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Comparison of the effects of exploitation on theoretical long-lived fish species with different life-history strategies and the implications for management

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Abstract
A stage-based simulation model is used to investigate the effect of exploitation on theoretical populations representing long-lived elasmobranch and teleost species with different life-history strategies. A comparison is made between the effect of exploitation on the elasmobranch 'k-strategists' and other teleost species that are 'r-strategists'. We demonstrate the effects of stage-based exploitation on a typical long-lived elasmobranch population and discuss the implications of this when designing a management plan to ensure survival of the stock.

Keywords: elasmobranch, k-strategy, r-strategy, exploitation, management plan

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1. Introduction
In this paper we use simulations of a simple fishery model to compare exploitation strategies on two virtual stocks, both of which are top predators in their ecological niches. The virtual stocks are fictional but have been designed to capture the key dynamics of real stocks that can be described as 'k-strategists' or 'r-strategists'. In general, a 'k-strategist' is typically slow growing, suffers low natural mortality and has low reproductive potential (characteristics that are typical of elasmobranches such as deep-water sharks). In contrast, an 'r-strategist' is typically fast growing, suffers high mortality (at least at young ages) and has very high reproductive potential (characteristics that are typical of cod *Gadus morhua*). We use a simple deterministic stage-based model in the simulations and compare results for different levels of exploitation. Results of this simple model suggest that at an optimal fishing level it is possible to catch approximately 80% of the spawning stock biomass (SSB) each year for the 'r-strategist' (cod) and maintain a sustainable fishery. However, for the 'k-strategist' (shark), the optimal fishing level only allows a catch of less than 5% of the SSB level each year, and higher exploitation results in population extinction (equilibrium SSB levels are similar for both stocks). We show that, by fishing on the juvenile sharks only and avoiding exploitation of the adults (a strategy that may be possible if the species is spatially discrete by size or age), it is possible to fish at a much higher level of F, although the overall yields are still low (as the juveniles are individually much smaller). Thus, we suggest that sustainable yields from k-strategists are very low and there is little value in directly exploiting shark stocks. The results also imply that fisheries that have a significant shark bycatch should aim to fish in areas where only juveniles are found (assuming the population is spatially discrete by age and that we have this information).

2. Methods

A simulation has been programmed in R (R Development Core Team, 2003) using a simplified version of a stage-based model suggested by Cortes (1999).

2.1 Species comparison

We compare two theoretical long-lived fish with different species and population characteristics. Both species are entirely fictional and exist only as 'virtual' stocks for the purposes of our simulation. However, we have tried to capture the key features of stocks that are considered top predators in their respective ecological niches but who can be classed as 'k-strategists' and 'r-strategists' respectively.

Species A:

- k-strategist;
- low productivity;
- low natural mortality;
- slow to mature;
- represents a 'typical' deepwater shark – top predator in deep-water areas.

Species B:

- r-strategist;
- high productivity;
- high natural mortality (at younger ages);
- fast growing and maturing;
- represents a teleost such as cod – top predator in shallow water areas.

For simplicity in our simulations, we assume a sex ratio of 50% for both species.

2.2 Stage-based model

We have adapted and simplified the stage-based model used by Cortes (1999) to run simulations to compare the effects of exploitation on our two virtual stocks.

In our model we have four separate stages corresponding to different age ranges for the two species:

Stage	Species A	Species B
Young (SY)	0-1	0-1
Juveniles (J)	1-15	1-2
Young adults (YA)	15-20	2-3
Adults (A)	20+	3+

Our model is different to standard age-based models because the virtual stock does not automatically move up to the next age (stage) at the end of each simulated year. Instead, only a fixed proportion of the population in each stage move on to the next stage. This proportion is related to the length of time typically spent in that stage – for example, only a very low proportion of species A juveniles will move up a stage to become young adults, while a large proportion of species B juveniles will move up a stage. The proportion moving between stages for each species is given by a 'growth' parameter G, see Section 2.4. Note that there are some limitations with this model, see Section 4.

2.3 Mortality

We use a standard exponential mortality model: $\exp(-Z_i)$ where $Z_i = F_i + M_i$, where $i = 1$ to 4 corresponds to the four different stages and F and M are fishing and natural mortality respectively.

2.4 Species parameters

We use the following stage-based parameters to describe each species characteristics. The vectors correspond to the values for each stage as given in Section 2.2, e.g. (SY, J, YA, A).

Natural mortality:
$M_A = (0.5^a, 0.1, 0.05, 0.01)$ [a] low mortality on young (SY)
$M_B = (4^b, 0.2, 0.2, 0.2)$ [b] high mortality on young (SY)

Maturity:
$Mat_A = (0, 0, 0.6, 1)$
$Mat_B = (0, 0.2, 1, 1)$

Weight (kg):
$Wght_A = (0.15, 1.5, 2.5, 5)$
$Wght_B = (0.05, 1, 2.5, 7)$

'Growth' (proportion moving between stages):
$G_A = (1, 0.07, 0.2, 0)$
$G_B = (1, 0.9, 0.9, 0)$

Initial population numbers (millions):
$N_A = (0.2, 2, 0.6, 1)$
$N_B = (20, 2, 0.5, 1)$

Thus, our two virtual stocks have similar initial adult population numbers, and similar weights across all stages. However, the growth and maturity dynamics of the two species are very different.

2.5 Reproduction

In our model, spawning takes place once a year at the end of the year (after mortality has affected the population). For simplicity, we use the same 'bell-shaped' recruitment function for both stocks. The function is given by

$$R = 4 * SSB * R_{Max} * (1 - SSB / K) / K, \qquad (1)$$

where R is the number of recruits entering the first stage (SY) in the next year, SSB is the spawning stock biomass in the year of spawning, R_{Max} is the maximum number of recruits that can be produced in any year, and K is the carrying capacity of the stock (in the sense that if SSB > K then recruitment is zero). Note that the function is symmetrical about an optimum SSB = K/2 (corresponding to the maximum possible recruitment) and is zero when SSB > K to represent density dependence, see Figure 1. The SSB of the virtual population can be greater than the carrying capacity K, but in recruitment will simply be zero if this is the case.

Recruitment parameters:
Carrying capacity, K species A = 30,000 tonnes
Carrying capacity, K species B = 50,000 tonnes

R_{Max} species A = 500,000 individuals
R_{Max} species B = 500,000,000 individuals

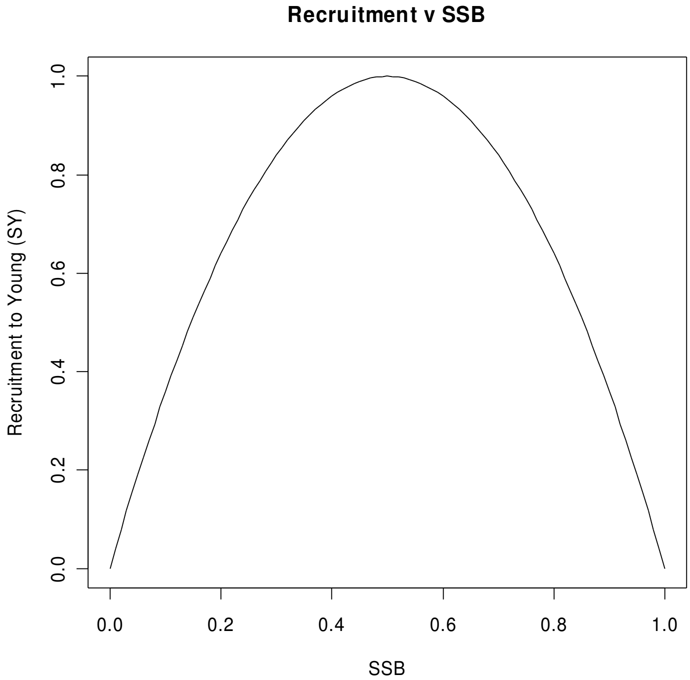


Figure 1. *'Bell-shaped' recruitment function used in simulations. The function in the plot has been rescaled so that K = 1 and R_{Max} = 1. Note that the function is symmetrical about the point K / 2, which is where the highest recruitment value (Max) occurs.*

Both our virtual stocks have similar spawning stock carrying capacities but Species B (teleost) is far more productive. However, species B also suffers much higher mortality of young recruits. This reflects a different recruitment strategy (the 'r' strategy: high production, high mortality) to species A (the 'k' strategy: low production, low mortality). Thus although our recruitment function is crude, it reflects the key points of real-life k and r strategists.

2.6 Exploitation

Fishing mortality is applied to both stocks (see Section 2.3). The F vector consists of a 'selection pattern' (a normalised vector) together with a corresponding F multiplier.

We look at two different exploitation strategies for species A (sharks):

- I: exploitation of adult population: selection pattern = (0, 0.5, 1, 1);
- II: exploitation of juvenile population only: selection pattern = (0, 1, 0, 0).

We argue that as shark populations are more likely than teleost species (cod in particular) to be segregated geographically by age or size, it should be theoretically possible to target a particular stage of the population only (e.g. juveniles).

With a species such as cod, it is only possible to target by size (e.g. the bigger, older fish only). Thus, we use one exploitation strategy for species B with selection pattern = (0, 0.5, 1, 1).
Different F multipliers are applied to each of the three selection patterns to give a range of final F vectors.

3. Results

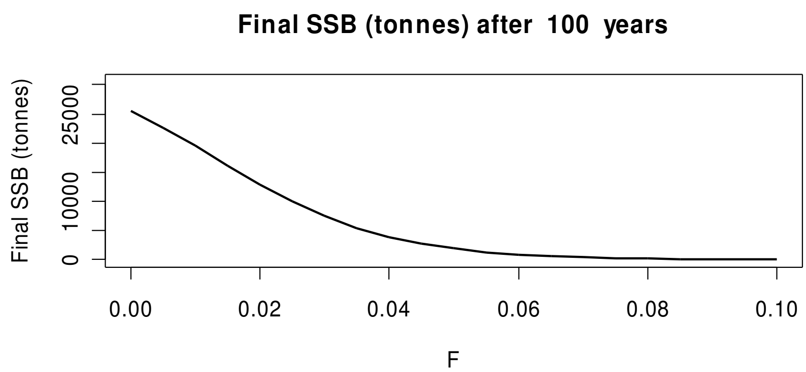
Simulations projecting the two stocks have been completed for 100 years to allow the fishery system to reach an equilibrium state. All simulations are deterministic – we are interested in the underlying dynamics of the model rather than trying to replicate a more complex (but more realistic) system.

Results are presented below for the three different exploitation strategies described in Section 2.6. For each strategy there is:

i) a figure showing plots of the final SSB and total catch over the 100-year projection run under a range of different F multipliers (applied to the normalised selection pattern);
ii) a figure showing four time series plots over the 100 years of the projection completed for the F multiplier that produces the largest total catch over the projection (i.e. the optimal F multiplier). Plots shown are population numbers at each stage, SSB, catch weight, and spawning production (recruitment).

3.1 Species A (k-strategist – 'shark')

3.1.1 Selection pattern I – (0, 0.5, 1, 1)



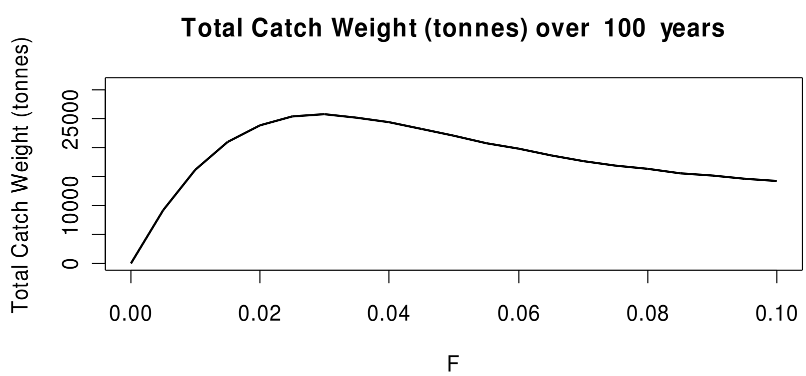


Figure 2. *Plots showing the SSB in the final year and the total catch over a 100-year deterministic projection using a selection pattern of (0, 0.5, 1, 1) to fish on species A*

(sharks). The optimal F-multiplier giving the largest total catch is approximately $F_{mult} = 0.025$. Note that even with exploitation as low as this, the population is still well below equilibrium SSB (approx 27,000 tonnes).

Figure 2 shows plots of a simulated 100-year projection of species A (shark) under different levels of F multiplier with selection pattern (0, 0.5, 1, 1). The first plot in the figure shows the final SSB of the virtual stock (i.e. SSB in year 100 – not the average SSB over the 100 years). The second plot shows the total catch weight over the entire projection (the sum of the catch in every year). It is clear that if $F_{mult} > 0.05$ (usually a very low fishing mortality) then the population is practically extinct at the end of the 100-year projection. The equilibrium SSB (final SSB given zero fishing) is approximately 27,000 tonnes. Note that this is less than the 'carrying capacity', K, (see Section 2.5) as might be expected – when the population is at K there is zero recruitment, so that the equilibrium population should be slightly less than K. From the second plot, it is clear that by fishing too intensively, the total yield over the 100-year projection is actually reduced (because the population is reduced to a low level). The optimal level of fishing is when $F_{mult} = 0.025$ (approximately).

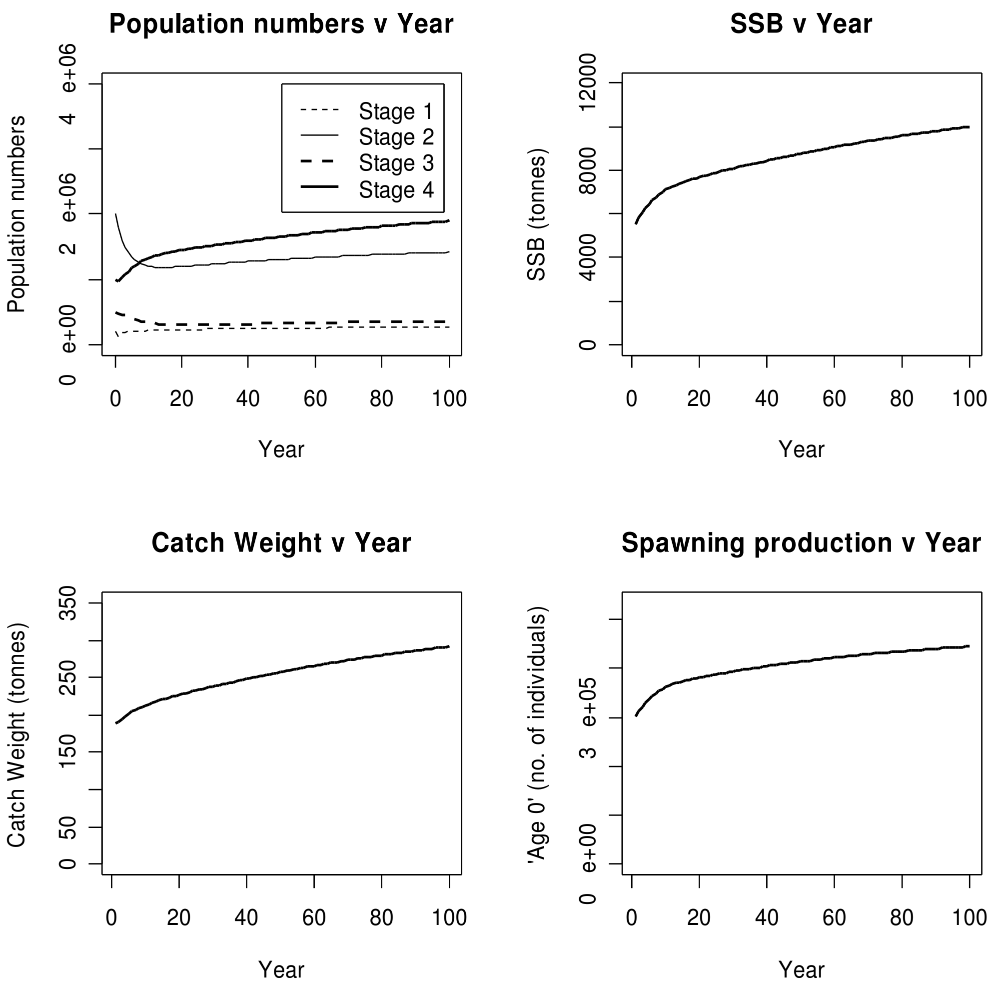


Figure 3. *Time-series plots from a 100-year simulation projection using a selection pattern of (0, 0.5, 1, 1) and $F_{mult} = 0.025$ (the approximate value of the optimal F-multiplier that gives the largest total catch weight from Fig. 2) to fish on species A (sharks). The plots show population numbers at each stage, SSB, catch weight and*

spawning projection for each of the 100 years of the projection. The approximate percentage yield from the stock (catch weight per year / SSB per year) is less than 5%.

Figure 3 shows time-series plots of a simulated 100-year projection of species A with selection pattern (0, 0.5, 1, 1) and $F_{mult} = 0.025$ (the approximate value of the optimal F-multiplier). The first plot shows how the population numbers at each stage change over the projection. As may be expected, the largest numbers are in the two stages that include the most ages (stage 2 – juveniles, and stage 4 – adults, see Section 2.2). The other plots show how SSB, catch weight, and recruitment change over the projection. Under this level of F_{mult} the population seems to still be increasing and has not reached equilibrium. This is due to the much lower mortality at older ages in the population, which means that there is a 'time-lag' before we can see the full effects of any exploitation strategy. If the projection is continued for longer (e.g. 1000 years) then the system reaches equilibrium. The approximate percentage yield from the stock (catch weight per year / SSB per year) is less than 5% suggesting that the fishery is not at all productive (as expected).

3.1.2 Selection pattern II - (0, 1, 0, 0)

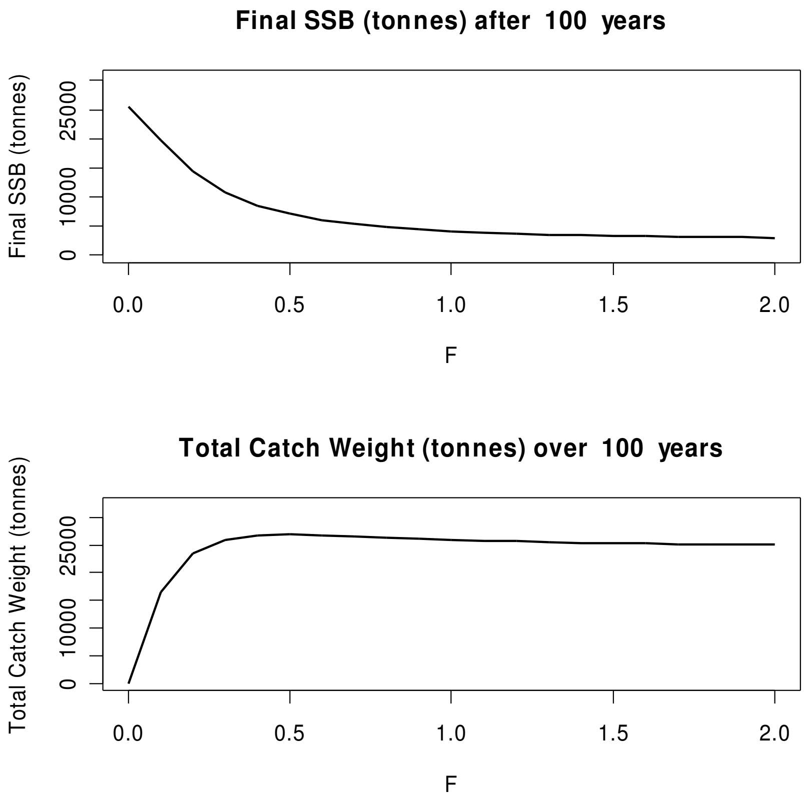


Figure 4. *Plots showing the SSB in the final year and the total catch over a 100-year deterministic projection using a selection pattern of (0, 1, 0, 0) to fish on species A (sharks). The optimal F-multiplier giving the largest total catch is approximately $F_{mult} = 0.5$. Note that by exploiting the juvenile part of the population only we are able to sustain the population at a much higher value of F_{mult} (although the yield may not actually be any higher than fishing with a low F_{mult} on the adult population). Also note that, due to the 'time-lag' effect due to the low mortality of*

adults, the effect of this exploitation strategy may not be obvious even over a 100-year period.

Figure 4 shows plots of a simulated 100-year projection of species A under different levels of F multiplier with selection pattern (0, 1, 0, 0), i.e. exploitation is only on the juveniles in the population (this may be a possible strategy if the stock is spatially discrete by age or size). It is clear that compared to the exploitation strategy in the previous section (including adults in the catch, see Figure 2), it is possible to sustain the population at a much higher level of F multiplier. The optimal multiplier is $F_{mult} = 0.5$ (approximately) and the total catch weight does not seem to be significantly diminished by fishing at higher levels of F_{mult}. However, fishing at higher levels still reduces the total population numbers. Because of the 'time-lag' effect mentioned previously, the effects of over-exploitation are unlikely to be seen in the short term. If we run a projection for longer than 100 years then over-exploitation ($F_{mult} > 0.5$) results in a much lower total catch than the optimal F multiplier (the adult population is driven to extinction as there is limited juveniles reaching adult age to sustain the population).

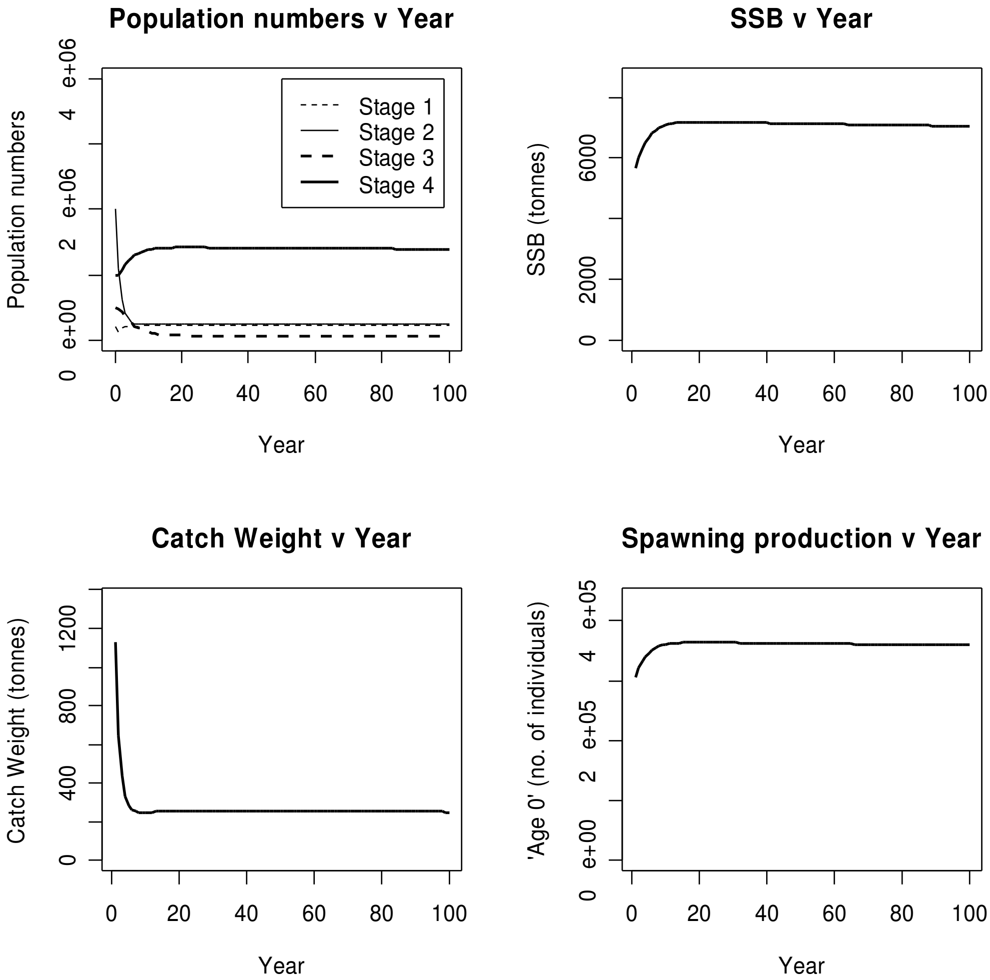


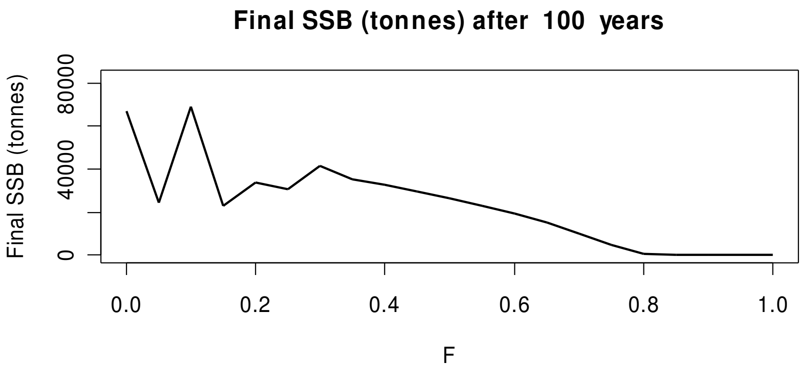
Figure 5. *Time-series plots from a 100-year simulation projection using a selection pattern of (0, 1, 0, 0) and $F_{mult} = 0.5$ (the approximate value of the optimal F-multiplier that gives the largest total catch weight from Fig. 4) to fish on species A (sharks). Note that even using this 'optimal' value of F_{mult} the population still*

appears to be gradually decreasing – this level of exploitation may not be sustainable over a long period than 100 years. The approximate percentage yield from the stock (catch weight per year / SSB per year) is less than 5%.

Figure 5 shows time-series plots of a simulated 100-year projection of species A with selection pattern (0, 1, 0, 0) and $F_{mult} = 0.5$ (the approximate value of the optimal F-multiplier). As may be expected, the largest numbers are now in the adult stage with reduced numbers of juveniles because of exploitation. Looking at the other plots, it appears that under this level of F_{mult} the population is actually slowly decreasing. This is due to the 'time-lag' effect discussed previously – it appears that even though this F multiplier is gives the largest catch over a 100-year projection, it is not sustainable in the long-term. The approximate percentage yield from the stock (catch weight per year / SSB per year) is less than 5% suggesting that the fishery is just as unproductive as the previous strategy of fishing for the adults.

3.2 Species B (r-strategist – 'cod')

Selection pattern – (0, 0.5, 1, 1)



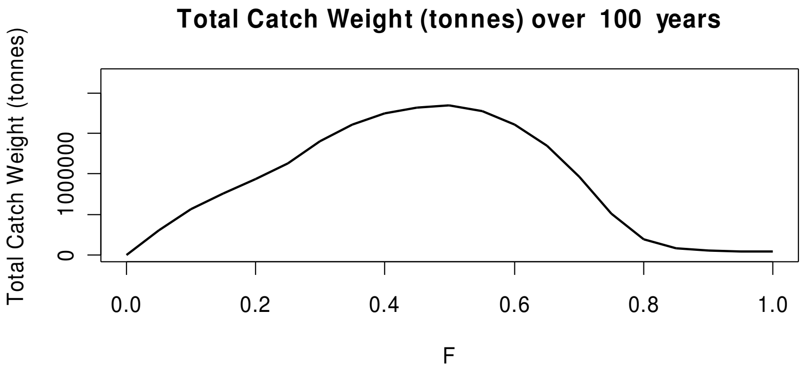


Figure 6. *Plots showing the SSB in the final year and the total catch over a 100-year deterministic projection using a selection pattern of (0, 0.5, 1, 1) to fish on species B (cod). The optimal F-multiplier giving the largest total catch is approximately $F_{mult} = 0.5$. Note that the fluctuations at low values of F_{mult} are because at low exploitation the stock dynamics are governed by the cyclical density dependent stock-recruit relationship (at these low values of F_{mult} the stock does not reach an equilibrium level but fluctuates around an equilibrium).*

Figure 6 shows plots of a simulated 100-year projection of species B (cod) under different levels of F multiplier with selection pattern (0, 0.5, 1, 1). It is clear that compared to species A, it is possible to sustain the population at a much higher level of F multiplier. The optimal multiplier is F_{mult} = 0.5 (approximately), which sustains the population at a high level close to the 'carrying capacity' (30,000 tonnes). Note that in the first plot the apparent fluctuations at low values of F_{mult} are because at low exploitation levels, the dynamics of species A are dominated by the cyclical density-dependent stock-recruit function. For example, the population will rapidly increase because of low fishing mortality, reach a peak, and then have reduced recruitment causing the population to crash. By applying different values of F_{mult} the period of the 'boom and bust' cycle is changed and this explains why the final SSB at the end of the projection differs in the first plot. The equilibrium SSB is likely to be similar for these low F multiplier values, but the population will not stay at this equilibrium value and will instead fluctuate around it. As with species A, at higher F multiplier levels the stock dynamics are dominated by the higher fishing mortality (the population never reaches a high enough level to cause density dependent reduced recruitment).

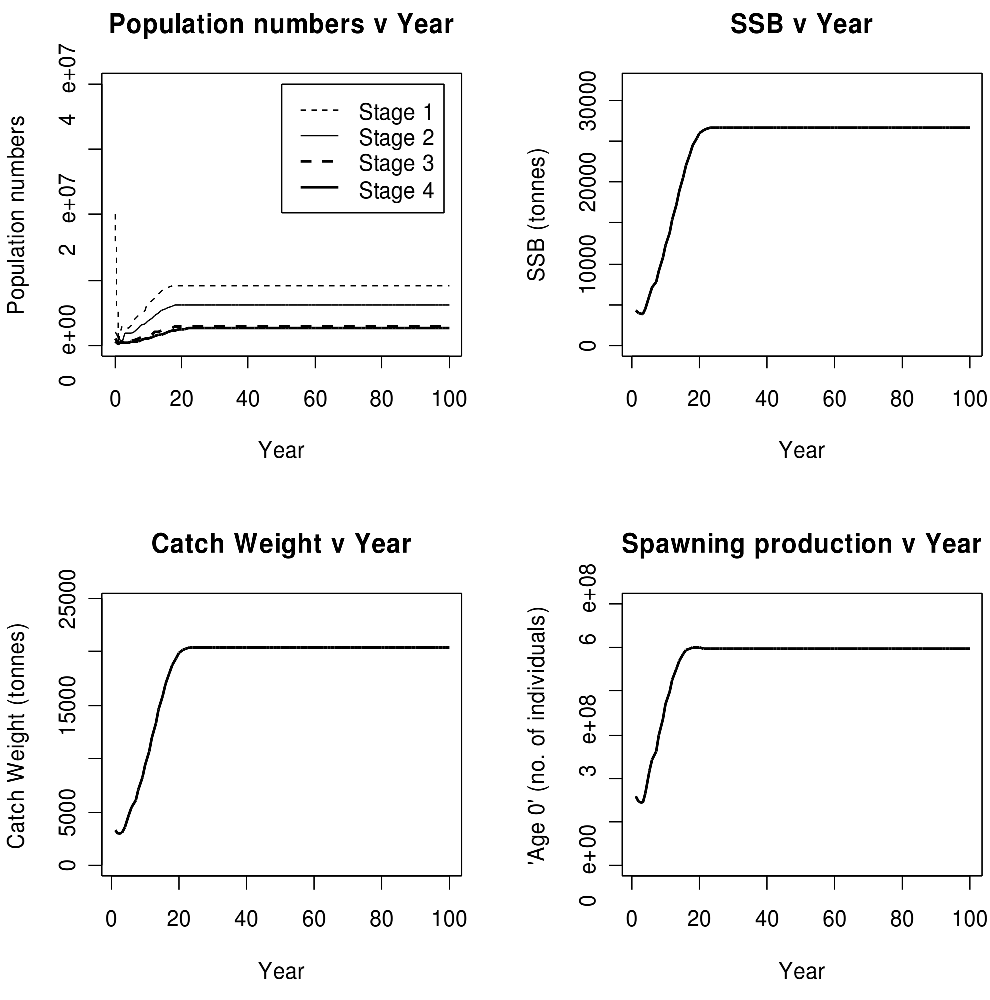


Figure 7. *Time-series plots from a 100-year simulation projection using a selection pattern of (0, 0.5, 1, 1) and F_{mult} = 0.5 (the approximate value of the optimal F-multiplier that gives the largest total catch weight from Fig. 6) to fish on species B*

(cod). The approximate percentage yield from the stock (average catch weight per year / average SSB per year) is almost 80%.

Figure 7 shows time-series plots of a simulated 100-year projection of species B with selection pattern (0, 0.5, 1, 1) and $F_{mult} = 0.5$ (the approximate value of the optimal F-multiplier). For this species, the largest numbers are in the youngest stages – this is expected in a stock that is highly productive but suffers high mortality. The approximate percentage yield from the stock (catch weight per year / SSB per year) is close to 80% suggesting that the fishery is highly productive compared to the fishery for species A.

4. Discussion

Although our simple model is quite basic there are some quite clear conclusions to be drawn. Results suggest that at an optimal fishing level it is possible to catch approximately 80% of the spawning stock biomass (SSB) each year for the 'r-strategist' (cod) and maintain a sustainable fishery. However, for the 'k-strategist' (shark), the optimal fishing level only allows a catch of less than 5% of the SSB level each year, and higher exploitation results in population extinction. The equilibrium SSB levels are similar for both stocks (approximately 30,000 tonnes). Using an alternative strategy of targeting only juvenile sharks (which may be possible with stocks that are spatially discrete by age or size) suggests that a much higher level of F could be used, although the overall yields are still low as the juveniles are much smaller. In terms of managing our two virtual stocks, it is clear that very high yields are attainable from the 'r-strategy' stock (species B) as long as the stock isn't over-exploited. However, there seems little point in trying to directly exploit the 'k-strategist' (species A) as the only sustainable fishing levels are extremely low and produce very low yields. This may be acceptable if the stock is extremely valuable on the marketplace but it would probably not be worthwhile otherwise. What is more interesting is to consider a fishery where sharks are caught as a bycatch and the aim is to minimise exploitation of the shark population. In this case, our results would suggest that if the fishery could avoid catching adult sharks and only allow catches of juvenile sharks as bycatch then this would be more sustainable. However, it remains to be seen whether we could obtain and use spatial information on currently exploited stocks in this way.
The simulations suggest that initial relatively high yields from k-strategy species (such as deep water sharks and teleosts such as orange roughy, *Hoplostethus atlanticus*) are not sustainable and are likely only produced by the fishing down of an unexploited population with an accumulation of biomass at old ages (reverse senescence, see Kenchington (2005)). Such strategies have been referred to as 'mining' and it may practical to consider the exploitation of k-strategists in such terms only. That is to say that a fishery is opened until the accumulated biomass has been removed after which the fishery is closed permanently.

The program files and R source code used to run the simulations described in this paper are freely available on request from the authors.

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