



Chapter 2

A Model of Enhancement Potentials in Open Ecosystems

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Abstract

Using mathematical modelling based on the Masfjorden cod (*Gadus morhua* L.) enhancement experiment, we explore the potential for increasing local populations by mass releases of juveniles. We develop an age-structured population model for a variable ecosystem with stochastic carrying capacity, stochastic recruitment and frequency-dependent cannibalism. We explore the potential impact of two enhancement options: a static release of a fixed number of juveniles every good year and a dynamic release to exactly match carrying capacity of 1-group fish every year when recruitment is below the current carrying capacity. We discuss the biological potential for enhancing populations in variable environments, in advective regimes, for migratory species, for age-structured populations and at different trophic levels. It seems difficult to increase the population size in a variable environment by stocking unless the release matches the current ecological conditions well.



Introduction

Is it possible to increase the output of a fishery by release of reared juveniles? Or can such releases stabilize the ecosystem or the fishery? We will study the impact of released fish in a model ecosystem, particularly to investigate under what circumstances a release program may be beneficial for a fishery. The discussion is intended to be general, but restricted to small scales and strongly biased towards cod-like situations. Norway has performed a series of scientific stock enhancement experiments on cod (*Gadus morhua*), European lobster (*Homarus gammarus*), salmon (*Salmo salar*) and shad (*Alosa alosa*) during the period 1983–98. The major results from the Masfjorden cod enhancement program have already been reviewed by Fosså *et al.* (1994) and Smedstad *et al.* (1994). In parallel with the field programme, the potential for cod enhancement in Masfjorden and similar western Norwegian ecosystems has been studied by ecological modelling, particularly by a biomass-based multispecies model (Giske *et al.* 1991, Salvanes *et al.* 1992, 1995,

Salvanes & Baliño 1998). These models show that cod production will depend on advective transportation of zooplankton to the fjord. In this paper we develop a stochastic age-structured population model using as parameters data originating from the field investigations in Masfjorden and incorporating environmental variability to illustrate possibilities and limitations of cod enhancement.

Model

A general k -age group population dynamics model can be formulated by the Leslie matrix approach (Leslie 1945). This specifies two matrices A and B :

$$A = \begin{bmatrix} F_0 & F_1 & F_2 & \dots & F_{k-1} \\ P_1 & 0 & 0 & \dots & 0 \\ 0 & P_2 & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & 0 & P_{k-1} & 0 \end{bmatrix}$$

of which each column is the age at time t , each row is the age at time $t+1$ and every entry to the matrix represents a change in the number of individuals from one age group to the next. In accordance with common practice in fisheries, we have termed the first age group '0', covering the eggs and their survival the first year. F_i is the average number of eggs produced by an individual in age group i (discounted for the sex ratio and the proportion of immatures) and P_i is the survival until age group i . The second matrix contains the number of individuals in each age group at time t

$$B = \begin{bmatrix} n_0(t) \\ n_1(t) \\ \dots \\ n_{k-1}(t) \end{bmatrix}$$

Population growth and age group development can now be studied by matrix multiplication. Numbers of age group i still alive 1 year later are denoted by

$$n_{i+1}(t+1) = P_{i+1} n_i(t)$$

and population egg production at time $t+1$ is the sum

$$n_0(t+1) = \sum_{i=0}^{k-1} P_i F_i n_i(t)$$

Any population that is characterized by deterministic age-dependent fecundity and survivorship will eventually achieve a stable age distribution (SAD, where the fraction of the population that belongs to age group i is constant) and a constant population growth rate r (Euler 1760, Lotka 1907).

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If carrying capacity, fecundity or recruitment success are fluctuating environmental variables, then the population size will not stabilize but will grow by the stochastic growth rate a (Tuljapurkar 1990, 1997, Yoshimura & Clark 1993). Although $a \approx 0$ over some extended time period, growth, survival and population size may vary considerably. For fish, ecosystem variation works differently for stationary and migratory populations. Migratory populations composed of individuals swimming long distances to find high quality and quantity food patches can reduce the effect of ecosystem variability by searching in an area that is large enough to overcome the variability. Stationary populations, however, rely strictly on locally available prey organisms. Thus, stationary fish populations in small areas can only grow large if they are fed by an advective supply of food (Aksnes *et al.* 1989).

Cod stocks in western norwegian fjords and coastal areas fall within the category of stationary predators (Svåsand & Kristiansen 1990, Salvanes & Ulltang 1992, Nordeide 1993) feeding on advective prey (Aksnes *et al.* 1989) in a variable ecosystem (Giske *et al.* 1991, Salvanes *et al.* 1992, 1995, Salvanes & Baliño in press). The dominant variable is the highly fluctuating advection of copepods, which are direct and indirect prey for 0- and 1-group cod (Giske *et al.* 1991), as well as food for the prey of elder cod and its gadoid competitors (Salvanes *et al.* 1992). Advective supply can vary in time and intensity (Aksnes *et al.* 1989) and autumn biomass of copepods can vary interannually by an order of magnitude (Giske *et al.* 1991) which again affects strongly the productivity of gobies (Fosså 1991), the principal prey for young cod (Salvanes & Nordeide 1993). We take this fjordic ecosystem as an illustration of the restricted ecological potential for stock enhancement.

Complex dynamic ecosystem

To the Leslie matrix approach above we therefore add the possibilities for fluctuating recruitment success, fluctuating carrying capacity for the two youngest age groups (impacting survival) and frequency-dependent cannibalism. The time step is 1 year:

- (1) Recruitment (survival of eggs to age group 1, i.e. during its first year of life) is variable. In general it is low, but with a probability of $1/x$ of being x times higher. In Fig. 2.2, $x = 5$.
- (2) Carrying capacities K for living up to age groups 1 and 2 vary randomly within a higher and lower limit around the average carrying capacities for these age groups. We assume the fish relies on zooplankton (through gobies as intermediate trophic level) these first 2 years and that K varies due to the variability in the physical advection rate of zooplankton. Survival to age groups 1 and 2 is also density-dependent, as it is increased if the density of one of these age group is below its current K and decreased if the density is above K .
- (3) Frequency-dependent cannibalism impacts survival to age groups 1, 2, 4 and 5. If the fraction of age groups 1 + 2 is higher than expected from the SAD (so

that fraction of ages 3–5 is lower than average), then predators are rare and have lots of prey. Hence, predation mortality rate on the younger ages is reduced and carrying capacity related survival of the elder is improved. The opposite is true if elder ages dominate.

Hence, we have put all environmental impact on survival while keeping fecundities constant. As recruitment is the product of survival and fecundity, this simplification should not cause trouble. The data used correspond to cod in the Masfjorden ecosystem. In sum, these natural ecological processes yield a highly variable population, where numbers of each age group typically vary by a factor of 10–50 among years. As the age structure has been included at the expense of explicit representation of other populations, the age groups in the model also represent the ecologically corresponding age groups of competing populations.

Survival to age 1 is a dynamic function of recruitment (R), cannibalism (C_j) and resource-mediated survival (Z_1):

$$P_1 = Z_1 C_j R$$

Recruitment is either poor or good:

$$R = \begin{cases} p_1 & \text{if random number} > x^{-1} \\ x p_1 & \text{if random number} < x^{-1} \end{cases}$$

Here, p_1 is the survival probability from eggs (age group 0) to age group 1 in the SAD population. Frequency-dependent cannibalism is

$$0.5 \leq C_j = u/v \leq 2$$

where u and v measure current deviations from the SAD among young and elder fish, respectively:

$$u = \frac{n_1 + 2n_2}{s_1 + 2s_2}$$

$$v = \frac{n_3 + 2n_4 + 4n_5}{s_3 + 2s_4 + 4s_5}$$

Here n_i and s_i are the current and SAD fractions of age group i in the population. As a large prey fills more of the stomach of the predator, and hence reduces the predation risk for the remaining potential prey, n_2 is given higher weighting than n_1 in u . Likewise, as a heavy predator needs more food than a smaller one, the weighting increases with age in v . The restriction on $0.5 \leq C_j \leq 2$ (and later on C_a) acts to reduce the efficiency of cannibalism, as other predators and prey species also occur in the ecosystem, and survival of juveniles and adults of this target species is balanced by these unspecified interspecific interactions. Restrictions are stronger among predators than prey, assuming that survival of the larger predators is more robust.

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Carrying capacity K for the first two age groups is variable due to physical advection of zooplankton

$$0.8 K_{avg(i)} \leq K_{rand(i)} \leq 1.3 K_{avg(i)} \quad (i = 0, 1)$$

Resource-mediated survival is linked to the fluctuating carrying capacity

$$Z_i = (K_{i-1,t-1} / n_{i-1,t-1})^{0.75} \quad (i = 1, 2)$$

The lower the exponent, the weaker the link between survival and carrying capacity. A low value will reflect that other species may potentially utilize some of the available K and also that individuals are restricted in their flexibility and efficiency.

Survival of elder age groups is formulated similarly, but more simply:

$$P_2 = p_2 Z_2 C_j$$

$$P_3 = p_3$$

$$P_4 = p_4 C_a$$

$$P_5 = p_5 C_a$$

where

$$0.7 \leq C_a = u/v \leq 1.3$$

and p_i is the survival probabilities from age group $i - 1$ to i in the SAD population:

$$p_1 = 2.03 \times 10^{-5}$$

$$p_2 = 0.264$$

$$p_3 = 0.382$$

$$p_4 = 0.643$$

$$p_5 = 0.643$$

The fecundities used in Figs 2.2 and 2.3 originate from estimated weight-dependent fecundity for coastal cod (Kjesbu *et al.* 1996) and estimated average individual weight at age from Masfjorden (Salvanes & Ulltang 1992). But as cod may live for more than 5 years, reproduction by older ages is included in F_4 and F_5 . The new value of F_{4-5} is obtained by searching for the fecundities that make total population egg production yield a SAD of the population.

$$F_0 = F_1 = 0$$

$$F_2 = 23622$$

$$F_3 = 109626$$

$$F_4 = F_5 = 305000$$

A deterministic version of the model gives a population in SAD and stable population size (Fig. 2.1). With frequency-dependent cannibalism, the population will oscillate but still be predictable. The predictability is lost if recruitment or prey advection is stochastic. In the more realistic ecosystems, both the closed system with stochastic recruitment, that with carrying capacity influence on survival, and that with frequency-dependent cannibalism, as well as the open system with

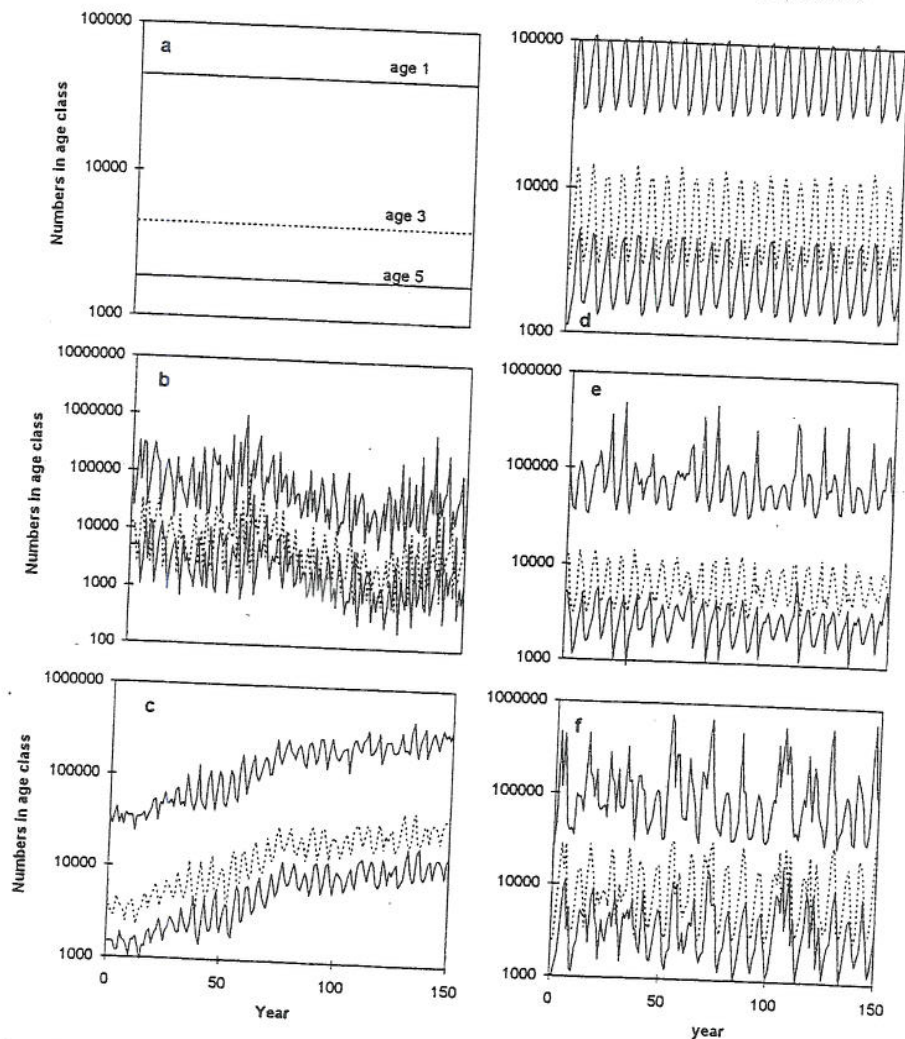


Fig. 2.1 Population dynamics by age-structured population models. Age groups 1, 3, and 5 in the age-structured population model of cod in Masfjorden under different scenarios: (a) fixed environment (gives stable age distribution); (b) stochastic recruitment (survival of eggs to age group 1); (c) stochastic prey advection to age groups 1–2; (d) frequency-dependent cannibalism (but constant carrying capacity, yielding density-dependent survival); (e) cannibalism and stochastic recruitment; (f) cannibalism, stochastic recruitment and variable prey advection. In all panels, age group 1 is most and age group 5 least abundant.

stochastic prey advection, yield age group dynamics that vary naturally by more than an order of magnitude (Fig. 2.1). This corresponds well with observations for cod in Masfjorden (Salvenes & Ulltang 1992), as well as for cod in the whole North East Atlantic (Daan *et al.* 1994, Dickson & Brander 1994, Nakken 1994). Can such an ecosystem be stabilized by stocking, or can its population size of cod be increased?

28 *Theoretical Considerations**Two release strategies*

We will now explore the effect of releasing juveniles within the framework presented here by simulating two scenarios:

- (1) We suppose that we know how to assess carrying capacity and recruitment success exactly, and that we are able to rear sufficient number of juveniles to release just enough individuals to match the variable K for age group 1.
- (2) More realistically, we suppose that we have far from perfect information, but are able to assess whether K at age group 1 in a particular year will be higher or lower than average, and that we can release a fixed number of individuals in years of higher-than-average K .

Our simulations show that 'perfect releases' tend to maintain the population at a much higher level (Fig. 2.2 upper panel). Due to the strong inherent stochasticity of the carrying capacity and egg production, and to the frequency-dependent cannibalism, it will not be possible to stabilize the population at or near a SAD by 'perfect releases'. However, if we do not have the necessary information, and can figure out only that the coming year will be 'good' or 'bad', then releases of juveniles will not enhance the population (Fig. 2.2 lower panel). In Fig. 2.2 lower panel, the number of juveniles released corresponds to a natural egg production that is 5 times higher than the number needed to match carrying capacity at age 1 in an average year. It will not help to release a higher but still constant number of juveniles. They will die off due to limited carrying capacity and give rise to unwanted frequency-dependent cannibalism (Fig. 2.3). This latter result is similar to the findings of Fosså and Nordeide (1991), who studied the effect of age-dependent cannibalism on the youngest age group of cod. They found that releases every third year (i.e. corresponding to the age at catch of cod) gave the best yield. More frequent releases increased the cannibalism but not the yield.

Discussion

In a closed ecosystem, for example a lake where dynamics depend on local conditions but may change with weather and season, inter-annual variability is generally much lower than in open ecosystems, particularly if local prey concentration is a function of (often a relatively stable) local carrying capacity and a strongly variable advective flow rate. If this flow can either give or take prey individuals, it is obvious that predator stocking should only be assessed in situations of a net food supply. The time horizon for variation is also of fundamental importance: while short-time fluctuations do not leave openings for releases, there is a potential for stocking with intermediate sized fluctuations, where natural recruitment cannot respond fast enough. However, there are obvious drawbacks:

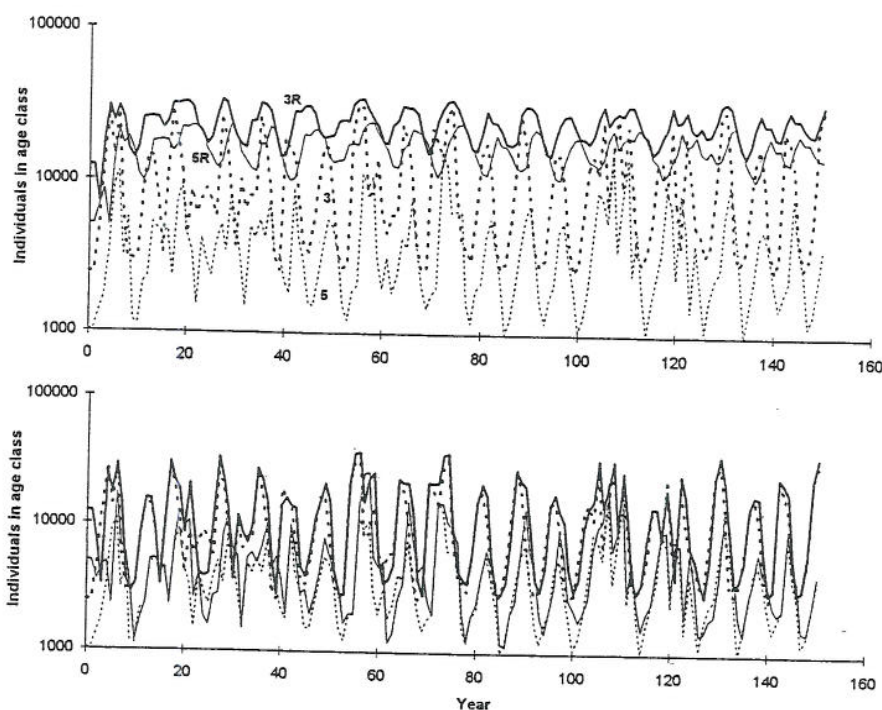


Fig. 2.2 Result of releases. Abundances of age groups 3 and 5 in the variable Leslie model of cod in Masfjorden, in the environment given by Fig. 1(f). Upper panel: releases assuming perfect knowledge of recruitment limitation and carrying capacity compared with no release. Key to symbols: 3R and 5R, natural and released numbers of ages 3 and 5, respectively; 3 and 5, numbers of age groups 3 and 5 in the absence of release. Lower panel: releases of a fixed number of individuals in years with higher than average carrying capacity compared with no release. Line types as above.

- (1) Release of predators is only of use in good years with strong natural year-classes (Giske *et al.* 1991, Salvanes *et al.* 1992, 1995). Does this imply that release cannot be used as a means of levelling harvests, but will amplify harvest variation?
- (2) The increased predator population may suffer food limitation whenever the favourable conditions change. There is thus a potential for subsequent density-dependent growth depression (Salvanes & Baliño 1998) and yield loss if the predator is not removed (fished) fast enough.

Can we improve the natural output of local fisheries by releases?

There are at least two questions related to this:

- Are population sizes limited by recruitment?
- Can we stabilize or increase the recruitment by mass releases?

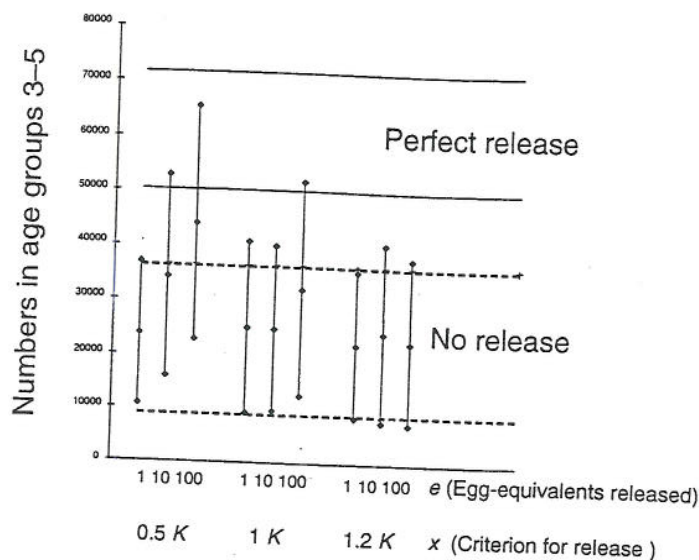
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Fig. 2.3 Benefits of fixed release. Average range (indicated by lines at ± 1 SD) of 'adults' (sum of age groups 3-5) at perfect release and at no release, and variation range (average ± 1 SD) of different fixed release scenarios. Release scenarios (x -axis) are converted to eggs, and given as multiplications ($e = 1, 10$ or 100) of the average carrying capacity of eggs. 0-Group fish are released in years where the actual carrying capacity (K) is at least x times the average carrying capacity.

The goal of the Norwegian cod release experiments was to level out natural variation in recruitment to local populations. It was hoped that by releasing juveniles in years with low natural recruitment, a more stable harvest level could be achieved. The conclusions of the investigations in Masfjorden are that an ecological basis for additional releases is found only in years when the natural recruitment is above the average (Salvanes *et al.* 1992). This result may seem contradictory to the common assumption that mass releases would overwhelm natural recruitment limitations. But it does not: due to variability in carrying capacity (zooplankton advection) and hence survival of 0- and 1- group cod, the average egg production of the cod population was large enough, except in years with a very favourable prey supply. This is also in accordance with theory of optimal behaviour in variable environments (Cohen 1966, Orzack 1993). In such an ecosystem, mass releases can only be used to increase the difference between years, not to level them out.

The interannual variability in recruitment may be caused by several factors. Feeding of fry and larvae will generally depend on available food, which for most species will be zooplankton (or organisms that eat zooplankton). Local zooplankton availability will vary extensively on an interannual scale due to variability of the current systems caused by weather fluctuations, e.g. regional variability in wind directions (Sætre *et al.* 1988) or large-scale climatic oscillations (Klyashtorin 1998). It is important to be aware of this trophic link between zooplankton production in remote areas, advective transportation to coastal areas and consumption by local

planktivores (e.g. the youngest age groups of species that are migratory later in life). The variability in both water transportation and zooplankton concentration in the currents is probably one of the more important factors determining variability in year-class strength.

This advection-driven variability is most pronounced for zooplankton, as their locomotive power is too weak to offset water transportation, and their reproductive rate too low to locally compensate for emigration losses. Fish eggs and fish larvae may also be advected in and out of local areas, yielding regional rather than local gene pools, as seen for haemoglobin types in coastal cod (Frydenberg *et al.* 1965). Planktivores will generally not advect, although they may form enormous migratory schools. Also local phytoplankton concentrations will be little impacted by advection, as their renewal rate may exceed even a considerable water transportation rate (Giske *et al.* 1991). This implies that the carrying capacity of even non-migrating phytoplanktivores (e.g. clams) will be much more stable than that of zooplanktivores.

Local recruitment will fail when zooplankton has not advected to an area. Releases of juveniles, which will be food competitors to the wild stock, will not improve the situation. However, if advection has been far above average, then local recruitment may be inadequate, and releases of juveniles may contribute to the population if other species do not fill the gap. Natural selection has established fish life histories in such systems to make fewer offspring than what can usually survive in a very good year (Orzack 1993). If a female can increase her fecundity only by elevating her mortality risk, then the potential fitness cost of producing too many offspring in a situation where almost all die will often be higher than the fitness cost of producing too few when many more survive (Gillespie 1977). Adapted life histories will tend to save energy to future reproductions. An average year may be well exploited, but not the exceptional good years.

Local predator-prey dynamics will also be influenced by animal behaviour, and in a non-linear fashion. This behavioural component will probably be least linear at lower trophic levels, where the variability in food supply is greatest. Individuals will continuously trade off between potential growth versus potential mortality risk, for example by feeding in exposed areas instead of hiding (Werner & Gilliam 1984, Aksnes & Giske 1990, Giske & Salvanes 1995). If zooplankton concentrations are high, planktivores will have enough food and will tend to be 'risk-averse' in their feeding behaviour. This will reduce their mortality rate at the expense of a very high growth rate (Rosland 1997). The availability of planktivores to the piscivores will therefore not be proportional to the increase in plankton. Similarly, if plankton concentrations are low, planktivores will have to risk more for a good meal, and food availability to higher trophic levels will be better than predicted from plankton concentrations (Fiksen 1997, Giske *et al.* 1997, Rosland 1997). Thus, animal behaviour will even out some of the effects of physical variability, and the further up in the food chains, the more stable will the carrying capacities be. A corollary is that increased food supply to a population may increase its survival by reducing its pre-

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dition mortality (Rosland & Giske 1994, Fiksen & Giske 1995, Fiksen 1997), instead of increasing its fecundity or weight-at-age.

Life forms suited for enhancements

The cultivation of Atlantic salmon (*Salmo salar* L.) in rivers is based on migratory predation that may involve searching for moving prey over large areas. Neither predator nor prey will depend on local conditions, and the dynamics of the predator may be expected to be much more stable than we may expect of coastal cod, which is fully dependent on receiving food aid from outside. However, the stationary predator depending on advected prey may still expect to gain far more food resources than a stationary predator dependent on local production. Aksnes (1988) estimated, for example, that if cod in Masfjorden fed on the local food chain (locally produced phytoplankton–locally produced zooplankton–nearshore fishes–cod) then the fjord could only hold a population of 1000 1-group individuals. This is more than two orders of magnitude below natural densities.

Food and energy contents of ecosystems generally peak in the lower trophic levels, and the potential for harvest will decrease with the trophic level of the catch. Algae-feeding bivalves thus have a much higher carrying capacity than piscivorous fishes, but this depends also on the level of advection of zooplankton to the area and density-dependent stocking (Parsons & Dadswell 1992, Cote *et al.* 1993, Emerson *et al.* 1994, Peterson *et al.* 1996). Individual growth-versus-survival trade-offs will act to even out resource variability between trophic levels, as will also the increased longevity of prey at higher trophic levels.

A critical question for the success of releases is at which age the strength of a year-class is established. Release strategies must depend on whether younger age groups will suffer from competition or predation from elder individuals, and also on whether the benefit of mass releases in a year with high advection will depend on high advection in the next year(s). Both these effects influence the survival of juvenile cod in Masfjorden.

The philosophy of releases of juvenile salmon is that oceanic conditions allow a far larger adult population than the river may allow for juveniles. For stationary organisms, production will strongly depend on the rate of food supply, i.e. the rate of advection of prey. If this rate is approximately constant, one cannot expect gain from enhancement, while that may be possible for a variable advective supply. Salmon is an example of a two-stage life history with different food bases and mortality risks. As both marine diets and mortality risks generally are size-dependent, many species will experience this shift to some extent. In such cases, growth and survival in the second 'niche' may be independent of survival through the first. If conditions are poor for early life stages, releases of individuals that have been reared through this 'bottleneck' may enhance the adult population.

However, it is also possible that populations are so local that recruitment may be hindered by extensive advective losses or overfishing. This will particularly apply to

species with low swimming ability and with pelagic larvae, as may be the case for large benthic crustaceans. Although they may feed on benthic prey, their continuous food supply will often depend on advective transportation of food to this community. The settlement of recruits will also depend on suitable habitats (Jensen *et al.* 1994) providing them with shelter for predators (Butler & Herrnkind 1997). Such populations are probably the principal candidates for a biological effect of stock enhancements. If they are prized, there may be economic gains in enhancing population sizes of such organisms by artificial recruitment.

The early Norwegian efforts to increase populations of cod involved releasing large numbers of yolk-sac larvae. However, as mortality rate at that age may be 0.1 day^{-1} over prolonged periods, enormous numbers of larvae were needed to enhance recruitment to even a small local population. A 10% daily mortality over 4 months implies only six survivors for each million larvae released (see discussion in Salvanes *et al.* 1994). Tveite (1971) could therefore not detect any effect of these releases in fjords in southern Norway. Recruitment programmes will only be successful if the larvae are kept in a low-mortality environment until they have grown to a size or age that makes them less vulnerable to high natural mortality (Salvanes *et al.* 1994). For benthic crustaceans, this will mean not releasing them before they can settle in the benthic habitat. The same is true for cod: mortality risk for pelagic cod larvae forbids an economically based release of such small individuals. (But although this juvenile survival is a prerequisite, it does not secure success – as seen in the Norwegian cod enhancement program (Fosså *et al.* 1994). Salvanes *et al.* 1994 found that the best yield of cod was achieved by rearing the 'juveniles' in net pens all through their lives. Aquaculture may be the best method for many species.)

Ecological advice for stock enhancement

Seek species with strong recruitment limitation Only a strong failure of natural reproduction or early life survival can give hope for increased long-term yield by artificial propagation.

Seek species with low variation in carrying capacity If K is difficult to assess, then the effect of the enhancement will be almost stochastic. Avoid releasing stationary zooplanktivores.

Seek species with low tendencies to cannibalism Releases of juveniles that end up as food for elder stocked individuals is expensive. The effect of variable K for elder individuals and cannibalism may yield a chaotic return rate from releases. It is also expensive to release individuals that end as food for a competing species. As diet is strongly size-dependent for most fish, it will probably pay to select species for enhancement with different habitats for juveniles and adults.

Don't play God Marine systems tend to have strong non-linear dynamics, and unless we are able to predict these dynamics over a relevant time horizon, our

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release efforts are not likely to benefit the stock to be enhanced. However, also under perfect information, where recruitment failure and carrying capacity fluctuations are perfectly balanced, this increase will eventually influence predators and competitors. It will probably influence prey, parasites and diseases, as well. The model developed here is inadequate to address all important ecological questions related to a stocking programme, and a suite of approaches should be utilized to study density-dependent behaviour, state-dependent decisions, complex trophic interactions and local adaptations, respectively (Giske *et al.* 1998). Ecological (and genetic and bioeconomic) modelling remains a cheap method to investigate pros and cons of an attempt to change Nature. Attempt 'artificial life' before artificial propagation.

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