

## RESEARCH ARTICLE

# The transition from resistance to acceptance: Managing a marine invasive species in a changing world

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## Abstract

1. Marine invasive species can transform coastal ecosystems, yet mitigating their effects can be difficult, and even impractical. Often, marine invasive species are managed at poorly matched spatial scales, and at the same time, rates of spread and establishment are increasing under climate change and can outpace resources available for population suppression. These circumstances challenge traditional conservation goals of maintaining a historic environmental state, especially for a species like the European green crab (*Carcinus maenas*), a formidable invader with few examples of successful long-term removal programs.
2. A management paradigm where decision alternatives include resisting or accepting a new ecological trajectory may be needed. We apply mathematical concepts from decision theory to develop a quantitative framework for navigating management decisions in this new resist-accept paradigm. We develop a model of European green crab growth, removal and colonization, and we find optimal levels of removal effort that minimize both ecological change and removal cost.
3. We establish a benchmark of colonization pressure at which green crab density becomes decoupled from a decision maker's actions, such that population control can no longer shape the invasion trajectory. For informing the decision boundary between resistance and acceptance, our results highlight that a decision maker's understanding of how removal cost scales with removal effort is more important than understanding the density-impact relationship.
4. We show that assuming stationary system dynamics can result in sub-optimal levels of species removal effort, highlighting the importance of developing anticipatory management strategies by accounting for non-stationary dynamics.
5. *Policy implications.* For marine invasive species that can disperse across long distances and recolonize rapidly after removal, the focus of conservation policy should shift away from understanding *how* to resist change to understanding *when to stop* resisting change. Navigating this decision problem involves trade-offs among competing objectives, highlighting the need for structured approaches to elicit objective weights that reflect the values of the decision maker.

Timothy D. Counihan—Posthumous authorship.

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For natural resource managers facing possible ecosystem transformation, this decision framework can enable proactive and strategic decisions made under uncertainty in a changing world.

#### KEYWORDS

invasive species management, Markov decision process, non-stationarity, RAD decision framework, structured decision making

## 1 | INTRODUCTION

Rates of ecological transformation are accelerating under global change (Williams et al., 2021), so long-standing conservation goals of maintaining ecosystems at baseline conditions may no longer be attainable. These novel situations warrant considering new approaches for stewarding ecosystems where the focus shifts to 'managing for change, not just persistence' (Stein & Glick, 2014).

This shift in focus will be critical for the management of marine invasive species that can drive profound ecological change, transform community structure and engineer ecosystems (Guy-Haim et al., 2018; Ruiz et al., 1997). In addition to human-mediated pathways, many marine organisms can naturally disperse broadly and rapidly, where dispersal at a regional scale influences the demographics of local populations (Kinlan & Gaines, 2003). These long dispersal distances contribute to spatial mismatches between scales of governance and population processes, such that institutional jurisdictions are often too small to affect the areal extent of the ecosystem (Crowder, 2006; Galaz et al., 2008). The rate of invader spread and recolonization after removal in marine systems can therefore outstrip resources available for control (Figure 1) (Green & Grosholz, 2021), yet historical conservation strategies have focused on resisting change through eradication or population suppression.

*When should a manager stop resisting change and accept a new ecological trajectory?* This question will become a hallmark of natural resource management under global climate change and has motivated the development of the resist-accept-direct (RAD) decision framework, an emerging classification system that encompasses the entire decision space in circumstances where maintaining historical or current conditions may no longer be possible (Schuurman et al., 2020). Two of the decision alternatives under this paradigm include *resist* to conserve historical or current conditions and *accept* due to insufficient resources or inability to shape the ecological trajectory (Lynch et al., 2021). While this new framework represents a paradigm shift in thinking necessary for developing climate-wise management strategies, the framework itself does not inform the decision to switch between decision alternatives (Williams & Brown, 2024).

The sole emphasis on minimizing impact and resisting change is becoming especially inadequate for a species like the European

green crab (*Carcinus maenas*). This resilient marine invader has no documented examples of eradication due to its enormous reproductive potential and its dispersive larval phase that facilitates the recolonization of suppressed populations from neighbouring habitats (Behrens Yamada et al., 2015; Young & Elliott, 2020). Field experiments with established populations demonstrate that although green crab removal programs can achieve short-term benefits in local areas, population suppression through removal is unlikely at larger temporal and spatial scales (Duncombe & Therriault, 2017; Flynn et al., 2024). Understanding the decision boundary between resistance and acceptance will therefore be critical for management in newly invaded areas. For example, estuaries in the Northeast Pacific have recently experienced a significant expansion in range and abundance, following colonization pressure associated with El Niño events that allow the survival and transport of larvae hundreds of kilometres from their source (Behrens Yamada et al., 2021). Natural resource managers will need to strategically allocate resources to locations where resistance is most feasible.

Under greenhouse warming, climate models project an increase in the frequency of these oceanographic conditions that favour larval dispersal and colonization pressure (Cai et al., 2021). Existing invasive species management policies may therefore become unsuitable for stewarding transforming ecosystems in a non-stationary world. Management strategies are often developed under the assumption that although system dynamics may be stochastic, the underlying processes are constant over time (Tucker & Runge, 2021). These stationary policies can be sub-optimal under non-stationary conditions, as past relationships can be insufficient predictors of the future (Dietze et al., 2018; Nichols et al., 2011). Proactive policies that include time as a state variable and account for changing system dynamics could be necessary for guiding anticipatory actions, yet are uncommon in natural resource management.

In this paper, we apply a decision-theoretic lens to characterize the boundary between resistance and acceptance when managing a marine invasive species under system change. We use stochastic dynamic programming to establish conditions when natural resource managers can no longer alter an invasion trajectory through their actions, and we contextualize our model through a case study with an invasive European green crab. This quantitative framework can provide critical decision support for managers of ecosystems on paths toward potential transformation.

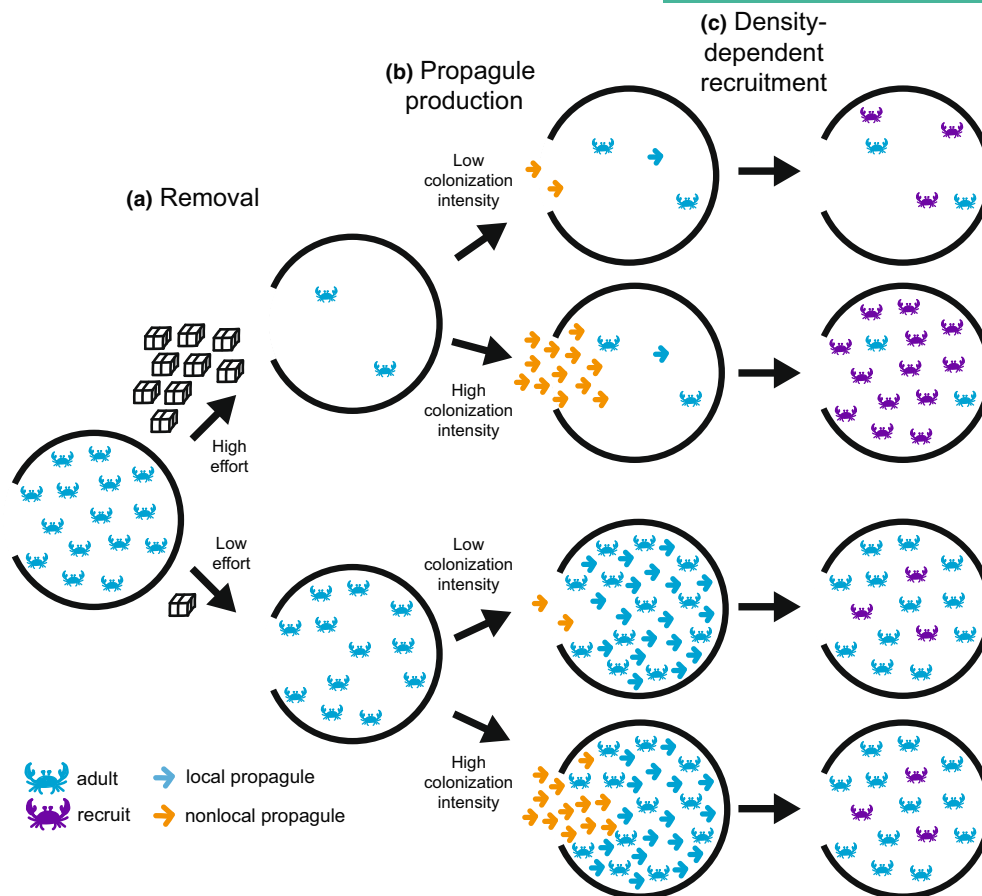


FIGURE 1 Conceptual diagram highlighting the resulting European green crab (*C. maenas*) density after (a) variable levels of removal, (b) propagule production under variable levels of colonization intensity and (c) density-dependent recruitment into the population.

## 2 | MATERIALS AND METHODS

To find optimal levels of invasive species removal effort, we formulated a Markov decision process (MDP) model to represent a decision problem faced by an invasive species manager tasked with controlling a single, local population. Solved with the established optimization technique of stochastic dynamic programming (SDP), MDPs are appropriate for finding optimal sequential decisions about dynamic biological systems where the outcomes of management actions are uncertain (Marecot et al., 2013). Here we present how we formulated the Markov decision process (MDP) model for a more general problem, and then we describe its application within the context of invasive European green crab management in the Northeast Pacific. Finally, we describe how we characterized the decision boundary between resistance and acceptance, and how we evaluated the impact of biological non-stationarity on optimal removal efforts. This study did not require ethical approval.

### 2.1 | MDP model formulation

A finite horizon stationary MDP is described by a tuple,  $(S, A, U, P)$ , where  $S$  represents the finite set of states that can be reached by the

system,  $A$  represents the finite set of actions that can be applied at each period,  $U$  is a utility function and  $P$  is a state transition function.

The set  $S$  reflects the species density in a decision maker's jurisdiction, where  $s = \{0, \dots, s_{\max}\}$ . The maximum available species density,  $s_{\max}$ , is chosen such that it is 40% greater than  $K$  or the carrying capacity of the habitat. In each period  $t$ , the manager decides the level of removal effort,  $a_t$ , where  $a_t = \{0, \dots, a_{\max}\}$ . Both the state and action spaces are discretized into 141 and 100 partitions, respectively. The harvest rate of the population,  $H_t$ , is a saturating function of the removal effort, the rate of saturation,  $b$  and a parameter,  $H_{\max} < 1$ , that describes the mean maximum removal rate, often smaller than one due to size-selective removal or intra-specific interactions (Young & Elliott, 2020).

$$H_t = H_{\max} \times e^{b \times a_t} + \epsilon_R. \quad (1)$$

$$\epsilon_R \sim \text{Normal}(0, \sigma_R). \quad (2)$$

We assume discrete-time, density-dependent population growth, building from a European green crab population dynamics model developed by Canary et al. (2014) that assumes a reproductive period during a brief interval at a specific time of the year. The local crab population size at the beginning of the  $t$ th season is represented by  $s_t$ . The population size at the beginning of the reproductive

period is denoted by  $s'_t$ , where  $S_A < 1$  and  $H_t$  are the adult survival and removal rate, respectively:

$$s'_t = (1 - H_t) \times s_t \times S_A, \quad (3)$$

$$S_A \sim \text{Normal}(S_{A,\text{mean}}, S_{A,\text{sd}}). \quad (4)$$

The growth function,  $g$ , is described using the Beverton-Holt equation (de Vries et al., 2006), where  $K$  is the carrying capacity of the local habitat. The maximum growth rate,  $r$ , is a function of maximum fecundity,  $F > 0$ ; larval recruitment,  $0 < S_L < 1$ ; and the proportion of the population that reproduces,  $0 < m < 1$  (Kanary et al., 2014):

$$g = s_{t+1} = \frac{r}{1 + \frac{r-1}{K} \times s'_t} \times s'_t, \quad (5)$$

$$r = m \times F \times S_L, \quad (6)$$

$$F \sim \text{Normal}(F_{\text{mean}}, F_{\text{sd}}), \quad (7)$$

$$S_L \sim \text{Normal}(S_{L,\text{mean}}, S_{L,\text{sd}}). \quad (8)$$

After spawning, green crab planktonic larvae exit the estuarine habitat to develop in high-salinity coastal waters. In these open waters, they complete development alongside larvae produced by neighbouring habitats before advection back into the estuary during recruitment (Young & Elliott, 2020). We account for this non-local larval supply produced by neighbouring source populations by considering the effective population size,  $E_t$ , which is the sum of the local population size,  $s'_t$ , and the size of neighbouring source population(s),  $\alpha \geq 0$ :

$$E_t = s'_t + \alpha. \quad (9)$$

Population growth can then be represented as:

$$g = s_{t+1} = \frac{r}{1 + \frac{r-1}{K} \times E_t} \times E_t. \quad (10)$$

Connectivity among neighbouring populations is variable, depending upon the strength and direction of currents, El Niño events and other oceanographic conditions, like temperature and salinity (Brasseale et al., 2019; See & Feist, 2010). The size of the neighbouring source population(s) scaled relative to the carrying capacity of the local population,  $K$ , is therefore represented stochastically to account for this variability. The expected value of  $\alpha$ ,  $E[\alpha]$ , is  $\beta_1 \times \beta_2 \times K$ .

$$\frac{\alpha}{K} \sim \text{Gamma}(\beta_1, \beta_2). \quad (11)$$

Removal and population growth are then combined to create the state transition function,  $P(s_{t+1}|s_t, a_t, \theta)$  in the MDP, representing the system transitions from one state,  $s_t$ , to another,  $s_{t+1}$ , after implementing the action,  $a_t$  and assuming  $\theta$ , parameters in the removal rate and growth functions

( $\theta = \{H_{\text{max}}, b, \sigma_R, S_{A,\text{mean}}, S_{A,\text{sd}}, m, F_{\text{mean}}, F_{\text{sd}}, S_{L,\text{mean}}, S_{L,\text{sd}}, K, \beta_1, \beta_2\}$ ; Equations 1, 2, 4–8 and 11; see Appendix S1 for values used for  $\theta$ ).

The transition function,  $P$ , is expressed fully:

$$P(s_{t+1}|s_t, a_t, \theta) = g(H_t, F, S_L, S_A, \alpha, s_t, m, K) \times \int P(H_t = h_t | a_t, \theta) \times \int P(F = f | \theta) \times \int P(S_L = s_L | \theta) \times \int P(S_A = s_A | \theta) \times \int P(\alpha = \nu | \theta). \quad (12)$$

The transition function,  $P$ , is discretized for numerical methods (further description of discretization and integration intervals is provided in Appendix S2).

This decision problem is a multi-objective programming problem, where the goal is to find the optimal level of removal effort that both minimizes the cost of removal and minimizes ecological change. The utility function,  $U$ , represents this trade-off between available removal resources and the management goal of minimizing ecological change. Since the relationship between species density and ecological impact is uncertain or depends upon the impacted resource, we examined two nonlinear ecological value functions,  $V_d(s_t)$  (Bradley et al., 2019; Yokomizo et al., 2009).

$$V_d(s_t) = \frac{l_{\text{sig}}}{1 - e^{-m_{\text{sig}} \times (s_t - n_{\text{sig}})}} \text{ (sigmoidal)}, \quad (13)$$

$$V_d(s_t) = l_{\text{exp}} \times e^{-m_{\text{exp}} \times s_t - n_{\text{exp}}} \text{ (exponential)}. \quad (14)$$

We considered two different value functions,  $V_c(a_t)$ , that describe the cost of removal to the decision maker.

$$V_c(a_t) = -a_t^{p_{\text{nonlinear}}} \text{ (nonlinear)}, \quad (15)$$

$$V_c(a_t) = -a_t \text{ (linear)}. \quad (16)$$

The utility function,  $U(s_t, a_t)$ , gives the reward for the outcome of applying action  $a$ , to state  $s$ , at time  $t$ . Creating a multi-objective programming problem requires dealing explicitly with the relative importance of the objectives to the decision maker (Converse, 2020). The utility function,  $U(s_t, a_t)$ , is calculated using a weighted-sum method, where weights are assigned to the two objectives and are used to develop a single criterion. These weights reflect the values of the decision maker; here, weights are selected to represent a scenario where a decision maker values minimizing ecological damage much more than minimizing removal cost ( $w_d = 0.98$ ,  $w_c = 0.02$ ) (see Appendix S1). Both  $V_d$  and  $V_c$  are normalized to range between  $-1$  and  $0$ .

$$U(s_t, a_t) = w_d V_d(s_t) + w_c V_c(a_t). \quad (17)$$

To solve the MDP, we used backward iteration over a finite horizon ( $t = 150$ ) to find a policy that maximizes the sum of the discounted utility values (discount factor = 0.99) (Marescot et al., 2013) (see Appendix S1). The discount factor represents inter-temporal trade-offs in rewards and ranges from 0 to 1, and a discount factor of 0.99 indicates that the value of future rewards is nearly equal to the value of immediate rewards. The optimal solution is a function,  $\pi^*$ , that maps each state to an optimal action.

## 2.2 | Application to invasive European green crab

Values for most model parameters,  $\theta$ , are drawn from previous literature estimates and are further described in Appendix S1. Carrying capacity,  $K$ , was selected based on population estimates from intensive mark-recapture experiments in an estuary in central California (Grosholz et al., 2021). European green crab's resilience to suppression is related to its extremely high fecundity, with gravid females producing hundreds of thousands of eggs (Cohen & Carlton, 1995). Although there is geographic variability in fecundity and survival, parameter values for adult survival, larval survival and fecundity were chosen based on those used in a population dynamics model of green crab invasion and control developed by Canary et al. (2014) (Cooper et al., 2012; Canary et al., 2014; Klassen & Locke, 2007). The primary method for green crab removal is through the use of baited traps, which can limit removal efficacy due to factors including foraging activity of crabs, size-selectivity of traps, tide, season and intra-specific interactions (Grosholz et al., 2000; Hunter & Naylor, 1993; Young et al., 2017; Young & Elliott, 2020). The exact relationship between removal effort and population suppression is unknown, but previous studies estimate that a maximum of 80% of the population can be removed (Crothers, 1968; Young & Elliott, 2020). We therefore use arbitrary units of removal effort ( $a_t = \{0 \dots 1\}$ ,  $a_{\max} = 1$ ), where the removal rate asymptotically reaches 0.8 (Equation 1).

Reproductive crab populations occupy sheltered bays and estuaries, whereas the dispersive larval phase occurs in open marine waters that can be connected to neighbouring habitats (Behrens Yamada et al., 2015; Klassen & Locke, 2007). Connectivity between a local population and non-local source populations, however, is variable, ranging from isolated populations that infrequently receive non-local propagules through intermittent oceanographic events, to highly connected populations, like those within a single estuary but are fragmented by jurisdictions of private shellfish farms, Tribal governments and state and federal entities (Behrens Yamada et al., 2021). Parameter values used to describe the stochastic size of the source population(s),  $\alpha$ , were chosen to reflect this range in connectivity (Table S1; Figure S1).

The green crab is considered an 'ecosystem engineer' because of its ability to modify ecosystem components, including mudflat, saltmarsh and eelgrass habitat through its foraging behaviour (Malyshev & Quijón, 2011). As a generalist predator, the green crab feeds on a diversity of bivalves and crustaceans, most notably exemplified through its devastating impact on an economically significant soft-shell clam industry in New England (Beal, 2002). Though likely nonlinear, the exact quantitative relationship between green crab density and ecological impact is unknown, so alternate utility functions in the MDP were parameterized to reflect this uncertainty (Equations 15 and 16) (Davis et al., 1998; Grosholz et al., 2011).

## 2.3 | Resistance and acceptance along an invasion trajectory

To assess how the decision boundary between resistance and acceptance varies along an invasion trajectory, optimal actions were

found for a range of invasion regimes, reflecting variation in both the magnitude of source population(s) and frequency with which they are connected to a local population managed by a single decision maker. Optimal actions were found for source population(s) size,  $\alpha$ , with expected values from 0.005K to 5K (Table S1; Figure S1).

To quantify a population's response to removal effort under these invasion regimes, the equilibrium population size was calculated by iterating through the state transition function with a constant action,  $P(s_{t+1}|s_t, a)$ , for 50 iterations and for  $a = \{0, 0.25a_{\max}, 0.5a_{\max}, 0.75a_{\max}, a_{\max}\}$  and  $s_{t=1} = 0.2K$ .

## 2.4 | Impact of non-stationarity on optimal decisions

We then evaluated the impact of biological non-stationarity on optimal removal efforts. As the abundance of nearby populations increases under range expansion and as conditions supporting long-distance colonization events increase in frequency and magnitude in a warming climate (Cai et al., 2021), the frequency and magnitude of colonization pressure from non-local source populations are likely to increase.

We assumed a progression through four invasion regimes at discrete intervals, where the expected value of  $\alpha$  increases from 0.005K, 0.05K, 0.5K, to  $K$  (Table S1). This progression reflects a transition from an isolated local population with infrequent colonization events to a population fully connected to a source population(s) equal to the size of the carrying capacity of the local habitat. A time-dependent transition function was used,  $P(s_{t+1}|s_t, a_t, \theta(t))$ , where the values of  $\theta$  related to the stochastic source population(s) size,  $\beta_1$  and  $\beta_2$ , varied across time (Equation 11). Regime transitions occurred discretely at  $t = 10, 20$  and  $30$ .

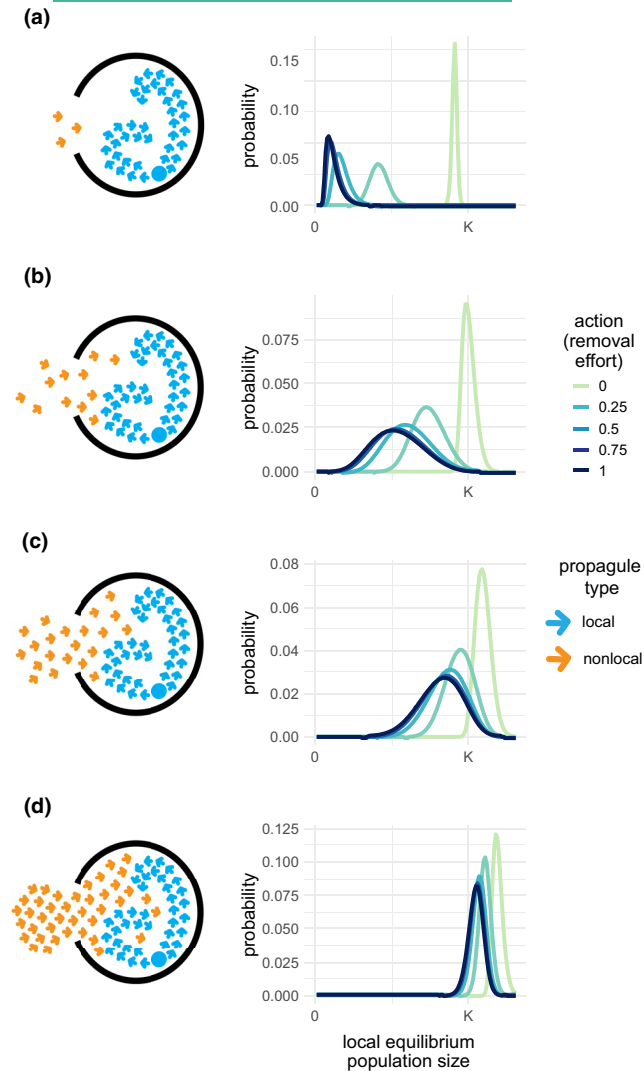
We used backwards iteration SDP to solve for optimal state- and time-dependent removal efforts that minimize ecological impact and removal cost over a 65-year time horizon with a discount factor of 0.99 (Tucker & Runge, 2021) (Appendix S1). We quantified the impact of non-stationarity on the optimal decision by calculating the difference in the time-dependent, non-stationary optimal policies and the time-independent optimal policy assuming stationarity in the regime ( $\Delta$  optimal removal effort).

## 3 | RESULTS

### 3.1 | Equilibrium population size depends on colonization intensity

The equilibrium population size under a constant action was calculated for four invasion regimes (Figure 2a:  $E[\alpha] = 0.005K$ ; Figure 2b:  $E[\alpha] = 0.2K$ ; Figure 2c:  $E[\alpha] = 0.5K$ ; Figure 2d:  $\alpha = K$ ). When propagule pressure from source population(s) is small and infrequent, the equilibrium population size is closely coupled to the action, or level of removal effort (Figure 2a). As the size of the source population(s) increases, the equilibrium population size becomes decoupled from the action or level of removal effort (Figure 2b-d).





**FIGURE 2** Probability density functions representing the local equilibrium population size under a constant action (removal effort) and four invasion regimes with increasing propagule pressure from non-local source populations. Panels represent increasing size of the stochastic source population(s),  $\alpha$ : (a)  $E[\alpha]=0.005K$ , (b)  $E[\alpha]=0.2K$ , (c)  $E[\alpha]=0.5K$ , (d)  $E[\alpha]=K$ . The  $x$ -axis represents the size of the local population at equilibrium, and line colours represent the constant action, ranging from 0 to 1 ( $a_{\max}$ ). [Table S1](#) provides more information about the parameters associated with the stochastic source population size.

### 3.2 | Characterizing the resist-accept decision boundary

As the size of the source population(s),  $\alpha$ , increases, the optimal management strategy shifts from resistance to acceptance ([Figure 3](#)). The continuous optimal removal effort is discretized to reflect the binary resist-accept decision space, where a removal effort greater than zero corresponds to ‘resist’ and a removal effort equal to zero corresponds to ‘accept’. Along this decision boundary, acceptance—a removal effort of zero—becomes optimal for higher species densities before lower species densities ([Figure 3b,c](#)).

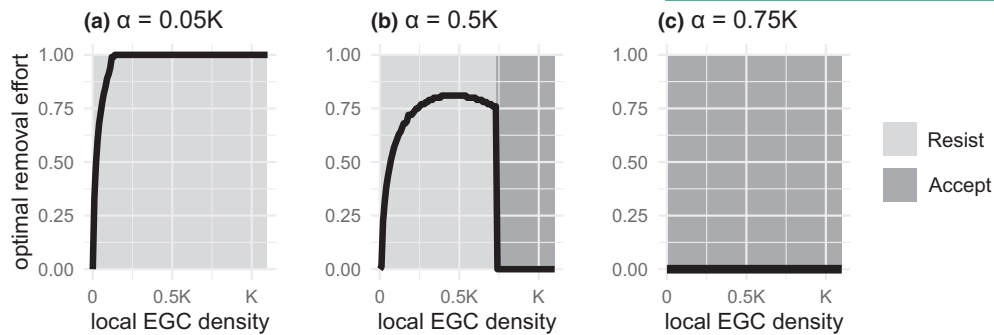
The path along the decision boundary between resistance and acceptance is nuanced, as the optimal policy depends on the removal cost function and action penalty function ([Figure 4](#); [Figure S2](#)). The optimal removal effort is more sensitive to variation in the removal cost function than variation in the ecological impact function ([Figure 4](#)), despite objective weighting such that the ecological impact contributes an order of magnitude more toward the overall reward than the removal cost ([Equation 17](#); [Appendix S1](#)). With a linear removal cost function, the optimal management effort switches rapidly from the maximum removal effort,  $a_{\max}$ , to no removal effort or acceptance ([Figures 3 and 4](#); [Figure S2](#)). Conversely, with a nonlinear removal cost function, the optimal management effort only reaches  $a_{\max}$  when the source population(s) size is low and never reaches complete acceptance (removal effort=0), even when the mean source population(s) size is five times greater than the local carrying capacity (i.e.  $E[\alpha]=5K$ ) ([Figure 4d](#)).

### 3.3 | Accounting for non-stationarity variably impacts the optimal decision

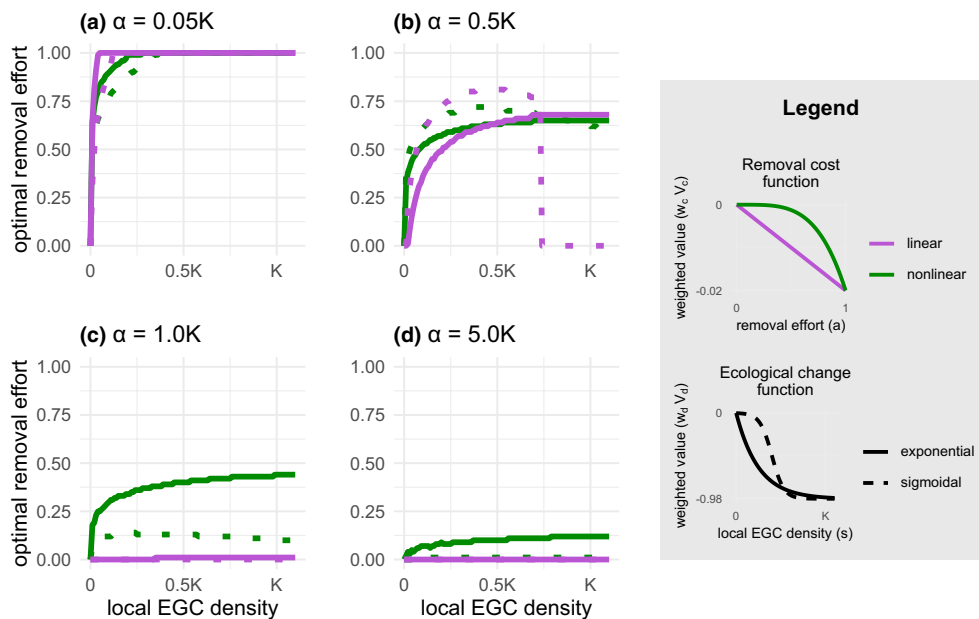
In anticipation of a regime shift, the optimal state- and time-dependent removal efforts that account for non-stationarity in the invasion regime differed from the optimal policy assuming stationarity in the current regime. In anticipation of a change from a regime where a local population is isolated from source population(s) and infrequently receives non-local propagules ( $E[\alpha]=0.005K$ ) to a regime with an increased source population(s) size ( $E[\alpha]=0.05K$ ), the optimal time-dependent removal effort is different than the optimal removal effort assuming stationarity in an isolated regime. This difference, however, depends upon the ecological change function. If the relationship between green crab density and ecological change is exponential, the optimal removal effort accounting for this non-stationarity is lower than the optimal removal effort assuming stationarity in the current isolated regime ([Figure 5b](#)). Conversely, if the relationship between green crab density and ecological change is sigmoidal, the non-stationary optimal removal effort is higher than the action assuming stationarity in the current isolated regime ([Figure 5c](#)). In anticipation of a further increased source population(s) size ( $E[\alpha]=0.05K$  to  $E[\alpha]=0.5K, 1.0K$ ), the non-stationary optimal removal effort is lower than the current regime’s stationary optimal removal effort ([Figure 5b,c](#)).

## 4 | DISCUSSION

This work establishes a quantitative framework for guiding the transition between resistance and acceptance when managing a resilient marine invader like the European green crab. We find that at high colonization intensities via a large source population(s), a decision maker’s action can no longer shape an invasion trajectory ([Figure 2d](#)) such that resistance, or continued removal effort, is no longer optimal ([Figure 3](#)). These high colonization intensities are



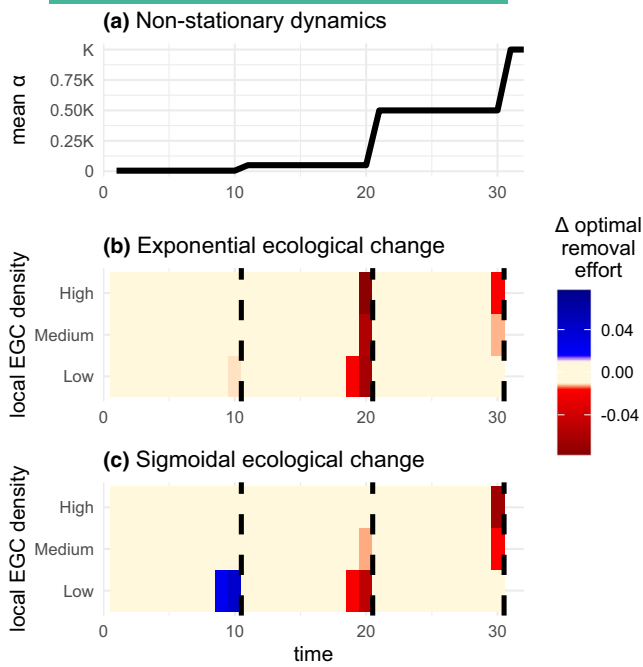
**FIGURE 3** The decision boundary between resistance and acceptance under increasing stochastic source population(s) sizes,  $\alpha$ : (a)  $E[\alpha]=0.05K$ , (b)  $E[\alpha]=0.5K$  and (c)  $E[\alpha]=0.75K$ . The continuous optimal removal effort is discretized to reflect the binary resist-accept decision space; the optimal state-dependent management strategy of ‘resistance’ (i.e. optimal removal effort  $>0$ ) is highlighted in light grey, and the optimal state-dependent management strategy of ‘acceptance’ (i.e. optimal removal effort  $=0$ ) is highlighted in dark grey. Optimal removal efforts are calculated using a sigmoidal ecological change function and nonlinear removal cost function (Equations 13 and 15) and with objective weights 0.02 and 0.98 for  $w_c$  and  $w_d$ , respectively (Equation 17).



**FIGURE 4** Stationary state-dependent optimal removal efforts for variations in removal cost function (line colours) and ecological change function (line types) (Equations 13–16). Panels show the optimal removal effort as a function of local European green crab (EGC, *C. maenas*) density under increasing size of stochastic source population(s),  $\alpha$ : (a)  $E[\alpha]=0.05K$ , (b)  $E[\alpha]=0.5K$ , (c)  $E[\alpha]=K$  and (d)  $E[\alpha]=5K$ . Legend indicates the objective weights used to develop the weighted-sum utility function (Equation 17). Optimal removal efforts for other source population(s) sizes are provided in Figure S2.

quite probable for some marine species, especially European green crab, where non-local recruitment can play a substantial role in local population dynamics (Behrens Yamada et al., 2021; Szuwalski et al., 2015). Additionally, the jurisdictions of individual decision makers can fragment highly connected subpopulations within an estuary with strong larval retention, and long-distance dispersal can transport larvae up to thousands of kilometres between estuaries (Kinlan et al., 2005). Climate change will increase oceanographic conditions supporting region-scale dispersal and high growth rates, so quantitative guidance for assessing the feasibility of long-term suppression will be critical for managing green crab in a changing world.

Our findings highlight the importance of identifying situations when accounting for non-stationary dynamics, especially the magnitude and frequency of connectivity to a source population, should impact today's decision. Time-dependent management strategies that embed changing conditions can outperform stationary strategies in maximizing management objectives (Nicol et al., 2015), suggesting the need for proactive actions that anticipate change. We show that in some scenarios where a population is isolated and receives infrequent propagule pressure from source populations, management should increase removal effort beyond the action that would be optimal assuming stationarity in the current regime (Figure 5c). Conversely, as the size of the source population(s) increases and is



**FIGURE 5** Accounting for non-stationarity in propagule pressure affects optimal removal efforts. (a) Plot depicts assumed non-stationary dynamics, represented as an increase in expected value of stochastic source population(s) size,  $\alpha$ . The source population(s) size increases discretely at  $t=10$ , 20 and 30. (b, c) Heatmaps represent the difference between the (1) time-dependent optimal removal effort accounting for non-stationarity and (2) optimal removal effort assuming stationarity in the current regime ( $\Delta$  optimal removal effort) (ex. blue indicates that by accounting for non-stationarity, the optimal removal effort is higher than if a decision maker assumed stationarity in the current regime). Transition between invasion regimes occurs at discrete intervals, indicated by the black dashed lines. European green crab (EGC, *C. maenas*) densities are aggregated such that low density = 0–0.3K, medium density = 0.3–0.7K and high density = 0.7–1.0K. Panels (b) and (c) show results assuming an exponential and sigmoidal ecological change function, respectively (Equations 13 and 14). Both panels assume a nonlinear removal cost function (Equation 15).

more frequently connected to the local population, management can save resources by anticipating change and lowering the removal effort below a strategy that assumes stationarity (Figure 5). These anticipatory strategies will be critical for managing green crab under changing ocean conditions in the northeast Pacific. Recent particle-tracking model simulations predict a double to quadruple increase in the frequency of green crab larval exchange across the Salish Sea with a water temperature increase of 0.5°C–1°C (Du et al., 2024). Decision making assuming the status quo will therefore be insufficient in anticipation of future climate warming and expectation of increased dispersal from oceanographic processes like El Niño and Pacific Decadal Oscillation.

Our results also reveal nuance along the boundary between the binary alternatives of resistance and acceptance (Figure 4). Although previous work highlights the importance of understanding the relationship between species density and effects, information that is

often lacking, we find that the optimal removal effort is more sensitive to the relationship between removal effort and cost (Figure 4) (Crystal-Ornelas & Lockwood, 2020; Yokomizo et al., 2009). When the relationship between removal effort and cost is linear, the optimal strategy shifts from resistance to acceptance when the mean size of the source population is as low as half of a local carrying capacity (Figure 4b). Whereas if this relationship is nonlinear, such that the cost of removal is relatively lower at low removal efforts, the optimal strategy does not shift to acceptance, even in scenarios with extremely large and highly connected source population(s) (Figure 4d). The contrasting optimal policy behaviour in response to the penalization of cost reinforces the need for decision makers to clearly articulate removal costs relevant to the decision, including the cost and availability of gear and personnel, institutional and budget constraints and species-specific removal attributes like site accessibility that affect the cost of removal (Bond et al., 2008).

The boundary between resistance and acceptance is ultimately a question of a decision maker's values, expressed through their discounting of future rewards, as well as the cost of removal relative to the cost of environmental change. The discount factor describes the value of future rewards relative to current rewards and can either reflect a decision maker's values (Runge, 2020), or a level of confidence in predictions of non-stationary dynamics (Marescot et al., 2013). Our multi-objective programming approach also makes explicit the need to minimize ecological change, while avoiding impractical levels of removal effort using a weighted-sum method (Converse, 2020). The optimal level of removal effort is highly sensitive to the weighting of objectives, and since the weights in our analysis conservatively penalize the cost of removal (Equation 17), we have created a RShiny app (<https://resist-accept.shinyapps.io/RShiny/>) to explore how discount factor, objective weighting and predicted non-stationary dynamics impact these trade-offs.

Operationalizing this decision framework will involve adapting and contextualizing the approach for a particular decision. This contextualization can be supported through structured decision making, or a deliberative process by which a complex problem is decomposed into its constituent elements to support transparent and rational decision making (Gregory et al., 2012). Structured methods will be necessary for developing objective weights that reflect the values of the decision maker. Objective weights can be elicited through swing weighting, a cognitive exercise used for obtaining weights that reflect both an objective's relative importance and the degree to which alternative actions vary on that objective (Converse, 2020). Additionally, developing time-dependent strategies involves predicting non-stationary system dynamics. When model-based forecasts are unavailable, expert elicitation can be used to develop predictions, plan scenarios and quantify uncertainty through methods like Bayesian belief networks, the IDEA protocol and Delphi process (Hemming et al., 2018; McCann et al., 2006; Runge et al., 2011).

Direct application of our results in developing actionable management strategies for European green crab has limitations, however. Our modelling framework uses a Markov decision process, which assumes perfect knowledge of the system state, including



local species density and the size and connectivity of source population(s). Methods from the Artificial Intelligence community, like partially observable Markov decision processes, will be a powerful addition to natural resource management for informing decisions based on imperfect observations of a managed system (Chadès et al., 2021). Further investment in genomics research could also help inform population connectivity, dispersal pathways and ultimately identify isolated populations for which resisting change through population suppression is most feasible (Tepolt et al., 2009). Additionally, the optimization method we used to account for non-stationarity requires complete omniscience of expected changes to the system. Future work could investigate methods like scenario optimization with forward simulation or reinforcement learning that can account for uncertain future change, yet have no guarantee of optimality (Lapeyrolerie et al., 2022; Pepin et al., 2022).

Invasive species managers at the precipice of potentially irreversible ecosystem transformation face the difficult decision of knowing whether to continue resisting change or accept a new ecological trajectory. We present a novel quantitative framework that uses mathematical concepts from decision theory to resolve the boundary between resistance and acceptance in the context of the invasive European green crab. This decision framework will therefore support anticipatory, informed and strategic choices when managing environments under continuous change.

#### AUTHOR CONTRIBUTIONS

Abigail G. Keller, Timothy D. Counihan and Carl Boettiger conceived the ideas; Abigail G. Keller, Carl Boettiger and Edwin D. Grosholz designed the methodology; Abigail G. Keller conducted analyses and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

All data and R code associated with this analysis are available in the Zenodo archive <https://doi.org/10.5281/zenodo.14344378> (Keller et al., 2025). Data and code are also available on GitHub <https://github.com/abigailkeller/resist-accept>.

#### STATEMENT ON INCLUSION

This study was conducted by a team of government and academic researchers and was conceived as the outcome of a structured decision making process for managing European green crab in the

Northeast Pacific. Co-managers and stakeholders, including members from tribal natural resource agencies, state and federal agencies, shellfish farmers and non-profit organizations in Washington State, United States, were interviewed and consulted to frame the decision problem, clarify objectives and define alternatives. This consultation determined the research questions addressed in this manuscript.

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## SUPPORTING INFORMATION

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

**Appendix S1:** Description of model parameters, parameter values used in model and selection of time horizon.

**Appendix S2:** Description of discretization used in Markov decision process model.

**Table S1:** Parameter values used to represent the stochastic source population size, scaled relative to the local carrying capacity ( $\alpha / K$ ).

**Figure S1:** Probability density functions with a range of parameter values used to describe the stochastic source population size, scaled relative to the local carrying capacity ( $\alpha / K$ ).

**Figure S2:** Stationary state-dependent optimal removal efforts for variations in removal cost function (line colors) and ecological change function (line types) under varying mean source population sizes: (A)  $\alpha = 0.005K$ , (B)  $\alpha = 0.05K$ , (C)  $\alpha = 0.2K$ , (D)  $\alpha = 0.5K$ , (E)  $\alpha = 0.75K$ , (F)  $\alpha = 1.0K$ , (G)  $\alpha = 1.25K$ , (H)  $\alpha = 1.5K$ , (I)  $\alpha = 2.0K$ , and (J)  $\alpha = 5.0K$ .

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