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Distribution, characteristics and condition of Arctic charr (*Salvelinus alpinus*) spawning grounds in a differentially eutrophicated twin-basin lake

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Abstract – Spawning is a key but often fragile event in the life cycles of fish populations. Nevertheless, it has been relatively little studied for lithophilic lacustrine species requiring hard spawning substrates, such as gravels or stones, largely devoid of fine sediments. Twelve demonstrated or putative spawning grounds of Arctic charr (*Salvelinus alpinus*) in shallow and deep areas of the north and south basins of the eutrophicated lake of Windermere, U.K., were described by hydroacoustic, physical and visual surveys. In addition, their current conditions were compared with their original qualitative descriptions made over 50 years ago. Spawning ground characteristics were found to be more complex than originally described, with considerable overlaps in depth ranges and only limited areas of appropriate hard substrates. Moreover, extensive gill netting surveys in recent years have found spawning Arctic charr at only seven of the original 12 demonstrated or putative spawning grounds, although several new spawning areas have also been found. The distribution of unsuitable fine sediments is widespread in the lake, particularly in the more eutrophicated south basin where suitable spawning habitat within the putative spawning areas is limited. Windermere faces a number of environmental problems including climate change and species introductions. However, the temporal and spatial patterns of the lake's eutrophication suggest that associated increases in fine sediments have been a major driver of the observed deterioration of Arctic charr spawning grounds and so may have also contributed to a marked decline recently observed in the local abundance of this species.

Key words: Arctic charr, *Salvelinus alpinus*, U.K., Windermere, spawning grounds, littoral, bottom substrate, eutrophication

Introduction

The act of spawning is a key but often fragile event in the life cycles of fish populations. In fresh waters, it has been well studied for lithophilic riverine spawners as reviewed by Klemetsen et al. (2003) for the widespread salmonids Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). Successful recruitment in such species requires their access to spawning grounds in appropriate condition, for which an absence of excessive fine sediments is a critical requirement. In contrast, the lacustrine spawning grounds of these and other lithophils have received much less attention. Although a few studies have investigated aspects of the lake spawning habitats of the salmonids Arctic charr (*Salvelinus alpinus*) (Jonsson and Hindar 1982), lake trout (*Salvelinus namaycush*) (Gunn and Sein 2000) and brook trout (*Salvelinus fontinalis*) (Blanchfield and Ridgway 2005), such detailed lacustrine investigations remain sparse for salmonids in general (Klemetsen et al. 2003; Winfield 2004).

Recently, Low et al. (2011) have partially addressed this lack of information for lacustrine lithophilic spawners by describing the littoral spawning habitats of the holarctic Arctic charr in three lakes in Ireland. Using a combination of fyke netting and snorkelling, the physical characteristics of 23 discrete spawning sites were described as narrow strips of hard substrates with clean interstitial spaces running parallel to the shore at a maximum depth of 1.2 m. The lacustrine spawning ecology of Arctic charr populations is further complicated by the fact that although many populations spawn in the littoral zone, some spawn at greater depths (Klemetsen et al. 2003). Furthermore, some lakes support both shallow- and deep-spawning populations, making this species of great interest for studies of evolutionary biology (e.g. Adams et al. 2006; Corrigan et al. 2011a). Within-lake diversity in Arctic charr spawning depth has been reported for a number of lakes in Europe and North America, including within the Faxälven water system in Sweden where shallow- (8 to 10 m) and deep-water spawning (up to c. 100 m depth) on a stony bottom was first described by Määr (1949).

In the twin-basin lake of Windermere, U.K., the first detailed observations of Arctic charr spawning in shallow and deep areas were made by Frost (1965). On the basis of netting, observations by divers and local knowledge, Frost (1965) concluded that Windermere's shallow spawning grounds ranged from 1 to 3 m depth and were used during the autumn (mainly November), while the deeper spawning grounds ranged from 15 to 20 m depth and were used during the spring (mainly February to March). The spawning substrate for shallow water sites was described as always hard with a range of particle sizes from sand through to large stones or small boulders up to 0.25 m in diameter, with some locations also having a little silt or a few macrophytes in the form of *Littorella* sp. Deep-water sites, based only on detailed descriptions from the single spawning ground of Holbeck Point, were characterised by Frost (1965) as having a stony bottom.

An improved understanding of Arctic charr spawning grounds is critical for the better management of this species, whether it be for fisheries purposes or biodiversity conservation. At a global level, the status and conservation of this widespread species have given concern for some time (Maitland 1995). More specifically within the British Isles, several Arctic charr populations have already been lost and many more are threatened (Igoe et al. 2003; Maitland et al. 2007; Winfield et al. 2010), including that of Windermere (Winfield et al. 2008). Notably, Igoe et al. (2003) emphasised the susceptibility of this species' shallow littoral spawning grounds to exposure due to falling lake levels or siltation by fine sediments. In particular, eutrophication has the potential to produce major impacts on littoral-spawning fish due to associated increases in fine sediments of algal origin deposited on stones, gravels and other substrates (Winfield 2004). Moreover, such sedimentation is likely to be even greater on deeper spawning grounds due to sediment accumulation processes (Mackay et al. 2012). In the face of this lack of fundamental knowledge and widespread conservation concerns, Low et al. (2011) understandably called for long-term monitoring and comparisons of Arctic charr spawning site habitats amongst lakes of differing conditions such as nutrient loading.

The objectives of the present study were to assess the current conditions of the demonstrated or putative Arctic charr spawning grounds of Windermere initially described by Frost (1965) but subsequently largely unstudied for approximately 50 years. During this period the lake has undergone significant eutrophication, particularly in its south basin (Jones et al. 2008; Winfield et al. 2008), and its Arctic charr population has declined (Winfield et al. 2010). This assessment was accomplished using multi-beam bathymetry, underwater video observations and the collation of historical and contemporary netting information on spawning Arctic charr.

Materials and methods

Study site

Windermere is situated (54° 22’ N, 2° 56’ W; altitude 39 m) in the English Lake District, U.K. It comprises a mesotrophic north basin (area 8.1 km^2, maximum depth 64 m) and a eutrophic south basin (area 6.7 km^2, maximum depth 44 m). The cultural eutrophication of the latter basin accelerated markedly in the mid 1960s due to nutrient enrichment attributed to a combination of growing human population in the catchment, changes in agricultural practice and increased sewage discharge (Parker and Maberly 2000). In recent years, the south basin has shown some response to the introduction in 1992 of tertiary chemical stripping of phosphate at the lake’s sewage treatment plants (Winfield et al. 2008). The fish community is relatively simple with Arctic charr, Atlantic salmon, brown trout, European eel (*Anguilla anguilla)*, perch (*Perca fluviatilis*), pike (*Esox lucius*) and in recent years roach (*Rutilus rutilus*) dominating it, although a number of minor species are also present (Winfield et al. 2011).

Hydroacoustic survey of the lake bottom

A multi-beam bathymetry of the lake bottom was produced in September 2010 using a SIMRAD Kongsberg EM3002D dual head system operating at 300 kHz on the British Geological Survey vessel R/V White Ribbon, providing 100% coverage of both the north and south basins in areas where water depth exceeded 5 m (Miller et al. 2013). Coverage of shallower areas was limited by technical constraints. The resulting hydroacoustic data were gridded at a resolution of 1 m and corrected to Ordnance Datum Newlyn using lake level data from an electronic gauge operated by the Environment Agency. Processed data were exported as xyz coordinates for subsequent analysis in ArcGIS Version 10, where slope, aspect, curvature and hillshade were derived using the Spatial Analyst extension, and subsequently used to calculate the area and depth range of each of the demonstrated or putative spawning grounds described by Frost (1965) by digitising them from the latter's Fig. 1.

Physical survey of the lake bottom

Sixty-nine sediment samples from the lake bed (33 in the north basin and 36 in the south basin) were collected in June 2011 using a 2 L Van Veen F42A grab as described in detail in Miller et al. (2013). Visual descriptions and grain size analysis were used to identify a number of distinct lake bed facies, i.e. gyttja (composed of fine to very coarse organic-rich, olive-green silt), finely-laminated mud, fine sand and gravel. Gyttja is the most prevalent lake bed sediment and covers more than 95% of the lake bed (Miller et al., 2013). Outcrops of bedrock were also identified through underwater video observations (see below).

Visual survey of the lake bottom

Two remotely-operated vehicles (ROVs) were used on visual survey in June 2011, April 2012 and May 2013 to record visual images of the lake bed (Fig. 1). The ROVs were a SeaBotix LBV 150-4MiniROV using a USBL system for precise positioning information, deployed primarily on offshore transects, and a VideoRay Pro 3 XEGTO deployed primarily on inshore transects. The two ROVs surveyed a total of 53 transects (33 in the north basin and 20 in the south basin) typically running from shallower to deeper water (Fig. 1) in order to facilitate the examination of areas of less than 5 m depth which had not been covered by the hydroacoustic survey. Video outputs from both ROVs, including their operating depths, were recorded and subsequently used to produce series of representative still images for each transect.

FIG 1 HERE (approximately)

Within the ROV survey, single transects each of approximately 100 m in horizontal extent running out perpendicularly from the shore at the demonstrated or putative spawning grounds of Frost (1965) at Holbeck Point, Low Wray Bay and North Thompson Holme in the north basin and Baswicks, Blake Holme, Bellman Landing, Stewardson Nab, South Rawlinson Nab and Tower Wood in the south basin undertaken in May 2013 were subjected to a further systematic examination. Following the procedure described by Coyle and Adams (2011) for vendace (*Coregonus albula*) spawning habitat requirements, which are similar to those of Arctic charr, depth-stratified still images were produced and classified as optimal, sub-optimal or poor spawning habitat. This assessment procedure is based on the presence of hard substrate types such as gravels, pebbles, cobbles and boulders, but also takes into account the presence of fine sediments which are unsuitable for spawning by lithophilic species. Such assessments of a total of 92 depth-stratified specific sites along the transects were pooled by basin into 0 to 5 m, 6 to 10 m, 11 to 15 m, 16 to 20 m and 21 to 25 m depth bands.

<u>Collation of information on use of demonstrated or putative spawning grounds and other areas</u>

Information on the historic and contemporary use by Arctic charr of the demonstrated or putative spawning grounds described by Frost (1965) and other potential spawning grounds was collated from published and unpublished studies, primarily by gill netting, undertaken during the autumn and spring spawning periods. Published sources comprised Frost (1965), Kipling and Le Cren (1975), Kipling (1984), Partington and Mills (1988), Winfield et al. (2008), Corrigan (2009) and Corrigan et al. (2011a), with most of these studies involving sampling in both the north and south basins. These observations were augmented by further and generally more recent information from a total of 60 netting events undertaken by some of the present authors between 1993 and 2012 (IJW, unpublished data).

Together, the above collated information covered all of the six north basin and six south basin demonstrated or putative spawning grounds described by Frost (1965) together with an additional two north basin and seven south basin locations containing potential spawning grounds, making a total of 21 locations. Given differing gill net designs and sampling effort, these data are interpreted here simply as the local presence or absence of spawning Arctic charr.

Results

Distribution, characteristics and condition of demonstrated or putative spawning grounds

Areas of the demonstrated or putative spawning grounds ranged from 28,150 m^2 (autumn-spawning ground of Blake Holme) to 186,800 m^2 (autumn-spawning ground of Balla Wray), while depth range varied from the lake margin (autumn-spawning grounds of Low Wray Bay, Red Nab and Stewardson Nab and spring-spawning ground of Holbeck Point) to 57.4 m (autumn-spawning ground of Balla Wray) (Table 1).

Gravels, stones and/or cobbles were present at all the north basin demonstrated or putative spawning grounds with the exception of the spring-spawning ground of Meregarth, which lies at a depth of 17.4 to 40.8 m and at which only gyttja was observed (Table 2, Fig. 2). Even when present, with one exception, such hard substrates were always restricted to less than 5.0 m depth and usually to less than 2.0 m depth. The sole exception was the spring-spawning ground of Holbeck Point, where stones and gravels were also recorded between 20.0 m and 27.0 m depth. No observations of substrate characteristics were made at either of the further two locations in the north basin investigated as potential spawning grounds.

In the south basin, gyttja was predominant at all sites and gravels and cobbles were either absent or restricted to a maximum of 2.4 m depth (Table 3, Fig 3). The exception to this was the autumn-spawning ground of Stewardson Nab, where scattered cobbles and boulders were found up to 15.0 m depth. Observations of substrate characteristics were made only at North Tower Wood amongst the further seven locations in the south basin investigated as potential spawning grounds, where gravels and cobbles were found at up to 1.2 m depth.

TABLE 1 HERE (approximately)

TABLE 2 HERE (approximately)

TABLE 3 HERE (approximately)

FIG 2 HERE (approximately)

FIG 3 HERE (approximately)

In terms of specific spawning requirements, appropriate contemporary spawning habitat was relatively limited within the demonstrated or putative spawning grounds of both basins but particularly so in the south basin (Fig. 4). In the north basin, optimal and sub-optimal spawning habitats together comprised 42% of observations from the 0 to 5 m depth band and were recorded only at the autumn-spawning grounds of Low Wray Bay and North Thompson Holme. Sub-optimal spawning habitat in this basin also occupied 86% of the 21 to 25 m depth band, although such observations were restricted to the spring-spawning ground of Holbeck Point. In the south basin, optimal and sub-optimal spawning habitats were restricted to the 0 to 5 m depth band where they comprised 12% of observations and were restricted to the autumn- spawning grounds of Baswicks, Blake Holme, Stewardson Nab and Tower Wood. Note that transects in the south basin did not encounter any depths beyond 20 m.

FIG 4 HERE (approximately)

<u>Historic and contemporary use of demonstrated or putative spawning grounds and other areas</u>

In the north basin, of the six demonstrated or putative spawning grounds described by Frost (1965), autumn spawning has only been observed at three sites (Low Wray Bay, North Thompson Holme and Red Nab) since the 1980s, and spring spawning at one site (Holbeck Point) as recently as 2006. In addition, two sites have been newly described (High Wray Bay and South Rough Holme) since 2004.

In the south basin, of the six demonstrated or putative spawning grounds described by Frost (1965), autumn spawning has only been observed at two sites (Baswicks and Tower Wood) in 2006, and spring spawning at one site (South Rawlinson Nab) in 2006. In addition, seven autumn spawning sites have been newly described (Beech Hill Sheds, East Grass Holme, North Grass Holme, North Tower Wood, North-west Grass Holme, South Grass Holme and West Grass Holme) since 1993, while spring-spawners have been found at one site (East Grass Holme).

Discussion

The present study assessed the current condition of 12 Arctic charr spawning grounds in Windermere first described by Frost (1965) after a period of approximately 50 years of eutrophication. In particular, the extent of Arctic charr investigations at this lake and the differential impact of eutrophication in its north and south basins together provide a unique opportunity to address the call of Low et al. (2011) for long-term comparisons of this species' spawning habitats under contrasting conditions of nutrient loading. Furthermore, population monitoring has shown that Arctic charr abundance has fallen markedly in the lake's two basins in recent years and particularly so in its more eutrophicated south basin (Winfield et al. 2010). In this basin, since the early 2000s the catch-per-unit-effort of recreational anglers has been consistently and considerably below that recorded at the time of Frost (1965) but in the north basin it has remained at a similar level. Previous studies of this decline have considered the potential effects of reduced oxygen availability (Jones et al. 2008), a recent increase in the potential competitor roach (*Rutilus rutilus*) (Winfield et al. 2008, Corrigan et al. 2011b), climate change (Winfield et al. 2010) and changing predation pressure from pike (Winfield et al. 2012). However, the present investigation is the first study to consider changes in the condition of Arctic charr spawning grounds in this lake.

On the basis of observations up to the mid 1960s, Frost (1965) summarised that Arctic charr in Windermere spawned in the autumn on shallow spawning grounds (1 to 3 m depth) and in the spring on deeper spawning grounds (15 to 20 m depth). In shallow water sites, the spawning substrate was described as hard with a range of particle sizes from sand through to large stones or small boulders up to 0.25 m in diameter. In deep-water sites, spawning areas were described as having a stony bottom. The hydroacoustic survey of the present study has revealed a much more complex picture: areas originally identified as demonstrated or putative autumn-spawning grounds ranged between the lake margin and 57.4 m depth, with all such sites extending to 19.0 m or beyond, while demonstrated or putative spring-spawning grounds extended to depths of 49.7 m. It is possible that the areas identified as demonstrated or putative spawning grounds (or specifically ‘spawning places’) by Frost (1965) are in fact spawning aggregation areas, with the act of spawning being confined to a more specific depth range within them, but it is also possible and perhaps more likely that the depth descriptions presented by Frost (1965) were limited in accuracy and extent by the technology available at that time. In addition, it is also possible that some or even all of the putative sites identified by Frost (1965) were not actually spawning grounds, although this seems unlikely given the degree of her awareness of local knowledge derived from earlier decades of extensive commercial fishing for Arctic charr on Windermere.

Physical and visual surveys between 2011 and 2013 revealed that hard substrates on the autumn-spawning grounds were largely limited to depths of less than 5 m and in many cases to less than 2 m. This finding is in agreement with the earlier description for Windermere provided by Frost (1965) and with those reported from elsewhere for Arctic charr (Klemetsen et al. 2003). Appropriate hard substrate, although not always in an appropriate condition in terms of the required limited presence of fine sediments, was also found in deeper areas of one spring-spawning ground (Holbeck Point) in the north basin and one autumn-spawning ground (Stewardson Nab) in the south basin.

In terms of the requirement of spawning Arctic charr for clean hard substrate largely devoid of fine sediments, the present observations give considerable cause for concern for parts of Windermere. The results suggest suitable spawning habitat within the demonstrated or putative spawning areas is limited. In the north basin, sub-optimal and optimal conditions were together widespread in areas of up to 5 m depth. Sub-optimal conditions were also evident at depths of 21 to 25 m in this basin’s deep-water spawning ground of Holbeck Point. However, in the south basin both sub-optimal and optimal conditions comprised only a small proportion of observations and were never recorded at depths beyond 5 m. Certainly, in the early 2010s no demonstrated or putative Arctic charr spawning sites in the south basin could be described as having at most ‘a little silt’ as was the case 50 years ago (Frost 1965).

The present observations and local knowledge from over 50 years ago presented by Frost (1965) suggest that siltation by fine sediments has occurred in the south basin. This may potentially have been brought about by four types of human impacts, i.e. changes in water level, mineral extraction, increased fluvial deposition and eutrophication. The level of Windermere is influenced by the operation of a sluice on its outflow for flood alleviation purposes and by the periodic limited abstraction of potable water (Pickering 2001). However, the environmental impact of each operation is strictly controlled and is unlikely to have a major impact on shallow water spawning grounds. Furthermore, it is also highly unlikely to have had a differential impact on the two basins. Substantial sand and gravel deposits were commercially exploited up to the early 1970s (Pickering 2001) and extensive traces of such extraction activities remain clearly visible on the bed of the lake (Miller et al. 2013), including on or near demonstrated or putative spawning grounds. While such past mineral extraction may have had some localised impacts on Arctic charr spawning grounds, they are unlikely to be widespread and are also unlikely to have resulted in the increase in fine sediments observed in the south basin. Increased fluvial deposition, for example arising from riverine erosion or landslides in the catchment, may greatly increase the amount of fine sediments on spawning grounds in lakes. Although a recent extensive fluvial audit of the Windermere catchment found relatively little fine sediment currently originating from such sources (Barlow et al. 2009a), it was concluded that local sediment sourcing, transfer and storage processes have been altered by the historical modification of river reaches in the middle and lower catchment and that future management of rivers and riparian land should aim to allow and embrace natural processes (Barlow et al. 2009b).

In contrast to the limited anthropogenic impacts arising from the above factors, the effects of eutrophication are more likely to have been responsible for the general deterioration inferred in the condition of Arctic charr spawning grounds in Windermere. As noted by Maitland (1995), Igoe et al. (2003), Maitland et al. (2007), Low et al. (2011) and many others, increased algal production generated by eutrophication frequently manifests itself as increased fine sediments of algal origin deposited on stones, gravels and other substrates. For Windermere, the local pattern of eutrophication matches the observed deterioration in the condition of spawning grounds both temporally and spatially. In terms of timing, the initial description of demonstrated or putative spawning grounds by Frost (1965) was made in the early 1960s before the lake underwent marked eutrophication and while its limited effects were still similar in the two basins. For example, at this time the mean concentrations of soluble reactive phosphorus during the first 4 weeks of the year varied between 2 and 5 mg m^{-3} in both basins (Winfield et al. 2008). In contrast, the present observations were made after a 30 years period of significant eutrophication such that by the early 2000s levels in the north basin had increased to 4 to 10 mg m^{-3} but in the south basin they had reached 10 to 20 mg m^{-3} and had been higher (Winfield et al. 2008). In terms of spatial differences between the two basins, we infer that a deterioration in the condition of demonstrated or putative spawning grounds is more marked in the more eutrophicated south basin (Winfield et al. 2008), which now exhibits a bottom covering of fine sediments even in large parts of its shallowest areas. Although the problem of eutrophication has been addressed by phosphate stripping of wastewater discharges since 1992, this action has only been partially successful and neither basin of Windermere has yet been returned to the conditions of the 1960s or earlier (Winfield et al. 2008).

The present study also assembled published and unpublished information from a considerable body of netting activities for spawning Arctic charr in Windermere undertaken since the time of Frost (1965). In recent years spawning Arctic charr have been recorded in the north basin at four of the original six demonstrated or putative spawning grounds described by Frost (1965) plus two newly described areas. In the south basin, where more extensive sampling has been undertaken in attempts to find spawning fish, they have been reported from only three of the original six demonstrated or putative spawning grounds. In addition, spawning fish have never been recorded at three south basin sites, and it is possible that these sites were rarely used as spawning grounds. Spawning fish have also been reported at seven newly described areas in the south basin, although five of these are closely clustered around the island of Grass Holme and this area could arguably be better classified as a single site.

Although spawning is not direct evidence of successful subsequent egg incubation and Arctic charr are known to move between the north and south basins of Windermere (Elliott et al. 1996), their high fidelity to their natal spawning grounds (Frost 1963) means that spawning is indicative of at least some recent successful hatching at the locations where fish currently return to spawn. Nevertheless, an overall population decline of Arctic charr in Windermere is evident and concerning (Winfield et al. 2010).

Finally, the production by Miller et al. (2013) of a detailed map of the geomorphological features and sedimentary processes shaping Windermere and its catchment allow the current observations of Arctic charr demonstrated or putative spawning grounds to be considered in the context of the lake’s glacial history. The retreat of the British and Irish Ice Sheet approximately 15,000 years ago resulted in nine sub-basins separated by steps, ridges and isolated topographic highs. These features have been interpreted as the surface expression of recessional moraines and ridge complexes formed during ice retreat (Pinson et al. 2013).

Gravels and other coarse substrates have been transported to the lake through fluvial action, resulting in their distribution in the lake's shallow inshore waters, and thus only a small fraction of the great physical diversity of the bottom of Windermere meets the spawning requirements of Arctic charr. In their mapping of this species' spawning grounds in three Irish lakes, Low et al. (2011) noted that such habitats comprised only 0.4 to 0.7% of the available littoral habitat. The majority of them were located adjacent to steeply shelving areas that Low et al. (2011) considered might have been selected because of their proximity to deep-water, non-spawning habitat that may minimise migratory energy costs or predation risk. In addition, Low et al. (2011) considered that the long and narrow shapes of these spawning grounds resulted from historical hydraulic sorting by wave action producing a localised hard substrate free of fine particles. Similar processes are likely to have occurred in Windermere where many of the spawning grounds are also adjacent to or even enclose steeply shelving areas (see again Fig. 1), particularly on the western shore which was strongly shaped by the retreat of the British and Irish Ice Sheet (Miller et al. 2013). Further consideration of such issues at Windermere would require a higher resolution mapping of the spawning grounds, for example through surveys for deposited eggs as performed by Low et al. (2011) combined with hydroacoustic bathymetric surveys focussed on inshore areas of less than 5 m depth.

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Tables

Table 1. Spatial characteristics of 12 demonstrated or putative Arctic charr spawning grounds described by Frost (1965) in the north and south basins of Windermere. Area and depth range (corrected to Ordnance Datum Newlyn) are derived here from multi-beam bathymetry data. Minimum depths not available due to limitations of the hydroacoustic coverage are indicated by NA.

Basin	Location	Putative spawning time	Area (m^2)	Depth range (m)
North	Balla Wray	Autumn	186,800	6.8 - 57.4
North	Holbeck Point	Spring	40,900	Lake margin – 49.7
North	Low Wray Bay	Autumn	56,360	Lake margin – 32.4
North	Meregarth	Spring	38,700	17.4 – 40.8
North	North Thompson Holme	Autumn	32,300	NA – 19.0
North	Red Nab	Autumn	57,820	Lake margin – 46.0
South	Baswicks	Autumn	88,730	NA – 36.0
South	Bellman Landing	Spring	31,780	NA – 25.2
South	Blake Holme	Autumn	28,150	NA – 33.4
South	South Rawlinson Nab	Spring	30,370	24.0 – 33.5
South	Stewardson Nab	Autumn	34,720	Lake margin – 26.6
South	Tower Wood	Autumn	42,160	NA – 39.0

Table 2. Substrate characteristics in the north basin of Windermere (from physical and visual surveys) and evidence of historic and contemporary use (from published sources and additional netting information) of six demonstrated or putative Arctic charr spawning grounds described by Frost (1965) and (where available) a further two locations containing potential spawning grounds (in italics).

Location	Substrate characteristics	Evidence of use from published sources	Evidence of use from additional netting
Balla Wray	No stones, but cobbles at 1.0 m depth or less to the west.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965); Autumn-spawners caught at 4.0 m depth between 2004 and 2006 at High Wray Bay to the west of this location (Corrigan 2009).	Autumn-spawners caught at 4.0 m depth in 2004 at High Wray Bay to the west of this location.
Low Wray Bay	Gravels and cobbles limited to less than 2.0 m depth, with gravel beach extending offshore at the north. Substrate of gyttja at 8.0 m depth.	Described as an autumn-spawning ground on basis of netting (Frost 1965); Autumn-spawners caught in 1950 (Kipling and Le Cren 1975); Autumn-spawners caught inshore annually from 1939 to 1973 (Winfield et al., 2008); Autumn-spawners caught at 4.0 m depth between 2004 and 2006 (Corrigan et al. 2011a).	No information available.
Holbeck Point	Stones to 5.0 m depth in north, with some gravels and stones also at between 20.0 m and 27.0 m depth.	Described as a spring-spawning ground on basis of netting and diver observations, including of gravel tongue at from 9.8 to 28.0 m depth (Frost 1965); Spring-spawners caught between 1951 and 1957 (Kipling and Le Cren 1975); Spring-spawners caught in 1980s (Partington and Mills 1988); Spring-spawners caught between 2004 and	Spring-spawners caught at up to 10.0 m depth in 1993, 1994, 2004 and 2005.

		2006 (Corrigan 2009); Spring-spawners caught at 10.0 m depth between 2004 and 2006 (Corrigan et al. 2011a).	
Meregarth	No gravels or cobbles, only gyttja.	Described as a probable spring-spawning ground on basis of local knowledge (Frost 1965).	No spring-spawners caught in four netting attempts in 2004.
North Holbeck Point	No information available.	No information available.	No spring-spawners caught in one netting attempt at 40.0 m depth in 2004.
North Thompson Holme	Stones at 1.5 to 2.5 m depth in south-east extending south towards Belle Isle. Gyttja in deeper water in north.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965); Autumn-spawners caught at 2.0 m depth annually from 1975 to 2004 (Winfield et al., 2008); Autumn-spawners caught between 2004 and 2006 (Corrigan 2009); Autumn-spawners caught between 2004 and 2006 (Corrigan et al. 2011a).	Autumn-spawners caught at 2.0 m depth annually from 2005 to 2012.
Red Nab	Gravels at 1.7 m depth in west.	Described as an autumn-spawning ground on basis of netting (Frost 1965); Autumn-spawners caught between 1950 and 1953 (Kipling and Le Cren 1975); Autumn-spawners caught in 1980s (Partington and Mills 1988).	No information available.
South Rough Holme	No information available.	Autumn-spawners and spring-spawners caught between 2004 and 2006 (Corrigan 2009); Autumn-spawners caught at 3.0 m depth and spring-spawners caught at 3.0 m depth between 2004 and 2006 (Corrigan et al. 2011a).	Autumn-spawners and spring-spawners caught at 4.0 m depth in 2004 and 2005 (autumn-spawners) and 2006 (spring-spawners).

Table 3. Substrate characteristics in the south basin of Windermere (from physical and visual surveys) and evidence of historic and contemporary use (from published sources and additional netting information) of six demonstrated or putative Arctic charr spawning grounds described by Frost (1965) and (where available) a further seven locations containing potential spawning grounds (in italics).

Location	Substrate characteristics	Evidence of use from published sources	Evidence of use from additional netting
Baswicks	Predominantly gyttja, with some cobbles in centre. Exclusively gyttja at and beyond 18.0 m depth.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965); Autumn-spawners caught at 4.0 m depth between 2004 and 2006 (Corrigan 2009).	No information available.
Beech Hill Sheds	No information available.	No information available.	Autumn-spawners caught in 1993.
Bellman Landing	No gravels or cobbles, only gyttja with some leaf litter.	Described as a probable spring-spawning ground on basis of local knowledge (Frost 1965).	No spring-spawners caught in four netting attempts in 2004.
Blake Holme	Very limited gravels and cobbles, predominantly gyttja.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965).	No information available.
East Grass Holme	No information available.	Autumn-spawners caught in unspecified area of Grass Holme at 4.0 m depth between 2004 and 2006 (Corrigan 2009).	Spring-spawners caught at 30.0 m depth in 1999.
North Grass Holme	No information available.	Autumn-spawners caught in unspecified area of Grass Holme at 4.0 m depth between 2004 and 2006 (Corrigan 2009).	No autumn-spawners caught in one netting attempt in 2004.
North Tower Wood	Gravels and cobbles at up to 1.2 m depth.	Autumn-spawners caught in 2005 (Corrigan et al. 2011a).	Autumn-spawners caught in 2005.
North-west Grass Holme	No information available.	Autumn-spawners caught in unspecified area of Grass Holme at 4.0 m depth	Autumn-spawners caught in 1993.

		between 2004 and 2006 (Corrigan 2009).	
South Grass Holme	No information available.	Autumn-spawners caught in unspecified area of Grass Holme at 4.0 m depth between 2004 and 2006 (Corrigan 2009).	Autumn-spawners caught at 4.0 m depth in 2004 and 2005.
South Rawlinson Nab	Some gravels and cobbles at up to 2.4 m depth to north-west, but predominantly gyttja with occasional cobbles in deeper areas.	Described as a probable spring-spawning ground on basis of local knowledge (Frost 1965); Autumn-spawners caught in shallow water and spring-spawners caught in deep-water in 1980s (Partington and Mills 1988); Spring-spawners caught to north of area at Rawlinson Nab between 2004 and 2006 (Corrigan 2009); Spring-spawners caught at 20.0 m depth between 2004 and 2006 (Corrigan et al. 2011a).	Spring-spawners caught in 1993, 1994, 1999 and 2004.
Stewardson Nab	Gyttja with scattered cobbles and boulders to 15.0 m depth, beyond which exclusively gyttja.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965).	No autumn-spawners caught in one netting attempt in 2004.
Tower Wood	Very limited gravels and cobbles, predominantly gyttja.	Described as a probable autumn-spawning ground on basis of local knowledge (Frost 1965); Autumn-spawners caught at 6.0 m depth between 2004 and 2006 (Corrigan 2009).	No information available.
West Grass Holme	No information available.	Autumn-spawners caught in unspecified area of Grass Holme at 4.0 m depth between 2004 and 2006 (Corrigan 2009).	No spring-spawners caught in one netting attempt in 1999.

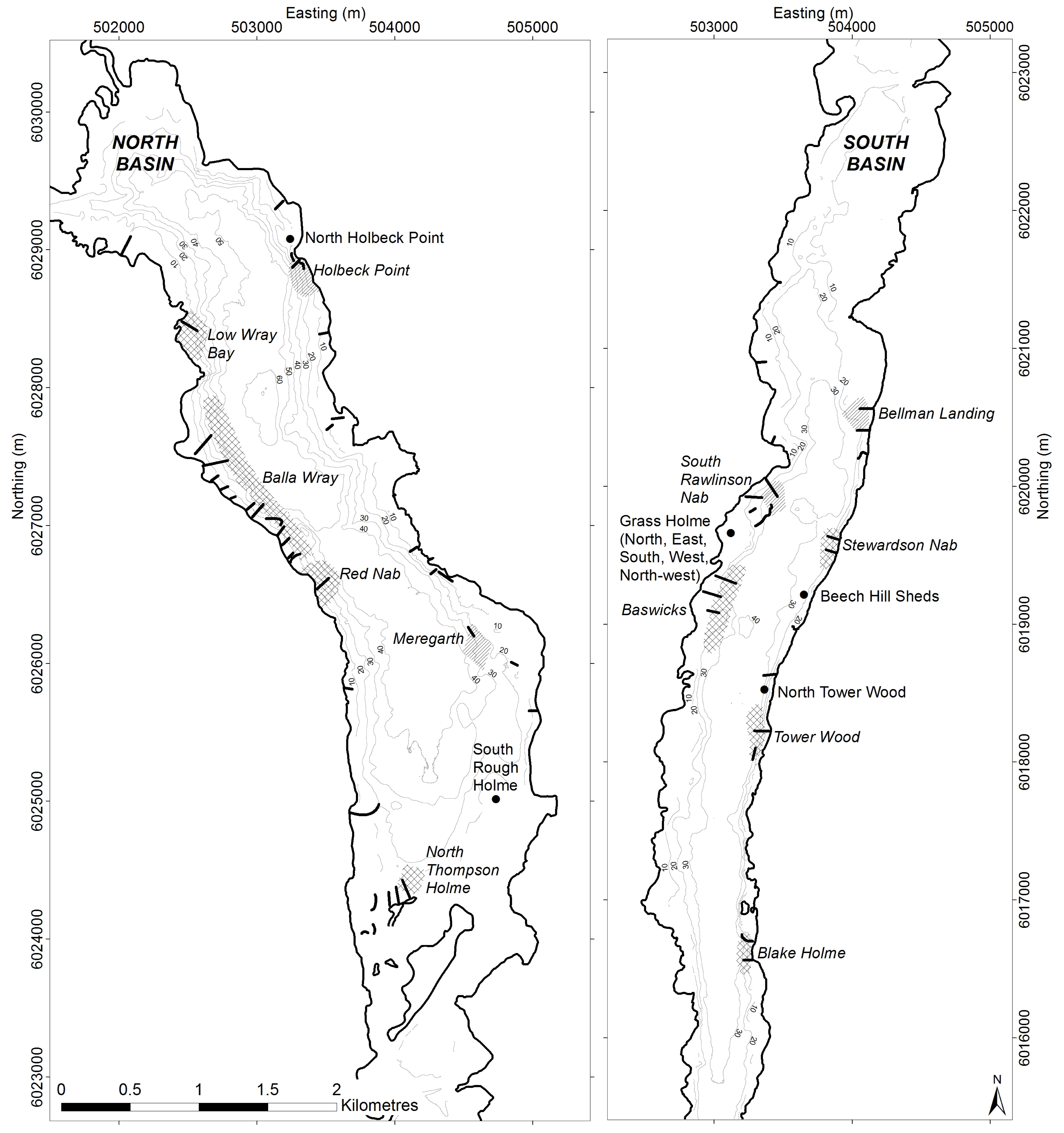
Figure legends

Fig. 1. Location of 12 named demonstrated or putative Arctic charr spawning grounds (cross-shading, eight autumn sites; single-shading, four spring sites) described by Frost (1965) in the north (left) and south (right) basins of Windermere, U.K. A further nine named locations containing potential spawning grounds assessed here are also indicated by closed circles, but note that five locations closely clustered around and named by their bearing relative to Grass Holme are represented by only one closed circle. The locations (solid lines) of visual transects of the lake bottom and 10 m depth contours are also shown.

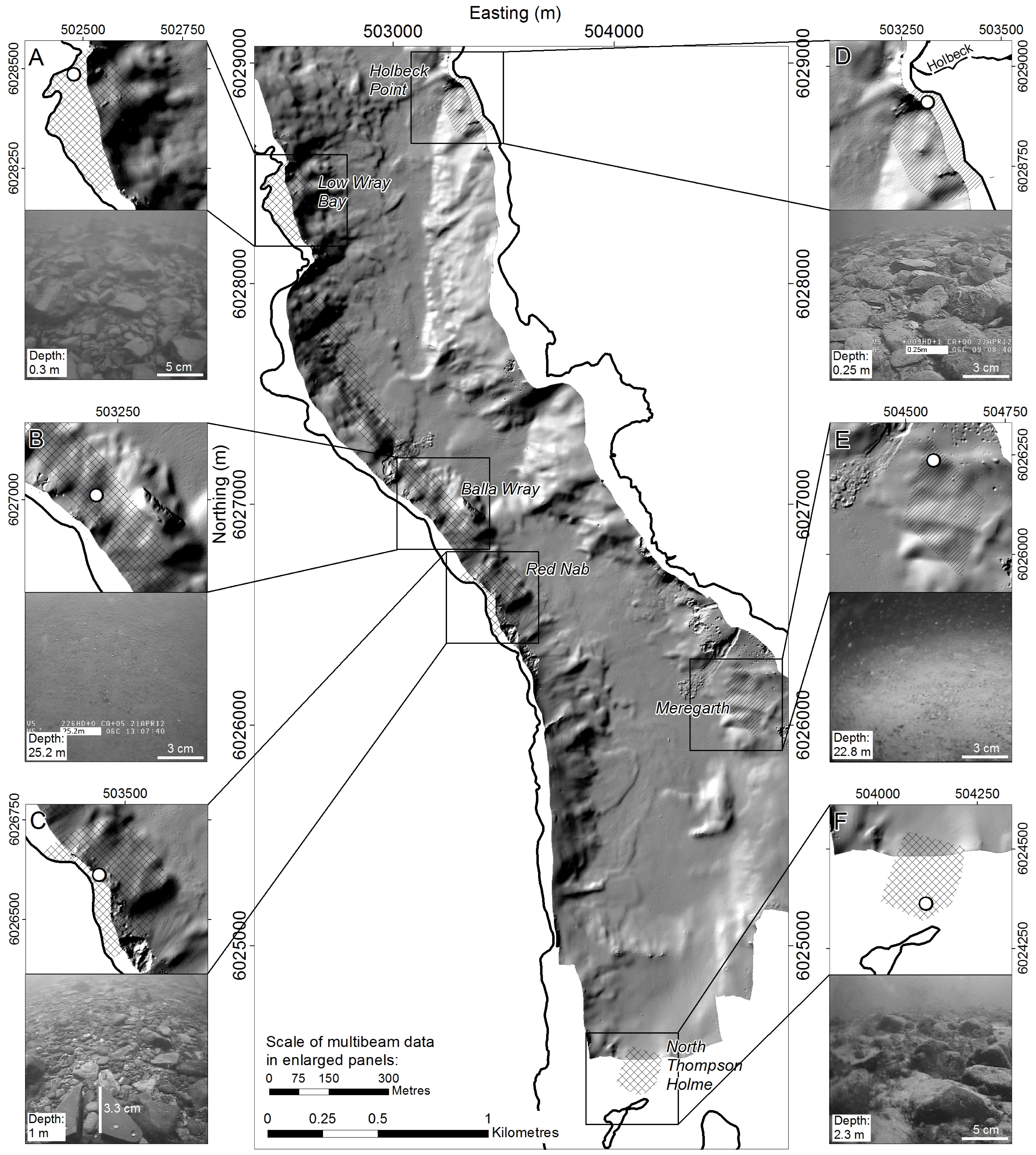
Fig. 2. Multi-beam bathymetry in the north basin of Windermere with inserts, each centred on one of six demonstrated or putative Arctic charr autumn (cross-shading) and spring (single-shading) spawning grounds described by Frost (1965), of bathymetry details and representative still images of the lake bottom. Within the inserts, the precise locations of the still images are indicated by an open circle. Adapted and developed by the addition of inserts from Miller et al. (2013).

Fig. 3. Multi-beam bathymetry in the south basin of Windermere with inserts, each centred on one of six demonstrated or putative Arctic charr autumn (cross-shading) and spring (single-shading) spawning grounds described by Frost (1965), of bathymetry details and representative still images of the lake bottom. Within the inserts, the precise locations of the still images are indicated by an open circle. Adapted and developed by the addition of inserts from Miller et al. (2013).

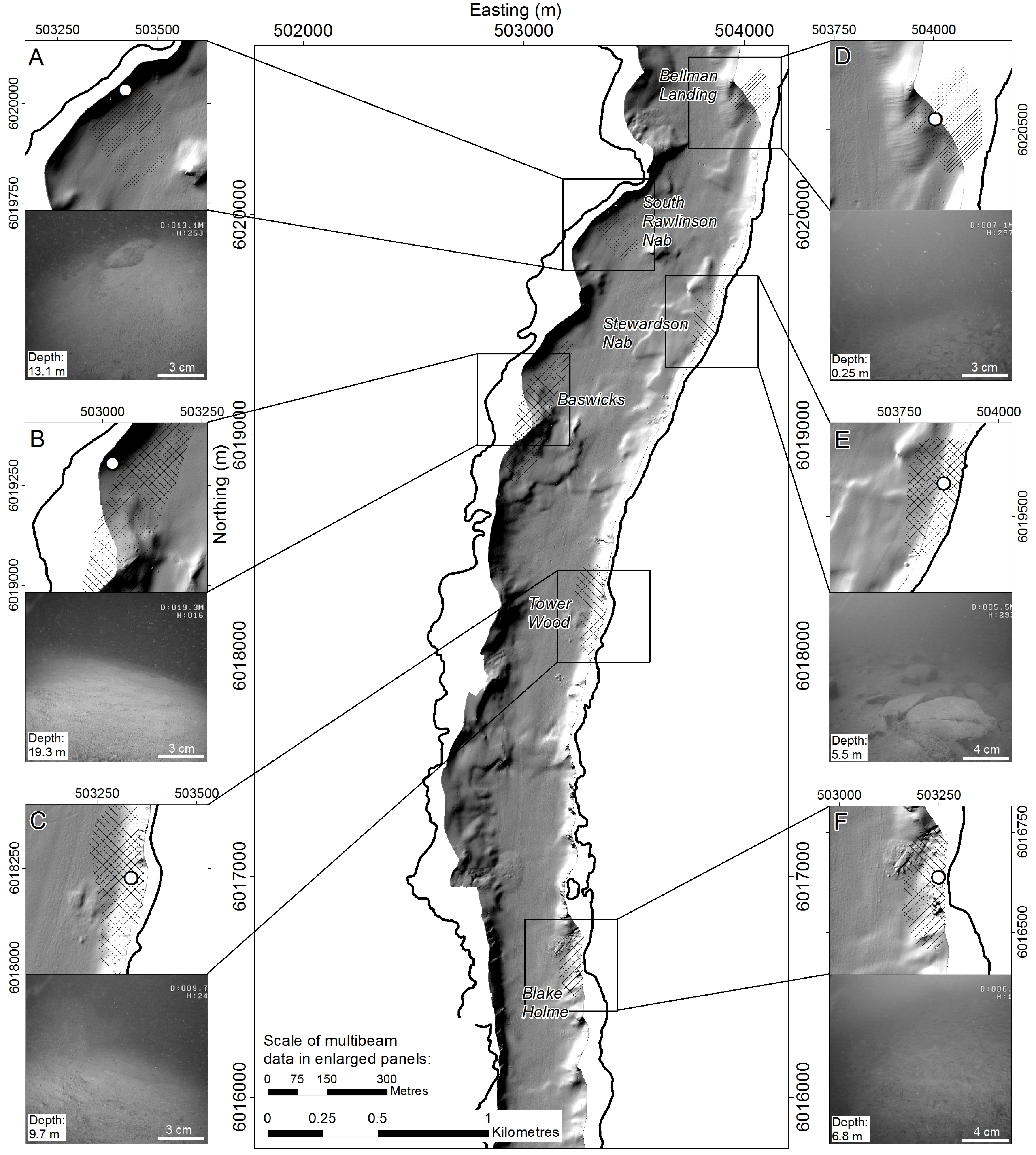
Fig. 4. The relative occurrence (expressed as percentage of all still image observations assessed within a depth zone) of optimal, sub-optimal and poor spawning habitat by 5 m depth zones in the north and south basins of Windermere. Demonstrated or putative spawning grounds examined in the north basin comprised Holbeck Point, Low Wray Bay and North Thompson Holme assessed by a total of 36 still images. Demonstrated or putative spawning grounds examined in the south basin comprised Baswicks, Blake Holme, Bellman Landing, Stewardson Nab, South Rawlinson Nab and Tower Wood assessed by a total of 56 still images. Note that transects in the south basin did not encounter any depths beyond 20 m.



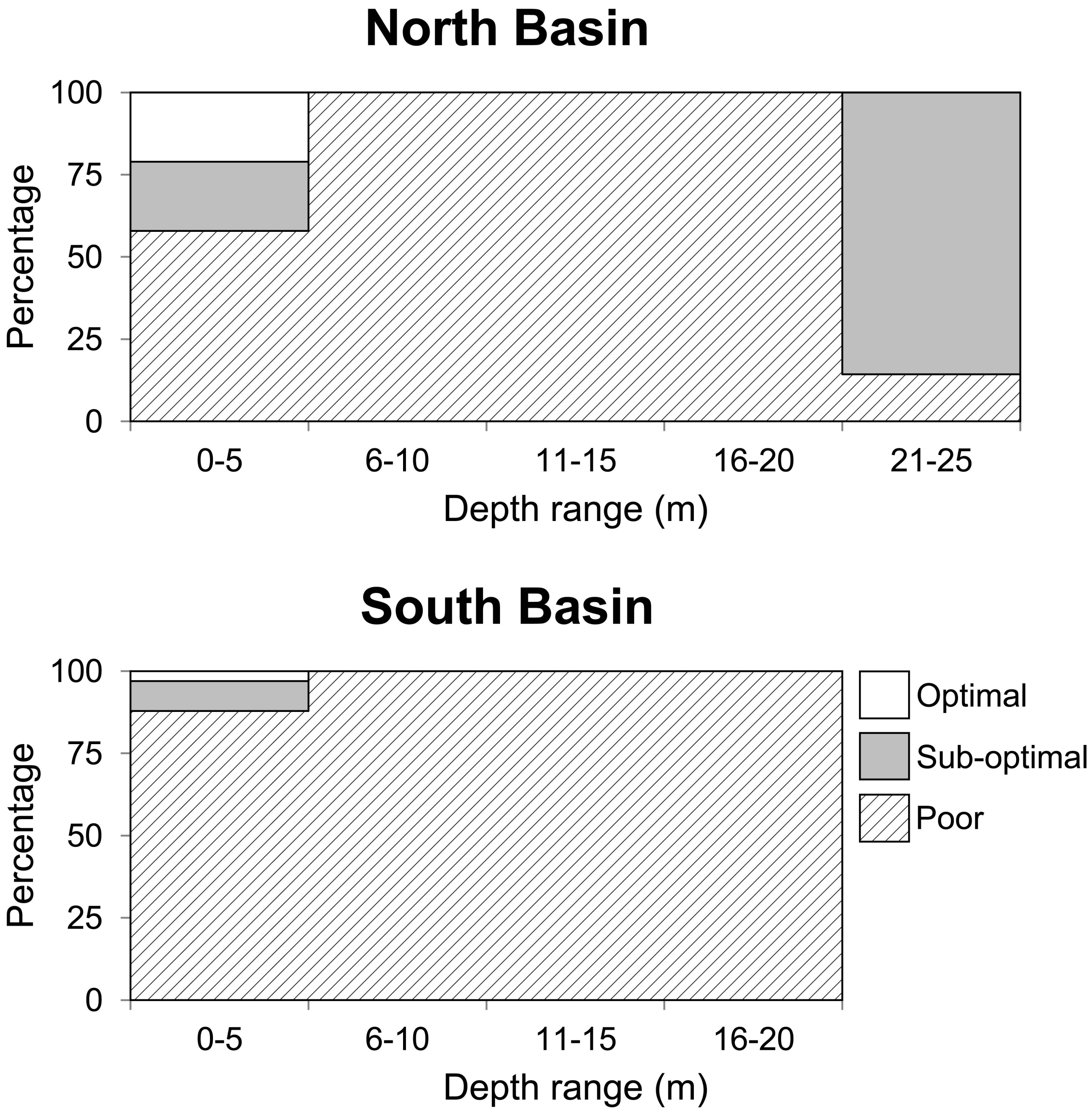
Easting (m)
502000
503000
504000
505000
Northing (m)
6030000
6029000
6028000
6027000
6026000
6025000
6024000
6023000
NORTH BASIN
North Holbeck Point
Holbeck Point
Low Wray Bay
Balla Wray
Red Nab
Meregarth
South Rough Holme
North Thompson Holme
0 0.5 1 1.5 2 Kilometres
Easting (m)
503000
504000
505000
Northing (m)
6023000
6022000
6021000
6020000
6019000
6018000
6017000
6016000
SOUTH BASIN
Bellman Landing
South Rawlinson Nab
Grass Holme (North, East, South, West, North-west)
Stewardson Nab
Beech Hill Sheds
Baswicks
North Tower Wood
Tower Wood
Blake Holme
N



Easting (m)
503000
504000
Northing (m)
6029000
6028000
6027000
6026000
6025000
Holbeck Point
Low Wray Bay
Balla Wray
Red Nab
Meregarth
North Thompson Holme
Scale of multibeam data in enlarged panels:
0 75 150 300 Metres
0 0.25 0.5 1 Kilometres
A
502500
502750
6028500
6028250
Depth: 0.3 m
5 cm
B
503250
6027000
Depth: 25.2 m
3 cm
C
503500
6026750
6026500
Depth: 1 m
3.3 cm
D
503250
503500
Holbeck
6029000
6028750
Depth: 0.25 m
3 cm
E
504500
504750
6026250
6026000
Depth: 22.8 m
3 cm
F
504000
504250
6024500
6024250
Depth: 2.3 m
5 cm



Easting (m)
Northing (m)
Bellman Landing
South Rawlinson Nab
Stewardson Nab
Baswicks
Tower Wood
Blake Holme
Scale of multibeam data in enlarged panels:
0 75 150 300 Metres
0 0.25 0.5 1 Kilometres
A
Depth: 13.1 m
3 cm
B
Depth: 19.3 m
3 cm
C
Depth: 9.7 m
3 cm
D
Depth: 0.25 m
3 cm
E
Depth: 5.5 m
4 cm
F
Depth: 6.8 m
4 cm


North Basin
100
75
50
25
0
Percentage
0-5
6-10
11-15
16-20
21-25
Depth range (m)
South Basin
100
75
50
25
0
Percentage
0-5
6-10
11-15
16-20
Depth range (m)
Optimal
Sub-optimal
Poor