



Effects of uniform rotational flow on predator–prey system

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ABSTRACT

Rotational flow is often observed in lotic ecosystems, such as streams and rivers. For example, when an obstacle interrupts water flowing in a stream, energy dissipation and momentum transfer can result in the formation of rotational flow, or a vortex. In this study, I examined how rotational flow affects a predator–prey system by constructing a spatially explicit lattice model consisting of predators, prey, and plants. A predation relationship existed between the species. The species densities in the model were given as S (for predator), P (for prey), and G (for plant). A predator (prey) had a probability of giving birth to an offspring when it ate prey (plant). When a predator or prey was first introduced, or born, its health state was assigned an initial value of 20 that subsequently decreased by one with every time step. The predator (prey) was removed from the system when the health state decreased to less than zero. The degree of flow rotation was characterized by the variable, R . A higher R indicates a higher tendency that predators and prey move along circular paths. Plants were not affected by the flow because they were assumed to be attached to the streambed. Results showed that R positively affected both predator and prey survival, while its effect on plants was negligible. Flow rotation facilitated disturbances in individuals' movements, which consequently strengthens the predator and prey relationship and prevents death from starvation. An increase in S accelerated the extinction of predators and prey.

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1. Introduction

A large number of organisms live in aquatic environments that are characterized by a predominantly running flow. Rivers and streams are particular examples of this type of environment. In lotic ecosystems, many organisms can be found occupying almost every available habitat, including the surfaces of stones, deep below the substratum, adrift in the current, and in the surface film. Insects have developed several strategies for living in the diverse flows of lotic systems. Some avoid high current areas, inhabiting the substratum or the sheltered side of rocks. In stronger current, species have developed weighted cases, attachments to anchored pads of silk, recurved clinging claws, suction cup-like appendages, and flattened, streamlined bodies [1,2]. Most organisms in lotic ecosystems rely heavily on the current to bring them food and oxygen [2]. As examples of positive and negative effects of flow on the predation, Trager et al. [3] showed that mean capture efficiency of *Artemia salina nauplii* by the barnacle, *Nobia grandis*, was maximized at the flow speed of 5 cm/s. On the other hand, Hansen et al. [4] reported that predation on black fly larvae by flatworms was shown to decrease with increasing flow as a result of reduced encounter rates (flatworms were less abundant in areas of high flow) and reduced probability of capture following encounters (flatworms are less efficient at capturing prey in higher flows). It has been known that in many cases, the water flow constitutes not only a foundation for the populations living therein, but also provides many ecological benefits to the populations [5,6].

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There are various interactions between biotic factors, such as animals, plants, and micro-organisms, and abiotic factors, such as temperature and water flow in lotic ecosystems. These interactions can be strengthened or weakened by flowing water, which directly affects the predation intensity. Variation in predation intensity has the potential to regulate species abundance in space and time in most systems [7–9]. The ability of predators to successfully detect and consume prey is a key factor in determining the potential regulating effect of predators on prey communities. Variation in many biotic and abiotic variables may affect a predator's ability to locate prey as well as escape or defense responses of prey to an approaching predator. For example, variations in water clarity [10], substrate type [11,12] and concentration of gases in aquatic systems [13,14] all have been shown to modify predator success.

Consequently, disruptions in the predation process can significantly affect the aquatic community [15,16]. The predation process is closely related to prey patch dynamics that can have significant consequences for the optimal foraging strategy of predators and the overall stability of predator–prey relationships [17–19].

In addition to lotic ecosystems, water flow also plays an important role in oceanic ecosystems. The impact of ocean hydrodynamic conditions on the biological activity of plankton species in predator–prey relationships has been a subject attracting the interest of researchers over the past several decades [20,21]. Two different processes, caused by flow, have been extensively studied. One process is vertical transport (e.g., advection, turbulent mixing) to bring nutrients to the upper layers of the ocean [22]. The other is horizontal (or lateral) transport mediated by mesoscale structures such as eddies, jets, and fronts [20,21,23–25]. These processes are the primary factors in the dynamics of plankton populations, providing the basic mechanism for patchiness in the plankton distribution and influencing key features, such as biological productivity.

As mentioned above, flow is one of the important keys to understand the aquatic ecosystems. However, to date, few simulation studies on the effects of the rotational flow on ecosystems have been performed because it is difficult not only to describe the interaction between organisms and flow mathematically, but also to quantify, by experimentally measuring, the changes in an organism's behavior caused by the flow characteristics [26]. Recently, along with the increase of the computer power, the method of computational fluid dynamics (CFD) has begun to attract considerable interest as a useful tool to theoretically understand an organism's behavior in fluid flow [27,28]. However, this approach still has limitations in terms of the short time dynamics. This method numerically solves the Navier–Stokes equation for fluid coupled with equations for the organism's behavior, which only focuses on the interaction between fluid and organism. The interaction occurs in a small area during a short time period, but not the stability of an aquatic ecosystem [29,30].

In the present study, to overcome the limitation, I constructed a simple lattice model consisting of three populations in a predator–prey system under uniform rotational flow. Using the model, I explored how the rotational flow affects the predator–prey system.

2. Model description

A simple ecosystem consisting of predator, prey, and plant was simulated on a 100×100 gridded space. A periodic boundary condition was used to minimize the boundary effect. Each lattice site was either occupied by predator, prey, or plant, or empty. Predators (and prey) could occupy the same site simultaneously. Double occupancy of plants at the same site was forbidden.

The initial distributions ($t = 0$) of the predator, prey, and plant were introduced into the lattice space by the distribution field for each species, $n_s(i, j)$, $n_p(i, j)$, and $n_g(i, j)$. The field denotes the number of individuals at lattice site (i, j) . I allowed at most one individual of each species to be present in any lattice site at $t = 0$. For $t > 0$, individuals can occupy the same lattice site while predator and prey move in the rotational flow effect.

The occupancy of the individual for each species in each lattice was given by thresholding based on the values S , P , and G , ranging from 0.0 to 1.0;

$$\begin{aligned} n_s(i, j), \\ n_p(i, j), \\ n_g(i, j) \end{aligned} = \begin{cases} 1, & \text{when } r(i, j) < S \text{ (for predator), } P \text{ (for prey), } G \text{ (for plant)} \\ 0, & \text{otherwise} \end{cases}$$

where $r(i, j)$ represents a randomly generated number at site (i, j) . Thus, the values of S , P , and G indirectly reflect the initially assigned species densities. In the simulation, the predator and prey initial density was $0.1 \leq S \leq 0.55$, $0.1 \leq P \leq 0.55$ with 0.05 increments, respectively. The value of G was set as 0.3. In the present study, each combination of S , P , and G was run for 10,000 iterations, and the simulation results were statistically averaged over 50 independent runs.

2.1. Homogeneous random space

In order to generate a lattice space in which individuals can randomly move, I assigned a random value, h , ranging from 0.0 to 1.0 to each lattice site. When a predator (or a prey) is surrounded by neighboring sites with h values, it is more likely to move into a site with a higher h value than a site with a lower h value (Fig. 1(a)). The probability for an individual to move to its neighbor sites is calculated as the ratio of the h value of a site to the summation of h values of the neighbor sites. For example, the probability for the individual to move in the top-right direction is calculated as $0.7/(0.7 + 0.1 + 0.5 + 0.2 + 0.1 + 0.3 + 0.4 + 0.3)$. The probability values for each direction were represented outside of the lattice box. In this figure, the predator has the highest probability to move into the top-right site.

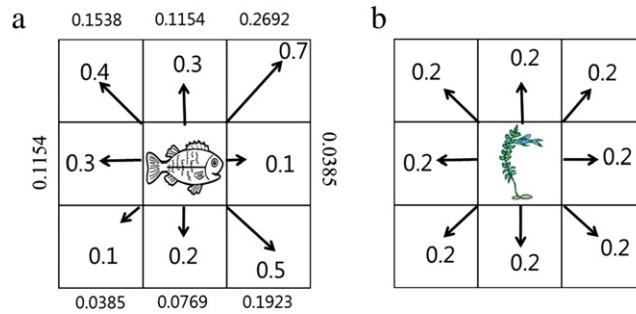


Fig. 1. (a) Example of a predator (or a prey) surrounded by eight neighbor sites (b) growth process of plants with growth probability of 0.2. Each neighbor site is labeled with its associated h value, reflecting the environmental property. The values on the outside of the lattice squares represent the probability for the predator (or prey) to move to each site. The length of an arrow indicates the probability that the predator (or prey) will move into a surrounding site.

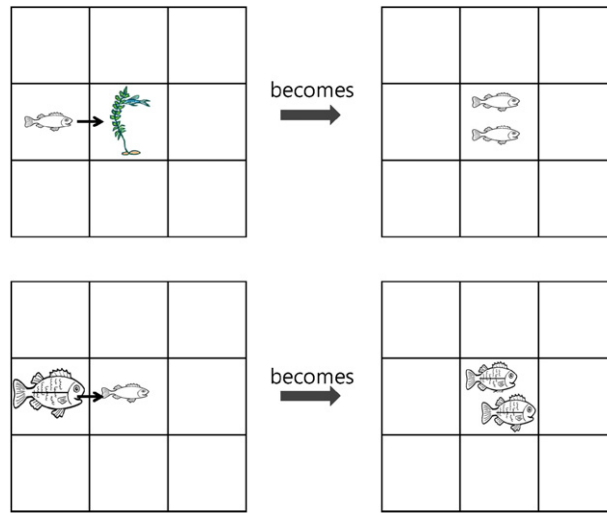


Fig. 2. Possible configurations encountered by a predator and a prey at a site. When the prey eats the plant (or the predator eats the prey), the prey (or predator) gives birth to an offspring. Here, the predator is depicted as a big fish eating a small fish and the prey is represented by a small fish eating a plant.

2.2. Species

Interactions among species were included in the model; namely, predators eat prey, prey eats plants, and plants grow by themselves. Predator and prey move on the lattice space without stopping. I pictorially represented predator and prey as a big fish eating a small fish and a small fish eating a plant in Fig. 2 to facilitate understanding. Although predator, prey, and plant individuals were positioned to lattice sites without overlapping at $t = 0$, the individuals (predator and/or prey) were allowed to occupy the same lattice site during evolution ($t > 0$). When different species are within the same site, the predation occurs. Predator and prey individuals have a reserve of food, represented by a counter containing its food rations. The reserve was interpreted as the health state in this study. The counter increased after each meal (eating plant by a small fish, and the small fish by a big fish). This rule was widely used in the lattice based model for predator–prey ecosystem [31,32]. Other values of the biological variables, such as health state and plant growth probability, were arbitrarily kept as constant. This is because the species in the model does not mean the specific species [33]. They are general agents representing predation interaction. The aim of this model is to understand characteristic properties underlying the simplified aquatic ecosystem, not explain a specific real ecosystem.

- When a plant site had neighboring sites that included at least one site not occupied by a plant, the plant could grow in that site according to its growth probability, which was arbitrarily set to 0.2. Note that it was possible for a given plant to grow into multiple neighboring sites during one iteration time step (Fig. 1(b)). Only a single plant could occupy a lattice site at any given time. The plant could occupy only a single lattice site.
- When predator and prey were present within the same site simultaneously, the number of prey that were eaten/killed was the same as the number of predators. The consumed prey were chosen randomly. In addition, the predators that eat the prey were also randomly selected. This rule was also applied to the relationship between the prey and plants.

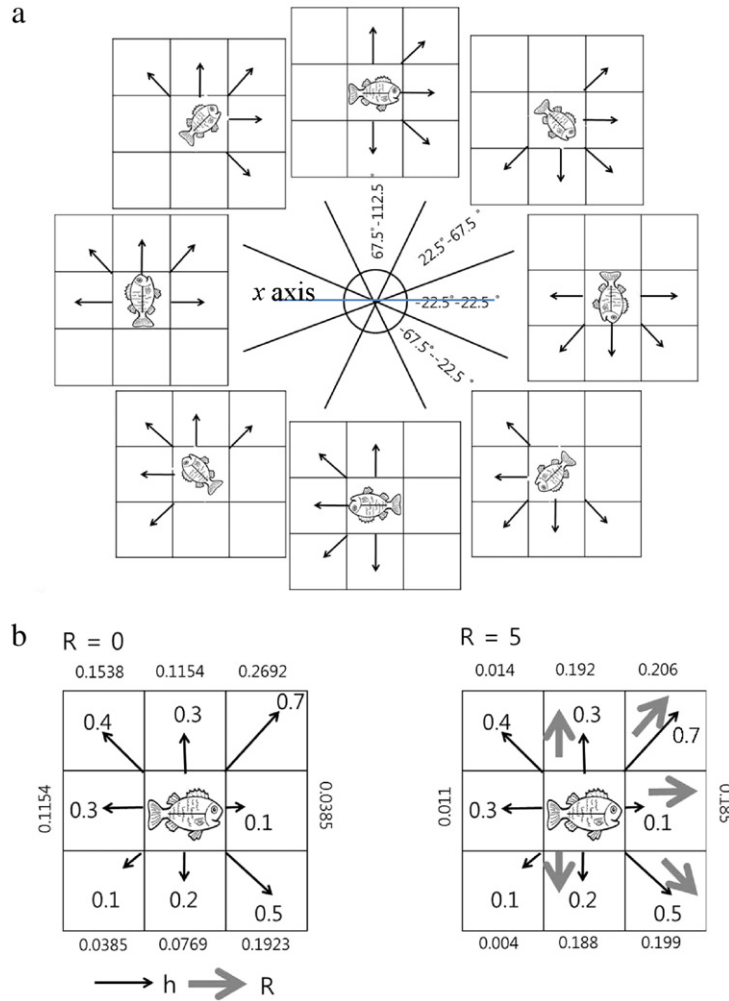


Fig. 3. (a) Rotational probability, R , characterizing the degree of flow rotation, is assigned to five neighbor sites of each individual. The neighbor sites are determined by the angle formed from the center of the lattice space and the location of the individual. The arrows indicate the neighbor sites assigned the rotational probability. (b) The probability for the predator (or prey) to move into a surrounding site when $R = 0$ (left side) and $R = 5$ (right side). The values on the outside of the lattice squares represent the probability for the predator (or prey) to move to each site. The values on the inside of the lattice square mean the h values.

- The state of health of a predator or prey was represented by a value ranging from 0 to 20. When a predator or prey was first introduced, or born, its health state was assigned an initial value of 20.
- When a predator or prey moved a step spatially, its health state decreased by 1. When its health state decreased to below zero, the predator or prey was considered dead, and it was removed from the system.
- If a predator or prey consumed food (plant for prey; prey for a predator) any time before death, its health state was restored to the original value of 20.
- When a predator ate a prey or a prey ate a plant, the predator or prey gave birth to a single offspring according to a birth probability of 0.2. The offspring was located within the same lattice site as its parent (Fig. 2).

2.3. Uniform rotational flow

In order to describe the rotational flow in the model, I assigned a value, R , ranging from 1 to 10 to five neighboring sites of each individual (predator or prey). The five sites were determined by the angle formed between the x axis and the straight line passing through the center point of the space and the x and y coordinate of an individual as shown in Fig. 3(a). As an example to aid understanding, let's suppose the situation where an individual positioned at site (i, j) at time t moves to site (i', j') after one time step. At time t , R value was given to the five neighboring sites of the individual positioned at (i, j) and used to determine the individual's moving direction. After the determination, the R value was removed from the sites. At time $t + 1$, the R value was newly assigned to the neighbor sites of (i', j') . The repetition of the process generated the rotational flow effect. Higher R values corresponded to stronger levels of rotation. In other words, the increase of R

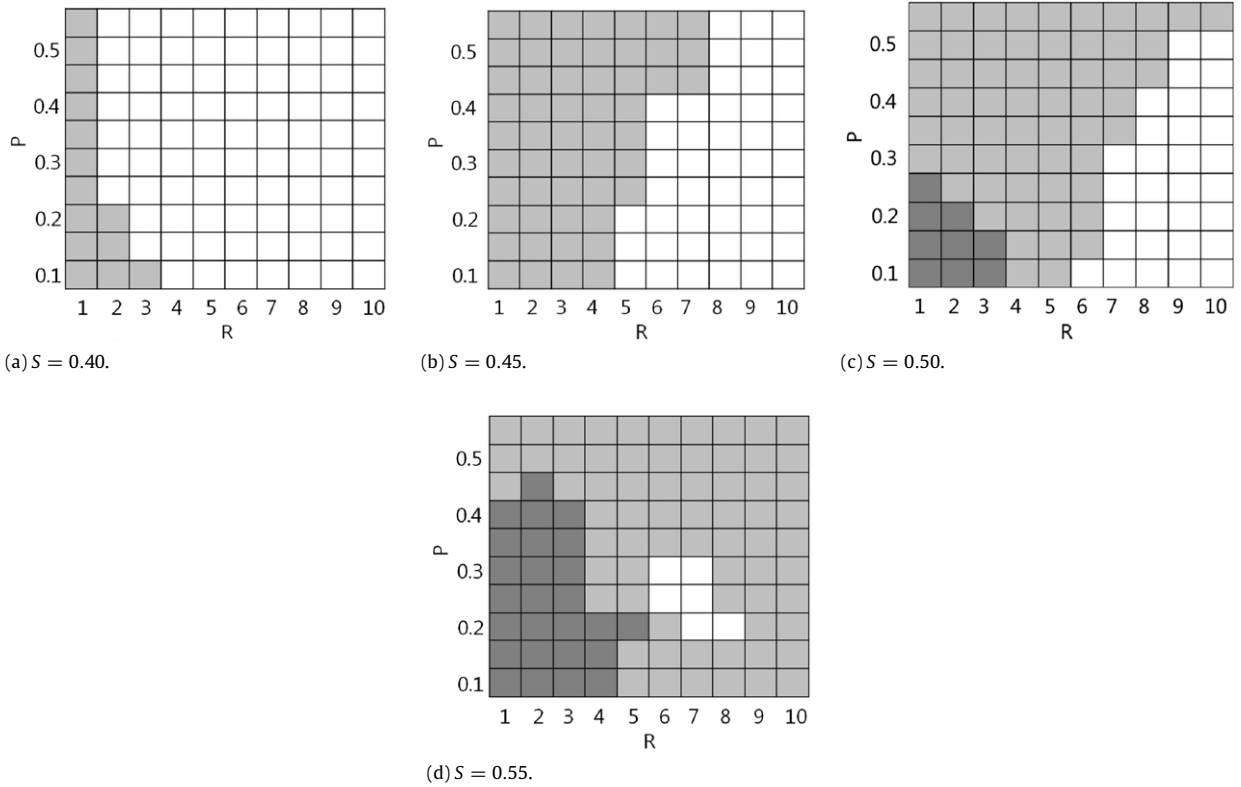


Fig. 4. The predator and prey results in the P – R space for $S = 0.4, 0.45, 0.5, 0.55$ and $P = 0.1, 0.2, \dots, 0.55$ where $R = 1, 2, 3, \dots, 10$. The lighter and darker grey colors at each site indicate the extinction of predators only and the extinction of both predators and prey, respectively. The white color represents the coexistence of both predators and prey.

decreased the randomness of individual movement. As mentioned in the earlier section, h values in the lattice sites describe the randomness of an individual's movement. On the other hand, R values characterize the directional movement of the individuals. Fig. 3(b) shows an example of how the value of R contributes to the probability for an individual to move its neighboring sites. In the case of no flow ($R = 0$), the probability for the individual to move in the top-right direction was $0.2692 (=0.7/(0.4 + 0.3 + 0.7 + 0.1 + 0.5 + 0.2 + 0.1 + 0.3))$. This value was calculated only based on the h values (represented inside of each lattice). When the flow effect was considered ($R = 5$), the probability for the top-right direction was $0.206 (=5.7/(5.4 + 5.3 + 5.7 + 5.1 + 5.5 + 5.2 + 5.1 + 5.3))$. Comparing the directional probabilities between the case of $R = 0$ and the case of $R = 5$, we can see without difficulty that the individual movement is strongly affected by the flow. I formulated the probability for an individual positioned at (i, j) to move to its neighboring site, $(i + \alpha, j + \beta)$ in consideration of R as follows,

$$P(i + \alpha, j + \beta) = \frac{h(i + \alpha, j + \beta) + R(i + \alpha, j + \beta)}{\sum_{\substack{k, l = -1, 0, 1 \\ k+l \neq 0}} [h(i + k, j + l) + R(i + k, j + l)]} \quad (\alpha, \beta = -1, 0, 1; \alpha = \beta \neq 0).$$

3. Simulation results

The typical survival and extinction results for a predator and prey for $S = 0.40, 0.45, 0.50$, and 0.55 and $P = 0.1, 0.15, \dots, 0.55$, where $R = 1, 2, \dots, 10$ are shown in Fig. 4. The lighter and darker grey colors in the plot represent the extinction of predators and both predators and prey, respectively. The white color indicates the coexistence of both predators and prey. The plant density was stable, regardless of predator and prey density. This is because it was possible for a given plant to grow into multiple neighboring sites during one iteration time step, which allowed for rapid recovery from being eaten by prey (see Fig. 1(b)). At $S = 0.40$, the predator became extinct when $R = 1$ and for all ranges of P (Fig. 4(a)). For $R > 1$, the predator survived, except for the range of $R \leq 2$ and $P \leq 0.2$. When S increased to 0.45 , the extinction area for predator was extended in the P – R space. However, strong flow rotation ($R > 6$) mitigated this extinction (Fig. 4(b)).

For $S = 0.50$, prey was heavily eaten by predators in the early simulation stage. This was caused by the initial predator density being too high, which, in turn, resulted in prey extinction. The extinction was observed in ranges of low R (≤ 3) and low P (≤ 0.25). On the other hand, the coexistence area decreased in the P – R space. When $S = 0.55$, the extinction for both

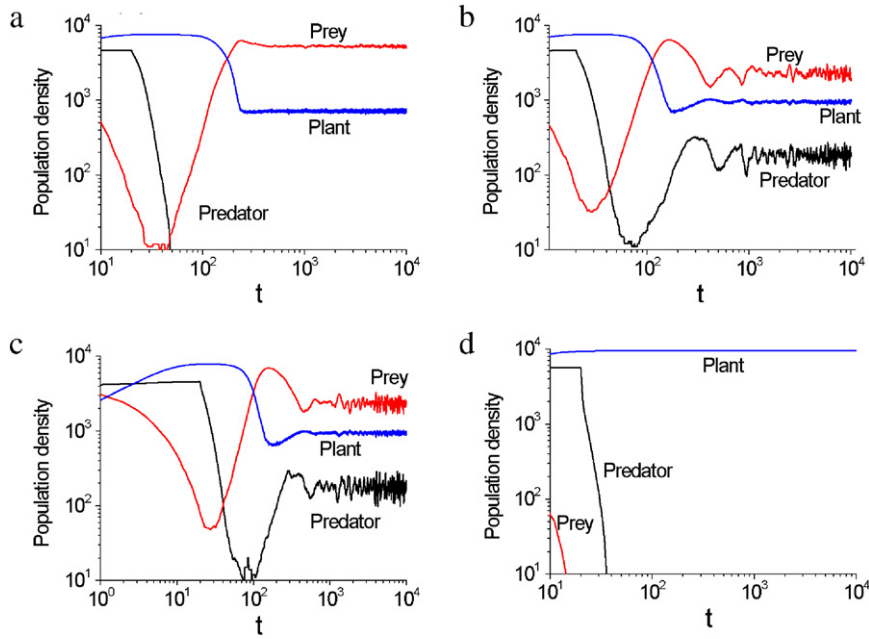


Fig. 5. Plots of the population density for predator, prey, and plant over time where (a) $S = 0.4$, $P = 0.5$, $R = 1$, (b) $S = 0.4$, $P = 0.5$, $R = 5$, (c) $S = 0.4$, $P = 0.5$, $R = 9$, and (d) $S = 0.55$, $P = 0.5$, $R = 9$.

predator and prey was more severe. The relationship between the strength of the rotational flow and a predator's density can be gleaned from this simulation. A higher value of R contributes to the coexistence of predator and prey, while a higher value of S forces the extinction of both species (Fig. 4(d)). A coexistence region in the P – R space appeared. This means that the R effect is relatively stronger than the S effect in the region. Interestingly, the coexistence region is not overlapped with the coexistence region of Fig. 4(c). This indirectly reflects that the competition between the two effects is nonlinear. Further investigation would be interesting. However, the problem was excluded in this study to avoid my focus becoming entangled.

I investigated the population dynamics for typical conditions, showing the three states. When the degree of rotation was low ($S = 0.4$, $P = 0.5$, $R = 1$), predators became extinct in the early stage (Fig. 5(a)). This is because a low R value means that individuals move with higher randomness on the lattice space. In this case, the number of directions that a predator can move is almost eight (see Fig. 2). Thus, even if prey is located at the neighboring sites of a predator, the predator has a relatively low probability of catching the prey. After predator extinction, prey and plant entered into stable coexistence. For a relatively high value of R ($S = 0.4$, $P = 0.5$, $R = 5$) (Fig. 5(b)), the probability that predators catch prey increased because predators and prey individuals have a tendency to move along a circular path. This tendency decreased the randomness, as shown in Fig. 5(a). Consequently, the tendency prevented the predator's extinction near $t = 100$ (Fig. 5(b)). When the value of R was considerably high ($S = 0.4$, $P = 0.5$, $R = 9$), predators could catch prey more easily. This caused stronger interaction between predator and prey, which in turn caused relatively more fluctuation in their population size (Fig. 5(c)). For the cases of higher values of S and higher values of R ($S = 0.55$, $P = 0.5$, $R = 9$), prey density abruptly decreased due to too many predators, finally leading to prey extinction. Starvation subsequently led to extinction of the predator (Fig. 5(d)).

In order to further investigate the effect of the rotational flow on the predator–prey system, I investigated the relationship between N and R for different values of S (Fig. 6). Here, the coexistence area, N , was defined as the number of sites where a predator and prey coexisted in the P – R space with 5 (for P) \times 10 (for R) grids, where $P = 0.1, 0.2, \dots, 0.5$ and $R = 1, 2, \dots, 10$. N increased with the increase of R , while for lower S values, the degree of the increase of N decreased.

4. Discussion and conclusion

In this study, I constructed a lattice model that simulates an ecosystem consisting of predators and prey moving under influence of a rotational flow, and plants in order to explore the effect of rotational flow on the ecosystem. In real aquatic systems, we can often observe rotational flow. When an obstacle (e.g., a rock) interrupts constant flow in a stream, rotational flow can be formed by way of energy dissipation and transfer of the momentum across the flow. In the presence of sufficiently strong circulation regions, some flows become trapped for a long time in the region of interest [34]. The uniform flow in the simulation model would correspond to the trapped flow. In the model, the degree of the rotational flow was characterized as the value of R . A higher value of R means a higher tendency of predators and prey to move in a circular path. For all combinations of S , P , and R , the predator and prey showed higher survival probability for higher R values, which means that the rotational flow played an important role in ecosystem stability. The plant was negligibly influenced by the dynamics of

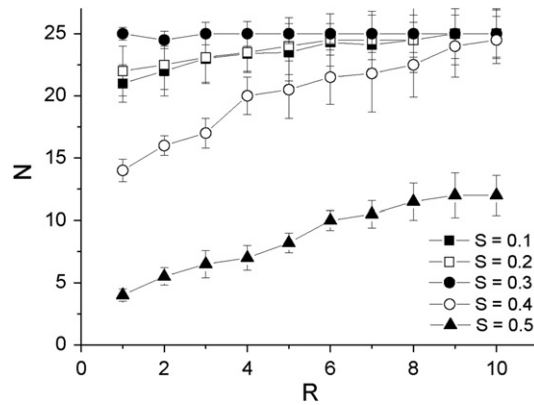


Fig. 6. Plots of the coexistence area of both predator and prey, N , against the degree of flow rotation, R , for $S = 0.1, 0.2, \dots, 0.5$ and $P = 0.1, 0.2, \dots, 0.5$, where $R = 1, 2, \dots, 10$. The area, N , is defined as the number of sites in 5 (for P) $\times 10$ (for R) grid spaces.

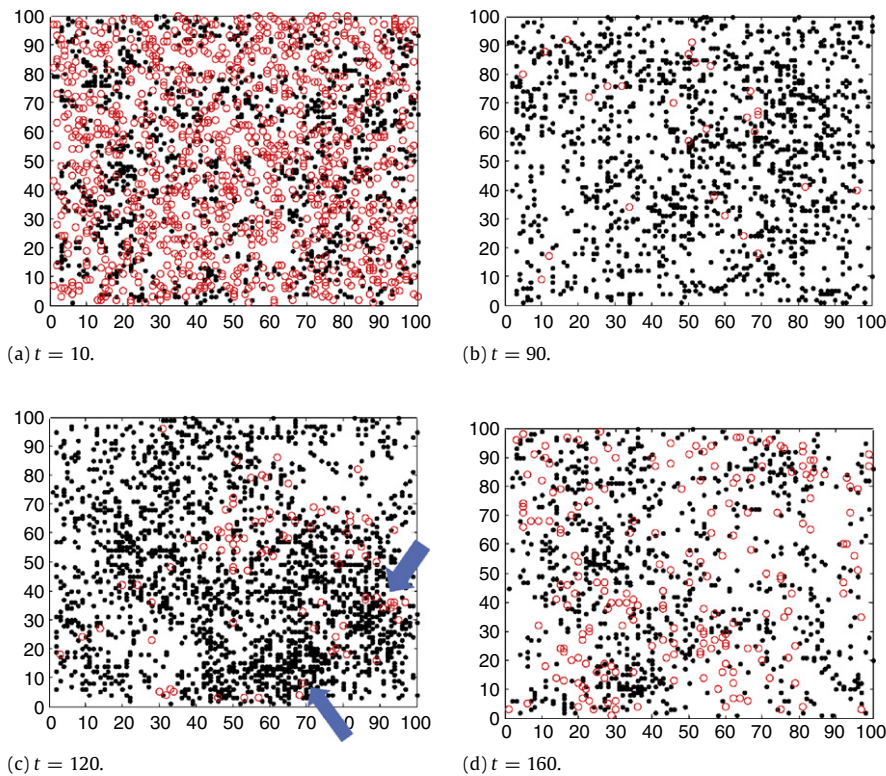


Fig. 7. The typical distribution patterns for predator (red circles) and prey (black dots) at different times. The arrows shown in the pattern at $t = 120$ represent the area with a higher density of prey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the predator and prey. Interestingly, in the simulation, the predator is almost faced with the crisis of extinction near $t = 100$ (see Fig. 5). For some cases, predator density recovered and stabilized with some fluctuation, while for other cases, the predator became extinct. To better understand this dynamic behavior, I investigated the predator and prey movement over time where $S = 0.1$, $P = 0.3$, and $R = 5$. In Fig. 7, at an early stage ($t = 10$), predator and prey were randomly distributed. As time progressed ($t = 90$), predator density abruptly decreased because too many prey were eaten by predators, which resulted from an imbalance between the initial density of the predator and prey. This decrease gave rise to the predator's extinction. Subsequently, the size of the prey population gradually increased, which, in turn, caused the prey population to homogeneously cover the lattice space. In this situation, individual predators, scattered in small amounts in the lattice area, acted as absorbers for the flow of prey individuals. Thus the predators disturbed the transfer of prey by water flow. Consequently, this disturbance resulted in the dynamic spatial heterogeneity of the distribution of prey individuals (see the typical pattern at $t = 120$). Some areas had higher prey density for a short time, while others had lower prey density.

The arrows in Fig. 7 indicate the higher density areas. When the predators entered the higher density area, they could suddenly increase the size of their population ($t = 160$). This dynamic heterogeneity seemed to be related to the degree of rotational flow. It will be interesting to explore this relationship in future studies.

In this study, to simplify the model, I assumed that the predator and prey had the same health state and movement speed. The maximum value of the health state was fixed at 20. In the preliminary test, when the maximum value was smaller than 13, predator and prey could not interact due to the short traveling distance, which in turn led to the extinction of both species. On the other hand, when the maximum value was in the range from 13 to 25, predator and prey individuals actively interacted and showed similar dynamics in their population size.

In addition, both species were assumed to be equally influenced by the rotational flow. Although these assumptions are unrealistic for actual animals (e.g., big and small fish) in a river or stream, the simulation results provide a possible explanation for the mechanism of how the rotational flow affects a predator–prey system in relation to extinction and coexistence of predators and prey. In the simulation study, the growth probability for plant was fixed at 0.2. This is because when I preliminarily tested for different values of the growth probability, 0.15, 0.2, 0.25, and 0.3, I found that the changes in the value little affected the dynamics of the predator–prey system.

The following observations in the field are indirectly linked to my simulation result that the flow could positively contribute on the stability of the ecosystem by enhancing the degree of the predation relationship. Fausch [35], and Hughes and Dill [36] reported that there exists a proportional relationship between flow velocity and the amount of prey eaten by a single predator. In particular, for turbulence flow, Mahjoub et al. [37] revealed in observations in the field that turbulence flow can enhance ingestion rates in larval fish by increasing encounters with prey.

In addition, the results provide a basis for future work on the dynamics of a predator–prey system with regard to the innate abilities of individuals, e.g., the ability to search for food in an intelligent manner or the ability to communicate with other members of the same species.

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