

The natural control of salmon and trout populations in streams

N.J. Milner^{a,*}, J.M. Elliott^b, J.D. Armstrong^c, R. Gardiner^c, J.S. Welton^d, M. Ladle^d

^a National Salmon and Trout Fisheries Centre, Environment Agency, 29 Newport Road, Cardiff CF24 0TP, UK

^b Freshwater Biological Association, The Ferry House, Far Sawrey, Ambleside LA22 0LP, UK

^c Fisheries Research Services, Fisheries Laboratory, Faskally, Pitlochry, Perthshire PH16 5LB, UK

^d CEH Dorset, Dorset, Winfrith Technology Centre, Winfrith Newburgh, Dorchester DT28ZD, UK

Abstract

This paper reviews current understanding of factors controlling salmonid populations in streams and how this contributes to better fisheries management. Salmonid populations are regulated by density-dependent mortality, typically during the early stages of free-living life after fry emerge from spawning gravels. After the early regulatory phase, mortality is controlled mainly by density-independent factors. The relative contributions of density-dependent and density-independent factors to population variability are outlined, noting the special importance of environmental impacts such as flow and temperature extremes. Stock–recruitment relationships are discussed, with an emphasis on understanding the uncertainties and risks inherent in modelling wild populations. Key subjects for future research are identified. The challenge for science in the future lies in two areas: first, incorporating uncertainties into population modelling and management decision making, and second improving the understanding of processes regulating populations through long term studies.

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1. Introduction

Fish populations are subject to natural control processes that continually modify and adjust the structure and abundance of populations and their life cycles in response to a wide range of factors. This paper discusses population dynamics of the Atlantic salmon (*Salmo salar* L.) and the migratory (sea trout) and non-migratory (brown trout) forms of trout (*S. trutta* L.).

Effective fisheries management is dependent upon, among other things, knowledge of how fish popula-

tions are regulated naturally and thus how they might respond to management intervention. Most salmonid populations are naturally highly variable, with respect to their abundance and life history features, both within populations over time and between populations. This can cause difficulties for managers because it introduces uncertainties into stock assessment and into the prediction of management outcomes. An understanding of population dynamics can show why these uncertainties arise, how to quantify them, and how to optimise management decisions.

The spatial and temporal variability of populations operate within constraints imposed by the environment and genetic predisposition of the fish, but within these limits there is often considerable flexibility. For example, in migratory salmonids, changes in growing conditions in fresh water are thought to influence smolt

* Corresponding author. Tel.: +44-29-20770088;
fax: +44-29-20798555.
E-mail address: nigel.milner@environment-agency.gov.uk
(N.J. Milner).

age and size, and thus survival at sea, resulting in complex, interrelated adjustments throughout the life cycle. Genetic adaptation to local stream conditions also exerts its effect by modifying the processes expressed through population dynamics.

Population dynamics is a wide subject and here we concentrate on those aspects that are particularly pertinent to management, namely processes regulating abundance, especially the compensatory mechanisms; stock–recruitment relationships; population variability, and the interdependence of traits such as growth, survival and maturation. We generalise across salmon and trout wherever possible, but note the species distinctions where they are known to be significant and take examples from other species where they are appropriate.

2. Populations, management units and sampling

Populations are usually defined as biological units that are reproductively discrete, but their dynamics have been studied at widely ranging scales from local sites (<10 m stream lengths) up to whole catchments (generally <500 km). As more is learnt about homing and genetics of salmonids, the points at which populations start and finish become more difficult to define, but also more critical as the evolutionary significance of sub-structuring within rivers becomes clearer (Youngson et al., 2003).

For economic, legal and practical reasons, fisheries management is usually applied to *stocks*, being groupings of populations that are regarded as having broadly similar biology and genetics, and experience similar environmental conditions and exploitation regimes, to which they display broadly similar responses. Distinctions have been made between evolutionarily significant units (ESUs) and operationally significant units (OSUs) (Dodson et al., 1998). ESUs are considered to be the appropriate unit to ensure biological conservation, but the OSU has been the conventional grouping for practical management, synonymous with stock here. This scale issue is important, because survival traits and other adaptive features of life cycles that influence the dynamics of each population (ESU) may not be measurable or applicable at an OSU scale. Therefore, without care, management choices could be sub-optimal for some ESUs. In the following

account the terms stock and population will be freely interchanged, and a distinction made only where it is necessary to clarify meaning.

The practical issues of sampling efficiency and survey design are important in understanding sources of variation in populations. The abundance of fish in a stream section is the net effect of births, deaths, immigration, and emigration. Typically, numbers decrease with age in the total population, but in a short stream section, where local habitat may favour a particular life stage of fish, the age structure is often unbalanced, with perhaps more 1- or 2-year olds present than younger fish. Consequently, adjacent stream sections may have very different salmonid population structures, depending on the habitat they offer. In practice, the information on stream populations usually comes from sampling comparatively short sections (e.g., 50–100 m), each containing a biased sample of the total population. Age structure may also vary between years as random events alter recruitment and survival. This combined with the varying efficiency of sampling in different habitat types, increases variability and attendant uncertainty in population data.

For migratory species, total counts of inputs (spawners) and outputs (smolts) from streams can be made using traps or counters. In theory these could be made without sampling error, but in practice measurement errors always arise. The total counting option is desirable, but it is expensive and not often available. Moreover, on its own, it does not help in understanding processes within streams. To properly understand population dynamics, a combination of whole catchment and local site sampling is required, over many years. This has rarely been achieved (e.g., Elliott, 1993a) and is a long-standing research need.

3. Life cycles of salmonids

Salmon and trout have life cycles that are comparatively complex and highly variable between populations (Elliott, 1994; Hutchings and Jones, 1998; Jonsson, 1985, 1989). The anadromous forms migrate between a freshwater reproductive and juvenile phase, typically in the upper reaches of rivers, and a growth phase, typically in the larger habitats of lower rivers, lakes or the sea.

The eggs are laid in redds in gravel in the autumn and winter and hatch in early spring. The alevins remain in the gravel for a short period, feeding on their yolk sacs, then emerge as fry to begin feeding on drifting invertebrates. The early post-emergence phase is a crucial one in which fry develop the swimming behaviour to maintain position and feed in flowing water and during which dispersion from the redds occurs. This phase is typified by aggressive, territorial behaviour and high mortality rates that regulate population size (Kalleberg, 1958; Le Cren, 1973; Elliott, 1994; Heland, 1999). The surviving parr spend between 1 and 3 (usually 2) years in streams in Britain, but longer (up to 7 years) in colder regions such as Scandinavia and Canada (Gibson, 1993). Finally, they undergo physiological changes that pre-adapt them to life in the sea and migrate as smolts in April–May. Smolts move in large numbers and are particularly vulnerable to predation in fresh water, estuaries and at sea (Feltham, 1990; Hvidsten and Møkkelgjerd, 1987; Kennedy and Greer, 1988). Both salmon and trout exhibit a wide range in life history strategies, expressed through, for example, different age-at-maturation and migration patterns. Although European Atlantic salmon are typically anadromous, there are examples of landlocked races (e.g., Berg, 1985). Trout in particular are highly variable in their degree of migratory habit, exhibiting a continuum from merely local spring redistribution (<100 m) within small streams (Milner et al., 1979), through to migrations into lakes, estuaries and sea feeding grounds (Jonsson, 1985; Northcote, 1992; Elliott, 1994; Baglinière and Maisse, 1999).

At sea, most European Atlantic salmon post-smolts make long migrations to feeding grounds off the Faroes or West Greenland (Hansen and Quinn, 1998) before maturing and returning to natal rivers after 1–4 years. For both species, growth is rapid in the marine phase, dependent upon sea-feeding. Sea trout exhibit considerable geographical variation in marine growth and pattern of maturation and return, that may be due partly to differences in coastal sea-feeding conditions (Fahy, 1978; Solomon, 1995), but may also be adaptations to particular river structures. In both species there is sex-selective migration with, in general, more females than males migrating to sea or lakes. Residency is often associated with early male maturation (Gibson, 1993; Jonsson, 1989) and can

occur in a high proportion of the males in some sea trout populations (Campbell, 1977). Maturing male parr form a significant part of the breeding population in some salmon stocks and represent one of two distinct reproductive tactics (the other being the production of anadromous males that compete aggressively for mates). Fleming (1996) has reviewed the evolutionary origins and implications of these strategies. Sex-linked migration is thought to provide an opportunity to increase fecundity and egg size, which are strongly, positively correlated with female size (Pope et al., 1961; Elliott, 1995; Fleming, 1996). The mechanisms behind trade-offs between life history traits and the interrelationships between genotypic and phenotypic variation are attracting more attention which will improve understanding of salmonid life history variation (Stearns, 1992; Fleming, 1996).

Homing to natal rivers is particularly strong in salmon (Stabell, 1984), maintaining reproductive isolation, with its implications for local genetic adaptation (Youngson et al., 2003). Sea trout make less extensive migrations, mainly confined to coastal waters, and tagging studies suggest that, like salmon, homing specificity is high (Sambrook, 1983; Le Cren, 1985; Solomon, 1995).

In summary, the generalised salmonid life cycle is capable of adaptation to a wide range of environmental conditions, but with a complex and still poorly understood interaction between environmental and genetic factors. It can involve extensive migrations, and thus exposure to many types of environmental influences from oceanic climate change to impacts of local land use. The migratory habit, seen to various degrees across most trout and salmon populations, leads to a spatial separation between a regulatory phase, mostly in the early juvenile stages in nursery areas, and a growth phase (benefiting egg production) in the larger habitats occupied by pre-adults.

4. Population regulation

4.1. Basic principles of stock and recruitment

Given the territorial nature of juvenile salmonids and their requirement for food, there is clearly a limit to the number of fish that any stream can support. At low spawning densities, because competition is

limited, reproduction is efficient and the number of juveniles produced is closely proportional to the spawning level. As spawning numbers increase so does competition amongst the young fry, and density-dependent factors serve to restrict the population as the carrying capacity is approached (Fig. 1a). Carrying capacity varies dependent upon species, age of fish, nature of the habitat, food availability and time of year (see Armstrong et al., 2003, for a detailed discussion). An example of a stock–recruitment curve from the River Bush in Northern Ireland is shown in Fig. 1b. This is based upon repeated annual measurement of the number of salmon smolts (recruits) emigrating from the river and the number of adults (expressed here as equivalent egg deposition) that produced them. The two curvilinear relationships between stock and recruitment in Fig. 1b are based upon the same data, but are calculated using different mathematical models. Survival rate (between eggs and older stages) does not suddenly change, as implied diagrammatically in Fig. 1a. It is usually found to decrease with increasing spawner density, changing most rapidly as the carrying capacity is approached (Fig. 1c). The term “recruits” can apply to any stage in the life cycle, such as the adult progeny of a year class just before they become vulnerable to a fishery, or to adult spawners returning to their natal stream. In migratory salmonid studies, consideration of parr or smolts as recruits is a convenience, because it marks the end of a distinct biological phase. It also has management significance, because it signals the production of the fresh water phase and is the last chance to measure the size of a year class until adults return from the sea 1–3 years later.

4.2. Factors influencing abundance

Abundance of stream-dwelling salmonids is influenced by two broad categories of process. First, density-dependent feedback mechanisms, such as territorial competition or limited food availability, can be said to truly *regulate* abundance. Secondly, density-independent processes (such as climate), which act unpredictably to *determine* abundance and, because they can have large effects on survival, may obscure the underlying density-dependent processes. Much of population dynamics is concerned with distinguishing between these processes, understanding

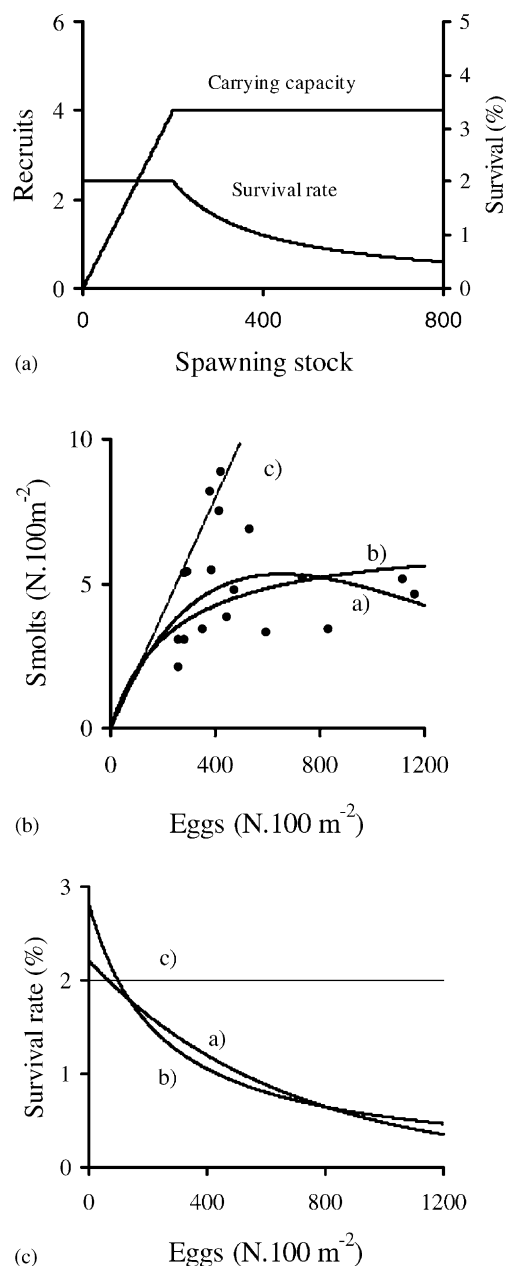


Fig. 1. (a) Diagrammatic representation of recruitment constrained by carrying capacity, showing survival rate (% egg to recruit) changing with spawning stock. (b) Stock-recruit curves for salmon from the River Bush (northern Ireland (adapted from Kennedy and Crozier, 1993), showing (a) dome-shaped (Ricker) and (b) asymptotic (Beverton and Holt) relationships. Line (c) shows directly proportionate survival (egg to smolt) at an arbitrary 2%. (c) Survival rates (%) between egg and smolt stages for the stock–recruitment relationships shown in figure (b).

their effects and assessing their relative contributions to population variation.

4.3. *Density-dependent effects on abundance*

Density-dependent mortality is a prerequisite for persistent populations that are apparently stable and by implication regulated (Elliott, 2001). Population regulation implies that the relationship between spawning stock and recruits is not random or simply proportionate. The stock–recruitment (S–R) relationship expresses the form that regulation takes in a population. However, it is notoriously difficult to collect the data required to elucidate S–R relationships, because it is necessary to measure populations over many generations or across many experimental populations, with appropriate variation in spawning stock size. This requires long-term programmes and sometimes elaborate facilities which are hard to fund. Moreover, in the field situation, there are practical problems, such as coping with long-term environmental changes that, by influencing survival or growth rates, for example may alter the relationship between spawners and recruits during the period of observations. Hilborn and Walters (1992) have reviewed the issues underlying this so-called non-stationarity.

Density-dependent processes can be positive or negative, i.e., the probability of individual survival increases or decreases with density. Positive density-dependence occurs with some forms of fishing pressure and predation, in which high density, possibly accompanied by shoaling behaviour, reduces the chances of individual deaths (Solomon, 1982; Hansen and Jonsson, 1985; Hvidsten and Johnsen, 1993). Negative density-dependence is more common and arises from the classic negative feedback mechanisms that regulate abundance, such as territorial competition for food and space, disease and parasitism. A further distinction should be made between internal density-dependent factors such as spawner abundance, density of each cohort of fish and external density-dependent factors such as the density of other cohorts of the same or different species, incidence of predators, disease or parasites. Habitat availability and quality is in a special category, being a resource that, by limiting carrying capacity, stimulates density-dependence to operate.

Factors may change from positive to negative depending on stock density. For example, increasing

spawner density at very low levels may be a positive factor, increasing the chance of finding a mate; whereas at higher densities behavioural interference between spawners or over-cutting of redds may lead to negative density-dependence (Solomon, 1985).

The evidence for density-dependent regulation of abundance in the salmonid life cycle is overwhelming and governs the general form of stock–recruitment relationships for salmon (Gibson, 1993) and trout (Elliott, 1994). However, the point at which it begins to operate, its intensity and thus the precise form of the stock–recruitment relationship is less clear.

4.4. *Timing of density-dependent mortality*

Density-dependent mortality only operates for comparatively short periods of the life cycle, during critical stages, when regulation is achieved by competition for limited resources. In a long-term study on sea trout, Elliott (1993a) showed that regulation of population size was achieved through density-dependent mortality operating over a short critical period (30–70 days) when the fry dispersed from the spawning gravels. Thereafter, survival was shown to be proportionate, influenced by density-independent factors. The detailed studies of Elliott have not been carried out for salmon, so the precise timing of any critical phase is not known. However a similar type of analysis on a Norwegian salmon population showed that density-dependent regulation operated in the early life of salmon too, sometime between the egg and smolt stages (Jonsson et al., 1998). Other studies have also demonstrated density-dependent regulation in salmon early in fresh water life, although it may be sustained for longer than trout, at least through the first summer (Gee et al., 1978; Egglisshaw and Shackley, 1977; Gardiner and Shackley, 1991). Thereafter, up to the smolt stage, survival has generally been found to be density-independent in salmon (Gee et al., 1978; Whalen et al., 2000). Competition between year classes has also been reported, but the evidence for it is conflicting and it has been proposed that, in most natural situations, the niche separation of different fish sizes and species is enough to keep inter-year class and inter-specific competition at low levels (see review by Gibson, 1993). However, it is difficult to distinguish between volitional niche preferences and active segregation due to competition. There is

evidence that inter-specific competition can occur between salmon and trout, with the latter generally out-competing salmon (Kennedy and Strange, 1986); but whilst there is overlap, the two species display adaptations to different preferred habitats (Armstrong et al., 2003; Bremset and Heggenes, 2000).

All the cases above show that the main density-dependent regulating processes act during the fresh water, mostly very early, juvenile phase. However, Elliott and Hurley (1998) have demonstrated regulation in the adult phase (female spawners), rather than the juvenile phase of a non-migrant brown trout population. This may have been a consequence of the harsh upland environment and low population densities that prevailed in this particular situation.

Studying population dynamics in the sea is practically difficult, but observations on salmon returning to the River Imsa, Norway, show that marine survival is density-independent (Jonsson et al., 1998). Similarly, for sea trout, Elliott (1993c) has shown that numbers of returning females were directly proportional to the numbers of smolt emigrants. This lack of observable density-dependence may be a consequence of the large scale of marine habitat in comparison with the limiting rearing capacity in fresh water. More research is required on marine population dynamics to establish when, where and how mortality occurs (Potter and Crozier, 2000).

4.5. Density-independent factors affecting survival

Density-independent factors include a wide range of variables that cause sometimes extensive, but unpredictable, mortality at any stage in the life cycle and at any density.

Examples include the impact of siltation that, by impairing water flow through gravels, reduces oxygen delivery and causes mortality of incubating eggs. Although much of the work relates to North American salmonid species (e.g., Chapman and McLeod, 1987), the principle applies equally to Atlantic salmon (Scott and Beaumont, 1994) and brown trout (Acornley and Sear, 1999). Other water quality parameters such as acidity (Lacroix, 1985; Milner and Varallo, 1988; Turnpenny et al., 1988) or pesticides (Alabaster, 1969; Moore and Waring, 1998; Fairchild et al., 1999) also cause proportionate, density-independent mortality through direct toxicity or secondary responses brought

about by reduced physiological tolerance. Impacts caused by extremes of flow are particularly important. Droughts and high temperatures were believed to be responsible for low survival in sea trout in Black Brows Beck that otherwise were controlled mainly by density-dependent mortality (Elliott et al., 1997). In contrast, Jensen and Johnsen (1999) reported low survival in trout resulting from low temperatures and high discharges acting during the alevin stage. Egg washout at high flows and desiccation at low flows have been reported (Milner et al., 1981; Crisp et al., 1984). Impacts from density-independent factors acting in fresh water may reveal themselves later in terms of maturation rates, smolt numbers, smolt size and marine survival (e.g., Whalen et al., 2000; Elliott, 1993c; Nieceza and Braña, 1993; Power and Power, 1994; Salminen, 1997). Such effects are likely to be increasingly important if, as predicted, climate change leads to greater extremes and variability of temperature, rainfall and flow regimes (McKenzie Hedger et al., 2000; Dempson et al., 2001).

Carrying capacity, as determined by habitat features (Armstrong et al., 2003), is independent of density, but creates a bottleneck, typically for space and food, that increases competition, thus leading to density-dependent effects. Key stages where such bottlenecks have been demonstrated are the early post-emergent fry stage, and at spawning when limited availability of spawning gravel can cause density-dependent regulation of breeding female trout numbers (Elliott and Hurley, 1998). For long periods of life, the density of stream-dwelling salmonids may be below the limiting carrying capacity appropriate to their life stage, having been controlled by an earlier limiting bottleneck.

The response of a population to density-dependent or independent factors is influenced by the fitness of individual fish. This in turn is influenced by their genetic makeup and so genotype is a crucially important density-independent variable (Youngson et al., 2003).

4.6. Self-thinning

At any given temperature, the resources needed by individual juvenile trout or salmon increase as they grow. Therefore, assuming that the total availability of space and food is constant, the number of fish in a given area can be expected to decrease as the mean

weight increases, due to competition for limiting resources. This process is termed “self-thinning”. On theoretical grounds, the gradient of the thinning slope (log number of fish against log mean weight) might be expected to vary, depending on whether food (energy) or space is limiting (Grant and Kramer, 1990; Grant, 1993). If the total available energy limits production and is constant, then self-thinning may be a special case of the energy equivalence hypothesis. This proposes that the total energy demand of a population filling a habitat to carrying capacity is constant, whether the population comprises many small or few large individuals.

There is compelling evidence for an inverse relationship between numbers and weights of salmonid fishes. Grant and Kramer (1990) showed that many populations of salmonids appeared to thin at gradients consistent with space being the factor that limited carrying capacity. Other studies suggested that populations of salmon and trout may self-thin at gradients consistent with the energy equivalence hypothesis (Bohlin et al., 1994; Elliott, 1993b). More recent work (Steingrímsson and Grant, 1999) showed that food and space limitations may in fact generate similar thinning gradients and moreover, because food supply changes with time, thinning gradients are plastic and can be expected to deviate from the energy equivalence hypothesis.

A reduction in numbers as fish grow is not itself an indication of self-thinning because mortality can be expected with time due to density-independent factors. A between-population comparison that suggests adherence to the energy equivalence hypothesis indicates that self-thinning may have occurred at some time previously (during a bottleneck) but cannot be used to infer that it is a continuous process (Armstrong, 1997). Furthermore, evidence shows that consistency between predicted thinning gradients and observed changes in weight and numbers can be coincidental and not a result of sustained density-dependent processes (Armstrong, 1997). Because of the potential variability in thinning gradients, depending on temporal variation in food availability, it may be difficult to assess whether populations are at their carrying capacity by measuring gradients of change in mean weight and density over time. Further variation in thinning gradients would be expected as the suitability of habitat varies with the size of the fish (Steingrímsson and

Grant, 1999; Armstrong et al., 2003). Self-thinning is an interesting process that no doubt occurs when salmonid fish are growing through bottlenecks (Elliott, 1990).

4.7. *Some issues with stock–recruitment relationships*

Stock–recruitment curves (Fig. 1b) describe how a population, or a stock comprising several populations, will respond to variation in spawner density, brought about for example fishing controls, habitat management or environmental factors affecting survival. However, there are several contentious issues surrounding their derivation and use.

The stock–recruitment curve may vary in shape according to the type of model fitted. The commonest choice is between a dome-shaped curve (Ricker, 1954) and an asymptotic one (Beverton and Holt, 1957) (Fig. 1b). These are both two-parameter models and with others, such as the three-parameter Shepherd model (Shepherd, 1982), provide for a wide family of curves ranging from continually ascending to sharply domed. The distinction is important, theoretically and for practical management, because the dome shape implies some optimum level of spawning; whereas an asymptote indicates that increasing spawners will also reduce survival, but not to the extent that absolute recruit numbers decrease. Depending on which model is applied, the management strategy might be different (Potter et al., 2003). It is important that the data are used to test for the most appropriate model (Elliott, 1985; Jonsson et al., 1998). It is also important, when fitting mathematical models, not to lose sight of the ecological processes controlling abundance; these are complex and may involve redistribution of fish in response to habitat availability, in addition to mortality.

The scale at which they are derived may influence the forms of these curves. A whole river stock–recruitment curve can be thought of as a weighted mean curve comprising many others typical of the representative stream types prevailing in the catchment (Wyatt and Barnard, 1997a,b). There is some pattern emerging for migratory salmonids in which studies at small scale (e.g., <50 m stream lengths) tend to produce dome-shaped, but rarely flat-topped curves (Elliott, 1994; Gee et al., 1978; Gardiner and Shackley, 1991). In contrast, those derived at whole tributary

or river scale may produce either flat-topped or gently rising curves (Buck and Hay, 1984; Ward and Slaney, 1993; Jonsson et al., 1998). If this is shown to be a real effect, it could be because at a small scale there are genuine functional relationships between individuals and between fish and their immediate habitat. When stock–recruitment curves are based on counts for whole rivers, the dilution of spawners spread out over a widely ranging habitat, with inevitably varying local intensities of spawning, coupled with some redistribution of juveniles, may mean that the over-compensatory effects are not so readily detected. Thus, it would be risky to draw conclusions about the management response of a whole river stock solely from the stock–recruitment relationship for a small stream section. Stock–recruitment curves should be developed for key habitat types (Gibson, 1993) and be expressed on a scale compatible with the management regime. This is the basis for current approaches to adjusting stock–recruitment curves for rivers where original data are lacking (Prévost and Porcher, 1996; Wyatt and Barnard, 1997a,b; Bradford et al., 2000; Milner et al., 2000).

The shape of curves at very low stock densities is a problem for two reasons. First, there is a paucity of data at low stock densities, which means that it has proved difficult to establish between-river differences in the initial slope of the curves, equivalent to density-independent survival. On the limited evidence available, density-independent survival appears similar across a range of river types (ICES, 1994), but this conclusion requires validation. Second, conventional models may not accurately describe populations at very low levels and lead to over-optimistic estimates of safe harvest levels (Barrowman and Myers, 2000). The line of the curve may not pass through the origin, because recruitment is effectively prevented at some very low spawner density. This effect has been reported in salmon by Chadwick (1985) and could be explained by a critical abundance of spawners, below which the chance of encounters between mating fish is greatly diminished (Solomon, 1985). The effect requires a switch from positive to negative density-dependent mortality as spawners increase at very low levels (see Section 4.3). This process, could have important implications for the survival, extinction rate and recovery of localised, small stocks, which would be susceptible to chance fluctuations in spawner abun-

dance and exhibit rapid terminal decline below some critical level (Routledge and Irvine, 1999). Research is needed to learn more about stock–recruitment at low stock densities and over a wider range of stream types than has been studied to date.

For many salmon stocks, current spawning abundance may be at levels where the distinction between dome or asymptotic curves becomes unimportant, because both predict increasing recruitment as stock increases over lower spawning levels. Stocks might be held at such levels by high exploitation and/or by high mortality in fresh water or at sea.

4.8. Applications of stock–recruitment curves

The two main phases of the life cycle, regulation and adult growth, can be brought together into a single life cycle model that offers several applications for management. An example is outlined below for salmon.

Consider the directly proportional relationship between smolts and adult spawners in a stock, brought about by density-independent marine survival (see above). This is conveyed in Fig. 2a by the straight line, with the dependent variable (spawners) on the x -axis. The survival of smolts, sex ratio and fecundity of spawners determine the slope of this line. Onto this relationship can be superimposed the freshwater stock–recruitment relationship (a Ricker curve is used for this example), with the dependent variable (smolts) on the y -axis. In this example, eggs are the unit of spawning stock, but numbers of females or total spawners could also be used. Both lines are estimated from river-specific data collected through long-term monitoring and assessment, or by extrapolation and transportation methods where necessary (Wyatt and Barnard, 1997b; Milner et al., 2000).

These two lines represent a full life cycle model and allow the estimation of abundance at two key stages (smolts and spawners) for any starting value of spawner density. Two important features are seen in Fig. 2a. First, at the intersection point of the two lines the number of smolts produced at that level of spawners results in the same number of spawners returning, so the population exactly replaces itself and remains in equilibrium. The straight line is termed the *replacement* line and the intersection the *replacement* point. Secondly, at spawning stock levels less than the

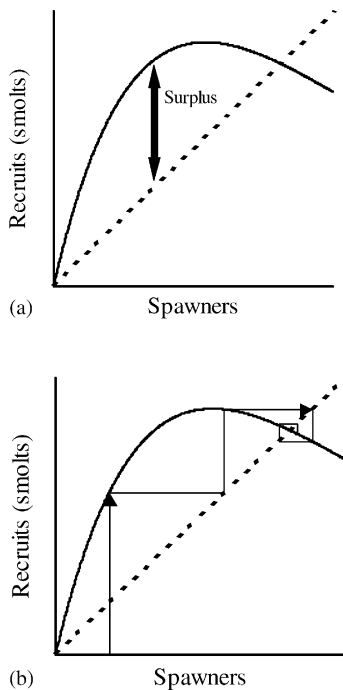


Fig. 2. (a) Full life cycle model showing a density-dependent freshwater regulatory component (solid line) and a marine stage having proportionate survival (dashed line). The surplus production of recruits is estimated by the difference between the two lines, and position of the maximum surplus is shown (arrow). (b) Life cycle model, showing how a population returns to an equilibrium point, starting from a low spawning level.

replacement point more smolts are produced than are needed to replace their parents, giving rise to a surplus of adults. This surplus production is the “spare” capacity that fisheries exploit, but it also has great biological significance. Surplus production insures the stock against random events that may reduce survival and, through density-dependent survival, regulates an unexploited stock at an average level around the replacement point. This can be seen by tracking generations, starting from some arbitrary low spawner level brought about by chance low survival, using the lines in Fig. 2b. At stock levels above the replacement point, lower egg-smolt survival produces a corresponding reduction in returning spawners. The same process applies to asymptotic (e.g., Beverton and Holt) curves, and in all cases the stability and response times will vary according to the model parameters shaping the S–R curve of a particular population (Ricker, 1954). This

introduces additional uncertainty into assessments if the OSU (see Section 2) comprises several different populations.

This simple model illustrates responses to variables that are relevant to fisheries management. For example, if stock experiences reduced survival at sea because of climate change then the replacement line will move to the left (because it will take more smolts to produce a returning spawner). The stock will then stabilise around a new replacement point. Similarly, if exploitation is applied to the stock, to cause a reduction in survival between smolt and spawner, then the same stock level change will occur. Inspection of Fig. 2a shows that changes in freshwater carrying capacity (equivalent to the peak, or asymptote, of the curve) or in density-independent survival (equivalent to the initial slope of the curve) will also cause predictable changes in equilibrium stock. Likewise, the returns to be expected from given spawner levels will vary as these conditions change.

Such changes are typical issues facing managers. Life cycle models, with the appropriate cautions (see below), introduce structure and objectivity into options appraisal and enable managers to predict the outcome of their actions. An important contemporary issue is the use of stock–recruitment curves to set reference points for stock management (Wyatt and Barnard, 1997a; Milner et al., 2000; Prévost and Chaput, 2001). Fig. 3 illustrates three common options for reference points. The replacement point (S_r) of an unexploited population defines the stock level expected with no

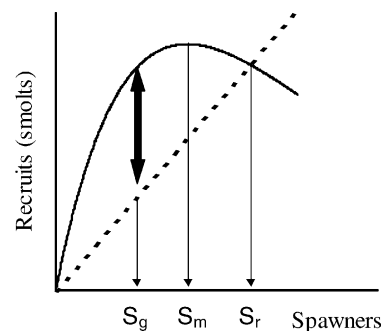


Fig. 3. Life cycle model showing three common options for biological reference points: S_r : equilibrium stock level for replacement in unexploited population, S_m : stock level providing maximum recruits, S_g : stock level providing maximum surplus production.

exploitation. The peak of a dome-shaped curve (S_m) defines a stock that produces the largest number of recruits and thus defines an exploitation level that maximises returning spawners. This point cannot be objectively defined for an asymptotic or rising curve, although some proportion of the asymptote could be arbitrarily set as a reference point. Finally, the stock level S_g , defines a spawning level that maximises the potential catch level. While this is attractive for fisheries management purposes, it has some drawbacks if used alone as a stock reference point (Milner et al., 2000). An advantage of S_g is that it can be estimated from any form of stock–recruitment curve. The merits of these reference points and their application to management are discussed elsewhere by Potter et al. (2003).

4.9. Variability in stock–recruitment

A feature of stock–recruitment curves is the high variability usually seen in the data (e.g., Fig. 1b). The resulting variance can mask the influence of density-dependent regulation causing the predictive power of some stock–recruitment relationships to be rather low, leading to uncertainty and risks when making management decisions. This uncertainty does not invalidate the use of such models, but does require that the errors and risks are quantified as far as practicable and taken into account for management (Hilborn and Walters, 1992). This area of work is rapidly expanding, as statistical methods develop and computing power increases.

Elliott (1994) showed that the variance in recruits increased over the lifetime of a year class, correspondingly, spawner level explained a reducing proportion of the recruit variance, presumably as random effects accumulated. In Black Brows Beck sea trout, egg density explained 95% of the variance seen in early summer fry, but only 44% of the variance in eggs laid by the returning survivors of the same year class. A similar trend has been reported in salmon. In a recent extension to the Shelligan Burn study, the proportion of variance of November parr explained by the density of early summer fry was 66% (Gardiner, unpublished), compared with earlier estimates of 46 and 63% for 1 and 2 year olds respectively (Gardiner and Shackley, 1991). Jonsson et al. (1998) found that initial egg density explained 49% of smolt variance in the

River Imsa, but only 22% of the variance in eggs from these smolts was accounted for by their parental egg density.

4.10. Processes controlling growth and maturation

Growth rate might be expected to be influenced by fish density, because it represents an individual's success in acquiring energy through food. But results on this point have been inconsistent, which may partly reflect species differences as well as the circumstances of individual studies. For sea trout in Black Brows Beck, mean growth rate and mean size were found to be independent of density, although *variability* in size was inversely density-dependent during the critical period for sea trout (Elliott, 1994). Gardiner and Shackley (1991) showed that growth was density-dependent in salmon, over the first growing season, but Gee et al. (1979) were unable to demonstrate density-dependent growth (expressed as production/biomass ratios) in salmon in the River Wye. Gibson (1993), in a review of salmon production, reported inconsistencies between various authors, in the effect of density on growth, and suggested that this may have been due to differences in food availability and/or habitat between different studies. He noted that over a range of streams varying greatly in productivity, high growth was positively associated with high density in relatively rich sites. However, in a single stream type, higher density usually gave lower growth. Comparisons should thus only be made under similar habitat and productivity conditions. Gibson (1993) also noted that the links between fish size for age, productive capacity and abundance, offered potential for models that might aid stock assessment. These models are related conceptually to the *percent habitat saturation* models discussed more recently by Grant et al. (1998).

The incidence of density-dependent growth may be variable and the mechanisms not yet fully understood, but it has significant implications for fishery scientists and managers. In sea trout and in salmon, the majority of females go to sea as smolts, but a sizeable minority of males (more in sea trout than salmon) remain in fresh water and mature (Jonsson and Jonsson, 1993; Jonsson et al., 1998). The choice between these two options (migration or maturation) seems to be based on the growth rates of young first year fish well before

either smolting or maturation take place, 7–10 months in the case of smolting and 12 months in the case of maturation (Metcalf, 1998). There are well-established latitudinal variations in growth rate and smolt age of both species (Jonsson and Jonsson, 1993; Metcalf, 1998) that may reflect temperature-related growth opportunity (Metcalf, 1998).

Metcalf (1998) has produced models of the life history responses based on hatchery experimental studies, showing systematic changes in life history features (smolt age, sex ratio of smolts, mean smolt size, etc.) that might be influenced by climate or habitat change, for example, it would be useful to test these models in populations of wild fish, which tend to grow more slowly than hatchery-reared fish.

Empirical links between freshwater performance (as revealed in smolt size and age) and subsequent growth, survival and maturation at sea have been well-established (Bilton et al., 1982; Ward and Slaney, 1988; Erikson, 1989; Elliott, 1993c; Nieceza and Braña, 1993; Salminen, 1997). However, there are inconsistencies between studies, probably reflecting variations in marine environments experienced by the stocks and species examined (Salminen, 1997). The underlying mechanisms controlling marine growth, survival and maturation, particularly the roles of environment and genetics, are still unclear and require further study (Mills, 2000).

5. Conclusions

Salmonid life cycles are highly variable, displaying flexibility in adapting to different and variable environments. The study of population dynamics still has a long way to go before the understanding of processes matches all the management questions that need to be answered. Nevertheless, many basic principles have emerged which, coupled with rapid improvements in statistics and computing, are permitting the translation of current understanding into management tools.

The regulation of salmonid populations through density-dependent feedback mechanisms is now a well-established principle, but studies on this have still only been applied to a very limited range of stream types and species. The application of stock–recruitment models to management has forced the

critical review of available data and will, hopefully, lead to long-term studies targeted on priority issues. Lack of such information will continue to be a major constraint until financial commitment is made to support long-term ecological studies.

Critical periods, when population regulation occurs in early freshwater life, have been demonstrated (most clearly for sea trout), but there is still ignorance about regulatory processes at other times and about how the small stream studies translate to larger habitats. Over-wintering habitat may be a further bottleneck, but its effect on populations has not yet been clearly or consistently shown.

The impacts of predation also remain unclear. Bird predation, for example, undoubtedly removes large numbers of salmonid juveniles in some cases, but overall population responses have remained surprisingly hard to demonstrate (Kennedy and Greer, 1988; Feltham, 1990; Carss and Marquiss, 1999). This may reflect the difficulty in detecting such effects against the high variability of whole river population sizes.

The reality of self-thinning as a discrete process is questionable, but the debate around it has been productive in establishing at least the questions about limiting factors, if not all the answers. Even if cohorts do not follow thinning lines, the carrying capacity may. Self-thinning may therefore be important in defining the carrying capacities for fish of different sizes for comparison with standing stock. This study area may offer good opportunities for developing alternative freshwater assessment models.

Multispecies models are also required. Interactions between salmon and trout are partly offset by niche separation, but migratory trout are sometimes the largest contributors of eggs in river systems and a complete lack of interaction would be surprising. Energetics and biomass production models also offer potential for better understanding of the processes at work in rivers. Nutrient flux between marine and freshwater environments by post-spawning salmon mortality is an important mechanism maintaining freshwater production in some Pacific salmon species (Elliott et al., 1997). Atlantic salmon and sea trout, because of their lower spawning densities and life cycle, have a less dramatic biomass transfer and lower mortality rate than Pacific species. Nevertheless, the process may be significant in very low nutrient status

waters (Lyle and Elliott, 1998). The topic requires further investigation.

The importance of random environmental events cannot be overstated. The variability that this introduces into population models can mask the underlying regulatory mechanisms and has previously led to fundamental debate over the existence and role of density-dependence (see Elliott, 1994, for a review relating to salmonids). The ability of density-dependent regulation to protect populations at low spawner densities is still not well understood and is an obvious subject for study. This knowledge gap, and the related issue of population structuring in large river systems, is particularly relevant to declining stocks, management of which requires a great degree of caution.

Most population dynamics studies have been carried out in fresh water. However, the mechanisms controlling salmon and sea trout at sea are still poorly understood, but in spite of the technical difficulties and high costs, further progress is anticipated as this becomes an increasingly important research area (Mills, 2000). Performance at sea may also be influenced by events in fresh water. The roles of stream habitat and population density in influencing the trade-offs between growth, maturation and smolting require further work, for both trout and salmon.

Almost all management decisions about fisheries involve “what if” testing of options, which may be implicitly or explicitly formalised through models that pull together our understanding of biological processes. In adopting models, scientists and managers come up against the issues of variability and uncertainty in application of the science to their problems. These difficulties stem variously from poor understanding of processes, forced errors in measurement and from the variability due to random events in nature. A tendency in the past has been to assume that science will be able to explain all or most of this variation. However, that may not be possible, practicable or affordable. So, the challenge for the future lies in two areas. First, in recognising such uncertainty as an inherent feature of natural systems and learning to incorporate it into decisions by re-phrasing management questions and scientific answers. Second, in agreeing what are the key issues for research and investing in targeted studies, which will often have to be long-term, to improve our understanding of processes regulating populations.

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