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# Internal phosphorus recycling promotes rich and complex dynamics in an algae-phosphorus model: Implications for eutrophication management

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# ABSTRACT

Internal phosphorus recycling in lakes is an important nutrient source that promotes algal growth. Its persistence impedes the effort to improve water quality and thus poses a challenge to the management of eutrophication in lakes, especially in shallow lakes where the occurrence of internal phosphorus recycling is reportedly more common. This paper aims to provide crucial insights on the effects of internal phosphorus recycling on eutrophication dynamics for effective management of lake eutrophication. For this purpose, a mathematical model for lake eutrophication, comprising two compartments of algae and phosphorus, is first formulated for application to a eutrophic tropical lake named Tasik Harapan in Universiti Sains Malaysia. Numerical bifurcation analysis of the model is then performed to assess the combined influences of internal phosphorus recycling, algal mortality and external phosphorus loading on Tasik Harapan eutrophication dynamics. Specifically, co-dimension one bifurcation analysis of algal mortality rate is carried out by means of XPPAUT for various external phosphorus loading rates. The emergence of limit cycle for a certain range of algal mortality rate could be related to the hydra effect (i.e., algal concentration increases in response to greater algal mortality) and the paradox of enrichment (i.e., destabilization of algae in nutrient rich environment). To trace the locus of co-dimension one bifurcation, co-dimension two bifurcation analysis is performed by means of MatCont. The analysis demonstrated that the inclusion of the internal phosphorus recycling term induces rich and complex dynamics of the model. These dynamics include saddle-node bifurcation, cusp, Bogdanov-Takens bifurcation, Generalized Hopf bifurcation and limit point bifurcation of cycles. The results suggest that high internal phosphorus recycling rate promotes bistability and catastrophic shift in a shallow and tropical lake like Tasik Harapan. Hence, the key to effective management of eutrophication in shallow and tropical lakes is the control of internal phosphorus recycling.

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#### 1. Introduction

Internal phosphorus recycling in shallow lakes has been the focus of intensive studies for eutrophication management purposes (Li et al., 2015; Welch and Cooke, 2005; Jeppesen et al., 2005; Kiani et al., 2020; Yang et al., 2020; Zou et al., 2020). It has been identified as one of the key factors leading to successful lake restoration (Søndergaard et al., 2007). Eutrophication refers to an ecological state where proliferation of algae occurs due to an increase in nutrient loading (Pang et al., 2018). It is well known that phosphorus is an essential nutrient driving algal growth

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(Carpenter, 2008). In a healthy lake, phosphorus occurs in limiting amount so the algal growth is restricted. However, residuals from human activities such as industrial, agricultural and urban domestic sewage increase the phosphorus concentration and subsequently lead to excessive algal growth. Algal concentration is a commonly-used indicator for eutrophication where a lake is deemed eutrophic when the algal concentration exceeds 10 µg/L Chl *a* (Chapra, 1997). Shallow lake ecosystem tends to exhibit alternative stable states, either oligotrophic, mesotrophic, or eutrophic (Xu et al., 2020). The oligotrophic state is the desired state with low algal concentration ( $A < 2.6 \mu g/L$ ) and low nutrients. In contrast, the undesired eutrophic state has high algal concentration ( $A \ge 10 \mu g/L$ ) and rich nutrient constitution. With intermediate level of algal and nutrient concentrations, mesotrophic is the state between oligotrophic and eutrophic (Chapra, 1997).







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A sudden change in the equilibrium state of an ecosystem may occur due to external or internal disturbances (Lin et al., 2019; Mohd, 2016; Mohd, 2018). This phenomenon is known as regime shift (Xu et al., 2020; Bannister et al., 2018). An external disturbance is characterised by a rapid change in an external environmental driver (Vermaire et al., 2017). For example, an increase in external phosphorus loading (external disturbance) may lead to the undesirable shift of a lake from oligotrophic to eutrophic. An internal disturbance refers to a gradual change in an environmental driver that moves the system close to regime shift threshold gradually (Vermaire et al., 2017). Internal phosphorus recycling is considered as an internal disturbance that slowly drives the lake system to eutrophic state (Zhao et al., 2020). The impact of regime shift is often visible, for example, a clear lake shifts to a turbid lake. However, the gradual changes induced by internal disturbance that moved the lake system close to a critical threshold have no visible impact until the point at which regime shift occurs. Hence, insights on the possible critical thresholds and transitions in eutrophication dynamics are needed for effective ecosystem management. In this study, bifurcation theory is used to identify such transitions between different regimes.

In lake study, several types of bifurcations are associated with the alterations between different regimes, including saddle-node bifurcation, transcritical bifurcation and Hopf bifurcation (Caen et al., 2019; Edwards and Bees, 2001; Zambrano et al., 2001; Cai et al., 2012; Ruan, 2001; Shi and Yu, 2017; Zhang and Wang, 2012). The abrupt and persistent change from low algal concentration (oligotrophic) to high algal concentration (eutrophic) due to a small change in external phosphorus loading will cause the lake system to undergo a saddle-node bifurcation (Caen et al., 2019). For such saddle-node bifurcation in lake eutrophication, alternative stable states exist and the oligotrophic, mesotrophic and eutrophic states represent the stable steady states. Regime shift in a lake's trophic state occurs when the nutrient level in the lake exceeds a critical threshold. Transcritical bifurcation is also commonly observed in lake ecosystems, where a stable and an unstable equilibrium collide and exchange stability at bifurcation point (Edwards and Bees, 2001). For example, in a lake ecosystem, transcritical bifurcation occurs during the transition of a stable survival steady state to the extinction of fish at higher fish loss rate (Zambrano et al., 2001). Changes in nutrient level can also result in a Hopf bifurcation, where an equilibrium loses its stability and a periodic solution bifurcates from the equilibrium (Cai et al., 2012; Ruan, 2001; Shi and Yu, 2017; Zhang and Wang, 2012). The oscillatory behaviour in algal dynamics is an early warning of eutrophication as the high amplitude of oscillation is a sign of a sudden increase in algal concentration (Chaudhuri et al., 2013). The insights on bifurcational changes in dynamics provide important limnological implications such as regime shift threshold and transition between oligotrophic and eutrophic states. This knowledge is vital for preventing undesirable shift in the lake trophic state.

It is generally assumed that external phosphorus loading is the main nutrient source for algal growth. However, internal phosphorus recycling can also contribute significantly to the total phosphorus available for algal consumption and may sometimes exceed the contribution from external phosphorus loading (Li et al., 2015). The lake sediment serves as a pool of phosphorus accumulation where some fractions of phosphorus in the sediment are permanently buried while some can be recycled back into the lake water. It has been recorded that the phosphorus can be released from sediment as deep as 20 cm (Søndergaard et al., 2003). Persistent release of phosphorus from the sediment into the water column can delay the improvement of water quality (Welch and Cooke, 2005; Horppila et al., 2017; Watson et al., 2016). It has been reported that internal phosphorus recycling can persist for 5–15 years after

reduction in external phosphorus loading (Welch and Cooke, 2005; Jeppesen et al., 2005; Søndergaard et al., 2013). This poses a challenge in managing eutrophication in shallow lakes where the occurrence of internal phosphorus recycling is commonly reported (Welch and Cooke, 2005; Søndergaard et al., 2003; Søndergaard et al., 2013; Bormans et al., 2016).

As an intrinsic process in lake, the gradual changes induced by internal phosphorus recycling often have no visible impact (Biggs et al., 2012). An early warning of lake system transition induced by internal phosphorus recycling would help prevent the undesirable shift in lake eutrophication. Published studies on regime shift in lake generally focus on the effects of external phosphorus loading (Zhang et al., 2021; Gebremariam et al., 2021; Xu et al., 2020). In recent development of regime shift in lake eutrophication, the effects of other external drivers such as hydrological factors and climate change are taken into considerations (Bao et al., 2021: Mao et al., 2021). But the discussions on lake system transition or change in eutrophication dynamics triggered by internal phosphorus recycling available in published literature are limited. Hence, in this paper, we demonstrate that the internal phosphorus recycling could be a significant nutrient source that (i) induces rich and complex dynamical behaviours and (ii) triggers catastrophic shift in a lake. First, a mathematical model consisting of two compartments of algae and phosphorus is formulated and used to analyse the eutrophication dynamics of the highly eutrophic Tasik Harapan. The analysis begins with co-dimension one bifurcation analysis of algal mortality rate by means of XPPAUT (Ermentrout, 2002; Mohd et al., 2019; Omaiye and Mohd, 2018) to reveal possible tipping points as algal mortality rate is varied. The effects of external phosphorus loading on bifurcation diagram of algal mortality rate are then demonstrated. Based on the simulation results, we discuss two paradoxical results, namely the hydra effect and the paradox of enrichment. This is followed by a co-dimension two bifurcation analysis by means of MatCont (Dhooge et al., 2008), performed to understand the transitions of algal dynamics as ecologically-relevant parameter values are varied. Parameter space of external phosphorus loading and algal mortality rate are considered in this analysis. Subsequently, the rich and complex model dynamics induced by internal phosphorus recycling are demonstrated and discussed. Based on these bifurcation results, we provide a discussion on their implications on eutrophication management. We conclude the paper with a summary of the key findings and highlight its biological significance.

#### 2. Mathematical model

In this study, a eutrophication model is formulated for the tropical Tasik Harapan in Universiti Sains Malaysia, Penang, Malaysia. Tasik Harapan is a small and shallow tropical lake with a surface area of about 6070  $m^2$  (1.5 acres) and a mean depth of 1.0 to 1.5 m (Teh et al., 2008). The reported algal concentration in Tasik Harapan may reach 300 µg/L, implying a highly eutrophic condition. Both algae and phosphorus, which are the two important components of eutrophication, are considered in the formulation of eutrophication model, as indicated in Equations (1) and (2). The sources of phosphorus input into the lake water include external phosphorus loading  $(l_p)$ , excretion associated with zooplankton grazing (egA) and recycling from sediment  $(rP^q | (P^q + n^q))$ . The loss of phosphorus from the lake water is due to flushing  $(h_1P)$  and uptake by algal for growth  $(bA(P - p_aA)/(h_a + P - p_aA))$ . Phosphorus is a nutrient limiting factor for algal growth and is represented by the term  $(P - p_a A)/(h_a + P - p_a A)$ , following the Michaelis-Menten or Monod function (Scheffer et al., 2004; O'Brien, 1974). The algal loss is due to flushing  $(h_1A)$ , grazing by zooplankton (gA) and mortality  $(s_{\nu}A)$ . Table 1 shows the definition and unit of the parameters in

Table 1	
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Definition and unit of the parameters in algae-phosphorus model for Tasik Hara	pan.
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Parameter	Definition	Unit	Value	Source	Range
Α	Algal concentration	μg/L	_	_	_
Р	Phosphorus concentration	μg/L	_	_	_
t	Time	$d^{-1}$	_	_	-
b	Algal growth rate	$d^{-1}$	0.7	(Tay et al., 2020)	0-1
$h_a$	Half saturation constant	μg/L	25	(O'Brien, 1974)	0-10
$p_a$	Phosphorus content percentage	_	1	(Jones, 2018)	0-1
$h_1$	Flushing rate	$d^{-1}$	0	_	0-0.8
g	Zooplankton grazing rate	$d^{-1}$	0.0011	(Genkai-Kato and Carpenter, 2005)	0-0.91
S <sub>V</sub>	Algal mortality rate	$d^{-1}$	0.0019	(Genkai-Kato and Carpenter, 2005)	0-0.9
$l_p$	External phosphorus loading rate	μg/L/d	0.3	(Tay et al., 2020)	-
r	Internal phosphorus recycling rate	μg/L/d	0.3	(Tay et al., 2020)	0-14
п	Half saturation value of recycling function	μg/L	10	(Carpenter, 2005)	0-10
q	Parameter for steepness of sigmoid function near n	_	20	(Carpenter et al., 1999)	0-20
е	Phosphorus excretion associated with grazing	μg/μg	0.65	(Genkai-Kato and Carpenter, 2005)	0.4-0.8

this algae-phosphorus model for Tasik Harapan. Key parameter values such as algal growth, external phosphorus loading and internal phosphorus recycling rates are estimated from curve fitting in a previous study (Tay et al., 2020) while the others are adopted from literature.

$$\frac{dA}{dt} = bA \frac{P - p_a A}{h_a + P - p_a A} - (h_1 + g + s_v)A \tag{1}$$

$$\frac{dP}{dt} = l_p + r \frac{P^q}{P^q + n^q} + egA - bA \frac{P - p_a A}{h_a + P - p_a A} - h_1 P$$
(2)

In a lake, the sediment serves as a pool of phosphorus accumulation, where mechanisms such as resuspension, temperature, redox condition and bioturbation may trigger the release of phosphorus from sediment (Søndergaard et al., 2003; Jalil et al., 2020; Tammeorg et al., 2020). Phosphorus can be recycled from lake sediment or by consumers (egestion or excretion by zooplankton, fish and other animals) (Carpenter, 2005; Vanni, 2002). In the formulation of internal phosphorus recycling  $(rP^q / (P^q + n^q))$  by Carpenter (Carpenter et al., 1999), it is assumed that (i) sediment is the major source of internal phosphorus recycling and (ii) the increase in internal phosphorus recycling follows a sigmoid-shaped curve. The sigmoid function  $(rP^q / (P^q + n^q))$  represents the probability of anoxia in lake, where the decomposition of algae is considered as one of the mechanisms driving oxygen depletion in hypolimnion (Carpenter et al., 1999). When phosphorus concentration is low, the hypolimnion is oxygenated. Internal phosphorus recycling is limited by low sediment resuspension and low decomposition of algae. On the other hand, high phosphorus concentration leads to the formation of algal bloom. Decomposition of algae forms the major source of organic matter in lake sediment, resulting in anoxic condition at the sediment-water interface. This promotes the release of phosphorus from sediment into the water column, causing the internal phosphorus recycling rate to reach almost the maximum rate. Hence, in our model, phosphorus release from algal decomposition is implicitly modelled through the sigmoid function  $(rP^q | (P^q + n^q))$ , while phosphorus recycling by excretion associated with zooplankton grazing is explicitly modelled through the term egA.

Although algae-phosphorus model is widely used to study lake eutrophication, most of these models are developed for temperate lakes. The formulation of internal phosphorus recycling in temperate lake is based on the concept of proportion of anoxic days during summer stratification. It is deemed not suitable to represent the internal phosphorus recycling in tropical Tasik Harapan with no summer stratification and with little fluctuation in temperature throughout the year. Hence, another internal phosphorus recycling term deemed appropriate for tropical lake, i.e.,  $rP^q / (P^q + n^q)$ , is considered. The choice of this term is based on three reasons: (i) the sigmoid term  $rP^q/(P^q + n^q)$  represents the probability of anoxia in lakes (Nürnberg, 1995; Nürnberg, 1984), (ii) the alternative stable states of lake can be illustrated by using this sigmoid term (Tay et al., 2021), and (iii) the major recycling mechanism in shallow lake is driven by phosphorus resuspension, which is represented by this sigmoid term, being proportional to the amount of phosphorus available in water (Nürnberg, 1984).

The parameter for steepness of sigmoid function, q is reported to be in the range of  $2 \le q \le 20$  (Carpenter et al., 1999). The value of q = 20 is suggested for a shallow and warm lake while q = 2 is suggested for a deep and cold lake. A greater value of q produces a steeper internal phosphorus recycling slope, which is appropriate for a shallow lake where the occurrence of alternative states is more common (Carpenter et al., 1999). Likewise, steep internal phosphorus recycling slope is also appropriate for lakes with warmer hypolimnions as warmer lake is more likely to undergo regime shift in alternative stable states (Carpenter et al., 1999). As a tropical shallow lake, Tasik Harapan is more vulnerable to the occurrence of internal phosphorus recycling (Søndergaard et al., 2003). Hence, we choose q = 20 for the tropical and shallow Tasik Harapan.

# 3. Model analysis results

To investigate the dynamical behaviours of the model, both codimension one and co-dimension two bifurcation analyses are performed by means of XPPAUT and MatCont, respectively (Ermentrout, 2002; Dhooge et al., 2008). Algal mortality rate is considered in co-dimension one bifurcation analysis for various external phosphorus loading rates. Co-dimension two bifurcation analysis is carried out in parameter space of external phosphorus loading and algal mortality rates where changes in model dynamics are detected.

#### 3.1. Co-Dimension one bifurcation analysis

## 3.1.1. Critical thresholds of algal mortality rate at different $l_p$

To understand the transition of algal dynamics as algal mortality rate,  $s_v$ , is varied, a co-dimension one bifurcation analysis of algal concentration, A (µg/L) against  $s_v$  (d<sup>-1</sup>) is performed and the result is illustrated in Fig. 1(a). In this case, both saddle-node and Hopf bifurcations exist. At the limit points L1 and L2, the stable equilibria collide with an unstable equilibrium and disappear. This is known as the saddle-node bifurcation. The value of A decreases as  $s_v$  increases. In the range 0.04543 d<sup>-1</sup> <  $s_v$  < 0.06732 d<sup>-1</sup>, bistability occurs and the value of A may converge to the stable steady state E1 (eutrophic) or to the stable steady state E3 (mesotrophic), depending on the initial values. As  $s_v$  increases, the solution behaviour changes from bistability to a stable equilibrium in the range



**Fig. 1.** (a) Bifurcation diagram of algal concentration,  $A(\mu g/L)$  against algal mortality rate,  $s_v(d^{-1})$  at  $l_p = 0.3 \ \mu g/L/d$ . (b) Hopf bifurcation occurs as algal mortality rate,  $s_v(d^{-1})$  is varied. The green and filled circles represent stable limit cycles while the blue circles denote unstable limit cycles.

0.06732 d<sup>-1</sup> <  $s_v$  < 0.1494 d<sup>-1</sup>. At  $s_v$  = 0.1494 d<sup>-1</sup> (H1), Hopf bifurcation occurs. The algal and phosphorus dynamics switch from a stable steady state to periodic solutions.

The Hopf bifurcation diagram shown in Fig. 1(a) is enlarged and displayed in Fig. 1(b). As shown in Fig. 1(b), subcritical Hopf bifurcation occurs at both H1 ( $s_v = 0.1494 d^{-1}$ ) and H2 ( $s_v = 0.1548 d^{-1}$ ). The first Lyapunov coefficients at H1 and H2 are 0.038 and 0.046, respectively. These positive values indicate the existence of unstable periodic orbits (the blue circles). At H1 ( $s_v = 0.1494 d^{-1}$ ), the stable equilibrium loses stability and unstable limit cycle is formed. The unstable limit cycle then gains stability at LPC1 ( $s_v = 0.1481 d^{-1}$ ). The stable limit cycle (indicated by the green and filled circles) disappears at LPC2 ( $s_v = 0.1560 d^{-1}$ ). A stable limit cycle appears to exist in the range LPC1 <  $s_v < LPC2$ . The unstable limit cycle connects LPC2 with H2 ( $s_v = 0.1548 d^{-1}$ ). Two ranges of bistability exist here, i.e., LPC1 <  $s_v < H1$  and H2 <  $s_v < LPC2$ , where a stable equilibrium coexists with a stable limit cycle.

The joint effects of external phosphorus loading rate  $(l_p)$  and algal mortality rate  $(s_v)$  on the dynamical behaviour of the model, are illustrated in Fig. 2. Three values of  $l_p$ , i.e.,  $l_p = 0.01$  (Fig. 2(a)), 0.05 (Fig. 2(c)) and 0.1 µg/L/d (Fig. 2(e)), are considered in the analysis using MatCont (Dhooge et al., 2008). Similar to Fig. 1(a), both saddle-node (LP1 and LP2) and subcritical Hopf (H1 and H2) bifurcations occur as  $s_v$  is varied under distinct external phosphorus loading scenarios. Within LP1 <  $s_v <$  LP2, the model exhibits bistability behaviour: (i) oligotrophic ( $A < 2.6 \mu g/L$ ) or mesotrophic ( $2.6 \le A < 10 \mu g/L$ ), and (ii) eutrophic ( $A \ge 10 \mu g/L$ ) states. Another two ranges of bistability exist at LPC1 <  $s_v <$  H1 and H2 <  $s_v <$  LPC2, where a stable equilibrium coexists with a stable limit cycle.

The Hopf bifurcation diagrams in Fig. 2(a), (c) and (e) are enlarged and illustrated in Fig. 2(b), (d) and (f), respectively. As  $l_p$ is decreased from 0.1  $\mu$ g/L/d to 0.01  $\mu$ g/L/d, the amplitude of oscillation increases. When oscillatory solution occurs, the algal concentration switches between two states: one with a higher algal concentration, A1 and another one with a lower algal concentration, A2. For example, in Fig. 2(f), at  $s_v = 0.18 \text{ d}^{-1}$ , the algal concentration switches between  $A1 = 3.7995 \ \mu g/L$  and  $A2 = 0.2137 \ \mu g/L$ . When  $l_p$  is decreased to 0.01  $\mu$ g/L/d in Fig. 2(b), A2 decreases and approaches to 0  $\mu$ g/L. This situation is expected as a decrease in nutrient source would result in a lower algal concentration. Ironically, A1 increases to 12.5  $\mu$ g/L when  $l_p$  is decreased to 0.01  $\mu$ g/L/d, which implies that the algal concentration reaches a higher value when the external phosphorus loading is reduced. Since this theoretical observation is unlikely to happen in a real lake system, it is more likely for the algal concentration to reach a value close to zero (red curve in Fig. 2(a)) as indicated by the decrease in stable equilibrium of algal concentration (red curve) when  $l_p$  is reduced from  $l_p = 0.1 \ \mu g/L/d$  to  $l_p = 0.01 \ \mu g/L/d$  in Fig. 2.

#### 3.1.2. Hydra effect and paradox of enrichment

It is also observed that the results presented in Fig. 2 exhibit a counter intuitive effect known as the hydra effect (Cortez and Abrams, 2016). It is generally assumed that an increase in mortality should result in a decrease in the population. However, our results indicate that in this ecological system, increased mortality causes an increase in population size. The model formulation suggests that the increased algal mortality reduces the phosphorus consumption by algae and this, in turn, increases the phosphorus concentration. Algae then proliferates due to the increased phosphorus levels (Pang et al., 2018). This is consistent with the fact that the decomposition of algae promotes phosphorus release from sediment (Wang et al., 2019). Consequently, the increase in phosphorus availability results in an increase in algal growth.

The effects of internal phosphorus recycling, r on the amplitude of oscillation in Hopf bifurcation is further demonstrated in Fig. 3. Here, two values of  $r = 0.1 \ \mu g/L/d$  (Fig. 3(a)) and  $r = 0.35 \ \mu g/L/d$ (Fig. 3(b)) are considered with  $l_p = 0.065 \ \mu g/L/d$ . When the *r* value is increased from 0.1  $\mu$ g/L/d to 0.35  $\mu$ g/L/d, the amplitude of oscillation increases. For example, in Fig. 3(a), at  $s_v = 0.184 \text{ d}^{-1}$ , the algal concentration switches between  $A1 = 1.7431 \mu g/L$  and A2 = 0.108 $9 \mu g/L$ . When r is increased to 0.35  $\mu g/L/d$  in Fig. 3(b), A1 increases to 5  $\mu$ g/L while A2 decreases to 0.0554  $\mu$ g/L. A higher value of r indicates that more phosphorus is recycled from the sediment into the water column. This increases the availability of phosphorus in water column and consequently, a higher value of algal concentration is obtained, as exhibited by the high amplitude of oscillation. But the result also suggests possible algal extinction as A2 is closer to zero when the amplitude of oscillation increases. Although in nature, the extinction of algal in nutrient rich environment is not evident, such model observation could be related to paradox of enrichment, where an increase in nutrient source would lead to destabilization of biodiversity with some species more prone to extinction (Rosenzweig, 1971).

#### 3.2. Co-Dimension two bifurcation analysis

# 3.2.1. Rich and complex bifurcational changes in dynamics of external phosphorus loading rate against algal mortality rate

Since various dynamical behaviours (stable equilibrium, saddlenode bifurcation, Hopf bifurcation) are observed in Fig. 1, the analysis is performed further in co-dimension two bifurcation to trace the locus of co-dimension one bifurcation. Here, we consider co-



**Fig. 2.** Graph of algal concentration,  $A(\mu g/L)$  against algal mortality rate,  $s_v(d^{-1})$  at external phosphorus loading rate,  $l_p = (a) 0.01$ , (c) 0.05 and  $(e) 0.1 \mu g/L/d$ , respectively. The corresponding Hopf bifurcation is enlarged as (b), (d) and (f). Internal phosphorus loading rate,  $r = 0.3 \mu g/L/d$  is considered in these cases. The cross marks indicate the values of A1 and A2 at  $s_v = 0.18 d^{-1}$ .

dimension two bifurcation in the external phosphorus loading rate,  $l_p$  and algal mortality rate,  $s_v$  parameter plane. Fig. 4(a) illustrates the possible scenarios of algal dynamics transitions with three types of bifurcation curves computed by MatCont, namely (i) saddle-node curve (red solid curve), (ii) Hopf curve (blue solid curve) and (iii) limit point of cycles (LPC) curve (black solid curve). When the two branches of saddle-node bifurcation curve meet tangentially, a cusp point (CP) is formed at  $(s_v, l_p) = (0.15, 0.3190)$ . Two Bogdanov-Takens points (BT), which mark the collision of saddle-node bifurcation curve and Hopf bifurcation curve, also occur at  $(s_v, l_p) = (0.1334, 0.3967)$  and (0.1397, 0.3676). An enlarged dia-

gram of the complex region where CP and BT occur is shown in Fig. 4(b). These curves divide the  $(s_v, l_p)$  parameter plane into regions with various dynamics: (i) region with a stable equilibrium (co-existence of algal and phosphorus), (ii) bistability region of two stable steady states, (iii) stable limit cycle and (iv) a stable equilibrium coexists with an unstable and a stable limit cycle. In region (i), a eutrophic state is obtained when the parameter values result in an algal concentration,  $A \ge 10 \mu g/L$ . In the region with alternative stable states (region (ii)), a small variation in parameter would significantly affect the simulation results, i.e., an oligotrophic state of lake will shift to the undesirable eutrophic state when the crit-



**Fig. 3.** The amplitude of oscillation increases as internal phosphorus recycling, *r* is increased from (a)  $r = 0.1 \ \mu g/L/d$  to (b)  $r = 0.35 \ \mu g/L/d$  at  $l_p = 0.065 \ \mu g/L/d$ . The cross marks indicate the values of *A*<sub>1</sub> and *A*<sub>2</sub> at  $s_v = 0.184 \ d^{-1}$ .



**Fig. 4.** (a) Bifurcation diagram of external phosphorus loading rate,  $I_p$  ( $\mu$ g/L/d) against algal mortality rate,  $s_v$  (d<sup>-1</sup>) at  $r = 0.3 \ \mu$ g/L/d. (b) Enlarged bifurcation diagram of the complex region. Dynamics of the regions: (i) region with a stable equilibrium (co-existence of algal and phosphorus), (ii) bistability region, (iii) stable limit cycle, and (iv) a stable equilibrium coexists with an unstable and a stable limit cycle.

ical threshold of  $s_v$  is crossed. In the region with Hopf bifurcation (regions (iii) and (iv)), oscillation between oligotrophic and eutrophic states will be obtained (refer to Fig. 2 for more details).

# 3.2.2. Influences of internal phosphorus recycling term on the dynamical behaviour of the system

The occurrence of rich and complex dynamics in Fig. 4 is due to the inclusion of the phosphorus recycling term  $(rP^q | (P^q + n^q))$  in the model. The choice of internal phosphorus recycling rate, r influences the dynamics of the model in  $(s_v, l_p)$  parameter plane. To identify the effects of internal phosphorus recycling, r on the model dynamics, Fig. 5 is plotted by considering r = 0.05 (Fig. 5(a)), 0.1 (Fig. 5(b)), 0.2 (Fig. 5(c)) and 0.4  $\mu$ g/L/d (Fig. 5(d)). Similar to Fig. 4, the  $(s_v, l_p)$  parameter plane is partitioned by the bifurcation curves into regions with various dynamics: (i) region with a stable equilibrium (co-existence of algal and phosphorus), (ii) bistability of two stable steady states region, (iii) stable limit cycle, and (iv) a stable equilibrium coexists with an unstable and a stable limit cycle. In Fig. 5(a)-(c), Generalized Hopf bifurcation (GH) is detected and it separates the branches of subcritical and supercritical Hopf bifurcations in the parameter space. As r increases, the saddlenode, LPC and Hopf curves move closer to each other until the saddle-node and Hopf curves intersect at Bogdanov-Takens (BT) point. The GH point then vanishes and only subcritical Hopf bifurcation exist (Fig. 5(d)).

To further explain the (dis-)appearance of Generalized Hopf bifurcation (GH) in this lake system,  $r = 0.2 \ \mu g/L/d$  is considered as an example and the Hopf bifurcation diagram is enlarged as displayed in Fig. 6(a). By taking some slices at  $l_p = 0.27$  (Fig. 6(b)), at  $l_p = 0.295$  (Fig. 6(c)) and at  $l_p = 0.32 \ \mu g/L/d$  (Fig. 6(d)), the codimension one bifurcation diagram of algal concentration, A against algal mortality rate,  $s_v$  is plotted. For  $l_p$  value lower than GH2 ( $l_p < 0.2893 \ \mu g/L/d$ ), subcritical Hopf bifurcation occurs at both H1 and H2 (Fig. 6(b)). The first Lyapunov coefficients at H1 and H2 are 0.0097 and 0.0055, respectively, indicating the existence of unstable limit cycles (the blue circles) at both subcritical Hopf H1 and H2.

Within the narrow range GH2 <  $l_p$  < GH1, for example, at  $l_p$  = 0. 295 µg/L/d (Fig. 6(c)), subcritical Hopf bifurcation occurs at H1 (with first Lyapunov coefficient of 0.0023), where bistability of stable equilibrium and stable limit cycle exists at LPC1 <  $s_v$  < H1. As a contrasting scenario, supercritical Hopf bifurcation appears at H2, implying the occurrence of smooth transition from stable equilibrium to oscillatory solution. The first Lyapunov coefficient at H1 is -0.0019, denoting the existence of stable limit cycle (green and filled circles). When  $l_p$  > 0.3012 µg/L/d (GH1), the model exhibits supercritical Hopf bifurcation at both H1 and H2 (Fig. 6(d)), driving the solution smoothly from a stable equilibrium to a stable limit cycle. The first Lyapunov coefficients at H1 and H2 are -0.0085 and -0.0125, respectively, implying the presence of stable limit cycles (green and filled circles) at both H1 and H2. Supercrit-



**Fig. 5.** Bifurcation diagram of external phosphorus loading rate,  $l_p$  ( $\mu g/L/d$ ) against algal mortality rate,  $s_v$  ( $d^{-1}$ ) at internal phosphorus loading rate, r = (a) 0.05, (b) 0.1, (c) 0.2 and (d) 0.4  $\mu g/L/d$ . Dynamics of the regions: (i) region with a stable equilibrium (co-existence of algal and phosphorus), (ii) bistability of two stable steady states region, (iii) stable limit cycle, and (iv) a stable equilibrium coexists with an unstable and a stable limit cycle.

ical Hopf bifurcation refers to a smooth and non-catastrophic transition between stable equilibrium and stable limit cycle while subcritical Hopf bifurcation gives rise to a catastrophic shift between stable equilibrium and stable limit cycle (Russo et al., 2019). Subcritical Hopf bifurcation is often dangerous due to its sudden shift to different stable attractors (Pandey and Singh, 2017). Based on Fig. 6(a), with the subcritical Hopf bifurcation, two catastrophic shifts may occur due to parameter perturbation. For a fixed value of  $l_n$ , if the system is at a stable equilibrium near the subcritical Hopf bifurcation point H1 or H2, a small perturbation of the parameter  $s_v$  would result in a sudden shift from stable equilibrium to stable limit cycle. In another scenario, when  $l_p$  is increased from a value below GH2 ( $l_p$  < 0.2893 µg/L/d) to a value greater than GH1  $(l_p > 0.3012 \ \mu g/L/d)$ , the subcritical Hopf bifurcation changes its nature to become supercritical Hopf bifurcation and the limit point of cycle (LPC) disappears. In this case, the shift between stable equilibrium and stable limit cycle is smooth and non-catastrophic.

#### 4. Discussion and conclusion

In lake eutrophication management, it is crucial to understand the algae-phosphorus interactions and to identify the critical transitions between possible dynamical regimes. Based on the simulation results presented in this paper, we would like to highlight three important biological implications useful in lake eutrophication management. The first implication identifies the role of nonlinearity in internal phosphorus recycling process. The second implication is the possible occurrence of (a) the hydra effect induced by increase in algal mortality and of (b) the probable paradox of enrichment phenomenon caused by elevated internal phosphorus recycling rate. The third implication is that active internal phosphorus recycling may induce (i) bistability of two stable steady states (saddle-node bifurcation) and (ii) catastrophic shift (subcritical Hopf bifurcation) in a shallow lake system. These three implications have significant impact on efficient eutrophication control in shallow tropical lakes such as Tasik Harapan and many shallow lakes in Malaysia including the Sunway Lagoon. Of particular importance is the suitability of the sigmoid function  $rP^q$  / ( $P^q + n^q$ ) in representing the role of internal phosphorus recycling.

#### 4.1. Role of nonlinearity in internal phosphorus recycling process

Internal phosphorus recycling in shallow lakes have been studied intensively for eutrophication management purposes (Li et al., 2015; Welch and Cooke, 2005; Jeppesen et al., 2005; Kiani et al., 2020; Yang et al., 2020; Zou et al., 2020). It has been identified as one of the key factors leading to successful lake restoration (Søndergaard et al., 2007). Based on published literatures (Carpenter et al., 1999; Nürnberg, 2009; Nürnberg et al., 2012), there are four possible approaches to quantify internal phosphorus loading: (i) *in situ* determination from hypolimnetic phosphorus increase, (ii) annual total phosphorus mass balance approach, (iii) estimate from anoxic active area and phosphorus release, and (iv) a sigmoid function of internal phosphorus recycling. Due to the lack of long-term monitoring data for Tasik Harapan, the



**Fig. 6.** (a) The slices of  $l_p$  taken in co-dimension two bifurcation diagram of external phosphorus loading rate,  $l_p$  ( $\mu$ g/L/d) against algal mortality rate,  $s_v$  ( $d^{-1}$ ) at internal phosphorus loading rate,  $r = 0.2 \ \mu$ g/L/d. (b) Subcritical Hopf bifurcation is observed at both H1 and H2 when  $l_p = 0.27 \ \mu$ g/L/d. (c) Subcritical Hopf bifurcation occurs at H1 while supercritical Hopf bifurcation happens at H2 when  $l_p = 0.295 \ \mu$ g/L/d. (d) Supercritical Hopf bifurcation is detected at both H1 and H2 at  $l_p = 0.32 \ \mu$ g/L/d.

approach (iv) of using the sigmoid function to represent internal phosphorus recycling is deemed the most appropriate for this study.

Identified as an intrinsic process, an increase in internal phosphorus recycling can be caused by many factors, including temperature increase, anoxia, wind-induced resuspension, and bioturbation (Welch and Cooke, 2005; Jeppesen et al., 2005; Søndergaard et al., 2013). The catastrophic shift induced by internal phosphorus recycling might be difficult to detect due to unknown thresholds or tipping points. The important task of identifying the critical tipping points in a lake system can be facilitated by the incorporation of the internal phosphorus recycling term such as  $rP^q \mid (P^q + n^q)$  (Tay et al., 2021) in our model (1)–(2). As demonstrated by our result presented in Fig. 2(a), the inclusion of such a sigmoid function in the internal phosphorus recycling term could induce saddle-node and subcritical Hopf bifurcations. The occurrence of regime shift or oscillations between oligotrophic and eutrophic states is possible with the existence of saddle-node or subcritical Hopf bifurcations. Further comparison of this result with that shown in Fig. 7 reveals that only stable equilibrium exists when the internal phosphorus recycling is a constant term (i.e., without the sigmoid function). Therefore, the incorporation of  $rP^{q}/(P^{q} + n^{q})$  into our model serves two primary purposes: (i) to illustrate the existence of alternative stable states as observed in natural lakes and (ii) to model the impact of internal phosphorus recycling on the eutrophication dynamics of the shallow tropical

lake such as Tasik Harapan. It should be noted that the bifurcation analysis results presented in this paper are appropriate for the shallow tropical Tasik Harapan. This bifurcation analysis is modelled through the choice of high steepness parameter q given by q = 20 in the sigmoid function.



**Fig. 7.** Graph of algal concentration, A (µg/L) against algal mortality rate,  $s_{v}$  ( $d^{-1}$ ) with constant internal phosphorus recycling term, r, at external phosphorus loading rate,  $l_p = 0.01$  µg/L/d.

#### 4.2. Implications of emergence of limit cycles

## 4.2.1. Real examples of lakes exhibiting cyclic behaviour

Cyclic behaviour or oscillations between oligotrophic and eutrophic states as simulated in this research can occur under certain situations in nature (Zhao et al., 2020). Two possible explanations for such cyclic behaviour are: (i) an external interference (such as meteorological fluctuations) or (ii) an intrinsic process (such as the internal phosphorus recycling) (van Nes et al., 2007). For example, the oscillations between oligotrophic and eutrophic states in Lake Botshol (mean depth 3 m) in the Netherlands is caused by an intrinsic process, in which the macrophytes adversely affect the sediment and water quality (van Nes et al., 2007). Although macrophytes commonly help improve water quality, in the long run, they might create a "slow internal eutrophication" through the retention of phosphorus in lake sediment (van Nes et al., 2007). In an oligotrophic lake with submerged macrophytes. a difference in the phosphorus concentration gradient might trigger the release of phosphorus from the sediment into water and might therefore shift the system towards eutrophic state slowly. This intrinsic process induced by submerged macrophytes has also been suggested to explain the cyclic behaviour in Alderfen Broad (mean depth 0.8 m, England), as well as in Lake Tåkern (mean depth 0.8 m, Sweden) and in Lake Krankesjön (mean depth 0.9 m, Sweden) (Hargeby et al., 2007; Perrow et al., 1994). Although macrophyte is not included in our model, these examples of lakes that exhibit cyclic behaviour suggest that internal phosphorus recycling could be an intrinsic process that triggers oscillations between oligotrophic and eutrophic states in a lake.

#### 4.2.2. The paradox of enrichment

The discussion of regime shift in lake studies generally focus on regime shift between two alternative stable states. However, our paper enriches the discussion by demonstrating the possibility of sudden shift between stable equilibrium and limit cycle. The oscillatory behaviour in algal concentration happens in certain cases when certain tipping points are crossed (van Nes et al., 2007). Hence, efforts are needed to identify the possible tipping points that trigger such behaviour and to provide insights when these tipping points are crossed using model simulation techniques. Our simulation results illustrate that the occurrence of oscillatory behaviour is possible through Hopf bifurcation. However, this oscillatory behaviour with high amplitude of oscillations would cause the algal concentration to oscillate to a very low density and might even result in extinction of this species (in the presence of stochastic factors in nature). Additionally, this paper reveals that internal phosphorus recycling is an important nutrient source, especially for shallow tropical lakes, as it leads to an enrichment effect when its rate is high. Interestingly, our analysis indicated that an increase in internally recycled phosphorus could possibly result in the destabilization of algae. It might even enhance the likelihood of extinction of this species (due to high amplitude of oscillation - refer to Fig. 3). This observation could be related to the paradox of enrichment proposed by Rosenzweig (Rosenzweig, 1971). Similar paradoxical phenomenon is also reported by Tubay et al. (Tubay et al., 2013). Their simulation results demonstrated the paradox of enrichment in which the increase in nutrients leads to phytoplankton diversity loss due to interspecific competition. Although algal diversity is not considered in our study, interspecific interactions between species may also induce the paradox of enrichment (Smith and Wollkind, 1983; Haque, 2011; Mohd and Noorani, 2021). Our research contributes to an enriched theoretical discussion on the paradox of enrichment for lakes. Such paradox might have significant bearing on lake eutrophication management.

#### 4.2.3. The hydra effect

Another paradoxical result that can be observed from our simulation results is the hydra effect, which occurs when increased mortality causes paradoxically an increase in algal population size. The increasing algal decomposition due to higher mortality depletes oxygen in the water, which in turn induces the release of phosphorus from the sediment. Such increase in phosphorus availability allows the proliferation of algae. Several mechanisms have been described to explain the hydra effect such as overcompensation in stage-structured populations and reduction in resource exploitation (Abrams, 2009; Cortez and Yamamichi, 2019). The knowledge of the hydra effect is important in ecosystem management such as pest control programme. The proposed pest control strategies should consider the possibility of this paradoxical effect, which can increase the population abundance of pest species despite the control efforts (Cortez and Yamamichi, 2019). In the management of lake eutrophication, reduction of external nutrient source is a more common approach in limiting algal growth compared to regulating algal mortality rate. The implication here is that increased algal mortality in a eutrophic system like Tasik Harapan could result in increase in algal population in a counter intuitive manner.

#### 4.3. Effects of active internal phosphorus recycling

Our simulation results demonstrate that the inclusion of internal phosphorus recycling into our model can induce rich and complex dynamics that can provide useful insights to lake management. These complex dynamics include saddle-node bifurcation, cusp, Bogdanov-Takens bifurcation, Generalized Hopf bifurcation and limit cycles. In general, a higher value of internal phosphorus recycling, r would induce a higher occurrence of alternative stable states (region (ii) in Fig. 5) and of limit cycle (regions (iii) and (iv) in Fig. 5). This higher value of *r* is attributed to the shallow depth of the lake, in which the phosphorus released from the sediment is more readily available to the photic zone of the shallow lake. Other processes such as wind-induced resuspension and bioturbation are also important mechanisms driving the internal phosphorus recycling in shallow lakes (Welch and Cooke, 2005). The roles played by wind-induced resuspension and by bioturbation on internal phosphorus recycling are not explicitly represented in our model. However, we provide some perspectives here by giving some examples of lakes in which these two mechanisms can induce internal phosphorus recycling that can consequently shifts the lake to a eutrophic state. It has been documented that in the shallow and temperate Yilong Lake, China (mean depth 3.9 m), intensive cage fish farming had induced regime shift to eutrophication (Zhao et al., 2020). It is well-known that intensive cage fish farming can cause an increase in external phosphorus loading that can lead to eutrophication resulting in high level of algal concentration. In short, the intensive aquaculture practice in Yilong Lake intensified eutrophication through an increase in internal phosphorus recycling and through heighted organic matter loads. The increase in internal phosphorus recycling in this lake occurred through bioturbation by fish. In another study in Lake Taihu, China (mean depth 1.9 m), the relationship between wind dynamics and algal concentration has proven to be significantly correlated, indicating the positive impact of wind dynamics on internal phosphorus recycling (Jalil et al., 2020). The resuspension of phosphorus induced by wind dynamics provided a higher availability of dissolved phosphorus that promoted algal growth and drove the system to eutrophic state.

# 4.3.1. Bistability of two stable steady states

An increase in internal phosphorus recycling rate, *r* would increase the region of bistability of two stable steady states (region

(ii) Fig. 5). In a lake exhibiting bistable behaviour, alternative stable states exist, and the lake tends to remain in that state unless a threshold is crossed (Biggs et al., 2012). Small changes in algal mortality rate might trigger an abrupt shift to a different stable steady state. The shifting between alternative stable states in a shallow lake has large impacts on the ecosystem and its restoration can be difficult and expensive (Genkai-Kato and Carpenter, 2005). The response of algal concentration to changes in nutrient concentration could be hysteretic, i.e., the lake ecosystem tends to remain in a steady state caused by internal stabilizing factors despite changes in external factors (Zhao et al., 2020; Ibelings et al., 2007). In such cases, eutrophication remediation become more difficult and additional restoration efforts are required to overcome the hysteresis in the lake (Li et al., 2015). Therefore, quantifying the effects of internal phosphorus recycling on the regime shift dynamics is essential for providing useful insights on effective management of eutrophication in lakes.

## 4.3.2. Catastrophic shift

Another message that could be derived from this research is that the lake is more likely to undergo catastrophic shift at higher value of internal phosphorus recycling, r. At higher rates of r, the dynamical behaviour of the system changes from the existence of both supercritical and subcritical Hopf bifurcations to subcritical Hopf bifurcation only (disappearance of GH in Fig. 5). Subcritical Hopf bifurcation is often dangerous because it can induce sudden shift to different stable attractors (Pandey and Singh, 2017). Catastrophic shift can be triggered by a small perturbation in the parameter value around the subcritical Hopf bifurcation point. Consequently, the algal concentration may jump to a different stable state, triggering a regime shift. Although the oscillatory behaviour in algal concentration occurs in certain real lake systems (Zhao et al., 2020), the analysis of dynamic change as illustrated in Fig. 5 could provide important indications on the early signs of regime shift. Early detection of potential regime shift can provide valuable time for preparatory intervention.

#### 4.4. Concluding remarks

Overall, a combination of external phosphorus loading, algal mortality, and internal phosphorus recycling rates plays an important role in lake eutrophication process. External phosphorus loading can be regulated by controlling or diverting the external sources of phosphorus flowing into the lake. However, both algal mortality and internal phosphorus recycling rates are difficult to detect and control. This research reveals that a small change in these two ecological parameter values might trigger a sudden shift in the lake dynamics once the tipping points of the system are crossed. These thresholds could serve as an early warning of a potential shift in lake trophic state. This early warning allows timely implementation of mitigation measures to prevent the undesired shift. The numerical bifurcation analysis performed in this study also reveals that internal phosphorus recycling is the most crucial parameter driving the dynamics of the shallow tropical Tasik Harapan. Therefore, methods to reduce internal phosphorus recycling such as sediment dredging and flushing are recommended, in conjunction with the control of external phosphorus loading, to facilitate lake restoration.

# **CRediT authorship contribution statement**

**Chai Jian Tay:** Conceptualization, Methodology, Software, Validation, Visualization, Writing – original draft. **Mohd Hafiz Mohd:** Conceptualization, Supervision, Writing – review & editing. **Su**  **Yean Teh:** Supervision, Funding acquisition, Writing - review & editing. **Hock Lye Koh:** Writing - review & editing.

#### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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