FISH and FISHERIES, 2001, **2**, 293–327

Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis

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Abstract

Density-dependent processes such as growth, survival, reproduction and movement are compensatory if their rates change in response to variation in population density (or numbers) such that they result in a slowed population growth rate at high densities and promote a numerical increase of the population at low densities. Compensatory density dependence is important to fisheries management because it operates to offset the losses of individuals. While the concept of compensation is straightforward, it remains one of the most controversial issues in population dynamics. The difficulties arise when going from general concepts to specific populations. Compensation is usually quantified using some combination of spawner–recruit analysis, long-term field monitoring or manipulative studies, and computer modelling. Problems arise because there are limitations to each of these approaches, and these limitations generally originate from the high uncertainty associated with field measurements. We offer a hierarchical approach to predicting and understanding compensation that ranges from the very general, using basic life-history theory, to the highly site-specific, using detailed population models. We analyse a spawner–recruit database to test the predictions about compensation and compensatory reserve that derive from a three-endpoint life-history framework designed for fish. We then summarise field examples of density dependence in specific processes. Selected long-term field monitoring studies, manipulative studies and computer modelling examples are then highlighted that illustrate how density-dependent processes led to compensatory responses at the population level. Some theoretical and empirical advances that offer hope for progress in the future on the compensation issue are discussed. We advocate an approach to compensation that involves process-level understanding of the underlying mechanisms, life-history theory, careful analysis of field data, and matrix and individual-based modelling. There will always be debate if the quantification of compensation does not include some degree of understanding of the underlying mechanisms.

Keywords compensation, density dependence, fish populations, fisheries management, life-history theory, sustainable harvest

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Received 3 Jul 2001
Accepted 6 Aug 2001

Introduction

Processes such as growth, survival, reproduction and movement are density dependent if their rates change as a function of the density or number of individuals in a population. Density-dependent processes are said to be compensatory if their rates change in response to variation in population density such that they result in a slowed population growth rate at high densities and promote a numerical increase of the population at low densities. Density-dependent processes are depensatory if they change with population density such that they slow the rate of population growth at low densities.

Density dependence is a fundamental concept in the study of fish population dynamics. Depensatory density dependence is a positive feedback on population size, and therefore tends to destabilise populations. Depensatory density dependence is especially important for depleted populations and for endangered species because it acts to accelerate further population decline and can delay recovery (e.g. Myers *et al.* 1995b; Shelton and Healey 1999). Compensatory density dependence is a negative feedback on population size, and therefore acts to stabilise populations. Compensatory density dependence is important to management because it operates to offset the losses of individuals, which can occur from natural fluctuations in environmental conditions or from anthropogenic activities such as power-plant operations and fishing. Lowered population density temporarily results in increased survival or reproduction of the remaining individuals which favours an increase in population size.

We will focus in this paper on compensatory density dependence. Myers *et al.* (1995b) analysed spawner–recruit relationships for a variety of marine fish species, and found little evidence of depensatory density dependence at low population sizes. However, Liermann and Hilborn (1997) reexamined the data and Shelton and Healey (1999) evaluated the analytical method, and both urged caution before dismissing the possibility of depensation. Liermann and Hilborn (2001) recently reviewed depensatory density dependence in fish and other taxa. We use the term density dependence in this paper to mean compensatory density dependence.

Compensation and compensatory reserve

Two terms used throughout this paper are: compensation and compensatory reserve. Compensation refers to the net effect of the density-dependent processes that cause negative feedback on population size. Strong compensation means that the processes are highly responsive to density changes. Strong compensation does not necessarily imply high population stability (i.e. population fluctuations within relatively narrow numerical bounds). Specific processes may be tightly coupled to variation in density at particular life stages, but the variation from environmental fluctuations affecting other processes or life stages may dominate overall population variability. Similarly, populations with weak compensation can exhibit low interannual variation if they inhabit relatively stable environments. The magnitude of compensation can be inferred from how tightly coupled the responses of specific processes are to changes in density.

Christensen and Goodyear (1988) defined compensatory reserve as the "excess reproductive capacity under 'ideal' conditions for individual reproduction (i.e. when population size is so low that compensatory mortality does not operate)." Compensatory reserve is the capacity of the population to offset variation in mortality, but is not necessarily related to the stability (interannual variation) of population size over time. Populations with high compensatory reserve can also exhibit large interannual fluctuations in abundance; the degree of fluctuation depends upon the net effects of environmental variation and compensation in multiple life stages. Compensatory reserve can be estimated via the maximum reproductive rate, which is the slope of the spawner–recruit relationship near the origin, where compensation effects would be small (Myers *et al.* 1999).

Compensation, fisheries management and controversy

The theory of compensatory density dependence underlies the management of fish populations. Two situations that permit sustainable harvest can be envisioned: a population with a net positive growth rate and a quasi-stable population. While sustainable harvest is theoretically possible without compensatory density dependence, it is ecologically unrealistic. In theory, a population that has a positive rate of increase can be harvested until the population growth rate is reduced to almost zero, and the population would persist. While such a population does not require compensation for sustainable harvest, in the absence of harvesting this population would eventually increase unbounded.

The second situation of sustainable harvest from a quasi-stable population requires compensation. Compensatory density dependence permits populations to persist under conditions of an increase in mortality, and is the basis of the concepts of surplus production and sustainable harvest (Schaefer 1954; Beverton and Holt 1957; Ricker 1975; Gulland 1977; Sissenwine 1984; Fogarty *et al.* 1991). Population stability, which can include bounded fluctuations (Turchin 1995), implies that, averaged over a long enough time period, reproduction is balanced by mortality. Despite the wide fluctuations in abundance typical of many fish populations, many populations have persisted (some with harvesting) within some defined upper and lower abundances for many generations, implying at least a modest degree of long-term stability. Without compensatory responses, any increase in mortality owing to harvesting in an already stable population would eventually result in population decline because, in the long term, mortality would exceed reproduction. Thus, compensatory density dependence must exist for naturally stable populations to persist under harvesting. The basis for surplus production and sustainable harvest is that populations have the ability, at some densities, to increase in numbers at a rate greater than that required for replacement (Goodyear 1993). However, inclusion of compensation in fishery management analyses does not automatically result in predictions of increased yield or higher sustained fishing rates (e.g. Helser and Brodziak 1998).

An illustration of the general magnitude of compensatory reserve in fish populations is that it is considered risk-averse and long-term sustainable to remove 60–70% of a virgin stock's reproductive potential (Goodyear 1993; Mace and Sissenwine 1993; Mace 1994). One of the principal sources of uncertainty and risk in fisheries management is determining the actual magnitude of the compensatory reserve in a specific population (Fogarty *et al.* 1992). The debates over compensation and compensatory reserve are rarely ever resolved, and often act to delay the initiation of needed management actions.

While the concept of compensatory density dependence is straightforward, it remains one of most controversial issues in population dynamics. As stated by Fletcher and Deriso (1988), "Why is it [density-dependent compensation] so easy to imagine but so hard to find?" In the aftermath of a long court case concerning the permitting of Hudson River power plants, Barnthouse *et al.* (1988) stated "The most controversial of the issues raised at these hearings was the potential importance of density-dependent regulatory mechanisms in offsetting direct mortality caused by power plants." The debate over the management of red snapper (*Lutjanus campechanus*) in the Gulf of Mexico has been contentious (e.g. Macaluso 1999). This has been partially fuelled by uncertainty about the appropriate assumptions concerning the magnitude of compensatory reserve in red snapper stock assessment. In lieu of better information, Schirripa and Legault (1999) assumed a range of compensation levels, which resulted in a five-fold variation in estimates of maximum sustainable yield (MSY). Everyone agrees that intraspecific competition for one or more resources ultimately will limit the size of a fish population (i.e. populations can not increase unbounded), and that, at least intuitively, survival and reproduction can be negatively related to density. The difficulties arise when extrapolating from density dependence, identified in a particular process or life stage, to its effect on long-term population size, and when going from very general statements about compensation and compensatory reserve to cases involving specific populations.

Extrapolation of density dependence in a particular life stage to the population level requires understanding of how density-independent and density-dependent factors interact to affect all life stages in the life cycle. Fish exhibit complex life-history strategies that make the comprehensive study of their full life cycle difficult. Quantifying the magnitude of compensation for a particular population requires years to decades of study to uncover the nuances of site-specific dynamics. The universal shortage of adequate data for specific populations results in alternative interpretations of available data, and has lead to acrimonious debate. Use of population dynamics and other models, in lieu of adequate data, only changes the tone of the debate – from inadequate data to uncertain models. The root cause of the debate remains our inability to adequately quantify and understand compensation for a particular population. In the absence of experimental controls, we cannot determine how much of population fluctuation is owing to environmental factors versus density-dependent responses. This is further confounded by environmental fluctuations not simply acting as density-independent factors, but also potentially causing density-dependent responses. Environmental variation can alter the quality and quantity of habitat, which can in turn cause changes in population density and thereby trigger density-dependent growth, survival, reproduction and movement.

Marine fisheries worldwide are in a dismal state (Garcia and Newton 1997; NMFS 1998), with many populations experiencing overfishing and harvesting rates that may not be sustainable (Botsford *et al.* 1997; Pauly *et al.* 1998; NRC 1999). The situation for many freshwater fish species is similarly pessimistic (Warren and Burr 1994), with the need for widespread use of management practices to limit harvest and extensive use of stocking to augment populations (e.g. Schramm *et al.* 1995; Fenton *et al.* 1996). Proper and effective management and restoration of fishery resources require progress on the issues surrounding the quantification and understanding of compensatory processes.

Statement of the problem

In our view, the problem is how to determine the magnitude of compensation and compensatory reserve accurately, and not how to incorporate known compensation and compensatory reserve into population analyses. The mathematics exist for including density-dependent processes in population dynamics models. For example, compensatory spawner–recruit relationships for egg to age-1 survival are often used in age-structured matrix models (Saila *et al.* 1991; Hilborn and Walters 1992); compensatory density dependence has also been included in other types of populations models (Jensen 1993; Marschall and Crowder 1996; Nisbet *et al.* 1996; Rose *et al.* 1996, 1999).

While the mechanics for including compensation in population and stock assessment models exist, limited data and lack of process-level understanding for a particular population often leads to dispute. The default assumption of no compensation is protective of the population (e.g. Ginzburg *et al.* 1990; Fogarty *et al.* 1992), but is so overly conservative that it becomes impractical and economically inefficient, given so many competing demands on fishery resources. The other extreme assumption of recruitment which is independent of spawning population size corresponds to effectively infinite compensation (Hilborn and Walters 1992), and puts the fish population at risk.

This review is organised as follows. We begin with a discussion of why compensation is so difficult to measure in the field. We suggest that life-history theory provides a framework for understanding and predicting the magnitude of compensation and compensatory reserve in populations. We use a three-endpoint life-history framework, developed specifically for fishes, to make first-order predictions of the magnitude of compensation and compensatory reserve. We then analyse an extensive spawner–recruit database to test the predictions about compensation from the life-history framework. This is followed by a description of how compensatory responses can arise from changes in the processes of mortality, growth, reproduction and movement. Selected empirical and computer modelling examples are then presented which illustrate how compensation operates at the process level and why detailed understanding of compensation can be elusive. Examples were chosen to span a wide variety of both freshwater and marine species. Theoretical and empirical advances that offer hope for progress in the future on the compensation issue are next discussed. Finally, we conclude with a synthesis and some suggestions for addressing the compensation problem.

Why direct measurement of compensation can be difficult

Compensation is usually quantified using a combination of spawner–recruit analysis, long-term field monitoring or manipulative studies, and computer modelling. A relationship between spawners and recruits that shows a less than proportional increase in recruitment with increasing spawning implies compensatory density dependence (Cushing 1975; Fogarty *et al.* 1992). Long-term field monitoring and manipulative studies allow for direct determination of population stability and quantification of density dependence in mortality, reproduction and other processes. Field measurements showing positive population growth rates at low densities imply that compensation exists. Ignoring how one arrives at a specific model formulation, realistic models of population dynamics can be developed that include documented compensatory mechanisms.

Problems arise because there are limitations to each of these approaches, and these limitations generally arise from the high uncertainty associated with field measurements (e.g. Bradford 1992). Uncertainty in field measurements is due primarily to lack of experimental controls and the often high measurement error associated with field data. The merits and drawbacks to spawner–recruit data have been debated for decades. Some of the drawbacks include the generally high variability of the data (Walters and Ludwig 1981; Goodyear and Christensen 1984), use of improper proxy variables for egg production (Goodyear and Christensen 1984; Rothschild and Fogarty 1989), the often poor fit of the assumed deterministic spawner–recruit function (Koslow 1992) and weaknesses in the statistical fitting methods (Christensen and Goodyear 1988). The lack of convincing relationships between spawners and recruits led some to assume no relationship, which implies extremely high compensation (Fogarty *et al.* 1992; Hilborn and Walters 1992), and others to propose flexible functional forms (Getz and Swartzman 1981; Mackinson *et al.* 1999). Because spawner–recruit data are annual, many years of monitoring are required before meaningful interpretation is possible. Also, while properly analysed spawner–recruit data provide direct evidence of the magnitude of compensation and compensatory reserve, spawner–recruit data often do not include definitive information on the specific processes that underlie the compensatory responses.

Inferring density dependence from long-term field and manipulative studies is convincing, although rarely adequate for definitive conclusions for most specific populations. For example, despite long-term data on Hudson River striped bass (*Morone saxatilis*), Pace *et al.* (1993) cautioned that the apparent density-dependent response could also be attributed to sampling limitations. Monitoring *in situ* is difficult because fish populations typically exhibit wide inter-annual variation in their numbers (Sissenwine 1984; Rothschild 1986; Fogarty *et al.* 1991). Often, much of this variation in abundance results from variability in hydrographic and climatic factors that affect individuals prior to recruitment (Shepherd *et al.* 1984; Laevastu 1993). Furthermore, these environmental factors vary simultaneously in nature, often exhibiting interactive (nonadditive) effects on recruitment (Rose and Summers 1992). When variation in abundances and in processes is large, and is strongly influenced by environmental variables, monitoring can often be unrepresentative of long-term conditions. Furthermore, detection of population stability or density-dependent components in these processes amongst environmental variation becomes very difficult (Bailey and Houde 1989; Bromley 1989; Hixon 1998). Monitoring is also complicated by many species being relatively long-lived with life stages that inhabit different habitats. Furthermore, the magnitude and process that shows density dependence can vary over time and space in a population (Goodyear 1980; Shima 1999), and changes in growth or mortality in one life stage can be offset by changes in subsequent life stages (e.g. Bertram *et al.* 1993). Thus, use of monitoring to document population stability or to detect density dependence in processes requires long-term and extensive data, which is impractical for many populations.

Manipulative approaches (laboratory experiments, mesocosms and field experiments) attempt to address some of the problems inherent with *in situ* monitoring. By addressing the issue of the lack of experimental controls in field data, experimental manipulation enables observed responses to be attributed to known causes. However, because manipulative studies are usually short-term and under contrived conditions, extrapolation to the broader temporal and spatial scales that operate in nature can be problematic. Also, detection of density dependence in a process for a particular life stage is necessary, but not sufficient, to conclude that the process regulates population size. The realism of manipulative approaches has been much discussed and debated (de Lafontaine 1987a,b; Fausch 1988).

Using models in place of good data simply shifts the focus from inadequate data to uncertain models. Population models have been at the centre of many ecological conflicts (e.g. Barnthouse *et al.* 1984; Swartzman 1996). The controversies associated with the use of models usually centre on what constitutes model validation (Rykiel 1996), alternative model formulations leading to different conclusions (e.g. Barnthouse *et al.* 1984), the inability to rigorously test the basic assumptions or the predictive power of a model (e.g. Mathur *et al.* 1985; Lindenmayer *et al.* 2000), and the high uncertainty often associated with model forecasts (Ludwig *et al.* 1993; Botsford *et al.* 1997). There is no generally accepted theory of population dynamics that would allow clear and unequivocal specification of the structure of a model (i.e. what processes and the correct biological, temporal and spatial scales) in specific situations (Getz 1998). Further, in many studies, the available data were deemed inadequate to address the questions of interest (thus models were needed); yet, the same data are used to develop and evaluate the model.

Measuring compensation and compensatory reserve is further complicated by compensatory responses being potentially site-specific. The site-specificity of compensatory responses can make the use of information from other populations or species problematic. The processes and life stages that respond to changes in abundance can vary among different populations of the same species (Rose and Cowan 2000). Differences in the composition and arrangement of the food web can also affect the compensatory responses of a population (McDermot 1998).

Measuring compensation and compensatory reserve is also hindered by the general lack of sufficient data at the extremes of population densities. Compensatory responses are strongest under conditions of high population densities, while compensatory reserve is estimated from spawner–recruit data at low population densities. Some have suggested that compensatory density dependence operates most strongly only at the extremes of densities (Strong 1986; Murray 1994). Unfortunately, the data available for many fish populations either do not adequately span the full range of densities, or if they do, the data usually cover decades and are therefore confounded with long-term environmental changes. All of these factors make it difficult to obtain accurate and precise long-term data sufficient to definitely quantify and understand compensation and compensatory reserve for specific populations.

We do not believe, however, that it is necessary or even possible to know everything to resolve the compensation quagmire. Further, we believe that with the proper care, spawner–recruit data, field monitoring, manipulative studies and modelling are useful approaches for quantifying and understanding compensation and compensatory reserve. Indeed, we use these approaches extensively later in this paper. We suggest that a hierarchical approach be used to study compensation. The detail to which compensation needs to be understood depends on the specifics of the population of interest and the questions being asked. Effective resource management is possible, whereby the risk taken by managers is commensurate with the level of understanding about the magnitude of compensation. Rough estimates of compensatory reserve, without detailed understanding of the underlying processes, may be adequate for a healthy population supporting a well-managed stable fishery, or when extensive data are available for other similar populations. At the other extreme, detailed understanding of compensation at the process level may be required to target management actions for the rebuilding of an overexploited, declining population. Toward this end, we offer in this paper a hierarchical approach to predicting and understanding compensation that ranges from the very general, using basic life-history theory, to the highly site-specific, using detailed population models. As one proceeds from the general to the specific in our hierarchy, the level of generality of predictions decreases while (hopefully) the level of accuracy of predictions increases.

Life-history theory

Strategies

Winemiller and Rose (1992) analysed data on 16 life-history parameters for 216 North American freshwater and marine species, and found that variation among life histories of these species could be described in terms of three general strategies (Fig. 1). These three strategies are defined as: (i) opportunistic – small, rapidly maturing, short-lived fishes; (ii) periodic – larger, highly fecund fishes with long life spans; and (iii) equilibrium – fishes of intermediate size that often exhibit parental care and produce relatively few, large offspring. For convenience, we use the three strategies here, keeping in mind that they represent endpoints; species can fall anywhere on the surface shown in Fig. 1.

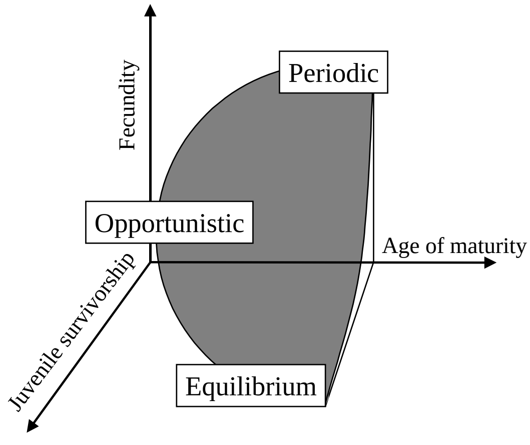

Figure 1 Three endpoint life-history strategies for fish derived by Winemiller and Rose (1992). The endpoint strategies are: opportunistic, equilibrium and periodic. Species can fall anywhere on the surface shown here.

The opportunistic strategy is associated with early maturation, frequent reproduction over an extended spawning season, rapid larval growth and high adult mortality. Examples of opportunistic life-history strategists include many anchovies (family Engraulidae), silversides (family Atherinidae) and killifishes (family Cyprinodontidae).

Equilibrium strategists tend to be intermediate-sized fish that inhabit relatively stable environments, produce small numbers of large eggs, and provide high parental investment in their young. Examples of equilibrium life-history strategists are tropical cichlids, sculpins (family Cottidae), many gobies (family Gobiidae) and some salmonids. Equilibrium life-history strategists are similar to the traditional K-strategy of adaptation to life in resource-limited and density-dependent environments (Pianka 1970), except for their smaller body size.

The periodic life-history strategy identifies fishes that delay maturation to attain a size sufficient for production of a large clutch and to improve adult survival during periods of suboptimal environmental conditions. Red snapper, striped bass and American shad (*Alosa sapidissima*) typify the periodic life-history strategy. Winemiller and Rose (1992) view the periodic strategy as the perennial tactic for spreading reproductive effort over many years (or over a large area), so that high larval or juvenile survivorship during one year (or in one spatial zone) offsets the many bad years (or zones).

Expectations from life-history theory

We formulate expectations for compensation and compensatory reserve based on the three endpoint life-history strategies. We expect compensation to be strongest in equilibrium strategists, while we expect compensatory reserve to be highest in periodic strategists. We use information derived from spawner–recruit relationships to evaluate these expectations. Compensatory reserve can be estimated from the slope of the spawner–recruit relationship (Myers *et al.* 1999). Use of fecundity alone to infer compensatory reserve is overly simplistic because compensatory reserve also includes the survival from egg to recruitment. Estimating the magnitude of compensation from data is problematic, as it is difficult to obtain consistent measures of the magnitude of compensation that can be compared across many species. Instead, we use an indirect measure based on the magnitude of interannual variation in recruitment derived from an assumed spawner–recruit relationship. We recognise that interannual variation in recruitment reflects both the general magnitude of compensation in the population (ability to adjust to new densities) and fluctuations in recruitment owing to environmental variation. Thus, we state our expectations in terms of the magnitude of interannual variation, rather than in terms of the magnitude of compensation.

Equilibrium strategists should have the lowest interannual variation because they inhabit relatively stable environments and because they generally exhibit the strongest compensation. Equilibrium strategists invest heavily in individual offspring (by trading off against fecundity) to enhance early survivorship. Their population abundance should tend to track a long-term mean value near the carrying capacity of the environment. Equilibrium strategists have relatively low fecundity, which, despite high early life stage survivorship, should result in low compensatory reserve. Interannual variation in recruitment should be higher in periodic and opportunistic strategists. Periodic strategists are typically broadcast spawners that rely on wide fluctuations in year-class strengths, with the occasional exceptional year carrying the population through poor years. Because they inhabit highly variable environments and seldom approach environmental carrying capacity, opportunistic strategists should also show high interannual variation. We note that Mertz and Myers 1996) had difficulty relating fecundity to recruitment variability in marine fishes, although more recent analyses have yielded stronger relationships (Rickman *et al.* 2000). The longevity and high fecundity of periodic strategists should more than offset their low early survivorship, resulting in periodic strategists having the highest compensatory reserve. Opportunistic strategists should have low-to-intermediate compensatory reserve, as they are small and short-lived with relatively low fecundity and low early survivorship.

Comparison of life-history expectations with data

Myers and colleagues assembled and analysed several hundred spawner–recruit data sets (see Myers *et al.* 1995a; Myers and Barrowman 1996; Myers *et al.* 1999). Below we further analyse the Myers' spawner–recruit database by examining measures of compensatory reserve and interannual variation in recruitment, grouped by life-history strategies. The spawner–recruit relationships of a total of 249 populations consisting of 57 species were analysed. A Ricker spawner–recruit relationship was fitted to each population using linear regression (Myers *et al.* 1999); recruitment and spawners were specified in the same units (thousand tonnes for all species, except numbers for salmonids).

We used the fitted spawner–recruit relationships to estimate the compensatory reserve and magnitude of interannual variation for each of the 249 populations. The estimate of the slope at the origin of the fitted spawner–recruit curve (i.e. the maximum rate of recruits per spawner) was converted from an annual rate to a lifetime rate by dividing by one minus the natural adult mortality rate (Myers *et al.* 1999), and then used to compute a steepness value (Hilborn and Walters 1992). The slope at the origin corresponds to the maximum rate of recruitment per spawner because spawners are at very low values where compensatory density dependence would least affect recruitment. The steepness parameter is the fraction of the maximum recruitment expected when the stock is at 20% of its unfished state. The magnitude of interannual variation in recruitment for each population (which we term sigma) was computed as the standard deviation of the natural log-transformed residuals between predicted and observed recruitment values (Mertz and Myers 1996). Use of sigma to infer interannual variation presumes that the spawner–recruit model is a reasonable representation of the true relationship between spawners and recruits, and that the deviations between predicted and observed recruitment are indicative of differences in population dynamics among species (i.e. process error) and are not overly influenced or biased by measurement error.

Each species in the spawner–recruit database was also assigned to a life-history strategy, based upon their egg diameter (mm) and fecundity (total annual egg production per female). Egg diameter was used as a proxy for the degree of parental investment in individual offspring. Species with fecundity ⩽ 25 000 eggs and egg diameter > 2 mm were assigned to the equilibrium strategist group. Species with fecundity ⩽ 25 000 eggs and egg diameter ⩽ 2 mm were definned as opportunistic strategists. Species with fecundity > 25 000 eggs and egg diameter < 2 mm were deemed periodic strategists. There were three exceptions: three

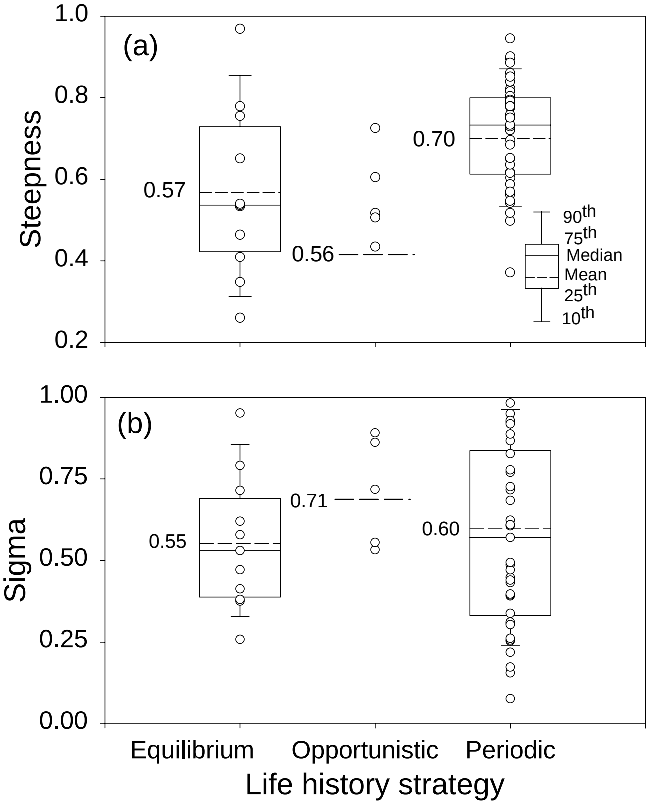

Figure 2 Steepness estimates (a) and sigma values (b), averaged over populations for each species, by life-history strategy. Steepness estimates were determined from the slope at the origin of Ricker spawner–recruit curves fitted to observed data for each population, and are interpreted as indicating the compensatory reserve in a population. Sigma values are the standard deviation of natural log-transformed residuals (observed recruitment minus predicted from the spawner–recruit curve), and are interpreted as reflecting the combined effects of environmental variation and the degree of compensation.

species with egg diameters > 2 mm were considered periodic strategists because of their high fecundity [pike (*Esox lucius*): 2.75 mm and 32 000 eggs; American shad (*Alosa sapidissima*): 3.0 mm and 125 000 eggs; Greenland halibut (*Reinhardtius hippoglossoides*): 4.25 mm and 165 000 eggs]. These rules resulted in 11 species (110 populations; 106 Salmonidae) being equilibrium strategists, 5 species (8 populations) being opportunistic strategists and 41 species (131 populations) being periodic strategists.

Steepness (of recruitment curves) and sigma values were generally consistent with our expectations from life-history theory. Single steepness and sigma values were obtained for each species by averaging over populations to reduce the effects of uneveness in the number of populations per species (Fig. 2). The overall average steepness value was highest for periodic species (0.70) and lower for equilibrium species (0.57) and opportunistic species (0.56). Overall average sigma values were lowest for equilibrium species (0.55), intermediate for periodic species (0.60) and highest for opportunistic species (0.71).

Our initial analysis of the Myers group spawner–recruit database generally supports the expectations from life-history theory. Our analysis is encouraging but admittedly superficial, as we did not perform statistical tests of group differences and we ignored any confounding effects of measurement error. Further analysis should focus on reducing the high variation in steepness and sigma values within each strategy by allowing species to have intermediate strategies, adding more equilibrium and opportunistic species to the database, and including a formal statistical analysis of the results.

Understanding compensation

Population regulation via compensatory responses must ultimately occur through density-dependent changes in rates of mortality or in reproductive success. Mortality and reproduction directly affect the numbers of individuals. Other responses, such as density-dependent changes in growth rate or movement are indirect, and must lead to changes in mortality rate or reproductive success if they are to affect population size. If growth or movement do not ultimately affect numbers of individuals, then changes in these processes would simply result in larger or smaller individuals (for growth) or the same number individuals, but in different locations (for movement).

There are multiple pathways by which mortality, reproduction, growth and movement can interact, leading to compensatory responses at the population level (Goodyear 1980; Jude *et al.* 1987; Saila *et al.* 1987). Compensation is achieved by density-dependent factors that may appear weak relative to the environmental influences, but act cumulatively over life stages and generations to stabilise the population (Hixon 1998). Below we describe several of the more common pathways that have been documented. We use reported studies of particular processes, results of long-term field and manipulative studies, and computer modelling examples to illustrate compensatory responses. The studies of particular processes provide evidence of density-dependent mortality, growth, reproduction and movement. The selected long-term empirical studies and model analyses demonstrate how density-dependent processes in life stages can lead to compensatory responses at the population level. The field studies involve real fish populations, but at the cost of the underlying processes causing the compensation to be weakly documented. The modelling examples provide explicit understanding of how compensation resulted from density-dependent processes, but in a virtual world.

Density-dependent processes

Density-dependent mortality can arise from density-dependent responses by predators, or via density-dependent growth, reproduction and movement affecting survival. While density-dependent mortality can lead directly to compensation, detecting density-dependent mortality from field data is difficult. For large-number fish populations (e.g. most marine commercial stocks), estimates of mortality rates and fish densities have large measurement errors (Beverton and Holt 1957; Ricker 1975; Houde 1987). Nevertheless, Myers and Cadigan (1993) explicitly accounted for measurement errors and isolated a density-dependent component in mortality rates of juvenile-stage demersal marine species. Crecco and Savoy (1987) used otolith data to infer that survival of American shad cohorts (grouped into 5-day hatching periods) was inversely related to initial cohort size. Density-dependent mortality in young-of-the-year (YOY) life stages has also been detected for other species (Crozier and Kennedy 1995; Bailey *et al.* 1996; Michaletz 1997; Planes *et al.* 1998).

Predation as the cause of density-dependent mortality results from the numerical or functional responses of the predators to prey density (Murdoch and Oaten 1975; Hassell 1978; Bailey 1994; Rose *et al.* 1999). Numerical responses involve increases in the number of predators when prey densities are high. Functional responses involve changes in the consumption rates of predators such that mortality rate of prey increases with increasing prey density. Recently, Hixon (1998) suggested that an aggregative response, whereby the local distribution of predators shifts in response to local prey density, is reasonable for density-dependent predation of reef fish (e.g. see Schneider 1989). Predation has been implicated for density-dependent mortality in a variety of juvenile fishes (Murdoch 1969; Murdoch and Oaten 1975; Peterman and Gatto 1978; Lockwood 1980; van der Veer 1986; Forrester and Steele 2000; Anderson 2001). Forrester (1995) and Steele (1997) manipulated both juvenile and adult goby densities over realistic ranges, and in both cases, recruit density was not linearly related to adult density, indicating density-dependent survival. Because growth rates of individuals were similar across all densities, the authors implicated predation as the likely cause of the density-dependent mortality. In a more recent study, Forrester and Steele (2000) showed that the intensity and cause of density-dependent mortality differed among three closely related goby species. Reductions in mortality rates due to density-dependent responses by predators are also possible if predators target other forage species owing to reduced profitability when densities are low (Werner and Hall 1974; Townsend and Hughes 1981; Werner and Mittlebach 1981; Hartman and Brandt 1995). Shima (2001) showed that per capita mortality rates of the reef-dwelling six-bar wrasse (*Thalassoma hardwicke*) were dependent on both the density and number of individuals.

Cannibalism, which can result in a strong density-dependent feedback, has been documented for a variety of fish species (Smith and Reay 1991). For example, adults eating their young is prevalent in walleye (Forney 1977) and northern pike (Treasurer *et al.* 1992). Egg cannibalism has been shown to be a significant cause of density-dependent predation mortality in some fishes via positive relationships between daily egg mortality rates and spawning biomass densities (Hunter and Kimbrell 1980; Smith *et al.* 1989). For example, simultaneous samples of eggs and adults for estimates of daily egg production indicate that cannibalism can amount to 20–30% of total daily egg mortality in northern anchovy (*Engraulis mordax*) and Peruvian anchovy (*E. ringens*) (MacCall 1981; Alheit 1987).

Density-dependent growth is not simply food limitation of growth rate. Rather, density-dependent growth refers to a situation where the feeding rate of an individual is reduced by the presence of other members of the same population, cohort, or year-class, i.e. intraspecific competition for food increases with increasing density of individuals (Heath 1992). In a recent review, Cowan *et al.* (2000) concluded that density-dependent regulation of cohort growth and biomass via feedbacks derived from reductions in prey resources is more likely to occur during the late-larval to juvenile stage than in the high-density early larval stage. Examples also exist which indicate slower individual growth rates in large cohorts or year classes (e.g. Bannister 1978; Rauck and Zijlstra 1978; Craig and Kipling 1983; Mills and Forney 1983; Rijnsdorp and van Leeuwen 1992). Adults also can exhibit density-dependent growth. Rieman and Myers (1992) found density-dependent growth in adult kokanee (*Oncorhynchus nerka*), but not in yearlings.

Density-dependent growth can result in density-dependent mortality; slower growth leads to prolonged stage duration (Houde 1989; Hovenkamp 1992), and mortality often decreases with body size (Cushing 1975; Dahlberg 1979; Anderson 1988; Sogard 1997). Larger individuals at the end of their first growing season often experience decreased probability of overwinter mortality (Post and Evans 1989; Johnson and Evans 1990), and increased survival to recruitment (e.g. Marshall and Frank 1999b). Growth rate can also affect mortality because size is important in determining the susceptibility of prey to predators and can influence competitive interactions (Miller *et al.* 1988; Bailey and Houde 1989; Fuiman and Magurran 1994; Bystrom and Garcia-Berthou 1999; Lundvall *et al.* 1999). The behaviour of individuals depends on their balancing of energy gain with predation risk; more time spent foraging generally translates into higher predation risk. Selection by individuals for spatial and temporal restriction of foraging activity to reduce predation risk can lead to density-dependent growth and mortality (Walters and Korman 1999; Walters 2000).

Density-dependent reproduction includes changes in fecundity (egg production, eggs per gram of female), maturation, spawning frequency, egg quality and spawning location. Changes in reproduction can arise directly from how individuals allocate their energy (Kjorsvik *et al.* 1990; Henderson *et al.* 1996; Van Winkle *et al.* 1997), and indirectly via density-dependent changes in growth and movement (e.g. Peterman and Bradford 1987). Within morphological upper limits (Roff 1982), the weight of mature ovaries in most fish species is an exponential allometric function of body weight (MacKinnon 1972; Delahunty and deVlaming 1980; Erickson *et al.* 1985; Sibly and Calow 1986). This suggests that fecundity is highly size-dependent (Rijnsdorp 1990, 1994; Koslow *et al.* 1995).

Examples of changes in fecundity that could provide a compensatory mechanism serving to stabilise fish populations have been reported (Nikolsky 1969; Nikolsky *et al.* 1973; Rothschild *et al.* 1989). However, several authors have expressed doubts that density-dependent changes in adult growth affecting fecundity can be large enough alone to stabilise recruitment (Craig and Kipling 1983; Koslow 1992; Koslow *et al.* 1995; Trippel 1995). Interannual changes in fecundity of northern anchovy (Lasker 1985) and Atlantic herring (*Clupea harengus*) (Almatar and Bailey 1989) were unrelated to changes in adult abundance; however, variation in fecundity consistent with density dependence has been reported for other species (Nikolsky 1969; Bagenal 1973; Nikolsky *et al.* 1973; Rothschild 1986; Rothschild and Fogarty 1989).

Density-dependent growth can affect fecundity via growth effects on lifetime egg production owing to either earlier maturation (Muth and Wolfert 1986; Peterman and Bradford 1987; Funakoshi 1992) or delayed maturation (Bowen *et al.* 1991; DeLeo and Gatto 1996), depending on how survival and fecundity vary with age. Trippel (1995) reviewed data from north-west Atlantic groundfish populations for 1959–92 and reported that age and size at maturity decreased by 15–55% in cod and by as much as 30% in haddock (*Melanogrammus aeglefinus*). He presumed the observed shift to a younger age and smaller size at maturity to be a compensatory response to reduced population size to maintain or achieve maximal reproductive output. Perrow *et al.* (1990) attributed 2-year cycles in roach (*Rutilus rutilus*) to density-dependent growth of YOY resulting in their reduced fecundity in the next year.

Serial or batch spawners may also respond to changes in density-dependent growth (actually per capita ration) by changing the frequency of spawning and the number of spawns. Both the interval between successive spawnings (Wootton 1977) and the numbers of spawnings during a season (Townsend and Wootton 1984) have been related to ration. Experimental results with Japanese anchovy (*Engraulis japonicus*) confirmed the dependence of batch-fecundity and interspawning interval on ration, with a lag of 11–21 days between increased ration and increased fecundity (Tsuruta and Hirose 1989). Based upon studies in Tampa Bay, Florida, Peebles *et al.* (1996) inferred that bay anchovy may be an "income breeder" (following Stearns 1993) that spawns soon after energy for egg production becomes available, implying that observed seasonal and spatial patterns in egg production could largely be explained by variation in metabolic rate and adult ration.

Density-dependent food availability (per capita ration) during the spawning season may also influence the size and quality of eggs spawned (reviewed by Kjorsvik *et al.* 1990; Bromage 1995). Egg size has been shown to increase with spawner body size for many species (e.g. Buckley 1967; Rogers and Westin 1981; Lobon-Cervia *et al.* 1986; Hislop 1988; Kjesbu 1989; Zastrow *et al.* 1989; Monteleone and Houde 1990; Buckley *et al.* 1991b; Kjesbu *et al.* 1992). Number of eggs spawned, and their condition and hatchability, have been related to the condition of female Japanese sardine (*Sardinops melanostictus*) spawners, which in turn, is influenced by the quantity and quality of their food (Lasker and Theilacker 1962; Takeuchi *et al.* 1981; Watanabe *et al.* 1984a,b,c; Morimoto 1996). In contrast, increasing egg number, rather than egg quality, in response to low densities was exhibited by Atlantic herring (Bradford and Stephenson 1992) and Japanese anchovy (Funakoshi 1992). Larger eggs leading to increased survival has been documented for some species (Rosenberg and Haugen 1982; Miller *et al.* 1988; Buckley *et al.* 1991a), but not for others (Chambers *et al.* 1989; Kjorsvik *et al.* 1990; Pepin and Myers 1991; Rijnsdorp and Vingerhoed 1994).

Density-dependent movement affecting mortality and reproductive success is well documented in fishes. Whenever these vital rates directly (or indirectly via growth) depend upon habitat that is both limiting in quantity and variable in quality, the movement of individuals to suboptimal habitats when densities are high can result in compensatory density dependence. For example, competition for feeding and spawning sites in many salmonids in rivers and streams involves fine-scale movement of individuals related to their body size (Caron and Beaugrand 1988; Grant *et al.* 1989; Hughes 1998; Reinhardt 1999); crowded conditions force individuals to occupy lesser quality habitats, where they presumably experience higher mortality or slower growth (Fausch 1984; Grant and Kramer 1990; Hughes 1992; Elliot 1994). Selection of pool, run, or riffle habitats by juvenile Atlantic salmon (*Salmo salar*) in experimental river enclosures depended on density (Butl *et al.* 1999). Superimposition of nests whereby, under high densities of spawners, late spawners destroy earlier spawned nests has been documented for some stream and riverine dwelling salmonids (Beall and Marty 1987; Maunder 1997). Large-scale movements related to density has been observed in the contraction and expansion of the distribution of populations that track fluctuations in their abundance (Swain and Sinclair 1994; McConnaughey 1995); presumably such movements force individuals to occupy inferior habitats when crowded (MacCall 1990). Density-dependent mortality of postsettlement coral reef fishes is related to the availability of, and movement between, optimal and suboptimal habitats (Hixon 1998).

There are also less-well-studied processes, such as sex change, parasitism and disease, that can lead to compensatory density dependence. Sex change in protogynous species, such as the gag grouper (*Myctoperca microlepis*), depends on population density (Lutnesky 1994; Collins *et al.* 1998). Sex change being both density dependent and socially mediated has led to speculation that species in the grouper-snapper complex in the Gulf of Mexico may be sperm limited (Coleman *et al.* 1996) and have diminished genetic variation (Chapman *et al.* 1999) owing to a long history of overfishing that targets males (Koenig *et al.* 1996). Parasitism and disease can be direct sources of density-dependent mortality and fecundity in fishes (Ivlev 1961; Moller 1990; Adlard and Lester 1994), and their prevalence is often facilitated by poor nutritional condition that could arise from density-dependent growth. For example, in a study of flounder (*Platichthys flesus*) in the Elbe estuary, Moller (1990) found that local differences in condition factor and disease prevalence seemed to be negatively correlated with local food supply. In contrast, Poulin (1995) concluded that larger (well-fed) hosts consume greater quantities of food and are therefore exposed to a wider range of parasite-infective stages.

Empirical field studies

Empirical evidence for compensatory responses can be found in long-term and manipulative studies of particular fish populations. However, while there are many examples of density dependence in particular processes and life stages (see above; Jude *et al.* 1987; Saila *et al.* 1987; Myers 1995; Cowan *et al.* 2000), there are fewer examples where the evidence is sufficient to infer how the density-dependent process in a life stage actually influenced population dynamics. To be useful for understanding how compensation works, population-level studies of density dependence must be long-term (multigenerational), and should involve multiple life stages and multiple processes (Hixon 1998). While not meant to be an exhaustive review, we describe below several examples that include species from marine, estuarine and freshwater environments. These examples include a variety of data analysis methods, the use of experimental manipulation, and they are field-orientated and focus on single populations. These studies are included because they provided insights about the underlying causes of the observed compensatory response.

Japanese anchovy

In response to long-term declines (1970–84) in stock levels and the numbers of large adults, Japanese anchovy (*Engraulis japonicus*) underwent a change in 'mode of life' whereby the spawning potential of small anchovy (7–12 cm in length) increased dramatically (Funakoshi 1992). Nutritional condition and the proportion of small females that matured and spawned increased. Spawning frequency changed from once every 4–5 days for large females (12–16 cm in length) to every 2–3 days for small anchovy. Batch fecundity increased by 1.2- to 2.2-fold, although egg size decreased. In combination, these changes in reproductive potential of smaller fish resulted in almost constant population egg production over the period of decline (Funakoshi 1992). Experimental results have confirmed that batch-fecundity and the intervals between spawnings in the Japanese anchovy depend on ration (Tsuruta and Hirose 1989).

Population cycles of vendace

The long-term study of vendace (*Coregonus albula*) in Lake Pyhajarvi in south-west Finland showed a 2-year cycle in year-class strength (Helminen *et al.* 1993; Helminen and Sarvala 1994). Vendace enter the fishery in their first autumn (defined as recruitment) and dominate the catch during the next winter. Individuals spawn the following year, with larval development in the summer. Abundances in the first autumn were estimated for 1971–90. A 2-year cycle was documented using autocorrelation analysis, which showed alternating signs with increasing lags (Helminen *et al.* 1993), and using multiple regression analysis with lagged abundances (Helminen and Sarvala 1994). The multiple regression model related autumn abundance to the following explanatory variables: autumn abundance lagged one year, summer water temperature lagged 2 years (index of abundance of age-2 perch, a major predator on YOY vendace), and a temperature-derived estimate of the duration of the larval stage of vendace. All three regression coefficients were negative and the model explained 77% of the interannual variation in autumn abundance. Additional analyses using bioenergetics modelling showed that vendace can affect the densities of their zooplankton prey (Helminen *et al.* 1990).

The cause of the 2-year cycles was asymmetric competition in which YOY out competed age-1 and older individuals for zooplankton prey (Hamrin and Persson 1986). Thus, a high autumn YOY abundance in one year would lead to lowered zooplankton prey for age-1 and older individuals in that year. However, in the previous year these age-1 individuals had experienced low abundances as YOY, and thus had faster growth rates, making them relatively large at the end of their first growing season. Larger size requires a larger ration, which further lowered their competitive abilities in the next year when compared with relatively small, but numerous, YOY. These age-1 and older individuals therefore had less surplus energy to devote to reproduction and produced fewer eggs, leading to low YOY abundance the next year. Similar 2-year cycles have been documented for vendace in other systems, and for other species with a similar life-history strategy (Hamrin and Persson 1986; Perrow *et al.* 1990).

Controlled exploitation of lake whitefish

Healey (1978, 1980) controlled the annual exploitation rates of lake whitefish (*Coregonus clupeaformis*) in four similar lakes at levels of 0, 10, 20 and 30%. Gill nets were used to sample each lake during various combinations of spring, summer and autumn from 1971 to 1978. Captured fish were aged using scales. Length-at-age (growth), fecundity and year-class strength (recruitment) were compared before and after exploitation was begun for each lake. Length-at-age data showed that growth rates of adults increased in relation to the level of exploitation, such that: (i) little or no change in growth rate of adults occurred in the unexploited lake; (ii) a small but temporary increase in growth rate (5 mm over ages) occurred in the lightly exploited lake; (iii) growth rate increased (12 mm over ages) and was maintained in the moderately exploited lake; and (iv) growth rate was still increasing at the end of the study for the heavily exploited lake. Relationships between fecundity and exploitation and between recruitment and exploitation were suggestive, but less definitive. Individual fecundity increased in response to exploitation, although the increases were not related to the magnitude of exploitation. Year-to-year patterns between lakes indicated that the most heavily exploited lake had a higher frequency of strong recruitments, especially just after exploitation was begun. Responses of recruitment to exploitation in the other lakes was less consistent. Removal of adults via fishing tended to stimulate good (but variable) recruitment of younger fish. The author proposed that adult suppression of young could be owing to relegation to marginal habitats, or inhibition of normal exploratory and foraging behaviour.

Orange roughy

Koslow *et al.* (1995) showed that individual fecundity of orange roughy (*Hoplostethus atlanticus*) females increased by 20% after the stock was fished down to around 50% of its virgin biomass. The authors suggested that the compensatory increase in individual fecundity was attributable to increased per capita food availability. Increased fecundity, combined with an apparent 17% increase in the proportion of females spawning, limited the expected decline in population egg production during 1987–92 to 15%, despite the 50% reduction in spawning biomass.

Walleye recovery in western Lake Erie

Muth and Wolfert (1986) documented changes in walleye (*Stizostedion vitreum*) growth and maturity during the recovery of the stock in western Lake Erie. The population declined during the 1960s, and a catch-quota system on recreational fishing was implemented in 1976. The estimated standing stock of yearling and older walleye increased from 14.6 million in 1976 to 44.7 million in 1983. Associated with this increase in abundance were downward annual trends in mean lengths and condition factors of YOY in the autumn, and in age-1 and age-2 fish sampled from the trap-net fishery. Percent-mature-by-age also declined with increasing abundance. The percent mature of age-2 females dropped from 90% in 1976 to 45% in 1977, plateaued until the 1980s, then dropped from 31% in 1981 to 7% in 1983. Nearly all age-1 males were mature (99%) in 1975, 78% were mature during 1978–81, followed by a rapid drop to 45% in 1982 and to 32% in 1983. The authors suggested that the piscivorous YOY walleye exceeded the carrying capacity of their forage fish prey in years of high walleye abundance. Thus, forage fish biomass declined in parallel with increasing walleye abundance. With less food per capita, walleye were unable to maintain growth, which ultimately resulted in delayed maturation and lowered reproductive potential.

Plaice in the North Sea

Beverton and Iles (1992) examined how density-dependent mortality during the first 16 months of life can explain the relatively low variation in recruitment observed in North Sea plaice (*Pleuronectes platessus*). They used regression analysis, and carefully estimated the density-dependent component of mortality for three time periods between settlement (June) and October 1 of the second year. While North Sea data were used to estimate the density-dependent components for the earliest and latest time periods, data both from within and outside of the North Sea were used for the middle period. They then determined that the dampening effect of the density-dependent mortalities was sufficient to reduce a 200-fold variation in abundance at settlement to 4-fold variation on October 1 of the second year. The dramatic reduction generally agreed with the decrease in variation observed in various surveys performed during the 16 months after settlement. They further concluded that all three periods of density-dependent mortality were important, but that the strong density dependence estimated for the earliest period from Wadden Sea data may be higher than is typical for other nursery areas. The explanations for the density-dependent mortality are only well understood for the earliest period, during which the functional response of shrimp predators in the Wadden Sea have been implicated as the causative agent (van der Veer 1986; van der Veer and Bergman 1987).

Haddock recruitment in the North Atlantic

Marshall and Frank (1999a,b) presented empirical evidence for compensatory control of haddock (*Melanogrammus aeglefinus*) recruitment in the south-west Scotian Shelf in the North Atlantic. They analysed summer surveys from 1970 to 1995 and autumn surveys from 1963 to 1986 and showed that: (i) mean length at age-1 was negatively related to adult (age-4 and older) abundance; (ii) differences in mean length at age-1 persisted through the adult stage; and (iii) recruitment was positively related to the mean length of age-4 adults (an indicator of spawning stock condition). The negative feedback on recruitment operated as follows: high adult abundance led to short mean length at age-1, which led, 3 years later, to short mean length at age-4, which led to low recruitment the next year, which led to low adult abundance 3 years later. Likewise, low adult abundance in a year resulted in a tendency towards high adult abundance 8 years later. Marshall and Frank (1999a) caution that this compensatory feedback occurs only during periods when both density-dependent growth of age-1 and recruitment dependent on mean length of age-4 adults were operating. They further suggested that this feedback could led to cyclic population behaviour, which has been observed in a variety of stocks, and hypothesised that competition for food between juveniles and adults was the cause of density-dependent age-1 growth.

Migratory brown trout

Elliott (1994) synthesised 25 years of study of anadromous brown trout (*Salmo trutta trutta*) in Black Brows Beck, a stream in the English Lake District. Abundances at successive life stages from eggs to spawning for each year-class were estimated for 1966–1990. Analysis of mortality rates between successive life stages (K-factor analysis) using spawner–recruit-type functions showed that there was a critical period from emergence to 30–70 days postemergence during which mortality was density-dependent. After this critical period, mortality was much lower and density-independent. More detailed studies of some year classes indicated that the likely cause of density-dependent mortality during the critical period was the effects of locating and defending feeding territories. Under high egg abundances, smaller young trout experienced reduced food because they could not locate good territories, and the larger young trout also suffered higher mortality because they incurred the greatest costs of territory defense. Locating and defending territories provided a simple explanation for Eliott's observation that both the smaller and larger individuals were lost under high abundances (i.e. variability of mean lengths at the end of the critical period decreased with increasing abundance).

Computer modelling examples

We present the results of three simulation models to illustrate how compensation works at the process level, and to illustrate several features of compensation that make understanding compensation from field measurements so difficult. The three models are: yellow perch (*Perca flavescens*)-walleye in Oneida Lake, New York; bay anchovy in the Chesapeake Bay, Maryland; and fish food web models in Lake Mendota, Wisconsin. The three examples are from our own work. They were selected because they illustrate important points about compensation and were convenient. There are numerous other examples we could have used, including examples that use modelling approaches other than the individual-based approach. The yellow perch-walleye example illustrates how compensation arises from complex relationships among multiple processes operating in multiple life stages. The bay anchovy example demonstrates how small, probably undetectable, density-dependent changes in multiple processes can combine to result in significant compensatory responses. The food web analysis demonstrates how density-dependent relationships in a species can depend on the specifics of the situation.

The models are all site-specific and individual-based. The advantage of site-specific models is that they provide a method for tracking the complex pathways of compensation under relatively realistic (albeit virtual world) conditions. These models were developed for specific locations, which were selected because of the extensive long-term data available for those populations. Thus, model predictions were extensively compared with observed data to ensure model realism. The reader is referred to the original publications cited under each example for the details of model calibration and validation. The individual-based approach used has several advantages for modelling fish population dynamics and predicting compensatory responses (DeAngelis *et al.* 1993, 1994). One such advantage is that density dependence can be an emergent property of the model, resulting from the summed effects over individuals, rather than having to be specified *a priori* in relationships (e.g. spawner–recruit curves) used to construct the model.

Yellow perch in Oneida Lake

Rose *et al.* (1999) used an extensive database to develop, calibrate and corroborate an individual-based model of yellow perch–walleye dynamics for Oneida Lake, New York. The model begins with spawning of individual females of yellow perch and walleye, and simulates growth and mortality of both species progeny as they develop through successive life stages (egg, yolk-sac larva, feeding larva, YOY juvenile, yearling and adult). YOY juvenile and yearling yellow perch are the dominant prey for adult walleye, and walleye predation is the major source of mortality of young yellow perch. Density-dependent growth, survival and reproduction emerge from the size-based interactions represented in the model. Predicted annual adult abundances of yellow perch and walleye under baseline conditions show weak, but consistent, prey–predator cycling (Fig. 3).

We use three simulations to illustrate how growth, survival and reproduction processes can lead to

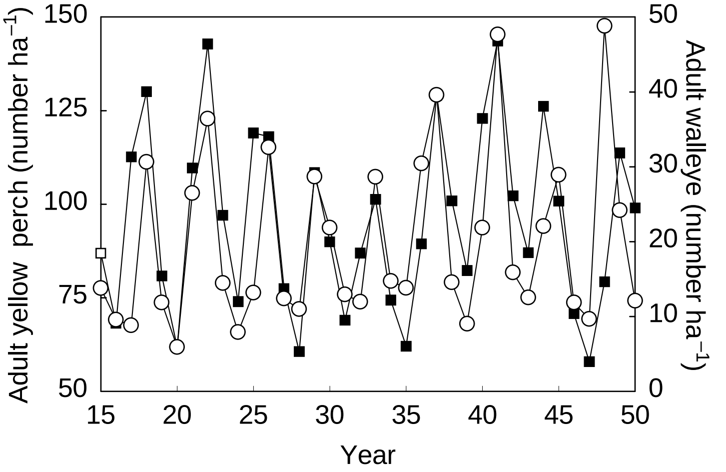

Figure 3 Simulated annual adult densities of yellow perch (■) and walleye (○) for years 15–50 of the baseline simulation of Oneida Lake (modified from Rose *et al.* 1999).

Table 1 Simulated responses of yellow perch to decreased and increased egg mortality rate based on an individual-based model of yellow perch–walleye in Oneida Lake (from Rose *et al.* 1999)

Variable	Units	Decreased egg mortality	Baseline	Increased egg mortality
Increasing egg mortality	Percentage	71	90	96
Lower number of first feeders	No. ha^{-1}	178 325	85 036	40 894
Lower 18 mm abundance	No. ha^{-1}	60 594	30 329	15 325
Increased 18 mm to recruitment survival	Percentage	0.41	0.85	1.56
Higher (slightly) recruitment	No. ha^{-1}	205	210	221
Longer recruitment mean length	mm	141.8	144.5	151.8
Faster adult growth	mm year^{-1} (age-4)	18.5	20.9	22.0
Longer adult mean lengths	mm (age-4)	205	215	221
Younger maturation	Percentage mature (age-4)	24	41	54
Higher (slightly) fecundity	Eggs per spawner	27 885	30 313	30 989
Similar adult abundance	No. ha^{-1}	103	106	112
More spawners	No. ha^{-1}	29.1	35.4	44.2
Higher egg production	$\times 10^6$ eggs ha^{-1}	0.80	1.11	1.35

The value of each variable is the average computed over the last 35 years of the 50-year simulation.

compensation in yellow perch. The baseline yellow perch egg mortality rate of 0.11 day^{-1} was increased to 0.15 day^{-1} and decreased to 0.06 day^{-1}. Predicted average values of abundances, mean lengths, growth rates, survival rates, fecundity and percent mature at age for yellow perch were analysed for density-dependent responses. To match how Oneida Lake data were reported, Rose *et al.* (1999) used several conventions in reporting model predictions: abundance at 18 mm roughly corresponds to metamorphosis (i.e. number of juveniles), recruitment is abundance at age-2, and age-4 responses are considered representative of adults. All simulations were for 50 years duration; average values of all variables were computed over the last 35 years of each simulation.

Yellow perch exhibited density-dependent responses to increasing egg mortality (Table 1). Increasing egg mortality led to the expected lower total number of yellow perch first feeders, and lower yellow perch abundance at 18 mm. The survival rate of yellow perch from 18 mm to recruitment increased with increasing egg mortality, resulting in slightly increased recruitment with increasing egg mortality. Yellow perch survival from 18 mm to recruitment increased owing to decreased walleye predation pressure; average adult walleye abundances in the three simulations decreased with increasing yellow perch egg mortality (20.2 per hectare (ha)$^{-1}$ to 19.9 ha^{-1} to 16.1 ha^{-1}). Walleye adult abundance decreased because there was less food available to the walleye. Fewer 18 mm yellow perch lead to faster growth rates of YOY yellow perch (density-dependent growth) and longer mean recruit lengths. Longer YOY yellow perch were less vulnerable to predation by walleye because yellow perch predation risk decreased with length. Fewer and longer YOY yellow perch resulted in less food for walleye, which resulted in increased cannibalism of YOY walleye by adults, and shorter walleye adults that produced fewer eggs; both of which caused walleye adult abundances to decrease with increasing yellow perch egg mortality. Adult yellow perch growth rates also increased with increasing egg mortality which lead to longer yellow perch adults at age, and resulted in a younger age-of-maturation and slightly higher fecundity of adult yellow perch. With adult yellow perch abundances near or slightly above baseline levels, younger age-of-maturation resulted in more spawners with increasing egg mortality. More spawners and higher fecundity resulted in increased egg production to compensate for increased egg mortality. Thus, despite a two-fold variation in the egg mortality rate between the high and low mortality simulations, predicted average adult abundances of yellow perch were similar (103 ha^{-1} and 112 ha^{-1}).

These results illustrate how understanding compensation requires knowledge of how multiple processes interact over the full life cycle, and how difficult it would be to try to monitor these process-level responses in nature. Recall that the values reported in Table 1 span all yellow perch life stages and are averages over 35 years, with the only difference among the three simulations being the egg mortality rate of the yellow perch. Sufficient monitoring of the variables listed in Table 1 would require an enormous amount of sampling over several decades.

Food webs in Lake Mendota

We configured six different food webs from a general, multispecies individual-based model (Fig. 4; McDermot

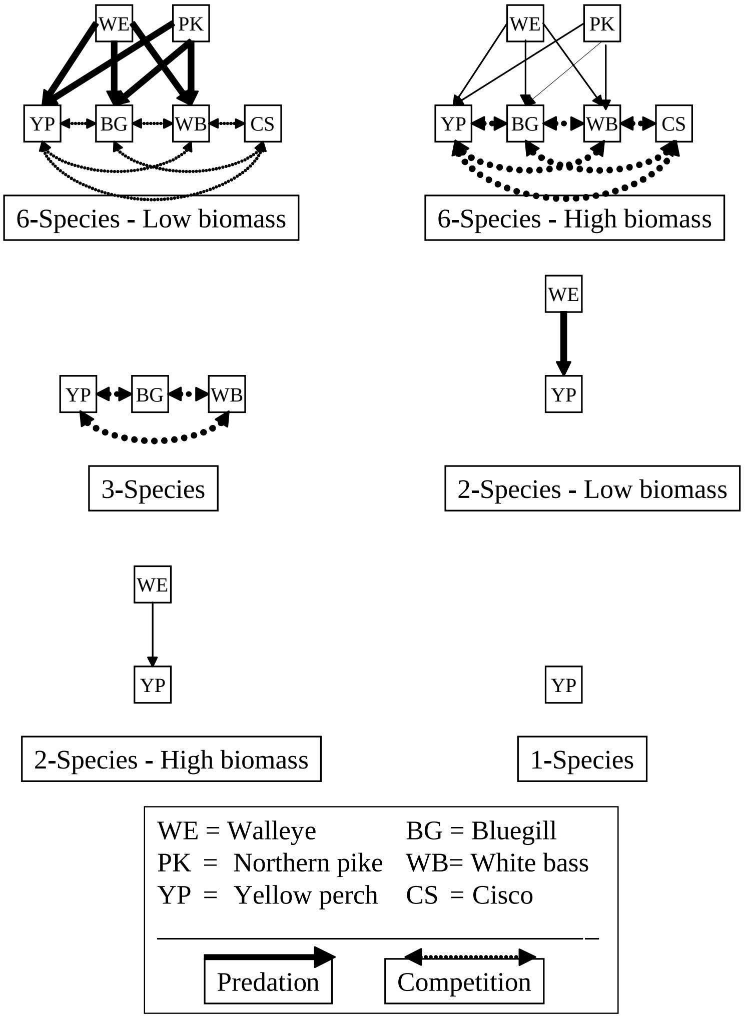

Figure 4 The six food webs used to compare density-dependent survival of juvenile yellow perch. The low- and high-biomass food webs differ in their average yellow perch biomass and their degree of coupling between piscivores (walleye and pike) and their prey. Differences in the feeding-related parameters of walleye and pike resulted in competition among the yellow perch and other planktivores being more important in the high-biomass versions, while piscivore predation was more important in controlling the planktivores in the low-biomass versions. Predator–prey interactions are shown as solid lines; competitive interactions are shown as dashed lines. Heavier lines indicate greater intensity of the interactions.

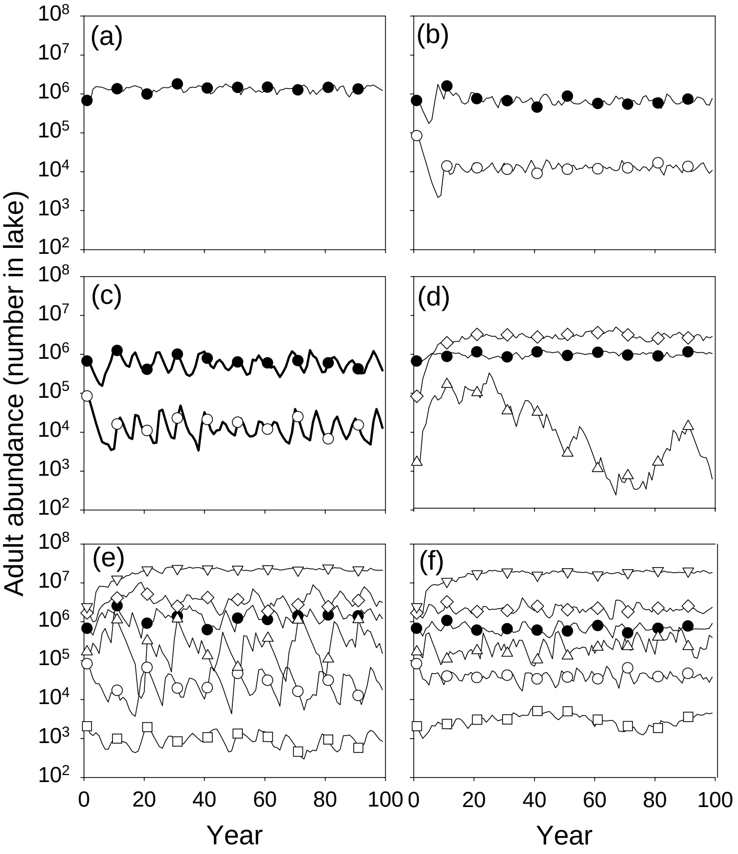

Figure 5 Simulated annual adult abundances of the species in each of the six food webs. (a) 1-species; (b) high-biomass, 2-species; (c) low-biomass, 2-species; (d) 3-species; (e) high-biomass, 6-species; and (f) low-biomass, 6-species. Yellow perch (●); walleye (○); bluegill (△); northern pike (□); white bass (◇); and cisco (▽). Symbols are shown every 10 years (Modified from McDermot 1998).

1998). McDermot and Rose (2000) present a detailed description of the model and analysis of the two of six food webs. All six of the food webs included yellow perch; two versions of the 6-species and 2-species food webs (denoted high and low biomass) were configured such that they differed in their average yellow perch biomass and degree of predator-prey coupling. Differences in the feeding-related parameters of walleye and pike resulted in competition among the yellow perch and other planktivores being more important in the high-biomass versions, while piscivore predation was more important in controlling the planktivores in the low-biomass versions. All six of the food webs shared the same environmental conditions, which were based on data from Lake Mendota, Wisconsin.

The six different food webs were standardised to permit cross-food web comparisons. Selected parameters were calibrated for each version until: (i) all species in the food web persisted for 100 years; (ii) mean lengths of adults (age-5) for all species were biologically reasonable; and (iii) average yellow perch adult biomass was similar to the value from the low-biomass 6-species food web. The 6-food webs used here are similar but not identical to those reported in McDermot (1998); some of the Northern pike parameter values were adjusted. Annual adult abundances for each of the food webs used in this paper are shown in Fig. 5. We examined the relationship between yearling survival and the number of entering yearlings for yellow perch in each of the 100-year simulations of the 6-food webs.

The strength of density-dependent mortality in the yearling stage varied among the different food webs (Fig. 6). Strong negative relationships ($r^2 = 0.34$ and 0.49) were observed in the 1-species (Fig. 6a) and the high biomass, 6-species (Fig. 6e) food webs. A statistically significant, but very weak, negative relationship ($r^2 = 0.04$) was observed in the high biomass, 2-species food web (Fig. 6b), and yearling survival was unrelated to the number of entering yearlings for the 3-species food web (Fig. 6d). Yearling survival actually increased with increasing numbers of entering yearlings for the low biomass 2-species (Fig. 6c) and the low biomass 6-species (Fig. 6f) food webs.

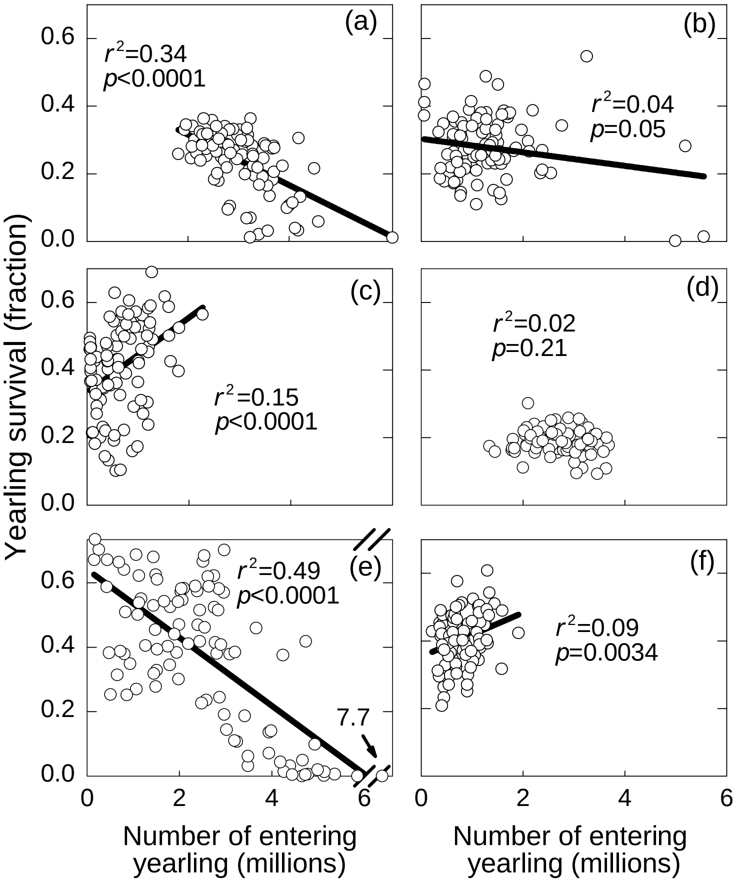

Figure 6 Simulated relationship between annual values of yearling yellow perch stage survival and the numbers of yearlings entering. Values are from the 100-year simulations shown in Fig. 6. Regression lines, and associated r^2 and P-values, are shown. (a) 1-species; (b) high biomass, 2-species; (c) low biomass, 2-species; (d) 3-species; (e) high biomass, 6-species; (f) low biomass, 6-species.

With a little imagination, these 6-food webs can be viewed as yellow perch in different systems or as yellow perch in a single system that is changing over time. Detecting density-dependent yearling mortality would then depend on the population studied, or on quantifying density dependence from a mixture of the relationships observed in various food webs.

Bay anchovy in Chesapeake Bay

Bay anchovy has been the subject of much research (Houde and Zastrow 1991) and has been shown to be important in the Chesapeake Bay as forage for striped bass, weakfish (*Cynoscion regalis*) and bluefish (*Pomatomus saltatrix*) (Hartman and Brandt 1995), and to the overall energy cycling of the bay (Baird and Ulanowicz 1989). The available data on bioenergetics, growth, survival and reproduction were sufficient to develop and verify an individual-based model of the bay anchovy population in the mesohaline region of Chesapeake Bay (Rose *et al.* 1999).

Cowan *et al.* (1999) used the model to examine the maximum compensatory response of bay anchovy, measured in terms of the largest amount of additional larval mortality that could be offset by compensatory increases in survival or reproduction in other life stages. First, a baseline simulation was performed in which the average fecundity, size-at-age, and population abundance closely matched values observed for the Chesapeake Bay. The maximum compensatory response of the population was then simulated by assuming that fecundity, egg mortality, and juvenile and adult mortality would all respond to lowered anchovy densities. The magnitude of the changes in each of these parameters was derived from an extensive review of the literature on bay anchovy population dynamics (Cowan *et al.* 1999). It was assumed that decreased density of bay anchovy would result in (i) an increase in reproduction by 3 batches per year (from 60 under baseline conditions to 63); (ii) a 10% increase in the number of eggs produced per gram of spawning anchovy; (iii) a decrease in egg mortality rate from 0.2 to 0.1 day^{-1}; and (iv) 10% decreases in the daily mortality rates of juvenile and adult bay anchovy.

A total of eight 50-year simulations were performed under maximum compensation conditions,

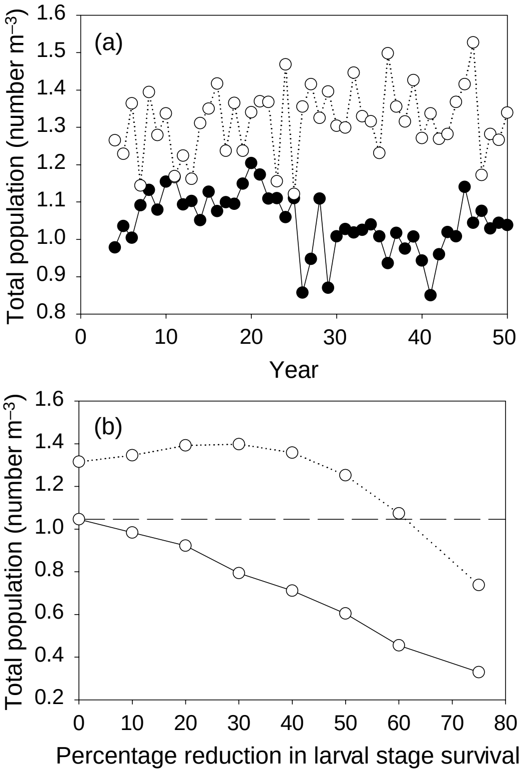

Figure 7 (a) Predicted annual total population density of bay anchovy for the baseline (●) and maximum compensation (○) simulations. (b) Average total population density (computed over the 50 years) for simulations with 0, 10, 20, 30, 40, 50, 60 and 75% reductions in larval stage survival. Maximum compensation conditions result from the imposition on baseline conditions of 3 more spawning batches per year, a 10% increase in individual fecundity, egg mortality rate being decreased from 0.2 to 0.1 day^{-1}, and a 10% decrease in the daily mortality rates of juvenile and adult bay anchovy. Note the different vertical scales on panels (a) and (b). (Modified from Cowan *et al.* 1999).

and average population abundance was computed for each simulation. The eight simulations corresponded to larval stage survival being reduced by 0% (baseline), 10, 20, 30, 40, 50, 60 and 75%; a 75% reduction meant that larval survival was 25% of the baseline value. Predicted average population abundances were compared with average abundance predicted under baseline conditions. The purpose of the simulations was to see how much larval survival had to be reduced before the compensatory reserve in the population was exceeded, and before predicted population abundances would drop below the baseline value.

The assumed compensatory increases in survival and reproduction increased the simulated density of the bay anchovy by 30% compared with the baseline simulation. Predicted population density under maximum compensation were higher than under baseline conditions (0.87 m^{-3} vs. 0.67 m^{-3}; see Fig. 7a). Higher densities were predicted because of the increased fecundity and lowered mortality rates assumed under maximum compensation conditions. Under the assumed changes in processes, baseline or higher population densities were predicted for up to 60% reductions in larval survival (Fig. 7b). Only at the highest (75%) reduction in larval survival was the compensatory reserve from lowered mortality and increased reproduction exceeded, resulting in a still stable population but at an average density 25% lower than baseline. Whether the changes in processes assumed under maximum compensation would occur in a particular situation is not known, but the changes imposed were relatively small compared with the variation observed in these processes *in situ* (see Cowan *et al.* 1999). Thus, relatively small changes in fecundity and survival of bay anchovy, which would probably be undetectable in field monitoring amongst the variation from density-independent sources, combined to produce substantial compensation.

Cause for optimism: recent technological and theoretical advances

There have been several technological and theoretical advances in the past decade that make us optimistic that further progress on the compensation issue is possible. These advances are: otolith ageing, new methods for marking of individuals, physiological measures of fish health, microchemical analysis of skeletal material, genetic and molecular approaches to stock identification, recognition of the importance of spatial heterogeneity in population dynamics, new acoustic and video measurement methods, new statistical estimation and time series methods, incorporation of stochasticity into population- and stock-assessment models, tailoring of classical life-history theory to fishes, assembly of large databases, and individual-based modelling.

Some of these advances are directly related to better measurement and modelling of compensation. Other advances do not involve compensation directly, but help by improving our knowledge of the causes of population dynamics and variation. Some of these advances have already had impact on population dynamics, while others are still in their infancy and their full impacts have yet to been realised. Below we briefly discuss these advances.

The developments of otolith ageing, new methods for marking of individuals, physiological measures of fish health, and microchemical analysis of skeletal material have enabled improved estimation of mortality, growth, movement rates and stock structure. Otolith ageing has added a new layer of resolution (i.e. cohorts within a year) in our ability to tease apart year-class strength. By separating cohorts within a year-class, otolith analysis has enabled much greater understanding of density dependence of growth and mortality (Crecco *et al.* 1983; Crecco and Savoy 1987), and of how survivorship of individuals during the critical first year of life relates to temporal and spatial variation in spawning and environmental variables (Rice *et al.* 1987; Zastrow *et al.* 1991; Limburg *et al.* 1999). The traditional mark-recapture approach to estimating mortality and movement has been greatly expanded by the use of chemicals for mass marking (Ennevor 1994; Secor *et al.* 1995), tags that permit information on individual fish (Bryan and Ney 1994; Achord *et al.* 1996), and ultrasonic telemetry that allow continuous tracking of marked individuals (Szedlmayer 1997). The rapidly growing field of biological indicators (see Adams 1990; Holdway *et al.* 1995) has increased our ability to detect the presence of sublethal effects and environmental stressors affecting individuals in a population. Microchemical analysis of skeletal material can yield vital information on broad-scale movement patterns and stock structure (Campana *et al.* 1994; Thorrold *et al.* 1998; Campana 1999), and on pollution exposure (Coutant 1990). These new advances have the potential to greatly improve our ability to estimate mortality rates and habitat usage, and to identify possible environmental causes for population variability not apparent from traditional monitoring.

Developments in the field of genetics and molecular biology have greatly increased our ability to identify fish populations or stocks (Carvalho and Hauser 1994; Lincoln 1994; Ferguson *et al.* 1995). Density dependence on a local scale may or may not translate into population compensation, depending on the degree of mixing with individuals from other locations (Stepien 1995; Policansky and Magnuson 1998). Being able to define the spatial extent of the unit of the population seems fundamental to understanding population dynamics, but is a continuing problem in many fish population studies. Continued work in the genetics area, as well in microchemical analysis of otoliths (Campana 1999), may ultimately resolve one of the major issues hindering our understanding of fish population dynamics.

The importance of spatial heterogeneity to understanding density dependence and population dynamics is receiving increasing attention (Kareiva 1990a; Stewart-Oaten and Murdoch 1990; Dunning *et al.* 1995). Space has been called the final frontier in ecological theory (Kareiva 1990b). Explicit consideration of spatial variability is possible from developments in measurement and analysis methods. The general availability of global positioning systems has permitted much greater accuracy in determining where samples are collected than previously possible. Geographic information systems has provided a means for storage and interpretation of spatially explicit data (Keleher and Rahel 1996; Johnson and Gage 1997; Wiley *et al.* 1997; Clark *et al.* 2001). Remote sensing provides simultaneous measurement of environmental variables over km scales (Cole and McGlade 1998; Polovina *et al.* 1999). Recognising that fish population dynamics are influenced by large-scale oceanic patterns and decadal climate patterns such as El Nino-Southern Oscillation (Sinclair *et al.* 1985; Lluch-Belda *et al.* 1989, 1992; Lenarz *et al.* 1995; Gargett 1997) and the North Atlantic Oscillation (Hoffmann and Powell 1998), has aided in explaining variation and trends that may appear random on the local level. There is increasing interest in Lagrangian-type models, where individual fish are imbedded into spatially explicit hydrodynamics models (Walters *et al.* 1992; Hinckley *et al.* 1996; Werner *et al.* 1996; Heath and Gallego 1997).

Video and acoustic technologies are two examples of new measurement methods that have recently become available. Video and acoustic methods have been used to augment and calibrate traditional sampling gear (Luo and Brandt 1993; Banneheka *et al.* 1995; Greene *et al.* 1998), and to permit sampling in situations where traditional gear cannot (Parker *et al.* 1994). They have also been used to simultaneously monitor biological and environmental variables on a meter scale over large areas (Brandt and Mason 1994), and for recording of detailed behavioural interactions between individuals (Fuiman and Batty 1994; Barnett and Pankhurst 1996).

New statistical methods are available that are well suited for analysing fish population dynamics data. Statistical analysis in ecology has in general been moving from hypothesis testing and linear models to multiple hypothesis evaluation (e.g. likelihoods) and nonlinear models (Maurer 1998). New methods, such as generalised additive models (Swartzman *et al.* 1995; Daskalov 1999), nonlinear time series (Dixon *et al.* 1999), neural networks (Lek *et al.* 1996; Thorrold *et al.* 1998), fuzzy mathematics (Saila 1992; Mackinson *et al.* 1999), geostatistical methods (Fletcher and Summer 1999) and methods that explicitly account for sampling and measurement error (Mertz and Myers 1995), are being applied to fisheries-related datasets. Statistical techniques are now available for valid detection of density dependence in time series (den Boer and Reddingius 1989; Dennis and Taper 1994; Dennis *et al.* 1998; Bjornstad *et al.* 1999), but not without controversy (see Wolda *et al.* 1994). Recent advances also allow for much greater flexibility in time series model formulation (Dixon *et al.* 1999; Sanderson *et al.* 1999). A promising trend is the focus on the interaction between environmental stochasticity and density dependence, and how they combine to control the long-term dynamics of populations (Fogarty *et al.* 1991; Higgins *et al.* 1997; Hixon and Carr 1997). Bayesian approaches using maximum likelihood methods are being used to estimate the many unknown parameters in population dynamics and stock assessment models (Hilborn *et al.* 1994; McAllister and Kirkwood 1998; Schirripa and LeGault 1999). Synthetic analyses involving diverse studies can now be rigorously analysed statistically using meta-analysis methods (Hilborn and Liermann 1998; Myers and Mertz 1998).

Explicit treatment of stochasticity in population models has increased their realism. Population modelling has moved from deterministic models of simple equilibrium to nonequilibrium approaches that explicitly include stochasticity and uncertainty (Turchin 1995; Uchamnski and Grimm 1996). The definition of a regulated population has been expanded from simple statements about equilibrium densities to more encompassing definitions appropriate for highly stochastic populations, such as a bounded variance of population densities and a long-term stationary probability distribution of population densities (Turchin 1995). The influence of stochastic modelling can be seen in the increasing use of uncertainity and risk in stock assessment (Hilborn and Walters 1992) and in fisheries management (Rosenberg and Restrepo 1994; Francis and Shotton 1997). Embracing the stochasticity that is characteristic of almost all fish populations, rather than using models that attempt to average the variability away and produce precise but inaccurate predictions, will increase model realism and credibility.

Finally, three areas of advance emphasised in this paper are life-history theory, large databases and individual-based modelling. Winemiller and Rose (1992) reconfigured the traditional 'r and K' life-history framework to a 3-endpoint framework specifically designed for fishes. We encourage continued efforts in relating fish population responses to stress within a life-history framework (e.g. Garrod and Knights 1979; Schaaf *et al.* 1987; Armstrong and Shelton 1990); others have since expanded on the Winemiller and Rose framework (McCann and Shuter 1997). Significant progress is occurring on the assembly of large databases (e.g. Myers *et al.* 1995a; Froese and Pauly 2000) and synthetic analyses (e.g. Miller *et al.* 1988; Li *et al.* 1996; Shuter *et al.* 1998). Individual-based modelling offers a promising approach for modelling population and community dynamics (Huston *et al.* 1988; DeAngelis *et al.* 1994; Judson 1994), and has features that should help to quantify compensatory responses of fish populations. Representing local interactions in space, size–based interactions, episodic effects, movement and stochasticity, all of which are important to realistic simulation of fish population dynamics and compensation, is relatively easy in individual-based models (DeAngelis and Rose 1992; DeAngelis *et al.* 1994; Tyler and Rose 1994). Additional critical review (*sensu* Grimm 1999) is needed to further the usefulness of individual-based modelling. Intuitively, if one can realistically represent how individuals grow, survive, reproduce and move, then population-level phenomenon such as compensation can be obtained by simply summing over all of the individuals in the model. There are also exciting advances occurring within the individual-based approach, including the use of state-dependent methods to allow individuals to respond dynamically to changing internal and external conditions (e.g. Huse and Giske 1998; Railsback 2001). In this paper, we used a large database to test some of the predictions from life-history theory, and used individual-based models to illustrate several features of compensation.

We have briefly mentioned some of the technical and theoretical advances that make us optimistic that significant progress on the compensation issue is possible in the near future. Our list is not meant to be comprehensive, but rather to illustrate that we are at a point where diverse advances are providing an opportunity for a major leap in our understanding of compensation. The growing emphasis on synthetic and comparative analyses, coupled with advances in measurement, statistical, and population modelling methods, is encouraging and critical for progress in understanding compensation and in the effective management of fish populations.

Synthesis and prognosis

Compensation must be included in management analyses that involve long-term predictions of fish populations. The fact that some resource will eventually limit the size of a fish population is not disputed. We also know how to incorporate density dependence into population dynamics and stock assessment models. Difficulties and controversy arise when the magnitude of compensation and compensatory reserve must be specified for a particular population. The details of compensation, such as the mix of magnitude, life stages, and processes, that exhibit density dependence can greatly influence the resulting population response. The consequences of over- or under-estimating compensation and compensatory reserve are serious; these include risk of population decline, unnecessary spending of monetary resources, and unneeded restrictions on fishers and energy generation.

Analysis of a particular population becomes difficult because model predictions are very sensitive to how compensation is represented, direct measurement of compensation and compensatory reserve in the field require many years of data, and the mechanisms underlying compensation can be highly site-specific. The sensitivity of model predictions to assumptions about compensation is practically legendary (e.g. Barnthouse *et al.* 1984). Simply measuring the details of compensation in the field is very difficult. Long-term studies that span multiple generations and involve multiple processes and all life stages are needed. As shown with the empirical examples of compensation presented in this paper, even with adequate long-term data, tracking density dependence through the full life cycle in the midst of large variation owing to environmental variables often results in conjecture as to the underlying causes of the compensatory response. The yellow perch-walleye and bay anchovy modelling examples illustrated how extensive monitoring must be to detect density-dependent processes and to track compensatory responses through the life cycle. Finally, we used a food web model to demonstrate that compensation can be site specific, and, thus, that using information from other species and locations can be problematic.

Turchin (1995), in a review chapter on population dynamics in general, asks “Is there no end to the density dependence debate?” He then emphatically answers that “the fundamental issues of the population regulation debate have been resolved … all recent empirical analyses agree that the frequency of detecting density dependence increases with the length of the data series. Thus, most field populations are regulated, and previous failures to show this were owing to inadequate data sets….” Unfortunately, this statement resembles similar earlier proclamations. For example, Royama began a 1977 paper with “A basic concept in many theories to explain the persistence of animal populations is the notion of density-dependent regulation, which is now widely accepted in spite of much controversial literature during the last half century.” We suspect that as long as there is lack of definitive proof of how compensation is operating in a specific population, the debates over the long-term consequences of harvesting, power plant effects and other stressors will continue.

We advocate an approach to compensation that involves process-level understanding of compensation, life-history theory, synthetic analyses, and matrix projection and individual-based models. There will always be debate if the quantification of compensation, from any source, does not include some degree of understanding of the underlying mechanisms. Quantifying compensation without adequate understanding is analogous to correlation without supporting information on cause and effect. Estimates of compensation, like correlative relationships, will hold for a while, but will eventually fail. Understanding compensation and compensatory responses is the key to making progress on this important issue.

We also advocate viewing compensation and compensatory reserve in a life-history framework, and endorse the trend towards synthetic analysis of large databases. Life history theory provides the general framework so that one can quickly appreciate (albeit qualitatively) the scope of compensation and compensatory reserve generally associated with a given configuration of attributes. Life history theory also permits interpopulation and interspecific comparisons of the scope of compensatory responses and compensatory reserve. We hope our initial attempt at a synthetic analysis of steepness parameters by life-history strategies using the Myers group spawner–recruit database will stimulate further similar investigations. One area ripe for extending the life-history framework using synthetic analysis is the inclusion into the framework of the plasticity of life-history traits (e.g. Belk 1995; Rodd and Reznick 1997). The Winemiller and Rose framework does not incorporate differences in the degree of flexibility in life-history characteristics among species and strategies.

This flexibility or phenotypic plasticity is probably important for understanding compensatory responses. Numerous other extensions to the life-history framework and potential synthetic analyses can also be envisioned.

When modelling is required for prediction, we suggest using aggregate models for screening and using individual-based models for detailed analyses. Aggregate models, such as age- and stage-structured matrix projection models (Caswell 2000), provide a screening tool for determining populations at risk. Matrix projection models use fecundity and survival data that are generally available for many species, and can applied to populations using site-specific data. Individual-based models should be developed for select species, either the species shown to be potentially adversely impacted by the screening analyses or for which understanding how compensation works is important. Individual-based modelling provides a powerful way to model compensation that avoids the pitfalls of more aggregate approaches by allowing individuals in the model to respond to changing conditions. Matrix projection-type models are relatively easy to apply and analyse but require compensation to be specified *a priori*; individual-based models are well-suited for detailed modelling of compensation at the process level, but are data hungry. A major role of individual-based modelling is to understand compensation and thereby bound the magnitude of compensation that is assumed *a priori* in aggregate models.

We are optimistic, although a bit worried. Focus on how compensation is working in specific populations can lead to constructive debate and better understanding of population regulation. Also, we described some recent advances that have greatly improved our ability to quantify and understand compensatory density dependence in fish populations; these advances are continuing to be refined and new advances are on the horizon. Yet, we still suffer from a lack of a unified theoretical framework for understanding and modelling population dynamics (Getz 1998). Greater attention to understanding compensation and to synthetic analyses and life-history theory, coupled with these technical advances and efforts towards advancing ecological theory of population dynamics, should enable progress on the important issue of compensation. Now is the time for some soul searching and for asking why important fish populations are seemingly overfished worldwide. Demands on fish stocks will only increase in the future.

Acknowledgements

Financial support for the preparation of this paper was provided by the Electric Power Research Institute. Some of the ideas in this paper originated during discussions among the authors during their involvement with permit preparation activities for a Public Service Enterprise Group (PSEG) facility. The comments of Jamie Gibson on an earlier draft greatly improved the paper.

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