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Abstract

This is a contribution to a paper by Rabe et al. describing the 'Loch Linnhe-Lynn of Lorn' system. This part deals with the pelagic habitat at the 'Lorn Pelagic Observatory', comprising for present purposes the station LY1 in the Lynn of Lorn, and the adjacent fjordic sea-lochs Creran and Etive. It summarises information about the plankton community and its production.

1 Introduction

The Firth of Lorn and Loch Linnhe comprise a fjordic system of several basins in which a multi-layer flow is interrupted by a series of sills. The Firth of Lorn is the outer basin, exchanging with the water on the western Scottish continental shelf and in particular with that in the Scottish Coastal Current (Simpson and Hill, 1986; Hill and Simpson, 1988). SAMS's 'Lorn Pelagic Observatory' (LPO) studies conditions at the head of this basin, and, for the present purpose, comprises the station LY1 in the Lynn of Lorn and the adjacent sea-lochs Etive and Creran.

Model simulations (D. Aleynik, SAMS, *pers. com*) suggest that conditions at LY1 and in the inflow to Creran are influenced by the outflow from Etive, which receives a freshwater discharge that is, in relation to the loch's volume, one of the largest in Scotland (Edwards and Sharples, 1986). Creran is better than Etive as type for sea-lochs in Scotland (Landless and Edwards, 1976), which are, in comparison with typical Norwegian fjords, rather small and shallow (Tett, 1986).

It is the Firth of Lorn itself, a large, deep, and deep-silled basin, which most resembles the Norwegian fjords.

This contribution briefly describes the 'pelagic habitat' in the LPO region, meaning the plankton and related nutrients and hydrography of the upper water column.These have been observed (with some interuptions) by SAMS and its precursor SMBA since the Dunstaffnage Laboratory was established in 1970. There have been changes over time, best understood and documented in the case of loch Creran. Many data remain to be analysed; any unsupported claim in the following material should be understood as the opinion of the author of this section on the basis of data that are being analysed.

2   Plankton community

In principle, physical and chemical environmental conditions determine the lifeform of marine primary producer that characterises a marine habitat-type or biome (Tett et al., 2007; van Leeuwen et al., 2015). Although macroalgal production and terrestrial organic matter input makes a significant contribution to the supply of organic matter in Loch Creran (Cronin and Tyler, 1980; Tyler, 1983), the characteristic primary producers in the region of the LPO are marine pelagic diatoms (Tett, 1973; Wood et al., 1973; Tett et al., 1981; Harris et al., 1995; Edwards et al., 2003; Fehling, 2004; Fehling et al., 2006). They include species of *Chaetoceros, Leptocylindrus, Pseudo-nitzschia, Rhizosolenia* (now partly renamed as *Guinardia*), *Skeletonema* and *Thalassiosira*. One reason for this diatom dominance may be that, although peak nutrient concentrations are comparatively low (maximum winter nitrate 6 - 8 μM) (Jones, 1979; Solórzano and Grantham, 1975; Solórzano and Ehrlich, 1979), the ratio of dissolved silica to oxidised nitrogen remains high. Furthermore, freshwater-driven estuarine circulation replenishes upper-water nutrients during summer and the freshwater input creates year-round salinity (and thus density) stratification over the whole LPO region except in the turbulent zones at the mouths of the loch. This can lead to an extended productive season.

In contrast to the Firth of Clyde, where there is a classical 'textbook' seasonal sequence from diatoms to dinoflagellates (both heterotrophic, such as *Protoperidinium*, and autotrophic or myxotrophic such as *Ceratium*) (Marshall and Orr, 1927; Tett, 1971; Boney, 1986; Tett et al., 1986), the dinoflagellate component of the LPO plankton seems naturally scant. The main dinoflagellate lifeform in Creran during the 1970s and 1980s was that of cyst-forming gonyaulacoids and similar, which typically formed short-lived blooms in late spring and again in late summer, probably seeded from cysts in the sediment

(Lewis et al., 1984, 1985; Lewis, 1985, 1988).

Three types of alteration of this phytoplankton community have been observed. The first occurs in loch Etive, where the freshwater diatom *Asterionella* and the estuarine euglenoid *Eutreptiella* are common (Wood et al., 1973). The other types are those associated with change over time and are best known for Creran (Lappalainen and Tett, 2014; Whyte et al., 2016). The first major change is that the diatom *Skeletonema*, which dominated the Spring bloom between 1971 and 1983, no longer does so, although it continues to form a part of the summer phytoplankton. The second change is that gonyaulacoid and other small armoured dinoflagellates, and photosynthetic flagellates, have increased in both numbers and seasonal persistence.

There is some evidence that similar temporal change has occurred at LY1 (Scherer et al., *in prep.*), which could imply large-scale drivers. Whyte et al. (2016) argued that the Creran changes could be related to changes in precipitation in this part of the west Highlands. Tett (2014) reported decreased transparency along the LY1-Creran transect compared to observations in the 1970s by Tyler (1983), suggesting it might be the result of increasing amounts of yellow-substance in freshwater discharges. The increases in dinoflagellates and flagellates in Creran are not incompatible with nutrient inputs from salmon farming, but it is more difficult to make this case in relation to LY1.

In Creran, the holoplankton community exploiting the primary production includes little crustacean zooplankton (Gowen, 1981). The main consumers of primary production might instead be heterotrophic pelagic protists, especially oligotrich ciliates, which were inversely correlated with flagellate abundance during microcosm experiments (Jones et al., 1978). Both they and unarmoured heterotrophic dinoflagellates have been observed feeding also on diatoms. Both groups of pelagic micro-heterotrophs have increased in abundance during recent years (Lappalainen and Tett, 2014; Whyte et al., 2016). However, it is also possible that some of the ciliates might be feeding on small heterotrophic flagellates, which might in turn be supported by allochthonous organic matter.

In Etive, despite the low surface salinity and the sometimes low oxygen in the deeper water, there are thriving populations of crustacean zooplankters, including the large copepods *Calanus finmarchicus* and *Euchaeta norvegica* and the small euphausiid *Thysanoessa raschii*. The sustained presence of these animals in a comparatively small and fluctuating volume of middle water with favourable conditions suggests that they might be resupplied from populations in the Firth of Lorn (D. Pond, SAMS, *pers.com.*), although there is currently no information about such populations. Finally, recent townet sam-

pling at LY1 and in Creran shows early spring blooms of the small gelatinous zooplankters *Obelia* spp., *Hydrocodon prolifer* and *Rathkea octopunctata* followed by larger summer/autumn blooms again dominated by *Obelia* spp. but with *Lizzia blondina*, *Clytia hemisphaerica* and *Coryne eximia* also abundant (Fox et al., ms). Casual observation shows the moon-jelly (*Aurelia aurita*) to be abundant in Creran during late spring and early summer.

3   Standing Crop

As observed in the 1970s, phytoplankton flourished in both Creran and Etive during a long productive season lasting from March through October. During this season chlorophyll concentrations in the upper water column rarely fell below 1 mg m^{-3}, were often between 2 and 4 , and commonly exceeded 10 mg m^{-3} during the Spring bloom (Wood et al., 1973; Tett and Wallis, 1978; Tett and Grantham, 1980; Gowen et al., 1983; Tett et al., 1985). This can be seen in the envelope for Creran in figure 1(a), drawn to include 80% of data-banked chlorophyll observations from 1970-1985.

In contrast, during the first decade of the 21st century, chlorophyll concentrations were much lower in Creran, especially during the Spring (figure 1(b)). This finding is counter-intuitive, as the moderate enhancement of nutrients by aquaculture in Creran would be expected to increase standing crop, especially in summer when ambient nutrients are lowest and fish excretion is greatest.

Chlorophyll time-series from LY1 and loch Etive have yet to be properly analysed. Analysis of a incomplete data-set could detect no significant temporal trend at LY1 between 1970 and 2005. This data set was used to prepare the Creran sea-boundary chlorophyll climate shown in both parts of figure 1 (Portilla and Tett, 2008; Portilla et al., 2009). Ongoing analysis including more recent data (Scherer et al., SAMS/Trinity, *in prep.*) suggests some decrease in spring bloom chlorophyll at LY1, although not to the same extent as seen in Creran.

4   Primary production

During 1970 and 1971 pelagic primary production was measured in Loch Etive by *in situ* incubation of water samples with ^{14}C. Most carbon fixation occurred in the top 10 metres, due to high attenuation of PAR (typical k_D 0.4 – 0.5 m^{-1}), and the annual total of gross production was 71 g C m^{-2} (Wood et al., 1973). The same method was used in loch Creran during the Spring Blooms of 1972 and 1973,

suggesting higher production in the clearer water of that loch (k_D 0.2 – 0.3 m^{-1} at that time). Without an estimate of algal respiration, however, it was not possible to estimate the production available for the rest of the food web.

Tyler (1983) used a mixed procedure in 1977-1978, with photosynthetic and respiratory parameters determined by oxygen change during incubations of water samples in the laboratory, chlorophyll and light penetration measured regularly in the loch, and production calculated from these data and irradiance measured by the meteorological station at the Dunstaffnage Laboratory. The light-and-dark bottle method allowed calculation of annual 'net microplankton production' (NMP), which is gross photosynthesis less respiration by all the micro-heterotrophs (micro-algae, protists and bacteria) that could not be excluded by screening from the incubation bottles. NMP is the part of production that is available to higher levels in the food web. Tyler estimated annual NMP as between 150 and 225 g C m^{-2}, implying typical values during a 240 day productive season of 0.6 to 0.9 g C m^{-2} d^{-1}.

There have been no subsequent direct measurements of production, but Tett (2014) adapted Tyler's calculations (without new measurements of the microplankton parameters) to a transect worked between loch Creran and LY1 in September 2013. This (figure 2) showed positive NMP only in the upper few metres of Creran. The transect shows how shallow (in present times) is the layer of significant production. Using climatic irradiance, the month's NMP was estimated as 0.18 g C m^{-2} d^{-1} in Creran and 0.17 g C m^{-2} d^{-1} in the Lynn of Lorn.

5   Simulations

The ACExR-LESV model has been developed to simulate layering and exchange in lochs, and the impact of aquaculture on production and microplankton on the basin scale (Portilla et al., 2009; Tett et al., 2012, 2011; Gillibrand et al., 2013). It has been tested against observations in loch Creran and (in the case of physical processes) the upper basin of loch Etive. The model describes a loch basin as a dynamic three-layer structure and simulates annual cycles of nutrients (N, P and Si) and two kinds of microplankton. Each biological compartment represents a combination of autotrophic and heterotrophic processes (Tett and Wilson, 2000; Lee et al., 2002, 2003); 'net microplankton production' NMP was calculated as the product of the specific growth rate and the biomass of each compartment, and, in the present case, integrated over the upper 10 metres of the water column.

Simulations have been run for two years during the 1970s and, with

altered parameters, for two years in the 2000s (details in appendix B). The alterations were intended to represent decreases in water transparency and *Skeletonema*. Simulated chlorophyll are shown in Fig 1 and compared with envelopes based on observations. The estimates of annual NMP were similar in all years, averaging 53 g C m^{-2}. However, the similarity hides dynamics that differed between the decades. The simulations for 1975 and 1978 combined often-high chlorophyll with often-low growth rates, whereas the 2003 and 2005 simulations multiplied lower chlorophyll by faster growth. Finally, in 1975 and 1978, the diatom-dominated 'microplankton 1' compartment contributed 68% of NMP; in 2003 and 2005, only 38%.

6   Discussion

Several sorts of change are taking place in the pelagic habitat in this part of the Loch Linnhe – Lynn of Lorn system. They include shifts in phytoplankton floristic composition towards more dinoflagellates and flagellates and a decrease in chlorophyll concentrations and the length of the productive season. Changes in the optical properties of seawater and nutrient inputs from aquaculture might provide some of the explanation, as might enhanced precipitation from climate change, but more research is needed on changes in microplankton at other sampling sites in the region, and on changes in the light-absorbing constitutents of seawater.

During the 1970s the mean concentration of chlorophyll in superficial waters inside lochs Creran and Etive was higher than that outside; given the continuous dilution of loch water by external sea-water, this implies that the lochs were at that time net sources of phytoplankton (Tett, 1986). In recent times the chlorophyll contrast has lessened, and Creran in particular may have become more of a sink than a source for pelagic primary production. The LESV simulations were only able to explain part of this change as a result of decreased water transparency; it was also necessary to postulate increased losses of diatoms.

A final problem concerns the reconciliation of the various estimates of production. The only published study (Wood et al., 1973) to use direct (^{14}C uptake) estimates of photosynthesis, resulted in a low estimate of GPP in loch Etive. The other 'observational' estimates used a combination of measured chlorophyll, k_D and surface PAR with photosynthetic and respiratory parameters either measured at the time or taken from published values. The combined approach was validated when it satisfactorily budgetted all production and loss terms in a near-closed water column replenished from the Firth of Lorn (Tett

et al., 1988). The method suggests that there was high NMP during 1977-1978 in loch Creran (Tyler, 1983) but lower values (at least during September) by 2013 (Tett, 2014). However, the LESV simulations do not agree with this conclusion. Although they fit the chlorophyll observations, and help to explain the changes in chlorophyll, they result in roughly the same NMP in the two decades. This is a matter that needs further investigation.

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7 Figures

11
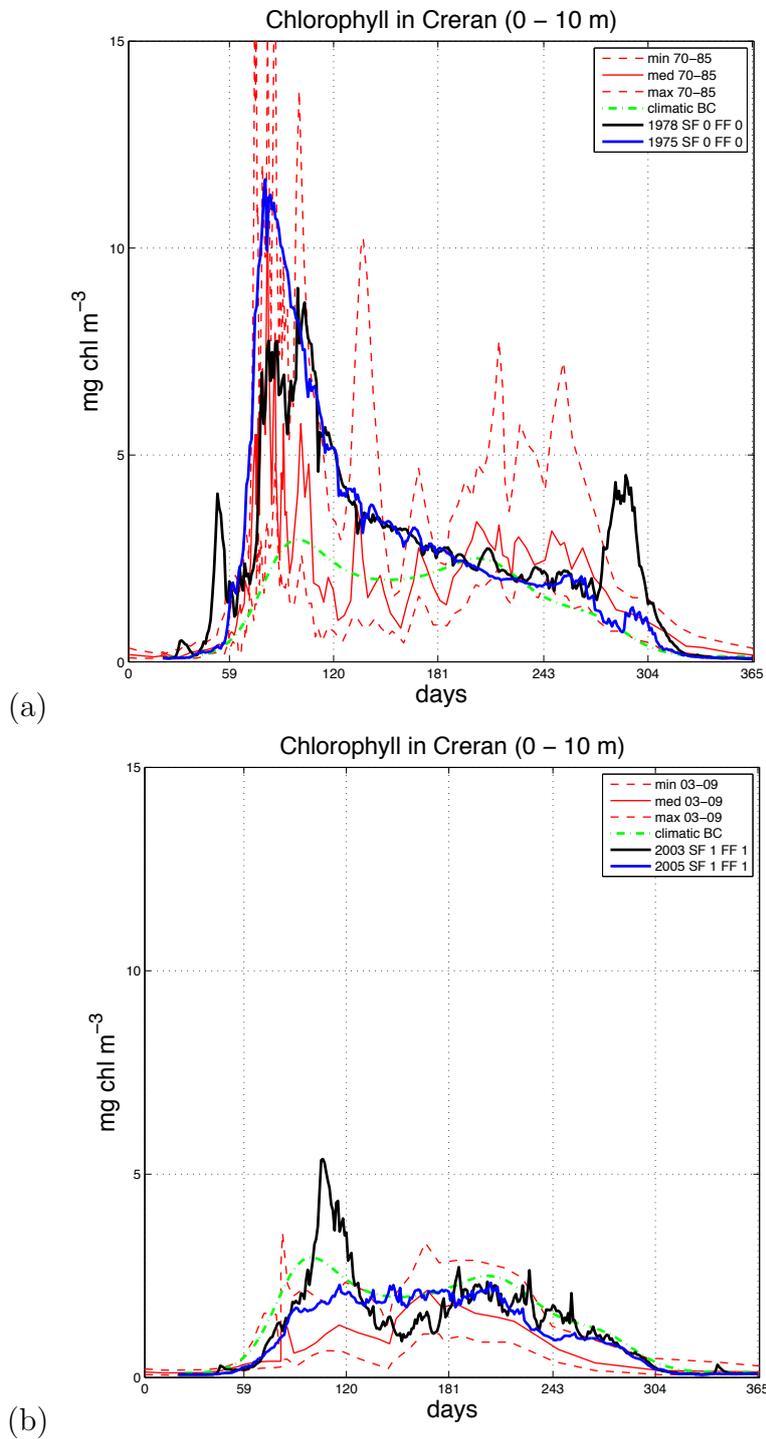
Figure 1: Chlorophyll simulated for loch Creran by the LESV model (Tett et al., 2011), compared with 10-50-90%ile envelopes of observations. (a) 1970-1985; (b) 2003-2009. Yellow-substance light absorption and MP1 loss rate and heterotroph fraction increased in (b). For methods, see appendices A and B.

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Figure 2: Section from the Greag Isles station in the Lynn of Lorn to station C5 Loch Creran, 10 September 2013, contoured for properties derived from CTD measurements (Tett, 2014).

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Appendices

A Envelopes

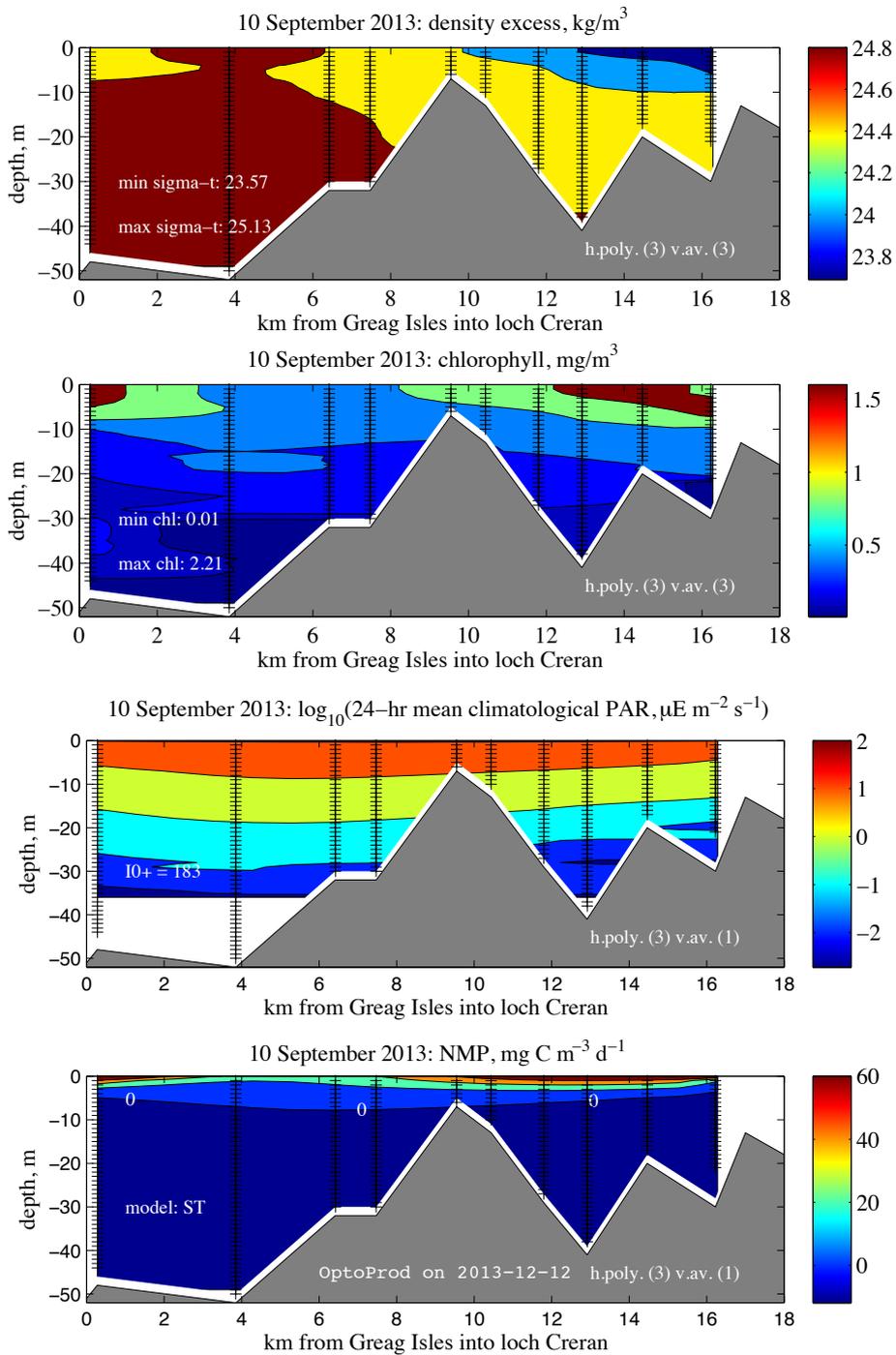The chlorophyll envelopes shown in figure 1 derive from water-bottle samples from which phytoplankton pigments have been extracted into 90% acetone after retention on glass-fibre filters. In most cases concentrations were calculated from measurements of fluorescence before and after acidification (Tett and Wallis, 1978; Tett, 1987). Some extracts in 2005-2006 were measured by HPLC (T. Nickell, SAMS, *pers.com.*). Since the latter estimated the pure pigment chlorophyll *a*, and the former a mixture of pigments including chlorophyllides as well, the HPLC values have been multiplied by 1.3, the average ratio of fluorescence-determined 'chlorophyll' to chromatographically-determined chlorophyll *a* (Gowen, 1981; Gowen et al., 1983).

Data were saved as a flat-ASCII data base in which each row specifies sample site, depth and date as well as concentration of 'chlorophyll'. A Matlab script (current version HPLP4B) was written to extract data from rows selected by site, depth and year, and to plot against year-day. The script also generated an envelope to include a specified fraction of values in discrete time-periods. Table 1 lists the sorting and analysis parameters used, and figure 3 provides an example of the results of the plotting script.

Table 1: Chlorophyll sorting parameters. Stations 302 – 306 are on the centre line of the main basin of loch Creran.

sort year range	1970 to 1985	2000 to 2009
actual year range	1972 – 1983	2003 – 2009
stations	302 – 306	302 – 306
depths (m)	0 – 10	0 – 10
samples	1343	328
envelope %iles	10 – 90	10 – 90
samples in block	10	10
blocks smoothed	3	3

B Simulations

The simulations shown in figure 1 were made with the ACExR-LESV model, which describes the main physical and biological processes af-
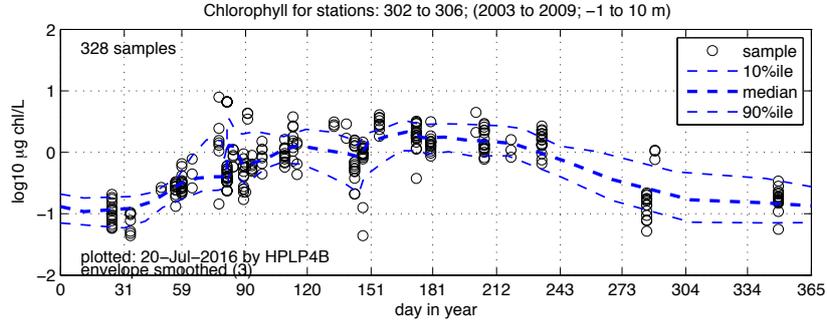
Figure 3: Recent chlorophyll data and fitted envelope, to exemplify the method for getting the envelope.

fecting the water columns of 'narrow regions of restricted exchange' such as fjord or sealochs. ACExR simulates a water-body as three dynamic layers, and LESV populates these with nutrients and 'microplankton', which comprises pelagic autotrophs and microheterotrophs. Some of these nutrients may emanate from fish-farms and some microplankton may be consumed by cultivated shellfish.

The model equations are coded in Matlab and were numerically integrated on a Windows-emulating Macintosh MacBook Pro using the suit of programmes described in the 'LESV handbook' (Tett, 2016). Parameter values particular relevant to the Creran changes are listed in tables 2 and 3, and boundary conditions an forcing data are summarized in table 4. NMP was calculated from:

$$\sum_{L} \sum_{MP} X_{(L,MP)} \cdot \mu_{(L,MP)} \cdot {}^{B}q^{X}_{(MP)} \cdot w_{(L)} \qquad (1)$$

where L is layer $(1 \ldots 3)$ and MP is microplankton (1 or 2), which have layer-dependent specific growth rate μ. X is chlorophyll concentration and $w_{(L)}$ is the proportion of loch volume, down to 10 m, occupied by layer L. For ${}^{B}q^{X}$ see table 3.

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Table 2: Values of the main bio-optical parameters. Value-1 = current 'standard' value used for 1975 and 1978; value-2 = altered value used for 2003 and 2005 (blank if no change).

symbol	description	value-1	value-2	units
$a*_{YS}$	increase in water (YS) absorption with (decreasing) salinity	-0.014	-0.028	$\mathrm{m^{-1}\ psu^{-1}}$
$a*_{SPM}$	SPM specific absorption	$3 \cdot 10^{-5}$	-	$\mathrm{m^{-1}\ mg^{-1}}$
a_w	(PAR) absorption pure water	0.02	-	$\mathrm{m^{-1}}$
$B*_{SPM}$	SPM specific scatterance	$1 \cdot 10^{-4}$	-	$\mathrm{m^{-1}\ mg^{-1}}$
$g_{440,c35}$	water-YS absorption at 35 psu	0.028	0.05	$\mathrm{m^{-1}}$
$a*_{PH}$	algal pigment absorption cross-section for MP1	0.0197	-	$\mathrm{m^{-1}\ mg\ chl^{-1}}$
	. . . . for MP2	0.03	-	$\mathrm{m^{-1}\ mg\ chl^{-1}}$

Table 3: Values of the main microplankton parameters. Value-1 = current 'standard' value used for 1975 and 1978; value-2 = altered value used for 2003 and 2005 (blank if no change). MP1 comprises 'spring' diatoms and associated microheterotrophs; there were relatively few of the latter during the 1970s when *Skeletonema* was abundant at this time, and relatively more after 2000. MP2 comprises summer diatoms, dinoflagellates and flagellates.

symbol	description	value-1	value-2	units
η	heterotroph fraction MP1	0.125	0.3	
	. . . . MP2	0.3	-	
q^N	chl. yield from N, MP1	2.6	2.1	$\mathrm{mg\ chl\ (mg\text{-}at\ N)^{-1}}$
	. . . . MP2	1.4	-	$\mathrm{mg\ chl\ (mg\text{-}at\ N)^{-1}}$
q^P	chl. yield from P, MP1	35	28	$\mathrm{mg\ chl\ (mg\text{-}at\ P)^{-1}}$
	. . . . MP2	28	-	$\mathrm{mg\ chl\ (mg\text{-}at\ P)^{-1}}$
q^{Si}	chl. yield from Si, MP1	2.6	2.1	$\mathrm{mg\ chl\ (mg\text{-}at\ Si)^{-1}}$
	. . . . MP2	2.8	-	$\mathrm{mg\ chl\ (mg\text{-}at\ Si)^{-1}}$
$^Bq^X$	chlorophyll:carbon MP1	26	41	$\mathrm{mg\ C\ (mg\ chl)^{-1}}$
	. . . . MP2	61	61	$\mathrm{mg\ C\ (mg\ chl)^{-1}}$
L_{20}	loss rate at 20°C, MP1	0.2	0.6	$\mathrm{d^{-1}}$
	. . . . MP2	0.2	0.2	$\mathrm{d^{-1}}$

Table 4: Boundary conditions and forcing data for simulations. (1) Discharge model for Creran catchment modified from the hydrological part of CHUM (Tipping, 1996), forced by rainfall and temperature. The simulation for 1978 was calibrated with daily flow-guage data (Tyler, 1983). (2) Sea-boundary climate for nutrients, chlorophyll and the fraction $\psi = $ MP1/(MP1+MP2) originally computed by E. Portilla (Napier) from data available c. 2006 for LY1 during 1970-2005. (3) Fish farm input (for 1 standard farm) based on feed supplied to a salmon farm of 1500 tonne consented maximum stock in the 2nd (most productive) year of the fish management regime. (4) Mussel farm effect based on a farm growing 400 (wet) tonnes during the year. See Tett et al. (2012) concerning (2) – (4).

variable	1975	1978	2003	2005
sea-boundary hydrography	climatic UKHO	observed LY1	climatic UKHO	climatic UKHO
freshwater discharge (1)	obsv. rain → model	obsv. rain → model	obsv. rain → model	% of climatic rain
wind	observed Tiree	observed Tiree	observed Tiree	observed Tiree
surface heat-flux	calc. from obsv. DML	calc. from obsv. DML	calc. from obsv. DML	climatic DML
solar irradiance	observed DML	observed DML	observed DML	climatic DML
sea-boundary nutrients (2)	climatic	climatic	climatic	climatic
sea-boundary chl & ψ (2)	climatic	climatic	climatic	climatic
Fish-farms (3)	0	0	1	1
Mussel farms (4)	0	0	1	1