Constant proportion harvest policies: Dynamic implications in the Pacific halibut and Atlantic cod fisheries

Abdul-Aziz Yakubu [a,*], Nianpeng Li [a], Jon M. Conrad [b], Mary-Lou Zeeman [c]

[a] Department of Mathematics, Howard University, Washington, DC 20059, United States
[b] Charles H. Dyson School of Applied Economics and Management, Cornell University, Ithaca, NY 14853, United States
[c] Department of Mathematics, Bowdoin College, Brunswick, ME 04011, United States

ARTICLE INFO

ABSTRACT

Overfishing, pollution and other environmental factors have greatly reduced commercially valuable stocks of fish. In a 2006 *Science* article, a group of ecologists and economists warned that the world may run out of seafood from natural stocks if overfishing continues at current rates. In this paper, we explore the interaction between a constant proportion harvest policy and recruitment dynamics. We examine the discrete-time constant proportion harvest policy discussed in Ang et al. (2009) and then expand the framework to include stock-recruitment functions that are compensatory and overcompensatory, both with and without the Allee effect.

We focus on constant proportion policies (CPPs). CPPs have the potential to stabilize complex overcompensatory stock dynamics, with or without the Allee effect, *provided* the rates of harvest stay below a threshold. If that threshold is exceeded, CPPs are known to result in the sudden collapse of a fish stock when stock recruitment exhibits the Allee effect. In case studies, we analyze CPPs as they might be applied to Gulf of Alaska Pacific halibut fishery and the Georges Bank Atlantic cod fishery based on harvest rates from 1975 to 2007. The best fit models suggest that, under high fishing mortalities, the halibut fishery is vulnerable to sudden population collapse while the cod fishery is vulnerable to steady decline to zero. The models also suggest that CPP with mean harvesting levels from the last 30 years can be effective at preventing collapse in the halibut fishery, but these same policies would lead to steady decline to zero in the Atlantic cod fishery. We observe that the likelihood of collapse in both fisheries increases with increased stochasticity (for example, weather variability) as predicted by models of global climate change.

© 2011 Elsevier Inc. All rights reserved.

1. Introduction

Fisheries throughout the world are in crisis [5,7,9,11,16,22,23,28,31,32]. In a recent paper, Ang et al. examine the degree of sub-optimality when fishery managers use the best constant proportion policy (CPP) instead of the optimal variable proportion policy (VPP). Sub-optimality was measured relative to the maximized discounted net revenue in a single-species, discrete-time, unstructured population model [1]. In their model, Ang et al. adopted a logistic escapement function. They identified the best constant proportion policy and the best variable proportion policy for the Pacific halibut fishery in Gulf of Alaska in Area 3A (see Fig. 1).

In this paper, we extend that framework to include discrete-time fisheries that exhibit compensatory stock dynamics, with and without the Allee effect (e.g. the Beverton–Holt and modified Beverton–Holt models) and overcompensatory stock dynamics

with and without the Allee effect (e.g. the Ricker and modified Ricker models) [2–4,6,9–14,17–27,29–32]. We use the model framework to assess performance of harvested fisheries that vary in levels of compensation with and without depensation (Allee effect) under constant harvest regimes. It is known that both CPPs can stabilize complex behavior caused by overcompensatory dynamics but they may result in a sudden collapse of the fish stock when the Allee effect is present. In the absence of the Allee effect, our models show that, as the harvest fraction increases, yield (harvest) first rises gradually to a maximum sustainable level and then declines continuously to zero.

As case studies, we apply the theoretical model framework to Gulf of Alaska Pacific halibut fishery data from the International Pacific halibut Commission (IPHC) annual reports and Atlantic cod fishery data from the North East Fisheries Science Center (NEFSC) Reference Document [1,5,22]. The Gulf of Alaska Pacific halibut fishery data is for Area 3A (see Fig. 1) and that of the Atlantic cod fishery is for the Georges Bank (see Fig. 2). Our analysis indicate that under CPP, mean harvest rates of the last 30 years are effective at preventing collapse in the halibut fishery but

---

* Corresponding author.
E-mail addresses: ayakubu@howard.edu (A.-A. Yakubu), sylnp@hotmail.com (N. Li), jmc16@cornell.edu (J.M. Conrad), mlzeeman@bowdoin.edu (M.-L. Zeeman).
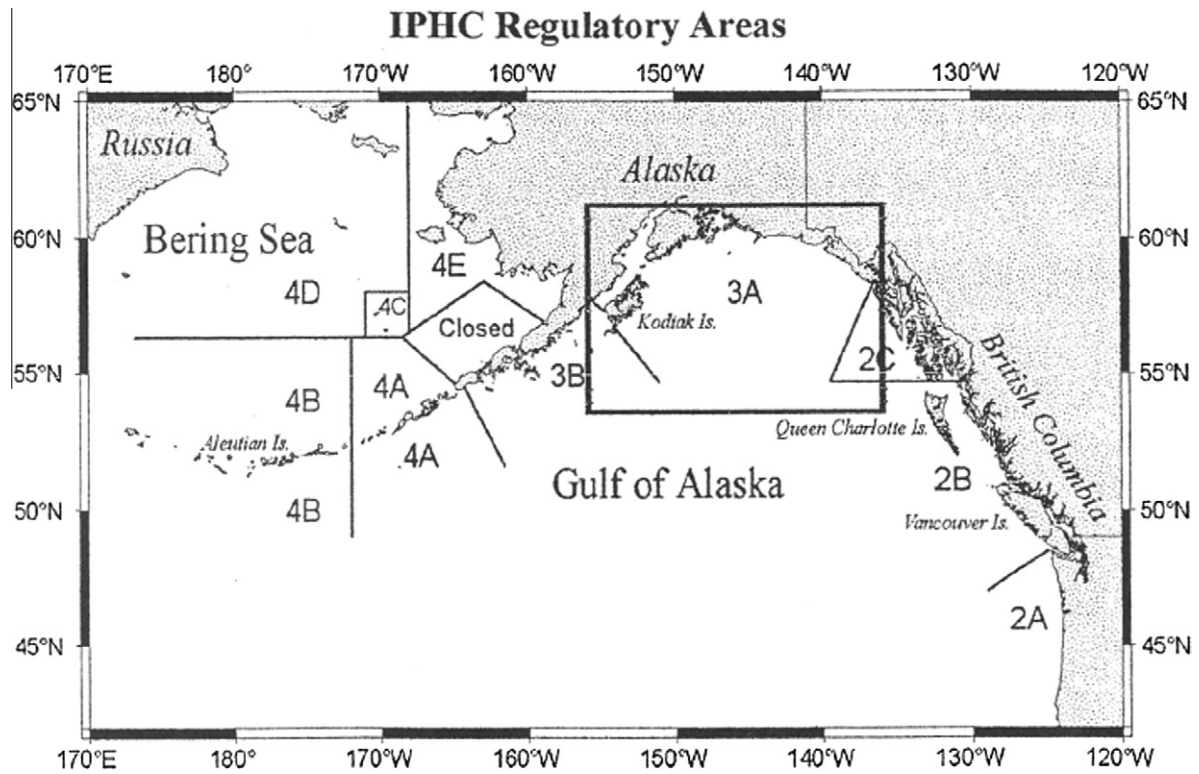
IPHC Regulatory Areas

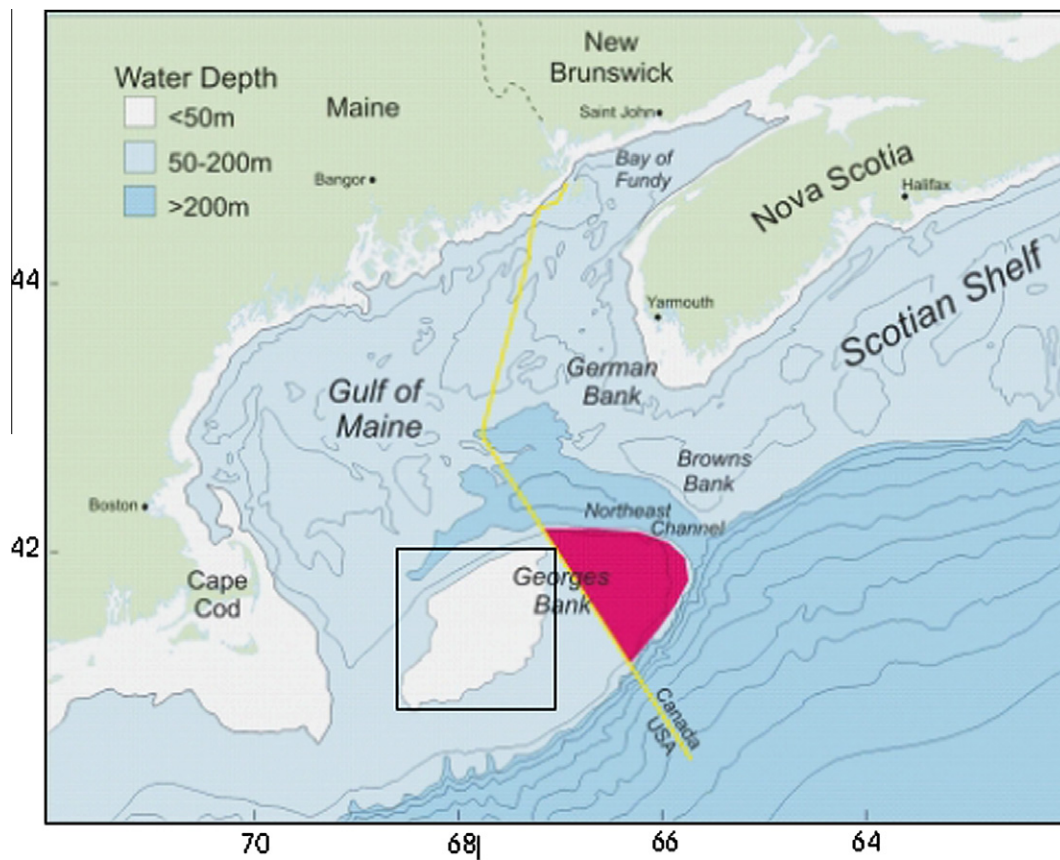
Fig. 1. IPHC Regulatory areas [1].

Fig. 2. Georges Bank Atlantic cod fishery area and the North-East Coastal areas.

endanger the cod fishery. Stochastic versions of the model indicate that the likelihood of the collapse of both halibut and cod fisheries increases with increased stochasticity in the fish environment.

The rest of the paper is organized as follows. In Section 2, we introduce the general model for regulation with a CPP and we define compensatory, overcompensatory and depensatory (Allee effect) recruitment dynamics. In Section 3 we explore the interactions between recruitment dynamics and CPP. Section 4 examines the Gulf of Alaska halibut fishery, Section 5 analyzes the Georges Bank cod fishery, and concluding remarks are presented in Section 6.

2. Harvested fisheries population model

In this section, we introduce the single species discrete-time fish stock mathematical model for regulation with a CPP. At the start of year t, we let $x(t)$ denote the fish stock (biomass) and $y(t)$ the total allowable catch (TAC). The total allowable catch is the fraction, $0 < a < 1$, of the estimated stock. That is,

$$y(t) = ax(t). \tag{1}$$

Since the harvesting fraction is constant $a \in (0,1)$, we refer to $y(t) = ax(t)$ as the *constant proportion policy* (CPP). The CPP is transparent, easily implemented and historically acceptable to fishers [1].

At the start of year t, the escapement is defined as

$$s(t) = x(t) - y(t) = (1-a)x(t). \tag{2}$$

We assume that reproduction occurs halfway through the season and is characterized by the recruitment function

$$f(s(t)) = s(t)g(s(t)), \tag{3}$$

where the per-capita growth function, $g : [0, \infty) \to [0, \infty)$, is assumed to be a continuously differentiable function.

The dynamics of the harvested stock are then described by the deterministic, discrete-time, unstructured population model

$$x(t+1) = (1-m)s(t) + f(s(t)), \tag{4}$$

where $m \in (0,1)$ is the (constant) natural mortality rate. The assumption about the timing of recruitment allows compression of the age-structure of the model so that one can work with a minimum number of equations. There are two terms for the population dynamics: survival of mature fish $(1-m)s(t)$, and recruits to the population, $f(s(t))$.

Using Eqs. (2) and (3), Model (4) becomes the exploited fish population model,

$$x(t+1) = G(x(t)) = (1-a)x(t)(1 - m + g((1-a)x(t))). \tag{5}$$

The set of iterates of the function G is equivalent to the set of stock sequences generated by Model (5). Note that when the per capita growth rate is the logistic model and

$$g(x(t)) = r\left(1 - \frac{x(t)}{K}\right),$$

then Model (5) reduces to that of Ang et al. [1].

The fish population is said to be *persistent* if $\underline{\lim}_{t\to\infty} G^t(x) > 0$ for all $x > 0$. Moreover, the population is said to be *uniformly persistent* when there exists a constant $\eta > 0$ such that $\underline{\lim}_{t\to\infty} G^t(x) \geqslant \eta$ for all $x > 0$.

In Section 3 we analyze the behavior of Model (5) under CPP, for stock populations exhibiting compensatory, overcompensatory and/or depensatory (Allee effect) recruitment dynamics. First, we define these terms in Section 2.1.

2.1. Compensatory, overcompensatory and depensatory vital rates

The per-capita growth rate, g, is said to be *compensatory* if for all $s \geqslant 0$

$$\frac{dg(s)}{ds} < 0,$$

$$\frac{df(s)}{ds} > 0$$

and

$$\lim_{s\to\infty} f(s) = \eta > 0.$$

When g is compensatory the decline in the per-capita growth rate with density exactly compensates for the increase in density so that the net growth rate is asymptotically constant [3].

For example, when f is the classic monotone Beverton–Holt stock recruitment model,

$$f(s) = \frac{\alpha s}{1 + \beta s}, \tag{6}$$

where the intrinsic growth rate, α, and the scaling parameter, β, are positive constants, then g is compensatory. If $\alpha > 1$, then $f'(0) > 1$, the Beverton–Holt model has a globally attracting equilibrium point at $x_\infty = \frac{\alpha-1}{\beta} \in (0, \infty)$ and all positive initial conditions converge to x_∞ *monotonically* under f iterations.

The per-capita growth rate, g, is said to be *overcompensatory* if

$$\lim_{s\to\infty} f(s) = 0.$$

When g is overcompensatory an increase in s is more than compensated for by a decrease in $g(s)$ at high densities [3].

For example, when f is the classic Ricker stock recruitment model,

$$f(s) = \alpha s e^{-\beta s}, \tag{7}$$

where the intrinsic growth rate, α, and the scaling parameter β are positive constants, then g is overcompensatory [29–32]. If $\alpha > 1$, then $f'(0) > 1$ and the one-humped Ricker model has a positive equilibrium point at $x_\infty = \frac{\ln \alpha}{\beta} \in (0, \infty)$. Depending on the model parameters, the Ricker model can exhibit oscillatory and chaotic dynamics.

When

$$\frac{dg(s)}{ds} > 0$$

for some $s > 0$, then the per-capita growth rate g is said to exhibit *depensation* or *the Allee effect* [3]. The Allee effect describes a positive relation between population density and the per capita growth rate of species. In the presence of the Allee effect, there is a decrease in population growth rate at low population sizes, and the effect usually saturates or disappears as populations get larger. Presence of the Allee effect in populations may be due to any number of causes. In some species, reproduction or finding a mate is increasingly difficult as the population density decreases [3–6,11,14,16,19,25].

For example, when f is either the modified Beverton–Holt stock recruitment model,

$$f(s) = \frac{\alpha s^2}{1 + \beta s^2}, \tag{8}$$

or the modified Ricker stock recruitment model,

$$f(s) = \alpha s^2 e^{-\beta s}, \tag{9}$$

g is depensatory.

Scramble and contest competition are two extreme forms of intraspecific competition for resources [21]. Systems that exhibit scramble competition try to support all individuals including those who are non-reproductive. In scramble competition, the resources

are equally divided among individuals, so that, beyond a threshold density, none can get enough of a share of the resource to survive and reproduce. Anadromous brown trout, *Salmo trutta*, exhibits scramble competition when it strives to secure broadcast food items by being better at searching and handling the items [23]. Models that are subject to overcompensatory dynamics, such as the Ricker model, provide examples of systems where new recruits experience scramble competition. In contest competition, some individuals get a big enough share of the resource to survive and reproduce at the expense of the rest. Anadromous brown trout exhibits contest competition when it interferes with other individuals for food items or for a territory [23]. Models that are subject to compensatory dynamics, such as the Beverton–Holt model (a special case of Smith–Slatkin model), provide examples of systems where new recruits experience contest competition.

3. Recruitment functions and stock dynamics

In this section, we study Model (5) where the stock population exhibits compensatory or overcompensatory dynamics with or without the Allee effect. We see that the behavior of discrete-time CPP regulated fishery systems with compensatory dynamics echoes the well known behavior of their continuous-time counterparts with constant proportion harvesting (see [4]). When there is no Allee effect, a gradual increase in harvesting fraction, a, leads to a gradual change in stock population and the corresponding catch. But when the stock system is subject to the Allee effect, then a gradual increase in the harvesting rate can lead to a sudden collapse of the fishery through an underlying fold bifurcation in the dynamics. In contrast, discrete-time CPP regulated fishery systems with overcompensatory dynamics in the presence of the Allee effect exhibit period-doubling bifurcations and chaotic dynamics combined with a similar fold bifurcation underlying fishery collapse. In Sections 3.1, 3.2, 3.3, 3.4 we describe these dynamics in more detail.

3.1. Compensatory stock dynamics

To study the effects of CPP and compensatory stock dynamics, we assume that in Model (5) the fish population dynamics are compensatory. That is, we assume that for all $x \geqslant 0$

$$\frac{dg(x)}{dx} < 0.$$

Whenever $a < a_{cr} = \frac{g(0)-m}{1-m+g(0)} > 0$, $G'(0) > 1$ and we assume that G has a globally attracting positive fixed point, x_∞, and all positive population sizes converge to x_∞ monotonically under G iterations.

Since g is a decreasing function, the maximum value of the effective per capita growth, $\frac{G(x)}{x}$, is $(1-a)(1-m+g(0))$. Thus, if

$$a > a_{cr}$$

then $\frac{G(x)}{x} = (1-a)(1-m+g((1-a)x(t))) < 1$ and the population size approaches zero for any initial biomass. That is, under CPP the model has a critical harvesting rate, a_{cr}, with the property that any larger harvesting rate will lead to the depletion of the exploited stock. However, when $a < a_{cr}$ then the stock persists on a globally attracting positive steady state biomass,

$$x_\infty = \frac{1}{(1-a)} g^{-1}\left(\frac{1-(1-m)(1-a)}{(1-a)}\right) \qquad (10)$$

and the corresponding positive steady state TAC

$$y_\infty = \frac{a}{(1-a)} g^{-1}\left(\frac{1-(1-m)(1-a)}{(1-a)}\right). \qquad (11)$$

Thus, G exhibits compensatory dynamics whenever the harvesting rate is below the critical value a_{cr}. Next, we use the Beverton–Holt

model (compensatory dynamics) to illustrate the continuous relationship between steady state TAC and harvest rates.

Example 1. When we adopt the Beverton–Holt form for the stock recruitment function, then

$$G(x) = (1-a)x\left(1 - m + \frac{\alpha}{1+\beta(1-a)x}\right),$$

and

$$a_{cr} = \frac{\alpha - m}{1 - m + \alpha}.$$

The stock goes extinct whenever $a > a_{cr}$. When $a < a_{cr}$ then $G'(0) > 1$, $0 < G'(x_\infty) < 1$, $G'(x) > 0$ and $G''(x) < 0$ for all $x > 0$. So, the stock persists at the globally attracting steady state biomass,

$$x_\infty = \frac{1}{\beta(1-a)}\left(\frac{(1-a)(\alpha+1-m)-1}{1-(1-a)(1-m)}\right),$$

and the corresponding steady state TAC is

$$y_\infty = \frac{a}{\beta(1-a)}\left(\frac{(1-a)(\alpha+1-m)-1}{1-(1-a)(1-m)}\right).$$

For example, if we let

$$\alpha = 3, \quad \beta = 1, \quad m = 0.223 \quad \text{and} \quad a \in (0,1),$$

then $a_{cr} = 0.735$. Fig. 3 shows that the steady state biomass, x_∞, declines gradually to zero with increasing levels of harvesting. However, in Fig. 4 the corresponding steady state TAC first increases to a maximum before it declines continuously to zero at $a = a_{cr}$ so that the maximum sustainable TAC is achieved at an intermediate value of a.

A CPP regulated fishery that exhibits compensatory dynamics and no Allee effects leads to continuous relationships between the steady state biomass, catch and harvest rates (see Figs. 3 and 4). Such continuous relationships are known to be useful in actual fisheries as they make it relatively easy to recognize when the fishery is being overharvested, and to remedy the situation by reducing the harvest rate to that yielding maximum sustainable TAC levels [4].

3.2. Allee effect and compensatory stock dynamics

To include the Allee effect in Model (5), we assume that whenever

$$0 < a < a_{cr} = \frac{(\max_x g(x)) - m}{1 - m + (\max_x g(x))},$$

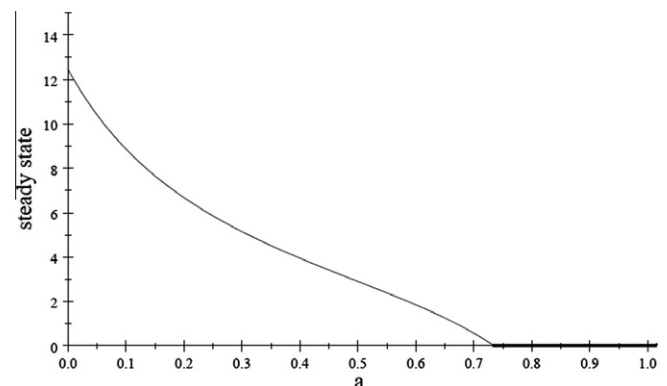then the effective density-dependent per-capita growth rate,

Fig. 3. The steady state biomass decreases continuously to zero with increasing levels of harvesting.
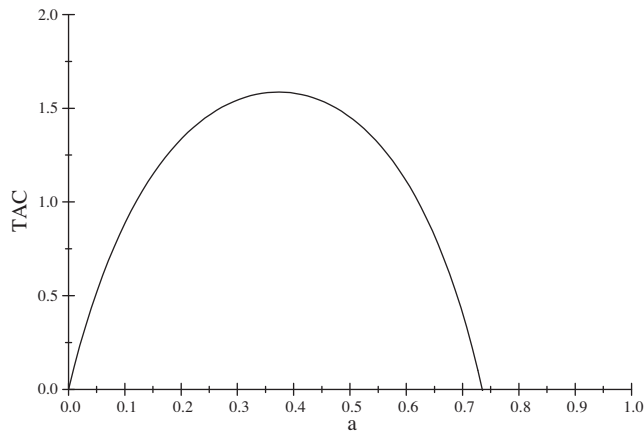
Fig. 4. TAC first increases to a maximum before it declines to zero with increasing values of a.

$$\frac{G(x)}{x} = (1-a)(1-m+g((1-a)x)),$$

increases continuously from positive values smaller than 1 to a maximum value greater than 1 and then decreases continuously to positive values smaller than 1 as the stock size is further increased.

By our assumptions, when $a < a_{cr}$ then G has two positive fixed points, the Allee threshold x_∞^A and a positive steady state $x_\infty > x_\infty^A$. All initial population sizes in the interval $[0, x_\infty^A)$ converge to $\{0\}$ under G iterations. Furthermore, we assume that all positive initial population sizes greater than x_∞^A converge *monotonically* to the attracting steady state biomass x_∞. Our assumptions guarantee a strong Allee effect and compensatory dynamics in Model (5) whenever the harvesting rate is below the critical value a_{cr}.

In the presence of the Allee effect, whenever the harvesting rate $a > a_{cr}$, then

$$\frac{G(x)}{x} < 1$$

for all $x > 0$ and the steady state biomass and TAC both collapse to zero. However, whenever the harvesting rate $a < a_{cr}$, then there is persistence of the fish population at high initial stock levels.

Example 2. To study the relationship between the steady state biomass, TAC and harvest rates in the presence of the Allee effect, we adopt the modified Beverton–Holt form for the stock recruitment function and let

$$G(x) = (1-a)x\left(1 - m + \frac{\alpha(1-a)x}{1+\beta(1-a)^2 x^2}\right).$$

Then the critical harvesting rate is

$$a_{cr} = \frac{\alpha - 2m\sqrt{\beta}}{\alpha + 2(1-m)\sqrt{\beta}},$$

the Allee threshold is

$$x_\infty^A = \frac{\alpha(1-a) - \sqrt{\alpha^2(1-a)^2 - 4\beta(1-(1-a)(1-m))^2}}{2\beta(1-a)(1-(1-a)(1-m))},$$

the positive steady state biomass is

$$x_\infty = \frac{\alpha(1-a) + \sqrt{\alpha^2(1-a)^2 - 4\beta(1-(1-a)(1-m))^2}}{2\beta(1-a)(1-(1-a)(1-m))},$$

and the corresponding steady state TAC is

$$y_\infty = \frac{a\left(\alpha(1-a) + \sqrt{\alpha^2(1-a)^2 - 4\beta(1-(1-a)(1-m))^2}\right)}{2\beta(1-a)(1-(1-a)(1-m))}.$$

When $a > a_{cr}$, then the stock size and TAC decline to zero. Furthermore, when $a < a_{cr}$ the stock and TAC collapse to zero for any initial stock size smaller than x_∞^A. However, when $0 < a < a_{cr}$, then for initial population sizes greater than x_∞^A the stock persists on the steady state biomass x_∞ and corresponding TAC $y_\infty = ax_\infty > 0$.

If $0 < a < a_{cr}$, then G has two positive fixed points, x_∞^A and x_∞. If $a = a_{cr}$, then $x_\infty^A = x_\infty$ and G has *only* one positive fixed point. G has *no* positive fixed points whenever $a > a_{cr}$. That is, in the presence of the Allee effect and compensatory stock dynamics, the steady state biomass and corresponding TAC exhibit a discontinuity at $a = a_{cr}$. The positive steady state and corresponding steady state TAC suddenly collapse to zero as a exceeds a_{cr}. We summarize this in the following result.

Theorem 1.

$$G(x) \equiv G(x, a) = (1-a)x\left(1 - m + \frac{\alpha(1-a)x}{1+\beta(1-a)^2 x^2}\right)$$

exhibits a fold bifurcation at

$$a = \frac{\alpha - 2m\sqrt{\beta}}{\alpha + 2(1-m)\sqrt{\beta}}.$$

Proof. Let $a = \frac{\alpha - 2m\sqrt{\beta}}{\alpha + 2(1-m)\sqrt{\beta}}$. Then

$$x_\infty^A = \frac{\alpha + 2(1-m)\sqrt{\beta}}{2\beta},$$

$$G\left(\frac{\alpha + 2(1-m)\sqrt{\beta}}{2\beta}, \frac{\alpha - 2m\sqrt{\beta}}{\alpha + 2(1-m)\sqrt{\beta}}\right) = \frac{\alpha + 2(1-m)\sqrt{\beta}}{2\beta},$$

and

$$\mu = G_x\left(\frac{\alpha + 2(1-m)\sqrt{\beta}}{2\beta}, \frac{\alpha - 2m\sqrt{\beta}}{\alpha + 2(1-m)\sqrt{\beta}}\right) = 1.$$

Now, apply the Fold Bifurcation Theorem to obtain the result [15,31].

Sudden collapse of fishery systems due to a small increase in exploitation rates, as predicted by Theorem 1, are also known to occur in continuous-time depensation models as well as discrete-time models with non-overlapping generations [31]. To illustrate this in a specific example of Model (11), we use the same parameter values as in Example 1.

$$\alpha = 3, \quad \beta = 1, \quad m = 0.223 \quad \text{and} \quad a \in (0,1).$$

With this choice of parameters, $a_{cr} = 0.561$. As predicted by Theorem 1, Figs. 5 and 6 show the sudden decline in the steady state biomass and corresponding TAC as a exceeds a_{cr}.

In the presence of the Allee effect and compensatory stock dynamics, a CPP regulated fishery exhibits a discontinuity in the steady state biomass and corresponding steady state TAC at $a = a_{cr}$. This sudden jump to zero in the biomass and corresponding steady state TAC gives little warning of the fishery collapse as harvesting levels gradually increase, and so is relevant to issues of species extinction, conservation, fishery management and stock rehabilitation [4].

3.3. Overcompensatory stock dynamics

To study the effects of CPP and overcompensatory stock dynamics in the absence of the Allee effect, we assume that G is a
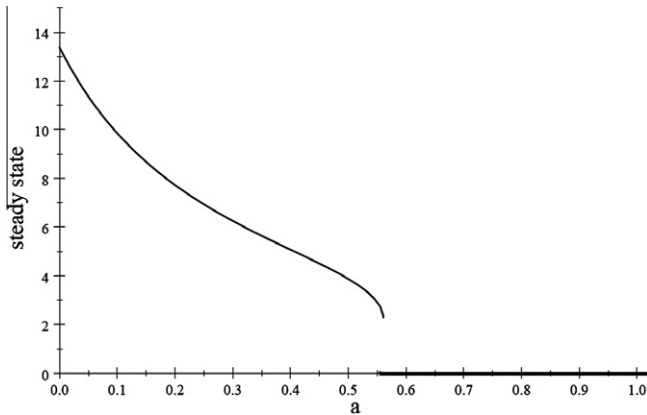
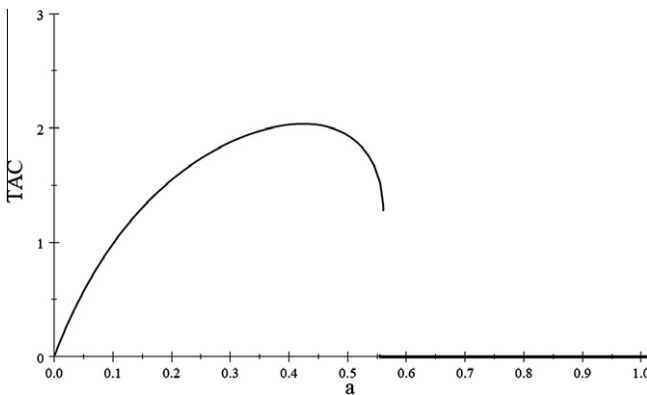**Fig. 5.** The steady state biomass suddenly jumps to zero as a exceeds a_{cr}.

Fig. 6. The TAC suddenly jumps to zero as a exceeds a_{cr}.

one-humped map and the per-capita growth rate in Model (5), g, is overcompensatory. Furthermore, whenever $0 < a < a_{cr} = \frac{g(0)-m}{1+g(0)-m}$, we assume that G has a unique positive fixed point, x_∞. That is, we assume that for all $x > 0$

$$\frac{dg(x)}{dx} < 0$$

and

$$\lim_{x \to \infty} f(x) = 0,$$

whenever

$$0 < a < a_{cr}.$$

Consequently, some positive population sizes "overshoot" x_∞ under G iterations. That is, G exhibits overcompensatory dynamics when the harvesting rate is below the critical value a_{cr}.

By the monotonicity assumption, if $a > a_{cr} = \frac{g(0)-m}{1+g(0)-m} > 0$ then the population size approaches zero for any initial population size. When $a < a_{cr}$, zero is a repelling fixed point and the positive closed interval $[c,d]$ is $G-$ *invariant*, where $c = \min_x\{G[x_\infty, \max_x(G[0,x_\infty])]\}$ and $d = \max_x\{G[0,x_\infty]\}$ Thus, the stock population persists when $0 < a < a_{cr}$.

Unstructured population models with overcompensatory dynamics can exhibit a period-doubling bifurcation route to chaos. In these models, it is possible for the stock to persist on a cyclic or chaotic attractor. Next, we use the Ricker model (overcompensatory dynamics) to illustrate the relationships between the cyclic attractors, TAC and harvest rates.

Example 3. Sockeye salmon (*Oncorhynchus nerka*) stocks of British Columbia provide one of the clearest examples of cycling fish populations (overcompensatory dynamics) [19,20]. In Myers et al. [19], obtained that the Ricker model accounts for the observed sockeye cycles. When we adopt the Ricker form for the stock recruitment function, then

$$G(x) = (1-a)x\left(1-m+\alpha e^{-\beta(1-a)x}\right)$$

and

$$a_{cr} = \frac{\alpha - m}{1 + \alpha - m}.$$

The stock goes extinct when $a > a_{cr}$ whereas it persists when $a < a_{cr}$. Moreover, when

$$\frac{1-(1-a)(1-m)}{1-a} < \alpha < \frac{(1-(1-a)(1-m))}{1-a} e^{\frac{2}{1-(1-a)(1-m)}},$$

then the steady state biomass is

$$x_\infty = \frac{1}{\beta(1-a)} \ln\left(\frac{\alpha(1-a)}{1-(1-a)(1-m)}\right)$$

and the corresponding steady state TAC is

$$y_\infty = \frac{a}{\beta(1-a)} \ln\left(\frac{\alpha(1-a)}{1-(1-a)(1-m)}\right).$$

However, when the intrinsic growth rate α exceeds $\frac{(1-(1-a)(1-m))}{1-a} e^{\frac{2}{1-(1-a)(1-m)}}$, then the steady state biomass and TAC undergo period-doubling bifurcation. To illustrate this in a specific example, we let

$$a = 0.3, \quad m = 0.135, \quad \beta = 1 \quad \text{and} \quad \alpha = e^r \quad \text{where } r \in (4,8).$$

Fig. 7 shows that with this choice of parameters, when $r \in (4, 4.494)$ then Model (5) with the Ricker stock recruitment exhibits a steady state positive fixed point biomass and a positive fixed point TAC. As r is increased past 4.494, the fixed point biomass and fixed point TAC exhibit a period-doubling bifurcation route to chaos. Thus, when $r > 4.94$, the example illustrates cyclic and chaotic attractors for the steady state biomass and corresponding TAC in Model (5) with CPP and overcompensatory stock dynamics.

To investigate the relationship between the cyclic attractors, TAC and harvest rates, we let

$$\beta = 1, \quad \alpha = e^4, \quad m = 0.135 \quad \text{and} \quad a \in (0.3,1).$$

With this choice of parameters, a_{cr} = 0.982 and Fig. 8 shows the gradual decline in the stock biomass and TAC as a exceeds a_{cr}. In addition, Fig. 8 shows a period-doubling bifurcation followed by a
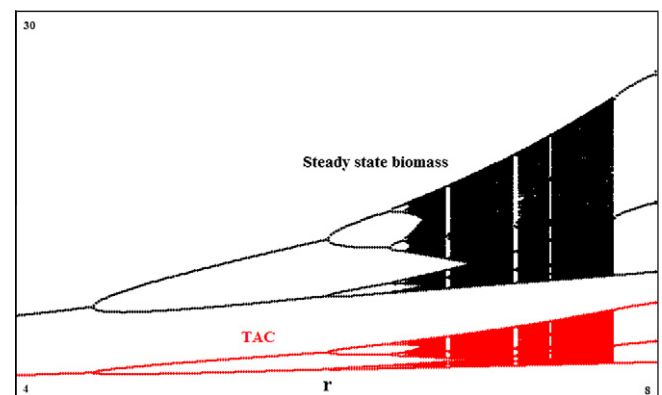

Fig. 7. Steady state biomass (black) and TAC (red) undergo period-doubling bifurcations route chaos as r is varied between 4 and 8. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

period-doubling reversal (bubble bifurcation) in both the stock biomass and TAC as the harvesting rate is varied between 0.3 and 0.982 [27].

As in Figs. 3 and 4, Fig. 8 shows that a CPP regulated fishery that exhibits overcompensatory dynamics and no Allee effect leads to continuous relationships between the steady state biomass, catch and harvest rates.

3.4. Allee effect and overcompensatory stock dynamics

To model overcompensatory dynamics in the presence of the Allee effect, we assume that G is a *one-humped* map and whenever

$$0 < a < a_{cr} = \frac{(\max_x g(x)) - m}{1 - m + (\max_x g(x))},$$

then the effective density-dependent per capita growth rate,

$$\frac{G(x)}{x} = (1-a)(1 - m + g((1-a)x)),$$

increases continuously from positive values smaller than 1 to a maximum value greater than 1 and then decreases continuously to positive values smaller than 1 as the stock size is further increased. Furthermore, we assume that the unique critical point of G is not in the basin of attraction of the origin and

$$\lim_{x \to \infty} f(x) = 0.$$

By our assumptions, when $a < a_{cr}$ then G has two positive fixed points, the Allee threshold x_∞^A and a positive steady state $x_\infty > x_\infty^A$. All initial population sizes in the interval $[0, x_\infty^A)$ converge to $\{0\}$ under G iterations. In addition, when $a < a_{cr}$ we assume that some positive population sizes "overshoot" x_∞ under G iterations and the stock persists for some initial population sizes in the open interval (x_∞^A, ∞). G is a *one-humped* map implies G can exhibit cyclic and chaotic attractors in the presence of the Allee effect. That is, depending on model parameters, positive initial population sizes greater than x_∞^A may converge to an attractor that is fixed, cyclic or chaotic whenever $a < a_{cr}$. The stock collapses and the corresponding TAC decline to zero whenever the harvesting rate $a > a_{cr}$ whereas for high initial population sizes there is persistence on fixed, cyclic or chaotic attractor when $a < a_{cr}$. That is, our assumptions guarantee the Allee effect and overcompensatory dynamics in Model (5) whenever the harvesting rate is below the critical value a_{cr}.

Example 4. To study the relationship between the attractors, TAC and harvest rates in the presence of the Allee effect, we adopt the modified Ricker form for the stock recruitment function and let

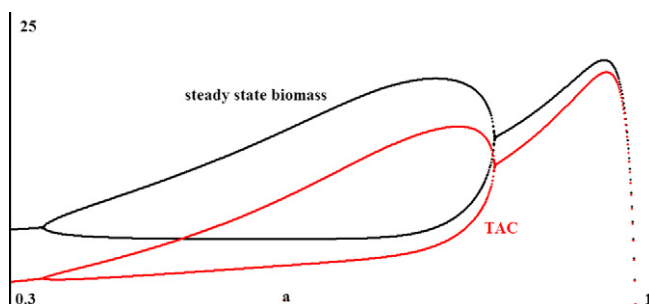$$G(x) = (1-a)x(1 - m + \alpha(1-a)xe^{-\beta(1-a)x}).$$

Fig. 8. Steady state biomass (black) and TAC (red) undergo period-doubling and period-doubling reversal bifurcations before declining smoothly to zero as a is varied between 0.3 and 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Then the critical harvesting rate is

$$a_{cr} = \frac{\alpha - m\beta e}{(1-m)\beta e + \alpha},$$

whenever the unique positive critical point of G is not in the basin of attraction of the origin. If $0 < a < a_{cr}$, then G has two positive fixed points, x_∞^A and x_∞. Typically, the stock persists on a cyclic or chaotic attractor when $0 < a < a_{cr}$. If $a = a_{cr}$, then $x_\infty^A = x_\infty$ and G has *only* one positive fixed point. G has *no* positive fixed points whenever $a > a_{cr}$. That is, independent of initial stock sizes, the stock collapses when $a > a_{cr}$. Therefore, in the presence of the Allee effect and overcompensatory stock dynamics, the stock size and corresponding TAC exhibit a discontinuity at $a = a_{cr}$. The stock size and TAC suddenly collapse to zero as a exceeds a_{cr}. We summarize this in the following result, where for simplicity we let $\beta = 1$.

Theorem 2.

$$G(x) \equiv G(x, a) = (1-a)x(1 - m + \alpha(1-a)xe^{-(1-a)x})$$

exhibits the fold bifurcation at

$$a = \frac{\alpha - me}{(1-m)e + \alpha}.$$

Proof. The proof is similar to that of Theorem 1. As in Theorem 1, let $a_{cr} = \frac{\alpha - me}{(1-m)e + \alpha}$. Then

$$G\left(\frac{1}{1 - a_{cr}}, a_{cr}\right) = \frac{1}{1 - a_{cr}}$$

and

$$\mu = G_x\left(\frac{1}{1 - a_{cr}}, a_{cr}\right) = 1.$$

Now, apply the Fold Bifurcation Theorem to obtain the result [15,31]. □

To use specific model parameters to illustrate the predicted sudden collapse in a CPP regulated fishery that exhibits overcompensatory dynamics in the presence of the Allee mechanism (Theorem 2), we use the same parameter values as in Example 3.

$$\beta = 1, \quad \alpha = e^4, \quad m = 0.135 \quad \text{and} \quad a \in (0, 1).$$

With this choice of parameters, $a_{cr} = 0.952$. As predicted by Theorem 2, Fig. 9 shows the sudden decline in the stock population and TAC as a exceeds a_{cr}.

When an unstructured exploited stock model has the Allee effect, its stock and TAC curves are strikingly different from that of the corresponding model without the depensation effect. In the presence of compensatory and overcompensatory stock dynamics, the Allee mechanism generates a discontinuity at $a = a_{cr}$, with the stock size and TAC suddenly collapsing to zero through a fold bifurcation as a approaches the critical value.

In the one-humped modified Ricker model with an Allee effect, if an initial stock size, x_0, is smaller than the unique positive critical point, x_{cr}, and the constant harvesting rate $a > \bar{a} = \frac{g((1-\bar{a})x_0) - m}{1 - m + g((1-\bar{a})x_0)} > 0$, then the small initial stock size leads to a collapse of the fishery. We summarize this in the following result.

Corollary 1. *Let*

$$G(x) = (1-a)x(1 - m + g((1-a)x),$$

have a unique positive critical point x_{cr}, where
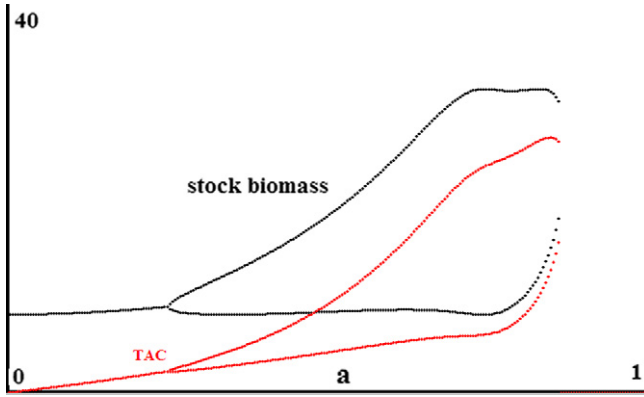
$$g((1-a)x) = \alpha(1-a)xe^{-\beta(1-a)x}.$$

If

Fig. 9. The stock size and corresponding TAC suddenly collapse to zero as a exceeds a_{cr}.

Table 1
Pacific halibut biomass ($\times 10^6$ pounds) and Harvest ($\times 10^6$ pounds) in Gulf of Alaska.

Year	X_t	Y_t	E_t	Year	X_t	Y_t	E_t
1975	90.989	10.6	192	1992	190.776	26.782	69.093
1976	89.339	11.044	154.848	1993	188.782	22.738	58.728
1977	89.484	8.641	141.639	1994	192.548	24.844	72.776
1978	96.987	10.295	132.051	1995	196.91	18.342	44.375
1979	106.831	11.335	131.86	1996	209.634	19.696	42.008
1980	116.954	11.966	101.441	1997	219.196	24.628	53.93
1981	129.693	14.225	100.211	1998	223.962	25.703	57.317
1982	142.881	13.53	79.529	1999	223.847	25.292	58.192
1983	159.637	14.112	58.629	2000	216.138	19.288	43.634
1984	173.717	19.971	37.729	2001	208.928	21.541	46.055
1985	184.207	20.852	40.54	2002	195.243	23.131	45.897
1986	194.695	32.79	66.398	2003	188.546	22.748	46.858
1987	194.991	31.316	65.258	2004	171.794	25.168	52.041
1988	198.127	37.862	78.25	2005	143.105	26.033	58.543
1989	193.12	33.734	77.341	2006	125.32	25.714	63.921
1990	189.684	28.848	84.873	2007	136.344	26.2	64.024
1991	189.582	22.926	75.455	2008	–	–	–

$$0 < x_0 < x_{cr}$$

and

$$a > \bar{a} = \frac{g((1-\bar{a})x_0) - m}{1 - m + g((1-\bar{a})x_0)} > 0,$$

then $\lim_{t \to \infty} G^t(x_0) = 0$ and the stock collapses to zero.

Proof. Since $a > \bar{a} = \frac{g((1-\bar{a})x_0)-m}{1-m+g((1-\bar{a})x_0)} > 0$, we have $(1-\bar{a})(1-m+g((1-\bar{a})x_0) = 1$. Using the fact that g is strictly increasing on $[0, x_{cr})$ and $0 < (1-a)x_0 < (1-\bar{a})x_0 < x_{cr}$, we obtain $g((1-a)x_0) < g((1-\bar{a})x_0)$. Hence,

$$(1-a)(1-m+g((1-a)x_0) < (1-\bar{a})(1-m+g((1-\bar{a})x_0)) = 1.$$

When the harvesting rate is $a > \bar{a}$ and the initial positive stock size is x_0, we have

$$G(x_0) = (1-a)x_0(1-m+g((1-a)x_0) < x_0 < x_{cr}.$$

Furthermore, $(1-a)G(x_0) < (1-a)x_0 < x_{cr}$ imply that $g((1-a)G(x_0)) < g((1-a)x_0)$ and $G^2(x_0) < G(x_0) < x_0$. Proceeding exactly as above, we obtain that the sequence $\{G^t(x_0)\}_{t \geqslant 0}$ decreases to zero.

4. Gulf of Alaska Pacific halibut

The Alaskan Halibut fishery, one of the few success stories in the book on USA fishery management, is currently regulated using a TAC within a system of individual transferable quotas. Ang et al. [1] extracted data from the International Pacific halibut Commission (IPHC) annual reports on the Pacific halibut estimated biomass $x(t)$ and harvest $y(t)$ for the years 1975–2007 in Area 3A of the Gulf of Alaska (see Fig. 1) [5]. The data is given in Table 1.

In Fig. 10, we use the data in Table 1 and $a(t) = \frac{y(t)}{x(t)}$ to obtain a graphical view of how the harvest rate $a(t)$ and stock biomass $x(t)$ change with time.

Next, for each model form $g(x)$ of interest, we use the Akaike Information Criterion (AIC) for the goodness-of-fit. That is, for each $g(x)$, we use χ^2-fitting to find the point estimates of parameter values and then compute the corresponding AIC value to measure the goodness-of-fit. We assume that the underlying errors are normally distributed and independent. Consequently, the likelihood function for each model form $g(x)$ is given by
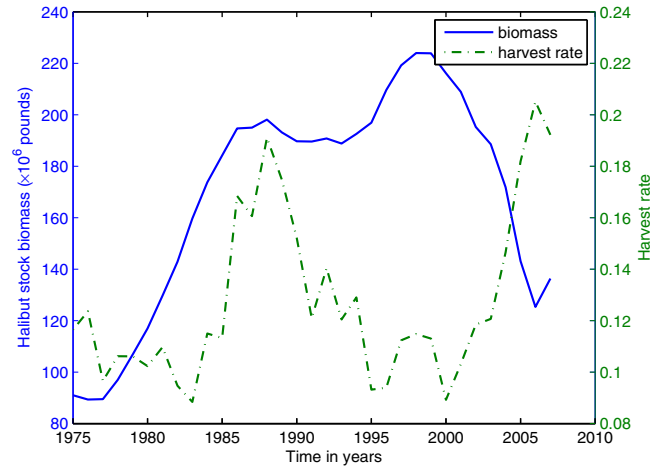

Fig. 10. The halibut harvest rate $a(t)$ (dashed curve) and the halibut observed biomass $x(t)$ (solid curve) versus time t in years.

$$L = \prod_{t=1976}^{2007} \left(\frac{1}{2\pi\sigma_t^2}\right)^{\frac{1}{2}}$$
$$\times \exp\left(-\sum_{t=1976}^{2007} \frac{\{x(t+1) - s(t)(1-m+g(s(t)))\}^2}{2\sigma_t^2}\right).$$

Therefore,

$$\ln L = \ln\left(\frac{1}{2\pi\sigma_t^2}\right)^{\frac{1}{2}} - \frac{1}{2}\sum_{t=1976}^{2007} \frac{\{x(t+1)-s(t)(1-m+g(s(t)))\}^2}{\sigma_t^2} = C - \frac{\chi^2}{2},$$

where C is a constant that is independent of the choice of model form, and

$$\chi^2 = \sum_{t=1976}^{2007} \frac{\{x(t+1) - s(t)(1-m+g(s(t)))\}^2}{\sigma_t^2}.$$

For χ^2-fitting, we seek the values of the model parameters that

Maximize $\ln L = C - \frac{\chi^2}{2}$,

subject to $s(t) = x(t) - y(t)$ and $m = 0.15$.

Furthermore, we assume that the variance in the observed data is directly proportional to the stock size. That is, $\sigma_t = cx(t)$ where c is a proportionality constant. Then the maximization process is equivalent to the following:

Table 2
Parameter estimates for the logistic, Beverton–Holt and Ricker models fit to stock (x) and harvest rate (a) data for the Alaskan halibut Using AIC.

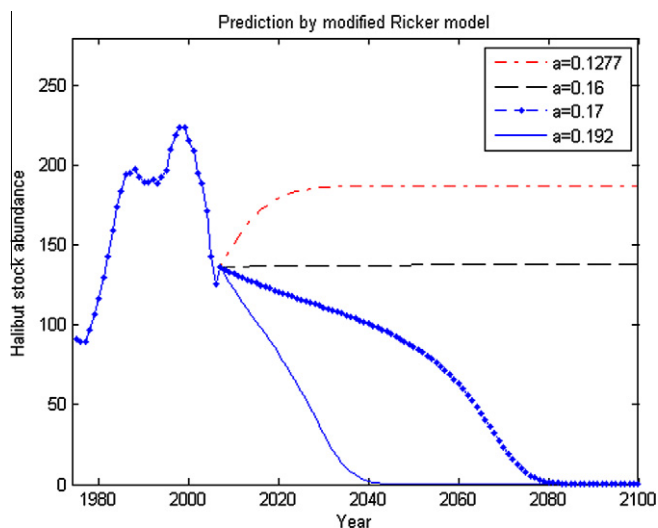| Model	$g(s)$	Parameters	$c^2\chi^2$
1. Beverton–Holt	$\frac{\alpha}{1+\beta s}$	$\alpha = 0.4455,\ \beta = 3.240 \times 10^{-3}$	0.1203
2. Ricker	$\alpha e^{-\beta s}$	$\alpha = 0.4273,\ \beta = 2.343 \times 10^{-3}$	0.1197
3. Modified Beverton–Holt	$\frac{\alpha s}{1+\beta s^2}$	$\alpha = 7.474 \times 10^{-3},$ $\beta = 1.180 \times 10^{-4}$	0.1158
4. Modified Ricker	$\alpha s e^{-\beta s}$	$\alpha = 9.504 \times 10^{-3},$ $\beta = 1.013 \times 10^{-2}$	0.1152
5. Logistic	$r(1-\frac{s}{K})$	$r = 0.4145,\ K = 551.6$	0.1191

Fig. 11. Modified Ricker model predictions of halibut stock size (in millions of pounds) after 2007 at the constant harvest values $a = 0.1277, 0.16, 0.17$ and $a(t) = 0.192$, where $\alpha = 0.0102$ and $\beta = 0.0104$ and initial population size $x(0) \equiv x(2007)$.

$$\text{Minimize} \quad c^2\chi^2 = \sum_{1976}^{2007} \frac{\{x(t+1) - s(t)(1 - m + g(s(t)))\}^2}{x(t+1)^2},$$

subject to $s(t) = x(t) - y(t)$ and $m = 0.15$.

Consequently,

$$AIC = 2k - 2\ln L = 2k - 2C + \chi^2,$$

where $k = 2$ is the number of parameters in each model. Since the same data points are used for each model fit,

$$AIC_{\chi^2} = \chi^2,$$

modulo a constant. By the χ^2-fitting, we obtain that the modified Ricker model has lowest AIC score (see Table 2). That is, the modified Ricker model "best" fits the halibut data with $\alpha = 9.504 \times 10^{-3}$, $\beta = 1.013 \times 10^{-2}$ and $c^2\chi^2 = 0.1152$. These values imply a no-harvest steady state of 286.0 million pounds. This value might be compared to that of Ang et al. [1], who found a carrying capacity of 309 million pounds in 2008.

4.1. Sustainability of Pacific halibut fishery

Using the AIC goodness-of-fit to the standard and modified Beverton–Holt and Ricker models, we obtain that the two models that "best" fit the halibut data are the modified Ricker and the modified Beverton–Holt models. This suggests that halibut population dynamics exhibit the Allee effect, and so the halibut fishery is susceptible to sudden collapse under CPP harvesting strategy at high levels, as shown in Sections 3. In this section, we use the modified Ricker model with point estimates of the parameters $\alpha = 9.504 \times 10^{-3}$ and $\beta = 1.013 \times 10^{-2}$ from Table 2 to predict the long-term population dynamics of the Pacific halibut under different harvesting regimes. In this case, using the modified Ricker model we obtain that $a_{cr} = 0.1633$. That is, the model predicts extinction of the Pacific halibut whenever the harvest rate is higher than a_{cr}.

If the harvest rate is kept constant at the 2007 harvest rate of $a = 0.192 > a_{cr}$, the model predicts halibut extinction by 2050
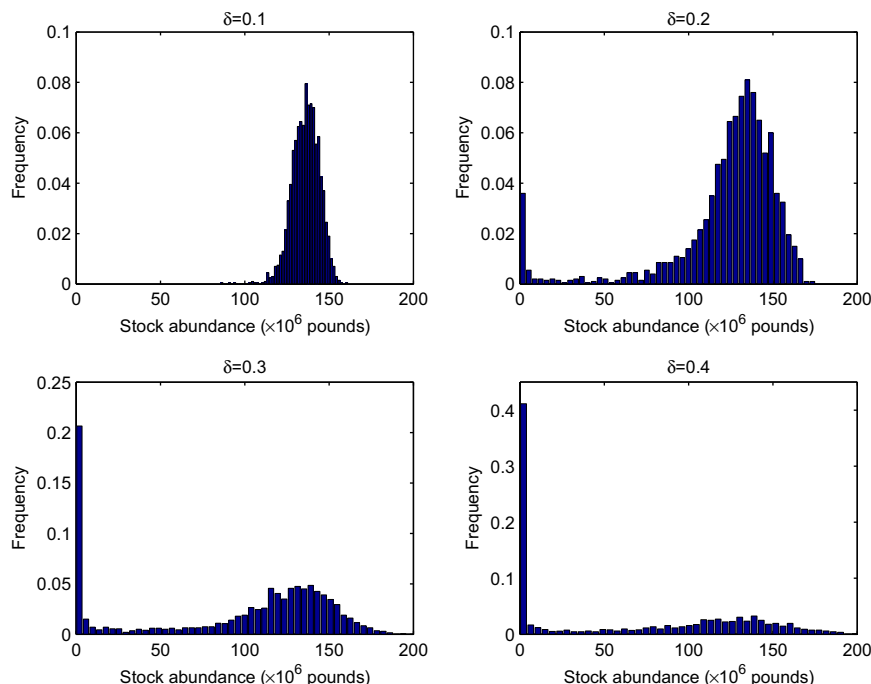

Fig. 12. Stochastic modified Ricker model predictions of halibut stock size (in millions of pounds) in 2100 at the constant harvest value $a = 0.16$, for $\delta \in \{0.1, 0.2, 0.3, 0.4\}$ where $\alpha = 9.504 \times 10^{-3}$ and $\beta = 1.013 \times 10^{-2}$.

(see Fig. 11). To make a model prediction under the recent constant mean harvesting rate, we assume that a_{mean} = 0.1277, where a_{mean} is the mean of the harvest rates from 1976 to 2007 (see Table 1 and Fig. 11). That is, we assume that the TAC, $y(t)$, is directly proportional to the stock size $x(t)$. The modified Ricker model with these parameters predicts persistence of the Pacific halibut with initial population size $x(0) \equiv x(2007) = 136.344 > x_{cr} = 98.72$. However, when the constant harvest rate is changed from $a = 0.1277$ to $a = 0.17$, an increase of 48.8%, then the Pacific halibut population collapses by 2085 (see Fig. 11).

Our analysis suggests that a CPP with mean harvesting levels of the last 30 years are sustainable in the halibut fishery. However, it is important to note that our analysis also indicates that a CPP at maximum recent levels, or at any harvesting level above $a_{cr} = 0.1633$, would lead to collapse of the halibut population.

We now explore the effects of uncertainty and environmental variation on the halibut fishery. We show that under increasing uncertainty, such as the more extreme weather variations predicted by models of global climate change, the otherwise well managed halibut fishery is vulnerable to sudden collapse.

A theoretical approach to understanding stock persistence under uncertainty is to include stochasticity in per-capita growth rate of the population. Consequently, we consider the stochastic modified Ricker model

$$x(t + 1) = (1 - a)x(t)(1 - m + \mathcal{E}(t)\alpha(1 - a)x(t)e^{-\beta(1-a)x(t)}), \qquad (12)$$

where $\mathcal{E}(t)$ is a random variable describing the environmental state. That is, in Model (12) the stochastic per-capita growth rate is $\mathcal{E}(t)\alpha(1 - a)x(t)e^{-\beta(1-a)x(t)}$. For simplicity, we assume that $\mathcal{E}(t)$ has uniform distribution on $(1 - \delta, 1 + \delta)$. That is, $\mathcal{E}(t)$ has mean-preserving spread; $E(\mathcal{E}(t)) = 1$ and $Var(\mathcal{E}(t)) = \frac{\delta^2}{3}$. Model (12), a stochastic model extension, reduces to the deterministic modified Ricker model when $\delta = 0$ and $Var(\mathcal{E}(t)) = 0$. Ellner [8], Benaim and Shreiber [2] and others have studied stochastic discrete-time population models in the absence of the Allee mechanism.

Next, we impose a constant harvesting policy and let $a = 0.16$ so that the deterministic modified Ricker model with $\delta = 0$ ($Var(\mathcal{E}(t)) = 0$), $\alpha = 9.504 \times 10^{-3}$ and $\beta = 1.013 \times 10^{-2}$ predicts persistence of halibut at a steady state halibut biomass of 137.7×10^{6} pounds (see Fig. 12). To link the variance to the probability of persistence under many realizations, we keep all the parameters constant at their current values except the variance parameter δ. For small values of δ, the stochastic model predicts persistence of halibut with probability one in 2100. Fig. 12 shows that, for small values of the variance, many realizations lead to a "bell curve" shape distribution centered around the halibut biomass of 137.7×10^{6} pounds. However, the probability of halibut persistence in 2100 decreases with increasing values of δ (see Fig. 12). When the variance is large enough, halibut goes extinct by 2100 with high probability, while the corresponding deterministic model predicts halibut persistence in 2100 (see Fig. 12).

5. Georges Bank Atlantic cod

Unlike the Alaskan halibut, Georges Bank Atlantic cod stock is overfished. Using the North East Fisheries Science Center (NEFSC) Stock Assessment Report of 2009 [22], we extracted data on the Atlantic cod estimated biomass $x(t)$ and harvest rate a (or h in Table 3) for the years 1978–2008 in the Georges Bank. The data is given in Table 3.

As in Section 4, we use the Akaike Information Criterion (AIC) for the goodness-of-fit. That is, we seek the values of the model parameters that fit the observed values of $x(t + 1)$ in Table 3 and the predicted values given by $s(t)(1 - m + g(s(t)))$, where $s(t) = x(t) - y(t)$ and $m = 0.20$. The NEFSC uses $m = 0.20$ as the

Table 3
Atlantic cod biomass (in metric tons) and harvest rate in Georges Bank.

Year	X_t	h_t	Year	X_t	h_t
1978	72,148	0.18847	1994	21,980	0.282701
1979	73,793	0.149741	1995	17,463	0.199275
1980	74,082	0.219209	1996	18,057	0,18781
1981	92,912	0.176781	1997	22,681	0.193574
1982	82,323	0.282033	1998	20,196	0.189526
1983	59,073	0.34528	1999	25,776	0.170108
1984	59,920	0.206545	2000	23,796	0.156601
1985	48,789	0.338185	2001	19,240	0.281787
1986	70,638	0.147236	2002	16,495	0.252869
1987	67,462	0.19757	2003	12,167	0.255417
1988	68,702	0.231541	2004	21,104	0.081034
1989	61,191	0.208597	2005	18,871	0.0873972
1990	49,599	0.335648	2006	21,241	0.0819517
1991	46,266	0.295344	2007	22,962	0.105181
1992	34,877	0.331848	2008	21,848	unknown
1993	28,827	0.350394	2009	–	–

current "working value" of the natural mortality of Atlantic cod. We use the values of a given in Table 3.

As in Table 2, we summarize in Table 4 the estimates of the parameter values that fit the standard and modified forms of the Beverton–Holt and Ricker models. From Table 4, in contrast to that the halibut data, the two models that "best" fit the cod data are the logistic and Ricker models with no Allee effect, suggesting that unlike Pacific halibut fishery, the Atlantic cod fishery is not susceptible to sudden collapse under CPP harvesting policy. The

Table 4
Parameter estimates for the logistics, Beverton–Holt and Ricker models fit to stock (x) and harvest rate (a) data for Georges Bank Cod.

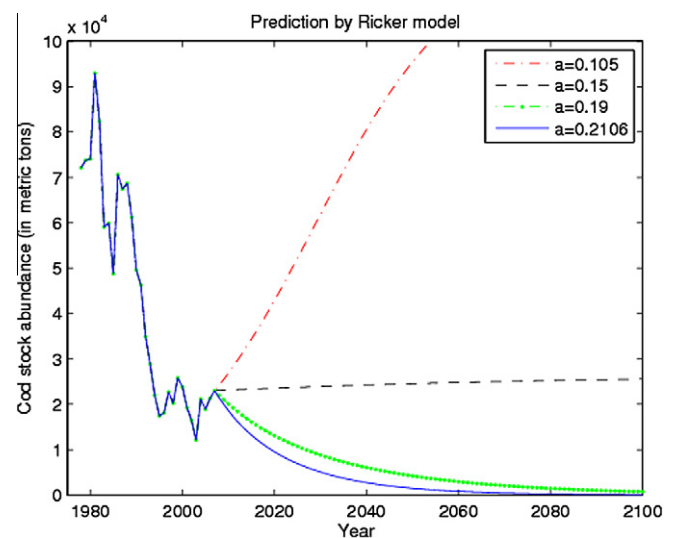| Model	$g(s)$	Parameters	$c^2\chi^2$
1. Beverton–Holt	$\frac{\alpha}{1+\beta s}$	$\alpha = 0.3949$ and $\beta = 2.179 \times 10^{-6}$	1.00362
2. Ricker	$\alpha e^{-\beta s}$	$\alpha = 0.3940$ and $\beta = 2.014 \times 10^{-6}$	1.00360
3. Modified Beverton–Holt	$\frac{\alpha s}{1+\beta s^2}$	$\alpha = 2.860 \times 10^{-5}$ and $\beta = 1.141 \times 10^{-6}$	1.06790
4. Modified Ricker	$\alpha s e^{-\beta s}$	$\alpha = 3.597 \times 10^{-5}$ and $\beta = 3.096 \times 10^{-6}$	1.0594
5. Logistic	$r(1 - \frac{s}{K})$	$r = 0.5999$ and $K = 170014$	1.00356

Fig. 13. The Ricker model predictions of cod stock size (in metric tons) after 2007 at the harvest values $a \in \{0.105, 0.15, 0.19, 0.2106\}$, where $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$ and initial population size $x(0) \equiv x(2008)$.
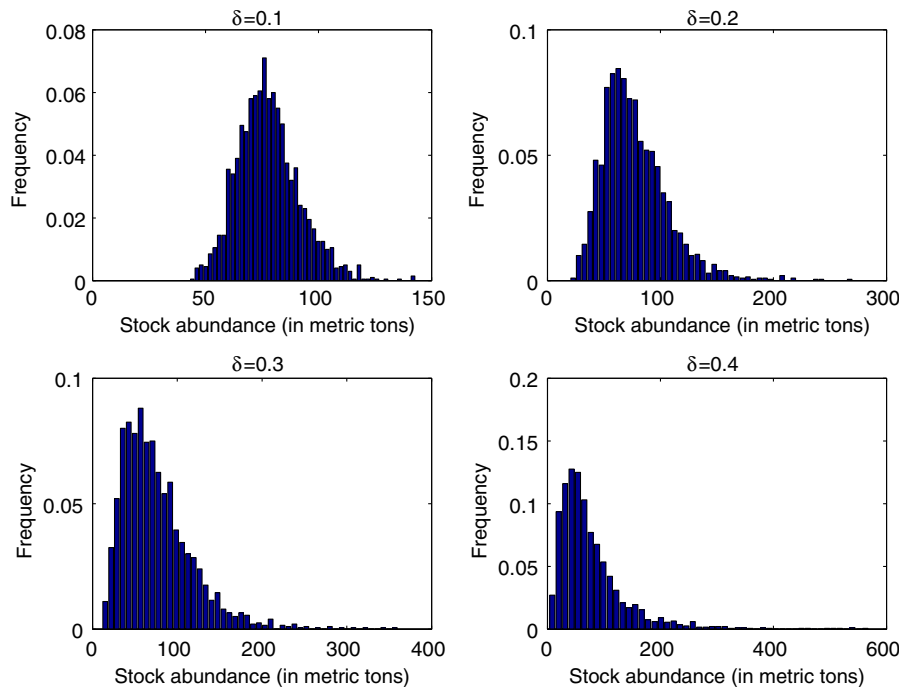
Fig. 14. Stochastic Ricker model predictions of cod stock size (in metric tons) in 2100 at the constant harvest value $a = 0.2106$, for $\delta \in \{0.1, 0.2, 0.3, 0.4\}$ where $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$.

more biologically relevant classic Ricker model with no Allee effect "best" fits the cod data with $\alpha = 3.94 \times 10^{-1}$, $\beta = 2.014 \times 10^{-6}$ and $c^2\chi^2 = 1.360$. These values imply a no-harvest cod steady state of 3.37×10^5 metric tons in Georges Bank.

5.1. Sustainability of Georges Bank Atlantic cod fishery

For over 200 years, the Georges Bank cod fishery enriched New England and the rest of the world. However, the North East Fisheries Science Center announced recently that the cod population of Georges Bank is collapsing [22]. In this section, we use the Ricker model with estimates of the parameters $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$ from Table 4 to assess the long-term performance of Georges Bank Atlantic cod under various constant harvesting parameter regimes.

To make a model prediction under different harvesting levels, we choose four different values of a (see Fig. 13). When $a = a(2007) = 0.1050 < a_{cr} = 0.1961$, the cod population rebounds and persists at a steady state value of 1.2×10^5 metric tons. That is, under the 2007 fishing mortality, the Ricker model predicts persistence of the Georges Bank cod. However, if $a = a_{mean} = 0.2106 > a_{cr}$ and initial population size $x(0) \equiv x(2008)$, then $x(2100) = 78$ metric tons and eventually the Atlantic cod goes extinct; where a_{mean} is the mean of the harvest rates from 1978 to 2007 (see Table 3 and Fig. 13). Thus, with the relatively small stock size in 2008, cod persists when $a \leqslant a_{cr}$ while it decreases gradually to zero as the harvesting values exceed a_{cr} (see Fig. 13).

From Table 3, we see that from 1988 to 1994, the harvesting level was above a_{mean}, and the cod population exhibited rapid decline. From 1995 to 2003, the mean harvesting level was 0.209, approximately equal to a_{mean}, and the stock population did not recover. As illustrated in Fig. 13, harvesting levels must be reduced below a_{cr} if the cod population is to recover, and the recovery is much faster with smaller harvesting levels. Our model provides the ground work for an economic analysis on the choice of

a harvesting strategy that optimizes the cod yield, while ensuring robust recovery of the stock.

As in Model (12), we now use a stochastic extension of the deterministic Ricker model to link environmental variability with probability of persistence under the mean harvesting level a_{mean}. That is, we consider the stochastic Ricker model

$$x(t + 1) = (1 - a_{mean})x(t)(1 - m + \mathcal{E}(t)\alpha(1 - a_{mean})e^{-\beta(1-a_{mean})x(t)}),$$
(13)

where $\alpha = 3.94 \times 10^{-1}$ and $\beta = 2.014 \times 10^{-6}$. Since $E(\mathcal{E}(t)) = 1$, Model (13) reduces to the deterministic Ricker model whenever $\delta = 0$. Recall that when $a = a_{mean}$ and the initial population size $x(0) \equiv x(2008) = 21{,}848$ metric tons, then the deterministic Ricker model predicts an Atlantic cod biomass of 78 metric tons in 2100, which is significantly small compared to the population in 2008. As with the halibut fishery, we now link the variance to the probability of persistence of cod fishery under many realizations. That is, we keep all the parameters of Model (13) constant at their current values except the variance parameter δ. For small values of δ, the stochastic model predicts persistence of cod with probability one in 2100 at the relatively small biomass of 78 metric tons. Fig. 14 shows that, for small values of the variance, many realizations lead to a "bell curve" shape distribution centered around the cod biomass of 78 metric tons in 2100. However, the probability of cod persistence in 2100 at the small biomass decreases with increasing values of δ (see Fig. 14).

6. Conclusion

We have used a discrete-time model without age-structure to assess the performance of a CPP in fisheries that vary in levels of compensation with and without the Allee effect (depensation). When there is no Allee effect, it is known that CPP regulated fishery systems decline to zero gradually under high harvesting levels. However, when the Allee effect is present, the fishery systems

exhibit a sudden decline to zero under high exploitation levels. We use a Fold Bifurcation Theorem to predict the sudden decline in such a fishery when it is managed using a CPP. As in [31], our fishery models illustrate that high fishing levels are capable of stabilizing complex overcompensatory dynamics via period doubling reversal bifurcations.

Using Gulf of Alaska Pacific halibut data from the International Pacific halibut Commission (IPHC) annual reports and Georges Bank Atlantic cod data from the North East Fisheries Science Center (NEFSC) Reference Document 08-15 [5,22], we demonstrate that the modified Ricker model with the Allee effect best fits the Pacific halibut fishery data while the Ricker and logistic models with no Allee effect best fit the Atlantic cod data. Consequently, under high fishing mortalities, the halibut fishery is vulnerable to sudden population collapse while the cod fishery is vulnerable to steady decline to zero. Under harvesting levels from the last 30 years, the CPP did a reasonable job of preventing the collapse of the halibut, but left the Atlantic cod at risk of collapse. Under increased uncertainty, such as more severe weather extremes as predicted by models of global climate change, fisheries managed using CPP may be more susceptible to collapse.

Acknowledgments

References

[1] M. Ang, J.M. Conrad, D. Just, Proportional harvest policies: An application to Pacific halibut Working Paper, Department of Applied Economics and Management, Cornell University, Ithaca, NY, 2009.
[2] M. Benaìm, S.J. Shreiber, Persistence of structured populations in random environments, Theor. Popul. Biol. (2009).
[3] H. Caswell, Matrix Population Models: Construction, Analysis, and Interpretation, second ed., Sinauer Associates, 2000.
[4] C.W. Clark, Mathematical Bioeconomics: The Optimal Management of Renewable Resource, Wiley, New York, 1976.
[5] W.G. Clark, S.R. Hare, Assessment and Management of Pacific Halibut Data, Methods, and Policy, International Pacific Halibut Commission, Scientific Report No. 83, Settle, 2006.
[6] F. Courchamp, L. Berec, J. Gascoigne, Allee Effects in Ecology and Conservation, Oxford University Press, 2009.
[7] J. Eilperin, World's fish supply running out researchers warn, The Washington Post 3 (2006).
[8] S. Ellner, Asymptotic behavior of some stochastic difference equation population models, J. Math. Biol. 19 (1984) 169.
[9] M. Fogarty, Chaos, complexity and community management of fisheries: an appraisal, Marine Policy 19 (1995) 437.
[10] J. Franke, A. Yakubu, Exclusion principles for density dependent discrete pioneer-climax models, J. Math. Anal. Appl. 187 (3) (1994) 1019.
[11] M.S. Fowler, G.D. Ruxton, Population dynamic consequences of Allee effects, J. Theor. Biol. 215 (2002) 39.
[12] E.E. Hackney, J.B. McGraw, Experimental demonstration of an Allee effect in American ginseng, Conserv. Biol. 15 (2001) 129.
[13] M.P. Hassell, J.H. Lawton, R.M. May, Patterns of dynamical behavior in single species populations, J. Anim. Ecol. 45 (1976) 471.
[14] M. Kussaari, I. Saccheri, M. Camara, I. Hanski, Allee effect and population dynamics in the Glanville fritillary butterfly, Oikos 82 (1992) 384.
[15] Y.A. Kuznetsov, Elements of Applied Bifurcation Theorey, Applied Mathematical Sciences, 112, Springer, New York, 1995.
[16] M. Liermann, R. Hilborn, Depensation: evidence, models and implications, Fish Fisheries 2 (2001) 33.
[17] R.M. May, Simple mathematical models with very complicated dynamics, Nature 261 (1977) 459.
[18] R.M. May, Stability and Complexity in Model Ecosystems, Princeton University Press, 1974.
[19] R.A. Myers, N.J. Barrowman, J.A. Hutchinson, A.A. Rosenberg, Population dynamics of exploited fish stocks at low population sizes, Science 269 (1995) 1106.
[20] R.A. Myers, G. Mertz, J.M. Bridson, M.J. Bradford, Simple dynamics underlie sockeye salmon (Oncorhynchus nerka) cycles, Can. J. Fish. Aquat. Sci. 55 (1998) 2355.
[21] A.J. Nicholson, Compensatory reactions of populations to stresses, and their evolutionary significance, Aust. J. Zool. 2 (1954) 1.
[22] Northeast Fisheries Science Center Reference Document 08-15, A Report of the 48th Northeast Regional Stock Assessment Workshop (July 2009).
[23] E. Petersson, T. Jarvi, Both contest and scramble competition affect the growth performance of brown trout, Salmo trutta, parr of wild and of sea-ranched orgins, Environ. Biol. Fishes 59 (2000) 211.
[24] W.E. Ricker, Stock and recruitment, J. Fish. Res. Board Can. II (5) (1954) 559.
[25] S.J. Schreiber, Allee effects, extinctions, and chaotic transients in simple population models, Theor. Popul. Biol 64 (2003) 201.
[26] L. Stone, Period-doubling reversals and chaos in simple ecological models, Nature 365 (1993) 617.
[27] A.W. Stoner, M. Ray-Culp, Evidence for Allee effects in an over-harvested marine gastropod: density dependent mating and egg production, Mar. Ecol. Prog. Ser. 202 (2000) 297.
[28] B. Worm, E.B. Barbier, N. Beaumont, J.E. Duffy, C. Folke, B.S. Halpern, J.B.C. Jackson, H.K. Lotze, F. Micheli, S.R. Palumbi, E. Sala, K.A. Salkoe, J.J. Stachwicz, R. Watson, Impacts of biodiversity loss on ocean ecosystem services, Science 314 (2006) 787.
[29] A. Yakubu, The effects of planting and harvesting endangered species in discrete competitive systems, Math. Biosci. 126 (1995) 1.
[30] A. Yakubu, Two-habitat dispersal-linked compensatory–overcompensatory discrete population models, J. Biol. Dynam. 1 (2) (2007) 157.
[31] A. Yakubu, M. Fogarty, Periodic versus constant harvesting of discretely reproducing fish populations, J. Biol. Dynam. 3 (2–3) (2009) 342.
[32] A. Yakubu, M. Fogarty, Spatially discrete metapopulation models with directional dispersal, Math. Biosci. 204 (2006) 68.