## West Sutherland Fisheries Trust



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# Habitat use and movements of sea trout in Loch Laxford: an acoustic telemetry study 

A report by the:
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Contributor Roles: A B-J \& SM (West Sutherland Fishery Trust) conceived the study, developed the study design, secured funding and contributed considerably to its execution. IM (SCENE) led the project execution, the analysis of the data and report writing. HH \& SG (SCENE) contributed to project execution and to data analysis. MN (Atlantic Salmon Trust/SCENE) contributed to project execution, study design and to data analysis. CA (SCENE) contributed to study design and project execution. Marine Scotland Science donated the tags to the study.

## I. NON-TECHNICAL SUMMARY

There is evidence that sea trout numbers in Scotland have declined over recent decades; and that they continue to do so.

Management of trout populations has primarily focused on the freshwater phase of the life cycle; this is in part, because we know much more about the requirements for trout in freshwater water.

By contrast, sea trout ecology in the marine environment is poorly understood. At its simplest, we know very little about where sea trout go when they reach the coast, and what they do when they get there.

We do know however, that the coastal zone around Scotland has changed considerably in the last few decades. The effects of such changes on sea trout are not well understood.

The aim of the study presented here was to address some very basic questions about marine activity by sea trout from the Laxford system, West Sutherland.

We did this by capturing and tracking trout that had smolted and were migrating to sea for the first time (post-smolts) and trout that were using marine habitats for a second (or more) year, (multiple year migrants).

In total 99 fish were tagged with a small tag which emits a coded sound signal that can be detected and logged when close to a receiver.

Thirty eight receivers were deployed in the River Laxford, its estuary and the sea loch, Loch Laxford. Some were positioned close to salmon cage farms and some close to mussel farms to address specific questions related to their potential impact on sea tout.

The study addressed 6 specific questions:

- Do sea trout remain within the sea loch of origin during their first summer at sea?

Our results showed that only $5 \%$ of sea trout migrated out of Loch Laxford and into more open coastal waters. Thus, the vast majority of sea trout remained within the sea loch of their natal river to feed over the summer.

- What is the extent of habitat use by sea trout in Loch Laxford?

Although sea trout were recorded across the whole of the Loch Laxford sea loch (Figure 1) sea trout use of the area in summer was highly concentrated in a very small patch of the total available habitat. This area comprised a shallow, tidal, estuarine area between the mouth of the river and where it opens out into the deeper sea loch. $75 \%$ of fish detected consistently were never detected outside this small ( $0.2 \mathrm{~km}^{2}$ ) shallow but energetically productive area.

- Does the pattern of coastal habitat use by sea trout change with time?

There were indications of the habitat use change with time. There was evidence that those fish that migrated out from the estuary into the wider sea loch did so later in the summer and after a period of residency in the estuary.

- Are sea trout interacting with a salmon open net pens at an aquaculture facility?

There was no evidence of sea trout being attracted to areas around the two salmon cage sites. In this study, no fish were detected at one of the cage sites and only 3 at the other. The total time spent by sea trout close to the cage sites was 46 minutes over the study period of ca 100 days.

- Is there an interaction between edible mussel, suspended rope farm units and sea trout habitat use?

There was evidence that sea trout were using habitat areas occupied by mussel farm units. Of the fish that dispersed from the estuary and entered the wider sea loch, $50 \%$ were detected close to a mussel farm unit and there was evidence of residency events of moderate duration in these areas. It is possible that sea trout are being attracted to mussel farms deployments, possibly because the structure of the farm provides physical protection from predators. More likely is that the habitat type preference of sea trout, at least in Loch Laxford, coincides with the habitat suitable for a mussel farm deployment.

- Does the marine habitat use and migration behaviour of sea trout on their first migration to sea differ from that of individuals making their second or third sea migration?

Although the sample size of multiple year migrant sea trout in this study was small ( $\mathrm{N}=8$ ) the pattern of behaviour observed was very similar to first year migrants. No multi-year migrants migrated out of Loch Laxford into the open coastal zone, all such fish remained
within the energy rich, shallow estuary area or lower reach of the river throughout the study.

We conclude that only a small percentage of sea trout from the River Laxford migrate out into open coastal waters, a larger percentage use the enclosed sea loch for summer feeding but the majority of sea migrants use only a very small, very specific habitat in the estuary. This very high concentration of marine feeding by sea tout in a very small area makes this stage of the life cycle vulnerable to negative effects of marine development and thus such areas in Loch Laxford (and elsewhere) need to be identified and consideration given to their protection.

## II. INTRODUCTION

The anadromous brown trout (Salmo trutta), hereafter referred to as sea trout, is an opportunistic salmonid species that can make use of a wide range of freshwater and marine habitats (Eldøy et al., 2015; Thorstad et al., 2016).) It is widely agreed that trout migrate to sea when the benefits of the habitat shift (thought to be more abundant feeding resources) outweigh the costs, which are likely to include increased predation risk and exposure to disease (Thorstad et al., 2016; Moore et al., 2018).

In a number of European countries sea trout populations are "vulnerable" and/or population declines have been reported in recent decades (ICES, 2017; Evans \& Harris, 2017; Hojesjo et al., 2017). Where the reasons behind declines have been identified, degradation of freshwater habitat, (used by sea trout for spawning, juvenile nursery areas and in some populations as overwintering habitat) has had an effect. However, there is also evidence that mortality in the marine environment may also play a significant role (Eldøy et al., 2015).

There is evidence of a decline in sea trout numbers in Scotland, particularly amongst west coast populations (Moore et al. in prep). However, there have been very few studies investigating potential drivers of population change.

Although some sea trout do migrate into the open ocean to feed, it is thought that in many populations, the majority of individuals mostly use near-shore coastal environments (see Pratten \& Shearer (1983), Jonsson et al. (1995), Middlemas et al. (2009), del Villar Guerra et al. (2014)). This may be particularly true of post-smolt sea trout migrating from rivers into sheltered fjord systems, (in Scotland known as sea lochs), for summer feeding. However, the nature of sea lochs has changed dramatically over the last few decades. In particular open net pen Atlantic salmon (Salmo salar) farming has expanded significantly in Scotland in recent decades (OECD, 2018) raising concerns around the quality of the marine environments used by sea trout (Gargan et al., 2012). One strand of this concern is that research has demonstrated that the presence of aquaculture facilities in a sea loch can lead to increased levels of ectoparasites, such as Lepeophtheirus salmonis (salmon lice), in the water column for up to 30 km from the facility (Middlemas et al., 2013, Thorstad et al., 2015) This in turn, can result in an increase in the parasite load on salmonids utilizing the same areas. High parasite loads, particularly on newly smolted sea trout, can result in changes in migratory patterns (such as premature re-entry into freshwater catchments), osmoregulatory issues,
secondary infections and weakened states, and ultimately increased mortality (Thorstad et al., 2015).

Acoustic telemetry is a technique that can be used to track the movements of fish in both marine and freshwaters. A small transmitter that produces a coded sound signal at intervals is implanted into fish and acoustic receivers are used to log the presence of a fish as it passes within range of the receiver. Frequently multiple receivers are deployed as an array to be able to determine patterns of fish movements or habitat use. This technique has been used in studies of migration patterns of Atlantic salmon (for Scottish examples see Honkanen et al., 2018; Lothian et al., 2018), and of sea trout in Scandinavia (Flaten et al., 2016; Eldøy et al., 2017; Kristensen et al., 2019), in contrast sea trout marine habitat use and the potential for interactions with salmon aquaculture facilities has had little attention in Scotland .

In the study reported here we use acoustic telemetry to address a number of questions related to marine habitat and fish farm interactions by sea trout in the marine feeding phase during summer.

Specifically, we test the following questions:

- Do sea trout remain within the sea loch of origin during their first summer at sea?
- Are sea trout interacting with salmon open net pens at an aquaculture facility?
- Does the pattern of coastal habitat use by sea trout change with time?
- Is there an interaction between edible mussel Mytilus edulis farm units and sea trout habitat use?
- Does the marine habitat use and migration behaviour of sea trout on their first migration to sea differ from that of individuals making their second or third sea migration?


## III. METHODS

This study was conducted in Loch Laxford, ( $58^{\circ} 24.12^{\prime} ; 005^{\circ} 05.32^{\prime}$ ) a sea loch located on the north west coast of Scotland (Figure 1).

The acoustic receiver array comprised eight TBR700 receivers (Thelma Biotel) and 30 Vemco receivers (11 Vemco VR2AR (with an acoustic release facility) and 19 VR2TX).

Figure 1. Map of the Loch Laxford receiver array with receiver locations, tagging sites, aquaculture pens and mussel farms identified.
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Receiver were placed in a grid system to monitor areas of particular interest in the study area. This specifically included coastal and estuarine tidal areas of Loch Laxford, two open pen salmon aquaculture facilities, the entry point into the River Laxford and exit of the sea loch into the more open coastal marine environment. The receiver array was designated into sections ("river", "estuary", "inner", "middle" and "outer") in order to concisely refer to specific study areas (Figure 1).

A total of 99 sea trout were tagged with an acoustic transmitter ( $7.3 \times 17 \mathrm{~mm}$, weight in air/water of $1.8 / 1.1 \mathrm{~g}, 69 \mathrm{kHz}$, Thelma Biotel, Trondheim, Norway) implanted into the abdominal cavity for this study. Forty-nine (49) tags were programmed to transmit coded acoustic pings at random intervals every 120 seconds, and 50 tags were programmed to transmit coded acoustic pings at random intervals every 90 seconds. The purpose of this difference in transmitter rates was to determine if the tags were producing similar fine scale data or if more detailed movements could be captured by the 90 second tags than the 120 second tags (for example, if fish tagged with 120 tags were only picked up at every other curtain array as they migrated through the sea loch, while the fish tagged with 90 second tags were detected at every curtain array). If the tags were to produce similar data, then future studies of sea trout movement could use 120 second tags which would prolong the battery life without sacrificing important data on migration patterns. This question will be addressed in future analyses.

The original estimated tag life for these tags was six months, however, tags used in this study were over a year old, having been repurposed from another study where they were not deployed. As such, there was no assurance that the battery life of each tag would function to its full capacity.

Tagged individuals comprised two age classes. Very recently smolted fish (hereafter referred to as post-smolts) were defined as fish making their first marine migration to sea (Aldvén \& Davidsen, 2017) and identified by length as fish less than 255 mm fork-length. Ninety one post-smolts were tagged. Multiple year migrants (MYMs) were defined as sea trout greater than 255 mm fork-length; eight MYM were tagged (Table 1).

Sea trout ( $\mathrm{N}=82$ ) were captured by seine net in the Loch Laxford estuary $\left(58^{\circ} 22.89^{\prime}\right.$; $005^{\circ} 02.05^{\prime}$ ) (Figure 1) on four days between the $15^{\text {th }}$ May and $14^{\text {th }}$ July 2018 (Table 1).

Fourteen (14) migrating post-smolts were captured in a smolt trap in Allt Bad na Baighe $\left(58^{\circ} 22.32^{\prime} ; 005^{\circ} 02.71^{\prime}\right)$ (Figure 1) on May $23^{\text {rd }} 2018$ and subsequently tagged.

A total of three individuals were caught on a rod and line, two were captured and tagged on July $13^{\text {th }}$ and one was captured and tagged on July the $14^{\text {th }}$.

To insert the tag, fish were anaesthetised using MS-222 and their mass (g) and fork length (mm) were measured. Visual counts of L. salmonis were conducted on each fish.

The tags and surgery equipment were sterilized in ethanol before washing with distilled water. The fish were placed on a V-shaped surgery sponge with their ventral side uppermost. A tag was inserted through a ventral incision made to one side of the ventral line. The incision was closed with three interrupted sutures. The fish was then allowed to fully recover (determined by the return of normal behaviour) in a well oxygenated recovery tank before being released back into the water, close to the tagging site.

## IV. RESULTS

The mean fork length of post-smolts tagged was $189.1 \pm 21.5 \mathrm{~mm}$ (mean $\pm$ standard deviation (SD)), while the mean weight of the cohort was $70.2 \pm 30.9 \mathrm{~g}$ (Table 1). The longest postsmolt tagged was 255 mm , while the shortest was 141 mm . The largest tagged post-smolt weighed 194 g , while the smallest weighed 36 g . The mean fork length of MYM fish was $322.1 \pm 27.4 \mathrm{~mm}$, while the mean weight of the cohort was $347.5 \pm 83.2 \mathrm{~g}$ (Table 1). The longest MYM tagged was 368 mm , while the smallest was 285 . The largest MYM fish tagged weighed 489 g , while the smallest weighed 235 g .

Of the 99 fish tagged during the course of this study, 77 tagged post-smolts and eight MYM fish were detected on the receiver array; a total of 85 individuals.

The Thelma V7 tags used in this study weighed 1.8 g . The mean tag burden ( $\%$ of body weight) of the post-smolt cohort was $2.6 \pm 1.1 \%$ (mean $\pm \mathrm{SD}$ ), while the mean tag burden of the MYM cohort was $0.5 \pm 0.1 \%$ (mean $\pm$ SD) (Table 1).

Of the 99 fish tagged, 17 were found to be infected with $L$. salmonis. The mean number of $L$. salmonis on this subset of fish was $4.4 \pm 3.5$ L. salmonis /individual. Tag 3596 had the highest number of $L$. salmonis with 13 attached individuals.

In order to remove detections that were most likely caused by either an expelled tag or a fish that had expired within range of a receiver, detections of each fish were examined individually before data analysis began. If a tag was last detected at a single receiver for more than 10 hours of continuous detections, it was assumed that this tag was no longer in a swimming fish. Any detections after that 10 hour waiting period were removed from the main data frame to avoid skewing the results. Four tags (Tags 3596, 3796, 3576 and 3683) were found to have exceeded the 10 hour detection limit and thus data from that point on for these four tags were removed from further analysis.

## 1. Survival over time

Of the 77 detected post-smolts, 45 fish were still being detected 20 tagging, and 32 at 40 days after tagging (Figure 2). Sixty (60) days after tagging, 22 post-smolts were still detected and at 120 days $5 \%$ of the original 77 tagged individuals (4) were still being detected.

Of the eight MYM fish detected, seven were detected 20 days after tagging, and five at 40 days after tagging; four were detected at 60 days but no MYM fish were detected at 120 days post tagging (Figure 3).

A fish's period of detection (as a response variable) was modelled as a negative binomial distribution on fish length (as an explanatory variable) to investigate the relationship between the two. Fish length did not significantly predict the period over which fish were detected ( P $=0.56)$.

## 2. Spatial habitat use

The receiver that detected the most tagged individuals was receiver 131691 located next to the main tagging site in the Laxford estuary (Figure 1). A total of 78 of the 85 detected fish were recorded there. The receivers that detected the second and third greatest number of individual tags were 482008 and 480414, detecting 58 and 29 tags respectively. Both were located in the estuary array of the study area.

Receiver 131693 did not detect any fish. This receiver was located at the outermost fish farm. Receivers 482006 and 482009 both at the entrance to embayments on the south west shore of Loch Laxford, detected only two individuals.

Number of tags detected (smolts)




Number of tags detected (MYM)


Receiver 480414 was located at the end of the estuary array, downstream of the tagging site, where the narrow bay opens into the wider sea loch and was used as a threshold marker to identify fish which migrated to the edge of the estuary array with the potential to move into wider Loch Laxford array. Only 29 fish were detected at this receiver over the course of the study, 28 were post-smolts that moved further into the estuary array from the tagging site.

The amount of time that a tagged individual spent within the detection range of a receiver, hereafter referred to as the residency event, was used to determine how much time fish spent in different areas of the sea loch. A residency event was defined as the period from first detection to last detection in the same detection range of single receiver, assuming there was no detection at any other receiver and/or no gap in detections exceeding 30 minutes during this period (Honkanen et al., 2018).

The receiver that reported the longest mean residency event over the course of the study was 131695 located at the mouth of the River Laxford and was the most downstream receiver of the river array. The mean duration time spent at this receiver was $505 \pm 1,619$ minutes (mean $\pm$ SD) and a total of 26 tagged individuals were detected here.

The receiver with the second longest mean residency event was 482009 , located on the south west shore of the sea loch. The receiver reported a mean residency event of 148 minutes (only one residency event was recorded here) and detected a total of two individuals. A receiver located near the main tagging site (482008) reported the third longest mean duration at $143 \pm 374$ minutes.

The three receivers with the lowest mean residency event were all located on the outer line of the array $(547517,547055$ and 547515$)$ and reported duration times of less than five minutes each. The majority of receivers making up the outer most section of the array, including the deep-water receivers located down the middle channel of the sea loch all reported shorter mean durations, generally $<20$ minutes, than receivers found in the inner and estuarine sections of the array, as well as receivers along the coastline.

## a) Post-Smolts

Since post-smolts made up the majority of the study population, their space use heavily influenced the overall results of this study. As such, the post-smolt study group followed a similar pattern as outlined above. The receivers reporting the highest total number of
individuals were 131691, 482008 and 480414 with 70, 53 and 28 individuals reported at each respective receiver. The highest concentration of individual tags detected at a receiver occurred in the estuary array and as the distance from the estuary tagging site increased, the number of individuals detected on a receiver decreased.

Receivers that detected the fewest individuals were 131693, which detected zero individuals, and Receivers 482006 and 482009, which each detected two individuals.

The mean residency event of post-smolts also exhibited the general patterns described above. Receiver 131695 again reported the longest mean duration at $560 \pm 1,792$ minutes. Receivers 482008 and 482009 reported the next longest mean residency, with values of $150 \pm 390$ and 148 minutes (only one residency event was detected here) respectively.

The three receivers with the lowest mean residency events were all located in the outer line of the array $(547517,547055$ and 547515$)$ and reported residency times of less than five minutes each.

Different patterns of space use by post-smolts were apparent from daily detection data (Figure 4). Although more than half of the fish from the post-smolt study group were detected continuously over the duration of the study, indicating that they spent the majority of their time in the study area, other individuals remained undetected for extended periods of time, suggesting that they were utilising areas that were either not in range of a receiver or left the array entirely.

Differences in post-smolt spatial use patterns were also apparent between months (Figure 5). There was a gradual increase in the number of post-smolts entering the main sea loch between May and June and mean residency events increased at receivers located outside the estuary array. On average, post-smolts spent longer periods of time at receivers located in the estuary array and along the coast than at receivers located in the deeper water in middle of the sea loch. June saw the highest number of post-smolt tags detected outside of the estuary as well as longer residency events spent at receivers in the sea loch than had been observed in May. Furthermore, tags were detected further along the coast line and towards the outer line of array receivers. Post-smolts were detected at all but one receiver in June, indicating that the entire sea loch was being utilised by at least some individuals albeit for different lengths of time.
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By July, the number of individuals detected in the sea loch, as well as the mean residency events, at the sea loch receivers began to decline. Receivers 131695 at the mouth of the River Laxford river and 126846 upstream well into the river itself, both reported the highest number of tagged individuals relative to their other monthly detections during the study. Receiver 131695 also reported the longest mean residency time of any receiver in the array during the month of July. These data would suggest that for some individuals there was a shift in habitat use from the estuarine and marine environment to the freshwater habitat use during July. With detections of three tagged fish at Receiver 126846, it is plausible that there was some upstream migration of post-smolts at this time.

August saw a decline in the number of fish detected at all receivers and a concentration of tagged fish in the estuary. Only one individual (Tag 3825) was detected by receivers in the outer and middle sections of the sea loch and, based on mean residency events, this fish also utilised habitats along the northern shore of the sea loch and in Loch a' Chadh'fi (a northern arm of the main Loch Laxford (Figure 1)). By September and October, post-smolts were detected almost exclusively within the estuary near the original tagging site.

## b) $M Y M s$

Of the 38 receivers within the Laxford array, MYM fish were only detected at six receivers located in the estuary and river arrays of the study site. The receivers that detected the highest total number of individuals were 131691, 126845 and 482008 (all in the estuary array area of study site) with eight, six and five tags reported at each respective receiver.

The longest mean residency event for MYM fish was reported by receiver 131695, the most downstream receiver of the river array. The mean residency time spent at this receiver was $301 \pm 638$ minutes (mean $\pm$ SD). Receivers 131691 and 482008 (both in the estuary array) reported the next longest mean duration times of $67 \pm 88$ and $58 \pm 74$ minutes (mean $\pm$ SD) respectively. The receivers with the shortest residency events (of those where a residency event was detected) were 126846 (in the river array) and 126845 (in the estuary array). Receiver 126846 reported a singular residency event of 18 minutes, from Tag 3830, and Receiver 126845 reported a mean residency time of $35 \pm 41$ minutes.

Based on presence/absence data (Figure 6), there was a similar temporal pattern of movement to that seen in the post-smolts; with some fish detected almost continuously and other relatively intermittently throughout the study period.

Seasonal changes in MYM fish spatial use were not as clearly demonstrated as they were in the post-smolt movement patterns, but some differences were observed (Figure 7). More tagged MYM fish were detected within the freshwater system in July and residency events were generally longer at the receiver located at the mouth of the river than in other locations. One MYM fish was detected at Receiver 126846 in the River Laxford in July, suggesting that it migrated upstream instead of remaining the marine environment at that time. However, from August until the end of the study, no fish were detected in the freshwater system. Based on detections, the remaining fish spent their time migrating between Traigh Bad na Baighe and Laxford estuaries (Figure 1). In October, only one fish was detected moving between Receivers 131691 and 126845.

## 3. Influence of $L$. salmonis on habitat preference

Of the 99 fish tagged, total of 17 individuals were found to be infected with L. salmonis. Given that previous research suggests that increased L. salmonis loads can lead to early freshwater re-entry by sea trout attempting to rid themselves of the parasites (Halttunen et al., 2014), the movement of these individuals into the River Laxford was examined to determine if similar behaviour could be observed in the Loch Laxford population.

Two receivers (131695 and 126846) were located in the River Laxford, at the river mouth and $\sim 1.5 \mathrm{~km}$ upstream respectively. A total of 26 fish were detected by these two receivers, 11 of which had been infected with L. salmonis when they were tagged. All 11 of these individuals were detected at Receiver 131695, while only two of the infected fish were detected at Receiver 126846, Tags 3830 (three L. salmonis at the time of tagging) and 3587 (one L. salmonis at the time of tagging) The mean number of $L$. salmonis on these 11 fish was $3.7 \pm 3.6$ L. salmonis /fish (mean $\pm \mathrm{SD}$ ). The remaining six fish that had been infected with $L$. salmonis during tagging but were not detected at the river receivers had a mean number of $L$. salmonis of $5.7 \pm 2.9$ L. salmonis /fish (mean $\pm \mathrm{SD}$ ).

The mean residency time that these 11 fish spent within range of the river array receivers was $221 \pm 486$ minutes (mean $\pm \mathrm{SD}$ ) and the mean residency time spent at the receivers in the rest

Tag ID


of the Laxford array was $30 \pm 51$ minutes. Therefore, despite that the zone of detection for receivers in the estuary was likely to be much higher than in the river, individuals infected with sea lice at the start of the study appeared more likely to spend more time close to freshwater receivers than to receivers in the marine environment.

A Chi-squared test was performed to examine the frequency of detection of fish with and without a $L$. salmonis infection at receivers located in marine or freshwater habitats. In this study sea trout infected with L. salmonis were more frequently detected at receivers in the river array and less likely to be detected at receivers in marine waters than sea trout that are not infected ( $\chi^{2}=7.69, \mathrm{df}=2, \mathrm{P}=0.021$ ).

## 4. Leaving the array

a) Post-Smolts

Four of the 77 detected post-smolts were last detected on the outer line of the array, indicating that they left Loch Laxford. These fish did not return for the duration of the study. Three were tagged in May. Two of those individuals left within a month of being tagged and the third at the beginning of July. All three post-smolts were last detected by receiver 547516, which was located in the middle of the outer receiver line (Table 1; Figure 1). The fourth fish was tagged in mid-July and was last detected at the outer line at the end of August. It was last detected by the most northern receiver (480412) in the outer line that was positioned between the coast and a small rocky outcrop in the sea. This would suggest that the individual left the sea loch following the coast.

Three post-smolts were last detected at the most upstream receiver located in the River Laxford (126846), however, their migration patterns before entering the river varied between individuals. One of these post-smolts (Tag 3793) was tagged in May and spent two months migrating around the majority of the sea loch array before entering the river at the beginning of the July. It was not detected on any receiver after being detected by the upstream receiver, suggesting that it did not return to the sea loch for the rest of the study. The remaining two post-smolts that were last detected by Receiver 126846 did not migrate out of the estuary array and were each detected by the upstream receiver on two separate occasions in mid-July with several days between detections. These fish were not detected by any other receivers once they had been detected at Receiver 126846 indicating that although they moved out of
the detection range of this upstream receiver, they did not return to the main array in the marine environment.

Only one post-smolt that was detected by the most upstream receiver was later detected by the downstream receiver located at the mouth of the river. This individual was detected on Receiver 126846 on two separate occasions but after both visits was detected back at Receiver 131695, indicating that it migrated back down stream instead of continuing an upstream migration.

However, in addition to these eight individuals, another seven post-smolts were last detected at the most downstream receiver of the River Laxford located in the river array, two in May soon after tagging, five in mid-July between the $14^{\text {th }}$ and $17^{\text {th }}$, and one in mid-August. Furthermore, two post-smolts were last detected by Receiver 126845 positioned in Traigh Bad na Baighe estuary (Figure 1) close to the mouth of Allt Bad na Baighe, one in August and one in September. It is likely that these nine post-smolts could have left the array via freshwater rivers but this cannot be confirmed because they were not detected further upstream. In the case of Allt Bad na Baighe, this cannot be confirmed because no receivers were stationed in the river.
b) $M Y M s$

One tagged MYM was last detected at the most upstream receiver located in the River Laxford, suggesting that it entered the freshwater environment and did not return to the sea loch. After it was tagged on July $13^{\text {th }}$, the fish spent several days at Receiver 131695, the most downstream receiver of the river array. It was last detected here on July 17 ${ }^{\text {th }}$ at 12:00. The next detection was reported at the upstream receiver, 126846, on July $22^{\text {nd }}$ at 01:00. These detections suggest that it took the fish just under five days to migrate through the 1.5 km stretch of river between the receivers.

Furthermore, four more MYM were last detected by the receiver positioned in Traigh Bad na Baighe estuary close to the mouth of Allt Bad na Baighe. One of these individuals was detected at the beginning of August, only a few weeks after tagging. Two of the fish were last detected between mid- and late September and the final individual was last detected at the end of October. These four fish may well have left the array via freshwater rivers but this cannot be confirmed because there were no receivers to allow detections further upstream.

No tagged MYM were detected on the outer array, suggesting that none of them left the study area for more open coastal marine habitat.

## 5. Home range

The majority of tagged fish spent the duration of the study within the Laxford estuary, an area of approximately $0.2 \mathrm{~km}^{2}$ at high tide. Of the 85 fish detected in this study, only 22 postsmolts were detected on receivers outside the estuary array, westward of Receiver 480414. Given the non-parametric distribution of the data, a series of Kruskal-Wallis tests were conducted to determine if fish length was influencing a fish's decision to migrate from the estuary array into the sea loch. Firstly, the fish length of all detected individuals was compared to their decision to leave or remain in the estuary array. There was no significant difference between the mean length of fish that stayed within the estuary array (202.8 $\pm$ 48.8 mm , mean $\pm \mathrm{SD}$ ) and the mean length of fish that left the estuary array ( $201.8 \pm 34.8 \mathrm{~mm}$ ) $\left(\chi^{2}=54.3, \mathrm{df}=55, \mathrm{P}=0.5\right)$.

The home range of individual fish was calculated using the Minimum Convex Polygon (MCP). This determines the smallest polygon around all points where an animal was located and is a common estimator of home range. However, MCP may sometimes include areas which are not utilised by the individual. To identify more clearly the space used by individuals the MCP level can be set so that 'outliers' or positions furthest from the core area of detections are removed. For example, setting the MCP level to ' $60 \%$ ' will remove the $40 \%$ furthest locations from the core detection area as determined by the mean of the coordinates of the relocations for each animal.

In this study the minimum number of receivers a fish was detected at before a polygon could be determined was set at five. This is due to the proximity of the receivers within the estuary array, and effective detection range of the tags. Using five receivers ensures that fish were actually moving out from the estuarine array.

The vast majority of fish (63) were not detected beyond receiver 480414 (the outermost estuary array receiver (Figure 1)), indicating that they did not move out into the main sea loch. They were not detected on five or more receivers and thus home range was not calculated. However, 15 individuals (all post-smolts) were detected on 5 or more receivers and thus home ranges were calculated. The mean total area covered ( $100 \% \mathrm{MCP}$ ) by this
group of sea trout was $937.2 \pm 917.4 \mathrm{~m}^{2}$ (mean $\pm$ S.D.; Range $85.7 \mathrm{~m}^{2}$ to $2696.3 \mathrm{~m}^{2}$ ). Home range at $60 \%$ MCP was smaller at $257.7 \pm 353.5 \mathrm{~m}^{2}$. As the majority of fish were not detected beyond the estuary and because the MCP area at the $60 \%$ level was considerably smaller than at $100 \%$, this indicates this population of fish is showing high site fidelity. A small number of excursions were made throughout the sea loch by a small number of individuals, however these do not equate to substantial time being spent elsewhere in the loch away from the estuarine array. This is further supported by the sudden jump in home range size at $>90 \%$ MCP level. For example, Tags $3797,3827,3685,3592,3568$ and 3559 all have a home range of 0 (detected on less than 5 receivers) up to the $80 \%$ MCP level where there is subsequently an increase in the area used, indicating that short excursions have occasionally occurred further out into the loch but the vast majority of the time fish are spending within the estuary zone.

A GLM model was developed to investigate the relationship between the $100 \% \mathrm{MCP}\left(\mathrm{m}^{2}\right)$ occupied by each of the 15 fish and fish length (mm). Fish length did not significantly predict the size of the area used $(\mathrm{P}=0.95)$.

## 6. Rate of movement

The mean swimming speed of sea trout was estimated using non residency events, or the period of time between subsequent receiver detections. This was the time from when a fish was last detected at Receiver A until when that fish was first detected by Receiver B. Using the distance (by sea) between receivers, and the travel time between outer edges of the detection ranges of receivers, a minimum speed of travel can be calculated.

A total of 63 tagged fish were only detected by receivers in the estuary and due to the number of residency events (approximately 700), it is apparent that these fish were moving between receivers constantly. However, due to the proximity of receivers in some sections of the study array, like the estuary, it is not always possible to accurately calculate the swimming speed of the sea trout because of an overlap in receiver ranges. With a large detection range, a receiver can report that a fish has reached the location of a receiver when it has in fact only reached the edge of the receiver's detection range that could still be over 150 m away from the coordinates of the receiver. This can lead to physically impossible swimming speeds.

To account for this effect, non-residency events were calculated for small subsets of fish that were detected by multiple receivers across the array. Receivers 480407, 547512, 131694, 547510 and 547516 (Figure 1) form a straight line through Loch Laxford and were thought to provide an accurate measure of the uninterrupted active swimming speed of a sea trout. A subset of the detections of seven sea trout post-smolts that were detected along this line was analysed. The mean swimming speed determined for this group of fish was $0.21 \pm 0.12 \mathrm{~m} / \mathrm{s}$ (mean $\pm$ SD).

The swimming speed of those individuals that migrated up the River Laxford during the course of the study was also calculated. A subset of five fish (four post-smolts and one MYM fish) reported a mean swimming speed of $0.04 \pm 0.06 \mathrm{~m} / \mathrm{s}$ between Receiver 131695 at the mouth of the river and Receiver 126846 located approximately 1.5 km upstream. Based on the detections of these five fish, migration through this section of river ranged from a few hours to almost five days.

## 7. Engagement with areas of interest

## a) Aquaculture facilities

Loch Laxford hosts two open net Atlantic salmon aquaculture units (Figure 1). A receiver was deployed at each farm site to monitor the movement of tagged sea trout in the area. The receiver that was located next to the outer most farm (131693) did not detect any fish over the course of the study. The inner most receiver (131694) detected a total of three tagged individuals.

Tag 3793, a post-smolt, was detected on two different days over a two-week period by this receiver in June 2018. It was detected twice over a 20-minute period around 05:00 on June $6^{\text {th }}, 2018$. It was later detected twice over a two-minute period around 07:00 on June $17^{\text {th }}$, 2018. Tag 3557, a second post-smolt, was detected twice over a ten-minute period around $06: 15$ on June $20^{\text {th }}, 2018$. Tag 3825 , also a post-smolt, was detected twice over a two-minute period around 06:00 on August $2^{\text {nd }}, 2018$.

It is clear that there are a very small number of both detections and residency events recorded by receivers located at the fish farms, strongly indicating that these units are not attracting fish.

## b) Mussel farm interaction

Of the 38 receivers within the Laxford array, three ( 000545,480407 and 547513) were within an estimated 200 m (the maximum detection range of a receiver for this study) of a mussel farm found in the sea loch (Figure 1). Therefore, tags that were detected by these three receivers were identified as fish that could have possibly used the same habitat as the mussel farms over the course of this study. In total, 12 individuals were detected by the three receivers, all from the post-smolt cohort (3558, 3557, 3792, 3793, 3682, 3796, 3579, 3560, 3788 and $3568,3825,3592$ ). Most of these fish were detected by one of the receivers, generally 480407 , located near a mussel farm with a few weeks of being tagged. As the study progressed, however, several of the 12 fish were detected multiple times within range of a mussel farm.

The mean duration of time reported by the three receivers varied slightly. Receiver 480407 was located near to the inner-most mussel farm in the sea loch and, of the three mussel farm receivers, was closest to the main tagging site in the estuary. It detected all of the 12 individuals and reported a mean residency event of $89 \pm 192$ minutes (mean $\pm$ SD). Receiver 547513 reported a similar mean residency event of $10 \pm 15$ minutes, but only detected eight individuals. Receiver 000545 was located in Loch a' Chadh'fi and detected four individuals but reported the longest mean duration time of the three receivers at $20 \pm 28$ minutes.

The mean residency event that these 12 individuals spent within range of the three receivers adjacent to mussel farms was $53 \pm 145$ minutes (mean $\pm \mathrm{SD}$ ) and the mean residency event spent at the remaining 38 receivers in the rest of the array was $38 \pm 100$ minutes.

## c) Loch a' Chadh 'fi use

Four tagged post-smolts were detected by receivers located in Loch a' Chadh'fi (Figure 1), a smaller and more sheltered inlet on the northern coastline of Loch Laxford, three of which were tagged in May (Tags 3557, 3560 and 3793) and one that was tagged in July (Tag 3825). These individuals are four of the most widely detected fish across the array, meaning that they were detected by a larger number of receivers compared to other fish in the study. These fish were detected at the mouth of Loch a' Chadh'fi by receiver 482007 soon after their respective tagging dates. Later, they were detected by the remaining three receivers located
further into the loch, however, the time that it took the fish to migrate entirely through Loch a' Chadh'fi (from Receivers 482007 to 482011 ) ranged from 12 days (Tag 3793) to three hours (Tag 3825). All four individuals were detected within Loch a' Chadh'fi on multiple occasions and would spend time ranging from hours to days within detection range of the receivers. They were also detected by other receivers in the main loch between periods of occupation of Loch a' Chadh'fi, suggesting that they migrated between Loch a' Chadh'fi and Loch Laxford several times over the course of the summer.

The mean time these individuals spent at each receiver within Loch a' Chadh'fi ranged from $10 \pm 11$ minutes (mean $\pm \mathrm{SD}$ ) at receiver 482007 to $56 \pm 76$ minutes at receiver 551. The mean residency event spent at the Loch a' Chadh'fi receivers was $32 \pm 52$ minutes and the mean residency event spent at the Loch Laxford receivers was $26 \pm 107$ minutes.

## V. DISCUSSION

In this study, 99 sea trout were tagged and 85 were detected on the receiver array. Of the 14 undetected individuals, 12 were tagged from fish trapped in Allt Bad na Baighe but were never detected in the estuary array. If post-smolts from the Allt Bad na Baighe had expired after tagging, research suggested the carcasses should have been washed downstream into the Traigh Bad na Baighe estuary, less than 0.5 km away, where they would most likely have been detected by the receiver located there (Strobel et al., 2008; Havn et al., 2017). Therefore, it is likely that these fish "de-smolted", a recognised process in salmonid smolts (Aarestrup et al., 2000; Jonsson \& Jonsson, 2008; Thorstad et al., 2012). Although the exact causes of de-smolting are unknown, it is thought that water temperature, stress or lack of access to the marine environment due to barriers could encourage a smolt to change its migratory physiology to remain in freshwater (Jonsson \& Jonsson, 2008). There is some evidence to suggest that salmonid smolts that undergo a de-smolting process are capable of re-smolting the following year (Shrimpton et al., 2000).

## 1. Post-smolts

The majority of the post-smolts tagged in this study were caught in May, however, based on fish length there were still a few post-smolts migrating into the estuary in July, with some as small as 141 mm and 155 mm (well below the mean length of the post-smolts tagged in May).

This late marine entry is not uncommon in sea trout which generally have a more prolonged migration period than other salmonids such as Atlantic salmon (Thorstad et al., 2016).

Based on the reported detection levels, there was a decline in sea trout post-smolts in the array within the first week of tagging. The first weeks in the marine environment are crucial to sea trout post-smolt survival and with unfamiliar pressures like predation and adjustment to saline conditions, high mortality rates amongst post-smolt as they enter the marine environment is suspected (Thorstad et al., 2016). Middlemas et al. (2009) reported a $50 \%$ loss in the number of fish detected in the first two weeks of their study, suggesting a similar decline to that reported here. Although some of this decline in the Laxford population could represent mortality, several tags were detected multiple times over the following weeks, indicating that some of the tagged individuals must have migrated to a location outside the receiver range before returning to the array. It is reasonable that the site fidelity exhibited within the estuary array receivers was shown in other locations outwith the detection area of acoustic receivers.

The decline in detection levels continued over the summer, likely influenced by mortality and decreasing battery life of the tags, however, it is apparent that sea trout post-smolts spent large amounts of their time foraging in Loch Laxford, particularly the estuary array, instead of moving out to the deeper water of the ocean or returning to freshwater. Of the 77 detected post-smolts, only $5 \%$ were detected leaving the array through the outer line and $3 \%$ were detected at the most upstream river receiver. Of those fish that remained active in the sea loch, longer residency events were recorded in areas within the estuary array of Loch Laxford and along the coastline than in more open water of the sea loch.

These patterns of habitat use are similar to those demonstrated in the few other studies of salmonid marine habitat use in Scotland. Sea trout have been documented remaining near to their natal river several weeks after their initial migration for several weeks (Pemberton, 1976; Middlemas et al., 2009). Coastal areas are also well documented as habitats used frequently by sea trout, particularly in the first few months of their marine migration (Davidsen et al., 2014; Thorstad et al., 2016).

As the summer progressed, more fish were detected on receivers in the middle and outer sections of the array (Figure 5), suggesting that as some post-smolts continued to feed, they would gradually expand their home range and feeding grounds. This gradual increase in home range over time has been observed in other Scottish studies (Middlemas et al., 2009).

Post-smolts that did enter the sea loch to feed exhibited marginally longer mean residency events at receivers located along the shores of the sea loch, suggesting that there was some benefit to remaining there, either a better food supply or shelter from predators. Interestingly, higher numbers of tagged post-smolts were being detected by the middle line of the array than were detected on most coastal receivers in June. This could suggest that as the postsmolts grew bigger, they were more comfortable travelling through deeper water and did so either to access larger prey items that would inhabit these areas or to migrate more swiftly to another location within the sea loch.

Several individuals were detected on more than half of the receivers in the array, indicating that they occupied a large proportion of the sea loch during their summer migration.

However, the receivers located in the estuary array continued to act as the primary habitat for the majority of the post-smolts; this relatively limited area consistently reported the highest number of tags and longest residency events.

Another area of importance for a proportion of the post-smolt population is Loch a' Chadh'fi. Of the 22 post-smolts that were detected beyond the estuary, $18 \%$ of the population ( 4 individuals) actively migrated into Loch a' Chadh'fi on several occasions, presumably feeding in the area, given the mean residency events reported at the receivers located there. This is supported by the finding that four post-smolts spent slightly longer at the Loch a' Chadh'fi receivers compared with the rest of the array. Due to the quiet location and sheltered coast line, Loch a' Chadh'fi would appear to provide a particularly suitable summer feeding habitat for feeding sea trout post-smolts.

The movement of several fish, primarily post-smolts, further into the River Laxford from July to August showed a different habitat use pattern from that observed in the wider study group and indicating a strong freshwater habitat use very early in the summer.

Four post-smolts were detected at the upstream receiver in the River Laxford. Two exhibited unique behaviour within the freshwater habitat. One post-smolt migrated between the upstream and downstream receivers several times in June before its last detection which was reported at the downstream receiver of the river array. Another post-smolt was last detected on the upstream receiver a single time on July $4^{\text {th }}$.

The other two post-smolts were detected at the upstream receiver twice over several days between July $18^{\text {th }}$ and August $2^{\text {nd }}$ with several days between detections, suggested that either they reached the receiver and fell back downstream and maintained an out of range position
between the upstream and downstream receivers, or migrated further upstream beyond the upstream receiver, only to fall back briefly within detection range before continuing up river again.

Due to high levels of precipitation, river height increased from 0.09 m on July $20^{\text {th }}$ to 0.42 m on July $23^{\text {rd }}$. The mean river height of the Laxford in July was $0.13 \pm 0.10 \mathrm{~m}$. It is thought that this increase in flow rate could have influenced the time of migration of the three fish that were first detected by the upstream receiver from July $18^{\text {th }}$ to $24^{\text {th }}$. Although these fish moved very differently around the estuary array, including entering freshwater at different times, all of these fish were firstly detected at the most downstream receiver (131695) for an extended period of time before they were detected further up the river, and secondly they were detected at the upstream river receiver (126846) between July $22^{\text {nd }}$ and $24^{\text {th }}$, indicating that some similar migration strategy during periods of peak rainfall. It was also noted that the individuals that were detected at the most upstream receiver in the river were not detected anywhere below the downstream receiver located at the mouth of the river after their first detection upstream. This would suggest that once the fish enter into the freshwater system over the summer, they are not returning to the estuary or sea loch to feed.

Post-smolts have been known to re-enter river systems after spending a summer at sea to over-winter in freshwater (Thorstad et al., 2016), however the upstream migration that occurred in July was earlier than expected. There are several freshwater lochs within the River Laxford system that could provide suitable habitat and feeding grounds for the sea trout that were detected last at Receiver 126846 and appeared to have continued their migration upriver.

## 2. Multi Year Migrants

Detections of the older age fish that had migrated into the marine environment in previous years also showed a strong preference for in the Laxford estuary array. There were no detections of an MYM individual beyond Receiver 480414, indicating that MYM fish were only using the Laxford and Traigh Bad na Baighe estuaries as feeding grounds.

One MYM was detected upstream in the River Laxford on July $22^{\text {nd }}$. This was its last detection. Its detection coincided with the movements of the post-smolts that migrated
upstream. This would suggest that this fish was also influenced by the high flow levels in the River Laxford during this month and migrated upstream.

In addition, a further four MYMs were last detected in Traigh Bad na Baighe estuary. Although there was no receiver positioned in Allt Bad na Baighe to determine if these individuals did actual enter the freshwater environment, most of these fish were detected in the Traigh Bad na Baighe estuary over the course of several days before their final detection, similar to the one individual that was detected in the upstream receiver of the Laxford River. River height was high in September (mean $\pm$ SD of the month was recorded at $0.67 \pm 0.23 \mathrm{~m}$ ), suggesting that any fish migrating upstream would be able to access the river at any time given the level of spate flows.

Given the variation in each fish's residency times at the freshwater and estuarine receivers located below the River Laxford and Allt Bad na Baighe, it is thought that these four sea trout ere using these nutrient rich and sheltered tidal areas as a final opportunity to feed and gain condition before entering freshwater during high water flow to await the spawning season.

Despite the potential for the majority of MYM fish to have left the array through freshwater rivers, there were still one fish detected in the array into October. The presence of this fish in the estuary array and not within the freshwater array, would suggest that a small portion of MYM sea trout remain in the marine environment over the winter to feed, a well-documented behaviour (Thorstad et al., 2016).

## 3. Influence of $L$. salmonis on movement

Early freshwater re-entry is a common behavioural response by sea trout, thought to be as an attempt to remove lice (Shephard et al., 2016). Fish that were infected with L. salmonis on the day that they were tagged were more likely to spend time in the river array than fish that were not infected. However, the majority of fish used in this study had low levels of L. salmonis at the time of tagging. Thorstad et al. (2015) referenced that natural levels of $L$. salmonis in areas without aquaculture had been reported at 4-8 individual lice per fish in the summer months, and fish in this study showed similar parasite burdens at time of tagging. Therefore, the infected individuals may not have been under heavy stress from their parasite loads and, as a result, may not have needed to move into freshwater habitats for extended periods of time to de-louse.

## 4. Areas of anthropogenic interaction

Although research suggests that a wide variety of wild fish can be attracted to aquaculture facilities, particularly in warmer climates (Uglem et al., 2014), less is known about wild salmonid-specific interactions with sea cages (Thorstad et al., 2012). Given the low number of detections at the two aquaculture pens in the sea loch, as well as the low number of detections at receivers located along the southern coastline closest to the pens, this study shows that salmon pens are not attracting sea trout to their immediate vicinity.

While the receiver array for this system was not dense enough to identify fine scale interactions between sea trout and mussel farms, some observations about the relationship could be made. $50 \%$ of the 22 fish that were detected beyond the estuary were detected at a least one of the three receivers adjacent to mussel farms. Mean residency events of the 12 fish detected near the mussel farms were similar at both the receivers adjacent to the mussel farm and the rest of the array indicating that mussel farms were neither attracting or discouraging habitat use near to these installations.

Overall, the data suggests that a large majority of Loch Laxford sea trout (both post-smolts and MYM) are remaining within the Laxford estuary to feed over the duration of the summer. The muddy intertidal and shallow sublittoral habitats of the Laxford estuary and Traigh Bad na Baighe, including sheltered Loch a' Chadh'fi, can support diverse marine communities structurally dominated by seaweed (James 2004). These nutrient rich areas were clearly capable of providing enough food sources and shelter to support the foraging of the majority of tagged sea trout during the summer months, more so than other rockier shores or deeper locations around the sea loch.

Although there was some deviation from this general behaviour pattern as roughly $20 \%$ of the 77 detected post-smolts migrated from the estuary into the main sea loch to forage, ultimately this study did demonstrate that very few sea trout are leaving their natal sea loch to feed and therefore reinforces the importance of sea loch "nursery" habitats not only to young anadromous trout, but also to older individuals that are feeding in the same areas.

This study has shown that:

- The sea trout in Loch Laxford have a strong preference for a small area with a very specific habitat for summer feeding
- Because the summer feeding habitat of sea trout is so geographically constrained, the potential impact on sea trout by an inappropriate anthropogenic activity if it were to affect this area is substantial
- Effort should be made to identify similar important habitats for sea trout elsewhere with a view to protecting this important component part of sea trout ecology

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| u！̣யəУ | ${ }^{1} \mathrm{lous}$－ $\mathrm{FSO}_{\mathrm{d}}$ | 8I0Z／¢0／6I | 8I0Z／S0／9 I | LS＇Z | 02 | 86I | projxe7 | 8IOZ／S0／¢I | ¢LSE |
| u！̣шวप |  | 8I0Z／80／ちI | 810Z／90／6I | $\varepsilon L^{\circ}$ 亿 | 99 | 861 | projxe7 | 8IOZ／S0／¢I | 七LSE |
| әлвวТ | ${ }^{1}\left[\mathrm{OUSS}-\mathrm{lsO}_{\mathrm{d}}\right.$ | 810Z／¢0／0¢ | 810Z／S0／¢ I | $60^{\circ} \mathrm{Z}$ | 98 | E0Z | projxe7 | 8IOZ／S0／¢I | ZLSE |
| u！̣யəУ | ${ }^{1}\left[\mathrm{OUS-}\right.$－ $\mathrm{SO}_{\mathrm{d}}$ | 8I0Z／80／0I | 8I0Z／S0／S I | $00^{\circ} \mathrm{\varepsilon}$ | 09 | 08I | projxe7 | 8IOZ／S0／¢I | ILSE |
| u！̣шəप |  | 8L0Z／¢0／9I | 810Z／¢0／¢ I | $00 \cdot \varepsilon$ | 09 | ¢8I | projxe7 | 8I0Z／S0／¢ I | $0 \angle \varsigma \varepsilon$ |
| u！̣шəप |  | 810Z／L0／0Z | 810Z／¢0／¢ I | $\varepsilon \downarrow$ ¢ | tL | I6I | p．ojxe7 | 8I0Z／S0／¢I | 69¢E |
| วлеวТ | $\mathrm{H}^{\text {［ous－}}$－ $\mathrm{SO}_{\text {d }}$ | 8L0Z／0I／0¢ | 8L0Z／S0／G I | L0\％ | L8 | E0Z | projxe7 | 8I0Z／S0／¢ | 89¢E |
| u！̣யшวप |  | 8I0Z／90／9I | 8I0Z／¢0／¢ I | I6 $\mathcal{E}$ | 9t | ZLI | profxe7 | 8IOZ／S0／¢ | L9¢E |
| u！̣யəप | ${ }^{1} \mathrm{lous}-\mathrm{lfO}_{\mathrm{d}}$ | 8I0Z／90／6I | 8I0Z／S0／S I | $98^{\circ} \mathrm{Z}$ | £9 | Z6I | projxe7 | 8IOZ／S0／¢ | 99¢£ |
| u！̣யəy |  | 810Z／90／L0 | 8I0Z／S0／S I | $\varepsilon L^{\circ}$ ¢ | 99 | L8I | projxe7 | 8IOZ／S0／¢I | ¢9¢E |
| u！̣யəУ |  | 810Z／90／90 | 8I0Z／S0／S I | ¢0＊$\varepsilon$ | 6 S | 88I | projxe7 | 8IOZ／S0／¢I | ャ9¢E |
| әлеวТ |  | 8［0Z／90／0I | 810Z／90／0I | $6 \varepsilon^{*} \downarrow$ | It | 29I | projxe7 | 8I0Z／S0／¢ | E9¢E |
| u！̣யəप | ${ }^{1}\left[\mathrm{OUSS}-\mathrm{FSO}_{\mathrm{d}}\right.$ | 8I0Z／S0／SI | 8I0Z／S0／S I | $6 \varepsilon^{*} \downarrow$ | It | \＆9I | projxe7 | 8IOZ／S0／¢I | Z9¢E |
| u！̣шәप |  | 810Z／80／9Z | 8I0Z／S0／¢ I | $9 \downarrow^{\bullet} \varepsilon$ | ZS | 8LI | profxe7 | 8IOZ／S0／¢ | ［9¢\＆ |
| әлвวТ | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\mathrm{d}}$ | 810Z／90／8て | 8I0Z／S0／9I | ¢6\％ | I9 | 06I | profxe7 | 8IOZ／S0／¢ | 09¢\＆ |
| әлеәТ |  | 810Z／60／80 | 8I0Z／S0／S I | $60^{\circ}$ ¢ | tt | \＆9I | projxe7 | 8IOZ／S0／¢I | 6¢¢E |
| әлвวТ |  | 8L0Z／S0／IE | 8I0Z／S0／S I |  | $\varepsilon L$ | 66 I | projxe7 | 8IOZ／S0／¢I | 8¢¢E |
| วлеวТ |  | 810Z／L0／ち0 | 810Z／¢0／¢ I | $\bigcirc 0^{\circ} \mathrm{E}$ | 6 S | L8I | p．ojxe7 | 8I0Z／¢0／¢I | L¢SE |
| әэ！๐чด K．Jentst |  |  |  | uәp．ng $\mathrm{Sb}_{\mathbf{L}}$ | （ $\mathbf{0})$ ทЧธ゚！จМ |  |  |  |  |



| u！̣шәу | ${ }^{7} \mathrm{HOUS-} \mathrm{q}^{\text {SO}}{ }_{\text {d }}$ | 8 IOZ／¢0／8I | 8IOZ／¢0／¢ | $0 \downarrow^{\bullet} \varepsilon$ | $\varepsilon \varsigma$ | †LI | p．ojxe7 | 8 IOZ／¢0／¢ | 018E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| แ！̣шวу |  | 810Z／01／90 | 8I0Z／S0／9I | 6でも | て† | 991 | p．ofxe7 | 8 IOZ／¢0／¢ | $608 \varepsilon$ |
| u！¢шวу |  | 810Z／¢0／0Z | 810Z／¢0／¢ | $9 \downarrow^{\circ} \mathrm{E}$ | ZS | ¢LI | profxe7 | 810Z／¢0／¢ ¢ | 808E |
| u！̣шวу |  | 810Z／L0／Z0 | 8I0Z／¢0／¢ | $06^{\circ} \mathrm{Z}$ | Z9 | E8I | profxe7 | 810Z／¢0／¢ ¢ | L08E |
| u！pшəУ |  | 810Z／¢0／¢ | 8I0Z／S0／¢ | $\varepsilon \varepsilon^{*} \varepsilon$ | 七S | E8I | profxe7 | 810Z／S0／¢ | $908 \varepsilon$ |
| әлеәТ | ${ }^{+1}{ }^{\text {Ous－}}$－ $\mathrm{SO}_{\text {d }}$ | 810Z／¢0／ちて | 8L0Z／S0／¢ I | $09^{\circ} \mathrm{E}$ | 0S | 6LI | profxe7 | 8 IOZ／¢0／¢ | ¢08E |
| әлеәТ |  | 810Z／¢0／ZZ | 810Z／¢0／¢ |  | I9 | 06 I | profxe7 | 810Z／¢0／¢ | †08\＆ |
| แ！̣шวу |  | 810Z／90／E0 | 810Z／¢0／¢ I | $98^{\circ}$ | $\varepsilon 9$ | 981 | p．ojxe7 | 8 IOZ／¢0／¢ | E08E |
| แ！̣шәу | ${ }^{+1}{ }^{\text {Ous－}}$－ $\mathrm{SO}_{\text {d }}$ | 8I0Z／L0／9I | 810Z／¢0／¢ I | 6 ¢ $^{\text {¢ }}$ | It | E9I | profxe7 | 8 IOZ／¢0／¢ | Z08E |
| u！̣шวу | ${ }^{+1}{ }^{\text {Ous－}}$－ $\mathrm{SO}_{\mathrm{d}}$ | 810Z／L0／8Z | 810Z／S0／¢ | Lで乏 | ¢S | ¢9I | p．ofxe7 | 810Z／¢0／¢ | ［08E |
| әлеәТ |  | 810Z／90／LZ | 8I0Z／S0／¢ I | $\varepsilon \varepsilon^{*} \varepsilon$ | tS | 6LI | profxe7 | 810Z／¢0／¢ | $008 \varepsilon$ |
| u！̣யəУ | ${ }^{7} \mathrm{OUS-4} \mathrm{SO}_{\mathrm{d}}$ | 810Z／S0／¢ | 8IOZ／S0／S I | $00^{\circ} \varepsilon$ | 09 | 8LI | projxe7 | 810Z／S0／¢ | 66LE |
| แ！̣шวУ |  | 810Z／¢0／LE | 810Z／¢0／¢ | $00^{\circ} \mathrm{Z}$ | 06 | Z0Z | profxe7 | 810Z／¢0／¢ | 86LE |
| u！pшวУ |  | 810Z／80／L0 | 8I0Z／S0／¢ | しナて | $\varepsilon L$ | ¢6I | p．ofxe7 | 810Z／¢0／¢ | L6LE |
| әлеәТ |  | 810Z／90／9Z | 810Z／¢0／¢ | $0 \downarrow^{\circ} \mathrm{E}$ | ES | 08I | p．oyxe7 | 8［0Z／¢0／¢ | 96LE |
| u！¢யวу |  | 810Z／¢0／¢ | 810Z／¢0／¢ | $00^{\circ} \mathrm{\varepsilon}$ | 09 | 781 | projxe7 | 8 I0Z／¢0／¢ | ¢6LE |
| u！̣шวу |  | 810Z／01／90 | 810Z／S0／¢ | tS＇Z | IL | 76I | p．ofxe7 | 810Z／¢0／¢ | †6LE |
| әлеәТ | ${ }^{+1}{ }^{\text {Ous－}}$－ $\mathrm{SO}_{\mathrm{d}}$ | 810Z／L0／E0 | 810Z／S0／¢ | しがて | $\varepsilon L$ | 681 | p．ofxe7 | 810Z／S0／¢ | £6LE |
| әлвәТ | ${ }^{7} \mathrm{OUS-4} \mathrm{SO}_{\mathrm{d}}$ | 810Z／90／L0 | 8I0Z／S0／SI | $00^{\circ} \mathrm{E}$ | 09 | L8I | projxe7 | 810Z／S0／¢ | Z6LE |
| u！pшวу | ${ }^{7} \mathrm{HOWS}-\mathrm{lSO}_{\mathrm{d}}$ | 810Z／90／E0 | 8IOZ／S0／¢ I | t＜＇t | $8 \varepsilon$ | LSI | projxe7 | 810Z／¢0／¢ | I6LE |
| แ！̣шวу | ${ }^{+}{ }^{\text {Ouss－}}$－ $\mathrm{SO}_{\text {d }}$ | 810Z／90／E0 | 8I0Z／¢0／¢ I | L9 ${ }^{\circ}$ | 6 t | ELI | profxe7 | 8 IOZ／¢0／¢ ¢ | 68LE |
| әлеәТ |  | 8I0Z／90／9I | 810Z／¢0／¢ | じて | $\varepsilon L$ | 8LI | profxe7 | 810Z／¢0／¢ | 88LE |
| u！¢யวу |  | 810Z／¢0／0¢ | 810Z／¢0／¢ | $0 \downarrow^{\circ} \mathrm{E}$ | $\varepsilon ¢$ | ¢ 21 | projxe7 | 8 I0Z／¢0／¢ | L8LE |
| и！ршวу |  | 810Z／L0／¢ | 8I0Z／S0／¢ I | $06^{\circ} \mathrm{Z}$ | 29 | 06I | profxe7 | 8IOZ／S0／S I | $989 \varepsilon$ |
| әлвәТ |  | 810Z／S0／0Z | 8I0Z／S0／¢ I | てİて | ¢8 | ［6I | projxe7 | 810Z／¢0／¢ | ¢89E |
| u！pшวу | ${ }^{7} \mathrm{HOWS}-\mathrm{lSO}_{\mathrm{d}}$ | 8I0Z／S0／¢ | 8IOZ／S0／¢ I | $06^{\circ}$ | 29 | ¢8I | p．ojxe7 | 8I0Z／S0／GI | †89E |
| แ！ршวу | ${ }^{+1}{ }^{\text {Ous－}}$－${ }^{\text {SOd }}$ | 810Z／¢0／LI | 8L0Z／¢0／¢ I | $06^{\circ} \mathrm{Z}$ | 29 | I6I | p．ofxe7 | 8 LOZ／¢0／¢ | E89E |
|  | ${ }^{\text {SsblD }}$ 2siv |  |  | $\begin{gathered} \hline \text { uәp.ng } \\ \mathbf{S B}_{\mathbf{L}} \end{gathered}$ |  |  |  | pəosib ${ }^{\text {L P7PG }}$ | $\begin{gathered} . \operatorname{rgqum} \\ \operatorname{se}_{\mathbf{L}} \end{gathered}$ |


| u！̣யəヤप | WXW | 8I0Z／60／8I | 8I0Z／L0／ZI | £9＊0 | 987 | L6Z | p．ojxe7 | 8I0Z／L0／ZI | 978E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| － | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\text {d }}$ | － | рәџәџәр ұои | E60 | L9 | ち6I |  | 810Z／S0／\＆Z | ¢8¢E |
| － | ${ }^{1} \mathrm{HOUS-} \mathrm{FSO}_{\mathrm{d}}$ | － | рәŋәдәр ұои | ¢0＊ | 0S | ZLI |  | 8IOZ／S0／EZ | †8¢E |
| － |  | － | рәџәдәр ґои | $00^{\circ} \mathrm{I}$ | $\varepsilon \varsigma$ | 08I |  | 8I0Z／S0／EZ | てZ8\＆ |
| － |  | － | рәџəдәр ґои | E6\％ | 99 | £6I |  | 8I0Z／S0／EZ | £8¢E |
| － |  | － | рәəәдәр ұои | $\pm 60$ | $\varepsilon 9$ | I6I |  | 810Z／S0／\＆Z | IZ8E |
| － | ${ }^{1} \mathrm{OHSS}-\mathrm{lsO}_{\mathrm{d}}$ | － | рәŋәџрр ұои | $00^{\circ} \mathrm{I}$ | 0¢ | 08I | 2पธ̊！${ }^{\text {eg eu peg liv }}$ | 810Z／S0／\＆Z | Z8¢E |
| － | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\mathrm{d}}$ | － | рәŋәџрр ұои | L80 | 98 | 802 |  | 810Z／S0／をZ | 0Z8E |
| － |  | － | рәџəəәр ґои | E1’］ | てt | 6¢ I |  | 8I0Z／S0／EZ | I8¢E |
| － |  | － | рәџəәәр ґои | $96^{\circ} 0$ | ¢9 | L8I |  | 8I0Z／S0／\＆Z | 6I8E |
| － | ${ }^{1}\left[\mathrm{OUSS}-\mathrm{FSO}_{\mathrm{d}}\right.$ | － | рәŋәдәр ґои | 20＊ | 9S | 9LI |  | 8I0Z／S0／EZ | 08¢£ |
| － |  | － | рәџวәәр ұои | $06^{\circ} 0$ | $t L$ | 007 |  | 810Z／S0／EZ | 818E |
| － | ${ }^{7}$［0us－${ }^{\text {S }} \mathrm{SO}_{\mathrm{d}}$ | － | рәџวәәр ұои | 860 | L9 | ¢81 |  | 810Z／S0／EZ | 8L¢E |
| u！̣யəप | ${ }^{1} \mathrm{OWOS}-\mathrm{lsO}_{\mathrm{d}}$ | 810Z／80／II | 810Z／S0／9Z | $L L^{\circ} \mathrm{Z}$ | ¢9 | I6I |  | 810Z／S0／\＆Z | £Z8\＆ |
| әлвวТ | ${ }^{7} \mathrm{OHSS}-\mathrm{lsO}_{\mathrm{d}}$ | 810Z／0I／0¢ | 810Z／¢0／8Z | $0 \downarrow^{\circ} \mathrm{Z}$ | SL | 26I |  | 810Z／S0／EZ | 6LSE |
| － |  | － | рәŋəдәр ґои | t0 ${ }^{\text {I }}$ | $\bigcirc \mathcal{E}$ | ELI | projxe7 | 8I0Z／¢0／¢ | 6L9E |
| － |  | － | рәџəәәр ұои | $90^{\circ} \mathrm{I}$ | Lt | 0LI | projxe7 | 8I0Z／S0／¢ | 06LE |
| u！̣யəप | ${ }^{1} \mathrm{HOUSS}-\mathrm{FSO}_{\mathrm{d}}$ | 810Z／60／80 | 810Z／S0／S I | $88^{\circ} \mathrm{I}$ | 96 | 012 | projxe7 | 8IOZ／S0／¢I | 918E |
| วлеวТ |  | 810Z／L0／ちI | 8I0Z／¢0／9I | $L S^{\circ} \mathrm{Z}$ | 0 L | Z0Z | p．ofxe］ | 8IOZ／S0／¢ | ¢18E |
| u！̣шวप | ${ }^{7}$［0us－${ }^{\text {S }} \mathrm{SO}_{\mathrm{d}}$ | 810Z／¢0／¢ ¢ | 8L0Z／¢0／¢ I | ¢9\％ | 89 | 26I | p．ofxe7 | 8IOZ／S0／¢ | $\dagger 18 \varepsilon$ |
| แ！̣யวบ |  | 810Z／L0／6Z | 8I0Z／S0／9 I | $\varepsilon \varsigma^{\bullet} \varepsilon$ | IS | 9LI | projxe7 | 8IOZ／S0／¢ | £I8E |
| u！̣யəУ |  | 810Z／80／8て | 8I0Z／S0／9I | $\varepsilon \varepsilon^{*} \varepsilon$ | tS | 08I | projxe7 | 8IOZ／S0／¢I | 2I8E |
| u！̣யəप | ${ }^{7}$［0us－1 ${ }^{\text {SO}}{ }_{\text {d }}$ | 810Z／90／LI | 8L0Z／S0／S I | LS＇Z | 02 | 002 | p．ojxe7 | 8I0Z／S0／¢ | ［18\＆ |
|  | SSEID ${ }^{\text {asiV }}$ |  | $\begin{gathered} \hline \text { ио!̣әәә I } \\ \text { IS.I! } \end{gathered}$ | $\begin{gathered} \text { uəp.mg } \\ \text { SB }_{\mathbf{L}} \end{gathered}$ |  |  |  |  | $\begin{gathered} \operatorname{raqumn}_{N} \\ \operatorname{si}_{\mathrm{L}} \mathrm{~L} \end{gathered}$ |


| u！̣யəəप | WXW | 810Z／80／S0 | 8I0Z／L0／ちI | てヤ＊0 | †で | $6 \downarrow \mathcal{E}$ | p．ojxe7 | 810Z／L0／tI | 96¢E |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| u！̣யəУ | ${ }^{7}$［0us－${ }^{\text {SOO}}{ }_{\text {d }}$ | 810Z／L0／LI | 810Z／L0／E I | L9＊ | 801 | ¢0Z | projxe7 | 810Z／L0／EI | 9 988 |
| u！̣யəəy |  | 8I0Z／60／9I | 8I0Z／L0／EI | $8 \varepsilon^{\circ} \mathrm{I}$ | $0 \varepsilon[$ | IEZ | projxe7 | 8I0Z／L0／EI | ¢£8E |
|  | ${ }^{1} \mathrm{HOUS-} \mathrm{FSO}_{\mathrm{d}}$ | 8L0Z／L0／tI | 8IOZ／L0／EI | LİI | $\dagger$ ¢ | カャて | projxe7 | 8I0Z／L0／EI | $\dagger$ ¢8ะ |
| u！̣шวบ | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\text {d }}$ | 810Z／L0／tI | 8IOZ／L0／E I | E60 | †6I | E¢Z | profxe7 | 810Z／L0／EI | £ย8ะ |
| u！̣¢วу | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\text {d }}$ | 810Z／60／tI | 8IOZ／L0／E I | 960 | L8I | ¢¢Z | profxe7 | 810Z／L0／EI | $678 \varepsilon$ |
| u！̣யəУ | ${ }^{1} \mathrm{lous}-\mathrm{lfO}_{\text {d }}$ | 8L0Z／L0／EI | 810Z／L0／E I | $0 S^{\circ} \mathrm{Z}$ | ZL | †6I | profxe7 | 810Z／L0／EI | ¢6¢E |
| u！̣шวप | ${ }^{1} \mathrm{lous}-\mathrm{lfO}_{\text {d }}$ | 810Z／0I／9Z | 8IOZ／L0／E I | 0s＇† | 0t | ¢SI | projxe7 | 810Z／L0／EI | †6¢E |
| u！̣шวप | ${ }^{1} \mathrm{lous}-\mathrm{lsO}_{\text {d }}$ | 810Z／60／ZI | 8IOZ／L0／E I | $9 \varepsilon^{*}$ I | て\＆I | 877 | projxe7 | 810Z／L0／EI | E6¢E |
| әлеวТ | $\mathfrak{7}$［0us－ $\mathrm{lSO}_{\text {d }}$ | 8102／80／Z0 | 8I0Z／L0／E | ¢で 1 | カワI | 0 0\％ | p．ofxe7 | 810Z／L0／EI | Z6¢E |
| u！̣யəУ |  | 810Z／0I／LZ | 810Z／L0／t | 6I｀1 | ISI | 8\＆Z | projxe7 | 810Z／L0／EI | I6SE |
| әлеәТ | NXW | 810Z／0I／90 | 8I0Z／L0／E I | S ${ }^{\circ} 0$ | 0¢E | てIE | projxe7 | 8I0Z／L0／EI | て£8ะ |
| u！̣யшวप | WAW | 810Z／0I／9Z | 810Z／L0／E I | t900 | 087 | $60 \varepsilon$ | projxe7 | 810Z／L0／EI | IE8E |
| әлвวТ | WXW | 810Z／L0／Zて | 810Z／L0／E I | LL＇0 | ¢¢Z | ¢82 | profxe7 | 810Z／L0／EI | $0 \varepsilon 8 \varepsilon$ |
| แ！̣யวप | WAW | 810Z／60／¢Z | 8I0Z／L0／E I | IS＇0 | \＆¢£ | \＆ZE | projxe7 | 810Z／L0／EI | 878E |
| u！̣யəप्ర | WAW | 810Z／80／S0 | 810Z／L0／E I | Lt＊0 | E8E | $\downarrow$ セย | projxe7 | 810Z／L0／EI | 06¢E |
| u！̣шวप | WAW | 8I0Z／60／0I | 8I0Z／L0／E I | LE＊0 | $68 t$ | $89 \varepsilon$ | p．ofxe7 | 810Z／L0／EI | 98¢E |
| u！̣шəप |  | 810Z／80／90 | 810Z／L0／ZI | L0\％ | L8 | L0Z | projxe7 | 810Z／L0／ZI | LZ8E |
| วлеวТ | $\mathrm{H}^{\text {ours－}}$－ $\mathrm{SO}_{\text {d }}$ | 810Z／80／LZ | 810Z／L0／ZI | ¢0\％ | 88 | E0Z | projxe7 | 810Z／L0／ZI | ¢78E |
|  |  | 810Z／80／ちI | 810Z／L0／ZI | 29 I | III | てIZ | projxe7 | 810Z／L0／ZI | $\dagger 78 \varepsilon$ |
|  |  | 810Z／60／ち0 | 810Z／L0／ZI | $98^{\circ} \mathrm{t}$ | LE | ItI | profxe7 | 810Z／L0／ZI | LI8E |
| u！̣шวप |  | 8I0Z／L0／ZI | 8I0Z／L0／ZI | $60^{\circ} \mathrm{t}$ | カt | 6SI | profxe7 | 810Z／L0／ZI | 68¢E |
| u！̣யəप | $\mathfrak{7}$［0us－ $\mathrm{FSO}_{\mathrm{d}}$ | 810Z／60／0I | 810Z／L0／ZI | ¢0\％${ }^{\text {\％}}$ | 88 | L0Z | projxe7 | 8I0Z／L0／ZI | 88¢E |
| วлеวТ |  | 810Z／L0／EZ | 810Z／L0／ZI | $67^{*}$ I | 0†I | てって | p．ofxe7 | 810Z／L0／ZI | L8¢E |
|  K．Jentst | SsbID 2sf |  |  | $\begin{gathered} \hline \text { uәp.ıng } \\ \mathbf{S B}_{\mathbf{L}} \end{gathered}$ |  |  |  |  | $\begin{gathered} \operatorname{raqumn}_{N} \\ \operatorname{si}_{\mathrm{L}} \mathrm{~L} \end{gathered}$ |

