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Assessment of long-term changes in habitat availability for Arctic charr (*Salvelinus alpinus*) in a temperate lake using oxygen profiles and hydroacoustic surveys

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Running Head: Effects of oxygen depletion on Arctic charr habitat

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Summary

1. Hydroacoustics (2002 to 2004) and long-term oxygen data (1969 to 2004) have been used in conjunction to examine the habitat of Arctic charr in the north and south basins of Windermere, U.K., a temperate lake subjected to cultural eutrophication and subsequent nutrient management.

2. Since 1969 there has been a gradual decline in the oxygen concentration in the bottom waters of both basins of 0.03 – 0.04 mg $L^{-1}yr^{-1}$, resulting in up to 43 % of the volume of the south basin having an oxygen concentration < 5 mg L^{-1} in the early autumn.

3. Hydroacoustic data indicate that most Arctic charr routinely avoid the upper 10 m of the water column irrespective of temperature, with the implication that an observed gradual warming of the lake has not yet directly impacted upon their habitat.

4. In recent years there has been a behavioural response of the Arctic charr population to migrate vertically to avoid oxygen concentrations < 2.3 to 3.1 mg L^{-1}. Further, the depth of the lower bound of the Arctic charr population is shown to be highly correlated with the deep water oxygen concentration throughout the year prior to autumnal overturn.

Introduction

The availability of oxygen, together with water temperature on which it is partially dependent, has been acknowledged as one of the most important abiotic environmental characteristics affecting the distribution of freshwater fish at the habitat scale (e.g. Rudstam & Magnuson, 1985; Spoor, 1990; Kalikhman, Walline & Gophen, 1992; Swierzowski, Godlewska & Poltorak, 2000; Burleson, Wilhelm & Smatresk, 2001; Klumb *et al.*, 2004; Larsson, 2005). Despite this widespread influence, the effects of this factor are taxa-specific to the degree that while many cyprinids and some percids can tolerate relatively low levels of dissolved oxygen, salmonids require significantly higher availabilities (Alabaster & Lloyd, 1980). In lake habitats, salmonids such as Arctic charr (*Salvelinus alpinus* (L.)) may consequently be amongst the species most sensitive to deteriorating oxygen conditions which typically accompany eutrophication. In addition, this holarctic species can also be expected to be impacted by further reductions in oxygen availability which are anticipated under climate change, particularly in the hypolimnia of productive systems (Carpenter *et al.*, 1992).

Windermere is the largest natural lake in England and, like many other large temperate lakes, has a long history of cultural eutrophication and subsequent nutrient management (reviewed by Pickering, 2001). Following increases in nutrients in the lake's north and particularly south basins between the 1940s and the late 1980s, when substantial deepwater anoxia became a recurring problem in the south basin during the late summer and autumn, phosphate stripping was introduced to local sewage treatment works in 1992 (Elliott & Reynolds, 1996). One of the main drivers behind this action was concern over the lake's populations of Arctic charr. In an early application of hydroacoustic techniques in 1988, Mills *et al.* (1990) observed that Arctic charr were displaced from the deepest areas of the south basin at a time when local oxygen levels were low.

In addition to supporting a small semi-commercial fishery (Mills, 1989), the Arctic charr of Windermere has a great importance for local tourism arising from its national rarity and perceived indication of a healthy environment. The local stocks also have a long-standing interest for evolutionary biologists because they comprise autumn- and spring-spawning sub-populations in both basins (Partington & Mills, 1988), while the species is recognised to hold significant biodiversity conservation value at a national level (Maitland *et al.*, 2007). On the basis of these attributes and the observations of Mills *et al.* (1990), the Arctic charr of both basins have been monitored by monthly hydroacoustic surveys since 1989 (Winfield, Fletcher & James, 2007a). To date, analyses of these hydroacoustic data have been restricted to changes in population abundance (Elliott *et al.*, 1996), horizontal distribution (Baroudy & Elliott, 1993) and survey design (Winfield, Fletcher & James, 2007b), that is, no further studies of vertical distributions in relation to oxygen concentration beyond the limited observations of Mills *et al.* (1990) have been undertaken.

It is unclear precisely what lower level of oxygen concentration will impact Arctic charr populations in terms of either direct mortality or restrictions in habitat use. Laboratory experiments on young Arctic charr from Windermere (Baroudy & Elliott, 1994) revealed that incipient lethal levels of oxygen (i.e. survival over seven days) were as low as 1.8 to 2.0 mg L^{-1} at low acclimation temperatures (5 and 10 ^{o}C) and

2.2 to 2.4 mg L^{-1} at higher acclimation temperatures (15 and 20 ^{o}C). Such values are similar to a threshold of 1.8 to 1.9 mg L^{-1} reported for the congeneric brook trout (*Salvelinus fontinalis* Mitchill) by Shepard (1955), but lower than values reported for related *Salmo* species (see Baroudy & Elliott (*op. cit.*)) leading Elliott & Baroudy (1995) to conclude that Arctic charr are amongst the most tolerant of salmonids to low oxygen levels. Such laboratory experiments cannot, of course, address the more complex issue of habitat avoidance due to low oxygen levels.

The aims of this study were to combine results from long-term dissolved oxygen profiles of the north and south basins of Windermere with more recently acquired fish vertical distribution data to assess changes in oxygen concentrations and to investigate their impacts on habitat availability for Arctic charr.

Methods

Windermere is situated in the English Lake District in the north-west of the country at approximately 54.5^{o}N, 3^{o}W. It is a mesotrophic, lowland, valley lake surrounded by fells of a few hundred metres height. The lake comprises two basins, one to the north and one to the south of a shallow sill populated with islets approximately halfway along the length of the lake. The north basin of Windermere has a surface area of 8.05 km^{2} and a maximum depth of 64 m, while the south basin covers 6.72 km^{2} and descends to a maximum of 42 m; the bathymetry of both basins being detailed by Ramsbottom (1976). The fish community is relatively simple with the only species of numerical importance being Arctic charr, Atlantic salmon (*Salmo salar* L.), brown trout (*Salmo trutta* L.), European eel (*Anguilla anguilla* (L.)), perch (*Perca fluviatilis*

L.), pike (*Esox lucius* (L.)) and, in recent years, roach (*Rutilus rutilus* (L.)), although Pickering (2001) notes the presence of a further nine minor species.

Oxygen concentrations and temperatures have been monitored in both basins of Windermere since June 1968. Initially this routine monitoring took place every week, but in 1980 monitoring in the winter was changed to once every two weeks, and in 1992 and onwards all monitoring has been at a frequency of once every two weeks. Measurements were routinely taken at the surface and the bottom and at a varying number of depths in between. Typically measurements were tightly spaced through stratification in order that the temperature measurements accurately resolved the thermocline, but less tightly spaced when the lake was isothermal and the oxygen well mixed. To avoid any inherent biasing from this spatial and temporal variation, the data have been linearly interpolated on to a 1 m resolution daily grid prior to analysis. Measurements were originally taken with an YSI model 58 sonde (YSI, Yellow Springs, Ohio, U.S.A.) and latterly with a WTW Oxi 340i probe (WTW, Weilheim, Germany).

For each day the volume of water in the south and north basins that had an oxygen concentration less than 5 mg L^{-1} was calculated. By comparing with the total volume of the basin and averaging over each month of each year the average monthly percentage of the basin with water less than 5 mg L^{-1} was calculated. Similar calculations were done for the percentage of water with an oxygen concentration less than 3 mg L^{-1} and less than 1 mg L^{-1}.

Day and night hydroacoustic surveys of Windermere have been conducted at approximately monthly intervals since 1989 as part of an Arctic charr monitoring programme (see Winfield *et al.,* 2007a). However, data appropriate for detailed vertical profile analysis have only been collected since January 2002, following upgrade of the hydroacoustic system to a BioSonics DT6000 echo sounder (BioSonics Inc, Seattle, U.S.A.). This system was subsequently upgraded to a BioSonics DT-X echo sounder in November 2004, although with no implications in the context of the present study. Accordingly, three years of hydroacoustic data were used here: 2002, 2003 and 2004. Throughout the surveys, the 200 kHz transducer (beam angle 6.5°) was mounted at 0.5 m below the lake surface, the data threshold was set at -70 dB, the pulse rate was set at 5 pulses s^{-1} with a width at 0.4 ms and data recorded from a range of 2 m from the transducer. For the present study, data were taken from single transects nearest the deepest areas of each of Windermere's two basins. For the north basin this transect ran from 54°, 23.480' N, 2°, 56.330 W to 54°, 24.030' N, 2°, 57.550 W, while for the south basin it ran from 54°, 18.950' N, 2°, 57.340 W to 54°, 18.050' N, 2°, 57.070 W. Of a theoretical total of 144 such transects (36 months x two basins x day and night), 13 transects were lost, primarily due to adverse weather conditions, leaving an actual total of 131 transects (91%) available for analysis.

Subsequent data analysis in the laboratory was performed by fish tracking using Sonar5-Pro Version 5.9.6 (Lindem Data Acquisition, Oslo, Norway, www.fys.uio.no/~hbalk/sonar4_5) with a target threshold of -70 dB. For hydroacoustic data files collected before 1 January 2004 and for which GPS data were not directly available, this information was later added using Sonar5-Pro as described by Balk & Lindem (2006). Data analysis involved the water columns of each transect being divided into 1 m deep strata from a depth of 2 m below the transducer down to the lake bottom. Fish population densities expressed as individuals per 1000 m^3 (converted to individuals ha^{-1} of lake surface area in some analyses – see results) for each transect were exported via the Winfield table function of Sonar5-Pro to a spreadsheet for further analysis including combination with oxygen concentration data. Estimates of target strengths produced by Sonar5-Pro were converted to fish lengths using the relationship described by Love (1971):

$$TS = (19.1 \log_{10} L) - (0.9 \log_{10} F) - 62.0,$$

where TS is target strength in dB, L is fish length in cm and F is frequency in kHz. A breakpoint of –43 dB was used to pool targets into two length classes of less than and greater than 200 mm. The above calculations of fish population densities were thus produced for both length classes and for total fish for each basin and for day and night of each month.

In addition to Arctic charr, significant numbers of small individuals of other species less than 200 mm in length are also seasonally present in the pelagic upper waters of Windermere (Winfield & Durie, 2004; CEH, unpublished data). Consequently, subsequent analyses combining hydroacoustic and environmental data were performed only for individuals of at least this length to ensure that they were based exclusively on Arctic charr. Using the bathymetry of Windermere, population densities were also converted to absolute numbers of individuals present in each depth stratum. These absolute population distributions were then used to calculate, for each transect, the depths at which 90% of the population was situated below or above the depth stratum; hereafter referred to as the lower and upper 90% bounds of the Arctic charr vertical distributions. These parameters gave a more robust measure of the vertical distributions of fish than that produced simply by the minimum and maximum recorded fish depths.

Results

Between 1969 and 2004 there has been a significant reduction in the annually averaged oxygen concentration in the bottom water of both basins of Windermere (Fig. 1a,b). In the north basin this decline has been at the rate of 0.030 mg $L^{-1}yr^{-1}$, while in the south basin a somewhat higher rate was noted (0.042 mg $L^{-1}yr^{-1}$). Oxygen concentrations have also typically been absolutely higher in the north basin than in the south basin throughout this period.

In the south basin, from January to the end of May, there were no occasions when the monthly average oxygen concentration was < 5 mg L^{-1}. In June and December there was only one occurrence each month and in July there were nine occurrences. For August, September, October and November there have been a number of years in which the monthly average oxygen concentration has been below 5 mg L^{-1}, 3 mg L^{-1} or even 1 mg L^{-1} (Fig. 2a–d). Although in the late 1960s and early 1970s virtually the whole basin had an oxygen concentration > 5 mg L^{-1}, in the 1980s much of the basin suffered severe oxygen depletion, with portions of the basin regularly experiencing < 1 mg L^{-1} in the early autumn. In years immediately following upgrading of sewage treatment works in early 1992, the percentage of the basin with low oxygen concentration was considerably reduced. Subsequently, however, the volume of water with a low oxygen concentration has increased, with the largest volume of water with a concentration < 5 mg L^{-1} since monitoring began occurring in September 2002 (43 %). The volume of low oxygen concentration water tends to be highest in September and October, shortly before the autumnal overturn. Since 1992, the percentage volume of water in October with an oxygen concentration < 3 mg L^{-1} has been increasing at a significant rate of approximately 1.5 % yr^{-1}.

In the north basin, only a few occasions with oxygen concentrations < 5 mg L^{-1} were noted. An average monthly concentration < 5 mg L^{-1} was recorded somewhere in the basin for a total of nine months during the 1980s and for five months post 2000. Thus, whilst there are signs of a recent increase in volume of low oxygen concentration water in the north basin, in comparison to the south basin the basin is relatively well oxygenated.

In the south basin, despite warming in the summer, the 16 ^{o}C isotherm rarely penetrated below 10 m, and the 12 ^{o}C isotherm was never lower than 20 m during 2002, 2003 and 2004 (Fig. 3a,b,c). Both the annual pattern of depleted oxygen concentration and the seasonal positioning of the upper and lower 90% bounds of Arctic charr were broadly similar each year (Fig. 3a,b,c). The lake was fully mixed throughout the winter, but routinely stratified between approximately April and November. Oxygen concentrations correspondingly declined in the hypolimnion to a minimum in autumn, shortly before overturn. It is notable that the lower 90 % bound exhibited the same trend each year, increasing from about 35 m in early summer to about 25 m in autumn. Another common trend was that the upper 90 % bound was rarely < 10 m depth, even during the isothermal hibernal months. Moreover, there is some indication of the upper 90 % bound increasing in tandem with the lower 90 % bound.

Isotherms in the north basin showed similar trends to those in the south but, despite being a deeper basin, oxygen concentrations were rarely < 5 mg L^{-1} (Fig. 4a,b,c). The lower 90 % bound was typically a few metres deeper in the water column than the corresponding bound in the south basin, but there was a less pronounced elevation in the bound through the summer and autumn. Once again the upper bound was almost always beneath 10 m depth throughout the year.

The average depths of the lower and upper 90% bounds of Arctic charr vertical distributions over the three years showed a clear increase in the lower bound between winter and autumn in the south basin, but less of an increase in the north basin (Fig. 5a). There was also a systematic greater depth of the lower bound in the north compared to the south basin. Though the average bound range over the three years was usually greater in the north than in the south basin, in neither basin was there an obvious systematic seasonal change in bound range (Fig. 5b). The average depths of the lower and upper bounds were 30.8 m and 15.9 m, respectively, in the south basin and 37.1 m and 16.3 m, respectively, in the north basin, leading to average band widths of 14.9 m in the south and 20.8 m in the north basins.

An indication of the oxygen concentrations that Arctic charr avoid in the south basin can be estimated from the minimum concentration of the interpolated oxygen data that the lower 90 % bound reached on a day when a hydroacoustic survey was carried out.

This was 2.3, 2.7 and 2.7 mg L^{-1} in 2002, 2003 and 2004, respectively, and in all three years occurred in October. Alternatively, the minimum preferred oxygen concentration can also be estimated from the monthly averaged concentration of oxygen at the depth the lower 90 % bound reached in October each year; using this method gave values of 2.8, 3.0 and 3.1 mg L^{-1} for the years 2002, 2003 and 2004, respectively. However, this latter method is likely to overestimate minimum concentration as it is based on a monthly average rather than a daily concentration and does not rely on temporal interpolation. The corresponding values for the north basin were somewhat greater compared to the south basin, namely 6.0, 6.2 and 5.7 mg L^{-1} for 2002, 2003 and 2004, respectively.

Oxygen concentrations for each month averaged from 2002 until 2004 at the depth of the annually averaged lower 90 % bound of Arctic charr vertical distributions (31 m depth in the south basin, 37 m depth in the north basin) were very similar in the two basins at the beginning of the year, but started to diverge in May (Fig. 6). Both showed a pattern of declining oxygen concentration until late autumn, followed by a steep increase. In the south basin the decline was much greater than in the north basin. The standard deviation of this monthly oxygen concentration was always small, with the exception of the oxygen concentration in the south basin in November when overturn occurs and concentrations consequently rapidly shift from near anoxia towards the hibernal maximum.

Depths of the lower 90 % bound of Arctic charr vertical distributions each month averaged over the three years were correlated with the corresponding monthly averaged oxygen concentration at the annual average depth of the lower bounds (Fig. 7). Only the pre-overturn months of January to October have been included in this Figure, as adult Arctic charr move to shallow waters in the late autumn to spawn and also at this time there is a radical change in the oxygen concentration at depth (Fig. 6) resulting from the autumnal overturn. The oxygen concentration at the average depths of the lower bounds were chosen as being indicative of the ambient oxygen concentration experienced by fish at depth in the lake.

Discussion

This study has clearly shown that the vertical distribution of Arctic charr in Windermere is significantly influenced by the availability of oxygen in the lower hypolimnion, particularly in the more nutrient-enriched south basin. The present findings also show that, despite the introduction of phosphate stripping in early 1992 and a subsequent initial improvement in water quality, the lake has not since recovered to the conditions observed in the 1960s. Indeed, recent measurements indicate further decreases in oxygen concentrations. This decline in oxygen concentration at depth, particularly in the south basin, signifies a potential loss of habitat volume for the Arctic charr. In theory, changes in the algal community, in lake temperature or in the duration of stratification could have effected this depletion.

One oxygen threshold for Arctic charr habitat relates to the minimum oxygen concentration which the Arctic charr can endure for prolonged periods of time. In the period 2002 to 2004, the lower 90 % bound of Arctic charr vertical distribution was observed at a minimum oxygen concentration of c. 3 mg L^{-1} in the south basin, allowing for uncertainties in the interpolation of the oxygen data. This suggests that, in the wild, the Arctic charr of Windermere will avoid spending prolonged periods in water below this oxygen concentration. This range is noticeably similar to the values observed in laboratory experiments on incipient lethal oxygen concentrations of individual Windermere Arctic charr parr carried out by Baroudy & Elliott (1994), but slightly below the avoidance level of 4 mg L^{-1} reported by Spoor (1990) for fingerlings of the closely related brook trout. A conservative approximation, therefore, to the recent (1992 – 2004) rate of Arctic charr habitat decline is shown by the volume of water with a concentration < 3 mg L^{-1} in October to be 1.5 % yr^{-1}.

Moreover, our results indicate a tendency for Arctic charr to seek more oxygenated waters by upward migration even when ambient oxygen concentrations are high. For example, we noted that the vertical distribution of Arctic charr in the south basin began in early spring, when oxygen concentrations were still well above incipient lethal levels. Although oxygen concentration is clearly not the only driver of positioning in the water column, the correlation that we noted in the south basin between oxygen at depth and Arctic charr positioning suggests that oxygen concentration is of considerable importance. Despite this increase in the lower 90% bound of Arctic charr vertical distributions, the upper bound rarely increased above a depth of 10 m in either basin. This suggests that avoidance of surface waters is another strong driver of Arctic charr positioning in the water column, irrespective of local oxygen concentrations. The near-surface distributions of Arctic charr may also be influenced by changes in basin-specific zooplankton abundances and distributions, given the dominance of such prey in their diet (Frost, 1977). Unfortunately, appropriate long-term zooplankton spatial distribution data are not available for

Windermere. Furthermore, any such influences may have recently been dramatically changed by the expanding epilimnetic population of roach (Winfield *et al.*, 2007a) and their predatory impacts on cladoceran zooplankton. Consequently, this issue remains unresolved although its potential importance is acknowledged.

In addition to eutrophication, another potential threat to the habitat of the Arctic charr in Windermere is a changing climate, which has recently warmed the lake above its long-term average (Winfield *et al.*, 2004). Mills *et al.* (1990), following Elliott (1981), suggested the preferred maximum temperature for Arctic charr was 16 ^{o}C and thus any deepening of this isotherm as the lake warmed could potentially restrict available habitat. In a more extensive study based on Arctic charr from eleven widespread European locations, Larsson *et al.* (2005) similarly found maximum growth to occur between 14.4 and 17.2 ^{o}C. In Windermere, the position of the upper 90 % bound for Arctic charr habitat was rarely above 10 m depth in either basin during the years 2002 to 2004 and so crossed the 16 ^{o}C isotherm only occasionally. However, Larsson (2005) reported notably lower actual preferred temperatures for Arctic charr from two populations in Sweden of 10.8 and 11.8 ^{o}C. Similarly, Mortensen, Ugedal & Lund (in press) observed a population in northern Norway to prefer a temperature of 11.5 to 11.8 ^{o}C from spring to autumn and then 8.7 ^{o}C in winter. Irrespective of whether Arctic charr in Windermere also occupy this preferred lower temperature range or they indeed inhabit warmer water allowing maximum growth rate, water at 10 m is still sufficiently cool to be inhabitable. Moreover, for the time being, the Arctic charr can still rise through the water column in the late summer, without needing to inhabit the top 10 m. Therefore, whilst there has been a significant rise in the surface temperature of Windermere with implications for littoral fish species (Winfield *et al.*, 2004), the increases in temperature have not yet directly impacted on the volume of habitat available to the Arctic charr. However, as changing temperatures and stratification are known to have other effects on lake ecosystems (Elliott, 1996; Winfield *et al.*, 2004; Elliott, Jones & Thackeray, 2006; Madgwick *et al.*, 2006; Winfield *et al.*, 2007a), an indirect but still significant impact upon the Arctic charr cannot be discounted.

The data presented in this paper have a number of implications. Firstly, despite phosphorus striping there has been a decline in oxygen concentration in England's largest lake. Secondly, recent hydroacoustic data suggest that, with the known exception of a brief inshore spawning season when mature individuals visit shallow areas (Kipling, 1984), the majority of the adult Arctic charr stay below the upper 10 m of the lake. As such, it is unlikely that the direct effects of climate warming have directly impinged upon this species. However, studies by Nakano, Kitano & Maekawa (1996) concerning the potential loss of habitat for the closely related Dolly Varden (*Salvelinus malma* (Walbaum)) and white-spotted charr (*Salvelinus leucomaenis* (Pallas)) of the Japanese archipelago and by Janssen & Hesslein (2004) for the closely related lake trout (*Salvelinus namaycush* (Walbaum)) in temperate zone lakes, clearly indicate the potential scope of this threat. Thirdly, while the combined oxygen measurements and hydroacoustic data suggest that Arctic charr populations in Windermere will avoid areas with oxygen concentrations which previous laboratory experiments have shown to be approaching lethal levels (Baroudy & Elliott, 1994), they also suggest sensitivity to all levels of oxygen. This was most apparent in the south basin of Windermere where a vertical migration was shown to begin in the spring as oxygen concentrations declined in the deep waters following the onset of stratification.

Although this study has exclusively addressed the Arctic charr populations of Windermere, our findings have a wider relevance given that Maitland *et al*. (2007) recognised eutrophication and climate change to be two of the major threats facing the conservation of this species elsewhere in the British Isles. The same threats are important on a global basis; both to the Arctic charr and to its congeners (see Magnan *et al*., 2002). With specific respect to climate change, in their examination of the potential effects of this threat on fish habitats including that of the closely related lake trout in temperate zone lakes, Janssen & Hesslein (2004) noted that the impact of oxygen deficits on habitat availability will be influenced by lake trophic status. In this context, the extensive datasets on Arctic charr vertical distributions and associated environmental parameters available for Windermere offer an invaluable opportunity for further studies of the detailed interactions between oxygen availability, water column temperatures and habitat use by this ecologically and economically important species.

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Figure Legends

Figure 1. Regression plots of annually-averaged oxygen concentration from 1969 to 2004 at the near-bottom for the south (A) and north (B) basins of Windermere.

Figure 2. Percentage of the south basin volume with oxygen concentration < 5 mg L^{-1} (♦), < 3 mg L^{-1} (x) and < 1 mg L^{-1} (o), from 1968 – 2004 in August (A), September (B), October (C) and November (D). A regression line is shown only for the percent volume < 3 mg L^{-1} in October (C) for the years 1992 – 2004.

Figure 3. Depths of lower (dashed line and circles) and upper (dashed line and crosses) 90 % bounds of Arctic charr vertical distributions in the south basin, depths at which oxygen concentration was < 5 mg L^{-1} (thin line), < 3 mg L^{-1} (thin dash-dot line) and < 1 mg L^{-1} (thin dashed line) and the 16 °C (thick line) and 12 ^{o}C (very thick line) isotherms for 2002 (A), 2003 (B) and 2004 (C).

Figure 4. Depths of lower (dashed line and circles) and upper (dashed line and crosses) 90 % bounds of Arctic charr vertical distributions in the north basin, depths at which oxygen concentration is < 5 mg L^{-1} (thin line) and the 16 °C (thick line) and 12 ^{o}C (very thick line) isotherms for 2002 (A), 2003 (B) and 2004 (C). Note that the oxygen concentration is always > 5 mg L^{-1} except briefly in 2004.

Figure 5. Average lower (circles) and upper (crosses) 90 % bounds of Arctic charr vertical distributions (A) and average range (squares) between lower and upper 90 %

bounds (B) for the south (thick line) and north (dashed line) basins for the years 2002 to 2004.

Figure 6. Oxygen concentrations (squares) averaged over 2002 to 2004 at the average depths of the lower 90 % bound of Arctic charr vertical distributions in each basin, i.e. 31 m in the south and 37 m in the north basins. Oxygen concentrations ± 1 SD are also shown in grey; dashed lines for the north basin, solid lines for the south basin.

Figure 7. Correlations between the depth of the lower 90 % bound of Arctic charr vertical distributions and the oxygen concentration at the annual average depth of the lower 90 % bound, averaged for the years 2002 to 2004 for each month, January – October, for the south (stars) and the north (triangles) basins.

Figure 1

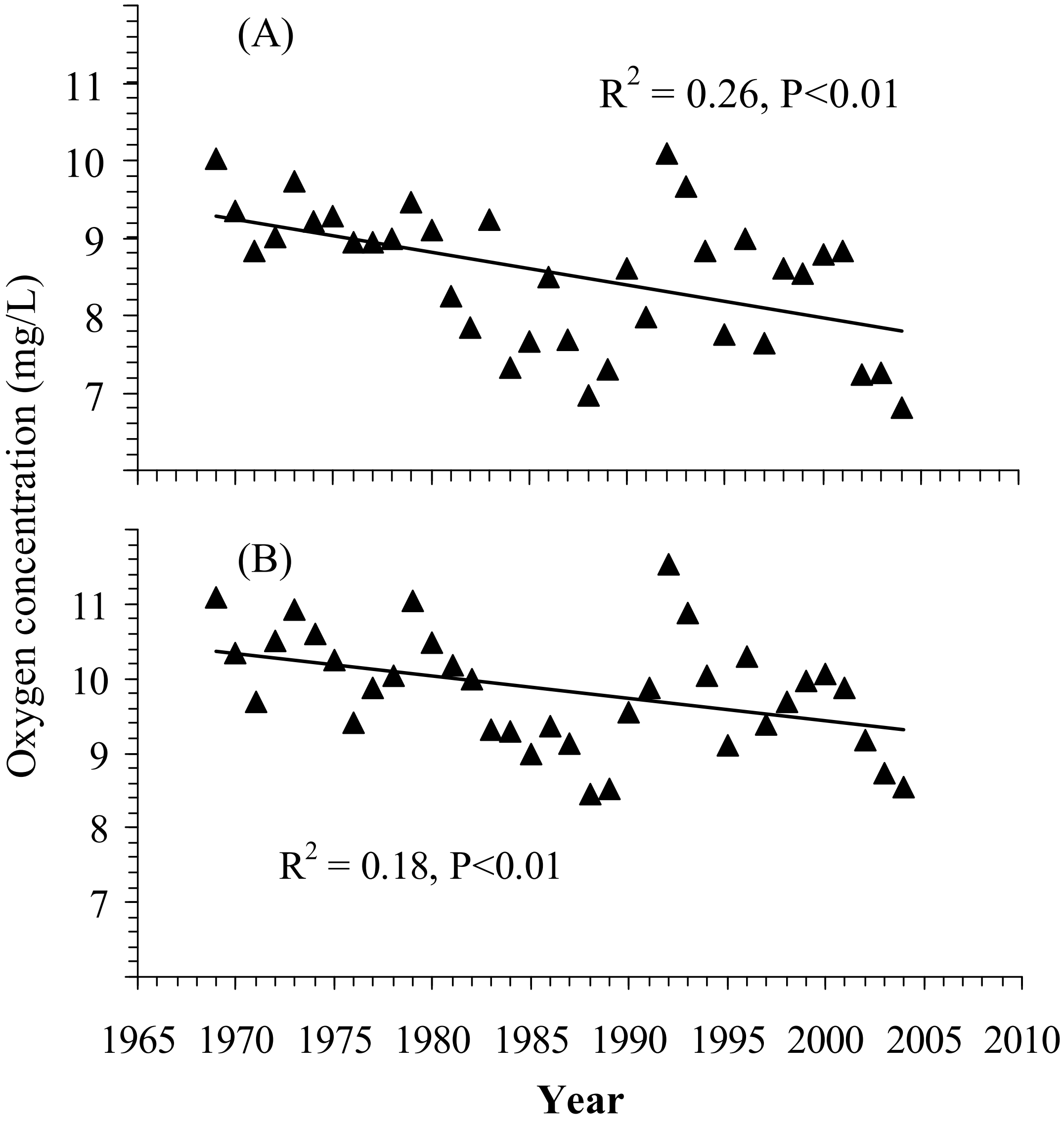
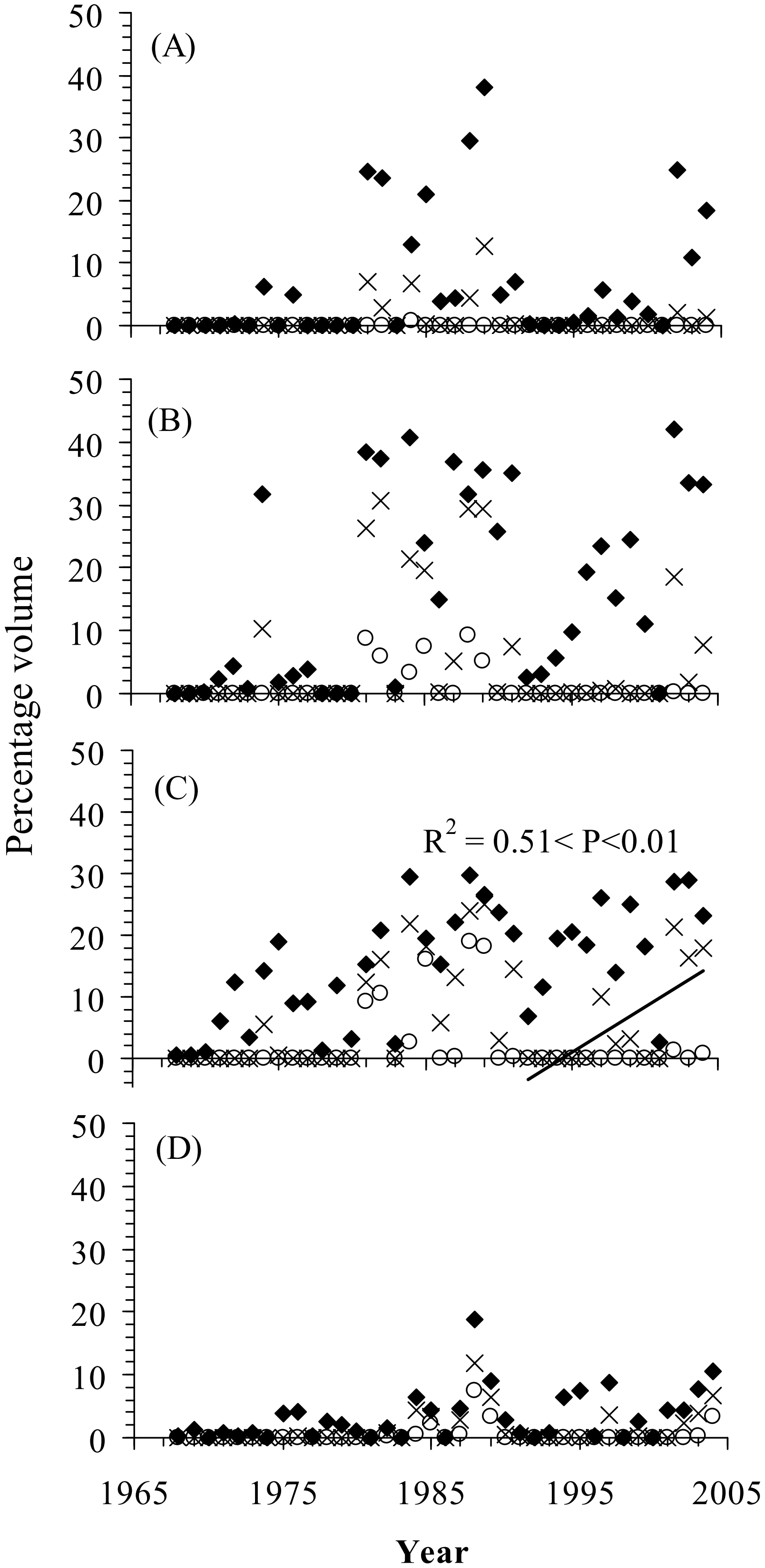

(A)
R² = 0.26, P<0.01
(B)
R² = 0.18, P<0.01
Oxygen concentration (mg/L)
11
10
9
8
7
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
Year

Figure 2



Percentage volume
(A)
(B)
(C)
R^2 = 0.51< P<0.01
(D)
0
10
20
30
40
50
1965
1975
1985
1995
2005
Year

Figure 3

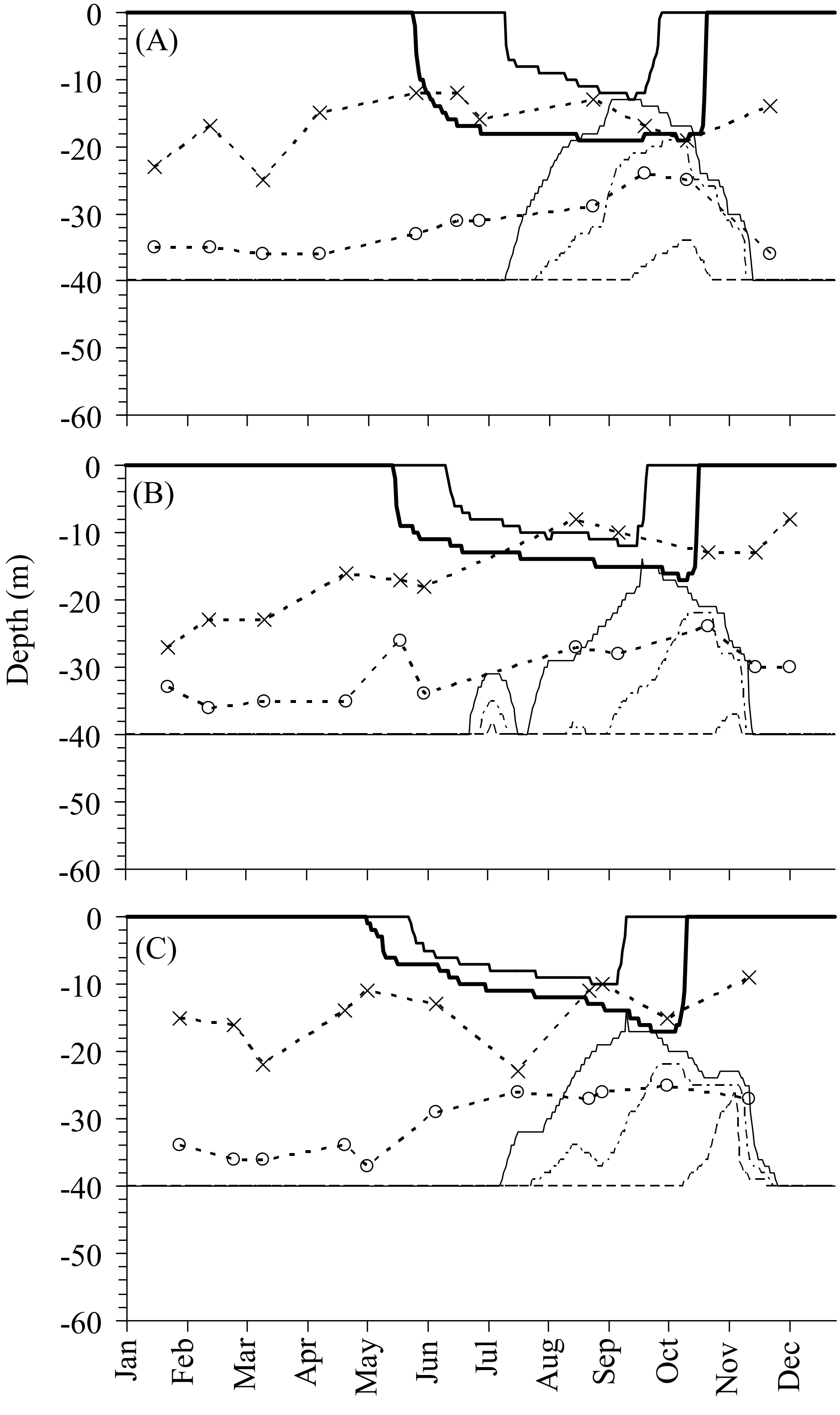

(A)
(B)
(C)
Depth (m)
0
-10
-20
-30
-40
-50
-60
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 4

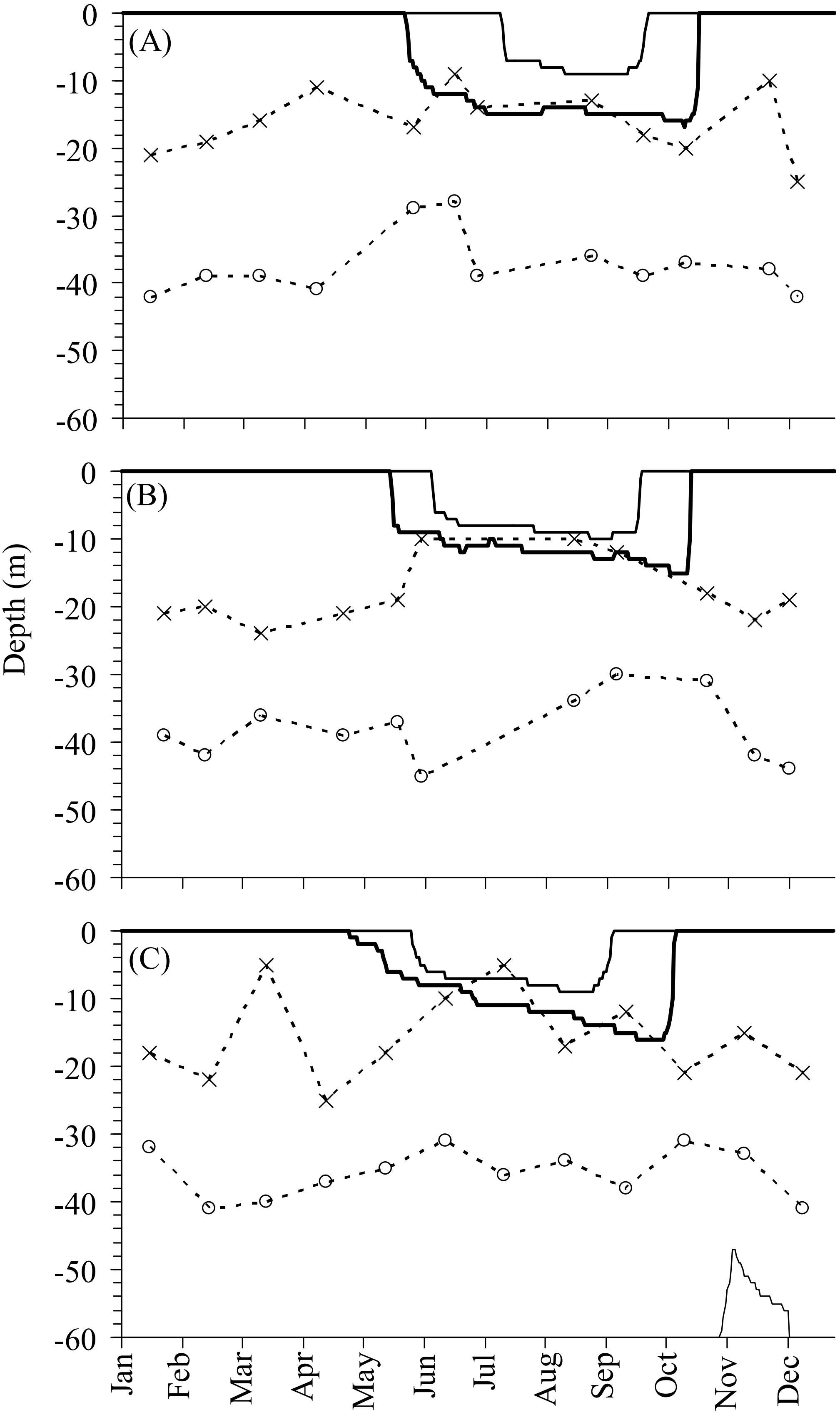

(A)
(B)
(C)
Depth (m)
0
-10
-20
-30
-40
-50
-60
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 5

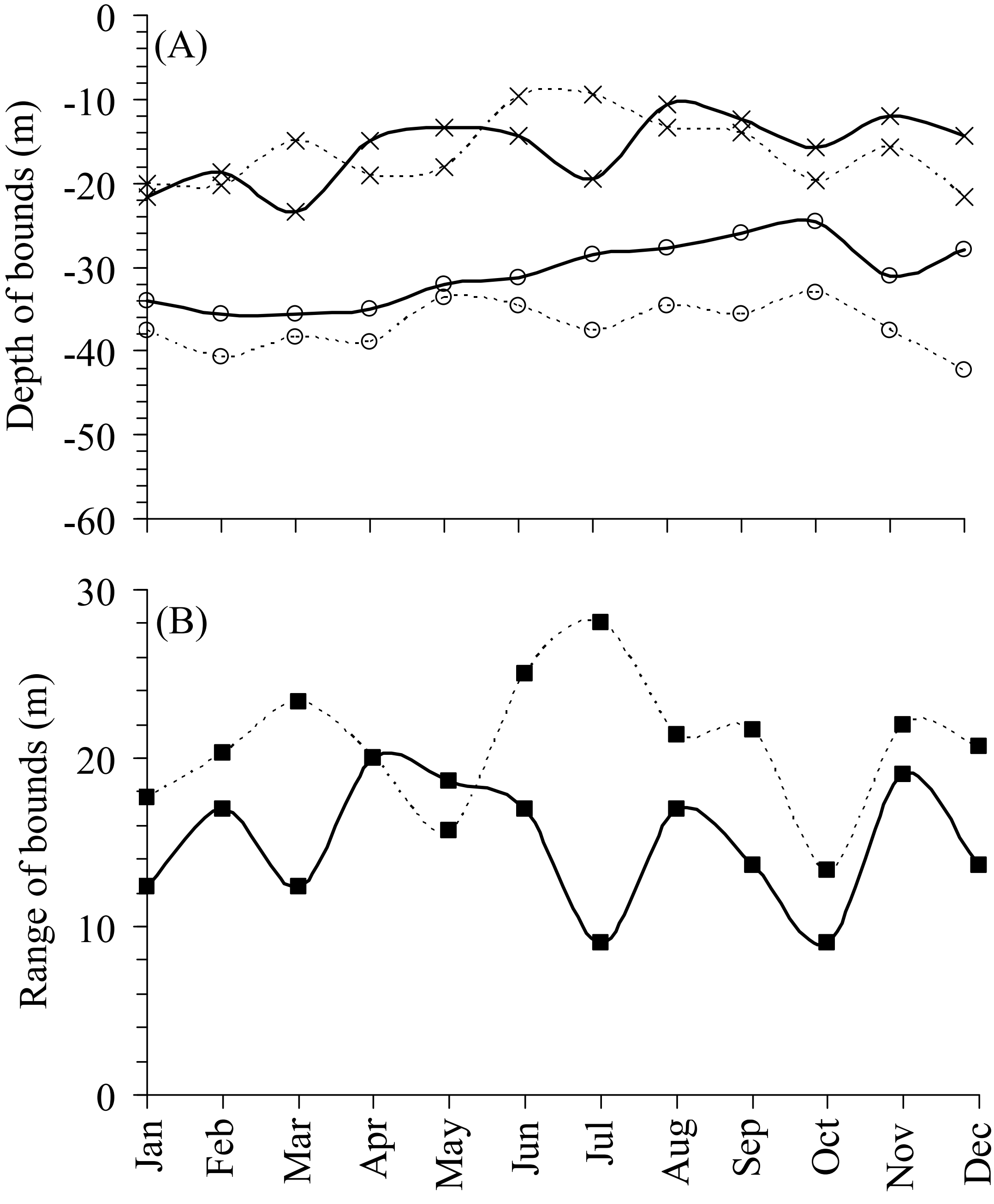

(A)
Depth of bounds (m)
0
-10
-20
-30
-40
-50
-60
(B)
Range of bounds (m)
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 6

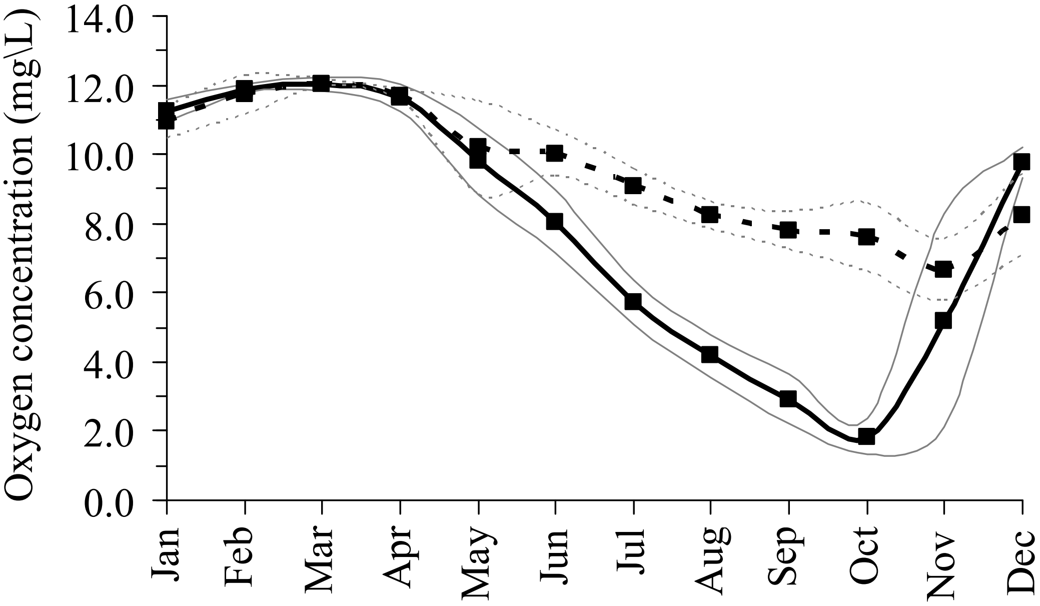
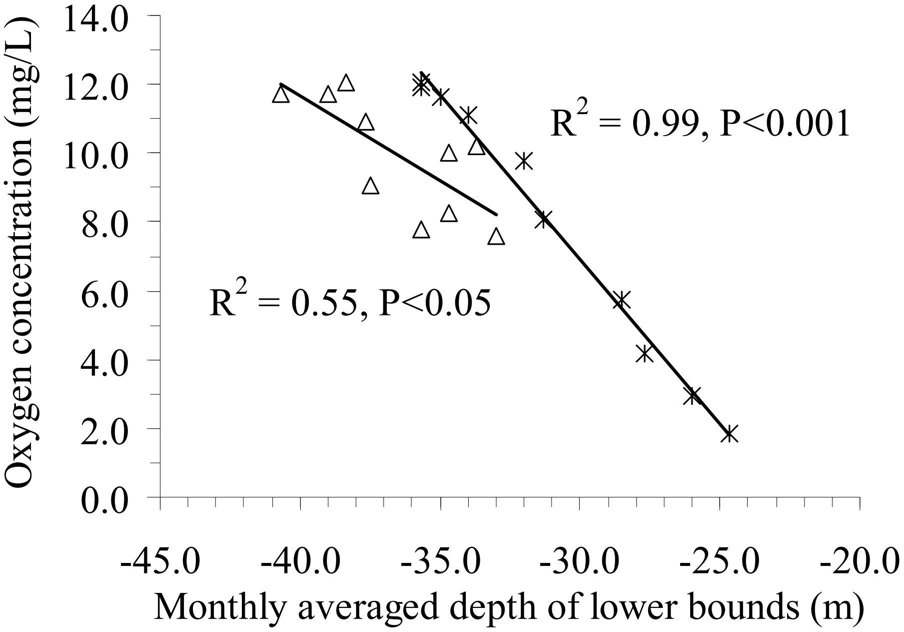

Oxygen concentration (mg\L)
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 7



Oxygen concentration (mg/L)
14.0
12.0
10.0
8.0
6.0
4.0
2.0
0.0
-45.0
-40.0
-35.0
-30.0
-25.0
-20.0
Monthly averaged depth of lower bounds (m)
$R^2 = 0.99$, $P<0.001$
$R^2 = 0.55$, $P<0.05$