

Rapid ecosystem recovery from diffuse pollution after the Great Irish Famine

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Abstract. Remarkably little is known about the effectiveness or rates of recovery of aquatic ecosystems from reductions in human-associated pressures at landscape scales. The retention of anthropogenic contaminants within ecosystems can retard rates of recovery considerably, while the trajectories of recovery processes vary with the extent of disturbance and the resilience of biotic assemblages. The Great Irish Famine of 1845–1850 comprised one of the most significant human disasters of the 19th century, causing the death of approximately one million people and the emigration of a further two million from the country between 1845 and 1855. We found, through analysis of detailed historical census data combined with paleolimnological investigation of sedimentary nutrient concentrations, stable isotope ratios, and diatom assemblages, that the trophic level of Lough Carra, a largely shallow calcareous lake in the west of Ireland with no urban areas or point sources of any significance in its catchment, reduced considerably during and immediately after the Great Famine, shifting to new equilibria within just 2–10 years. Our results demonstrate that the reduction of human pressures from diffuse sources at landscape scales can result in the rapid and monotonic recovery of aquatic ecosystems. Moreover, the recovery of ecosystems from diffuse pollution need not necessarily take longer than recovery from pollution from point sources.

Key words: *depopulation; disturbance; eutrophication; lake; landscape; Lough Carra, western Ireland; nutrients; paleolimnology; point source; resilience.*

INTRODUCTION

As the extent and intensity of human influence on the biosphere continue to increase, there is a critical need to manage ecosystems in ways that maximize their integrity. Inherent in this is the ability to predict rates and trajectories of recovery after disturbance (Peterson et al. 2003, Lotze et al. 2006). Remarkably little is known, however, about the effectiveness or rates of ecosystem recovery from rapid and large-scale human depopulation and the consequent reduction in their associated pressures. Anthropogenic contaminants can be retained within ecosystems for long periods (Withers et al. 2001, Kretzschmar and Schäfer 2005, Banks et al. 2006), and can thus retard rates of recovery considerably (Peterson et al. 2003, Schippers et al. 2006). Consequently, historic land use can have persistent effects for centuries (Knops and Tilman 2000, Fraterrigo et al. 2005, McLauchlan et al. 2007, Matamala et al. 2008). Moreover, in some cases full recovery may never occur owing, for example, to hysteretic shifts in ecosystem structure, loss of native species pools and genotypic diversity, shifts in species dominance and

trophic structure, or changes in landscape connectivity and organization (Rietkerk et al. 2004, Suding et al. 2004, Reusch et al. 2005, Lotze et al. 2006). Further, both rates and trajectories of recovery can differ significantly from those of impact processes (Hjermann et al. 2004, Zhao et al. 2005, Ibelings et al. 2007), which makes our ability to predict the nature and rates of recovery at ecosystem scales remarkably poor.

Eutrophication from nutrient enrichment comprises a globally important anthropogenic pressure on aquatic ecosystems (Smith et al. 2006, Smith and Schindler 2009). Increased transfer of phosphorus to water is considered as the primary cause of eutrophication of freshwaters, particularly in northern temperate lakes (Schindler 1978, Schindler et al. 2008). Lake-restoration efforts based on reducing external loading of phosphorus have, however, met with varied levels of success and can be affected significantly by, for example, the relative importance of internal nutrient loading (Marsden 1989, Sas 1989, Søndergaard et al. 2003, Jeppesen et al. 2005), historical loading history (Jeppesen et al. 1991), lake retention time (Kilinc and Moss 2002, Søndergaard et al. 2005), and food-web structure (Jeppesen et al. 1990, Hansson et al. 1998). The length of time required to achieve discernable decreases in lake water-column total phosphorus concentrations after reduction in point-source nutrient loading has been shown to vary commonly from 10 to 15 years (Jeppesen et al. 2005).

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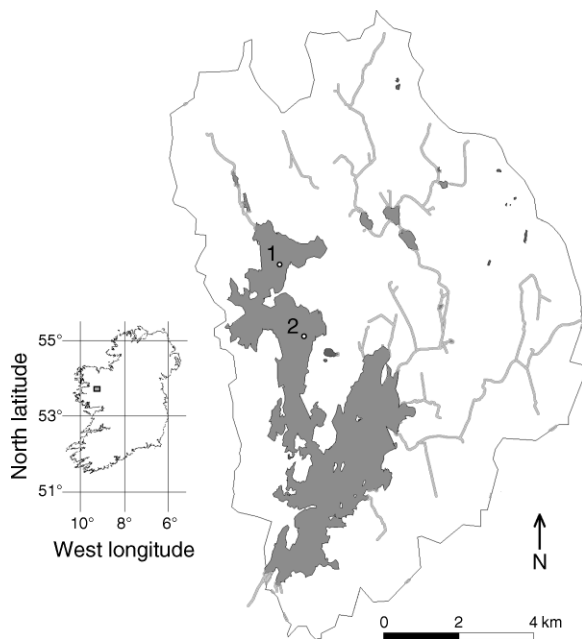


FIG. 1. Lough Carra (in western Ireland) and its catchment, showing the locations of (1) the north-basin and (2) the mid-basin cores (outlined open circles).

Some lakes have, however, shown no signs of recovery even 20 years after reduction of phosphorus input (Jeppesen et al. 2005, Moss et al. 2005).

The great majority of, if not all, efforts to restore lakes through the reduction of external nutrient loading has been based primarily upon diversion, removal, or improved treatment of point sources of nutrients (see, for example, Marsden 1989, Sas 1989, Jeppesen et al. 2005). Owing, however, to the considerable difficulties involved with the effective manipulation and management of whole catchments, little is known about rates of lake recovery from catchment-scale reductions in anthropogenic disturbance. Rates of recovery from diffuse pollution may be lengthened considerably compared with those from point sources due to the retention of nutrients and other substances within soil matrices (e.g., Johnston and Poulton 1992, Withers et al. 2001, Kretzschmar and Schäfer 2005, Banks et al. 2006, Bunemann et al. 2006). Lag times of the order of years to decades might, therefore, be expected to occur between initial reductions of agricultural intensity and consequent decreases in rates of diffuse nutrient transfer to drainage networks (Schippers et al. 2006).

The Great Irish Famine of 1845–1850 comprised one of the most significant human disasters of the 19th century, causing the death of approximately one million people and the emigration of a further two million from the country between 1845 and 1855 (Póirtéir 1995). This altered permanently the demographic, political, and cultural landscape not only of Ireland, but also, in particular, of the United States and Great Britain. The famine resulted in the dramatic depopulation of the Irish

landscape, particularly in western regions where reductions of over 40% of the human population were recorded between 1841 and 1861. Because lakes act as sinks for materials from their catchments, paleolimnology is one of the few techniques supporting quantification of rates of ecosystem-scale change over discrete intervals of time (Carpenter 2003, Smol 2008) and has, therefore, the potential to provide holistic insight into rates and trajectories of ecosystem recovery after the Great Famine. To this end, we took sediment cores from the two deepest and most geochemically distinct basins (Hobbs et al. 2005) of Lough Carra, a mostly shallow (mean depth, 1.8 m; maximum depth, 19 m) calcareous lake (surface area, 15.6 km²) located in a low-lying (mean elevation, 30 m above sea level) agricultural landscape in the west of Ireland (Fig. 1). The catchment of Lough Carra (area 114 km²) has never contained urban areas or contaminant point sources of any significance and, thus, provides an excellent location for the examination of rates of ecosystem recovery from human depopulation and associated reductions in diffuse nutrient pollution at the landscape scale. After establishing radiometric chronologies for the cores, we quantified the structure of historic diatom assemblages, ratios of the stable isotopes $\delta^{13}\text{C}$ (for organic material only) and $\delta^{15}\text{N}$, and the concentrations and accumulation rates of particulate organic matter and key nutrients. Further, using historic census data with high spatial and temporal resolutions, we were also able to estimate historic human and livestock population densities for the Carra catchment and use those data to estimate changes in both nutrient loading and the primary sources of nutrients to the lake from the period immediately following the Great Famine through to the present day.

MATERIAL AND METHODS

Core sampling and analyses

Sediment cores were taken from the deepest points in the northern (17 m water depth; 53°22'15.6" N, 9°15'46.8" W) and middle (19 m water depth; 53°42'50.4" N, 9°15'10.8" W) basins of Lough Carra (Fig. 1) in July 2002 using a piston corer (Livingstone 1955) of 5 cm diameter. Core sediments were extruded into 1-cm segments immediately after collection, placed in polygrip plastic bags and stored in darkness at 4°C. Quantification of sedimentary total phosphorus (TP) followed Eisenreich et al. (1975) after nitric acid digestion in a CEM MDS-2000 microwave (CEM Corporation, Matthews, North Carolina, USA). Percentage organic matter was determined by loss-on-ignition of ~2 g of dry sediment at 550°C for 3 h (Heiri et al. 2001). Organic carbon and nitrogen were quantified by flash combustion at 900°C in a Carlo Erba 1112 series elemental analyzer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) after removal of inorganic carbon with sulfuric acid. Ratios of the stable isotopes $\delta^{15}\text{N}$ and $\delta^{13}\text{C}_{\text{org}}$, the latter corrected for historic $\delta^{13}\text{C}$ depletion of atmospheric CO₂ (Schelske and Hodell

1995), were quantified with a Thermo Deltaplus continuous-flow isotope-ratio mass spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and are reported relative to, respectively, air and Vienna Pee Dee Belemnite.

Radiometric dating

After grinding to less than ~ 1 -mm particle size, the concentrations of gamma-emitting ^{210}Pb , ^{214}Pb , ^{214}Bi , ^{137}Cs , and ^{241}Am were determined by placing dried sediments in a calibrated geometry and counting in a high-resolution, low-background, p-type germanium well detector. Energy and efficiency calibration was done using a mixed radionuclide standard supplied by Cerca Framatome ANP (Pierrelatte, France; code, 7081/4) and a separate ^{210}Pb standard supplied by Amersham International (Amersham, UK; code, S6/19/110). “Excess” or “unsupported” ^{210}Pb ($^{210}\text{Pb}_{\text{exc}}$) activity was calculated from the total ^{210}Pb activity by subtracting the terrestrial (“supported”) ^{210}Pb component, which was calculated as the mean activity of ^{214}Pb and ^{214}Bi for the sample. Chronologies and sediment accumulation rates were estimated using the constant rate of supply (CRS) model (Appleby and Oldfield 1978). Application of the CRS model required the careful determination of the unsupported ^{210}Pb inventory of the core. This was achieved by using the “1986” and “1963” chronostratigraphic markers in the ^{137}Cs profile to obtain the full-core inventory, as recommended for lakes with low ^{210}Pb surface activity concentrations (Appleby 2008). Modeled CRS chronologies were validated using dates determined independently from the well-known pattern of nuclear fallout input from anthropogenic ^{241}Am and ^{137}Cs . Although the applicability of ^{210}Pb dating techniques is limited by its half-life to periods spanning ~ 150 years, it is in principle possible to extend the established chronologies below the ^{210}Pb dating horizon. This extrapolation is likely to yield accurate dates at sites where sediment accumulation rates have not changed significantly over the ^{210}Pb age range (Binford 1990, Appleby 2000). As this was the case in our study, we used the mean and variability of the sediment accumulation rate quantified directly for the CRS-dated portion of the core to estimate chronologies and their associated uncertainties for the lower regions of the core where $^{210}\text{Pb}_{\text{exc}}$ activity was not detectable. The core from the northern basin was dated radiometrically with the chronological model extended to the middle-basin core by correlation of down-core variation in sediment properties. Chemical accumulation rates, expressed as $\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, were calculated as the product of chemical concentrations and dry-mass accumulation rates.

Census data and modeling of historic TP loads

Data on historical human population densities were obtained from the Central Statistics Office of Ireland for the period 1841–2002, with 8 ± 4.2 years (mean \pm SD)

between each census (range, 2–20 years). Human population data were available for the entire period at the level of the District Electoral Division (DED), which is the finest census resolution possible. The Carra catchment encompasses 10 DEDs, each with an area of $28.1 \pm 9.3 \text{ km}^2$ (mean \pm SD). Agricultural census data, comprising historical land cover, livestock density and farm holding data, were obtained for the period 1851–2002, with 8.3 ± 3.1 years (mean \pm SD) between each census (range, 3–15 years). These data were, however, available at DED level only for 1851 and 1937–2002, and were recorded at the level of the Rural District (RD) between 1861 and 1933. The Lough Carra catchment is located within two RDs, Castlebar (588 km^2 ; 14% in catchment) and Ballinrobe (570 km^2 ; 6% in catchment). Calculations of human and livestock densities, land cover, and farm holdings in the catchment were estimated by weighted averaging based on the proportion of DEDs and, where necessary, RDs located within the catchment. This method thus assumed a homogenous distribution of people, livestock, and land use within DEDs and RDs.

Historic TP loads from the catchment of Lough Carra to the lake were estimated using the export coefficient model of Johnes et al. (1996) for calcareous catchments. The application of this model to the Carra catchment works extremely well and has been validated with actual measurements of nutrient loading from the catchment in addition to measurements of in-lake nutrient concentrations (I. Donohue, *unpublished data*).

Diatom analyses

Diatom remains were quantified from, respectively, 10 and 11 samples located throughout the north- and middle-basin cores. High quality of valve preservation was found throughout the samples, with no evidence of valve dissolution or breakage present. Diatom slides were prepared following Battarbee et al. (2001), with 300–500 valves counted per slide, all of which were identified to species level following Krammer and Lange-Bertalot (1986–1991). Variation in the structure of diatom assemblages in these samples among the three main phases of lake productivity indicated by the biogeochemical data from the cores (i.e., pre-famine, post-famine, and post-1960; see *Results*, below) was examined with permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, McArdle and Anderson 2001). Lake basin (random factor) and productivity phase (fixed factor) were independent variables in the model, which was based on a Bray-Curtis (Bray and Curtis 1957) similarity matrix calculated from $\log(x + 1)$ -transformed proportional abundance data and was done with 9999 permutations under the reduced model as recommended by Anderson et al. (2008). Diatom species that were contributing most to pairwise dissimilarities between productivity phases were identified using similarity percentages (SIMPER) analyses (Clarke and Warwick 2001) with lake basin and

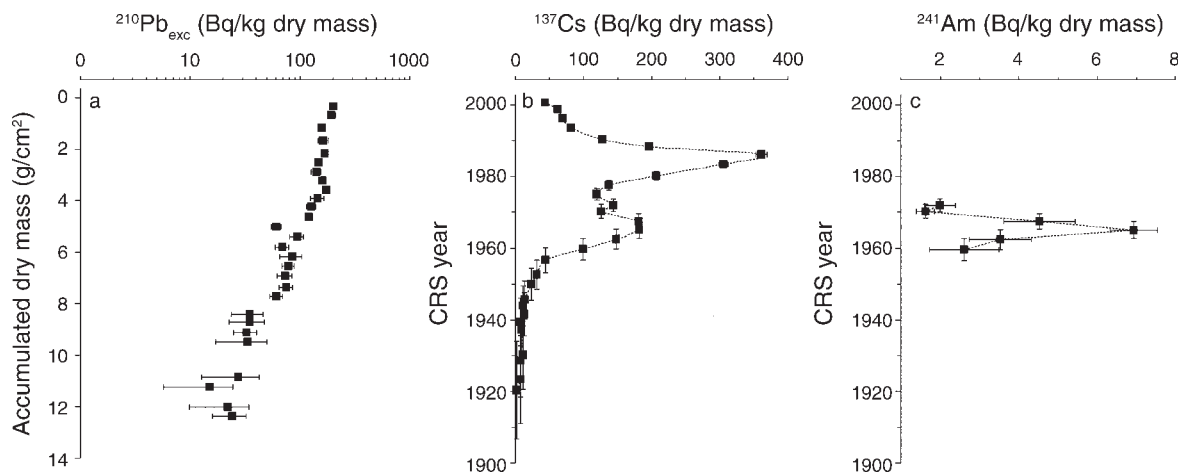


FIG. 2. Activity profiles in the Lough Carra north-basin core of (a) $^{210}\text{Pb}_{\text{exc}}$, (b) ^{137}Cs , and (c) ^{241}Am . Data are means \pm SD. In panels (b) and (c) the activity profiles are shown with CRS (constant rate of supply) dates (the CRS model was used to estimate sediment accumulation rates); ^{241}Am was above detection limits in only a limited section of the core.

productivity phase incorporated as independent variables. All multivariate analyses were done with PRIMER version 6.1 (PRIMER-E 2007).

The composition of diatom assemblages from the north-basin core was used to infer historic water-column TP concentrations in Lough Carra using European Diatom Database (EDD) software for palaeoenvironmental reconstructions (Juggins 2001). Match analogue technique (Birks et al. 1990, Jones and Juggins 1995) was used to identify data sets with the closest matches to the fossil samples. Historic diatom-inferred water column TP (DI-TP) concentrations were estimated using locally weighted weighted averaging (Birks et al. 1990) with inverse de-shrinking because reconstructed values lay closer to the mean of the training-set values (Juggins 2001). Analysis of variance (ANOVA) was then used to examine whether temporal patterns in modeled DI-TP concentrations concurred with those of the biogeochemical data from the cores by examining whether they varied among the three lake-productivity phases described previously. No attempt was made to model DI-TP concentrations from the mid-basin core because >25% of diatom species from the core were absent from the EDD (Birks 1998).

RESULTS

$^{210}\text{Pb}_{\text{exc}}$ activity concentrations declined exponentially with depth in the north-basin core (Fig. 2), consistent with a relatively constant rate of sediment accumulation. Application of the constant rate of supply (CRS) radiometric-dating model yielded a sediment accumulation rate of $0.137 \pm 0.031 \text{ g}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ (mean \pm SD). The core chronology (Appendix A) is supported strongly by the ^{137}Cs profile (Fig. 2), which shows two relatively well-resolved peaks corresponding to radioactive fallout from Chernobyl (1986; CRS date, 1986 ± 1 year) and global nuclear weapons fallout (onset, 1954; peak, 1963; CRS dates, 1954 ± 3 and 1963 ± 2 years, respectively).

The presence of ^{241}Am in the layers corresponding to the deeper peak in ^{137}Cs confirm its origin as weapons fallout. Moreover, the resolution of the peaks in ^{137}Cs is suggestive of little post-depositional mixing of core sediments.

Chronologies for the highly consistent geochemical profiles from the two sediment cores (Appendix B) show a dramatic and monotonic decline in both sedimentary $\delta^{15}\text{N}$ and organic matter in the period during and immediately following the Great Famine of 1845–1850 (Fig. 3). Considerable depletions in $\delta^{15}\text{N}$ of the order of 1.25‰ and 1.13‰ in the northern and mid-basin cores, respectively, were found over a two-year period (CRS estimate 2.4 ± 0.4 years; from 1852 ± 18 years to 1854 ± 18 years) immediately after the famine while the concurrent monotonic reduction in sedimentary organic matter content took place over ~ 10 years (CRS estimate 9 ± 1.5 years) commencing immediately after the onset of the famine (from 1846 ± 19 to 1856 ± 18 years). These decreases were coincident with a 39.8% reduction in the human population recorded between 1841 and 1861 (Fig. 3). These shifts to new equilibria were also contemporaneous with considerable reductions in concentrations of sedimentary phosphorus (reductions of 32.9% and 43% were recorded in the north- and mid-basin cores, respectively, between 1846 ± 19 and 1863 ± 16 years; Fig. 4). Phosphorus accumulation rates declined by 32% and 32.8% in the north- and mid-basin cores, respectively, in the same period (Fig. 4).

Molar ratios of $\text{C}_{\text{org}}:\text{N}$ and sedimentary $\delta^{13}\text{C}_{\text{org}}$ (Fig. 4) were highly consistent (Pearson product-moment correlation; $r = 0.906$, $P < 0.0001$, $df = 28$) and generally increased over a ~ 20 -year period during and following the famine. This pattern was, however, punctuated by a distinct peak in both ratios (CRS date, 1854 ± 18 years), which took place immediately after the phase of declining sedimentary $\delta^{15}\text{N}$ stable-isotope ratios immediately after the famine. Simultaneous and consistent

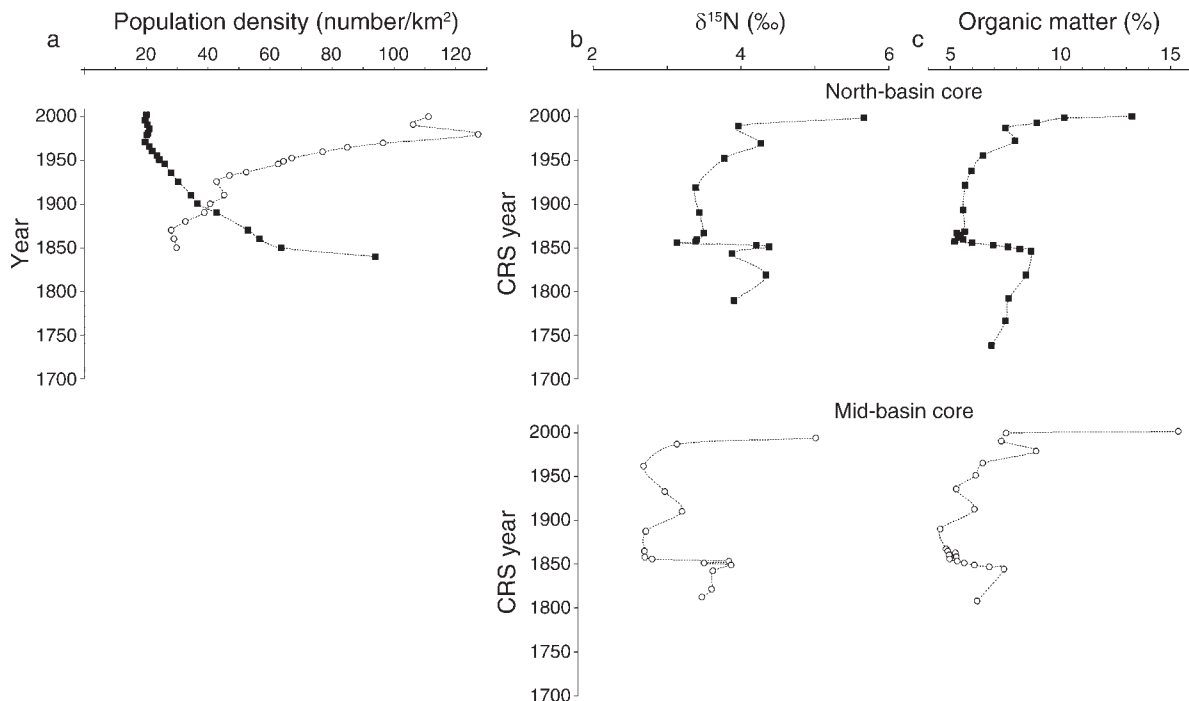


FIG. 3. (a) Estimated population densities of humans (solid squares) and cattle (open circles) in the Lough Carra catchment, 1841–2002. (b, c) Profiles (with CRS dates) of (b) sedimentary $\delta^{15}\text{N}$ and (c) organic matter in the cores taken from the north (solid squares) and middle (open circles) basins of Lough Carra.

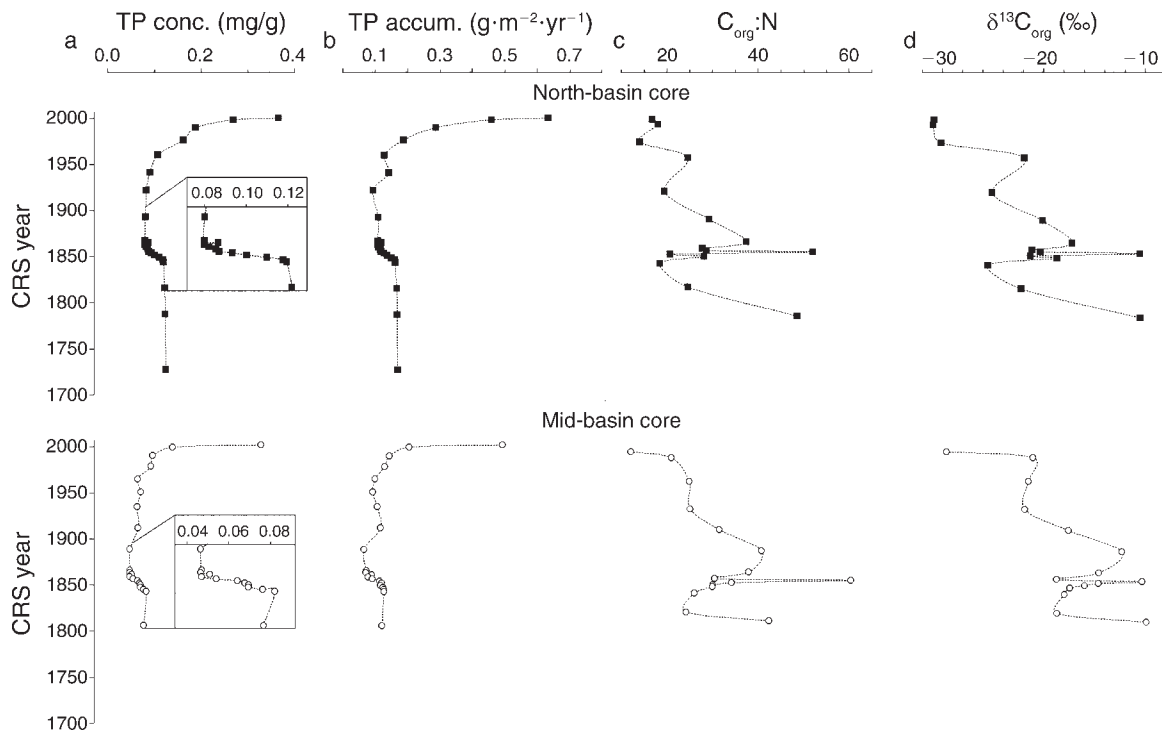


FIG. 4. Profiles (with CRS dates) of (a) total phosphorus (TP) concentrations (with insets) and (b) accumulation rates of TP together with (c) ratios of organic carbon to nitrogen and (d) $\delta^{13}\text{C}_{\text{org}}$ in the cores taken from the north (solid squares) and middle (open circles) basins of Lough Carra. In panel (a), the y-axes on the insets were not modified; the x-axes were expanded to show detail.

TABLE 1. Results of (a) PERMANOVA analysis of diatom assemblage structure and (b) ANOVA analysis of diatom-inferred total P (DI-TP) concentrations during the three main phases of lake productivity indicated by the biogeochemistry of core sediments.

Source of variation	df	SS	MS	F ratio	P
a) PERMANOVA analysis					
Lake basin, B	1	5401.4	5401.4	6.8†	≤0.0001
Productivity phase, P	2	4616.9	2308.4	2.6†	0.033
B × P	2	1776.8	888.4	1.1†	0.33
Residual	15	11 944	796.3		
b) ANOVA analysis					
Productivity phase	2	83.3	41.7	5.3	0.039
Residual	7	54.6	7.8		

† Pseudo-F ratio.

enrichment of sedimentary $\delta^{15}\text{N}$, organic-matter content, and both concentrations and accumulation rates of phosphorus were found toward the top of both cores, from the latter half of the 20th century to the present and particularly in the last two decades, concurrent with declining molar organic $\text{C}_{\text{org}}:\text{N}$ ratios (Figs. 3 and 4).

Even though the structure of lake diatom assemblages differed significantly between the two lake basins (Table 1a), significant differences were also found among the three main phases of lake productivity indicated by the biogeochemistry of the cores (i.e., pre-famine, post-famine [spanning diatom assemblages from 1868 ± 16 to 1941 ± 5 years] and post-1960 ± 3 years). A posteriori pairwise tests found that the structure of diatom assemblages during the post-famine phase differed significantly from those prior to the famine ($t = 2.06$, $P = 0.02$). SIMPER analysis (Table 2) found that the five most important species contributing to the differences between the pre- and post-famine diatom assemblages comprised *Mastogloia smithii*, *Amphora pediculus*, *Fragilaria brevistriata*, *Denticula küentzingii*, and *Cymbella microcephala* (Fig. 5). Concentrations of historic diatom-inferred water-column total phosphorus (DI-TP) estimated from the north-basin core (Fig. 5) correlated highly significantly with concurrent sedimentary TP (Pearson product-moment correlation; $r = 0.881$, $P < 0.001$, $df = 8$). Moreover, they also varied significantly with lake productivity phase (Table 1b) and comprised 15 ± 2.6 $\mu\text{g/L}$ (mean \pm SD) for the period prior to the famine, 11.8 ± 2.5 $\mu\text{g/L}$ for the post-famine phase, and 18.2 ± 3.1 $\mu\text{g/L}$ since 1960.

In spite of the variability in the spatial resolution of the agricultural census data used to estimate phosphorus loading to the lake, patterns of modeled P loads (Fig. 6) were similar to those of DI-TP (Fig. 5), sedimentary TP (Fig. 4), and organic-matter (Fig. 3) concentrations in that they decreased after the famine and have been increasing consistently since the mid-20th century. The modeled TP load for 2002 was estimated as 2078 kg/yr, which compares remarkably well with the TP load of 2070 ± 484 kg/yr (mean \pm SD), measured from July 2001 to July 2003 (I. Donohue, unpublished data). Moreover, the relative importance of the primary sources of phosphorus to the lake (Table 3; Appendix C) appear to have changed considerably in the last 150 years, with human effluent comprising the main source up to 1900, whereas cattle have provided the majority of TP loading to the lake since 1970 (Fig. 6). This increase in the importance of cattle farming (Fig. 3a) has been concurrent with a consistent increase in the number of larger farms (>20 ha) in the catchment (Fig. 6) owing to the aggregation of small farms and the associated removal of field boundaries.

DISCUSSION

Our results suggest strongly that the trophic level of Lough Carra (sensu Rodhe 1969, Wetzel 2001) reduced dramatically over <10 years during and after the rapid and large-scale depopulation of the landscape and reduction of associated human pressures that occurred as a result of the Great Famine. The sedimentary profiles of $\delta^{15}\text{N}$ and organic matter from the two sediment cores indicate that considerable and monoton-

TABLE 2. Results of SIMPER analyses identifying the five diatom species contributing most ($>3\%$) to the dissimilarity between pre- and post-famine periods and their associated relative change in abundance.

Diatom species	Change in abundance†	Contribution to total dissimilarity (%)	Cumulative contribution (%)
<i>Mastogloia smithii</i>	↑	9.55	9.55
<i>Amphora pediculus</i>	↑	5.61	15.16
<i>Fragilaria brevistriata</i>	↑	5.19	20.34
<i>Denticula küentzingii</i>	↓	4.52	24.86
<i>Cymbella microcephala</i>	↓	4.29	29.15

† Relative change in post-famine abundance compared with pre-famine abundance.

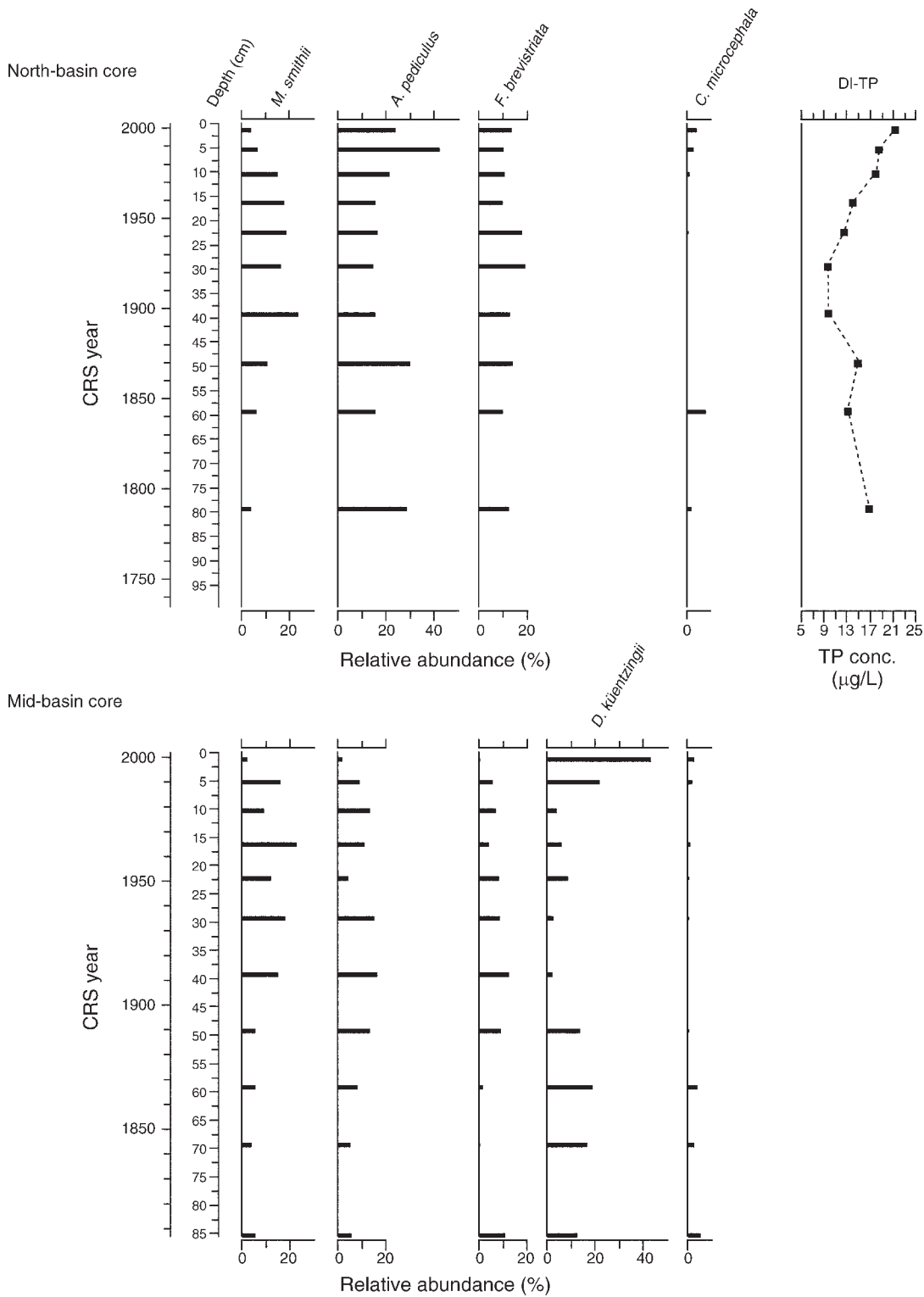


FIG. 5. Percentage abundance of the species contributing most to the differences between pre- and post-famine diatom assemblages (*Mastogloia smithii*, *Amphora pediculus*, *Fragillaria brevistriata*, *Denticula küentzingii*, and *Cymbella microphala*); see Table 2). Diatom-inferred concentrations of water-column total phosphorus (DI-TP) calculated from the north-basin core are also shown. DI-TP could not be estimated from the mid-basin core. *D. küentzingii* was not found in the north-basin core.

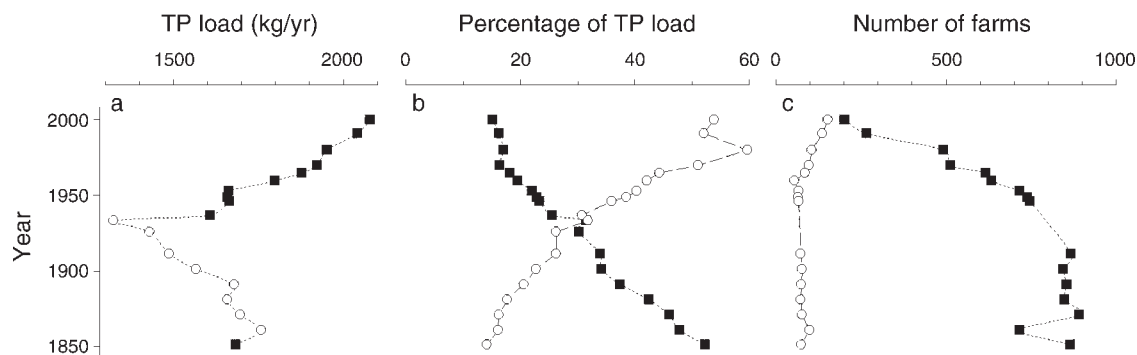


FIG. 6. (a) Historical change in the modeled TP loading to Lough Carra, (b) the percentage of that loading that is attributable to humans (solid squares) and cattle (open circles), and (c) the number of farms <20 ha (solid squares) and >20 ha (open circles) in area in the lake catchment. The different symbols in panel (a) correspond to the modeled TP loads estimated using data from fine (District Electoral Divisions; solid squares) and coarse (Rural Districts; open circles) spatial resolutions.

ic declines in the transfer of nutrients and particulate organic matter from the catchment and associated reductions in lake productivity took place over ~2 and 10 years, respectively, concurrent with a 40% decline in human population density. The depletion in sedimentary $\delta^{15}\text{N}$ during this period likely reflects both reduced input of diffuse N from the catchment and associated decreased utilization of nitrate by algae in the lake. Diffuse nitrogen loading has been shown previously to be a key driver of $\delta^{15}\text{N}$ signatures in lake sediments (e.g., Bunting et al. 2007). Although abandonment of agriculture and the associated tightening of the N cycle has also been found to reduce $\delta^{15}\text{N}$ in upper soil layers (Compton et al. 2007), it is unlikely that decreases of the magnitude observed here could be accounted for by this mechanism over such a short time scale as two years. These shifts to new equilibria were also concurrent with considerable reductions (of the order of approximately one third) in both concentrations and accumulation rates of sedimentary phosphorus, which further supports the premise that nutrient losses from the catchment to the lake declined as a result of reductions in human population pressure and associated agricultural intensity. The possibility of post-depositional mobilization of phosphorus upon sediment deposition is considered to be low in Lough Carra owing to the low likelihood of historical changes in redox states in the lake (Hobbs et al. 2005). Moreover, the highly significant correlations between concentrations of DI-TP (diatom-inferred water-column total phosphorus) and sedimentary TP in the north-basin core and the strong similarity between the sedimentary TP profiles and those of both organic matter and $\delta^{15}\text{N}$ in both cores support this strongly.

The remarkable similarity and consistency between the two cores, which were taken from the two most geochemically distinct basins in the lake (Hobbs et al. 2005), demonstrate that the patterns found here occurred throughout the lake system. The $C_{\text{org}}:N$ ratios from both cores suggest strongly that the organic matter deposited in Lough Carra comprised significant contributions from both allochthonous (produced in the

catchment) and autochthonous (produced in the lake) sources. Profiles of both $C_{\text{org}}:N$ and $\delta^{13}C_{\text{org}}$ indicate that the relative contributions of these sources have varied considerably over the last 200 years and particularly during and after the Great Famine. Increasing ratios of both $C_{\text{org}}:N$ and $\delta^{13}C_{\text{org}}$ during this period indicate reduced contribution of lacustrine productivity to sedimentary organic matter and increased dominance of terrestrial organic matter, for which $C_{\text{org}}:N$ ratios vary typically between 20 and 100 (Jasper and Gagosian 1989). This is consistent with reduced nutrient losses from the catchment during and after the famine resulting in decreased in-lake productivity. These gradual increases in both $C_{\text{org}}:N$ and $\delta^{13}C_{\text{org}}$ were punctuated by a dramatic peak in both ratios in both cores at the end of the period of decreasing lake concentrations of sedimentary nutrients and organic matter after the famine, which is highly indicative of a pulse of terrestrial organic matter into the lake. Historical records (Board of Public Works 1853) suggest strongly that this pulse is attributable to drainage works that took place in the lake catchment in the summer of 1852 and later flooding that obliterated those works later that winter, two years after the famine. The fact that the CRS date for this event, at 1854 ± 18 years, is so close to this date supports strongly this assertion and, equally, supports the quality of the chronological model for the region of the core where $^{210}\text{Pb}_{\text{exc}}$ was not detectable. That this pulse was not discernable in the

TABLE 3. Contributions of the primary sources of phosphorus to the total modeled annual catchment TP loading to Lough Carra for the period 1851–2002 ($n = 19$).

Source of P	Contribution (%)†	Range of contribution (%)
Cattle	33.8 ± 14.3	14.1–59.8
Humans	29.1 ± 11.8	15.1–52.3
Tillage	13.4 ± 6.9	0.6–25.5
Grassland	10.5 ± 5.4	0–17
Sheep	9.5 ± 3.3	4.5–14.8
Pigs	3.8 ± 1.2	0–5.4

† Mean \pm SD.

profiles of organic matter, $\delta^{15}\text{N}$, or sedimentary phosphorus from either core suggests, however, that the event had a limited effect on overall sedimentation patterns in the lake system.

Results from our biogeochemical indicators of historical catchment conditions and inferred shifts in ecosystem equilibria are supported strongly by the fact that the structure of diatom assemblages varied significantly among the three phases of lake productivity indicated by the geochemistry of the cores. Further, diatom-inferred water column TP concentrations also varied significantly among the lake productivity phases and, similar to sedimentary TP concentrations and modeled TP loads to the lake, were lowest in the period following the famine and highest in the most recently deposited sediments. *Mastogloia smithii*, the diatom species that contributed most to the difference between pre- and post-famine diatom assemblages, is considered to be very sensitive to pollution (Van Dam et al. 1994). In both sediment cores, the relative abundance of *M. smithii* increased during the post-famine phase only to decline again in the most recently deposited sediments. Similar patterns were found for *Fragilaria brevistriata*, a species that has been associated previously with reduced nutrient conditions (Finney et al. 2000). Patterns of relative abundance of both *Denticula küentzingii* and *Cymbella microcephala* were, however, opposite to this, being highest prior to the famine and in the most recently deposited sediments in both cores. Species of the genus *Denticula* have been shown to be robust indicators of nutrient enrichment in Irish lakes (Chen et al. 2008), and both *Denticula küentzingii* and *Cymbella microcephala* have been associated previously with mesotrophic conditions (Van Dam et al. 1994, DeNicola et al. 2004). Results from the analyses of diatom assemblages in the cores therefore support the assertion that biological change occurred in the lake coincident with the biogeochemical shifts to new equilibria that occurred after the Great Famine. Even though our present study suffers from the constraints associated normally with uncontrolled observational studies, the fact that such consistent results were obtained from the analysis of a number of independent proxies provides strong support for our conclusions.

Sources of phosphorus to the lake appear to have changed dramatically since the famine, driven initially directly by reductions in human populations in the catchment. The majority of recent inputs of phosphorus to the lake was, however, derived directly from intensification of catchment use associated with cattle farming, and demonstrates a dramatic change in catchment land use and sources of nutrients over the last 150 years. Further, the size of farms has also increased considerably, in particular since the 1950s. These factors, coupled with the associated removal of field boundaries, suggest that the process of recovery from current anthropogenic pressures would likely differ from, and could be considerably more difficult and

lengthy than, that which occurred as a result of the Great Famine. Further, there is evidence that the surface lakebed sediments in Lough Carra have approached their maximum sorption capacity for phosphorus (Hobbs et al. 2005). Beyond this point, there is a strong possibility that the lake could switch rapidly from its current state of relatively clear water with extensive macrophyte growth to an alternative stable state with a highly turbid water column (Scheffer et al. 2001). Recovery from the latter state would be expected to take considerably longer than was required after the Great Famine and would necessitate much management effort, potentially incurring substantial financial cost.

The fact that Lough Carra is largely shallow with, therefore, a relatively important contribution of benthic processes to lake ecology, would have been expected to retard recovery of the lake significantly (Moss et al. 1996). The rapid establishment of new ecosystem equilibria within 2–10 years after the Great Famine is, however, comparable with the most expeditious response of lakes whose nutrient loading from point sources have been reduced using modern engineering solutions (Jeppesen et al. 2005). This is in spite of the fact that nutrients and other substances can be retained by soil matrices for long periods, potentially delaying recovery from landscape-scale anthropogenic disturbance significantly (Schippers et al. 2006). The legacy of historic anthropogenic disturbance can potentially last for centuries, even after rapid human depopulation has taken place (Webb and Newman 1982, Paul 1991, Knapp 1992, Brown 2000). Our results demonstrate, however, that the swift reduction of human-associated pressures from diffuse sources at landscape scales can, in some circumstances, result in the rapid and monotonic recovery of lake ecosystems. Therefore, recovery of ecosystems from diffuse pollution need not necessarily take longer than from pollution from point sources.

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APPENDIX A

CRS dates estimated for each sample from the north-basin core (*Ecological Archives* A020-063-A1).

APPENDIX B

Geochemical data from the north- and mid-basin cores (*Ecological Archives* A020-063-A2).

APPENDIX C

Modeled total phosphorus loads to Lough Carra (1851–2002) and the percentage contribution of the primary sources of the loading (*Ecological Archives* A020-063-A3).