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Territorial behavior and its role in population regulation of young brown trout (*Salmo trutta*): new perspectives

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Territorial behavior and factors which influence aggression in young stream salmonids are briefly reviewed, as are characteristics of the territory and determinants of territory size. Population regulation of brown trout (*Salmo trutta*) fry is also reviewed and used as a type example for coupling stream-salmonid behavioral ecology to population dynamics. A comprehensive working hypothesis is proposed to explain the mechanisms behind population regulation which result in a dome-shaped stock-recruitment relationship in a migratory brown trout population: Parr recruitment increases with increasing egg or alevin (initial) density on the ascending portion of the curve; i.e. recruitment is positively density-dependent. Aggression rates among newly-emerged fry increase with progressively higher initial population densities, as does selection pressure for individuals with greater growth potential (GGP dominants). Beyond the optimum initial density where maximum parr recruitment is attained, GGP dominants continue to progressively increase their territory size by increasing attack distance toward territorial intruders, and exclude subordinates from assuming even suboptimal feeding positions. Increasing numbers of subordinates are forced to move downstream where they die due to malnutrition. Consequently, parr recruitment gradually decreases; i.e. recruitment becomes negatively density-dependent. The time taken to regulate numbers from high densities at emergence to stable, first-summer population levels becomes progressively shorter with increasing initial population density.

1. Introduction

The purpose of this paper is to update theory on the role of territorial behavior in population regulation of stream-dwelling salmonids, using the migratory form of brown trout (*Salmo trutta)* as the primary type example (for an earlier review, see Chapman 1966). Le Cren (1965, 1973) first suggested that intraspecific aggressive behavior of young brown trout as they establish feeding territories plays an important role in their population regulation. However, little progress has been made in linking stream-salmonid behavioral ecology to population dynamics. In this paper, results from the literature in various fish-research areas are pooled together to develop a conceptual framework with which to explore the mechanisms of population regulation in juvenile populations of territorial stream salmonids.

In order to understand regulatory mechanisms in fish populations, it is necessary to consider events occurring at the individual level within the population. Fish population parameters are too generalized by traditional fishery statistics to reveal such mechanisms. Great efforts in fisheries science have been devoted to determining non-mechanistic stock-recruitment relationships in fish populations, leaving what occurs in the pre-recruit stages (i.e. eggs, larvae, juveniles) as a *black box* (Gulland 1983). More interest has developed in the last 20 yr or so in the early life history of fishes and in determining mechanisms behind recruitment variation (e.g. Lasker & Sherman 1981, Miller et al. 1988). For stream salmonids, the concept of profitable stream positions (Fausch 1984) is quite useful as a theoretical framework because it relates the energetics of the fish to its chances for growth and survival. Another advancement, otolith microstructure analysis (e.g. Campana & Neilson 1985), has proven to be helpful in, for example, studying characteristics of individual fish larvae on a temporal basis (e.g. Rice et al. 1987, Titus & Mosegaard 1990) and elucidating selection processes during early recruitment stages. These developments can now be applied to further our understanding of how the behavioral ecology of young migratory brown trout acts as a mediator of population regulation and long-term maximization of fitness.

2. Terminology for different morphs and life stages

The brown trout is a polymorphic species which exhibits a variety of life history patterns. Although "brown trout" is the common name given for the species as a whole, it is also more specifically used to describe the morph which spends its entire life cycle in its natal stream (i.e. resident brown trout). Migratory trout are also common; in these anadromous populations, the juveniles remain in the natal stream for 1 yr or more before migrating either to a downstream lake ("lake-trout"), or to the sea as smolts ("sea-trout"), where they grow to maturity. (Note also that both resident and migrant morphs may exist within the same breeding population). Various life history patterns as well as other aspects of brown trout ecology are presented by Alm (1950), Allen (1951), Frost & Brown (1967), Elliott (1985a), Jonsson (1985), Elliott (1989b), and L'Abée-Lund et al. (1989).

Because the terminology for the early life stages of salmonids is often unclear, the convention of Allan & Ritter (1977) for migratory trout will be followed. The alevin stage lasts from hatching of the egg to the end of dependence on the yolk sac as the primary nutrition source. The fry stage begins at this point and lasts until dispersal from the redd (gravel nest) occurs, i.e. through emergence. The juvenile migratory trout is then termed a parr until it emigrates from the stream (sea-trout emigrate as smolts). The stream-resident morph follows the same early ontogeny but with omission of the migratory (smolt) stage. In the present context, "young" brown or migratory trout is used as a collective term for fry and parr.

3. Territorial behavior

Aggressive behavior of underyearling stream salmonids in connection with territorial defense was described during the 1950's (Hoar 1951, Stringer & Hoar 1955, Newman 1956, Kalleberg 1958, summarized by Chapman 1962). These studies gave definition to such behaviors as frontal and lateral threat displays, nipping, chasing, and fighting. Specific reference is often made to threat displays and nipping, the latter of which is generally assumed to be a more intensive act of aggression. In the present context, the various behaviors will be referred to primarily by their collective name, agonistic or aggressive behavior, because it is the result of this behavior in relation to the population that is of interest here.

Aggressive behavior begins shortly after emergence of the fry from the gravel redd and is associated with first-feeding in the free-swimming stage (Dill 1977). Kalleberg (1958) observed aggression between fry of Baltic (Atlantic) salmon (*Salmo salar*) as early as the first day after emergence. Similarly, Titus & Mosegaard (1990) observed aggressive behavior in migratory trout fry beginning 2.5 d after emergence. Aggressive interactions lead to dispersal of emerging fry clusters and aggression has been noted as a cause of downstream migration, e.g. in coho salmon (*Oncorhynchus kisutch*) by Chapman (1962).

The influence of various factors on intraspecific aggression has been investigated. Stringer & Hoar (1955) investigated the relationship between aggressiveness of underyearling Kamloops rainbow trout (*Oncorhynchus mykiss kamloops* formerly *Salmo gairdneri kamloops*) and decreasing light intensity (c. 162 to 3 lux, measured at the water surface). No major reduction in aggressiveness (no. nips/10 min) occurred until illumination was reduced to c. 43 lux, below which aggressiveness declined rapidly. With increasing illumination, aggressiveness increased rapidly and reached an asymptote, also at c. 43 lux. Because aggressive behavior ceased to occur at low light intensity, the authors reasoned that the releaser mechanism for aggressive behavior was visual in nature (see also Kalleberg 1958, Yamagishi 1962).

Kalleberg (1958) suggested that the development rate of aggression between fry was accelerated by increasing current velocity from 15 cm/s (development rates and higher current velocities were not quantified). As velocity increased, the fry were pressed toward the aquarium bottom and their aggressiveness increased. Hartman (1963) better quantified this relationship and found that with increasing current velocity (8 to 9, 18 to 19, and 28 to 30 cm/s) under spring conditions, the rate of aggressiveness (no. nips, displays and totals/fish/100 min) increased in yearling brown trout. He also found that intensity of aggressive behavior increased because rate of nipping increased at higher current velocities while rate of threatening decreased. Hartman reasoned that holding a stream position while assuming a threat display posture became progressively more difficult at higher velocities, and so intrusions by competing trout were more often met with nips. Grant & Noakes (1988) found that aggressiveness in young brook trout (*Salvelinus fontinalis*) also increased initially with increasing current velocity to a maximum at 6 cm/s for 20 to 29 mm fry. Aggressiveness decreased at higher current velocities, probably because of increased energetic costs of defense.

In relation to fry density, Kalleberg (1958) found that aggression among fry of trough-reared Baltic salmon increased with increasing fry density. At a relatively low density (2.5 fry/m^2), all fry held well-spaced territories and aggressive interactions were minimal. Aggressiveness (unquantified) increased as densities were increased to between 24.8 and 31.0 fry/m^2, beyond which interactions became so intense that stable occupation of territories no longer existed.

Yet another aspect is the influence of food and feeding on aggressive behavior. Kalleberg (1958) found that the frequency of aggressive contacts among Baltic salmon or brown trout fry was greatest during intensive feeding periods (e.g. during early morning and evening). Diel periodicity in aggressiveness as related to feeding activity was also reported for coho salmon fry (Mason & Chapman 1965), and rainbow and brook trouts (Newman 1956). Hartman (1963) observed an increase in aggression rates (nips plus threats/fish/unit time) in yearling brown trout after feeding in 78% of studied cases. Similar results were reported for young Atlantic salmon by Keenleyside & Yamamoto (1962). Thus, it seems that, within a feeding regime, aggression increases during intensive feeding periods. Between feeding regimes, Symons (1968) found that juvenile Atlantic salmon deprived of food were more aggressive than those receiving an abundance of food. Slaney & Northcote (1974) also reported a higher aggression rate between rainbow trout fry at a low prey level, and vice versa.

Studies on the influence of relative fish size on aggressiveness have produced somewhat disparate results. Stringer & Hoar (1955) showed that, between groups of underyearling Kamloops trout with lengths 60 to 65 mm, 50 to 55 mm, and 40 to 45 mm, the rate of attacks by larger fish upon smaller ones was 8.5 nips/10 min, while the rates for fish of equal size and for smaller fish attacking larger ones were much lower and about equal (2.5 and 2.6 nips/10 min, respectively). Similarly, Grant et al. (1989) found that 65.4% of aggressive acts among brook trout fry were directed at smaller fish, 16.4% at even-sized fish, and 18.2% at larger fish. In contrast, Chapman (1962) reported that coho salmon of near-equal length (57 to 58 mm) had nearly twice the nipping frequency (6.1 nips/10 min) as coho of unequal length (51 to 58 mm; 3.3 nips/10 min). Wankowski & Thorpe (1979) also found that the relationship between size differences and aggressiveness was inverse among juvenile Atlantic salmon. In the latter two cases, lower aggression rates between fish of widely differing size may have been due to one of the following reasons: either the size discrepancy was so large that the fish did not regard each other as competitors, or the larger fish was so clearly dominant over the smaller that, once established, the hierarchy did not require frequent reinforcement (i.e. the smaller fish avoided interaction with the larger and did not provoke aggression). More evenly-sized fish may take longer to establish a stable relationship.

Mason & Chapman (1965) claimed that aggressiveness (nips/fish/10 min) among coho salmon fry increased with increasing (seasonal) water temperature, and that this trend was paralleled by an increase in emigration rates from stream channels. These results should be regarded dubiously because the observations were made under uncontrolled experimental conditions where changes in fish size and season (photoperiod) were not accounted for. Similar results with identical experimental limitations were also reported by Hartman (1965). Temperature may nevertheless have an important influence on aggressiveness and should be investigated further using modern experimental methods.

4. Characteristics of the territory

Kalleberg (1958) first described how juvenile Baltic salmon and brown trout position themselves at a fixed station in the stream, with the point of their snout consistently oriented a short distance from some reference structure on the stream substrate. This fixed station for stream fishes is now termed the focal point (e.g. Fausch 1984, Moyle & Baltz 1985) and is defined as the dominant holding position of the stream salmonid within its territory. The territory is cardioid (cordate) in shape (McNicol & Noakes 1981, Noakes & McNicol 1982), with the resident stationed at the downstream end facing into the current. From the focal point, the fish makes its feeding excursions and defense attacks.

Habitat utilization studies on stream salmonids with reference to feeding ecology (Chapman & Bjornn 1969, Everest & Chapman 1972, Griffith 1972, Wankowski & Thorpe 1979, Fausch & White 1981) have demonstrated that salmonids prefer stream positions with the focal point in low velocity current to minimize energy expenditure for swimming, yet near a high velocity current where invertebrate drift rate is high (Waters 1972), thus providing a readily available energy source. Fausch (1984) demonstrated experimentally that juvenile salmonids select these "profitable stream positions" to achieve a positive net energy balance, and that social hierarchies are formed through aggressive interactions with dominant fish holding the positions which offer "maximum potential profit". Puckett & Dill (1985) showed that juvenile coho salmon which assumed such positions had greater net energy gain than those which did not. Of course, the availability of profitable stream positions for juvenile salmonids can vary widely between streams, and even between rearing areas within the same stream, and is contingent upon the physical and biological aspects of the stream or stream section. These aspects include substrate configuration and resultant current patterns, invertebrate production, amount of juvenile rearing area — that is, elements of the so-called "carrying capacity" for stream salmonid production (e.g. Allen 1969, Burns 1971).

The size of the territory, although lacking distinct borders, is in part dependent upon the size of the defending fish (Kalleberg 1958, reviewed by Allen 1969). For example, Titus & Mosegaard (1990) found that newly-emerged migratory trout fry in artificial stream sections had a territory size of c. 0.04 m^2. By 11 days after emergence, territory size had expanded to about 0.15 m^2 per individual, and by 17 days to about 0.30 m^2. These approximate territorial dimensions were maintained to the end of the 28 d experiment, during which time the trout had grown from a mean total length of 27.1 mm at emergence to 49.7 mm after 28 d. Similarly, Grant et al. (1989) demonstrated a significant log-log linear relationship between territory area and increasing fork length of young brook trout. Fish require larger territories as they grow because they demand larger amounts of food, and thus outgrow the food supply of smaller territories.

Territory size is also influenced by prey abundance. Slaney & Northcote (1974) found that territory size of rainbow trout fry decreased hyperbolically as a function of increasing prey density. Dill et al. (1981) also found this relationship for young coho salmon, and determined further that the fish possess a mechanism to adjust territory size to local prey abundance, whereby attack distance toward intruders is increased with increasing hunger.

The releaser mechanism for aggressive behavior in young stream salmonids is visual (see section 3). It follows to reason then that territory size is also partially determined by and negatively correlated with substrate complexity from which visual blocks, and thus isolation, are provided (Kalleberg 1958). Ontogenetic territorial shifts will occur in this respect as the fish grows; that is, the fish will outgrow a territory when existing stream-bottom components (stones, cobbles, vegetation, woody debris, etc.) no longer provide the necessary visual isolation from intraspecific competitors. In addition, the fish will seek deeper water as it grows (reviewed by Heggenes 1988).

Current velocity may also be an important determinant of territory size for salmonid fry. Kalleberg (1958) reported an increase in territorial occupation of Baltic salmon fry in a stream aquarium from c. 250 fry at 18 cm/s (1 fry /3.2 dm^2) to c. 280 fry at 29 cm/s (1 fry /2.9 dm^2); thus, mean territory size decreased when current velocity was increased. Kalleberg reasoned that the focal point of the salmon was depressed toward the stream bottom at the higher velocity, and that visual isolation by existing structures was enhanced thus enabling more salmon fry to occupy territories. However, the relationship between territory size and current velocity is complicated because faster flows result in a greater supply of drift food per unit time (Waters 1972). Thus, an alternative or complimentary explanation is that the observed decrease in territory size was perhaps a consequence of an increased drift rate, a function discussed above.

5. Population regulation of young brown trout

Brown trout fry are present in high densities following emergence in late spring, but loss (mortality) rates are also high through the first summer (Allen 1951, Le Cren 1973, Mortensen 1977a, b, c, Elliott 1984a). By autumn, population densities are regulated to much lower levels, and loss rates are also much lower and more constant. It is during these first few months of the life cycle when year-class size is essentially established. This pattern of regulation has been observed in fry populations of other stream salmonid species as well, including brook trout (Latta 1962) and Atlantic salmon (Egglishaw & Shackley 1977).

Numbers of recruits and hence population densities of young brown trout parr are dependent upon egg or alevin (initial) densities (Le Cren 1965, 1973, Elliott 1984a). Elliott (1984a) demonstrated that maximum recruitment of young parr (7 fish/m^2) in 18 year-classes of migratory trout in Black Brows Beck (English Lake District) was related to an optimum initial population density of about 50 alevins/m^2; recruitment decreased when initial density was higher or lower, resulting in a dome-shaped stock-recruitment curve (Fig. 1; see also Gee et al. 1978). Density ranges for stock and recruits, respectively, were c. 12 to 133 eggs/m^2 and c. 2 to 8 early-stage parr/m^2. In contrast, population densities of young brown trout parr in a nearby resident population (Wilfin Beck) had a simple linear relationship to egg densities; i.e. parr densities increased with increasing egg densities (Elliott 1987). However, in this case, egg densities ranged from only 3 to 6 eggs/m^2, and young parr densities from only c. 0.6 to 1.4 parr/m^2, which corresponds to only a short linear segment beneath the ascending portion of the dome-shaped model for the Black Brows Beck population (Elliott 1989a).

Instantaneous loss (mortality) rates of brown trout during their first summer are also density-dependent, and increase linearly in proportion to initial densities of eggs, alevins, or fry (Le Cren 1965, 1973, Egglishaw & Shackley 1977, Mortensen 1977b, Elliott 1984a). Moreover, density-dependent mortality appeared to be the main process behind population regulation of young brown trout in these populations. An exception was Wilfin Beck where instantaneous loss rates of newly-emerged brown trout fry were rather constant between year-classes and thus density-independent (Elliott 1987).

The contrasting results from Elliott's (1984a, 1987, summarized in 1989a) long-term investigations of a migratory and a resident brown trout population indicate that population density changes are due primarily to negative density-dependent factors in favorable habitat with high population density (e.g. Black Brows Beck with stable flow regime), and density-independent factors in unfavorable habitat with low population density (e.g. Wilfin Beck with unstable flow regime).

Indeed, density-independent factors such as unpredictable environmental changes are important as regulatory mechanisms in many juvenile stream-salmonid populations. These events, due to instability in the physicochemical environment, are responsible for what Grossman et al. (1982) referred to as stochasticity in stream fish populations. For example, floods greatly reduce entire year-classes of salmonids, especially among fall-spawning species whose eggs, alevins, or fry are mechanically destroyed because of scouring caused by the transport of streambed material (Allen 1951, Elwood & Waters 1969, Seegrist & Gard 1972, Erman et al. 1988). Short-term flooding associated with anchor ice formation may cause mortality and thus regulate numbers of all age-classes of salmonids as well as other fish species (Maciolek & Needham 1952, Needham & Jones 1959). Droughts also reduce fish populations, especially in small streams, by reducing flow and therefore drifting food supply and space, and because of mortality caused by high water temperatures and low dissolved oxygen concentrations (see references in Grossman et al. 1982; Borgstrøm & Heggenes 1988, Titus & Mosegaard 1989 for juvenile migratory trout).

6. Synthesis and hypothesis building

6.1. Dynamics of aggressive behavior in population regulation

It is clear that aggressive behavior, in conjunction with territory acquisition and defense, is a fundamental component in population regulation of young brown trout (but see argument by Bachman 1984 against the term "territoriality" as applied to stream salmonids). For a given individual, the instantaneous probability of having aggressive interactions with other fry (P_a) is predicted to be greatest from emergence through early summer, corresponding with the period when instantaneous loss rates are density-dependent. Thereafter, P_a must be much lower because instantaneous loss rates become density-independent (e.g. Egglishaw & Shackley 1977, Elliott 1985a). Furthermore, P_a, and thus the degree of influence that territorial behavior will have on population regulation, may be expected to vary over a continuum related to population density and habitat quality. High-density fry populations associated with favorable habitat, where aggression rates would potentially be high, would occur at one end of the continuum. In these populations, the influence of territorial behavior on the resultant population would be great. In contrast, low-density fry populations associated with unfavorable habitat, where aggression rates would be comparatively low, would occur at the other end of the continuum. In these populations, the influence of territorial behavior on the resultant parr population would be much less. These generalities will be developed further through the next several sections.

6.2. Selection for greater growth potential

Upon emergence from the redd, the brown trout fry must begin external feeding in order to grow, while simultaneously defend a feeding position in order to reduce its risk of extinction. These conflicting, trade-off activities must be accomplished so as to achieve a positive net energy balance. Therefore, establishing a feeding territory at a favorable stream position (sensu Fausch 1984) as soon as possible is crucial, because the majority of fry will not survive (see references in section 5).

Which individuals then have the best chance of obtaining a favorable stream position once emergence has begun? Inferences from previous studies suggest that size- or growth-selection may be a mechanism involved in the initial population regulation and spatial structuring of brown trout fry populations. For example, relative to fry which establish territories, downstream-emigrating brown trout fry have lower activity levels (Heland 1980a,b), are smaller in size (Heland 1980a, Ottaway & Forrest 1983), and are in poor nutritional condition or moribund (Elliott 1986).

Titus & Mosegaard (1990) applied otolith microstructure analysis to determine differential size and/or growth characteristics between newly-emerged migratory trout fry in artificial stream sections which established territories, and those which emigrated into downstream traps. Sagittal otolith size at emergence was used as an index of metabolic performance among individual fry based on evidence that otolith growth rate in salmonids is coupled to fish metabolic rate (Mosegaard 1986, Mosegaard & Titus 1987, Mosegaard et al. 1988). Fish functioning at a high metabolic rate are predicted to have a corresponding high rate of otolith formation, and otolith size at emergence will reflect the standard metabolic level of the fish. There was a clear-cut selection for individuals with larger otoliths at emergence among parr which maintained feeding territories to the end of the 28 d experiment. This process was interpreted as selection for greater growth potential, based on the premise that natural selection will favor genotypes which are metabolically efficient and able to increase their metabolic scope at lower power outputs (Priede 1985). Selection for individuals with larger otoliths at emergence suggested that these fish had a higher metabolic scope. By having a high metabolic turnover rate, energy may be allocated to both somatic growth and territorial defense at higher rates, assuming energy intake (food abundance) is also high. These individuals were regarded as having a greater metabolic, and hence growth, potential from emergence, which later in the growth history was reflected in larger body size by virtue of their growth advantage (i.e. high somatic growth rate). Greater body size generally confers dominance in the social hierarchy of stream salmonid fry populations (e.g. Chapman 1962, Mason & Chapman 1965, Fausch 1984).

Thus, as a social hierarchy is established within the fry population in a given stream area, it may be assumed that individuals with greater growth potential will achieve dominance status and hence assume the stream positions affording maximum potential profit (sensu Fausch 1984). According to Metcalfe (1986), subordinates, being forced to assume less than optimal feeding stations, may adopt one of two feeding strategies in order to survive in the face of competition with dominants. Some subordinates may adopt a high-return/high-cost strategy where more energy is expended than is gained. In such cases, subordinates attempt to maintain temporary stations in areas of slow current (and consequently low prey abundance), or in fast current with little shelter, where much energy is consumed by swimming and interacting with dominants. The result in either case is that net energy gain, and hence growth, is negative and chances for survival are presumably reduced. In contrast, other subordinates adopt a strategy whereby they avoid competition with dominants altogether by assuming sheltered (poor) feeding positions away from faster currents where dominants occur. These fish reduce their metabolic costs to a minimum and continue to grow (albeit slowly) and survive despite a low level of feeding. As Metcalfe (1986) concluded, the optimum growth strategy for subordinates may not be one of attempting to maximize food intake, but one of minimizing energy expenditure (see also Puckett & Dill 1985). Therefore, it could be argued that under conditions of overall low prey abundance that selection could be reversed to favor individuals with lower metabolic scope (smaller otoliths at emergence) and lower energy demands for growth and survival (i.e. selection for lesser growth potential).

6.3. Regulation in relation to initial population density

Earlier in this paper, the influences of various factors on intraspecific aggression in young stream salmonids were described (e.g. illumination, current velocity, initial population density, etc.). Because aggressive behavior plays a major role in population regulation of young stream salmonids, factors which influence aggressive behavior should also influence population regulation. The results of these influences on regulation may later be expressed in growth patterns and population density.

As an example, Elliott (1984b) found that growth of young migratory trout in Black Brows Beck was density-independent. In contrast, the coefficient of variation in individual sizes of young trout varied inversely with initial population density. As initial egg or alevin density increased, variation in length or weight decreased, its magnitude being established in the first month following emergence and remaining fairly constant throughout the life-cycle (Elliott 1985b). Elliott (1984b) hypothesized that size-selective mortality could explain this relationship, its effect increasing with increasing egg or alevin density.

Size variation could arise from differences in growth potential among individual fish as previously described. Within a redd area, individuals with greater growth potential (GGP) should have faster development times through the egg and alevin stages than individuals with lesser growth potential (LGP), and should therefore emerge earlier as fry. Thus, GGP fry may be referred to as early emergers, and LGP fry as late emergers. Early-emerging fry would be expected to dominate later-emerging fry because of their advantage in having first choice of favorable stream positions, and because of the size advantage they are able to gain. Experiments in laboratory stream channels have in fact shown that early-emerging coho salmon and steelhead (sea-run rainbow) trout fry dominate numerically and are significantly larger at a given time after emergence than late emergers (Mason & Chapman 1965, Chandler & Bjornn 1988).

Therefore, in the wild under high population-density conditions, dominating early emergers are predicted to displace and increase mortality of large numbers of smaller, less-active late emergers (Mason & Chapman 1965, Heland 1980a,b, Elliott 1986, Chandler & Bjornn 1988). At the same time, growth of the larger, early emergers may be suppressed because of energy expended in displacing large numbers of late emergers through aggressive behavior. The overall effect would be that variation in individual size is reduced (Fig. 1). In the case of low initial density, no significant size-selective mortality would occur between fry emerging at different times. However, subordinates would still be forced to assume suboptimal feeding positions and therefore grow slower than dominants whose growth would be largely unaffected. The overall effect would be a greater variation in individual fry/parr sizes (Fig. 1). Thus, the type of regulation that occurs under different initial-density conditions is expected to determine size variation within a cohort as described by Elliott (1984b).

The growth-potential mechanism in relation to initial density may now be applied in an attempt to explain the dome-shaped stock-recruitment relationship Elliott (1984a) determined for the Black Brows Beck migratory trout population. Parr recruitment increases as a function of increasing egg or alevin (initial) density on the ascending portion of the curve; i.e., recruitment is positively density-dependent. At the peak of the dome-shaped curve, maximum recruitment is attained in relation to territory availability. The process which leads to a decline in parr recruitment beyond the optimum initial density appears to be more complicated. However, accepting the idea that dominants are GGP individuals provides a feasible mechanism with which to explain the observed decline in recruitment.

As mentioned earlier, territory size of dominants increases when food supply is reduced (Slaney & Northcote 1974, Dill et al. 1981). Therefore, as increasing numbers of fry emerge from the gravel, and prey abundance per fry decreases, GGP dominants are predicted to increase their attack distance and thereby increase their territory size. At progressively higher initial densities, increasingly greater numbers of LGP subordinates should not even be allowed to assume suboptimal feeding positions at the fringes of territories held by dominants (see Symons 1971). These displaced individuals will be unable to feed, lose weight, and will be forced to move downstream where they die due to malnutrition (e.g. Elliott 1986). The result will be progressively decreasing recruitment with initial densities greater than the optimum; i.e., recruitment will become negatively density-dependent. Thus, the type of population regulation that occurs in relation to initial density is expected to not only determine size variation within a cohort but also an associated level of recruitment. These processes are summarized in Fig. 1.

6.4. Regulation time

A parallel aspect is the time taken to reach density regulation as the result of differential behavioral

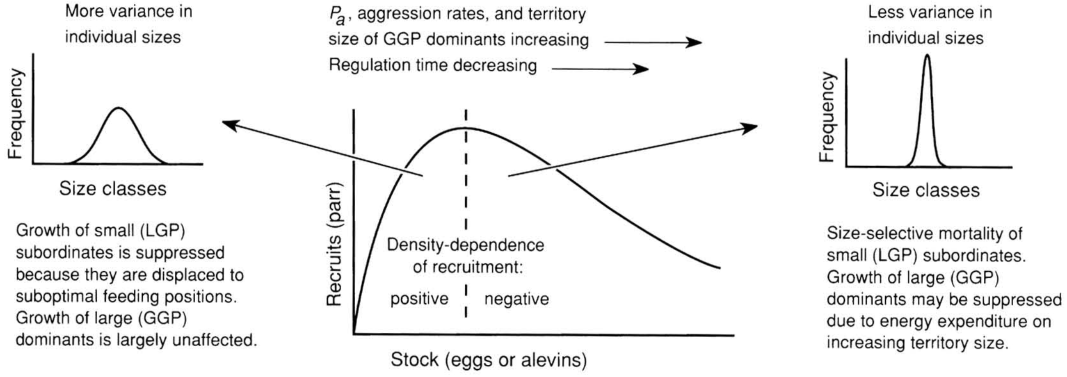

Fig. 1. Dynamics of territoriality in young brown trout as a function of increasing stock size (egg or alevin density). The influence of population regulation on recruitment and variation in fish size is indicated in relation to stock size. P_a is the instantaneous probability for aggressive interactions at the individual level. LGP is Lesser Growth Potential, GGP is Greater Growth Potential. The stock-recruitment curve is adapted from Elliott (1984a).

responses of fry to population density and environmental factors. As a reference point, it will be assumed that factors which increase aggression rates will decrease the regulation time to population stability (i.e. regulation from high initial densities at emergence to a stable, first-summer population level).

Regulation time would be expected to decrease with increasing egg or alevin densities (Fig. 1). As GGP dominants increase attack distance and defend larger territories because of lower prey abundances at progressively higher initial densities, the time required for LGP subordinates to reach a poor nutritional state and be forced to move downstream should become progressively shorter. This is supported by Elliott's (1989c) application of the critical period concept to newly-emerged migratory trout fry in Black Brows Beck. He found that critical survival time (time from emergence until a nutritional "point of no return" was reached) for fry which were unable to establish feeding territories was inversely density-dependent on egg density. That is, regulation time to population stability decreased with increasing initial density.

Following Grant & Noakes (1988), aggressiveness is expected to initially increase with increasing current velocity, reach a maximum at an optimal current velocity, and decrease at higher current velocities. Therefore, regulation time is predicted to initially decrease with increasing current velocity, reach a minimum at the optimal current velocity, and subsequently increase at higher current velocities. At some maximum critical current velocity (dependent on water temperature, fish size and species; Heggenes & Traaen 1988), the young salmonid will become vulnerable to downstream displacement. Newly-emerging fry are susceptible to being "flushed out" at high velocities (Ottaway & Forrest 1983), with the critical velocity at this stage being less than 25 cm/s (Heggenes & Traaen 1988). At this point, a transition will occur where density-dependent regulation is replaced by density-independent regulation, caused by, for example, an unpredictably high increase in stream flow.

Substrate complexity in the area of emergence might also be expected to influence regulation time although this relationship is more difficult to define based on present knowledge. Generally, aggression rates should be inversely related to the degree of visual isolation provided by substrate components; thus, regulation time should be longer when complexity is high.

Water temperature, because of its overriding importance for fish growth and activity, is most likely another important influence on regulation time, although there exists only a paucity of information regarding its influence on aggression in stream salmonid fry. However, swimming ability, and presumably fighting ability, increases from low temperatures up to an optimal range, beyond which performance is reduced (e.g. Brett & Glass 1973). Therefore, as with current velocity, aggression rates should initially increase, and regulation time decrease, with increasing water temperature through an optimal range, beyond which aggression rates would again decrease and regulation time increase.

One final environmental factor which must be considered is prey abundance. Aggression rates are high at low prey levels and vice versa (Symons 1968, Slaney & Northcote 1974); thus, regulation time should vary directly with increasing prey abundance. However, this basic relationship is confounded because increases in drifting prey are associated with increases in current velocity, the latter of which is predicted to increase aggressiveness to a maximum and decrease regulation time to a corresponding minimum. Based on present knowledge, it is difficult to predict the influence of prey level on regulation time.

6.5. Working hypothesis

As a summary, a working hypothesis is proposed to explain the mechanisms behind population regulation of young stream salmonids which result in a dome-shaped stock-recruitment relationship (Fig. 1): Parr recruitment increases with increasing egg or alevin (initial) density on the ascending portion of the curve; i.e. recruitment is positively density-dependent. Aggression rates among newly-emerged fry increase with progressively higher initial population densities, as does selection pressure for individuals with greater growth potential (assuming high prey abundance). Beyond the optimum egg density where maximum parr recruitment is attained, GGP dominants continue to progressively increase their territory size by increasing attack distance toward territorial intruders, and exclude LGP subordinates from assuming even suboptimal feeding positions. Increasing numbers of subordinates are forced to move downstream where they die due to malnutrition. Consequently, parr recruitment gradually decreases; i.e. recruitment becomes negatively density-dependent. The time taken to regulate numbers from high densities at emergence to stable, first-summer population levels becomes progressively shorter with increasing initial population density (Fig. 1).

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