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Marine and freshwater influences on the hydrography, oxygen dynamics and ecology of an anoxic lagoonal estuary, Lough Furnace, Mayo, Ireland

A thesis submitted to the National University of Ireland, Galway for the degree of Doctor of Philosophy

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July 2019
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DECLARATION

I, Seán Kelly, certify that this thesis is all of my own work. I have not obtained a degree in this University or elsewhere on the basis of any of this work. My contribution to each article presented herein is explicitly stated in section 1.3.

Signed:
Date:
FUNDING

This Cullen Fellowship project (Grant-aid Agreement No. CF/15/03) was carried out with the support of the Marine Institute and funded under the Marine Research Programme by the Irish Government. Funding from the Marine Institute Networking and Travel Awards, Thomas Crawford Hayes Research Fund and Global Lake Ecological Observatory Network Student Travel Award are also gratefully acknowledged.
ABSTRACT

Estuarine and coastal water bodies are amongst the most productive and diverse habitats, providing crucial ecological and economic benefits. However, owing to their position at the interface between continents and the oceans, they are highly sensitive to natural and anthropogenic environmental change. Deoxygenation is increasingly recognised as a major threat to coastal ecosystems, with climate change heavily implicated in the expansion of oxygen depletion. Thus, there is a need to discern the physical processes that heighten susceptibility to severe deoxygenation. This project used Lough Furnace, a lagoonal estuary with deep anoxia, to address the following: what are the relative roles of marine, freshwater and meteorological variables in controlling hydrography and dissolved oxygen dynamics? This was investigated using timeseries of hydrographic and meteorological observations. The anoxic inner basin revealed significant interannual oxygen variability over the past decade, with bottom water ventilations occurring every 2 years on average. Ventilations followed prolonged periods of low rainfall, allowing increasingly saline spring tides to traverse the long connecting channel and dense oxygen-rich water descend to the basin bottom. A simple model indicated that these oxygenations have become less frequent since 1979, due in large part to the higher rainfall in this region in the past 10-15 years. The implications of anoxia on resident fish ecology was assessed and it was revealed that wind-induced baroclinic seiches can cause deep anoxic water to encroach into oxygenated nearshore zones. The marine-species dominated deep chlorophyll maximum was more conspicuous following low freshwater input and increased tidal inflows, sharing
similar physical drivers with oxygen dynamics. Overall the study has indicated that oxygen dynamics result from a delicate interplay between freshwater, tidal and wind forces, which are all subject to modification under climate change, putting into uncertainty the future oxygen regimes in such systems.
Chapter 1

Chapter 1. INTRODUCTION

1.1. Background and Motivation

Coastal habitats and estuaries form the interface region between freshwater and marine environments and are among the most productive ecosystems globally, providing crucial environmental and economic value. Near-coastal (within 100 km) human population densities are nearly 3 times higher than the global average density (Small and Nicholls 2003). Furthermore, 10% of the global population resides in the low-elevation coastal zone situated directly along coastlines, which only encompasses 2% of the earth’s total land area (Ramesh et al. 2015). These coastal areas provide vital economic benefits to the tourism and recreation sector, fisheries and the shipping and ports industry. Coastal zones and estuaries also provide important ecosystem services including shoreline stabilization and flood defence, food and energy resources and the sequestration and detoxification of pollutants and organic waste from terrestrial runoff (Wolanski 2007). From an ecological perspective they can also provide nursery grounds for juvenile fish species (Beck et al. 2001) and connect the migratory route between freshwater and marine environments for diadromous fish.

Owing to dual physical and biogeochemical inputs from freshwater and marine environments, estuaries and coastal waters often showcase complex interactions and are typically highly dynamic systems, varying enormously depending on their geomorphology and the local climatic conditions (Dyer 1997; Robins et al. 2016). Classification can therefore be difficult and throughout this dissertation when referring to estuarine waters a broad
definition is used: a semi-enclosed coastal water body which receives tidal input through a connection with the open sea and freshwater input from terrestrial runoff. The nature of the connection to the sea may be natural or man-made, periodically closed or open and/or severely constricted; the tidal input may be minimal; the magnitude of freshwater input may vary temporally, even being absent during certain time periods. This broader definition allows the inclusion of various estuarine systems from various geographic regions such as drowned river valleys and coastal plains (see Davidson et al. 1991), coastal lagoons (see Kjerfve 1994) and fjords (see Farmer and Freeland 1983). It also allows the inclusion of larger scale semi-enclosed oceanic basins with estuarine characteristics such as the Black Sea (Murray et al. 1991) and the Baltic Sea (Stigebrandt 1985).

This thesis is primarily concerned with the category of transitional water bodies that have a restricted connection to their adjacent oceanic basins and because of this typically have a restricted rate of exchange. These coastal basins are usually bounded by land on each side apart from a single, often narrow (and sometimes shallow) entrance through which estuarine exchange with the open sea must occur. The topographically constrained connecting channel limits flow in each direction. Such semi-enclosed coastal waters have been referred to as regions of restricted exchange (Tett et al. 2003) and are often important sites for human settlement and activities; their saline waters are relatively well sheltered and easily accessible compared with open coastal areas and thus they are often chosen as sites for aquaculture and fisheries development. For example in Ireland, the vast majority of salmonid farm sites are located in sheltered, enclosed inlets and bays (https://www.marine.ie/Home/site-area/areas-
activity/aquaculture/locations-salmonid-farms) while in Scotland and Norway aquaculture sites are predominantly located in sea-lochs and fjords (Gillibrand and Turrell 1997; Bannister et al. 2016). However such human activities can lead to increased nutrient and chemical loading and because of the nature of the restricted exchange and longer residence times, these habitats may be particularly sensitive to water quality issues and eutrophication (Tett et al. 2003). It is therefore important to develop an understanding of the mixing and exchange mechanisms that occur within these environments in order to assess susceptibility to water quality degradation as well as overall suitability for aquacultural activities (Stigebrandt 2012; Gillibrand et al. 2013). Moreover, understanding the hydrodynamics in these transitional water bodies is integral from an overall ecological perspective, as resident flora and fauna must be adapted to the highly variable conditions that exist and are dependent on waterborne materials and properties (e.g. temperature, salinity, dissolved gases and nutrients), the supply and distribution of which are ultimately a function of circulation, stratification and mixing dynamics.

Transitional coastal basins with restricted horizontal exchange with the open coastal area may develop strong saline stratification of the water column due to reduced surface salinities from freshwater runoff. The combination of vertical stratification and restricted horizontal exchange often isolates the bottom waters of these systems, leading to the development of stagnancy and increasing the likelihood of deoxygenation. There is a great need to develop an understanding of the physics that control exchange and renewal of the deep basin water and whether similar control mechanisms exist between individual systems. Furthermore, it remains to be seen how
climate change will impact upon these physical controls and whether projected modifications of meteorology (e.g. air temperature, rainfall patterns, wind speeds) and hydrography (e.g. sea level rise) will increase mixing dynamics in these systems or reinforce the restricted exchange. Finally, aside from being important from a human activity and ecological perspective, these transitional coastal systems can serve as excellent models for readily observing and studying many fundamental hydrographic processes in physical oceanography and limnology related to naturally stratified flows.

1.2. Research objective

The primary objective of this dissertation was to assess how the combination of marine, freshwater and meteorological variables control the hydrography of a semi-enclosed estuarine basin and what the resulting implications are for dissolved oxygen dynamics and resident ecology.

The study used Lough Furnace, a deep lagoonal estuary that experiences natural anoxia of its deeper waters. In order to achieve this objective, a series of targeted observational field studies were combined with routine environmental monitoring work carried out by the Marine Institute. The main research objective was divided into the following four sub-aims:

1. Use in-situ, high-resolution monitoring over a multiyear period to assess inter- and intra-annual variability in hydrography and dissolved oxygen dynamics in the Lough Furnace system. (Article I)

2. Quantify the volume fluxes associated with the horizontal exchange flow between the semi-enclosed inner basin and the
adjacent open coastal region in order to determine the renewal times of the basin water. An additional component of this objective was to develop an empirical model capable of accurately predicting the occurrence of deep-water ventilations based on hydro-meteorological input data. (Article II)

3. Investigate the potential ecological implications of wind-driven upwelling of oxygen-depleted bottom water on nearshore benthic fish ecology. (Article III)

4. Determine bio-physical controls of the spatio-temporal dynamics of the Furnace phytoplankton population, with specific focus on the deep chlorophyll maximum (DCM). (Article IV)

1.3. Thesis outline and article contributions

This thesis is arranged into 7 Chapters and 3 Appendices. The overall layout of the thesis, with relevant linkages between the articles, is shown schematically in Fig. 1. Following this general background and motivation for the project in Chapter 1, a general review of the literature pertaining to the relevant hydrodynamical and bio-physical processes in stratified estuarine systems is presented in Chapter 2. The main body of the thesis is a collection of articles I-IV related to the four sub-aims listed in section 1.2. and arranged into Chapters 4-7. Each of these chapters contains a specific introduction, review of the relevant literature, methodology, results and discussion. Chapter 8 provides a short synthesis of the overall findings and discusses avenues for prospective research. An additional 3 articles are included in the Appendices (A-C), with relevance to the overall research objectives of the project.
1.3.1 Articles (and contributions)

I. **Kelly, S.**, Eyto, E. de, Dillane, M., Poole, R., Brett, G., White, M. 2018. Hydrographic maintenance of deep anoxia in a tidally influenced saline lagoon. Marine and Freshwater Research 69, 432–445. (Collated and processed the raw data, analysed the data and wrote the first draft of the paper (included integrating a subsection written originally by M. White relating to data collected in 2010))

II. **Kelly, S.**, Eyto, E. de, Dillane, M., Poole, R., White, M. Volume fluxes, oxygen dynamics and a predictive model of deep-water ventilation in an anoxic estuarine basin. (in prep for submission). (Collected, processed and analysed the data and wrote the first draft of the paper.)

III. **Kelly, S.**, Eyto, E. de, Poole, R., White, M. 2018. Ecological consequences of internal seiches in a semi-enclosed, anoxic coastal basin. Marine Ecology Progress Series 603, 265–272. (Collected, processed and analysed the data and wrote the first draft of the paper.)

IV. de Eyto, E., **Kelly, S.**, Ryder, E., Dillane, M., Archer, L., O’Cathain, D., Daly, S., Lyons, K., Obrador, B., Brentrup, J., Naumoski, A., Poole, R., Lucy, F.E., Jennings, E. 2019. High frequency monitoring reveals fine scale spatial and temporal dynamics of the deep chlorophyll maximum of a stratified coastal lagoon. Estuarine, Coastal and Shelf Science 218, 278–291. (Performed data processing and analysis pertaining to physical processes and assisted in generating figures and writing.)
1.3.2 Appendices


Chapter 1. Introduction
Coastal & estuarine waters, deoxygenation, motivation & aims

Chapter 2. Literature Review
Overview of density stratification, influence on oxygen dynamics, hydrodynamics of semi-enclosed, stratified estuaries

Chapter 3. (Article I)
Physical: Stratification & oxygen dynamics

Chapter 4. (Article II)
Physical: Estuary-ocean fluxes & oxygen dynamics
Kelly et al. (2019). Volume fluxes, oxygen dynamics and a predictive model of deep-water ventilation in an anoxic estuarine basin. *in prep*

Chapter 5. (Article III)
Bio-physical: fish ecology

Chapter 6. (Article IV)
Bio-physical: phytoplankton ecology

Chapter 7. Synthesis
Summary of findings and future research

Appendix A.

Appendix B.

Appendix C.

Fig. 1. Thesis outline.
REFERENCES


Chapter 2. LITERATURE REVIEW

2.1. Density stratification in aquatic environments

Vertical stratification exerts a large influence on the physics of aquatic environments and therefore profoundly affects chemical and biological processes (Imberger, 1998). Stratification refers to a vertical gradient in water density, with mean water density increasing with depth. The density of water ($\rho$, kg m\(^{-3}\)) is dependent upon its salinity ($S$), temperature ($T$, °C) and pressure ($P$, decibars) with the equation of state for seawater density (at the normal atmospheric pressure, $P = 0$) given by Fofonoff and Millard (1983):

$$\rho = \frac{\rho(S, T, 0)}{1 - \frac{p}{K(S, T, P)}}$$

(1)

where $K(S, T, P)$ is the secant bulk modulus (seawater compressibility, see Fofonoff and Millard (1983) for further details). Warm water will have a lower density than cold water (above 4°C) and saline water will have a higher density than pure freshwater. As a point of reference and to illustrate the influence of salinity on water density, surface water (at a standard atmospheric pressure of 1 atm) with a practical salinity of ~0 (i.e. freshwater) and at a temperature of 10 °C has a density of 999.7 kg m\(^{-3}\). The density of water with a typical surface seawater salinity of 35 and at the same pressure and temperature is 1027 kg m\(^{-3}\).

A body of water with volume $V$ and density $\rho$ will have a weight of $g\rho V$, where $g$ is the acceleration due to gravity, generally taken as 9.81 m s\(^{-2}\) (Thorpe 2007). The effect of density-stratification is
to separate fluid masses of different densities into vertically stacked layers with lighter, lower density fluid overlying denser fluid due to the differential (upward) buoyancy forces at work. Density variations with depth are a ubiquitous and distinguishing feature of naturally occurring geophysical flows on Earth (Cushman-Roisin and Beckers 2011). In a stably stratified fluid, ignoring brief states of static instability, density generally increases uniformly with depth (i.e. $\frac{dp}{dz} < 0$); thus a displacement of a parcel of water of density $\rho_1$, from its original position (either upwards or downwards) to a position where it is surrounded by water of density $\rho_2$, will produce a simple oscillatory motion as the particle accelerates back towards (and overshoots) its equilibrium position. The acceleration is a function of the buoyancy force, and the frequency at which the particle will oscillate following vertical displacement is given by the buoyancy frequency, $N$, (Gill 1982):

$$N = \left[-\frac{g}{\rho_0} \frac{dp}{dz}\right]^{1/2}$$  \hspace{1cm} (2)

where $\rho_0$ is a mean density and $\frac{dp}{dz}$ is the density difference over the displacement depth. Thus $N$ represents a measure of the local stability of the density stratification (Thorpe 2007). For $N > 0$ the parcel accelerates back toward its initial position and the stratification is stable; for $N < 0$ the parcel accelerates away from its initial position and the stratification is unstable or in a state of static instability, which eventually leads to convection and overturning and a local breakdown of the density stratification.

The maximum value of $N$ recorded in a depth profile of a stratified water column corresponds with the region where the
density gradient \((dp/dz)\) is greatest. This depth zone is referred to as the pycnocline and represents a region where a physical interface occurs between the layers of water situated above and below (Affholder and Valiron 2001). The pycnocline region is important from a physics perspective as it influences circulation, currents and heat budgets and is also crucial to biological and chemical processes as it can inhibit vertical mixing of nutrients and dissolved gases between layers (Imberger 1998; Fiedler et al. 2013). The depth and strength of the pycnocline region (and the severity of the exchange restriction between upper and lower layers) varies temporally (e.g. seasonally) and between different geographical regions (Longhurst 2007).

One of the defining physical characteristics of the ocean is the near universal presence of stable stratification. Warm near-surface water overlies cold, denser water, with the sharp drop off in temperature with depth generating a pycnocline, referred to as the thermocline. This thermocline is situated below the mixed upper layer of the ocean and its shape varies seasonally, reflecting the temporal changes in the interaction between the upper ocean and the atmosphere (Fiedler et al. 2013); a second, permanent thermocline lies deeper below in the ocean interior, separating the upper stratified region from the deep, dense abyssal ocean (Gnanadesikan 1999).

In temperate freshwater lakes and reservoirs, thermal stratification during the warmer seasons restricts vertical mixing, creating a gradient of dissolved substances which greatly affects important lake processes such as phytoplankton productivity (MacIntyre and Jellison 2001), CO\(_2\) fluxes from surface waters to the atmosphere (Åberg et al. 2010) and whole-lake metabolism (Coloso et al. 2011; Staehr et al. 2012). Understanding the pathways that exist for
nutrient and particle transport between layers, which effectively controls the ecology of the lake during prolonged stratified periods, has been a key focus of limnological research for several decades (e.g. Mortimer 1952; Thorpe 1977; MacIntyre et al. 1999; Saggio and Imberger 2000; Hondzo and Haider 2004).

Density gradients and the related stratification in aquatic basins play a pivotal role in circulation by moderating the interaction between the deep interior basin water and the atmospheric forcing, which in turn influences the Earth’s surface climate (e.g. Oglesby et al. 2005; Lofgren 1997). Buoyancy fluxes at the water surface driven by temperature differences across the air-water interface modify the density of surface waters (Csanady 2001). For example, cooling by the overlying atmosphere reduces the buoyancy of the sea surface water, which may induce overturning in the ocean which can extend from the surface to the deep interior (Wunsch and Ferrari 2004). In contrast, heating at the sea surface by the atmosphere adds buoyancy, reinforcing the thermal stratification with depth. In addition to heating and cooling, surface water buoyancy is modified by evaporation and precipitation, which increase and decrease salinity respectively (Sathiyamoorthy and Moore 2002; Karstensen and Lorbacher 2011). Thus the buoyancy-driven circulation of oceans and lakes is intrinsically linked to modification of the stratification and the deep convection that can occur following a large removal of surface buoyancy (e.g. Killworth 1983; Marshall and Schott 1999; Isachsen et al. 2007; Yang et al. 2018; Boehrer and Schulze 2008; Stigebrandt 1985). Buoyancy fluxes through the air-water interface also directly influence mixing layer depth and near-surface turbulence, which regulates gas flux dynamics between aquatic
environments and the overlying atmosphere (Imberger 1985; MacIntyre et al. 2010).

Density stratification also supports internal waves, which are oscillating motions that occur within the interior of a stratified fluid, propagating along the interfaces that separate fluid layers of different densities (Thorpe 2007). These internal gravity waves can be thought of as analogous to the more familiar surface gravity waves that propagate along the air-water interface but because the density difference between water masses is much less than that between surface water and the overlying atmosphere, internal waves propagate at much slower speeds and resemble “slow motion” surface waves (Gill 1982). Internal waves, which can be forced by wind stress acting on the water surface (e.g. D’Asaro 1985; Alford 2001; Mortimer 1952) or by the interaction of tidal flow with topography (e.g. Garrett and Kunze 2004; van Haren 2012), are one of the predominant sources of mixing and turbulence within stratified systems (Munk and Wunsch 1998; Thorpe 2010; Saggio and Imberger 2000; Arneborg and Liljebladh 2001). Because of their horizontal and vertical currents and the turbulent mixing associated with their breaking, internal waves redistribute and supply important water properties, playing a well-documented role in biological processes within the ocean (e.g. Holligan et al. 1985; Leichter et al. 1998; Muacho et al. 2013), lakes (e.g. MacIntyre et al. 1999) and estuaries (e.g. Friedrichs and Wright 1995).

In estuarine systems salinity is generally the dominant contributor towards the water density *i.e.* a 1°C change in temperature creates a density difference equivalent only to a 0.2 psu change in salinity (Geyer and Ralston 2011). In such systems a large salinity gradient can arise with surface freshwater runoff providing
buoyancy input into a saline receiving basin, leading to the formation of a very strong halocline separating the two layers. However the strength of stratification varies among estuarine systems and is dependent upon the magnitude of freshwater inflow and the mixing rate, which is typically a function of the tidal forcing (Fischer et al. 1979; Simpson et al. 1990; Geyer and Ralston 2011). This makes transitional water bodies with a restricted connection to the open sea excellent candidates for studying stratification dynamics, as the constrained entrance channel usually limits the ability of tidal mixing to prevent the formation of a strongly stratified interior basin, with a seaward surface freshwater or brackish layer overriding and remaining separated from a deeper saline layer.

In this regard, fjords (and other strongly stratified estuarine basins mostly cut-off from the circulation of open coastal waters) have attracted much attention from physical oceanographers, as a wide range of fluid dynamics related to naturally stratified flows can be readily observed. Examples include internal waves generated by tides (Staalstrøm et al. 2012; Arneborg and Liljebladh 2009) and by wind (Arneborg and Liljebladh 2001), wind-driven upwelling in nearshore areas (Cushman-Roisin et al. 1994), interaction of stratified flow with topography (Farmer and Armi 1986; Inall et al. 2005), internal hydraulic control (Stigebrandt 1981), vertical diffusion of deep basin water (Stigebrandt and Aure 1989) and the exchange of deep resident basin water by a bottom-intruding turbulent gravity current (Liungman et al. 2001; Arneborg et al. 2004; Belzile et al. 2015) [for a comprehensive review of the physical oceanography and hydrodynamics of fjords see Farmer and Freeland (1983) and Stigebrandt (2012)]. Apart from being crucial to developing an understanding of the physical processes involved in the interaction
between terrestrial and oceanic environments, such fluid dynamics are of even greater general interest as many of these processes are important to understanding flows and circulation in large-scale oceanic basins.

2.2. Dissolved oxygen dynamics in aquatic environments

An important ecological concept is the association between stratification of the water column and the depletion of dissolved oxygen in bottom layers. In water bodies with strong and stable stratification, the bottom layers may become isolated from any interaction with the atmosphere and oxygenated near-surface waters for a prolonged time period. This separation causes a reduced downward transport of dissolved oxygen (e.g. Stanley and Nixon 1992; Burns 1995; Sharples et al. 2003). Over time, dissolved oxygen in the isolated lower layer is depleted through biochemical activity in the water column (biological oxygen demand (BOD)) and in the bottom sediments (sedimentary oxygen demand (SOD)). BOD involves the biological oxidisation of organic matter by microorganisms present in the water column (Jouanneau et al. 2014). SOD involves the uptake and consumption of dissolved oxygen by microbial and chemical processes in the sediments following the sinking and sedimentation of organic detritus (Jørgensen and Revsbech 1985; Higashino 2011).

Eutrophication in aquatic environments occurs following increased loading of nutrients and dissolved organic matter from anthropogenic sources (Nixon 1995). This can lead to an over-production of particulate organic matter including specific groups of bacteria (e.g. Fodelianakis et al. 2014; Xiong et al. 2015) and phytoplankton (e.g. Paerl et al. 1998; Jiang et al. 2013; Song et al. 2017)
favoured by the eutrophic conditions. The large quantities of particulate organic matter produced may exceed grazing rates by primary consumers and will accumulate in the water column and in bottom sediments after sinking, consuming dissolved oxygen through microbial degradation (Gray et al. 2002). This consumption of dissolved oxygen, which in stratified conditions is coupled with a lack of replenishment from an oxygenated source, leads to the development of hypoxia, usually defined in aquatic environments as oxygen concentrations lower than 2 mg O$_2$ L$^{-1}$ (Diaz and Rosenberg 2008). Evidence suggests however that this defined hypoxic threshold may be too low and could underestimate the ecological impacts of hypoxia, particularly for sensitive benthic fauna (Vaquer-Sunyer and Duarte 2008). In severe cases, where bottom waters remain stagnant for prolonged periods and/or eutrophication is particularly intense, anoxia (0 mg O$_2$ L$^{-1}$) will develop (Gray et al. 2002).

The development and spread of hypoxic and anoxic zones in coastal and marine ecosystems and the potentially negative consequences for biodiversity and productivity have been extensively documented (e.g. Gray et al. 2002; Diaz and Rosenberg 2008; Vaquer-Sunyer and Duarte 2008; Rabalais et al. 2010; Steckbauer et al. 2011). Benthic fauna may be particularly vulnerable, as regions with severe bottom hypoxia such as the Baltic Sea can have large areas with impoverished species diversity or that are completely devoid of any benthic macrofauna (Karlsson et al. 2002; Villnäs and Norkko 2011). There is also considerable evidence of the harmful physiological effects of acute low oxygen exposure in laboratory settings on a variety of fish (e.g. Tallqvist et al. 1999; Chabot and Claireaux 2008; Nishizawa et al. 2017) and invertebrate
species (e.g. de Zwaan et al. 1995; Cheung et al. 2008; Villnäs et al. 2012). Aside from the obvious outcome of mortality, hypoxic conditions can have more insidious impacts on aquatic organisms such as reduced growth rates and modification of foraging, avoidance and predatory behaviour (Wannamaker and Rice 2000; Domenici et al. 2007). Less is known however about how long-term exposure to sub-lethal concentrations of dissolved oxygen affects the physiology and behaviour of aquatic organisms or what the larger-scale population and ecosystem impacts of low oxygen concentrations will be (Townhill et al. 2017). Certain species inhabiting environments with chronically low levels of dissolved oxygen may have a higher tolerance to oxygen depletion and could gain a competitive advantage. For example, in a coastal inlet with significant bottom layer hypoxia, inter-species variation in hypoxia and anoxia tolerance explained why some species of medusae thrived in low oxygen conditions whilst more sensitive taxa disappeared (Rutherford Jr. and Theusen 2005). Similarly, in a seasonally hypoxic fjord, pelagic fish species were found to be consistently distributed in the moderately hypoxic bottom zone, often in oxygen concentrations below the threshold shown in laboratory settings to initiate behavioural changes in pelagic species, which may confer a competitive advantage in terms of predator avoidance or food acquisition (Sato et al. 2016).

Aside from its impacts on aquatic organisms, dissolved oxygen depletion also fundamentally modifies biogeochemical processes that control nutrient concentrations in the water column (Conley et al. 2009). In systems with hypoxic bottom water, dissolved inorganic phosphorus is released from iron-bound phosphorus in the oxygen-deplete sediments into the overlying water column (Rozan et
In addition, rates of denitrification are influenced by low-oxygen conditions and may be reduced depending on multiple conditions including the duration of the hypoxic conditions and initial concentrations of nitrates in the bottom water at the onset of hypoxia (Middelburg et al. 1996; Kemp et al. 2005; Conley et al. 2009). The release of phosphate from sediments and enhanced recycling of nitrogen because of reduced denitrification efficiency may boost phytoplankton productivity and support more intense blooms under hypoxic conditions, which can function as a positive feedback loop for continued deoxygenation (Kemp et al. 2005; Conley et al. 2009).

Whilst eutrophication is an important driver of dissolved oxygen depletion, hydrography is ultimately the most critical factor in determining whether a system develops persistent hypoxia or anoxia (Gray et al. 2002). For example, in pristine freshwater lakes without appreciable external sources of nutrient loading, oxygen depletion can occur in the deep water below the thermocline during periods of stable thermal stratification (Nürnberg 2004). In contrast, in estuarine systems with very high nutrient loading but with rapid flushing rates of the bottom water, hypoxia can be avoided (e.g. Wang et al. 2004). It is therefore not surprising that it is in coastal and estuarine systems with strong vertical stratification, limited horizontal exchange with other oxygenated basins and long deep-water residence times that the most drastic occurrence of oxygen depletion, anoxia, commonly occurs. This includes silled fjords, where tidal exchange with the open ocean is generally restricted to above-sill depths and the below-sill basin water inside the fjord can remain stagnant for prolonged periods (Gade 1973; Farmer and Freeland 1983). This can have profound implications in some deeper fjords with shallow sills, with perennially (e.g. Stigebrandt et al. 2015)
or even permanently (e.g. Skei 1988; Yao and Millero 1995) anoxic water comprising a considerable portion of the total basin volume. Additional examples of large estuarine systems showing natural development of deep anoxia include basins separated by shallow, narrow or long outlets to adjacent seas such as Nitinat Lake (Pawlowicz et al. 2007), Saanich Inlet (Zaikova et al. 2010) and the Black Sea (Murray et al. 1991; Özsoy et al. 2001). Whilst the hydrography of some of these systems make them naturally susceptible to the development and maintenance of anoxia there is evidence that increased anthropogenic eutrophication exacerbates the extent and intensity of anoxic conditions and the associated negative ecological impacts (e.g. the Baltic Sea (Stigebrandt et al. 2014), the Black Sea (Zaitsev 1992)).

In anoxic conditions, benthic metabolism switches from aerobic to anaerobic respiration, with the mineralisation of organic matter resulting in the formation of various reduced substances including ammonium, hydrogen sulphide and methane (Middelburg and Levin 2009). Hydrogen sulphide (H2S) in particular is toxic to aquatic animals as it inhibits cytochrome c oxidase (Grieshaber and Völkel 1998). Because the physiological response to sulphide exposure in animals increases oxygen consumption (Grieshaber and Völkel 1998), H2S toxicity may work synergistically with low oxygen concentrations and has been observed to further increase mortality rates in organisms already exposed to hypoxia (Vaquer-Sunyer and Duarte 2010). In the past, significant fish kills have been strongly associated with the upwelling and intrusion of anoxic, H2S-rich bottom water (Bagarinao and Lantin-Olaguer 1998; Luther et al. 2004; Marti-Cardona et al. 2008; Lamberth et al. 2010). Therefore there is a need to understand the physical dynamics that moderate upwelling
and mixing events in aquatic environments with deep anoxia in order to assess potential ecological consequences.

Modification of biogeochemical cycles may lead to the oxygen-deplete bottom water becoming nutrient-rich compared to the photic surface waters, where nutrients become limited due to phytoplankton activity (Hecky and Kilham 1988). The pathways of mixing and exchange between deeper nutrient-rich waters and well-lit layers further up the water column in the pycnocline region may be critical in maintaining levels of primary productivity (e.g. Sharples et al. 2001; Tweddle et al. 2013). Research indicates that renewal and uplifting of the old, oxygen-deplete, nutrient-rich basin water toward the surface in fjords (Arneborg et al. 2004) and nearshore breaking of internal waves along the pycnocline in lakes (e.g. MacIntyre et al. 1999; Lorke 2007) play a large role in facilitating the flux of nutrients into productive upper layers. However how such mixing events might support phytoplankton populations in stratified basins with naturally occurring deep anoxia is largely unknown.

Climate change is predicted to lead to an increased occurrence of dissolved oxygen depletion in bottom waters primarily through decreasing the solubility of oxygen in warmer surface water and intensifying the effects of thermal stratification and is expected to affect oceans (e.g. Deutsch et al. 2015; Schmidtko et al. 2017), coastal estuarine systems (e.g. Hordoir and Meier 2012) and lakes (e.g. Foley et al. 2012; North et al. 2014; Missaghi et al. 2017). In some coastal regions, increased river runoff could also increase vertical saline stratification and nutrient loading which could compound the occurrence and severity of coastal ‘dead zones’ (Altieri and Gedan 2014). Therefore systems that experience natural anoxia under
contemporary climate conditions represent ideal test-beds for developing an understanding of the hydro-meteorological controls of oxygen dynamics.

2.3. *Hydrodynamics in stratified estuarine systems with restricted exchange*

Using the Lough Furnace study site as a template, Fig. 2. represents a schematic overview of the range of hydrodynamic and biological processes often encountered in these coastal environments and highlights their use as model systems.

**Fig. 2.** Schematic showing physical and biological processes often encountered in stratified estuarine basins such as Furnace.

2.3.1. *Estuary-ocean exchange fluxes and renewal times*

Because of the large vertical density gradients typically present in semi-enclosed estuarine basins, exchange of water with the adjacent coastal ocean through the connecting channel is dominated by horizontal transport processes. These are mainly driven by tides and the gravitational (density-driven) circulation caused by the discharge of freshwater into the surface of the estuarine basin which creates a horizontal density and pressure
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gradient; the result (often referred to as “estuarine circulation”) is a seaward flowing surface layer, beneath which is an inward flow of seawater drawn in to replace the outflowing water (Stigebrandt 1981; Geyer and MacReady 2014). A simplified, effective approach to understanding circulation and exchange dynamics is to represent the water column structure within the estuarine basin as two or three horizontally-uniform layers, separated by primary and secondary pycnoclines (Gillibrand et al. 2013). The presence of two or three layers depends upon the morphology of the basin and the connection to the adjacent ocean; a deeper basin with a shallow outlet or sill may have a third layer, containing dense water below the level of the sill that is generally isolated both horizontally and vertically (outside of deep-water renewal events (see section 2.3.2)). The surface layer salinity depends upon the amount of saltwater entrained across its density interface with the stratified layer below (Kato and Phillips 1969; Strang and Fernando 2001a), with the energy for these turbulent vertical fluxes between layers primarily supplied by tidal and wind-driven flows (see section 2.3.3). The intermediate, tidally-exchanged layer has properties that may change based upon variations in coastal water density outside the basin (Klinck et al. 1981; Arneborg 2004).

The simplified, time-averaged exchange flow for the upper two layers, assuming steady state conditions in relation to volume and salt, can be expressed using Knudsen’s relation, originally derived for the Baltic Sea (Knudsen 1900; MacCready and Geyer 2010):

\[ Q_1 = Q_f + Q_2 \]  

(3)
where $Q_1$ is the volume leaving the basin in the upper layer through the mouth, $Q_2$ is the volume entering the basin in the lower layer through the mouth and $Q_f$ is the volume of freshwater entering the basin. Salt balance requires that:

$$Q_1 S_1 = Q_2 S_2$$

(4)

where $S_1$ is the mean salinity of the surface layer outflow and $S_2$ is the mean salinity of the bottom layer inflow through the mouth. This important relation states that for an estuarine system with constant volume and salt balance, the amount of salt and water volume transported into the estuary during a flood tide must be balanced by an equal export of salt and volume during the ebb tide and from the residual surface outflow arising from the estuarine circulation. Thus, the exchange flow between an estuarine basin and the ocean is inextricably linked to the renewal rate and residence time of basin water, which are key parameters when assessing the susceptible of a specific system to water quality issues and dissolved oxygen depletion (e.g. Gillibrand 2001; Dettmann 2001; MacDonald 2006).

Transport timescales in estuaries and lagoons often have overlapping and inconsistent definitions (see Monsen et al. 2002). The residence time generally refers to individual water particles and is a measure of the timescale associated with a single particle exiting the system through the coastal boundary (Andutta et al. 2014). Age is similar to residence time in that it refers to a single water particle or parcel, although it is commonly defined as the length of time spent by a water particle in the estuarine system since entering through any of its boundaries (Monsen et al. 2002). Accurate computations of either age or residence time requires individual water parcels to be
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represented by discrete particles within the study domain, often invoking significant computational costs (de Brauwere et al. 2011). In contrast, the renewal time ($T_R$) (sometimes referred to as flushing time) is an integrative system measure and simply describes the exchange characteristics of a water body in terms of the time needed to replace (‘renew’) its volume ($V$) based on a volumetric flow rate ($Q$) i.e. $T_R = V/Q$. Accurate calculations of $T_R$ in this scenario require that the water body in question is homogeneously mixed, which generally is not the case. For an estuarine system with stratification tendencies, a bulk renewal time is difficult to quantify and a more useful approach is to define renewal times for different stratified layers, as significant renewal of these different water masses is dependent on advective fluxes of ‘new’ water of equal density. In stratified estuarine systems, a surface freshwater or low salinity layer often exists above a shallow halocline and the time it takes to completely replace or renew this layer is generally a function of the magnitude of the incoming river discharge (Sheldon and Alber 2002). Thus a simple renewal time could be given as $T_r = h_1 A_s/Q_f$, where $h_1$ is the height of the surface layer and $A_s$ is the surface area of the basin (e.g. Green et al. 2004).

A complementary renewal time for saline water in stratified estuarine systems is more problematic to quantify, given the complexities associated with tidal exchange dynamics and particularly in the case of enclosed basins with deep water that is not exchanged on each tidal cycle (section 2.3.2.). The renewal time of the intermediate saline layer (below the surface freshwater layer and above any isolated deep-water) is a function of the volume flux associated with the tidal exchange, for which several calculation methods exist. As a starting point, a simple first order estimate of the
renewal time of the entire estuary basin, based on volume fluxes associated with tidal exchange, can be obtained using the tidal prism method (Dyer 1997):

\[ T_r = \frac{V_{lw} + P}{P} \]  

(5)

where \( V_{lw} \) is the basin volume at low tidal water and \( P \) is the tidal prism, \( a_0 \times A_s \) (\( a_0 \) is the average barotropic tidal amplitude in a given location). The tidal prism quantifies the theoretical volume of water exchanged between the basin and the ocean over a complete tidal cycle and assumes that the estuary is well-mixed and that there is 100% replacement of resident estuarine water by tidal inflows, which are unrealistic assumptions in the case of stratified basins with constricted exchange flow. The tidal prism method was adapted by Gillibrand (2001) and calculated for individual sub-basins and depth layers in a Scottish sea-loch and was found to consistently underestimate the residence times compared to a 2-D circulation model. The tidal prism method performed particularly poorly in relation to estimating the residence time of deeper layers which are not exchanged on each tidal cycle.

Another consideration when calculating the tidal exchange is that the water entering the estuary on the flood tide will likely be a mixture of “new” ocean water and water that was discharged from the estuary on the preceding ebbs (Fischer et al. 1979). It is the volume of “new” water that should be estimated in order to accurately assess the renewal time and implications for water quality issues such as flushing of pollutants or susceptibility to deoxygenation. Following analysis based upon Knudsen’s relation
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(eq. 3 and 4), Fischer et al. (1979) derived a tidal exchange ratio \( R_f \) that accounts for the proportion of the total water volume entering the estuary during the flood tide \( V_f \) that is comprised of “new” oceanic water \( V_{NO} \), such that \( R_f = V_{NO}/V_f \). Similarly, the discharge of estuarine water during the ebb will be comprised of “new” oceanic water that entered on the flood and resident estuarine water already present from previous floods. This exchange ratio \( R_e \) of “new” estuarine water leaving on the ebb \( V_{NE} \) can be determined from \( R_e = V_{NE}/V_f \). The estimates of exchange ratios for the flood \( R_f \) and ebb \( R_e \) tides can be combined to calculate an estuarine renewal time associated with the overall tidal exchange (MacDonald 2006):

\[
T_r = \frac{V_{est}}{R_f R_e V_f} T_p
\]

where \( V_{est} \) is the mean volume of the estuarine basin and \( T_p \) is the dominant (e.g. \( M_2 \)) tidal period. Estimates of \( R_f \) and \( R_e \) can be made from measurements of average salinities and velocities during the flood and ebb flows of a complete tidal cycle (Fischer et al. 1979; Macdonald 2006).

One shortcoming of the tidal exchange methods described thus far is that they may have limited applicability in strongly stratified ‘layered’ estuaries, where the tidal exchange mechanism may only operate within a specific depth zone and will not necessarily cause an exchange to occur in the surface freshwater/brackish layer (or in deep basin water below the depth of the connecting channel or sill through which the tide flows). Assuming that the pycnocline separating the surface (fresh) layer
and intermediate (tidally-exchanged) layer moves as a horizontal rigid lid\textsuperscript{1}, the volume of the intermediate layer ($V_2$) is given by:

$$V_2 = \int_{-d}^{\eta_1} A(z) dz$$

(7)

where $z$ is depth, $A$ is the horizontal area of the basin at depth $z$, $d$ is the depth of the sill (or bottom of the channel where tidal inflow into the basin occurs) and $\eta_1$ is the depth of the pycnocline separating the upper two layers. Renewal of $V_2$ is assumed to be caused primarily by volume fluxes into the basin transporting water of similar density. In the case of stratified baroclinic exchange through the entranceway, net volume transport to the intermediate layer through the lower layer ($Q_2$) can be directly estimated (e.g. from moored current profilers). When coupled with information of the densities associated with inflows and outflows and the density of the receiving basin waters, direct estimates of renewal times of the intermediary saltwater masses in the basin can be estimated.

Another method that can be used to estimate the net estuarine exchange flow in two layers (above sill/entrance channel depth) is once again based on Knudsen’s relation and requires only knowledge of the freshwater discharge and the mean salinity of the upper and lower layer through the mouth of the basin. By combining Eq. 3 and 4 the transport in the upper and lower layer through the mouth can be determined (Stigebrandt 1981; 2012):

\textsuperscript{1} This assumption is valid if the timescales used in the volume flux calculations are longer than the periods associated with oscillations of the halocline due to baroclinic waves.
Thus $Q_1$ and $Q_2$ may be estimated if the freshwater discharge ($Q_F$) and the average salinities of the upper ($S_1$) and lower ($S_2$) layers at the mouth are known.

2.3.2. Deep-water renewal

A crucial component of the exchange flux between the coastal sea and deep enclosed estuarine basins with an isolated lower layer is deep-water renewal. The parent water of the deepest basin water below the sill or entrance channel depth will be the dense water associated with the most recent deep-water renewal (Farmer and Freeland 1983). Until a subsequent inflow of water of equal or greater density occurs, the deep resident basin water will essentially remain isolated and become stagnant. A range of timescales can persist between individual renewals of the basin water from spring-neap tidal periods (e.g. Geyer and Cannon 1982) to decades or more (e.g. Gade 1973). Renewal events in individual basins tend to occur with some degree of recurring regularity (e.g. during specific times of the year and separated by a relatively standard time period) (Gade 1973).

Exchange of the basin water may be activated by several processes. Larger tidal flows, such as a spring tide during the vernal or autumnal equinox, may transport water of sufficient density across the entrance channel to cause a renewal (Inall and Gillibrand 2010). Vertical diffusion and mixing in the basin water may gradually reduce the density, preconditioning the basin water for a
renewal by a denser tidal inflow (Stigebrandt and Aure 1989; Belzile et al. 2015). Variations in the coastal water density, often caused by upwelling of denser offshore water onto the continental shelf, can lead to water masses of greater density arriving at the entrance channel (Skreslet and Loeng 1977; Gillibrand et al. 1995; Thomson et al. 2017). Low freshwater runoff may reduce blockage and mixing (dilution) of tidal inflows, allowing sufficiently dense water to enter the estuarine basin and cause a renewal (Allen and Simpson 1998; Austin and Inall 2002). A coordinated sequence of such conditions may be required in order for a deep-water renewal event to occur (e.g. Gillibrand et al. 1995; Thomson et al. 2017).

Once water dense enough to initiate a renewal of the deep water crosses the entrance channel into the basin it descends as a turbulent gravity current (Edwards and Edelsten 1977; Arneborg et al. 2004). If the inflow has a higher density than the densest resident basin water then it will sink along the bottom slope to the maximum basin depth; however as it entrains ambient water of lower density along its descent, the inflow may reach a depth at which it becomes neutrally buoyant and where it may spread out laterally as an intrusion (Farmer and Freeland 1983; Liungman et al. 2001). Thus, the properties of the inflow and the density profile of the basin water are important parameters for assessing the dynamics of the deep-water renewal. However because of their somewhat unpredictable nature, detailed observations of actual deep-water inflows and large scale renewal events as they occur and the resulting physical, chemical and biological changes are rare (Edwards and Edelsten 1977; Liungman et al. 2001; Arneborg et al. 2004).

A potentially significant outcome of deep-water renewal events in anoxic basins is the fate of the old, resident water being
replaced, which may have built up concentrations of methane and hydrogen sulphide in the intervening stagnant period (e.g. Yao and Millero 1995; Schmale et al. 2012). Some of the old basin water will likely be mixed into the entraining dense inflow (e.g. Liungman et al. 2001); the remainder may be uplifted toward the normally well-oxygenated shallower zones where it might be mixed and incorporated into the surface layers (Arneborg et al. 2004; Stigebrandt et al. 2015). In the latter case, research is required to assess both the short-term ecological implications and how long the uplifted oxygen-deplete, H₂S-rich water stays in the system before being flushed out by the surface outflow (with the possibility that for a system with stratified basin water, it could remain “trapped” in a quiescent layer of equal density below the intermediate or surface layers regularly exchanged by tidal and freshwater flows). For example, following a deep-water inflow into the stagnant anoxic basin of a fjord, there was a large transport of nutrients and H₂S toward shallower depths as well as a subsequent appearance of high concentrations of methyl mercury in subsurface zones, which can easily accumulate in fish species (Pakhomova et al. 2014). Given the potential significance of these events and in light of the increased likelihood of dissolved oxygen depletion in many aquatic environments with climate change, further research on the processes that occur in the beginning, midst and aftermath of deep-water renewal events are needed.

2.3.3. Wind forcing

In addition to the influence of freshwater runoff and tidal currents, surface wind stress can also be expected to have significant impacts on important hydrodynamic processes in stratified estuarine basins. Wind forcing can generate turbulent entrainment of water
across the upper pycnocline into the surface freshwater or brackish layer from the more saline layer immediately below. Significantly, this can increase the salinity of the surface outflow and thus play a crucial role in regulating the overall salt balance in the inner basin (Eq. 4). An entrainment velocity across the pycnocline due to wind stress was presented by Stigebrandt (1981, 1985) based on the Kato-Phillips formula (1969):

\[ W_e = \frac{2C_o u^3}{g' h_1} \]  

(8)

where \( g' \) is the reduced gravity, \( g\Delta\rho/\rho_0 \) (\( \Delta\rho \) is the density difference across the pycnocline and \( \rho_0 \) is a mean density), \( h_1 \) is the depth of the upper layer, \( C_o \) is an empirical constant (≈ 0.6) and \( u_* \) is the friction velocity (m s\(^{-1}\)) given by:

\[ u^2_* = \frac{\rho_a}{\rho_w} C_d W^2 \]  

(9)

where \( \rho_a \) is the density of air, \( \rho_w \) is the density of surface water, \( C_d \) is a surface drag coefficient for air flow over water and \( W \) is wind speed (m s\(^{-1}\)). Aside from transporting salt across the pycnocline, the wind-driven entrainment may also act to deepen the surface mixed layer, thus influencing the magnitude of heat and gas fluxes at the air-water interface (e.g. Lincoln et al. 2016). This wind-driven dynamic could be especially important for surface heat fluxes in estuarine systems with strong vertical salinity gradients, as convective mixing may be limited due to the surface buoyancy input from freshwater inflows.
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An additional outcome in relation to the wind stress is the interaction between wind-driven flows and basin boundaries. In this regard, semi-enclosed stratified estuarine basins may experience similar wind-effect dynamics as stratified freshwater lakes. A surface current driven in the same direction as a strong wind can lead to a piling of water at the downwind end of the basin; this can lead to a downward tilting of the pycnocline in this region which must be balanced by an upward tilt at the upwind end (Mortimer 1952; Monismith 1986; Shintani et al. 2010). For intense, sustained winds, the upward tilt may be severe enough to upwell deeper saline water toward the surface layer causing localised turbulence and mixing, as shear stresses develop between the lower layer and the bottom slope and also between the interface separating upper and lower layers (Monismith 1986; Niño et al. 2003). The magnitude of the pycnocline tilt in response to a wind event can be assessed using the Wedderburn number ($W_N$), which parameterises the surface wind stress and the baroclinic restoring forces of the vertical stratification in relation to the basin geometry:

$$W_N = \frac{g' h_1^2}{u^2 L_e}$$  \hspace{1cm} (10)

where $L_e$ is an effective horizontal length scale, typically the length of the unbroken pycnocline (Shintani et al. 2010). A $W_N$ value > 3 implies that only minimal upwelling occurred and the basin essentially remains horizontally stratified whilst for $W_N < 3$ some upwelling of the pycnocline at the upwind end occurs (and horizontal isopycnals are sufficiently destabilised to necessitate significant baroclinic readjustment (Horn et al. 2001)). The critical
value for complete upwelling of the lower layer to the surface at the upwind end is $W_N < 0.5$ (Niño et al. 2003; Shintani et al. 2010). Thus $W_N$ is an effective way to scale the changes that may occur in the pycnocline depth during a wind event and the subsequent generation of internal standing waves (seiches) following the cessation of the wind (Horn et al 2001). Such wind-forced internal seiches can contribute energy used for basin water mixing in stratified estuarine basins, which in some cases may exceed the energy supplied by the internal tides (e.g. Arneborg and Liljebladh 2001). The occurrence of wind-induced upwelling events and the associated seiching that occurs when the deep water is hypoxic or anoxic requires special consideration. The impacts of such internal seiche events in lake basins with a stratified thermocline have been observed as temperature fluctuations in nearshore areas following a wind event (e.g. Lorke et al 2008; Coman et al. 2012; Cossu and Wells 2013). However observations of such events are less common for systems with deep anoxia. Internal seiche events could potentially lead to upwelling of oxygen-depleted water into nearshore areas that normally serve as an oxygenated refuge for fauna. For example, wind events and upwelling of anoxic water were linked to fish kills in the extremely eutrophic Salton Sea (Marti-Cardona et al. 2004) and a wind-induced onshore movement of deep hypoxic water led to a fish kill along the northern shoreline of Lake Erie (Rao et al. 2014). Dissolved oxygen variability in shallower nearshore zones has also been linked to wind events in estuaries (e.g. Sanford et al. 1990; Reynolds-Fleming and Luettich 2004) and lagoons (e.g. Chikita 2000). Lower frequency basin-scale waves often generate higher frequency non-linear waves which can shoal and break along sloping topography in boundary areas, causing localised turbulence.
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(Boegman et al. 2005). This can enhance boundary mixing in lakes and similar bounded water bodies such as semi-enclosed estuaries, leading to a redistribution of water properties between deeper and shallower water masses (e.g. Goudsmit et al. 1997; MacIntyre et al. 1999). Thus, internal wave related diapycnal fluxes across isopycnals separating oxic from anoxic water masses may play an important role in deoxygenated systems. Assessing the precise ecological implications of internal seiching and dissolved oxygen dynamics requires further investigation, particularly the impact of upwelling anoxic water on slow-moving or immobile benthic species inhabiting the littoral zone.

2.4. Study site

The setting for this research project was Lough Furnace, a deep, semi-enclosed lagoonal estuary with a surface area of 1.5 km² and max depth of 21 m (Fig. 3). Furnace is located along the Atlantic coastline of Co. Mayo, Ireland, with the deep inner basin connected to the coastal waters of Clew Bay by a long, shallow and narrow channel. Clew Bay is a large westerly facing bay, notable for its multiple glacially formed drumlin islands. The semi-diurnal $M_2$ tide is the dominant tidal motion. Tidal currents transporting saltwater from Clew Bay must traverse the long connecting channel and two topographic constrictions either side of Nixon’s Island before reaching the main inner basin of the Furnace system (Parker 1977). Furnace is located at the base of the Burrishoole watershed, a ~100km² blanket peatland catchment (Doyle et al. 2019; Ryder et al. 2014). The freshwater lake Lough Feeagh drains into Furnace through two rivers, the Salmon Leap and (man-made) Mill Race. This river runoff forms a seaward low salinity surface layer,
overlaying denser, saltier water of coastal origin (Parker 1977). The inner basin is notable for this strong salt stratification, and given its morphometry, resembles a meromictic saline lake, in which the water column does not overturn and mix completely at specific times of the year (e.g. Jellison and Melack 1993; Rogozin et al. 2010; Boehrer and Schulze 2008). Although classified and protected as a coastal lagoon habitat under the EU habitats directive (EU, 1992), Furnace also shares many physical similarities with fjordic-type estuaries and sea lochs, in particular the deep inner basin with its oxygen-deplete bottom waters and restricted horizontal exchange with open coastal waters (e.g. Farmer and Freeland 1983; Pawlowicz et al. 2007; Inall and Gillibrand 2010). Based on a palaeolimnological reconstruction, the evolution of Furnace toward a saline basin, with meromictic conditions and deep anoxia, is suggested to have occurred during the late Holocene (from ca. 3400 cal. yr BP) as a response to sea level rise (Cassina et al. 2013). Like most estuarine and lagoonal habitats, Furnace has a diverse faunal assemblage comprising marine, euryhaline, oligohaline and freshwater species (Healy et al. 1997). In spite of its deoxygenated conditions, Furnace provides habitat for important populations of European eel (Anguilla anguilla) (Poole 1990), multiple ecotypes of the three-spined stickleback (Gasterosteus aculeatus) (Ravinet et al. 2015) and fluctuating populations of the euryhaline invertebrate Neomysis integer (Parker and West, 1979). Furnace also comprises a key transitional zone of the migratory pathway of wild diadromous salmonid populations of the Burrishoole catchment (de Eyto et al. 2016). The Marine Institute maintains fish trapping facilities on both rivers connecting Furnace to upstream Lough Feeagh, with a complete daily timeseries of diadromous fish movements (Atlantic salmon, sea trout, adult
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European eels) between marine and freshwater existing from 1970 to the present day (Appendix C). Thus Furnace is ideally positioned for monitoring the interaction between the changing environment and changes in the populations of these sensitive species. Less is known about the floristic composition of Furnace, with routine phytoplankton sampling and high-frequency monitoring of chlorophyll a concentrations currently performed in an effort to assess the resident phytoplankton dynamics.
Fig. 3. Map of Lough Furnace study site, showing the main inner basin and the tidal channel connecting Furnace to the coastal waters of Clew Bay. North of the inner basin is Lough Feeagh, the freshwater lake that drains the Burrishoole watershed.
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Chapter 3. HYDROGRAPHIC MAINTENANCE OF DEEP ANOXIA IN A TIDALLY INFLUENCED SALINE LAGOON

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\textbf{ABSTRACT:} Low dissolved oxygen concentrations are of increasing concern in aquatic ecosystems, particularly at the interface between freshwater and marine environments. Oxygen depletion occurs naturally in many perennially stratified systems and it remains to be seen how climate change will affect these habitats. This is due, in part, to a lack of high-resolution, long-term data describing interannual variability in dissolved oxygen concentrations within stratified basins. Physicochemical parameters for Lough Furnace, an ecologically important tidal lagoon, were assessed using daily measurements (2009–14) from an undulating CTD (conductivity, temperature and depth) profiler and observations of tidal exchange flow. Continuous vertical saline stratification existed, with anoxia (<0.1 mg L\textsuperscript{-1}) typically persisting below 6 m. Tidal inflows were generally restricted, with deep-water renewal events by intrusions of denser spring tidal water occurring episodically (three times in 6 years), following prolonged periods of low fresh water input. Although wind forcing alone was not sufficient to generate basin-scale mixing, the conditions that led to deep-water renewals may also be conducive to wind-driven upwelling events in nearshore areas. These findings have wider application to larger-scale two-layered stratified systems with deep anoxia because the ability to
forecast such dynamic events is important for assessing the ecological implications of dissolved oxygen depletion.

**Additional keywords:** deep-water ventilation, high-resolution monitoring, hypoxia, stratification, wind-driven upwelling.

**INTRODUCTION**

Transitional waterbodies, such as coastal lagoons, tidal inlets, estuaries and fjords, form an interface between marine and terrestrial environments. These habitat types are often highly dynamic and variable systems, where complex physical and biogeochemical processes from marine and freshwater environments interact. Owing to their coastline location, transitional water bodies are naturally susceptible to freshwater floods and drought, as well as coastal subsidence and storm surges, and they may also be heavily affected by natural or anthropogenic disturbances (Viaroli et al. 2008). The nature of each system can vary enormously depending upon the relative magnitude of marine and freshwater inputs combined with geomorphologic and climatic features. These combinations determine hydrographic conditions, including stratification and mixing regimes, which have implications for resident biotic communities and human activities, such as aquaculture and fisheries. An increasing concern for productivity and biota in these vulnerable transitional aquatic ecosystems is the depletion of dissolved oxygen, which is becoming more widespread in global oceanic regions (Schmidtka et al. 2017), coastal zones (Diaz and Rosenberg 2008; Steckbauer et al. 2011) and freshwater lakes (Foley et al. 2012; Missaghi et al. 2017). Hypoxic and anoxic conditions in the deeper waters of aquatic systems can arise naturally, when vertical
exchange with a well-oxygenated near-surface layer is prevented because of the presence of a strong density gradient (pycnocline) and horizontal exchange with adjacent oxygenated basins is restricted. Knowledge gained by studying the natural dynamics at work in these stratified systems can be readily applied when assessing the sensitivity of normoxic systems to oxygen depletion following a disturbance such as eutrophication or modification of meteorological or hydrological regimes by climate change. At the largest scale, the Black Sea (Murray et al. 1989) and the Baltic Sea (Stigebrandt 1985) are well-documented examples of systems where vertical saline stratification and limited horizontal exchange have led to the development of deep hypoxia or anoxia. Anoxic conditions are often present in the deep water of fjords, which are typically connected to open coastal waters by a shallow sill (e.g. Skei 1988; Arneborg et al. 2004; Staalstrøm and Røed 2016). The length of the connecting channel between the enclosed and open basin may also exert significant control on horizontal exchange. Nitinat Lake, an anoxic fjord, has a shallow 3-km long channel connecting it to the open ocean, with significant mixing of ocean and fjord water along the sill extent (Pawlowicz et al. 2007). Shallow, sedimentary coastal lagoons do not often develop hypoxia naturally owing to their well-mixed water column, although increasing nutrient and organic waste input can deplete oxygen in bottom waters, particularly in lagoons with low flushing rates and long residence times (Kennish and Paerl 2010) and in those lagoons that do undergo periods of vertical saline stratification (e.g. Paerl et al. 2010).

Once bottom waters become isolated, dissolved oxygen is depleted through uptake by the sediments (sedimentary oxygen demand; e.g. Jørgensen and Revsbech 1985) and by respiring micro-
organisms breaking down organic matter (biochemical oxygen demand; e.g. Jouanneau et al. 2014). Once oxygen has been fully exhausted, hydrogen sulphide (H\(_2\)S) is produced as a by-product of bacterial activity (Yao and Millero 1995). Because H\(_2\)S is toxic to many resident fauna, problems can arise if H\(_2\)S is released from deep to surface waters, with major fish kills having been associated with upwelling of H\(_2\)S-rich deep water towards the surface (e.g. Luther et al. 2004; Marti-Cardona et al. 2008).

A waterbody with seaward-flowing freshwater discharge and tidal input in the opposite direction may become vertically stratified if tidal currents do not generate sufficiently intense mixing (Fischer et al. 1979). Aside from tides, wind forcing can also modify stratification and cause mixing between fresh and saline layers (Stigebrandt 1981); this is often the case in shallow or wide estuarine systems (e.g. Geyer 1997). For stably stratified waterbodies in a confined basin, an important effect of surface wind stress is the interaction between wind-driven flows and boundaries. In particular, downward tilting of the pycnocline can occur at the downwind end of the basin with a subsequent upward tilt at the upwind end (Monismith 1986; Shintani et al. 2010). This wind-induced upward tilting of the pycnocline may be great enough to directly expose deeper water to the surface, leading to upwelling events in boundary regions; the magnitude of this tilt can be assessed through the parameterisation of the surface wind stress, the baroclinic restoring forces of the vertical stratification and the basin geometry (e.g. Wedderburn Number; Thompson and Imberger 1980).

The objective of the present study was to determine the primary physical controls on vertical gradients of dissolved oxygen in a deep tidal lagoon. Inter- and intra-annual variability in mixing
and stratification dynamics were investigated over a continuous multiyear period in order to identify mechanisms responsible for observed trends in dissolved oxygen concentrations. The effects of surface wind stress and horizontal exchange flow in and out of the lagoon from freshwater and tidal sources on mixing dynamics were assessed. Quantification of these physical parameters is an important step in determining how patterns in dissolved oxygen vary over time at different depth zones in aquatic environments, how these controlling hydrographic parameters may become modified by climate change and what the implications may be for resident ecological communities should natural physical regimes that promote stagnancy and depletion of oxygen become exacerbated by anthropogenic effects and climate change.

**METHODS**

*Study site*

Lough Furnace is a natural, deep saline lagoon situated in north-east Clew Bay, County Mayo on the macrotidal Atlantic coast of Ireland (53°55’04”N, 9°34’20”W; Fig. 1). Tidal input of coastal water comes from the Burrishoole estuary, a 1-km long shallow, constricted channel connecting the southern part of Lough Furnace to Clew Bay. At the northern end, Furnace receives freshwater input at a typical rate of 3–3.5 m³ s⁻¹ from upstream Lough Feeagh through two connecting channels: the natural Salmon Leap and man-made Mill Race rivers. Lough Feeagh is at the base of the Burrishoole catchment, a small upland peat oligotrophic catchment, measuring ~100 km² (Dalton et al. 2014). Lough Furnace is protected as a coastal lagoon habitat under both the European Union Habitats and Water
Framework Directives (European Union Environment Council 1992, 2000) and forms part of the Clew Bay Special Area of Conservation (SAC Site Code 001482; NPWS 2001). Furnace is an ecologically important site, providing a nursery for juvenile marine fish and forming a key component of the migratory route of important diadromous fish species (Atlantic salmon (Salmo salar), European eel (Anguilla anguilla) and sea trout (Salmo trutta); de Eyto et al. 2016). A palaeolimnological reconstruction of the ecology of Furnace suggests that its current hydrological status as a brackish coastal lagoon occurred during the late Holocene in response to sea level rise (Cassina et al. 2013).

The Furnace system (comprising a deep main basin, with shallower channels to the south-west and side bays to the east) has a total combined surface area of $1.5 \times 10^6$ m$^2$ (Fig. 1). The surface area of the main basin is $8.5 \times 10^5$ m$^2$, with a maximum depth of 20 m (mean depth 7.9 m) and a volume of $6.75 \times 10^6$ m$^3$ (calculated by linear volume interpolation of 1-m interval depth contours). The volume development of the main basin (= 1.1) indicates that the bathymetry closely resembles an upturned cone shape, with a deep central point and steep sloping sides (Johansson et al. 2007).

**Hydrographical and meteorological measurements**

Wind speed and direction, and hydrographical profiles were measured over the period January 2009–October 2014 from an Automatic Water Quality Monitoring Station (AWQMS) anchored in the centre of the main basin (S1; Fig. 1). This station comprises a floating platform with a meteorological station and a multiparameter Hydrolab DS5 CTD (conductivity, temperature and depth; OTT, Kempton, Germany) attached to an automated winch system, which
initiated downcasts at four daily time points (0000, 0600, 1200 and 1800 hours). Each water column profile recorded temperature (accuracy 0.1°C), conductivity (accuracy 0.001 mS cm\(^{-1}\)), dissolved oxygen (accuracy 0.015 mg L\(^{-1}\)) and pressure (converted to depth following Fofonoff and Millard (1983)). Profiles were measured from a fixed starting depth of 0.6 m below the surface down to a depth of ~13 m. Additional meteorological data (air temperature, rainfall, short-wave radiation and relative humidity) were recorded at a shoreline weather station (S2; Fig. 1). Gaps in wind speed data when the AWQMS failed were filled using a regression with the shoreline wind data, and missing wind direction data were replaced with data from the shore station.

Point observations of temperature, salinity and currents were also made between late July and mid-September 2010 at several strategic locations along the entrance channels connecting Lough Furnace to Clew Bay (Fig. 1). In addition, pressure (depth) was recorded at the lower Burrishoole estuary (S6), a mid-estuary location (S5) and on the Lough Furnace side of one of the channel constrictions (S4). Measurements were also made in the relatively deep (~3 m) part of the connecting channel close to the entrance to the main upper Furnace basin (S3). At all locations, temperature (T) and conductivity (C; resolution of T = 0.001°C, C = 0.001 mS cm\(^{-1}\)) were measured using an SBE-37 MicroCAT (Sea-Bird Scientific, Bellevue, WA, USA) mounted on a concrete block with sensor height ~0.25 m above the bed and sampled every 10 min. The MicroCAT deployed at S6 also contained a pressure sensor that gave readings of relative depth at the seaward end of the system.
A time series of horizontal currents, at 0.1-m vertical intervals, was measured between 29 July and 22 September 2010 at Site S3 using a 2-MHz Nortek AquaDopp three-beam current profiler (ADP) with a right-angled transducer head (Nortek AS, Rud, Norway). This configuration allowed the instrument to be mounted flat on a weighted base plate such that the first measurement could be made at 0.2 m above the bottom (mab) and to a maximum height of 2.2 mab. The ADP also had a pressure sensor that was used to provide a record of relative lake depth at the ADP location.

Data analysis

Practical salinity (derived from actual C and T) and water density (derived from salinity and T) were computed according to the UNESCO algorithm (Fofonoff and Millard 1983). Surface heat flux and evaporation were calculated following Woolway et al. (2015) using net short-wave and long-wave radiation, wind speed, relative humidity, air temperature and surface water temperature.

For all individual water column profiles, observations were vertically interpolated to consistent, successive 0.15-m depth intervals from 0.6 m down to a cut-off depth of 12.9 m, with a total of 83 observations in every profile. The strength of stratification was expressed by calculating the square of the buoyancy frequency \(N^2\) for each successive depth interval as follows:

\[
N^2 = -\frac{g}{\rho_0} \frac{d\rho}{dz}
\]

(1)

where \(g\) is gravitational acceleration (9.81 m s\(^{-2}\)), \(\rho_0\) is mean density and \(d\rho/dz\) is the change in density over depth \(z\). The depth and strength of the pycnocline (i.e. the region of largest vertical density
gradient, hence strongest stratification) were defined as the depth and value of maximum $N^2$ for each profile. Anoxic conditions were defined as dissolved oxygen concentrations below 0.1 mg L$^{-1}$.

To assess the response of vertical stratification in the main basin to wind forcing, the Wedderburn Number was calculated. Specifically, the Wedderburn Number represents the magnitude of the basin-scale tilt of the pycnocline following the application of a surface wind stress and is defined for a two-layered simple rectangular basin by Thompson and Imberger (1980); considering that the bathymetry of the main Furnace basin deviates from that of a simple rectangular one with symmetrical bottom slopes, an ‘effective’ Wedderburn Number ($W_e$; Shintani et al. 2010) was calculated and used in the analysis, as follows:

$$W_e = \frac{g' h_1^2}{u^2 L_e}$$  \hspace{1cm} (2)$$

where $g'$ is the reduced gravity, $g \Delta \rho / \rho_0$ (where $\Delta \rho$ is the density difference across the pycnocline and $\rho_0$ is mean density), $h_1$ is height (m) of the surface layer and $u^2$ is the friction velocity on the water surface, calculated as:

$$u^2 = \frac{\rho_a}{\rho_w} C_d W^2$$  \hspace{1cm} (3)$$

where $\rho_a$ is the density of air, calculated following Verburg and Antenucci (2010), $\rho_w$ is the density of surface water, $C_d$ is a surface drag coefficient for air flow over water and $W$ is wind speed (m s$^{-1}$). Both $C_d$ and $W$ (scaled to 10 m above the water surface using a logarithmic profile of air velocity change with height) were
calculated following the methods of Woolway et al. (2015), which accounts for a range of atmospheric stabilities.

In Eqn 2, \( L_e \) is the effective lake length, which represents the internal fetch length of the unbroken pycnocline and considers that as the pycnocline is tilted at opposite basin ends along the axis of wind stress it becomes non-linear, with the result that asymmetrical bottom slopes shorten or stretch the effective internal fetch depending on whether wind direction is towards the shallower or steeper side of the basin respectively (Shintani et al. 2010).

Wind speeds were filtered over a period of 30 min, which corresponds to approximately one-quarter the period of the dominant first vertical mode internal seiche \( (T_1) \) in Lough Furnace, where \( T_1 = \frac{2L}{c_1} \), with \( L \) the length of the basin along the dominant wind axis (south-west to north-east) and \( c_1 \) the phase speed of the Mode 1 internal wave. The tilted condition of the pycnocline denoted by (2) occurs at a time equal to \( T_1/4 \) (Spigel and Imberger 1980). In order to estimate the vertical Mode 1 seiche period, monthly averages of vertical \( N^2 \) profiles were used to obtain theoretical vertical modes and \( c_1 \), calculated from normal mode theory (Gill 1982) using the numerical code of Klinck (1999). A mean representative value from these monthly averages of the phase speed of the vertical Mode 1 internal seiche was used to account for any seasonal variations in the vertical density structure.

Values of \( W_e \) were grouped into three broad categories following Shintani et al. (2010). For \( W_e \geq 3 \), the basin remains horizontally stratified with minimal upwelling of lower layer fluid; for \( 0.5 < W_e < 3 \), some tilting of the pycnocline towards the surface at the upwind end occurs, with upwelling of lower-layer water along the basin slope and some small-scale turbulence at the upper–lower
layer interface; for $W_e \leq 0.5$, the lower layer may surface fully at the upwind end, with further increases in bottom and interfacial shear stresses. Some entrainment of deep water across the density interface into the surface layer is expected to occur in this nearshore region at critically low Wedderburn values (Monismith 1986; Niño *et al.* 2003). However, it is noted that $W_e$ is not a direct estimate of vertical mixing across isopycnals, but rather a scale for the degree of pycnocline tilting at the upwind and downwind ends of the basin and the associated internal seiching that will occur following a wind event (Stevens and Imberger 1996; Horn *et al.* 2001; Shintani *et al.* 2010). Therefore, in the present study, $W_e$ values are simply indicative of the potential energy gained from a surface wind stress that may contribute to turbulent mixing within a stratified basin and are not representative of full basin-scale mixing events.

Previous observations suggest that Lough Furnace undergoes periods of stagnancy and anoxia in the deeper parts of the basin because of the formation of strong density gradients with depth (Parker 1977; Cassina *et al.* 2013). In order to assess rates of vertical mixing in the stable basin interior during stagnant periods (which is effectively buffered from the surface wind-mixed layer by a stable pycnocline), a vertical turbulent eddy diffusivity coefficient ($K_z$) was calculated using the budget method defined for a stratified fluid contained within a closed basin (e.g. Gargett 1984; Stigebrandt and Aure 1989; Arneborg and Liljebladh 2001). Using temperature, $T$, as a scalar in the laterally bounded lower layer, assuming a negligible molecular diffusion rate and neglecting heat transport through the sides and bottom of the basin, the rate of change in horizontally averaged temperature was integrated vertically from the bottom
boundary depth \( z = 0 \) to height \( z = H \), the upper depth limit of the lower layer basin water, to give \( K_z \):

\[
K_{z=H} = \frac{\int_0^H A \frac{\partial \langle T \rangle}{\partial t} \, dz}{(A \frac{\partial \langle T \rangle}{\partial z})_{z=H}}
\]  

where \( z \) is depth, \( A \) is horizontal surface area of the basin at depth \( z \), \( t \) is time and \( T \) is temperature, with parentheses indicating the horizontal average at depth \( z \). \( K_z \) is only valid during times when stagnant conditions are fulfilled (i.e. there is no horizontal advection of new water (e.g. by tides) into the stratified bottom layer).

RESULTS

Meteorology and physicochemical parameters

In the present study, seasons are defined as winter (December–February), spring (March–May), summer (June–August) and autumn (September–November). Weekly summaries of key meteorological variables indicated a temperate, oceanic climate without extreme air temperatures in winter (mean 5.5°C) or summer (mean 14.3°C) and with rainfall spread throughout the year without a pronounced wet or dry season (although broad rainfall patterns are discernible, with wetter autumns and winters and drier springs and summers; Fig. 2a). Net surface heat flux showed a seasonal warming and cooling of the surface water, with average weekly values ranging from a maximum of 134.2 W m\(^{-2}\) in May 2012 to a minimum of –117.1 W m\(^{-2}\) in November 2009 (Fig. 2b). The net weekly average surface heat flux over the full 5-year period of 2009–13 was negative (–11.2 W m\(^{-2}\)). Wind speeds recorded on the AWQMS had an average
value of 5.2 m s\(^{-1}\), reaching maximum speeds of 15.2 m s\(^{-1}\) (Fig. 2c). The prevailing wind directions were south-westerly and south-easterly (Fig. 2d), with the average of these two wind direction axes along the surface area of the main basin used to assess the effective fetch length (~1200 m).

The predominant physical feature in the upper basin of Furnace was the presence of the highly stable two-layered stratified structure formed by the large salinity contrast between surface and deeper water (Fig. 3). The two layers remained separated by a strong, relatively shallow pycnocline at an average depth of 2.4 m (Fig. 3d), which reached maximum depths of 7 m following persistent rainfall in autumn–winter of 2011. Buoyancy frequency \((N^2)\), used to assess the strength and stability of the pycnocline, showed a buoyancy period \((2\pi/N)\) dropping below 5 s during wetter periods, highlighting the exceptionally stable configuration of the two-layered structure of Furnace.

The strong density gradient severely restricted vertical exchange and isolated the deeper water, evident in the vertical gradients of temperature and dissolved oxygen (Fig. 3b, e). Surface water temperatures followed the seasonal trend of the air–water heat flux whereas predominantly isothermal (~11.6°C) conditions were typically maintained below the pycnocline, with thermal stratification in summer and inverted thermal stratification in winter, stratification maintained solely by the strong salinity gradient (Fig. 3b). Dissolved oxygen concentrations were high, often supersaturated in the surface layer, with anoxic conditions persisting below depths of ~6–7 m on average (Fig. 3e). However, despite the highly stable configuration of this two-layered structure, three distinct periods were visible when both temperature and oxygen
values changed over the course of a single day in the bottom layer (Fig. 3b, e, black arrows) and these events are indicative of exchange and mixing of the deeper water.

Although a strong salinity or density gradient with depth was always maintained throughout the study period, seasonal variability in salinity profiles was apparent, with lower salinity values occurring, on average, at greater depths during the wetter winter and autumn months (Fig. 4a). As a result, a deeper pycnocline region occurred during these same months (Fig. 4b). Depth profiles of oxygen (Fig. 4b; and, to a lesser extent, temperature (Fig. 4a)) showed greater intra-annual variability than salinity below the pycnocline depth, with a wider range of values occurring at different times of the year.

The change in bottom-layer oxygen concentration is evident for some years only (e.g. 2010 and 2013), with other years showing that bottom anoxia remained throughout. The depth of the oxycline also varied from year to year depending on pycnocline depth (i.e. the thickness of the oxygenated surface layer; Fig. 5). The timing of the oxygenation of the deeper, normally anoxic zone of the lagoon coincided with discernible changes in the normally constant deeper layer temperatures, which again provided further indication that a mixing and exchange of the stagnant basin water occurred during these time periods (Fig. 3).

**Saline water inflow**

Pressure recorded at S6 measured a tidal range of 1.5–3 m at the lower end of the Burrishoole Estuary (Fig. 6a). Salinities measured at strategic locations (S6, S5, S4) along the channel connecting the Furnace system to coastal waters indicated a spring
neap tidal variability, with maximum salinities at high water during spring tides (Fig. 6b–d). However it was apparent that salinity values decreased moving from location S6 up to S4 (at the entrance to the main basin) due, in part, to mixing or dilution of the incoming tidal saline water by outflowing ‘upstream’ water from Furnace (Fig. 6d).

Measurements at the main basin entrance (S3) demonstrated spring neap variability in bottom inflow, as well as the effects of rainfall and freshwater outflow on the system dynamics (Fig. 7). A fortnightly increase in lagoon level was observed peaking on Days 225, 239 and 253; levels rose by ~0.7 and 0.45 m on Days 225 and 239 respectively, but a steeper 1-m rise was measured in the third spring tide period (Fig. 7a). Comparison with rainfall measured at S1 at this time showed that the heaviest rainfall for the observation period was recorded (Day 250), reaching 20 mm in a 6-h period and ~10 cm during the 2-day period before the rise in lagoon level (Fig. 7d).

Interestingly the salinity measured close to the bottom of the lough at S3 did not show a spring neap variability, but was more influenced by freshwater (rainfall) input, actually decreasing during the first spring tide period after a period of intermittent rainfall (Fig. 7b). Thereafter salinity remained fairly constant and increased gradually during a dry spell between Days 240 and 250, before decreasing after the period of most intense rainfall at Day 250. Overall, this would suggest significant dilution of the saline inflow from the constrictions (S4) to the entrance of the main basin (S3) resulting from mixing between upper and lower layers, particularly when freshwater discharge was high.

A time series of 6-h averaged flow at 0.2 and 2.2 mab revealed opposite mean flow directions (Fig. 7c). At 2.2 mab, a near persistent mean outflow (south-east-directed flow) of 5 cm s$^{-1}$ was measured
(reaching up to 15 cm s\(^{-1}\)) with only occasional short periods of inflow (north-west directed). A low mean inflow (1.2 cm s\(^{-1}\)) at 0.2 mab was measured with numerous reversals in direction. This would imply that rather episodic and brief phases of saline water inflow into upper Lough Furnace occurred during the observation period with freshwater blockage of saline inflow during periods of heavy rainfall and run-off. Flow directed into the lough was recorded for each spring tide period, although it was less apparent for the second spring tide (centred at Day 239), which caused the lowest relative rise in lagoon level (Fig. 7a). The full-depth ADP profile (see Fig. S1, available as Supplementary Material to this paper) highlighted the spring neap variability on the general flow direction out (neap tides) and stalled or inward (spring tides, which peaked on Days 224, 238 and 253), as well as the two-layer character of the flow, with generally little or weak inflow in the bottom 0.5-m of the channel and an increasingly stronger mean outflow from 1 mab to the extent of current measurements at 2.2 mab.

The full ADP data was used to quantify the mean and time-varying volume fluxes in and out of upper Lough Furnace (at location S3; Fig. 1), with the in- and outflow direction determined from a scatterplot of the east and north velocity vectors. The deeper channel at the ADP location was measured as 30 m wide. In total, a resultant volume flux, based on 6-h averaged data of the full velocity vector depth profile in this channel, varied between approximately −6 m\(^3\) s\(^{-1}\) (outflow) to 2–3 m\(^3\) s\(^{-1}\) (inflow), with overall inflow occurring during the spring tidal phases. Over the 54.5-day observation period, a mean volume flux of −1.86 m\(^3\) s\(^{-1}\) was found, which comprised contributions of outflow = −2.78 m\(^3\) s\(^{-1}\) and inflow = 0.92 m\(^3\) s\(^{-1}\). This area connecting the two lower channels to upper Lough Furnace (S3)
also has a shallow (<1.5 m) region where current measurements were not made. To take this region into account, a second volume flux estimate was made whereby the volume flux for the upper-most current measurement level was used to represent the flow for the shallow region, which has approximately the same width as the deeper channel (30 m). If the estimate for the shallow region outside the deep channel was included, then the total volume flux was found to be ~3 m$^3$ s$^{-1}$ (~1.86 m$^3$ s$^{-1}$ in the deep channel plus ~1.14 m$^3$ s$^{-1}$ additional transport).

The overall outflow of 3 m$^3$ s$^{-1}$ was comparable to the outflow that may be expected given rainfall measurements and mean estimates of summertime river input into Furnace based on sample flow measurements (3–3.5 m$^3$ s$^{-1}$). A total of 325 mm of rain was recorded during the 55 days of the observations. A value of 110 mm was calculated as representative evaporation rate over the observation period, leaving a net precipitation of 215 mm rainfall over the catchment of ~90 km$^2$. Over a 55-day period, this resulted in a mean input of 4 m$^3$ s$^{-1}$ into Lough Furnace, comparable to the outflow value measured given the simplistic assumptions made and likely storage effects of groundwater throughout the catchment.

Response of stratified lagoon structure to surface wind forcing

Overall, $W_E$ values were high, falling below the critical value threshold of 0.5 in only 0.25% of occurrences, indicative of strong resistance to destabilisation by wind stress. However, the capacity of the baroclinic restoring forces of the two-layered stratification to abate wind-induced upwelling varied over the course of a typical year, as shown by summary statistics of monthly mean Wedderburn values (Fig. 8). On average, $W_E$ values were highest in winter
(because of a thicker freshwater surface layer), despite often elevated wind speeds during this time period (e.g. 2011–12, 2013–14; Fig. 2c). In contrast, the lowest \( W_E \) values occurred during spring and autumn months (e.g. March, April, October; Fig. 8). However, it should be noted that this pattern was highly inconsistent between years, with average \( W_E \) values for March, for example, ranging from the most stable period to among the least stable (Fig. 8), indicating that the stratification response to wind forcing was not predictable on a seasonal basis and was more likely related to the occurrence of the same conditions that led to basin water renewal.

**Mixing and renewal of basin water**

Based on observations of water column profiles, \( K_z \) was calculated for stagnant periods only and integrated from the greatest measured depth up to a depth of 6 m (Fig. 3e; anoxia typically persists below 6–7 m outside of oxygenation events, so it was assumed that the condition of stagnancy was fulfilled, that is no horizontal intrusions of new water into the basin below this depth). Basin water mixing was estimated and time averaged over the stagnant period August 2012 until March 2013 (before the changes in deep water properties in spring 2013). Time averaging over a several-month period allowed any effects of sporadic internal mixing events in the basin water (e.g. by internal waves, tides) to be minimised and a turbulent diffusivity coefficient representative of a stagnant regime to be obtained (Gargett 1984). \( K_z \) values ranged from \( 4 \times 10^{-7} \) to \( 8.16 \times 10^{-5} \) m\(^2\) s\(^{-1}\), with an overall average of \( 9.35 \times 10^{-6} \) m\(^2\) s\(^{-1}\) during this period of stagnancy.

The relationship between interior basin mixing and wind-induced tilting of the pycnocline (\( W_E \)) was assessed before and
during the spring 2013 renewal event (21 March–18 April; Fig. 9). The results show that the minimum daily $W_e$ value dropped to ~0.5 on 31 March and 1 April, before the oxygenation of the stagnant basin water; these critically low values co-occurred with a noticeable rise in $K_z$, indicating that turbulent mixing rates in the interior basin of Furnace increased with maximal up- or downwelling of the pycnocline along boundary slopes. However, large-scale changes in the water column structure were evidently not induced by wind forcing at this point. Deep-water renewal and oxygenation of the stagnant lower layer was initiated several days later during spring tides (8 April). The time series of oxygen concentrations at 12, 8, 4 and 2 m showed that oxygenation occurred in the anoxic, deeper parts of the basin first with a subsequent decrease in oxygen closer to the surface, implying that an incoming dense intrusion of oxygenated water of tidal origin replaced the old oxygen-depleted basin water, lifting it upward, where it subsequently mixed with and reduced oxygen concentrations in the oxic intermediate and surface waters (e.g. anoxic conditions were observed at 4 m following the onset of the deep-water renewal, whereas before this event water at this depth was comparatively well oxygenated; Fig. 9).

**DISCUSSION**

Lough Furnace functioned as a stably stratified inshore coastal waterbody over the 6-year study period, with river run-off forming a seaward surface freshwater layer, overriding a landward tidal intrusion of saline water. Exchange of deep saline water in the upper main basin was vertically and horizontally restricted under typical conditions, resulting in anoxic conditions at depth (>6–7 m). In this
regard, Furnace shares many physical traits with fjords, including gravitational circulation and naturally stagnant deep water (e.g. Stigebrandt 1981; Farmer and Freeland 1983; Arneborg et al. 2004; Pawlowicz et al. 2007). Lough Furnace also functions in a similar manner to larger-scale oceanic systems with oxygen-depleted basin water resulting from restricted communication with adjacent waterbodies and strong vertical salinity gradients, such as the Black Sea (Murray et al. 1989), Baltic Sea (Stigebrandt 1985) and North Aegean Sea (Zervakis et al. 2003). As such, Furnace represents a natural small-scale analogue for studying the hydrodynamics of restricted two-layer horizontal exchange flow and vertical stratification and the associated physical, chemical and biological implications.

Residence time and deep-water renewal estimate

A first order residence time \( T_r \) for deep-water renewal within the upper lough can be estimated from the inflow volume calculated from Fig. 7. For a basin volume of \( V = 6.74 \times 10^6 \) m\(^3\) and inflow transport of \( 0.9 \) m\(^3\) s\(^{-1}\), \( T_r = \frac{6.74 \times 10^6 \text{ m}^3}{0.9 \text{ m}^3 \text{ s}^{-1}} \), or \(~87\) days (~3 months). This is certain to be an absolute minimum value because some mixing at the in- and outflow interface (S3; Fig. 1) will reduce the amount of the original saline inflowing water to reach the deepest northern portion of the lough. It is noted again that the saline inflow at the basin entrance is already significantly diluted from its entrance through the constrictions. The dilution of the seawater entering the system, together with the low inflow at the shallow basin entrance and the typically higher salinity or density of resident basin water, implies that renewal of the deep water in the main Furnace basin is on a long time scale, in the order of years.
perhaps, and this was evident in the water column profiles, where prolonged periods of stagnancy and anoxic conditions in the basin interior were observed (e.g. 2010–13; Fig. 3c).

*Irregular basin water mixing events and wind-driven upwelling*

Despite the hydrographic constraints on mixing, infrequent and irregular exchanges of basin water were apparent during prolonged dry periods when an increase occurred in oxygen concentrations over several days in the normally anoxic zone (e.g. March 2010, April 2013 and October 2014). This would indicate that elevated deep oxygen concentrations were not caused by gradual processes, but rather resulted from sporadic, single renewal events where an exchange of the old anoxic resident saline water with new oxygenated saline water occurred for a limited time only. The new resident basin water then became isolated once the hydrographic conditions that facilitated the exchange events changed, and oxygen was gradually depleted once again by biochemical and sedimentary oxygen demand (for an overview, see Fig. 3c; for 2010 and 2013 renewals, see Fig. 5). The oxygen depletion rate in the isolated basin water (below an average oxycline depth of 7 m) was calculated based on the timescale ($\Delta t$) between a re-oxygenation event (at time $t$) and a return to anoxic conditions (at time $t + \Delta t$); i.e. $DO_t - DO_{t + \Delta t} / \Delta t$, where $DO_t$ is the dissolved oxygen concentration at time $t$). Calculations for 2010 and 2013 give an observed oxygen depletion rate of 0.04–0.05 mg L$^{-1}$ day$^{-1}$; this is likely to be a reasonable minimum estimate of biological and sedimentary oxygen demand in the basin water, which was largely isolated from horizontal and vertical exchange with oxygenated water after the initial renewal events (and assuming that downward diffusion of oxygen from
surface waters is predominantly going to be close to molecular values during the stagnant regime).

The proposed mechanism for the renewal of stagnant deeper water in the main Furnace basin is due to tidal inflow of oxygenated water of sufficient density (equal to or greater than basin water density), whereupon entering the mouth of the basin the tidal current descends before reaching neutral buoyancy and causes upward displacement of the older, anoxic water in the process (Fig. 9). This mechanism of deep-water renewal has been observed in fjords, where the intruding gravity current entrains the surrounding resident fluid as it sinks, changing water properties in the lower basin (e.g. Farmer and Freeland 1983; Arneborg et al. 2004). The prerequisite condition for these renewal events is very low freshwater input into (and subsequently out of) the Furnace system, allowing saline inflow during large spring tides to reach the upper main basin unimpeded and without significant dilution by outflowing surface fresh water, which is usually the case (Fig. 6). The correlation between prolonged low freshwater run-off and renewal of deep basin water by dense tidal inflows has also been observed in several Scottish sea lochs (Edwards and Edelsten 1977; Gillibrand et al. 1995; Allen and Simpson 1998). Similarly, reduced river run-off encourages and intensifies major inflow events of dense, saline water to stagnant deep basins of the Baltic (Matthäus and Schinke 1999). This is a salient point, because changes in both the intensity and timing of freshwater run-off regimes in estuaries are likely given current climate projections (e.g. Robins et al. 2016), meaning that the dynamics of stagnancy and renewal will likely be affected in such environments. This could have wide-ranging implications, from biological productivity (e.g. large pulses of nutrients to surface layers
from deeper zones and major fish kills due to upwelling of H:2S) to fluxes of nitrous oxide from the upper water column to the atmosphere following upwelling events (Naqvi et al. 2010). In the present study, direct measurements of inflowing tidal salinities are lacking during the time of the irregular renewal events; however, evidence of reduced stratification stability and an increase in turbulent mixing in the interior of the receiving basin were apparent and are considered here.

Values of $K_z$ in the stratified basin interior of Furnace during a prolonged stagnant period were low, similar to values calculated in the hypolimnion of stratified lakes (e.g. Jassby and Powell 1975; Lewis 1982; Jellison and Melack 1993; MacIntyre et al. 2006). Furnace $K_z$ values were also comparable to those calculated in the stagnant basin water in a small shallow-silled fjord (Svensson 1980) and in the low tidal range Gullmar fjord, during calm periods when wind-induced internal seiching of the basin water was low (Arneborg and Liljebladh 2001). During the stagnant intervening period between renewal events in fjords, background rates of vertical turbulent diffusion ($K_z$) gradually decrease the density of basin water, priming the basin for a renewal by an inflowing dense intrusion (Stigebrandt 1979; Stigebrandt and Aure 1989; Arneborg and Liljebladh 2001). In fjords, the energy for increased turbulent diffusion is typically supplied by internal tides interacting with sloping bottom boundaries (e.g. Stigebrandt 1979; Inall 2009; Staalstrøm and Røed 2016). However, in the case of systems with weak or no tidal forcing (e.g. in stratified lakes, coastal lagoons and well-confined coastal inlets), an alternative process contributing to these changes in deep-layer water properties may come in the form of wind-driven internal waves.
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Lower values of $W_e$ indicate the generation of internal waves following the cessation of a wind stress (Horn et al. 2001). Potential energy from these internal waves may contribute directly to turbulence within the stratified basin interior largely because of shear-driven instabilities forming along density interfaces (Boegman et al. 2003; Saggio and Imberger 2001). In addition, turbulent boundary layers may be formed by localised mixing because of internal wave interaction with sloping topography and up- or downward turbulent flow of density interfaces along a basin slope (e.g. De Silva et al. 1997; MacIntyre et al. 1999; Lorrai et al. 2011). These turbulent boundary layers may ultimately form horizontal offshore intrusions, transporting homogeneous fluid into the basin interior along isopycnals (Gloor et al. 2000; Inall 2009; Wain and Rehmann 2010).

In Lough Furnace, deep-water renewal events have been observed to occur during the same time periods as low $W_e$ values (~1; Fig. 9) and more generally, a lower range of $W_e$ values typically occurred during the same time periods when a deep-water renewal event was most likely to occur (i.e. lowest in spring and autumn months; Fig. 8). The low rates of freshwater input into Furnace that caused the tidally induced renewal events to occur also led to a decrease in the resistance of the saline stratification to wind-induced destabilisation. Although freshwater input is also often lower during summer, thermal stratification may reinforce the vertical density gradient (and hence resistance to wind forcing) during dry spells in summer. In addition, higher wind speeds appeared to occur more often during spring and autumn than during summer (e.g. spring 2013, autumn 2014; Fig. 2c).
A sudden increase in the estimated $K_z$ value of up to $2.5 \times 10^{-5}$ m$^2$ s$^{-1}$ (above the average value of $9.35 \times 10^{-6}$ m$^2$ s$^{-1}$, representative of the prolonged stagnant period before the 2013 renewal event) occurred at the same time as $W_E$ values approached critically low values indicative of full upwelling, supporting the proposal that mixing in the basin interior increased before the renewal and was largely wind driven (Fig. 9). A similar relationship between $K_z$ values increasing from order $10^{-6}$ to $10^{-5}$ m$^2$ s$^{-1}$ and Lake Number values (an integral form of the basic Wedderburn Number accounting for basin morphometry) dropping below 1 was reported by MacIntyre et al. (2006) for a thermally stratified Arctic lake. Thus, in the time interval between deep-water renewals, individual wind events may cause small amounts of mixing in the strongly stratified basin interior that may gradually modify the density gradient, reducing the density of the deepest basin water, which then lowers the density required of tidal inflows to mix with and replace this basin water. An additional important consideration is that the physical conditions (i.e. low freshwater input) that led to a tidal renewal of basin water in the first instance may persist following this initial renewal. Therefore, the basin may remain susceptible to wind forcing and boundary upwelling of anoxic water; this is observed in the low range of $W_E$ values recorded following the renewal event on 8 April, where values often dropped below the critical value of 0.5 for several days (Fig. 9). For $W_E \leq 0.5$, the magnitude of the pycnocline tilt at the upwind basin end towards the surface of the lough (given by $H/2W_E$, where $H$ is height of the surface layer (m)) is of the order $\sim 1.4$ m, with maximum displacements of up to 2.5 m occurring; given that anoxic water is displaced upward to shallower depths following a renewal, a wind-induced pycnocline tilt of 1.4–2.5 m should be
sufficient to cause further significant upwelling of anoxic water into the normally well-oxygenated nearshore regions, with likely implications for inhabiting organisms.

The results of such nearshore upwelling events were not detected directly by hydrographic profiles from the centre of the lough basin. In order to assess the nature of localised upwelling of anoxic water in nearshore areas of stratified basins, the implications for resident ecological assemblages and to fully understand the boundary-initiated mixing processes that may prime the basin for renewal, additional hydrographic measurements in boundary regions are essential.

Conclusion

The results of the present study reveal large inter- and intra-annual variability in oxygen concentrations in a strongly stratified, horizontally constricted tidal lagoon over the course of several years. Irregular, transient renewals of anoxic resident basin water were directly related to changes in horizontal exchange flow, where reduced surface freshwater outflow from the lagoon facilitated an unimpeded intrusion of tidal water during spring tides. In addition, these large-scale renewal events occurred during the vernal and autumnal equinoxes when tidal range is largest. Observations taken during the renewal and ventilation of stagnant deep water in aquatic systems are rare and have typically been described for fjordic systems only. In addition, it was found that the same physical conditions facilitating deep water renewals may also make the basin susceptible to wind-driven upwelling, indicating that tidal and wind forces may work synergistically to drive short, intense mixing events in what is normally a highly stable, predictable system. These
findings have application to larger systems that undergo long periods of stratification and deep-water stagnancy. With climate change predicted to intensify stratification in a wide variety of aquatic systems (e.g. Holt et al. 2010; Hordoir and Meier 2012; Schmitdtko et al. 2017; Woolway et al. 2017), susceptibility to hypoxia or anoxia will increase and the importance of horizontal exchange flow with adjacent oxygenated water bodies becomes critical in the maintenance of normoxic conditions.
Fig. 1. Lough Furnace (boundary highlighted by the thicker line) showing bathymetry (2-m contours) and locations of sampling stations: S1, Automatic Water Quality Monitoring Station; S2, shore line weather station; S3, AquaDopp three-beam current profiler for salinity, temperature and pressure monitoring; S4 and S5, salinity and temperature monitoring; S6, salinity, temperature and pressure monitoring. S3–S6 were deployed during the summer of 2010 only.
Fig. 2. Meteorological summaries for key parameters affecting physical structure and dynamics in Lough Furnace over the study period, 2009–14, measured from a shore line weather station and an automatic weather station on the lake. (a) Total weekly rainfall, (b) mean weekly water surface heat flux (W), (c) mean weekly wind speed at 10 m above the lake surface and (d) windroses of daily wind speed and direction frequencies (meteorological convention) for each year.
Fig. 3. Summary of hydrographic profiles (0.6 m to a depth of 12.9 m), showing the two-layered vertical structure of water column over 2009–14 for (a) salinity, (b) temperature, (c) density, (d) square of buoyancy frequency (the black line is the pycnocline, defined as the depth of maximum buoyancy frequency) and (e) dissolved oxygen. Shown are weekly averages taken from four daily profiles. Black arrows indicate the onset of the deep-water renewal event. (White gaps indicate longer periods when the profiler was inactive because of a mechanical failure or was removed for servicing.)
Fig. 4. Mean monthly water column profiles over the study period, 2009–14, showing months representative of seasonal change for: (a) salinity (solid line) and temperature (dashed line); and (b) density ($\sigma_t$; solid line) and dissolved oxygen (dashed line). Lines represent the overall monthly mean profile for all 6 years combined, whereas the shaded regions highlight variation around the mean between years (± s.d.).

Fig. 5. Mean monthly depth profiles for (a) salinity and (b) dissolved oxygen over a 4-month period before and during spring for each year (2009–14), highlighting irregular interannual variation in oxygen at depth.
during this time period. (Black lines represent overall monthly mean for all 6 years combined; coloured lines represent monthly mean depth profile for individual years, as indicated in the key.)

Fig. 6. Time series of (a) bottom pressure (relative depth) at location S6, and salinity at locations (b) S6, (c) S5 and (d) S4. (See text for details and Fig. 1 for locations.)
Fig. 7. Time series of 6-h averaged (a) water depth, (b) bottom salinity and (c) north-west-directed current velocity at 0.2 (thick line) and 2.2 m above the bottom (thin line) at the AquaDopp three-beam current profiler location (S3), 29 July–22 September 2010 (days of year 210–265). (d) Time series of 6-h rainfall at the Furnace meteorological station (S2).

Fig. 8. ‘Effective’ Wedderburn Number ($W_E$; Shintani et al. 2010) summary statistics by month, 2009–14. Boxplots show the median, 25th and 75th percentiles (mid, lower and upper horizontal lines), maximum and minimum values (whiskers) and statistical outliers (dots) for monthly mean $W_E$ for all years.
Fig. 9. Spring 2013 mixing or renewal event, 21 March–18 April. (a) Vertical turbulent diffusion coefficient ($K_z$) for stagnant basin water (depth >6m) before the renewal event and minimum daily ‘effective’ Wedderburn Number ($W_e$; Shintani et al. 2010) before and after the renewal event. The dashed horizontal line indicates the critical $W_e$ threshold value of 1; the solid vertical line denotes 1 April and the dashed vertical line denotes 8 April. (b) Time series of oxygen concentrations over the course of renewal at depths of 2, 4, 8 and 12 m.

Supplementary material

Fig. S1. Timeseries of the 6-hourly averaged velocity component (m s$^{-1}$) into the main Lough basin (Direction 325°T) from 0.2–2.2 m above the lake bed from the ADP mooring (location S3, Fig. 1 between 29th July (Day 210) – 22nd Sept (Day 265), 2010). Positive values denote flow into the basin and a velocity scale (m s$^{-1}$) is shown to the right.
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Conflicts of interest

The authors declare that they have no conflicts of interest.

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Chapter 4. VOLUME FLUXES, OXYGEN DYNAMICS AND A PREDICTIVE MODEL OF VENTILATION EVENTS IN AN ANOXIC ESTUARINE BASIN

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ABSTRACT: Observations of prolonged anoxic periods in the deep water of a small semi-enclosed coastal basin (Lough Furnace) prompted 15 months of continuous sensor deployment at strategic locations between the inner basin and adjacent coastal waters, to measure water levels, currents, oxygen and density. The objective was to determine basin water renewal times and discern the estuary-ocean exchange dynamics leading to irregular and ephemeral deep-water ventilation. Measured densities and direct estimates of volume fluxes were used to close a steady-state mass balance budget and compute typical renewal times of individual water masses in the stratified inner basin. Freshwater flux and the spring-neap tidal cycle were the primary determinants of mass transport in and out of Furnace. The deployment period culminated with observations of a ventilation of the basin water which had been stagnant for over 2.5 years. Volume transport of the dense inflowing plume doubled through entrainment of ambient resident water, diluting oxygen content in the process. Following ventilation, the volumetric extent of anoxia expanded by 20% within several months, owing to uplifting of old basin water and oxygen consumption in the new basin water. Founded on these analyses, a predictive machine learning model was
constructed using readily available hydro-meteorological variables and successfully recreated ventilation events over the past decade. This model offers a diagnostic tool to assess how climatic change may modify the frequency of such events in Furnace and similar estuarine systems that experience contrasting regimes of anoxia and ventilation.

INTRODUCTION

Deoxygenation is a growing global concern across coastal and marine environments (Breitburg et al. 2018; Levin 2018; Oschlies 2018). In many habitats, the leading cause for this concern is anthropogenic eutrophication which increases primary productivity, with subsequent sinking of organic material amplifying respiration rates and oxygen consumption in deeper waters (Diaz and Rosenberg 2008). Climate change may compound these increased rates of oxygen consumption, as warming of near-surface waters decreases oxygen solubility and intensifies vertical stratification, reducing downward mixing of oxygenated surface waters in the process (Schmittko et al. 2017; Keeling et al. 2010). Therefore it is usually deeper waters, isolated below a strong pycnocline, that are most susceptible to severe deoxygenation. Whilst untenable rates of biological activity associated with nutrient loading can ultimately generate an hypoxic or anoxic environment, the natural hydrography is often the primary factor in determining how prone a system is to oxygen depletion in the first instance (Gray et al. 2002).

One step toward understanding the links between physics and oxygen dynamics is to study naturally anoxic basins. Case studies of anoxic basins have offered considerable insight into the
oceanographic control of oxygen dynamics with large-scale examples including semi-enclosed seas, basins and fjords (e.g. Murray et al. 1991, Astor et al. 2003, Mohrholz et al. 2015, Pawlowicz et al. 2007a, Thomson et al. 2017, Sørhaug et al. 1988, Stigebrandt et al. 2015). In some of these systems, anoxia is almost exclusively a function of the natural oceanography (e.g. Saanich Inlet (Anderson and Devol 1973), Framvaren Fjord (Sørhaug 1988)) whilst others show the increasingly delicate interplay between hydrodynamics and anthropogenic disturbance in controlling the severity of oxygen depletion (e.g. Baltic Sea (Meier et al. 2018), Black Sea (Capet et al. 2016)). Current evidence suggests that different climate change variables (e.g. increased thermal stratification, altered river flow climatology) could compound the occurrence and severity of ‘dead zones’ in coastal regions (Altieri and Gedan 2014). Thus there is a need to discern the precise hydrographic mechanisms that cause the formation, maintenance and ventilation of anoxic water masses under current climate conditions.

This study used Lough Furnace, located on the west coast of Ireland, as an example of a coastal basin that experiences natural anoxia in its deeper waters (Fig. 1). The system is comprised of a distinct meromictic inner basin (max depth 20 m), with deoxygenated conditions typically prevalent at depths below 5 - 8 m (Parker (1977); Kelly et al. (2018a)). The vertical saline stratification blocks direct ventilation of the deeper water by convection in winter and during storm events; ventilation is only achieved through lateral inflows of sufficiently dense, oxygenated external water. The inner Furnace basin communicates through a topographically constrained, shallow (< 2 m) 1-km-long connecting channel with the North Atlantic coastal waters of Clew Bay, a large westerly facing bay (Fig.
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Tidal currents transport saltwater across this channel and through two narrow topographic constrictions either side of Nixon’s island before reaching the main inner basin (Fig. 1b). Tidal range in the inner basin during spring tides is ~ 0.3 m. The principal source of freshwater runoff into Furnace comes from the upstream Lough Feeagh, which drains the ~100 km² Burrishoole catchment. Two rivers flow into the northern end of the Furnace main basin (mean annual discharge of 4 m³ s⁻¹), forming a thin, seaward flowing fresh layer usually less than 2 m deep. Its small size, complex bathymetry, stratification and the multiple inflows and outflows, makes Lough Furnace an ideal natural laboratory for investigating hydrodynamical processes relevant to larger-scale stratified estuarine basins. Furnace has also served as a model system for important ecologically-motivated research including the population dynamics of euryhaline invertebrates (Parker and West 1979), a paleolimnological reconstruction of it’s evolution toward anoxic conditions (Cassina et al 2013), divergent evolution in fish ecotypes (Ravinet et al. 2015), bio-physical interactions between benthic fish and internal waves (Kelly et al. 2018b) and dynamics of sub-surface chlorophyll maxima (SCM) (de Eyto et al. 2019). Although deoxygenation in open coastal areas and well-flushed estuaries was reported as being rare in an Irish context (O’Boyle et al. 2009), documented examples of other perennially or periodically deoxygenated coastal systems along the Atlantic coast of Ireland include Ardbear Salt Lake (Henry et al. 2008) and Lough Hyne (Trowbridge et al. 2017).

The fundamental hydrographic parameter toward determining how susceptible a given water body is to deoxygenation is the frequency at which resident water is exchanged for new,
oxygenated water. The importance of using precise definitions in reference to transport time scales in water bodies (e.g. residence time, age, flushing rate) was discussed in Monsen et al. (2002). With this in mind, here we use the term renewal time ($T_r$) to refer to the time required for the entire volume of the basin to be replaced by new water from either freshwater or tidal sources (following Andutta et al. 2014). This renewal time is not a measure of the transport and fate of individual water parcels through the system but rather a simple integrative measure at a fixed spatial and temporal point (Eulerian) based on basin volumes and advective/diffusive fluxes. Thus in systems with long renewal times, the exchange rate is low and the potential for exchanging oxygen-poor with oxygen-rich water becomes limited.

A simple exchange rate assumes 100% mixing efficiency between advective fluxes of external water into the basin and the flushing out of prior resident water. This assumption becomes more problematic in stratified basins, where vertical density gradients introduce a complexity, as different water masses of specific densities will have different renewal times, with significant replacement of resident water dependent upon advective fluxes of new water of similar density. Thus a simplistic yet useful approach is to divide stratified basins into appropriate layers of uniform densities (‘mixed-boxes’) and derive individual flux rates and renewal times for each layer. In estuarine coastal systems, this typically includes a surface freshwater layer (here denoted by $L_1$), an intermediate tidally-exchanged saline layer ($L_2$) and in the case of confined basins deeper than their inflow/outflow channels, a third layer below the extent of the channel depth containing the densest resident basin water ($L_3$). The usefulness of variations of this layered
box model approach is evident through its successful application to a variety of coastal systems that could be classified as regions of restricted exchange (e.g. Babson et al. 2004; Gillibrand et al. 2013; Pawlowicz et al. 2007b; Stigebrandt 2012).

Renewal of the deep basin water $L_3$ (termed ventilation in cases of suboxic waters) is of particular interest as it can cause profound biogeochemical changes over a very short timeframe (Arneborg et al. 2004; Bergen et al. 2018; Lehmann et al. 2015). Of particular concern are the potential impacts of releasing toxic hydrogen sulphide ($\text{H}_2\text{S}$) gas, which has accumulated in anoxic deep water, to aquatic life in oxygenated surface waters (Luther et al. 2004) or to the atmosphere (Capet et al. 2016). In Furnace, deep-water ventilations have been linked to mass fish kills (SRA, 1995) and phytoplankton population dynamics (de Eyto et al. 2019).

The parent water of $L_3$ will be the dense water associated with the most recent deep-water renewal, with the subsequent decreases in density occurring very slowly through diffusivity with the water in the overlying layer (e.g. Farmer and Freeland 1983; Stigebrandt 2012). This gradual reduction in density will eventually precondition the resident basin water to a replacement by an inflow carrying water of sufficient density; the slow nature of this process however means that renewal of the basin water based on this mechanism alone is typically of order years (Farmer and Freeland 1983). Understanding the mechanisms that control the temporal variability of the inflow density and volume fluxes at the entranceway of the basin is therefore crucial in determining a typical renewal time of the interior waters and has been a focus of estuarine and coastal oceanography for several decades (e.g. Geyer and Cannon 1982; Griffin and LeBlond 1990; Schinke and Matthäus 1998;
Allen and Simpson 1998; Laval et al. 2003; Thomson et al. 2017). However owing to their stochastic nature, few direct observations have been made during a dense, oxygenated intrusion (e.g. Liungman et al. 2001; Arneborg et al. 2004; Holtermann et al. 2017). More generally, the dynamics associated with the intrusion of dense gravity currents into ambient basin water form a key component of overall vertical circulation and sedimentation in oceanic basins (e.g. Wåhlin and Cenedese 2005; Ivanov et al. 2004) and lakes (Fer et al. 2001).

In this paper, observations of currents, temperature, salinity, water levels and meteorology over a 15-month period were analysed in an attempt to estimate freshwater and saltwater volume fluxes between Lough Furnace and the adjacent open coastal waters, with the objective of calculating renewal times in the main inner basin. The motivation was to understand the processes responsible for ventilation of the deep anoxic waters and attempt to predict these events based on the observational data. A key aspect of this was to utilise an empirical approach rather than a numerical model and provide a simple, computationally inexpensive assessment of how climatic changes may potentially alter deep water oxygen dynamics in Furnace and similar systems.

**METHODS**

*Instrumentation and observations*

From March 16th 2016 to July 3rd 2017 the deepest (mean depth 5.8 m) section of the entrance channel to the main inner basin of Lough Furnace was instrumented with an upward looking 1-MHz Nortek Aquadopp 3-beam current profiler (ADCP) (Nortek AS, Rud,
Norway) (MR01, Fig. 1b and 1c). The ADCP was mounted to a steel frame and the sensor head, with a 25° beam angle to the vertical, was fixed at 0.2 m above the bed. An L-shaped mooring configuration was used to avoid measurement interference by the surface marker buoy and line. The ADCP recorded in 0.5 m bin ensembles, with a blanking distance of 0.4 m and a velocity measure averaged over 60 seconds. Two SBE-37 MicroCATs (Sea-Bird Scientific, Bellevue, Washington, USA) recording temperature (resolution = 0.001°C) and conductivity (resolution = 0.001 mS) were also attached to the same mooring with one MicroCAT mounted on the bottom ADCP frame and the second MicroCAT positioned ~1 m below the surface on the L-shaped mooring. An additional MicroCAT, also recording pressure, was located further downstream closer to the estuary proper, on the lough side (upstream) of one of the entrance constrictions (MR02, Fig. 1). All of these instruments had synchronised internal clocks and logged measurements every 30 minutes. Mooring turnaround occurred at approximately 4-6 week intervals, for data downloads, instrument cleaning and (ADCP) battery replacement.

Additional data sources available for use throughout the experimental period included several of the Marine Institute’s long-term monitoring stations. An Automatic Water Quality Monitoring Station (AWQMS) located in the central main basin (Fig. 1b), recorded 4-daily full water column profiles (00, 06, 12 and 18 hours) of temperature, conductivity and dissolved oxygen using a Hydrolab DS5 datasonde (OTT, Kempton, Germany) attached to an undulating winch profiler. The AWQMS also included a surface meteorological station with wind speed and direction, air temperature and solar radiation measured every 2 minutes. Missing gaps in the AWQMS
wind data were filled using a regression model with a Met Éireann station located directly on the shoreline of Furnace (MET, Fig. 1b) – this land station also recorded rainfall. A tidal gauge was located at the northern landward limit of the main Furnace basin (TG01, Fig. 1b) and one was installed in the lower reaches of the Burrishoole estuary (TG02, Fig. 1b) midway through the deployment in November 2016, which provided a direct measure of tidal influence from the adjacent coastal waters.

Data Processing

Profiles from the AWQMS were processed following Kelly et al. (2018a), with individual profiles extrapolated onto a standard depth grid spanning the water column from 0.6 m – 12.9 m in 0.15 m depth increments. Practical salinity (derived from actual conductivity and temperature) and water density (derived from salinity and temperature) were computed according to the UNESCO algorithm (Fofonoff and Millard 1983) for all sensors recording temperature and conductivity.

Harmonic analysis of the time series of water levels recorded at TG02 was performed to obtain tidal constituents, using the ‘tidem’ function from the ‘oce’ R package (Kelley and Richards, 2018). Using these constituents, a tidal model was then constructed and used to predict a timeseries of tidal heights spanning the full deployment period.

The analyses pertaining to exchange flow and volume flux calculations in and out of the inner Furnace basin presented here were primarily concerned with subtidal residual currents. Thus, higher-frequency tidal fluctuations (subject of a separate analysis) were attenuated by applying a 4th order Butterworth filter to the
ADCP velocity vectors with a cut-off frequency of 40 hours (Thompson, 1983). Horizontal current velocity vectors from the ADCP were then rotated into along- (V) and across-channel (U) components using principal components analysis (PCA) (Emery and Thomson, 2001). Wind speed and direction were decomposed into zonal and meridional vectors and given the wind measurement site (AWQMS, see Fig. 1b), true north and east essentially corresponded to the along- and across-channel wind stress at MR01 without requiring rotation. In order to assess the influence of coastal winds on the density of tidal inflows into Furnace, a separate set of wind vectors were derived using the same wind parameters measured at Furnace but rotated into along-shore (U) and across-shore (V) components relative to the coastline of Clew Bay following PCA (Fig. 1a). Wind stress components $\tau_x$ and $\tau_y$ were computed from the equation $\tau_{x,y} = \rho_{air} c_d W_{x,y}^2$, where $\rho_{air}$ is the density of air (kg m$^{-3}$), $c_d$ is a surface drag coefficient (computed based on wind speed and atmospheric stability (Woolway et al. 2015)) and $W_{x,y}^2$ is windspeed squared at 10m above the water surface in the $x$ or $y$ direction.

Volume flux and renewal time calculations

Volume fluxes in and out of the main inner basin through the deepest part of the channel were determined from the along-channel low-pass filtered horizontal velocity vectors. A volume flux $Q$ through the entrance channel is defined as:

$$Q = \int_A v \, dA$$  \hspace{1cm} (1)
where \( v \) is the along-channel velocity and \( A \) is the depth-varying cross-sectional area. Volume fluxes were computed through each ADCP bin based on channel width at each bin depth; an echosounder transect of the entranceway provided accurate bathymetry (Fig. 1c). Whilst the standard ADCP bin sizes spanned 0.5 m in the vertical, the lowest bin was weighted to account for the bottom 1.1 m of the channel (i.e. 0.5 m bin size + 0.4 m blanking distance + 0.2 m frame height above the bed). For each individual ADCP profile, the uppermost usable bin was defined as the shallowest bin below the computed depth of sidelobe interference.

In order to account for upper water column measurements discarded due to sidelobe contamination, initially each current profile was extrapolated to the surface level using a constant velocity from the uppermost usable bin. However, the upper halocline in Furnace was often very close to the surface (< 1.5 m deep for one third of the deployment period) and it is probable that using velocities from below this depth would not accurately capture shallow flow dynamics during periods with a thin surface layer. Furthermore, the entrance section widens significantly at depths shallower than 2 m (Fig. 1c) and using a constant velocity from the ADCP moored in the deeper trough section to approximate volume transport through this unmonitored, shallow rocky region to the east yielded erroneous flux estimates. Thus an alternative method used the ADCP to directly estimate volume fluxes through the lower layer \( (Q_2) \) by integrating velocities up to the depth of the density interface \( (\eta_1) \) that divided the fresher upper \( (L_1) \) and saline lower \( (L_2) \) layers such that:
where $u$ and $W$ are along-channel velocity and width at the entranceway at depth $z$ and $H$ is the depth to the channel bottom. Using this configuration positive (negative) values indicate flow into (out of) the inner basin through the lower layer. A timeseries of $\eta_1$ was inferred using daily averaged CTD profiles from AWQMS and calculating the shallowest depth at which the salinity differed from that at the surface by a value of 2. This finite difference criteria was chosen after comparison with gradient-based approaches (e.g. depth of max buoyancy frequency or salinity gradient); the latter was often inaccurate during periods where the greatest salinity gradient occurred at the deep halocline between the intermediate ($L_2$) and basin ($L_3$) water, which was not applicable when defining stratification in the shallower entranceway.

Using appropriate assumptions of volume conservation in the inner basin and considering the primary inflows and storage capacity, subtidal barotropic volume fluxes were estimated as:

$$Q_{baro} = -A_s \frac{d\eta_0}{dt} + Q_F$$

where $A_s$ is the surface area of the inner basin and $\eta_0$ is the surface water level (monitored at TG01). The barotropic seiche speed in Furnace is such that surface level oscillations forced by tidal motions through the mouth have a period of < 10 minutes, meaning that the surface is horizontal on the subtidal timescales considered here. $Q_F$ is the freshwater flux associated with the following parameters:
\begin{equation}
Q_F = Q_R + Q_P - Q_E
\end{equation}

\(Q_R\) is river discharge and was quantified through a series of flow measurements at various river stages on the Mill Race and Salmon Leap, the primary freshwater inflows, to derive a ratings curve of discharge based on the lake level at the southernmost tip of upstream Lough Feeagh. \(Q_P\) represented the volumetric flux rate of precipitation (recorded at MET, Fig. 1b) to the basin. \(Q_E\) represented a volumetric flux rate associated with evaporation (calculated using net shortwave and longwave radiation, wind speed, relative humidity, air and surface water temperatures following Woolway et al. (2015)).

For steady-state subtidal conditions, remaining volume fluxes through the unmonitored upper layer at the entrance (\(Q_1\)) were deduced by subtracting \(Q_2\) from \(Q_{baro}\).

The final set of volume flux estimates were used to compute renewal times for each water mass of the inner basin. The surface freshwater renewal time was given by \(T_{r1} = \frac{\eta_1 A_s}{Q_F}\). Due to fluctuating thickness of the intermediary saline water mass, the renewal time was determined by first calculating the volume of this layer, \(V_2\), at each timestep as:

\begin{equation}
V_2 = \int_{\eta_2}^{\eta_1} A(z) \, dz
\end{equation}

where \(A\) is the horizontal area of the inner basin at each depth \(z\) and \(\eta_2\) is the depth of the interface separating the intermediate from deep basin water. Timescales associated with the fundamental mode baroclinic wave forced by tidal motions into the inner basin are typically < 4 hours (Kelly et al. 2018b) meaning internal density
interfaces could be considered horizontal at lower frequencies. Renewal times of the intermediary layer $T_{R2}$ were calculated by $V_2/Q_{2in}$, where $Q_{2in}$ was the inflow contribution through the lower layer during periods when the inflow density ($\rho_{in}$, measured by the bottom MicroCAT at MR01) was less than mean density of the deep basin water ($\rho_3$, computed from AWQMS profiles).

Separate renewal time estimates of the deep basin water ($L_3$) were derived depending on whether the renewal or stagnant regime prevailed. When $\rho_{in} < \rho_3$, no advective fluxes of external water occurs and density reduction in the basin water is primarily dependent upon diffusive fluxes with the overlying water (e.g. Stigebrandt, 2012). A diffusive flux between $L_2$ and $L_3$ was estimated using observed data as:

$$Q_{K3} = \frac{V_3 \, d\rho_3}{\Delta \rho \, dt}$$  \hspace{1cm} (6)

where $V_3$ is the basin water volume and $\Delta \rho$ is the density difference between $L_2$ and $L_3$. If $\rho_{in} > \rho_3$, a switch was initiated in the calculation workflow and an estimate of basin water renewal time was given by $V_3/Q_{2in}$.

**Predictive model**

In an effort to predict the occurrence of deep-water ventilations, a simple model was constructed based on the time series of observations. The primary response variable in the model was represented by bottom densities at MR01. Because the objective of the modelling exercise was to be able to hindcast over a timeframe longer than the 15-month deployment period, independent variables
in the model were restricted to data sources that could be derived over the period 2009-2018, for which dissolved oxygen profiles were available to validate against model predictions (Kelly et al. 2018c). It was assumed \textit{a priori} that the density of the inflow would be dependent in some combination on the local magnitude of freshwater discharge and tidal forcing and this assumption is validated in the Results section. Thus predictor variables included freshwater discharge (from the ratings curve developed for inflows to Furnace) and tidal elevation (from the tidal model of TG02). The potential influence of coastal dynamics on inflow densities were also assessed by including timeseries of atmospheric pressure (recorded at MET) and along-shore wind stress relative to the geometry of Clew Bay as predictors. Two time-lagged freshwater discharge datasets were created – one with a 7-day lag and one with a 14-day lag to allow any influence of freshwater conditions during the preceding neap and spring tides on instantaneous values of density to be incorporated into the model.

A machine learning approach was adopted which allows the analyst to map a set of input values to a set of output values, crucially without requiring numerical interpretation of the mechanisms involved. The advantage of this method were: 1) the dataset of input values was limited and a complete algorithm to temporally resolve inflow densities over a multi-year period would have required additional data sources (e.g. some measure of mixing) and 2) such an empirical approach is relatively simple and computationally inexpensive compared to configuring and executing a full hydrodynamic model. The obvious major drawback of this method is that it omits an understanding of the underlying physics. However predictive machine learning techniques have been
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successfully applied toward water quality assessment in reservoirs (Chou et al. 2018) and predicting salinity intrusion in estuaries (Nguyen et al. 2018).

A random forest algorithm (Breiman, 2001) was implemented in R (following Liaw and Wiener 2018). A general overview of the random forest procedure applied to a continuous variable (water density in this case) is as follows: multiple regression trees are independently constructed, each using a different bootstrap sample of the dataset (bootstrap aggregating, see Breiman (1996)). For each regression tree, each root split (node) is optimised for only a subset of the predictor variables, randomly chosen at each node (in contrast, a standard regression tree selects an optimal split amongst all predictor variables at each node). This additional layer of randomness in the decision procedure gives random forests added robustness against overfitting compared with traditional regression and classification trees (Breiman 2001). The predictions from each tree are then aggregated and a final prediction consensus is reached by selecting the most common output.

The dataset was first randomly split into training and test subsets and the model was initially fit on the training data. This trained model was then applied to the independent test dataset and model performance assessed - a similar model fit on both training and test data indicated that minimal overfitting occurred and the model was generalised further and used to predict inflow densities over the period 2009-2018.
RESULTS

Observations

A histogram of salinities recorded at the surface (blue) and bottom (red) of the entranceway for the deployment period are shown in Fig. 2. Black lines are histogram density curves for salinities recorded from the inner basin over the same timeframe (normalised for the same number of observations), with the solid black line including salinities throughout the full water column and the dashed line including salinities down to the average depth of the oxycline only (6 m). This plot illustrates that separate lower and higher salinity water masses occurred in the entranceway, which correspond to the waters above and below the upper halocline in the inner basin ($L_1$ and $L_2$). It also shows a third water mass in the inner basin below the deep halocline and oxycline depth, with salinities typically higher than those of any other water mass ($L_3$ (deep basin water)). A histogram following the same criteria for density closely resembled the salinity histogram highlighting the minimal influence of temperature on density variations in the system (Fig. 2). The appearance of water of salinity/density higher than the basin water at the entranceway is thus the necessary condition for a large-scale exchange of the stagnant deep water.

Fig. 3 shows the full timeseries of (a) along-channel velocity profiles (MR01), (b) spring-neap tidal forcing (red line shows low-pass filtered tidal elevations at site TG02 and black line is salinity at MR02), (c) surface (blue) and bottom (red) salinities (MR01) (d) freshwater inflow from LoughFeeagh ($Q_F$) and (e) along-channel wind speeds (positive values indicate winds blowing up-estuary...
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toward the inner basin). The flow structure is complex and it is evident that the variability likely depends on all three primary forcing mechanisms. The strongest flows occurred at the bottom and nearer the surface (visible immediately below the sidelobe cut-off depth) with generally weaker flows at intermediate depths.

The low-pass filtered mean flow often featured baroclinic exchange (Fig. 3a). This was most apparent during spring tides, with positive velocities (into Furnace inner basin) near the bottom (~2 m above the bed) sometimes exceeding 0.2 – 0.3 m s\(^{-1}\). At neaps, inflow nearer the bottom was attenuated or reversed completely. Currents closer to the surface (within ~2 m) showed less fortnightly tidal influence and outflow (negative velocities) was the primary flow dynamic. At intermediate depths (2 – 4 m) weaker outflow was predominant, with occasional weak inflows during spring tides. The influence of wind was also apparent with some reversals of the surface outflow during strong up-estuary winds (e.g. early October 2016, late January 2017, late March/early April 2017 (Fig. 3a and 3e)). Similarly, surface outflow was often accelerated during strong down-estuary winds (e.g. April/May/June 2016, November 2016 (Fig. 3a and 3e)). The extent of ADCP measurements meant that some of the finer details of wind influence on surface layer reversals may not have been adequately captured.

The influence of spring-neap tidal forcing on salinity was most apparent at the shallow MR02 site, with the minimal salinity fluctuations observed during mid-neaps implying that generally nominal quantities of saltwater reached the Furnace basin during these times (Fig. 3b). During large freshwater events (e.g. September 2016, March 2017), the overall salinity at MR02 was reduced even at spring tides, indicating that tidal inflows were diluted further
downstream by the flushing out of this lower salinity water from upstream or perhaps blocked by large volumes of freshwater outflow (Fig. 3b and 3d). Surface and bottom salinities at the entranceway (MR01) remained distinctive throughout the 15 month deployment with stratification being maintained (Fig. 3c). Lower layer salinities were more stable over the period with a mean value of 17, with short-lived decreases during freshwater events (e.g. March 2017) and gradually increasing over consecutive spring tides during dry spells (e.g. April/May 2017). Above the halocline in the freshwater-influenced surface layer, salinities were generally lower (mean value of 4.6) but during periods (weeks) of low freshwater discharge, surface salinities converged toward lower layer salinities during spring tides (June 2016, late October 2016, May 2017 Fig. 3c). The general increase in bottom layer salinity from the onset of the deployment should be noted, as the 2016 spring period followed an abnormally wet winter period 2015/16, with lingering effects on salinity levels in Furnace still apparent in early spring.

Variance-preserving spectra of the unfiltered along-channel currents for each depth section of the water column are displayed in Fig. 4. Currents at all depths of the water column show pronounced spectral energies associated with the semi-diurnal (M2) frequency band. Higher order harmonics (M4 (3.8 cpd) and M6 (5.79 cpd)) were also observed, which are associated with tidal asymmetries between the flood and ebb arising from the distortion of M2 tidal currents through non-linear interactions as the water depth shallows (Aubrey and Friedrichs 1988). The bottom (black line) portion of the water column notably showed increased spectral peaks at 0.06 cpd (spring-neap tides) and all depths showed significant spectra at 1 cpd
(related to the mixed nature of the semi-diurnal tide and with possible contribution from the pronounced diurnal coastal winds).

Volume fluxes

Table 1. shows summary statistics for $Q_F$, $Q_1$, $Q_2$, and $Q_{net}$. Using $Q_2$ and $Q_F$, the mean volume transport through the surface layer $Q_1 = -3.45 \text{ m}^3\text{s}^{-1}$. This value equated to the combined fluxes from catchment runoff plus volumetric fluxes of precipitation and evaporation over the surface area of Furnace ($Q_F = +3.30 \text{ m}^3\text{s}^{-1}$) and the net lower layer volume transport directly measured by the ADCP, which over the full deployment provided a small net mean inflow contribution of $Q_2 = +0.155 \text{ m}^3\text{s}^{-1}$. Therefore, the overall mean volume flux over the full deployment period through the entranceway, $Q_{net} = -3.29 \text{ m}^3\text{s}^{-1}$. This value was comparable to the mean volume flux estimate of $-3 \text{ m}^3\text{s}^{-1}$ measured over summer 2010 by an ADCP positioned in shallower water further downstream (Kelly et al (2018a)).

From March 2016 to March 2017 the basin water density decreased at a rate of $1.7 \times 10^{-7} \text{ kg m}^3\text{s}^{-1}$. A timeseries of density differences between $L_2$ and $L_3$ over the same period had a mean value of $\Delta \rho = 2.4 (\pm 1.55) \text{ kg m}^3$, thus giving a diffusive flux to the basin water from above of $Q_{K_3} = 0.023 (\pm 0.019) \text{ m}^3\text{s}^{-1}$. Mean volumetric fluxes associated with direct precipitation ($Q_P = 0.036 (\pm 0.05) \text{ m}^3\text{s}^{-1}$, based on a mean rainfall rate of $3.6 \text{ mm day}^{-1}$) and evaporation ($Q_E = 0.019 (\pm 0.01) \text{ m}^3\text{s}^{-1}$, based on a mean open water evaporation rate of $1.7 \text{ mm day}^{-1}$) over the small surface area of the inner basin provided only minor contributions to the overall water balance. Groundwater inflows were not accounted for and thus likely contribute a (small) error to the overall estimates presented in Table 1.
Timeseries of upper layer ($Q_1$, thick black line Fig. 5a) and lower layer ($Q_2$, thin grey line Fig. 5a) mean daily volume fluxes through the entranceway to the inner Furnace basin both showed contrasting periods of net positive and negative fluxes into and out of the inner basin. The black dashed line shows the transition between positive and negative fluxes with opposing baroclinic volume transport between the two layers a predominant feature, which was anticipated based on the observed flow structure previously described (Fig. 3a). The magnitude of negative volume fluxes generally exceeded positive fluxes and this is clearly observed in the timeseries of net volume transport (Fig. 5b) with only weak and rare occasions of net inflow. Significant temporal variability around the overall mean volume flux was observed (solid black horizontal line Fig. 5b and Table. 1). Large negative fluxes in Fig. 5b were associated with freshwater events and overall volumes through the mouth closely matched $Q_F$ (Fig. 3d), indicating the dominating influence of freshwater outflow on flux dynamics.

Volume transport through $Q_2$ showed spring-neap fluctuations (Fig. 5c). During large spring tides, typical volume fluxes of $\approx +10$ m$^3$s$^{-1}$ were estimated, which were an order of magnitude larger than the mean volume transport to the inner basin over the full deployment period (Table 1.). A maximum influx of (+) 22 m$^3$s$^{-1}$ was recorded in April 2016, which occurred during a 2 month period of persistent inflows. This period was relatively unusual with regard to the frequent southward blowing winds (Fig. 3e), which often attained windspeeds greater than the average for the region (~5 m s$^{-1}$ (Kelly et al. 2018a)). These down-estuary winds appeared to reinforce the strength of the estuarine circulation. However, the salinity
(density) associated with these large volume fluxes was not great enough to renew the deep basin water at this time.

During neap tides, negligible amounts of tidal water reached the entranceway to the main basin and generally negative fluxes were observed near the bottom (Fig. 5c). There was evidence suggesting that freshwater conditions increased the magnitude of these negative fluxes through the lower layer at neap tides. Larger negative fluxes were observed over autumn and winter months (September through March) when freshwater discharge was higher compared to spring and (early) summer months (April through July) when drier freshwater conditions prevailed (Fig. 3d for freshwater discharge; Fig. 5c for lower layer net fluxes).

The net volume flux through the lower layer was partitioned into contributions in and out for each 30 minute timestep, using velocities measured through each individual depth bin of the ADCP (Fig. 5d). As expected, the volume transport was primarily either into or out of the inner basin, although there were instances of simultaneous positive and negative fluxes of comparable magnitude (e.g. February and April 2017). This dynamic was highly relevant when estimating renewal times for the inner basin's intermediate and deep saline waters as it meant that during periods of significant outflow, small positive fluxes of salt water may still occur. It also highlights the complexity of the flow through the shallow entranceway and may be related to tidal asymmetries and the differential influence of tidal forcing on currents closer to the bottom compared to currents at intermediate depths (Fig. 4).
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Renewal times

Using a mean daily timeseries of the relevant volume flux, renewal times were calculated for each water mass and then averaged over 7 day periods. Renewal time summary statistics for $L_1$, $L_2$ and $L_3$ are displayed in Table 2. Separate renewal times are presented for $L_3$ based on whether renewal was primarily a function of advective or diffusive fluxes.

Basin water renewal and ventilation

On May 9th 2017, a significant renewal and ventilation of the deep basin water occurred (Fig. 6). Based on the prolonged dry weather conditions that occurred, the ventilation event was anticipated and a dissolved oxygen sensor (miniDOT) was deployed near the bed next to the MR01 mooring (Fig. 1b) to monitor oxygen of the inflowing water. The change in basin water properties from this date onward (Fig. 6a-c) indicated that the source water for the inflow was comprised of the warm, salty and oxygenated bottom water (relative to the ambient resident water) presented at the entranceway (Fig. 6d). The necessary condition for this large-scale basin renewal was when the bottom layer inflow density (red line) equalled or exceeded the mean basin water density (blue line ~ 1015 kg m$^{-3}$) during a spring tidal phase (Fig. 6e). (A small (partial) renewal, limited to the uppermost part of the basin water, occurred ~ 7 days prior during the preceding spring tides, when the inflow density briefly exceeded the mean basin density during flood tides (27th April onwards, Fig. 6e)). The bottom density at MR01 gradually increased over successive spring-neap tidal cycles in the lead up to the ventilation, as denser (saltier) inflows traversed downstream channels of the Furnace system at flood tides and the mean density
during neaps remained relatively high as denoted by the density timeseries at MR02 (black line, Fig. 6e).

Temperature-salinity (T-S) relations (Kelley and Richards, 2018) were utilised to trace basin water properties at 4-day intervals relative to the external water recorded at the entranceway prior to and during the renewal event (Fig. 7; lines with symbols represent T-S curves from the AWQMS depth profiles, single symbols represent corresponding T-S relations of bottom water at the entranceway for the same date). Initially on the 6th May (prior to renewal (black, circles)) the basin water was saltier and warmer than the inflow. On the 11th May (red, stars) the inflow water was warmer and saltier (denser) and a new warmer water mass is observable along the basin water T-S curve. The salinity of this warmer water is slightly higher than the saltiest resident basin water and much lower than the water presented at the entranceway, indicating that substantial mixing occurred between resident water and the inflow as it entered the inner basin. This created a water mass of intermediate density, warmer than the ambient basin water, with slightly higher salinity and occupying roughly the same density space on the T-S plot as the old basin water (when comparing the densest portions of the black and red T-S curves). However, water warmer and saltier than the resident basin water was continually presented at the mouth over the following 4 days and on 15th May (blue, triangles) a new arm can be seen on the T-S curve for the basin water, this time containing warmer water that was salty enough to surpass the density of the old basin water, reaching densities > 1015 kg m$^3$. The position of this new arm between the old resident water and the inflow implies that the new basin water was a mixture of old and external water. A second post-renewal T-S curve 4 days later on
19\textsuperscript{th} May (green, diamonds) showed little change in the properties of the new basin water. A reduction of the inflow density compared to 15\textsuperscript{th} May meant that the upper limit of new basin water density had already been reached. This was related to the transition from spring to neap tides (Fig. 6e) and a rainfall event on 15\textsuperscript{th} May (already observable in the decreased surface salinities of the 15\textsuperscript{th} May T-S profile), which together brought about a conclusion to the major renewal event which only lasted 7 days.

The mean volume flux into the basin through the lower layer calculated directly from the ADCP during the 7 day period (between the dashed vertical lines Fig. 3 and Fig. 5) was $= + 2.02 (\pm 0.83) \text{ m}^3\text{s}^{-1}$. This estimate was two orders of magnitude higher than the average diffusive flux computed during the stagnant period. Using the volume fluxes calculated during the renewal, the basin water would take 13.3 days to renew completely, meaning that only a partial renewal occurred. The mean oxygen content of the volume flux from 10\textsuperscript{th}–15\textsuperscript{th} May was 8.4 mg l\textsuperscript{-1} (Fig. 6d).

Some of the old basin water was upwelled to an intermediate depth ($\sim 3.5 – 5.5$ m) in the aftermath of the initial deep-water inflow, where it remained as an isolated band of salty, cooler, oxygen-depleted water (Fig. 6a-c, Fig. 8). This water experienced slower rates of renewal than the previous intermediary water, given that its density was higher than typical inflow densities. In contrast, the newly ventilated basin water returned to a stagnant regime once the dense oxygen-rich inflows ceased (Fig. 6) and by September 2017, fully anoxic conditions had re-occurred (Fig. 8). Somewhat counterintuitively, 4 months post-ventilation the vertical extent of anoxia in the inner basin had increased with a shallower oxic-anoxic
interface (6.6 m up to 4.2 m) and the overall volume of anoxic water had expanded from 34.5% to 53.5% (Fig. 8).

**Predictive model**

Variables related to freshwater conditions (30-day running mean and both the 7- and 14-day lagged values) were most important in predicting inflow densities, followed by max daily tidal elevation (TG02), mean daily atmospheric pressure and mean daily along-shore coastal wind stress, in that order. This model explained 75.47% of the variance, with a mean absolute error of 0.73 kg m$^{-3}$ between predicted and measured values of density (root mean square error of 1.02 kg m$^{-3}$). The agreement between mean daily bottom layer densities at the entranceway predicted by the final iteration of the random forest model and the actual measured values over the full deployment is shown in Fig. 9. Timeseries of the two mean daily water densities showed that the model captured the overall pattern in density variability over time, and crucially for the prediction of deep water ventilations, recreated periods of higher than average density values.

By generating timeseries of relevant driver variables, the predictive model was hindcast over the 10-year period 2009-2018 and compared to the AWQMS timeseries of density and oxygen profiles in the inner basin over the same timeframe, which documented the occurrence of 5 major ventilation events (Fig. 10). (Two separate significant deep-water inflows occurred in 2010, on 26$^{th}$ February and 16$^{th}$ May, although the basin water remained oxygenated throughout the intervening period and therefore we considered it a single ventilated period). The model successfully predicted the occurrence of 4 out 5 of these major ventilation events, as highlighted by the
predicted bottom densities exceeding the mean basin water density (the event in 2013 was almost captured as the modelled inflow density equalled the bottom water density).

DISCUSSION

The observations presented here has allowed the development of a general framework for assessing the influence of tidal, river and meteorological forcing on deep-water oxygen dynamics in the semi-enclosed anoxic lagoonal estuary, Lough Furnace. In aquatic systems, the oxidation and breakdown of organic matter creates a biological oxygen demand (BOD), which utilises oxygen in the water column (e.g. Robinson 2019) and sediments (e.g. Livingstone and Imboden 1996). In order to maintain oxygenated conditions, the rate at which oxygenated water is supplied to a basin must exceed this rate of oxygen consumption. Thus, the primary control of oxygen levels in the inner Furnace basin was renewal of (and delivery of fresh oxygen to) resident water masses, which was mainly dependent upon lateral fluxes of external water of similar density. The exchange processes observed in Furnace shared many similarities with those of coastal systems with restricted exchange (e.g. Tett et al. 2003) and have good analogies on much larger scales with fjords (e.g. Farmer and Freeland 1983) and semi-enclosed seas that are poorly ventilated (e.g. Schinke and Matthäus 1998; Murray et al. 1991).
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Volume fluxes and renewal of surface and intermediate waters

The primary flux pathways with mean renewal time estimates for the layered water masses in the inner Furnace basin are recapped schematically in Fig. 11.

The thin surface freshwater layer $L_3$ had the shortest renewal time and was generally replaced entirely within 10 days (Table 2). This renewal time depends upon the rate of river runoff, with shortest renewal times occurring following periods of heavy rainfall. However as increased runoff also increased the depth of the surface layer, the renewal time decreased slowly with increasing freshwater input. Given the fast transit time of freshwater through the system, Furnace likely has a limited capacity to sequester quantities of dissolved organic carbon exported from the Burrishoole watershed, which drains a blanket peatland catchment (Doyle et al. 2019).

Renewal of the saline water at intermediate depths $L_4$ in the inner basin was dependent upon positive fluxes of saltwater. The topographically constricted connecting channel was a key determinant of the overall small positive volume fluxes (Table 2) and effectively functioned as a long, shallow sill between the basin interior and the adjacent open coastal waters, limiting tidal inflows. Spring-neap tidal forcing modulated the pattern of exchange fluxes between the inner basin and the adjacent coastal water, a general dynamic that has been previously documented in other semi-enclosed estuarine and coastal systems (e.g. Griffin and LeBlond 1991; Geyer and Cannon 1982). Large freshwater fluxes, opposing the general direction of landward tidal inflows, also appeared capable of limiting the magnitude of tidal intrusions, even during spring tides (e.g. September 2016, February/March 2017 Fig. 5).
The overall significance of this spring-neap volume flux asymmetry through the lower layer was that major positive fluxes to the inner basin and hence renewal of $L_2$ effectively had a fortnightly frequency. This led to a relatively long mean renewal time of 46 days. Thus a practical timeframe for the complete exchange of this water is over approximately 3 spring-neap tidal cycles. This long residence time (compared to the rapidly flushed surface layer) and the spring-neap modulation of influx may have biological implications. In Furnace, the SCM was found to occupy this intermediate depth zone below the upper halocline (de Eyto et al. 2019) and pelagic productivity in this stable region could potentially be influenced by fortnightly variability in tidal fluxes. For example, chlorophyll concentrations were found to fluctuate at spring-neap timescales in a shallow coastal sea (Blauw et al. 2012).

**Volume fluxes during renewal of deep basin water**

Prior to the deep-water renewal and ventilation event on the 9th May 2017, the Furnace basin water had been stagnant since September 2014 (Fig. 10b). The set of observations taken during the 7-day event allowed some description of the dynamics involved. This is useful, as aside from the irregular and ephemeral nature of these events, exchange of basin water by intruding dense gravity currents form a fundamental link in the vertical circulation of oceanic, estuarine and lake basins of all sizes. Yet detailed observations are relatively rare, with fjords and semi-enclosed basins traditionally offering the most complete recounts of the hydrodynamic processes occurring during basin water exchange (e.g. Edwards and Edelsten 1977; Arneborg et al. 2004; Liungman et al. 2001; Holtermann et al. 2017; Fer et al. 2004 ).
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The changes in the Furnace basin water is perhaps best observed from the progression of the T-S curves in Fig. 7. A straight line traced directly from the old basin water (black curve) to the densest water presented at the entranceway during the renewal (red star) reveals that the new densest basin water (additions at the ends of the blue and green T-S curves on 15th and 19th May, which lie halfway along the straight line) was a mixture comprising ~50% old basin water and ~50% new basin water. This estimate was validated by considering that the mean oxygen concentration of the inflowing new water was 8.5 mg L\(^{-1}\) (Fig. 6d), the old basin water was 0 mg L\(^{-1}\) and the new basin water immediately following the ventilation was 4.5 mg L\(^{-1}\) (Fig. 8). Based on oxygen content, the new basin water should therefore contain ~48% old anoxic basin water and ~52% from the oxygenated inflow.

The creation of new deep basin water with intermediate properties could have occurred due to the turbulent entrainment of ambient resident water by the dense inflow as it descended into the basin water (Princevac \textit{et al.} 2005). If the oxygen, salt and heat content of the Furnace inflow were reduced along its passage to the basin interior through entrainment of old water (Fig. 7, Fig. 8), then its overall volume transport should also have increased. This can be confirmed by comparing the volume fluxes estimated directly from the ADCP during the renewal, to the volume of the new basin water. By integrating the horizontal area of the inner basin from the upper depth limit of the new basin water (~6 m (Fig. 8 (blue profile))) down to the deepest point we obtain the approximate volume of the new deep basin water, \(V_{3new} = 2.61 \times 10^6 \text{ m}^3\). The mean volume influx of dense new water at the entranceway over the 7-day renewal yielded a volume, \(V_{in} = 1.22 \times 10^6 \text{ m}^3\). This was only ~47% of the new basin
water volume, meaning that the remaining ~53% was entrained from the old resident water and the initial inflow volume flux doubled. This value for volume increase of the inflow through entrainment fits well with the estimates that were obtained from analysis of temperature-salinity (50%) and oxygen (48%) properties. A two-fold increase in the volume of a dense inflowing plume as it enters ambient water of lower density is consistent with observational values reported for deep-water inflows into fjords (Liungman et al. 2001) and for outflows from straits into receiving oceanic waters (e.g. Baringer and Price 1997; Girton and Sanford 2003).

**Significance of deep-water ventilation**

The rapid delivery of relatively warm, oxygen-rich water triggered a sudden shift in basin water conditions (Fig. 6a-c). Understanding the precise impact of oxygenated inflows to the bottom of Lough Furnace on biogeochemical processes remains elusive and represents an obvious avenue for prospective research. Profound changes in phosphorus, nitrogen and methane dynamics have been reported following ventilation of a deep anoxic lake (Lehmann et al. 2015) and large changes to the bacterial community of an anoxic deep basin of the Baltic were detected following oxygenation (Bergen et al. 2018). The fate of basin water H₂S and methane during and following ventilation also deserves further investigation and are relevant to larger-scale analogues (Capet et al. 2016).

The fate of the remaining ~50% of the old basin water not entrained into the gravity current can be seen in Fig. 6b and 6c, where an uplifting of cold, anoxic basin water to shallower depths occurred in the aftermath of the renewal. A new oxygen minimum
zone occupies the depth range between ~3.3 and ~5.5 m, overlying the new (relatively) well-oxygenated basin water (Fig. 8). It is evident that some mixing with shallower oxygenated water occurred given the increase in oxygen concentrations above anoxic levels. However the average oxygen content of this new intermediate low oxygen zone is only 0.7 mg L$^{-1}$; average oxygen values at this depth range prior to the ventilation (black line, Fig. 8) were ~7.4 mg L$^{-1}$. This implied that the majority (>90%) of the water constituting this oxygen minimum zone is from the remaining anoxic basin water not entrained into the dense gravity current. It also indicates that only minimal amounts of the old basin water were mixed into the shallower waters and exported. This ‘trapping’ of old basin water below the surface layer suggests that diffusive efflux of gaseous elements accumulated in anoxic water to the atmosphere may be avoided, although this dynamic certainly warrants further investigation.

The shallower oxic-anoxic interface observed in the months following ventilation has potential consequences for resident fauna inhabiting surface oxygenated zones. In particular, the shallower depth where the oxycline now intersects the basin slope around the perimeter of the inner basin will essentially translate to a reduction in the extent of viable habitat for aerobic organisms. In Furnace (Kelly et al. 2018b) and similar deoxygenated estuaries (e.g. Sanford et al. 1990; Chikita 2000) baroclinic waves can dramatically influence dissolved oxygen conditions in nearshore areas. A shallower oxycline following ventilation will therefore mean that upwelling anoxic water could encroach further on communities of nearshore benthic organisms.
Following the initial ventilation, conditions in the deep basin water once again became stagnant and oxygen declined due to internal oxygen consumption related to BOD. BOD per unit volume of basin water is clearly of interest and the post-ventilation stagnant period affords us the opportunity to estimate this parameter in Furnace. Using the new basin water oxygen content as a starting point, the rate of oxygen decline over time, $dO/dt$, was estimated. However some of this consumed oxygen may be replenished through the downward diffusive flux of oxygenated surface water to the deep basin water. Therefore, using the mean estimate of vertical diffusive flux between the basin water and overlying water, $Q_{K3} = 0.023 \, \text{m}^3 \, \text{s}^{-1}$, the rate of internal oxygen utilization (BOD) in the new basin water is given by:

$$BOD = \frac{Q_{K3}}{V_3} (O_1 - O_3) - \frac{dO}{dt}$$  \hspace{1cm} (7)

where, $O_1$ and $O_3$ are the mean oxygen concentrations of the basin water and surface oxygenated water (note that water at intermediate depths was also anoxic following ventilation hence the relative oxygen gradient involved in diffusion was across the oxic-anoxic interface). $BOD$ in the basin following ventilation was $0.06 \, \text{mg L}^{-1} \, \text{day}^{-1}$, with the diffusive flux contributing less than a 5% replenishment.

In a broader context, recent evidence suggests that many lake basins, comparable in size and morphometry to Furnace inner basin, will experience decreased basin-scale mixing events and increased isolation of hypolimnetic water, related to warming surface water temperatures (Woolway and Merchant, 2019). The impact of
intensified thermal stratification has already been linked to hypolimnetic oxygen depletion in lakes (e.g. Jankowski et al. 2003). Based on our observations from Furnace, the mean downward diffusive flux of oxygen from surface waters to deep water alone would not be sufficient to prevent anoxic conditions from occurring within several months, although BOD will vary from system to system based on supply of organic matter.

Dynamics and drivers of deep-water ventilations in Furnace

Given the overall significance of deep-water renewal and ventilation, discerning the mechanisms involved and being able to predict their occurrence has considerable pertinency to the study of physical, chemical and biological regimes in semi-enclosed deoxygenated coastal systems. The inflow density and density gradient of the receiving water column determines the intrusion depth of inflows into the inner basin, which interleave at a depth of neutral buoyancy. Based on our profiles of the water column density in the inner basin and entranceway, this intrusion depth was typically somewhere below the upper halocline and above the depth of the densest resident water in Furnace (Fig. 2). Less than 5% of observed inflow densities were sufficiently dense ($\geq 1016$ kg m$^{-3}$) to activate a deep-water renewal (i.e. 2 red histogram bars with density greater than solid black line in bottom panel Fig. 2). Whilst the precise drivers of deep-water renewal and ventilation vary from system to system, a number of general processes have been shown to play a role in activating a basin water exchange and we now examine which ones may be most relevant to Furnace.

Basin water density
Vertical diffusion and mixing will gradually reduce the density of basin water over time, preconditioning it for a renewal by reducing the density contrast with external water (Stigebrandt 2012). From 2016-2017 prior to the renewal event, the Furnace basin water density reduced at a rate of $1.5 \times 10^3$ kg m$^{-3}$ d$^{-1}$ (or 0.5 kg m$^{-3}$ yr$^{-1}$). Given that renewals are typically separated by at least one year (Fig. 10), the rate at which the resident basin water density reduces appears not be a limiting factor in the occurrence of dense intrusions. Sources of energy for this mixing are typically derived from internal tides (e.g. Inall 2009). In Furnace, wind may be a significant factor as previous estimates of turbulent diffusivity in the stagnant basin water indicated a mean value of $9.35 \times 10^{-6}$ m$^{2}$ s$^{-1}$, which increased by an order of magnitude following wind-induced internal seiching (Kelly et al. 2018a). Another important consideration is the dynamics of the dense inflowing plume, as the rate of entrainment and density reduction will set the upper limit of the basin water density at the outset of subsequent stagnant periods (Liungman et al. 2001). Our analyses showed that the density of new basin water is significantly reduced compared to the inflow source water (Fig. 7) and thus rule the density of the inflow as a factor that restricts future ventilations.

*Tidally-modulated exchange*

The timescales of basin water exchange have often been linked to the spring-neap tidal cycle, primarily through two different mechanisms. Firstly, larger tidal excursions during spring flood tides may enhance the likelihood of deep-water renewal as large volumes of dense coastal water are transported toward the basin entrance (e.g. Edwards and Edelsten 1977; Gade and Edwards 1980). Secondly, changes in mixing regime between springs and neaps may modify
the density of tidal water as it is transported through the entrance constriction. Often, spring tides may intensify this mixing, reducing the inflow density and lessening the likelihood of deep-water inflows (e.g. Geyer and Cannon, 1982; Griffin and LeBlond 1990). In such systems, basin water exchange is thus more likely to occur during neaps. In Furnace, the former mechanism is much more fitting given that significantly higher salinities and larger advective fluxes into the inner basin are recorded during spring tides (Fig. 3, Fig. 5), related to the long excursion length between the inner basin and the open coastal water.

*Freshwater flux*

Freshwater runoff may indirectly control basin water exchange dynamics by physically blocking tidal inflows and diluting inflowing coastal water especially along constricted or shallow connecting channels. Complete blockage would require the surface freshwater layer to extend down to or below sill depth and in Furnace this would likely only occur during periods of exceptional run-off, given a mean surface freshwater depth of only 1.8 m and a depth of ~5 m through the deeper portion of the entrance section (Fig. 1c). The role of freshwater flux on controlling basin water exchange through mixing with inflows has previously been documented in the fjords and sea-lochs of Scotland, with several systems showing an inverse correlation between river runoff and inflow density (Allen and Simpson 1998; Gillibrand *et al*. 1995; Edwards and Edelsten 1977). Reduced freshwater runoff has been shown to play a considerable role in the large-scale ventilation of the deep Baltic sea (so-called ‘major Baltic inflows’), with the drastically reduced frequency of these events in recent decades being linked to
changes in large-scale atmospheric circulation over the North Atlantic and Europe (Schinke and Matthäus 1998; Mohrholz et al. 2015).

Water entering an estuarine basin during a flood tide is comprised of ‘old’ water that exited the during the preceding ebbs and ‘new’ water that is transported in from the adjacent coastal region. We can assess the role that freshwater flux through the Furnace system plays in modifying inflow densities by quantifying the fraction of inflow water comprised of actual ‘new’ coastal source water compared to recirculated water. In Furnace, inflowing coastal water remains relatively unchanged through the lower part of the tidal channel (Fig. 1b). A timeseries of salinities recorded in 2010 at a mooring next to TG02 revealed consistent values of ~31 during flood tides (Kelly et al. 2018a). As this water traverses the remainder of the connecting channel and passes Nixon’s Island, it mixes with outflowing Furnace surface water, evident in the reduced salinities of tidal water measured at MR02 and MR01 (Fig. 4b and 4c). Following Pawlowicz et al. (2007b) and using salinity as a tracer, the lower layer inflow water at MR01 ($S_2$) is comprised of the following mixture:

$$S_2 = \gamma S_1 + (1 - \gamma)S_0$$

where $S_1$ is the surface outflow water from Furnace measured at MR01, $S_0$ is the coastal water entering the lower estuary (taken to be 31) and $\gamma$ is the recirculating fraction. Solving for $\gamma$ gave a mean value of 0.52 ($\pm 0.08$). This indicates that on average, 52% of the water flowing into the inner Furnace basin through the lower layer is comprised of prior resident water that was flushed out (or alternatively, 48% is comprised of ‘new’ oceanic water).
In practical terms, this means that the salinity of the inflowing tidal water should be diluted by the outflowing surface water by roughly 52% by the time it reaches the inner basin. As salinity of the outflowing surface water increases during periods of low river runoff (blue line, Fig. 3c) the salinity of the inflow will be diluted less. Given a mean surface outflow salinity of 13.5 (observed on May 9th 2017) and taking a value of 31 for incoming water at the coastal boundary of the estuary, the inflow salinity to the inner basin was 22-23 at the onset of the renewal and would go on to reach values as high as 26 at peak flood tide (red line, Fig. 3c). It was also probable that the salinities of inflows from the adjacent coastal waters were slightly higher than 31 at this time, given the very low inputs of freshwater around Clew Bay. In contrast, a surface layer outflow close to fully fresh, which occurs following heavy rainfall events (blue line, Fig. 3c), would give a bottom inflow salinity of only ~15.

A climatology of freshwater discharge from the Burrishoole watershed with the timestamp of observed deep-water ventilations over the ten year period 2009-2018 reveals that significant ventilations occurred only during months with negative discharge anomalies (Fig. 12a). This further highlights that in Lough Furnace, freshwater flux plays the preeminent role in determining the salinities (densities) of inflows, thereby modulating the exchange of basin water to a larger extent than any other variable. It also implies that the frequency and magnitude of ventilations will be highly sensitive to climate-induced modification of precipitation and run-off patterns.

Coastal forcing
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Variations in coastal water density have long been recognised to play an important role in regulating exchange processes in semi-enclosed coastal basins (Arneborg 2004; Stigebrandt 2012; Klinck et al. 1981). In particular, the role of regional winds in determining coastal water density in the vicinity of the basin entranceway has been implicated, with wind patterns that promote offshore transport of low salinity surface water often inducing upwelling of denser water from greater depths in return (e.g. Thomson et al. 2017; Arneborg et al. 2004). In Clew Bay (Fig. 1a), the dominant mode of wind variability is related to the south-westerly sea breezes coming in from the North Atlantic, which would tend to block outflow of low-salinity surface water (i.e. positive toward 107°T Fig. 12b). A climatology of wind stress along the primary axis of wind forcing in the bay revealed that deep-water ventilations in Furnace occurred during or immediately following months with negative wind stress anomalies. The 2017 and 2018 events occurred during weaker than average south-westerly winds and the 2010, 2013 and 2014 events during or following persistent north-easterly winds (Fig. 12b). The 2013 event in particular is interesting, as the magnitude of the ventilation was particularly large (Fig. 10b) despite the freshwater conditions not being as low as other months with ventilations (Fig. 12a). Given the timing of the ventilation in 2013 (April 9th) the vernal equinox tides may also have played a role in the magnitude of this renewal. It is for these reasons that the predictive model did not adequately recreate inflow densities exceeding basin water densities for 2013; the set of wind conditions in the lead-up to that event were not recorded during the observational period of this study (2016-2017) which was used as the basis for the model drivers. It is therefore likely that the current iteration of the model
underestimates the impact of prolonged offshore winds on inflow densities and this could be remedied by training the model using a longer set of observations which ideally captured sufficient variability in coastal winds.

**Summary and future outlook**

An understanding of the main drivers of renewal times and deep-water ventilation in the semi-enclosed estuarine basin Lough Furnace has allowed predictions of when and how significant alterations to basin water oxygen dynamics will occur. Ventilations essentially depend on two primary parameters: 1) a prolonged reduction in local rainfall leading to very low river runoff into (and subsequently out of) the inner basin and 2) spring tides capable of transporting dense (salty) coastal water across the long connecting channel. Wind-induced upwelling of denser coastal water may also play a role and at the very least, it would appear that a weakening of the predominant south-westerly sea breezes may reduce blockage and backing up of lower salinity surface outflows from the adjacent coastal bay. Sufficient reduction in basin water density between renewals and entrainment of the dense plumes as they intrude into receiving basin waters appear to prevent the basin water density from prolonging the internal timescale between ventilations.

Using the set of observations described, a simple predictive model was constructed using only 4 commonly measured hydro-meteorological variables: catchment freshwater discharge, tidal elevation, atmospheric pressure and wind. The predictive model was capable of accurately recreating the density of inflows to the inner Furnace basin (Fig. 9). Given a relatively stable mean basin water density over the last ten years of 1015.57 kg m$^{-3}$, we can deduce based
on the predicted inflow densities when a deep-water ventilation event will occur (Fig. 10). This model provides a simple diagnostic tool for assessing the likelihood of future ventilation events and also for diagnosing the frequency of past events.

Compared to tidal and wind forcing, changes in precipitation patterns are most likely to be altered by climate change in the near future and it would appear based on the climatology of Burrishoole discharge that the last ten years have experienced wetter winters on average relative to the long-term mean (1976-2018) (Fig. 12a). Whilst increased total rainfall and larger rates of terrestrial discharge have been linked to reduced ventilation of the vast Baltic basin (Schinke and Matthäus 1998; Mohrholz et al. 2015), in a smaller system like Furnace the relevant parameter may be the distribution of rainfall intensity across the year. An increase in total rainfall should only increase the occurrence and extent of anoxia should the rainfall be spread evenly throughout the year. In contrast, an increased occurrence of prolonged dry periods in spite of an overall increase in total annual precipitation could see the frequency of ventilation events increase. For example, the most recent decade (2006-2015) of a 305-year-long rainfall analysis for Ireland was found to be the wettest (Murphy et al. 2018), yet Furnace experienced ventilation events in five out of the ten most recent years related to anomalously dry spring or autumn periods. Ascertaining whether climate change will alter the frequency of deep-water ventilation events in Furnace and other specific deoxygenated estuarine systems strongly influenced by local runoff conditions is difficult, as model projections of hydrological patterns throughout Europe are typically focused at the regional scale or coarser (Lobanova et al. 2018). In a national context, decreased summer precipitation and discharge is anticipated
although the high uncertainty associated with hydrological modelling is emphasised (Bastola et al. 2011). A relevant next step toward understanding future oxygen dynamics in Lough Furnace could be to assess the individual catchment-scale response to changes in timing and intensity of future precipitation and more broadly, assessing how modified hydrological regimes in catchments might affect physical, chemical and biological processes in receiving coastal waters.

### TABLES & FIGURES

*Table 1. Advective volume flux estimates in/out of the inner Furnace basin. Positive (negative) values indicate fluxes into (out of) the inner basin.*

<table>
<thead>
<tr>
<th>Flux</th>
<th>Mean (±s.d.) (m³s⁻¹)</th>
<th>Min/Max (m³s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Q_F)</td>
<td>3.30 (±3.26)</td>
<td>0.43/28.56</td>
</tr>
<tr>
<td>(Q_1)</td>
<td>-3.45 (±4.97)</td>
<td>-27.55/22.11</td>
</tr>
<tr>
<td>(Q_2)</td>
<td>0.155 (±4.28)</td>
<td>-24.46/22.63</td>
</tr>
<tr>
<td>(Q_{net})</td>
<td>-3.29 (±3.28)</td>
<td>-25.94/2.26</td>
</tr>
</tbody>
</table>
Table 2. Renewal time ($T_R$ in days) of each water mass in the inner Furnace basin. $T_R$ values shown here represent an average over 7-day periods. ($T_{R3\text{stagnant}}$ refers to time periods when renewal of basin water occurred due to diffusive fluxes only; $T_{R3\text{renewal}}$ refers to periods when advective fluxes to the basin water occurred.)

<table>
<thead>
<tr>
<th>Layer</th>
<th>Mean (Median)</th>
<th>Min/Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_{R1}$</td>
<td>8.5 (7.3)</td>
<td>2.4/29.8</td>
</tr>
<tr>
<td>$T_{R2}$</td>
<td>46.0 (31.6)</td>
<td>7.2/254.6</td>
</tr>
<tr>
<td>$T_{R3\text{stagnant}}$</td>
<td>1663.3 (1347.7)</td>
<td>309/4789.6</td>
</tr>
<tr>
<td>$T_{R3\text{renewal}}$</td>
<td>13.3 (13.3)</td>
<td>14.3/12.2</td>
</tr>
</tbody>
</table>

Fig. 1. (a) Clew Bay with Lough Furnace highlighted in the north-east corner. (b) Lough Furnace with 2-m depth contours and sampling locations. The main inner basin is continuously connected to adjacent coastal waters of Clew Bay. (c) Cross-section of the entranceway to the inner Furnace basin, showing the set-up of the ADCP and MicroCat Temperature-Salinity sensors in the deep channel section.
Fig. 2. Probability histograms of salinity (top) and density (bottom) based on measurements made in the entrance to the inner basin at MR01 (blue – surface layer, red – lower layer) and in the inner basin at AWQMS (black solid line – full water column, dashed black line – water column only to mean depth of oxycline).
Fig. 3. Timeseries of (a) along-channel (350°T) current velocity profiles at MR01, (b) salinity (black) at MR02 with 40-h low-passed tidal elevations at TG02 (red), (c) surface (blue) and bottom (red) salinities at MR01, (d) freshwater flux (Qf), (e) along-channel wind-stress at MR01 (positive (red) is toward inner basin and negative (blue) out of inner basin).

Fig. 4. Variance-preserving spectra of along-channel (350°T) velocities at MR01 recorded over the full deployment period (March 16\textsuperscript{th} 2016 – July 7\textsuperscript{th} 2017). Depths are metres above the bed.
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Fig. 5. Timeseries of mean daily volume fluxes through the entrance section to the inner Furnace basin. Positive values indicate volume flux in and negative values out. (a) volume flux through upper layer $Q_1$ (thick black line) and lower layer $Q_2$ (thin grey line), (b) net volume flux $Q_{net}$, (c) net volume flux through lower layer $Q_2$ (red positive, blue negative) with 40-h low-pass filtered tidal elevations at TG02 (thin grey line), (d) partition of lower layer volume flux into contributions in (red) and out (blue). Dashed vertical lines denote the time period of deep-water ventilation.
Fig. 6. Observations of lead up and occurrence of deep-water renewal and ventilation on 9th May 2017. Timeseries of contours measured at AWQMS of (a) salinity, (b) temperature, (c) dissolved oxygen. (d) Salinity (red), temperature (black) and oxygen (blue) recorded at the bottom mooring MR01. (e) Density recorded at MR02 (black), MR01 bottom (red) and mean basin water density recorded at AWQMS (blue).

Fig. 7. Temperature-salinity diagram for inner basin AWQMS profiles (lines with symbols) and bottom inflow water through entranceway recorded at MR01 in the leading up to and following deep-water renewal event on 9th May 2017.
Fig. 8. Oxygen profiles in inner basin recorded at AWQMS for 1\textsuperscript{st} April 2017 (pre-ventilation), 20\textsuperscript{th} May 2017 (immediately post-ventilation) and 1\textsuperscript{st} September 2017 (several months post-ventilation).

Fig. 9. Validation of predictive model of mean daily bottom ventilation, 2017.
densities through entranceway to the inner basin (MR01). (a) predicted vs observed densities, (b) timeseries of observed (grey dots) and predicted (red line) densities for the full deployment period.

Fig. 10. Hindcast of predictive model of mean daily bottom densities through entranceway to the inner basin (MR01) over the period 2009-2018. (a) predicted inflow densities (black line) and mean basin water densities recorded by AWQMS profiler, (b) mean inner basin bottom water oxygen recorded by AWQMS profiler. The inflow densities exceeding the bottom basin water density is the criteria for basin water ventilation.

Fig. 11. Schematic indicating main flux pathways in Furnace and estimates of the typical renewal times of each water mass of the inner basin computed based on the observations presented here.
Fig. 12. (a) Monthly mean freshwater discharge (thick black line) into upper Lough Furnace from the Burrishoole catchment, relative to the long-term monthly mean discharge (dashed black line) over the period 1976-2018. (b) Monthly mean along-shore component of wind stress in Clew Bay with positive values indicating winds blowing toward 107°T (see Fig. 1a), relative to the long-term monthly mean (dashed black line) over the period 2005-2018. Black vertical arrows indicate the onset of deep-water ventilations in the inner Furnace basin.

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REFERENCES


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Chapter 5. ECOLOGICAL CONSEQUENCES OF INTERNAL SEICHEs IN A SEMI-ENCLOSED, ANOXIC COASTAL BASIN

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ABSTRACT: Climate-related increase of near-surface water temperatures in aquatic environments both decreases oxygen solubility and intensifies vertical stratification of the water column, prompting concern over the depletion of dissolved oxygen (DO) in deep interior waters. Understanding bio-physical interactions in affected ecosystems is therefore paramount, as physical processes often determine the spatial extent of deoxygenated zones. One pertinent example, often linked to mass-mortality events of marine organisms, is wind-driven upwelling of low-DO deep waters into shallower, nearshore oxygenated areas. In this note, mortalities recorded during routine fishery surveys in Lough Furnace, a semi-enclosed estuarine basin with deep anoxia, are shown to result from significant wind events. Advection of deoxygenated deep water into nearshore areas occupied by fishing nets occurred following strong winds. Relaxation of the initial wind stress generated a baroclinic standing wave (internal seiche) and a succession of upwelling and downwelling events which caused drastic fluctuations in nearshore DO concentrations that persisted for several hours. The internal seiche dynamics were confirmed following analysis of water density oscillations at a mid-basin and boundary location. These results
highlight the importance of bio-physical interactions in aquatic ecosystems with DO-depleted deep waters, as hydrodynamic processes can mediate the exposure of biota to deoxygenated water conditions.

**KEY WORDS:** Anoxia · Fish kill · Upwelling · Stratification· *Anguilla Anguilla*

**INTRODUCTION**

Dissolved oxygen (DO) depletion in aquatic environments is a growing concern globally, with profound negative implications for biodiversity and ecosystem productivity (Diaz & Rosenberg 2008, Breitburg et al. 2018). Climate change is anticipated to intensify deoxygenation in bottom waters, with warming of near-surface waters decreasing oxygen solubility and strengthening stratification of the water column, limiting downward mixing of DO-rich surface water (Keeling et al. 2010). This climate-related escalation of bottom water DO depletion is expected to affect oceans (Schmidtko et al. 2017), coastal and estuarine systems (Zhang et al. 2010) and freshwater lakes (North et al. 2014). Microbial degradation of organic material in the water column and bottom sediments consumes DO, and in isolated bottom waters without a replenishing DO source, hypoxic (< 2 mg O² l⁻¹) and eventually anoxic (0 mg O² l⁻¹) conditions will develop (Diaz & Rosenberg 2008).

The effects of hypoxia on aerobically respiring aquatic organisms vary from reducing scope for growth and fecundity (Gray et al. 2002) to more insidious effects such as compressing viable habitat space and necessitating changes in movement and feeding behaviours (e.g. Wannamaker & Rice 2000, Domenici et al. 2007). Hydrogen sulphide (H₂S) is a microbial by-product of anoxic
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conditions and toxic to aerobic species (Vacquer-Sunyer & Duarte 2010), giving anoxic H₂S-rich water the capacity to cause mass mortalities of aquatic organisms during single exposure events (e.g. Luther et al. 2004).

In stratified waters with deep hypoxic/anoxic zones isolated from oxygenated upper layers by a stable density gradient (pycnocline), an important consideration is the effect of wind-induced upwelling events, where an episodic upslope movement of deoxygenated sub-pycnocline water masses into shallower nearshore oxygenated refuges occurs. This phenomenon has been previously documented in coastal ecosystems (e.g. Grantham et al. 2004), estuaries (e.g. Sanford et al. 1990, Reynolds-Fleming & Luettich 2004), saline lagoons (e.g. Chikita 2000) and lakes (e.g. Bernhardt et al. 2014). In confined basins, wind-driven surface currents are piled against the downwind basin boundary, raising the surface water level at this end. This horizontal pressure gradient leads to a depression in the pycnocline below its equilibrium depth (downwelling) at the downwind end. This is balanced by a return flow of deeper water and an uptilt of the pycnocline at the upwind boundary (upwelling) (e.g. Shintani et al. 2010). Calming of the initial wind stress allows the tilted condition of the pycnocline to relax back toward its equilibrium position with the momentum generating a standing gravitational wave at the pycnocline (internal seiche) which reflects back and forth from each basin end and causes a series of regular, basin-wide internal oscillations (Münnich et al. 1992, Shintani et al. 2010).

In this note, mortalities of European eel Anguilla anguilla observed in catches from routine fishery surveys in a stratified estuarine basin with deep anoxia are linked to wind-induced internal
seiching and consequent upwelling of anoxic water into susceptible nearshore regions, for which few observations exist. The initial focus was on the gravest internal seiche mode (referred to hereafter as $T_1$), which shifts the whole water column up and down and has opposite horizontal flow between a surface and bottom layer separated by a pycnocline of constant thickness (e.g. Münnich et al. 1992). Whilst the fishery surveys offered an unusual, opportunistic experiment to test this, the wider ecological implications of upwelling of DO-depleted deep water are considered, as similar physical dynamics related to wind-driven water movements are ubiquitous in stratified water bodies.

**METHODS**

*Study site*

The study was conducted in Lough Furnace, a semi-enclosed estuarine basin on the Atlantic coast of Ireland (53° 55’ 04’ N, 9° 34’ 20’ W) (Fig. 1). The northern main inner basin (max depth 20 m) receives surface freshwater input from river runoff and tidal inflow of saline water from the southern entrance channel. Tides are semi-diurnal, with spring and neap tidal ranges of 0.3 m and 0.1 m respectively. Stagnant hypoxic and anoxic conditions are typically maintained below 7–8 m (35–40% of the total basin volume) by the strong halocline (usually at 1–4 m depth) and the restricted estuary–ocean exchange, with significant ventilation of the deep water by dense tidal intrusions only occurring at approximately 2-year intervals (Kelly et al. 2018).

*Fishery surveys*
Stock assessment surveys for critically endangered European eel *Anguilla anguilla* have been carried out intermittently in Lough Furnace since 1987 and annually since 2011. In these surveys, 10 fyke nets (each 15 m long unit consists of 2 funnel-shaped nets connected by a leading net, with the openings facing each other) are joined together end-to-end to form a single net chain laid along the bed starting at the shoreline and extending ~150 m directly offshore (Poole & Reynolds 1996). Fyke net locations are shown in Fig. 1, with dead eels often recovered at site C (see Table 2). Given the frequency of westerly winds in this system (Kelly et al. 2018), it was hypothesised that the location of site C near the shallower western side of the main basin would make it susceptible to upwelling of deep anoxic water. This was tested during two 2016 fyke net surveys, S1 and S2 (Table 1). Numbers of live and dead eels per net were recorded, and dead eels were sampled for signs of injury and for stomach contents.

*Hydrographic observations*

Table 1 summarises instruments deployed during each net survey, and Fig. 1 indicates locations of moorings MR01 and MR02. In addition to these moorings, transects of DO depth profiles measured at 0.15 m increments were made using a handheld probe (*In-Situ* smarTROLL) at 4 locations along the length of each fyke net chain, immediately after nets had been set (Table 1). An echosounder transect from 165 m offshore to the shoreline was taken to assess bathymetry at net sites. Wind speed and direction at 2 min intervals and water column profiles of density and DO every 6 h (using a Hydrolab DS5 data sonde attached to an undulating winch) were recorded from an automatic water quality monitoring station.
(AWQMS) in the central basin (Fig. 1). Both S1 and S2 occurred during neap tidal phases (<0.1 m change in water level height).

The internal wave field was assessed using normal mode analysis of the density stratification. Density profiles measured at the AWQMS (at 0.15 m increments) were averaged for the duration of S1 and S2 and used to calculate vertical profiles of the buoyancy frequency squared: $N^2(z) = (−g/ρ) \frac{dρ}{dz}$, where $g$ is gravity, $ρ$ is density and $z$ is depth. By imposing rigid level boundary conditions at the surface ($z = 0$) and bottom ($z = −H$, where $H$ is the full water column depth), and in the absence of background shear, the modal structure and corresponding phase speeds of long, linear internal wave motions that would result from an initial perturbation to a stratified fluid characterised by $N^2(z)$, were determined through solution of the eigenvalue problem (e.g. Gill 1982):

$$\frac{d^2ψ_i(z)}{dz^2} + \frac{N^2(z)}{c_i^2}ψ_i(z) = 0,$$

$$ψ(−H) = ψ(0) = 0,$$

where the eigenfunction $ψ_i(z)$ and its eigenvalue $c_i$ are the vertical modal structure and phase speed respectively of a horizontally propagating wave of the $i^{th}$ vertical mode. The largest eigenvalue is the phase speed of the fundamental baroclinic mode ($c_1$) and was used to estimate $T_1$ for S1 and S2, with $T_1 = 2L/c_1$, where $L$ is an effective horizontal scale (i.e. basin length at the pycnocline depth along the axis of wind forcing).

Time series of water densities were calculated for each sensor at moorings MR01 and MR02 for the 5 d period overlapping with the S2 survey (Table 1). Spectral analysis was carried out on each time
series by calculating power spectra and 95% confidence intervals using a multitaper spectrum estimate (Rahim & Burr 2014) in R (R Core Team 2017). Water density at 3 m at MR01 and MR02 was analysed to compare vertical oscillations between the site C net location and at a location near the opposite side of the basin.

RESULTS

Fishery surveys

Anoxic water spatially overlapped with the outermost parts of the site C net chain during both surveys (Fig. 2). Eleven eels were captured during survey S1 at site C (Table 2) with dead eels recovered in the outermost nets containing any catch (10 and 8) and the remaining live catch in nets 1, 2 and 5. One dead eel was recovered from site Y (net 10) with no mortalities in sites X or Z. For survey S2, dead eels were recovered from site C in nets 4 and 6, at depths that initially did not experience severely low-DO conditions (Fig. 2c); interestingly, live eels were also recovered in deeper nets 6 and 5 (in addition to 4 eels in net 1) (Table 2). Dead eels were also discovered at site X (net 8) and site Y (net 10).

Dead eels showed no evidence of clogged gill tissue or obvious disease or injury. Eight of 9 fish had full stomachs, indicative of recent feeding. Several dead fish had wide, open mouths and expanded gills upon initial recovery, likely a symptom of having been asphyxiated.

Hydrography

During survey S1, winds were primarily northerly, occasionally veering westerly (Fig. 3a). Comparison of bottom DO
concentrations with the wind stress indicates that a downwelling of oxygenated surface water occurred initially as the northerly wind blew surface water toward site C (between 15:00 and 19:00 h; Fig. 3a, b). Relaxation of the wind generated a baroclinic seiche, evident as 5 successive upwelling and downwelling events in the MR02 DO time series during the ensuing calmer period (from 19:30 to 07:00 h; Fig. 3b). A periodogram of the DO time series during this post-wind focal period revealed a prominent periodicity of 2 h (Fig. 3c). Another strong wind from the north at ~07:00 h disturbed this internal seiche by causing another downwelling event and possibly re-energising a second internal seiche (upwelling of low DO water at ~11:00 h). $T_i$ calculated for the ~1100 m NW–SE basin axis (roughly aligned with the predominant wind direction during S1) was 2.03 h ($c_1 = 0.30$ m s$^{-1}$, using the $N^2$ profile in Fig. 2b), confirming that the DO oscillations matched the fundamental internal seiche period (Fig. 3c).

The timeseries of wind during the S2 survey and overlapping observation period showed that winds were predominantly westerly with southerly and northerly components (Fig. 4a). Contrasting the initial downwelling during S1, strong westerly winds at the onset of S2 caused upwelling of low-DO water into shallower regions (Figs. 2c & 4a). Water density fluctuations from the daily mean value at 3 m at MR01 and MR02 showed distinct oscillations, with values periodically increasing and decreasing above and below the mean; fluctuations also appeared directly out of phase between the 2 locations (Fig. 4c). Spectral analysis of the water density at 3 m for MR01 (Fig. 4c) and MR02 (Fig. 4d) showed pronounced spectral peaks at ~1.25 cycles per hour (cph) with MR01 also showing a peak
at ~0.6 cph (although a flatter peak around this frequency was also observable for MR02).

Between S1 and S2, the upper freshwater layer deepened following rainfall events and stratification was greater during S2, resulting in a higher $c_1$ value calculated from the mean $N^2$ profile for this period (Fig. 2d) of 0.44 m s$^{-1}$. Using this phase speed and considering the main wind dynamics, $T_1$ was calculated for a wave travelling directly across the E–W axis of the main basin (~650 m) and also across the longer NE–SW axis (~1200 m, slightly longer than the NW–SE axis). $T_1$ across the shorter E–W axis was 0.81 h and along the longer NE–SW axis was 1.5 h. Both $T_1$ values appeared to correspond with peaks in the MR01 and MR02 power spectra, which were more apparent for the MR01 site, possibly related to larger internal wave amplitudes in this deeper part of the basin (Fig. 4c,d).

A spectral peak was also observable at the lower frequency of ~0.25 cph (~4 h periodicity) for both MR01 and MR02 (Fig. 4c,d). Given the estimated phase speeds of the first few vertical wave modes and basin geometry, it appears that this peak is not directly related to a cross-basin, wind-generated internal seiche with a central nodal point. It is proposed that the origin of this 4 h periodicity may therefore be related to a tidally-forced pycnocline displacement originating from the open mouth at the southern end of the main basin (Fig. 1). This open boundary represents a nodal line, since external water masses outside the inner basin are involved in the seiche oscillations, and therefore the gravest mode response to tidal forcing occurring through the (narrow) entrance channel is a progressive standing wave radiating away from the node with a wavelength of 4 times the basin length (e.g. Wilson 1972). By using the range of $c_1$ values calculated (0.3 to 0.44 m s$^{-1}$) and a basin length
from the mouth to the northern boundary of ~1200 m, a resulting seiche period of 3 to 4.4 h was estimated, which may explain these lower frequency density oscillations at 3 m for MR01 and MR02, noted in Fig. 4c,d.

In the immediate aftermath of each pronounced wind event (wind >8–10 m s⁻¹) density oscillations at 3 m appeared directly out of phase between MR01 and MR02 (Fig. 4b). Vertical displacement of water masses in different directions at opposite basin ends along the general axis of wind stress (E–W or NE–SW) led to the conclusion that the initial major fluctuations observed in DO (S1) and density (S2) appeared to be correlated to the mode 1 internal seiche response to cross-basin wind-forcing (Figs. 3 & 4). Subsequent density oscillations were generally not directly out of phase between MR01 and MR02, often appearing to be of similar phase. This was consistent with a seiche, likely tidally-forced, propagating south-north (i.e. from the mouth to the head), with MR01 and MR02 both located north of the entrance channel. The significance of this lower frequency (~0.25 cph) oscillation for nearshore DO remains unclear.

DISCUSSION

Results indicated that dissolved oxygen fluctuations, related to wind-induced baroclinic motions, led to mortalities in captured fish held in nearshore areas that are within the upwelling limits of deoxygenated water from the deep zone of the main basin.

The fishery surveys offered a novel method for assessing the extent of upwelling and subsequent bio-physical interactions. Whilst the setting was unnatural (i.e. captured eels were unable to escape from developing harmful conditions) they illustrated the potential
implications of deoxygenated deep water for commercial fisheries in similar habitats, which could experience a reduction in viable catch or fishing grounds. Eels were obviously alive as they entered a specific net location meaning that DO conditions were reasonably favourable at that time and location. Thus, if an eel enters a deeper, offshore net during a downwelling phase it cannot escape and move to a shallower net in the event of a subsequent upwelling, likely explaining why eels were caught in nets which normally experience very low DO concentrations.

Using the slowest baroclinic wave speed ($c_1 = 0.30 \text{ m s}^{-1}$), the Rossby radius of deformation ($L_R = c_1/f$, where $f$ is the latitude-dependent Coriolis frequency) was 2500 m. The ratio of $L_R$ to the radius of the basin’s major axis was 4.2, allowing any weak rotational influence to be discounted for the present analysis (e.g. Gill 1982). Spectral analysis of the wind data (not shown) indicated a pronounced 24 h periodicity in wind speed. The strongest winds occurred in the afternoon, diminishing toward night (Fig. 4a), meaning afternoon wind energy may generate overnight internal seiche activity. In each of the focal periods presented, the most dramatic patterns of upwelling and downwelling were observed during night time hours (Figs. 3b & 4b) when many benthic fish, including eels, actively forage. Tidal forcing may also generate pycnocline oscillations and the influence of these motions on nearshore DO dynamics requires further investigation.

Disproportionately higher numbers of eels caught in shallower nets indicate that eels generally avoid the deep, low-DO zones. However live eels were retrieved from fyke nets that also contained dead eels (Fig. 2c; S2 catch, Table 2); these eels may have only entered the net shortly before nets were recovered or were able
to tolerate short periods of deoxygenation. Amongst teleosts, European eel have one of the highest tolerances to low DO, with a critical O\textsubscript{2} value (level below which a stable O\textsubscript{2} uptake cannot be maintained) of ~1 mg l\textsuperscript{–1} (Rogers et al. 2016). Other species however may not share the robustness of eel toward low-DO conditions, as evident in the absence of any other live species in the site C fyke net apart from nets 1 and 2 which contained crab, flounder and pollack. Overall it is noted that historically, eel mortalities amongst the site C catch are generally associated with nets further offshore than inshore, with deep offshore sites more likely to be exposed to deoxygenated water conditions during seiche activity (Table 2).

In a broader context, these findings show that wind-induced baroclinic motions in a stratified basin with deoxygenated bottom waters can dramatically influence DO conditions in oxygenated nearshore areas that are considered productive fish habitat. Similar episodic movements of seemingly stable, low-DO deep water masses by wind-induced seiching have been documented in very similar environments (Sanford et al. 1990, Chikita 2000, Reynolds-Fleming & Luettich 2004). Therefore, when assessing the spatial extent of hypoxic/anoxic ‘dead-zones’, a potential exposure zone at shallower depths, particularly around the boundaries where the oxycline meets basin slopes, should be considered. Deoxygenated deep waters may not only affect demersal and benthic fauna, but also nearshore communities inhabiting slopes and banks that are within upwelling limits. Fish movement and feeding may be affected by such upwelling events and sessile or slow-moving benthos may be most vulnerable to lateral intrusions of anoxic water transported upslope by internal waves. Further work is required to assess such biophysical interactions, with high-resolution acoustic tracking of fish in
affected areas in conjunction with hydrographical observations being one potentially informative method.

TABLES & FIGURES

Table 1. Schedule of fishery surveys S1 and S2 with measurement details taken during each survey. See Fig. 1 for location details

<table>
<thead>
<tr>
<th>Survey/measurement</th>
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<th>Depth (m)</th>
<th>Sampling interval (min)</th>
<th>Date</th>
<th>Time UTC (h)</th>
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<td>S1</td>
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<td></td>
<td></td>
<td>13–14 June</td>
<td>~15:00–10:00</td>
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<tr>
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<td></td>
<td>13 June</td>
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<td>DO sensor (JFE Advantech ARO-USB)</td>
<td>MR02</td>
<td>7.5</td>
<td>5</td>
<td>13–14 June</td>
<td>15:00–16:00</td>
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<tr>
<td>S2</td>
<td>C, X, Y, Z</td>
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<td></td>
<td>28–29 June</td>
<td>~15:00–10:00</td>
</tr>
<tr>
<td>DO transect</td>
<td>C</td>
<td></td>
<td></td>
<td>28 June</td>
<td>~15:30–16:15</td>
</tr>
<tr>
<td>Temperature/salinity (Sea-Bird Scientific SBE-37)</td>
<td>MR01</td>
<td>1, 3, 5, 7</td>
<td>5</td>
<td>27–02 July</td>
<td>15:00–14:00</td>
</tr>
<tr>
<td>Temperature/salinity (Sea-Bird Scientific SBE-37)</td>
<td>MR02</td>
<td>3, 7</td>
<td>5</td>
<td>27–02 July</td>
<td>15:00–14:00</td>
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### Table 2. Total eel catch per net during surveys S1 and S2 and total historical catch at site C. Number of dead eels per net indicated in parentheses. Net 1 is inshore and net 10 furthest offshore (see Fig. 2)

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<th>Site</th>
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<th>Net 3</th>
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<th>Net 6</th>
<th>Net 7</th>
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<td>(8)</td>
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Fig. 1. Lough Furnace (thick outline is the semi-enclosed main basin and thin outline the shallow tidal channel connecting to the ocean) showing fyke net (red lines) and measuring sites: automatic water quality monitoring station (AWQMS); MR01; and MR02 (see Table 1 for mooring instrumentation)
Fig. 2. (a) Dissolved oxygen (DO) transect at site C ('x' indicates profile locations); (b) average buoyancy frequency squared ($N^2$) profile for S1; (c) and (d) show the same for S2. Schematic illustration of fyke net chain in (a) and (c) with nets 1–10 numbered (recovery of live eels denoted by the subscript ‘o’, of dead eels by superscript ‘*’). Arrows indicate location of MR02.
Fig. 3. Survey S1 timeseries of (a) U (solid line) and V (dashed line) wind vector azimuths (i.e. positive values indicate wind blowing towards east and north, respectively); (b) dissolved oxygen (DO) measured at MR02. Black arrow in (a) denotes time of S1 DO profile (see Fig. 2a); (c) periodogram of DO during the focal period denoted by vertical dashed lines in (b). Red vertical dashed line in (c) indicates theoretical frequency (cycles per hour) of the fundamental mode internal seiche along the NW–SE axis during S1
Fig. 4. Survey S2 timeseries of (a) U (solid line) and V (dashed line) wind vector azimuths (i.e. positive values indicate wind blowing towards east and north, respectively) and (b) comparison of water density deviations from the daily mean value at 3 m depth at MR01 and MR02. Black arrow in (a) denotes time of S2 dissolved oxygen profile (Fig. 2c); (c) spectral density (black line) and 95% confidence intervals (red and green dashed lines) for the S2 water density timeseries at 3 m for MR01; (d) shows the same for MR02. Vertical dashed lines in (c) and (d) show fundamental mode internal seiche frequencies (cycles per hour) along the SW–NE axis (black) and E–W axis (red) of the main basin during S2

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Chapter 6. HIGH FREQUENCY MONITORING REVEALS FINE SCALE SPATIAL AND TEMPORAL DYNAMICS OF THE DEEP CHLOROPHYLL MAXIMUM OF A STRATIFIED COASTAL LAGOON


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ABSTRACT: Coastal lagoons are a dynamic habitat, with varying marine and freshwater inputs determining the presence and extent of stratification, and the physical and chemical environment of the epilimnion and hypolimnion. As a result, the biotic assemblages that thrive in such environments are a diverse mix of species, with wide ranges of tolerances. While annual succession and vertical distribution of phytoplankton assemblages in marine and freshwater ecosystems are
well documented, few data are available which describe the spatial and temporal variability of phytoplankton in coastal lagoons, even though these are a protected habitat under the European Union’s Habitat Directive. In this study, high frequency monitoring (HFM) of chlorophyll fluorescence (ChlF) using a vertical profiling sonde was used to describe the variation in algal biomass over six annual cycles and through the water column of Lough Furnace, a perennially stratified coastal lagoon on the west coast of Ireland. Spot sampling, and species enumeration of phytoplankton were used to confirm the patterns observed in the fluorescence data, which indicated a general pattern of increasing biomass starting in spring, and a deepening of the deep chlorophyll maximum (DCM) over the summer. Typical of a stratified system, the DCM was often situated below the surface mixed layer, in saline hypoxic water. The best predictors of daily maximum ChlF were the depth of the surface mixed layer and daily solar radiation. We conclude that HFM allows an unprecedented glimpse into the substantial variability and complexity of phytoplankton distributions, a key biotic variable.

INTRODUCTION

Coastal lagoons occur at the transitional zone between marine and freshwater ecosystems, and make up 13% of the world’s coastline (Nixon, 1982) and 5.3% of the European coastline (Kjerfve, 1994). Coastal lagoons can be defined as sea-water bodies situated at the coast, but separated from the sea by land spits or similar land features (UNSD, 2006), leading to restricted marine connectivity which distinguishes lagoons from estuaries. Semi-isolated from the adjacent coastal waters, lagoon ecosystems are characterized by a
natural exchange of water between land and sea (Barnes, 1980). This exchange of tidal water and freshwater inputs from rivers, rainfall and groundwater, results in a dynamic environment with extreme fluctuations in salinity, water volume, temperature and other chemical properties. The combination of these features make coastal lagoons highly variable habitat types that are difficult to define (Barnes, 1980; Kjerfve, 1994). This difficulty also creates complexities when trying to classify coastal lagoons into a unique habitat category for legislative purposes (Bamber, 2010; Tagliapietra and Ghirardini, 2006). A common generalisation is to define a lagoon as “open” (a significant intertidal area), “choked” (connected to the sea by a single or few narrow and shallow entrances) or “leaky” (multiple channels between the water body and the sea) as these terms give some indication of the extent of their hydrodynamic exchange properties with the adjacent open sea (Newton et al., 2014). Although common on the microtidal coasts of the Mediterranean, Baltic, and Black sea, coastal lagoons are particularly rare on the macrotidal North Atlantic seaboard (Beer and Joyce, 2013; JNCC, 1996; Newton et al., 2014). Compared to estuaries and other marine and freshwater habitats, there are also large gaps in scientific knowledge about lagoon ecology, and again this is particularly so for the North Atlantic fringe (Beer and Joyce, 2013). The vulnerability of coastal lagoons to climatic and anthropogenic impacts has led to their classification as an Annex I priority habitat (“in danger of disappearance”) under the EU Habitats Directive (EU, 1992). However, by their nature, coastal lagoons can change rapidly in response to sea-level rise (Buzer, 1981; Cassina et al., 2013b), or changes in salinity regime (Cassina et al., 2013a; Obrador et al., 2008; Obrador and Pretus, 2008) as a result of local actions such as dredging or sluice gate operations.
protection of these habitats therefore represents a unique challenge in terms of interpretation of conservation needs – what habitat and ecological features are we trying to preserve?

Phytoplankton, aquatic macrophytes and phytobenthos are the primary producers in coastal lagoons, with phytoplankton being of greater importance in deeper lagoons where light limitation restricts the growth of benthic organisms (Knoppers, 1994). Spatial and temporal patterns in the phytoplankton of Mediterranean (e.g. Bernardi Aubry et al., 2013), Baltic (Pilkaityte and Razinkovas, 2007), and Adriatic (Sfriso et al., 2014) microtidal lagoons have been relatively well studied when compared to North Atlantic lagoons, where research to date has largely focused on invertebrate and macrophyte assemblages (Bamber et al., 1992; Barnes et al., 2008; Barnes, 1987; Healy, 1997; Joyce et al., 2005), with relatively few studies including phytoplankton (Chapman et al., 1997; Crawford et al., 1979; Pybus and Pybus, 1980). In this context, the perceived status of coastal lagoons as a “neglected habitat” (Barnes, 1980), due in part to the lack of studies into the processes which influence the structure and composition of lagoonal communities (Barnes, 1991; Beer and Joyce, 2013), appears to be particularly relevant to phytoplankton. There has however been more recent focus on the phytoplankton of coastal lagoons in Britain and Ireland (Durante et al., 2013; Roden and Oliver, 2010), due to the requirement under the EU Water Framework Directive (EC, 2000) to monitor the ecological status of transitional waters using phytoplankton as a quality element (Murphy et al., 2002). A survey of Irish coastal lagoons (Roden and Oliver, 2010), which examined the phytoplankton from 21 sites, is among the first databases of its kind for the phytoplankton of Irish lagoons, establishing provisional reference conditions for these sites.
Coastal lagoon habitats can support a diverse phytoplankton flora composed of co-occurring marine and freshwater species, as well as those with a salinity tolerance that allow them to bloom in this dynamic brackish environment (Caljon, 1984; Reynolds et al., 2006; Willén, 1962). In contrast to benthic organisms, which show an impoverished diversity in brackish environments (Remane and Schlieper, 1971), records show plankton to be especially species rich (Reyes et al., 2008; Telesh et al., 2011). High phytoplankton diversity in brackish waters is attributed to phytoplankton adaptations, namely rapid reproduction rate, motility, and the ability to enter resting stages periodically during unfavourable conditions, which allow them to exist in an environment of fluctuating salinity levels (Telesh et al., 2013). Colonization of lagoons by marine phytoplankton species carried in with tidal flow, as well as freshwater species carried in riverine inputs are likely to augment species richness (Bode et al., 2017). Where there are large and sustained salinity fluctuations, a lagoon’s phytoplankton may alternate between marine, and freshwater dominated phases (e.g. Comin and Valiela, 1993; Rojo and Miracle, 1989).

The position of coastal lagoons at the land-sea interface means the seasonal development of phytoplankton is subject to multiple temporal influences including tidal phase, seasonal freshwater inputs and meteorological conditions, as well as anthropogenic perturbations of these factors (Duarte et al., 2009). Nevertheless, a reoccurring seasonal pattern may be influenced to a greater degree by the annual climate cycle (Cloern and Jassby, 2008). Spring diatom blooms associated with increasing solar radiation and nutrient availability, occur widely in temperate coastal waters (Carstensen et al., 2015; Hitchcock and Smayda, 1977), and have been commonly
observed in coastal lagoons (e.g. Bode et al., 2017). Dinoflagellate blooms have also been reported in coastal lagoon (e.g. Giacobbe et al., 1996; Gilabert, 2001; Macedo et al., 2001). The onset of these blooms has been attributed to a variety of causes, including periods of stable surface water temperature and weak winds (Laanaia et al., 2013), anthropogenic eutrophication (Sorokin et al., 1996), increased inputs of freshwater following rainfall (Macedo et al., 2001), and the seasonal germination of overwintering resting stages (Voltolina, 1993). Cyanobacterial blooms are documented from lagoons which are highly impacted by cultural eutrophication (e.g. Serrano et al., 2004). Another characteristic feature of the phytoplankton of near-shore and lagoon habitats are outbursts of rapidly growing nanoplanktonic flagellates (Reynolds et al., 2006).

Deep chlorophyll maxima (DCM) occur in a variety of aquatic environments where their development is often associated with water column stratification (e.g. Cullen, 2015; Sharples et al., 2001). In brackish waters where salinity induced stratification is common, peaks in phytoplankton biomass are frequently found within, or in close association with, physical and chemical gradients bounding fresh and saline water-masses. Examples are documented from estuaries (Falco et al., 2006; O’Boyle and McDermott, 2014), fjords (Menden-Deuer, 2008), brackish lakes (Laybourn-Parry and Bell, 2014) and a small number of coastal lagoons (Borrego y and García-Gil, 1994; Miracle et al., 1992; Moyà et al., 1987). The underlying mechanism behind DCM formation is generally accepted to be the growth of phytoplankton at a depth where two vertically opposing resource gradients (for example, light supply from the surface and nutrient supply from nutrient-rich deep waters) favour in-situ growth in a stratified region of the water column that is sheltered.
from turbulent mixing (Sharples et al. 2001; Mellard et al., 2011; Williams et al. 2013). However whilst the primary mechanism for DCM formation is well-documented, the precise vertical location within the water column and specific species composition are attributed to a variety of phenomena, including sinking phytoplankton reaching neutral buoyancy (Piwosz et al., 2008), motile species actively retaining a favourable position in the stable pycnocline region (Ross and Sharples, 2008), behavioural aggregation of flagellates (Galvez et al., 1988), grazing by zooplankton (Coon et al., 1987) and the aggregation of mixotrophic ciliates (Pérez et al., 2002) which are a prey item for some dinoflagellates (Velo-Suárez et al., 2014). While some DCMs have been attributed to elevated cellular chlorophyll levels at depth (Fennel and Boss, 2003; Mikaelyan and Belyaeva, 1995), the majority are found to consist of an increase in algal biomass (Camacho, 2006; Longhi and Beisner, 2009). Along with these biological influences, turbulent mixing in the water column has been found to have a strong impact on the spatio-temporal DCM dynamics (Abbott et al., 1984; Alexander and Imberger, 2009), with chlorophyll maxima being weak and diffuse where there is high turbulent diffusion, and becoming deeper and more stable with increasing water column stability. Turbulence has been hypothesised to determine the thickness of the DCM, which may form a thin layer during stable conditions with a sharp, abrupt pycnocline region and thicken during turbulent conditions, particularly in the presence of a weaker, more continuous density gradient (Abbott et al., 1984; Durham and Stocker, 2012; Fee, 1976)).

While the protection of coastal lagoon habitats is warranted given their unique nature, there are significant gaps in our current
knowledge of what constitutes “normal” temporal and spatial variation in phytoplankton, a key biotic element. Beer and Joyce (2013) recommend targeted surveys and monitoring to determine the North Atlantic lagoon resource base more accurately and better establish its baseline ecology. A vital tool in detecting the impacts of environmental change and anthropogenic disturbance are long-term data sets (Dodds et al., 2012), which until recently have been composed of spot samples. However, this infrequent sampling method may not capture the detail of a rapidly changing phytoplankton assemblage (Pomati et al., 2011), particularly one influenced by drivers such as upstream floods, tidal patterns and varying stratification dynamics. Recent developments in the use of high frequency chlorophyll sensors, in combination with automated profiling winches, now allow the investigation and characterisation of both the hydrological conditions (Kelly et al., 2018) and the phytoplankton variability at high frequency (Brentrup et al., 2016; Doubell et al., 2014). Profiling winches are a relatively new technology which requires a high level of maintenance. As a result, consistent multi-annual operation is rare. In this paper, we report on data from a protected stratified coastal lagoon on the Atlantic coast of Ireland, where a profiling multiparameter sonde has been successfully maintained for six consecutive years. The aims of this paper were to describe the seasonal and spatial (vertical) variability in algal biomass using chlorophyll fluorescence as a proxy, to ascertain the presence and extent of DCM and finally, to determine the main environmental drivers controlling the development of algal biomass, and the depth of the DCM. In addressing these aims, we hope to ascertain the variability in this key biotic element, and hence
inform efforts to preserve and protect the unique nature of coastal lagoons.

METHODS

Site description
Lough Furnace is located at the southern end of the Burrishoole catchment (N 53°55′22″, W9°34′20″) at the north-eastern corner of Clew Bay (northwest Ireland) (Fig. 1). It is a glacially excavated basin with a permanent, constricted connection to open coastal waters through the Burrishoole channel (Kelly et al., 2018). It is best described as a “choked” coastal lagoon (Newton et al., 2014), as it is only connected to the sea by one narrow entrance. The upper part of the catchment is considered to be one of the best examples of an active blanket bog in Ireland (NPWS, 2017), which represents 71% of the catchment today whilst forest plantations occupy 23% of the catchment (Dalton et al., 2014). Furnace is part of the Clew Bay Complex Special Area of Conservation (SAC site code 1482) and is described as a good example of a deep, stratified coastal lagoon in a very natural state (NPWS, 2011). It has a surface area of 141 ha, a maximum depth of 21 m, a diameter of 1850 m, and it is approximately 800 m wide on average. It receives highly coloured river inflows (brown humic substances from the peatland catchment) (52 – 112 mg l⁻¹ PtCo; Marine Institute, unpublished data) from the freshwater lakes upstream, that strongly limit the photic zone depth (average secchi depth over the time period = 1.75m). The length and shallowness of the connecting channel greatly restricts the magnitude of northward flowing tidal water from the Atlantic ocean (via Clew Bay), which coupled with the buoyancy input from freshwater runoff, allows strong vertical saline stratification to
The exceptionally strong halocline and restricted lagoon-ocean exchange is conducive to the development of stagnant, deoxygenated conditions in the deep basin water, with large-scale deep-water renewals by dense tidal inflows only occurring every 2.25 years on average (Kelly et al., 2018). Palaeoenvironmental reconstructions suggest that meromixis first formed as a result of sea level rise prior to ca.4000 BP. (Cassina et al., 2013b)

**High frequency monitoring**

The water column in Furnace was monitored with an Automatic Water Quality Monitoring Station (AWQMS) (Lakeland Instrumentation: www.lakelandinstrumentation.co.uk) (Fig. 1). The AWQMS was stationed in the middle of the main Furnace basin where water depth is at least 14 metres. The station comprised of a Datasonde DSX5 (Hydrolab OTT) attached to a winch, which profiled the water column 4 times daily (0000, 0600, 1200, 1800 hours) from 0.6 m to 13 m depth. Each downward profile took circa 90 minutes. Data were recorded at two minute intervals by a Campbell Scientific CR1000 datalogger, with an average of 0.17 m between measurement intervals (depending on lake level). The datasonde was fitted with sensors measuring temperature, dissolved oxygen, salinity, conductivity and chlorophyll fluorescence (ChlF). Data from the AWQMS were collated for the period 1st Jan 2009 to 30th October 2014. Chlorophyll fluorescence (in RFU - relative fluorescence units) was extracted from the midnight profile for each calendar day. Midnight profiles were used to avoid possible
misinterpretation of RFU as a result of photo-inhibition during sunlight hours (Scofield et al., 2017). Out of a possible 2191 calendar days in the sampling period, 1659 midnight profiles were included in the dataset (de Eyto et al., 2018). Equipment malfunction was the primary reason for discarding profiles. For each profile, the maximum ChlF (maxChlF) was determined, and the depth (m) from the surface at which that maximum occurred (depth). Light attenuation (Secchi depth) and nutrients were measured approximately monthly. Total Phosphorus was measured using a modified Molybdate – ascorbic acid method following digestion of the unfiltered sample with persulphate and sulphuric acid in an autoclave at 121°C for 30 minutes. Total Nitrogen was measured using an automated colorimetric method following digestion of the unfiltered sample with potassium persulphate and boric acid in an alkaline solution in an autoclave at 121°C for 30 minutes. High frequency data characterising driving variables (representing water column stratification, water column conditions, meteorological conditions, freshwater influence, marine influence) were collated from various sources in the Burrishoole catchment (de Eyto et al., 2018). Full water column profiles of temperature and salinity were obtained from the automated winch profiler detailed above (only those profiles recording to a depth of 7m or greater were used) and water density profiles were calculated following Millero and Poisson (1981). $Z_{mix}$, the depth of the bottom of the surface mixed layer (m), was determined as the shallowest depth with a vertical density gradient higher than 2 kg m$^{-3}$ m$^{-1}$, following procedures in Read et al (2011). The stability of the stratification around the pycnocline was expressed as the squared Brunt–Väisälä frequency, $N^2$ (rad s$^{-1}$) (Thorpe, 2007). Mean daily $Z_{mix}$ was used to differentiate between the
epilimnion and hypolimnion, and mean dissolved oxygen concentration, salinity, ChlF and temperature were estimated for each of those layers from data collected by the profiling Datasonde. Daily meteorological data (global solar radiation, wind speed, air temperature) were collated from a Met Éireann automatic weather station on the shore of Lough Furnace (Fig. 1). Sunshine hours and daily cumulative rainfall were taken from a manual weather station operated by the Marine Institute (Fig. 1). Water level in Lough Feeagh was taken from an OTT thalimedes (www.ott.com, OTT Hydromet, Kempten, Germany) installed on the southern shore of Feeagh (Fig. 1). The water level in Feeagh determines the primary freshwater inflow into Furnace through two inflows; the Mill Race (200 m long) and the Salmon Leap (100 m long), each of which have an elevation drop of 10 m (Fig. 1). Feeagh water level was therefore used as a proxy indicator of freshwater inflow. In order to determine the potential tidal influence on the main basin in Furnace, the tidal signal was extracted from a water level recorder (Orpheus mini water level recorder, www.ott.com, OTT Hydromet, Kempten, Germany) on the northern shore of Furnace. The tidal signal was extracted using the MATLAB T_TIDE software package (Pawlowicz et al., 2002) and this was adjusted to the mean level at Furnace using a 30-day running mean of the Furnace water level. The daily maximum tidal range (Max range), maximum tidal height (Max tide) and minimum tidal height (Min tide) were then extracted from this data set for use in the current analysis.

Veriﬁcation of the chlorophyll fluorescence sensor signals

Two methods were used to conﬁrm that the chlorophyll sensor was representative of phytoplankton biomass. Monthly epilimnetic water
samples were taken using a 1 metre tube. Two litres of each sample were filtered (Whatman glass microfiber filter GF/F 0.45 µm pore size) and measured for chlorophyll a using standard ethanol extraction (Standing Committee of Analysts, 1983). In addition, 500 ml of these monthly samples was preserved with Lugol’s iodine solution (Merck with a composition of I₂ = 3.2 g L⁻¹ and KI = 6.8 g L⁻¹) and stored in the dark. Monthly phytoplankton biomass from 2010 and 2013 were enumerated and identified with an inverted microscope using a method adapted from Utermöhl (1958). Identification was carried out to the highest taxonomic level possible using a mix of marine and freshwater keys (Dodge, 1982; Hoppenrath et al., 2009; John et al., 2002; McDermott and Raine, 2006; Sykes, 1981; Tomas, 1993, 1997).

Counts were carried out at a magnification of x200 or x400. Phytoplankton biomass was calculated by multiplying the number of cells of a given species by its average cell volume (calculated using digital photographs and the direct measurement of the linear dimensions) (Hillebrand et al., 1999). In addition to temporal verification of the chlorophyll sensor, spatial verification was also carried out by collecting water from 6 depths (surface, 2,4,6,8,10 m) using a 5 L Van Dorn sampler. These water samples were analysed for phytoplankton biomass using both the ethanol extraction and inverted microscope methods described above. This was done on two occasions in 2012 (April 18th and May 30th). The results from both these analyses (chl a extraction and phytoplankton biomass) were matched by date and water depth to the readings from the fluorometer.
Chapter 6

Statistical analysis

Generalised additive mixed modelling (GAMM) with a cubic smoothing regression spline was used to explore the main drivers controlling chlorophyll fluorescence (~ algal biomass) over the study period. The response variable was the maximum midnight ChlF in the water column (maxChlF) which was log transformed prior to the analysis. Driving (explanatory variables) included are described above in section 2.2. Cross validation was used to determine the main drivers of maxChlF using the mgcv package (Wood, 2011) in R (version 3.4.3, R Core Team, 2017). There was a high degree of temporal autocorrelation in the datasets, which could not be accounted for using a correlation structure in a model with daily data, and therefore all data were aggregated to five-day means. Since collinearity between independent variables can be an issue in GAMs (Zuur et al., 2009), variables were not included in the same model where they breached a conservative threshold of a Pearson's r <0.4 (Dormann et al., 2012). Alternate models were tested where there were strong correlations between explanatory variables. The optimum model was selected following the protocol described in Zuur et al. (2009). The gam.check function in mgcv (Zuur et al., 2009) was used to check for any breach of the assumption of equal variance. Since this assumption was breached in the final model, it was accounted for by including an exponential variance structure. An auto-correlation function plot of the residuals of this model indicated a breach of the assumption of independence which was accounted for by inclusion of an autocorrelation-moving average (corARMA) correlation structure. The optimum values of p and q in this structure were selected based on the Akaike Information Criterion (AIC) (Sakamoto et al., 1986).
General additive modelling was also used to investigate the driving variables of the depth of the DCM, but was unsuccessful – i.e. no significant relationships were found. We therefore used an alternative statistical method to look for thresholds in the driving variables that may account for the position of the DCM in the water column. Two complementary unbiased recursive partitioning methods, conditional inference forests (cforest: CIF) and regression conditional inference tree (ctree: CIT) (Hothorn et al., 2006; Strobl et al., 2007, 2008) were run using the party (v.1.3-0) package in R (version 3.4.3, R Core Team, 2017). For more details regarding the advantages of recursive partitioning and random forests over classical regression methods (linear and logistic regression) see Strobl et al. (2009). Firstly, the CIF method was used to rank the importance of the driving variables, measuring the impact of each driver variable individually, as well as in multivariate interactions with other variables. We set the ntree parameter in party: cforest control function to 2000 as compromise between accuracy and computational effort. The number of randomly pre-selected variables was set to 3 (Strobl et al., 2008). After this, the CIT method was used to build a single tree representative of the statistically significant driving variables of the depth of the DCM. The CIT method uses unbiased variable selection through conditional permutation tests to select the driver variable with the most significant association (smallest $p$-value) with the response variable (depth of the DCM). The CIT method terminates once the global null hypothesis of independence can no longer be rejected or no explanatory variables remains. Treating the $p$-value as hyperparameter (calculated either by exact calculation, Monte Carlo or asymptotic approximation) can be computational expensive, especially for large datasets, so we set
an exact value of 0.99 ($p < 0.001$) for the `mincriterion` parameter in `party:ctree` package. All other method parameters were left to their default values. The well-known statistical theory embedded in this method ensures that the right-sized tree is grown without additional pruning, cross-validation and independent of overfitting (Hothorn et al., 2006). The output of the CIT method is an easily interpreted hierarchical tree-structured model, in which the tree root variable has strongest association with the response variable, and then less significant driving variables are arranged with binary splits lower in the tree, each representing a certain partition of the dataset under the given conditional control statements in that particular tree branch. For both the CIF and CIT analyses, statistical metrics of RMSE and $R^2$ metric are calculated to estimate model performance.

**RESULTS**

Data from the AWQMS confirmed that, for the years between 2009 and 2014, Lough Furnace was permanently stratified, with a $Z_{\text{mix}}$ situated at an average depth of 2.12 m (range: 0.7 – 6.4 m) (Fig. 2). The epilimnion was predominantly freshwater (mean salinity = 4.06, range: 0.02 – 22.12) and was well oxygenated throughout the study period (mean dissolved oxygen = 10.63 mg l$^{-1}$, range: 6.86 - 14.23 mg l$^{-1}$). In contrast, the hypolimnion was saline (mean salinity = 19.25, range: 15.42 – 24.09) and hypoxic conditions prevailed below $Z_{\text{mix}}$ (mean dissolved oxygen = 2.34 mg l$^{-1}$, range: 0.08 - 7.57 mg l$^{-1}$). Average Secchi depth over the study period was 1.8 m (range 1.1 – 2.7 m). Using the correction of Koenings and Edmondson (1991) ($K_d=2.7/\text{Secchi depth}$), these Secchi depths indicate that the average $K_d$ was 1.6 m$^{-1}$ (range: 1.0 – 2.5 m$^{-1}$) over the time period. This corresponds to 1% Par ($= \ln100/K_d$ (Leach et al., n.d.)) situated at an
average depth of 3 m (range: 1.9 – 4.6 m). The average total phosphorus (TP$_\text{conc}$tration over the study period was 8 µg TP l$^{-1}$ (range 4-17 µg TP l$^{-1}$), while total nitrogen averaged 0.23 mg TN l$^{-1}$ (range 0.02-0.47 mg TN l$^{-1}$).

A consistent annual pattern in ChlF was apparent across all years, with values increasing from a winter baseline of <14 RFU in mid-February and dropping back to baseline values in the middle of November (Fig. 3). ChlF had a mean of 20.35 rfu (± s.d. 28.65 rfu) for the whole time series, and ranged between 3.89 and 266.66 rfu. In all six years, maxChlF generally occurred below $Z_{\text{mix}}$ and high values of ChlF were often recorded relatively deep in the hypolimnion, 3 to 5 metres below the surface. The average depth of the DCM over the entire time series was 4.1 m (range 0.5 - 13 m). Missing data in 2009 meant that the annual succession pattern was not captured in that year. ChlF recorded in 2011 and 2012 was relatively low and quite patchy throughout the year. In contrast, a strong persistent ChlF signal was recorded in 2010, 2013 and 2014 (Fig. 4). In these three years, a dynamic DCM was apparent, developing near the surface in February, and deepening as the spring and summer progressed through to September. Maximum ChlF was often recorded just below the depth of maximum water stability. In both 2013 and 2014, ChlF was apparent throughout the water column for a number of days in autumn. In both years, this phenomenon occurred when the freshwater epilimnion was very shallow, and $Z_{\text{mix}}$ was close to the surface of the lake.

The overall correlation between ChlF and ethanol extracted Chl-$a$ was 0.53 (Pearson correlation, p<0.001, n=83) (Fig. 5). This included both epilimnetic samples collected approximately monthly between 2009 and 2014, and those collected vertically through the
water column in April and May 2011. ChlF was also correlated with total biomass of phytoplankton ($\log_{10}$ transformed $\mu m^3$ ml$^{-1}$) counted using an inverted microscope (Pearson correlation = 0.37, p<0.05, n=34).

The phytoplankton of Lough Furnace comprised a mix of freshwater and marine species from the following phyla: Bacillariophyta, Chlorophyta, Cryptophyta, Dinophyta, Haptophyta and Euglenophyta, (Fig. 6). Very small amounts of Chrysophyta (two individuals of a Dinobyron sp.) were recorded in July 2013 but are not included in Fig. 6 for clarity. Euglenophyta were often recorded in 2010, but not at all in 2013. Haptophyta were recorded in 2013 (Pavlova sp. and Pseudopedinella sp), but not at all in 2010. We attribute these differences to an issue with preservation of samples and/or familiarity of the scientist doing the counts with certain groups. Changes in biomass and species composition through the years 2010 and 2013 (the years for which we have detailed phytoplankton counts) showed a seasonal pattern consistent with the ChlF signal, initially progressing from a winter biomass minimum to a ‘spring-bloom’ phase of diatom predominance between March and May. This bloom was a little later in 2013, in comparison to 2010. Freshwater diatoms Asterionella formosa, Aulacoseira spp. and Diatoma sp. were frequent throughout the year, and formed the greater part of the spring bloom maximum. The spring diatom bloom was dominated by freshwater taxa, but the marine centric diatoms Thalassiosira spp. and Skeletonema spp. also occurred. Although chlorophytes never attained great biomass in Furnace, the species Monoraphidium contortum and Closterium acutum occurred in all but one monthly sample. The cryptophyte nanoflagellate Chroomonas acuta was present in every sample. Samples from spring and early
summer showed the greatest range of marine species in Lough Furnace. Of these, the most abundant were the dinoflagellate *Heterocapsa triquetra*, and a number of nanoplanktonic flagellates, including the cryptophyte *Teleaulax acuta*, as well as the Haptophytes *Pavlova* sp. and *Pseudopedinella* sp. The dinoflagellates *Prorocentrum micans* and *Dinophysis* sp occur also. *Oxyrrhis marina* was recorded in April, June, July and October 2010 samples. A bloom of *Prorocentrum minimum* in Lough Furnace was evident in the surface samples enumerated from August and September 2013. Bloom conditions ceased by the end of October, and *P. minimum* was absent by November. As the fluorometer indicated biomass of phytoplankton throughout the water column in October 2013 and 2014, archived samples from 2014 were examined to ascertain the source of this chlorophyll fluorescence. As with 2013, the dominant species in August and September 2014 was *P. minimum*, and we assume that this species contributed significantly to the chlorophyll signal picked up by our sensor at all depths during those short periods in the autumn of 2013 and 2014.

The vertical distribution of phytoplankton species was examined in April and May 2012 (Fig. 7). Similar to the surface samples, the main components of these phytoplankton assemblages were Bacilliarophytes and Dinophytes. The microscope counts confirmed that there was significant phytoplankton biomass in April and May 2012 below the epilimnion, which is where the fluorometer also signalled maximum ChlF. In April, the main biomass at depth comprised the dinoflagellates *Heterocapsa triquetra* and *Oxyrrhis marina*, both of which actually occurred at all depths, but peaked at 4 m.
GAMM analysis based on five day mean values indicated that the main drivers of maxChlF were the depth of the surface mixed layer ($Z_{mix}$) and average daily solar radiation, and the optimum model explained 32% of the deviance in maxChlF (Table 1). There was a generally negative relationship between maxChlF and $Z_{mix}$ - that is maxChlF was highest when the epilimnion was shallow, and decreased as $Z_{mix}$ got deeper. MaxChlF increased with higher solar radiation, and was lowest in the winter months when days were short (Fig. 7). We note that $Z_{mix}$ was correlated with epilimnetic temperature, and a model including epilimnetic temperature on its own explained nearly as much variation as the optimum model (28% of deviance) The analysis also highlighted the fact that many of the potential explanatory variables were significantly correlated (supplemental information), and while $Z_{mix}$ and solar radiation were the best numerical predictors of maxChlF, these two variables may act as proxies for other explanatory variables such as the tidal influence, the amount of freshwater input from the upper catchment, epilimnetic physicochemical conditions and the general seasonal weather patterns for this geographic area. In particular, $Z_{mix}$ was highly correlated with the water level in Lough Feeagh, which determines the amount of freshwater flowing into Lough Furnace.

According to the variable importance chart produced by the CIF analysis, epilimnetic water temperature and epilimnetic salinity were the two top highest rated driving variables of the depth of the DCM (RMSE = 1.13, $R^2$ (adj) = 0.25). The optimal CIT also included epilimnetic water temperature and epilimnetic salinity, in addition to $Z_{mix}$. (Fig. 8, RMSE = 1.34, $R^2$ (adj) = 0.21). The CIT indicates that the deepest DCMs occurred in warmer months when the epilimnetic water temperature exceeded 13.92 °C ($n = 295$, mean depth = 2.76),
but also when the epilimnion was a little more saline (n = 147, mean depth = 3.92). This branch of the tree contains almost 70% (449/663) of days in the dataset and comprises measurements taken between May and October of each year. The deepest DCMs during these summer and autumn months (right hand node of Fig. 8) were associated with periods of low freshwater inflow, and greater intrusion of tidal water into the main basin. This increased the salinity throughout the water column, including the epilimnion (as indicated by increased epilimnetic salinity), and during these periods, the DCM was often well below Z_{mix}. When the epilimnion was cooler (30% of the dataset), deeper DCMs tended to occur when Z_{mix} was shallow (i.e. less than 2.14 m).

**DISCUSSION**

Our findings show that an automatic, high frequency chlorophyll fluorescence sensor can provide unprecedented insight into the interannual and spatial dynamics of phytoplankton in a coastal lagoon, systems that are, by their nature, generally more dynamic than the upstream and downstream habitats which they bridge. Owing to their fast generation time, phytoplankton can be highly sensitive to environmental change, responding through changes in taxonomic composition, structure, and seasonal dynamics (Winder and Sommer, 2012). We would therefore expect that lagoon phytoplankton would respond to both freshwater and tidal influences, as well as vary seasonally as predicted by the PEG model for freshwater systems –i.e. display a distinct spring bloom, followed by highest phytoplankton biomass in mid-summer (Brentrup et al., 2016; De Senerpont Domis et al., 2013; Sommer et al., 1986). Our results confirmed this expectation, with ChlF increasing as spring
progresses to summer. The GAMM indicated that either solar radiation or water temperature, two variables which co-vary, could adequately describe the seasonal increase and decrease of phytoplankton biomass (as indicated by maxChlF). However, we also found that the inclusion of $Z_{mix}$, (the depth of the freshwater epilimnion) increased the descriptive power of the model, and that as $Z_{mix}$ increased, maxChlF decreased. $Z_{mix}$ is primarily determined by the amount of freshwater flowing into Furnace from upstream Lough Feeagh, and is a reflection of rainfall in the upper catchment in the preceding days. As high rainfall events are common in this catchment, it is likely that freshwater inflow leads to either a wash out of phytoplankton to sea, or alternatively a dilution of the standing stock of algal biomass in the epilimnion. Either alternative explanation could lead to a reduced ChlF signal in the lagoon. Dilution is a possibility if the inflowing water from upstream Lough Feeagh contains less phytoplankton than that of Lough Furnace. This is the case throughout the year, but particularly in mid-summer, when the ethanol extracted Chl a in Furnace can reach 5-6 $\mu$g l$^{-1}$, while that of Lough Feeagh is rarely greater than 2 $\mu$g l$^{-1}$ (de Eyto et al., 2016). As the inclusion of both variables (solar radiation and $Z_{mix}$) better explain ChlF than solar radiation alone, we conclude that increased freshwater inflow into the lake decreases algal biomass, irrespective of the season.

The high density of phytoplankton in the hypolimnion over 6 years confirms that at certain times of the year, the phytoplankton assemblage in this lagoon thrives in the dark, hypoxic environment of the hypolimnion. While there are many reports of phytoplankton thriving below oxyclines in freshwater lakes (reviewed in Gervais et al., 2003), it is hard to find literature describing this phenomenon in
coastal lagoons, where there is the added dimension of salinity. Both
top down and bottom up explanations for the occurrence of DCM’s
in this habitat are both likely, as are physical processes. A top down
driver for the positioning of the DCM might include reduced
grazing, or avoidance of zooplankton predation. Monthly
zooplankton samples taken with a vertical haul through the top 8
metres of Lough Furnace comprised a mix of marine, brackish and
freshwater copepods (particularly in the summer months), as well as
a species rich assemblage of rotifers (McKenna, 2013). However,
these samples encompassed both the hypo- and epilimnia and so we
cannot be conclusive about where, in the water column, predation
pressure might be greatest. This will be a fruitful line of enquiry for
future studies.

A physical driver of this observed pattern of hypolimnetic
phytoplankton abundance is likely the difference in turbulent flow
between the epilimnion, comprising a fast flowing seaward
freshwater layer (with an average freshwater residence time of ~4
days) and the more stable saline hypolimnion, which generally
experiences weak tidal currents and long residence times (Kelly et al
2018). Buoyancy frequency profiles indicated that an extremely large
density jump occurs abruptly over a very thin depth interval at the
base of the freshwater epilimnion (i.e. $Z_{mix}$ depth) but below this
depth a more continuous region of saline stratification exists, often
several metres thick and frequently occupied by the DCM (yellow-
coloured pycnocline region in Fig. 4). This region of stratification,
despite experiencing lower light availability than further up in the
water column, appears to function as a stable shelf for
phytoplankton, where they avoid advection out of the lagoon by
surface outflow and may be sheltered from the intense shear that is
anticipated to regularly occur directly at the density interface between the fresh and saline layer, as a result of tidal straining and wind entrainment (e.g. (Simpson et al., 1990). Our results support the occurrence of this bottom up control by physical drivers, as the deeper DCM were associated with time periods in summer and autumn when freshwater inflow was low, and the epilimnion was shallow, warm and saline. It is likely in these conditions, that the hypolimnion offers a more stable environment for tolerant species to thrive.

The fine temporal resolution of the fluorometer data was particularly useful to capture short lived blooms that may have been missed with monthly, or even fortnightly manual sampling. In both 2013 and 2014, blooms of *Prorocentrum minimum*, which lasted only a couple of days, were captured throughout the water column by the fluorometer. Microscope counts of the samples taken close to these dates confirmed a high density of *P. minimum*, reaching a peak of 570 individuals per ml in September 2013. Although *P. minimum* has a wide geographical distribution, blooms generally occur in coastal and inshore areas that are affected by fresh water and/or anthropogenic inputs. Some clones of this species have been reported to produce toxic blooms, but *P. minimum* is not considered to be persistently toxic (Macedo et al., 2001). In Portugal, *P. minimum* blooms have been reported in the Óbidos Lagoon after heavy rainfall (Silva, 1985). However, the occurrence of these whole column phytoplankton blooms in Furnace coincided with years when an unusually low freshwater input into (and hence out of) the inner basin was accompanied by large spring tides (and potentially, variations in coastal water density), resulting in a dynamic renewal of the stagnant, anoxic deep water (Kelly et al 2018). Therefore, the
presence of ChlF (probably *P. minimum*) through the water column in 2013 and 2014 was likely the result of a bulk advection of marine phytoplankton from the adjacent coastal waters by larger than usual tidal inflows which may have seeded the subsequent bloom. Phytoplankton blooms were found to have occurred following a deep-water renewal by tidal intrusion in a Scottish fjord (Watt et al. 1998) and more generally, the impact of deep-water renewal and the release of nutrients accumulated in stagnant anoxic bottom waters can fuel profound changes in biogeochemical processes (e.g. Lehmann et al. 2015). Weekly phytoplankton sampling of Clew Bay is carried out as part of the Harmful Algal Bloom (HABS) program run by the Marine Institute (www.marine.ie/Home/site-area/dataservices/interactive-maps/weekly-hab-bulletin), and *P. minimum* was recorded in the north of Clew Bay during August and September of both years. These observations add some weight of evidence to the idea that the blooms in Furnace of this species originated in coastal waters, and were transported into the lough with high tides. More generally, the results from the CIT analysis on the depth of the DCMs indicated that deeper DCMs coincided with time periods when low fresh water input allowed larger than normal intrusion of tidal waters (as indicated by higher epilimnetic salinity). The data presented here do not allow us to conclude whether this resulted from migration of coastal phytoplankton into the hypolimnion of Furnace, or active migration of resident phytoplankton to greater depths. Combining the fluorometer data with high frequency sampling of the estuary and incoming tide would confirm which explanation is more plausible.

A severe limitation of this study is the lack of high frequency nutrient data which we presume accounts for a proportion of the
variation in ChlF. Bottom up control of phytoplankton biomass by nutrient availability has been demonstrated around the coast of Ireland, with reductions in phosphorus input resulting in decreases in chlorophyll a concentrations in several estuaries (Ní Longphuirt et al., 2016), and we presume that the spring bloom of diatoms is controlled to a large extent by nutrient availability (including micronutrients such as silica). Total phosphorus measured in Loughs Feeagh and Furnace during the study period indicate that both systems are oligotrophic (average of 7.5 and 8 µg TP l\(^{-1}\) respectively), while nutrient levels measured in Clew Bay by the Irish EPA are also relatively low (supplemental information). Average values of PO\(_4\)-P, NH\(_3\)-N and TON were 16 µg l\(^{-1}\), 0.04 mg l\(^{-1}\), and 0.07 mg l\(^{-1}\) respectively in the main tidal inflow into Lough Furnace, measured in the summer months from 2009 to 2014. The work described in the current study indicates that targeted sampling of nutrients flowing into and out of Lough Furnace at crucial times of the year will be required to ascertain the role of nutrients in controlling the development of algal biomass, particularly at depth. Sampling during spring tides and when the epilimnion is shallow would be particularly informative.

However, it is of note that nutrients have been found to play a secondary role in explaining phytoplankton biomass variability in other coastal lagoons, where physical forcing such as riverine flow and wind-induced turbulence are more important (Artigas et al., 2014). Our microscopy provided some insight into the complexity of the phytoplankton assemblage that made up the DCM. The occurrence of motile and mixotrophic species indicates that the food web in this lagoon is complex, with a blurred boundary between producers and consumers, as described by Ward and Fallows (2016),
Chapter 6

allowing energy and biomass to enter the food web across multiple trophic levels. For example, dinoflagellates were a common component of the phytoplankton, both in the surface samples enumerated from 2010 and 2013, and from samples taken at depth in 2012. Species such as *Heterocapsa triquetra* and *Dinophysis acuta* were found in conjunction with the ciliate *Mesodinium sp.*, a prey item which dinoflagellates are known to feed on (Litaker et al., 2002; Reguera et al., 2012; Velo-Suárez et al., 2014). Cryptophytes were also very common in Lough Furnace, and because they are motile, can be found deeper in the water column where they may utilise nutrients that have been depleted in the epilimnion (Gervais, 1998), but also use a heterotrophic diet if required. On many occasions, the DCM was located well below where we estimate 1% PAR was reaching. While we couldn’t include our low frequency light measurements in our data analysis, the variability in light availability, as indicted by monthly Secchi depth readings, is far less than the variability in the depth of DCM, indicating that light availability may not be one of the main drivers of DCM formation in Furnace. The occurrence, location and composition of the DCM in Lough Furnace indicates that the classic descriptors of bottom up (nutrient availability) and top down (predation) control of algal biomass need to be supplemented by additional information about food web structure.

In this study, we have used chlorophyll fluorescence as a proxy for algal biomass. However, while there was a significant positive correlation between fluorescence and both extracted chlorophyll *a* and phytoplankton biomass, the relationships were not particularly strong. Chlorophyll fluorescence is measured and used as a proxy for phytoplankton biomass through use of the
carbon/chlorophyll ratio (C:Chl) (Banse, 1977). However, the ratio of carbon to chlorophyll does not remain constant and can vary widely between taxonomic groups and within species depending on external conditions, leading to situations where detectable chlorophyll levels may not be representative of the actual distribution of phytoplankton biomass (Cullen, 1982). For example, diatoms generally have a lower C:Chl ratio than the smaller dinoflagellates and cyanobacteria (Chan, 1980; Sathyendranath et al., 2009), meaning that use of average C:Chl ratios, for example during a dinoflagellate bloom, can underestimate plankton biomass (Domingues et al., 2008). The C:Chl ratio has also been shown to be influenced by light, nutrient and temperature conditions in algal culture experiments (Geider et al., 2004; Laws and Bannister, 1980; Spilling et al., 2015). For example, phytoplankton may photoinhibit through down-regulation of their photosynthetic pigments during high light exposure in order to prevent photooxidative damage (Long et al., 1994). This would lead to a reduction in the levels of detectable chlorophyll a fluorescence, which if measured, would not be representative of actual chlorophyll a concentrations or more importantly, phytoplankton biomass. We have avoided this being an issue in our analysis by only using profiles collected at midnight. The significant correlation in this study between ChlF and both extracted Chl a and biomass of phytoplankton indicates that the fluorometer was capturing biological meaningful signals, but at a spatial and temporal resolution which would be challenging to achieve with traditional methods. We are not advocating that autonomous sensing is a better monitoring method than traditional Chl a extractions or phytoplankton counts. Instead, we suggest that a combination of autonomous sampling and targeted spot samples can be used to gain
a full understanding of how phytoplankton are responding to seasonal changes in a very dynamic environment.

**Conclusion**
We conclude that the spatial and temporal dynamics of phytoplankton assemblages in stratified coastal lagoons are highly variable, but somewhat predictable at an annual scale. The development of a spring bloom, followed by the deepening of a deep chlorophyll maximum occurred in all of the years of this study, although this pattern was more defined in some years. High frequency monitoring using a vertical profiling fluorometer allowed us to locate and quantify phytoplankton biomass in this dynamic environment, and demonstrated that significant phytoplankton biomass occurred in the dark, hypoxic hypolimnion, below a very strong stratification. Areas of future research might include the contribution of mixotrophs to this hypolimnetic biomass, quantifying the contribution of marine migrants to the lagoon biomass and determining the role of physical controls, specifically quantifying the role of freshwater-tidal exchange fluxes with the coastal ocean. It is inevitable and expected that coastal lagoons will change more rapidly than the marine and freshwater habitats which they bridge, particularly as sea levels rise and freshwater inflow undergoes seasonal modification. Programs aimed at conserving and managing the unique dynamic nature of coastal lagoons are needed, and the development of 3-D models for threatened lagoons is warranted. The data presented here provides a sound platform for such work, which would then enable the investigation of potential impacts under future climate scenarios.


**Table 1.** Generalized additive mixed model of chlorophyll fluorescence in Lough Furnace between 2009 and 2014. The response variable, (5 day average of maxChlF) was $\log_{10}$ transformed maximum daily fluorescence measured by a chlorophyll fluorometer. Explanatory variables included were $Z_{mix}$ (m) and solar radiation $(J / \text{cm}^2)$. $R^2$ (adj) = 0.32, Scale est. = 0.16 and $n = 258$

<table>
<thead>
<tr>
<th>Parametric coefficients</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t-value</th>
<th>p</th>
</tr>
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<tbody>
<tr>
<td>Intercept</td>
<td>1.16</td>
<td>0.06</td>
<td>18.68</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

Approximate significance of smooth terms:

| s(Solar radiation)     | 1.85     | 1.85       | 7.76    | <0.01 |
| s($Z_{mix}$)           | 4.62     | 4.62       | 10.97   | <0.01 |
Fig. 1. Location of Lough Furnace on the Atlantic coast of Ireland. S1 is the location of the automatic monitoring station and S2 is the Met Éireann automatic weather station.
Fig. 2. Top: Depth (m) of $Z_{\text{mix}}$ (grey lines) and 1 % PAR (black dots); middle: epilimnetic (grey lines) and hypolimnetic (black lines) dissolved oxygen concentration (mg l$^{-1}$); bottom: epilimnetic (grey lines) and hypolimnetic (black lines) salinity measured from daily profiles of Lough Furnace between 2009 and 2014. Years separated by vertical grey lines.
Fig. 3. Contour plot of midnight chlorophyll fluorescence (rfu – relative fluorescence units) in Lough Furnace for each day from 2009 to 2014. White areas indicate days where data were missing. \( Z_{mix} \) (the bottom of the surface mixed layer) is indicated by the red line, and estimated 1% PAR by black dots.
Fig. 4. Contour plots of the stability around the pycnocline in Lough Furnace (expressed as the squared Brunt–Väisälä frequency, $N^2$, rad s$^{-1}$) for 2010 (top), 2013 (middle) and 2014 (bottom). Green dots represent the depth where the Chl fluorometer sensed significant chl fluorescence (>14RFU). The black line shows the daily maximum tidal height, while the dashed black line indicates the water level in upstream Lough Feeagh, which is a proxy for freshwater inflow in Lough Furnace. The left hand y-axis indicates water column depth while the right hand y-axis indicates the water levels in Furnace and Feeagh.
Fig. 5. Relationship between ChlF (measured in RFU by a profiling sonde at the relevant depth) and chlorophyll $a$ ($\mu$g L$^{-1}$) measured in spot samples and processed using a standard ethanol extraction method (top), and between ChlF and biomass of phytoplankton counted with an inverted microscope (bottom). Manual surface water samples were taken approximately monthly (black dots), or at various depths on two occasions in 2011 (grey dots). Chlorophyll $a$ was extracted approximately monthly between 2009 and 2014 (top), while only 2 years of monthly phytoplankton samples (2010 and 2013) were enumerated (bottom). Dashed lines indicate the linear relationship between the two variables for all samples.
Fig. 6. Biomass of phytoplankton phyla recorded in the epilimnion of Lough Furnace in 2010 (top left) and 2013 (bottom left), and through the water column in April 2012 (top right) and May 2012 (bottom right).

Fig. 7. Smoothers for the optimum general additive model, with maximum chlorophyll fluorescence (RFU, log_{10} transformed) as the response variable and global solar radiation (J cm^{-2}) and mixing depth (Z_{mix}) as significant independent variables; y axis units represent the centred linear predictor of the model with the estimated degrees of freedom in the brackets.
Fig 8. Conditional inference tree showing the main driving variables (statistically significant variables with $p < 0.001$) of the depth of maxChlF in Lough Furnace. RMSE error rate between measured and predicted values was 1.34 and $R^2$ (adj) = 0.21. The mean depth of the DCM in each node is given underneath each boxplot.

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REFERENCES


Chapter 6


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Chapter 6


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CHAPTER 7. SYNTHESIS

7.1. Summary of findings & wider context

The objective of this project was to assess how the combination of marine, freshwater and meteorological variables control the hydrography of the lagoonal estuary Lough Furnace, and what the resulting implications are for dissolved oxygen dynamics and resident ecology. An 18-month observational field study was carried out on the Furnace system and supplemented with longer term hydrological and meteorological data collected as part of the Marine Institute’s environmental monitoring program based in the Burrishoole. Detailed summaries of results can be found in each of the thesis articles I-IV. A general summary and synthesis of these findings is presented here.

High-resolution monitoring of the deep inner basin water column over a continuous 6-year period from automated profiles taken by an undulating CTD, revealed the maintenance of strong saline stratification and isolation of water below a depth of approximately 6 – 8 m. This isolated basin water displayed persistent anoxic conditions. The vertical thermal structure of the water column was primarily determined by the salt stratification, with heat loss and gain through the air-water interface generally influencing only the surface layer. Exchange of heat properties between the surface and deep waters was restricted to diffusive fluxes, with isothermal conditions generally existing in the basin water year-round. As the strong vertical stratification precluded full water column mixing, exchange of basin water properties was primarily a function of lateral intrusions of sufficiently dense water presented at the basin
entranceway, a dynamic commonly encountered in silled fjords and coastal basins with restricted connections to open coastal waters (Farmer and Freeland 1983; Inall and Gillibrand 2010; Stigebrandt 2012).

These basin water exchange events were infrequent (only 5 recorded in 10 years) and irregularly spaced. However, because they caused changes in basin water temperature and oxygen concentrations, understanding the precise mechanisms leading to their occurrence was a primary focus of this research. The set of current and density observations between the inner basin and the adjacent coastal waters provided insight in the horizontal exchange dynamics between Furnace and Clew Bay. Significant tidal inflows were generally limited to fortnightly spring tides. Overall, the flow dynamics were dominated by freshwater discharge, with Furnace providing a mean net volume transport of low salinity water toward the adjacent coastal region. As such, there was a pronounced seasonality observable in the lagoon/ocean volume transport. Deep water ventilation only occurred following a sequence of processes, beginning with a prolonged reduction in rainfall and river discharge followed by larger tidal excursions along the long connecting channel (i.e. spring tides). A reduction in both the salinity of the surface outflow and overall volume of water exiting Furnace allowed progressively saltier (denser) tidal intrusions to reach the inner basin, which eventually attained a large enough density to sink into the anoxic basin water as a dense gravity current.

The dynamics of the entraining gravity current were assessed and water mass analysis implied that the new inflow of dense water entrained significant amounts of ambient basin water along it’s passageway to the basin interior. The result was the formation of
new basin water, an almost 50:50 mixture of old basin water and juvenile water from the inflowing dense plume. The remainder of the old anoxic basin water was uplifted toward the surface layer, where it remained at an intermediate depth. Crucially, this generated a shallower oxic-anoxic interface. Once stagnant conditions reoccurred in the new basin water below this intermediate anoxic zone, biochemical oxygen consumption once again led to anoxic conditions and the overall volume of anoxic water increased by ~20% compared with pre-ventilation conditions.

Some insight into the influence of changing climatic conditions on the frequency of ventilations in Lough Furnace has been gained through the results presented in this study. Specifically, the role of freshwater discharge was well delineated, with analysis of the ten-year timeseries showing that ventilation of the anoxic zone only occurred during or immediately following months with drier conditions compared to long-term averages in the Burrishoole system. This finding has potentially major implications for oxygen dynamics in Furnace, as future climate change scenarios may modify temporal distribution and intensity of precipitation (Bastola et al. 2011). If the frequency of prolonged dry spells increases, then so too will the frequency of ventilation events. The precise manner in which climate change will affect local rainfall conditions is difficult to predict, given that most hydrological forecast modelling studies typically focus on the regional scale or coarser (Lobanova et al. 2018).

At a national level, total precipitation across the year in Ireland is expected to increase, although this is due in large part to the anticipated increase in rainfall intensity during winter months (Bastola et al. 2011). Analysis of a 305-year-timeseries of reconstructed rainfall records for Ireland also indicated that the most
recent period analysed (2006-2016) was the wettest on record (Murphy et al. 2018). A creation of a 250-year historic drought catalogue also revealed that Ireland in recent decades has experienced less severe periods of drought (Noone et al. 2017). These studies taken together would appear to imply that with increasing rainfall and freshwater discharge, ventilation is perhaps likely to become less frequent in Furnace, reinforcing the anoxic conditions.

However if heatwaves and droughts become more frequent under future climate scenarios then ventilations could occur more often. Using the most severe end-of-century climate model, Matthews et al. (2016) expected the occurrence of extreme heatwave or drought periods to increase significantly in Ireland. The warmest recorded summer over the time period of their analysis (1900-2014) was 1995, a summer in which a major fish kill was recorded in Furnace. A profile of oxygen taken in the aftermath of the fish kill is reproduced from the Salmon Research Agency annual report (SRA 1995) in Fig. 1 and shows the typical post-ventilation upward lifting of the old anoxic, sulphidic basin water outlined in Chapter 4. This implies that following the exceptionally hot and dry summer, successive deep-water inflows ventilated the basin with some of the unmixed old anoxic water lifted toward the surface where it encroached on fish held in aquaculture cages. A startling finding of the analysis by Matthews et al. (2016) was that the occurrence of summers as dry as 1995 may increase by a factor of 10 by the end of the century, which would certainly mean that Furnace could be ventilated more frequently, perhaps annually. However, it is reemphasised here that multiples studies (Bastola et al. 2011; Matthews et al. 2016; Murphy et al. 2018) are all in agreement that Ireland is and will experience wetter winters. Furthermore, evidence
of recent wetter winters in Burrishoole can be observed in the freshwater discharge climatology over the last decade compared to long-term means over the period 1976-2018 (Fig. 12a, Chapter 4). Thus it is highly likely that even if the basin water is ventilated annually, anoxic conditions will re-occur during winter months, as the results of this research have shown that once the basin water becomes isolated from deep inflows, anoxic conditions develop within 2-3 months.

Fig. 1. Oxygen profile taken on 13th September 1995, the day following a major fish kill event in Furnace. An anoxic mass of water is evident very close to the surface with oxygenated conditions at depth, indicative of a deep water renewal with the old anoxic basin water pushed toward the surface. (Reproduced from The Salmon Research Agency 1995 Annual Report).

A very simple assessment to stimulate future work in this area was carried out by hindcasting the machine learning algorithm used to predict inflow densities presented in Chapter 4 back to 1979 (Fig. 2). This was achievable by utilising the long-term discharge records,
extending the tidal elevation model back in time and using wind stress and atmospheric pressure from the ERA-interim gridded climate reanalysis dataset\textsuperscript{2} (Dee \textit{et al.} 2011). As no inner basin water column profiles of density are available pre-2009, whether or not a ventilation occurred is anticipated based on setting a typical mean basin water density equal to 1015.5 kg m\textsuperscript{3} (which was the mean basin water density over the period 2009-2018). Aside from 1995, no way of validating whether a predicted ventilation actually occurred exists, although it is worth noting that running the model back in time did successfully recreate the 1995 event (Fig. 2a). Despite the simplicity and limitations of this approach, it does appear as if the frequency of ventilations has decreased in the last 10-15 years, in accordance with results that this time period is the wettest on record in Ireland (Murphy \textit{et al.} 2018).

\textsuperscript{2} The 0.75° X 0.75° sized grid containing Lough Furnace and the Burrishoole catchment was used for obtaining wind and atmospheric pressure reanalysis data, which were then averaged to a daily timestep.
black periods of basin water exchange anticipated based on whether the predicted inflow densities exceed the typical basin water density in (a).

By comparing a climatology of modelled mean monthly inflow densities over the period 2008-2018 with those for the period 1979-2007 it appears that over the most recent decade the distribution of inflow densities across the year has been modified (Fig. 3). Specifically, since 2008 lower densities in mid- and late summer were predicted compared to the period 1979-2007. In contrast, highest monthly inflow densities were predicted for late spring and early summer. Using the observed data from the Furnace profiler for 2009-2018 (Fig. 11, Chapter 4) it is noted that 4 out of 5 ventilations occurred in spring/early summer. The model hindcast would indicate that in the past (pre-2008), ventilations were more likely to occur in mid-summer (June-August) and were more frequent (Fig. 2). Thus some of the possible effects of changing climatic conditions on deep water oxygen dynamics in Furnace are beginning to emerge, with this evidence tentatively suggesting that runoff modifications may promote stagnancy in Furnace and other strongly stratified estuarine systems in similar climatic zones. In addition, altered rainfall patterns across the year may modify the timing of ventilations with an apparent shift to spring or earlier summer months (April-June).
Fig. 3. Predicted mean monthly inflow densities for (a) 1979-2007 and (b) 2008-2018. Values were obtained by hindcasting the predictive model outlined in Chapter 4. The red horizontal dashed line represents a typical mean basin water density of 1015.5 kg m$^{-3}$. Error bars represent 95% coverage probability.

Along with the influence of freshwater flux, the other primary driver of deep water ventilations in Furnace highlighted in Chapters 3 and 4 was spring tides. The larger tidal excursions across the long connecting channel associated with fortnightly spring tides were necessary to deliver dense, oxygenated inflows to the confined inner Furnace basin. Thus, the influence of climate-modulated sea level rise may enhance tidal transport from the adjacent coastal area. An analysis of the projected magnitude of sea level rise along the entire European coastline revealed that the largest increases are most likely to occur in the North Sea and along North Atlantic coasts (Vousdoskas et al. 2017). The major relevance of this for Furnace, which is situated on the North Atlantic coastline of Ireland, is that a significant increase in mean sea level could see larger tidal intrusions into the Furnace system, possibly increasing the frequency of
ventilations. Furthermore, coastal storm surges and waves may act synergistically with these relative mean sea level rise projections, leading to increased risks of extreme sea levels and coastal flooding which could potentially flush out the inner Furnace basin entirely. Again, much uncertainty relating to future oxygen dynamics in Furnace arises from these projections. Whether anoxic or oxic conditions will prevail in the basin water is ultimately dependent upon the frequency of these ventilations; should mean sea level rise increase sufficiently such that oxygenated dense coastal water reaches the deep water of Furnace during each spring tidal phase for example, then Furnace may no longer experience fully anoxic conditions.

An additional component of this work was to assess the potential influence of meteorological forcing on the water column structure and consequently, deep water oxygen dynamics. Even the strongest wind events could not create significant breakdown of the stratification. However, upwelling of the deep, oxygen-deplete waters was examined through Wedderburn number computations which revealed critical upwelling limits were reached on occasion. This would imply localised mixing between stratified water masses around the basin boundaries and wind-induced internal wave activity. A particular significance of the Wedderburn number calculations was the observation that turbulent diffusivity in the isolated basin water increased by an order of magnitude following critical upwelling of the pycnocline. The implications of this finding was that wind forcing may gradually decrease the density of the isolated basin water and pre-condition the basin water to a renewal by a dense inflow.
The low freshwater conditions that lead to a deep water renewal also reduce the overall vertical density gradient. Thus, prior to and during deep water renewals, susceptibility to wind-induced upwelling is greatest given the reduced baroclinic restoring forces and this was evident in the low Wedderburn numbers computed in the days leading up to and following these events. The consequences of increased upwelling in nearshore areas are especially pertinent in systems with deoxygenated conditions and this was illustrated through a case study carried out during a stock assessment survey of the critically endangered European eel (*Anguilla anguilla*) (See Appendix C). Results indicated that temporal variability in oxygen concentrations were correlated with fundamental mode internal seiche motions associated with wind events. Crucially, during the upwelling phase of the seiche, oxygen-deplete (and likely hydrogen sulphide-rich) deep water encroached on oxygenated nearshore zones where fishing nets were situated. This led to mortalities of captured fish but more broadly it implied that internal seiche dynamics are capable of necessitating changes in movement and behaviour of aerobic organisms that inhabit the littoral zone of basins with deep deoxygenated water.

The hydro-meteorological conditions in Furnace were also related to the phytoplankton population dynamics over a 6-year period, using chlorophyll fluorescence as a proxy for phytoplankton biomass. As anticipated, the results highlighted how phytoplankton biomass increased with increasing surface water temperature and solar radiation; however the depth of the surface freshwater layer was negatively correlated with maximum chlorophyll fluorescence. Thus, larger volumes of freshwater runoff led to a decrease in phytoplankton productivity, irrespective of season. Furthermore, out
of a large set of hydro-meteorological variables, surface water temperature and salinity were shown to have the largest influence on the depth of the deep chlorophyll maximum (DCM). Warmer water temperatures and higher surface salinities were correlated with the deepest DCMs. This dynamic was again likely related to the freshwater-tidal interaction – during low freshwater runoff, which tended to happen during warmer months, surface layer salinities increase as larger, saltier tidal intrusions into the inner basin occur. This could potentially impact phytoplankton population dynamics by enhancing advective fluxes of phytoplankton from the adjacent coastal habitat into Furnace and by creating an environment conducive to phytoplankton productivity. The phytoplankton composition of the most pronounced DCMs was primarily comprised of marine species recorded in Clew Bay around the same time period, which lends support to this hypothesis.

Another highlight of this work showed that over the period 2009-2014, the most intense, prolonged DCMs occurred in years following a deep water renewal event. Whilst this observation requires further detailed analysis over a longer time period, it fits with the proposal that larger tidal intrusions enhance phytoplankton productivity in Furnace, either through enhanced transport of phytoplankton cells or nutrients from the adjacent coastal area or a combination of both. In the case of a deep water renewal, it could also potentially be related to the upward release of nutrients that have built-up in the stagnant basin water, stimulating phytoplankton growth in the photic zone.

In a broader context, understanding the physical processes that govern dissolved oxygen dynamics is a crucial step toward assessing how susceptible individual habitats are toward
deoxygenated conditions and what the resulting ecosystem consequences could be. For systems that are strongly stratified like Furnace, bottom waters are prone to isolation and stagnancy. Estuaries and coastal systems may be particular vulnerable in this regard (e.g. Gray et al. 2002; Diaz and Rosenberg 2008; Middelburg and Levin 2009) given the strong density gradients associated with dual marine and freshwater inputs. However, warming surface water temperatures due to climate change can also increase stratification of the water column and reduce vertical mixing, with mounting evidence of increasing open ocean deoxygenation (Keeling et al. 2010; Schmidtko et al. 2017; Levin 2018).

Outside of similar stratified coastal habitats, the results from Lough Furnace are perhaps most applicable to lakes, as the morphometry of the semi-enclosed anoxic inner basin closely resembles a steep-sided lake. Modulation of air-water surface heat fluxes due to climate change will lead to increasingly stable thermal stratification and reduced basin-scale vertical mixing events (Woolway and Merchant 2019; see Appendices A and B). This could potentially lead to increased isolation of bottom water and the occurrence of hypoxia in freshwater lakes (e.g. North et al. 2014; Jankowski et al. 2006). Thus in future, the physics of many lakes could resemble those observed in Furnace currently, owing to its strong stratification. The Furnace work has indicated that fluxes of oxygen across the oxycline could only replenish 5% of the oxygen consumed in the basin water through biochemical processes during the stagnant regime. In lakes under future climate scenarios, fluxes of oxygen across the thermocline may not be sufficient to prevent deoxygenated conditions from occurring in isolated bottom waters.
The results from this research have also revealed that in the absence of significant vertical mixing, sources of oxygen to isolated deep water must come primarily from horizontal intrusions. In fjordic-estuaries, this dynamic generally occurs during deep water ventilation (e.g. Thomson et al. 2017; Farmer and Freeland 1983; Arneborg et al. 2004). In lakes, possible sources of ventilation could come from river inflows that are denser (colder) than surface waters and that sink as dense plumes upon entry (e.g. Churchill et al. 2003) or from lateral advection from shallower embayments, where water may cool more rapidly compared to deeper locations (e.g. MacIntyre et al. 2002; Cannaby et al. 2007). An additional pathway for oxygen fluxes to isolated deep water is through mixing around the basin perimeter. For example, in stratified basins localised turbulence along boundary slopes created by shoaling internal waves (e.g. Boegman et al. 2005) could lead to mixing between oxic and suboxic water masses. However, the implications for biological communities inhabiting these areas needs to be considered, as the research in Furnace has highlighted.

7.2. Future research

The findings from this dissertation have opened up several new avenues for future work. Of particular interest would be understanding the changes in biogeochemical processes in the anoxic basin water during and after the occurrence of a deep water ventilation event. Whilst the hydro-meteorological drivers of basin water exchange and some of the physical dynamics occurring during and after these events have been described here, little is known about the fate of hydrogen sulphide or methane for example, which may have accumulated during the preceding stagnant period. The work
on surface heat fluxes (Appendices A, B) could also be expanded to incorporate analyses of gaseous efflux from Furnace, particular following a ventilation event. The anoxic basin water of Furnace represents an ideal opportunity to study microbial processes and ecology in an anaerobic environment. The fate of bacterial communities in the aftermath of ventilation would be one area of prospective research with wider application, for example to larger deoxygenated basins that experience contrasting regimes of anoxia and ventilation.

Having highlighted the possible impact of internal seiche events on nearshore dissolved oxygen variability, a logical next phase would be to assess shoaling and mixing dynamics where the oxycline intersects the benthic boundary layer. This research has highlighted that internal seiche events do lead to drastic oxygen fluctuations in shallower nearshore regions but it remains to be seen to what extent breaking non-linear waves cause intermittent oxygen fluxes from the basin interior and oxygenated shallow layers into the anoxic bottom boundary layer.

From an ecologically-motivated perspective, numerous research questions have arisen from this work. For example, the behaviour of fish species in relation to the variability in nearshore dissolved oxygen remains elusive. Aside from resident fish species, returning migratory fish such as adult Atlantic salmon (*Salmo salar*) often use Furnace as a holding ground before moving up into the freshwater Lough Feeagh, especially during dry spells when the rivers are too low to traverse. Understanding how these fish navigate the potentially treacherous waters of Furnace, particularly if internal seiche events are generating upwelling of anoxic water, remains to be seen. In addition, the work presented here on phytoplankton
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dynamics has opened up several questions and in particular, understanding precisely how tidal inflows stimulate phytoplankton productivity would be valuable. Targeted sampling of tidal inflows in the lower estuary could reveal whether the advection of coastal phytoplankton are effectively generating the observed DCMs in the inner Furnace basin for example.

Finally, a holistic approach toward understanding the linkages between hydrodynamics and biogeochemistry, and how these dynamics are subject to change under future climate scenarios, would be to set-up and execute a full hydrodynamic model of the Furnace system. The set of observations collected and analysed throughout the course of this research, including multi-year water column profiles of temperature, salinity and oxygen, high-resolution meteorological data and volume fluxes from the adjacent marine and freshwater environments, could serve as boundary conditions to initiate the model and also be used to validate model performance. Following accurate simulation of the Furnace system under current and past climate, the model could be coupled to climate projections of important environmental variables including air temperature and precipitation climatologies. Disentangling the role of climate change on local rainfall, which is a key determinant of deep water oxygen in Furnace, would likely require specific modelling studies of the Burrishoole watershed to accurately simulate future discharge climatologies. This would allow an unprecedented look into how the physical dynamics of a deoxygenated environment such as Furnace may be subject to change and what the implications will be for biogeochemical and ecological processes.
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APPENDICES
Latitude and lake size are important predictors of over-lake atmospheric stability

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Abstract

Turbulent fluxes across the air-water interface are integral to determining lake heat budgets, evaporation, and carbon emissions from lakes. The stability of the atmospheric boundary layer (ABL) influences the exchange of turbulent energy. We explore the differences in over-lake ABL stability using data from 39 globally distributed lakes. The frequency of unstable ABL conditions varied between lakes from 71 to 100% of the time, with average air temperatures typically several degrees below the average lake surface temperature. This difference increased with decreasing latitude, resulting in a more frequently unstable ABL and a more efficient energy transfer to and from the atmosphere, toward the tropics. In addition, during summer the frequency of unstable ABL conditions decreased with increasing lake surface area. The dependency of ABL stability on latitude and lake size has implications for heat loss and carbon fluxes from lakes, the hydrologic cycle, and climate change effects.

1. Introduction

Temperature gradients between lake water surfaces and air influence the exchange of heat, gas, and energy fluxes from lakes. Lake surface temperatures are governed by the interactions with the overlying atmosphere and radiative fluxes [Schmid et al., 2014]. Lake surface temperature exceeding surface air temperature tends to produce an unstable atmospheric boundary layer (ABL), which is the lower layer of the troposphere that is influenced directly by the Earth’s surface [Garratt, 1994]. In general, the higher the lake surface temperature is relative to the air temperature, the more unstable the ABL, although other factors play a role as well. In turn, the thermodynamic interaction of lakes with the atmosphere is influenced by the stability of the ABL.

Unstable ABL conditions can result in enhanced heat loss (where heat loss is defined as heat transport from lakes to the atmosphere) by sensible and latent heat transfer from the lake surface to the atmosphere [Brutsaert, 1982], thereby influencing the local climate [Bonan, 1995; Lofgren, 1997], altering hydrological cycles at catchment scales [Rouse et al., 2005], and enhancing lake evaporation and water level decline [Grenweald and Stow, 2014], with consequences for water security [Vörösmarty et al., 2000] and supply [Brookes et al., 2014]. This is of significance to lakes which are an important supply of national water demand and can have considerable consequences for water management strategies [Vörösmarty et al., 2000; Immerzeel et al., 2010; Vörösmarty et al., 2010]. The turbulent heat and moisture fluxes can also enhance the gas transfer coefficient and thereby the emission of carbon dioxide and methane from lakes [Polsenaere et al., 2013; Podgajskie et al., 2015].

Unstable ABL conditions have been shown to persist above lakes for long periods [Rouse et al., 2003], resulting in enhanced turbulent heat loss. ABL conditions have been reported in lake studies from around the world, in tropical [Verburg and Antenucci, 2010] and temperate regions [Derecki, 1981; Lofgren and Zhu,
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2000; Laird and Kristovich, 2002; Rueda et al., 2007) but no study has compared ABL stability across a range of latitudes and other lake attributes.

In view of increasing temperature gradients reported between lake surfaces and air in the past few decades as a result of climate warming [O’Reilly et al., 2015; Woolway and Merchant, 2017], and the acceleration expected in the hydrologic cycle [Wentz et al., 2007], an understanding of the extent, causes, and effects of variations in the stability of the ABL above lakes is of great interest. However, until recently, in situ high-frequency measurements at the air-water interface of wind speed, water temperature, air temperature, and relative humidity, that are required to examine patterns in the stability of the ABL, have not been widely available, preventing a comprehensive comparison across lakes.

The recent establishment of scientific networks dedicated to the collaborative analysis of high-frequency lake buoy data has provided an opportunity for a large-scale analysis. We have collated data from 39 lakes from around the globe to quantify variability and identify patterns in annual, seasonal, and diurnal ABL conditions above the water surface and analyze how these patterns vary across different lake types and climatic gradients. To understand the overarching controls on ABL stability, we examine the influence of four variables that might be expected to have an effect, altitude, latitude, lake surface area, and lake depth. Latitude determines variation in net radiation flux and thus has a strong influence on lake temperature and the seasonal temperature cycle [Straskraba, 1980] and ultimately on ABL stability [Verburg and Antenucci, 2010]. Altitude can influence air-water temperature relationships via differential lapse rates [Livingstone et al., 1999] and can thus be expected to influence ABL stability [Rueda et al., 2007]. Lake area has been shown to affect lake temperatures at diurnal timescales [Woolway et al., 2016]. Lake depth influences the thermal capacity of water and thus air-water temperature relationships [Balsamo et al., 2010; Woolway and Merchant, 2017].

2. Materials and Methods

We collected high-frequency observations (measurement interval range from 4 min to 1 h) of lake surface temperatures and meteorological conditions from 39 lakes on 5 continents, ranging in surface area between 0.001 km$^2$ and 32,900 km$^2$, in altitude between 0 m above sea level (asl) and 1987 m asl, in latitude between 38.8°S and 71.24°N, and in maximum depth between 2 m and 1470 m (Table S1 in the supporting information). Instrumented buoys measured near-surface water temperatures ($T_w$, K) at an average depth of about 0.5 m, always within the surface mixed layer. In this study, we assume that the measured water temperature equals that at the surface, although it must be noted that under certain conditions (e.g., under intense heating conditions) temperatures can vary considerably within the upper meter of a lake [Tedford et al., 2014]. Meteorological conditions including wind speed ($u_w$, m s$^{-1}$), air temperature ($T$, K), and relative humidity (RH, %) were measured on average 2.9 m (range 1.3 to 10 m) above the lake surface. Fourteen lakes had observations available throughout at least 1 year (i.e., 12 months of observations). All lakes had observations for the summer months (defined as July to September in the Northern Hemisphere and January to March in the Southern Hemisphere) for at least 1 year. Each lake had measurements at one location, except for Lake Tanganyika (two locations) and Lake Tahoe (four locations). We analyzed the data from each monitoring station in these two lakes independently before combining the results.

Stability of the atmospheric boundary layer is characterized by the nondimensional atmospheric stability parameter, determined from surface measurements which we obtained from the lake buoy monitoring stations. It is given by $\zeta = z \vec{w}^{-1}$ [Brutsaert, 1982], which is the ratio of the sensor measurement height above the water surface ($z$; in meters) to the Monin-Obukhov stability length

$$L = \frac{-\rho_a u_w^2 T_w}{\gamma g \left( \frac{z}{h} + 0.61 \frac{h}{L} \right)}$$

where the absolute value of $L$ is the height above ground level above which buoyancy-generated turbulence dominates wind shear-generated turbulence, $\rho_a$ is air density (kg m$^{-3}$), $u_w$ is the air friction velocity (m s$^{-1}$), $T_w = (T_0 + 0.61q_r)$ is virtual air temperature (K), which we assume to be approximate to the virtual potential temperature and thus are neglecting the influence of adiabatic expansion and compression on $T_w$ [Mowbray et al., 2002; Hipsey et al., 2014], $q_r$ is the specific humidity (kg kg$^{-1}$) calculated from relative humidity, air temperature, and air pressure, $\gamma = 0.41$ is the von Karman constant, $g = 9.81$ m s$^{-2}$ is the gravitational acceleration, $Q_h$ and $Q_Q$ are the sensible (equation (21)) and latent (equation (31)) heat fluxes,
respectively, positive when heat flux is from the lake surface to the atmosphere (W m$^{-2}$), $C_{pu} = 1005$ J kg$^{-1}$ K$^{-1}$ is the specific heat of air at constant pressure, and $L_f$ is the latent heat of vaporization (J kg$^{-1}$). A negative $\zeta$ indicates an unstable ABL, a convective atmosphere above the lake, and increased potential for heat loss from lakes via turbulent heat fluxes. The opposite is the case when $\zeta$ is positive and the ABL is stably stratified. ABL conditions are neutral when $\zeta = 0$. We analyzed the incidence of an unstable ABL as the percentage of time in which $\zeta < 0$, using hourly data, and examined the incidence against lake attributes using a multiple regression model.

Air pressure was not measured on all instrumented buoys, and since local variability in air pressure has negligible effect on the estimation of ABL stability, transfer coefficients, and turbulent fluxes [Verburg and Antenucci, 2010], a constant air pressure was assumed for each site, based on the altitude of the lake [Woolway et al., 2015a]. With the exception of air pressure, all data used to estimate the stability of the ABL were measured directly above each lake, as opposed to over land. Previous work has often relied on overland weather data [e.g., Derecki, 1981; Croley, 1989; Rueda et al., 2007].

Sensible heat and latent heat fluxes were estimated with bulk aerodynamic methods [Brutsaert, 1982]

$$Q_h = \rho \rho_u C_{pu} u(z_0)(T_s - T)$$

(2)

$$Q_e = \rho \rho_v C_{pu} u(z_0)(q_s - q)$$

(3)

where $q_s$ is the specific humidity at saturation (kg kg$^{-1}$). The turbulent transfer coefficients for heat ($\rho_u$) and humidity ($\rho_v$), which regulate $Q_h$ and $Q_e$ energy exchanges, were assumed to be equal and adjusted for ABL stability by applying stability functions [Verburg and Antenucci, 2010]. Estimates of the surface turbulent fluxes of $Q_h$ and $Q_e$ taking into account varying ABL conditions were compared with estimates that assume ABL neutrality to elucidate the role of ABL stability in regulating air-water exchanges.

The air-water surface temperature difference ($\Delta T = T - T_0$) has been used as a measure of ABL stability in previous studies [Croley, 1989; Derecki, 1981]. However, stability of the ABL is more accurately related to the virtual air-water temperature gradient [Verburg and Antenucci, 2010], which is estimated as the difference between $T_s$ and the virtual temperature of saturated air at the water surface ($T_{sv}$, K): $\Delta T_v = T_s - T_{sv}$. When $\zeta < 0$ (unstable ABL), then $\Delta T_v < 0$ is also true (Figure S1), while $T - T_0$ can be several degrees higher [Verburg and Antenucci, 2010]. Therefore, in addition to $\zeta$, we use $\Delta T_v$ as an alternative measure of ABL stability and estimate the incidence of an unstable ABL as the percentage of time in which $\Delta T_v < 0$. As the meteorological measurement heights vary among lakes, we converted $T$ and $q_s$ to a surface elevation of 10 m ($T_{sv}$ and $q_{sv}$ respectively) following Zeng et al. [1998], using the algorithms of Woolway et al. [2015a], prior to calculating $\Delta T_v$. In addition, to ensure that ABL conditions that were close to neutral were not inferred as unstable as a result of measurement uncertainty, we included an uncertainty threshold to our estimates of percent unstable conditions by determining the prevalence of unstable ABL conditions as the proportion of time during which $\Delta T_v < -0.5$ K.

All statistical analyses in this study were performed in R [R Development Core Team, 2014], including bilinear regressions computed with the “Segmented” package [Vito and Muggeo, 2008], used to relate the frequency of unstable ABL conditions to lake surface area.

To evaluate further the influence of latitude on ABL stability, we also examined incoming solar radiation (i.e., shortwave; $Q_{sw}$) and thermal radiation (i.e., longwave; $Q_{lw}$). A number of lakes ($n = 28$) had in situ measurements of $Q_{lw}$ but to be consistent among all lakes, we used $Q_{sw}$ and $Q_{lw}$ estimates from the ERA-Interim reanalysis product [Dee et al., 2011], available at a spatial resolution of 0.75°. Data were extracted for the grid point situated closest to the center of each lake, and the reanalysis data were verified using in situ measurements when available. To estimate net incoming longwave radiation, $Q_{lw,\text{net}} = (1 - \alpha_{lw}) Q_{lw}$, 3% of $Q_{lw}$ was assumed to be reflected at the lake surface ($\alpha_{lw} = 0.03$) [Brutsaert, 1982]. Emitted, outgoing longwave radiation was estimated as $Q_{lw,\text{out}} = 0.972 \sigma T_s^4$, where $\sigma$ is the Stefan-Boltzmann constant ($= 5.67 \times 10^{-8}$). The shortwave albedo ($\alpha_{lw}$), estimated from Fresnel’s equation [Woolway et al., 2015a], was used to account for the amount of $Q_{lw}$ reflected at the lake surface and to estimate the net incoming shortwave radiation: $Q_{lw,\text{net}} = (1 - \alpha_{lw}) Q_{lw}$. These surface radiative fluxes were then used to calculate net radiation, as $Q_{\text{net}} = Q_{lw,\text{net}} + Q_{lw,\text{in}} - Q_{lw,\text{out}}$.
3. Results

The ABL over lakes was unstable ($\zeta < 0$ and $\Delta T_0 < 0$) 82% of the time on an annual basis ($n = 14$) averaged across this globally distributed set of lakes (Figure 1 and Table S1). However, the stability of the ABL varied at both seasonal and diurnal timescales and differed between lakes. Unstable ABL conditions were most prevalent in summer (91% of time) and least common in spring and winter (74% and 70% of time, respectively; Figures 1b and S2). Since an unstable ABL can enhance surface heat loss considerably [Verburg and Antenucci, 2010], this suggests seasonal differences in heat transfer efficiency [Lofgren and Zhu, 2000; Rouse et al., 2003; Woolway et al., 2015b]. Unstable ABL conditions were most common during the late evening to early morning hours (Figures 1c and S3), when air temperatures tend to be cooler while the surface temperature of the lake retains daytime heat longer. In addition, at night, winds are often less intense, producing less mixing of the lower ABL. The magnitude of the diurnal cycle in ABL stability also varied among the seasons, similar to that of $T_0$ [Woolway et al., 2016] with greatest diurnal variability in spring (Figure S3).

For lakes with data available throughout the year ($n = 14$), a multiple linear regression model including latitude, altitude, lake surface area, and lake depth explained 94% of the variation in annual mean frequency of occurrence of unstable ABL conditions ($\zeta < 0, \Delta T_0 < 0$, Table S2 and 95% for $\Delta T_0 < -0.5$, Table S3). Latitude was the most important covariate ($R^2 = 0.81$, $p = 0.001$), and lake surface area was also significant ($p < 0.1$). The ABL was most commonly unstable near the equator (Figure 2a), with $\zeta < 0$ more than 99% of the year in Lake Tanganyika. Unstable conditions decreased with increasing latitude, to $\zeta < 0$ occurring about 72% of the year for lakes situated in the English Lake District. $Q_{\text{out}}$, increased with decreasing latitude ($R^2 = 0.93$, $p < 0.001$). $Q_{\text{out}}$ correlated significantly with $T_{0}$ ($R^2 = 0.88$, $p < 0.01$) and also with $\Delta T_0$ ($R^2 = 0.69$, $p < 0.01$), with a more negative $\Delta T_0$, at higher $Q_{\text{out}}$. $\Delta T_0$ decreased (i.e., became increasingly negative) at a rate of 0.28 K per 10 W m⁻² increase in $Q_{\text{out}}$. Similarly, $\Delta T_0$ decreased at a rate of 0.49 K per 10⁴ decrease in latitude, meaning that while $T_0$ increases toward the tropics, the increase in $T_{0}$ is larger, as a result of higher $Q_{\text{out}}$ received by tropical lakes.

When restricting the analysis to summer, latitude and lake surface area were statistically significant predictors as well of the frequency of unstable ABL conditions ($n = 39$, Tables S2 and S3), with latitude being the stronger factor. The relationship between latitude and ABL stability was strongest among the larger lakes ($> 10 \text{ km}^2$) during summer ($R^2 = 0.70$, $n = 18$; Figure 2b) with, similar to the annual data, a higher incidence of unstable ABL conditions at lower latitude.

Assuming neutral turbulent transfer coefficients to estimate the transfer efficiency to and from the atmosphere of vapor and heat resulted in a mean annual ($n = 14$) underestimate of 8.6 W m⁻² (12% difference) and 3.4 W m⁻² (28% difference) in estimates of $Q_v$ and $Q_h$, respectively, compared to transfer coefficients adjusted for ABL stability. This bias in $Q_v$ increased with decreasing latitude ($R^2 = 0.65$, $p < 0.001$; Figure 2c). The bias was even greater, an average 14.0 W m⁻² and 4.4 W m⁻² for $Q_v$ and $Q_h$, respectively, if a constant, such as $1.35 \times 10^{-3}$ [Hicks, 1972, 1975] was assumed for the transfer coefficients $C_v$ and $C_h$, as opposed to transfer coefficients accounting for ABL stability. Moreover, in summer ($n = 39$), there was a mean difference of 12.7 W m⁻² (16% difference) and 4.1 W m⁻² (28% difference) for $Q_v$ and $Q_h$, respectively, between estimates assuming neutral transfer coefficients and those which account for ABL stability, with largest differences at low latitudes ($R^2 = 0.56$; Figure 2d). Similar to the annual data, the bias was greater, 21.5 W m⁻² and 5.5 W m⁻² for $Q_v$ and $Q_h$, respectively, in summer if constant transfer coefficients were assumed. A difference of 27 W m⁻² in $Q_v$ and $Q_h$ combined equates to a 22% change in the surface energy budget as given by the summer average $Q_{\text{out}}$ among the study lakes (131.9 W m⁻²).

The transfer coefficients for momentum ($C_u$) and water vapor and heat ($C_v = C_h$), which describe the transfer efficiency to and from the atmosphere, are higher when the ABL is unstable [Verburg and Antenucci, 2010] and when wind speeds are low, such as during summer (Figures S4 and S5). Mean wind speed ($u_{10}$) in summer correlated significantly with lake surface area ($R^2 = 0.36$, $p < 0.001$), but not with latitude or altitude ($p > 0.1$), suggesting an effect of lake fetch. A strong lake size dependence also existed for the mean transfer coefficients (Figure 2e and Table S4). We also found a weak but statistically significant relationship ($R^2 = 0.12$, $p = 0.04$) between summer average wind speed and the percentage of time in which the ABL was unstable ($\zeta < 0$ and $\Delta T_0 < 0$; Figure S6). The greatest change in the transfer coefficients following accounting for ABL
Appendix A

Figure 1. Comparisons of atmospheric stability above lakes across temporal and spatial scales. (a) Location of each lake, colored according to the summer (July–September in the Northern Hemisphere and January–March in the Southern Hemisphere) average air-water virtual temperature difference ($\Delta T_v = T_v - T_0^v$). (b) Monthly averaged percentage of time in which $\zeta < 0$, with confidence intervals, as well as with colors indicating mean $\Delta T_v$. The number of lakes with available data for each month contributing to the average is indicated. Monthly average percentage of time in which $\zeta < 0$ in lakes with data available throughout the year ($n = 14$) is shown in Figure S2. (c) Average diurnal cycles of the percentage of time in which $\zeta < 0$, for winter (January, February, March (JFM), triangles, $n = 16$), spring (April, May, June (AMJ), squares, $n = 30$), summer (July, August, September (JAS), diamonds, $n = 39$), and autumn (October, November, December (OND), circles, $n = 24$) months, with 95% confidence intervals. Colors represent the average diurnal cycles in surface wind speed adjusted to a height of 10 m ($u_{10}$). Southern Hemisphere lakes were shifted by 182 days.
Figure 2. Relationships between lake location and size, atmospheric stability, and the accurate estimation of turbulent energy fluxes. Shown are the relationships between latitude (shown as absolute latitude) and (a) the annual percentage of time in which \( \zeta < 0 \) \((n = 14)\), (b) the summer percentage of time in which \( \zeta < 0 \) \((n = 39)\), (c) the annual average difference in the latent heat flux \( (Q_e) \) which arises by not accounting for atmospheric stability in the estimation of transfer coefficients and (d) the summer average difference in \( Q_e \) which arises by not accounting for atmospheric stability in the estimation of transfer coefficients. For the summer data (Figures 2b and 2d), a linear fit is shown for the lakes (black) with surface area > 10 km\(^2\) \((p < 0.1)\). A linear fit is also shown for the smallest lakes (<10 km\(^2\); blue circles) where significant \((p < 0.1)\). R\(^2\) values are shown for each linear fit. (e) Relationship between lake surface area and the transfer coefficients (adjusted to a height of 10 m) for the latent heat flux \( (C_{e10}) \) and momentum \( (C_{d10}) \), accounting for atmospheric stability. All values are shown as summer averages. A bilinear trend is shown. Coefficient values are in Table S4.
stability was observed in lakes \(<1 \text{ km}^2\) (Figure 2e). These results demonstrate that lake surface area and its effect on ABL stability affects \(C_p\) and \(C_d\) and that the stability of the ABL has a greater influence on the transfer coefficients in smaller lakes during summer. Latitude showed no significant effect on the transfer coefficients \((p > 0.1)\). However, after removing the lake area effect (i.e., the bilinear trends in Figure 2e; \(C_{d,pp}\) adjusted to a height of 10 m, \(R^2 = 0.19, p = 0.006\) and \(C_{v,pp}\) \((R^2 = 0.16, p = 0.01)\) were both significantly correlated with latitude, consistent with the aforementioned effect of \(Q_{net}\) on ABL stability.

4. Discussion

This global-scale analysis has identified latitude and lake surface area as significant predictors of the variability in ABL stability over lake surfaces. Previous studies have shown evidence of a high incidence of unstable ABL conditions and its influence on the turbulent energy fluxes in individual lakes [Verburg and Antenucci, 2010; Lorenzetti et al., 2015; Yusup and Liu, 2016]. This paper investigated the effects of geographic location and lake morphometry on ABL stability, the turbulent transfer coefficients, and on energy fluxes across the air-water interface. High-frequency data recorded on lakes showed variability in ABL stability on diurnal, seasonal, and annual timescales. Our results reveal that the ABL was unstable on average \(>80\%\) of the year across the examined lakes and that a strong latitudinal and lake size dependence exists for the incidence of unstable ABL conditions. An unstable ABL is more common above low-latitude lakes on seasonal and annual timescales and above small lakes during summer.

Lake size can affect lake temperatures (and the overlying atmosphere) and thereby the ABL and lake-air interactions. Small lakes are often well sheltered from the wind and experience lower wind speeds than large lakes with greater fetch [Hondo and Stefan, 1993], resulting in less mechanical mixing of the lower ABL and, consequently, a higher incidence of unstable ABL \((\zeta < 0)\) conditions. Moreover, small lakes tend to have higher dissolved organic carbon concentrations [Hanson et al., 2007], resulting in more stratified distributions of thermal energy, higher lake surface temperatures, and more negative \(\Delta T\) due to higher attenuation of light in the water column [Read and Rose, 2013]. The effects of high dissolved organic carbon concentrations in small lakes on lake surface temperature and on ABL stability would be especially notable in summer when the lake water column is stratified. This is consistent with the relationship between lake size and the frequency of unstable conditions, which was negative during summer but not the rest of the year. The transfer coefficients \(C_p\) and \(C_d\) increased sharply as lake surface area fell below 1 km\(^2\). This lake size threshold is similar to that reported for transitions in the relative contribution of convective mixing in the gas transfer coefficient [Read et al., 2012] and in the magnitude of diurnal heating and cooling in surface waters [Woolway et al., 2016].

Net radiation received by lakes is higher in the tropics, due to higher \(Q_{net}\) and \(Q_{wave}\) and lower shortwave albedo. The latter is a result of a smaller zenith angle at low-latitude lakes [Cogley, 1979], thus increasing the proportion of shortwave radiation being absorbed annually. Higher \(Q_{wave}\) likely explains why, while lake water temperatures are typically higher than air temperatures in most lakes, they are more so in tropical lakes, on an annual average. \(\Delta T\) becomes increasingly negative toward the tropics indicating a more frequently unstable ABL.

Comparisons of turbulent energy fluxes calculated without taking ABL stability into account with those calculated by applying stability functions demonstrate substantial differences. Assuming neutral transfer coefficients instead of accounting for ABL stability in the estimation of turbulent transfer coefficients resulted in evaporation being underestimated on average by 16\% during summer. Note that this is not a comparison with turbulent energy fluxes in a truly neutral ABL \((\zeta = \Delta T = 0)\), because then \(Q_p\) and \(Q_w\) are close to zero. Many lake models that use a physically based approach [Imberger et al., 1978; Imberger and Patterson, 1981; Hipsey et al., 2014] apply fixed transfer coefficients [Fischer et al., 1979] when simulating lake temperatures at daily or longer timescales, as it is often assumed that only at diurnal timescales is the thermal inertia of water too great to use constant values. However, our results illustrate that on seasonal and annual timescales \(C_p\) and \(C_d\) can be over twice as large as assumed fixed values, particularly for small lakes (Figure 2e). This challenges the validity of neglecting the effect of ABL stability on transfer coefficients by using neutral coefficients or, more generally, of applying constant transfer coefficients at seasonal and longer timescales.

The inclusion of variable ABL conditions in the formulation of turbulent transfer coefficients has consequences for the simulation of heat transfer, and thus lake thermal dynamics, which are fundamental to understanding lake biogeochemistry and ecology and the role of lakes in the global carbon cycle.
Variable ABL conditions, and the accurate estimation of their effect on the turbulent energy fluxes, are likely to influence estimates of rates of gas transfer, in particular, at lower latitudes [Erickson, 1993], where lakes generally have persistent carbon dioxide supersaturation [Cole et al., 1994; Marotta et al., 2009; Marotta et al., 2014]. In addition, small lakes, which have recently been demonstrated to be important in the study of global and regional processes including carbon and nutrient cycling [Cole et al., 2007], vastly outnumber large lakes globally [Downing et al., 2006; Verpoorter et al., 2014]; thus, our findings of the effect of lake size on ABL stability are important when evaluating the role of lakes in global cycles.

Given the importance of ABL stability in influencing the exchange of water and energy at the air-water interface, our findings highlight the importance of lake location and size for evaluating the role of lakes in the Earth’s hydrologic cycle, which is expected to accelerate with climate change [Wentz et al., 2007; Wu et al., 2013]. Our results show that water surface temperatures are on average higher than air temperatures. While air temperature increases toward the tropics, the surface temperature is larger. Climate warming will likely increase the destabilization of the ABL as suggested by the observation that temperature in many lakes has increased more than air temperatures in the past few decades [Desai et al., 2009; O’Reilly et al., 2015; Woolway and Merchant, 2017]. Such enhanced lake-air temperature gradients by climate warming are likely to result in enhanced heat loss, gas fluxes, and evaporation from lakes.

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Appendix A
Appendix A


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Geographic and temporal variations in turbulent heat loss from lakes: A global analysis across 45 lakes

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Abstract

Heat fluxes at the lake surface play an integral part in determining the energy budget and thermal structure in lakes, including regulating how lakes respond to climate change. We explore patterns in turbulent heat fluxes, which vary across temporal and spatial scales, using in situ high-frequency monitoring data from 45 globally distributed lakes. Our analysis demonstrates that some of the lakes studied follow a marked seasonal cycle in their turbulent surface fluxes and that turbulent heat loss is highest in larger lakes and those situated at low latitude. The Bowen ratio, which is the ratio of mean sensible to mean latent heat fluxes, is smaller at low latitudes and, in turn, the relative contribution of evaporative to total turbulent heat loss increases toward the tropics. Latent heat transfer ranged from ~ 60% to > 90% of total turbulent heat loss in the examined lakes. The Bowen ratio ranged from 0.04 to 0.69 and correlated significantly with latitude. The relative contributions to total turbulent heat loss therefore differ among lakes, and these contributions are influenced greatly by lake location. Our findings have implications for understanding the role of lakes in the climate system, effects on the lake water balance, and temperature-dependent processes in lakes.

Wind stress and surface heating/cooling are two of the most important factors driving physical processes within lakes (Wüst and Lorke 2003), wherein water movements forced by the wind produce turbulent mixing that combines with surface heating/cooling to determine the physical environment of the lake ecosystem. Lake thermal structure regulates key aspects of lake ecosystems and is influenced by the interactions between the lake surface and the overlying atmosphere (Edinger et al. 1968). Some of the most important physical effects of climate change on the physics, chemistry, and biology of lakes (De Stasio et al. 1996) are associated with changes in thermal structure, heat budgets, and ultimately the fluxes of heat and energy at the air–water interface.

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Additional Supporting Information may be found in the online version of this article.
By modifying the key processes of mixing and stratification (Peeters et al. 2002; Perroud and Goyette 2010; Stainsby et al. 2011), climate-driven modulation of surface heat fluxes can alter key aspects of lake ecosystems, such as an increased occurrence of toxic cyanobacterial blooms (Johnk et al. 2008), deep-water hypoxia (Jankowski et al. 2006; North et al. 2014), and changes in lake productivity (Verburg et al. 2003; O’Beirne et al. 2017). Evaporative heat fluxes also alter lake levels (Gronevold and Stow 2014), with consequences for water security and supply (Brookes et al. 2014) and, in turn, water management strategies (Vörösmarty et al. 2000; Immerzeel et al. 2010).

Heat loss at the lake surface can modify the intensity of near-surface turbulence (Imberger 1985; Brubaker 1987; Schladower et al. 2002) and thereby influence the efflux of gases such as carbon dioxide and methane from lakes to the atmosphere (MacIntyre et al. 2010; Vachon et al. 2010; Dugan et al. 2016). A detailed understanding of surface heat loss processes is therefore essential given the growing realization of the importance of lakes in the global carbon cycle (Cole et al. 2007; Raymond et al. 2013). Surface energy fluxes from lakes can also influence the climate directly (Bonan 1995; Löfgren 1997; Samuelsson et al. 2010; Thiyer et al. 2015). The surface fluxes of latent and sensible heat, representing the turbulent exchange of energy between a lake and the atmosphere, are critical components of the global surface energy cycle (Dutra et al. 2010; Le Moigne et al. 2016) and can influence the hydrological cycle (Rouse et al. 2005), which is sensitive to climate change (Wentz et al. 2007; Wu et al. 2013).

Until recently, in situ high-frequency measurements at the air–water interface that are required to accurately examine patterns in surface heat loss fluxes from lakes (e.g., wind speed, water temperature, air temperature, and relative humidity) were not widely available, thus preventing a consistent and comprehensive comparison across lakes. The recent establishment of scientific networks (e.g., Networking Lake Observatories in Europe and Global Lake Ecological Observatory Network) dedicated to the collaborative analysis of high-frequency lake buoy data has provided opportunities for global-scale analyses to be undertaken (Hamilton et al. 2015; Rose et al. 2016). We collated data from 45 lakes across 5 continents (Fig. 1 and Supporting Information Table S1) to examine patterns in turbulent surface heat fluxes (i.e., latent and sensible heat fluxes) and determine how these patterns vary across time, space, and different lake attributes, such as latitude and depth. To understand the controls on turbulent heat fluxes, we examine the influence of additional variables that we hypothesize may have an effect, including altitude, lake surface area/wind speed, and lake-air differences in temperature and humidity (Woolway et al. 2017a). We predicted that absolute latitude, which is strongly related to annual mean air temperature and net radiation, would have a strong influence on lake temperature (Straskraba 1980; Picololroaz et al. 2013) and thus heat fluxes at the air–water interface. Altitude can influence air–water temperature relationships via differential lapse rates (Livingstone et al. 1999), and we thus predicted it would influence the cooling fluxes (Rueda et al. 2007; Verburg and Antenucci 2010). We predicted that lake area would be an important predictor of surface energy fluxes given that it regulates surface temperature at diel timescales (Woolway et al. 2016) and thereby surface cooling in lakes and has also been shown as an important predictor of the relative importance of convective vs. wind-driven mixing (Read et al. 2012). Finally, lake depth can influence the interactions between a lake and the atmosphere and is often correlated strongly with annual lake heat budgets (Gorham 1964), and so we predicted that depth could also influence the surface energy fluxes.

Materials and methods

We collected mostly continuous observations (measurement intervals range from 4 min to 1 h) of lake surface temperatures and meteorological conditions from 45 lakes (Fig. 1a), ranging in surface area between 0.005 and 32,900 km$^2$, in altitude between 0 m above sea level (a.s.l.) and 1897 m a.s.l., and in latitude between 38.8°S and 72.4°N (Supporting Information Table S1). Instrumented buoys measured near-surface water temperature ($T_w$, °C) at an average depth of approximately 0.5 m (range 0–1 m), always within the surface mixed layer. Meteorological conditions including wind speed ($U$, m s$^{-1}$), air temperature ($T_a$, °C), and relative humidity ($RH$, %) were measured on average $z = 2.5$ m (range 1.3–10 m) above the lake surface. Fourteen lakes had observations available throughout at least 1 yr. All lakes had observations for the months of July to September (January to March in the southern hemisphere) for at least 1 yr. Note that lake variables were not measured annually in some lakes as a result of the monitoring stations being removed prior to the formation of ice cover in winter. Throughout the text, we refer to July to September (January to March in the southern hemisphere) as “summer,” in-line with previous studies (Woolway et al. 2017a). Each lake had measurements taken at a single location, except for Lake Tanganyika (two locations) and Lake Tahoe (four locations). We analyzed the data independently from each monitoring station in Lakes Tanganyika and Tahoe before combining the results in our statistical analyses (see below). Specifically, for lakes with more than one monitoring station, we calculated the surface heat fluxes (see below) for each site individually and then calculated a lake-wide average.

This article focuses on sensible ($Q_h$) and latent ($Q_e$) heat fluxes at the lake surface, each of which is positive when the direction of heat transfer is from the lake to the atmosphere (i.e., during surface cooling). The turbulent fluxes, $Q_h$ and $Q_e$, were calculated as:
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\[ Q_h = \rho_a C_{pa} C_h U_z (T_0 - T_z) \]  \hspace{1cm} (1)

\[ Q_e = \rho_a L_v C_e U_z (\eta - \eta_s) \]  \hspace{1cm} (2)

where \( \rho_a \) is air density (kg m\(^{-3}\)), estimated as a function of air pressure, air temperature, and humidity (Chow et al. 1988; Verburg and Antenucci 2010), \( C_{pa} = 1005 \text{ J kg}^{-1} \text{ K}^{-1} \) is the specific heat of dry air at constant pressure, \( C_h \) and \( C_e \) are the transfer coefficients for heat and humidity, which were assumed to be equal and adjusted for atmospheric boundary layer stability, measurement height, and wind speed (at \( z \) meter above the lake surface) by following...
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the computational method of Verburg and Antenucci (2010), and

\[ L_v = 2.501 \times 10^6 - 2370T_0 \]  

is the latent heat of vaporization (J kg\(^{-1}\)).

The humidity difference, \( q_s - q_z \), which influences evaporative heat transfer at the air-water interface, was calculated as the difference between the specific humidity of saturated air at the water surface temperature, \( q_s \) (kg kg\(^{-1}\)), and the specific humidity of unsaturated air at the measurement height, \( q_z \) (kg kg\(^{-1}\));

\[ q_s = 0.622e_{sat}/p \]  

and

\[ q_z = 0.622e_a/p \]  

where \( e_{sat} \) is the saturated vapor pressure at \( T_0 \) (mbar), calculated as:
Fig. 3. Across-lake monthly averaged (a) latent ($Q_e$, gray), sensible ($Q_h$, black), and the sum of turbulent heat fluxes ($Q_e + Q_h$, red) at the water–air interface, (b) the water–air humidity difference, (c) the water–air temperature difference, and (d) the wind speed adjusted to a height of 10 m ($u_{10}$). Averages are shown for 14 lakes with data available throughout the year (as shown in Fig. 2). The 95% confidence intervals are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 4. Across-lake summer (July–September in northern hemisphere and January–March in southern hemisphere) average diel cycles of (a) latent ($Q_e$, gray), sensible ($Q_h$, black), and the sum of turbulent heat fluxes ($Q_e + Q_h$, red) at the water–air interface, (b) the water–air humidity difference, (c) the water–air temperature difference, and (d) the wind speed adjusted to a height of 10 m ($u_{10}$). Averages are shown for 45 lakes. The 95% confidence intervals are also shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
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\[ e_a = 6.11 \exp\left[\frac{17.27T_a}{(237.3 + T_a)}\right] \]  \hspace{1cm} (6)

and \( e_s \) is the vapor pressure (mbar), calculated as:

\[ e_s = \frac{RHe_s}{100} \]  \hspace{1cm} (7)

with \( e_s \), the saturated vapor pressure at \( T_a \) (mbar), calculated as:

\[ e_s = 6.11 \exp\left[\frac{17.27T_a}{(237.3 + T_a)}\right] \]  \hspace{1cm} (8)

and \( RH \) is relative humidity (%), and \( p \) is air pressure (mbar).

In this study, we also calculate the Bowen ratio (\( B \)), which is commonly used with the energy budget method to estimate evaporation rates in lakes and reservoirs (Gibson et al. 1996; Lenters et al. 2005; Riveros-Iregui et al. 2017) and is defined as the ratio of mean \( Q_h \) to mean \( Q_e \):  

\[ B = \frac{Q_h}{Q_e} \]  \hspace{1cm} (9)

We also calculate the relative contribution of evaporation to the total turbulent heat flux, referred to hereafter as the evaporative fraction (EF), as:

\[ EF = \frac{Q_e}{(Q_h + Q_e)} = 1/(1 + B) \]  \hspace{1cm} (10)

As air pressure was not measured on all instrumented buoys and as local variability in air pressure has a negligible effect on the turbulent fluxes (Verburg and Antenucci 2010), a constant air pressure was assumed for each lake in this study, calculated based on the altitude of the lake (Woodway et al. 2015a). With the exception of air pressure, all data used to estimate the turbulent surface fluxes were measured directly above the lake surfaces, as opposed to over land. The latter approach was...
formally more common in limnology (Derecki 1981; Croley 1989; Lofgren and Zhu 2000) but has often been shown to cause large errors (Croley 1989), perhaps contributing to annual mean net surface fluxes that differ substantially from zero (Lofgren and Zhu 2000).

To understand the drivers of variations in turbulent heat fluxes among lakes, we modeled the summer and (where available) annual mean fluxes, calculated from the raw, high-resolution data, against lake attributes using a multiple linear regression model. Latitude, altitude, lake surface area, and depth were used as predictors in each multiple linear regression model evaluated in this study. Altitude and latitude are proxies for climatic variables (e.g., annual mean temperature and/or net radiation). Thus, we are not attempting to comprehensively isolate the ultimate climatic drivers of surface heat fluxes in this study but to identify patterns that would be of utility for simple geographic models.

All statistical analyses in this study were performed in R (R Development Core Team 2014). As the height of air temperature and relative humidity measurement varied among the lakes, we converted $T_a$ and $q_a$ to a surface elevation of 10 m ($T_{10}$ and $q_{10}$) prior to performing comparisons among lakes (Woolway et al. 2015). Similarly, in the across-lake comparisons, surface wind speed was adjusted to a height of 10 m ($u_{10}$) following the methods of Woolway et al. (2015a).

Results

Seasonal and diel cycles in turbulent surface fluxes

Many of the lakes investigated in this study followed a distinct seasonal cycle in their turbulent surface cooling terms (Figs. 2 and 3), albeit less pronounced over, or even absent, in tropical lakes (Fig. 2), where the turbulent fluxes demonstrate near-constant monthly mean values (e.g., Corumba). The latent heat flux ($Q_e$), and also the sum of the turbulent fluxes ($Q_h + Q_e$), followed a clear seasonal cycle in many lakes, especially those situated in temperate regions, being highest in summer as a result of a greater air–water humidity difference (Fig. 3a,b). The sensible heat flux ($Q_h$) followed a less pronounced seasonal cycle among all lakes but was, on average, highest in autumn as a result of a greater air–water temperature difference (Fig. 3a,c). Specifically, the surface temperatures of lakes typically retain summertime heat well into autumn, resulting in a larger air–water temperature difference at this time of year. This is particularly the case for deep, mid-latitude lakes such as Tahoe (California/Nevada; max. depth = 501 m) and Taupo (New Zealand; max. depth = 186 m), which experience highest turbulent heat fluxes well into autumn and winter as a result of their greater heat storage capacity. This also results in a higher Bowen ratio ($B = Q_h/Q_e$) in late autumn and winter (Supporting Information Fig. S1). The variation in surface wind speed, $u_{10}$, which was highest in winter, did not covary strongly with $Q_e$, $Q_h$, or $Q_h + Q_e$ at seasonal timescales (Fig. 3d).

Fig. 6. Relationship between lake surface area (log$_{10}$) and summer-mean (July-September in northern hemisphere and January-March in southern hemisphere) sum of turbulent heat fluxes ($Q_h + Q_e$) at the water–air interface across 45 lakes. Points are coloured according to climatic zones, which are defined by the absolute latitude of each lake: tropical (< 30°, black), temperate (30–60°, gray), and polar (> 60°, white). A statistically significant ($p < 0.05$) linear fit to the data is shown.

Table 1

The sensible and latent heat fluxes generally follow a clear diel cycle in summer, but the mean diel cycles are out-of-phase with each other, resulting in a minimal diel cycle in the sum of the turbulent fluxes (Fig. 4a) but considerable diel variability in $B$ (Supporting Information Fig. S2). $Q_h$ is highest during mid-afternoon and lowest during late evening and early morning hours as a result of the diel cycles in wind speed (Fig. 4d) and the humidity difference (Fig. 4b) at the air–water interface (see Eq. 2), both of which are highest during mid-afternoon. Sensible heat flux follows an opposite diel cycle, with highest $Q_h$ during the late evening and early morning hours, as a result of a greater air–water temperature difference during that time of day (Fig. 4c). Air temperatures above the lake surface tend to be cooler during the evening while the surface water temperatures retain daytime heat longer, resulting in a larger temperature difference. Interestingly, the diel cycle in $Q_h$ is opposite to that of $u_{10}$, to which $Q_h$ is related (see Eq. 1). This illustrates that the air–water temperature difference in the studied lakes is the main driver of the diel variability of $Q_h$, and that the magnitude of the air–water temperature difference outweighs the opposite influence of $u_{10}$ at diel timescales.

Relationships between surface fluxes and lake attributes

A multiple linear regression model including latitude, altitude, lake surface area, and depth demonstrates a statistically
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significant \((p < 0.05)\) effect of lake surface area and latitude on \(Q_e\) during summer and annually (Supporting Information Table S2). \(Q_e\) was higher in larger lakes (Fig. 5a and Supporting Information Table S2) and in lakes situated at low latitudes (Fig. 7a and Supporting Information Table S2). Lake surface area also had a statistically significant \((p < 0.05)\) relationship with \(Q_h\) (Fig. 5b) within the multiple linear regression model, with \(Q_h\) typically being higher in larger lakes during summer but not annually (Supporting Information Table S2). The relationship between lake surface area and both \(Q_e\) and \(Q_h\) was not always statistically significant when computing the linear regression within specific climatic zones, but this was primarily a result of the limited number of lakes with available data in some climatic regions (e.g., \(n = 8\) in the tropics; \(n = 7\) in polar regions).

The relationship between lake size and both \(Q_e\) and \(Q_h\) is explained, in part, by the lake-size dependence in over-lake wind speed. Larger lakes with greater fetch typically experience higher wind speeds (Fig. 5c) via the acceleration of wind over water. In the lakes studied, there was a statistically significant positive linear relationship between lake size and \(u_{10}\) during summer \((r^2 = 0.23, p < 0.001, n = 45)\) but not with latitude or altitude \((p > 0.1)\), thus suggesting an effect of lake fetch. However, we must note that the linear lake-size dependence in \(u_{10}\) is not likely to extend indefinitely to the world’s largest lakes, because once a lake reaches a certain (unknown) size threshold, the atmospheric boundary layer has essentially adjusted to the lake surface area, and so any further increases in lake size would not lead to further increases in over-lake wind speed.

The relationship of lake size and \(u_{10}\) results in greater \(Q_h\) and \(Q_e\) (Eqs. 1 and 2) in the lakes studied. However, \(Q_h\) and \(Q_e\) are also influenced by the air-water temperature and humidity differences, respectively; thus, the lake-size dependence of these differences must also be considered. There is no statistically significant lake-size dependence in the air-water humidity difference \((r^2 = 0.04, p = 0.17, n = 45)\), to which \(Q_e\) is related, in the studied lakes. However, \(Q_h\) and \(Q_e\) are also influenced by the air-water temperature difference \((r^2 = 0.16, p < 0.05, n = 45)\), with a greater temperature difference in smaller lakes (Fig. 5d). Therefore, the influence of lake size on \(T_{0} - T_{10}\) to which \(Q_h\) is related, is opposite to that of

Fig. 7. Relationship between latitude (shown as absolute latitude) and (a) latent \((Q_e)\), (b) sensible \((Q_h)\), and (c) the sum of turbulent heat fluxes \((Q_e + Q_h)\) at the water-air interface, and (d) the ratio of the summer-mean \(Q_e\) to summer-mean \(Q_h\) \((B = Q_e/Q_h\); gray), and the relative contribution of summer-mean \(Q_e\) to the summer-mean total turbulent heat flux \((EF = Q_e/(Q_h + Q_e)\); black). Statistically significant \((p < 0.05)\) linear fits to the data are shown, except for Fig. 7d, where an exponential relationship is shown.

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$u_{10}$, resulting in the relationship between lake size and $Q_h$, being weaker than the observed relationship between lake size and $Q_e$ (Supporting Information Table S2).

Relative contributions to total turbulent heat loss

In terms of the total turbulent heat fluxes ($Q_h + Q_e$), a multiple linear regression model (testing the influence of latitude, altitude, lake surface area, and lake depth) demonstrates that latitude and lake surface area are statistically significant predictors (Supporting Information Table S3). More total turbulent heat loss was found in lakes with greater surface area (Fig. 6) and in lakes situated at low latitude (Fig. 7c). In contrast to the diel cycle, which shows an out-of-phase covariance between $Q_h$ and $Q_e$ (Fig. 4a), lakes often show in-phase covariance on seasonal timescales (Fig. 3a). The magnitude of these turbulent fluxes, however, can differ considerably among lakes. The ratio of $Q_h$ to $Q_e$ (i.e., the Bowen ratio) demonstrates that $Q_h$ is consistently lower than $Q_e$ (Fig. 7d), with an average $B (= Q_h/Q_e)$ across all lakes of 0.23 ($\pm 0.11$ SD) during summer ($n = 45$). Fitting a multiple linear regression model (testing the influence of latitude, altitude, lake surface area, and lake depth) demonstrates that latitude is the only statistically significant ($p < 0.05$) predictor of $B$ (Supporting Information Table S4). As would be expected, the relevant contribution of $Q_e$ to total turbulent heat loss, in turn, increases toward the tropics (Fig. 7d). Specifically, $Q_e$ can contribute $>90\%$ of the total turbulent heat exchange in some lakes during summer (Fig. 7d). The contribution of $Q_h$ to total turbulent heat exchange increases at higher latitude, where summer $Q_h$ can contribute approximately 40\% of the total turbulent heat exchange. It is important to note that—particularly for deep lakes in mid-latitudes—significantly higher $Q_{sw}$ and therefore $B$, can occur in late autumn and into winter (Fig. 3 and

**Fig. B.** Relationship between latitude (shown as absolute latitude) and (a) the specific humidity above the lake surface ($q_{10}$; black) and at saturation ($q_s$; gray); (b) the specific humidity difference ($q_s - q_{10}$); (c) mean surface air temperature ($T_{10}$; black) and lake surface temperature ($T_0$; gray); (d) the temperature difference at the water–air interface ($T_0 - T_{10}$). Relationships are shown for summer (July–September in northern hemisphere and January–March in southern hemisphere) means across 45 lakes. Statistically significant ($p < 0.05$) linear fits to the data are shown, except for Fig. 8b,c where an exponential relationship is shown.
The decrease in $B$ with decreasing latitude is a result of the Clausius-Clapeyron relationship, with $Q_e$ higher in warmer lakes situated in warmer climates. To explain the effect of latitude on $Q_e$ (Fig. 7a), but not $Q_h$ (Fig. 7b), we compared, across lakes, the humidity and temperature differences at the air-water interface, to which $Q_e$ and $Q_h$ are, respectively, proportional. With decreasing latitude, we calculated a rapid and statistically significant ($p < 0.05$) increase in $Q_e - Q_h$, $T_s - T_a$, and $T_{10}$ (Fig. 8). We find no relationship of latitude to the air-water temperature difference in these lakes ($T_s - T_{10}$), while there was a statistically significant increase in the humidity difference ($q_e - q_h$) with decreasing latitude. The latter results from the nonlinearity of the Clausius-Clapeyron relationship and the resulting dependence of vapor pressure difference on temperature (Eqs. 6–8), which is strongly related to absolute latitude both annually ($r^2 = 0.89, p < 0.001$) and during summer ($r^2 = 0.79, p < 0.001$). Thus, at low latitudes, $q_e - q_h$ will be greater, resulting in higher $Q_e$ and lower $B$.

Discussion

We investigated the differences in turbulent surface heat fluxes from 45 lakes across 5 continents. These turbulent fluxes have been investigated in lakes around the world for many years (Dutton and Bryson 1962; Lofgren and Zhu 2000; MacIntyre et al. 2002; Momil and Ito 2008), but our study is the first, to our knowledge, to investigate and compare these fluxes across a range of climatic zones and lake attributes. In addition, many earlier studies that have calculated surface heat fluxes from lakes have used remotely sensed water temperature in combination with land-based meteorological measurements (Derecki 1981; Crole 1989; Lofgren and Zhu 2000) or reanalysis data (Moukomla and Blanken 2017), which can lead to erroneous estimates of air-water interactions. Studies that have calculated heat fluxes using in situ temperature and meteorology data have dealt primarily with single lakes (Laird and Kristovich 2002; MacIntyre et al. 2002; Lenters et al. 2005; Verburg and Antenucci 2010; Lorenzetti et al. 2015; Dias and Vissotto 2017), or a number of lakes from a confined region (Woolway et al. 2015a). Prior to this investigation, no known previous studies have compared turbulent surface fluxes from continuously recorded buoy data at so many lakes across the globe and at diel, seasonal, and annual timescales.

Using in situ observations from 45 lakes, we show that the turbulent surface fluxes of latent and sensible heat and their relative contributions to total turbulent heat loss at the air-water interface can vary considerably across temporal and spatial scales. Our analysis demonstrates that latent and sensible heat fluxes follow a pronounced diel cycle in summer and, for lakes with data available throughout the year, follow a predictable seasonal cycle in small to medium-sized temperate lakes, with high $Q_e$, $Q_h$, and $Q_e + Q_h$ in summer (later in the year for deeper lakes). In tropical lakes, the turbulent surface fluxes follow a less pronounced seasonal cycle, but rather experience comparatively high turbulent heat loss throughout the year, which is expected given the increase in heat gain toward the equator (Verburg and Antenucci 2010; Woolway et al., 2017a). The reduced seasonality of the lake heat content (the difference between minimum and maximum heat content) toward the equator demonstrates that heating and cooling are more separated by season at higher latitudes, resulting in a greater amplitude of the heat budget. In deep and large temperate lakes, such as Tahoe and Taupo, the turbulent energy fluxes are greatest during autumn and winter, as a result of the large heat capacity that causes their surface waters to cool more slowly during winter than the ambient surface air, as has been reported in other studies focusing on large, deep North American lakes (Blanken et al. 2011; Moukomla and Blanken 2017). These results indicate that the season in which the turbulent surface energy fluxes from lakes interact most strongly with the overlying atmosphere (and also affect internal lake mixing processes) can vary considerably among lakes.

A comparison across lakes of the relative contributions of $Q_e$ and $Q_h$ to the total turbulent heat flux demonstrates interesting relationships. The Bowen ratio ($B = Q_h/Q_e$) is found to decrease toward the tropics, as $Q_e$ increases with decreasing latitude (i.e., increasing lake surface temperature), while $Q_h$ does not. $B$ is lower in a warmer climate, both in summer and annually. Similar to lakes at low latitude, one might also expect that $Q_h$ would vary with altitude, as a result of the decrease in air temperature with increasing altitude and the temperature dependence of the specific humidity differences (for a given relative humidity). Specifically, we would expect an altitudinal dependence of $Q_h$ and also $B$ in the studied lakes. However, our global-scale analysis demonstrated that altitude did not have a statistically significant effect when investigated alongside latitude, lake surface area, and depth. Latitude was the only statistically significant predictor of $B$. In turn, the relevant contribution of $Q_e$ to total turbulent heat loss is greater in tropical lakes (upward of 90%) and then decreases toward higher altitude (~60% to 70%). While this relationship is expected due to the temperature dependence of specific humidity differences, this study is the first to calculate $B$ across a global sample of lakes using in situ high-resolution data collected at the lake surface. The lowest annual mean $B$ calculated in this study was 0.06 for Lake Tanganyika, while the highest annual mean $B$ was 0.31 for Rotoana. The lowest summer mean $B$ calculated was 0.04 for Lake Tahoe, while the highest summer mean $B$ calculated was 0.69 for Emalikson Lake, Alaska. Even higher values of $B$ have been reported on seasonal or shorter timescales in other lake studies. For example, Lenters et al. (2005) calculated a $B$ of 0.85 during early November in Sparkling Lake (Wisconsin), and other studies have demonstrated that $B$ can approach and even exceed 1 for some lakes during winter (Lofgren and Zhu 2000; Blanken...
et al. 2011), indicating that $Q_h$ can occasionally be larger than $Q_e$. This highlights the need for continued and expanded analysis of high-frequency heat flux measurements on lakes, particularly during the cold season when such measurements are difficult and infrequently undertaken.

Our results, in particular, those that illustrate the nonlinear functional form of $B$ with latitude, are useful for measuring/predicting the energy balance of lakes globally because a number of methods (and models) use estimates of $B$ to solve the energy balance and/or to estimate $Q_h$ or $Q_e$. A constant $B$ is used commonly in, for example, palaeoclimate studies and also in simplified lake models (Bultot 1993; Blodgett et al. 1997). Our results demonstrate that a common value of $B$ should not be assumed, and our findings can provide ways of estimating $B$ for lakes as a function of latitude, for example (e.g., in the absence of expensive instrumentation), which can help advance prediction of lake thermal processes. Moreover, our results challenge the validity of neglecting the effect of varying $B$, which has consequences for estimating lake thermal processes, which are fundamental to understanding lake biogeochemistry and ecology. The proportion of $Q_h$ : $Q_e$ is also important for understanding the influence of climate change on the water balance of lakes and in evaluating the role of lakes in the Earth’s hydrologic cycle, which is expected to accelerate with climate change (Wentz et al. 2007; Wu et al. 2013; Wang et al. 2018).

While our analysis included observations from lakes across five continents, these were typically restricted to specific years and, as such, may not have captured “normal” meteorological conditions for a particular lake, nor a reasonable range of interannual variability. As such, any lake-to-lake comparisons could have been biased by the presence of “abnormal” years (e.g., drought, flood, and heat waves). For example, one lake may have experienced temperatures above the mean while another lake experienced temperatures below the mean, which could bias our global relationships. Nevertheless, we have found the relationships between the turbulent heat fluxes, in particular with latitude and lake size, to be statistically significant. This occurs despite potential errors in the data and “noise” introduced into the global relationships by any one anomalous lake or anomalous weather during a given year. A caveat to our results regarding the relationship between latitude and the turbulent surface heat fluxes is that not all latitudes are equally represented by our study lakes, with fewer or no lakes in areas of critical climate gradients, such as the descending branches of the Hadley cell, which can influence local climate. In addition, latitude serves as a proxy for climatic variables (e.g., air temperature and net radiation) but not completely, as factors such as altitude also controls these same variables.

Although $Q_h$ is a relatively minor component of total turbulent heat loss in some lakes, contributing ~10% during summer in the tropics, it can be much larger during certain times of the year (and at diel timescales), which could influence greatly convective mixing in a lake and gas transfer at the lake surface. In particular, estimates of carbon dioxide emissions from lakes can be considerably biased when $Q_h$ is not considered (Podgrajsek et al. 2015). Climatic warming will likely increase $Q_h$ in the future, as suggested by the observation that summer-mean water surface temperatures in many lakes have increased more than air temperatures in the past few decades (O’Reilly et al. 2015), thereby increasing the lake-air temperature difference, to which $Q_h$ is proportional. Lake surface temperatures in high-latitude lakes, in which $Q_h$ is a relatively large contributor of total turbulent heat loss, have been suggested to experience an amplified response to air temperature variability (Woolway and Merchant 2017). Thus, as a result of the expected increase in $Q_h$ with climate change, there will be a relatively greater increase in total turbulent heat loss at high latitude. Any enhanced lake-air temperature differences induced by climate warming are also likely to be accompanied by enhanced heat loss via $Q_e$ and, in turn, affect gas fluxes into and out of lakes. However, we must note that changes in other meteorological variables associated with the turbulent fluxes, in particular surface wind speed (Woolway et al. 2017b), must also be considered.

This large-scale analysis of the spatial and temporal variations in turbulent surface heat flux processes among lakes has implications for carbon dioxide and methane emissions (Polienae et al. 2013; Podgrajsek et al. 2015). Previous studies have demonstrated that convective mixing dominates wind-induced mixing in small lakes (Read et al. 2012) and that a simple wind-based approach for estimating the gas transfer coefficient can underestimate lake metabolism and gas exchange with the atmosphere. While our results verify some aspects of this previous work, such as the significantly positive relationship between lake area and wind speeds, we also arrive at some important conclusions regarding the surface cooling processes that lead to convective mixing. For example, we show that turbulent surface cooling (especially $Q_h$) is considerably lower in small lakes whereas large lakes have considerably larger $Q_h$ and overall turbulent heat loss. These results indicate that the higher wind speeds that lead to greater wind-induced mixing on large lakes also lead to greater turbulent heat loss and potentially convective mixing, especially during times when such cooling processes are not offset by significant surface radiative heating (e.g., strong incoming solar and thermal radiation). Similarly, high rates of $Q_h$ and total turbulent surface heat loss are also found for lakes situated in warmer climates (e.g., tropical lakes). Therefore, our results suggest that convective mixing may be more important in large and tropical lakes than has been suggested previously and that convection may be a greater contributor to gas exchange in these systems as well.

Conclusions

We have analyzed high-resolution monitoring data from 45 lakes across 5 continents to study the global variation in
mean (summer and annually) turbulent surface heat fluxes at the air–water interface. Our results indicate the relative importance of lake location and lake-specific characteristics (e.g., surface area and depth) to the turbulent exchange of heat and energy at the lake surface and also how these fluxes vary at diel, seasonal and annual timescales. We demonstrate that the turbulent fluxes follow predictable diel and seasonal cycles in many lakes, and that, on average, the sum of the turbulent fluxes are greater in larger lakes and in those situated at low latitude. The ratio of mean sensible to mean latent heat fluxes, often referred to as the Bowen ratio and used commonly to estimate evaporation rates in lakes, was shown to vary predictably with latitude, being lower in the tropics. In turn, our study demonstrates that the relative contribution of latent to total turbulent heat loss in lakes varies predictably with latitude. In monsoon areas, evaporation is a major contributor to global energy balance of lakes globally, in particular in the absence of effective instrumentation required to solve the lake energy budget.

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Appendix B

A global turbulent heat flux analysis across lakes


Acknowledgments

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Conflict of Interest

None declared.

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Appendix C

Original Article

Long-term variation in numbers and biomass of silver eels being produced in two European river systems

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The European eel (Anguilla anguilla) population has been in decline at least since the 1960s and reliable regional information, particularly on the spawner production and escapement (i.e. the silver eel life stage), is a requirement of the EU stock recovery regulation. Two comparable time series exist in Burrishoole (Ireland) and Imsa (Norway), with monitoring of total silver eel production since the early 1970s. Numbers of emigrating silver eels fell significantly (p < 0.0001) in the 1980s (breakpoints: Burrishoole 1982; Imsa 1988), in both catchments from >4000 eels per annum to ~2000 eels per annum. The proportion of male eels dropped and the average size of female eels increased. Biomass of silver eels escaping has remained similar in Burrishoole (1.1/1.2 kg/ha), but not in Imsa (2.1/0.9 kg/ha) between the early period and the 2000s.

Factors that govern the onset of eel maturation (silvering) and the annual production of silver eels are little understood. In this paper, the influence of time-lagged environmental variables on silver eel production is examined. Annual variation in the time series was partly explained by variation in water temperature and water level. Annual number of migrating eels in both catchments was positively related to summer temperature and summer water flow, negatively related to summer temperatures in the previous year, and in the Burrishoole, also negatively related to high water levels in September/October. The models did not transfer well between catchments, indicating likely catchment specific environmental factors impacting on eel production. The reduction in eel numbers observed in both catchments, accompanied by the change in sex ratio and mean weight of females that contribute to maintain biomass production, calls into question the advisability of basing a spawner escapement recovery target on biomass alone, while numbers and proportions of males decline.

Keywords: Anguilla anguilla, annual production, biomass, silver European eel, temperature, water level

Introduction

European eel (Anguilla anguilla) spawn in the Sargasso Sea and recruit to the European and north African continental habitats following a trans-Atlantic larval migration. On arrival, the larvae metamorphose into glass eel and a proportion migrates upstream into inland waters where they are subject to many natural and anthropogenic pressures. The growth phase, when they are known as yellow eels, takes many years (sometimes decades) and varies between sexes, with males typically smaller and younger than females. The onset of sexual maturation or “silvering” occurs...
towards the end of their life cycle and is associated with prepara-
tion for the downstream and oceanic migration back to the
Sargasso Sea (Tesch, 2003). Triggers for the silverying process,
apart from size of the eel, are little understood, but are likely to
be linked to growth (Durif et al., 2005). Little is known about the
influence of environmental factors on this process. The long-term
datasets in this article provide an opportunity to examine the role
of time lagged environmental drivers, i.e. water temperature and
level, on the amount of annual silver eel production.

The eel population, which is genetically panmictic (Palm et al.,
2009), has been in decline at least since the 1960s, with a severe re-
duction in glass eel recruitment occurring in the early 1980s
(Moriarty, 1990a; Dekker, 2003; Alton et al., 2016; ICES, 2016).
This prompted eel conservation and stock recovery measures within
the European Union (European Council, 2007). EU Member States are now required by legislation (EC No. 1100/2007)
to contribute to the restoration of the European eel stock by imple-
menting eel management plans. The Regulation seeks to reduce an-
thropogenic mortalities to permit the escapement of 40% of the
silver eel biomass relative to the best estimate of the escapement
that would have existed if no anthropogenic influences had affected
the stock (European Council, 2007). Setting the historical baselines and
monitoring in biomass, rather than numbers, adds an extra
challenge for Member States when assessing compliance with the
Regulation, considering the overall paucity of relevant historical
data and limited opportunities for ground truthing outputs from
modelling exercises (e.g. Walker et al., 2011).

Long-term datasets of silver eel production and escapement are
few, and many are based on fishery yield or some form of es-
capement estimate, using one or a combination of methods such
as mark and recapture, acoustics and fisheries landings (Dekker,
2000a; Rosell et al., 2005; ICES, 2010). It is often difficult to de-
termine the representativeness (proportion of run captured, bias
in size or sex ratio) of such monitoring (Feunteun et al., 2000;
Allen et al., 2006; MacNamara and McCarthy, 2014; McCarthy
et al., 2014). Biases can occur when the fishing season does not
dcover the full migration period, when there is significant eel pro-
duction downstream of the fishery area assessed, or when the
implementation of management measures on fisheries introduces
discontinuities in the data.

Direct assessments of silver eel leaving a given catchment are
difficult to obtain due to the migration behaviour of the eel.
Silver eels tend to migrate at night, during dark moon periods
and in high water discharges making high capture efficiency diffi-
cult, especially in larger rivers (Vollestad et al., 1986; Bruijs and
Durif, 2009; Sandlund et al., 2017). Wolf traps (Wolf, 1951) or
similar capture systems can be used to provide precise estimates of
migrating eels and in some instances allow all silver eels to be
counted and measured. Full quantification of the number, size
and sex of silver eel leaving catchments has only been carried out
on a few systems with trapping facilities (Vollestad and Jonsson,
1986, 1988; Poole et al., 1990; Feunteun et al., 2000; Lafaille
et al., 2006; Acou et al., 2009). Only the time series in the Imsa
(Norway) and Burrishoole (Ireland) presented in this article in-
clude data collected before the collapse in recruitment during the
1980s. Such historical data are a requirement for setting historical
baselines for the EU (Piggins, 1985; Vollestad and Jonsson, 1986,
1988; Poole et al., 1990).

This study brings together the silver eel data sets from two
contrastingwatersheds in Ireland and Norway describing the
stock composition and long-term trends of the silver eel
production over a more than 40-year time span in rivers that
have experienced little or no exploitation. Neither river has been
stocked, nor had hydropower obstruction to migration. The eel
data represent the complete annual number of escaping silver eels
which are combined with environmental variables (temperature, 
water level) to explain how time lagged environmental drivers in-
fluence the year-to-year variation in annual numbers of migrating
silver eel being produced in each catchment. Similarities and dif-
fences between the catchments are discussed, and the use of
biomass as a management indicator in the light of continually
falling numbers and changing sex ratios is questioned.

Material and methods

Site descriptions
The Burrishoole system in western Ireland (53° 56’N, 9° 35’W:
Figure 1; and Supplementary Material) has a catchment area
of 100 km² and drains through two channels, the Mill Race and the
Salmon Leap, into the north-east Atlantic. The catchment has a
total productive wetted area of 474 ha (449 ha lacustrine, 25 ha
fluval). Feegh and Bunavela, the two largest freshwater lakes,
have mean depths >12 m, are oligotrophic (TP < 10 µg l⁻¹), col-
oured (c. 80 mg l⁻¹ PtoCo), and have low alkalinity (c. 20 meq
CaCO₃) and pH (c. 6.7). Average combined water discharge at
the river outlets is 4.2 m³ s⁻¹, ranging between 0.4 and 13 m³ s⁻¹,
although higher discharges have been observed but not quanti-
fied. Strongly influenced by the Atlantic Ocean (Jennings et al.,
2000), the climate is temperate and oceanic, with mild winters
and cool summers. Maximum air temperature rarely exceeds
20°C, while minimum winter temperatures are usually between 2
and 4°C. The geology is predominantly of low buffering capacity,
leading to acidic runoff, and overlaid with poorly drained pre-
dominantly peaty soils. There has been no commercial or recrea-
tional yellow or silver eel fishery and no stocking of eel.

The Imsa River in southwestern Norway (58° 54’ N, 5° 57’ E:
Figure 1; and Supplementary Material) has a catchment area of
128 km². The catchment has a productive wetted area of 1160 ha
(~800 ha of lake and ~360 ha fluval habitat). Maximum depths
of the five major lakes vary between 27 and 48 m. Water discharge
at the river outlet varies between 0.5 and 30 m³ s⁻¹ (mean 4.5 m³
s⁻¹). Similar to Burrishoole, climatic conditions are influenced by
the Atlantic Ocean, and it is relatively warm, considering the
northern location. Winter air temperatures are rarely below
−4°C and summer temperatures rarely above 24°C. The Imsa
has an average pH >6.8 and acid-neutralizing capacity ranging
between 150 and 230 µeq l⁻¹. There has been no stocking of eel,
but there was a restricted seasonal yellow and silver eel fishery up-
stream of the trapping station, which in the 1990s became rela-
tively small due to fewer landowners participating in eel fishing
and only hobby fishing, and the fishery closed from 2006. The
catches, when known, from this limited fishery were taken into
account in the production data in this study.

Silver eel trapping and recording of
environmental variables
Trapping of downstream migrating silver eel has been in opera-
tion in Burrishoole since 1958 and in Imsa since 1975. The traps
at the freshwater outflows of both catchments include Wolf type
downstream traps of similar design (Wolf, 1951; McGrath, 1969)
eploying horizontal grids with 10 mm gaps on a 1:10 inclina-
tion. Trapping at Burrishoole involves a fish fence and wolf trap

Appendix C
on the Mill Race outflow installed in 1958 and a full flow controlled Wolf trap on the Salmon Leap outflow (McGrath, 1969 and map in the Supplementary Material) installed in 1970 (Poole et al., 1990; Poole, 1994). Total annual captures probably represent about 90 ± 10% of the total run (Piggins, 1985). Years when extreme flood events led to known major losses of eel were 1978, 1984, and 1989 and these have been removed from the data.

In Imsa, trapping commenced in 1975 (Vøllestad and Jonsson, 1986, 1988). The total weight of the catch biomass from commercial silver eel fishing in the river upstream of Imsa was reported annually to the Research Station at Ims (Vøllestad and Jonsson, 1988). This was converted to numbers using the mean weight data of the eels caught in the trap that year, and added to the trap catch to give total silver eel production [in numbers and weight (kg) per ha]. No other fishing takes place on a regular basis (Vøllestad and Jonsson, 1988; Bergesen, pers obs.).

Daily water level and temperature (°C) were recorded on both the Burrishoole and Imsa outflow rivers. In Imsa, water discharge is estimated based on an empirical relationship between water level and discharge. The water level is recorded 15 m above the fish fence on the Mill Race and this is influenced by the amount of debris in the water. For this project, we used the lake water level, taken at the outflow of the lake 75 m upstream and away from any influence of the traps. Since the water level measurements from Burrishoole were obtained from two locations and with varying recorder setups and influences, a standardized Lake Feeagh water level time series was reconstructed, based on relationships estimated from periods with parallel recordings. Over the time-period, daily water temperature ranged from 1.5 to 23.5°C in Burrishoole and 0.2 to 24.2°C in the Imsa, with corresponding annual means of 9.2–12.4 and 7.7–10.7°C respectively. Imsa has warmer summer and colder winters than Burrishoole (Figure 2 upper graph). An examination of the temperature anomalies compared with the period 1971–2000 (1975–2000 for Imsa) indicated a period of warming in both catchments since 1997/1998 (Figure 2 lower graph).

### Appendix C

#### Data collection and analysis

In both catchments, traps were attended at least once a day and all silver eels were counted and recorded. Annual numbers analysed in this paper are the summation of the daily trap counts from 1 May to the 30 April in the following year, called "Silver Season". Samples of descending silver eels were taken throughout the run, measuring total length (TL: to the nearest 0.1 cm Burrishoole, 0.5 cm Imsa) and weight to the nearest 1 g (Imsa) or 5 g (Burrishoole). Length and weight data were not collected in the Imsa between 1993 and 2011 and only batch weights were taken in Burrishoole between 1971 and 1975, 1978/1979 and 1980–1983. For consistency, the sex ratio was determined from length frequency analysis of the sampled eels. The overlap between the male and female modes was separated using the technique described by Bhattacharya (1967). These analyses were confirmed by random dissections (Burrishoole; n = 1303; 1986–2016; Imsa; see Vøllestad and Jonsson 1986) using gross macroscopic examination (Frost, 1945; Bertin, 1956).

Production of silver eel was calculated in numbers and biomass (kg) per hectare (wetted area) of the watershed upstream of the trap. Biomass was calculated using the mean weight and total count, including the reported catches upstream of the trap in the Imsa.

Structural changes, or breakpoints, in the time series were dated using the function breakpoint in the R package strucchange (R Core Team, 2016) where we assume that coefficients shift from one stable relation to another (e.g. Bai and Perron 2003). A Two Sample t-test was used to verify that the difference in the means of the two time series before and after the breakpoint was significant. After the structural breaks in the data were accounted for, time series analyses were performed (e.g. Wei, 2006) to evaluate possible serial dependencies. For each catchment, autoregressive (AR) integrated moving average models were fitted to each time series segment and tested whether the same AR structure existed within a catchment before and after the break. Finally, with the break points and potential time series structures established, generalized models (GLMs) with a Poisson error distribution were fitted to look for covariates that together with, or instead of, the AR terms explained the variance in the number of emigrating eels.

Statistical modelling of variation in eel run and the relationship to environmental parameters was carried out using the statistical software R (R Core Team, 2016). In the initial models of the annual eel count in both catchments, monthly averages for temperature \( T_{Y,M} \) and water level \( W_{Y,M} \) were used as explanatory variables. The water level time series was standardized, since we assumed that it is the variation around the mean that is informative and not the absolute value at some arbitrary location. The 2-year period was chosen, assuming that the various underlying processes preparing for migration may last for an extended period. Different river systems likely have different bottlenecks or optimal periods for maturation and migration, so we should initially include a long period in the analysis. The effects of temperature and water level were assumed
to be accumulated over a few months, but rather than determining these periods \textit{a priori}, subsequent months that had the same effect on the model response were pooled to quantify the mean value over a longer period. For example, \( T_{e-1, \text{May-Nov}} \) will denote the mean water temperature from May to November the preceding year.

A maximum linear regression model including all explanatory variables was simplified by stepwise reduction based on the Akaike information criterion (AIC) (Sakamoto \textit{et al.}, 1986). If consecutive monthly averages for either water level or temperature had the same effect on the response, a model where these consecutive monthly averages for either water level or temperature were the same in both periods and that the covariates can-
dent from the model fitted to the time series after the break. Assuming the same AR structure before and after the break, the AR model still showed a weak significance \([\text{AR}(1) = -0.061; p = 0.061]\). A negative AR(1) coefficient indicates a temporal pattern where high emigration in 1 year may lead to a reduced emigration the next year.

\textbf{Results}

\textbf{Annual variation in number of silver eels}

There was considerable annual variation in silver eel counts in both Burrishoole and Imsa rivers (Figure 3). In both rivers, there was a downward shift in the 1980s in the annual numbers of migrating eels. In Burrishoole, breakpoint analysis indicated a break in the time series after 1982 (95% CI = 1980–1985), when the average count changed significantly (two sample t-test; \( p < 0.0001 \)) from 4719 eels to 2821 eels. In Imsa, breakpoint analysis indicated a break after 1988 (95% CI = 1987–1990) when the average count changed significantly (two sample t-test; \( p < 0.0001 \)) from 5815 eels to 2201 eels (data supplied in the Supplementary Tables S1 and S2). It should be noted that before the abrupt shifts, the average number of eels in Imsa was higher than in Burrishoole, while after the shift, the counts were higher in Burrishoole (Figure 3).

For Burrishoole, after the break in 1982 had been accounted for, no significant AR terms were found in either of the time series segments. For the Imsa time series with a break in 1988, the AR model with lag 1 year was close to being significant before the break \([\text{AR}(1) = -0.404; p = 0.085]\), and not significantly different from the model fitted to the time series after the break. Assuming the same AR structure before and after the break, the AR model still showed a weak significance \([\text{AR}(1) = -0.281; p = 0.061]\). A negative AR(1) coefficient indicates a temporal pattern where high emigration in 1 year may lead to a reduced emigration the next year.

\textbf{Influence of water temperature and level on annual eel run}

Finally, with break points accounted for and weak serial dependencies established for the time series, we fitted GLMs with a Poisson error distribution to the annual eel runs. The 1 year lagged autocorrelations of the time series were better explained by lagged covariates of water temperature, so no AR terms were retained in the models.

By fitting a model to the whole detrended time series, i.e. breaks accounted for, we assume that the modelled relationships were the same in both periods and that the covariates cannot explain the shift in mean level. Models fitted to the two periods separately gave similar results, and there was no obvious
relationship between the shift in eel numbers and the temperature or water level variables, which supported these assumptions. The fit of the models (Table 1) shows that the eel run in most years is well described by the model (Figure 4), although a few years have large residuals, indicating that there are some environmental variables affecting the eel run in some years that are not accounted for by the model. The years with large residuals occur in different years in the two systems (Figure 4).

The maximum model for Burrishoole, including all explanatory variables, had an AIC of 683.5. Stepwise removal of variables that did not improve the AIC, and biologically sensible pooling of months that had the same effect on the response, resulted in a simplified model with four variables and an AIC of 670.6 and $R^2 = 0.43$ (Table 1).

The detrended eel numbers in Burrishoole can be explained by a negative relationship with a warm previous season ($T_{t-1, May–Nov}$ - mean water temperature over all months from May to November), and a positive relationship to the current year’s conditions in August (both temperature and water level), while high mean water levels in September and October caused a decrease in the number of migrating eels (Table 1).

The maximum model for Imsa, including all explanatory variables, had an AIC = 652.6. Applying the same variable selection approach as for Burrishoole resulted in a model with an AIC = 644.8 and $R^2 = 0.48$ (Table 1). The detrended eel numbers in Imsa have a negative relationship with the mean temperature in June and July the previous year, and a positive relationship with mean temperatures in September and October the previous year. There was a positive relationship with mean temperatures in the summer (June and July) of the same calendar year, and with the mean standardized water level in January and February in the same year (Table 1).

When Imsa data were used to validate the Burrishoole model, the validation $R^2$ was close to zero. A similar result was obtained using Burrishoole data to validate the Imsa model, i.e. $R^2$ almost equal to zero. Thus, predicting the quantity of annual eel runs in one of the catchments from a model fitted in the other catchment gave poor results.

Size and sex

We used length as the indicator of eel size, while noting that there is a highly significant exponential relationship between length and weight allowing conversion to biomass. Although the Burrishoole eels were on average 10% heavier than the Imsa eels of the same length, the slopes in the log-log models were similar [Burrishoole $\log(\text{Weight}) = 3.11\log(\text{Length}) – 6.72$, $R^2 = 0.94$; Imsa $\log(\text{Weight}) = 3.12\log(\text{Length}) – 6.83$, $R^2 = 0.97$].

### Table 1. Significant variables and their coefficients and significance levels for the Burrishoole and Imsa run models.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimate</th>
<th>s.e.</th>
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<td>107</td>
<td>2.72</td>
<td>0.010</td>
</tr>
<tr>
<td>$WL_{Jan–Feb}$</td>
<td>–384</td>
<td>176</td>
<td>–2.18</td>
<td>0.036</td>
</tr>
</tbody>
</table>

$T$, water temperature (°C); $WL$, water level (m in Imsa, standardized lake water level in Burrishoole); $t$, year; and $t-1$, preceding year.

Figure 3. Annual counts of eels emigrating from the Burrishoole and Imsa Rivers between the early 1970s and 2015, with means for each period indicated by dashed lines. The breakpoints are indicated by vertical dotted grey lines and the 95% CIs around the breakpoints are shown above the x-axis.

Figure 4. Model run predicted outputs plotted against detrended silver eel counts for the Burrishoole and Imsa catchments. The straight line gives the 1–1 relationship.
There was a strong sex-related bimodal distribution of eel length in both Burrishoole and Imsa although the proportions differed between locations and over time (see Figure 5 for sample years). In Burrishoole, male eels ranged from 27.6- to 45.4-cm body length (dissected eels, n = 445) and females ranged from 37.5 to 105.3 cm (dissected eels, n = 859). Only three females were <40 cm. In Imsa, male eels ranged from 32.5- to 46.0-cm body length (n = 119) and females from 39.0 to 107.0 cm (n = 4164).

A multivariate linear regression model showed differences in the size of eels for each sex; both over time and between locations (see Supplementary Table S2). For male eels, and noting the large disparity in numbers of males between the two catchments, the males in Burrishoole were significantly smaller than those in the Imsa (−3.7 cm; p < 0.0001) in all periods. The males in Burrishoole decreased significantly in size by decade (p < 0.001) over the sample period, with males averaging 37.0 cm in the 1980s, 36.7 cm in the 1990s and 35.7 cm after 2000 (Figure 6). There were too few males in the Imsa to examine any change over time.

The female length model was highly significant (p < 0.001) with both decadal differences in each catchment and a significant interaction between catchments, noting the missing data in the Imsa in the 1990s and 2000s, and with competing tendencies in the 2010s when the Burrishoole females decreased in length while Imsa females increased. The female eels in Burrishoole were significantly shorter (−11.6 cm; p < 0.001) than those in the Imsa in all years sampled (Figure 5; and Supplementary Material). The female eels in Burrishoole increased in length from the 1970s until 1998, stabilised until 2005 and then started to decline in size again (Figure 7), averaging 50.3 cm in the 1970s/1980s, 52.0 cm in the 1990s, 52.8 cm in the 2000s and 49.6 cm in the 2010s (Figure 7; and Supplementary Table S3). In the Imsa, females were similar in length from 1982 to 1991 (61.9 cm in the 1980s and 62.8 cm in 1991/1992) and then increased to 68.7 cm in the last 4 years of the 2010s (Figure 7).

There has been a drop in the proportion of male eels in both catchments, in Burrishoole from >55% male before 1985 to...
both numbers and biomass in the Imsa. Weighed their increased average size, leading to the reduction in few in both periods. The reduction in numbers of females out-
erage weight of the females while the number of females remained
not significant (ANOVA), but the Imsa had a significantly (ANOVA, 
p < 0.0001) higher production in biomass per ha due to the larger size of the female eels (Table 2, Figure 8). In Burrisheoole, the redu-
ction in numbers over time was accompanied by a slight, but not significant (p = 0.134) increase in biomass while, in contrast, both the numbers and biomass fell significantly (ANOVA, p < 0.0001) in the Imsa (Figure 8; ANOVA outputs supplied in the Supplementary Table S4). This was due to the larger reduction in the number of males in the Burrisheoole and the increase in the average weight of the females while the number of females remained similar in both periods (Table 2). In the Imsa, males were relatively few in both periods. The reduction in numbers of females out-
weigthed their increased average size, leading to the reduction in both numbers and biomass in the Imsa.

**Production**

The average silver eel production in numbers per ha was higher in Burrisheoole than in Imsa for both periods (Analysis of variance (ANOVA), p < 0.0001) (pre- and post-1982 in Burrisheoole; pre-
and post-1988 in Imsa), but the Imsa had a significantly (ANOVA, 
p < 0.0001) higher production in biomass per ha due to the larger size of the female eels (Table 2, Figure 8). In Burrisheoole, the redu-
ction in numbers over time was accompanied by a slight, but not significant (p = 0.134) increase in biomass while, in contrast, both the numbers and biomass fell significantly (ANOVA, p < 0.0001) in the Imsa (Figure 8; ANOVA outputs supplied in the Supplementary Table S4). This was due to the larger reduction in the number of males in the Burrisheoole and the increase in the average weight of the females while the number of females remained similar in both periods (Table 2). In the Imsa, males were relatively few in both periods. The reduction in numbers of females out-
weigthed their increased average size, leading to the reduction in both numbers and biomass in the Imsa.

**Discussion**

The Burrisheoole (Ireland) and Imsa (Norway) rivers have been independently monitored using full river trapping systems of sim-
ilar design (see McGrath, 1969) for >45 years. Although the eel stock in each catchment has its own particular characteristics, some of the similarities are striking. In the 1980s, both catch-
ments experienced a sudden drop in numbers of eels emigrating, a reduction in the proportion of males in the silver eel run and an increase in the size of females. It seems likely that maturation (sil-
vering), and hence the level of annual production of silver eel, was positively related to summer temperature and summer water flow, negatively related to summer temperatures in the previous year, and in the Burrisheoole, also negatively related to high water levels in September/October.

Both catchments have experienced higher temperatures in the last 20 years compared with the 30 years before that, the Imsa more so than Burrisheoole (Fealy et al., 2014; this paper). Burrisheoole has also shifted towards mesotrophic conditions since the 1950s, associated with the commencement of commer-
cial coniferous plantations (Dalton et al., 2014). Untangling the relative influence of different factors, such as temperature, eel density and trophic changes, on eel stocks is difficult. Changing eel growth across Europe has been associated with rising tempera-
ture over the last century (Daverat et al., 2012) and the silver eel run has been commencing earlier (on average 0.8 days/year) in Burrisheoole (Sandlund et al., 2017). However, to our knowledge there are no previous studies showing how the level of annual production of silver eel might be influenced by time-lagged envi-
ronmental factors.

Little is known about the mechanism that governs the decision to mature and migrate, once an eel is in the optimum size range for the river, or about the factors that influence the physiological readiness to migrate, although these are likely to involve signifi-
cant changes in body constitution and energy (e.g. fat, protein, and dry matter) and also raised cortisol levels in the autumn linked to energy mobilisation (Van Ginneken et al., 2007). The environmental or physiological conditions that trigger the onset of maturation and silverying are still poorly understood (Durif et al., 2009).

Environmental variables (e.g. water level, water temperature) likely to influence the onset of silverying, using variables from the year of the migration and from the preceding year, explained ap-
proximately half the variation in annual eel count in each catch-
ment. Although there was little evidence of a regular pattern of low years following high years in either catchment, high summer temperatures were associated with greater numbers migrating in that year, and consequently lower numbers migrating the follow-
ing year. This was shown by a significant relationship with tem-
terature in June/July (Imsa) and May/November (Burrisheoole) in the previous year, and high temperatures in the current year in June/July (Imsa) and in August (Burrisheoole). Water level in August in Burrisheoole was also positively related to eel count. The onset of migration in the Loire River (France) was correlated with August temperature, discharge and sunshine hours (Durif and Elie, 2008). Temperature-related increases in growth and physiological activity could encourage a higher proportion of eels to reach the required physiological threshold switch for the onset of silverying in that year. Consequently, in the following year, there will be a lower proportion of eels near that threshold as they had migrated in the previous season and therefore less eels are available to migrate in those years following high tempera-
tures. The significant positive relationship in Imsa, with high

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**Appendix C**

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Figure 7. Boxplots for length (cm) of female silver eels in Burrisheoole and Imsa. The central box depicting the middle half of the data (25th–75th percentiles), the horizontal line across the box marks the median, the whiskers indicate the main extent of the connected data (−1.5*IQR) and extreme values are indicated by starbursts.

**Table 2**

<table>
<thead>
<tr>
<th>Year</th>
<th>Burrishoole female</th>
<th>Imsa female</th>
</tr>
</thead>
<tbody>
<tr>
<td>1976</td>
<td>70</td>
<td>90</td>
</tr>
<tr>
<td>1987</td>
<td>80</td>
<td>90</td>
</tr>
<tr>
<td>1993</td>
<td>90</td>
<td>100</td>
</tr>
<tr>
<td>1999</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>2005</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>2011</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>
temperatures in September/October leading to a higher migration in the following year, also supports that argument, where eels that were not quite at the threshold in the current season may have a longer growing season thereby facilitating silvering in the following year.

The relationship with water level in the Imsa in January and February may be related to an interaction between warm winters and higher precipitation or less ice, and therefore earlier influences on eel physiology than in colder drier winters. Such cold winters usually do not occur in Burrishoole. In Burrishoole, eel counts were lower than expected with increasing water level in September/October. This is counter-intuitive, unless we consider that this was an artefact related to high floods reducing trapping efficiency, which is considered unlikely.

The size of female silver eel and proportion of males observed in the two catchments in this study are consistent with the cline in these parameters demonstrated for American eel *Anguilla rostrata* (Helfman, 1988; Oliveira, 1999; Jessop, 2010) and European eel (Vøllestad, 1992), with less males and larger females with increasing latitude and distance from the Sargasso Sea. In the 1960s, partial trapping in Burrishoole indicated a silver eel male sex ratio of over 94% (Piggins, 1985), a fact supported by a yellow eel fyke net survey (Moriarty, 1974). The male ratio declined to circa 30% in the 1980s (Poole et al., 1990), and is currently around 44% in the most recent decade (this study). In contrast, the silver eel run in Imsa was dominated by females in the 1970s and 1980s, with the male sex ratio between 1 and 7% (Vøllestad and Jonsson, 1986, 1988), and this has now decreased to <0.5% males. These changes in sex ratio in both catchments have been accompanied by an increase in the average size of females. The number of females per annum in Burrishoole has remained similar while it has fallen in the Imsa since the mid-1980s. Andersson et al. (2012) noted a considerable decline in escapement of eels in the southern areas of Sweden over the past 50 years, but particularly in the 1960s and 1970s, inferred from fishing records and fisheries independent surveys. It seems likely that falling density of eel leads to lower proportions of males and some compensation by an increase in mean weight of silver eel (De Leo and Gato, 1996; Andersson et al., 2012; this study). The ratios of number to biomass observed in this study are probably catchment specific influences on eel physiology than in colder drier winters. Such cold winters usually do not occur in Burrishoole. In Burrishoole, eel counts were lower than expected with increasing water level in September/October. This is counter-intuitive, unless we consider that this was an artefact related to high floods reducing trapping efficiency, which is considered unlikely.

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Annual silver eel production and migration

and are likely to vary with latitude (Vøllestad, 1992) depending on the proportion and size of the female eels present in the catchments. Recruitment and escapement estimates are rare, especially before the 1980s (see review Supplementary Table S4) with the majority based on fishing yield or on estimates of escapement using mark-recapture or partial counts. In recent years, the Burrishoole has been producing about 1.1–1.4 kg/ha or 5.3–6.9 eels/ha, which is a similar weight per hectare as estimated for the Fremur catchment (1.3 kg/ha; Feunteun et al., 2000), the Shannon (1.5–1.6 kg/ha; MacNamara and McCarthy, 2014) and the Erne (1.5–1.7 kg/ha, McCarthy et al., 2014). However, it is a lower production in weight per hectare than estimated for the Imsa (3.51 kg/ha; Vøllestad and Jonsson, 1988), the Oir (4.8–6.9 kg/ha; Acou et al., 2009) and the Lake Ijsselmeer (4.4 kg/ha; Dekker, 2008b). Production in the Burrishoole and these other freshwater catchments is much lower than estimated for coastal lagoons in southwestern France (Bages-Sigean: 30 kg/ha; Amilhat et al. (2008) and the Mediterranean (Comacchio: 20 kg/ha; Rossi, 1979, Sardinia: 19 kg/ha; Rossi and Cannas, 1984). High yields have also been reported from some freshwater catchments where the yield was maintained by active transport and stocking of glass eels and elvers, such as Lough Neagh in Northern Ireland (>20 kg/ha; Moriarty, 1988).

Although the biomass production in Burrishoole has remained similar since the 1970s, the number of eels has decreased from an average of 11.5 eels/ha in the late 1970s to an average of 5.8 eels/ha in the 2000s. Production in 2015 was the lowest on record in the Burrishoole and second lowest in Imsa. In contrast, both biomass and numbers have fallen in the Imsa over a similar period. A decline in silver eel production has also been reported in the Irish River Shannon, at least since 1992, but due to changing fishing management practices it is difficult to understand the dynamics of that stock (Moriarty, 1990b; McCarthy and Cullen, 2000; MacNamara and McCarthy, 2014).

Mature eels are sexually dimorphic in size, with males being smaller than females. Both genetic and environmental factors have been implicated in sex determination and, for European eel, it has been related to various factors including population density, levels of recruitment and catchment characteristics (Davey and Jellyman, 2005). In general, male silver eels are more abundant at high densities whereas females predominate at lower densities (Parsons et al., 1977; Vøllestad and Jonsson, 1988). It is generally understood that in the European eel, optimum size for each sex is promoted, rather than age, and that this optimum size, especially in females, varies with distance from the Sargasso and with latitude (Vøllestad, 1992). The majority of female silver eels in Imsa are larger than in Burrishoole (this article; Haraldstad et al., 1985; Vøllestad and Jonsson, 1986; Poole et al., 1990; Poole and Reynolds, 1996), and in recent years this difference has increased.

Sex ratios can vary widely between catchments and over time (Parsons et al., 1977; Jessop, 1987; Poole et al., 1990; Oliveira, 1999; Oliveira and McCleave, 2000; Oliveira et al., 2001; Tesch, 2003). Changes in stocking densities (Parsons et al., 1977; Wickstrom et al., 1996) and natural recruitment (Rossi et al., 1988; Bark et al., 2007) have been implicated in altered sex ratios in some systems. It seems likely, therefore, that the changes observed in the Burrishoole and Imsa Rivers are a response to the observed low recruitment, which has been consistent with the decline observed across Europe since the early 1980s (Poole, 1994; Bornarel et al., 2017; Durif et al., in prep.), with falling local stock densities and maybe also changes induced by rising temperatures and catchment enrichment. Bark et al. (2007) illustrated temporal changes in population density and population structure in the River Piddle and other rivers in England and Wales, where a decline in population density since the mid-1970s was accompanied by a profound change in population structure, from one dominated by small eels to one currently dominated by large eels, clearly suggestive of a major recruitment failure. In rivers where eel populations were stable, the populations were male biased, while rivers with declining populations were female biased (Bark et al., 2007). Similarly, Lafaille et al. (2006) associated a shift from male to female dominance with a falling number of silver eels in the Fremur in France in an 8-year period after 2000, likely due to a number of factors including the installation of eel passes on the main hydraulic engineering structures in 1992 and 1996. Although sex ratio and eel size have been changing over a longer time scale in Burrishoole (Poole et al., 1990), likely influenced by environmental changes in the catchment (Dalton et al., 2014), it is not easy to find an explanation for the sudden drop in numbers of eels in Burrishoole and in Imsa, particularly as the annual silver eel run is composed of up to 20 or more age classes of eel (Poole and Reynolds, 1996; Durif et al., in prep.). The 6-year difference between catchments in the main drop in numbers during the 1980s is also difficult to explain.

The collapse in recruitment observed in the 1980s across Europe was preceded by a longer-term decline in landings, indicating a probable decline in the continental potential spawning stock (Dekker, 2003) and leading to a conclusion that insufficient spawning stock biomass might have caused the recruitment collapse. More current observations indicate possible Allee-effects (Allee, 1931), or depensatory mechanisms (Hilborn and Walters, 1992), taking place in the stock–recruitment relationship and likely caused by a disruption in the social mating system below a minimum spawning density (Dekker, 2004, 2008). The spawning target set in the EU Regulation is based on biomass of the combined sexes (European Council, 2007). If the demographics (e.g. numbers, size, and sex ratio) of the eel stock are changing, as indicated in these catchments (this article), and other areas (e.g. Ile Leo and Gato, 1996; Bark et al., 2007; Andersson et al., 2012), it is possible that by concentrating on a biomass only approach we may overlook social aspects of eel reproduction and miss the opportunity to positively influence the spawning stock recovery and further contribute to the decline in the stock.

In conclusion, annual counts and biomass of silver eels in the Burrishoole and Imsa rivers were remarkably similar: the numbers of eels emigrating from the 1980s to present decreased in both catchments, the Imsa lagging 6 years behind the Burrishoole. In both catchments, the proportion of silver males decreased and the size of the females increased, likely due to a combination of stock density and changing productivity of the catchments. Silver eel runs were more important after warm summers and this resulted in a reduction of the number of silver eels in the following year. Warm autumn temperatures in the Imsa may extend the growing season, facilitating more eels to silver the following year. The reduction in numbers observed in both catchments, accompanied by the change in sex ratio and mean weight of females that contribute to maintain biomass production, especially in the Burrishoole, calls into question the advisability of basing the silver eel recovery target under the EU Regulation.
solely on biomass, while numbers and proportions of males continue to decline.

Supplementary data
Supplementary material is available at the ICES/JMS online version of the manuscript.

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Appendix C

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