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Influence of the habitat on the potential for cannibalism and population dynamics in stream-dwelling European grayling (Thymallus thymallus L.)

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Habitatets betydelse beträffande potentialen för kannibalism och populationsdynamik hos strömlevande harr (Thymallus thymallus L.)

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Keywords: Cannibalism, European grayling, *Thymallus thymallus*, habitat mapping, Jämtland, population dynamics, recruitment, size structured population model, stream environment

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Abstract

Cannibalism can have major influence on fish population dynamics. A prerequisite for cannibalism is that the cannibal and the potential victim meet, and besides density effects, the encounter rate between cannibals and their victims is therefore also largely dependent on habitat use and habitat heterogeneity. In this study I quantified and compared the potential for cannibalism in stream-dwelling European grayling populations in three rivers in Jämtland by means of habitat classifications. I also analyzed population dynamic consequences of varying the potential for cannibalism in terms of intensity, using a physiological structured population model. Findings based on habitat characteristics were that the potential for cannibalism is in general not favourable in these types of streams. However, some sections had optimal conditions for cannibalism. The population dynamic model predicted that cannibalism can regulate the dynamic if sufficiently intense. It might also induce population cycles, and a fishing mortality will increase the destabilizing effect. It is the younger cohorts that drive the cycles by delayed density regulation. Cannibalism can be important to take into consideration in management actions. Hence, sections with favorable conditions for cannibalism also has a capacity for high fish production, and can thus be important as a source to less productive areas of a watercourse. Cannibalism can therefore indirectly decrease the fish density in more sections than in the few sections with favorable conditions for cannibalism. Moreover, if a population has fluctuating dynamics, some years the population will be dominated by young individuals, which not is desirable for watercourses used for sportfishing.

Sammanfattning

Kannibalism har stor potential att påverka fiskpopulationers dynamik. En förutsättning för att kannibalismen skall kunna ha någon större betydelse är att lekområden, yngeluppväxtområden och vuxenhabitat antingen överlappar eller finns i nära anslutning till varandra. Syftet med denna studie var att undersöka och jämföra tre vattendrags förutsättningar för kannibalism hos strömlevande harr i Jämtland, baserat på yngel- kontra vuxenhabitatens lokalisering samt kvalitet med hjälp av fältbaserade habitatklassificeringar. För att undersöka hur dessa förutsättningar kan tänkas påverka populationsdynamiken gjordes även analyser med hjälp av en fysiologiskt strukturerad populationsmodell. Resultatet från habitatundersökningarna visade att även om det finns sektioner som har optimala egenskaper för kannibalism, så är goda förutsättningar för kannibalism inte vanligt förekommande i denna typ av vattendrag. Den populationsdynamiska modellen visade att kannibalism kan reglera dynamiken även om graden av kannibalism är låg och kan framkalla mer eller mindre regelbundna populationsfluktuationer. Ett uttag via fiske ökar den effekten ännu mer och det är de unga kohorterna som skapar cyklerna genom fördröjd täthetsregleringen. Kannibalism kan vara viktigt ur förvaltningssynpunkt även om det inte är så vanligt förekommande. Sträckor med goda förutsättningar för kannibalism har vanligen även kapacitet för hög fiskproduktion och kan således vara viktiga som källa till mindre produktiva områden av vattendraget. Kannibalism kan följaktligen minska fisktätheten på fler lokaler än på de få sektioner som har gynnsamma förutsättningar för kannibalism. Dessutom, om fluktuationer förekommer så kommer populationen vissa år att domineras av unga individer, vilket inte är önskvärt om vattendraget utnyttjas för sportfiske.

Introduction

Cannibalism is common in many fish species (Fox 1975; Polis 1981). For some species e.g. arctic char (*Salvenius alpinus* L.) and perch (*Perca fluviatilis* L.), cannibalism is considered to be an important mechanism for population regulation, stabilization or destabilization with alternated age- and size structure (Amundsen 1994; Hammar 2000; Finstad *et al.* 2001; Claessen *et al.* 2002; Claessen *et al.* 2003; Persson *et al.* 2003; Svanbäck and Persson 2004). Cannibalism increases prey mortality and may or may not enhance the cannibal's growth, and lowers intraspecific exploitation competition among the survivals (Claessen *et al.* 2002; Claessen *et al.* 2003; Finstad *et al.* 2006).

Mechanisms determining the ontogeny of piscivory in fishes are many. The size at which a predator can enter the piscivorous niche depends on the prey size a predator can handle in combination with the size distribution of available prey (Mittelbach and Persson 1998). For most fishes, the different age stages have specific habitat requirements (Rabeni and Sowa 1996) A prerequisite for cannibalism is that the cannibal can encounter the potential victim, i.e. that they occur in the same habitat. Quantitative measures of the occurrence of cannibalism in stream-dwelling European grayling (*Thymallus thymallus* L.) populations are lacking. While the general view is that grayling mainly feeds on invertebrates they may eat fish prey if the opportunity arise (Bo-Göran Persson, *personal communication*). Their tendency for piscivory is also indicated by that they can be captured using small fish-like lures when sportfishing. According to Näslund *et al.* (2004) the recruitment of young grayling declined when the number of large fish and potential spawners was high. While these authors did not link this negative correlation to cannibalism, it shows the typical outcome of cannibalism. Moreover, between 2005 and 2008 censuses in Idsjöströmmen also displayed an asynchronous pattern with high number of yoy (young of the year) when the numbers of individuals in older cohorts were few and vice versa (Kjell Leonardsson, *unpublished data*).

Keast (1985) divided piscivores into two categories, specialist- and secondary piscivores. Specialist piscivores switch to fish diet early and achieve higher energetic returns from fish prey than from invertebrate prey, as predicted by optimal foraging theory. Secondary piscivores mainly prey on invertebrates and passively choose fish prey based on foraging efficiency and encounter rates (Brian *et al.* 2004; Turesson *et al.* 2002). In many stream living populations, grayling may be restricted to be a secondary cannibal since the distance between different age-cohorts habitats probably often limits the encounters. However, where habitat characteristics causes high encounter rates, a high cannibal rate and even switching to specialist piscivory could be possible. Potential for grayling cannibalism should therefore be dependent on the distance between juvenile- and adult habitats, a representation of the appearance of prey availability.

In Sweden small grayling emerge in April to early June (Fabricius and Gustafsson 1955) with a length of approximately 15 mm (Nykänen and Huusko 2003). After hatching they will stay in the nursery gravel for some days. When the yolk sac is consumed they migrate at night time to suitable habitats (Bardonnet and Gaudin 1990). During the ontogenetic development of grayling, the habitat selection is mostly based on the geomorphology/topography in the streams, for example suitability of a stream section for juvenile habitats is determined by the bottom substrate and stream velocity (Nykänen and Huusko 2003). The first two-six weeks they are aggregated in the surface waters, generally close to the river banks (Nykänen and Huusko 2003). This period they expose themselves and will be vulnerable for predation if the habitat is also suitable for larger fish. As they grow larger they can utilize the outer, deeper and faster running parts of the stream where larger graylings (potential cannibals) are more abundant.

One of my aims was to investigate the potential for cannibalism in stream-dwelling grayling, based on the topographic characteristics in the field. The potential and presumed cannibalism intensity will depend on both the distance between yoy- and the older fishes' habitats, and the quality of each habitat. Another aim was to analyze how the intensity of cannibalism modified by for example habitat heterogeneity can affect stability, growth, size- and age-structure in grayling populations. For these analyses I used a physiological structured population model of a cannibalistic fish population that links population dynamics to the behaviour of individual fishes (see Persson *et al.* 1998 and Claessen *et al.* 2002), in this case of grayling. Furthermore, since sportfishing occur in almost all Swedish streams and rivers with salmonid populations, the modelling were performed with and without including fishing induced mortality for comparison.

Material and methods

Study localities

The habitat classification was carried out in central Sweden in the county of Jämtland between 2007-08-15 and 2007-09-01. The data was collected for three rivers: Gimån, Ammerån and Hårkan.

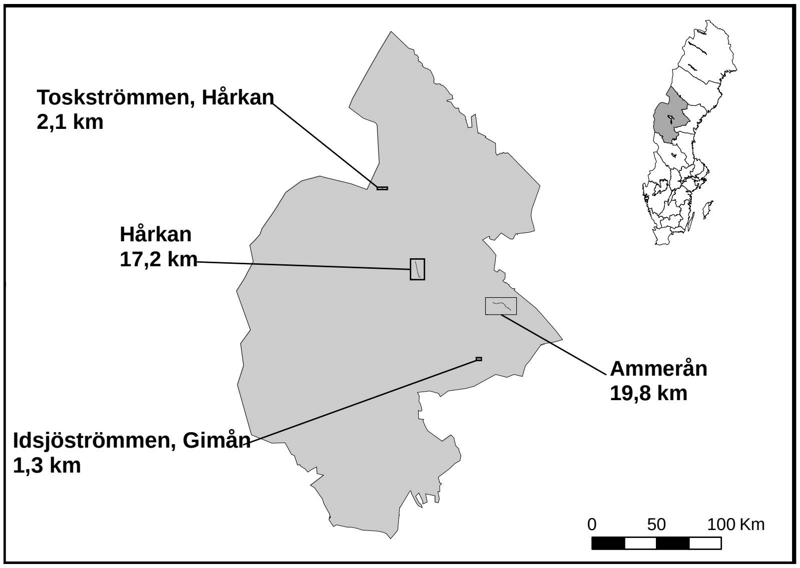


Figure 1. Map showing sampled rivers and surveyed distances.

Gimån

Gimån (62°28′N and 16°19′E), belongs to the drainage basin of Ljungan. The section in Gimån that was sampled is called Idsjöströmmen (62°47′N and 15°44′E). Idsjöströmmen forms the outlet of Lake Idsjön, which gives favourable nutrition conditions. The stream has been used for timberfloating, but extensive restoration has made the topography varied. I surveyed an 1135 m section that had a mean width of 74 m and a mean depth of 1.1 m (during this survey). The substrate is dominated by boulders and cobbles. Stream velocity was dominated by slow riffle and annual mean flow is 19.1 $m^3 s^{-1}$. During the survey the mean flow was much less than normal, only 4 $m^3 s^{-1}$. Fish species generally present in this stream section are: grayling (dominates), brown trout (*Salmon trutta* L.), pike (*Esox lucius* L.), perch (*Perca fluviatilis* L.*)*, minnow (*Phoxinus phoxinus* L.), ide (*Leuciscus idus* L.) and whitefish Coregonus spp. (Näslund *et al.* 2004)

Ammerån

Ammerån (63°91′N and 16°13′E) originates from Lake Fyrsjön in the north and belongs to the catchment of Indalsälven. I surveyed ~19800 m, which has a mean width of 66 m and the mean depth was 0.7 m (during this survey). The substrate in the mapped section is dominated by boulders and cobbles. Stream velocities were dominated by slow riffle and glide and the annual mean flow is 38 $m^3 s^{-1}$. During the survey the mean flow was 10 $m^3 s^{-1}$, which is less than normal. Fish species generally present in this section are: grayling, trout, pike, perch, minnow, common dace (*Leuciscus leuciscus* L.), burbot (*Lota lota* L.), bullhead (*Cottus gobio* L.*),* roach (*Rutilus rutilus* L.) ide, and whitefish.

Hårkan

Hårkan (63°19′N and 14°52′E) begins in the Norwegian mountains of Liernes and also belongs to the drainage basin of Indalsälven. Hårkan flows through among others: Valsjön, Hotagen, Lövsjön, Ockern and Sandvikssjön and is regulated from the lake Hotagen. Toskströmmen forms the outlet of Lake Valsjön in the upper part of River Hårkan. This section of Hårkan deviates in characteristics from the lower part of Hårkan. Toskströmmen is 2100 m in length, the mean width is 75 m and the mean depth was 0.9 m. The substrate is dominated by boulders and cobbles. Stream velocities were dominated by slow riffle and pool and the annual mean flow is 35 $m^3 s^{-1}$. Under the survey the mean flow was 15 $m^3 s^{-1}$. Grayling dominate the stream fish fauna but brown trout is also quite numerous. Downstream Toskströmmen, I surveyed 17230 m that has a mean width of 103 m and the mean depth was 0.7 m. The substrate is also dominated by boulders and cobbles. Stream velocity was dominated by pool and glide, but slow riffle is also quit numerous. The annual mean flow is 75 $m^3 s^{-1}$. During the survey the mean flow was 35 $m^3 s^{-1}$. Grayling and trout are present here, but downstream Toskströmmen non-salmonid fish species becomes more common.

Habitat mapping

To collect the data I used a Swedish standard method for classifications of habitats (Swedish Environmental Protection Agency 2003). This method gives a natural division of extents that is mostly based on substrate and velocity characteristics, which suites the aim of this investigation. Here will follow a short description of the approach in the method, however, in the results, only the features important for grayling habitat and grayling cannibalism will be presented.

A detailed description of each habitat was noted in a protocol. The standard protocol includes the following variables: general site description, length, width, depth, substrate, vegetation, velocity, shadiness, dead wood, flow, affect by humans, structure elements, habitat suitability for brown trout. All criteria together provide a good overall description of a stream and its potential as grayling habitat. The habitat mapping started upstream of the selected part of each stream, and proceeded downstream. Coordinates for the upstream position of each subsection were noted and stored, using a GPS (Garmin 60CS). A visually based classification of the dominating and sub dominating protocol variables was made. While proceeding downstream, a new protocol was processed when the habitat characteristics changed. Water depth was measured using a wading rod marked at 25-cm intervals. To estimate length and area of each habitat, coordinates and air photograph were analyzed in ArcMap 9.2. The classification of the substrate and stream velocity characteristics followed a nominal scale with four categories: Missing 0 = 0%, 1 $\leq$5%, 2 = 5-50% and 3 $\geq$50%. The classification for stream velocity was: pool (deep and slow-flowing water), glide (no turbulence), slow riffle (turbulent water) and riffle (very turbulent water). The surface area of dominant substrate was classified either as: clay (<0.02 mm), sand (0.02-2 mm), gravel (2-20 mm), cobbles (20-200 mm), boulder (> 200 mm) or rock (>4000 mm). For further information about the habitat mapping method see Swedish Environmental Protection Agency (2003).

Complement to the habitat mapping method

In order to obtain a description that is useful for interpretation of potential for cannibalism, I complemented the standard protocol with following variables: quantification of potential grayling habitats and distance between older cohorts- and the yoy' habitat. The grayling habitat variable contains the same criteria as the classification of the brown trout habitat (Swedish Environmental Protection Agency 2003). They were: habitat for juveniles, habitat for adults, and spawning suitability, see table 1. Grayling habitats were classified following Gönczi (1989), Bardonnet *et al.* (1991), Sempeski and Gaudin (1995), Greenberg *et al*. (1996), Mallet *et al*. (2000), Nykänen *et al.* (2001), Nykänen & Huusko (2002), Nykänen and Huusko (2003), Vehanen *et al. (*2003) and Nykänen *et al*. (2004).

Table 1. Summary of classification on grayling habitats: spawning habitat, juvenile habitat, and adult habitat.

Classes	***Habitat characteristics***
0	*Not suitable*
1	*Poor conditions*
2	*Good*
3	*High quality*

To improve my knowledge about the larval grayling habitat requirements, behaviour and appearance, a pilot study "in situ" was performed. The 29th June of 2007 I studied habitat characteristics in Idsjöströmmen, Gimån, where larval grayling were present. A few larval grayling were caught to study them closely. To improve my skill in classification of spawning- and adult habitat, I visited previously known spawning and adult habitats in river Ammerån the 8th August of 2007 (Ingemar Näslund; Birger Ajax *personal communication*). The final grayling habitat classification of spawning habitat and suitability as adult and juvenile habitat was a weighted result of many different features, and the characteristics with the most negative impact being most influential on the classification.

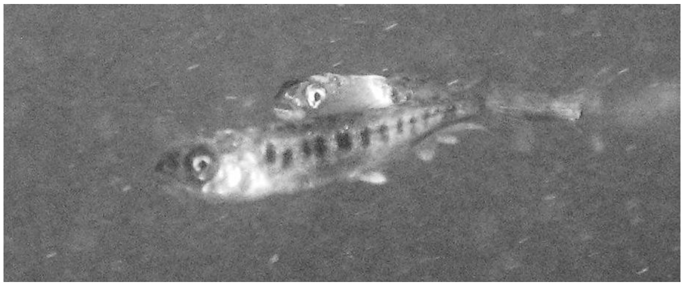


Figure 2. YOY (young of the year) graylings. Photo: Carl-Johan Lindström

Distance between older cohorts' and the yoy's habitat

Encounter rate is normally defined as the product of victim abundance and the attack rate. With a given population size, the attack rate (search rate) will scale to the volume the population of interest is occupying. In this study it is the distance between the different habitats that is measured and I will make the assumption that the attack rate in a stream section instead will scale to the linear distance between the distances between older cohorts′ and the yoy's habitats. This variable (hereafter *Distance variable*) can thus be used to get a relative measure on the presumed level of the attack rate on different sections.

For simplicity I applied a four-level scale (0-3) also for the *Distance variable*. The intention was that a class-3 score should imply that the older cohort and the yoy habitat overlap considerably. Available data on how far an grayling can see in different types of streams are lacking. However, Arctic grayling, a close relative to European grayling, with sizes of about 40 cm has a maximal width of the search window of about 70 cm at moderate velocities (10 - 30 $cm*s^{-1}$) (O'Briean and Showalter 1993). This search window is applicable for successful attacks on drifting invertebrates. The detection window for fish prey is probably much wider, at least in clear water, and the distance between habitats on a section with a class 3-score was therefore set to be in the range 0-3 m. The average distance between the habitats is then 1.5 m and the probability that older individuals in a section with a class-3 score detect the yoy individuals will be very high. For a class-2 score the habitats do not overlap at all, thus older cohorts has to move if encounters with yoy should occur. According to Nykänen *et al.* (2004), daily grayling movements in the late summer period were quite short (mean 18 m). For a class-2 score the distance between the habitats was thus set to be in the range of 4-16 m, i.e. in the distance of normal daily movement for adult grayling and some daily encounters are expected. For a class-1 score the encounter rate should be rare since the distance between habitats (17-80 m) mainly exceeds the distance of the daily mean movement. In the field the distances between adult and juvenile habitat were visually estimated.

Quantification of the potential for cannibalism

As total consumption rate in the habitat also depends on predator and victim abundances, some measurement on their abundances was needed. The best would be to use empirical data on population densities, but this information was only available from a small part of each stream.

Therefore grayling habitat quality was used as a relative measure of abundance and some rearrangements were needed. The relationships between the different grayling habitat variables in the method are not linear. For example, a spawning habitat with a score of 2 does not have twice as high quality as a habitat with a score of 1. It actually has four times higher quality, see below. Today available knowledge about grayling habitat is not that precise and a section with a score of 1 will have a range of characteristics from poor quality to some quality. Moreover, the range of characteristics that would give a section a class-2 score is not the same as in the class-1 score, i.e. the pattern is not linear.

To facilitate the ecological interpretation, I rescaled the scores for each class, corresponding to a proportion of optimum conditions. All classes except 0 have a range of habitat characteristics that will result in the same classification (Table 2.). To get a relative abundance value the scores 1-3 were rescaled using the average between the range boundaries, which are: 0.125, 0.5 and 0.875, respectively. The interpretation of the rescaling is that a section with a classification of 2 has an average quality of 50 % of optimal condition and (most important) four times higher quality than a section with classification of number 1, hence (0.5 / 0.125 = 4).

Table 2. Range boundaries, average range boundaries and the description for different classes of the characteristics describing grayling habitat.

Classes	***Range boundaries***	***Interpretation***	***Relative Abundance* (RA)**
0	0	Sections where characteristics is missing will have the classification of 0	0
1	>0 ↔ 0.25	Sections with a habitat quality between >0% to 25 % of optimal condition will have the classification of 1	0.125
2	>0.25 ↔ 0.75	Sections with a habitat quality between >25 % to 75 % of optimal condition will have the classification of 2	0.5
3	>0.75 ↔ 1.00	Sections with a habitat quality between >75 % to 100 % of optimal condition will have the classification of 3	0.875

In a similar way I rescaled the *Distance variable*. To do this I used the relation between the average distance between habitats of class 1 (48.5 m) to the average distance of class 2 (10 m) and 3 (1.5 m). The distance between habitats of a section with a classification of 2 is then 48 / 10 = 4.8 times shorter and the attack rate will be 4.8 times higher than for a section with class-1 score. For a class 3-score sections, the distance is 48/1.5 = 32 times shorter and the attack rate is consequently 32 times higher than for a section with a *Distance variable* class-1 score. A Class 1 score will then be equivalent to the rescaled value of 1, class 2 is equivalent to the value 4.8 and class 3 corresponds to 32. See (Table 3).

When combining the "habitat quality variable" and the *Distance variable*, the potential for cannibalism (hereafter *Cannibalism value*) will depend on both the *Distance variable* (the habitat heterogeneities effect on the attack rate) and the quality of each habitat (the relative measure of abundance), as it would do in a natural system. At very high prey densities, handling time may limit the feeding rate due to satiation. However, in this study most of the victims are small, thus, handling time can be assumed to be short and it is therefore unlikely that cannibalism would occur at such rate that they become satiated. The only situation when this could occur would be in habitats with the highest *Cannibalism value*, and then probably only during a short period of time.

All together this implies that a section with all "habitat value" of 3 (for each of yoy, older individuals, and spawning areas) and *Distance variable* of 3 will score to $0.875*0.875*0.875*32 = 21.4$, which will be the maximum value a section can get. The scores from all sections were divided with this maximum (21.4) and the expression $RA_{Adlut}*RA_{Spawning}*RA_{Juveniels}*a/21.4$ will facilitate the interpretation of the final *Cannibalism value,* which will vary between 0 and 1.

Table 3. Distances between adult- and juvenile habitats and values used to rescale the classes describing distance between habitats.

Classes	**Distance between habitats (m)**	**Average distance between habitats (m)**	**Scaled attack rate (a)**
0	*> 80*	…	**0**
1	17 *-80*	48.5	**1**
2	*4-16*	10	**4.8**
3	*0 – 3*	1.5	**32**

Population modeling

I used a physiological structured population model that accounts for the food intake, growth and reproduction of individuals; see e.g. Persson *et al.* (1998). The core of the model is based on two state variables: the state of the individuals (e.g. physiological condition) and the state of the population, which is defined as the frequency of possible individual states. The dynamic is shaped by for exampel individual's: birth, death and growth. The growth season represent the summer in Jämtland (90 days) and the winter is overlooked, based on the assumption that the biological activity is insignificant in the winter season. The model is in principal identical to the one described by Claessen *et al.* (2002), except for the re-parameterization to grayling, a constant food resource, and intra-cohort variation in food conversion efficiency.

As food cannot regulate the grayling population in this model system, (there is a lack of competition for this particular resource since there is no feedback of resource consumption on the resource density), the ultimate regulation was instead set by a maximum allowed recruitment. This regulation will mimic the general conception of regulation of salmonid populations in streams (Finstad *et al.* 2008).

An important feature of the model is the "cannibal window", which refers to the variety of different prey sizes a predator of a given size can eat. Individuals that can cannibalize are those that have prey in their "cannibal window". The attack rate is defined as the search area per unit of time for a particular length relation between predator and prey and the actual feeding rate will follow a Hollings type II functional response (Hollings 1959).

The individual net energy intake per unit of time is the energy intake per unit of time minus the metabolic demands per unit of time. The energy intake equals the feeding rate multiplied by a conversion efficiency factor and the metabolic demand is a power function of body mass. The individuals of a cohort in my analysis are acquired one of five food conversion efficiencies that will facilitate the development of an intra-cohort size-distribution that resembles the size variation seen in nature (Kjell Leonardsson, *personal communication*). All newborn have the same size, but their sizes start to deviate as soon as the individuals start to grow. Individuals characters (e.g. metabolic demands, attack rate and prey manipulation times) are all functions of body mass.

When introducing cannibalism the model opens for cannibalism to override the competitive recruitment regulation. In contrast, the allowance for a divergence in size among individuals within each age-class opens for a wider range of cannibal-victim interactions compared to in the model formulation used by e.g. Claessen *et al.* (2002) analyses. Thus, the scope for energy transfer from potential victims to cannibals is higher in this model formulation than in models that lack intra-cohort variation. Furthermore, the modelling issue here involves varying the potential and intensity for cannibalism caused by the habitat complexity rather than being a species specific property. Thus, for examples prey manipulation times, and morphology will only be important if predators and prey meet.

Model parameterization

There is a lack of knowledge for a complete model parameterization for grayling based on empirical data. The functional response parameters have been scaled to provide growth rates that correspond to the range of observed growth rates for the food densities available in these streams. Data on total length (mm) gape width (mm) and gape height (mm), collected in Jämtland between 2008-07-01 and 2008-09-01 by me and John Niklasson revealed that the upper limit of the cannibal window (maximum victim size relative to cannibal length) for grayling is ~0.43. However, I mainly used 0.25 as a conservative measure not to overestimate the piscivory feeding capacity of grayling.

The intra-cohort variation in food conversion efficiencies were introduced by multiply the assimilation efficiency with the five different conversion efficiency constants k_1-k_5 (table 4.). The share of the newborn that allocated the different constants (k_1-k_5) followed a normal distribution. The distribution can be varied by changing the coefficient of variation, in this study the CV was set to 0.095. Thus, the variation (CV) in the assimilation coefficient among the newborn were 0.095. The parameter values used in the model and their origin are presented in table 4. Parameter values not presented here were the same as in Claessen *et al.* (2002)

Table 4. Variables, values, constants and their definitions, used in the model for European grayling.

Subject or Symbol	Value	Unit	Interpretation
Environment			
Year	90	Days	Represents the length of the growth season.
Stream	$50*10^6$	Litres	Volume of the stream (e.g. 1000m*50m*1m)
Maxeggs	10^7 and 10^5	Recruiters	The maximum number of recruiters from eggs, regardless the number of adults and their fecundity.
R	0.7	L^{-1}	Resource density (the resource consists of unspecified drifting invertebrates)
Rm	$3{,}0*10^{-5}$	g	Resource mass
Cannibalism			
β	varied	$\text{Stream}*d^{-1}*mm^{-\sigma}$	Determines the cannibalistic intensity by defining the different sized cannibals attack rate (foraging capacity).
δ	0.00	…	Lower limit of the cannibal window.
ε	0.25 and 0.15	…	Upper limit of the cannibal window.
φ	0.16 and 0.10	…	Optimal victim length defines how the attack rate of different sized predators is changing in relation to prey size. I used the same ratio to δ and ε that was used in (Claessen *et al.* 2002). $\varphi \approx (\delta + \varepsilon) / (2 * 0.785)$.
ζ	0.6	…	Allometric exponent used in the attack rate function. For prey with optimal victim length φ the maximum cannibal attack rate A_c is given by $A_c = \beta c^{\sigma}$ where c is cannibal length.
Drift feeding			
$W\text{opt}$	500	g	The grayling size at maximum attack rate on the invertebrate resource.

Table 4. Continued...			
Subject or Symbol	**Value**	**Unit**	**Interpretation**
$A_{\max}$	$8*10^5$	Stream*d^{-1}	maximum attack rate on resource
Invertebrate encounter	x	g* d^{-1}	The encounter rate on the resource is given by $A_{\max}* R*Rm$
Metabolism			
k	0.49, 0.55, 0.61,0.67, 0.73		Assimilation efficiency among cohorts in each year class, corresponding to a coefficient of variation of 0.095 among the cohorts at birth.
Mortality			
…	0.008	Day $^{-1}$	Background mortality.
...	0.75	...	Egg/newborn mortality
...	0.64	Year^{-1}	Fishery induced mortality, probability
Reproduction			
Fecundity	3.33	Egg/gram*individual	The individuals are a mix of a female and a male and the fecundity has been adjusted to that. Data from Nordwall *et al.* 2002.

Analyses using the population model

In the model I focused on varying the cannibalistic intensity by varying β to represent varying degree of habitat suitability for offspring and older fish. I also studied the effect of carrying capacity for the grayling (by changing the maximum number of recruiters from eggs), adding a fishing mortality to individuals of 25 cm and larger (a previously common harvest strategy) and changes in the “cannibal window” parameters. I analyzed the results in bifurcation diagrams, and for dynamics of special interest, time series were studied and interpreted. For each β-value the model was run for a time span corresponding to 200 years and the population was sampled the first day each season

Results

Habitat mapping

In total about 40 km where mapped, with a wetted area of about 318 ha, divided on 113 sections. Most results concerning habitat quality, used as relative measure of abundance, showed high values. For example, the proportion of the total area with good and optimal juvenile habitat areas was 63%, and for adult habitat it was 78 % and for spawning area it was 50 %. Hence, the sampled streams have naturally high prerequisites for grayling populations. It should be noted that a habitat score of class-2, having the widest range of different characteristics, will also contribute to make a class-2 score more common than the other scores in these types of streams. The detailed habitat results are presented in table 5.

Table 5. The absolute and relative frequencies of good and optimal, (class 2 and 3, see table 1) grayling- spawning area, adult habitat area and juvenile habitat area (ha) for each of the streams.

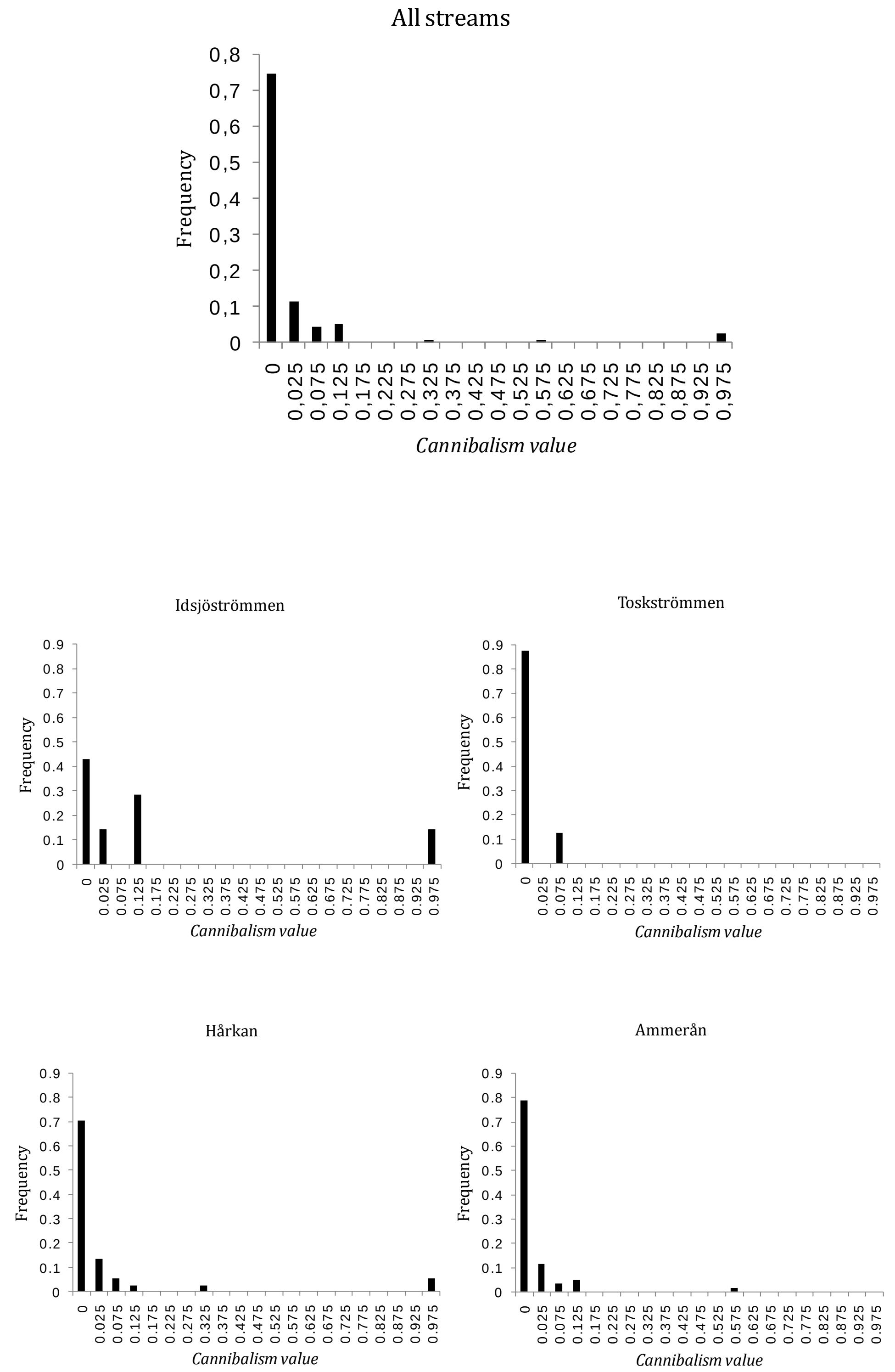
Stream	**Spawning area ha**	**Adult habitat area ha**	**Juvenile habitat area ha**	**N#**	**Total area ha**
Ammerån	73 (56 %)	90 (69 %)	78 (60 %)	61	131
Hårkan	71 (44 %)	140 (86 %)	107 (66 %)	37	162
Tokströmmen	6 (38 %)	11 (69 %)	7 (44 %)	8	16
Idsjöströmmen	9 (90 %)	9 (90 %)	9 (90 %)	7	10
Total	159 (50 %)	250 (78 %)	201 (63%)	113	319

Potential for cannibalism

The *Cannibalism value* is constrained between 0 and 1 due to rescaling. In total there were 11 sections (10% of the total 113 sections) with a *Cannibalism value* between 0.15 and 1. The total area for those "cannibal values" was 23.1 ha (~7.3 %) (Fig. 2). For all sampled streams the "cannibal values" was: 5th percentile = 0, median = 0 and 95th percentile = 0.15. These values show that most *Cannibalism values* were low. For the distribution of the *Cannibalism values* among the streams, see table 6.

Table 6. *Cannibalism values* at the 5th, median and 95th percentile.

Rivers	***Cannibalism values***			
	5th percentile	Median	95th percentile	Highest value
Idsjöströmmen	0	0,05	0,15	1
Toskströmmen	0	0	0,01	0,09
Ammerån	0	0	0,15	0,57
Hårkan	0	0	0	1
All streams	0	0	0,15	1


All streams

Idsjöströmmen

Toskströmmen

Hårkan

Ammerån

Figure 2. Frequency distributions of *Cannibalism values* from mapped stream sections in each of the three investigated rivers.

Comparison of the potential for cannibalism between streams

To compare the streams' potential for cannibalism, the product of each sections length (m) and *Cannibalism value*, divided with each stream's total length (m) was used. These length weighted values describing the proportion of each stream that has optimal potential for cannibalism comes in the following order: Idsjöströmmen (0.25), Hårkan (0.05), Ammerån (0.02) and Toskströmmen (0.02) (Fig. 3)

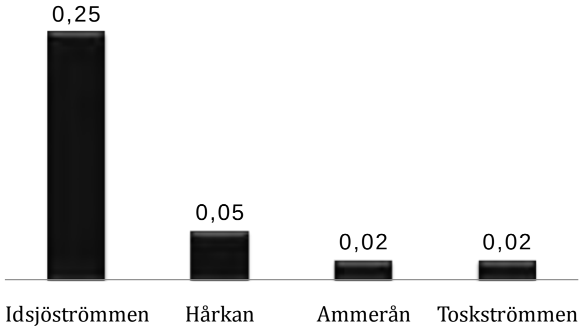


Figure 3. Length weighted value describing the proportion of each stream that has optimal potential for cannibalism.

Modelling

For zero cannibalism ($\beta = 0$), the model generated stable dynamics and stationary age and size distribution (Fig. 4). With a constant "drifting" invertebrate resource there will not be any competition for food between the different cohorts and consequently, with a maximum number of recruits, the population size as well as the size distribution has to be stable.

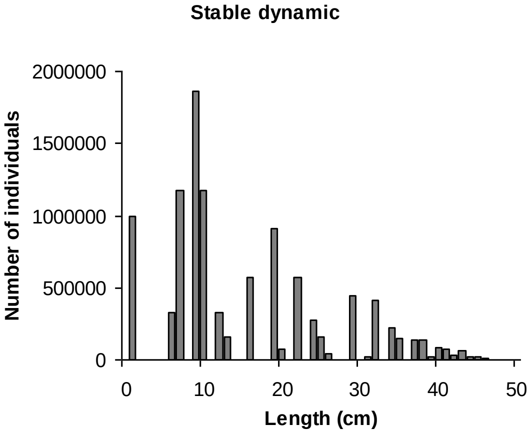


Figure 4. An example of a size distribution for a population without fishing mortality and cannibalism.

When cannibalism is introduced it reduces the population density. The maximum size of the individuals is also decreased, hence cannibalism only affects mortality and there will not be any response with higher population birth rate (maximum number of recruiters is constant). With increased mortality, fewer fish will get old enough to reach the same size as could be the case without cannibalism. The occurrence cannibalism also destabilizes the population dynamics (Fig. 5). For the population with higher recruiters from eggs (10^7) and no fishing mortality, all β-values produced irregular cycles (quasi periodic cycles) with a dominating frequency of five years (Fig. 6). The size distributions at the start of the season from year 1 to 5 for the irregular cycles are shown in figure 7. Cannibalism will in this population favour some cohort more than others and every 5th year (sometimes every 4th year) a strong cohort is born that will face low mortality from cannibalism (See Year = 5 in figure 7). When this cohort becomes the next 1+ cohort and entering the cannibal niche, they are so numerous that they can consume a considerable amount of the new YOY cohort. When the dominating cohort is reduced in numbers by background mortality and to a lesser extent due to cannibalism from larger individuals, they will fail to control the younger ones and a new strong cohort will be born, and the cyclic pattern will be repeated. The cannibalism in these scenarios introduces a density dependent mortality that will cause fluctuating dynamics. The population-cycles are an outcome of the delayed regulation, hence, the strong YOY cohort that is born every fourth or fifth year cannot start to cannibalize until the next season.

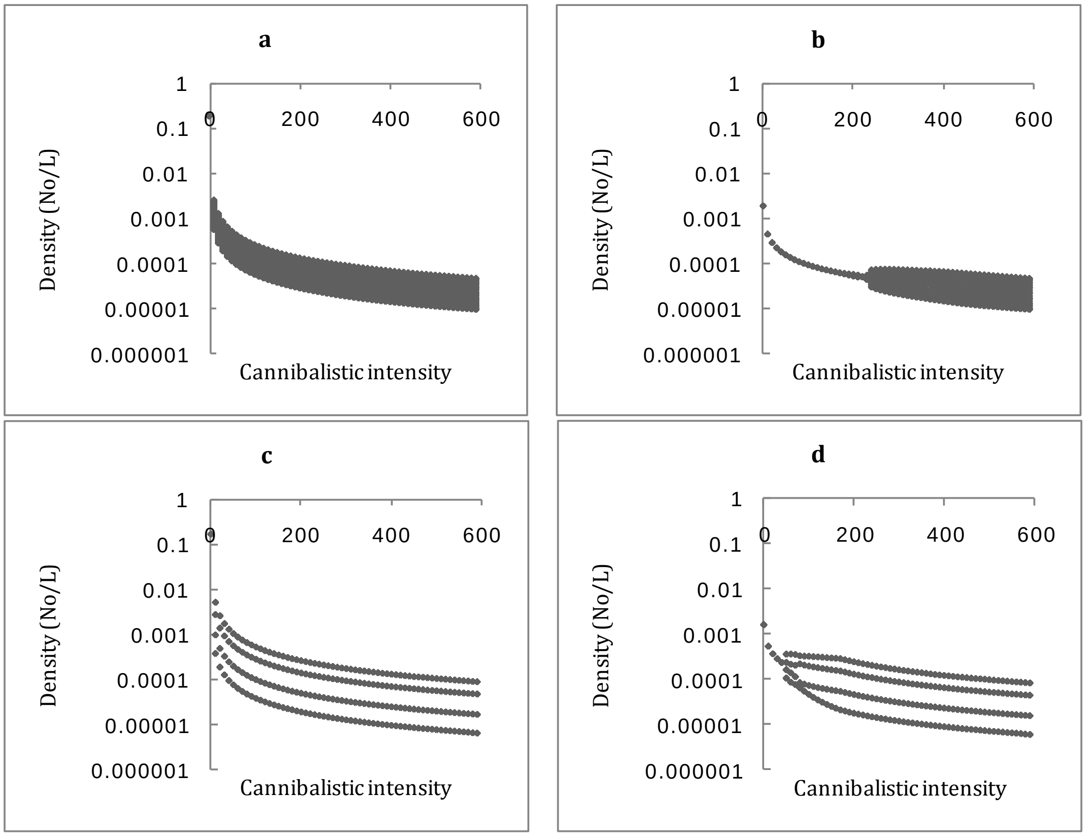


Figure 5. Bifurcation diagrams for two different values of maximum recruiters from eggs, panel (a) and (c) with 10^7 recruiters and panel (b) and (d) with10^5 recruiters. In the panel (c) and (d) a fishing mortality of 60 % is also added to individuals of the size of 25 cm and larger. The upper limit of the predation window was set to $\varepsilon = 0.25$. For each β value the model was run for 200 years and the population was sampled the last 100 years when the final dynamics were approached

With fewer recruits from eggs the population remain stable for β-values between 0 and 230 (Fig. 5 panel b). For this range of β-values no cohort will be large enough or have the required encounter rate that is needed to create sufficient mortality on younger cohorts. It is a consequence of that no birth pulse will be large enough to create a dominating cohort that can suppress the next YOY cohort adequate. There will thus be both fewer cannibals and available preys for the cannibals to eat. For high cannibal intensity $\beta > 230$ the encounter rate will be high enough, and the older cohorts can cannibalize a YOY cohort to such level that the population will start to fluctuate.

When the fishing mortality was added in the model, the amplitude of the fluctuations were larger and the cycles got regular with a period of 4 years (Fig. 6) Cycles also occurred at much lower intensities of cannibalism in the population with a lower recruitment regulation scenario (Fig. 5 panel d). The increased destabilizing effect of the fishing mortality is an outcome of individuals over 25 cm will face higher mortality, and hence, the 1+ will be even more dominant due to lowered predation on them. Furthermore, more prey will be available to the 1+ when older individuals suffer a higher mortality from fishing. In the second year the dominant cohort leaves the protected refuge of being smaller that 25 cm and they will also face the fishing mortality. Their number is severely decreased by the fishing, but also the background mortality is complementing the depletion. In Year = 4, see (Figure 8.) a new strong cohort is born and the cycle will repeat itself.

Analyses with the $\varepsilon = 0.15$ instead of 0.25 was also made, i.e. reducing the maximum victim size relative to the cannibal length from 25 % to 15 %. With this limit, especially the younger cohorts will have fewer available prey in their "cannibal window". The model predicted in principle the same dynamic as the other simulations did, i.e. with the 1+ as the dominating cohort driving the population cycles.

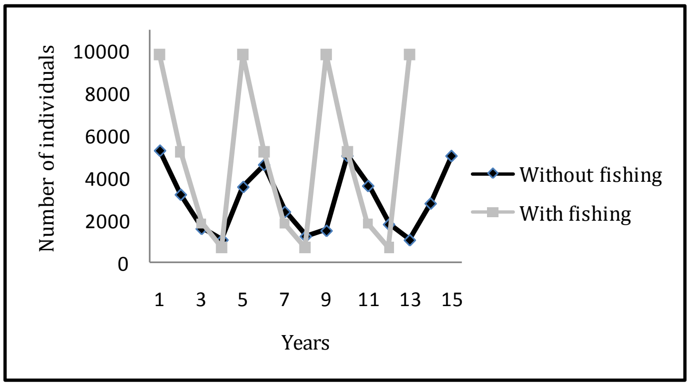


Figure 6. Time series of cannibal driven cycles predicted by the model: The black line shows the irregular cycles that are found without fishing mortality, dominating cycle is 5 years. The gray line shows the stable 4 year cycles produced when a 60 % fishing mortality is added to individuals of the size of 25 cm and larger.

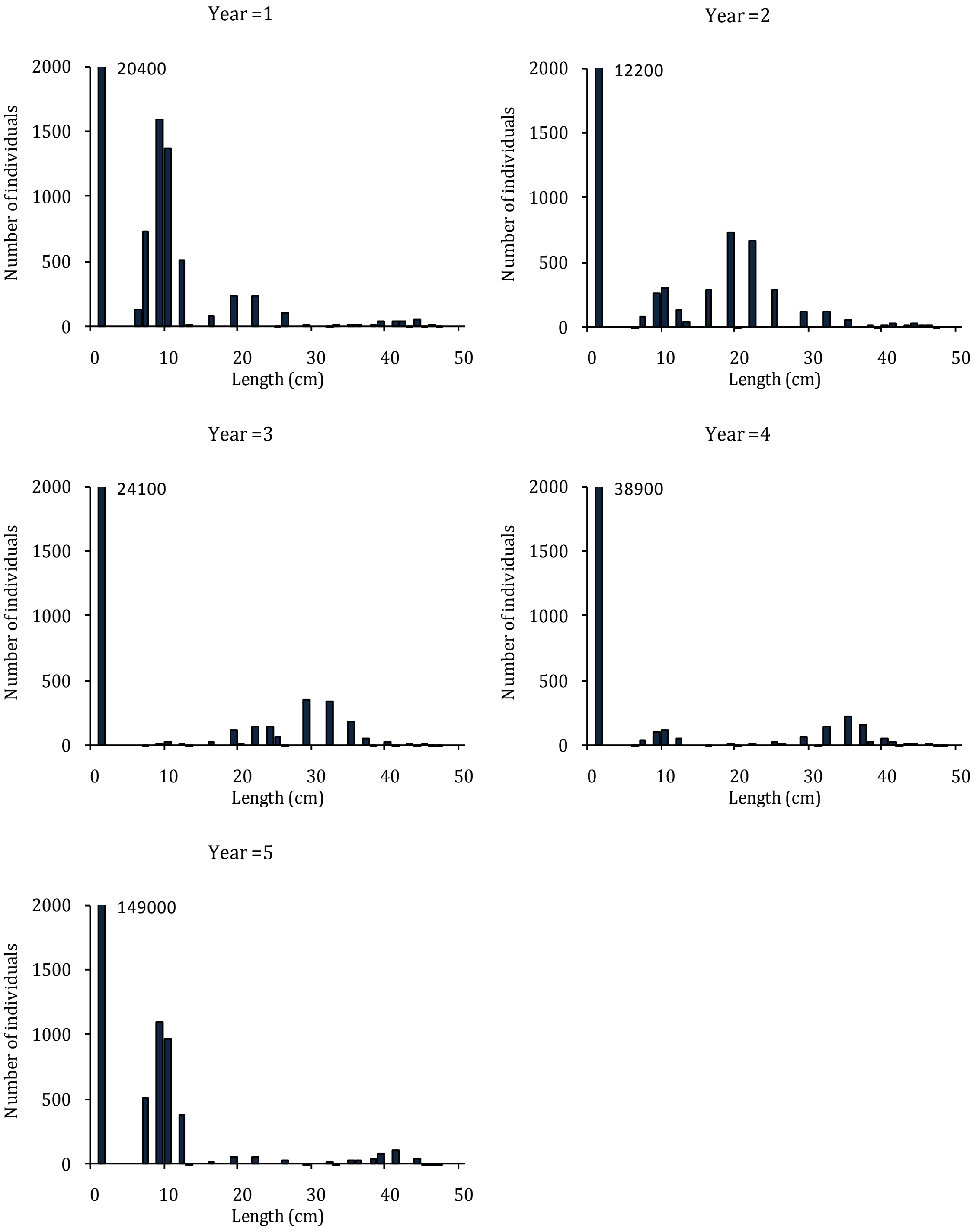


Figure 7. Change in size distributions for a population with a five year “cannibal cycle”, shown in Fig. 6.

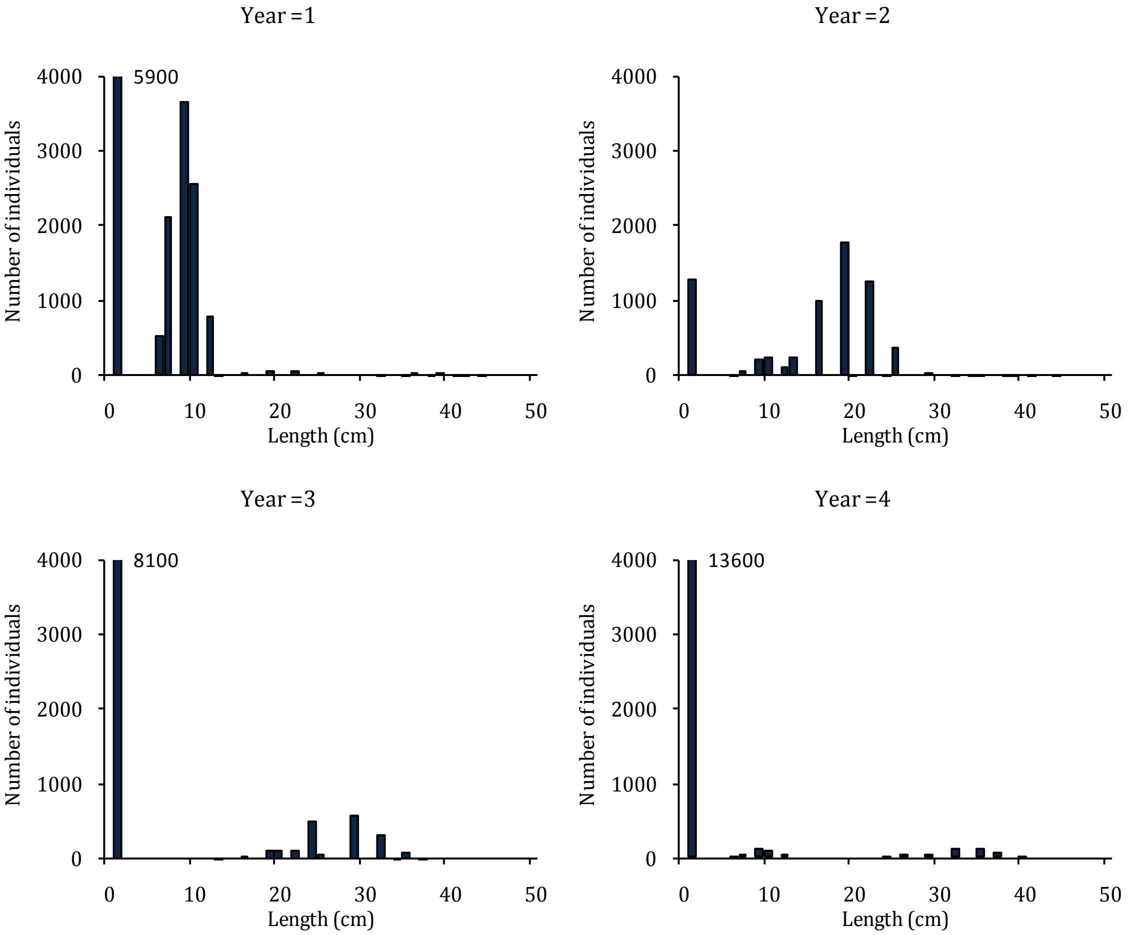


Figure 8. Size distribution for a population with cannibal driven regular cycles produced when a 60 % fishing mortality is added to individuals of the size of 25 cm and larger.

Discussion

The habitat mapping results showed that the potential for cannibalism based on habitat characteristics are not in general favourable in this type of streams. The distances between high quality juvenile- and adult habitat are mostly large and encounter rates will consequently be low. Only about 10 % of the total area had *Cannibalism values* between 0.15 – 1, and the most frequent value was 0 for all streams. Good and optimal juvenile habitat area, spawning area and adult habitat was numerous in the sampled rivers and it is consequently mainly the distance between the habitats that keep the numbers low. To a large extent it is the hydrodynamic capacity of the fish and reigning water velocity which determine what part of the stream graylings utilise (Nykänen and Huusko 2002). Grayling choose most times quite fast water velocity due to the feeding opportunity increases with the water speed. Favourable conditions for cannibalism include the combination of proper depth, velocity and substrate for adults close to the banks where juveniles resides at least during the first few weeks of life. However, it is more common that both the current velocity and the depth increase from the river banks towards the middle of the stream, which will keep the habitats separated. All the investigated streams have been used for timberfloating with associated cleaning and channelization of the streams which have caused higher flows and reduced structural complexity. That is, the potential for cannibalism may be more favourable in undisturbed streams. Of the investigated rivers, Idsjöströmmen had the most favourable conditions for cannibalism. Part of the explanation for this may be the extensive restoration that has made the topography very varied in this stream.

Population dynamics

A general finding from size-structured modelling is that small individuals can have higher competitive ability than larger ones because they are more energetic effective (Persson *et al.* 1998). It is the ontogenetic scaling of foraging- and metabolic rates that determines the strength of the competitive ability of differently sized individuals. If smaller individuals are competitively better than larger ones they can out-compete adult cohorts and hence create population cycles if sufficiently many offspring are produced to reduce the resource. However, if cannibalism occurs in this type of system, older cohorts will reduce the intraspecific competition, and dampen the population cycles by decreasing the recruit density (Claessen *et al.* 2002) With a constant "drifting" resource and a density dependent recruitment the population dynamic will instead be stable without cannibalism, due to a stable birth and death rate. Cannibalism will introduce a density dependent death rate which will affect the population dynamics when sufficiently intense. Using a constant food resource in combination with a bottleneck recruitment will thus produce a different type of dynamic compared systems with a dynamic resource, but mainly so in the absence of cannibalism or at low cannibalism intensities. A dynamic resource with feedback from the consumption rate is hard to motivate for grayling, however, other regulation mechanism is possible for example a limit in the number of adults a section can hold, is also a plausible regulation mechanism. In line with van Kooten *et al.* (2007), also my analysis showed a pronounced effect of sportfishing on the dynamics in a cannibalistic species. My results indicated that especially in low productive streams there probably has to be an extra size-selective mortality, such as sportfishing, if cannibal driven population fluctuations should occur. Otherwise my results show the same pattern as other studies of size specific interactions i.e. a single dominant cohort driving the dynamics and that the magnitude of the reproduction pulse is important if fluctuations should occur. Thus, when cannibalism occurs in populations with high production (many recruiters) the tendency for destabilization is much higher, compared to populations in low-productive systems. In a management perspective this is an important aspect, because high production of recruiters is desired in management actions. The explanation is that in a cannibalistic interaction predator and prey belong to the same species. This simple trophic interaction will shape population dynamics like the model predicts, hence, cannibals and preys reciprocally control one another's numeral (e.g. lower population size means fewer cannibals).

An evolutionary consequence due to this dependence is that victims will have difficult to escape the limiting effect of the predators/cannibals by changing their life history and produce more juveniles (more juvenile's means more cannibals). Selection will then favour other traits for example foraging behaviour, habitat use and activity pattern. This is in line with my results i.e. the study shows that the juveniles, at least during their first weeks of life, has a refuge due to their habitat use. Consequently, there may also be a selection for habitats separation between the adults and yoy habitats.

Linking the modelling and habitat mapping results

The cannibal mapping result were derived from measures of potential for encounter between different age cohorts based on different habitat characteristics. In the model I have varied the cannibalistic intensity by changing the encounter rate between cannibals and their victims. A low *Cannibalism value* (i.e. habitats are separated and/or low quality of the habitats) of the collected data resembles low cannibalism intensity in the model. In the simulations of the productive system, i.e. many recruiters, the high population density implied high encounter rate also at low β-values. I will therefore use these simulations to represent the sections that have maximal potential for cannibalism. There are three sections with maximal conditions for high encounter rate, one in Idsjöströmmen and two in Hårkan. In Idsöströmmen catch and release angling is practiced and if the model assumption is fulfilled the expected population dynamic should be described by irregular population cycles driven by cannibalism of younger cohorts on the yoy individuals. Hårkan is a popular stream for sportfishing, and the fishing mortality is considered as high and a destabilized dynamic with stable cycles should be expected.

Further on only the results from simulations of the low productive system will be used for predictions. If I make the assumption that the maximum β a Grayling can have in a stream section is approximately 250, then I can relate the habitat results to this maximum, and a habitat value of 0.1 would resemble a β-value of about 25 and a habitat value of 0.5 would resemble a β-value of about 125, and so on. This will consequently imply that all sections with *Cannibalism value* < 0.9 in a low productive stream with no fishing mortality should have stable dynamics. On the contrary, all stream sections with intermediate to high fishing mortality will destabilized the dynamics for all *Cannibalism value*s > 0.2, which shows the pronounced effect fishing has on the population, if cannibalism occurs. Based on this, there are two more stream sections with the potential for influence of cannibalism on the population stability, one in Ammerån (*Cannibalism value*=0.58) and one in Hårkan (*Cannibalism value*=0.33) hence both these streams have a quite high fishing mortality. In contrast, for Toskströmmen all cannibal values were low which also implies low potential for cannibal driven population cycles.

In total there were only five sections out of 113 with the potential for a destabilized population dynamic in this investigation, i.e. in streams high grayling cannibalism intensity may be rare. However, if a section gets a high cannibal value it also implies that it has close to optimal habitat quality for both juveniles and adult, hence, the section can produce and hold a large population. Such high quality sections may be an important source for other sections (sinks); consequently, cannibalism can then affect a large part of a stream and, even if the cannibalism doesn't induce population cycles it will always lower the population size.

Grayling has a high recreational value, and for a river that is used for sportfishing it is not desirable to have population cycles; hence, there will be years when the population almost only have young (small) individuals. The risk for disappointed visiting sportfishers is obvious. These systems have reproduction regulation and to lessen the overcompensatory response it is the non regulatory stages' mortality that should be increased (Schröder *et al.* 2009). Common for all scenarios are that it is the 1+ cohort that is shaping the dynamics and these are the ones that should be harvested if one wants to reduce the cannibal cycles amplitudes. The problem is that this size is not interesting either as food or for sportfishing. Such management action has to be considered as a form of culling to keep the desired population structure. It would be a strategy that contrasts from todays' normal practice in fish management. This type of management is common in e.g. forestry and it may be something to learn from.

In Idsjöströmmen, some of the favourable potential for cannibalism is manmade, hence, actions to create more suitable habitats for adult grayling might also improve the conditions for newborn to reside in the vicinity of the older grayling and thus increase the potential for cannibalism driven (unstable) dynamics. When improving habitats in the future, it might be worth considering providing refuges for the yoy, to prevent the larval grayling of being an easy target for potential cannibals and other piscivores as well.

If it is cannibalism that causes the decrease of small fish when the older age cohorts are increasing in Idsjöströmmen, remains to be verified. In a natural system the dominance of the 1+ cohort may be dampen by competition that involves direct interactions e.g. exclusion of some individuals from territories (interference competition). Moreover, community dynamics due to interactions between other species is an unexplored area for grayling populations (Nordwall 2002), and other species like perch, pike and trout can mediate trophic interactions in the community that may affect the level of grayling cannibalism. However, my result shows that the potential for cannibalism is maximal in the most productive stream section in Idsjöströmmen, i.e. cannibalism is a plausible explanation. To answer this question, data on actual amount of cannibalism when juveniles and adults encounter each other is needed, with, stomach content analysis, video recording at interesting sites and studies of the species specific properties (like e.g. teeth's, speed and digestive capacity). More model analyses of what harvest strategies that is best in different scenarios are also needed and studies in lake systems would be interesting, thus, the potential for cannibalism will most times be favourable there. Finally, if cannibalism is occurring in grayling populations, understanding will enhance the possibility to choose a proper management plan for entrepreneurs and other stakeholders in the future.

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