SYNTHESIS

Adaptive landscapes and density-dependent selection in declining salmonid populations: going beyond numerical responses to human disturbance

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Abstract

Theory suggests an important role for population density in shaping adaptive landscapes through density-dependent selection. Here, we identify five methodological approaches for studying such selection, review the existing empirical evidence for it, and ask whether current declines in abundance can be expected to trigger evolutionary responses in salmonid fishes. Across taxa we find substantial amounts of evidence for population density influencing the location of adaptive peaks for a range of traits, and, in the presence of frequency dependence, changing the shape of selection (stabilizing versus disruptive). For salmonids, biological and theoretical considerations suggest that the optimal value of a number of traits associated with juvenile competitive ability (e.g. egg size, timing of emergence from nests, dominance ability), may depend on population density. For adults, more direct experimental and comparative evidence suggest that secondary sexual traits can be subject to density-dependent selection. There is also evidence that density affects the frequency-dependent selection likely responsible for the expression of alternative male reproductive phenotypes in salmon. Less is known however about the role of density in maintaining genetic variation among juveniles. Further efforts are required to elucidate the indirect evolutionary effects of declining population abundances, both in salmonids and in other anthropogenically challenged organisms.

Introduction

Anthropogenic disturbances of natural populations commonly entail a reduction in population abundance, and in this context salmonids are not an exception. Abundance declines can be ascribed to problems such as climate change, degradation of freshwater stream habitats, exploitation, water quality problems, dam construction and influences from the aquaculture industry. Ecologically, such reductions in abundance are worrying not only from the single-species perspective, but also due to the cascading effects through ecosystems (Wipfli et al. 1998; Helfield and Naiman 2001). Genetically, declines may lead to inbreeding and loss of genetic diversity (reviewed in Frankham et al. 2002). Additionally, gene flow from

neighbouring populations (Consuegra et al. 2005) or cultured fish (Fleming and Gross 1993; Fleming et al. 1997) may increase in reduced populations.

A less studied genetic effect of abundance declines is the potential for population density to influence adaptive landscapes. In an adaptive landscape, the surface elevation represents the mean fitness as a function of the characteristics of the population, and changes in the topography (e.g. peak movement) caused by changing densities are predicted to cause evolutionary responses in the population. The lack of empirical efforts to evaluate the potential for such effects of changing densities in salmonids is surprising, given the interest in salmonid population dynamics on the one hand (e.g. Elliott 1994; Jonsson et al. 1998; Einum et al. 2003) and the

potential for and importance of their adaptive genetic divergence on the other (reviewed in Garcia de Leaniz et al. 2007). Here, we review the theoretical and empirical advances that enable an understanding of links between population abundance and evolution, and evaluate the potential role of such links in salmonid contemporary evolution.

Density-dependent selection

Under density-dependent selection (DDS), conspecific density is an environmental variable which, similar to many other environmental variables, determines genotype-specific fitnesses. Early theory commonly considered a situation where events of high density-independent mortality, for example due to environmental seasonality, reduce population density (e.g. Pianka 1970; King and Anderson 1971; Roughgarden 1971). Alternatively, low density may occur initially following colonization of new habitats. If the fitness surface of a character changes with such changes in density, its evolutionary trajectory can be understood in the light of DDS theory.

r/K selection

Early attempts at understanding DDS distinguished between two types of selection, r-selection and K-selection (MacArthur and Wilson 1967). Different models of population dynamics can be applied, and here we use the one for logistic population growth with discrete generations. If the absolute fitness of the genotype A_iA_j, W_{ij}, is assumed to be equal to the realized per capita growth rate, it can be expressed as:

$$W_{ij} = 1 + r_{ij} - \frac{r_{ij}}{K_{ij}}N \qquad (1)$$

(Roughgarden 1971). Here, r_{ij} is the genotype's growth rate given no density dependence, K_{ij} is the genotype's carrying capacity and N is the total population size. The decrease in fitness with increasing N is given as r/K. Increasing the value of K for a given N always increases the fitness of the genotype. At population sizes below the carrying capacity ($N < K$), increasing r increases fitness. As the population reaches its carrying capacity ($N = K$), variation in r no longer influences fitness, and selection acts on K only (i.e. K-selection). Thus, K is viewed as not only a characteristic of the environment, but also as a parameter that varies among genotypes. Because of trade-offs between r and K (e.g. Mueller et al. 1991) an evolutionary increase in one is likely to be accompanied by a decrease in the other. The optimal values of r and K will then depend on the population dynamics experienced.

Early application of the above theory included verbal arguments for a priori categorization of life-history traits resulting from the two types of selection (Pianka 1970), and some naïve interpretations of comparative life-history data. Such studies spurred justified criticism (Stearns 1977; Boyce 1984; Mueller 1997). However, disagreements about the use and misuse of the theory should not be used to denounce the importance of DDS as a potential force in shaping life-histories. The introduction of r/K selection was an important contribution towards the development of a mathematically and empirically rigorous approach to studies of life-history evolution (reviewed by Reznick et al. 2002), and it sometimes serves well as a simplified model of density-dependent natural selection (Boyce 1984).

Adding realism to r/K selection

The model described above becomes problematic if competition is asymmetric. In a given resource-limited population, K will increase with decreasing per capita resource requirements. Thus, according to equation (1), one would predict resource requirements to evolve towards ever diminishing values when a population is kept at its carrying capacity. However, this reasoning ignores the possibility that a genotype can have a different competitive effect on itself than on others (i.e. asymmetric competition). Such effects can be studied using a DDS model expressing fitness as:

$$W_{ij} = 1 + r_{ij} - \sum_{k,l=1,2,\ldots,m} \alpha_{ijkl}N_{kl}. \qquad (2)$$

In this version of the model (e.g. Joshi et al. 2001), α_{ijkl} refers to the reduction in realized per capita growth rate of genotype A_iA_j due to the addition of one individual of genotype A_kA_l and N_{kl} is the number of individuals of genotype A_kA_l. This expression allows for genetic variation in competitive ability and decomposes it into two components; the effect of one's own genotype on itself (α_{ijij}) and the effect of other genotypes (α_{ijkl}). If competitive ability is constant (i.e. $\alpha_{ijij} = \alpha_{ijkl}$), α may be replaced by r/K, and hence equation (1) can be used to predict evolution of reduced resource requirements and increased equilibrium population size. However, in the presence of genetic variation in competitive ability, equation (2) is required to predict selection. Selection at high density will then not necessarily result in increased K; in fact if competitive ability and resource requirements are positively correlated, K will likely decrease. Thus, selection at high density is not synonymous with selection for large K, and depending on the biology of the focal organism, DDS may act in qualitatively different ways.

Similar to the trade-off between r and K, there may well be trade-offs between r and α. For example, high competitive ability may be linked with higher levels of steroid hormones, particularly during sexual selection, which may influence susceptibility to parasitism (Folstad and Karter 1992). Furthermore, fast growing genotypes may have higher competitive abilities due to their accumulating size advantage, but rapid growth may also entail costs such as increased susceptibility to low levels of oxygen (Sundt-Hansen et al. 2007) and increased levels of predation (Brodin and Johansson 2004). In the presence of such trade-offs, different genotypes may be optimal under different densities.

Using adaptive landscapes in a scenario for a colonizing population, we can visualize how density might influence selection on traits that influence r and α (Fig. 1A–C). During the initial period following colonization, the population experiences low density, and hence a high r (and low α) will be favoured. Thus, assuming that the founders originate from a population evolved under a higher density, there will be selection for increased r in the new environment (Fig. 1A). As the population grows, the benefits of competitiveness increase, and the adaptive peak shifts towards increasing values of α (Fig. 1B). When the population approaches its carrying capacity, selection becomes stabilizing due to costs of being overly competitive (e.g. injury, energy, time; Fig. 1C). As such, density-dependence can cause adaptive landscapes to become dynamic features that change through time with changing densities in otherwise constant environments.

Frequency dependence and maintenance of genetic variation

Up to this point we have considered how density may influence the location of a single peak (i.e. the optimum)
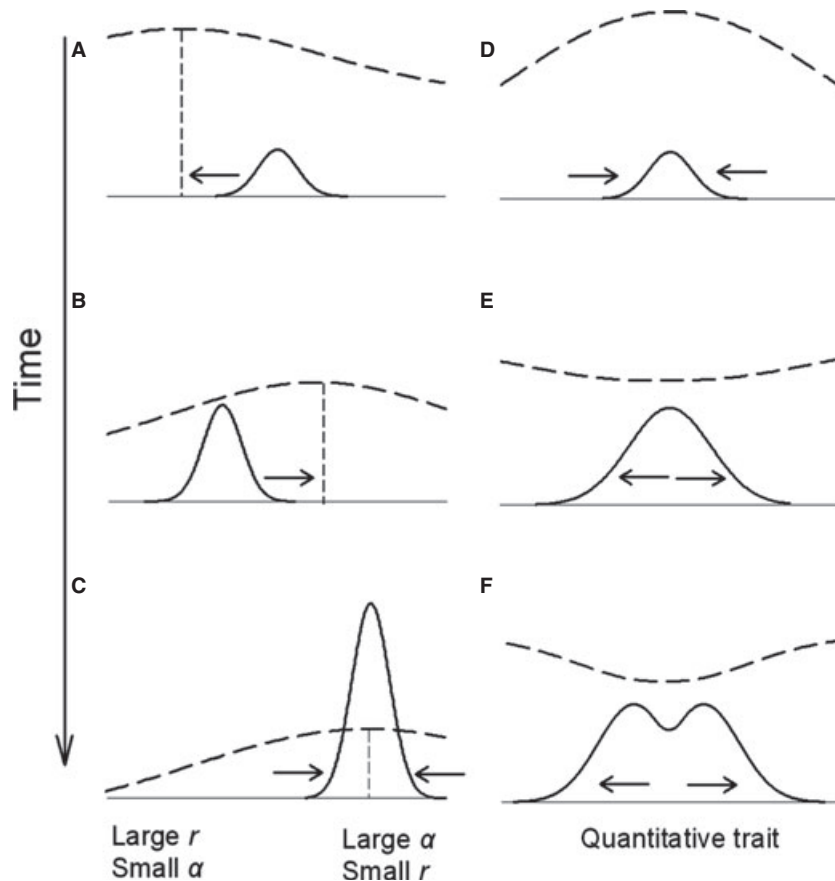

Figure 1 Frequency distributions of phenotypes (solid curves) responding to density-induced changes in the adaptive landscape (broken curves). Panels to the left represent development in a colonizing population through time (A–C). Selection goes from being directional during the period of population growth (A, B, selection towards optimum indicated by vertical broken lines) to becoming stabilizing at population carrying capacity. Panels to the right represent a situation where the adaptive landscape moves due to changes in the frequency distribution of different qualities of the limiting factor. As the population grows (D–F), the previously most common quality of the resource becomes depleted, and selection changes from being stabilizing (D) to becoming disruptive (E, F).

in an adaptive landscape. However, density effects may also influence the slopes of the landscape surrounding such a peak, or even cause a prior peak to become a depression. This occurs under frequency-dependent selection, when the fitness of a phenotype is dependent on its frequency relative to other phenotypes in the population. Because such effects are commonly caused by intraspecific interactions (i.e. competition), the effect of frequency-dependent selection will depend on population density (e.g. Fitzpatrick et al. 2007). For example, consider a situation where prey size in the absence of predators is continuously distributed, and its frequency distribution is curved with a single peak. Under low predator density, the prey size frequency distribution remains relatively unaffected, and this will lead to stabilizing selection to utilize the most abundant prey size (Fig. 1D). However, as population density increases, the previous peak in the frequency distribution of the resource may turn into a local minimum due to depletion (Fig. 1E). The resulting disruptive selection is expected to produce increased phenotypic variation through phenotypic plasticity, increased genetic variation, or both (reviewed by Rueffler et al. 2006). Under certain circumstances, such dynamics may lead to divergence of phenotypes into discrete morphs (Fig. 1F), and given sufficient assortative mating, even sympatric speciation (e.g. Dieckmann and Doebeli 1999). This mechanism is thus similar to the ecological character displacement occurring during adaptive radiation (Schluter 2000). Disruptive selection appears to be relatively common in natural populations (Kingsolver et al. 2001), and although other mechanisms may contribute (i.e. frequency-independent bimodal fitness functions), striking examples demonstrate the role frequency-dependent selection can play in maintenance of stable polymorphisms in natural populations [e.g. direction of mouth-opening in scale-eating cichlid fish (Hori 1993) and bill crossing in crossbill birds (Benkman 1996)].

Are fluctuating populations r-selected?

It may be argued that fluctuating populations are more likely to be r-selected than more stable populations that are constantly at, or near their carrying capacity. An implicit assumption in this argument is that the cause of reduced population abundance is density-independent mortality. An alternative cause for fluctuations in population size is fluctuations in the level of a limiting resource (Boyce and Daley 1980; Berryman 2004). For example, in salmonids, annual variation in juvenile production has been shown to be strongly influenced by water discharge (e.g. Jensen and Johnsen 1999) and water discharge is known to influence the amount of habitat suitable for the juveniles (Nislow et al. 2000). Thus, discharge may influ-

ence dynamics more indirectly through effects on carrying capacity than directly through density-independent mortality. In this case, mortality rates may depend on both the water discharge and initial abundance, and hence will be density dependent (Einum 2005). Although there may be selection for large r during the subsequent increase in abundance when environmental conditions have improved, selection for competitive ability may be intensified during years of unsuitable conditions. General predictions about selection in fluctuating versus stable populations should therefore be made cautiously.

Types of anthropogenic disturbance – does it matter?

Anthropogenic disturbances may cause a decrease in population abundance either indirectly following a reduction in limiting factors, or directly by reducing N through density-independent losses (see 'Are fluctuating populations r-selected?'). The distinction between these two types of disturbance can be illustrated if we modify equation (2):

$$W_{ij} = (1 - d)(1 + r_{ij} - \sum_{k,l=1,2,\ldots,m} \alpha_{ijkl}N_{kl}c). \qquad (3)$$

In this new version of the model, two new parameters are introduced to allow (i) for effects on fitness with changes in the number of individuals in the population to vary (c) and (ii) for density-independent nonselective reductions in fitness (d). For a given population, a reduction in a limiting factor will increase the degree to which adding individuals will reduce fitness, and hence it can be modelled by setting $c > 1$. Increasing the effect of adding individuals will reduce the equilibrium population abundance, but not the level of competition at this equilibrium, nor the optimal solution to the r/α trade-off (Fig. 2). For salmonids, examples of such disturbances may include flow depletions due to water removal, in-stream habitat degradation and competition from introduced species.

Extrinsic factors causing increased density-independent mortality (d) may maintain the population abundance below its carrying capacity over longer time periods. This has a more dramatic effect on DDS, because the selective advantage of being highly competitive is reduced. Imposing density-independent mortality may therefore cause a shift in the optimal genotype (Fig. 2). For salmonids, exploitation, pollution, pathogens/diseases and unsuitable oceanic conditions may represent the examples of such disturbances which nonselectively remove individuals from the population, but which indirectly may change the adaptive landscape due to a change in the level of competition.
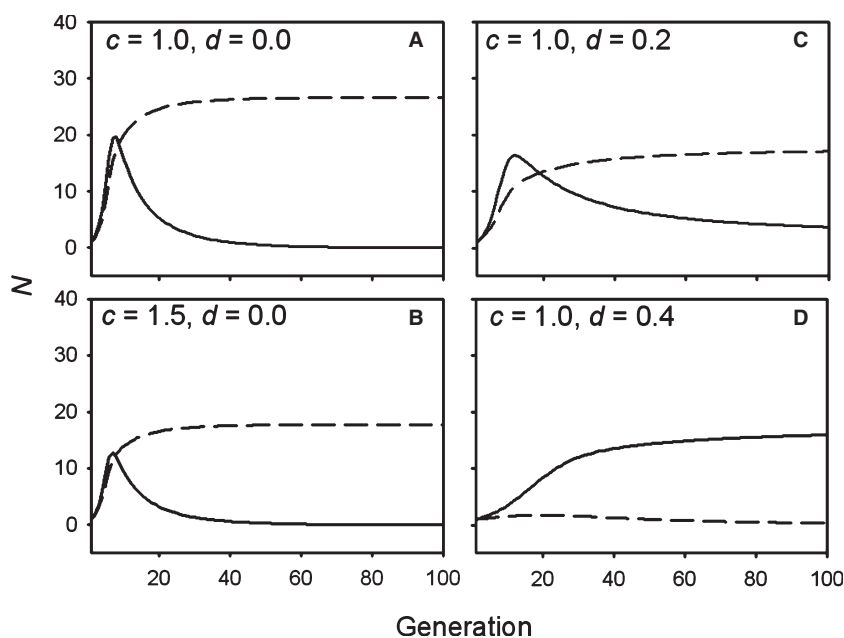
Figure 2 Population growth of genotypes A_iA_j (solid lines) and A_kA_l (dashed lines) according to equation (3) for different values of total resource abundance (c) and density-independent mortality (d). In this example, there is a trade-off between the genotype's rate of increase in absence of competition and its competitive ability, such that genotype A_iA_j has the highest r ($r_{ij} = 1$, $r_{kl} = 0.8$), but has a lower competitive ability than A_kA_l ($\alpha_{ijij} = 0.02$, $\alpha_{klij} = 0.01$, $\alpha_{klkl} = 0.03$, $\alpha_{ijkl} = 0.04$). At equilibrium in the absence of density-independent mortality, the genotype with superior competitive ability (A_kA_l) approaches fixation independent of c (A, B). In contrast, nonselective density-independent mortality may delay fixation or even cause a shift in the optimal genotype (C, D).

Does stage-structure have implications for DDS?

Above we considered anthropogenic changes in limiting factors [c in equation (3)] to have a low potential for causing evolutionary changes through DDS. However, this reasoning ignores potential effects of stage structure. Many organisms, including salmonids, have complex life cycles in which more or less distinct morphological, physiological and behavioural changes occur throughout ontogeny. An important property of such stage-structured populations is that reduced resources available for a given stage may influence the intensity of competition in another. This will be particularly relevant under situations of sequential density dependence (cf Åström et al. 1996). For example, if a salmonid population experiences density dependence both during breeding and the juvenile stage, a reduction in the amount of breeding habitat will cause intensified competition during breeding but relaxed competition for juveniles (Einum et al. 2008). Thus, the optimal solution to the α/r trade-off changes during both life stages. Stage-structured organisms such as salmonids may therefore be more likely to experience change in DDS due to anthropogenic disturbance than organisms without such structure.

Approaches to study DDS and empirical evidence

The theoretical advances made over the last decades have been accompanied by numerous studies providing empirical evidence for DDS in a wide variety of model organisms including bacteria, plants and animals, and by using a wide range of approaches. The majority of existing studies focus on the location of fitness peaks in relation to density, but an increasing amount of evidence suggests that density may also be important for the dynamics of genetic diversity (see Supplementary material). The studies illustrate the range of traits that can be expected to respond evolutionarily to changes in density, and also the variety of available empirical approaches, and in this context they represent an important contribution towards progress within this field for nonmodel organisms such as salmonids. Some organisms, such as *Drosophila* spp., have been utilized more extensively than others and provided large amounts of information on the process of DDS and its evolutionary implications. The various approaches that exist to study DDS can be divided into two main categories. The first one represents methods for direct observations of DDS within cohorts. Typically, one or

more measures of performance (e.g. growth, survival, fecundity) that can be assumed to be correlated with fitness are quantified across densities for different phenotypes and/or genotypes. This process-oriented approach is discussed below under the heading 'Density-dependent performance'. The second category represents methods for comparing evolutionary changes arising from DDS and is therefore to a larger extent pattern-oriented. We discuss these under the heading 'Density-dependent evolution'. Both categories contain observational and experimental approaches. Generally, observational studies do not attempt to manipulate density, and cause–effect relationships may not be easily determined. In experimental approaches, densities are manipulated and these are thus more likely to provide information on causal relationships.

Density-dependent performance: individual level

Density-dependent performance can be studied using individual level data on phenotypic traits and performance measures across densities. The direct forces of DDS on a trait can then be obtained by estimating selection gradients (relative fitness regressed on trait values) (Lande and Arnold 1983) at different population densities. In the absence of data on phenotypic traits, information on the potential for DDS to act in a population can be estimated by quantifying the opportunity for selection (variance in relative fitness, Arnold and Wade 1984) across densities.

Density-dependent performance of individuals has been studied observationally or experimentally, and over short or long terms. Short-term studies are often replicated spatially, whereas long-term studies are replicated temporally. One example of a study with both spatial and temporal replication is that by Conner (1989) who studied DDS on horn length in male *Bolitotherus cornutus* (fungus beetle) populations of naturally and experimentally varying densities. Males of this species have horns that vary greatly in length and are used in fights over females, where longer-horned males win the majority of contests. However, and perhaps contrary to *a priori* expectations, the relative success (measured as the observed access to females and overall insemination success) of longer-horned males decreased at high densities. It may be that long-horned males have to contend with each other more often at higher than lower densities, making female defence increasingly difficult, and providing easier access to fertilizations by shorter-horned males. In addition, male encounter rate is high even at 'low' density in this organism, such that absence of male–male competition is unlikely (Conner 1989). Indeed, selection intensity on male secondary sexual traits has been shown

to be positively correlated to population density in organisms where males rarely encounter each other at low density (e.g. Zeh 1987). Thus, even the qualitative evolutionary response to changes in density may to a large degree depend on the detailed biology of the focal organism.

Individual level approaches to studies of DDS can elucidate processes by which population dynamics influence patterns of selection. A remarkable amount of such information comes from the long-term observational studies by Clutton-Brock et al. on the unmanaged *Ovis aries* (Soay sheep) population of St Kilda. These studies suggest that selection on a large number of traits (e.g. coat colour, horn type, hindlimb length and body size) depend on temporally fluctuating densities (e.g. Milner et al. 1999; see Supplementary material for complete list). Another example of links between population dynamics and evolution has been demonstrated in *Uta stansburiana* (side-blotched lizard). Long-term experimental field studies in this species indicate that two different female colour morphs, which are genetically correlated to clutch size, egg size and immune function (Sinervo et al. 2000; Svensson et al. 2001), participate in an offspring quantity and quality game that generates cycles in density and morph frequency (Sinervo et al. 2000; Sinervo 2001). Orange-throated females, which produce large clutches and therefore are favoured at low density, can cause an overshoot of the carrying capacity within a single year. At the resulting high density, yellow-throated females, which produce fewer and larger offspring, will have an advantage. The high density, however, will induce a population crash, after which orange-throated females will again have an advantage (Sinervo et al. 2000). Thus, observations made in both these systems suggest that temporally varying densities may contribute to the maintenance of genetic variation within a population. Furthermore, the lizard studies suggest that not only can population dynamics influence evolution, but also that evolutionary changes can modify population dynamics.

Density-dependent performance: family level

The performance of families across differing densities is another approach to studying DDS experimentally or observationally. Individuals within families are usually more similar to each other than to individuals from other families in their population. One advantage of this method is that it is technically straight forward because the only prerequisite is that individuals can be assigned to families.

An experimental study of DDS at the family level was performed by Coman et al. (2004), who found differences

in family response to conspecific density in rearing tanks of juvenile *Penaeus japonicus* (Kuruma shrimp). Family growth rate was not consistent at high and low densities (i.e. families with fast growth at low density did not necessarily grow fast at high densities). This indicates that genotypes respond differently to varying population densities. Additional insights may be gained from such studies if phenotypic traits that vary among families are quantified. Such data may enable tests for associations between trait values and density-specific performance of the different families.

Density-dependent performance: population level

Density-dependent selection can also be studied by quantifying effects of density on fitness in populations of individuals with different genetic origins. Often such studies have compared different laboratory strains carrying different morphological markers. For example, different strains of *Musca domestica* (housefly) and *Tribolium castaneum* (flour beetle) seem to respond differently to larval competition (e.g. Sokal and Huber 1963; Bhalla and Sokal 1964; see Supplementary material for complete list). Considerable variation in fitness in response to crowding among various strains of *Drosophila* has also been found (e.g. Lewontin 1955; see Supplementary material). Such studies provide evidence that the fitness of different populations can respond differently to changes in population density. However, studies at the population-level can rarely provide information about the direct effect of specific traits involved.

Density-dependent evolution: comparative studies

One of the most straightforward methods to detect evolutionary trends is to compare life-history traits across species or among populations (Endler 1986). If life-history traits are found to correlate with population density, DDS can be proposed to explain some of the character variation. The effects of phenotypic plasticity and phylogenetic constraints must, however, be considered. An important shortcoming of these types of studies is that species/populations may differ with respect to environmental variables other than density in an unknown and uncontrolled fashion. Furthermore, the population densities observed today may not be correlated with the ones experienced in the past. Thus, as with other observational approaches, it does not allow for causal mechanisms to be identified (Endler 1986). However, strong inferences may be made if accompanying studies of a more mechanistic nature exist. For example, Tomkins and Brown (2004) studied frequency variation in forcep size dimorphism among populations of *Forficula auricularia* (European earwig),

and found that the proportion of males with long forceps increased with population density. Males with long forceps have been shown to have an advantage over those with short forceps when competing for females (Radesä-ther and Halldórsdóttir 1993). Thus, if competition for access to females is more intense at higher density, the advantage of elongate forceps is also expected to be greater, and this may explain the variation in frequencies observed (Tomkins and Brown 2004). Although indirect, this comparative study suggests that population density is a parameter influencing relative fitness of different phenotypes and driving local evolution of male dimorphism.

Density-dependent evolution: multiple generation selection studies

A large proportion of our empirical understanding of DDS comes from multiple generation selection experiments. This approach is appealing as it involves direct observations of evolutionary change occurring in a controlled environment. Model organisms with short generation times are typically required.

Selection studies on laboratory populations of *Drosophila melanogaster* kept at different densities for multiple generations have yielded considerable empirical evidence for DDS (reviewed in Joshi and Mueller 1996; Mueller 1997; Joshi et al. 2001). Some traits have evolved repeatedly in populations subjected to high density compared to control populations reared at low larval densities. The most important traits observed to evolve in a high-density environment are increased population growth rate when tested at high densities, and increased carrying capacity (K). These populations also show enhanced competitive abilities when competed against control strains at high, but not at low densities. In low-density environments, however, such populations have impaired growth rates compared to controls, supporting the notion of a trade-off between traits beneficial at high versus low density (Mueller et al. 1991). Other traits observed to evolve in response to density include larval feeding rate, pupation height, larval tolerance to metabolic waste, foraging path length and minimum food required for pupation (Supplementary material).

Studies in *Drosophila* have also indicated a potential role for population density in the evolution of niche width. Bolnick (2001) subjected populations to a spatially heterogenous distribution of toxic cadmium, and observed a more rapid adaptation to cadmium in high density populations than in low density ones. This supports predictions arising from frequency- and density-dependent competition. At low density, competition in cadmium-free patches is low and the relative fitness cost of reproducing in patches with cadmium is high.

However, at high density, this fitness cost is reduced due to high local competition in cadmium-free patches. Thus, studies using multiple generations of selection have repeatedly shown density to be a factor in evolution, not only determining the location of peaks, but also the steepness of surrounding adaptive landscapes.

Empirical evidence for DDS in salmonids

In the previous section, we reviewed the wide variety of organisms used in studies of DDS and the range of empirical approaches available. Yet, despite the extensive use of salmonids in empirical work on evolutionary biology (Hendry and Stearns 2004), the role of DDS has received little attention within this taxon. Only a few studies have addressed this issue explicitly but, together with more circumstantial evidence and detailed considerations of salmonid biology, it appears clear that DDS plays an important role in salmonid evolution.

Juveniles

For anadromous salmonid species that spend substantial amounts of their juvenile life in streams, both temporal (Elliott 1994; Jonsson et al. 1998) and spatial density dependence (Einum and Nislow 2005; Einum et al. 2006, 2008) are likely pronounced during this period. Furthermore, because they commonly defend feeding territories following emergence, traits that provide a competitive advantage during direct interactions will be important. In species that are born in or migrate to lakes and estuaries following emergence (e.g. sockeye salmon *Oncorhynchus nerka*, pink salmon *Oncorhynchus gorbuscha*, chum salmon *Oncorhynchus keta*), there may be a reduced potential for individuals to monopolize resources. For these species, competitive abilities may be related to the efficiency of exploiting resources when they become scarce at high densities. It is, however, less obvious which traits can influence r and α in opposite directions under such circumstances, and we therefore focus on traits of importance for stream-rearing species here.

Egg size is one obvious candidate trait for DDS (see Marshall et al. 2006 for an invertebrate example). Salmonid egg size has been shown to have a direct influence on size at emergence, juvenile growth rate and survival during competition (Hutchings 1991; Einum and Fleming 1999, 2000a; Einum 2003). Furthermore, under favourable growth conditions, and particularly in the absence of inter-phenotypic competition (i.e. when different egg sizes are reared separately), egg size effects are marginal or absent (Hutchings 1991; Einum and Fleming 1999). Selection on egg size is particularly interesting due to its trade-off with egg number. If the positive effect of larger

egg size on fitness is assumed to decrease with decreasing density [as in equation (2)], and there is a trade-off between egg size (and hence competitive ability) and egg number (and hence r), different egg size-number combinations will be optimal at different densities. However, it remains to be shown whether density *per se* influences the effect of egg size on fitness in salmonids.

Another trait of potential interest with respect to DDS is the timing of emergence from nests. Under competition, earlier emerging juveniles outperform later ones (Einum and Fleming 2000b). However, early emergence may also entail costs in terms of increased susceptibility to predation (Brännäs 1995) and possibly unsuitable environmental conditions. Thus, r may be maximized by emerging late (avoid unsuitable environmental conditions at low density), whereas competitive abilities may be maximized by emerging early (competitive advantage at high density).

Variation in levels of aggression and dominance ability has been linked to variation in innate metabolic rate, with dominant individuals being those with a high metabolic rate (Metcalfe et al. 1995; Yamamoto et al. 1998). The ability to dominate other individuals is beneficial for growth rates in competitive situations (Metcalfe et al. 1989, 1992), and hence at high densities, there should be selection for increased dominance abilities. However, in the absence of competition, this ability should be of less importance. Furthermore, traits associated with high dominance ability may be disadvantageous in the absence of competition, and may therefore reduce r (Vøllestad and Quinn 2003). The positive effect of both dominance and metabolic rate on growth is contradicted by several studies performed in semi-natural or natural streams (Höjesjö et al. 2002; Martin-Smith and Armstrong 2002; Harwood et al. 2003; Alvarez and Nicieza 2005). This loss of a correlation between dominance status or metabolic rate and growth rate indicates that a trait profitable in one environment could be neutral or negative in another. However, it remains to be tested whether different selection pressures in relation to population densities could be one parameter explaining these results.

The three traits identified above (egg size, emergence time and dominance ability) are among those few where empirical and theoretical considerations together enable predictions not only about the existence of DDS in juvenile salmonids, but also the direction of selection. A range of other morphological, behavioural and physiological traits may be speculated to be subject to DDS. It seems less clear whether a flattening of the adaptive landscape surrounding a peak can occur under high density in juvenile salmonids, i.e. whether frequency-dependent selection during juvenile life stages may play a role in trait evolution. For example, experimental evidence suggests that

the level of egg size heterogeneity within a population has no effect on the intensity of intraspecific competition in Atlantic salmon (Einum and Fleming 2004). Fish originating from different egg sizes appear to utilize identical or very similar resources, which would preclude high density to select for rare phenotypes (i.e. frequency dependence). On the other hand, Griffiths and Armstrong (2001) stocked different stream locations with either mixed family groups or full sibling groups, and found that the mixed groups outperformed the full sibling ones. Although circumstantial, this may indicate genetically based specialization, which would allow for a rare-phenotype advantage at high density. It is possible that frequency-dependent selection is more likely among salmonids relying on exploitative competition in lakes where resources are not defensible but can be depleted, and where sympatric divergence of morphs have been observed (Gislason et al. 1999).

Adults

There is no reason to expect competition for limited resources at reproduction (e.g. mates, territories, nest sites) to be fundamentally different from that at other life stages, and as such, DDS is likely to be important in shaping reproductive strategies. Density and its influence on sexual selection may even influence the potential for speciation; the sexual conflict during mating can cause a coevolution of male and female sexual traits, and the potential for a runaway coevolution may increase with increasing population density (Gavrilets 2000). Thus, high-density allopatric populations may have a higher potential to diverge in sexual traits, and hence become reproductively isolated from each other, than low-density populations. This prediction was recently supported in experiments with *Sepsis cynipsea* (dung fly, Martin and Hosken 2003).

In salmonid fishes, the operational sex ratio (i.e. the ratio of sexually receptive females to males) is commonly male biased, even when the ratio of returning adults to the spawning streams is female biased (Fleming and Reynolds 2004). This generates intense male–male competition for mating opportunities (e.g. Schroder 1982; Fleming and Gross 1994; Quinn 1999), and males in some salmonid fishes develop among the most elaborate secondary sexual traits seen in breeding fishes (Fleming and Reynolds 2004). Population density affects the operational sex ratio, becoming increasingly male biased with increasing density because of the asynchronous nature of spawning among females that is accentuated as access to breeding territories becomes limiting (Fleming and Gross 1994). Such changes in population density can thus alter the selective advantage of particular male traits, such as secondary sexual traits and body size that afford mating success.

Few studies have explicitly addressed the role of density in shaping the direction and strength of selection targeting male breeding traits in salmon. Seamons et al. (2007) found that although the opportunity for selection increased linearly with breeding density in *Oncorhynchus mykiss* (steelhead trout), selection on the two male traits examined, body size and arrival timing, was unaffected. Because success was estimated over the life time of the fish (i.e. from adult to adult), selection at other life history episodes may have masked or opposed that during breeding. To understand how changes in breeding density, independent of events during other periods of life, affect selection we need to focus on the specific life-history episode. In an experimental study of breeding success in the absence and presence of competition, as well as across three breeding densities, Fleming and Gross (1994) found that competition alone can generate a 52-fold increase in the opportunity for selection among male *Oncorhynchus kisutch* (coho salmon). The resultant sexual selection targeted two traits directly, body size and the size of the hooked snout, a specialized weapon for fighting that is perhaps equivalent to horns, antlers or tusks. Selection on body size shifted from exponential to linear to disruptive with increasing breeding density. At the lower densities, large males were clearly favoured and small males disfavoured, however, at the high density, it was the more intermediate-sized males that incurred the greatest selective disadvantage while the success of small males had improved markedly. Under high density conditions, small size and crypsis appear to afford male salmonids an alternative tactic for accessing ovipositing females that involves sneaking. It is likely that such frequency-dependent sexual selection, as affected by breeding density, has been responsible for the evolution of the alternative, early maturing 'jack' phenotype in coho salmon (Gross 1985, 1996) and other similar phenotypes observed commonly among male salmonids (Fleming 1998). Accordingly, Young (1999) observed that the proportion of early-maturing jack males among coho salmon populations increased with breeding density.

Among females, the opportunity for selection during reproduction appears to increase with breeding density in the two salmonid species where it has been examined (Fleming and Gross 1994; Seamons et al. 2007). Increasing competition for nest sites increases the probability of female displacement, nest superimposition and destruction by later spawning females, and delays in spawning that can reduce egg fertility and increase the likelihood of the retention of eggs unspawned (Quinn et al. 2007; reviewed in Fleming and Reynolds 2004). A comparison of the adult morphology of female coho salmon across populations found that the expression of two secondary sexual characters, hooked snout and breeding colouration,

was related to breeding density (Fleming and Gross 1989). It has been, however, much more difficult to detect evidence for breeding density shaping the direction or intensity of selection on female morphological traits, including body size (Fleming and Gross 1994; Seamons et al. 2007). Whether this has been a consequence of the restricted range of densities examined or masking by selection at other life-history episodes is unknown.

Selection on other female traits, particularly those likely to influence embryo and early offspring survival and performance (i.e. maternal effects), should also be expected to be shaped by breeding density. For example, timing of breeding is likely to influence the probability of nest destruction by later spawning females, which in turn may vary with breeding density (e.g. Hendry et al. 1999; Dickerson et al. 2005). In sockeye salmon, nest destruction is shown to cause strong selection for increased longevity (time from start of breeding until death) among early, but not late breeding females due to the benefits of prolonged nest guarding (Hendry et al. 2004). However, under low population density, and hence low risk of nest destruction, no such temporal trend in selection is predicted (Morbey and Ydenberg 2003). Thus, in this case density may influence the selection on the genetic covariance between arrival time and longevity.

Another density-dependent factor that can alter the shape of selection on both males and females during breeding is predation. Quinn et al. (2003) found that the number of salmon killed in the spawning streams by bears increased with salmon abundance, but at a declining rate and the proportion killed generally decreased. Moreover, bears selectively kill large salmon and males (Quinn 2005). Thus, the reduction in the intensity of sexual selection for large body size at low population densities will be compounded by proportionately greater size-selective mortality by bears.

Conclusions

There is currently a solid theoretical background for predicting evolutionary changes in populations as a response to changes in abundance. The introduction of the terms r- and K-selection, and later developments that include the competitive ability coefficient α, predicts that the location of peaks in the adaptive landscape depends on population density. In the presence of frequency-dependent selection, whereby rarer phenotypes gain an advantage, population density is also predicted to influence the shape of the landscape surrounding such peaks, and with increasing density stabilizing selection may turn into disruptive selection. A substantial amount of empirical evidence from across taxa suggests that DDS can play

an important role in evolution, and a range of methodological approaches are available to study the phenomenon. For salmonids, the extent of intraspecific competition during both juvenile and adult life stages, and its role in population regulation, suggests that competitive ability may well show evolutionary responses to changes in abundance. There is also evidence that density can affect frequency-dependent selection and the expression of alternative male reproductive phenotypes in salmon. Less, however, is known about the role of density in maintaining genetic variation among juveniles. Furthermore, due to their pronounced stage-structure, a change in resources available for one stage may influence the intensity of competition in another. Thus, both disturbances that act directly on mortality as well as those influencing limiting resources are in theory capable of causing evolutionary responses through DDS in salmonids. The pervasive extent of anthropogenic disturbance to salmonid abundances underlines the importance that DDS may have in contemporary evolution of their populations.

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Supplementary Material

The following supplementary material is available for this article online:

Table S1. Studies of density-dependent selection across taxa using different empirical approaches. The type of effect density has on the adaptive landscape is indicated (1 = shifting peak location, 2 = shape of landscape surrounding peak or valley, i.e. including disruptive selection).

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