Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis

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The population dynamics of fisheries stock enhancement, and its potential for generating benefits over and above those obtainable from optimal exploitation of wild stocks alone are poorly understood and highly controversial. I review pertinent knowledge of fish population biology, and extend the dynamic pool theory of fishing to stock enhancement by unpacking recruitment, incorporating regulation in the recruited stock, and accounting for biological differences between wild and hatchery fish. I then analyse the dynamics of stock enhancement and its potential role in fisheries management, using the candidate stock of North Sea sole as an example and considering economic as well as biological criteria. Enhancement through release of recruits or advanced juveniles is predicted to increase total yield and stock abundance, but reduce abundance of the naturally recruited stock component through compensatory responses or overfishing. Economic feasibility of enhancement is subject to strong constraints, including trade-offs between the costs of fishing and hatchery releases. Costs of hatchery fish strongly influence optimal policy, which may range from no enhancement at high cost to high levels of stocking and fishing effort at low cost. Release of genetically maladapted fish reduces the effectiveness of enhancement, and is most detrimental overall if fitness of hatchery fish is only moderately compromised. As a temporary measure for the rebuilding of depleted stocks, enhancement cannot substitute for effort limitation, and is advantageous as an auxiliary measure only if the population has been reduced to a very low proportion of its unexploited biomass. Quantitative analysis of population dynamics is central to the responsible use of stock enhancement in fisheries management, and the necessary tools are available.

Keywords: stocking; supplementation; density dependence; mortality; growth; evolution

1. INTRODUCTION

(a) *Overview*

Stock enhancement is a fisheries management approach involving the release of cultured organisms to increase abundance and yield of natural fish or invertebrate stocks. Releases may be carried out on a long-term basis to raise yields above the level supported by natural recruitment, or temporarily to rebuild depleted populations. Stock enhancement describes a continuum of hatchery release and associated harvest regimes, the extremes of which are culture-based fisheries and supplementation. In culture-based fisheries or ranching systems, recruitment is largely or entirely based on hatchery releases, and release and harvesting regimes may be designed to maximize production. By contrast, in supplementation, hatchery fish are released to bolster the natural spawning stock, and release and harvesting regimes may be designed to maximize natural recruitment. In the current analysis, I deal with enhancement in its full breadth but exclude considerations specific to the supportive breeding of small populations such as depensation, demographic stochasticity and the genetics of low effective population size. Stock enhancement may be implemented under a variety of different institutional settings such as private or communal enterprises, or for public benefit under open access.

Stock enhancement is one of the oldest, yet most controversial and least well-understood approaches to fisheries management. Stocking of hatchery fish has been practised on a large scale since the mid-nineteenth century, and systematic transfers of wild juveniles probably have a much longer history. Current global production by stock enhancement and culture-based fisheries has been estimated at *ca.* 2 Mt yr^{-1} (Lorenzen *et al.* 2001). This includes some enhancement programmes conducted on a very large scale by government agencies (notably for Pacific salmon) and many small, often resource-user-led initiatives.

Stock enhancement as a management approach is more common in freshwater than in marine systems, reflecting differences in scale, institutional arrangements and state of hatchery technology (Welcomme & Bartley 1998). For well over a hundred years, stock enhancement has been the subject of fierce controversy regarding its effectiveness and possible adverse impacts on wild stocks (reviewed in Hilborn 1999; Taylor 1999; Smith *et al.* 2002). Generally, this 'hatchery controversy' has divided stakeholders along disciplinary lines, with aquaculture practitioners, scientists and some fisheries managers broadly in favour, but fisheries ecologists vigorously against the use of stock enhancement. The result has been a plethora of poorly conceived and managed enhancements, and a very uneven development of relevant science. Advances in the science and

practice of hatchery management have allowed increasingly effective production of fish for release, but the crucial, broader issues of using hatchery fish in population management and conservation have received little systematic attention (Hilborn & Winton 1993). The few studies to address the population dynamics of enhancement (reviewed in § 1d) have been largely ignored by both management practitioners and scientists. Poor appreciation of the dynamics of enhancements limits their potential for achieving management objectives (Botsford & Hobbs 1984; Lorenzen 1995), and allows their misuse as an apparent 'quick fix' for management problems they cannot effectively address (MacCall 1989; Hilborn 1999). Without quantitative assessment, it is difficult to gauge the true potential of enhancement and refute unrealistic proposals and claims. The need for a critical and realistic assessment, a 'common version of reality' (Waples 1999) of stock enhancement is now widely recognized (Blankenship & Leber 1995; Hilborn 1999; Leber 2001; Lorenzen *et al.* 2001). The aim of this paper is to contribute to a common reality by developing and analysing a general model for the dynamics of stock enhancement.

(b) *Rationale for stock enhancement*

In theory, successful stock enhancement can yield significant production, social and ecological benefits. First, it can increase the use of natural aquatic productivity beyond the level achievable by harvesting alone, providing high quality food at relatively low external inputs of energy and protein and with limited effects on aquatic habitats and their competing uses (Lorenzen *et al.* 2001). Second, enhancement can create new economic opportunities for fisheries-related livelihoods, and provide incentives for active management of fisheries resources (Pinkerton 1994; Lorenzen & Garaway 1998). Third, enhancement can maintain the abundance of exploited stocks above the level supported by natural recruitment alone. This may provide partial mitigation against the ecosystem effects associated with depletion of key species by fishing (Pauly *et al.* 1998; Jackson 2001; Mehner *et al.* 2002; Pauly *et al.* 2002). Fourth, and rather more speculatively, genetic resource management of enhanced stocks could be employed to mitigate against the evolutionary effects of fishing (Stokes *et al.* 1993; Conover & Munch 2002) by replenishing stocks with offspring from the genotypes most susceptible to harvesting which are otherwise selected against.

The biological rationale for stock enhancement has three key components: recruitment limitation, hatchery advantage, and manipulation of population structure. Fish populations in general are believed to be recruitment limited in the sense that under most conditions, additional recruits will increase the abundance of the recruited stock (Munro & Bell 1997; Walters & Korman 1999; Hixon *et al.* 2002). This view is also implicit in dynamic pool fisheries models (Beverton & Holt 1957). Recruitment limitation may be exacerbated by anthropogenic factors such as fishing or degradation of juvenile habitat (Blankenship & Leber 1995; Blaxter 2000). If adult abundance is recruitment limited, increasing the level of recruitment through hatchery releases can be expected to increase abundance and yield of the recruited stock. For this to be beneficial overall, hatcheries must be able to produce a higher number of recruits per spawner than are produced in natural stocks.

This 'hatchery advantage' is substantial and well documented. On average, juvenile survival in aquaculture facilities is several orders of magnitude higher than in the wild, and even though this is partially offset by increased mortality upon release an overall advantage is likely to remain (Lorenzen 1996b, 2000). A significant hatchery advantage is of course possible only in organisms of very high fecundity. The hatchery advantage not only allows increased recruitment above natural levels, it paves the way for structural manipulations of fish populations. It enables, for example, the construction of populations of fast growing juveniles harvested at the optimal size for production, replenished with offspring from a relatively small hatchery broodstock. Such stock management strategies are used to raise productivity in extensive aquaculture systems or culture-based fisheries on scales from ponds to large reservoirs (Walter 1934; Lorenzen 1995; Lorenzen *et al.* 1997). Whether such manipulations are ecologically acceptable and economically viable in natural populations will depend on specific circumstances, but the biological potential is a crucial, and much underexplored aspect of stock enhancement.

(c) *Reality check: problems and progress in addressing them*

Despite clear rationale and potential benefits, the actual performance of stock enhancements has been mixed and, more often than not, disappointing. Many enhancements have failed to deliver significant increases in yield or economic benefits, and/or have had deleterious effects on the naturally recruited components of the target stocks (Hilborn 1998; Levin *et al.* 2001; Arnason 2001). For enhancement to produce net benefits and avoid unacceptable deleterious effects on the wild-stock component, several conditions must be met. First, only certain stocks offer the potential for biologically effective and economically viable enhancement, even with the best stock management and aquaculture technology (Blankenship & Leber 1995; Travis *et al.* 1998). Second, where potential exists in principle, appropriate release and harvesting regimes must be developed with respect to both the wild and stocked components of the target stock (Botsford & Hobbs 1984; Lorenzen 1995). Third, hatchery production and release strategies must provide fish that perform well in the wild, at a low cost. Inadvertent developmental and genetic adaptations of the hatchery environment, which are deleterious in the wild, make this a major challenge (Olla *et al.* 1998; Lorenzen 2000; Fleming & Petersson 2001). Fourth, hatchery and fisheries management strategies must be developed that minimize genetic hazards to the wild stock (Utter 1998). Many stock enhancement programmes have paid little attention to some or all of these conditions, and their success or otherwise has been a hit or miss affair. The need for a more informed and responsible approach to the development of stock enhancements has been widely recognized, however, and various conceptual frameworks proposed to guide the process (Cowx 1994; Blankenship & Leber 1995; Lorenzen & Garaway 1998). At the same time, there has been substantial progress in hatchery production and genetic management of enhancements. Hatchery management and release techniques such as nutrition optimization, behavioural enrichment and conditioning, and soft release can greatly reduce developmental

adaptation to the hatchery environment and improve post-release performance in the wild (Olla *et al.* 1998; Brown & Dey 2002). Genetic resource management can effectively address, but not entirely eliminate, problems arising from limited effective population size in the hatchery, disruption of the genetic structure of the wild population, and genetic adaptation to the hatchery environment (Utter 1998; Price 2002; Miller & Kapuscinski 2003). Deliberate manipulations of hatchery organisms including hybridization, triploidization and artificial selection provide means of minimizing genetic interactions with wild conspecifics, or improving performance traits of stocked fish (Jonasson *et al.* 1997; Bartley *et al.* 2001). Obviously, even a rigorous and responsible development approach using the best available science does not guarantee the emergence of effective and sustainable enhancements. This is well illustrated, for example, by the Alaskan pink salmon and Norwegian cod enhancement programmes, both of which have a history of systematic investigation and enlightened management but have proved uneconomic under current conditions (Boyce *et al.* 1993; Hilborn 1998; Svasand *et al.* 2000). By contrast, the equally well-developed Japanese chum salmon enhancement programme, as well as various smaller initiatives in freshwaters, is believed to be effective as well as economically viable (Hilborn 1998; Arnason 2001). Indeed, some enhancements provide very high physical and economic returns to limited investment (Ahmad *et al.* 1998; Lorenzen *et al.* 1998). Overall, this suggests a potential for certain, well-conceived and managed enhancements to be technically effective and economically beneficial. In such systems, moderate quantitative differences in biological or economic parameters can make all the difference between success and failure. For example, decline in salmon prices owing to the large supply from aquaculture may have turned many salmon enhancement projects from economic successes into failures (Boyce *et al.* 1993; Arnason 2001). A good, quantitative understanding of the dynamics of an enhanced fishery is therefore crucial to its sustainable development.

(d) *Understanding the dynamics of stock enhancement*

At the heart of the enhancement system are the enhanced stock and its dynamics in response to harvesting, hatchery releases and environmental factors. These dynamics remain poorly understood beyond the most basic information gleaned from empirical recapture rates for, at best, a small set of management options. A handful of studies, however, have covered significant ground towards a more comprehensive and theory-based assessment. Botsford & Hobbs (1984) conducted the first general, quantitative analysis of stock enhancement as a fisheries management policy. Recognizing that density-dependent processes at different life stages are fundamental to enhancement dynamics but poorly understood, they used a set of alternative and very general assumptions to derive robust insights and decision rules. Cuenco (1994) took a similarly general approach to the problem of supplementing declining salmon populations, providing simple decision rules for populations of semelparous organisms

with non-overlapping generations. An alternative to such general but abstract analyses has been the use of conventional fisheries models incorporating empirically based representations of certain population processes (Polovina 1990). However, conventional fisheries models disregard size and density-dependent processes that are central to the dynamics of enhancements. Simple and empirically robust models for two such processes, density-dependent growth and size-dependent mortality, form the basis of an assessment methodology for culture-based fisheries developed by Lorenzen (1995, 2000) and Lorenzen *et al.* (1997). The dynamic implications of genetically-based performance differences between wild and hatchery components of enhanced stocks were first analysed by Byrne *et al.* (1992), and more recently by Ford (2002).

In this paper I build on the earlier work reviewed here to develop a general and practical theory of fisheries enhancement, an integrated framework for the evaluation of release and harvest regimes with respect to yield and abundance of different population components. As a case study, I explore the potential of enhancing the North Sea sole stock, using stock assessment data and integrating basic economic considerations. I close by discussing general implications for the development and management of enhancements, and their future role in fisheries management.

2. POPULATION DYNAMCIS THEORY FOR ENHANCED FISHERIES

A practical theory of stock enhancement must allow analysis of the impacts of management variables such as stocking size and density, post-release performance, and harvest regulations on fisheries yield, as well as the status of the wild and hatchery stock components. It must be based on biologically meaningful process models that are simple, robust and general with parameters that can be estimated from widely available data or inferred from comparative analyses. The dynamic pool theory of fishing (Beverton & Holt 1957) provides a practical and widely used methodology for the assessment of capture fisheries, which can be extended to the analysis of enhancements. Three extensions are necessary to achieve this. First, the stock–recruitment relationship must be 'unpacked' in order to analyse the effect of releasing pre-recruit juveniles. Second, population regulation in the recruited stage must be accounted for because it determines to what extend additional recruits can increase stocks and yields: the potential of enhancement. Third, biological differences between hatchery and wild fish have important implications for the dynamics of enhancements and must be accounted for. The following sections set out how this may be done.

(a) *Unpacking recruitment*

Conventional dynamic pool theory divides the life history of exploited fish and invertebrates into a density-dependent and possibly stochastic pre-recruit phase, and a density-independent and deterministic recruited phase. Recruitment, the transition between these phases, may be associated with identifiable biological processes but is often assumed to occur at a somewhat arbitrary age. I define recruitment as the transition from a juvenile stage subject to density-dependent mortality, to a recruited stage subject to density-dependence in growth and reproductive parameters.

Most stock enhancement efforts are likely to involve releasing fish in the pre-recruit stage; hence unpacking recruitment is a necessary step to analysing the effects of different release sizes and densities.

Precise size or stage-specific data on population dynamics of pre-recruits are available for only a handful of populations (e.g. Elliott 1994). In general, an overall stock–recruitment relationship is the most an analyst can hope for, and this must be unpacked without recourse to more detailed data. Three pieces of information provide the basis for doing this: the general allometry of natural mortality, empirical and theoretical information on density-dependent processes at different life stages, and a mathematical way for breaking stock–recruitment relationships into successive stages.

Natural mortality rates within natural fish populations are strongly size-dependent with an allometric weight exponent of *ca.* -0.29 to -0.37 (McGurk 1986; Lorenzen 1996*b*). In other words, natural mortality is approximately inversely proportional to length:

$$M(L) = M_1 \frac{1}{L} \tag{2.1}$$

where $M(L)$ is the natural mortality rate at length L, and M_1 is the natural mortality rate at unit length. Lorenzen (2000) gives survival equations based on this mortality–length relationship for different growth models; these are used in equations (2.10) and (3.1). The average M_1 in wild fish is 15 yr^{-1} at unit length of 1 cm, while that of stocked hatchery fish may be in a similar range or substantially higher (Lorenzen 1996*b*, 2000). Because models based on an inverse relationship between mortality and length provide good predictions of survival in relation to release size in fish stocking experiments (Lorenzen 2000), average mortality rates in consecutive phases of the recruitment process may be expected to follow this relationship. This is a first major step in unpacking recruitment.

The next question is where and how stochastic and/or density-dependent processes generate variation around the 'average' allometry and thus give rise to variable and often density-dependent stock–recruitment relationships. The general pattern that has emerged in this respect may be summarized as follows. Vital rates of early life stages (eggs and larvae) tend to be highly variable, but density independent (Myers & Cadigan 1993*a*; Leggett & DeBlois 1994). Small changes in the very high rates of mortality suffered by these stages cause major variation in cohort survival, and are believed to account for a large part of variability in recruitment (Beyer 1989; Rothschild 2000). By contrast, vital rates in juveniles are often density dependent and thereby tend to dampen the variability created at early life stages (Myers & Cadigan 1993*b*; Elliott 1994). Density-dependent survival at this stage may arise directly from density effects on the mortality rate (Elliott 1994), or indirectly from the interaction of size-dependent mortality with density-dependent growth (Shepherd & Cushing 1980; Post *et al.* 1999). Either mechanism or a combination may arise from trade-offs between foraging and predation risk-taking in juveniles, and result in density-dependent survival to recruitment (Walters & Korman 1999). Density-dependent growth replaces density-dependent mortality as the dominant regulatory mechanism in larger fish (Walters & Post 1993; Post *et al.*

1999; Lorenzen & Enberg 2002). Most probably, this transition is gradual and related to declining effects of growth variation on mortality (as overall mortality rates are declining), and increasing effects on biomass (as body mass is increasing). Broadly in parallel with ontogenic changes in regulatory mechanisms, there is a transition from intra-cohort to inter-cohort density dependence. The appropriate metric of density therefore changes from stage-specific numerical abundance to whole population biomass or similar measures that reflect aggregated effects on resources (Walters & Post 1993; Lorenzen 1996*a*). Even though the transition in mechanisms and metrics of density-dependence is likely to be gradual, it is practical to assume distinct phases of intra-cohort density-dependent mortality before, and inter-cohort density-dependent growth after recruitment. This is unlikely to misrepresent dynamics provided recruitment is assumed to occur at a size most probably within the growth-dominated phase of regulation, and dynamics in the recruited phase takes account of size-dependent mortality as well as density-dependent growth. I now focus on pre-recruit processes and return to regulation in the recruited population in § 2b.

Having established that within the pre-recruit stage, density dependence is most likely to act on juvenile mortality in a manner dependent on stage-specific numerical abundance, it is possible to partition the stock–recruitment relationship into a density-independent larval phase, and a density-dependent juvenile phase. The latter may again be subdivided into a pre- and post-release phase according to the stage or size at which juveniles will be released. Mathematically it is straightforward to partition an overall Beverton–Holt stock–recruitment relationship into consecutive relationships of the same functional form (Beverton & Holt 1957; Walters & Korman 1999). The overall relationship is given by

$$N_r = \frac{a^* S}{1 + b^* S} \tag{2.2}$$

where N_r is the number of recruits, S is spawner biomass, a^* is the maximum number of recruits produced per unit spawner biomass (the product of larval production and subsequent survival) and b^* describes the degree of density dependence in recruitment. This may be partitioned into a three-stage model with density-independent larval production

$$N_0 = fS \tag{2.3}$$

and two consecutive phases of potentially density-dependent survival according to a Beverton–Holt relationship, e.g. for the first stage:

$$s_1 = \frac{N_1}{N_0} = \frac{a_1}{1 + b_1 N_0} \tag{2.4}$$

The parameters f, a_1, b_1, a_2, and b_2 of the three-stage model are related to a^* and b^* by

$$a^* = fa_1 a_2 \tag{2.5}$$

and

$$b^* = fb_1 + fa_1 b_2. \tag{2.6}$$

The three-stage model thus has three free parameters, which are, however, constrained within certain ranges

given that a_1 and a_2 are survival rates and thus must be between zero and unity.

The key to unpacking recruitment in a meaningful way, of course, is in relating the abstract phases of the model to actual life stages or sizes, and this requires good biological knowledge of the target organism. In demersal fish with pelagic larvae for example, settlement represents a clear transition to the juvenile stage and often coincides with density-dependent mortality (Van der Veer 1986). It may thus be assumed that the period from settlement to recruitment corresponds to the density-dependent juvenile phase of the model. If this is indeed the case, field measurements or comparative data on survival from settlement to recruitment should be broadly consistent with predictions from the stock–recruitment model at observed levels of spawner biomass. Subdivision of the juvenile phase before and after release may be informed by the allometry of mortality, or further empirical data. If stage-specific survival s_1 is known for some level of initial density N_0^* entering the stage (e.g. the estimated abundance when field measurements were taken), the stage-specific density-dependent parameter b_1 is given by rearranging the Beverton–Holt survival model as:

$$b_1 = \left(\frac{a_1}{s_1} - 1\right)\frac{1}{N_0^*}. \qquad (2.7)$$

Note that b_1 is constrained by $s_1 \leqslant a_1 \leqslant 1$; hence stage-specific survival at N_0^* puts an upper limit on the potential degree of density dependence within the stage. If survival in consecutive stages reflects the general allometry of mortality, this translates into declining potential for density-dependent mortality with increasing size.

The unpacking approach is illustrated with an example in § 3a. It is possible, of course, that survival rates implied by the unpacked stock–recruitment relationship and specific biological data are inconsistent. Where this happens, reviewing fundamental assumptions will probably prove productive, not only as a basis for assessment but in terms of basic biology.

Recruitment variation is a pervasive feature of fish population dynamics. A large share of variability in recruitment appears to be generated in the egg and larval stages, prior to the action of density-dependent processes (Myers & Cadigan 1993a; Leggett & DeBlois 1994; Secor & Houde 1998). However, environmental variability may also affect the intensity of density-dependent processes in juvenile stages (Giske & Salvanes 1999; Levin *et al.* 2001). Episodes of low larval survival or weak juvenile density dependence may create temporary opportunities to increase recruitment through juvenile releases, but regulation in the recruited stock may limit the overall benefits of such strategies. I do not explore the implications of recruitment variability further, but note that this can easily be done by defining parameters f, a or b in the unpacked model as stochastic variables.

(b) *Regulation in the recruited population and recruitment limitation*

Regulation in the recruited phase determines the ultimate biological limits of enhancement, particularly (but not only) when hatchery fish are released as recruits or late pre-recruits. Density dependence in the recruited population may act on growth, reproductive traits such as age or size at maturity, and mortality (Rose *et al.* 2001). Density-dependent growth appears to play a key role in regulating abundance, and is well described by a von Bertalanffy growth function with asymptotic length $L_\infty(B)$ defined as a linear function of population biomass B (Lorenzen 1996a; Lorenzen & Enberg 2002):

$$L_\infty(B) = L_{\infty L} - gB \qquad (2.8)$$

where $L_{\infty L}$ is the asymptotic length in the absence of competition ($B \to 0$), and g measures the strength of density dependence. Interactions between density-dependent growth and size-dependent mortality only have a weak regulating effect in the recruited stock because overall mortality is low. By contrast, strong density-dependent effects on reproductive traits may arise from interactions of density-dependent growth and size-dependent maturation and fecundity schedules. Rochet (1998) and Beverton (2002) show that many populations respond to increases in fishing effort and concomitant reduction in density with reduced age, but little or no change in size at maturity. Overall reproductive allocation at a given size appears to be largely independent of density, but a tendency to produce more and smaller eggs at low density has been noted (Rijnsdorp *et al.* 1991; Rochet *et al.* 2000). Some populations, however, have undergone substantial changes in both age and size at maturity in response to exploitation. These changes defy simple generalizations, and may well reflect a combination of phenotypic plasticity and natural selection by fishing. Life-history theory holds the key to unravelling the proximate dynamics of these responses (Thorpe *et al.* 1998), but to date satisfactory predictive models remain elusive. I note this as a key area of research interest, and confine my analysis here to populations that show essentially constant size at maturity.

The concept of recruitment limitation is an important element of the biological rationale for enhancement. Recruitment limitation is defined here as a state in which natural recruitment is limited to a level at which the addition of further recruits increases the abundance of the recruited stock (i.e. elicits a less than complete compensatory response). The notion that the abundance of recruited stocks can be increased by additional recruits is borne out by the observation that in many stocks, very large year classes raise biomass and fisheries yield far above the long-term average (Myers *et al.* 1990; Munro & Bell 1997). That does not mean that direct density-dependent processes are absent in the recruited phase: episodes of strong recruitment can depress growth significantly. The ratio of asymptotic length at current B to asymptotic length at very low biomass ($B \to 0$), $L_\infty(B)/L_{\infty L}$ is typically above 0.9 at the long-term average biomass $\overline{B}$ of exploited populations, but may decline to less than 0.7 during periods of high abundance (Lorenzen & Enberg 2002). Direct density dependence thus has a significant compensatory effect on biomass, but is not sufficient to effect complete compensation. In extensive aquaculture systems, stocking can maintain high biomass densities that depress $L_\infty(B)/L_{\infty L}$ well below 0.9 on a permanent basis (Lorenzen 1996a; Lorenzen *et al.* 1997). Why, then, is the long-term average abundance (i.e. carrying capacity) of wild populations reached at a relatively low biomass so that $L_\infty(\overline{B})/L_{\infty L}$ remains above 0.9? The answer must lie in compensatory

processes that act on future recruitment, and are stronger than effects on current biomass. The action of such processes is borne out, for example, by the observation that in a highly variable fish population, strong year classes are followed by weak recruitment and vice versa (Marshall & Frank 1999). Compensatory effects on future recruitment may act on reproductive output of the parent generation, or on survival of their offspring. Density-dependent growth combined with constant size at maturity alone implies strong regulation of reproductive output, and there may be further effects on size-related fecundity or egg quality. Density-dependent survival in the juvenile phase appears to be ubiquitous (§ 2a) and probably contributes significantly to the degree of recruitment limitation observed in fish populations. However, recruitment limitation as defined here is likely to arise even without juvenile density dependence, as a consequence of the nature of compensatory processes in the recruited stock. This implies a general potential for enhancing abundance of the recruited stock, and an equally general expectation of significant compensatory decline in natural recruitment.

(c) *Ecological differences between wild and hatchery fish*

Ecological differences between wild fish and hatchery fish derived from a local founder stock arise from plastic developmental responses to, and natural or artificial selection in, the hatchery environment (Price 2002). Experimental evidence for the success of conditioning and soft release in improving performance on the one hand (Olla *et al.* 1998; Jonsson *et al.* 1999), and heritability of poor performance on the other (Reisenbichler & Rubin 1999) shows that both developmental and genetic factors can be important. Their relative contribution is likely to vary and must be assessed experimentally for specific fisheries. Differences due to developmental plasticity diminish over the lifetime of a cohort due to increasing adaptation of individuals and the action of natural selection, and are not passed on to offspring produced in the wild (bar possible maternal effects). Differences induced by selection in the hatchery are passed on to the following generation, subject to natural selection that will act in the direction of the wild phenotype and reduce differences over successive generations. The rate at which this phenotypic change occurs is given by the heritability h^2 of the traits in which the wild and hatchery phenotypes differ. Heritability is the change in a quantitative trait due to selection within one generation, relative to the selection differential between the current and the optimal trait value. Heritability of morphological traits is generally *ca.* 0.2; that of fitness traits tends to be lower at between 0.01 and 0.1 (Mousseau & Roff 1987; Burt 1995).

Which ecological traits are most likely to differ between wild and hatchery fish, and by how much? In general, natural mortality rates of released hatchery fish are higher than those of wild conspecifics of similar size, often by a substantial margin (Lorenzen 2000; Fleming & Petersson 2001). Reproductive success of hatchery fish in the wild also tends to be substantially below that of their wild conspecifics, at least in salmonids (Fleming & Petersson 2001). By contrast, no strong or consistent differences have been reported for growth (Svasand *et al.* 2000; Fleming & Petersson 2001). Most life-history differences between wild and hatchery fish are expressed even when the two groups do
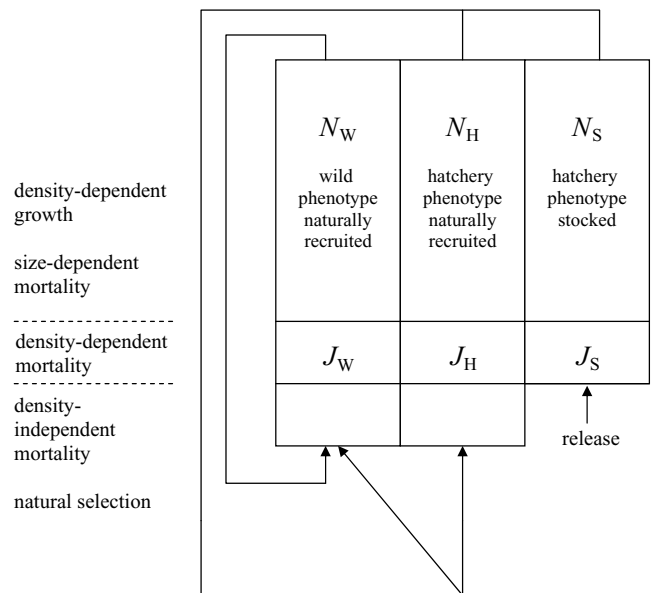

Figure 1. Structure of the fisheries enhancement model, showing the population components, flows and key processes.

not interact ecologically (e.g. Lorenzen 2000), but asymmetric interactions may further modify relative performance. Evidence for the effects of asymmetric interactions is complex and mixed (Weber & Fausch 2003). I will not consider such interactions in this paper, but again note this as an area of further research and population-level analysis.

A simple and straightforward way of accounting for ecological differences between wild and hatchery fish in population dynamics modelling is to disaggregate the population into components with different life-history parameters. Normally the hatchery component will be less well adapted than the wild component, and this will be reflected in poorer values of performance traits. Natural selection will act to move the average performance of the combined population towards that of the wild component, and this process may be modelled as transition of offspring from the hatchery component into the wild component at a rate equal to the heritability h^2. The result is a simple model of phenotypic evolution in the enhanced fishery that can be used to assess the implications of a wide range of possible ecological differences and assumptions about their genetic and/or developmental basis.

(d) *Population model for stock enhancement*

To explore the dynamics of stock enhancement, I use a population model incorporating the key aspects identified above: an unpacked stock–recruitment relationship, regulation in the recruited phase, and a population differentiated into components according to phenotype and origin (figure 1). The three components considered are wild (wild phenotype, naturally recruited), hatchery (hatchery phenotype, naturally recruited) and stocked (hatchery phenotype, stocked). This differentiation allows us to address a range of different questions, including the contributions of stocking and natural recruitment to yield, and the implications of releasing genetically maladapted fish.

Growth is described by the density-dependent von Bertalanffy model defined in equation (2.8), starting with a

constant length at recruitment $L(1, t)$. All population components are assumed to share the same growth pattern. A discrete time model to predict mean length $L(a, t)$ of age group a at time t from mean length of the cohort in the previous year $L(a - 1, t - 1)$ is given by

$$L(a,t) = L_\infty(B) - (L_\infty(B) - L(a-1,t-1))\exp(-K) \quad (2.9)$$

where $L_\infty(B)$ is the asymptotic length at biomass density B (equation (2.8)).

I assume that fishing occurs in discrete events once a year, and that natural mortality is size dependent and acts continuously between the fishing events. Population numbers N_I of the different components $(I = W, H, S)$ are given by

$$N_I(a,t) = N_I(a-1,t-1)\exp(-F(a-1,t-1))$$
$$\times \left(\frac{L(a-1,t-1)}{L(a-1,t-1) + L_\infty(B)(e^k - 1)}\right)^{\frac{M_{1,I}}{L_\infty K}} \quad (2.10)$$

where F is the fishing mortality rate, and $M_{1,I}$ is the natural mortality rate at unit length (Lorenzen 2000). Catch at age $C_I(a, t)$ is given by

$$C_I(a,t) = N_I(a,t)(1 - \exp(-F(a,t))). \quad (2.11)$$

Gear selectivity and proportional maturity are described by length-dependent logistic functions. Fishing mortality is given by

$$F(a,t) = \frac{F_\infty}{(1 + \exp(q(L(a,t) - L_c)))} \quad (2.12)$$

where F_∞ is the fishing mortality at fully selected length, L_c is the length at 50% gear selection and q describes the steepness of the selectivity curve. The proportion mature $Q(a, t)$ is given by

$$Q(a,t) = \frac{1}{(1 + \exp(p(L(a,t) - L_m)))} \quad (2.13)$$

where L_m is the length at 50% maturity and p describes the steepness of the maturity curve.

Total biomass B, spawner biomass S and yield Y of the population components are given by

$$B_I(t) = \sum_a \alpha L(a,t)^\beta N_I(a,t) \quad (2.14)$$

$$S_I(t) = \sum_a Q(a,t)\alpha L(a,t)^\beta N_I(a,t) \quad (2.15)$$

$$Y_I(t) = \sum_a \alpha L(a,t)^\beta C_I(a,t) \quad (2.16)$$

where α and β are parameters of the length–weight relationship.

Natural juvenile production $\mathcal{J}$ up to the stage at which hatchery fish are released is described as follows. Survival of naturally spawned juveniles to the stage at which hatchery fish are released is given by a Beverton–Holt type survival function s_1 dependent on total larval production:

$$s_1 = \frac{a_1}{1 + b_1 f(S_W + r(S_H + S_S))} \quad (2.17)$$

where f is the larval production per unit of spawner biomass, and r is the reproductive performance of the hatchery and stocked components relative to the wild phenotype

$(0 \leqslant r \leqslant 1)$. Natural selection is assumed to act during the first juvenile stage, described by transition of a proportion h^2 (heritability) of larvae produced by the hatchery and stocked components to juveniles of the wild component. The numbers of wild and hatchery juveniles $\mathcal{J}_W$ and $\mathcal{J}_H$ are thus given by:

$$\mathcal{J}_W = fs_1(S_W + rh^2(S_H + S_S)) \quad (2.18)$$

$$\mathcal{J}_H = fs_1 r(1 - h^2)(S_H + S_S). \quad (2.19)$$

Survival from release to recruitment is subject to the second Beverton–Holt survival function s_2, dependent on the combined abundance of naturally produced juveniles $(\mathcal{J}_W + \mathcal{J}_H)$ and stocked fish R.

$$s_2 = \frac{a_2}{1 + b_2(\mathcal{J}_W + \mathcal{J}_H + R)}. \quad (2.20)$$

Recruitment into the different population components at age 1 is then given by:

$$N_W(1,t) = s_2 \mathcal{J}_W \quad (2.21)$$

$$N_H(1,t) = s_2 \mathcal{J}_H \quad (2.22)$$

$$N_S(1,t) = s_2 R \quad (2.23)$$

where R is the number of hatchery fish released. This formulation allows release at any juvenile size or stage to be represented by a particular combination of before- and after-release survival functions, within the extremes of either function being density independent $(b_1 = 0$ or $b_2 = 0)$ and the other accounting for the full extent of compensation.

Although the focus of my analysis is on population dynamics, management decision-making almost inevitably involves making trade-offs between inputs and outcomes measured and valued in different ways, such as fishing effort and release numbers or yield and abundance. Valuing inputs and outcomes in monetary terms and combining them in economic performance indicators allows trade-offs to be considered directly, even though valuation may be difficult in practice. I use two simple indicators of economic performance of different management regimes: the overall resource rent generated at equilibrium, and the net present value of stock rebuilding strategies. In both cases I value hatchery releases, fishing effort, and yield in monetary terms. Assuming that the costs and value are proportional to the number of hatchery fish released, fishing effort and yield, respectively, net benefit (or utilty) U^* at equilibrium is given by

$$U^* = \pi Y^* - \gamma_1 R - \gamma_2 F \quad (2.24)$$

where Y^* is the equilibrium yield at release numbers R and fishing mortality F, π is the ex-vessel price of fish, γ_1 is the unit cost of hatchery fish released, and γ_2 is the cost of generating a unit of fishing mortality. The net present value (NPV) of a management strategy implemented from time $t = 0$ is given by

$$\text{NPV} = \sum_{t=0}^{\infty} \frac{\pi Y_t - \gamma_1 R_t - \gamma_2 F_t}{(1 + \delta)^t} \quad (2.25)$$

where δ is the discount rate.

3. DYNAMICS AND POTENTIAL OF STOCK ENHANCEMENT

I use the above model to explore key issues in the management of stock enhancements: interactions between fishing and release regimes in long-term enhancement programmes and stock rebuilding, and the implications of releasing hatchery fish that are maladapted due to developmental or genetic factors. Throughout I use biological (yield and abundance of stock components) and economic (net benefit and NPV) criteria, as both sets of criteria are required to understand the potential and implications of enhancement. As a case study, I use North Sea sole (*Solea solea*), a candidate stock for enhancement, with good stock assessment data but as yet no experimental releases.

(a) *Case study: North Sea sole*

Sole (*Solea solea*) is among the most valuable flatfish in Europe and has long been considered as a candidate species for stock enhancement. Culture technology posed some initial difficulties but is now well developed (Howell 1997), and laboratory experiments have been carried out to assess behavioural attributes of hatchery fish relevant to post-release survival (Ellis *et al.* 1997). No experimental releases of sole have been documented, but experiments with other flatfish such as age-1 turbot (*Psetta maxima*) have demonstrated survival in the wild and numerical recapture rates of 1–11% in the commercial fishery (Stottrup *et al.* 2002).

The North Sea sole stock supports a valuable beam trawl fishery, yielding *ca.* 20 000 t yr^{-1}. The fishery has been routinely monitored and assessed for over 40 years. The stock is considered overfished, with yield marginally below maximum sustainable yield (MSY) but spawner biomass (S) estimated at only 20% of unexploited S (ICES 2003). Recruitment is highly variable but virtually independent of S, implying strong density dependence in pre-recruit mortality. In the recruited stock, growth is strongly density dependent, giving rise to density-dependent age at maturity while length at maturity is approximately constant (Rochet 1998; Lorenzen & Enberg 2002).

While many population parameters can be estimated with a high degree of precision from survey data, there is considerable uncertainty about the true natural mortality rate. Because natural mortality is difficult to estimate, it is common practice to use a reasonable 'guesstimate' in stock assessments. The North Sea sole assessment, upon which most of the parameter values used here are based, assumes a constant $M = 0.1$ yr^{-1} in all recruited age groups (ICES 2003). Estimates of most derived quantities such as stock biomass, recruitment and fishing mortality are conditional on the natural mortality rate assumed. To construct a baseline scenario close to the reported assessment, I use a size-dependent natural mortality of $M_1 = 3$ yr^{-1} cm so that $M = 0.1$ yr^{-1} at $L = 30$ cm. It should be noted, however, that the assumed natural mortality rate is very low compared with the wild population average (Lorenzen 1996b) and direct field measurements of juvenile mortality in sole (Jager *et al.* 1995). Underestimating true natural mortality in assessments leads to conservative exploitation regimes for the capture fishery (Punt 1997), but overestimates
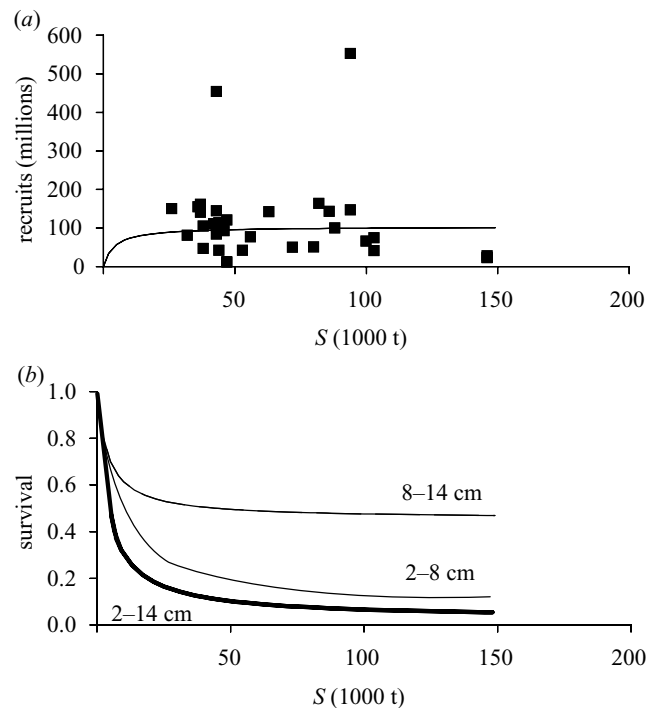
Figure 2. Stock–recruitment relationship and juvenile survival in North Sea sole (1957–1991). (*a*) Observed spawner biomass (S) and subsequent recruits (age 1), and Beverton–Holt stock–recruitment relationship with $a^* = 25\,500$ t^{-1} and $b^* = 0.000243$ t^{-1}. (*b*) Survival in relation to spawner biomass, predicted by the unpacked stock–recruitment relationship for the full juvenile stage (2–14 cm length) and the sub-stages of 2–8 cm and 8–14 cm (assuming $a_1 = a_2 = 1$). Data from ICES (2003).

potential benefits from enhancement. I briefly explore the implications of different values of M_1 in § 3e.

The relationship between spawner biomass (S) and recruitment (at age 1) in North Sea sole is shown in figure 2a. Note that recruitment is virtually independent of S over the observed range, indicating strong density dependence in recruitment, but the relationship is poorly defined for low S. For further analysis, I use a Beverton–Holt type relationship with parameters $a^* = 25\,500$ t^{-1} and $b^* = 0.000243$ t^{-1} (figure 2a). This relationship implies a more gradual increase in recruitment over the range of low S for which no data are available other than the best fitting curve, from which it is not significantly different. In keeping with the stock assessment I assume that recruitment occurs at age 1; hence no density-dependent mortality other than that mediated by growth affects fish aged 1 and older. This may be an overly positive assumption, given that Myers & Cadigan (1993b) detected density-dependent mortality in sole up to age 1.5. To unpack the relationship I assume $a_1 = a_2 = 1$; therefore $f = a^*$, and $b^* = a^*(b_1 + b_2)$. The resulting survival rate over the full juvenile period (figure 2b) is $s = 0.093$ at spawner biomass $S = 40\,000$ t, broadly consistent with a field estimate of $s = 0.14$ for juvenile sole from settlement to age 1 (Jager *et al.* 1995). Because growth over the six months from settlement at 2 cm to age 1 at 14 cm is approximately linear, survival s between any lengths L_0 and L_t within this period can

be predicted from

$$s = \left(\frac{L_0}{L_t}\right)^{\frac{M_1}{v}} \tag{3.1}$$

where v is the linear length growth rate (Lorenzen 2000). Applying this relationship to the full juvenile period and solving for M_1 gives $M_1 = 29.3 \text{ yr}^{-1}$ cm. Note that this is far higher than the baseline value assumed for the recruited stock, and see § 3f for further discussion. To evaluate release of hatchery fish at an intermediate size of 8 cm, applying equation (3.1) with $M_1 = 29.3 \text{ yr}^{-1}$ cm to the stages from 2 to 8 cm, and from 8 to 14 cm length gives $s_1 = 0.18$ and $s_2 = 0.51$. Together with $a_1 = a_2 = 1$, this implies $b_1 = 4.35 \times 10^{-9}$ and $b_2 = 5.22 \times 10^{-9}$ (equation (2.7)). The resulting stage-specific survival rates are also shown in figure 2b. Note that the constancy of second-stage survival at high S reflects near-constant entry into the second stage due to prior density dependence, rather than absence of density dependence in the second stage.

In the economic assessment I assume an ex-vessel price $\pi = 10$ US\$ kg^{-1} for whole sole, and a cost of $\gamma_1 = 1$ US\$ per piece for 1 year old hatchery fish (Moksness & Stole 1997). The cost of fishing mortality (effort) γ_2 is difficult to estimate, but its precise value is not essential here because my aim is merely to illustrate general trade-offs. For simplicity, I assume that the fishery is currently at its open access equilibrium, i.e. the cost of fishing equals the value of the catch and the resource generates zero rent (Clark 1976). This assumption is arbitrary but not unrealistic: although the North Sea sole fishery is regulated through quotas, the latter assume the character of open-access resources and lead to rent dissipation even if they succeed in conserving the stock. An overview of all parameter values is given in table 1.

(b) *Enhancement as a long-term strategy*

Key issues in the biological dynamics of enhancement as a long-term strategy for increasing yield concern the effects of releasing fish at different life stages, and trade-offs between harvesting and release regimes. I explore the effects of releasing larvae of 2 cm before, juveniles of 8 cm during, or recruits of 14 cm after juvenile density-dependent mortality, over a wide range of fishing mortality rates. For each life stage released, the numbers of hatchery fish are set to equal the equilibrium numbers of wild fish produced at the same stage given a fishing mortality of $F = 0.6 \text{ yr}^{-1}$. Equilibrium effects of continuous enhancement on total and naturally recruited yield and spawner biomass are shown in figure 3. The effectiveness of enhancement in terms of raising total yield (figure 3a) increases as more advanced life stages are released. At current levels of fishing mortality ($F = 0.6 \text{ yr}^{-1}$), increasing the abundance of larvae, juveniles and recruits by 100% raises total yield by 4%, 29% and 81%, respectively. Underlying the differential effects of the same proportional enhancement at different life stages are compensatory responses that differ in their strength and dynamics. Releasing larvae elicits the strongest compensatory response in naturally recruited yield (figure 3b) and spawner biomass (figure 3d), except at low fishing mortality when responses to juvenile and recruit stocking are stronger. Larval releases elicit compensatory responses

mainly through juvenile density-dependent mortality, while releases of recruits elicit growth responses in the recruited stock. Intermediate juvenile stages may elicit strong responses in both juvenile mortality and post-recruit growth, and the combined effect may be stronger than from either larval or recruit releases when exploitation levels are low. Effects on total spawner biomass (figure 3c) mirror those on yield in terms of the relative effectiveness of different life stages. It is striking, however, that the effect of enhancement on spawner biomass is small compared to that of fishing mortality. At the current $F = 0.6 \text{ yr}^{-1}$, increasing recruits by 100% through enhancement would raise spawner biomass from 44 000 t to 78 000 t, still far below the unexploited spawner biomass of 205 000 t.

Direct and effective (net of compensatory responses in the naturally recruited stock) yield per stocked fish increase with release size (figure 4). Importantly, the two measures also converge as the magnitude of compensatory responses declines with increasing release size. Direct yield per stocked fish as estimated from tag returns can be much higher than effective yield where compensatory processes are strong. Optimizing release size requires assessment of compensatory responses and cannot be based on returns from tagged hatchery fish alone. Density dependence in juvenile mortality is quite ubiquitous and precludes effective enhancement with larval releases except when natural larval production is very low (Secor & Houde 1998). Indeed, rather large juveniles may be required to bypass density-dependent mortality, which is detectable up to age 2.5 in some demersal stocks (Myers & Cadigan 2003b). Even releases of advanced juveniles such as cod yearlings or Pacific salmon smolts have been shown to elicit density-dependent mortality to the extent of complete compensation (Hilborn 1998; Svasand et al. 2000).

It has previously been pointed out that releases of hatchery juveniles will only be effective if regulation in the juvenile phase is either weak (Travis et al. 1998), or can be bypassed by releasing larger juveniles (Hilborn 1999). The current study corroborates this point, but also shows that when enhancement bypasses juvenile density dependence it may face stronger compensatory responses in the recruited stock. It is impossible to evade compensatory responses completely, but it may be possible to develop release and harvesting regimes that provide sufficient net gain in the face of such responses. Quantitative analysis of population dynamics, integrating over the full life cycle and several generations, holds the key to doing this. Field studies testing for displacement of wild by stocked juveniles (e.g. Leber et al. 1995) provide important information, but are not sufficient to establish the full extent of compensation.

Enhancement increases total spawner biomass, but very high levels of enhancement are required to compensate for the reductions in S associated with even moderate levels of fishing mortality. Fishing drastically reduces the proportion of wild and hatchery recruits reaching large size and providing significant reproductive output (see also § 3c). Heppell & Crowder (1998) and Salonen et al. (1998) allude to this problem in the contexts of sea turtle bycatch mortality and biomanipulation. Enhancement is fundamentally an approach to exploitation, allowing increased production while maintaining a high biomass of mostly small and immature fish, but relatively ineffective as

Table 1. Model parameters and their baseline values.
(Population parameter values approximately reflect those of the North Sea sole stock (Lorenzen & Enberg 2002; ICES 2003).)

parameter	baseline value (range)	definition
growth		
$L_{\infty L}$	46 m	asymptotic length at $B \to 0$
K	0.3 yr^{-1}	growth rate
g	4.6×10^{-5} cm t^{-1}	competition coefficient
$L(1)$	14 cm	length at recruitment (age 1)
α	1.0×10^{-8}	coefficient of length–weight relationship
β	3	exponent of length–weight relationship
natural mortality		
$M_{1,\mathrm{W}}$	3 yr^{-1} cm	mortality of wild phenotype at $L = 1$ cm
$M_{1,\mathrm{H}}$	3 (3–13) yr^{-1} cm	mortality of hatchery phenotype at $L = 1$ cm
b	0.2 (0.1–0.5)	density dependence of juvenile mortality
reproduction		
L_{m}	26 cm	length at maturity
F	25 500 t^{-1}	juvenile production per unit spawner biomass
p	1	steepness of maturity function
r	1, 0	relative reproductive performance of stocked fish
recruitment		
a_1	1.0 yr^{-1}	survival over first juvenile period at $\mathcal{J} \to 0$
b_1	0, 9.53, 4.35×10^{-9}	density-dependent parameter
a_2	1.0 yr^{-1}	survival over second juvenile period at $\mathcal{J} \to 0$
b_2	9.53, 0, 5.22×10^{-9}	density-dependent parameter
fishing		
F_{∞}	0.6 (0–2) yr^{-1}	fishing effort asymptote
L_{c}	26 cm	gear selection length
q	1	steepness of selectivity curve
evolution		
h^2	0.2 (0.0–1.0)	heritability of life-history traits
economics		
γ_1	1 (0–2) US$	cost of hatchery fish at age 1 ($L = 14$ cm)
γ_2	330 million US$ yr^{-1}	unit cost of fishing mortality
π	10 000 US$ t^{-1}	ex-vessel price of fish
δ	10%	discount rate

an approach to conserving stocks subject to high mortality on large and mature fish.

(c) *Bio-economics*
Population dynamics theory suggests that release of additional recruits may well allow significant production increases in many stocks, and this is supported by predictions for the North Sea sole case study. The crucial question is under what conditions this would be economically beneficial (Peterman 1991), considering costs of enhancement itself and trade-offs between enhancement and effort regulation. Figure 5 sets out the key considerations and reference points of a basic bio-economic analysis of enhancement, using the North Sea sole example. Point A is the bio-economic open access equilibrium of the non-enhanced fishery, where revenue equals the opportunity costs of fishing. Enhancement as a welfare programme without cost recovery or effective effort restrictions would allow the fishery to expand to a new open access equilibrium B. By contrast, if costs of enhancement were recovered from the fishing sector, for example through a tax, the enhanced open access equilibrium would be at point C. All three open access equilibria are suboptimal in that they imply rent dissipation, albeit to a different degree. The greatest resource rents would be achieved at point D for the non-enhanced, and at point E for the enhanced fishery. Of

the two options considered here, enhancement with optimal effort management would generate only marginally higher resource rent than optimal effort management without enhancement. Which of these or other outcomes are considered optimal depends on the economic and social objectives of management. What this simple analysis shows, however, is the importance of considering trade-offs between fisheries regulation and hatchery releases in the overall assessment of enhancement as a management strategy.

Botsford & Hobbs (1984) have shown that optimal fishery policy with enhancement is strongly dependent on costs, prices and biological returns. In figure 6, I analyse optimal policy with respect to resource rent as a function of the price of hatchery fish. If hatchery fish are free or very cheap, the optimal policy would be stocking at over five times the current level of recruitment combined with a fishing mortality of $F = 0.8$ yr^{-1}. This would generate a rent of over 400 million US$, three times the maximum rent obtainable from a pure capture fishery (figure 6b). At the other extreme, no enhancement is feasible at costs of hatchery fish above 1.2 US$ per piece when optimal (with respect to rent) management of the capture fishery would generate a rent of 130 million US$ at a low fishing mortality of $F = 0.2$ yr^{-1}. Total spawner biomass is fairly
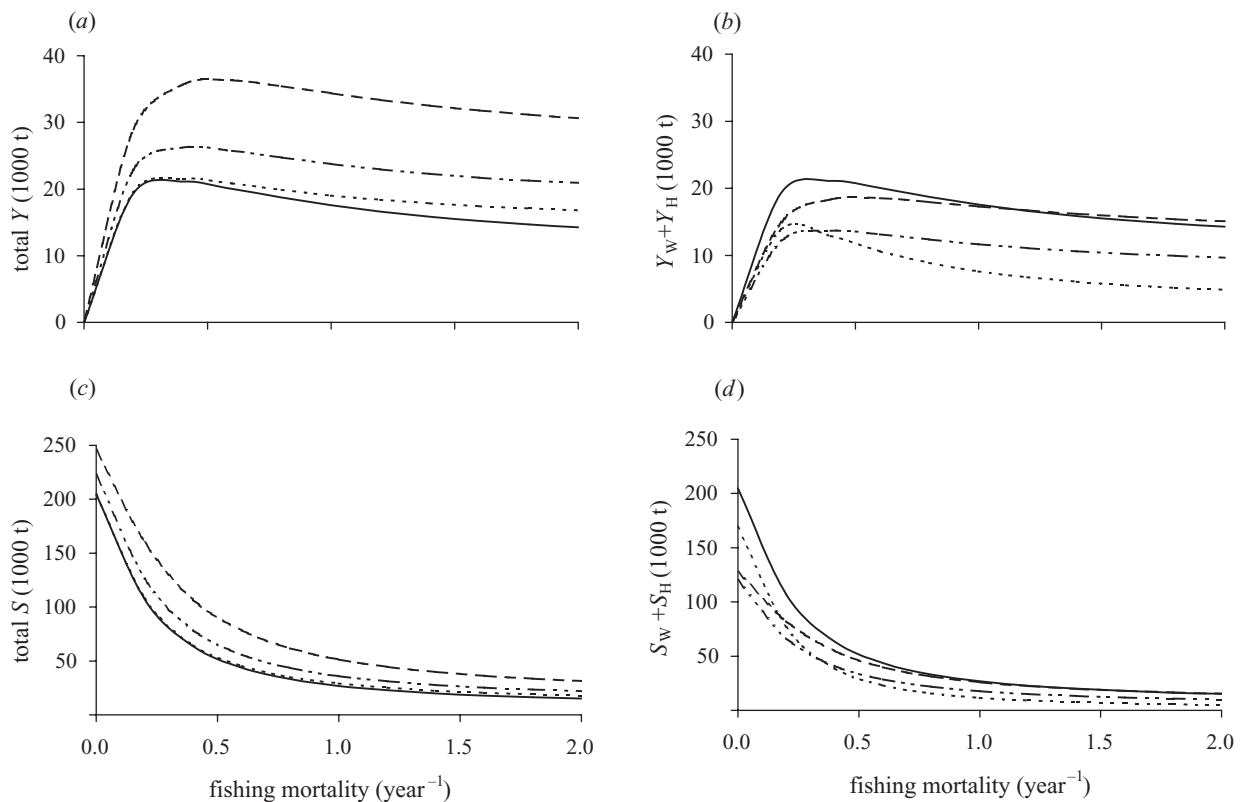
Figure 3. Effect of stock enhancement on total yield (*a*), yield of naturally recruited fish (*b*), total spawner biomass (*c*) and naturally recruited spawner biomass (*d*). Non-enhanced baseline (solid line) and releases of recruits (dashed line), juveniles (dashed-dotted line) and larvae (dotted line). Hatchery releases increase abundance at the stage of release by 100% of the natural level at $F = 0.6$ year^{-1}.

insensitive to hatchery costs and consequent levels of stocking and fishing mortality, but its naturally recruited component ($S_W + S_H$) is increasingly depressed as costs decline and levels of stocking and fishing mortality increase (figure 6*d*). This illustrates how enhancement can support intensive fisheries while maintaining high population abundance and, thus, key aspects of ecosystem structure and functioning. The trade-off however is that naturally recruited spawners are increasingly replaced with stocked fish. Enhancement can help to reconcile intensive exploitation with certain ecosystem management objectives, but this will be at the expense of the natural component of the target stock.

There are clear trade-offs between production and the conservation of wild stocks in enhancement. When enhancement is biologically effective and stocking costs are low, optimum economic policy may depress the abundance of the naturally recruited stock component even when the concomitant loss of natural production is taken into account. Hence, where wild stock abundance has a value in addition to that of the associated fishery productivity, this must be included explicitly in the economic analysis, and/or direct conservation safeguards need to be introduced in order to maintain an abundant wild stock (at the expense of some production benefit). Hatchery-enhanced stocks can supply many but not all of the production and ecosystem services provided by wild stocks (Holmlund & Hammer 1999). Ecological services provided by juveniles prior to the stage at which hatchery fish are released, the value of fish stocks as indicators of ecological integrity, and the

existence value of wild populations are among the attributes at which enhanced stocks will fall short of the value of wild populations. The values attached to different aspects of the enhanced stock will differ between systems (pristine versus highly modified environments, developing versus developed countries), and between stakeholders within systems (fishers versus conservationists). Bio-economic analysis cannot resolve such differences, but it can help greatly to make informed choices.

The analysis presented here remains economically simplistic, but still provides key insights for fisheries policy. It can be extended by integrating the biological models developed here into more sophisticated economic models which, so far, have relied on abstract biological models (Arnason 1991, 2001). It must also be realized that in practice, many of the reference points used in the static bio-economic analysis can only be reached via complex temporal patterns of investment, cost recovery and deliberate effort control.

(d) *Enhancement for stock rebuilding*

What is the potential for enhancement to contribute to rebuilding of spawner biomass in depleted stocks? In the North Sea sole stock, spawner biomass at the present level of exploitation is *ca.* 20% of its unexploited level. Rebuilding spawner biomass to *ca.* 40% is called for by the precautionary approach (ICES 2003) and may also have beneficial ecosystem effects. I therefore explore rebuilding trajectories and evaluate the time needed to rebuild to target biomass and net present value of alternative recovery scenarios with or without enhancement (table 2; figure 7).
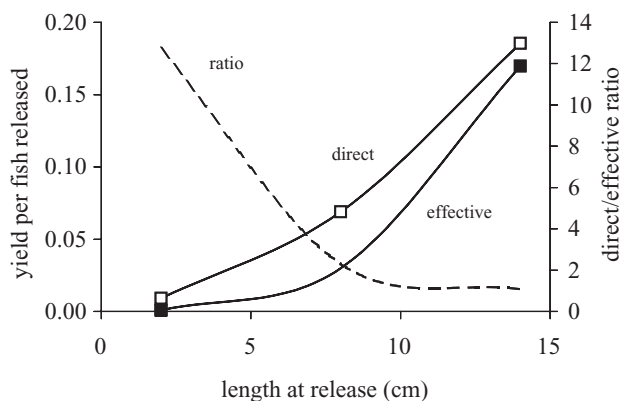
Figure 4. Direct and effective yield per stocked fish as a function of release size. Also shown is the ratio of direct to effective yield, i.e. the factor by which direct returns of tagged fish overestimate their effective contribution to yield. Fishing mortality $F = 0.6 \text{ yr}^{-1}$ and hatchery releases increasing abundance at the stage of release by 100%.
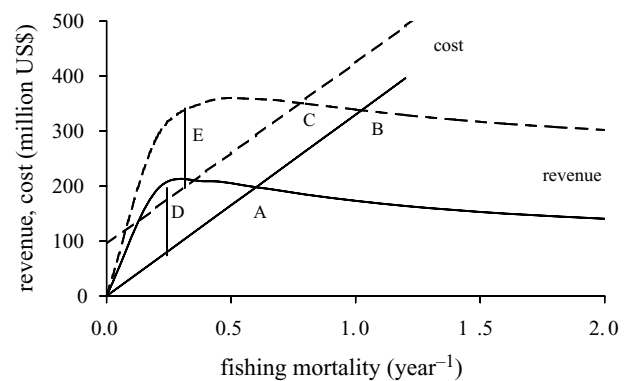

Figure 5. Bio-economic reference points for sole stock enhancement. Revenue and cost curves without enhancement (continuous lines), and for releases increasing natural recruitment by 100% at $F = 0.6 \text{ yr}^{-1}$ (dashed line). Open access equilibria for the baseline case without enhancement (A), enhancement as a welfare programme without cost recovery (B) and as a commercial operation with cost recovery (C). Also shown are the maximum resource rents achievable without (D) and with (E) enhancement.

Simply closing the fishery until target spawner biomass is reached and subsequent harvesting at $F = 0.3 \text{ yr}^{-1}$ (strategy B) achieves rebuilding after only 2 years of closure, and has the highest NPV of all options. The same scenario with temporary enhancement (strategy C) is the second best option, closely followed by reducing exploitation to $F = 0.3 \text{ yr}^{-1}$ without and with enhancement (strategies D and E, not shown in figure 7). The option of enhancing to rebuild spawner biomass before reducing effort (strategy F) avoids temporary yield loss, but foregoes the economic benefits of immediate effort reduction. It delays recovery and has a much lower NPV than the options that involve immediate effort reductions. Reducing effort immediately is far more advantageous in NPV terms than attempting stock enhancement and postponing effort reductions. However, simply closing the fishery will result in effort being redirected elsewhere and/or hardship to fishers, so that combining gradual effort adjustment with compensation and decommissioning programmes may be ecologically and socially advantageous. The contribution of enhancement to rebuilding is likely to be limited in either case, but continuous enhancement could be considered as an alternative to rebuilding the natural spawning stock. The predicted, rapid rebuilding of spawner biomass after effort reduction is based on gains in biomass due to growth and increased survival of already recruited fish. It therefore takes almost immediate effect, while enhancement and increased natural recruitment will become effective only after at least one generation. However, there are situations where enhancement can help to rebuild stocks more quickly than closure of the fishery alone (figure 7c). This is the case principally where stocks have been reduced to such low levels that natural rates of biomass growth are insufficient to achieve rebuilding within one or two generations, or in semelparous species. Enhancement may be particularly beneficial in populations that show depensatory density dependence at low abundance (Liermann & Hilborn 1997; Walters & Kitchell 2001). To be effective in rebuilding stocks from very low abundance, the level of enhancement must be high relative to the natural recruitment capacity of the depleted stock. A high level of enhancement also implies a high level of genetic risks to the

target stock, and necessitates careful genetic resource management (see Utter 1998; Miller & Kapuscinski 2003).

Experience with stock rebuilding efforts involving enhancement broadly corroborates the theoretical results obtained here. A retrospective analysis of the successful striped bass (*Morone saxatilis*) stock rebuilding programme in Chesapeake Bay points to a predominant role of effort reduction, and at best a marginal contribution of enhancement (Richards & Rago 1999). Where hatchery releases have played a major role in fisheries restoration, this is typically in the context of bolstering very small, or re-establishing locally extinct populations (Philippart 1995). Overall, this suggests that enhancement is of limited use for rebuilding of overexploited stocks. Any proposals for enhancement as a rebuilding strategy must be carefully evaluated against alternative or additional measures, and the methodology developed here provides the basis for doing this even where data are very limited. Where enhancement may be effective in principle, it must also be considered that developing hatchery production and release protocols and scaling up production to meet requirements for rebuilding large stocks is likely to take years if not decades.

(e) *Maladapted hatchery fish*
Maladaptation of hatchery fish to the natural environment may be reflected in a variety of life-history traits, and be based on developmental and/or genetic factors. I consider increased natural mortality of hatchery fish in the post-recruit phase as an example, using different assumptions on the biological basis of maladaptation and the reproductive competence of hatchery fish. The latter assumptions include release of sterile fish, and releases of reproductively competent fish that either produce wild phenotye offspring (implying that parental maladaptation results from developmental plasticity), or produce maladapted offspring subject to different levels of selection pressure towards the wild (optimum) phenotype. Total yield declines with increasing mortality of hatchery fish under all assumptions, gradually approaching the non-enhanced level (figure 8a). Reproduction of released hatchery fish makes a very slight contri-
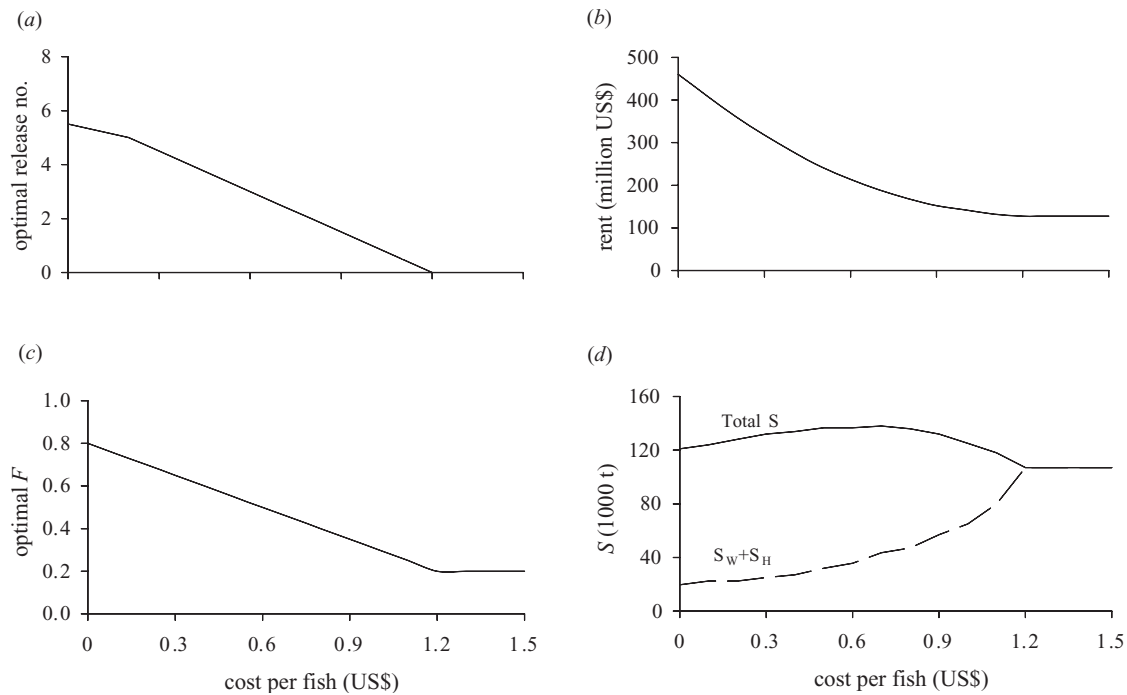
Figure 6. Influence of the unit cost of hatchery fish on optimal fishery policy with respect to resource rent. (*a*) Optimal release numbers as multiples of natural recruitment at $F = 0.6 \text{ yr}^{-1}$. (*b*) Resource rent at optimal release and effort regime. (*c*) Optimal fishing mortality F. (*d*) Abundance of total and naturally recruited (wild and hatchery phenotype) spawners.

bution to yield if maladaptation is moderate and arises from developmental plasticity only. If maladaptation has a genetic basis and is perpetuated through reproduction, reproduction depresses equilibrium yield below the level achieved by release of non-reproducing fish. The demographic effect of maladaptation is greatest if the genetically-determined reduction in performance is only moderate (here, a doubling of the base rate of natural mortality). Hatchery releases always depress wild phenotype spawner biomass (figure 8*b*), and this effect is greatest if maladaptation is weak, genetically based and subject to low heritability. Continuous release of genetically (and phenotypically) fit hatchery fish does not depress productivity because the fish perform as well as their wild conspecifics, but carries a great risk of displacing the wild genotype for precisely the same reason. This is of conservation concern where the hatchery and wild genotypes are not identical. Releasing genetically maladapted individuals reduces yield (figure 8*a*) but causes less displacement of the wild genotype. Effective yield per released hatchery fish (figure 8*c*) indicates that, in the case of North Sea sole, no enhancement will be economically viable (produce a yield per hatchery fish above the break-even level of 0.1 kg) if maladaptation causes M_1 to rise above 7 yr^{-1}. If maladaptation is genetically based, the threshold is even lower at approximately $M_1 = 5$ yr^{-1}.

This analysis provides important insights into the genetic risks of enhancement. Continuous release of well-adapted hatchery genotypes is likely to cause introgression to the extent of virtual replacement of the wild genotype, but have no effect on productivity. Moderately maladapted hatchery genotypes pose the greatest combined risk of introgression and loss of productivity. The demographic and genetic impact of poorly adapted genotypes is predicted to be effectively self-limiting, but several caveats are in order. Even

poorly adapted genotypes can have significant ecological and genetic effects on wild conspecifics if released in very large numbers, or when maladaptation is manifested only under extreme environmental conditions (Philipp & Whitt 1991). Results are broadly consistent with those obtained by Byrne *et al.* (1992) and Ford (2002), and illustrate the importance of considering interactions between demographic and genetic processes in the analysis of fisheries enhancement. Due to such interactions, outcomes of enhancement in terms of yield, abundance and the level of introgression are more sensitive to small differences in the performance of released organisms than expected from either demographic or genetic considerations alone.

Releasing sterile fish has the potential of minimizing the risks of both ineffective enhancement if hatchery fish are maladapted, and displacing the wild genotype if they are not. Moreover, potential benefits from successful reproduction of hatchery fish in the wild are predicted to be small. Release of sterile fish is thus indicated as a management strategy provided they do not compromise the reproductive performance of wild conspecifics, e.g. through behavioural interactions.

(f) Feasibility of North Sea sole enhancement: conclusions

While the primary aim of my analysis has been to derive general insights into the dynamics and potential of stock enhancement, it has also provided a preliminary assessment of the potential for enhancing the North Sea sole stock in particular. Overall, results are not encouraging: if the assumptions and parameter values used here are correct, enhancement could be technically effective but would generate only marginal economic benefits. A natural mortality rate more in line with comparative information for other wild stocks (let alone released hatchery fish) would

Table 2. Performance of different options for rebuilding the North Sea sole stock to a spawner biomass of 80 000 t. Economic assumptions as before, i.e. fishery is assumed to be at bio-economic open access equilibrium and cost of seed fish is 1 US$ per juvenile, and discount rate 10%.

strategy	description	time to ($S = 80\ 000$ t)	NPV (million US$)
A	no change ($F = 0.6$ yr^{-1}, no enhancement)	∞	0
B	close fishery until target S is reached	2	761
C	close fishery and enhance until target S is reached	2	733
D	reduce exploitation to $F = 0.3$ yr^{-1}, no enhancement	10	656
E	reduce exploitation to $F = 0.3$ yr^{-1} and enhance until target S is reached	4	607
F	maintain $F = 0.6$ yr^{-1} and enhance until target S is reached, then set $F = 0.3$ yr^{-1} and discontinue enhancement	10	142

imply far lower returns and all but preclude the prospect of economic feasibility. Any further assessment of enhancement as a management option for North Sea sole should involve a release experiment to assess mortality rates, and estimation of the true costs of hatchery production and fishing. Such new information is easily integrated into the model developed here.

4. IMPLICATIONS AND OUTLOOK

Stock enhancement holds significant potential for raising yields of target stocks where effective hatchery production, release and harvest regimes can be developed. However, both economic and conservation considerations pose strong constraints on the sustainability of enhancements, and only a small subset of technically feasible enhancements will be beneficial overall compared to alternative fisheries management options. Understanding the dynamics of stock enhancements is crucial to identifying such beneficial applications, and the current study provides both general insights in this respect and a methodology for the evaluation of specific systems.

(a) *Dynamics and potential of stock enhancement*

There appears to be good biological potential for increasing yields through releases of hatchery fish that bypass juvenile density-dependent processes at least partially. Effective enhancement will increase total abundance, but reduce abundance of the naturally recruited component of the stock below its non-enhanced optimum either through compensatory density dependence or through overfishing. The key challenge is thus to design release and harvesting regimes that provide sufficient net returns in the face of compensatory processes acting at all life stages. Whether this is possible at all will depend on specific biological and economic conditions. While enhancement will generally involve negative impacts on the naturally recruited component of the target stock, raising total stock abundance under heavy exploitation may contribute to maintaining structure and functioning of heavily exploited ecosystems.

Despite biological potential, economic benefits of stock enhancement in commercial fisheries will often be marginal or negative given current market prices and post-release performance of hatchery fish. Strong trade-offs exist between the costs of fishing and hatchery releases. Cost and post-release survival of hatchery fish strongly influence optimal policy, which may range from no enhancement at high cost (low survival) to high levels of stocking, to fishing effort and yield at low cost (high survival).

Release of genetically maladapted hatchery fish reduces the effectiveness of enhancement, and is most detrimental overall if fitness is only moderately lower than in the natural population. Releasing sterile fish minimizes risks from maladaptation to both the enhancement programme and the wild stock, provided sterile fish do not interfere with the reproductive performance of wild fish.

As a temporary measure for stock rebuilding, enhancement is beneficial only if the population has been reduced to a very low proportion of its unexploited biomass. Effort restrictions are the most effective short-term measure, and delaying such restrictions in favour of enhancement may incur large economic loss as well as ecological damage. Enhancement may contribute to the rebuilding of overexploited stocks under certain conditions, but cannot substitute for effort restrictions.

These general insights into enhancement dynamics and potential should not substitute for a careful and objective analysis of specific enhancement proposals or programmes. There is no general answer to the question whether stock enhancement is effective or sustainable—it depends on specific circumstances, technology and management, and not least the values that stakeholders attach to outcomes.

(b) *Development and management of enhancements*

Quantitative assessment of biological and economic outcomes is crucial to the rational evaluation of enhancement and alternative or additional management measures, and should be central to any responsible enhancement programme. The theoretical framework and model developed here provide a powerful and general tool for the evaluation of enhancement programmes, from early planning to full-scale operation. Preliminary assessments (such as the one conducted here for North Sea sole) can and should be carried out before significant investment in experimental research or production facilities, and before any alternative management options are dismissed or delayed in favour of enhancement. Combining population dynamics and bio-economic modelling with participatory planning will promote a broad-based assessment of alternatives, and reduce the influence of unrealistic expectations and partisan views on decisions. Often, preliminary assessments will rule out enhancement as an effective and economically beneficial option. Where this is not the case, further research and development may be justified.

Where available, stock assessments provide information on the values of model parameters pertaining to the wild stock, while release experiments allow the estimation of
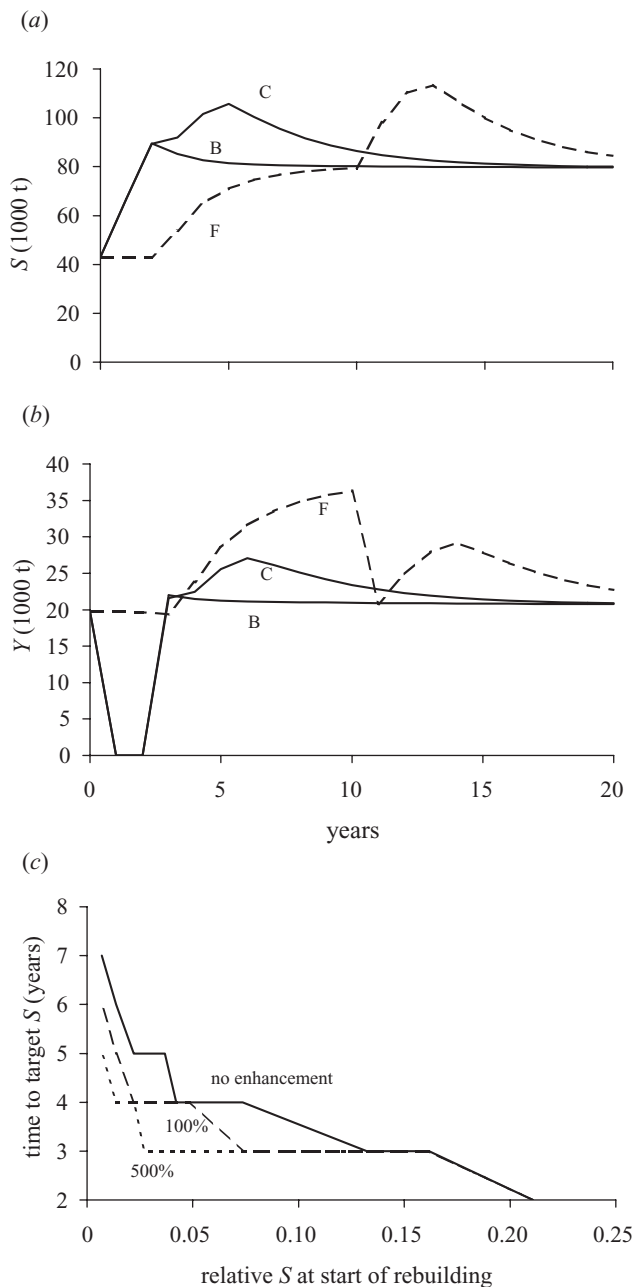
Figure 7. Rebuilding the sole stock to a target spawner biomass S of 80 000 t with and without enhancement. Development of spawner biomass (a) and yield (b) over 20 years following adoption of rebuilding policies B (close fishery until target B is reached), C (close fishery and enhance until target B is reached) and F (enhance until target B is reached, then reduce fishing effort to $F = 0.3$ yr^{-1}). See table 2 for further details of rebuilding policies. Also shown (c) is the time needed to rebuild to target S from different levels of initial S (relative to unexploited S) without enhancement and with enhancement at 100% and 500% of natural recruitment at initial S.

Figure 8. Effect of increased natural mortality M_1 of hatchery fish due to developmental or genetic maladaptation on yield (a), abundance of wild phenotype spawners (b), and effective yield per released fish (c). Assumptions: stocked fish do not reproduce (bold solid line), stocked fish reproduce and all offspring are of the wild phenotype (i.e. maladaptation is developmental only, $h^2 = 1.0$; solid line), and stocked fish reproduce and maladaptation is genetically based with heritabilities of $h^2 = 0.2$ (dashed line) and $h^2 = 0.0$ (dotted line). The horizontal line in (c) denotes the economic break-even level of yield per released fish.

wild and hatchery fish (Fleming & Petersson 2001). Comparative information allows prognostic evaluations to be conducted even in very data-poor situations, exploring alternative management options for a range of scenarios that capture the uncertainty imminent in biological and economic assumptions.

Should a proposed enhancement programme pass the prognostic evaluation and continue to pilot or operational stage, experimental studies will be required to resolve key uncertainties (Leber 1999; Hilborn 2004). Experimental studies must encompass monitoring of the wild, as well as stocked, components of the enhanced population, and be

others including the mortality rate of stocked fish. Comparative studies can provide invaluable *a priori* information on parameter values including those of the stock–recruitment relationship (Myers 2001), size-dependent mortality in wild and released hatchery fish (Lorenzen 1996*a*, 2000), density-dependent growth in the recruited phase (Lorenzen & Enberg 2002), and comparative performance of
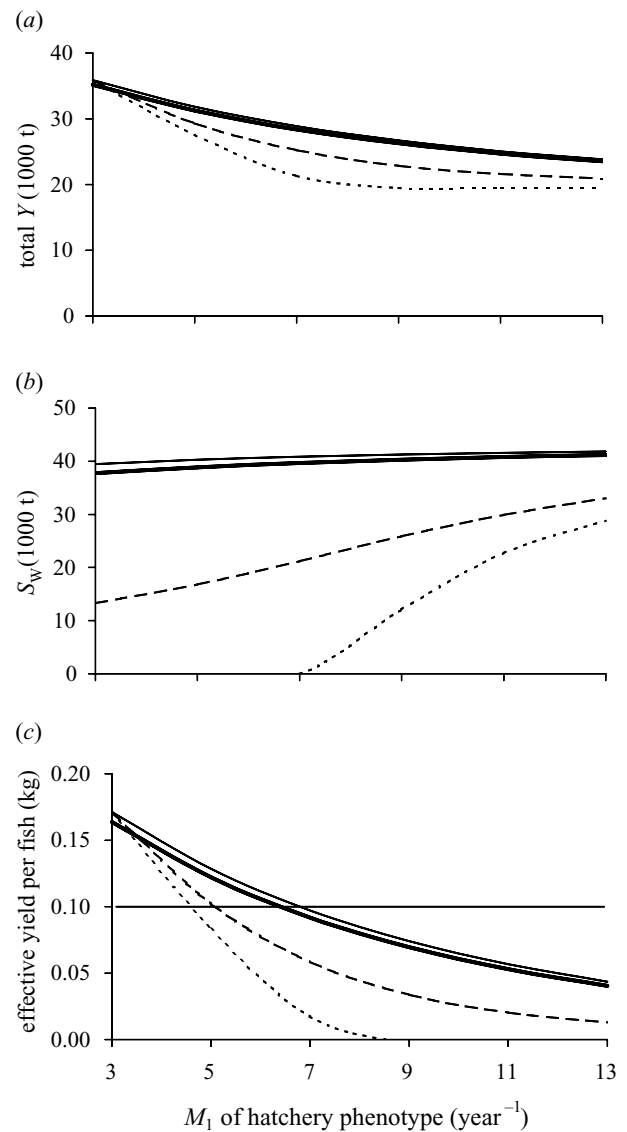
carried out on a large scale to capture the compensatory effects that ultimately determine biological enhancement success (see also Peterman 1991; Hilborn 2004). Population analysis can help to identify the most pertinent uncertainties, and aid the design of experiments to resolve them. Given the dynamic complexity of enhancements and the time-scales involved in responses, experimental approaches alone are unlikely to be efficient in evaluating potential and optimizing release and harvesting regimes. Close integration of population modelling and experimental management is likely to be the most efficient approach to assessing and developing enhancements, and should be a prominent element of planning frameworks (e.g. Cowx 1994; Blankenship & Leber 1995).

(c) Research

Further development of the theory presented here is required, in particular with respect to five areas: interaction of size and density-dependent processes throughout the life cycle, proximate basis of life-history plasticity, combined effects of natural selection by hatchery production and fishing, competitive asymmetries between wild and hatchery fish, and community-level interactions. The approach used here is an extension of conventional fisheries stock assessment models, and treats these problems in a separate and largely phenomenological manner (describing measurable responses in population parameters rather than underlying biological processes). However, the emerging evolutionary ecology of fisheries suggests that these aspects are closely connected. Recruitment limitation may arise from natural selection for use of restricted feeding habitats due to predation risk, a multi-species interaction (Walters & Korman 1999). This provides a theoretical framework for linking recruitment to the dynamics of prey and predator species, which in turn may be subject to 'cultivation' effects by the very population whose recruitment is being studied (Walters & Kitchell 2001). An evolutionary perspective will provide a deeper understanding of how the ecological interactions underlying enhancement dynamics arise, and most probably reveal new relationships between key parameters and processes. Fisheries enhancements may provide the most effective, if not the only, way of testing such theories on relevant ecological scales. Hence, enhancement research is likely to make significant contributions to fundamental fisheries ecology.

(d) Future role of enhancements

What, if any, role does the future hold for stock enhancement in fisheries management? Conditions for the development of sustainable stock enhancements have never been better than at present. Emerging theory and assessment methodology for stock enhancement will facilitate realistic and quantitative policy analysis, weeding out ineffective or damaging enhancements, identifying new opportunities and optimizing operational systems (this study). Aquaculture technology is increasingly capable of cost-effectively producing fish that perform well in the wild, a crucial precondition for economically viable enhancement (Olla *et al.* 1998; Brown & Dey 2002). Genetic resource management can mitigate, if not fully eliminate, genetic risks to wild populations (Waples 1999; Miller & Kapuscinski 2003). The tendency in many regions of the world to replace open access to fisheries with common or private use

rights regimes (Hilborn *et al.* 2003) establishes institutions conducive to investment into fisheries resources, including enhancement approaches. The potential for enhancement to increase productivity and thus reward active stewardship may in itself provide incentives for resource users to cooperate in management, provided they contribute to costs and external institutional arrangements support collective action (Pinkerton 1994; Lorenzen & Garaway 1998). Real prices of fisheries products are high and increasing, as demand will continue to outgrow supply despite a further expansion of aquaculture (Delgado *et al.* 2003).

Even though the general conditions are thus conducive, stock enhancement will remain subject to strong biological, economic and institutional limitations. These arise from natural processes and conditions beyond management control, and inherent difficulties of establishing compatible institutional regimes in larger systems where stakeholders are diverse and often have conflicting interests. Strong public support for conservation of natural aquatic resources makes large-scale manipulations for production ends all but unacceptable. Stock enhancement is therefore likely to remain a niche form of aquatic resource use, dominated in output by both capture fisheries and aquaculture. However, enhancement can make significant contributions to fisheries-related livelihoods where basic biological and economic conditions are met, and help to reconcile intensive exploitation with certain (but not all) ecosystem management objectives. Effective conservation of aquatic resources on a scale beyond individual protected areas and conservation schemes can be achieved only if the burgeoning demand for fisheries products, and the needs of the many people relying on fisheries for all or part of their livelihoods can be satisfied. Where stock enhancement is biologically effective and economically feasible, its environmental and socio-economic impacts may well compare favourably to realistic production and livelihoods alternatives. Research on stock enhancement issues will remain a dynamic and exciting area of fisheries science, and continue to make major contributions to the advancement of fisheries ecology as well as aquaculture science.

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GLOSSARY

MSY: maximum sustainable yield
NPV: net present value