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Modeling the refuge effect of submerged macrophytes in ecological dynamics of shallow lakes: A new model of fish functional response

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ABSTRACT

Submerged macrophytes often provide refuge for zooplankton from fish predation in temperate and subtropical shallow lakes. However, since the relationship between submerged macrophyte abundance and its refuge effect has not been well established, the refuge effect is difficult to be simulated. In this paper, we constructed mathematical models to describe the refuge effect of submerged macrophytes on fish foraging activities and ecological dynamics of shallow lakes based on the previous studies. We clarified the underlying behavioral mechanisms of the observed functional responses through analyses of the fish foraging behavior, extracted the affected variables related to the refuge effect, formulized the relationship between the affected variables and submerged vegetation density, and determined parameter values with a compensative procedure. Calibration and validation results indicated that the new functional response model was successful to simulate the refuge effect on interfering with fish foraging behavior. Moreover, the model was cooperated into a minimal ecological model for shallow lakes. Modeling results showed that the model was able to simulate the refuge effect in ecological dynamics, and made the ecological model produce significantly different results from those with the existing functional response models.

1. Introduction

Submerged macrophytes are crucial for the stabilization of the clear water state in shallow lakes for leading to lower phytoplankton abundance and higher water transparency (Lauridsen and Buenk, 1996; Van Donk and Van de Bund, 2002). It has been proved that the refuge provided by submerged macrophytes is one of the most important mechanisms for the positive effects. Timms and Moss (1984) firstly demonstrated submerged macrophytes as refuge for herbivorous zooplankton against fish. Lauridsen et al. (1996) pointed out that the edge zone between macrophyte bed and open water was an important daytime refuge for potentially migrating pelagic cladocerans. Utilizing the refuge to escape from diurnal visual predation by fish, large-bodied zooplankton keeps high grazing pressure on phytoplankton. Therefore, clear water state is easy to maintain in shallow lakes accompanied with abundant submerged macrophytes (Jeppesen et al., 1999; Van Donk and Van de Bund, 2002).

For modeling ecological dynamics of shallow lakes, different models have been developed, most of which include processes of nutrition, phytoplankton, zooplankton, and fish in the modeling structures. Increasingly, submerged macrophytes have been introduced in some models to study shallow lake dynamics (e.g. Xu et al., 1999; Zhang et al., 2003; Janse et al., 2010). However, in the models without considering the refuge effect, impact of macrophytes on the lake system is mainly through two mechanisms: completing nutrient and other resources with phytoplankton and providing habitat and food for fish. Even though some phenomenological approaches have been used to describe the refuge effect in a few models (Genkai-Kato, 2007; Carusela et al., 2009; Wang et al., 2009b), the approaches are mostly based on ideal and strict assumptions, such as vegetation abundance as a constant or strictly determined by phytoplankton density. Since such assumptions are hardly satisfied in reality, these models are not applicable in a complex ecological system.

Thus far, the refuge effect of submerged macrophytes is rarely simulated directly in dynamic models of shallow lakes. The reason is probably because how vegetation density affects fish predation has not been clarified, and the relationship between macrophyte abundance and its refuge effect on fish foraging rate has not been well documented (Genkai-Kato, 2007). In fact, numerous previous laboratory and field studies have observed that submerged vegetation greatly influences various aspects of fish foraging behavior, such as movement, visual sight, consuming time, and probability and success rates of attacking prey. The refuge effect of submerged macrophytes often result in lower fish capture rate, encounter rate, swimming speed, visual field and foraging success and higher han-

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Table 1
Data sources of the essential model hypotheses.

Variables	H1[a]	H2	H3	H4	DE
Swimming speed (v)	4, 6, 18, 21, 23, 32, 34, 38, 44[b]		4, 6, 18, 21, 23, 32, 34, 38, 44		4, 6, 18, 21, 23, 32, 34, 38, 44
Visual field (K)	3, 7, 14, 19, 32, 35		3, 7, 14, 19, 32, 35		3, 14, 32, 35
Foraging success (s)	3, 5, 13–15, 38, 49	3–7, 14–15, 18, 21, 23, 32, 34, 38, 44, 49	3, 5, 13–15, 38, 49	3–5, 14–15, 21, 32, 38	3, 13–15, 38, 49
Handling time (t_h)	3–5, 15, 21, 24		3–5, 15, 21, 24		3–4, 15, 21, 24
Attack ratio (a)	14, 21, 36, 44, 49		14, 21, 36, 44, 49		14, 21, 36, 44, 49
Encounter rate (E)	3–5, 12, 14–15, 21, 25, 36, 38, 44, 48–49		–	–	3–4, 12, 14–15, 21, 25, 36, 38, 44, 48–49
Capture rate (C)	1–3, 6–12, 14, 16–18, 20, 22–23, 25–34, 36–49		–	–	1–3, 6, 8–12, 14, 16–18, 20, 22–23, 25–34, 36–49

[a] H1, H2, H3, H4, and DE denote hypothesis 1, hypothesis 2, hypothesis 3, hypothesis 4, and data extraction, respectively.

[b] References: [1]Crowder and Cooper (1982); [2]Stoner (1982); [3]Savino and Stein (1982); [4]Anderson (1984); [5]Cook and Streams (1984); [6]Winfield (1986); [7]Main (1987); [8]Russo (1987); [9]Wilson et al. (1987); [10]Butler (1988); [11]Diehl (1988); [12]Ryer (1988); [13]Gotceitas and Colgan (1989); [14]Savino and Stein (1989); [15]Gotceitas (1990a); [16]Gotceitas (1990b); [17]Gotceitas (1990c); [18]Persson (1991); [19]Lillie and Budd (1992); [20]Savino et al. (1992); [21]Christensen and Persson (1993); [22]Roca et al. (1993); [23]Eklöv and Diehl (1994); [24]Eklöv and Persson (1995); [25]Kenyon et al. (1995); [26]Persson and Eklöv (1995); [27]Tátrai and Herzig (1995); [28]Gregory and Levings (1996); [29]Jacobsen et al. (1997); [30]Nyström and Pérez (1998); [31]Aarnio and Mattila (2000); [32]Manatunge et al. (2000); [33]Harrel and Dibble (2001); [34]Priyadarshana et al. (2001); [35]Asaeda et al. (2002); [36]Valley and Bremigan (2002); [37]Harris et al. (2004); [38]Ryer et al. (2004); [39]Abdel-Tawwab (2005); [40]Okun and Mehner (2005); [41]Van de Meutter et al. (2005); [42]Godinho and Ferreira (2006); [43]Scharf et al. (2006); [44]Priyadarshana and Asaeda (2007); [45]Stuart-Smith et al. (2007); [46]Mattila et al. (2008); [47]Henninger et al. (2009); [48]Michel and Adams (2009); [49]Stoner (2009).

dling time and attack ratio (e.g. Savino and Stein, 1989; Manatunge et al., 2000; Priyadarshana and Asaeda, 2007). All these influences finally lead to the impact on fish functional response, defined as the consumption rate of individual fish changing with zooplankton density (Wong and Barbeau, 2006). It is feasible to establish the relationship of between submerged macrophytes and fish functional response from organizing the previous research results.

Hence, the aim of this study was to construct a new mathematical model to describe the refuge effect, based on systematic analyses of data in the literature. Then the new model was incorporated into a minimal ecological model for shallow lakes to test its efficacy of simulating the refuge effect in ecological dynamics.

2. Material and methods

2.1. Data of the refuge effect from the literature

To construct the model, data related to fish foraging behavior in the submerged vegetation environment were collected from the literature, resulting in 49 papers published from 1982 to 2009 (Table 1). Based on the literature, hypotheses for the modeling construction were summarized as follows: Hypothesis 1 (H1) included that fish capture rate (C), encounter rate (E), swimming speed (v), visual field (K), and foraging success (s) decreased, while handling time (t_h) and attack ratio (a) increased under the refuge effect. Hypothesis 2 (H2) was that the changes of v, K, s, t_h and a under the refuge effect would result in corresponding changes of C and E. Hypothesis 3 (H3) included that the changes of v, K, s, t_h and a were nonlinear and usually with threshold levels, at which the changes were from significant to gentle (even sometimes capricious), and the change tendency of a fixed variable among different cases was similar. For hypothesis 4 (H4), the macrophyte density (M_D), at which v, K, s decreased 50% and t_h and a increased 100% in a certain case, was approximately equal. The relative change of the variables (p_{MD}/p_0, $p = v, K, s, t_h, a, E, C$) and theirs corresponding M_D values and the prey density were extracted from the references. The references related to the hypotheses and data extraction (DE) are listed in Table 1. The details of data extraction were given in Section 2.3.

2.2. Construction of the new functional response model

For the frequently observed functional response in fish foraging activity (Johansson, 1987; Jeschke et al., 2002), the functional response is often modeled as Holling type II function (e.g. Xu et al., 1999; Zhang et al., 2003):

$$f_{FR}(Z) = \frac{Z}{Z + h_Z} p_F \tag{1}$$

where Z (g/m^3) is zooplankton biomass; p_F (/d) is the maximum predation rate of fish on zooplankton; h_Z (g/m^3) is the half saturation constant for fish predation. The underlying behavioral mechanisms of the observed functional responses can be found out through the analysis of fish foraging behavior. Fish as an active swimming searcher, its prey encounter rate (E, ind./s) is expressed by (Aksnes and Giske, 1993; Priyadarshana and Asaeda, 2007):

$$E = Kvn \tag{2}$$

where K (m^2) is the fish visual field plane, v (m/s) is the fish swimming speed, and n (ind./m^3) is the prey density. Then the amount of prey encountered by fish (m_E, ind.) in the time period of T_S (s) is:

$$m_E = ET_S = KvnT_S \tag{3}$$

However, fish is not likely to attack all prey encountered. Also, fish cannot always successfully capture all preys attempted to