On a Stochastic Model of Gulping Behavior of Larval Fish to Planktonic Prey[†]

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(Received January 13, 1995)

We present a stochastic model that describes the gulping behavior of fish larva to planktonic prey. The model basically deploys the Yule's process, for it conveys the situation that the previous experience on feeding bouts is influential to the sequential volition of gulping.

Let $P_x(t)$ indicate the probability of how larval fish gulp x prey during the time interval $[0, t]$, and $\lambda_x(t)w + o(w)$ ($o(w)/w \rightarrow 0$) the conditional probability that larval fish gulped x preys by the time t and the next gulping behavior occurs once during the time interval $[t, t+w]$. In order to characterize $\lambda_x(t)$, $\lambda_x(t) = \lambda x + k$ (λ, k : constants) is adopted. This arrangement shows that the gulping behavior is dependent upon conditional experiences (λx) and non-conditional potential (k). Then, the differential equation system with respect to $P_x(t)$ is solved under an initial condition.

When $\lambda > 0$, $P_x(t)$ shapes the probability distribution function of the negative binomial type; when $\lambda = 0$, $P_x(t)$ shapes of the Poisson's type; and when $\lambda < 0$, $P_x(t)$ shapes of the binomial type, respectively. Thus, the parameter λ may operate as an indicator which distinguishes the dietetic maneuvers of larval fish and its ramifications.

Key words: plankton feeding, larval fish, gulping behavior, Yule's process, binomial distribution, Poisson's distribution, negative binomial distribution

One of the most prevailing causes in the fish population fluctuation is the sizable mortality in the early life histories: only a few fish larvae survive. On the ontogenetic profile they feature the lack of versatility. They do not swim fast nor cover a distance; therefore, they are not always tactful in food acquisition. From the viewpoint of energetics, elongated fast duration or vacancy in alimentary canals can impair their vitality and result in incurable conditions such as "point of no return".¹⁾ Many kinds of fish larvae depend upon plankton for their initial exogenous nourishment, so to encounter with planktonic prey is crucial to the larvae under field conditions.²⁻⁴⁾ Such is also the case for intensively reared ones which can indulge with feed but suffer intraspecific competition.⁵⁾ Thus, feeding success is a serious issue for every larva which subsists both penned and unpenned, and a better understanding will be attained through collecting evidence regarding feeding dynamics in how larvae encounter prey patches, how their prey patches are distributed, and then how they forage enough prey to survive. Evidently, such facets of the early biology of fish stem from the synergies between physiological and ambient conditions in which various effective durations or periodicities inhere, hence the characteristics of these phenomena should be monitored at several degrees of temporal scales. To date, however, considerable effort has been expanded on those on a day or so,⁶⁻⁸⁾ but those on smaller, such as, over a time span of less than an hour, are few.⁹⁾ Among them is

the larval behavior in feeding bouts.

We present here a plausible model that describes the gulping behavior of fish larva, not in a critical condition, but with enough vitality to forage habitually, to planktonic prey. It is helpful to analyze reactions when fish locate prey patches in the field or to comprehend preference in feed items. In order to facilitate understanding the context, some mathematical definitions and denotations are elucidatively exemplified in the appendices section.

Model Composition and Its Characteristics

An observation on prandial modes of larval fish revealed that after the initial voracity, fish become satiated with prey, which implies the condition of how the gut is packed per se effects the sequential foraging tactics.⁹⁾ This may indicate that a series of gulping behaviors on a feeding bout of larval fish is mathematically processed as a dynamics on a certain feed-back system. The stochastic calculus shows the conditional probabilities that larval fish gulped x preys by the time t and the next gulping behavior occurs during the time interval $[t, t+w]$ less than once, once, and more than once are denoted as

$$1 - \lambda_x(t)w + o(w), \quad \lambda_x(t)w + o(w), \quad o(w) \quad (1)$$

respectively, where

$$\lim_{w \rightarrow 0} \frac{o(w)}{w} = 0 \quad (2)$$

[†] Biometrics in Aquaculture-II.

(2) indicates that larval fish does not gulp plankton twice or more in a brief time span w .¹⁰⁾

Let $P_x(t)$ indicate the probability how larval fish has gulped x preys during the time interval $[0, t]$, then it gives rise to $P_0(t+w)$ and $P_x(t+w)$,

$$P_0(t+w) = \{1 - \lambda_0(t)w\} P_0(t) + o(w) \quad (3)$$

$$P_x(t+w) = \{1 - \lambda_x(t)w\} P_x(t) + \lambda_{x-1}(t)w P_{x-1}(t) + o(w) \quad (x=1, 2, \dots) \quad (4)$$

respectively.

In order to characterize $\lambda_x(t)$, Yule's process can be significantly feasible,¹⁰⁾ for it conveys the situation that the previous experience on feeding is quite influential to the sequential volition of gulping, as mentioned above. Thereby, instead of giving the original assumption $\lambda_x(t) = \lambda x$,¹⁰⁾ we deployed a modification such as

$$\lambda_x(t) = \lambda x + k \quad (\lambda_x(t) > 0) \quad (5)$$

for the constants λ and k . This arrangement shows mathematically a generalization of Yule's assumption, and semantically that the gulping behavior is dependent not only upon conditional experiences (λx) but upon non-conditional potential (k).

When larval fish gulped r times by the time $t=0$, convergence of w to zero leads (3) and (4) to develop into serial stochastic differential equations such as

$$\frac{dP_0(t)}{dt} = -(\lambda r + k) P_0(t) \quad (6)$$

$$\frac{dP_x(t)}{dt} = -\{\lambda(r+x) + k\} P_x(t) + \{\lambda(r+x-1) + k\} P_{x-1}(t) \quad (x=1, 2, \dots) \quad (7)$$

respectively. Larval fish does not gulp at $t=0$, then such initial conditions are introduced that

$$P_0(0)=1, \quad P_x(0)=0 \quad (x=1, 2, \dots) \quad (8)$$

Then the solution for (6) is

$$P_0(t) = e^{-(\lambda r + k)t} \quad (9)$$

and (9) yields the solutions for (7) sequentially

$$P_x(t) = {}_{r+k/\lambda+x-1}C_x (e^{-\lambda t})^{r+k/\lambda} (1 - e^{-\lambda t})^x \quad (x=1, 2, \dots) \quad (10)$$

Depending upon the equation (A1.3), (9) and (10) are obviously colligated into (11).

$$P_x(t) = P_n(x; r+k/\lambda, e^{-\lambda t}) \quad (x=0, 1, 2, \dots) \quad (11)$$

Meanwhile, (11) may connote the probability distribution functions of types other than the negative binomial one. Namely, when $\lambda < 0$ and $-r-k/\lambda$ is a natural number, (A2.1) induces

$$P_x(t) = P_b(x; -r-k/\lambda, 1 - e^{\lambda t}) \quad (x=0, 1, \dots, -r-k/\lambda) \quad (12)$$

If this is the case, the requisites $\lambda < 0$ and $r+k/\lambda < 0$ give $r\lambda + k > 0$, which assuredly stands the assumption denoted in (5).

By extension, when $k > 0$, convergence of λ to zero drives (11) and (12) to similarly turn to limiting values such as

Fig. 1. Examples of the probability distribution function $P_x(t)$ which equips numerically different parameter λ .

(A) $\lambda = 0.25$; (B) $\lambda = -0.25$; (C) $\lambda = 0$; (D) $\lambda = 0.025$. The other parameters are common such that $t=1$, $r=1$ and $k=2$.

$$\lim_{\lambda \rightarrow \pm 0} P_x(t) = \frac{(kt)^x}{x!} e^{-kt} = P_p(x; kt) \quad (x=0, 1, \dots) \quad (13)$$

Evidently these are solutions of the stochastic differential equation system (6) and (7) under the condition that $\lambda=0$ in (5):

$$\lambda_x(t) = k \quad (k > 0) \quad (14)$$

This is just an example of Poisson's process. Therefore, an arbitrary λ and a certain combination of r and k formulate, without inconsistency in the hypotheses, the probability distribution function for (6) and (7), or (11).

Discussion

An applied procedure of Yule's process introduces a convertible probability distribution function which generates binomial, Poisson's and negative binomial types. These are easily distinguishable if only to estimate the numerical relativity between the average and the variance, or the coefficient of variation (CV) value: if $CV < 1$, the process is the binomial type; if $CV = 1$, Poisson's type; and if $CV > 1$, the negative binomial type. Among them, Poisson's case is the most perceivable example where larval fish are represented to gulp randomly irrespective of previous forage records.¹⁰⁾ In the case of the binomial type, the conditional probability figures maximal value at $x=0$ and then is reduced to 0 at the maximal number in which the fish has gulped, which can be interpreted such that the less experience enhances the motivation to gulp and a frequent operation restrains it, or consequently ceases the activity. This may indicate that the fish is under a starved condition. The negative binomial case, finally, gives the contrary situation to the previous one: the conditional probability is minimum at $x=0$ and then increases. In this case, however, there may be the substantial limit in x that sustains the conditional probability at the utmost less than 1. Thereby more experience motivates the sequential assault, but once disinclined for feeding, fish assails still more seldom. This may indicate that the fish can afford to do so without feeding. These speculative delineations on the

feeding bout should be verified in order to address the uncertainty whether to ensure model realism and to concretely evaluate the parameters. This is achieved by such an experiment that can control the dietary situation of the wild and/or the nurtured fish larvae.

Admittedly, a certain combination of some parameters in each probability distribution function can resemble these instances to the Gaussian process. Then, it is next to impossible to distinguish the specific conditions mentioned above, and the whole fashion can be utterly noticed as a random process. Moreover, it is evident that modifying (1)–(4) induces the other stochastic process such as Langevin's equation, which exemplifies and discusses the multigale.¹¹⁾ Whenever we are dependent on these models, however, whether or not the physiological and functional response of larvae validates the applicability should be simultaneously inspected.

Acknowledgments We greatly appreciate all the members of the Yamaguchi Prefectural Naikai Sea Farming Center for their advisory contributions. This study was planned upon the ideas and drafts proposed by Mr. Kenya Kuwahara, a former researcher at the Yamaguchi Prefectural Gaikai Sea Farming Center.

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Appendices

Denotation of the probability distribution functions

Binomial distribution:

$$P_b(x; n, p) = {}_nC_x p^x (1-p)^{n-x} \quad (\text{A1.1})$$

Poisson's distribution:

$$P_p(x; \lambda) = \frac{\lambda^x}{x!} e^{-\lambda} \quad (\text{A1.2})$$

Negative binomial distribution:

$$P_n(x; n, p) = {}_{n+x-1}C_x p^n (1-p)^x \quad (\text{A1.3})$$

and the coefficient in (A1.3) can be transformed as follows:

$$\begin{aligned} {}_{n+x-1}C_x &= \frac{(n+x-1)!}{x!(n-1)!} = \frac{1}{x!} n(n+1) \cdots (n+x-2) \\ &\quad \times (n+x-1) \\ &= \frac{(-1)^x}{x!} (-n)(-n-1) \cdots (-n-x+2) \\ &\quad \times (-n-x+1) \\ &= \frac{(-1)^x (-n)!}{x!(-n-x)!} \\ &= (-1)^x {}_{-n}C_x \end{aligned} \quad (\text{A1.4})$$

Transformation of a negative binomial distribution function

$$\begin{aligned} P_n(x; n, e^{-m}) &= {}_{n+x-1}C_x (e^{-m})^n (1-e^{-m})^x \\ &= (-1)^x {}_{-n}C_x (e^m)^{-n} \{(-1)e^{-m}(1-e^m)\}^x \\ &= {}_{-n}C_x (1-e^m)^x (e^m)^{-n-x} \\ &= P_b(x; -n, 1-e^m) \end{aligned} \quad (\text{A2.1})$$

where $-n$ is a natural number and $m < 0$.