

# Kelp-urchin model discrete time CC 4pop v0

- spatially implicit model, with 4 patches (closed/within patch dynamics for kelp, closed population/among patch dynamics for urchins)
- builds on “Kelp-urchin model discrete time CC v6a”

## State Variables

Predators:  $N_{i,t}$  biomass density (i.e., normalised to area) of predators size  $i$  at time  $t$

Kelp:  $k_{i,t}$  biomass density of kelp stage  $i$  at time  $t$

$k_{J,t}$  standing juvenile kelp

$k_{A,t}$  standing adult kelp

$k_{D,t}$  drift kelp

(note that standing kelp collectively refers to juv and adult kelp)

Urchins:  $u_{i,t}$  biomass density of urchins stage  $i$  at time  $t$

$u_{J,t}$  juvenile (small, sexually immature) urchins

$u_{H,t}$  hiding (cryptic) adult urchins

$u_{E,t}$  exposed (barren) adult urchins

## Notes

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- Time steps are quarterly (3 months). This matches with kelp maturation times and the average time before starvation affects urchin gonads.
- Order of events
  - Within-matrix: changes state then survives (natural, grazing, predation, or fishing)
  - Within-season: get densities at end of last time step ( $t$ ) → use those in functions → do matrix multiplication to calculate densities at the end of current time step ( $t+1$ )
  - urchin recruitment -> urchin culling -> kelp seeding -> urchins eat kelp

## Kelp

Using a vec-permutation approach (Hunter and Caswell 2005).

$$\mathbf{K}_{t+1} = \mathbf{P}^T \mathbf{D}_K \mathbf{P} \mathbf{M}_K * \begin{bmatrix} k_{J,t} \\ k_{A,t} \\ k_{D,t} \end{bmatrix}$$

$$\mathbf{M}_K = \begin{matrix} & \text{juvs} & \text{adult} & \text{drift} \\ \begin{matrix} \text{juvs} \\ \text{adult} \\ \text{drift} \end{matrix} & \begin{bmatrix} 0 & \theta_{K,t} R_K s_Y r_S \kappa_{Y,E} \gamma & 0 \\ r_S g_K (1-c) \kappa_{A,E} \gamma & r_S g_K (1-c) \kappa_{A,E} \gamma & 0 \\ c r_D \kappa_{D,H} & c r_D \kappa_{D,H} & (1-d) r_D \kappa_{D,H} \end{bmatrix} \end{matrix}$$

- Recruitment** of young/juvenile (recruited) kelp biomass

Juveniles are defined as sporophytes that are visible to the naked eye, but not reproductive. They are 0-3 months old. They are also considered standing kelp and contribute to the production of drift.

$R_K$  = zoospore production, successful fertilization, and settlement of spore\*\* (biomass of kelp recruited), per biomass of adults

=  $norm(\overline{R_K}, \sigma_{RK})$ , where  $\overline{R_K}$  = yearly mean biomass of incoming settlers &  $\sigma_{RK}$  = yearly variance of incoming settlers

$\theta_{K,t}$  = recruitment timing function for kelp

- DD survival**: density-dependent survival (ricker function)

Incoming recruits are affected by shading of larger plants. Since plants grow quickly, its reasonable to assume that they are affect by the biomass of standing juveniles and adults.

$$s_Y = e^{-\beta (k_{J+A,t})}$$

$\beta$  = strength of density dependence (strength of shading effect by local adult kelp)

Since kelp dynamics occur at the local (~transect scale), we can approximate the landscape scale density dependent survival (following White 2011) as

$$\bar{s}_Y \approx e^{-\beta k_{J+A,t}} + 0.5 \beta^2 e^{-\beta k_{J+A,t}} var(k_{J+A,t})$$

$var(k_{J+A,t})$  = Spatial variance in the density of kelp across the model unit space

- Growth/Maturation**

All juveniles become adults in the next season, reflecting quick maturation rates (on the order of months; Schiel and Foster 2015 pg 31)

$g_K$  = increase in adult kelp biomass from season to season as it ages

- Natural mortality & loss**

$\gamma$  = change in standing (juvs & adults) kelp biomass over the season\*\*

(Note that  $g$  exists to capture losses in biomass due to decreased growth and conditioning in low nutrient/high temp conditions. This is relative to the baseline value of 1)

$r_S$  = proportion of standing kelp biomass that remains at the end of the season (1-proportion of plants lost, usually dues to storms/waves)

- Drift production**

$c$  = proportion of juvenile and standing kelp biomass converted to drift

$(1-c)$  = proportion of standing kelp biomass that remains as standing kelp biomass (or juveniles that become standing)

**Commented [JH1]:** Burgan & Gerard 1990 and Nisbet & Bence 1989 refer to "recruitment windows", which are months with favourable environmental conditions for production and survival

**Commented [JH2]:** If want to inc light availability explicitly, see Stewart et al 2009. However, I don't think this is necessary to answer questions about management actions atm...

**Commented [JH3R2]:** we also implicitly include it in the timing function and could add it through time-series of noise

$d$  = decomposition of drift kelp biomass (through things other than grazing by urchins)  
 $r_D$  = proportion of drift kelp biomass retained in system

- Grazing survival:**

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

$\Omega_{i,j}$  = instantaneous rate of mortality of kelp stage  $i$  due to grazing by urchins stage  $j$  (hiding or exposed): Holling Type II functional response, but parameters redefined for discrete time and per-capita. This assumes that there is no effect of increasing urchin densities (Rennick et al. 2022).

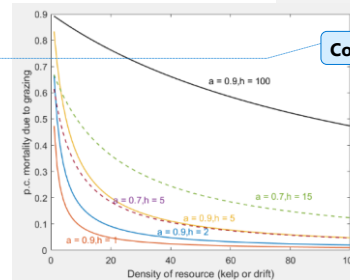
$$\Omega_{i,j} = \frac{a_{i,t}}{1 + \frac{1}{p_i} a_{i,t} \kappa_{i,t}} u_{j,t},$$

$a_i > 0$  per kg mortality due to grazing by an urchin in the absence of conspecifics (search/attack rate), *which varies seasonally*

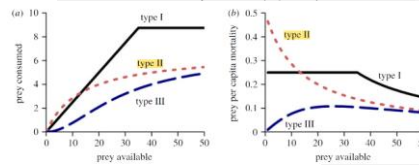
$p_i > 0$  the asymptotic (max) kg of prey consumed by an urchin in a time step (handling & ingestion time<sup>-1</sup>)

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

$$\mathbf{a}_t = \begin{matrix} & \begin{matrix} \text{hiding} & \text{exposed} \end{matrix} \\ \begin{matrix} \text{juvs} \\ \text{adult} \\ \text{drift} \end{matrix} & \begin{bmatrix} 0 & a_{J,E,t} \\ 0 & a_{A,E,t} \\ a_{D,H,t} & 0 \end{bmatrix} \end{matrix} \quad \mathbf{p} = \begin{matrix} & \begin{matrix} \text{hiding} & \text{exposed} \end{matrix} \\ \begin{matrix} \text{juvs} \\ \text{adult} \\ \text{drift} \end{matrix} & \begin{bmatrix} 0 & p_{J,E} \\ 0 & p_{A,E} \\ p_{D,H} & 0 \end{bmatrix} \end{matrix}$$



Commented [JH4]: Dunn & Hovel 2020



## Urchins

Using a vec-permutation approach (Hunter and Caswell 2005).

$$\mathbf{U}_{t+1} = \mathbf{P}^T \mathbf{D}_U \mathbf{P} \mathbf{M}_U * \begin{bmatrix} u_{J,t} \\ u_{H,t} \\ u_{E,t} \end{bmatrix}$$

$$\mathbf{M}_U = \begin{matrix} & \begin{matrix} juvs & hiding & exposed \end{matrix} \\ \begin{matrix} juvs \\ hiding \\ exposed \end{matrix} & \begin{bmatrix} (1-g_J) s_J & R_U \theta_{U,t} (s_J)^\tau & \psi R_U \theta_{U,t} (s_J)^\tau \\ g_U s_H (1-\phi) & s_H (1-\phi) & s_H (1-\phi) \\ g_U s_E \phi & s_E \phi & s_E \phi \end{bmatrix} \end{matrix}$$

- Recruitment** of juvenile urchins

$R_U$  = per kg larval production (fecundity), dispersal and settlement for urchins

$R_U = norm(\overline{R_U}, \sigma_{RU})$ , where  $\overline{R_U}$  = yearly mean biomass of incoming urchin recruits &  $\sigma_{RU}$  = yearly variance of recruits

$\theta_{U,t}$  = recruitment timing function for urchins

- Growth/maturation**

$g_U$  = proportion maturing from juvenile to adult urchin

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

$g_{mat}$  = average age of maturation

- Survival**

$s_j$  = survival of stage  $j$

Juveniles:  $s_J = e^{-M_J}$

or  $s_J = e^{-M_J} (1 - e^{-\alpha(u_{H+E,t})})$  (with Allee effect; Pfister and Bradbury 1996),

where  $\bar{s}_J \approx e^{-M_J} (1 - e^{-\alpha \overline{u_{H+E,t}}} - 0.5 \alpha^2 e^{-\alpha \overline{u_{H+E,t}}} var(u_{H+E,t}))$

Hiding:  $s_H = e^{-M_H - P_H N_t - F}$

Exposed:  $s_E = e^{-M_E - \psi(P_E N_t + F)}$

$M_i$  = natural mortality rate of stage  $i$

$\alpha$  = strength of recruitment facilitation by adults

$F$  = fishing mortality (if applicable to species, and only affects adults)

$P_i$  = predation mortality (rate of consumption by a predator, only affects adults) ← this assumes Type I (linear/constant p.c. rate), but need to consider sensitivity to Type II (shown for lobsters) and Type III (possible for Sheephead under low urchin densities). Note that urchins only make up a small portion of SH diet, so it is unlikely that urchin mortality decreases with more urchins...

$\tau$  = discount rate for juvenile survival to account for mismatch between long PLD and time step.

$$\tau = 1 - \frac{PLD}{91}, \quad PLD < 90$$

Note:  $\tau \leq 0$ , and when  $\tau = 1$ ,  $(s_J)^\tau = s_J$ .

- Urchin barren state**

$\psi$  = Step function to turn off predation and urchin reproduction when has been in a kelp barren state (no standing kelp) for >3months

$$\psi = \begin{cases} 0, & k_{J+A,t-1} < k_{J+A}^{min} \\ 1 & \end{cases}$$

$k_D^{min}$  = standing kelp threshold below which a kelp barren state is declared

- **Behaviour switching** of urchins between hiding and exposed as a function of drift density, urchin biomass & max feeding rate.

Rennick et al. 2022 shows that urchin barrens are more likely when drift availability < urchin consumptive capacity (biomass of urchins x max kg of drift consumed in a time step).

$\phi$  = Proportion of urchins exposed in the open grazing standing kelp

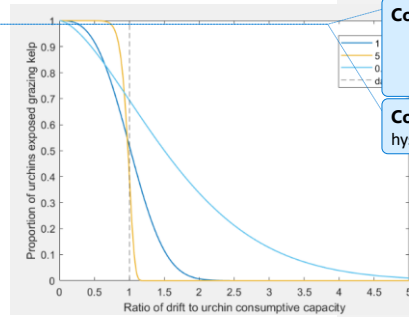
$$\phi = e^{-v_1 \left( \frac{k_{D,t}}{u_{H+E,t} P_{D,H}} \right) v_2}$$

where the following are satisfied:

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

and  $w_1$  = inflection point (drift density at which urchin hiding:exposed = 1:1) and  $w_2$  = slope around the inflection point.

$w_1=1$  (where urchin consumptive capacity = drift availability)



**Commented [JH5]:** Note this impacts:  
 1) When urchins switch with a steady decline in kelp, and  
 2) When urchins start to return to crevices, following a disturbance

**Commented [JH6R5]:** I wonder if this explains hysteresis...?

	Symbol	Description	Baseline value (Heatwave value)	Units	References	Notes
kelp (macrocystis)	$\overline{R_K}$	mean zoospore production and successful fertilization and settlement of spore (in the absence of DD), <i>per kg standing kelp</i>	$4 \times 10^4$ (x 1/7)	kg.year <sup>-1</sup>	(Dayton et al. 1984, Schiel and Foster 2015)	<ul style="list-style-type: none"> <li>- assume one recruit = 1g = 0.001kg</li> <li><u>Per kg adult:</u></li> <li>- 10<sup>11</sup> zoospores per plant (S&amp;F 2015 pg 31), halve this cas 50:50 sex ratio = 5x10<sup>10</sup> (Graham 2007 pg 47)</li> <li>- 0.01 survival for settled spores-microsporophytes (S&amp;F 2015 pg 77)</li> <li>- Dayton et al. 1984: ~20% survival 0-3 months (0 = microsporophytes)</li> <li>- One adult plant ~0.5kg dry = 10kg wet (using conversion below)</li> <li>- 5x10<sup>10</sup> x 0.01 x 0.2 = 10<sup>8</sup> individuals per plant</li> <li>= 10<sup>8</sup> x 0.1 = 10<sup>7</sup> individuals per kg adult (assuming weight of the reproductive blades, sporophylls, is proportional to total plant weight)</li> <li>= 10<sup>7</sup> x 0.001 = 10<sup>4</sup> kg recruits per kg adult (per season)</li> </ul> <u>Total settlement/recruitment numbers NOT USED:</u> <ul style="list-style-type: none"> <li>- Schiel &amp; Foster (2015 book, Fig 4.2A inset) have initial settlement rates ~10<sup>6</sup>-10<sup>8</sup>.m<sup>2</sup></li> <li>- Reed 2004 (San Clemente): 6 recruits.m<sup>-2</sup>.season = 6*10<sup>4</sup>*4 = ~24*10<sup>4</sup> recruits.ha.year = 240 kg recruits. However, this is plants &lt;1m, so later-stage recruits</li> </ul> <b>**Warming scenario:</b> <ul style="list-style-type: none"> <li>- x1/7 (7-fold decrease in sporophyte production with temps &gt;20°C for San Diego collected kelp; Hollarsmith et al. 2020). Applies throughout the year (note that it is multiplied by the recruitment timing function)</li> </ul>
	$\sigma_{RK}$	variance of incoming settlers	0.389			<ul style="list-style-type: none"> <li>- normalised variance from kelp recruits PISCO data for Channel Islands CA. See PISCO_kelp-urchin-sheephead_data.Rmd for details.</li> </ul>
	$\beta$	strength of density dependence effect of shading by adults	3.5x10 <sup>-4</sup>	NA		<ul style="list-style-type: none"> <li>- Set to standing kelp densities (~700kg.60m<sup>2</sup>/0.006 = ~ 1.17x10<sup>5</sup>kg.ha) observed in kelp forested state, based on PISCO data for Channel Islands at Anacapa East MPA</li> <li>Conversion used in calc (from stipe density to wet kg):</li> <li>- stipe (plant) density to dry biomass (kg) density: y = 0.33x + 0.16 (Reed et al. 2009)</li> <li>- wet-to-dry ratio = 0.094 (Rassweiler et al. 2018)</li> <li>- note: S&amp;F 2015 pg 27 has wet weight of 1.25kg per frond from North 1971</li> </ul>
	$var(\overline{k_{J+A,t}})$	Variance in the density of standing kelp across the model unit space	189,090	(kg)		<ul style="list-style-type: none"> <li>- spatial variance at transect level, averaged over years. Data from PISCO kelp surveys at the Channel Islands, which measures all plants over 1m tall. See PISCO_kelp-urchin-sheephead_data.Rmd for details</li> </ul>
	$\theta_{K,t}$	kelp recruitment timing function	[0.1, 0.1, 0.4, 0.4]		(Reed et al. 2008)	([Winter, Spring, Summer, Autumn]) <ul style="list-style-type: none"> <li>- Baseline: Reed et al. 2008 has recruitment (&gt;1m) peaks in summer-Autumn (July-Nov) for Sth CA</li> </ul>

						<ul style="list-style-type: none"> <li>- although main reproduction ('fecundity') peaks in winter &amp; spring (Santa Barbara Reed et al. 1996)</li> </ul>
$r_S$	proportion of standing kelp biomass that remain at the end of the season	0.5688	season <sup>-1</sup>	(Hobday 2000)		<ul style="list-style-type: none"> <li>- Rassweiler et al. 2018 data: avg daily plant loss rate = 0.0062. Conversion: <math>\exp(-0.0062 \times 91) = 0.5688</math> for proportion of plants surviving per season.</li> <li>- Hobday 2000: value (0.17) is proportion of plants lost per season. 0.83 NOT used.</li> <li>- We are assuming that biomass is proportional to number of plants.</li> <li>- Evidence that this varies by season: more during winter/spring storms (Hobday 2000, Rassweiler et al. 2018)</li> <li>- This captures loss due to wave exposure, which is <b>highly variable</b> at the small scale and can have a large impact in kelp loss, especially during El Nino events (Edwards and Estes 2006).</li> <li>- <b>Note:</b> this is where storm effects/removal would be included, if we wanted to go there. See Reed et al. 2008, Rassweiler et al. 2018 data</li> </ul>
$g_K$	increase in adult kelp biomass as it ages	6.825	kg.season <sup>-1</sup>			<ul style="list-style-type: none"> <li>- Stewart et al. 2009 (fig 4): avg growth rate = 0.075kg frond biomass added per day. Conversion: <math>0.075 \times 91 = 6.825</math>kg fronds per season. Note this changes over the seasons (which is captured below in the growth function).</li> </ul>
$\gamma$	change in standing kelp biomass over the season	[1 1 0.8 0.9] (x [0,0,0.5,0.5])				<p><b>**Warming scenario:</b> growth declines as temp increases: 50% reduction from 18 to ~20°C in Channel Islands (Zimmerman and Kremer 1986, see also data in folder). This only applies during the summer/autumn when temps can peak above 20°C</p>
$c$	proportion of standing kelp biomass converting to drift ( <i>drift production</i> )	0.9	season <sup>-1</sup>	(Rennick et al. 2022)		<ul style="list-style-type: none"> <li>- Rennick 2022 (Fig S1): value (0.025) is proportion of biomass converted to drift per day. Conversion = <math>1-(1-0.025)^{91}</math> for proportion of drift produced per season.</li> <li>- Rennick calc this from Rassweiler et al. 2018 data as the fraction of biomass lost as frond and blades.</li> </ul>
$r_D$	proportion of drift biomass retained locally	0.7	season <sup>-1</sup>	(Hobday 2000, Figurski 2010)		<ul style="list-style-type: none"> <li>- using value to allow Anacapa East MPA to be a persisting kelp forest</li> <li>- ~50% drifting rafts stayed within 100km of source (Hobday 2000)</li> <li>- local retention (of drift) is highest in summer/fall and lowest in winter (Figurski 2010)</li> <li>- depends on local wave action: high wave areas can experience 90% loss of drift, where as low wave areas can experience 10% loss (Figurski 2010, pg 130).</li> <li>- <b>Note: model (drift/kelp persistence) is highly sensitive to this value (relative to grazing and decomposition)</b></li> </ul>
$d$	proportion of drift decomposing	0.1	season <sup>-1</sup>	(Figurski 2010)		<ul style="list-style-type: none"> <li>- Figurski 2010, pg 123 avg of controls</li> <li>- <b>highly variable</b>, depending on water flow in crevices, light and (mostly) density of drift (Figurski 2010, pg 108, 123)</li> <li>- <b>Note: model (drift/kelp persistence) is highly sensitive to this value (relative to grazing and drift production)</b></li> </ul>

**Commented [JH7]:** also:  
[https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/11-0377.1?casa\\_token=1TkGLzjDn20AAAAA%3ApB9eYQmatsfgi-yxtSm7Y0ZpudtiXxVhU6Vgf4UXzzD8fZrC-pfZlk-uHL8CF3esk53xF44nvTk9nNeW7](https://esajournals.onlinelibrary.wiley.com/doi/full/10.1890/11-0377.1?casa_token=1TkGLzjDn20AAAAA%3ApB9eYQmatsfgi-yxtSm7Y0ZpudtiXxVhU6Vgf4UXzzD8fZrC-pfZlk-uHL8CF3esk53xF44nvTk9nNeW7)

urchins	$a_{i,j}$	per kg mortality of kelp stage $i$ due to grazing by an urchin, stage $j$ , in the absence of conspecifics ( <i>search/attack rate</i> )	<div><div><div>hiding</div><div>exposed</div></div><div><div>juv k</div><div>adult</div><div>drift</div></div><div><div><div>0</div><div>0</div><div>1</div></div><div><div>0.5</div><div>0.5</div><div>0</div></div></div></div>	kg kelp .kg urchin <sup>-1</sup> .season <sup>-1</sup>		<ul style="list-style-type: none"><li>- Can't find 'exact' data on this. It is a hard parameter to quantify. So set relatively high, assuming that without other kelp/drift around, it will get eaten pretty quickly (i.e., that urchins don't have to spend long finding kelp)</li><li>- Kriegisch 2019: attack rate for standing &lt; drift, since they have similar consumption rates at low resource density (barrens), but kelp has lower consumption than drift at high resource density (kelp forests). Can't quantify from study though, so will go with 0.5.</li><li>- <i>Note: model is not very sensitive to these values</i></li></ul>
	$p_{i,j}$	the max kg of kelp stage $i$ consumed by an urchin, stage $j$ , in a time step ( <i>1/handling time</i> )	<div><div><div>hiding</div><div>exposed</div></div><div><div>juv k</div><div>stand</div><div>drift</div></div><div><div><div>0</div><div>0</div><div>2.985</div></div><div><div>2.985</div><div>2.985</div><div>0</div></div></div></div> <div>(x 1.2)</div>	kg kelp .kg urchin <sup>-1</sup> .season <sup>-1</sup>	(Rennick et al. 2022, Spindel 2023)	<ul style="list-style-type: none"><li>- Rennick 2022 (Fig 2): 0.02 (0.009 reds) g detritus.g urchins<sup>-1</sup>.day<sup>-1</sup> at 14.5°C. Conversion = <del>*1000/1000</del>*91. Purples = <b>1.82 kg kelp.kg urchin<sup>-1</sup>.season<sup>-1</sup></b>, Reds = 0.8281(note reds are bigger). Urchins were taken from a kelp forest and fed for a week prior to experiments. Experiments were run at 14.5°C water temp.</li><li>- Foster 2015: purples collected from urchin barrens = 1.14 g kelp.urchin<sup>-1</sup>.day<sup>-1</sup>. Conversion = 1.14/1000*91 = 0.104 kg kelp.urchin<sup>-1</sup>.season<sup>-1</sup> = 0.104/0.025 = <b>4.15 kg kelp.kg urchin<sup>-1</sup>.season<sup>-1</sup></b> with avg urchins in experiments = 25g (from supp data file "foster_etal_2014_peerj_urchin_final_20110209.csv"). Urchins were taken from an established urchin barren and starved for a week prior to experiments. Experiment: water temp varied (with ambient temp) 11.6 to 16.3°C</li><li>- Taking the average of Rennick &amp; Foster = <b>2.985 kg kelp.kg urchin<sup>-1</sup>.season<sup>-1</sup></b></li><li>- Assuming max feeding rate is the same for drift and standing. Kriegisch et al. 2019 suggests that it is (at least in Aust), as consumption rates were the same for drift and kelp in urchin barrens (when resources are low).</li><li>- juv kelp is supposedly more tasty (Karatayev et al. 2021), but I haven't found evidence or rates for this.</li><li>- <i>Note: drift/kelp persistence depends on these values relative to retention.</i></li></ul> <p><b>**Warming scenario:</b></p> <ul style="list-style-type: none"><li>- ~40% increase in grazing rates between 13-16°C and El Nino heatwave (up to 21 °C) (Spindel 2023 fig3.2b), BC Canada</li><li>- (didn't used Spindel as baseline cas units were per urchin, not biomass, and conversion adds uncertainty when its not necessary)</li></ul>
urchins	$\overline{R_U}$	mean larval production (fecundity), dispersal and settlement for urchins (assumes open population)	<div>3x10<sup>5</sup></div>	kg.yr <sup>-1</sup>		<ul style="list-style-type: none"><li>- Set to observed in kelp forested state, based on PISCO data for Channel Islands</li><li>- Conversion used for numbers of urchins to wet biomass:<ul style="list-style-type: none"><li>- Biomass (kg) = (0.0499* test dimeter (cm) + 0.0019) (Ling et al. 2015, <a href="#">supp Table1</a>)</li><li>- using PISCO data: avg purple urchin weight is 0.21kg</li></ul></li><li>- larval mortality may <b>depend on CC</b></li><li>- No recruit data from PISCO for Channel Islands, only further north</li></ul>

(x 1.2)

**Commented [JH8]:** no idea where the authors got this, but I think their units are wrong, as using kg and cm makes sense following this: [https://link.springer-com.oregonstate.idm.oclc.org/article/10.1007/s00227-010-1541-2/figures/5](https://link.springer.com/oregonstate.idm.oclc.org/article/10.1007/s00227-010-1541-2/figures/5)



$\sigma_{RU}$	variance of incoming recruits	0.522				<ul style="list-style-type: none"> <li>- normalised variance from PISCO data for central and northern CA. See PISCO_kelp-urchin-sheephead_data.Rmd for details. No urchin recruit data exists for Channel Islands.</li> </ul>
$\theta_{U,t}$	urchin recruitment timing function	[0.05 0.54 0.36 0.05]				<p><b>Will likely depend on CC</b></p> <ul style="list-style-type: none"> <li>- ([Winter, Spring, Summer, Autumn])</li> <li>- baseline: 90% evenly across March-July (Okamoto et al. 2020)</li> </ul>
$\alpha$	strength of recruitment facilitation by adults	$1 \times 10^{-3}$				<ul style="list-style-type: none"> <li>- purples: flexible in recruitment habitat &amp; have weaker effects (Tegner and Dayton 1977, Clemente et al. 2013)</li> <li>- reds: depend strongly on adults (Tegner and Dayton 1977, Nishizaki and Ackerman 2007), but effect varies site-to-site (Zhang et al. 2011)</li> <li>- Pfister and Bradbury 1996 explore two extremes for strength value</li> </ul>
$var(u_{H,t} + u_{E,t})$	Variance in the density of adult urchins across the model unit space	5,751,518	(kg)			<ul style="list-style-type: none"> <li>- Spatial variance at transect level, averaged over years. Data from PISCO kelp surveys at the Channel Islands. See PISCO_kelp-urchin-sheephead_data.Rmd for details</li> </ul>
$g_{mat}$	average urchin maturation age	2	yrs	(Gonor 1972)		<ul style="list-style-type: none"> <li>- Gonor 1972: purples (~24mm test), central Oregon</li> <li>- See Zhange et al 2011 for possible red info</li> </ul>
$M_j$	instantaneous natural mortality rate of stage $j$	$\begin{matrix} juvs \\ hiding \\ exposed \end{matrix} \begin{bmatrix} 0.1 \\ 0.1 \\ 0.1 \end{bmatrix}$	season <sup>-1</sup>	(Russell 1987, Dunn et al. 2017)		<ul style="list-style-type: none"> <li>- purples: adult mortality based on tidepool experiments NW pacific coast (Russell 1987) (also used as natural mort. in Dunn et al. 2017)</li> <li>- reds: similar rates (M = 0.1), although this is in the presence of predators (Ebert and Russell 1992)</li> <li>- Juvs unclear from lit, Dunn et al 2017 uses 0.1, but should be lower than adults?</li> </ul>
$F$	fishing mortality					
$P$	instantaneous predation mortality rate of stage $j$ (per kg predator)	$\begin{matrix} hiding \\ exposed \end{matrix} \begin{bmatrix} 0.0065 \\ 0.013 \end{bmatrix}$	kg pred <sup>-1</sup> .season <sup>-1</sup>	(Nichols et al. 2015, Selden et al. 2017)		<ul style="list-style-type: none"> <li>- see Selden2017_UrchinPredRates.xlsx (uses biomass from Fig. 2 inside &amp; outside MPA to get a linear relationship for the effect of increasing predators Fig. 4). Prop eaten per trial = 0.01.kg sheephead = 0.01 instantaneous rate.</li> <li>- Nichols et al. 2015, demonstrates that predation mortality is approx. halved with cover (Fig. 3).</li> <li>- Assuming that Selden values are average of exposed and covered.</li> <li>- Check out <b>Dunn &amp; Hovel 2019 as well</b></li> </ul>
PLD	Planktonic larval duration	65	days	(from Nur et al 2024 table)		<ul style="list-style-type: none"> <li>- middle of range (40-90) in Nur et al, took average. To clarify ref. <b>will depend on CC.</b></li> </ul>
$w_1$ $w_2$	Behaviour switching function: Inflection point Slope	1 0.5				<ul style="list-style-type: none"> <li>- functional form from Randell 2022</li> <li>- values are arbitrary; w2 value set so that kelp forest switches to urchin barren around observed urchin biomass thresholds for California (~1.3 kg.m; Ling et al. 2015)</li> </ul>
$k_{J+A}^{min}$	standing kelp density threshold below which a kelp barren state is declared	1170	kg			<ul style="list-style-type: none"> <li>- 1% of the average standing kelp densities (~700kg.60m<sup>2</sup>/0.006 = ~ 1.17*10<sup>5</sup>kg.ha) observed in kelp forested state, based on PISCO data for Channel Islands at Anacapa East</li> </ul>

	Winter DJF	Spring MAM	Summer JJA	Autumn SON	
Pre-heatwave daily avgs	13.8	12.8	15.6	16	SBC LTER - Reef bottom temp data
Heatwave daily avgs	15.5	14.2	17.2	18.4	SBC LTER – Heatwave period
spore production	peaks				(not explicitly in model) Reed et al. 1996
Seasonal change in recruitment	0.1	0.1	0.4	0.4	Reed et al. 2008
MHW recruitment	0.1x0.7	0.1x0.7	0.4x0.7	0.4x0.7	Hollarsmith et al. 2020
'growth'	1	1	1	1	
MHW growth	1	1	0.5	0.5	Zimmerman & Kremer 2986
Seasonal change in grazing rates	x1	x0.9	x1.15	x1.2	Baseline grazing = 2.985 (see Spindel fig 3.2 datasheet)
MHW seasonal change grazing	X1.15	x1.05	x1.2	x1.3	
Management (when on)					

**Commented [JH9]:** x1/7 (7-fold decrease in sporophyte production with temps >20°C for San Diego collected kelp; Hollarsmith et al. 2020). Applies throughout the year (note that it is multiplied by the recruitment timing function)

**Commented [JH10]:** growth declines as temp increases: 50% reduction from 19 to ~20°C in Channel Islands (Zimmerman and Kremer 1986, see also data in folder). This only applies during the summer/autumn when temps can peak above 20°C

	Winter DJF	Spring MAM	Summer JJA	Autumn SON
Seasonal change in recruitment	0.1	0.1	0.4	0.4
MHW recruitment	0	0	0.4	0.4
'growth'	1	1	1	1
MHW growth	0.5	0.5	1	1
grazing rates	2.985	2.985	2.985	2.985
MHW grazing rates	X1.4	X1.4	X1	X1
Management (when on)				