

OLM12.4. Kelp forests and urchin barrens as alternative stable states

The difference between the species diversities of forests and deserts is huge. It is no different in the oceans either. The highly productive “forests” or “beds” of brown macroalgae (*Laminariales*) are far more diverse than the deserts of crustose red algae (*Corallinales*) on rocky subtidal reefs. Evidence accumulates in support of the view that these two habitats might be two alternative stable states of the same community, any one transforming into the other by hysteresis. We have shown by the example of forests and savannas in the last chapter of our book (Ch12.3, p. 273-4) that a dynamical system admitting alternative stable states may show a patchy pattern even if the environment is spatially homogeneous. Multispecies kelp forest patches alternating with crustose coralline algal “urchin barrens” are examples of such systems. The patches are persistent if the transition between the alternative stable states admits hysteresis. It was possible to demonstrate that alternative stable states and hysteresis characterize a simplified three-component model system with an inedible but competitively inferior algal species facilitating the occurrence of a herbivore consuming the dominant competitor alga (Baskett and Salomon 2010). In contrast with the example presented in the previous OLM (OLM 12.3) pertaining to shallow lakes, changes in the physical environment are not indispensable for positive feedback and hysteresis to occur in this case (vs. Kéfi et al. 2016). Based on the model of Baskett and Salomon (2010) we show in the following that the shift between the alternative states of the system may be induced by changing the equilibrium density of the herbivore in itself.

The map of Figure 12.4.1 shows that transitions between diverse kelp forests and urchin barrens have been repeatedly observed in both directions in different regions of the world. Since no global survey has been carried out, the frequency of these transitions is not yet reliably determined. What we can say even from the data we have so far is that the transition, if it occurs, is usually relatively abrupt both ways, completed within just a few years. At locally different threshold densities sea urchins, which are normally generalist foragers, invade kelp forest and switch to herbivory instead of consuming the detritus otherwise produced at high abundance by the forest, thus increasing the growth potential of their population substantially. Kelp forests quickly recover in place of barrens when grazing intensity is dropped. The actual events crucially depend on urchin density that changes from time to time and place to place for different reasons: it depends on the presence and the population size of sea otters or some predatory fish, the intensity of urchin harvesting, the protection of regularly harvested kelp forests from urchin invasions, El Niño-Southern

Oscillation, and diseases. The review of Filbee-Dexter and Scheibling (2014) presents a case-to-case account of these causes.

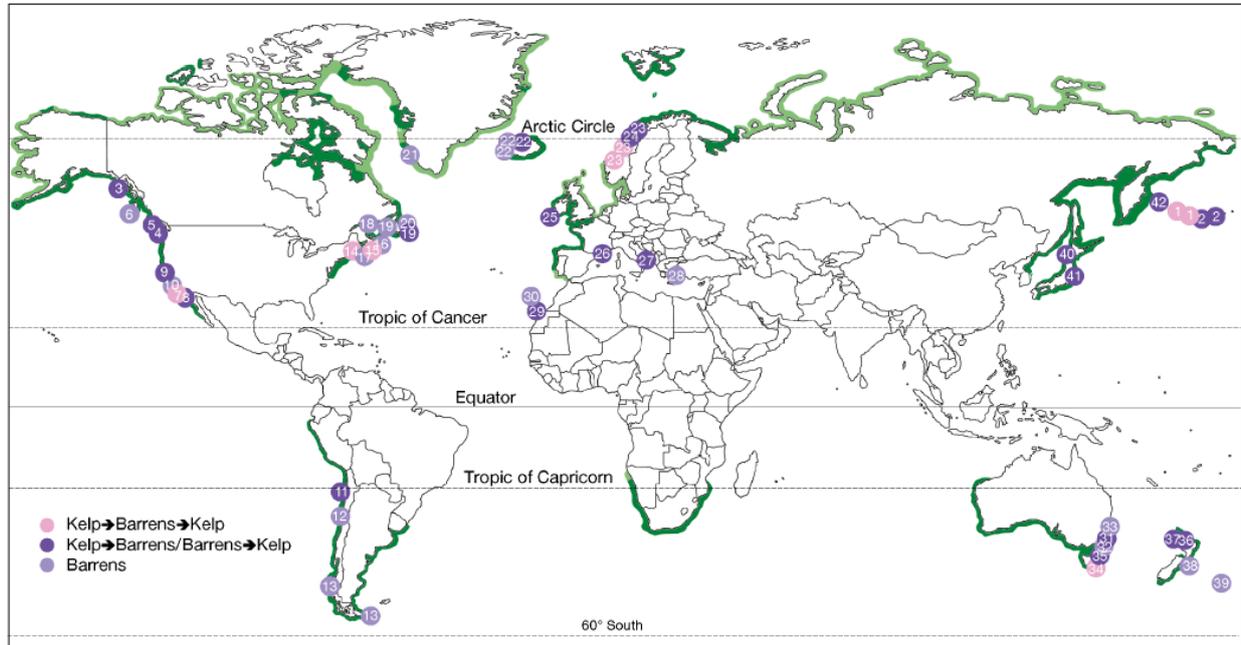


Figure 12.4.1 The global distribution of sea urchin barrens and macroalgae (Filbee-Dexter and Scheibling 2014). © 2014 Inter-Research

Original legend: Numbered locations (colored circles) indicate areas where urchin barrens have been documented: (1) through the course of multiple phase shifts between kelp beds and barrens (pink), (2) following a single phase shift from a kelp to a barrens state, or vice versa (dark purple), and (3) in areas that might otherwise support kelp, although a phase shift has not been observed (light purple). Locations outside the kelp range indicate barrens within communities of canopy-forming brown algae that are functionally and taxonomically similar to kelps. Dark green shading represents observed range of kelp (Raffaelli and Hawkins 1996, redrawn from Steneck et al. 2002). Light green shading represents the range of potential occurrence of kelp, based on the light and temperature requirements for kelp (approximated by latitude) (Krumhansl and Scheibling 2012, K. A. Krumhansl pers. comm.). Dark green areas in the Beaufort Sea, Canadian Arctic, Greenland and northern Europe represent recorded kelp beds within the potential range of kelp.

This review presents a more detailed version of Table 12.4.1. that contains the most important data supporting the empirical occurrence of hysteresis. This shows that the urchin barren to kelp forest transition occurs at an urchin biomass density about an order of magnitude lower than the threshold density of kelp forest collapse.

Table 12.4.1 Sea urchin density and biomass required to trigger system shifts at six sites (after Filbee-Dexter and Scheibling 2014). © 2014 Inter-Research

Data from field observations (Obs) and experimental transplantation or removal of sea urchins (Exp). Biomass decrease (%) provides the percentage decrease in threshold biomass between forward and reverse shifts. See sources of data in Filbee-Dexter and Scheibling (2014).

Region	Method	Threshold density (ind /m ²)		Threshold biomass (kg /m ²)		Biomass decrease (%)
		K→B	B→K	K→B	B→K	
Alaska, USA	Exp	72	16	1.81	0.41	77
California, USA	Obs	14	2–3	2.81	0.4–0.61	82
Chile	Obs	36	20–28	–	–	–
Nova Scotia, Canada	Obs, Exp	31–65	–	1.5–3.2	0.15–0.25	91
Norway	Obs, Exp	45–75	10	1.0–1.7	0.22	84
Tasmania, Australia	Obs, Exp	4–10	0.2–1.2	0.9–2.3	0.05–0.28	90

The model of Baskett and Salomon (2010) was designed to studying the consequences of the excretion of chemicals by crustose coralline algae which promote the colonisation and development of herbivores including sea urchins. The urchins, feeding on the microalgal films and macroalgal recruits, prevent the recruitment of brown algae. The three components of the system studied are brown algae, sea urchins and crustose coralline algae. Each component is composed of more than a single species, but they are treated as single species in the model which is based on the following observations: 1.) Sea urchins consume brown algae, but not the crustose corallines; 2.) In the absence of herbivores the two algae compete for light, which is advantageous for the taller brown algae and detrimental for the crustose ones; 3.) The crustose algae excrete a chemical substance that facilitates the settling of urchin larvae. The state variables of the model and the relations of its components are shown in Figure 12.4.2.

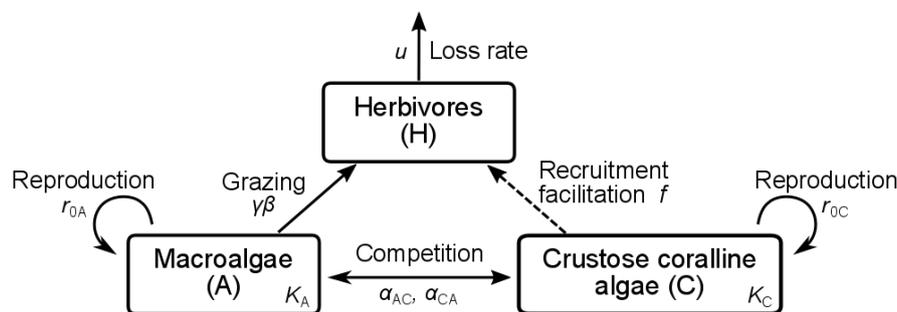


Figure 12.4.2 The sketch of the three-component system showing the processes modelled and the notations used (after Baskett and Salomon 2010). Reprinted by permission of John Wiley & Sons.

Let us write down the equations of the dynamics of the three species. *a* is the forest- or bed-forming alga, *c* is the crustose alga, and *h* is the herbivore, whose state variables (densities or biomasses) are *A*, *C* and *H*. The competitive interaction between the kelp and the crustose alga is represented in an implicit manner by a Lotka-Volterra model of parameters r_0 and a_{ij} as usually (TBox 9.1, p.171). The equation for the crustose alga is the simpler one:

$$\frac{1}{C} \frac{dC}{dt} = r_c = r_{0c} - a_{cc}C - a_{ca}A \quad (12.4.1)$$

As shown also in OLM 9.1, the conditions of coexistence are typically expressed as functions of the parameters r_{0i} , K_i and a_{ij}/a_{ii} . Introducing the notations $K_c = r_{0c}/a_{cc}$ and $\alpha_{ca} = a_{ca}/a_{cc}$ (the first of which is the equilibrium density of the crustose alga and the latter the strength of interspecific relative to intraspecific competition) the equation can be re-written into the form used by (Baskett and Salomon 2010):

$$r_c = \frac{r_{0c}}{K_c} (K_c - C - \alpha_{ca}A) \quad (12.4.2)$$

The equation for kelp algae will be given in the corresponding form, with the loss term due to herbivory added assuming Holling Type I, i.e., linear functional response (TBox 6.3, p.108) and where factor β stands for herbivore foraging efficiency.

$$\frac{1}{A} \frac{dA}{dt} = r_a = \frac{r_{0a}}{K_a} (K_a - A - \alpha_{ac}C) - \beta H \quad (12.4.3)$$

The facilitating effect of crustose algae was included by a proportion f of potential herbivore population increase linearly depending on the density of facilitating algae, and the remaining $(1-f)$ proportion being independent of it. The loss rate of the herbivore is u and its resource conversion factor is γ :

$$\frac{1}{H} \frac{dH}{dt} = r_h = \gamma\beta A \left(1 - f + f \frac{C}{K_c}\right) - u \quad (12.4.4)$$

Consequently, the growth rate of the herbivore depends only on the density of the algae (exclusive resource limitation, p.115) and both types of algae have a positive effect on herbivore population growth.

The possible fixed points of the dynamical system and the transitions between them are shown on Figure 12.4.3.

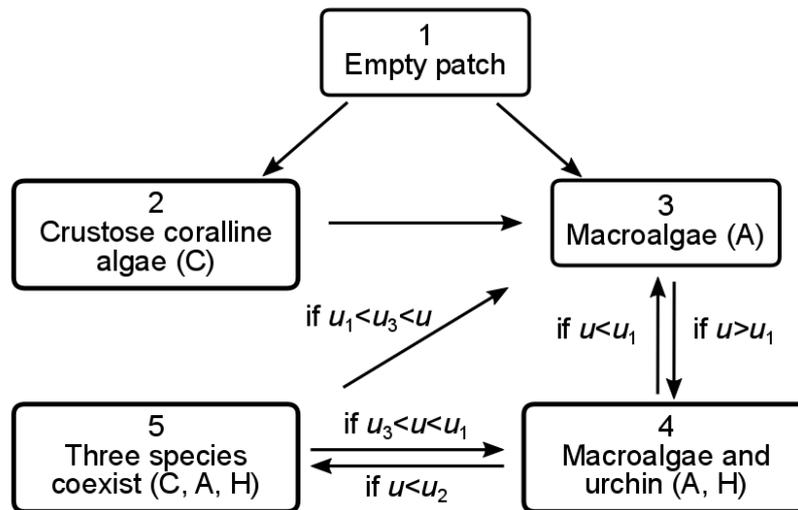


Figure 12.4.3 The three-component system with 5 equilibria and the transitions among them (model of Baskett and Salomon 2010).

Transitions occur if the fixed points are perturbed. The first two equilibria are unstable, so there are no conditions assigned to the arrows originating on them. The other three fixed points may or may not be stable or unstable, depending on the loss rate (u) of the sea urchin population. At certain specific values of the loss rate some of these fixed points may not exist at all. The critical values of the loss rate (u_1, u_2, u_3) are explained in the text.

Let us discuss the stability properties of the fixed points! The first fixed point is the trivial one with no populations at all – this is obviously unstable, because any one of the algae can invade. The second and the third fixed points correspond to the two algal populations in themselves, at densities K_a and K_c . The parameters are set so that the kelp alga can exclude the crustose in the absence of herbivores. This translates to the condition that the initial growth rate of the kelp alga be positive in the equilibrium population of the crustose, but that of the crustose alga be negative at the equilibrium density of the kelp, i.e., $r_{Ia} > 0$ and $r_{Ic} < 0$ if $H=0$.

$$r_{Ia} > 0 \text{ if } K_a - \alpha_{ac}K_c > 0 \quad (12.4.5)$$

$$\frac{K_a}{K_c} > \alpha_{ac} \quad (12.4.6)$$

and

$$r_{Ic} < 0 \text{ if } K_c - \alpha_{ca}K_a < 0 \quad (12.4.7)$$

$$\frac{K_c}{K_a} < \alpha_{ca} \quad (12.4.8)$$

The fourth equilibrium state of the community is the coexistence of the kelp alga with the herbivore. The herbivore can spread in the equilibrium population of the kelp alga:

$$r_{Ih} > 0 \text{ if } \quad \gamma\beta K_a(1-f) - u > 0 \quad (12.4.9)$$

that is,

$$u < \gamma\beta K_a(1-f) := u_1 \quad (12.4.10)$$

As we have already seen (Eq.6.21, p.109) the settlement of a consumer is easier if it has a small loss rate and the unconsumed equilibrium density of its resource population (K_A in this model) is high. Increasing $\gamma\beta$, i.e., the efficiency of resource utilisation, has also a positive effect on consumer settlement. If there is no crustose alga present, then there is no facilitation, i.e., $f = 0$. The density of brown algae necessary for the settlement of the urchin population is the highest in this case. We do not detail the calculations of the equilibrium of the brown alga and the herbivore (r_a and r_h must be set equal to 0 in Equations (12.4.3) and (12.4.4) and the resulting algebraic equations solved with the condition $C = 0$). The result is shown in the fourth line of Table 12.4.2 In accordance with the expectation (Figure 6.14, p.108) the equilibrium alga density increases with the loss rate of the herbivore, and it decreases with the efficiency of resource utilisation.

We explore under what conditions the crustose alga can settle in this system. Urchins – as top consumers – decrease the equilibrium density of kelp algae, thus enabling crustose algae to invade, provided that their initial rate of increase is positive on this lower kelp density.

$$r_{Ic} > 0 \text{ if } \quad K_c - \alpha_{ca}\hat{A}_4 > 0 \quad (12.4.11)$$

Rearranging,

$$\hat{A}_4 < \frac{K_c}{\alpha_{ca}} \quad (12.4.12)$$

Substituting the equilibrium density of the kelp algae (Table 12.4.2) yields

$$\frac{u}{\gamma\beta(1-f)} < \frac{K_c}{\alpha_{ca}} \quad (12.4.13)$$

$$u < \frac{K_c\gamma\beta(1-f)}{\alpha_{ca}} := u_2 \quad (12.4.14)$$

That is, crustose algae can invade if the loss rate of the herbivore decreases below the critical u_2 level, because the equilibrium density of the macroalgae decreases along with the loss rate of the consumer.

Now we have two critical loss rate values for the herbivore: u has to be lower than u_1 for the kelp forest to maintain the herbivore, and it has to be lower than u_2 for its helper to be able

to invade. The relationship of these two criteria can be studied by expressing the $\gamma\beta(1-f)$ product from Eq.(12.4.10) and substituting into Eq.(12.4.14), which reveals that

$$u_1 \frac{K_c}{K_a} \frac{1}{\alpha_{ca}} = u_2 \quad (12.4.15)$$

From Eq.(12.4.8) (the crustose alga is the weaker competitor) it follows that

$$\frac{K_c}{K_a} \frac{1}{\alpha_{ca}} < 1, \quad (12.4.16)$$

thus $u_2 < u_1$. That is, the kelp forest is a stable fixed point when herbivore loss rates are sufficiently high. If the loss rate is lower than u_1 but higher than u_2 the herbivore can invade but the crustose alga cannot. If the loss rate of the herbivore decreases below u_2 , then the density of the kelp alga becomes so low that the crustose alga can invade, too. The necessary condition for the three components of the system to coexist is thus $u < u_2$. However, the fact that the crustose alga can invade the kelp alga – urchin patch does not necessarily imply long-term coexistence.

Coexistence requires that all the three components have zero growth at the equilibrium point. Starting from the three equations representing the dynamics of the three components we ask at which u the condition that the three growth rates are zero is met. The equilibrium density of the crustose alga does not depend on that of the urchins, only on the kelp's, so it can be calculated by rearranging Eq. (12.4.2):

$$\hat{C} = K_c - \alpha_{ca}\hat{A} \quad (12.4.17)$$

Substituting this in Eq.(12.4.4) the growth rate of the herbivore is zero if

$$\beta\gamma\hat{A} \left(1 - f + f \frac{K_c - \alpha_{ca}\hat{A}}{K_c} \right) - u = 0 \quad (12.4.18)$$

This equation contains the equilibrium density of the kelp alga (\hat{A}) alone, and it is of second degree in that variable. Rearranging into the usual form of second degree equations

$$-\frac{f\gamma\beta\alpha_{ca}}{K_c}\hat{A}^2 + \gamma\beta\hat{A} - u = 0 \quad (12.4.19)$$

This equation has a real solution if

$$\gamma^2\beta^2 - \frac{4f\gamma\beta\alpha_{ca}u}{K_c} = \gamma\beta \left(\gamma\beta - \frac{4f\alpha_{ca}u}{K_c} \right) \geq 0 \quad (12.4.20)$$

Since the parameters are positive, this condition is equivalent to

$$\gamma\beta - \frac{4f\alpha_{ca}u}{K_c} \geq 0 \quad (12.4.21)$$

Rearranging the latter we get a new condition for the loss rate of the herbivore:

$$u \leq \frac{\gamma\beta K_c}{4f\alpha_{ca}} := u_3 \tag{12.4.22}$$

The coexistence of the three species is possible if the loss rate of the herbivore is below this value. If $u < u_3$ holds, then Eq. (12.4.19) has two solutions, of which only the smaller one is a locally stable equilibrium (Baskett and Salomon 2010); therefore we discuss only that one here.

It follows from Eqs. (12.4.14) and (12.4.22) that

$$u_3 = \frac{u_2}{4f(1-f)} \tag{12.4.23}$$

Since $f(1 - f) \leq 0.25$ (as this product has its maximum at $f=0,5$) $u_3 \geq u_2$; that is, the coexistence of the three species – once it has occurred – may be stable even at high herbivore loss rates at which the initial growth rate of the crustose alga is already negative.

The values of the state variables at the five possible fixed points are given in Table 12.4.2 Let us consider the results so far from the viewpoint of the possible state transitions in Figure 12.4.3, in which the conditions of the transitions just obtained are assigned to the arrows. High urchin loss rate (mortality) and the consequential low population density is advantageous for the maintenance of the kelp forest, whereas low urchin mortality (high herbivore density) results in the collapse of the kelp forest, in accordance with the observations.

Table 12.4.2 Equilibrium densities of the three populations in the 5 possible fixed points of the system. The labelling of the equilibria is the same as in Figure 12.4.1

State	crustose \hat{C}	kelp \hat{A}	urchin \hat{H}
1	$\hat{C}_1 = 0$	$\hat{A}_1 = 0$	$\hat{H}_1 = 0$
2	$\hat{C}_2 = K_c$	$\hat{A}_2 = 0$	$\hat{H}_2 = 0$
3	$\hat{C}_3 = 0$	$\hat{A}_3 = K_A$	$\hat{H}_3 = 0$
4	$\hat{C}_4 = 0$	$\hat{A}_4 = \frac{u}{\gamma\beta(1-f)}$	$\hat{H}_4 = \frac{r_{0a}}{\beta K_a}(K_a - \hat{A}_4)$
5	$\hat{C}_5 = \frac{K_c - \alpha_{ca}\hat{A}_5}{K_c - \alpha_{ca}\hat{A}_5}$	$\hat{A}_5 = \frac{\gamma\beta - \sqrt{\gamma^2\beta^2 - \frac{4f\gamma\beta\alpha_{ca}u}{K_c}}}{\frac{2f\gamma\beta}{K_c}}$	$\hat{H}_5 = \frac{r_{0a}}{\delta K_a}(K_a - \hat{A}_5 - \alpha_{ac}\hat{C}_5)$

Next we analyse more closely how the composition of the community changes with the loss rate of the herbivore (Figure 12.4.4). We start at a high loss rate (grey arrows on the figure) where the kelp forest is the stable equilibrium state – neither sea urchins nor crustose algae persist. Decreasing the loss rate to under u_1 the herbivore could establish, and even lower, below u_2 , the crustose alga appears, too, thus the three species coexist. With the loss rate shrinking, the density of the brown alga decreases and that of the crustose increases. Starting from a low value and increasing the loss rate (with high initial densities of herbivores and crustose algae) the trajectory of changes is different: until the critical $u_3 > u_2$ loss rate the coexistence of the three species is maintained with the dominance of the crustose alga. Above u_3 the crustose alga disappears; what remains in equilibrium is either the kelp alga and the herbivore or just the kelp alga. The two trajectories (increasing and decreasing loss rate) are different between the critical loss rates u_2 and u_3 . Comparing this picture to Figure 12.35 of our book (TBE, p.273) the similarity is obvious. The forward and the backward phase shift occur at different values of the critical variable, i.e., the system shows hysteresis. The reason behind this is the facilitating effect of the crustose alga on the settlement of the herbivore which, in turn, helps the growth of the crustose alga, thus creating a positive feedback loop. This is why the crustose alga may persist under conditions at which its initial growth rate is already negative, i.e., at which it could not invade.

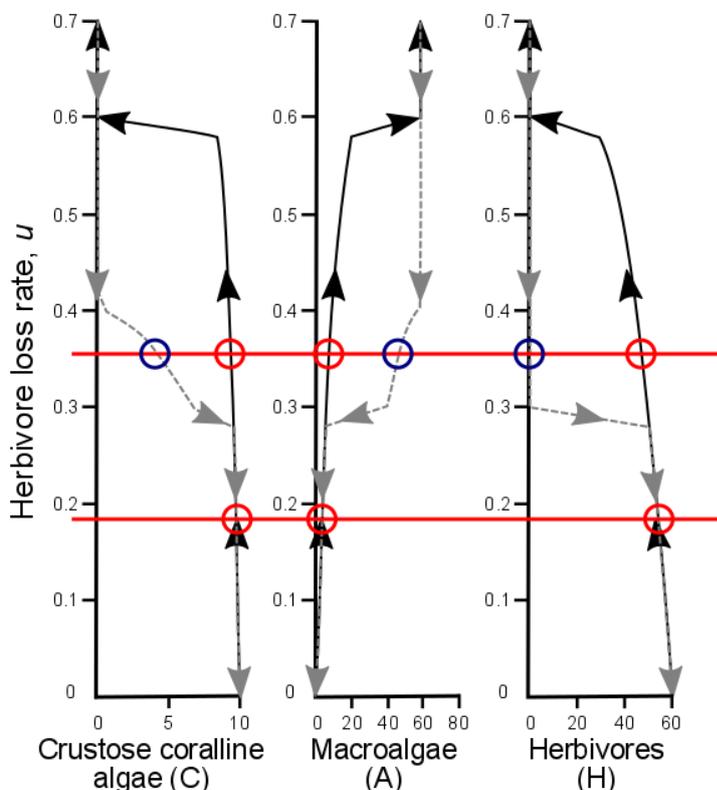


Figure 12.4.4: Hysteresis in the urchin-macroalga-alga system (after Baskett and Salomon 2010).

Changes in the densities of the three populations with the loss rate of the herbivore decreasing from a high value, i.e., with the conditions of its population growth improving (grey arrows) or with increasing the loss rate from a low value (black arrows). At the actual parameter values ($r_{0c} = 50$, $r_{0a} = 100$, $K_c = K_a = 60$, $\alpha_{ca} = 1.5$, $\alpha_{ac} = 0.5$, $\gamma\beta = 0.05$, and $f = 0.85$) there are two alternative stable states between the loss rates 0.3 and 0.6: kelp forest and urchin barren. Reprinted by permission of John Wiley & Sons.

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