highest densities estimated to exist on the juvenile outplant sites are assumed to be below their carrying capacity. The most successful sites, Omaha and Baytown, have observed abalone densities $>1\text{ m}^{-2}$, and estimated densities substantially higher. Index station surveys from Haida Gwaii, Canada, in 1978 and 1979 showed an average pinto abalone density of 2.7 m^{-2} , with a maximum value of 16.6 m^{-2} (Hankewich, Lessard, & Grebeldinger, 2008).

Lastly, the target abalone reproductive threshold of 0.3 m^{-2} is derived from the approximate density below which a population of another species, on another continent, crashed (Babcock & Keesing, 1999). More proximal work in California has suggested a similar minimum stocking density (0.23 m^{-2}) for white abalone (*Haliotis sorenseni*) to show positive growth in a population projection model (Catton, Stierhoff, & Rogers-Bennett, 2016). Is it possible that pinto abalone in Washington State have a very different threshold density, which would change restoration strategies substantially. Getting a better estimate of the relationship between adult density and fertilization efficiency in field or laboratory experiments in an important piece of designing a cost-effective large-scale restoration programme.

Future restoration planning for *H. kamtschatkana* will begin by reconstructing the historical range of the species in Washington State to guide the calculation of available habitat for supplementation. If refined using continued data collection, population projection models developed in this study will be used to estimate the time and resources needed for regional recovery on the identified habitat. Meanwhile, monitoring of the wild remnant population will continue, in hopes of finding the first evidence of juvenile recruitment in many years.

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ORCID

Henry S. Carson  <https://orcid.org/0000-0002-3428-9231>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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