Final Report: "Trophic Modeling of Oregon's Nearshore Reefs"

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Project Summary

Bull kelp (*Nereocystis luetkeana*) forests in Oregon have declined substantially in recent decades due to interacting effects of marine heatwaves, reduced predator control, and overgrazing by sea urchins (*Strongylocentrotus purpurates* and *Mesocentrotus franciscanus*). Several management actions have been proposed to promote kelp persistence, including sea urchin removal, kelp seeding, and sea otter (*Enhydra lutris*) reintroduction. However, these actions differ in their mechanisms, expected effectiveness, and potential ecological or socioeconomic tradeoffs. In particular, sea otter reintroduction may benefit kelp forests by restoring top-down control of urchins, but it may also affect commercially important invertebrates in nearby habitats, such as Dungeness crab (*Metacarcinus magister*).

We developed a multi-species trophic population model to evaluate how alternative management strategies influence bull kelp persistence and fishable Dungeness crab density in Oregon nearshore ecosystems. The model represented a one hectare rocky reef system with a) bull kelp and sea urchin populations, and key demographic, behavioral, and trophic interactions between them; b) an adjacent soft-bottom habitat containing a Dungeness crab population, include important age- and sex-based demographics; and c) the potential for sea otter predation on urchins and crabs, depending on diet preferences and relative abundance. We evaluated kelp seeding, urchin removal, and combined

management under continuous and intermittent implementation timings, both with and without sea otter reintroduction. We also assessed how sea otter prey-switching behavior influenced fishable crab density through time.

Kelp seeding alone produced only minor increases in kelp persistence, whereas urchin removal generated stronger responses. The greatest improvements occurred when urchin removal and kelp seeding were combined, indicating that effective bull kelp restoration benefits from simultaneous reduction of grazing pressure and enhancement of recruitment. Combined management produced synergistic effects, increased kelp persistence, and promoted recovery from barren states to kelp-dominated conditions. Continuous combined management generated the most durable outcomes, although intermittent combined management also improved persistence and may provide a realistic option when continuous intervention is not feasible. Sea otter reintroduction increased baseline kelp persistence by reducing urchin grazing pressure, but it did not eliminate the benefits of direct restoration.

Sea otter predation reduced fishable Dungeness crab density across all prey-switching scenarios, relative to no-otter conditions. Crab responses were temporally variable following otter introduction, with an initial decline, partial intermediate recovery, and later sustained reduction. These patterns reflected direct predation, prey-switching behavior, kelp forest conditions, and compensatory dynamics within the crab population. However, modeled crab reductions are best interpreted as localized effects within kelp-associated habitats where sea otters and crabs overlap, rather than coastwide predictions for the Oregon fishery.

Overall, this study suggests that bull kelp restoration in Oregon will likely require integrated management strategies that combine active restoration, predator recovery, and consideration of fishery tradeoffs. Sea otters may improve kelp forest persistence, but their reintroduction should be evaluated as a broader socioecological intervention with uneven benefits and costs across habitats, species, and stakeholder groups.

Project Outputs

• The project supported one graduate student, Andrés Pinos-Sánchez, in completing his M.S. in Fisheries, Wildlife, and Conservation Sciences at OSU.

• Project results were disseminated to scientific audiences at multiple regional and international venues:

- Western Society of Naturalists, Portland, OR, Nov. 2024 (poster)

- Western Society of Naturalists, San Diego, CA, Nov. 2025 (oral)

- International Phycological Congress, Bohol, Philippines, June 2025 (oral, invited)

- National Academy of Sciences/Royal Academy of Sciences workshop on marine ecosytem resilience, London, UK, May 2026 (oral, invited)

- Hatfield Marine Science Center seminar series, Newport, OR, May 2026 (oral, invited)

- Public M.S. thesis defense, Hatfield Marine Science Center, Newport, OR, June 2026

• Project results were disseminated to the general public at multiple events and formats:

- State of the Coast, Seaside, OR, 2024 (poster)

- State of the Coast, Coos Bay, OR, 2024 (oral + poster)

- Hatfield Marine Science Center 'Tap Talk', Newport, OR, April 2026 (oral)

- Radio interview, KYAQ, Newport, OR, April 2026 (radio)

• Project results will be disseminated in a peer-reviewed publication, currently being prepared for submission to *Ecological Applications*

• The PIs leveraged OOST funding to obtain a contract for ancillary work from the Nearshore Ecology Program at Oregon Department of Fish and Wildlife, leading to a publication:

White JW, Hopf JK, Pinos-Sánchez A, Rasmuson LK, Schmid MS, Novak M. 2026. Models reveal potential synergies in management actions for bull kelp forest resilience and restoration. *Journal of Applied Ecology* 63:e70448

Project Outcomes

• The results of our model analysis have been communicated to the main group performing kelp restoration actions in Oregon, the Oregon Kelp Alliance. They are using our model analysis to inform restoration planning.

• The results of our model analysis have been communicated to the Marine Resources and Nearshore Ecology groups, who will use these results to guide management recommendations surrounding kelp restoration, urchin removal, and sea otter reintroduction.

• The model code is publicly available (on GitHub) and can be used by future investigators to analyze alternative hypotheses about trophic interactions and restoration in Oregon's nearshore environment.

1. Introduction

Ecosystems across the globe have experienced widespread loss and degradation over recent decades as a consequence of overexploitation, pollution, and climate change, creating an urgent need to better understand and promote ecosystem management actions (IPBES, 2019). Kelp forests are a clear example of both the scale of ecosystem loss and the ecological and socioeconomic value of effective management. These ecosystems are found along ~20% of the world's coastlines (Jayathilake & Costello, 2020) and are dominated by highly productive, habitat-forming seaweeds that support high species richness and provide multiple ecosystem services, including fisheries production, nutrient cycling, shoreline protection, and carbon sequestration (Eger et al., 2022, 2023; Jayathilake & Costello, 2020; Springer et al., 2006). Yet, kelp forests have declined across many regions worldwide. Global syntheses report average cover losses of approximately 1-2% per year over the last century and document multiple regional collapses associated with interacting environmental and ecological stressors (Krumhansl et al., 2016; Wernberg et al., 2019). Common drivers of kelp forest collapse include marine heatwaves, overgrazing by herbivores, and sedimentation. These stressors, which frequently occur simultaneously, can interact to push kelp systems beyond ecological thresholds and into persistent urchin barrens or turf-dominated reefs (Hamilton et al., 2024; McPherson et al., 2021; Rogers-Bennett & Catton, 2019; Springer et al., 2006).

Worldwide, efforts to manage kelp forests have traditionally focused on passive management activities in which managers attempt to improve environmental or ecological conditions without direct manipulation of kelp populations or their consumers. Examples of these actions include improving water quality, regulating kelp harvest, and protecting species that facilitate kelp forest persistence (Eger et al., 2022; Foster & Schiel, 2010). In regions such as Chile, Norway, Ireland, and France, low levels of kelp exploitation and harvest regulations have contributed to more sustainable kelp harvesting practices (Buschmann et al., 2017; Eger et al., 2022; Frangoudes & Garineaud, 2015; Lorentsen et al., 2010; Werner & Kraan, 2004). Similarly, protecting important predators of herbivores that graze kelp, such as sea otters and sea stars, can maintain top-down control on grazer populations, promoting kelp forest persistence (Eger et al., 2022; Estes et al., 2004; J. Smith et al., 2021).

However, many passive management measures have failed to re-establish lost kelp populations, leading to increased consideration of more direct restoration approaches (Eger et al., 2022; Wernberg et al., 2019). Active restoration involves the intentional addition or removal of biotic or abiotic components within an ecosystem to recover degraded, damaged, or destroyed kelp systems (Eger et al., 2022). For example, when kelp

reproduction is limited, reproductive material may be introduced through the addition of spores or gametophytes, or through the transplantation of mature individuals that subsequently act as local spore sources (Eger et al., 2022; Layton & Johnson, 2021). Alternatively, when excessive grazing is pushing kelp towards collapse, managers may reduce grazer abundance by removing, culling, transporting, or harvesting herbivorous species such as sea urchins or herbivorous fishes (Eger et al., 2022; Lee et al., 2021; Strand et al., 2020; Tracey et al., 2015; Watanuki et al., 2010). Nevertheless, these restoration actions often carry substantial uncertainty regarding the effort level required to achieve restoration goals. In addition, some interventions may generate unintended ecological consequences that negatively affect other species or ecosystem components.

On the coast of the state of Oregon in the Pacific Northwest region of the United States, the dominant canopy-forming kelp species is *Nereocystis luetkeana*, commonly known as bull kelp. Recent assessments indicate that more than two-thirds (67-73%) of Oregon's kelp canopy disappeared between 2010 and 2022, with evidence suggesting reproductive failure during marine heatwaves and overgrazing by sea urchins (*Strongylocentrotus purpurates* and *Mesocentrotus franciscanus*) being the main reason for bull kelp substantial decline. Additionally, Oregon's kelp forests are under weakened top-down control of urchin populations due to the lack of urchin predators (Hamilton et al., 2024). Historically, the two primary predators of sea urchins in Oregon were sea otters (*Enhydra lutris*) and sunflower sea stars (*Pycnopodia helianthoides*). Both species are now functionally absent throughout much of the Oregon coast. Sea otters were hunted to local extinction during the early twentieth century and have not recovered or reinvaded (Bodkin, 2015; Kenyon, 1969). More recently, sunflower sea stars experienced catastrophic declines due to a widespread epizootic wasting disease that caused mass mortality throughout the species' range. This most recent loss of sea stars likely exacerbated the loss of kelp during a subsequent multi-year heatwave across the region (Burt et al., 2018; McPherson et al., 2021; White et al., 2026).

Several management actions have been proposed to promote kelp persistence and recovery in Oregon. Current direct restoration discussions primarily focus on two broad direct pathways: physical removal or culling of sea urchins, and kelp "seeding" (i.e., introducing kelp spores or juvenile macrophytes into the system). Concurrently, there has been a growing interest by many stakeholder groups in restoring sea otter populations along the Oregon coast (Kone, 2019; Tinker et al., 2023; USFWS, 2022), which could benefit kelp persistence, hence, opening a third management pathway. However, substantial uncertainty remains regarding both the magnitude and duration of effort required for these actions to succeed, as well as their potential unintended consequences. For example, urchin removal and kelp seeding may require sustained effort over long periods and may

only succeed under specific environmental or ecological conditions (Hopf et al., 2025; Springer et al., 2006; Tegner & Dayton, 2000; White et al., 2026). Similarly, although sea otter reintroduction may facilitate kelp recovery by reducing urchin populations through top-down control (Hamilton et al., 2024), it may also impact commercially important fisheries such as the Dungeness crab (*Metacarcinus magister*) fishery by reducing the available stock through predation (Garshelis et al., 1986). The Oregon Dungeness crab fishery is the state's most valuable single-species commercial fishery, generating tens of millions in revenue per year (Oregon Department of Fish and Wildlife & Marine Resources Program, 2022). Beyond its economic importance, this fishery sustains coastal communities, supports local tourism, and acts as a cultural icon for the Pacific Northwest (Oregon Dungeness Crab Commission, 2026).

Sea otters are generalist predators with complex foraging behaviors and flexible prey preferences that vary spatially and among individuals (Garshelis et al., 1986; Kenyon, 1969; Novak & Tinker, 2015; J. Smith et al., 2021). Consequently, they have had different ecological and socioeconomic impacts in the different regions of the North American west coast in which they have recovered or been reintroduced. In some regions, such as the estuaries and embayments of Alaska, sea otter predation has substantially reduced Dungeness crab populations and contributed to the displacement of local fisheries (Pitcher & Imamura, 1990). In contrast, studies from central and southern California have reported little to no detectable negative effect of sea otters on crab landings and, in some cases, have even documented positive correlations between sea otter presence and crab fishing success (Boustany et al., 2021). These contrasting outcomes highlight the need to better understand the ecological tradeoffs associated with sea otter reintroduction and kelp management within Oregon's bull kelp forest ecosystems.

Motivated by these uncertainties, we analyzed a multispecies population model to evaluate how alternative management actions may influence bull kelp persistence in Oregon. Prior work using a similar modeling framework for giant kelp (*Macrocystis pyrifera*) communities in southern California (Hopf, et al., 2025), and bull kelp communities in Oregon (White et al., 2026) have explored how each of those systems are influenced by discrete marine heatwaves, and how specific management actions have different effects in respect to marine heatwaves timing. Those studies' main findings suggest that management actions are more effective when implemented before or during heatwaves, urchin predators enhance the direct effect of management, and specific responses to management depend on the natural history of kelp species. Building on those results, we wanted to explore broader questions regarding management over long time periods, rather than specifically in regards to marine heatwaves: (1) How do the duration and intensity of sea urchin removal and kelp seeding influence the degree to which these management

actions are successful in promoting bull kelp persistence?, (2) Does the concurrent implementation of these two management actions produce synergistic outcomes relative to implementing either action independently?, and (3) How is the reintroduction of sea otters likely to influence kelp persistence and what could be their potential effect on the biomass density of fishable Dungeness crabs? To address these questions, we used a minimal-realistic simulation modeling approach (Plagányi, 2007), building a model that explores the intra- and inter-specific dynamics of bull kelp communities in the absence of marine heatwaves and across different stages/ages of kelp, urchins, and Dungeness crabs.

2. Methods

In what follows we describe the methodology used in the development of this study; detailed information regarding equations, assumptions, and justifications can be found in the **Error! Reference source not found.**. All the materials, data, code and additional documentation can be found in the project repository: GitHub-ORPM.

2.1. Model overview

We developed a spatially implicit, stage- and age-structured model of a shallow rocky-reef kelp forest ecosystem. The model explicitly represented the population dynamics of bull kelp (*Nereocystis luetkeana*), sea urchins (*Strongylocentrotus purpuratus* and *Mesocentrotus franciscanus*), and Dungeness crabs (*Metacarcinus magister*), and linked these dynamics to a sea otter (*Enhydra lutris*) predation model. We did not model sea otter population dynamics explicitly. Instead, we used sea otter density trajectories generated by the Oregon Sea Otter (ORSO) model as an external forcing variable. The model represented a spatial domain equivalent to 1 ha and operated at seasonal time steps of three months corresponding to winter, spring, summer, and autumn.

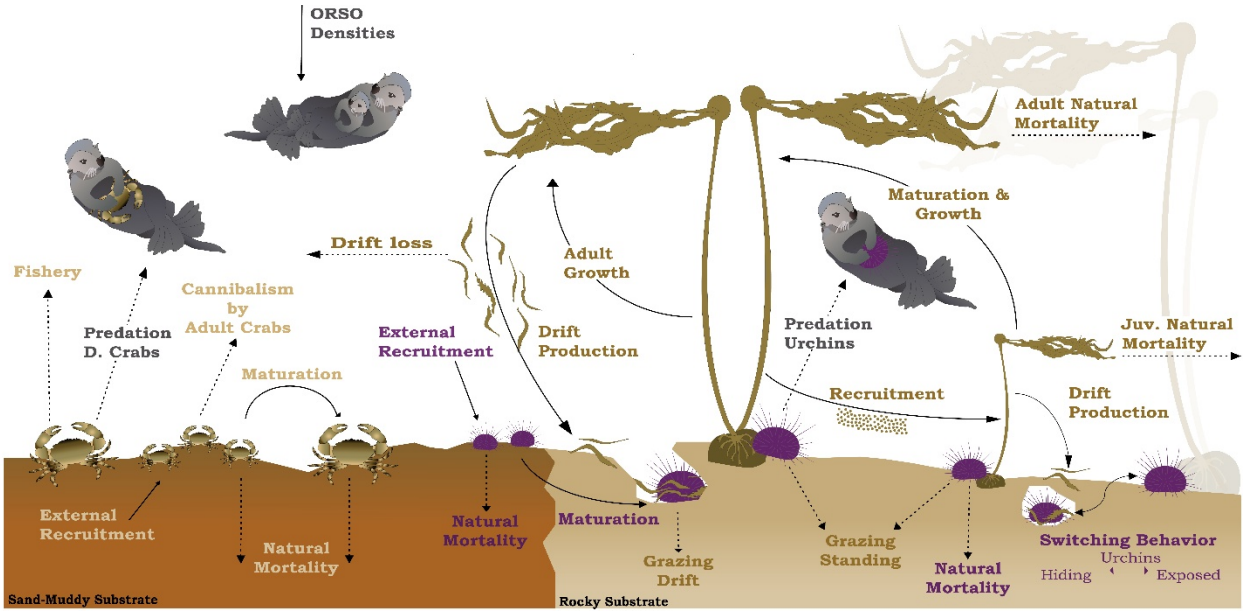


Figure 1. Model overview. Main biological processes and interactions included in the three linked sub-models: the kelp-urchin stage-structure sub-model, the Dungeness crab age-structure sub-model, and the sea otter predation model. Text colors correspond to the species affected by each process. Dotted arrows indicate processes that reduce biomass or abundance, including mortality, grazing, harvest, and predation. Solid arrows indicate additive or transition processes, including recruitment, growth, aging, and behavioral state changes. Illustration by Andrés Pinos-Sánchez. Original artwork was obtained from the Integration and Application Network image library and modified for this study: sea urchin by Jess K. Hopf; Dungeness crab by Kim Kraeer and Lucy Van Essen-Fishman; sea otter by Tracey Saxby; and kelp by Jane Thomas. Source: ian.umces.edu/media-library.

The model structure reflected key ecological traits and interactions among the focal species (**Figure 1**). Bull kelp is an annual species whose seasonal growth, reproduction, and mortality influence both standing kelp and the availability of detached drift material. We represented bull kelp using three-stage components (**Table 1**): juvenile standing kelp, adult standing kelp, and drift kelp. Drift kelp represented detached fronds and fragments produced from standing kelp and provided an important food source for urchins.

Table 1. State variables.

Functional group	State variable	Description	Units
Bull kelp - $K_{i,t}$ (*Nereocystis luetkeana*)	$K_{J,t}$	Biomass density of juvenile kelp at time t	kg ha^{-1}
	$K_{A,t}$	Biomass density of adult kelp at time t	kg ha^{-1}
	$K_{D,t}$	Biomass density of drift kelp at time t	kg ha^{-1}
Sea urchins - $U_{i,t}$ (*Strongylocentrotus purpurates & Mesocentrotus franciscanus*)	$U_{J,t}$	Biomass density of juvenile urchins at time t	kg ha^{-1}
	$U_{H,t}$	Biomass density of hiding adult urchins at time t	kg ha^{-1}
	$U_{E,t}$	Biomass density of exposed adult urchins at time t	kg ha^{-1}
Female Dungeness crabs - $C_{fi,t}$ (*Metacarcinus magister*)	$C_{f0,t}$	Density of age-0 female crabs (newly settled) at time t	Crabs ha^{-1}
	$C_{f1,t}$	Density of age-1 female crabs (juveniles) at time t	Crabs ha^{-1}
	$C_{f2-10,t}$	Density of age-2 to age-10 female crabs (adults) at time t	Crabs ha^{-1}
Male Dungeness crabs - $C_{mi,t}$ (*Metacarcinus magister*)	$C_{m0,t}$	Density of age-0 male crabs (newly settled) at time t	Crabs ha^{-1}
	$C_{m1,t}$	Density of age-1 male crabs (juveniles) at time t	Crabs ha^{-1}
	$C_{m2-3,t}$	Density of age-2 to age-3 male crabs (adults) at time t	Crabs ha^{-1}
	$C_{m4-10,t}$	Density of age-4 to age-10 male crabs (fishable adults) at time t	Crabs ha^{-1}
Sea otters (*Enhydra lutris*)	N_t	Biomass density of sea otters at time t	kg ha^{-1}

We represented the aggregate urchin population using three stages (**Table 1**): juveniles, hiding adults, and exposed adults. This distinction captured differences in adult urchin foraging behavior. Hiding urchins fed primarily on drift kelp, whereas exposed urchins grazed directly on standing kelp. The proportion of adults occupying each state changed dynamically in response to drift-kelp availability. Thus, low standing kelp biomass could reduce drift production, increase the proportion of exposed urchins, and intensify grazing on the remaining standing kelp. These feedbacks allowed the model to represent transitions between kelp forest and urchin barren states, which are characteristic of kelp-urchin ecosystems.

We modeled Dungeness crabs as an open, sex- and age-structured population (**Table 1**). We tracked female and male crabs separately across eleven annual age classes from age 0

to age 10. This structure represented changes in size, mortality, and vulnerability to predation as crabs grew through successive molts. Separating sexes was necessary because the Oregon Dungeness crab fishery is managed through size, sex, and seasonal restrictions, with harvest focused on legal-sized males. The modeled crab population represented a component of the broader population occupying habitat adjacent to the shallow rocky reef.

The sea otter predation model linked sea otters to the kelp-urchin and crab sub-models through predation on adult urchins and adult Dungeness crabs. It also included an alternative prey pool representing other sea otter prey available within kelp forest ecosystems. We modeled sea otter predation at daily time steps within each season to allow predation rates and feeding allocation to respond to changes in prey biomass. The predation model incorporated prey-specific functional responses, intrinsic prey preferences, and alternative prey-switching scenarios.

We used the overall model to evaluate the effects of sea otter reintroduction and management interventions on two primary response variables: kelp persistence and fishable Dungeness crab density. Kelp persistence represented the proportion of stochastic replicates that remained in a kelp forest state through time. Fishable crab density represented the density of male Dungeness crabs in ages 4 and 5, which were the age classes available to the modeled fishery. We provide full model equations, parameter values, and implementation details in the **Error! Reference source not found.**. All analyses were conducted in MATLAB R2025a (The MathWorks, Inc, 2025).

2.2. Sub-model 1: kelp-urchin stage structure model

We modeled bull kelp and sea urchin dynamics using a stage-structured model that represented the main demographic processes and species interactions occurring within a shallow rocky-reef kelp forest (Appendices

A1. Urchin Population Model., A2. Bull-Kelp Population Model., and A8. Parameters table.). Model parameterization primarily reflected purple sea urchin dynamics, while red sea urchins were implicitly included within the aggregate sea urchin biomass because they were not represented as a separate functional group.

We represented the rocky-reef spatial domain as an approximately 1-ha patch. Within this domain, we modeled bull kelp as a demographically closed population and sea urchins as a demographically open population. These contrasting assumptions reflected the short planktonic duration of kelp spores relative to the longer pelagic larval duration of sea urchins. Consequently, kelp recruitment depended entirely on reproductive output from adult kelp within the modeled patch, whereas the urchin population received a persistent

influx of recruits from outside the modeled area. Under this framework, juvenile kelp experienced density-dependent limitation through both intra- and inter-cohort competition (Nisbet & Bence, 1989), while urchin dynamics reflected local survival, maturation, behavioral state changes, grazing, and external recruitment.

We structured the kelp component to reflect the annual and seasonal life history of Oregon bull kelp (A6. Bull kelp seasonal life history). Adult standing kelp experienced near-complete winter dieback, which contributed to drift material, whereas juvenile kelp settlement and rapid growth occurred primarily during spring (Amsler & Neushul, 1989; Maxell & Miller, 1996; Springer et al., 2006). Adult kelp then contributed to spore production during summer and autumn, providing the basis for recruitment in the following spring. This structure implicitly incorporated the non-modeled gametophyte stage during winter and represented the time lag between seasonal spore production and subsequent sporophyte recruitment. Together, these seasonal processes captured the strong annual turnover characteristic of bull kelp forests and linked kelp production, drift availability, and grazing pressure across seasons.

We incorporated environmental and demographic stochasticity through interannual variation in recruitment. We drew annual kelp and sea urchin recruitment from data-parameterized probability distributions, using a normal distribution for kelp recruitment and a lognormal distribution for sea urchin recruitment. This stochastic structure generated variation among replicates in kelp persistence, kelp decline, and transitions to barren states.

We modeled kelp-urchin interactions through a grazing functional response that incorporated density-dependent resource use by adult urchins (Randell, 2022; Randell et al., 2025). Specifically, adult urchins shifted between hiding and exposed behavioral states according to drift-kelp availability. When drift kelp was abundant, urchins fed primarily on drift material and exerted limited grazing pressure on standing kelp. As drift availability declined relative to urchin feeding demand, a greater proportion of adult urchins became exposed and increasingly grazed on standing kelp. This drift-dependent behavioral switch allowed the system to transition from kelp-dominated states to urchin barrens when drift production was insufficient to buffer grazing pressure on standing kelp.

2.3. Sub-model 2: Dungeness crab age-structure model

We modeled Dungeness crab dynamics using a demographically open, age-structured population model that tracked female and male crabs separately. We divided the population into annual cohorts from age 0 to age 10 to capture age-specific demographic

processes and the sex- and size-selective structure of the commercial fishery (A3. Dungeness Crab Population Model, and A8. Parameters table.).

We interpreted the modeled crab population as a local segment of a larger Dungeness crab population adjacent to the modeled kelp forest. This distinction was important because Dungeness crabs primarily inhabit deeper soft-substrate habitats, whereas bull kelp, sea urchins, and sea otters in our model occupied a shallow rocky-reef domain. Thus, we did not treat the crab population as restricted to the 1-ha kelp forest patch. Instead, we represented the portion of the crab population that could overlap spatially with sea otter foraging near the modeled kelp forest.

We modeled age-0 crab recruitment as an external stochastic input during spring and summer. Each year, we drew total age-0 recruitment from a lognormal distribution to represent the episodic recruitment pulses and cyclic variability commonly observed in Oregon Dungeness crab populations (Higgins et al., 1997; Rasmuson et al., 2022). We assigned recruits a 1:1 sex ratio at settlement and allowed individuals to age seasonally through annual age classes under age-specific natural mortality (A3.2. Crab transition matrix:). To represent density-dependent juvenile mortality, we included cannibalism as an inter-cohort, Ricker-style reduction in age-0 survival driven by larger crabs (Botsford, 1984; Botsford et al., 2019; Botsford & Wickham, 1978; Hobbs & Botsford, 1989).

We modeled the commercial crab fishery following Oregon's Triple-S management strategy, which regulates harvest by size, sex, and season (Oregon Department of Fish and Wildlife & Marine Resources Program, 2022; Rasmuson, 2013). Under this framework, we allowed harvest only on legal-sized male crabs, defined in the model as age-4 and older, during the open fishing season from winter through summer. This concentrated fishing mortality rates (Botsford & Hobbs, 1995) on males entering the fishable age classes. We therefore assumed that harvest effectively removed most legal males during their first fishing season, resulting in no survival into older fishable age classes.

2.4. Sub-model 3: Sea otter population and predation model

We implemented sea otter abundance using density time series generated by the Oregon Sea Otter (ORSO) model (Tinker, 2023; Tinker et al., 2023). Thus, sea otter biomass functioned as an external forcing variable that influenced sea urchin and Dungeness crab dynamics without receiving feedback from prey availability (e.g., no otter mortality or immigration responses under prey limitation).

We obtained sea otter densities directly from the ORSO R implementation rather than the online interface (Tinker, 2023; Tinker et al., 2023; A5. ORSO implementation on this model (ORPM).). We used ORSO to evaluate multiple reintroduction scenarios across the Oregon

coast and retained only section S6 (i.e., north of Port Orford), because it produced the highest projected sea otter densities. We expanded annual ORSO estimates of sea otter density (otters km^{-2}) to seasonal time series, converted density to biomass using simulated individual body masses (mean = 32 kg, SD = 4.38 kg; Kenyon, 1969), and rescaled the resulting biomass density from km^2 to hectares to match the spatial resolution of the kelp-urchin model.

We further adjusted sea otter densities to represent effective habitat area by retaining only suitable habitat cells with carrying-capacity values of $K \geq 2$. This reduced the ORSO modeled area from 123.96 km^2 to 36.66 km^2 (Tinker et al., 2023). We then calculated otter biomass density over this suitable habitat area, thereby concentrating projected biomass within habitat considered available to sea otters.

We modeled sea otter predation across three prey categories: sea urchins, Dungeness crabs, and an alternative prey pool, hereafter prey X. This prey X represented a constant biomass pool of other sea otter prey available within the modeled kelp forest. This pool represented the broader diversity of prey available in kelp forest ecosystems and provided an additional resource over which sea otters could distribute feeding effort when sea urchin or crab biomass declined.

Within each seasonal time step, we modeled sea otter predation as a daily process over 91-time steps. This temporal resolution allowed predation pressure and prey preferences to respond to changes in prey biomass within each season. We used prey biomasses at the beginning of each season as initial conditions for the daily predation loop. Daily predation reduced prey biomasses over the 91-day period, and we used the resulting biomasses at the end of the loop as inputs for subsequent seasonal processes, including natural mortality, grazing, cannibalism, and seasonal transitions.

Available sea urchin biomass consisted of hiding and exposed adult urchins, whereas available crab biomass consisted of adult crab age classes summed across both sexes. We assumed that juvenile urchins and juvenile (ages 0-1) crabs were invulnerable to sea otter predation. Predation rates followed a Type II functional response (Dunn & Hovel, 2020), in which prey consumption increased with prey density but approached a maximum as handling time constrained feeding rates. We applied prey-specific attack rates and maximum consumption rates to account for differences in prey vulnerability and handling efficiency. For example, exposed adult urchins were more vulnerable to predation than hiding adult urchins.

We allocated sea otter feeding effort among prey types using a modified Yodzis-style prey-switching function (Koen-Alonso & Yodzis, 2005; Randell et al., 2025). This approach

accounted for the ability of sea otters to forage across multiple prey types and adjust feeding effort as relative prey availability changed. The function combined intrinsic prey preferences, defined as the tendency of a predator to select a prey type when all prey types occur at equal abundance, with dynamic responses to changes in prey biomass through time.

We assigned intrinsic preferences to sea urchins, Dungeness crabs, and prey X based on the biomass of each prey type required to satisfy the estimated daily energetic requirements of an adult sea otter and the corresponding number of individual prey items required to provide that biomass (A8. Parameters table.). We then adjusted these preferences to reflect prey accessibility within the modeled foraging arena. Sea urchins and prey X were assumed to be directly available within the kelp forest, which represented the sea otter spatial domain in the model. In contrast, we penalized the intrinsic preference assigned to Dungeness crabs because crabs were assumed to occupy adjacent habitat rather than the kelp forest itself and were therefore less accessible to foraging sea otters. Thus, intrinsic preference values represented both the energetic contribution of each prey type and its expected accessibility within the modeled seascape.

Because the empirical strength and direction of prey switching by sea otters remains uncertain, we evaluated three prey-selection scenarios in response to relative prey availability: (1) no prey switching, in which prey preferences remained constant regardless of prey abundance; (2) negative frequency-dependent switching, in which preference increased toward less common prey; and (3) positive frequency-dependent switching, in which preference increased toward more abundant prey.

We also allowed prey preferences to respond to the state of the kelp forest. Under prolonged low-kelp conditions, we assumed that sea urchin gonad condition declined and that sea otters reduced their preference for sea urchins as prey (Foster et al., 2015; Gonor, 1972). Therefore, when kelp biomass remained below the barren-state threshold for two consecutive seasons, we assumed that sea otters did not consume exposed urchins and that hiding urchins had a reduced intrinsic preference. This distinction reflected the assumption that hiding urchins retained better gonad condition than exposed individuals under barren conditions. Feeding effort no longer allocated to sea urchins was redistributed toward Dungeness crabs and prey X, increasing the relative feeding of sea otters on these alternative prey types during barren states.

2.5. Model simulations and evaluation, management strategies, and variables of interest

We ran the model on discrete seasonal time steps corresponding to Northern Hemisphere seasons, with winter beginning on December 1 and each season represented as a three-month period. We included season-specific parameters and processes, such as kelp reproduction, to match the phenology of the modeled species. We ran each scenario for 10,000 stochastic replicates over 40 years to obtain probabilistic predictions of system behavior. The daily sea otter predation loop contained 91-time steps within each seasonal step.

We designed the model as a stochastic system to characterize overall behavior across replicate simulations rather than a single deterministic trajectory. Stochasticity occurred primarily through kelp and sea urchin recruitment (A1.1. Urchin recruitment: and A2.2. Kelp recruitment (sporophytes):). Because the modeled kelp patch received no external kelp recruitment, this design represented a closed-patch recovery scenario without rescue effects from neighboring kelp populations (Hopf et al., 2025; White et al., 2026).

Under these assumptions, variation in kelp and sea urchin recruitment could cause a replicate to transition from a kelp forest to an urchin barren (**Figure 2**). For instance, low kelp recruitment reduced adult kelp and drift-kelp biomass, whereas large sea urchin recruitment pulses could exceed the available drift-kelp supply. Either process increased the proportion of exposed urchins and intensified grazing on standing kelp. When these processes reduced standing kelp biomass below the barren-state threshold, the replicate transitioned to an urchin barren. In the absence of management, this state was absorbing because kelp recovery could not occur without an external source of recruitment. Consequently, kelp persistence in unmanaged simulations could only decline through time.

We defined kelp persistence as the proportion of replicate simulations that remained in a kelp forest state at each time step. The barren-state threshold corresponded to a minimum standing kelp biomass density of ~408 kg ha^{-1}, equivalent to 1% of the mean standing kelp biomass across simulations. We evaluated management performance as the increase in kelp persistence relative to the unmanaged baseline through time.

We evaluated three management strategies designed to prevent or delay transitions to urchin barrens and, when possible, facilitate recovery of barren state replicates: (1) sea urchin removal, (2) kelp seeding, and (3) a combined strategy including both sea urchin removal and kelp seeding. Although all simulations ran for 40 years, we focused the kelp-persistence analysis on the first 15 years because this period captured the direct effects of

management before longer-term stochastic trajectories became the primary source of variation. Management actions began seven years after the start of each simulation. By this time, some replicates had already transitioned to barren states, allowing us to evaluate both the capacity of management to maintain existing kelp forests and its potential to promote recovery following kelp loss.

We defined management effort as the target biomass of sea urchins removed and kelp recruits added under each intervention. We designed the timing of management actions to align with current Oregon Kelp Alliance pilot restoration efforts, regional oceanographic conditions, and species natural history. Accordingly, we applied sea urchin removal only during summer, whereas kelp seeding occurred from spring through summer. We determined target intervention biomasses from model simulations under undisturbed conditions. The total sea urchin removal target was ~4,630 kg ha^{-1}, whereas the total kelp-seeding target was ~40,380 kg ha^{-1} of kelp recruits. We used a relatively high kelp-seeding target because only a small proportion of seeded recruits were expected to settle and survive.

We evaluated multiple implementation schedules that differed in management duration, continuity, and the temporal allocation of total effort. In continuous management scenarios, interventions occurred in consecutive years, and the total planned effort was distributed evenly across the management period. For example, a three-year management plan allocated ~1,540 kg ha^{-1} yr^{-1} of sea urchin removal and ~13,460 kg ha^{-1} yr^{-1} of kelp seeding. In intermittent management scenarios, interventions included planned gap years without action. These discontinuous schedules represented logistical and economic constraints that can affect restoration programs, including variation in diver availability and Oregon's biennial budgeting cycle. Together, these scenarios allowed us to examine how management duration, continuity, and effort allocation influenced kelp persistence and potential cost efficiency.

We evaluated all management scenarios under two ecological conditions: one without sea otters and one with a reintroduced sea otter population represented by the ORSO-derived density timeseries. We retained Dungeness crabs and prey X in both conditions to preserve the structure of the modeled food web. However, when sea otters were absent, neither crabs nor prey X influenced kelp-urchin dynamics and therefore had no functional effect on kelp-persistence outcomes. To isolate the effects of sea otter presence within the management analysis, we evaluated kelp persistence under sea otter reintroduction using only the no-prey-switching scenario. Under this scenario, sea otter foraging allocation remained determined by intrinsic prey preferences and did not change in response to relative prey availability.

In addition to kelp persistence, we evaluated the potential consequences of sea otter predation for the Dungeness crab fishery. For this analysis, we focused on model years 5 to 25 of the 40-year simulation period. Sea otters were introduced in year 5, and this subsequent 20-year interval allowed us to evaluate sea otter foraging under two contrasting ecosystem states. During the earlier portion of this period, more than half of the stochastic replicates remained in a kelp forest state. During the later portion, most replicates had either transitioned to, or were transitioning toward, an urchin barren state. This comparison allowed us to evaluate sea otter foraging under relatively intact versus degraded kelp forest conditions.

We defined fishable crab density as the density of male Dungeness crabs in ages 4 and 5, which represented the age classes available to the fishery under the modeled size, sex, and seasonal regulations. For each sea otter predation and prey-switching scenario, we calculated mean fishable crab density across stochastic replicates through time and compared these values with the no-otter baseline. This comparison quantified how sea otter predation and alternative prey-switching assumptions altered modeled crab availability to the fishery. We interpreted these outputs as relative changes in fishable crab density within the modeled system rather than direct predictions of coastwide crab abundance or fishery landings.

3. Results

We present the results of our analysis in two parts, first focusing on the results related to kelp forest dynamics and management strategies, and second the results related to Dungeness crab fishery dynamics under sea otter reintroduction. Although both components are linked through the structure of the model, presenting them separately facilitates interpretation of the ecological mechanisms underlying each set of outcomes.

3.1. Kelp forests dynamics and management strategies

Overall, the kelp-urchin sub-model produced dynamics consistent with empirical observations of temperate kelp forest ecosystems (A7. Kelp-Urchin model validation.). In particular, the model captured shifts in sea urchin feeding behavior in response to the availability of kelp drift. In simulations where kelp reproduction failed or stochastic pulses of urchin recruitment occurred, sea urchins shifted their feeding behavior as drift kelp became scarce. Drift availability declined either because standing kelp was limited or because high urchin densities depleted kelp biomass. As drift kelp declined, sea urchins moved from hiding to exposed feeding behavior, increasing herbivory on standing kelp and ultimately driving the system toward an urchin barren state.

To illustrate these dynamics, we present two representative simulations conducted under the current state of nature without sea otters (**Figure 2**). In both examples, declines in drift kelp triggered increases in exposed urchin biomass, which subsequently caused rapid reductions in standing kelp biomass. Following collapse, exposed urchins dominated the system, generating the persistent barren-state dynamics characteristic of heavily grazed kelp ecosystems.

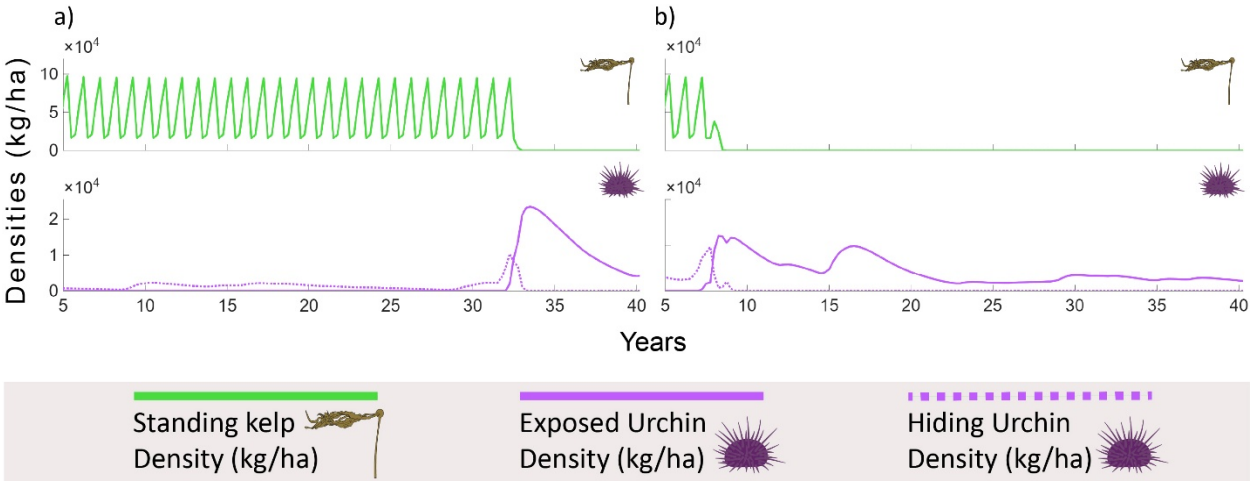


Figure 2. Simulation examples of standing kelp and adult urchin biomass densities (kg ha^{-1}) through time. Green solid lines represent standing kelp biomass, purple solid lines represent exposed adult urchins, and purple dotted lines represent hiding adult urchins. Simulations were selected from 10,000 model replicates under the current state of nature without sea otters. Panel (a) corresponds to simulation ID 7,973 and panel (b) to simulation ID 9,912.

The stochastic structure of the model produced substantial variation in the timing of kelp collapse among simulations. Because the system represented a closed kelp population without external recruitment subsidies, all simulations eventually transitioned to a barren state; however, the timing of collapse differed considerably among replicates due to stochastic variability in kelp recruitment, episodic pulses of urchin recruitment, and fluctuations in drift production. For example, kelp persisted until late in the simulation in **Figure 2a**, whereas collapse occurred substantially earlier in **Figure 2b** under a different sequence of stochastic conditions.

Across all management scenarios, both continuous and intermittent strategies increased kelp persistence relative to unmanaged baseline conditions under both states of nature (i.e., with and without sea otters; **Figure 3** and **Figure 4**). However, management effectiveness varied substantially among strategies, durations, and effort allocations. Overall, kelp seeding alone produced the weakest effects on persistence, urchin removals generated substantially larger responses, and combined management actions consistently produced the strongest and synergistic outcomes.

Under continuous management strategies (**Figure 3**), both kelp seeding and urchin removal produced additive increases in kelp persistence as management duration increased. Because total management effort was distributed evenly across the duration of the intervention window, longer-duration strategies applied lower annual effort. For example, single-year interventions applied 100% of the total management effort in one year (**Figure 3a,d**), whereas three-year strategies distributed effort evenly across years, resulting in approximately 33% of the total effort being applied annually (**Figure 3c,f**). Despite this reduction in annual effort, longer-duration combined strategies produced stronger increases in kelp persistence and substantially improved recovery from barren states back to kelp-dominated conditions.

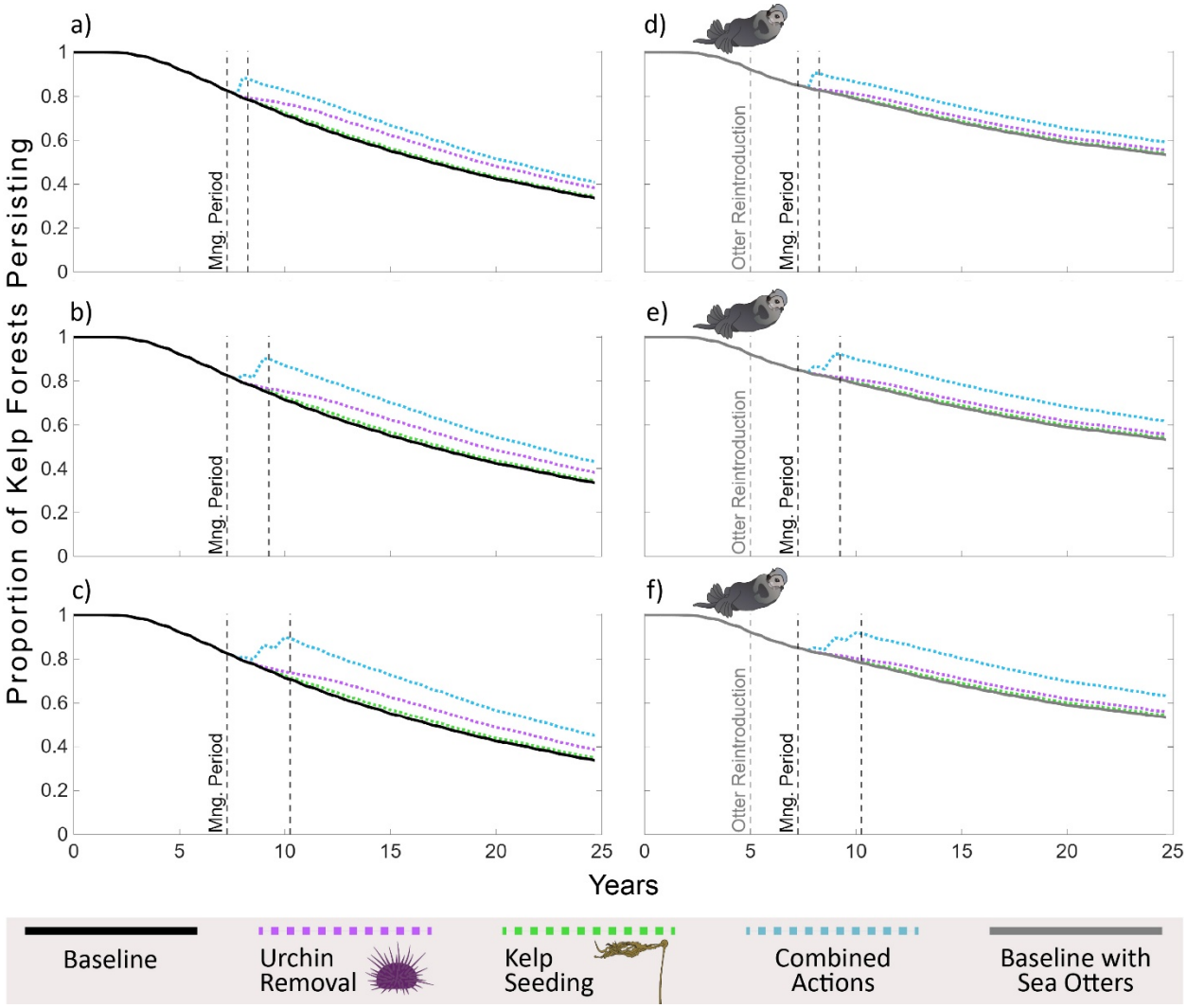


Figure 3. Kelp persistence through time under continuous management strategies. Values represent the proportion of model simulations ($n = 10{,}000$) remaining in a kelp-dominated state under different management scenarios and states of nature. Panels (a-c) represent simulations without sea otters, whereas panels (d-f) represent simulations with successfully reintroduced sea otters. Management strategies differed in implementation duration and annualized effort

allocation. Panels (a,d) show single-year management, panels (b,e) show effort distributed evenly across two consecutive years (50:50), and panels (c,f) show effort distributed evenly across three consecutive years (33.3% per year).

Management effects remained qualitatively consistent across both states of nature; however, their relative magnitude differed depending on sea otter presence. Under sea otter reintroduction (**Figure 3d-f**), baseline kelp persistence was already elevated relative to no-otter simulations because sea otter predation reduced urchin biomass and grazing pressure. Consequently, management actions produced higher absolute persistence values under sea otter presence. Nevertheless, proportional gains relative to baseline conditions were generally smaller because kelp forests already occupied comparatively healthier ecological states in the presence of sea otters.

Intermittent management strategies (**Figure 4**) produced patterns similar to those observed under continuous management. Individual management actions remained less effective than combined actions across both states of nature. Because all intermittent scenarios applied the same initial management effort during the first intervention year, early increases in kelp persistence were identical among simulations within each state of nature. Subsequent differences emerged as the interval between management years increased. Longer gaps between interventions reduced overall management effectiveness; however, these reductions remained relatively modest, particularly for combined strategies, which consistently generated strong increases in kelp persistence and facilitated recovery from barren states.

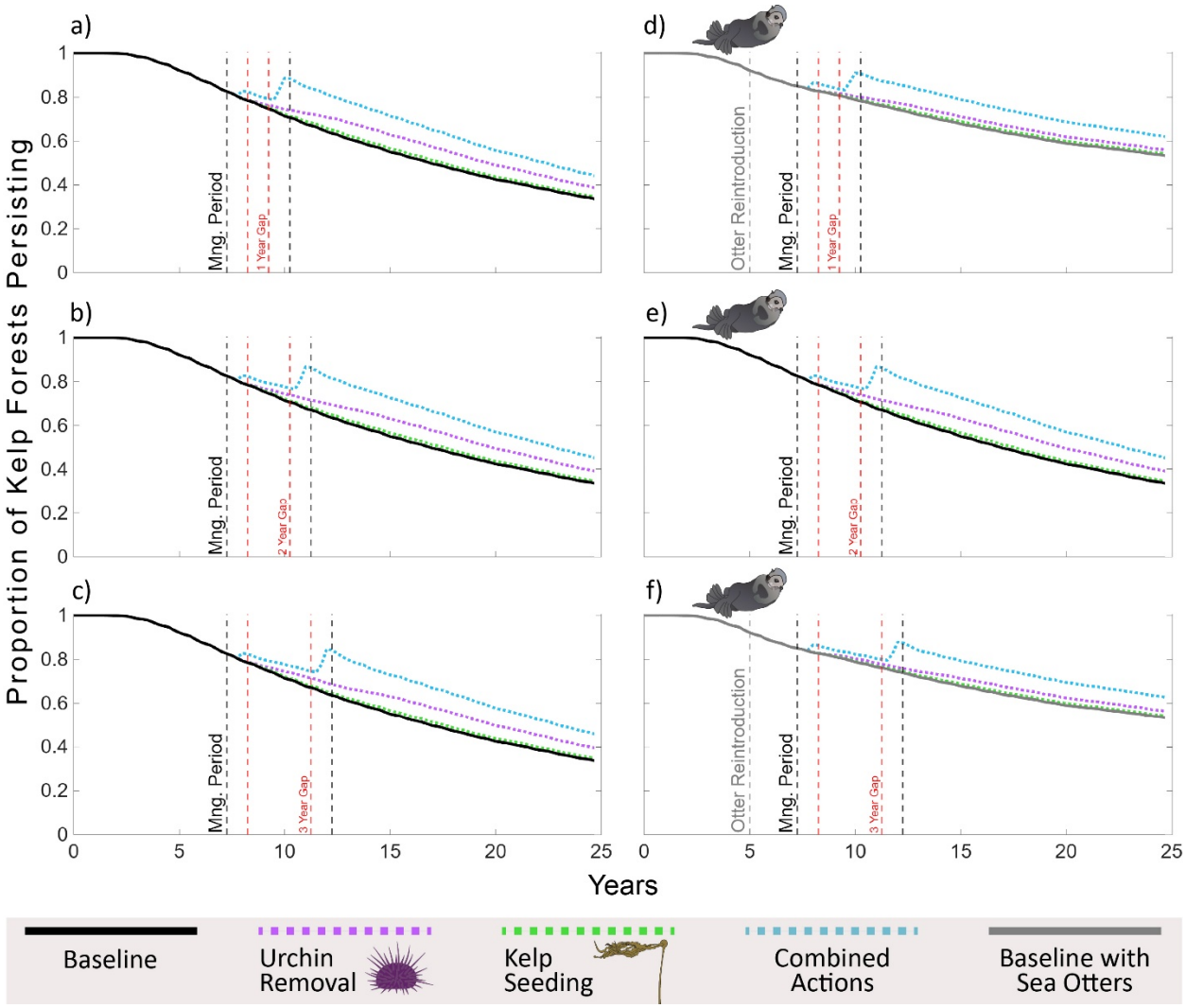


Figure 4. Kelp persistence through time under intermittent management strategies. Values represent the proportion of model simulations ($n = 10{,}000$) remaining in a kelp-dominated state under different management scenarios and states of nature. Panels (a-c) represent simulations without sea otters, whereas panels (d-f) represent simulations with successfully reintroduced sea otters. Management strategies differed in the interval between intervention years. Panels (a,d) show two management years separated by a one-year gap, panels (b,e) by a two-year gap, and panels (c,f) by a three-year gap.

Overall, all management actions increased the probability of kelp persistence relative to unmanaged conditions. Kelp seeding alone consistently produced the weakest responses, whereas urchin removals generated substantially larger increases in persistence. Combined strategies consistently produced the strongest effects and were the only strategies that facilitated recovery from barren states back to kelp forest conditions. Across all scenarios, sea otter presence elevated baseline kelp persistence by reducing urchin grazing pressure, thereby increasing the absolute persistence achieved under

management. However, relative improvements above baseline remained smaller than those observed under no-otter conditions.

3.2. Dungeness crab fishery dynamics under sea otter reintroduction

Sea otter predation reduced fishable Dungeness crab density across all modeled scenarios relative to baseline no-otter conditions (**Figure 5**). Fishable crab density was defined as the density of male crabs aged 4 years and older, corresponding to the legally harvestable component of the Oregon commercial fishery.

Under all sea otter scenarios, crab density declined immediately following sea otter establishment (**Figure 5b-d**). However, this decline was not constant through time. Between approximately years 10 and 15, crab densities partially recovered and approached values closer to the no-otter baseline before declining again during later years.

Temporal patterns differed among prey-switching scenarios, although these differences were relatively modest when compared visually (Figure 5). The scenario in which sea otters preferentially consumed more abundant prey ($\phi = 2$; **Figure 5d**) consistently maintained the highest fishable crab densities among predation scenarios. In contrast, the no-switching scenario ($\phi = 0$; **Figure 5b**) produced the lowest crab densities throughout most of the simulation period. The intermediate prey-switching scenario ($\phi = 1$; **Figure 5c**) generally produced intermediate outcomes.

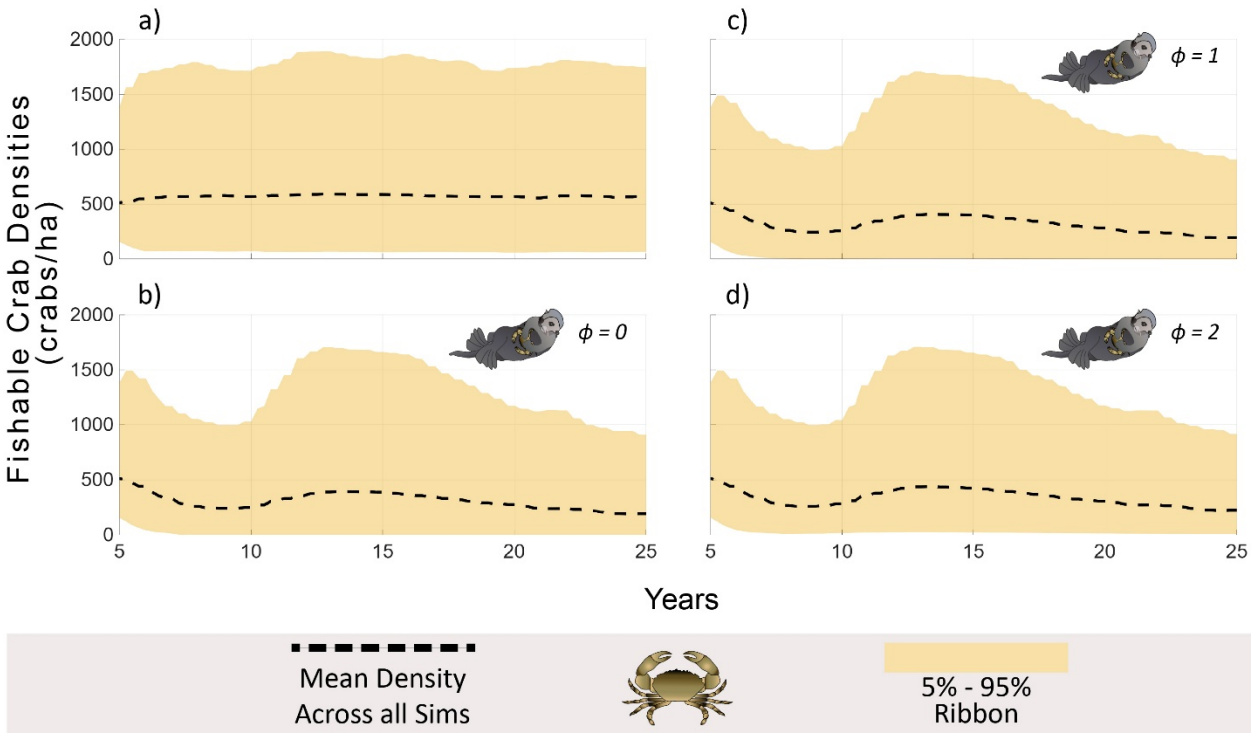


Figure 5. Fishable Dungeness crab density (crabs ha^{-1}) through time across all simulations ($n = 10{,}000$). Fishable density includes male crabs aged 4-10 years, although values primarily reflect ages 4-5 because older age classes are virtually inexistent due to high levels of fishing. Panel (a) shows baseline crab density in the absence of sea otters. Panels (b-d) show crab density under sea otter predation with different prey-switching sensitivities: $\phi = 0$ indicates no prey switching, $\phi = 1$ indicates increased preference for less common prey, and $\phi = 2$ indicates increased preference for more abundant prey.

Summarizing fishable crab density across 5-year intervals clarified these differences among scenarios (

Table 2). Across all time periods and prey-switching sensitivities, sea otter predation reduced fishable crab density by an average of approximately 44% relative to baseline conditions. Mean reductions were 42% during years 5-10, 35% during years 10-15, 40% during years 15-20, and 58% during years 20-25. The strongest preference for more abundant prey ($\phi = 2$) produced the smallest overall reduction in fishable crab density, with an average decline of 41% relative to baseline conditions. The intermediate switching scenario ($\phi = 1$) produced an average reduction of 45%, whereas the no-switching scenario ($\phi = 0$) produced the largest decline at 46%.

Table 2. Fishable Dungeness crab densities (crabs ha^{-1}) summarized across all simulations over 5-year intervals under each modeled state of nature.

Sampled Period	Baseline (no-otters)	Sea otters (ϕ = 0)	Sea otters (ϕ = 1)	Sea otters (ϕ = 2)
Year 5 - 10	536.63	310.15	311.90	319.32
Year 10 - 15	556.97	339.81	352.81	382.05
Year 15 - 20	548.22	313.62	323.41	346.46
Year 20 - 25	542.29	212.99	219.50	245.43

Overall, sea otter reintroduction consistently reduced fishable Dungeness crab density across all modeled prey-switching scenarios. Although crab densities partially recovered during the intermediate period of the simulations, all predation scenarios ultimately produced substantial long-term reductions relative to no-otter conditions. However, these reductions are context dependent to the ecology and state of the kelp forests, as this heavily influences sea otter foraging behavior, and will be further explained in the discussion section.

4. Discussion

We evaluated how direct restoration actions and sea otter reintroduction may influence bull kelp persistence and fishable Dungeness crab density in Oregon nearshore ecosystems. Overall, our results suggest that bull kelp persistence depends strongly on reducing grazing pressure, that combined management actions are more effective than either kelp seeding or urchin removal alone, and that sea otter reintroduction can increase kelp persistence while also creating localized tradeoffs for Dungeness crab availability. Together, these findings emphasize that kelp restoration, predator recovery, and fisheries management are connected through shared ecological pathways and should be evaluated as interacting components of nearshore ecosystem management.

4.1. Kelp forests dynamics and management strategies

Kelp forests worldwide face increasing risk of collapse from interacting stressors, including marine heatwaves, extreme herbivore, and weakened top-down control (Krumhansl et al., 2016; Wernberg et al., 2019). As these stressors intensify, direct management interventions are becoming increasingly important for maintaining kelp forest persistence and supporting ecosystem recovery (Eger et al., 2020, 2023; Hopf et al., 2025; Johnson, 2020; Springer et al., 2006; Steneck et al., 2002; Wernberg et al., 2019; White et al., 2026). Because kelp forests and urchin barrens can function as alternative stable states, reversing a barren state often requires greater effort than preventing collapse in the first place

(Springer et al., 2006; Tegner & Dayton, 2000). Therefore, management actions that maintain kelp persistence before complete ecosystem degradation may be particularly valuable.

We evaluated the effects of urchin removal and kelp seeding, both independently and in combination, across continuous and intermittent management strategies. We also examined these strategies under two contrasting ecological contexts: one without sea otters, representing current Oregon conditions, and one with a successfully reintroduced sea otter population. This comparison allowed us to evaluate how direct restoration actions interact with the restoration of top-down predator control.

Our results (**Figure 3** and **Figure 4**) reflect the interpretation that excessive urchin grazing is the main threat to bull kelp persistence in degraded systems lacking urchin predators (Dean et al., 1984; Karatayev et al., 2021; Kriegisch et al., 2019; Ling et al., 2015; Steneck et al., 2002). Kelp seeding alone produced only marginal increases in kelp persistence, whereas urchin removal generated stronger responses across management strategies and ecological contexts. However, the strongest and synergistic outcomes occurred when we combined urchin removal with kelp seeding. These combined interventions increased kelp persistence consistently and promoted recovery from barren states back to kelp-dominated conditions.

This pattern highlights the importance of treating kelp restoration as a two-part problem: increasing kelp recruitment alone may not be sufficient if grazing pressure remains high, and reducing grazing alone may produce limited recovery if local recruitment is weak. In this model, kelp seeding provided additional recruitment, but that recruitment only translated into stronger persistence when urchin removal reduced the grazing pressure that would otherwise suppress juvenile kelp establishment. Therefore, combined management produced a synergistic response because each action addressed a different ecological constraint.

The weak effect of kelp seeding alone differs from restoration outcomes reported for giant kelp (*Macrocystis pyrifera*) systems, where direct restoration practices such as seeding or outplanting can produce stronger short-term recovery responses (Arroyo-Esquivel et al., 2024; Hopf et al., 2025). This contrast likely reflects important differences in life history and seasonal dynamics between bull kelp and giant kelp. Bull kelp is an annual species with strong seasonal turnover, whereas giant kelp is perennial and can recover through multi-year growth and recruitment processes (Schiel & Foster, 2015; Springer et al., 2006). In bull kelp systems, winter dieback converts standing kelp into drift material that temporarily support urchins, but reductions in drift availability may subsequently shift urchins toward active grazing on juvenile standing kelp during spring. Under those conditions, additional

kelp recruits (i.e., seeding) may be rapidly consumed before establishing. Thus, seeding alone cannot overcome the main bottleneck limiting persistence: intense grazing pressure during the early development of kelp.

Our findings are also consistent with parallel recent bull kelp modeling work showing that kelp seeding alone was less effective than urchin culling or combined restoration under heatwave conditions (White et al., 2026). Together, these results suggest that bull kelp restoration may require management actions that directly reduce herbivore pressure, especially when systems have already shifted toward degraded or barren conditions.

The strong response to combined management likely reflects the interaction between bull kelp life history and the timing of management actions. Summer urchin removal reduced grazing pressure during the critical growing seasonal window, allowing seeded kelp recruits to establish more effectively. Because adult bull kelp die-back during winter, juvenile kelp experience reduced shading and competition during the following growing season. Therefore, seeded juveniles can take advantage of the rapid growth rates characteristic of bull kelp and potentially rebuild canopy biomass within a single growing season (Maxell & Miller, 1996; Pontier et al., 2024; Springer et al., 2006). This annual life cycle may allow bull kelp systems to respond rapidly to successful intervention, but only when recruitment and reduced grazing occur together.

These results also suggest that urchin removal may have even greater restoration potential in open kelp systems than in the closed-population scenario represented here. In natural systems, kelp populations may receive recruitment subsidies from nearby populations (Burnett et al., 2024). Under reduced grazing pressure, this external recruitment could function similarly to artificial kelp seeding by supplying new individuals to recovering habitat. Therefore, in areas with strong connectivity to existing kelp forests, urchin removal alone may produce stronger recovery than predicted by this closed-population model. Conversely, isolated kelp patches or regions with widespread canopy loss may require both grazing reduction and active recruitment enhancement.

Sea otter reintroduction increased kelp persistence by restoring top-down control over urchin populations. In this sense, sea otters acted as a form of passive or biological management by shifting the system toward a higher baseline level of kelp persistence relative to the no-otter scenario. This finding reinforces the broader ecological importance of predator recovery in kelp forest ecosystems, where predators can suppress herbivores and reduce the likelihood of transitions to urchin-dominated states (Burt et al., 2018; Hamilton et al., 2024; Hopf et al., 2025). However, in our model, sea otters did not eliminate the benefits of direct restoration. Management actions still increased kelp persistence under sea otter presence, although proportional gains were smaller because

otter predation had already improved baseline conditions. This result has important implications for restoration planning. Sea otter reintroduction may improve the ecological context in which restoration occurs, but it should not be treated as a complete substitute for targeted management. Instead, predator recovery and direct restoration may act as complementary tools. Sea otters can reduce background grazing pressure across time, whereas urchin removal and kelp seeding can provide targeted intervention during critical periods or in locations where kelp recovery remains limited.

Management duration and temporal strategy (i.e., continuous vs intermittent) also influenced restoration outcomes. Under continuous management, redistributing the same total effort across longer durations produced different effects depending on the management strategy. For single-action strategies, spreading effort across multiple years produced mostly additive responses, with relatively modest differences among one-, two-, and three-year interventions. In contrast, combined management became more effective when distributed across longer continuous management windows. The three-year combined strategy produced more durable and stronger increases in kelp persistence while requiring lower annual effort than the single-year strategy. This suggests that sustained, moderate combined intervention may be more effective than short, intensive intervention because repeated reductions in grazing pressure and repeated recruitment enhancement increase the probability that management overlaps and carryover management effects with favorable ecological conditions.

Intermittent management strategies produced similar qualitative patterns but differed in the timing and persistence of their effects. Because intermittent strategies included years without intervention, they created pulses of management pressure rather than sustained annual intervention. As a result, their initial effects were similar across scenarios, as we applied the same first-year effort, but their longer-term performance depended on the length of the gap between intervention years. Longer gaps reduced the continuity of grazing control and recruitment support, allowing the system more time to return toward degraded dynamics before the second intervention occurred. This explains why intermittent strategies produced weaker or less durable responses than continuous strategies when total management effort was otherwise comparable.

From a practical management perspective, this distinction is important. Continuous management may provide stronger ecological consistency, but intermittent management may better reflect real-world constraints such as funding cycles, diver availability, permitting, weather, and agency capacity. The results suggest that if management must be intermittent, combining urchin removal with kelp seeding is likely to provide more durable benefits than implementing either action alone. However, long gaps between interventions

may reduce effectiveness, especially in systems already close to collapse or dominated by high urchin grazing pressure.

Overall, the kelp results indicate that effective bull kelp restoration will likely require management strategies that reduce grazing pressure and enhance recruitment at the same time. Continuous combined management produced the most reliable and persistent improvements, but intermittent combined management also increased kelp persistence and may represent a realistic compromise when continuous intervention is not feasible. These findings support a restoration framework in which managers prioritize sustained or repeated combined actions, adjust intervention timing to seasonal kelp dynamics, and consider predator recovery as a complementary process that can improve baseline ecological conditions.

4.2. Dungeness crab fishery dynamics under sea otter reintroduction

Sea otters are known predators of Dungeness crabs in regions where both species overlap (Kenyon, 1969). In several areas where sea otters have recovered after historical extirpation, conflicts have emerged between sea otter expansion and nearshore invertebrate fisheries. In parts of Alaska, for example, local Dungeness crab landings declined after sea otter recovery, likely because legal-sized male crabs experienced both fishery harvest and sea otter predation (Garshelis et al., 1986; Pitcher & Imamura, 1990). These cases are especially relevant to Oregon because the Dungeness crab fishery is the state's most valuable commercial fishery and supports coastal economies, fishing communities, and regional identity (Richerson et al., 2020).

Our results suggest that sea otter reintroduction could substantially reduce fishable Dungeness crab density in habitats where sea otters and crabs overlap. Across all prey-switching scenarios, fishable crab densities declined relative to the no-otter baseline (**Figure 5**). However, this response was not temporally uniform and depended on ecological context. Simulations showed three broad phases: an initial decline, a partial intermediate recovery, and a later sustained decline. This pattern indicates that sea otter effects on fishable crabs are shaped by more than direct predation alone; they also depend on prey availability, prey-switching behavior, kelp forest condition, and internal crab population dynamics.

The initial decline in fishable crab density reflects the addition of sea otter predation as a new source of mortality. This outcome was expected because sea otters are efficient benthic predators and can consume adult crabs when they occur within otter foraging habitat (Garshelis et al., 1986). However, fishable crab density partially recovered between years 10 and 15. This recovery likely reflects compensatory dynamics within the crab

population. Dungeness crabs are strongly cannibalistic, and larger crabs can reduce the survival of younger cohorts through predation on recently settled individuals (Botsford, 1984; Botsford et al., 2019; Botsford & Hobbs, 1995; Botsford & Wickham, 1978). When sea otter predation reduced adult crab abundance, cannibalistic pressure on younger crabs also declined. This reduction in density-dependent mortality likely increased juvenile survival and produced larger cohorts that later recruited into the fishable population.

The later sustained decline suggests that this compensatory response did not fully offset sea otter predation through time. As simulations progressed, fishable crab densities declined more consistently, particularly after year 15. This pattern reflects a shift in the broader ecological context that influenced sea otter foraging allocation. During earlier periods, many simulations still retained kelp-dominated conditions, allowing sea otters to distribute predation across the full prey assemblage, including urchins, crabs, and the hypothetical alternative prey assemblage. However, as more simulations transitioned into degraded or barren states, the prey field available to sea otters became more restricted (A1.4. Predation on urchins:). Under barren conditions, exposed urchins became unavailable to predation because they entered a starvation state that made them less desirable to sea otters (Dean et al., 1984; Karatayev et al., 2021; Rogers-Bennett, 2013). At the same time, hiding urchins became increasingly scarce and were more likely to transition into the exposed state, further reducing their availability as prey. As a result, predation pressure became increasingly concentrated on the remaining prey groups, primarily crabs and prey X. Thus, sea otter foraging allocation depended not only on relative prey abundance, but also on the condition of the kelp forest ecosystem in which predation occurred.

Prey-switching behavior influenced the magnitude of crab decline, although differences among scenarios were modest (**Figure 5**). The scenario in which sea otters increased preference for more abundant prey produced the smallest reduction in fishable crab density. In contrast, the no-switching scenario and the scenario favoring less common prey produced larger declines in the fishable crab biomass. This pattern suggests that impacts on crabs may be lower when sea otters shift predation away from crabs as crab density declines. Conversely, when predation remains less responsive to prey abundance, or when predators maintain pressure on rarer prey, crabs experience stronger long-term reductions.

These results highlight the importance of prey-switching uncertainty in predicting fishery outcomes after sea otter reintroduction. Sea otters are generalist predators with flexible diets, and their effects on prey populations can vary across habitats, prey communities, and individual foraging specializations (Boustany et al., 2021; Laidre & Jameson, 2006; Smith et al., 2025; Tinker et al., 2008). Therefore, the impact of sea otters on Dungeness

crabs in Oregon will likely depend on the relative availability of alternative prey, the condition of kelp forests, and the degree to which individual otters specialize on crabs or other prey.

The interaction between kelp condition and crab predation is especially important. Our results suggest that healthier kelp forest states may buffer crab predation by maintaining a broader and more diverse prey base for sea otters. In kelp-dominated systems, otters can distribute feeding effort among urchins, crabs, and other prey. In degraded or barren states, the available prey base may narrow, increasing the relative exposure of crabs to predation. Therefore, kelp restoration and crab fishery outcomes should not be viewed as independent management issues. Actions that maintain productive kelp forests may also influence how sea otter predation is distributed across prey groups.

However, these results apply most directly to areas where Dungeness crabs, kelp forests, and sea otter foraging habitat occur within the same spatial units. This overlap is not representative of the broader Oregon nearshore ecosystem, where much of the commercial Dungeness crab fishery occurs offshore, over soft-sediment habitats with limited spatial overlap with rocky kelp forests and potential sea otter foraging grounds (Kone et al., 2021). Sea otters are capable swimmers, but they typically forage within localized nearshore areas associated with suitable habitat rather than distributing predation evenly across the entire coastal fishery landscape (Bodkin, 2015; Kenyon, 1969; Smith et al., 2025). As a result, sea otter predation may strongly affect crabs in localized kelp-associated habitats while producing weaker effects at the broader scale of the Oregon fishery.

This distinction between local ecological effects and coastwide fishery outcomes is central for interpreting the management implications of sea otter reintroduction. In areas where sea otters, kelp habitat, and Dungeness crabs overlap, fishable crab densities may decline substantially, as our findings suggest. However, the broader fishery may be buffered by spatial separation between major crab fishing grounds and sea otter foraging habitat. Therefore, the model results are best interpreted as a localized estimate of potential crab exposure under strong habitat overlap, rather than as a direct forecast of Oregon-wide fishery losses.

Overall, the crab results illustrate the ecological tradeoffs associated with sea otter reintroduction. Sea otters can increase kelp persistence by reducing urchin grazing pressure, but they may also reduce local availability of fishable Dungeness crabs. These effects are not contradictory; rather, they reflect the role of sea otters as generalist predators that restructure nearshore food webs. From a management perspective, this means that sea otter reintroduction should be evaluated not only as a kelp restoration tool,

but also as a socioecological intervention with uneven benefits and costs across habitats, species, and stakeholder groups.

5. Conclusion

We used a minimal-realistic multispecies model to evaluate how sea urchin removal, kelp seeding, and sea otter reintroduction could influence bull kelp persistence and fishable Dungeness crab density in Oregon nearshore ecosystems. The results show that bull kelp persistence depends strongly on reducing grazing pressure from sea urchins and that management strategies are most effective when applied together.

Kelp seeding alone produced only small improvements in kelp persistence, suggesting that adding recruits is unlikely to restore bull kelp forests when grazing pressure remains high. Urchin removal produced stronger effects, but the greatest and most consistent increases in kelp persistence occurred when urchin removal and kelp seeding were combined. These combined actions generated synergistic responses, increased the probability of kelp persistence, and promoted recovery from barren states back to kelp-dominated conditions. Continuous combined management produced the most durable outcomes, although intermittent combined management also improved kelp persistence and may represent a practical compromise when continuous intervention is not feasible.

Sea otter reintroduction increased kelp persistence by restoring top-down control over sea urchins, thereby shifting the system toward a higher ecological baseline. However, sea otters did not replace the need for direct restoration. Instead, predator recovery and active management acted as complementary pathways: sea otters reduced background grazing pressure, while urchin removal and kelp seeding provided targeted intervention during critical periods of kelp establishment.

At the same time, sea otter reintroduction created tradeoffs for fishable Dungeness crabs. Across prey-switching scenarios, sea otter predation reduced fishable crab density, reflecting the likely cases where crabs could overlap with sea otter foraging areas. These reductions were strongest over longer time horizons and depended on prey availability, prey-switching behavior, kelp forest condition, and internal crab population dynamics. However, these modeled effects should be interpreted as localized impacts within kelp-associated habitats rather than direct predictions of coastwide fishery collapse.

Overall, this study highlights the need to evaluate kelp restoration, predator recovery, and fisheries management as interconnected components of Oregon's nearshore ecosystem. Effective management will likely require strategies that combine active restoration with

ecological context, recognize spatial variation in stakeholder impacts, and account for the tradeoffs generated by recovering predators in human-used seascapes.

Appendices

A1. Urchin Population Model.

As we are including urchin feeding behavior switching between standing kelp and drift kelp, we chose a stage-based matrix model for the kelp-urchin sub-model, which easily allows attribution of different demographic rates to different life-history or behavioral stages. Following a stage-based matrix approach (Caswell, 2001), the biomass density of urchins in the next time-step ($\mathbf{U}_{t+1}$) is a product of the biomass of urchins in the current time step ($\boldsymbol{U}_{J,t}, \boldsymbol{U}_{H,t}, \boldsymbol{U}_{E,t}$) and the transition matrix ($\mathbf{M}_{\mathbf{U,t}}$), plus recruits ($\boldsymbol{R}_{\boldsymbol{U,t}}$), such that

$$\mathbf{U}_{t+1} = \mathrm{M}_{\mathrm{U,t}} * \begin{bmatrix} \boldsymbol{U}_{J,t} \\ \boldsymbol{U}_{H,t} \\ \boldsymbol{U}_{E,t} \end{bmatrix} + \begin{bmatrix} R_{U,t} \\ 0 \\ 0 \end{bmatrix},$$

where ***J***, ***H***, and ***E*** are the urchin life-stages: juveniles, hiding adults, and exposed adults, respectively.

A1.1. Urchin recruitment:

For urchins, we assume open-patch dynamics, representing the case that the urchin patch is a portion of a larger population. This is a fair assumption at the scale of our model (1 ha), as urchins have long larval durations and dispersals (Groth, 2024; Kinlan & Gaines, 2003). Urchin recruitment varies seasonally, with 20% of recruitment settling on winter, 20% on spring, 50% on summer, and 10% on autumn, and with interannual variation (Okamoto et al., 2020). Therefore, the biomass of incoming urchin recruits ($\boldsymbol{R}_{\boldsymbol{U,t}}$) is:

$$\boldsymbol{R}_{\boldsymbol{U,t}} = lognorm\left(\overline{R_U}, \sigma_{RU}\right) \theta_{U,t} \left(s_J\right)^{\tau},$$

where $\overline{\boldsymbol{R}_{\boldsymbol{U}}}$ is the yearly mean biomass and $\boldsymbol{\sigma}_{\boldsymbol{RU}}$ is the yearly variance of incoming urchin recruits, and $\boldsymbol{\theta}_{\boldsymbol{U,t}}$ is the timing function for urchin recruitment, hence capturing seasonal variation. Note that each year in the model, the total yearly recruit biomass is drawn from a lognormal distribution, and $\boldsymbol{\theta}_{\boldsymbol{U,t}}$ distributes this recruitment proportionally over the seasons and sums to one each year. A lognormal distribution best fits the recruitment patterns observed for Oregon, reflecting the infrequent but large urchin recruitment pulses of this region (Okamoto et al., 2020; Tegner & Dayton, 1981).

A1.2. Urchin transition matrix:

The stage transition matrix ($\mathbf{M}_{\mathbf{U}}$) in time steps t for urchins is:

$$\mathbf{M_{U,t}} = \begin{matrix} \\ juvenile \\ hiding \\ exposed \end{matrix} \begin{matrix} \begin{matrix} juvenile & hiding & exposed \end{matrix} \\ \begin{bmatrix} (1-g_U)\,s_J & 0 & 0 \\ g_U\,s_H\,(1-\Phi_t) & s_H\,(1-\Phi_t) & s_H\,(1-\Phi_t) \\ g_U\,s_E\,\Phi_t & s_E\,\Phi_t & s_E\,\Phi_t \end{bmatrix} \end{matrix},$$

where $\boldsymbol{g_U}$ is the proportion of juvenile biomass maturing to adults in a season, $\boldsymbol{s_i}$ is the proportion of stage i (juvenile, hiding adult, exposed adult) surviving the season, and $\boldsymbol{\Phi_t}$ (*uppercase Phi*) is the proportion of exposed urchin biomass grazing on standing kelp in a given season (t), also known as the grazing behavior switching function. We explain these parameters further in the following sections.

A1.3. Urchin growth and maturation:

$$\boldsymbol{g_U} = \frac{1}{(4 * g_{mat})},$$

reflecting the probability that a juvenile will mature that season given the average age of urchin maturation ($\boldsymbol{g_{mat}}$).

Urchin survival ($\boldsymbol{s_i}$) is a function of the natural instantaneous mortality rates ($\boldsymbol{M_i}$) for the three stages: juveniles ($\boldsymbol{J}$), hiding adults ($\boldsymbol{H}$), and exposed adults ($\boldsymbol{E}$):

$$\boldsymbol{s_i}\begin{cases} \boldsymbol{s_J} = e^{-M_J} \\ \boldsymbol{s_C} = e^{-M_H} \\ \boldsymbol{s_E} = e^{-M_E} \end{cases}.$$

A1.4. Predation on urchins:

In previous versions of this model, predation was treated as a seasonal mortality rate incorporated directly into the survival terms ($\boldsymbol{s_i}$) described above (see: Hopf, et al., (2025) and White et al., (2026). However, in this iteration and to represent more realistic predator-prey dynamics, predation was implemented as a daily process (inside each season) that reduces biomass in daily timestep ($\boldsymbol{tt}$), through a Type II functional response and a Yodzis prey switching function (Koen-Alonso & Yodzis, 2005). This process is therefore implemented outside the projection matrix. This also means that we use start of the season prey biomasses and the result of the predation inner loop goes into the seasonal processes.

For sea urchins (prey $\boldsymbol{S}$), the total available biomass available for predation is:

$$\boldsymbol{S_{t,tt}} = U_{H,t,tt} + U_{E,t,tt},$$

where $\boldsymbol{u_{H,t,tt}}$ and $\boldsymbol{u_{E,t,tt}}$ are the biomasses of adult hiding ($\boldsymbol{H}$) and adult exposed ($\boldsymbol{E}$) urchins during season $\boldsymbol{t}$ and at day $\boldsymbol{tt}$, respectively.

Predator relative preference was represented using a modified Yodzis switching functional response (Randell et al., 2025), which describes how sea otters adjusts their feeding preference among sea urchins (prey $\boldsymbol{S}$), Dungeness crabs (prey $\boldsymbol{A}$), and an alternative source of prey (prey $\boldsymbol{X}$), depending on their relative abundances:

$$\boldsymbol{p_{S,t,tt}} = \frac{w_u S_{t,tt}^{\phi}}{w_u S_{t,tt}^{\phi} + w_c A_{t,tt}^{\phi} + (1 - w_u - w_c) X_{t,tt}^{\phi}},$$

where $\boldsymbol{p_{S,t,tt}}$ (*lowercase p*) is the fraction of otter's total feeding effort allocated to urchins ($\boldsymbol{S_{t,tt}}$) at a giving daily time step. $\boldsymbol{A_{t,tt}}$ and $\boldsymbol{X_{t,tt}}$ represent the biomass of the other prey *Note: prey X is a constant biomass set to represent anything else that might be in a kelp forest that could be part of the sea otters' diet (e.g., abalone, clams, mussels, snails, etc.)*. The intrinsic preference ($\boldsymbol{w_i}$), or preference when prey are at equal abundances, are specific to each prey: crabs ➡ $\boldsymbol{w_c}$ urchins ➡ $\boldsymbol{w_u}$, and prey X ➡ $1 - \boldsymbol{w_c} - \boldsymbol{w_u}$. Lastly, $\boldsymbol{\phi}$ (*lowercase phi*) controls the strength of switching, introducing density-dependent predation because preference changes with the relative abundance of prey types. *Note: The same $p_{S,t,tt}$ term is applied to both hiding and exposed urchins*.

The feeding rates $\boldsymbol{P_{i,t,tt}}$ (*uppercase P*) on urchin biomass ($\boldsymbol{S}$) follows a Type II functional response that includes the fraction of otter's total feeding effort allocated to urchins ($\boldsymbol{p_{S,t,tt}}$) implemented separately for hiding ($\boldsymbol{H}$) and exposed ($\boldsymbol{E}$) adults through the functions:

$$\boldsymbol{P_{H,t,tt}} = e^{\left(-\frac{a_{1,H,t} * p_{S,t,tt}}{1 + \frac{1}{b_{1,H,t}}(a_{1,H,t} * p_{S,t,tt})\, S_{t,tt}} N_t\right)},$$

$$\boldsymbol{P_{E,t,tt}} = e^{\left(-\Psi_t\left(\frac{a_{1,E,t} * p_{S,t,tt}}{1 + \frac{1}{b_{1,E,t}}(a_{1,E,t} * p_{S,t,tt})\, S_{t,tt}} N_t\right)\right)},$$

where $\boldsymbol{N_t}$ is predator density; $\boldsymbol{a_{1,i,t}}$ is the per kg mortality of urchins, stage $\boldsymbol{i}$ (hiding or exposed), due to predation, in the absence of conspecifics (*search/attack rate*), $\boldsymbol{b_{1,i,t}}$ is the max kg of urchins, stage $\boldsymbol{i}$ (hiding or exposed), consumed by a kilogram of predator, in a time step (*1/handling time*). *Note: both $a_{1,i,t}$ and $b_{1,i,t}$ account for the fact that hiding urchins are relative harder to capture than exposed urchins (see* ***Error! Reference source not found.*** *for details)*.

The binary switch $\boldsymbol{\Psi_t}$ (Psi) controls whether exposed urchins are vulnerable to predation. In the current version of the model $\Psi_t = 1$ or $\Psi_t = 0$, this is controlled by the availability of kelp in the system, essentially regulating whether the model is on a kelp state ($\Psi_t = 1$) or barren state ($\Psi_t = 0$) in which predation of exposed urchins by sea otters gets turned off.

Therefore Ψ_t is a function in which if for 2 seasons kelp biomass is bellow a specific threshold ($k_{\min}$) then $\Psi_t = 0$. Furthermore, we included a rule in which for those simulations where $\Psi_t = 0$ (aka: barren state) the intrinsic preference of sea otters on all prey items changes from the defaults to $w_u = 0.1$ and $w_c = 0.75$, to account for feeding efforts being reallocated.

This multiplier ($\boldsymbol{P_{i,t,tt}}$) then updates the biomasses of urchin stages in a daily basis (daily predation):

$$\mathbf{U_{i,t,tt+1}} \begin{cases} U_{J,t,tt+1} = U_{J,t,tt} & ,juveniles \\ U_{H,t,tt+1} = U_{H,t,tt}\, P_{H,t,tt} & ,hiding \\ U_{E,t,tt+1} = U_{E,t,tt}\, P_{E,t,tt} & ,exposed \end{cases},$$

and at the end of the daily predation loop ($tt = 91$), we get the post-predation biomasses which are the biomasses of urchins that survived predation on that specific season:

$$\mathbf{U}_{\boldsymbol{i,t}}^{\boldsymbol{post_pred}} = U_{i,t,tt=91}\,,$$

these post-predation biomasses are then used in the projection matrix (see above) for the remaining seasonal demographic processes.

A1.5. Urchin grazing behavioral switching:

The urchin behavioral grazing switch function ($\boldsymbol{\Phi_t}$) captures the shift between hiding urchins grazing on drift kelp, to being exposed and actively grazing on standing kelp when drift resources are relatively low (Ebeling et al., 1985; Kriegisch et al., 2019; Randell, 2022; Randell et al., 2025; Rennick et al., 2022).

Following (Randell, 2022), the proportion of adult urchins that are exposed and grazing on standing kelp is modelled as a declining function of drift availability relative to grazing demand. In this model, drift availability is normalized by total urchin consumptive capacity through the grazing-capacity ($\boldsymbol{GC_t}$) ratio:

$$\boldsymbol{GC_t} = \frac{\overbrace{\widetilde{k_{D,t}}}^{drift\ kelp\ density}}{\underbrace{\left(U_{H,t}^{\text{post_pred}} + U_{E,t}^{\text{post_pred}}\right)^{b_{2,i,j,t}}}_{urchin\ consumptive\ capacity}},$$

and the proportion of exposed urchins grazing on standing kelp us then given by:

$$\boldsymbol{\Phi_t} = e^{(-v_1 {GC_t}^{v_2})}\,,$$

where $\boldsymbol{GC_t}$ represents the ratio of drift kelp supply to total urchin grazing capacity, $\boldsymbol{b_{2,i,j,t}}$ is the max kg of kelp stage i consumed by an urchin, stage j, in a time step (1/handling time).

*Note: in practice $b_{2,i,j,t}$ is scaled to the seasonal level into a variable called **hij** this is only done in MATLAB for coding reasons*.

The parameters $\boldsymbol{v_1}$ and $\boldsymbol{v_2}$ are derived from the more interpretable quantities $\boldsymbol{w_1}$ and $\boldsymbol{w_2}$ (slope around inflection point of behavior switching function), which controls the location and steepness of the behavioral switch (**Figure 6**). Specifically,

$$\boldsymbol{v_1} = \frac{v_2 - 1}{v_2 w_1{}^{v_2}} \text{ and } (\boldsymbol{v_2} - 1)e^{\frac{1-v_2}{v_2}} = w_2 w_1 .$$

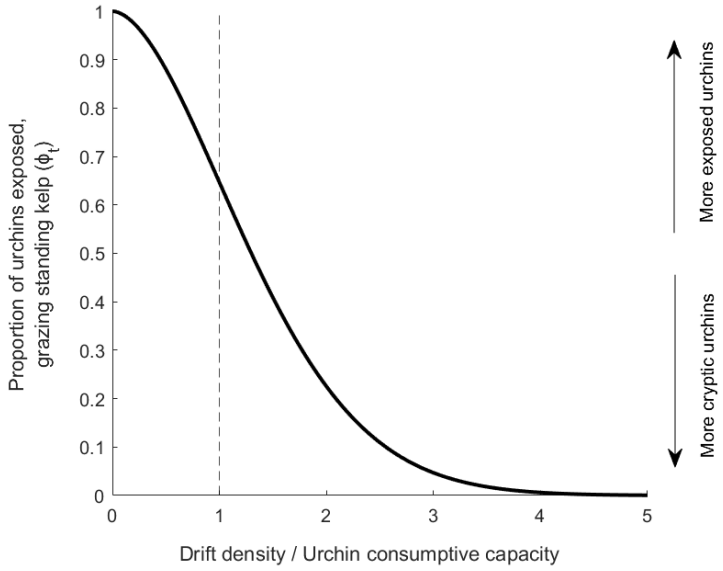


Figure 6. Urchin behavioral feeding switch function ($\boldsymbol{\Phi_t}$). As the availability of drift kelp to urchin consumptive capacity (biomass of urchins x urchin grazing rate) decreases (left-to-right along the x-axis) more urchins shift to grazing standing kelp. The rate of change of this shift is determined by the slope of the curve ($\boldsymbol{w_2}$), here $\boldsymbol{w_2} = 0.5$.

A2. Bull-Kelp Population Model.

Following a stage-based matrix approach, the biomass density of kelp in the next time-step ($\mathbf{K}_{t+1}$) is the product of the current three stages of kelp biomass ($\boldsymbol{K_{J,t}}$, $\boldsymbol{K_{A,t}}$, $\boldsymbol{K_{D,t}}$) and the transition matrix ($\mathbf{M_{K,t}}$), plus the newly arrived juveniles ($\boldsymbol{J_{K,t}}$), such that

$$\mathbf{K_{t+1}} = \mathrm{M_{K,t}} * \begin{bmatrix} \boldsymbol{K_{J,t}} \\ \boldsymbol{K_{A,t}} \\ \boldsymbol{K_{D,t}} \end{bmatrix} + \begin{bmatrix} J_{K,t} \\ 0 \\ 0 \end{bmatrix}.$$

Bull kelp in Oregon release zoospores during summer and autumn before mass sporophyte dieback in winter (Maxell & Miller, 1996; Springer et al., 2006). Fertilized eggs then grow into juvenile sporophytes the following spring (Amsler & Neushul, 1989). Mathematically, this requires recruitment in a given time-step to be a function of adult biomass density 2-3 time-steps prior. To capture this lag correctly, the total biomass density of recruiting juvenile sporophytes ($\boldsymbol{J_{K,t}}$) must exist outside the transition matrix and associated matrix multiplication. We will first describe the transitions matrix ($\mathbf{M_{K,t}}$), before detailing with $\boldsymbol{J_{K,t}}$.

A2.1. Kelp transition matrix:

The stage transition matrix ($\mathbf{M_K}$) in time steps *t* for bull kelp is:

$$\mathbf{M_{K,t}} = \begin{array}{c} \\ juvs \\ adult \\ drift \end{array} \begin{array}{c} \begin{array}{ccc} juvs & adult & drift \end{array} \\ \begin{bmatrix} 0 & 0 & 0 \\ r_S\, g_K\, (1-c)\, K_{A,E}\, \gamma & r_S\, g_K\, (1-c)\, K_{A,E}\, \gamma & 0 \\ c\, r_D\, K_{D,H} & c\, r_D\, K_{D,H} & (1-d)\, r_D\, K_{D,H} \end{bmatrix} \end{array}.$$

Reflecting fast maturation rates (on the order of months; (Schiel & Foster, 2015)), we assumed that juvenile sporophytes become adults, or contribute to drift, in the next season. Adult sporophyte growth over time is captured through $\boldsymbol{g_K}$, the seasonal increase in standing kelp biomass, and $\boldsymbol{\gamma}$, the relative change in standing (juvenile and adult) kelp growth over the seasons.

Non-grazing loss of standing kelp biomass is captured in two terms: $\boldsymbol{c}$, proportion of juvenile and adult standing kelp biomass converted to drift kelp in a time step, and $\boldsymbol{r_S}$, the proportion of non-grazed standing kelp biomass that survives the season. $\boldsymbol{r_S}$ accounts for storm and wave damage, senescing blade material, boat propeller damage, and dissolved material released from blades and stipes (Rassweiler et al., 2021). Drift kelp biomass is either lost through decomposition ($\boldsymbol{d}$) or removed from the system via processes such as transportation through wave action or storm events, where $\boldsymbol{r_D}$ is proportion of non-decomposed drift biomass retained in system.

We assumed a Type-II grazing functional response for standing and drift kelp by urchins, following Randell, (2022a)). This is reasonable given that, like most herbivores following a Type-II saturating function, urchins require handling time between kelps stipes (Boada et al., 2017). $\boldsymbol{K_{i,j}}$ is the proportion of kelp stage i (juvenile, adult, or drift), grazed by urchins' stage j (juvenile, hiding adult, exposed adult), such that:

$$\boldsymbol{K_{i,j}} = e^{-\Omega_{i,j}},$$

where the instantaneous rate of grazing $\boldsymbol{\Omega_{i,j}}$ of kelp stage i, by urchins' stage j, is a per-kilogram Type-II response:

$$\boldsymbol{\Omega_{i,j}} = \frac{a_{2,i,j,t}}{1+\frac{1}{b_{2,i,j,t}} a_{2,i,j,t}\, k_{i,t}}\, U_{j,t}\,.$$

$\boldsymbol{a_{2,i,j,t}}$ is the per kilogram kelp mortality due to grazing by a kilogram of urchins in the absence of conspecifics (search/attack rate), and $\boldsymbol{b_{2,i,j,t}}$ is the asymptotic (max) biomass of prey consumed by an urchin in a time step (1/handling and ingestion time), in season t. This assumes that there is no effect of increasing urchin densities (Rennick et al., 2022).

Note: exposed urchins graze on recruits and standing kelp, and hiding urchins only graze on drift:

$$\boldsymbol{a_2} = \begin{matrix} \\ juvs \\ adult \\ drift \end{matrix} \begin{matrix} \begin{matrix} cryptic & exposed \end{matrix} \\ \begin{bmatrix} 0 & a_{2,J,E,t} \\ 0 & a_{2,A,E,t} \\ a_{2,D,C,t} & 0 \end{bmatrix} \end{matrix} \qquad \boldsymbol{b_{2,t}} = \begin{matrix} \\ juvs \\ adult \\ drift \end{matrix} \begin{matrix} \begin{matrix} cryptic & exposed \end{matrix} \\ \begin{bmatrix} 0 & b_{2,J,E,t} \\ 0 & b_{2,A,E,t} \\ b_{2,D,C,t} & 0 \end{bmatrix} \end{matrix}.$$

A2.2. Kelp recruitment (sporophytes):

The total biomass density of recruiting juvenile sporophytes, $\boldsymbol{J_{K,t}}$ captures all processes between spore release, recruitment of settled juvenile sporophytes, and survival through their first season.

$$\boldsymbol{J_{K,t}} = R_{K,t}\, s_{Y,t}\, \gamma\, r_S\, K_{Y,E}\,.$$

We break this down as follows:

a) Settling microscopic sporophytes:

As bull kelp spores have short dispersal distances (generally <1 km; (Gaylord et al., 2002; Reed et al., 2004; Schiel & Foster, 2015)), we assume closed-patch dynamics, where the total incoming biomass density of settling microscopic sporophytes at time t ($\boldsymbol{R_{K,t}}$) is a function of local adult standing kelp biomass densities 2-3 seasons prior (as per the lag in zoospore release to settling sporophytes). Since 90% of adults release

zoospores in the autumn, with the rest releasing in the summer (Maxell & Miller, 1996), we weight the contribution of adults in those timesteps accordingly. Note that ($\boldsymbol{R_K}$) includes zoospore production, survival and development through the gametophyte phase, successful fertilization, and settlement survival, and interannual variation in settlement, where $\overline{\boldsymbol{R_K}}$ is yearly mean biomass and $\boldsymbol{\sigma_{RK}}$ is the yearly variance of in settling sporophytes. Therefore:

$$\boldsymbol{R_{K,t}} = \ norm\left(\overline{R_K}, \sigma_{RK}\right) \theta_{K,t} \ (0.9k_{A,t-2} + 0.1k_{A,t-3}) \ .$$

To capture spring settlement of new sporophytes, $\boldsymbol{\theta_{K,t}}$ (the kelp recruitment timing function), is set to zero in summer, autumn and winter, and **one** in spring, as all recruitment settlement happens in spring.

b) Density dependent survival of settle sporophytes:

Incoming kelp recruits compete for space among themselves and are also negatively affected by shading of older standing adult kelp biomass that survived the winter storms (Nisbet & Bence, 1989; Reed, 1990; Stewart et al., 2009). As such, we used a combined Ricker and Beverton-Holt function, that captures both inter- and intra-cohort density dependent effects (C. White, 2009). Per biomass recruit survival ($\boldsymbol{s_Y}$) is therefore:

$$\bar{\boldsymbol{s}}_{\boldsymbol{Y,t}} = \ \frac{(D-1)\ K_{A,t}\ e^{\beta_{RK}\ D\ K_{A,t}}}{D\ Y_t\ e^{\beta_{RK}\ D\ K_{A,t}} + e^{\beta_{RK}\ K_{A,t}}\ ((D-1)\ K_{A,t} - D\ Y_t)} \ ,$$

where $\boldsymbol{\beta}$ is the strength of density dependence and $\boldsymbol{D}$ is the relative strength of inter- versus intra-cohort density-dependent processes ($0 < \boldsymbol{D} < 1$). As D is unquantifiable, we set D as relatively high ($D = 0.9$) reflecting that majority of density dependent as competition among recruits given the very low adult survival rates over winter and into the recruiting period (spring) (Maxell & Miller, 1996; Springer et al., 2006). Note that, in a similar model, Hopf, et al., (2025) previously demonstrated that kelp forest responses were not overly sensitive to the value of *D*.

Since kelp dynamics occur at a smaller scale than our 1 ha model domain (i.e., at the local transect scale), we approximated the model landscape scale density dependent survival following J. W. White, (2011) as:

$$\boldsymbol{s_{Y,t}} \approx \ \bar{s}_{Y,t} + 0.5\ \bar{s}"_{Y,t} + var(k_{A,t}) \ ,$$

where $\boldsymbol{var\left(K_{A,t}\right)}$ is the spatial variance in the density of adult standing kelp across the model unit space.

c) Survival and grazing of recruited sporophytes:

Juveniles are considered standing kelp and are, therefore, grazed by urchins and contribute to the production of drift.

A3. Dungeness Crab Population Model

In contrast to kelp and urchins where we used a stage-based matrix approach, here we followed an age-based matrix approach to better represent the life history of Dungeness crabs, in which different cohorts of crabs have different sizes, traits, and characteristics as they age, furthermore, certain processes (e.g., fishing) are age specific. We modelled two densities of Dungeness crabs, one for females and one for males. This was done to account for the sex-age fishery management strategy in which only male crabs of certain size (age) are harvested during the open season. Therefore, the density of female crabs in the next time-step ($\mathbf{FC}_{t+1}$) is the product of the current eleven female age classes ($Fc_{0,t}$, $Fc_{1,t}$, $Fc_{2,t}$, $Fc_{3,t}$, $Fc_{4,t}$, [...], $Fc_{10,t}$), and the transition matrix ($\mathbf{M}_{\mathbf{CF,t}}$) plus one half of the newly arrived age-0 ($\boldsymbol{R}_{C,t}$) individuals. And the density of male crabs in the next time-step ($\mathbf{MC}_{t+1}$) the product of the current eleven male age classes ($Mc_{0,t}$, $Mc_{1,t}$, $Mc_{2,t}$, $Mc_{3,t}$, $Mc_{4,t}$, [...], $Mc_{10,t}$), and the transition matrix ($\mathbf{M}_{\mathbf{CM,t}}$), plus the other half of the newly arrived age-0 ($\boldsymbol{R}_{C,t}$) individuals such that

$$\mathbf{FC}_{t+1} = \mathbf{M}_{\mathbf{CF,t}} * \begin{bmatrix} Fc_{0,t} \\ Fc_{1,t} \\ Fc_{2,t} \\ Fc_{3,t} \\ Fc_{4,t} \\ \vdots \\ Fc_{10,t} \end{bmatrix} + \begin{bmatrix} R_{C,t} * 0.5 \\ 0 \\ 0 \end{bmatrix} \quad \& \quad \mathbf{MC}_{t+1} = \mathbf{M}_{\mathbf{CM,t}} * \begin{bmatrix} Mc_{0,t} \\ Mc_{1,t} \\ Mc_{2,t} \\ Mc_{3,t} \\ Mc_{4,t} \\ \vdots \\ Mc_{10,t} \end{bmatrix} + \begin{bmatrix} R_{C,t} * 0.5 \\ 0 \\ 0 \end{bmatrix},$$

The key differences between all ages and the two sexes are:

Female Dungeness crab ($\mathbf{FC}_i$)			**Male Dungeness crab ($\mathbf{MC}_i$)**		
$Fc_{0,t}$	Age-0/recruit	- Cannibalized - Non-preyed	$Mc_{0,t}$	Age-o/recruit	- Cannibalized - Non-preyed
$Fc_{1,t}$	Juvenile	- Not cannibalized - Non-preyed	$Mc_{1,t}$	Juvenile	- Not cannibalized - Non-preyed
$Fc_{2,t}$	Adult	- Not cannibalized - Preyed	$Mc_{2,t}$	Adult	- Not cannibalized - Preyed
$Fc_{3,t}$			$Mc_{3,t}$		
$Fc_{4,t}$			$Mc_{4,t}$		- Not cannibalized - Preyed **- Harvested by fishery**
$Fc_{5,t}$			$Mc_{5,t}$		
$Fc_{6,t}$			$Mc_{6,t}$		
$Fc_{7,t}$			$Mc_{7,t}$		
$Fc_{8,t}$			$Mc_{8,t}$		
$Fc_{9,t}$			$Mc_{9,t}$		
$Fc_{10,t}$			$Mc_{10,t}$		

Note: Unlike the kelp urchin sub-model where densities are expressed in biomass (kg ha $^{-1}$), this Dungeness crab sub-model tracks crab age classes in crabs ha $^{-1}$ densities. However, these densities are transformed into biomasses using age-weight specific vectors for the predation inner loop and transformed back again into crabs ha $^{-1}$ for the other processes outside the predation inner loop.

A3.1. Crab age-0 arrival (recruitment):

For crabs, we assume open patch dynamics, representing the case that the crab patch is a fraction of a much larger population. The reasoning behind this logic is fair, as crab recruitment dynamics happen both at the regional and local scale, with most recruits input at the local scale coming from other populations. Furthermore, we are assuming this crab patch to be adjacent (very close) to our kelp forest spatial domain, this is to make sea otter predation on crabs plausible. Dungeness crab habitat and kelp forests (domain in which our sea otters exist) do not overlap much in Oregon, therefore our simulated crab patch represents the border portion of a much larger crab population that is close enough to our kelp forest hectare. Arrival of newly settled age-0 crabs occur through spring and summer. Therefore, the density of incoming age-0 crabs ($\boldsymbol{R_{C,t}}$) is:

$$\boldsymbol{R_{C,t}} = \left(lognorm\left(\overline{R_C}, \sigma_{RC}\right) \theta_{C,t}\right) * \ e^{-\beta\ (\sum(NCIF(Fc_{1-10,t} + Mc_{1-10,t})))}\ ,$$

where $\overline{\boldsymbol{R_C}}$ is the yearly mean number of age-0 crabs, $\boldsymbol{\sigma_{RC}}$ is the yearly variance of incoming age-0 crabs, and $\boldsymbol{\theta_{C,t}}$ is the timing function for age-0 arrival (capturing seasonal variation). Note that each year in the model, the total yearly number of age-0 arrivals is drawn from a lognormal distribution, and $\boldsymbol{\theta_{C,t}}$ distributes this proportionally over the seasons and sums to one each year. A lognormal distribution alongside our other parameters approximations best fits the ~10 year cyclic patterns observed for Dungeness crab recruitment (Higgins et al., 1997; Rasmuson, 2013), reflecting the large pulses in crab recruitment observed in Oregon.

Additionally, age-0 crabs experience cannibalism by all older age classes. Where, $\boldsymbol{\beta}$ is the cannibalism intensity coefficient, set to achieve the general demographic patterns and age distributions observed in crab populations; and $\boldsymbol{NCIF}$ is the normalize influence function for cannibalism per age class, where older age classes have a stronger influence in cannibalism due to larger body sizes (Botsford et al., 2019).

A3.2. Crab transition matrix:

The age transition matrix ($\mathbf{M_{Ci,t}}$) in time steps t for female (F) crabs is:

$$\mathbf{M_{CF,t}} = \begin{array}{c} \\ age0 \\ age1 \\ age2 \\ age3 \\ age4 \\ age5 \\ age6 \\ age7 \\ age8 \\ age9 \\ age10 \end{array} \begin{array}{c} \begin{array}{ccccccccccc} 0 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 & 9 & 10 \end{array} \\ \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ s_{f,R} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_{f,J} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_{f,A} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & s_{f,A} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_{f,A} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_{f,A} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_{f,A} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{f,A} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{f,A} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_{f,A} & 0 \end{bmatrix} \end{array},$$

where $\boldsymbol{s_{f,i}}$ is the proportion of female crabs i (R = age-0, J = age-1, A = ages-2-10) surviving and aging into the next group.

The age transition matrix ($\mathbf{M_{Ci,t}}$) in time steps t for female (M) crabs is:

$$\mathbf{M_{CM,t}} =$$

	0	1	2	3	4	5	6	7	8	9	10
$age0$	0	0	0	0	0	0	0	0	0	0	0
$age1$	$s_{m,R}$	0	0	0	0	0	0	0	0	0	0
$age2$	0	$s_{m,J}$	0	0	0	0	0	0	0	0	0
$age3$	0	0	$s_{m,A}$	0	-0	0	0	0	0	0	0
$age4$	0	0	0	$s_{m,A}$	0	0	0	0	0	0	0
$age5$	0	0	0	0	$s_{m,A2}$	0	0	0	0	0	0
$age6$	0	0	0	0	0	$s_{m,A2}$	0	0	0	0	0
$age7$	0	0	0	0	0	0	$s_{m,A2}$	0	0	0	0
$age8$	0	0	0	0	0	0	0	$s_{m,A2}$	0	0	0
$age9$	0	0	0	0	0	0	0	0	$s_{m,A2}$	0	0
$age10$	0	0	0	0	0	0	0	0	0	$s_{m,A2}$	0

,

where $\boldsymbol{s_{m,i}}$ is the proportion of male crabs i (R = age-0, J = age-1, A = ages-2-3, $A2$ = ages-4-10) surviving and aging into the next group.

Note: in this document both crab's transition matrices have been simplified to 11x11 dimensions, reflecting the eleven annual age classes described on the state variables section. However, in practice this matrix is 44x44, this is because the time steps in our model are at the seasonal scale (four timesteps per year); therefore, for every age class to move into the next one (age-0 to age-1), it has to go through four seasons. Therefore, in order to account for crabs aging seasonally through annual ages, we had to create seasonal cohorts, which allowed us to capture this more realistic dynamics. Hence, in practice this matrix is 44x44 where every four rows corresponded to a specific age class per season, but due to spatial constraints and simplicity here we are simplifying the model back to the 11 annual age classes.

Dungeness crab survival ($\boldsymbol{s_{i,i}}$) is a function of the natural instantaneous mortality rates ($\boldsymbol{M_i}$) for all age classes (age 0-10), and the fishing mortality rates ($\boldsymbol{F_{i,t}}$) for the applicable sex-age classes, such that:

$$s_{f,i}\begin{cases} s_{f,R} = e^{-M_{RC}}, age0 \\ s_{f,J} = e^{-M_{JC}}, age1 \\ s_{f,A} = e^{-M_{AC}}, age2-10 \end{cases},$$

and

$$s_{m,i}\begin{cases} s_{m,R} = e^{-M_{RC}}, age0 \\ s_{m,J} = e^{-M_{JC}}, age1 \\ s_{m,A} = e^{-M_{AC}}, age2-3 \\ s_{m,A2} = e^{-(M_{AC}+F_{C,t})}, age4-10 \end{cases}.$$

A3.3. Predation on crabs:

In previous versions of this model, predation was treated as a seasonal mortality rate incorporated directly into the survival terms ($\boldsymbol{s_i}$) described above (see: Hopf, et al., (2025) and White et al., (2026)). However, in this iteration and to represent more realistic predator-prey dynamics, predation was implemented as a daily process (inside each season) that reduces biomass in a daily timestep ($\boldsymbol{tt}$), through a Type II functional response and a Yodzis prey switching function (Koen-Alonso & Yodzis, 2005). This process is therefore implemented outside the projection matrix. This also means that we use start of the season prey biomasses and the result of the predation inner loop goes into the seasonal processes.

Note: as mentioned earlier, the Dungeness crabs sub-model works on units of crabs ha $^{-1}$, however, for the predation inner loop (this section), those densities have been transformed into biomass values that match each age class (e.g., older age classes have more biomass).

For Dungeness crabs (prey $\boldsymbol{A}$), the total available biomass available for predation is:

$$\boldsymbol{A_{t,tt}} = \sum_{i=9}^{44}\left[\mathrm{FC}_{i,t,tt} + \mathrm{MC}_{i,t,tt}\right],$$

where $\boldsymbol{FC_{i,t,tt}}$ and $\boldsymbol{MC_{i,t,tt}}$ are the biomass of female ($\boldsymbol{F}$) and male ($\boldsymbol{M}$) crabs in age class i during season $\boldsymbol{t}$ and day $\boldsymbol{tt}$, respectively. *Note, the lower index limit $i = 9$ reflects the fact that only adult crabs (ages 3-10 on 11x11 matrix, or ages 9-44 on the 44x44 matrix) are vulnerable to sea otter predation in the model.*

Predator relative preference was represented using a modified Yodzis switching functional response (Randell et al., 2025), which describes how sea otters adjusts their feeding preference among Dungeness crabs (prey $\boldsymbol{A}$), sea urchins (prey $\boldsymbol{S}$), and an alternative source of prey (prey $\boldsymbol{X}$), depending on their relative abundances:

$$\boldsymbol{p_{A,t,tt}} = \frac{w_c A_{t,tt}^{\phi}}{w_u S_{t,tt}^{\phi} + w_c A_{t,tt}^{\phi} + (1 - w_u - w_c) X_{t,tt}^{\phi}},$$

where $\boldsymbol{p_{A,t,tt}}$ (*lowercase p*) is the fraction of otter's total feeding effort allocated to crabs ($\boldsymbol{A_{t,tt}}$) at a giving daily time step. $\boldsymbol{S_{t,tt}}$ and $\boldsymbol{X_{t,tt}}$ represent the biomass of the other prey *Note: prey X is a constant biomass set to represent anything else that might be in a kelp forest that could be part of the sea otters' diet (e.g., abalone, clams, mussels, snails, etc.)*. The intrinsic preference ($\boldsymbol{w_i}$), or preference when prey are at equal abundances, are specific to each prey: crabs ➡️ $\boldsymbol{w_c}$ urchins ➡️ $\boldsymbol{w_u}$, and prey X ➡️ $1 - \boldsymbol{w_c} - \boldsymbol{w_u}$. Lastly, $\boldsymbol{\phi}$ (*lowercase phi*) controls the strength of switching, introducing density-dependent predation because preference changes with the relative abundance of prey types.

The feeding rates $\boldsymbol{P_{i,t,tt}}$ (*uppercase P*) on crab biomass ($\boldsymbol{A}$) follows a Type II functional response that includes the fraction of otter's total feeding effort allocated to urchins ($\boldsymbol{p_{A,t,tt}}$):

$$\boldsymbol{P_{A,t,tt}} = e^{\left(-\frac{a_{3,i,t} * p_{A,t,tt}}{1+\frac{1}{b_{3,i,t}}(a_{3,i,t} * p_{A,t,tt})\, A_{t,tt}} N_t\right)},$$

where $\boldsymbol{N_t}$ is predator density, $\boldsymbol{a_{3,i,t}}$ is the per kg mortality of crabs, ages $\boldsymbol{i}$ (ages: 2-10), due to predation, in the absence of conspecifics (*search/attack rate*), $\boldsymbol{b_{3,i,t}}$ is the max kg of crabs, ages $\boldsymbol{i}$ (ages: 2-10), consumed by a kilogram of predator, in a time step (*1/handling time*). *Note, this multiplier is only applied to the adult age classes*.

This multiplier ($\boldsymbol{P_{i,t,tt}}$) then updates the biomasses of crabs in a daily basis (daily predation)

$$\mathbf{FC}_{\boldsymbol{i,t,tt+1}} \begin{cases} \mathrm{FC}_{Fc_{\leq 1},t,tt+1} = \mathrm{FC}_{Fc_{\leq 1},t,tt} & , age0-1 \\ \mathrm{FC}_{Fc_{\geq 2},t,tt+1} = \mathrm{FC}_{Fc_{\geq 2},t,tt}\, P_{A,t,tt} & , age2-10 \end{cases},$$

and

$$\mathbf{MC}_{\boldsymbol{i,t,tt+1}} \begin{cases} \mathrm{MC}_{Mc_{\leq 1},t,tt+1} = \mathrm{MC}_{Mc_{\leq 1},t,tt} & , age0-1 \\ \mathrm{MC}_{Mc_{\geq 2},t,tt+1} = \mathrm{MC}_{Mc_{\geq 2},t,tt}\, P_{A,t,tt} & , age2-10 \end{cases},$$

and at the end of the daily predation loop ($tt = 91$), we get the post-predation biomasses which are the biomasses of urchins that survived predation on that specific season:

$$\mathbf{FC}_{\boldsymbol{i,t}}^{\boldsymbol{post_pred}} = \mathrm{FC}_{i,t,tt=91} \quad \& \quad \mathbf{MC}_{\boldsymbol{i,t}}^{\boldsymbol{post_pred}} = \mathrm{MC}_{i,t,tt=91},$$

these post-predation biomasses are then used in the projection matrix (see above) for the remaining seasonal demographic processes.

A4. Parameters clarification

Currently the Greek letter “phi” is being used twice, this is because in both cases “phi” is part of a switching function, but it is being used in different context, for which we have tried to differentiate them. The first “phi” is $\boldsymbol{\Phi}$ (upper case) which is being used as part of the sea urchin grazing switching behavior equations. The second “phi” $\boldsymbol{\phi}$ (lower case) which is being used in the Yodzis switching in predator preference.

Similarly, the letter *p* is being used twice in two different but related contexts. The first $\boldsymbol{p}$ (lower case) is predator preference term for the Yodzis equation, while /p/ $\boldsymbol{P}$ (upper case) is the daily predation survival multiplier, also interpreted as the feeding rate.

A5. ORSO implementation on this model (ORPM).

In this version of the model, sea otter densities derived from ORSO were used to represent N_t, defined as predator biomass (kg·ha^{-1}) exerting predation pressure on urchins and crabs. ORSO provides an online, user-friendly Shiny application (link) that generates sea otter population trends, density maps, and mean projected abundances per year across defined coastal sections (see **Figure 7** for details on ORSO's coastal sections). Although the ORSO app is a useful exploratory tool, the full *ORSO_Rversion* implementation was used here to extract raw projected abundances across all replicates. This approach allowed pairing ORPM (our model) replicates with ORSO replicates to preserve variability and enabled conversion of ORSO outputs into units compatible with the predation model.

We run ORSO for 100 years across 10,000 replicates, simulating sea otter reintroductions in sections S6, C7, and N5. For the present model configuration, only section S6 (representing the simulated population north of Port Orford) was used, as it exhibits the highest projected sea otter densities due to high habitat suitability (i.e., elevated carrying capacity, K).

ORSO outputs were extracted as time series of otter density (individuals·km^{-2}·year^{-1}). These annual densities were expanded to match the model's four-season temporal resolution by replicating each yearly value across seasons. Densities were then converted to biomass by assigning each individual a mean mass of 32 kg with a standard deviation of 4.38 kg, drawn from a normal distribution to introduce variability across time-steps and replicates. These values were based on reported ranges in Kenyon, (1969) and were intended to approximate mixed sex and age classes. Subsequently, densities were converted from km^2 to hectares (ha) to align with the spatial scale of the kelp model domain.

Finally, otter densities were adjusted to reflect effective habitat area. The S6 section in ORSO spans 123.96 km^2; however, ORSO densities are calculated as total abundance divided by total section area, which can underestimate local densities because sea otters do not occupy all available space uniformly. To correct this, habitat suitability information embedded within ORSO was used. Each coastal section is subdivided into smaller spatial units ("cells"), each assigned a carrying capacity (K) value based on limiting resources such as prey availability, refuge habitat, and other ecological constraints (see Appendix A, "Estimating *K* and Habitat Effects" section in Tinker et al., (2023) for more details). Cells with low Kvalues (approaching zero) are effectively unsuitable for occupation. By filtering S6 cells with $K \geq 2$, the effective habitat area was estimated at approximately 36.66 km^2.

Otter densities were therefore rescaled to this reduced area to better represent realistic spatial aggregation.

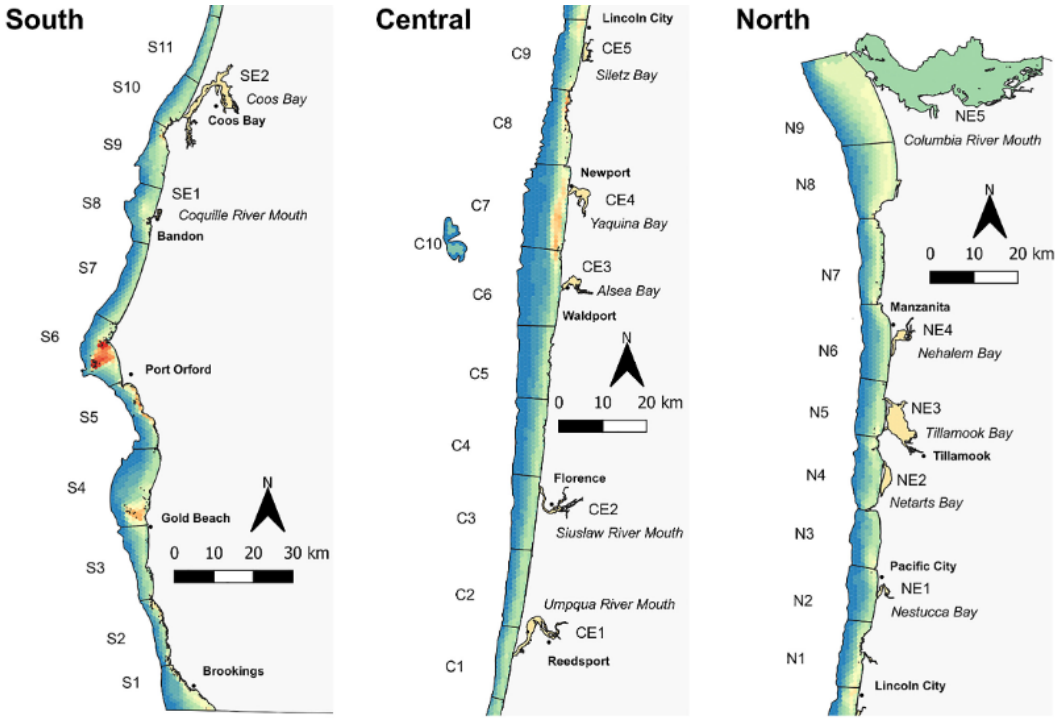


Figure 7. Results of a habitat-based model of sea otter K to the Oregon coast (D. V. Kone et al., 2021; Tinker et al., 2023). It illustrates the spatial configuration of coastal habitat in Oregon used for ORSO's population modeling. Coastal habitat sections (labeled polygons) show the basic geographic unit for modeling demographic processes, while the colored spatial grids within these polygons show the relative expected density at K (carrying capacity) based on a previously developed model of habitat-density relationships.

Oregon Sea Otter Model (ORSO) R version setting parameters: reps = 10000, StartYear = 2026, Nyrs = 100, Mltplscn = 0, Initseg = c("S6","C7","N5"), Initpop = c(60,60,60), AddOt = c(0,0,0), AddYrs = 0, PpnFem = .65, PpnAd = .40, Ephase = 5, AddMortE = .15, ProbMv = .4, EstryMvAdj = .3, AgeMvAdj = .5, Mvmort = .55, sig = 0.1, rmax = 0.18, theta = .9, V_sp = 2.5

A6. Bull kelp seasonal life history

Box 1. Bull kelp life cycle

Winter (Spores/Gametophytes): Microscopic spores released the previous summer-fall survive on the ocean floor in cold, nutrient-rich, dark conditions, waiting to germinate.

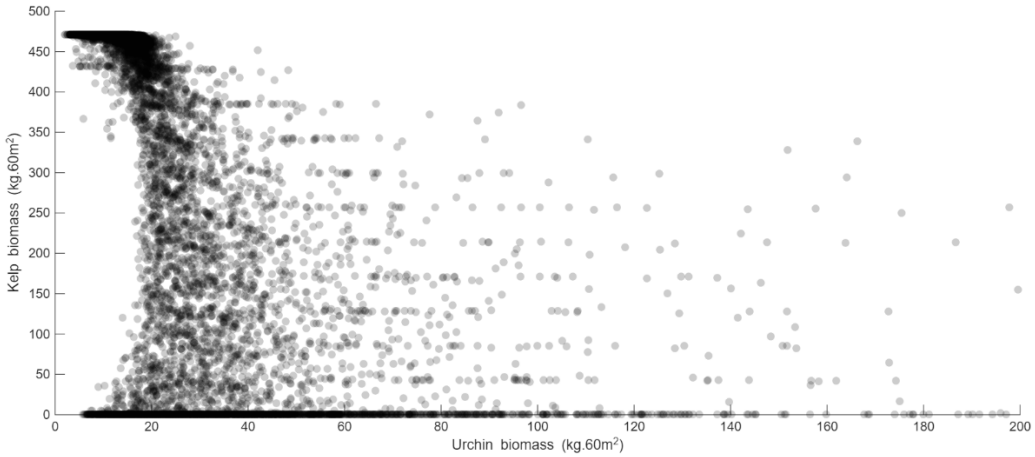
Spring (Germination & Rapid Growth): As days lengthen, spores germinate into microscopic gametophytes, which produce eggs and sperm. Once fertilized, the sporophyte (visible plant) grows rapidly, sometimes 25 centimeters or more per day until maturity.

Summer (Maturation & Canopy Formation): The kelp reaches the surface (between spring and summer, depending on depth), forming thick forests. Reproductive patches called sori develop on the blades, each capable of releasing millions of spores.

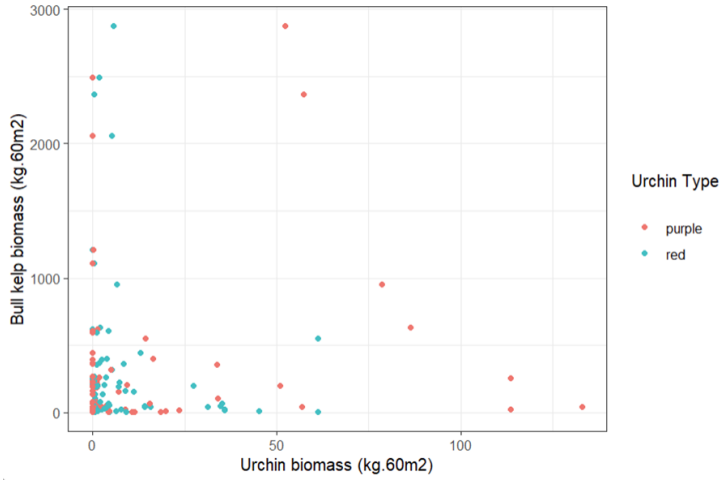
Fall (Reproduction & Decay): Mature plants release their spores (sometimes during summer too) to the water column to begin the next cycle. Storms in late fall and winter tear the adult plants from the rocky seabed, causing them to die and wash ashore

A7. Kelp-Urchin model validation.

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=10,000)



Site-averaged standing kelp and urchin biomass densities along the Oregon coast 2001-2011.



A8. Parameters table.

Symbol	Description	Baseline value	Units	References	Notes & Math
$\overline{R_U}$	Mean larval production, dispersal and settlement	2*10^2 (Tuning parameter)	kg/year		Value set to achieve a range of urchin biomasses that fall within observed values for Oregon coast kelp forests. Based on PISCO data. *Assumes open population.*
σ_{RU}	Variance of incoming recruits	1.89			Normalized variance from PISCO data.
R_{Udist}	Recruitment distribution	{lognormal}			Distribution from which urchin recruitment is drawn. Based on anecdotal and Okamoto et al. (2020) information.
$\theta_{U,t}$	Recruitment timing function	[0.2 0.2 0.5 0.1]		(Okamoto et al., 2020)	Northern California: 90% recruitment from January to September, with large peaks on July, February, and March. Visual interpretation of plot [20%, 20%, 50%, 10%] (Okamoto et al., 2020).
g_{mat}	Average urchin maturation age	2	years^{-1}	(Gonor, 1972)	Urchins become adults (~24mm test), two years after being recruitment.
M_{Ui}	Natural instantaneous mortality rate	$\begin{matrix} juvs \\ hiding \\ exposed \end{matrix} \begin{bmatrix} 0.1 \\ 0.1 \\ 0.1 \end{bmatrix}$	season^{-1}	(Russell, 1987)	Purple sea urchin mortality based on tidepool experiments at Vancouver Island at different seasons. mean = 0.1115 or 0.1 per season.
$a_{1,i,t}$	Per kg mort of urchins, stage *i,* due to predation, in the absence of conspecifics (*search/attack rate*)	$\begin{matrix} exposed \\ hiding \end{matrix} \begin{bmatrix} 0.597 \\ 0.2985 \end{bmatrix}$	kg urchin/ kg urchin/ kg pred^{-1}/ day^{-1}		Set to obtain an average per-capita otter consumption of 30.94 urchins per day. Assuming an urchin weights 0.2 kg (max), this is an average of 9.28 kg of food per day. Otters need at least 30% of body weight in food per day (8.4 - 13.2 kg/day**)** to meet energetic demands.

$b_{1,i,t}$	Max kg of urchins, stage *i*, consumed per predator kg (*1/handling time*)	$\begin{matrix} exposed \\ hiding \end{matrix} \begin{bmatrix} 1/0.0366 \\ 1/0.0366 * 0.5 \end{bmatrix}$	kg urchin/ kg urchin/ kg pred^{-1}/ day^{-1}		Set to obtain an average per-capita otter consumption of 30.94 urchins per day. Handling efficiency reported for specialist sea otters feeding on urchins is 20.5 seconds/urchin (Tinker et al., 2008). Sea otters may spend 30-60 min (avg ~2800 sec) handling prey during a 24h period. Assuming an urchin weight of 0.2 kg (max). $\frac{0.2\ kg\ per\ prey * 2800\ s\ day^{-1}}{20.5\ s\ per\ prey}$ $= 27.31\ (max) kg\ per\ day$ 27.31 (max) kg in urchins = 136.5 urchins max.
w_U	Predator intrinsic preference (*Yodzis func*)	0.5			Default set to simulate desired dynamics. Predator intrinsic preference *w* corresponds to the preference when all prey are equally abundant. $\sum w_i = 1$
$w_U Psi$	Predator intrinsic adjusted preference for $\boldsymbol{\Psi_t}$ (Psi) = 0 (*Yodzis func*)	0.1			Parameter $\boldsymbol{\Psi_t}$ (Psi), controls predation on exposed urchins. When $\boldsymbol{\Psi_t} = 0$, predation on exposed urchins is off, and the intrinsic preference on urchins gets adjusted to 0.1 (new preference for hiding urchins) For those cases, intrinsic preference for all other prey get proportionally reallocated so that: $w_U Psi = 0.1$ $w_C Psi = w_C/(1 - UPsi)$ $w_X Psi = 1 - w_U Psi - w_C Psi$
ϕ	Preference sensitivity to the relative abundance of prey (*Yodsis func*)	$\begin{matrix} No\ sensitivity \\ sen.\ less\ common \\ sen.\ common \end{matrix} \begin{bmatrix} 0 \\ 1 \\ 2 \end{bmatrix}$			Default value is ϕ = 0, so that there is no sensitivity to the relative abundances of different prey items. ϕ = 0, no sensitivity to prey abundances. $0 < \phi > 1$, increased preference for the less common (rare) prey. $\phi > 1$, increased preference for the common prey.
F_U	Fishing mortality rate	0			No urchin fishery.
PLD	Planktonic Larval Duration	91	days	(Groth, 2024)	PLD for Oregon is 62 to 131 days (Groth, 2024) - 96 days median. We are choosing arbitrary 91, as that is the max number of days per season.

τ	Discount rate for juvenile survival	1-*PLD*/91			This is to account for mismatch between long PLD and timestep.
w_1 w_2	Slope around inflection point of behaviour switching function	1 0.5			Value set so that kelp forest switches to urchin barren around observed urchin biomass thresholds.
k_{J+A}^{min}	Minimum standing kelp biomass density before barren state	408.33	kg ha^{-1}		Barren = 1% of average standing kelp densities. Based on PISCO data: Otter Rock = ~11,333.3kg ha^{-1} * 0.01 = **113.33 kg ha^{-1}** Redfish Rock = ~40,833.3kg ha^{-1} * 0.01 = **408.33kg ha^{-1}**
$\overline{R_K}$	Yearly mean zoospore production, successful fertilization and settlement of spore, per kg standing kelp	6.21x10^3 (Tuning parameter)	kg/year	(Amsler & Neushul, 1989)	Calculated as follows: *Spore release:* ~50 blades per kelp (Springer et al., 2006) blade area ~1.2m^2. and sori covers ~45% (0.54m^2) of blade area (Amsler & Neushul, 1989) mean spore release is is 2.3 x 10^9 per m sori per year (Amsler & Neushul, 1989) 50 x 1.2 x 0.45 x 2.3 x 10^9 = ~6.21 x 10^{10} spores released per kelp *Spore survival:* sex ration is 50:50 ~1% survival probability to settled microsporophytes ~20% survival probability for settled spores lasting 3 months 6.21x10^{10} x 0.01 x 0.2 x 0.5 = 6.21x10^7 *Individuals to weight:* We assumed that one recruit weighs, on average, 1g. And 1 adult plant wights ~10kg 6.21 x 10^7 x 0.001 x 0.1 = 6210 kg recruits per kg adult
σ_{RK}	Variance of incoming settlers	0.32			Normalised variance from PISCO data.

β_{RK}	Strength of density dependence	$3x10^{-5}$			Value set to achieve a range of standing kelp biomasses that fall within observed values for Oregon coast kelp forests, based on PISCO data.
D	Relative strength of inter- versus intra-cohort density-dependent processes	0.9			Mix density dependence (0.9). D = 0 for Ricker (inter-cohort DD) D = 1 for Beverton-Holt (intra-cohort DD)
$var(\overline{k_{J+A,t}})$	Variance in the density of standing kelp across the model unit space	116,535			Spatial variance at transect level, averaged over years, based on PISCO data.
$\theta_{K,t}$	Recruitment timing function	[0, 1, 0, 0]		(Maxell & Miller, 1996)	New recruits observed in early March to late May (spring).
lag	Recruitment lag	[2 3]		(Maxell & Miller, 1996)	Kelp recruits depend on adult biomass from the previous summer and autumn.
repro weight	Reproduction weightings	[0.9 0.1]		(Maxell & Miller, 1996)	~80-90% of spores are released in summer. ~20-10% of spores are released in autumn.
g_K	Maximum increase in adult kelp biomass as it ages	29.65	kg/season	(Pontier et al., 2024)	Value calculated as follows: Mean blade and stipe growth is 0.0465 m/day Assuming 10m kelp = 70kg Daily seasonal growth is 0.0465 x 7 x 91 = 29.65 kg per season
γ	Relative change in standing kelp biomass over the seasons	[0.1 0.8 1 0.9]			This value comes from the interpretation of existing literature and anecdotical data for Oregon. The *y* change in kg of kelp over the season: *winter*: almost full loss of kelp coverage. *spring*: recruitment and fast growth. *summer*: maximum growth rate. *autumn*: close to maximum growth rate.

r_S	Proportion of non-grazed standing kelp biomass remaining at the end of the season	0.6	season^{-1}	(Rassweiler et al., 2018)	Following giant kelp in Southern California, as no data exists for bull kelp in Oregon. Conversion from average daily plant loss rate to proportion surviving a season (91 days): exp(-0.0062*91) = 0.5688.
c	Proportion of standing kelp biomass converting to drift	0.9	season^{-1}	(Rennick et al., 2022)	Following giant kelp in Southern California, as no data exists for bull kelp in Oregon. Conversion from daily to seasonal proportion of biomass converted to drift = 1-(1-0.025)^{91}.
r_D	Proportion of drift biomass retained locally	0.7	season^{-1}	(Figurski, 2010; Hobday, 2000)	Following giant kelp in Southern California, as no data exists for bull kelp in Oregon.
d	Proportion of drift decomposing	0.1	season^{-1}	(Figurski, 2010)	Following giant kelp in Southern California, as no data exists for bull kelp in Oregon.
$a_{2,i,j,t}$	Per kg mort of kelp, stage *i* due to grazing by urchins, stage *j*, in the absence of conspecifics (*search/attack rate*)	$\begin{matrix} & hiding & exposed \\ juv\ k \\ adult \\ drift \end{matrix}\begin{bmatrix} 0 & 0.5 \\ 0 & 0.5 \\ 1 & 0 \end{bmatrix}$	kg kelp/ kg kelp/ kg urchin/ season^{-1}	(Kriegisch et al., 2019)	No data is available to parameterize this, so we assumed very high attack rates with near-zero standing or drift densities. Kriegisch et al., (2019a) findings suggest that attack rates for standing are less than that for drift as kelp has lower consumption than drift at high resource density (kelp forests).
$b_{2,i,j,t}$	Max kg of kelp, stage *i,* consumed by kg urchins, stage *j* (1/*handling time*)	$\begin{matrix} & hiding & exposed \\ juv\ k \\ stand \\ drift \end{matrix}\begin{bmatrix} 0 & 2.985 \\ 0 & 2.985 \\ 2.985 & 0 \end{bmatrix}$	kg kelp/ kg kelp/ kg urchin/ season^{-1}	(M. C. Foster et al., 2015; Rennick et al., 2022)	Kriegisch et al., (2019a) findings suggest that the maximum feeding rate is the same for drift and standing kelp, as consumption rates were the same for drift and kelp in urchin barrens (when resources are low). We assume they are the same. Experimental data (Randell, 2022; Rennick et al., 2022) have a range of maximum feeding rate values and we used the average of these to obtain the baseline value. Rennick et al. (2022): 0.02 g detritus per urchins^{-1} per day^{-1}. Conversion = 0.02*1000/1000*91 = 1.82 kg kelp.kg urchin^{-1}.season^{-1}

$\overline{R_c}$	Mean larval production, dispersal and settlement of age-0 crabs	1000 (Tuning parameter)	crabs/year		Value set to achieve a range of crab biomasses that fall within observed patterns in Oregon for a 1 ha spatial domain. See: Cannibalism_Inf_Func_Exploration.m Dungeness_size_weight.xlsx *Assumes open population.*
σ_{RC}	Variance of incoming age-0 crabs	1.26			Set to simulate observed pattern of larval/age-0 settlement, and crab demographics.
R_{Cdist}	Recruitment (age-0) distribution	{lognormal}			Distribution from which crab recruitment is drawn. Set to match 7-10-year pulses cycles (Higgins et al., 1997; Rasmuson, 2013).
$\theta_{C,t}$	Recruitment (age-0) timing function	[0 0.5 0.5 0]		(Botsford & Hobbs, 1995; Higgins et al., 1997)	On average age-0 individuals (step after Megalopa stage) arrive in settle in Oregon though Spring and Summer. Here we have set the system to have half of the new age-0 to arrive on spring and the other half in summer.
β	Cannibalism intensity	1.0000e-03			This cannibalism intensity coefficient is set to achieve the demographic patterns and age distributions observed in crab populations. See: Cannibalism_Inf_Func_Exploration.m Dungeness_size_weight.xlsx
M_{Ci}	Natural instantaneous mortality rate	$recruits(age\ 0)$ $juveniles(age\ 1)$ $adults(age\ 2-10)$ $\begin{bmatrix} 0.05 \\ 0.05 \\ 0.05 \end{bmatrix}$	season^{-1}	(Botsford & Hobbs, 1995)	Average instantons mortality rates for different crab age classes.
F_c	Fishing mortality rate	[0.33 0.33 0.33 0]	season^{-1}	(Botsford & Hobbs, 1995; Rasmuson, 2013)	Average Fishing harvest rates (Botsford & Hobbs, 1995). In Oregon the commercial fishery is open from December to August, and effort is relative even through the season (Rasmuson, 2013).
$a_{3,i,t}$	Per kg mort of crabs, ages *i* (2-10), due to predation, in the absence of conspecifics (*search/attack rate*)	0.897	kg crab/ kg crab/ kg pred^{-1}/ day^{-1}		Set to obtain an average per-capita otter consumption of 6.54 crabs per day. Assuming a crab weights 1.2 kg (max), this is an average of 7.85 kg of food per day. Otters need at least 30% of body weight in food per day (8.4 - 13.2 kg/day**)** to meet energetic demands.

$b_{3,i,t}$	Max kg of crabs, ages *i* (2-10), consumed per predator kg (*1/handling time*)	1/0.0545	kg crab/ kg crab/ kg pred^{-1}/ day^{-1}		Set to obtain an average per-capita otter consumption of 6.54 crabs per day. Handling efficiency reported for specialist sea otters feeding on crabs is 183.2 seconds/crab (Tinker et al., 2008). Sea otters may spend 30-60 min (avg ~2800 sec) handling prey during a 24h period. Assuming a crab weight of 1.2 kg (max). $\frac{1.2\ kg\ per\ prey * 2800\ s\ day^{-1}}{183.2\ s\ per\ prey} = 18.34\ (max) kg\ per\ day$ 18.34 (max) kg in crabs = 15.28 crabs max. One adult sea otter can consumed between 10 - 14 crabs per day (Pitcher & Imamura, 1990)
w_C	Predator intrinsic preference (*Yodzis func*)	0.3			Default set to simulate desired dynamics. Predator intrinsic preference *w* corresponds to the preference when all prey are equally abundant. $\sum w_i = 1$ On equal abundances and conditions, and according to literature, otters should prefer crabs ($w_C > w_u$) over all other prey in this model. However, w_C gets a penalization to account for the spatial domain of the model in which otters inhabit and forage inside the kelp, while crabs are in the vicinity (outside) the kelp forest; and therefore, are harder to obtain.
$NCIF$	Normalized Cannibalism influence function	$\begin{matrix} age\ 1 \\ age\ 2 \\ age\ 3 \\ age\ 4 \\ age\ 5 \\ age\ 6-10 \end{matrix} \begin{bmatrix} 0.0028 \\ 0.0315 \\ 0.0516 \\ 0.0772 \\ 0.1085 \\ 0.1457 \end{bmatrix}$		(Botsford et al., 2019)	The relative influence of cannibalistic pressure from older age classes to age-0. The older and larger the age class the strongest influence on cannibalism. Obtained from Botsford et al. (2019) modelling work repository.

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