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Overlooked biological and economic implications of within-season fishery dynamics

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Abstract

Catch equations relate fisheries catch to initial fish abundance and the applied fishing pressure. Baranov catch equation, often simply referred to as the catch equation, is the commonest one. However, there are exactly three ways of describing seasonal progression of fishing parsimoniously with a single parameter: either catch rate, fishing effort, or fishing mortality is constant, the last being the assumption underlying the Baranov catch equation. These assumptions imply different dynamics, and only in special cases two of these assumptions can hold true simultaneously. Whether this happens is dictated by the concentration profile, i.e. the dependence of average fish density where fishing takes place on total stock abundance. We show that the assumed seasonal progression of fishing and the type of the concentration profile have major implications for fishery dynamics as well as biological and economic consequences of fishing, calling for increased awareness of these overlooked assumptions of fishery dynamics. However, in many cases the Baranov catch equation serves as a good approximation, even when its assumption of constant fishing mortality is violated.

Introduction

Dynamics of closed populations are determined by birth and death rates. In harvested populations, harvesting is a major source of death and must be accounted for. For exploited fish populations, dynamics are typically described at an annual time scale, with some assumptions about when natural and fishing mortality as well as recruitment occurs within a year. Ricker (1940, 1975) distinguished two types of fisheries, "type 1" fisheries where natural mortality occurs during a time of year other than the fishing season, and "type 2" fisheries where natural mortality occurs along with fishing. In modern literature, these are sometimes referred to as the discrete and continuous formulation of the fishing

process, respectively (e.g., Branch 2009). The latter is more commonly assumed in marine fisheries where fishing season is prolonged (although discrete approximations of the continuous formulation are common, see Pope 1972; Schnute 1985). For type 2 fisheries it is usually assumed that natural and fishing mortality rates are constant within a season. In this case, the total catch for one season, as shown by Russian scientist Fedor Baranov almost a century ago (Baranov 1918), is $F/(F + M) \left(1 - e^{-(F+M)}\right) N_0$, where M and F are natural and fishing mortality rates, respectively, and N_0 is population abundance in the beginning of a season. This equation, often referred to as the Baranov catch equation, is a cornerstone of quantitative fisheries science (Quinn 2003). In economics, the same equation is sometimes known as the Beverton-Holt model (Steinshamn 2011), after Beverton and Holt (1957).

Assuming constant fishing mortality rate is mathematically convenient. This was probably the reason why Baranov made that assumption in the first place. However, fishing mortality is a parameter that neither fishermen nor fishery managers can directly observe. It is far from obvious that it will naturally occur that fishing mortality stays approximately constant during a fishing season. Yet this assumption is usually left implicit or only mentioned in passing, and it has rarely been challenged. We are aware of only few notable exceptions. Mertz and Myers (1996) introduced a formulation where seasonal changes in catches determine fishing mortality but where fishing mortality does not appear as a parameter. Xiao (2005) derived generalized catch equations allowing for time-dependent fishing mortality. These formulations permit flexible, data-driven generalizations. In contrast, in a more theoretical approach, Steinshamn (2011) derived a catch equation by assuming that fishing effort within a season is constant. He pointed out that the Baranov catch equation is obtained as a special case in his model. This happens when catch per unit effort is directly proportional to overall abundance, which can apply for a fish population that is uniformly distributed within a fixed area or volume. The implication is that the Baranov catch equation does not hold when the dependence of exploited fish density on total abundance is different from strict proportionality. This is considered to be common (Clark 1990; Hilborn and Walters 1992). Steinshamn's finding casts further doubt on generality of the Baranov catch equation, although we should notice that constant effort within a season is just another specific assumption.

The purpose of this paper is to draw attention to the limitations of the Baranov catch equation and highlight simple, alternative catch equations. We use the word "simple" in a specific, precise sense: a simple model is one with just one parameter to describe seasonal pattern of fishing, just like the Baranov catch equation has. In fact, there are only three such models: one that assumes that mortality rate is constant (the Baranov catch equation itself), one assuming that fishing effort is constant, and one assuming that catch rate is constant. It is not a priori clear which one, if any, of these assumptions should have supremacy over the others. In the end, this can be seen as an empirical question to be decided by data. However, an important issue is whether the choice matters, i.e., can the Baranov catch equation still be a good approximation of fishery systems where constant seasonal catch rate or effort is closer to the truth? As we shall show, the answer depends critically on the shape of the concentration profile (sensu Clark 1990), as Steinshamn (2011) has already shown under more restricted conditions. In the following, we first build our alternative seasonal fishery models from the first principles, before exploring the implications of different assumptions about the control parameter defining the dynamics and the shape of the concentration profile.

Methods

The core of theory of fishing is the relationship between stock abundance and catch, which are linked together through the act of fishing. Fishing is quantified as either fishing mortality or fishing effort, depending on whether one is interested in quantifying the consequences of fishing or in quantifying the amount fishing per se. The latter is interesting in the economic perspective (effort is costly) as well as because fishing effort, or at least proxies of it, is more directly observable than fishing mortality and can be helpful in estimating fishing mortality and stock abundance.

Short-term dynamics

In a short term the relationships between stock abundance, catch and fishing effort are straightforward. Instantaneous catch rate C_t at time t is determined as a function of instantaneous fishing mortality rate F_t and stock abundance N_t,

$$C_t = F_t N_t. \tag{1}$$

Notice that it is not essential for our argument whether N_t here represents abundance at a certain age or an aggregate abundance. N_t can also be interpreted as biomass provided that mean weight of fish is constant during the considered period.

Fishing mortality can be expressed as a product of fishing effort E_t and catchability coefficient q, $F_t = q E_t$. The former characterizes the amount of fishing (input) and the latter the efficiency in which fishing effort translates into fishing mortality; in a structured population model q would also reflect selectivity with respect to age or size. Effort is expressed in units of effort over time (e.g., hours trawled or number of hooks set per day) and catchability in the reciprocal units of effort (e.g., one over hours trawled or number of hooks set). This gives rise to an alternative version of eq. (1),

$$C_t = q E_t N_t. \tag{2}$$

When recruitment is ignored, stock abundance declines as dictated by the differential equation

$$\frac{dN_t}{dt} = -(F_t + M)N_t, \tag{3}$$

where M is the instantaneous natural mortality rate, assumed constant in this paper.

Linking total abundance and local density

The instantaneous relationships above skip the issue that catchability (q), as defined above, is unlikely to be constant over any longer period of time. Equation (2) suggests proportionality between catch rate and abundance, but this is often known to be not true (Clark 1990; Hilborn and Walters 1992; Harley et al. 2001). Schooling species, in particular, can provide high catch rates even when their total abundance is strongly reduced, simply because total stock abundance is a poor predictor of local density. By expressing catch rate as a function of local density, and local density as a function of stock abundance, one can separate the local catching process from the processes that determine local fish density.

Clark (1982, 1990) introduced the concept of concentration profile to describe how the density ρ of fish depends on total stock abundance. More specifically, we follow the definition from Clark (1990) and interpret this density as the local density experienced by fishers, reflecting the highest densities available for fishing. The functional form usually assumed is the power function (Clark 1990):

$$\rho(N) = a\bar{N}^b, \tag{4}$$

where exponent $b \geq 0$ determines the shape of concentration profile (also interpreted as stock elasticity of harvest, see Steinshamn 2011), a is a scaling parameter, and $\bar{N}$ is normalized abundance, such that $\bar{N} \leq 1$. This normalization is necessary for the function to have its intended behaviour, i.e., that increased degree of schooling (lower b) leads to a slower decline in the local density when total abundance declines. A natural choice is to normalize N with respect to carrying capacity K, $\bar{N} = N/K$. Already Clark (1990) used this normalization, without making it explicit. Notice that catch will now be expressed on the same scale as stock abundance. To make this explicit, we denote this normalized catch $\bar{C}$. Simple back-transformation will give results in the original scale (e.g., $C = K\bar{C}$).

The shape of concentration profile depends on behaviour of both the fish and the fishers: the spacing behaviour of fish (i.e., the degree of schooling), and the ability of fishers to find and target fish aggregations. Case $b = 1$ corresponds to strict proportionality of abundance and density, and is obtained when fish are uniformly distributed over a fixed area, immediately redistributing themselves if density somewhere is reduced. Moreover, $b \sim 1$ is also obtained for non-uniform distributions if fishers cannot find or effectively target aggregations, such that the fish distribution is random from their perspective. The limiting case $b = 0$ is obtained when fish are always fully aggregated and fishers can find even the last school, and the effective density stays constant until the moment when the last fish is taken.

Catch as a function of local density

Using the concept of concentration profile, we can derive a more mechanistic model of fishing. At a local scale, as long as there are no gear saturation or interference effects (Ricker 1940; Paloheimo and Dickie 1964), it is reasonable to assume that catch is proportional to effort and to the local fish density:

$$\bar{C}_t = q'E\rho(\bar{N}_t), \tag{5}$$

where q' is a parameter describing the capture efficiency. When concentration profile is given by the power function (4), we obtain

$$\bar{C}_t = \tilde{q}E_t\bar{N}_t^b, \tag{6}$$

where we for simplicity have merged parameters a and q' into $\tilde{q} = aq'$. We term $\tilde{q}$ the local catchability coefficient; its interpretation is similar to the catchability coefficient in eq. 2 but it is defined in terms of local density (instead of total stock abundance).

Models for seasonal fishery dynamics

Eq. 6 is general but not directly helpful because it requires that effort and stock abundance are known. However, by assuming that fishing mortality is constant, it is easy to derive

expressions for stock abundance and effort. However, as we have already emphasized, constant fishing mortality is just one way of describing the seasonal progression of fishery with a single parameter. There are two other options, constant catch rate and constant effort. There are no other one parameter models that would work for general concentration profiles, unless one relaxes one of the underlying assumptions (i.e., that natural mortality, local catchability, and concentration profile shape are constant).

When either catch rate, effort, or fishing mortality is assumed constant, stock abundance and the remaining fishing-related parameters at time t within a season can be calculated as follows. When fishing mortality is constant $(F = F_t)$, $F_t = F = \tilde{q} E_t \bar{N}_t^{b-1}$. $\bar{N}_t$ is known from $\bar{N}_t = \bar{N}_0 e^{-(F+M)t}$. Thus E_t can be solved, $E_t = F/\tilde{q}\bar{N}_t^{b-1}$. For catch rate, the relationship $\bar{C}_t = F\bar{N}_t$ holds. When catch rate is constant $(\bar{C} = \bar{C}_t)$, F_t can be solved from $\bar{C} = F_t \bar{N}_t$, provided that we find $\bar{N}_t$ by solving the differential equation $d\bar{N}/dt = -M\bar{N} - \bar{C}$. This gives $\bar{N}_t = \bar{N}_0 e^{-Mt} - (1 - e^{-Mt})\bar{C}/M$. E_t is obtained from e.g. $\bar{C} = \tilde{q} E_t \bar{N}^b$. When effort is constant $(E = E_t)$, one can find $\bar{N}_t$ by solving the differential equation $d\bar{N}/dt = -M\bar{N} - \bar{C}_t = -M\bar{N} - \tilde{q}E\bar{N}^b$; this task is facilitated when one notices that this non-linear, first-order differential equation is a Bernoulli equation when $b \neq 1$. F_t and $\bar{C}_t$ are obtained similarly as above. The results of these calculations are shown in Table 1.

Often one is primarily interested in the outcome of fishing in the end of a season in terms of stock abundance, total catch and effort, and average fishing mortality. These can be calculated by integrating equations in Table 1 over time. Unfortunately, many of these have no general closed-form solutions, the Baranov catch equation being an important exception. The results are summarized in Table 2.

Table 1: Equations for alternative seasonal catch models at time t.

Variable kept constant	Abundance $\bar{N}_t$	Fishing mortality F_t	Catch rate $\bar{C}_t$	Effort E_t
Fishing mortality $F_t = F$	$\bar{N}_0 e^{-(F+M)t}$	F	$F\bar{N}_0 e^{-(F+M)t}$	$\dfrac{F}{\tilde{q}(\bar{N}_0 e^{-(F+M)t})^{b-1}}$
Catch rate $C_t = C$	$(\bar{N}_0 + \bar{C}/M)e^{-Mt} - \bar{C}/M$	$\dfrac{\bar{C}}{(\bar{N}_0+\bar{C}/M)e^{-Mt}-\bar{C}/M}$	$\bar{C}$	$\dfrac{\bar{C}}{\tilde{q}((\bar{N}_0+\bar{C}/M)e^{-Mt}-\bar{C}/M)^b}$
Effort $E_t = E$ $b \neq 1$	$\left\{\left[\bar{N}_0^{1-b}+\dfrac{\tilde{q}E}{M}\right]e^{-M(1-b)t}-\dfrac{\tilde{q}E}{M}\right\}^{\frac{1}{1-b}}$	$\dfrac{\tilde{q}E}{\left[\bar{N}_0^{1-b}+\frac{\tilde{q}E}{M}\right]e^{-M(1-b)t}-\frac{\tilde{q}E}{M}}$	$\tilde{q}E\left\{\left[\bar{N}_0^{1-b}+\dfrac{\tilde{q}E}{M}\right]e^{-M(1-b)t}-\dfrac{\tilde{q}E}{M}\right\}^{\frac{b}{b-1}}$	E
$b = 1$	$\bar{N}_0 e^{-(\tilde{q}E+M)t}$	$\tilde{q}E$	$\tilde{q}E\bar{N}_0 e^{-(\tilde{q}E+M)t}$	

Table 2: Equations for alternative seasonal catch models: seasonal totals or averages. Where integrals are shown, general closed form solutions do not exist.

Variable kept constant	Average fishing mortality $\mathbb{F}$	Total catch $\mathbb{C}$	Total effort $\mathbb{E}$
Fishing mortality			
$b \neq 1$	F	$\dfrac{F}{F+M}\left(1-e^{-(F+M)T}\right)\bar{N}_0$	$\dfrac{F\bar{N}_0^{1-b}(e^{-(F+M)(1-b)T}-1)}{\tilde{q}(F+M)(b-1)}$
$b = 1$			$FT/\tilde{q}$
Catch rate	$\int F_t dt/T$	$\bar{C}T$	$\int E_t dt$
Effort			
$b \neq 1$	$\int F_t dt/T$	$\int \bar{C}_t dt$	ET
$b = 1$	$\tilde{q}E$	$\dfrac{\tilde{q}E}{\tilde{q}E+M}\left(1-e^{-(\tilde{q}E+M)T}\right)\bar{N}_0$	

Bioeconomic implications

The decision to fish is ultimately an economic decision: fishers are only expected to fish when they have a chance to make profit. Economic rent from a fishery operation is defined by the revenues from the catch and the costs of operation, here assumed to scale with fishing effort. A simple model allowing for price that declines with total catch (reflecting price elasticity of demand) is

$$p = p_0 \frac{C_t^{\alpha_p - 1}}{C_0^{\alpha_p}}, \tag{7}$$

where p_0/C_0 is the price per unit catch when $C_t = C_0$, C_0 is a normalization constant (here 1 unit of catch), and exponent α_p measures the dependence of unit price on the total catch. $\alpha_p < 1$ implies that unit prices declines with increasing catches; if $\alpha_p = 1$, unit price is constant at p_0/C_0. Similarly for costs,

$$c = c_0 \frac{E_t^{\alpha_c - 1}}{E_0^{\alpha_c}}, \tag{8}$$

where c_0/E_0 is the cost per unit effort when $E_t = E_0$, E_0 is a normalization constant (here 1 unit of effort), and exponent α_c reflects economies of scale, provided that $\alpha_c < 1$ ($\alpha_c = 1$ results in fixed cost c_0/E_0). Putting these equations together, we obtain for economic rent (profit)

$$P_t = p_0 (C_t/C_0)^{\alpha_p} - c_0 (E_t/E_0)^{\alpha_c}. \tag{9}$$

Results

There are three seasonal fishery dynamics models that use one parameter to parsimoniously describe seasonal pattern of fishing: constant fishing mortality, constant catch rate, and constant effort. From Table 1 we see that assuming constant fishing mortality tends to lead to the simplest and constant effort to the most complex equations describing the dynamics. We illustrate these results through a concrete example. Figure 1 shows seasonal dynamics of abundance, fishing mortality, catch rate, effort, and catch per unit effort for the three alternative assumptions of the constancy defining the dynamics as well as for different values of the concentration profile parameter b. The initial abundance, fishing mortality, catch rate, and effort are set to be identical. However, depending on the assumed constancy, they can take quite different paths later on. The differences are most striking for fishing mortality and effort: fishing mortality can decline during the season (for constant E when $b > 1$), be constant (for constant F by definition, and for constant E when $b = 1$), or increase (for constant C and for constant E when $b < 1$). Similar qualitative differences are obtained for time evolution of effort. On the other hand, catch per unit effort is not much influenced by the assumed constancy, but it is strongly influenced by the concentration profile. The patterns illustrated in this figure are general, but the magnitude of these differences increases with the intensity of fishing.

Some predictions in Figure 1 look unrealistic. For example, it looks unlikely that constant catch rate can be maintained if there is little schooling ($b \sim 1$ or larger) because this would require a large increase in effort. On the other hand, maintaining constant fishing mortality with a schooling stock (low b) would require that effort is gradually
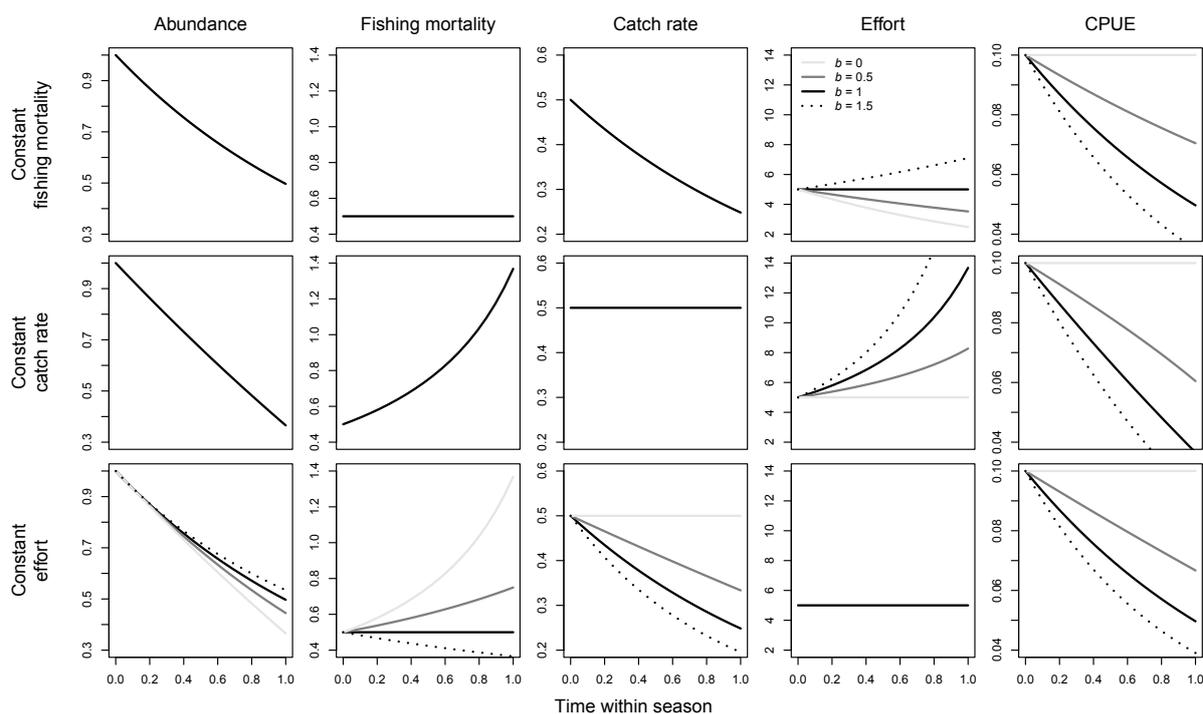
Figure 1: Dynamics of population abundance, fishing mortality, catch rate, effort, and catch-per-unit-effort (CPUE) for alternative assumptions regarding what is constant within a season (fishing mortality, catch rate, or effort) and the shape of the concentration profile (parameter b in eq. 5). Initially the displayed variables are identical for all scenarios but usually diverge during the season. Initial stock abundance $\bar{N}_0 = 1$, natural mortality $M = 0.2$, local catchability $\tilde{q} = 0.1$.
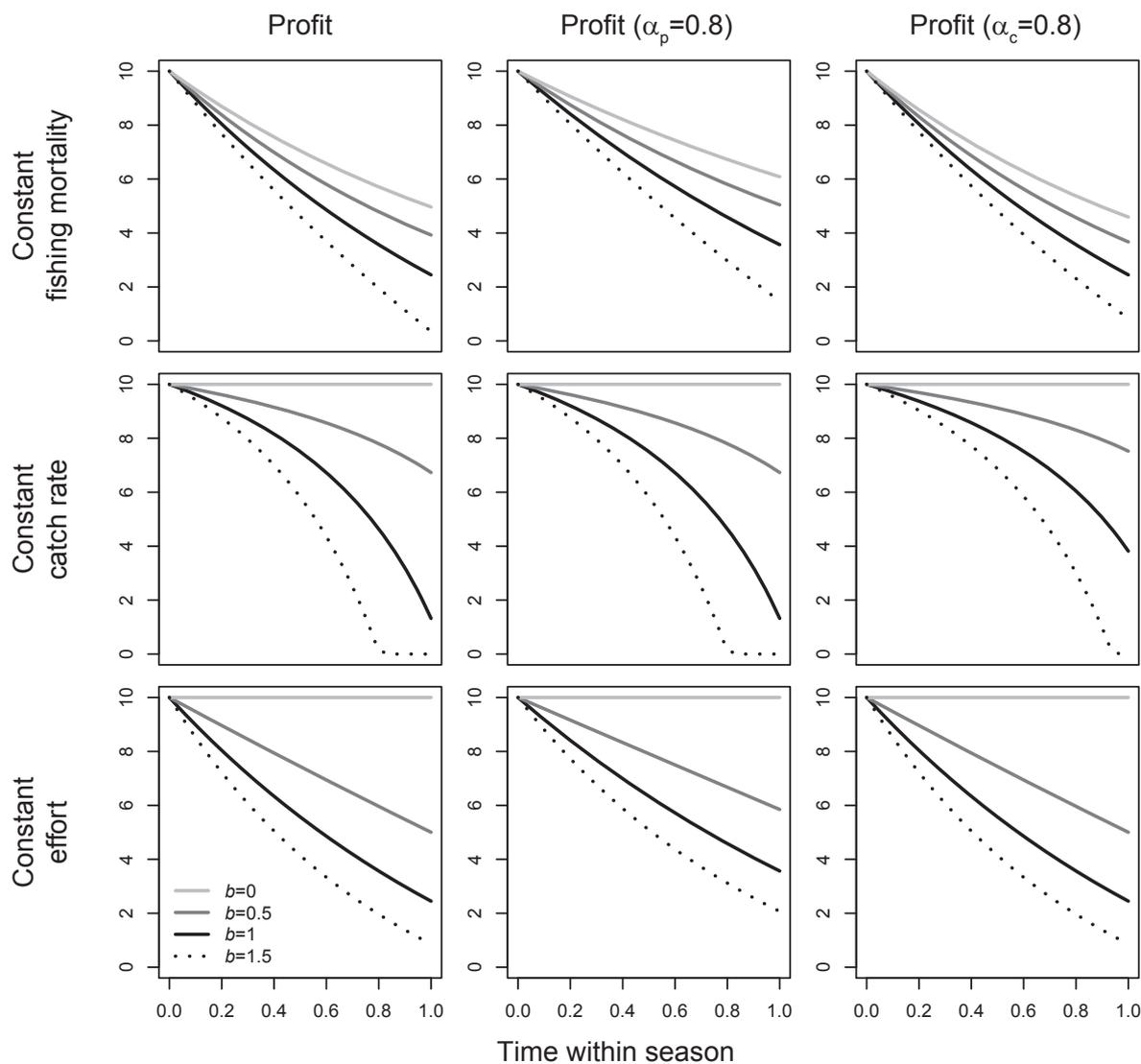
Figure 2: Economic rent (profit) for the scenarios studied in Figure 1 is given in the left column. Constant profit is possible only in the special case of $b = 0$. In the left column, unit price $p_0 = 15$ and unit cost $c_0 = 1$. In the second and third column, respectively endogenous price (increasing catches results in reduced unit price) and economies of scale (fishing operations get more cost-efficient when scaled up) are considered; p_0 and c_0 are rescaled such that the initial revenue and cost are the same as for fixed price and cost. Other parameters as in Figure 1.
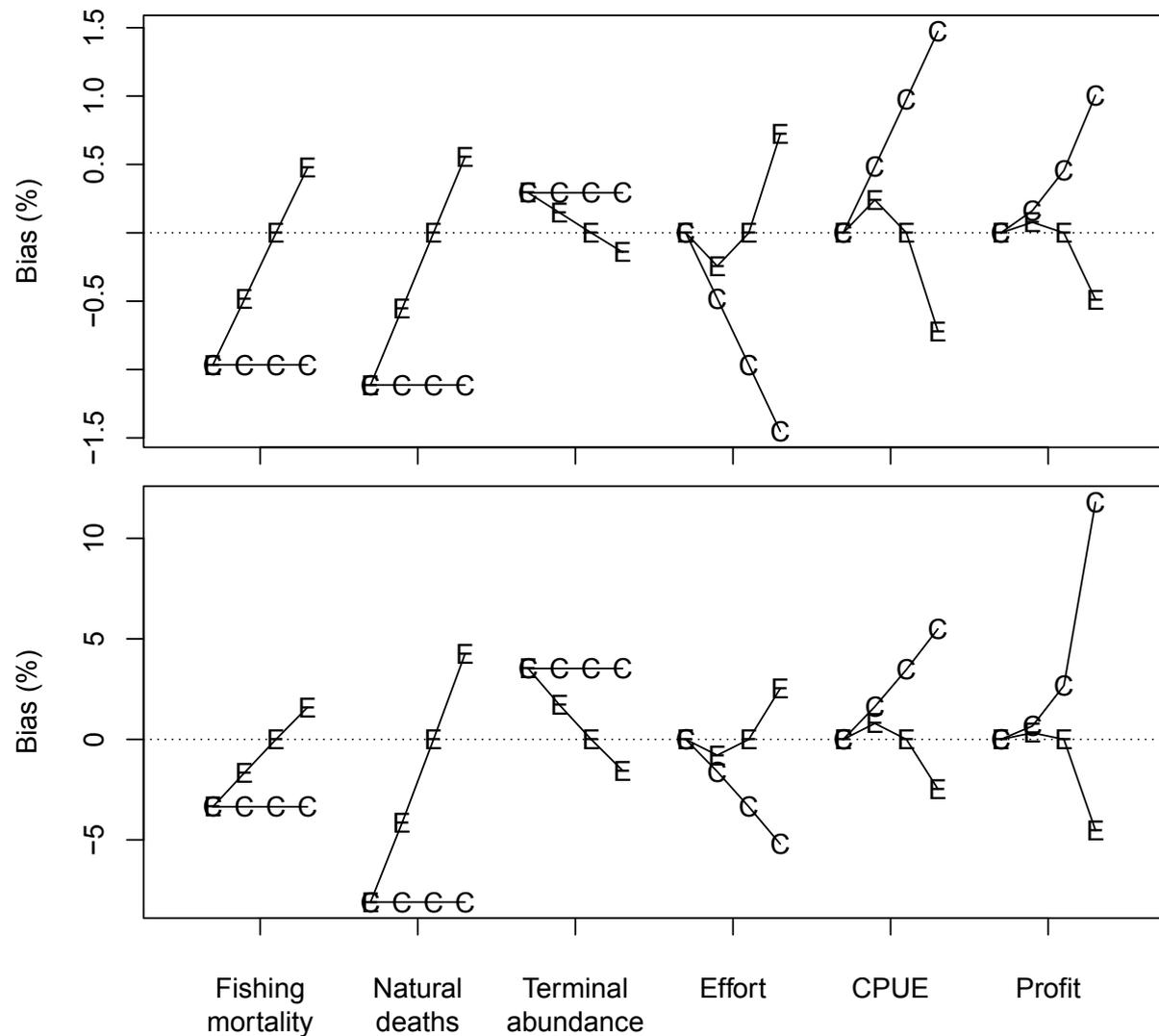
Figure 3: The influence of assuming constant fishing mortality (i.e., the Baranov catch equation) through a season when either catch rate is constant (curves with plot symbol 'C') or fishing effort is constant (curves with 'E'). The influence is expressed as bias relative to the true values obtained when correct assumption on the seasonal pattern is made. Target fishing mortality is low ($F = 0.3$) in the top panel and high ($F = 1$) in the bottom panel. In both panels, four different shapes of the concentration profile (b) are tested (from left to right: 0, 0.5, 1, 1.5). Other parameters: initial stock abundance $\bar{N}_0 = 0.8$, natural mortality $M = 0.2$, local catchability $\tilde{q} = 1$, unit price $p_0 = 5$ and unit cost $c_0 = 1$.

reduced during the season, which seems unlikely to happen given that also catch rate is declining. In such cases, one should consider whether another catch model would better describe the dynamics.

The three seasonal fishery dynamics models can be used to assess the outcomes of a fishery in the end of a season (Table 2). Perhaps the most interesting ones are the catch equations. The expression for the total catch is trivial when constant catch rate is assumed and takes the familiar Baranov form for constant fishing mortality. However, the catch equation becomes very complex for constant effort in all but special cases: the general solution for the total seasonal catch when effort is constant is an infinite, hypergeometric series; simpler solutions exist for some concentration profile parameters b that are rational numbers, but only for $b = 1$ (the Baranov catch equation) and $b = 0$ (which reduces to constant catch rate) the solution is simple enough to have practical appeal.

The economic implications of different seasonal models are illustrated in Figure 2. Typically economic rent declines during the season, reflecting seasonally declining catch rates and/or increasing effort. Economic rent can be constant and positive as a special case for $b = 0$, which allows constant catch rate and effort to be maintained simultaneously. The concentration profile has a strong effect on economic rent. The seasonal decline in economic rent is steeper the less schooling the stock is (i.e., the larger is b). The effect is most drastic for the scenario with constant catch rate. Even for the least sensitive case (constant fishing mortality), the differences are large in the end of the season. In contrast, the patterns are only little influenced by unit price or costs that depend on supply or effort, respectively.

The examples above show that the alternative assumptions on seasonal dynamics, combined with the type concentration profile, can have large impact on development of catch rate, effort, and cash flow during the season. Yet it is not obvious how much these differences might matter in practice. We now look at the case where target level of fishing is expressed through fishing mortality, but fishing is regulated through a catch quota. Initial stock abundance and natural mortality are assumed to be known. Using the Baranov catch equation, it is now possible to predict the stock abundance in the end of the season; similarly, one can calculate how many fish are expected to be eaten by predators. With additional assumptions, total effort and profit can also be calculated. A pertinent question is how much these predictions are biased if effort or catch rate is constant, instead of fishing mortality?

Figure 3 illustrates a number of representative cases. The decisive factor for the magnitude of the bias is how large is the abundance decline during one season. If the decline is modest, then biases will generally be small, often negligible (about 1 % or less). However, if the decline is large, which occurs when either fishing or natural mortality is high, then the biases can become more marked. Also the concentration profile plays a role. When effort is constant, the bias is zero when $b = 1$, changing the sign at this point. When catch rate is constant, parameters related to population dynamics are not influenced by b, but effort and profits are influenced by departures from $b = 0$.

Discussion

In this paper we have shown that the Baranov catch equation is just one of three generic catch equations where the seasonal pattern of fishing is parsimoniously described by one

constant. Mathematically, the Baranov catch equation is the most convenient catch equation, but it is not the one resulting from the most natural assumptions about seasonal pattern of fishing intensity, namely that either fishing effort or catch rate is constant. Only in the special case of fish stocks where local fish density is strictly proportional to stock abundance, assuming constant fishing effort implies constant fishing mortality.

Baranov catch equation is valid whenever fishing mortality is constant. However, it is difficult to envisage a situation in which fishing mortality is constant during a fishing season, except when this occurs as a secondary consequence of the behaviour of fishermen and fish. Our results suggest that one such case, and perhaps the only realistic one, is when effort is constant and fish have a uniform distribution ($b = 1$). While the former assumption may often be reasonable, the latter one is more questionable. Hyperstability ($b < 1$), where catch per unit effort does not decline proportionally with declining abundance, is probably more like a rule rather than an exception (Radovich 1976; Winters and Wheeler 1985; Hilborn and Walters 1992; Harley et al. 2001). Hyperdepletion ($b > 1$), though seldom implicated, is also possible (Hilborn and Walters 1992).

The starting point of Baranov's derivation of the famous catch equation was a body of water where fishing mortality, or 'intensity of fishing' using his own phrasing, was constant (Baranov, 1918). It is almost certain that Baranov assumed constant fishing mortality because it was mathematically convenient, but there might have been more to it: Baranov also assumed a uniformly distributed fish stock, and though his text is not clear about this, it seems plausible that he was thinking that fishing effort was constant.

Alternative catch equations can be derived by assuming that catch rate or fishing effort is constant. The latter was first derived by Steinshamn (2011), although he did not highlight that the decisive feature of his catch equation was the constant fishing effort. A number of mechanisms can lead to near-constant effort. When fishing effort is regulated through licensing or by gear limitations (i.e., numbers of allowed gear) and profitable fishing can be maintained throughout a season, we expect the full fishing capacity to be employed, and within-season effort can be expected to be constant. More in general, in a fishery where input is capacity-limited, constant within-season effort could be expected. Note, however, that constant-effort fishing may imply strongly declining catch rates (Figure 1).

We are not aware of earlier derivations of the catch equation assuming constant catch rate. Constant catch rate is assumed in some bioeconomics models (e.g., Hannesson 2007; Liu and Heino 2013), albeit while assuming "type 1" fisheries (sensu Ricker 1940). Constant catch rate could occur when the market is easily saturated, leading to price drop when output increases. If this drop is strong enough, it acts as an incentive to maintain moderate output. Limitations of storage or processing capacity can also tend to stabilize the output. A quota-regulated fisher might also attempt to spread his total quota evenly across time, so as to maintain steady revenues. Constant catch rate may also be predicated by the regulation. Some fisheries in the European Union are managed through monthly catch quotas that are constant or near-constant (Goodlad 2005; Marine Management Organisation 2013). Many recreational fisheries have daily bag limits, which leads to near-constant catch rate if the bag limit is restrictive and if the numbers of fishers do not vary too much (e.g., Cockcroft et al. 2002; Beard et al. 2003). Note that in non-schooling species constant catch rate may require strong increases in effort (Figure 1).

Using the Baranov catch equation when its assumptions are not met has practical implications. In general, it leads to wrong predictions about:

- *Biological effects of exploitation.* The stock in the end of season and the numbers that perish from predation are systematically biased relative to the predictions. Importantly, the terminal abundance is almost always overestimated, and the natural deaths are almost always underestimated.

- *Socio-economic effects of exploitation.* Total effort and total profit are systematically biased relative to the predictions. Especially if $b > 1$, predicted effort and profit can become seriously biased.

In a system where total catch is controlled, using a wrong catch equation results in misestimation of the stock left behind and the effort used. Similarly, in a system where total effort is controlled, using a wrong catch equation results in misestimation of the stock left behind and the total catch. Fortunately, the magnitude of the resulting biases is quite small unless fishing mortality is high, such that fishing causes a significant decline in stock abundance during the fishing season. Also high natural mortality aggravates the biases. This suggests that using the correct catch equation is most important for short-lived species with naturally high mortality, or for stocks that are very intensively exploited. Small pelagic species can satisfy both criteria, moreover, they are often schooling which implies that the Baranov catch equation is unlikely to describe their fishery dynamics well.

Of course, catch equations are always 'wrong', yet they may be useful approximations of reality. What are the options if the Baranov catch equation is deemed to offer a poor description of the dynamics?

- It is possible to formulate catch equations that allow for complex time-dependency of fishing and natural mortality (Mertz and Myers 1996; Xiao 2005). However, this approach implies much increased complexity (i.e., more parameters) and may often be impractical.

- Another solution is to split fishing season into shorter periods within which constant fishing mortality can be assumed (e.g., Xiao 2005). Again, this implies that the model has to deal with a larger number of parameters.

- Alternatively, if model complexity is not to be increased, assuming constant catch rate or constant effort could be more realistic. The resulting catch equations have one parameter describing the seasonal pattern of fishing, as also the Baranov catch equation does.

Of the three simple alternative assumptions about seasonal progression of fishing, constant seasonal effort or catch rate are the more realistic ones. The Baranov catch equation may imply unrealistic seasonal patterns of fishing effort. It is unfortunate that the more realistic catch equations do not generally take a simple form. Instead, numeric integration may be needed. This is not a serious restriction, but it would be unrealistic to expect that the Baranov catch equation will be seriously challenged in the future. Fortunately, our results suggest that despite the conceptual importance of alternative catch equations, in many situations the practical implications of this distinction are minor: the Baranov catch equation can be a reasonable approximation of systems even when its assumption about constant fishing mortality is violated. An important exception occurs when natural mortality is high or fishing mortality is high. We call for greater awareness

of the specific assumptions of this cornerstone of quantitative fisheries science, and greater readiness to consider alternative catch equations.

Acknowledgements

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