Fine-scale habitat use and behaviour of Arctic charr (Salvelinus alpinus) morphs in a remote Arctic lake

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Abstract

The Arctic charr (*Salvelinus alpinus*) is the most northerly distributed species of freshwater fish and is biologically and culturally important throughout the Arctic region. Lacustrine populations of high-latitude Arctic charr exhibit considerable phenotypic variability, specifically adapted to occupy multiple niches in order to maximise the limited resources available. The inhospitable environment, in which this species can reside, creates difficulties in studying this species in all seasons, with research under ice severely limited. The objectives of this study were to determine whether phenotypic variation influences the spatial behaviour of Arctic charr and to investigate the year-round strategies of this species.

An autonomous acoustic telemetry positioning system was deployed to record the near complete, 3-dimensional spatial distribution of 28 acoustically tagged Arctic charr, from an Arctic lake, Lake Ellasjøen (surface area; 0.72 km^2, max depth; 34 m) on Bear Island (74° N) over a 12 month period (September 2009–2010). Discriminant analysis of meristic data identified sympatric morphotypes within the study sample.

Spatial distribution (lake zone habitat, fish depth and fish distance from lake bed) space use (core and excursive home range area) and activity were compared for two morphs; a robust littoral form and a delicate limnetic form. Each morph exhibited discrete habitat use over almost the entire study period and divergence in space use and activity reflected different behavioural patterns. Both phenotypes exhibited similar behavioural responses to the Arctic annual cycle, with fish less active under ice, however diel patterns of fish activity were observed during polar night, autumn and spring which were absent during the months of polar day (May – July).

These findings likely manifest as a result of resource-driven divergence of morphs in a harsh, Arctic environment. Seasonal behavioural adaptations reveal dynamic responses to the Arctic year, warranting further attention, particularly in light of predicted climate change in this region.

Contents

Declaration

I, Kate Louise Hawley, hereby declare that this thesis entitled:

"Fine-scale habitat use and behaviour of Arctic charr (*Salvelinus alpinus*) morphs in a remote Arctic lake"

Is to the best of my knowledge, a presentation of my own original work and that no work done by any other person or group is included, except where due reference is given in the text. I have acknowledged any sources of help with written work or field work in my acknowledgements.

Statement of copyright

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1 Introduction

The freshwater environments of the Arctic regions present unique challenges to the fish that inhabit them. Arctic fishes have to overcome extreme variations in solar radiation and low temperatures resulting in widespread freezing where streams and rivers can become frozen solid (Svenning and Gullestad 2002) and rapid expansion of water bodies associated with ice-melt and the resulting high levels of suspended-solids (Lucas and Baras 2001). The low temperatures characteristic of high-latitudes can reduce swimming performance (Finstad et al. 2007), while low light and increased suspended solids may prevent foraging (Helland et al. 2011). Fish are ectotherms, thus low temperatures will likely limit metabolic capacity for energy intensive processes such as feeding, growth and activity, with feeding and growth often being limited to warmer summer months (Lucas and Baras 2001). As a result there is limited diversity and abundance of freshwater fishes in the Arctic (Power 1997), with Arctic charr (*Salvelinus alpinus*) often being the dominant species (Reist et al. 2006b) and top of lacustrine food webs (Johnson 1980).

1.1 The physical environment of Arctic freshwater systems

The Arctic Circle is a vast circumpolar area consisting of seasonally ice-covered ocean, surrounded by continental land masses and islands and which ends at 66° 32’ N (AMAP 1998). This latitude is the southern limit of at least one 24-hour period a year during which the sun does not set and one 24-hour period during which it does not rise. The Arctic can also be classified by the northern limit of upright tree growth (Hustich 1979), the 10 °C July isotherm, or the southern extent of discontinuous permafrost (Heginbottom 2002) (Figure 1-1). These classifications are climate dependent and the polar regions are considered indicators for the magnitude and pace of global climate change (Wrona et al. 2006). The high-latitude regions also include the forest-tundra ecozone, referred to as the sub-Arctic or low Arctic, which grades into shrub tundra, true tundra and finally high Arctic polar desert (AMAP 1998) (Figure 1-1).

The availability of light is an important factor in the productivity of Arctic freshwater environments. During the polar night (periods of 24 hour darkness), the Arctic receives very little, or no solar radiation. When light levels increase in late winter and early spring, Arctic lakes are often covered with snow or ice which then reflects the light. The albedo, or reflectance of snow is approximately 80 % (Welch et al. 1987, Vincent et al. 2008). Thus, less light reaches the lake ecosystem and the longer it takes for the snow and ice to melt, with some high Arctic lakes being ice-covered year-round (Salonen et al. 2009). Oxygen may also be low in Arctic lakes during winter when there is no photosynthesis. If oxygen drops below critical levels, fish in the lake will die, this

is termed winterkill. Winterkill generally occurs in lakes that are less than 4.5 m in maximum depth and 1.8 m in mean depth. In these shallow lakes, the oxygen supply is depleted before spring (Welch and Bergmann 1985, Hurst 2007).

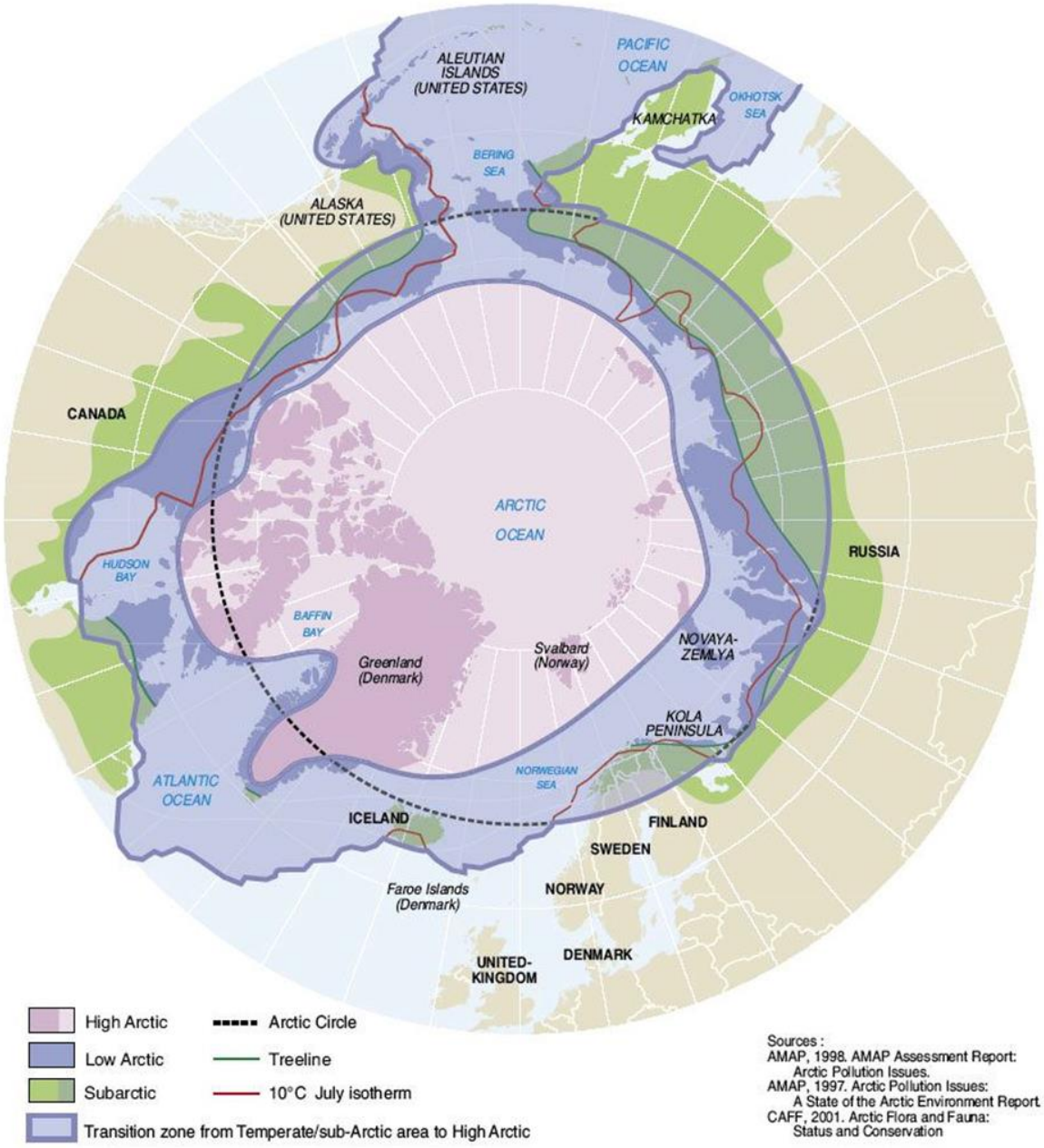


Figure 1-1: Map of Arctic region, showing Arctic boundaries dependent upon classification. Shaded areas divide the high, low and subarctic regions. Modified from the Arctic Monitoring and Assessment Programme (AMAP, 1998).

Arctic lakes are often ultra-oligotrophic (nutrient poor), characterised by low species diversity, short nutrient pathways and simple food webs (Salonen et al. 2009). Hobbie et al. (1999) ranked Arctic lacustrine habitats by linking the structure and diversity of a food web to the trophic state of the lake. In this scale Type I lakes are ultra-oligotrophic, that is they have very low primary productivity and support few plankton and no zooplankton. Type II are very oligotrophic and increased in productivity, supporting microzooplankton. Type III lakes are more productive still

and allow copepods to survive. Type IV lakes are oligotrophic and the most productive of the Arctic, these sustain both copepods and Cladocera, much like a typical temperate lake.

As lakes in higher latitudes are subject to extended periods of polar darkness and the resulting extended period of ice-coverage, summer water temperatures will be lower than those of lower latitudes (Vincent et al. 2008). There is little difference in winter water temperatures between dimictic lakes (mix from top to bottom during two mixing periods each year) and cold monomictic lakes (mix from top to bottom during one mixing period each year), as inverse temperature profiles develop under the ice, thus temperatures are coldest at shallower depths directly below the ice (Lewis Jr 1983). Winter water temperature is more dependent on local weather conditions in autumn, pre ice-cover, as strong winds can prolong circulation and result in lower temperatures before ice-cover (Svenning et al. 2007).

1.2 Fish of the Arctic region

There are approximately 99 species in 48 genera of freshwater fish present in the Arctic region (Reist et al. 2006a). These fishes consist of those which conduct their entire life history in freshwater habitats, and those which move between freshwater and marine areas (i.e. diadromous forms consisting of both anadromous fishes which spawn in freshwater and feed in the sea and catadromous fishes which do the reverse). These represent 17 families, the most species rich being Salmonidae, represented by 33 different species, most of which are important in north-latitude fisheries (see Reist et al. 2006a for detailed inventory of Arctic fish species). Fish species residing in the Arctic must possess the behavioural and physiological adaptations fundamental for survival in environments characterised by limited light availability, low productivity and low temperatures (see Section 1.1). Table 1-1 (adapted from Power 2002, Power et al. 2008), lists the main physiological and behavioural adaptations required for survival in this environment. Taken collectively, the traits describe the attributes of the species adapted for survival in the northern latitudes (Power 2002). Traits are often linked, with changes in one trait holding significant implications for expression of other traits. For example, delayed maturation will tend to lead to an increase in body size, which in turn often leads to an increase in egg size and survivorship (Hindar and Jonsson 1982). Delayed maturation also often results in increased longevity, this acts to offset possible consequences for lifetime reproductive potential (Power et al. 2008).

Table 1-1: Life history adaptations of fishes inhabiting Arctic aquatic environments (adapted from Power, 2002; Power et al. 2008). Traits are grouped by their main effect on the population processes of reproduction, growth and survival. Traits within each category are not necessarily independent of those in other categories. For example, variable growth will likely influence reproductive strategies.

Life History trait	Description of effect/advantage
Reproductive traits	
Autumn spawning	Facilitates maximum energy acquisition for gonadal development. Allows young to assimilate enough resources for first winter survival (Johnson 1980).
Large egg size	Development of larger progeny, reducing early stage mortality. Less immediate dependence on exogenous food sources (Byström et al. 2004).
Facultative nest selection	Protection from biotic (e.g. predation) and abiotic (e.g. freezing) factors, thereby increasing egg survival (Jonsson and Jonsson 2001).
Variable reproductive cycles	Allows individuals to determine reproductive events with respect to environment conditions; by postponing reproduction in poor years and accelerating gonadal development in good years (Johnson 1980).
Variable age at maturity	In combination with longevity facilitates development of larger body sizes associated with improved fecundity (Hindar and Jonsson 1982).
Iteroparity	Multiple reproductive events promotes greater reproductive success and population persistence (Power et al. 2008).
Growth traits	
Variable growth	Variability promotes growth with respect to feeding conditions and environmental stochasticity. This is linked to variability of spawning events, to promote individual survival during adverse environmental periods (Adams and Huntingford 1997).
Adaptation to low temperatures	Ability to complete all life stages in extreme conditions (Larsson and Berglund, 2005).
Adaptation to low-light levels	Ability to detect both prey and conspecifics, implies good low-light vision and/or alternate means of detection (Elliott 2011).
Diet flexibility	Consume a variety of prey in a variety of habitats. Opportunistic predation, including cannibalistic behaviour (Adams et al. 1998, Hammar 2000).
Metabolic efficiency/variability	Ability to feed to satation during summer and tolerate food deprivation during winter (McKeown 1984).
Survival	
Habitat generalists	Ability to reside in a variety of habitats and to change habitats in regular or variable sequence means that optimal residence timing can be exploited (Jonsson and Jonsson 2001).
Variable life histories	Results in optimal resource use; either as individuals (e.g. facultative anadromy) or collectively as a population (e.g. development of land-locked populations) (Rikardsen et al. 2000, Power et al. 2002).
Exploratory behaviour/migrations	Ability to select the best resources with respect to environmental stochasticity (e.g. low flows preventing re-entry into freshwater) (Gulseth and Nilssen 2000, Svenning and Gullestad 2002). Established movement between reproductive, feeding and overwintering habitats promotes migratory pathways.
Low aggression	Limited agonistic behaviour allows energy to be preserved for somatic and gonadal purposes (Huusko et al. 2007).

1.3 The Arctic charr

The circumpolar Arctic charr is the most northerly distributed of all freshwater and anadromous fish. It is also one of the most thoroughly studied (for a review of the species life history see Johnson 1980, Jonsson and Jonsson 2001, Klemetsen et al. 2003a). This species promotes such interest because of the diversity of forms and range of aquatic habitats in which it exists. Dependant on latitude, season and life history stage Arctic charr may occupy lakes, rivers, streams or sea. There are fluvial and lacustrine populations and populations in which individuals migrate between both habitats. However, lacustrine populations dominate throughout the Arctic distributional range (Power et al. 2008).

The Arctic charr is the only fish species that is truly Holoarctic, being present on all land masses of the Arctic region (Reist et al. 2006a). This species occurs in the northern extremes of land distribution (ca. 84° N) (Reist et al. 2006a). North of 75° latitude, Arctic charr are the only fish species present in fresh water (Johnson 1980). This species also exhibits the widest latitudinal range of all Arctic fish (Reist et al. 2006a), the southern limit of distribution extending to 43° N in North America and 45° N in Europe (Power et al. 2008). As a result, Arctic charr are biologically and culturally important throughout the Arctic regions. It is a valuable sport and household fish, particularly for the indigenous peoples of the North (Johnson 1980) and important commercial fisheries are developed in Canada (Reist et al. 2006b).

Tremendous morphological, ecological and genetic variability and plasticity within this species, has been reported, which makes Arctic charr an excellent model for studying evolutionary processes (Adams and Huntingford 2002, Magnan et al. 2002, Knudsen et al. 2006, Corrigan et al. 2011). With only a few exceptions, all the fresh waters presently occupied by Arctic charr were directly influenced by the climatic and topographic changes of the Pleistocene glaciations (Johnson 1980); therefore this species has been subjected to many episodes of isolation, divergence and recontact (Magnan et al. 2002). Variations in Arctic charr phenotype may be a result of allopatric (i.e. geographically isolated) differentiation, in that formerly isolated populations remain morphologically distinct and reproductively isolated after coming into contact with each other (Power 2002). Divergence may also result from sympatric (i.e. co-occurring) differentiation, where a single genotype can produce multiple phenotypes as a function of the environment, which due to behavioural isolation (especially at breeding) may result in eventual genotype divergence (Skulason and Smith 1995). Genetic studies of Arctic charr have indicated that in most cases, phenotypes are derived from a single sympatric origin, with the number of different morphs likely depending on ecological conditions such as the number of available niches (Klemetsen et al. 2003a). However, allopatric divergence of phenotype in Arctic charr populations

does also occur (Power et al. 2009), thus both sympatric and allopatric processes of diversification can intermix, causing complications in delineating causation (Corrigan et al. 2011, Reist et al. 2012). Despite being much discussed the mechanisms by which diversification of this species occurs are not yet fully understood (Jonsson and Jonsson 2001).

1.3.1 Variable life-histories of Arctic charr

Within lakes they inhabit, Arctic charr can use all habitat types (e.g. pelagic, littoral and profundal), with usage dependent on age, and life-stage of the charr and co-occurring species in the lake (Klemetsen et al. 2003b, Amundsen and Knudsen 2009). Arctic charr appear to be adapted to low-aggression (Power 2002, Huusko et al. 2007) and in instances of interspecific competition habitat niche shifts are commonly observed. For example, Arctic charr have been shown to segregate from brown trout (*Salmo trutta*) (Hammar 1998, Klemetsen et al. 2003b, Helland et al. 2011), brook charr (*Salvelinus fontinalis*) (Halvorsen et al. 1997, Hammar 1998) lake trout (*Salvelinus namaycush*) (Fraser and Power, 1989), European whitefish (*Coregonus lavaretus*) and grayling (*Thymallus thymallus*) (Amundsen et al. 2010). High levels of intraspecific competition have also been shown to result in habitat shifts, with resource use separation occurring when Arctic charr is the only fish species present (Klemetsen et al. 1997, Adams et al. 1998, Jonsson and Jonsson 2001, Knudsen et al. 2007, Amundsen et al. 2008). Stable isotope studies of feeding patterns show that this intraspecific niche separation has the effect of lowering resource competition (Power et al. 2002). However, this may impose developmental energetic constraints, such as dictating limits on body size, maturation rate and fecundity (Guiguer et al. 2002). For example, the ability to deal with low food availability through selective allocations of energy to somatic growth or reproduction has been implicated in the development of stunted populations of Arctic charr (Power et al. 2002). Phenotypical or morphological variation in lacustrine populations of Arctic charr is characteristic of the species and has been described in numerous instances (Johnson 1980, Klemetsen et al. 2003a, Reist et al. 2012).

The term ecophenotype has been used to describe sympatric forms of a single species that may be morphologically, genetically and/or ecologically distinct (Klemetsen et al. 2003a). In many cases, where ecophenotypes exist there is evidence of an ecological basis for its occurrence and in Arctic charr this is often linked with functional differences in feeding ecology (Adams et al. 1998, Guiguer et al. 2002). For example, there is often a small or 'dwarf' epibenthic form that feeds on zoobenthos and a large, pelagic form that feeds on zooplankton (e.g. Lake Vangsvatnet, Hindar and Jonsson 1982). A larger piscivorous form can also exist that predates on the other forms (Finstad et al. 2006). Perhaps the greatest example of ecophenotypic diversity known for Arctic charr occurs in Thingvallavatn, Iceland, where four distinct morphs are known to exist: small

benthic, large benthic, pelagic piscivorous and pelagic planktivorous forms (Sandlund et al. 1992). This morphological diversity observed in Arctic charr is considered to be an adaptive strategy as a result of localised environmental pressures (Sandlund et al. 1992), with morphologically specialised forms appearing to feed more effectively than intermediate forms (Klemetsen et al. 1997, Knudsen et al. 2006).

Flexibility in habitat usage extends to include flexibility in spawning site requirements, with both spatial and temporal segregations between sympatric ecophenotypes observed (Sandlund et al. 1992, Elliott and Baroudy 1995, Klemetsen et al. 1997). For example, the Arctic charr population of Windermere, England is composed of two autumn (November – December) and two spring (February – March) spawning populations, which spawn in shallow littoral (2 – 4 m) and deeper profundal (15 – 8 m) habitat, respectively (Elliott and Baroudy 1995).

Anadromous populations of Arctic charr are numerous, particularly in high-latitude populations (Rikardsen and Amundsen 2005, Siikavuopio et al. 2009). Factors determining anadromy are primarily environmental (Power et al. 2008). These may be ecological for example; productivity in natal freshwater versus accessible marine waters, predation costs versus benefits of migration (Gross et al. 1988) or physical including; duration of ice cover in natal freshwater (Svenning and Gullestad 2002) and low/high marine temperatures (Rikardsen and Amundsen 2005). Where anadromy does occur, individuals feed annually for only a 6 – 8 week period post ice break (Klemetsen et al. 2003a). Despite the limited time spent at sea, these feedings are associated with rapid growth, with individuals increasing body size by as much as 42 % in this period (Johnson 1980). Arctic charr populations are suspected of being facultative with respect to anadromy (Power 2002). In some high-latitude Arctic charr populations with access to the sea the phenomenon of 'partial migration' exists, with a fraction of individuals remaining resident in freshwater (Rikardsen et al. 2000). The rapid growth that is characteristic of the brief feeding periods in marine waters means that anadromous fish grow faster than lake resident fish over a simultaneous period (Rikardsen et al. 2000, Rikardsen et al. 2003).

Regardless of life-history type, all Arctic charr utilise freshwater during the first few years of life and for spawning and overwintering (Klemetsen et al. 2003a). A simplistic overview of the life-history variation of Arctic charr, as influenced by environmental and physical factors is provided in Figure 1-2 (adapted from Power et al. 2008).

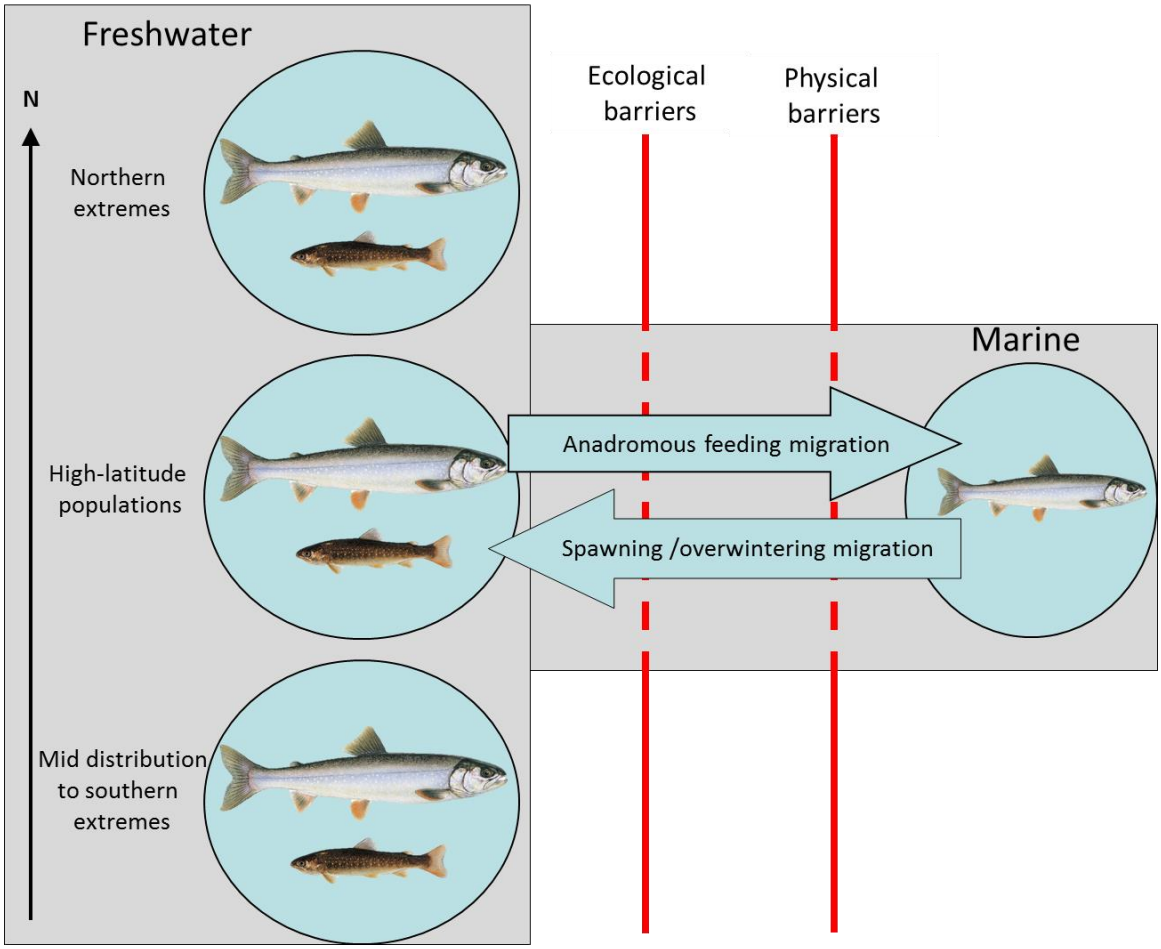


Figure 1-2: A generalised overview of possible Arctic charr life histories, modified from Power et al. (2008). Resource-driven morphological variation in sympatry can occur, depicted by the large and small morph Arctic charr figures. Life history strategies of fishes vary by latitude, as depicted by the north arrow. The red lines represent physical and ecological barriers to marine migration. In the northern extremes, river and sea ice, stream gradients and discharge and low marine temperatures may all physically prevent marine migration. In the range from the mid-distributional latitude to the southern extremes, high stream and marine temperatures may prevent anadromy. At these latitudes the ecological costs of anadromy including increased predation and less productive marine waters can outweigh potential benefits. At higher latitudes, the physical and ecological barriers are relaxed (represented by dashed red lines) and anadromous migration is possible. Land-locked populations are most common in the northern and mid-to southern extremes, within which co-occurring morphotypes commonly occur. Different morphotypes can also occur within an anadromous population.

1.4 Coping with winter in the Arctic

Low temperatures and poor light conditions under ice and snow make winter in Arctic lakes a challenging period for many fishes. Poor light conditions are demanding for visual search and capture of prey and predator avoidance. In addition, lower productivity and reduced prey

availability are expected to result in marked differences between winter and summer seasons, both in diet composition and feeding rates. However, due to practical reasons, our understanding of the liminogical conditions during this season lags behind that of summer (Salonen et al. 2009).

Fish may use a number of strategies in order to survive the winter, these may include physical migrations into specific overwintering habitats (McKeown 1984), building up of energy stores in the form of lipids in autumn (Rikardsen et al. 2003), and reducing activity during winter (Huusko et al. 2007). Fish are ectotherms, thus low temperatures will severely limit metabolic capacity for energy intensive processes such as feeding, growth and activity. Consequently, most fish are assumed to reduce their swimming activity and aggressive feeding behaviour during winter (Huusko et al. 2007). A decline in body temperatures during winter will likely result in reduced metabolism and energy use (Jobling 1983). Fish may even become dormant, stop feeding, and rely solely on their energy reserves to survive the winter (Rikardsen et al. 2003). The accumulation of energy stores for overwintering may serve to increase reproductive performance the following spring (Rikardsen et al. 2004). Therefore, the rate at which energy stores are depleted during winter can affect not only over-winter survival, but also future reproductive output (Brodersen et al. 2011). The overwintering success of an individual can therefore be divided into primary success (i.e. survival) and secondary success (i.e. condition) at the end of the winter (Brodersen et al. 2011).

1.4.1 Feeding and metabolic performance

In fish, ambient temperatures influence lipid accumulation rates before winter (Brodersen et al. 2011) and depletion rates during winter (Sogard and Olla 2000), as enzyme processes and basal metabolic rates generally slow with a decrease in temperature. As food consumption and rates of assimilation are likely to drop with decreasing temperatures, most organisms may be challenged at the low temperatures during winter if intake and assimilation rates are below the level needed for maintenance metabolism (Amundsen and Knudsen 2009). The food intake in fish, including the ability to capture (Svenning et al. 2007), process (Nicieza and Metcalfe 1999) and evacuate food (Jobling 1983), are all slowed as a result of reductions in metabolic rate. The rate of food intake and the motivation to feed are closely linked to both stomach fullness and rate of gut emptying, with appetite reduced by the presence of food in the stomach or its slow movement through the digestive system (Bull and Metcalfe 1997). When feeding occurs at low temperatures, the consumption rates are usually considered too low for growth (Klemetsen et al. 2003b, Amundsen and Knudsen 2009).

Few studies have been conducted investigating the overwintering strategies of fishes in high-latitudes, despite winter being the dominant season, with lacustrine environments being ice-covered for much of the year. Many populations of fish undergo specific feeding migrations in the more productive summer months in order to obtain the necessary energy reserves to survive the winter (McKeown 1984, Gross et al. 1988), during which feeding to satiation may occur in order to tolerate low food availability during winter (McKeown 1984). Where anadromy of Arctic charr occurs, the anadromous individuals can maintain a higher growth rate in late summer and early autumn than those residing year-round in freshwater (Rikardsen et al. 2004). In freshwater resident Arctic charr, reduced autumn growth rate, higher levels of lipid accumulation and low lipid depletion in winter allows sexual maturation the following summer, without marine migration being required (Rikardsen et al. 2004). Evidence suggests that mature anadromous charr seem to feed little, or not at all during winter (Rikardsen et al. 2003). Studies have also shown that anadromous charr experience severe depletion in weight and energy reserves whilst overwintering in freshwater (Jorgensen et al. 2000). Conversely, land-locked or lacustrine Arctic charr are observed to feed throughout the entire winter period, despite water temperatures being close to 0 °C (Brannas and Wiklund 1992, Klemetsen et al. 2003b, Svenning et al. 2007, Amundsen and Knudsen 2009).

The seasonal feeding and habitat use of Arctic charr has been investigated by static, point sampling using gill nets set under ice (Brannas and Wiklund 1992, Klemetsen et al. 2003b, Svenning et al. 2007, Amundsen and Knudsen 2009). The stomach contents of Arctic charr from two subarctic Norwegian lakes showed that the fish fed continuously during winter despite the cold water and poor light, with amphipods and chironomid larvae dominating the diet (Klemetsen et al. 2003b). Arctic charr were more concentrated in the littoral zones (0 – 15 m depth) of the lakes during the entire winter period (December to May), despite these temperatures being the lowest within the lake. At ice break in June, all Arctic charr moved to the profundal zone in response to the sudden light increase and profundal resource peak of chironomid pupae (Klemetsen et al. 2003b).

Svenning et al. (2007) deployed a similar methodology to study the Arctic charr from a high Arctic lake on Svalbard (Norway). These fish also fed continuously during the nine month long Arctic winter. The food intake was lowest during the darkest period and increased towards the end of the ice-free period. Although most fish occupied the littoral zone during winter, the highest catch densities in April and October were found in deeper areas (20 m) of the lake. The diet of smaller charr (< 15 cm in length) was found to vary strongly with season, with prey choice reflecting the greatest density of food items available; zooplankton in late autumn and chironomids in winter

(larvae) and summer (pupae). Whereas larger fish (> 15 cm in length) were shown to be mostly cannibalistic.

Both studies observed strong changes in net-catch abundance during winter, from very low values mid-winter to high values in June. This likely reflects an increase in feeding activity with increasing light. Svenning et al. (2007), also indicate that the seasonal rapid shift of light in April, likely increases the availability of light under the ice significantly, allowing feeding in deeper water at that time. This is in contrast to the subarctic lakes where Klemetsen et al. (2003b) found that the charr populations lived in the littoral zone the entire winter. The differences observed between the subarctic and high Arctic studies may be caused by the seasonal differences in light regime shifts, differences in albedo on the lake surface and/or a difference in prey densities with water depth (Svenning et al. 2007).

The ability to visually detect prey can be severely limited during the extended periods of polar darkness. However Arctic charr have been shown to feed in darkness during the Arctic winter (Klemetsen et al. 2003b, Svenning et al. 2007, Amundsen and Knudsen 2009). The retina of Arctic charr is an example of a multi potential teleost retina that is able to cope with a wide range of light conditions and temperatures (Ali et al. 1984). Ali et al. (1984) examined the retinal characteristics of Arctic charr from a lake in Iceland and found no structural differences between the retinal photoreceptors of fish from deep waters (40 m) and shallow waters (< 20 m). Svenning et al. (2007) found a high incidence of mud in the stomachs of Arctic charr which may indicate that fish browse bottom sediments in pursuit of chironomid larvae, the dominant winter prey during the polar winter by use of tactile and chemical senses.

Under experimental conditions Arctic charr have been shown to maintain positive growth in darkness, when high prey abundance is available (Siikavuopio et al. 2009). Whereas the actual overwinter assimilation of prey in sub-Arctic lakes, was found to be similar to estimates of the standard metabolism at the temperatures observed (Klemetsen et al. 2003b). These findings indicate that Arctic charr were able to compensate for the metabolic costs of overwintering but not for the costs of growth and activity. Thus, even when feeding occurs in winter, the winter may represent a serious bottleneck for resource acquisition, possibly resulting in a depletion of energy reserves (Siikavuopio et al. 2009). Little is known about the activity of Arctic charr under winter temperatures and light conditions but studies indicate that winter feeding may compensate for at least the standard metabolic costs associated with overwintering at high-latitudes (Klemetsen et al. 2003b, Amundsen and Knudsen 2009).

1.4.2 Behavioural strategies

In shallow, Arctic, lacustrine habitats fish are unable to migrate or select the ideal water temperatures in order to regulate their metabolism according to the availability of food. Instead they may increase their feeding rate by choosing a habitat with greater food availability, but often with the trade-off of accepting a higher predation risk (Amundsen and Knudsen 2009). Alternatively, fish may choose to decrease their food intake during winter and thereby decrease their overwintering success both in terms of survival or condition at the benefit of a lower risk of predation (Brodersen et al. 2008). Different strategies and cost versus benefits will vary both between individuals and species (Brodersen et al. 2008).

Arctic charr have been shown to exhibit ontogenetic differences in habitat use during winter and summer seasons, with this being most pronounced for small-sized Arctic charr (Amundsen and Knudsen 2009). The smaller fish often reside in the profundal zone during the ice-free period, but move to the littoral zone before the time of ice formation, remaining there over winter (Amundsen and Knudsen 2009). This habitat shift may increase the resource for littoral prey, but simultaneously also alters the predation risk for small-sized Arctic charr. High predation risk in the littoral zone during summer time is suggested as the main reason why small Arctic charr tend to reside in the profundal at this time of the year (Klemetsen et al. 1997, Klemetsen et al. 2003a). Potential predators in the littoral zone of high-latitude lakes can include; piscivorous fish, cannibalistic Arctic charr and predatory birds. Predatory birds are obviously absent from frozen lakes, and piscivorous fish may be less efficient predators under winter conditions (Hammar 1998, Huusko et al. 2007). The littoral zone can therefore be considered a less dangerous habitat for small-sized fish during winter than summer. However Amundsen and Knudsen (2009), showed that Arctic charr dominated the diet of brown trout in a sub-Arctic lake during winter. Thus, the use of the littoral habitat by small-sized Arctic charr overwinter is associated with an enhanced predation risk. This suggests that the shifting of the small Arctic charr into the littoral zone during winter is a trade-off to offset their food demand that is likely more critical than the threat of predation (Amundsen and Knudsen 2009). This may be related to the observation that small Arctic charr are likely to starve to death during winter if they are unable to feed (Byström et al. 2006) and the availability of food resources is therefore a critical factor for their survival during this period.

1.5 Arctic fish populations and climate change

Variations in the strength of ecological interactions between seasons have received little attention. The winter situation is often neglected when studying behaviour and competitive

interactions (Helland et al. 2011). Under ice, research is limited, with the methodology of most studies being predominately static point sampling (Klemetsen et al. 2003b, Svenning et al. 2007). However, low temperatures and poor light conditions will influence the spatial requirements of fish (Blanchfield et al. 2009), leading to differences in resource use during winter and summer periods. In general, the Arctic freshwater-terrestrial system will warm more rapidly than the global average, particularly during the autumn and winter season (Wrona et al. 2006). Changes in temperature, snow, ice-cover, and nutrient availability exert major influences on the biological dynamics in the Arctic, which will in turn affect the ecology of Arctic lakes (Vincent et al. 2008). The suite of adaptations exhibited by Arctic charr is likely a competitive advantage compared to other fish species in subarctic and Arctic areas (Reist et al. 2006b). In a scenario of global warming, it is expected that the seasonal melt cycle will change and the duration of ice-formation will be reduced (Hobbie et al. 1999). Such conditions, with a reduced period of water temperatures close to zero, could be a disadvantage for Arctic charr, due to increased competition from more southerly species, with higher optimal temperatures like the European whitefish (Reist et al. 2006a, Reist et al. 2006b).

Climate change can be expected to affect organisms both directly, e.g. through temperature effects on consumption and metabolism and indirectly through effects on trophic dynamics, such as resource availability and predation (Helland et al. 2011). Research on the interactions of trophic levels is needed to fully understand the effects of climate change on ecosystem dynamics (Wrona et al. 2006). The development of new techniques has opened new possibilities to address these issues, with the logistics of studying all seasons in the high-latitudes made feasible. Recent studies have deployed techniques to address also fish activity under ice. Using a radio-linked acoustic telemetry positioning system Blanchfield et al. (2009), found that lake trout were equally active during winter and summer but were in winter confined only to a shallow water layer in the middle of the lake. Jurvelius and Marjomaki (2008), observed a distinct diel vertical migration of European whitefish under ice. Such examples emphasise that, in winter, activity and behaviour of organisms can be complex and comparable to summer.

2 Research aims

This study set out to investigate the year-round strategies of a high-latitude population of Arctic charr; explicitly to elucidate the specific behavioural adaptations as a result of the energetic limitations imposed by overwintering in the Arctic. Specifically, it was hypothesised that because of the near absence of light and very low ambient temperatures, and their resultant effects on feeding opportunities and food processing, Arctic charr activity and home range size during winter ice cover would be significantly smaller than during autumn, spring and summer.

Arctic charr populations often exhibit ecophenotypic variation (see section 1.3) and habitat use may change with ontogeny. This investigation consequently aimed to determine whether ecophenotypic variation occurred in the study population, and if so whether this or ontogenetic factors influenced spatial behaviour.

As this study was the first to apply a Vemco Positioning System (VPS) autonomously over a period of one year, it was considered necessary to carefully evaluate the performance of the system and its suitability for studying Arctic aquatic systems.

3 Study site

3.1 Bear Island, Lake Ellasjøen

Bear Island (Bjørnøya, Figure 3-1) (74° 30’ N, 19° 00’ E) is a remote, high Arctic island, situated in the Barents Sea; equidistant between Spitsbergen (Svalbard archipelago) and mainland Norway.

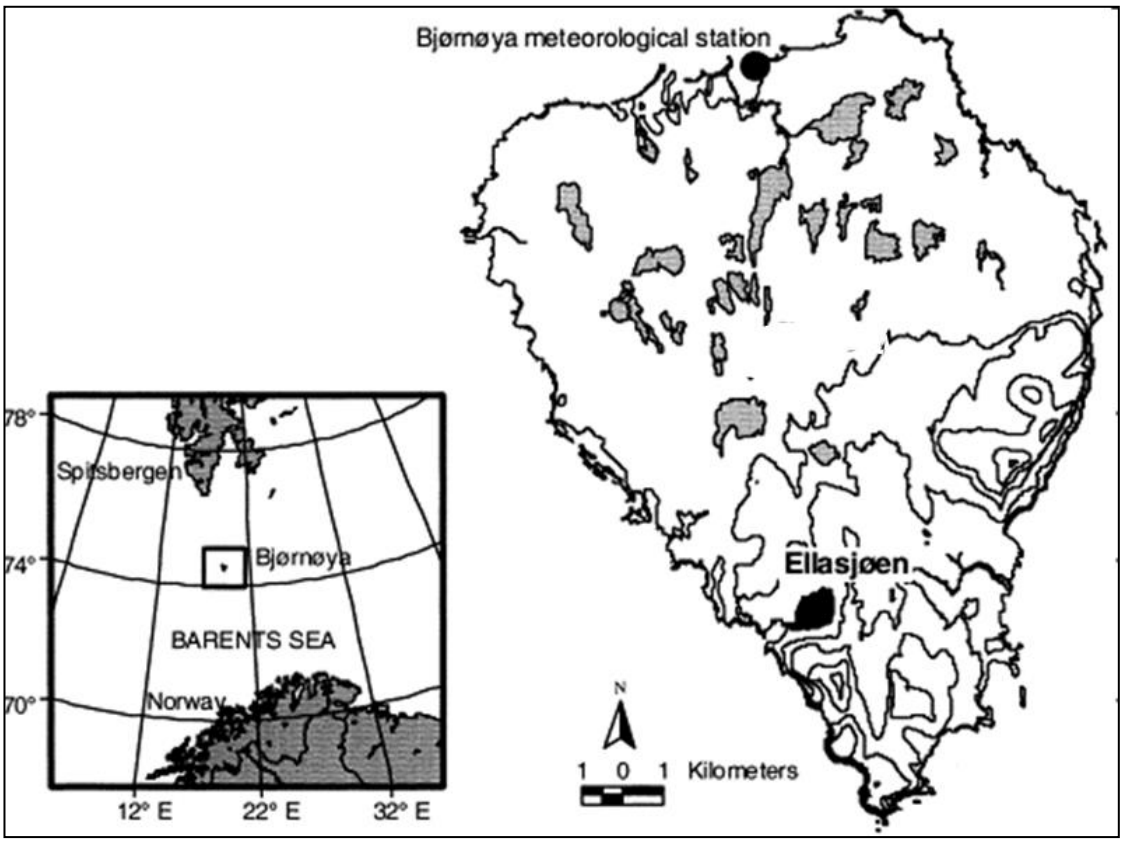


Figure 3-1: Map of Bear Island (Bjørnøya), to the south of the Svalbard archipelago, Barents Sea.

The island has an area of approximately 178 km^2 and measures 20 km from north to south. The island’s only inhabitants are the nine staff employed to run the meteorological station, located on the island’s north shore (Figure 3-1 closed circle). The average annual temperature is - 3.8 °C and 24 hour darkness occurs for a period of 88 days. Precipitation is low, an average of 367 mm per year, of which 60 % is snow (Norwegian Meteorological Institute, unpublished data). The island was glaciated during the Pleistocene and the surrounding sea was permanently ice-bound. Topographically the island is split in two; the northern region forms low-lying plains, the south being mountainous, with the highest peak, Mount Misery reaching 536 m. The south coast sea cliffs form important colonies for seabirds, in particular kittiwakes (*Rissa tridactyla*). The island has several river systems and due to glacial impact, is rich in lakes and ponds, forming 11 % of the island’s surface. The majority of these water bodies are shallower than 2 m and located in the

northern plains. These are prevented from drying due to permafrost, which also prevents the transport of groundwater. Ellasjøen, with a maximum depth of 34 m is the only deep lake on the island and is also the largest, with a surface area of 0.72 km^2. Figure 3-1 shows the locality of Ellasjøen (shaded black) in the mountainous southwest region of the island. The lake is situated 0.5 km from the coast, at an elevation of 21 m.

The duration of ice-cover on Ellasjøen is for a period of 8.5 – 9.5 months, with the ice free months being between late June and early September. Water temperatures are low, with an average summer temperature of 7.5 °C. Summer stratification does not develop in Ellasjøen, thus the lake is defined as cold monomictic (Lewis Jr 1983). During summer, large flocks of kittiwakes, sometimes forming thousands of individuals, use the lake for bathing and preening (Figure 3-2a). Their presence contributes a heavy allochthonous nutrient input, and accounts for the alkalinity of the lake (pH 7.3 – 7.6) and the low transparency of the water (Secchi depth transparency 3.5 m, colour: grey green) (Klemetsen et al. 1985).

Figure 3-2: a) The large numbers of kittiwakes that use the lake during summer; b) the un-vegetated rocky shore of Lake Ellasjøen (photographs taken by author).

The littoral zone of Ellasjøen is composed of a steep rocky margin up to a metre high, and except for occasional submerged mosses there is no macro-vegetation present (Figure 3-2b). Low diversities of protozoans and phytoplankton are present, with only six species of phytoplankton recorded in Ellasjøen (Klemetsen et al. 1985, and references therein). Among crustaceans the tadpole shrimp (*Lepidurus arcticus*) is a dominant species in fish-less lakes, but is much reduced in Ellasjøen. The cladoceran, *Daphnia longispina* forms much of the plankton population in Ellasjøen. Chironomidae is the dominant aquatic insect group in Ellasjøen, both in diversity and abundance (Klemetsen et al. 1985).

3.2 Bear Island Arctic charr

The presence of Arctic charr, the only fish species on the island, was first registered by Andersson and Herwig (1900) (cited in Klemetsen et al. 1985), during Swedish and German expeditions to the island. Since initial discovery, limited observations constituted the only published information on Bear Island charr. In 1977 and 1978 the University of Tromsø conducted scientific expeditions to Bear Island. These findings published by Klemetsen et al. (1985) form a comprehensive overview of Bear Island Arctic charr.

Klemetsen et al. (1985) observed that present day anadromy does not appear to exist in Bear Island charr. There are no biological reasons for the disappearance of anadromy. Bear Island is situated in the middle of the highly productive Barents Sea and anadromy occurs both to the north and to the south. A combination of small catchment areas and low precipitation on the island means that river outlets to the sea appear to be too steep and high to allow fish to ascend. In effect, Bear Island charr are landlocked, descent is possible but ascent is physically prohibited.

Fishing by Klemetsen's team in 1977 was conducted using 1.5 m deep 25 m long mixed mesh (16 – 39 mm) bottom-set gill nets, placed either singularly or linked and set perpendicular from the shore and left overnight. During 1978, 10 and 12.5 mm mesh size nets were also used, as well as, floating nets (6 m deep 25 m long, mesh size 10 – 39 mm) set mid lake. During August 1978 a total of 921 charr was caught in Ellasjøen. Of these 618 (67 %) were caught in benthic gill nets and 303 (33 %) were caught in floating nets. The bottom nets caught fish sized 8 – 52 cm in length, the floating caught fish 14 – 42 cm in length. Klemetsen et al. (1985) observed a bimodal length distribution in the 1977 Ellasjøen littoral samples, with the modal lengths of the two groups recorded as 16 and 38 cm, and only one fish was between 19 and 29 cm long. The littoral bottom net catches of 1978 displayed a broadly similar distribution to those of 1977, but included substantial numbers of intermediate-sized fish, suggestive of a tri-modal distribution (Figure 3-3). The length distribution of the pelagic net catches showed no such bimodality. However, a bimodal distribution became re-apparent (8 – 21 and > 29 cm), when only sexually mature fish were considered (Figure 3-3). The fish were aged from examination of otoliths; fish of the small mode were aged between 6 – 14 years and fish of the large mode were 12 – 23 years. Figure 3-4 shows the bimodality of length distribution with respect to age, which becomes apparent from 8 years and over, suggesting separation into slow growing and fast growing morphs, often attributed to trophic polymorphism (Knudsen et al. 2006).

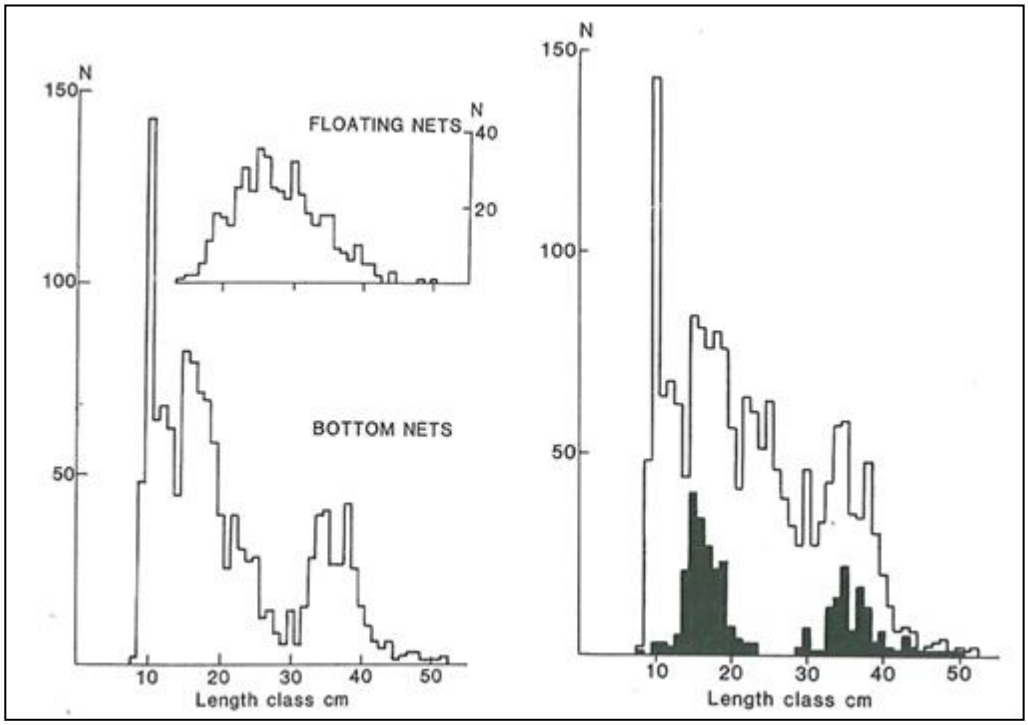


Figure 3-3: Length distribution of Arctic charr from bottom and floating gill nets, during the 1978 sampling of Ellasjøen. Values shaded black show fish at an advanced stage of gonad maturation. Reproduced from Klemetsen et al. (1985).

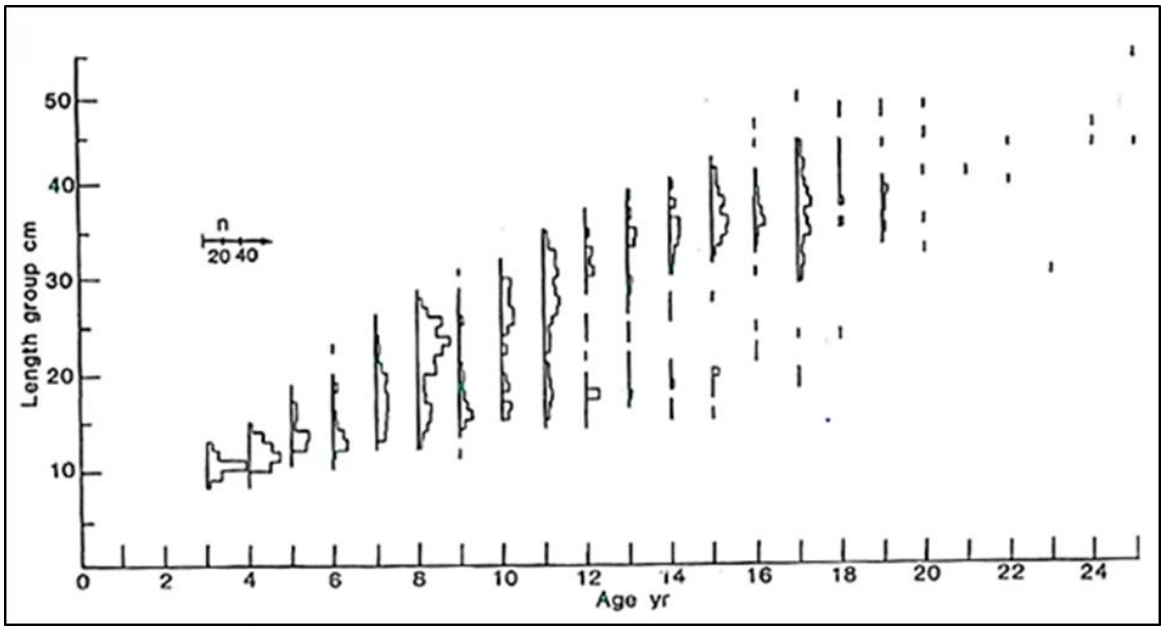


Figure 3-4: Length distribution by age of Arctic charr from bottom and floating gill nets, during the 1978 sampling of Ellasjøen. Reproduced from Klemetsen et al. (1985).

Klemetsen et al. (1985), found a statistical difference in the number of gillrakers between small and large mode charr, with the small mode having fewer gillrakers. In addition, small mode charr were found to have their pelvic fins set further back along the body, smaller relative head length, smaller relative eye diameter, shorter snout and shorter jaw, than large mode fish. Spawning

colours were also noted to be different, with bright yellow bellies of large mode fish and more muted bronze coloured bellies of small mode fish.

Klemetsen et al. (1985) also sampled the stomach content of Ellasjøen charr and found plankton (*Daphnia longispina*) and benthos (Chironomidae and *Apatania zonella* larvae) to co-dominate, both in occurrence and stomach fullness. Stomach contents from pelagic and benthic sampled fish were similar, although plankton was found to be more dominant in pelagic-caught fish. The co-dominance of both benthos and plankton implies that Ellasjøen fish exhibited habitat shifts between the littoral and pelagial zones (Klemetsen et al. 1985). As small mode charr were not often caught in the floating nets, the authors assume plankton feeding must occur close to the shore, in the littoral zone. Arctic charr remains were also found in significant numbers in the stomachs of large-mode fish. The stomachs of small-mode charr were not quantitatively analysed as they were often empty, the authors presume this to be a sign that spawning had initiated (in late August, when samples were taken). Nevertheless, these results are in agreement with the suggestion of at least a degree of trophic polymorphism that could be associated with different growth rates.

4 Methods

4.1 Methodology appraisal

The key data required to determine the year-round behaviour of high-Arctic lake-dwelling charr in Lake Ellasjøen were activity levels and local distribution during all seasons both under ice and in open water conditions. Example outputs could have included measures of daily movement and seasonal home ranges. Information on Arctic charr habitat selection was also necessary, therefore positional information was required, again on a seasonal basis. It was also valuable to distinguish between diel rhythms of activity during an Arctic solar cycle (continual darkness, light/dark, continual sunlight), therefore data was also needed on a 24 hour basis.

In addition, the study aimed to determine whether these variables (activity levels, home range, habitat use) differed between the two putative morphs identified (Klemetsen et al. 1985). This information was therefore gathered for individual Arctic charr of both groups. Thus, individual, fine scale movement and position data were required, allowing conclusions to be drawn with respect to population and sub-population habitat utilisation and activity. The study required data to be collected from an Arctic lake (Ellasjøen is appropriate), on a near-continual basis over a period of a year. Therefore non-automated, manual methods of data collection were eliminated as access to the study site was physically impossible overwinter. Automated data storage technology was therefore required, which could be distributed during the accessible, ice-free summer season and left *in-situ* until access was possible again (9 – 12 months later). In summary, the methodology adopted was capable of; a) collecting fine-scale, individual movement and positional data of Arctic charr *in-situ*, b) collecting data over an extended year-long period and c) deployment in an Arctic lake above or below ice.

Limited research has been conducted in Arctic freshwater environments during all seasons, primarily due to the practical difficulties associated with this inhospitable environment (Vincent et al. 2008, Salonen et al. 2009), with the predominant winter season and the short but dynamic spring and autumn seasons often absent from the literature. Under ice, research on biota, including fish is somewhat limited, with the approaches of most studies being predominately static and manually deployed, for example point sampling of fish using gill nets set through ice (Rikardsen et al. 2003, Svenning et al. 2007). However, the development of new techniques has opened possibilities to measure fish activity under ice. One such method is the application of hydroacoustics, employing advanced fixed station echo-sounding techniques. This method has been used to observe diel vertical migration of lake fishes under ice (Jurvelius and Marjomaki 2008, Gjelland et al. 2009, Kahilainen et al. 2009). However, this method is not appropriate for

determining activity on a wide spatial scale for known individuals and it cannot be deployed autonomously over long periods.

Biotelemetry methods, employing information acquisition from an animal borne transmitter, have a long history of application in fish behaviour research and allow data to be collected on an individual scale, due to the tagging of individual fish. Radio-telemetry has been deployed to determine Arctic charr movement under ice in Northern Labrador (Beddow et al. 1998) and is convenient because radio signals pass easily from water upwards through ice. However, it is not possible to obtain precise positional data using passive (fixed location) application of radio telemetry (Cooke et al. 2013). Therefore radio-telemetry is most feasible using manual active tracking which requires regular access to the study site (Cooke et al. 2013) which would be impossible in this instance, or conducted from air (Beddow et al. 1998), again difficult but, crucially, incapable of giving fine-scale spatial and temporal resolution of animal fixes. Acoustic telemetry has also been applied to determine individual fish movement and habitat use (e.g. Blanchfield et al. 2009, Dick et al. 2009, Baktoft et al. 2012, Bass et al. 2013). Recent advances have been made, which allow the remote (passive) monitoring of acoustically tagged fish using receivers placed in the water column that are capable of detecting and storing tag positions over a considerable period of time. This method has become relatively cheap and easy to deploy and is capable of resolving fine-scale spatial behaviour (Heupel et al. 2006, Cooke et al. 2013).

4.2 Acoustic telemetry

Acoustic telemetry is the transmission in water of sound waves, typically at ultrasonic frequencies of 20 – 500 kHz, which must be detected using an underwater microphone (hydrophone), unlike radio signals which if generated in fresh water, can be detected in air. Acoustic telemetry is generally used for transmitting data underwater because compared to VHF radio frequencies (100 – 200 MHz) acoustic frequencies are absorbed much less. However, acoustic signals, due to their lower frequencies, experience more distortion than radio and cannot transmit as much information per time unit (Vemco Division 2008). Acoustic transmitters emit very short pings of ultrasound, singly or, more commonly, as a series. The train of pings, with short but differing time periods between them forms a digital ID code that identifies that individual transmitter. This code burst occurs over a few seconds and is then followed by a delay, this delay sets the 'repeat rate' of the transmitter. Code repeat rate is set according to study requirements, since factors such as the number of tagged fish, swimming speed and detection range will influence this. The repeat rate is randomized to minimize chances of pings from multiple tags overlapping or colliding repeatedly. This type of transmission scheme allows many tags to transmit on the same frequency (e.g. 69 KHz) enabling multiple transmitters within a single system. The transmitter code is then

detected by an acoustic receiver which detects, decodes and stores the transmission in an internal memory. Acoustic receivers may be used in passive (fixed station) or active tracking modes. Passive receivers, typically with omnidirectional hydrophones, are designed to be moored in a fixed location to detect the presence/absence of tags. Active tracking is used to manually locate tags, using a boat-mounted hydrophone. Passive monitoring was ideal for use in Lake Ellasjøen as receivers could be deployed during the accessible summer months, and left *in-situ*, under ice, until access was possible again 9 – 12 months later.

4.3 Vemco Positioning System (VPS)

This study used the Vemco VR2W Positioning System (VPS), one example of an acoustic telemetry array system. This is a non-real-time, underwater acoustic positioning system, which uses the same equipment used in conventional Vemco remote logging acoustic telemetry studies at a frequency of 69 kHz. The system consists of acoustic transmitters (also referred to here as tags) and receivers with omnidirectional hydrophones (VR2Ws) that are deployed in an individually designed grid formation optimised for maximum coverage of the study area. The acoustic receivers are downloaded on a periodic basis and the data is then extracted and processed. The deployment of this system can provide near-continual spatial and temporal data of a subject in an aquatic environment, provided the animal remains within the instrumented zone. When applied to a 'closed' system such as a lake, the system can effectively 'track' numerous tagged subjects for the entire duration of the study. Transmitters with a pressure sensor can be used which provides the depth at each position received, therefore mapping the 3-dimensional spatial distribution of the animal. Publications utilising this method are emerging (Espinoza et al. 2011a, Farrugia et al. 2011, Andrews and Quinn 2012, Dean et al. 2012, Furey et al. 2013) and results have shown that tagged organisms can be tracked almost continuously, with a positional error equivalent to manual active tracking methods (Andrews et al. 2011, Espinoza et al. 2011b). However, as yet no published studies have utilised this method continuously over a full-year completely unattended. This is not the only such method available, as 3-dimensional telemetry in aquatic systems is also possible solely using 3-dimensional arrays of hydrophones (Lucas and Baras 2000, Cooke et al. 2005, Cooke et al. 2013).

The VPS system is ideal for research in the Arctic, when water is frozen and inaccessible for sustained periods, as once deployed it requires little maintenance. The system can be deployed during the summer months and left unattended for an extended period, if combined with depth-sensing tags, it can effectively provide near continuous temporal and 3-dimensional spatial data, with deployment and data collection required only during the accessible Arctic summer months.

VPS initialisation and deployment was conducted by Dr Carolyn Rosten and Guttorm Christensen. The VPS system design and data extraction was provided by Vemco. VPS retrieval was conducted by the author and Guttorm Christensen.

4.3.1 Theory of operation

The VPS system, as with other hydrophone arrays including some of the earliest (e.g. Hawkins et al. 1974), uses the principle of hyperbolic positioning, also known as time-difference-of-arrival positioning. The basis of this technique is to convert differences in arrival times of a transmitted sound wave to hydrophones in different locations, to distance (range), using the speed of sound in water. The location of the transmitter can then be determined from the distance calculated between the known locations of the detecting receivers. The difference in range between a transmitter and two receivers determines one hyperbola, i.e. any point on which the transmitter may be located, as all points on the hyperbola result in the same difference in range. Figure 4-1a, shows a transmitter hyperbola between two receivers. When three receivers are used, a second difference in range can be determined, resulting in two hyperbolas. Where these hyperbolas intersect is the location of the transmitter (Figure 4-1 b). Therefore, in order to calculate a tag position in two dimensions a transmitter must be detected on a minimum of three receivers, which gives a single tag position.

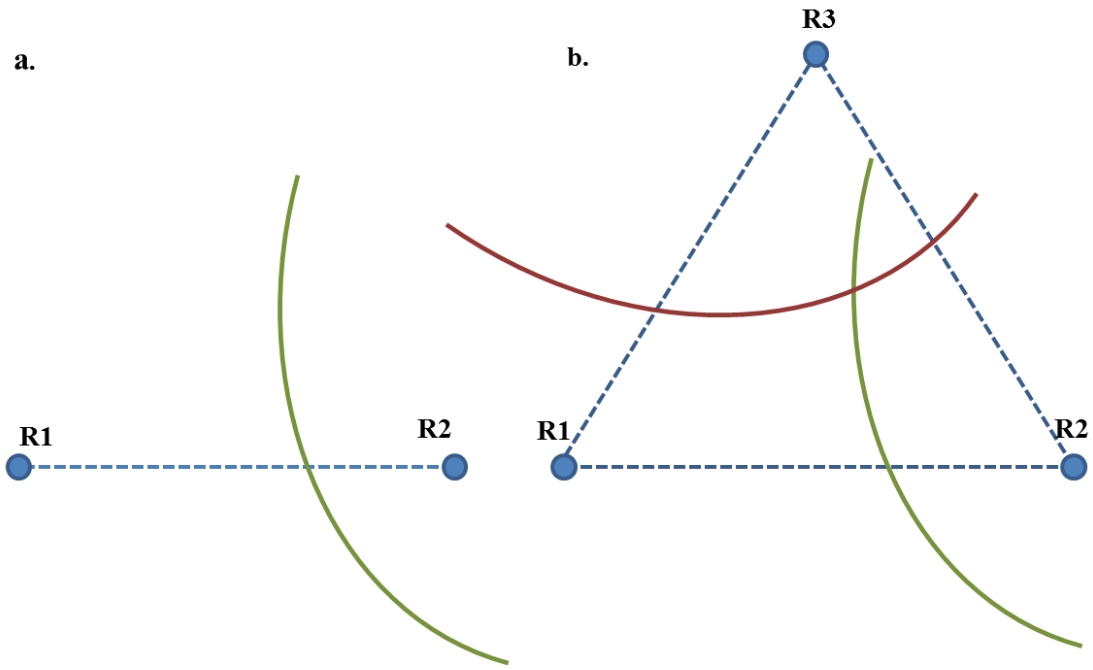


Figure 4-1: a) one side of a hyperbola b) two intersecting hyperbolas. Reproduced from Vemco Division (2008).

The above example shows an ideal receiver arrangement from which to determine the location or position of a transmitter. The three receivers form an equilateral triangle, with the transmitter located within it. If the transmitter were located outside this triangle, the potential error in determining the location of hyperbolic intersection increases. Figure 4-2 (Vemco Division 2008) illustrates the error potential for determining hyperbolas, using a triangle of receivers. The most accurate location will be calculated when the transmitter is within the triangle (green, light blue). Outside of the triangle potential error increases (dark blue, violet, pink). Positioning using detections from four or more receivers is better than with three, as it is more likely that at transmitter will be in a geometrically favourable position, as square arrangement of four receivers forms four triangles.

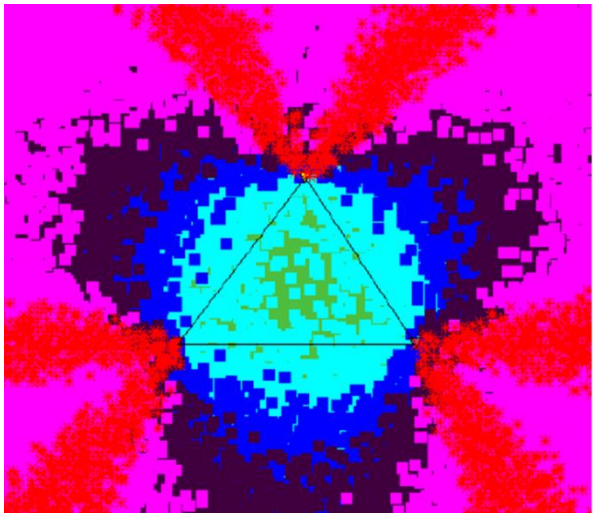


Figure 4-2: Potential error plot for a triangle arrangement of receivers, see text for explanation of what colours represent. Reproduced from Vemco Division (2008)

Because of the drift in receiver clocks, due to changes in water temperature and because of inherent variability between digital clock oscillators, time synchronisation between receivers is required. This issue is solved by using transmitters which are moored with a respective receiver. These transmitters are termed co-located sync tags. Figure 4-3 (Vemco Division 2008) illustrates a typical receiver and co-located sync tag arrangement.

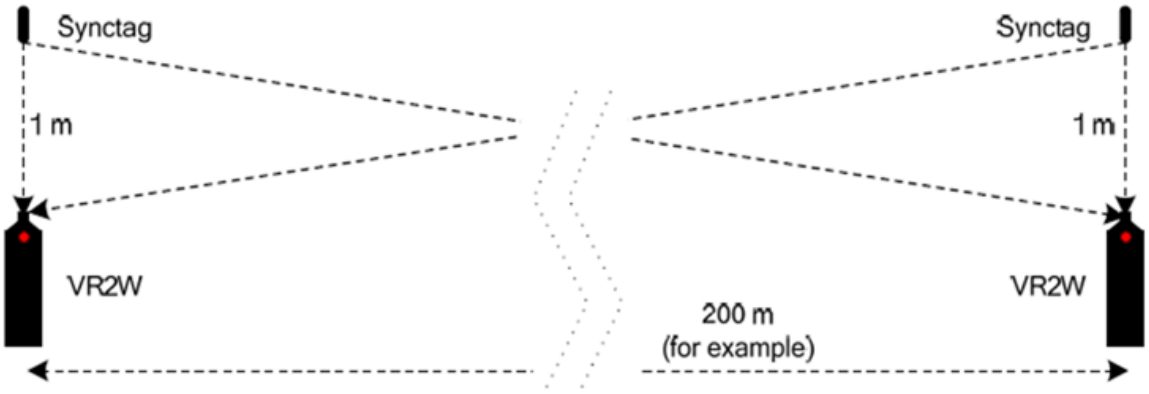


Figure 4-3: Neighbouring receiver and co-located sync tag pair. Reproduced from Vemco Division (2008).

In the VPS system, VR2Ws are placed in an array or grid of triangles or squares. The objective is to ensure that every tag transmission is detected by at least three receivers. Ideally the area of interest is covered with enough receivers to ensure that animals are always inside of a triangle of receivers. Synchronisation tags, 'sync tags', remaining in known location (co-located with receiver), are used to correct for clock drift and/or movement between receivers.

4.3.2 System design

The VPS system is tailored to individual requirements, dependent on site size, bottom topography and depth, study duration and the number of animal transmitters required. Table 4-1 lists the key parameters of consideration and technical specifications of the equipment used in Ellasjøen. Vemco have a central role in both the design of the receiver (VR2W) array and in the extraction of the tag detection data and derivation of tag positions, the customer pays for this service in addition to any equipment costs (fish/sync-tags, VR2Ws). A sample size of 30 animal tags was selected as this was the largest sample funds would allow. It was deemed sufficient to allow for statistical interrogation of the data.

The key concern for Lake Ellasjøen was that the system, once set would not be accessible until retrieval, 12 months later. It is usual to download the receivers and collect data on a periodic basis, thus preventing receiver memory reaching capacity and allowing maintenance of the system e.g. changing receiver batteries, or making position adjustments. However, access to Bear Island is only possible with transportation by the Norwegian coastguard during the summer months; therefore the system was designed with this in mind. Transmitters, both sync tags and animal tags, were set at a reduced repeat rate; an average of every 80 minutes, so receiver memory would not be filled prematurely. Also, the sync tags were set 'co-located' with receivers, meaning that a sync tag was moored on the same line as its receiver pair (see section 4.3.4 System deployment). Therefore, if a receiver drifted or moved, its new position could be

calculated from detections of the co-located sync tag. Transmitters, both sync tags and animal tags were set at a reduced repeat rate; an average of every 80 minutes. This interval was selected after discussion with Vemco as it provided the greatest capacity for data collection but without the receiver memory being filled prematurely, i.e. before retrieval was possible.

Table 4-1: Key parameters and specifications of the Vemco Positioning System (VPS) deployed at Ellasjøen.

Parameter	Specification
Lake area	0.71 km^2
Maximum depth	34 m
Study period	1 year, August 2009 – August 2010
No. of fish tagged	30
Fish tag (transmitter) specification	30 × V9P-6L (depth sensors) (code repeat rate 80 min) Estimated tag life: 3650 days
No. of receivers (VR2W)	19
No. of sync tags	19
Sync tag specification	13 × V13-1L (code repeat rate 80 min) Estimated tag life: 3650 days 6 × V16-4L (code repeat rate 20 min) Estimated tag life: 3650 days
Temperature tag specifications	3 × V13T-1L, set at 3, 25 and 31 m (code repeat rate 80 min) Estimated tag life: 3650 days

Figure 4-4 maps the receiver array formation in Lake Ellasjøen. A total of 19 VR2W-sync tag pairs were required to monitor the full lake, each assigned a station number (e.g. R01). The array was designed so that any position in the lake was in acoustic 'sight' of at least one receiver triangle. This distribution maximises the chance of a transmitter being detected by at least three receivers at any point within the lake. Three temperature loggers were also set at depths of 3, 25 and 31 m so as to enable interpretation of the approximate temperature at which tagged fish resided. All tags had an expected battery life of 3560 days.

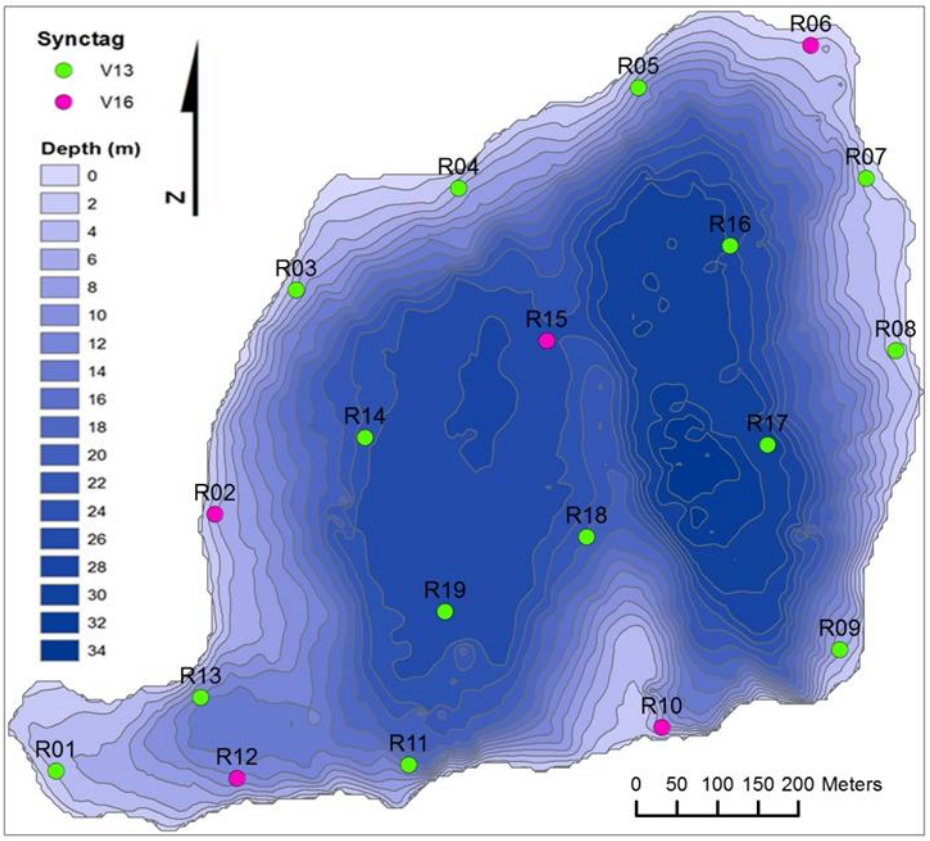


Figure 4-4: Map of VPS receiver array deployed in Lake Ellasjøen, Bear Island. R number denotes station name and co-located receiver/sync tag pair. Depth contours are at 2 m intervals, maximum depth of 34 m (see 4.5 Bathymetry of Lake Ellasjøen). Green markers show the V13 sync tag deployment locations, pink markers V16 sync tag locations.

4.3.3 System initialisation

Prior to deployment each receiver, powered by a single 3.6 V Lithium D cell, was activated (initialised). The serial number of each receiver was recorded and designated a station name (R number) according to the array deployment map (Figure 4-4). Vemco User Environment (VUE) freeware, a programme interface for receivers, was used to create a database allowing the initialisation and data retrieval from multiple Vemco receivers. It was used, via a bluetooth dongle to assign a station name, and check the internal clock and settings of the connected receiver ready for deployment.

4.3.4 System deployment

Each initialised receiver was attached to a line of rope approximately 2 – 3 m shorter than the total depth at the assigned deployment position. This was considered deep enough to prevent receivers being frozen into ice, which may have caused receiver damage or receiver stations being moved with ice currents. A handheld echo sounder was used to determine depth. A large rock

was wrapped in a net and secured to the line, in order to anchor the receiver in position. More sophisticated anchors were not possible due to the remoteness of the location. A small surface marker buoy was attached to the other end of the line to keep the receiver vertical in the water column. The receiver was attached to the rope with five strong cable ties, approximately 1 m above the anchor, with the hydrophone pointing upwards. For each receiver a sync tag was 'co-located' and attached to the same line, approximately 1 m above the receiver. Care was taken to ensure each sync tag and receiver serial number matched the station name assigned in VUE. The line was then lowered into the water at the designated position and a GPS waypoint was recorded. A minimum of three GPS locations were taken for each receiver station, in order to maximise accuracy of the GPS location. Figure 4-5 shows the attachment method and necessary equipment. Equipment was deployed on the 28 August 2009.

Figure 4-5: Receivers used for VPS deployment in Lake Ellasjøen, Bear Island. The figure also illustrates the attachment method used for receiver deployment.

4.3.5 System retrieval

Where possible each receiver was retrieved and the data downloaded on the 23 – 24 August 2010. A line between two small boats was used to 'trawl' for the marker buoy in the vicinity of the deployment position. A GPS waypoint was taken for each retrieval position. Each receiver was then downloaded using VUE, using the communication process described in 4.3.3 (System initialisation). In some formats the user is able to download the receiver and use VUE to view the data directly. However the VPS arrangement in Lake Ellasjøen did not allow this; to maximise

memory capacity on the receivers (due to the extended deployment period) this was disabled during initialisation. Therefore all download files had to be sent to Vemco for an extraction process. This generated individual fish positions from receiver detections (see 4.3.1 Theory of operation).

4.4 Fish sample

Fish capture, surgery and morphology measurements were conducted by Dr Carolyn Rosten and Guttorm Christensen.

4.4.1 Capture methods

Fish were caught on the 27 August 2009 during daylight, by rod and line using a single barbed hook from two locations; either from the lake shore at the north east corner of the lake to target littoral fish, or by boat over the deepest area of the lake to target pelagic fish. This method was the most effective at catching fish and a fishing effort of just two to three hours was required to achieve a sample suitable for tagging (see 8.4.2). Nordic multi-mesh (12 mesh sizes, 5 – 55 mm) bottom set gill nets (30 × 1.5 m) were also set in the deeper areas of the lake, to target benthic, profundal fish. They were set for a 24 hour period from the 27 – 28 August 2009. As the fish were required alive and fit for tagging the nets were lifted every two to six hours over this period. Fishing effort was limited to one 24 hour period due to the limited time access on Bear Island and the high number of fish caught during that time.

4.4.2 Tagging procedure

The animal transmitters used in this study were 9 mm acoustic transmitters with pressure sensors, capable of measuring depths up to 50 m (resolution 0.22 m) (model V9P-6L Vemco Ltd). Each tag had a code repeat rate of every 80 minutes. This was selected for a number of reasons; a) so the battery capacity was capable of lasting the study period; b) so the memory capacity on the VR2W receivers would not become full before the study was complete; c) to avoid transmitter collisions (see 4.2 Acoustic telemetry) and; d) to maximise data collection within the constraints listed in (a) to (c).

Each tag weighed 2.9 g in air and it was considered that the maximum proportion of body mass the tag should represent should be 8 % in order to minimize impacts on physiology and behaviour (Cooke et al. 2013). These tags were used as the lightest model with pressure transducers capable of measuring depth with a resolution applicable to the relatively shallow water depth of Lake Ellasjøen. Therefore the fish selected for surgery weighed a minimum of 35 g, and in all but two

cases the tag to body mass ratio was less than 4 %. Fish were selected for tagging if they fulfilled this weight criterion, and were fit in external appearance and movement. Where possible, an equal number of fish from both small and large mode charr were selected (as identified by Klemetsen et al. 1985). These were identified using a combination of length, key morphological traits (e.g. head and snout shape, judged by eye in the field) and colouration in order to distinguish as best as possible the two putative groups of Arctic charr.

Fish tagging was conducted in the field, as close to the lake as possible, thus minimising transportation stress on the fish. Post capture, all fish were kept in the same large keep net, in the lake and transported to tanks shortly prior to surgery. A pre and post-operative tank was built on the shoreline with rocks and a plastic sheet. Fish were individually anesthetised in a benzocaine solution (0.5 ml l^{-1}). Once sedated the fish were placed on a latex mat, which was sterilised (wiped with ethanol, and allowed to dry) between each fish. A 2 cm incision was then cut through the ventral body wall and peritoneum of the fish using a scalpel. A pre-sterilised (washed in 96 % ethanol and dried) tag was inserted into the incision, rounded end first, and positioned to sit horizontal in the abdominal cavity. The incision was then closed using two monofilament sutures. The entire procedure was conducted in as sterile conditions as possible. Scalpel blades and suture needles were changed between each fish and latex gloves were worn by both the surgeon and the assistant. Each fish was then allowed to recover in a large tank, until full reflexes and movement had returned, and no visible impairment as a result of surgery observed. The fish were then returned to the lake, as it was considered that a swift release provided the fish with the least stressful from of recovery (Crossman 1977).

Prior permission was granted to use live animals for research purposes by the Norwegian Ethical Committee for Animal Experimentation (Forsøksdyrutvalget) and all surgery procedures were conducted by a person licensed in Norway to conduct research using live animals.

4.4.3 Morphometric measurements

For each fish a series of morphometric measurements were taken, whilst the fish was sedated and before tagging was undertaken. Head measurements, including; head length, head depth, lower jaw length and eye diameter (Figure 4-6 orange arrows) were selected based on their relationship to prey acquisition and handling (Adams et al. 1998). These measurements have been successfully used to discriminate between sympatric phenotypically divergent populations (e.g. Adams et al. 1998). Body measurements, including; caudal peduncle width, pelvic and pectoral fin lengths were also used to describe individual body shape (Figure 4-6 blue arrows). Body shape morphology is generally adapted to different modes of swimming in different foraging habitats.

Limnetic fish tend to have narrow, streamlined bodies and smaller fins to minimise drag when swimming in open-water, whereas benthic fish tend to have relatively deeper, robust bodies and larger fins for improved manoeuvrability (Webb 1984).

Morphological variation amongst individuals for any given trait is expected to be small relative to the size of the trait, therefore any potential variation will be confounded by further variance such as measurement error. For this reason, care was taken to minimise measurement error; all fish were measured using precision callipers and measured to the nearest 0.1 mm and all measurements were taken from the left side of the fish.

The traits measured were (Figure 4-6):

1. FL - Fork Length; distance from the tip of the snout to the fork of the tail fin.
2. TL - Total Length; distance from tip of the snout to the tip of the tail
3. CP - Greatest depth of the caudal peduncle
4. PEC - Pectoral fin length
5. PEL - Pelvic fin length
6. HL - Head length. Distance from the tip of the snout to the operculum
7. HDO - Head depth at the operculum
8. HDE - Head depth at the eye
9. LJ - Length of the lower jaw
10. ED - Diameter of the eye

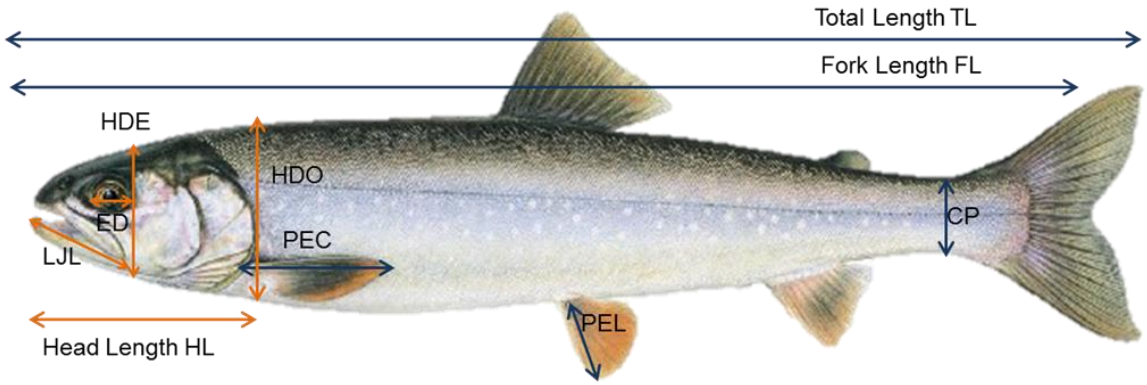


Figure 4-6: Body (blue arrows) and head (orange arrows) morphological measurements: CP, caudle peduncle width; PEC, pectoral fin length; PEL, pelvic fin length. LJL, lower jaw length; ED, eye diameter; HDE, head width at eye; HDO, head width at operculum (illustration reproduced from Government of Maine, U.S.A; www.maine.gov).

Photography was also used as additional evidence of any intra-population variation. This is useful for determination of markings and colour variations between individuals. A photograph was taken of each individual from the left side of the fish (camera specifications: optical sensor size 6.17 ×

4.55 mm, focal length 27 mm). From these photographs each fish was visually assigned to a morphology grouping according to size, colouration and markings of each individual.

As the morphological measurements are correlated to the fork length of the fish, it was necessary to determine a measure of morphological shape irrespective of individual size. Size independent measures of head and body shape were therefore derived by calculating the proportion of each measured variable with individual fork length. Discriminant analysis was selected as the groups were defined according to visual inspection of the photographs taken at processing (i.e. the groups were known *a priori*). Using JMP v 9.03 software (SAS institute Inc.) discriminant analysis was applied to the size-adjusted traits (using forward direction stepwise insertion of variables) to test for group membership. Stepwise insertion of variables was used to minimise the sum of unexplained variance for all groups and to identify those meristic traits which discriminate between the visually identified groups (Solem 2011).

4.5 Bathymetry of Lake Ellasjøen

The detailed bathymetry of Lake Ellasjøen was not known prior to this investigation, therefore a bathymetric GIS map was created specifically for this study by the author. A GPS bathymetry sounder (Garmin GPSmap 178C) recorded the lake depth at 4,412 XY positions on Lake Ellasjøen (25 August 2010). The sounder was attached to a small boat and numerous transects of the lake were undertaken covering as much of the surface area of the lake as possible (Figure 4-7). The data were transferred to ArcMAP10 (ESRI, 2010) where a bathymetry map was created from these raw XYZ positions, with a resolution of 1 m. The lake outline, defined from the GPS positions taken around the lake edge was overlaid with satellite images (Norges Kart) of Lake Ellasjøen to confirm the accuracy of the bathymetry map outline. The Spatial Join tool in ArcMap 10 was utilised to calculate the density distribution of fish positions. The area of Lake Ellasjøen was divided into a grid formed of 25 m^2 squares, allowing the number of fish positions in each grid square to be calculated as a percentage density of the total number.

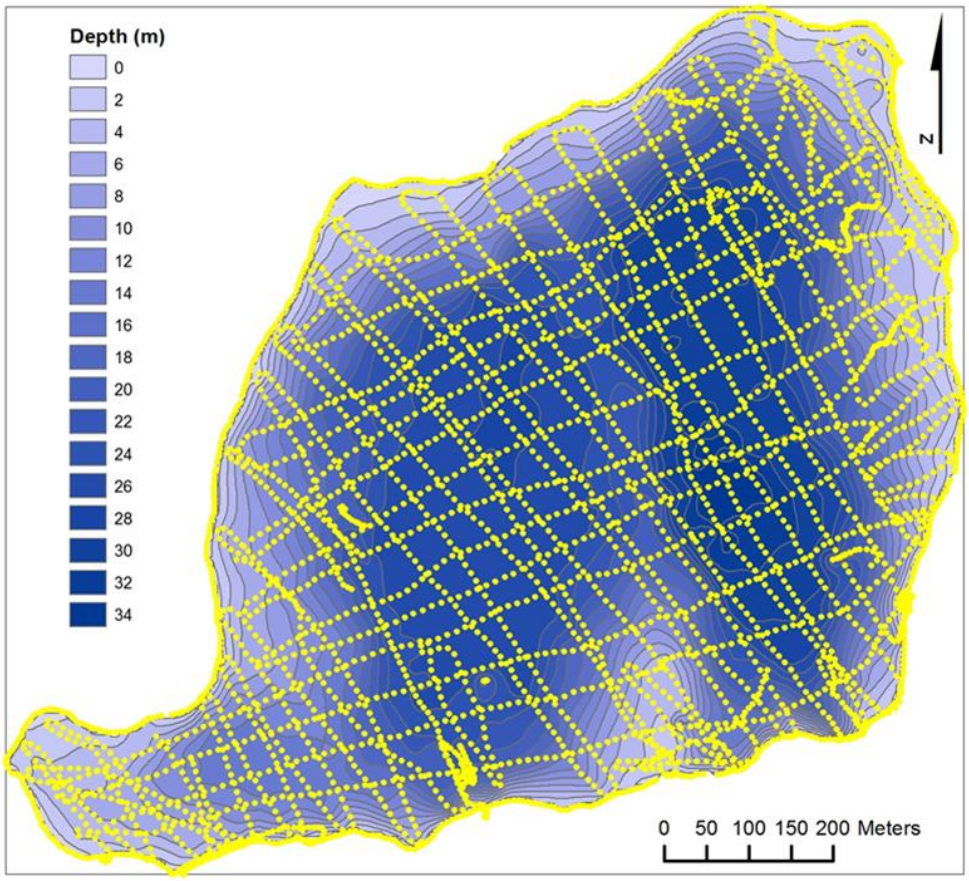


Figure 4-7: Transects travelled to collect the raw bathymetry data of Lake Ellasjøen, Bear Island. A GPS bathymetry sounder (Garmin GPSmap 178C) recorded the lake depth at 4,412 locations (yellow markers). From this a bathymetry map was created in ArcMap 10 (ESRI, 2010) (see Figure 4-4).

4.6 Statistical analyses

All statistics were performed by the author using JMP v 9.03 software; a p value < 0.05 was considered statistically significant unless specifically stated.

Statistical analyses of fish behavioural patterns were largely based on Generalised Linear Models (*GLMs*). Individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals.

Linear regressions were conducted to investigate the effect of the physical environment on fish behaviour. Linear models were selected in all instances due to time constraints. Where multiple linear regressions were conducted Bonferonni correction was applied in order to correct for possible false rejection of the null hypothesis (type I errors). The Bonferonni corrected significance (p) value is stated in each instance.

Linear regressions were also applied to investigate fish length and weight effects on activity. Data for Robust and Delicate morphs were pooled, as sample sizes were relatively small and individuals were tracked for varying durations. Data acknowledgements

Fish capture, surgery and system deployment was conducted by Dr Carolyn Rosten (Norwegian Institute of Water Research, NIVA) and Guttorm Christensen (AvkaplanNIVA). The VPS system design and data extraction was provided by Vemco. Data retrieval and analyses were conducted by the author.

5 Results

5.1 Fish sample

5.1.1 Visual determination of phenotype

A total of 32 (two fish were processed but not considered in a sufficiently fit condition for surgery to be conducted) Ellasjøen Arctic charr (fork length; 166 – 505 mm) were processed and 28 were photographed in late August 2009, at a time of reproductive maturation. From this sample 30 fish were implanted with an acoustic transmitter (V9P-6L). Visual analysis of the photographs taken during the tagging procedure, and notes taken during processing revealed six visually distinct groups based on size, sex and colouration/markings:

1. Robust - male (1M): Large size, strong orange/red colouration, hooked lower jaw, white fin edges.
2. Robust - female (1F): Large size, red/orange colouration below lateral line- silver above, blunt snout, white spots, white fin edges.
3. Robust - undetermined sex (1?): Large size, silver colouration with white spots, blunt snout, white fin edges.
4. Delicate (2): Smaller size, sex undetermined, silver colouration, pointed snout, large eye.
5. Dwarf -maturing (3): Small size, mixed sex (gametes released when gentle pressure was applied), 'parr' markings.
6. Other (4): Small size, immature (no gametes released when gentle pressure was applied), silver /parr colouration.

The first three groups were combined, generating three different phenotypes/morphs and one ontogenetic group:

Group 1: Robust morph (1M, 1F, 1?)

Group 2: Delicate morph (2)

Group 3: Dwarf maturing morph (3)

Group 4: Other (ontogenetic group) (4)

An example individual assigned to each of the four visually determined groups are shown in Figure 5-1. All 28 of the photographed fish and their designated grouping are exhibited in 9.1 Appendix I- fish sample.

1 (M): Robust - male

Large size, red /orange colouration, hooked lower jaw, white fin edging

1 (F): Robust - female

Large size, orange / silver colouration, blunt snout, white fin edging

1 (?): Robust - undetermined sex

Large size, silver colouration, blunt snout, white fin edging

2: Delicate – undetermined sex

Smaller size, silver colouration, large eye, pointed snout

3: Dwarf - small maturing

Small size, parr markings, mature (gametes released)

4: Other

Small size, silver/parr markings, immature (no gametes released)

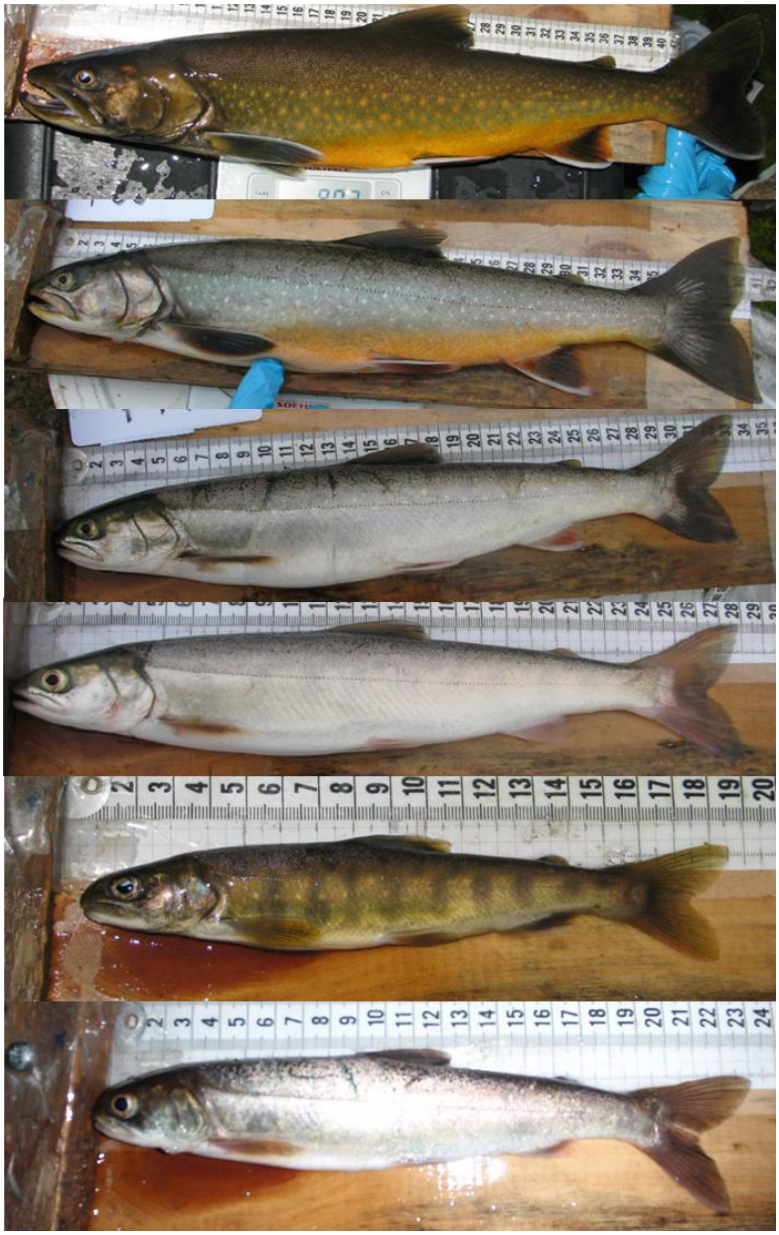


Figure 5-1: An example individual from each of the six visually determined groups, from a sample of 32 Arctic charr from Lake Ellasjøen, Bear Island. The groups were derived according to size, sex, colouration and markings.

5.1.2 Distribution of morphology measurements

The raw values from the series of morphological measurements taken for each of the 32 fish are shown (Table 5-2), for descriptions of the measurements refer to the Methods chapter 4.4.3 Morphometric measurements. The individuals D1 and D2 were included in the meristic analysis but not implanted with a transmitter. The morphological code according to the visual analysis is shown (1 – 4), when no photograph was taken N/A is stated.

Descriptive statistics for each morphological measurement are presented in (Table 5-1). Values of skewness (g1) ranged from 0.11 (Eye diameter, ED) to 0.29 (head depth at operculum, HDO) and kurtois (g2) -1.27 (head depth at eye, HDE) to -0.59 (lower jaw, LJ). A Shapiro Wilk W test was used to test for significant deviation from a normal distribution. Regression statistics showed a highly significant regression of each variable with fork length (FL) (R^2 = 0.72 – 0.98, p < 0.0001). Regression fits indicated that measurements for the individual T20 were outliers. No photograph was available for this individual, making post- verification of the measurements impossible, thus meristic data from this individual is omitted from Table 5-1 and not included in further morphological analysis.

Table 5-1: Descriptive statistics of each morphology measurement (cm) (for a description of the measurement refer to the Methods chapter, 4.4.3 Morphometric measurements) taken from a sample of 31 Arctic charr (T20 excluded, see text above for explanation), from Lake Ellasjøen, Bear Island. Abbreviations: FL, fork length; CP, caudal peduncle width; PEC, pectoral fin length; PEL, pelvic fin length; HL, head length; HDE, head depth at eye; HDO, head depth at operculum; LJ, lower jaw length; ED, eye diameter; SD, standard deviation; Min, minimum; Max, maximum; g1, skewness; g2, kurtosis; p, the outcome of the Shapiro Wilk W test for a non-normal distribution, significance at p < 0.05 is indicated by*; a, intercept; b, slope; R^2, regression coefficient.

	Descriptive statistics							Regression statistics (p < 0.0001)		
Measurement (cm)	Mean	SD	Min	Max	g1	g2	p	a	b	R^2
FL	32.5	9.2	16.6	50.5	0.21	-0.90	0.277	-	-	-
CP	1.9	0.7	0.7	3.4	0.19	-0.62	0.436	-0.33	0.01	0.93
PEC	4.8	1.7	1.9	8.1	0.26	-1.11	0.058	-1.05	0.02	0.93
PEL	3.6	1.3	1.4	6.2	0.24	-1.23	0.034*	-0.89	0.01	0.92
HL	6.7	2.2	3.2	10.7	0.25	-1.03	0.067	-0.89	0.02	0.98
HDE	3.0	1.1	1.4	5.1	0.21	-1.27	0.043*	-0.66	0.01	0.95
HDO	4.1	1.4	1.8	7.0	0.29	-0.90	0.120	-0.75	0.01	0.93
LJ	3.0	1.3	1.1	6.1	0.60	-0.59	0.035*	-1.35	0.01	0.88
ED	0.8	0.2	0.5	1.2	0.11	-0.91	0.322	0.25	0.00	0.72

Table 5-2: Table of raw morphology measurements for all 32 sampled Arctic charr from Lake Ellasjøen, Bear Island. Fish ID T01 – T30 indicates those fish implanted with an acoustic transmitter. Fish ID 'D' identifies those fish that died during processing. Morphology measurements are in mm, weight in grams; see Methods chapter 4.4.3 Morphometric measurements for a description of measurements. Abbreviations: W, weight; FL fork length; TL, total length; HL, head length; HDE, head depth at eye; HDO, head depth at operculum; LJ, lower jaw length; ED, eye diameter; PEC, pectoral fin length; PEL, pelvic fin length; CP, caudal peduncle width. Sex is given as M for male, F for female and ? for unknown. See 5.1.1 Visual determination of phenotype, for an explanation of morph group code (1 – 4), N/A lists individuals for which a photo is unavailable.

Fish ID	Morph group	Sex	W	FL	TL	HL	HDE	HDO	LJ	ED	PEC	PEL	CP
T01	1	F	387	405	432	79	39	51	35	9	58	44	22
T02	1	F	630	435	455	97	46	60	47	12	69	55	25
T03	1	M	1127	495	527	107	47	70	61	10	81	62	34
T04	1	F	808	505	543	107	51	66	52	11	75	57	30
T05	1	F	548	418	452	90	43	43	40	9	63	50	26
T06	2	?	203	297	333	56	22	34	24	7	41	29	17
T07	1	M	488	362	386	79	38	53	44	10	58	41	21
T08	4	?	76	212	241	40	19	24	16	6	30	19	11
T09	1	F	578	420	416	84	38	51	35	9	54	43	25
T10	1	?	314	314	341	60	25	36	26	7	44	30	17
T11	1	M	923	460	501	102	43	63	51	10	77	56	30
T12	N/A	?	125	240	260	45	20	29	17	6	29	22	11
T13	1	F	666	385	424	79	37	54	33	9	58	42	24
T14	1	M	481	350	375	76	37	45	38	9	56	47	23
T15	3	M	49	166	180	33	14	20	14	6	26	19	10
T16	N/A	?	130	248	270	56	26	34	22	10	36	29	19
T17	1	?	594	398	427	83	39	51	29	10	60	44	24
T18	2	?	185	275	286	51	22	33	18	7	34	25	16
T19	2	?	201	265	291	50	23	31	22	8	32	24	17
T20	N/A	?	149	281	301	85	55	65	54	12	77	68	50
T21	1	F	608	392	427	84	39	51	39	11	62	47	24
T22	2	?	216	281	300	54	24	33	17	7	36	26	16
T23	4	?	162	251	271	49	20	21	21	7	32	23	13
T24	N/A	?	90	224	242	42	17	24	15	5	28	22	12
T25	1	F	291	308	392	72	34	44	32	9	56	45	22
T26	2	?	220	290	315	58	24	33	22	7	38	28	15
T27	3	F	114	219	237	42	18	27	15	6	33	22	12
T28	4	?	35	175	189	32	14	18	11	5	19	14	7
T29	2	?	195	271	289	52	22	31	19	7	35	28	14
T30	1	M	412	369	386	79	34	50	44	8	64	47	23
D1	4	?	56	178	190	34	12	19	11	4	22	15	8
D2	3	F	119	220	236	42	19	27	16	7	24	24	12

5.1.3 Determination of shape morphology

As the morphological measurements revealed a strong correlation to FL, it was necessary to determine a measure of morphological shape irrespective of individual size. Size independent measures of head and body shape were therefore derived by calculating the proportion of each measured variable with FL, head length (HL), head depth at eye (HDE) and head depth at operculum (HDO). Discriminant analysis was then applied to the size-adjusted traits (using forward direction stepwise insertion of variables) to test for group membership. Stepwise insertion of variables was used to minimise the sum of unexplained variance for all groups and to identify those meristic traits which discriminate between the visually identified groups (Solem 2011). The model selected ED/HDE, PEL/FL and HDO/HL as the first, second and third discriminant functions respectively. The first discriminant function explained 85.8 % of the variation, the second 7.6 % and the third 1.6 %. An ordination of the canonical scores of the model (Figure 5-2) reveals that the four groups' are well separated. Wilk's Lambda test showed the difference between the groups centroids was highly significant (Wilk's Lambda value = 0.07, $F = 7.86$, $df = 9$, $p < 0.0001$) (Solem 2011).

The model calculated the probability of each individual being correctly assigned to the visually designated groupings, based on how close the meristic values of the individual were to the mean values of the group being predicted (Table 5-3). According to the covariates selected by the discriminant model, three fish (T08, T10, T27) were visually misclassified into a morphology group, i.e. the probability of them being a different morph, was greater (Table 5-4). Fish were grouped according to the output of the discriminant model and checked for compatibility against existing biological and photographic data. In all cases these complied, except for T27 which, since it was a reproductively mature female (was expressing ova when abdomen gently stroked) at a FL of 23 cm, and showed classical parr markings was identified as a Dwarf Maturing charr (9.1 Appendix I-fish sample), even though the morphometric characteristics were similar to a Delicate fish. These phenotype classifications were then used for subsequent analysis of the telemetry data and to distinguish Robust from Delicate fish for comparison of spatial behaviour of these two groups. Thus, the sample of 32 Lake Ellasjøen Arctic charr were classified as; 14 Robust individuals, 10 Delicate, 4 Dwarf maturing, 3 Other and 1 Unclassified (T20).

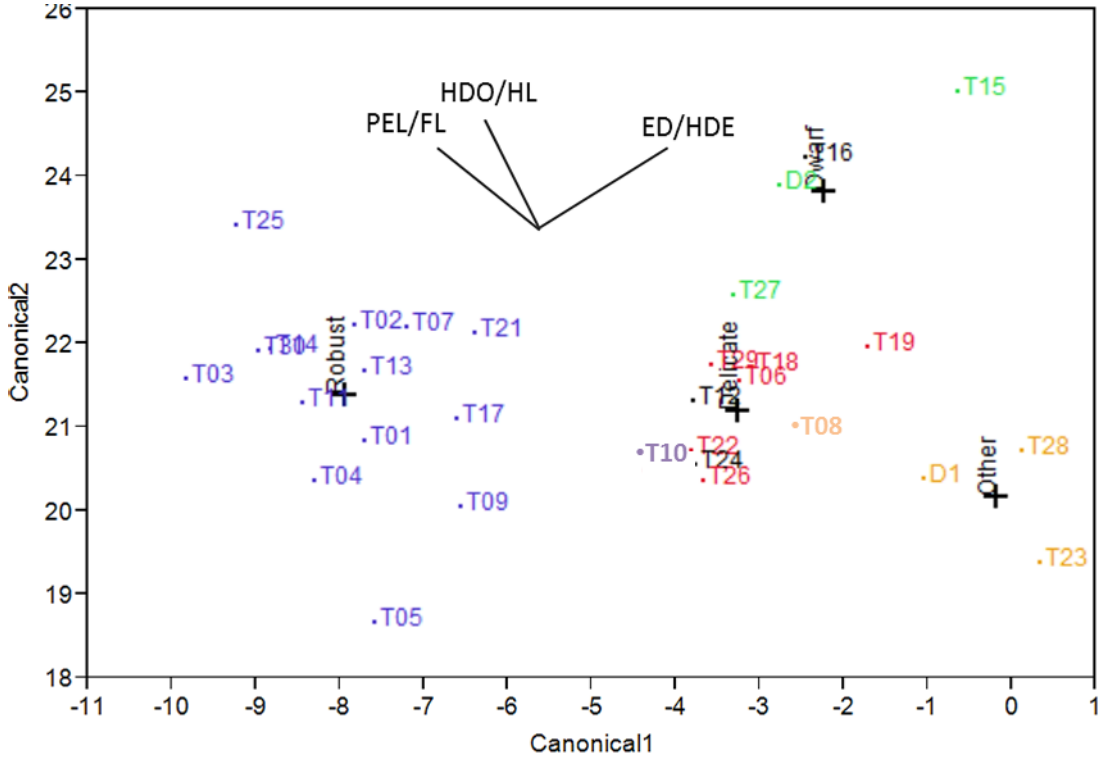


Figure 5-2: Ordination of the three discriminant functions (PEL/FL, ED/HDE and HDO/HL) selected according to a stepwise discriminant analysis model to test individual membership according to the four visually identified groups from a sample of 31 Arctic charr from Lake Ellasjøen, Bear Island. Individuals are identified by markers according to their visually assigned morphology group; blue, Robust; red, Delicate; green, Dwarf maturing and orange, Other. Non-photographed individuals were also included in the model, shown with black markers. Group centroids are marked (+). Ordination rays are shown for each discriminating covariate, to illustrate the direction of each function in canonical space, where ED/HDE is canonical 1, PEL/FL canonical 2 and HDO/HL canonical 3. The individual T20 was excluded, see section 5.1.2 for further explanation.

Table 5-3: Mean values (mm) of each discriminant function (PEL/FL, ED/HDE and HDO/HL) selected according to a stepwise discriminant analysis model to test individual membership according to the four visually identified groups from a sample of 31 Arctic charr from Lake Ellasjøen, Bear Island.

		mean value (mm)		
Morph group	*n*	PEL/FL	ED/HDE	HDO/HL
Robust	14	0.12	0.24	0.62
Delicate	10	0.09	0.31	0.61
Dwarf	4	0.11	0.38	0.62
Other	3	0.09	0.35	0.52

Table 5-4: Probability scores for the three misclassified fish according to the discriminant analysis model, for which the three covariates PEL/FL, ED/HDE and HDO/HL were selected to discriminate between the four visually, identified groups from a sample of 31 Arctic charr from Lake Ellasjøen, Bear Island. The morphological designation and probability of the three non-photographed individuals are also given. The model was accepted in all instances with the exception of T27, which was classified according to the photographic and biological data, i.e. Dwarf maturing.

Fish	Visually assigned phenotype	Probability of visual phenotype	Discriminant model assigned phenotype	Probability of discriminant model phenotype
T08	Other	0.21	Delicate	0.79
T10	Robust	0.05	Delicate	0.92
T27	Dwarf	0.27	Delicate	0.71
T12	N/A	-	Delicate	0.97
T16	N/A	-	Dwarf	0.99
T24	N/A	-	Delicate	0.88

5.2 The physical environment of Lake Ellasjøen

5.2.1 Environmental conditions

Three temperature tags (V13T-1L) recorded the water temperature of Lake Ellasjøen approximately every 80 minutes over the entire study period (28/8/2009 – 23/8/2010). Tags were set at three depths; 3, 25 and 31 m. The lake showed little evidence of stratification over the summer months (Figure 5-3) but an inverse temperature gradient occurred over winter, inferring the likely period of complete ice coverage (16/12/2009 – 24/5/2010, 158 days), with temperatures close to zero at 3 metres between December and June. Maximum temperature was recorded at 8.0 °C on the 29th July 2010 at 3 metres. Minimum temperature was recorded at -0.1 °C at all three depths during January.

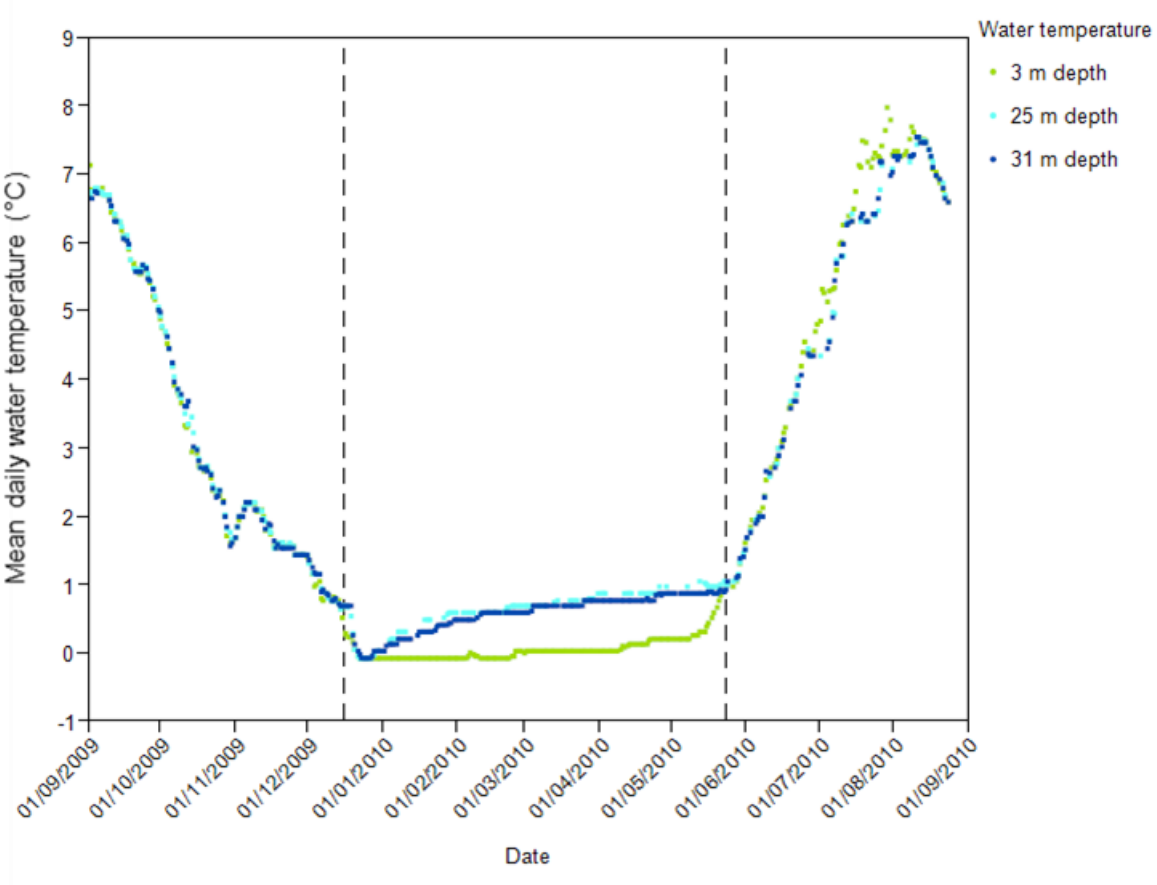


Figure 5-3: Mean daily water temperature (°C) at 3 (green), 25 (light blue) and 31 (dark blue) metre depths in Lake Ellasjøen, Bear Island, over the study period (28/8/2009 – 23/8/2010). Dashed reference lines on the date axis show the period of inverse temperature gradient (16/12/2009 – 24/5/2010, 158 days), inferring the likely period of complete ice coverage.

Daily meteorological records were obtained from the Norwegian Meteorological Institute (accessed online from the eklima database) for the Bear Island Radio climate station, located on the north coast of the island, 14 km from Lake Ellasjøen (straight line distance). These included; daily mean air temperature, ground snow cover (presence/absence, not precipitation), mean daily wind speed and time of sun rise/set. Daily average wind speed ranged from 1.6 ms^{-1} recorded on 16/7/2010 to; 16.5 ms^{-1} on 19/01/2010 (Figure 5-4). The highest average air temperature was 9.5 °C on 10/7/2010, the lowest -13.7 °C on 27/3/2010 (Figure 5-4, Figure 5-5). Snow presence occurred between 14/12/2009 and 7/6/2010, 173 days (Figure 5-4, Figure 5-5) At the latitude of Bear Island (74° N) polar night occurred between 8/11/2009 – 3/2/2010 (88 days) and polar day occurred between 31/4/2010 – 12/8/2010 (102 days), based upon time of sun rise and sun set (Figure 5-5).

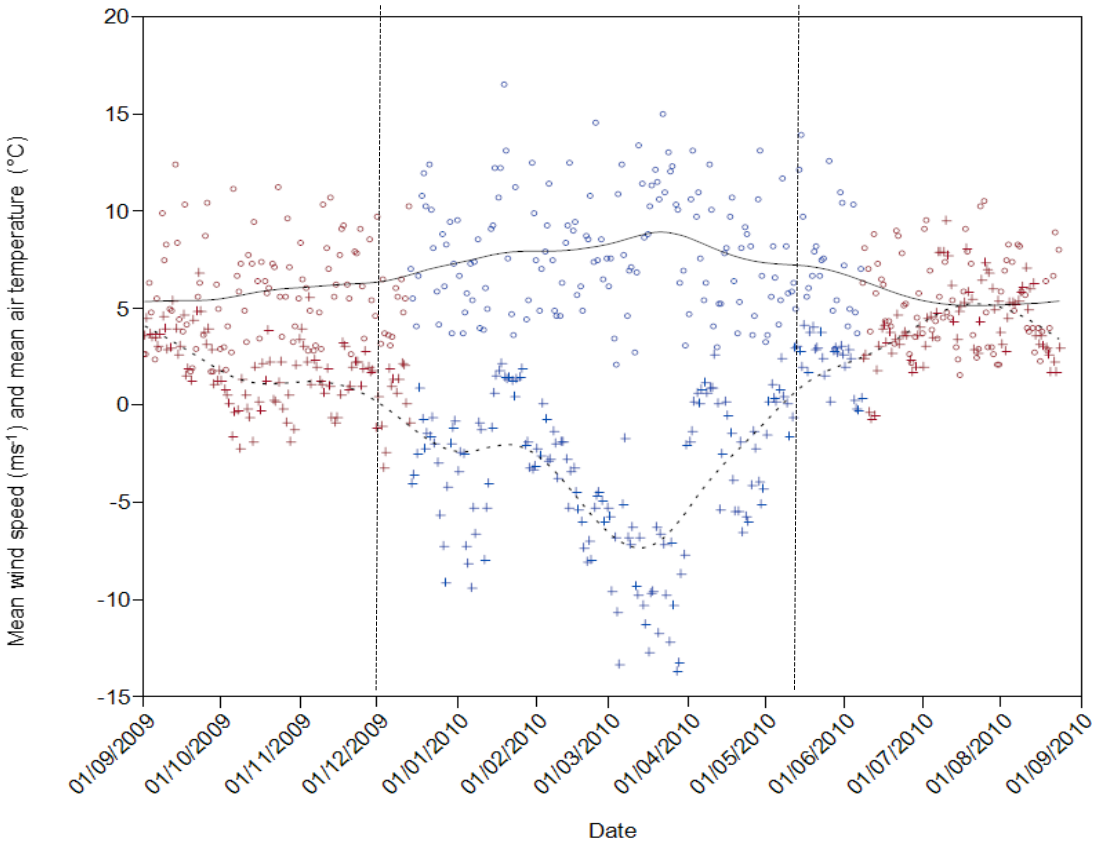


Figure 5-4: Daily meteorological data recorded at the Bear Island Radio climate station (Norwegian Meteorological Institute; data accessed online via eklima database). Mean values of daily air temperature (**+**) (°C) and wind speed (**o**) (ms^{-1}) are given and smoothed curves fitted. Data values are coloured according to presence (blue) or absence (red) of snow ground cover at the station. Dashed reference lines on the date axis show the period of likely complete lake ice coverage (16/12/2009 – 24/5/2010, 158 days).

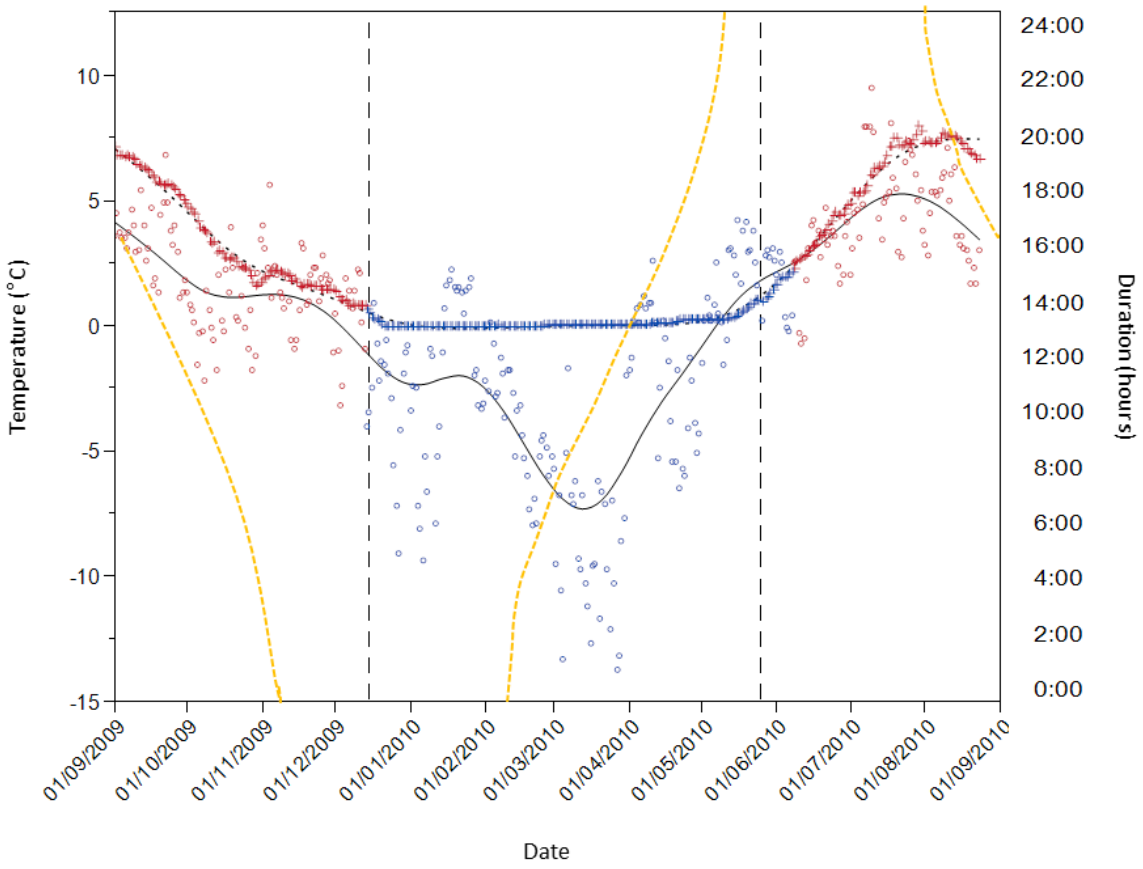


Figure 5-5: Daily meteorological data recorded at the Bear Island Radio climate station (Norwegian Meteorological Institute; data accessed online via eklima database). Mean values of daily air temperature (+) and water temperature of Ellasjøen at 3 m depth (o) are given (°C) and smoothed curves fitted. Data values are coloured according to presence (blue) or absence (red) of snow ground cover. The duration of daylight, as hours between daily dawn and dusk, is shown with the orange dashed line. Dashed reference lines on the date axis show the period of inferred complete lake ice coverage (16/12/2009 – 24/5/2010, 158 days).

5.2.2 Bathymetry and zonation of Lake Ellasjøen

The bathymetry map of Ellasjøen (see 4.5 Bathymetry of Lake Ellasjøen) shows the lake is characterised by steep sloping sides and partially divided into two relatively flat basins with a maximum depth of 34 metres. The euphotic zone (Zeu) of a lake can be defined by Equation 5-1 (Moss 2010):

$$Zeu = 1.7 \times Zs$$

where Zs is Secchi depth (Equation 5-1)

Using this model the euphotic zone of Ellasjøen is 6 m (Secchi depth of 3.5 m measured in August, Klemetsen et al. 1985). The fish tags used in this study had a vertical accuracy of ± 2.2 m;

therefore an additional two metres were added to the euphotic zone, to allow for error in vertical fish position. Ellasjøen was thus divided into three zones:

1 Littoral: Depth 0 – 8 m where total water column depth is ≤ 8 m. In Ellasjøen this occurred exclusively around the shores of the bowl shaped lake.

2 Limnetic: Depth 0 – 8 m, where the total depth of Ellasjøen is greater than 8 m.

3 Profundal: Depth 9 – 34 m (the maximum depth of the lake).

Using the Spatial Analyst add-on for ArcMAP10 (ESRI, 2010) the surface area (m^2) and volume of water (m^3) in each of the three zones of Ellasjøen was calculated, as well as the offshore area, the sum of limnetic and profundal zones and the total lake area (Table 5-5).

Table 5-5: Surface area (km^2) and water volume (km^3) of the three defined zones (littoral, limnetic and profundal) of Lake Ellasjøen. The offshore area, defined as the limnetic and profundal zones combined, and total lake area and volume are also given.

Lake zone	Surface area (km^2)	% Area	Water volume (km^3)	% Volume
Littoral (0 – 8 m where total depth is ≤ 8 m)	0.16	22.54	0.71	5.72
Limnetic (0 – 8 m where total depth is > 8 m)	0.55		4.4	35.45
Profundal (9 – 34 m)	0.55		7.3	58.83
Offshore (limnetic and profundal)	0.55	77.46	11.7	94.28
Total lake	0.71		12.41	

5.3 Performance of the Vemco Positioning System (VPS)

As this study was one of the first to apply a Vemco Positioning System (VPS) autonomously over a period of one year, it was considered necessary to carefully evaluate the performance of the system. It was also crucial to develop a suitable method to filter and interrogate the data.

5.3.1 Vemco processing output

The VPS was deployed on 28/8/2009 and retrieved on 23 – 24/8/2010. GPS (Garmin, GPSMAP60) positions of the deployment and retrieval locations of each VR2W were taken. These positions and the raw VR2W log files were sent to Vemco for data processing. The data received from Vemco is formatted as individual text files of raw position data for each retrieved VR2W. These include; a latitude and longitude value of each position (as degrees, minutes and seconds), date and time of each position, transmitter (tag) ID code associated with each position, a depth (metres) or temperature value (°C) (where applicable) for each position and a list of detecting VR2Ws from which each position is calculated. These files are provided by Vemco for both fish and sync tags.

Two Vemco derived estimates of position accuracy are also included in the processed data. These are: Horizontal Position Error-metres (HPEm) and Horizontal Position Error (HPE). HPEm is a value, in metres of the positional error for each VPS derived sync tag position i.e. the distance in metres between the known 'fixed' position and the VPS calculated position of each sync tag based on time of arrival information to receiver hydrophones (see 4.3.1 Theory of operation). The second, HPE, is an error value assigned to each VPS-derived position for both sync and fish tags. This value is estimated by assessing the relationship between HPEm and Horizontal Position Error-sensitivity (HPEs). HPEs is a theoretical measure of the sensitivity of a position to timing error within the VPS; however these values are not included in the processed data from Vemco. As HPE is a value derived by Vemco using an unknown algorithm (unknown to the customer, and which Vemco were not willing to release or explain in detail for this study), HPE values were not used in this study. Alternative methods were derived in order to estimate the validity and accuracy of individual fish positions; these were explained in section 5.4.2 Pre-treatment of fish positional data.

5.3.2 System retrieval and movement

In total 19 VR2W receivers were deployed in Lake Ellasjøen, each with a co-located sync tag (13 × V13-1L and 6 × V16-4L). The receivers R01 – R12 were deployed around the lake edge in the

littoral zone, R13 – R19, were deployed offshore. Of the 19 receivers deployed, four (and their co-located sync tags) could not be located; R12, R14, R18 and R19 (Figure 5-6), therefore these VR2Ws could not be used to derive any positional information. In effect all fish tag and sync tag detections logged onto these receivers were lost. Of the seven VR2Ws deployed offshore, four were recovered, R13, R15, R16 and R17 (and their co-located sync tags). Twelve VR2Ws were deployed around the lake edge (littoral zone), of these only one, R12, was not recovered. This is illustrated in Figure 5-6, which also depicts the littoral zone (0 – 8 m) and offshore area; the latter comprising the limnetic and profundal zones where the total depth of the lake is greater than 8 metres (9 – 34 m).

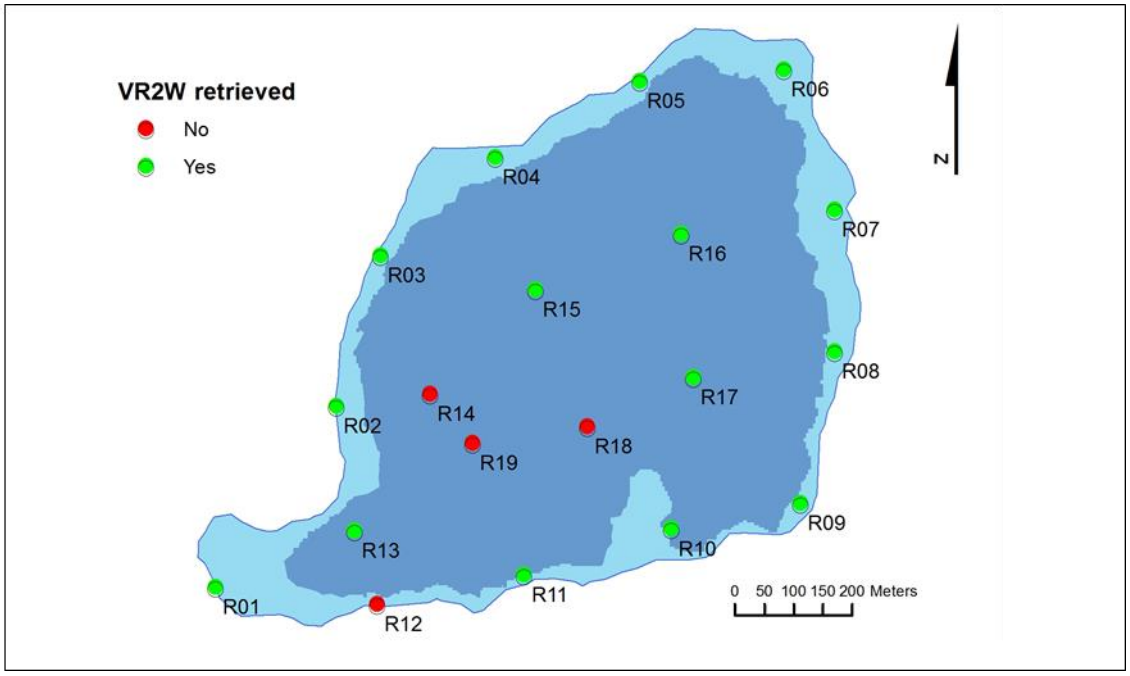


Figure 5-6: Deployment location of the 19 VR2Ws (and co-located sync tags) of the VPS, Lake Ellasjøen, Bear Island (28/8/2009 – 23/8/2010). Green markers, represent those VR2Ws recovered, red those not recovered. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

Over the course of the study, seven VR2Ws moved from their original deployment location; R05, R10, R14, R15, R16, R18 and R19. Only one (R12) of the four VR2Ws not recovered remained in the original deployment location at the time of system retrieval. The date of these movements was established by Vemco during the initial data processing phase and each piece of equipment that moved was assigned a different location (from positions of the co-located sync tag) after the movement occurred. All but one movement (R16) occurred during the period of ice closure over the lake (mid-December) and during the period of ice break up (late May to early June) (Table 5-6).

Table 5-6: Summary of VR2W and sync tag movement during the VPS study in Lake Ellasjøen, Bear Island, deployed between 28/8/2009 and 23/8/2010.

VR2W	Date of movement	Distance moved (m)
R05	Dec 19 – Dec 24	3
R10	Dec 22 – Dec 23	5
R14	Dec 19 – Dec 24	62
	June 2 – June 3	42
R15	Dec 21 – Dec 25	46
	May 28 – June 2	42
	June 2 – June 3	149
R16	Sept 8 – Sept 10	5
R18	Dec 19 – Dec 24	222
R19	Dec 19 – Dec 24	81

A total of 29 locations were identified for the 19 VR2Ws (Figure 5-7). Five VR2Ws moved once (R05, R10, R16, R18 and R19), one (R14) moved three times and one (R15) moved four times.

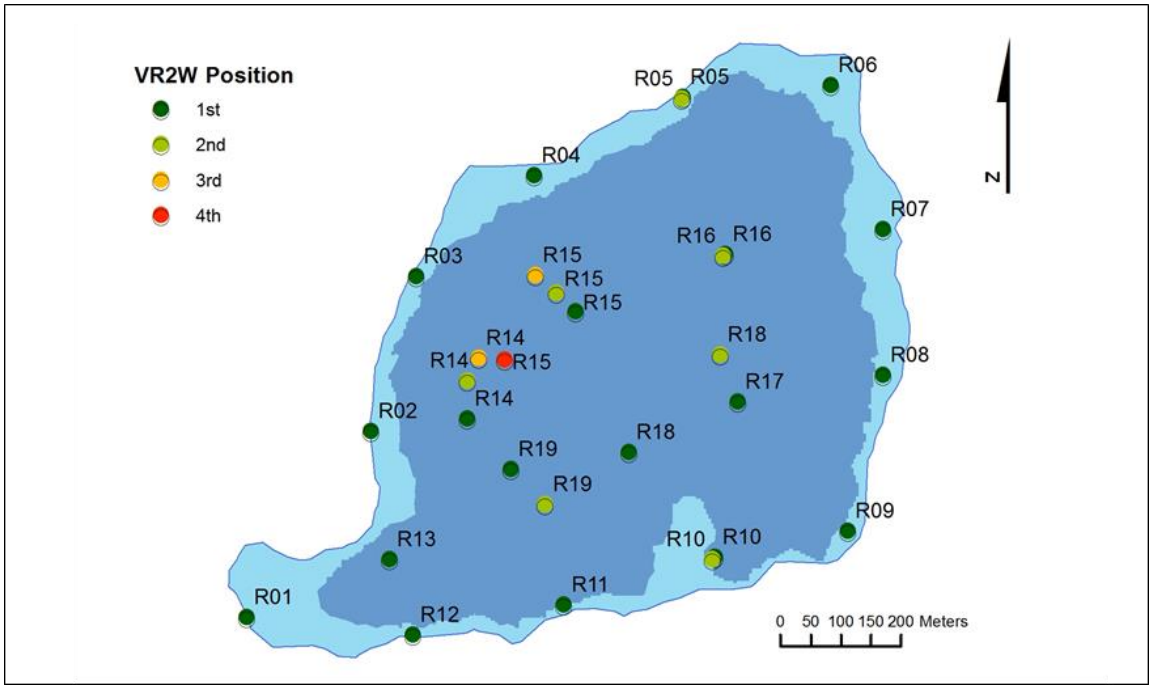


Figure 5-7: All 29 locations of the 19 VR2Ws (and co-located sync tags) of the VPS, deployed in Lake Ellasjøen, Bear Island (28/8/2009 – 23/8/2010). Locations are coloured to illustrate the order of locations. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

5.3.3 Detection data

A total of 3,679,720 detections were logged onto the 15 retrieved VR2Ws, 1,922,707 of these were fish tags (52.25%) and 1,757,013 were sync tags (47.75%). Each receiver logged an average of 251,871 detections during the study period, an average of 29 per hour. The receiver located at the southwest bay (R01) logged the least, 12 per hour. R08 on the eastern edge of the lake logged the most, 36 per hour (Figure 5-8). Figures of the total daily number of fish and sync tag detections for each individual receiver are presented in Appendix II- VR2W fish tag and sync tag detections.

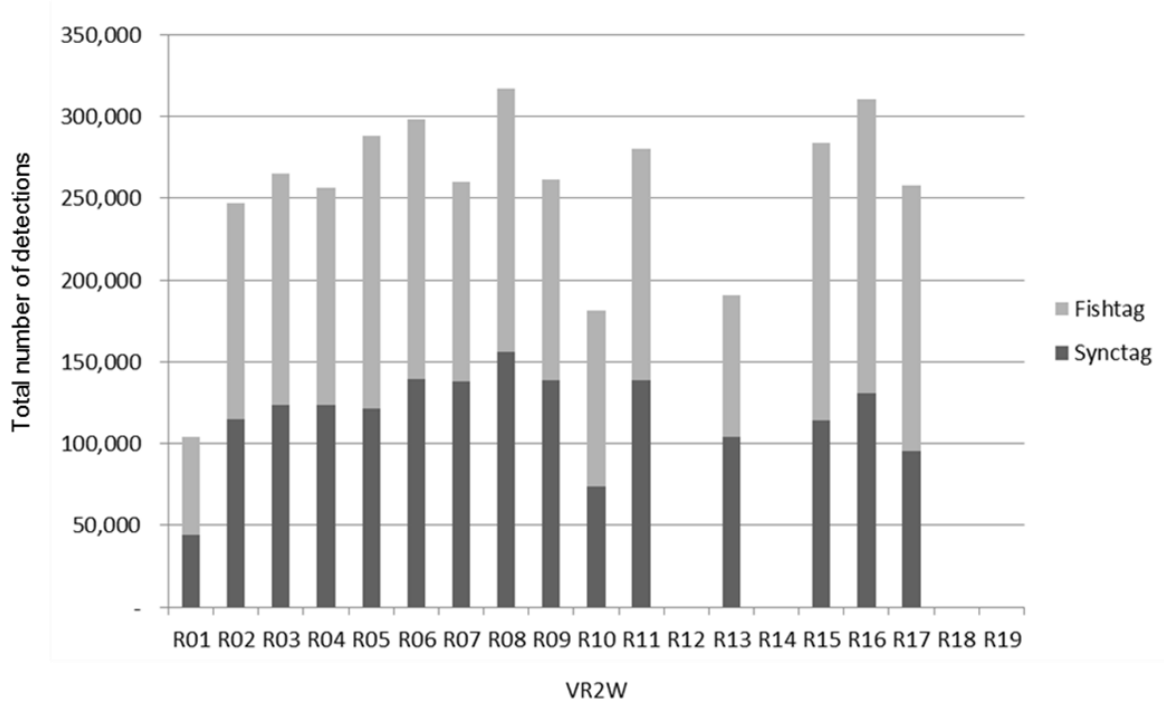


Figure 5-8: Total number of fish tag (*n* = 30) and sync tag (*n* = 19) detections logged on each VR2W for the duration of the VPS deployment (28/8/2009 – 23/8/2010) in Lake Ellasjøen, Bear Island. R12, R14, R18 and R19 were not recovered and hence data for these is unavailable.

The daily number of detections per fish- and sync tag was calculated (Figure 5-9). The number of detections was divided by the number of fish tags (*n* range = 0 – 28, mean = 25) and sync tags (*n* range = 0 – 19, mean = 19) operating per day. A reduction in both sync and fish tag detections was apparent from 25/5/2010, at the time of ice break up, which continued for the remainder of the study (Figure 5-9). However, no signifcant difference in the daily number of detections was observed between the ice covered and ice free periods of Lake Ellasjøen, for either fish- or sync tag detections (*ANOVA*, $p > 0.05$, 1 *df*). Sync tag detections were more frequent during the ice free period (mean = 256.25, S.E. = 3.04), than during ice coverage (mean = 252.99, S.E. = 3.38).

Converesly, fish tag detections were more frequent under ice (mean = 211.19, S.E. = 4.75), than during the ice free period (mean = 205.24, S.E. = 4.75).

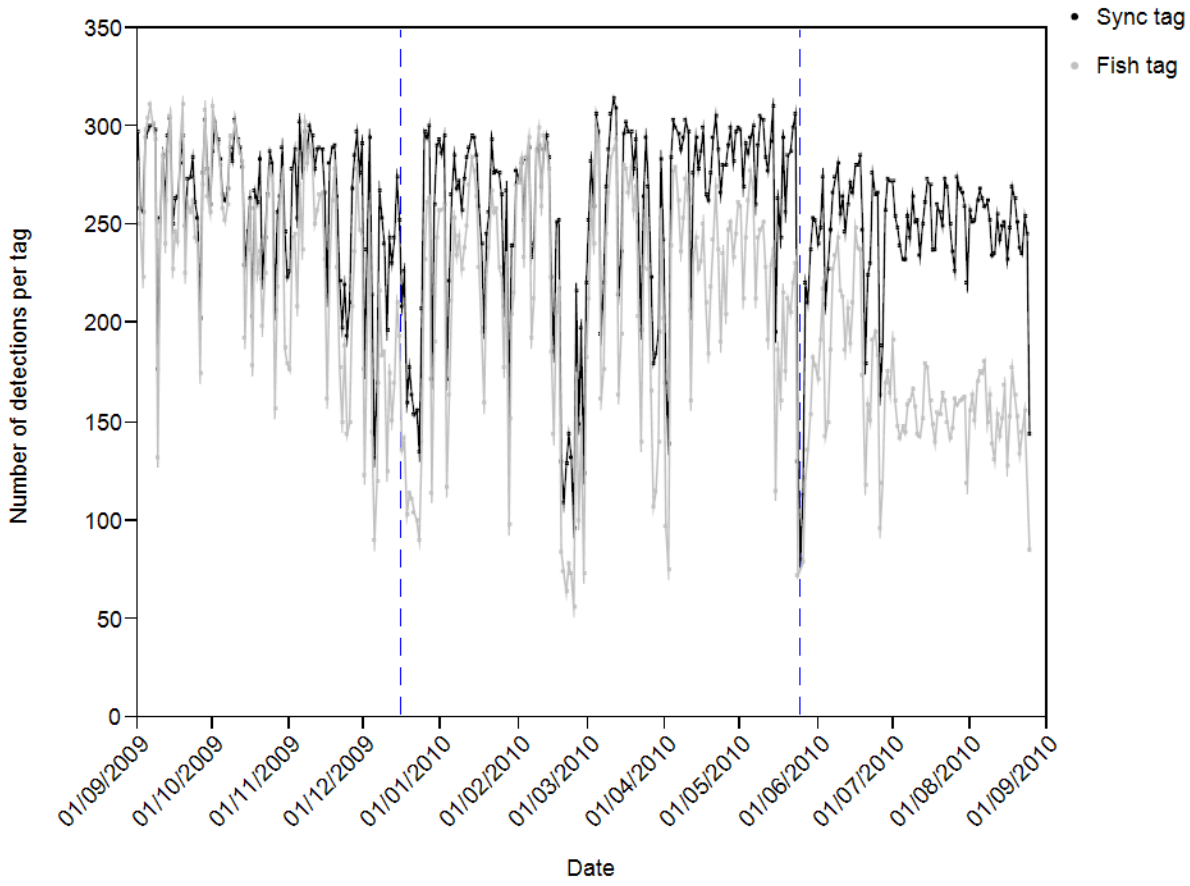


Figure 5-9: The daily number of detections per fish tag (grey) and sync tag (black), recorded during the VPS deployment in Lake Ellasjøen, Bear Island. The number of detections was divided by the number of fish tags (*n* range = 0 – 28, mean = 25) and sync tags (*n* range = 0 – 19, mean = 19) operating per day. The dashed reference lines on the date axis show the period of inferred lake ice coverage (16/12/2009 – 24/5/2010, 158 days), according to meteorological data, water temperature of Ellasjøen (Figure 5-3) and movement of the VPS (5.3.2).

5.3.4 Positional data

A total of 335,942 positions were derived from the VPS tag detection data. Of these 172,987 were sync tag positions (43.7 %), this equates to an average of one sync tag position per sync tag per hour. On average each sync tag position was calculated from 10.2 VR2W detections. The number of positions were consistent for each sync tag and power (Figure 5-10) (mean *n* positions: V13 = 7,525, R.S.D = 4.9 %; V16 = 15,879, R.S.D. = 3.7 %), with the clear exceptions of S01 (*n* = 1,253) and S13 (*n* = 1,979), both of which are located on the western edge of Lake Ellasjøen, close to the southwest bay and in line-of-sight detectability by only a small number of receivers.

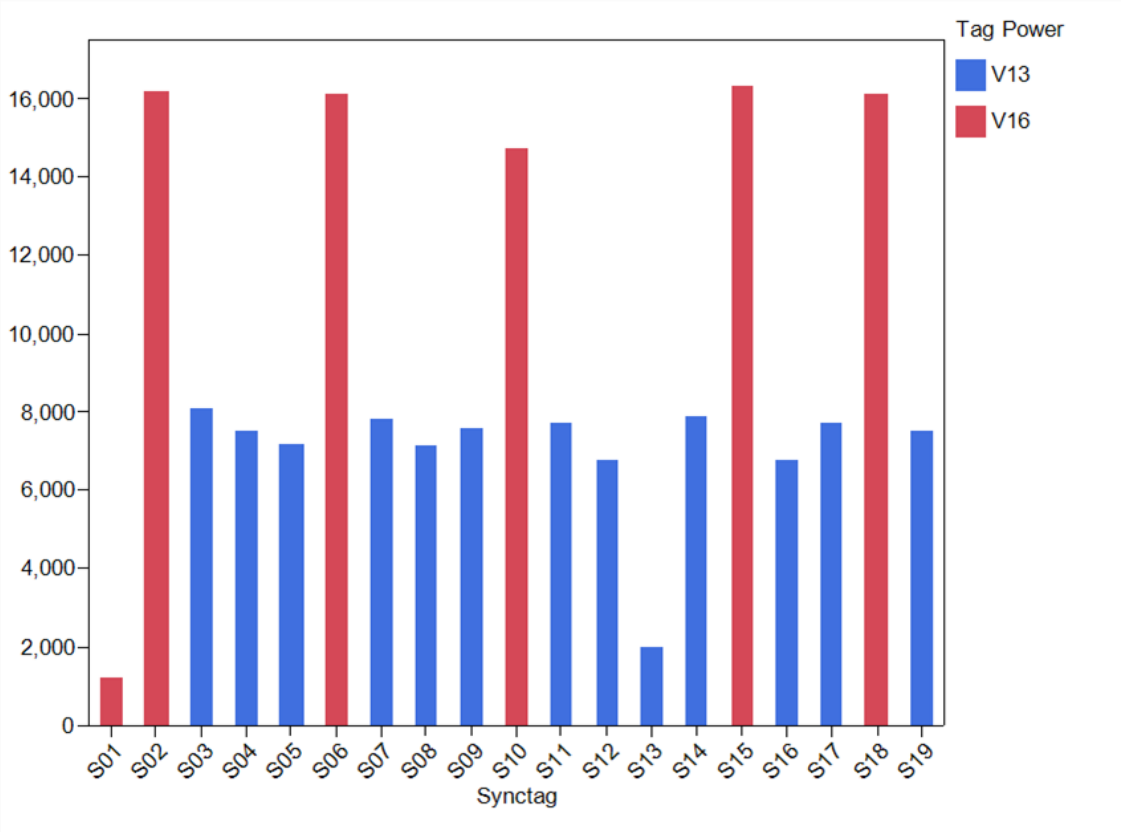


Figure 5-10: Total number of individual sync tag positions derived from the detection data of the VPS deployed between 28/8/2009 and 23/8/2010, in Lake Ellasjøen, Bear Island. Bars are coloured according to sync tag power: V13; blue, V16; red.

A total of 222,955 fish positions were derived with the VPS system, this equates to an average of 25.7 positions per hour or 0.9 positions, per fish per hour. On average, each fish position was calculated from 8.6 VR2W detections. From the sample of 30 tagged Arctic charr, no positions were recorded for the two individuals; T19 (Delicate morph) and T23 (classified as other). A total of 123,201 positions were calculated for the Robust morph Arctic charr (mean = 8,800 per fish, R.S.D. = 11.8 %), 76,884 positions (mean = 6,989 per fish, R.S.D. = 42.7 %) of delicate morph and 7,654 positions (mean = 3,827 per fish, R.S.D. = 40.1 %) of Dwarf morph fish, with these data presented for individual fish in Figure 5-11.

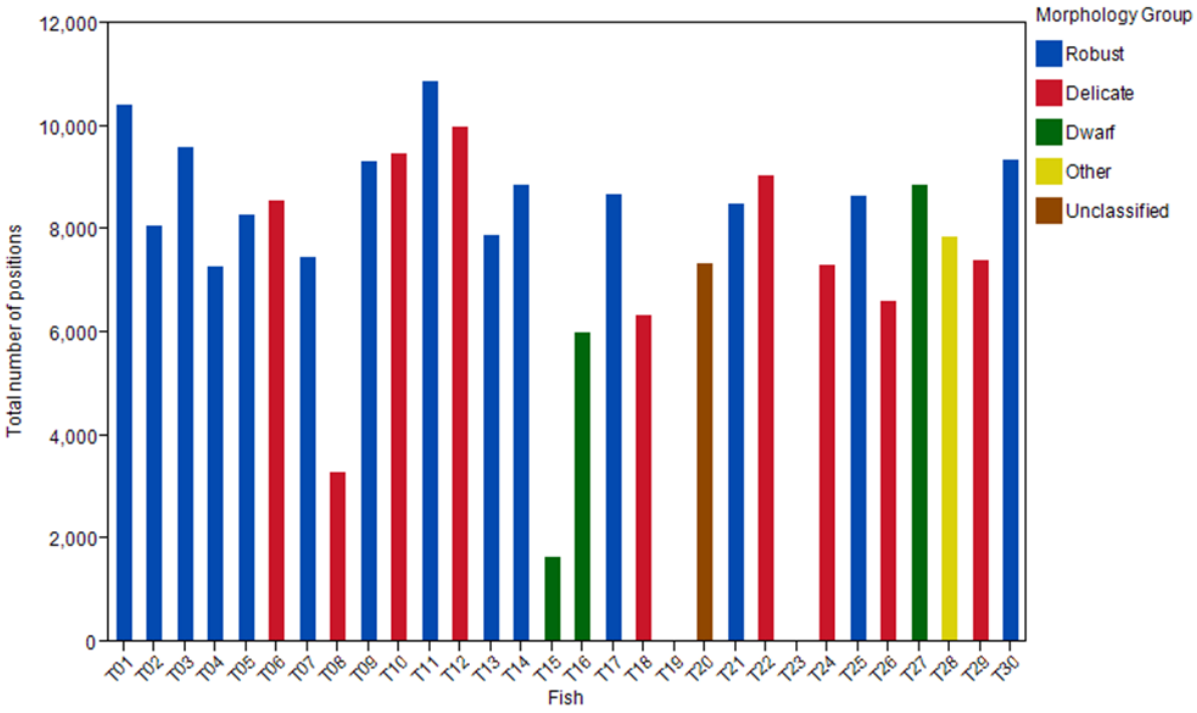


Figure 5-11: Total number of individual fish tag positions derived from the detection data of the VPS deployed between 28/8/2009 and 23/8/2010, in Lake Ellasjøen, Bear Island. Bars are coloured according to the morphology grouping of the Arctic charr sample. Tags 19 and 23 failed to transmit.

The daily number of positions per fish- and sync tag was calculated (Figure 5-12). The number of positions was divided by the number of fish tags (*n* range = 0 – 28, mean = 25) and sync tags (*n* range = 0 – 19, mean = 19) operating per day. A reduction in the number of fish tag positions was apparent from 25/5/2010, at the time of ice break up, which continued for the remainder of the study. A signifcant difference in the daily number of positions was observed between the ice covered and ice free periods of Lake Ellasjøen, for both fish tags (F = 4.42, p = 0.0363) and sync tags (F = 8.47, p = 0.0038) (*ANOVA*, 1 *df*). Sync tag positions were more frequent during the ice free period (mean = 25.61, S.E. = 0.25), than during ice coverage (mean = 24.53, S.E. = 0.28). Converesly, fish tag positions were more frequent under ice (mean = 25.09, S.E. = 0.58), than during the ice free period (mean = 23.46, S.E. = 0.52).

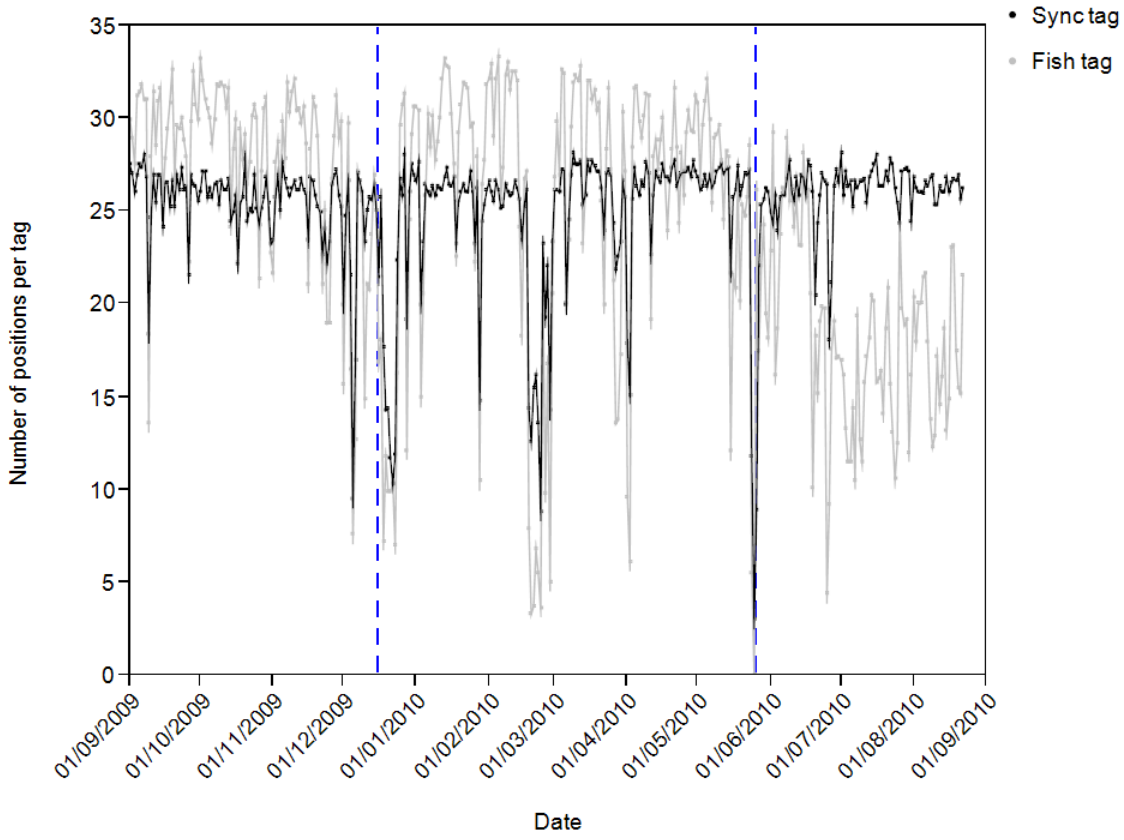


Figure 5-12: The daily number of positions per fish tag (grey) and sync tag (black), recorded during the VPS deployment in Lake Ellasjøen, Bear Island. The number of positions was divided by the number of fish tags (*n* range: 0 – 28, mean: 25) and sync tags (*n* range: 0 – 19, mean: 19) operating per day. The dashed reference lines on the date axis show the period of inferred lake ice coverage (16/12/2009 – 24/5/2010, 158 days), according to meteorological data, water temperature of Ellasjøen (Figure 5-3) and movement of the VPS (5.3.2).

5.4 Evaluation of VPS

5.4.1 Accuracy of sync tag positions

A commonly used measurement of horizontal position accuracy is twice the root mean squared of the horizontal error (e.g. Patterson et al. 2010, Larson et al. 2013), otherwise referred to as; twice the Distance Root Mean Squared (2DRMS). This measurement corresponds to the 95 % confidence interval (Clarke 1994), thus if the absolute position accuracy of a global positioning system (GPS) receiver is 100 m 2DRMS, then 95 % of the horizontal positions will be within 100 m of the correct value. This measurement was calculated to quantify the position error, according to a 95 % confidence limit, for the stationary or 'fixed' co-located sync tag positions. The 2DRMS value (m), for all VPS-derived sync tag positions of each of the 29 VR2W/co-located sync tag locations was calculated according to the formula below (Equation 5-2):

$$2\text{DRMS} = 2\sqrt{\sigma_x^2 + \sigma_y^2} \qquad \text{(Equation 5-2)}$$

where σ_x is the standard deviation of the Easting values, and σ_y is the standard deviation of the Northings

All VPS derived sync tag positions are shown in Figure 5-13 (n = 172,987), together with circles with radii of 2DRMS for all 29 VR2W/sync tag positions. The radius of 95 % error for the VR2W located in the southwest bay (R01) was clearly larger than the other VR2W locations (Figure 5-13, Table 5-7). The 2DRMS value for all 29 locations of the 19 VR2Ws and co-located sync tags, as well as the mean Vemco derived HPEm, of each location were calculated (Table 5-7). Where HPEm refers to a value, in metres of the positional error for each VPS derived sync tag position i.e. the distance in metres between the known 'fixed' position and the VPS calculated position of each sync tag. Calculated 2DRMS values ranged from 3.85 m (R15, location 1) to 137.63 metres (R01). Mean HPEm values ranged from 6.58 metres (R18, location 2) to 1,617.55 metres (R01). Sync tag 2DRMS was significantly greater in the littoral (R01 – R12: mean = 26.99 m, S.E. = 5.99, S.D. = 32.18) than offshore (R13 – R19: mean = 7.51 m, S.E. = 5.79, S.D. = 2.78) (*ANOVA*, *1 df*, F = 5.47, p = 0.027). There was a significant positive linear relationship between log 2DRMS and log mean HPEm of each sync tag location (linear regression, 1 *df*, R^2 = 0.63, $p < 0.0001$). The percentages of positions outside of the lake boundary (i.e. on land) are also given as an indicator of sync tag position accuracy (Table 5-7). Only those sync tags located around the lake edge (R01 – R12) resulted in positions on land, of which the highest proportion was 43.4 % (R12).

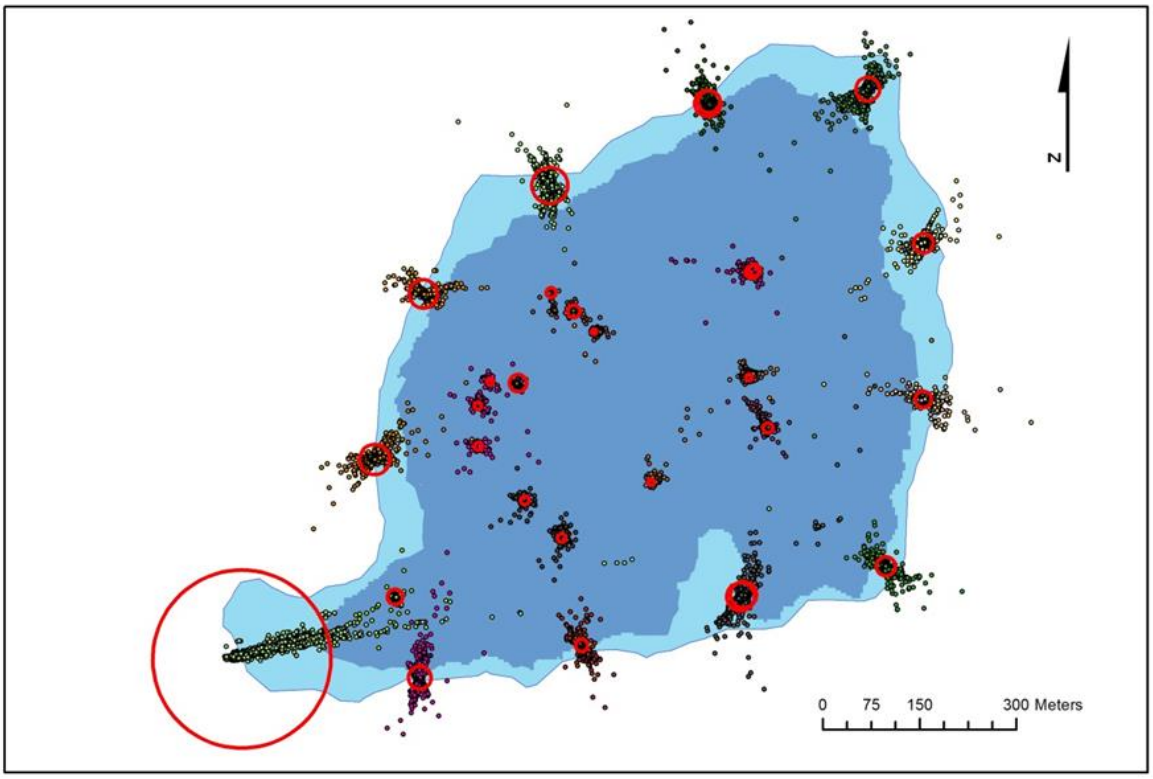


Figure 5-13: All VPS derived positions of the 29 locations of the 19 co-located sync tags deployed as a VPS in Lake Ellasjøen, Bear Island. Circles with 2DRMS radius values, representing a 95 % confidence contour of each sync tag location are shown in red. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

Table 5-7: The number and duration of co-located sync tag positions of the 29 locations of VR2Ws deployed as a VPS in Lake Ellasjøen, Bear Island. The percentages of positions outside the lake boundary are stated, in addition to the 2DRMS and HPEm of all sync tag positions of each location. 2DRMS and HPEm values are stated in metres, duration in days.

VR2W/ co-located sync tag	Location number	*n* of days in location	*n* of positions	% of positions outside lake	2DRMS (m) of location	Mean HPE (m) of location
R01	1	356	1,253	12.9	137.63	1617.55
R02	1	356	16,172	28.9	23.4	11.82
R03	1	356	8,088	1.9	21.91	11.43
R04	1	356	7,497	2.3	27.91	22.02
R05	1	111	2,174	21.2	16.82	14.47
R05	2	240	5,024	4.1	20.29	17.19
R06	1	356	16,119	0.1	18.43	21.91
R07	1	356	7,789	0.2	15.14	19.15
R08	1	356	7,154	0.4	12.62	10.27
R09	1	356	7,576	0.7	14.75	24.42
R10	1	114	4,833	0.2	20.24	22.41
R10	2	241	9,869	0.1	21.68	32.28
R11	1	356	7,727	1.5	9.47	20.82
R12	1	356	6,770	43.4	17.6	55.89
R13	1	356	1,979	0	11.82	24.25
R14	1	111	2,510	0	6.01	31.2
R14	2	158	3,543	0	5.64	7.51
R14	3	81	1,847	0	5.25	7.26
R15	1	113	5,239	0	3.85	6.6
R15	2	153	7,053	0	9.52	6.81
R15	3	4	247	0	7.55	6.8
R15	4	81	3,757	0	13.51	6.58
R16	1	10	255	0	8.97	7.41
R16	2	344	6,523	0	10.1	7.85
R17	1	356	7,686	0	7.7	7.85
R18	1	111	5,116	0	4.78	6.69
R18	2	241	10,991	0	4.86	6.56
R19	1	111	2,435	0	6.47	9.41
R19	2	240	5,106	0	6.6	8.5

5.4.2 Pre-treatment of fish positional data

Five potential sources of pre-treatable error in the fish position data were identified: 1) Tagging effects, 2) Impossible horizontal position, 3) Impossible vertical position, 4) Poor quality of fish position and 5) High probability of VPS positional error. Fish tag positions were removed and excluded from further analysis according to the five sources on a step-wise basis according to the following method:

1st. Tagging effects:

In order to prevent bias of fish positions due to post tagging effects, all fish positions recorded before the 1st of September 2009 were excluded from analysis (*n* = 3,093, 1.39 % of all fish tag positions). This period of at least 3 days is considered to have allowed the fish to recover sufficiently from any effects of tag implantation, with normal movement behaviour resumed (Hitt et al. 2011)

2nd. Impossible horizontal position:

All positions outside of the lake boundary (i.e. on land) were removed (*n* = 2,710, 1.22 % of all fish tag positions).

3rd. Impossible vertical position:

In order to determine vertical fish position relative to the bathymetry map of Lake Ellasjøen (see 4.5 Bathymetry of Lake Ellasjøen), a Spatial Join was conducted using ArcMap10. This tool was used to overlay the XY coordinates of each fish position onto the bathymetry map of Lake Ellasjøen, creating an extra data field of total lake depth for each fish position, thus the fish distance to lake bed could be calculated. A total of 51,367 fish positions were at a depth greater than the depth of the lake, according to their horizontal position (range = 0.1 – 32.8 m, mean = 1.6 m). Where this difference was greater than 5.0 m those positions were removed (*n* = 2,307). This equates to 4.49 % of those positions with a depth greater than lake depth and 1.03 % of all fish positions derived. All remaining positions were adjusted so the vertical position was equal to lake depth.

As error in vertical position may be due, in actuality to an error in horizontal position, particularly given the steep bathymetry of Lake Ellasjøen (Figure 4-4), the positions removed during this step were also checked according to the methods applied to horizontal position filtering (step 4 a. b. and step 5). Of the 2,307 positions removed during this step, only 17 of these positions would not be removed according to the criteria set in the horizontal position filtering process. Of these

positions the mean difference between the depth of fish position and lake depth was 7.1 m (range: 5.0 – 16.1 m).

4th. Quality of fish position:

For each fish position the following calculations were made in order to assess the positional quality based on the VPS design and the principles of time to arrival triangulation (4.3.1 Theory of operation).

a) Detection geometry of fish positions:

A triangle of three VR2Ws forms the minimum number of detections required for the VPS to calculate a fish position. Therefore, the three detecting VR2Ws closest to each fish position were identified; these form the minimum detection triangle of VR2Ws. The three furthest detecting receivers from each fish position were also identified; they formed the maximum detection triangle of VR2Ws. Using the principle of barycentric coordinates, the following formula (Equation 5-3) was applied to determine if each fish position was either inside or outside the a) minimum detection triangle of VR2Ws and b) maximum detection triangle of VR2Ws (Figure 5-14 box 1).

$$b0 = (x2 - x1) * (y3 - y1) - (x3 - x1) * (y2 - y1)$$

$$b1 = \frac{\big((x2 - x0) * (y3 - y0) - (x3 - x0) * (y2 - y0)\big)}{b0}$$

$$b2 = \frac{\big((x3 - x0) * (y1 - y0) - (x1 - x0) * (y3 - y0)\big)}{b0}$$

$$b3 = \frac{\big((x1 - x0) * (y2 - y0) - (x2 - x0) * (y1 - y0)\big)}{b0}$$

If $b1$, $b2$ and $b3$ are > 0 then ($x0$,$y0$) is inside the triangle ($x1$,$y1$) ($x2$,$y2$) ($x3$,$y3$).

(Equation 5-3)

b) The two-dimensional minimum detection distance:

The three closest detecting VR2Ws to each fish position were identified (i.e. those forming the minimum detection triangle). The straight line distance between the fish position and each of the three VR2Ws was calculated and summed to give a total minimum detection distance (in metres) (Figure 5-14 box 2). Two-dimensional distance was calculated according to Equation 5-4.

$$\sqrt{(x_2 - x_1)^2 + (y_2 - y_1)^2}$$

(Equation 5-4)

The distribution of minimum detection distance was calculated. If the value was between the 97.5 percentile (1,294.5 m) and the maximum (3,106.9 m) and the estimated fish position was outside

of both the minimum detection triangle and the maximum detection triangle then that fish position was excluded (*n* = 4,773, 2.14 % of all fish positions).

5th. High positional error of VPS:

A daily mean value of HPEm for each of the 29 sync tag locations was calculated. This value was summed for the three minimum-distance detecting VR2Ws and co-located sync tags, to give a daily value of ± error of minimum detection distance (step 4 b) in metres (Figure 5-14 box 3). The distribution of these values was plotted. If the result was between the 97.5 percentile (141.04 m) and the maximum value (1,293.91 m) the position was removed (*n* = 4,779, 2.14 %).

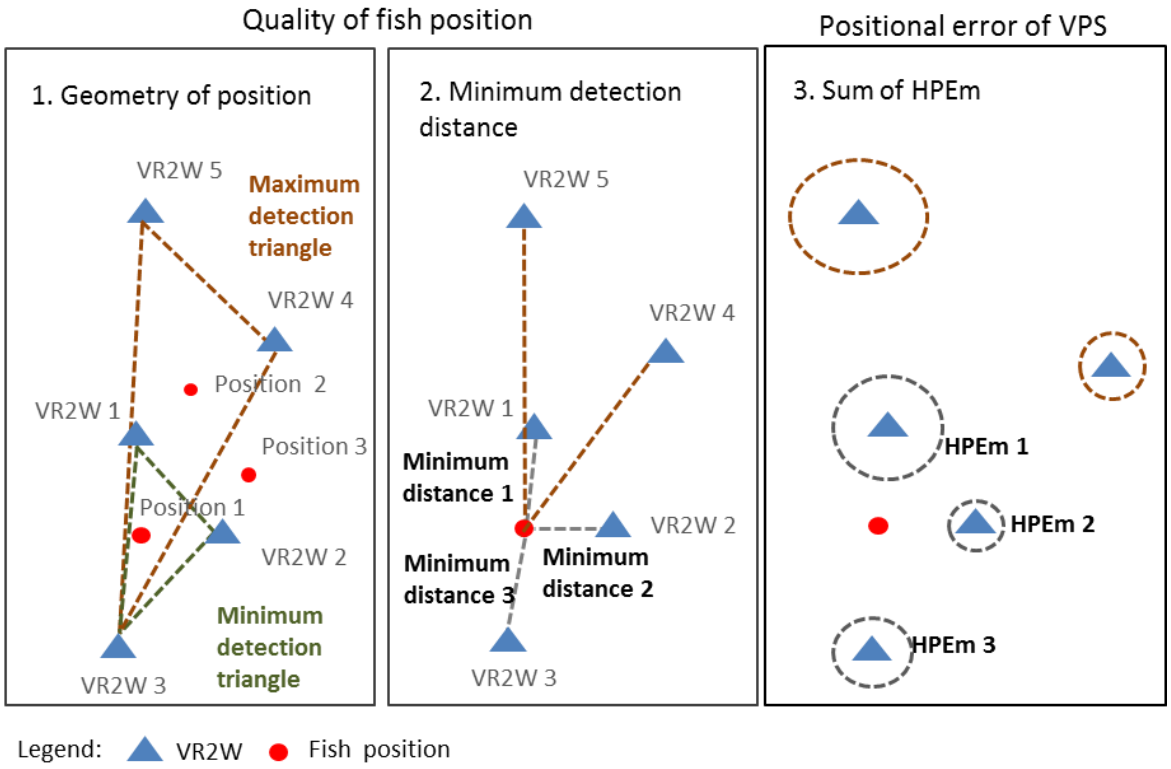


Figure 5-14: An illustration of the measurements used to calculate the quality and error of each fish position derived from the VPS deployed in Lake Ellasjøen, Bear Island. Boxes 1 and 2 show steps 4 a) minimum (green dashed line) and maximum (orange dashed line) detection triangle of VR2Ws, and 4 b) minimum detection distance (sum of grey dashed lines), required to assess the quality of each fish position. In box 1, fish position (red dot) 1, is inside both the minimum and maximum detection triangle, fish position 2 is outside the minimum detection triangle but within the maximum and fish position 3 is outside both the minimum and maximum detection triangles of VR2Ws. Box 3 describes the daily error in minimum detection distance (step 5) as a measure of the positional error of the VPS, derived by summing the daily average HPEm values of the minimum detection triangle of VR2Ws (indicated by the grey dashed contours around each VR2W).

A total of 17,662 (7.92 %) fish positions were removed as part of the pre-treatment of potential fish positional error. The number and percentage of the total removed as well as the number and percentage remaining after each step of the positional data pre-treatment process is shown in Table 5-8.

Table 5-8: The number and percentage of fish positions removed from further analysis during each step of the pre-treatment of fish positions derived from a VPS deployment in Lake Ellasjøen, Bear Island (28/8/2009 – 23/8/2010).

Position removal rationale	Total *n* positions removed	% positions removed	Total *n* positions remaining	% positions remaining
Tagging effects	3,093	1.39	219,862	98.61
Impossible horizontal position	2,710	1.22	217,152	97.40
Impossible vertical position	2,307	1.03	214,845	96.36
Poor positional quality	4,773	2.14	210,072	94.22
Positional error of VPS	4,779	2.14	205,293	92.08
Total	17,662	7.92 %	205,293	92.08 %

The area of Lake Ellasjøen was divided into a grid formed of 25 m^2 squares, and the sum of excluded fish positions in each grid square was calculated as a percentage density of the total number (Figure 5-15). This was conducted using the Spatial Join tool in ArcMap 10. The greatest densities of excluded fish positions were located close to the lake edge; between the southwest corner, along the southern edge of the lake and upwards towards the northwest point. Of the positions removed, 29.91 % (*n* = 5,282) were located in the littoral zone (0 – 8 m depth) and 54.75 % (*n* = 9,670) were located in the offshore zone (9 – 34 m depth). This equates to 11.07 % of all littoral fish positions derived (*n* = 47,701) and 5.60 % of all offshore positions (*n* = 172,544). Of the 205,293 fish positions remaining, 20.66 % (*n* = 42,419) of fish positions are located in the littoral area and 79.34 % (*n* =162,874) in the offshore area. The distribution of fish positions was altered by -0.73 % in the littoral zone and 1.95 % in the offshore zone as a result of the data cleaning, pre-treatment methodology (steps 1- 5).

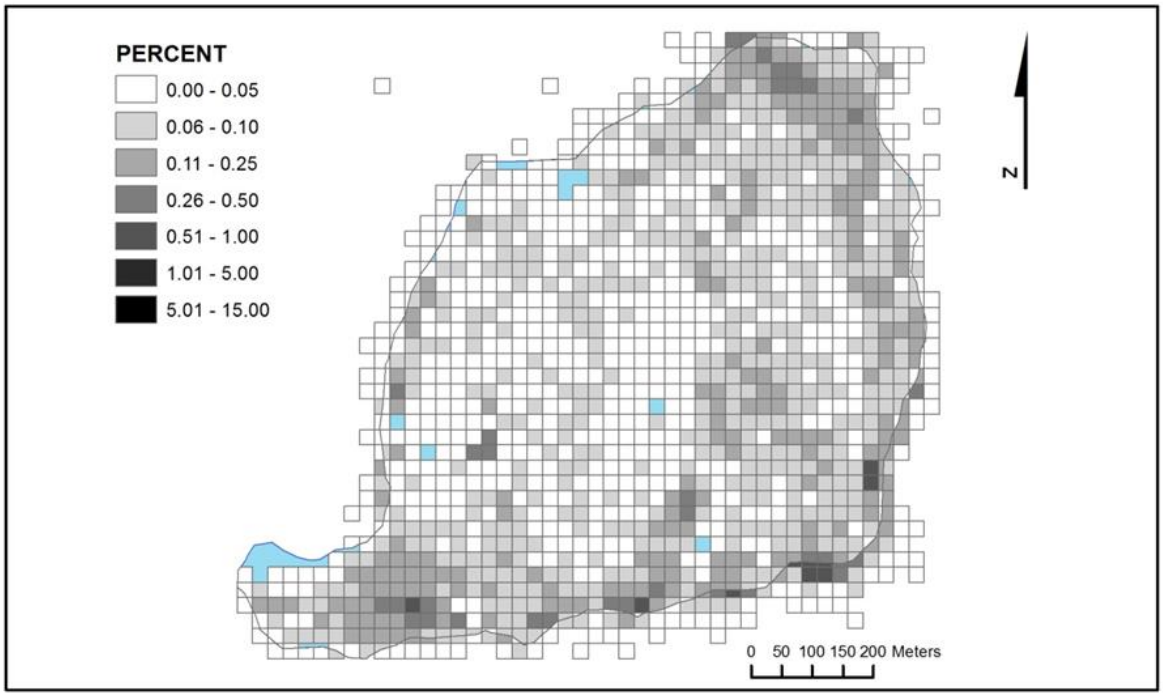


Figure 5-15: The percentage density of 17,662 fish positions excluded as a result of the pre-treatment of positional data derived from a VPS deployed in Lake Ellasjøen, Bear Island. The lake is divided into a grid formed of 25 m^2 squares; the percentage density of fish position within each square is shown and shaded according to the figure legend. Blue squares represent an absence of fish positions.

5.4.3 Individual fish fate and validity of VPS fish positions

In order to assess the validity of VPS calculated fish positions, temporal 'tracking' information of individual Arctic charr was calculated (summarised in Table 5-9). For each tagged individual, daily mean values of; the three dimensional minimum distance travelled (metres), fish depth (negative metres) and fish distance from lake bed (metres) were calculated and plotted for the entire study period (1/9/2009 – 23/8/2010). Individual plots are given in 9.3 Appendix III - individual fish tracks. The straight line distance travelled between consecutive positions was calculated according to Equation 5-4. The depth value of each fish position (z coordinate) was also included, thus the 3-dimensional distance could be calculated according to Pythagoras (Equation 5-5.), where c^2 represents the three dimensional distance squared.

$$a^2 + b^2 = c^2$$

(Equation 5-5)

From these figures it was possible to observe; a) the duration of positional data, b) gaps in positional data and c) stationary positional data relative to lake depth, for each tagged individual. From this, the spatial validity of each fish track could be assessed on a temporal scale for the

study duration (1/9/2009 – 23/8/2010, 357 days). Validity of positions was determined by manually as**s**essing the individual fish tracks for any periods of sustained lack of movement, horizontally and vertically, with fish depth being equal to lake depth (see 9.4 Appendix IV- incomplete fish positional data for further description). A lack of movement was identified in four (13 %) individuals; T02, T08, T15 and T30. In all instances the mean daily values of distance travelled (m) and distance to the lake bed (m) were significantly different (*ANOVA*: 1 *df*, $p < 0.0001$) during this stationary period than observed in previous tracking activity. It is most probable that these fish died during the study, these positions were therefore deemed stationary or static and were excluded from further analysis. The horizontal distribution (calculated as 2DRMS), the number of positions and duration of the stationary period were defined for the four fish (9.4.1 Static positions: an indicator of fish position accuracy, Table 9-1).

A 'gap' in position data was defined by an absence of fish position for any given date over the study duration. For five (17 %) individuals a sustained gap in positional data was observed, with no positions derived for these fish for between 55 to 64 consecutive days mid- deployment, i.e. tracking data of these individuals resumed after this gap in tracking data (see 9.4.3 Gap in positional data, for further description).

The individual with the shortest duration of valid positional data (other than T19 and T23 which did not transmit) was identified as T15, just 17 days. The longest period of valid position data was 349 days; T01, T11 and T25. These three fish had just one, eight consecutive day's gap in position data. This period was between 25/5/2010 and 2/6/2010, at ice break-up. All individuals were missing positional information during this period. Valid tracking data over 12 months (complete dataset) was derived for 16 (53 %) of the 30 tagged Arctic charr. For three (10 %) fish, transmitter detections stopped before the VPS was retrieved and two (7 %) were not detected by the VPS at all (these tags failed to transmit properly).

Table 5-9: Summary of the 'valid' period of VPS derived individual fish positions, as determined by temporal tracking data. Mean daily values of; minimum distance travelled (m), fish depth (m) and fish distance from lake bed (m) were calculated for each tagged Arctic charr, sampled from Lake Ellasjøen, Bear Island (9.3 Appendix III - individual fish tracks). Positions were considered in-valid if the fish had become stationary, and fish depth was equal to lake depth. Significant difference in distance travelled and fish distance to lake bed was observed between this stationary period and previous tracking activity (*ANOVA*: 1 *df*, $p < 0.0001$). The date of final position and final valid position are stated, as well as the number of days of missing data, where total study duration was 357 days. The number of months of valid data are given and an explanation if the tracking duration was different to the duration of the study (12 months).

Fish ID	Date of final position	Date of final 'valid' position	*n* of date gaps in positional data	Total *n* of 'valid' position days	*n* of months of 'valid' positional data	Explanation for incomplete positional data
T01	23/08/2010	23/08/2010	8	349	12	Complete
T02	23/08/2010	16/07/2010	9	310	11	No movement- stationary
T03	23/08/2010	23/08/2010	13	344	12	Complete
T04	09/06/2010	09/06/2010	35	247	10	Detections stopped
T05	23/08/2010	23/08/2010	32	357	12	Complete
T06	19/06/2010	19/06/2010	9	283	10	Detections stopped
T07	23/08/2010	23/08/2010	18	339	12	Complete
T08	22/07/2010	25/01/2010	3	133	5	No movement- stationary
T09	23/08/2010	23/08/2010	10	347	12	Complete
T10	23/08/2010	23/08/2010	10	347	12	Complete
T11	23/08/2010	23/08/2010	8	349	12	Complete
T12	23/08/2010	23/08/2010	34	323	12	Complete
T13	23/08/2010	23/08/2010	19	338	12	Complete
T14	23/08/2010	23/08/2010	13	344	12	Complete
T15	23/08/2010	17/09/2009	0	17	0	No movement - stationary
T16	19/08/2010	24/05/2010	7	259	9	Gap in data (64 consecutive days)
T17	23/08/2010	23/08/2010	11	346	12	Complete
T18	23/08/2010	23/08/2010	63	294	11	Gap in data (55 consecutive days)
T19	No data				0	Tag did not transmit
T20	24/07/2010	24/05/2010	61	266	9	Gap in data (58 consecutive days)
T21	23/08/2010	23/08/2010	13	344	12	Complete
T22	23/08/2010	23/08/2010	21	336	12	Complete
T23	No data				0	Tag did not transmit
T24	23/08/2010	23/08/2010	70	287	11	Gap in data (56 consecutive days)
T25	23/08/2010	23/08/2010	8	349	12	Complete
T26	23/08/2010	23/08/2010	71	286	10	Gap in data (55 consecutive days)
T27	23/08/2010	23/08/2010	29	328	12	Complete
T28	23/08/2010	23/08/2010	23	334	12	Complete
T29	07/06/2010	07/06/2010	12	268	10	Detections stopped
T30	23/08/2010	23/06/2010	13	283	10	No movement- stationary

5.4.4 Morphological variation of fish fate

The majority of individuals with a complete positional dataset were Robust morph Arctic charr (*n* = 11) (Table 5-10). No Robust fish were amongst those individuals with a 'gap' in detection data, but three individuals with a gap were Delicate morph, one individual was a Dwarf morph and one was the unclassified fish T20 (Table 5-10). The numbers of individuals from each morph per study month (September 2009 – August 2008) are stated in 9.5 Appendix V - fish sample overview. Only those fish belonging to the Robust and Delicate morphology groups were analysed further (*n* = 24) as these were the largest samples.

Table 5-10: Summary of the fate of fish revealed by tracking analysis of consecutive VPS derived fish positions of each tagged individual (*n* = 28, two fish tags filed to transmit). Fish fate is grouped according to the morphology of the sampled Arctic charr (see 5.1.1 Visual determination of phenotype).

Morphology group	Complete data (12 months)	Detections stopped	Gap in detections	No movement
Robust	11	1	0	2
Delicate	3	2	3	1
Dwarf	1	0	1	1
Immature	1	0	0	0
Unclassified	0	0	1	0
Total	16	3	5	4

5.5 Spatial and temporal analyses of fish position data

5.5.1 Horizontal fish position and habitat use

The horizontal distributions of fish positions are presented in Figure 5-16 (Robust morph) and Figure 5-17 (Delicate morph). The area of Lake Ellasjøen was divided into a grid formed of 25 m^2 squares and the sum of fish positions in each grid square is shown as a percentage density; this was calculated using the Spatial Join tool in ArcMap 10. More Robust fish positions (mean: *n* = 9295; 677 positions per fish) (Table 5-11) were derived from the VPS than for Delicate morph Arctic charr (mean: *n* = 5238, 637 positions per fish) (Table 5-11). For both morph groups the minimum number of fish positions was recorded in August (Robust; *n* = 4,891; 444 per fish, Delicate; *n* = 1,374; 229 per fish) and the maximum in October (Robust; *n* = 12,188; 871 per fish, Delicate; *n* = 8,042; 894 per fish). The number of positions per number of fish was significantly different between months (*ANOVA*: *n* = 24, *F* = 15.91, 11 *df, p* < 0.0001) but not between morph groups (*ANOVA*: *n* = 24, *F* = 0.23, 1 *df, p* > 0.05).

Both morphs occupied the offshore lake zone more than the littoral zone (Table 5-11), with 73.09 % (S.E. 2.96) of Robust fish positions and 92.42 % (S.E. 2.06) of Delicate fish positions located in the offshore lake habitat (mean of monthly mean values). Robust Arctic charr utilised the littoral habitat, on average 19.33 % more than Delicate charr. The only month Delicate fish occupied the littoral zone more predominantly than Robust was in October. Both morphs show a variation in habitat use with month; greatest littoral use was recorded in July (53.96 %) and October (21.62 %) for Robust and Delicate morphs respectively. Greatest use of the offshore habitat was during February (83.02 %) for Robust Arctic charr and in June (98.90 %) for Delicate Arctic charr.

Table 5-11: The total number of Arctic charr positions located in either the littoral (lake depth 0 – 8 m) or offshore habitat (8 – 34 m) divided by the total number of individual Arctic charr per month per morphology group (Robust or Delicate). The percentage of fish positions located in each habitat, per month per morph are also presented. Positions are derived from a VPS deployed September 2009 – August 2010, in Lake Ellasjøen, Bear Island. *n* varies per month, see Figure 5-16 (Robust morph) and Figure 5-17 (Delicate morph).

	Littoral zone (lake depth 0 – 8 m)				Offshore zone (lake depth 8 – 34 m)			
	Robust morph		Delicate morph		Robust morph		Delicate morph	
Month	*n* positions per *n* fish	% of fish positions	*n* positions per *n* fish	% of fish positions	*n* positions per *n* fish	% of fish positions	*n* positions per *n* fish	% of fish positions
Sep	290	34.74	43	5.34	546	65.26	766	94.66
Oct	186	21.4	193	21.62	684	78.60	700	78.38
Nov	202	25.05	154	18.74	605	74.95	666	81.26
Dec	147	26.41	84	14.98	410	73.59	475	85.02
Jan	178	21.17	74	9.12	663	78.83	737	90.88
Feb	95	16.98	8	1.35	464	83.02	519	98.65
Mar	148	17.89	51	6.04	680	82.11	794	93.96
Apr	175	22.30	18	2.15	611	77.70	815	97.85
May	169	30.15	4	0.66	392	69.85	619	99.34
Jun	187	32.91	5	1.10	382	67.09	450	98.90
Jul	253	53.98	9	3.50	216	46.02	244	96.50
Aug	89	19.96	15	6.40	356	80.04	214	93.60
mean	176	26.91	54	7.58	500	73.09	583	92.42

The positional data, as a percentage of the total number per month, per morph group was fitted to a Generalised Linear Model (*GLM*) with fish morph, month and lake zone (littoral or offshore) as model predictors. Individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. No significant morph x month x zone interaction ($p > 0.05$, 11 *df*) was found, but significant morph x zone interaction was observed ($F = 65.69$, 11 *df*, $p < 0.0001$). The sum of individual monthly values was used ($n = 439$).

Figure 5-16: The percentage density distribution of Robust morph Arctic charr on a monthly basis, from September 2009 to August 2010. The number of fish positions and number of individual fish are stated per month. Grid square area is 25 m^2, percentage density increases with shading intensity, blue represents those lake areas for which no fish positions were recorded.

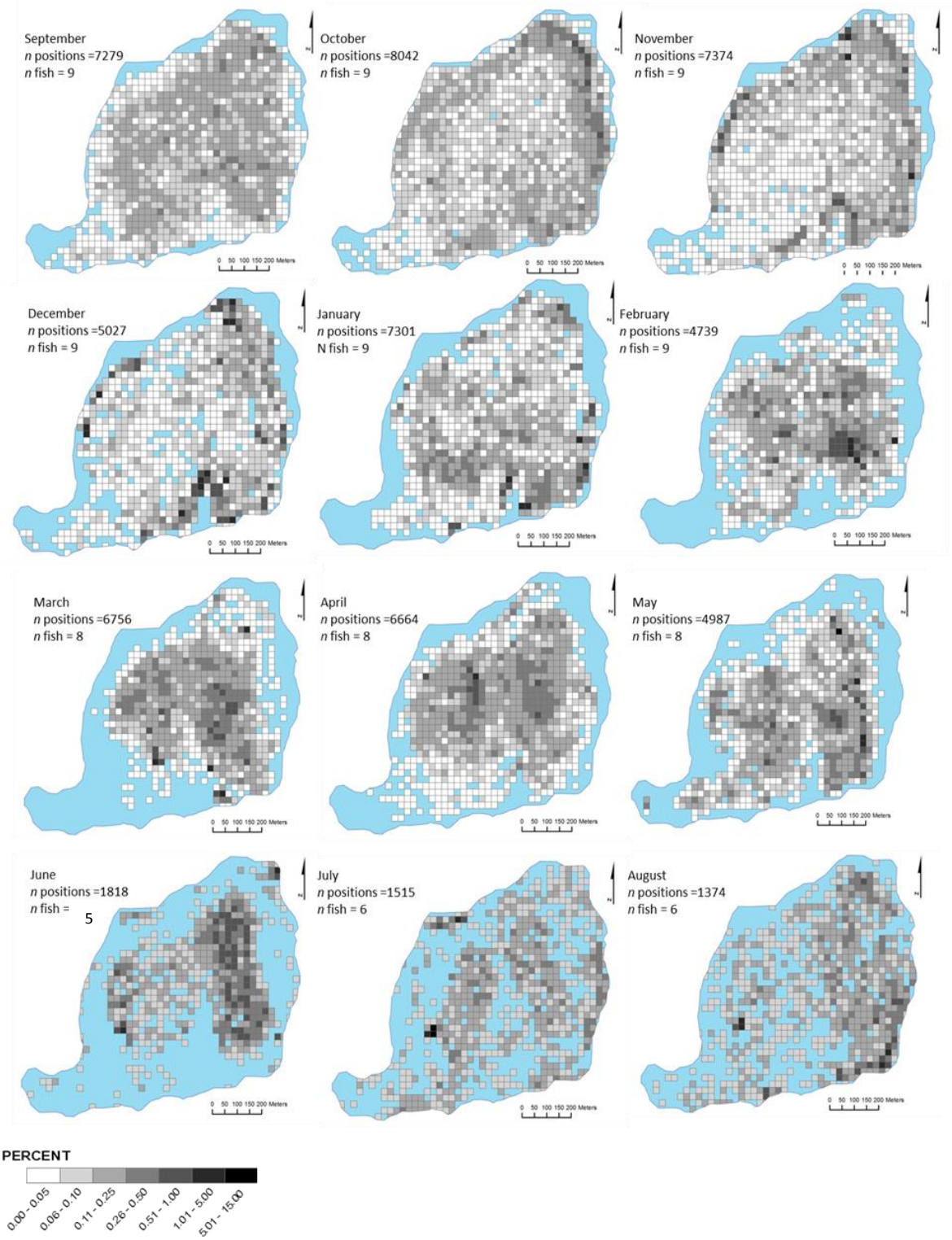


Figure 5-17: The percentage density distribution of Delicate morph Arctic charr on a monthly basis, from September 2009 to August 2010. The number of fish positions and number of individual fish are stated per month. Grid square area is 25 m^2, percentage density increases with shading intensity, blue represents those lake areas for which no fish positions were recorded.

To further explore the patterns of monthly habitat selection as a proportion of the available lake zone habitat, Jacobs index (Jacobs 1974) was calculated (Figure 5-18) according to Equation 5-6 (the sum of individual monthly values was used (n = 439).

$$D = (r - p)/(r + p - 2rp) \quad \text{Equation 5-6}$$

Where r is the proportion of habitat used and p the proportion of habitat available.

D varies from -1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that the habitat is used proportionally to its availability. The 95 % confidence limits of the means were calculated to test whether they differed significantly from the 'neutral' value 0. If 0 was not included within the range of confidence limits, the use of the habitat type was considered not random but the habitat was either favoured or avoided ($p < 0.05$). This method was selected as only two habitats were defined, thus this index gives the full range of values ($-1 < D < 1$) for any value of r or p (Lechowicz 1982). Surface area measurements, not volumes (see 5.2.2 Bathymetry and zonation of Lake Ellasjøen) were used to define the proportion of available habitat (littoral zone 22.6 %; offshore 77.4 %) as the positional distribution is presented in two dimensions (Figure 5-16 and Figure 5-17).

Delicate fish exhibited no selection for the littoral zone, with smallest values of D occurring from October – December, the only months in which significant offshore habitat selection did not occur (Figure 5-18). Conversely, Robust morph fish exhibited significant selection of littoral habitat in July and a non-significant preference in September and June. Robust morph fish mainly utilised the offshore habitat in the remaining months, however significant selection was only observed during February and March.

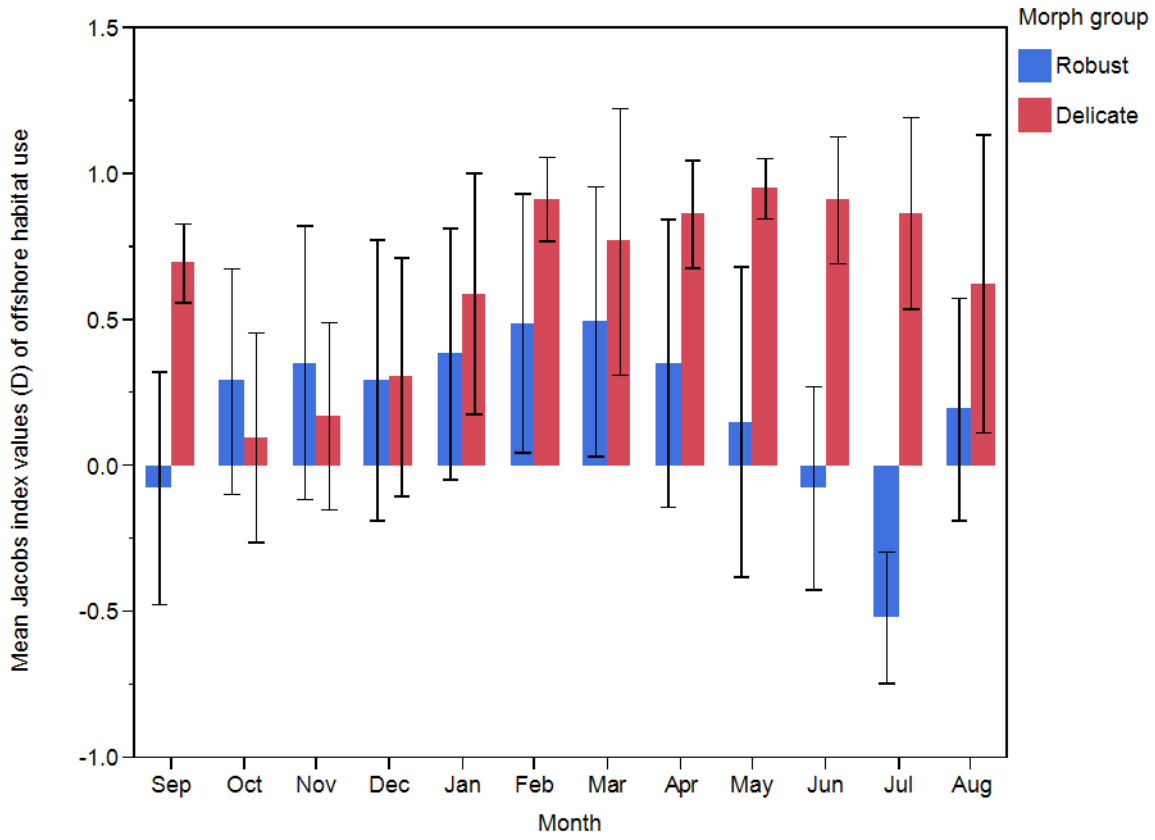


Figure 5-18: Monthly mean values of Jacobs selectivity index D, for the offshore habitat (lake depth 8 – 34 m, 77.4 %) of Lake Ellasjøen, Bear Island (see 5.2.2 Bathymetry and zonation of Lake Ellasjøen). D varies from -1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that the habitat is used proportional to its availability. Error bars represent the 95 % confidence limits of the means, if 0 was not included within the range of confidence limits, the use of the habitat type was considered not random but the habitat was either favoured or avoided ($p < 0.05$). Habitat use was calculated from VPS derived positional data, calculated as a percentage of total positions per morph per month. Individual n varies for each month; values are stated in Figure 5-16 (Robust fish) and Figure 5-17 (Delicate fish). Months are listed from September 2009 – August 2010. Bars are coloured according to the morphology group of the sampled Arctic charr (Robust; blue, Delicate; red).

5.5.2 Variations in fish activity and depth use

Fish activity is presented as average relative speed (given in body lengths per second, BLs[1] to standardise for body length) per day, per Arctic charr morphology group (Figure 5-20: Robust morph; blue, Delicate morph; red). Thus, enabling comparison between months to examine patterns in activity, but actual activity is in all cases likely to be underestimated, especially that which is very localised but continuous (since valid fish detections were approximately every 80 minutes). Speed was calculated between consecutive positions of each fish. If consecutive positions were greater than two hours apart these values were excluded (n = 12,891). Daily average values of fish distance from lake bed (m) and fish depth (negative m), for the Robust and

Delicate morphology groups, were calculated from the tracking data (see 5.4.3 Individual fish fate and validity of VPS fish positions) as the mean of individual daily means (Figure 5-20). Linear regression analysis of mean fish speed, averaged over the 12 month sampling period revealed that individual fork length and weight had a significant ($p < 0.05$) negative effect on mean fish relative swimming speed, R^2 values were 0.23 and 0.18 respectively (Figure 5-19), i.e. smaller fish tended to be more active. Statistical comparison of size versus morph effects is compromised by little overlap in sizes between morphs and has not been attempted. No significant linear relationship was observed between mean fish distance from lake bed, mean fish depth and individual fork length or weight. Both Robust and Delicate morphs were pooled, as sample sizes were relatively small and individuals were tracked for varying durations (see Table 5-9 for details of individual track duration).

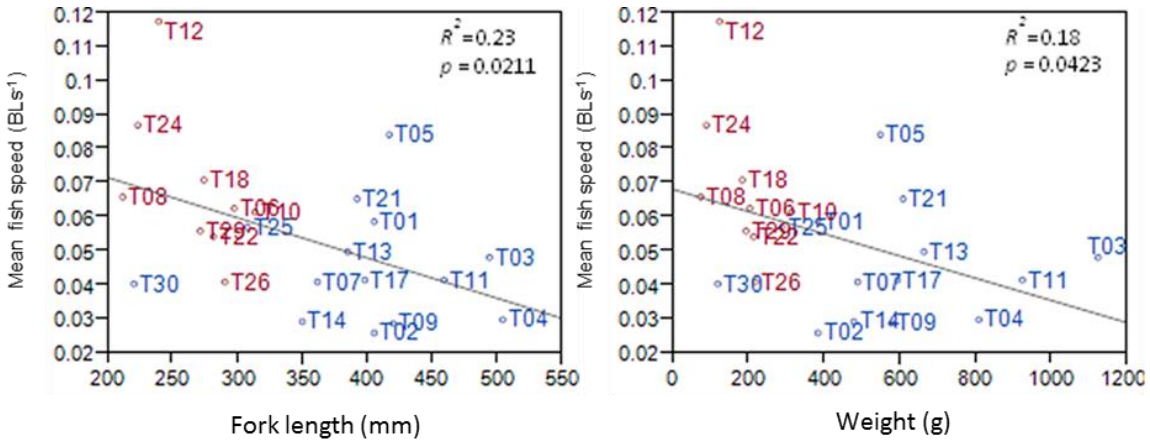


Figure 5-19: Linear regression fits of mean fish speed (BLs^{-1}), averaged over the 12 month sampling period (September 2009 – August 2010) on individual fork length (mm) and weight (grams). Labels refer to individual fish ID; Robust morph fish are blue (n = 14), Delicate red (n =9).

The individual tracking data (Figure 5-20) was fitted to a *GLM* with fish morph and month as model predictors. Individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. Significant morph x month interactions ($p < 0.0001$, 11 *df*) were found for each of the response variables (fish speed; $F = 50.48$, fish distance from lake bed; $F = 21.54$ and fish depth; $F = 174.69$), individual daily mean values were used (n = 7,165). For further exploration of among treatment level effects, *post hoc* Tukey-Kramer HSD tests were applied, where months are not connected by the same letter, these are significantly different (Table 5-12). Total means were calculated as the mean of monthly means per morphology group (Table 5-12).

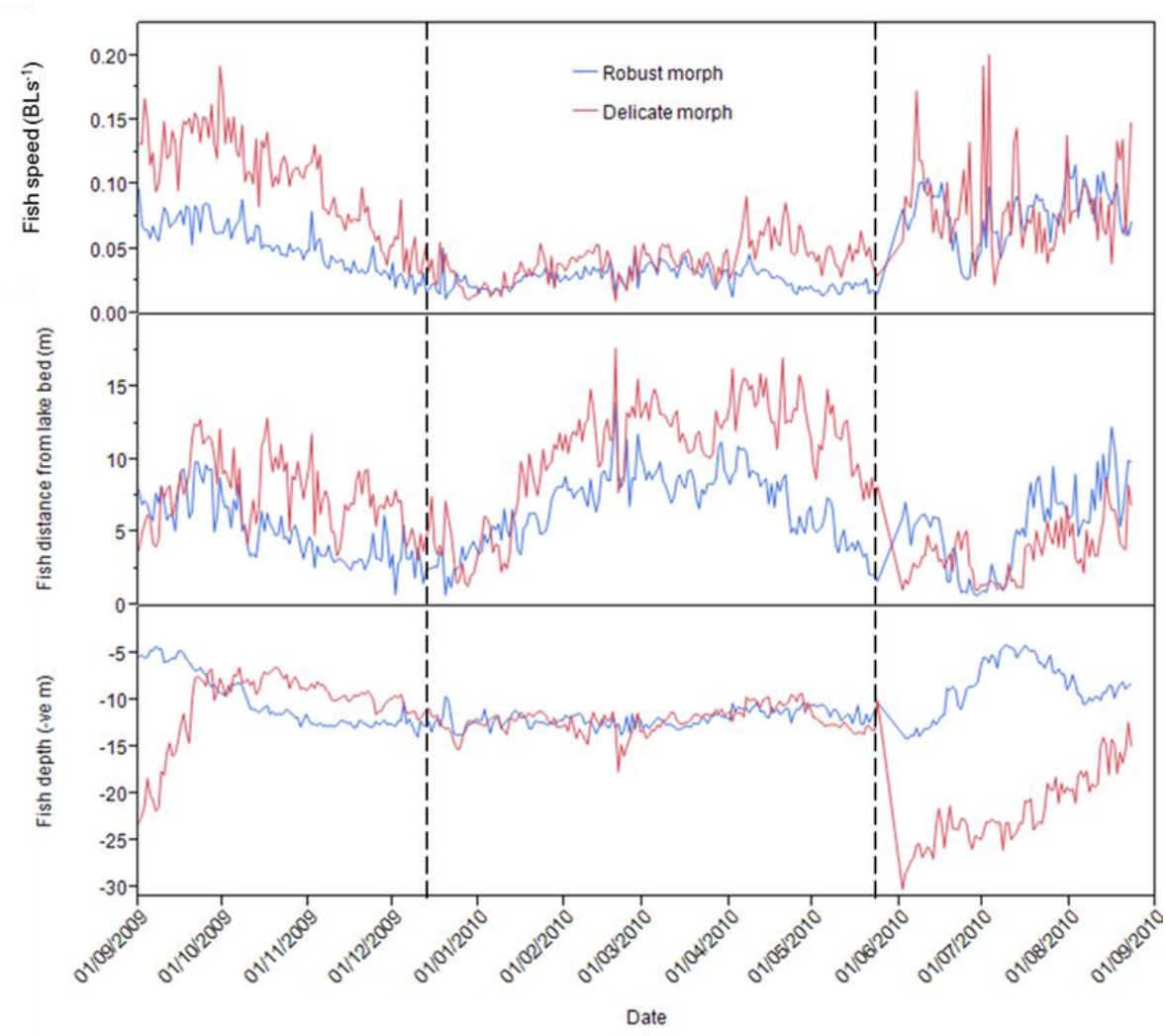


Figure 5-20: Daily average values of relative fish speed (BLs^{-1}), fish distance from lake bed (m) and fish depth (negative m) (*n* = 349), for the Robust (blue) and Delicate (red) morphology groups of sampled Lake Ellasjøen Arctic charr. Average values were calculated as the mean of individual daily means per fish morphology. Speed values from consecutive fish positions greater than two hours apart were not included. Estimated dates of lake ice formation (1/12/2009) and breakup (24/5/2010) (see Figure 5-3 and 5.3.2) are represented by the dashed reference lines on the date axis.

In all months except July and August, Delicate fish were more active than Robust fish, the mean speeds of monthly mean values were 0.069 and 0.047 BLs^{-1} respectively (Table 5-12). Robust morph fish were significantly less active between November and May, with slowest speeds recorded in January and February (0.024 BLs^{-1}). Delicate morph fish were significantly less active between December and May with least activity recorded between December – March (range: 0.029 – 0.041 BLs^{-1}). Robust morph fish were most active in August (0.087 BLs^{-1}) and Delicate fish in September (0.137 BLs^{-1}).

Delicate fish were further from the lake bed than Robust morph fish in all months except June – August. The mean (calculated as the mean of monthly means) fish distance from the lake bed was

8.21 m and 5.87 m for Delicate morph and Robust morphs respectively (Table 5-12). Robust morph fish were significantly further from the lake bed in; September, Feb – April and August (mean: 8.01 m), than during October – January and May – July (mean: 4.35 m). Delicate fish were significantly further from the lake bed between Feb – April (mean: 12.78 m) then for the remainder of the year (mean: 6.68 m). Robust morph fish were furthest from the lake bed in March (8.67 m) and closest in December (2.91 m). Delicate fish were also closest to the lake bed in December, but also during June and July (range: 4.02 – 4.90 m).

Overall mean depth values revealed that Robust morph fish occupied shallower lake depths (10.47 m) than Delicate morph fish (14.11 m) (Table 5-12). However during the months of October – January, March and April Delicate fish were shallower than Robust fish. Robust fish were significantly deeper between October – June (mean: 11.76 m) than during September, July and August (mean: 6.61 m), conversely Delicate fish were significantly deeper in June – August (21.64 m) than the remainder of the year (11.60 m). Robust morph fish were shallowest in July (5.08 m) and September (6.04 m) and deepest in November and December (12.50 m). Delicate fish were shallowest in October (7.85 m) and deepest in June (25.22 m).

To compare the effect of lake ice on the behaviour of the tagged Arctic charr, the tracking data (Figure 5-20) was fitted to a *GLM* with fish morph and ice coverage (present or absent) as model predictors. Individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. Significant morph x ice coverage interactions ($p < 0.0001$, 1 *df*) were found for each of the response variables (fish speed; $F = 147.65$, fish distance from lake bed; $F = 23.11$ and fish depth; $F = 189.62$), individual daily mean values were used (total $n = 7{,}165$). The period of ice coverage (16/12/2009 – 24/5/2010, Figure 5-20) was estimated according to meteorological data, water temperature of Ellasjøen (see Figure 5-3) and movement of the VPS (5.3.2). Robust fish were 58.49 % faster, 21.15 % closer to the lake bed and 30.98 % shallower during the ice free period (Table 5-13). Delicate fish were also observed to be faster (61.15 %) and closer to the lake bed (34.63 %) when lake ice was absent. However in contrast to Robust morph, Delicate fish occupied deeper water (7.31 %) during the ice free period (Table 5-13).

Table 5-12: Least squares mean values and post-hoc Tukey-Kramer HSD test outputs, from a Generalised Linear Model in which significant Arctic charr morph x month interactions ($p < 0.0001$, 11 *df*) were observed for each of the response variables; fish speed (BLs^{-1}), fish distance from lake bed (m) and fish depth (m). Individual daily mean values were used (total $n = 7{,}165$) and individual fish identification was modelled as a random effect. Where months are not connected by the same letter, these are significantly different. Total means were calculated as the mean of monthly means per morphology group, standard error (S.E) is shown in parentheses. Data was derived from a VPS deployed in Lake Ellasjøen, Bear Island, from September 2009 to August 2010.

	Fish speed (BLs^{-1})				Fish distance from lake bed (m)				Fish depth (m)			
	Robust		Delicate		Robust		Delicate		Robust		Delicate	
Month	L Sq mean	Tukey test	L Sq mean	Tukey test	L Sq mean	Tukey test	L Sq mean	Tukey test	L Sq mean	Tukey test	L Sq mean	Tukey test
Sep	0.072	B	0.137	A	7.60	AB	8.57	CDE	6.04	F	13.80	D
Oct	0.057	C	0.120	B	5.28	CD	8.59	CD	10.54	D	7.85	H
Nov	0.040	D	0.079	C	3.44	EF	7.10	EF	12.50	A	9.52	G
Dec	0.024	FG	0.036	F	2.91	F	4.33	G	12.50	A	11.73	EF
Jan	0.024	FG	0.029	F	5.66	C	7.16	DEF	12.16	ABC	12.06	E
Feb	0.031	EF	0.037	F	8.54	AB	12.10	B	12.32	AB	13.04	DE
Mar	0.034	DE	0.041	F	8.67	A	12.31	B	12.31	AB	12.11	E
Apr	0.028	EFG	0.056	DE	7.98	AB	13.96	A	11.03	D	10.44	FG
May	0.020	G	0.043	EF	4.38	DE	10.14	C	11.30	BCD	13.82	D
Jun	0.072	B	0.087	C	4.13	DEF	4.02	G	11.13	CD	25.22	A
Jul	0.075	B	0.073	CD	4.66	CDE	4.90	G	5.08	F	21.87	B
Aug	0.087	A	0.085	C	7.25	B	5.29	FG	8.72	E	17.84	C
Total mean (S.E.)	0.047 (0.007)		0.069 (0.010)		5.87 (0.59)		8.21 (0.97)		10.47 (0.73)		14.11 (1.47)	

Table 5-13: Least squares mean values from a Generalised Linear Model in which significant Arctic charr morph x lake ice presence/absence interactions ($p < 0.0001$, 11 *df*) were observed for each of the response variables; fish speed (BLs^{-1}), fish distance from lake bed (m) and fish depth (m). Individual daily mean values were used (total n = 7,165) and individual fish identification was modelled as a random effect. The period of ice coverage (16/12/2009 – 24/5/2010) was estimated according to meteorological data and water temperature of Ellasjøen (see Figure 5-3 and 5.3.2).

	Fish speed (BLs^{-1})		Distance to lake bed (m)		Fish depth (m)	
	Robust	Delicate	Robust	Delicate	Robust	Delicate
Lake ice absent	0.065	0.103	5.31	7.23	9.13	12.86
Lake ice present	0.027	0.04	6.43	9.73	11.96	11.92

Regression analyses were conducted to investigate the effect of the physical environment on; relative fish speed, fish distance to lake bed and fish depth. Linear regression was performed using the covariates; duration of night (minutes) and water temperature (°C) at depths of 3, 25 and 31 metres (Figure 5-21). Daily mean values were calculated from the mean of individual means (n = 349) per morphology group. Significant (df = 1, $p < 0.002$ after Bonferonni correction) linear relationships were observed in all instances with the exception of water temperature at 3 m and fish distance to lake bed, for Robust morph fish. Linear models were selected in all instances due to time constraints, however more complex non-linear modelling should be applied in future work. Water temperature accounted for the greatest proportion of observed variation in fish speed, with little R^2 variation between the three water depths. A stronger relationship was observed between fish speed and water temperature for Robust morph fish (mean R^2 = 0.71) than Delicate morph (mean R^2 = 0.39), with the latter exhibiting a drop in speed at higher water temperatures (Figure 5-21). A negative relationship between fish speed and duration of night was shown (R^2: Robust = 0.24, Delicate = 0.06). Both water temperature and duration of night were poor explanatory factors for fish distance from lake bed (Figure 5-21), with the strongest relationship observed between water temperature at 3 m depth for Delicate morph fish (R^2 = 0.24). The relationship to water temperature was positive in Robust fish with increasing water temperature increasing the fish distance to lake bed, conversely a negative response was observed in Delicate morph fish. Water temperature at 25 and 31 m depth explained the greatest proportion of variation in fish depth for Robust fish R^2 = 0.72 and 0.66 respectively, with water temperature at 3 m showing a considerably poorer relationship (R^2 = 0.27). Depth use of Delicate fish, in contrast, showed a stronger relationship to water temperature at 3 m (R^2 = 0.27), than for the deeper temperature measurements (R^2 = 0.15, 0.18), (for which there appeared to be a distinctly biphasic relationship, with ambient temperature a poor indicator of depth use) with duration of night a better explanatory factor than water temperature (R^2 = 0.37). A negative response in fish depth to water temperature was observed in Robust fish but a positive response was shown for Delicate fish (Figure 5-21).

Figure 5-21: Regression plots of relative fish speed (BLs^{-1}), fish distance from lake bed (m) and fish depth (m) (left to right) and water temperature (°C) at 25 m depth for Robust (blue) and Delicate (red) morphs of Arctic charr. Daily mean values were calculated from the mean of individual means (n = 349) per morphology group. Regression lines were significant (df = 1, p < 0.002), values of intercept, slope and regression coefficient (R^2) are stated in Table 5-14. Data was derived from a VPS deployed in Lake Ellasjøen, Bear Island, between 28/8/2009 and 23/8/2010. Limited stratification of water temperature occurred (Figure 5-3), thus plots are presented for water temperature at 25 m depth only.

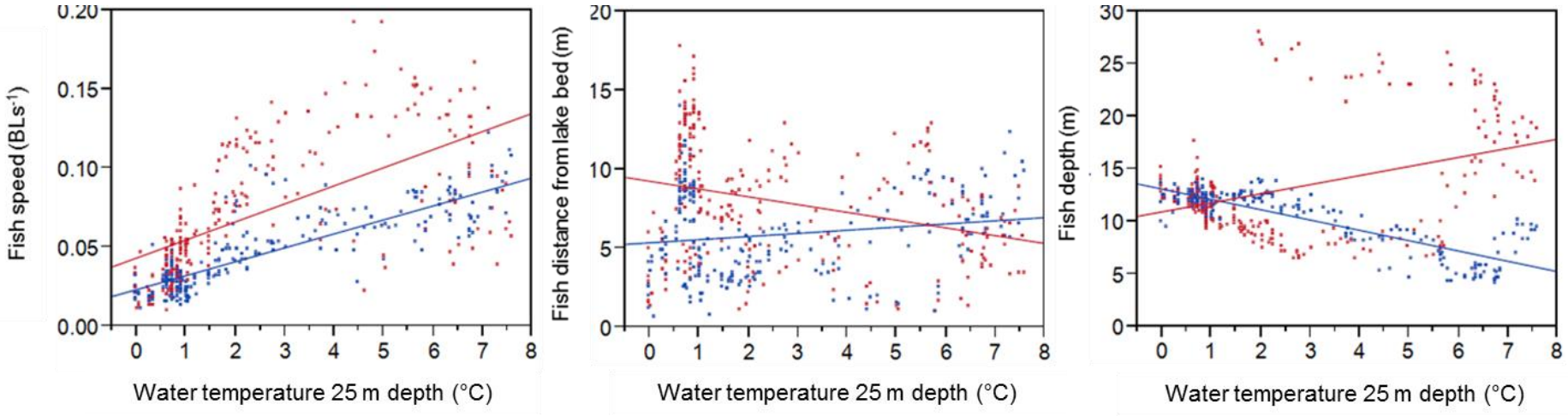


Table 5-14: Linear regression statistics of fish speed (BLs^{-1}), fish distance from lake bed (m) and fish depth (m). Using the covariates; duration of night (minutes), water temperature (°C) at depths of 3, 25 and 31 metres, for Robust and Delicate morphs of Arctic charr. Daily mean values were calculated from the mean of individual means (n = 349) per morphology group. Where significant (df = 1, p < 0.002), intercept (a), slope, (b) and regression coefficient (R^2) are stated. Data was derived from a VPS deployed in Lake Ellasjøen, Bear Island, between 28/8/2009 and 23/8/2010.

	Fish speed (BLs^{-1})						Fish distance from lake bed (m)						Fish depth (m)					
	Robust			Delicate			Robust			Delicate			Robust			Delicate		
Covariate	*a*	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2	*a*	*b*	R^2
Duration of darkness	0.06	0.00	0.24	0.08	0.00	0.06	6.28	0.00	0.01	7.35	0.00	0.02	8.89	0.00	0.26	17.38	-0.01	0.37
Water temp. 3 m	0.03	0.01	0.69	0.05	0.01	0.37	-	-	-	9.70	-0.73	0.24	12.39	-0.79	0.27	11.64	0.96	0.24
Water temp. 25 m	0.02	0.01	0.72	0.04	0.01	0.41	5.36	0.19	0.03	9.24	-0.49	0.09	13.09	-0.98	0.72	10.94	0.86	0.15
Water temp. 31 m	0.02	0.01	0.71	0.04	0.01	0.38	5.70	0.14	0.02	9.79	-0.64	0.14	12.72	-0.83	0.66	11.23	0.91	0.18

Diel movements

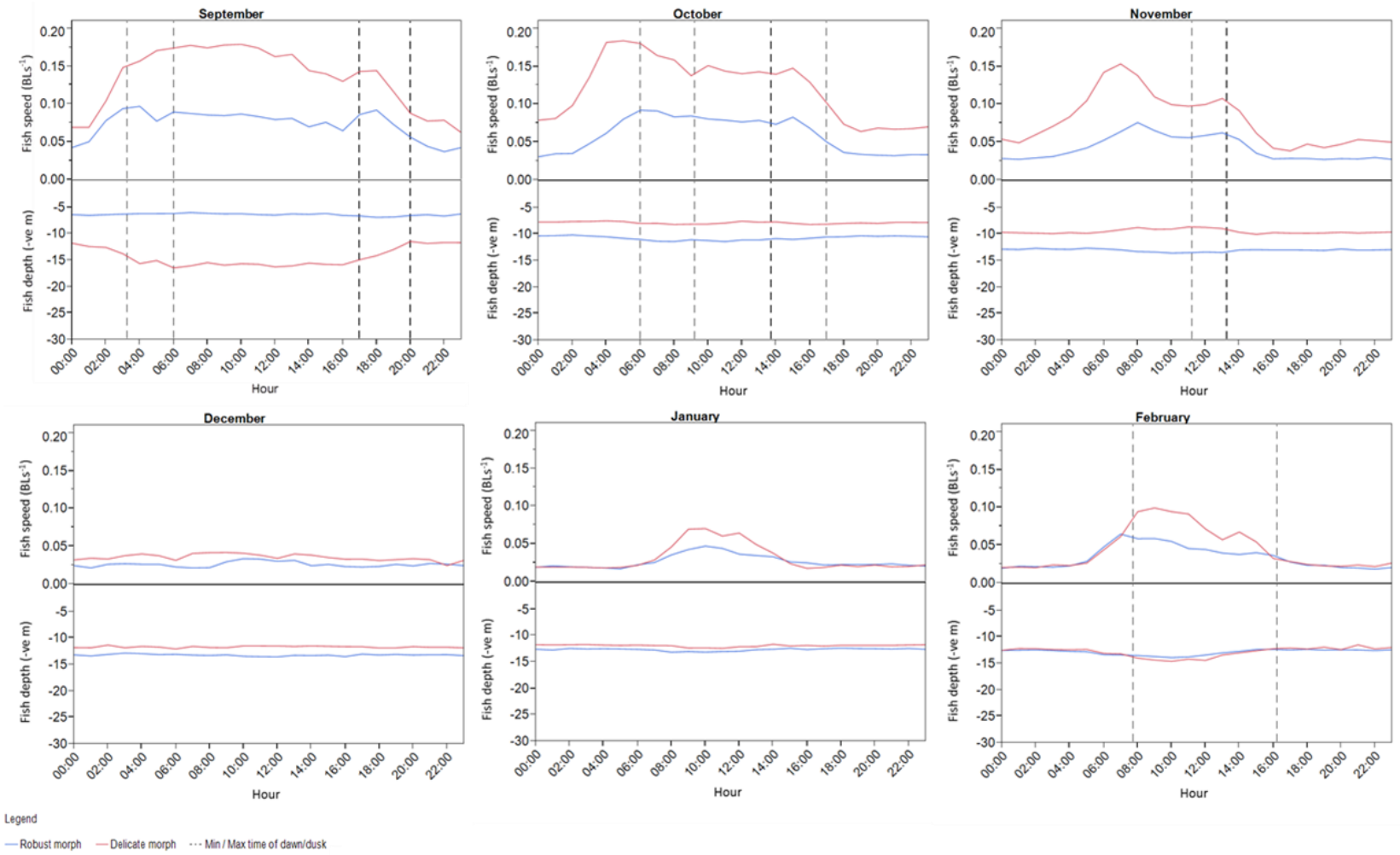
Diel activity is presented as the average relative speed (BLs^{-1}) and depth (m), per hour, per month for both Robust and Delicate morphs of sampled Arctic charr (Figure 5-22). The data was fitted to two *GLMs,* one per fish morph (Robust and Delicate) with hour and month as model predictors. Individual mean values per hour per month were used (n = 5,870) and individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. Significant hour x month interactions ($p < 0.0001$, 253 *df*) were found for the response variable fish speed for both Robust and Delicate morphs; F = 2.42 and 1.55 respectively. No significant interaction was observed for fish depth for either morph ($p > 0.05$, 253 *df*). A *post hoc* Tukey-Kramer HSD test was applied to the speed data for both the Robust and Delicate morph models, in order to further explore hourly effects (Table 5-15, where hours are not connected by the same letter, these are significantly different).

In all months except May – August a diel peak in fish speed is visible for both morphs (Figure 5-22). A diel change in depth use is also indicated during September (Delicate morph only) and February – March, however this was not found to be signicant according to either model. During the months in which dawn and dusk occurs (the earliest and latest time of sunrise and sunset for each month is represented by a dashed line on the hour axis in Figure 5-22) a bimodal peak in fish speed is visible for both morphs e.g. September – November and February – March. With the exception of November, these peaks correspond to dawn and dusk periods, indicating crepuscular increases in activity. A significant diel pattern of fish speed was observed during the months of polar night; December and January (*GLM*: hour x morph, fish ID random effect; n = 1,056, *df* = 23, F = 1.58, $p < 0.05$), but not during the months of polar day; May – July (*GLM*: hour x morph, fish ID random effect; n = 1,353, *df* = 23, F = 0.68, $p > 0.05$).

Tukey-Kramer outputs (Table 5-15) indicate that both morph groups undertook a similar diel pattern of activity, with greatest speeds recorded between 09:00 and 10:00 (range: 0.093 – 0.096 BLs^{-1}) for Delicate morph fish and during 07:00 (0.060 BLs^{-1}) for Robust fish. Delicate fish were least active between 21:00 – 23:00 (range: 0.048 – 0.051 BLs^{-1}), Robust fish at 00:00 (0.042 BLs^{-1}). Delicate morph fish were significantly less active in the hours of 00:00 – 01:00 and 18:00 – 23:00 (mean: 0.052 BLs^{-1}) than between 07:00 – 10:00 (mean: 0.091 BLs^{-1}). Robust morph fish were significantly less active between 00:00 – 03:00 and 16:00 – 23:00 (mean: 0.044 BLs^{-1}) than during 07:00 – 08:00 (mean: 0.060 BLs^{-1}). In all instances Delicate fish were more active than Robust morph fish (Figure 5-22, Table 5-15).

Table 5-15: Least squares mean values and post-hoc Tukey-Kramer HSD test outputs, from two Generalised Linear Models, one for each morph of Arctic charr; Robust and Delicate. Significant hour x month interactions ($p < 0.0001$, 253 *df*) were found for the response variable fish speed for both Robust and Delicate morphs; $F = 2.42$ and 1.55 respectively. Individual mean values per hour per month were used (n = 5,870) and individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. Where hours are not connected by the same letter, these are significantly different. Data was derived from a VPS deployed in Lake Ellasjøen, Bear Island, between 28/8/2009 and 23/8/2010.

	Fish speed (BLs^{-1})			
	Robust morph		Delicate morph	
Hour	L Sq mean	Tukey test	L Sq mean	Tukey test
00:00	0.042	I	0.050	F
01:00	0.043	FGHI	0.049	F
02:00	0.042	HI	0.060	CDEF
03:00	0.048	CDEFGHI	0.066	BCDEF
04:00	0.052	ABCDEFGHI	0.073	ABCDEF
05:00	0.054	ABCDEF	0.080	ABCDE
06:00	0.056	ABCD	0.085	ABC
07:00	0.060	A	0.086	AB
08:00	0.060	AB	0.090	AB
09:00	0.058	ABC	0.093	A
10:00	0.058	ABC	0.096	A
11:00	0.054	ABCDEFG	0.086	ABC
12:00	0.054	ABCDEFGH	0.081	ABCD
13:00	0.056	ABCDE	0.079	ABCDE
14:00	0.051	ABCDEFGHI	0.081	ABCD
15:00	0.049	BCDEFGHI	0.077	ABCDE
16:00	0.044	EFGHI	0.067	BCDEF
17:00	0.046	DEFGHI	0.065	BCDEF
18:00	0.044	FGHI	0.059	DEF
19:00	0.044	FGHI	0.058	DEF
20:00	0.044	FGHI	0.054	EF
21:00	0.042	HI	0.048	F
22:00	0.043	FGHI	0.050	F
23:00	0.043	GHI	0.051	F


September
October
November
December
January
February
Fish speed (BLs⁻¹)
Fish depth (-ve m)
Hour
Legend
Robust morph
Delicate morph
Min / Max time of dawn/dusk

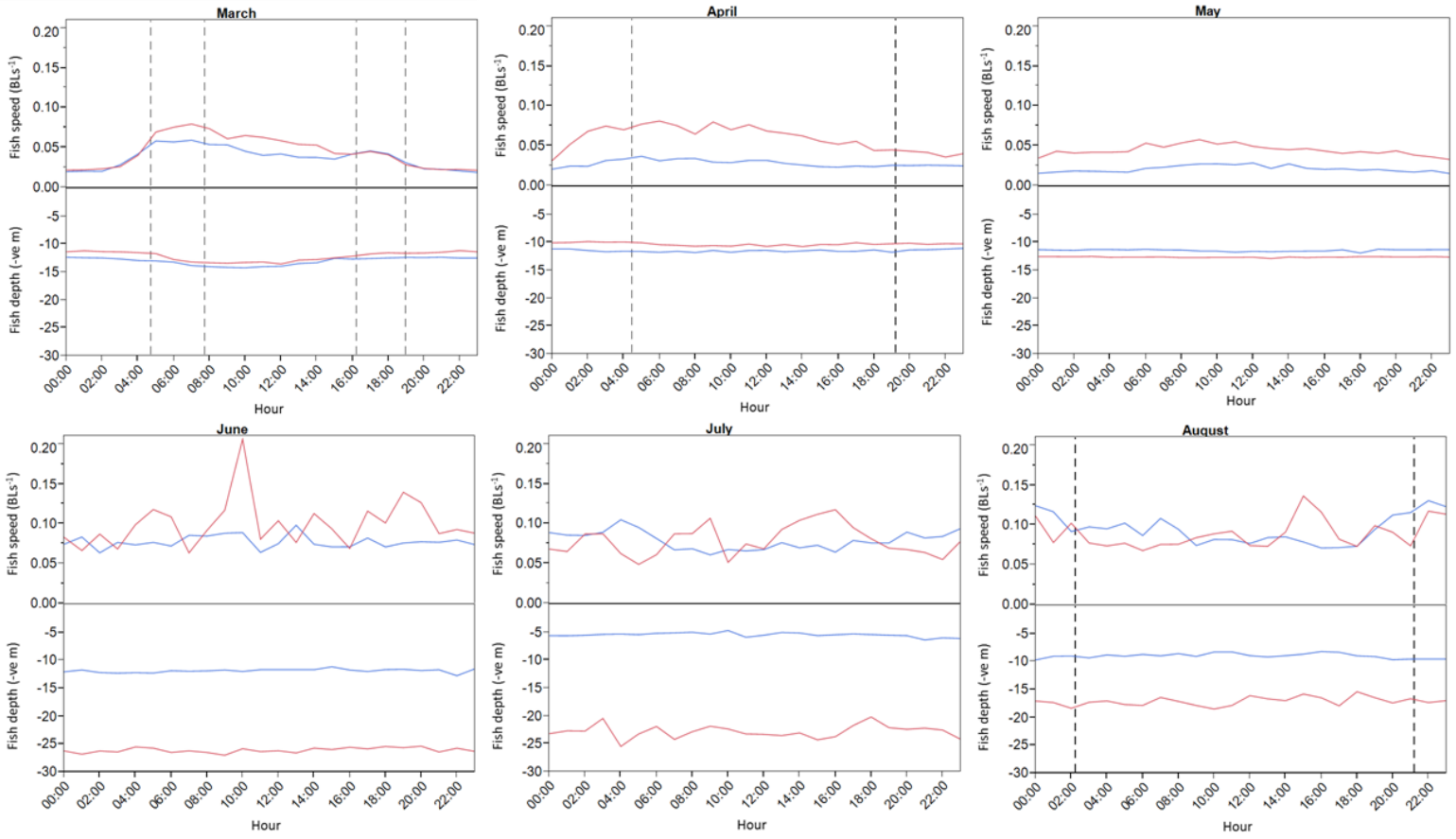


Figure 5-22: The average speed (BLs^{-1}), per hour, per month for both Robust (blue) and Delicate (red) morphs of sampled Arctic charr. Average fish depth (negative metres) per hour, per month is also given. Months are presented from September (2009) to August (2010). All mean values were calculated as the mean of individual means per hour per month for each morph. Speed was calculated from individual fish positions less than (or equal to) two hours apart. The earliest (min) and latest (max) time of sunrise and sunset for each month is shown. The months of polar day and polar night are shown by the absence of dashed lines. For April and August only the earliest time of dawn/dusk is shown, for November and February only the latest time of dawn/dusk

5.5.3 Home range estimates

Subsampling of fish position data

A standardised sample of 54 positions per fish was used to estimate monthly home range. This number was chosen to maximise the number of individuals included for which analysis could be conducted. Incremental Area Analysis was conducted in Ranges 8 (Anatrack Ltd, 2008); according to Hodder et al. (2007), to ensure that a sample of 54 positions was sufficient to represent the full range span area or maximal home range area (K100) of each individual. Positions in the sample were selected randomly to represent the correct proportion of the number of hours in each time of day category (day, night, polar day, and polar night) during each month, in order to reflect the highly varied Arctic photoperiod. For the months where dawn and dusk occurred, fish positions from within an hour of sunrise/sunset were included to represent a third of the total number of dawn and dusks per month, when they occurred at an interval of four hours or greater (Table 5-16).

Table 5-16: The sample size of *n* = 54 positions for each home range, broken-down according to the time of day class of each fish position, representing a proportion of the total number of hours in each class per month. The number of individual Arctic charr from each morph group; Robust or Delicate for which home ranges were calculated for each month (September 2009 – August 2010) is also stated.

	n positions included in home range sample						*n* individuals per month	
Month	Dawn	Day	Dusk	Night	Polar day	Polar night	Robust morph	Delicate morph
Sep	2	29	2	21	0	0	14	9
Oct	2	15	2	35	0	0	14	9
Nov	0	1	0	11	0	42	14	9
Dec	0	0	0	0	0	54	14	9
Jan	0	0	0	0	0	54	14	9
Feb	2	11	2	39	0	1	14	8
Mar	2	24	2	26	0	0	14	8
Apr	4	17	4	25	3	0	14	8
May	0	0	0	0	54	0	14	8
Jun	0	0	0	0	54	0	14	5
Jul	0	0	0	0	54	0	12	5
Aug	0	24	1	3	27	0	11	5

For each home range sample the positions were randomly selected from each time class using JMP v 9.03 software (SAS institute Inc.). Where a sample from a time of day class was larger than or equal to 10 positions, the random sample was stratified according to the hour of fish position. All positions were grouped according to the hour position on a clock face. Thus, hours 1 – 3 and 13 – 15 were grouped; 4 – 6 and 16 – 18 were grouped; 7 – 9 and 19 – 21 were grouped and 10 – 12 and 22 – 24 were grouped, thus minimising auto-correlation in the sampled data.

Kernel analysis

Kernel Analysis was selected as the most appropriate home range estimator for fish, due to the restricted (i.e. aquatic) environment in which they live (Knight et al. 2009). The 95 % probability distribution area, K95, was used to estimate the outer maximum range area, K50 (50 % probability distribution zone) the core range area. As home range estimates extended beyond the lake edge boundary (i.e. onto land), the estimates of K95 and K50 were 'clipped' when necessary to the feasible boundary, Lake Ellasjøen. All kernel analyses were conducted in Ranges 8 (Anatrack Ltd, 2008) the lake boundary polygon (vesfile) was imported into Ranges as a shapefile from ArcMap 10. Examples of each home range estimate for two individuals, one Robust (T01), one Delicate (T06) for the months October and April are given (Figure 5-23).

Home range estimates are presented as the average K50 and K95 areas (ha), per month for both Robust and Delicate morphs of sampled Arctic charr (Table 5-17, Figure 5-24). The data was fitted to two *GLMs,* one per home range estimator (K50, K95) with fish morph and month as model predictors. Individual values per month were used (n = 255 per model) and individual fish identification was modelled as a random effect to account for observational dependency caused by repeated measures from the same individuals. Significant morph x month interaction (F = 2.11, p = 0.0202, 11 *df*) was found for the response variable K50. No significant morph x month interaction was observed for K95 (F = 1.52, p > 0.05, 11 *df*) but significance was observed for both responses individually (morph F = 4.35, p = 0.0380, 1 *df*; month F = 4.57, p < 0.0001, 11 *df*). A *post hoc* Tukey-Kramer HSD test was applied to both models, in order to further explore monthly effects on K50 and K95 estimates (Figure 5-24).

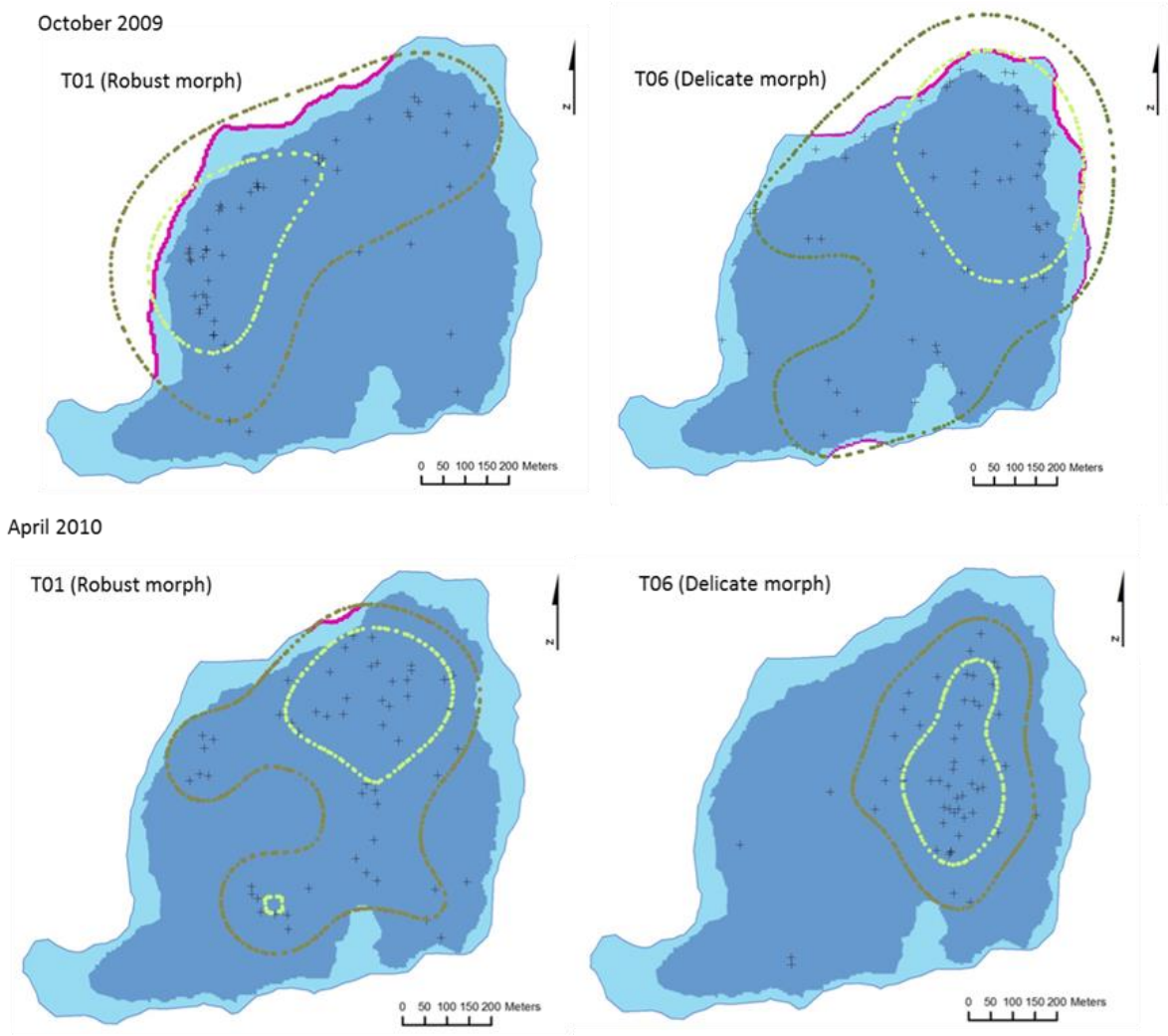


Figure 5-23: Example home range area estimates of the Robust morph individual T01 (left) and the Delicate morph individual T06 (right) for the months October (top) and April (bottom). The 54 fish positions used to calculate the home range are represented with black crosses. The K50 core estimate and K95 maximum home range estimates are shown by light green and dark green contour lines respectively. The pink line represents the clipped boundary of the K50 and/or K95 estimates, where these extend beyond the range boundary of Lake Ellasjøen. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

Overall average estimates (mean of monthly means) of Delicate morph home range area were 25.64 % (K50) and 17.74 % (K95) larger than Robust morph fish (Table 5-17). This significant difference between morphology groups was observed to be significantly different between months for K50 estimates but not for K95 estimates. Robust fish occupied larger home ranges than Delicate fish during the months of December (K50), March (K50, K95) and June – August (K50, K95) (Table 5-17). Robust morph fish occupied the largest home range area during October (K50: 11.46 ha) and September (K95: 34.11 ha) (Table 5-17). Delicate fish also occupied the largest

home range during October for both K50 and K95 estimates, 18.12 and 40.82 ha respectively (Table 5-17). The greatest difference in mean monthly home range areas between morph groups occurred during September (7.46 ha), October (7.23 ha) and November (6.68 ha) for K50 estimates and in October (13.74 ha) and November for K95 (18.88 ha) estimates (Table 5-17, Figure 5-24). K50 estimates were significantly larger during September – October (mean: 17.75 ha) than December – May (mean: 6.96 ha) (Figure 5-24). K95 estimates were significantly larger during September – October (mean: 37.60 ha) than February – March (mean: 18.44 ha) (Figure 5-24). K95 estimates of home range area were 65.90 % and 63.61 % larger than K50 estimates for Robust and Delicate morphs respectively, with greatest differences occurring in February (Robust; 73.15 %) and December (Delicate; 78.18 %). Smallest difference occurred in July (61.29 %) and September (55.61 %) for Robust and Delicate morphs respectively.

Table 5-17: Least squares mean values of K50 and K95 home range estimates in hectares, for both Robust and Delicate morphs of sampled Arctic charr, for each month of VPS deployment in Lake Ellasjøen, Bear Island (September 2009 – August 2010). *n* varies for each month; values are stated in Table 5-16. Overall mean values are calculated as the mean of monthly means, standard error (S.E.) is shown in parentheses. Analyses were conducted in Ranges 8.

	Least squares mean values			
	K50 area (ha)		K95 area (ha)	
Month	Robust	Delicate	Robust	Delicate
September	10.66	18.12	34.11	40.82
October	11.46	18.78	30.88	44.62
November	7.59	14.27	22.29	41.17
December	6.34	5.88	22.07	26.95
January	6.12	7.19	19.19	21.92
February	4.00	8.95	14.90	23.15
March	6.86	6.58	17.90	17.81
April	7.49	10.41	21.19	26.42
May	5.08	8.71	16.08	27.35
June	10.77	8.28	28.94	24.47
July	10.71	7.96	27.67	19.31
August	11.14	8.27	32.85	25.17
Overall mean (S.E.)	8.18 (0.76)	10.28 (1.26)	24.00 (1.92)	28.26 (2.58)

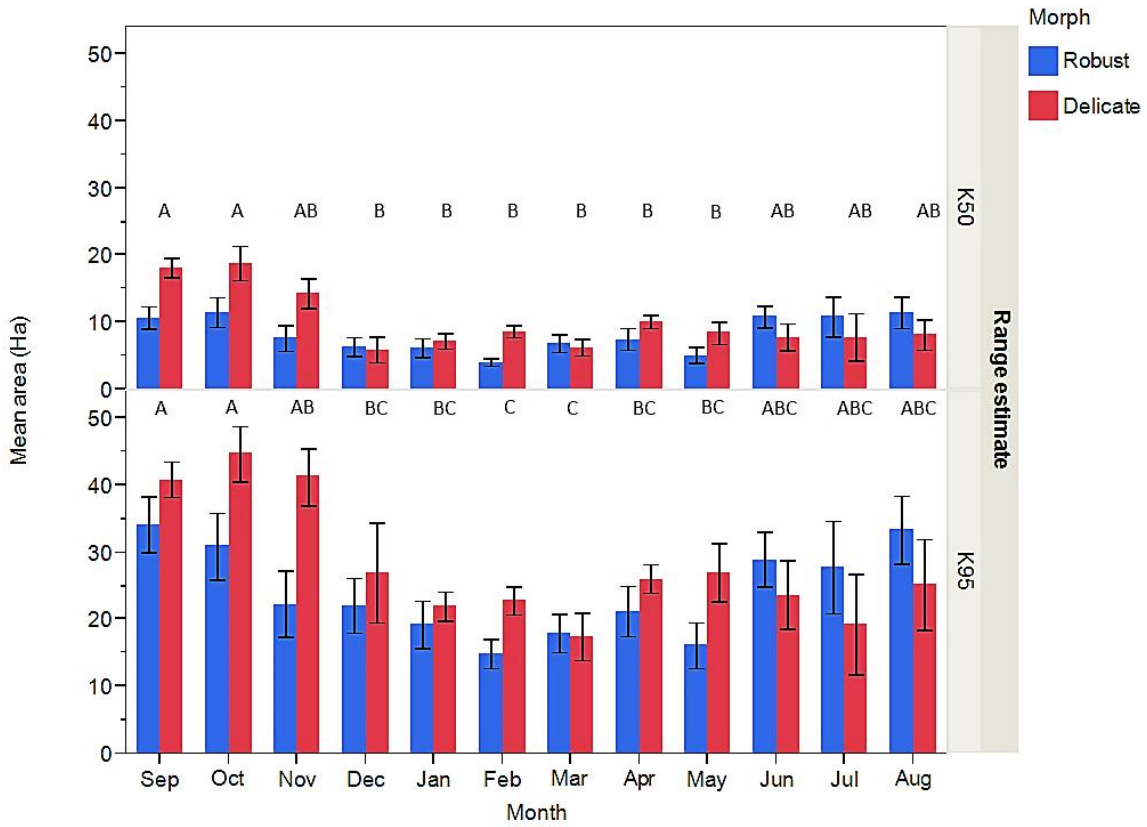


Figure 5-24: Mean monthly home range areas (hectares) calculated using the kernel analysis estimates; K50 (top) and K95 (bottom) that have been clipped to within the boundary of Lake Ellasjøen, Bear Island. Bars are coloured according to the morphology group of the sampled Arctic charr. *n* of individuals varies for each month; values are stated in Table 5-16, total *n* = 510. Months are listed from September 2009 – August 2010. Error bars represent +/- one standard error. Letters above each pair of bars represent the output of a post-hoc Tukey-Kramer HSD test, for the significant effect of month (*GLM*; *df* = 11, $p < 0.0001$), for both K50 ($F = 5.70$) and K95 ($F = 4.57$) estimates. Months not connected by the same letter are significantly different ($p < 0.05$).

Regression analyses revealed no effect of individual fork length or weight on the mean area estimate of K50 or K95 for either morph ($p > 0.05$, 1 *df*), although sample size was quite small (Robust *n* = 14, Delicate *n* = 10). The *n* of individuals varied between months (Table 5-16) with smaller sample sizes for June – August. Regression analyses of home range on individual fork length and weight was therefore also calculated on a monthly basis (Robust and Delicate morphs combined), to prevent potential confounding effects due to different tracking periods of individuals (Figure 5-25). A significant negative response to fork length was observed in November and February for K50 home range and in November only for K95. An inverse relationship was also observed with fish weight. A significant effect was found during September, November and February for K50 and September and November for K95. However, after application of Bonferonni

correction, no significance was sustained (∝ level $p < 0.004$). All such relationships were contrary to expectation.

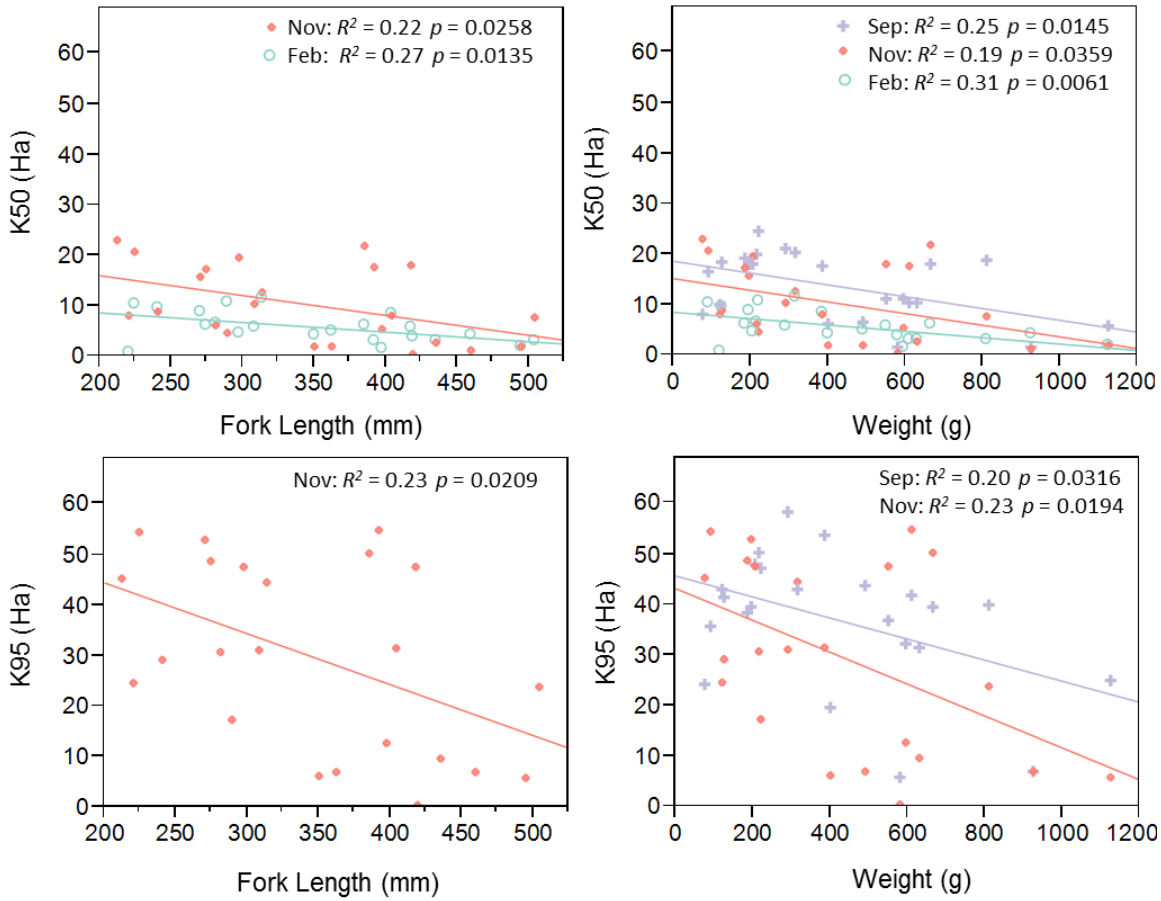


Figure 5-25: Linear regression fits of K50 (top) and K95 (bottom) estimates of home range area (ha) on individual fork length (mm) and weight (g). Regression analyses were conducted for each sampled month (September 2009 – August 2010) (Robust and Delicate morphs combined), to prevent potential confounding effects due to different tracking periods of individuals (Table 5-16). Significance was observed for September (+), November (•) and February (○). Regression coefficient (R^2) and p values (1 *df*) are stated on each plot. After application of Bonferonni correction, no significance was sustained (∝ level $p < 0.004$).

Regression analyses were conducted to investigate the effect of the physical environment on K50 and K95 estimates of home range area. Linear regression was performed using the covariates; duration of night (minutes), water temperature (°C) at depths of 3, 25 and 31 metres. Mean values were calculated per fish morphology per month (n = 12). Water temperature significantly affected both home range estimates for Robust morph fish (*ANOVA*: $df = 1$, $p < 0.05$). A positive response was shown, with limited variation in R^2 between estimates or the three water depths

(K50 R^2= 0.71, 0.68, 0.68; K95 R^2 = 0.76, 0.74, 0.74 at 3, 25 and 31 m depth respectively). No effect of water temperature was shown for Delicate morph fish. No relationship between home range area and duration of night was shown for either morph.

Habitat composition of home range

The habitat use, represented as either littoral or offshore (i.e. both limnetic and profundal zones) was calculated as the percentage composition of the K50 home range area (Figure 5-26). The major component of home range habitat was the offshore area of Lake Ellasjøen (Robust mean; 72.3 %, min; 0 %, max; 100 %; Delicate mean; 92.7 %, min; 63.2 %, max; 100 %), with the littoral habitat forming an average of 22.7 % (min; 0 %, max; 100 %) of the home range area for Robust fish and 7.25 % (min; 0 %; max; 36.8 %) for Delicate fish, for all months. Seasonal variation of habitat use was shown by both groups of fish, with a higher proportion of littoral home range area in October – December and again in June – August. The greatest difference in littoral use between morphs was exhibited in September (Robust; mean 14 %, Delicate; 1 %).

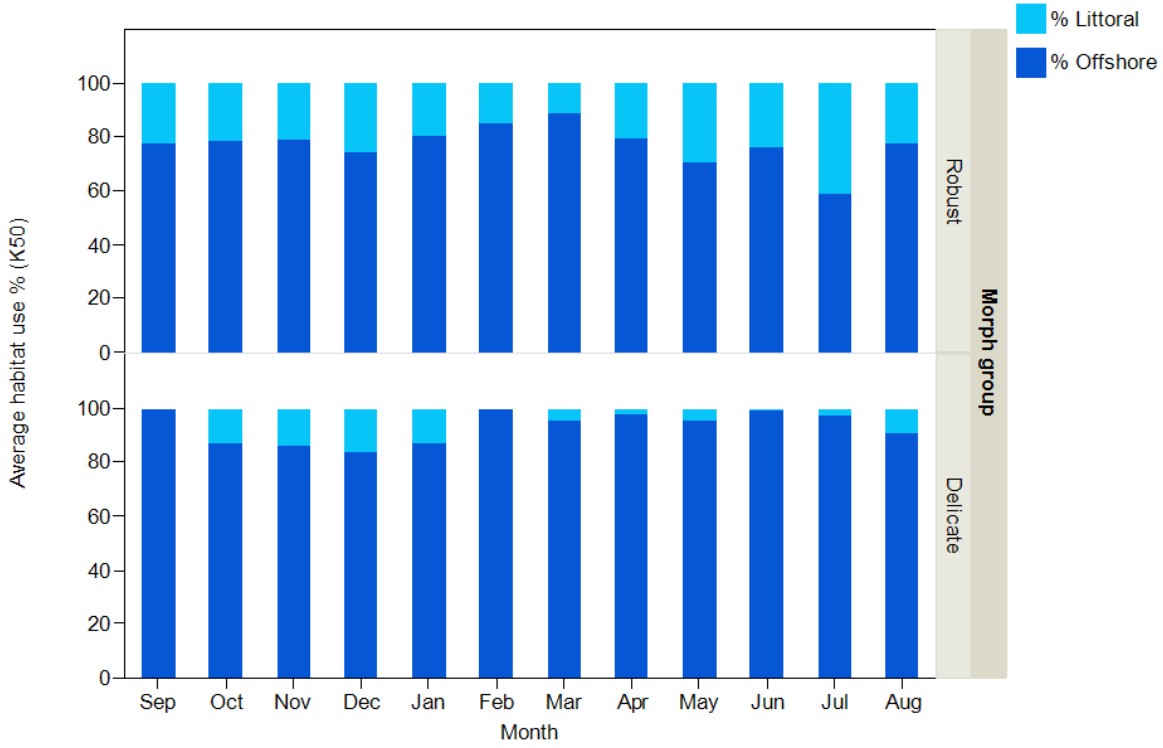


Figure 5-26: Mean percentage habitat composition of the K50 home range area (hectares) estimates of the two morphology groups (Robust; top, Delicate; bottom), of tracked Arctic charr, per month (September 2009 – August 2010). *n* of individuals varies for each month; values are stated in Table 5-16. Offshore habitat (dark blue) includes both the limnetic and profundal zones. The littoral zone (light blue) of Lake Ellasjøen is defined as the lake edge habitat to a maximum depth of 8 m.

To calculate the patterns of habitat selection as a proportion of the available habitat, monthly values of Jacobs index, *D* (Jacobs 1974) were calculated according to Equation 5-7. Surface area measurements, not volumes were used to define the proportion of available habitat (littoral zone 22.6 %; offshore 77.4 %) as the home range area K50 (proportion of habitat used) was only estimated in two dimensions. The only months Delicate fish did not show a significant selection for the offshore area were December and August (Figure 5-27). Conversely, Robust morph only showed a significant selection for offshore habitat during February and March, in all other months, no significant habitat selection was observed. A negative value of *D* was calculated for Robust fish in July, indicating a preference for littoral habitat during this month, however this was not significant.

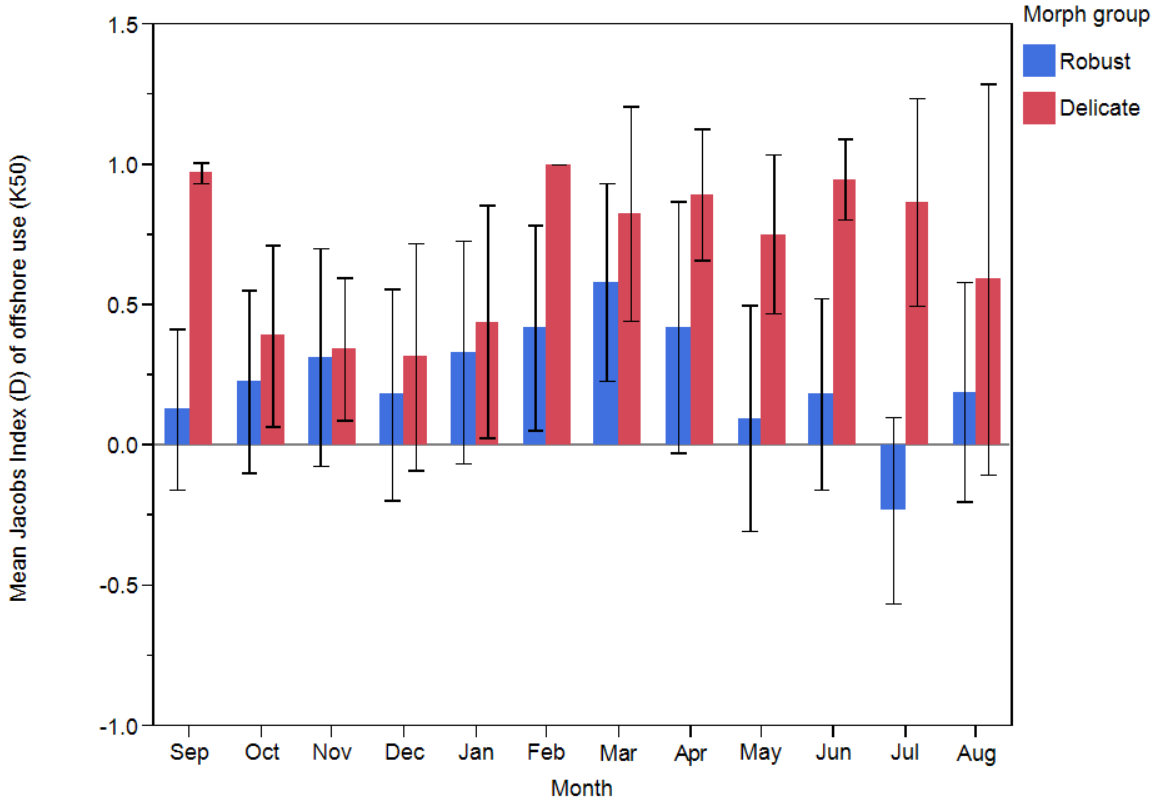


Figure 5-27: Monthly mean values of Jacobs selectivity index D, for the offshore habitat (77.4 %) of Lake Ellasjøen, Bear Island (see 5.2.2 Bathymetry and zonation of Lake Ellasjøen). D varies from -1 (strong avoidance) to +1 (strong preference), and values close to zero indicate that the habitat is used proportional to its availability. Error bars represent the 95 % confidence limits of the means, if 0 was not included within the range of confidence limits, the use of the habitat type was considered not random but the habitat was either favoured or avoided ($p < 0.05$). Habitat use was calculated from K50 estimates of home range, individual n varies for each month; values are stated in Table 5-16. Months are listed from September 2009 – August 2010. Bars are coloured according to the morphology group of the sampled Arctic charr (Robust; blue, Delicate; red).

6 Discussion

6.1 A unique data set

This study is amongst the first to study the fine-scale, spatial distribution and activity of polymorphic organisms in sympatry within a natural setting. The application of a novel, autonomous method of passive data collection derived hourly movements of the sampled population over the near-complete habitat range, for a full year.

This study set out to investigate the year-round strategies of a high-latitude population of Arctic charr; explicitly to elucidate the specific behavioural adaptations as a result of the energetic limitations imposed by residing in the Arctic. Deployment of an autonomous method of acoustic telemetry (VPS) derived an activity metric (fish speed) and spatial distribution (core and excursive home range area), from which the study aims could be investigated. A further aim was to reveal whether ecophenotypic variation occurred in the Arctic charr population of Lake Ellasjøen, and if this influenced spatial behaviour. Meristic analysis was utilised to distinguish between four putative morphs within the sampled population. Of the four Arctic charr morphotypes identified, fine scale positioning analyses and activity metrics were calculated for two, identified as Robust and Delicate forms. Significant temporal and spatial patterns of divergence were exhibited between the two morphotypes. Habitat use revealed that each morph tended to occupy a discrete habitat niche (though with overlap at times), over the entire year-long study. The activity metrics disclosed different strategies between phenotypes, which vary seasonally. These differences likely manifest as a result of resource-driven divergence, in a harsh, Arctic environment and are considered in section 6.2.

Biotelemetry methods, employing information acquisition from an animal-borne transmitter, have a long history of application in fish behaviour research (Lucas and Baras 2000, Cooke et al. 2013) and allow data to be collected on an individual scale, due to the tagging of individual fish. Yet to date, no study has applied these methods continuously and autonomously over a complete annual cycle (including under ice) and in such a remote, inaccessible location i.e. completely unattended over the duration of data collection. Using this method extensive positional data was derived, from which hourly movements of the sampled population were mapped in three dimensions over a complete year within an Arctic lake.

6.2 Niche separation between phenotypes -ecological significance of polymorphism

The meristic analysis used in this study distinguished four morphs of Lake Ellasjøen Arctic charr based on the diameter of the eye, pelvic fin length and head depth, as well as conspicuous differences in size and colouration, albeit based on smaller samples than ideal for such analyses. In a review of polymorphism in Arctic charr, Jonsson and Jonsson (2001) state that one to four sympatric morphs are exhibited in postglacial lakes. Of these one or two are epibenthic zoobenthos feeders (one small form, one large form), one is a limnetic planktivore and one is a piscivorous form, with phenotypic differences in sympatric forms of Arctic charr linked to divergence in feeding ecology (Adams et al. 1998, Knudsen et al. 2006). In fishes a larger eye is related to acuity for detecting small prey under poor light conditions (Holling 1959), the paired pelvic fins are associated with a passive, stabilising function in locomotion (Standen 2008) and a slender, hydrodynamic body shape, will reduce swimming cost (Boily and Magnan 2002, Ohlberger et al. 2006). Body size influences diet, with larger fish able to handle a larger range of prey sizes (Wootton 1998).

Accordingly, the large Robust morph charr from the current study, with their small eye, long pelvic fins and broad head shape, characterise this morph as littoral dwelling, with a generalist piscivorous and/or epibenthic diet (Sandlund et al. 1992, Hammar 2000). The smaller Delicate morph express the phenotype of a pelagic, zooplankton feeding fish, with large eye and slender head and body shape (Sandlund et al. 1992, Guenard et al. 2010). Although diet analyses were not carried out in this study due to limited field time, fin tissue samples have been taken which would enable dietary comparisons to be made by stable isotope analyses of carbon and nitrogen (Grey 2001, Rubenstein and Hobson 2004), but were beyond the scope of this study. The small size of maturation, large eye, sub-terminal mouth position and parr markings of the Dwarf maturing morph, are archetypal of ‘dwarf’, epibenthic feeding charr (e.g. Hindar and Jonsson 1982, Sandlund et al. 1992). The small size, combined with an absence of released gametes at processing depicts the group of charr defined as Other as a juvenile grouping, likely feeding upon epibenthos (Johnson 1980, Byström et al. 2004). Therefore, according to these distinctions the Ellasjøen charr population is likely composed of three sympatric morphotypes; a littoral piscivorous/epibenthic (Robust) morph, a limnetic planktivorous (Delicate) morph and a profundal, epibenthic (Dwarf maturing) morph, with phenotype manifestation indicative of feeding specialisation.

In their initial investigation of Bear Island charr, Klemetsen et al. (1985) identified only two modes of Arctic charr in Ellasjøen based on length distributions; a large mode (30 – 40 cm) and a small

mode (15 – 20 cm); both of which were sexually ripe at the time of sampling (August 1977 – 78) with bottom-set gill nets. These two modes are likely those described as Robust and Dwarf maturing morphs respectively within the scope of this study. Klemetsen et al. (1985) described a bi-modal length-frequency catch distribution, attributing this to the two modes they identified from bottom-set gill nets, however they appear to disregard, the non-sexually ripe fish caught in the floating, pelagic-set gill nets (Figure 3-3), which if included indicate a tri-modal population distribution. These non-ripe, pelagic caught fish (20 – 30 cm) are most likely identified as Delicate morph fish within this investigation. The application of meristics in this study has facilitated identification of a distinct phenotype, previously unrecognised within the population of Lake Ellasjøen and better characterised other phenotypes in terms of morphological traits. Finstad and Berg (2004) emphasise the importance of methodological verification when obtaining population measures by passive sampling gear. They observed that Arctic charr of intermediate size (15 – 30 cm), lacking in gillnet samples, were often present within populations (verified by electric fishing). The three morphs of Arctic charr identified in Lake Ellasjøen are discrete according to phenotype and likely in existence over at least 31 years (1978 – 2009).

Morphological diversity in Arctic charr is thought to be adaptive and differences in phenotype and morphology are often linked to resource partitioning in feeding ecology (Adams et al. 1998, Knudsen et al. 2006), with intermediate forms having a reduced ability to exploit available resources than specialised forms (Jonsson and Jonsson 2001, Klemetsen et al. 2003b, Finstad et al. 2006, Knudsen et al. 2006). Polymorphic populations of Arctic charr tend to follow patterns of morphological divergence along ecological gradients that correlate with the number and availability of habitats and food resources in the lake (Gíslason et al. 1999). In many lakes, including Lake Ellasjøen (Klemetsen et al. 1985, Evenset et al. 2004), discrete limnetic, littoral and profundal habitats are available and specialised morphotypes associated with these habitats coexist.

Resource partitioning (in terms of habitat use) was clearly defined between the Robust and Delicate morphs in Lake Ellasjøen. Robust charr utilised the littoral zone significantly more than the Delicate morph, whereas Delicate fish, exhibited limited littoral use and significant selection for limnetic, open water habitat (offshore zone). As generalists, trophic polymorphism of Arctic charr has been described in numerous examples (e.g. Adams et al. 1998, Guiguer et al. 2002, Klemetsen et al. 2006, Knudsen et al. 2011). Stable isotope studies of feeding patterns show that this intraspecific niche separation has the effect of lowering resource competition (Power et al. 2002, Helland et al. 2011). For example, in Thingvallavatn, the planktivorous Arctic charr morph fed extensively on zooplankton in open water, whereas the piscivorous form preyed in littoral areas (Sandlund et al. 1992). The vertical distribution of Lake Ellasjøen Arctic charr revealed that

Robust and Delicate morphs maintained discrete vertical niches year-round. This was most distinct directly after ice break, when Delicate fish moved into deeper water, close to the lake bed and Robust fish were at shallow depths, exclusively within the littoral zone. This is most probably a seasonal response to food availability, with fry hatching in the littoral (Johnson 1980) and a peak of zooplankton in the water column and emerging chironomids in the epibenthos (Primicerio 2000, Klemetsen et al. 2003b, Mousavi and Amundsen 2012). Prior observations have shown that separation between Arctic charr phenotypes breaks-down when food is abundant (Jonsson and Jonsson 2001), yet this is clearly not the case in this instance.

The extent of individual habitat use on fine spatial and temporal scales has not been demonstrated for Arctic charr in this manner previously. This has only been possible by utilising a passively deployed method of autonomous data collection. Prior investigations of sympatric fish populations have often utilised gill-netting and inspection of stomach contents to determine habitat selection and diet (e.g. Klemetsen et al. 2003b, Svenning et al. 2007). The use of terminal methods (i.e. that involve death of the animal) is advantageous in that, stomach content, fullness and associated parasitic fauna can be determined, as well as age, sex and stage of sexual maturity. However Berg et al. (2010) warn against the use of test fishing in remote polymorphic Arctic lakes, as limited knowledge is available on the productivity and composition of these isolated systems. As a result sustainable harvest quotas cannot be derived, with large piscivorous fish particularly sensitive due to their over-representation in gill net catches due to greater fishing pressure, long-life span and late maturation. For example, an annual surveillance programme conducted in a small Arctic lake (Lake Trestikkelen) removed the majority of large charr individuals from the population (Finstad and Berg 2004). More recently, stable isotope methods have been utilised to determine trophic level as a proxy for habitat use in fish (Power et al. 2005, Gallagher and Dick 2010, Eloranta et al. 2013, Woods et al. 2013). These methods when coupled with terminal fishing have the ability to elucidate persistent foraging specialisms. Knudsen et al. (2011), state that resource use identified by measures that integrate over very short temporal periods (stomach content) showed clear evidence of persistent foraging specialism over much longer temporal periods, when used in combination with muscle stable isotope signatures, which integrate over months (Perga and Gerdeaux 2005) and parasite fauna which integrates over years (Knudsen et al. 1997). However, neither method is capable of deriving activity or behavioural responses, and currently there is little known about possible physiological variation amongst morphs (Jonsson and Jonsson 2001).

Fish activity, measured as size-corrected metric of fish speed, and space use, calculated as home range area (both core and excursive usage) were compared for both the Robust and Delicate phenotypes. Delicate charr used larger home range areas and were more active, exhibiting higher

swimming speeds than Robust charr. Only during June, July and August were Robust charr more active than Delicate and their habitat usage almost exclusively littoral. This period of intense activity undertaken by Robust charr likely corresponds to a peak in feeding on littoral prey resources i.e. young-of year Arctic charr and zoobenthos. Young-of-year Arctic charr probably form an important component of the diet for the Robust morph, with young-of-year habitat use restricted to the near-shore, littoral habitat during summer (Byström et al. 2004). The profitability of this energy-rich food resource, coupled with a reduction of metabolic rates in a period of reduced rations (i.e. winter), may account for the annual variation in activity for this morph. Similar patterns of activity are known among fish, and supports an energy conservation strategy in periods of resource scarcity (Wieser et al. 1992, O'Connor et al. 2000). Conversely invertebrate prey is a lower resource level than piscivory (Finstad et al. 2006), so the capacity for energy storage during periods of plentiful resources (summer in Arctic lakes) will be limited for Delicate morph fish, thus greater feeding activity over a wider seasonal period might occur. However, smaller individuals can often sustain themselves on lower resource levels than larger ones because of the size scaling of metabolic demands (Byström et al. 2006), thereby the smaller Delicate morph may be able to remain more active than Robust over a more sustained period.

Further evidence of disparity in metabolic capacity and feeding strategy may be evident when considering the effect of temperature on fish activity. A clear effect of water temperature was shown on the activity levels of Robust morph fish, with increasing water temperature, associated with larger home range areas and faster swimming speeds at shallower water depths. An effect of water temperature was also indicated on the Delicate morph activity levels, but to a much lesser extent than for Robust morph fish. As Robust and Delicate morphs exploit environments with different feeding opportunities, temperature and light conditions, it could be expected that variation in oxygen metabolism and growth efficiencies in relation to water temperature would be observed (Larsson and Berglund 2005). However, at present limited investigations have been conducted, and as yet no such variation has previously been reported (Elliott and Baroudy 1995, Larsson and Berglund 2005). With this evidence presented it is highly likely that different morphotypes of Arctic charr exhibit local adaptations in physiological traits, with polymorphism in Arctic charr resulting in variations of growth conditions between different habitats (Finstad et al. 2006).

Limited agonistic and aggressive behaviour is considered a specific adaptation of salmonids inhabiting high-latitudes, as it allows energy to be preserved for somatic and gonadal purposes (Huusko et al. 2007). This likely contributes to differential habitat use over large parts of the year by Lake Ellasjøen morphotypes. Even during winter ice-cover, when food availability and feeding activity was likely at a minimum (Klemetsen et al. 2003b, Mousavi and Amundsen 2012) Robust

and Delicate fish remained spatially separated. Under ice, both groups maintained an equal, stable depth of about 12 m but Delicate fish occupied more open water i.e. they were further from the lake bed and further from the lake edge than Robust morph fish. Based on gape size limitations, the maximum prey length of cannibalistic Arctic charr have been estimated to be approximately 40 % of the length of the predator (Damsgård 1995). Therefore a Robust morph charr at a maximum size of 50 cm is able to feed only on fish smaller than approximately 20 cm. Thus, Delicate Lake Ellasjøen fish are too large, at the sizes tagged to be predated upon by Robust morph charr of the size tagged. Consequently, the high degree of separation between Robust and Delicate morphs is unlikely a predator-prey response, but probably a means of preserving energy over-winter.

Thirteen of the Robust morph fish from Lake Ellasjøen were exhibiting the red/orange spawning colouration, typical of Arctic charr (Johnson 1980) and exhibited secondary sexual morphological features (e.g. kype, albeit small, in male) at the time of capture and tagging in August 2009. Most often, but not always (e.g. Windermere, England, Corrigan et al. 2011), Arctic charr spawn in the autumn in order to coincide with availability of resources for the first feeding of juveniles in the following spring (Power et al. 2008). Consequently, Robust charr likely spawned during September-October in Lake Ellasjøen, as processing was undertaken in late August. It has been observed that Arctic charr populations at high-latitudes tend not to spawn every year (Johnson 1980), hence those Robust morph fish not exhibiting spawning colouration, probably did not spawn during this study. The Dwarf maturing Lake Ellasjøen charr were releasing gametes at the time of processing, consequently spawning of these fish probably occurred shortly after processing also. Delicate morph fish did not exhibit external signs of spawning colouration nor were they releasing gametes, therefore it cannot be determined if this morph was mature. It is possible that this morph spawns in late autumn, as observed in Thingvallavatn, where the four morphs segregate with respect to spawning time and habitat (Sandlund et al. 1992). There, the large benthivorous charr spawn earliest in the season, from late July to early August. Small benthivorous charr spawned in the shallow littoral zone (0 – 10 m) from early September until November. The planktivorous and piscivorous charr both spawned from mid-September to mid-October, on stony littoral substrata around the lake. Sandlund et al. (1992) also noted however, that ripe piscivorous charr were observed from late August, while spawning planktivorous charr were also observed in November. This suggests that although the planktivorous and piscivorous forms spawned concurrently in Thingvallavatn, piscivorous charr matured earlier in the season. According to the spatial distribution data derived for Lake Ellasjøen, the only months in which Delicate morph charr utilised the littoral zone more than Robust was during October and November, where this morph occupied significantly shallower depths than during other months. It is therefore a possibility that the Delicate morph fish were utilising the littoral region for

spawning in this period. Alternatively, they could have used deep-water gravel substrate as found for example, for Windermere, England spring-spawning charr (Frost 1977, Corrigan et al. 2011). However within the scope of this study, maturity of Delicate morph fish cannot be determined.

Most teleost fishes have indeterminate and plastic growth, retaining the potential for growth throughout life, and with growth often determined by environment. Hence ontogenetic niche shifts in order to compensate for decreasing foraging gain is common in Arctic charr populations (Forseth et al. 1994, Finstad et al. 2006). However, once sexual maturity has been attained, It is usual that phenotype is fixed in adult Arctic charr (Jonsson and Jonsson 2001). Therefore both Robust and Dwarf maturing morphs, can be defined as ecophenotypes; i.e. they exhibit distinct trophic morphology and behaviour, which is unlikely to undergo further ontogenetic development (Adams et al. 1998). Delicate morph fish did not exhibit external signs of spawning colouration nor were they releasing gametes, therefore it cannot be ascertained with full certainty whether this morph was immature, and yet to develop into the piscivorous Robust morph i.e. ontogenetic polymorphism according to Adams et al. (1998). However, the Delicate morph charr exhibit both the morphology and niche distinction typical of a planktivorous, pelagic morph of Arctic charr, with mostly year-round resource partitioning with a littoral-generalist ecophenotype. The meristic analysis discriminates between the Robust and Delicate morphs clearly, between similar sized fish, with transition from one shape to another during an individual's lifetime seeming improbable (Adams et al. 2003).

As the sole fish occupant of many high-latitude and Arctic lakes, Arctic charr are able to occupy different habitat types that inter-specific resource competition would normally prevent (Jonsson and Jonsson 2001). The development of individuals into specific morphotypes is probably a conditional strategy whereby individual development is determined by the size of the individual at a specific ontogeny and influenced by a combination of ecological, environmental and /or genetic factors (Jonsson and Jonsson 2001, Reist et al. 2012). The resource driven polymorphism exhibited in Lake Ellasjøen Arctic charr likely manifests as a result of reducing intra-specific competition. This is characteristic of simple fish communities and broadens the range of habitat and food resource available in often low-productivity, high-latitude aquatic environments (Hindar and Jonsson 1982, Skulason and Smith 1995). Ecological speciation can occur when divergent natural selection between populations that exploit distinct ecological niches leads to the evolution of reproductive isolation (Bolnick and Fitzpatrick 2007, Corrigan et al. 2011). An example of incipient speciation has been identified between profundal and littoral reproductively isolated phenotypes of Arctic charr, in Fjellfrøsvatn, Norway (Knudsen et al. 2006). Divergence according to this process often varies continually, even if the endpoint is the development of a discontinuity (Smith and Skúlason 1996, Skúlason et al. 1999, Johannesson 2001). The occurrence

of allochrony (temporal spawning variation), with respect to reproductive isolation between Lake Ellasjøen morphotypes has not been investigated; neither has genetic analysis been undertaken. Without this knowledge, it is not possible to further infer the degree of ecological speciation within the population. According to the four stage process of ecological speciation as proposed by Skúlason et al. (1999), Robust and Delicate morphs of Ellasjøen Arctic charr have undergone the first two stages. That is, alternative, adaptive traits are expressed in individuals (stage one) and behavioural phenotypes show discrete alternatives within a population (stage two), often with behavioural specialisation resulting in modification of morphological traits through phenotypic plasticity in anatomical traits (Skúlason et al. 1999). Once this stage is reached, reproductive segregation may occur through differential habitat use or through mate selection by different phenotypic variants (stage three). As a consequence, different forms are exposed to different selection pressures and hence genetic fixing of traits can occur (stage four). However, the mechanisms by which phenotypic and genetic divergence may occur between sympatric polymorphic populations have been widely discussed but are still not understood (Jonsson and Jonsson 2001, Adams and Huntingford 2004, Corrigan et al. 2011).

The modes of differentiation and the constraints of classification provide the basis for the 'charr problem' (Jonsson and Jonsson 2001, Reist et al. 2012). That is, should the diverse forms of Arctic charr be each recognised as a distinct species, or is it more appropriate to simply refer to the many morphs as a single taxonomic entity? Resolution is likely fundamental for conserving biodiversity and for further insight of the drivers and maintenance of polymorphism in this species.

6.3 Temporal variations in habitat use and activity: a response to the Arctic year

Few studies have been conducted during all seasons in Arctic, aquatic systems, with the majority of research focusing on the ice-free, summer period despite winter being the dominant season (Reist et al. 2006a, Salonen et al. 2009, Shuter et al. 2012). As a result, there has been limited research on the seasonal patterns of habitat use and behaviour of fishes, including Arctic charr. In Ellasjøen, there was a clear seasonal effect in the distribution and behaviour of both Robust and Delicate Arctic charr morphs. Average fish speed (for both morphs) was reduced by more than 50 % under ice cover when compared to open water, and home range area was significantly smaller during February and March than for the remainder of the year. Thus, the hypothesis that Arctic

charr activity and home range size during winter ice cover would be significantly smaller than during autumn, spring and summer can be accepted.

Habitat use of Lake Ellasjøen Arctic charr also varied according to season, with both the littoral dwelling Robust morph and the limnetic Delicate morph inhabiting offshore water under ice, with greatest use of the offshore zone during February and March. A clear effect of water temperature was shown on the activity rates of Lake Ellasjøen Arctic charr, with increasing water temperature, resulting in larger home range areas and faster swimming speeds. Under ice, both morphotypes maintained the same mean depth of 12 metres, albeit in different lake habitats (Delicate occupied more offshore waters than Robust), thus both morphotypes were exposed to the same ambient water temperature. Water temperature was measured at three different depths throughout the study; 3, 25 and 31 metres, with limited stratification of water temperature observed during summer but a small inverse temperature gradient occurring over winter. Stratification albeit less than 1 °C occurred between 3 and 25 m under-ice, with virtually no difference in temperature recorded between 25 and 31 m. It is probable therefore, that both morphs predominantly resided at the depth of maximum ambient temperature occurring due to stratification under ice, at a temperature closest, but still below the thermal preferendum for this species (4.6 °C, Larsson 2005).

Seasonal changes in ecosystem processes at the high-latitudes are often driven by the extreme variations in solar photoperiod. Yet, limited research has been conducted especially *in-situ*, in aquatic systems during all phases of the solar cycle, principally, the phase of 24- hour darkness (polar night) and the short but dynamic spring and autumn seasons are absent from the literature. In fish, the ability to visually detect prey can be severely limited during the extended periods of polar darkness (Amundsen and Knudsen 2009, Elliott 2011). Nonetheless, Arctic charr are capable of preying upon macro-invertebrates at light levels equivalent to star-lit night sky (0.001 lux) and of grazing bottom sediment for macro-invertebrates in complete darkness (Elliott 2011). This indicates that Arctic charr are capable of feeding in low-light, over-winter conditions, which may account for the continued Arctic charr activity recorded over winter in Lake Ellasjøen, albeit at a much reduced level. However, no structural differences between the retinal photoreceptors of Arctic charr from deep waters (40 m) and shallow waters (< 20 m) have been found (Elliott 2011), and a high incidence of mud in the stomachs of Arctic charr has also been observed during winter (Svenning et al. 2007). This may indicate that fish browse bottom sediments in pursuit of chironomid larvae, the dominant prey during the polar winter by use of tactile and chemical senses (Svenning et al. 2007). In Atlantic salmon (*Salmo salar*), increasing photoperiod has an immediate, stimulatory effect on growth (Hansen et al. 1992), while exposure to a decrease in photoperiod has a depressing effect on growth (Skilbrei et al. 1997). By contrast, in a study

conducted on anadromous Arctic charr a change from short day to continuous light in late winter did not result in an immediate growth increase (Bottengård and Jørgensen 2008) and when kept at constant ambient temperature (4 °C), marked annual rhythms of appetite and growth were seen in laboratory held Arctic charr when natural light conditions were simulated (Tveiten et al. 1996). Thus, growth is not as prone to acute photo-stimulation in Arctic charr as seen in other fish. This may indicate that there is a stronger endogenous component in the seasonal regulation of appetite and growth in the high-latitude Arctic charr than in more temperate species and may explain why a limited effect of photoperiod (duration of day/night) was observed on fish speed and home range area of Lake Ellasjøen charr.

The seasonal timing of life-history events is often under strong natural selection as fitness depends on forecasting the optimal timing of season specific activities, such as migration and reproduction, to exploit favourable conditions. Photoperiod is a predictable environmental cue that organisms use to respond to seasonally varying conditions (Quinn and Adams 1996). This view is supported by a previous study in which it was concluded that the seasonal rhythms of appetite and growth in anadromous Arctic charr follow an endogenous rhythm and that the circa-annual clock runs with a periodicity close to 12 months (Sæther et al. 1996). It is therefore likely that the temporal changes in activity and behaviour observed in Lake Ellasjøen are a seasonally regulated process on which temperature and photoperiod only partly influence. Evidence of this in Lake Ellasjøen is shown in the diel pattern of fish activity observed during the months of polar night (when diel periodicity is absent); during which sub-surface light levels under lake ice and snow cover must be minimal (but unfortunately not measured in this study). Yet, conversely no diel periodicity in activity was exhibited during the months of continual solar radiation i.e. polar day.

One explanation is that these observations may be a response to endogenous circadian rhythms in the production of melatonin. The daily molecular oscillator, known as the circadian clock, senses changes in the photoperiod and mediates a diverse number of photoperiodic responses such as flowering time in plants (Yano et al. 2000) and hormone secretion in mammals (Goldman 2001). In vertebrates the prevailing photoperiod is transformed into neuroendocrine signals which include the pineal hormone melatonin (Reiter 1993). The production of melatonin mirrors the light-dark cycle with high production in the hours of darkness and low production in daylight. In this way concentrations of melatonin impart temporal information that is believed to influence many physiological processes, including those linked to seasonal events (Reiter 1993). However, in terrestrial high-latitude animals such as Svalbard ptarmigan (*Lagopus mutus hyperboreus*) (Reierth et al. 1999) and Svalbard reindeer (*Rangifer tarandus tarandus*) (van Oort et al. 2005) production of melatonin levels remain low and non-rhythmic during 24-hour daylight. In Svalbard

ptarmigan and reindeer this coincides with a period of high activity levels and feeding, mirroring food availability during the Arctic summer. Similarly, the non-diel activity observed during summer in Lake Ellasjøen Arctic charr could be a strategic adaptation of polar habitation, in response to the extreme seasonal fluctuations in food availability. Strand et al. (2008), described the diel plasma melatonin profiles at different times of the year (June, September, February and April) in a population of high-latitude Arctic charr held in their natural (lacustrine) environment, under prevailing *in-situ* irradiance. In June melatonin was low throughout the 24 hour cycle; despite there being a sub-surface difference in irradiance between night and day. During June the irradiance at night (5.9×10^{-2} W/m^2) probably remained above the threshold for suppression of melatonin production (Strand et al. 2008). In September, February and April a diel profile in melatonin was seen in the charr, which reflected the ambient light conditions above the water surface, even during February when there were minimal changes in irradiance between midday (8.0×10^{-3} W/m^2) and midnight (3.0×10^{-3} W/m^2), at the water depth at which the fish were held (10 m). The irradiance threshold for suppression of melatonin production has been shown to be very low in Atlantic salmon (Migaud et al. 2006), therefore Strand et al. (2008), suggest that the irradiance levels measured at midday in February remain above the threshold for suppresion of melatonin production in Arctic charr, thus diel periodicty of melatonin production still occurred. These results demonstrate that there are diel and seasonal rhythms of melatonin production in Arctic charr and that these rhythms appear to reflect the seasonal changes in photoperiod observed above the water/ice surface. Such circadian rhythms likely contribute towards the seasonal responses exhibited in Lake Ellasjøen Arctic charr, with these fish appearing to keep track of time even under the extreme conditions of high-latitudes during winter, when lakes are covered by thick ice and snow.

A diel change in depth use, although not significantly so, was observed during the months of September (Delicate morph only), February and March. A migration to greater depth during day corresponded to an increase in fish speed, with greatest speeds recorded at dawn and dusk. Such behaviour is likely an indicator of diel vertical migration (DVM), a behavioural strategy commonly observed in many aquatic organisms (Steinhart and Wurtsbaugh 1999, Jurvelius and Marjomaki 2008, Gjelland et al. 2009). The usual pattern of DVM is to stay in the deeper parts of the lake during the day, ascend into shallower layers at dusk, reside there during the night, and descend back to deeper layers at dawn (Johnson and Mehner 2011, Gutowsky et al. 2013). There are three main explanations for the evolution of this strategy; bioenergetics efficiency, feeding opportunities and predator avoidance (Mehner 2012). In Lake Ellasjøen fish, the likely triggers are bioenergetic strategy and feeding opportunities, or a combination of the two, with fish moving into colder, deeper water to feed on epibenthos and/or deeper-water plankton, during maximum irradiance. The key trigger of DVM in freshwater fishes is thought to be the diel cycle of

illumination (Mehner 2012). There is a broad consensus for several fish genera that the decline in illumination at dusk stimulates ascent, whereas the increasing illumination at dawn induces descent within the water column (Mehner 2012). Support for the triggering effect of light cycles has been gained by studies at high-latitudes in summer and on fish under ice. In these examples migrations only occurred where there were diel phases of rapid changes in illumination but stopped when the difference between day and night was low (Kahilainen et al. 2004). This pattern was mirrored in Lake Ellasjøen, with DVM only visible during autumn and spring, when photoperiod was most dynamic.

Variations in the strength of ecological interactions between seasons in Arctic limnology have received little attention, with the winter situation often neglected when studying behaviour (Helland et al. 2011). Yet, the seasonal trends in Lake Ellasjøen reveal that during each season, behaviour of Arctic charr can be significant and complex. A distinct annual cycle with seasonal patterns in habitat use and activity was realised in two morphs of Lake Ellasjøen charr. Changes in temperature, snow, ice-cover, and nutrient availability exert major influences on the biological dynamics in the Arctic, and extensive ecological consequences of recent warming-related trends in these parameters will affect the ecology of Arctic lakes (Rouse et al. 1997). Arctic charr are the most northerly distributed freshwater fish and hence exhibit a suite of adaptations, for inhabiting these harsh aquatic environs (Power 2002). Climate change will affect Arctic charr by direct effects of temperature change together with the secondary influences of the resulting environment and food source changes. These changes will affect both the individual physiological and behavioural processes of Arctic charr and key characteristics of their habitat (Power et al. 2008).

6.4 Evaluation of methodologies

The use of passive deployed acoustic telemetry has become an increasingly common approach to answering questions on animals' habitat use, activity and life-history strategy in aquatic systems. This study used the Vemco VR2W Positioning System (VPS), one such example of a passively-deployed, acoustic telemetry positioning array. This study was the first to deploy this methodology in the Arctic. As shown, the system can be deployed during the accessible summer months and left unattended for an extended period, making such systems an ideal research tool for difficult to access, aquatic systems. Lake Ellasjøen is ice-covered for at least six months of the year and is situated on a remote island in the Barents Sea. Yet, this method effectively produced continual temporal and three-dimensional spatial data of the tagged individuals, during the

deployment time frame, over the near-complete habitat range of the lake; making the VPS a powerful tool for fisheries researchers. The data derived from the Lake Ellasjøen VPS was extensive and constitutes the longest-deployed, unattended system to date (Andrews et al. 2011).

The use of VPS is increasing, with a number of studies utilising this method emerging (Espinoza et al. 2011a, Espinoza et al. 2011b, Dean et al. 2012, Furey et al. 2013). However, limited research has been published which assesses the validity, both spatially and temporally of the positions derived by this system. Those studies that do filter the positional data, filter according to HPE, with an HPE threshold set between 10 and 20 (Andrews et al. 2011, Espinoza et al. 2011a, Espinoza et al. 2011b, Dean et al. 2012, Furey et al. 2013). Transparent dissemination of the algorithm information, underlying the assumption of HPE, for which there are no associated units, is required for this metric to be used transparently. Until Vemco disclose this information, alternate methods must be utilised, in order to elucidate erroneous tag positions. Thus, considerable effort was undertaken during this study in order to define an alternative process for identifying and removal of poor quality positional data, on a daily temporal scale (see 5.4.2 Pre-treatment of fish positional data).

The VPS generates an extensive dataset (a total of 3,679,720 independent tag detections by all loggers combined during this study); therefore comprehensive interrogation of the data, as well an appropriate method of data management is required by the user. To utilise all VPS derived positions would create erroneous values of fish activity and spatial distribution, for example, 2,710 fish positions were recorded as outside the lake boundary i.e. on land, with one fish position recorded 245 metres (straight line distance) outside of the lake boundary. According to the principle of hyperbolic positioning (by which positions are derived, see 4.3.1 Theory of operation), those positions outside the boundary of the receiver array will be of poorer quality, as positioning is less accurate and the tag is more likely to be detected by fewer receivers. Hence, position accuracy is not consistent throughout Lake Ellasjøen. Fish positions located around the lake edge (littoral zone) are more likely to be less accurate than those positions mid-lake (offshore), because a number of the littoral positions lie outside of the receiver array. This is shown by analysing the littoral-located stationary sync tag positions, which had significantly larger 2DRMS radii (mean 26.99; S.D. 32.18 m) than those sync tags located offshore (mean 7.51; S.D. 2.78 m). The sync tag located in the south west corner of the littoral zone in Lake Ellasjøen (R01) had a considerably larger 2DRMS radius (137.63 m), as the line of sight to this receiver was very poor due to its isolated, corner location (the neighbouring receiver R12 was not retrieved, thus the line of sight to this receiver was severely restricted). Hence fish positions in this area, were of poorer quality as shown by the higher density of erroneous fish positions removed in this area

(Figure 5-15). The 2DRMS radii of littoral-located sync tag positions are considerably improved if this sync tag is not included (mean 18.48; S.D. 4.88 m). Similar findings were shown by Espinoza et al. (2011b), who recorded a mean positional accuracy of 5.12 (S.D. 4.11) m of fish tags outside the receiver array and 2.13 (S.D. 1.31) m inside the array (over a 1.6 hour deployment period). This is important to consider as the littoral area is narrow and comprises only 22 % of the total surface area of Lake Ellasjøen, yet forms an important habitat for lacustrine fish populations (Johnson 1980, Sandlund et al. 1992). This potential bias in position resolution for the offshore zone may account for the greater preference for offshore habitat observed by Lake Ellasjøen Arctic charr. However, both the frequency of sync tag detections and resulting positions derived show no significant difference in frequency between the littoral located sync tags and those sync tags in the offshore zone. The pre-treatment process of erroneous positional data did remove a higher percentage of littoral (11.07 % of the total) than offshore positions (5.60 % of the total), however the overall distribution of total fish positions was altered by -0.73 % in the littoral zone and 1.95 % in the offshore zone as a result of the data cleaning, this was considered minor and no post-correction of positional frequency/habitat availability was conducted.

In addition to spatial variation in position quality, temporal variation in position quality was observed in Lake Ellasjøen. Periods of noise, such as high winds, ice formation/breakup and changes in temperature and salinity can affect the efficiency of acoustic telemetry (Heupel et al. 2006). For example a seven day gap in both sync and fish tag positions was observed at the time of ice breakup, this likely occurred due to the physical movement of the receivers trapped and dragged by moving ice. Therefore a daily mean value of HPEm for each sync tag was calculated, to give a daily value of ± error in detection in metres. HPEm is a valuable metric because it shows how sync tag location error can change over time due to environmental conditions and between receiver locations. Thus all positions formed during periods (daily) and within a locality (sync tag) of poor detection quality could be identified and removed from further analysis. In addition, individual fish tracks were inspected to observe; a) the duration of positional data, b) gaps in positional data and c) stationary positional data relative to lake depth, for each tagged individual. From this, the spatial validity of each fish track could be assessed on a temporal scale for the study duration. According to these tracks four individuals became stationary when compared to the prior tracking data of the individual. These fish were presumed dead and all stationary positions were removed from further analysis. However these now stationary or sentinel individuals were used to assess the positional accuracy of fish tags for the reminder of the study. One fish, presumably as a result of the capture and tagging procedure died after only 17 days, thus the horizontal distribution (2DRMS: 5.54 m) of this fish tag was determined over a 335 day period, thereby deriving a measure of fish position accuracy in this VPS deployment. However the

use of stationary fish tags are likely to be less accurate than fixed sentinel tags for testing positional error, as the fish may be moved around by moving water or other animals.

For five of the tagged Arctic charr an extended 'gap' in detection data occurred; positional data disappeared at the time of ice break (25th June) with detections returning 55 – 64 consecutive days later (16 – 21 July). There are two explanations for these gaps, the first is that the fish remained in the lake but were located in an area of non-detection. This could be in the southwest corner of the lake, or on the west side of the ridge on the southern edge of the lake (see Figure 4-4), where line of sight by VR2Ws is poor. Movement of the VR2Ws at the time of ice-break caused re-distribution of the receiver array, which probably reduced the detection coverage of Lake Ellasjøen (see Figure 5-7). The second explanation is that these fish left the lake and then returned. Anadromy in Arctic charr usually occurs at the time of ice-break up for a period of around six weeks (Rikardsen et al. 2000, Svenning and Gullestad 2002, Rikardsen et al. 2007). Yet Klemetsen et al. (1984), state that anadromy is physically prohibited with descent possible, but physical ascent impossible due to the steepness of the outlet stream. Complete anadromy is therefore unlikely, but Arctic charr do migrate within systems (Klemetsen et al. 2003a); at a time of flood due to ice/snow melt the outlet stream is likely to be of sufficient volume and flow to hold fish. The spatial tracks of these five individuals do not give any indication that this is what has occurred, i.e. they showed no physical track towards the outlet. However, a tag code repeat rate of every 80 minutes does mean that a fish could traverse a considerable length of the lake without being detected, particularly during a period of poor VPS detection, when probability of detection was low due to high levels of noise.

All consecutive locations (excluding those removed according to the pre-treatment process and where they occurred at an interval greater than two hours apart), were used to calculate individual fish displacement. Position fixing frequency may affect several aspects of swimming behaviour, such as estimating swimming speeds, activity rhythms and movement patterns. For example, Løkkeborg et al. (2002) found that for cod (*Gadus morha*), a position fix interval of two minutes resulted in an underestimate of speed by about 60 % in comparison to a cod tracked at intervals of every 17 seconds. The greater the sampling interval the greater the likelihood that the true track of the fish is not recorded and the swimming speed during all deviations from the straight line between consecutive locations is therefore underestimated. However, finer temporal scale increases autocorrelation and generates measurements in which random deviations result from 'noise' of imprecision in the tag location system. An incomplete resolution of distance travelled and hence fish speed has been derived from the VPS deployment in Ellasjøen. Activity levels were therefore likely to be seriously underestimated as the frequency of detections was approximately every 80 minutes, thus actual levels of swimming speeds and foraging activity

cannot be determined. The values presented are however a length adjusted metric for the temporal patterns of fish activity and all speed values were below the critical swimming speed of Arctic charr (0.51 m/s at 15 °C; fork length 170 mm (Beamish 1980), therefore all values were included.

Despite the inherent issues discussed with passive acoustic telemetry arrays, comparative studies have shown that positioning accuracy is comparable to manual (active) tracking methods of acoustic telemetry (Andrews et al. 2011, Espinoza et al. 2011b), and the temporal information derived from this method is advantageous over static, gill net sampling. For example, it was assumed that intermediate-sized Arctic charr exhibited low levels of activity, due to their under-representation in gill net catches (Finstad et al. 2000), yet the intermediate sized Delicate morph charr were overall, most active in Lake Ellasjøen. However, as most net-fishing is conducted during the shorter ice-free period, when the Robust morph were most active, large Arctic charr are likely over-represented in gill net catches. Therefore, this method can be a valuable tool for autonomous data collection, particularly if individual spatial and temporal information is required. However, an understanding of the system design and theory of the method should be known and sufficient interrogation of the data should be conducted before the derived positional information is utilised.

The application of meristic analysis was effective in discriminating between the four putative Arctic charr morphs sampled in Lake Ellasjøen. Similar techniques have been applied in numerous instances to determine phenotypic divergence in fishes (e.g. Reist 1985, Adams et al. 1998, Solem and Berg 2011). There are many approaches to size standardisation to correct size effects in morphological analyses and the method utilised has been criticised for not fully removing size information (Reist 1985). The use of image processing computer programmes to standardise the measurements taken, minimising human sampling error e.g. ImageJ (http://rsb.info.nih.gov/ij/), have also been used in similar studies. However a simple methodological approach was adopted, due to small sample sizes, particularly for the Dwarf maturing and Other Arctic charr morphs and also because fish length/body size is a key phenotypic trait, which should be considered when studying life-history and habitat use (Jonsson and Jonsson 2001).

6.5 Future research

This study, by application of a novel methodology has provided new insights into Arctic charr ecology in a remote, high Arctic lake, at a northerly extreme of this species' distribution. An obvious comparison would therefore be to apply similar methodologies to investigate the ecology

and behaviour of sympatric Arctic charr morphotypes at a southerly extreme of distribution. This could provide a reference in which to model potential ecological effects and interactions of speculated climate change effects. This would also provide insight into latitudinal effects as a potential driver in the processes of niche divergence and eventual speciation. Another possible comparative study would be to investigate an anadromous charr lifecycle system. In order to elucidate the effects of anadromy and the resulting responses of these fish to the Arctic year, and how sympatry with an anadromous morphotype affects the behaviour of those Arctic charr exhibiting facultative, lacustrine exclusivity.

Although identified as an ecophenotype of Lake Ellasjøen, no behavioural analysis was conducted for the Dwarf maturing charr (individual fish tracks are presented in Appendix III) as a sample of two individuals (T16 and T27) was deemed insufficient for comprehensive analysis . Such examples of dwarf-maturing forms have been shown to exhibit discrete habitat use (Klemetsen et al. 2006, Knudsen et al. 2007), spawning isolation (Sandlund et al. 1992, Klemetsen et al. 1997) and even speciation between sympatric Arctic charr morphs (Knudsen et al. 2006). It would therefore be of great interest to elucidate the seasonal behaviour and extent of niche divergence for this morph in Lake Ellasjøen. Additionally, to further understand and define the development of potential speciation between the Arctic charr phenotypes of Lake Ellasjøen as defined by Skúlason (1999), three factors should be addressed. The first is to determine if Delicate morph charr have reached maturity, thus defining this morph as a true ecophenotype according to Adams et al. (1998). Secondly to elucidate if reproductive segregation occurs between the Lake Ellasjøen ecophenotypes and if this occurs spatially, temporally or by mate selection according to phenotype. Thirdly, yet perhaps the first of these tasks to undertake, is to determine if the ecophenotypes of Lake Ellasjøen are genetically distinct. This would provide further insight into the mechanisms by which phenotypic and genetic divergence may occur between sympatric populations of Arctic charr, a process which has been much discussed but still not understood (Jonsson and Jonsson 2001, Adams and Huntingford 2004, Corrigan et al. 2011).

This study focused on the identification of life-history strategies and the ecological interactions and behaviour of Arctic charr. However, this could be significantly strengthened with improved knowledge on the physiological processes and drivers by which Arctic charr are both able to select and maintain these life-histories. For example, greater knowledge on the metabolic requirements of different charr morphotypes would give much insight into the seasonal distribution and activity of these fish and the differences identified. It is highly probable that the seasonal responses of these fish are also under some form of hormonal control, yet this theory has been little investigated. It would be of particular interest to observe if similar hormonal effects are observed

in southern populations of this species, where seasonal photoperiod and productivity is more regulated, or if this is a specific adaptation of those Arctic charr inhabiting high-latitudes.

In short, despite the extensive research that has been previously undertaken, there is still much to learn about this species and its environs. Rapid developments in research techniques and methodologies mean that the tools in which to answer key questions and overcome the logistical difficulties in studying the inhabitants of Arctic aquatic systems are increasingly available. Therefore, it seems pertinent to embrace this momentum in order to improve our understanding and to develop informed management strategies for this unique species as the sole fish inhabitant of high Arctic freshwater, particularly in light of potential climate change effects.

7 Conclusions

The findings of this study reveal that the year-round ecology of fish in Arctic freshwater systems can be complex, with seasonal behaviour more variable than previously perceived. Sympatric morphotypes of Arctic charr exhibiting discrete, phenotypic resource specialisations were defined. Spatial analyses revealed that each morphotype maintained a distinct habitat niche over much of the year-long study. Fish activity patterns inferred different life-history strategies between morphotypes; however similar behavioural responses to the Arctic annual cycle were exhibited in both morphs. These findings likely manifest as a result of resource-driven divergence, in a harsh, Arctic environment. The unique and extensive data derived reveal the utility of autonomous telemetry methods for increasing the understanding of behavioural ecology in poorly accessible and inhospitable environments.

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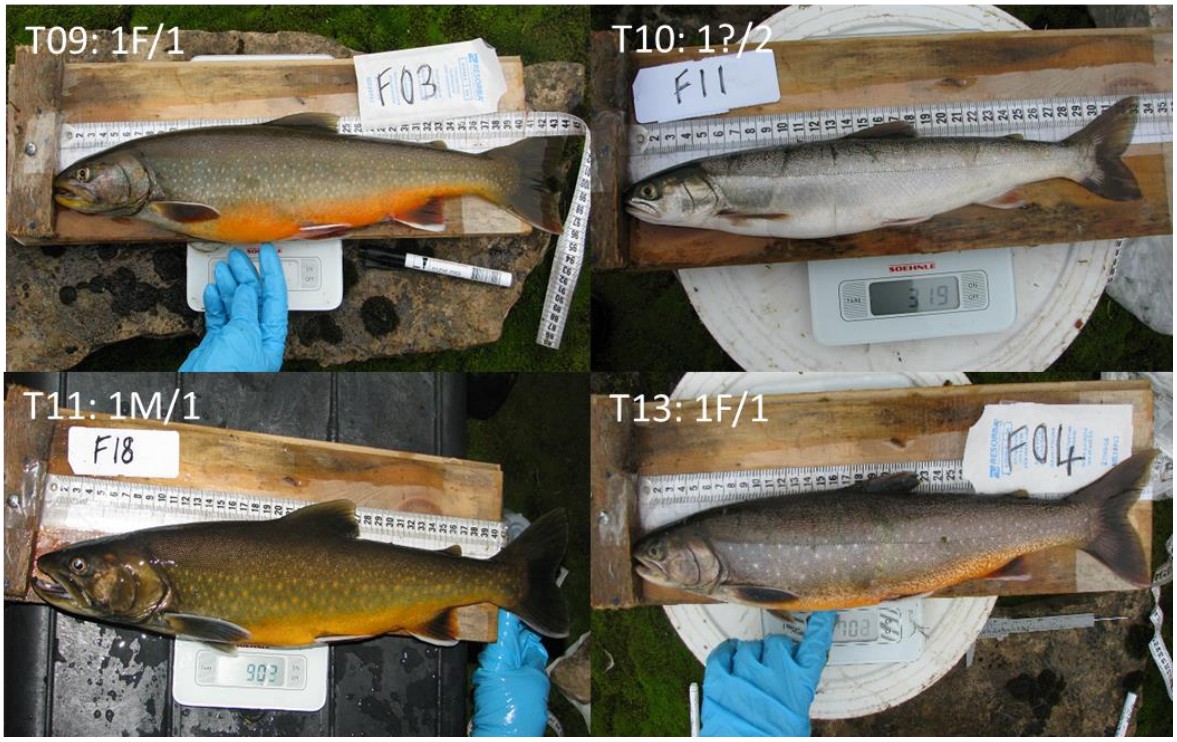
9 Appendices

9.1 Appendix I- fish sample

Each photographed Arctic charr from Lake Ellasjøen, Bear Island is shown below. Fish were sampled between 23 – 24/8/2009 (*n* = 28). Individuals are labelled (in white text) according to their acoustic transmitter number (T01 – 30). The individuals D1 and D2 were photographed and included in the meristic analysis but were not implanted with a transmitter. The visually determined morphology group (1 – 4) and final morphology grouping are also shown respectively (e.g. 1/2 refers to an initial grouping (1) followed by a subsequent recoding (2) based upon meristic analysis). Final morphology groups were designated according to a discriminant analysis model including the covariates; pelvic fin length (PEL) proportional to individual fork length (FL), head depth at operculum (HDO) proportional to head length (HL) and eye diameter (ED) proportional to head depth at eye (HDE) (see 4.4.3 Morphometric measurements, for a description of each measurement). The individuals T12, T16, T20, T24 are absent as no photo was available. Fish ID during field sampling was indicated by 'F number' in the photo, duplicate F codes, in several cases, were resolved from field notes and can be ignored here. Key for morphological grouping: 1; Robust, 2; Delicate, 3; Dwarf maturing, 4; Other. Group 1, Robust morph fish and group 3, Dwarf morph fish were further divided into: F: female, M: male, ?: unknown sex.

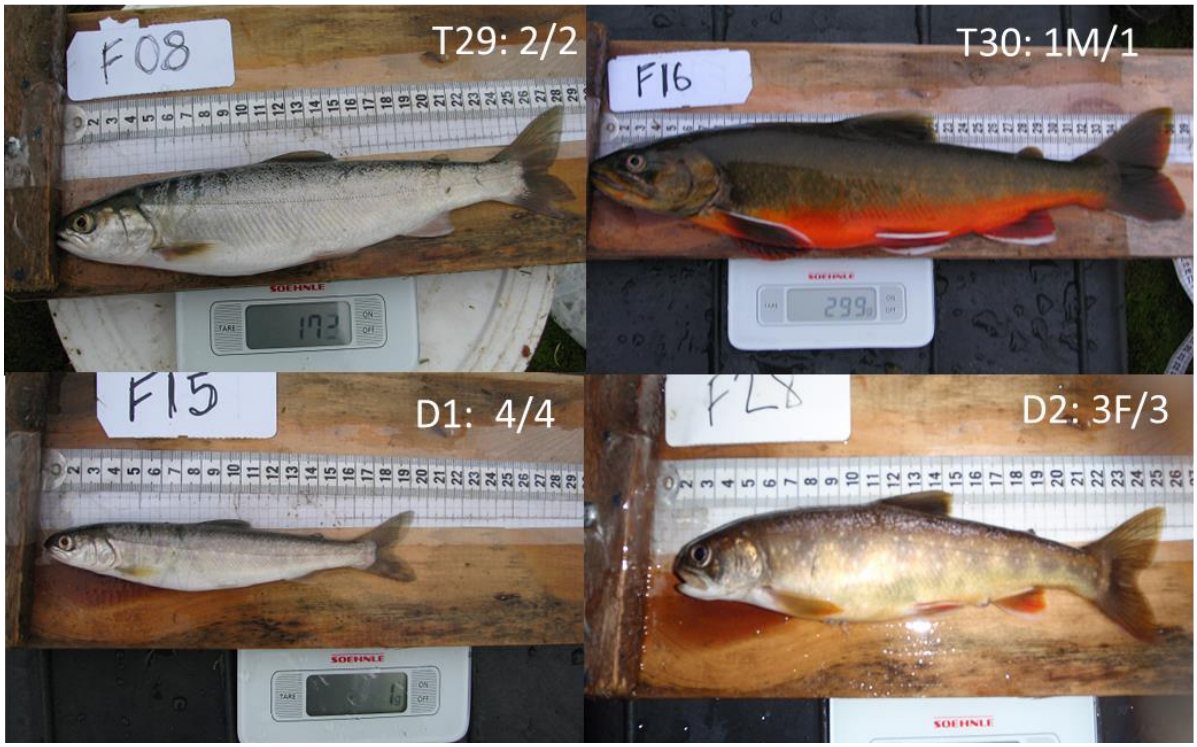

T05: 1F/1
F02
T06: 2/2
F11
T07: 1M/1
F18
500
T08: 4/2
F27


T09: 1F/1
F03
T10: 1?/2
F11
319
T11: 1M/1
F18
903
T13: 1F/1
F014


T14: 1M/1
F12
T15: 3M/3
F20
T17: 1?/1
F05
T18: 2/2
F13

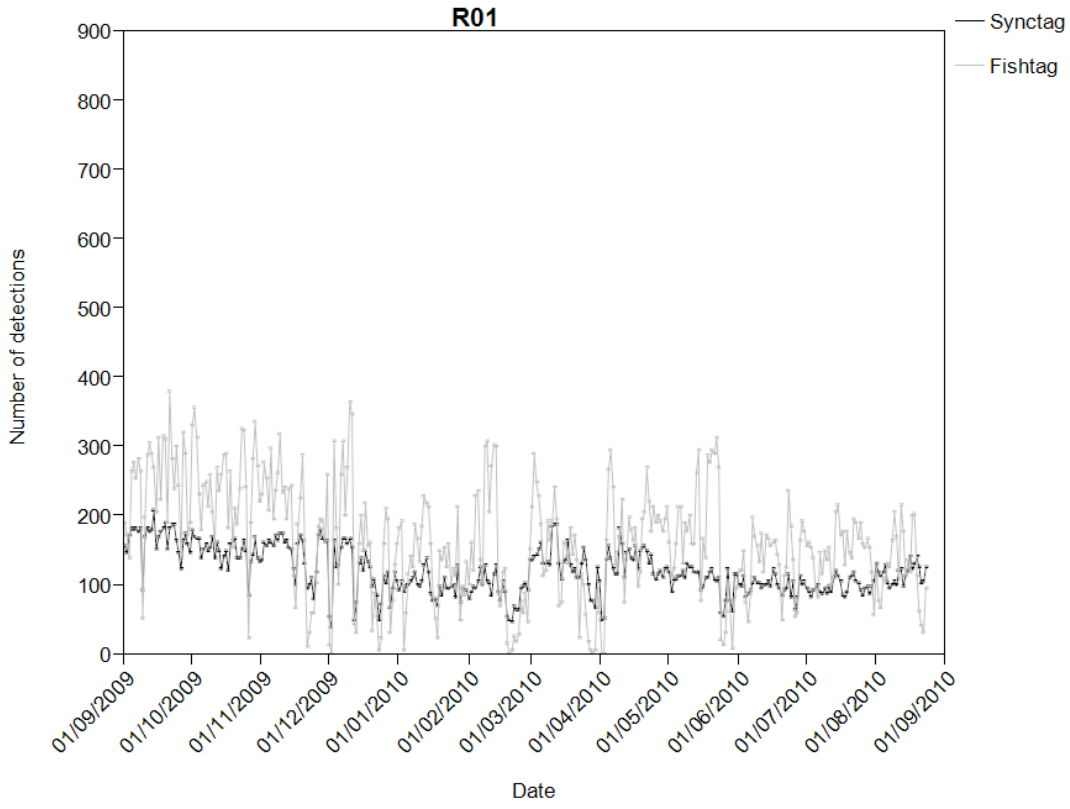

T19:2/2
F21
T21: 1F/1
F06
T22: 2/2
F14
T23: 4/4
F22

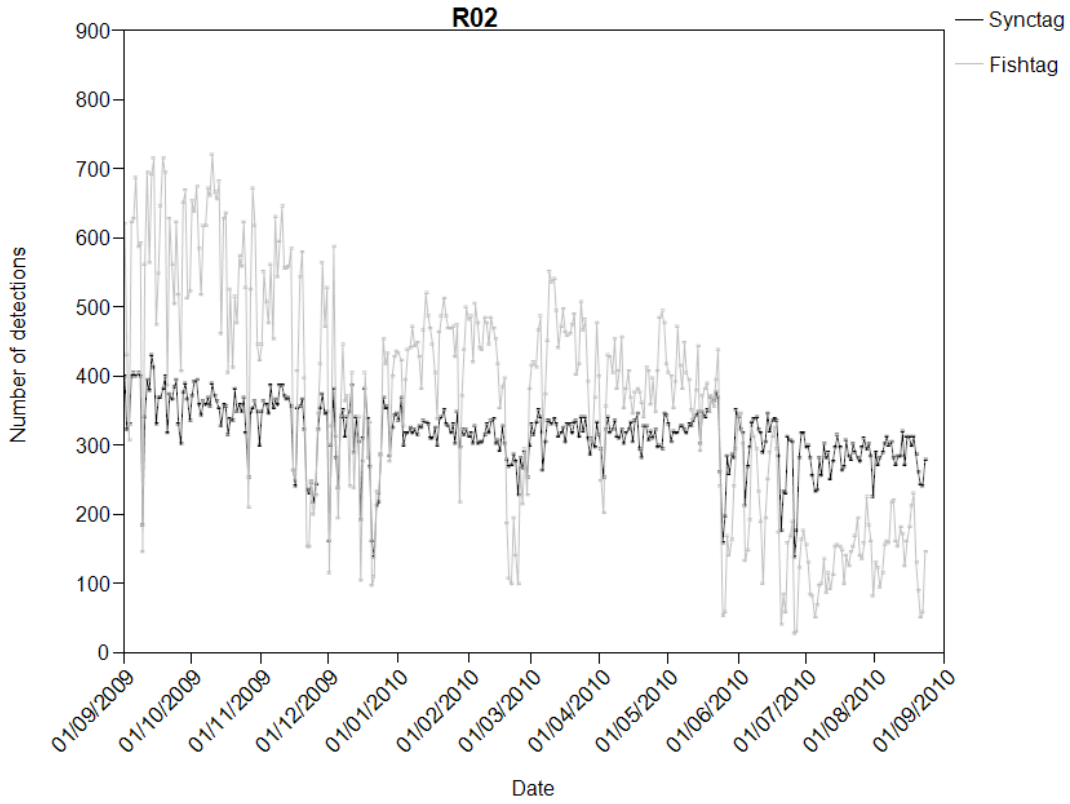

T25: 1F/1
F07
T26: 2/2
F26
T27: 3F/3
F23
F25
T28: 4/4

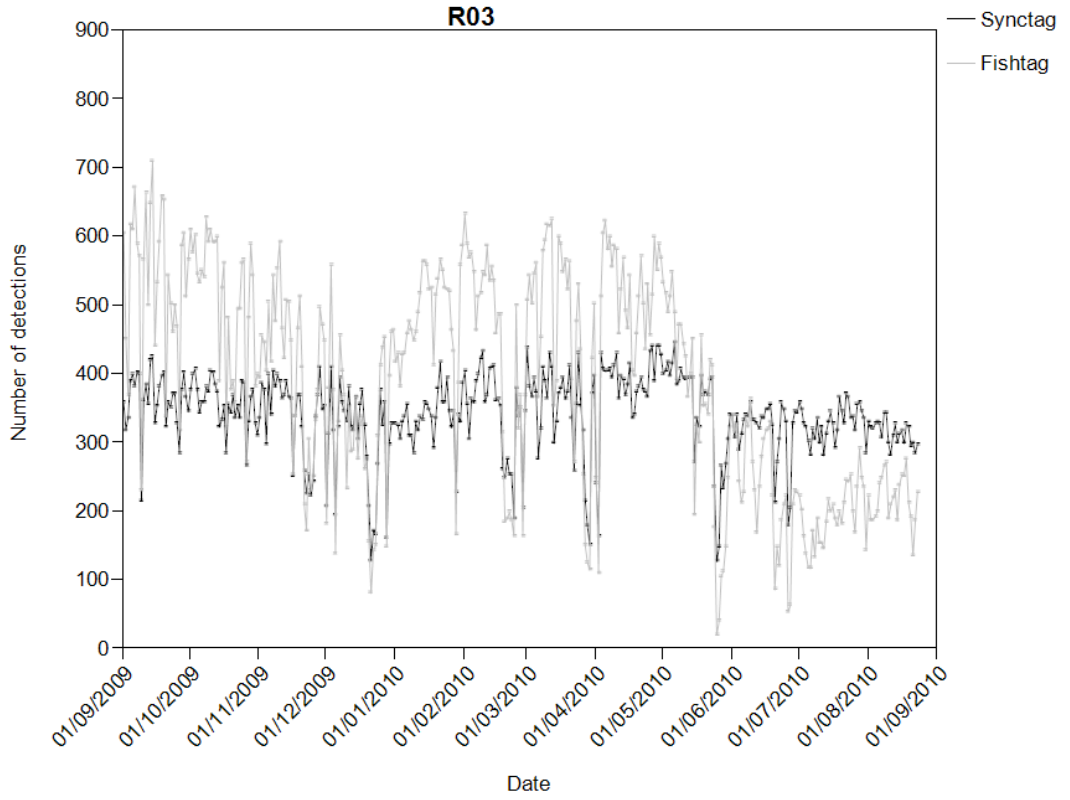

F08
T29: 2/2
T30: 1M/1
F16
F15
D1: 4/4
D2: 3F/3

9.2 Appendix II- VR2W fish tag and sync tag detections

Figures presenting the total number of daily fish tag and sync tag detections recorded on each VR2W retrieved during the Vemco Positioning System (VPS) deployment in Lake Ellasjøen, Bear Island. The VPS was composed of 19 VR2Ws and co-located sync tags and 30 fish tags. VR2Ws are labelled R01 – R19. The VR2Ws R12, R14, R18 and R19 were not retrieved and, therefore, all detections recorded onto these receivers were lost. Trends in sync tag detections over the study period can be used to infer changes in tag detection efficiency of a given VR2W, while changes in fish tag detection numbers may indicate changes in tag detectability and/or the number of fish tags within the VR2W locality. VR2W deployment locations are shown in Figure 4-4.




R02
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R03
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
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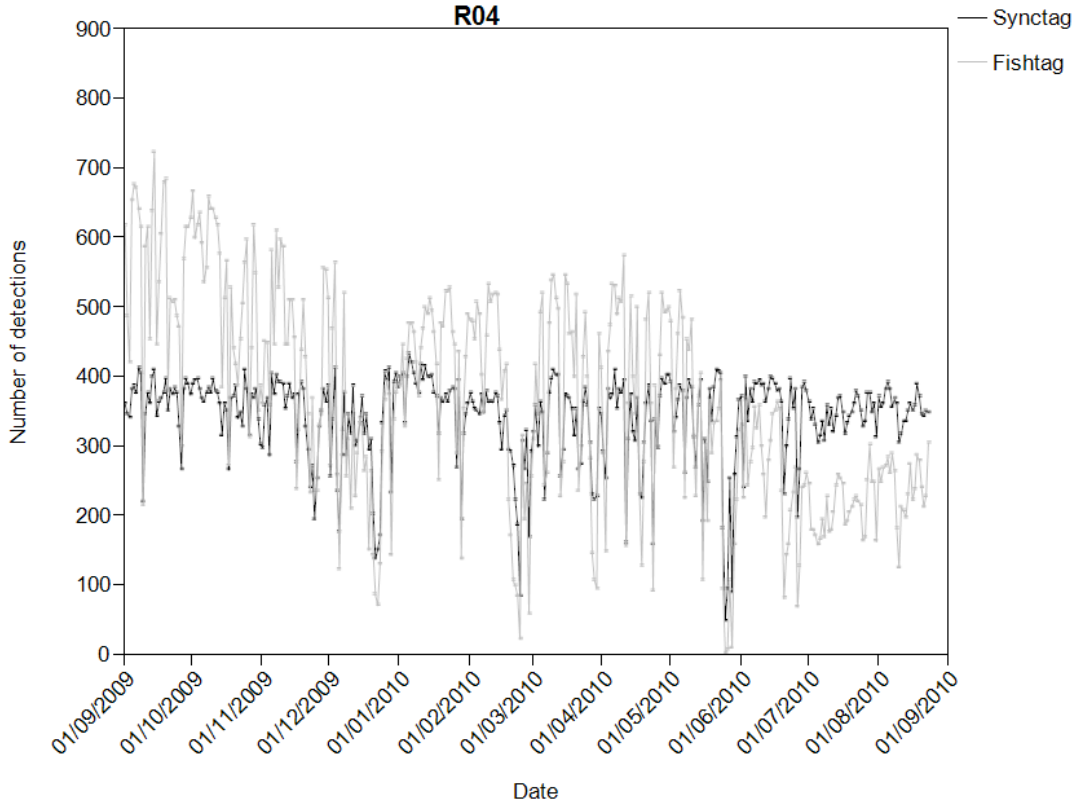
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R04
Synctag
Fishtag
Number of detections
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800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
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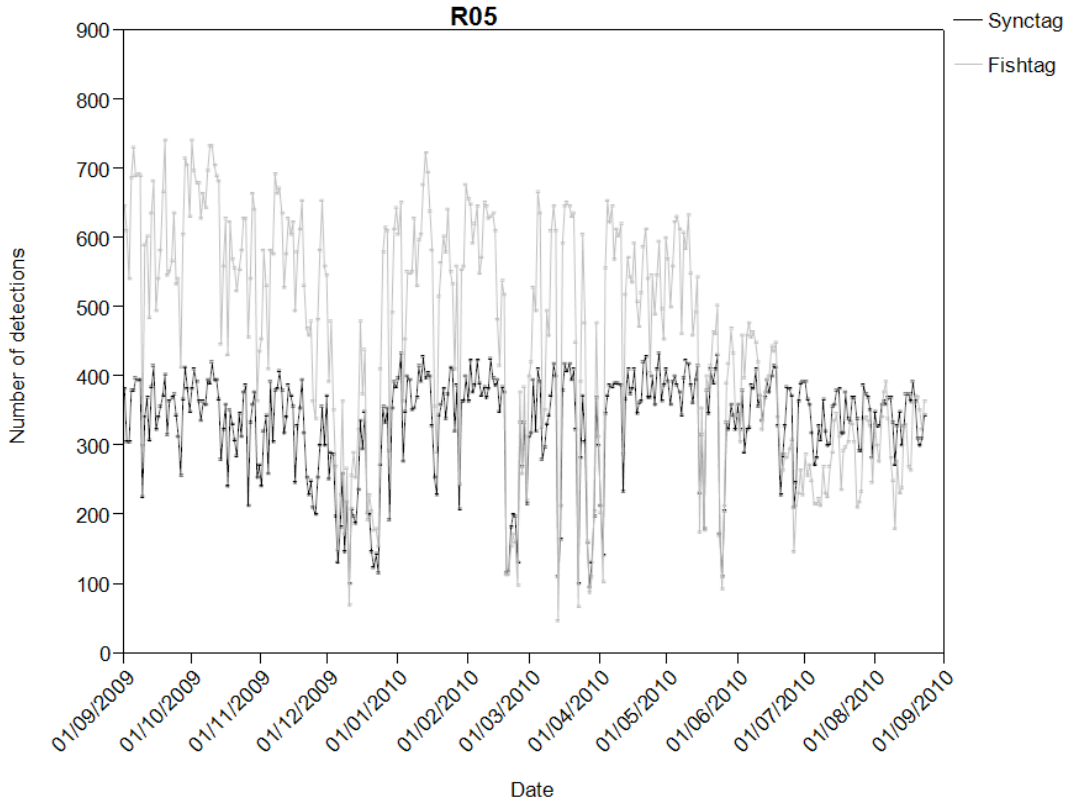
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R05
Synctag
Fishtag
Number of detections
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800
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600
500
400
300
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100
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01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
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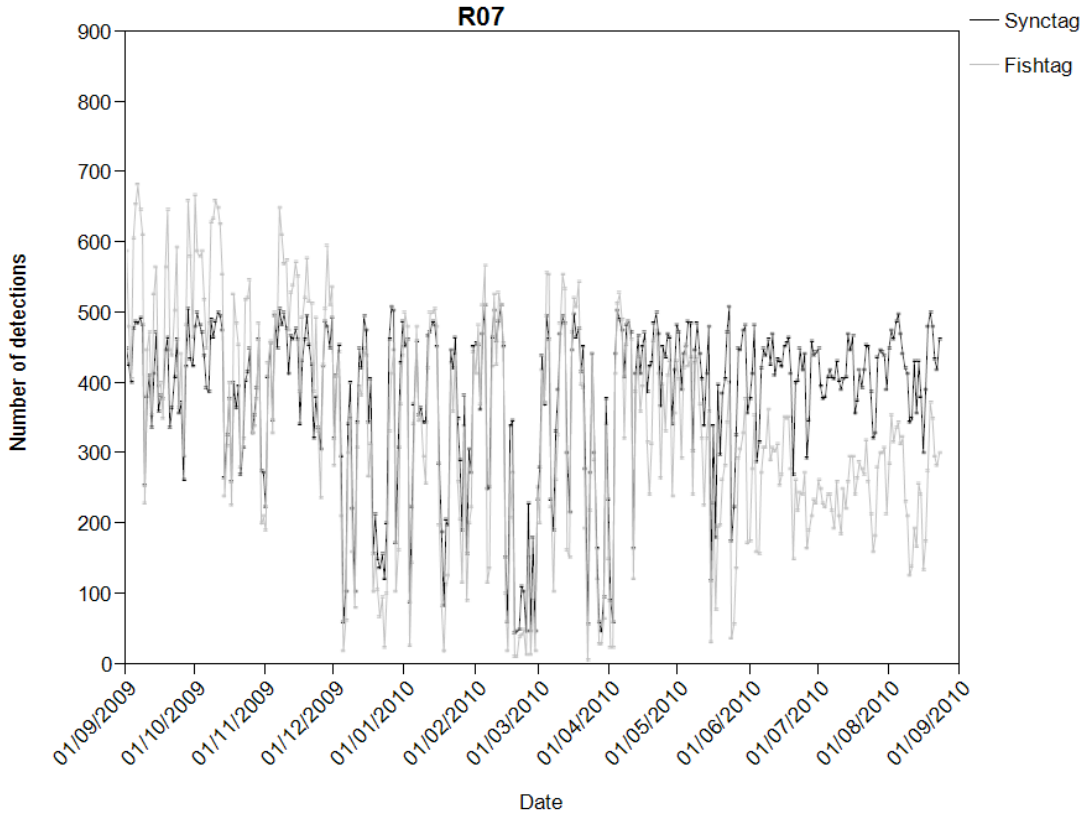
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R07
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
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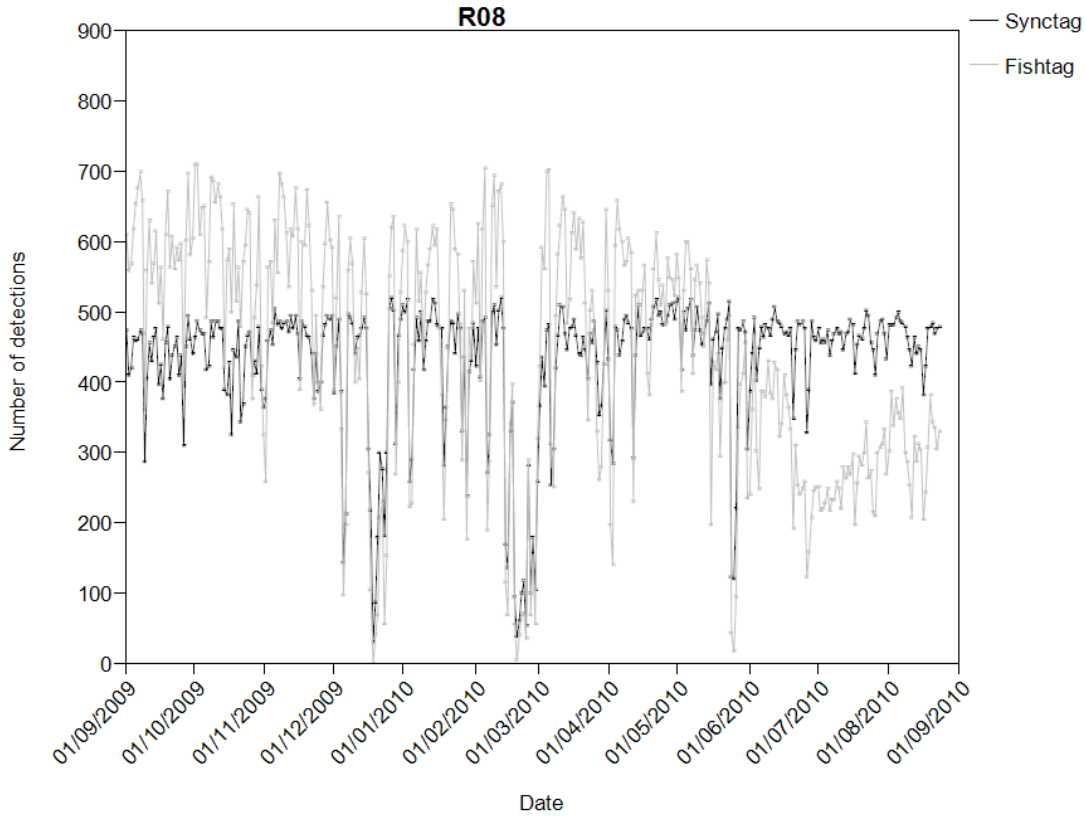
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R08
Synctag
Fishtag
Number of detections
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800
700
600
500
400
300
200
100
0
01/09/2009
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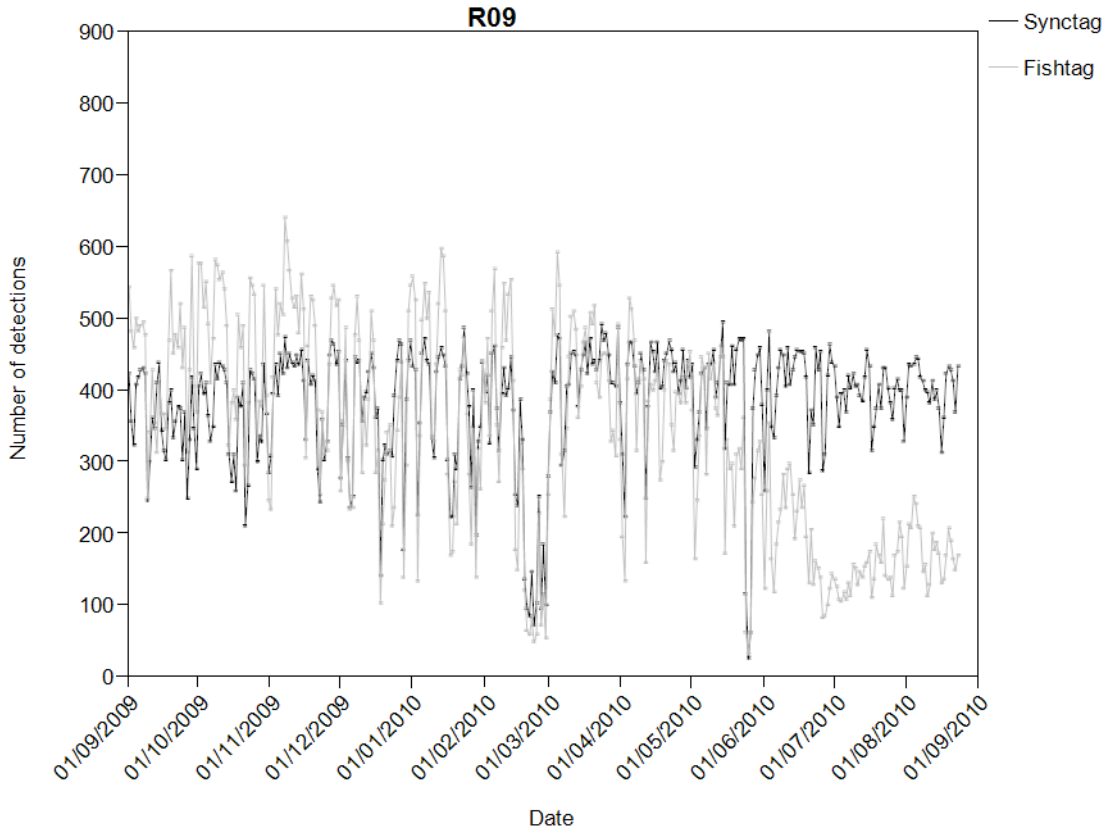
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R09
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
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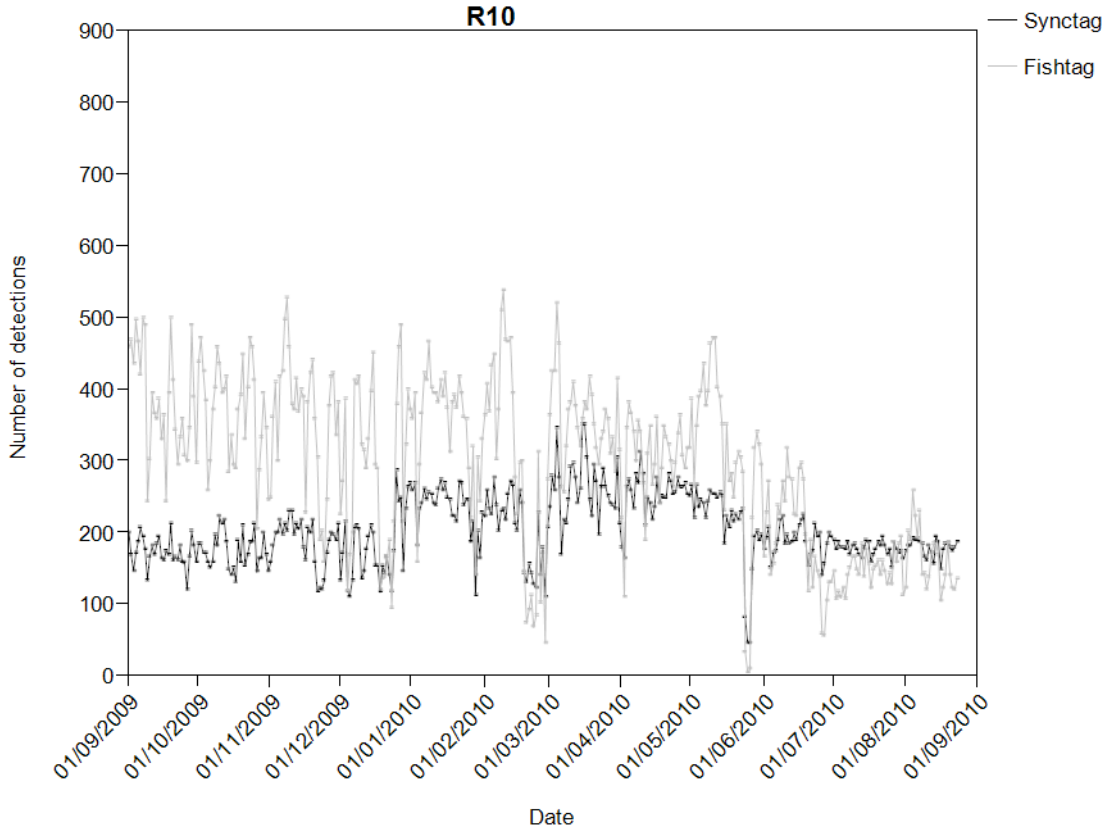
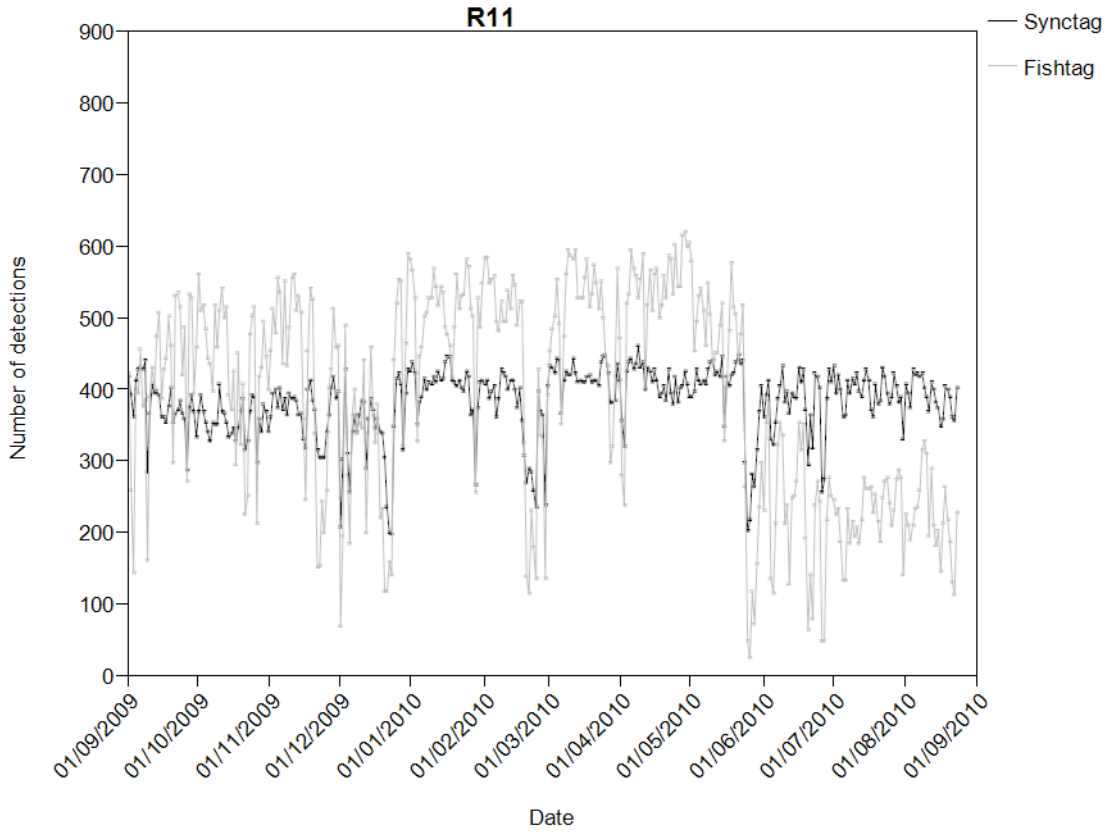
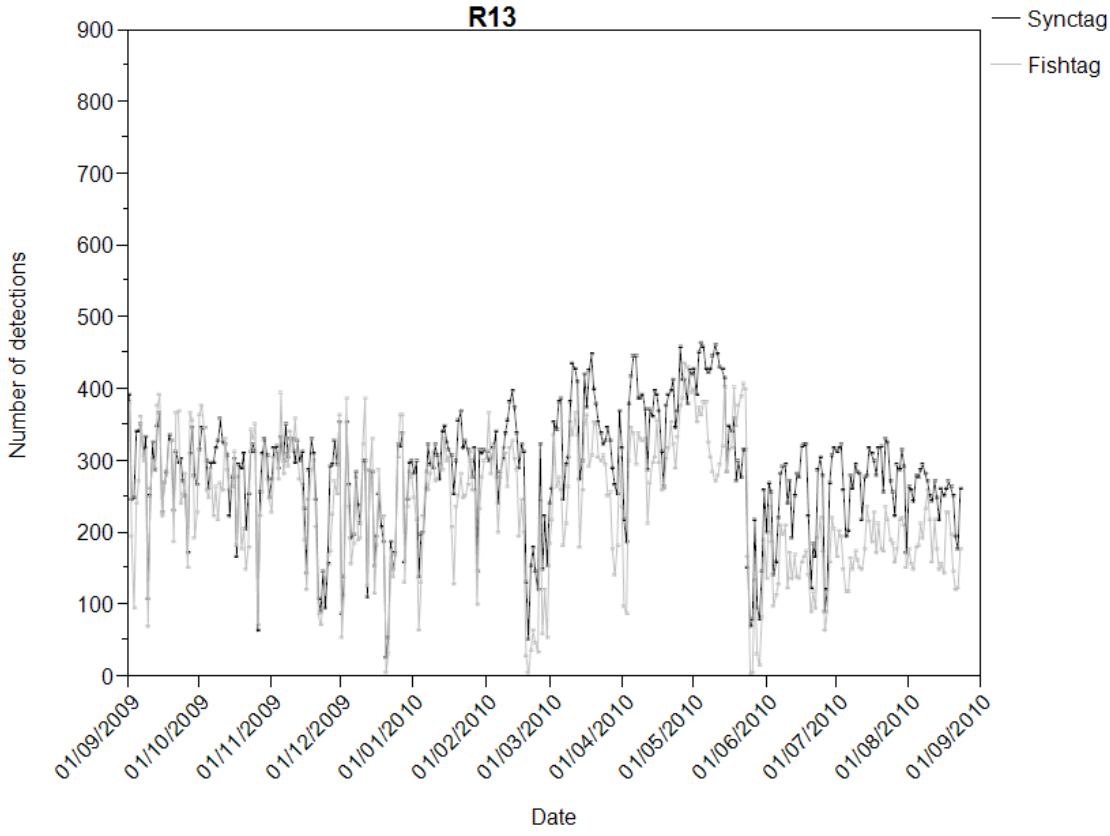
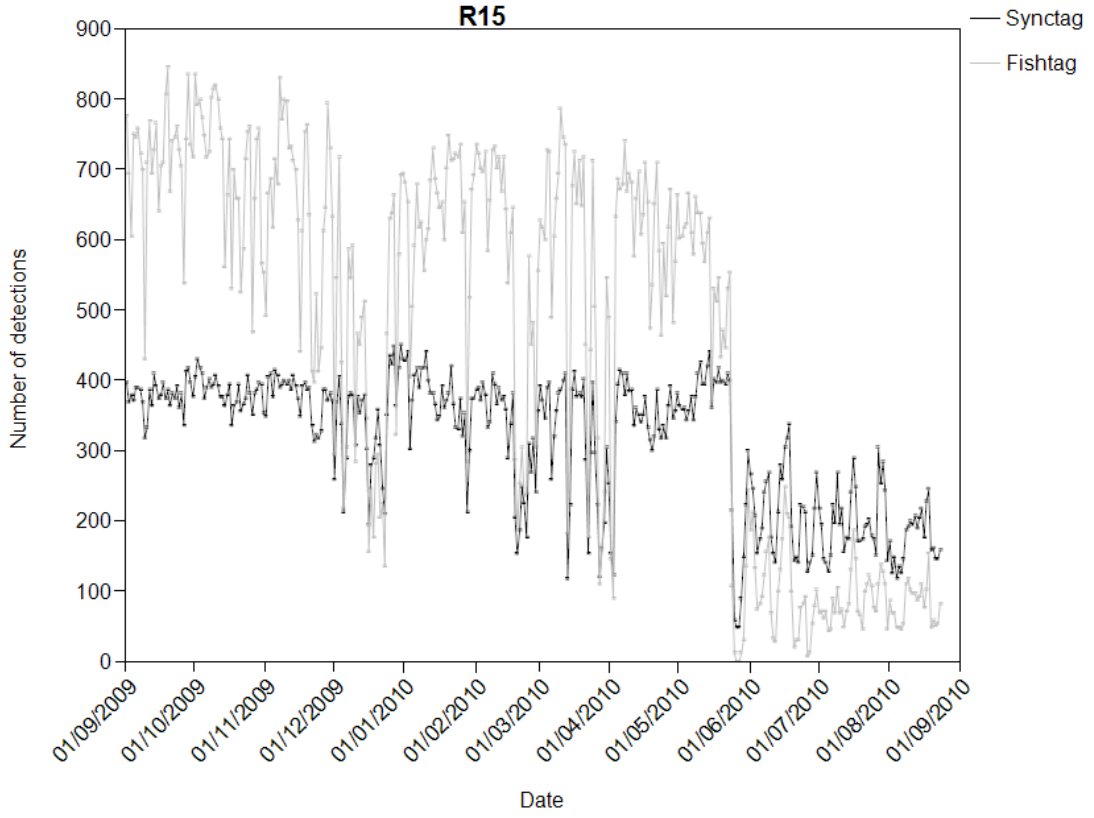
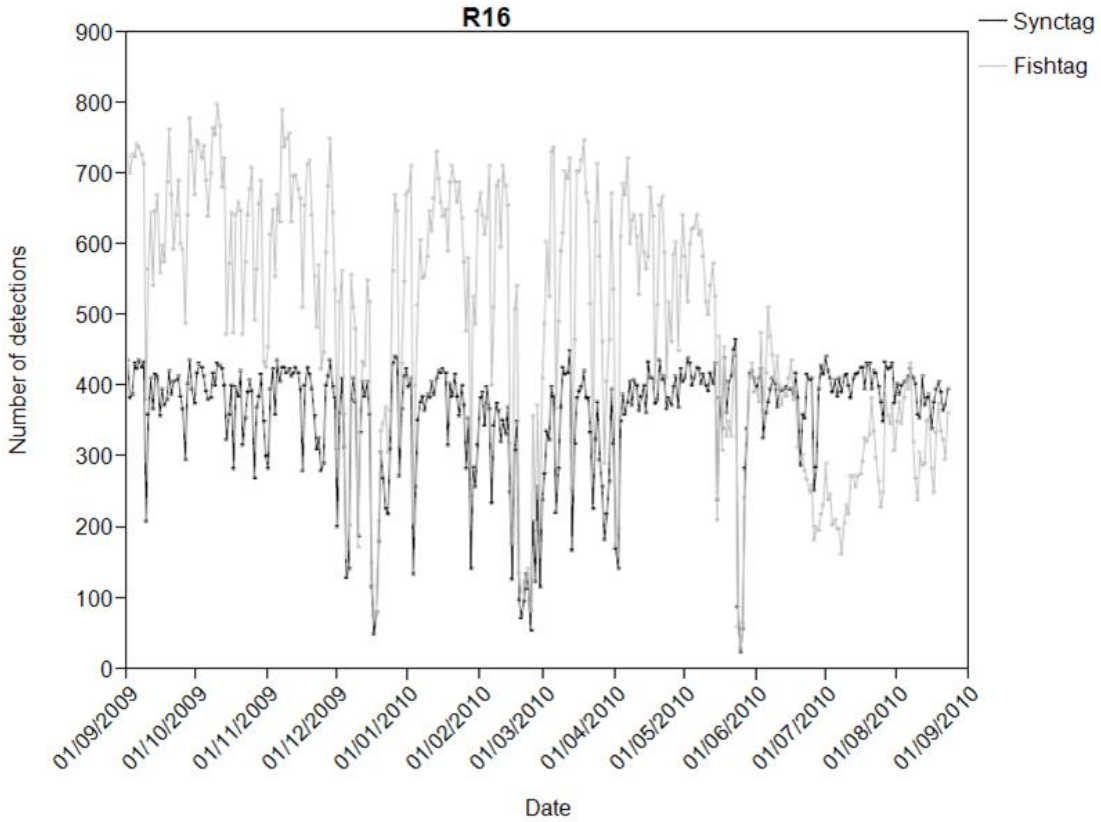
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date

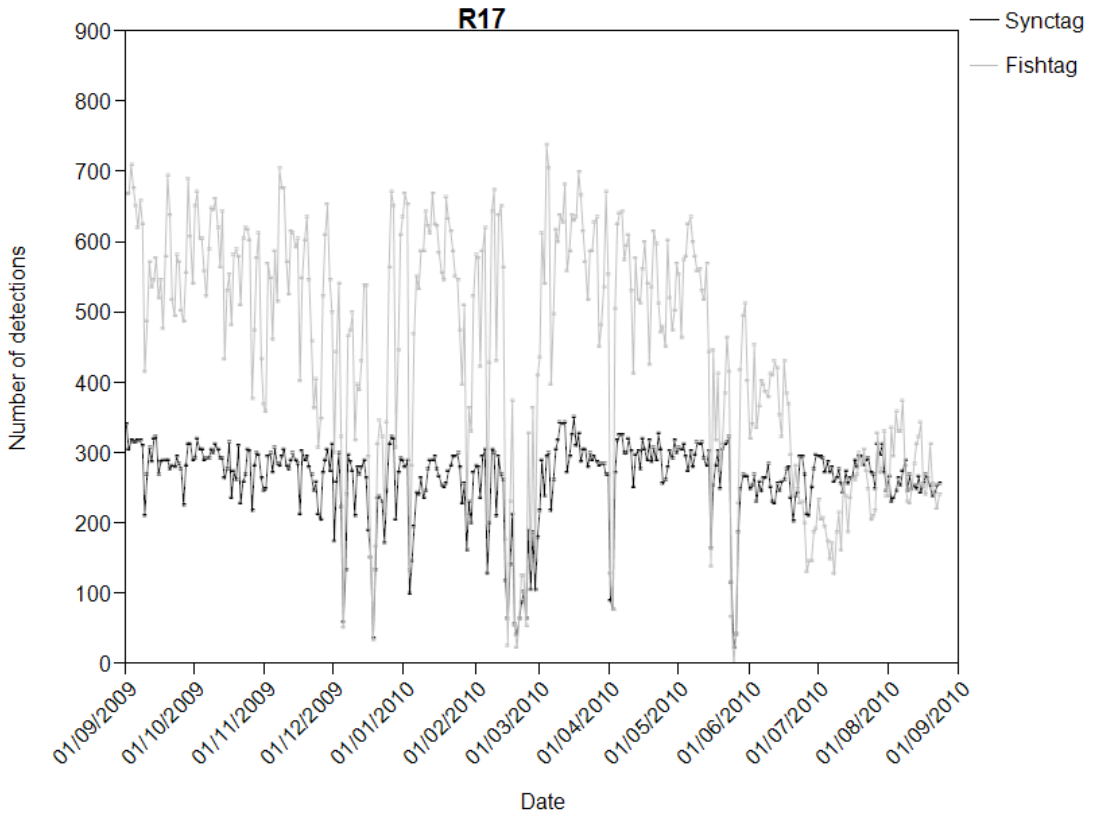

R10
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R11
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date


R13
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date

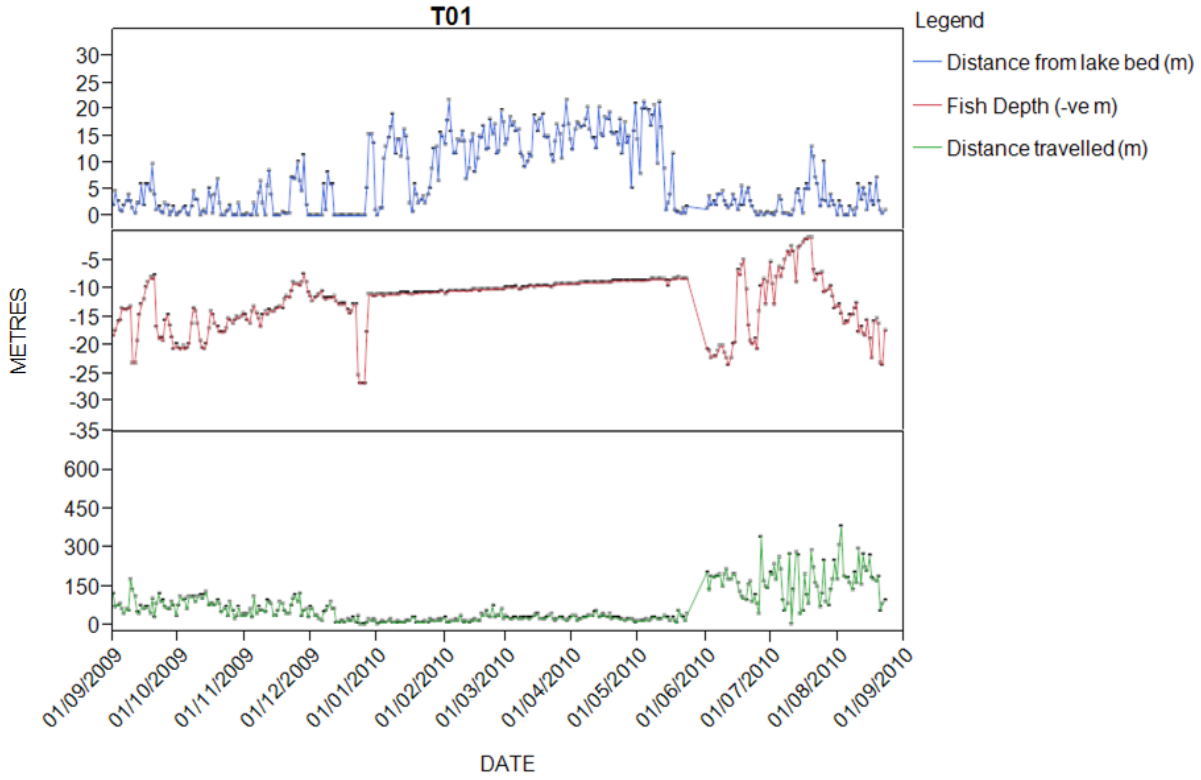

R15
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date

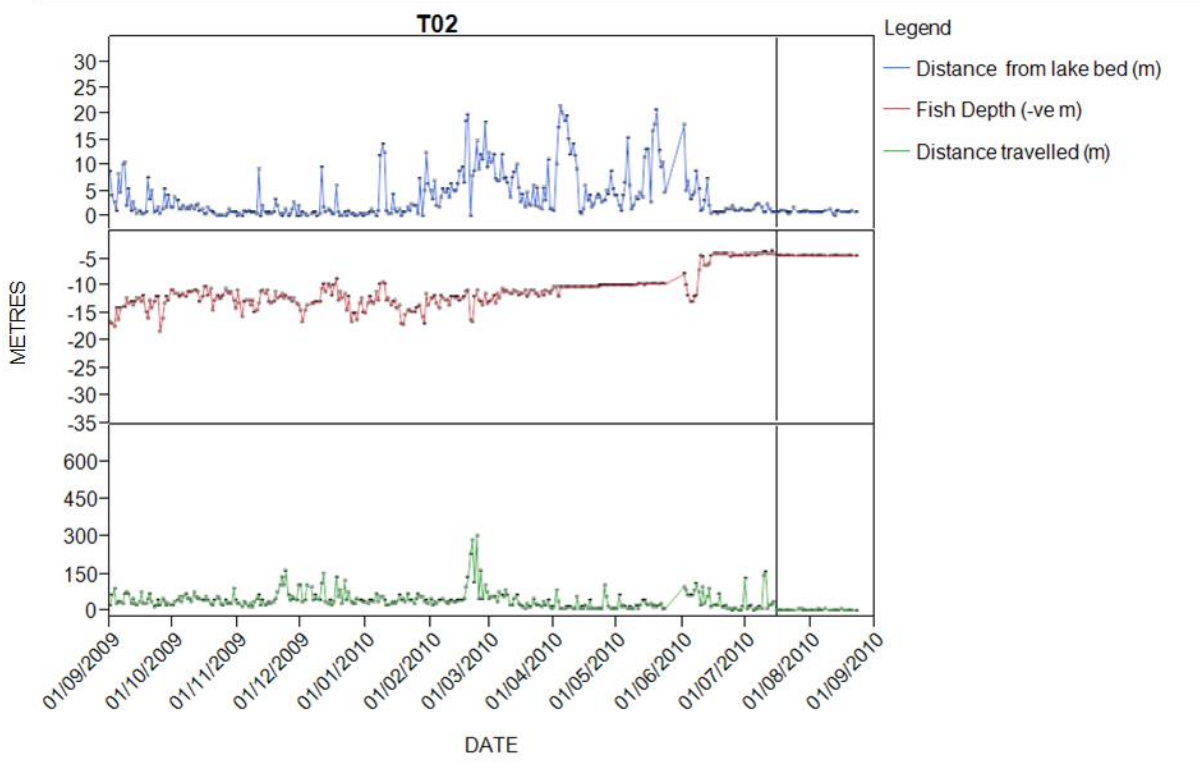

R16
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date

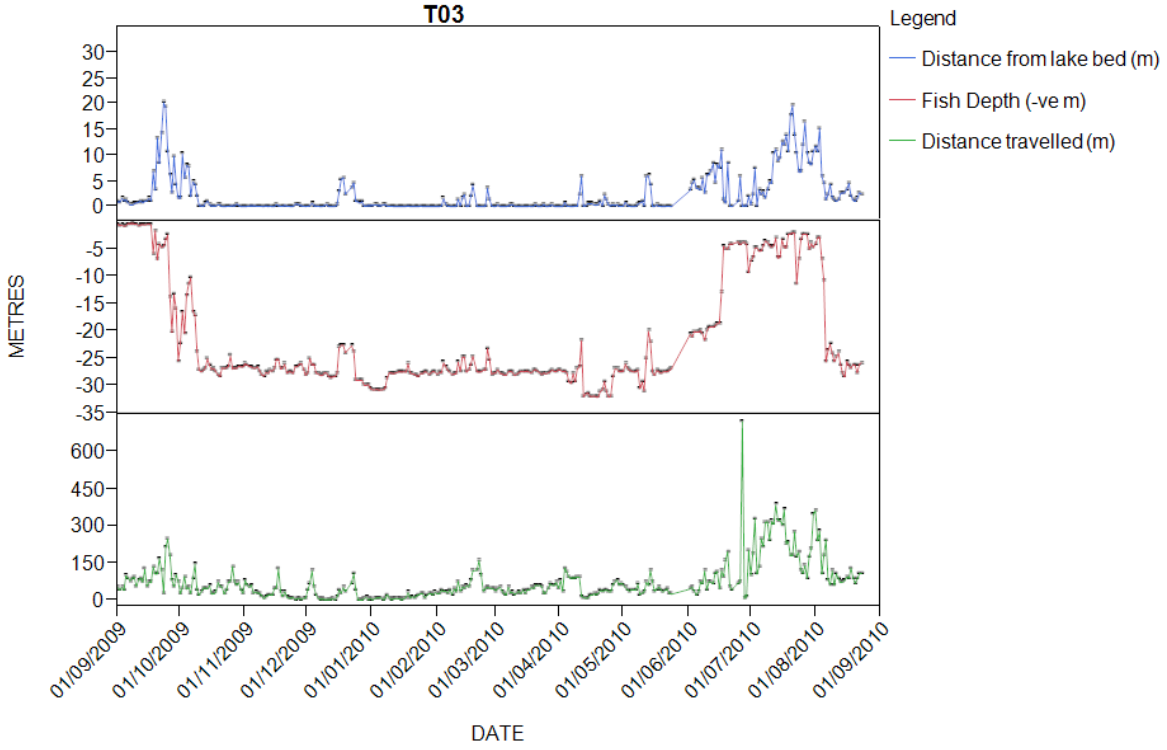

R17
Synctag
Fishtag
Number of detections
900
800
700
600
500
400
300
200
100
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
Date

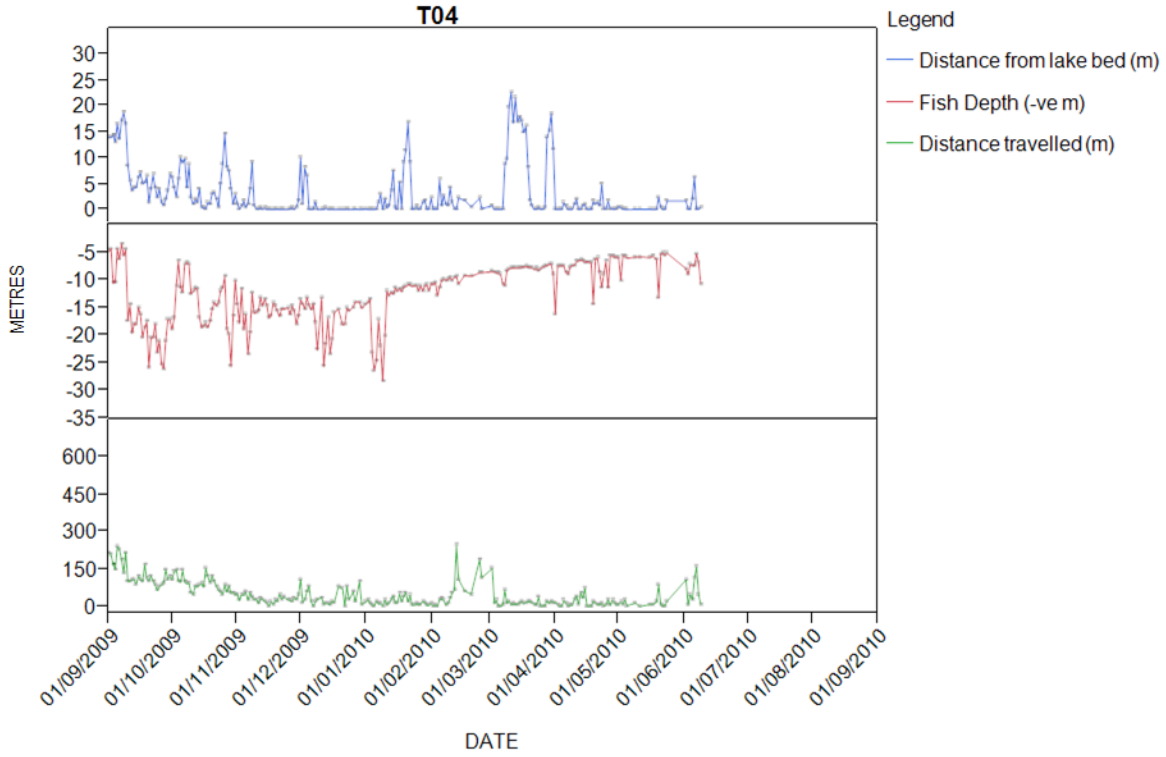
9.3 Appendix III - individual fish tracks

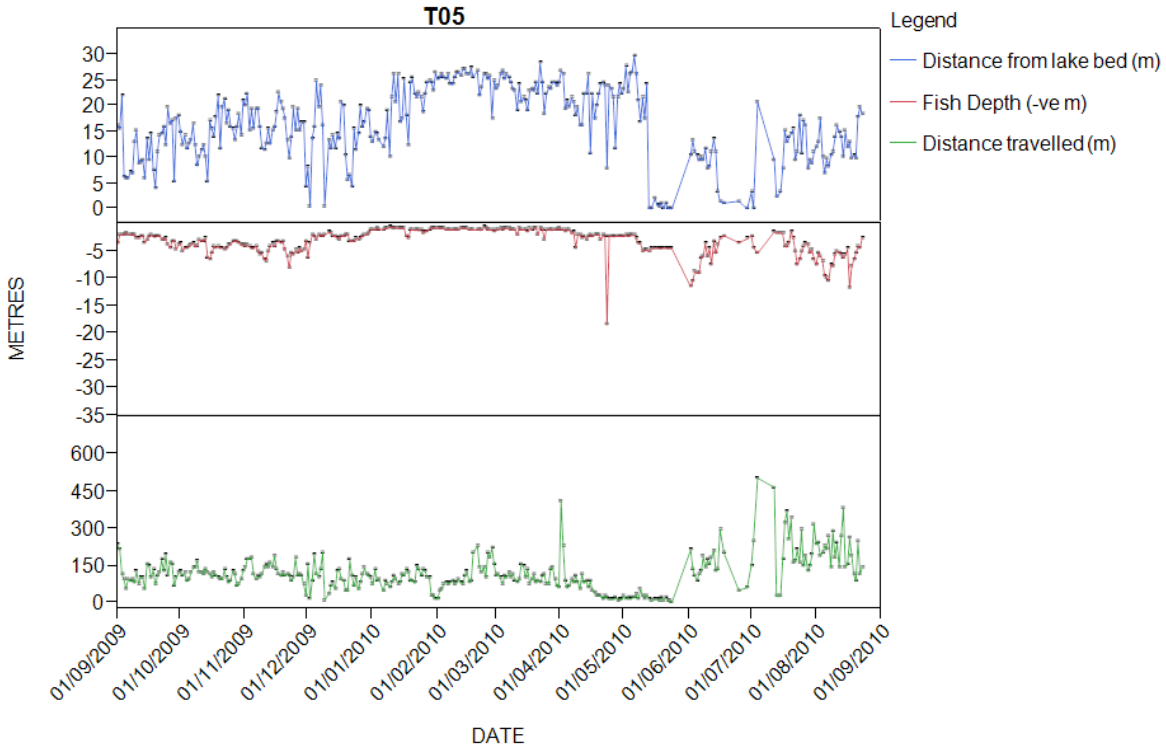
The temporal 'tracking' of each tagged Arctic charr calculated from the VPS deployed in Lake Ellasjøen, Bear Island is shown below. For each individual, daily mean values of; the three dimensional distance travelled (metres), fish depth (negative metres) and fish distance from lake bed (metres) were calculated and plotted for the entire study period (1/9/2009 – 23/8/2010). Likely erroneous positions identified according to 5.4.2 (Pre-treatment of fish positional data) were not included. The 3-dimensionsonal distance travelled was calculated according to Equation 5-4 and Equation 5-6. Activity is likely to be underestimated (as transmitter code rate was set at 80 minutes) therefore activity is presented as a metric only. No data was derived for the fish T19 and T23, likely due to malfunctioning transmitters and therefore plots for these fish are absent. From these figures it was possible to observe the 'valid' positional data of each fish. For those fish for which stationary tag positions were identified (T02, T08, T15 and T30), the start of the 'static' positional period is indicated by a vertical black reference line (see 5.4.3 Individual fish fate and validity of VPS fish positions). The pressure sensor for the individual T12 became faulty after the 1/5/2010 (no change in depth/vertical movement corresponding to horizontal movement was recorded from this period onwards); therefore all depth values for this individual were removed from further analysis from this date.

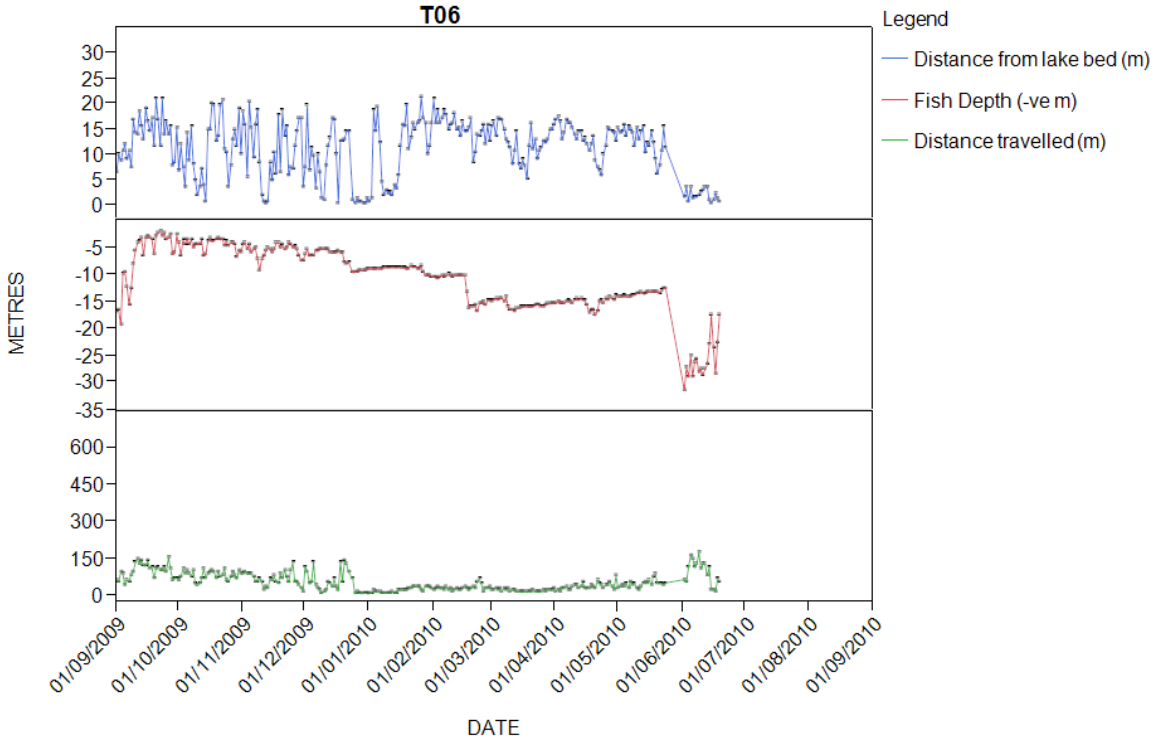


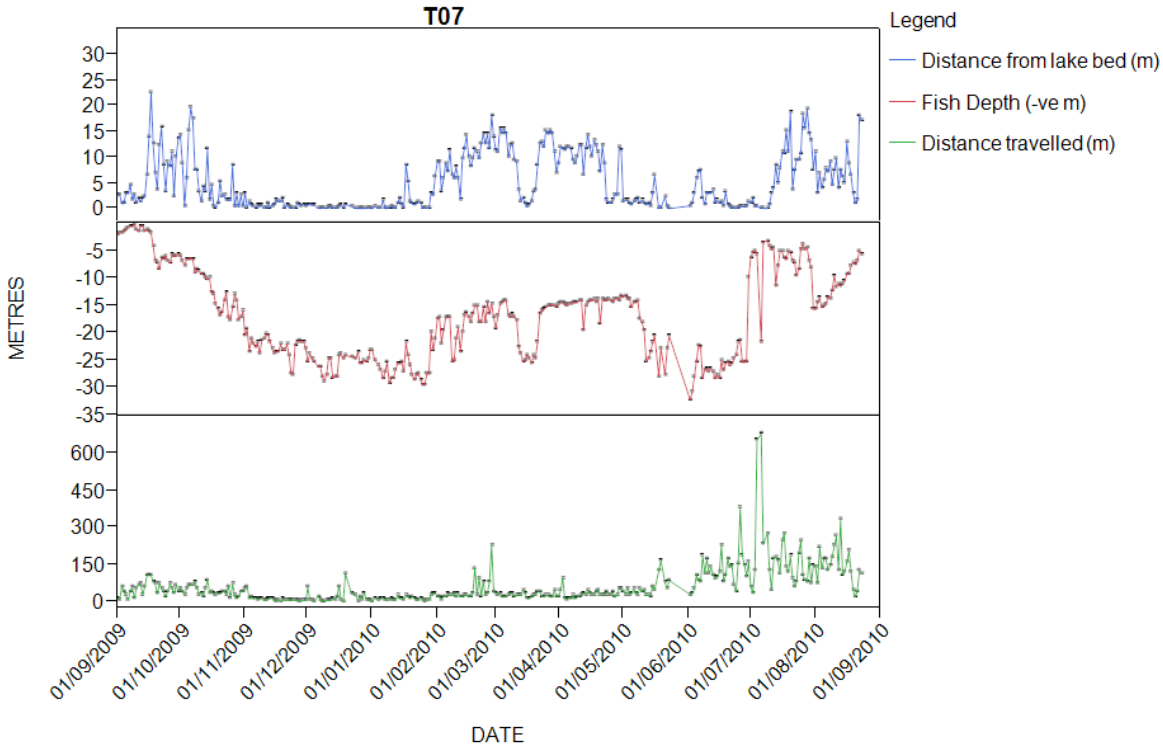

T02
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
DATE
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010

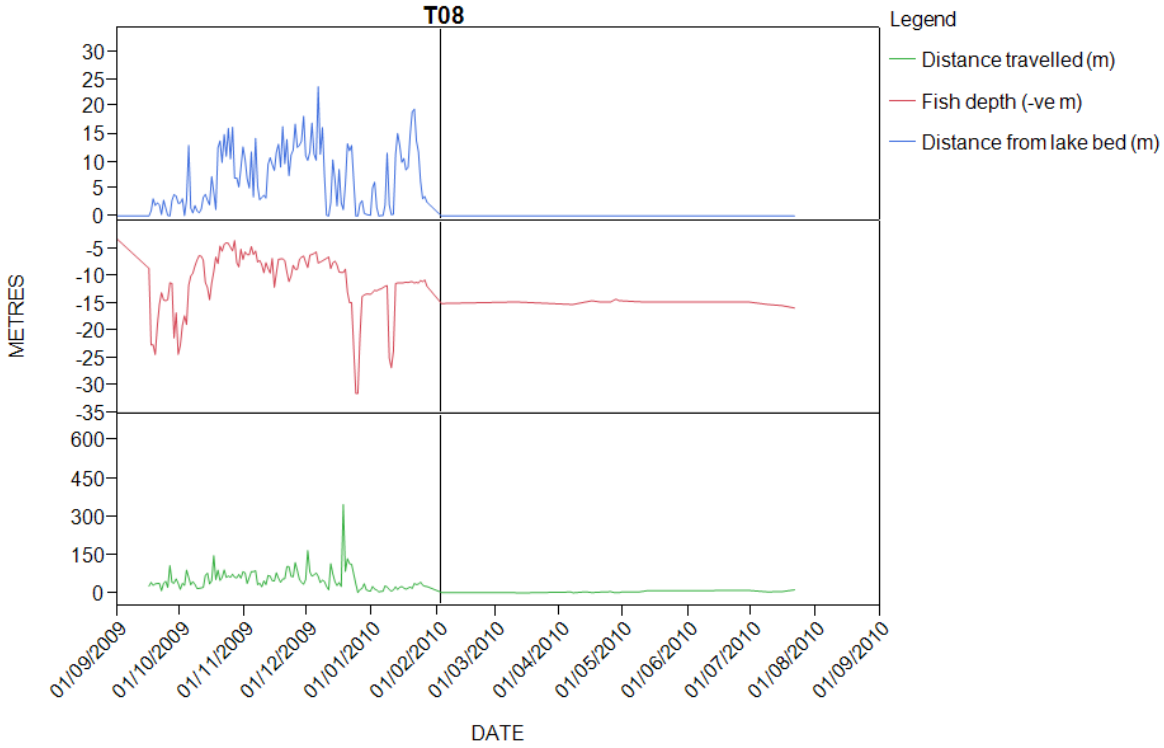

T03
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
DATE
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010

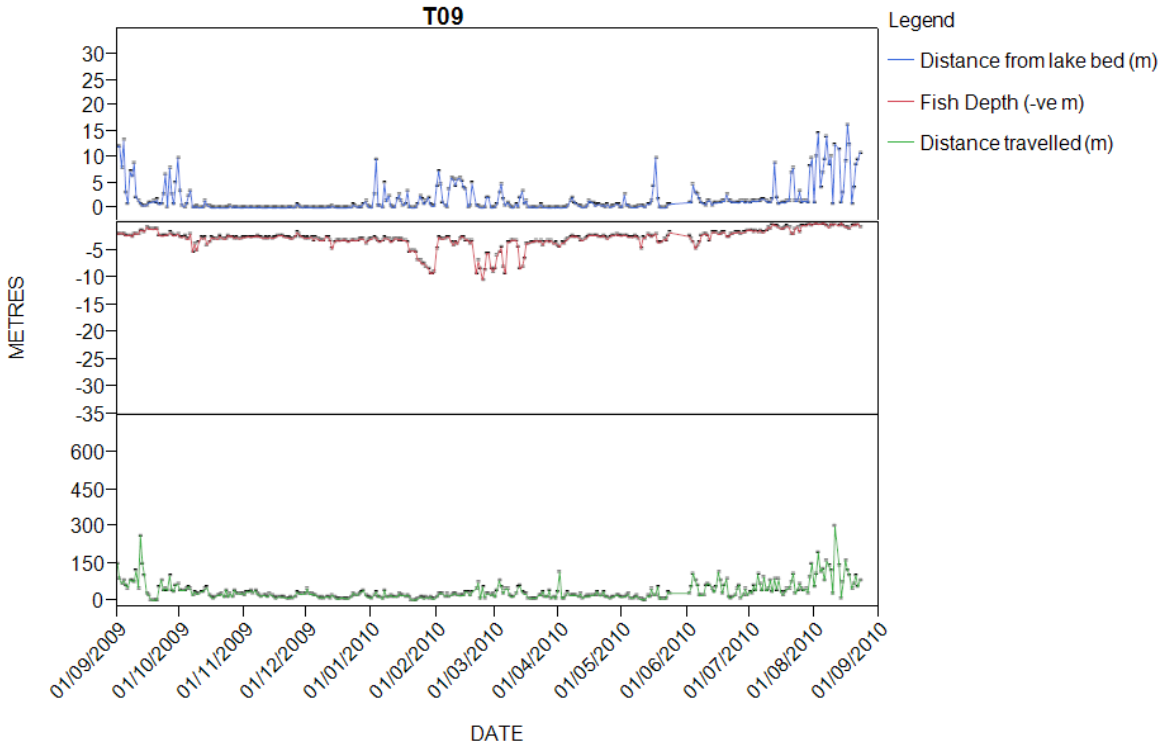

T04
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T05
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T06
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T07
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T08
Legend
Distance travelled (m)
Fish depth (-ve m)
Distance from lake bed (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T09
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
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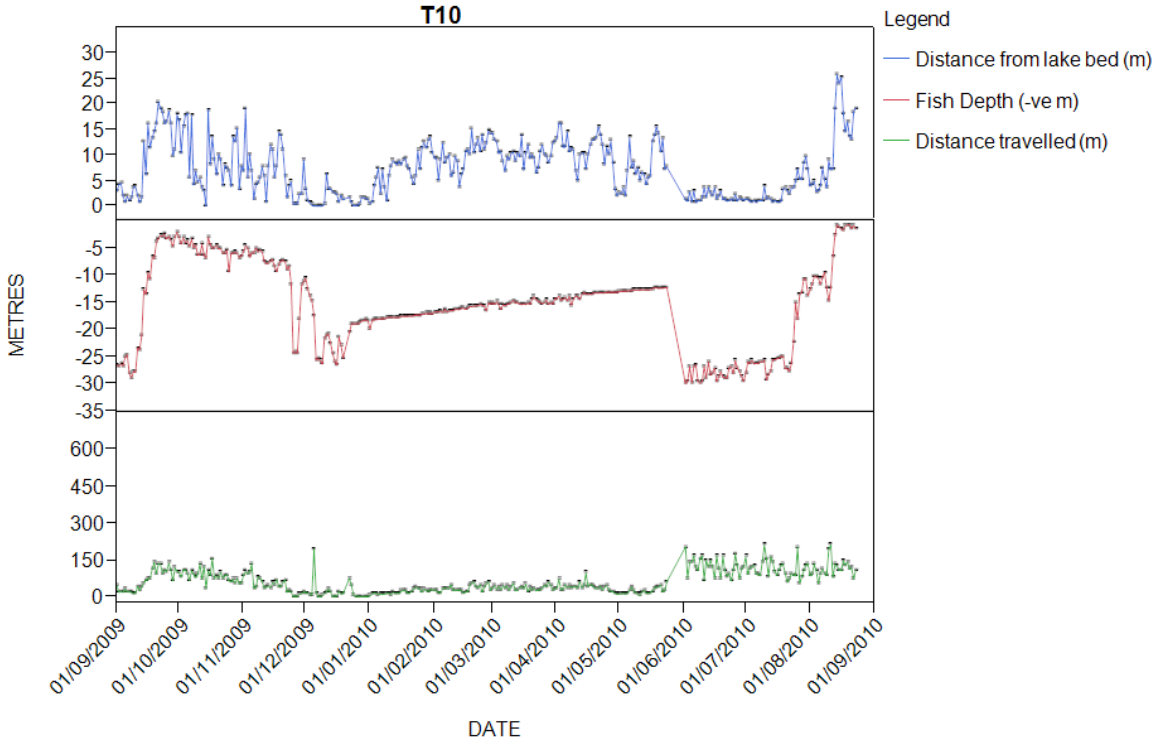
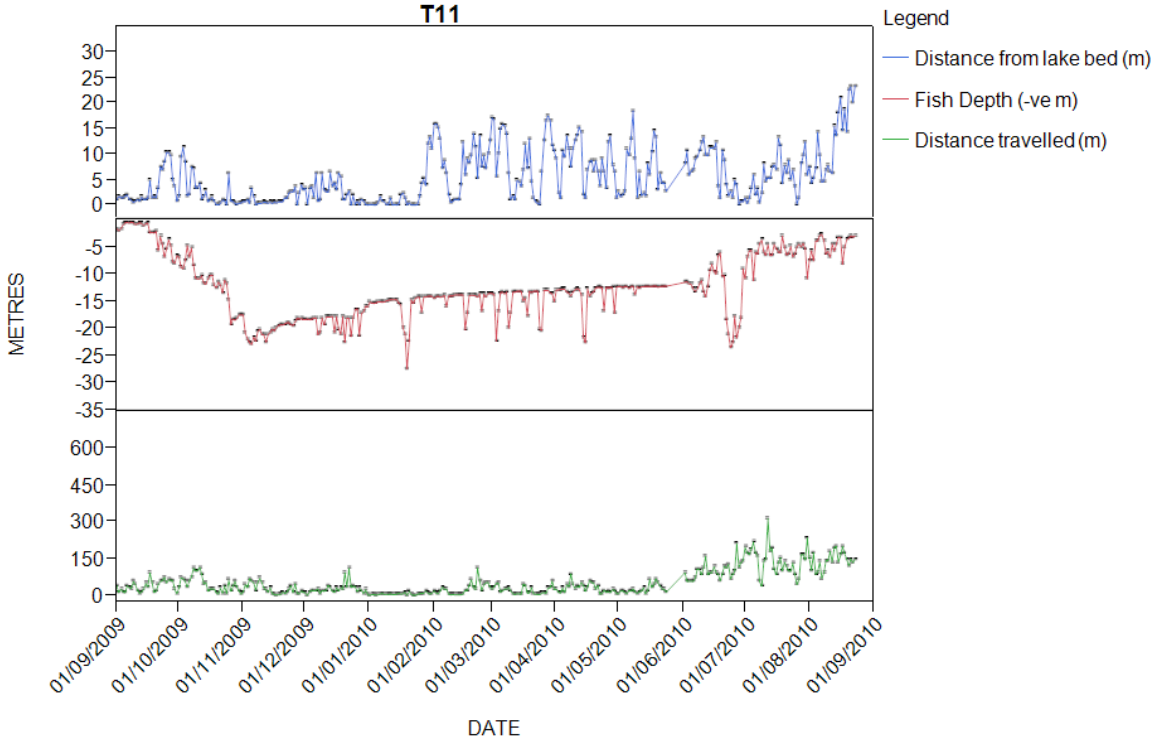
01/08/2010
01/09/2010
DATE


T10
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T11
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
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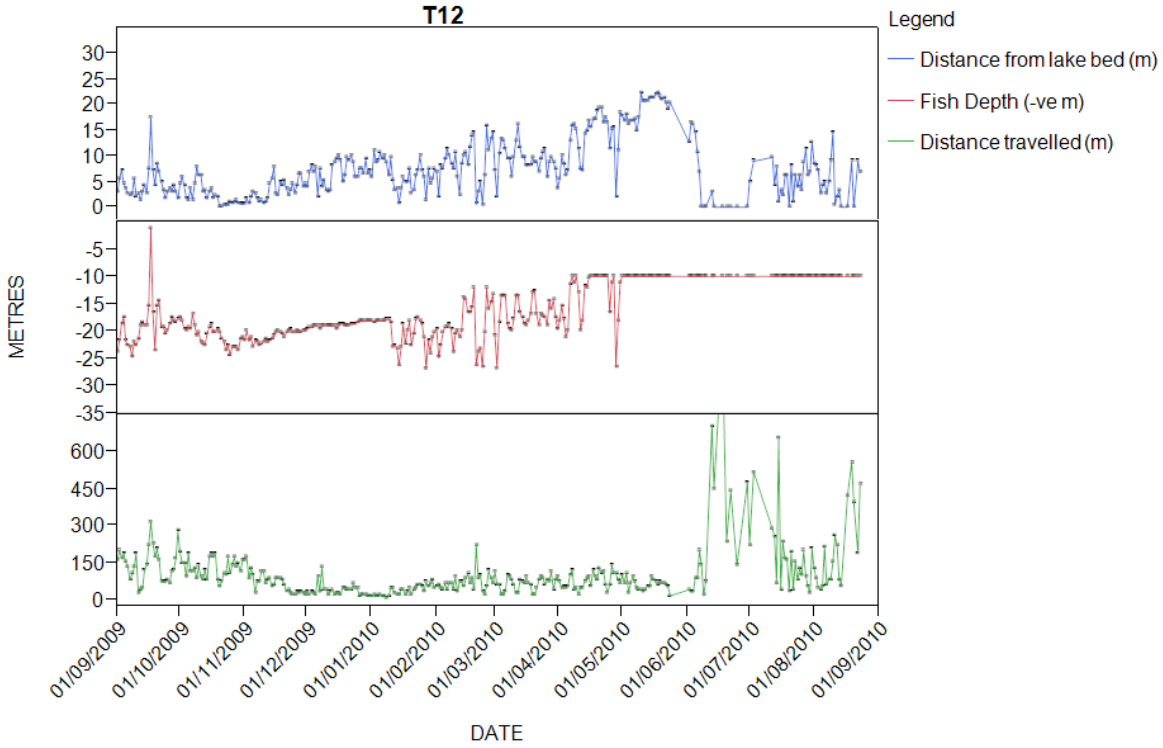
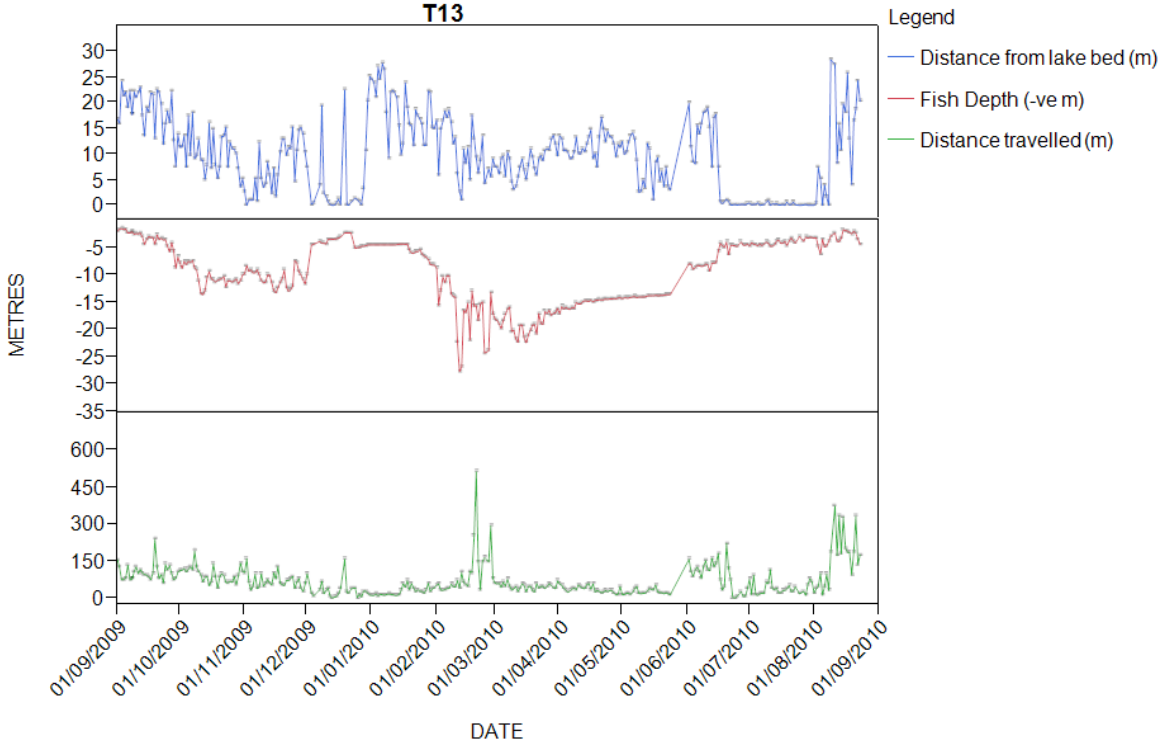
01/08/2010
01/09/2010
DATE


T12
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T13
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
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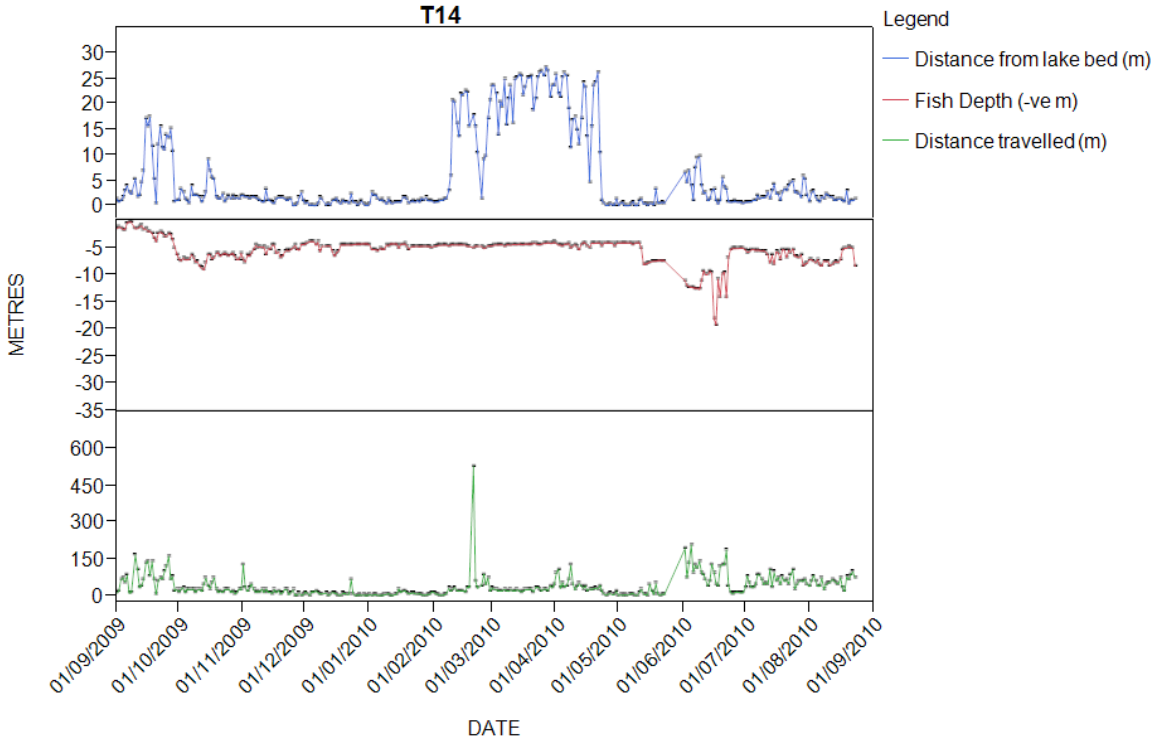
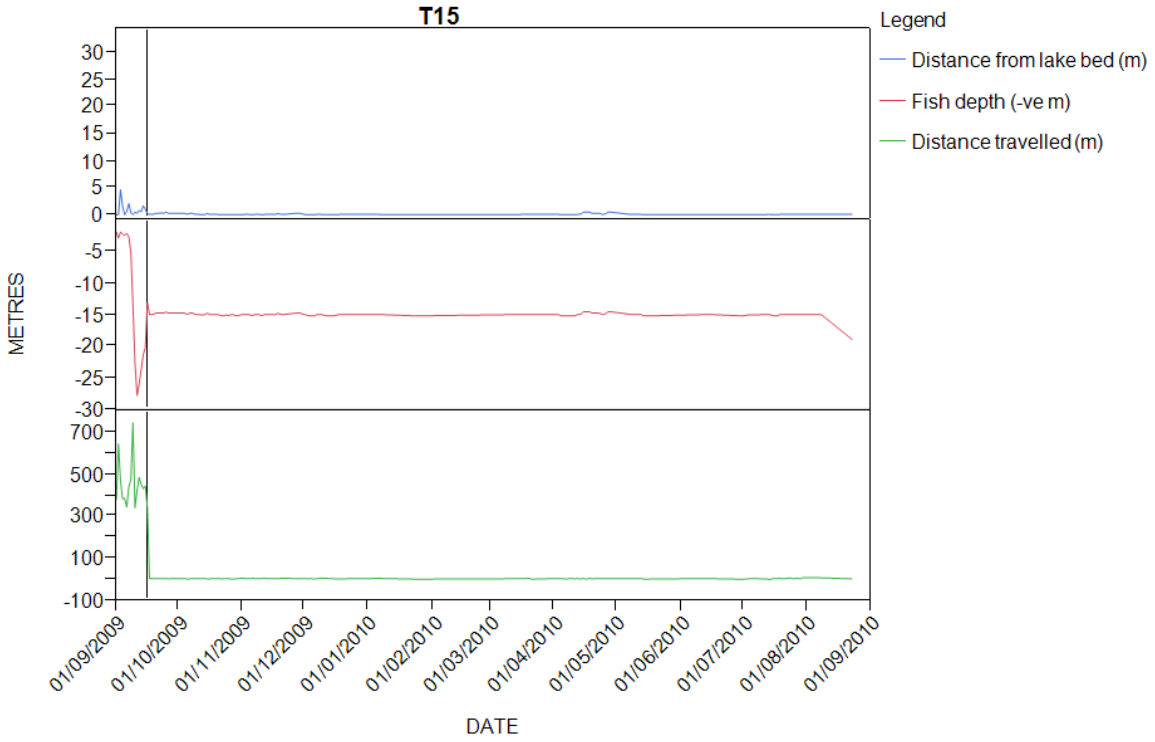
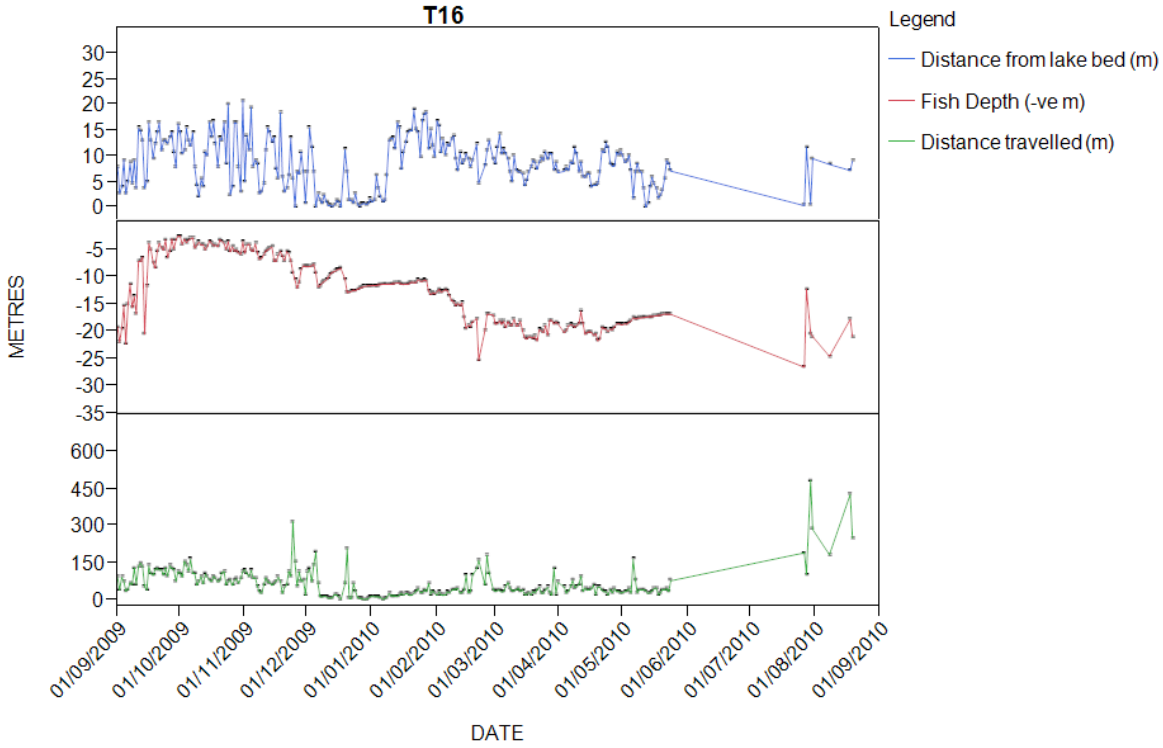
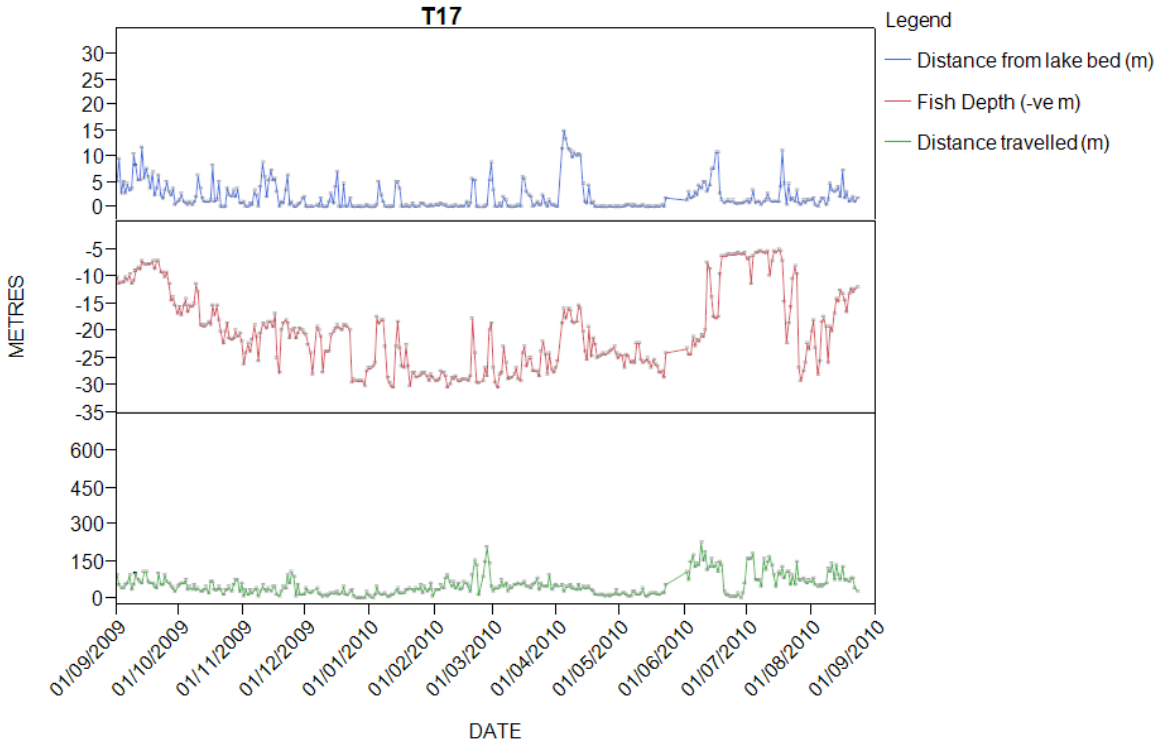
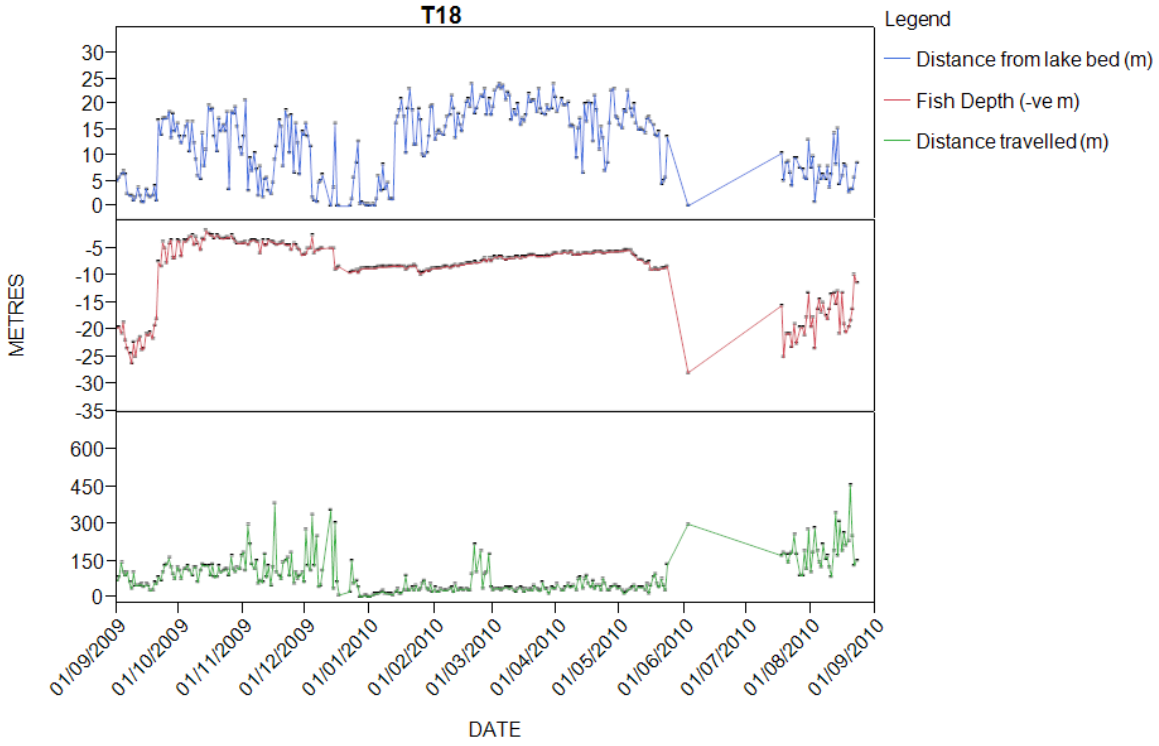
DATE

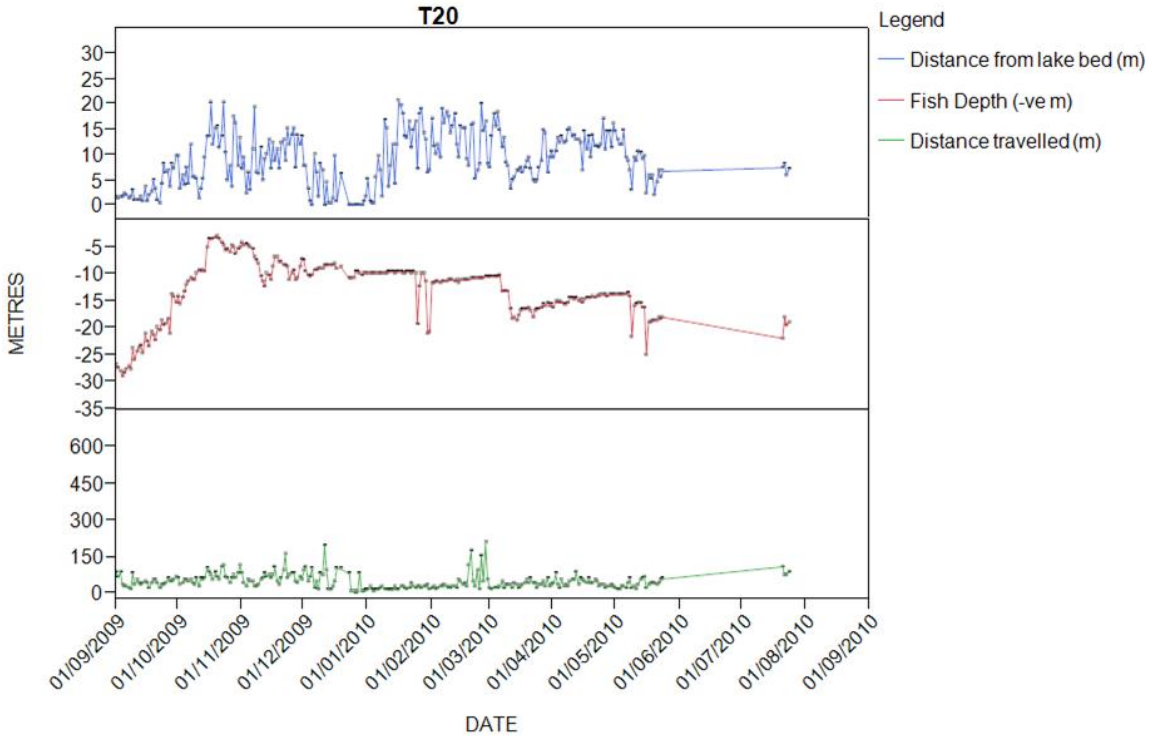

T14
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

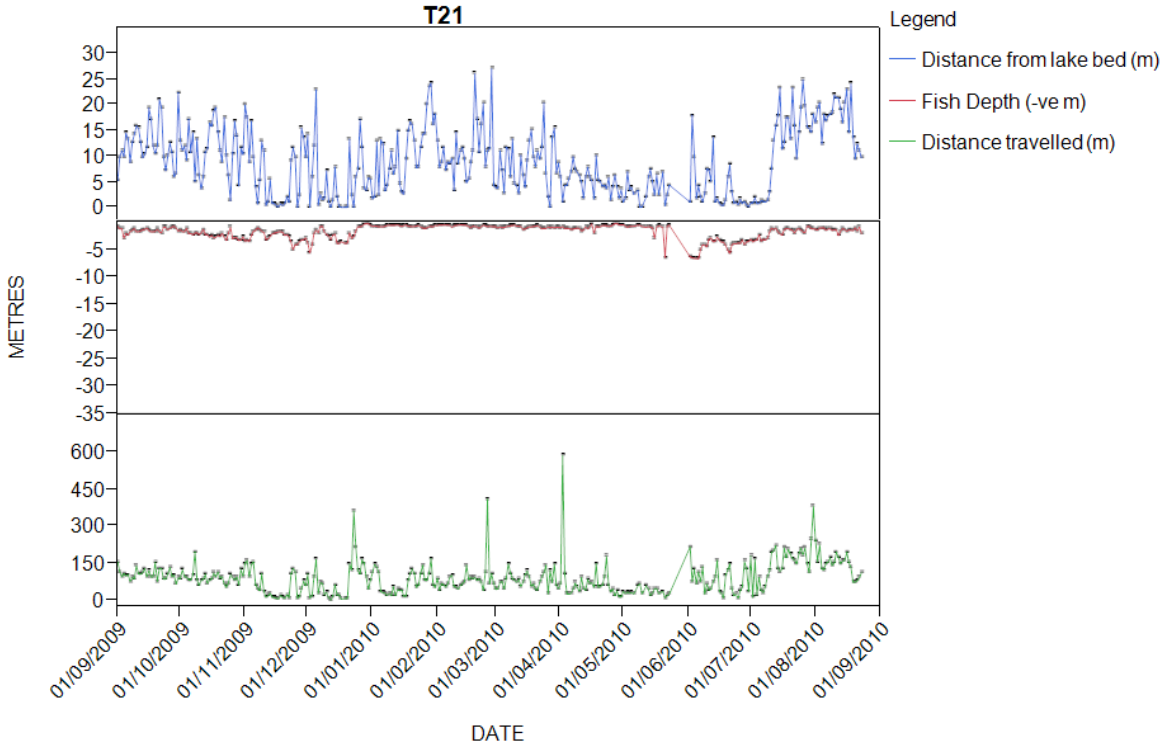

T15
Legend
Distance from lake bed (m)
Fish depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
700
500
300
100
-100
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

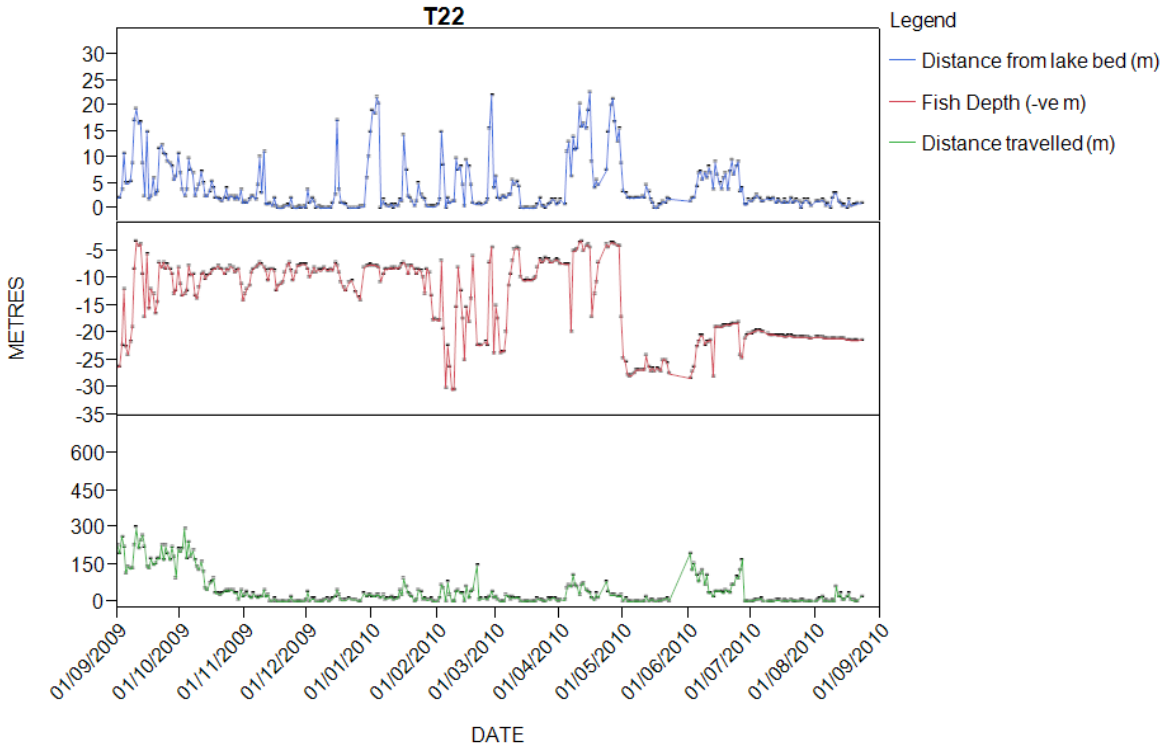

T16
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

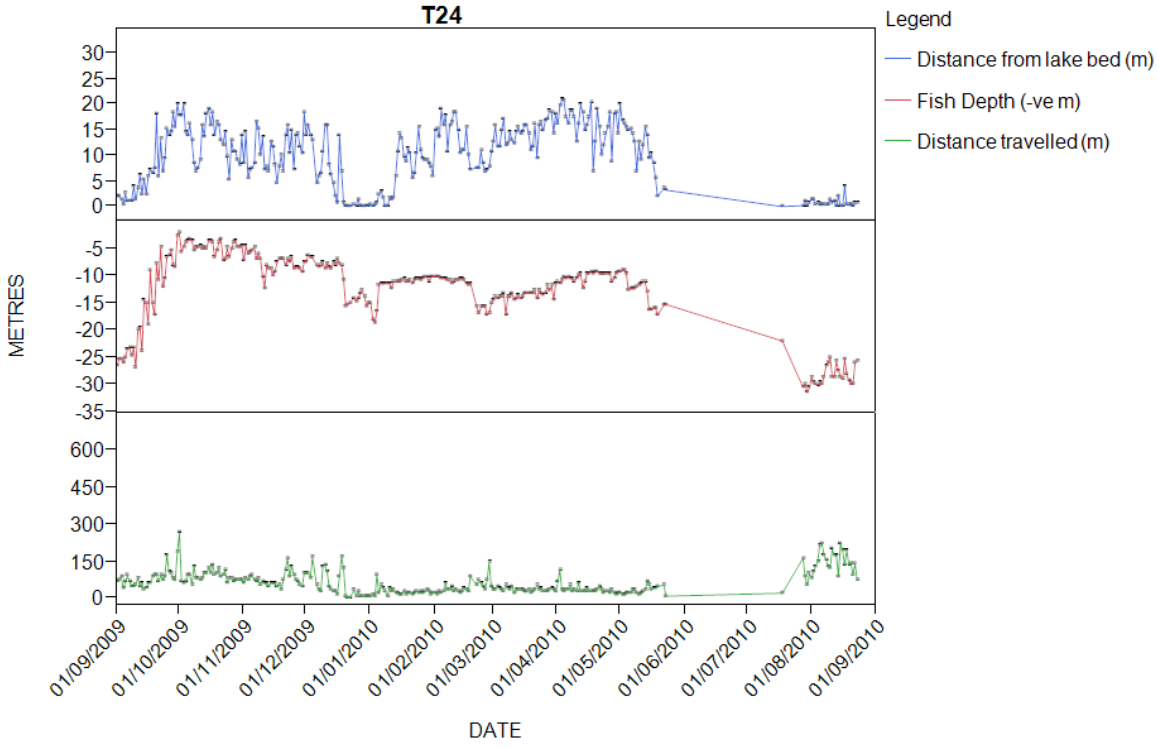

T17
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

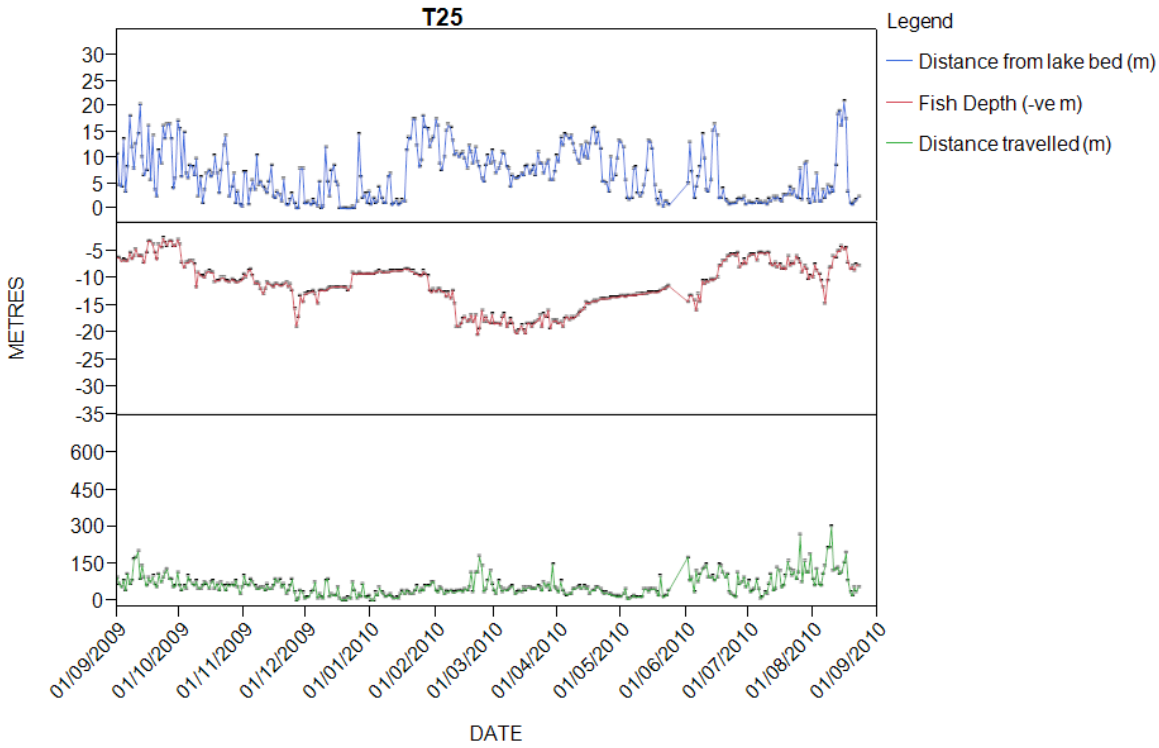

T18
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

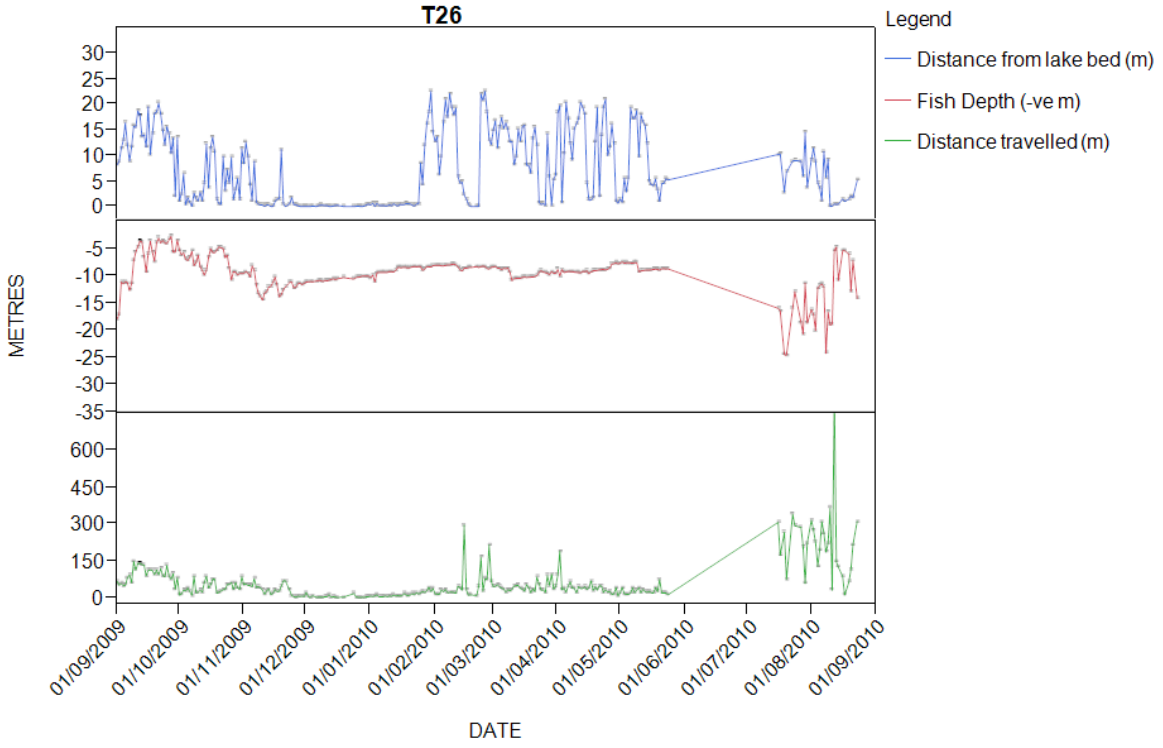

T20
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

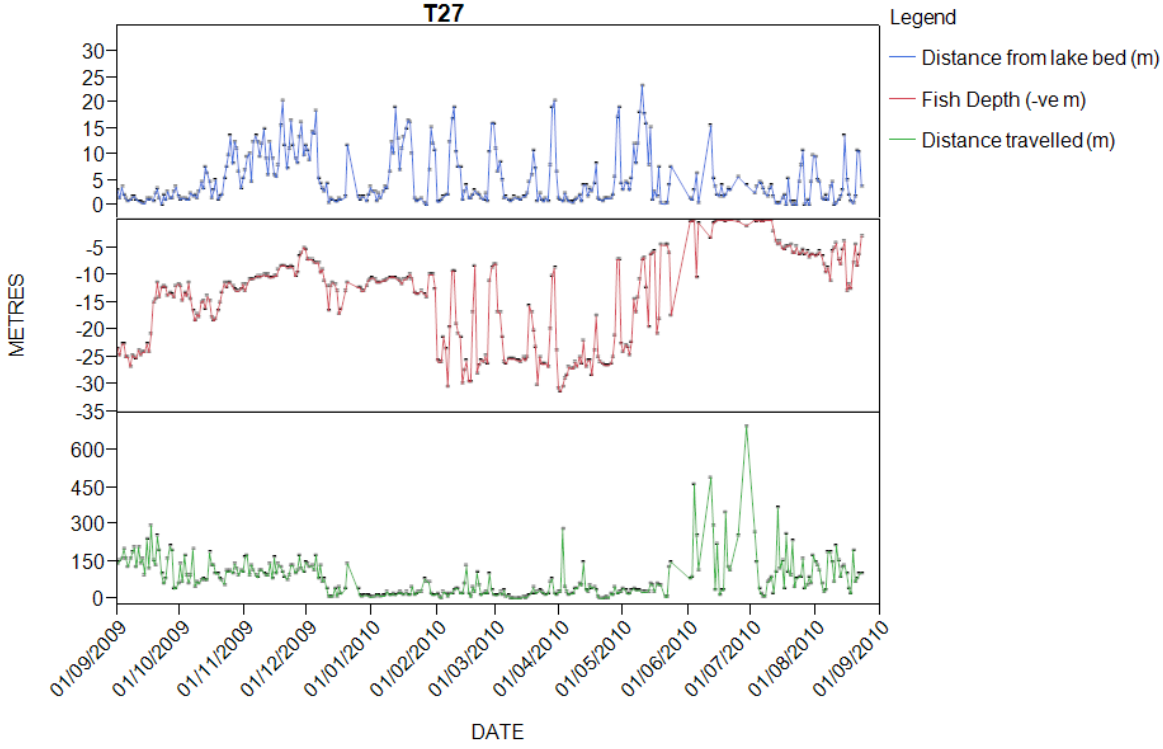

T21
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

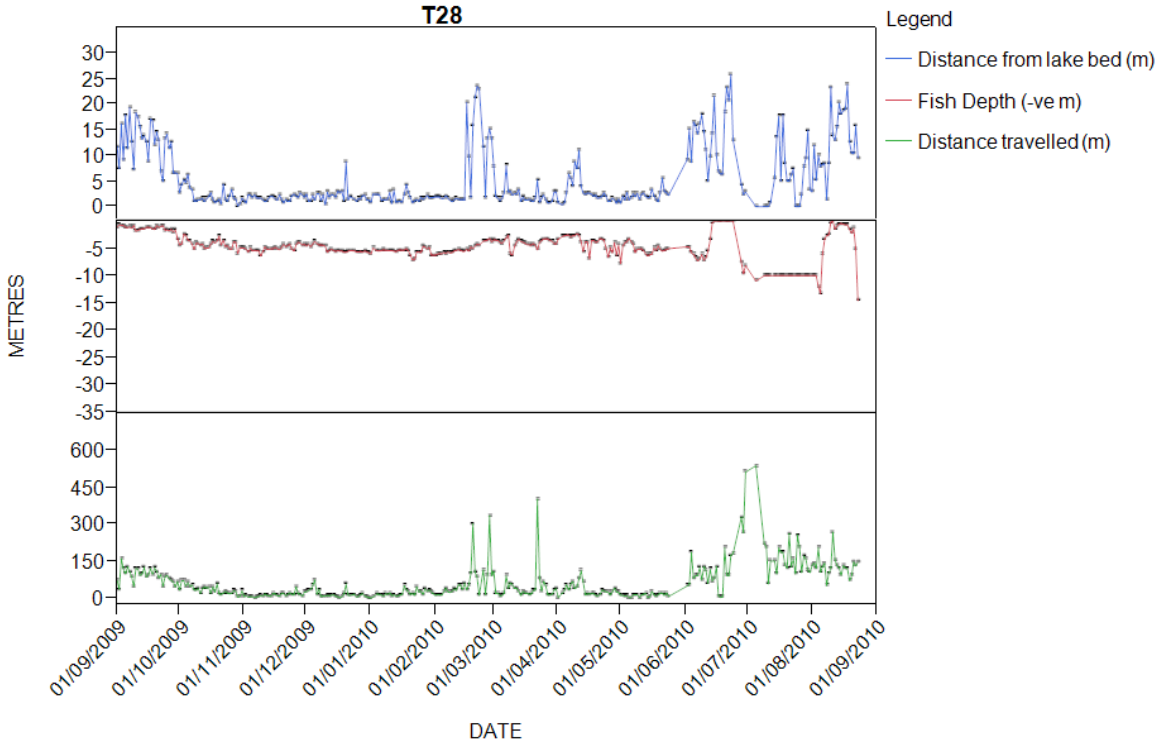

T22
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

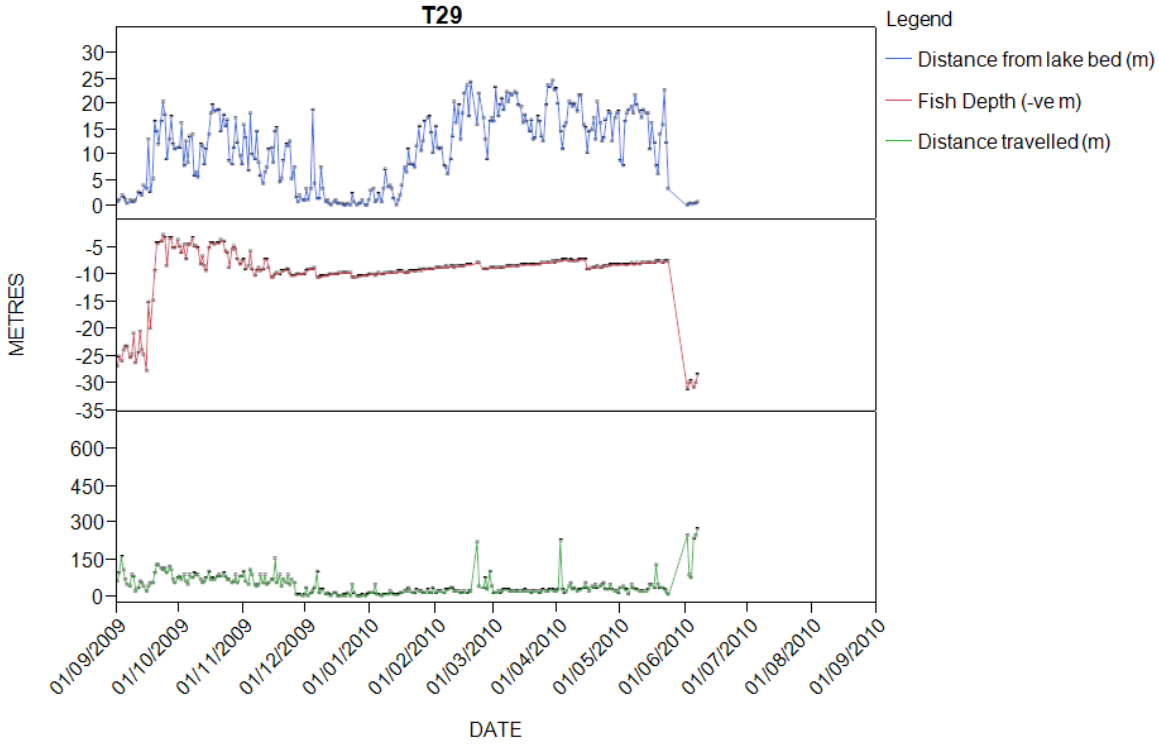

T24
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE

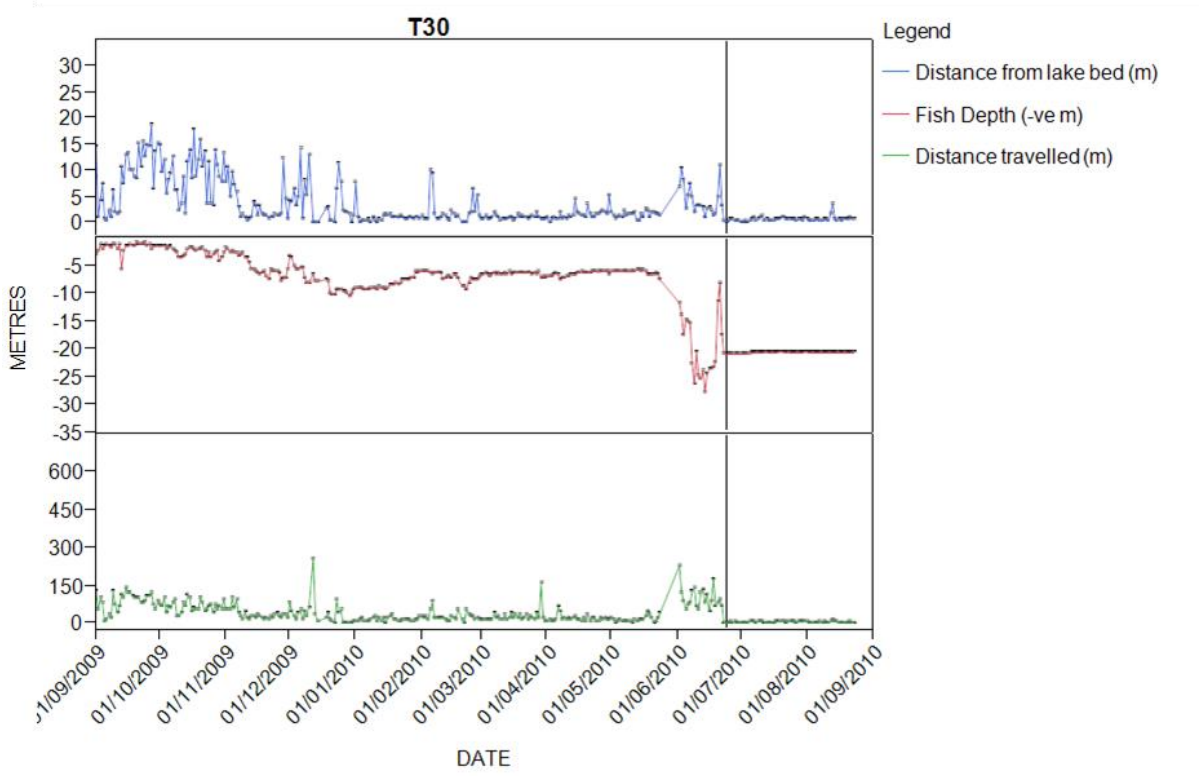

T25
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T26
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T27
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T28
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T29
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
01/06/2010
01/07/2010
01/08/2010
01/09/2010
DATE


T30
Legend
Distance from lake bed (m)
Fish Depth (-ve m)
Distance travelled (m)
METRES
30
25
20
15
10
5
0
-5
-10
-15
-20
-25
-30
-35
600
450
300
150
0
01/09/2009
01/10/2009
01/11/2009
01/12/2009
01/01/2010
01/02/2010
01/03/2010
01/04/2010
01/05/2010
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01/07/2010
01/08/2010
01/09/2010
DATE

9.4 Appendix IV- incomplete fish positional data

Temporal 'tracking' information of individual Arctic charr was calculated (summarised in Table 5-9) and individual plots are given in 9.3 Appendix III - individual fish tracks. From these figures it was possible to observe; a) the duration of positional data, b) gaps in positional data and c) stationary positional data relative to lake depth, for each tagged individual. From this, the spatial validity of each fish track could be assessed on a temporal scale for the study duration (1/9/2009 – 23/8/2010, 357 days). Validity of positions was determined by manually as**s**essing the individual fish tracks for any periods of sustained lack of movement, horizontally and vertically, with fish depth being equal to lake depth (see 5.4.3 Individual fish fate and validity of VPS fish positions, for further description).

9.4.1 Static positions: an indicator of fish position accuracy

According to the tracking of consecutive positional data, four fish displayed no significant movement, i.e. fish positions became stationary when compared to prior tracking data of the individual (see 5.4.3 Individual fish fate and validity of VPS fish positions, for further description). An example is given in Figure 9-1, which plots the daily averaged distance travelled (metres), fish depth (negative metres) and fish distance from lake bed (metres) of the fish T15. It is clear from the graph that the fish stops moving in both a horizontal and vertical direction. According to the figure, all fish positions after the 16/9/2009 (indicated by black line on the date axis) show the fish is on the lake bed.

When shown spatially (Figure 9-2), the lack of horizontal movement after the 16/9/2010 (red positions) becomes apparent. This lack of movement both vertically and horizontally indicates that T15 is almost certainly dead and the tag signal is being detected from the bottom of the lake. All 'no movement' positions can therefore be considered stationary or 'static'. Accordingly, the 2DRMS value of these static fish tags can be calculated to estimate the accuracy of a 95 % confidence radius of VPS derived fish tag positions (see 5.4.1 Accuracy of sync tag positions, for further description). The 2DRMS radius of the static positions of T15 (5.54 metres) is shown in Figure 9-2.

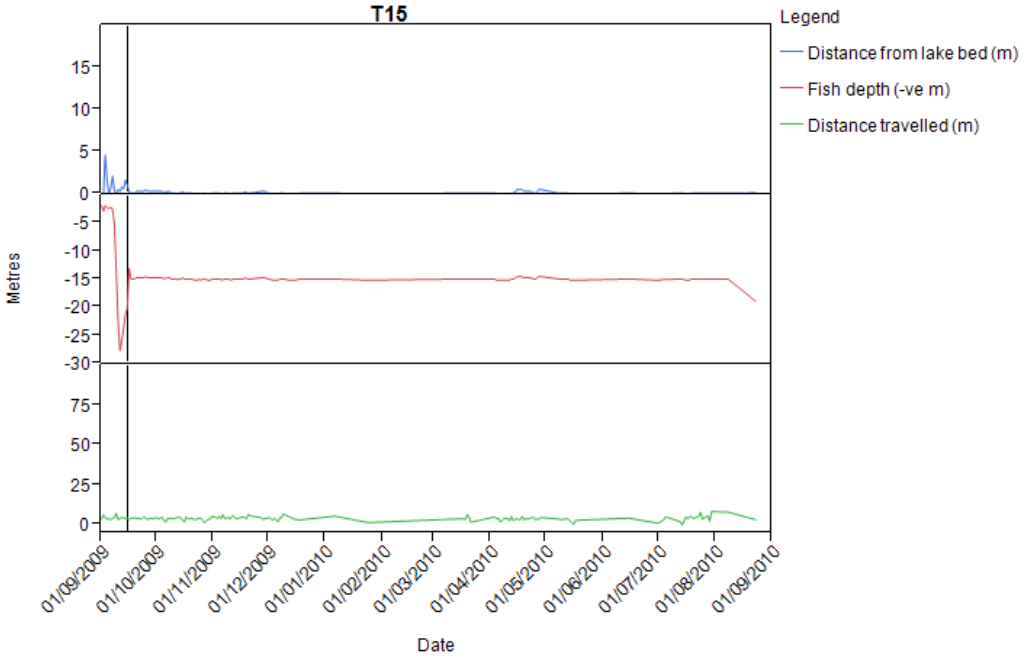

Figure 9-1: Daily average values of; fish distance from lake bed (metres), fish depth (negative metres) and minimum distance travelled (metres) for the individual fish T15. The black line on the date axis marks the 16/9/2010, the date movement of this individual becomes static.

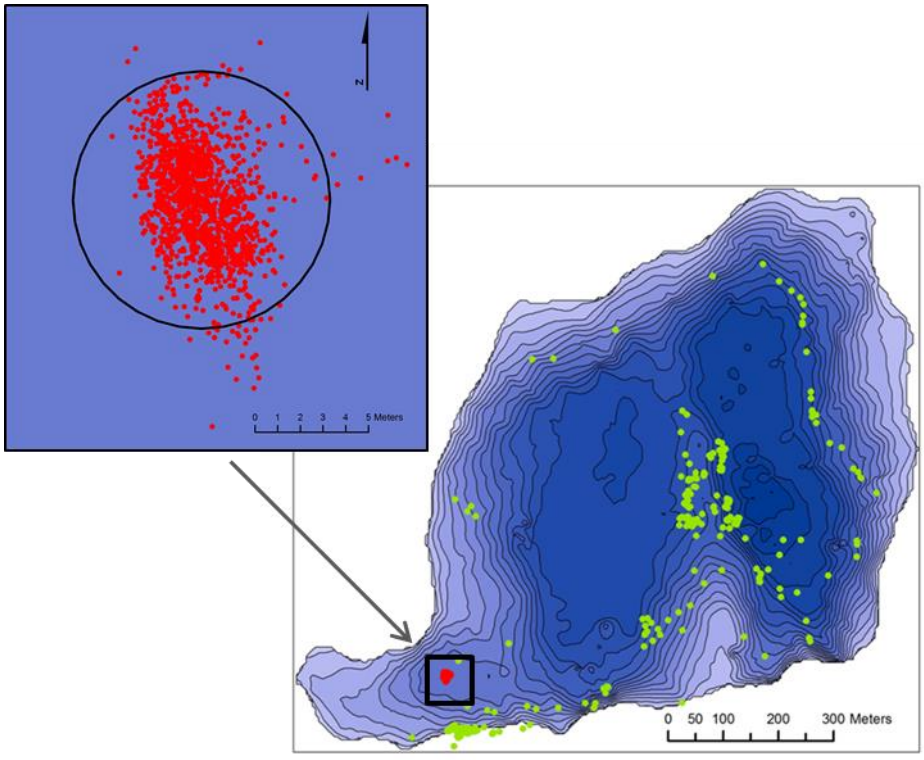

Figure 9-2: All VPS derived fish positions for T15. The green points are the valid positions, during the period of fish movement. The red positions recorded between the 17/9/2009 – 23/8/2010 when the fish tag becomes 'static'. The radius of 2DRMS, 5.54 m is shown in the insert. Map shading is darker with increased lake depth, with contour lines at 2 m depth intervals.

A lack of movement was identified in four individuals; T02, T08, T15 and T30. In all instances the mean daily values of distance travelled (m) and distance to the lake bed (m) were significantly different (*ANOVA*: 1 *df*, $p < 0.0001$) during this stationary period than observed in previous tracking activity. These positions were therefore deemed static or in-valid and were excluded from further analysis. The horizontal distribution (calculated as 2DRMS), the number of positions and duration of the stationary period were defined for the four fish (Table 9-1). The static positions of the four 'no movement' fish are shown in Figure 9-3.

Table 9-1: The duration and number of each static fish tag position is given, including a daily average number of static positions. The radii of 2DRMS values for each fish tag are also stated.

Static fish ID	Period of static position data	*n* of days in static position	*n* of static fish tag positions	Average *n* of daily static positions	Radius of 2DRMS of static positions (m)
T02	17/7/2009 – 23/8/2010	36	423	12	8.01
T08	25/1/2009 – 22/7/2010	176	69	< 1	7.04
T15	18/9/2009 – 23/8/2010	335	1367	4	5.54
T30	24/6/2009 – 23/8/2010	60	1149	19	12.75
					Average: 8.33

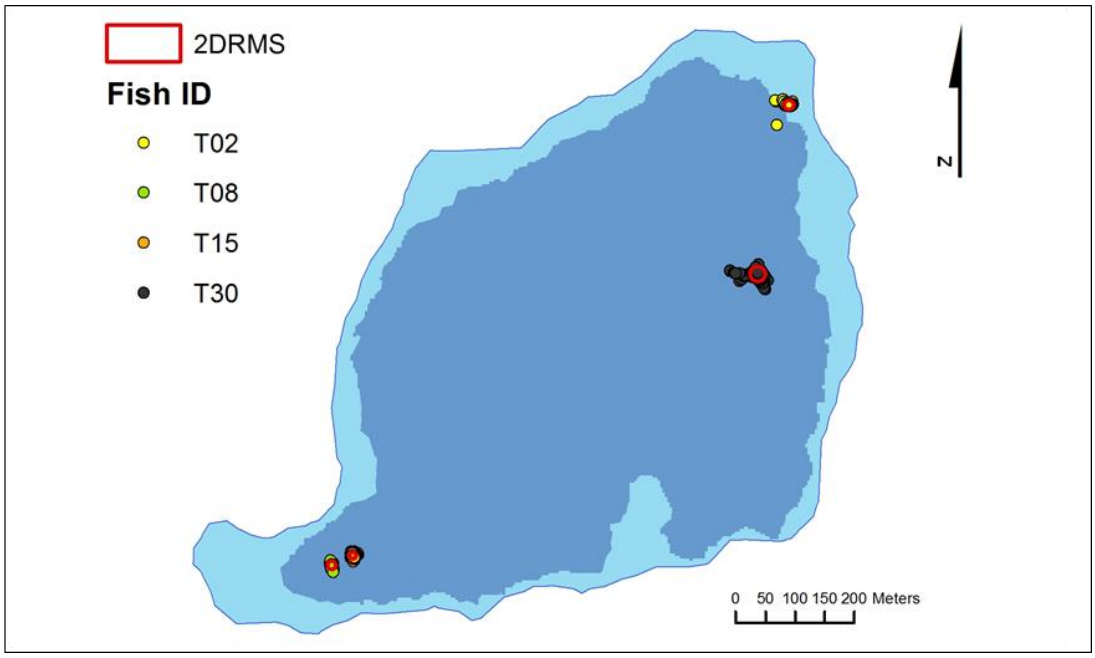

Figure 9-3: The VPS derived positions of the four fish identified as static are plotted and 2DRMS radius is shown in red. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

9.4.2 Premature ceasing of positional data

The positional data of three individuals (T04, T06 and T29) stopped before the retrieval of the VPS (23/8/2010), see 5.4.3 Individual fish fate and validity of VPS fish positions for further description. The spatial distributions of the final ten, valid positions of these three fish were plotted for visual assessment (Figure 9-4).

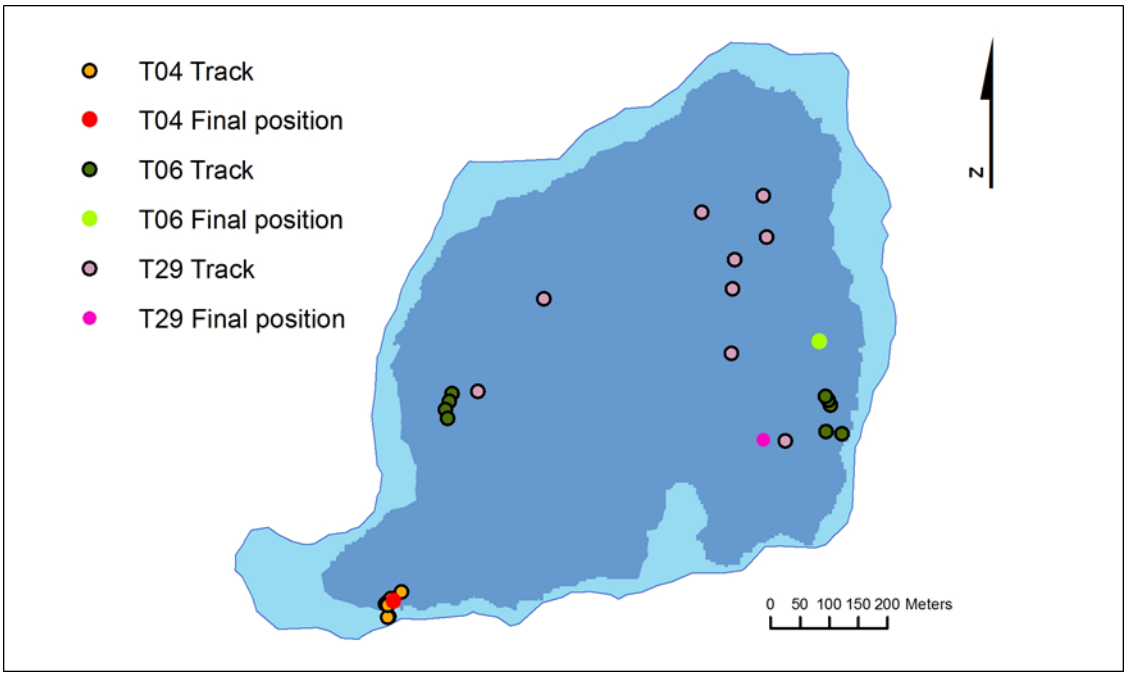

Figure 9-4: The final ten, valid positions of each of the three Arctic charr for which transmitters detections stopped prior to the retrieval of the VPS. Positions are coloured by individuals according to the legend, with the bright coloured points representing the final position. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

9.4.3 Gap in positional data

A 'gap' in position data was defined by an absence of fish position for any given date over the study duration. For five individuals a sustained gap in positional data was observed, with no positions derived for these fish for between 55 to 64 consecutive days mid-deployment, i.e. tracking data of these individuals resumed after this gap in tracking data (see 5.4.3 Individual fish fate and validity of VPS fish positions for further description). The track of the ten consecutive true positions both prior to and post this gap in detections were plotted in order to assess the spatial distribution of these fish immediately pre and prior a gap in data occurred (Figure 9-5).

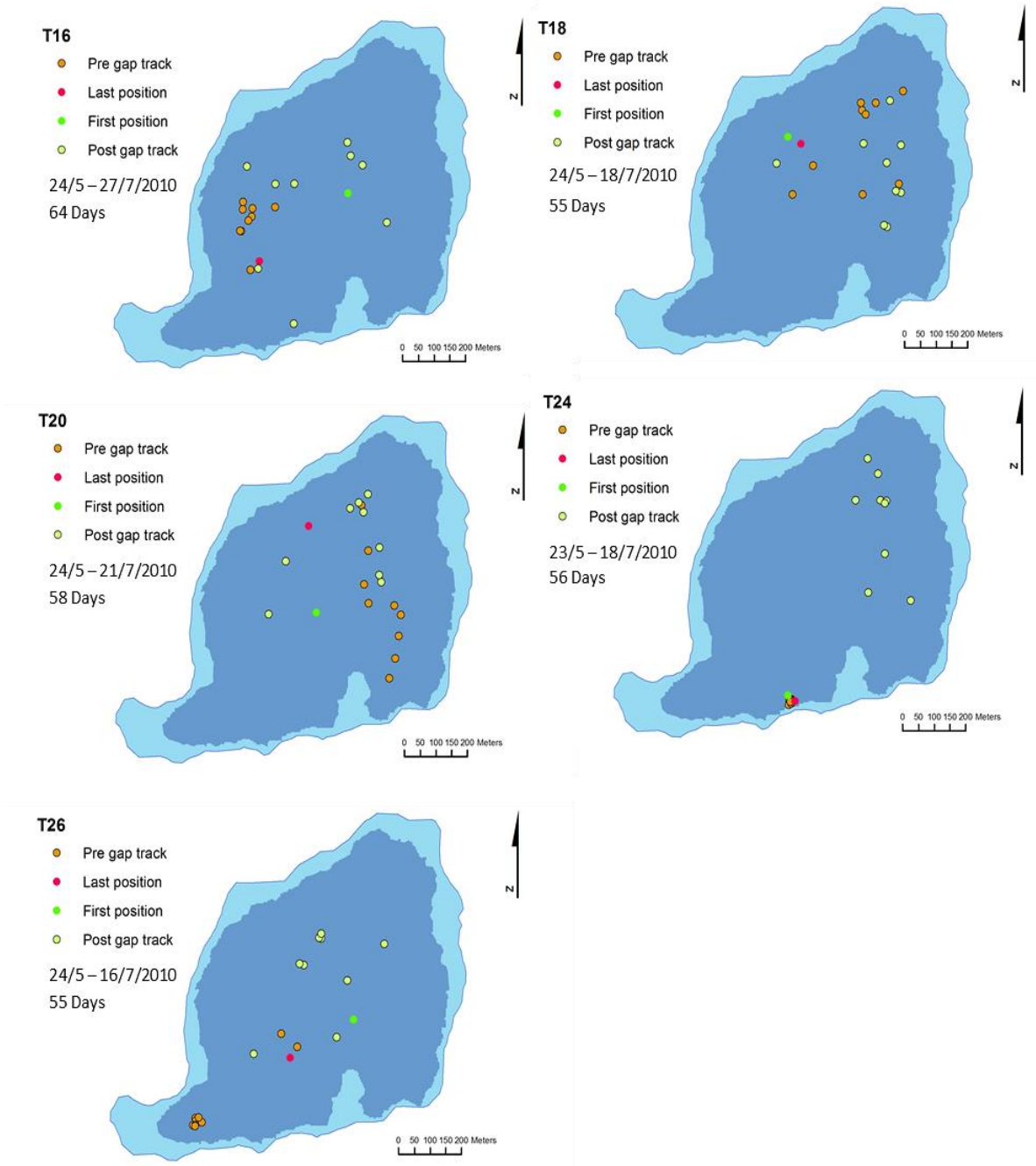

Figure 9-5: The track of the ten consecutive true positions both prior to and post a gap of a least 55 days in individual fish positional data. The five fish are presented individually, the last position pre data gap is shown in red, and the first position post detection gap is green. The background map of Ellasjøen is shaded according to the depth of the lake; light blue 0 – 8 m (littoral zone), darker blue 9 – 34 m (offshore zone).

9.5 Appendix V - fish sample overview

A summary of the number of individuals for which valid positional data was derived (i.e. post data treatment) according to each of the morphology groups identified in 5.1.1: Visual determination of phenotype.

Table 9-2: The number of individuals for which valid positional data was derived for each morph group identified per month of study duration (September 2009 – August 2010).

	n of individuals per Arctic charr morph				
Month	Robust	Delicate	Dwarf maturing	Other	Unclassified
Sep	14	9	2	1	1
Oct	14	9	2	1	1
Nov	14	9	2	1	1
Dec	14	9	2	1	1
Jan	14	9	2	1	1
Feb	14	8	2	1	1
Mar	14	8	2	1	1
Apr	14	8	2	1	1
May	14	8	2	1	1
Jun	14	5	1	1	0
Jul	12	6	1	1	0
Aug	11	6	1	1	0