Personality of sea trout: A case study on ecology, conservation and dynamics in coastal Skagerrak

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Drawing by Yvonne Cunnane

On an autumn day in 2017, Esben and I was hauling the beach seine in Stølsviga, Hisøya, looking to catch sea trout. We were captured on paper by artist Yvonne Cunnane, who generously presented me the drawing.

Preface

Setting out to disentangle the relationship between behaviour, personality and conservation of the interesting fish that is the sea trout, has been a fascinating journey for me. The results presented herein have been acquired with help from colleagues and supervisors to whom I would like to express my gratitude. The practical work described in this thesis has been carried out at the Institute of Marine Research.

I would like to thank my main supervisor, Esben Moland Olsen, for guiding me in the interesting field that is fish behaviour. You have an extensive knowledge of animal behaviour, life history theory, telemetry and conservation that it has been very valuable for me to learn from. Especially useful to me, has been your ability to sort out what is really interesting and really represents something novel, in the myriad of data and questions to ask from them. Thank you for interesting discussions on fish behaviour, help with writing and statistics, and for assistance in the field. Additionally, you and Even have designed an exceptional telemetry study system in the Tvedestrand fjord, which I have come to realise is quite unique in its configuration and suitability for performing detailed studies on fish behaviour.

Furthermore, I would like to thank my supervisor Even Moland for discussions on biology and for being of great help with statistics and writing. Also, you have carried out the continuous maintenance of the receiver array in which all of the telemetry work reported in this thesis has taken place. I have on several occasions joined in on this work, and it has always been a pleasure for me, even in freezing cold weather, to spend some time on the fjord with you and your stories and humour. My third supervisor, Halvor Knutsen, has contributed with extensive knowledge on the sea trout's way of life. Also, you have made an important contribution to mine and other students' working environment by introducing us to fellow students and researchers across countries and institutions, and by working to strengthen the marine biology research environment at University of Agder.

Also, I want to thank my co-authors for their contributions to the work presented herein. In the fall of 2016, I was lucky enough to be welcomed into the research lab of Colin Simpfendorfer at James Cook University in Townsville, Australia. Both from Colin Simpfendorfer and Michelle Heupel, I received valuable guidance in data analysis of my telemetry data, also thanks to their specific knowledge of the Tvedestrand telemetry array. Moreover, I would like to thank my colleague, Katinka Bleeker, with whom I have cooperated closely during field work for both our theses. We have spent many hours together hauling the beach seine in the Tvedestrand fjord looking for fish to tag, quite a few downloading data from the receivers, and also some electrofishing for trout in the stream. In the latter case, I have also received some well-appreciated help from colleague Tormod Haraldstad. I would also like to thank David Villegas-Ríos for guiding me in the analysis of behavioural data and being always very positive and excited both when receiving new drafts and when discussing statistics.

For assistance in the laboratory, I want to thank Stian Stiansen and Tor Birkeland, and the latter has also provided great help when it comes to technical support. For commenting on the thesis part of my dissertation, I would like to thank my supervisors and colleague Angela Helen Martin.

I also want to thank all the students, staff and researchers at Flødevigen research station, where I have been part of a welcoming and engaging research environment.

Susanna Huneide Thorbjørnsen

Abstract

Variation in fish behaviour seems to be an important part of species' life-history and adaptation to environmental change. Interestingly, variation occurs not only in response to environmental cues, but can also be consistently different between individuals, reflecting differences in personality. By means of acoustic telemetry tracking, I set out to measure the movement and behavioural composition of sea trout (*Salmo trutta*) in the marine habitat. The study system was located in the Tvedestrand fjord, a Norwegian fjord bordering the Skagerrak coast, where a no-take marine reserve was also located. This enabled me to study how behavioural variation can be maintained in a population by means of spatial protection, by potentially protecting fish from fishing-induced evolution. Firstly, I found that home ranges varied both in size and location for individual sea trout. The amount of protection received by the marine reserve for individual sea trout was affected by both the home range size of the individual, and initial capture location (inside or outside of the reserve). Sea trout tagged in the reserve also spent the most time there, although an increase in home range size resulted in a marginal reduction in degree of protection. For individuals tagged outside of the reserve, an increase in home range size resulted in an increase in protection. Secondly, I found that sea trout spatial behaviour was repeatable, hereby representing differences in spatial personality which is likely to be partly heritable. Moreover, selection on fish 'spatial personality' differed between the reserve and the fished area. Here, individuals tagged inside the reserve experienced a decrease in survival with increasing home range size, whereas individuals tagged outside the reserve experienced an increase in survival with increasing home range size. Effectively, the fitness landscape of sea trout was affected by the no-take marine reserve as a spatial management measure. Third, using

accelerometer tags, I obtained high-resolution spatial behaviour data, and found evidence of personality, temperature and light conditions (time of day) driving variation in activity of sea trout. Fourth and last, I investigated trends in sea trout catches along the Skagerrak coast using data from a scientific beach seine survey conducted during the past 100 years, and found that catches have been increasing for the past four decades in six Norwegian coastal regions. Conclusively, sea trout behaviour as measured in the wild, was found to vary both in response to environmental cues and as an effect of innate individual differences in behaviour, i.e. personality. To protect behavioural variation in a population from fishing-induced selection, marine reserves are a useful management tool, and optimally, a network of marine reserves can provide heterogeneity in fishing pressure and the selective landscape through which the sea trout moves when occupying its coastal marine habitats.

List of contents

1 Introduction

1.1 Fish behaviour and personalities

What makes fish behave differently? On one hand, they must constantly adapt to a changing environment, where access to food, predator density and abiotic environmental factors like temperature vary. On the other hand, consistency in behaviour that is stable over time, and differ between individuals seem to exist; individuals do not always react alike to changes in the environment. The advantages of this consistency in behaviour may arise through a trade-off between survival and reproduction, where individuals adopt strategies to invest either in future or current reproduction (Wolf et al., 2007). Individuals that invest in future reproduction are expected to adopt a “low-risk” behavioural strategy to increase the probability of surviving until that event; this involves avoiding risks, both when facing conspecifics and predators, by being shy and non-aggressive. Additionally, they must also take the time to search for the best resources available in their environment, which upon discovery can generate long-term benefits (Wolf et al., 2007). The latter will be more difficult and less rewarding as population densities are higher. Conversely, individuals that invest in current reproduction are expected to be aggressive and bold, and investigate their environment less thoroughly (Wolf et al., 2007). Different behavioural strategies will be favoured in response to changes in a range of environmental variables, including food availability, population density and predator density. Populations that maintain a range of behavioural strategies are therefore likely to be more resilient towards environmental change (Dingemanse and Réale, 2013).

Individual consistency in behaviour, termed personality, has recently been identified in several fish species (Kortet et al., 2014; Alós et al., 2016; Byrnes and Brown, 2016; Villegas-Ríos et al., 2017b). Personalities are often described as occurring along a scale from shy to bold (Sih et al., 2004) or on a spectrum from reactive to proactive (Quinn et al., 2012), where reactive fish are shy and thorough explorers whereas the proactive ones are bold, superficial explorers. Reactive fish are more prone to adjusting their behaviour in response to environmental change, as seen in cod (*Gadus morhua*) (Villegas-Ríos et al., 2018). Here, reactive fish reduced their home range size in response to an increase in sea temperature, while proactive fish did not. It was hypothesised that while reactive fish could afford to avoid the stressor that higher temperatures represent for cod (Freitas et al., 2015), proactive fish maintained their home range sizes to sustain the higher energy demands of being bold, aggressive and active (Careau et al., 2008).

Behavioural differences are already apparent in early life stages of fish. In a lab study of brown trout fry experiencing different levels of hunger, the activity and aggression levels shown during food search were affected more by differences in personality than starvation itself (Näslund and Johnsson, 2016). In behavioural ecology studies, personality is quantified as repeatability: the proportion of the total variance that is explained by individual identity (Falconer and Mackay, 1996). Bell et al. (2009) reported an average repeatability of 0.37 across a range of studies, meaning that 37 % of the variation in behaviour is attributable to consistent differences between individuals. Dochtermann et al. (2015) found that heritability of personality ranged from 0 to 96 % across studies, with an average of 52 %. This makes behaviour and personality an important piece of the puzzle that constitute individual selection – and ultimately evolution.

1.2 Harvesting and management measures affect fish behaviour

Being subject to selection, personality must also be considered in management. We already know that fishing gear such as nets and trawls typically induce selection on fish body size, where larger fish are more likely to be captured (Olsen et al., 2004; Kuparinen and Merila, 2007). In this case, a fish is better off being small and maturing and reproducing earlier. In the long run, this selective pressure will likely change the total production of a population (Kuparinen et al., 2016). When the old and large individuals are removed from the population, the quality of the produced offspring is reduced (Birkeland and Dayton, 2005). Fishing may also select on behaviour. Angling (rod-and-line fishing) has been shown to select strongly against active individuals with large home ranges and leaving behind individuals with localised and low-intensity movement patterns (Alós et al., 2016). Interestingly, different types of fishing gear can have opposite effects. While passive gear types, like hook-and-line and traps, can select against boldness and large home range sizes (Olsen et al., 2012), active gear types, like trawls, can select for increased boldness (Andersen et al., 2018). The latter scenario could be explained by positive correlations between basal metabolic rates, swimming ability and boldness (Careau et al., 2008). As pointed out by Killen et al. (2015), it is vital to have species specific information on harvest-induced behavioural selection, as the vulnerability to harvest will likely vary between species.

Marine reserves and marine protected areas are widely used as a conservation tool to protect fish populations from harvest. These defined areas can protect both fish abundance and size structure (Lester et al., 2009; Fenberg et al., 2012; Baskett and Barnett, 2015), but to what degree can they protect the behavioural variation in a population? It has been hypothesised that marine reserves, where no fishing is allowed, can select for individuals with smaller home ranges, unless the reserves are large enough to protect a sufficiently large portion of movement ranges occurring within a population (Villegas-Ríos et al., 2017a). Field studies on behavioural selection in relation to marine reserves are scarce but needed to investigate the potential of this management tool to protect behavioural variation.

To summarise, behavioural variability is likely to be partly heritable and an important part of a population's resilience to environmental change. The degree to which fishing and/or protection can alter the behavioural composition of a population is therefore of broad interest.

1.3 The sea trout

The brown trout (*Salmo trutta*) is a salmonid species with a highly variable life history. Some individuals live their whole life in a stream or lake, while the anadromous form, called sea trout, will venture out to marine areas. Seaward migrations can last from only a few weeks (Eldøy et al., 2015) to two or more years (Jonsson and Jonsson, 2002), followed by returning to the river to spawn during fall. Food acquisition is the main driver of migration, as sea trout will expectedly have access to more food in the marine environment (Thorstad et al., 2016). However, the sea trout will also have to make a costly adaption to salt water, tackle a potentially higher predation risk, and pay the energetic cost of moving longer distances. The balance between growth, resulting in increased fecundity, on one side, and increased risk of mortality on the other, could explain why we observe a range of migration strategies within and among populations (Thorstad et al., 2016).

Migratory strategy is only one aspect of which the sea trout show large variations in behaviour; others include habitat use at sea (Eldøy et al., 2015), dominance (Höjesjö et al., 2002), feeding behaviour (Alanärä et al., 2001) and spawning behaviour (Jonsson, 1985). Within confined laboratory conditions, sea trout also show individual consistency in behaviours like swimming activity, aggression, boldness, exploratory behaviour and tendency to freeze (Kortet et al., 2014; Näslund and Johnsson, 2016). However, data on individual consistency of behaviour in sea trout in the wild has rarely been collected.

In Norway, sea trout is highly valued by recreational fishers. Fishing is only allowed using hook and line equipment, and with specialised traps during one month in summer. This means that sea trout are likely subject to angling-induced behavioural selection when moving in coastal marine habitats.

1.4 Fish tracking using acoustic telemetry

Acoustic telemetry is a tracking method that can be used to acquire long-term, detailed data on movement of aquatic animals. The animal carries a tag transmitting an acoustic signal to a network of nearby receivers. The signal transfers an identity code and may also include information measured and/or stored by the tag, for example depth-use measured by a pressure sensor, or acceleration measured by an accelerometer. Such raw data on presence and absence at multiple receivers forms the basis for estimating short-term centres of activity and long-term home ranges (Simpfendorfer et al., 2002).

2 Objectives

Within my doctoral research project, I set out to evaluate a hypothesis that sea trout (*Salmo trutta*) exhibit variation in their movement behaviour in the wild (paper 1) that is partly due to variation within individuals and partly due to variation between individuals (paper 2 & 3). The existence of the latter indicates that sea trout exhibit individually consistent behaviour in the wild, in other words, differences in personalities. This is quantified as repeatability: the proportion of the total variance that is explained by individual identity (Falconer and Mackay, 1996). I also hypothesised that sea trout exhibiting consistently different behaviours will receive unequal benefits from spatial management measures (paper 2). The amount of protection received is likely to vary and will ultimately result in differences in survival between individuals.

To quantify long-term spatial behaviour of sea trout in the wild, I used a network of acoustic telemetry receivers located in the Tvedestrand fjord in southern Norway (Figure 1). The Tvedestrand fjord has a no-take marine reserve in which no fishing is allowed. Bordering the reserve are two marine protected areas (MPAs) where fishing regulations do not protect sea trout (hook-and-line type gear are allowed). Through the study, 132 sea trout were fitted with acoustic transmitters, sending information on presence and depth-use to the receivers. 15 of these sea trout were tagged with accelerometer tags, which provide temporally and spatially detailed information on individual activity (paper 3). From the collected data, I estimated a range of movement metrics relating to depth-use, activity and home range.

Lastly, I will present a century of scientific survey data on sea trout abundance from the Norwegian Skagerrak coast, and discuss catch trends in the different southern and eastern coastal regions of Norway (paper 4).

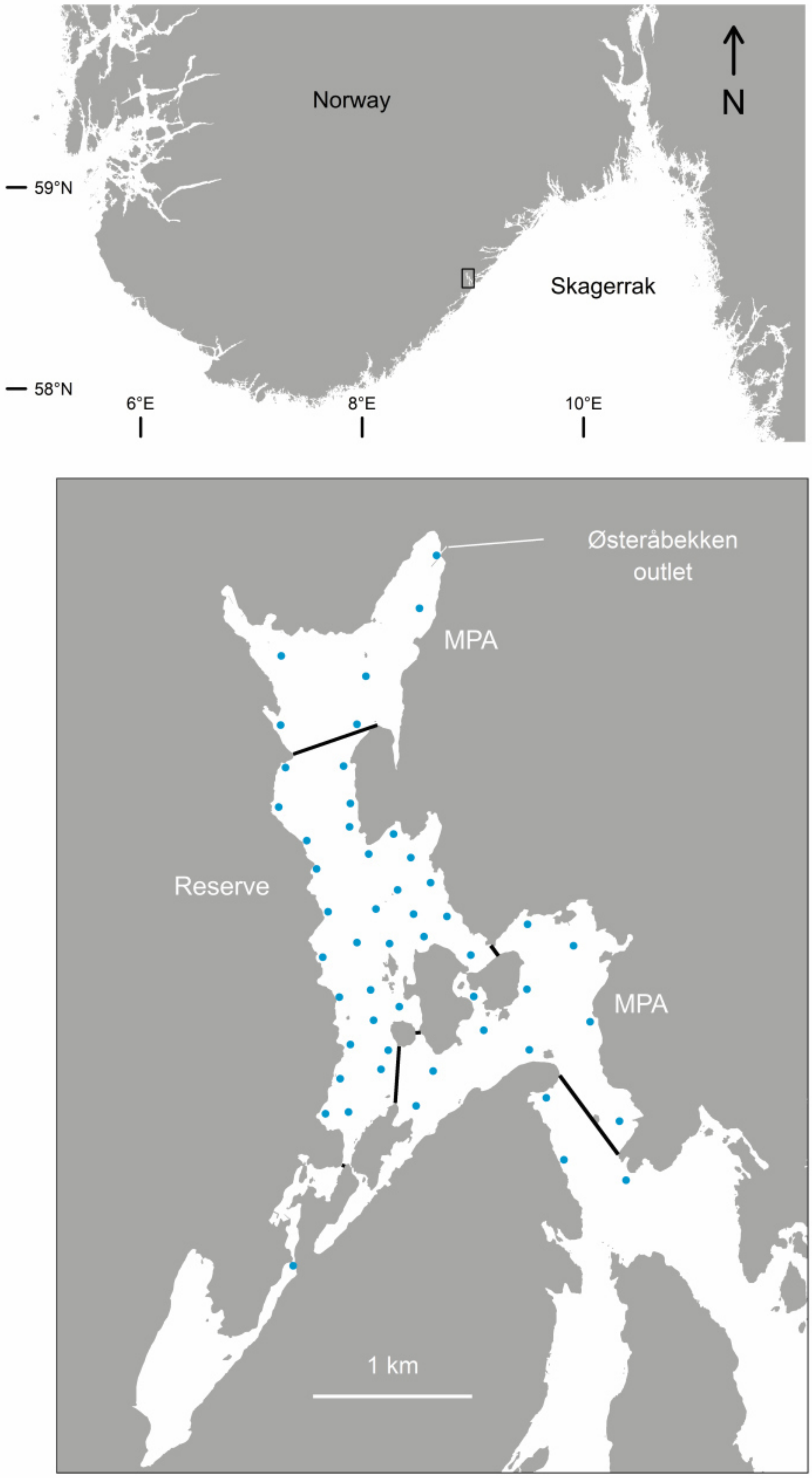

Figure 1 The Tvedestrand fjord study area (lower panel) and its position on the Skagerrak coast (upper panel). The central part of the fjord is a no-take marine reserve where all types of fishing are forbidden. The reserve is located between two marine protected areas where sea trout are not protected.

3 Results and discussion

3.1 A marine reserve can protect home ranges of sea trout

Sea trout tagged in the study made extensive use of the Tvedestrand fjord, and their individual spatial behaviour varied substantially (paper 1). The main finding was that home range size affected how much protection the reserve provided to an individual sea trout, and that this effect varied with initial capture location (Figure 2). In general, sea trout tagged inside the reserve also spent the most time there, although an increase in home range size resulted in a marginal reduction in protection level. For individuals tagged outside of the reserve, an increase in home range size resulted in an increase in protection. According to previous research, fish home range sizes can be repeatable (Villegas-Ríos et al., 2017b), and can thus also be prone to selection by fishing. Recently, there has been concern that marine reserves can select against large home ranges when individuals straying outside reserve borders are continuously removed by fisheries (Villegas-Ríos et al., 2017a), but the results of the present study might address that concern (paper 1). I argue that marine reserves and marine reserve networks have the potential to affect the selective landscape through which the sea trout travels in two ways: Firstly, there is an increase in protection with larger home ranges for individuals originally located outside the reserve, potentially opposing selection towards smaller home ranges within the reserves (Villegas-Ríos et al., 2017a). Secondly, there will be protection from selection on behaviour from the fishing gear itself (in this case, angling) within the reserve. However, I note that estimates of fishing effort are not included in the present study, thus I can only comment on the potential for protection from fishing by reserves.

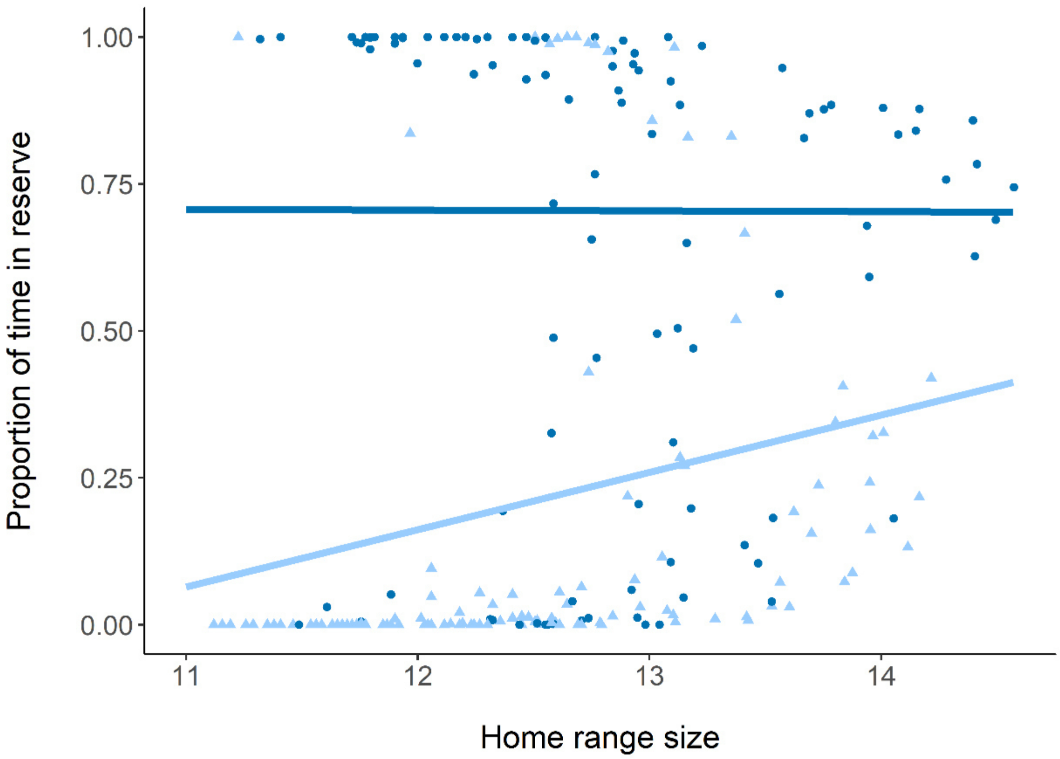

Figure 2 Proportion of time spent in the reserve per month plotted against 95 % monthly home range size (log-transformed). Light blue triangles represent observations from fish that were caught outside the reserve, while dark blue circles represent observations from fish that were caught inside the reserves. The light blue and dark blue lines show the predicted relationship between home range size and proportion of time spent inside the reserve for trout initially caught outside and inside the reserve, respectively.

Anadromous species do, to some degree, have a predictable movement pattern considering having to return to the river for spawning, but there is great variation in marine habitat use (Jonsson and Jonsson, 2002; Eldøy et al., 2015). This variation was also observed in the present study, where 21 % of the tagged population dispersed from the fjord without returning during tag life (paper 1). Further, 26 % of the tagged population spent time outside the study area, possibly in outer coastal areas, before returning. The remaining individuals (53 %) spent most of their time in the Tvedestrand fjord. Sea trout do stray to non-natal rivers, and straying rates of up to 57 % have been observed in some populations, often being directed towards larger rivers (Degerman et al., 2012). To protect sea trout from fishing, it could therefore be advisable to locate marine reserves in fjords connected to major spawning rivers.

3.2 Selection on fish home range size differs between a marine reserve and fished areas

To evaluate whether marine reserves can protect sea trout behaviour, I first assessed whether behaviours are consistent (repeatable) within individuals and thus represent personalities. Secondly, I focused on whether fitness is affected by individual behaviour and protection regime (paper 2). Home range size was consistently different between individuals in the population (repeatability: 21 %), indicating that home range size represents a personality-dependent spatial trait in sea trout. Median sea survival of sea trout was almost 11 months, and survival differed for fish tagged within and outside the reserve. Individuals tagged inside the reserve experienced a decrease in survival with increasing home range size, while individuals tagged outside the reserve experienced an increase in survival with increasing home range size (Figure 3). This shows that the fitness landscape of sea trout is affected by spatial management.

Based on these findings, and in line with previous studies showing that fishing selects against large home ranges (Alós et al., 2016), I suggest that networks of marine reserves can be used to provide spatial heterogeneity in fishing pressure and hereby protect populations against fishing-induced selection on fish behaviour. Optimally, network design would incorporate various habitat types, as different habitats favour different behaviours (Killen et al., 2016).

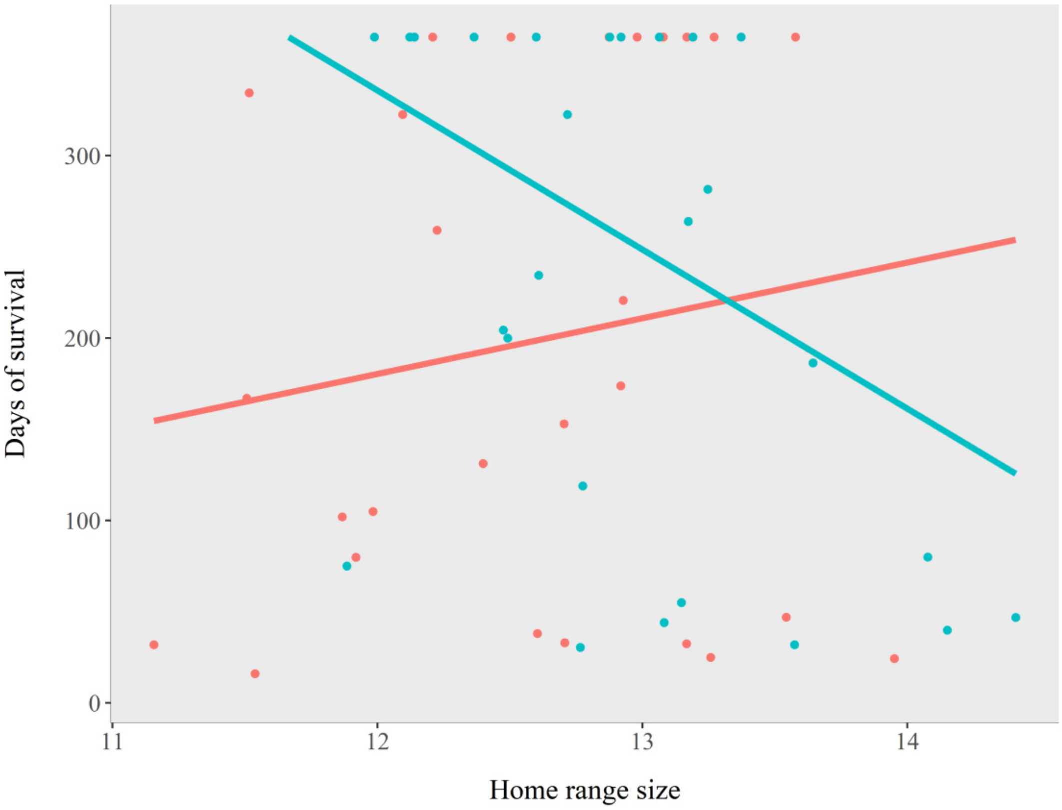

Figure 3 Days of survival as an effect of average monthly 95 % home range size (log-transformed) of sea trout in the Tvedestrand fjord. Red and blue dots represent trout initially caught outside and inside the reserve, respectively. The red and blue lines show the predicted relationship between home range and days of survival for trout initially caught outside and inside the reserve, respectively. Trout tagged in spring had lower survival than trout tagged in the fall, but this effect is averaged in the figure.

3.3 Individual consistency in activity of sea trout estimated from accelerometer measurements

Fifteen sea trout were caught in the spawning river Østeråbekken and fitted with acoustic transmitters measuring the acceleration of the fish across three axes, providing a high-resolution measure of activity in the wild. As found for home range (paper 2), activity measured as acceleration was consistently different between individuals in the tagged population (paper 3). Repeatability was estimated at 38 %, indicating that activity represents a personality trait in sea trout. Furthermore, sea trout activity was affected by an interaction between hour of day and temperature, meaning that the diel pattern of acceleration varied with temperature. Generally, trout were more active during daylight hours and activity increased with temperature (Figure 4). Accordingly, sea trout activity varied as a result of both consistent individual differences and environmental factors like temperature and daylight. Furthermore, by providing a high-resolution measure of activity, I argue that accelerometer tags may enable classification of fish personality directly during tracking in the wild (paper 3).

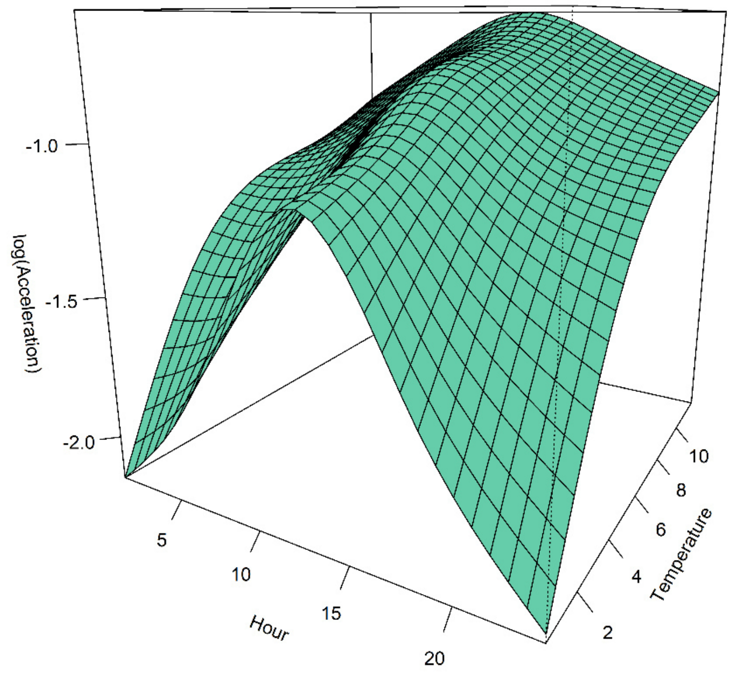

Figure 4 Average hourly acceleration (log-transformed) through the 24-hour cycle across temperatures for sea trout.

3.4 100 years of scientific beach seine sampling reveal trends in sea trout dynamics

Using data from a unique and extensive time series of scientific beach seine sampling conducted along the Norwegian Skagerrak coast during the past 100 years (see eg. Fromentin et al., 1997; Durif et al., 2011; Barceló et al., 2016), I investigated trout catch-per-unit-effort, representing a proxy for abundance, in six Norwegian coastal regions. Overall, these data suggest that sea trout abundance have increased in all regions for the past four decades, and even longer in some regions (paper 4, Figure 5). Identifying the causes of this is beyond the scope of this study, but some potential explanatory variables could be discerned. For instance, increasing temperatures may have led to more favourable feeding temperatures for sea trout feeding in the marine habitat and more optimal growth temperatures for juvenile trout on the stream (Klemetsen et al., 2003). Additionally, temperature may have affected sea trout catchability at sea, as any alteration in feeding behaviour would be accompanied by a shift in feeding activity levels, and relocation. Acidification of surface water, originating from acidic deposition from European industry, has long been known as a stressor for trout while residing in fresh water (Bulger et al., 1993). Several international agreements have reduced the amount of acidic deposition and, combined with liming (Miljødirektoratet, 2016), likely had a positive effect on sea trout populations (Saksgård and Schartau, 2011). Moreover, changes in legislation governing sea trout fishing have occurred since the first law was implemented in 1848. Some important changes were the ban on fishing sea trout with nests in marine areas, implemented in 1979, and the shift from an open fishery with regulations to a closed fishery with exceptions, which occurred in 1992. Today, sea trout can only be fished using hook and line in marine areas, and specialised traps are permitted during one month in summer.

Interestingly, Skagerrak is almost free of salmonid aquaculture, and thus represents a valuable reference area to e.g. Western Norway, where sea trout are exposed to the excess export of sea lice from aquaculture facilities using net pens (Torrissen et al., 2013). This has been shown to reduce survival (Serra-Llinares et al., 2014) and growth (Thorstad et al., 2015) of sea trout in marine habitats.

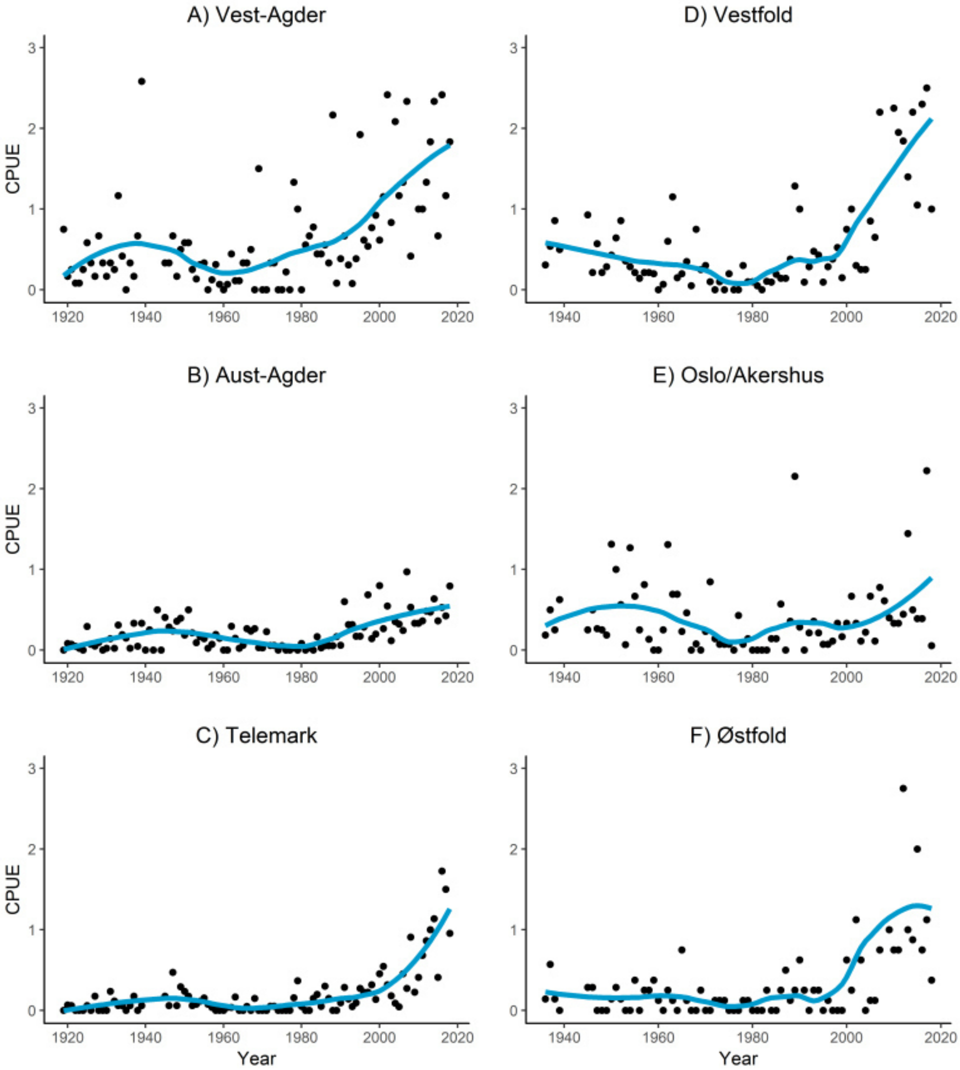

Figure 5 Yearly catch-per-unit-effort (CPUE) of sea trout in the beach seine survey in Skagerrak. Loess smoothers were fitted to the six regions: A) Vest-Agder, B) Aust-Agder, C) Telemark, D) Vestfold, E) Oslo/Akershus and F) Østfold. CPUE values larger than 3 are not plotted in the figure (n = 3).

4 Conclusion

Fish behave differently and, interestingly, the variation in behaviour is founded both in response to environmental cues, as well as in consistent individual differences (personality). In this study, I found that sea trout exhibit consistent innate individual differences in both spatial behaviour (home range size) and activity (paper 2 & 3), and further adapted their behaviour to the environmental variables of temperature and daylight (paper 1 & 3). As consistent individual differences in behaviour are often partly heritable, the behavioural composition of a population is affected by the selective landscape in which its individuals move and reside. I found that selection on fish ‘spatial personality’ differed between a no-take marine reserve and adjacent fished areas, where individuals tagged inside the reserve experienced a decrease in survival with increasing home range size, and individuals tagged outside the reserve experienced an increase in survival with increasing home range size (paper 2). This supports the notion that marine reserves can protect individuals from fishing-induced evolution acting on behavioural traits, and optimally, networks of marine reserves can be used to further provide spatial heterogeneity in fishing and selection pressure.

Sea trout seem to prosper in Skagerrak (paper 4), and the individual variation in behaviour shown herein is part of the diversity and biocomplexity that makes this species resilient. This variation can be further promoted and maintained if taken into account when managing this highly valued species.

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6 List of papers

Paper I	Thorbjørnsen S.H., Moland E., Simpfendorfer C., Heupel M., Knutsen H., Olsen E.M., 2018. Potential of a no-take marine reserve to protect home ranges of anadromous brown trout (*Salmo trutta*). Ecology and Evolution 00:1-10. https://doi.org/10.1002/ece3.4760
Paper II	Thorbjørnsen S.H., Moland E., Villegas-Ríos D., Bleeker K., Knutsen H., Olsen E.M. Selection on fish spatial personality differs between a no-take marine reserve and fished areas. (*Manuscript*).
Paper III	Thorbjørnsen S.H., Moland E., Villegas-Ríos D., Olsen E.M. Drivers and individual consistency of sea trout (*Salmo trutta*) activity in the wild. (*Manuscript*).
Paper IV	Thorbjørnsen S.H., Knutsen H., Olsen E.M. Dynamics of anadromous brown trout at sea inferred from 100 years of scientific beach seine sampling. (*Manuscript*).

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ORIGINAL RESEARCH

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Potential of a no-take marine reserve to protect home ranges of anadromous brown trout (*Salmo trutta*)

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Abstract

1. The extent to which no-take marine reserves can benefit anadromous species requires examination.
2. Here, we used acoustic telemetry to investigate the spatial behavior of anadromous brown trout (sea trout, *Salmo trutta*) in relation to a small marine reserve (~1.5 km^2) located inside a fjord on the Norwegian Skagerrak coast.
3. On average, sea trout spent 42.3 % (±5.0% *SE*) of their time in the fjord within the reserve, a proportion similar to the area of the reserve relative to that of the fjord.
4. On average, sea trout tagged inside the reserve received the most protection, although the level of protection decreased marginally with increasing home range size. Furthermore, individuals tagged outside the reserve received more protection with increasing home range size, potentially opposing selection toward smaller home range sizes inflicted on fish residing within reserves, or through selective fishing methods like angling.
5. Monthly sea trout home ranges in the marine environment were on average smaller than the reserve, with a mean of 0.430 (±0.0265 *SE*) km^2. Hence, the reserve is large enough to protect the full home range of some individuals residing in the reserve.
6. *Synthesis and applications*: In general, the reserve protects sea trout to a varying degree depending on their individual behavior. These findings highlight evolutionary implications of spatial protection and can guide managers in the design of marine reserves and networks that preserve variation in target species' home range size and movement behavior.

KEYWORDS
acoustic telemetry, behavior, marine reserve design, movement, sea trout, selection, space use

1 | INTRODUCTION

Marine protected areas (MPAs) are widely used as a means to protect species in their habitat and have been shown to increase numbers and/or biomass of protected species, both inside MPAs (Lester et al., 2009) and as spillover beyond MPA borders (Abesamis & Russ, 2005; Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010; Roberts, Bohnsack, Gell, Hawkins, & Goodridge, 2001). Efficacy of MPAs is expected to be higher for less mobile species (Pilyugin, Medlock, & Leenheer, 2016), but positive effects have also been found for wide ranging species, such as coastal sharks. For example, Knip, Heupel, and Simpfendorfer (2012) found that coastal shark species resided in an MPA 22%–32% of their time, and that the MPA provided similar protection to all size classes. MPAs can protect mobile species if strategically situated, as shown for white stumpnose (Kerwath et al., 2008) and migratory sea turtles (Hays, Mortimer, Ierodiaconou, & Esteban, 2014). Since migratory species move in predictable patterns, there is potential to recognize and protect key areas of their habitat using MPAs or strictly no-take zones (marine reserves).

A number of fish species are known to undertake migrations for a variety of purposes such as spawning and feeding (Block et al., 2001; Hunter, Metcalfe, & Reynolds, 2003; Klemetsen, 2003). Salmonids are often anadromous, migrating between spawning areas in fresh water (rivers) and the marine environment. Brown trout (*Salmo trutta*, Figure 1) is a salmonid species with an anadromous component called sea trout. It has a highly variable life history, with some trout spending their whole life in the river, and others spending most of their time in the marine environment (Klemetsen et al., 2003). Predicting the efficiency of marine reserves for species with highly variable migratory patterns, such as the sea trout, is a major challenge. Variation in how sea trout use marine habitats is substantial and ranges from spending only a few weeks at sea (Eldøy et al., 2015) to spending two or more years at sea (Jonsson & Jonsson, 2002; Klemetsen et al., 2003). In addition, there is great variation in habitat use in marine regions, with some sea trout spending most of their time in fjords and some venturing out to the open seas (Bordeleau et al., 2018; del Villar-Guerra, Aarestrup, Skov, & Koed, 2014). Seaward migration can occur as a response to reduced energetic surplus available for growth (Forseth, Næsje, Jonsson, & Hårsaker, 1999) and is also more likely for individuals with a lower body condition (Bordeleau et al., 2018). Decisions made regarding staying in fjord habitats or moving to the open sea are made shortly after entering the fjord (del Villar-Guerra et al., 2014). Additionally, sea trout may stray to rivers other than their natal river, also to spawn (Berg & Berg, 1987; Degerman, Leonardsson, & Lundqvist, 2012; Thorstad et al., 2016 and references therein). Acquiring knowledge on habitat use of sea trout in relation to a no-take zone can assist managers in positioning of reserves and in evaluating a potential MPA network design.

FIGURE 1 Brown trout (*Salmo trutta*). Photo: Erlend A. Lorentzen

A study of wild-origin zebrafish (*Danio rerio*) revealed that size-selective harvesting alters the behavioral composition in a target population, resulting in less explorative and bold individuals (Uusi-Heikkilä et al., 2015). Angling selects against bold behavior and large home ranges (Alós, Palmer, Rosselló, & Arlinghaus, 2016; Klefoth, Skov, Kuparinen, & Arlinghaus, 2017), and one mechanism behind this is that fish that utilize larger areas and have a higher movement rate have a higher risk of encountering hooks (Enberg et al., 2012). In Norway, fishing for sea trout is mainly by hook and line, leaving sea trout vulnerable to angling-induced selection. Marine reserves also have the potential to select against large home range size depending on an individual's home range size relative to reserve size (Villegas-Ríos, Moland, & Olsen, 2016). Selection on behavior and movement can indirectly select on life-history traits like growth and fecundity (Biro & Stamps, 2008) and thus alter the productivity in a population, which in turn will affect fishing yields. The interplay between these selective effects will determine how a marine reserve succeeds in protecting a population and its different behavioral components (see Baskett & Barnett, 2015).

Acoustic telemetry can be used to acquire long-term detailed information on movement in marine animals and using a dense network of acoustic receivers allows for calculating centers of activity (Simpfendorfer, Heupel, & Hueter, 2002) and home ranges (Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2017). We used acoustic telemetry to quantify spatial use of sea trout in a southern Norwegian fjord in relation to a no-take marine reserve, as well as adjacent partially protected marine habitats and areas open to all types of fishing. We expected that habitat use during the marine phase would vary substantially among individual sea trout, and that the amount of protection afforded by the no-take marine reserve would be influenced by tagging location and home range size.

2 | MATERIALS AND METHODS

2.1 | Study species

The brown trout (*Salmo trutta*) is a salmonid fish that spawns in fresh water and subsequently adopts various migratory strategies, with some individuals spending their whole life in fresh water and others being anadromous and undertaking marine migrations (Jonsson, 1985; Jonsson & Jonsson, 1993). Spawning occurs during autumn, and migrations are cued by river flow (Jonsson & Jonsson, 2002). The sea trout is highly valued by recreational fishers. In Norway, sea

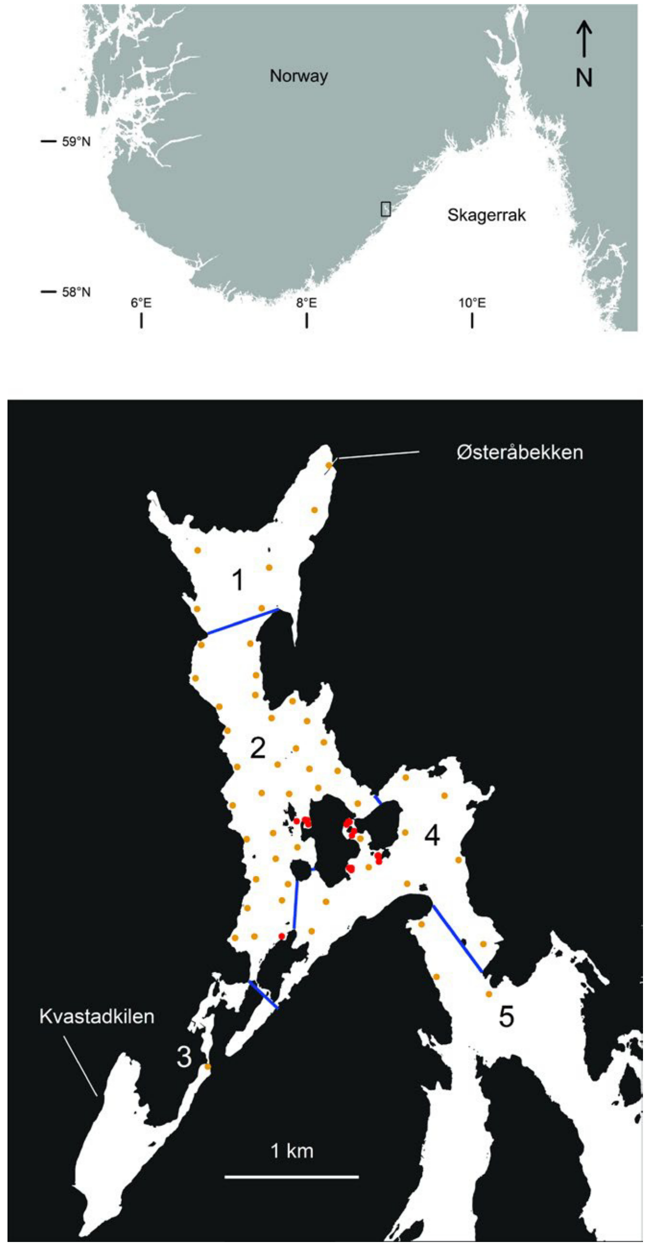

FIGURE 2 Map of the Tvedestrand fjord with zones (bottom) and its location along the Norwegian coastline (top). Red and yellow dots represent tagging and receiver locations, respectively, and blue lines section the fjord into the five different zones: The Northern MPA, including the spawning river Østeråbekken (1); the marine reserve (2); Kvastadkilen (3); the central fjord MPA (4); and the outer zone with no fishing restrictions (5)

trout can be fished using hook and line equipment all year in marine locations, and traps are allowed for 1 month in summer in the southern part of Norway.

2.2 | Study site and data collection

The Tvedestrand fjord is located on the Skagerrak coast in southern Norway and covers an area of approximately 3.8 km^2, with depths reaching 87 m. Outside the receiver array, the fjord splits into Oksefjorden and Eikelandsfjorden, which connect to the open ocean, hereby referred to as outer fjord and sea areas. A network of 50 VR2W receivers (Vemco Ltd., Halifax, Canada) was deployed in the fjord. All receivers were attached to moorings and deployed at ~3 m depth where they were kept in place by subsurface buoys. Receivers were deployed to cover most regions of the fjord, including the no-take reserve, adjacent MPAs, and potential spawning rivers. A no-take marine reserve designated in 2012 to protect fishes and lobsters from commercial and recreational fishing, hereafter referred to as "the reserve" (1.5 km^2), is located in the central area of the Tvedestrand fjord (Figure 2). One receiver was deployed close to the inlet of the main spawning stream, Østeråbekken, to monitor freshwater migrations. Fish were classified as being in the river if both the last detection before an absence and the first detection after an absence occurred at the receiver in the spawning river inlet or the second closest receiver (Figure 2). One receiver was positioned to identify fish moving to the inner basin in the southwest part of the fjord (Kvastadkilen). Three receivers were located in the outermost section of the Tvedestrand fjord to identify fish movements between the fjord and the outer fjord and sea areas bordering the Skagerrak ocean. Receiver coverage was good in all zones of the fjord (see Supporting Information Figure S1).

Sea trout were caught around the center islands of the fjord using a beach seine between April and November 2013. This active fishing gear was chosen to avoid selecting individuals with a more active behavior that would potentially be favored if using angling or passive nets (Olsen, Heupel, Simpfendorfer, & Moland, 2012). Immediately following capture, individuals bigger than 23 cm were anesthetized by a 9:1 ethanol—clove oil solution added at 2 ml per 5 L of water and tagged with Vemco V9P-L transmitters, positioned in the abdominal cavity (see Olsen et al., 2012). The transmitters were equipped with pressure sensors with an accuracy of ±2.5 m and a resolution of 0.22 m to a max depth of 50 m. Time lag between signal emissions was 120 ± 60 s and expected battery life was 550 days. The detection intervals were similar in the different zones (see Supporting Information Figure S1). All fish were released from shore at the capture location.

2.3 | Data preparation and analyses

Detection data were downloaded from the receivers and processed using VUE software (VEMCO). An individual was defined as dead at the point where vertical and horizontal movement ceased, and the remaining data were deleted from the dataset. Detections below 50 m and single detections within 1 day were removed, as they are likely to be false. All following calculations and analyses were performed in the R environment (R Core Team, 2016). Horizontal locations were estimated using position averaging (PAV), following Simpfendorfer et al. (2002). PAVs were calculated as centers of activity for 30-min time intervals and assigned to the appropriate fjord zone and time of day (day/night). Day and night was defined

TABLE 1 Proportion of time (days) spent in the Tvedestrand fjord zones for all sea trout combined

Zone	Proportion ± *SE*
Zone 1	7.07 ± 2.14
Zone 2	42.3 ± 5.04
Zone 3	0.669 ± 0.547
Zone 4	47.9 ± 5.02
Zone 5	2.13 ± 0.985

by positive and negative solar elevation, respectively. Monthly 95% home ranges (HR) for each fish were calculated from PAVs using Kernel Utilization Distributions (bandwidth = 60, extent = 0.5).

For the purpose of this study, the Tvedestrand fjord was divided into five zones: a northernmost zone comprising an MPA where no fixed gear is allowed, also including the main spawning river Østeråbekken where no fishing is allowed (Zone 1); the no-take marine reserve (Zone 2); Kvastadkilen (Zone 3); central fjord area MPA (no fixed gear; Zone 4); and the outermost section of the Tvedestrand fjord with no restrictions (Zone 5; Figure 2). The proportion of time spent in each zone was calculated using the number of PAVs (each representing 30 min) assigned to a specific zone for both individual trout and the tagged population as a whole. In the latter case, all PAVs calculated for the tagged population were pooled.

Linear modeling was used to test if body length (mean = 0, *SD* = 1) had an effect on the proportion of time spent in the reserve. Further, to test whether home range size, tagging location (two levels: within/outside the reserve) and the interaction between these affected the proportion of time spent in the reserve, a linear mixed-effects (lme) model was constructed based on monthly estimates of home range size, with individual as a random effect. The lme model was compared to a generalized least squares (gls) model to assess the necessity of including individual as a random effect. The model selection was based on AIC-values, and significant improvement was assigned following a minimum reduction in two AIC units. Sizes of home ranges were log-transformed for normality. To ensure that estimated home ranges were representative of sea trout habitat use, all months with <14 days of presence were excluded from the dataset in models including home range as a variable. A linear model fitted using generalized least squares was used to test whether season had an effect on the proportion of time spent in the reserve on a monthly basis. As sea trout spent different amounts of time within the study site in the Tvedestrand fjord, a linear model was used to test whether observation time (in months) affected the proportion of time spent in the reserve. A linear model was also used to check whether calculated home ranges were related to the number of PAVs available for a given month (Becker et al., 2016).

How often and in which direction sea trout ventured from the reserve was examined, excluding individuals that did not visit the reserve (*n* = 4). To test whether there were more excursions from the reserve during day or night, a Pearson's chi-squared proportionality test was used. Since there were more observations during day than night, proportions were corrected accordingly by multiplying the number of detections during night by the ratio of day/night detections. The effect of body length, body condition (Fulton's $K = 100 \times \text{Weight (g)} \times \text{Length [cm]}^{-3}$), and sex on the average daily number of excursions was also assessed by linear modeling. The effect of home range on monthly number of excursions was assessed by a lme model including individual as a random effect, and compared to a gls model to assess the necessity of including individual as a random effect. Similarly, a separate model was fitted to test for the effect of season on monthly number of excursions. Significance of temporal autocorrelation was tested for in all models where monthly averages represented replicates for each fish.

Sea trout excursions from the Tvedestrand fjord to outer fjord and sea areas and to Østeråbekken were quantified and related to season. Excursions were defined as having a minimum length of 3 days. Additionally, the effects of length, body condition, and sex on time spent at sea were explored by linear modeling. The effect of length, body condition and sex on the probability of dispersing was assessed by a binomial generalized linear model (glm). We defined sea trout as dispersers if they left the study site within 2 months of tagging, followed by either not returning to the study site during tag life or spending >50% of their time outside the study area and river system. Dispersing sea trout were defined as receiving no protection from the reserve. Sea trout postsmolts have shown a low probability of migrating to sea if they did not exit the fjord within the first 41 days after leaving the river (del Villar-Guerra et al., 2014); hence, sea trout that exited the fjord at a later stage were assumed to be expanding their home range beyond the fjord, rather than dispersing. To examine what proportion of the population is protected in the reserve, the proportion of time spent in the reserve given that the sea trout was in the fjord was multiplied with the proportion of time spent in the fjord by the tagged sea trout population as a whole. Here, dispersing sea trout were defined as spending no time in the fjord.

3 | RESULTS

In total, 60 sea trout (mean body length: 34 cm, range 23–64 cm) were captured and tagged in the Tvedestrand fjord in 2013. Three individuals were excluded from the study due to postsurgical mortality (*n* = 1) and tag malfunction (*n* = 2). The remaining 57 fish generated 2,269,920 detections during the study, after removing false detections. The amount of time spent in the telemetry array by each fish ranged from 1 to 18 months (mean = 5.9, *SE* = 0.62).

On average, sea trout spent 42.3% (±5.0% *SE*) of their time in the fjord inside the reserve (Table 1). Individuals utilized the reserve differently, with most trout spending either a large or a small proportion of their time in the reserve. Approximately half (53%) of sea trout spent less than 25% of their time in the reserve, whereas 33%

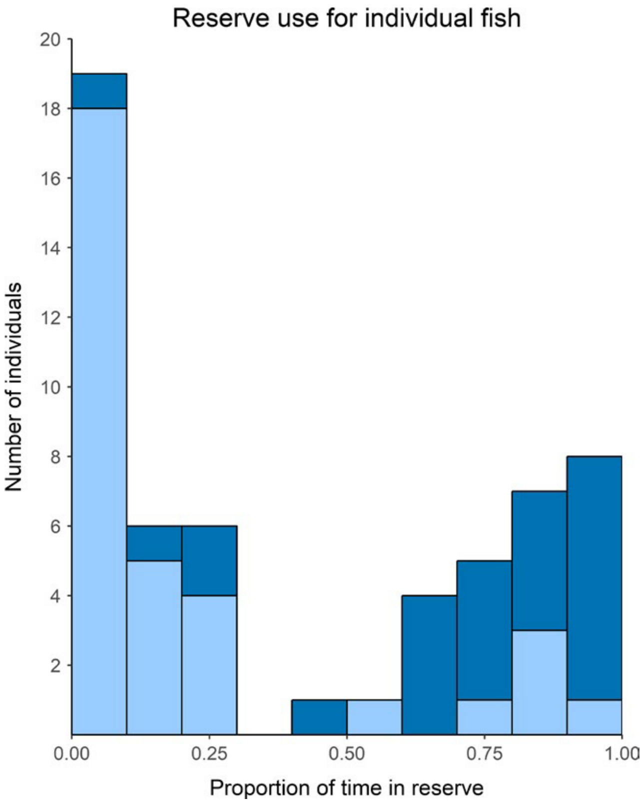

FIGURE 3 Distribution of the proportion of time spent in the reserve relative to time present in the fjord for all trout. Light blue and dark blue represent trout initially caught outside and inside the reserve, respectively

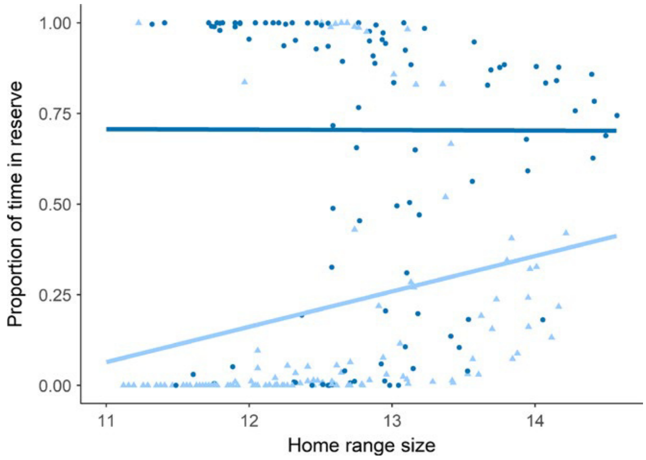

FIGURE 4 Proportion of time spent in the reserve plotted against 95% monthly home range size (log-transformed). Light blue triangles represent observations from fish that were caught outside the reserve, while dark blue circles represent observations from fish that were caught inside the reserve. The light blue and dark blue lines show the predicted relationship between home range and proportion of time spent in the reserve for trout initially caught outside and inside the reserve, respectively

spent more than 75% of their time in the reserve (Figure 3). Four individuals apparently did not visit the reserve during the study. The proportion of time spent in the reserve was not affected by fish length ($df = 55$, $p = 0.240$) or observation time ($df = 55$, $p = 0.373$). There was a marginally significant effect of season on time spent in the reserve ($df = 334$, $p = 0.0574$), where trout spent the least amount of time in the reserve during fall (34.4%) and the most in spring (46.0%). Furthermore, there was a significant interaction effect between home range size and capture location on the proportion of time spent in the reserve ($df = 223$, $p = 0.0029$). For trout captured within the reserve, home range size had a weak negative effect on proportion of time spent in the reserve (Figure 4). For trout captured outside the reserve, home range size had a stronger positive effect on proportion of time spent in the reserve (Figure 4). Including the identity of the trout as a random effect did not improve the model (ΔAIC = 1.88). Mean home range size was 0.430 km^2, ranged from 0.0675 to 2.14 km^2 (for examples, see Figure 5) and was not related to the number of PAVs calculated for a given month ($df = 221$, $p = 0.106$).

Sea trout made an average of 0.38 (±0.052 *SE*) excursions from the reserve every day, and 92.8% of excursions were made to the central fjord area MPA (Zone 4). Movement out of the reserve occurred significantly more often during the day (60%) than at night ($p < 0.001$). Number of daily excursions was not affected by fish length ($df = 51$, $p = 0.815$), body condition ($df = 50$, $p = 0.35$), or sex ($df = 46$, $p = 0.74$). However, the monthly number of excursions was significantly affected by season ($df = 322$, $p = 0.044$). Summer and spring were the most different ($p = 0.0765$, $SE = 1.89$) with the fewest number of monthly excursions in summer (4.04) and the most in spring (8.59). Fish with larger home range sizes did more excursions from the reserve ($df = 223$, $p < 0.001$). Including the identity of the trout as a random effect did not improve the models.

The 15 individuals (26.3%) that utilized outer fjord and sea areas and returned spent on average 86.1 (±28.0 *SE*) total days at sea, and the average length of one excursion was 34.0 (±9.12 *SE*) days. Combined for all seagoing fish, there was little difference in time spent at sea in the different seasons (Table 2), and time spent at sea was not affected by fish length ($df = 55$, $p = 0.115$), body condition ($df = 54$, $p = 0.28$), or sex ($df = 50$, $p = 0.21$). Sea trout almost exclusively spent time in Østeråbekken during the spawning season in fall, with some stays extending into winter. Average total time spent in the river was 37.0 (±8.92 *SE*) days per fish, with the average duration of one excursion being 24.6 (±5.79 *SE*) days.

A total of 35.1% of the sea trout were outside the study system at the end of tag life ($n = 20$), including the dispersed sea trout. Fish that dispersed to outer fjord and sea areas ($n = 12$) accounted for 21.1% of all tagged individuals. Fish length was close to having a significant positive effect on whether the trout dispersed from the fjord ($\beta_{\text{Length}} = 0.56$, $df = 55$, $p = 0.0722$). Body condition ($df = 54$, $p = 0.21$) and sex ($df = 50$, $p = 0.67$) did not affect dispersal. Time spent in the fjord by nondispersers was 96.6% (±1.4% *SE*), and the protection level afforded to all tagged sea trout by the current reserve was 32.3%.

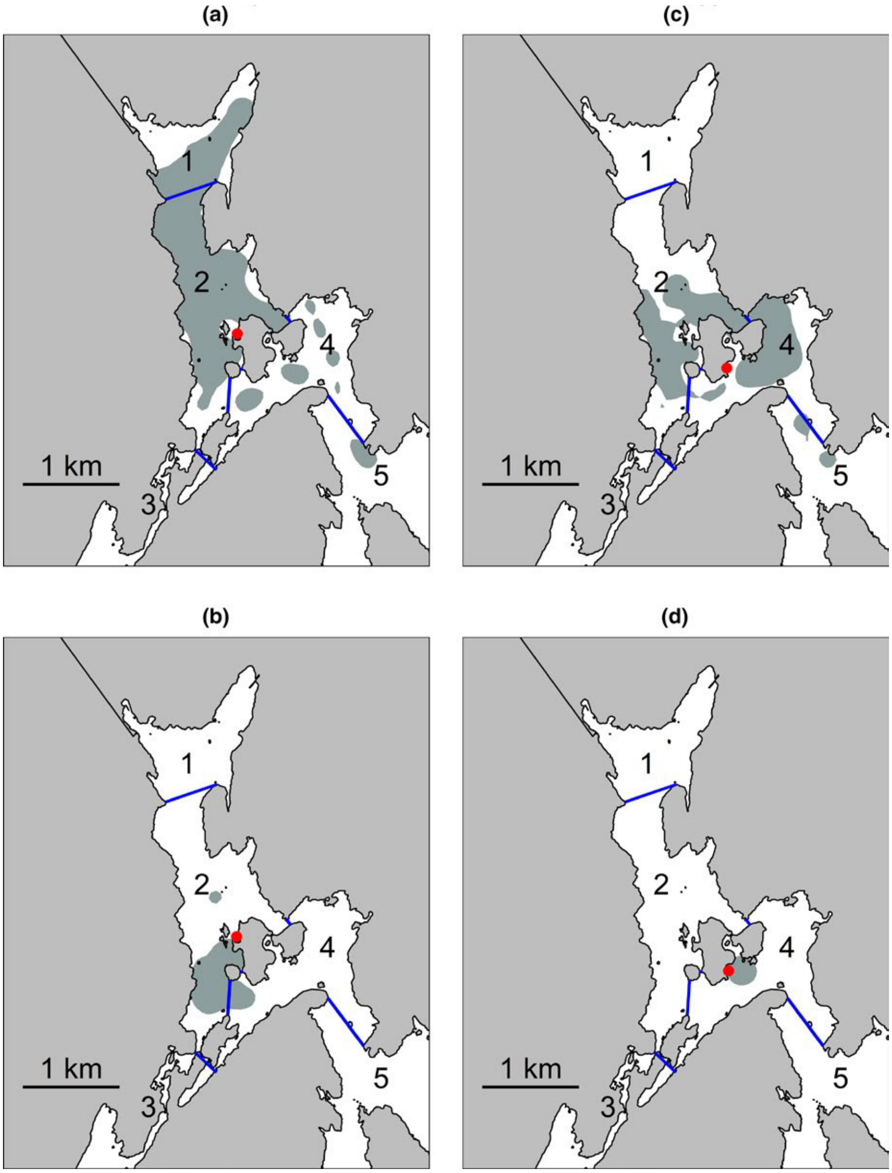

FIGURE 5 Examples of 95% home ranges of trout (a) with large home range caught inside the reserve, (b) with small home range caught inside the reserve, (c) with large home range caught outside the reserve and (d) with small home range caught outside the reserve. Blue lines delineate the zones, and red dots represent tagging locations. All home ranges are from May 2013 and selected among all tagged fish for illustrative purposes. The numbers on the map represent the different zones in the fjord

4 | DISCUSSION

This study evaluates factors determining the efficacy of a marine reserve for protecting anadromous brown trout. Overall, sea trout utilized the fjord extensively, spending only a quarter of their time in outer fjord and sea areas. While in the fjord, they spent on average 42% of their time inside the reserve, a proportion that corresponds to the size of the reserve relative to the study area. Sea trout caught within the reserve generally spent a larger proportion of their time within the reserve and for this group the effect of home range size on protection level was small, but slightly negative (Figure 4). In contrast, sea trout caught outside the reserve spent a smaller proportion of their time within the reserve and the effect of home range size was positive. Interestingly, this shows that home range size has a different effect on the amount of protection a sea trout receives from the reserve depending on capture location in the fjord.

TABLE 2 Days spent at sea (*n* = 15) and in Østeråbekken river (*n* = 14) by season

Season	Days at sea	Days in Østeråbekken
Spring	313	5
Summer	311	0
Fall	328	403
Winter	339	109

Protection afforded by a reserve might be influenced by movement and home range size, with wide ranging and bold individuals experiencing less protection from a reserve (Parsons, Morrison, & Slater, 2010). There may be a heritable component to home range size and dispersal, implying that different genotypes may receive different levels of protection from a reserve (Harrison et al., 2015). Accordingly, based on a study of cod home ranges, it was theorized that having a larger home range could result in higher exposure to fishing outside the reserve and lead to fishery induced selection toward smaller home ranges (Villegas-Ríos et al., 2016). In this study, we found that trout received a higher degree of protection with increasing home range size if initially captured outside the reserve (Figure 4). The different response to increasing home range size for individuals tagged within and outside the reserve indicates that if selection pressure toward smaller home ranges was to exist within the reserve, it can be opposed by the individuals outside the reserve. However, the selective landscape must be seen in concert with the selection pressure inflicted by angling in itself. Angling has been shown to select against boldness in carp (*Cyprinus carpio*) (Klefoth et al., 2017), and Alós et al. (2016) show that pearly razorfish (*Xyrichthys novacula*) individuals characterized by a high exploration intensity and a large home range radius are quickly removed from the population when exposed to an intense angling fishery. In total, abundance was reduced by 60% within a few days. In the present study, we do not present rates of fishing induced mortality and can thus only comment on the potential for protection within reserves. Also, potential selection on home range sizes within and outside the reserve may be limited if the tagged trout originate from different populations. We tagged sea trout within a limited area and assumed that most individuals belonged to the same gene pool.

Length, body condition, and sex of sea trout were not related to movement at sea, but size was close to having a significant positive effect on dispersal. The latter is in line with findings by Flaten et al. (2016) and Bordeleau et al. (2018), showing that female sea trout migrating to the outer fjord areas were larger than females migrating to inner fjord areas in Norwegian fjords. In contrast to our findings, an earlier study found that low body condition correlated with increased migration distance in sea trout, potentially for the purpose of maximizing feeding opportunities (Eldøy et al., 2015). Haraldstad et al. (2018) also found that poor condition correlated with an extended marine stay and skipped spawning migrations in sea trout in Skagerrak. Furthermore, home range size has been shown not to correlate with size for trout (Závorka, Aldvén, Näslund, Höjesjö, & Johnsson, 2015), and it has also been shown that migratory decisions in the fjord are not affected by size (del Villar-Guerra et al., 2014). Overall, our results imply that the reserve does not inflict a size-selective protection regime on the sea trout population within the fjord. In our study, the potential selectivity of the sampling location must be taken into account, as sampling was only conducted around the islands in the center part of the fjord (Figure 2) and not in the river or outer fjord and sea areas. Individuals that disperse from the fjord within a short time frame are less likely to have been sampled, and the length distribution and body condition of these fish is unknown. In general, individuals and behavioral types that mainly utilize the inner parts of the fjord or the outer fjord and sea areas are less likely to have been sampled.

Excursions from the reserve were mainly to Zone 4, which comprises the central fjord MPA. Movement between these zones is likely to represent random movements within a home range. However, the relatively few excursions to Zone 1, combined with the low proportion of time spent there (Table 1), may indicate that sea trout find the area outside the river inlet less favorable than the central part of the fjord. This may be related to higher availability of food further out in the fjord which has previously been suggested as a migratory decision characteristic (del Villar-Guerra et al., 2014) and an explanation for trout to spend less time in inner fjord areas (Morris & Green, 2012). Previously, low biodiversity has been observed at sampling stations in Zone 2, close to the border between Zone 1 and 2, indicating a reduced selection of prey for sea trout in this habitat (Kroglund, Dahl, & Oug, 1998). More likely, the low proportion of time spent in the inner part of the fjord is due to no individuals being tagged in this region. There were significantly more excursions from the reserve during day than night, implying greater horizontal movement during day. Salmonids have shown great differences in movement rates contrasting day and night (Alanärä, Burns, & Metcalfe, 2001; Candy & Quinn, 1999; Eldøy et al., 2017; Goetz, Baker, Buehrens, & Quinn, 2013), and it has been shown for steelhead trout (*Oncorhynchus mykiss*) that horizontal movement rates increase twofold during daylight compared to night in the marine habitat (Ruggerone, Quinn, Mcgregor, & Wilkinson, 1990). This may lead to a higher exposure to fishing during the day.

Sea trout resided in Østeråbekken stream almost exclusively during spawning season in fall, including some extended stays into the winter season. Also, sea trout spent significantly less time in the reserve during fall. This confirms the theories about spawning behavior previously documented for sea trout (Klemetsen et al., 2003; Knutsen, Knutsen, Olsen, & Jonsson, 2004; Olsen, Knutsen, Simonsen, Jonsson, & Knutsen, 2006).

Following the predictable spawning migration of sea trout, it can be expected that individuals receive protection from the reserve in the fjord while migrating to and from river spawning areas. A study on Arctic charr (*Salvelinus alpinus*) showed that an MPA located in a fjord, also encompassing the nearest spawning river, on average protected the tagged population one-third of the time (Morris & Green, 2012). In the present study, there were seasonal differences in reserve use, with sea trout spending a larger proportion of time in the reserve and performing most excursions from the reserve during spring, the latter indicating more horizontal movement in this period. Furthermore, protection extends to straying trout that arrive in the spawning river. In a study of how stocked sea trout uses nearby rivers, Degerman et al. (2012) suggest straying rates were twice as frequent for individuals stocked in small rivers as a consequence of less available habitat. Overall straying rates (including nonspawners) of up to 57% were observed, and temporary use of non-natal rivers occurred more often in large rivers (Degerman et al., 2012). This indicates that situating reserves in fjords with large spawning rivers may increase the number of individuals that receive protection from the reserve, and thus also protect individuals from nearby river and fjord systems during migrations. Further studies may reveal more detailed habitat preferences in sea trout, but previous studies indicate that individual fish exhibit highly variable movement patterns in marine areas (Middlemas, Stewart, Mackay, & Armstrong, 2009). However, sea trout have shown slower rates of movement away from spawning rivers than salmon (Finstad, Økland, Thorstad, Bjørn, & McKinley, 2005; Thorstad et al., 2007), thus spending more time in the fjord may improve protection by reserves.

Given their broad distribution and desirability in fisheries, there are a range of areas where implementation of reserves may be useful in maintaining sea trout populations. For example, populations are threatened by overfishing such as in the Gulf of Bothnia and the Gulf of Finland in the Baltic Sea (HELCOM, 2011). In these regions, sea trout are bycatch in other fisheries, such as whitefish and pikeperch, and fishing mortality may reach 80%. With high mortality rates occurring in fisheries, protection of fjord based populations or spawning areas may be crucial to sustaining sea trout populations.

In conclusion, this study revealed that even a relatively small no-take marine reserve has potential to protect the full home range of sea trout displaying small to intermediate home range size while residing in the marine habitat. Furthermore, sea trout initially tagged in the reserve received more protection than individuals tagged outside the reserve, while individuals tagged outside the reserve received more protection with increasing home range size. This attribute of the no-take/partially protected zone mosaic studied herein can potentially oppose the combined effects of “protection-induced selection” toward smaller home ranges within reserves—and angling-induced selection toward less bold behavior and smaller home ranges outside reserves. From a selection perspective, MPA and MPA network design can affect the selective landscape through which sea trout are moving during the marine phase. This perspective has important evolutionary implications for marine reserve and MPA network design. Although “Darwinian MPA design” requires good knowledge regarding key features of target species’ movement ecology and life histories, it is worthwhile to develop design criteria that will improve the protective qualities of spatial management measures and ensure long-term benefits to protected populations.

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AUTHOR CONTRIBUTIONS

All authors were involved in conceiving and developing ideas and designing methodology; EMO and EM collected the data; SHT analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data is available from the Dryad Digital Repository: http://doi.org/10.5061/dryad.fq3d127

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Selection on fish spatial personality differs between a no-take marine reserve and fished areas

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Abstract

Marine reserves can protect fish populations by increasing abundance and body size, but there is little knowledge on the effect of protection on fish behaviours. We looked for individually consistent behaviours, or personalities, in spatial use of sea trout in the marine habitat using acoustic telemetry, and investigated how personalities affect survival in relation to a marine reserve. We found individual consistency of 21 % in home range size for sea trout, indicating that this measure represents a personality trait. Survival differed for fish tagged within and outside a marine reserve, where individuals tagged inside the reserve experienced a decrease in survival with larger home ranges and individuals tagged outside the reserve experienced an increase in survival with larger home ranges. In line with previous studies showing that fishing selects against large home ranges, we suggest that a diversity of personality traits within populations of fish can be preserved by establishing networks of marine reserves encompassing different habitat types, ensuring both a heterogeneity in environmental conditions and fishing pressure.

Introduction

Fishing-induced evolution and the consequences for populations has now been extensively documented (Kuparinen and Festa-Bianchet, 2016). For example, selective fisheries can reduce population productivity through a shift towards maturation at earlier ages and smaller body sizes (Olsen et al., 2004; Kuparinen et al., 2016). However, fisheries-induced evolution on behaviour has received far less attention (Diaz Pauli and Sih, 2017). Interestingly, body size can be related to behavioural expression, and a selection regime targeting larger individuals may reduce the overall boldness in the population compared to a selection regime where small individuals are targeted (Biro and Post, 2008; Uusi-Heikkilä et al., 2015). Harvesting may also select directly on behaviour. Passive fishing gear can select against traits such as strong diel vertical migration and large home ranges (Olsen et al., 2012; Alós et al., 2016), while active fishing gear such as trawling may actually favour bolder individuals (Diaz Pauli et al., 2015; Andersen et al., 2018). Moreover, since the vulnerability to certain harvest conditions may vary from one fish species to another (Killen et al., 2015), species specific information on behavioural responses to fishing restrictions and protection will be important for management.

Interestingly, such behavioural selection processes may entail evolutionary consequences as long as the selected behavioural traits have a heritable basis. Consistent individual differences over time and through context, or personalities, are likely a result of a trade-off between mortality on one side, and growth and fecundity on the other (Wolf et al., 2007). Evolutionary modelling predicts that a spectrum of life-history strategies is concurrent with a spectrum of risk-taking and explorative behaviours that are stable over time. For example, individuals that invest more in future reproduction are expected to explore their environment more thoroughly and be less aggressive and bold, as they have more to lose

(Wolf et al., 2007). Assessing the heritability of behavioural traits may be difficult, and repeatability has been used as a proxy of it. Although not equivalent, recent studies have reported that it is a valid proxy (Dochtermann et al., 2015). Often, studies on repeatability of behaviour have been conducted in the lab, but in recent years, researchers have started to investigate repeatability of spatial behavioural traits in the wild (Harrison et al., 2014; Villegas-Ríos et al., 2017b). Such studies may be relevant to understand how behavioural variation is maintained in nature which in turn may provide useful input to adapting conservation strategies.

Marine reserves have long been used as a conservation tool to protect populations against depletion from fishing (Lester et al., 2009). While protecting fish abundance and body sizes (Baskett and Barnett, 2015), it is less known to which degree they help to preserve behavioural variation within populations by neutralizing fishing-induced selection. However, marine reserves may also result in unanticipated selection processes due to their spatial configuration in relation to the spatial movements of the individuals, which might ultimately erode expected benefits of marine reserves, e.g. spillover (Villegas-Ríos et al., 2017a). It is important thus to understand how selection may differ between harvested and protected areas and to what degree marine reserves may help in maintaining the behavioural diversity within populations which ultimately represent resilience to environmental change (Dingemanse et al., 2004). Here we focus on the former.

We used acoustic telemetry to quantify spatial behaviour of anadromous brown trout (*Salmo trutta*) in marine habitats in a Southern Norwegian fjord. We hypothesised that sea trout spatial behaviour, here quantified as the movement metrics home range, mean depth use, activity and diurnal vertical migration, was repeatable among individuals and represented an aspect of fish personality. Spatially-explicit management measures may alter the fitness of the individuals depending on how and where they move, which ultimately depend on their spatial behaviour. Therefore, we further hypothesised that survival in both fished and protected areas will differ among individuals.

Materials and methods

STUDY SPECIES

The brown trout (*Salmo trutta*) is a salmonid species in which the anadromous component of a population is referred to as sea trout. Sea trout has a highly variable life history with some individuals spending only summer at sea, and some spending most of their time in marine areas only returning to the river to spawn during fall and winter (Klemetsen et al., 2003). Marine migrations are motivated by access to more food, with important trade-offs being adjustment to different salinities, increased energetic cost of movement and a potentially higher predation risk (Thorstad et al., 2016). The balance of these trade-offs is likely an important part of the explanation for the range of migration strategies within populations (Thorstad et al., 2016) and population differentiation between streams (Knutsen et al., 2001; Olsen et al., 2006). Also, the balance of these trade-offs may change temporally within individual water systems and lead to coexistence of different migration strategies (Jonsson and Jonsson, 2011). In Norway, sea trout in marine locations can be caught only by hook-and-line equipment, except for one month in summer where specialised traps are permitted in the southern part of Norway.

STUDY SYSTEM AND DATA COLLECTION

Movement data was collected in the Tvedestrand fjord (3.8 km^2) located in southern Norway along the Skagerrak coast (Figure 1). A telemetry array consisting of 50 Vemco VR2-W receivers (VEMCO Ltd., Halifax, Canada) was deployed in the fjord, with the receivers being attached to moorings and kept at three m depth aided by sub-surface buoys (for more details, see Villegas-Ríos et al., 2017b). One receiver was located close to the spawning river, Østeråbekken, in order to monitor river migrations, and three receivers located in the outer part of the fjord served as a gate for monitoring marine stays in outer fjord and sea areas. The high density of receivers ensured a good coverage of the fjord. A marine protected area (1.5 km^2) prohibiting all types of fishing was established within the spatial coverage of the telemetry array in 2012. Fishing is also prohibited in Østeråbekken and up to 100 meters from the outlet of the stream.

Sea trout were caught around the centre islands of the fjord in 2013 (n = 60), 2015 (n = 22) and 2016 (n = 11) using a beach seine, and also by electrofishing in the spawning river at November 11, 2016 (n = 23). Beach seine was chosen in an attempt to minimise sampling-induced selection of particular behavioural types (Olsen et al., 2012). Electrofishing was added because of low catches in the beach seine. Individuals were anaesthetised with clove oil and a transmitter was inserted in the abdominal cavity (for details, see Olsen et al., 2012). We used Vemco V9P or Vemco V13P transmitters, which had a maximum lifetime of 701 and 1297 days, respectively. Signals were emitted with a random time lag of 120 ± 60 seconds. Accuracy and resolution of depth measurements were ± 2.5 m and 0.22 m, respectively, and max depth was 50 m and 68 m, respectively.

DATA PREPARATION AND ESTIMATION OF BEHAVIOURAL METRICS

Detections were downloaded from the receivers and processed using the VUE software (VEMCO Ltd., Halifax, Canada), and further data preparation and analyses were done in the R environment (R Core Team, 2018). All detections after presumed death were censored, which was defined to have occurred when continuing detections showed that horizontal and vertical movement had ceased (Olsen et al., 2012). Note that this could also represent transmitter loss. Fish were defined as dispersed after having followed a directional path out of the reserve with final detections occurring at the outermost receivers. Single detections within one day were removed to eliminate potential code collisions and false detections, and positive depth measurements were defined as NA. Four movement traits were used to describe the spatial behaviour in the marine phase: home range, mean depth use, activity and diurnal vertical migration. Monthly 95 % home ranges were calculated using locations based on position averages (PAVs, centres of activity), following Simpfendorfer et al. (2002). PAVs are mean locations within an array of receivers, based on the number of detections at each receiver during a specified time period (Simpfendorfer et al., 2002), in this case 30 minutes. Home ranges were then calculated from PAVs using Kernel Utilization Distributions (bandwidth = 60, extent = 0.5). Depth measurements were averaged over months after removing replicated measurements occurring when a signal is detected at more than one receiver. Following Freitas et al., (2015), activity was defined as the standard deviation of depth and was calculated hourly and then averaged over months. Diurnal vertical migration was calculated as the difference in mean depth from day to night within a calendar day and then averaged over months. Day and night phases were defined by solar elevation. Behavioural metrics were only calculated for months where the fish was present in the fjord for a minimum of 15 days (not necessarily consecutive), to make the estimate representative of monthly behaviour.

REPEATABILITY ESTIMATION

The variation in behaviour within a population is composed of variation within the individuals (short-term environmental variation and variation due to measurement error) and among the individuals (additive genetic variation and permanent environmental variation) (Dingemanse and Dochtermann, 2013). In behavioural ecology studies, repeatability is operationally defined as the proportion of the total variance that is explained by individual identity (Dingemanse and Dochtermann, 2013).

Univariate mixed effects models were fitted for each behavioural trait using the nlme package (Pinheiro et al., 2018) in R. For modelling purposes, home range and activity were log-transformed for normality. Monthly averages of each behavioural metric served as replicates for individual fish and individual sea trout identity was included as a random effect. We considered a trait to be repeatable when the inclusion of the random effect significantly improved the model fit. Provided that the random effect was supported, repeatability was calculated as:

$$Repeatability = \frac{V_{ind_0}}{V_{ind_0}+V_{e_0}} \qquad \text{(Eqn. 1)}$$

Where $V_{ind_0}$is the among-individual variance and V_{e_0} is the within-individual variance (Dingemanse and Dochtermann, 2013). Model selection was done in two steps: 1) selecting the overall model structure by assessing if including the identity of the fish as a random effect and temporal autocorrelation between months improved the model (method = restricted maximum likelihood), followed by 2) selecting the fixed effects structure (method = maximum likelihood). Model selection was done using AIC-values, and a minimum reduction of > 2 units was required to assign significant improvement. When two or more models received equivalent support, the model with the simplest structure was selected. Fixed effects included in the models were body length (standardised to mean = 0, SD = 1), season (categorical variable with four levels, as defined by the UK calendar with spring starting on March 1), sex and capture location (two levels: fjord or river). Sex was determined using a sex-determining marker loci based on Eisbrenner et al. (2014).

SURVIVAL

A survival curve was generated by computing a Kaplan-Meier estimator for right-censored data (Cox and Oakes, 1984) using the survival package in R (Therneau, 2015). Day of tagging was set to 0 for all individuals. Furthermore, linear modelling (LM) was used to assess the fixed effects of home range size and reserve use on survival (number of days alive after tagging). Reserve use was included in models either as the proportion of time spent in the reserve given that the fish was in the study area (calculated from PAVs), or as capture location (two levels: reserve or fished area), which served as a proxy for core area. Fish that were tagged on the river were excluded in this analysis. Both home range size and proportion of time spent in the reserve were calculated as the average of monthly estimates from tagging until death or end of study. Home range sizes were log-transformed for normality. As the most recent addition to the tagged population were tagged one year prior to the end of the study, the end of the survival period was set to one year for the analysis, with fish that dispersed before that time being excluded from the model. Thus, mean monthly averages were calculated based on one to 12 months. Additionally, the fixed effects fish length and season of capture (two levels: spring and fall) were also included in all models. Model selection was based on AIC and done in two steps: (1) selecting the best model structure related to the main variables of interest (home range size, proportion of time spent in reserve, tagging location) and (2) selecting the best model structure related to the additional covariates body length and season of capture.

Results

In total, 116 sea trout (mean body length: 337 mm, range: 215-635 mm) were caught, tagged and monitored in the Tvedestrand fjord during a 1669 day study period (spring 2013 – fall 2017). A total of 20 individuals were excluded from the study due to tag malfunction (n = 4), post-surgical mortality (n = 5) or limited presence in the study area (<14 days, n = 11). Time spent in the study ranged from 1 to 20 months. Initial data exploration revealed that sex had no effect on any behavioural trait. Including autocorrelation led to significant improvement of all models with a behavioural trait as the response variable (Tables 1-4).

Home range size was the only movement trait exhibiting significant repeatability (repeatability = 0.21), while mean depth use, activity and diurnal vertical migration did not (Tables 1-4). Mean monthly home range size was 0.407 km^2 (range: 0.065 - 2.14 km^2), increased with body length, and was larger for fish caught in the fjord than fish caught in the river (Table 1 & 5). Home range size was also affected by season, being the largest in spring, followed by fall and summer, and the smallest in winter (Table 1 & 5).

Analysis of monthly mean depth use (mean = 2.27 m, range: 0.35 - 9.44 m) showed that fish caught in the fjord swam deeper than fish caught in the river (Table 2 & 5). Mean depth use was also affected by an interaction between length and season. Mean depth use increased with body length and differed between seasons, with fish being located at more shallow depths during fall compared to all other seasons. The interaction between length and season indicated a stronger positive effect of body length on mean depth use in summer, followed by spring, winter and fall (Table 5).

Activity (standard deviation of depth; mean = 0.47 m, range: 0.018 - 3.67) increased with length and was higher for fish caught in the fjord (Table 3 & 5). Activity differed between the seasons, and fish were most active during spring and summer, and least active during fall and winter (Table 3 & 5).

Diurnal vertical migration (mean = 0.95 m, range: -0.75 - 5.08) was larger for fish caught in the fjord than fish caught in the river, and was affected by an interaction between length and season (Table 4 & 5). Diurnal vertical migration increased with body length and differed between seasons, with fish having a larger daily movement span during spring and summer than in winter and fall. The interaction between length and season indicated a stronger positive effect of body length on diurnal vertical migration in spring and summer than in winter and fall (Table 4 & 5).

Estimated median survival occurred after 323 days (10.8 months, Figure 2). At this point in the curve, estimated survival was 0.494 (95 % CI 0.392 - 0.623). The best model for predicting days of survival included average monthly home range size, capture location and the interaction between these, in addition to season of tagging (Table 6, df = 49, $R^2 = 0.133$). In the first step of the model selection, the model with an interaction effect between home range and proportion of time spent in the reserve was not significantly different from the model with an interaction effect between home range and capture location ($\Delta AIC < 2$). The latter model was chosen due to its reduced complexity. Home range size had a negative impact on survival for trout tagged in the reserve, while it had a positive impact on survival for trout tagged in the fished area (Table 7,

Figure 3). Survival was higher for fish tagged in the fall than fish tagged in the spring.

Discussion

Our study of sea trout behaviour in the marine environment revealed individual consistency in home range size over a period of several months/years, reflecting that home range can be considered an aspect of the spatial personality of sea trout. Further, we found that home range size correlated with survival, and this relationship differed between individuals having a core home range inside the reserve versus in the fished area. For individuals caught in the reserve, an increase in monthly average home range size led to decreased survival, while individuals caught in the fished area experienced increased survival with increasing home range size. In other words, the fitness landscape of sea trout appears to be influenced by spatial management, here represented by a no-take marine reserve. As discussed below, this suggests that fish behaviour could evolve in response to conservation.

We found that home range size had a repeatability of 0.21, indicating that about a fifth of the variation in home range size is variation that occurs between the individuals. This is not unexpected given that mean repeatability of behavioural traits was reported to be 0.37 (Bell et al., 2009). Moreover, our results confirm previous studies showing repeatable home range in wild fish (0.43 for Atlantic cod *Gadus morhua*; Villegas-Ríos et al., 2017b; 0.33 for burbot *Lota lota*; Harrison et al., 2014) suggesting that consistent spatial behaviour may be a general pattern for aquatic organisms. In accordance with estimates of how much additive genetic variation contributes to personality, Dochtermann et al., (2015) estimated that the ratio of heritability to repeatability collected from literature averaged at 0.52 and ranged from 0 to 0.96 (Dochtermann et al., 2015). Repeatability was not detected for any depth related trait. An apparent disadvantage of the registration of depth use in this study was that trout mainly utilised shallow depths, giving little room for detecting, if present, fine scale differences in depth use with our given accuracy and resolution of depth measurements. In future studies of fine scale depth use of sea trout, tags with higher resolution would be advisable. Furthermore, other behavioural traits that could be investigated for individual consistency in sea trout could be activity as measured by accelerometer tags, providing high resolution measurements of fish acceleration across three axes.

Our main finding is that the effect of home range size on survival differed between the protected and the unprotected population. For trout caught in the fished area, days of survival increased with increasing home range. This may be explained by fish with larger home ranges having a higher probability of being located in the reserve where it will receive protection from fishing. Note that this is the opposite pattern as previously found by Alós et al. (2016) who reported selection against large home ranges in harvested areas; but the main difference is that the harvested area in our study is adjacent to a marine reserve that may serve as a refuge for fish and that fundamentally alters the fitness landscape for the sea trout living in it. For trout caught in the reserve, the opposite pattern was observed: days of survival decreased with increasing home range, following that a large home range implies a higher probability of being located in the fished area. It was recently hypothesised that the consistent removal of fish that strand out beyond reserve boundaries may eventually lead to selection against large home ranges in marine reserves (Villegas-Ríos et al., 2017a). These findings, combined with the fact that home range is repeatable, and likely heritable (Dochtermann et al., 2015), may entail profound evolutionary consequences for populations residing in relation to a marine reserve.

Body length affected all movement traits, with larger fish having larger home ranges, utilizing a larger range of depths and having a higher activity. The same pattern was true for fish tagged in the sea as opposed to fish tagged in the river. Home ranges were the largest in spring, and fish were more active during spring and summer than fall and winter. This is in accordance with sea trout intensifying their food search as temperatures increase during spring and summer (Klemetsen et al., 2003). Fish also swam deeper during spring and summer, which can be associated both with different habitat use and that the trout seek out colder water temperatures optimal for growth when surface temperatures rise (Eldøy et al., 2017; Kristensen et al., 2018).

Survival is higher in the river as compared to sea (Solomon, 2006), and the duration of migration varies both within populations and among populations and latitudes (Klemetsen et al., 2003). This implies that yearly survival will vary substantially between river systems. Return rates from 193 sea trout tagged in the nearby river Storelva (< 5 km from our study system) revealed 40 % survival for trout spending one or two years at sea (Haraldstad, 2015). The fact that survival was higher for fish tagged in the fall could be explained by the upcoming spawning ascent, where sea trout received protection from fishing and experienced a lower predation risk in the river (Thorstad et al., 2016). Median survival in the wild was close to 11 months. Survival may have been underestimated due to tag excretion, which would have led individuals to be falsely defined as dead. Also, there might be a negative effect of tagging on survival. A study on gastrically tagged salmonids found that small (9 mm) and large (13 mm) tags reduced survival from 94 % in the control group to 90 % and 72 %, respectively. (Kennedy et al., 2018). However, there are differences in tagging procedures between this study and the present study, including tag positioning, time from capture to tagging and type of sedation agent, that may have had different unconsidered effects on survival.

Interestingly, fish with different personalities adjust their behaviour differently when faced with environmental change (Závorka et al., 2015; Villegas-Ríos et al., 2018). Reactive fish (being less bold, exploratory and aggressive than proactive fish) reduced their home ranges in response to increasing temperature, while proactive maintained, or even slightly increased theirs (Villegas-Ríos et al., 2018). This could further enhance the effect of fishing-induced selection towards smaller home range sizes for proactive fish. A field study of trout in the stream revealed that trout with low activity showed increasing growth rates with increasing home range size, while high activity individuals had lower growth with increasing home range size (Závorka et al., 2015). Here, personality scoring was made in the lab prior to the field study, and it was assumed that the increase in home range size for low activity individuals was a response to reduced food availability. These examples show some disadvantages of reduced plasticity when facing environmental change that are likely to affect proactive individuals. Consequently, preserving a spectrum of different personalities will help sustaining a population's resistance to environmental change, as different personalities are favoured across variable environmental conditions (Dingemanse et al., 2004). Accordingly, spreading fishing effort over a range of habitats could reduce capture bias even more, as different environmental conditions favour different behaviours (Killen et al., 2016). Moreover, a study of wild-collected guppy populations showed that reproductive behaviour diversified in populations that were exposed to heterogeneity in predator biomass (Barbosa et al., 2018). By rearranging reserve locations across years, managers can also use reserves to provide temporal heterogeneity in “predator biomass”.

Our results have clear managerial consequences. The fact that spatial behaviour may affect survival differently inside and outside marine reserves implies that ideally, a mosaic of marine reserves and areas (partially) open to harvest, hereby representing a variation in fishing pressure, can provide a heterogeneous selection regime that can oppose selection in any one direction.

Figures and tables

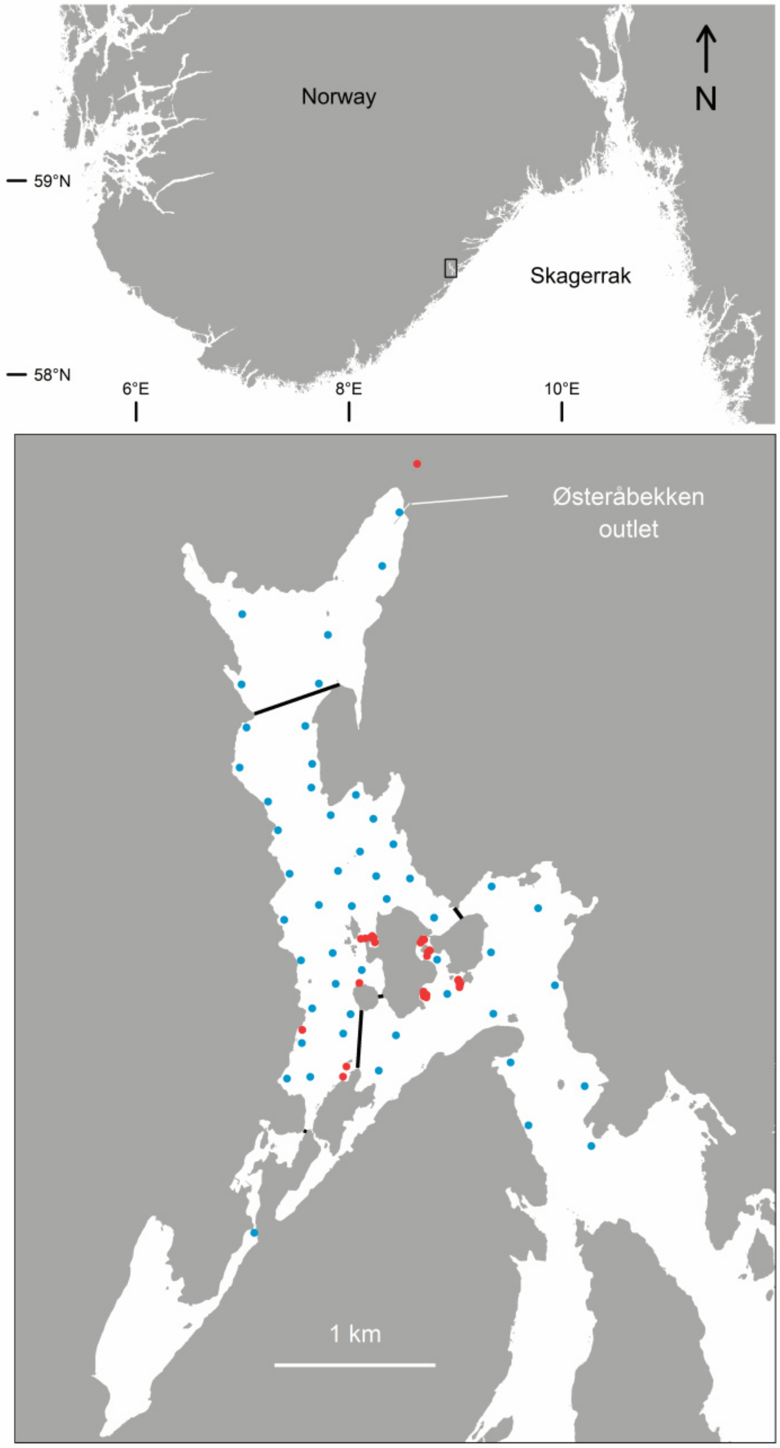

Figure 1 Map of the Tvedestrand fjord (below) and its location along the Norwegian Skagerrak coast (above). The marine reserve in the centre of the fjord is delineated with black lines. Blue dots represent receiver locations and red dots represent capture locations.

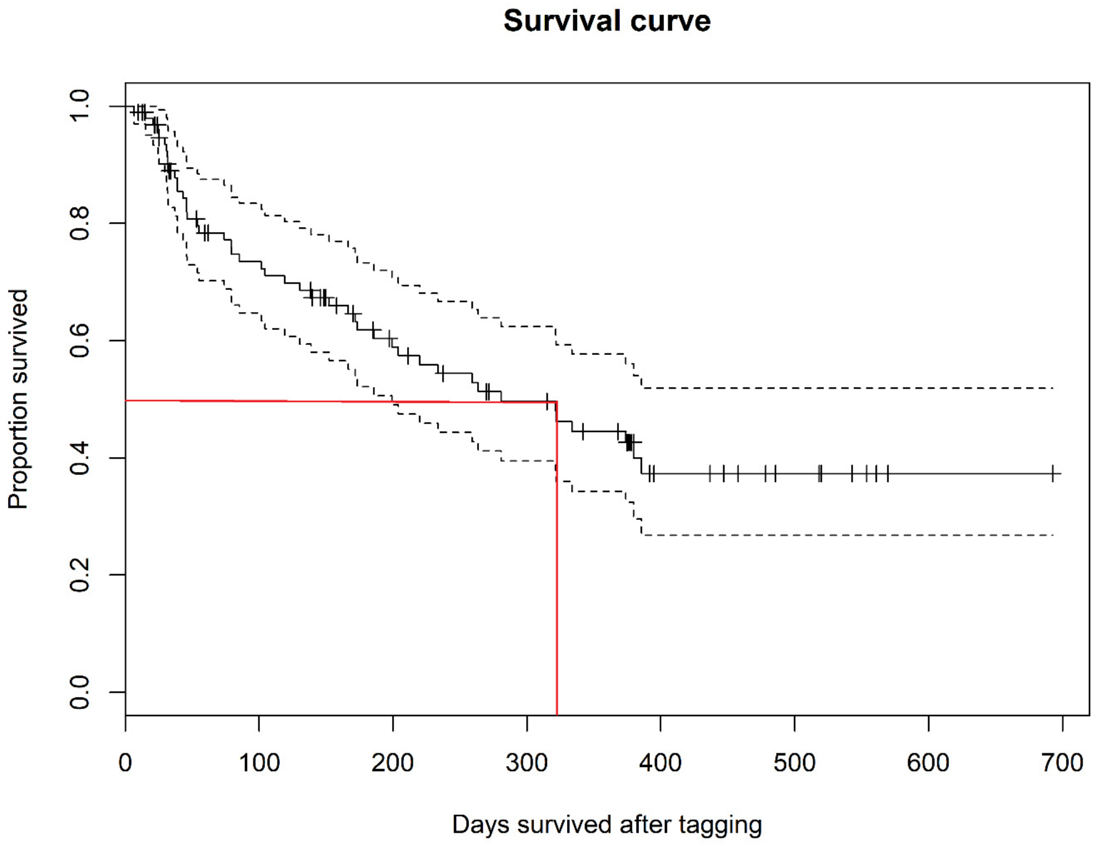

Figure 2 Right-censored Kaplan-Meyer survival curve for sea trout in the Tvedestrand fjord. Red lines show median survival at 323 days. Tagging day was set to zero for all individuals.

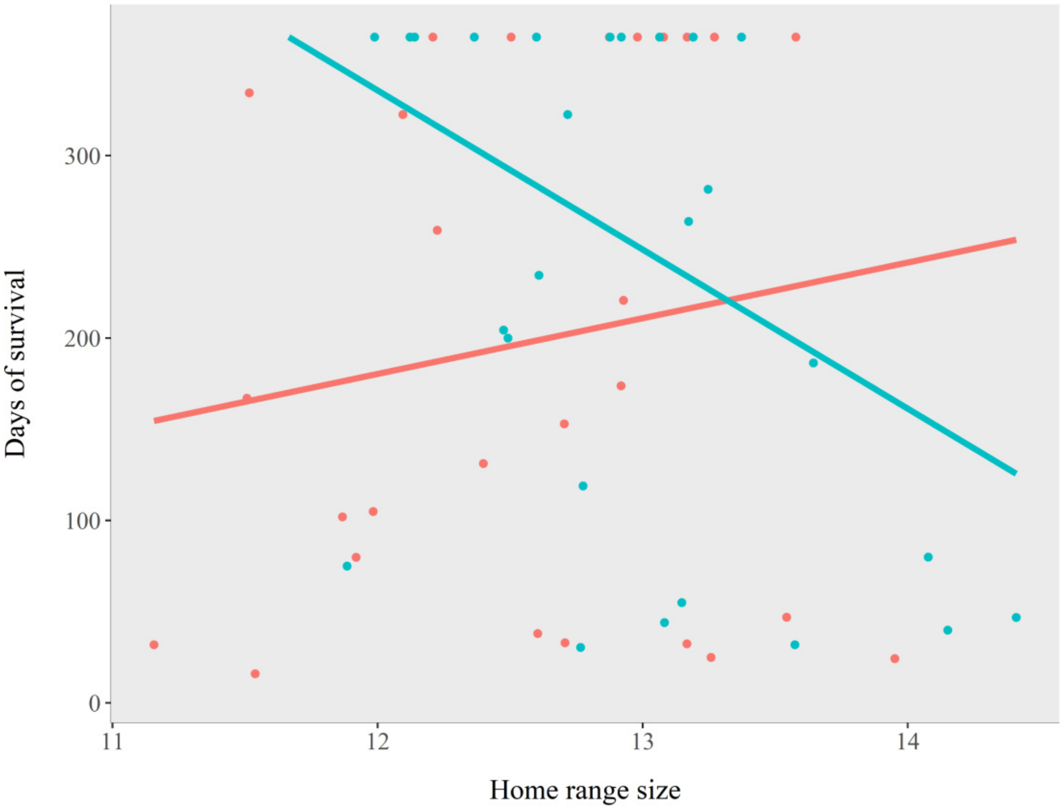

Figure 3 Days of survival as an effect of average monthly 95 % home range size. Red and blue dots represent trout initially caught outside and inside the reserve, respectively. The red and blue lines show the predicted relationship between home range and days of survival for trout initially caught outside and inside the reserve, respectively. Trout tagged in spring had lower survival than trout tagged in fall, but this effect is averaged in the figure.

Table 1 Model selection for response variable home range size (log-transformed for normality). The random effects and correlation structure is selected in the first step and the fixed effects structure is selected in the second step. Model selection was done using AIC values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	**Home range = β_0 + β_1 * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**795.54**
2	Home range = β_0 + β_1 * Season * β_2 * Length * β_3 * Capture location + $COR_{Month\|Fish\ ID}$	801.62
3	Home range = β_0 + β_1 * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID	810.23
No	(2) Model structure	AIC
1	Home range = β_0 + β_1 * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID + COR_{Month}	775.48
4	**Home range = β_0 + β_1 * Season * β_2 * Length + β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**766.89**
5	Home range = β_0 + β_1 * Season * β_3 * Capture location + β_2 * Length + b_1 * Fish ID + COR_{Month}	771.34
6	**Home range = β_0 + β_1 * Season + β_2 * Length * β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**767.72**
7	**Home range = β_0 + β_1 * Season + β_2 * Length + β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**767.07**
8	Home range = β_0 + β_1 * Season + β_2 * Length + b_1 * Fish ID + COR_{Month}	772.43
9	Home range = β_0 + β_1 * Season + β_3 * Capture location + b_1 * Fish ID + COR_{Month}	769.15
10	Home range = β_0 + β_2 * Length + β_3 * Capture location + b_1 * Fish ID + COR_{Month}	783.78

Table 2 Model selection for response variable mean depth use. The random effects and correlation structure is selected in the first step and the fixed effects structure is selected in the second step. Model selection was done using AIC values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	**Mean depth use = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**1049.80**
2	**Mean depth use = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $COR_{Month \mid Fish\ ID}$**	**1050.10**
3	Mean depth use = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location	1113.08
No	(2) Model structure	
2	Mean depth use = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $COR_{Month \mid Fish\ ID}$	1043.77
4	**Mean depth use = $\beta_0 + \beta_1$ * Season * β_2 * Length + β_3 * Capture location + $COR_{Month \mid Fish\ ID}$**	**1032.67**
5	Mean depth use = $\beta_0 + \beta_1$ * Season * β_3 * Capture location + β_2 * Length + $COR_{Month \mid Fish\ ID}$	1041.66
6	Mean depth use = $\beta_0 + \beta_1$ * Season + β_2 * Length * β_3 * Capture location + $COR_{Month \mid Fish\ ID}$	1039.60
7	Mean depth use = $\beta_0 + \beta_1$ * Season + β_2 * Length + β_3 * Capture location + $COR_{Month \mid Fish\ ID}$	1037.91

Table 3 Model selection for response variable activity (log-transformed for normality). The random effects and correlation structure is selected in the first step and the fixed effects structure is selected in the second step. Model selection was done using AIC values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	**Activity = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID + $\mathrm{COR}_{\mathrm{Month}}$**	**565.60**
2	**Activity = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$**	**563.60**
3	Activity = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location	651.77
No	(2) Model structure	
2	Activity = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	534.32
4	Activity = $\beta_0 + \beta_1$ * Season * β_2 * Length + β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	524.00
5	Activity = $\beta_0 + \beta_1$ * Season * β_3 * Capture location + β_2 * Length + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	525.72
6	**Activity = $\beta_0 + \beta_1$ * Season + β_2 * Length * β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$**	**522.79**
7	**Activity = $\beta_0 + \beta_1$ * Season + β_2 * Length + β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$**	**521.58**
8	Activity = $\beta_0 + \beta_1$ * Season + β_2 * Length + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	525.96
9	Activity = $\beta_0 + \beta_1$ * Season + β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	539.82
10	Activity = $\beta_0 + \beta_2$ * Length + β_3 * Capture location + $\mathrm{COR}_{\mathrm{Month\mid Fish\ ID}}$	539.56

Table 4 Model selection for response variable diurnal vertical migration. The random effects and correlation structure is selected in the first step and the fixed effects structure is selected in the second step. Model selection was done using AIC values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	**Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + b_1 * Fish ID + COR_{Month}**	**680.83**
2	**Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $COR_{Month\mid Fish\ ID}$**	**678.83**
3	Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location	730.25
No	(2) Model structure	
2	Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_2 * Length * β_3 * Capture location + $COR_{Month\mid Fish\ ID}$	662.17
4	**Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_2 * Length + β_3 * Capture location + $COR_{Month\mid Fish\ ID}$**	**650.85**
5	Diurnal vertical migration = $\beta_0 + \beta_1$ * Season * β_3 * Capture location + β_2 * Length + $COR_{Month\mid Fish\ ID}$	659.87
6	Diurnal vertical migration = $\beta_0 + \beta_1$ * Season + β_2 * Length * β_3 * Capture location + $COR_{Month\mid Fish\ ID}$	658.81
7	Diurnal vertical migration = $\beta_0 + \beta_1$ * Season + β_2 * Length + β_3 * Capture location + $COR_{Month\mid Fish\ ID}$	656.86

Table 5 Summary of selected linear mixed effects- and lme models explaining movement behaviour in sea trout. Associated parameter estimates, standard errors (S.E.), degrees of freedom (df) and p-values are given. The table continues on to the next page.

Response	**Parameter**	**Estimate**	**S.E.**	**df**	**p-value**
Home range	Intercept	12.1	0.224	272	< 0.001
	Length	0.134	0.0666	75	0.048
	Capture location, Fjord	0.604	0.224	75	0.0086
	Season, Winter	-0.342	0.123	272	0.0058
	Season, Spring	0.177	0.118	272	0.135
	Season, Summer	-0.145	0.111	272	0.193
Mean depth	Intercept	0.678	0.331	324	0.0415
	Length	0.127	0.152	324	0.404
	Capture location, Fjord	0.996	0.326	324	0.0024
	Season, Winter	0.487	0.219	324	0.0268
	Season, Spring	0.881	0.203	324	< 0.001
	Season, Summer	0.827	0.190	324	< 0.001
	Season, Winter: Length	0.133	0.227	324	0.560
	Season, Spring: Length	0.441	0.213	324	0.0395
	Season, Summer: Length	0.671	0.206	324	0.0012

Response	**Parameter**	**Estimate**	**S.E.**	**df**	**p-value**
Activity	Intercept	-1.67	0.174	322	< 0.001
	Length	0.251	0.0536	322	< 0.001
	Capture location, Fjord	0.445	0.175	322	0.0114
	Season, Winter	-0.0953	0.105	322	0.364
	Season, Spring	0.317	0.0977	322	0.0013
	Season, Summer	0.339	0.0896	322	< 0.001
Diurnal vertical migration	Intercept	0.00313	0.231	279	0.989
	Length	0.155	0.103	279	0.133
	Capture location, Fjord	0.475	0.224	279	0.0348
	Season, Winter	0.00867	0.156	279	0.956
	Season, Spring	0.716	0.144	279	< 0.001
	Season, Summer	0.643	0.138	279	< 0.001
	Season, Winter: Length	0.0835	0.155	279	0.590
	Season, Spring: Length	0.476	0.143	279	0.001
	Season, Summer: Length	0.280	0.140	279	0.046

Table 6 Model selection for estimating days of survival for the sea trout. First, the best model structure related to the main variables of interest (home range size, proportion of time spent in reserve, tagging location) was selected, followed by selection of the best model structure related to the additional covariates body length and season of capture. Model selection was based on AIC-values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	Days of survival = $\beta_0 + \beta_1$ * Home range + β_4 * Body length + β_5 * Season of capture	689.01
2	Days of survival = $\beta_0 + \beta_2$ * Prop. of time in reserve + β_4 * Body length + β_5 * Season of capture	689.24
3	Days of survival = $\beta_0 + \beta_3$ * Capture location + β_4 * Body length + β_5 * Season of capture	754.03
4	**Days of survival = $\beta_0 + \beta_1$ * Home range * β_2 * Prop. of time in reserve + β_4 * Body length + β_5 * Season of capture**	**684.11**
5	Days of survival = $\beta_0 + \beta_1$ * Home range + β_2 * Prop. of time in reserve + β_4 * Body length + β_5 * Season of capture	690.89
6	**Days of survival = $\beta_0 + \beta_1$ * Home range * β_3 * Capture location + β_4 * Body length + β_5 * Season of capture**	**685.45**
7	Days of survival = $\beta_0 + \beta_1$ * Home range + β_3 * Capture location + β_4 * Body length + β_5 * Season of capture	687.80
	(2) Model structure	
6	Days of survival = $\beta_0 + \beta_1$ * Home range * β_3 * Capture location + β_4 * Body length + β_5 * Season of capture	685.45
8	**Days of survival = $\beta_0 + \beta_1$ * Home range * β_3 * Capture location + β_5 * Season of capture**	**685.66**
9	Days of survival = $\beta_0 + \beta_1$ * Home range * β_3 * Capture location + β_4 * Body length	688.78
10	Days of survival = $\beta_0 + \beta_1$ * Home range * β_3 * Capture location	689.10

Table 7 Parameter estimates with associated standard errors (S.E.) and p-values for the model predicting days of survival for sea trout.

Parameter	**Estimate**	**S.E.**	**p-value**
Intercept	-143.30	447.10	0.75
Home range	30.57	35.58	0.39
Capture location, Reserve	1569.25	681.74	0.026
Season of tagging $_{\text{Spring}}$	-86.46	37.92	0.027
Home range : Capture location $_{\text{Reserve}}$	-117.82	53.20	0.0315

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Drivers and individual consistency of sea trout (*Salmo trutta*) activity in the wild

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Abstract

Consistency in individual behaviour, or personalities, of fish can be investigated in the wild by means of acoustic telemetry tracking. Using tags measuring acceleration, we investigated activity patterns of 15 sea trout in a Southern Norwegian fjord and found variation in behaviour relating to both individual identity and environmental conditions. Firstly, we found 38 % of the variation in sea trout activity was explained by individual identity. Furthermore, sea trout activity varied across the hours of the day, being higher during daylight hours. This pattern changed with temperature, and periods of higher activity increased both in intensity and duration as temperatures increased. Accelerometer tags provide a high-resolution measure of activity and can potentially be used to assess fish personality directly in the wild.

Introduction

There are selective advantages of individual consistency in behaviour, or personality, arising through trade-offs between survival and reproduction (Wolf et al., 2007). Individuals that invest more in future reproduction than their conspecifics will have an advantage off adapting a more risk-averse behaviour, reducing the chances of an early death, and vice versa (Wolf et al., 2007). In turn, behavioural variation increases the resilience of the populations to environmental change in for example resource abundance, population density and predation risk, where different conditions will favour different behavioural strategies (Wolf et al., 2007; Dingemanse and Réale, 2013).

Harvest selection on fish behaviour has been observed. Indirectly, this could happen through selection on physical traits that are in turn correlated to behavioural traits. For instance, a laboratory experiment revealed that size-selective harvesting resulted in adaption towards less explorative and bold behaviour in zebrafish (*Danio rerio*) (Uusi-Heikkilä et al., 2015). Direct selection on behaviour has also been documented. Examples include passive fishing gear like traps and hook-and-line that select against large home ranges (Alós et al., 2016) and strong diel vertical migration (Olsen et al., 2012), and active methods like trawling that can select for boldness (Diaz Pauli et al., 2015) and swimming performance (Killen et al., 2015). Interestingly, harvest selection on behaviour can have consequences for population productivity in the long run, as bolder fish have higher growth rates (Biro and Post, 2008). Also, selection on one behavioural type could reduce the resilience of the population to environmental change.

Recent research has revealed individual consistency also in the behaviour of fish (Kortet et al., 2014; Alós et al., 2016; Byrnes and Brown, 2016; Näslund and Johnsson, 2016; Villegas-Ríos et al., 2017).

Previous studies of consistency in movement behaviour of fish in the wild were often based on acoustic telemetric methods (Harrison et al., 2014; Alós et al., 2016; Villegas-Ríos et al., 2017). From a network of receivers one can calculate fish positions that can be later used to estimate behavioural traits such as home range. Fish telemetry can also provide depth information, which has been previously used to investigate diel patterns of migration and water column use, but also activity patterns. For instance, activity has been estimated as the standard deviation of depth (Freitas et al., 2015) However, such a measure of activity is not direct and may not be applicable to all aquatic animal species, especially those with a limited vertical movement (e.g. species that move close to the bottom). Recent advancements in the field of acoustic telemetry include tags that measure acceleration, a more direct proxy of activity. This enables the study of fine scale movement patterns across time and space and provides a useful measure of individual activity for a wider range of fish species. Interestingly, such measures of activity can be linked to reproductive or feeding behaviour (Brownscombe et al., 2014) and fleeing events (Noda et al., 2013), and differing activity patterns across varying habitats (Taylor et al., 2018).

The brown trout (*Salmo trutta*), including its anadromous component called sea trout, is a salmonid species with a highly variable life history, largely determined by migratory decisions (Klemetsen et al., 2003). Migration to sea occurs after spawning in fall, and is largely motivated by food availability (Thorstad et al., 2016). Sea trout increase their feeding activity during spring and summer, as temperatures are rising (Klemetsen et al., 2003). Moreover, consistency in swimming activity and aggression have been shown in lab studies of juvenile sea trout (Adriaenssens and Johnsson, 2013; Näslund and Johnsson, 2016), but estimates of repeatability in mature sea trout in the wild for those or other behavioural traits are scarce.

We hypothesised that activity levels are consistent between individual trout, hereby indicating differences in personalities. Further, since activity is normally influenced by a variety of environmental variables (Freitas et al., 2015; Killen et al., 2016), we also hypothesised that sea trout activity would vary across the day and with temperature. To test these hypotheses, we tagged 15 sea trout with acoustic telemetry accelerometer tags to investigate movement activity of sea trout in the marine environment. Our results suggest that sea trout activity in the wild is strongly dependent on the surrounding environment but also holds a considerable degree of variation between individuals.

Materials and methods

STUDY SYSTEM AND DATA COLLECTION

The study was conducted within a network of 50 VR2W receivers deployed in the Norwegian fjord, Tvedestrand fjord, situated along the Skagerrak coast (Fig. 1). The network covers approximately 3.8 km^2, and includes one receiver positioned by the inlet of the main spawning stream, Østaråbekken, to register migrations between salt- and fresh water. Receivers where submerged and positioned at ~ 3 m depth, where they were held in place aided by moorings and sub surface buoys. Temperature was measured hourly at 1 m at one location in the fjord and averaged over days.

Sea trout (n = 15) were caught after spawning using electrofishing in the spawning stream on November 20, 2017. The fish were collected and stored in a tank on site, equipped with an oxygen pump supplying a continuous flow of oxygen. Fish were anaesthetised using a 9:1 ethanol - clove oil solution added at 2 mL per 5 L of water. Then they were tagged with VEMCO V13AP transmitters (VEMCO Ltd., Halifax, Canada), positioned in the abdominal cavity, following Olsen et al. (2012), before being released in the river upon resuming swimming activity. The tags measure acceleration (ms^{-2}) at a sampling frequency of 10 Hz across three axes (x, y, z) for a time period of 33 seconds and calculates the root mean square (RMS) of these measurements averaged over time, T (Eq. 1).

$$ms^{-2} = \frac{\sqrt{x^2+y^2+z^2}}{T} \qquad \text{(Eq. 1)}$$

These acceleration measurements served as a proxy for sea trout activity level in the wild. Time lag between signals is 180 ± 50 and the acceleration range the tags can sample is ± 3.43 ms^{-2}. Estimated tag life is 364 days.

DATA PREPARATION, ANALYSIS AND STATISTICAL MODELS

The detection and acceleration data was downloaded from the receivers and processed in VUE software (VEMCO Ltd., Halifax, Canada). An individual was defined as dead when acceleration measurements were zero or near zero (< 0.1 ms^{-2}) for a long period without increasing again. Data analysis was performed in the R environment (R Core Team, 2016).

We used a generalised additive mixed effects model (GAMM) to investigate drivers of variation of acceleration of sea trout. Acceleration, the response variable, was averaged per hour and log-transformed to meet normality assumptions. To detect any influence of temperature on the shape of the relationship between acceleration and hour of day, the explanatory variables temperature and “hour of day” were included in the model as a tensor product (continuous by continuous interaction).

Fish identity was included as a random effect and a variable representing hours since the start of the study was included to account for temporal autocorrelation.

Repeatability (Eq. 2) of acceleration was calculated following Dingemanse and Dochtermann (2013), and represents the share of total variance in acceleration that is attributable to between-individual variance, V_{ind_0}. $V_{e_0}$is within-individual variance.

$$Repeatability = \frac{V_{ind_0}}{V_{ind_0}+V_{e_0}} \qquad \text{(Eq. 2)}$$

Variance components for the repeatability estimation were calculated using a linear mixed effects model (LMM). For the response variable daily average acceleration, only detections made during day were used, to avoid bias due to potential differences in detection rates between day and night. Day was defined by solar elevation, and days with < 15 detections were excluded from the study. Acceleration averages were log-transformed to meet normality assumptions. The fixed effects temperature and fish length (scaled and centred: mean = 0, SD = 1) was included in the model. Individual identity was included as a random effect and must represent a significant improvement of the model for the trait to be considered repeatable. A variable representing day since the start of the study was included to account for temporal autocorrelation. After assessing the overall model structure related to random effects and autocorrelation (method = restricted maximum likelihood), we proceeded with model selection of fixed effects (method = maximum likelihood).

Model selection was based on AIC-values, and significant improvement was awarded following a minimum reduction of > 2 AIC-units. When two or more models received the same support, the model with the simplest structure was selected. To assess the dispersion in the acceleration measures used to calculate daily averages, coefficients of variance were calculated for each daily activity measure.

Results

Fifteen sea trout (mean body length: 36 cm, range: 32 - 42 cm) were caught in Østeråbekken and tagged with acoustic transmitters in November 2017. Three individuals were not included in the study, as they had either few (n = 1) or no (n = 2) detections in the fjord. Number of days that the different individuals were detected in the study area ranged from one to 155, which marks the end of the study period. During the study, 42412 acceleration measurements were registered, 96 % of which came from five individuals. Hourly averages of acceleration ranged between 0.0272 and 3.46 (S.E. = 0.00344) (Figure 2). Daily estimates of activity ranged from 0.0666 – 1.55 ms^{-2} and had an average of 0.415 ms^{-2} (Figure 4). Coefficients of variance associated with averages of daily acceleration ranged from 0.275 – 2.65 and averaged to 0.942. Day length ranged from 6.28 – 15.27 h, and temperature ranged from 0.45 – 11.73 °C.

The GAMM investigating drivers of variation of acceleration yielded a significant effect of the interaction between hour of day and temperature (Table 1), meaning that the diel pattern of variation in acceleration depended on temperature. Generally, acceleration was higher around midday and increased with temperature. At lower temperatures differences in acceleration between midnight and midday were much more pronounced as compared to higher temperatures, when the variation of acceleration across the day was less pronounced (Fig. 3).

Including individual identity as a random effect led to significant improvement of the model predicting activity of sea trout in the wild (Table 2). Repeatability of activity as approximated by acceleration was 0.38. Temperature was included as a fixed effect in the final model, and as in the GAMM, it had a positive effect on activity (Table 3). Including temporal autocorrelation significantly improved the model.

Discussion

Using acoustic telemetry tags measuring acceleration, we were able to detect consistent individual differences in activity of sea trout, and find that activity varied with time of day and temperature. Repeatability of activity was 0.38, meaning that 38 % of the variation in this behavioural trait is attributable to individual identity. This estimate is in line with meta-analyses reporting that on average 37 % of the variation occur between individuals (Bell et al., 2009). Furthermore, on average, half of the variation between individuals is reported to be genetically founded, indicating that there could be a heritable component to sea trout activity (Dochtermann et al., 2015).

Consistent individual differences in activity in the wild has previously been detected for cod (*Gadus morhua*) (Villegas-Ríos et al., 2017), and many other studies support the notion that fish behaviour in the wild is repeatable (Harrison et al., 2014, 2017; Alós et al., 2016, 2017; Monk and Arlinghaus, 2018). Repeatability estimates are generally higher when measured in the wild as compared to the laboratory, possibly a consequence of repeatability to some degree reflecting individual differences in habitat use (Bell et al., 2009). Also, repeatability increases when the behavioural traits are measured within short time intervals, as individuals are likely to experience similar environments and be in similar states (Bell et al., 2009). Conversely, activity as a behavioural trait is generally less repeatable than e.g.

aggression (Bell et al., 2009). Note that most of the activity measures in this study came from five of the 12 individuals. Although LMMs account for uneven sample sizes (Zuur et al., 2017), this must be taken into account when inferring general patterns from the data. Including autocorrelation in the LMM significantly improved the model. However, previous studies have suggested that weekly replicates provide the best temporal averages for unbiased parameter estimates (Villegas-Ríos et al., 2017), but there was not enough data for using weekly averages in the present study.

Sea trout activity through the day increased with temperature, with both the amplitude and the width of peak activity increasing. This is in line with current knowledge stating that feeding activity of brown trout increase with temperature (Klemetsen et al., 2003). Also, previous studies of sea trout movement in the marine environment show higher vertical movement rates during daylight hours (Eldøy et al., 2017). Sea trout were more active during daylight hours, and the temperature effect is likely intertwined with an effect of day length. In spring, the length of the day will be increasing with temperature. As the effect of day length on activity was not tested for, we cannot disentangle these two effects in the present study. Including autocorrelation between the hourly measurements in the GAMM significantly improved the model. However, as there is likely also correlation between the data across longer time frames than hours, there will still be autocorrelation present that is not accounted for in the model.

Personality is often described as occurring along an axis from shy to bold (Sih et al., 2004), but can similarly be explained using a reactive-proactive spectrum (Quinn et al., 2012). Here, the proactive fish are bold, risk prone and fast and superficial in their exploratory behaviour, hence having larger home ranges, while the reactive fish are shy and thorough explorers within smaller home ranges. Studying covariation between home range and activity could give an insight into how fish behave within their respective home ranges. Variation in home range size has an environmental component, and responds for example to changes in food availability (Závorka et al., 2015). Linking lab activity with home range and growth in the river, the authors found that active individuals experienced decreased growth with increasing home range size, assuming that an increase in home range size was a response to a decrease in food abundance. Conversely, individuals with low activity experienced increased growth with increasing home range size (Závorka et al., 2015). In addition to responding to environmental conditions, home range is also partly consistent within the individual (Villegas-Ríos et al., 2017). Nevertheless, their results are in line with there being a difference in individuals' response to environmental factors across the reactive-proactive spectrum. This was also shown in cod, where home ranges of reactive fish decreased with increasing temperatures, while proactive fish did not react (Villegas-Ríos et al., 2018). These fish were also assigned as being reactive or proactive using lab tests prior to being tracked at sea. Possibly, since activity as measured by acceleration shows high consistency within the individual, acceleration tags can enable classification of fish personality directly during tracking in the wild.

Our study suggests that acceleration is a useful measure in identifying within- and between individual variation in activity of sea trout. SD of depth can be used as a measure of activity, and have been successful in identifying personality traits in cod (Villegas-Ríos et al., 2017). However, as trout utilise a small depth range, with mean daily depth ranging between 0.5 and 1.9 m during winter in a Norwegian fjord (Eldøy et al., 2017), detecting variation between individuals could be difficult without high resolution in depth measurements. Acceleration tags have also been successful in detecting certain types of behaviour within individuals. Yellowfin bream tagged with accelerometer tags revealed increased activity in seagrass habitats as compared to artificial reefs, and authors suggest this represents foraging behaviour as opposed to using the artificial reef as a refuge (Taylor et al., 2018). Furthermore, external accelerometer tags have been successful in detecting feeding and fleeing events in great sculpin (*Myoxocephalus polyacanthoceaphalus*) at a detection probability of 69 % and 91 %, respectively (Broell et al., 2013). The tags used stored acceleration data continuously, had a sampling frequency of 100 Hz and a storage capacity of 10 h. Such high-resolution data is thus currently not obtainable in the wild for longer time periods. Acceleration data in the present study has a lower resolution as acceleration measurements are averaged across axes and time, but options exist to reduce the duration of the sampling event and/or increase sampling frequency to obtain higher resolution.

Using acceleration tags, we were successful in detecting individual consistency in activity of sea trout in the marine environment and activity responses to temperature and light. We argue that accelerometer tags provide high resolution activity data that may potentially enable classification of fish personality directly during tracking in the wild.

Figures and tables

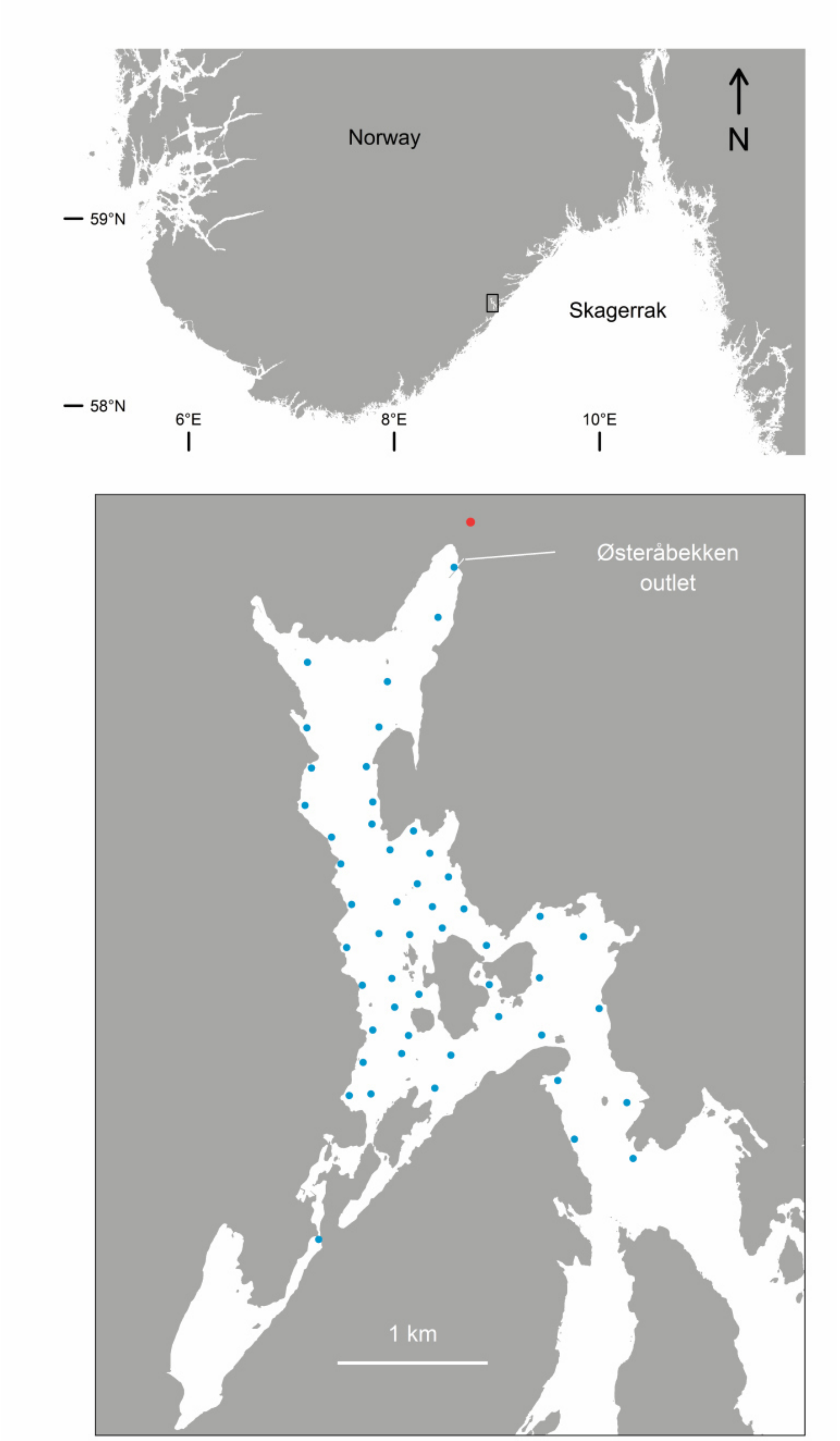
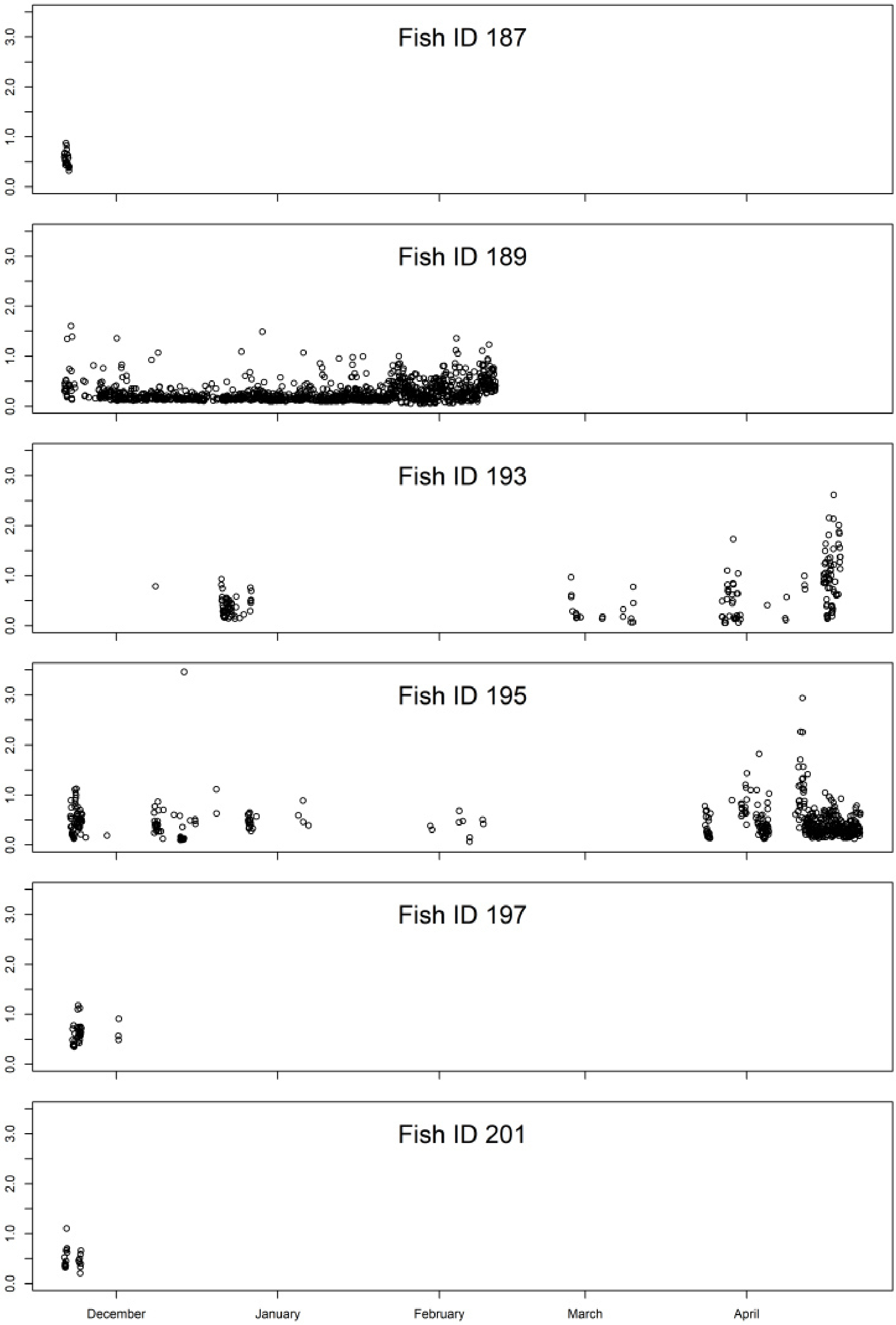


Figure 1 The Tvedestrand fjord study system. Receiver locations are indicated with blue dots, capture location in Østeråbekken is indicated with a red dot.


Fish ID 187
Fish ID 189
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0.0
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December
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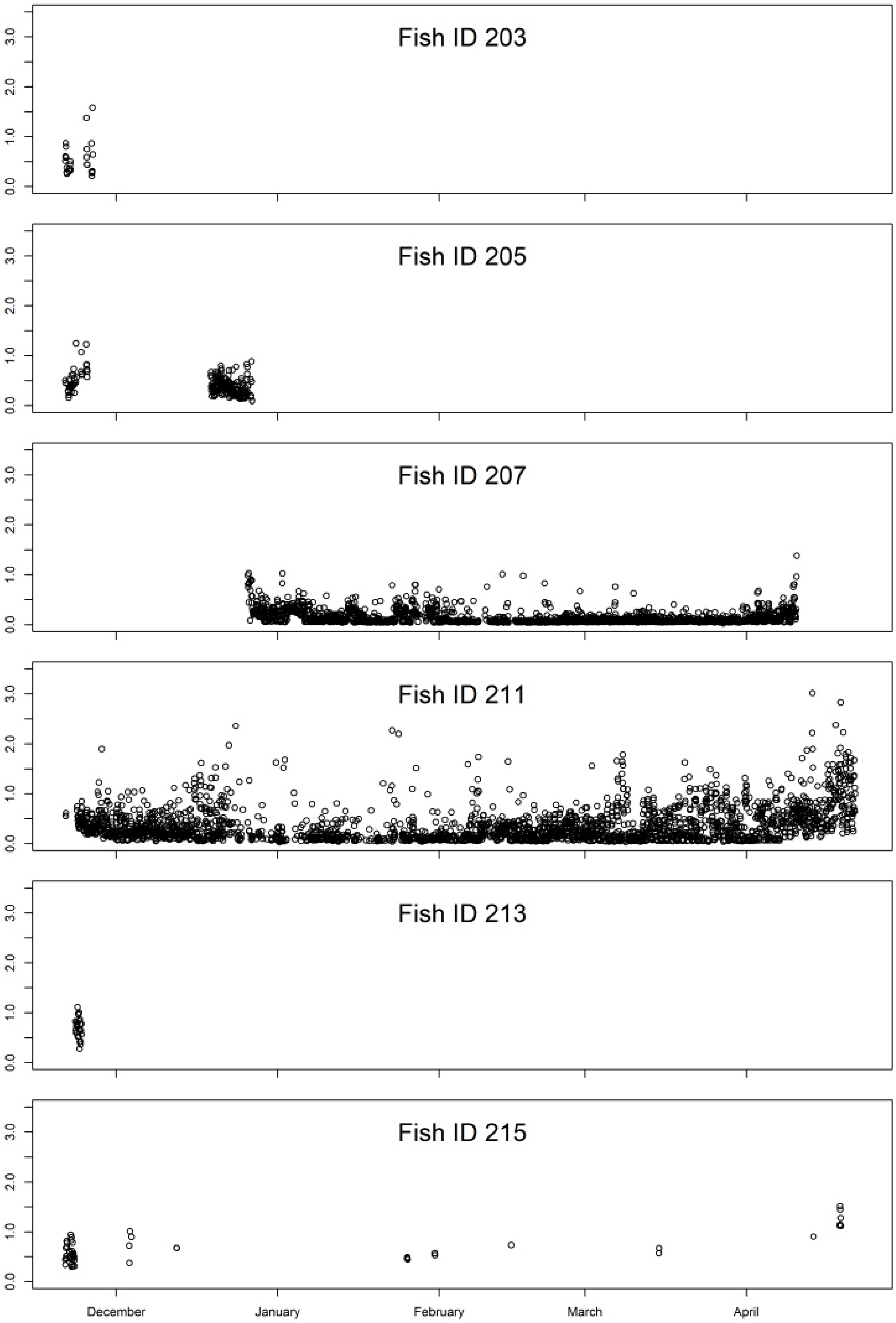
March
April


Fish ID 203

Fish ID 205

Fish ID 207

Fish ID 211

Fish ID 213

Fish ID 215

Figure 2 Average hourly acceleration for all fish from tagging in November 2017 until the end of the study in April 2018.

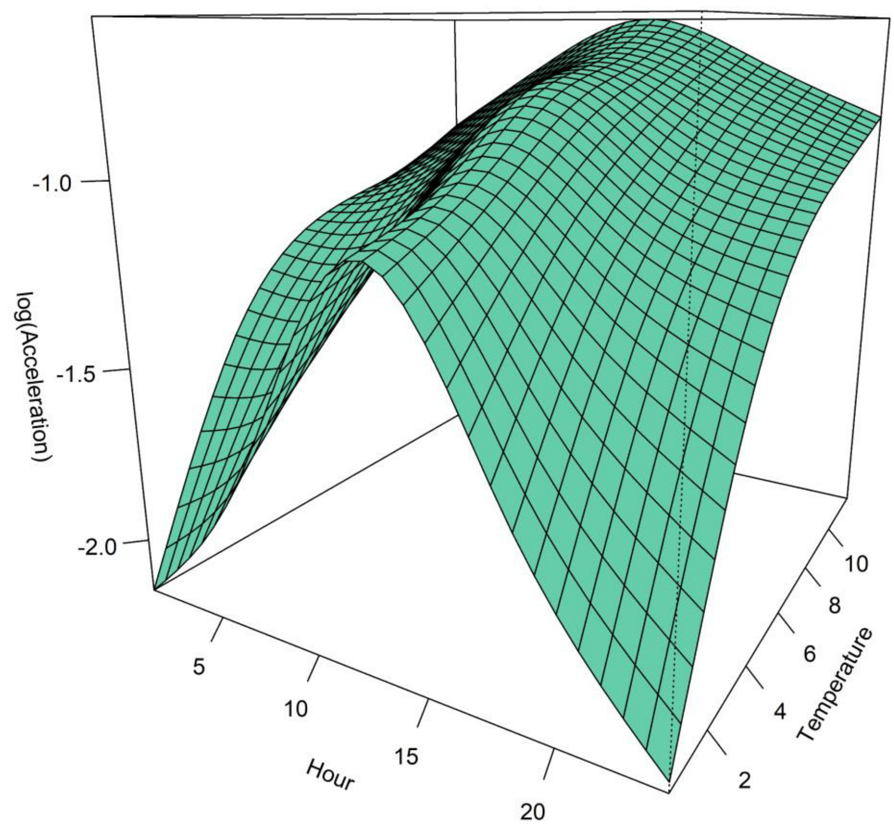


Figure 3 Average hourly acceleration through the 24-hour cycle across temperatures.

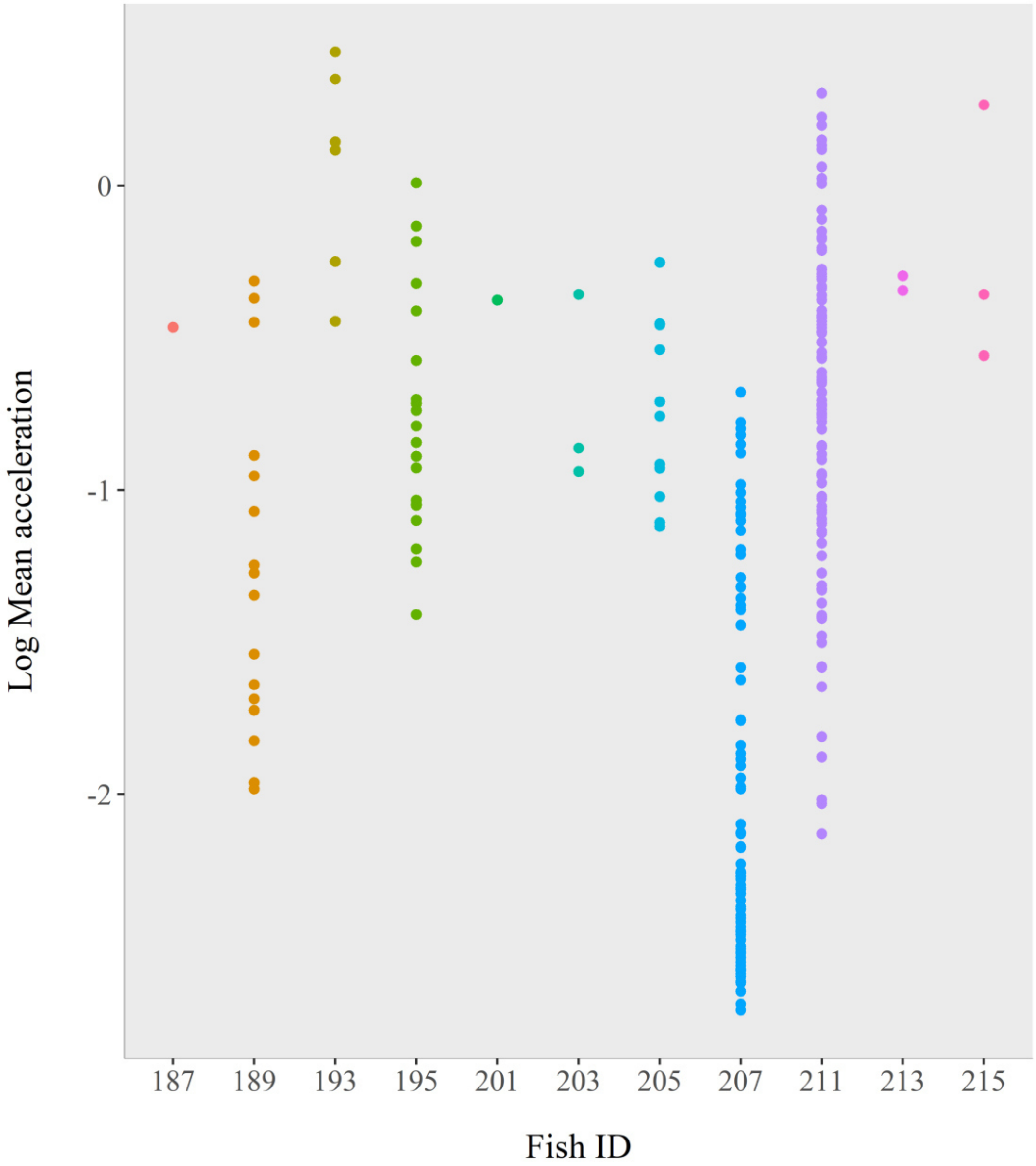


Figure 4 Average daily acceleration (based on detections during day, log-transformed) for individual sea trout. Colours represent individual trout.

Table 1 Parameter estimates with associated standard errors (S.E.), estimated degrees of freedom (edf) and p-values for the GAMM assessing the influence of temperature on the shape of the relationship between acceleration and hour of day for sea trout.

Response variable	Model component	Estimate	S.E.	edf	p-value
Log (Average hourly acceleration)	Intercept	-1.25	0.117		< 0.001
	Tensor (Hour of day, Temperature)			15.6	< 0.001
	R-square (adjusted)	0.196			
	Random variance (Between-individual variance)	0.133			
	Residual variance (Within-individual variance)	0.502			
	Autocorrelation parameter (phi)	0.575			

Table 2 Model selection of random effects structure (1) and fixed effects structure (2) for response variable daily activity. Model selection was done using AIC values. The best models from each selection step are shown in bold, and the selected model is enclosed.

No	(1) Model structure	AIC
1	**Daily activity = $\beta_0 + \beta_1$ * Temperature * β_2 * Length + b_1 * Fish ID + $\text{COR}_{\text{Julian day}}$**	**286.30**
2	Daily activity = $\beta_0 + \beta_1$ * Temperature * β_2 * Length + $\text{COR}_{\text{Julian day\|FishID}}$	298.88
3	Daily activity = $\beta_0 + \beta_1$ * Temperature * β_2 * Length + b_1 * Fish ID	428.18
	(2) Model structure	
1	Daily activity = $\beta_0 + \beta_1$ * Temperature * β_2 * Length + b_1 * Fish ID + $\text{COR}_{\text{Julian day}}$	271.68
4	**Daily activity = $\beta_0 + \beta_1$ * Temperature + β_2 * Length + b_1 * Fish ID + $\text{COR}_{\text{Julian day}}$**	**269.71**
5	**Daily activity = $\beta_0 + \beta_1$ * Temperature + b_1 * Fish ID + $\text{COR}_{\text{Julian day}}$**	**267.71**
6	Daily activity = $\beta_0 + \beta_2$ * Length + b_1 * Fish ID + $\text{COR}_{\text{Julian day}}$	274.98
7	Daily activity = $\beta_0 + b_1$ * ID + $\text{COR}_{\text{Julian day}}$	272.98

Table 3 Parameter estimates with associated standard errors (S.E.), degrees of freedom (df) and p-values for the LMM predicting average daily acceleration for sea trout.

Response variable	Model component	Estimate	S.E.	df	p-value
Average daily acceleration	Intercept	-1.21	0.226	233	< 0.001
	Temperature	0.0661	0.0240	233	0.0064
	Random variance (Between-individual variance)	0.178			
	Residual variance (Within-individual variance)	0.289			
	Autocorrelation parameter (phi)	0.710			

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Dynamics of anadromous brown trout at sea inferred from 100 years of scientific beach seine sampling

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Abstract

Safe management of fish populations rests on basic knowledge about population dynamics. Unfortunately, long-term reliable data on population abundance are often incomplete or absent for species outside of the commercial fishing industry. For instance, the anadromous brown trout (*Salmo trutta*) is a popular catch in recreational fisheries. Therefore, understanding current trends and drivers of change in sea trout populations in Norway is important for management and conservation. To this end, we analysed 100 years (1919-2018) of scientific sampling data from the Norwegian Skagerrak coast to study population dynamics of sea trout across six coastal regions. These data suggest that the abundance of sea trout has been increasing since the 1980's, and also that the positive trend started earlier in some regions and included some setbacks in other regions. We discuss potential causes for the observed dynamics and highlight changes in temperature, the reduction in acidic precipitation and changes in fishing legislation as some of the most interesting candidates for future studies.

Introduction

The brown trout (*Salmo trutta*), including its anadromous form called sea trout, is a highly valued species in the recreational fishery in Norway. Population fluctuations and their causes are therefore of interest to managers, researchers and the general public. Norwegian brown trout populations have experienced changes in population size and productivity in response to several well-known anthropogenic effects, such as acidification of surface waters originating from deposition of sulphur oxides and nitrogen from European industry (Jenkins et al., 2003). Furthermore, trout populations have also been affected by fishing regulations that have been constantly changing since the first law on salmon and trout fishing was implemented in 1848 (Langset and Staldvik, 2011). In the western and central part of Norway, sea trout experience increased mortality risk in marine areas due to high concentrations of salmon lice associated with aquaculture of salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Serra-Llinares et al., 2014), which can also affect growth and thus fecundity (Thorstad et al., 2015). Recognizing drivers of change in sea trout population productivity, both when it comes to anthropogenic stressors and natural fluctuations, are of interest to further optimise the fishing legislation and management of brown trout.

Partly due to the abovementioned threat from salmon lice in western Norway, sea trout populations have received some additional attention in this region (Birkeland and Jakobsen, 1997; Fjørtoft et al., 2014; Skaala et al., 2014). Brown trout populations in fresh water habitats have also been studied in southern regions of Norway, where acidic precipitation has been particularly severe (Bulger et al., 1993). Furthermore, sea trout populations in southern Norway are sampled in a unique beach seine series extending from 1919 until 2018 through most regions of the

Norwegian Skagerrak coast. During this fishery-independent sampling, all species are registered and counted, providing standardised measures of catch per unit effort of various species (Tveite, 1971; Johannessen and Sollie, 1994; Fromentin et al., 1997; Durif et al., 2011; Rogers et al., 2011; Barceló et al., 2016).

Here, we utilise this century-long sampling program for presenting catch-per-unit-effort, a proxy for population abundance of sea trout for six southern Norwegian coastal regions. Furthermore, we comment on the potential causes for the observed dynamics, indicative of an increase in trout abundance in marine habitats during the past 60 to 40 years, depending on region.

Materials and Methods

DATA COLLECTION

Data on trout abundance has been collected along the southern Norwegian coast from a unique marine time series extending from 1919 until 2018. The survey, being a series of beach seine hauls, was initiated to study cod recruitment in nursery areas such as eel grass beds (Fromentin et al., 1997). Sampling started in 1919 in the three western Skagerrak regions; Vest-Agder, Aust-Ager and Telemark. In 1936 in the study expanded into three eastern Skagerrak regions; Vestfold, Oslo/Akershus and Østfold (Fig. 1). Thus, new stations were added later, and stations are sampled for an uneven number of years. Currently, IMR perform 130 beach seine hauls along the Skagerrak coast every year, and 38 of these stations have been sampled since the start of the survey (Barceló et al., 2016). However, as some stations existed only for a few years, there are 295 stations in total with data on trout (two were excluded in this study due to missing information on location). Sampling takes place from mid-September to early October. The beach seine is 40 m long, 3.7 m deep and has a stretched mesh size of 1.5 cm. The total area sampled is up to 700 or 1000 m^2, depending on the length of the hauling ropes, being either 20 or 30 m long, respectively. Sampling depth varies between 3-15 m. See Fromentin et al., (1997) for detailed sampling description. During sampling, all trout were counted and released.

DATA ANALYSIS

Yearly catch per unit effort (CPUE) was calculated for each region as the average number of trout per haul. Then, loess smoothers (span = 0.5) were fitted to the CPUE data for each of the 6 sampling regions. The catch data was given as number of trout per haul. Stations that were sampled less than 30 times (years) were excluded from the dataset. Also, the survey was affected by WWII (1940-1944), when only a few stations in Aust-Agder were sampled.

Results

In total, 295 stations have been sampled in the six regions during the Skagerrak time series. After removing stations that were sampled less than 30 years, 158 stations were kept (Table 1). Number of stations per region per year ranged from 4-44. In total, 9839 beach seine hauls were included in the data, and the average number of trout per haul ranged from 0.20 – 0.67 between the different regions. The proportion of zeroes in the data were large (Fig. 2), and varied between 0.74 and 0.90 for the six different regions in the study.

Loess smoothers fitted to the CPUE data in the six regions revealed differing patterns of catches across years (Fig. 3). In Vest-Agder, catches are increasing from the 1920's and decreasing from early 1940's until early 1960's, before beginning a gradual increase until present (Fig. 3A).

For Aust-Agder, the change in catches across years is more moderate (Fig. 3B). Catches are increasing until the late 1940's and decreasing towards early 1980's, before increasing towards present. In Telemark, changes are moderate until the early 2000's, where catches are increasing more prominently towards present (Fig. 3C). However, there are still weak signs of an increase in catches towards the late 1940's, followed by a decrease that lasts until the mid-1960's, before a gradual increase begins. For stations sampled from 1936 until present, there are also similarities. In Vestfold, catches are decreasing from the 1940's until late 1970's (Fig. 3D). Hereafter, catches are largely increasing until present, except from a small dip in the 1990's. In Oslo and Akershus, catches are increasing until the early 1950's and then decreasing towards the mid 1970's (Fig. 3E). And increase is then observed until present, but also here including a small dip in the late 1990's to early 2000's. In the Østfold region, the patterns are similar to Vestfold, decreasing towards the early 1970's, but showing a small positive tendency in the early 1960's (fig. 3F). A later increase in catches is observed, but including a similar dip in the 1990's as observed in Vestfold and Oslo and Akershus. In these three easternmost regions and Telemark, the increase in catches seems to be accelerating after the 1990's. Unlike in other regions, the positive trend does not seem to continue in the last few years of the study in Østfold.

Discussion

By analysing 100 years of scientific survey data on sea trout catch-per-unit-effort, this study suggests that there is an overall increase in the abundance of sea trout in marine habitats along the Norwegian Skagerrak coast. In all regions, a dip in abundance occurs either in the 1960's or 1970's, although less prominent in Aust-Agder, Telemark and

Østfold. In the three eastern regions, there is also a dip in abundance in the 1990's or early 2000's. Identifying drivers of this dynamics is beyond the scope of this chapter, but we will discuss potential explanatory variables; temperature, pH in associated spawning rivers, quality of spawning river habitat and fishing regulations. We also note that catches of trout in the beach seine could also be influenced by catchability related to behaviour and habitat use, perhaps in response to temperature changes (Klemetsen et al., 2003).

Temperature at sea may have affected trout catches in the seine, both via recruitment effects on true abundance, and also by affecting trout behaviour and thus catchability. Feeding activity of brown trout is increasing as sea temperatures are rising in the spring and summer (Klemetsen et al., 2003). The optimal temperature for growth of brown trout is 14-17°C (Elliott and Hurley, 2000), and prolonged periods of optimal temperatures may increase growth and thus reproductive output (Roff, 1984) in sea trout. Sea trout actively seek out water bodies with optimal temperatures, either by migrating to outer sea areas or by performing horizontal movements (Kristensen et al., 2018). Here, sea trout resided in water warmer than the average for the area during spring, and water colder than the average during summer (Kristensen et al., 2018). Accordingly, temperature may have affected the whereabouts of the trout from year to year, and also their behaviour in relation to feeding activity. Furthermore, higher temperatures on the spawning stream could have increased the growth rate of juvenile trout (Klemetsen et al., 2003).

Acidification of surface waters from deposition of mainly sulphur oxides and nitrogen has led to a decline in pH in European waters since the mid-1800s (Jenkins et al., 2003). Several protocols have been adopted to reduce emissions since the first agreement in 1985 (UNECE, 1985). Southern Norway has received moderate levels of acid deposition, but have had elevated problems with highly acidified lakes due to naturally low acid neutralizing capacity (Jenkins et al., 2003). Populations of brown trout in Norwegian lakes have shown great declines as a response to low pH and acid neutralizing capacity (Bulger et al., 1993). However, there has been a significant reduction in sulphur oxide deposition in Europe since the 1980's (Jenkins et al., 2003). Southern Norwegian surface waters still have problems with acidity, but positive trends can be seen also here (Saksgård and Schartau, 2011). Liming of lakes and rivers has been a part of a national strategy to reduce the effect of acidification since 1983 (Miljødirektoratet, 2016). In several regions in the present study, the increase in trout catches begins earlier than the reduction in deposition of acidic components, so there are likely also other important effects at play. However, in Telemark and Vestfold, Østfold and to some degree also Oslo and Akershus, catches have increased much faster since the late 1990's (see below).

In 1979, a total ban on fishing sea trout with nets in marine areas was introduced (Langset and Staldvik, 2011). This co-occurs with the increase in trout catches starting in the 1980's in Aust-Agder, Vestfold, Oslo and Akershus and Østfold. In Vest-Agder and Telemark, catches are also increasing in this period, but had already started when the ban was introduced. Furthermore, laws regulating trout fishing, both at sea and in the river, has been continuously changing since the first law was established in 1848. Another important change occurred in 1992, when instead of limiting the fishery using regulations, all fishing was banned unless otherwise stated. Today, fishing for sea trout is allowed all year using hook and line, and by specialised traps during one month in summer, effectively reducing the fishing pressure on sea trout in marine habitats. This change co-occurs with the abovementioned accelerated increase in catches beginning in the 1990's.

Other factors that may have affected sea trout population size is restoration of spawning rivers, which today is a popular activity among sea trout and salmon fishing enthusiasts in Norway. The conditions on the spawning river, including the amount of high-quality territories for spawning, are of high importance for population productivity (Klemetsen et al., 2003). One can speculate that an increase in effort to improve fresh water habitats could coincide with an increase in awareness and public concern for sea trout populations, effectively resulting in a reduction in illegal fishing practices.

We also note that, in contrast to western Norway, Skagerrak is almost free of salmonid aquaculture, and thus represents a valuable reference area where sea trout are not exposed to the excess export of sea lice from aquaculture facilities using net pens (Torrissen et al., 2013). Catch data from the recreational river fishery in western, central and northern parts of Norway indicate an overall increase in population size, amounting to 15 % per decade (Otero et al., 2017). However, when breaking down long term trends, river catches were decreasing in western regions and increasing in northern regions. The study did not report detailed effort data and must thus be interpreted with care (Otero et al., 2017). Other records of sea trout population sizes in the western, central and northern part of Norway, being based on drift dive counting, video or catch statistics and having an extent of 4 to 50 years, show great variety in population trends (Anon., 2018). Here, population sizes were increasing in 25 % of the watercourses, decreasing in 46 % and being stable in the rest (Anon., 2018). Salmon lice infestations can affect marine growth of sea trout (Thorstad et al., 2015) and lead to decreased marine survival (Serra-Llinares et al., 2014; Skaala et al., 2014).

The beach seine data series in the Skagerrak region was originally designed to study recruitment of cod (Tveite, 1971). Hence, locations chosen for sampling do not necessarily cover habitats suitable for sea trout, and there was a large number of zeroes in the data (hauls containing no trout). Accordingly, the trends shown in this study represent changes in sea trout catches in the marine habitat with stations being located randomly with respect to sea trout habitat. Furthermore, the beach seine is an active sampling gear and may selectively catch less active trout. More active fish have a higher chance of escaping active gear types like trawls (Diaz Pauli et al., 2015). Sea trout catches in the different regions will also depend on migration patterns in the related spawning rivers. There is a large variation in time spent at sea depending on the size of spawning rivers (Klemetsen et al., 2003). Generally, sea trout return earlier to fresh water when homing to a larger river. This could have had an effect on the difference in catches between the regions, as sea trout will be homing to rivers of different sizes, and thus possibly at different points in time.

In conclusion, by presenting 100 years of fishery-independent data sea trout catch-per-unit-effort from the Norwegian Skagerrak coast, our study strongly suggests that sea trout abundance is increasing in all regions. The positive trend started as early as 1960 in some regions, and had started in all regions in the beginning of the 1980’s. There are many interesting potential explanatory variables for the observed change in catches, including temperature, acidification of surface waters in streams and lakes and changes in fishing restrictions, and their importance should be investigated in future studies.

Figures and tables

Figure 1 Map of the Norwegian Skagerrak coast showing the six coastal regions Vest-Agder, Aust-Agder, Telemark, Vestfold, Oslo/Akershus and Østfold where the beach seine sampling has been conducted.

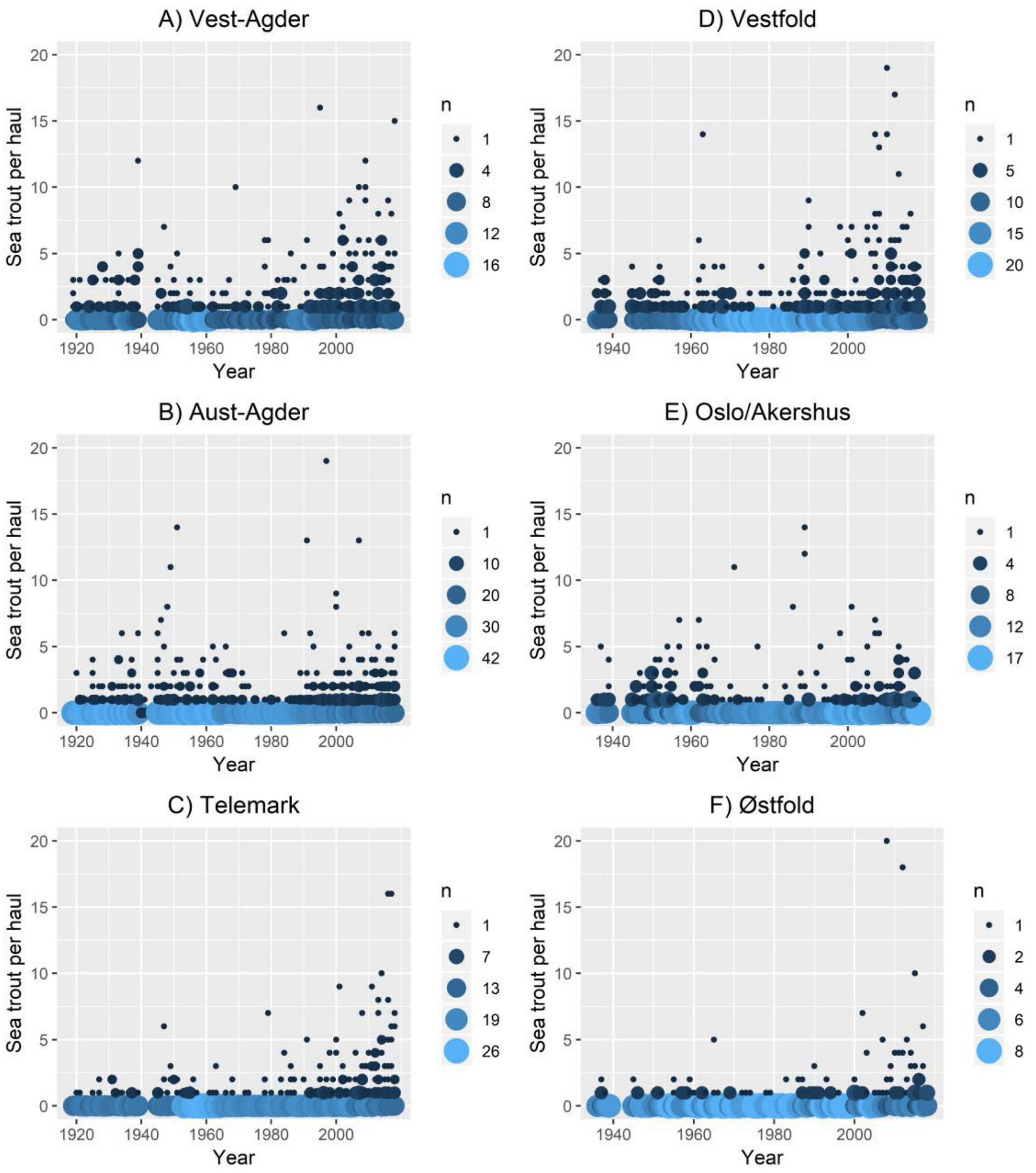

Figure 2 Trout per haul across years for the six different regions. The size and colour of circles indicate at how many stations the given number of trout per haul occurred per year. Note that the circles represent different numbers across plots. The smallest circle always represents one instance (e.g. five trout in one haul occurred at one station in a given year), while the largest circle represents the maximum number of catches of the same size within a year for that given region (e.g. in A) Vest-Agder, zero trout in one haul occurred at up to 16 stations in a given year). The regions plotted are A) Vest-Agder, B) Aust-Agder, C) Telemark, D) Vestfold, E) Oslo/Akershus and F) Østfold. Catches larger than 20 trout per haul are not presented in the figure (n = 7).

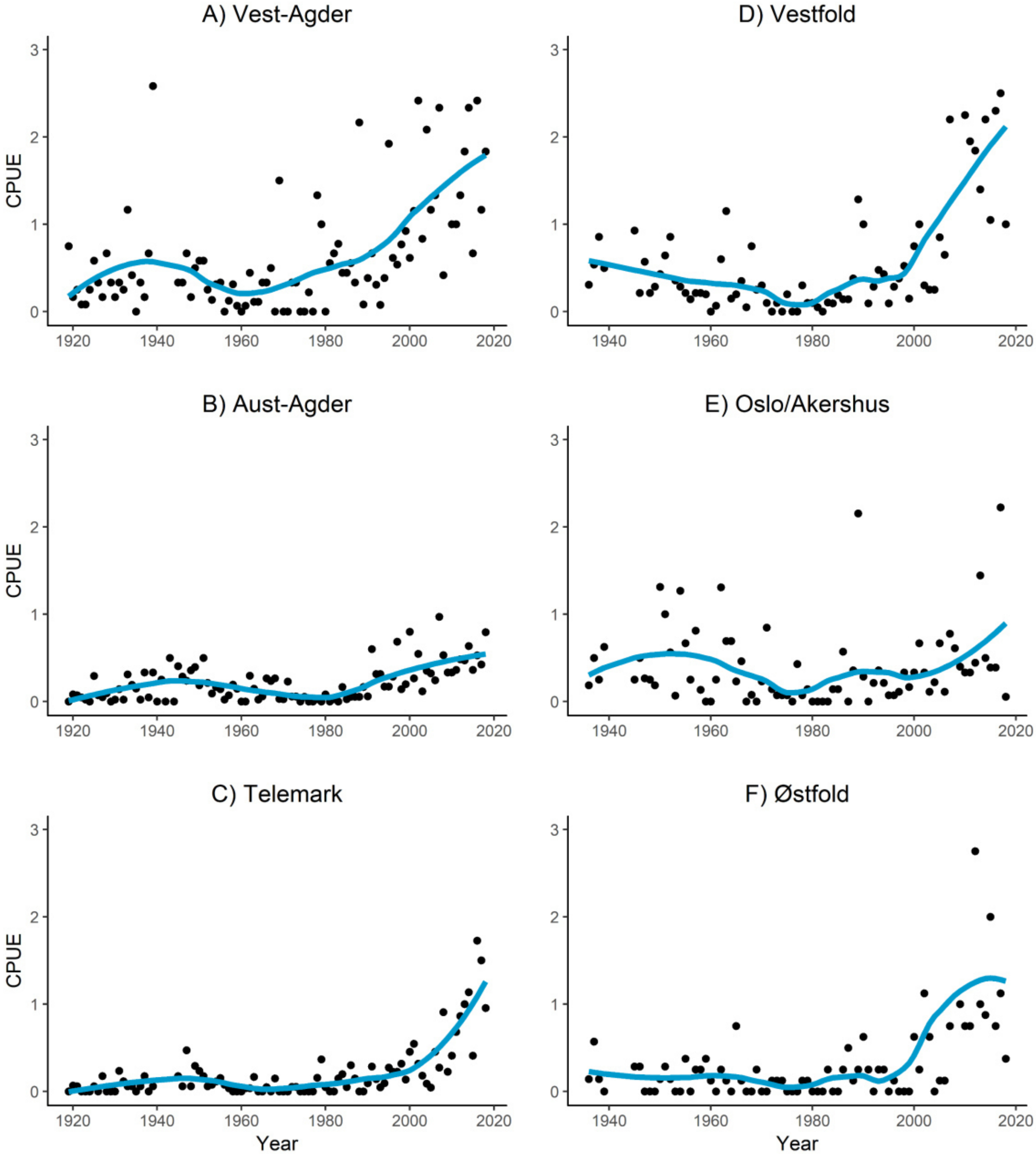

Figure 3 Yearly catch per unit effort (CPUE) of sea trout in the beach seine survey. Loess smoothers were fitted to the six regions: A) Vest-Agder, B) Aust-Agder, C) Telemark, D) Vestfold, E) Oslo/Akershus and F) Østfold. CPUE values larger than 3 are not plotted in the figure (n = 3).

Table 1 Number of stations, stations per year (mean and range), sample size and trout per haul (mean and range) for the six study regions.

Region	Number of stations	Stations per year (mean, range)	Sample size (Σ $_{\text{station x years}}$)	Trout per haul (mean ± S.E, range)
Vest-Agder	20	12, 8-16	1096	0.67 ± 0.054, 0-26
Aust-Agder	52	36, 4-44	3595	0.20 ± 0.014, 0-19
Telemark	33	20, 13-26	1918	0.21 ± 0.022, 0-16
Vestfold	24	19, 13-22	1429	0.60 ± 0.054, 0-30
Oslo/Akershus	20	15, 5-18	1193	0.40 ± 0.041, 0-30
Østfold	9	8, 5-8	608	0.39 ± 0.075, 0-31

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Cartoon: Seppo Leinonen, www.seppo.net

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