

Maternal Fitness Consequences of Different Causative Agents of Offspring Mortality in  
Early Life

by

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For my parents, with thanks for all their support,  
and for Sam (who is entirely to blame).

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## **ABSTRACT**

Maternal effects can be key determinants of female fitness through their influence on early life survival. In salmonids, three main sources of mortality in early life can be attributed to redd superimposition, predation, and starvation (mediated by territory limitation). The influence of different agents of mortality will depend on maternal phenotype (e.g. body size) and within-season reproductive timing. An individual-based model, incorporating both stochastic and deterministic processes, was developed to assess how the relationships between maternal fitness, maternal phenotype (body size) and spawning timing were affected by these different sources of mortality. I found that maternal size influenced fitness under some, but not all circumstances. Larger size was beneficial when predation mortality was low, territories were limited, and/or spawner density was high. Spawning time also influenced maternal fitness; early spawned juveniles were favoured when territories were limited, whereas later spawned juveniles were favoured when predation mortality was high. Component Allee effects at low spawned densities were also detected in some simulations. These results suggest that the fitness consequences of maternal phenotype depend on the sources of mortality present. The fact that these context-dependent sources of offspring mortality in early life may vary between habitats or between years increases the difficulty in identifying the correlates of maternal fitness in salmonid fishes.

## **LIST OF ABBREVIATIONS USED**

IBM-individual based model

YOY-young-of-the-year

S-Spawner

R-Recruit

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## CHAPTER 1: INTRODUCTION

Fitness functions can be invaluable when addressing questions of fundamental importance in evolutionary and behavioral ecology. These descriptions of how fitness varies with a trait (Schluter 1988) or environmental feature (Pen et al. 1999) can reflect the selection pressures experienced by individuals within a population and provide information on the fitness value of a trait in a given environment (Schluter 1988). The shape, slope, and scatter of fitness functions provide information on the direction, type (Kelly and Levin 1997) and intensity of selection; for example, steep, tight, fitness functions imply strong selection with large consequences for individuals of inferior quality. Fitness functions can be modified by both abiotic and biotic conditions (Roff 2002, Einum et al. 2008), as well as by the phenotypes of the offspring. Traditionally, parental influence on offspring phenotype was considered to occur primarily via genetic inheritance, however it has become apparent that non-genetic mechanisms of inheritance can also be important (Bonduriansky and Day 2009). One kind of non-genetic inheritance, maternal effects, wherein maternal phenotype affects offspring phenotype in a manner not mediated by the offspring's maternally derived genes (Bernardo 1996), can also have important fitness repercussions (Mousseau and Fox 1998).

There are several means by which maternal effects can be manifested. They can influence maternal fitness directly, for example, through differential feeding of offspring (e.g. Couvillon and Dornhaus 2009). Indirect influences also occur, whereby different female phenotypes confer differences in the offspring's subsequent ability to fend for itself. Offspring production site can also be important in this respect (Bernardo 1996), given that females may choose to produce offspring in areas where there are higher resources (McLoughlin et al. 2008), lower predation or

reduced competition (Resetarits and Wilbur 1989). Maternal effects can be a consequence of both physical and behavioural maternal phenotypes (Mousseau and Fox 1998).

Much of the work on physically mediated maternal effects, with the exception of a limited number of studies on the role of maternal condition (e.g. Nazarova and Evsikov 2008), has been concerned with effects mediated by maternal size (Bernardo 1996). These effects include increased allocation of yolk antibodies by large females (Addison et al. 2009), increased size of eggs (see Kamler 2005 for an overview in fish) or increased size of offspring produced from large females (e.g. Monteith et al. 2009), and better chance of acquiring or defending higher quality territory by larger females (Foote 1990). Accordingly female size has been considered an especially important determinant of female fitness in fishes (Green 2008).

Salmonid fishes represent a good taxonomic group in which to study maternal effects because of the high variability in maternal fitness that exists in this taxonomic group (Taggart et al. 2001, Seamons et al. 2004, Anderson et al. 2010). Often the importance of maternal effects for survival of offspring are most influential in early life (Heath et al. 1999, Green 2008, Sman et al. 2009), and early life corresponds to a critical period during which high levels of mortality are experienced in salmonids (Elliott 1989, Einum and Fleming 2000). Through a variety of mechanisms, maternal size is expected to be a key determinant of female fitness (Table 1), with large size generally considered to be a positive correlate thereof (Holtby and Healey 1986, McPhee and Quinn 1998). There is, however, evidence that this trend is not ubiquitous (Holtby and Healey 1986, Table 1), and may be dependent on the stage at which juvenile survival is evaluated. Therefore, overall patterns need to be considered to obtain a fuller understanding of how female size influences fitness in salmonids (McPhee and Quinn 1998).

On average, in salmonids, female fecundity increases with female size (see summary in Hendry et al. 2001a). The fitness benefits associated with larger size are in excess of the benefit from fecundity alone (Anderson et al. 2010). Another mechanism providing fitness benefits with female size is the positive correlation between egg size and female size (Hendry et al. 2001a). Female size is also important during spawning. Prior to spawning, females excavate the bottom substrate to create a redd, or egg nest (Burner 1951): eggs are laid in this depression and covered with gravel after fertilization (Quinn 2005). In many semelparous salmonids, redd sites are guarded after spawning to prevent later-spawning females from constructing redds in the same area (Quinn 2005). Reuse of redd sites can lead to superimposition, i.e. the partial or complete destruction of the initial female's eggs during redd construction by the subsequent female (McNeil 1964).

The empirical evidence is mixed as to whether female size confers an advantage on the spawning grounds during redd site acquisition and post-spawning redd defense: larger females are generally considered to acquire better quality sites, and to be better at defending these sites (van den Berghe and Gross 1989) through dominance over smaller females (Foote 1990). However, studies in sockeye salmon (*Oncorhynchus nerka*) have found that larger females may not acquire better quality redd sites (Hendry et al. 2001b), and have, at best, a small advantage in terms of redd defense duration or level of aggression (McPhee and Quinn 1998). Unguarded redds are at risk of superimposition from subsequent females reusing redd sites: even in species exhibiting redd defense, female death prior to the end of the spawning season means that redds are usually left unguarded for some period of time during the spawning season (McPhee and Quinn 1998). Redd site reuse is frequent (Hayes 1987, Blanchfield and Ridgway 1997, Essington et al. 1998). Deep redds may be protected from superimposition if a subsequent female digs to a

shallower depth (Weeber et al. 2010) which confers an advantage to larger females which dig deeper (Ottaway et al. 1981, van den Berghe and Gross 1984, Crisp and Carling 1989, Steen and Quinn 1999, Edo et al. 2000). Superimposition can have a large detrimental effect on offspring production (McNeil 1964).

The fitness costs associated with redd superimposition for egg survival makes it of considerable interest within an adaptive framework. Thus, my first objective is to construct fitness functions between body size and number of offspring, given the egg mortality that can be caused by redd superimposition.

There are a number of sources of mortality during the egg stage. Studies have shown survival to be higher in eggs from both larger females (Montgomery et al. 1996, DeVries 1997), and eggs from smaller females (Beacham and Murray 1985), or for there to be an inconsistent effect with female body size (Holtby and Healey 1986). Once juveniles emerge from the gravel, there are two primary sources of mortality: predation (Henderson and Letcher 2003) and starvation (Elliott 1984, Keeley 2001). Maternal effects mediated by female size have the potential to affect both of these factors. Juveniles from larger eggs often experience higher survival early in life (Bagenal 1969, Einum and Fleming 1999, Heath et al. 1999) because of either increased time to starvation of larger juveniles (Elliott 1984, Miller et al. 1988) or reduced predation risk for larger juveniles (West and Larkin 1987, Sogard 1997), although the benefits of larger size may not be consistent between years (Good et al. 2001) or across habitats (Bailey and Kinnison 2010). It is not clear how much of a size difference is necessary to cause an appreciable difference in survival probabilities for fish of roughly similar size. Predators may not show a size preference between conspecifics from the same spawning period (Fresh and Schroder 1987, Reinhardt et al. 2001).



My second objective is to explore how the fitness functions driven by redd superimposition and female fecundity generated in the first objective vary with changes to starvation and predation mortality of offspring in early life.

In addition to those mediated by physical phenotype, maternal effects can be generated by behaviour (Mousseau and Fox 1998). Behavioural phenotypes which can mediate maternal effects include choice of offspring production site (Resetarits Jr and Wilbur 1989, Bernardo 1996, Green 2008, McLoughlin et al. 2008), level of care (Bernardo 1996, Couvillon and Dornhaus 2009), maternal rank (hyenas: Dloniak et al. 2006, Watts et al. 2009; ungulates: Guilhem et al. 2002, Dusek et al. 2007; primates: Holekamp and Smale 1991, Kutsukake 2000), and within-breeding season timing of offspring production (Bernardo 1996).

Within-breeding season timing of offspring production, which has been investigated in a variety of taxa, can have effects on both size and survival of offspring (e.g. Einum and Fleming 2000). Timing of reproduction can affect body size through increased time for feeding or growth (birds: Cooke et al. 1984; fish: Cargnelli and Gross 1996, Saito and Nakano 1999, Einum and Fleming 2000; insects: Landa 1992, mammals: Armitage et al. 1976, Pilastro et al. 1994, Rieger 1996, Rödel et al. 2004, Feder et al. 2008, Barber-Meyer et al. 2009, Barber-Meyer et al. 2009; reptiles: Bauwens and Verheyen 1985). Faster growth is also possible when the timing of offspring production coincides with a peak in resource quantity or quality (fish: Wright and Bailey 1996, Reznick et al. 2006; mammals: Green and Rothstein 1993, Réale and Boussès 1999, Côté and Festa-Bianchet 2001), or due to production at temperatures which allow for higher growth (fish: Crecco and Savoy 1985). Timing of reproduction does not always, however, affect size of offspring (Boltnev and York 2001, Skibieli et al. 2009).

Differences in size or condition of offspring born at different times can affect offspring survival (fish: Henderson et al. 1988, Cargnelli and Gross 1996, Slater et al. 2007; insects: Landa 1992; mammals: Armitage et al. 1976, Cooke et al. 1984, Harris et al. 1992, Rieger 1996, Rödel et al. 2004, Feder et al. 2008; reptiles: Civantos et al. 1999). Timing of offspring production can more directly impact survival through factors such as predator dilution (birds: Patterson 1965, Robertson 1973, Emlen and Demong 1975, Findlay and Cooke 1982, Hatchwell 1991, Grand and Flint 1996, Götmark 2002; fish: Narimatsu and Munehara 1999, Pine et al. 2000; insects: Sweeney and Vannote 1982, Williams et al. 1993; mammals: Estes 1976, Rutberg 1987, Whittaker and Lindzey 1999, Testa et al. 2000, Gregg et al. 2001, Jarnemo et al. 2004, Barber-Meyer et al. 2009), starvation risk (fish: Crecco and Savoy 1985, Schultz 1993, Reznick et al. 2006; mammals: Watts 1969, Halle 1993, O'Donoghue and Boutin 1995, Boltnev et al. 1998, Gillis 1998, Réale et al. 2003, Kraus et al. 2005, Reading et al. 2009), and competitive ability (birds: Verhulst et al. 1995, Svensson 1997). The effect of timing on offspring quality may be confounded if different quality females breed at different times (Price et al. 1988, Verhulst et al. 1995, Lomas and Bender 2007). Some studies have reported no effect of timing of reproduction on offspring survival (Bowyer et al. 1998, Côté and Festa-Bianchet 2001, Franken and Hik 2004, Chilvers et al. 2007, Kaplan et al. 2008).

In salmonids, timing of reproduction can have important fitness repercussions (Metcalf and Thorpe 1992, Einum and Fleming 2000,) which can interact with the fitness repercussions of female size (Fleming and Reynolds 2004). Risk of redd superimposition mortality is higher the longer a redd is undefended on the spawning ground. As a consequence, later spawners are expected to lose fewer eggs to superimposition than earlier spawners (McNeil 1964, McPhee and Quinn 1998). Size and timing may also interact with one another such that small females may be

forced to spawn relatively late to avoid superimposition, whereas larger females may be able to avoid superimposition, even if they spawn early, because of the deeper depths at which they are able to bury their eggs (Taniguchi et al. 2000, Nomoto et al. 2010, Weeber et al. 2010).

Timing of reproduction is also important for post-emergence survival (Einum and Fleming 2000). In salmonids, one important component regulating starvation mortality is territory acquisition (Elliott 1984). Juveniles that do not acquire territories fail to feed, move downstream and starve (Elliott 1986), or feed at low rates (Puckett and Dill 1985, Nakano 1995, Huntingford and Garcia de Leaniz 1997, Cutts et al. 1999a, O'Connor et al. 2000, Harwood et al. 2003). In juvenile salmonids, territory acquisition occurs primarily through the prior residence effect whereby the first fish to acquire a territory maintains itself on that territory (Huntingford and Garcia de Leaniz 1997, Cutts et al. 1999b Harwood et al. 2003), provided the fish are similar in size (Cutts et al. 1999a). Because of this, earlier-produced juveniles have a higher chance of acquiring a territory and, therefore, of surviving in the absence of other mortality sources (Brännäs 1995).

Predation mortality is also expected to be affected by offspring emergence time from the redds (Brännäs 1995). All else being equal, early emergers experience longer periods of time under predation. Additionally the saturating functional feeding responses of predators on juvenile salmonids (Fresh and Schroder 1987, Petersen and DeAngelis 1992) means that individuals in populations of smaller size experience higher per capita predation rates (Daan and Tinbergen 1979, Foster and Treherne 1981, Liermann 2001). Earlier emerging juveniles are likely to experience higher per capita predation rates because these juveniles emerge when the population is smaller in abundance. However, early emergent fish on any given day are, on average, larger than later emergers (Svärdson 1948, Einum and Fleming 2000, Seamons et al. 2004) and,

therefore, would be expected to have a lower chance of being preyed upon at any given time given the existence of size-dependent predation.

There is evidence of early-, intermediate- and late-produced juveniles being favoured in different studies (Table 2). In salmonids, the effect of size is not variable – early-emerging juveniles are larger than their later-emerging conspecifics (Einum and Fleming 2000, Seamons et al. 2004, Einum et al. 2006). In terms of survival of juveniles as a function of offspring production time, the effect is context dependent (Table 2). Anderson et al. (2010) found that early breeders were favoured in the first year of colonizing a new stretch of river, when spawning population size was small, but in subsequent years selection on timing was stabilizing. Seamons et al. (2004) found no effect of breeding time on survival of offspring in their first year. In a single-year study, (Einum and Fleming 2000) found that early emerging juveniles were favoured. Brännäs (1995) reported that earlier emerging juveniles experienced higher survival when predators were absent, whereas later-emerging juveniles had higher survival when predators were present.

My third objective is to construct fitness functions between timing of reproduction and number of offspring, and to explore how these fitness functions are affected by changes with in both the starvation and predation mortality experienced by juveniles.

Table 1- Summary of female size-fitness relationships for salmonids.

Female size fitness relationship	Species	Source
Larger females have higher fecundity	Atlantic salmon Brown trout Chinook salmon Coho salmon  Pink salmon White spotted charr Salmonids	Jonsson et al. (1996) Jonsson and Jonsson (1999) Quinn and Bloomberg (1992) van den Berghe and Gross (1989) Fleming and Gross (1994) Holtby and Healey (1986) Dickerson et al. (2002) Morita et al. (2002)  See summary in Hendry et al. (2001a)
Larger females more dominant in competition	Sockeye salmon	Foote (1990)
Larger females get access to better quality redd sites	Coho salmon	van den Berghe and Gross (1989)
Larger females do not acquire better quality redd sites	Sockeye salmon	Hendry et al. (2001b)
Larger females are better able to defend redds	Coho salmon	van den Berghe (1989)
Weak or no advantage of larger size for redd defense duration or aggression	Sockeye salmon	McPhee and Quinn (1998)
Larger females dig deeper redds	Atlantic salmon Brown trout  Coho salmon Sakhalin taimen Salmonids	Crisp and Carling (1989) Crisp and Carling (1989) Ottaway et al. (1981) van den Berghe and Gross (1984) Edo et al. (2000) See review in Steen and Quinn (1999)
Deeper redds are less likely to be destroyed by scour	Chum salmon Salmonids	Montgomery et al. (1996) DeVries (1997)

Female size fitness relationship	Species	Source
Larger females have larger eggs/larger offspring	Atlantic salmon Brook charr Brown trout Chinook salmon Chum salmon Coho salmon Sockeye salmon White spotted charr Salmonids	Berg et al. (2001) Perry et al. (2004) Elliott (1984) Quinn and Bloomberg (1992) Beacham and Murray (1985) Holtby and Healey (1986) Nadeau et al. (2009) Morita and Yokota (2002)  See summary in Hendry et al. (2001a)
Smaller females have higher egg survival	Chum salmon	Beacham and Murray (1985)
No consistent benefit of female size for egg survival	Coho salmon	Holtby and Healey (1986)
No effect of female size on egg survival	Brown trout (eggs in high O <sub>2</sub> environments)	Einum et al. (2002)
Larger eggs/ larger offspring have higher survival	Chinook salmon Brown trout  (eggs in low O <sub>2</sub> environments)	Heath et al. (1999) Bagenal (1969) Elliott (1984) Einum and Fleming (1999) Einum et al. (2002)
Variable effect of offspring size on survival	Atlantic salmon	Good et al. (2001) Bailey and Kinnison (2010)
Larger females have more surviving offspring	Coho salmon YOY rainbow trout	Anderson et al. (2010) Seamons et al. (2004)

Table 2- Summary of suggestions and evidence on effects of spawning time for post-emergent juvenile salmonid success

	Early	Intermediate	Late
Survival	<p>Earlier had higher survival (Einum and Fleming 2000)</p> <p>Early emergers had best survival in the absence of predators (Brännäs 1995)</p> <p>Early breeders had higher fitness in 1 study year (Anderson et al. 2010)</p>	<p>Stabilizing selection on breeding time in 2 study years (Anderson et al. 2010)</p> <p>No effect of breeding time on survival after 1 year (Seamons et al. 2004)</p>	<p>Late emergers had best survival in the presence of predators (Brännäs 1995)</p>
Size	<p>Earlier emergers larger (Seamons et al. 2004, Einum and Fleming 2000, Einum et al. 2006)</p>		

## CHAPTER 2: METHODS

Individual-based models (IBMs) follow every individual of interest in a simulated population, and therefore allow for modeling of how individual traits interact among individuals and with the environment in a direct manner (Huston et al. 1988).

Additionally individual-based models are useful when stochastic processes at the individual level are deemed important (Neuheimer et al. 2009). In general, IBMs often allow for more biologically reasonable assumptions than coarser scale models (Huston et al. 1988) by allowing for modeling at the individual scale instead of relying on population averages (Crowder et al. 1992). IBMs are ideally suited to model the complexities of the interactions between female body size and timing of maternal effects in salmonids, and the importance of stochasticity in predation risk, because they allow for the combination of multiple processes to influence each offspring of each female in the simulation in an individually appropriate manner. Additionally, this method allows for each individual to have mortality risks set individually and to be changed according to an individual's trait, such as body size or age.

### *I. Model Set-up*

#### *I. Overview*

I used an individual-based model (IBM) with a combination of deterministic and stochastic elements to address both individual-level variability and population-level processes (Figure 1). As much as possible, parameterization of the model was empirically grounded in literature on Atlantic salmon (*Salmo salar*). When data on Atlantic salmon were not available, I relied on data for other salmonid species. The model follows a population of offspring from egg deposition until 30 days post-emergence (and first



exogenous feeding) of the youngest individual (Figure 1). The mortality structure for this model was loosely based on the IBM of Neuheimer et al. (2009). The three sources of mortality are redd superimposition, starvation by individuals following the initiation of exogenous feeding (mediated by territory availability), and predation of individuals (mediated by population size and individual length).

## *2. Spawning*

### *a. Generating the spawning population*

The spawning population is described by three attributes: spawner density; the distribution of spawner body sizes; and the distribution of female spawning dates. The range of spawner densities used (Table 3) was based on the reported range of spawner densities found in the literature for which superimposition values were available (Figure 2).

The remaining two attributes of the spawning populations are body length and spawning date. These attributes are used to determine individual characteristics of the females in any given simulation. Given that the number of females on the spawning ground over time typically follows a humped distribution (Blanchfield and Ridgway 1997, Hendry et al. 1999), I assumed that the distribution of spawning dates would follow a normal frequency distribution. This normal distribution was established in such a way that all females spawned within a 2-week period (mean=7 days, standard deviation=2 days). Each individual female's spawn date was randomly chosen from this normal distribution.

Previous models of spawning population length-frequency distribution have incorporated the assumption that this variable is normally distributed within a population

(Grover 2005). Additionally, there tends to be a negative correlation between female size and spawning ground arrival or spawning time (Elliott 1984, Elliott and Hurley 1998, Hendry et al. 1999, Quinn et al. 2006) of -0.1 (Doctor and Quinn 2009; although van den Berghe and Gross 1989 reported no evidence of delay in spawning time by small females). Length for each female in the spawning population is assigned as:

$$\Phi = -3 * \zeta + \bar{x} + \sigma * \nu \quad , \quad (1)$$

where  $\Phi$  is the maternal body length in mm, and  $\zeta$  is the randomly chosen spawning date for that female.  $\bar{x}$  and  $\sigma$  are the mean and standard deviation of a normal distribution from which the random number  $\nu$  is drawn. The parameters for the normal distribution used for assigning female length ( $\bar{x}=700$  mm,  $\sigma=50$  mm) were based on data from (Fleming 1996).

Using (1), length distributions for populations comprising a density of 0.44 females/100 m<sup>2</sup> were drawn 1000 times. This yielded an average correlation between female size and spawning date of -0.1. Any given set of random numbers used in simulations was checked to ensure that this correlation was  $-0.1 \pm 0.05$  for a population of 0.44 females/100 m<sup>2</sup> or higher.

#### *b. Egg production*

In the model, each female spawns once on her assigned spawn date. Egg size is assumed to vary with female size, according to the relationship constructed by Beacham and Murray (1985) for chum salmon (*O. keta*):

$$\Psi = 20.62 + 0.56 * \Phi \quad , \quad (2)$$

where  $\Psi$  is the mass of the eggs in mg.

Female fecundity is also assumed to increase with maternal size, based on a relationship for Atlantic salmon (Einum et al. 2004):

$$\gamma = 2.03 * \Phi \quad , \quad (3)$$

where  $\gamma$  is female fecundity in units of number of eggs produced.

### *c. Superimposition*

#### *i. Modelling superimposition*

On her spawning date, each female is randomly assigned to one of a limited number of redd sites. The potential for redd superimposition in the model occurs if a new redd is assigned to an already occupied spawning site. Redd site reuse did not automatically mean that superimposition occurred because nest depth is positively associated with female size. Therefore, if the subsequent spawner is much smaller than the previous spawner, no egg loss will occur (Ottaway et al. 1981, van den Berghe and Gross 1984, Crisp and Carling 1989, Steen and Quinn 1999, Edo et al. 2000). In the wild, complete egg loss due to redd superimposition does not always occur; partial superimposition is possible (Hayes 1987, Taggart et al. 2001). To account for such partial superimposition events, I assumed that egg mortality resulting from superimposition increased with the ratio in body size between the later spawning female and that of the earlier spawning female. Thus, the proportion of eggs lost to superimposition was assumed to depend primarily on the ratio of the body size of the later spawning female with that of the earlier spawning female. This relationship was assumed to be sigmoidal (Figure 3). To parameterize this function, I used Essington et al.'s (1998) estimate that, on average, 34% of brown trout (*S. trutta*) redds experience superimposition (there is very limited information on superimposition rates in the wild, but see Figure 2). I used

this average because it represented superimposition over a wider range of spawner densities than those considered in other papers. On average, when generating all possible ratios from female pairs for multiple simulations of the spawner population (at a density of 0.44 spawners/100m<sup>2</sup>), 34% of female pairs had a ratio greater than 1.07. I therefore parameterized the superimposition function such that there was a 50% egg loss at a ratio of female sizes of 1.07. Under this formulation, there is some loss of eggs even when the second female is slightly smaller than the previous one because disturbed depth by female digging exceeds burial depth (Steen and Quinn 1999). The formula for superimposition is:

$$\Gamma = \frac{1}{1 + e^{\eta - 1.07}} \quad , \quad (4)$$

where  $\Gamma$  is the proportion of eggs lost to superimposition and  $\eta$  is the ratio in body size between the second female and the initial female. A redd in the model is considered to have been superimposed if there is any mortality of eggs in that redd attributable to redd site reuse. Individuals develop (i.e. increase in age) during the egg stage until they attain the specified age at emergence.

#### *ii. Relationship between superimposition and spawner density*

The number of redd sites utilized by females is often quite limited (Hayes 1987, Blanchfield and Ridgway 1997, Essington et al. 1998). Egg loss from superimposition increases with female density (McNeil 1964), although Essington et al. (1998) found no relationship between spawner density and superimposition. In order to assess the relationship between spawner density and superimposition, and to determine reasonable ranges of spawner densities, I consulted papers which reported both level of redd superimposition and female density in the field. My criteria for these papers were that

they had to provide information on number of females, an estimate of overall study area (e.g. length and width of study site), and observed levels of superimposition. The studies which met these criteria were then used to perform a logistic regression to determine the relationship between percent of redds which were superimposed and spawner density (5 studies: see Figure 2). Percent superimposition was significantly related to redd density ( $p < 0.05$ ), based on the fit of a logistic regression.

Model outputs for percent of redds experiencing superimposition across a range of densities were generated and compared to the fitted line. Neither an assumption about preferred redd sites nor constant number of spawning sites nor a linear relationship between number of redds and female density resulted in a pattern of percent redd superimposition that mirrored the one from the literature. However, a function which generally gave a close match between the observed and model superimposition levels was:

$$\kappa = 0.0015 * \varphi^2 + 1.31 * \varphi + 17.35 \quad , \quad (5)$$

where  $\kappa$  is the number of available redd sites to which spawning females are randomly assigned, and  $\varphi$  is the number of females in the spawning population (ranging from 20-640 females). This formula was used to generate number of redd sites for subsequent simulations.

### *iii. Potential sources of egg mortality not included in the model*

Redd superimposition was assumed to be the only source of egg mortality. This simplifying assumption ignores other potential sources of mortality during the egg stage. For some post-spawning sources of egg mortality, maternal size may influence the risk of

mortality. Between egg production and emergence movement of gravel, scour, can have a large impact on fry survival (Holtby and Healey 1986, Scrivener and Brownlee 1989). Increased maternal size is expected to provide an advantage during scour events, because deeper redds are more likely to be below the scour depth (Montgomery et al. 1996, DeVries 1997). Winter temperature regime is also an important determinant of embryo survival (Chadwick 1982). Although inadequate oxygen leads to egg mortality (Turnpenny and Williams 1980, Ingendahl 2001), the evidence as to whether this effect is size-dependent is equivocal (e.g. Einum et al. 2002, Rombough 2007). Overall, egg survival has been shown to be higher amongst the offspring of smaller females (Beacham and Murray 1985), or to have an inconsistent effect with maternal body size (Holtby and Healey 1986). These other potential mortality sources were not included in the model because they are either poorly understood or they vary from year to year (e.g. scour Lapointe et al. 2000) instead of within years and are, therefore, not suitable to include in a model tailored to the effects of within-breeding season maternal effects.

### *3. Individual Random Events*

IBMs allow for individual, random events, whereby individuals undergo a state change based on their traits or environment (e.g. Neuheimer et al. 2009). State changes which may be of interest include developmental stage (e.g. Gentleman et al. 2008), location (e.g. Batchelder and Williams 1995), territoriality (e.g. Tyler and Rutherford 2007), mortality (e.g. Höök et al. 2008), reproductive state and reproductive mode (e.g. Zadereev et al. 2003). IBMs need to select  $x$  individuals from the population to undergo state changes, where  $x$  is the number of individuals in the population that will undergo a state change. Because each individual is accounted for in an IBM, the model requires one

to specify which individuals will undergo the state change. There are two methods commonly used to determine which individuals are chosen for this state change. The first approach incorporates the assumption that the identity of individuals which undergo the state change is completely random:  $x$  individuals are randomly selected either from the total population or from a subset of the population, such as from a single age cohort (Neuheimer et al. 2009). The second method is to rank individuals based on some metric of fitness (e.g. size, age), and to have  $x$  individuals with the lowest or highest trait values undergo the state change (Neuheimer et al. 2009). The former method assumes inherent stochasticity in the process, while the latter assumes that the relevant trait is the key driver in the process.

Commonly, the theoretical basis behind these state changes rests on not just one but rather on both of these assumptions: that the occurrence of a state change is to some degree stochastic, but that the susceptibility to the state change is dependent on individual trait(s). For example, fish predation events (the initial interaction between predator and prey) may occur at random, but the probability of a given fish being eaten is strongly size-dependent (Parkinson et al. 2004, Bestgen et al. 2006). In addition to size-dependent mortality, examples of this kind of state change include size- or experience-dependent resource or territory acquisition, age-, condition- or size-dependent life stage transitions, and size-, condition- or age-dependent reproductive decisions. For the present model, two processes required these kinds of state changes: size-dependent predation and territory acquisition. In order to deal with this, I used a shifting critical value,  $\rho$ , to determine whether an individual should undergo a state change or not;  $\rho = f(\text{trait})$ , where *trait* is a changeable trait of the individual, such as body size. A random number,  $v$ , is then drawn

from a uniform  $[0,1]$  distribution for that individual. If  $v \leq \rho$  then the individual changes state. But if  $v > \rho$ , there is no state change.

#### 4. Juveniles

##### a. Emergence

Emergence of juveniles from a redd occurs over a period of days typically ranging between 5 and 14 days (Jones et al. 2003) with most emergence occurring during a period of 8 days (Brännäs 1995). Emergence of juveniles from a redd tends to be unimodal (Godin 1980). An 8-day period for emergence of all juveniles from a single redd was used in the present model and, for simplicity, the timing of emergence was assumed to follow a normal distribution (although there is evidence that it may not always be normal in the wild; Godin 1980).

When necessary, length was converted to mass, using an equation for juvenile rainbow trout (*Oncorhynchus mykiss*) based on information provided by Post and Parkinson (2001):

$$\Omega = (W_t * 100 - 0.15)^{0.32} \quad (6)$$

where  $\Omega$  is juvenile length in mm, and  $W_t$  is weight (g).

##### b. Territory acquisition

The relationship between population size and probability of territory acquisition has not been empirically described in the literature, so the relationship included in the present model is somewhat arbitrary. Nonetheless, Elliott (1990) has reported that all early-emerging juvenile brown trout initially have territories, and that subsequently emerging juveniles that do not obtain territories quickly starve or move downstream and die, implying that the number of territories is limited. The probability of securing a



feeding territory with changes in juvenile population size is assumed here to follow a rectilinear function (Figure 4). The juvenile population size used in this function is comprised of only the number of juveniles that have territories. The logic applied here is that the number of juveniles with territories will be the major determinant of how likely it is that subsequent juveniles will be able to secure a territory. The relationship is described as:

$$\begin{aligned} &\{If \ \mu < \lambda_T \\ &\rho_s = M \\ &If \ \mu > \lambda_T \\ &\rho_s = -\delta * \lambda_T + \vartheta \} \end{aligned} \quad (7)$$

Where  $\delta$  is:

$$\delta = \frac{M}{\omega - \mu} \quad (8)$$

and  $\vartheta$  is:

$$\vartheta = -\delta * \omega \quad (9)$$

where  $\rho_s$  represents the probability that the juvenile acquires a territory and is used as a critical value to determine whether an individual acquires a territory by comparing  $\rho_s$  to a randomly chosen number (as described in 3. *Individual Random Events*);  $\lambda_T$  is the number of juveniles in possession of a territory at the start of the time step,  $\mu$  is the largest population size at which the highest probability of territory acquisition is found,  $M$  is the highest probability of territory acquisition ( $M=1$  in most runs) and  $\omega$  is the population size at which there is a 0% probability of acquiring a territory.  $\omega$  and  $\mu$  can be converted to densities:

$$w = \omega / a, \quad (10)$$

and:

$$u = \mu/a, \quad (11)$$

where  $w$  is the maximum density (juveniles per  $m^2$ ) the environment can support (i.e. the density beyond which there is a 0% probability of acquiring a territory), and  $u$  is the density (juveniles/ $m^2$ ) at which the probability of territory acquisition begins to decline, and  $a$  is the amount of available habitat suitable for territories. All juveniles without territories are assessed in random order at each time-step as to whether they will acquire a territory (Figure 1). Changes in territory size during growth of salmonids could affect the population density supported in the environment over time (Steingrímsson and Grant 1999). Although territory size in salmonids is size-dependent (Grant and Kramer 1990, Keeley and Grant 1995, Keeley 2000, Steingrímsson and Grant 2008), during approximately the first month after emergence, territory size is relatively constant, after which territory size rapidly increases (Gustafson-Greenwood and Moring 1990). I assumed here that territory size would remain constant for the duration of the simulations, given that the model applied here pertains only to the period of very early life.

Once a juvenile is assigned a territory, it keeps it for the duration of the simulation, unless it was victim to predation mortality. This protocol is consistent with the prior residence effect, whereby territory acquisition and maintenance is determined by first access (Huntingford and Garcia de Leaniz 1997, Cutts et al. 1999b, Harwood et al. 2003). Also, in keeping with the prior-residence effect, it was assumed that there was no effect of juvenile size on territory acquisition. For newly emerged juveniles that do not immediately receive a territory, the number of days until starvation is calculated. This is meant to represent the time to a "point of no return", i.e. the time at which juvenile fish

will starve to death if they do not have food (Miller et al. 1988). For every day that a fish is without a territory, its time to point of no return declines. When time to point of no return is equal to zero, the juvenile is assumed to die because of starvation. The initial time to point of no return (time to starvation) is assumed to be a function of body size:

$$P = 8.33 * \Omega - 19.66 \quad , \quad (12)$$

where P is the initial time to point of no return (starvation).

There are foraging costs for non-territorial juveniles (Table 4). When compared to non-territorial conspecifics, juveniles with territories grow at a faster rate because they have more surplus energy (Puckett and Dill 1985) and engage in significantly more foraging activities (e.g., 40% more feeding motions by territory holders according to one estimate; Puckett and Dill 1985, Cutts et al. 1999a). Prior residents under experimental conditions can grow twice as fast as later introduced fish (Huntingford and Garcia de Leaniz 1997) and dominant fish generally grow at faster rates than subordinate ones (e.g., O'Connor et al. 2000). In the model considered here, juveniles that do not acquire a territory are assumed to grow at half the rate of juveniles with a territory.

### *c. Predation*

The second primary source of mortality for juveniles in the present model is that attributable to predation. There are two levels of predation mortality: population mortality and individual predation risk. Population-level mortality is assumed to follow a Type II functional response (Figure 5), based on Fresh and Schroder (1987)'s study of juvenile coho salmon (*O. kisutch*)

$$\alpha = \frac{\lambda}{v + \lambda} * \beta \quad , \quad (13)$$

where  $\alpha$  is the total population level mortality,  $\lambda$  is the juvenile population size,  $v$  is half saturation constant, and  $\beta$  is the maximum specific ingestion rate (Note that this Michaelis-Menten formulation is mathematically equivalent to the Holling Type II curve; Gentleman et al. 2003). The population mortality represents the total number of individuals which need to undergo a state change (i.e. need to undergo the transition from life to death). The probability of mortality for individual fish is considered to be size dependent (Parkinson et al. 2004, Bestgen et al. 2006). The critical value for each individual fish is calculated as:

$$\rho_p = \kappa * \Omega^{-0.3017}, \quad (14)$$

where  $\rho_p$  is the probability of mortality for fish at a given size (and is used as a critical value to determine whether an individual is killed by comparing  $\rho_p$  to a randomly chosen number, as described in 3. *Individual Random Events* ) and  $\kappa$  is a parameter used to scale individual probability of predation (Mogensen and Post, submitted). Individual predation risk was assumed to differ for territorial and non-territorial fish. Because non-territorial individuals tend to be more mobile than territorial fish, they are likely more vulnerable to predators (Puckett and Dill 1985, Brännäs 1995). Therefore, in the model, juveniles which do not acquire a territory were assumed to experience double the predation risk of juveniles with a territory (i.e.  $\rho_p$  for non-territorial fish is twice that of territorial ones).

#### *d. Growth*

Once all juveniles have emerged, their growth rate is based on individual size and temperature (updated on a daily time step). Based on the literature on mass-specific

growth rates with temperature (Table 5), model parameterization was derived from data provided by Elliott et al. (1995) and by Jonsson et al. (2001) because these sources provided data for young Atlantic salmon across a range of populations. Because of the wide range of possible parameter choices provided by Jonsson et al. (2001)'s work, parameter values were chosen such that the resultant growth trajectories were similar to those reported by Einum and Fleming (2000):

$$W_t = \left( \frac{W_{t-1}^{0.31} + 0.31 * 2.2(T - T_{Lim})}{100(T_M - T_{Lim})} \right)^{1/0.31}, \quad (15)$$

where  $W_{t-1}$  is weight at the start of the timestep (g),  $T$  is the temperature,  $T_M$  is the temperature at which peak growth is obtained (18.5°C), and  $T_{LIM}$  is specified by:

$$\begin{aligned} \{ & \text{If } T \leq T_M \quad T_{LIM} = T_L \\ & \text{If } T > T_M \quad T_{LIM} = T_U \} \end{aligned} \quad (16)$$

where  $T_L = 6.98^\circ\text{C}$ , and  $T_U = 24.9^\circ\text{C}$ . Temperature regimes used in the model are based on daily average air temperature data for spring available from Environment Canada for northern Nova Scotia (<http://climate.weatheroffice.gc.ca/index.html>) over a period of at least the last 20 years.

## II. Simulations

Base-line simulations were run across the range of population densities (Table 3) to represent the range of densities for which redd superimposition levels are reported in the literature (Figure 2). The densities examined were weighted more heavily for low densities because this region was more data rich. Ranges of population predation parameters and territory availabilities were used.

The level of post-emergence mortality juveniles experience is environment dependent (Henderson and Letcher 2003). Territory availability is expected to vary between habitats (Titus 1990). Estimates of juvenile densities for small fish vary greatly from as high as 30 emergent fry/m<sup>2</sup> (Gardiner and Shackley 1991) to as low as 2 (Elliott 1990) or even 1 juvenile/m<sup>2</sup> (Keeley and Grant 1995). Predation pressure is also expected to vary between habitats due to differences in predator abundance (Henderson and Letcher 2003) or due to differences in abiotic environment features that influence predator efficiency (Laplane-Albert et al. 2010). Although there are a limited number of examples of parameterized functional responses available in the literature (but see Fresh and Schroder 1987), levels of population-level predation mortality are known to be variable (Peterman and Gatto 1978, Fresh and Schroder 1987, Henderson and Letcher 2003), therefore predation was scaled in the present formulation to encompass the range from almost no mortality attributable to predation to almost all (or all) mortality being caused by predation. Because of these environmental differences, simulations were run across the widest range of feasible territory availabilities and predation pressures (Table 6). For comparison, the simulations were also run under the assumptions that either starvation mortality or predation mortality was nil.

Table 3: Female spawner population densities used in the model simulations.

Population density (females/100m <sup>2</sup> )
0.13
0.22
0.33
0.44
0.54
0.66
0.76
0.88
2
3
4

Table 4: Examples of the costs of not having a territory for juvenile salmonids.

<b>Advantage</b>	<b>Species</b>	<b>Source</b>
Territorial fish made ~40% more feeding motions than non-feeding	Coho salmon	Puckett and Dill (1985)
Territorial fish show ~37% more feeding motions than non territorial fish	Atlantic salmon	Cutts et al. (1999a)
Prior-residents grew twice as fast as other fish	Atlantic salmon	Huntingford and Garcia de Leaniz (1997)



Table 5: Literature models of temperature and mass specific growth rates for Atlantic salmon (*Salmo salar*) or brown trout (*S. trutta*). \* Indicates growth models or parameterizations used in the present model.

Model Presented	Comments	Source
*Growth model with temperature and weight	Parameterized for brown trout but subsequent studies have parameterized for other organisms (including for Atlantic salmon).	Elliott et al. (1995)
Parameterization of Elliot et al.'s (1995) model	Parameterization for Atlantic salmon parr	Forseth et al. (2001)
*Parameterization of Elliot et al.'s (1995) model	Parameterization for Atlantic salmon	Jonsson et al. (2001)
Separate growth models for temperature and weight	Parameterization for Atlantic salmon smolts	Handeland et al. (2008)
Growth model for temperature and weight	Parameterization for age 1+ Atlantic salmon	Koskela et al. (1997)
Parameterization of Elliott et al.'s (1995) model	Parameterization for ~8g Baltic Atlantic salmon	Larsson and Berglund (2005)
Growth model (but not as a function of temperature)	Parameterization for pre-smolt Atlantic salmon	Noble et al. (2008)
Growth model with changing temperature	Parameterization for juvenile brown trout	Ojanguren et al. (2001)

Table 6: Summary of territory availability (territories/m<sup>2</sup>) and predation parameters used in the model simulations. Lower territory availability densities correspond to reduced habitat availability, and hence higher levels of starvation.  $w$  is the maximum density of territories the environment can support (i.e. the density beyond which there is a 0% probability of acquiring a territory), and  $u$  is the density at which territory starts to be limited (i.e. probability of territory acquisition begins to decline). The predation parameter  $v$  refers to the half saturation constant for the type II functional response and  $\beta$  is the maximum specific ingestion rate

Territory parameters	
$u$	$w$
0.9	1.95
1.3	2.6
2.3	4.6
2.6	5
3.5	6.8
4.7	9.1
Unlimited territories	
Predation parameters	
$\beta$	$v$
No predation	
100	20
1000	900

1375	1237
1500	1350
2050	1855
2750	2470

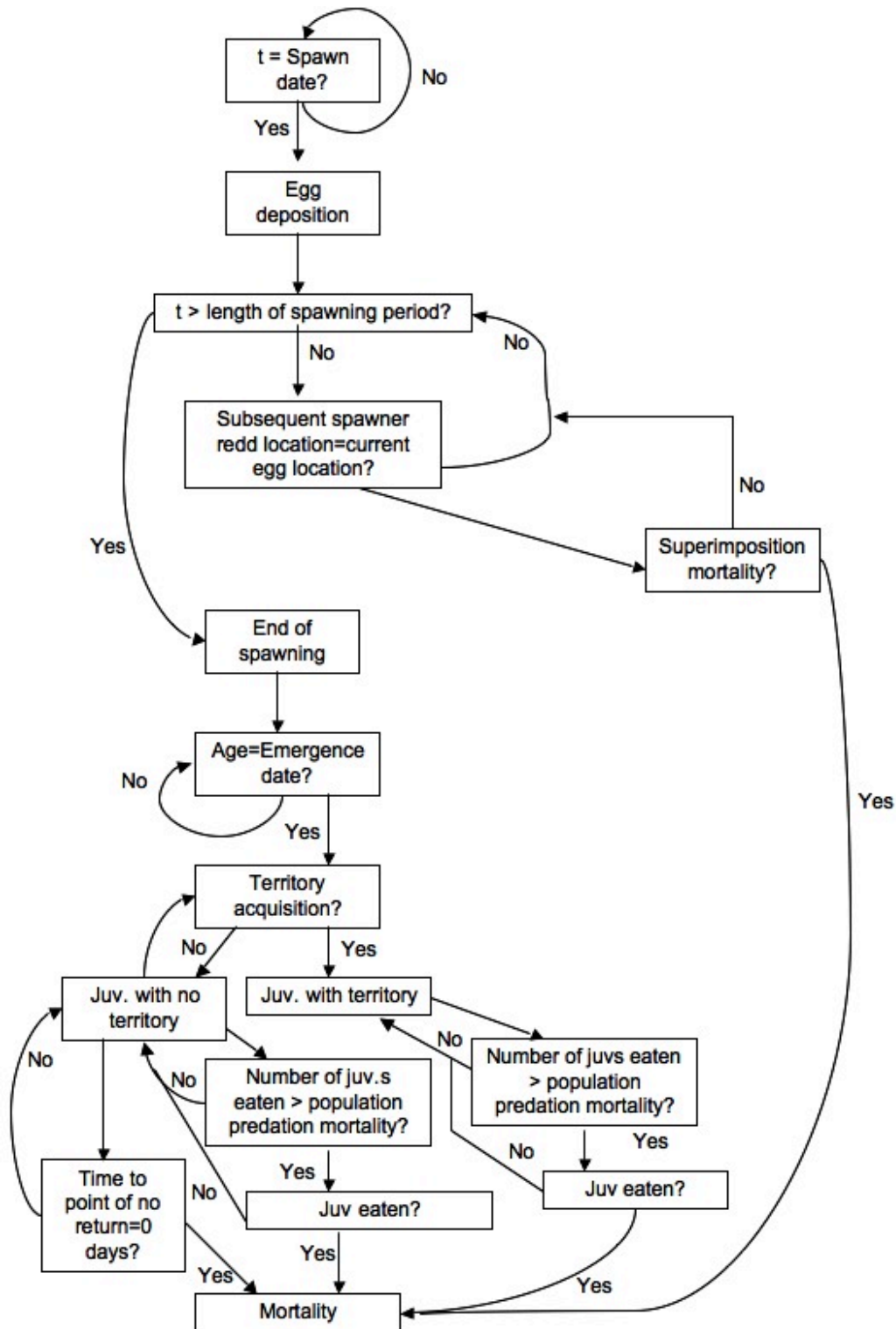


Figure 1: Conceptual frame-work of the model.  $t$  represents the current time-step of the model. Mortality events remove juveniles from the population.

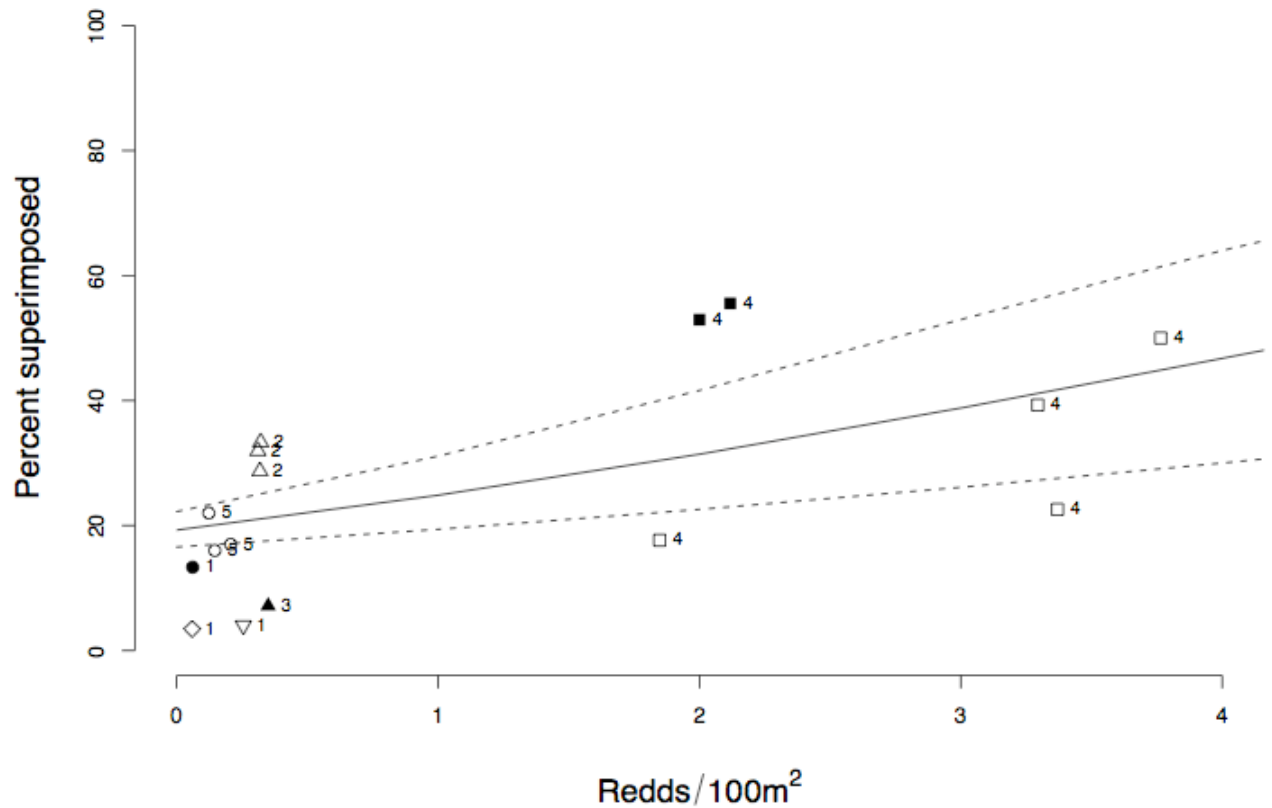


Figure 2-Relationship between number of redds per 100m<sup>2</sup> and the percent of those redds which were superimposed. Logistic regression for the data (solid line) and 95% confidence intervals (dashed lines) are shown. The species used were white spotted charr(◇), dolly varden(●), rainbow trout(▽), taimen and rainbow trout(△), taimen(▲), brown trout(□), brook trout (■), and Atlantic salmon (○). Data is from (1) Taniguchi et al. (2000), (2) Nomoto et al. (2010), (3) Edo et al. (2000), (4) Essington et al. (1998), and (5) Taggart et al. (2001) .

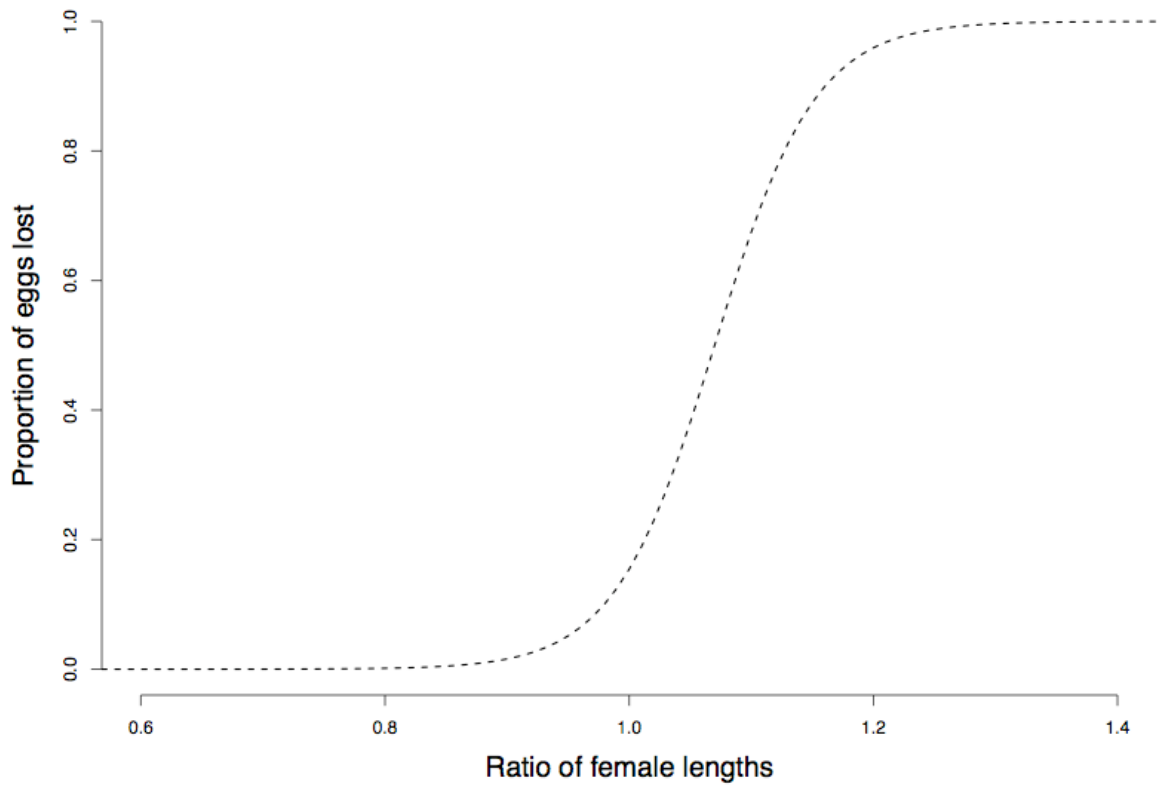


Figure 3: Function used to determine the proportion of eggs originally in the nest lost to redd superimposition (see Equation 4) when a subsequent female digs her redd in the same location as that of a pre-existing redd.

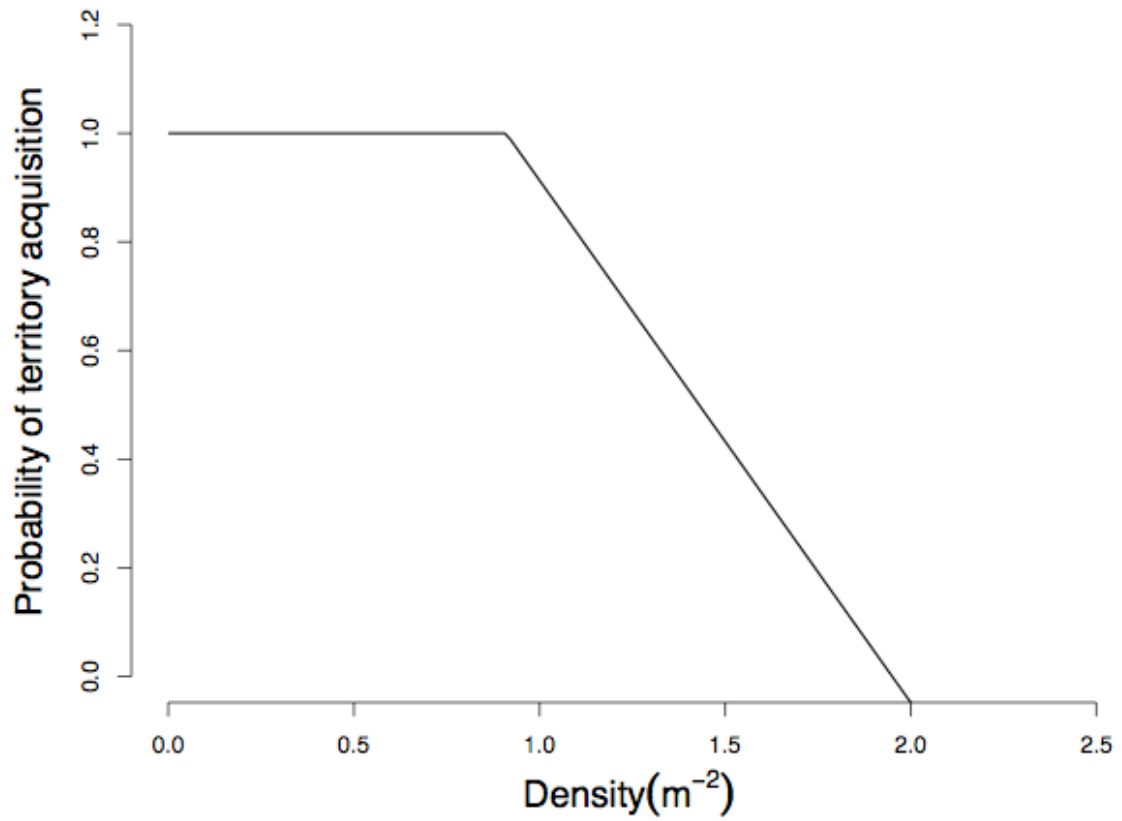


Figure 4: Probability of territory acquisition in the model was assumed to be a rectilinear function of the number of juveniles who already have territories (see Equation 7).

Parameters used for this figure were  $u=0.9$ , and  $w=1.95$ .

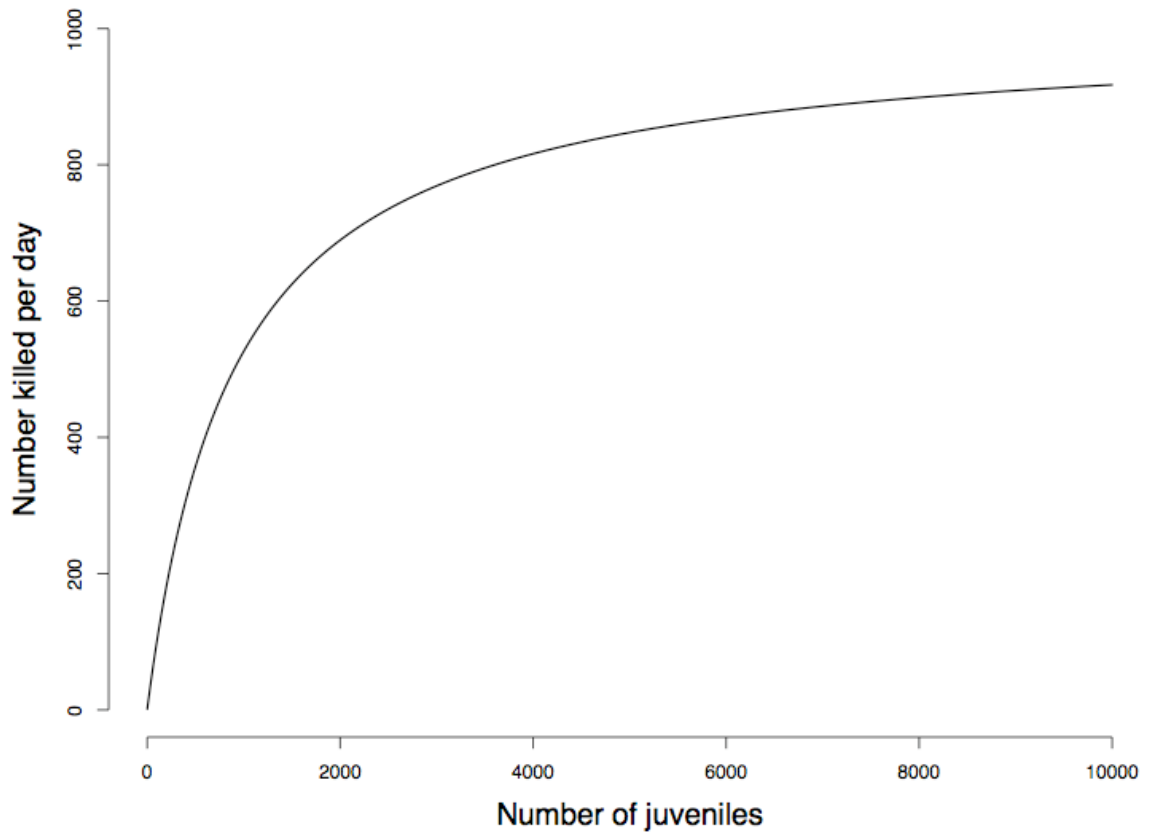


Figure 5: The assumed relationship between total population mortality (number killed per day) as a function of the number of emerged juveniles used for simulations in the present model (see Equation 14). The functional response was assumed to be a Type II functional response. Parameters used in this figure:  $\beta=1000$ ,  $v=900$ .



## CHAPTER 3: RESULTS

### *I. Egg stage*

The probability of a redd being superimposed (where superimposition occurs when there is egg loss due to redd reuse) was modeled using logistic regression. The best model (evaluated by lowest AIC) included spawning time, maternal size, spawner density, and a spawning time\*maternal size interaction (tested for 2 sets of random numbers). Only spawning time, spawner density and the spawning time\*maternal size interaction were significant for both sets of random numbers (Table 7). The earlier a redd had been used for spawning, or the greater the density of the spawning population, the higher the probability of superimposition. The larger the female, the lower the probability that her redd would be superimposed, although this effect was significant for only one of the two random number sets tested. Redds excavated by smaller females had a lower probability of superimposition when spawn date was later, while the superimposition risk for redds produced by larger females was relatively low irrespective of when they spawned, although this interaction was also only significant in one of the two random number sets tested.

Redd superimposition was the primary determinant of egg survival. Female body size was also an important factor, especially in non-superimposed redds for which the number of eggs surviving was strictly a function of maternal size (in accordance with the fecundity: maternal size relationship; equation 3). A logistic regression was used to identify the factors responsible for determining the proportion of eggs surviving in superimposed redds. However, the proportion of eggs surviving within each redd was not independent, but rather the result of redd-level superimposition events. This correlation

of binary events violates the assumption of the binomial distribution and resulted in overdispersion (Collett 2003). In order to account for this overdispersion ( $X^2_{934} = 553$  and  $X^2_{945} = 562$  for the two random number sets explored), a quasibinomial distribution was used (McCullagh and Nelder 1983). For both sets of random numbers explored, the significant terms ( $p < 0.05$ ) included in the model were the same: maternal size, spawning time and spawner density (Table 8). For superimposed redds, the later spawning occurred, the lower the proportion of eggs lost to superimposition. The larger the spawner, the fewer the eggs lost to superimposition, and the higher the spawner density, the greater the proportion of eggs lost to superimposition.

## *II. Post emergence*

### *1. Size*

#### *a. Selection differentials*

Selection differentials can be used to illustrate the difference between the original mean population trait value (i.e. maternal size) and the population trait value after selection events (Ridley 2004). The original mean maternal size (trait value) of the population was calculated by taking the average size of all females responsible for producing all eggs in the simulated population, prior to any kind of mortality. The post-selection average maternal size was determined by accounting for the average maternal size of all juveniles at the end of the simulation (or at the end of the spawning season for the egg stage). Either the estimated selection differential for maternal size was zero (21% of simulations), or larger females (reflected by negative selection differentials) were favoured. The maximum differential was -35mm (5% of female body size prior to selection). The selection differential was very small or zero at low densities but

increased in absolute value as density increased (Figure 6). The selection differential and the pattern with density were greatest when predation pressure was low, and when territories were very limited, or both (Figure 6).

*b. Correlation coefficients*

Correlation coefficients between log-number of juveniles and female body size were calculated (log-transformations were used in order to meet correlation assumptions). These correlation coefficients were compared across the range of simulated spawner densities. Correlation coefficients were calculated separately for females whose redds had been superimposed and for those whose redds had not. These correlation coefficients provided a measure of the relationship between female size and log number of juveniles. When there was a benefit to size, larger females were always favoured.

At the egg stage, there was a perfect correlation between log juvenile number and maternal length for non-superimposed redds because of the fecundity: maternal size relationship used here (equation 3). For superimposed redds, the correlation was less than this (Figure 7). When territory was not limiting (meaning that starvation mortality was nil), the correlation between log number of juveniles and maternal size was higher for females whose redds had not been superimposed than for those whose redds had been superimposed (Figure 7a). At the highest densities, for females whose redds had not been superimposed, the correlation coefficient approached unity; again this was driven by the fecundity relationship (equation 3). For females whose redds had been superimposed, the correlation coefficients were initially low, but did increase with density (Figure 7a).

In the absence of predation mortality, there was a decline in correlation between log number of juveniles and maternal size with increasing spawner density (Figure 7b).

This occurred because territories were more limiting at high spawner density than at low densities. As more territories became available, this relationship with density became less and less steep (Figure 7c).

When both sources of post-emergence mortality sources are present, a hump-shaped pattern is observed with an initial increase to a peak driven by predation followed by a decline driven by limited territories (Figure 7d). The post-emergence sources of mortality result in an increasing amount of scatter in the relationship between log number of juveniles and female size. The higher the mortality, the greater the degree to which this effect was observed.

## *2. Stock Recruitment Relationships*

The stock-recruitment curves followed a saturating relationship when there was territory limitation (Figure 8a). When there was no territory limitation, there was an increase in number of recruits as spawner density increased across the range of densities modeled (Figure 8b). The average number of recruits per spawner (a metric of fitness) depended on the mortality sources. When superimposition was the only source of mortality, an increase in spawner density resulted in a decline in recruits/spawner (Figure 9). The addition of starvation mortality (in the absence of predation mortality) was associated with a decline in recruits per spawner (“None” in Figure 10) such that there were fewer recruits per spawner, especially at high spawner densities, than that associated with superimposition mortality alone. As territory became increasingly limited, this decline became increasingly steep with reduced number of recruits per spawner, especially at high population densities. Overall, the number of recruits per spawner declined with increasing predation, and with increasing territory limitation.

When predation was the only source of post-emergent mortality (i.e. territories were unlimited), the number of recruits per spawner increased with spawner density to an asymptotic level (Figure 11). The fewest number of recruits per spawner was produced at low female density. As predation increased, the number of recruits per spawner declined (Figure 10).

At very low predation levels ( $\beta=100$ ,  $\nu=20$ ), a curve, similar to that seen for the mortality condition of ‘no predation’, was maintained across all levels of territory limitation. However, when both sufficient predation mortality ( $\beta \geq 1000$ ,  $\nu \geq 900$ ) and territory limitation was present, recruits per spawner were related to spawner density in accordance with a hump-shaped relationship (Figure 10). The steepness of the approach to the maximum was dependent on the level of predation: the approach was steeper when predation was lower (Figure 10). As mortality increased, the density at which the maximum number of recruits per spawner occurred also increased while the overall number of recruits per spawner decreased (Figures 10 and 11). As predation increased, an increasing number of low density simulations resulted in no survival among juveniles (Figure 10). When territories were highly limited, there was a decline in recruits per spawner as spawner density increased (territory parameters:  $u \leq 1.3$ ,  $w \leq 2.6$ , Figure 11). When both predation mortality and territory limitation were high, there was no survival of juveniles at any of the simulated densities (territory parameters:  $u \leq 0.9$ ,  $w \leq 1.95$ , predation parameters  $\beta \geq 1375$ ,  $\nu \geq 1237$  and territory parameters:  $u \leq 1.3$ ,  $w \leq 2.6$ , predation parameters  $\beta \geq 2050$ ,  $\nu \geq 1855$ ).

### 3. *Timing of Reproduction*

The average number of juveniles surviving to the end of the simulation was estimated for early-emerging juveniles (i.e. those produced in the first half of the spawning season) and for late-emerging juveniles (i.e. those produced in the latter half of the spawning season). Superimposition mortality favoured late-spawning females (Tables 7 and 8). The addition of post-emergence mortality affected the fitness associated with spawning early and late in a manner which depended on the relative importance of the mortality sources. On average, early-spawning females produced an equal number or more juveniles at the end of the simulation period than late-spawning females (Figure 12). Early-spawning females had more surviving offspring than late-spawning females at high densities; as density declined this difference disappeared (Figure 12).

When territory limitation was high, early-spawning females had more surviving offspring than late spawners (Figure 13). When territory was the only source of post-emergence mortality, late-produced offspring were favoured (“Unlimited” in Figure 13). However, as territory limitation increased there was an equal success of early- and late-produced juveniles (Figure 13).

Across all densities at which predation mortality was the only source of post-emergence mortality, females that spawned later in the spawning season had more surviving offspring at the end of the spawning season than those that had spawned earlier (“Unlimited” in Figure 13). When predation was not a source of post-emergence mortality, early-spawning females produced more surviving offspring per spawner than those spawning late (Figure 14). As predation mortality increased, the number of recruits per spawner declined for both early- and late-spawning females, however the decline was

more abrupt for early-spawning females: at higher predation levels, on average, early- and late-spawned offspring experienced similar survival (Figure 14).

Although on average early-spawned females did better or as well as late-spawning females in these simulation sets, there were certain scenarios that favoured late-produced offspring. Again, at higher predation mortality, or at a mix of higher predation mortality and high territory limitation, or at low spawner density and higher predation mortality, none of the juveniles was predicted to survive. As territories become increasingly limited, early-produced juveniles were increasingly favoured (Figure 12). Overall, when territory was limiting, early-produced juveniles are favoured.

For specific simulations in which both predation mortality and territory limitation occurred, the patterns of the benefit of spawning time depended on the relative importance of the two sources of post-emergence mortality, as well as on the spawning population density. At very low densities (0.13 and 0.22 spawners/100 m<sup>2</sup>), the addition of low levels of predation mortality (predation parameters:  $\beta=100$ ,  $\nu=20$ ) resulted in similar levels of survival for early- and late-spawned juveniles. However, increasing the predation (predation parameters:  $\beta \geq 1000$ ,  $\nu \geq 900$  for 0.13 spawners/100 m<sup>2</sup> and  $\beta \geq 1375$ ,  $\nu \geq 1237$  for 0.22 spawners/100 m<sup>2</sup>) led to no juvenile survival at any level of territory limitation. At higher densities, there were also predation mortality levels which resulted in no juvenile survival (predation parameters:  $\beta \geq 2050$ ,  $\nu=1855$  for 0.33 spawners/100 m<sup>2</sup> and  $>\beta=2750$ ,  $\nu=2470$  for 0.44 spawners/100 m<sup>2</sup>). At the very highest densities (i.e. 4 spawners/100 m<sup>2</sup>), early-spawned juveniles were always favoured. As predation mortality increased, early-spawned juveniles were less favoured. When predation mortality dominated (at lower densities or when there was little territory

limitation), later spawned juveniles were favoured over early (Figure 15).

Superimposition mortality also resulted in later spawned juveniles being favoured.

However, at low spawner densities, the difference in survival between early- and late-emerging juveniles was not as great as it was in the presence of predation mortality, indicating that although redd superimposition favoured late-produced offspring, the effect is not as strong as that associated with predation at low densities. When density was high, however, the difference in survival between early and late produced juveniles due to superimposition was greater than that associated with predation mortality indicating that, at high spawner densities, superimposition is more likely to favour late-produced offspring than predation.



Table 7: Terms present in the best models (assessed by lowest AIC), for the two sets of random numbers explored, explaining probability of superimposition in the egg stage.

Factor	Random number set 1		Random number set 2	
	Coefficients	P-value	Coefficients	P-value
Spawning time	-1.18	0.0014	-1.27	0.0012
Maternal size	-0.01	0.0083	-0.007	0.10
Spawner density	1.095	$8.8 \times 10^{-13}$	0.5	$2 \times 10^{-16}$
Spawning time *Maternal size	0.0013	0.017	0.0018	0.052

Table 8: Significant terms ( $p < 0.05$ ) included in the logistic models (using quasibinomial distributions) used to determine the factors responsible for determining the proportion of eggs surviving in superimposed redds.

Factor	Random number set 1		Random number set 2	
	Coefficients	P-value	Coefficients	P-value
Spawning time	0.128	$2 \times 10^{-16}$	0.179	$2 \times 10^{-16}$
Maternal size	0.025	$9.8 \times 10^{-6}$	0.026	$2.1 \times 10^{-9}$
Spawner density	-0.27	$2.9 \times 10^{-11}$	-0.16	$2.8 \times 10^{-5}$

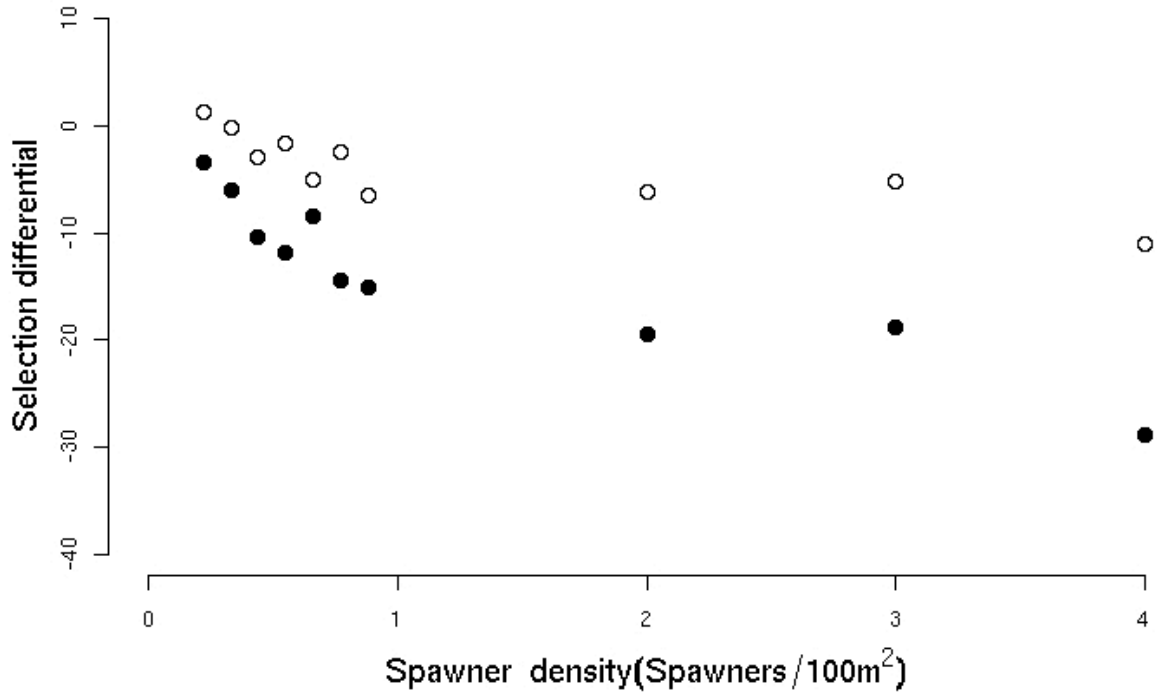


Figure 6: Output of simulations run over a consistent set of random numbers for selection differentials of maternal size (average maternal size prior to egg stage mortality-average maternal size of surviving juveniles at end of simulation) at different spawner densities (spawners/100m<sup>2</sup>). Simulations were run across a range of parameters for predation and territory limitation (for full range of parameters investigated see Table 6). Parameters used for the simulations shown; open symbols are for territory parameters:  $u=0.9$ ,  $w=1.95$ , predation parameters:  $\beta=1000$ ,  $\nu=900$ , closed symbols are for no territory limitation, predation parameters:  $\beta=1000$ ,  $\nu=900$ .

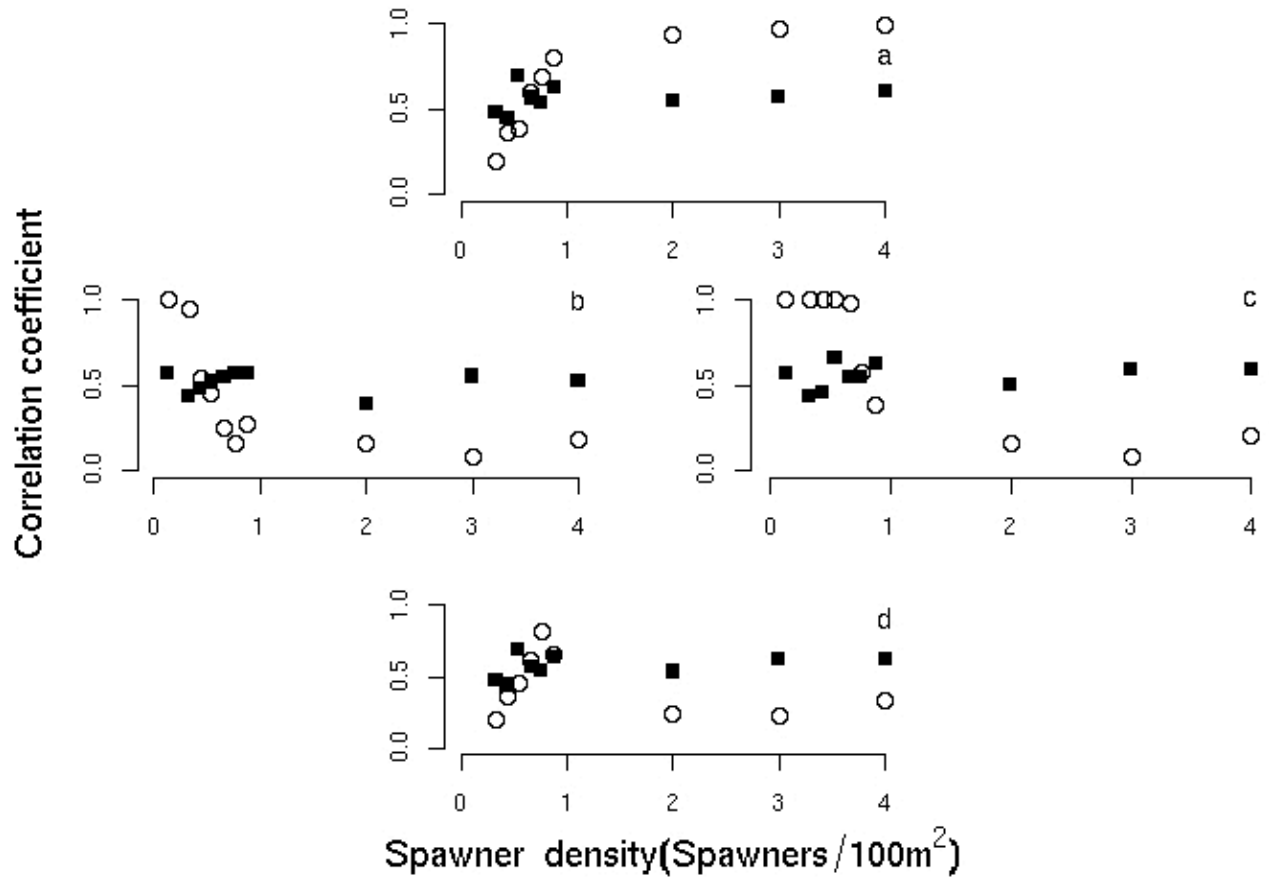


Figure 7-Output of simulations run over a consistent set of random numbers for correlation coefficients between log number of surviving juveniles and maternal size, at different spawner densities (spawners/100m<sup>2</sup>). Simulations were run across a range of parameters for predation and territory limitation (for full range of parameters investigated see Table 6). Filled symbols indicate calculations for females with superimposed redds, whereas open symbols indicated calculations for females with non-superimposed redds. Parameters used for these simulations: a) No territory limitation, predation parameters:  $\beta=1375$ ,  $\nu=1237$ , b) Territory parameters:  $u=2.3$ ,  $w=4.6$  (note that lower parameters result in greater territory limitation), no predation mortality, c) Territory

parameters:  $u=4.7$ ,  $w=9.1$ , no predation mortality, d) Territory parameters:  $u=4.7$ ,  $w=9.1$ ,  
predation parameters:  $\beta=1375$ ,  $\nu=1237$ .

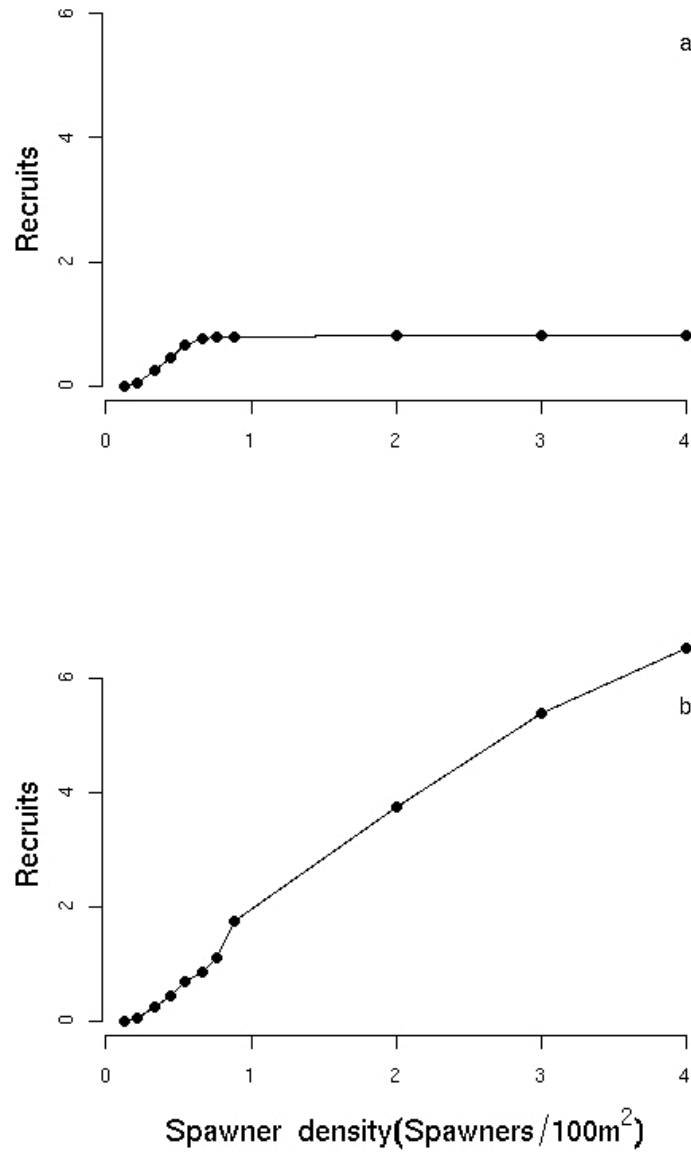


Figure 8- Output of simulations run over a consistent set of random numbers for number of surviving recruits (number of juveniles at the end of the simulation in 100 000s) at different spawner densities (spawners/100m<sup>2</sup>). Simulations were run across a range of parameters for predation and territory limitation (for full range of parameters investigated see Table 6). Parameters used for the simulations shown: a) Territory parameters:  $u=3.5$ ,  $w=6.8$ , predation parameters:  $\beta=1000$ ,  $\nu=900$ , b) No territory limitation, predation

parameters:  $\beta=1000, \nu=900$ .

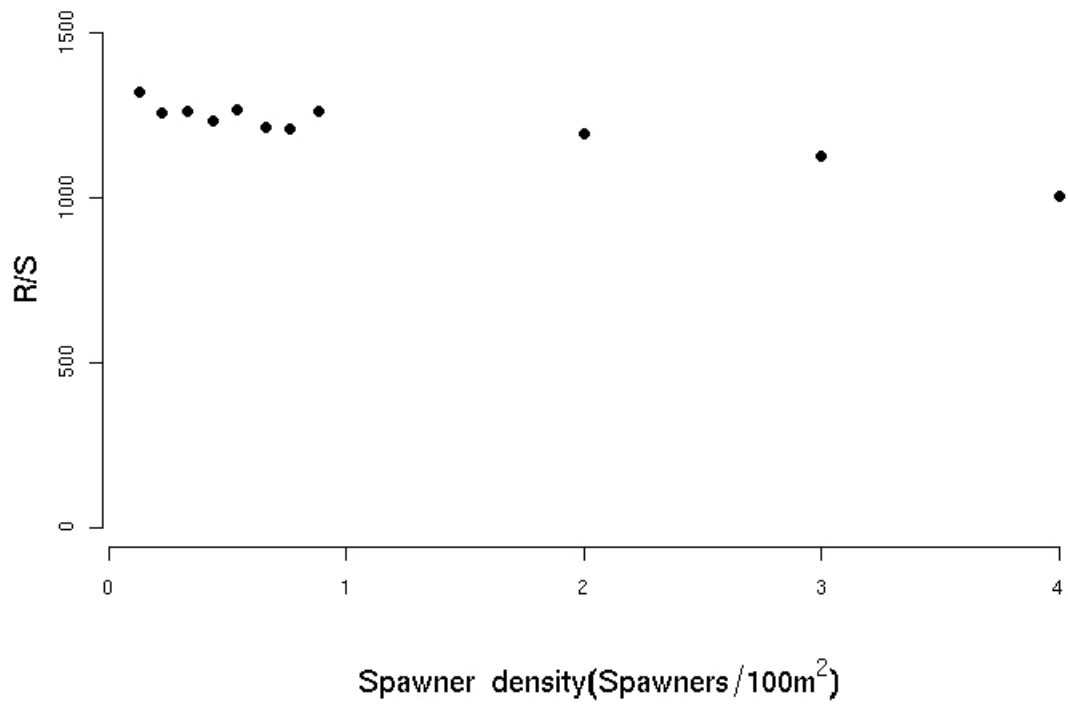


Figure 9-Output of simulations run over a consistent set of random numbers for number of surviving eggs per spawner (R/S) at different spawner densities (spawners/100m<sup>2</sup>). Simulations to the end of the egg stage only (i.e. not including post emergent mortality).



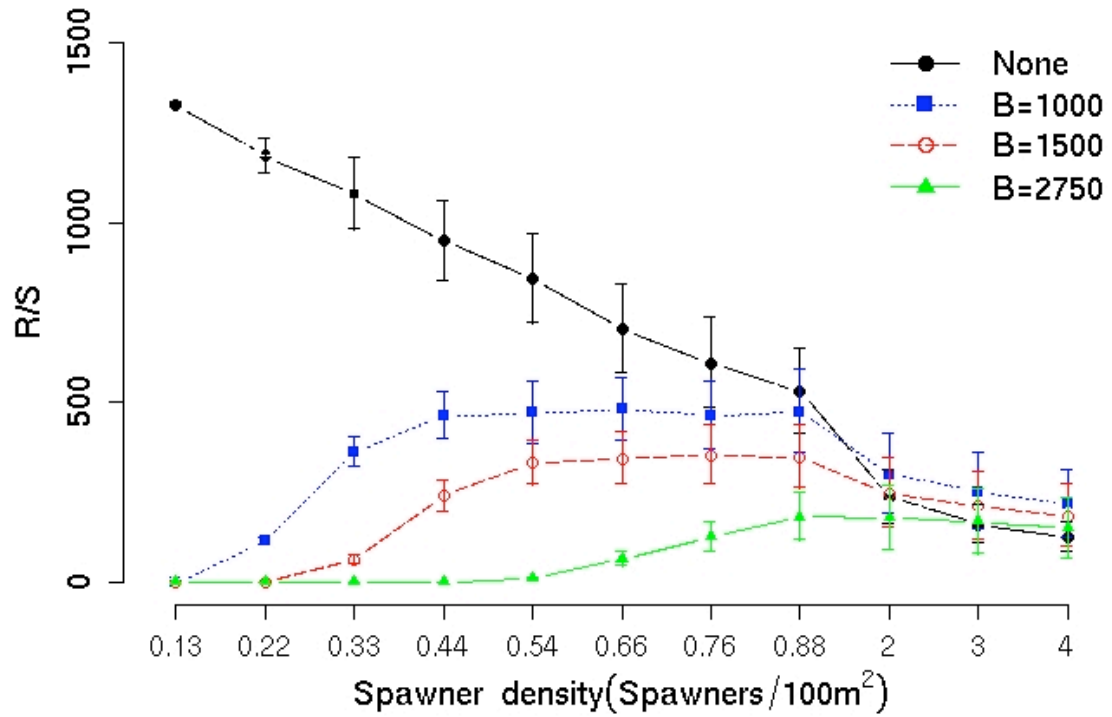


Figure 10-Number of recruits per spawner (R/S), for a range of predation parameters, averaged across densities. The full set of predation parameters investigated are shown in Table 6. Standard errors of the averages are shown. None refers to no predation mortality.

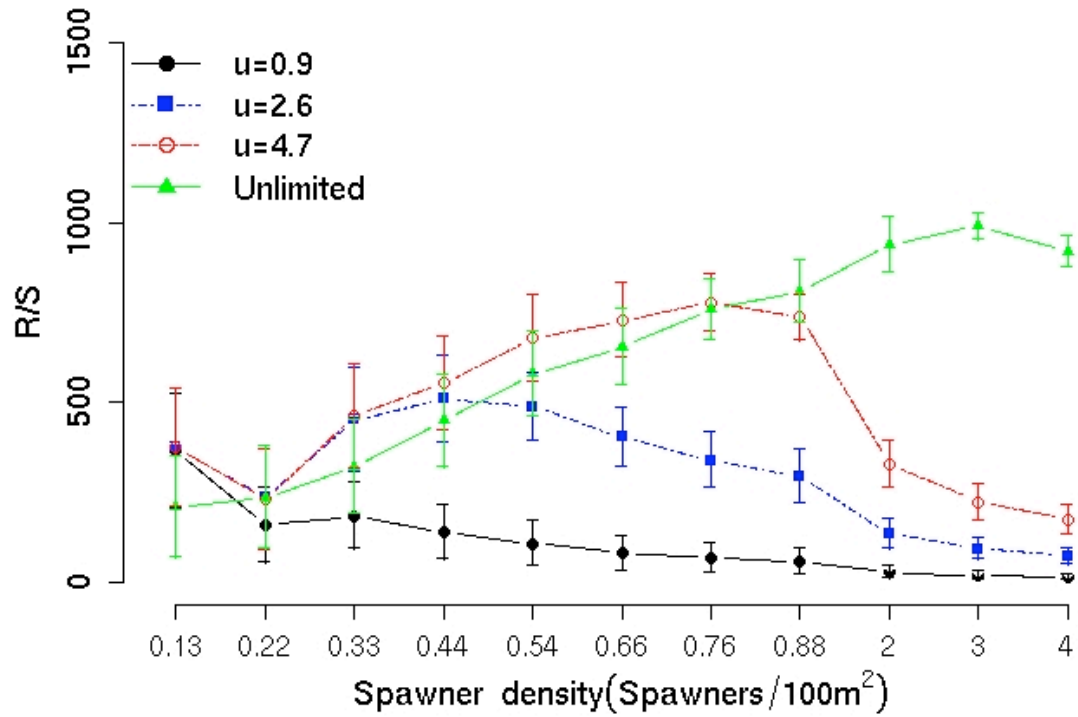


Figure 11-Number of recruits per spawner (R/S), averaged across each territory simulation. Full set of territory parameters investigated are shown in Table 6. Standard errors of the averages are shown. Unlimited refers to unlimited territory availability.

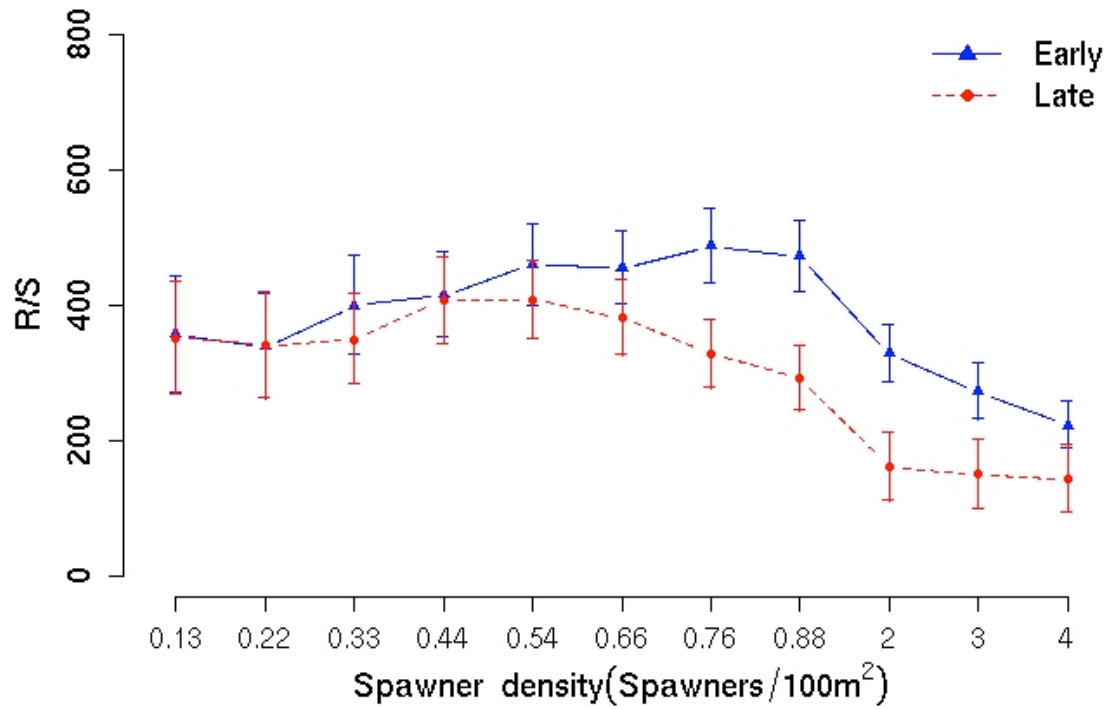


Figure 12-Number of recruits per spawner (R/S), averaged across each simulated density for early and late spawners. The full set of parameters investigated are shown in Table 6. Standard errors of the averages are shown.

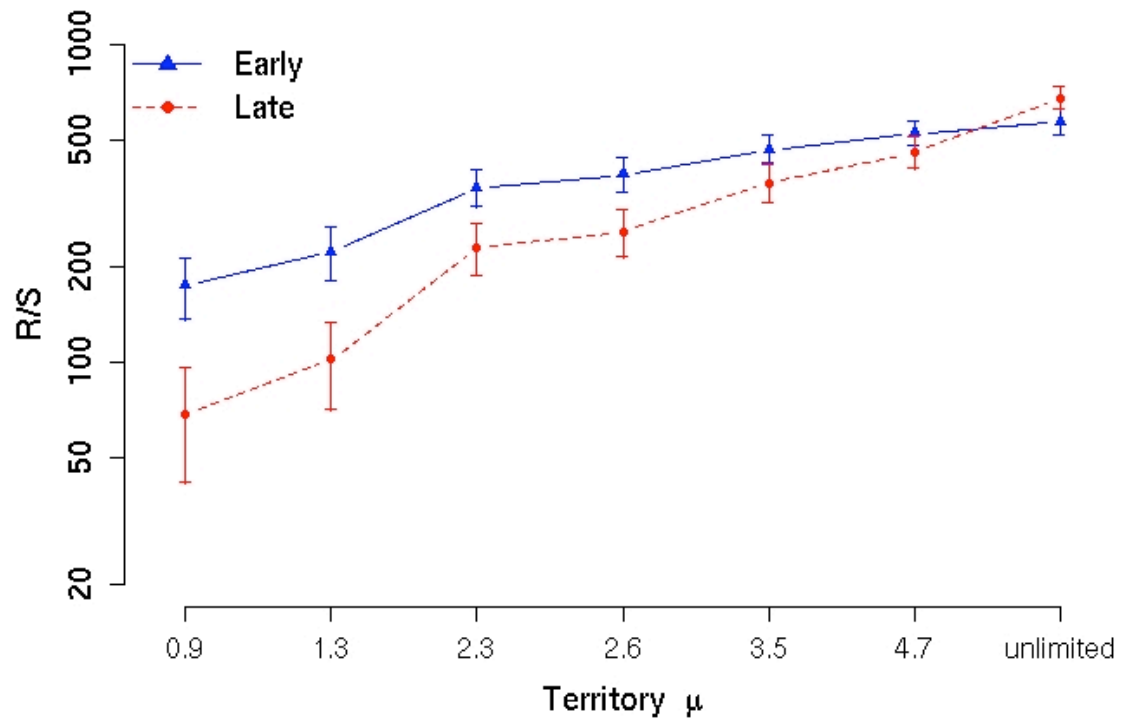


Figure 13-Number of recruits per spawner (R/S), averaged across each set of territory parameters for early and late spawners. The full set of parameters investigated are shown in Table 6. Standard errors of the averages are shown. Unlimited refers to unlimited territory availability.

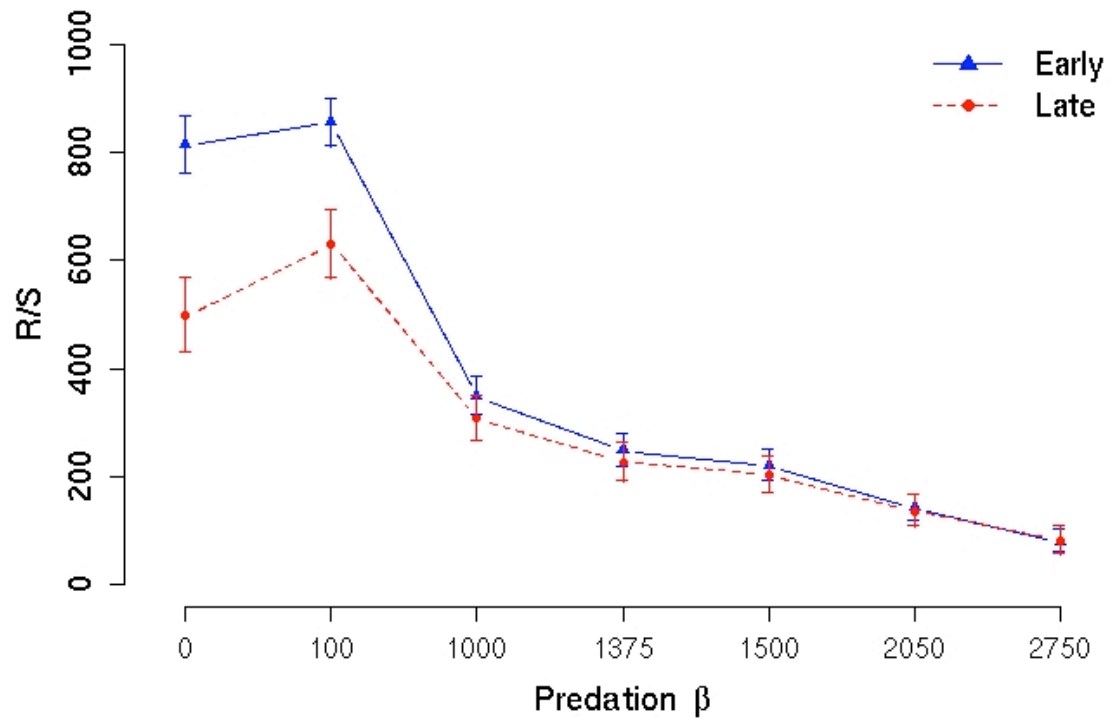


Figure 14-Number of recruits per spawner (R/S), averaged across each set of predation parameters for early and late spawners. The full set of parameters investigated are shown in Table 6. Standard errors of the averages are shown.

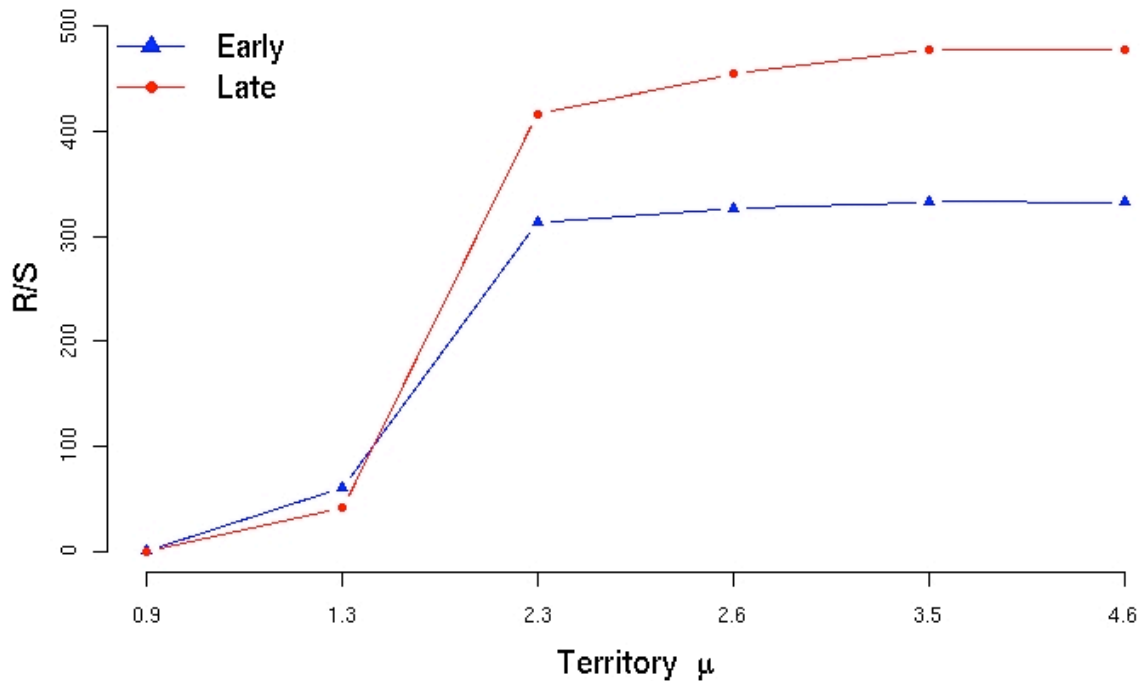


Figure 15- Average number of surviving early juveniles (those produced before the midpoint of the spawning season) and average number of surviving late juveniles (those produced after the midpoint of the spawning season) per spawner (R/S), across simulations of different territory limitation parameters (the territory parameters refer to  $\mu$ , see Table 6 for respective  $w$ 's, as well as full range of parameters investigated). Parameters used for these simulations: spawner density: 0.44 spawners/100m<sup>2</sup>. Predation parameters for all simulation shown here:  $\beta=1375$ ,  $\nu=1237$ .

## CHAPTER 4: DISCUSSION

The present study explored the influences of various sources of mortality during the egg and early juvenile stages on maternal fitness in salmonids. The model simulations indicated that the probability of redd superimposition during the egg stage declined with increasing maternal size, reductions in spawner density, and delayed spawning date. For redds which had been superimposed, each of these factors was also found to positively influence the proportion of surviving eggs. Maternal fitness was also affected by post-emergent sources of juvenile mortality which were, in turn, influenced both by maternal size and spawning date. Under those circumstances in which maternal size influenced fitness, increased rather than reduced body size was favoured. This effect was more intense when predation mortality was low, territories were limited, and/or spawner density was high. Spawning time also influenced maternal fitness, although the manner in which this occurred depended on the source(s) of mortality. Overall, early-spawned juveniles were more highly favoured (i.e. experienced higher survival probabilities) than later-spawned juveniles. This association was largely influenced by circumstances in which territories were highly limited and predation mortality was low, thus allowing for many more early-spawned juveniles to survive than later-spawned juveniles. However, when predation mortality was high, later-spawned juveniles experienced higher survival. Territory limitation tended to favour early-spawned juveniles whereas high predation mortality tended to favour later-spawned individuals. Additionally, component Allee effects in juvenile survival were detected in some of the modeled scenarios.

### *I. Superimposition*

Risk of redd superimposition increased with spawner density, and decreased for females who were larger or who spawned later. A function relating increased risk of superimposition with increased spawner density was built directly into the simulations (i.e. Equation 5; Figure 2) based on existing literature. Increased risk of superimposition with increased size was consistent with the implications of salmonid redd-depth:body-size relationships (Charnov and Krebs 1974, van den Berghe and Gross 1984). Early-spawning females have also been shown to experience an increased risk of redd superimposition (McPhee and Quinn 1998).

Spawner density, maternal size, and spawning date also influenced the proportion of eggs lost in superimposed redds. To the best of my knowledge, post-superimposition, within-redd survival has not been examined empirically. The present work suggests that not all redds offer the same protection to eggs: even in the event of superimposition, the degree of egg loss (and hence cost to maternal fitness of superimposition) is dependent on both spawner density and maternal phenotype (i.e. size and spawning time). When redds of large or late-spawning females are superimposed (which they have reduced risk of), they will have higher egg survival than superimposed redds produced by earlier spawning, small females. It is often implicitly assumed that the occurrence of redd site reuse is indicative of superimposition, and the cost (in terms of egg loss) is the same for all redds (but see Taggart et al. 2001). The simulation results presented here suggest that this assumption is incorrect and, in the event of superimposition, the cost in terms of egg loss will differ among females and be dependent on their phenotype.



Overall, the model results indicate that spawner density, maternal body size and spawning timing can significantly affect egg survival. These variables also influence both intra- (McNeil 1964) and inter-specific competition for redd sites (Essington et al. 1998, Taniguchi et al. 2000). In the case of interspecific competition, this may mean that one species may be more (Taniguchi et al. 2000) or less vulnerable to redd superimposition and its detrimental consequences to eggs (Weeber et al. 2010), depending on relative spawner density, size and spawning time.

## *II. Population pattern*

The stock-recruitment curves that were generated from the simulations are consistent with those characteristic of a Beverton-Holt curve (i.e. recruitment increases at progressively slower rates towards an asymptotic value). Previous work does suggest, however, that the relationship between recruitment and spawning stock size in salmonids might better fit a Ricker curve (Gardiner and Shackley 1991, Crozier and Kennedy 1995), albeit with a lot of variability in the relationship (Gardiner and Shackley 1991). In order for there to be a decline in recruitment at high spawner densities (i.e. to match the dominant characteristic of a Ricker curve), there would have to be additional costs associated with high densities beyond those included in the present model. In the current model, juvenile population size at high densities is dictated primarily by territory limitation. Superimposition does act in the model to cause greater mortality at high spawner densities, however the number of juveniles produced at these higher spawner densities is still sufficient to ensure that all there are many more juveniles than available territories and, hence, that juvenile survival is still regulated by the number of available territories. One example of a mechanism not represented in this model, which could lead

to lower juvenile survival when spawner density was high, would be competition among juveniles for food at very small spatial scales (Keeley 2001).

### *III. Maternal size*

In the model simulations presented here, large maternal size was more favoured (i.e. was associated with higher maternal fitness) when predation mortality was low, territories were limited, and/or spawner density was high. The effect of territory limitation was not unexpected because of longer time to starvation for the larger juveniles that emerged from the larger eggs produced by larger females (Equation 12). The effect of low predation was, however, unexpected. Even though there was a term in the model that had the effect of reducing the probability of predation for larger juveniles (Equation 14), the difference in size among newly emerged juveniles was not large enough to have greatly influenced the predation risk, and was smaller than the differences in body size (at a given time) between early- and later-emerged juveniles.

Given that there was little effect of maternal size on juvenile predation risk, predation mortality might have been expected to increase the variation in the relationship between maternal size and number of surviving juveniles. Increased juvenile density would be expected to have an effect similar to that associated with increased territory limitation because there are fewer territories per capita at high densities than there are at lower densities. Based on the model presented here, it is only disadvantageous to be a small female under certain circumstances, such as when juvenile density is high or when territory limitation is the primary source of juvenile mortality (which is sometimes equivalent). Overall, post-emergent mortality reduced the strength of the relationship between maternal size and fitness (number of juveniles produced). Selection for large

maternal size is widespread in fish because of both fecundity-size relationships and other beneficial correlates of large size (see review in Green 2008). In salmonids, evidence is mixed as to whether large or small size is favoured overall (see Table 1). Although the present work did not identify circumstances for which small maternal size was beneficial to fitness, there were simulation results for which there was little or no benefit to large maternal size. Thus, the benefits of large size in salmonids may well be context dependent.

#### *IV. Spawning timing*

In general, juvenile survival depended on the source of mortality. As juvenile territories became increasingly limited, there was a switch in the fitness benefits associated with spawning relatively early or relatively late in the spawning season. At low juvenile densities, late-spawning females tended to have a fitness advantage over early-spawning females. However, as territories became increasingly limited, the model simulations indicated that females who had spawned comparatively early produced more juveniles than those who had spawned late. Territory limitation could be achieved both through reduction in number of territories (reduction in territory parameters), or through increased juvenile density, which essentially decreases the number of territories available per capita. Territory limitation favoured early-emerging juveniles because of their higher probability of acquiring a territory when juvenile density was low. This result matches the experimental findings reported by Brännäs (1995) for Atlantic salmon. The model simulations presented here suggest that, at low levels of predation mortality, early-spawned juveniles were favoured; however, as predation mortality increased, the fitness advantage enjoyed by early-emerging juveniles over late-emergents declined and then

disappeared. For some of the model simulations presented here, when juvenile predation was high and territory availability low, later-spawned juveniles were favoured over early-emergents. This result is also consistent with previous experimental work (Brännäs 1995). Predation may have favoured later-emerging individuals because time spent exposed to predation was shorter. Also, because juvenile density increases as time progresses and more juveniles emerge, and because the functional response is a saturating one, the per capita predation rate is correspondingly lower.

Although late- and early-emerging juveniles experienced similar survival at low densities, on average, early-emerging juveniles experienced higher survival as spawner density increased and as territories became increasingly limiting. Although others have identified conditions under which early-produced offspring might be favoured (Einum and Fleming 2000), the present work suggests that the actual effect is context dependent and that, under some conditions, late-produced juveniles would be favoured. Indeed, Anderson et al. (2010) concluded that the direction of selection on timing of spawning changes annually. They found that in the first year of re-colonization of a stream stretch by coho salmon, early spawning time was favoured; however, in subsequent years, selection on spawning time was of a stabilizing nature.

#### *V. Allee effects*

Component Allee effects (i.e. an Allee effect which influences a portion of fitness Stephens et al. 1999) were evident in the model simulations presented here (Figures 10 and 11). When territory limitation was the only source of post-emergent mortality, the number of recruits (i.e. juveniles) per spawner declined with increasing spawner density, as would be expected under compensatory population dynamics. However, when

territories were not limiting and when predation was the only source of post-emergent mortality, there was a pattern of increasing recruits per spawner as spawner density increased: this constituted a component Allee effect for which lower spawner densities resulted in lower reproductive output.

Saturating functional feeding responses by predators can result in the expression of Allee effects in their prey (Gascoigne and Lipcius 2004). In the present model, the lower per capita predation risk at high densities, caused by the type 2 functional response, lead to a component Allee effect. The pattern became more complicated when territories were limiting. At very limited territories, no Allee effect was present. When territory limitation was present but not extreme, an Allee effect was still evident at low densities because of the saturating nature of predation mortality. There was, however, a threshold beyond which recruits per spawner began to decline. The compensatory decline in recruits per spawner at high densities was caused by territory limitation at high densities. As territories become less limiting, the threshold between Allee and compensatory dynamics shifted to higher densities.

Component Allee effects have been identified in fishes. In salmonids, the attributed mechanism for these effects is predator saturation (see review in Kramer et al. 2009). In a study on experimentally released juvenile Atlantic salmon, Ward et al. (2008a) found that Allee effects were increasingly likely to be observed with increases in predation mortality, an observation consistent with what is reported here. Although Ward et al. (2008a)'s results reveal how predation mortality could result in an Allee effect, they do not identify an effect of spawner density, which in these simulations could lead to a

threshold between Allee and compensatory effects (when coupled with territory limitation).

The presence of Allee effects depends not only on the relative predation level (Ward et al. 2008a, present study) and on the degree of territory limitation, but also on the density of the spawner population. Given that component Allee effects have been reported in salmon (Wood 1987, Ward et al. 2008a, present study), an important question is whether these scale up to demographic Allee effects (i.e. reduced per-capita population growth-rate; Stephens et al. 1999). Compensation in other aspects of fitness could mean that a component Allee effect does not result in a demographic one (Stephens et al. 1999). Ward et al. (2008b) found, for example, that there was a positive relationship between the number of surviving young-of-the-year Atlantic salmon and the number of yearlings in the next year, implying that compensation does not negate the component Allee effects at the yearling stage. Evidence for demographic Allee effects have also been documented in some Pacific salmon stocks (Myers et al. 1995, Chen et al. 2002), although Barrowman et al. (2003) found that, when evident at all, demographic Allee effects occurred only at very low densities. It can, however, be difficult to detect Allee effects because of the few data points that are typically available at low densities (Gurney et al. 2010). If component Allee effects translate to demographic effects, there will be population-level implications for extinction risks of small populations. This is especially true if Allee effects are likely to be realized in conjunction with variable recruitment, given that this further increases the probability of extinction in small populations (Routledge and Irvine 1999). The effect of variable recruitment may strengthen the negative consequences of the Allee effect.

## VI. Overall implications

Overall, the direction and amount that the traits explored here are predicted to be favoured by selection could vary from year to year, depending on the conditions present. Selection on spawning timing, for example, almost certainly varies with spawner density (Einum et al. 2008), but, as these simulations suggest, the benefit of maternal size varies with the environmental context. Increased benefit of large maternal size, for instance, may only be apparent in situations for which spawner density is low, or for which the availability of territories for juveniles at the time of emergence is limited. Additionally, non-density related factors may be important; predation, for example, is known to reverse the direction of density dependence in juvenile salmonids (Ward et al. 2008a). Low-water years could result in less useable habitat which could, in turn, favour early emergence, whereas higher water years could result in more useable territories, but higher predation pressure, thereby favouring later emergence.

Changes in population size are also likely to affect maternal fitness. As spawner population increases, it becomes increasingly important to emerge earlier and it will also be more important to be larger to survive long enough to acquire a territory. However, there will also be increased risk of superimposition, which affects small females more than large ones. To avoid superimposition, small females might have to spawn later in the season which would then put them at a further fitness disadvantage at higher population sizes. The fundamental point here, then, is that selection on traits such as body size, which is almost always positively correlated with fitness *ceteris paribus*, is likely to be context dependent.

## *VII. Influence of assumptions*

As with all models, there are a number of simplifying assumptions that were incorporated into the present model. Some the functional relationships in the model did not have empirically based equivalents that could be obtained from the literature. At the superimposition stage, for example, there are three major assumptions which have the potential to affect the results. The first of these is the function between number of redds and spawner density (Equation 5). The output of this equation was intended to match literature values associated with superimposition, while still allowing the identity of superimposed redds to vary, thus allowing one to explore how various maternal attributes, such as spawning time and body size, might affect superimposition risk and egg survival after superimposition. Because this function was assigned empirically, and not mechanistically, this could result in undue simplicity. However, by using this formulation, it allowed me to describe the relationship between spawner density and percentage of redds superimposed, thereby setting the stage for an exploration of the remaining aspects in a realistic framework. I decided that this was preferable to a superimposition-spawner density relationship that was not consistent with available evidence.

The second simplifying assumption that females excavate a single redd, rather than multiple redds, is not always biologically accurate (e.g. Taggart et al. 2001). However, an increase in the number of redd sites would likely be associated with an increased risk of superimposition at the population level, given that there would be more digging by females, and this may well overcome any substantive benefit that might accrue from the construction of more redds. Furthermore, in terms of number of



surviving juveniles post-emergence, the production of multiple redds, unless they were spaced out in time, may not be sufficient to dominate the maternal fitness consequences associated with the production of late- versus early-emerging offspring.

The third key assumption at the superimposition stage is spawning season duration. A longer spawning season (and hence a longer period of emergence by juveniles) than the one considered here would increase the duration of the post-emergence period. It may also result in a greater disparity in body sizes among emergent offspring, which may then have consequences to offspring survival, and may result in the persistence of a greater range of body size differences through time than that considered here.

There are a number of model assumptions for the simulations of the post-emergence period which could affect the qualitative results outlined here. Two of the major ones include the functional shape of the territory acquisition function (Equation 7) and predation functional response (Equation 13).

The predator functional response is based on information provided by Fresh and Schroder (1987). The saturating nature of the type 2 functional response chosen here was important for generating patterns such as the Allee effects. However, it is fairly reasonable *a priori* to assume that the functional response would represent some kind of saturating curve (e.g. type 2 or type 3 functional response) and this assumption would seem justifiable. A non-saturating function (e.g. type 1) would not have included a predator satiation effect and would, as a consequence, have been expected to affect the qualitative results presented. This was not modeled because it is unlikely that salmonid predators would exhibit such a functional response in nature, given that at some level

predator constraints in handling time or feeding rate will cause a limit to the number of prey which can be eaten at any one time (Peterman and Gatto 1978), and given the ubiquity of saturating functional feeding responses in nature (Hassell, 1979).

The other function of concern is the territory function. To the best of my knowledge, this function has not been previously quantified and is not, thus, empirically grounded quantitatively. However, the important qualitative patterns arising from this function are attributable to the way in which it limits the total number of territories. Essentially, as long as functional choices limited the absolute number of territories, and probability of territory acquisition does not increase as density increases (which is biologically unlikely), the qualitative patterns reported here should remain unaltered.

Temperature also has the potential to influence the fitness consequences associated with body size because of its influence on growth rate. However, given that the size differences between juveniles considered here are not large (within 0.2g for early compared to late spawned juveniles at the start of the spawning season), differences in temperature would be expected to have the same effect on all individuals and would not be expected to alter the relative size differences sufficiently to generate significant differences in predation risk.

This model focused on egg and early life survival, this time frame was selected primarily because it reflects a window during which mortality is highest in life (Elliott 1989). Towards the latter parts of the initial season post emergence, other factors are expected to influence juvenile survival, such as the changes in territory size concomitant with fish growth (Grant and Kramer 1990), changes in growth trajectories affected by

maturation and smoltification (e.g. Jonsson and Jonsson 1998), and energetically-based preparations for winter survival (Post and Parkinson 2001).

### *VIII. Conclusions*

The present study identifies areas that remain to be explored. These include the effect at the individual level of superimposition on egg survival within redds. More work is needed to better understand how population density affects territory acquisition. Additionally, further investigation into population behaviour at low density is needed to try to better understand whether Allee effects are evident at small population sizes and, if so, to try to identify the circumstances under which they arise.

The present study explored the influences of various sources of mortality during the embryo and early juvenile stages on maternal fitness in salmonids. In cases for which maternal size influenced maternal fitness, large body size was favoured. This occurred throughout the egg stage, and when post emergence predation was low, territories were limited, and/or spawner density was high. Spawning time was also important for juvenile survival although in a manner which was dependent on mortality sources. At the egg stage, the influence of superimposition favoured later-spawning females. Territory limitation tended to favour early-spawned juveniles whereas high predation mortality tended to favour later-spawned individuals. There were also component Allee effects evident, driven by predation saturation, although the magnitude depended on mortality sources. The fitness consequences of maternal phenotype can vary greatly depending on the sources of mortality present. These sources of offspring mortality in early life are context-dependent, and may vary between habitats or between years. This context-

dependence increases the difficulty in identifying the correlates of maternal fitness in salmonid fishes.

## WORKS CITED

- Addison B. A., K. C. Klasing, W. D. Robinson, S. H. Austin, and R. E. Ricklefs. 2009. Ecological and life-history factors influencing the evolution of maternal antibody allocation: a phylogenetic comparison. *Proceedings of the Royal Society B: Biological Sciences* **276**:3979.
- Anderson J. H., P. L. Faulds, W. I. Atlas, G. R. Pess, and T. P. Quinn. Selection on breeding date and body size in colonizing coho salmon, *Oncorhynchus kisutch*. *Molecular ecology* **19**: 2562–2573.
- Armitage K. B., J. F. Downhower, and G. E. Svendsen. 1976. Seasonal changes in weights of marmots. *American Midland Naturalist* **96**:36-51.
- Bagenal T. B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L. *Journal of fish biology* **1**:349-353.
- Bailey M., M. Kinnison. 2010. Habitat-mediated size selection in endangered Atlantic salmon fry: selectional restoration assessment. *Evolutionary Applications* **3**:352-362.
- Barber-Meyer S. M., L. D. Mech, and P. J. White. 2009. Elk calf survival and mortality following wolf restoration to Yellowstone National Park. *Wildlife Monographs* **169**:1-30.
- Barrowman N. J., R. A. Myers, R. Hilborn, D. G. Kehler, and C. A. Field. 2003. The variability among populations of coho salmon in the maximum reproductive rate and depensation. *Ecological Applications* **13**:784-793.
- Batchelder H. P., R. Williams. 1995. Individual-based modelling of the population dynamics of *Metridia lucens* in the North Atlantic. *ICES Journal of Marine Science* **52**:469.
- Bauwens D., R. F. Verheyen. 1985. The Timing of Reproduction in the Lizard *Lacerata vivipara*: Differences between Individual Females. *Journal of Herpetology* **19**:353-364.
- Beacham T. D., C. B. Murray. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1755-1765.
- Berg O. K., A. P. Hendry, B. Svendsen, C. Bech, J. V. Arnekleiv, and A. Lohrmann. 2001. Maternal provisioning of offspring and the use of those resources during ontogeny: variation within and between Atlantic salmon families. *Functional Ecology* **15**:13-23.

- Bernardo J. 1996. Maternal Effects in Animal Ecology. Integrative and Comparative Biology **36**:83-105.
- Bestgen K. R., D. W. Beyers, J. A. Rice, and G. B. Haines. 2006. Factors affecting recruitment of young Colorado pikeminnow: synthesis of predation experiments, field studies, and individual-based modeling. Transactions of the American Fisheries Society **135**:1722-1742.
- Blanchfield P. J., M. S. Ridgway. 1997. Reproductive timing and use of redd sites by lake-spawning brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **54**:747-756.
- Boltnev A. I., A. E. York. 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. Journal of Zoology **254**:219-228.
- Boltnev A. I., A. E. York, and G. A. Antonelis. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. Canadian Journal of Zoology **76**:843-854.
- Bonduriansky R., T. Day. 2009. Nongenetic Inheritance and Its Evolutionary Implications. Annual Review of Ecology, Evolution, and Systematics **40**:103-125.
- Bowyer R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy **79**:1332-1344.
- Brännäs E. 1995. First access to territorial space and exposure to strong predation pressure: A conflict in early emerging Atlantic salmon (*Salmo salar* L.) fry. Evolutionary Ecology **9**:411-420.
- Burner C. J. 1951. Characteristics of spawning nests of Columbia River salmon. Fishery Bulletin **52**:97.
- Cargnelli L. M., M. R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size, and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Canadian Journal of Fisheries and Aquatic Sciences **53**:360-367.
- Chadwick E. M. P. 1982. Stock-recruitment relationship for Atlantic salmon (*Salmo salar*) in Newfoundland rivers. Canadian Journal of Fisheries and Aquatic Sciences **39**:1496-1501.
- Charnov E. L., J. R. Krebs. 1974. On clutch-size and fitness. Ibis **116**:217-219.

- Chen D. G., J. R. Irvine, and A. J. Cass. 2002. Incorporating Allee effects in fish stock–recruitment models and applications for determining reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:242-249.
- Chilvers B. L., B. C. Robertson, I. S. Wilkinson, and P. J. Duignan. 2007. Growth and survival of New Zealand sea lions, *Phocarctos hookeri*: birth to 3 months. *Polar Biology* **30**:459-469.
- Civantos E., A. Salvador, and J. P. Veiga. 1999. Body size and microhabitat affect winter survival of hatchling *Psammmodromus algirus* lizards. *Copeia* **1999**:1112-1117.
- Collett D. 2003. Modelling binary data. Chapman and Hall, London.
- Cooke F., C. S. Findlay, and R. F. Rockwell. 1984. Recruitment and the timing of reproduction in Lesser Snow Geese (*Chen caerulescens caerulescens*). *The Auk* **101**:451-458.
- Côté S. D., M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**:230-238.
- Couvillon M. J., A. Dornhaus. 2009. Location, location, location: larvae position inside the nest is correlated with adult body size in worker bumble-bees (*Bombus impatiens*). *Proceedings of the Royal Society B: Biological Sciences* **276**:2411.
- Crecco V. A., T. F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissima*, in the Connecticut River. *Canadian Journal of Fisheries and Aquatic Sciences* **42**:1640-1648.
- Crisp D. T., P. A. Carling. 1989. Observations on siting, dimensions and structure of salmonid redds. *Journal of fish biology* **34**:119-134.
- Crowder L. B., J. A. Rice, T. J. Miller, and E. A. Marschall. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. Pages 237-255 *In* D. L. De Angelis and L. J. Gross, editors. Chapman & Hall, New York.
- Crozier W. W., G. J. A. Kennedy. 1995. The relationship between a summer fry (0+) abundance index, derived from semi-quantitative electrofishing, and egg deposition of Atlantic salmon, in the River Bush, Northern Ireland. *Journal of Fish Biology* **47**:1055-1062.
- Cutts C. J., B. Brembs, N. B. Metcalfe, and A. C. Taylor. 1999a. Prior residence, territory quality and life-history strategies in juvenile Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* **55**:784-794.

- Cutts C., N. Metcalfe, and A. Taylor. 1999b. Competitive asymmetries in territorial juvenile Atlantic salmon, *Salmo salar*. *Oikos* **86**:479.
- Daan S., J. Tinbergen. 1979. Young Guillemots *Uria lomvia* leaving their Arctic breeding cliffs: a daily rhythm in numbers and risk. *Ardea* **67**:96-100.
- DeVries P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:1685-1698.
- Dickerson B. R., T. P. Quinn, and M. F. Willson. 2002. Body size, arrival date, and reproductive success of pink salmon, *Oncorhynchus gorbuscha*. *Ethology Ecology & Evolution* **14**:29-44.
- Dloniak S. M., J. A. French, and K. E. Holekamp. 2006. Rank-related maternal effects of androgens on behaviour in wild spotted hyaenas. *Nature* **440**:1190-1193.
- Doctor K., T. Quinn. 2009. Potential for adaptation-by-time in sockeye salmon (*Oncorhynchus nerka*): the interactions of body size and in-stream reproductive life span with date of arrival and breeding location. *Canadian Journal of Zoology* **87**:708-717.
- Dusek A., L. Bartos, and L. Svecová. 2007. The effect of a mother's rank on her offspring's pre-weaning rank in farmed red deer. *Applied Animal Behaviour Science* **103**:146-155.
- Edo K., H. Kawamura, and S. Higashi. 2000. The structure and dimensions of redds and egg pockets of the endangered salmonid, Sakhalin taimen. *Journal of Fish Biology* **56**:890-904.
- Einum S., I. A. Fleming. 2000. Selection against late emergence and small offspring in Atlantic salmon (*Salmo salar*). *Evolution* **54**:628-639.
- Einum S., I. A. Fleming. 1999. Maternal effects of egg size in brown trout (*Salmo trutta*): norms of reaction to environmental quality. *Proceedings of the Royal Society B: Biological Sciences* **266**:2095-2100.
- Einum S., L. Sundt-Hansen, and K. H. Nislow. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. *Oikos* **113**:489-496.
- Einum S., M. T. Kinnison, and A. P. Hendry. 2004. Evolution of egg size and number. Pages 127–153 In A. P. Hendry and S. C. Stearns, editors. *Evolution Illuminated: Salmon and their Relatives*, Oxford University Press, Oxford.



- Einum S., A. P. Hendry, and I. A. Fleming. 2002. Egg-size evolution in aquatic environments: does oxygen availability constrain size? *Proceedings of the Royal Society of London. Series B: Biological Sciences* **269**:2325.
- Einum S., G. Robertsen, and I. Fleming. 2008. Adaptive landscapes and density-dependent selection in declining salmonid populations: going beyond numerical responses to human disturbance. *Evolutionary Applications* **1**:239-251.
- Elliott J. M. 1984. Numerical changes and population regulation in young migratory trout *Salmo trutta* in a Lake District stream, 1966-83. *Journal of Animal Ecology* **53**:327-350.
- Elliott J. M. 1986. Spatial distribution and behavioural movements of migratory trout *Salmo trutta* in a Lake District stream. *The Journal of Animal Ecology* **55**:907-922.
- Elliott J. M. 1989. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. I. The critical time for survival. *The Journal of Animal Ecology* :987-1001.
- Elliott J. 1990. Mechanisms responsible for population regulation in young migratory trout, *Salmo trutta*. III. The role of territorial behaviour. *The Journal of Animal Ecology* :803-818.
- Elliott J. M., and M. A. Hurley. 1998. An individual-based model for predicting the emergence period of sea trout fry in a Lake District stream. *Journal of Fish Biology* **53**:414-433.
- Elliott J. M., M. A. Hurley, and R. J. Fryer. 1995. A new, improved growth model for brown trout, *Salmo trutta*. *Functional Ecology* :290-298.
- Emlen S. T., N. J. Demong. 1975. Adaptive significance of synchronized breeding in a colonial bird: a new hypothesis. *Science* **188**:1029.
- Essington T. E., P. W. Sorensen, and D. G. Paron. 1998. High rate of redd superimposition by brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in a Minnesota stream cannot be explained by habitat availability alone. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:2310-2316.
- Estes R. D. 1976. The significance of breeding synchrony in the wildebeest. *African Journal of Ecology* **14**:135-152.
- Feder C., J. G. A. Martin, M. Festa-Bianchet, C. Berube, and J. Jorgenson. 2008. Never too late? Consequences of late birthdate for mass and survival of bighorn lambs. *Oecologia* **156**:773-781.

- Findlay C. S., F. Cooke. 1982. Breeding synchrony in the lesser snow goose (*Anser caerulescens caerulescens*). I. Genetic and environmental components of hatch date variability and their effects on hatch synchrony. *Evolution* **36**:342-351.
- Fleming I. A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Reviews in Fish Biology and Fisheries* **6**:379-416.
- Fleming I. A., J. D. Reynolds. 2004. Salmonid Breeding Systems. Pages 278-281 *In* A. P. Hendry and S. C. Stearns, editors. *Evolution Illuminated*, Oxford University Press, USA.
- Fleming I. A., M. R. Gross. 1994. Breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*): measures of natural and sexual selection. *Evolution* **48**:637-657.
- Foot C. J. 1990. An experimental comparison of male and female spawning territoriality in a Pacific salmon. *Behaviour* **115**:283-314.
- Forseth T., M. A. Hurley, A. J. Jensen, and J. M. Elliott. 2001. Functional models for growth and food consumption of Atlantic salmon parr, *Salmo salar*, from a Norwegian river. *Freshwater Biology* **46**:173-186.
- Foster W. A., J. E. Treherne. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature* **293**:466-467.
- Franken R. J., D. S. Hik. 2004. Interannual variation in timing of parturition and growth of collared pikas (*Ochotona collaris*) in the southwest Yukon. *Integrative and Comparative Biology* **44**:186.
- Fresh K. L., S. L. Schroder. 1987. Influence of the abundance, size, and yolk reserves of juvenile chum salmon (*Oncorhynchus keta*) on predation by freshwater fishes in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:236-243.
- Gardiner R., P. Shackley. 1991. Stock and recruitment and inversely density-dependent growth of salmon, *Salmo salar* L., in a Scottish stream. *Journal of Fish Biology* **38**:691-696.
- Gascoigne J. C., R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Applied Ecology* **41**:801-810.
- Gentleman W. C., A. B. Neuheimer, and R. G. Campbell. 2008. Modelling copepod development: current limitations and a new realistic approach. *ICES Journal of Marine Science* **65**:399.

- Gentleman W., A. Leising, B. Frost, S. Strom, and J. Murray. 2003. Functional responses for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. *Deep-Sea Research* **50**:2847-2875.
- Gillis E. A. 1998. Survival of juvenile hares during a cyclic population increase. *Canadian Journal of Zoology* **76**:1949-1956.
- Godin J. G. J. 1980. Temporal aspects of juvenile pink salmon (*Oncorhynchus gorbuscha* Walbaum) emergence from a simulated gravel redd. *Canadian Journal of Zoology* **58**:735-744.
- Good S. P., J. J. Dodson, M. G. Meekan, and D. A. J. Ryan. 2001. Annual variation in size-selective mortality of Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **58**:1187-1195.
- Götmark F. 2002. Predation by sparrowhawks favours early breeding and small broods in great tits. *Oecologia* **130**:25-32.
- Grand J. B., P. L. Flint. 1996. Survival of northern pintail ducklings on the Yukon-Kuskokwim Delta, Alaska. *Condor* **98**:48-53.
- Grant J. W. A., D. L. Kramer. 1990. Territory size as a predictor of the upper limit to population density of juvenile salmonids in streams. *Canadian Journal of Fisheries and Aquatic Sciences* **47**:1724-1737.
- Green B. S. 2008. Maternal effects in fish populations. *Advances in Marine Biology* **54**:1-105.
- Green W. C. H., A. Rothstein. 1993. Persistent influences of birth date on dominance, growth and reproductive success in bison. *Journal of Zoology* **230**:177-186.
- Gregg M. A., M. Bray, K. M. Kilbride, and M. R. Dunbar. 2001. Birth synchrony and survival of pronghorn fawns. *The Journal of Wildlife Management* **65**:19-24.
- Grover M. C. 2005. Changes in size and age at maturity in a population of kokanee *Oncorhynchus nerka* during a period of declining growth conditions. *Journal of Fish Biology* **66**:122-134.
- Guilhem C., J. F. Gerard, and E. Bideau. 2002. Rank acquisition through birth order in mouflon sheep (*Ovis gmelini*) ewes. *Ethology* **108**:63-73.

- Gurney W. S. C., P. J. Bacon, E. McKenzie, P. McGinnity, J. Mclean, G. Smith, and A. Youngson. 2010. Form and uncertainty in stockrecruitment relations: observations and implications for Atlantic salmon (*Salmo salar*) management. *Canadian Journal of Fisheries and Aquatic Sciences* **67**:1040-1055.
- Gustafson-Greenwood K. I., J. R. Moring. 1990. Territory size and distribution of newly-emerged Atlantic salmon (*Salmo salar*). *Hydrobiologia* **206**:125-131.
- Halle S. 1993. Wood mice (*Apodemus sylvaticus* L.) as pioneers of recolonization in a reclaimed area. *Oecologia* **94**:120-127.
- Handeland S. O., A. K. Imsland, and S. O. Stefansson. 2008. The effect of temperature and fish size on growth, feed intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture* **283**:36-42.
- Harris M. P., D. J. Halley, and S. Wanless. 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. *Ibis* **134**:335-339.
- Harwood A. J., J. D. Armstrong, N. B. Metcalfe, and S. W. Griffiths. 2003. Does dominance status correlate with growth in wild stream-dwelling Atlantic salmon (*Salmo salar*)? *Behavioral Ecology* **14**:902.
- Hassell, M.P. 1978. The dynamics of arthropod predator-prey systems. Princeton University Press: New Jersey.
- Hatchwell B. 1991. An experimental study of the effects of timing of breeding on the reproductive success of common guillemots (*Uria aalge*). *The Journal of Animal Ecology* **60**:721-736.
- Hayes J. W. 1987. Competition for spawning space between brown (*Salmo trutta*) and rainbow trout (*S. gairdneri*) in a lake inlet tributary, New Zealand. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:40-47.
- Heath D. D., C. W. Fox, and J. W. Heath. 1999. Maternal effects on offspring size: variation through early development of chinook salmon. *Evolution* **53**:1605-1611.
- Henderson J. N., B. H. Letcher. 2003. Predation on stocked Atlantic salmon (*Salmo salar*) fry. *Canadian Journal of Fisheries and Aquatic Sciences* **60**:32-42.
- Henderson P., R. Holmes, and R. Bamber. 1988. Size-selective overwintering mortality in the sand smelt, *Atherina boyeri* Risso, and its role in population regulation. *Journal of fish biology* **33**:221-233.

- Hendry A. P., T. Day, and A. B. Cooper. 2001a. Optimal Size and Number of Propagules: Allowance for Discrete Stages and Effects of Maternal Size on Reproductive Output and Offspring Fitness. *The American Naturalist* **157**:387-407.
- Hendry A. P., O. K. Berg, and T. P. Quinn. 2001b. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (life span, energy stores). *Oikos* **93**:407.
- Hendry A. P., O. K. Berg, and T. P. Quinn. 1999. Condition dependence and adaptation-by-time: breeding date, life history, and energy allocation within a population of salmon. *Oikos* **85**:499.
- Holekamp K. E., L. Smale. 1991. Dominance acquisition during mammalian social development: the "inheritance" of maternal rank. *Integrative and Comparative Biology* **31**:306.
- Holtby L. B., M. C. Healey. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Sciences* **43**:1946-1959.
- Höök T. O., E. S. Rutherford, T. E. Croley, D. M. Mason, and C. P. Madenjian. 2008. Annual variation in habitat-specific recruitment success: implications from an individual-based model of Lake Michigan alewife (*Alosa pseudoharengus*). *Canadian Journal of Fisheries and Aquatic Sciences* **65**:1402-1412.
- Huntingford F., C. Garcia de Leaniz. 1997. Social dominance, prior residence and the acquisition of profitable feeding sites in juvenile Atlantic salmon. *Journal of Fish Biology* **51**:1009-1014.
- Huston M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. *Bioscience* **38**:682-691.
- Ingendahl D. 2001. Dissolved oxygen concentration and emergence of sea trout fry from natural redds in tributaries of the River Rhine. *Journal of Fish Biology* **58**:325-341.
- Jones M., A. Laurila, N. Peuhkuri, J. Piironen, and T. Seppa. 2003. Timing an ontogenetic niche shift: responses of emerging salmon alevins to chemical cues from predators and competitors. *Oikos* **102**:155.
- Jonsson B., T. Forseth, A. J. Jensen, and T. F. Naesje. 2001. Thermal performance of juvenile Atlantic Salmon, *Salmo salar* L. *Functional Ecology* **15**:701-711.

- Jonsson N., B. Jonsson, and I. A. Fleming. 1996. Does early growth cause a phenotypically plastic response in egg production of Atlantic salmon? *Functional Ecology* **10**:89-96.
- Jonsson N., B. Jonsson. 1998. Body composition and energy allocation in life-history stages of brown trout. *Journal of Fish Biology* **53**:1306-1316.
- Jonsson N., B. Jonsson. 1999. Trade-off between egg mass and egg number in brown trout. *Journal of Fish Biology* **55**:767-783.
- Jarnemo A., O. Liberg, S. Lockowandt, A. Olsson, and K. Wahlström. 2004. Predation by red fox on European roe deer fawns in relation to age, sex, and birth date. *Canadian Journal of Zoology* **82**:416-422.
- Kamler E. 2005. Parent-egg-progeny relationships in teleost fishes: an energetics perspective. *Reviews in Fish Biology and Fisheries* **15**:399-421.
- Kaplan C. C., G. C. White, and B. R. Noon. 2008. Neonatal survival of Steller sea lions (*Eumetopias jubatus*). *Marine Mammal Science* **24**:443-461.
- Keeley E. 2000. An experimental analysis of territory size in juvenile steelhead trout. *Animal Behaviour* **59**:477-490.
- Keeley E. 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* **82**:1247-1259.
- Keeley E. R., J. W. A. Grant. 1995. Allometric and environmental correlates of territory size in juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **52**:186-196.
- Kelly M. G., D. A. Levin. 1997. Fitness consequences and heritability aspects of emergence date in *Phlox drummondii*. *Journal of Ecology* **85**:755-766.
- Koskela J., J. Pirhonen, and M. Jobling. 1997. Feed intake, growth rate and body composition of juvenile Baltic salmon exposed to different constant temperatures. *Aquaculture International* **5**:351-360.
- Kramer A. M., B. Dennis, A. M. Liebhold, and J. M. Drake. 2009. The evidence for Allee effects. *Population Ecology* **51**:341-354.
- Kraus C., D. L. Thomson, J. Kuenkele, and F. Trillmich. 2005. Living slow and dying young? Life-history strategy and age-specific survival rates in a precocial small mammal. *Journal of Animal Ecology* **74**:171-180.

- Kutsukake N. 2000. Matrilineal rank inheritance varies with absolute rank in Japanese macaques. *Primates* **41**:321-335.
- Landa K. 1992. Seasonal declines in offspring fitness and selection for early reproduction in nymph-overwintering grasshoppers. *Evolution* :121-135.
- Laplante-Albert K., M. Rodriguez, and P. Magnan. 2010. Quantifying habitat-dependent mortality risk in lacustrine fishes by means of tethering trials and survival analyses. *Environmental Biology of Fishes* **87**:263-273.
- Lapointe M., B. Eaton, S. Driscoll, and C. Latulippe. 2000. Modelling the probability of salmonid egg pocket scour due to floods. *Canadian Journal of Fisheries and Aquatic Sciences* **57**:1120-1130.
- Larsson S., I. Berglund. 2005. The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* L.) from four Swedish populations. *Journal of thermal biology* **30**:29-36.
- Liermann H. 2001. Depensation: evidence, models and implications. *Fish and Fisheries* **2**:33-58.
- Lomas L. A., L. C. Bender. 2007. Survival and cause-specific mortality of neonatal mule deer fawns, north-central New Mexico. *Journal of Wildlife Management* **71**: 884-894.
- McCullagh P. N., J. A. Nelder. 1983. *Generalized Linear Models*. Chapman and Hall, Great Britian.
- McLoughlin P. D., T. Coulson, and T. Clutton-Brock. 2008. Cross-generational effects of habitat and density on life history in red deer. *Ecology* **89**:3317-3326.
- McNeil W. J. 1964. Redd superimposition and egg capacity of pink salmon spawning beds. *Journal of the Fisheries Research Board of Canada* **21**:1385-1395.
- McPhee M. V., T. P. Quinn. 1998. Factors affecting the duration of nest defense and reproductive lifespan of female sockeye salmon, *Oncorhynchus nerka*. *Environmental Biology of Fishes* **51**:369-375.
- Metcalf N., J. Thorpe. 1992. Early predictors of life-history events: the link between first feeding date, dominance and seaward migration in Atlantic salmon, *Salmo salar* L. *Journal of fish biology* **41**:93-99.
- Miller T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**:1657-1670.

- Monteith K. L., L. E. Schmitz, J. A. Jenks, J. A. Delger, and R. T. Bowyer. 2009. Growth of male white-tailed deer: consequences of maternal effects. *Journal of Mammology* **90**:651-660.
- Montgomery D. R., J. M. Buffington, N. P. Peterson, D. Schuett-Hames, and T. P. Quinn. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Canadian Journal of Fisheries and Aquatic Sciences* **53**:1061-1070.
- Morita K., A. Yokota. 2002. Population viability of stream-resident salmonids after habitat fragmentation: a case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual based model. *Ecological Modelling* **155**:85-94.
- Mousseau T. A., C. W. Fox. 1998. The adaptive significance of maternal effects. *Trends in Ecology & Evolution* **13**:403-407.
- Myers R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. *Science* **269**:1106.
- Nadeau P. S., S. G. Hinch, L. B. Pon, and D. A. Patterson. 2009. Persistent parental effects on the survival and size, but not burst swimming performance of juvenile sockeye salmon *Oncorhynchus nerka*. *Journal of fish biology* **75**:538-551.
- Nakano S. 1995. Individual differences in resource use, growth and emigration under the influence of a dominance hierarchy in fluvial red-spotted masu salmon in a natural habitat. *Journal of Animal Ecology* **64**:75-84.
- Narimatsu Y., H. Munehara. 1999. Spawn date dependent survival and growth in the early life stages of *Hypoptychus dybowskii* (Gasterosteiformes). *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1849-1855.
- Nazarova G. G., V. I. Evsikov. 2008. Effect of Mother's Physical Condition during Pregnancy and Lactation on Postnatal Growth and Reproductive Success of Offspring in Water Vole *Arvicola terrestris*. *Russian Journal of Developmental Biology* **39**: 100-107.
- Neuheimer A. B., W. C. Gentleman, P. Pepin, and E. J. H. Head. 2009. How to build and use individual-based models (IBMs) as hypothesis testing tools. *Journal of Marine Systems* **81**:122-133.
- Noble C., S. Kadri, D. F. Mitchell, and F. A. Huntingford. 2008. Growth, production and fin damage in cage-held 0 Atlantic salmon pre-smolts (*Salmo salar* L.) fed either a) on-demand, or b) to a fixed satiation–restriction regime: Data from a commercial farm. *Aquaculture* **275**:163-168.



- Nomoto K., H. Omiya, T. Sugimoto, K. Akiba, K. Edo, and S. Higashi. 2010. Potential negative impacts of introduced rainbow trout on endangered Sakhalin taimen through redd disturbance in an agricultural stream, eastern Hokkaido. *Ecology of Freshwater Fish* **19**:116-126.
- O'Connor K. I., N. B. Metcalfe, and A. C. Taylor. 2000. The effects of prior residence on behavior and growth rates in juvenile Atlantic salmon (*Salmo salar*). *Behavioral Ecology* **11**:13-18.
- O'Donoghue M., S. Boutin. 1995. Does reproductive synchrony affect juvenile survival rates of northern mammals? *Oikos* **74**:115-121.
- Ojanguren A. F., F. G. Reyes-Gavilán, and F. Brana. 2001. Thermal sensitivity of growth, food intake and activity of juvenile brown trout. *Journal of Thermal Biology* **26**:165-170.
- Ottaway E., P. Carling, A. Clarke, and N. Reader. 1981. Observations on the structure of brown trout, *Salmo trutta* Linnaeus, redds. *Journal of Fish Biology* **19**:593-607.
- Parkinson E. A., J. R. Post, and S. P. Cox. 2004. Linking the dynamics of harvest effort to recruitment dynamics in a multistock, spatially structured fishery. *Canadian Journal of Fisheries and Aquatic Sciences* **61**:1658-1670.
- Patterson I. J. 1965. Timing and spacing of broods in the Black-headed Gull *Larus ridibundus*. *Ibis* **107**:433-459.
- Pen I., F. J. Weissing, and S. Daan. 1999. Seasonal sex ratio trend in the European kestrel: an evolutionarily stable strategy analysis. *American Naturalist* **153**:384-397.
- Perry G. M. L., C. Audet, B. Laplatte, and L. Bernatchez. 2004. Shifting patterns in genetic control at the embryo-alevin boundary in brook charr. *Evolution* **58**:2002-2012.
- Peterman R. M., M. Gatto. 1978. Estimation of functional responses of predators on juvenile salmon. *Journal of the Fisheries Research Board of Canada* **35**:797-808.
- Petersen J. H., D. L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:2551-2565.
- Pilastro A., T. Gomiero, and G. Marin. 1994. Factor affecting body mass of young fat dormics (*Glis glis*) at weaning and by hibernation. *Journal of zoology* **234**:13-23.

- Pine III W. E., S. A. Ludsin, and D. R. DeVries. 2000. First-summer survival of largemouth bass cohorts: is early spawning really best? *Transactions of the American Fisheries Society* **129**:504-513.
- Post J. R., E. A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. *Ecology* **82**:1040-1051.
- Price T., M. Kirkpatrick, and S. Arnold. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240**:798-799.
- Puckett K. J., L. M. Dill. 1985. The energetics of feeding territoriality in juvenile coho salmon (*Oncorhynchus kisutch*). *Behaviour* **92**:97-111.
- Quinn T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Canada.
- Quinn T. P., S. Bloomberg. 1992. Fecundity of chinook salmon (*Oncorhynchus tshawytscha*) from the Waitaki and Rakaia Rivers, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **26**:429-434.
- Quinn T. P., P. McGinnity, and T. F. Cross. 2006. Long - term declines in body size and shifts in run timing of Atlantic salmon in Ireland. *Journal of Fish Biology* **68**:1713-1730.
- Reading R. P., D. Kenny, S. Amgalanbaatar, A. DeNicola, and G. Wingard. 2009. Argali lamb (*Ovis ammon*) morphometric measurements and survivorship in Mongolia. *Mammalia* **73**:98-104.
- Réale D., P. Boussès. 1999. Effects of summer and winter birth on growth of lambs in a population of feral sheep. *Journal of Mammalogy* :1028-1037.
- Réale D., A. G. McAdam, S. Boutin, and D. Berteaux. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**:591.
- Reinhardt U. G., T. Yamamoto, and S. Nakano. 2001. Effects of body size and predators on intracohort competition in wild and domesticated juvenile salmon in a stream. *Ecological Research* **16**:327-334.
- Resetarits Jr W. J., H. M. Wilbur. 1989. Choice of oviposition site by *Hyla chrysoscelis*: role of predators and competitors. *Ecology* **70**:220-228.
- Reznick D., E. Schultz, S. Morey, and D. Roff. 2006. On the virtue of being the first born: the influence of date of birth on fitness in the mosquitofish, *Gambusia affinis*.

- Oikos **114**:135-147.
- Ridley M. 2004. Evolution. Blackwell Publishing, USA.
- Rieger J. F. 1996. Body size, litter size, timing of reproduction, and juvenile survival in the Unita ground squirrel, *Spermophilus armatus*. Oecologia **107**:463-468.
- Robertson R. J. 1973. Optimal niche space of the Redwinged Blackbird: spatial and temporal patterns of nesting activity and success. Ecology **54**:1085-1093.
- Rödel H. G., A. Bora, P. Kaetzke, M. Khaschei, H. Hutzelmeyer, and D. von Holst. 2004. Over-winter survival in subadult European rabbits: weather effects, density dependence, and the impact of individual characteristics. Oecologia **140**:566-576.
- Roff D. A. 2002. Life History Evolution. Sinauer Associates Inc, USA.
- Rombough P. J. 2007. Oxygen as a constraining factor in egg size evolution in salmonids. Canadian Journal of Fisheries and Aquatic Sciences **64**:692-699.
- Routledge R. D., J. R. Irvine. 1999. Chance fluctuations and the survival of small salmon stocks. Canadian Journal of Fisheries and Aquatic Sciences **56**:1512-1519.
- Rutberg A. T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. American Naturalist **130**:692-710.
- Saito T., S. Nakano. 1999. Reproductive-timing-dependent alternation of offspring life histories in female threespine sticklebacks. Canadian journal of zoology **77**:1314-1321.
- Schluter D. 1988. Estimating the form of natural selection on a quantitative trait. Evolution **42**:849-861.
- Schultz E. T. 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformes: Embiotocidae). Evolution **47**:520-539.
- Scrivener J. C., M. J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences **46**:681-696.
- Seamons T. R., P. Bentzen, and T. P. Quinn. 2004. The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. Environmental Biology of Fishes **69**:333-334.
- Skibiell A. L., F. S. Dobson, and J. O. Murie. 2009. Maternal influences on reproduction in two populations of Columbian ground squirrels. Ecological Monographs **79**:325-

341.

- Slater J. J., T. E. Lankford, and J. A. Buckel. 2007. Overwintering ability of young-of-the-year bluefish *Pomatomus saltatrix*: effect of ration and cohort of origin on survival. *Marine Ecology Progress Series* **339**:259-269.
- Sman J., N. E. Phillips, and C. A. Pfister. 2009. Relative effects of maternal and juvenile food availability for a marine snail. *Ecology* **90**:3119-3125.
- Sogard S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**:1129-1157.
- Steen R. P., T. P. Quinn. 1999. Egg burial depth by sockeye salmon (*Oncorhynchus nerka*): implications for survival of embryos and natural selection on female body size. *Canadian Journal of Zoology* **77**:836-841.
- Steingrímsson S. O., J. W. A. Grant. 2008. Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**:448-457.
- Steingrímsson S. Ó., J. W. A. Grant. 1999. Allometry of territory size and metabolic rate as predictors of self-thinning in young-of-the-year Atlantic salmon. *Journal of Animal Ecology* **68**:17-26.
- Stephens P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? *Oikos* **87**:185-190.
- Svärdson G. 1948. Natural selection and egg number in fish. *Reports of the Institute of Fresh-water Research* **29**: 115-122.
- Svensson E. 1997. Natural selection on avian breeding time: causality, fecundity-dependent, and fecundity-independent selection. *Evolution* **51**:1276-1283.
- Sweeney B. W., R. L. Vannote. 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* **36**:810-821.
- Taggart J. B., I. S. McLaren, D. W. Hay, J. H. Webb, and A. F. Youngson. 2001. Spawning success in Atlantic salmon (*Salmo salar* L.): a long-term DNA profiling-based study conducted in a natural stream. *Molecular ecology* **10**:1047-1060.
- Taniguchi Y., Y. Miyake, T. Saito, H. Urabe, and S. Nakano. 2000. Redd superimposition by introduced rainbow trout, *Oncorhynchus mykiss*, on native charrs in a Japanese stream. *Ichthyological Research* **47**:149-156.

- Testa J. W., E. F. Becker, and G. R. Lee. 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. *Journal of Mammalogy* **81**:162-168.
- Titus, R. 1990. Territorial behavior and its role in population regulation of young brown trout (*Salmo trutta*)-New Perspectives. *Annales Zoologici Fennici* **27**:119-130.
- Turnpenny A. W. H., R. Williams. 1980. Effects of sedimentation on the gravels of an industrial river system. *Journal of Fish Biology* **17**:681-693.
- Tyler J. A., E. S. Rutherford. 2007. River Restoration Effects on Steelhead Populations in the Manistee River, Michigan: Analysis Using an Individual-Based Model. *Transactions of the American Fisheries Society* **136**:1654-1673.
- van den Berghe E. P., M. R. Gross. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (coho: *Oncorhynchus kisutch*). *Evolution* **43**:125-140.
- van den Berghe E. P., M. R. Gross. 1984. Female size and nest depth in coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of Fisheries and Aquatic Science* **41**:204-206.
- Verhulst S., J. H. Van Balen, and J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology* **76**:2392-2403.
- Ward D. M., K. H. Nislow, and C. L. Folt. 2008a. Predators reverse the direction of density dependence for juvenile salmon mortality. *Oecologia* **156**:515-522.
- Ward D. M., K. H. Nislow, and C. L. Folt. 2008b. Do native species limit survival of reintroduced Atlantic salmon in historic rearing streams? *Biological Conservation* **141**:146-152.
- Watts C. H. S. 1969. The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire. *The Journal of Animal Ecology* **38**:285-304.
- Watts H. E., J. B. Tanner, B. L. Lundrigan, and K. E. Holekamp. 2009. Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proceedings of the Royal Society B* **276**:2291-2298.
- Weeber M. A., G. R. Giannico, and S. E. Jacobs. 2010. Effects of Redd Superimposition by Introduced Kokanee on the Spawning Success of Native Bull Trout. *North American Journal of Fisheries Management* **30**:47-54.
- West C. J., P. A. Larkin. 1987. Evidence for size-selective mortality of juvenile sockeye salmon (*Oncorhynchus nerka*) in Babine Lake, British Columbia. *Canadian Journal*

- of Fisheries and Aquatic Sciences **44**:712-721.
- Whittaker D. G., F. G. Lindzey. 1999. Effect of coyote predation on early fawn survival in sympatric deer species. Wildlife Society Bulletin **27**:256-262.
- Williams K. S., K. G. Smith, and F. M. Stephen. 1993. Emergence of 13-Yr periodical cicadas (*Cicadidae: Magicicada*): phenology, mortality, and predators satiation. Ecology **74**:1143-1152.
- Wood C. C. 1987. Predation of juvenile Pacific salmon by the common merganser (*Mergus merganser*) on eastern Vancouver Island. I: Predation during the seaward migration. Canadian Journal of Fisheries and Aquatic Sciences **44**:941-949.
- Wright P. J., M. C. Bailey. 1996. Timing of hatching in *Ammodytes marinus* from Shetland waters and its significance to early growth and survivorship. Marine Biology **126**:143-152.
- Zadereev E. S., I. G. Prokopkin, V. G. Gubanov, and M. V. Gubanov. 2003. Individual-based model of the reproduction cycle of *Moina macrocopa* (Crustacea: Cladocera). Ecological Modelling **162**:15-31.