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HERBIVORE HARVESTING AND ALTERNATIVE STEADY STATES IN CORAL REEFS

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Abstract. Coral reefs can undergo relatively rapid changes in the dominant biota, a phenomenon referred to as phase shift. Degradation of coral reefs is often associated with changes in community structure towards a macroalgae-dominated reef ecosystem due to the reduction in herbivory caused by overfishing. We investigate the coral-macroalgal phase shift due to the effects of harvesting of herbivorous reef fish by means of a continuous time model in the food chain. Conditions for local asymptotic stability of steady states are derived. We have shown that under certain conditions the system is uniformly persistent in presence of all the organisms. Moreover, it is shown that the system undergoes a Hopf bifurcation when the carrying capacity of macroalgae crosses certain critical value. Computer simulations have been carried out to illustrate different analytical results.

Keywords: phase shift; coral bleaching; harvesting; Hopf bifurcation

MSC 2020: 34A34, 34D20, 92D25

1. Introduction

The role of macroalgae as an essential nursery ground for many coral reef fish species is well documented [9]. Macroalgae serve as a major food source for a wide variety of herbivores in coral reefs. Despite the recognized roles of macroalgae in coral reefs, proliferation of macroalgae in coral reefs is increasingly related to coral reef decline [3], [13]. As observed by Bruno et al. [5], reefs have shown a tendency to exist in alternate coral- or algae-dominated states. Degradation of coral reefs

often involves phase shifts in community structure for which abundance of corals declines with an increase in abundance of macroalgae [7]. Phase shifts in coral reefs are mostly driven by the competition for light and space between corals and macroalgae. According to Lirman [17], macroalgae may compete with corals by basal encroachment, shading or abrasion and allelopathic chemical defenses. Also, macroalgae can dominate corals through space pre-emption by reducing available space for the successful settlement of coral larvae [29]. As observed by Mumby et al. [22], coral can inhibit algae growth by shading, stinging, allelopathic chemical defenses, the occupation of space, mucus secretion, and overgrowth. Although corals grow in the range of approximately 2–185 mm per year [12], the collective growth of many colonies across a large area can return the area to coral dominance within a few years [1].

Coral reefs throughout the world have suffered substantial declines in coral cover and species diversity due to the proliferation of macroalgae and overfishing of herbivorous reef fish [23]. In coral reef ecosystems, macroalgae and corals compete for space and when herbivores are not present, the faster growing macroalgae often overgrow corals, depriving them of essential sunlight and causing their decline [4]. The grazing of macroalgae by herbivores contributes to the resilience of the coral-dominated reef. There is substantial evidence that herbivore removal by harvesting has resulted in increased algal growth on coral reefs at the expense of living coral cover [18], [28]. This resulted in a phase shift from coral-dominated reef to algal reef with proliferation of macroalgae, resulting in coral bleaching [10].

Parrotfish are some of the most abundant fish on Caribbean reefs, dominating the biomass of herbivorous fishes. They are known to prefer macroalgae to living corals and infrequently feed on actual live coral tissue. Concerned about the harmful consequences of phase shifts towards increased macroalgal cover, Mumby [21] pointed out that prevalence of Parrotfish actually benefits coral reefs. The phase shift could be a result of overfishing of Parrotfish which favour macroalgae over coral. It can result in permanent shift in state in which macroalgae, once dominant, inhibit coral settlement. This leads to the disruption of symbiosis between coral polyps and microalgae zooxanthellae, resulting in the expulsion of zooxanthellae and loss of photosynthetic pigments. As observed by McManus and Polsenberg [20], if stresses continue for long enough, corals can suffer extensive mortality, and eventually bleach.

We study a model in which the interacting organisms, macroalgae and corals, exhibit modified logistic growth in the absence of Parrotfish. Herbivorous Parrotfish feed mostly on macroalgae but also on a small amount of corals. Experimental observations by Murray et al. [24] reveal that Holling II functional response is quite accurate in predicting the observed functional response of fishes. This prompts us to use Holling II response function in our model. Parrotfish are harvested with a non-

constant harvesting policy [16]. In particular, for a more realistic approach, a rational harvesting function has been considered in the model which provides diminishing marginal returns of the harvesting organization.

In the present paper, the main emphasis will be put on studying the dynamic behaviour of the system and role of harvesting and coral-macroalgal competition parameters in coral-macroalgal phase shifts. We have studied the model analytically as well as numerically; proofs are all relegated to the Appendix.

2. THE BASIC MODEL

We take a model in which algae and corals are growing with concentration $P(t)$ and $C(t)$, respectively, at time t. Herbivorous Parrotfish are growing in the system by feeding on algae as well as corals having concentration $x(t)$ at time t. Parrotfish are harvested at a density-dependent harvesting policy [11].

We make the following assumptions in formulating the mathematical model:

(H1) In the absence of corals and herbivores, macroalgae follow the logistic growth with intrinsic growth rate r_1 and carrying capacity K_1.

(H2) In the absence of macroalgae and herbivores, corals follow the logistic growth with intrinsic growth rate r_2 and carrying capacity K_2.

(H3) The effect of coral on macroalgae is expressed by the competition coefficient α_1, representing the rate of inhibition of macroalgal growth by corals due to shading, stinging, allelopathic chemical defenses and mucus secretion [19].

(H4) The rate of inhibition of the growth of corals by macroalgae due to shading, abrasion, allelopathic chemical defenses and macroalgal overgrowth is represented by the sigmoidal Hill function $\alpha_2 P^n/(a^n + P^n)$, where α_2 is the interspecific competition coefficient, a is the macroalgal concentration at which coral concentration is half its carrying capacity and n is the measure of macroalgal effect on coral as the community structure of algae shifts. Figure 1 shows that at larger values of n, corals are less sensitive to low concentration of macroalgae, but macroalgae outcompete corals when their concentration crosses a certain threshold.

The basic equations with all the parameters are:

$$(2.1) \quad \frac{\mathrm{d}P}{\mathrm{d}t} = r_1 P\left(1 - \frac{P + \alpha_1 C}{K_1}\right) - \frac{m_1 P x}{a_1 + P + b_1 C} \equiv F^1,$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = r_2 C\left(1 - \frac{C + \alpha_2 P^n/(a^n + P^n)}{K_2}\right) - \frac{m_2 C x}{a_2 + P + b_2 C} \equiv F^2,$$

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x\left(\frac{e_1 m_1 P}{a_1 + P + b_1 C} + \frac{e_2 m_2 C}{a_2 + P + b_2 C} - \frac{h}{b + x} - D\right) \equiv F^3,$$
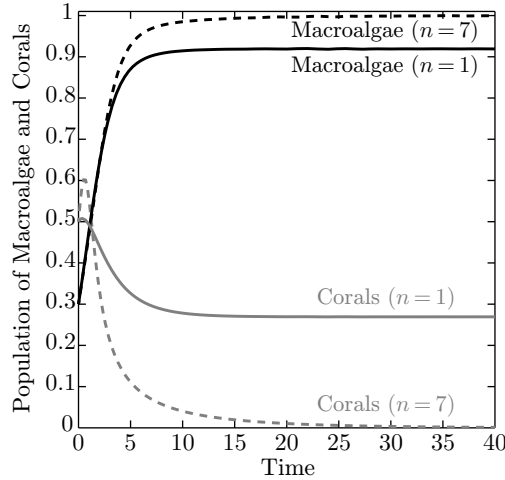
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Figure 1. The effect of macroalgae (in black) on the growth of coral (in gray) for $n = 1$ (solid) and $n = 7$ (dashed).

where $P(0) \geqslant 0$, $C(0) \geqslant 0$, $x(0) \geqslant 0$.

Here, D is the death rate of Parrotfish, h is the maximum harvesting rate of Parrotfish and b is the concentration of Parrotfish for which the rate of harvesting is half its maximum, m_i are the maximal uptake rates, a_i are the half-saturation constants and $P + b_i C$ is the interference of coral and macroalgae on the per-capita growth rate of Parrotfish ($i = 1, 2$). Also, e_i is the growth efficiency ($0 < e_i < 1$, $i = 1, 2$) of Parrotfish on macroalgae and coral, respectively; all of these are positive quantities.

Obviously, the right-hand sides of system (2.1) are continuous smooth functions on $\mathbb{R}_+^3 = \{(P, C, x): P, C, x \geqslant 0\}$. Indeed, they are Lipschitzian on $\mathbb{R}_+^3$ and so the solution of the system (2.1) exists and is unique. Therefore, the interior of the positive octant of $\mathbb{R}^3$ is an invariant region.

3. Boundedness and uniform persistence of the system

Theorem 3.1. *For all $\varepsilon > 0$, there exists $t_\varepsilon > 0$ such that for $t \geqslant t_\varepsilon$, all the solutions of (2.1) enter into the set*

$$\left\{ (P, C, x) \in \mathbb{R}^3 \colon P(t) + C(t) + x(t) \leqslant \frac{K(r_1 + r_2)}{D_0} + \varepsilon \right\},$$

where $K = \max\{K_1, K_2\}$ and $D_0 = \min\{r_1, r_2, D\}$.

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The above theorem states that, with non-negative initial values and other parameter values in the ecosystem, the concentrations P, C and x will always remain finite and bounded.

By definition, the system will be uniformly persistent if there exist $u_{1_i}, M_i \in (0, \infty)$ such that $u_{1_i} \leqslant \liminf\limits_{t \to \infty} u_i(t) \leqslant \limsup\limits_{t \to \infty} u_i(t) \leqslant M_i$, for each organism $u_i(t)$ in the system [26], [6]. Uniform persistence represents convergence on an interior attractor from any positive initial conditions and so it can be regarded as a strong form of coexistence [8]. From a biological point of view, uniform persistence of a system ensures the survival of all the organisms in the long run.

Since $\limsup\limits_{t \to \infty}\{P(t) + C(t) + x(t)\} \leqslant K(r_1 + r_2)/D_0$ as $t \to \infty$, it follows that there exists a positive number $M < K(r_1 + r_2)/D_0$ such that $x(t) \leqslant M$ for large values of t.

The following theorem rules out the possibility of extinction of any organism in the system:

Theorem 3.2. *For large t, if $h \leqslant \bar{h}$ and $K_1 > \alpha_1 \alpha_2$ hold, there exists $x_1 > 0$ such that all the solutions of (2.1) enter into the set $\{(P, C, x) \colon p_1 \leqslant P(t) \leqslant K_1,$ $c_1 \leqslant C(t) \leqslant K_2,\ x_1 \leqslant x(t) \leqslant M\}$ and will remain there forever, where*

$$\bar{h} = b\Big(\frac{e_1 m_1 p_1}{a_1 + b_1 K_2 + K_1} + \frac{e_2 m_2 c_1}{a_2 + b_2 K_2 + K_1} - D\Big),$$

$$p_1 = K_1\Big(1 - \frac{m_1 M}{a_1 r_1}\Big) - \alpha_1 K_2, \ \ c_1 = K_2\Big(1 - \frac{m_2 M}{a_2 r_2}\Big) - \alpha_2$$

and

$$0 < M < \min\Big\{\frac{a_1 r_1 (K_1 - \alpha_1 K_2)}{m_1 K_1}, \frac{a_2 r_2 (K_2 - \alpha_2)}{m_2 K_2}, \frac{K(r_1 + r_2)}{D_0}\Big\}.$$

Thus, if the carrying capacity of macroalgae exceeds $\alpha_1 \alpha_2$, then restricted harvesting of Parrotfish can lead to coexistence of all the organisms in the system.

4. Equilibria and their stability

System (2.1) possesses the following equilibria:

(i) Organism-free equilibrium $E_0 = (0, 0, 0)$;

(ii) coral- and fish-free equilibrium $E_1 = (K_1, 0, 0)$;

(iii) coral-free equilibrium $E_2 = (p_2, 0, x_2)$, where p_2 is a positive root of the equation

$$\frac{e_1 m_1 P}{a_1 + P} - \frac{h m_1 K_1}{b m_1 K_1 + r_1 (K_1 - P)(a_1 + P)} - D = 0 \quad \text{and} \quad x_2 = \frac{r_1 (K_1 - p_2)(a_1 + p_2)}{m_1 K_1};$$

(iv) macroalgae- and fish-free equilibrium $E_3 = (0, K_2, 0)$;

(v) macroalgae-free equilibrium $E_4 = (0, c_4, x_4)$, where c_4 is a positive root of the equation

$$\frac{e_2 m_2 C}{a_2 + b_2 C} - \frac{h m_2 K_2}{b m_2 K_2 + r_2 (K_2 - C)(a_2 + b_2 C)} - D = 0$$

and

$$x_4 = \frac{r_2 (K_2 - c_4)(a_2 + b_2 c_4)}{m_2 K_2};$$

(vi) fish-free equilibrium $E_5 = (p_5, c_5, 0)$, where c_5 is a positive root of the equation

$$K_2 - C - \frac{\alpha_2 (K_1 - \alpha_1 C)^n}{a^n + (K_1 - \alpha_1 C)^n} = 0$$

and $p_5 = K_1 - \alpha_1 c_5$;

(vii) positive equilibrium $E^* = (p^*, c^*, x^*)$, where p^* is a positive root of

$$\frac{f(P) + \alpha_2 P^n / (a^n + P^n)}{K_2} + \frac{m_2 g(P)}{a_2 + P + b_2 f(P)} = 1,$$

$f(P)$ is a positive root of $\beta_1 C^2 + \beta_2 C + \beta_3 = 0$,

$$\beta_1 = r_2 m_1 K_1 b_2 - \alpha_1 m_2 b_1 r_1 K_2,$$
$$\beta_2 = m_2 r_1 K_2 \{ b_1 (K_1 - P) - \alpha_1 (a_1 + P) \}$$
$$+ r_2 m_1 K_1 \left\{ (a_2 + P) + b_2 \left(K_2 - \frac{\alpha_2 P^n}{a^n + P^n} \right) \right\},$$
$$\beta_3 = m_2 r_1 K_2 (K_1 - P)(a_1 + P) - r_2 m_1 K_1 (a_2 + P) \left(K_2 - \frac{\alpha_2 P^n}{a^n + P^n} \right)$$

and

$$g(P) = \frac{r_1 \{ a_1 + P + b_1 f(P) \}}{m_1} \left(1 - \frac{P + \alpha_1 f(P)}{K_1} \right)$$

so that $c^* = f(p^*)$ and $x^* = g(p^*)$. The equilibria E_0, E_1, and E_3 always exist, whereas E_2 exists if $0 < p_2 < K_1$, E_4 exists if $0 < c_4 < K_2$ and E_5 exists if $0 < c_5 < K_1 / \alpha_1$. Also, E^* exists if $0 < p^* < K_1$ and $0 < c^* < (K_1 - p^*) / \alpha_1$.

We note that the organism-free critical point E_0 of the system is always a saddle point.

4.1. Macroalgae-dominated irreversible regime. Due to increasing frequency of coral bleaching, there can be a permanent shift from coral-dominated ecosystems to macroalgae-dominated ones. We study macroalgae-dominated systems

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following mass coral bleaching in which there is no possibility of reversal of the regime.

Let us define $\lambda_1 = a_1 D/(e_1 m_1 - D)$, where $e_1 m_1 > D$. Then λ_1 is the break-even concentration of $x(t)$, representing the concentration of macroalgae for which the population of Parrotfish is constant, in the absence of harvesting.

The following lemma states the condition followed by coral bleaching under which Parrotfish cannot survive, even in the absence of harvesting:

Lemma 4.1.1. *In the absence of corals,*
 (i) *if $m_1 \leqslant D/e_1$, then $\lim\limits_{t\to\infty} x(t) = 0$;*
 (ii) *if $m_1 > D/e_1$ and $K_1 < \lambda_1$, then $\lim\limits_{t\to\infty} x(t) = 0$.*

Under the hypothesis of Lemma 4.1.1 it follows that, in the absence of corals,
(i) low growth rate of Parrotfish on macroalgae leads to its extinction from the system;
(ii) low macroalgal cover leads to the extinction of Parrotfish from the system.

Therefore, for the survival of Parrotfish in a macroalgae-dominated system following coral bleaching, we must have $m_1 > D/e_1$ and $K_1 \geqslant \lambda_1$.

Now we analyze the stability of the system, assuming that $m_1 > D/e_1$ holds throughout our study.

Lemma 4.1.2. *Coral- and Parrotfish-free equilibrium E_1 is locally asymptotically stable if $K_1 > \lambda_1$,*

$$\alpha_2 > \frac{K_2(K_1^n + a^n)}{K_1^n} \quad \text{and} \quad h > \frac{b(e_1 m_1 - D)(K_1 - \lambda_1)}{a_1 + K_1}.$$

Thus, if macroalgae outcompete corals with high interspecific competition coefficient α_2, then for high harvesting rate of Parrotfish the system stabilizes at E_1 with complete elimination of corals and Parrotfish.

Corollary 4.1.1. *In the absence of harvesting, the critical point E_1 is locally asymptotically stable if $K_1 < \lambda_1$ and*

$$\alpha_2 > \frac{K_2(K_1^n + a^n)}{K_1^n}.$$

The conditions for stable coexistence of macroalgae and Parrotfish after mass coral bleaching are given by the following lemma.

Lemma 4.1.3. *The critical point E_2 is locally asymptotically stable if*

$$\alpha_2 > \frac{K_2(a^n + p_2^n)}{p_2^n}\left\{1 - \frac{m_2 x_2}{r_2(a_2 + p_2)}\right\}$$

and any one of the following two conditions holds:

(i)

$$\frac{r_1(a_1 + p_2)^2}{m_1} < K_1 < \frac{r_1 p_2(a_1 + p_2)^2(b + x_2)^2}{m_1 p_2 x_2(b + x_2)^2 + hx_2(a_1 + p_2)^2};$$

(ii)

$$K_1 < \min\left\{\frac{r_1(a_1 + p_2)^2}{m_1}, \frac{r_1 p_2(a_1 + p_2)^2(b + x_2)^2}{m_1 p_2 x_2(b + x_2)^2 + hx_2(a_1 + p_2)^2}\right\}$$

and

$$h < \frac{e_1 a_1 m_1^2 K_1(b + x_2)^2}{(a_1 + p_2)\{r_1(a_1 + p_2)^2 - m_1 K_1\}}.$$

4.2. Coral-dominated irreversible regime. Most healthy coral-dominated reefs have pockets of turf algae and occasional macroalgae. Even though a coral reef without macroalgae is unusual in ecology, from a mathematical standpoint we consider the case when corals are dominating the system in the absence of macroalgae.

Let us define

$$\lambda_2 = \frac{a_2 D}{e_2 m_2 - b_2 D},$$

where $m_2 > b_2 D/e_2$. Then λ_2 is the break-even concentration of $x(t)$, representing the concentration of coral for which the population of Parrotfish is constant, in absence of harvesting.

The following lemma states the conditions under which Parrotfish, when solely dependent on corals, cannot survive, even in the absence of harvesting:

Lemma 4.2.1. *In the absence of macroalgae,*
 (i) *if $m_2 \leqslant b_2 D/e_2$, then $\lim_{t \to \infty} x(t) = 0$;*
 (ii) *if $m_2 > b_1 D/e_2$ and $\lambda_2 > K_2$, then $\lim_{t \to \infty} x(t) = 0$.*

Under the hypothesis of Lemma 4.2.1 it follows that, in absence of macroalgae,

 (i) low growth rate of Parrotfish on corals leads to its extinction from the system;
 (ii) low coral cover leads to the extinction of Parrotfish from the system.

Therefore, for the survival of Parrotfish in a coral-dominated system in the absence of macroalgae, we must have $m_2 > b_2 D/e_2$ and $\lambda_2 \leqslant K_2$.

Now we analyze the stability of the system by assuming that $m_2 > D/e_2$ holds throughout our study.

Lemma 4.2.2. *Macroalgae- and Parrotfish-free critical point E_3 is locally asymptotically stable if*

$$K_2 > \max\left\{\lambda_2, \frac{K_1}{\alpha_1}\right\} \quad and \quad h > \frac{b(e_2 m_2 - b_2 D)(K_2 - \lambda_2)}{a_2 + b_2 K_2}.$$

Therefore, in the absence of macroalgae, high harvesting rate of Parrotfish can lead to its elimination even with sufficient coral cover.

Lemma 4.2.3. *The critical point E_4 is locally asymptotically stable if*

$$K_1 < \frac{r_1 \alpha_1 c_4 (a_1 + b_1 c_4)}{r_1 (a_1 + b_1 c_4) - m_1 x_4}$$

and any one of the following two conditions holds:

(i)

$$\frac{r_2 (a_2 + b_2 c_4)^2}{m_2 b_2} < K_2 < \frac{r_2 c_4 (a_2 + b_2 c_4)^2 (b + x_4)^2}{m_2 b_2 c_4 x_4 (b + x_4)^2 + h x_4 (a_2 + b_2 c_4)^2};$$

(ii)

$$K_2 < \min\left\{\frac{r_2 (a_2 + b_2 c_4)^2}{m_2 b_2}, \frac{r_2 c_4 (a_2 + b_2 c_4)^2 (b + x_4)^2}{m_2 b_2 c_4 x_4 (b + x_4)^2 + h x_4 (a_2 + b_2 c_4)^2}\right\}$$

and

$$h < \frac{e_2 a_2 m_2^2 K_2 (b + x_4)^2}{(a_2 + b_2 c_4)\{r_2 (a_2 + b_2 c_4)^2 - m_2 b_2 K_2\}}.$$

4.3. Reversible regimes. Corals and macroalgae can coexist under restricted circumstances. We now consider the cases when macroalgae and corals coexist in the system.

Lemma 4.3.1. *System (2.1) is locally asymptotically stable at E_5 if*

$$\alpha_2 < \frac{(a^n + p_5^n)^2}{n a^n \alpha_1 p_5^{n-1}}$$

and

$$h > b\left(\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - D\right).$$

Thus, with a higher rate of harvesting of Parrotfish, the system becomes stable at E_5 if coral-macroalgal competition effect is low.

When Lemma 4.3.1 holds, E_5 is (i) macroalgae-dominated and stable if

$$\frac{K_1}{1 + \alpha_1} < c_5 < p_5 < \min\{K_1, K_2\};$$

(ii) coral-dominated and stable if $K_1/(1 + \alpha_1) < p_5 < c_5 < \min\{K_2, K_1/(\alpha_1)\}$.

Lemma 4.3.2. *The positive equilibrium $E^* = (p^*, c^*, x^*)$ is locally asymptotically stable if $h < h^*$ and $\eta^* > 0$, where*

$$h^* = \frac{(b + x^*)^2}{x^*} \left\{ \frac{r_1 p^*}{K_1} + \frac{r_2 c^*}{K_2} - \frac{m_1 p^* x^*}{(a_1 + p^* + b_1 c^*)^2} - \frac{m_2 b_2 c^* x^*}{(a_2 + p^* + b_2 c^*)^2} \right\}$$

and

$$
\begin{aligned}
\eta^* = \ & F_C^1|_{E^*} F_x^2|_{E^*} F_P^3|_{E^*} + F_x^1|_{E^*} F_P^2|_{E^*} F_C^3|_{E^*} - 2 F_P^1|_{E^*} F_C^2|_{E^*} F_x^3|_{E^*} \\
& + (F_C^2|_{E^*} + F_x^3|_{E^*}) \{ F_x^2|_{E^*} F_C^3|_{E^*} - (F_P^1|_{E^*})^2 \} \\
& + (F_P^1|_{E^*} + F_x^3|_{E^*}) \{ F_x^1|_{E^*} F_P^3|_{E^*} - (F_C^2|_{E^*})^2 \} \\
& + (F_P^1|_{E^*} + F_C^2|_{E^*}) \{ F_C^1|_{E^*} F_P^2|_{E^*} - (F_x^3|_{E^*})^2 \}.
\end{aligned}
$$

When Lemma 4.3.2 holds, the equilibrium E^* is
(i) coral-dominated and stable if $p^* < c^* < K_1/(1 + \alpha_1)$;
(ii) macroalgae-dominated and stable if $c^* < p^* < \min\{K_1, K_2\}$.

Lemma 4.3.3. *System (2.1) undergoes a Hopf bifurcation at $K_1 = K_{1_{\text{cr}}}$ if and only if*

(i) $Q_i(K_{1_{\text{cr}}}) > 0$ $(i = 1, 2, 3)$,
(ii) $f_1(K_{1_{\text{cr}}}) = f_2(K_{1_{\text{cr}}})$,
(iii) $\{M(K_1)K(K_1) + N(K_1)L(K_1)\}_{K_{1_{\text{cr}}}} \neq 0$, *where* $f_1(K_1) = Q_1(K_1)Q_2(K_1)$, $f_2(K_1) = Q_3(K_1)$,

$$
\begin{aligned}
K(K_1) &= 3\gamma_1^2(K_1) - 3\gamma_2^2(K_1) + 2Q_1(K_1)\gamma_1(K_1) + Q_2(K_1), \\
L(K_1) &= 6\gamma_1(K_1)\gamma_2(K_1) + 2Q_1(K_1)\gamma_2(K_1), \\
M(K_1) &= Q_3'(K_1) + \{\gamma_1^2(K_1) - \gamma_2(K_1)\}Q_1'(K_1) + \gamma_1 Q_2'(K_1), \\
N(K_1) &= 2\gamma_1(K_1)\gamma_2(K_1)Q_{1'}(K_1) + \gamma_2(K_1)Q_2'(K_1);
\end{aligned}
$$

$\gamma_1(K_1)$ and $\gamma_2(K_1)$ are real and imaginary parts, respectively, of a pair of eigenvalues in $K_1 \in (K_{1_{\text{cr}}} - \varepsilon, K_{1_{\text{cr}}} + \varepsilon)$.

Condition (iii) of Lemma 4.3.3 is equivalent to

$$\frac{\mathrm{d}g(K_1)}{\mathrm{d}K_1}\big|_{(K_1 = K_{1_{\text{cr}}})} \neq 0,$$

where $g(K_1) = f_1(K_1) - f_2(K_1)$. By using numerical methods, condition (ii) of Lemma 4.3.3 can be verified by showing that the curves $y = f_1(K_1)$ and $y = f_2(K_1)$ intersect at $K_1 = K_{1_{\text{cr}}}$, whereas condition (iii) can be verified by showing that the tangent to the curve $y = g(K_1)$ at $K_1 = K_{1_{\text{cr}}}$ is not parallel to the K_1 axis [27].

Corollary 4.3.1. *The period T of the bifurcating periodic orbits close to $K_1 = K_{1_{cr}}$ is given by*

$$T(K_{1_{cr}}) = \frac{2\pi}{\sqrt{Q_2(K_{1_{cr}})}}.$$

We investigate the orbital stability of the Hopf-bifurcating periodic solution by using Poore's sufficient condition [25]. The supercritical and subcritical nature of the Hopf-bifurcating periodic solution is determined by the positive and negative sign of the real part of Φ, where

$$\begin{aligned}
\Phi = {} & -a_l F^l_{u_j u_m u_s} b_j b_m \bar{b}_s + 2a_l F^l_{u_j u_m} b_j (J_{E^*}^{-1})_{mr} F^r_{u_p u_q} b_p \bar{b}_q \\
& + a_l F^l_{u_j u_k} \bar{b}_j (J_{E^*} - 2\mathrm{i}\omega_0)_{kr}^{-1} F^r_{u_p u_q} b_p b_q,
\end{aligned}$$

the repeated indices within each term imply a sum from 1 to 3 and all the derivatives of F^l ($l = 1, 2, 3$) are evaluated at E^* with $u_1 = P, u_2 = C, u_3 = x$ and J_{E^*} is the variational matrix of (2.1) calculated at E^*. $[(J_{E^*})^{-1}]_{mr}$ denotes the element in row m, column r of $(J_{E^*})^{-1}$. Also, $\mathbf{a} = (a_1, a_2, a_3)$ and $\mathbf{b} = (b_1, b_2, b_3)^{\top}$ are left and right normalized eigenvectors of J_{E^*} with respect to the eigenvalues $\pm \mathrm{i}\omega_0$ at $K_1 = K_{1_{cr}}$ such that $\mathbf{a} \cdot \mathbf{b} = 1$. The detailed calculations for supercritical and subcritical Hopf bifurcation are given in the Appendix. Also, from numerical simulations it is observed that the system undergoes a Hopf bifurcation when the macroalgal carrying capacity (K_1) crosses a certain threshold.

5. Numerical simulations

In this section, we investigate numerically, as demonstrated in [2], the effect of the various parameters on the qualitative behavior of the system using parameter values given in Table 1 [15] throughout, unless otherwise stated.

We will verify the feasibility of the stability criterion from Section 4.

E x a m p l e 5.1. Under the set of parameter values as given in Table 1, the system is locally asymptotically stable at $E^* = (0.3487, 0.5642, 0.586)$ with eigenvalues $-1.0535, -0.0339 \pm 0.586\mathrm{i}$ (cf. Figure 2 (unshaded)). In this case we obtain $p^* < c^* < K_1/(1 + \alpha_1) = 0.615$, and so E^* is coral-dominated.

For $h = 0.15$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E^* = (0.4386, 0.1622, 0.5460)$ with eigenvalues $-0.0199, -0.0950 \pm 0.3820\mathrm{i}$ (cf. Figure 2 (shaded)). In this case we obtain $c^* < p^* < \min\{K_1, K_2\} = 0.7$, and so E^* is macroalgae-dominated.
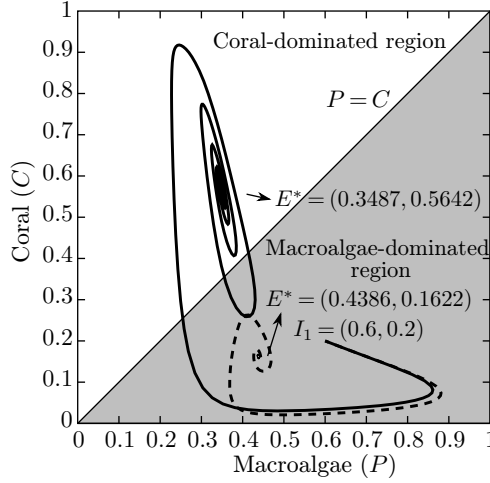
Figure 2. Phase plane diagram of the system projected on the CP-plane with initial values $I_1 = (0.6, 0.2)$ and parameters as given in Table 1; the system has a stable focus at E^* with corals dominating macroalgae (solid trajectories). For $h = 0.15$, other parameter values as given in Table 1, the system is LAS at E^* with macroalgae dominating corals (dashed trajectories).

Parameters	Description	Value	Dimension
r_1	Intrinsic growth rate of macroalgae	0.3	1/time
r_2	Intrinsic growth rate of coral	0.2	1/time
K_1	Carrying capacity of macroalgae	0.8	mass/volume
K_2	Carrying capacity of coral	0.7	mass/volume
a	Half-saturation constant	0.3	mass/volume
α_1	Effect of coral on macroalgae	0.3	-
α_2	Effect of macroalgae on coral	0.75	-
n	Order of the Hill function	0.7	-
D	Death rate of Parrotfish	0.1	1/time
m_1	Maximal growth rate of x on P	1	1/time
m_2	Maximal growth rate of x on C	0.1	1/time
a_1	Half-saturation constant for uptake of P by x	1.5	mass/volume
a_2	Half-saturation constant for uptake of C by x	1.5	mass/volume
b_i	Interference of P and C on the growth of x	1	-
e_1	Growth efficiency of x on P	0.7	-
e_2	Growth efficiency of x on C	0.8	-
h	Maximal rate of harvesting	0	1/time
b	Half-saturation constant on harvesting	5	mass/volume

Table 1. Default parameter values used in the numerical analysis.

Example 5.2. For $h = 1.5$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_1 = (0.8, 0, 0)$ with eigenvalues $-0.3, -0.82, -0.09$ (cf. Figure 3 (a)). In this case we obtain

$$\alpha_2 > \frac{K_2(K_1^n + a^n)}{K_1^n} = 0.7,$$

$$h > \frac{b(e_1 m_1 - D)(K_1 - \lambda_1)}{a_1 + K_1} = 0.7174$$

and $K_1 > \lambda_1 = 0.25$, satisfying Lemma 4.1.2.

Example 5.3. For $h = 0.4$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_2 = (0.5062, 0, 0.2211)$ with eigenvalues $-0.1036, -0.0794 \pm 0.0879i$ (cf. Figure 3 (b)). In this case we obtain

$$\alpha_2 > \frac{K_2(a^n + p_2^n)}{p_2^n}\left\{1 - \frac{m_2 x_2}{r_2(a_2 + p_2)}\right\} = 0.6784,$$

$$K_1 < \min\left\{\frac{r_1(a_1 + p_2)^2}{m_1}, \frac{r_1 p_2(a_1 + p_2)^2(b + x_2)^2}{m_1 p_2 x_2(b + x_2)^2 + h x_2(a_1 + p_2)^2}\right\} = 1.2074$$

and

$$h < \frac{e_1 a_1 m_1^2 K_1(b + x_2)^2}{(a_1 + p_2)\{r_1(a_1 + p_2)^2 - m_1 K_1\}} = 28.015,$$

satisfying Lemma 4.1.3 (ii).

Also, for $h = 0.4$ and $K_1 = 1.3$, other parameter values as given in Table 1, $E_2 = (0.4981, 0, 0.3698)$ is locally asymptotically stable with eigenvalues -0.0268, $-0.0318 \pm 0.1512i$.

We obtain
$$\alpha_2 > \frac{K_2(a^n + p_2^n)}{p_2^n}\left\{1 - \frac{m_2 x_2}{r_2(a_2 + p_2)}\right\} = 0.6535$$

and

$$1.1977 = \frac{r_1(a_1 + p_2)^2}{m_1} < K_1 < \frac{r_1 p_2(a_1 + p_2)^2(b + x_2)^2}{m_1 p_2 x_2(b + x_2)^2 + h x_2(a_1 + p_2)^2} = 2.9149,$$

satisfying Lemma 4.1.3 (i).

Example 5.4. For $K_1 = 0.2$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_3 = (0, 0.7, 0)$ with eigenvalues -0.015, -0.2, -0.0745 (cf. Figure 3 (c)). In this case we obtain $K_2 > \max\{\lambda_2, K_1/\alpha_1\} = 0.6667$ and

$$h > \frac{b(e_2 m_2 - b_2 D)(K_2 - \lambda_2)}{a_2 + b_2 K_2} = -0.3727,$$
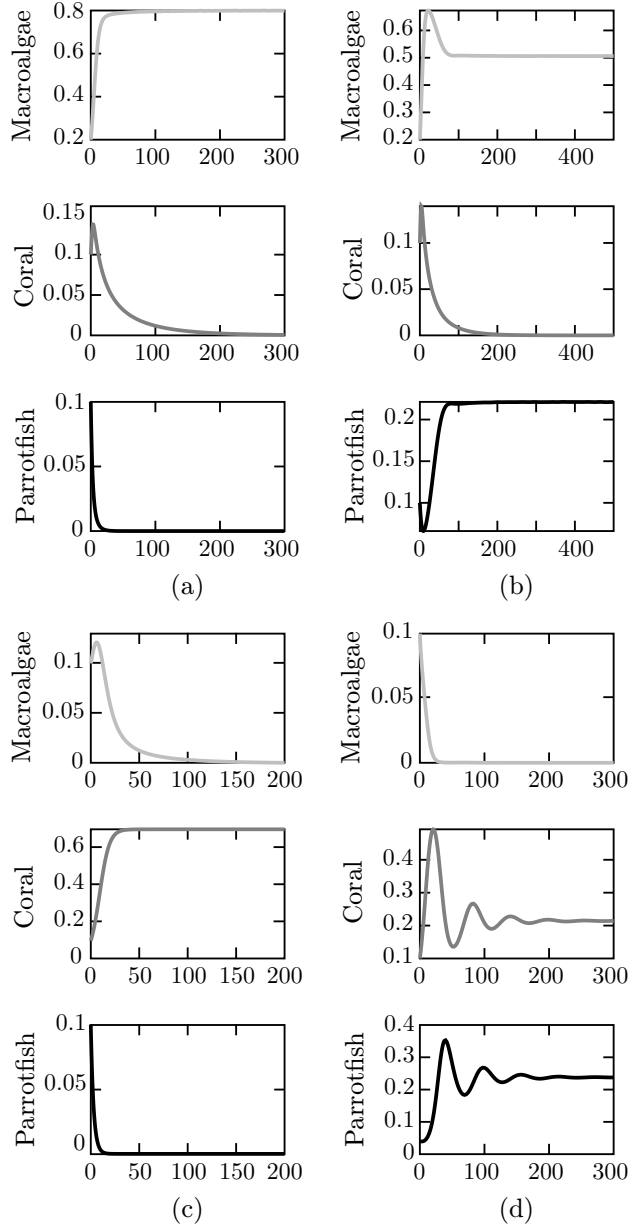
satisfying Lemma 4.2.2.

Figure 3. Time series analysis of the system for (a) $h = 1.5$, other parameter values as given in Table 1, the system is LAS at E_1; (b) $h = 0.4$, other parameter values as given in Table 1, the system is LAS at E_2; (c) $K_1 = 0.2$, other parameter values as given in Table 1, the system is LAS at E_3; (d) $K_1 = 0.1, K_2 = 0.4$ and $m_2 = 1$, other parameter values as given in Table 1, the system is LAS at E_4. (Horizontal axes show the time.)

E x a m p l e 5.5. For $K_1 = 0.1$ and $m_2 = 1$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_4 = (0, 0.2143, 0.2379)$ with eigenvalues -0.0316, $-0.0219 \pm 0.1080i$. Also, we obtain

$$K_1 < \frac{r_1 \alpha_1 c_4 (a_1 + b_1 c_4)}{r_1 (a_1 + b_1 c_4) - m_1 x_4} = 0.1196, \ 0.5878 = \frac{r_2 (a_2 + b_2 c_4)^2}{m_2 b_2}$$

$$< K_2 < \frac{r_2 c_4 (a_2 + b_2 c_4)^2 (b + x_4)^2}{m_2 b_2 c_4 x_4 (b + x_4)^2 + h x_4 (a_2 + b_2 c_4)^2} = 2.4706,$$

satisfying the analytical conditions of stability at E_4 as given in Lemma 4.2.3 (i).

For $K_1 = 0.1$, $K_2 = 0.4$ and $m_2 = 1$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_4 = (0, 0.2143, 0.1592)$ with eigenvalues 0.0143, $-0.0478 \pm 0.0764i$ (cf. Figure 3 (d)). Also, we obtain

$$K_1 < \frac{r_1 \alpha_1 c_4 (a_1 + b_1 c_4)}{r_1 (a_1 + b_1 c_4) - m_1 x_4} = 0.0931,$$

$$K_2 < \min \left\{ \frac{r_2 (a_2 + b_2 c_4)^2}{m_2 b_2}, \ \frac{r_2 c_4 (a_2 + b_2 c_4)^2 (b + x_4)^2}{m_2 b_2 c_4 x_4 (b + x_4)^2 + h x_4 (a_2 + b_2 c_4)^2} \right\} = 0.5878$$

and

$$h < \frac{e_2 a_2 m_2^2 K_2 (b + x_4)^2}{(a_2 + b_2 c_4) \{ r_2 (a_2 + b_2 c_4)^2 - m_2 b_2 K_2 \}} = 39.6944,$$

satisfying the conditions of stability at E_4 in Lemma 4.2.3 (ii).

E x a m p l e 5.6. For $K_1 = 0.4$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_5 = (0.2043, 0.6523, 0)$ with eigenvalues -0.0541, -0.2855, -0.0172 (cf. Figure 4 (unshaded)). In this case we obtain

$$\alpha_2 < \frac{(a^n + p_5^n)^2}{n a^n \alpha_1 p_5^{n-1}} = 1.6326,$$

$$\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} < D$$

and

$$0.3077 = \frac{K_1}{1 + \alpha_1} < p_5 < c_5 < \min \left\{ K_2, \frac{K_1}{\alpha_1} \right\} = 0.7,$$

satisfying the conditions of stability at E_5 with a coral-dominated regime.
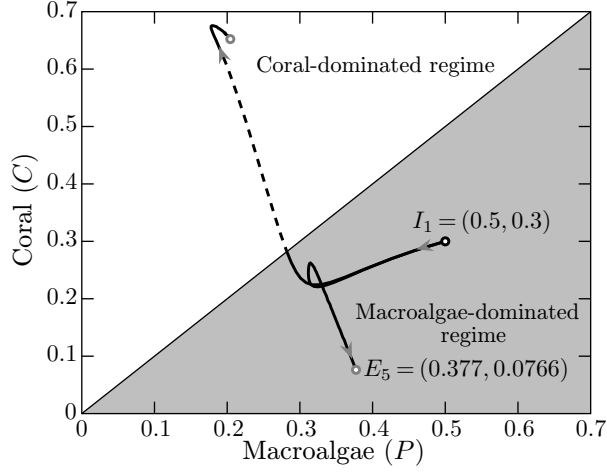
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Figure 4. Phase plane diagram of the system projected on the CP-plane with initial values $I_2 = (0.5, 0.3)$, $K_1 = 0.4$ and other parameter values as given in Table 1; the system has a stable node at E_5 with corals dominating macroalgae (dashed trajectories). For $K_1 = 0.4, h = 0.3$, other parameter values as given in Table 1, the system is LAS at E_5 with macroalgae dominating corals (solid trajectories).

Also, for $K_1 = 0.4$, $h = 0.3$, other parameter values as given in Table 1, the system is locally asymptotically stable at $E_5 = (0.377, 0.0766, 0)$ (cf. Figure 4 (shaded)). In this case we obtain

$$\alpha_2 < \frac{(a^n + p_5^n)^2}{n a^n \alpha_1 p_5^{n-1}} = 1.2842,$$

$$h > b\left(\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - D\right) = 0.1911$$

and

$$0.3077 = \frac{K_1}{1 + \alpha_1} < c_5 < p_5 < \min\{K_1, K_2\} = 0.4,$$

satisfying the conditions of stability at E_5 with a macroalgae-dominated regime.

Effects of macroalgal carrying capacity and harvesting: With low carrying capacity of macroalgae ($K_1 < 0.503$) and in the absence of harvesting of Parrotfish, the system becomes oscillatory around E^* (cf. Figure 5 (a)). When the carrying capacity of macroalgae is lowered below $K_1 = 0.4083$, the system stabilizes at E_5 followed by the extinction of Parrotfish from the system. In the presence of harvesting of Parrotfish (viz. $h = 0.1$) and with low carrying capacity of macroalgae ($K_1 < 0.4168$), the system becomes oscillatory around E^* (cf. Figure 6 (a)) followed by the extinction of Parrotfish when the carrying capacity of macroalgae is lowered below $K_1 = 0.3917$. Also, with high macroalgal carrying capacity (viz. $K_1 > 2.1569$), the system becomes oscillatory. In this case, due to moderate increase of maximal
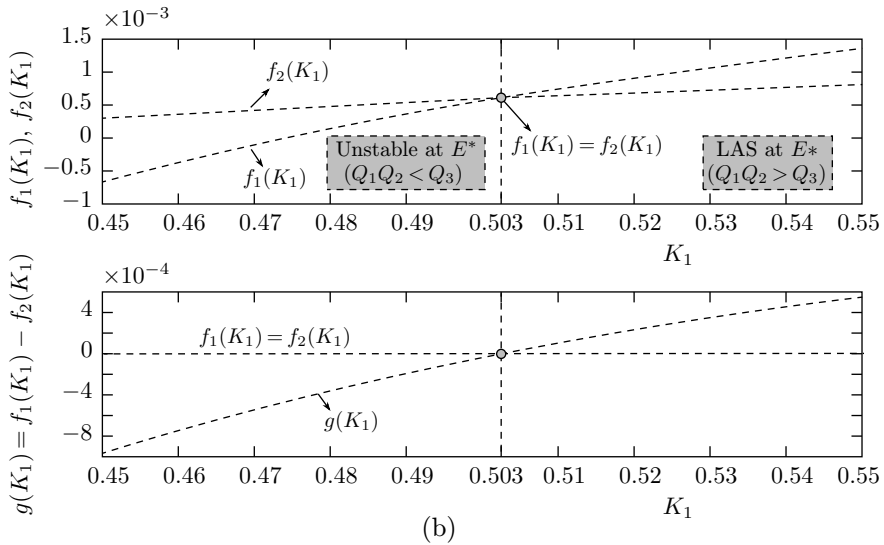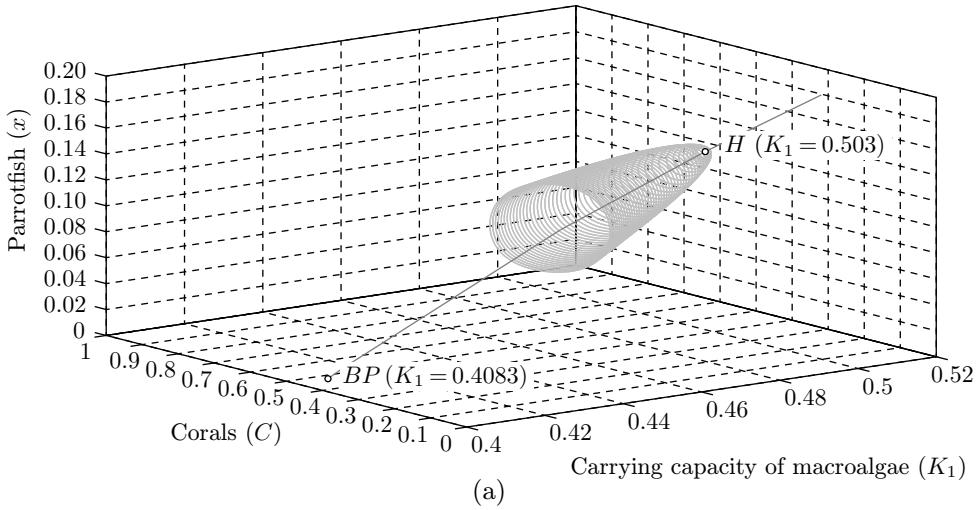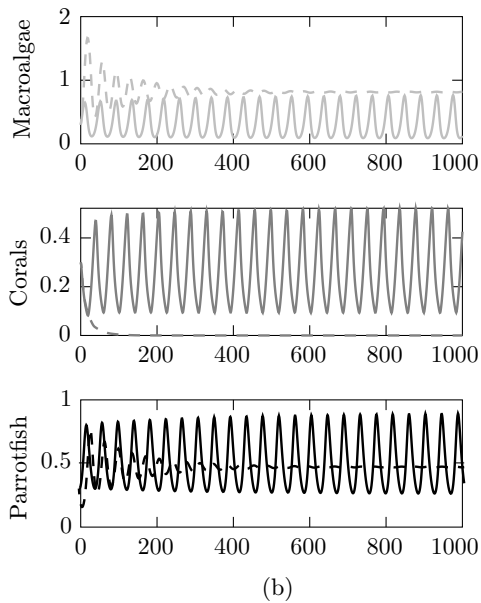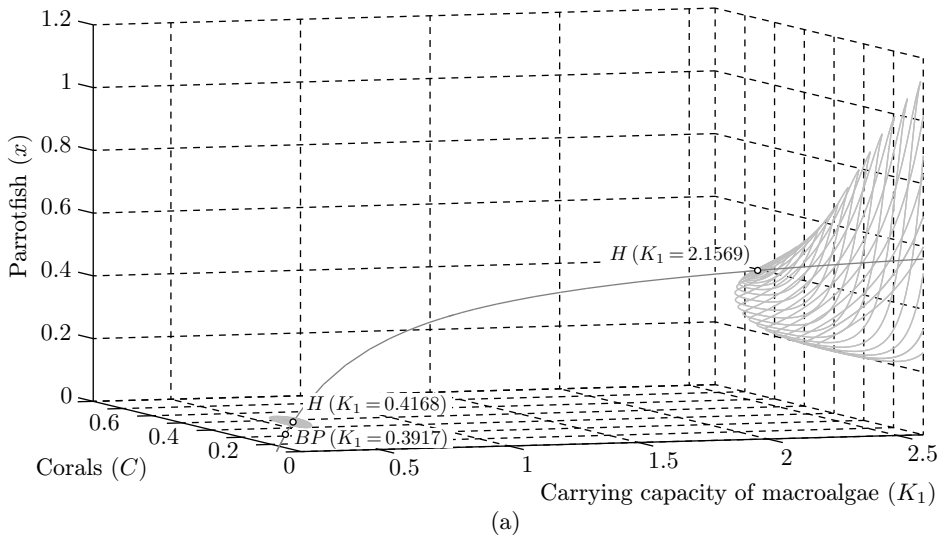
Figure 5. (a) Bifurcation diagram of macroalgal carrying capacity (K_1) versus the equilibrium value of the concentrations of Parrotfish and corals. The system undergoes a Hopf bifurcation at E^* when K_1 crosses $K_1 = 0.503$. Limit cycle branches originate at the Hopf point (H). The system becomes stable at E_5 when K_1 is lowered below $K_1 = 0.4083$. (b) The relative positions of $f_1(K_1)$, $f_2(K_1)$ and $g(K_1)$, showing that Hopf bifurcation occurs when the two curves intersect at $K_1 = 0.503$.

harvesting rate of Parrotfish (viz. $h = 0.8$), the system becomes stable at E_2 (cf. Figure 6 (b)).

Effects of coral carrying capacity and harvesting: In the absence of harvesting and with low carrying capacity of corals $(K_2 < 0.1825)$, the system becomes

macroalgae-dominated followed by the elimination of corals (cf. Figure 7 (a)). Due to the increase of K_2 (viz. $K_2 = 0.3$), initial coral mortality is observed followed by its subsequent recovery. But, in the presence of harvesting of Parrotfish (for $K_2 = 0.3$ and $h = 0.1$), the system becomes stable at the coral-depleted steady state E_2, representing an irreversible shift of regime (cf. Figure 8 (a)). With high carrying capacity of corals ($K_2 > 2.0467$), the system becomes coral-dominated followed by the extinction of Parrotfish (cf. Figure 7 (a)).
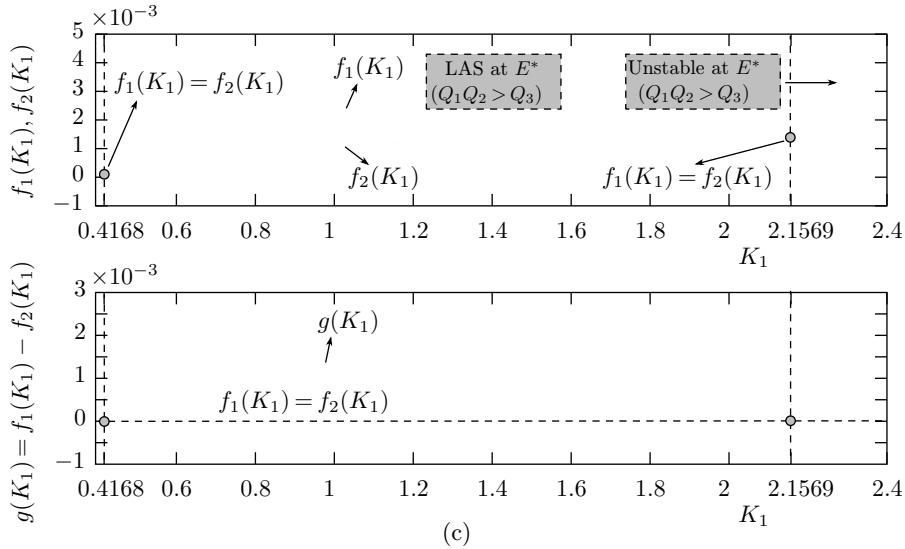

(a)

(b)

Figure 6. (a) For $h = 0.1$, the bifurcation diagram of macroalgal carrying capacity (K_1) versus the equilibrium value of the concentrations of Parrotfish and corals. The system undergoes Hopf bifurcations at E^* when K_1 crosses $K_1 = 0.4168$ and $K_1 = 2.1569$, generating limit cycle branches at the Hopf points (H). The system becomes stable at E_5 when K_1 is lowered below $K_1 = 0.3917$. (b) For $K_1 = 2.5$, $h = 0.1$, the system becomes oscillatory around E^* (solid). For $K_1 = 2.5$, $h = 0.8$, the system stabilizes at E_2 (dashed). (c) The relative positions of $f_1(K_1)$, $f_2(K_1)$ and $g(K_1)$ showing that Hopf bifurcations occur when the two curves intersect at $K_1 = 0.4168$ and $K_1 = 2.1569$. (Horizontal axes in the part (b) of the figure show the time.)

Effects of coral-macroalgal competition and harvesting: For $\alpha_2 = 1.7$, other parameter values as in Table 1, it is observed that corals recover after extensive mortality (cf. Figure 8 (b)). This refers to the coral reef's ability to recover from bleaching in the absence of harvesting. But for $\alpha_2 = 1.7$ and $h = 0.1$, the system becomes stable at E_2 and so corals fail to recover from bleaching in the presence of herbivore harvesting (cf. Figure 8 (b)).

Hopf bifurcation: We observe that the system becomes oscillatory when the carrying capacity of macroalgae (K_1) crosses certain thresholds (cf. Figures 5 and 6). We therefore consider K_1 as a bifurcation parameter.

In the absence of harvesting of Parrotfish, from Figure 5 (b) we observe that $f_1(K_1)$ and $f_2(K_1)$ intersect at $K_1 = 0.503$, indicating that the system changes its stability when the parameter crosses the threshold $K_1 = 0.503$. More specifically, for $K_1 > 0.503$ we see that $f_1(K_1) > f_2(K_1)$, satisfying the Routh-Hurwitz condition and therefore the system is locally asymptotically stable at E^*. For $K_1 < 0.503$ we see that $f_1(K_1) < f_2(K_1)$ and so the system is unstable at E^*. Moreover, we observe
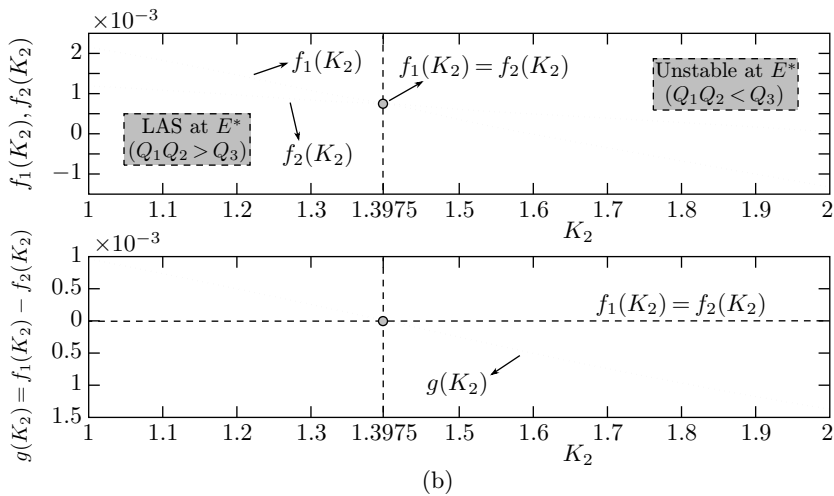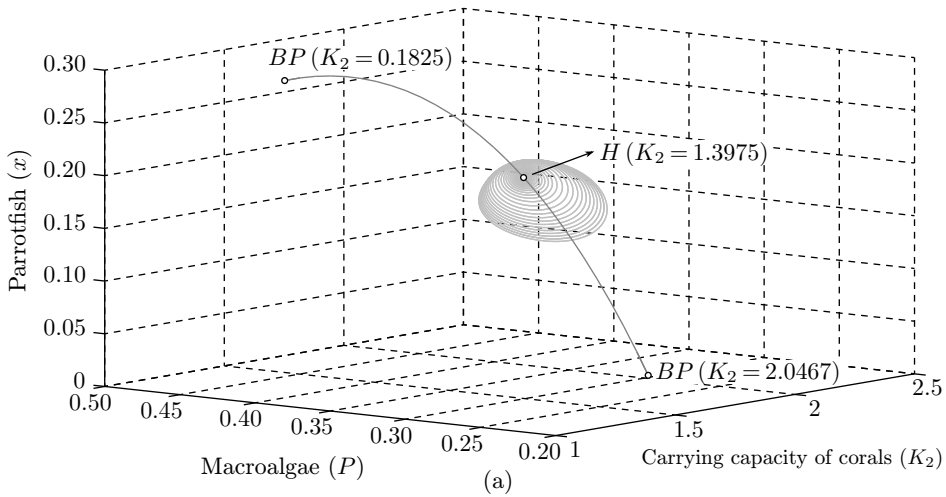
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Figure 7. (a) Bifurcation diagram of coral carrying capacity (K_2) versus the equilibrium value of the concentrations of Parrotfish and macroalgae. The system undergoes a Hopf bifurcation at E^* when K_2 crosses $K_2 = 1.3975$, generating limit cycle branches at the Hopf point (H). The system becomes stable at E_2 when K_2 is lowered below $K_2 = 0.1825$ and becomes stable at E_5 when K_2 is increased beyond $K_2 = 2.0467$. (b) The relative positions of $f_1(K_2), f_2(K_2)$ and $g(K_2)$ showing that Hopf bifurcation occurs when the two curves intersect at $K_2 = 1.3975$.

that the tangent to $g(K_1)$ at $K_1 = 0.503$ is not parallel to the K_1 axis, satisfying the condition

$$\frac{\mathrm{d}g(K_1)}{\mathrm{d}K_1}\bigg|_{(K_1=0.503)} \neq 0$$

and therefore, the system undergoes a Hopf bifurcation when K_1 crosses $K_1 = 0.503$.

In the presence of harvesting of Parrotfish (viz. $h = 0.1$), from Figure 6 (c) we observe that $f_1(K_1)$ and $f_2(K_1)$ intersect at the two points $K_1 = 0.4168$ and $K_1 = 2.1569$, indicating that the system changes its stability when the parameter crosses the thresholds $K_1 = 0.4168$ and $K_1 = 2.1569$. It is observed that for $0.4168 < K_1 < 2.1569$ we have $f_1(K_1) > f_2(K_1)$, satisfying the Routh-Hurwitz condition for stability at E^*. Moreover, the tangents to $g(K_1)$ at $K_1 = 0.4168$ and $K_1 = 2.1569$ are not parallel to the K_1 axis, satisfying the conditions

$$\frac{\mathrm{d}g(K_1)}{\mathrm{d}K_1}\bigg|_{(K_1=0.4168)} \neq 0$$

and

$$\frac{\mathrm{d}g(K_1)}{\mathrm{d}K_1}\bigg|_{(K_1=2.1569)} \neq 0.$$

Therefore, the system undergoes Hopf bifurcations at $K_1 = 0.4168$ and $K_1 = 2.1569$.

We also observe that the system becomes oscillatory when the carrying capacity of corals (K_2) exceeds $K_2 = 1.3975$ (cf. Figure 7 (a)). The system changes its stability when the curves $f_1(K_2)$ and $f_2(K_2)$ intersect at $K_2 = 1.3975$. For $K_2 < 1.3975$, we have $f_1(K_2) > f_2(K_2)$, satisfying the Routh-Hurwitz condition for stability at E^* and the transversality condition

$$\frac{\mathrm{d}g(K_2)}{\mathrm{d}K_2}\bigg|_{(K_2=1.3975)} \neq 0$$

(see Figure 7 (b)) and consequently, a Hopf bifurcation occurs when K_2 crosses $K_2 = 1.3975$.

6. Discussion

We have considered a mathematical model of a coral reef ecosystem with mutual interspecific competition between macroalgae and corals and harvesting of herbivorous Parrotfish. Parrotfish are harvested with a rational harvesting policy. A simple linear competition coefficient of coral on macroalgae is used in the growth equation of macroalgae. The model treats the effect of macroalgae on corals differently than the effect of corals on macroalgae by incorporating the Hill function in the interspecific competition term of the growth function of corals. We have shown that solutions of the system are bounded in the long run. We have obtained conditions for uniform persistence at the coexistence steady state. Also, we have derived the conditions for local asymptotic stability of the system at different steady states. It is observed that low harvesting of Parrotfish ensures the survival of the organisms

in the coral-dominated coexistence state. Also, it is observed that if macroalgae outcompete corals, then limited harvesting of Parrotfish can lead to its survival in a macroalgae-dominated irreversible regime. We have also provided numerical simulations to substantiate our analytic results. Further, from analytical and numerical observations we get the following conclusions:
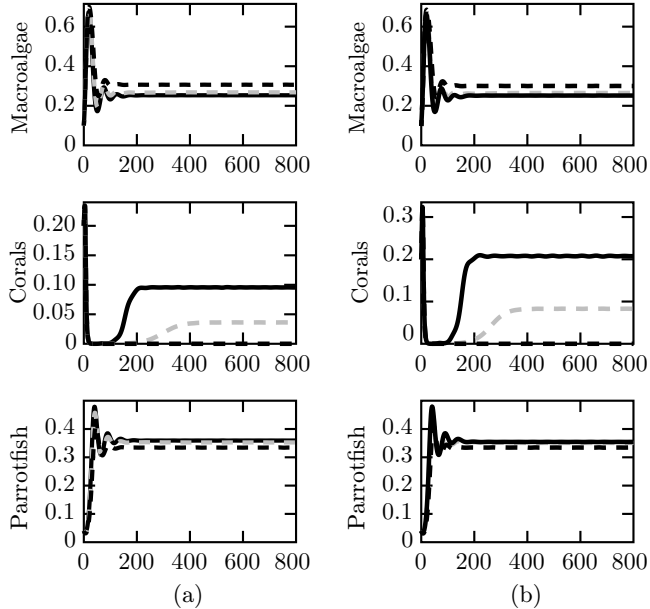

Figure 8. (a) For $K_2 = 0.3$, the system is LAS at E^* (solid black). For $K_2 = 0.3$ and $h = 0.03$, the system becomes LAS at E^* (dashed gray) with late recovery of corals. For $K_2 = 0.3$ and $h = 0.1$, the system becomes LAS at E_2 (dashed black). (b) For $\alpha_2 = 1.6$, other parameter values as given in Table 1, the system is LAS at E^* (solid black). For $\alpha_2 = 1.6$ and $h = 0.03$, the system becomes LAS at E^* (dashed gray) with late recovery of corals. For $\alpha_2 = 1.6$ and $h = 0.1$, the system becomes LAS at E_2 (dashed black). (Horizontal axes show the time.)

(i) Harvesting of Parrotfish leads to phase shifts from a coral-dominated to macroalgae-dominated regime, representing the coral-macroalgal phase shift phenomenon in the coral reef ecosystem as a result of the loss of herbivory. This supports the observations of [14] that reductions in Parrotfish grazing could have deleterious impacts on the reef habitat.

(ii) In the absence of harvesting of Parrotfish, corals can recover after extensive mortality even with high coral-macroalgal interspecific competition. But in the presence of harvesting, corals do not recover with high coral-macroalgal competition. This justifies the observations of Mumby [21] that herbivory helps control macroalgae which compete with corals and can impede reef resilience if allowed to bloom.

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(iii) With low coral cover, if there is no harvesting, corals can recover after extensive initial mortality. But in the presence of harvesting, the system becomes macroalgae-dominated with complete elimination of corals.

(iv) High macroalgal cover leads to dynamic instability of the system around the equilibrium of coexistence. In this case, an increase in harvesting of Parrotfish leads to the extinction of corals from the system.

Throughout the article, an attempt is made to search for a suitable way to control the growth of macroalgae, corals and Parrotfish for stable coexistence of all the species in the system. From analytical and numerical observations, it is seen that lowering the rate of harvesting of Parrotfish can induce a coral-dominated regime. From numerical simulations we observe that corals can recover even after extensive mortality if the harvesting of Parrotfish is minimized.

<div align="center">APPENDIX</div>

P r o o f of Theorem 3.2. Since $\limsup\limits_{t\to\infty}\{P(t) + C(t) + x(t)\} \leqslant M$, it follows that exists $T_1 > 0$ such that $x(t) \leqslant M$ for all $t \geqslant T_1$.

Also,
$$\forall t \geqslant T_1, \quad \frac{\mathrm{d}P}{\mathrm{d}t} \geqslant P\Big[r_1\Big(1 - \frac{P + \alpha_1 K_2}{K_1}\Big) - \frac{m_1 M}{a_1}\Big]$$
implies
$$\liminf_{t\to\infty} P(t) \geqslant p_1 = K_1\Big(1 - \frac{m_1 M}{a_1 r_1}\Big) - \alpha_1 K_2,$$
where $0 < M < a_1 r_1 (K_1 - \alpha_1 K_2)/(m_1 K_1)$ and $K_1 > \alpha_1 K_2$.

Therefore, exists $T_2 > 0$ such that $p_1 \leqslant P(t) \leqslant K_1$ for all $t \geqslant T_2$, where
$$M < \frac{a_1 r_1 (K_1 - \alpha_1 K_2)}{m_1 K_1} \quad \text{and} \quad K_1 > \alpha_1 K_2.$$

Again,
$$\forall t \geqslant T_1, \quad \frac{\mathrm{d}C}{\mathrm{d}t} \geqslant C\Big[r_2\Big(1 - \frac{C + \alpha_2}{K_2}\Big) - \frac{m_2 M}{a_2}\Big]$$
implies
$$\liminf_{t\to\infty} C(t) \geqslant c_1 = K_2\Big(1 - \frac{m_2 M}{r_2 a_2}\Big) - \alpha_2,$$
where
$$0 < M < \frac{r_2 a_2 (K_2 - \alpha_2)}{m_2 K_2} \quad \text{and} \quad K_2 > \alpha_2.$$

Thus, exists $T_3 > 0$ such that $c_1 \leqslant C(t) \leqslant K_2$ for all $t \geqslant T_3$, where
$$M < \frac{r_2 a_2 (K_2 - \alpha_2)}{m_2 K_2} \quad \text{and} \quad K_2 > \alpha_2.$$

Therefore, for all $t \geqslant \max\{T_1, T_2, T_3\}$, we have $p_1 \leqslant P(t) \leqslant K_1$ and $c_1 \leqslant C(t) \leqslant K_2$, where

$$M < \min\left\{\frac{a_1 r_1 (K_1 - \alpha_1 K_2)}{m_1 K_1}, \frac{a_2 r_2 (K_2 - \alpha_2)}{m_2 K_2}, \frac{K(r_1 + r_2)}{D_0}\right\}$$

and $K_1 > \alpha_1 \alpha_2$.

Again,

$$\forall\, t \geqslant \max\{T_1, T_2, T_3\}, \quad \frac{\mathrm{d}x}{\mathrm{d}t} \geqslant x\left(\frac{e_1 m_1 p_1}{a_1 + K_1 + b_1 K_2} + \frac{e_2 m_2 c_1}{a_2 + K_1 + b_2 K_2} - \frac{h}{b} - D\right).$$

Therefore, $\mathrm{d}x/\mathrm{d}t \geqslant 0$ implies

$$h \leqslant b\left(\frac{e_1 m_1 p_1}{a_1 + K_1 + b_1 K_2} + \frac{e_2 m_2 c_1}{a_2 + K_1 + b_2 K_2} - D\right).$$

Thus, exists $T_4 > 0$ such that for all $t \geqslant T_4$, we can find $x_1 > 0$ such that $x_1 \leqslant x(t) \leqslant M$.

Therefore, for large values of t, if $h \leqslant \bar{h}$ and $K_1 > \alpha_1 \alpha_2$ hold, where

$$\bar{h} = b\left(\frac{e_1 m_1 p_1}{a_1 + b_1 K_2 + K_1} + \frac{e_2 m_2 c_1}{a_2 + b_2 K_2 + K_1} - D\right),$$

$$p_1 = K_1\left(1 - \frac{m_1 M}{a_1 r_1}\right) - \alpha_1 K_2, \quad c_1 = K_2\left(1 - \frac{m_2 M}{r_2 a_2}\right) - \alpha_2,$$

$$M < \min\left\{\frac{a_1 r_1 (K_1 - \alpha_1 K_2)}{m_1 K_1}, \frac{a_2 r_2 (K_2 - \alpha_2)}{m_2 K_2}, \frac{K(r_1 + r_2)}{D_0}\right\},$$

there exists $x_1 > 0$ such that all the solutions of the system with positive initial values enter into the compact set $\{(P, C, x)\colon p_1 \leqslant P(t) \leqslant K_1, c_1 \leqslant C(t) \leqslant K_2, x_1 \leqslant x(t) \leqslant M\}$ and will remain there forever. $\qquad\square$

P r o o f of Lemma 4.1.1. Since $P(t) \leqslant K_1$ as $t \to \infty$, corresponding to $\varepsilon_1 > 0$, exists $t_\varepsilon > 0$ such that $P(t) \leqslant K_1 + \varepsilon$ for all $t \geqslant t_\varepsilon$.

Therefore, in the absence of corals,

(i) if $m_1 \leqslant D/e_1$ for all $t \geqslant T_\varepsilon$, we have

$$\frac{\mathrm{d}x}{\mathrm{d}t} \leqslant -\frac{a_1 x D}{a_1 + K_1 + \varepsilon} \Rightarrow \int_{x(T_\varepsilon)}^{x(t)} \frac{\mathrm{d}\xi}{\xi} \leqslant \frac{-a_1 D (t - T_\varepsilon)}{a_1 + K_1 + \varepsilon}$$

and so $x(t) \to 0$ as $t \to \infty$;

(ii) if $m_1 > D/e_1$, for all $t \geqslant T_\varepsilon$, we have

$$\frac{\mathrm{d}x}{\mathrm{d}t} \leqslant x\frac{(e_1 m_1 - D)(K_1 + \varepsilon - \lambda_1)}{a_1}$$

and so

$$\int_{x(T_\varepsilon)}^{x(t)} \frac{\mathrm{d}\xi}{\xi} \leqslant \frac{(e_1 m_1 - D)(K_1 + \varepsilon - \lambda_1)(t - T_\varepsilon)}{a_1}.$$

In this case, if $\lambda_1 > K_1$, then $x(t) \to 0$ as $t \to \infty$. $\qquad\square$

P r o o f of Lemma 4.1.2.   The variational matrix at E_1 is

$$(6.1) \qquad V(E_1) = \begin{bmatrix} -r_1 & -r_1\alpha_1 & -\dfrac{m_1 K_1}{a_1 + K_1} \\[3ex] 0 & r_2\left\{1 - \dfrac{\alpha_2 K_1^n}{K_2(a^n + K_1^n)}\right\} & 0 \\[3ex] 0 & 0 & \dfrac{e_1 m_1 K_1}{a_1 + K_1} - \dfrac{h}{b} - D \end{bmatrix}.$$

At E_1, the eigenvalues of the variational matrix are

$$-r_1, \quad r_2\left\{1 - \frac{\alpha_2 K_1^n}{K_2(a^n + K_1^n)}\right\} \quad \text{and} \quad \frac{e_1 m_1 K_1}{a_1 + K_1} - \frac{h}{b} - D.$$

The system is stable at E_1 if

$$K_1 > \lambda_1, \quad \alpha_2 > \frac{K_2(a^n + K_1^n)}{K_1^n} \quad \text{and} \quad h > \frac{b(e_1 m_1 - D)(K_1 - \lambda_1)}{a_1 + K_1} > 0$$

(since $m_1 > D/e_1$). $\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad\qquad$ □

P r o o f of Lemma 4.1.3.   The variational matrix at E_2 is

$$(6.2)$$

$$V(E_2) = \begin{bmatrix} \dfrac{m_1 p_2 x_2}{(a_1 + p_2)^2} - \dfrac{r_1 p_2}{K_1} & -\dfrac{r_1 \alpha_1 p_2}{K_1} + \dfrac{m_1 b_1 p_2 x_2}{(a_1 + p_2)^2} & -\dfrac{m_1 p_2}{a_1 + p_2} \\[3ex] 0 & r_2\left\{1 - \dfrac{\alpha_2 p_2^n}{K_2(a^n + p_2^n)}\right\} - \dfrac{m_2 x_2}{a_2 + p_2} & 0 \\[3ex] \dfrac{e_1 m_1 a_1 x_2}{(a_1 + p_2)^2} & \dfrac{e_2 m_2 x_2}{a_2 + p_2} - \dfrac{e_1 m_1 b_1 p_2 x_2}{(a_1 + p_2)^2} & \dfrac{h x_2}{(b + x_2)^2} \end{bmatrix}.$$

One eigenvalue is

$$r_2\left\{1 - \frac{\alpha_2 p_2^n}{K_2(a^n + p_2^n)}\right\} - \frac{m_2 x_2}{a_2 + p_2} < 0$$

if

$$\alpha_2 > \frac{K_2(a^n + p_2^n)}{p_2^n}\left\{1 - \frac{m_2 x_2}{r_2(a_2 + p_2)}\right\}.$$

The other two eigenvalues are given by the equation $\mu^2 + A_1\mu + B_1 = 0$, where

$$A_1 = \frac{r_1 p_2}{K_1} - \frac{h x_2}{(b + x_2)^2}$$

and

$$B_1 = x_2 p_2\left[\frac{h\{m_1 K_1 - r_1(a_1 + p_2)^2\}}{K_1(a_1 + p_2)^2(b + x_2)^2} + \frac{e_1 a_1 m_1^2}{(a_1 + p_2)^3}\right].$$

E_3 is stable if $A_1 > 0, B_1 > 0$ and

$$\alpha_2 > \frac{a^n + p_3^n}{r p_3^n}\left(r - \frac{m_2 x_3}{a_2 + p_3}\right).$$

Now, $A_1 > 0$ implies

$$K_1 < \frac{r_1 p_2 (a_1 + p_2)^2 (b + x_2)^2}{m_1 p_2 x_2 (b + x_2)^2 + h x_2 (a_1 + p_2)^2}.$$

if

$$K_1 > \frac{r_1 (a_1 + p_2)^2}{m_1}$$

then $B_1 > 0$.

For

$$K_1 < \frac{r_1 (a_1 + p_2)^2}{m_1}, \quad B_1 > 0$$

if

$$0 < h < \frac{e_1 a_1 m_1^2 K_1 (b + x_2)^2}{(a_1 + p_2)\{r_1 (a_1 + p_2)^2 - m_1 K_1\}}$$

holds.

Therefore, E_2 is stable if

$$\alpha_2 > \frac{K_2 (a^n + p_2^n)}{p_2^n}\left\{1 - \frac{m_2 x_2}{r_2 (a_2 + p_2)}\right\}$$

and any one of the following two conditions holds:

(i)

$$\frac{r_1 (a_1 + p_2)^2}{m_1} < K_1 < \frac{r_1 p_2 (a_1 + p_2)^2 (b + x_2)^2}{m_1 p_2 x_2 (b + x_2)^2 + h x_2 (a_1 + p_2)^2};$$

(ii)

$$K_1 < \min\left\{\frac{r_1 (a_1 + p_2)^2}{m_1}, \frac{r_1 p_2 (a_1 + p_2)^2 (b + x_2)^2}{m_1 p_2 x_2 (b + x_2)^2 + h x_2 (a_1 + p_2)^2}\right\}$$

and

$$h < \frac{e_1 a_1 m_1^2 K_1 (b + x_2)^2}{(a_1 + p_2)\{r_1 (a_1 + p_2)^2 - m_1 K_1\}}.$$

$\square$

P r o o f of Lemma 4.2.1. In the absence of macroalgae, we have

$$\frac{\mathrm{d}x}{\mathrm{d}t} \leqslant x\left(\frac{e m_2 C}{a_2 + b_2 C} - D\right).$$

(i) If $m_2 \leqslant b_2 D/e$, then

$$\frac{dx}{dt} \leqslant \frac{-a_2 Dx}{a_2 + b_2 C} < 0.$$

Since $\lim\limits_{t \to \infty} C(t) \leqslant K_2$, corresponding to $\varepsilon_2 > 0$, exists $T_{\varepsilon_2} > 0$ such that for all $t \geqslant T_{\varepsilon_2}$, $C(t) \leqslant K_2 + \varepsilon_2$.

Therefore,

$$\forall t \geqslant T_{\varepsilon_2}, \quad \frac{dx}{dt} \leqslant \frac{-xa_2 D}{a_2 + b_2(K_2 + \varepsilon_2)} \Rightarrow \int_{x(T_{\varepsilon_2})}^{x(t)} \frac{d\eta}{\eta} \leqslant \frac{-a_2 D(t - T_{\varepsilon_2})}{a_2 + b_2(K_2 + \varepsilon_1)} \Rightarrow x(t) \to 0$$

as $t \to \infty$.

(ii) If $m_2 > b_2 D/e$, then

$$\frac{dx}{dt} \leqslant x \frac{(em_2 - b_2 D)(C - \lambda_2)}{a_2 + b_2 C}.$$

Therefore, for all $t \geqslant T_{\varepsilon_2}$, if $\lambda_2 > K_2 + \varepsilon_2$, then

$$\int_{x(T_{\varepsilon_2})}^{x(t)} \frac{d\eta}{\eta} \leqslant \frac{(em_2 - b_2 D)(K_2 + \varepsilon_2 - \lambda_2)(t - T_{\varepsilon_2})}{a_2}$$

and so if $\lambda_2 > K_2$, then $x(t) \to 0$ as $t \to \infty$. $\qquad\square$

P r o o f of Lemma 4.2.2. The variational matrix at E_3 is

$$(6.3) \qquad V(E_3) = \begin{bmatrix} r_1\left(1 - \dfrac{\alpha_1 K_2}{K_1}\right) & 0 & 0 \\[2mm] 0 & -r_2 & -\dfrac{m_2 K_2}{a_2 + b_2 K_2} \\[2mm] 0 & 0 & \dfrac{e_2 m_2 K_2}{a_2 + b_2 K_2} - \dfrac{h}{b} - D \end{bmatrix}.$$

At E_3, the eigenvalues of the variational matrix are

$$r_1\left(1 - \frac{\alpha_1 K_2}{K_1}\right), -r_2 \quad \text{and} \quad \frac{e_2 m_2 K_2}{a_2 + b_2 K_2} - \frac{h}{b} - D.$$

Therefore, the system is stable at E_3 if

$$K_2 > \max\left\{\lambda_2, \frac{K_1}{\alpha_1}\right\} \quad \text{and} \quad h > \frac{b(e_2 m_2 - b_2 D)(K_2 - \lambda_2)}{a_2 + b_2 K_2} > 0$$

(since $m_2 > D/e_2$). $\qquad\square$

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P r o o f of Lemma 4.2.3.   The variational matrix at E_4 is

$$(6.4) \quad V(E_4) = \begin{bmatrix} r_1\left(1 - \dfrac{\alpha_1 c_4}{K_1}\right) - \dfrac{m_1 x_4}{a_1 + b_1 c_4} & 0 & 0 \\[2ex] \dfrac{m_2 c_4 x_4}{(a_2 + b_2 c_4)^2} & \dfrac{m_2 b_2 c_4 x_4}{(a_2 + b_2 c_4)^2} - \dfrac{r_2 c_4}{K_2} & \dfrac{-m_2 c_4}{a_2 + b_2 c_4} \\[2ex] \dfrac{e_1 m_1 x_4}{a_1 + b_1 c_4} - \dfrac{e_2 m_2 c_4 x_4}{(a_2 + b_2 c_4)^2} & \dfrac{e_2 m_2 a_2 x_4}{(a_2 + b_2 c_4)^2} & \dfrac{h x_4}{(b + x_4)^2} \end{bmatrix}.$$

One eigenvalue is

$$r_1\left(1 - \frac{\alpha_1 c_4}{K_1}\right) - \frac{m_1 x_4}{a_1 + b_1 c_4} < 0,$$

if

$$0 < K_1 < \frac{r_1 \alpha_1 c_4 (a_1 + b_1 c_4)}{r_1(a_1 + b_1 c_4) - m_1 x_4}.$$

The other two eigenvalues are given by the equation $\mu^2 + A_2 \mu + B_2 = 0$, where

$$A_2 = \frac{r_2 c_4}{K_2} - \frac{m_2 b_2 c_4 x_4}{(a_2 + b_2 c_4)^2} - \frac{h x_4}{(b + x_4)^2}$$

and

$$B_2 = x_4 c_4 \left[\frac{h\{m_2 K_2 b_2 - r_2(a_2 + b_2 c_4)^2\}}{K_2(a_2 + b_2 c_4)^2(b + x_4)^2} + \frac{e_2 a_2 m_2^2}{(a_2 + b_2 c_4)^3} \right].$$

E_4 is stable if $A_2 > 0, B_2 > 0$ and

$$0 < K_1 < \frac{r_1 \alpha_1 c_4 (a_1 + b_1 c_4)}{r_1(a_1 + b_1 c_4) - m_1 x_4}.$$

Now, $A_2 > 0$ implies

$$K_2 < \frac{r_2 c_4 (a_2 + b_2 c_4)^2 (b + x_4)^2}{m_2 b_2 c_4 x_4 (b + x_4)^2 + h x_4 (a_2 + b_2 c_4)^2}.$$

If

$$K_2 > \frac{r_2(a_2 + b_2 c_4)^2}{m_2 b_2},$$

then $B_2 > 0$.
   For

$$K_2 < \frac{r_2(a_2 + b_2 c_4)^2}{m_2 b_2}, \; B_2 > 0$$

if

$$0 < h < \frac{e_2 a_2 m_2^2 K_2 (b + x_4)^2}{(a_2 + b_2 c_4)\{r_2(a_2 + b_2 c_4)^2 - m_2 b_2 K_2\}}$$

holds.

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Therefore, E_4 is stable if

$$K_1 < \frac{r_1\alpha_1 c_4(a_1 + b_1 c_4)}{r_1(a_1 + b_1 c_4) - m_1 x_4}$$

and any one of the following two conditions holds:

(i)
$$\frac{r_2(a_2 + b_2 c_4)^2}{m_2 b_2} < K_2 < \frac{r_2 c_4(a_2 + b_2 c_4)^2(b + x_4)^2}{m_2 b_2 c_4 x_4(b + x_4)^2 + h x_4(a_2 + b_2 c_4)^2};$$

(ii)
$$K_2 < \min\left\{\frac{r_2(a_2 + b_2 c_4)^2}{m_2 b_2}, \frac{r_2 c_4(a_2 + b_2 c_4)^2(b + x_4)^2}{m_2 b_2 c_4 x_4(b + x_4)^2 + h x_4(a_2 + b_2 c_4)^2}\right\}$$

and

$$h < \frac{e_2 a_2 m_2^2 K_2(b + x_4)^2}{(a_2 + b_2 c_4)\{r_2(a_2 + b_2 c_4)^2 - m_2 b_2 K_2\}}.$$

$\square$

P r o o f of Lemma 4.3.1.   The variational matrix at E_5 is

$$(6.5) \qquad V(E_5) = \begin{bmatrix} \dfrac{-r_1 p_5}{K_1} & \dfrac{-r_1\alpha_1 p_5}{K_1} & \dfrac{-m_1 p_5}{a_1 + p_5 + b_1 c_5} \\ \dfrac{-r_2\alpha_2 n a^n c_5 p_5^{n-1}}{K_2(a^n + p_5^n)^2} & \dfrac{-r_2 c_5}{K_2} & \dfrac{-m_2 c_5}{a_2 + p_5 + b_2 c_5} \\ 0 & 0 & \Gamma \end{bmatrix},$$

where

$$\Gamma = \frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - \frac{h}{b} - D$$

One eigenvalue is

$$\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - \frac{h}{b} - D < 0,$$

if

$$h > b\left(\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - D\right).$$

The other two eigenvalues are given by the equation $\mu^2 + A_3\mu + B_3 = 0$, where

$$A_3 = \frac{r_1 p_5}{K_1} + \frac{r_2 c_5}{K_2} > 0 \quad \text{and} \quad B_3 = \frac{r_1 r_2 p_5 c_5}{K_1 K_2}\left\{1 - \frac{n\alpha_1\alpha_2 a^n p_5^{n-1}}{(a^n + p_5 n)^2}\right\}.$$

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E_5 is stable if $B_3 > 0$ and

$$h > b\Big(\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - D\Big).$$

Now, $B_3 > 0$ implies

$$\alpha_2 < \frac{(a^n + p_5^n)^2}{n a^n \alpha_1 p_5^{n-1}}.$$

Therefore, E_5 is stable if

$$\alpha_2 < \frac{(a^n + p_5^n)^2}{n a^n \alpha_1 p_5^{n-1}} \quad \text{and} \quad h > b\Big(\frac{e_1 m_1 p_5}{a_1 + p_5 + b_1 c_5} + \frac{e_2 m_2 c_5}{a_2 + p_5 + b_2 c_5} - D\Big).$$

<div style="text-align:right">□</div>

P r o o f of Lemma 4.3.2. The characteristic equation of the variational matrix at E^* is $\mu^3 + Q_1 \mu^2 + Q_2 \mu + Q_3 = 0$, where

$$Q_1 = -(F_P^1|_{E^*} + F_C^2|_{E^*} + F_x^3|_{E^*}),$$

$$Q_2 = F_P^1|_{E^*}(F_C^2|_{E^*} + F_x^3|_{E^*}) + F_C^2|_{E^*} F_x^3|_{E^*} - F_C^3|_{E^*} F_x^2|_{E^*}$$
$$\qquad - F_C^1|_{E^*} F_P^2|_{E^*} - F_x^1|_{E^*} F_P^3|_{E^*},$$

$$Q_3 = F_P^1|_{E^*}(F_C^3|_{E^*} F_x^2|_{E^*} - F_C^2|_{E^*} F_x^3|_{E^*})$$
$$\qquad + F_C^1|_{E^*}(F_x^3|_{E^*} F_P^2|_{E^*} - F_P^3|_{E^*} F_x^2|_{E^*})$$
$$\qquad + F_x^1|_{E^*}(F_P^3|_{E^*} F_C^2|_{E^*} - F_P^2|_{E^*} F_C^3|_{E^*}),$$

$$F_P^1|_{E^*} = \frac{m_1 p^* x^*}{(a_1 + p^* + b_1 c^*)^2} - \frac{r_1 p^*}{K_1},$$

$$F_C^1|_{E^*} = p^*\Big\{\frac{m_1 b_1 x^*}{(a_1 + p^* + b_1 c^*)^2} - \frac{r_1 \alpha_1}{K_1}\Big\},$$

$$F_x^1|_{E^*} = -\frac{m_1 p^*}{a_1 + p^* + b_1 c^*},$$

$$F_P^2|_{E^*} = \frac{m_2 c^* x^*}{(a_2 + p^* + b_2 c^*)^2} - \frac{n r_2 \alpha_2 c^* a^n (p^*)^{n-1}}{K_2\{a^n + (p^*)^n\}^2},$$

$$F_C^2|_{E^*} = c^*\Big\{\frac{m_2 b_2 x^*}{(a_2 + p^* + b_2 c^*)^2} - \frac{r_2}{K_2}\Big\},$$

$$F_x^2|_{E^*} = -\frac{m_2 c^*}{a_2 + p^* + b_2 c^*},$$

$$F_P^3|_{E^*} = x^*\Big\{\frac{e_1 m_1 (a_1 + b_1 c^*)}{(a_1 + p^* + b_1 c^*)^2} - \frac{e_2 m_2 c^*}{(a_2 + p^* + b_2 c^*)^2}\Big\},$$

$$F_C^3|_{E^*} = x^*\Big\{\frac{e_2 m_2 (a_2 + p^*)}{(a_2 + p^* + b_2 c^*)^2} - \frac{e_1 m_1 b_1 p^*}{(a_1 + p^* + b_1 c^*)^2}\Big\},$$

$$F_x^3|_{E^*} = \frac{h x^*}{(b + x^*)^2}.$$

E^* is locally asymptotically stable if $Q_1 > 0$ and $Q_1 Q_2 > Q_3$.

Now,

$$Q_1 = \frac{r_1 p^*}{K_1} + \frac{r_2 c^*}{K_2} - \frac{m_1 p^* x^*}{(a_1 + p^* + b_1 c^*)^2} - \frac{m_2 b_2 c^* x^*}{(a_2 + p^* + b_2 c^*)^2} - \frac{h x^*}{(b + x^*)^2} > 0 \Rightarrow h < h^*,$$

where

$$h^* = \frac{(b + x^*)^2}{x^*} \left\{ \frac{r_1 p^*}{K_1} + \frac{r_2 c^*}{K_2} - \frac{m_1 p^* x^*}{(a_1 + p^* + b_1 c^*)^2} - \frac{m_2 b_2 c^* x^*}{(a_2 + p^* + b_2 c^*)^2} \right\}.$$

Therefore, E^* is stable if $h < h^*$ and $\eta^* > 0$, where

$$\begin{aligned}
\eta^* = {}& F_C^1|_{E^*} F_x^2|_{E^*} F_P^3|_{E^*} + F_x^1|_{E^*} F_P^2|_{E^*} F_C^3|_{E^*} - 2 F_P^1|_{E^*} F_C^2|_{E^*} F_x^3|_{E^*} \\
& + (F_C^2|_{E^*} + F_x^3|_{E^*})\{F_x^2|_{E^*} F_C^3|_{E^*} - (F_P^1|_{E^*})^2\} \\
& + (F_P^1|_{E^*} + F_x^3|_{E^*})\{F_x^1|_{E^*} F_P^3|_{E^*} - (F_C^2|_{E^*})^2\} \\
& + (F_P^1|_{E^*} + F_C^2|_{E^*})\{F_C^1|_{E^*} F_P^2|_{E^*} - (F_x^3|_{E^*})^2\}.
\end{aligned}$$

$\square$

P r o o f of Lemma 4.3.3.   The characteristic equation of the variational matrix at E^* is $\mu^3 + Q_1 \mu^2 + Q_2 \mu + Q_3 = 0$.

The necessary and sufficient conditions for a Hopf bifurcation to occur at $\alpha_1 = \alpha_{1_{cr}}$ are that

(i) $Q_1(K_{1_{cr}}) > 0, Q_2(K_{1_{cr}}) > 0$ and $Q_3(K_{1_{cr}}) > 0$,

(ii) $Q_3(K_{1_{cr}}) = Q_1(K_{1_{cr}}) Q_2(K_{1_{cr}})$,

(iii) $\mathrm{Re}[\mathrm{d}\mu_j / (\mathrm{d}K_1)]_{K_1 = K_{1_{cr}}} \neq 0$, $j = 1, 2, 3$.

For $K_1 = K_{1_{cr}}$, the characteristic equation becomes $(\mu + A)(\mu^2 + B) = 0 \Rightarrow$ $\mu = -Q_1, \pm i\sqrt{Q_2}$.

For $K_1 \in (K_{1_{cr}} - \varepsilon, K_{1_{cr}} + \varepsilon)$, the roots are in general of the form:

$$\begin{aligned}
\mu_1(K_1) &= \gamma_1(K_1) + i\gamma_2(K_1), \\
\mu_2(K_1) &= \gamma_1(K_1) - i\gamma_2 K_1), \\
\mu_3(K_1) &= -Q_1(K_1).
\end{aligned}$$

Therefore,

$$\frac{\mathrm{d}}{\mathrm{d}K_1}(\mu^3 + Q_1 \mu^2 + Q_2 \mu + Q_3) = 0$$

gives

$$(K + iL)\frac{\mathrm{d}\mu}{\mathrm{d}K_1} + (M + iN) = 0,$$

where
$$K(K_1) = 3\gamma_1^2(K_1) - 3\gamma_2^2(K_1) + 2Q_1(K_1)\gamma_1(K_1) + Q_2(K_1),$$
$$L(K_1) = 6\gamma_1(K_1)\gamma_2(K_1) + 2Q_1(K_1)\gamma_2(K_1),$$
$$M(K_1) = Q_3'(K_1) + \{\gamma_1^2(K_1) - \gamma_2(K_1)\}Q_1'(K_1) + \gamma_1 Q_2'(K_1),$$
$$N(K_1) = 2\gamma_1(K_1)\gamma_2(K_1)Q_1'(K_1) + \gamma_2(K_1)Q_2'(K_1).$$

Therefore,
$$\frac{\mathrm{d}\mu}{\mathrm{d}K_1} = -\frac{\{M(K_1)K(K_1) + N(K_1)L(K_1)\} + \mathrm{i}\{N(K_1)K(K_1) - M(K_1)L(K_1)\}}{K^2(K_1) + L^2(K_1)}.$$

If $\{M(K_1)K(K_1) + N(K_1)L(K_1)\}_{K_1=K_{1_{\mathrm{cr}}}} \neq 0$, then
$$\mathrm{Re}\Big[\frac{\mathrm{d}\mu_j}{\mathrm{d}K_1}\Big]_{K_1=K_{1_{\mathrm{cr}}}} \neq 0.$$

Therefore, if
  (i) $Q_i(K_{1_{\mathrm{cr}}}) > 0$ $(i = 1, 2, 3)$,
  (ii) $f_1(K_{1_{\mathrm{cr}}}) = f_2(K_{1_{\mathrm{cr}}})$,
  (iii) $\{M(K_1)K(K_1) + N(K_1)L(K_1)\}_{K_{1_{\mathrm{cr}}}} \neq 0$
all hold, then a Hopf bifurcation occurs at $K_1 = K_{1_{\mathrm{cr}}}$ and also it is non-degenerate.
  Also, at E^* we obtain $(J_{E^*} - 2\mathrm{i}\omega_0)^{-1} = (Q_{\omega_0}^{ij})_{3\times3}$ where

$$Q_{\omega_0}^{11}\Delta_{\omega_0} = (F_C^2 F_x^3 - F_x^2 F_C^3 - 4\omega_0^2) - 2\mathrm{i}\omega_0(F_C^2 + F_x^3),$$
$$Q_{\omega_0}^{12}\Delta_{\omega_0} = (F_x^1 F_C^3 - F_C^1 F_x^3) + 2\mathrm{i}\omega_0 F_C^1,$$
$$Q_{\omega_0}^{13}\Delta_{\omega_0} = (F_C^1 F_x^2 - F_x^1 F_C^2) + 2\mathrm{i}\omega_0 F_x^1,$$
$$Q_{\omega_0}^{21}\Delta_{\omega_0} = (F_x^2 F_P^3 - F_P^2 F_x^3) + 2\mathrm{i}\omega_0 F_P^2,$$
$$Q_{\omega_0}^{22}\Delta_{\omega} = (F_P^1 F_x^3 - F_x^1 F_P^3 - 4\omega_0^2) - 2\mathrm{i}\omega_0(F_P^1 + F_x^3),$$
$$Q_{\omega_0}^{23}\Delta_{\omega_0} = (F_x^1 F_P^2 - F_x^2 F_P^1) + 2\mathrm{i}\omega_0 F_x^2,$$
$$Q_{\omega_0}^{31}\Delta_{\omega_0} = (F_P^2 F_C^3 - F_P^3 F_C^2) + 2\mathrm{i}\omega_0 F_P^3,$$
$$Q_{\omega_0}^{32}\Delta_{\omega_0} = (F_C^1 F_P^3 - F_C^3 F_P^1) + 2\mathrm{i}\omega_0 F_C^3,$$
$$Q_{\omega_0}^{33}\Delta_{\omega_0} = (F_P^1 F_C^2 - F_C^1 F_P^2 - 4\omega_0^2) - 2\mathrm{i}\omega_0(F_P^1 + F_C^2)$$

and for Δ_{ω_0} we have

$$\Delta_{\omega_0} = \{F_P^1 F_C^2 F_x^3 - 4\omega_0^2 F_P^1 - F_P^1 F_x^2 F_C^3 - 4\omega_0^2(F_C^2 + F_x^3)$$
$$- F_C^1 F_P^2 F_x^3 + F_x^2 F_C^1 F_P^3 + F_x^1 F_P^2 F_C^3 - F_x^1 F_C^2 F_P^3\}$$
$$- 2\mathrm{i}\omega_0\{F_C^2 F_x^3 - 4\omega_0^2 - F_x^2 F_C^3 + F_P^1(F_C^2 + F_x^3) - F_C^1 F_P^2 - F_x^1 F_P^3\}.$$

Putting $\omega_0 = 0$ we get the components of $(J_{E^*})^{-1} = (Q^{ij})_{3\times3}$.

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The left and right normalized eigenvectors $\mathbf{a} = (a_1, a_2, a_3)$ and $\mathbf{b} = (b_1, b_2, b_3)^{\top}$ of the variational matrix J_{E^*} are

$$\mathbf{a} = \frac{\xi_1}{F_C^3\{(F_P^1 F_C^3 - F_C^1 F_P^3)^2 + \omega_0^2 (F_C^3)^2\}}$$
$$\times (a_1 + \mathrm{i}\omega_0 a_2, \; F_C^3\{(F_P^1 F_C^3 - F_C^1 F_P^3)^2 + \omega_0^2 (F_C^3)^2\}, \; a_3 + \mathrm{i}\omega_0 a_4)$$

and

$$\mathbf{b} = \frac{\xi_2}{F_x^2\{(F_x^2 F_P^1 - F_x^1 F_P^2)^2 + \omega_0^2 (F_x^2)^2\}}$$
$$\times (b_1 + \mathrm{i}\omega_0 b_2, \; F_x^2\{(F_x^2 F_P^1 - F_x^1 F_P^2)^2 + \omega_0^2 (F_x^2)^2\}, \; b_3 + \mathrm{i}\omega_0 b_4)^{\top},$$

where ξ_1, ξ_2 are complex numbers,

$$a_1 = F_C^3\{(F_P^3 F_C^2 - F_P^2 F_C^3)(F_P^1 F_C^3 - F_C^1 F_P^3) + \omega_0^2 F_P^3 F_C^3\},$$
$$a_2 = F_C^3\{F_C^3(F_P^3 F_C^2 - F_C^3 F_P^2) - (F_P^1 F_C^3 - F_C^1 F_P^3) F_P^3\},$$
$$a_3 = F_C^2\{(F_P^1 F_C^3 - F_C^1 F_P^3)^2 + \omega_0^2 (F_C^3)^2\}$$
$$\qquad + F_C^1\{(F_P^3 F_C^2 - F_C^3 F_P^2)(F_P^1 F_C^3 - F_C^1 F_P^3) + \omega_0^2 F_P^3 F_C^3\},$$
$$a_4 = F_C^1\{F_C^3(F_P^3 F_C^2 - F_C^3 F_P^2) - F_P^3(F_P^1 F_C^3 - F_C^1 F_P^3)\}$$
$$\qquad - (F_P^1 F_C^3 - F_C^1 F_P^3)^2 - \omega_0^2 (F_C^3)^2,$$
$$b_1 = F_x^3\{(F_x^1 F_C^2 - F_x^2 F_C^1)(F_x^2 F_P^1 - F_x^1 F_P^2) + \omega_0^2 F_x^1 F_x^2\},$$
$$b_2 = F_x^3\{F_x^2(F_x^1 F_C^2 - F_C^1 F_x^2) - (F_x^2 F_P^1 - F_x^1 F_P^2) F_x^1\},$$
$$b_3 = - F_P^3\{(F_x^1 F_C^2 - F_C^1 F_x^2)(F_x^2 F_P^1 - F_x^1 F_P^2) + \omega_0^2 F_x^1 F_x^2\}$$
$$\qquad - F_C^2\{(F_x^2 F_P^1 - F_x^1 F_P^2)^2 + \omega_0^2 (F_x^2)^2\},$$
$$b_4 = - F_P^2\{F_x^2(F_x^1 F_C^2 - F_C^1 F_x^2) - F_x^1(F_x^2 F_P^1 - F_x^1 F_P^2)\}$$
$$\qquad + (F_x^2 F_P^1 - F_x^1 F_P^2)^2 + \omega_0^2 (F_x^2)^2.$$

Using $\mathbf{a} \cdot \mathbf{b} = 1$ we can obtain $\xi_1 \xi_2$.

Now

$$-a_l F^l_{u_j u_m u_s} b_j b_m \bar{b}_s = -(a_1 F^1_{PPP} + a_2 F^2_{PPP} + a_3 F^3_{PPP}) b_1 |b_1|^2$$
$$- (a_1 F^1_{CCC} + a_2 F^2_{CCC} + a_3 F^3_{CCC}) b_2 |b_2|^2 - a_3 F^3_{xxx} b_3 |b_3|^2$$
$$- (a_1 F^1_{PPx} + a_2 F^2_{PPx} + a_3 F^3_{PPx})(2 b_3 |b_1|^2 + b_1^2 \bar{b}_3)$$
$$- 2(a_1 F^1_{PCx} + a_2 F^2_{PCx} + a_3 F^3_{PCx}(b_1 b_2 \bar{b}_3 + b_1 b_3 \bar{b}_2 + b_2 b_3 \bar{b}_1)$$
$$- (a_1 F^1_{PPC} + a_2 F^2_{PPC} + a_3 F^3_{PPC})(b_1^2 \bar{b}_2 + 2 b_2 |b_1|^2)$$
$$- (a_1 F^1_{CCx} + a_2 F^2_{CCx} + a_3 F^3_{CCx})(b_2^2 \bar{b}_3 + 2 b_3 |b_2|^2)$$
$$- (a_1 F^1_{CCP} + a_2 F^2_{CCP} + a_3 F^3_{CCP})(b_2^2 \bar{b}_1 + 2 b_1 |b_2|^2),$$

$$a_l F^l_{u_j u_m} b_j (J_{E^*}^{-1})_{mr} F^r_{u_p u_q} b_p \bar{b}_q$$

$$= \left\{ \sum_{i=1}^{3} a_i (F^i_{PP} b_1 + F^i_{CP} b_2 + F^i_{xP} b_3) \right\} \left(\sum_{i=1}^{3} Q^{1i} A^i \right)$$

$$+ \left\{ \sum_{i=1}^{3} a_i (F^i_{PC} b_1 + F^i_{CC} b_2 + F^i_{xC} b_3) \right\} \left(\sum_{i=1}^{3} Q^{2i} A^i \right)$$

$$+ [a_1 (F^1_{Px} b_1 + F^1_{Cx} b_2) + a_2 (F^2_{Px} b_1 + F^2_{Cx} b_2)$$

$$+ a_3 (F^3_{Px} b_1 + F^3_{Cx} b_2 + F^3_{xx} b_3)] \left(\sum_{i=1}^{3} Q^{3i} A^i \right)$$

and

$$a_l F^l_{u_j u_k} \bar{b}_j [(J_{E^*} - 2i\omega_0)^{-1}]_{kr} F^r_{u_p u_q} b_p b_q$$

$$= \left\{ \sum_{i=1}^{3} a_i (F^i_{PP} \bar{b}_1 + F^i_{CP} \bar{b}_2 + F^i_{xP} \bar{b}_3) \right\} \left(\sum_{i=1}^{3} Q^{1i}_{\omega_0} A^i_{\omega_0} \right)$$

$$+ \left\{ \sum_{i=1}^{3} a_i (F^i_{PC} \bar{b}_1 + F^i_{CC} \bar{b}_2 + F^i_{xC} \bar{b}_3) \right\} \left(\sum_{i=1}^{3} Q^{2i}_{\omega_0} A^i_{\omega_0} \right)$$

$$+ [a_1 (F^1_{Px} \bar{b}_1 + F^2_{Cx} \bar{b}_2) + a_2 (F^2_{Px} \bar{b}_1 + F^2_{Cx} \bar{b}_2)$$

$$+ a_3 (F^3_{Px} \bar{b}_1 + F^3_{Cx} \bar{b}_2 + F^3_{xx} \bar{b}_3)] \left(\sum_{i=1}^{3} Q^{3i}_{\omega_0} A^i_{\omega_0} \right),$$

where

$$A^1 = F^1_{PP} |b_1|^2 + F^1_{PC} (b_1 \bar{b}_2 + b_2 \bar{b}_1) + F^1_{Px} (b_1 \bar{b}_3 + b_3 \bar{b}_1)$$
$$+ F^1_{CC} |b_2|^2 + F^1_{Cx} (b_2 \bar{b}_3 + b_3 \bar{b}_2),$$
$$A^2 = F^2_{PP} |b_1|^2 + F^2_{PC} (b_1 \bar{b}_2 + b_2 \bar{b}_1) + F^2_{Px} (b_1 \bar{b}_3 + b_3 \bar{b}_1)$$
$$+ F^3_{CC} \bar{b}_2^2 + F^2_{Cx} (b_2 \bar{b}_3 + b_3 \bar{b}_2),$$
$$A^3 = F^3_{PP} |b_1|^2 + F^3_{PC} (b_1 \bar{b}_2 + b_2 \bar{b}_1) + F^3_{Px} (b_1 \bar{b}_3 + b_3 \bar{b}_1)$$
$$+ F^3_{Cx} (b_2 \bar{b}_3 + b_3 \bar{b}_2) + F^3_{CC} |b_2|^2 + F^3_{xx} |b_3|^2,$$
$$A^1_{\omega_0} = F^1_{PP} b_1^2 + 2F^1_{PC} b_1 b_2 + 2F^1_{Px} b_1 b_3 + F^1_{CC} b_2^2 + 2F^1_{Cx} b_1 b_3,$$
$$A^2_{\omega_0} = F^2_{PP} b_1^2 + F^2_{CC} b_2^2 + 2F^2_{PC} b_1 b_2 + 2F^2_{Px} b_1 b_3 + 2F^2_{Cx} b_1 b_3,$$
$$A^3_{\omega_0} = F^3_{PP} b_1^2 + F^3_{CC} b_2^2 + F^3_{xx} b_3^2 + 2F^3_{PC} b_1 b_2 + 2F^3_{Px} b_1 b_3 + 2F^3_{Cx} b_2 b_3.$$

For these values of $F^l_{u_i u_j u_k}$, $F^l_{u_i u_j}$, $\mathbf{a}$, $\mathbf{b}$ and components Q^{ij} and $Q^{ij}_{\omega_0}$ we obtain the value of $(\Phi)_{K_1 = K_{1\mathrm{cr}}}$. If $(\Phi)_{K_1 = K_{1\mathrm{cr}}} > 0$, then system (2.1) undergoes a supercritical Hopf bifurcation as K_1 is increased through $K_{1\mathrm{cr}}$ so that the bifurcating periodic orbit is asymptotically orbitally stable.

References

[1] *D. Bender, G. Diaz-Pulido, S. Dove*: Effects of macroalgae on corals recovering from disturbance. J. Exp. Mar. Biol. Ecol. *429* (2012), 15–19. `doi`

[2] *J. Bhattacharyya, S. Pal*: Coexistence of competing predators in a coral reef ecosystem. Nonlinear Anal., Real World Appl. *12* (2011), 965–978. `zbl` `MR` `doi`

[3] *S. J. Box, P. J. Mumby*: Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar. Ecol. Prog. Ser. *342* (2007), 139–149. `doi`

[4] *J. F. Bruno, W. F. Precht, P. S. Vroom, R. B. Aronson*: Coral reef baselines: How much macroalgae is natural? Marine Pollution Bull. *80* (2014), 24–29. `doi`

[5] *J. F. Bruno, H. Sweatman, W. F. Precht, E. R. Selig, V. G. W. Schutte*: Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology *90* (2009), 1478–1484. `doi`

[6] *R. S. Cantrell, C. Cosner*: On the dynamics of predator-prey models with the Beddington-DeAngelis functional response. J. Math. Anal. Appl. *257* (2001), 206–222. `zbl` `MR` `doi`

[7] *A. J. Cheal, M. A. MacNeil, E. Cripps, M. J. Emslie, M. Jonker, B. Schaffelke, H. Sweatman*: Coral-macroalgal phase shifts or reef resilience: Links with diversity and functional roles of herbivorous fishes on the Great Barrier Reef. Coral Reefs *29* (2010), 1005–1015. `doi`

[8] *J. Cui, Y. Takeuchi*: Permanence, extinction and periodic solution of predator-prey system with Beddington-DeAngelis functional response. J. Math. Anal. Appl. *317* (2006), 464–474. `zbl` `MR` `doi`

[9] *R. D. Evans, S. K. Wilson, S. N. Field, J. A. Y. Moore*: Importance of macroalgal fields as coral reef fish nursery habitat in north-west Australia. Mar. Biol. *161* (2014), 599–607. `doi`

[10] *J. Feng, H. Wang, D. Huang, S. Li*: Alternative attractors in marine ecosystems: A comparative analysis of fishing effects. Ecological Modelling *195* (2006), 377–384. `doi`

[11] *R. P. Gupta, P. Chandra*: Bifurcation analysis of modified Leslie-Gower predator-prey model with Michaelis-Menten type prey harvesting. J. Math. Anal. Appl. *398* (2013), 278–295. `zbl` `MR` `doi`

[12] *V. J. Harriott, S. A. Banks*: Latitudinal variation in coral communities in eastern Australia: A qualitative biophysical model of factors regulating coral reefs. Coral Reefs *21* (2002), 83–94. `doi`

[13] *T. P. Hughes, N. A. J. Graham, J. B. C. Jackson, P. J. Mumby, R. S. Steneck*: Rising to the challenge of sustaining coral reef resilience. Trends Ecol. Evol. *25* (2010), 633–642. `doi`

[14] *C. Jessen, C. Roder, J. F. V. Lizcano, C. R. Voolstra, C. Wild*: In-situ effects of simulated overfishing and eutrophication on benthic coral reef algae growth, succession, and composition in the Central Red Sea. Plos One *8* (2013), Article ID e66992, 13 pages. `doi`

[15] *D. B. Kramer*: Adaptive harvesting in a multiple-species coral-reef food web. Ecol. Soc. *13* (2007), Article ID 17, 25 pages. `doi`

[16] *P. Lenzini, J. Rebaza*: Nonconstant predator harvesting on ratio-dependent predator-prey models. Appl. Math. Sci., Ruse *4* (2010), 791–803. `zbl` `MR`

[17] *D. Lirman*: Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs *19* (2001), 392–399. `doi`

[18] *M. M. Littler, D. S. Littler, B. L. Brooks*: Harmful algae on tropical coral reefs: Bottom-up eutrophication and top-down herbivory. Harmful Algae *5* (2006), 565–585. `doi`

[19] *L. J. McCook, J. Jompa, G. Diaz-Pulido*: Competition between corals and algae on coral reefs: A review of evidence and mechanisms. Coral Reefs *19* (2001), 400–417. `doi`

[20] *J. W. McManus, J. F. Polsenberg*: Coral-algal phase shifts on coral reefs: Ecological and environmental aspects. Progress in Oceanography *60* (2004), 263–279. `doi`

[21] *P. J. Mumby*: Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. Coral Reefs *28* (2009), 761–773. `doi`

[22] *P. J. Mumby, N. L. Foster, E. A. G. Fahy*: Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs *24* (2005), 681–692. `doi`

[23] *P. J. Mumby, R. S. Steneck*: Coral reef management and conservation in light of rapidly evolving ecological paradigms. Trends Ecol. Evol. *23* (2008), 555–563. `doi`

[24] *G. P. D. Murray, R. A. Stillman, R. E. Gozlan, J. R. Britton*: Experimental predictions of the functional response of a freshwater fish. Ethology *119* (2013), 751–761. `doi`

[25] *A. B. Poore*: On the theory and application of Hopf-Friedrichs bifurcation theory. Arch. Ration. Mech. Anal. *60* (1976), 371–393. `zbl` `MR` `doi`

[26] *S. Ruan*: Persistence and coexistence in zooplankton-phytoplankton-nutrient models with instantaneous nutrient recycling. J. Math. Biol. *31* (1993), 633–654. `zbl` `MR` `doi`

[27] *I. Siekmann, H. Malchow, E. Venturino*: An extension of the Beretta-Kuang model of viral diseases. Math. Biosci. Eng. *5* (2008), 549–565. `zbl` `MR` `doi`

[28] *J. E. Smith, C. L. Hunter, C. M. Smith*: The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia *163* (2010), 497–507. `doi`

[29] *J. E. Smith, M. Shaw, R. A. Edwards, D. Obura, O. Pantos, E. Sala, S. A. Sandin, S. Smriga, M. Hatay, F. L. Rohwer*: Indirect effects of algae on coral: Algae-mediated, microbe-induced coral mortality. Ecol. Lett. *9* (2006), 835–845. `doi`

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