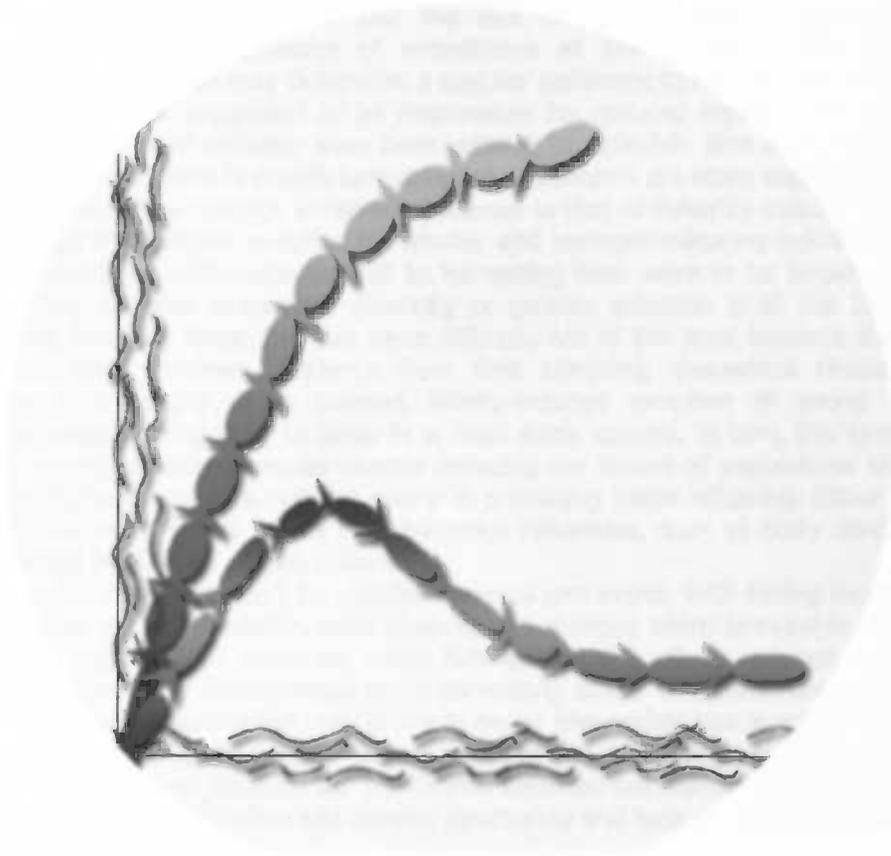


Evolving dynamics of exploited fish populations



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Abstract

Modern fishing industries have been harvesting marine fish populations in increasing amounts. It is becoming clear that despite increasing efforts, catches are diminishing and more and more harvestable stocks are depleted. Exploitation has led to worrisome losses in biomass and disruption of the age and size structure of fish populations. Classical fisheries' science is engaged in the assessment of stock abundance and in clarifying the interplay between stock constitution and the different harvesting regimes executed. Especially defining the relationship between adult stock size and the production of offspring is challenging and affected by numerous factors. The importance of this relationship for setting secure catch quota, combined with the difficulty in predicting it accurately, has attributed to the mismanagement of stocks. Overfishing has been held responsible for the collapse of several commercially important populations and the lack of their recovery, suggests complex mechanisms to rule the dynamics of populations at low densities. The capacity for compensatory reproduction may determine a species' resilience to exploitation. The opposite, depensation, has been suggested to be responsible for reduced reproductive capacity but exact reasons for lack of recovery have been difficult to establish. Size dependent predator-prey interactions and shifts in equilibrium states of ecosystems are other explanations given.

A relatively new concept in fisheries' science is that of fisheries-induced evolutionary change through the positive selection for smaller and younger maturing individuals. The life history of a species and the selectivity of its harvesting fleet seem to be largely responsible for determining whether phenotypic plasticity or genetic selection is at the base of this. Discriminating between these two has been difficult, not in the least because they are not mutually exclusive. However, evidence from field sampling, theoretical simulations and experiments is mounting which support fishery-induced evolution of young and early maturing genotypes being likely to occur in at least some species. In turn, this selection may provoke a cascade of consequences directly reducing the fitness of populations since young and early maturing genotypes perform poorly in producing viable offspring. Other properties determining the resilience of stocks to detrimental influences, such as body condition, may also be affected by the size of maturation.

Fisheries may thus select for disadvantageous genotypes. With fishing mortality being far greater than natural mortality, such maladaptive changes seem favourable above being caught before reproduction. However, when fishing mortality will be reduced in the future, either by adjustments in management or by harvesting stocks to commercial extinction, the genetic load of the remaining fish may prove to be an irreversible loss in stock viability. How such loss relates to other detrimental factors affecting the subsistence of marine populations remains to be elucidated. As does the interaction between harvesting-induced selection and population dynamics with spatial- and genetic structuring and local adaptations of stocks.

Keywords: fisheries, population dynamics, stock structure, life-history evolution

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1. Introduction

In the last century, fisheries have resulted in overexploitation of 25% of commercially valuable fish species (fig. 1; FAO 2004). Industrial fisheries are estimated to have reduced the biomass of predatory fish in the oceans by 90% and community biomass of diverse marine ecosystems with typically 80% within the last 15 years time (Myers & Worm 2003). Collapses¹ of several fish stocks (Myers *et al.*, 1997; Dulvy *et al.*, 2003; FAO 2004) together with the observation of globally declining catches (Myers & Worm 2003; Pauly *et al.*, 2003), show that our understanding of the impact of fisheries on marine resources, has been insufficient for their descent management. As Hutchings and Myers (1994) put it: "only when management fails, resulting in declining catches and stock collapses, its strategies may be evaluated". It is becoming increasingly clear that harvesting marine resources does not merely reduce biomass but is likely to affect population structure and dynamics of the exploited species and their communities as well, resulting in – initially unexpected – additional losses of recovery potential (Hutchings 2000; de Roos & Persson 2002), resilience (Hsieh *et al.* 2006) and ecosystem productivity (Worm *et al.* 2006). Furthermore, evidence is growing that species fished upon respond to exploitation by earlier maturation and changes in growth rate.

Younger maturation ages have been observed for a diversity of severely depleted fish stocks including cod (Hutchings 2004; Olsen *et al.* 2004), plaice (Rijnsdorp 1993; Morgan & Colbourne 1999) and herring (Engelhard & Heino 2004a,b). These observations go hand in hand with changes in growth rate and are most commonly explained by two processes. First, decreased densities of phenotypically plastic species may result in compensatory growth due to increased availability of- and reduced competition for resources. Faster individual growth then allows for earlier maturation or a larger size at the same maturation age (Engelhard & Heino 2004a; de Roos *et al.* 2006). Second, selective fishing for large individuals may result in genetic adaptations to the harvesting regime to which small, early mature fish may have a reproductive advantage above larger or late mature individuals (Olsen *et al.* 2004; de Roos *et al.* 2006). It has been a subject of debate if, and if so to what extent, observed changes in size and age of maturation are a plastic or an evolutionary response with a genetic basis; and entangling these two, not mutually exclusive, processes is challenging fisheries' scientists. Furthermore, there is an ongoing debate on whether processes taking place on an evolutionary timescale could seriously affect population dynamics in response to harvesting over several decades. If so, mapping out these effects is of utter importance, since size-selective harvesting leading to evolution may irreversibly affect the preservation of fisheries' yield in the long run (Conover & Munch 2002; de Roos *et al.* 2006).

From a fishes' point of view, it would be interesting to know whether genetic adaptations to harvesting would be truly beneficial in the long run or perhaps be a mere postponement of execution. Whilst small size and early maturity may seem beneficial in an exploited environment, irreversible changes in life-history strategy may affect population dynamics in an undesirable way and reduce, for example, the capacity of stocks to resist and recover from unfavourable circumstances or catastrophic events. In this essay, I will therefore try to answer the following question:

How do exploited populations respond to harvesting and would evolutionary adaptations increase population resilience in the long run?

In order to answer this question, I will discuss studies on fisheries-induced evolution but first will provide a review of the principle processes affecting the dynamics of exploited fish populations. First, I present insights in the basic principles and models involved in classical fisheries' science. There are several parameters which have gained a great deal of attention in the literature and underlie commonly used models, namely: stock-recruitment- and density dependent relationships; and the structure of stocks in cohorts of different sizes and ages. Second, I focus mainly on processes taking place in highly fecund species with high juvenile mortality, since many exploited species belong to this category.

¹ Collapse: catches reduced to less than 10% of the recorded maximum (Worm *et al.* 2006).

The dynamics discussed below are general, underlying processes and no doubt assuming them crucial for exploited fish – assuming processes to be generally comparable for species with different life histories, distributions and dynamics – can be justly criticised. However, in light of the question posed in this study, discussing these general processes will provide a handhold to evaluate possible evolutionary effects of exploitation on population resilience. This forms the second part of the present review, in which I discuss adaptations to harvesting, and how these may affect life history characteristics. What implications this may have for the future of stocks is evaluated in the final section.

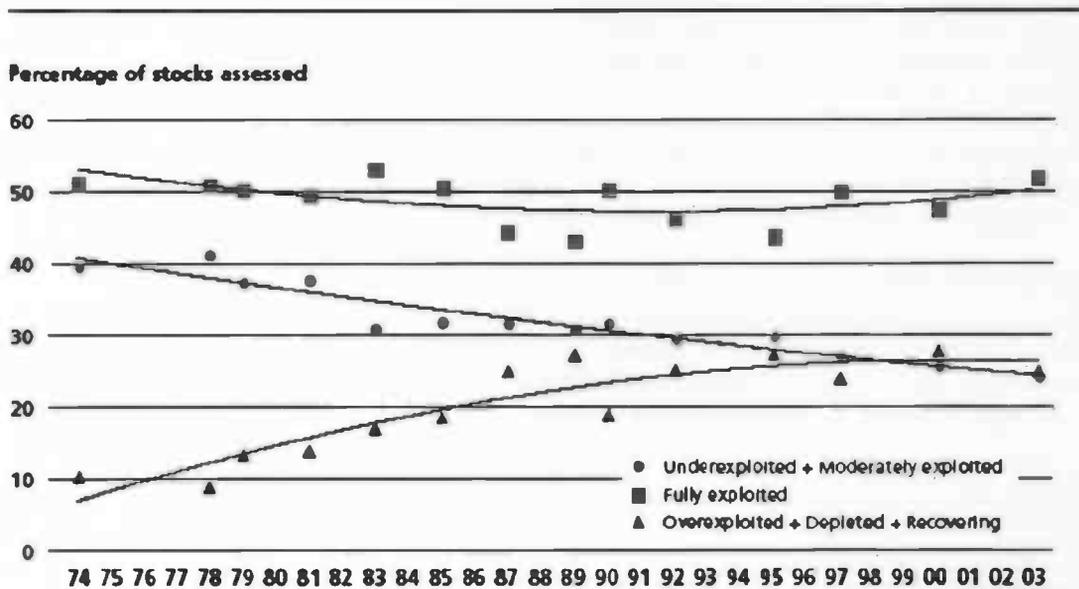


Fig. 1. Global trends in the state of world marine stocks since 1974. A consistent downward trend of stocks offering potential for expansion of fishing coincides with an increasing trend in the proportion of overexploited and depleted stocks. From: FAO 2004.

2. Basic principles in fisheries' science

2.1 The definition of stock

Prior to elaborating on population dynamics, evolution and fisheries, a brief note on the definition of stock is necessary. Unfortunately, no single uniform definition can be given for stock. In the present review, I use a slightly modified version of the definition by Ihssen *et al.* (1981): "a stock is an intraspecific group of individuals with temporal or spatial integrity". Note that, with this definition, the stock concept does not imply any *specific* amount of phenotypic, genotypic or spatial segregation. This makes it a useful working definition for fish species, since these characteristics typically vary between stocks. The stock concept has recently been reviewed by Waples and Gaggiotti (2006) who state that the definition of population depends on the objectives and context of the question proposed (fig. 2). Depending on the questions of interest, one can define a stock as a genetically separated, reproductively isolated, unit; or a group responding differently to exploitation compared to another. In this case genetic isolation may be irrelevant. These form the two extremes of a continuum of stock definitions – the former being especially of interest for conservation matters and long-term management, the latter for short-term management and exploitation (Carvalho & Hauser 1994).

One has to keep in mind this continuum and the interaction between stock definition and the question of interest while reading this study: the stock concept is a means to convert biological objectives, practical feasibility and political interests and constraints, into a manageable unit. I have chosen for such a pragmatic definition of stock since, in light of the broad nature of the issues dealt with, setting strict margins to the definition is not appropriate.

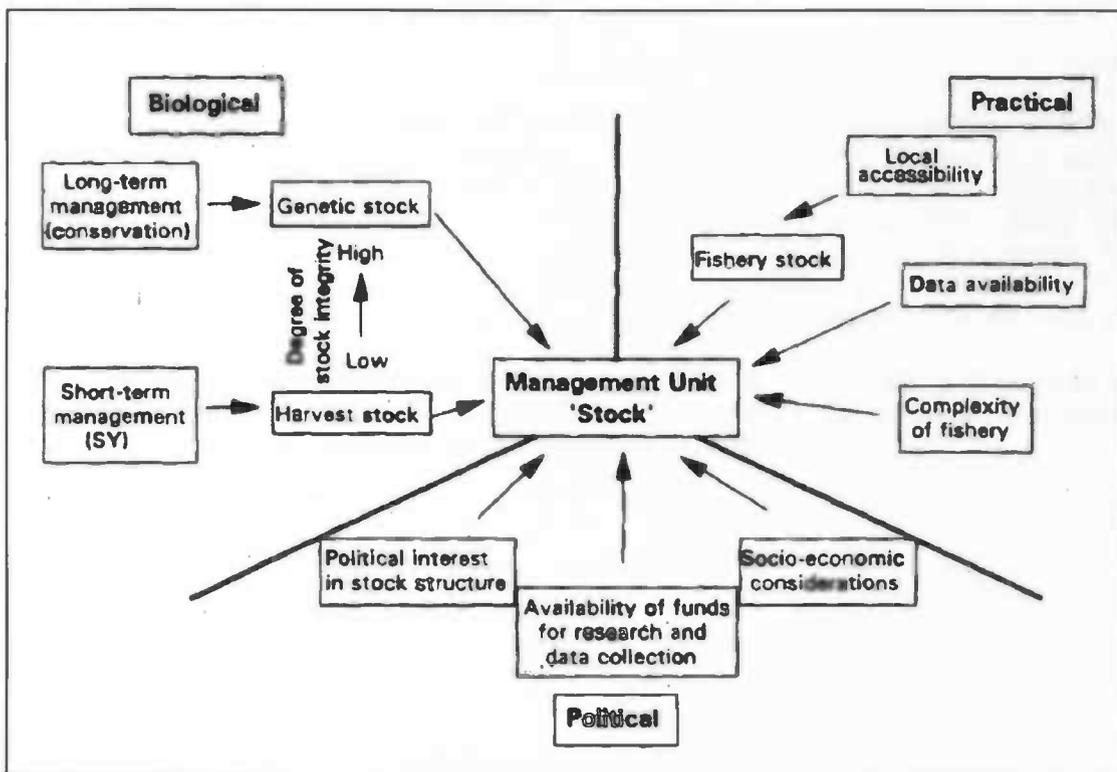


Fig. 2. Schematic representation of factors affecting the stock concept and types of stock commonly used in fisheries biology. (From Carvalho & Hauser 1994).

2.2 Modelling fishing mortality

Early studies on fish population dynamics and fisheries focused on estimating stock sizes and the component of mortality for which fisheries are responsible. In its most basic form, decrease in population size N over time, can be given by:

$$\frac{dN}{dt} = -ZN \text{ or: } N_{t+1} = N_t e^{-Zt} \quad (1)$$

In which Z , the instantaneous rate of mortality, in fisheries' science is estimated from changes in age distribution of the stock density in numbers (N) from year to year. Since Z is comprised of natural mortality (M) and fishing mortality (F), a year's catch C – the proportion of N which dies due to fishing – can be regarded as the fraction F of Z :

$$C = \frac{F}{Z}(N_t - N_{t+1})$$

or:

$$C = \frac{F}{Z} N_t (1 - e^{-Zt}) \quad (2)$$

(Cushing 1975; pers. comm. Rijnsdorp)

Already in 1900, Garstang (1900-3) proved a negative correlation to exist between fishing pressure and average catch. The catch per unit effort (effort as day's absence or hours' fishing), can be estimated by:

$$C_N / F = (R' / Z)[1 - \exp(-Z_t)] \quad (3)$$

In which C_N is the catch in numbers over the instantaneous coefficient of fishing mortality. C_N/F thus represents the catch per unit effort; CPUE, (in Cushing 1975 referred to as stock density d). The right-hand side represents the remaining stock in numbers, with R' being the number of recruits to a year class λ at the start of the fishing season and Z being the instantaneous coefficient of total mortality ($Z = F + M_{\text{natural mortality}}$). Equation (2) is referred to as the catch equation and expressed as catch per unit of effort (3) has become very important in fisheries research since catch per unit effort can be shown to be an index of stock:

Fishing mortality (F) = catchability (q) * fishing intensity (f), or $F = qf$. Fishing intensity (f) is equivalent to fishing effort (E) per unit area (A). C being FN , it can be shown that stock density (d , as catch C per unit effort E) and true density ($D: N/A$) relate as:

$$q = \frac{F}{f} = \frac{C/N}{E/A} = \frac{C A'}{N E} = \frac{C A'}{E N} = \frac{d}{D} \quad (4)$$

or:

$$D = \frac{d}{q} = \frac{C/E}{F/(E/A)} = \frac{C}{F/A} \quad (5)$$

(Modified from Cushing 1975)

The principle of CPUE being a measure for stock underlies most models in fisheries science. However, using this straightforward relationship does not allow space for variation in abundance due to stochastic effects or biological processes (Munyangorero 2001) and assuming a straightforward relationship may have serious consequences for the maintenance of stocks, resulting in biased estimates and mismanagement (Hutchings & Myers 1994; Walters & Maguire 1996). To encompass variable processes, the different components of the catch equation: mortality (Z), catchability (q), and recruitment (R') have to be assessed.

2.2.1 Estimating biomass and mortality

Fishing mortality F can be inferred from changes in Z with changing fishing effort. Natural mortality then is assumed to be constant. Aside from this, it can be deduced from catch data. Catch data are obtained primarily by two methods for estimating biomass and age structure of fish populations: research surveys and Virtual Population Analysis.

Research surveys use catch data on numbers and biomass from trawl series at different depths and at random locations. This method is designed to produce unbiased estimates of mean and variance in abundance but has the disadvantage of producing very large variances (Myers *et al.* 1997). Besides, it has been shown that the method is less efficient for smaller fish and the gear efficiency varies from year to year (Myers & Cadigan 1995, in Myers *et al.* 1997). Many survey series do not go back longer than the early seventies, which makes it difficult to impossible to obtain information on long-term trends from them.

Virtual Population Analysis (VPA) or cohort analysis on the other hand, uses data from commercial catches to reconstruct size/age-structure and abundance of the populations in a previous year. It estimates the numbers N for each class (size or age) a at the beginning of year y , using the numbers at size/age $a+1$ in year $y+1$, the catch C at a and y and estimated natural mortality M . Depending on the species, M is set at a constant of 0.1-0.2 (pers. comm. Rijnsdorp). VPA thus predicts what must have been there, based on what has been taken (C), what has died (M) and what is still there the next year.

Since catch at age data are routinely collected for many species, VPA is a convenient way to obtain information on recruitment, fishing mortality and such. However, it relies on the crucial assumption that catch-at-age data are flawless, which may be violated due to discarding practices or mis- or underreporting (e.g. Rijnsdorp *et al.* 2007). Biased estimates of natural mortality may cause biased abundance assessments (Lapointe *et al.* 1989, in Myers *et al.* 1997) but a more pressing problem seems to be increasing discrepancies between actual and reported catches.

Myers *et al.* (1997) demonstrated significant underestimation of recruitment by VPA, compared to research surveys for each of six collapsed Atlantic cod (*Gadhus morhua* L.) populations.

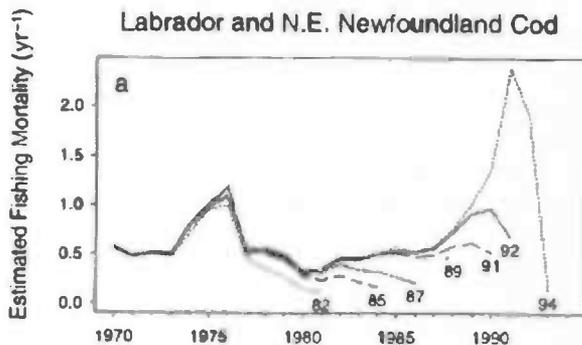


Fig. 3. Fishing mortality of cod estimated by Virtual Population Analysis in the years '82, '85-'94 for Labrador and N.E. Newfoundland cod. The last year of each time series represents the year in which the analysis was performed. Note that fishing mortality is almost always underestimated in the most recent years of the assessment, compared to later analyses.

(From: Myers *et al.* 1997).

Underestimation of recruitment combined with the observation of increased mortality of young individuals evident from research surveys but not from VPA, indicated an increasing discrepancy between actual and reported catches, i.e. increased discarding of juvenile fish and underestimated juvenile mortality. This observation is in agreement with underestimation of fishing mortality by VPA, which has been a persisting problem as fig. 3 shows and has led directly to the collapse of the northern cod (Walters & Maguire 1996).

2.2.2 Catchability

Aside from biased estimates of natural mortality and misreporting of actual catches, discrepancies between estimated and true abundances can further be explained by not meeting the assumption of fishing fleets having complete access to stocks, or by incorrect estimation of the catchability coefficient q . Catchability is defined as a measure of the interaction between fish abundance and fishing effort (Arreguín-Sánchez 1996) and is the third parameter determining catch (see eq. 3). For those management strategies setting quota not as a maximum catch in number but regarding fishing mortality as catch/unit effort

– thereby assuming constant catchability – correct assessment of this parameter evidently is of major importance for determining the effect a fishery has on any population (Arreguín-Sánchez 1996; Rijnsdorp *et al.* 2006).

Catchability is most commonly assessed by VPA: by analyses of catch fluctuations over time, variation- and trends in fishing mortality can be detected. Specifically comparing catch rates of vessels equipped with different gear, the origin of variation in catchability may be assessed. This was, for example, done recently for the North Sea beam trawl fleet by Rijnsdorp *et al.* (2006). These authors demonstrated the mortality per unit effort of European plaice (*Pleuronectes platessa* L.) and sole (*Solea solea* L.) to be positively correlated with vessel power.

Tagging studies are another means used to obtain information on catchability and abundance (e.g. Rijnsdorp & Pastoors 1995; Bolle *et al.* 2005). A major problem with data derived from such mark-recapture experiments is their reliance on fishing vessels, which determine the date and location of release and recapture: the data obtained from tags may better reflect the behaviour of the fishing fleet than that of the fish themselves. Electronic Data Storage Tags (DST) solve this problem to some extent, since they record information on the fishes' movement regularly but these are not used widely as yet (Bolle *et al.* 2005). Moreover, acquiring parameter estimates from tagging studies involves elaborate statistics and methods such as Markov Chain and Maximum Likelihood analyses (Kendall & Bjorkland 2001 and references therein). It goes too far to discuss them here in detail.

Three factors determine catchability: 1) fishing gear; 2) fishing strategy and 3) fish behaviour. Catchability can thus reflect changes in abundance (Beverton & Holt 1957), technological advances in the fishing industry or variation in the stock itself. The latter includes behaviour, such as avoidance and swimming activity, and environmental factors like temperature (Arreguín-Sánchez 1996). MacCall (1990, in Arreguín-Sánchez 1996) redefined catchability by allowing it to be affected by fraction a of the population habitat A being susceptible to fisheries. The ratio a/A is closely related to the *accessibility* of a population in geographical terms and its *availability* on a temporal scale. Temporal availability can for example be affected by diurnal or seasonal migration, mortality and recruitment processes. Both sources of variation were also observed for plaice and sole by Rijnsdorp *et al.* (2006). Catchability variation can thus be explained by temporal and spatial changes in fishing gear, - strategy and fish behaviour.

Different models have been developed for estimating catchability. Examples of early models vary between catchability being linearly dependent on estimates of population density, to catchability coefficients directly estimated from tagging studies or affected by habitat or temperature (see Arreguín-Sánchez 1996 for a review). However, they all are variations of the same relationship:

$$q = \left(\frac{1}{s}\right)\left(\frac{1}{D}\right)\left(\frac{C}{E}\right) \quad (6)$$

Where s is a constant related to fishing gear, D is the number of individuals per area (population density) and C/E the catch per unit effort.

Another feature these models share, is considering neither population structure, nor temporal variation, and hardly ever regarding more than one variable. By not taking population structure into account, these models implicitly assume fishing effort, population size and catchability to be constant and uniform over all age or size classes. However, catchability is a highly variable parameter and assumed constant, it is most probable the largest source of error in catch/unit effort models (Ricker 1975). Arreguín-Sánchez (1996) proposed a model taking into account both selectivity of fishing gear, varying q with age or time and saturation of fishing gear. The model was applied to the red grouper (*Epinephelus mori* Valenciennes) and resulted in clear effects of size and density-dependence on the catchability quotient. Such models are promising tools for deriving stock specific catchability coefficients. However, by implementing multiple parameters the models immediately become highly complex and a mathematical explanation goes beyond the scope of this study.

Box 1. Maximum Sustainable Yield, Yield per recruit and Reference Points

An important concept in fisheries' management is that of the maximum sustainable yield (MSY). Sustainable yield is defined as "the amount of biomass or the number of units that can be harvested currently in a fishery without compromising the ability of the population/ecosystem to regenerate itself" (FAO, 1997). The MSY concept is important because optimal management tries to maximise the yield per recruit. Common stock assessment methods aim to establish what levels of fishing effort and/or mortality correlate with long-term sustainable catch levels (Munyandorero 2001). It is based on the idea that fish stocks have a surplus which can be harvested without affecting recruitment (Carvalho & Hauser 1994). The MSY-concept was introduced by Beverton and Holt (1957) and is founded on the yield per recruit (Y/R) relationship, which is given by the integral of:

$$Y_w = \int FN_t W_t dt$$

In which Y_w is the yield in weight units, N_t the stock in numbers at age t and W_t gives the weight at age t (Beverton & Holt 1957; Cushing 1975). The MSY is the maximum of the Y/R plot. In fig. 4, MSY lies at a fishing mortality (F) of about 0.2. This F reference point is commonly referred to as F_{msy} . Gulland and Boerema (1973, in Beverton 1998) introduced the slightly more precautionary $F_{0.1}$, relative to the slope of the yield curve, as "the F value at which the slope of the yield curve is one tenth of that at the origin". In the same light, several other F reference points have been defined which one frequently encounters in literature and management objectives in fisheries' science.

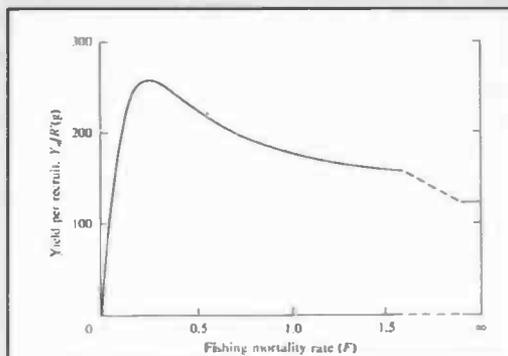


Fig. 4 Dependence of catch (Yield per recruit) in weight on Fishing mortality F (Beverton & Holt 1957). From: Cushing 1957.

F_{med} represents the level at which recruitment to stock more than compensates mortality in half of the observed years. It lies there where Spawning Stock Biomass (SSB) per recruit equals the median of observed recruits per unit of SSB. Other reference points are related to F_{med} , e.g. points at which recruitment compensates for 95% of losses (F_{high}), 5% (F_{low}) or none (F_{crash}) (Sissenwine & Shepherd 1987, in Beverton 1998). See also Gabriel and Mace (1999) for an extensive review of reference points.

Total Allowable Catch (TAC) was then derived as the, from reference points proposed, F multiplied by the assessed stock size (Walters & Maguire 1996). However, quota systems based on TAC's do not depend on recruitment levels but are mostly established on a *per recruit* basis. With many fisheries catching mixed species and by-catch discards often being underestimated, they easily contribute to overfishing which is indeed what was observed (Beverton 1998). Common F values for the 1980s are twice or triple those suggested by reference points (Beverton 1998). *Per recruit* MSY-related F values have therefore been subject to criticism in more recent discussions on stock management. Beverton (1998) proposed F_{95} as the mortality at which yield is 95% of the maximum yield. The major difference between this reference and previous ones, is that it is not based on a *per recruit* curve but on a yield curve, comprising stock and recruitment relationships (see 2.5.2). It may be estimated from Y/F curves or indirectly from natural mortality M , being approx. $2M$ for long-lived species down to less than $0.5M$ for short-lived ones. Walters & Maguire (1996) suggest it necessary for F to stay below M for cod, given the difficulties of assessing stock and recruitment levels with certainty. Nowadays, MSY is more and more regarded as associated with a too high target F (Cook *et al.* 1997; Beverton 1998), leaving no space for biased assessments and therefore enhancing overfishing and stock decline.

VPA does not make the assumptions of q being constant or the absence of population structure. With VPA, a specific catchability coefficient is estimated for each age or size class within a population. With age VPA, catchability is assumed to be equal for all individuals of the same year class or *cohort*. It thus is linked to cohort-specific characteristics whereas for size-specific q , this link is not established. Instead, the parameter changes with body length. Whatever being the trait catchability is connected to, it is assumed to change according to a certain pattern (Arreguín-Sánchez 1996). Megrey (1989) showed models to be extremely sensitive to variations in this pattern, emphasising the need for accurate estimates and knowledge on stock structure. As pointed out in 2.2.1, VPA estimates parameters indirectly

from commercial catch data. For q specifically, this is a potential problem due to the inverse relationship between catchability and abundance (see Arreguín-Sánchez 1996 for a review but also Walters & Maguire 1996). This, perhaps counterintuitive, correlation comes from the tendency of many schooling fish species to aggregate in response to decreasing population sizes. A decreased searching effort for fishermen and thereby increased catchability follows. Assuming a pattern therefore may not be incorrect but determining the exact relation can be notoriously difficult. There are few studies known which made an attempt to establish the correlation of catchability with age or size. Except for deriving it from catch data, the only possibility is by mark-recapture studies. The reduced effort required for catching populations at low abundance levels has the problematic side effect of increased catchability being mistaken for increased abundance. The concern for such a misinterpretation evidently lays in an increased risk of overexploitation (Arreguín-Sánchez 1996). In the fishing industry, it pays to minimise effort and maximising catchability is therefore desirable from a short term economic perspective. In a larger timeframe however, the risk of overexploitation should be taken into account. Especially when Maximum Sustainable Yield estimates are violated – when stocks are exploited below the level at which they can continue to be optimally harvested over the long run (see Box 1). This leads us to the third parameter of the catch equation: recruitment.

2.3 Recruitment

Recruitment is regarded as "the number of individuals surviving to the age (or size) of vulnerability to harvesting" (Fogarty *et al.* 1991). It is an extremely variable parameter in marine species, largely affected by life history traits such as fecundity, density-dependent growth stages, longevity and environmental parameters such as availability of food, predation and variations in the physical environment. Consequential variation in mortality, especially in egg- and larval life stages, results in high variation in year-class strengths.

2.3.1 Recruitment variability

Species with low fecundity and high offspring survival rates are characterised by relatively constant mortality rates and, consequently, levels of survival/ recruitment. On the other extreme, species with high fecundity, especially those with long larval life stages, are characterised by large variations in juvenile mortality and recruitment levels (Fogarty *et al.* 1991). Many exploited fish species (e.g. European plaice; clupeids such as herring and gadoids such as Atlantic cod) belong to this last category and their management should therefore take into account recruitment variability.

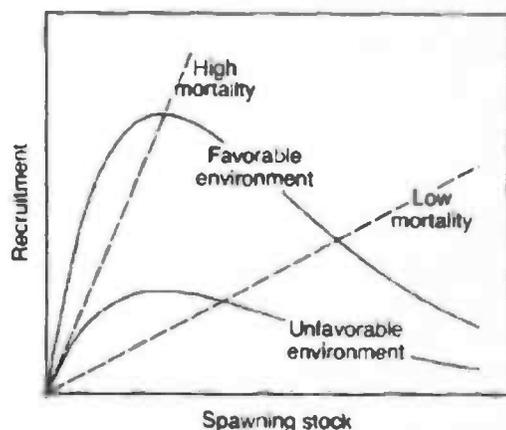


Fig. 5 Representation of a simple spawning stock-recruitment model (Ricker) in two hypothetical environments (favourable and unfavourable). The straight lines represent spawning stock as a density-independent function of recruitment under high and low (fishing) mortality. The intersections of the stock-recruitment curves and recruitment-stock lines represent equilibria. From: Fogarty *et al.* 1991.

Myers (2001) performed an extensive meta-analysis on over 700 populations of diverse exploited fish species (from the database of Myers *et al.* 1995a), regarding the effect on recruitment of different parameters such as: 1) depensation², 2) density-dependent processes at different age classes and 3) maximum reproductive rate. He found no depensatory effects for most exploited fish species but did find increased variance in recruitment rates at low population levels. He hypothesised this increased variability to be an effect of a different ratio of density-independent mortality in egg and larval stages and density-dependent mortality affecting juveniles. He concluded the relative contributions of environmental variation in recruitment and variability due to the life history strategy of a species to form the direct foundation of their *compensatory* capacities.

When recruitment of juveniles to the spawning stock does not match or overrule the loss in numbers (stock-recruitment relationship, see 2.5.2), population levels will decrease and populations may ultimately collapse (Fogarty *et al.* 1991; Hutchings & Myers 1994). The resilience of fish stocks to high levels of exploitation or other detrimental forces is closely related to their capacity to compensate for such losses and to persist under heavy exploitation (Iles & Beverton 2000).

Stock collapses have been suggested to be an effect of recruitment failures by unfavourable environmental conditions prolonged over several seasons (De Young & Rose 1993; Lear & Parsons 1993). However, this hypothesis does not get support from more recent analyses on several collapsed populations of cod (Hutchings & Myers 1994; Myers *et al.* 1997) which attribute the collapse to overexploitation, as do Frank and Brickman (2001) and Dulvy *et al.* (2003). The latter determined overfishing as the cause of collapse for 55% of the cases in their extensive analyses of 155 extinction events. Collapse due to overfishing is only possible when individuals are caught before they are able to reproduce, i.e. to produce recruits (Myers 2001), which is something indeed increasingly observed (e.g. Walters & Maguire 1996; Myers *et al.* 1997). This form of overexploitation is generally referred to as recruitment overfishing. Nevertheless, disadvantageous environmental circumstances may very well help to tip the scale by decreasing recruitment levels as indicated by fig. 5: whereas high levels of mortality still allow for equilibrium on a stock-

² Depensation: the marine variant of the Allee effect (Thompson 1993): the observation of decreased reproduction/recruitment at low population density.

recruitment curve in favourable surroundings, equilibrium does not occur when environmental conditions are less helpful to produce sufficient recruits.

Recruitment overfishing did not use to be regarded as a potential risk for highly fecund species, because they were not believed to have a strong stock-recruitment relationship – i.e. recruitment not to be affected by fishing mortality. High fecund species which gain a lot of weight during their adult lives may be more sensitive to growth overfishing: fisheries capturing the largest individuals, reducing fish sizes but not affecting recruitment (Cushing 1975). However, it is becoming increasingly clear that recruitment overfishing does take place in high fecund species as well (Walters & Maguire 1996). The age structure of a stock can play an important role in this matter, as is explained in 3.2.2.

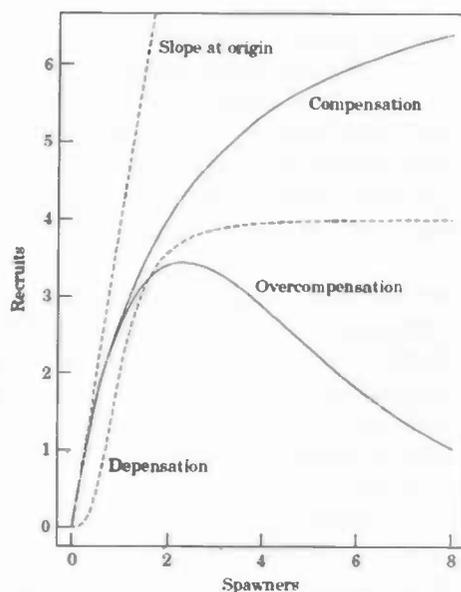


Fig. 6 Three models describing S-R relationships: Depensation (sigmoid Beverton-Holt model), overcompensation (Ricker model) and compensation (Beverton-Holt model). The slope at the origin is also shown for the latter two models. From: Myers 2001.

2.3.2 Stock-Recruitment relationships

Compensatory capacity (or resilience) of exploited stocks thus depends on the stock-recruitment relationship and on environmental circumstances (Fogarty *et al.* 1991; Beverton 1998). Recruitment has proven to be a crucial parameter when it comes to understanding the interplay between exploitation and population dynamics. The relationship between recruitment and spawner abundance is regarded as the most important one in fisheries research (Myers 2001) and numerous examples exist of studies and models investigating how the two relate to each other (e.g. references mentioned in this section). Any model describing population dynamics must describe population behaviour at high and low numbers of individuals (Myers 2001) and thereby density-dependence in at least one life stage. The most widely used models describing population dynamics by the stock-recruitment (S-R) relationship analyse individual data sets, using the classical Ricker (1954) (eq. 7) or Beverton-Holt (1957) (eq. 8) equations:

$$R = \alpha S e^{-\beta S} \quad (7)$$

$$R = \alpha S^\delta / (1 + (S^\delta / K)) \quad (8)$$

Where α – the slope of the curve at $S=0$ – is a parameter describing the recruitment per spawner unit and β and K are measures of curvature, or in other words: of the degree of compensation, which is embedded in the shape of the S-R curve. δ Signifies the level of depensation for the Beverton-Holt equation. When $\delta=1$ no depensation occurs. For $\delta>1$, depensation occurs and for $0<\delta<1$, recruitment will be larger at low population levels than for a normal ($\delta=1$) Beverton-Holt relationship (Myers 2001). Fig. 6 shows the S-R relationship for the three models, showing different compensatory behaviours.

The main difference between the two lies in the effect large spawner abundance has on recruitment: for the Beverton-Holt model, recruitment increases to a maximum and is not affected by adult abundance when numbers are large. In contrast, for a Ricker relationship, adult density determines pre-recruitment mortality directly, resulting in increased juvenile mortality or overcompensation when spawners are abundant (pers. comm. Weissing).

For semelparous³ species, the slope a through 0 can be interpreted directly as the maximum per capita reproductive rate and be used to estimate compensatory capacity (Rose *et al.* 2001). For iteroparous³ species, the parameter has to be standardised (since then R and S are not in the same units) but it goes too far to elaborate on this process here. The important point is that the value of a can (in)directly be interpreted as maximum reproductive rate and thereby determines the biological limit to exploitation (Myers 2001): when mortality would exceed a for a prolonged period of time, SBB would inevitably decrease (Rose *et al.* 2001).

When a linear relationship between stock and recruitment occurs, little to no compensation for large losses can take place, since the S:R ratio is constant. More precisely; it is the curvature of the S-R relationship – or its deviation from a linear relationship – which determines a population's compensatory capacity and thereby a population's resilience to exploitation (Fogarty *et al.* 1991; Beverton 1992; Iles & Beverton 2000). This can also be illustrated by fig. 5: a linear S-R relationship would not yield equilibrium points at low abundance levels and the maximum difference between the S-R curve and the R-S relationship or replacement line⁴ are a measure of compensation (Iles & Beverton 2000).

Ricker's model illustrates an overcompensatory S-R relationship, in which the number of recruits decreases when the number of spawners becomes large, causing overcrowding at a given life stage and reduced recruitment as a consequence. The Beverton-Holt model does not show this behaviour but rather an asymptotic maximum to which recruitment approaches at large stock sizes. At small stock sizes, both the Ricker and Beverton-Holt (given $0 < \delta < 1$) model show compensation, where the steeper curvature indicates the stronger increase in recruitment at low population levels and thus resilience.

Fitting actual data to stock-recruitment curves is problematic due to the substantial amount of variance in true recruitment. Also, when several stocks are combined in an attempt to fit an S-R relationship, this may prove to be much weaker than for each sub-stock separately.

This turned out to be the case for North Sea herring, where the combined S-R relationship for three sub-stocks seemed to be weak, in contrary to the relationships of individual stocks (Nash & Dickey-Collas 2005). Messy data allow practically any model to be fitted to a given data set (Beverton 1998, see fig. 7 for an example). Estimating compensatory capacity from a stock-recruitment relationship is tricky due to this high uncertainty on the shape of the curve. The distribution of the variance however may be indicative of at which life stage density dependence occurs (Iles & Beverton 2000) which will be central in the next section.

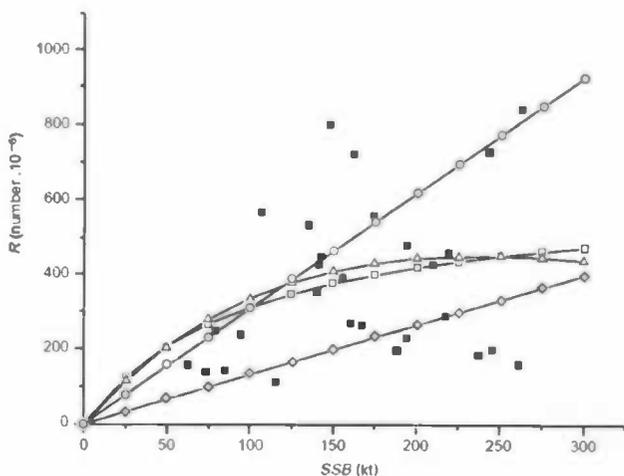


Fig. 7 Stock and recruitment data for North Sea cod with fitted Beverton-Holt (\square _ \square) and Ricker (Δ _ Δ) stock-recruitment curves. Lines represent replacement lines⁴ at low (\diamond _ \diamond) and high (o _ o) fishing mortality. From: Beverton 1998.

³ Semelparity: adult individuals spawn only once in their life. This in contrast with iteroparity; where individuals reproduce repeatedly throughout their adult life and thus overlapping generations may occur (www.marlin.as.uk).

⁴ Replacement line: the number of recruits required to replace any given spawning stock in the future.

3. The Structure of stocks

So far, I have discussed some principal theory underlying most classic models used in fisheries' science and subsequent management issues. The way I presented these basic principles, they do not take into account any demographic structure of stocks. The focus of this section will be on that matter. The study of the effect of structure in populations on their dynamics and response to exploitation is a very extensive field. Numerous examples can be given of factors affecting the way a given stock responds to exploitation but I focused on several key features that can explain for a large part the different responses of species and stocks to exploitation: density dependence and age/size structured populations.

The importance of understanding the structure of fish stocks has been emphasised when stocks of several commercially interesting species collapsed. The realisation arose that effects of fishing may not be reversible (Frank & Brickman 2001). For example, the Atlantic cod off the Canadian coast was estimated to suffer losses of over 75 – 99% of the spawning stock biomass and collapsed in the early 1990s (Hutchings & Myers 1994; Myers *et al.* 1997). Moreover, even after a ban on fishing, the stocks did not recover. Similar observations of non-recovery have been observed for other species such as flatfish (Hutchings 2000). Collapsed herring stocks on the other hand, such as the Downs herring in the North Sea in the 1970s, recovered within ten years time (Cushing 1992; Nash & Dickey-Collas 2005). The observation of non-recovery of some collapsed stocks and recovery of others is – at least partially – underscored by differences in their respective life histories and population dynamics, of which one main ingredient is density-dependent regulation at different life stages (Frank & Brickman 2001; Rose *et al.* 2001).

3.1 Density dependence

Understanding the interaction between the density-dependent- and density-independent life stages, is crucial in order to apply the general S-R and compensatory mechanisms to specific stocks (Rose *et al.* 2001). Especially unravelling the relative contributions of the different regulatory mechanisms to abundance estimates, is notoriously difficult for fishes because of high natural variation and sampling problems (see 2.3).

Density-dependent processes may vary between stocks of the same species, between life stages and, temporarily, for a given life stage. Furthermore, environmental variation can affect density-dependent regulation (Rose *et al.* 2001). However, understanding the link between the change in abundance over time and the S-R relationship is crucial if one wants to grasp at what life stage variability is damped (Iles & Beverton 2000) – i.e. at what life stage numbers are controlled not so much by stochastic processes but rather by carrying capacity. The shape of a S-R relationship, as well as the distribution of the variance around it, may be indicative of at which life stage density dependence occurs (Beverton 1995; Iles & Beverton 2000).

3.1.1 Compensatory recruitment

The Concentration Hypothesis

In terms of stock and recruitment, density-dependent processes can act upon two stages: before and after recruitment. When density-dependent processes act upon the former, the maximum number of recruits would be reached before the adult population size would reach its carrying capacity. This would result in a sharply curved, asymptotic relationship, as

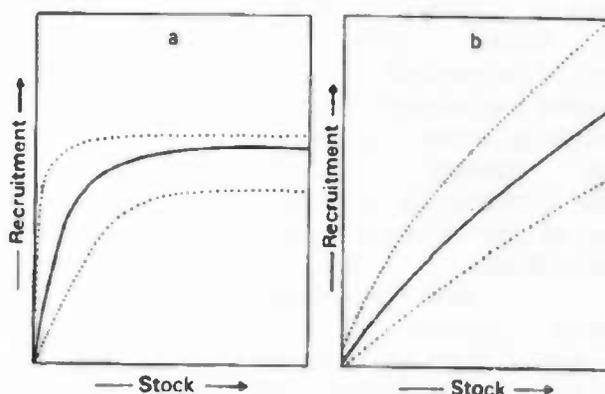


Fig. 8. Stock-recruitment diagrams which illustrate the probability of the recruitment distribution around a fitted S-R curve when density-dependence acts upon (a) the juvenile and (b) the adult life stage. Recruitment limits are indicated by dotted lines and distributions are assumed to be log-normal. From: Beverton 1995.

illustrated by fig. 8a. Recalling fig 6, a S-R curve of this kind indicates strong compensatory capacity of the corresponding species. When density-dependent processes do not act upon the juvenile phase, the corresponding S-R curve would be more linear (though eventually it would have to curve to some limit) since spawning stock biomass (SSB) would be limited not by recruitment but by the adult habitat, allowing the stock to increase further and not being suppressed by forces that limit recruitment. This principle is embedded in Beverton's *Concentration Hypothesis* (Beverton 1995), which he proposed to explain low recruitment variability in highly fecund species which tend to settle as juveniles in so-called 'nursery areas'. These nursery areas would limit numbers of juveniles in the 2-dimensional nursery habitat just after metamorphoses by e.g. overcrowding and food availability. Fig. 9 illustrates this concept for a strong concentrator: North Sea plaice. The concentration concept also implies that the distribution of recruitment variability may contain important information: when numbers approach the carrying capacity of the juvenile habitat, above-average recruitment years would become rare, resulting in downwards-skewed variation probabilities (fig. 8a). For non-concentrators or species with density-dependence operating on the adult life stage, such a skewed variance around a fitted S-R plot would not be visible (fig. 8b).

Iles & Beverton (2000) provided the statistical evidence for the Concentration Hypothesis analysing S-R series of 63 stocks of species with different degrees of concentration in the juvenile phase. Based on their analyses, they categorised high fecund species into three categories: The strongest concentrators are 'benthic' species such as the flatfish plaice, sole and halibut. A second group, 'proxima-benthic', consists of species that have pelagic egg phases and which move to the sea bed shortly after metamorphosis. This group includes mainly gadoids, for example Atlantic cod. Concentration is less pronounced in these species and one gadoid, North Sea haddock (*Melanogrammus aeglefinus* L.), does not concentrate at all. To the third group, 'pelagic', minor concentrators such as herring and

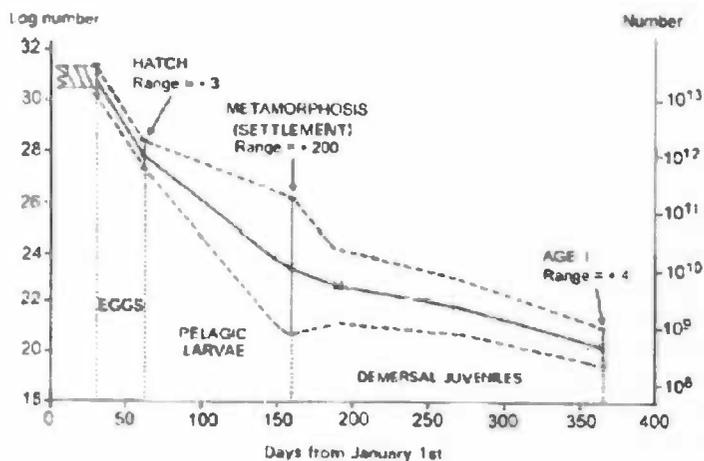


Fig. 9. Survival curve of first year of North Sea plaice showing averages (solid line) and variance (dotted lines). A decrease in variance after metamorphosis and settlement of juveniles, illustrates the concentration hypothesis. From: Beverton 1998.

entirely pelagic, non-concentrating, species as sardine (*Sardinops* sp.) and mackerel (*Scomber* sp.) belong. The authors found a strong correlation between the amount of concentration and variance in recruitment, as well as with a standardised compensation index. In general, spatial regulation by adult habitat is less common than by that of juveniles. For most demersal fish (to which commercial species such as cod, plaice and sole belong), strong density dependence in the juvenile habitat determines the stock size. (Beverton 1995; Myers 2001). Even when present, adult phase density-dependence may be limiting the maximum population size but would probably not be powerful enough to prevent stocks from collapsing (Beverton 1995): stock collapse by reduction of recruitment could still take effect and would not likely be compensated by the potential of larger stock sizes due to the lack of restrictions on recruitment. On the contrary: non-concentrating species, spending their entire life in the pelagic environment, may be much more vulnerable to variability in recruitment and less resilient to exploitation (Iles & Beverton 2000).

The role of life history strategies in compensation

Rose *et al.* (2001) looked at compensatory capacity from a different perspective. They did not focus on presence/absence of a concentrated life phase but regarded compensatory capacity to be a result of the life-history strategy. The latter as a function of three parameters: age of maturity, fecundity and juvenile survivorship. They discriminated specifically between compensation – as the process of strong response to changes in abundance – and compensatory reserve; the excess reproductive capacity. These two are not mutually inclusive. Fig. 10 illustrates their hypothesis which is discussed below.

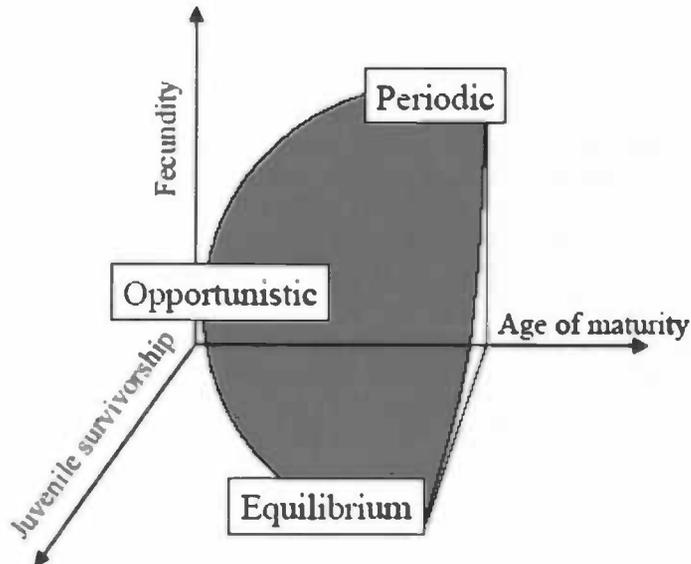


Fig. 10. Three endpoint life-history strategies derived from fecundity, age of maturity and juvenile survivorship. Adopted strategies of fish species can lay anywhere on the surface between the three endpoint strategies opportunistic, periodic and equilibrium. From: Winemiller & Rose 1992 in Rose *et al.* 2001.

An equilibrium strategy (low fecundity, old maturation age and high juvenile survival) can be found with, mostly intermediate sized, species in stable environments. Such strategists invest much energy in their offspring and as a result, recruitment variability is fairly low. However, the trade-off between high offspring survival and low fecundity results in density-dependent processes acting upon the adult population and very low compensatory capacities. Thus: high compensation and low compensatory reserve.

Opportunists (relatively low fecundity, low juvenile survivorship and early maturation) are characterised by frequent reproduction, long spawning periods, fast growing larvae and high adult mortality. They are mostly small species that do not grow very old. The low value of all three parameters results in compensatory capacity intermediate between equilibrium and periodic strategists. The latter are species with both high fecundity and juvenile mortality that mature late in life, after they have attained sufficient body weight to produce large broods. They are often long-lived and spread their reproductive output to spread risks and consequently have large inter-annual variances in recruitment and abundance, seldom exploiting the full carrying capacity of their environment. Due to this periodicity, the authors argue periodists to have the largest compensatory reserve.

Testing the validity of the described pattern of life-history traits and compensatory capacity on 249 populations of the world's largest stock-recruitment database (from Myers *et al.* 1995a) supported their expectations but superficially, since in-depth statistical analyses on group differences and possible measurement errors were not performed. Rose *et al.* emphasised as well the notorious difficulty of acquiring useful S-R data and the tremendous variance, clouding possible trends and correlations.

3.1.2 Depensation

Depensation² is another process engaged in density-dependent regulation. Commonly given explanations for the observation of depensation are; reduced opportunities for finding a partner, less defence against predators and decreased offspring survival at low densities (Liermann & Hilborn 2001). Myers (2001, supported by Myers *et al.* 1995b) did not find strong proof for depensation to play an important role in decreasing recruitment at low population levels of most fish stocks: for only three of 129 analysed stocks, δ (eq. 8) was significantly larger than one. Even then, he argued that changes in the environment would be a more likely explanation for the decreased recruitment. Liermann and Hilborn (1997)

reanalyzed the same data with a Bayesian method which resulted in low probabilities of depensation as well. Nevertheless, they did advise to incorporate the possibility of depensation in S-R analyses, since the obtained depensation levels covered a broad range of probabilities and certainty on its importance is therefore very difficult to obtain.

Obtaining reliable information on S-R relationships is especially challenging at low population levels due to the increase in variation around this relationship by stochastic processes and consequently decreased detectability of patterns. Collapse of a stock may follow when recruitment falls below equilibrium (Frank & Brickman 2001; Lierman & Hilborn 2001; Hsieh *et al.* 2006). When depensation is an issue, collapse is an even larger risk since the S-R curve then has a concave shape, causing the equilibrium at small population sizes to be unstable and recovery to be problematic.

Frank and Brickman (2001) state that assuming no depensation in management can seriously increase the risk of stock collapse not followed by recovery. Not only are data rare and difficult to read for low population levels, but levels defined as "low population levels" may still be above the levels at which depensation would take place, resulting in low statistical power of tests, while not covering data actually indicating depensation (Liermann & Hilborn 2001). Lack of evidence due to a lack of proper data should thus not be automatically interpreted as absence of depensation (Frank & Brickman 2001; Liermann & Hilborn 2001). However, assuming it *a priori* is not satisfactory for the endeavour of understanding population dynamics at low abundance levels. In section 3.2.3, I discuss a possible explanation for depensation by alternative equilibrium states of populations.

Minimal Spawning Stock

In the same paper, Frank and Brickman discuss another assumption, underlying virtually all fitted S-R curves: crossing the axes at the origin. While it is undoubtedly true that zero spawners will produce zero recruits, one can put a question mark when stating more than zero spawners will produce at least some recruits. Data are rare and variable and in fact are not so supportive of this assumption which, they state, "has probably done more harm than good". A SSB threshold may exist at which stocks are still relatively numerous but below which, extinction is inevitable. Removing the zero-intercept assumption results in a whole different curve: no recruitment will take place unless a minimum SSB threshold is present. Falling below the threshold then would eliminate any prospects to stock recovery.

Serebryakov (1990) suggested several reference points for defining a SSB threshold in terms of survival rates (as recruits per unit of SSB): Safe SSB and Minimum SSB defined as the average survival resulting in respectively a strong and an average year class, and Dangerous SSB, where high survival is needed to produce an average year class. Such thresholds could reflect the vulnerability of stocks to collapse and did in fact correspond with the collapsed Northern cod stocks off the coast of Canada. Nevertheless, they were not regarded as applicable reference points and not implemented in management. Frank and

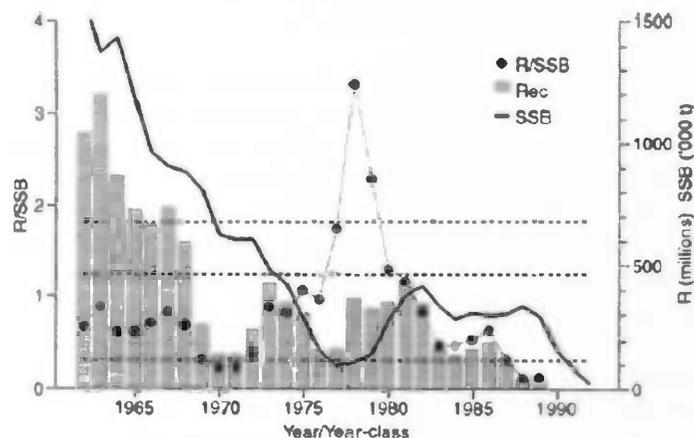


Fig 11. The Serebryakov method applied to Northern cod. Dashed horizontal lines indicate SSB thresholds, bars represent Recruits and lines respectively SSB (-) and R/SSB (•). From: Maguire & Mace 1993 in Frank & Brickman 2001.

Brickman (2001) cannot explain why but regard it not unlikely to be due to distrust in strong S-R relationships. Examining fig 11, it is evident that it could have been wise to reckon with a threshold SSB, since collapse in the 1990's coincides perfectly well with passing the threshold of Dangerous SSB. It has to be said that cod is argued to be one of only few examples of species that show a clear stock-recruitment relationship. The reluctance of management to act accordingly, may well come from a lack of convincing data at the time (Walters &

Maguire 1996).

Fig. 11 illustrates another feature which may add up to the confusion around depensation. Whilst indicating the importance of a minimum SSB, fig. 11 seems also supportive of compensation in cod: after all, the R/SSB increased at low SSB levels in the late 1970's. Frank and Brickman do not pay attention to this specific observation in this figure but they do give a possible explanation by elaborating in a more general manner on apparent compensation: not only do the Serebryakov Reference points change with available data and variations in stock and recruitment over time – and thereby cannot be used as a reference for management over prolonged time – but (in this example at least) they are based upon data derived from management stocks units, thereby ignoring stock structure and differences between biological stocks. This can have several implications (Frank & Brickman 2001). Frank and Brickman (2000, in Frank & Brickman 2001) simulated Northern cod as six sub-stocks, keeping track of stock, recruitment and R/S levels. When abundance decreased, the stock displayed strong compensatory response (as increased survival rates R/S) but with closer examination it became evident that all stock structure had disappeared by decreased recruitment and extinction of sub-stocks (see also Berkeley *et al.* 2004). Depensatory effects at sub-stock level may thus be covered when multiple stocks are managed as one unit. Due to constraints on time I will not review spatial- and sub-stock structure in more detail but will discuss another important feature of stocks, also ignored by Serebryakov's – and many other's – reference points, by assuming no effects of age-structure on a population's resilience to exploitation.

3.2 Age and size structured populations

More and more it is realised that our failure in managing fish stocks in a sustainable manner is at the least partially underlain by regarding harvestable-, adult- and spawning stocks as one and the same unit. This not being true has serious implications but is so far not taken into account in management issues (Berkeley *et al.* 2004). Not all harvested individuals are adults and not all adults contribute to the next generation. Data, supported by models, are telling a clear story: fish stocks are not uniform. Specifically, they consist out of multiple year classes or *cohorts* and spawning is not a single event, nor does spawning or maturation take place at the same instant for the entire cohort. These latter two features are typically assumed for management purposes, which set maturation age and capture age as an average below which the probability of capture or maturity is zero and above which it is 100%. Such "knife-edge" assumptions⁵ do not meet reality but underlie many reference points and models on fish dynamics. Serebryakov's initial SSB thresholds are an example.

Models and stock assessments assume, at least to some extent, SSB as being an index of recruitment and thereby implicitly assume spawners to attribute to the recruitment pool in a predictable manner. However, when due to exploitation sudden changes in the age and size structure of stocks take place, or when spawning gets disturbed, this assumption becomes unrealistic (Murawski *et al.* 2001). Evidence supporting such disturbing effects of fishery – affecting age structure and equilibrium state of populations – is growing.

3.2.1 Viability and survival of progeny

Not all spawning individuals produce new cohorts in equal amounts. In most teleost fish, it is the larger and especially the older, more experienced females that contribute most to recruitment by producing more, and more viable offspring. On the other hand, first- and second time spawners perform especially badly (Murawski *et al.* 2001 and references therein; Berkeley *et al.* 2004). Well-studied examples are cod, which show a positive correlation between maternal age/ size and egg size (the latter correlated with egg viability) and flatfish, having a positive correlation between fecundity and maternal length/weight (Armstrong *et al.* 2001). Furthermore, older fish tend to time their spawning better, often earlier in the season, thereby increasing the chances of offspring survival (Berkeley *et al.* 2004). Hedgcock (1994) hypothesised recruitment of many oceanic species to take

⁵ Knife-edge exploitation patterns assume that below the age at first capture – i.e. the age attained by 50% of the captured individuals of a given sex (modified from FAO, www.fao.org) – fishing mortality = 0, but at or above the age at first capture, the cohort is fully vulnerable to the same rate of fishing mortality (Gabriel & Mace 1999).

place in a 'sweepstakes' pattern: a winner-takes-all strategy in which only those individuals that time their spawning well with environmental conditions, produce surviving progeny. Hilborn *et al.* (2003) describe sockeye salmon (*Oncorhynchus nerka* Walbaum) to time their spawning in early spring according to the long-term average thermal conditions, causing embryos to develop in cold water but juvenile development to match planktonic abundance upon which they can feed.

Another strategy to reach the same goal, exercised by many long-lived species, is to spread reproductive output over multiple seasons (so-called iteroparity). Fisheries intervene with this bet-hedging strategy and disrupt the age structure of stocks by recruitment overfishing – killing juveniles before they get the chance to reproduce (Myers *et al.* 1997) and by removing mostly the oldest, largest, individuals.

3.2.2 Age structure and population resilience

In addition to fisheries eliminating the most reproductive fraction of stocks in the above manner, truncation of age structure also increases the impact of stochastic events on populations and reduces their resilience to environmental change (Hilborn *et al.* 2003; Hsieh *et al.* 2006). The latter authors were able to explicitly separate environmental effects from fishery effects by comparing the coefficients of variation in temporal larval abundance of 13 exploited and 16 virgin fish species, using larval abundance as an index of parent stock. They discovered a strong increase in variability of larval abundance in the exploited stocks compared to the unexploited ones, even after correcting for life history differences. They attribute the increased variability of exploited stocks to the disruption of the "long-tailed" age distribution (a tail of old individuals) and consequent undermining of bet-hedging strategies. A significant relationship between age at maturation and the coefficient of variation was also found. This would result in populations being more susceptible to temporal variability and secondly, may occur even when reductions in numbers are not an apparent threat (Hsieh *et al.* 2006). The fact that fisheries also provoke increased variance in abundance levels can be deduced from a simple population model illustrated by the same authors. Let adult abundance in the next time step N_{t+1} be described by the number of adults N_t lessened by mortality (M, F) and increased by recruitment R_t :

$$N_{t+1} = N_t e^{-(M-F)} + R_t \quad (9)$$

It then becomes obvious that the importance of recruitment increases when abundance N_t is low. Since recruitment variation is regarded as the most influential factor on abundance variability, fishing may cause increased variability and the accompanying decreased resilience (Hsieh *et al.* 2006). The authors ignore the fact that recruitment is, at least to some extent, dependent on N itself. This is presumably done for the purpose of simplicity when explaining the increased importance of recruitment variability at low population levels. Nevertheless, the two individual effects of removing large individuals and decreasing abundance, both increase recruitment variability and thereby provoke stochastic variation even more. Even catch levels which are considered sustainable can half the number of age classes of a population (Berkeley *et al.* 2004).

The Atlantic cod can be used as a biological example to stress the importance of age structure. Cod are an iteroparous species that can attain 15 years of age and thus have around 15 cohorts thriving in a single population (Trippel 1995). The age of 50% maturity was around five in the mid 1990s (Olsen *et al.* 2004) but cod were caught as young as three years of age (Myers *et al.* 1997). The latter authors explain how high catches of juveniles contributed to the collapse of Canadian cod populations: the high catches of adult cod were associated with high juvenile mortality resulting in recruitment overfishing and ultimately in the collapse of the stocks (see also 1.3). Secondly, cod continue to grow after maturing and are more likely to produce successful broods each time they spawn. By fishing away the older individuals, recruitment success was reduced and in addition, truncation of age structure reduced the number of year classes present in stocks. Stocks have not returned to this day (Trippel 1995, Berkeley *et al.* 2004; Hsieh *et al.* 2006).

Numerous publications have stressed the importance of preserving the complex age structure of stocks (e.g. Frank & Brickman 2001; Berkeley *et al.* 2004; Hsieh *et al.* 2006).

Next to affecting recruitment and perhaps less straight-forward, size-selective fishery may affect population structure by altering equilibrium states between predators and their prey.

3.2.3 Size structure and equilibrium state

De Roos and Persson (2002) modelled the dynamics of a predator-prey-resource system mathematically and implemented predation as being size-selective: only prey smaller than a certain length, were susceptible to predation. Food intake and maturation of prey (or consumers) were modelled as size-dependent as well and growth took place by a von Bertalanffy growth function (see Box 2). Predator mortality was introduced as a variable.

They found that varying the predator mortality rate yielded different equilibria between resource, juvenile and adult prey and predators. Most importantly, they observed collapse of the predator population not followed by any prospect on recovery when their mortality was set above a certain 'persistence threshold'. Predator density had to be high and mortality much lower (below an 'invasion threshold') in order for predators to be able to invade a stable consumer-resource equilibrium.

In their simulations, depensation was hence a result of merely the dynamics of size-dependent growth of prey and size-selective predation by predators. No assumptions about underlying depensatory mechanisms were required (e.g. low probability of finding a partner) which are often assumed to explain depensatory dynamics in other models and field observations (see Liermann & Hilborn 2001 for a review on the latter). Predator density also greatly affected the constitution of the prey/consumer population.

Fig. 12 describes some of their results: high predator densities coincide with abundant adult consumers, few juveniles and high resource levels. Since predators feed on juvenile consumers, increasing predator mortality enhances initially only juvenile and resource density (thick solid curves) but when passed the persistence threshold (vertical dotted line), instable equilibria (dashed curves) between predator and prey communities arise and result in collapse of the predator population and a stable equilibrium with high juvenile, low adult consumer biomass and low resource levels (solid horizontal lines).

They looked at the effect of size-selective mortality on the constitution of the consumer population as well. Assuming a resource-dependent growth response of consumers, size-selective predation results in both larger individuals and more adult and vulnerable juvenile biomass of the consumer population, and higher resource levels (fig. 13). Counter-intuitively, decreased predation causes overcrowding of juveniles and reduces growth by resource competition. The maximum length attained by adult consumers is thereby decreased and so is biomass of juveniles upon which can be predated – inhibiting the re-establishment of the stable equilibrium. Predators may thus increase the availability of suitable prey by feeding on them (de Roos & Persson 2002).

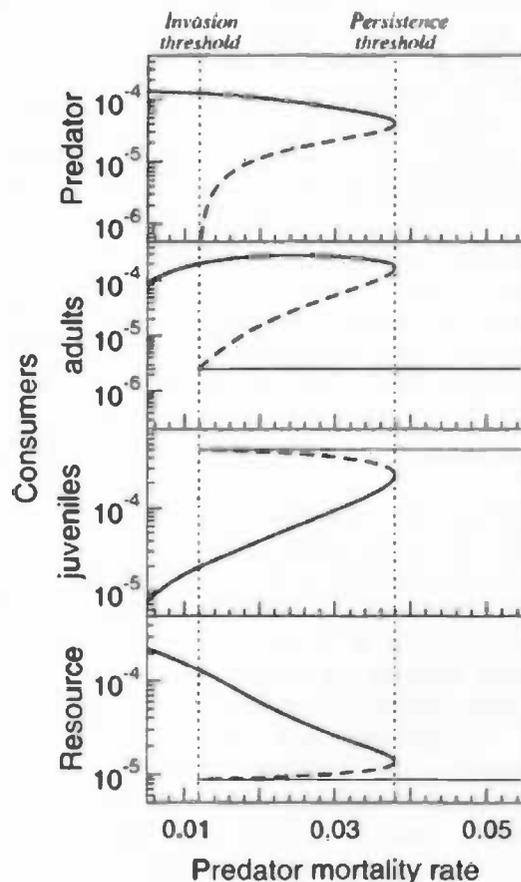


Fig. 12. Variation in predator density (individuals/l) and adult and juvenile consumer and resource biomass (g/l) as a function of predator mortality rate. Solid lines represent stable equilibria, dashed lines unstable ones. Solid horizontal lines represent stable equilibria without predators, which can occur alternatively between the invasion and persistence threshold predator mortalities. From: De Roos & Persson 2002.

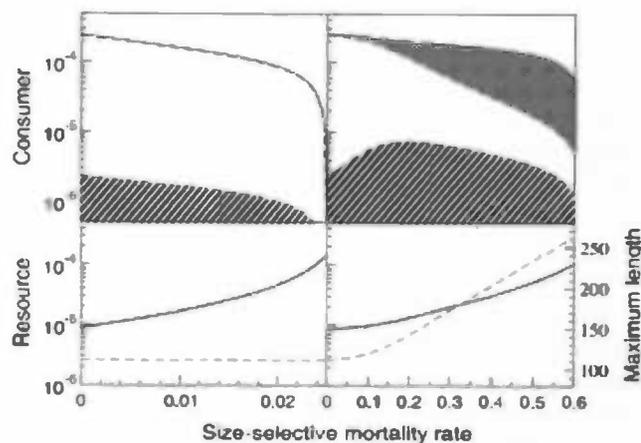


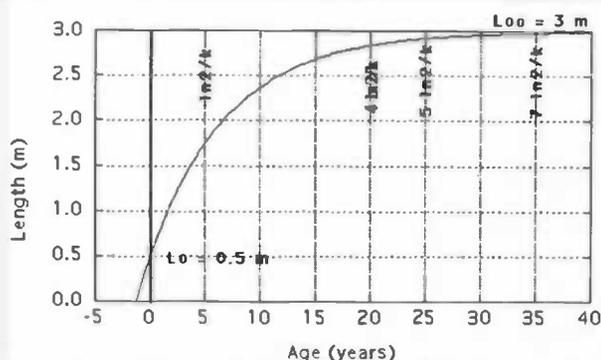
Fig. 13. Variation in biomass of the size structured consumer-resource system by varying size-selective mortality rate (day^{-1}). Upper charts: total biomass (g/l) is partitioned in juveniles vulnerable to predation (hatched), non-vulnerable juveniles (white) and adults (speckled). Lower charts: resource biomass (solid line, g/l) and maximum individual length (dashed line, mm). The left-side graphs represent the case of non-resource dependent growth, in which maximum length thus is a constant. The right side shows what happens when individual growth and maximum length increase with resource availability. Both vulnerable juvenile- and adult biomass increase. From: De Roos & Persson 2002.

Box 2. The von Bertalanffy growth function

Von Bertalanffy (1938) was the first to describe length as a linear function of age. Length L at age t is determined on the basis of the difference between length at birth L_0 and maximum length L_∞ and some growth constant K :

$$L(t) = L_\infty - (L_\infty - L_0)e^{-Kt}$$

(Beverton & Holt 1957; pers. comm. Weissing 2006). The resulting curve looks similar to the following:



From: <http://homepage.mac.com/mollet/VBGF/VBGF.html>

the size at which individuals are safe for predators. When maturation would be possible at a size when individuals could still be at risk of predation, the dynamics would likely be different. Such a model would be interesting to study the dynamics of maturation size and growth rates in the presence of different predation levels and perhaps could be used to study the predator-prey-resource system of fishing industry-cod-capelin.

Since the model was founded on very wide-spread traits – i.e. predator selection for small prey and resource-dependent growth – the obtained size-dependent dynamics may apply to a whole range of community systems. Though optimised for a fresh water community, the results may give an explanation for the observation of large shifts in capelin (*Mallotus villosus* Müller) populations after the disappearance of their main predator, cod, in the Northwest Atlantic: here capelin became smaller but their abundance higher and the numbers of their planktonic food sources increased as well. This, together with the non-reappearance of cod, is in agreement with the model and figs. 12 and 13.

Furthermore, the authors stress the importance of the observation of a different invasive and persistence threshold for predators. This is a characteristic typically ignored by classical food-chain models but important, since it allows for the coexistence of different equilibria for identical levels of predator mortality. Whereas classical models cannot explain collapses without specifically assuming the presence of a depensatory mechanism, the 'instability region' between the two thresholds in the size-structured model is itself sufficient to explain depensation: predators may exist over a broad range of mortality rates but in order to invade an equilibrium system, mortality has to be substantially lowered (de Roos & Persson 2002).

One drawback of their study is the assumption of maturation length being larger than

Equilibrium shifts

Frank *et al.* (2005) provide evidence for the collapse of cod populations at the Scotian Shelf, Canada, resulting in a 'trophic cascade': they demonstrated the disappearance of the large benthic predatory community to cause a shift in the constitution of the dominant species: from a very productive benthic community, dominated by cod and other large predators such as haddock and American plaice (*Hippoglossoides platessoides* Dery), the system shifted towards a community dominated by pelagic fish and large invertebrates like shrimp and crab, associated with smaller plankton species and low ecosystem productivity.

Beverton (1998) mentioned the collapse of Norwegian spring-spawning herring in the Barents Sea in the 1960s. He hypothesises how capelin took over the niche of herring in the Barents Sea after this stock had been effectively fished away. Herring could not recover until a large year class of cod eliminated the majority of capelin.

Another explanation given for the recovery of collapsed herring stocks, in contrary to those of cod for example, is connected to their clupeid life history of forming isolated schools in pelagic environments. In contrary to many benthic (gadoid) species, such schools are fished upon by very selective gear and can be effectively get round when overfishing demands such a measure. In the example of cod, which coexists with other exploited species in the same habitat, the diminished stocks get still depleted further when other species are targeted. Furthermore, herring mature relatively young which increases their resilience to exploitation (Hutchings 2000). Whilst for cod, a substantial part of the juvenile individuals already belongs to the harvestable stock (Cook *et al.* 1997) this number is lower in herring. However, indications are accumulating for early maturation being a strategy being employed by an increasing number of species to avoid the detrimental effects of exploitation to their subsistence.

Box 3. Maturity ogives

Maturity ogives are the most common way to describe maturation in fisheries' science. They represent "the proportion of mature individuals in a population as a function of age and or size" in histograms such as fig. 14. Knife-edge ogives assume a vertical slope between at the age class at which 50% of the individuals is mature (T_{mat} in fig. 14). Maturity ogives do not discriminate between first-time or repeat spawners (Heino *et al.* 2002) and it is important to keep in mind that the ogive merely indicates the proportion of mature individuals in a cohort over time and not the maturation process itself. Changes in the maturation rate as inferred from an ogive therefore do not necessarily indicate changes in the maturation process but can reflect modifications of growth and mortality rates as well (ICES 2006).

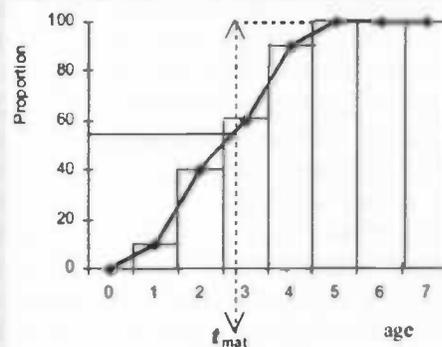


Fig. 14. Example of a simple maturity ogive. From: Cadima 2003.

4. Adaptation to exploitation

The relationships between stock size and recruitment, combined with the structuring of stocks in size classes and different age groups, yield a differential contribution of stock components to the next generation. In the previous section, I already described how the disruption of structure by exploitation may cause violation of the assumed reproductive output and predictions on recruitment and future levels of abundance. In this section, I discuss another feature simultaneously caused- and overlooked by management: the adaptation of stock structure to exploitation. The disruption of structure by excessive fishing mortality does not only result in biased assessments and predictions but consequently allows for alternative life-history strategies and age- and size structures to occur. To what extent such observations may be caused by phenotypic plasticity as a response to changing conditions or have a genetic basis, is explained in this section.

4.1 Plasticity and adaptation

Two alternative explanations are most commonly given for the observed changes in maturation age and size of exploited populations. First, the compensatory response hypothesis predicts younger maturity to come forth as a phenotypically plastic response from increased growth rates due to less competition in exploited populations. The required length of maturation (L_{mat}) is then reached at an earlier age. The second, evolutionary response hypothesis, predicts selection to increase the frequency of early maturing genotypes, since harvesting greatly diminishes the chances for late matures (Engelhard & Heino 2004a). Which hypothesis is in accordance with observed trends may depend on both the harvesting regime and life-history of the species (Engelhard & Heino 2004a; de Roos *et al.* 2006).

4.1.1 Estimating selection

Early studies on life-history effects of fisheries had difficulties in distinguishing between effects of exploitation and environmental variation, phenotypic plasticity and genetic selection and still these are challenging to unravel. Whether changes in e.g. maturation rate have a genetic basis or not, had to be inferred from the persistence of traits after transferring to another environment (Reznick 1982, 1990) or from discrepancies between e.g. the expected and observed change in age at maturation based on changes in growth rate.

Rijnsdorp (1993) performed such a study for European plaice. He observed an increase in growth rate of juvenile plaice from 1950-1980 – a period when fishing mortality greatly increased – and demonstrated this to result in a younger age of maturation, which was in principle in agreement with the compensatory hypothesis. Rijnsdorp (1993) observed maturation probability to increase with size attained by fast growth early in life but to decrease with fast growth shortly before maturation: the highest probability of maturation was observed for the larger of two fish of the same age but also for the older of two fish of the same size. The slopes of the maturity ogives (see box 3) were steeper for older ages and had shifted to smaller sizes at the end of the monitoring period. The largest, but also slowest growing fish thus being most likely to mature implied an effect of growth history on maturation: recent fast growth reduced the probability of maturation. Expected maturation probability was calculated by a general linear model⁶ incorporating maximum length and previous growth rates obtained from back calculations. However, the predicted shift in maturation age and length based on changes in growth rate did not fully cover the observed changes: a net decrease in L_{mat} remained unexplained. Comparing L_{mat} with length at age four in two different periods (1930s and 1980s) resulted in similar unexplained discrepancies. This brought the author to conclude that a genetic component was likely to be involved in decreasing maturation age and length due to selective harvesting. Computer simulations confirmed a selective advantage of young maturity under high fishing mortality and predicted similar shifts to those observed. However, other factors than selective exploitation, such as temperature, could not be ruled out as a cause of the decreased L_{mat} . Later studies could confirm a genetic component by applying probabilistic reaction norms.

⁶ General Linear Model (GLM): extension of multiple regression, in which each component can represent a whole set of variables (www.socialresearchmethods.net).

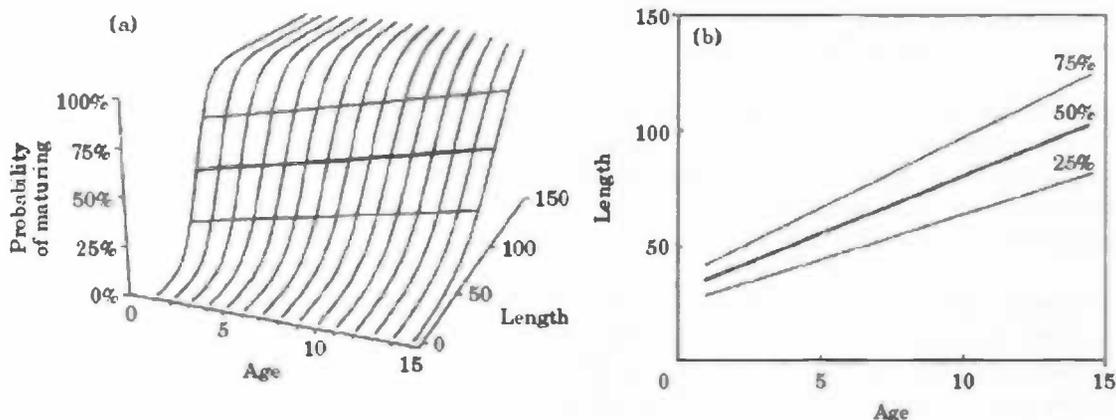


Fig. 15. (a) Reaction norms for age and size at maturation describing the probability of immature individuals to mature at certain size and age. (b) Projection of the 50% midpoint and width, results in a 2-dimensional representation of the reaction norm. From: Heino *et al.* 2002.

Maturation and Reaction norms

Disentangling selection from phenotypic variation can be notoriously difficult. However, one can describe the probability of maturing at a certain age or size by an age-size plot. When assuming phenotypic variation in maturation to be related to environmental variability, such a curve reflects the plastic component of maturation that varies with environmentally induced changes in growth. This principle is underlying reaction norms (Stearns & Koella 1986, in Grift *et al.* 2003) which describe how one genotype can be expressed as different phenotypes depending on environmental conditions. More specifically, the probabilistic reaction norm for age and size "describes the probability of immature fish maturing at a certain age and size during a given time interval" (Heino *et al.* 2002). In contrary to maturity ogives, the reaction norm thus calculates the probability of reaching maturity *given* a certain age and size and is not affected by the probability or rate of attaining this age or size. By this, it disentangles the environmental processes affecting growth and survival from the genetic component determining whether attaining a certain age or size makes maturation likely. Furthermore, by focusing on the maturation process itself, complications with discriminating between first-time or repeat spawners are also eliminated (Heino *et al.* 2002).

Maturation probabilities can be estimated from the combined information from ogives and growth rates. Details on the estimation procedure can be found in Heino *et al.* (2002) and Grift *et al.* (2003) and are based on the observed proportion of mature individuals at given ages a and $a-1$ plus the length gained between these two ages.

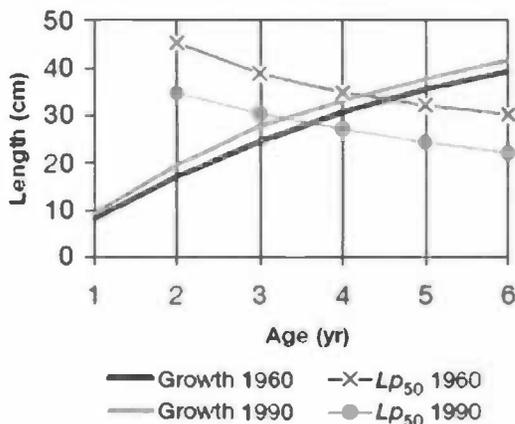


Fig. 16. Probabilistic reaction norms at size and age for plaice born in 1960 and 1990. -x- and -o- Lines connect identical probabilities: 50% midpoints. Solid lines indicate average growth trajectories for these two periods. From: Grift *et al.* 2003.

The probability to mature at age a , is then expressed as the ratio of individuals which have matured, relative to the number of individuals which could have matured in theory. Reaction norm midpoints – at which the probability to mature equals 50% – and e.g. 25% and 75% probabilities can then be projected in a 2-dimensional plot, as is represented by fig. 15 (Heino *et al.* 2002; Grift *et al.* 2003). The latter authors estimated growth rates, age and length at maturity (i.e. at which 50% of individuals mature) and reaction norms for North Sea plaice from 1955-1995. They observed over time increasing maturation probabilities at smaller sizes, simultaneously with increased lengths-at-age. More precisely: they found the reaction norm midpoints to lie well above the average length-at-age at the beginning of the

monitored period and 30 years later, the midpoints laid well below. The probability to mature at a smaller size thus had increased, even though the average length-at-age had increased (fig. 16).

Since shifts in reaction norm probabilities cannot be due to (environmentally induced) changes in growth/ survival rates, Grift *et al.* (2003) hereby confirmed the selection for younger and smaller maturing genotypes, as proposed by Rijnsdorp (1993). They considered fishery-induced selection as the most likely selective force. Olsen *et al.* (2004) observed similar trends for Northern cod of, on average, a year younger and 10 cm smaller maturing individuals in 1987 than seven years before.

Lowered reaction norm midpoints thus indicate maturation at smaller sizes and younger ages. Secondly, the slope of the reaction norm can be informative of the size dependent mortality acting upon maturing individuals. While a horizontal slope of a reaction norm would indicate age-independent maturation probabilities and a vertical slope would result from size-independence, a tilted slope indicates plasticity in both traits and maturation to be affected by both. The shape of the reaction norms in fig. 16 indicates increased size-at-age, or younger maturation for fast-growing individuals. Heino *et al.* (2002) and Engelhard & Heino (2004a) translate this to lower maturation probabilities than size would suggest. Ernande *et al.* (2003) explain this to be an effect of more severe harvesting pressure (and thereby selection) on fast-growing individuals and consequently differential selection along the reaction norm. I discuss different selective patterns of harvesting in more detail in 4.2. Here, the main point to make is that reaction norms thus suggest a long-term genetic response to harvesting, dominating short-term phenotypic fluctuations (Grift *et al.* 2003). However, cases where selection does not seem to be the dominant force affecting maturation are known as well.

4.1.2 Compensatory growth response

Engelhard and Heino (2004a,b) investigated Norwegian spring-spawning herring, mentioned briefly in 3.3.2. This is one of few exploited stocks considered to have completely recovered from fifteen years of commercial extinction. The variability in abundance of the herring stock is believed to be sensitive to environmental conditions but little doubt exists about the severe impact of harvesting resulting in collapse of the stock. During the period of depletion, Engelhard & Heino (2004b) observed higher growth rates, decreased maturation age (age 3-4 compared to 6-7 before the collapse) and slightly increased sizes of maturing individuals. After recovery of the stock, maturation age and growth rate seemed to return to pre-collapse levels – they were intermediate between the former two periods – but data were inconclusive due to variation between the recent cohorts and the absence of the most recent data. Since the temperature conditions (juveniles at low densities tend to dwell in more southern, warmer regions which induce faster growth) and compensatory growth by reduced densities could largely explain the observed pattern, Engelhard and Heino (2004b) concluded phenotypic plasticity to be the most likely cause of the changes in maturation but by their analyses, could not exclude an evolutionary force underlying them.

Engelhard and Heino (2004a) computed reaction norms for this herring stock and hereby confirmed the compensatory growth hypothesis: they found a mere 3% of observed reduction in maturation age of only two cohorts to be explainable by lowered reaction norm midpoints and argue themselves that this may be due to the high statistical power of their analysis. Furthermore, they suggested assuming age and length to be the only two variables responsible for plasticity of maturation is not always realistic. For example, improved body condition due to increased juvenile growth may be responsible for the in herring observed earlier maturation after severe depletion. They argued that the specific harvesting pattern on herring (catching either mature or young juvenile individuals) results in the plastic maturation changes and the absence of an evolutionary driving force. In contrast, mixed fisheries, as those on e.g. cod and plaice, would lead to stronger selective shifts.

If indeed evolution, and not a variable unaccounted for, drives the observed shifts in reaction norms, the next step should be identifying the key processes responsible for the selective procedure at stake (Ernande *et al.* 2004). In other words: mutants should have a fitness advantage under the present harvesting regime in order to be able to invade a stock.

In the next section I will discuss two studies theoretically investigating selective advantages under different exploitation patterns.

4.2 Selective harvesting of structured stocks

4.2.1 Harvesting-induced selection

Ernande *et al.* (2003) modelled the evolution of reaction norms under three different patterns of exploitation: 1) maintaining constant catch levels 2), constant F , or harvesting being proportional to stock size and 3) maintaining constant biomass. These three regimes are corresponding with mortality being, respectively, negatively dependent, independent and positively dependent on population density. Furthermore, they investigated the differential effects of state-dependent (juvenile or adult) and size-dependent harvesting.

As one may expect, evolution of the reaction norms was most pronounced when fishing mortality was negatively related to density – i.e. increasing at low population levels. Evolution was tempered by a positive density-dependent harvesting scheme. Opposing directions of selection were observed for fisheries targeting juveniles or adults: whereas high adult mortality resulted in evolution towards individuals maturing older and at larger sizes, catching juveniles resulted in younger, smaller maturing individuals. In addition, they detected targeting juveniles to result in stronger selection than was the case for adults. When both juveniles and adults were caught, the net result was therefore still a decrease in size- and age of maturation. These results are in agreement with the later proposed effects of differing harvesting schemes by Engelhard and Heino (2004a, see the previous section).

A second effect of selective harvesting was reflected in its yield: not only did harvesting result in – as one might expect – lower density and biomass of harvestable individuals but the evolving size and age at maturity lead to a smaller fraction of the populations being susceptible to end up in the nets. Based on this model, high levels of fishing mortality thus seem to cut their own rewards but for fish, a fitness advantage of altering maturation may indeed drive the evolution of maturation norms. The observation of decreased selection rates when the minimal harvesting size was close to the resident maturation norm supports this statement.

Harvesting-induced alternative stable states

De Roos *et al.* (2006) investigated size-selective harvesting by modelling cohorts, subdivided into several phenotypic groups, differing in L_{mat} , which was positively correlated with growth rate. They used a consumer-resource model in which maximum feeding rate increased with L_{mat} and they monitored the change of cohort maturation length (as a mean L_{mat} of the different phenotypes) under different harvesting pressures. They regarded harvesting as mortality increasing with size, not explicitly depending on either juvenile- or adult life stage and affecting only individuals above a certain size threshold. They let it take place annually, prior to reproduction and recruitment. For several combinations of L_{mat} and harvesting pressure, they investigated the evolution of age- and size of maturation. In contrast to Ernande *et al.* (2003), maturation was regarded as a stepwise process, which had an important effect on the simulation outcome: in their analysis, de Roos *et al.* (2006) observed the arousal of different evolutionary stable strategies (ESS), depending on the harvesting intensity and the stepwise maturation and spawning events.

In the absence of harvesting, no shifts in abundance and maturation size were observed: one stable strategy emerged and remained. For a mild harvesting intensity – only seriously affecting individuals well above the threshold – an increase in size at maturation was observed but maturation age was not affected. The opposite occurred when harvesting intensity was severe – maturation size decreased. As a second effect of such a regime, compensatory growth led individuals to mature one year earlier. These changes were irreversible when severe harvesting was left to continue for too long; resulting in permanent loss of biomass and yield. Most notably, when the harvesting threshold was set at too small a size, a partial ban on fishing resulted in even stronger selection for small and young maturing individuals than continued harvesting would lead to. The authors explained this observation by the early, small maturation type and the late, large one being two alternative, stable strategies, both optimizing the amount of growth before reproduction in different years (due to the stepwise maturation process). Fig. 17 explains the underlying principle. Due to their

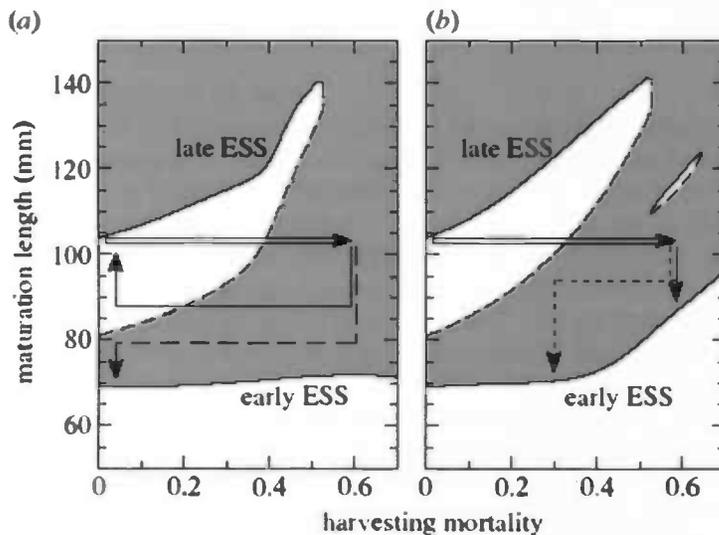


Fig. 17. The evolution of maturation sizes depending on harvesting intensity and threshold size, the latter being high (a) or low (b). Solid lines between the white and grey areas (where evolution to respectively larger and smaller sizes takes place) indicate evolutionary stable strategies (ESS), the dashed line indicates a saddle point. The solid arrow in (a) represents a moratorium on fishing after 25 years, the dashed arrow the same measure after 50 years. In (b) the arrows represent continuous harvesting (solid) and a partial moratorium (dotted). Only solid arrows embody a reversible shift. From: De Roos *et al.* 2006.

prolonged period of high feeding as juveniles, the individuals maturing late in life are large and fecund. With a large harvesting threshold, they are most affected by harvesting, compared to the early maturing type, reproducing one year earlier due to faster growth. However, when the threshold is set at a smaller size, the "early" phenotype is also affected by harvesting, resulting in increased maturation sizes (fig. 17b). This response is plastic (i.e. a moratorium would result in returning to the "late type", comparable to fig. 17a) but a *partial* ban on fishing would result in even stronger selection for the small, early phenotype since its fitness remains higher when harvested.

De Roos *et al.* (2006) suggested the results to be concordant with the observed stepwise changes in maturation age and continuous changes in maturation size in cod by Olsen *et al.* (2004). Such changes would lead to irreversible changes in the life history of an exploited species due to their genetic base and the establishment of a different ESS. A plastic response to harvesting, such as observed by Engelhard and Heino (2004a,b) may be the result of increased growth rates leading to decreased maturation age and limited changes in size. The opposite; increased size of maturation but no change in age seems also possible concluding from the model: it occurs when harvesting is milder (40% catch probability in their study) and compensatory growth is not sufficient to result in spawning a season earlier.

4.2.2 Considerations with modelling harvesting-induced selection

However, though in principle supportive of harvesting-induced selection for early-maturing genotypes, the models discussed have some unrealistic assumptions which should make one cautious in drawing conclusions about true populations too fast.

Ernande *et al.* (2004) implied fitness as long-term *per capita* growth rate, with fecundity being proportional to the cube of body length. De Roos *et al.* (2006) did model fitness as specifically depending on fecundity of the sub-cohorts (selection rate depending on the size of the sub-cohort and the number of eggs it produces) but, to my knowledge, neither study investigated the effect of a trade-off between growth rate and the survival of offspring, nor between maturation age and juvenile survival. Both processes are observed to play an important role in fish' population dynamics (see 3.2.1). Whilst fecundity is likely to increase with length, attaining this size faster may well do the opposite. For example, Rijnsdorp (1993) indicated faster growth to reduce maturation probability in plaice. Regarding the fitness of a phenotype thus merely as an effect of faster growth, irrespective of what this may do to the survival of the reproductive output, to me seems unrealistic.

Furthermore, Ernande and his team neglected the possibility of increased growth rates at low densities. De Roos *et al.* did not do so, but on the other hand implemented maturation age purely as plastic response of attaining maturation sizes earlier. Both studies argue the model's assumptions to most likely affect the results only quantitatively but nevertheless, these assumptions should make one cautious in interpreting the obtained

results as applicable when assessing the effect of harvesting on natural fish populations. For such purpose, experiments may certainly be helpful.

4.3 Selection at Sea

In the previous paragraph, I have discussed evidence and indications for evolution to drive maturation sizes and ages in at least some harvested stocks, subject to certain harvesting regimes. Difficulties with studying natural populations (discriminating between genetic and environmentally induced changes of traits and sampling problems) and theoretical simulations (simplifying systems to graspable dynamics) can be partially overcome by comparing them to experiments designed to detect heritable changes in life history traits – or age and size of maturation. Below I discuss two such studies which attribute to our understanding of selection in exploited populations.

4.3.1 Experimental selection – two examples

Reznick (Riverside, CA) has been studying selection in natural populations of guppies (*Poecilia reticulata* Peters) in Trinidad. These guppies live in streams which differ by their predator species, which predate size-specifically on guppies: a cichlid predator eating large, mature individuals and a killifish preferring small juveniles. Previous studies have demonstrated that guppies from sites with the cichlid (the 'adult predation' environment) mature earlier and allocate more resources to reproduction than individuals from communities in which the killifish predator prefers juveniles (the 'juvenile predation' environment): the former reproducing more frequently and producing more but smaller offspring than the latter. These differences have a genetic basis (Reznick *et al.* 1982). The different populations are fully isolated from each other by waterfalls and such and can be used as study systems of natural selection under different levels of mortality. Reznick *et al.* (1990) studied how new mortality regimes affected the traits described above.

They relocated guppies from an adult predation environment to a juvenile predation environment and after eleven years, evaluated whether traits related to reproduction had changed. This proved to be the case. Males and females introduced at the new site attained maturity at an older age and larger size than in their original habitat. The females produced fewer and larger offspring and less energy was allocated to reproduction. Persistence of the differences between the two groups by rearing their descendants in a common environment, confirmed the genetic basis of these traits. Replicate experiments demonstrated similar results and are therefore very supportive for the hypothesis of predator-induced selection resulting in changes of the maturation scheme and not of random drift or founder effects (Reznick *et al.* 1990).

Conover and Munch (2002) performed a different experiment examining predator-induced selection, with human harvesting regarded as the predator. They subjected six captive populations of Atlantic silverside (*Menidia menidia* L.) of about 1000 individuals each to harvesting mortalities of 90% according to three different regimes: 1) catching the largest 90%, 2) the smallest 90% and 3) harvesting 90% of the individuals irrespective of their size. The offspring of the remaining 10% of all populations were reared under identical conditions and during four generations their respective biomasses and the yield from the three different harvesting regimes were measured.

While catching the largest individuals initially resulted in the highest yield, after four generations, the yield from catching small individuals was nearly double that of the large harvesting regime, which had declined significantly. No clear trends were observed for the randomly harvested populations. Spawning stock biomass transformed in a similar way but the pattern here was even stronger: the mean weight of individuals from the small harvested populations rising to six times that of large harvested individuals. As an effect, reproductive potential of the small harvested populations greatly increased as well. This was further supported by increased egg sizes for these groups; suggestive of high embryo quality (see 3.2.1). Both juvenile- and larval growth rates increased in the small harvested populations and decreased in the large harvested ones, resulting in the observed differences in yield from adult biomass. Interestingly, survival of juveniles was not so much affected by the harvesting regime. Selection was thus upon growth rates and not on 'general' viability. Since density-

dependent effects and competition for food were eliminated by the experimental set-up, compensatory growth did not occur.

Walsh *et al.* (2006) analysed the progeny of the differently harvested populations of Conover and Munch (2002). They discovered major differences in traits affecting population viability and capacity to recover: in the large harvested populations, egg volume, size at hatching, viability and growth rate of larvae, size-specific fecundity, consumption rate and conversion efficiency of food and willingness to forage of adults, had all declined significantly. Furthermore, adults developed a vertebral column containing fewer vertebrae, signifying irreversible smaller sizes. In the small harvested populations, all these traits evolved in the opposite direction.

Conover and Munch (2002) estimated the heritability of body length at 0.2 – a common value for life-history traits – but the rate of changes observed was much higher than one may expect from a classic evolutionary viewpoint. Naturally, the size of the experimental populations was smaller than in nature and selective mortality was very high, most likely increasing the selective rate. Nevertheless, the experiments discussed here, demonstrate predation being capable of driving the evolution of life history traits in a time-frame of several generations.

4.3.2 The rate of change

Reznick *et al.* (1997) estimated the rate of change for a.o. the experiment described above (Reznick *et al.* 1990) and found the genetic base of age and size of maturation to be strongly correlated: evolution of the one trait thus strongly affecting – and affected by – the other. Observed rates of evolution (3.700-45.000 Darwins⁷) were orders of magnitude higher than those observed in fossil records but in the same order of magnitude as those for smaller size of maturation observed in cod by Olsen *et al.* (2004). These authors estimated the selective rate of changes in maturation length (as the shift of the reaction norm midpoint at age six) at -18.810 – -13.600 Darwins and argued these rates to be high but also comparable to other studies of contemporary evolution. Within four generations, Conover and Munch (2002) observed genetic selection to affect growth rates and body sizes in their experiments. The discussed evolution of age and size of maturation of exploited stocks took place over a time-span of several decades (Rijnsdorp 1993; Grift *et al.* 2003; Olsen *et al.* 2004). How can these genetic changes – assuming the evidence for fishery-induced evolution indeed is conclusive – occur within such brief periods?

Three factors affect the rate of evolution on a given trait: 1) its heritability, 2) the intensity of selection and 3) the selection on correlated traits (Reznick *et al.* 1997; Law 2000). Heritability of life history characteristics as age and size of maturation is well-accepted though may differ between sexes and species (Rijnsdorp 1993; Reznick *et al.* 1997; Conover & Munch 2002). A heritability of life history traits of 0.24 is common in teleost fish (Roff 1991 in Rijnsdorp 1993; Law 2000). The intensity of selection is furthermore affected by the amount of change in the environment and the fitness advantage of the trait in its new surroundings. When a new optimum is achieved by the trait, directional selection of the trait is expected to come to a halt (Reznick *et al.* 1997). The increasing exploitation and devastation of marine populations in the last decades can surely be regarded as rapidly changing conditions to which residents must adapt. It is not hard to imagine size-selective harvesting and recruitment overfishing to result in a fitness advantage of small, young mature fish. The correlation between age and size of maturation as observed by Reznick *et al.* (1997) will speed up selection even more. Fishery-induced evolution may thus seem surprising at first but not unlikely to be capable of result in changes in life history characteristics of the exploited species. Importantly, models and analysis of fishing activity and individual length of North Sea cod (Law 2000) show fishery-induced evolution to be likely but very hard to reverse since selection in the opposite direction under relaxed mortality conditions will be weak. What this may mean for the future of these species and the fisheries depending on them, I discuss in the last part of the present review.

⁷ Darwin: measurement for the rate of evolutionary change, expressed as the difference between the logarithm of the mean of a trait X at two moments in time, divided by the length of the time interval Δt : $(\ln X_1 - \ln X_2) / \Delta t$ (http://www.blackwellpublishing.com/ridley/a-z/Rate_of_evolution.asp).

5. Discussion

5.1 Harvesting dynamic populations

In the course of this review, I have discussed several features of fish' population dynamics and how they can be affected by exploitation. Intense fishery may, besides increased mortality rates and reduced biomass, result in increased catchability of populations, which reinforces the two former named effects. The knife-edge maturity ogives by which stocks are managed cause harvestable- and adult stocks to be substantially different. The increased harvesting of more, and eventually also younger individuals, has resulted in recruitment overfishing of an increasing number of stocks. 29% of species fished upon is currently considered collapsed (Worm *et al.* 2006) and for many of these, the future does not seem to bring improvement.

Stock assessments have to cope with complicating aspects of sampling: interpreting data from commercial catches, tagging studies and research surveys correctly; dealing with biased data-sets and extremely large confidence intervals. Evidence is mounting that dynamics of depleted populations do not follow the same rules as when they were abundant: while assessing the relationship between stock and recruitment is already a major challenge in abundant populations, depleted stocks are even more defying.

Since environmental variation may in principle drive similar changes, one can never be fully certain on the importance of a S-R relationship when observing variation in abundance of stocks (Cook *et al.* 1997). At low stock sizes however, as Hsieh *et al.* (2006) put it: "the only regulatory process operating may be a stochastic one". Bayesian- and meta-analyses on long-term datasets such as from Myers *et al.* (1995a) seem the most promising tools available to discriminate between stochastic and density-dependent processes and to obtain accurate estimates of unknown variables for specific stocks (Hilborn & Lierman 1998). Indeed, environmental variation seems to have much greater impact on the abundance of collapsed populations than of abundant ones but assuming obscured evidence for S-R related processes being a lack of evidence would be a very dangerous strategy (Frank & Brickman 2001; Liermann & Hilborn 2001). Recovery of stocks has been slow or even be absent, even after fishing activities were brought to halt. The lack of recovery of, for example, collapsed cod populations, suggests their productive capacity to be negatively affected by the harvesting regime executed. It does not need further explanation that unravelling the relative roles of the factors at stake at low population densities is of sheer importance if one wants to prevent history to repeat itself.

The model of de Roos and Persson (2002) demonstrates how very basic size-dependent interactions between predators, prey and their resources may, at least in theory, lead to separate threshold mortality rates for persistence and invasion in an ecosystem. These could explain the lack of return of predator populations even after mortality rates had been lowered by reducing fishery. Hsieh *et al.* (2006) show truncation of age structure by fisheries to increase variability in larval abundance and thereby decrease population resilience, since then stochastic processes become relatively more important in determining recruitment levels. The importance of preserving size and age structure of stocks in order to maintain a productive population is stressed by these authors and others discussed in the present review (e.g. Murawski *et al.* 2001; Berkeley *et al.* 2004).

However, with studies on stock-recruitment relationships focusing mainly on density-dependent processes, one has to be careful not to loose sight of other participating factors: compensation and depensation may or may not be important processes affecting abundance levels at low densities – they are certainly not the only ones. Recruitment depends on both survival of youngsters and on reproductive output, in their turn depending largely on the quality of the parent stock.

5.2 The power of exploitation

I have discussed how large, old and repeat spawners are often responsible for the vast majority of recruited individuals. It is these fish which are most valuable to both the populations and the fishing industry. Based on the studies I encountered while writing this review, it seems to me that the industry has been getting more than her fair share and thereby promotes losing these valuable fish for the future. By truncation of age structure

(Hsieh *et al.* 2006), recruitment overfishing (Myers *et al.* 1997) and fishing mortality being far greater than natural mortality, fisheries provoke increased frequencies of traits not optimal in natural circumstances (Walsh *et al.* 2006).

Engelhard and Heino (2004a,b) demonstrated how growth rates in collapsed herring populations increased while age of maturation decreased. The observation of these traits returning to their pre-collapse levels after recovery of the stock suggested plastic changes in growth rate to lead to faster maturation. Increased growth could be due to reduced competition, e.g. by increased food availability at low densities. The authors refer to this observation as compensatory growth. Although commonly used to indicate increased growth, it is advisable to bear in mind that this term does not imply determination: the increased growth rates here observed are merely a result of relaxed density dependent constraints on growth and not an adaptation in order to compensate for high losses.

However, not only plasticity but also directional selection seems to be driving the increased prevalence of younger and smaller maturing individuals in at least some exploited species. For example, natural populations of cod (Olsen *et al.* 2004) and plaice (Rijnsdorp 1993; Grift *et al.* 2003) were observed to mature younger and smaller after intense harvesting pressure was imposed on them. Experimental studies by Reznick *et al.* (1990, 1997) and Conover and Munch (2002) strongly support the capability of fisheries (although the former indirectly; investigating reduced predation mortality) to drive the evolution of life-history parameters such as age and size of maturation.

Discriminating between plastic and genetic changes in maturation has been difficult, moreover since the two processes are not mutually exclusive. Reaction norms have been very useful in clarifying the most important drivers behind observed changes but have shortcomings of their own. To obtain a norm, length at age data for both adults and juveniles have to be known. For the latter, such data may be very hard to obtain since juveniles often occupy different localities and/ or life styles than adults. Therefore, back-calculations are often used to convert indirect data from age-based maturity ogives of adults into information on juvenile lengths-at-age (Heino *et al.* 2002). However, back-calculations typically assume the predictability of a pattern not to change over time. In my opinion, exactly that assumption will be violated when new selective forces become influential, which is what reaction norms intend to unravel when estimating contemporary selection. The authors argue that caution should be taken with the application of back-calculations but do find their data, though noisy, sufficiently accurate. Furthermore, both Heino *et al.* (2002) and Olsen *et al.* (2004) warn for the necessity of a substantial part in length and age of maturation to be due to environmental factors. If not, the norm may be more representative of genetic variation in other traits responsible for maturation, such as body condition and growth, than of phenotypic plasticity of age and length of maturation. I have found no more information on this requirement but it seems to me, reaction norms push forward at least part of the problem of entangling environmental and genetic variation to another trait.

Be it with considerations to some extent and certainly with uncertainties to be solved, reaction norms of exploited populations, as well as experiments and theoretical studies do support the hypothesis of current harvesting regimes being capable of inducing selection for smaller size and age of maturation. What may this hold for the viability of populations?

5.3 The strength of stocks

Several features brought up in the present review hold worrisome perspectives for the sustainability of both the harvested populations and their exploiters. With plastic changes being reversible when mortality would be reduced, it is especially the genetic adaptations I want to underline here. The conclusion of plastic change in herring by Heino *et al.* (2004a) was made for a stock which actually recovered from a collapse by overfishing. The opposite joined observations of genetic change and no recovery in cod suggests irreversible maladaptive changes to have occurred. Though, to my knowledge, the lack of recovery of cod has not been proven to be associated with genetic changes in their age and size of maturation, this is at the least a disturbing coincidence.

The theoretical study on selective harvesting effects of Ernande *et al.* (2003) observed reaction norms to evolve to decreased densities and harvestable biomass. Moreover, fewer individuals became susceptible to harvesting since they escaped being caught by their

reduced sizes. In this light, early maturity at smaller sizes may seem to lead to improved survival of exploited stocks since adaptations to fishery result in reduced catchability of the remaining stock. However, I have discussed several papers which indicate recruitment not to improve simply with a higher number of spawning individuals.

Rijnsdorp (1993) demonstrated how increased reproductive investment in plaice may result in decreased body condition and vulnerability to detrimental influences from the environment, such as diseases. Younger maturity may thus be weakening the quality of the spawning stock. Especially with iteroparous species such as plaice – which will reproduce multiple times throughout their adult life – this may be reflected in their spawning output.

Convincing arguments for excessive harvesting to result in unfavourable effects on the quality of stocks also come from the experiments of Conover and Munch (2003) and Wash *et al.* (2006). These authors demonstrated a whole range of life-history parameters to be affected when the largest individuals are selectively removed from a population. Both yield and viability of the stocks were irreversibly, negatively affected by this harvesting regime. Heino *et al.* (2004a) emphasized how selection for early maturation, being directly correlated with reduced fecundity by low age-specific fertility, is selection for reduced fitness. Walsh *et al.* (2006) support this suicidal adaptation by their analyses of the differently harvested laboratory populations of Atlantic silverside. It seems as if reduced fitness by unfavourable adaptations does not seem to outweigh the selective forces imposed by harvesting. Then are such adaptations likely to pose a serious threat to exploited populations in the long run?

5.4 The evolution of fisheries

Recalling to the main question asked in the introduction of this review; “*how do exploited populations respond to harvesting and would evolutionary adaptations increase population resilience in the long run?*”, I come to the conclusion that fishery-induced evolutionary change does not increase the strength of stocks fished upon. It will depend on the future management regimes of stocks, whether negative fitness effects induced by selective harvesting will be expressed.

If patterns of exploitation remain at present levels in the future, early reproduction and small size may still be the better of two evils if the other option would be extinction. However, current fisheries are bound to change their directives at some point in the near future since at the present course, commercially exploitable stocks are disappearing at a very swift pace (Worm *et al.* 2006). What could happen when fishing mortality would be elevated – when fishing mortality would not dominate natural mortality any longer? Law (2000) demonstrated fishery-induced selection likely to be hard to reverse. What is more, reducing catches may not be the most sensible solution to halt the observed trend: de Roos *et al.* (2006) demonstrated how, at least in theory, reduced fishing effort may lead to even faster selection for small and early maturing genotypes. The reluctance of stocks to recover after relaxation of harvesting pressure supports the assertion of a solution likely to be more complicated than this. However, complete moratoria on fishing are not a realistic suggestion in the current society. Selective harvesting for small individuals, as done in the experiments of Conover and Munch (2003) and Wash *et al.* (2006) could perhaps reverse both the changes in life history and the decreasing yield of fisheries.

In any case, a malicious genetic load would surely not be helpful for depleted stocks to recover but I cannot give an unambiguous conclusion on the magnitude of the consequences reduced fitness may have on stocks compared to other devastating influences on their subsistence. Loss in biomass, habitat degradation, pollution – they all play their part in the dynamics and resilience of fish populations. Unravelling their relative importance for stock survival would be highly desirable but was not the intention of the present study.

I have made an attempt to evaluate the effects of exploitation on basic population dynamics and evolution of fish stocks. By trying to grasp such extensive topics within a relatively short time frame, several recent developments in fisheries' science have most likely been overlooked, which could have been a valuable contribution to the information presented. Furthermore, I have not paid attention to local adaptation and genetic structure of fish stocks. These features form vast research fields by themselves but are intertwined with the topics discussed here.

Amongst others, Hilborn *et al.* (2003) emphasised the importance of biocomplexity, different life histories and local adaptation of stocks in their resilience to exploitation. Beverton (1998) suggested variance around stock-recruitment relationships to increase at the limits of a species' geographical distribution area. The constitution of stocks out of different, locally adapted sub-stocks may greatly influence their response to harvesting. Genetic techniques are now being used to unravel this sub structuring and to assign catches to different sub-stocks which is, according to Manel *et al.* (2005), one of the greatest challenges in fisheries science. Furthermore, genetic erosion and complex genetic structuring have been suggested for several fish species (e.g. plaice, Hoarau *et al.* 2002). Each of these features would certainly affect the way evolution acts upon populations. A broad interface between these research fields and fishery-induced selection awaits exploration.

6. References

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