

Spatial and temporal scale of density-dependent body growth and its implications for recruitment, population dynamics and management of stream-dwelling salmonid populations

Simone Vincenzi ·
William Hallowell Satterthwaite ·
Marc Mangel

Received: 16 June 2011 / Accepted: 6 November 2011
© Springer Science+Business Media B.V. 2011

Abstract Density-dependent variations in body growth and size have important consequences for the population dynamics of stream-dwelling salmonid populations, since body size is related to a variety of ecologically relevant characteristics. These include survival and fecundity, competitive and predatory abilities, and foraging behavior. However, little work has been done to understand how density-dependent body growth varies across temporal and spatial scales and when this compensatory process is relevant for recruitment and population dynamics of stream-dwelling salmonids. Increased intra- or inter-cohort competition reduces growth rates of juveniles. Both within- and among-cohort differences at the juvenile stage are likely to be maintained through the lifetime. Limited movement or dispersal can lead to subdivision

of a population into several local populations with independent dynamics. The spatial and temporal variation in movement and the patchy distribution of resources make fish likely to experience density-dependence across location, life-stage, and season. The relaxation of density-dependent suppression of body growth at low densities constitutes a potential mechanism for salmonids to persist in the face of environmental perturbation and may contribute to explaining the peculiar resilience to population collapses often showed by salmonids. The inclusion of density-dependent growth in population models may increase the usefulness of model predictions in management contexts. Models not accounting for density-dependent growth may underestimate the recovery potential of resident salmonid populations when they collapse to low densities.

S. Vincenzi (✉) · W. H. Satterthwaite · M. Mangel
Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, USA
e-mail: simon.vincenz@gmail.com

S. Vincenzi
MRAG Americas, POB 1410, Capitola, CA 95010, USA

W. H. Satterthwaite
National Marine Fisheries Service, 110 Shaffer Road,
Santa Cruz, CA 95060, USA

M. Mangel
Department of Biology, University of Bergen,
P.O. Box 7803, 5020 Bergen, Norway

Keywords Compensatory recruitment · Population regulation · Population dynamics · Resilience

Introduction

The regulation of populations is a fundamental area of study for theoretical ecology, conservation, and management of our interaction with wild and cultured species. For fish species, the debate on population regulation has recently become both increasingly important and increasingly contentious, since the

investigation of mechanisms that allow populations to resist extinction risks and to respond to declines and collapses with either rapid or time-lagged recoveries are particularly important in the face of climate change. Although density-dependent regulation of fish numbers is a widely studied subject (Rose et al. 2001), density-related changes in body growth are an important, but understudied potential component of population regulation in fishes.

Density-dependent effects on population dynamics have been frequently detected in salmonids (e.g., Rose et al. 2001; Milner et al. 2003) and ecologists largely agree that density-dependent mortality during the early stages of life is their most important mechanism of population regulation (e.g., Elliott 1994; Milner et al. 2003). The debate over the regulation of recruitment and population size has been historically confined to densities close to carrying capacity. Hence, the effects of reduced intra-specific competition on population persistence and resilience at low spawner densities, especially in low-fecundity fishes like salmonids, is still not well understood (Milner et al. 2003).

Variation in the body size of fish within- and among-cohorts may have important implications for population structure and dynamics (Peters 1983; Werner and Gilliam 1984; Łomnicki 1988). Body size is positively associated with various metrics of fitness, such as fecundity (e.g., Wootton 1998), egg size (e.g., Rollinson and Hutchings 2010), and survival (e.g., Hutchings 1994; Sogard 1997). Density-dependent body growth has been observed in many studies on juvenile salmonids. A number of empirical studies have shown a negative power relationship between average growth rates and density of 0 + individuals in resident (e.g. for brown trout Crisp 1993; Jenkins et al. 1999; Lobón-Cerviá 2007; for marble trout Vincenzi et al. 2007a) and anadromous salmonid populations (for Atlantic Salmon: Imre et al. 2005; Imre et al. 2010; for coho salmon Hartman and Scrivener 1990; Roni and Quinn 2001; for a meta-analysis of salmon and trout populations see Grant and Imre 2005). Exploitation or scramble competition for drifting prey is commonly considered responsible for the occurrence of density-dependent body growth (e.g., Jenkins et al. 1999; Imre et al. 2005). However, competition for space (i.e., contest competition) has been suggested as a potential mechanism for the observed growth-density relationship (Ward et al. 2007).

Recently, Imre et al. (2010) tested the site-quality hypothesis using data from Imre et al. (2005) for young-of-year Atlantic Salmon living in Catamaran Brook (New Brunswick, Canada) and convincingly showed that the observed density-growth pattern was consistent with exploitative competition.

Density-dependent growth is also widely proposed as a plausible general mechanism of population regulation at the juvenile stage (e.g., regulation of early life-stages densities, size-dependent mortality, Imre et al. 2005; Einum et al. 2006; Lobón-Cerviá 2007), but the emerging picture is that the influence of density-dependent body growth on population dynamics may extend to egg production. Several review and in-depth works on density-dependent body growth have already been published (e.g., Grant and Imre 2005; Lorenzen 2008). Here, we clarify some of the less investigated aspects of density-dependent body growth and their implications for the population dynamics of stream-dwelling salmonids, which may stimulate further experimental research and modeling applications.

We explore the importance of early experience in shaping the lifetime individual growth trajectories of fish, the importance of spatial scale and structure for the occurrence and detection of density-dependent body growth, and the persistence of within- and among-cohort differences in size and growth after the early life-stages. We then investigate the implications of strength, timing and scale of density-dependent body growth for recruitment, population dynamics and selection of life-histories in stream-dwelling salmonids. Finally, we discuss why including density-dependent body growth in models of population dynamics can increase the usefulness of model predictions and help the effective implementation of management and conservation actions for threatened populations.

Temporal and spatial scale of density-dependent body growth

Temporal scale

Lower growth rates of juveniles at increasing densities can be the result of competition with other juveniles and/or adults. Although stream salmonids have different habitat requirements depending on their size and life-stage (juveniles typically occupy marginal

and shallow habitats, while older individuals occupy deep habitats more centrally located in the stream channel), habitat use may overlap and thus inter-cohort competition can occur (Cattaneo et al. 2002; Einum et al. in press). Jenkins et al. (1999) found for brown trout that the per-capita separate effects of underyearlings and older fish on underyearling growth were similar. Lobón-Cerviá (2005) found that the relative importance of intra- and inter-cohort density varied greatly and in a site-specific manner for a population of brown trout living in Rio Chaballos (Spain). Vincenzi et al. (2008b, 2010b) found for stream-dwelling marble trout that total population density better predicted growth patterns than cohort density for both yearlings and older age classes of fish, a result that holds at different spatial scales. The relationship between total population density and fish body growth can have alternative explanations, as it can be either a direct effect of total population density in the newly recruited cohort (i.e. inter-cohort competition) or, if density were proportional to the spawning stock, the effect of intra-cohort competition for resources among underyearlings. In the latter case, the negative relation between body size growth of the newly recruited cohort and population densities of older cohorts should be through overall egg production. Moreover, the occurrence of density-dependent inter-cohort competition in brown trout causing a reduction in growth rates were confirmed by Nordwall et al. (2001) and Kaspersson and Höjesjö (2009).

The persistence through the lifetime of within- and among-cohorts differences in size and growth experienced at early life-stages may have important implications for population dynamics. It is well known that environmental factors affecting an entire cohort (i.e., individuals born in the same year) early in life can influence subsequent individual performances (i.e., carry-over effects) and may have delayed consequences on population dynamics (e.g., Albon et al. 1983). The implications of the influence of early conditions (e.g., density, food, experience etc.) on the demographic and behavioral characteristics of fish are potentially both ecological and evolutionary and range from the evolution of life-histories to population dynamics and regulation. In many vertebrate taxa the environmental conditions experienced early in life affect growth of individuals and several related properties, such as metabolism and immunocompetence (Lindstrom 1999). Hence, presently observed

phenotypic traits may have developed through ontogenic trajectories influenced by a previous environment (Schlichting and Pigliucci 1998).

Elliott (1994) found that fry weight and water temperature were the chief factors affecting trout growth in freshwater and that within-cohort variation (expressed as coefficient of variation in mass) remained constant through cohort life. No year-to-year variation in growth was observed (individuals were growing very close to the predicted maximum at maximum ration according to a bioenergetic model), so that smaller fry were likely to be small at subsequent life-stages. Also in brown trout, Lobón-Cerviá (2005) found a negative power relationship between initial cohort size and lifetime growth in weight of the same cohort (Rio Chaballos, Spain). In marble trout, Vincenzi et al. (2007a, 2008b, 2010a) found long-term consequences of early density (i.e., during the first year of life) on life-time growth trajectories.

Growth performance through the lifetime can thus vary in response to early conditions, and may impact lifetime reproductive success. Jonsson et al. (1996) reported that in Atlantic Salmon juvenile growth explained part of the variation in the number of eggs produced by females. Lobón-Cerviá et al. (1997) found that the number of eggs produced by brown trout age-1 females was determined when trout were still age-0 (Esva River, Spain). However, the effect of early conditions on subsequent reproduction can be mediated by conditions later in life (Lindstrom 1999; Metcalfe and Monaghan 2001; Beckerman et al. 2003). For example, the environment experienced by adults may exert a stronger influence on performance than early environment. Habitat requirements of fish change over ontogeny and patterns of competition may change as a result, but density-dependent effects on body growth during the post-recruit phase have rarely been investigated in salmonids. Utz and Hartman (2009) found that adult growth and excess energy acquisition was density-dependent in brook trout *Salvelinus fontinalis*, but only during periods when temperature was warm and energy intake was low. In marble trout, density-dependent individual growth in sub-adults and adults in the wild may occur depending on variations in population density (Vincenzi et al. 2007a). By examining nine contrasting brown trout populations living in the North of Spain, Parra et al. (2011) observed that the main effects of within-cohort

competition on body growth were detected in the size attained at the second year of life and resulted from different levels of competition at multiple occasions through the period prior to that time. In some of the studied rivers, competition was sufficiently intense to cause a growth reduction since the first year of life, while in others the highest influence on growth was observed during the second year of life.

There is increasing evidence across taxa showing potential for compensatory growth (Ali et al. 2003; Jespersen and Toft 2003). This indicates that rapid growth can be costly, because growth rates are usually below the physiological maximum (Arendt 1997). Most experiments in the wild have been carried out on juveniles and thus we generally lack evidence of compensatory growth in sub-adults and adults. In yearling brown trout, structural body growth compensation in the wild led to increased winter mortality (Johnsson and Bohlin 2006). In contrast, Alvarez and Nicieza (2005) found that food-deprived brown were able to restore mass and energy levels after normal feeding was restored, but no structural compensation was observed.

In summary, increased intra- or inter-cohort competition lowers growth rates of juveniles and there is strong evidence indicating that both within- and among-cohort differences in early growth are maintained though the lifetime. Growth can be mediated by conditions experienced later in life, but early environment conditions during early phases of life seem to largely shape lifetime growth trajectories with clear implications for individual fitness of fish.

Spatial scale

Density-dependent processes may operate on spatial scales smaller than that of whole populations even in continuous habitats, and their detection may depend on the spatial scale at which the pattern is investigated. The appropriate spatial scale is likely to depend on the species and its ecology (e.g., territoriality, movement, ontogenetic shifts in diet), physical features of the stream and discontinuities in habitat quality.

Jenkins et al. (1999) investigated the occurrence of density-dependent growth in brown trout underyearlings at different spatial scales and concluded that a sampling area needs to be at least 100 m² to capture the trout density experienced by the average individual

over the preceding growth period. Einum et al. (in press) investigated the spatial scale at which high underyearling density can decrease parr (overyearlings) growth in Atlantic salmon. They created realistic spatial variation in recruitment in a natural stream and tested models integrating multiple spatial scales. Results showed that underyearling density within 16 m had the strongest influence on overyearling growth. The selected model suggested parr daily mass increase to be reduced by about 40% when increasing underyearling density from 0.0 to 1.0 m⁻². The spatial scale estimated in Einum et al. (in press) are similar to those obtained for effects of underyearling densities on their own growth in streams located in the River Conon catchment (Einum et al. 2011).

Another layer of complexity is provided by the estimation of food available, such as invertebrate drift, which may be affected by individuals living upstream. It follows that local abundance of food, a potential major driver of density-dependent growth, may depend on population abundance over a much larger area than that directly experienced by an individual trout. Here, trout density is not only the density of the focal species, but the density of the focal species and its competitors for resources and space.

The mobility of an organism influences the scale at which density-dependent growth may be detected. Trout may move over considerable distances (Gowan et al. 1994) both within- and among life-stages (Morales et al. 2004). Movement is also highly heterogeneous among-individuals (Rodriguez 2002). This possibility reconciles observations of generally sedentary behavior in stream-dwelling salmonids (e.g., Gerking 1959) with observations of long distance movements (Gowan et al. 1994). Downstream movement is commonly observed for alevins of stream-dwelling salmonids (e.g., Elliott 1987; Ottaway and Forrest 1983) and during ontogeny fish move typically from fast riffles to deeper pools (Nakano 1995, but see Gibson et al. 2008). In a recent study on stream-dwelling brook trout, Morrissey and Ferguson (2011) found that the mean dispersal during the alevin stage was comparable to the distances dispersed by individuals over large portions of the rest of their lives. The upstream movement that was observed in brook trout throughout the majority of the life cycle (i.e., after the alevin stage) may thus be compensatory for downstream movement during the alevin stage.

Lobón-Cerviá (2005) found for stream-living brown trout in Rio Chaballos (Spain) that the interactions between body size and density occurred at the spatial scale of 60–80 m. The relationship varied in nature among sites to the extent that the density-dependent patterns were site-specific (as also found by Vollestad et al. 2002 and Vincenzi et al. 2010b), and thus revealed a different effect of density depending on habitat quality. Fish can move from areas with high population densities and reduce the effects of initial patchiness in fish distribution on overall population dynamics by relaxing local density-dependent pressure on body growth and survival (Einum et al. 2006). However, dispersal is costly for the individual across taxa (Rankin and Burchsted 1992; Larsen and Boutin 1994; Aars et al. 1999) and this might prevent movement among local patches (as assumed by site-quality model) and thus cause the emergence of density-dependent responses in mortality and growth.

Individual variation around the mean size of an age-class increased with age-class density in some stream salmonid populations (Newman 1993; Jenkins et al. 1999; Keeley 2001 for confined populations; Einum et al. 2006; Lobón-Cerviá 2010; Kvingedal and Einum 2011), but exceptions were noted, from inverse density-dependence (i.e., decreased variability with increasing densities, Elliott 1994 for the Black Brows Beck population) to no effect detected (Fraser 1969; Gee et al. 1978; Elliott 1994 for the Wilfin Beck population; Harvey and Nakamoto 1996; Keeley 2001 for unconfined populations). An increase in the variability of size with increasing densities suggests that fish distribute according to habitat quality and consequent differential monopolization of resources driven by competitive abilities. Bigger individuals are those that acquired higher quality sites and smaller individuals those negatively affected by density-dependent interactions at lower quality sites (Keeley 2001). Martinussen et al. (2010) found an increase in diet breadth with increasing densities in young-of-the-year Atlantic Salmon (ca. 2 months after their emergence from nests), as predicted by optimal foraging theory. However, since spatial variation in prey availability was not estimated, either exploitative and interference competition were proposed as potential explanations of the wider range of prey size with increasing densities. In any case, the elucidation of competitive mechanisms from patterns in data (see Ward et al. 2007) must be approached with caution,

since an increase in size or growth variation with deteriorating environmental conditions, including an increase in population density, is widely observed in a variety of taxa, which probably differ in competition patterns (Łomnicki 1988).

In summary, the emerging picture is that the spatial and temporal variation in movement and the patchy distribution of resources make fish likely to experience density-dependence across location, life-stage and season. Limited movement or dispersal can provide the conditions for the subdivision of a population into several local populations with independent dynamics. Whether intra-cohort variations in body size and growth rates are related to density is still unclear.

Implications of density-dependent body growth for recruitment and population dynamics

A central and inevitable challenge when investigating regulatory factors involves the actual magnitude of compensatory responses such as density-dependent survival, body growth, reproduction and migration (e.g., Fogarty et al. 1992; Rose et al. 2001) and variation in both their occurrence and strength in response to density-independent factors (e.g., Cianelli et al. 2004; Stenseth et al. 2004).

In the study of fish population dynamics, the common view is that when the number of eggs produced is sufficient, the early life stage abundances are subject to both density-independent environmental factors that generate variability in recruitment, and density-dependent regulation that stabilizes recruitment (Cushing 1974; Rothschild 1986; Houde 1994). However, early life-stage abundances in fish populations appear to vary strongly and show a weak correlation to either spawning stock, population size or egg deposition (e.g., Walters and Juanes, 1993; Lorenzen 2005). Strong (1986) argued that for many species vital rates are clearly affected by density only at high population densities; while over medial densities, where populations spend most of the time, there is a lack of trend in vital rates, given their high variance (“density-vagueness”).

Lorenzen (2005) presented a clear and general pattern that gives rise to variable and often density-dependent stock-recruitment relationships in fish populations. The pattern is adaptable to stream-dwelling salmonids and also introduces the role of

density-dependent body growth as presented in the previous sections. According to Lorenzen (2005), vital rates of eggs and larvae tend to be highly variable and generally density-independent (Myers and Cadigan 1993; Leggett and DeBlois 1994), although density-dependent processes can be observed at those stages (e.g., redd superimposition). Small variation in the very high mortality rates experienced in those early stages cause major changes in the number of fish surviving, and potentially account for a large part of variability in the early stages (Rothschild 2000). On the contrary, mortality after the very early stages of life are density-dependent and tend to dampen the variability previously created (e.g., Elliott 1994). Density-dependent survival may arise directly from density effects on the mortality rate (Elliott 1994), or indirectly from the interaction of size-dependent mortality with density-dependent growth (Shepherd and Cushing 1990; Post et al. 1999). Density-dependent mortality is then replaced by density-dependent body growth as the dominant regulatory mechanism (Walters and Post 1993; Post et al. 1999; Lorenzen and Enberg 2002; Einum et al. 2006), with a parallel transition from intra-cohort to inter-cohort density-dependence. Local competition may also increasingly cause dispersal away from areas of high density, suggesting an ontogenetic increase in dispersal abilities (Einum et al. 2006) (Fig. 1).

The life-stage at which density-dependence has probably received the least attention is the egg (Vandenbos et al. 2006). Mechanisms occurring during the egg stage will affect juveniles and can often be linked to characteristics of the subsequent life-stages. Egg number and quality are affected by body size of sub-adults and adults, since both sexual maturation and fecundity are related to body size. Thus, a negative correlation between abundance and body growth that persists from the juvenile to the adult stage combined with constant size at maturity implies strong regulation of reproductive output (Jenkins et al. 1999; Lorenzen 2005). However, quantifying the number and fate of eggs in the wild is often difficult, and usually only one of either egg production or survival are estimated (Fox 1994; Post et al. 1998), even though egg production and egg survival are rarely correlated (e.g., Cole and Sadovy 1995).

Modeling investigations on the role of density-dependent body growth in the dynamics of populations are limited. For instance, a recent comprehensive

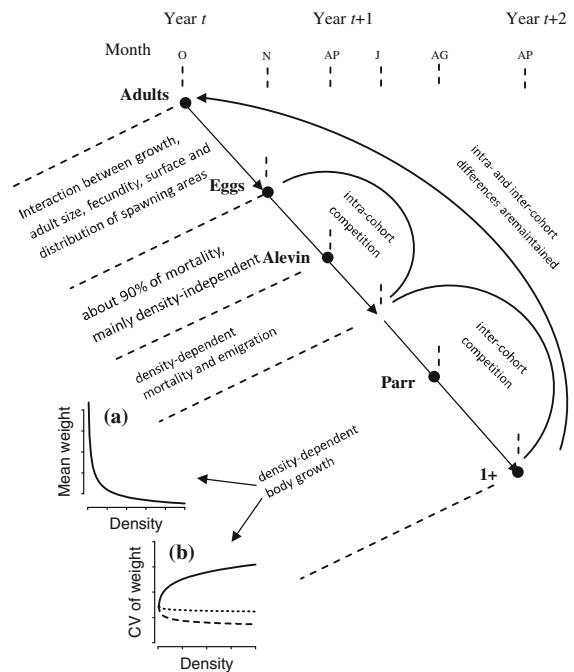


Fig. 1 The main regulatory (endogenous) factors in an ideal stream-living salmonid. Egg production can be constrained by lack of spawners or unsuitable spawning substratum and influenced by body size of spawners. The most critical period for survival (early bottleneck) is immediately after the start of external feeding and the establishment of territories in suitable micro-habitats. Small variations in the very high rates of mortality experienced in those early stages cause major changes in the number of fish surviving. In general, large size increases the survival probability of alevins. Mortality after the very early stages of life is density-dependent (intra-cohort) and tends to dampen the variability previously created, except in streams with low population density or influenced by extreme environmental conditions. Density-dependent mortality is then replaced by density-dependent body growth (inter-cohort) as the dominant regulating factor. Mean weight of cohorts decreases with increasing densities following a negative power curve (a), while intra-cohort variability (CV of weight) may increase (solid line), decrease (dashed line) or remain constant (dotted line) with increasing densities (b). Although growth may be influenced by conditions later in life, intra- and inter-cohort differences in body size established in the first stages of life are likely to be maintained through the lifetime. Additional details on the life-cycle of stream-dwelling salmonids can be found in Jonsson and Jonsson (2011)

review of population dynamics models for brown trout reported that density-dependent body growth is seldom included (Frank et al. 2011). Vincenzi et al. (2008a) provided insights on the effects of density-dependent body growth on population regulation in stream-dwelling salmonids through a simulation study using a simple data-driven individual-based model of

population dynamics of marble trout populations living in Slovenian streams. Both density-dependent early survival and body growth were modeled, along with the effects of autumnal severe flood events like those frequently occurring in the study area (Slovenia, Vincenzi et al. 2008a). At carrying-capacity, marble trout females reach sexual maturation at age-3 or age-4, while at very low densities, following a massive mortality event, increased growth rates may allow maturation at age-2 assuming constant size at sexual maturity. The simulations confirmed that density-dependent body growth (with purely stochastic and density-independent within-cohort variability in body size) may increase the chances of recovery of small populations of resident salmonids at low spawner densities, such as after the occurrence of heavy perturbations inducing a considerable reduction in population size. Density-dependent body growth may allow a faster recovery after population collapses due to severe disturbance events through a cascade of direct and indirect impacts, as described hereafter with reference to catastrophic floods.

Severe floods, flash-floods or debris-flows dramatically reduce population abundance by “washing-out” or killing fish. Although some within-population variation in morphological and behavioural adaptations to floods may exist (Ward et al. 2003; Lytle and Poff 2004), random death of fish is a reasonable assumption in the case of catastrophic events. Body growth of surviving individuals and of the emerging cohort then increases due to the relaxation of density-dependent pressure, potentially reaching the maximum growth allowed by water temperature and stream productivity. As previously described, there might be a costly structural compensatory response for sub-adults and adults, depending on early restrictions and post-disturbance availability of resources. In addition, the reduced availability of prey following the disturbance event may limit body growth in piscivorous fish.

With increased body growth rates, females may mature faster (Wilson et al. 2003; Vincenzi et al. 2008a) and produce more eggs, since both sexual maturity and egg production are size- and growth rate-dependent. In the case of marble trout, female length was peculiarly linked to egg production via a linear relationship. Further simulations showed a greater increase of per-capita egg production at very low densities when the relationship was modelled through a power curve (Vincenzi et al. 2010a). In addition,

bigger females are likely to produce bigger eggs with increased probability of early survival (e.g., Ojanguren et al. 1996), although with a trade-off between egg number and size (Lobón-Cervía et al. 1997). The decreased density-dependent pressure on body growth can have both immediate (through increased growth of sub-adults and adults) and delayed (through carry-over effects of early growth) effects on egg production. The increased per-capita egg production and the relaxation of density-dependent first-year survival (Vincenzi et al. 2007b) allow the surviving population to return faster to pre-event population size, thus reducing the years at low densities and consequently the risk of after-flood extinction. This picture holds for system in which immigration of fish living in neighbouring populations is either prevented or particularly difficult, either due to characteristics of the species (i.e., highly sedentary) or because of habitat fragmentation. Otherwise, neighbouring populations are likely to rapidly recolonize the stream affected by the flood event.

Vincenzi et al. (2008a, 2010a) showed that density-dependent individual growth was less important in determining population size and persistence when the population was not heavily affected by heavy perturbations with respect to a scenario with density-independent body growth (i.e., fish growing according to a density-independent Von Bertalanffy growth curve). This is a consequence of the negative power law relationship between growth and density often observed in salmonids; at persistently high population densities close to stream carrying capacity, year-to-year variations in growth rates are too low to provide substantial variations in per-capita egg production.

The importance of density-dependent growth for recovery after massive mortalities was proposed, but not quantitatively investigated, in other studies. Jenkins et al. (1999) pointed out that high individual growth rates at low densities may theoretically enable stream-dwelling salmonid populations to rebound quickly after high-amplitude stochasticity, such as extreme floods caused by snow-melt peaks or ice dams dewatering stream reaches. A localized massive flood event provided greater growth opportunities for the surviving individuals by drastically reducing competitors in an Atlantic salmon population living in the Sawmill River (Letcher and Terrick 1998). Cannibalistic pressure is widespread across salmonids (Aymes et al. 2010) and may be reduced after massive

mortalities. This might in part explain the spike of juveniles often observed after heavy perturbations. In addition, relaxed intra-specific pressure induces higher maturation rates which seem to contribute to a faster population recovery. Roghair et al. (2002) suggested that an increase in juvenile growth, such as that observed immediately following a flood event reducing population density, can decrease age-at-maturity due to faster growth rates and/or an increase in fecundity when body size of females at sexual maturation is bigger.

Stream-dwelling salmonids present strikingly different life-histories both within- and among-populations and species (e.g., Hendry and Stearns 2004; Jonsson and Jonsson 2011). This can have profound implications for the relevance of density-dependent body growth for population and recruitment dynamics and resilience to heavy perturbations. A diversity of life histories thus urges species- and population-specific explorations. Among largely variable life-histories within- and between-species there are differences in age and size at maturity, semelparity versus iteroparity, body growth trajectories after sexual maturation, trade-off of egg size and number, and breeding tactics (e.g., Klemetsen et al. 2003; Hendry and Stearns 2004; Jonsson and Jonsson 2011). For instance, body growth and size in brown trout vary considerably within and among-populations, where older fish may vary in size from about 20 g in slow growing fish in small streams up to 1 kg in piscivorous and anadromous populations with optimal feeding and temperatures (Klemetsen et al. 2003). Ferox trout, a phenotypic morph of brown trout, is exceptionally large (up to 100 cm in length) and long-lived (sometimes more than 20 years). Brown trout crossing a threshold in size can become piscivorous and then follow a different growth trajectory (and are thus identified as ferox trout). Their larger size makes them immune from cannibalism, thus causing the greater longevity (Mangel and Abrahams 2001). Freshwater resident populations of brown trout mature sexually at an age between 1 and 10 years, with fish maturing older in colder localities. Lobón-Cervia (2000) reported that slow growing adults spawned fewer but larger eggs that result in larger offspring, which may also contribute to size variation among populations. However, while the trade-off between egg size and number is widespread among salmonid species, there are numerous exceptions (Carlson and Seamons 2008).

The implications of density-dependent individual growth for compensatory recruitment seem to be strongly context- and species-dependent. Lobón-Cervia (2009) investigated the mechanisms allowing brown trout living in Rio Chaballos (Spain) to recover after years of dramatic and persistent low population densities. He suggested that the recovery trajectories can be fully explained in terms of parabolic recruitment-stream discharge relationships, year-to-year variations in stream discharge, and high fecundity relatively to juvenile carrying-capacity. He also noted that enough eggs to produce the observed recruits in the 2 years leading to recovery could be produced by one mid-sized female or a few smaller females, but did not account for the density-independent and often very high egg mortality. According to Lobón-Cervia (2009), when the discharge conditions are optimized (i.e., peak of the parabolic recruitment-discharge relationship) the “normal” egg production should allow the population to recover from collapses without a prominent role of density-dependent body growth.

While the analysis is interesting, the peculiarity of the monitored brown trout population in Rio Chaballos showing the boom-and-bust dynamics (more than 80% of population between age-0 and age-1, short life span, strong relationship between recruitment and stream discharge) limits the ability to generalize to other salmonid populations and species. For instance, suitable habitat for juveniles and spawning grounds may be altered by disturbances. This may influence both the overall reproductive output and recruitment dynamics and potentially modify the relative role of regulatory factors for recovery. Moreover, as also reported by Lorenzen (2005), egg survival is highly variable and a simple egg-to-recruit proportion may be too optimistic. In the context of the potential for recovery, the question concerning density-dependent body growth is not whether depressed populations are able to rebound to pre-event levels without growth-mediated increases in per-capita egg production, but how the intensity and variation in density-dependent body growth will influence the probability of recovery.

Natural selection for maximal lifetime reproductive success shapes the life-histories of a given species in a given environment (Kozłowski 2006). Life-histories include age and size at maturity, reproductive output and also the timing of the expression of these traits through the lifetime (Hutchings 2003). Like any heritable feature of an organism affecting its fitness,

body growth will be under some type of selection for increasing lifetime reproductive success. Plastic effects of poor diets and high densities of individuals can be consequences of low resources without any clear adaptive value. However, there is some evidence that size is more plastic in species adapted to fluctuating resources (Nylin and Gotthard 1998). We thus hypothesize that where fluctuating resources over time are related to variation in density, the adaptive value of a stronger body growth response to density is greater. The simultaneous maximization of all life-history traits influencing reproductive success and thus fitness is not possible, thus leading to an allocation compromise between conflicting traits (Roff 1992; Stearns 1992). For instance, increased growth rates in genetically-modified coho salmon lowered survival with respect to wild genotypes in the presence of predators and did not increase survival in the absence of predators (Sundström et al. 2005). Therefore, the existence of selection of stronger body growth responses in environments when variations in density are closely related to variations in resources needs to be carefully tested by taking into consideration heritability of body growth traits (e.g., Carlson and Seamons 2008) and trade-offs with other traits (Roff 1992; Kingsolver et al. 2001; Carlson and Seamons 2008).

Implications of density-dependent body growth for management of salmonid populations

In order to develop a proper focus for management efforts, the picture emerging from this work highlights the importance of understanding those stages that are under density-dependent regulation and how different regulatory pathways interact. For many years, the management of threatened salmonids focused primarily on the stock-recruitment relationship, but this greatly limited the advancement of knowledge in the regulation of populations and often led to the application of erroneous management actions (Einum et al. 2008). Density-dependent body growth has important implications for the development and application of models of population dynamics and Population Viability Assessments (PVAs), in particular given the increasing impact of floods, droughts, landslides on stream-dwelling salmonids expected with climate change.

Populations change through time according to processes that are rarely captured with reasonable accuracy by population viability models, such as variable environmental conditions (e.g., Ludwig 1979; Beissinger 1995), differences in individual performance (e.g., Kendall and Fox 2002) and regulation through density-dependent patterns. The implications of density-dependent body growth for population regulation and/or resilience to drops in population size might be non-trivial. Therefore, management and conservation plans based primarily on matrix model projections and elasticity analyses should be approached with caution and the possibility of developing individual-based models should be explored. Large fluctuations in population densities may affect both individual growth and age at maturity and lead to compensatory changes in life-histories through phenotypic plasticity or evolutionary adaptation (Thorpe et al. 1998). Life history responses to altered freshwater growth could extend to age at smolting in anadromous fish (Satterthwaite et al. 2009) or even an altered balance between residency and anadromy in facultatively anadromous fish (Satterthwaite et al. 2010), with considerable impacts on population dynamics. Therefore, the results and perspective provided by models of population dynamics in matrix form may not reflect the outcomes of management actions and thus put conservation efforts at risk. On the one hand, when density-dependent growth is expected to enhance the resilience of fish populations to disturbances, leaving out this compensatory response makes the conservation strategy more conservative. On the other hand, higher risk of extinctions predicted by models not including density-dependent body growth may call for unnecessary conservation actions (e.g., translocations of fish, habitat modifications), waste of financial resources and selection of particular life-histories by multiple restocking (i.e., selection of better competitors at high population densities). Finally, the inclusion of density-dependent growth in models of population dynamics may lead to better predictions of PVAs of salmonid populations, which may otherwise underestimate their recovery potential when they “naturally” (i.e., no size-selective exploitation) collapse at low densities.

Density-dependent body growth has clear implications for reintroduction and restocking of salmonids. The general objective of stocking programs is to maximize recruitment without wasting resources by

risking density-dependent mortality or growth in either the stocked or the native fish populations. Similarly, restoration plans typically target the limiting habitat type for the limiting life stage (Dodson et al. 1998). Models of population dynamics, where the main life-history and demographic traits have been estimated for the species and system in question (e.g. McCallum 1994; Towns and Ferreira 2001), usually confirm that compensatory responses are likely to regulate population size around the stream carrying capacity in a few years after the initiation of the population.

It is worth noting that since low numbers are generally released when the chances of success of the reintroduction are deemed to be poor, there is a bias in the literature in favour of larger release groups. However, reducing monetary expenses by releasing fewer individuals whenever possible can make further conservation efforts achievable. For instance, a greater number of populations can be obtained with the same total stocking material and money investment. This would reduce the risk of rapid extinction due to high-amplitude stochastic events through a portfolio effect (Moore et al. 2010; Carlson and Satterthwaite 2011). In simulations using models of population dynamics for marble trout, Vincenzi et al. (2008c, *in press*) found that given the observed compensatory responses (density-dependent early survival and growth), the same risk of quasi-extinction of newly created population would be expected by introducing about one-fifth of the numbers of marble trout originally stocked for the initiation of populations. Increased growth rates at low densities following small introductions may prove particularly advantageous for anadromous fish reintroductions, if rapid growth facilitates large smolts with increased marine survival probability (Ward and Slaney 1988; Mangel 1996; McGurk 1996).

Acknowledgments The authors thank Alain Crivelli, Giulio A. De Leo and Dusan Jesensek for providing helpful discussion.

References

- Aars J, Johannesen E, Ims RA (1999) Demographic consequences of movements in subdivided root vole populations. *Oikos* 85:204–216
- Albon SD, Guinness FE, Clutton-Brock TH (1983) The influence of climatic variation on the birth weights of red deer (*Cervus elaphus*). *J Zool* 200:295–298
- Ali M, Nicieza A, Wootton RJ (2003) Compensatory growth in fishes: a response to growth depression. *Fish Fish* 4:147–190
- Alvarez D, Nicieza AG (2005) Compensatory response “defends” energy levels but not growth trajectories in brown trout, *Salmo trutta* L. *P R Soc Lond B* 272:601–607
- Arendt JA (1997) Adaptive intrinsic growth rates: an integration across taxa. *Q Rev Biol* 72:149–177
- Aymes J-C, Larrieu M, Tentelier C, Labonne J (2010) Occurrence and variation of egg cannibalism in brown trout *Salmo trutta*. *Naturwissenschaften* 97:435–439
- Beckerman AP, Benton TG, Lapsley CT, Koesters N (2003) Talkin’ bout my generation: environmental variability and cohort effects. *Am Nat* 162:754–767
- Beissinger SR (1995) Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. *Ecol Appl* 5:618–631
- Carlson SM, Satterthwaite WH (2011) Weak portfolio effect in a collapsed fish population complex. *Can J Fish Aquat Sci* 68:1579–1589
- Carlson SM, Seamons TR (2008) A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evol Appl* 1:222–238
- Cattaneo F, Lamouroux N, Breil P, Capra H (2002) The influence of hydrological and biotic processes on brown trout (*Salmo trutta*) population dynamics. *Can J Fish Aquat Sci* 59:12–22
- Ciannelli L, Chan KS, Bailey KM, Stenseth NC (2004) Non-additive effects of the environment on the survival of a large marine fish population. *Ecology* 85:3418–3427
- Cole KS, Sadovy Y (1995) Evaluating the use of spawning success to estimate reproductive success in a Caribbean reef fish. *J Fish Biol* 47:181–191
- Crisp DT (1993) Population densities of juvenile trout (*Salmo trutta*) in five upland streams and their effects upon growth, survival and dispersal. *J Appl Ecol* 30:759–771
- Cushing DH (1974) The natural regulation of fish populations. In: Harden-Jones FR (ed) *Sea fisheries research*. Elek Science, pp, pp 399–412
- Dodson JJ, Gibson RJ, Cunjak RA, Friedland KD, Garcia de Leaniz C, Gross MR, Newbury R, Nielsen JL, Power ME, Roy S (1998) Elements in the development of conservation plans for Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 55:312–323
- Einum S, Sundt-Hansen L, Nislow KH (2006) The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* 113:489–496
- Einum S, Nislow KH, Reynolds JD, Sutherland WJ (2008) Predicting population responses to restoration of breeding habitat in Atlantic salmon. *J Appl Ecol* 45:930–938
- Einum S, Robertsen G, Nislow KH, McKelvey S, Armstrong JD (2011) The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. *Oecologia* 165:959–969
- Einum S, Nislow KH, McKelvey S, Armstrong JD (in press). The spatial scale of competition from recruits on an older cohort in Atlantic salmon. *Oecologia* 167:1017–1025
- Elliott JM (1987) The distances traveled downstream-moving trout fry, *Salmo trutta*, in a Lake District stream. *Freshw Biol* 17:491–499

- Elliott JA (1994) Quantitative ecology and the brown trout. Oxford University Press, London
- Fogarty M, Rosenberg A, Sissenwine M (1992) Fisheries risk assessment sources of uncertainty: a case study of Georges Bank haddock. *Environ Sci Technol* 26:440–447
- Fox MG (1994) Growth, density, and interspecific influences on pumpkinseed sunfish life histories. *Ecology* 75:1157–1171
- Frank BM, Piccolo JJ, Baret PV (2011) A review of ecological models for brown trout: towards a new demogenetic model. *Ecol Freshw Fish* 20:167–198
- Fraser FJ (1969) Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. In: Northcote TG (ed) Symposium on salmon and trout in streams. University of British Columbia, Vancouver, pp 253–266
- Gee AL, Milner NJ, Hemsworth RJ (1978) The effect of density on mortality in juvenile Atlantic salmon (*Salmo salar*). *J Anim Ecol* 47:497–505
- Gerking SD (1959) The restricted movement of fish populations. *Biol Rev* 34:221–242
- Gibson AJF, Bowlby HD, Amiro PG (2008) Are wild populations ideally distributed? Variations in density-dependent habitat use by age class in juvenile Atlantic salmon (*Salmo salar*). *Can J Fish Aquat Sci* 65:1667–1680
- Gowan C, Young MK, Fausch KD, Riley SC (1994) Restricted movement in resident stream salmonids: a paradigm lost? *Can J Fish Aquat Sci* 51:2626–2637
- Grant JWA, Imre I (2005) Patterns of density-dependent growth in juvenile stream-dwelling salmonids. *J Fish Biol* 67:100–110
- Hartman GF, Scrivener JC (1990) Impacts of forestry practices on a coastal stream ecosystem, Carnation Creek, British Columbia (Canada). *Canadian Bulletin of Fisheries and Aquatic Sciences* No. 223
- Harvey BC, Nakamoto RJ (1996) Effects of steelhead density on growth of coho salmon in a small coastal California stream. *Trans Am Fish Soc* 125:237–243
- Hendry AP, Stearns SC (eds) (2004) Evolution illuminated: salmon and their relatives. Oxford University Press, Oxford
- Houde ED (1994) Differences between marine and freshwater fish larvae: implications for recruitment. *ICES J Mar Sci* 51:91–98
- Hutchings JA (1994) Age- and size-specific costs of reproduction within and among populations of brook trout, *Salvelinus fontinalis*. *Oikos* 70:12–20
- Hutchings JA (2003) Life histories of fish. In: Hart PJB, Reynolds JD (eds) Handbook of fish biology and fisheries Vol. 1. Fish biology. Blackwell Science, Oxford, pp 149–174
- Imre I, Grant JWA, Cunjack RA (2005) Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. *J Anim Ecol* 74:508–516
- Imre I, Grant JWA, Cunjak RA (2010) Density-dependent growth of young-of-the-year Atlantic salmon (*Salmo salar*) revisited. *Ecol Freshw Fish* 19:1–6
- Jenkins TM Jr, Diehl S, Kratz KW, Cooper SD (1999) Effects of population density on individual growth of brown trout in streams. *Ecology* 80:941–956
- Jespersen LB, Toft S (2003) Compensatory growth following early nutritional stress in the wolf spider *Pardosa prativaga*. *Funct Ecol* 17:737–746
- Johnsson JI, Bohlin T (2006) The cost of catching up: increased winter mortality following structural growth compensation in the wild. *P R Soc Lond B* 273:1281–1286
- Jonsson B, Jonsson N (2011) Ecology of Atlantic salmon and brown trout. Springer, Berlin
- Jonsson N, Jonsson B, Fleming IA (1996) Phenotypically plastic response of egg production to early growth in Atlantic salmon, *Salmo salar*. *Funct Ecol* 10:89–96
- Kaspersson R, Höjesjö J (2009) Density-dependent growth rate in an age-structured population: a field study on stream-dwelling brown trout *Salmo trutta*. *J Fish Biol* 74:2196–2215
- Keeley ER (2001) Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* 82:1247–1259
- Kendall BE, Fox GA (2002) Variation among individuals and reduced demographic stochasticity. *Conserv Biol* 16:109–116
- Kingsolver JG et al (2001) The strength of phenotypic selection in natural populations. *Am Nat* 157:245–261
- Klemetsen A, Amundsen P-A, Dempson JB, Jonsson B, Jonsson N, O'Connell MF, Mortensen E (2003) Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. *Ecol Freshw Fish* 12:1–59
- Kozłowski J (2006) Why life histories are diverse. *Pol J Ecol* 54:585–605
- Kvingedal E, Einum S (2011) Intracohort and intercohort spatial density dependence in juvenile brown trout (*Salmo trutta*). *Can J Fish Aquat Sci* 68:115–121
- Larsen KW, Boutin S (1994) Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. *Ecology* 75:214–223
- Leggett WC, DeBlois E (1994) Recruitment in marine fishes: is it regulated by starvation and predation in egg and larval stages. *Neth J Sea Res* 32:119–134
- Letcher BH, Terrick TD (1998) Maturation of male age-0 Atlantic salmon following a massive, localized flood. *J Fish Biol* 53:1243–1252
- Lindstrom J (1999) Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348
- Lobón-Cervia J (2000) Determinants of parr size variations within a population of brown trout *Salmo trutta* L. *Ecol Freshw Fish* 9:92–102
- Lobón-Cervia J (2005) Spatial and temporal variation in the influence of density dependence on growth of stream-living brown trout (*Salmo trutta*). *Can J Fish Aquat Sci* 62:1231–1242
- Lobón-Cervia J (2007) Density-dependent growth in stream-living Brown trout *Salmo trutta* L. *Funct Ecol* 21:117–124
- Lobón-Cervia J (2009) Why, when and how do fish populations decline, collapse and recover? The example of brown trout (*Salmo trutta*) in Rio Chaballos (northwestern Spain). *Freshw Biol* 54:1149–1162
- Lobón-Cervia J (2010) Density-dependence constrains mean growth rate while enhancing individual size variation in stream salmonids. *Oecologia* 164:109–115
- Lobón-Cervia J, Utrilla C, Rincon P, Amezcua F (1997) Environmentally induced spatio-temporal variations in the fecundity of brown trout *Salmo trutta* L.: trade-offs between egg size and number. *Freshw Biol* 38:277–288

- Lomnicki A (1988) Population ecology of individuals. Princeton University Press, Princeton
- Lorenzen K (2005) Population dynamics and potential of fisheries stock enhancement: practical theory for assessment and policy analysis. *Philos Trans R Soc B* 360:171–189
- Lorenzen K (2008) Fish population regulation beyond “stock and recruitment”: the role of density-dependent growth in the recruited stock. *Bull Mar Sci* 83:191–196
- Lorenzen K, Enberg K (2002) Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc R Soc Lond B* 269:49–54
- Ludwig D (1979) Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310
- Lytle DA, Poff NL (2004) Adaptation to natural flow regimes. *Trends Ecol Evol* 19:94–100
- Mangel M (1996) Computing expected reproductive success of female Atlantic salmon as a function of smolt size. *J Fish Biol* 49:877–882
- Mangel M, Abrahams M (2001) Age and longevity in fish, with consideration of the ferox trout. *Exp Gerontol* 36:765–790
- Martinussen P, Robertsen G, Einum S (2010) Density-dependent diet composition of juvenile Atlantic salmon (*Salmo salar*). *Ecol Freshw Fish*. doi: [10.1111/j.1600-0633.2010.00468.x](https://doi.org/10.1111/j.1600-0633.2010.00468.x)
- McCallum H (1994) Modelling translocation strategies for the bridled naitail wallaby *Onychogalea fraenata* Gould, 1840. In: Serena M (ed) Reintroduction biology of Australian and New Zealand fauna. Surrey Beatty, Sydney, pp 7–14
- McGurk MD (1996) Allometry of marine mortality of Pacific salmon. *Fish Bull* 94:77–88
- Metcalfe NB, Monaghan P (2001) Compensation for a bad start: grow now, pay later? *Trends Ecol Evol* 16:254–260
- Milner NJ et al (2003) The natural control of salmon and trout populations in streams. *Fish Res* 62:111–125
- Moore JW, McClure M, Rogers LA, Schindler DE (2010) Synchronization and portfolio performance of threatened salmon. *Conserv Lett* 3:340–348
- Morales J, Haydon D, Friar J, Holsinger K, Fryxell J (2004) Extracting more out of relocation data: building movement models as mixtures of random walks. *Ecology* 85:2436–2445
- Morrissey MB, Ferguson MM (2011) Individual variation in movement throughout the life cycle of a stream-dwelling salmonid fish. *Mol Ecol* 20:235–248
- Myers RA, Cadigan NG (1993) Density-dependent juvenile mortality in marine demersal fish. *Can J Fish Aquat Sci* 50:1576–1590
- Nakano S (1995) Competitive interactions for foraging microhabitats in a size-structured interspecific dominance hierarchy of two sympatric stream salmonids in a natural habitat. *Can J Zool* 73:1845–1854
- Newman RM (1993) A conceptual model for examining density dependence in the growth of stream trout. *Ecol Freshw Fish* 2:121–131
- Nordwall F, Naslund I, Degerman E (2001) Intercohort competition effects on survival, movement, and growth of brown trout (*Salmo trutta*) in Swedish streams. *Can J Fish Aquat Sci* 58:2298–2308
- Nylin S, Gotthard K (1998) Plasticity in life-history traits. *Annu Rev Entomol* 43:63–83
- Ojanguren AF, Reyes-Gavilán FG, Brana F (1996) Effects of egg size on offspring development and fitness in brown trout, *Salmo trutta* L. *Aquaculture* 147:9–20
- Ottaway EM, Forrest DR (1983) The influence of water velocity on the downstream movement of alevins and fry of brown trout, *Salmo trutta* L. *J Fish Biol* 23:221–227
- Parra I, Almodóvar A, Ayllón D, Nicola GG, Elvira B (2011) Ontogenetic variation in density-dependent growth of brown trout through habitat competition. *Freshw Biol* 56:530–540
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- Post DM, Kitchell JF, Hodgson JR (1998) Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. *Can J Fish Aquat Sci* 55:2588–2600
- Post JR, Parkinson EA, Johnston NT (1999) Density-dependent processes in structured fish populations: interaction strengths in whole-lake experiments. *Ecol Monogr* 69:155–175
- Rankin MA, Burchsted JCA (1992) The cost of migration in insects. *Annu Rev Entomol* 37:533–559
- Rodriguez MA (2002) Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology* 83:1–13
- Roff DA (1992) The evolution of life histories: theory and analysis. Chapman and Hall, New York
- Roghair CN, Dolloff CA, Underwood MK (2002) Response of a brook trout population and instream habitat to a catastrophic flood and debris flow. *Trans Am Fish Soc* 131:718–730
- Rollinson N, Hutchings JA (2010) Why does egg size increase with maternal size? Effects of egg size and egg density on offspring phenotypes in Atlantic salmon (*Salmo salar*). *Evol Ecol Res* 12:949–960
- Roni P, Quinn TP (2001) Density and size of juvenile salmonids in response to placement of large woody debris in western Oregon and Washington streams. *Can J Fish Aquat Sci* 58:282–292
- Rose KA et al (2001) Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish Fish* 2:293–327
- Rothschild BJ (1986) Dynamics of marine fish populations. Harvard University Press, Cambridge
- Rothschild BJ (2000) “Fish stocks and recruitment”: the past thirty years. *ICES J Mar Sci* 57:191–201
- Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M (2009) Steelhead life history on California’s central coast: insights from a state dependent model. *Trans Am Fish Soc* 138:532–548
- Satterthwaite WH, Beakes MP, Collins EM, Swank DR, Merz JE, Titus RG, Sogard SM, Mangel M (2010) State-dependent life history models in a changing (and regulated) environment: steelhead in the California Central Valley. *Evol App* 3:221–243
- Schlichting CD, Pigliucci M (1998) Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Sunderland
- Shepherd JG, Cushing DH (1990) Regulation in fish populations: myth or mirage? *Philos Trans R Soc B* 330:151–164

- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129–1157
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Stenseth NC, Chan KS, Tavecchia G, Coulson T, Mysterud A, Clutton-Brock T, Grenfell B (2004) Modelling nonadditive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proc R Soc Lond B* 271:1985–1993
- Strong DR (1986) Density-vague population change. *Trends Ecol Evol* 1:39–42
- Sundström LF, Löhmus M, Devlin RH (2005) Selection on increased intrinsic growth rates in coho salmon, *Oncorhynchus kisutch*. *Evolution* 59:1560–1569
- Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA (1998) Modelling the proximate basis of life history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol Ecol* 12:581–600
- Towns DR, Ferreira SM (2001) Conservation of New Zealand lizards (Lacertilia: Scincidae) by translocation of small populations. *Biol Conserv* 98:211–222
- Utz RM, Hartman KJ (2009) Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). *Can J Fish Aquat Sci* 66:1072–1080
- Vandenbos RE, Tonn WM, Boss SM (2006) Cascading life-history interactions: alternative density-dependent pathways drive recruitment dynamics in a freshwater fish. *Oecologia* 148:573–582
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2007a) Density-dependent individual growth of marble trout (*Salmo marmoratus*) in the Soca and Idrijca river basins, Slovenia. *Hydrobiologia* 583:57–68
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2007b) Early survival of marble trout *Salmo marmoratus*: evidence for density dependence? *Ecol Freshw Fish* 16:116–123
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2008a) The role of density-dependent individual growth in the persistence of freshwater salmonid populations. *Oecologia* 156:523–534
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2008b) Total population density during the first year of life as a major determinant of lifetime body length trajectory in marble trout. *Ecol Freshw Fish* 17:515–519
- Vincenzi S, Crivelli AJ, Jesensek D, Rubin J-F, Poizat G, De Leo GA (2008c) Potential factors controlling the population viability of newly introduced endangered marble trout populations. *Biol Conserv* 141:198–210
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2010a) Individual growth and its implications for the recruitment dynamics of stream-dwelling marble trout (*Salmo marmoratus*). *Ecol Freshw Fish* 19:477–486
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (2010b) Detection of density-dependent growth at two spatial scales in marble trout (*Salmo marmoratus*) populations. *Ecol Freshw Fish* 19:338–347
- Vincenzi S, Crivelli AJ, Jesensek D, De Leo GA (in press). Translocation of stream-dwelling salmonids in headwaters: insights from a 15-year reintroduction experience. *Rev Fish Biol Fish*
- Vollestad A, Olsen EM, Forseth T (2002) Growth rate variation in brown trout in small neighbouring streams: evidence for density-dependence? *J Fish Biol* 61:1513–1527
- Walters CJ, Juanes F (1993) Recruitment limitation as a consequence of natural selection for use of restricted feeding habitats and predation risk taking by juvenile fishes. *Can J Fish Aquat Sci* 50:2058–2070
- Walters CJ, Post JR (1993) Density-dependent growth and competitive asymmetries in size-structured fish populations: a theoretical model and recommendations for field experiments. *Trans Am Fish Soc* 122:34–45
- Ward BR, Slaney PA (1988) Life history and smolt-to-adult survival of Keogh River steelhead trout (*Salmo gairdneri*) and the relationship to smolt size. *Can J Fish Aquat Sci* 45:1110–1122
- Ward DL, Schultz AA, Matson PG (2003) Differences in swimming ability and behavior in response to high water velocities among native and nonnative fishes. *Environ Biol Fish* 68:87–92
- Ward DM, Nislow KH, Armstrong JD, Einum S, Folt CL (2007) Is the shape of the density–growth relationship for stream salmonids evidence for exploitative rather than interference competition? *J Anim Ecol* 76:135–138
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425
- Wilson AJ, Hutchings JA, Ferguson MM (2003) Selective and genetic constraints on the evolution of body size in a stream-dwelling salmonid fish. *J Evolution Biol* 16:584–594
- Wootton RJ (1998) Ecology of Teleost fishes, 2nd edn. Kluwer Academic, Dordrecht