Original Article

Environmental drivers of a decline in a coastal zooplankton community

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Major changes in North Atlantic zooplankton communities in recent decades have been linked to climate change but the roles of environmental drivers are often complex. High temporal resolution data is required to disentangle the natural seasonal drivers from additional sources of variability in highly heterogeneous marine systems. Here, physical and plankton abundance data spanning 2003–2017 from a weekly long-term monitoring site on the west coast of Scotland were used to investigate the cause of an increasing decline to approximately -80± 5% in annual average total zooplankton abundance from 2011 to 2017. Generalized additive mixed models (GAMMs), with an autoregressive correlation structure, were used to examine seasonal and inter-annual trends in zooplankton abundance and their relationship with environmental variables. Substantial declines were detected across all dominant taxa, with ∼ 30–70% of the declines in abundance explained by a concurrent negative trend in salinity, alongside the seasonal cycle, with the additional significance of food availability found for some taxa. Temperature was found to drive seasonal variation but not the long-term trends in the zooplankton community. The reduction in salinity had the largest effect on several important taxa. Salinity changes could partly be explained by locally higher freshwater run-off driven by precipitation as well as potential links to changes in offshore water masses. The results highlight that changes in salinity, caused by either freshwater input (expected from climate predictions) or fresher offshore water masses, may adversely impact coastal zooplankton communities and the predators that depend on them.

Keywords: coastal, dominant taxa, salinity, time series, zooplankton

Introduction

Coastal regions are highly important due to their productivity and fisheries, and in the northern hemisphere these regions are particularly vulnerable to climate change impacts (Ramírez *et al.*, 2017; Stock *et al.*, 2017). Concern about these impacts on zooplankton are due to their importance as a food source for higher trophic levels and role in controlling phytoplankton blooms. While large inter-annual changes in the zooplankton communities of shelf seas have been linked to ocean-scale processes affecting circulation and temperature regimes (Edwards *et al.*, 2002;

Reid *et al.*, 2003), coastal ecosystems also respond to local conditions.

Multi-annual changes in zooplankton abundance and community structure are mostly attributed to changes in oceanic regime shifts as reflected by climate indices such as the North Atlantic Oscillation (NAO) or the Atlantic Multidecadal Oscillation (AMO; Goberville *et al.*, 2014; Montero *et al.*, 2020) and there are numerous literature reports and predictions of temperature linked zooplankton declines (Roemmich and McGowan, 1995; Piontkovski and Castellani, 2009; Chust *et al.*, 2014). The mechanisms underlying these changes have been linked to bottom up effects on

the timing and productivity of the phytoplankton community, or direct effects of temperature on thermal tolerance and development. In coastal waters the mechanisms driving the variation in zooplankton abundance are complex, often with a higher influence of local factors (Fanjul *et al.*, 2018, 2019), with temperature responses sometimes different from trends at the wider shelf sea-scale (Martens and van Beusekom, 2008; Bedford *et al.*, 2020).

Physical processes such as wind forcing and tidal advection play a role in the temporal variation of coastal zooplankton (Wiafe and Frid, 1996; Cheriton *et al.*, 2007). Freshwater input also influences local stratification, circulation, and salinity, which can affect coastal zooplankton diversity and biomass (Oghenekaro and Chigbu, 2019). Variability in salinity can cause osmotic stress if exceeding an aquatic organism's tolerance range, which varies greatly depending on species affinities, rate of change, exposure time, life history stage, and so on. Generally, those which are oceanic and neritic have optimal salinity ranges of ∼ 30–35 (although many neritic species are also found in salinities < 30), while estuarine species can tolerate much lower salinities. Osmotic stress may lead to increased mortality and reduced hatching success in some species (e.g. for crustaceans, Zajaczkowski and Legezyńska 2001; Anger, 2003; Chinnery and Williams, 2004). Salinity may also interact with other factors, such as temperature and food availability, to impact zooplankton community composition and abundance (Diekmann *et al.*, 2012). Additionally, terrestrial run-off may increase turbidity, affect nutrient concentrations, or release organic matter that can stimulate or inhibit plankton growth.

Declines across a large number of zooplankton taxa associated with increased freshwater input have been reported in Norwegian fjords (Kaartvedt and Aksnes, 1992; linked to hydroelectric activity) and Arctic fjords (Zajaczkowski and Legezyńska, 2001; linked to glacial meltwater). Species-specific declines related to salinity reductions have also been reported, e.g. for *Pseudocalanus elongatus* in the Baltic Sea (Möllmann *et al.*, 2000), for *Acartia* spp. and *Paracalanus* spp. at coastal sites in Chile (Krautz *et al.*, 2017), and for *Calanus finmarchicus* in the Massachusetts Bay (Turner *et al.*, 2011).

Few papers describe zooplankton communities in western Scottish coastal waters (e.g. Marshall, 1949; Gamble *et al.*, 1977; Heath, 1995) and there are no sustained plankton recorder (CPR) routes that cover western Scottish shelf seas. Nevertheless this region is of high economic and environmental importance due to aquaculture, fisheries and eco-tourism. The long term monitoring station at Loch Ewe, a sea loch on the Scottish west coast, is the only available sustained source of information on zooplankton dynamics in this region.

The wider circulation context of western Scottish shelf seas (Figure 1A) involves cross slope intrusions of "salty and nutrient rich" Atlantic waters on to the shelf (Ellett, 1979; Inall *et al.*, 2009), although recently Jones *et al.* (2018, 2020) found only limited exchange between Atlantic Water and coastal water. Intrusions of Atlantic Water are transported on the shelf and form part of the Scottish Coastal Current (SCC; Hill *et al.*, 1997), with one path flowing along the coast northwards past Loch Ewe. Due to the strong mixing of Loch Ewe waters with the coastal waters just offshore, some Atlantic Water influence and its associated changes can be expected in Loch Ewe. During high transports, which can be associated with Atlantic Water intrusions, much of the Atlantic Water might travel along the west side of the Outer Hebrides (Jones *et al.*, 2020) but further investigations on pathways of Atlantic Water and its signals are needed.

In Loch Ewe, the spring plankton bloom begins in March with fluorometric chlorophyll "a" concentrations increasing to a first peak in April and a secondary peak again around September, with the phytoplankton community being dominated by diatoms in spring and autumn, and dinoflagellates over the summer months (Bresnan *et al.*, 2015). The zooplankton community is dominated by copepods throughout the year, although Cirripedia larvae also dominate in spring coinciding with the phytoplankton spring bloom. The Cladocera, Hydrozoa, and Appendicularia are also highly abundant over summer months and the Chaetognatha over autumn and winter (Bresnan *et al.*, 2016).

In this study, seasonal and annual variability in zooplankton abundance was examined at Loch Ewe at a weekly resolution, in addition to concurrent measurements of phytoplankton and physical parameters. The purpose of this study was to identify (i) long-term variation in the zooplankton community and (ii) the environmental factors that may have an important role in explaining trends in the dominant zooplankton taxa.

Methods

Study site

Loch Ewe is a large (46 km^2) semi-enclosed coastal marine inlet (Figure 1) formed due to glacial erosion similar to fjordic marine environments. It is relatively shallow with an average depth of 20 m and maximum depth of 75 m, and with a low aspect ratio (length/width) in comparison with other Scottish lochs (Bresnan *et al.*, 2015). The 33 m sill depth at the opening of Loch Ewe provides regular exchange with coastal waters (flushing time of 3.5 days) that are dominated by the relatively fresh SCC, which consists of a mix of oceanic water (received through North Atlantic water inflow from the Atlantic Inflow Current (Porter *et al.*, 2018) as indicated in Figure 1a), freshwater runoff and coastal waters. The loch lies within a mountainous catchment area of 441 km^2 that receives high levels of precipitation, annual average of 203 ± 29 mm from 2003 to 2017, seasonally varying from extremes of 19 mm in the summer to 526 mm in the winter (Supplementary Figure S1). In excess of 95% of the catchment drains through Loch Maree (freshwater loch, surface area 30 km^2) which dominates the flow regime of the River Ewe (average of 30 ± 17 m^3 s^{-1} from 2003 to 2017, seasonally varying from extremes of 2 m^3 s^{-1} in the summer to 150 m^3 s^{-1} in the winter, Supplementary Figures S2 and S3). The river is the main source of freshwater input, although influxes of denser water from further offshore influence the salinity in Loch Ewe and long-term changes of water mass characteristics may be reflected in loch conditions. Surface salinity of the loch ranges from 20.0 (during extreme events measured at 1 m) to 34.7 at 10 m, while the near-bed layer (30–35 m) shows values from 32.0 to 35.1.

Loch Ewe is exposed to strong westerly winds, which enable mixing. Strong tidal forcing also plays an important role (Edwards and Sharples, 1986), with tidal mixing being another mechanism to entrain river water. Loch Ewe is dominated by the semi-diurnal (M2) tide in a northwest to southeast direction with a tidal range of around 4 m.

The monitoring site at Loch Ewe (57° 50.99' N, 05° 38.97' W), operated by Marine Scotland Science (MSS) as part of the Scottish Coastal Observatory (SCObs), has been sampled since 2003 (Bresnan *et al.*, 2016). The depth of the sampling site is 40 m and situated mid-loch, approximately 3 km from the sill and 9 km from
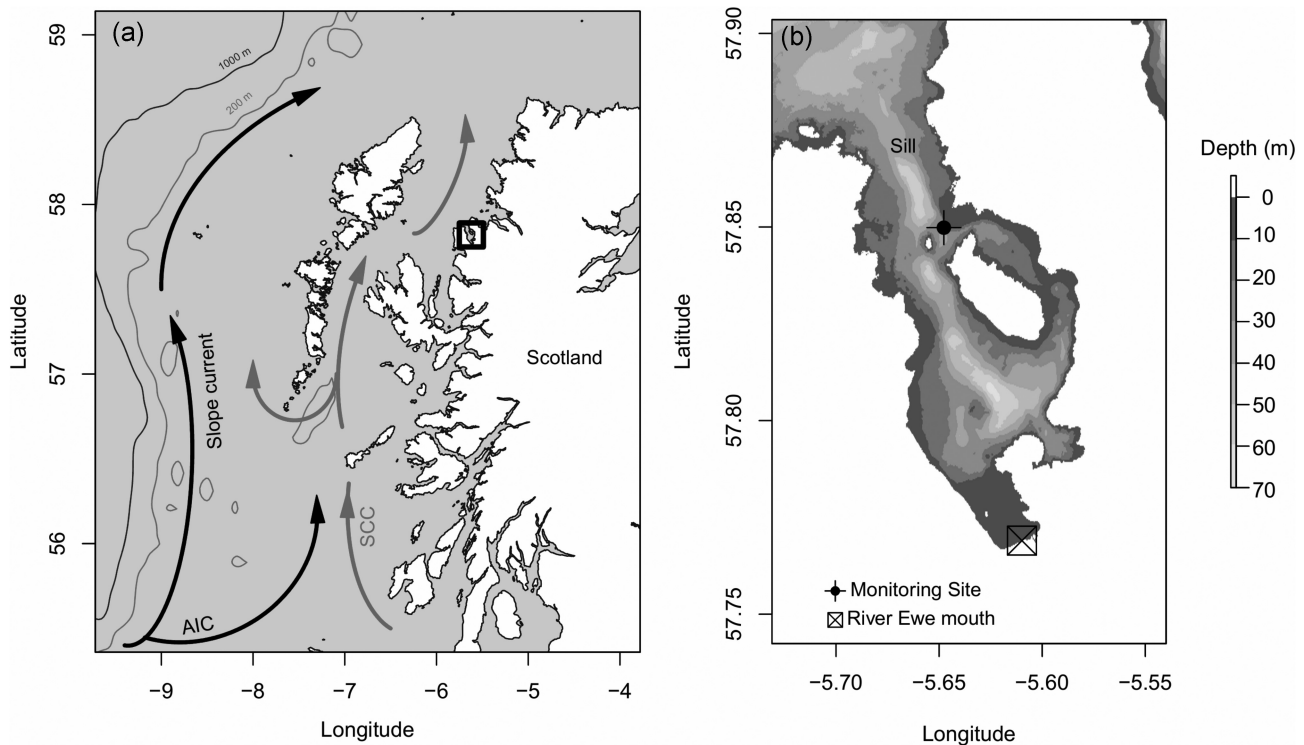
Figure 1. The location of Loch Ewe in Scotland with arrows indicative of the main current pathways (a). The saltier Slope Current and Atlantic Inflow Current (AIC) are represented by the black arrows and the fresher Scottish Coastal Current (SCC) by the grey arrows. The bathymetry of Loch Ewe and the positions of the monitoring site, sill and River Ewe mouth (b).

the River Ewe mouth, where riverine input may be more mixed. A number of smaller streams flow into the loch along the eastern and western coastlines and high precipitation and groundwater run off also contribute to the freshwater layer.

Sample collection and analyses

The sampling protocols for physical and biological parameters are described in detail in Bresnan *et al.* (2015, 2016). Briefly, between the 6th January 2003 and the 31st December 2017, temperature, salinity, (fluorometric) chlorophyll "a," phytoplankton and zooplankton community measurements were taken on a weekly basis. Secchi disk measurements were also taken from the 12th January 2012 to the 31st December 2017, excluding 2015. Sampling has continued to present, however zooplankton community analysis was temporarily suspended from 2018 to 2021, so the present study spans the period 2003–2017. Temperature and salinity were measured at the surface (at 1, 5, and/or 10 m) and at near-bed depths (30 or 35 m) using Niskin bottles fitted with digital reversing thermometers. Surface sampling depths varied over the years with 2003–2008 sample collections occurring consistently at 5 m and occasionally at 1 m, from 2008 to 2011 covering 1, 5, and 10 m, and from 2011 onwards only at 1 m. Supplementary Figure S4A shows the (uncorrected) 2003–2017 salinity record for all surface sampling depths, all measurements generally show the same changes, with the 1 m samples being strongly influenced by river flow events leading to drops in salinity. Supplementary Figure S4B illustrates an overlap period where this can be more clearly seen. From 2008 onwards more freshening events can be observed based on the shallower sampling depth. Averages for each parameter were obtained when

multiple samples were taken at the same date. Freshwater events in the surface layer are usually short-lived and entrained quickly into the deeper layers but the potential bias of the 1 m depth layer from 2011 and variations in sampling depths are detailed in the statistical method section. Near-bed samples were collected at 30 m from 2003 to 2008, and at 35 m from 2008 onwards. Phytoplankton were identified and enumerated as described in Bresnan *et al.* (2016). Counts (cells l^{-1}) of total diatoms and dinoflagellates were used in the present study. Zooplankton samples were taken using vertical 200 μm mesh bongo net hauls from 35 m to the surface. Samples were preserved in 4% borax-buffered formaldehyde and later analysed under a stereomicroscope. All copepods were identified to the lowest taxonomic level possible, whilst other taxa were grouped into categories. Where life history stages were counted these were pooled to give a total abundance for that taxa. The abundances of zooplankton are expressed as numbers of individuals per cubic metre (ind. m^{-3}). All methods follow quality assurance procedures in the MSS joint code of practice or UKAS ISO17025 with each data point assigned a quality flag based on the SEADATAnet quality flag system (Bresnan *et al.*, 2016).

River Ewe gauged daily flow rate data for the full study period and daily precipitation data (from 2003 to 2015) were obtained from the UK National River Flow Archive, station 94001 Ewe at Poolewe. Monthly accumulated precipitation data (from 2010 to 2017) was obtained from SEPA, station 115356 Inverewe Garden.

Statistical analyses

Prior to model fitting, data exploration was applied following Zuur *et al.* (2010). There were negligible missing data, with only three

(non-consecutive) weeks not sampled out of the 781 weeks in the study period. In addition to total zooplankton, dominant zooplankton taxa were selected based on their numerical abundance throughout the year and to represent different components of the community. These included broader taxonomic groups: the Hydrozoa, Appendicularia, Decapoda, Chaetognatha, Cirripiedia cypris, and nauplii; and species or genera in the Copepoda: *C. helgolandicus*, *C. finmarchicus*, *A. clausi*, *Pseudocalanus* spp., *P. parvus*, *T. longicornis*, and *Oithona* spp.; and the Cladocera: *E. nordmanni* and *P. leuckartii*. Of these taxa, *A. clausi* and *T. longicornis* are typical coastal neritic species and *Pseudocalanus* spp., *P. parvus* and *C. helgolandicus* are wide-spread in the North Sea, whereas *C. finmarchicus* is thought to originate from Atlantic waters (Fransz *et al.*, 1991). The Chaetognatha were dominated by *Parasagitta setosa*, a species known to be an indicator of coastal water with reduced salinities (Russell, 1935). In the Cladocera, *E. nordmanni* is a widely distributed euryhaline species and *P. leuckartii* is typically neritic, both are associated with lower salinity surface waters and cooler temperatures (Gieskes, 1971; d'Elbee *et al.*, 2014).

Seasonal and inter-annual trends in the physical data, phytoplankton, and zooplankton abundance were estimated using generalized additive mixed models (GAMMs). The models were fitted with two explanatory variables, "day of year" to model seasonal patterns and "time" to model inter-annual variation. The term "day of year" was defined as the day number within a year from 1 to 365. This represented the seasonal component and was fitted using a cyclic cubic regression spline, with value and first two derivatives matching at the year ends (Wood, 2003). The term "time" was defined as the number of days since sampling began, and was fitted using a cubic regression spline. As zooplankton abundances are highly seasonal, effectively modelling intra-annual variation (here using the "day of year" term) alongside any auto-correlation is important in order to establish whether there is a significant over all long-term trend. The term "time" represents the trend component of the model, i.e. long term changes in zooplankton abundance that would not be correctly captured without accounting for the seasonal component. The splines were penalized by the conventional integrated square second derivative cubic spline penalty (Wood, 2006), although the cyclic cubic regression spline had its penalty modified to shrink towards zero. Potential temporal dependence of the residuals and lags were assessed using autocorrelation function and partial autocorrelation function plots and Akaike's information criterion (AIC). Including a first-order auto-regressive correlation structure, nested within each year, was optimal and further helped to prevent over complex smoothing. A restricted maximum likelihood (REML) estimator of autoregressive parameters was used as opposed to maximum likelihood (ML), as REML estimators have been found to be less biased for time series of short to moderate length (Cheang and Reinsel, 2000). A second set of GAMMs were further used to investigate environmental variables that may explain the inter-annual variability in zooplankton abundances. The explanatory variables used in the model selection process were surface salinity, near-bed salinity, chlorophyll "a," dinoflagellate abundance, and diatom abundance. Collinearity between explanatory variables was assessed using multi-panel scatter plots, Pearson correlation coefficients and variance inflation factors (VIF). Explanatory variables that were collinear were not included in the same model (e.g. surface salinity and near-bed salinity). Backward selection using AIC was used to find the optimal model for each taxon. All models were fitted with the "day of year" term in order to account for seasonal variation.

The fits of all the models (both those first estimating patterns in temporal variation and then those with the addition of explanatory variables) were checked by examining residual plots and smoothing parameter estimation convergence information. Residual distributions were close to normal after transformations were made on some data. Specifically, the zooplankton data were fourth-root transformed, and the chlorophyll "a" data $\log_{10}$ transformed. The salinity data was handled according to Hughes *et al.* (2018); data from the surface was defined as that collected from depths less than 10 m, near-bed as that collected from within 10 m of the sea bed, and smoothed using a 12-week trailing running median with outliers greater than 4 *SD* difference removed. This method helped account for the variation in sampling depth and removed the impact of extreme single values, normalizing the distribution of residuals and allowing the salinity data to meet the underlying assumptions of the GAMMs To further validate this method and ensure the changes in sampling depth (sampling only at 1 m from 2011 onwards) did not have a significant impact on and bias in the surface salinity trend, the data from 1 m only (2008–2017) were tested separately and were found to still show a significant decline (results not shown). The approximate significance of smooth terms were checked to determine if the variable had a strong association to the seasonal cycle and/or inter-annual trend predicted by the model, or any environmental variables. The significance of whether smooth terms differ from zero in additive models is based on an approximate test. Although the test is low power, performance is improved with increasing sample size and so fairly robust in time series (Wood, 2013). The probability values were therefore used to determine the presence or absence of a given association, whereas statistical inference was based on the residual sum of squares and the degrees of freedom. All calculations were conducted using R 3.6.2 (R Core Team, 2019) and the *mgcv 1.8–31* package (Wood, 2006).

Results

Temporal trends

Long-term average variation in the total zooplankton abundance was high (mean annual abundance $\pm 1SD = 4031 \pm 1512$ ind. m^{-3}), but a clear inter-annual trend was nevertheless detected ($F_{4.3,773} = 31.61$, $p < 0.001$, Figure 2). Annual total zooplankton abundance remained stable between 2003 and 2011, after which an increasing decline was seen leading to very low abundances in 2017, which were on average 20% of the average annual abundance in 2011. The total zooplankton abundance also displayed a strong seasonal cycle with two annual peaks on average ($F_{6.9,770} = 61.89$, $p < 0.001$), with a rapid increase in March, declining in May before a larger secondary increase in July and remaining high until October after which it declined to a low stable level over winter (Figure 2). This predicted pattern was clear in the observed data in all years except for 2008 and 2012 where a sustained single peak in abundance was observed after March, and in 2017 where there was a complete breakdown of the seasonal cycle (Figure 2).

Surface salinity and near-bed salinity both displayed a clear freshening trend between 2003 and 2017 ($F_{1,776} = 21.77$, $p < 0.001$; $F_{1,776} = 15.74$, $p < 0.001$; respectively. Figure 3A). Both surface and near-bed salinity also displayed seasonal signals, with highest values over summer and lowest values in winter ($F_{4.9,772} = 6.93$, $p < 0.001$; $F_{6.8\ 770} = 26.3$, $p < 0.001$ respectively). A significant negative relationship with the River Ewe flow rate with a one week lag was found to explain 33% of the variation in surface salinity (GAM:
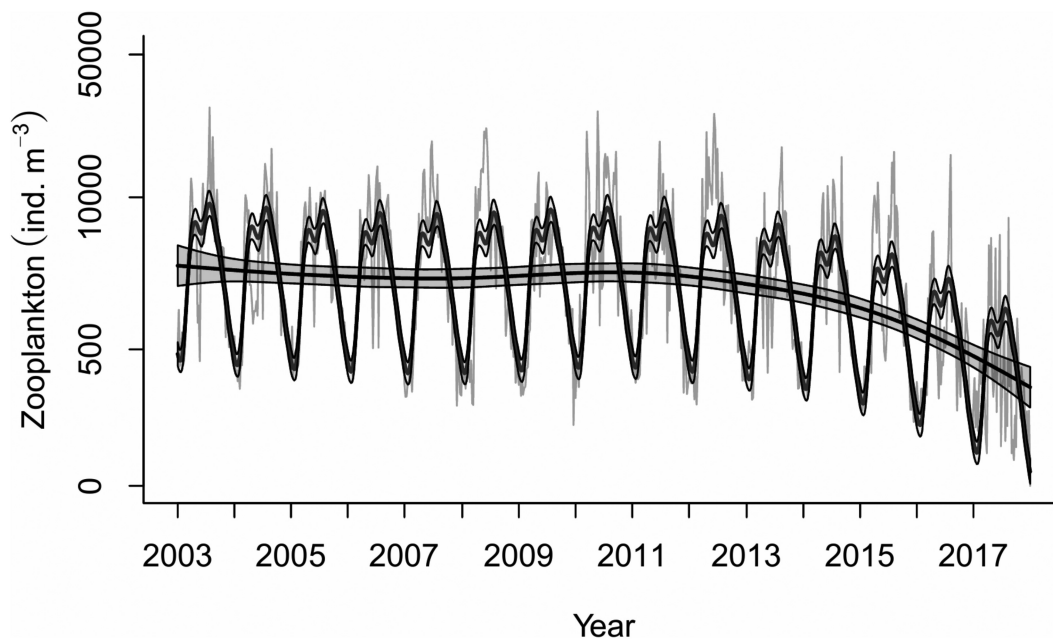
Figure 2. Weekly abundance of total zooplankton between 2003 and 2017 at Loch Ewe (grey line). The data are fourth root transformed and the *y*-axis is scaled to reflect this. The thick black lines represent the fitted seasonal and inter-annual trends for the time series, the thin black lines enclosing the shaded grey areas the respective 95% *CI*.

$F_{3.5,763} = 103.3$, $p < 0.001$; Supplementary Figure S5) and a 2-week lagged flow rate 29% of the variation in near-bed salinity (GAM: $F_{6.5,760} = 46.91$, $p < 0.001$; Supplementary Figure S5).

Significant inter-annual trends were also observed for sea surface temperature (SST) and chlorophyll "a" concentration. SST displayed a steady decrease from 2003 to 2013 after which it gradually increased again up to 2017 ($F_{3.2,774} = 8.08$, $p < 0.001$; not shown). Chlorophyll "a" concentrations were lower on average from 2013 to 2017, than between 2003 and 2012 ($F_{3.5,774} = 5.24$, $p = 0.001$, Figure 3B), however, there were no significant inter-annual trends for total diatoms ($F_{1.8,775} = 1.32$, $p = 0.187$) or total dinoflagellates ($F_{2.2,775} = 2.21$, $p = 0.086$).

Environmental drivers of zooplankton trends

Temperature did not significantly explain inter-annual variation in zooplankton abundances at Loch Ewe. The small temperature decline mid time series was not sustained. Temperature was associated with zooplankton seasonality, but there was no correlation between inter-annual trends of temperature and total zooplankton. Given this study's focus on multiannual trends in zooplankton, temperature was removed as an explanatory variable during model selection.

Temporal variation in total zooplankton abundance was best explained by surface salinity and chlorophyll "a," in addition to the seasonal component, but also displayed a significant relationship with near-bed salinity (Table 1). Total zooplankton abundance showed a positive relationship with surface salinity, near-bed salinity, and chlorophyll "a" (Figure 4). Along with the seasonal component, surface salinity was the most important variable in explaining the temporal variation of the dominant zooplankton taxa, being included in the most models following the model selection process (Table 1). Near-bed salinity was included in fewer models following model selection than surface salinity (Table 1) and no significant

relationships were found with *A. clausi*, *T. longicornis*, *C. finmarchicus*, and Appendicularia. The relationships of all the taxa in Table 1 with salinity were positive.

The most important explanatory variable after salinity was chlorophyll "a," which was included in the models for Decapoda and *Oithona* spp., in addition to total zooplankton (Table 1). Both taxa showed significant positive linear relationships with chlorophyll "a." *Paracalanus parvus* and Appendicularia also both showed significant relationships with diatom abundance (Table 1); which was positive and non-linear in the Appendicularia but in *P. parvus* the relationship was negative when diatom abundances exceeded 250000 cells l^{-1}. Dinoflagellate abundance was also included in the model for *A. clausi*, which showed a positive linear relationship (Table 1).

Several dominant taxa had no significant inter-annual trend and/or no significant relationship with either surface or near-ned salinity. There were no significant inter-annual trends in the Cladocera *E. nordmanni* ($F_{1,776} = 1.54$, $p = 0.215$) or *P. leuckartii* ($F_{3.2,774} = 2.03$, $p = 0.108$) and inter-annual variability in the abundances of both species could not be significantly explained by salinity, chlorophyll "a" or the phytoplankton community. Likewise, no explanatory variables were found to explain the slightly negative inter-annual trend in Cirripedia cypris, which was marginally non-significant ($F_{3.2,774} = 2.25$, $p = 0.052$). However, a significant negative inter-annual trend found in Cirripedia nauplii ($F_{5.1,773} = 6.65$, $p < 0.001$) was partially explained by diatom abundances in addition to the seasonal component ($F_{1,776} = 35.55$, $p < 0.001$).

Discussion

A synchronous multi-annual decline in the majority of zooplankton taxa from a planktonic community, as seen at Loch Ewe, is unusual for coastal ecosystems. The importance of salinity was contrasted by the lack of a temperature effect. Although
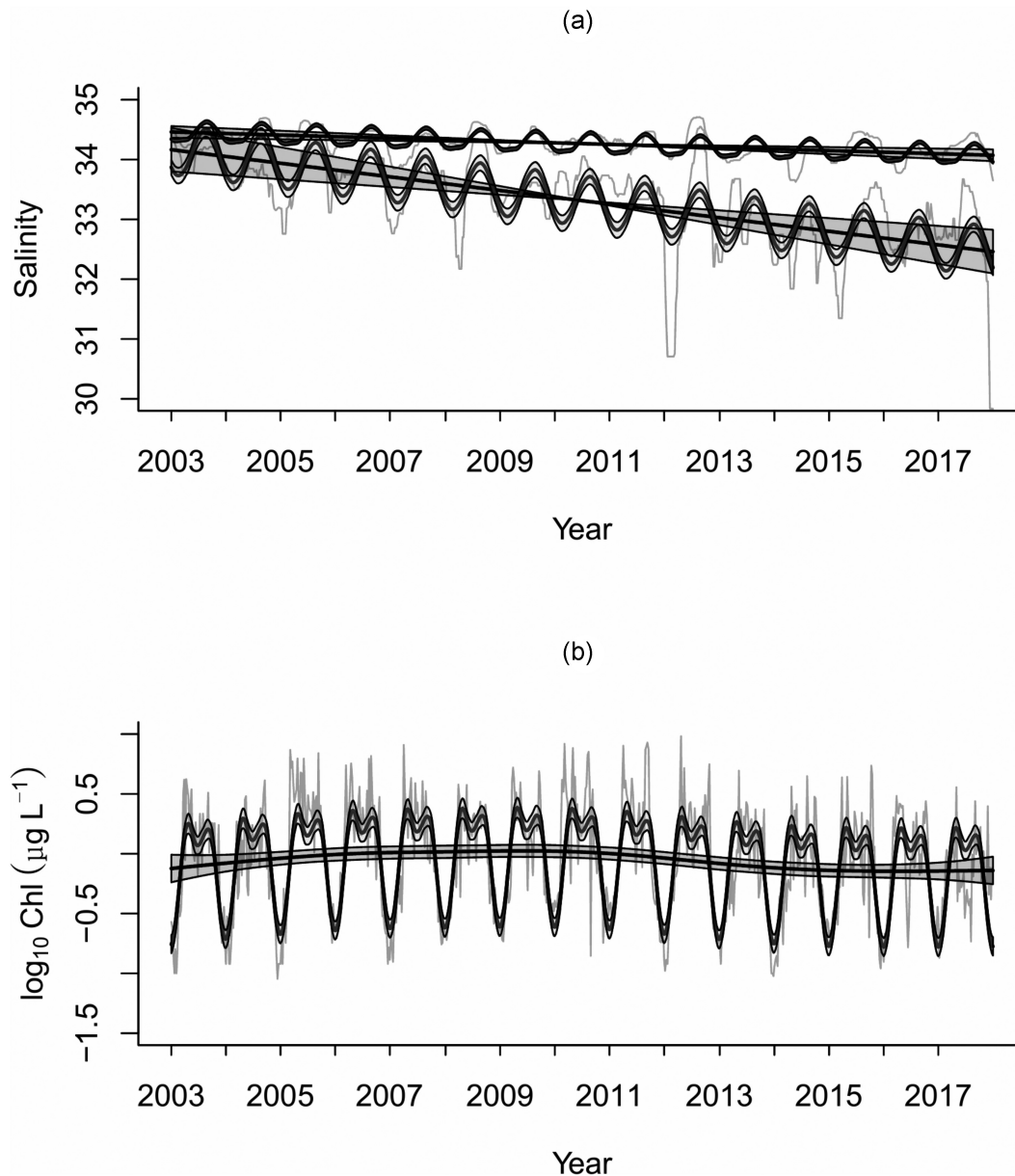
(a)

(b)

Figure 3. Twelve week rolling median near-bed salinity and surface salinity (a, upper and lower time series respectively) and weekly fluorometric chlorophyll "a" (b) measurements between 2003 and 2017 at Loch Ewe. The grey lines represent the observed data. The black lines represent the fitted seasonal and interannual trends for the time series with the thin black lines enclosing the shaded grey areas the respective 95% *CI*.

warming trends have been increasingly found to affect zooplankton dynamics (Chust *et al.*, 2014), temperature had no significant association with long term zooplankton abundances at Loch Ewe. There are several mechanisms that could instead explain the salinity-associated declines across a large number of zooplankton taxa.

Physical processes and the reduction in salinity at Loch Ewe

One component of the decreasing salinity trends at Loch Ewe resulted from an increased number and intensity of freshening events. The River Ewe flow rate explained more variation in surface salinity

compared to near-bed (33% vs. 29%). This is consistent with basic physical dynamics and estuarine circulation where strong freshwater inflow leads to a two-layer flow, with a fresh upper layer resulting in a buoyancy-driven flow (and more variability in salinity in the surface layer) (Rabe and Hindson, 2017). However, greater mixing of the water column at Loch Ewe, likely driven by the shallow depth, is indicated by the variation in near-bed salinity that is explained by River Ewe outflow.

Another component driving changes in physical characteristics in Loch Ewe is the link of conditions to those in the North Atlantic via the SCC, although no measurements of coastal inflow into the loch exist. An extreme freshening in the subpolar North Atlantic existed during 2012–2016 (Holliday *et al.*, 2020) and further anal-

Table 1. The GAMM results for total zooplankton and dominant taxa showing model outcomes following the model selection process. Environmental variables included in the models alongside the seasonal component and surface salinity are shown, and the approximate significance of each. Results from the second set of GAMMs are also shown for taxa that showed a significant association with near-bed salinity (bold). The estimated degrees of freedom (d.f) for each variable and the adjusted R^2 for each model (including the seasonal component) are also shown.

Taxa (ind. m^{-3})	Explanatory variable(s)	F-value	p	d.f	R^2
Total zooplankton	Surface salinity	10.10	< 0.001	2.1, 775	0.56
	Chlorophyll "a"	4.13	0.042	1, 776	
	Near-bed salinity	**9.83**	**0.002**	**1, 776**	**0.53**
	Chlorophyll "a"	**4.68**	**0.031**	**1, 776**	
Decapoda	Surface salinity	21.27	< 0.001	3.42, 774	0.68
	Chlorophyll "a"	8.08	0.005	1, 776	
	Near-bed salinity	**13.04**	**< 0.001**	**2.03, 775**	**0.64**
	Chlorophyll "a"	**9.15**	**0.003**	**1, 776**	
Acartia clausi	Surface salinity	10.32	< 0.001	1, 776	0.64
	Dinoflagellates	3.89	0.049	1, 776	
Temora longicornis	Surface salinity	6.78	0.009	1, 776	0.61
Hydrozoa	Surface salinity	8.17	< 0.001	3.09, 774	0.57
	Near-bed salinity	**6.92**	**< 0.001**	**2.62, 774**	**0.55**
Oithona spp.	Surface salinity	17.69	< 0.001	2.41, 775	0.47
	Chlorophyll "a"	4.63	0.032	1, 776	
	Near-bed salinity	**17.75**	**< 0.001**	**1.33, 776**	**0.43**
	Chlorophyll "a"	**5.37**	**0.021**	**1, 776**	
Paracalanus parvus	Surface salinity	12.77	< 0.001	2.20, 775	0.42
	Diatoms	3.70	0.045	1.96, 775	
	Near-bed salinity	**5.66**	**< 0.001**	**3.23, 774**	**0.42**
	Diatoms	**3.18**	**0.043**	**2.01, 775**	
Appendicularia	Surface salinity	7.92	0.005	1, 776	0.38
	Diatoms	9.38	< 0.001	3.52, 773	
Calanus finmarchicus	Surface salinity	3.08	0.035	1.9, 775	0.36
Calanus helgolandicus	Surface salinity	13.08	< 0.001	2.77, 774	0.35
	Near-bed salinity	**23.51**	**<0.001**	**2.77, 774**	**0.35**
Pseudocalanus spp.	Surface salinity	8.98	< 0.001	2.22, 775	0.31
	Near-bed salinity	**8.76**	**< 0.001**	**1.40, 776**	**0.29**
Chaetognatha	Surface salinity	7.18	0.002	1.42, 776	0.16
	Near-bed salinity	**4.47**	**0.010**	**1.80, 775**	**0.29**

ysis of the pathway of this fresh water along the Scottish coast is required. Preliminary analysis of long-term monitoring sites shows that this signal could indeed have been advected into Loch Ewe, but the underlying physics need further exploring.

Short-term high salinity intrusions of Atlantic Water during storm-driven across-shelf flows towards the coastal mooring site at the Tiree Passage further south at 56.6 °N have been investigated by Jones *et al.* (2020). These coastal waters then flow northwards but the Minch region (located between the Tiree Passage and Loch Ewe) could act as a potential barrier to the flow of the SCC, forcing the flow around the western side of the Outer Hebrides. Therefore, water mass changes observed at the Tiree Passage could have limited possibilities to influence down-stream conditions in Loch Ewe, although a proper analysis of signals and pathways and correlations between sites is still needed, but beyond the scope of this paper. With a flushing time of Loch Ewe of 3.5 days (Edwards and Sharples, 1986) conditions within the loch will generally reflect conditions on the shelf but unfortunately a long-term mooring does not exist in the northern part of the Minch closer to Loch Ewe. Future work might however be able to create links to data from the Tiree passage mooring, for example, or other relevant monitoring sites along the pathway.

Potential changes in water masses in the SCC and their influx into Loch Ewe, along with an analysis of terrestrial freshwater inputs, could be used to explain the residual variation in salinity and the zooplankton community at Loch Ewe, and the role of advec-

tive processes. The positive associations of several dominant taxa with near-bed salinity may be an indication of advection, as direct impacts from salinity and freshwater inflow are unlikely to be the mechanism driving zooplankton variation at near-bed depths. However, regional assessments do not suggest overall declines in North Atlantic mesozooplankton (Bedford *et al.*, 2020). In future, sampling of zooplankton would benefit from discrete sampling at depths and towards the sill to determine transport processes of zooplankton in Loch Ewe.

Surface flow

Zooplankton in surface waters could be flushed sea-ward by strong buoyancy-driven flows, according to typical estuarine circulation which relies on tidal mixing and freshwater inflow. However, many zooplankton taxa maintain their horizontal position through vertical migrations (Kaartvedt and Nordby, 1992; Epifanio and Cohen, 2016). The stable inter-annual abundances of surface inhabiting species, e.g. the Cladocera *E. nordmanii* and *P. leuckartii*, indicate that the freshwater flushing of zooplankton, out of Loch Ewe, is unlikely to be causing the observed declines.

Osmotic effects

Osmotic stress may explain salinity driven declines in zooplankton at Loch Ewe. The mechanisms by which it acts on individual species
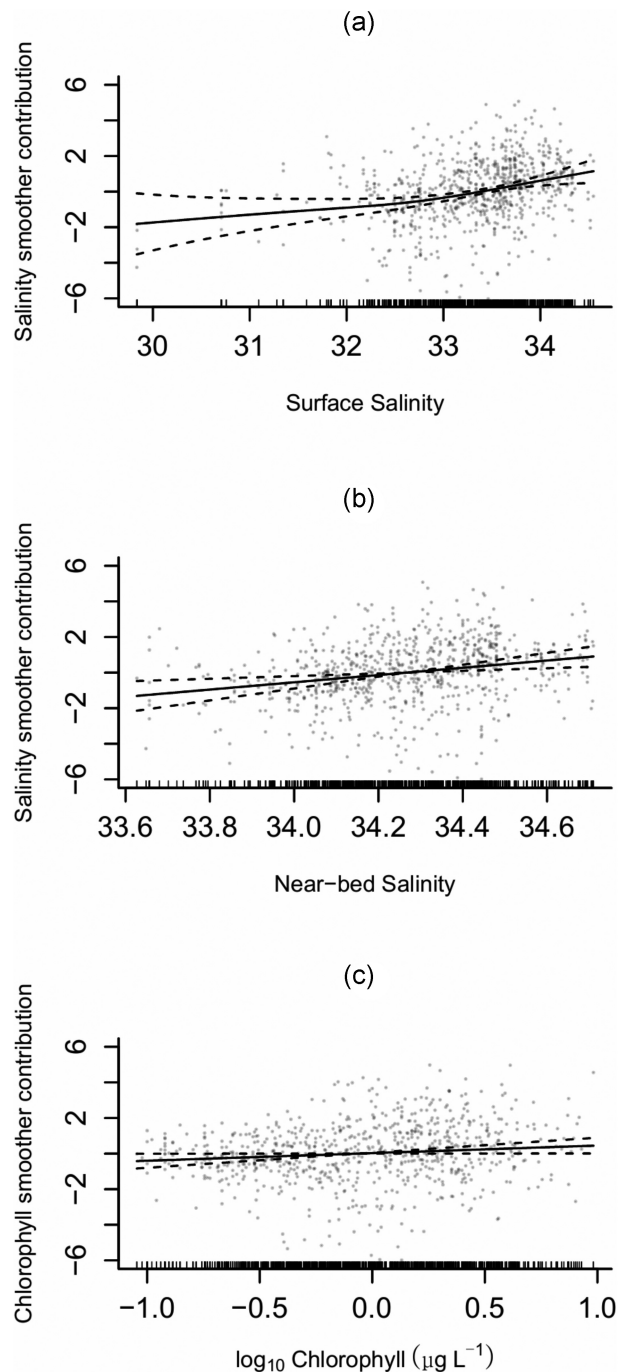
(a)

(b)

(c)

Figure 4. The smooth terms for surface salinity (a), near-bed salinity, (b) and fluorometric chlorophyll "a" (c) on total zooplankton abundance obtained by the GAMMs Note the salinity scales are different. The *y*-axes show the values of the smooth term centred around the intercept. The solid line represents the cubic regression spline and the dashed lines indicate 95% *CI*. The grey points show the partial residuals for each smooth term.

are likely complex, and will vary between species based on species physiologies and locations in the water column. Taxa in surface waters, where salinity is highly variable, are more likely to experience osmotic stress.

For several taxa in the present study associations with salinity were only significant at the surface. The impacts of reduced salinity may be lethal for some species, e.g. *Calanus* spp. exposed to salinities of 24 in laboratory experiments, experienced 25–100% mortality within an hour (Zajaczkowski and Legezyńska, 2001). In other species, such as many of the dominant species at Loch Ewe, there may be tolerance of a wide range but preference for higher salinities (Andersen and Nielsen, 2002). Additionally, sub-lethal impacts of reduced salinity may depend on the life stage. In *T. longicornis* nauplii from acclimatized females successfully hatch at salinities as low as 8, but hatching success and nauplii survival increases with salinity and is optimal > 24 (Holste *et al.*, 2009). In *A. clausi,* nauplii appear to be the more sensitive life stage with the highest hatching success and naupliar survival at a salinity of 33.3 (Chinnery and Williams 2004).

There was no positive trend for taxa with wide salinity tolerances, and the occurrences of the brackish water copepods *Acartia discaudata* and *A. bifilosa* did not increase over the study period (*A. bifilosa* was only recorded twice in 2003 and *A. discaudata* 12 times overall in the years 2002, '04, '07, '14, '15, and '16; all with relatively low abundances between 0.3 and 13 ind. m^{-3}), suggesting the decline in zooplankton is likely complex.

Disrupted feeding

Zooplankton may change their vertical position to avoid a freshwater layer. However, if maximal phytoplankton growth occurs near the surface, particularly in stratified waters (Durbin *et al.*, 2003), then zooplankton movement out of that layer means they would also be avoiding optimal feeding conditions. Freshening events may therefore create a trade-off between avoiding osmotic stress and exposure to phytoplankton food availability for zooplankton.

Disrupted feeding may also result from increased turbidity events following periods of heavy rainfall that can carry terrestrial run off in the form of soils and inorganic matter. High quantities of suspended particulate matter are known to disrupt zooplankton feeding through avoidance behaviour, rejection or regurgitation of the inedible particles, or by filling the gut in place of nutritional food particles (Arendt *et al.*, 2011; Sew *et al.*, 2018). As well as decreasing salinity, intense precipitation events will also increase groundwater run-off at Loch Ewe which is more likely to carry particulate matter, as indicated by a positive association between salinity and secchi disk depth at Loch Ewe, particularly for secchi disk depths of 3.5 m and associated salinities of < 30 (Supplementary Figure S6).

Taxa showing different trends or less likely to be driven by salinity

The Cladocera *E. nordmanii* and *P. leuckartii* are known to be associated with lower salinity surface waters (Poggensee and Lenz, 1981; d'Elbee *et al.*, 2014) and were two of the very few taxa that did not exhibit a significant decline at Loch Ewe. In addition to the Cladocera, the Cirripedia larvae (cypris and nauplii) were some of the few taxa that did not show significant relationships with salinity. This was not unexpected as many Cirripedia species, as meroplanktonic intertidal crustaceans, have evolved to tolerate a wide salinity range (Harms, 1986) and may also have been sustained by adult populations. It was likewise unsurprising that food availability, expressed as chlorophyll or phytoplankton community, did not explain inter-annual variation in the cypris, which is a non-feeding

developmental stage. Additionally, although the Chaetognatha had a positive relationship with salinity, given the wide salinity tolerance of *P. setosa* this may have been driven by salinity-associated declines in copepod prey.

Trophodynamics: food availability and predation

The added significance of chlorophyll "a," dinoflagellates or diatoms for some dominant taxa is not unexpected and drove the positive association between total zooplankton and chlorophyll "a" concentration. The importance of dinoflagellates and diatoms as food sources for zooplankton are very well documented in the literature. Some relevant examples include the selective grazing on dinoflagellates by *A. clausi* (Fileman *et al.*, 2010) and *Oikopleura* spp. timing reproduction with diatom dominated spring blooms (Troedsson *et al.*, 2002).

Mortality from predation was not accounted for in this study and may need consideration, e.g. an estimated 67–75% of total zooplankton mortality is accounted for by predation globally (Hirst and Kiørboe, 2002). Increased predation by predatory mesozooplankton (e.g. Hydrozoa and Chaetognatha) may be ruled out given their parallel declining trends. Other important predators of mesozooplankton such as Scyphozoa and planktivorous fish can have high feeding clearance rates (Olesen, 1995; Heath, 2007). Over the study period, stock trends in herring, sprat, and mackerel abundance have not reflected the changes in zooplankton found in Loch Ewe, with a declining trend in herring recruitment and high mackerel abundance (ICES, 2021).

Future considerations based on these results

In the coming decades, increased precipitation and extreme weather events are predicted for many regions across the globe (Min *et al.*, 2011). Extreme precipitation will increase freshening events in coastal marine systems. Reduced salinities caused by increasing freshening events may be accompanied by other stressors such as increased suspended particulate matter. If environmental changes, caused by either increasing precipitation or changes in offshore water masses, are leading to community wide declines in zooplankton, the ecological consequences can be severe, with trophic impacts extending to both ecologically and economically important fisheries (Beaugrand *et al.*, 2003). Sustained monitoring of zooplankton communities and environmental conditions is required to detect changes and link them to drivers. Zooplankton data are notoriously heterogeneous through time. The Loch Ewe time series showed this heterogeneity however the high frequency of sampling enabled the detection of fine scale variability in zooplankton abundances and other environmental parameters. This allowed the seasonal signals and noise to be robustly accounted for in the models and the long-term trends to be extracted. Careful interpretation of these inter-annual variations is required however, as the minimum recommended time period for the accurate assessment of inter-annual trends in plankton time series is 30 years, and > 40 years for decadal regime shifts (Edwards *et al.*, 2010). This highlights the need for maintaining high resolution monitoring.

Conclusions

The mesozooplankton community at Loch Ewe between 2003 and 2017 exhibited a substantial decline in abundance towards 2017.

This trend was found in all dominant taxa excluding the Cladocera and Cirripedia cypris. The declines coincided with concurrent decreases in salinity, with increased high intensity freshening events occurring between 2012 and 2017 and potentially fresher water masses offshore getting advected into the loch. The additional significance of chlorophyll "a," diatom or dinoflagellate abundances were found in some taxa. Although other factors influencing zooplankton abundance such as predation and advective processes could not be accounted for, these results, along with those from other studies, indicate the importance of salinity as a predictor of coastal zooplankton dynamics. This will potentially become increasingly relevant in the future, as increased precipitation and extreme weather events are expected to increase in many regions across the globe. These results also highlight the importance of maintaining high temporal resolution sampling in order to understand fluctuating trends in heterogeneous seasonal coastal systems.

Data availability statement

The Loch Ewe Scottish Coastal Observatory data underlying this article are available at https://data.marine.gov.scot/dataset/scottish-coastal-observatory-loch-ewe-site (doi: 10.7489/948–1).

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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