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THE LIMNOLOGY OF SLAPTON LEY

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ABSTRACT

Slapton Ley, a freshwater lake, located in south Devon (National Grid Reference SX 825 439), has been the focus of a wide range of research studies since the foundation of the Field Studies Council Centre in Slapton village in 1959, and the creation of the Slapton Ley Nature Reserve. Early concerns over eutrophication of the Lower Ley led to a range of studies focused on the impacts of land use change in the catchment, on nutrient delivery to the Ley, and on interpreting the impact of long-term nutrient enrichment of the Ley from palaeolimnological studies. What has been missing to date, however, is a focused study of the impacts of nutrient enrichment on the chemical and ecological structure and function of the combined Lower and Higher Ley systems. This paper attempts to draw together the various areas of study on the Ley to date in order to provide a review of current understanding of the limnology of Slapton Ley and to identify gaps in our knowledge. The past, present and future trophic status of the Ley is re-interpreted in the light of current understanding of the eutrophication process in the wider scientific community. Recommendations for future research are then made, with a view to the monitoring and management of Slapton Ley and its catchment.

INTRODUCTION

Early studies on Slapton Ley sought to describe the morphology and origins of the lake basin (Mercer, 1966; Morey, 1976), the hydrology of the Ley and its connectivity with its catchment and the adjacent marine environment (Mercer, 1966; Troake & Walling, 1973; Ratsey, 1975; Morey, 1976), its characteristic phytoplankton community (Benson-Evans *et al.*, 1967), its flowering plants (Brookes & Burns, 1969) and its fish community (Kennedy, 1975). These early studies still serve as a valuable background reference for modern research studies on the Ley.

In the early 1970s, an increase in the incidence of algal blooms in Slapton Ley raised concerns over the present and potential future trophic status of the Ley. This led to the initiation of a water quality monitoring programme on the streams draining into Slapton Ley from its catchment, conducted by researchers and staff at the Field Centre (see Burt, Heathwaite & Johnes, 1996). Early results suggested that nutrient loading on the Ley from its catchment was increasing, possibly resulting from the discharge of effluent into the streams from sewage treatment works serving a growing human population, and intensification and expansion of agricultural production in the catchment (see Troake & Walling, 1975; Troake *et al.*, 1976). Research was also being conducted on the Ley itself at this time, seeking to explain the dynamics of the phytoplankton community through detailed studies of the physico-chemical environment of the Ley (see Van Vlymen, 1979, 1980). This was the first study which substantially advanced understanding of the processes and mechanisms controlling the structure and function of Slapton Ley. Early findings from this programme suggested that the species composition of the phytoplankton community was characteristic of nutrient-enriched waters.

In the 1980s, research in the wider scientific community on eutrophication was concerned with the identification of the sources of nutrient enrichment in eutrophic waters. In particular, this research was focused on the easily visible point sources of pollution deriving from sewage treatment works and farm pollution incidents, as a function of North American pre-occupations with such sources in studies of the eutrophication of the Great Lakes, despite the very different nature of land use in lake catchments in lowland Britain (Johnes *et al.*, 1994a; Moss *et al.*, 1996). At Slapton, this led to two separate areas of research effort which have continued to the present day. One research group has focused on the catchment, aiming to develop an understanding of the hydrological pathways in the Slapton catchment along which nutrients and sediments are transported from the land to the adjacent streams and thence to the Ley. The early work in this field was conducted by researchers at the Universities of Huddersfield, Oxford and Sheffield (see Burt *et al.*, 1983; Trudgill, 1983; Coles & Trudgill, 1985; Burt & Arkell, 1987). The second main area of research concentrated on Slapton Ley, using palaeolimnological techniques to investigate time trends in nutrient loading and sediment delivery from the catchment and associated changes in the diatom community of the Ley as recorded in the lake sediments, and was largely conducted by researchers and undergraduates from the University of Plymouth. A comprehensive review of this work is provided by O'Sullivan (1994). However, whilst there was some overlap between the two areas, improved by the initiation of a substantive NERC funded research programme on the eutrophication of Slapton Ley in the late 1980s (see Heathwaite *et al.*, 1989, 1990a, 1990b, Heathwaite & O'Sullivan, 1991; Heathwaite, 1994; Heathwaite & Johnes, 1996), the two areas have remained essentially divorced.

Research on some elements of the floral and faunal communities of the Ley continued throughout the 1980s to the present day (see for example Kennedy, 1996), but what has been missing is a co-ordination of research on the processes and mechanisms controlling the structure and functioning of Slapton Ley as a whole. This raises problems when we try to forecast the likely impact of different management strategies on Slapton Ley (see, for example, Johnes & Heathwaite, 1996). We can claim to understand in some depth the pathways along which nutrients and sediments arrive in the Ley. Equally, we can argue that we have a fair understanding of the historical changes in sediment delivery and changes in the diatom community in the Ley, as evidenced from the sediment record (see O'Sullivan, 1994), although Foster *et al.* (1996) contest the validity of this source as a complete reflection of catchment history. However, what we cannot conclude with any confidence is the impact that these changes in nutrient loading have had on the structure and function of the ecological community of Slapton Ley, and this is the key to evaluating the likely impact of potential catchment and lake management strategies on Slapton Ley.

In this paper, the various areas of research will be reviewed to provide an insight into the limnology of Slapton Ley, the history of nutrient loading and sediment delivery to the Ley, and its past, present and future trophic status. Using classification schemes devised for the National Rivers Authority (Johnes *et al.*, 1994a, 1994b) and by the Nature Conservancy Council (Palmer, 1989), the data collected to date on this history and the past and present ecological communities of the Ley will be used to describe changes in the trophic status of the Ley. Gaps in our present understanding of Slapton Ley are then identified, and recommendations made for future research on the Ley in the context of our current general understanding of the eutrophication process.

The Morphology and Hydrology of Slapton Ley

In the first of a series of papers published in *Field Studies* on *The Natural History of Slapton Ley Nature Reserve*, Mercer (1966) describes Slapton Ley as 'a coastal lagoon impounded behind the shingle ridge that is Slapton Sands' (p. 388), and goes on to describe the Ley as a shallow, freshwater lake lying almost wholly above sea level. The shingle ridge is some 3.5 km in length and is thought to have formed in its present position between 1,500 and 2,000 years B.P. (Morey, 1976; Van Vlymen, 1979) as a result of the landward migration of the ridge during the Holocene period. The Ley would have originated as a tidal, saltwater lagoon (Hails, 1975; Morey, 1976) which, as the shingle ridge migrated landwards under the prevailing wind direction and tidal currents to its present position, would have become progressively a brackish water and then freshwater lake. Radio-carbon dating of sediment accumulated in the lake basin has revealed that Slapton Ley is unlikely to have existed as a freshwater lake for more than 1,000 years (Morey, 1976). Data presented by Morey (1976) suggest that the hydraulic gradient between the Ley and Start Bay is from freshwater to saltwater, with the springs draining from the Ley through the shingle ridge evident on the seaward side of the ridge at extreme low water during spring tides. The storm beach which has formed on top of the ridge prevents saltwater overflow into the Ley at extreme high water, even during spring tides, although some marine incursions may occur through the ridge at times when a low water level in the Ley is combined with high spring tides in Start Bay when the hydraulic gradient may be reversed.

The Slapton Ley wetland system is shown in Fig. 1. The total area of the wetland is 116 ha, of which over 60% lies within the boundaries of Slapton Ley Nature Reserve. The Ley is oriented on a North-South axis, running parallel to the shingle ridge and is divided into two distinct basins, the Higher Ley at the northern end, and the larger open water body of the Lower Ley to the south. The two basins are joined by a narrow open-water channel at Slapton Bridge, with the major outflow situated at the extreme southern end of the Lower Ley, flowing through a culvert built in 1856 through the shingle ridge to discharge into Start Bay at Torcross.

The Higher Ley

The Higher Ley is the smaller of the two basins with an area of 39 ha, a lake volume half that of the Lower Ley, and a maximum depth of 3m (see Table 1). Morey (1976) describes this basin as being bound by rock promontories at Broadstone Point to the north, and Slapton Bridge at its point of outflow into the Lower Ley, with the landward edge of the shingle ridge abutting the old cliff line at the base of Middlegrounds (see Fig. 1). As a result, the bed of this basin is underlain by beach gravels which, in turn, are overlain by riverine sediments. The River Gara drains into the Higher Ley at the northern end, contributing 70% of the total catchment runoff to Slapton Ley (Van Vlymen, 1979). The Slapton Wood stream flows into the Higher Ley from the west, but constitutes only 1.9% of the total catchment runoff (Van Vlymen, 1979).

Morey (1976) suggests that the River Gara would originally have flowed out into Start Bay through a natural overflow channel at Strete Gate, and that in association with

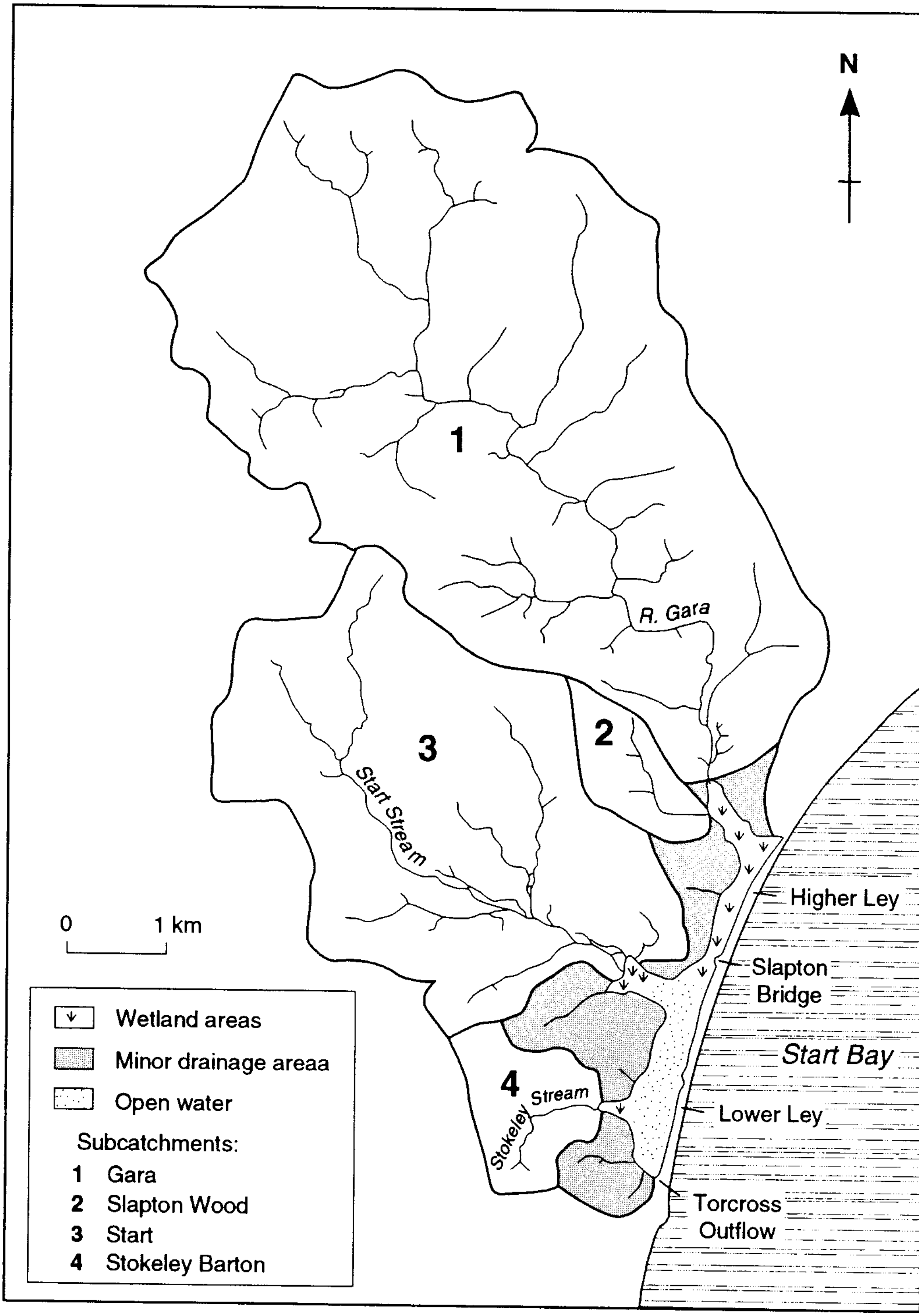

FIG. 1
Site map, showing the two lake basins and the catchment of Slapton Ley

TABLE 1 *The morphology and hydrology of Slapton Ley (based on data from Morey, 1976; Van Vlymen, 1979; Meteorological Office, 1989, 1992; Johnes et al., 1994a, 1994b)*

Catchment variables	
Catchment area (ha)	
Lower Ley	4556
Higher Ley	2902
Total	4556
Maximum altitude (m OD)	183
Minimum altitude (m OD)	2.71
Mean annual rainfall for the period 1941–1971 (mm)	1280
Mean annual actual evapotranspiration for the period 1961–1988 (mm)	529
Mean annual runoff (mm)	751
Lake variables	
Retention time (days)	19.0
Lake volume ($m^3 \times 10^6$)	
Lower Ley	1.19
Higher Ley	0.60
Total	1.79
Lake area (ha)	
Lower Ley	77
Higher Ley	39
Total	116
Maximum Depth [Z_{max} (m)]	
Lower Ley	2.8
Higher Ley	3.0
Total	3.0
Mean Depth [Z (m)]	
Lower Ley	1.55
Higher Ley	1.55
Total	1.55
Spread of depth (Z_{max}:Z)	1.8:1
Length of shoreline in the Lower Ley (km)	6.67
Shoreline development in the Lower Ley [D_L]	2.14

the building of the road along the shingle ridge to connect Strete with Torcross in 1856 and construction of the outflow culvert at Torcross, the outflow from the River Gara was diverted to Slapton Bridge. Morey (1976) also reports that the level of the weir at Torcross was raised by the Whitley Estate, possibly in the 1920s, to increase the area of the wetland available for water sports. If so, this may account to a large extent for the relatively rapid rates of sediment accumulation reported in the Higher Ley (see Morey, 1976; Jenns, 1994). Intensification and expansion of agricultural production in the Gara and Slapton Wood catchments, combined with the reduction in flow rates within the Ley resulting from these alterations to the natural flow patterns, would have made the Higher Ley an effective sediment trap, particularly during periods of low rainfall when evapotranspiration rates may exceed rainfall inputs. At such times, water may flow back into the Higher Ley from the Lower Ley, promoting further sediment deposition within the Higher Ley system. Jenns (1994) reports that sediment accumulation in the Higher Ley has increased markedly since 1945, and calculates an accumulation rate of 22.2 mm yr^{-1} in the period 1954–1963, ameliorated to 15 mm yr^{-1} in the period 1963–1993 which ties in closely with trends in agricultural land use and management during this period (see Johnes & Heathwaite, 1996). Jenns (1994) attributes these trends to the increases in stocking densities on grazing land, the recent cultivation of winter crops and the intensification of arable cultivation in the catchment. Cattle poaching in the riparian zone may also have played a role.

The wetland system of the Higher Ley is dominated by an extensive reed bed which covered approximately 84% of the total area of the wetland in 1945 (Cannell, 1992). Since then, sediment accumulation and colonisation of areas of the wetland by terrestrial plant species has reduced the area of both reed bed and open water. At present, open water is restricted to a few small pools and to a clearly visible, if somewhat discontinuous, water channel running close to the western landward shore of the Higher Ley from the inflow of the River Gara at its northern end to the outflow at Slapton Bridge (Benson-Evans *et al.*, 1967; Brookes & Burns, 1969; Van Vlymen, 1979, 1980; Cannell, 1992; Jenns, 1994).

The Lower Ley

The Higher Ley functions as an important buffer for the Lower Ley, reducing the loading of sediment and sediment-associated pollutants on the Lower Ley. In contrast to the Higher Ley, emergent macrophytes are restricted to a marginal shoreline fringe. The greatest extents of reed bed occur around the inflow deltas of the Start Stream in Ireland Bay, the Stokeley Stream in Stokeley Bay, and around the inflow from the Higher Ley at Slapton Bridge (see Fig. 2). The total area of the Lower Ley wetland is 77 ha (Brookes & Burns, 1969; Morey, 1976; Van Vlymen, 1979, 1980), of which more than 80% is open water. Of the total runoff arriving in the Lower Ley, 72% derives from the Gara and Slapton Wood catchments, running into the Lower Ley at Slapton Bridge, with 23% derived from the Start catchment running into Ireland Bay, and a further 1.6% from the Stokeley Barton catchment running into the Lower Ley near the outflow in Stokeley Bay (Van Vlymen, 1979). The remainder runs into the Ley from minor drainage sources around the lake margins. The culvert at Torcross provides the only major point of outflow from the Ley, and does become blocked by shingle at the seaward end, resulting in the raising of water levels in the Ley, and an increase in retention time and sediment trapping efficiency. Further freshwater leaves the Ley as seepage losses through the shingle ridge.

The morphology and hydrology of the Lower Ley have been reported in detail by Morey (1976) and Van Vlymen (1979, 1980), and these are still the standard references for modern studies on the Lower Ley. Morey (1976) describes the bed of the lake as comprising a sequence of slate gravels in the shallow eastern zone, grading to beach gravels over-spilling from the adjacent shingle ridge, which are gradually overlain by layers of estuarine clay, peat, silts and clays, and a diatom-rich layer. Delta sediments

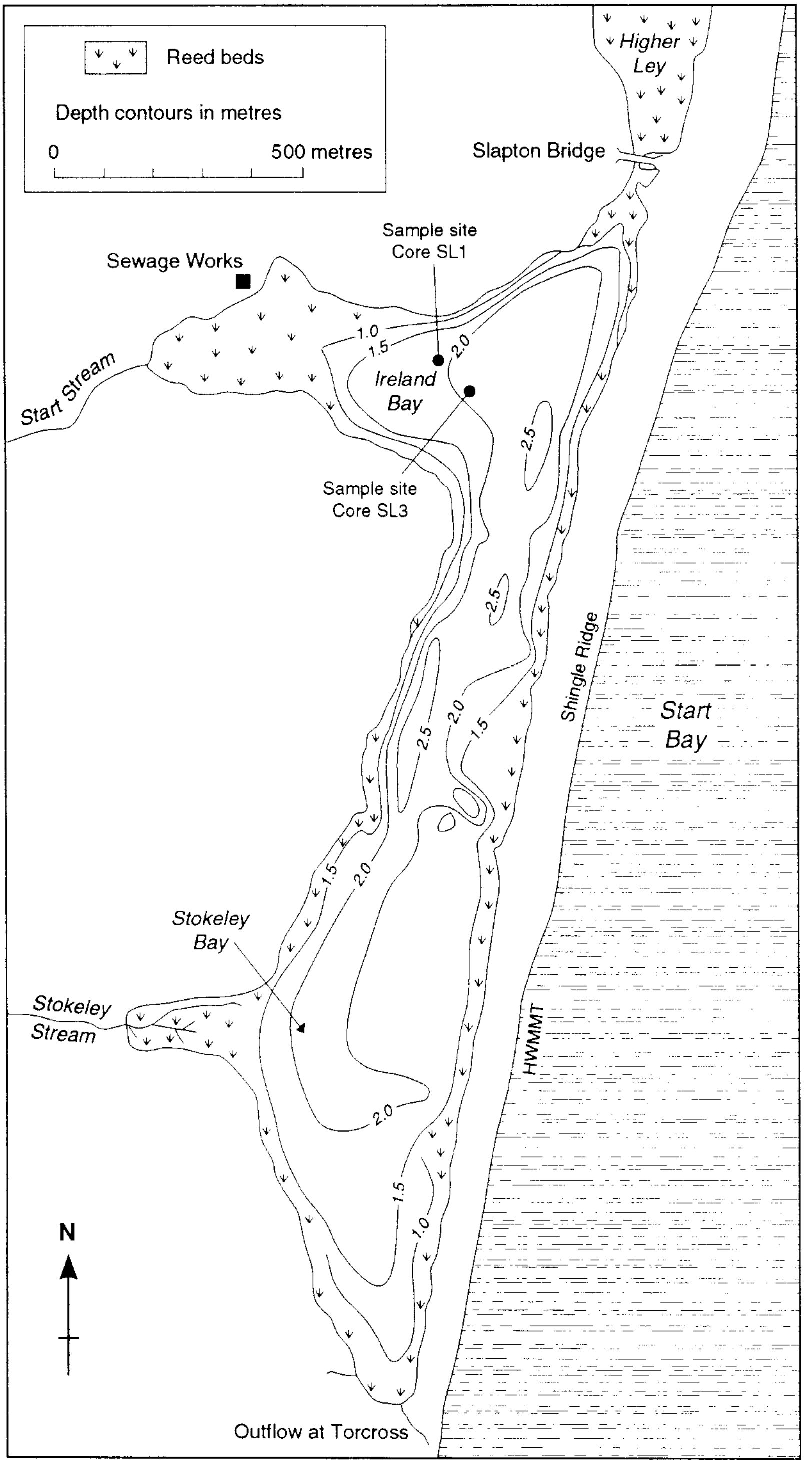

FIG. 2.
The bathymetry of the Lower Ley (after Morey, 1976; Van Vlymen, 1979)

comprising thicker layers of peat overlain by clay extend out into the Lower Ley from each of the major points of inflow at Slapton Bridge, Ireland Bay and Stokeley Bay. It is this sequence of sediments which has led to the Lower Ley being a focus for palaeolimnological research studies (see O'Sullivan, 1994), although there is currently a debate over the intactness of the sediment record and the extent to which it reflects catchment history (see Foster *et al.*, 1996).

Through collation of data collected by Troake, Morey and Van Vlymen in the early 1970s, a bathymetric map has been produced for the Lower Ley which provides valuable information for the limnologist on the morphological structure and hydrological functioning of this system (see Fig. 2). The morphometric and hydrological characteristics of Slapton Ley are shown in Table 1, representing a compilation of data reported in a range of studies (Morey, 1976; Van Vlymen, 1979, 1980; Johnes *et al.*, 1994a, 1994b). The key morphometric variables for the Ley are the retention time of 19 days (computed using mean annual runoff to the Ley calculated from MORECS database), a volume of 1.79×10^6 m^3 (of which the Lower Ley comprises 1.19×10^6 m^3), and a mean depth of 1.55m (Van Vlymen, 1979). These determine the type of plankton community likely to develop in the lake, the rate of nutrient supply, the degree to which any stratification and accumulated sediment may be disturbed by turbulent inflow, and the nature of the inflow streams as spawning sites for Salmonid fish.

The maximum depth (Z_{max}) of the Lower Ley is 2.8m, with a mean depth (Z) of 1.55m, giving a spread of depth ratio (Z_{max}:Z) of 1.8:1. This indicates that the Lower Ley is a shallow lake, with few depressions in the bed other than the shallow sub-lacustrine channel running from Slapton Bridge to Stokeley Bay and thence to the outflow at Torcross (see Fig. 2). This means that the Lower Ley is likely to be well mixed for most of the year, with little if any summer stratification. The shallow depth of the Ley, the relatively high lake volume, and the high exposure of the site to wind action also indicate that the bed of the lake will be exposed to a relatively high degree of scour, leading to high turbidity during the winter months through re-suspension of bed sediments, and a disturbance of the sediment record. This has implications for the integrity of the sediment record, since the historical sequence on which palaeoenvironmental reconstructions depend will be displaced (see Foster *et al.*, 1996).

The retention time of 19 days indicates that water flowing into the Ley has a relatively short contact time with the plant and animal communities. This is an average annual retention time, and during storm flow periods may be reduced to as little as one day (Foster, *pers. comm.*). At such times, pollutants transported to the Ley from its catchment may bypass the ecological communities of the Ley, flowing direct from the catchment to the outflow at Torcross. The pollutants with the greatest potential impact on the ecological structure and function of the Lower Ley will, therefore, be those which are delivered along sub-surface flow pathways from the catchment, arriving in the Ley during the spring and summer low flow periods, and those stored within the bed sediments and released at the same time. Since the Lower Ley is a shallow lake, it will have a high degree of contact between the lake sediments and the water column. As such, phosphorus stored in the bed sediments is likely to be rapidly mobilised and released to the water body during summer low flow periods when deoxygenation of the hypolimnion could occur.

The morphology of the Lower Ley will also determine the structure and function of the ecological community can support. The degree of shoreline development (the length of shoreline divided by the circumference of a circle of equal area) indicates the proportion of the lake area likely to occur in the shallow littoral zone. For the Lower Ley this is a factor of 2.14, suggesting a high proportion of shallow littoral areas in the Ley. This indicates that much of the lake lies within the euphotic zone, and is therefore potentially available for colonisation by rooted aquatic macrophytes, but is also available for the growth of epiphytic and benthic algae on the lake bed. It also indicates a potential to support coregonid and salmonid fish species through the provision of spawning grounds. However, high turbidity levels in the Ley throughout the spring and autumn months resulting from resuspension of bed sediments will restrict light penetration at depth and, therefore, the extent to which aquatic macrophytes can colonise the lake bed. Colonisation by rooted plants will be restricted to expansion from the margins of existing beds, rather than colonisation of new sites in higher flow environments. In an undisturbed system, this process could eventually lead to the complete colonisation of the bed of the Ley lying within the euphotic zone. However, in a turbid system where plant beds may have been disturbed through engineering works, or lost through nutrient enrichment of the water body, recolonisation by rooted macrophytes will be limited in the short term by the physical nature of the environment.

THE NUTRIENT CHEMISTRY OF THE LEY

The nutrient chemistry of Slapton Ley is largely unknown, despite nutrient enrichment and sediment accumulation being key causal factors in the eutrophication of the Ley over the past two decades. Recently, Slapton Ley was chosen as one of 100 standing waters monitored as part of the first phase in the development of a Lake Classification and Monitoring scheme for the National Rivers Authority (see Johnes *et al.*, 1994a, 1994b; Moss *et al.*, 1996). Some preliminary data are available from this source, and are reviewed later in this paper, but these only provide a broad indication of likely changes in the chemistry (and morphology and ecology) of the Ley over the past 60 years, and cannot make up for the lack of direct observations of changes in the chemical character and functioning of the Ley. The only detailed sources of information on these changes are derivative trends available from two sources: hindcasted nutrient loadings on Slapton Ley from its catchment using modelling approaches (see for example Johnes & O'Sullivan, 1989; Johnes & Heathwaite, 1996), and palaeolimnological reconstructions of nutrient concentrations based on direct measurements of the sediment chemistry (see for example Heathwaite & O'Sullivan, 1991; Heathwaite, 1994; O'Sullivan, 1994; Foster *et al.*, 1996). The modelling studies provide information on the nitrogen and phosphorus loadings delivered to both the Lower Ley and Higher Ley in inflowing streams, but do not give a direct indication of the nutrient dynamics of the lake itself. In contrast, the palaeolimnological studies provide information on the nutrient chemistry of the Lower Ley as recorded in the sediments, although very little research has been conducted to date on the Higher Ley (but see Jenns, 1994).

One method for assessing past nutrient loadings on Slapton Ley has involved the development of models of nutrient export from the catchment, based on contemporaneous records of catchment history. The export coefficient modelling approach, originally developed in North American studies of eutrophication, was adapted for the Slapton catchment to give an indication of the nature and location of nutrient sources in the catchment contributing to the nutrient enrichment of the Ley (see Johnes & O'Sullivan, 1989; Johnes, 1996; Johnes & Heathwaite, 1996). The model calculates the total nutrient load delivered to a surface water body as the sum of the exports from each individual nutrient source in the catchment. The model operates on an annual basis, using the field as the spatial unit. Each field unit is treated as a black box, with nutrient export from each unit calculated as a function of the total nutrient load input to that field in the study year. Export coefficients are derived from the published literature or field experimental studies for each major land use and livestock type in the catchment, and applied to each field unit. The export of nutrients from human sources to a water body are calculated on a *per capita* basis, taking account of the nutrient content of the wastes, the use of detergents, and the degree of treatment given to the wastes prior to discharge. However, the relative importance of nutrient export from human sources is also strongly determined by the number of households connected to the main sewage treatment works as opposed to having a soak-away or septic tank system (see Johnes, 1996), and this is difficult to establish in any catchment, as is the degree of treatment of the wastes. Ultimately, this export may be best assessed using direct measurements of effluent nutrient loading from field monitoring programmes. The sum of the exports from each of the field units together with export from human sources is equal to the total annual nutrient load exported from the catchment to the water body in tonnes per annum. Taking account of mean annual discharge from the catchment, the model predictions can then be expressed as mean annual total nitrogen and total phosphorus concentrations in the inflowing streams. Model output should then be compared with observed nutrient concentrations in the streams in a calibration step to determine the accuracy of the model and the extent to which it reflects the behaviour of the environment being modelled. If the model predictions agree well with observed water quality in the calibration year, then the model must be further evaluated in a validation step. Here, the same set of export coefficients originally selected in the calibration year are applied to a changing scenario of land use and management in the catchment, and model output is compared with trends in observed water quality in the inflowing streams for the validation period. If the model still proves accurate in simulating these water quality trends, it can then be accepted as a valid tool for evaluating the impact of land use change on water quality in that catchment. If the model output does not fit observed water quality, either at the calibration or validation step, then it should not be used for either forecasting or hindcasting purposes, since it will misrepresent the likely impact of different catchment management strategies on nutrient export to the water body.

In a preliminary application of this technique to the Slapton catchment, Johnes (1986) mapped land use and nutrient inputs on a field by field basis throughout the Slapton catchment (see Johnes & O'Sullivan, 1989). This took account of inputs from livestock and fertilisers, but did not include information on nitrogen input through nitrogen fixation. In this application, all export coefficients used were derived from earlier published nutrient export studies, predominantly from North American research, with a strong emphasis on the export of phosphorus from sewage treatment works. At this stage, there was insufficient information from field experimental studies in the Slapton catchment to allow a more catchment specific selection of coefficients. The model output was expressed in tonnes of nitrogen and phosphorus exported to the Ley in 1986. However, the model was neither calibrated nor validated against observed water quality data.

In a more detailed study, Johnes & Heathwaite (1996) combined further research by Johnes (1990, 1996) in developing the export coefficient modelling approach for a research catchment in the Cotswolds with findings from research by Heathwaite, Burt & Trudgill (1989, 1990a, 1990b) regarding nutrient export rates and pathways in the Slapton catchment. A new export coefficient model was constructed for the Slapton catchment, using findings from the field experimental studies to inform the selection of representative export coefficients for the Slapton catchment. The model included information on spatial variations in nitrogen fixation rates, and more accurate information on nutrient export from human sources in the catchment. It also incorporated a distance-decay function to take account of the hydrological connectivity of different nutrient sources in the catchment to the surface drainage network. In the calibration step, the model predicted total nitrogen and total phosphorus concentrations delivered to the Ley from inflowing streams within 1.3% of observed nitrogen and 2.2% of observed phosphorus in the calibration year (see Johnes & Heathwaite, 1996, for a full description). The benefits of following this more rigorous modelling procedure are illustrated in Table 2. The calibrated model is a valuable tool for predicting the impact of past, present and future proposed management of land in the Slapton catchment on the nutrient loading delivered to Slapton Ley. However, this approach cannot provide information on in-lake processes, and whilst equations do exist in the literature relating inflow to lake nutrient concentrations (see for example OECD, 1982), these can only give a broad picture of the mean annual nutrient concentrations in the lake, and do not reflect the impact of changes in nutrient loading on the chemical and ecological structure and functioning of the lake.

The alternative approach to reconstructing past nutrient concentrations in Slapton Ley has been to focus on historical records in the sediment core. Heathwaite & O'Sullivan (1991) provide the most detailed palaeolimnological interpretation of changes in the nutrient chemistry of the Lower Ley to date, based on mineral magnetic and geochemical analysis of sediments from a core (SL3) taken from a site in Ireland Bay (see Fig. 2). The core was ^{210}Pb dated to give a baseline date of *ca* 1860 at a depth of 40cm, with an upper date at the sediment water interface of 1987. The sediment from the core was fractionated into allogenic, authigenic and biogenic components, following the procedure outlined by Engstrom & Wright (1984), and then analysed to determine the concentration of a range of major ion and nutrient fractions. The initial findings from this study indicated both nitrogen and phosphorus concentrations in the core had increased in the 20th century, most notably since 1945, with a parallel increase in biogenic silica. Heathwaite & O'Sullivan (1991) argue that this indicates a trend in nutrient enrichment of the Lower Ley, paralleled by an increase in the production of diatom species as evidenced by the silica trend. Heathwaite (1994) and O'Sullivan (1994) suggest that intensification of livestock production on permanent grass in the catchment, increased use of artificial fertilisers on all agricultural land, and the connection of a number of new domestic sources to the sewage treatment works in Slapton village in 1953 (see Fig. 2) all contributed to this nutrient enrichment. These data are essentially qualitative, and provide a broad indication of the trends in nutrient enrichment in the Ley. However, Foster *et al.* (1996) question the integrity of these sediments as a record of catchment history, since much of the sediment and sediment-associated pollutant load exported from the catchment is either retained in depositional zones behind hedgerows and within floodplains along the inflowing streams, or is transported through the Ley to the outflow during extreme storm events at times when the sediment trapping efficiency of the Ley is low. As such, the sediments may only contain a record of nutrient fractions selectively exported and retained during medium to low flow periods and may not reflect the whole catchment history.

Current understanding of phosphorus dynamics in shallow eutrophic lakes also suggests a number of problems in interpreting historical phosphorus loading from sedimentary phosphorus profiles. Of most concern is the process of phosphorus release

TABLE 2. *Modelling errors associated with the use of uncalibrated export coefficient models: comparison of model output for the Slapton catchment using uncalibrated (Johnes & O'Sullivan, 1989)* versus *calibrated (Johnes & Heathwaite, 1996) models*

	Uncalibrated model Nutrient export (tonnes a^{-1})	**Calibrated model** Nutrient export (tonnes a^{-1})	**% error** in output from uncalibrated model
NITROGEN			
Inorganic sources (Agricultural land)	56	77.4	−27.6
Organic sources (Livestock)	92	101	−8.91
Human sources (sewage, detergents)	7.9	4.4	+79.5
Background sources (non-agricultural land, rainfall)	4.6	55.1	−91.7
Total nitrogen export	160	238	−32.8
PHOSPHORUS			
Inorganic sources (Agricultural land)	0.5	1.96	−74.5
Organic sources (Livestock)	2.0	2.22	−9.91
Human sources (sewage, detergents)	2.3	0.78	+195
Background sources (non-agricultural land, rainfall)	0.05	0.39	−87.2
Total phosphorus export	4.8	5.35	−10.3

Observed data for the Slapton catchment in water year 1985/86:
Mean annual runoff for the period 1941–1971 for Slapton = 23,900,000 $m^3\ a^{-1}$
Mean annual total nitrogen concentration in water year 1985/86 = 10.1 mg l^{-1} N
Mean annual total phosphorus concentration in water year 1985/86 = 0.229 mg l^{-1} P

Uncalibrated model predictions:
Mean annual total nitrogen concentration in water year 1985/86 = 6.69 mg l^{-1} N (33.8% error)
Mean annual total phosphorus concentration in water year 1985/86 = 0.201 mg l^{-1} P (12.2% error)

Calibrated model predictions:
Mean annual total nitrogen concentration in water year 1985/86 = 9.96 mg l^{-1} N (1.39% error)
Mean annual total phosphorus concentration in water year 1985/86 = 0.224 mg l^{-1} P (2.18% error)

from the sediments during periods of anoxia in the hypolimnion (see for example Lijklema, 1994), particularly from sediments with a high phosphorus:iron ratio. This process is dependent on the redox conditions at the sediment water interface, as well as the nature of the sediment, leading to a dynamic exchange of bioavailable phosphorus between sediments and the water column, disturbing the original sequence of the phosphorus record in the upper layers of the sediment record. As a result, phosphorus may show a diffusion curve up the sediment core from older to more recent layers, such that the post-depositional record is disturbed. This causes problems in interpreting the sedimentary phosphorus record in shallow eutrophic lakes, particularly where there is a history of changes in redox conditions in the hypolimnion for which there is some evidence in the Lower Ley. Further problems occur when the sediments are disturbed through biological action, or turbulent flow, and again at Slapton, with the recession of the submergent plant beds, much of the bed sediment is exposed, leading to resuspension during turbulent periods.

Anderson *et al.* (1993) argue that whilst there are some sites in which an accurate, undisturbed record of epilimnetic phosphorus concentrations is preserved in the lake sediment history, many sites have a history of redox changes and physical disturbance at the sediment water interface which will mean that the sedimentary phosphorus record can only give a broad indication of marked changes in nutrient concentrations in the water body. The preferred technique in these instances is to infer a phosphorus record for the lake from changes in the diatom community as recorded in the sediments (see Anderson *et al.*, 1993; Bennion, 1994; Bennion *et al.*, 1995; Bennion *et al.*, 1996). Work currently underway in testing the Lake Classification and Monitoring scheme for the NRA may involve the application of this approach to Slapton Ley as a means of comparing the accuracy of a diatom-inferred phosphorus record for the Ley with model hindcasts of nutrient loadings on the Ley from its catchment, and observed phosphorus loadings from its inflow streams.

On a more positive note, there appears to be a reasonable degree of correlation between the model hindcasts of phosphorus loading on the Ley (Johnes & Heathwaite, 1996), and a reconstruction of phosphorus concentrations from sedimentary records presented for core SL1 (see Fig. 2) by Foster *et al.* (1996). The two trends are plotted together with observed total phosphorus concentrations in the inflowing streams in Fig. 3. Since the core was not dated, the results of this comparison are only tentative at present. However, there does appear to be very close agreement between the model hindcasts and the sediment reconstruction for the period 1930 to the mid 1970s. O'Sullivan (1994) suggests that the extreme drought of 1976 was a critical phase in the development of the Ley, since the Lower Ley became hydrologically isolated from the Higher Ley at this time, and argues that this may have been the trigger event which switched the Ley over from a clear water, highly productive, plant-dominated lake to a turbid lake exhibiting phytoplankton blooms and a recession of the plant beds. Certainly, after this time, the sedimentary phosphorus and model hindcasts do not correlate well (see Fig. 3). We know from observed water quality records for the inflowing streams for the period 1974 to the present day that the model hindcasts are in close agreement with observed nutrient loadings in the streams (Johnes & Heathwaite, 1996). We also know from the observations of a number of researchers that the hypolimnion in the Lower Ley has been de-oxygenated in the recent past during the summer months (Bark, unpublished), and that this was likely to be a less frequent occurrence before 1970 (see for example, O'Sullivan, 1994). Foster (*pers. comm.*) argues that whilst

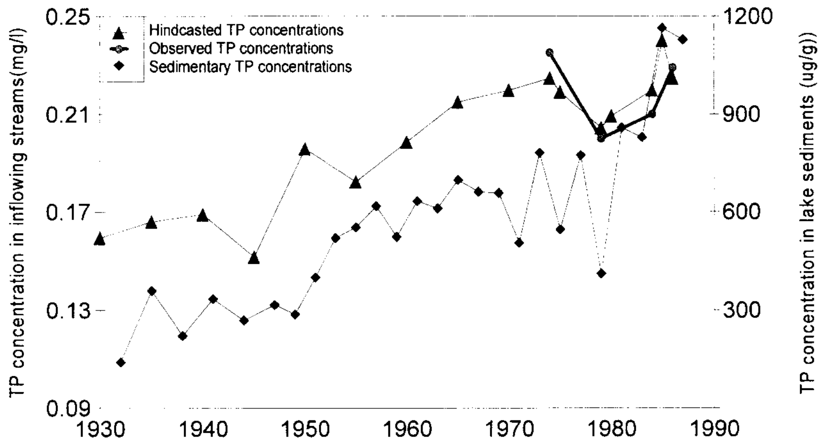

FIG. 3.
Reconstructions of nutrient loading on Slapton Ley for the period 1930–1990 (based on Johnes and Heathwaite, 1996; Foster *et al.*, 1996)

the post-1976 trend might reflect an increase in particulate phosphorus entering the Ley as a result of increased soil erosion, there is no direct evidence of this occurring at Slapton. Alternatively, evidence from studies on other shallow eutrophic lakes suggests that the more recent sediment record has undergone post-depositional change, with the release of phosphorus from the sediments to the water column under anoxic conditions. The post-1976 phosphorus profile may be reflecting a diffusion curve from the lower to the upper layers, rather than increases in catchment derived epilimnetic phosphorus loads. Foster argues, however, that although there is a marked up-core increase in the iron:manganese ratio in core SL1, suggesting loss of the more soluble manganese from the upper 10cm of the core, which would support this hypothesis, the profiles of other components do not follow the expected pattern. Nevertheless, it would appear from this preliminary analysis that internal loading is likely to be an important factor in driving phosphorus dynamics in the Lower Ley at present, as has been observed in many studies of shallow eutrophic lakes (see for example Phillips *et al.*, 1994; Lijklema, 1994). If so, then this is an important factor to be taken into account in devising suitable management strategies for Slapton Ley and its catchment.

THE PHYTOPLANKTON, ZOOPLANKTON AND FISH COMMUNITIES

It can be argued that the evidence from the modelling and palaeolimnological studies on the Lower Ley demonstrates a marked increase in the loading of both nitrogen and phosphorus to Slapton Ley over the past 60 years, and most notably in the post-war period since 1945. Further support for this trend of nutrient enrichment can be gained from a review of changes in the species composition and dominance of the different biotic communities of the Ley in the light of current understanding of the eutrophication process.

The coarse fish community at Slapton Ley is characteristic of eutrophic waters and has been discussed in detail by Bregazzi *et al.* (1982) and Kennedy (1996). A long history of the fishery at Slapton has meant that this is perhaps the best understood of the ecological communities of the Ley. For further information, the reader is referred to the paper by Kennedy (1996).

In contrast to the wealth of information on the fish community, the zooplankton community in the Ley has been almost wholly ignored to date, except in a few instances. This is a substantial flaw in the research programme at Slapton to date. We know from recent research on shallow eutrophicated lakes, and from the experiences of a wide range of researchers attempting to restore turbid, phytoplankton-dominated waters to a clear water, plant-dominated state, that the presence or absence of a viable zooplankton community plays a vital role in sustaining eutrophic waters in these two alternative steady states (see for example Irvine *et al.,* 1989; Scheffer, 1989; Moss *et al.,* 1991; Scheffer *et al.,* 1993). The zooplankton are the natural prey of the planktivorous fish community, which in turn are predated upon by the piscivorous fish. They also play an important role in the control of phytoplankton abundance, since the zooplankton, particularly the larger cladocerans, exert a grazing pressure on the phytoplankton. The nature of these biological interactions is almost wholly unknown at Slapton, and as a result, we do not know at present whether this "top-down" control mechanism is in place in the Ley. It is likely that there is a reasonably abundant zooplankton population in the Lower Ley, since there are planktivorous fish present, and there is an abundant supply of phytoplankton. However, with the recent dieback in the extent of the submergent macrophyte beds in the Lower Ley (discussed below), there has been a concomitant loss of refugia in which the zooplankton can shelter from predation. In an open, unstructured environment, created by the scarcity of submerged plants, the large cladoceran grazers may be more vulnerable to fish predation (see Irvine *et al.,* 1989). The lack of suitable habitat, or alternative large-invertebrate food sources, may also have long-term implications for the fish community, reducing populations of larger fish, and encouraging small zooplanktivores. These conditions would be conducive to higher populations of phytoplankton, and thus further reduce the abundance of submerged plants. Clearly, research on the zooplankton community must be a priority at Slapton in the future.

The phytoplankton community in the Ley has been investigated by a number researchers, possibly because the increase in phytoplankton abundance noted in the Lower Ley in the late 1960s was a key factor in promoting concerns over the trophic status of the Ley. The first quantitative study of the planktonic communities of Slapton Ley was conducted by Benson-Evans *et al.* (1967). In this, the authors demonstrated marked seasonal, horizontal and vertical variations in the composition of the phytoplankton community and relative abundance of individual species within the Ley. A high diversity of benthic algae was recorded in this survey, with epilithic algae occurring on rocks and stones in the River Gara, at Slapton Bridge and in the shallow littoral margins of the Lower Ley. Epipelic algae were also found in the shallow littoral areas on silt deposits, and epiphytic algae were abundant on the extensive submergent plant beds of the Lower Ley at that time (Benson-Evans *et al.,* 1967). This suggests that the Ley was unlikely to be the turbid water body we see today, since the present turbidity is sufficient to restrict light penetration at depth, reducing the extent of the euphotic zone available for macrophytic and benthic algal production in much of the Lower Ley. Benson-Evans *et al.* (1967) also noted that whilst a high diversity of phytoplankton species was present in the Ley, summer phytoplankton blooms in the Ley were dominated by species commonly associated with eutrophic condition such as *Tabellaria* spp., *Asterionella* spp. and *Anabaena* spp.. This study provided an important snapshot of the status of the phytoplankton community at that time, but was not repeated until the work of Van Vlymen in the mid 1970s (see Van Vlymen, 1979, 1980). Again, this more recent study provides a wealth of detail on the status of the phytoplankton community at that time, with evidence emerging for an increase in the abundance of centric diatom species associated with nutrient enriched waters. A further snapshot of the phytoplankton community is available from a summer net sample collected for the Lake Classification and Monitoring scheme database (see Johnes *et al.*, 1994a, 1994b; Moss *et al.*, 1996). This was essentially a qualitative survey, recording three cyanophyte genera (*Oscillatoria* spp., *Microcystis* spp., *Anabaena* spp.), two diatom genera (*Synedra* spp., *Asterionella* spp.), *Pediastrum, Dictyospherium* and one desmid species, *Staurastrum,* as common in the sample. The balance of species present in this sample suggests eutrophic conditions prevail at Slapton, but the high degree of temporal and spatial variation in phytoplankton communities negates the extent to which results from a single sample are applicable in describing a complex system.

These neo-limnological studies have value in describing the phytoplankton community at these date points. However, they cannot contribute to our understanding of the impact of long-term nutrient enrichment on the overall ecology of Slapton Ley over past 60 years. Again, this has perhaps been a flaw in the research programme at Slapton to date in that there has been no long-term monitoring of changes in phytoplankton community composition and dominance within the Ley.

This balance is redressed somewhat by palaeolimnological research studies (see for example Crabtree & Round, 1967; O'Sullivan *et al.*, 1991; O'Sullivan, 1994). O'Sullivan (1994) provides a valuable synthesis of the palaeolimnological evidence collected to date, including a useful conceptual model of long-term changes in the composition of the phytoplankton community and relative dominance of different species. This is based on analyses of the diatom record in a number of sediment cores from the Lower Ley. A key study was that conducted by Moscrop (1987). The core record is divided into four phases. The first reflects the period 1850–1910, when the dominant genera were *Cymbella* spp., *Cocconeis* spp., and *Fragilaria* spp., switching to phase two with an increase in the abundance of centric diatoms in from 1910–1960 linked to a change from arable farming to more intensive livestock production in the Slapton catchment (O'Sullivan, 1994). Heathwaite (1994) and O'Sullivan (1994) both argue that the diatom evidence for these early phases suggest that Slapton Ley was a clear water, plant-dominated lake up to the 1950s, with an abundant epiphytic algal community dominated by *Fragilaria* spp., and a low abundance of open water planktonic species. Phase three, reflecting the period 1960–1978 was characterised an increase in the abundance of centric diatom species such as *Cyclostephanus dubius, Stephanodiscus hantzschii* and *Melosira* spp. (O'Sullivan, 1994). Phase four, 1978–1987 is dominated by centric planktonic diatoms occupying the open water environment, with a concomitant reduction in the abundance of epiphytic species. The dominant species in this phase are *Cyclostephanus dubius, Melosira* spp. and *Asterionella formosa* which O'Sullivan (1994) suggests reflects a switch from a clear water plant-dominated system with a high degree of light penetration, to a turbid system with reduced light penetration in the recent period. The trigger events thought to have switched the Ley between the four phases have been essentially catchment based, with a switch to livestock production in 1910, post-war agricultural intensification and expansion from 1945 onwards, and the hydrological isolation of the Lower Ley during the 1976 drought at which time point source discharges of nutrient rich sewage effluent to the Lower Ley would have been proportionally more significant than nutrient loading from agricultural sources in the catchment. Certainly, this pattern

TABLE 3. *The relative abundance of macrophyte species in Slapton Ley recorded in 1969 (Brookes & Burns, 1969)*

Species	Estimate of Abundance
Ranunculus circinatus	Rare
Ranunculus trichophyllus	Locally abundant
Ranunculus peltatus ssp. *peltatus*	Occasional
Ranunculus baudotii	Occasional
Ceratophyllum demersum	Uncommon
Ceratophyllum submersum	Very rare
Elatine hexandra	Two areas
Myriophyllum spicatum	Locally frequent
Elodea canadensis	Locally abundant
Potamogeton pusillus	Occasional
Potamogeton crispus	Occasional
Potamogeton pectinatus	Rare
Zannichellia palustris	Rare, two patches

fits in well with the model hindcasts and sedimentary phosphorus records for the Ley (see O'Sullivan, 1994; Johnes & Heathwaite, 1996; Foster *et al.*, 1996).

THE MACROPHYTE COMMUNITY

The macrophyte community has, like the fish community, benefited from more frequent and detailed qualitative studies since the late 1960s, and has recently been studied in some detail by Wilson (1991). As such, it provides an important corollary to information derived from phytoplankton and palaeolimnological studies on the ecological impacts of nutrient enrichment in Slapton Ley.

The first qualitative survey of the flora of Slapton Ley Nature Reserve was undertaken by Brookes & Burns (1969). Thirteen species of aquatic macrophytes were recorded from the open water, as listed in Table 3. The survey also recorded areas of *Polygonum amphibium* and *Nymphaea alba*, particularly well developed in the more sheltered parts of the western side of the Lower Ley. Free-floating plants (e.g. *Lemna minor*) were restricted to the still water among the reed beds. This survey excluded all non-vascular plants, so that Charophytes and other macroalgae were not recorded.

TABLE 4. *The relative abundance of submerged macrophyte species in Slapton Ley recorded in 1990 (Wilson, 1991)*

Species	Relative Abundance (%)
Ceratophyllum demersum	72.90
Myriophyllum spicatum	12.36
Elodea canadensis	7.64
Chara sp.	6.54
Ranunculus circinatus	0.32
Potamogeton pectinatus	0.15
Potamogeton crispus	0.04
Zannichellia palustris	0.02
Callitriche sp.	0.02
Bryophyte	0.01

A further qualitative survey of the flora of the Reserve was carried out by Cole (1984). The following species of aquatic macrophytes were recorded: *Myriophyllum spicatum, Ranunculus peltatus, R. penicillatus v. penicillatus, Potamogeton berchtoldii, P. trichoides, P. pectinatus, Ceratophyllum demersum*, and *Elodea canadensis.* All submerged species were represented in the northern two-thirds of the Ley, whereas only *C. demersum* was apparent in the south. *Nymphaea alba* formed extensive patches near Torcross and Stokeley Bay, whilst *Lemna* species were confined to the sheltered areas among the fringing reed beds. Although this survey was not intended to include non-vascular plants, significant amounts of algal species, including those of *Enteromorpha* and *Cladophora*, were observed in the Lower Ley, covering the submerged macrophytes, and forming extensive rafts on the surface. A species of charophyte was also recorded.

The first quantitative survey of the aquatic macrophytes of Slapton Lower Ley was carried out between July and September 1990 (Wilson, 1991). Owing to the turbidity of the water, normal quadrat surveying and visual estimates of abundance were not possible. Samples were therefore collected using a grab along a total of eight transects, and species abundance quantified by fresh weight. Although floating-leaved and free-floating macrophytes were not the prime focus of this survey, their presence was noted along the transects. A total of ten species of submerged macrophyte were recorded, which are listed in Table 4 together with their relative abundance. In addition, three species of floating-leaved or free-floating macrophytes were encountered, namely *Lemna minor, Polygonum amphibium* and *Nymphaea alba*. Despite the limitations imposed by the turbidity of the water, the results of the surveys revealed a number of factors which correlate well with general limnological theory, as well as some which indicate characteristics peculiar to conditions within the Lower Ley. The overall distribution of submerged species reflect the physical limitations on macrophyte growth, particularly those of wave action in shallow water, and reduced light penetration with depth (Jupp & Spence, 1977a, 1977b). At all sampling points of 25cm depth, water clarity was good, yet mean abundance and species richness were considerably lower than might be expected. Low productivity at this depth is attributable to the effects of wave action, in removing fine sediments and displacing seedlings. Mean abundance of species reached a maximum at 50cm, and decreased rapidly with depth (correlation coefficient of -0.805).

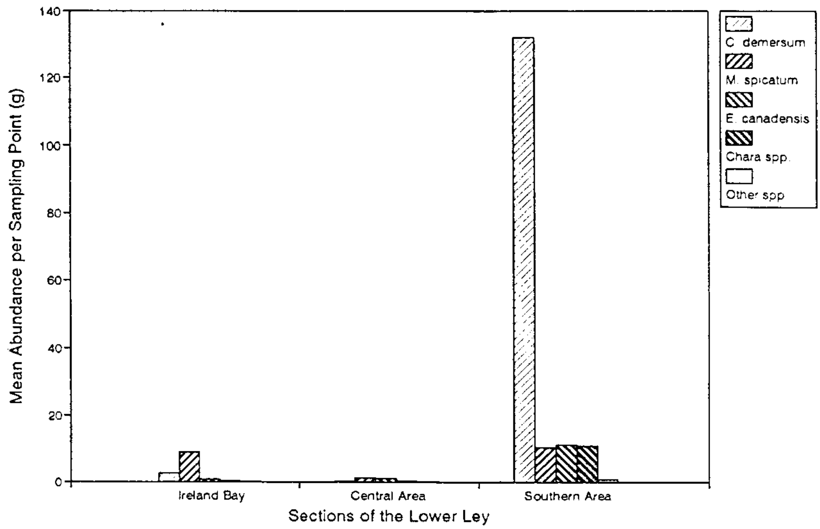

FIG. 4
Mean abundance of macrophyte species in sections of the Lower Ley

A limitation on abundance at relatively shallow depths is likely to be the result of rapid light attenuation by phytoplankton. Mean Secchi disc transparency (SDT) decreased with depth (correlation coefficient of −0.977), consistent with the tendency of phytoplankton populations to become more concentrated in deeper waters (Wetzel, 1983).

By far the most prevalent species, *Ceratophyllum demersum* accounted for nearly 73% of the total fresh weight. Its mean abundance reached a maximum at 50cm and declined with depth. *C. demersum* is a tall-growing, rootless species, which can occur attached or free-floating (Hutchinson, 1975) and its prevalence in the shallower waters of the Ley may well exclude low-growing species (Hough *et al.*, 1989). One of the few species able to coexist with *C. demersum*, was the similarly tall-growing *Myriophyllum spicatum*. Although far less abundant, its pattern of mean abundance with depth followed that of *C. demersum* in peaking at 50cm, but decreasing less rapidly in deeper water, in accordance with the low light requirements of this species (Nichols & Shaw, 1986).

The mean abundance of *Elodea canadensis* with depth did not appear to follow any recognisable pattern. Although this species is normally rooted, it demonstrates an ability to flourish as floating mats (Hutchinson, 1975), a phenomenon often encountered in the Lower Ley. This factor, combined with its tolerance of low light levels when rooted (Nichols & Shaw, 1986), enables *E. canadensis* to occupy a wide range of water depths. A definite pattern of mean abundance was demonstrated by the charophyte, but one that increased, rather than decreased, with depth. Maximum mean abundance occurred at 175cm, and this was the only species collected at 200cm. Its apparent preference for deeper water is consistent with surveys conducted by Spence (1975), which showed that charophytes are generally recorded at greater depths than angiosperms.

It was apparent, however, that the horizontal distribution of the submerged macrophytes was not uniform, and that *Ceratophyllum demersum*, in particular, was concentrated in certain areas. Fig. 4 illustrates the marked differences in species abundance between Ireland Bay, the central section, and the southern area around Stokeley Bay and Torcross. Of the total fresh weight of all species, 89% occurred in the southern area, 80% of which was composed of *C. demersum*. This suggests that parts of the Lower Ley may be subject to differing physical and chemical influences, which, in turn, affect the distribution and abundance of the submerged plant community. The most important variables affecting the submerged macrophytes appeared to be the degree of shelter from prevailing winds, and the proximity to sources of allochthonous nutrients, whilst the volume of inflow to the area, and the mean depth, may also have some bearing.

Several authors (e.g. Brookes & Burns, 1969; Van Vlymen, 1980) have suggested that parts of Ireland and Stokeley Bays are sheltered from the prevailing winds, which, during the growing season, are mainly southwesterlies (Ratsey, 1975). To the southwest of both Ireland and Stokeley Bays lie hills which provide a degree of shelter. Southwesterly winds are funnelled through the intervening valley, on to the central part of the Lower Ley. Since the flow is in a southerly direction, a conflict of the forces of wind and current may cause a great deal of turbulence in this area. In a shallow lake, such turbulence would deter the growth of taller submerged plants. The absence of floating-leaved species, the presence of Charophyte beds in the deeper water, and the low abundance of tall-growing species is consistent with these factors. This section featured the lowest number of species, yet proved to be the most diverse, since no single species predominated.

Ireland Bay contained the highest number of species, but at relatively low mean abundance and frequency. Three species, *Potamogeton crispus*, *Zannichellia palustris* and *Callitriche* spp., were only encountered in single samples in the shallows, and may be described as rare. *Myrophyllum spicatum* was by far the most common species, but since Ireland Bay only contributed less than 8% to the total fresh weight of vegetation, even this species cannot be described as abundant here. These characteristics of the submerged plant community were consistent with the low mean SDT of 29cm, which suggests the presence of dense phytoplankton populations.

The southern section, from north of Stokeley Bay to Torcross, stood in marked contrast to the other two. The fairly high degree of shelter it receives extends over most of its area, but decreases towards the northeast, as demonstrated by extensive stands of *Nymphaea alba*, and smaller patches of *Polygonum amphibium*, to the west, southwest and south. The area also appears to be the preferred habitat of many freshwater birds. The sheltered aspect probably accounts for the relatively high mean abundance, and high frequency, of submerged plants.

Since the influence of submerged macrophytes is proportional to their biomass and productivity (Carpenter & Lodge, 1986), their demise with eutrophication may have profound implications for the ecosystem. A comparison of the results of the 1990 survey with those of previous ones should reveal the extent of any changes, and thus provide some indication of the repercussion for the Lower Ley as a whole.

The survey of flowering plants undertaken in 1969 by Brookes & Burns did not include any indication of the distribution of submerged macrophytes within the Lower Ley, and provided only subjective estimates of their abundance. The fact that these estimates could be made implies that the water, at that time, was relatively clear. Certain species recorded in 1969 were not encountered in this survey; whilst this may be attributable to differences in sampling methods, some inference can be drawn. Three out of four members of the family Ranunculaceae recorded in 1969 were absent from this survey. Since Ranunculaceae are early-flowering, and senescence of some species may have occurred by July, these omissions cannot be taken as a definite indication of change in species composition. However, *Ranunculus peltatus*, according to TWINSPAN classification (Palmer, 1989), is strongly associated with mesotrophic waters, and only weakly with eutrophic, so that a decline in this species would not be unexpected. *R. circinatus* was apparently rare in 1969, but now seems to occur fairly frequently, at lower abundance levels. The same observation can be applied to *Potamogeton pectinatus*. Both species are common in eutrophic waters, and appear to have become more frequent in the Lower Ley. *P. pusillus* and *P. crispus*, described as occasional in 1969, were, respectively, absent and rare in this survey. Both species are strongly associated with eutrophic waters, and the reason for their demise may be associated with shading by phytoplankton. Two further species recorded by Brookes & Burns were not encountered in this survey. *Elatine hexandra* is very scattered and rare in the British Isles, and prefers acid, mesotrophic water, so that its absence from the Lower Ley would not be unexpected. *Ceratophyllum submersum*, the trophic requirements of which are unknown, was very rare in 1969, and may well have disappeared since then.

The frequency of *Zannichellia palustris*, a species strongly associated with eutrophic waters, does not appear to have altered, it being rare in 1969, and remaining so at present. *Elodea canadensis*, common in both mesotrophic and eutrophic waters, was described as locally abundant in 1969. This species now appears to be locally frequent, but not abundant. Another species of eutrophic waters, *Myriophyllum spicatum*, was locally frequent in 1969, but may now be described as locally abundant. The most significant change revealed by this comparison is the increase in the abundance and frequency of *Ceratophyllum demersum*. In 1969 it was uncommon, yet it is now the most prevalent species. Needless to say, this species is strongly associated with eutrophic waters.

The survey of the submerged plants carried out by Cole in 1984, gave some idea of the distribution and frequency of species, but did not comment on the abundance of them all. The results give the impression that *Ceratophyllum demersum* was, by this time, far more frequent than in 1969, appearing in 64% of sample points. On transects covering the southern part of the Ley, *C. demersum* was the sole submerged species recorded. Since only *Myriophyllum spicatum* and fine-leaved *Potamogeton* species were said to be widespread and abundant, it must be assumed that *C. demersum* was not as prolific as it is today.

The Trophic Status of Slapton Ley: Past, Present and Future

Changes in the physical environment and nutrient chemistry of Slapton Ley have clearly been paralleled by changes in the nature and dominance of the various biotic communities in both the Higher and Lower Ley systems over the past 60 years, with a loss of aquatic plants, and increase in phytoplankton dominance in the Lower Ley, and a progressive terrestrialisation of the Higher Ley. Using two recently developed schemes we can attempt to quantify the extent of this change.

The Nature Conservancy Council scheme for the classification of trophic status of standing water bodies is based on changes in the macrophyte community (see Palmer, 1989; Palmer *et al.*, 1992). This is based on a relationship between the species composition of macrophyte community in a standing water body and its water chemistry as defined by pH, conductivity and alkalinity, derived from studies on a large number of British lakes surveyed in the period 1975–1988. There is a sample bias in this scheme towards lakes which are particularly rich in macrophyte species, and those of high conservation value. As such, it has limited reliability when applied to lakes which have lost, or are in the process of losing their plants. Nevertheless, it does provide a means of quantifying the changes in the macrophyte community at Slapton Ley over the past 25 years in terms of the trophic status of the Ley. The scheme operates on the principle of assigning an averaged trophic ranking score to a water body on a scale of 1–10, with higher scores pertaining to eutrophic waters and lower scores to oligotrophic waters. The scores are derived from individual scores for each plant species recorded in the water body on the basis of the relative abundance of each species in waters of differing trophic status (see Palmer *et al.*, 1992 for a detailed discussion). When applied to the plant survey data for the past 25 years, a trend towards nutrient enrichment is identified. Many of the macrophyte species recorded during the 1969 survey are commonly found in eutrophic waters, whilst some are associated with the mesotrophic category. The average Trophic Ranking Score (TRS) of these species was 8.77, which indicates that the Lower Ley was already in an eutrophic condition by this time. The average TRS of species recorded in the 1984 survey was 8.53, a slightly lower figure than in 1969, and not significantly different, still indicating eutrophic conditions. TRS of the 1990 survey averaged 8.85, the highest of the three results, but again not significantly different from the scores for earlier surveys, and perhaps reflecting the short time period between the surveys, all of which post-date the observed shift of the Ley to eutrophic conditions.

Evidence from the modelling and palaeolimnological studies indicates that by the time the first plant survey was conducted in 1969, Slapton Ley had already undergone a period of marked nutrient enrichment. We also know that classification schemes based on a limited range of variables are not reliable when those variables fall outside the range of observations on which the scheme is based. In the case of the NCC macrophyte classification scheme, it cannot make distinctions in trophic state between lakes with similar nutrient loadings but different ecological structure. In order to quantify this period of change, an alternative scheme can be used which allows a reconstruction of the baseline state of Slapton Ley in the 1930s prior to the major phase of nutrient enrichment in the post-war period. This is the lake classification and monitoring scheme currently being tested for the National River Authority (see Johnes *et al.*, 1994a, 1994b; Moss *et al.*, 1996). Slapton Ley was one of 100 sites selected to provide a database from which the scheme was initially developed. Preliminary findings for Slapton are presented in Table 5, which provide an initial classification of changes in trophic state from the baseline to the present day. It must be stressed, however, that these are only preliminary data, and cannot be confirmed until the scheme has been fully tested in ongoing studies and then re-applied to Slapton Ley.

The lake classification and monitoring scheme has as its central concept the idea that the present state of any lake should be assessed according to the degree to which it has changed over time, rather than whether it exhibits a particular set of characteristics which make it appear as the same 'type' as other lakes with similar characteristics in the present state, but with a different catchment and lake history (Moss *et al.*, 1996). If the ultimate aim in managing freshwater systems is to attain a desirable and sustainable state, then we need to know whether the system is in a period of equilibrium with its environment, or undergoing change, the extent to which the system has changed over time and the cause of such change. By adopting this approach we are able to distinguish between lakes which are eutrophic and lakes which have become eutrophicated over time, and this in turn allows us to determine whether lake restoration through lake and catchment management is attainable in the future. The scheme uses a series of simple models to provide a hindcast of lake state in the baseline period detailing the likely range

TABLE 5. *Preliminary output from the Lake Classification & Monitoring Scheme for Slapton Ley (Johnes* et al., *1994a, 1994b)*

Variable	Baseline State	Present Day	% Change
Retention time (days)	19	19	0
Conductivity (ms cm^{-1})	350	300	−14
Inflow total P (mg l^{-1})	0.20	0.17	−15
Inflow total N (mg l^{-1})	4.38	11.2	157
Volume ($m^3 \times 10^6$)	1.80	1.80	0
Maximum depth (m)	3.50	3.50	0
Minimum Secchi depth (m)	0.87	0.65	25
pH	7.73	8.63	0
Lake total alkalinity (meq l^{-1})	1.62	1.89	16
Lake calcium (mg l^{-1})	35.9	10.1	−72
Lake total P (mg l^{-1})	0.105	0.150	43
Lake total N (mg l^{-1})	4.56	9.21	102
Winter nitrate (mg l^{-1})	1.67	5.88	252
Max chlorophyll a (mg l^{-1})	99.2	126	7
Plant score (0–10)	8.16	8.85	8
Fish population	Present	Present	N
EUTROPHICATION CLASS		3	
ACIDIFICATION CLASS		1	
OVERALL CLASS		2	

for a number of water quality variables as outlined for Slapton Ley in Table 5. From a field monitoring programme conducted on Slapton Ley in water year 1991–1992, the present day values of this same group of variables were determined. In the scheme, the extent to which change has occurred in the lake is evaluated to indicate the percentage change in each variable since the baseline period. The overall degree of deviation from the baseline state is then calculated for all variables. Then, by grouping together variables associated with particular axes of environmental change, the direction of change is also identified, and a class assigned based on pre-set classification bands. At present this scheme quantifies the extent of eutrophication as between 50–100% since the baseline period, largely attributable to intensification and expansion of agricultural production in the Slapton catchment since the baseline period, but also linked to increases in the human population, and the number of homes linked to the sewage treatment works in the catchment. At present, change is being driven by the increases in nutrient loading from the catchment, reflected in a decrease in the minimum Secchi depth of the Ley caused by resuspension of sediments and increased phytoplankton abundance in the water column, increases in chlorophyll *a* concentrations in the Ley, also as a function of increased phytoplankton abundance, and an increase in the trophic ranking score for the macrophyte community reflecting the change from short submergent species associated with clear water systems to the tall rank species currently found in the turbid waters of Slapton Ley.

The implications of the demise of submerged macrophytes over extensive areas of the Lower Ley, and the change in relative abundance of certain species, may be highly significant. The consequences of any changes within the submerged plant community of the Lower Ley may be inferred from other studies of plant loss in shallow eutrophic lakes (see for example Phillips *et al.*, 1978; Irvine *et al.*, 1989). In areas where a decline in submerged macrophyte productivity has been recorded, reductions in the level of dissolved oxygen and organic carbon may occur (Carpenter & Lodge, 1986). The rate of phosphorus cycling, and deposition of fine sediments, may also be adversely affected. These effects are likely to have implications for other organisms, but a more profound consequence of the demise of submerged macrophytes would be the loss of habitat structure provided by these plants. Benthic fauna, invertebrates, epiphytes, zooplankton and fish all depend on submerged plants to fulfil a variety of functions.

The decrease in rudd populations observed in the Lower Ley (see Kennedy, 1996) may well be attributable to the scarcity of submerged plants, their main food source and preferred habitat. The dependence of perch and pike on plants for spawning, cover, and as habitat for prey may be a key factor in their lower population levels. The changes in the phytoplankton community of the Lower Ley provide further cause for concern, with the decline in epiphytic and benthic phytoplankton and increase in abundance of the open water species following the well marked path to a phytoplankton-dominated turbid state. From the recorded decline in epiphytic diatoms since 1976, it might be assumed that other epiphytes, insects, gastropod molluscs, and isopod and decapod crustaceans that graze or inhabit submerged plants are now less abundant, although without observed data such conclusions are tentative. Birds that consume large quantities of underwater plants, such as mute swan and coot, may have been similarly affected. Certainly, the latter species is not as abundant now as it was during the coot shoots of the 1930s (Stanes, 1983).

The impression given by a comparison of the three macrophyte surveys is that some species, such as *Elatine hexandra*, have probably declined since 1969, whilst others, notably *Ceratophyllum demersum*, have increased. It is difficult to assess, on the basis of previous surveys, whether any change in overall abundance has occurred, but indirect evidence from palaeolimnological studies suggests that a decline has taken place (Crabtree & Round, 1967; Moscrop, 1987; O'Sullivan, 1994). However, the results of the 1990 survey show that such a decline has not affected all sections of the Lower Ley. Ireland Bay and the central area of the Lower Ley may be perceived as entering a later phase of eutrophication, in which turbid water associated with dense phytoplankton populations largely exclude submerged plants. The southern region, in contrast, appears to be in an earlier phase, in which tall-growing plants are still abundant. Whilst the rest of the Ley may indeed have crossed the threshold to mainly phytoplankton production, conditions in the south may not have been conducive, as yet, to such a transition.

The persistence of an abundant submerged plant community in part of a lake that is thought to be in an advanced state of eutrophication, confirms that responses to increased nutrient loading are not of a purely linear nature. The prime factor maintaining the current distribution of submerged macrophytes appears to be variations in physical and chemical conditions within the Lower Ley, and the existence of mechanisms that serve to buffer the effects of eutrophication in the south. In particular, the action of prevailing southwesterly winds, in removing phytoplankton to the north during periods of low flow, may be the prime factor in preserving a submerged macrophyte community in the southern part of the Lower Ley. However, it may also be argued that both the Lower Ley and Higher Ley are currently in a state of transition and have not yet achieved a steady state equilibrium. The Higher Ley appears to be moving to a terrestrial state in some areas, with a single channel becoming more defined from the River Gara to Slapton Bridge. The Lower Ley is changing in a different direction, perhaps towards a stable phytoplankton-dominated state, with the complete loss of submergent macrophytes and the valuable habitat they provide in the near future. If either system attains these projected states, particularly if nutrient loading continues to increase from the catchment, then this may have severe implications for the future amenity and conservation value of Slapton Ley.

Conclusion and Recommendations for Future Research

The evidence reviewed here on recent changes in the nutrient loading on Slapton Ley and its ecological communities suggests that the system is in a state of change. The sediment accumulation and infilling of the Higher Ley can be seen as part of the evolution of this system, dating from the engineering works in the mid-nineteenth century, and exacerbated by agricultural intensification and expansion in the present century. These trends are possibly mirrored by those observed by Foster *et al.* (1996) in the Start catchment. The floodplains of the Gara and Start catchments as well as the Higher Ley may currently be acting as important sediment and nutrient traps for the Lower Ley. The rapid rates of sedimentation within these systems, and the colonisation of the Higher Ley by terrestrial plants has immediate implications for the future ecology and hydrology of the Higher Ley as a wetland system. However, what is of equal concern is the potential effects of this trend for the Lower Ley which is already losing its submergent plants and switching to a phytoplankton-dominated state. Further nutrient enrichment and increased suspended sediment loads delivered to the Lower Ley in future if the Higher Ley ceases to operate as a sediment and nutrient sink will only accelerate this switch. Both systems, therefore, require prompt and targeted management if these trends are to be reversed to re-create a Higher Ley wetland, and a clear water, plant-dominated Lower Ley in which a viable coarse fishery can be maintained. However, we currently know very little about the chemical and ecological functioning of these systems, and without this knowledge, we cannot determine an effective catchment and lake management strategy which would permit the management of Slapton Ley in a stable, sustainable state. There is a clear need for co-ordinated research on both the Lower and Higher Ley basins as a complex system if we are resolve these issues in future and play some role in determining the future state of Slapton Ley.

References

Anderson, N. J., Rippey, B. and Gibson, C. E., (1993). A comparison of sedimentary and diatom-inferred phosphorus profiles: implication for defining pre-disturbance nutrient conditions. *Hydrobiologia,* **253**, 357–366.

Bennion, H., (1994). A diatom-phosphorus transfer function for shallow, eutrophic ponds in southeast England. *Hydrobiologia* **275/276**, 391–410.

Bennion, H., Wunsam, S. and Schmidt, R., (1995). The validation of diatom-phosphorus transfer functions: an example from Mondsee, Austria. *Freshwater Biology,* **34**, 271–283.

Bennion, H., Allott, T. E. H., Monteith, D. T., Duigan, C. A., Haworth, E. Y., Anderson, N. J. and Juggins, S., (1996). The Anglesey lakes, Wales, UK: changes in trophic status of three standing waters as inferred from diatom transfer functions and their implications for conservation. *Aquatic Conservation,* **6**, in press.

Benson-Evans, K., Fisk, D., Pickup, G. and Davies, P., (1967). The Natural History of Slapton Ley Nature Reserve II: preliminary studies of the freshwater algae. *Field Studies,* **2**, 493–519.

Bregazzi, P. R., Burrough, R. J. and Kennedy, C. R., (1982). The Natural History of Slapton Ley Nature Reserve XIV: the history and management of the fishery. *Field Studies,* **5**, 581–589.

BROOKES, B. S. and BURNS, A., (1969). The Natural History of Slapton Ley Nature Reserve. XIV. the flowering plants and ferns. *Field Studies,* **3**, 125–157.

BURT, T. P. and ARKELL, B. P., (1987). Temporal and spatial patterns of nitrate losses from an agricultural catchment. *Soil Use and Management,* **3**, 138–143.

BURT, T. P., BUTCHER, D. P., COLES, N. and THOMAS, A. D., (1983). Hydrological processes in the Slapton Wood catchment. *Field Studies,* **5**, 731–752.

BURT, T. P. and HEATHWAITE, A. L., (1996a). Long-term study of the natural environment at Slapton Ley. *Field Studies,* **8**, 533–542.

BURT, T. P. and HEATHWAITE, A. L., (1996b). The hydrology of the Slapton catchments. *Field Studies,* **8**, 543–557.

CANNELL, S., (1992). *Slapton Higher Ley—its history, ecology and conservation.* Unpublished paper, Slapton Ley Field Centre.

CARPENTER, S. R. and LODGE, D. M., (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany,* **26**, 341–370.

CHAPPELL, N. A. & FRANKS, S. W., (1996). Property distributions and flow structure in the Slapton Wood catchment. *Field Studies,* **8**, 559–575.

COLE, E., (1984). *Description and maps of the plant communities of Slapton Ley Nature Reserve.* Unpublished report, Slapton Ley Field Centre.

COLES, N. and TRUDGILL, S. T., (1985). The movement of nitrate fertiliser from the soil surface to drainage waters by preferential flow in weakly structured soils, Slapton, South Devon. *Agriculture, Ecosystems and Environment,* **13**, 241–259.

CRABTREE, K. and ROUND, F. E., (1967). Analysis of a core from Slapton Ley. *New Phytologist,* **66**, 255–270.

ELPHICK, DENNIS, (1996). A review of 35 years of bird-ringing at Slapton Ley (1961–95) together with a brief historical review of ornithological observations. *Field Studies,* **8**, 699–725.

FOSTER, I. D. L., OWENS, P. N. and WALLING, D. E., (1996). Sediment yields and sediment delivery in the catchments of Slapton Lower Ley, South Devon, UK. *Field Studies,* **8**, 629–661.

HAILS, J. R., (1975). Some aspects of the Quaternary history of Start bay, Devon. *Field Studies,* **4**, 207–222.

HEATHWAITE, A. L., (1994). Chemical fractionation of lake sediments to determine the effects of land-use change on nutrient loading. *Journal of Hydrology,* **159**, 395–421.

HEATHWAITE, A. L. and JOHNES, P. J., (1996). The contribution of catchment sources of nitrogen and phosphorus to stream water quality. *Hydrological Processes,* **10**, in press.

HEATHWAITE, A. L. and O'SULLIVAN, P. E., (1991). Sequential inorganic chemical analysis of a core from Slapton Ley. *Hydrobiologia,* **214**, 125–135.

HEATHWAITE, A. L., BURT, T. P. and TRUDGILL, S. T., (1989). Runoff, sediment and solute delivery in agricultural drainage basins—a scale dependent approach. In Lagone, S. (Editor) *Regional Characterization of Water Quality.* IAHS Publ. 182, Wallingford, pp. 290–218.

HEATHWAITE, A. L., BURT, T. P. and TRUDGILL, S. T., (1990a). The effect of land use on nitrogen, phosphorus and suspended sediment delivery to streams in a small catchment in southwest England. In Thornes, J. B. (Editor) *Vegetation and Erosion.* John Wiley, Chichester, pp. 161–179.

HEATHWAITE, A. L., BURT, T. P. and TRUDGILL, S. T., (1990b). Land use controls on sediment production in a lowland catchment, southwest England. In Boardman, J., Foster, I. D. L. and. Dearing, J. A (Editors) *Soil Erosion on Agricultural Land.* John Wiley, Chichester, pp. 69–86.

HOUGH, R. A., FORNWALL, M. D., NEGELE, B. J., THOMPSON, R. L. and PUTT, D. A., (1989). Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. *Hydrobiologia,* **173**, 199–217.

HUTCHINSON, G. E. (1975) *A Treatise on Limnology. Volume III. Limnological Botany.* John Wiley & Sons.

IRVINE, K., MOSS, B. and BALLS, H., (1989). The loss of submerged plants with eutrophication II: relationships between fish and zooplankton in a set of experimental ponds, and conclusions. *Freshwater Biology,* **22**, 89–107.

JENNS, N., (1994)/ *Sedimentation in Slapton Ley: an indicator of evolving land use.* Unpublished BSc dissertation, University of Oxford.

JOHNES, P. J., (1986). *An investigation into aspects of agriculture and water quality at Slapton Ley, South Devon.* Unpublished BSc dissertation, University of Plymouth.

JOHNES, P. J., (1990). *An investigation of the effects of land use upon water quality in the Windrush catchment.* Unpublished D.Phil. thesis, University of Oxford.

JOHNES, P. J., (1996). Evaluation and management of the impact of land use change on the nitrogen and phosphorus load delivered to surface waters: the export coefficient modelling approach. *Journal of Hydrology,* in press.

JOHNES, P. J. and HEATHWAITE, A. L., (1996). Modelling the impact of land use change on water quality in agricultural catchments. *Hydrological Processes,* in press.

JOHNES, P. J., MOSS, B. and PHILLIPS, G. L., (1994a). *Lakes—Classification and Monitoring. A strategy for the classification of lakes.* National Rivers Authority R&D

JOHNES, P. J., MOSS, B. and PHILLIPS, G. L., (1994b). *Lakes—Classification and Monitoring. A strategy for the classification of lakes.* National Rivers Authority R&D Project Record 286/6/A, Bristol.

JOHNES, P. J. and O'SULLIVAN, P. E., (1989). The Natural History of Slapton Ley Nature Reserve XVIII: nitrogen and phosphorus losses from the catchment—an export coefficient approach. *Field Studies,* 7, 285–309.

JUPP, B. P. and SPENCE, D. H. N., (1977a). Limitations on macrophytes in a eutrophic lake, Loch Leven I: Effects of phytoplankton. *Journal of Ecology,* **65**, 175–186.

JUPP, B. P. and SPENCE, D. H. N., (1977b). Limitations on macrophytes in a eutrophic lake, Loch Leven II: Wave action, sediments and waterfowl grazing. *Journal of Ecology,* **65**, 431–446.

KENNEDY, C. R., (1975). The Natural History of Slapton Ley Nature Reserve VIII: the parasites of the fish, with special reference to their use as a source of information about the aquatic community. *Field Studies,* **4**, 177–189.

KENNEDY, C. R., (1996). The fish of Slapton Ley. *Field Studies,* **8**, 685–697.

LIJKLEMA, L., (1994). Nutrient dynamics in shallow lakes: effects of changes in loading and role of sediment-water interactions. *Hydrobiologia,* **275/276**, 355–348.

MERCER, I. D., (1966). The Natural History of Slapton Ley Nature Reserve I: introduction and morphological description. *Field Studies,* **2**, 385–404.

METEOROLOGICAL OFFICE, (1989). *Climatological Data for Agricultural Land Classification.* The Meteorological Office, Bracknell.

METEOROLOGICAL OFFICE, (1992). *MORECS—the Meteorological Office Rainfall and Evaporation Calculation System database.* The Meteorological Office, Bracknell.

MOREY, C. R. (1976) The Natural History of Slapton Ley Nature Reserve IX: the morphology and history of the lake basins. *Field Studies,* **4**, 353–368.

MOSCROP, C. J., (1987). *A diatom profile of recent sediments in Slapton Ley, south Devon.* Unpublished BSc Dissertation, University of Plymouth.

MOSS, B., STANSFIELD, J. and IRVINE, K. (1991) Development of daphnid communities in diatom- and cyanophyte-dominated lakes and their relevance to lake restoration by biomanipulation. *Journal of Applied Ecology,* **28**, 586–602.

MOSS, B., JOHNES, P. J. and PHILLIPS, G. L., (1996). The monitoring of ecological quality and the classification of standing waters in temperate regions—a review and proposal based on a worked scheme for British waters. *Biological Reviews,* **71**, 301–339.

NICHOLS, S. A. and SHAW, B. H., (1986). Ecological life histories of three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodea canadensis. Hydrobiologia,* **131**, 3–21.

O'SULLIVAN, P. E. (1994) The Natural History of Slapton Ley National Nature Reserve XXI: the palaeolimnology of the uppermost sediments of the Lower Ley, with interpretations based on ^{210}Pb dating and the historical record. *Field Studies,* **8**, 403–449.

O'SULLIVAN, P. E., HEATHWAITE, A. L., APPLEBY, P. G., BROOKFIELD, D., CRICK, M. W., MOSCROP, C., MULDER, T. B., VERNON, N. J. and WILMHURST, J. M., (1991). Palaeolimnology of Slapton Ley. *Hydrobiologia,* **214**, 115–124.

PALMER, M. A., (1989). *A botanical classification of standing waters in Great Britain and a method for the use of macrophyte flora in assessing changes in water quality.* Nature Conservancy Council, Peterborough.

PALMER, M. A., BELL, S. L. and BUTTERFIELD, I., (1992). A botanical classification of standing waters in Britain: applications for conservation and monitoring. *Aquatic Conservation,* **2**, 125–144.

PHILLIPS, G. L., EMINSON, D. and MOSS, B., (1978). A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquatic Botany,* **4**, 103–126.

PHILLIPS, G. L., JACKSON, R., BENNETT, C. and CHILVERS, A., (1994). The importance of sediment phosphorus release in the restoration of very shallow lakes (The Norfolk Broads, England) and implications for biomanipulation. *Hydrobiologia,* **275/276**, 445–456.

RATSEY, S., (1975). The climate at Slapton Ley. *Field Studies,* **4**, 191–206.

SCHEFFER, M., (1989). Alternative stable states in eutrophic shallow freshwater systems: a minimal model. *Hydrobiol. Bull.,* **23**, 73–85.

SCHEFFER, M., HOSPER, S. H., MEIJER, M. L., MOSS, B. and JEPPESEN, E., (1993). Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution,* **8**, 275–279.

SPENCE, D. H. N., (1975). Light and plant response in fresh water. In: Evans, G. C., Bainbridge, R. and Rackham, O. (Eds) *Light as an Ecological Factor.* Blackwell Scientific, Oxford.

STANES, R. (1983) *A Fortunate Place: the history of Slapton in south Devon.* Occasional Publication of the Field Studies Council.

TROAKE, R. P. and WALLING, D. E., (1973). The Natural History of Slapton Ley Nature Reserve VII: the hydrology of the Slapton Wood stream. *Field Studies,* **3**, 719–740.

TROAKE, R. P., TROAKE, L. and WALLING, D. E., (1976). Nitrate loads of south Devon streams. *MAFF Tech. Bull.,* **32**, 340–351.

TRUDGILL, S. T., (1983). The Natural History of Slapton Ley Nature Reserve XV: the soils of Slapton Wood. *Field Studies,* **5**, 835–840.

VAN VLYMEN, C. D., (1979) The Natural History of Slapton Ley Nature Reserve XIII: the water balance of Slapton Ley. *Field Studies,* **5**, 59–84.

VAN VLYMEN, C. D., (1980). *The Water Balance, Physico-Chemical Environment, and Phytoplankton Studies of Slapton Ley, Devon.* Unpublished PhD thesis, University of Exeter.

WETZEL, R. G., (1983). *Limnology.* Second Edition. Saunders College Press.

WILSON, H. M., (1991). *The effects of eutrophication on the submerged macrophyte community of Slapton Ley, Devon.* Unpublished BSc dissertation, University of Plymouth.