Inherent bias in using aggregate CPUE to characterize abundance of fish species assemblages

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ABSTRACT

We have analyzed the practice of assessing an assemblage of fish species in a multispecies fishery on the basis of aggregate catch per unit effort (CPUE), which is the summed catch of all species per unit of effort. We show that at the onset of fishing or of a large positive or negative change in fishing effort, aggregate CPUE will be hyper-responsive, that is, relative change of aggregate CPUE will be greater than that of aggregate abundance. We also show that as the fishery reaches equilibrium, the aggregate CPUE in most circumstances will continue to be hyper-responsive, with a greater relative change from its value at the start than the aggregate abundance. However, there are less likely circumstances in which the aggregate CPUE will be hyper-stable compared to aggregate abundance. The circumstances leading to hyper-responsiveness or hyper-stability depend on the distribution of productivity and fishery vulnerability parameters among the species in the aggregation.

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1. Introduction

As the demands on fishery management have grown from consideration of a single target species harvested by a single gear to multiple species harvested by multiple gears, the challenge for fish stock assessment has grown commensurately and is evolving into notions of community or ecosystem assessment in which an assemblage of species is assessed in aggregate. A preferable strategy for evaluating the status of a community of species would be to incorporate biological and fishery information on each species into an integrated model of the community. However, in some cases, assessment of individual species and their interactions is not feasible because of the sheer number of species encountered in the fishery or because catches are not reported to species level. This difficulty predates the call for ecosystem assessment and has led to the strategy of treating the composite catch of all species as if it were the catch of a single species, for example, Marten and Polovina (1982), Ralston and Polovina (1982), Agnew et al. (2000), Halls et al. (2005), Lorenzen et al. (2006). Myers and Worm (2003) cite a rapid drop of aggregate catch per unit effort (CPUE) of large pelagic marine predator fishes in many longline fisheries in support of their claim that world-wide populations of large predatory fishes have declined to less than 10% of their abundance prior to the onset of industrial fishing.

In countering Myers' and Worm's (2003) assertion, Hampton et al. (2005) assert that aggregate catch per unit effort cannot be a valid index of aggregate abundance. Furthermore, Maunder et al. (2006) claim that declines in aggregate CPUE tend to exaggerate declines in aggregate abundance. Our purpose here is to show that such a bias exists even in the ideal situation where the CPUEs of individual species are valid indices of their individual abundances.

2. Analysis

In the assessment of single species, CPUE is often taken to be an index of abundance on the assumption that catch is proportional both to abundance and to fishing effort, i.e.

$$C_i = q_i E N_i \tag{1}$$

where C_i is catch of species i, q_i is the proportionality constant, or "catchability", E is effort,[1] and N_i is the abundance, whence it is easy to see that CPUE, C_i/E, would be an index of abundance for species i under the assumptions that catchability is constant in time and

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[1] Note that effort in aggregate CPUE must be identically defined for all species. Therefore, E is not indexed by species. Species specific aspects of the gear are relegated to the units of q_i.

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effort is a good measure of the effective magnitude of deployed fishing gear. Both assumptions are questionable unless the effort data have been appropriately standardized to account for variation in effective magnitude of fishing gear and other departures from Eq. (1). But assuming that the data are well standardized and Eq. (1) is true for individual species, we want to examine if the proportionality in (1) still holds for aggregate catch given by

$$C^T = \sum C_i = \sum q_i E N_i \tag{2}$$

and therefore whether aggregate CPUE given by

$$CPUE_A = \frac{C^T}{E}$$

is a valid index of aggregate abundance $N^T = \Sigma N_i$. Eq. (2) can be written analogously to (1) as

$$C^T = (\Sigma q_i p_i) E N^T \tag{3}$$

where $p_i = N_i/N^T$ is the abundance of species i as a proportion of N^T. It is evident that the proportionality holds only if $\Sigma q_i p_i$ is constant, and because the q_i are presumed to be constant, the p_i would also have to be constant, i.e. the distribution of abundance across species would have to remain stable as N^T changes. This would require the proportional rate of change to be the same for all species. We maintain that the only reasonable way this could happen is if the q_i are the same for all species.

Assume a simplified situation in which all species vulnerable to a fishery are at equilibrium with zero fishing effort. Then at a point in time when a level of fishing effort E is applied, the instantaneous rate of change for any species would be simply the catch C_i because all other forces driving the population are at equilibrium. The proportional rate of change for a particular species would then be

$$\frac{C_i}{N_i} q_i E$$

and the only way for it to be the same for all species is if q_i is the same for all i. With time following onset of fishing, forces of growth and mortality other than fishing come into play. It is possible to imagine that these forces would always precisely balance the differing values of q_i in such a way that the distribution of abundances across species would remain constant while aggregate abundance is changing, but such a supposition is extremely fanciful. In the development of industrial fishing it has been noted that the larger fish species have declined faster and sooner than the smaller species (Pauly et al., 1998). This is both because the larger fishes are preferentially targeted and because they tend to have slower production processes than the smaller fishes. It is to be expected that this picture will often be reflected in single gear, multiple species fisheries where the larger species would initially decline faster than smaller ones because of preferred targeting (and therefore higher catchability), and the lower productivity of the larger species would exacerbate the decline of the larger species.

Thus it is highly unlikely that the proportionality in (3) can be maintained unless catchability across species is constant, which is itself highly unlikely. Therefore, even if the assumptions inherent in Eq. (1) are satisfied, CPUE$_A$ is not expected to be a valid index of aggregate abundance. We are, however, interested in characterizing the biases to be expected if CPUE$_A$ is used as such an index, i.e. whether we expect CPUE$_A$ to exhibit *hyper-depletion* or *hyper-stability* as defined by Hilborn and Walters (1992).

We again envisage a simplified scenario in which a constant level of effort is applied to a hitherto unexploited mix of species and in which, prior to exploitation, all species are at equilibrium abundances which would be their respective carrying capacities.
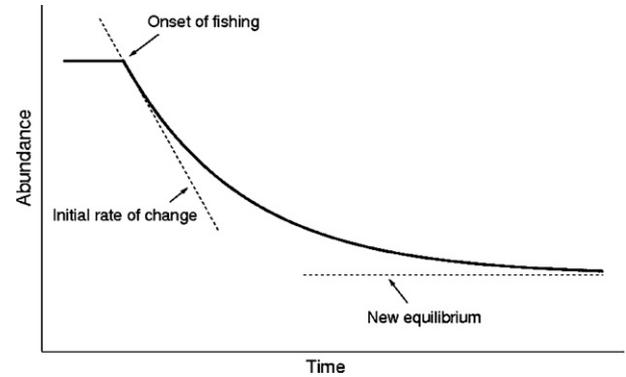

Fig. 1. Simple scenario with transition from equilibrium prior to exploitation to new equilibrium with constant fishing effort.

From the onset of exploitation, the abundance of all vulnerable species will decline toward new equilibrium levels (Fig. 1), as will CPUE$_A$. We investigated two questions mathematically: (1) in the short term, is the initial rate of change in CPUE$_A$ hyper-depleted or hyper-stable in relation to the rate of change in abundance?… and (2) in the long term as the system approaches a new equilibrium, is the equilibrium level of CPUE$_A$ hyper-depleted or hyper-stable in relation to the level of aggregate abundance? We also investigated by simulation the overall hyper-depletion versus hyper-stability throughout a time series from onset of fishing towards a new equilibrium.

3. Initial rate of change

We assume that the population of each species is governed by a very general population dynamic equation

$$\frac{\partial N_i}{\partial t} = P_i(N_i)N_i - C_i = P_i(N_i)N_i - q_i E N_i \tag{4}$$

where $P_i(N_i)$ is a net production function of abundance. The functional form of P is unspecified but has the stricture that net production is zero when abundance of species i is at the carrying capacity K_i, for that species. Furthermore, P can take on different functional forms for different species. From this very general model, we find that the initial decline in CPUE$_A$ in proportion to its level at the onset of exploitation must be steeper than the initial decline in N^T in proportion to its onset level, i.e. CPUE$_A$ exhibits hyper-depletion. The proof is detailed in Appendix A, and numerical examples are shown for a simple two-species case in Fig. 2a and b. Also, in the case where a mix of fish populations is held at some equilibrium level by constant fishing effort and is then subjected to increased effort, Appendix A shows the same result of steeper proportional decline in CPUE$_A$ than in N^T. Furthermore it is shown that when fishing effort is reduced, the recovery of CPUE$_A$ is steeper than that of N^T. Numerical examples are in Fig. 2c and d. It is thus to be expected that fishery driven fluctuations in aggregate CPUE would exaggerate fluctuations in aggregate abundance. Since the exaggeration works in both directions, we could define this property as *hyper-responsiveness*.

4. Equilibrium depletion level

In examining the eventual equilibrium of CPUE$_A$ in relation to the eventual equilibrium abundance with application of constant effort E, we find that the results do not generalize as well as they do for the initial rate of decline. We have found that it is impossible to say with certainty how the aggregate CPUE at equilibrium will relate to aggregate abundance at equilibrium. This is because the
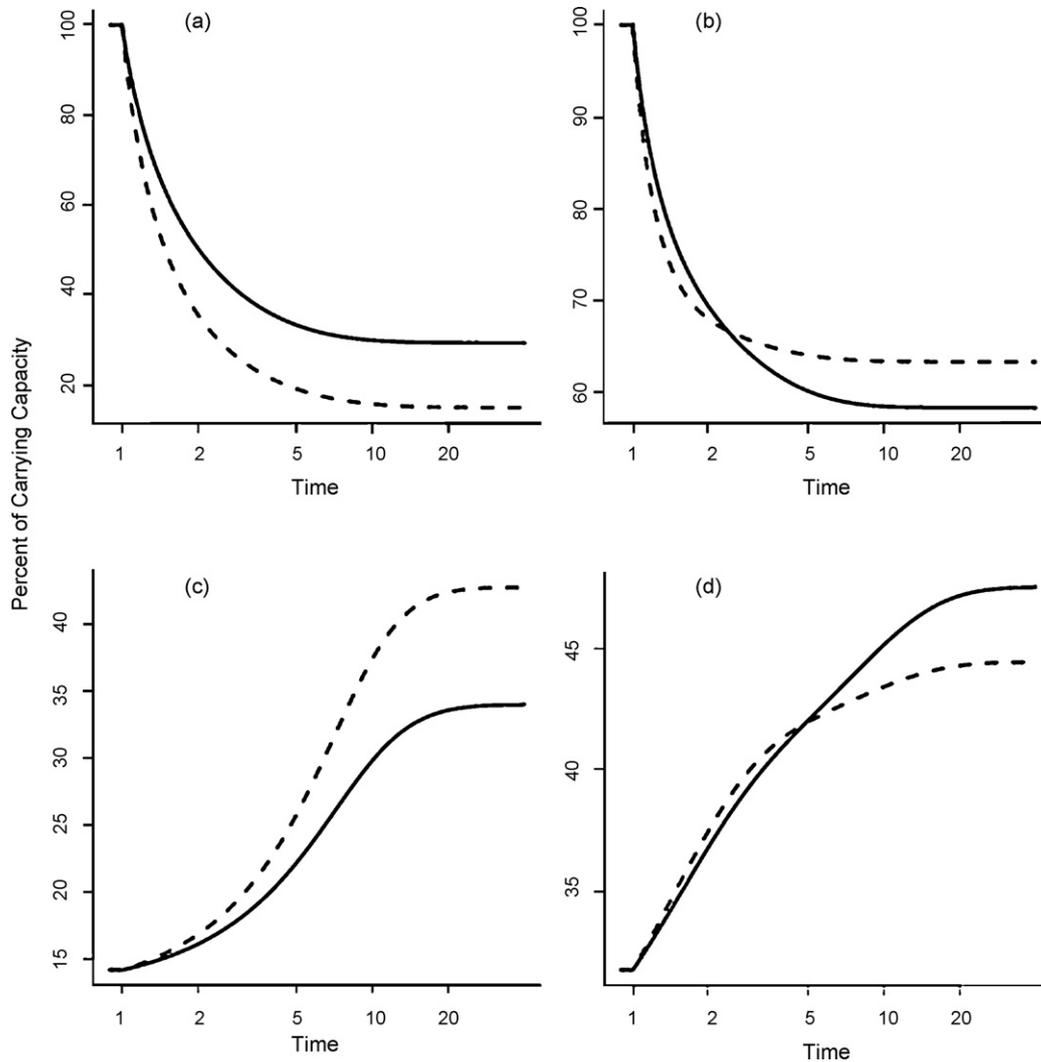
Fig. 2. Cartoon examples of aggregate abundance (solid line) and aggregate CPUE (dashed line) with two species having Schaefer model dynamics with production parameter r_i, carrying capacity K_i, and catchability q_i for each species i. Abundance in percent of carrying capacity. CPUE scaled to match abundance at start. Time scale stretched near onset to reveal differences in initial rate of change. There is no attempt to make these figures quantitatively match any real situation. (a) Start at equilibrium with no fishing and impose fishing effort at time = 1. $r_i/r_j < q_i/q_j$. Hyper-responsive throughout. (b) Same as (a) except $r_i/r_j > q_i/q_j$. Hyper-responsive at onset, eventually hyper-stable. (c) Start at equilibrium at some level of fishing effort and shift to lower level of effort at time = 1. $r_i/r_j < q_i/q_j$. Hyper-responsive throughout. (d) Same as (c) except $r_i/r_j > q_i/q_j$. Hyper-responsive at onset, eventually hyper-stable.

final levels are dependent on the balance between catchability and production. It is possible that N^T would decline to an equivalent or lower relative level than $CPUE_A$ as in Fig. 2b. This would require the steeper initial decline in $CPUE_A$ to be overcome by a particular mix of productivities for the various species. Intuitively this would require that the catchabilities and productivities of the various species be correlated in some way. We were unable to derive mathematical results for the case of the general production function $P_i(N_i)$ as defined above. However, we examined a particular case of the production function

$$P_i(N_i) = r_i \left(1 - \frac{N_i}{K_i} \right)$$

in the familiar Schaefer (1954) model where r_i is the maximal production parameter. It is shown in Appendix B that the relationship between the equilibrium values of $CPUE_A$ and N^T depends on the joint distribution of production parameters (the rs) and catchabilities (the qs). For the $CPUE_A$ to be hyper-stable in relation to N^T as in Fig. 2b and d would require a positive correlation between the

rs and qs plus a higher relative variability in the rs. While such a regime of rs and qs is not impossible, we are not aware of a mechanism by which this would be so. If anything, we expect the opposite to be more likely because larger fish, which tend to have lower rs, are often preferentially targeted and therefore have higher qs. We therefore surmise that a fishery driven decline in aggregate CPUE at equilibrium would most likely be hyper-responsive to aggregate equilibrium abundance, at least for populations with Schaefer-type dynamics.

5. Overall response of aggregate CPUE[2]

As a way to characterize $CPUE_A$ during transition from onset of fishing toward a new equilibrium, we simulated 5000 pairs of

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[2] The analysis in this section made heavy use of R language, in particular the R packages *odesolve* and *rgl* (R Development Core Team, 2008).
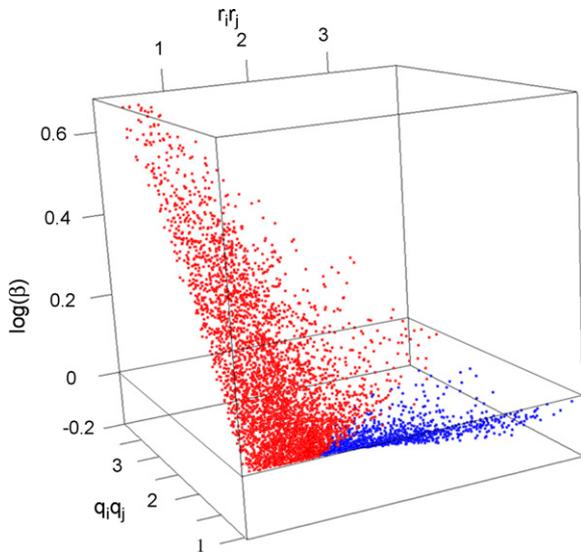
Fig. 3. Response of CPUE$_A$ from 5000 simulated Schaefer model populations following imposition of fishing. log of response parameter, β, plotted as function of q- and r-ratios. Red indicates hyper-responsiveness (i.e. log(β) > 0), and blue indicates hyper-stability (i.e. log(β) < 0). Pairs of q- and r-values were randomly chosen from a uniform [0.1–0.4] distribution.

species having Schaefer population dynamics:

$$\frac{\partial N_i}{\partial t} = r_i \left(1 - \frac{N_i(t)}{K}\right) N_i(t) - C_i; \quad C_i = q_i E N_i(t); \quad i = \{1, 2\}. \quad (5)$$

Carrying capacity K was set to 100 in all cases, and effort E was set to 1. For each species pair $\{r_1, r_2\}$ and $\{q_1, q_2\}$ were given randomly assigned values from a uniform [0.1–0.4] distribution. Equation system (5) was solved for 30 time steps starting at

$$N_i(0) = K; \quad i = \{1, 2\}$$

giving 5000 pairs of r-values and corresponding pairs of q-values from which vectors of aggregate abundance ($X(t) = \sum_1^2 N_i(t)$) and CPUE$_A$ ($Y(t) = \sum_1^2 C_i(t)/E$) were calculated and the coefficient β from the regression

$$\log(Y(t)) = \alpha + \beta \log(X(t))$$

was estimated. If CPUE$_A$ were unbiased, the slope, β, should be 1.0, otherwise, $\beta > 1$ would indicate hyper-responsiveness, and $\beta < 1$ would indicate hyper-stability. Fig. 3 is a 3D plot of log(β) against the q- and r-ratios. To simplify the plot, and taking advantage of the fact that the order of the i and j indices in each species pair was arbitrary, the order of the indices was chosen in each pair so that $q_i > q_j$. Thus the q-ratios are all greater than 1.0 whereas the corresponding r-ratios range above and below 1.0. Fig. 3 shows that hyper-responsiveness occurs where the r-ratios are less than the q-ratios, and hyper-stability occurs in a more restricted area where the r-ratios are greater than the q-ratios. Note that as theory would predict, there is no bias when the q-ratio is 1.0 regardless of the r-ratio. Also bias, as measured by log(β), is much more sensitive to the q-ratio than to the r-ratio. Thus the results for overall response substantially match the theoretical results for the eventual equilibrium state (Appendix B) in that a hyper-responsive bias is to be expected more often than not from a random assortment of rs and qs. Hyper-responsiveness is even more likely considering the expectation that larger fish, which tend to have lower rs, are probably targeted preferentially and therefore have higher qs.

6. Discussion

The analytical results shown here for initial rate of change are more robust than those for final equilibrium level or overall response in that they depend only on a general production function, whereas the other results depend on a particular production function and end up with a certain amount of indeterminacy. All results assume that (1) changes in the abundances of various fish species in the community are driven primarily by direct effects of harvest and not by secondary trophic effects or by other natural forces, (2) nominal effort is an accurate measure of effective effort, (3) the catchabilities do not change with time, (4) the abundances of all species were at equilibrium prior to a change in exploitation, and (5) effort was constant over the time period examined. If these assumptions are violated to a significant extent for some or all the species in the community, then the direction of bias in aggregate CPUE is unpredictable.

In light of the first assumption above, we have expressed our results here in terms of fishery driven changes in abundance. This is not to say that the forces behind changes in abundance can be easily parsed into fishery driven forces and other forces. Nor are violations of the second and third assumptions uncommon. Such violations have the effect of biasing CPUE as an index of single-species abundance and thereby place the suitability of aggregate CPUE as index of aggregate abundance further in doubt. Ideally, a stock assessment for any one species will deal with these issues by allowing for changes in environmental conditions that could affect recruitment and growth as well as changes in fishing gear that could affect catchability and selectivity. Such work needs to incorporate multiple sources of information into appropriately complex stock assessment models and procedures, and cannot be accomplished with simplistic examination of single-species CPUE trends, much less aggregate CPUE trends.

The fourth assumption, that of equilibrium starting conditions, was originally made to simplify the analysis. Further examination showed that the assumption could be relaxed somewhat but that if the system at the start is poised some distance away from equilibrium, then the direction of bias in aggregate CPUE becomes indeterminate. The fifth assumption is unrealistic, but it is likely to only effect the conclusions if there are large fluctuations in effort.

Fig. 2 demonstrates a cartoon model of various kinds of discrepancies between aggregate CPUE and aggregate abundance. To be able to demonstrate these effects in a real-world situation is unlikely partly because any real situation is likely to violate the stipulations above to some degree, also because real fishery data are notoriously error prone, and finally because there are few real examples where an independently known time series of aggregate abundance could serve as ground truth. Nevertheless, the type of bias shown here must be inherent in any interpretation of aggregate CPUE as a measure of abundance.

7. Conclusion

We assert that aggregate CPUE cannot be relied on as an index of aggregate abundance, and that under certain ideal circumstances it has a predictable bias which tends to exaggerate fishery-caused fluctuations in abundance. Aggregate CPUE might be a convenient summarization of events in a fish community, but it is vulnerable to misleading interpretation. At best it would indicate the variations in abundance of those species having predominantly high combinations of abundance and catchability. It is certainly not an appropriate substitute for careful stock assessment of the various species involved, either individually or in an integrated analysis that accounts for differences among species and their interactions.

Appendix A. Initial rate of decline

Assume a mix of species with very general population dynamics given by

$$\frac{\partial N_i}{\partial t} = P_i(N_i)N_i - q_i E N_i; \quad P_i(K_i) = 0 \ \forall \ i \tag{A1}$$

for each species i with symbols defined in the main text and catch given by

$$C_i = q_i E N_i \tag{A2}$$

we wish to show that the initial rate of decline in aggregate CPUE in proportion to its level at the onset of exploitation is steeper than the initial rate of decline in aggregate abundance, N^T, in proportion to its onset level. We assume that equilibrium has prevailed with no fishing and all species are at their respective carrying capacities prior to time $t = 0$ at which point a constant level of effort E is imposed. Thus

$$N_i|_{t=0} = K_i; \quad P_i|_{t=0} = 0; \quad C_i|_{t=0} = q_i E K_i \tag{A3}$$

Defining D_{CPUE_A} as the proportional decline of $CPUE_A$ we have

$$D_{CPUE_A} = \frac{1}{CPUE_A} \frac{\partial(CPUE_A)}{\partial t}\bigg|_{t=0} = -\frac{1}{(\Sigma C_i/E)} \frac{\partial}{\partial t}\left(\frac{\Sigma C_i}{E}\right)\bigg|_{t=0}$$

$$= -\frac{1}{\Sigma C_i} \frac{\partial}{\partial t}(\Sigma C_i)\bigg|_{t=0} \tag{A4}$$

From Eqs. (A1) and (A2)

$$\frac{\partial C_i}{\partial t} = q_i E \frac{\partial}{\partial t} N_i = q_i E[p_i(N_i)N_i - q_i E N_i]$$

and from (A3) we have at time zero

$$\frac{\partial C_i}{\partial t}\bigg|_{t=0} = -q_i^2 E^2 K_i$$

which from Eq. (A4) gives

$$D_{CPUE_A} = \frac{\sum q_i^2 K_i}{\sum q_i K_i} E \tag{A5}$$

For abundance, the proportional rate of decline at time zero is

$$D_N = -\frac{1}{\sum N_i} \frac{\partial}{\partial t}\left(\sum N_i\right)\bigg|_{t=0} = \frac{\sum q_i K_i}{\sum K_i} E \tag{A6}$$

To prove that D_N is always less than D_{CPUE_A} when the catchabilities differ, we show that the opposite premise leads to a falsehood. That opposite premise is

Premise 1 : $\quad D_N \geq D_{CPUE_A} \tag{A7}$

that is, from Eqs. (A5) and (A6)

$$\frac{\sum q_i K_i}{\sum K_i} E \geq \frac{\sum q_i^2 K_i}{\sum q_i K_i} E$$

which, written as follows, can be seen as comparing weighted averages of the q-parameters.

$$\frac{\sum q_i K_i}{\sum K_i} \geq \frac{\sum q_i(q_i K_i)}{\sum q_i K_i} \tag{A8}$$

Because the weights in the right-hand side are positively correlated with the values being averaged it would seem that the right-hand side must be greater, not less, than the left-hand side, which would violate Premise 1. To prove this (A8) can be manipulated to

$$\sum_{i<j} 2q_i q_j K_i K_j \geq \sum_{i<j} (q_i^2 + q_j^2) K_i K_j \tag{A9}$$

wherein each cross product term on the left of the inequality can be paired with a corresponding term on the right. Noting that q_i and q_j are positive numbers and $q_i \neq q_j$ (since catchabilities differ), it is elemental algebra that

$$2q_i q_j < q_i^2 + q_j^2$$

So because K_i and K_j are positive

$$2q_i q_j K_i K_j < (q_i^2 + q_j^2) K_i K_j$$

This is true for all pairs of terms in (A9) and contradicts the sense of the inequality in all cases. Therefore (A9) must be wrong, and since our premise in (A7) has led to a falsehood, it must be wrong as well. So D_N must be less than D_{CPUE_A}. Thus, the rate of decline in aggregate CPUE is necessarily an exaggeration of the rate of decline in aggregate abundance unless catchability is the same for all species.

By very similar analysis to the above, the same results are obtained for rates of decline following a sudden increase in effort applied to populations that had previously been held at equilibrium by a constant effort, $E_0 < E$. In this case, the factor E in Eq. (A5) and following becomes $E - E_0$ and K_i becomes $N_i(0)$, i.e. Premise 1 becomes

$$\frac{\sum q_i N_i(0)}{\sum N_i(0)}(E - E_0) \geq \frac{\sum q_i^2 N_i(0)}{\sum q_i N_i(0)_i}(E - E_0) \tag{A10}$$

which proves to be false by the same reasoning as above. Furthermore, the result must hold in the opposite sense if the population grows following a decrease in effort, i.e. $E_0 > E$. This is because a negative number is now canceled out of (A10), which reverses the sense of the inequality.

Appendix B. Eventual equilibrium

The following results presume that dynamics are given for species i by the Schaefer (1954) model:

$$\frac{\partial N_i}{\partial t} = r_i \left(1 - \frac{N_i}{K_i}\right) N_i - q_i E N_i \tag{B1}$$

where r_i is the maximal production parameter, and K_i is the carrying capacity.

Setting $\partial N_i/\partial t$ to zero in (B1), the eventual equilibrium abundance is

$$\tilde{N} = \sum N_i|_{t\to\infty} = \sum \left(1 - \frac{q_i E}{r_i}\right) K_i \tag{B2}$$

and the eventual equilibrium $CPUE_A$ is

$$\widetilde{CPUE_A} = \sum q_i \left(1 - \frac{q_i E}{r_i}\right) K_i \tag{B3}$$

As before, we will examine $\tilde{N}$ and $\widetilde{CPUE_A}$ in relation to their values at onset, and again we start with a premise, in this case

that under equilibrium conditions aggregate abundance is lower in proportion to its initial level than is the aggregate CPUE

Premise 2 : $\quad \dfrac{\tilde{N}}{\sum K_i} < \dfrac{\widetilde{CPUE_A}}{\sum q_i K_i}$ (B4)

or from Eqs. (B2) and (B3)

$$\frac{\sum(1-(q_iE/r_i))K_i}{\sum K_i} < \frac{\sum q_i(1-(q_iE/r_i))K_i}{\sum q_i K_i}$$

which simplifies to the following inequality

$$\frac{\sum(q_i/r_i)K_i}{\sum K_i} > \frac{\sum(q_i/r_i)(q_iK_i)}{\sum q_i K_i}$$ (B5)

which juxtaposes weighted averages of the ratios of q to r with the same two sets of weighting factors as in the similar inequality (A8) in Appendix A. In that case there is a positive correlation between the weighting factors and the values being averaged which causes the sense of the inequality to be violated. In this case the sense of the inequality in (B5) may be preserved if there is enough positive correlation between the rs and the qs (i.e. negative correlation between $(1/r)$ and q). So we expect the validity of Premise 2 to be indeterminate, which is proven by manipulating (B5) to

$$\sum_{i<j}\left(\frac{1}{r_i}+\frac{1}{r_j}\right)q_iq_jK_iK_j > \sum_{i<j}\left(\frac{q_i^2}{r_i}+\frac{q_j^2}{r_j}\right)K_iK_j$$ (B6)

wherein individual terms in the sum on the left can be paired with corresponding terms on the right. Since we are free to order the indices in (B6) any way we like, we declare them to be ordered by decreasing values of q, that is for every i and j in (B6), $i < j$ and $q_i > q_j$. To examine the sense of inequality for individual paired terms in (B6) we first consider the case where the ratio of rs is greater than the ratio of qs, i.e.

Case 1 : $\quad \dfrac{r_i}{r_j} > \dfrac{q_i}{q_j}$ (B7)

From (B7), and given that $q_i > q_j$, it follows that

$$(q_i - q_j)(r_iq_j - r_jq_i) > 0$$

which leads to

$$\left(\frac{1}{r_i}+\frac{1}{r_j}\right)q_iq_j > \left(\frac{q_i^2}{r_i}+\frac{q_j^2}{r_j}\right)$$

and since the carrying capacities, K, in (B6) are all positive numbers we have for Case 1

$$\frac{r_i}{r_j} > \frac{q_i}{q_j} \Rightarrow \left(\frac{1}{r_i}+\frac{1}{r_j}\right)q_iq_jK_iK_j > \left(\frac{q_i^2}{r_i}+\frac{q_j^2}{r_j}\right)K_iK_j$$

If all pairs of terms in (B6) acted this way, it would confirm the sense of the inequality in (B6) and hence confirm Premise 2 with results like Fig. 2b. However, examination of the alternative case where the r-ratio is less than the q-ratio, i.e.

Case 2 : $\quad \dfrac{r_i}{r_j} < \dfrac{q_i}{q_j}$

leads by similar algebra to the opposite conclusion, namely

$$\frac{r_i}{r_j} < \frac{q_i}{q_j} \Rightarrow \left(\frac{1}{r_i}+\frac{1}{r_j}\right)q_iq_jK_iK_j < \left(\frac{q_i^2}{r_i}+\frac{q_j^2}{r_j}\right)K_iK_j$$

and if all pairs of terms in (B6) acted like that, it would contradict Premise 2 giving results like Fig. 2a.

Thus the truth or falsity of Premise 2 is indeterminate. However, we note that for Premise 2 to be true, the r-ratios in the ordered pairs in (B6) should tend to be greater on average than the q-ratios. Furthermore, all q-ratios must be greater than 1 because of the way we ordered the indices in (B6). In other words,

$$\frac{r_i}{r_j} > \frac{q_i}{q_j} > 1$$ (B8)

should be true more often than not for Premise 2 to be true. This would require the rs to be positively correlated with the qs and the relative variation of the rs to be greater than that of the qs. A random assortment of the rs would violate (B8) more often than not.

Consideration of a case where fishing effort is changed to a level E in a fishery hitherto at equilibrium with constant effort E_0 involves cancelling a factor $(E - E_0)$ in derivation of (B6). This leads to the same findings above with respect to the rs and qs whether the effort increases or decreases, but with the sense of Premise 2 reversed if effort decreases.

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