Ecological Complexity 8 (2011) 258–264

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Fish kairomones, its benefits and detriments: A model based study both from releaser and acceptor perspective

S. Samanta [a,1], S. Chakraborty [b], S. Bhattacharya [a], J. Chattopadhyay [a,*]

[a] Agricultural and Ecological Research Unit, Indian Statistical Institute 203, B. T. Road, Kolkata 700108, India
[b] Department of Mathematics, Harimohan Ghose College, J-206 & 208A Paharpur Road, Garden Reach, Kolkata 700024, India

ARTICLE INFO

Article history:
Received 21 February 2011
Received in revised form 12 May 2011
Accepted 18 May 2011
Available online 16 June 2011

Keywords:
Infochemical
Zooplankton
Vertical migration
Mathematical models

ABSTRACT

Kairomones have been documented as an infochemicals to convey information between individuals in aquatic system. However, whether the effect of fish kairomones on acceptor (zooplankton) is beneficial or detrimental is a debatable and unanswered issue. This may be due to lack of feasibility of experimentation. In this study, we theoretically explore how fish kairomones affect the aquatic food chain and provide possible explanation of such different behaviors of kairomones. To do this, we propose two hypotheses and formulate two simple mathematical models which resemble more realistic scenario synergetic with natural complex system. Our study suggests that vertical migration helps zooplankton species for proper conservation of its abundance by avoiding unnecessary over predation.

1. Introduction

Planktonic interactions and the role of infochemicals in aquatic systems are highly complex in nature. To avoid mortality due to predation by higher trophic levels, many plankton species have developed a wide variety of defence mechanisms. Many organisms are receptive to chemical signals exuded by potential predators. We are now accumulating knowledge about the nature of infochemicals, but are still in infancy stage on its identification and isolation. In 1999, Boriss et al. identified trimethylamine (TMA) as a major component of fish kairomone. They explored that, whatever the migration trigger substance may be; it is produced only by fish in presence of bacteria. Such infochemicals are regarded as chemical compounds that convey information between individuals and thereby evoke changes in morphology (e.g., formation of spine and colonies), biochemistry (e.g., production of toxins, repellents), behavioral responses (e.g., migration, refuge use) in the receiver life history traits (e.g., age at maturity, size at maturity, clutch size) (Dicke and Sabelis, 1988). The chemical (kairomones) released from predators gives benefit to receivers rather than releasers (Brown et al., 1970). Extensive laboratory based study are being carried out on kairomones. For characterization of such compounds, *Daphnia* is the best choice of researchers. A lot of experimental studies have been performed to observe morphological and behavioral responses of *Daphnia* to kairomones (e.g., Miyakawa et al., 2010; Laforsch and Tollrian, 2004; Hanazoto et al., 2001; Hanazato, 1998, 1995; Hanazato and Dodson, 1995; Dodson, 1988a). However, the adaptive significance of such changes is the cost of induced morphological change or independent antipredator adaptation is not clearly understood (Tollrian, 1995; Black, 1993). Surprisingly, the reported results of such studies are not consistent with the results of other similar studies or even with other results in the same study (e.g., see, Table 8 in Tollrian, 1995). Although, food concentration and fish kairomones both can influence the life history of zooplankton, response to fish induced kairomones are strongly influenced by food conditions for zooplankton (Hülsmann et al., 2004; Weber, 2001). Again there are also controversial outcomes. For example, a study by Machacek (1991) revealed no effect of food concentration whereas the study of Reede and Ringelberg (1995) showed the effect of food concentrations on the changes induced by kairomones. These controversial outcomes may be due to the fact that those experiments have been performed in standing water or at laminar flow in laboratory conditions (Zimmer et al., 1999).

Despite the increasing interest on inducible defences against fish-kairomone, only a few model based work have been performed to study the cost and benefit of inducible defences against predators (Ramos-Jiliberto et al., 2008a,b; Ramos-Jiliberto and González-Olivares, 2000; Vos et al., 2004, 2002; Chase, 1999; Frank, 1998, 1993). Recently, Abrams (2008) study the impact of dynamic antipredator traits on predator–prey–resource interactions through comparison of density (or fitness) in presence and

---

* Corresponding author. Tel.: +91 33 25753231; fax: +91 33 25773049.
E-mail address: joydev@isical.ac.in (J. Chattopadhyay).

[1] The research work is supported by Council of Scientific and Industrial Research (CSIR), Human Resource Development Group, New Delhi.

1476-945X/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.ecocom.2011.05.001

absence of the cue with presence and absence of functional predator. But, none of them studied the contrast between different effects of kairomone (morphological and behavioral changes) on zooplankton and fish. Another drawback of such studies is the lack of field based experiments; however, recently Boeing and Ramcharan (2010) performed some field based experiments on *Daphnia pulex* and golden shiner (*Notemigonus crysoleucas*) in Costello Lake. Although inducible defences mediated through infochemicals (kairomone) have been investigated extensively (in laboratory set up) at the individual or on population level, but the effect of such kairomone on population dynamics or in food chain ecosystem has not yet been properly investigated.

Whether the effect of fish kairomones on zooplankton is beneficial or detrimental is a debatable and an unanswered issue which demands in depth researches both from experimental (laboratory and field) and modeling point of view. Some authors argued that fish kairomones are beneficial to zooplankton and the others claimed that it has detrimental effect on zooplankton. Fish kairomones can reduce zooplankton growth and reproductive rates and extend its maturation time (Black and Dodson, 1990). It is also known that, kairomone reduces tolerance of zooplankton to environmental stress, such as, starvation (Hanazato, 1991a), high water temperature (Hanazato, 1991b) and pesticide contamination (Hanazato and Dodson, 1992). Furthermore, a synergism in the effects of fish kairomones with food deficiency (Hanazoto et al., 2001), low oxygen concentration and pesticide (Hanazato and Dodson, 1995) has been observed. These studies suggest that fish kairomones might alter zooplankton behavior, morphology or some other characteristics and force to lose more energy or gain less energy. On the other hand, some other studies (Hanazato, 1995; Machacek, 1993, 1991; Weider and Pijanowska, 1993; Stibor, 1992) explained the life-history shifts as positive responses of *Daphnia*, because reduced size at maturation and offspring size produce small adults, which are less vulnerable to visually oriented predator fish. Also, reduced maturation time and increased brood size increase the population growth rate to compensate for population reduction by predation. Helmet formation of *Daphnia cucullata* (Laforsch and Tollrian, 2004)and neck teeth formation in *D. pulex* at juvenile stage (Miyakawa et al., 2010) are also considered to be a positive effect of kairomone on zooplankton as the predation risk decreases due to such morphological changes. Despite such increasing interest on fish kairomones and its effect on the releaser as well as on the acceptor, there are still large gaps in the knowledge. It has already proven difficult to simulate the natural environment artificially in static laboratory set up. So, the inclusions of some important natural issues such as complete food chain capturing, vertical migration of zooplankton and cost of zooplankton due to predation avoidance mechanism etc. are almost unattainable in lab experiments, although their amalgamated effects may have a different conclusion than the outcomes of experimental setup.

We like to be a part of the on-going debate by representing our thought through proposing two hypotheses and those to be tested by analyzing two simple mathematical models. In Hypothesis-1, we would like to test whether the initial formulated model based on simple phytoplankton–zooplankton system, incorporating the reduced growth rate of zooplankton in presence of kairomone, resembles the same result as Hanazoto et al. (2001). The drawback of the model is that though it includes the fish kairomone, but, the original source of fish kairomone has not been considered in model system. By introducing the fish population into the initial model we can capture the entire food chain. Whenever, considering fish and fish exudates (kairomones) in model system, one must be aware of two very common ecological phenomenons, (i) diel vertical migration (DVM) of zooplankton (Lampert and Loose, 1992; Dodson, 1988a; Gliwicz, 1986; Stich and Lampert, 1981) and (ii) cost of predation avoidance mechanism through DVM in zooplankton (Loose and Dawidowicz, 1994; Dawidowic and Loose, 1992; Lampert, 1989). Including these key parameters we modify previous model system and study 'whether kairomone released from predators (fish) gives benefit to receivers (zooplankton) rather than releasers?' This is our Hypothesis-2 needs to be tested through the simulated output of modified model.

2. Mathematical model-I: phytoplankton–zooplankton system based on laboratory set up

We formulate a mathematical model consisting of phytoplankton, zooplankton and fish kairomone similar to the laboratory experiment performed by Hanazoto et al. (2001). Let, $P(t)$ is the phytoplankton population, $Z(t)$ is the zooplankton population, and $C(t)$ is the concentration of kairomone present at time t. We assume that phytoplankton population follows logistic growth in the absence of grazer zooplankton. Let, r is the constant intrinsic growth rate and K is the carrying capacity of phytoplankton population. Let β be the rate at which phytoplankton are consumed by zooplankton, β_1 denotes the efficiency of phytoplankton conversion into zooplankton population and μ is the per capita-mortality rate of zooplankton. Let, kairomone is added into the system at a constant rate C_0 and d is the washout rate of kairomone.

To capture the effect of reduction in zooplankton growth in presence of kairomone we assume that α_1 be the parameter corresponding to the suppression of zooplankton growth due to increase in kairomone concentration in the system (Hanazoto et al., 2001; Loose and Dawidowicz, 1994). So the reduced growth rate should be a fraction $(1/\alpha_1 C)$ of $\beta_1\beta$ i.e., $\beta_1\beta \times (1/\alpha_1 C)$. But, for satisfying the initial condition of growth rate (i.e., the reduced growth rate should be equal to the growth rate $\beta_1\beta$, when the effect of kairomone was not present), the reduced growth rate should be $(\beta_1\beta/1+\alpha_1 C)$ – a monotonically decreasing function of kairomone concentration (C).

All the variables are connected through the following system of differential equations:

$$\begin{aligned} \frac{dP}{dt} &= rP\left(1-\frac{P}{k}\right)-\frac{\beta PZ}{a+P}, \\ \frac{dZ}{dt} &= \frac{\beta_1\beta PZ}{(1+\alpha_1 C)(a+P)}-\mu Z, \\ \frac{dC}{dt} &= C_0 - dC. \end{aligned} \tag{1}$$

System (1) has to be analyzed with the following initial conditions: $P(0)>0$, $Z(0)>0$, $C(0)>0$.

Equilibrium points, existence criteria and the local stability analysis of the system (1) are given in the Appendix A. Analytically we observe that, at high rate of addition of kairomone, zooplankton abundance remains low and above some critical level of kairomone input rate $(C_{crit}=(d/\alpha_1)[((\beta_1\beta k)/((a+k)\mu))-1])$, zooplankton extinct from the system (1). To validate and extrapolate our analytical findings through numerical simulation, we consider the set of fixed parameter values, mostly taken from various literature sources and are given in Table 1. With these set of parameter values, we find $C_{crit}=0.0871$. Numerically, to observe the effect of kairomone input rate on zooplankton abundance, we vary the parameter C_0 and plot zooplankton abundances keeping other parameter values fixed (Fig. 1). We observe that, whenever the value of C_0 remains below the critical value 0.0871, both phytoplankton and zooplankton coexist and increase in C_0 results decrease in zooplankton abundance; but whenever, C_0 crosses that critical value, zooplankton population extinct. Therefore, both the analytical and numerical results reveal that, kairomone has a negative impact on the zooplankton population which qualitatively resembles with the main outcome of the experimental