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ANALYSIS

Unobserved diversity, depletion and irreversibility The importance of subpopulations for management of cod stocks

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ABSTRACT

Diversity is often associated with resilience but in this model, *unobserved* genetic or behavioral diversity can explain the collapse of supposedly regulated fish stocks such as cod. Recent studies have shown the existence of separate sub stocks of cod even at a very fine geographical scale. We show that modeling a group of distinct stocks as if it were one large stock will tend to over-estimate the growth and harvest potential. If quotas are based on such over-estimates, the unobserved stock diversity can explain sudden stock collapses and unexpectedly slow recovery as observed for Canadian cod. It is a lack of information concerning diversity that leads to irreversibility. The differences between the various stocks may be behavioral or genetic but cannot be observed by the fishermen or regulators who believe that there is a gradual decline in one big stock while in fact they are witnessing the successive disappearance of a series of sub stocks.

1. Introduction

There is widespread concern that many fisheries are under severe stress; a comprehensive study showed that many fisheries have experienced serious stock reductions and that many with dramatic declines (50–80% over a 15 year period) failed to recover in the subsequent 5–15 year period, Hutchings (2000). This shows that though over-fishing may be reversible in principle, the time required for recovery can be long. One important example is cod: after years of warnings from biologists, the large fisheries on the great banks off Canada collapsed in 1992. Despite more than a decade of moratorium the cod have failed to come back. According to Svedäng and Bardon 2003, North Sea cod fisheries are also likely on the verge of collapse.

There is considerable evidence that the Canadian cod stock collapse is due to over-fishing rather than environmental factors.[1] The tendency of cod to aggregate and technological progress in finding and catching cod are important underlying factors which also explain why catch per unit effort (CPUE) continued to be high right up until the crash. Fishing effort needs to be limited and experience shows that we must involve fishermen as stakeholders to be able to deal with compliance and monitoring issues. The countries that have given fishermen secure property rights (such as ITQs) have generally had more success in enforcing a reasonable Total Allowable Catch (TAC) and thus avoiding stock depletion.[2]

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[1] Fletcher (2003), Myers et al. (1996), (1997).

[2] See Arnason (1996) and NRC (1999). Note that we are in no way claiming that ITQs lead to full social optimum nor that they lack specific problems of their own (such as severe conflicts over wealth accumulation) but they do appear to have the potential to avoid stock depletion, see also Escapa and Prellezo (2003) on the optimal distribution of harvest rates.

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The purpose of this article is to explore one additional mechanism that contributes to irreversible depletion or at least very slow recovery rates. This mechanism is the existence of separate spawning stocks within what is traditionally treated as one stock. There is an unobserved but biologically important structure of local populations that are either genetically (or perhaps behaviorally) separate which implies that the grand "stock" of cod we analyze is not actually one stock but consists of several stocks with very limited interbreeding. Normally we associate biodiversity with resilience (Perrings and Walker, 1997; Hughes et al., 2005) but in this case the connection is somewhat unexpected. Section 2 summarizes relevant biological literature, Section 3 shows how this structure can be incorporated into simple, standard fishery models and Section 4 analyzes the effect of this unobserved diversity on stock assessments and growth potential in terms of the non-convexity of the production set. Section 5 shows that standard regulation that ignores sub stock diversity can lead to depletion of at least some stock components and thus irreversible change in the total population. Section 6 illustrates this with a number of simulations for various differences in growth and catchability parameters as well as introducing straying and nonlinear catchability. In Section 7 we discuss how policy instruments might be designed based on very partial information on subpopulations. Section 8 concludes.

2. The existence of sub stocks in cod populations

Management of fish stocks relies on stock assessments that are typically carried out for administrative areas that do not generally coincide with population habitats. To take the case of cod, the relevant areas are defined by ICES[3] which has divided the Atlantic into a number of distinct areas which governments and fishery agencies use for managing stocks. For each division, biomass is estimated for commercial species often disaggregated by age groups. Recent research however shows that population structure, genetics and behavior of cod may be extremely complicated and in one limited area such as the Gulf of Maine or the Kattegatt, there is not a single stock, but numerous sub stocks that aggregate and reproduce separately. Thus the "stocks" used for stock assessments are "stocks" merely in an administrative not a biological sense.

The fecundity of many fish, including cod, is so phenomenal that researchers, in the past, thought cod would never be threatened. Evidently they were wrong. There are many factors making stocks vulnerable to depletion and slow recovery if over-fished. One of these is spatial: not all spots are suitable for reproduction. Cod prefer certain types of bottom and water parameters (salinity, oxygen etc.) and have a high degree of philopatry, i.e. they tend to reproduce in the same place they themselves come from. Everyone knows salmon return for spawning to the river they were born. Cod do the same but the spawning grounds are hard to see and thus this has passed unnoticed until recently. There is a small but fairly established literature on this subject, see for instance Ruzzante et al. (1999) for a review.[4] DNA mapping has made it possible to trace genetic differences among subpopulations in detail. Ruzzante et al. (1997) used microsatellite DNA variation to show the similarity between two cod samples and the difference vis-à-vis a third sample off Newfoundland and they also show that such genetic differences between different localities are stable over time. As they point out, these genetic differences can only be maintained as long as the sub stocks are (to a significant extent) separated during reproduction. Ames (2004) uses a variety of historical and biological data to describe the population structure of cod in the Gulf of Maine. A complex picture emerges with populations that reproduce independently of other populations, subpopulations within these that are semi-independent and thus have some, but very limited exchange and spawning components within the populations that have separate spawning grounds. Robichaud and Rose (2004) provide very convincing evidence that different subpopulations have different behaviour ranging from completely sedentary to accurate homing and to dispersal.

Hutchings (1996, 2000) shows how important subpopulation structure can be for a correct interpretation of stocks, when he analyzes the apparent southward movement of Canadian cod (said to be linked to environmental factors) but concludes that this was a miss-representation: the cod did not "move". They did not even consist of a single population but several and the northern sub stocks were more rapidly and severely depleted than the southern ones which created the impression of "movement".

3. Introducing subpopulation structure into fishing models

The exact definition of what constitutes a stock has critical importance since it is the stock size that is the main determinant of growth, and thus potential harvest in our standard fishery models, such as the simple Gordon Schaeffer models (1) and (2).[5]

$$\frac{dX}{dt} = g(X_t) - H_t \tag{1}$$

$$H_t = qE_tX_t \tag{2}$$

In this model, growth depends on stock size[6], X and harvests H. The harvest in turn depends on stocks, effort, E,

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[3] International Council for the Exploration of the Sea, http://www.ices.dk

[4] Other articles include Ames (2004), Frank and Brickman (2000), Knutsen et al. (2003), Lande (1988), Larkin (1977), Mork and Giaever (1999), Smedbol and Stephenson (2001), and Stephenson (1999). Imsland and Jonsdottir (2003) discuss what genetic differences might mean in terms of different growth rates and behaviour for the sub stocks.

[5] X is stock, dX/dt growth in stock, $g(X)$ is the growth function such as the logistic one, H is harvest, q is a catchability coefficient and E is effort. Eq. (2) assumes harvesting is cheaper with higher density of fish, an assumption we will discuss later since it may not hold very well for schooling fish.

[6] With the logistic function $g(X) = rX_t(1 - X_t/K)$ growth first increases (at the intrinsic rate r) with stock size and then declines as carrying capacity K is approached.

and catchability q. If the "stock" really consists of different sub stocks this has profound implications for the model used.[7]

Naturally, fishery boards have more sophisticated models with, amongst other features, size or year classes. We however keep the model as simple as possible to make our point clearer: the effects would carry over to more complex models. For the same reason we need a prototype model for the behavior of fishermen and regulators and again choose the simplest reasonable representation available. We chose the model of open access which although simplified, unfortunately is a rather apt description of many fisheries today. (The model is described in most textbooks on environmental or resource economics, see for instance Sterner 2003, chapter 4). It implies that fishermen (who compete with each other while none of them owns or controls the stock) will continue to fish until the marginal yield is so low that it just covers the short run marginal costs. At this point the fishery is over-fished and the potential resource rents for fishermen have been eroded away.

$$PH - (C + T)E = 0 \tag{3}$$

P is the market price of fish, C, the unit cost of fishing effort and T the policy instrument used by the regulator, for instance, a tax on fishing effort. In the absence of policy ($T=0$), open access effort would be $E=PH/C$. If there had been a sole owner of the resource, the optimal effort $\hat{E}$ selected by that owner would have been much lower — leaving in place a much higher stock with bigger annual growth and lower cost of fishing. A possible (though not necessarily popular!) policy instrument to force the (open-access) fishermen to restrain effort (to get closer to the optimum level) is to set a tax T on effort as in Eq. (3). As we show in Section 5, an optimal tax T^* can be chosen to stop the fishermen from going below a minimum target stock level X^*. Another instrument that is often preferable is to allocate property rights to the stock — usually referred to as Individually Transferable Fishing Quotas (ITQs) that allow the fishermen to land a harvest of suitable size.

We will now consider the effects of genetic diversity in this model: Assume there are n separate sub stocks ($i=1\ldots n$). They are physically so similar they cannot (readily) be distinguished by the regulator or fishermen. They may mix during most of the year, possibly for migration in search of food but the essential characteristic is that they have separate spawning aggregations. They may or may not be genetically differentiated but they have different behavior and therefore possibly different growth rates, r_i, individual carrying capacities X_i and perhaps different catchability coefficients q_i. Allowing for the possibility that a certain number of individuals stray we introduce spatial dispersion matrices D_{ij} to denote the fraction of individuals that, although they come from stock i, for some reason move to and reproduce with stock j. This implies thus that our biological model is modified to Eqs. (1′) and (2′).

$$\begin{gathered} \mathrm{d}X_{it}/\mathrm{d}t = g_i(X_{it,K_i}) + \sum_{i \neq j} D_{ji}X_{jt} - \sum_{j \neq i} D_{ij}X_{it} - H_{it} \quad K = \sum K_i \\ X = \sum X_i \end{gathered} \tag{1′}$$

$$H_{it} = q_i E_t X_{it} \qquad H = \sum H_i \quad i = 1 \ldots n \tag{2′}$$

Eqs. (1′) and (2′) defines a metapopulation model following Levins (1969, 1970) and Smedbol and Wroblewski (2002). The model is close to the models of Sanchirico and Wilen (1999, 2001a,b, 2002, 2005). The distinguishing feature here is that the diversity is unobserved and that the sub stocks may mix freely throughout the year (except during reproduction). This implies that they will be caught together and effort therefore is normally not specific to a single sub stock "i". The growth of each stock is however limited by individual carrying capacities which may be interpreted as carrying capacities for the breeding ground itself. In this model, the regulator can still only observe *aggregate* stock, *aggregate* harvest and *average* growth rates and catchability. The concept of metapopulation emphasizes the balance between extinction of local subpopulations and recolonization. However the degree of genetic differentiation shows that cod display significant site fidelity in reproduction, which would suggest that recolonization would be so slow and as to be almost irrelevant and we will therefore generally assume $D \approx 0$).[8] The models (1′) and (2′) are very similar to the multi-species model of differential productivity analyzed by Clark (1990, chapter 10). Clark shows that such a system is susceptible to over-fishing and extinction in a way that the single stock open access model with logistic growth is not.

4. Growth potential of a group of subpopulations

In this section we show that the same effort may lead to varying rates of sub stock depletion and even extinction if the sub stocks have different growth rates or catchability. Assuming the straying in Eq. (1′) is insignificant, we simply have the sum of growth minus harvest for each stock. If the regulators analyze a group of stocks as if it were a single stock they will misjudge the growth (and harvest) potential of such a system (the sum of n separate stocks) compared to that of a single stock of corresponding size. The sum of a set of growth functions is far from simple. The sum of several logistic functions is, for instance, not itself a logistic function. If the total stock is known (but not its distribution among sub stocks) the error in the growth estimate would be ΔG as in Eq. (4).

$$\Delta G = \sum_i^n g_i(X_{it}) - g\left(\sum_i^n X_{it}\right) \tag{4}$$

For logistic functions this is. $\sum_i^n r_i(X_{it})(1 - X_{it}/K_i) - r\sum_i^n (X_{it})(1 - (\sum_i^n X_{it})/\sum_i^n K_i)$.

Assuming the functions for the growth rates are concave, growth declines if stocks are either big or small (heavily or lightly depleted) and the average of two sub stocks' growth rates will be smaller than the growth rate for a corresponding single stock with a stock size (and depletion rate) equal to the average of the two component stocks. This result follows

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[7] As stated by Lande et al. (2003), "Population subdivision and spatial heterogeneity of the environment can exert a strong influence on population dynamics and extinction risk".

[8] However, as pointed out by Smedbol and Wroblewski (2002) genetic structures reflect past behavior and it is possible that straying and colonization rates will increase in a severely depleted population.

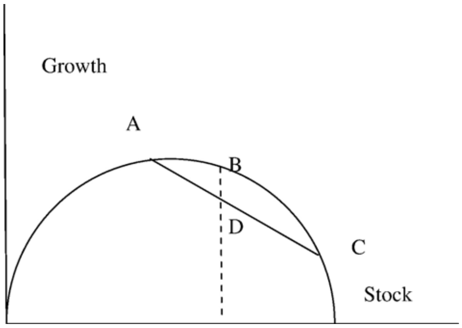

Fig. 1 – Average growth of two sub stocks compared to growth of a single (combined) stock.

immediately from the definition of convexity.[9] The only exception is the trivial case when all the stocks have been depleted to an identical percentage in which case the growth rates will be equal. This is illustrated in Fig. 1 where the observed growth for a mixture of two subpopulations (with identical growth parameters) will be the average growth at *D*, of the two sub stocks A and C which is lower than the hypothetical growth of a single combined stock at *B*.

The only case the error is zero is when A and C coincide in Fig. 1. The trouble is that equal depletion is trivial because then all stocks are behaving the same and there is little actual diversity. Furthermore this is an unlikely state in nature. Random events will be enough to give greater depletion of one sub stock than another. Similarly differences in growth rate or catchability would give different degrees of depletion. As soon as this happens, the growth potential of the aggregate system will be over-estimated, and this fact provides one reason for additional caution when regulating fishing effort or catches.[10]

4.1. *Differences in catchability or growth rate*

If two subpopulations vary with respect to growth or catchability parameters, we have a situation of multi-species competition. As shown by Clark (op cit.), the same effort level *E* will lead to different levels of sub stock depletion for the two subpopulations. The decisive variable is the ratio between the growth parameter *r* and the catchability *q*. Clark refers to this as the biotechnical productivity of a given stock *i* ($\text{btp}_i = r_i/q_i$). The btp acts as a form of “effective growth” (taking fishing mortality into account). If the effort *E* is sufficiently high then the sub stock with the lower biotechnical productivity will be driven to extinction. This extinction may be ascribed either to a higher level of catchability, a lower intrinsic growth parameter or some combination of the two.

If sub stocks have different spawning grounds and (slightly) different genomes they may well have differences in either growth or catchability parameters. What is special here is that the two species are virtually indistinguishable to the fishermen and regulator alike. In fact the sub stocks are not recognized as such but their sum is thought of as if it were one stock. For low levels of depletion the parameters of a joint system may be quite similar to the component population figures but with greater (and uneven) depletion the growth of the sum of the stocks will be different as shown above. Even if fishermen and regulators choose a level of effort that would have been appropriate for a single stock, this same level of effort may imply a moderate level of catch for the stock with a high btp but severe depletion or extinction for the slow growing or more easily catchable stock.

5. Stock management with imperfect information

The problem of fisheries management under imperfect information is that regulators cannot observe the subpopulation diversity and fishermen are unable to target their effort at any particular subpopulation, it is spread evenly across all the populations present. The regulator believes there is a single stock and he can optimize Eqs. (1) (2) and (3) but in reality he is faced with Eqs. (1′) and (2′) + Eq. (3). He sets out to calculate the tax T^* which will keep the stock at some minimum (“safe”) level X^*. To do this he sets net growth to 0 in Eq. (1). For a given X^* there exists an equilibrium harvest $H^*=g(X^*)$. To attain this harvest with the stock X^* the regulator must elicit an effort $E^*=g(X^*)/qX^*$ from Eq. (2). The regulator knows the open access mechanism (3) and thus $E=PH/(C+T)$. Simple insertion gives the optimal tax rate T^* as in Eq. (5)

$$T^* = PqX^* - C \tag{5}$$

T^* does indeed give the desired effort E^* (Eq. (3) still applies) but this effort is not the appropriate effort level for the multi-stock fishery. Applying Eq. (2′) we see that the total harvest *H* will still be at the level H^* that would have been optimal for a single stock of the same size as the sum of the sub stocks. As shown in Section 4 it suffices for the sub stocks to have different depletion rates — even when they have the same growth and catchability parameters for the growth of the sum of sub stocks to be reduced. The harvest level that would have been sustainable for a single stock will thus not be sustainable for the case of several sub stocks.

6. Simulating sub stock extinction due to differences in catchability or growth rates

Thus far we have shown that unobserved diversity can lead to overestimation of growth and thus over harvesting when sub stocks have different rates of depletion. We also discussed the case when biotechnical productivities vary which, as shown by Clark, may lead to the depletion of the less productive populations unless fishing effort can distinguish between them. In reality there may be additional aspects such as spatial dispersion and extinction thresholds all of which are difficult to treat analytically. In order to illustrate their importance we carry out some numerical simulations. The idea here is to illustrate a matter of principle and thus the model used is not calibrated to the specificities of any particular fishery but is a

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[9] If the growth function is concave, the production set will be convex and any linear combination of points on the frontier will be inside the set.

[10] There are also many other factors (not discussed here) causing quotas to be too large.

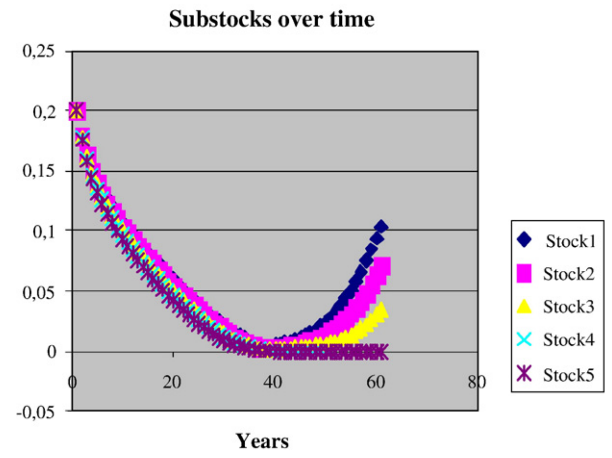

Fig. 2 – Five sub stocks with a moratorium in year 37.

generic model — in fact, a very slight adaptation of the model above (Eqs. (1″) and (2″)) to allow for the *possibility* of extinction at very low stock levels through the introduction of an Allee effect. The ecologist Allee emphasized the advantages of large numbers for a species. With low population numbers, difficulties in finding a partner, random differences in sex ratios and other factors concerning for instance genetics, may result in low or even zero reproduction and thus extinction (Allee et al., 1949; Frank and Brickman, 2000). The effect modeled here thus acts as an extinction threshold: Below "*a*", the subpopulation goes extinct: otherwise, simulations could give arbitrarily low population numbers even down to a single fish (or fractions thereof) which obviously makes no sense.

$$\Delta X_{it} = r_i(X_{it}-a)(1-X_{it}/K_i) + \sum_{i\neq j} D_{ji}X_{jt} - \sum_{j\neq i} D_{ij}X_{it} - H_{it} \qquad (1'')$$

$$X = \sum X_i$$

$$H_{it} = q_i E_t X_{it} \qquad H = \sum H_i \quad i = 1\ldots n \qquad (2'')$$

To make the model tractable, we have simulated it with five sub stocks that start off at equal size and compared this outcome to the corresponding results for a single stock of equal size as the combined biomass of the five sub stocks. In the first simulation the Allee effects are set very low and there is no straying or geographical diffusion. The sub stocks are identical except for their catchability.[11]

The development of the five stocks is shown in Fig. 2. Sub stock 5 declines the fastest since it has the highest catchability (the same pattern emerges if we instead vary growth rates). If nothing is done, the stocks go extinct one by one, consecutively in the years 40–44. However, if the regulator introduces a moratorium on fishing effort from the year 37 then three of the stocks are able to start rebuilding. The other two are already below the threshold defined by the Allee effect and go extinct. It is interesting to note that this creates a form of irreversibility that is illustrated in Fig. 3.

The interpretation of Fig. 3 is facilitated if we start at the point of "natural" equilibrium at the far right corner (at "N") where the total stock biomass, is normalized to 1, (but actually consists of 5 stocks of size 0.2). Increasing effort leads to decreasing stock and first increasing and then decreasing harvests as suggested by the arrows. If fishing effort continues long enough all sub stocks will be depleted but if, as in Fig. 2 above, there is a moratorium the sub stocks that are not extinct can start to rebuild. We assume they cannot (within relevant time frames) colonize the spawning grounds abandoned by the sub stocks that go extinct, and thus the total population does not recover to its original size but follows, for instance, the curve denominated "C" in the case when 3 out of five sub stocks recover. The diagram shows the different recovery paths that occur if a moratorium on fishing effort is enacted in different years. The differences are due to the fact that if a moratorium comes early then more sub stocks can be rebuild. If it is enacted fast enough (year 35) there is full recovery as shown by the path indicated A (although it still takes more than three decades to get back 90% of original biomass). If however the moratorium is delayed just one year (to year 36), sub stock 1 will be extinct and the moratorium will eventually lead to the recovery of only four out of five sub stocks and thus 80% of the original spawning biomass following path B. Similarly a delay of 5 years will lead to extinction of all but one sub stock along the path E.[12]

The response of the system to this differential impact will depend on a number of factors. If the size of sub stocks is only limited by competition for food, one single sub stock could grow and fill the niche left by those sub stocks that become extinct.[13] Such a system might be viable in some respects but would certainly be very vulnerable to local fishing pressure, pollution or other local incidents.

Let us instead assume (as in our model above) that sub stock size is limited by, for instance, resources related to the reproductive area itself so that each sub stock has a (roughly) constant maximum carrying capacity that is unaffected by the disappearance of other sub stocks. In this case, we have the gradual extinction of the sub stocks with the highest catchability (or lowest growth rates) as shown in Figs. 2 and 3. If fishing effort was to be cease the sub stocks that had not

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[11] For completeness we note here all the parameters used in this estimation: Growth rate $r=100\%$ (per year) for all stocks. Both total stock and total effort is normalized to unity in year 1. Catchability q_i is spread evenly from 0.1 for sub stock 1 to 0.105 for stock 2 and up to 0.12 for stock 5. Dispersal coefficients $D_{ij}=0$. Allee effects $a=0.001$ which means that net growth essentially falls to 0 when only 0.5% of the original stock levels remain. The number of fishermen is constant but effort grows at 4% per year because of technical improvements.

[12] A moratorium in year 37 saves 3 stocks, path C, in year 38 it saves 2 stocks, path D; in year 40 it saves one (path E) and if the moratorium comes year 41, all the substocks are lost.

[13] If there are interactions between differences in catchabilitiy and differences in intrinsic growth rates, matters would be more complex. If for instance it was the fast growing species that had lower catchability then indiscriminate fishing with joint fishing pressure would in fact favor the sub stock with higher-than-average growth rates which could be seen as positive from the viewpoint of avoiding stock depletion and for enhancing maximum sustainable yield (but at the expense of higher cost parameters in the cost of fishing function).

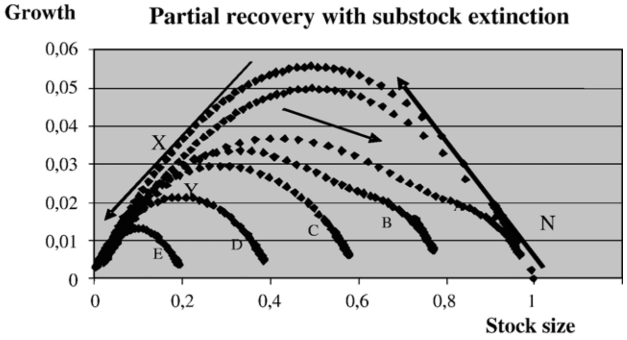

Fig. 3 – Depletion and partial recovery of a set of multiple subpopulations.

become extinct may be assumed to recover relatively fast but the extinct sub stocks can of course not do so (except on evolutionary time scales that permit re-colonization of abandoned niches which may be expected to be significantly longer[14] — see below). This implies that we have introduced a form of irreversibility — or perhaps rather an alternative explanation for irreversibility that is sometimes assumed in a more ad-hoc manner.

This may be one of the mechanisms behind such phenomena as the *sudden collapse and slow recovery* of the Canadian cod fisheries. A regulator who does not observe sub stock structure but thinks he is regulating a single stock would believe that the regulated fishery is at a point such as X on the top curve representing a single stock in Fig. 3, when in fact he is at Y on a multi-stock model where some stocks are already extinct. Although X clearly represents heavy fishing pressure, there is still reason to believe the stock would at least recover with a properly enforced fishing moratorium. If however we are at a point such as Y then only very limited recovery is possible.

Another possible difference between sub stocks is variation in intrinsic growth rates. These are likely to vary with parameters such as the temperature of the water in the area from which a certain genetic material originates. We found that different growth rates were quite sufficient *on their own* (without any difference in catchability) to lead to extinction of some sub stocks and survival of others.[15] We also found that *random variations* in the stock size (or in the intrinsic growth rate parameter) could lead to certain sub stocks becoming extinct. This may in practice be very important since it seems that random variation in recruitment is a typical feature of cod stocks. On the other hand simulations showed that a "disadvantage" in slow growth could be fully compensated by a lower catchability — reflecting the fact mentioned earlier that the crucial criterion is biotechnical productivity. In as much as catchability can be affected by policy instruments this suggests that the policy maker could, if this is desirable, ensure the survival of slow growing sub stocks by affording them greater protection (through spatially explicit regulations or other means).

6.1. *Straying and density independent catchability*

One positive aspect of the genetic diversity is that total extinction is less likely. The fact that some sub stocks have low catchability protects them (pointing to the importance of refuges). Depending on their ability to recolonize and to take over niches of the other sub stocks, this could be very valuable. A straying coefficient D_{ij} of only 0.03% (in Eq. (1′)) will have the effect of saving stock 5 in the simulation marked "B" in Fig. 3 above.[16] If straying is sufficiently common then the model essentially becomes a single stock model.[17] If, on the other hand, straying is uncommon – as it appears to be with cod – then recolonization will not happen within relevant timeframes.

We have spoken much about the tendency for cod to aggregate in this article. A consequence that has been described in the literature is that harvests (and most notably catch per unit effort CPUE) can continue to be good even though a stock is dwindling. Clearly this ruins the value of CPUE as an indicator of impending scarcity or stock collapse. In our model this can most easily be modelled as in Eq. (2*) with $\lambda < 1$.

$$H_t = qE_tX_t^{\lambda} \tag{2*}$$

Of all the parameter variations tested in our simulations this had the most powerful effect on extinctions. Extinction came much faster and CPUE remained high along the path towards extinction just as observed in for instance Canadian cod fishing. Catchability had to be lowered considerably to compensate.[18]

7. Targeting of fishing effort

Strict unobservability of the genetic differences between threatened and nonthreatened stocks only leaves two policy options. The first of these policies is to adjust total fishing effort to the level that would be sustainable for the most vulnerable subpopulation. If this population is severely threatened this may be an effort level of zero — for the whole fishery including some subpopulations that may be very healthy. This may well be considered to be too high a price to be paid for the conservation of a single subpopulation.[19] The other option is to accept extinctions of some sub stocks.

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[14] Unless, as discussed in Smedbol and Wroblewski (op cit), the behavior itself of cod were to change as stocks become very seriously depleted.

[15] We ran a simulation that was identical in all parameters except that catchability was $q = 0.0022$ for all sub stocks while growth rates varied from 80 to 120% instead of being 100% for each sub stock. The results were almost identical as those in Fig. 3.

[16] With D_{ij} of 0.02% sub stock 5 goes extinct in spite of the moratorium on fishing effort but with 0.03% it recovers.

[17] With straying rates of 0.5% sub stock 5 did not even go extinct in spite of a "catchability" that was ten times as large as the other sub stocks.

[18] In the simulation above with $q = 0.0022$ for all sub stocks and growth rates of 100%, a reduction in λ from 1 to 0.8 speeded up extinction so it occurred after 30 instead of 60 years. Catchability had to be lowered from 22 to 9 to counteract the effect of lowering λ from 1 to 0.8.

[19] Sanchirico and Wilen (2005) show that the optimal policy instruments should be spatially differentiated: uniform instruments will lead to an underregulation of threatened stocks and an over regulation of non-threatened stocks.

In some cases the biodiversity may be valued highly or some sub stocks may have an intrinsic value of their own. One possible such case would be local coastal populations of particular importance for sport fishing or artisanal fishing. If we further assume that there is some form of geographical information then we might explore the possibility of spatially (and temporally) differentiated instruments.[20] Building on information concerning the life history or behavior of the various stocks may for instance make it possible to designate areas that should not be fished or should at least not be fished during certain times of the year. In one set of simulations we tested a harvest function in which local stocks are *partially* protected or marine reserves *partially* respected. This was modelled through a harvest function such as Eq. (2**) in which local protection is a parameter Φ_{it} for sub stock i.

$$H_{it} = qE_{it}X_{it} * \Phi_{it} \tag{2**}$$

In this context, $\Phi_i=0$ is a no-take marine reserve, $\Phi_i=0$ is a temporary protection during time *t* of an area big enough and sufficiently enforced to fully protect the sub stock *i*. If a sufficiently large share of the sub stock *i* is in fact protected the "effective" fishing effort on that particular stock will be lowered, $E_i=E\Phi_i$. An alternative way of stating this is that the effective catchability[21] $q\Phi_{it}$ is reduced for fish in the reserve. In the simulations we found that it was sufficient to choose a parameter Φ_i that corresponds to the difference in biotechnical productivity. In other words, a single sub stock that was on the verge of extinction due to a lower growth rate (or higher catchability) could be saved if effective effort was reduced to compensate for the difference. If one sub stock had a growth rate 10% smaller than the others, then this disadvantage which would otherwise lead to extinction could be corrected for by an instrument that lowered fishing mortality by just 10% on that particular sub stock. This shows that we might not need very detailed information on a stock nor full compliance in order, at least in some circumstances, to have sufficient effect.

There has been increasing interest in marine reserves and other geographically differentiated instruments such as limits for certain types of equipment (trawls) in certain in-shore or close-to-shore areas, and local or seasonal moratoria. The usefulness of marine reserves is hotly debated. Hannesson (1998) questioned their use compared to optimal quotas while Armstrong and Reithe (2001) showed that under some assumptions they may in fact be very valuable instruments. Neubert (2003) shows that some percentage of waters under reserve protection should be profitable even from a strict fisheries perspective. Sanchirico (2004) shows that the design of marine reserves is a complicated trade-off between the degree of connectivity of sites and the biological and economic heterogeneities. Possibly this discussion should include quasi property rights (ITQs) for the spawning aggregations. When the cod are indistinguishable and mix throughout most of the year, fishing on the spawning aggregations may be the only practical way of targeting a particular subpopulation. This may go against the intuition that spawning aggregations should be protected and for this reason be seen as a risky strategy. However, with careful monitoring – and strong property rights to make sure that the fishermen have the appropriate conservation incentives – it might be the best policy.

Generally speaking it is healthy to move to better definitions of property rights including a broader use of ITQs. Allocating property rights to fishermen gives them a healthy self-interest in the sustainability of the stock. However an ITQ system could also create problems if shares in a fictitious stock (the sum of all sub stocks) were handed out without sufficient knowledge of its underlying components. The regime of property rights must to a reasonable degree correspond to biological reality. If spawning stocks could be identified then it is possible that property rights should be allocated specifically to these stocks or to the actual breeding grounds but this will certainly require some more research.

8. Conclusion

We started this paper by referring to recent biological literature on the tendency of cod to return to their origin for spawning and that this creates genetically and behaviourally separate sub stocks with limited dispersion. This has important consequences for modelling of stocks, growth and harvest potential that appear not to have been given proper attention. Effectively the single stock models used for stock assessments become misleading. We should be dealing with the joint exploitation of several stocks that are indistinguishable. Normally genetic diversity is associated with resilience — and it can play this role here too. Thanks to diversity the likelihood that some sub stocks survive is indeed enhanced. Failure to observe the diversity will however also lead to overestimations of the growth and harvest potential. Furthermore it was shown that hidden differences in growth parameters or catchability could lead to extinction of subpopulations. This applies even if fisheries are properly regulated and follow conventional rules for sustainable harvesting (except for the nonrecognition of sub stock diversity). Such extinctions are likely to be irreversible on conventional time scales and could thus imply that even if a moratorium is applied, only some sub stocks will be able to rebuild. This will in turn imply that the total population size and harvest potentials are not recovered.

Naturally the issue discussed here is not the only problem for fisheries policies. We still have underreporting, monitoring difficulties, lobbying for higher quotas, interjurisdictional problems and such issues as discards and discard mortality that are particularly serious in multi-species fisheries.[22] The number of fishermen in most industrialized countries is very

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[20] For a general discussion of related issues in the design of policy instruments see Sterner (2003).

[21] We have earlier seen that it is the relative biotechnical productivity parameter r/q that is decisive for sub stock growth and survival. In this case, the relevant parameter will be $r/q\Phi$ which indicates how the policy instrument Φ_{it} can be used to differentiate policies between sub stocks.

[22] Under current Swedish regulation, fishermen catch cod as long as there is a cod quota left. When that quota is "used up" they continue to fish with similar equipment in the same areas for other species such as Norway lobster for which they have separate, quota. They still catch significant quantities of cod but this is now classified as "by-catch" and discarded into the sea (with 90% mortality) or sold illegally, see further Sterner and Svedäng, 2005.

small but they carry quite a large weight as lobbyists and politicians want to keep the "sector" alive for reasons related to regional unemployment and politics. The fishermen are caught in a race for increased efficiency and tend to invest very heavily in new equipment, since they know only the most efficient will survive and partly because they know the politicians will support them since the public opinion is sensitive about this dwindling sector.

Above all we still have the fundamental problem of open access: fishermen compete for a common pool resource none of them owns and one of the few policy instruments that has any chance of solving that problem is the devolution of property rights to the stock — such as is implied by ITQs. This paper serves to show that there is actually a further layer of complication: spatially separate stocks that need individual, spatially sensitive management. This implies that we need more local decision-making and decision-making that builds on more detailed biological knowledge. It is also going to require the development of new property rights and instruments that take local complexity into account. Examples could include separate ITQs or local management instruments for separate sub stocks. Another possibility[23] is to think in terms of complementing quotas or other general instruments with marine reserves.

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[23] There are naturally many complex issues related to the design of such reserves but this falls outside the realm of the current paper, see for instance Boersma and Parrish (1999).

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