REVIEW

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Environmental Enrichment and its effects on *Welfare* in fish

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Contents:

Chapter Page

1 Introduction 4

2 Historical perspective of environmental enrichment 5

3 Definition of environmental enrichment 6

  3.1 Enrichment types 7

  3.2 Aims of enrichment 7

  3.3 Welfare and pain perception 8

  3.4 Areas of application 10

4 Functions of natural structures in the wild 11

5 Natural structures in in-stream restorations and their influences of the fish fauna 37

6 Structures in cultural / captive environment of salmonids 39

  6.1 Structures as shelters 39

  6.2 Structures for the reduction of aggression 40

  6.3 Structures for sensory and cognitive stimulation 42

  6.4 Tank floor substrates 44

  6.5 Incubation substrates 45

  6.6 Toys 47

  6.7 Structures in periphyton-based aquaculture 48

  6.8 Tank covers providing shade and visual protection 48

  6.9 Organic aquaculture 50

7 Discussion and conclusion 51

8 Acknowledgments 54

9 References 55

Abstract

Although public and consumer awareness is increasing fast in regard to welfare in captive fish; one often neglected aspect of fish welfare is the complexity of their holding environment. Increasing the complexity in any given way is termed environmental enrichment. Enriching the environment of fishes can have various positive effects on physiology, health, survival and therefore general welfare. However, it usually is also increasing labor through increasing maintenance and handling time and is lowering thus the efficiency. Fish welfare in general includes also the acceptance that fish can feel a certain degree of pain and should be considered, at least to a certain degree, sentient and conscious beings, which is scientifically still under serious debate.

Under the assumption that fish have the capabilities to feel pain and are, at least to a certain extent, conscious and sentient beings, the often neglected welfare-aspect of environmental enrichment and its effects on fish under captive conditions are discussed in this review. This includes farmed fish for human consumption and restocking purposes (aquaculture) and fish kept for research. A definition of environmental enrichment is as well provided as a historical context, different enrichment types and the aims of environmental enrichment and areas of its application. Whether or not fish can feel pain is also debated.

An extensive table is included, providing natural micro-, meso- and macrohabitat preferences of some important freshwater salmonids (rainbow and brown trout, Arctic char), Eurasian perch and common carp in different life stages (fry, juveniles, adults). Furthermore the environmental enrichment is considered under the perspective of in-stream restorations and its effect on, primarily, salmonids in culture. Environmental enrichment includes physical structures added to the captive environment to provide increase the structural complexity while other forms of environmental enrichment may include sensory, social, nutritional or even occupational enrichment. The latter, however, is usually not of higher importance for fish. In the various research papers reviewed, it is obvious that environmental enrichment can provide several beneficial advantages although some negative effects have been observed too. Observations of environmental enrichment effects on a production or farm-level are basically completely missing in the literature and therefore a large knowledge gap exists between laboratory studies and practical application. While several types of environmental enrichment have been adapted to aquaculture out of necessity, mainly in terms of reproduction success, little is known of environmental enrichment effects on fish welfare under production conditions and whether benefits may outweigh the drawbacks like increased installation costs or increased effort for maintenance.

1.0 Introduction

It is well known that aquaculture has been for the last decades the fastest growing food producing sector in the world. Although the largest absolute growth in terms of produced quantity is located in Asia (SOFIA 2014), there is growing interest of the public, government, media and potential investors all over the world, including Switzerland. The public awareness of problems related to sea food produced via capture fisheries (overfished and declining fish stocks, destruction of habitats by fishing gear) but also of problems associated with aquaculture production (fish meal production needed for carnivorous species, destruction of sensible ecosystems like mangroves for farm space, application of anti-biotics and chemicals) increases the sensibility of consumers in industrialized countries. Especially in Switzerland the consumer demand for high quality products fuels an unprecedented increase in sustainable and healthy sea food products. In addition to the product quality in terms of healthy and clean sea food, one emerging aspect of fish production is that of animal welfare. The debate about fish welfare is comparably younger the one about terrestrial animals. This is to a certain degree comprehensible as most terrestrial farm animals have been domesticated over hundreds, sometimes thousands of years while fish production is, with few exceptions (ancient Chinese carp and ancient Egyptian tilapia production), a comparatively young business and has started to be documented by the FAO (Food and Agricultural Organization of the UN) only in the 1950s with a global production volume of 640.000 t while the overall production in 2012 was 90.4 mio. t, resembling a 140-fold increase (FAO 2014). Furthermore several other differences besides the taxonomical affiliation exist. The production of fishes occurs in a complete different medium, water. It proves to be rather complicated to estimate the state of welfare. Fish are hard to observe during the day except for the feeding time and for a really close inspection (for detection of diseases, for example) they need to be removed from the water which in itself is great stress. Fish do not have any familiar facial or body expressions and usually do not make any noise which would help the farmer or an observer in judging the state of welfare in the respective holding system. One of the most heavily discussed issues about fish welfare is the ongoing debate whether or not fish are capable of feeling pain and discomfort. Another striking difference complicating research and definitions of fish welfare regulations compared to terrestrial livestock production is the significantly higher diversity of produced species in aquaculture. The FAO lists just below 20 terrestrial livestock species in comparison to around 500 fish and invertebrate species (plants not included) produced in aquaculture and listed in the FAO database FishStatJ (FAO 2014). Several intensively discussed aspects in fish welfare are species specific. For example a detrimentally high stocking density for one fish species is not necessarily detrimental for another (for example, growth (can) declines with too high stocking densities of rainbow trout, *Oncorhynchus mykiss* (Ellis et al 2002), while in young Arctic char, *Salvelinus alpinus*, it is usually positively correlated with stocking density (Wallace et al., 1988; Jørgensen et al., 1993).

Especially under production conditions where stocking densities are always, even under the most extensive conditions for most fish species, higher than found in nature, the fish welfare is of major concern for involved scientists, animal rights organizations, governmental departments of veterinary and animal rights affairs and consumers. Of course also for producers since a low welfare usually also goes along with a reduced production efficiency. While several aspects of fish welfare received significant attention in the last two decades, the question whether fish under production conditions need a certain degree of environmental enrichment or not is much less discussed in scientific literature. Here, we aim at shedding light on enrichment in a context of practical application of physical structures and of natural behavior of fish and what can be deduced for armed fish. The primary species investigated here are the rainbow trout, *O. mykiss*, and the Atlantic salmon, *Salmo salar* as they are among the most important high value farmed species in Europe with a high degree of research being conducted over the last few decades.

2.0 Historical perspective of environmental enrichment

At the beginning of the 20th century, concepts of enrichment were described first by Yerkes (1925), a primatologist, and later by Hediger (1950, 1969), a zoo biologist, in terms of occupying captive animals with playing and working. The physical and social as well as the management regimes and diet were recognized to be important for animals living in captivity. Markowitz and Woodworth (1978) and Markowitz (1982) gave the animals the possibility to choose within their environment and taught animals how to procure food. This also allowed getting insights into the way of learning of these animals. Psychology literature with a different focus than environmental enrichment provided deeper insights into enrichment. Housed in a barren box, the authors observed the animals' responses when fed after a certain schedule independent of the animal's behavior at that moment (schedule of reinforcement, conditioning). The animal learnt to predict and anticipate the arrival of next feeding and developed a stereotypic behavior (Ferster and Skinner, 1957). A highly predictable way of feeding can cause stereotypies in zoo animals as was stated by Carlstead (1998).
In the sixties, zoo designers started to implement animals' history into exhibition plans (Kortland, 1960). Fraser (1975) studied enrichment in farm animals (sows, *Sus scrofa*) by providing bedding material such as straw. In the eighties, many ideas in the area of environmental enrichment were developed by animal caretakers in zoos while the implementation was rather rare.

The research in environmental enrichment began with maturation of the subject (in the late 1980s) to be oriented towards improving animal welfare of laboratory and farm animals (Chamove, 1989; Mench, 1994; Markovitz and Gavazzi, 1995). As an example for farm animals, in the eighties enriched-housing-systems were designed that answered to the natural needs of pigs (Stolba and Wood-Gush, 1984). More recently research also focused on improving welfare of pets at home (Milgram et al., 2006).

Since the nineties environmental enrichment became a part of the management of captive animals in zoos as well as of farmed animals. Guidelines of housing enrichment were then developed for farm animals. In Switzerland, the Swiss Animal Welfare Act stipulates that housing systems must meet the animals' needs. The Centre for Proper Housing of the Federal Food Safety and Veterinary Office is testing housing systems for farm animals.
In aquaculture, more sophisticated technology, especially in water treatment and oxygenation, allowed for increasing stocking densities, for example in trout and salmon aquaculture. This intensification has also roused public awareness and therefore policy makers paying more attention to fish welfare for more than a decade in Europe (Kadri et al., 2005 in Kadri, 2008).

While welfare aspects have been quite broadly developed in terrestrial animals, this knowledge cannot be transferred to aquatic animals. The challenges in teleosts and other aquatic animals are novel and not necessarily comparable (Turnbull and Kadri, 2007). While knowledge and implementation of terrestrial animals has progressed significantly, the knowledge and implementation of fish welfare or even common definitions on general terms is lacking behind. With raising public and subsequent governmental awareness, also concerns about fish welfare in production are increasing (Lymbery, 2002;

Conte, 2004; Huntingford et al., 2006). It was in the late 1990s and early 2000s that stocking density became an issue. Growing interest in the welfare of fishes is rising also in regard of animal friendly slaughter techniques and husbandry systems promoting welfare of captive fishes (Huntingford and Kadri, 2009). One of the most striking differences between terrestrial and aquatic animals is the lack of known and easily observable behavioral patterns enabling the farmer to observe the welfare of his animals. As they live in a different environment in which a direct observation is often impossible few indicators exist to judge the current welfare state of the fish. Therefore one of the most important research areas is to elucidate easy applicable and if possible non-invasive welfare indicators providing a fish farmer the opportunity to estimate the welfare status in his production system. Up to now, the benefits of environmental enrichment have been demonstrated mainly under laboratory conditions and an up-scaled implementation on farm level is needed (Huntingford et al., 2012).

3.0 Definition of environmental enrichment

Environmental enrichment refers to improving the environment of captive animals. Shepherdson (1998) defined it as “an animal husbandry principle that seeks to enhance the quality of captive animal care by identifying and providing the environmental stimuli necessary for optimal psychological and physiological well-being”. Mellen and MacPhee (2001) suggested a more holistic approach in a framework integrating enrichment into the daily management. They use the ‘natural history’ of the animal as an initial guide for defining an appropriate environment for the specific species. Natural history, including instinctive pattern, evolutionary history and ecological niche was considered essential to adequately understand, predict or control the behavior of any species (Breland and Breland 1961). It is important to define environmental enrichment as it depends on this definition how it should be measured or what indicator should be used for it (Williams et al., 2009). How, for example, normal behavior is defined requires an understanding of the repertoire of the various behavioral patterns of the specific captive animal. On the other hand, Newberry (1995) suggested that functionality and adaptiveness of behavior in captivity could be more useful than “naturalness” as it is difficult to specify natural behavior and to define to what extent it should be similar to the behavior performed in extensive or natural environments. Besides, the author noted to differentiate between animals kept in captivity as livestock and as populations for release (for conservation or stocking purpose), remembering that natural environment should be preserved and life in captivity minimized. In the wild, the behavior adapted to a typical captive environment (which is normally characterized by high population densities, limited space, readily available food etc.) would be maladaptive. Therefore, captive environments for animals destined for conservation purpose should resemble as closely as possible the environment of the future release site– and thus enriched. For example, a kind of circular shoaling of Atlantic salmon (*S. salar*) in cages as reported in Martins et al. 2012) is an abnormal behavior. Also vacuum pit digging in tilapia when housed in the absence of substrate (Galhardo et al., 2008). Young salmon tend to be naturally territorial but when kept at high densities, this behavior is suppressed and they start shoaling in incessant circles around the cage (Juell, 1995; Oppedal et al., 2011; Lymbery, 2002). Since the start of salmonid farming, farmers have observed similar patterns (Branson, 2008). When in a shoal, a reduction in aggression and also risk taking during feeding has been recognized (Grand and Dill, 1999). Similarly, Wallace (1988) notes: “It would appear that high population density affects young Arctic char (*Salvelinus alpinus*) such that agonistic behavior is inhibited and schooling behavior stimulated”.

Thus to define the goals of environmental enrichment (see chapter 3.2) may be more helpful, also in terms of practicality of implementing enrichment (Young, 2003; Leach, 2000).

3.1 Enrichment types

The different types of environmental enrichment can be subdivided into five categories (Bloomsmith et al., 1991):

- Social enrichment with direct or indirect contact with conspecifics or humans. Indirect contact may imply visual, olfactory or auditory cues
- Occupational enrichment, which can encompass psychological (devices that provide animals with control or challenges as well as enrichment encouraging exercise such as mechanical devices
- Physical enrichment which can imply an alteration of the size or the complexity of the animal's enclosure. This includes the addition of objects, substrate etc.
- Sensory enrichment which could include visual, auditory, olfactory, tactile or taste stimuli
- Nutritional enrichment involving the type and delivery of food. The type of food can be varied or novel, while the delivery of food may imply the variation in frequency or presentation of food

For farmed fish, the main environmental enrichment comprises physical structures (for a review see Näslund and Johnsson, 2014). These structures, including for example bottom substrate such as gravel or pipes in order to offer shelter, may at the same time function for example as visual stimuli.

3.2 Aims of enrichment

The overall goal of environmental enrichment is the improvement of the husbandry conditions of captive animals; thus, to enrich the environment by means which augment the welfare of the animals held in captivity.

The purposes of environmental enrichment suggested by Chamove and Anderson (1989) for example are a reduction of abnormal behaviors, an increase of the behavioral repertoire, furthermore to enable the animal to cope with challenges in a normal way.
However, according to Ashley (2007), “abnormal” behavior in farmed fish should be interpreted with caution and stresses on further research to elucidate the importance of the possibility to express natural behavioral patterns.
Results of the enrichment efforts shall provide a complex environment with stress reducing stimuli allowing the animals a species-specific behavior (Shepherdson 1998). An understanding of the behavior is crucial to maximizing normal behavior and minimizing stress-induced behavior by means of environmental enrichment as was underlined by Mench (1998, 1998a).
Often, environmental enrichment is applied with the purpose to reduce or abolish stereotypic behavior (Würbel, 2006; Mason et al., 2007). For example in Atlantic halibut (*Hippoglossus hippoglossus*) held at high densities, Kristiansen et al. (2004, 2007) observed an increase in stereotypic behavior,

described as loops of vertical swimming behavior. Adapted feed types, such as sinking food, can reduce such behavior and thus increase welfare.

The following goals of enrichment were defined by Young (2003): a) Increasing behavioral diversity; b) reducing the frequency of abnormal behavior; c) increase the range or number of normal (i.e. natural behavior patterns); d) increasing positive utilization of the environment and increasing the ability to cope with challenges in a more normal way (Shepherdson 1989 as modified by Young 2003; Chamove and Moodie 1990).

Similar goals (modified from Mellen and McPhee, 2001) and also some other aspects are: - Animal welfare as primary goal.

- Successfully reproducing animals exhibiting adequate parental care as a goal of captive management. Enriched environment enhance an adequate care and thus successful reproduction.
- The identification and reduction of potential sources of chronic stress and/or the enhancement of an animal’s ability to cope successfully with acute stress by providing enrichment.
- The reduction or elimination of aberrant behaviors and concurrently to provide opportunities for species-appropriate behaviors and activity patterns.
- The rearing of animals for re-introduction or re-stocking purposes appears to be more successful when they are reared under conditions that are sufficiently rich (and close to the environmental diversity of the habitat they are going to be stocked into) to allow the performance and maintenance of species-appropriate behaviors (modified from Mellen and McPhee, 2001).

3.3 Welfare and pain perception

Welfare refers to both, physical and mental well-being, and thus to overall quality of life (Duncan and Fraser, 1997 in Young, 2003). There are different ways of defining welfare. The ‘Five Freedoms’, as defined by the Farm Animal Welfare Council (FAWC, 1979) which is an advancement of the proposal made by the Brambell Committee in 1965, provide a valuable basis in animal welfare (freedom from hunger, thirst and malnutrition; freedom from fear and distress; freedom from physical and thermal discomfort; freedom from pain, injury and disease; and freedom to express normal patterns of behavior). Freedom from pain requires the acceptance that fish are sentient beings (see below) which is still a controversial issue. A good health status is of course essential for the well-being of an animal, but health does not necessarily imply that welfare is good - this also raises the question how to measure good or bad welfare (Dawkins, 2006; Ashley, 2007). And how it is measured depends on its definition (Huntingford and Kadri, 2009). Thus welfare can be defined according to three approaches, in which most definitions can be divided in: The feelings, the nature and the function based approach (Huntingford et al., 2006; Segner et al., 2012). Feelings or emotion based approach implies that the animal is not only free of negative experience such as fear and pain but also experiences positive situations or events (social companionship for example). This type of research is conducted with the help of behavioral and physiological measurements (Désrié et al., 2002). “Pain, fear, and psychological stress are likely to be experienced by fish” (Chandroo et al., 2004). The nature based approach offers the animal an environment that allows expressing its natural behavior and the function based approach implies the biological-physiological functions of the animal in terms of stress that can for example provoke a reduction in growth or a disturbed immune system.

It is basic for the concept of animal welfare to consider that animals are sentient beings with an ability to experience good or bad feelings or emotional states (Dawkins 1990).

Improving welfare in fish consists for example in making a careful choice of which fish to culture. Continued selection might have brought fourth certain species which are more amendable for a life in captivity, for example regarding aggressive behavior. In Arctic char, often two forms exist in lakes and usually the pelagic form is less aggressive than the benthic (Huntingford et al., 2012). Another point is to design culture facilities and equipment that satisfies the needs of the fish. Furthermore, to adapt the husbandry practices and management systems to promote welfare (Huntingford et al., 2012).This includes not only farmed fish, but also a lot of aquatic animals that are used as pets (ornamentals) in private or public displays, as well as the many fish used in research, for example in ecotoxicological studies. Certain species (like carp, *Cyprinus carpio*, in China or Nile tilapia, *Oreochromis niloticus*, in Egypt) have been managed for millennia but very few of the globally produced species are truly "domesticated" (Hastein et al., 2005).

The debate whether fish are able to feel pain or not is still going on (Rose et al., 2014) despite the fact that in the last years several publications have shown that fish got the functional prerequisites to do so (e. g. Portavella et al., 2002; Sneddon, 2002; Sneddon et al., 2003, 2003a). The discussion held up to date has been reviewed by Segner (2012). Concerning the sensation of pain it must generally be differentiated between two issues: the pain reception (nociception) leading a stimulus from pain receptors (e. g. nervous termini in the skin) to the spinal cord followed by a reflexive reaction as an answer on the stimulus with the brain not being involved in this reaction. On the other side there is the cognitive pain perception in the brain in case of sending the message "external negative stimulus" via further nerve fibers to the brain. In this case the pain is registered as an experience that should be avoided in the future.

According to some scientist's view, pain perception at the level of the central nervous system (CNS) requires two general structures that are seen as accepted in primates but not or not fully accepted in all other vertebrates (Rose, 2002). Firstly, this is the cerebral cortex or neo-cortex including the limbic system associated with pain reception, emotional behavior and memory performance. Secondly, further nerve fibers are needed sending a signal to the brain's pain center after having received an external stimulus (mechanical, thermal, chemical, etc.). Reactions on painful stimuli in the view of Rose (2002, 2007) are just pure reflexes in all animals except primates – pain perception via the brain therefore would not occur.

The works of Stevens (1992), Gentle (1992), and Gentle and Tilsten (2000) are contradictory to this view. They published results of their work which they did on birds and amphibians showing that pain might also occur, besides in fish in birds and amphibians. Furthermore Davis and Kassel (1983) and Portavella et al. (2002) could show that the telencephalon in teleost fishes has a functional similarity with the limbic system of the tetrapods. Sneddon (2003) showed that rainbow trout have pain receptors (nociceptors) in the skin. In the head regions of rainbow trout 22 nociceptors were detected (Sneddon, 2003). These receptors are free ending nerves which are micro-anatomical analogous to the pain receptors in humans (Sneddon, 2004). The transmission of stimuli to the brain occurs via the trigeminal nerve (Sneddon, 2003a). Based on her research on the influence of morphine Sneddon (2003b) also concluded that pain responses in trout cannot be just reflex-based. Fishes that had been treated with noxious stimuli under the influence of morphine did not show abnormal behavior to the same extend than fish showed without morphine medication. As morphine is acting also on the trigeminus tract in the brain of rat (besides other areas as well) (Ebersberger et al., 1995) Sneddon (2003b) concludes that the painful stimulus must also be sent to the brain of the treated fishes. Dunlop and Laming (2005) have shown neuronal activity in all brain areas including the telencephalon of the goldfish (*Carassius auratus*) and the rainbow trout after treatment with mechanical and nociceptive stimuli, suggesting a nociceptive pathway from the periphery to the higher central nervous system of the fish. Nordgreen et al. (2007) could show clearly distinguishable electric potentials in the telencephalon of salmon that had been treated with electric stimuli of two different intensions (non-noxious and putatively noxious ones). The authors concluded that salmon are able to distinguish between putatively noxious and putatively non-noxious stimuli. Never-the-less these experiments did not give an answer to the question how fish feel pain and if they can feel pain in a similar way humans can.

The question of consciousness of fish was highlighted by the work of Chandroo et al. (2004) who could show reward behavior in fish after having been given amphetamines as dopaminergic agonists. The neurotransmitter dopamine functions in motivation and reward behavior. As the fish in the experiments showed similar reactions (reward behavior) as mammals, this could be seen as an indication of some capability of fish to experience emotions like fear (Segner, 2012) and maybe also to possess a certain degree of consciousness. Rose (2007) denied consciousness in fish which would implicate pain perception. Besides the fact that there is still no proof of these two points of discussion, the above summarized findings on (possible) pain reception in fish should be worth considering when fish are kept in culture environments to fulfill animal welfare in terms of behavioral needs and requirements regarding their peripherals. As it is assumed by the author of this review that fish have the capability to feel pain and thus have at least a certain degree of consciousness and sentience they should also be given similar rights and benefits in terms of animal welfare (including environmental enrichment) than terrestrial animals are granted.

3.4 Areas of application

Environmental enrichment is a concept that is widely used in zoo and laboratory animals, and to a lesser extent in pet animals, to improve the animals' welfare (Young, 2003). In farm animals (Mench et al. 1998) the theoretical understanding of animal welfare has been advanced massively by scientists in the last decades (Appleby and Hughes, 1997 in Young 2003) but Young (2003) regrets that the implementation of the gained knowledge has not progressed simultaneously. This is visible in various countries through large differences in implementing new welfare related changes in laws and regulations. For example, in Switzerland it was decided in 1981, with a 10-year phase out, to ban battery keeping of hens for egg production (BLW 2004). In comparison, in the European Union similar changes to battery hen keeping took longer. Only in 1999 the European Union Council Directive EC No 74/1999 banned the conventional battery cage in the EU beginning in 2012, after a 12-year phase-out. Germany banned conventional battery cages from 2007 (five years earlier than required by the EU Directive) and prohibited most types of cage production including enriched cages from 2012 onwards. Also in 1981 the legal basis was set (Schweizer Tierschutzgesetz, TSchG) for testing and licensing housing systems and installations that are mass-produced and sold for an application inside Switzerland. These systems and installations have to answer the demands of species-appropriate husbandry.

Despite the high activity in adapting terrestrial animal keeping and production systems to higher animal welfare, a look into fish production shows that an implementation of the different possibilities of enrichment for farmed or aquarium fish is complex, as it is very species specific. Compared with the number of species of farm animals, the number of produced animal species in aquaculture is extremely high. While just 17 terrestrial species are listed by the FAO there are around 500 animal species in aquaculture (fish and invertebrates; FAO, 2014). Notably in contrast to terrestrial animals, aquatic animals comprise very diverse taxonomic groups (Hastein et al., 2005). And while in terrestrial animals considerable improvements have been made in environmental enrichment, in fish (or non-mammalian aquatic species) a similar progress is not obvious or even completely missing (Williams et al., 2009).

4.0 Functions of natural structures in the wild

It is argued that domesticated animals have adapted to captive environments (Price, 1999)and it is subject of debate whether or not and if so, which natural behavior is beneficial in captivity (Newberry, 1995). However, knowledge and understanding of the natural situation might be of importance when the aim is to offer captive animals an environment that respects the animal's well-being (Fraser, 1997), keeping in mind that the environment of the farm animals ancestors having formed their behavioral patterns (Wechsler, 2007). According to Price (1984) domestication means the adaptation to a captive environment by the combination of genetic changes occurring over generations and by environmentally induced changes. On the other hand, it has been shown that domesticated animals still show behavioral patterns similar to their wild ancestors, once offered a semi-natural environment as was shown in the Japanese quail (*Coturnix japonica*) by Schmid and Wechsler (1997) and in domestic pigs by Stolba and Wood-Gush (1989). Accordingly, husbandry systems should be conceptualized in a way that allows the animals to perform a certain repertoire of behavioral patterns. At the same time an adapted system has the ability to prevent abnormal behavior such as stereotypies (Fraser, 1975).

In fish, for conservation or stocking purpose, it has been shown that an enriched hatchery environment promotes a more natural behavior (e.g. Roberts et al., 2011) and increased post-release survival in the wild (e.g. Maynard, 1994a). Olla et al. (1998) suggested that fish reared in a psycho-sensory-deprived hatchery environment are less able to carry out basic survival strategies (such as eating and not being eaten; Olla et al., 1995). 'Psycho-sensory-deprived environments' means barren, void areas without stimuli such as prey types (live prey), predator or habitat refugia etc. which can create behavioral deficits. Early life exposure to the 'psychosensory deprived' hatchery environment has been associated with deficits e.g. in feeding after release, when fish are confronted with the change from hatchery-supplied inanimate food to live prey, as these areas are typically void of all kind of natural stimuli (Olla et al., 1998). In comparison to barren artificial environments natural habitats are rich in stimuli although that depends primarily on the habitat itself as they can show high variation in physical structure. Major variables influencing the habitat use of stream-living salmonids are current velocity, water depth, substrate structure and -composition and shelter opportunities (Jonsson and Jonsson, 2011). Shelter opportunities are of great importance for salmonids and are influencing their positioning, densities and growth (Jenkins, 1969).

In streams, salmonids prefer solitary habitats with substrates of rather small particles, stones or gravel; and physical cover such as fallen trees, undercut banks and overhead vegetation (Groot and Margolis, 1991 in Flagg and Nash, 1999). However, fish reared in production hatcheries in uniform concrete raceways under environmentally sterile conditions are distinctly different from their wild conspecifics regarding behavior, morphology and physiology. Due to these deficiencies, hatchery reared fish often do not thrive as well after release as their wild conspecifics (Flagg and Nash 1999).

As an indication of the sizes of different substrate types, table 1 shows codes of WDF (Washington State Department of Fisheries, 1983) from Campbell and Neuner (1985) in comparison to the Wentworth scale (1922) modified from Cummins (1962):

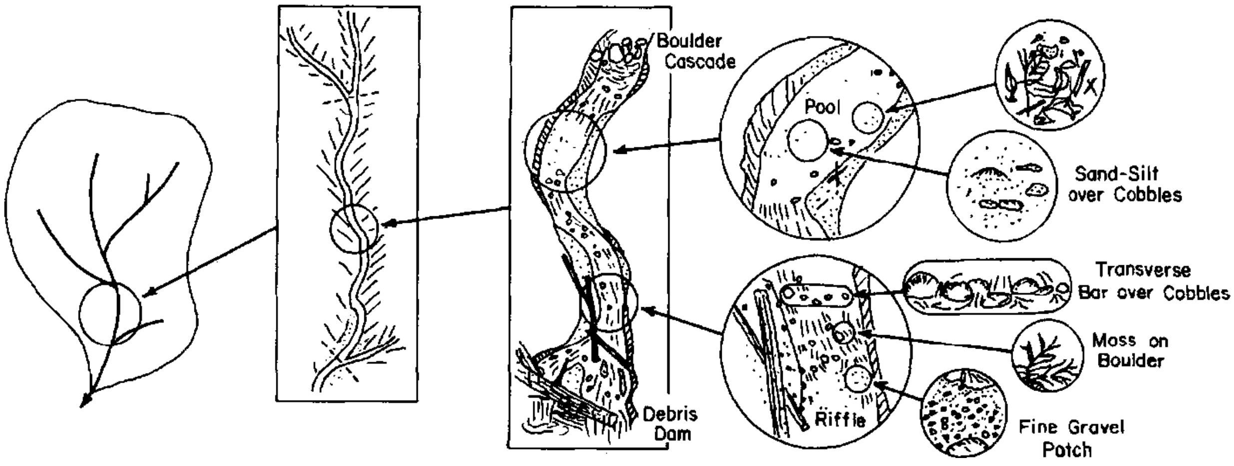
Table 1: Substrate type and particle size after WDF Washington State Department of Fisheries (1983) modified by Campbell and Neuner (1985) and after Wentworth (1922, modified from Cummins, 1962).

Type of substrate WDF (1983)	Particle size [mm]	Code	Type of substrate Wentworth (1922)	Particle size [mm]
Bedrock		9		
Boulder	>305	8	Boulder	>256
Large cobble	152-305	7	Cobble	64-256
Small cobble	76-152	6		
Large gravel	38-76	5	Pebble	16-64
Medium gravel	12-38	4		
Small gravel	2-12	3	Gravel	2-16
Sand	<2	2	Sand	0.0625-2
Silt, Clay	<2	1	Silt	0.0039-0.0625
			Clay	<0.0039
Organic detritus		0		

Furthermore, types of mesohabitats such as pools or riffle and structure (including undercut banks, woody debris, in-stream and riparian vegetation) are listed in table 2. This table includes mainly important freshwater species produced in Switzerland like rainbow and brown trout, Arctic char, Eurasian perch and common carp. Mesohabitats are physical habitat units at an intermediate level (Maddock, 1999) while microhabitats design hydraulic and structural features (substrate) including living space of the organisms at a much smaller scale (Bovee, 1982).

After Bisson et al. (1981) pool, riffle, glide (often also called "run", depending on the author) and cascades are hydraulic mesohabitats of stream reaches, differentiating through current velocity, water depth and gradient. Riffles are rather shallow (20 cm), having turbulences with fast current velocity (from 20 to more than 50 cm/sec) and quite coarse substrate (2-256 mm) with a gradient of up to ca. 4%. Cascades, categorized as the steepest type of riffles, are described as a series of small steps alternating small waterfalls and shallow pools. Rapids, another type of riffles, have an even gradient compared to cascades of more than 4% with swiftly flowing water (> 50 cm/sec). Glides, with moderate water depth and even flow often form the transition between pools and riffles. Pools are often quite deep with slow water flow. Plunge pools are called pools with a kind of cascade formed of large wood debris for example; see also fig. 1.

As habitat use can roughly be assigned to the developmental state of the fish, a classification in fry, juvenile and adult seemed to be adequate. In some publications clear indications regarding live-history states were presented, in other cases there was need to deduce life-history state from the given size-related information. Furthermore habitat-related abundance depends on availability and is also variable according to diel or seasonal influences (Heggenes et al., 1991, 2002). Also the occurrence of sympatric populations of fish species might influence habitat use (e.g. Fausch and White, 1981; Glova, 1986, 1987).



Stream System	Segment System	Reach System	“Pool/Riffle System”	Microhabitat System
10^3 m	10^2 m	10^1 m	10^0 m	10^{-1} m

Fig. 1: Hierarchical organization of a stream system with its habitats and an approximate spatial scale in meter; from Frissell et al. (1986).

Chapman (1966) considers that habitat availability (protection from predation, displacement and physical damage), is the primary regulator of salmonid population density during winter when low temperatures decrease the demand for food, while in warmer seasons “space-food convention” may be the most important regulator. In winter a “desirable” place associated with structure and cover seems being more important than feeding, while in summer space *and* food are the major determinants. Juvenile trout use for their daytime concealment during winter cobble and boulder substrate, woody debris, undercut banks and submerged aquatic macrophytes (Campbell and Neuner 1985; Griffith and Smith 1993). Adult trout, probably because not finding suitable-sized concealment, overwinter above the substrate in deep pools in large aggregations (Cunjak and Power, 1986; Meyer und Gregory 2000; Bjornn and Reiser, 1991; Cunjak, 1996;).

Table 2: On the following pages an extensive literature review, primarily about the commercially most important salmonid species produced in Switzerland (rainbow trout, brown trout, Arctic char), the European perch and the common carp about natural habitat types and preferences in early, juvenile and mature life stages of the aforementioned species is presented.

	Species			
Characteristics & Preferences	Salmonidae			
	Oncorhynchus mykiss			
	Rainbow trout			
Biotic	**Rainbow trout**			
	Fry	**Juveniles**	**Adults**	**Literature**
Feeding	Zooplankton	< 7 cm more on benthic organisms; >14 cm more terrestrial insects	Piscivore; drifting & benthic invertebrates Brief feeding forays also during night time (in summer)	Irvine & Northcote 1982 Kwain 1983 Elliot 1973 Campbell & Neuner 1985
Cannibalism			Cannibalism rarely observed in steam dwelling fish	Frost 1939; Jonsson & Sandlund 1979; Haraldstad et al 1987
Migration	Natural drift; movement towards river edges and pools	Migration to stream nursery areas and downstream Migration upstream and downstream		Erman et al 1975; Hutchings 1991 Stauffer 1972

		into lake habitats Migration influenced by water temperatures	Variations in movement patterns (highly migratory – non-migratory	Northcote 1962 Kwain 1983 Meka et al 2003
Territoriality	Territorial feeding patterns	Territory size increased with increasing fish size	In summer territorial behavior in association with substrate except in pool areas	Campbell & Neuner 1985 Keeley & McPhail 1998 Campbell & Neuner 1985
Schooling			In summer schooling common in pools; then hierarchical relationships based upon sizes observed	Campbell & Neuner 1985
Population density			0.64 fish/m^2 highest in pools areas	Campbell & Neuner 1985
Abiotic	**Rainbow trout**			
	Fry	**Juveniles**	**Adults**	**Literature**
Fluvial system	Edges of streams and lakes	Streams and lakes	Streams and lakes	Bjornn & Reiser 1991 Hartmann & Gill 1968

Water depth	Shallow water in small bays at the stream margin; 0.06-1.34 m; Differing diel and seasonal preferences of water depth Closer to bottom and selection of deeper, lower-velocity water in winter	0.18 m – 1.71 m Closer to bottom and selection of deeper, lower-velocity water in winter	Closer to bottom and selection of deeper, lower-velocity water in winter 0.15-1.89 m; in summer: pools <0.6 m deep and moving in mid-column depth ≥ 18 cm (=>spawning area)	Hartman 1965; Campbell & Neuner 1985 Riehle & Griffith 1993 Campbell & Neuner 1985 Baltz et al 1991 Campbell & Neuner 1985 Smith 1973 in Bjornn & Reiser 1991
Water flow	Require velocities of < 10 cm/s Low velocities (0-0.7m/s) along stream margins within 1-2 m off shore; Nose velocity 0-0.4 m/s Movement to lower-velocity water in winter	Movement to lower-velocity water in winter;	Movement to lower-velocity water in winter In summer more offshore; near fast	Chapman & Bjornn 1969 in Bjornn & Reiser 1991 Campbell & Neuner 1985 Baltz et al 1991

		Nose velocity 0-1.1 m/s	moving water, mostly areas with reduced current velocity; 94% trouts observed in moderate velocity sheltered positions. 6% exposed to the full force current, max nose velocity ca 1 m/s	Campbell & Neuner 1985
Structure				
- **Substrate (ground structure)**	Sand/gravel (0.6-5.2 cm) Boulders (25-30 cm) Near-shore: cobbles as shelter; Winter refuge in streambed	Seeking interstitial shelter; emerged at night to feed. Cobbles and boulders as cover especially during winter	Varying shelter; summer: in lee of objects (daytime); or shallow quiet water, resting on substrate (night) Winter: interstitial shelter	Smith 1973 in Bjornn & Reiser 1991 Hartman 1965 Campbell & Neuner 1985 Hartman & Gill 1968, Contor & Griffith 1995 Campbell & Neuner 1985

- **pools**	Seasonal differences; in winter highest density in pools			Hartman 1965
	Nearshore area of pools (winter)			Campbell & Neuner 1985
		Use of plunge pools		Hartmann & Gill 1968
			Pools preferred by largest specimen	Vondracek & Longenecker 1993
			Slow velocity pools	Contor (1989) in Simpkins et al 2000
			Clear preference of pools (winter: deeper pools)	Campbell & Neuner 1985
- **woody debris**	Preference of small crevices in log jam areas			Hartman 1965
		Small debris (branches, leaves) preferred cover type	Use of woody debris as cover	Zika & Peter 2002
			Winter concealment	Meyer & Gregory 2000
- **runs**		Runs with intermediate depth and velocities	Runs with intermediate depth and velocities	Vorndracek & Longenecker 1993, Hartman & Gill 1968
			Rapidly flowing areas such as runs, cascades, rapids	Campbell & Neuner 1985

- **riffle**		Mainly smaller trouts in shallow riffles In gravel riffles	Shallow riffles	Vondracek & Longenecker 1993 Hartman and Gill 1968
- **riparian/in-stream vegetation**	Use of submerged and overhanging vegetation as cover Association with *Chara* (algea), mainly in summer and winter nights	Seasonal occurring vegetation as shelter Submerged sedges and grasses for concealment in winter		Campell & Neuner 1985 Riehle and Griffith 1993 Simpkins et al 2000 Riehle and Griffith 1993
- **shade**	Shade along stream margin for cover Preference for shaded areas	Preference for shaded areas	22% in visually open areas and 56% in unshaded areas.	Campbell & Neuner 1985 Gatz et al, 1987 Campbell & Neuner 1985
- **undercut bank**	Use of undercut banks and shade or accumulated leaves along the stream margins.	Concealment during nights (au-		Campbell & Neuner 1985

		tumn/winter) Fish density and bank cover positively related	Trout in riffles with closest cover and undercut bank (night)	Riehle and Griffith1993 Gordon & McCrimmon 1982 Meyer & Gregory 2000
	Species			**Literature**
Characteristics & Preferences	*Salmonidae*			
	Salmo trutta fario			
	Brown trout f			
Biotic	**Brown trout**			
	Fry	**Juveniles**	**Adults**	
Feeding	Small invertebrates Chironomid larvae, zooplankton and Plecoptera (stonefly) larvae	Insects and fish (7%)	Insects and fish	Jonsson & Jonsson 2011 Skoglund & Barlaup 2006
Cannibalism			Coarse riverbed structure & low discharge facilitate cannibalism	Vik et al 2001
Migration	Downstream movement after emer-			Elliott 1986

	gence	Mechanisms determining age and size at juvenile migration	Spawning migration	Forseth et al 1999 Saranieni et al 2008
Territoriality	Aggressive; shortly after emerging from the gravel in spring, fry start to defend feeding territories	Young trout defend territories	No clearly defined territories	Elliot 1994 in Johnsson et al 1999; Kalleberg 1958 Keenleyside 1962 Bachman 1984
Schooling		Greater propensity to aggregate in winter	Greater propensity to aggregate in winter Aggregations in deep-slow areas in river during day (winter)	Cunjak & Power 1986 Heggenes et al 1999
Population density		Underyearlings: up to 0.76 specimen/m^2		Jenkins et al 1999
Abiotic	**Brown trout**			
Water depth	Shallow water (5 - 30 cm) Swift stream areas (<20-30 cm) Often located along the river bank in shallow areas	Fish >7cm: depth positively related to		Heggenes et al 1999 Roussel & Bardonnet 1999 Heggenes et al 1999

		size; in slow water velocity areas; General range of depth: 5-120 cm	Fish >7cm depth positively related to size, largest trout selecting deepest stream areas Spawning fish: 6-82 cm; Feeding fish: 14-122 cm	Jonsson & Jonsson 2011 Heggenes et al 1999 Shirvell & Dungey 1983
Water flow	21-64 cm/s Velocity mesohabitat 10-50 cm/s; velocity microhabitat 0-10 cm/s Fry in slow moving, shallow water along the river's edge, Moderately fast flowing water (0.2–0.5 m/s	Water column velocity 0-70 cm/s; snout water velocity < 20 cm/s		Thompson 1972 in Bjornn & Reiser 1991 Heggenes et al 1999 Keenleyside 1962 Roussel & Bardonnet 1999 Jonssson & Jonsson 2011 Heggenes 2002

		With age and size preference of deeper, more slowly flowing parts of stream	Range of water velocity of spawning fish: 15-75 cm/s; Of feeding fish: 0-65 cm/s Spawning site: upwelling hyporheic	Shirvell & Dungey 1983 Webster & Eiriksdottir, 1976 in Geist & Daube 1998
Structure				
- **substrate** (ground structure)	Substrate size of 0.6-7.6 cm Cobble substrate Conceal under cobble/bouler	Prefer coarse substrate Substrate size 0.8-15 cm Hiding among boulders; prefer stony bottoms to hide under cover; Positions on or close to streambed Passive shelter in the substrate in winter, no activity during daylight		Hunter 1973 in Bjorrn & Reiser; Roberge et al 2002 Heggenes et al 1999 Jonsson and Jonsson 2011 Bohlin, 1977; Klemetsen et al 2003 Jenkins, 1969; Heggenes et al 1993 Hunter 1973 in Bjorrn & Reiser; Mäki-Petäys et al

			Prefer coarse substrate; In summer smaller substrates preferred, in winter areas with cobble-boulder substrate preferred Spawning on stone and gravel bottoms (5-28 mm) Eggs embedded in bottom substrate	1997 Klemetsen et al 2003; Shirvell and Dungey, 1983 Jonsson and Jonsson, 2011
- **pools**		Using microhabitat in pool area Pools in the river during night more than day time	With increasing size brown trout move to pool areas (slow, deep) Microhabitats in pool area	Bremset and Berg, 1999 Heggenes et al 1999 Heggenes et al 1999 Bremset and Berg, 1999
- **woody debris**		Most frequently chosen among debris, undercut banks and pool Occurrence and fish size bigger with larger woody debris		Zika and Peter 2002

			Occurrence and fish size bigger with larger woody debris	Degerman et al 2004
- **riffle**		Shallow riffles of moderate water velocity areas		Heggenes et al 1999
			Pool or riffle−pool combination	Burell et al 2000
- **riparian, overhanging /in-stream vegetation**	Summer and autumn: stream areas with aquatic vegetation favored	Summer and autumn: stream areas with aquatic vegetation favored		Mäki-Petäys et al 1997
		Winter: passively sheltering in the substrate or submerged vegetation		Heggenes et al 1993
		Influence of overhead bank cover and primarily riparian vegetation on population density		Wesche et al 1987
			Selected spawning adjacent to undercut banks and overhanging vegetation	Johnson et al 1966, Reiser & Wesche 1977 in Bjornn & Reiser 1991
- **shade**	Use more shaded area than rainbow trout	Use more shaded area than rainbow trout		Gatz et al 1987
- **undercut bank**		In large rivers close to the river banks		Heggenes et al 1999
			Frequent use of sites	Young 1995 Cunjak &
			Under or near overhead cover	Power 1986; Clapp et al

			during the day, especially larger individuals	1990
	Species			**Literature**
Characteristics & Preferences	Salmonidae			
	Salvelinus alpinus			
	Arctic char			
Biotic	**Arctic char**			
	fry	juvenile	adult	
Feeding	Zooplankton	Invertebrates/fish	Invertebrates (crustacean zooplankton, chironomid pupae, Zoobenthos, zooplankton, surface insects) Char > 20 cm is piscivorous 1–4 sympatric forms In post-glacial lakes: piscivorus, limnetic planktivorous, epibenthic zoobenthos feeders and potential anadromous populations	Forseth et al 1994 Grant & Noakes 1987 Sandlund et al 1992 Gregerson et al 2006 Amundsen 1994 Jonsson & Jonsson 2001

Cannibalism			Variable extent of piscivory and cannibalism	Amundsen 1994
Migration	Migration to surf zone or pelagic zone in the fall			Sandlund et al 1992
		Downstream movements in river for feeding		Craig & Poulin 1975
		Shift from zooplankton to zoobenthos feeding in deeper water		Forseth et al 1994
			Anadromous or resident freshwater populations	Bradbury et al 1999
			Seasonal habitat shift (upstream movements)	Näslund 1990
			In lakes seasonal movement from littoral to the pelagic zone	
			Maturity at age 4-8 (size ~40cm)	Hindar and Jonsson 1982; Riget et al 1986; L'Abee-Lund et al 1992, 1993
Territoriality		Defend territories, territory size dependant of body size, food abundance		Gunnarson & Steingrímsson 2011
			Males defending redd (spawning nest)	Johnston 2008, Fabricius 1995 in Wilson and Herbert, 1993
Schooling	Small schools above substrate			Sandlund et al 1992
Population density	In surf zone average 1.83 - 4.7 fish/m^2			Sandlund et al 1988

Abiotic	Arctic Char			
Fluvial system	Stream/Lake	Stream/Lake	Stream/lake	Roberge et al 2002
Water depth	Shallow water areas (littoral, sometimes more open environments)			Johnston 2008
		In shallow nearshore waters		Sandlund et al 1992
		Juveniles typically inhabit deeper (>5 m) benthic habitats		Hegge et al 1989; Bjoru and Sandland 1995 (in Bradburry et al 1999)
				Heggenes & Salveit 2007
			mean 170.1 +/- 72.1 cm (river)	Dick et al 2009
			13.5 mean depth in lakes	Bradbury et al 1999
			Spawning in 1-5m	
Water flow			Mean velocity 7.2 +/- 16.5 cm/s	Heggenes & Salveit 2007
Structure				
- **substrate**	substrates including cobble, rubble and boulders			Klemetsen et al 1992; L'Abee-Lund et al 1993
		Cobble, rubble substrates		Sandlund et al 1987 in Bradbury et al 1999

		Bottom substrate as boulders Pebble and gravel in shallow zone cover use: cobble, rubble and boulders, bedrocks Seasonal preferences gravel or sand and rubble substrata	Particle size 9.3 +/- 1.6 cm Spawning substrate: Gravel and cobble	Dick et al 2009 Sandlund et al. 1987 L'Abee-Lund et al. 1993 Halvorsen et al. 1997 Adams et al 1988 Heggenes & Salveit 2007 Scott and Scott 1988 in Bradbury 1999
- **pools**			Preferred: slow deep pools	Heggenes et al 2007
- **woody debris**	Disperse in debris and rocks			Johnston 2008
- **riffle /log weir**			Presence in riffles	Heggenes et al 2007
- **riparian/in-stream**		Aquatic vegetation		Sandlund et al 1987 in

vegetation				Bradbury 1999
	Species			**Literature**
Characteristics & Preferences	Percidae			
	Perca fluviatilis			
	Eurasian perch			
Biotic	**Eurasian Perch**			
	fry	juvenile	Adult	
Feeding	Zooplankton	Benthic macroinvertebrates, become piscivore	Macroinvertebrate, piscivore	Smyly 1952, Guma’a 1978 Persson & Greenberg 1990 Craig 1974
Cannibalism	Beginning at fry stage (> 2.1-2.5 cm)	Common	Common	Thorpe 1977
Migration	To pelagic habitat and a second shift back to littoral zone (feeding shift)	1-year old in littoral zone, ≥ 2 years old in pelagic and littoral habitats	Sedentary behaviour in adult perch (lake)	Byström et al 2003 Eklöv 1997 Kipling & Le Cren 1984 in Gerlach et al 2001
Territoriality				

Schooling	Schooling of (related?) animals	Shoal of related perch even with increasing age	Aggregations observed in littoral zone	Gerlach et al 2001 Lorke et al 2008
Population density		Small fish estimate of 0.135 perch/m2 in a river Estimation of 6059 ind/ha for perch >5cm (backwater) and 1655 ind/ha (small bay)	312 ind/ha (Lake) 0,01 fish/m2 fish >10 cm (estimation; small and larger fish)	Williams 1965 Guti 1992 Viljanen & Holopainen, 1982 Williams 1965
Abiotic	**Eurasian Perch**			
Fluvial system	estuarine lagoons, lakes of all types to medium sized streams	estuarine lagoons, lakes of all types to medium sized streams	estuarine lagoons, lakes of all types to medium sized streams	Kottelat & Freyhof 2007
Water depth	Shallow water	deeper waters during winter; near bottom at depth of more than 30 m in winter, within 5 m depth in summer	deeper waters during winter	Wang & Appenzeller 1998; Wang & Eckmann 1994 Viljanen & Holopainen

			In 6-20 m depth (Lake Constance) eggs in 0-3 m depth zone	1982
Water flow	slow-flowing (or lentic), silted, trapezoidal (regulated) areas	slow-flowing (or lentic), silted, trapezoidal (regulated) areas		Copp, 1992
Structure				
- **substrate**	Silted areas	Silted areas In sand area (lake); At bottom at night;	eggs on stones and other structures in littoral zone	Copp, 1992 Eklöv 1997 Wang & Eckmann 1994 Gerlach et al 2001
- **pools**				
- **woody debris**			Use of tree structure Egg-strand attached to fallen trees eggs favorably deposited amongst structures such as woody debris	Eklöv 1997 Eg Echo 1955 in Thorpe 1977 Gillet & Dubois 2007
- **riparian/in-stream vegetation**		Preference of submerged macrophytes within 5 m depth habitat mainly in the vegetation zone of lakes; rivers		Wang & Eckmann 1994 Persson 1983; Copp 1992; Rossier et al 1995

		Vegetated habitats (e. g. Carex spec) as a possible protection against predators.	in vegetation in the littoral zone Spawning substrate: Egg-strand attached to plants	Eklöv 1997; Byström et al 2003 Eg Holcik 1969 in Thorpe 1977 Gillet & Dubois 2007
- **cover and shade**	Indications that fry aggregate in bright diffuse light until about 2 months after hatching. Then select darker areas, cease to be pelagic, and become demersal.	Shelter and shade in littoral zone	Activity favoured by certain of visual irradiance at dawn and dusk. Possible explanation for the inactive period at noon might be excess of light.	Thorpe 1977 Lorke et al 2008 Craig 1977
Characteristics & Preferences	Cyprinidae			
	Cyprinus carpio			
	Common Carp			

Biotic	**Common carp**			
	Fry	**Juveniles**	**Adults**	**Literature**
Feeding	Zoo- and phytoplankton (phytoplancton if density of zooplankton is low)	Littoral fauna and later bottom fauna (crustacean, worms, insect larvae); seeds, algae, detritus.	Omnivore, benthic feeding behavior Bottom fauna (tubifex, chironomidae, mussels, etc.)	Gill 1907, Akikunhi 1958 in Edwards & Twomey, 1982 Vaas and Vaas-van Oven 1959 Edwards & Twomey 1982 Steffens, 1980, Sibbing, 1988
Cannibalism	Hypothesis of cannibalism in experimental situation Cannibalism observed under experimental conditions			Charlon et al 1986 Stadtlander (pers. observation)
Migration			Stationary	Brown et al 2001
Territoriality			Not aggressive, not territorial	Lubinski et al 1986
Schooling			Large schools of spawning carps	Balon 1995
Abiotic	**Common carp**			

	Fry	Juveniles	Adults	
Fluvial systems	middle and lower streams of rivers, in inundated areas, shallow confined waters, lakes, oxbow lakes, water reservoirs	middle and lower streams of rivers, in inundated areas, shallow confined waters, lakes, oxbow lakes, water reservoirs	middle and lower streams of rivers, in inundated areas, shallow confined waters, lakes, oxbow lakes, water reservoirs	FAO 2015
Water depth	shallow water		0-20 m	Garcìa Berthoud 2001
Water flow	Inundated areas , lakes or streams	Stream or lake	Stream or lake	Roberge et al 2002
Structure				
- **substrate**	Sluggish waters	Sluggish waters	Mud or silt, riverine and lacustrine habitats, preference to enriched, shallow, warm and sluggish waters; well-vegetated;	Edwards &Twomey, 1982 Swee & McCrimmon 1968, Pflieger 1975 Edwards & Twomey 1982
- **pools**				
- **woody debris**				
- **boulders**				
- **riffle /log weir**				
- **riparian/in-stream vegetation**	adhesive eggs on aquatic or submerged terrestrial vegetation => fry associated with vegetation	In lacustrine habitats in association with	In lacustrine habitats in associa-	Sigler 1958 Sigler 1955 in Edwards &

		abundant vegetation	tion with abundant vegetation submersed aquatic plants as spawning substrate	Twomey 1982 June 1977 in Edwards & Twomey 1982
- **cover and shade**				
- **overhead bank**				

5.0 Natural structures in in-stream restorations and their influence on the fish fauna

The main focus of the following chapter is on restoration of in-stream structures in aquatic habitats and its influence on fish populations.

Returning an aquatic system or habitat to its undisturbed state is the aim of restorations and rehabilitations (Roni and Beechie, 2012). Impacts by human activity such as degradation, pollution, modification and channelization of aquatic habitats occur since centuries, particularly in the late nineteenth and twentieth century in Europe, the United States of America, Australia and other industrialized countries (Roni, 2005; Zika and Peter, 2002). In Western and Central Europe straightening/damming of rivers became common and has profound consequences on the fish fauna. In Switzerland, around 52’000 km or 78% of the fluvial system exhibit a good or to a lesser extent impaired ecomorphological structure. Around 42% of the total fluvial system (around 66’000 km) did not have sufficient riverine zones. Approximately 14’000 km rivers or some 22% of the Swiss fluvial system are in poor condition (Zeh Weissmann et al., 2009). Poor conditions include strongly impaired rivers, artificial ones or rivers buried in underground pipes. According to Kirchhofer et al. (2007) 58% of the endemic fish and cyclostomata species of Swiss water bodies are on the red list. In Germany, for example, a similar percentage (55%) of the freshwater fish species and lampreys are on the red list (Ellwanger et al. 2012).

Disturbance may be provoked by a modification of the channel morphology, depth, water velocity and accessibility to migration routes (Morrow and Fischenich, 2000). Hydropower plants for example play an important role in such modifications (EAWAG Factsheet Hydropower and ecology). It further includes the alteration or loss of riverine habitats, the impact of wetland drainage, and the destruction of forests or settlement areas (Roni and Beechie, 2012). Water quality changes such as rise in temperature, eutrophication, decrease or rise of pH and pollution through chemicals or heavy metals (Kirchhofer et al., 2007) influence fish populations and fish health as well. A very recent study showed, that in five tested rivers in Switzerland a total of 104 different pesticides were found which in 78% of all samples added up to a total concentration higher than 1 mg/l (Wittmer et al. 2014). The effects on the aquatic fauna including fish are completely unclear but several of the substances might be considered as endocrine disruptive chemical and therefore they might have impacts on various physiological functions including stress and disease resistance, reproduction and growth.

Restoration and protection of stream habitat for salmonids is a quite new and growing field in fisheries science (Jonsson and Jonsson, 2011). During the last 15-20 years, with conservation biology, methods of water body restoration have been developed. Results show that abundance and growth of fish can be increased with habitat restoration. In Atlantic salmon, brown and brook trout, populations have been improving by enhancing water quality in Canada and Norway (Lacroix, 1996; Hesthagen et al., 1999a), increasing the spawning habitat by introducing gravel in segments of three Wisconsin streams (Avery, 1996; Scruton et al., 1997), increasing the productive area by constructing side channels (Pethon et al., 1998 in Jonsson and Jonsson 2011), removing blockages and constructing fishways in a river estuary in the USA (Simenstad et al., 2005) and changing flow regime (Armstrong et al., 2003). Jong et al. (1997) described that the addition of boulder clusters, V-dams and half-log covers at selected sites of channelized reaches in Newfoundland, Canada, increased the abundance of salmonids. V-dams were effective through the creation of different pool habitats, while half-log covers increased cover for juvenile fish. In a meta-analysis of in-stream restoration structures, it could be shown that salmonid density increased significantly when more than one type of structure was installed (weirs, deflectors, cover, boulder, woody debris) (Whiteway, 2010). It is also reported in literature that rehabilitation did not have the desired effect on fish species. A combination of morphological aspects as for example cover and river widening with natural hydrological regime or riparian vegetation however, offers more potential (Weber et al., 2007; Roni et al., 2008). If the natural production of a river is to be restored, the limiting factors for salmonid production need to be identified and these constraints must be removed (Ebersole et al., 1997). But it should be kept in mind that any river has a limited carrying capacity, although this may, to some degree, be expanded by habitat improvements. To enhance population abundance, the easiest means may be to increase the nursery area for the juvenile fish (Jonsson and Jonsson, 2009 in Jonsson and Jonsson, 2011).

In a general way, instream structures (large boulders, woody debris, vegetation) offer cover to fish to hide from predators, or provide a refuge from velocity or attachment sites for adhesive fish eggs. It also creates habitats for invertebrates. Instream structures are an important aspect for the fish habitats and more instream cover often means higher habitat quality. The influence of structures and covers on water quality could be negative too. In case of neophyta, an overabundance could lead to a decrease of water flow and water depth and even to lowered oxygen levels (Morrow and Fischenich, 2000). Suitable substrate, consisting of sand, silt, clays, gravel etc., depending on species, is of major importance as fish can otherwise not reproduce successfully. Riparian vegetation does not only provide cover for fish but is very important for a river as it increases bank stability, reduces sedimentation, reduces summer water temperatures and offers recruitment of large woody debris. Leaves and other organic matter from riparian vegetation are an important source of nutrients for many low order streams (the lower the order, the less influx rivers are leading to that river). Riparian vegetation can also be a buffer zone to urban runoff or agriculture. Furthermore, riparian vegetation is important for the formation of habitat components such as pools and undercut banks (Morrow and Fischenich, 2000).

In some cases, descriptive models can predict the presence or absence of fish species. Habitat requirements are often inferred for an effective species management and habitat restoration. On the basis of correlative habitat associations in the wild, models can predict distribution of fish on different habitat levels (Rosenfeld, 2003).

To recapitulate briefly: The physical habitat requirements of salmonids are adequate quantities of spawning gravel (size range of 16-150 mm) and low fines content. Extensive nursery areas for fry and under-yearlings shall be found close to spawning grounds (water depth of around 20-40 cm and velocities of ca 20-75 cm/s). Cover should be provided by small cobble (up to 64 mm) as well as overhead cover and shade by bankside vegetation. Deeper and faster water (up to 46 cm depth, 100 cm/s) shall be near to fry habitats, with coarse substrate and boulder as in-stream cover. Adults must have free access to spawning areas (Hendry et al., 2003).

6.0 Structures in cultural / captive environment of salmonids

Physical structures and substrates for fish in captive environments (fish in aquaculture, for restocking purpose and conservation, research and display aquaria) were reviewed by Näslund and Johnsson (2014). Physical structure as environmental enrichment aims among others at reducing environmental stressors (e.g. intraspecific aggression or human activity). The effects of structure often interact, as a structure might have different functions (see for example chapter 3.1, sensory and social enrichment) and as they usually are species-specific (Näslund and Johnsson, 2014), and can have different effects in closely related species or even different environmental adaptation types of the same species (pelagic or demersal Arctic char in lakes).

Different structure types and functions are discussed in the following chapters in terms of a practical application in aquaculture, notably for trout. According to a survey of Näslund and Johnsson (2014), providing the number of publications investigating the effects of environmental enrichment, Salmoniformes was the taxonomical order with the highest amount of published articles. Furthermore, around 86% of the total Swiss fish production in aquaculture is rainbow trout and therefore the most important fish species (FAO 2014) and the focus of the following chapters is thus set to salmoniformes.

6.1 Structures as shelters

Fish that use shelters in their natural environment make also frequently use of shelters when held in captivity. Shelters in captivity offered to fish are e.g. pipes, tiles and non-buoyant plastic strips. These provide mainly hiding places, whereas entangled plastic stripes or net structures can inhibit cannibalism and aggressive behavior. In an experiment using semicircular plastic pieces as shelter for Atlantic salmon, fish without shelter had a 30% increased metabolic rate compared to fish with shelter (Millidine et al., 2006;). A decrease in fin erosion, when shelters were present, could also be observed in several studies with different fish species like Atlantic salmon (Näslund et al., 2013), cutthroat trout, *Oncorhynchus clarkii* and rainbow trout, *Oncorhynchus mykiss* (Bosakowsky and Wagner, 1995).

Accordingly, Berejikian and Tezak (2005) found that juvenile *Oncorhynchus mykiss* from enriched rearing environments (submerged tree tops, camouflage nets and underwater feeder) showed better fin condition than the fish from the conventional tanks. Tree branches as submerged structure on the tank bottom, overhead cover (camouflage netting), natural prey and simulated predator attacks were used by Roberts et al. (2011) in juvenile *Salmo salar* as enrichment. The authors found in a behavior test, that fish from an enriched environment showed 2.1 times less risk-taking behavior (measured by the latency to leave the shelter). Therefore they were considered to be more suitable as stocking fish. This less risky behavior can be considered comparable to behavior of natural fish and is thus better suited for survival in the wild. No significant differences could be found in hatchery survival, size or fin damages (Roberts et al., 2011).

Näslund et al. (2013) used shredded plastic bags and plastic tubes as enrichment in an experiment with juvenile Atlantic salmon. In the barren tanks, fish showed higher cortisol levels indicating higher stress levels and more fin damage than fish reared in structured environment. Fish from barren tanks had on average two to three times higher basal levels of plasma cortisol than fish from the enrichment treatments (enrichment treatment with (i) plastic bags and (ii) plastic tubes having been similar). Likewise, in juvenile catfish, *Rhamdia quelen*, in combination with darker tank color, PVC tubes used as shelters reduced the whole-body plasma cortisol level, while white or blue colored backgrounds in the tanks had no effects on the cortisol response to an acute stressor (Barcellos et al., 2009). In brook trout fry (*Salvelinus fontinalis*) a clear effect of structure (brick fragments) in combination with tank wall color on survival in a predation context was observed. A color acclimation in colored tanks rendered fish more cryptic to the birds (Hooded mergansers, *Lophodytes cucullatus*), as fish produced morphological color changes during the acclimation in the tank. The mortality by bird predation accounted for 37% in the color-acclimated fish and for 63% without acclimation (Donnelly and Whoriskey, 1991). In a study of Brockmark et al. (2007), structure did not have any effect on postrelease survival but low density and enriched environments had a positive effect on growth. For this experiment in-water structure was provided by 10 green plastic bags (17 L) per tank. A stone was placed in each bag to keep it in place, increase flow variation, and provide additional protective cover for the fish. Each bag was sliced to make them flutter in the water, resembling water plants.

The fact that fish kept in aquaculture systems, which comprised structures, showed better fin condition and subsequently impeding infections, or an improved behavioral flexibility illustrates the advantage and importance to implement structure in aquaculture. Plastic tubes as structure element in aquaculture might offer hiding possibilities for farmed fish. Size of tubes would have to be adapted and need to be large enough that the fish make use of it. Shredded plastic is sometimes used as enrichment in experiments. In practice, material should be easy to handle and to clean and if possible made of natural materials that would be recommendable. Submerged tree branches or rootstock could be a possibility for aquaculture as structure element for an artificial environment. Woody debris is a natural component in streams (see chapter 5.0, stream restorations), as fish find easily hiding possibilities and it might influence water flow and appears to be the most natural element in culture raceways etc. However, it is necessary to choose the elements carefully as they have to be easily removable for handling (cleaning, harvesting, etc.). Neither water quality shall be negatively influenced nor food availability. And of course, the material must not provoke injuries in fish or leak chemicals into the water. Interestingly, the presence of shelters per se can already be of utility, as shown in Millidine et al. (2006). Fish provided with semicircular Plexiglas as shelters were observed to stay rather outside or adjacent to the shelter and showed even a lower metabolic rate then fish without shelter. Structure can be of different form and offer e.g. visual barriers, at the same time create different flow areas in a raceway.

6.2 Structures for the reduction of aggression

Effects on behavior such as a reduction in aggression in salmonids could be observed in some studies as for example shown by Mork et al. (1999) for Atlantic salmon. In this experiment river cobbles with a diameter of 4-8 cm were used. Aggressive behavior of wild and farmed juvenile salmon was significantly decreased when kept in structured tanks. Other studies did not show effects as for example in rainbow trout (*Oncorhynchus mykiss*) by Riley (2005). In salmonids, a decrease in fin damage (Bosakowski and Wagner, 1995; Wagner et al., 1996; Arndt et al., 2001) indicates that aggressive behavior was reduced in the enriched environment, whereas fin erosion also can be due to abrasion with rough surfaces (Latremouille, 2003).

In Eurasian perch juveniles (*Perca fluviatilis*) Mikheev et al. (2005) found increased aggression in enriched tanks. They did work with one plastic tube per tank also showing, that too few structures can lead to high aggression levels, probably due to fighting over this attractive habitat feature, while there was no direct competition for food resources. The authors argue that using a shelter is an alternative to antipredator schooling behavior of perch in the littoral zone. Näslund et al. (2013) used shredded plastic bags and plastic tubes as enrichment in an experiment with juvenile Atlantic salmon. In the barren tanks, fish showed higher cortisol levels indicating higher stress levels and more fin damage than fish reared in structured environment. The authors suppose that more fin damage is potentially due to more aggression in the barren environment.

Another type of enrichment elements are tow wire shopping baskets (34 cm x 48 cm x 15 cm) filled with cobbles used in a hatchery of *O. mykiss* alevins (Tatara et al., 2008, 2009). This was in addition to overhead cover (camouflage netting) and underwater cover (tops of two fir trees) in 1.8 m diameter circular indoor tanks. The authors found that fry from conventional and enriched environment had similar survival, while natural reared fry showed significantly higher survival. Contrary to other studies (Berejikan et al., 2000, 2001), Tatara et al. (2008) did not find aggression to be affected by the rearing treatments. However, the behavior of natural resident fry differed depending on the type of hatchery fry they were stocked together. When stocked together with hatchery reared fry from enriched environments, natural fry significantly increased aggression and decreased foraging relative to stocking with fry of conventional rearing. The laboratory experiment of the same hatchery populations studied by Riley et al. (2004a) did not show differences in behavior when natural reared fry was stocked together with conventional reared or hatchery reared fry from enriched environments, while density had the strongest influence in a way that threats and attacks were higher at high density. In the same context Riley et al. (2004b) found that fish density, but not hatchery rearing environment, played an important role in determining dominance. This discrepancy suggests conducting studies with the assessment of behavior and performance under field conditions (Tatara et al., 2008). Berejikian et al. (2000, 2001) found, that juvenile rainbow trout reared in habitat-enriched tanks socially dominated size-matched competitors grown in conventional tanks. The structure comprised a combination of in-water structure (submerged tops of Douglas-fir and underwater feeders) and overhead cover (camouflage netting providing ca. 60% overhead shade cover) while the conventional tanks contained no structure and were hand-fed (all fish equal frequency). The authors discuss interactions between hatchery-reared and wild fish after release and concluded that a more naturalistic rearing environment probably results in post-release fish that behave more similar as wild fish but that potential impacts of the hatchery-reared fish in the wild should be clarified.

Contrariwise Riley et al. (2005, 2009) applied the enrichment as described in Berejikian et al. (2001) and Berejikian and Tezak (2005) in six conventional and six enriched tanks and found that attack rate of fry stocked for experimental trials in a laboratory flume tended to increase with density and was reduced in the presence of predators, but was not influenced by the rearing treatment. Threat display of naturally fry reared (stocked in river after emergence) was highest compared to fry reared in laboratory (conventional and enriched tanks) when predators were present. On the other hand, aggression (attack and threat display) rate of hatchery and natural reared fry observed in the two rivers was generally lower than those observed in the laboratory flume and did not increase with density. Aggression rate in naturally reared fry was higher than the rate of hatchery reared fry. However, as other factors like stocking density of *O. mykiss* fry and absence/presence of predators varied, these results are not directly comparable. With a similar experimental design, varying release density and testing for aggression, feeding dominance, position choice and territory size, Riley et al. (2009) could not find significant effects of the rearing treatment (conventional and enriched tanks) but instead of stocking density. However, naturally (in rivers, in situ) reared fry chose more upstream positions closer to the food source when stocked with conventional fry than with fry reared under enriched hatchery conditions. Their result suggests releasing similar sized fish to wild conspecifics at low density (Riley et al., 2009).

As mentioned, tree branches or small tree tops in hatchery tanks might be a good solution for enrichment. This material is easy to handle and in bigger tanks or ponds larger tree tops might be suitable. Clear disadvantage of any structures in grow-out facilities is always the increased effort during harvesting and maintenance work. Camouflage netting is certainly a solution for hatchery and indoor tanks. For outdoor facilities, nets as cover need to be adapted to environmental conditions. It certainly is practical in summer, but in autumn and winter it might need to be removed because of foliage, debris or snow that presses it down. In hatchery environments baskets with cobbles might provide interstitial space to hide and could be an alternative to substrate on the whole tank floor. Here as well, the structure itself shall be as easy to clean as the tank. Besides that, an important point is the quantity of structure. If too little, aggression of the fish can increase as they might fight over a shelter or territory.

6.3 Structures for sensory and cognitive stimulation

In captivity, animals live in an impoverished environment regarding sensory stimulation. In the natural habitat the animal is experiencing a permanent change of sensory stimuli that trigger the senses as vision, audition or scent (Wells, 2009). In fish, positive effects of sensory enrichment have been shown for example in an African cichlid (*Simochromis pleurospilus*) with feeding enrichment (Kotrschal and Taborsky, 2001) and its effects on learning behavior. Possible negative effects were observed on neurogenesis as for juvenile Coho salmon (*Oncorhynchus kisutch*) in Lema et al. (2005). Salmon parr of the enriched tanks had restricted mitotic activity in a certain proliferation zone in the telencephalon compared to fish from unstructured tanks. The applied physical structures comprised cinder blocks and gravel and the hydrodynamic environment was uniform. The unstructured environment was barren with spatial variation in water flow. In an experiment conducted by Salvanes et al. (2013) with Atlantic salmon, environmental enrichment consisted of treatment tanks containing pebbles and rocks (8-12 cm and covering a minimum 75% of the base of the tank) and vertically floating plastic structures. The enrichment led to increased forebrain expression of NeuroD1 mRNA and improved learning ability assessed in a spatial task. The authors argued that the addition of enrichment to the captive environment promotes neural and behavioral changes that are supposed to promote behavioral flexibility and by this way, post-release survival is improved. In rainbow trout, Kihslinger and Nevitt (2006) demonstrated that small stones (diameter ca. 4 cm) in rearing tanks can alter the growth of specific brain structures. The alevins, reared in enriched tanks, grew brains with significantly larger cerebella than genetically similar fish reared in conventional tanks. River-reared fish had similar cerebella volumes as alevins from enriched tanks. Kihslinger et al. (2006) found that in juvenile Chinook salmon (*Oncorhynchus tshawytscha*) olfactory bulb and telencephalon volumes relative to body size were larger in wild fish compared to hatchery fish. The former developed in wild streams until collection, while the hatchery fish were artificially spawned and incubated in Heath Trays and were kept until transfer to a conventional or enriched raceway. All fish were offspring of one genetically-similar run of wild fish from a river. Enriched raceways were equipped with camouflage-painted walls, underwater (denuded trees) and floating structures (camouflage netting attached to floating hoops). Wild fish had significantly larger volumes of olfactory bulb and telencephalon relative to body size than hatchery reared fish.

They did not observe significant differences of the relative volume of forebrain structure between fish from conventional and enriched treatments. Thus, considerable difference in the size of forebrain structures can occur (in salmonids) within a single generation and must not be a result of artificial selection in captive rearing situations. The authors suggest factors as environmental stimuli acting on neural growth and proliferation, which is documented in other taxa. Brain growth, on the other hand, can be hindered by stressful conditions in captivity as shown in jewel fish (*Hemichromis bimaculatus*; Burgess and Coss, 1982). Contrary to those studies having found an influence of environmental enrichment on brain size, Kihslinger et al. (2006) could not affirm and question whether the enrichment used in their study was inadequate or whether the timing of enrichment should start earlier in the hatchery during alevin life stage.

As enrichment in aquaria, Lee and Berejikian (2008) used stones (70 -100 mm in diameter) and plastic plants (580 by 60 mm) and found that juvenile rainbow trout (*O. mykiss*) from enriched tanks increased their exploratory behavior, given that the structures were not regularly varied in position over time. Here, the structured-unstable treatment consisted of changing the position of rocks and plastic plants every 2-3 days without perceived predation risk. Furthermore, behavioral variation among individuals of the enrichment treatment was smaller, while feeding behavior (number of bites on novel prey) was similar in fish of structured and barren environment. A reduced variation of behavioral patterns could mean an increased competition or a certain variation allows on the other hand to persist in changing environments. As this study showed, this effect did not involve selection but evolved during development. Further, the authors conclude, that an increased exploratory behavior, which was expressed in a context specific way (only when predation risk was low), may increase post-release success (Lee and Berejikian, 2008). Strand et al. (2010) reported that enrichment with rounded stones of 5 to 20 cm in diameter and plastic kelp seaweed, 30 to 40 cm long, influences social learning in juvenile cod (*Gadus morhua*) that were reared either in enriched or plain tanks. Thus, enrichment had significant effects on learning behavior from a tutor demonstrating to hunt and consume gammarid or mysid shrimp prey.

A visual stimulus as enrichment might include “landmarks” or a spatially relevant cue helping to orientate. Disorientation might occur because of production-related noise (filters, pumps). These structures might provide fish the ability to form and use mental maps in culture systems. For example in the wild, young tuna gather at floating objects during the night as their vision is poor in darkness. On transfer to cages, mortality of juvenile yellowfin tuna (*Thunnus albacares*) can be reduced by providing additional light, hence reducing collisions with cage walls. Structure such as shelters (e.g. lengths of pipe) can provide refuge from current and act as landmarks at the same time (Huntingford et al., 2012).

Positive effects of environmental enrichment on different specific brain structures and thus on related abilities of fish have been observed experimentally. The consequences for early development and locomotion or learning abilities support the application of enrichment. Notably, the environmental aspect for early development might have influences on adult life. If the early conditions were not optimal, animals may compensate and thus “pay” for the deficiency later on (Taborsky, 2006; Metcalfe and Monaghan, 2001). Like for example, in Arctic char, the cost of compensatory growth (little or no growth for some time due to limited food supply with subsequently increased growth given sufficient food is provided) can be muscle lesions (Christiansen et al., 1992, in Metcalfe and Monaghan, 2001).

Floating structures are interesting as enrichment in an experimental context, but they seem not very practical in aquaculture as they can impede feeding (regular distribution of the food). Plastic plants might be used in tanks but they are quite an expensive solution and need to be cleaned regularly.

Stones on the bottom of tanks and ponds (see tank floor substrates) are an element of stream-dwelling fish and therefore very suitable. Again the maintenance aspect is the drawback of this enrichment.

6.4 Tank floor substrates

For a lot of species, tank floor substrates have positive effects such as reduced injuries like decreased fin damage (Bosakowsky and Wagner, 1995; Wagner et al., 1996) or reduced agonistic behavior (Mork et al., 1999). The aspect of reduced aggression seems interesting as it could give bottom substrate an "occupational" value as salmonids use this habitat strongly in the wild (Batzina et al., 2014 in Näslund and Johnsson, 2014).

The addition of substrate in the fattening phase (fingerlings reared for 6 and 10 month respectively) is suggested by Bosakowsky and Wagner (1995) who found that fin erosion in rainbow trout and cutthroat trout *(Oncorhynchus clarkii*) fingerlings was significantly reduced when adding cobble substrate in concrete raceways. In rainbow trout, growth, fat levels and mortality were similar in both treatments – structured raceways and barren ones with no differences in water quality between the treatments (Bosakowsky and Wagner, 1995).

Similarly, the fin condition of albino rainbow trout was found superior in fish held in cobblestone (2-4 cm) and pea gravel raceways when compared to fish held in concrete raceways (Wagner et al., 1996). No significant differences were found in feed conversion (control 0.98, cobble 1.15) or mortality (control 10.4%, cobble 10.6%). A reduction in mean fat indices and total length seems to be due to the substrate, because the sinking pellets used throughout the experiment were probably more difficult to find in the cobble (as the insignificant but still higher FCR in the cobble treatment suggests) and the authors suggest floating pellets, which are nowadays used generally in rainbow trout production. Also, substrate size can be chosen accordingly. In that regard, Arndt et al. (2001) found that fin erosion was reduced in rainbow trout juveniles when held in raceways with gravel, where growth, feed conversion and mortality was not influenced. Moreover, the authors conducted four trials with different bottom types. A first trial compared conventional concrete raceways as control with raceways in which cobble and a false floor through which water and waste materials could flow have been included with the aim of a self-cleaning gravel substrate. The second trial compared concrete raceways as control and raceways containing two-dimensional painted gravel patterns and raceways with three-dimensional gravel substrate fixed to the raceway bottom. Trial three compared the control with raceways which had walls and bottoms smoothed by the application of a resin. Trial four consisted of cross-flow (with increased water flow) systems with a concrete and gravel substrate respectively and controls. Trials one and four with gravel significantly improved fin condition compared to controls. Arndt et al. (2001) concluded that the physical presence of gravel and not the appearance of gravel is what improves fin condition. The 3D treatment in trial 2 suggested a beneficial influence of the embedded gravel substrate but fin condition decreased as fish age increased. Smoothing the surfaces was not effective. Finally, the cross-flow raceway design (with or without gravel substrate) improved fin condition. The applicability of gravel is evaluated as a realistic alternative for production-scale hatcheries although gravel substrate used in this study is not very practical.

Furthermore, Tipping (2008) compared adult survival (in a conservation context) of *O. mykiss* and found that return was significantly greater when they were reared as juveniles in an earthen pond than return of fish reared in an asphalt-bottom pond; fish reared in earthen ponds had a mean survival 41.7% higher compared to fish reared in asphalt-bottom ponds. Even though both groups were fed nearly identical rations (~ 1% body weight/d), the earthen-pond fish were longer and weighed more than the asphalt pond fish at release suggesting that the earthen pond fish had access to additional forage (aquatic insects) which may have improved their foraging skills. Differences in loadings might have influenced the result, since in asphalt bottom ponds it was with 530 $g{\cdot}L^{-1}{\cdot}min^{-1}$ higher compared to the 339 $g\ L^{-1}\ min^{-1}$ in earthen ponds. Rearing density was with 5.2 kg/m^3 similar in both ponds. In a study with Sea-run cutthroat trout (*Oncorhynchus clarkii*) Tipping (1998) found that fish reared in gravel-earth bottom ponds showed significantly more adult returns than fish reared in standard raceways (60% increase) and that more fish returned from the standard raceway than those kept in a baffled raceway beforehand. The author adds that also concrete raceways with added earth and gravel could show a similar advantage.

Advantages of various substrates have been mentioned and include primarily improved fin condition but also a higher return rate to the spawning site (therefore lower mortality in the wild, thus a higher fitness). As a higher fin condition is usually positively correlated with improved fish welfare, adding substrate, where appropriate, can improve fish welfare. In table 2 it is shown, that the substrates in a river are important habitats for the fish, further substrate is crucial for spawning of fish and egg development. The other side is the maintenance of a tank, pond or raceway as it can become more laborious and time consuming than e.g. concrete raceways or ponds. Moreover, the risk of pathogen infection due to this difficulty in cleaning is increased (Näslund and Johnsson, 2014).

6.5 Incubation substrates

In the wild, salmonid yolk-sac fry are buried in the gravel, while hatchery environments lack this structural component. Hatcheries experimented with copying the conditions of nature by adding gravel substrate because of the inferior status of the reared fry. As Näslund and Johnsson (2014) describe, yolk-sac constrictions and malformations can be the consequence of barren incubation substrate (Emadi, 1973; Hansen and Møller, 1985). Products like hatching mats (fig. 2) are nowadays commercially available.

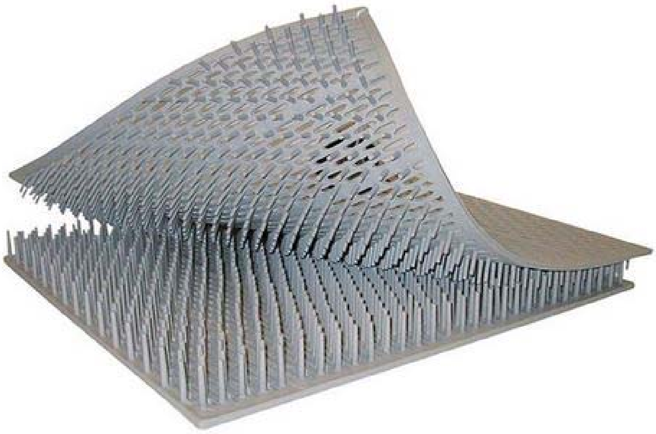


Fig. 2: Commercially available hatching mat (www.fiap.com/profibreed-schlupfmatte.html).

Natural gravel (Bams and Simpson, 1977) or synthetic material like artificial turf mats (Nortvedt, 1986) used in the breeding phase of rainbow trout led to higher survival of alevins. In the breeding of salmon, several authors reported about positive effects on survival rates and development of the fry, when incubated on synthetic substrates (e.g. Fuss and Johnson, 1982, 1988; Bams, 1983; Boyd, 2001). The reasons for this improved performance are seen in improved yolk utilization efficiency due to lower swimming activity and reduced occurrence of yolk-sac deformations which could often be seen in the case of barren trays. The difference to the findings of Tatara et al. (2008, 2009) could be seen in the period of the substrate application: The effects on free swimming alevins are not as big as on non-buoyant yolk-sac fry due to the above mentioned effects on the yolk-sac.

As mentioned, Kihslinger and Nevitt (2006) demonstrated that stones in rearing tanks can alter the growth of specific brain structures in steelhead salmon alevins (*Oncorhynchus mykiss*): Alevins reared in enriched tanks had brains with significantly larger cerebella than fish reared in conventional tanks. Further, larger cerebella were accompanied by changes in locomotion behavior which are correlated to the function of this brain region. This behavior is involved in controlling movement, body position and orientation in fish, thus fish reared in cobble could hold a more stable position in the tank which might lead to a more efficient use of the yolk reserves. The authors also showed, that hatchery fish reared in a natural environment had significantly larger brains than the lab-reared fish, and similar cerebella volumes as those reared in enriched environment in the laboratory. Variations that are commonly characterized by generations of selection have here been observed within the first three weeks of life in a rearing environment. The authors underline the need to implement enrichment strategies in rearing facilities (Kihslinger and Nevitt 2006).

Hansen (1985) found that alevins of sea trout (*Salmo trutta*) reared in astro-turf, a commercial type of artificial turf, absorbed their yolk faster and more efficiently than alevins reared on flat system. The author assumed that the difference is due to increased stress due to a high swimming activity in the flat system. Growth and survival were finally higher in the alevins from the astro-turf system. With a “Nortene” plastic mesh (8x5 mm) Krieg et al. (1988) found positive effects on survival, alevin growth and yolk conversion efficiency in *Salmo trutta*.

Alanärä (1993) used a gravel cylinder (fig. 3) and could show positive effects on yolk conversion efficiency during the yolk-sac period, resulting in significantly larger Arctic char alevins at emergence. The efficiency with which yolk can be converted to larval biomass (yolk conversion efficiency) compares the gain in larval weight to the loss in yolk weight at hatch and any time after hatch. The author used a PVC hatching cylinder with water inlet at the bottom and water distribution to the gravel inside. Covered with a lid, a cone with a small opening was installed for emerging alevins. The cylinder itself was placed inside of a start-feeding tank where the emerging alevins could swim in. Different timing of start-feeding were compared: 9 and 34 days after hatching for the two flat-screened bottom treatments and estimation of time point at which 50 % of gravel-reared alevins emerged was 52 days after hatching. During the initial feeding phase, growth rates as well as mortality was significantly reduced in gravel reared alevins. Differences between the treatments might be due to the timing of food introduction. Näslund et al. (2012) demonstrated that brain size of salmon was increased in enriched hatchery trays (cobble and plastic grate). Growth of the alevins was increased in the tray with the plastic grate.

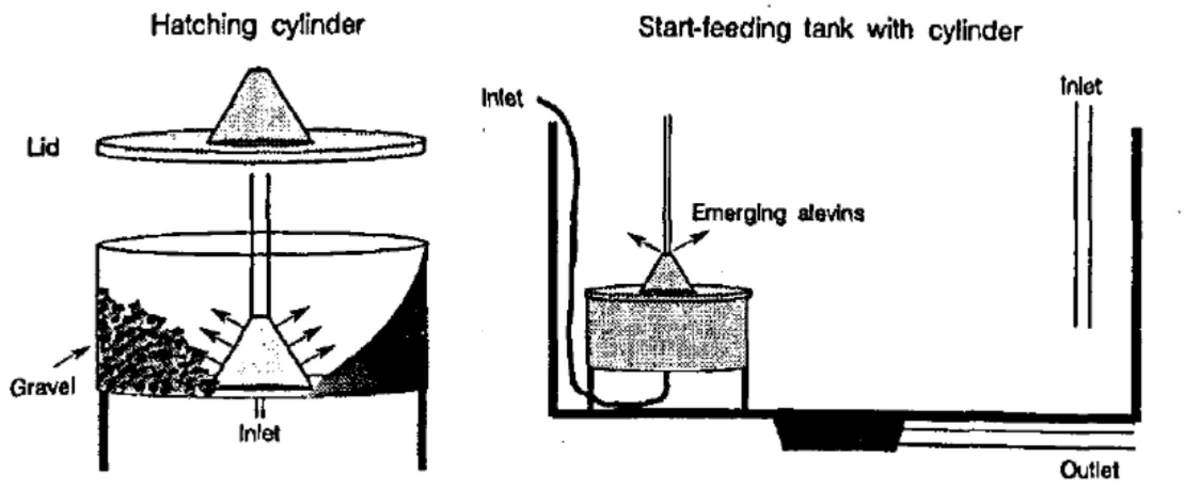


Fig. 3: Schematic illustration of the PVC cylinder for rearing the alevins (from Alanärä, 1993).

As mentioned, by offering a grooved surface instead of a plain, alevins' activity decreased (Kihslinger and Nevitt, 2006). Likewise in a study conducted by Benhaïm et al. (2009), where Arctic char were given PVC agricultural drain pipes in their hatching trays, activity decreased and growth increased. The PVC drain pipe provides shelter and allows the fish to stabilize in a vertical position without being forced to move and find and keep such a position. It was demonstrated that rearing fish embryos in trays with gravel leads to higher yolk conversion efficiency and more yolk was converted to body tissue than in a flat bottom (Alanärä, 1993). However, high density of alevins can abolish the positive effect of the incubation substrate. Thus densities in the incubation trays need to be adapted (Murray and Beacham, 1986).

In nature, after salmonids hatch, they need shelters which they usually find in interstitial spaces in the gravel of the streambed, where they are hiding from light due to their negatively phototactic behavior during that life stage until they emerge, developed enough to swim and cope with the currents. The addition of structure in hatching trays provides the alevins with such hiding possibilities allowing better growth. Gravel might not be the ideal substrate in hatcheries as there is a risk of fungal infections and to remove embryos mechanically without injuring them is difficult (Alanärä, 1993); removable artificial substrates might be more suitable and the positive effects, mainly on growth and survival, have been demonstrated. On the other hand, densities need to be adapted to the environment and substrate shall not hurt or "clamp" the alevins. These findings have already found application in practice. Hatching mats, slatted substrate, tube substrates or honeycomb substrates as well as boxes for salmonid eggs to be incubated in natural waters in spawning areas, are commercially available. Accordingly, different types of spawning brush are available for specific spawning behaviors as found in common carp, pike perch etc.

6.6 Toys

Zimmermann et al. (2012) studied the reaction of Atlantic cod when they were given two kinds of ball toys as a "stimulatory object". Overall number of interactions with the balls was small. Toys might have an occupational character of environmental enrichment, and as Näslund and Johnsson (2014) state further, evidence for play behavior in fish is anecdotal and thus the relevance of toys remains unclear. Moreover outdoor ponds or raceways offer a natural variability and unpredictable events (change of positions of structures, or varying water level, direction and velocity of current (Rodewald et al., 2011) and a practical application is not realistic on-farm. The situation might change when fish spend their whole life-cycle indoor under artificial conditions as in recirculation aquaculture systems.

6.7 Structures in periphyton-based aquaculture

Periphyton is the microbial, algal and invertebrate community that develops successively on submerged surfaces (Bosma and Verdegem 2011). Utilizing suspended and dissolved organic matter, this biological matrix reduces sedimentation and accumulation of organic matter at the pond bottom (van Dam et al., 2002). The organic matter trapped by substrates in the water column is decomposed in more oxygen-rich water which contributes to a beneficial microbial food web (Verdegem et al., 2005). Primary production can be increased and herbivorous and omnivorous fish can graze on periphyton and can find shelter from predators. As submerged surfaces serve branches, bamboo or stones and periphyton based aquaculture systems are mainly used in pond systems in Asia, growing herbi- and omnivorous fish like cyprinids and cichlids (often in polyculture), and according to van Dam et al. (2002) it is not clear to which extent periphyton can be applied to intensive aquaculture systems.
In aquaculture systems in Switzerland, notably for salmonids, carnivorous fish like trout, which require cold, clear and well-oxygenated water, this method is not suitable. But, it could be a possibility for carp ponds. Carps are omnivorous and prefer relatively warm, slow or standing water and vegetative sediments and as such are excellent fish for organic or sustainable aquaculture

6.8 Tank covers providing shade and visual protection

Cover can be provided for example on the top of fish tanks to limit stressful influences from the external environment. Näslund and Johnsson (2014) suggested to not consider full cover of tanks as enrichment structure, although it might reduce stress. But the aim of full cover is rather to limit information flow from outside the tank than to provide enrichment per se. Another use of such cover might be to vary light conditions (as e.g. for nocturnal species). On the other hand, partial cover can be regarded as environmental enrichment (e.g. providing light gradient, shelter).

Underyearling Atlantic salmon were provided with floating annular covers, constructed of fiberglass and polystyrene, to conventional tangential-flow rearing tanks which increased growth rate and decreased stress (Pickering et al., 1987).

Wagner et al. (1995) worked with plywood covered raceways. In a preference test in an observation tank with partial cover, cutthroat trout from two different groups (one being adapted to covered and one being adapted to uncovered raceways, respectively) made use of cover. Wagner and his coworkers furthermore mentioned the problems with sunburn lesions in Atlantic salmon as already described by Corson and Brezosky (1961) where they covered circular pools with saran cloth for shade, and different hatchery manuals also advice against exposure of eggs and alevins to direct sunlight

(Piper et al., 1986). Furthermore, *Oncorhynchus clarkii* reared in outdoor raceways with plywood cover showed better fin conditions than without cover during early rearing (Wagner et al., 1995). That cover in a aquaculture context is important, also in terms of sun shade, was furthermore demonstrated by Bullock and Roberts (1981) who described a case of sunburn lesions (white pectoral and dorsal fins) in rainbow trout fry. Once tanks were covered and thus protected from sunlight exposure, condition of the fish improved and mortalities (have not been reported in detail) ceased within two days. Furthermore avoidance behavior of solar radiation as well as infectious diseases has been observed in different salmonid species (Kelly and Bothwell, 2002 in newly emerged and juvenile Coho salmon; Holtby and Bothwell, 2008 in juvenile Coho salmon). For an overview of implication of solar UV exposure for fish see review of Zagarese and Williamson (2001) describing effects of UV radiation (egg and larval mortality), sunburn, oxidative stress and phototoxicity, further examining potential implications for aquaculture and fisheries.

Overhead cover is considered by Barnes et al. (2005) as an essential component of the habitat of wild brown trout *Salmo trutta* and state that it is typically lacking during hatchery rearing. To evaluate the effect of cover during hatchery rearing, the authors grew feral brown trout in circular tanks that were either completely open on top or partially (29%) covered. Results of growth and feed conversion were not consistent but Barnes et al. (2005) conclude the use of partial tank covers can increase the growth of feral juvenile brown trout in circular tanks during hatchery rearing.

It was demonstrated by Nordgreen et al. (2013) not only, that Atlantic salmon parr used the partial cover (PVC plate of the experimental tank, measured by scoring the time the fish spent using it) but also that their time budget was significantly different between day and night and between days. Less hiding behavior was observed during the night in comparison to the day. The salmon were held individually and of the enrichment types "hiding place", "inlet current" and "gravel box", fish used the hiding place and inlet current most frequently.

Heggenes and Traaen (1988) tested swim-up fry of four species in an experimental channel and found that fry of Atlantic salmon showed preferences for overhead cover (opaque plastic plates), brown trout fry showed moderate preferences, whereas lake trout fry had preferences depending on the temperatures, while brook trout fry showed no cover preferences. Size of overhead cover varied in a study of Butler and Hawthorne (1968). They compared plywood cover of 1 by 1, 2 by 2 and 3 by 3 feet. All three trout species tested (brook, rainbow and brown trout) showed preference for the large overhead cover, which was most used by brown trout showing lowest activity and less used by rainbow trout but showing highest activity in movements outside of the shaded area. The behavioral movement pattern of brook trout was in between brown and rainbow trout.

But the observation that fish make use of cover (Nordgreen, 2013) and the positive effects such as less fin erosion or reduced cortisol levels give indications for a better welfare and are reasons for an application on-farm. Wagner et al. (1995) noted that preference by salmonids for low light intensities is often ignored in intensive outdoor fish culture. In practice it needs to be easily applicable. Sometimes, natural cover as shade by vegetation at the pond banks is given on a fish farm. Floating covers are not suitable as distribution of food may be interfered. A resistant tissue or a dense network might be spanned above the pond as sun protection in summer without derange of feeding. Often nets are above the tanks to control bird predation – another dense net or tissue can be fixed on them if it is of lightweight material not straining the construction too much.

Even though hatchery performance such as growth in salmonids was similar or smaller with the addition of cover (Wagner et al., 1996 in albino trout; Lema et al., 2005), maybe one could mention that growth can be elucidated from different angles. From an economic point of view, it might be interesting to optimize or maximize growth and an optimized feed conversion ratio has ecological advantages as well. Under natural conditions, fish grow much slower with of course another feeding behavior. A (relatively) long rearing duration is supposed to lead to a high flesh quality. The Bio Suisse directives prescribe therefore a minimum rearing period. In France, the "Label Rouge" demands to keep slow growing broilers (genotype), arguing for a better meat (Bokkers and Koene, 2003). Castellini et al. (2002) found that slow- and fast-growing boilers showed a good meat quality and that the fast-growing genotype meat had more fat.

In the introduction, Butler and Hawthorne (1968), who made an experiment with overhead artificial cover, wrote: "Fisherman familiar with stream environment know where trout can be caught. These places of catch are generally located near objects of cover such as a boulder, an overhanging bank, a floating log or an area of turbulence. Although the term, cover, is difficult to define, it does include the features of shade or shadow".

6.9 Organic aquaculture

In farmed fish, besides the laws of the Swiss Act on animal protection regulating requirements regarding stocking density or water quality for example, the Swiss organic (Bio Suisse) guidelines demand additionally a structured environment such as a shaded area above ponds, protection of current and structured pond bottom. Bio Suisse Standard and Directive (Art 5.8.3) specifies the following: "The pond/facility needs to be equipped with hiding and cover possibilities. Fish shall be allowed to express species specific behavior (shoaling, territorial behavior) while flow screens (removable for cleaning) serve e.g. as additional structure. New ethological findings can sharpen the directives. Also fish have to be offered light shade (minimum 10% of the water surface). Ponds shall possibly be natural or at least the pond bottom has to be of natural substrate. Furthermore, Bio Suisse, as most other organic certification schemes, does not certify recirculation aquaculture system as RIAs are two technologically advanced and by that too distant from the principles of organic production. As demonstrations of effects of habitat complexity in practical aquaculture are rare, the Bio Suisse directives are based on practical experience and observation of fish farmers and aquafeed producers.

Interestingly, Pulcini et al. (2012) reported that rainbow trout differed significantly in phenotypic body profile when reared under organic or intensive farming conditions. The organically reared fish showed a higher body profile, particularly in the head and trunk region, shorter median fins and a deeper caudal peduncle. The authors conclude that a combined effect of lower stocking density and increased habitat complexity might have provoked more functional shape.

European Commission regulation EC No 710/2009 (rules on organic aquaculture production demands) demands that husbandry environments are designed in such a way that it is in accordance with their species specific needs and thus to have sufficient space for their wellbeing, species-specific light conditions and of at least 5% of the pond perimeter to be of natural vegetation at the land-water interface.

7.0 Discussion and conclusions

With the increasing public awareness and the rising interest in animal welfare of fish, questions about the containment environment and whether or not an enrichment adds to an increased welfare are getting more important over time. Although aquaculture is, due to the small size of the produced animals (0.4-0.6 kg rainbow trout vs. 600 -800 kg cow), always a kind of mass rearing it depends very much on the prevailing conditions if a higher stocking density leads to detrimental welfare conditions or not. Several factors have been intensively studied in regard to their effects on fish welfare, primarily in the most important farmed species like Atlantic salmon and rainbow trout but also for Nile tilapia, carp, sea bass, sea bream and others. The fish welfare research has progressed significantly in the last two decades although one of its major questions, whether or not fish can feel pain and negative (and also positive) emotions, is still under debate. The question, however, if environmental enrichment is meaningful for fish kept for various reasons like food for human consumption, animal models in biological, pharmaceutical, chemical or ecotoxicological research or as ornamentals in private or public aquaria, is a very young one and has up to now not raised similar research efforts than fish nutrition, disease resistance or treatment or genetical improvement due to breeding programs. Only in organic aquaculture certain structures inside the holding compartments like natural pond bottom and current and light shade are compulsory (although the amount or extent of the structuring is not specified and varies from farm to farm) while in conventional aquaculture any type of structuring is usually considered a nuisance and an extra effort for maintenance like cleaning or for sorting and harvesting the fish. The recently published very extensive review of Näslund and Johnsson (2014) showed that there is a lot of literature already published presenting various positive but also some negative effects of environmental enrichment for fish in captive environments. They do not, however include natural structures occurring in the habitat of a specific species and how that might influence welfare or behavior of fish. Therefore these parts were included into this review to a certain extent and primarily for the fish species produced in Switzerland.

The diversity of the different natural habitats is quite high although most of the studies reviewed in table XY are dealing mainly with macro- or mesohabitats and habitat preferences of the fish. It is quite obvious that the habitat preference is strongly depending on the investigated species and its life stage. The fish are adapted to certain habitats and environments in terms of survival by avoiding predators and finding sufficient food (this is important for all life stages but more so the younger and less experienced and simultaneously more vulnerable the fish are) and for mature fish, meaning later life stages, for reproduction purposes. In nature the structures therefore usually fulfill crucial roles in day to day survival which is typically not required in captivity since the predation pressure is usually low or non-present (with exceptions in extensive or near-natural production systems like carp production), food availability is, compared to nature, extremely high and reproduction before harvest is usually undesirable in aquaculture production. Similarly it goes with environmental enrichment in captive environments as their effect not only depends on the type and amount of enrichment but also very much on the kept species, its life stage and the production or holding system.

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Still, structures copied from the natural habitat might reduce stress and aggression, improve health, growth, development and metabolic performance and therefore nutrient utilization which in themselves improve animal welfare to a certain degree or even production efficiency. Some potential enrichment types are hardly an option for aquaculture as they are not only impractical but also very hard to apply like for example current changes in a raceway or tank as the current is depending on supplied water volume over time, width and depth of the system. All of which are factors hardly influenceable as water supply often is limited and changing the dimensions of a holding system is almost impossible except on a long term basis and only with high effort. Other enrichment types are comparably easy to apply like tank covers or structures inside the tank but again it is strongly depending on the holding or production system. Small trout ponds or raceways could be covered way easier than large carp ponds with an surface area of several hectares. Structure inside the holding system can become a problem during maintenance (sorting or harvesting) and need to be cleaned on a regular basis to avoid areas where feed residues and dead fish can accumulate unseen or hard to be seen and thus represent potential pathogen sources. However, several of the presented papers show medium to strong benefits in terms of fish welfare after applying environmental enrichment types. These effects strongly depend on the type of EE applied and on fish species and life stage so it is impossible to generalize results. Given the positive effects described in various papers, more research into the specific benefits, especially in trout culture, should be self-evident.

In aquaculture one of the upcoming trends is an increasing number of indoor recirculating systems (RAS, Recirculation Aquaculture System) and in these highly sterile and basically barren environments with potentially high noise from pumps, aerators and filters EE might compensate some of the potentially negative effects or even provide positive effects. But again any type of environmental enrichment needs to be easy applicable, handle, clean, free of noxious substances leaking into the water and should not be too expensive, since otherwise the already high costs for a RAS, making it an act of balance whether or not they can be operated financially viable, would increase even further.

Considerable evidence exists showing that environmental enrichment could have a positive impact on fish welfare in general although more research, especially under practical and on-farm conditions, is needed. Such a research needs to concentrate on the most important (farmed) species and the most important life stages in which the fish are most vulnerable to stress and any negative effects coming due to a prevailing production system or production conditions. Usually the earliest life stages are the ones in which fish are most vulnerable and where the resilience against any type of stress is lowest and therefore the research should focus on effects of EE on larval and early juvenile rearing with the goal to find types of EE being beneficial for different rearing systems. Given the case such studies reveal that under practical on-farm conditions the benefits of EE outweigh any given negative effects through increased maintenance and incurring costs species and life stage specific guidelines for EE could be developed. However, it might turn out, that effects of EE need to be analyzed on a case-by-case basis and might not be transferable into practice easily by being to system-specific to be applied in a broad context.

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