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RESEARCH ARTICLE

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Models reveal potential synergies in management actions for bull kelp forest resilience and restoration

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Abstract

1. Heatwaves are a growing threat to marine ecosystems. Kelps are particularly vulnerable because they require cool, nutrient-rich water to thrive. Heatwaves can also trigger increased herbivory by sea urchins.
2. Management interventions—including re-seeding kelp spores and manually removing urchins—could mitigate heatwave damage or aid recovery. However, we do not yet know the optimal timing of these management actions or whether combining them enhances their effectiveness.
3. We used a stochastic, stage-structured model of kelp-urchin population dynamics, which included an urchin-grazing behavioural switch and was parameterized to represent bull kelp (*Nereocystis luetkeana*) forests along the coast of Oregon, USA. We simulated a 2-year heatwave and considered two urchin predator scenarios: one in which the sunflower seastar *Pycnopodia helianthoides* was driven to local extinction by seastar wasting disease during the heatwave (the historical reality), and the counterfactual where seastar densities remained constant.
4. All management interventions individually were notably more effective when seastars were present. When each was enacted alone, kelp seeding was less effective than urchin removal. Both interventions improved kelp forest persistence most when begun before or during the heatwave, but were not effective if started and completed before the heatwave began. The effectiveness of both interventions increased with increasing effort (% biomass removed or added), but with diminishing returns.
5. Combining urchin culling and kelp seeding was highly effective, and even more so if urchin culling started first, with large synergistic gains starting at low intensities of kelp seeding (5% of pre-heatwave biomass) and higher intensities of urchin removal (25% of pre-heatwave biomass). Those synergies can be achieved when actions start after a heatwave has begun, easing the need to anticipate heatwaves.
6. *Synthesis and applications*. We found that urchin culling and kelp seeding interventions can be effective at rebuilding kelp forests, but require intensive effort (e.g.

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removing 25%–50% of urchins over multiple years), especially in the absence of predators. Our results provide recommendations for the magnitude and timing of culling and seeding that would be needed to provide desired levels of kelp forest resilience.

KEYWORDS
kelp forest, marine heatwaves, *Nereocystis*, restoration, stage-structured model, *Strongylocentrotus*, urchin barren

1 | INTRODUCTION

There is an urgent need to understand how local actions can mitigate the impacts of global climate change, even as the ultimate solutions are international in scope. Such local mitigation actions must respond not only to steady increases in average temperatures but also to the increasing frequency and magnitude of extreme events (Johnstone et al., 2016; Smith et al., 2023; Turner, 2010). In coastal oceans, the increased frequency and duration of marine heatwaves in particular are a growing threat to the structure and function of those ecosystems and the services they provide (Frölicher et al., 2018; Smith et al., 2021, 2023). Heatwaves can be defined as discrete pulses of extreme ocean temperatures occurring against the background of chronic warming (Amaya et al., 2023; Hobday et al., 2016). Recognizing the need for long-term, large-scale solutions to climate change, there remains a need to understand how local, short-term interventions can buffer systems against heatwaves or restore them after heatwave damage. The key questions then are what management actions will be most effective and efficient, and how best to implement them, whether in isolation or in concert (Ainsworth et al., 2020; Pinsky et al., 2021; Smith et al., 2021, 2023).

Heatwaves can have differential effects on species, producing complex ecosystem responses. In north-eastern Pacific kelp forests, warm, low-nutrient conditions during heatwaves reduce growth and recruitment of the dominant canopy-forming species, bull kelp *Nereocystis luetkeana* (Johnson, 2020; Rogers-Bennett & Catton, 2019; Spiecker & Menge, 2022). In contrast, during heatwaves, sea urchins (the dominant herbivores in the system; *Mesocentrotus franciscanus* and *Strongylocentrotus purpuratus*) exhibit increased grazing rates (Spindel, 2023). The heatwave-induced decrease in standing kelp also reduces production of detached kelp fronds ('drift kelp'), a preferred food source for urchins (Kriegisch et al., 2019; Randell, 2022). The loss of drift kelp combined with increased grazing rates can trigger urchins to switch behaviour, from feeding on drift and detritus while sheltered in rocky crevices to exposed roaming and targeting standing kelp stipes (Kriegisch et al., 2019; Rennick et al., 2022; Smith & Tinker, 2022; Figure 1). As a result, heatwaves can tip kelp forests to overgrazed urchin barrens

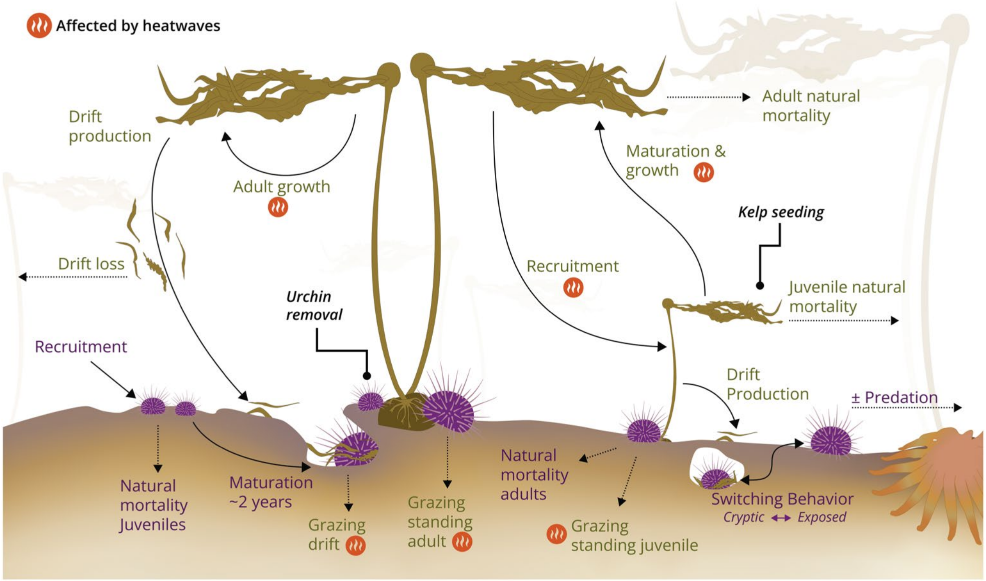


FIGURE 1 Model schematic. Main processes included in our model, including those affected by heatwaves (denoted by the orange 'flame' symbol). Purple and green text show processes included in the kelp and urchin components of the model, respectively. Dashed arrows indicate processes of biomass loss, and thin solid arrows indicate stage transitions. Bold solid lines indicate mitigation actions. Two predation scenarios were considered: A constant or declining biomass of seastars (following the onset of seastar wasting disease). Kelp and urchin icons by Jane Thomas sourced from ian.umces.edu/media-library under the CC BY-SA 4.0 licence.

(McPherson et al., 2021). Recovery from the barren state can be challenging even after kelp-beneficial conditions return (i.e. the system exhibits hysteresis; Filbee-Dexter & Scheibling, 2014; Ling et al., 2015) largely because the barren-state urchins exhibit high survival despite low food availability and exposure to predators. In fact, some urchin predators actively avoid consuming barren-state urchins (Eurich et al., 2014; Liebergesell, 2022; Smith & Tinker, 2022).

There is considerable societal and management interest in direct interventions to buffer kelp forests against heatwaves and restore impaired kelp populations (Johnson, 2020). This is because the loss of kelp following a heatwave can have severe impacts on associated kelp forest species and society. These impacts include the loss of habitat (particularly nursery habitat; Fennie et al., 2023; Pérez-Matus et al., 2025; Teagle et al., 2017), the loss of resources for herbivorous species (e.g. abalone; Rogers-Bennett et al., 2021), and the degradation in quality and hence economic value of urchins available to the urchin fishery (Spindel et al., 2021). The two main actions relevant to bull kelp address the two sides of the kelp-urchin dynamic (Figure 1): direct kelp restoration could increase kelp biomass via seeding spores or transplanting sporophytes (Eger et al., 2022), while herbivore removal via harvest, culling or translocation could promote kelp recovery by reducing herbivore density (Eger et al., 2022).

A previous analysis by Hopf et al. (2025) used a multispecies population model to understand the efficacy of different management actions in response to heatwaves in the kelp forests of southern California where the dominant canopy-forming species is giant kelp *Macrocystis pyrifera*, and the key urchin predators—the Californian Sheephead *Bodianus pulcher* (a labrid fish) and the California spiny lobster *Panulirus interruptus*—are harvested. Their model simulated the stochastic dynamics of this community in a spatially implicit manner (with lobster abundances assumed to be constant), considering a single isolated kelp forest that experiences a 2-year heatwave to replicate the 2014–2016 heatwave that affected kelp forests in the region (Free et al., 2023; Rogers-Bennett & Catton, 2019). Hopf et al. (2025) found that the most effective management action was to close Sheephead harvesting for as long as possible before the heatwave and throughout the duration of the heatwave, equivalent to having placed the kelp forest within a marine reserve. Removing urchins was also shown to be effective, but only if that action was taken immediately before the heatwave or soon after it started; if done too early, new urchin recruitment simply replaced the removed urchins. Kelp restoration was not effective when implemented alone, but if combined with urchin removals (timed to be before or at the onset of the heatwave, and persisting throughout it), low levels of both actions had approximately additive benefits for kelp persistence. Together, these results led to the recommendation that heatwave responses should be proactive and nimble, relying either on marine reserves to protect key urchin predators or on careful heatwave forecasting to time interventions together (Hopf et al., 2025).

Here, we applied a similar modelling approach to the kelp forest communities of Oregon and northern California where bull kelp is the primary canopy-forming species. We focus on purple sea urchins (*Strongylocentrotus purpuratus*), which are currently not targeted by fisheries and typically more aggressive consumers of standing kelp (Rogers-Bennett & Okamoto, 2020). Several key differences between bull kelp and giant kelp communities led us to anticipate the emergence of different management recommendations. First, bull kelp and giant kelp have distinctly different life histories. While giant kelp sporophytes may live for multiple years and giant kelp forests often persist intact for years or decades, most bull kelp sporophytes are lost in winter storms each year so that the entire kelp forest regrows from gametophytes each spring (Maxell & Miller, 1996; Springer et al., 2006). Second, the dominant urchin predators in Oregon and northern California are not harvested, so fishery closures are not a management action that would directly affect kelp persistence. Indeed, the major urchin predator, the sea otter *Enhydra lutris*, was regionally extirpated by hunting a century ago (Ravalli, 2009), and the only other major predator, the sunflower seastar *Pycnopodia helianthoides*, was effectively driven to local extinction by the epizootic seastar wasting disease which began in Oregon in spring 2014 (Hamilton et al., 2021), concurrent with the start of the 2014–2016 heatwave (Harvell et al., 2019; McPherson et al., 2021). It stands to reason that the presence versus absence of urchin predators would affect the kelp community response to a heatwave and the efficacy of alternative management interventions.

We followed Hopf et al. (2025) in assessing how the two management actions, kelp seeding and urchin removal, could be used to reduce the likelihood of a bull kelp forest shifting to an urchin barren because of a heatwave, in either the presence or absence of urchin predators (seastars). This allowed us to investigate the hypothetical past (what might have happened in the absence of the seastar wasting disease), the predator-free status quo and the hypothetical future: what if sunflower star populations suddenly recover before the next heatwave, as other seastar species have (Menge et al., 2016; Moritsch & Raimondi, 2018), or what if other predators such as otters are introduced (U.S. Fish and Wildlife Service, 2022). In all cases, we considered the outcomes when the two actions are implemented before, during or after a 2-year heatwave, considering these actions as possibly strategies to both pre-emptively reduce the likelihood of phase-shifting to an urchin barren state and restore a degraded kelp forest. Additionally, given the growing interest in the value of synchronous versus sequential multispecies ecosystem restoration actions (Samhouri et al., 2021), we also considered different relative timings of the two interventions (e.g. urchin removal before or after kelp seeding).

2 | MATERIALS AND METHODS

2.1 | Two-species population model

Our discrete-time single-patch model focused on the interactions between bull kelp and herbivorous purple urchins (Figure 1). The model was stage-based for both kelp and urchins, tracking the biomass of key life stages: juvenile and adult standing kelp, drift kelp (hereafter often referred to as 'drift'), juvenile urchins, exposed adult urchins and hiding adult urchins. To account for seasonal variations in ecological processes (recruitment, kelp growth, urchin grazing and heatwave effects), the model used seasonal (3 months) time steps. We also modelled predation by sunflower stars on urchins, but as sunflower stars have highly uncertain reproduction and recruitment dynamics and are generalist predators with many potential prey on rocky reefs, we did not explicitly model their dynamics; rather, we modelled a mean background density with year-to-year variation in the baseline scenario. For the 'seastar absent' scenario, we reduced this density over time to reflect a seastar wasting disease outbreak and subsequent population crash (see the Section 2.2; Hamilton et al., 2021). Details on the model and full equations are provided in the Supporting Information. As this study was desk-based, no ethics approval nor permission for fieldwork was required.

The model captured the characteristic dynamic of a kelp forest, where overgrazing by urchins shifted the system from a kelp forest to an urchin barren with local kelp extinction. Underpinning this was an urchin behavioural feeding switch: when drift kelp was abundant, urchins fed passively on drift, and they actively grazed on standing kelp only when drift kelp was scarce. To achieve this, we modelled the proportion of exposed urchins as a declining function of drift biomass density relative to urchin consumptive capacity (Rennick et al., 2022), building on the approach taken by Randell (2022) and assuming an overall Type-II functional response. We also assumed a Type-II functional response for urchin predation by sunflower stars, and that exposed urchins had a higher rate of predation mortality than cryptic urchins (Nichols et al., 2015).

We assumed a spatial domain equivalent to a spatially isolated kelp forest, at which scale the urchin population would be open with external recruitment and the kelp population would be largely closed (i.e. 1–10 ha; Kinlan & Gaines, 2003). Kelp reproduction was thus a function of local adult biomass, with juvenile sporophytes experiencing density dependence through both inter-cohort competition (shading by adult kelp, modelled with a Ricker function) and intra-cohort competition among the juveniles (modelled with a Beverton–Holt function; Nisbet & Bence, 1989). As discussed in Hopf et al. (2025), this closed population scenario can be viewed as a worst-case scenario for kelp resilience, without rescue effects from external kelp populations and with a consistent influx of urchin recruits. Kelp phenology in the model matched the pattern documented for Oregon bull kelp, with peaks in recruited juvenile sporophytes in spring (March–May) following summer and autumn spore production (Maxell & Miller, 1996). We included high summer growth and near-complete winter dieback for adult sporophytes, reflecting the annual nature of bull kelp in Oregon (Maxell & Miller, 1996; Springer et al., 2006). Stochasticity was captured through year-to-year variation in recruitment for all species, with recruitment each year drawn randomly from data-parametrized normal (for kelp) or lognormal (for urchins) distributions. All parameter values were based on published literature or data from Oregon or similar regions (Table S1).

It is important to emphasize that this type of modelling analysis is intended to characterize the general dynamics of the kelp-urchin system in order to understand how different interacting nonlinear processes will lead to different management outcomes (a *strategic model*, e.g. Arroyo-Esquivel et al., 2023). We do not intend it to describe or be fitted to data in any one specific kelp population, for which predictions of future management outcomes would be shaped by the historical patterns of stochastic variability in that population (a *tactical model*, e.g. Nickols et al., 2019). Thus, we understand the reliability of our model in terms of how well it recaptures the known dynamics of kelp-urchin systems. This consideration is particularly important in terms of our assumption that the kelp population being modelled is demographically closed. Kelp forests exist as metapopulations, with individual subpopulations frequently going locally extinct and being recolonized by neighbouring populations (this has been well documented in *Macrocystis* by Castorani et al. (2015, 2017), and similar patch dynamics have been observed in *Nereocystis* populations; McPherson et al., 2021). However, because we were interested in keeping the model relatively simple and investigating local-scale management actions, we did not include those metapopulation rescue effects. As a result, our simulated kelp populations all eventually go extinct and remain that way, without rescue from another patch in the metapopulation.

2.2 | Modelling heatwaves & management strategies

We initialized all scenarios in an undisturbed kelp forest state. Reflecting the known effects of heatwaves on kelp and urchins, we implemented a heatwave as a period of reduced kelp recruitment (Korabik et al., 2023) and growth (Supratya et al., 2020), and of increased urchin-grazing rates (Spindel, 2023). The heatwave started in winter and lasted 2 years (eight 3-month time steps), mimicking the 2014–2016 heatwaves that severely affected Oregon and Northern California kelp forests, as well as the more recent 2019–2020 heatwave (Cervantes et al., 2024; Michaud et al., 2022).

We considered two possible management actions: urchin removal (a set biomass of adult urchins removed each season) and kelp seeding (a set biomass of juvenile kelp sporophytes added each season). We focused on kelp seeding, rather than transplantation of adult kelp, as seeding is a more viable approach on large scales (Eger et al., 2022). We modelled scenarios where actions began up to 2 years before the heatwave (i.e. pre-emptive actions), began during the heatwave or began up to 3 years after the heatwave ended, with actions lasting 1 to 5 years after initiation. We explored a wide range of magnitudes for both actions (0%–100% of pre-disturbance biomass for each species), and assessed the consequences of combining them either simultaneously or sequentially, with one action following the start of the other with up to a 7-year delay. Finally, we repeated all simulations under two different states of nature. The first reflected the historical situation in which seastar wasting disease began 3 months after the onset of the marine heatwave and steadily reduced the abundance of sunflower stars over a course of 33 months (11 seasons/time steps; we refer to this as the

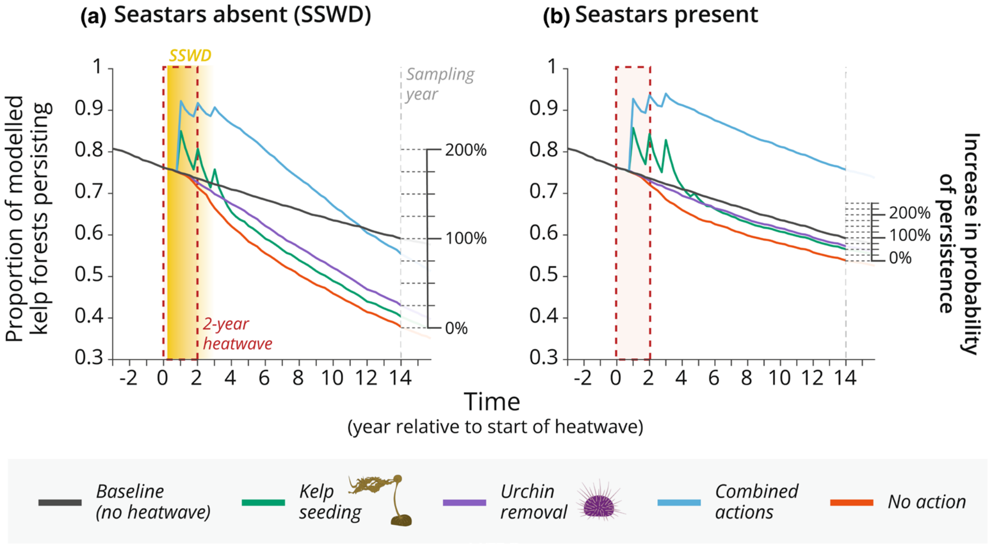


FIGURE 2 Example scenario simulations. The proportion of simulations in which kelp persisted in each model year, with different simulated management actions indicated by the colour of each curve. The percentage increase in probability of kelp persistence is calculated at the sampling year (12 years post-heatwave), as indicated by the scale bar marked with percentage increments. In these examples, management actions began the same year as the heatwave started, were implemented for 3 years, and 100% of the pre-heatwave biomass was removed (for urchins) or added (for kelp) yearly. The two panels illustrate scenarios with (a) and without (b) seastar wasting disease (SSWD) that began to eliminate seastars at the onset of the heatwave.

'seastars absent' case; Hamilton et al., 2021). The second state of nature ('seastars present') was a hypothetical scenario in which sunflower star densities remained unchanged during the simulations. Reflecting the real logistical challenges of undertaking field work in Oregon waters, management actions only occurred during summer months.

With 5000 replicates for each scenario, we simulated the system's dynamics for 20 years (80 model time steps) prior to the heatwave and then assessed the proportion of simulations in which kelp persisted (defined as non-zero kelp biomass for at least a year) 12 years after the heatwave ceased. Twenty pre-heatwave years was long enough to eliminate any sensitivity to starting conditions, with 12 post-heatwave years being long enough to complete and extend beyond the transient effects of all potential management actions. We present the response variable of kelp persistence as the percentage increase in probability of kelp forest persistence relative to the effect of the heatwave with no management intervention, and to a baseline scenario with no heatwave (Figure 2). More specifically,

$$\text{percentage increase in probability of persistence} = \frac{P_{\text{MHW \& action}} - P_{\text{MHW \& no action}}}{P_{\text{no MHW \& no action}} - P_{\text{MHW \& no action}}} \times 100,$$

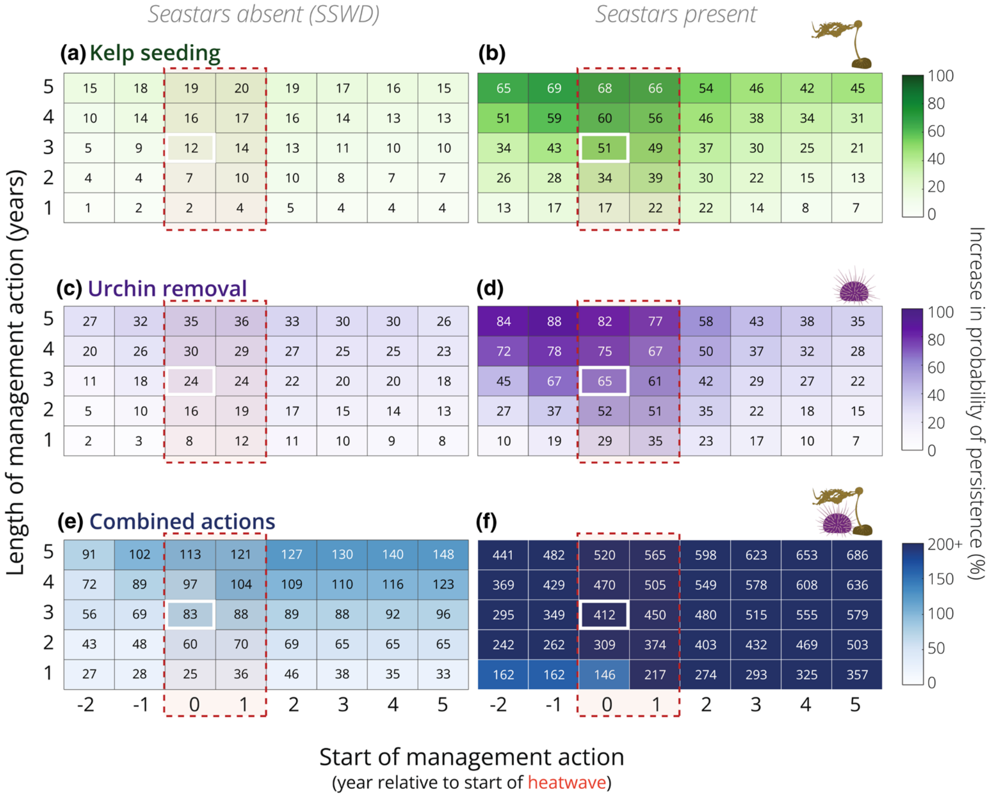
where P_i is the proportion of simulations with persistent kelp under scenario i.

Note that even without a heatwave, the proportion of kelp persisting declined over time (Figure 2) because in a stochastic system (and with our assumption that there is no kelp or drift immigration from other kelp forest patches in the metapopulation), there is a small, constant probability that a given forest will switch to a barren in any given time step due to a series of poor kelp recruitment years and/or substantial urchin recruitment events, and that barren state is trapping (without restoration actions).

3 | RESULTS

Because of the many sources of stochasticity in our model, we found that the probabilities of kelp persistence could vary by ~10 percentage points among sets of simulations of the same scenario. This occurred even when the number of simulations increased beyond 5000. Therefore, in interpreting the results, we do not consider differences of <10 percentage points to be meaningful.

When implemented individually, both management actions peaked in effectiveness when they were started before or during the heatwave, but this peak was less notable when seastars were absent (Figure 3a–d). Kelp seeding alone was consistently less effective than urchin culling alone, and both actions were more effective the longer they were undertaken (Figure 3a–d). With seastars present, both actions were at least moderately effective (>25% increase in probability of persistence) if begun after the heatwave ended but decreased in effectiveness the longer the delay in implementing the management action (Figure 3b,d). This was also true for urchin removal in the absence of seastars if removal was enacted for a long duration (>4 years; Figure 3c). However, neither urchin removal of a short duration nor any duration of kelp seeding was effective when seastar wasting disease removed seastars (Figure 3a,c). If both actions were started and completed before the heatwave began, they were relatively ineffective (<25% increase in probability of persistence; Figure 3a–d).



(a) Kelp seeding

	-2	-1	0	1	2	3	4	5
5	15	18	19	20	19	17	16	15
4	10	14	16	17	16	14	13	13
3	5	9	12	14	13	11	10	10
2	4	4	7	10	10	8	7	7
1	1	2	2	4	5	4	4	4

(b)

	-2	-1	0	1	2	3	4	5
5	65	69	68	66	54	46	42	45
4	51	59	60	56	46	38	34	31
3	34	43	51	49	37	30	25	21
2	26	28	34	39	30	22	15	13
1	13	17	17	22	22	14	8	7

(c) Urchin removal

	-2	-1	0	1	2	3	4	5
5	27	32	35	36	33	30	30	26
4	20	26	30	29	27	25	25	23
3	11	18	24	24	22	20	20	18
2	5	10	16	19	17	15	14	13
1	2	3	8	12	11	10	9	8

(d)

	-2	-1	0	1	2	3	4	5
5	84	88	82	77	58	43	38	35
4	72	78	75	67	50	37	32	28
3	45	67	65	61	42	29	27	22
2	27	37	52	51	35	22	18	15
1	10	19	29	35	23	17	10	7

(e) Combined actions

	-2	-1	0	1	2	3	4	5
5	91	102	113	121	127	130	140	148
4	72	89	97	104	109	110	116	123
3	56	69	83	88	89	88	92	96
2	43	48	60	70	69	65	65	65
1	27	28	25	36	46	38	35	33

(f)

	-2	-1	0	1	2	3	4	5
5	441	482	520	565	598	623	653	686
4	369	429	470	505	549	578	608	636
3	295	349	412	450	480	515	555	579
2	242	262	309	374	403	432	469	503
1	162	162	146	217	274	293	325	357

FIGURE 3 Effect of timing and length of mitigation actions. Percentage increase in the probability of kelp persistence through a 2-year marine heatwave, with (a, c and e) and without (b, d and f) seastar wasting disease (SSWD), under individual (a–d) and combined (e, f) management actions, over length and timing of action. The percentage increase is indicated by the colour shading as well as by the text in each grid cell. These modelled scenarios present the most intensive management scenario in which 100% of the pre-heatwave urchin and kelp biomass was removed or seeded each year, respectively. The orange dashed box indicates the action scenarios that began during the heatwave. White boxes indicate the scenarios that are shown in Figure 2.

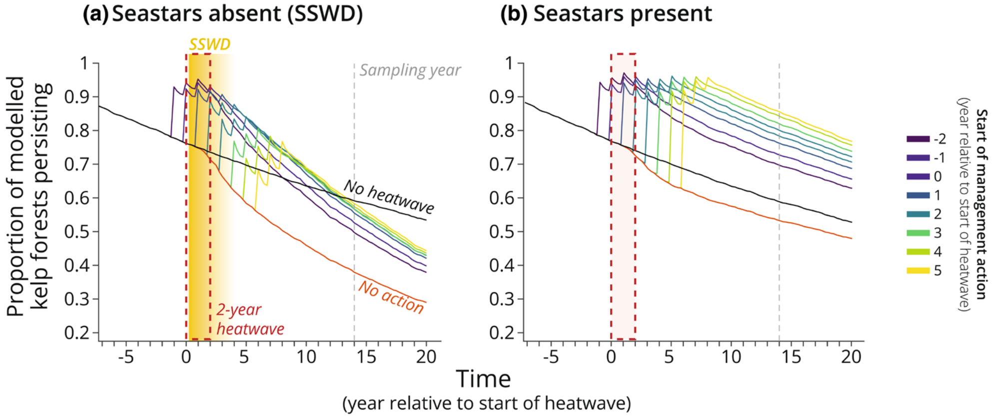
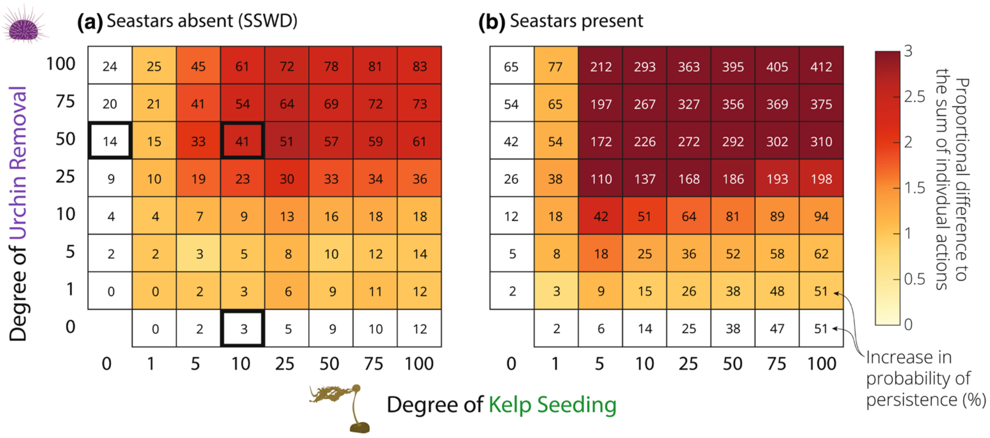


FIGURE 4 Example scenario runs with combined action. The proportion of simulations with kelp persisting over time when intensive kelp seeding and urchin removal were combined, either with (a) or without (b) the removal of seastars by SSWD. In this example, actions lasted 3 years and began at varying times relative to the heatwave (red box), as indicated by the line colour.

Combining urchin culling and kelp seeding could provide benefits with or without seastars but was notably more effective in the presence of seastars (Figures 3–5). Combining actions was exceptionally effective when both actions were implemented intensively (i.e. 100% of the pre-heatwave urchin removed and kelp biomass seeded each year; Figure 3e,f). The timing of actions relative to the start of the heatwave was less important when they were enacted in combination than when they were enacted alone. Combined actions were only less than moderately effective (<50% increase in probability of persistence) if started and completed before the heatwave began (Figure 3e,f).

It is important to note that the apparent increase over time in the effectiveness of combined actions (Figure 3e,f) was partly a



(a) Seastars absent (SSWD)

Urchin removal \ Kelp seeding	0	1	5	10	25	50	75	100
100	24	25	45	61	72	78	81	83
75	20	21	41	54	64	69	72	73
50	14	15	33	41	51	57	59	61
25	9	10	19	23	30	33	34	36
10	4	4	7	9	13	16	18	18
5	2	2	3	5	8	10	12	14
1	0	0	2	3	6	9	11	12
0		0	2	3	5	9	10	12

(b) Seastars present

Urchin removal \ Kelp seeding	0	1	5	10	25	50	75	100
100	65	77	212	293	363	395	405	412
75	54	65	197	267	327	356	369	375
50	42	54	172	226	272	292	302	310
25	26	38	110	137	168	186	193	198
10	12	18	42	51	64	81	89	94
5	5	8	18	25	36	52	58	62
1	2	3	9	15	26	38	48	51
0		2	6	14	25	38	47	51

FIGURE 5 Effect combining actions over varying intensities. Percentage increase in the probability of a kelp persistence through a 2-year marine heatwave (numbers in cells), and the proportional difference between the efficacy outcome of the combined actions compared with the expected summed outcome of the actions based on their individual efficacy (warm colour scale), over a range of urchin removal and kelp seeding efforts in the presence (a) or absence (b) of seastar wasting disease (SSWD). In this illustrative scenario, actions occur simultaneously at the start of the heatwave and last for the same 3-year time period. White boxes show the efficacy of individual actions. As an example (boxes outlined in thick black in panel a), adding 10% kelp seeding and 50% urchin removal has a synergistic effect (3% effect of kelp alone +14% effect of urchin alone < 41%, the combined effect of both). The degree of urchin removal and kelp seeding effort is the percentage of pre-heatwave urchin and kelp biomass removed or seeded each year, respectively.

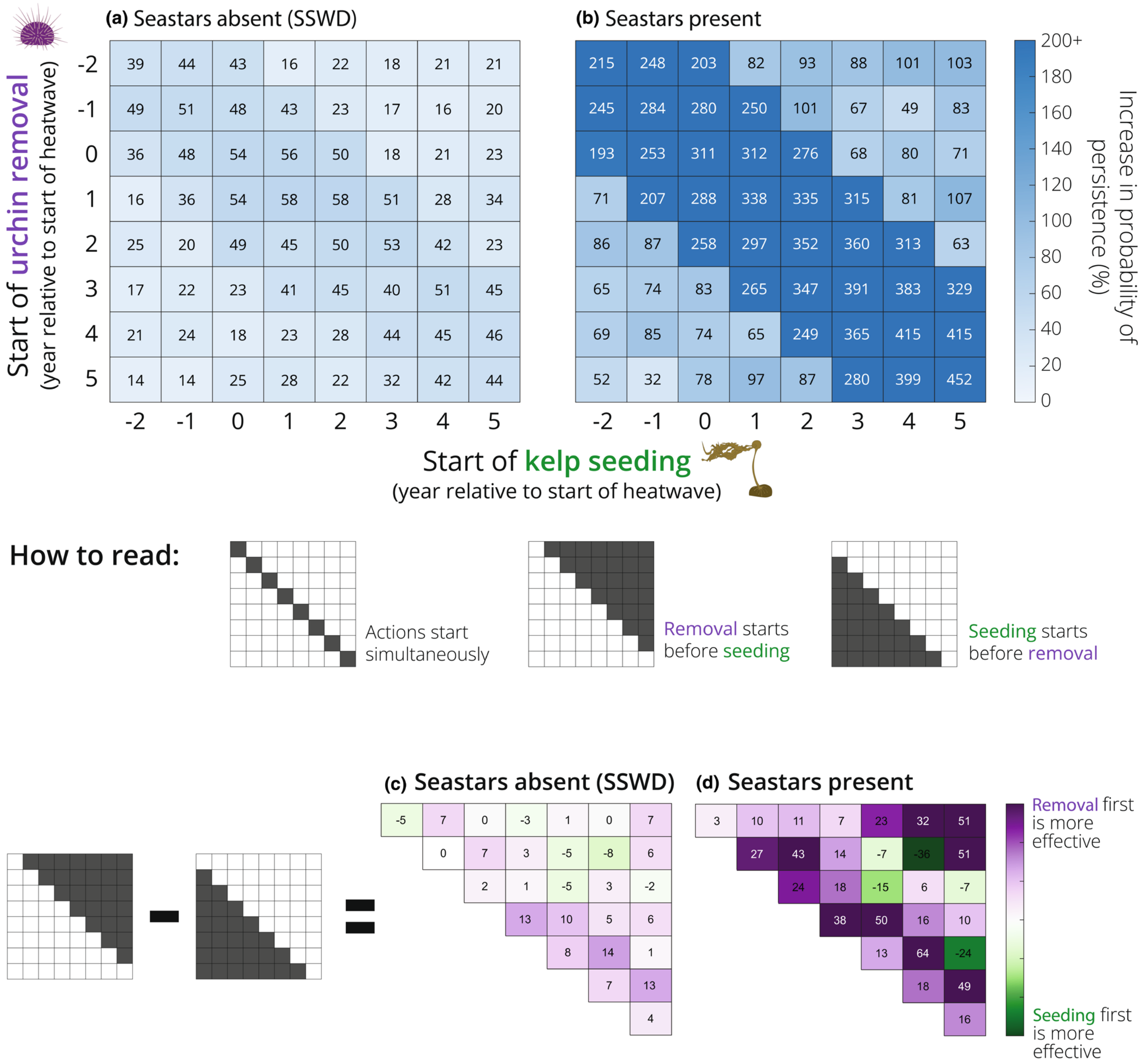
consequence of our baseline model scenario. In the baseline simulations, kelp persistence gradually decreased over time due to stochastic events, even in the absence of disturbances or interventions (see Section 2, black line in Figure 2). As such, the number of simulations with the potential to recover from an urchin barren increased over time (Figure 4). However, there is a ceiling on the absolute value of persistence (100%) if all simulated kelp populations have non-zero biomass in a given model year. The combined management actions often brought the system to that 100% ceiling, regardless of the level of persistence when the actions were initiated. This means that the later the actions were initiated, the greater the difference between the current system state and full recovery, and thus greater effectiveness by our metric. The potential for this artefact was also present in the simulations with single actions alone, but those single actions were not effective enough to raise the system to the persistence ceiling.

The effectiveness of both kelp seeding and urchin removal increased with increasing intensity of the action (measured as the percentage of pre-heatwave biomass removed/added), regardless of whether seastars were present or not (white panels, Figure 5). However, there were diminishing returns in those benefits, as measured by decreased marginal increases in effectiveness with increasing effort (see also Figures S2.1 and S2.2). Nonetheless, and remarkably, combining actions had synergistic effects, with the large synergistic gains beginning at low intensities of kelp seeding (≥5% of pre-heatwave biomass) and moderate intensities of urchin removal (≥25% of pre-heatwave biomass; denoted by the darker red coloration in Figure 5).

When combining management actions in a temporal sequence, there was a distinct benefit to overlapping actions as opposed to beginning one action after the other ended (Figure 6). For example, overlapping actions of three-year duration affected no less than a doubling of their effectiveness (compare the dark diagonal band where actions overlap with bottom-left and top-right in Figure 6a,b). In the absence of seastars, there was no consistent benefit to beginning either action first if the first action began before or concurrent with the start of the heatwave (first three rows in Figure 6c). However, a marginal benefit to removing urchins first occurred if it started after the heatwave had begun (bottom-left corner of Figure 6c). Beginning urchin removal first was generally more effective regardless of timing when seastars were present (Figure 6b). Here, we present results where 50% of the pre-heatwave urchin and kelp biomass was removed or seeded each year. Our results are consistent with higher and lower intensity actions (Figures S2.3 and S2.4), but due to the low effect of lower intensity actions, smaller differences are present in that scenario. Note that the average variation across simulations in this analysis was particularly high (±10 units).

4 | DISCUSSION

Local, short-term management actions may be essential to supporting Pacific Coast bull kelp forests through marine heatwaves. Given the high costs of the mitigation actions we considered (Eger et al., 2022), it is important to ensure that they are timed and implemented at levels that are likely to have the desired effect on kelp forest persistence. Our analysis showed that the most effective timing of single mitigation actions was immediately before and during the heatwave. Timing for combined actions, however, mattered less, and they could be successful if implemented after the heatwave. Critically, intensive effort (e.g. removing 25%–50% of urchins over multiple years) was required. Our results also suggest that heatwave mitigation actions could be successful in bull kelp forests regardless



(a) Seastars absent (SSWD)

	-2	-1	0	1	2	3	4	5
-2	39	44	43	16	22	18	21	21
-1	49	51	48	43	23	17	16	20
0	36	48	54	56	50	18	21	23
1	16	36	54	58	58	51	28	34
2	25	20	49	45	50	53	42	23
3	17	22	23	41	45	40	51	45
4	21	24	18	23	28	44	45	46
5	14	14	25	28	22	32	42	44

(b) Seastars present

	-2	-1	0	1	2	3	4	5
-2	215	248	203	82	93	88	101	103
-1	245	284	280	250	101	67	49	83
0	193	253	311	312	276	68	80	71
1	71	207	288	338	335	315	81	107
2	86	87	258	297	352	360	313	63
3	65	74	83	265	347	391	383	329
4	69	85	74	65	249	365	415	415
5	52	32	78	97	87	280	399	452

(c) Seastars absent (SSWD)

-5	7	0	-3	1	0	7
	0	7	3	-5	-8	6
		2	1	-5	3	-2
			13	10	5	6
				8	14	1
					7	13
						4

(d) Seastars present

3	10	11	7	23	32	51
	27	43	14	-7	-36	51
		24	18	-15	6	-7
			38	50	16	10
				13	64	-24
					18	49
						16

FIGURE 6 Effect of temporal sequencing when combining kelp seeding and urchin culling. Percentage increase in the probability of kelp persistence through a 2-year marine heatwave, with (a, c) and without (b) seastar wasting disease (SSWD), when combining urchin removal and kelp seeding sequentially. Panels (c) and (d) show the difference between starting urchin removal before or after kelp seeding, at the same times indicated in panels (a) and (b). For example, the top left boxes in (c) and (d) depict the increase in persistence probability when enacting urchin removal at $t=-2$ followed by kelp seeding at $t=-1$, *minus* enacting kelp seeding at $t=-2$ followed by urchin removal at $t=-1$. In this illustrative scenario, actions lasted for 3 years and 50% of the pre-heatwave urchin and kelp biomass was removed or seeded each year, respectively.

of whether sunflower seastars were present or not, but would be greatly more effective overall if seastars were present. This predator effect echoes both modelling and empirical findings from studies on southern California giant kelp forests (*Macrocystis*), where protecting urchin predators from harvest is found to be highly effective in enhancing kelp persistence, but only if that protection was started well before the heatwave to allow the size structure of the predator population to rebuild (Dunn et al., 2021; Eisaguirre et al., 2020; Hopf et al., 2025). While that result does not directly apply to the bull kelp system because there are no widely harvested urchin predators in that kelp forest community, collectively these studies highlight the importance of healthy predator populations in supporting heatwave mitigation.

We found that combining kelp seeding and purple urchin removal could have a significant, synergistic effect, especially when predators are present. This differs from an earlier analysis of the giant kelp system in which Hopf et al. (2025) found that combining these actions with predator protection produced additive effects at best. Several key distinctions between the two systems may explain this. First, the saturating nature of Type-II predation exhibited by sunflower seastars (Galloway et al., 2023) limited the extent to which seastar predation suppressed urchin population density. Hopf et al. (2025) characterized predation by Californian Sheephead on urchins with a linear functional response, resulting in the Sheephead population having greater capacity to suppress urchins. As such, in the bull kelp model, urchin removals by humans as a mitigation action (which are not modelled as being dynamically limited by a functional response in the same way the predator is) has a greater capacity than the predator to cause large, rapid declines in urchin density and increase kelp persistence, especially when combined with direct kelp seeding. This capacity remained in the bull kelp system even when the seastars declined over time. Second, while bull kelp and giant kelp recruits likely exhibit a mix of both inter- and intra-cohort density dependence, the relative importance of intra-cohort density dependence is expected to be greater in bull kelp given that adult densities are typically very low during spring following winter die-backs (Maxell & Miller, 1996; Springer et al., 2006). By contrast, incoming giant kelp recruits compete for space and are negatively affected by shading of older, perennial adult kelp sporophytes (Nisbet & Bence, 1989; Reed, 1990; Stewart et al., 2009), as Hopf et al. (2025) modelled accordingly. The lower negative effects of adults on juveniles in bull kelp provides artificially seeded juveniles with a greater chance of survival, especially given their relatively fast growth rate and when also released from herbivory through urchin removals (Pontier et al., 2024). Finally, the effectively annual lifespan of bull kelp means that recovery to a full canopy is possible within a single growing season, as opposed to giant kelp forests that grow with additional recruitment over multiple years (Carr et al., 2016).

An additional key finding was that if both urchin removal and kelp seeding were carried out over multiple years, the combined actions were most effective when they were performed simultaneously in at least 1 year. Intuitively, removing urchin-grazing pressure is beneficial to supporting successful direct restoration processes, such as kelp seeding (Eger et al., 2022). We found that removing urchins before seeding kelp was generally more effective than the reverse, unless the two actions were undertaken during the heatwave and when predators were absent, in which case there was no greater benefit to undertaking either action first. Furthermore, the time between urchin removal and kelp seeding had little effect so long as they overlapped for at least 1 year. This is a promising result to guide mitigation efforts with limited resources, suggesting that there may be flexibility in the timing of combined actions and little cost to adapting ‘on-the-fly’ to field or logistical conditions. However, these results may have been influenced by our assumption that the purple urchin population was demographically open; at the much larger scale of the urchin metapopulation, a relationship between population size and reproductive output would likely exist. We might expect a coast-wide loss of kelp to decrease urchin reproductive output (Botsford et al., 2004; Claisse et al., 2013; Lang & Mann, 1976) and thereby increase the effectiveness of urchin removals. Yet, in Oregon there was no evidence of a decrease in urchin recruitment following the widespread loss of bull kelp during the 2014–2016 heatwave (L. Rasmuson, pers. comm.).

Our results are consistent with other recent models of kelp-urchin dynamics in the context of kelp restoration, as well as with empirical studies of restoration actions. For example, Arroyo-Esquivel et al. (2023) used a spatially explicit model to examine kelp restoration actions in the context of small, local ‘oases’ of remaining kelp forests, focusing only on within-season dynamics. They found that addressing local, within-patch dynamics was most effective relative to a lower level of action over a larger spatial scale: in their analysis, kelp recovery required reducing urchin density below a certain threshold, and adding kelp (or starting with a higher abundance of kelp in the oasis) increased that threshold. Essentially, it was important for restoration actions to establish enough kelp to induce urchins to switch from feeding on standing kelp to drift. This is similar to our result for the effectiveness of simultaneous urchin removal and kelp seeding, although Arroyo-Esquivel et al. (2023) did not consider multiyear processes and so could not consider the potential effects of urchin recruitment following removal or the sequencing of actions relative to a disturbance. Both that modelling result and our own also match the empirical evidence for the importance of urchin removal as a part of kelp restoration (Layton et al., 2020; Morris et al., 2020; Sanderson, 2003), even if the spatial scale of field studies on bull kelp specifically have been limited (Ward et al., 2022). It is also clear that a key component of these models is the explicit representation of the urchins' behavioural diet shift from drift to standing kelp (Arroyo-Esquivel et al., 2023; Hopf et al., 2025; Karatayev et al., 2021), which is consistent with our general understanding of urchin-grazing-driven alternate states in kelp forest systems (Johnson et al., 2017; Ling et al., 2015; Marzloff et al., 2016; McPherson et al., 2021; Smith & Tinker, 2022). However, a better empirical understanding of that behavioural shift would improve our confidence in how it is represented in models (Randell, 2021).

While we focused on the maintenance of persistent kelp per se, the heatwave mitigation actions we describe here would be expected to have positive effects for the many other fish and invertebrate species that depend on kelp habitat (Carr et al., 2016) and exhibit declines in abundance following heatwaves (Arafeh-Dalmau et al., 2019; Smith et al., 2024; Tolimieri et al., 2023). For example, based on the empirical relationship between giant kelp abundance and recruitment success of kelp forest fishes, such as kelp bass (*Paralabrax clathratus*; White & Caselle, 2008), Hopf et al. (2022) used population models to quantify how post-disturbance kelp restoration would lead to increases in kelp bass population, particularly if the restoration was conducted inside marine reserves, though they also noted that such beneficial effects could be difficult to detect empirically because of transient fluctuations in population density. Similar positive benefits could be expected for species that utilize bull kelp habitat in Oregon and Northern California, particularly juvenile stages of nearshore rockfishes, such as copper and black rockfishes (*Sebastes caurinus* and *S. melanops*, respectively) and striped surfperch (*Embiotoca lateralis*; reviewed by Markel et al., 2017; Springer et al., 2010).

Here, we focused on the effects of heatwaves as a pre-eminent stressor of kelps and their interaction with urchins. During heatwaves in upwelling systems, warm temperatures couple with low-nutrient conditions (McPherson et al., 2021). Due to limited experimental data, we have parameterized our model with a focus on temperature changes. As nutrient limitation is important for kelp growth, growth rates during heatwaves may be overestimated in our current model, and thus the effectiveness of kelp seeding during heatwaves may be less in nutrient limited systems that our model suggests (Hopf et al., 2025). Furthermore, coastal kelp communities will be affected by other dimensions of anthropogenic global change in the coming decades. In particular, the California current region experiences a spatially heterogeneous pattern of regular exposure to low-pH and hypoxic water, with the intensity of those stresses increasing with climate change (Cheresh & Fiechter, 2020; Kroeker et al., 2023), leading to negative consequences for nearshore organisms (Chan et al., 2019; Feely et al., 2016). Those two particular climate stressors do not have direct negative effects on kelp; indeed there is some evidence that kelp forests modify the biogeochemistry of the water column in ways that provide a limited refuge from acidified conditions to other kelp forest organisms (Bednaršek et al., 2024; Hirsh et al., 2020). Perhaps of more interest, however, is the nature of the spatial heterogeneity in stressors. In the California Current region, coastal upwelling draws to the surface deeper waters that are cold and nutrient-rich, but low in oxygen and high in dissolved inorganic carbon (Chan et al., 2019). In this region, coastal upwelling is concentrated in hotspots associated with headlands and similar topographic features, and those areas experience more frequent exposure to low temperatures, low pH and low dissolved oxygen; areas between those upwelling centres experience higher and more variable temperatures (Cheresh & Fiechter, 2020; Hamilton et al., 2023; Kroeker et al., 2023). As a consequence, future marine conservation planning will have to grapple with this mosaic of locations that will face greater exposure to acidified, low-oxygen water (but also cooler, high-nutrient conditions favourable to kelp) and other locations that are more likely to experience high-temperature heatwave stress. Those differences in conditions across the seascape would lead to the need to use models like ours to prioritize restoration interventions over space, to determine how to allocate resources to achieve the best coast-wide outcomes for kelp forests. Future implementations of the model developed here will therefore investigate these spatially heterogenous dynamics, as well as the implications of possible future reintroduction of sea otters. It will also become necessary to grapple with the ongoing warming trend in average temperatures, which will eventually push coastal systems into a perpetual 'heatwave' state relative to historical climatology (Amaya et al., 2023). Models that consider this reality will have to include the potential for selection and adaptation among kelp and other organisms.

Restoration activities are time and resource intensive, and should be implemented as part of an adaptive management programme (Walters, 1986). This adaptive management can take the form of 'learning by doing', but there are too many possible combinations of actions and intensities to determine the best practices empirically. Models like ours are essential for guiding the next round of experimental work, within an adaptive management cycle in which we predict the expected outcome of actions, then assess the empirical outcomes to determine whether they match expectations. In this case, two clear recommendations arising from our model are that (a) kelp seeding is unlikely to be successful without urchin culling (or the restoration of urchin predators), and (b) the most effective outcomes will come if urchin culling precedes kelp restoration (or the two are done simultaneously), particularly if those actions are taken after a heatwave has started.

AUTHOR CONTRIBUTIONS

J. Wilson White, Jess K. Hopf and Moritz S. Schmid conceived the study. Jess K. Hopf and Andrés Pinos-Sánchez wrote the model code. Jess K. Hopf performed the analysis, with suggestions and advice from all other authors. Jess K. Hopf and J. Wilson White interpreted the results and led the writing of the manuscript. J. Wilson White and Jess K. Hopf contributed equally, with their order of authorship determined by a wager on the lounging behaviour of Cashie, the wolfhound-cross. J. Wilson White, Jess K. Hopf, Andrés Pinos-Sánchez, Leif K. Rasmuson, Moritz S. Schmid, Mark Novak contributed critically to the drafts and gave final approval for publication. Our study focuses on the geographical region where all the authors are based, and we included coauthors from the management agency that is responsible for the nearshore kelp forest ecosystem that is the focus of the work.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All code and relevant data can be found at : https://doi.org/10.5281/zenodo.19717785 (JKHopf, 2026).

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SUPPORTING INFORMATION

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

Figure S1.1. Urchin behavioural feeding switch function (ϕ_t). As the availability of drift kelp to urchin consumptive capacity (biomass of urchins × urchin grazing rate) decreases (left-to-right along the x-axis) more urchins shift to grazing standing kelp. The rate of change of this shift is determined by the slope of the curve (w_2), here $w_2 = 0.5$.

Figure S1.2. Example average standing kelp and urchin biomass densities in the last 10 years of the model run, sampling only in summer and fall (to match sampling seasons in Oregon). Each point is an individual model simulation ($n = 5000$).

Figure S1.3. Site-averaged standing kelp and urchin biomass densities along the Oregon coast 2001–2011, pre-seastar wasting disease.

Figure S2.1. Changes in efficacy with effort *when seastars are absent (SSWD)*. Percentage increase in the probability of kelp forest persistence through a 2-year marine heatwave with varying degrees of urchin removal (a–c) and kelp seeding efforts (d–f), and lengths of actions (colours), at different times relative to the start of the heatwave (rows). Degrees of effort are measured as the percentage of pre-heatwave urchin and kelp biomass removed or seeded each year, respectively.

Figure S2.2. Changes in efficacy with effort *when seastars are present*. Percentage increase in the probability of kelp forest persistence through a 2-year marine heatwave with varying degrees of urchin removal (a–c) and kelp seeding efforts (d–f), and lengths of actions (colours), at different times relative to the start of the heatwave (rows). Degrees of effort are measured as the percentage of pre-heatwave urchin and kelp biomass removed or seeded each year, respectively.

Figure S2.3. Percentage increase in the probability of kelp persistence through a 2-year marine heatwave, with (a) and without (b) seastar wasting disease (SSWD), when combining urchin removal and kelp seeding sequentially. Panels (c) and (d) show the difference between starting urchin removal before or after kelp seeding, at the same times indicated in panels (a) and (b). For example, the top left boxes in (c) and (d) depict the increase in persistence probability when enacting urchin removal at $t = -2$ followed by kelp seeding at $t = -1$, *minus* enacting kelp seeding at $t = -2$ followed by urchin removal at $t = -1$. In this illustrative scenario, actions lasted for 3 years and 25% of the pre-heatwave urchin and kelp biomass was removed or seeded each year, respectively.

Figure S2.4. Percentage increase in the probability of kelp persistence through a 2-year marine heatwave, with (a) and without (b) seastar wasting disease (SSWD), when combining urchin removal and kelp seeding sequentially. Panels c-d show the difference between starting urchin removal before or after kelp seeding, at the same times indicated in panels (a) and (b). For example, the top left boxes in (c) and (d) depict the increase in persistence probability when enacting urchin removal at $t = -2$ followed by kelp seeding at $t = -1$, *minus* enacting kelp seeding at $t = -2$ followed by urchin removal at $t = -1$. In this illustrative scenario, actions lasted for 3 years and 100% of the pre-heatwave urchin and kelp biomass was removed or seeded each year, respectively.

Table S1.1. State variables for the urchin-kelp sub-model. Each state variable is the biomass density (per ha) at season t.

Table S1.2. Parameter symbols, descriptions, values and references (where applicable) for the urchin-kelp sub-model. Values in red indicate values used during heatwave periods, and their associated references, where applicable. Unless otherwise specified, urchin data are for purple urchins (*Strongylocentrotus purpuratus*) and kelp data are for giant kelp (*Macrocystis pyrifera*; hereafter 'kelp'). Note that all relevant values are per hectare (ha^{-1}).

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