



Review

Predictions from simple predator-prey theory about impacts of harvesting forage fishes



Carl Walters^{a,*}, Villy Christensen^a, Beth Fulton^b, Anthony D.M. Smith^b, Ray Hilborn^c

^a Institute for the Oceans and Fisheries, University of British Columbia, Vancouver B.C. V6T1Z4, Canada

^b Commonwealth Scientific and Industrial Research Organization, Oceans and Atmosphere Hobart, TAS 7001, Australia

^c School of Aquatic and Fishery Sciences University of Washington Seattle, Box 355020, WA 98195-5020, USA

ARTICLE INFO

Article history:

Received 21 May 2016

Received in revised form 16 July 2016

Accepted 20 July 2016

Keywords:

Fisheries

Forage fish

Predator prey models

Ecosystem models

Depensatory mortality

Atlantis

Ecosim

ABSTRACT

Simple predator-prey models make widely divergent predictions about impact on piscivores of harvesting forage fish species, depending on structural assumptions about the fine-scale spatial structure of trophic interactions (presence or absence of foraging arena structure in prey availability) and about limitation in predator or prey recruitment due to foraging and habitat restrictions on early juvenile survival. This sensitivity to structural assumptions warns us about possible mistakes that can arise in much more complex and realistic models, where we have to make equivalent assumptions. Recruitment limitation implies risk of depensatory impact on forage species as fishing rate on these species increases, with attendant risk of development of predator-prey cycles and strong responses to relatively small changes in basic forage fish productivity due to environmental factors.

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Contents

1. Introduction	272
2. Predator-prey model structure and isocline analysis	273
3. How key assumptions change predicted patterns of forage fish-piscivore covariation	273
3.1. Classic Renshaw-MacArthur model for non-interacting piscivores	273
3.2. Effect of foraging arena limitation on predation rates	275
3.3. Effect of piscivore recruitment limitation due to early life history	275
3.4. Effect of stock recruitment limitation in forage fish combined with size-selective predation	276
3.5. Role of predator prey interactions in responses of forage fish to regime shifts	277
4. Discussion	277
Acknowledgements	279
Appendix A. Supplementary data	279
References	279

1. Introduction

Growing insistence on ecosystem based management has led to greater concern about the impacts of fishing on ecosystem trophic structure, and particularly the impacts of fishing “forage” species (invertebrates, small pelagics) on productivity and viability of larger predatory species (Cury et al., 2012; Pikitch et al., 2014;

Engelhard et al., 2014). Fisheries on smaller, lower trophic level species can typically result in higher biomass yields than fisheries for piscivores (Salcido-Guevara and Arreguin-Sanchez, 2014), and demand for harvesting of smaller species can be expected to grow both for feeding people and for feed in agricultural and aquacultural production. Fisheries on schooling small pelagics also have a particularly low lower carbon footprint (Tyedmers, 2004). The notion that it may be possible to both take such higher yields and still maintain overall ecosystem structure and function has been actively promoted through the concept of “balanced harvesting”

* Corresponding author.

E-mail addresses: c.walters@oceans.ubc.ca, carlwalt@gmail.com (C. Walters).

(Zhou et al., 2010; Garcia et al., 2012; Kolding and van Zwieten, 2014; Jacobsen et al., 2014), but this concept has been greeted with much suspicion by some senior fisheries scientists (Froese et al., 2015; other references in the same ICES J. Marine Science issue).

Field evidence of negative impact of forage species harvesting on higher trophic levels has been difficult to interpret, with little clear evidence of impact on piscivores (e.g. Hanneson, 2013) but better evidence of impact on piscivorous birds and mammals that are central place foragers with restricted spatial access to forage species (e.g. Cury et al., 2012). However for central place foragers the link between harvesting and local abundance is tenuous as local abundance is dominated by distribution change. This lack of clear field evidence has led to extensive use of ecosystem models and food web data to predict impacts (e.g. Smith et al., 2011; Garcia et al., 2012; Pikitch et al., 2014; Jacobsen et al., 2014; Plaganyi and Essington, 2014; Smith et al., 2015; Essington et al., 2015). Unfortunately, the various ecosystem models have not been consistent in their predictions of impact, with simpler models (mainly Ecosim) tending to predict quite strong impacts but more complex models (Atlantis, Osmose, some size-spectrum models) tending to predict much weaker impacts (see e.g. Smith et al., 2011, 2015; Woodworth-Jefcoats et al., 2015), though impacts are typically predicted to be qualitatively similar, e.g. Forrest et al. (2015).

It would be a grave mistake to assume that the more optimistic predictions from more complex ecosystem models are better simply because they represent ecosystem structure and large-scale spatial organization in more detail than the simpler models. The divergence in predictions does not arise simply from modeling prey community structure and the stabilizing effects of predator switching behaviors across the community in greater detail; at least some of the “simpler” Ecosim models used in model comparisons have represented forage species and size structure in substantial detail, along with changes in predator feeding rates as prey species composition changes. Taxonomic aggregation is not the cause of the differences among models, nor can we claim that predictions from simpler models are somehow better.

Rather, some of the differences in ecosystem model predictions may arise from basic assumptions about predator-prey interactions in general. This paper reviews basic predator-prey model theory, and shows how different basic structural assumptions, particularly about fine-scale spatial interaction patterns and factors other than food production that may limit predators, could well be the cause of divergent predictions by the more complex ecosystem models. The resilience and stability patterns (e.g. cyclic changes) that we see in the complex models are often very similar to, and can be explained largely by, the patterns we see in single prey-single predator differential equation models; that is, model complexity does not negate or mask the dynamic behaviors predicted by simple models.

2. Predator-prey model structure and isocline analysis

The dynamic predictions of simple predator-prey models have been well understood since the early 1970s, following the recommendation of Rosensweig and MacArthur (1963) to focus on the model “isocline” structure. The prey isocline is the set of all points where prey abundance has zero rate of change, and the predator isocline is the set of points where predator abundance has zero rate of change. The simplest models are defined by two rate equations, one for prey (B) abundance and one for predator (P) abundance, with four rate processes for prey surplus production $G(B)$, predation $q(B,P)P$, predator reproduction $gq(B,P)P$ proportional to (with efficiency g) food intake, and predator mortality ZP :

$$dB/dt = G(B) - q(B, P)P \quad (1a)$$

$$dP/dt = gq(B, P)P - ZP \quad (1b)$$

It is typically assumed that prey surplus production (excess of growth and recruitment over mortality rate not due to the predator) is a dome-shaped function of B, e.g. the logistic model

$$G(B) = rB(1-B/K), \quad (2)$$

where r is intrinsic growth rate and K is equilibrium biomass in the absence of the predator. Per-capita predation rate $q(B,P)$ is typically predicted with a Holling type II functional response, sometimes modified to have negative effects of increasing P due to vaguely defined “predator interference”. Absent such interference or other mechanism that reduces prey availability when P is high, q is given by

$$q(B, P) = q(B) = aT_t B / (1 + ahB). \quad (3)$$

Here, the predator rate of effective search (a) has units area or volume searched per time, divided by total area over which the interaction is distributed, T_t represents the proportion of time that predators are actively foraging (and/or prey are available in cases where prey are inactive or hiding much of the time), and h represents time spent handling or digesting each prey such that maximum q at high B is given by T_t/h .

In Ecosim models, prey biomass is assumed to be distributed between two vulnerability states, with V prey actually vulnerable at any moment and $B-V$ prey in safe places or hiding behaviors; in this “foraging arena theory” representation (Ahrens et al., 2011), V replaces B in Eq. (3), and V is assumed to vary dynamically according to the rate equation

$$dV/dt = v(B-V) - v'V - q(V)P \quad (4)$$

so that prey move into the vulnerable state at instantaneous rate v , leave that state at rate v' , and are removed by predators at rate $q(V)P$ where $q(V)$ is typically modeled using the type II Eq. (3) but with V replacing B . Rapid equilibration of V is expected if the v and v' rates are high, and if V remains near equilibrium the resulting overall relationship $q(B,P)$ shows apparent predator interference (and so-called “ratio dependence” in the $q(B,P)$ relationship) since predation rate $q(V)P$ can severely reduce V as P increases even if overall B is not strongly affected by this depletion.

3. How key assumptions change predicted patterns of forage fish-piscivore covariation

Changes in assumptions about how predator feeding rates vary with prey abundance and how predator food intake is translated into population growth cause profound changes in simple model predictions about the stability and abundance responses of both predators and prey to harvesting the prey species. The following paragraphs examine four main model structures that illustrate the range of predictions. Numerical parameter values and calculations used to produce figures for the models shown below are all in an Excel spreadsheet (“predator prey fat model isocline equations.xlsx”) provided as Supplementary material; for interested readers, this spreadsheet allows for easy change of model parameters to test sensitivity to them.

3.1. Classic Rosensweig-MacArthur model for non-interacting piscivores

The classic Rosensweig-MacArthur model (Rosenweig and MacArthur, 1963) uses only Eqs. (2) and (3), i.e. dome-shaped prey surplus production combined with type II predation with no predator interaction and no dynamics in the predator mortality rate Z . The basic isocline structure for this model involves a vertical predator isocline, i.e. predators are just holding their own ($dP/dt = 0$) only at a single prey density B^* and are increasing whenever B exceeds this

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