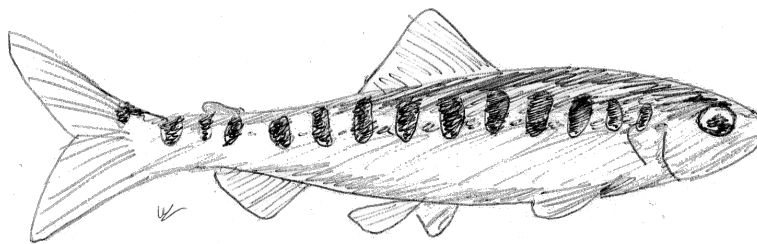


Master's research project

**Density-dependent micro-habitat selection of  
Atlantic salmon (*Salmo salar* L.) parr in winter**

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## Abstract

In nature, evolutionary pressure is often driven by deficits, and organisms have developed an array of coping mechanisms. One potent adaptation is density-dependent habitat selection, where animals take into account their surroundings and their potential competitors when choosing where to reside. Many models exist to predict the distribution of individuals over space, all with their own strengths and assumptions. The current study examines the distribution of wild underyearling Atlantic salmon (*Salmo salar* L.) between deep and shallow waters in winter, depending on size, density, presence of daylight and presence of overyearlings. In addition to being an interesting case study on the applicability of different models, the results address an imminent conservation issue. Hydro power installations induce rapid drops in stream water levels, causing Atlantic salmon in shallow parts of the river to strand, with severe fitness consequences. This research helps to predict the proportion of Atlantic salmon parr to be at risk in different circumstances. We find that during winter underyearling Atlantic salmon is uninfluenced by the tested factors, and maintain a preference for deep water. This means that stream bed prone to exposure is largely avoided, compensating for the increased wintertime risk and consequences of stranding when in the shallow. These observations differ from those from summer and autumn experiments, and illustrate the importance of including a seasonal timescale in experiments and models.

**Keywords:** *Salmo salar*, Hydropeaking, Density-dependent habitat selection, Ideal Free Distribution

## Introduction

All organisms are faced with a limitation in resource availability of some sort, whether it be breeding opportunities, shelter or nutrition [1]. The ability to cope with scarcities is a driving force behind population regulation, and is favored by evolution through natural selection. Species have evolved adaptations to best utilize resources, and individual fitness is in large part determined by the extent of optimization of traits accommodating this, within the boundaries of natural limitations [2,3]. As resources tend to be heterogeneously spread within the environment, a common adaptation is the use of mobility to maximize access to limiting resources. Combined with senses enabling the estimation of habitat suitability, it provides a potent mechanism to actively optimize individual fitness by habitat selection [1, 4, 5]. In the presence of competitors for the same resources, the resource availability per individual is reduced as resources have to be shared. Thus, competitor density is to be taken into account when assessing habitat suitability, and in many organisms there is evolutionary pressure on the ability to estimate potential habitat yields as a function of resource availability as well as competitor density, leading to density-dependent habitat selection [6]. Consequently, when the best habitats become over-crowded, individuals may resort to less suitable habitats [4, 7–12].

When population size exceeds sustainable levels, the source-sink model predicts that individuals from a suboptimal ‘sink’ habitat, in which mortality is higher than natality, may come to occupy vacant places in the productive ‘source’ habitat when they arise [1,2]. Thus, sink habitats provide a buffer effect to the population against steeply decreasing animal numbers in times of dearth, as first described by Kluyver and Tinbergen for titmice populations [13–15]. This provides a potent explanatory model for observed persistence of unsustainable settlement in animal populations, and an aid in establishing management and conservation objectives [16,17]. It demonstrates, for example, the need to distinguish between source- and sink habitats in population preservation, as protecting even a substantial part of a population’s habitat range is ineffective when that area

consists solely of sink habitats.

A classical approach to model the behavior and resulting distribution of individuals in such density-dependent circumstances is the Ideal Free Distribution, IFD. Coined by Fretwell and Lucas in 1970 [18], the model assumes negligible traveling time within a patched distribution of constant resources that are never depleted, and equally shared by any number of omniscient competitors that are equal in all respects. The IFD predicts a stable neutral equilibrium in which individuals divide themselves over habitats proportionally in regard to the availability of resources, so that their intake rates are the same regardless of which patch they reside in [12, 19].

The assumptions of the IFD prove unrealistic in most if not all natural environments, and a higher than predicted exploitation of poorer patches is a common observation [19, 20]. Especially the assumptions of perfect competitive symmetry between individuals and their assumed omniscience seem to be oversimplifications that undermine the model's validity in many field studies [8, 21–26]. Since the observed overuse of poorer habitat patches is a shift towards a more random distribution than the IFD would predict, one suggested adaptation of the IFD model is the incorporation of a limited ability to assess habitat quality or competitor density, thus reintroducing a random component as decisions are founded on incomplete information of the environment [19]. A more common approach, however, is the addition of interference among competing individuals by assigning costs to competitive interactions [19, 27] or introducing competitive inequality [28].

An integrative approach of the latter has been put forth by the introduction of the so-called Ideal Despotic Distribution, IDD. Proposed as an alternative to the IFD [22, 29], it incorporates competitive asymmetry, allowing superior competitors to prevent inferior competitors from gaining access, effectively monopolizing an attractive resource patch. As a consequence, rich patches come to contain fewer individuals than predicted by the IFD model alone, thereby accounting for the observed relative overuse of low quality patches [25, 30]. The monopolization consequentially leads to a reduction of the predicted

territory size in good habitats, since the exclusion of competitors means that a smaller area can suffice for the inhabitants' resource requirements. Reduced territory size is an advantage in terms of reduced energy expenditure allocated for territory defense, shifting the cost-benefit balance towards improved economic defendability [21].

As field studies often demonstrate deviations from the predictions made by these models, it is commonplace to introduce novel factors to retrofit the observations within a model's framework. As germane as such hypothesizing is, not in the least place as a reminder of complexity, predictions based on models incorporating observed distributions and densities alone are of limited use [26]. Apt numerical predictions on habitat selection are thus to be based on measurements on underlying factors that are often difficult to quantify, such as habitat quality, costs of competing and (re)settlement, as well as the costs, benefits and limitations of assessing habitat quality and competitor densities [6]. For this, it is paramount that measurements are derived from as natural settings as possible in order to predict behavior of individuals and consequences of management decisions in wild populations [24, 31].

In this respect the Atlantic salmon (*Salmo salar* L.) provides an especially well-suited study species. During its pre-smolt life stage in fresh water streams, fitness and survival are in large part determined by its ability to occupy habitats that provide shelter from predators as well as sufficient foraging opportunities. These requirements severely reduce the suitability of much of the potential habitat area, with the emergence of intraspecific competition and density-dependent habitat selection as a consequence [32]. A large amount of research has been done on this anadromous salmonid and elaborate semi-natural study facilities have been constructed, in large part due to the economic value of the stocks, the complex relationship with its environment throughout its life cycle and the degradation of its habitat caused by human activity. This research has brought about an ever-increasing understanding of the ecology and human-induced declines of Atlantic salmon populations, providing researchers and managers with tools to model the effects of various anthropogenic disturbances and thus strive for the minimization thereof.

The current research aims to test for density-dependent wintertime micro-habitat water depth preferences of pre-smolt Atlantic salmon, while taking into account effects of average body size, presence of larger conspecifics, and time of day. Atlantic salmon behavior conforming to the predictions of the source-sink model would exhibit a density-dependence in which the preferred habitat is increasingly saturated with higher densities, resulting in increasing residence in less preferred habitats. A similar pattern is to be expected in a model incorporating despotism, where dominant individuals force competitors into suboptimal habitats. We expect however that as despotism during wintertime is reduced [33, 34], the assumptions of the Ideal Free Distribution are effectively valid, causing a shift towards the equal spread predicted by the IDF model, unaffected by the aforementioned factors.

Besides providing added fundamental understanding of the habitat preferences and factors influencing habitat selection in Atlantic salmon parr, results may be utilized to address an imminent conservation issue. As human energy demands rise, Atlantic salmon populations are increasingly confronted with sudden fluctuations in river flow caused by hydro power plant-induced hydropeaking. In Norway, legislation has been passed allowing the export of hydroelectricity in order to meet the demands of a globally increasing market for renewable energy. This has and will continue to lead to an increase in hydropeaking, further altering the river habitat of the Atlantic salmon. This is especially pronounced during winter, when electricity demands are high [35]. Apart from a general reduction of food availability in ramping zones and numerous other effects on biotic and abiotic factors in the habitat [36], hydropeaking will adversely affect juvenile Atlantic salmon survival directly where stranding occurs. Individuals may sustain physical harm when flow is reduced with such a rate and to such an extent that fish residing in shallows become stranded, leading to mortality or reduced fitness. It has been reported that the likelihood of stranding is at least in part affected by season, time of day and cohort, as well as an interaction between these predictors [37, 38].

Previous results suggest a gradient in water depth preference over increasing age that

leads younger Atlantic salmon to reside in more shallow water, causing an increased risk of stranding [39,40]. A general tendency to seek refuge in deeper water during winter [41] may however cause cohort segregation to be less pronounced in this study. It has been established previously that stranding in general is far more common in winter due to reduced activity, especially during daytime as fish shift towards nocturnality [37,38]. As a result, fish in the shallow are more likely to strand when acute water flow reductions occur during daytime, whereas at nighttime they may be more able to avoid stranding but will still experience a drop in foraging opportunity as they are forced to leave their territories. While occurrence of despotism as in an Ideal Despotic Distribution would render both timing and population composition important considerations in hydropeaking planning, the predicted conformity to the Ideal Free Distribution model would leave a constant proportion of a population prone to stranding, regardless of these factors. Results of the current study will be of importance when estimating the respective risks of stranding different cohorts face, and will ultimately be integrated into advises on possible measures to minimize the impact of hydro power plants on Atlantic salmon populations.

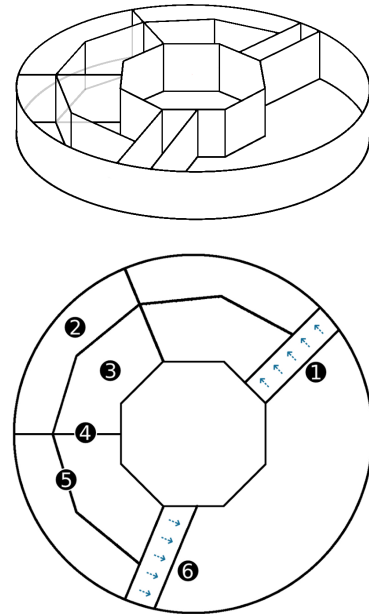
## Material and methods

### Study site and facilities

Field experiments were executed between February 8<sup>th</sup> and February 24<sup>th</sup> 2011 at the NINA Research Station near Ims, Norway (58°54'N, 5°57'E). The facility comprised four partial-ring shaped streams or 'arenas' (see figure 1), each with a surface area of 30 m<sup>2</sup>. Water originating from a nearby lake flowed through these arenas at a constant rate. In each arena, escape-proof mesh separators were present that separated the stream from the water in- and outlet, as well as separating the stream into three sections of 10 m<sup>2</sup> each. The bottom of each stream was filled with natural substrate with a depth gradient that ranged from a shallow 18 cm on the inner side of the ring to a deep 31 cm on the outer side. Along the length of the stream, vertical rails containing two framed mesh hatches



that could be slid up and down were present in the center of each section. When lowered these hatches separated the deep from the shallow part of that particular section (see figure 2). When lifted above the water surface, metal pins could be placed in the rails, thus suspending the hatches well above the water surface, leaving that section undivided. Ropes leading to the center of the arena were attached to each pin to allow its removal from the rail, thereby providing a triggering mechanism for the hatches to drop down. A white tarp was spanned across the middle of each section, covering an estimated 50% of the total surface area of that section to provide overhead cover.



**Figure 1:** 3D and top view of an 'arena'. Numbers indicate : (1) Water inlet (2) Deep subsection, surface area  $10 \text{ m}^2$  (3) Shallow subsection, surface area  $10 \text{ m}^2$  (4) Escape-proof mesh section boundary (5) Escape-proof mesh hatch that when lowered separates subsections (6) Water outlet.

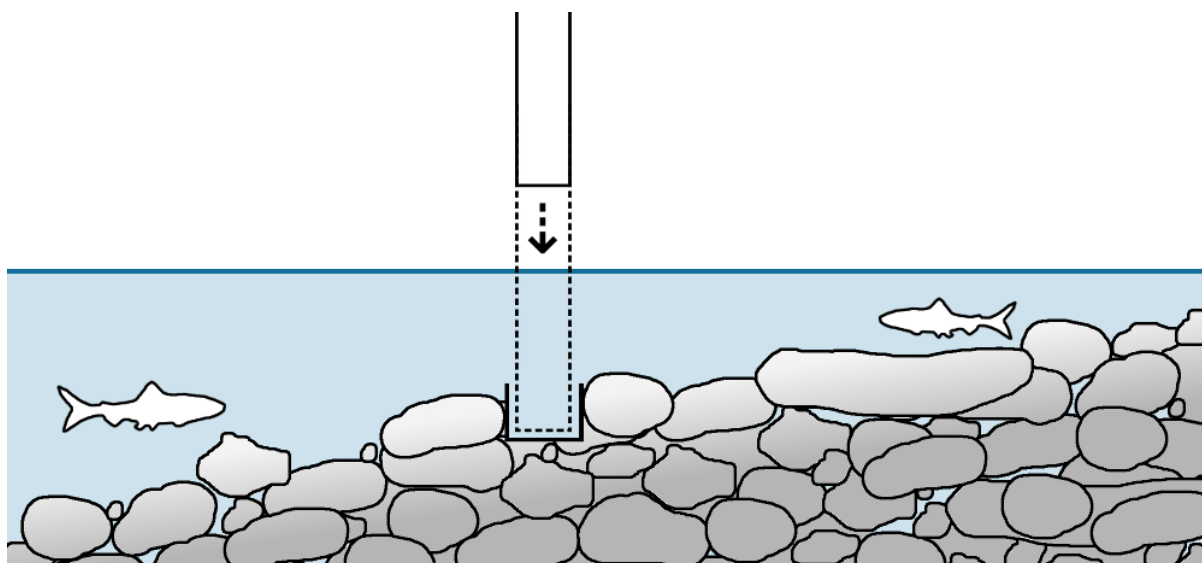
## Experimental animals and setup

Experimental animals (4032 in total) were part of a hatchery reared wild Atlantic salmon population originating from the nearby river Imsa. Over the 192 executed trials, 3840 young-of-the-year (YOY) individuals were used, with fork lengths ranging from 56 to 150 mm. In addition, 192 larger (fork lengths ranging from 142 to 206 mm) one-year-old fish were used to test the effects of the presence/absence of larger conspecifics.

The trials were carried out in accordance with a full factorial experimental design, with the fraction of YOY individuals in the deep as the response variable. This led to a total of eight possible setups (see Appendix), where experiments would be executed:

- with either low ( $1 \text{ per m}^2$ ) or high ( $3 \text{ per m}^2$ ) densities of YOY
- with either the addition or omission of two larger, one-year-old individuals
- in daylight (noon) or in the dark of night (midnight)

Prior to each trial, the hatches were suspended above the water surface with the triggering



**Figure 2:** Cross section of arena, consisting of a sloped gravel stream bed and a hatch that can be dropped to separate the deep from the shallow.

mechanism in place. The tarps were spanned across the center of each section, providing cover for the experimental animals in both shallow and deep water. The required number of YOY and large, one-year-old individuals were then extracted from their reservoirs, selecting for a minimal spread in fork lengths among YOY and a maximal fork length difference between large fish and YOY. These individuals were placed in the appropriate sections, with all sections within an arena containing the same composition to prevent any effects from adjacent sections. After stocking, fish were left to habituate for a minimum of 20 hours, as previous observations in the same facility proved this to be an ample amount of time. During habituation, any activity close to the arenas was avoided in order not to disturb the settling process. After the habituation period, experimenters would inconspicuously approach the center of the arena and drop the hatches by pulling the ropes attached to the pins holding the hatches in their suspended positions, thus instantly separating the shallow from the deep. After removing the tarps to gain access to the sections, all fish would be caught by electro-fishing and have their fork-lengths measured. All individuals were then put in separate reservoirs to avoid reuse in the experiment, after which the arenas were reset and restocked for the next series of trials. At any given time, two arenas were used for nighttime trials, and two arenas for daytime

trials. Halfway through the experiment this was reversed.

## Statistics

Statistical analysis were done using R version 2.13.1 for Ubuntu linux [42]. The effects of average YOY fork length, density, presence of large fish, time of day and all two-way interactions on the proportion of YOY in the deep were examined using linear mixed effect models by means of the *lme* command from the nlme package [43]. Model comparisons suggested that a random intercept model with sections as a random effect was superior to alternative models with either no random effect or with both a random intercept and -slope. A further visual inspection suggested no violation of assumptions, after which a full model was constructed including all terms and their two-way interactions.

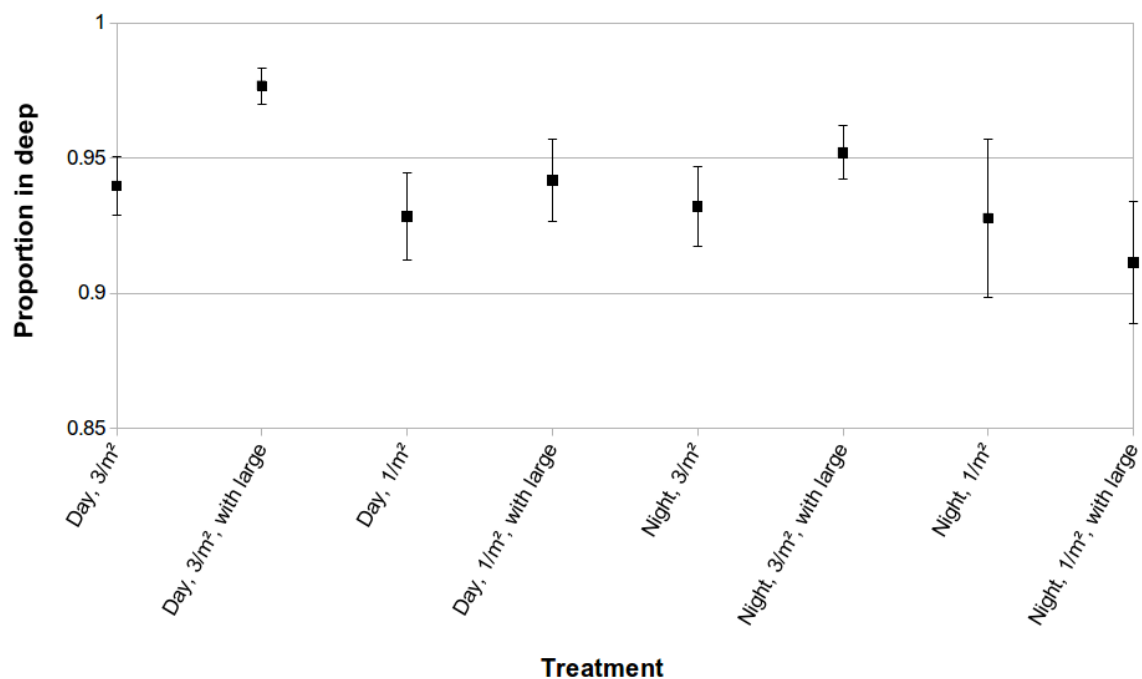
Using the protocol described by Zuur et al. [44], the maximum likelihood estimation of the models allowed for model comparison and sequential backward removal of terms until all terms had significant predictive value for the observations.

During the field experiments, frozen trigger mechanisms and/or hatches incidentally lead to suboptimal separation of deep and shallow. Such malfunctions were always resolved and noted as anomalies, although personal observations did not suggest a change in fish whereabouts after such incidents. The entire statistical analysis was executed on the entire data set (192 trials) as well as a data set omitting data following any suboptimal subsection separation events (leaving 155 trials). This had no effect on the resulting model or the orders of significance. Discussed results will henceforth consider those derived from the latter, most conservative data set.

## Results

Overall, fish exhibited a strong preference for the deep water; over 94% of YOY individuals were recaptured in the deep subsections. The sequential backward removal of terms from the maximal model (see Appendix) retained only the average fork length as a significant

factor ( $p = 0.0013$ ). Examining the magnitude of the effect fork length had on the proportion of fish in the deep, it amounts to an increase of 0.006% more fish in the deep for every centimeter increase of average fork length. Considering the limited range of fork lengths within a cohort, the infinitesimal effect renders this result biologically insignificant, in spite of its statistical significance. We therefore conclude that neither of the measured factors significantly influenced the proportion of individuals residing in the deep.



**Figure 3:** The proportion of YOY in the deep per treatment (time of day, density of YOY, large present/absent). Error bars indicate standard errors.

## Discussion

As none of the tested factors significantly influenced the proportion of YOY swimming in the deep in winter, it seems evident that these individuals maintain their preference for residing in deeper waters, irrespective of time of day, presence of larger conspecifics, density or fork length of the YOY. These findings contrast with those of similar experiments

carried out during summer and autumn. In those experiments, YOY were significantly more abundant in shallow water when sharing their habitat with larger fish [45,46]. Proposed underlying mechanisms in these cases were that aggressive territorial behavior of large fish displaced YOY to the less preferred, shallow micro-habitats, and/or that YOY avoided such large individuals whose size difference was sufficient to pose a potential predation risk [47]. Furthermore, a day/night difference that could not be tested during summer due to a lack of real dark of night, was found to have an effect on YOY habitat use during autumn. Individuals tended to reduce their residence in deep water during night, possibly due to a shift toward benthic feeding and a decrease in risk of predation by visual predators at night, both contributing to a less pronounced preference for deep water. The deep/shallow abundances found in this wintertime study are equivalent to those from the summer and autumn trials where overyearlings were absent.

One explanation for the apparent lack of a reaction to large fish during winter could be a reduction in the ability to detect the presence of conspecifics. Although relying on several visual and chemical cues to detect other individuals [48,49], some loss of resolution is to be expected at night. Shifting to a nocturnal foraging regime in winter, foraging individuals will be less able to detect each other unless in very close proximity, leading to lower nocturnal aggression rates. This hypothesis is supported by the observations that the territory radii approximate the limit at which individuals can detect prey items [50–52], and that wintertime aggression is higher in daylight [53]. When foraging strictly at night and sheltering at daytime, it is possible that densities examined here have not reached a level of saturation where significant competition for space occurs.

Another, perhaps more parsimonious explanation lies in the observation that fish are less active during winter, leading to a reduction in foraging behavior to the point of anorexia [54–57]. Whether through a reduction in competitive interactions or predation pressure from large individuals, it allows underyearlings to reside in closer proximity to larger, overyearling parr. A resulting move to deeper water has been observed [58], the decreased competition for food and space giving individuals the opportunity to compen-

sate for their decreased ability to escape predators by seeking shelter there. Displacement by larger fish, if occurring, may then be reduced to a spatial scale smaller than that of the deep/shallow distinction. The observation of the less than total absence of YOY in the shallow may in that case reflect preference for particular patches within that section.

One might hypothesize that rather than more benign circumstances in the deep allowing YOY to reside there, it may be that an increased risk of staying in the shallow effects the observed shift towards the deep. While this possibility cannot be disregarded completely, the known reduction in foraging and aggression during winter [33, 34] suggest this latter possibility is at best one amongst several, more influential factors. There is also no evidence for an upheaval of competitive differences through a disproportionate disadvantage for large individuals during winter, as the only temperature dependent competitive disadvantage for large individuals has been found to occur at the highest of summer temperatures [59, 60].

A factor that is not included in the present experimental setup is the influx of nutrients originating from riparian vegetation. More abundant in the shallow habitat adjoining the banks [61], it introduces an incentive to enter shallow waters. This incentive is absent in the artificial streams. As during winter this influx is reduced, and foraging less crucial in habitat choice, this absence is arguably irrelevant. In summer and autumn it may however partially compensate for the preference of deep habitat, resulting in less skewed habitat selection.

To allow for a distinct comparison between habitat selection during light and dark conditions, no experiments were conducted around dawn and dusk, when foraging is known to be intensified [62–64]. A shift in behavior and ultimately distribution may thus be present those periods, outside the scope of the present experiments. Again, the known decrease in foraging behavior as a whole and the shift towards nocturnal foraging would make this effect of less significance during winter than during summer and autumn.

When considering the suitability of a habitat selection model to predict the behavior of Atlantic salmon in winter, one has to consider the properties of individuals as well

as their interactions. On an individual level, the reduced foraging behavior takes away a strong incentive to prefer certain habitats on the basis of foraging opportunities. As shelter thus becomes both relatively and absolutely more important as a factor in habitat selection [65], this change in priorities does not necessarily mean that suitable habitats are more available or easier to find as such. It does seem likely, however, that the suitability of a habitat can be more readily assessed, since in contrast to food, the presence of shelter is stable over time for a given patch [53, 66, 67]. In modeling terms, this means that an individual is more well informed when selecting a habitat, in some ways approaching the omniscience in ideal models such as the Ideal Free Distribution (IFD).

The observed patterns of habitat use disqualify the source-sink model as an explanation in this case, as the density independence of the occupation of deep water indicates that individuals are free in their settlement. Had the source sink model been applicable, it would predict saturation of the preferred habitat, leading to an increasing proportion of individuals inhabiting the shallow as densities increase [1, 2]. Since all seasons fail to find a relation between proportion of individuals in the deep and density, fish do not seem to be forced into unsustainable habitats as would be the case in a sink habitat. Whereas the identification of a source habitat would render this habitat a conservation priority, the preference for deeper habitats is in itself an indication to the importance for Atlantic salmon, and an argument for its preservation.

The suggested lack of aggressive interactions, whether due to reduced activity or reduced detection of competitors, invalidates the Ideal Despotism Distribution (or any other model incorporating despotism) as an explanatory model. While in other seasons individuals monopolize resources and displace subdominant individuals to less preferred habitats [45, 46], the winter experiments fail to find any evidence for such behavior. Regarding the assumption of freedom in the IFD, the reduced territoriality observed in literature as well as indicated by the results presented here have to be taken into account. Different than in the Ideal Despotism Distribution, where stronger individuals monopolize certain habitats, Atlantic salmon in winter do not seem to compete over

habitats. Although different from the IFD assumption of equal competitive abilities, an apparent lack of competitive behavior renders the inclusion of despotism in the model unwarranted. Although movement is never without energetic cost (and relatively even more costly during winter due to lowered metabolism), thus violating the assumption of freedom of movement in the sense that it is not for free, individuals are indeed free to settle where they choose.

To conclude, on the spatial scale of the current study, individuals are both relatively free and ideal in deciding where to reside. If on grounds of parsimony alone, the most elementary model is to be preferred, the fact that nearly all individuals were recaptured in the deep end of the habitat suggests that the behavior of Atlantic salmon during winter is in concurrence with an unsaturated Ideal Free Distribution.

## **Management and research**

Through the refinement of knowledge of how species interact with their habitat, we are able and obliged to strive for the preservation of population numbers where under anthropogenic strain. A better understanding of the prerequisites and vulnerabilities of species and populations can help identify the habitat management strategies increasing carrying capacity or individual fitness. In the case of Atlantic salmon, the challenges posed by hydro power plant-induced hydropеaking and subsequent risk of stranding is an imperative conservation issue [39, 40, 68–70] that can be more aptly addressed as our understanding of micro-habitat selection increases.

The consequences of the current findings from a management perspective include the observation that no distinction can be made between effects of hydropеaking over different population compositions or diel time frames. Whereas during summer and autumn distinctive predictions can be made regarding likelihood of stranding depending on time of day and the presence of larger cohorts, no such differentiation is present during winter. While fish in the shallow are less likely to avoid stranding and face graver fitness consequences during winter, residence in the shallow during winter is on par with the



lowest levels found in summer and autumn. This leaves populations less vulnerable to wintertime stranding events when local water depth is sufficient to avoid exposure of the deepest substrate, but eliminates the opportunity to minimize effects by appropriate timing.

From a modeling perspective the current findings emphasize some vital considerations for the formulation of hypotheses. An important realization remains that quantities and distributions alone are fundamentally insufficient to assess the validity of any particular model in regard to observations when no underlying mechanisms are examined. To include these explanatory factors, experimental procedures as implemented here remain all but indispensable. It is important to note as well, however, that the current research studies the behavior of hatchery reared individuals, whose behavior is known to be somewhat dissimilar from that of wild individuals [71–73]. This further emphasizes the need to view results in a broader context of underlying mechanisms and behavioral patterns in order to avoid overgeneralizing results and to guide future research.

A final key consideration regarding the modeling of findings as those presented here is the importance of season as a substantial factor. When addressing the validity of a model that predicts the spatial properties of a population, a temporal factor such as season is easily obscured by averaging findings, or excluded from analysis when executing trials only at specific times of year. While the winter experiments examined here produced observations that are in accordance with an Ideal Free Distribution, those from identical trials on the same population and the same location within a different season were not. This demonstrates the necessity of the inclusion of temporal factors not only in the models themselves, but also in the actual selection of models, in order to do justice to the dynamic nature of behavior within populations over extended time scales.

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## Appendix: Tables

Time	Treatments		N	YOY size	1+ size	Size 1+ - YOY	
	YOY/m <sup>2</sup>	1+				mm	% of YOY
Day	3	absent	21	108.01 (21.27)			
Day	3	present	16	114.19 (17.89)	177.31 (11.20)	63.13	62%
Day	1	absent	19	105.62 (22.60)			
Day	1	present	18	104.78 (21.07)	172.78 (10.79)	67.97	71%
Night	3	absent	18	118.82 (13.51)			
Night	3	present	23	119.41 (14.56)	176.46 (9.51)	57.12	52%
Night	1	absent	19	112.25 (20.40)			
Night	1	present	19	107.74 (18.81)	172.00 (15.76)	64.01	64%

**Table 1:** Overview of treatments, number of trials (N), fork lengths of underyearling (YOY) and overyearling (1+) individuals, and their absolute and relative differences within each trial. Numbers in parentheses denote standard deviations. All sizes are in mm.

Factor	Significance
Size * Large present	0.9762
Size * Density	0.8461
Day/night * Density	0.4454
Size * Day/night	0.5081
Large present * Density	0.2783
Density	0.9312
Day/night * Large present	0.2074
Large present	0.4827
Day/night	0.1803
Size	0.0013*

**Table 2:** The p-values for the sequential removal of each factor of the full model, in order of removal.