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River fish habitat inventory phase III: multi-species models

Science Report: SC040028/SR

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Steve Killeen

Head of Science

Executive Summary

It has been recognised for many years that the physical habitat of rivers has a strong influence on the spatial occurrence of fish communities and upon the abundance and age-structure of species populations, notwithstanding the influences of water chemistry and climatic variation.

Scientists' understanding of these relationships has advanced considerably in recent years for some salmonid species, and a number of tools now exist for assessing and quantifying the quality of juvenile salmonid habitat.

In contrast, scientists' understanding of the relationships between coarse fish and habitat remains poor. Even the basic biology of common coarse fish species is not well understood compared with that of species such as the brown trout. Understanding these relationships is essential for the Environment Agency to carry out its duties and to help deliver the aspirations of the Fisheries Strategy.

The overall objective of this project was, therefore, to model the relationship between coarse fish populations and broad habitat features, in order to develop a River Fish Habitat Inventory (RFHI) that will allow habitat quality to be classified in terms of map-based and field-based features.

The project's specific objectives were as follows.

1. To develop fish abundance models to establish habitat-species, species-species and geographic relationships for coarse fish, using the framework developed in RFHI Phase 2 and appropriate datasets on coarse fish species.
2. To apply the model for coarse fish species abundance to national data sets in order to produce maps of habitat quality (predicted abundance) for each species, maps of observed values, and maps of the difference between observed and predicted values.
3. To develop models for the spatial patterns of coarse fish population parameters (recruitment, growth and survival), using the framework developed during Phase 3 of the R&D project 'Factors Affecting Recruitment of Riverine Coarse Fish', and apply these models to selected case-study catchments.

Using data from fisheries surveys undertaken during 2004, combined with map-based environmental variables, the models were able to generate maps of abundance and prevalence for several fish species, according to site width, gradient and geographical location. The following trends were observed.

Brown Trout – Prevalence and abundance decrease with increasing width, but increase with increasing altitude. Even after having allowed for altitude and width, prevalence and abundance are highest in the north, west and south-west of England and in Wales.

Barbel – Prevalence increases with increasing width, but abundance is highest at medium width. Prevalence is highest at medium altitudes, but abundance does not vary with altitude. Barbel are most prevalent and abundant in central and southern England.

Pike – Prevalence increases with increasing width, but abundance is highest at medium width. Prevalence and abundance decrease with increasing altitude. Pike are most prevalent and abundant in central and south-east England.

Chub – Prevalence increases and abundance decreases with increasing width. Prevalence and abundance are both highest at medium altitudes. Prevalence and abundance are highest in central and south-east England.

Grayling – Prevalence increases and abundance decreases with increasing width. Prevalence and abundance increase with increasing altitude. Prevalence and abundance are highest in central and south-west England.

Roach – Prevalence increases with increasing width, but abundance shows a less clear-cut relationship. Prevalence and abundance decrease with increasing altitude. Prevalence and abundance are highest in central and south-east England.

These models will be used as the basis of an approach for assessing the fish elements of ecological status, as required under the EU Water Framework Directive (WFD).

To test the models, spatial patterns in population parameters for roach, chub and dace were investigated using the Suffolk Stour fisheries survey dataset. The models were able to elicit marked differences in the parameters between different sub-catchments in the Stour, providing an indication of varying impacts on the fish populations arising from water quality and flow, and habitat modification. This modelling approach can be used to describe the age-structure of fish populations, which will be required under the WFD as part of the assessment of the ecological status for fish. The approach could also be used to assist in the diagnosis and remediation of pressures on the fish community, which will be required as part of the WFD's programmes of measures and as part of the Environment Agency's statutory duties to maintain, improve and develop fisheries.

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1. Introduction

1.1 Background

It has been recognised for many years that the physical habitat of rivers has a strong influence on the spatial occurrence of fish communities and upon the abundance and age-structure of species populations, notwithstanding the influence of water chemistry and climatic variation.

Scientists' understanding of these relationships has advanced considerably for some salmonid species in recent years, and a number of tools now exist for assessing and quantifying the quality of juvenile salmonid habitat. They include: Phase II of this project (River Fish Habitat Inventory); the Fisheries Classification Scheme (FCS) (Mainstone *et al.* 1994); HabScore (Wyatt *et al.* 1995); salmon conservation limit procedures (Wyatt and Barnard 1997); and methods for interpreting semi-quantitative electrofishing data (Wyatt and Lacey 1998). These tools are proving essential in formulating and implementing Salmon Action Plans and other measures aimed at protecting and restoring stocks of salmonid fishes.

In contrast, scientists' understanding of the relationships between coarse fish and habitat remains poor, although FCS does address coarse fish communities. This lack of understanding is partly due to the fact that coarse fish generally live in multi-species communities, are sometimes longer-lived than salmonid species, exhibit a variety of life-history strategies and show fewer ties to particular physical habitats, often having specific life-stage and seasonal habitat requirements and movements. Even the basic biology of common coarse fish species is poorly understood compared to that of the brown trout. However, both the ecological and socio-economic value of coarse fish species is now widely acknowledged. The Environment Agency has a duty to maintain, improve and develop sustainable coarse fisheries and to increase fishing opportunities and optimise the socio-economic benefits that these fisheries can bring. It is obliged under the EU Water Framework Directive (WFD) to assess, monitor and report on the condition of fisheries and to take measures to bring them up to good ecological status where they have been degraded. Understanding the relationships between coarse fish and their habitats is essential for the Environment Agency to carry out these duties and to help deliver the aspirations of the fisheries strategy.

1.2 Project history

The proposal for a coarse fish 'habitat inventory' was first put forward in the River Fish Habitat Inventory (RFHI) scoping study (Phase 1) in 1997 (R&D Technical Report W95). The basic idea was that the RFHI should be closely linked to the FCS, which produces two classifications – the 'absolute classification' (A, B, C,...) and the 'relative classification' (a, b, c, ...). The absolute classification is based on observed fish abundances, while the relative classification is based on the observed abundance relative to the expected abundance for a given river type (defined by width and gradient). However, the FCS does not provide a definition of this expected abundance (which can act as a measure of habitat quality). The RFHI was intended to fill this gap.

Phase 2 of the RFHI project concentrated exclusively on salmonids, which require a habitat inventory so that conservation limits can be set and management options assessed. Phase 3

of the RFHI project began in 2005 and included both coarse fish and salmonids in order to assess habitat quality for all river fish species. The primary objective of the Phase 3 project was to apply the salmonid RFHI methodologies to the monitoring data held on the National Fish Population Database (NFPD) for a range of species.

Modelling techniques developed within Phase 3 of the project, which was entitled 'Factors Affecting Recruitment of Riverine Coarse Fish' (FARRCoF) (Wyatt, Sedgwick & Burrough 2007), provided estimates for a range of coarse fish population metrics. These were derived from basic fisheries monitoring data covering parameters such as recruitment (in this context defined as the number of fish surviving to the end of their first summer), survival and growth. Combining these metrics with the GIS (Geographical Information Systems) approach from Phase 2 of the RFHI offers the possibility of developing a much better understanding of the relationship between coarse fish and catchment and habitat features.

1.3 Objectives

Overall objective

- To model the relationship between coarse fish populations and broad habitat features, in order to develop a RFHI that will allow habitat quality to be classified in terms of map-based and field-based features.

Specific objectives

1. To develop fish abundance models for establishing habitat-species, species-species and geographic relationships for coarse fish, using the framework developed in RFHI Phase 2 and appropriate datasets on coarse fish species.
2. To apply the model for coarse fish species abundance to national data sets, in order to produce maps of habitat quality for each species (predicted abundance), maps of observed values and maps of the difference between observed and predicted values.
3. To develop models for the spatial patterns of coarse fish population parameters (recruitment, growth and survival) using the framework developed in Phase 3 of FARRCoF and apply these models to selected case-study catchments.
4. To produce a peer-reviewed paper.

2 Abundance models (objectives 1 and 2)

2.1 Introduction

The original FCS classified salmon and trout, as well as a number of coarse fish species groups (such as rheophiles and limnophiles). The FCS employed two classifications: a classification of observed abundance ('absolute FCS'); and a classification of the observed abundance relative to that expected for the river type ('relative FCS'), based on the river gradient and wetted width. RFHI is designed to provide a third classification – expected abundance – whilst also updating the underlying models that relate fish abundance to environmental variables.

2.2 Methods

2.2.1 Overview

The design criteria for the multi-species RFHI models were set out in the Phase 1 report and are summarised in Table 2.1. Defining habitat quality as expected fish abundance and regarding environmental gradients as continuous are both features of the original FCS. However, the RFHI differs from the FCS in that it quantifies habitat requirements at a species level, whereas the FCS combined coarse fish species into groups. Nevertheless, the classification of observed abundance, expected abundance or the observed:expected ratio can be reported for any species group, including all species.

The original FCS was designed to be utilised without the need for a computer and was based on look-up charts. One of the major differences between the original FCS and the RFHI is that the RFHI replaces the look-up charts with statistical models, which require computer software.

Table 2.1 Requirements for the RFHI reported in the Phase 1 scoping study

Design criteria (RFHI Phase 1 report)	RFHI solution
1 'Habitat quality' should be defined as the expected fish abundance at a survey site (not just presence/absence) (p46).	The RFHI model uses three parameters to describe the frequency distribution of fish abundance (see below).
2 Ecological responses to environmental gradients are treated as continuous (no concept of discrete fish communities or river types) (p47).	Smooth curves are used to describe the relationship between fish abundance and environmental variables.
3 Habitat requirements should be quantified at a species level (p49).	Habitat models are developed for individual species, but species interactions can also be quantified.
4 Reporting should be possible for any species group (p49).	Model outputs can be combined to give the expected abundance (or species richness) of any species group (such as the original FCS groups).
5 To avoid the proliferation of habitat assessment methods, the FCS and RFHI should be based on the same underlying models (p54).	The RFHI model can be used to classify 'habitat quality' (expected fish abundance) as well as observed fish abundance (replacing FCS).

The development of the salmonid RFHI raised some additional issues. This resulted in additional modifications being made to the salmonid models and these modifications have also been applied to this project for coarse fish. First, not all **geographic patterns** of fish abundance can be explained by physical habitat measurements and so the RFHI model includes both geographic patterns of abundance and the habitat relationships. Second, estimating the **uncertainty** associated with model outputs is fundamental for fishery management decision-making. The RFHI uses Bayesian statistics to describe this uncertainty in terms of probabilities.

2.2.2 Parameters describing fish abundance.

A key feature of the RFHI models is that they describe the expected abundance of fish in a water body by means of a frequency distribution characterised by three distinct parameters:

- the 'prevalence' – the probability that the species is present;
- the 'average abundance' at sites where the species is present;
- the 'variability in abundance' at sites where the species is present.

These parameters are illustrated in Figure 2.1. Because the average abundance is defined only at sites where the species is present, this parameter is not the same as the overall average abundance, which is termed the 'expected abundance'. The expected abundance is defined as the product of the abundance and the prevalence. Thus, if a species is present at 50 per cent of sites and at those sites has an average abundance of 20 fish per unit area, then over all sites the expected abundance is 10 fish per unit area.

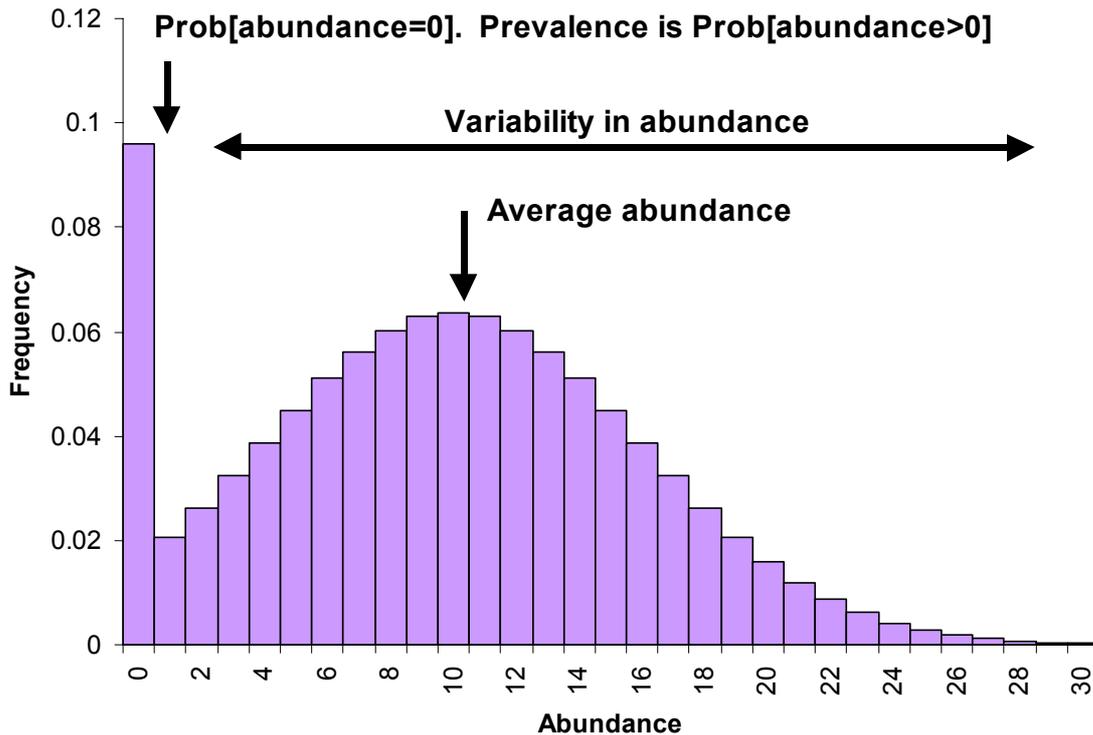


Figure 2.1 Illustration of average abundance, variability in abundance and prevalence

2.2.3 Model relating environmental variables to fish abundance

For each fish species, the RFHI models track the changes in prevalence and average abundance in response to environmental gradients and geographic location. Environmental gradients can be described in terms of map-based variables (such as altitude, gradient, distance to source) and field-based variables (such as wetted width, substrate type, depth). Linear models, such as straight lines or quadratic curves, are rarely adequate descriptors of the relationship between fish populations and environmental variables, and so the RFHI models use smooth non-linear curves to describe these relationships. The effect of geographic location is modelled by assuming that survey sites are not independent, with sites that are geographically close to each other more likely to be similar in terms of their fish populations than sites that are further apart. The existence of geographic patterns in fish abundance in England and Wales will in part reflect environmental variables that have not been included in the models.

Initial development of the multi-species RFHI has been undertaken for the 23 most prevalent species in the NFPD for 2004. The original FCS used environmental variables to describe the size and nature of the river (wetted width and gradient), and this report outlines an equivalent model that uses width and altitude as illustrative environmental variables.

2.2.4 Classification method

Classification of observed abundance ('absolute' FCS)

The FCS classification of observed abundance ('absolute' FCS) is based on a quintile classification (A–E) of abundance, with F denoting zero fish. This classification does not utilise a habitat model and will not be discussed further.

Classification of expected abundance (RFHI classification)

The RFHI models will predict the prevalence and average abundance of fish species for a river of a given width, altitude and location. These predictions provide two potential measures of habitat quality. For example, one habitat type may be predicted to support a particular species at 50 per cent of locations (prevalence = 0.5), with an average density at those locations of 20 fish per unit area. Another habitat type may be predicted to support the same species at 100 per cent of locations (prevalence = 1.0), but with an average density at those locations of only 10 fish per unit area. The quality of these two habitats for this species is clearly different, and it would be possible to describe and map habitat quality in terms of these two parameters. However, for simplicity, the RFHI measures habitat quality in terms of the expected abundance. This means that the two different habitats described above would be classified as having the same level of quality, with an expected abundance of 10 fish per unit area.

Classification of observed relative to expected abundance ('relative' FCS)

One of the primary objectives for quantifying habitat quality is to be able to assess the observed abundance of fish relative to what would be expected for a given habitat. This is achieved with the relative FCS, which is measured for a single species in terms of the probability of observing an equal or lower number of fish at another site of similar altitude, width and location. This probability is classified on a five-point scale, with probabilities over 0.8 classified as 'a', probabilities between 0.6 and 0.8 classified as 'b', and so on.

For a species with a low prevalence in a particular river type, a large proportion of sites will have zero fish (

Figure 2.2a). If this proportion is 0.8 or more, then even a site with zero fish will be classified as 'a', since the probability of observing this many fish or less at other sites will be greater than 0.8. Even for a species that is locally abundant (

Figure 2.2b), sites with zero fish can still be classified relatively highly, since zero fish may not be unusual. As prevalence increases (

Figure 2.2c&d), however, zero fish is increasingly likely to be classified as 'e'. For a site where the species is abundant and prevalent (Figure 2.2d), the number of sites in each of the five classes will be approximately equal.

For two species, the FCS for a particular site is based on the probability of observing an equal or lower number of species A and an equal or lower number of species B at another similar site. The abundance and classification can no longer be represented by a histogram (Figure 2.2), but can be represented by a pair of contour plots showing the fish abundance and FCS class (Figure 2.3).

For two independent but equally abundant species, the classification boundaries will be as shown in

Figure 2.3a. Consider a site that has eight individuals of both species present. This corresponds to a median ($p=0.5$) abundance for both species, and so around 25 per cent ($0.25 = 0.5 \times 0.5$) of sites will have less than or equal to eight of both species. If this percentage is calculated for all sites, around 59 per cent of sites would be found to have this value of 25 per cent or less. This site would therefore be given a value of 0.59 and be classified as 'c' (nearly 'b').

Sites with both species present will tend to be classified higher than sites with just one of the species present. For example, in

Figure 2.3a, 10 of the sites containing both species will be classified as a high 'b', whereas 20 of those containing one species and zero of those containing the other species will be classified as 'e'. Thus, this classification system will tend to favour sites where both abundance and species richness are high. For two independent species, where one is usually more abundant than the other (

Figure 2.3b), the class boundaries will automatically be weighted to reflect the difference between the two species.

The abundances of different species are unlikely to be independent, either due to direct interactions, such as competition or predation, or due to habitat preferences not explicitly included in the model. This is allowed for in the model by a spatial variance-covariance matrix (Table 2.2). The numbers on the diagonal represent the spatial variability of the species, while the off-diagonal numbers give the covariance for the species pair. Thus on the River Stour, for example (Table 2.2), the abundance of bream is more variable between survey sites (10.51) than the abundance of pike (0.80). This would be expected from knowledge of their respective behaviours, as bream are a shoaling species while pike are usually solitary and so spread more evenly. But the findings may also be affected by the efficiency of the fishing techniques employed in the surveys.

The correlations between species on the Stour can quantify what is already known about their habitat preferences. For example, bream are negatively correlated with trout (-4.12), but positively correlated with roach (3.77). The matrix could therefore be used as the basis for a multivariate analysis to define a number of species guilds, in which roach and bream may occur in the same guild but bream and trout would occur in different guilds. However, one of the objectives of the RFHI project is that the models are species-specific and that artificial clustering of either species or river types should be avoided. The species interactions are therefore simply used to adjust the calculation of probabilities and class boundaries

(
Figure 2.4).

The principles illustrated here for two species can be generalised to any number of species in order to provide an overall classification for any species group.

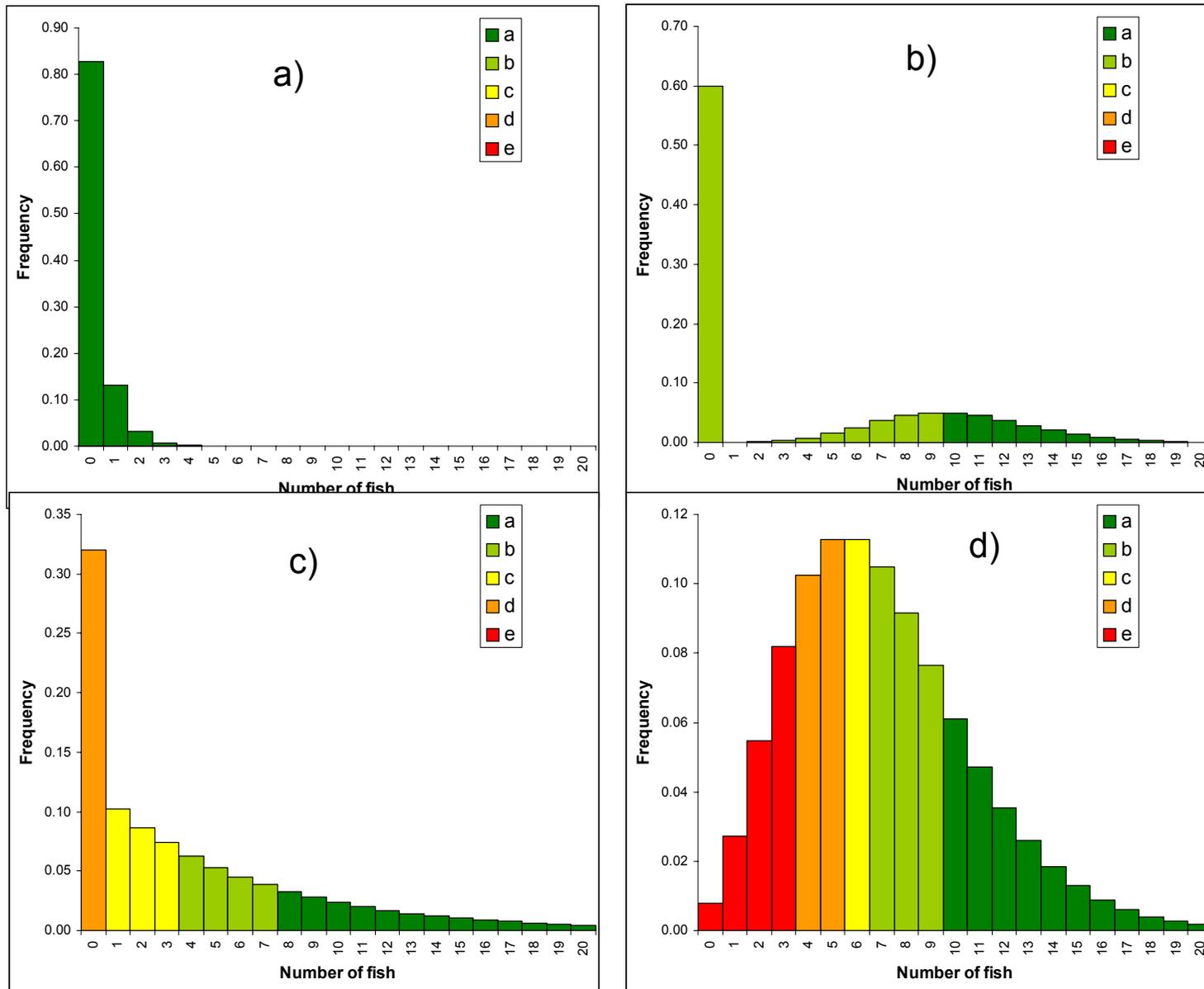


Figure 2.2 Classification of four species: a) rare; b) locally abundant; c) variable abundance; and d) prevalent and abundant

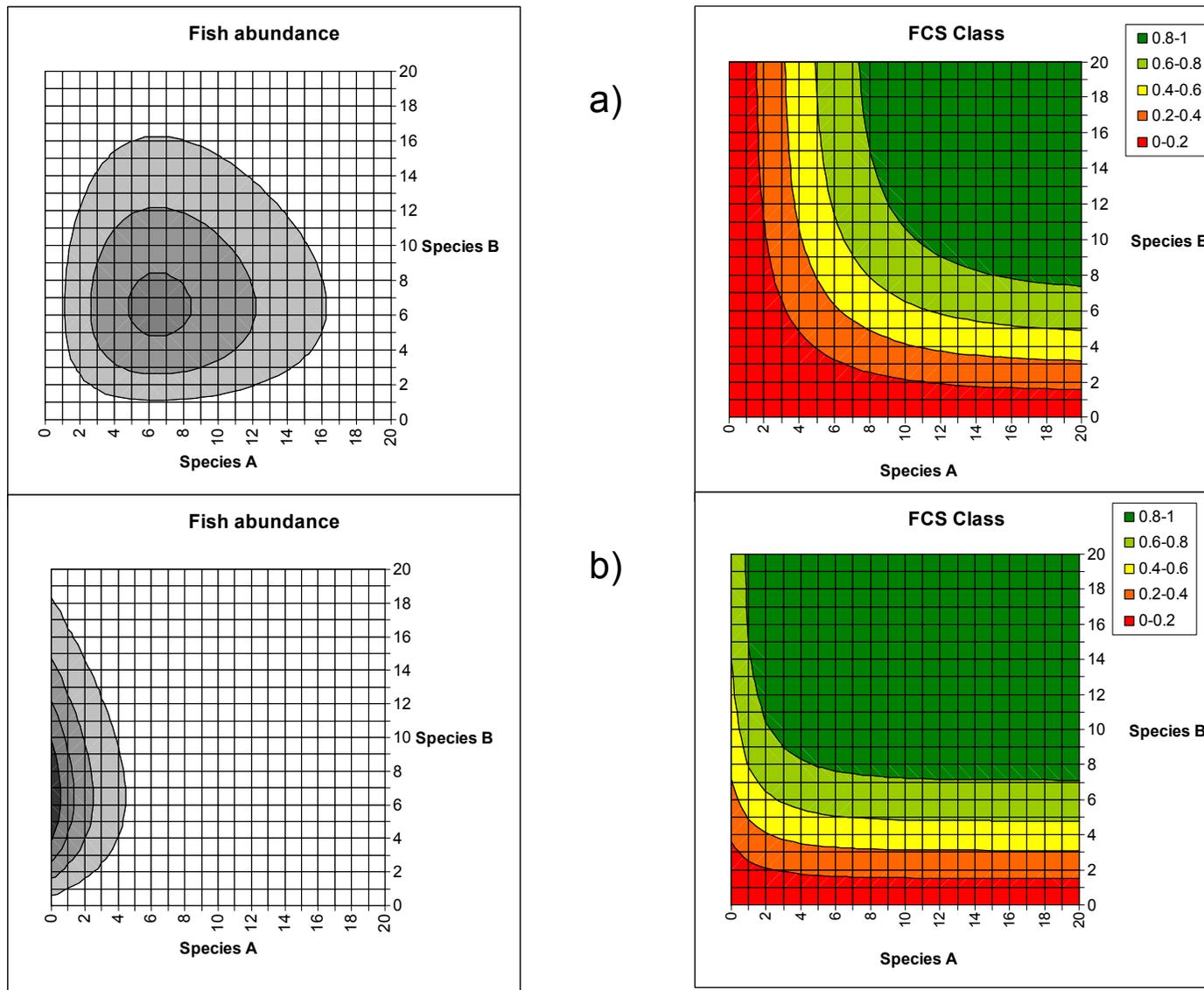


Figure 2.3 Joint classification of two independent species: a) both abundant; b) one abundant, one rare

Note: The left hand graph is a contour plot showing the frequency (dark grey = high, white = low) of sites with different numbers of the two species; the right hand plot shows the corresponding classification of abundance.

Table 2.2 Variance-covariance matrix for fish species in the River Stour

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Common bream	10.51																									
2 Eel	-0.78	3.24																								
3 Stone loach	-4.40	1.48	4.22																							
4 Barbel	2.83	0.87	0.54	7.62																						
5 Silver bream	-0.44	-0.11	0.16	0.06	2.10																					
6 Feral goldfish	1.93	-0.60	-1.68	-1.32	-0.30	4.22																				
7 Crucian carp	2.57	-0.62	-2.53	-2.84	-0.04	1.86	5.73																			
8 Spined loach	-0.13	0.53	-0.43	-0.71	0.10	0.35	0.77	2.00																		
9 Bullhead	-4.43	0.52	2.62	0.53	0.64	-2.30	-2.54	-0.47	4.77																	
10 Mirror carp	1.94	-0.97	-1.97	-1.95	-0.79	2.55	2.46	0.33	-3.24	4.58																
11 Pike	0.84	-0.40	-0.68	-0.35	0.03	0.21	0.54	-0.09	-0.20	0.04	0.80															
12 3sp stickleback	-5.69	0.71	3.52	-0.12	0.42	-1.98	-2.92	-0.64	3.96	-2.71	-0.56	5.03														
13 Gudgeon	1.09	-0.59	1.63	3.15	-0.36	-0.80	-2.51	-1.32	0.36	-1.05	-0.26	0.81	5.38													
14 Ruffe	7.11	0.16	-3.10	1.46	-0.55	1.74	2.08	0.22	-4.04	2.17	0.47	-4.45	0.03	6.83												
15 Brook lamprey	-3.20	0.72	2.30	1.15	0.45	-2.11	-2.07	-0.47	2.88	-2.48	-0.32	2.82	1.45	-2.63	4.08											
16 Chub	-0.06	0.54	1.72	2.69	-0.15	-0.91	-2.37	-0.81	1.62	-1.58	-0.32	1.59	2.48	-0.59	1.71	3.27										
17 Dace	-0.39	0.06	1.64	3.17	0.06	-1.38	-3.09	-1.13	2.47	-2.03	-0.43	2.10	3.05	-1.68	2.32	3.30	4.96									
18 Perch	2.14	-0.91	-1.35	-0.10	0.01	0.24	0.80	-0.26	-0.62	-0.21	0.89	-1.10	0.17	1.30	-0.54	-0.30	-0.50	2.09								
19 Minnow	-4.67	-1.06	3.32	-0.08	0.12	-1.69	-3.24	-1.29	2.85	-1.46	-0.51	3.92	3.04	-4.42	2.56	1.67	2.85	-0.76	6.43							
20 Flounder	-0.32	1.02	-0.11	0.16	-0.19	0.12	0.78	0.74	-1.06	0.81	-0.35	-0.70	-0.81	0.70	-0.38	-0.49	-1.17	-0.67	-1.44	3.46						
21 10sp stickleback	-1.51	0.52	0.96	-0.20	-0.11	-0.25	-0.92	0.18	0.67	-0.17	-0.31	0.95	0.22	-1.00	0.43	0.35	0.37	-0.54	0.81	0.15	2.24					
22 Roach	3.77	-0.38	-0.94	1.34	-0.30	0.50	0.37	-0.53	-1.39	0.32	0.57	-1.55	1.45	2.33	-0.69	0.49	0.55	1.20	-0.48	-0.52	-0.51	2.69				
23 Trout	-4.12	0.95	3.84	0.10	-0.85	-0.06	-2.72	-0.72	0.82	1.19	-1.38	3.02	2.56	-2.77	1.73	2.53	2.67	-2.61	4.66	0.47	1.84	-0.92	10.02			
24 Zander	3.85	0.86	-1.52	1.35	-0.40	0.82	1.14	0.27	-1.73	0.34	0.21	-2.12	-0.57	3.51	-1.13	0.51	-0.45	0.60	-3.44	0.83	-0.27	0.97	-1.48	4.75		
25 Rudd	-0.96	0.54	1.72	0.15	-0.53	0.20	-1.08	-0.62	-0.28	0.80	-0.49	1.06	2.11	-0.62	0.68	1.16	1.44	-0.69	2.52	-0.01	0.68	0.51	4.62	-0.84	3.51	
26 Tench	3.46	-0.42	-2.53	0.78	0.16	0.66	1.50	0.35	-1.13	0.18	0.42	-2.25	-1.46	2.23	-1.53	-0.87	-0.91	0.89	-2.97	0.12	-0.68	0.74	-3.98	1.74	-2.20	3.28

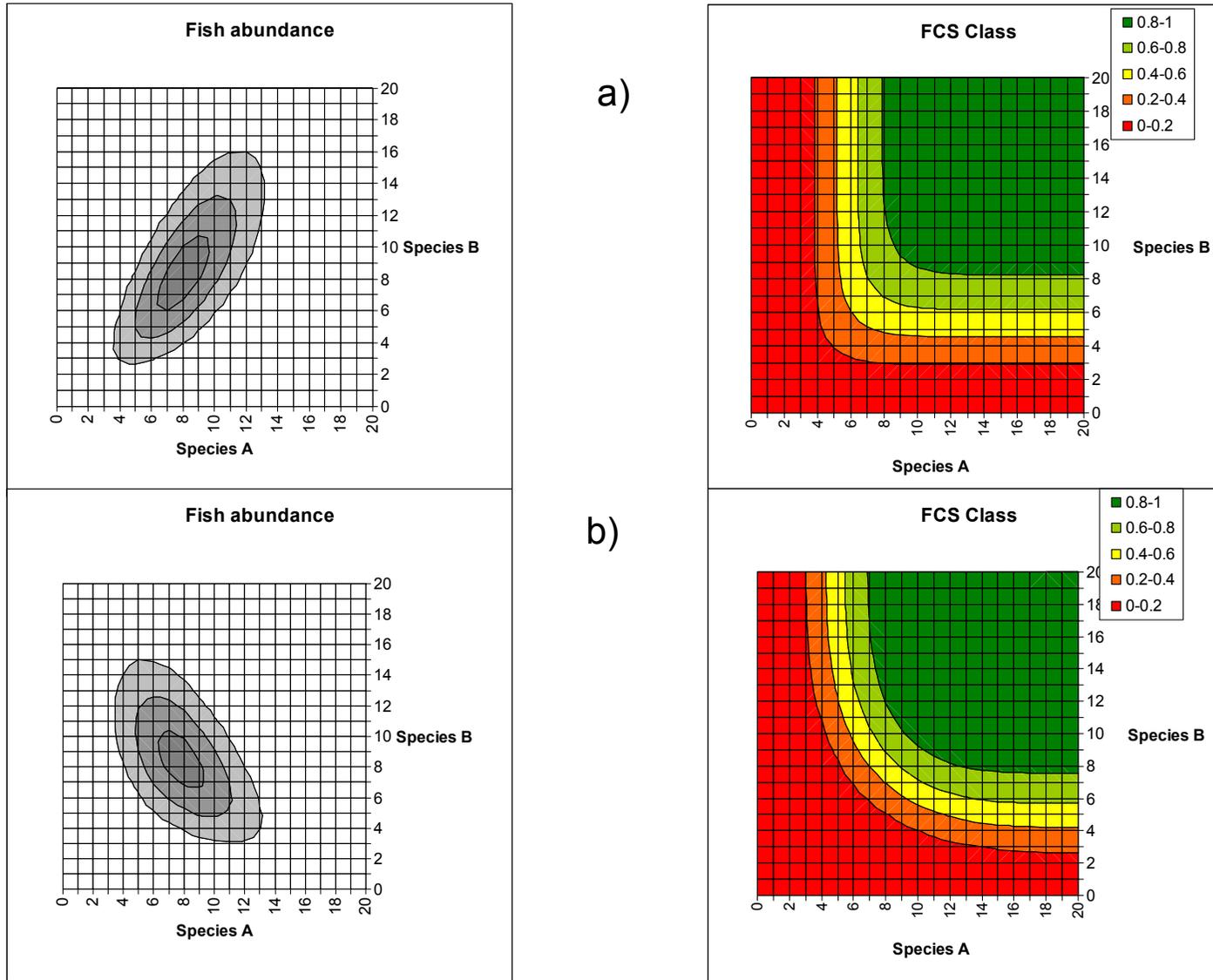


Figure 2.4 Joint classification of two correlated species: a) positive correlation; b) negative correlation

Note: The left hand graph is a contour plot showing the frequency (dark grey = high, white = low) of sites with different numbers of the two species; the right hand plot shows the corresponding classification of abundance.

2.3 Results

2.3.1 Model development

The RFHI models relate the prevalence and average abundance of 23 fish species to environmental variables (illustrated by width and altitude) and geographic location. Results for trout are shown in

Figure 2.5. On the maps, green denotes high values and orange denotes low values. On the graphs, the lines show contours (confidence intervals) of diminishing probability (25 per cent, 10 per cent, 5 per cent, 2.5 per cent) away from the central (most likely) relationship. The prevalence and abundance of trout decrease with increasing width, but increase with increasing altitude. Even after having allowed for altitude and width, prevalence and abundance are highest in the north, west and south-west of England.

Results for a further five species are given in Appendix A. The following highlight some of the main features for each species.

Barbel – Prevalence increases with increasing width, but abundance is highest at medium width. Prevalence is highest at medium altitudes, but abundance does not vary with altitude. Barbel are most prevalent and abundant in central and southern England.

Pike – Prevalence increases with increasing width, but abundance is highest at medium width. Prevalence and abundance decrease with increasing altitude. Pike are most prevalent and abundant in central and south-east England.

Chub – Prevalence increases and abundance decreases with increasing width. Prevalence and abundance are both highest at medium altitudes. Prevalence and abundance are highest in central and south-east England.

Grayling – Prevalence increases and abundance decreases with increasing width. Prevalence and abundance increase with increasing altitude. Prevalence and abundance are highest in central and south-west England.

Roach – Prevalence increases with increasing width, but abundance shows a less clear-cut relationship. Prevalence and abundance decrease with increasing altitude. Prevalence and abundance are highest in central and south-east England.

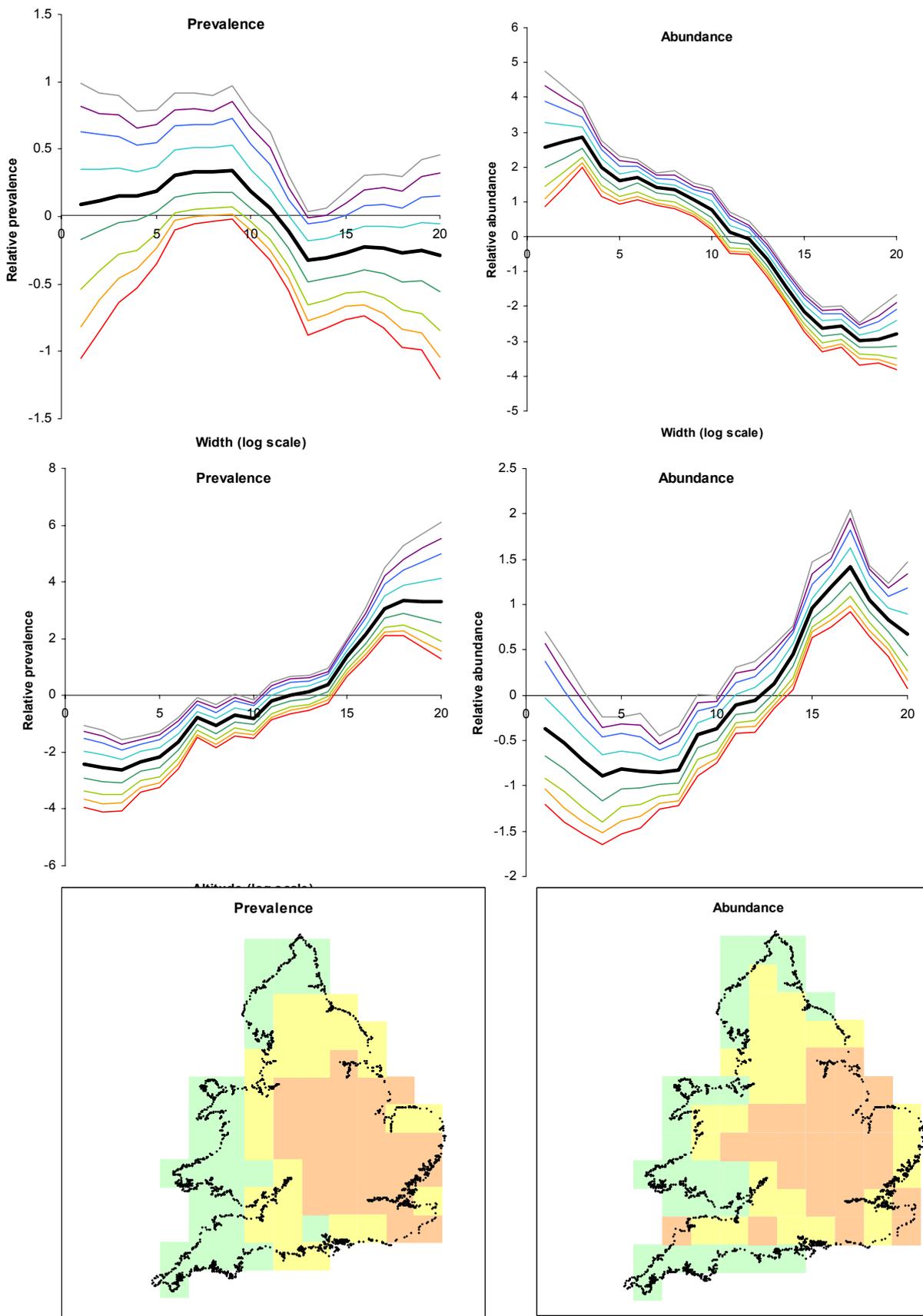


Figure 2.5 Variation in abundance and prevalence of trout with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

2.3.2 Production of national maps.

A national map of observed trout abundance in 2004 (absolute FCS) is shown in Figure 2.6 and a map of expected abundance is shown in Figure 2.7. The expected abundance of trout is highest in the south-west and north of England, and south-west Wales.

The FCS 'relative classification' (observed:expected ratio) for trout is shown in Figure 2.8. Sites with a low relative FCS class (red/black) show where the observed abundance is lower than expected and where management intervention may be required. Examples include the upper (northern) Tamar on the Devon-Cornwall border, where trout densities are lower than other comparable rivers in south-west England.

At many sites, such as those in the east of England, the expected trout abundance will be very low and species-specific impacts are impossible to detect. Even if trout are absent, the 'relative' FCS class may be 'a', reflecting the low expected abundance rather than a high observed abundance (see also Figure 2.2a). Figure 2.8 can therefore be re-drawn, omitting sites that have a high relative FCS class due to a low expected abundance and retaining sites that have a high class due to a high observed abundance (Figure 2.9). Maps for additional species are given in Appendix A.

The overall relative FCS for the 23 most prevalent species in England and Wales is shown in Figure 2.10.

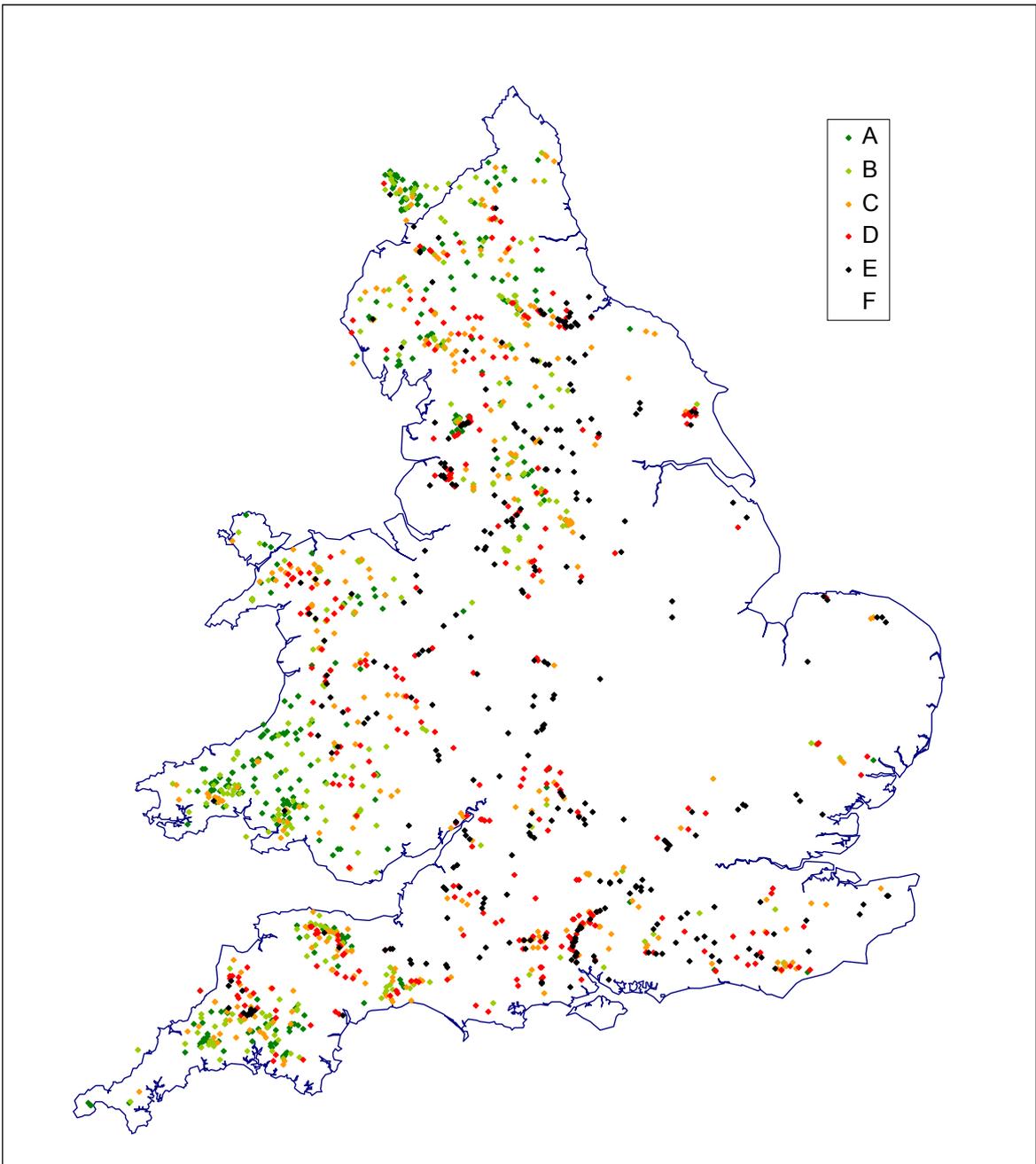


Figure 2.6 Classification of trout abundance (absolute FCS) in 2004
Note: Class F (no symbol) represents absence of the species in question.

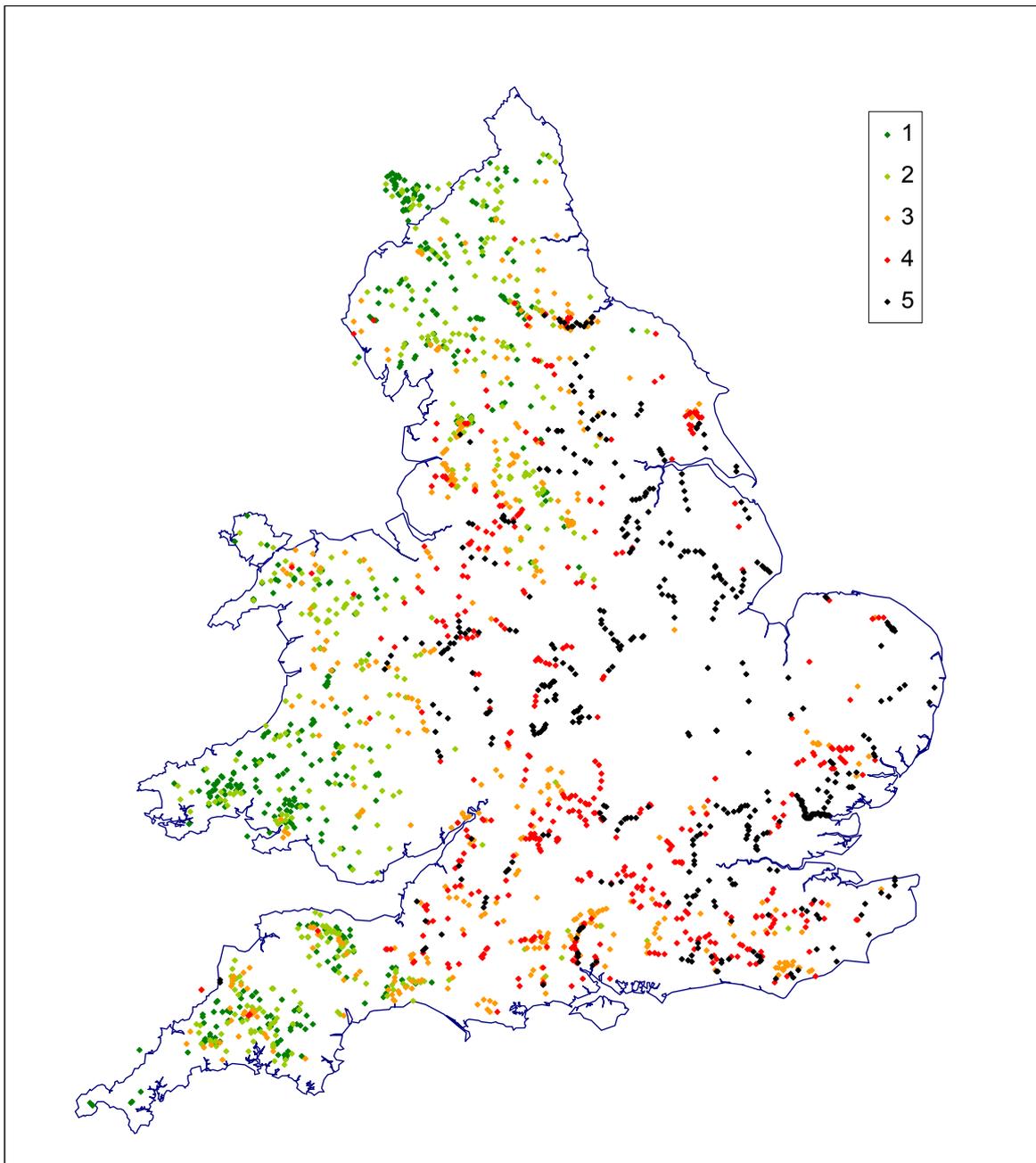


Figure 2.7 Expected abundance (=habitat quality) for trout
Note: 1 (green) is high, 5 (black) is poor.

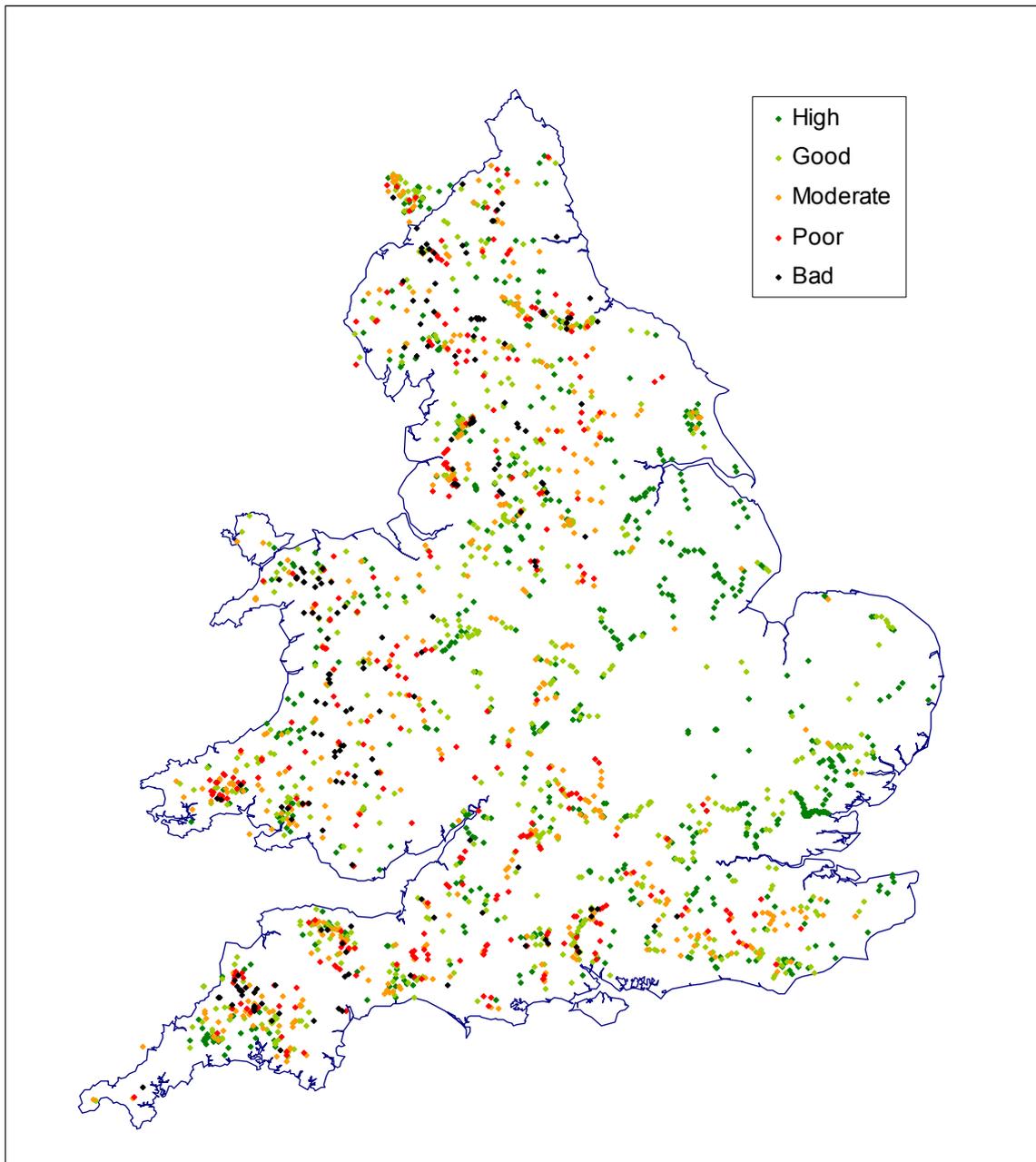


Figure 2.8 Observed:expected ratio for trout abundance (relative FCS) in 2004 (all sites are shown)

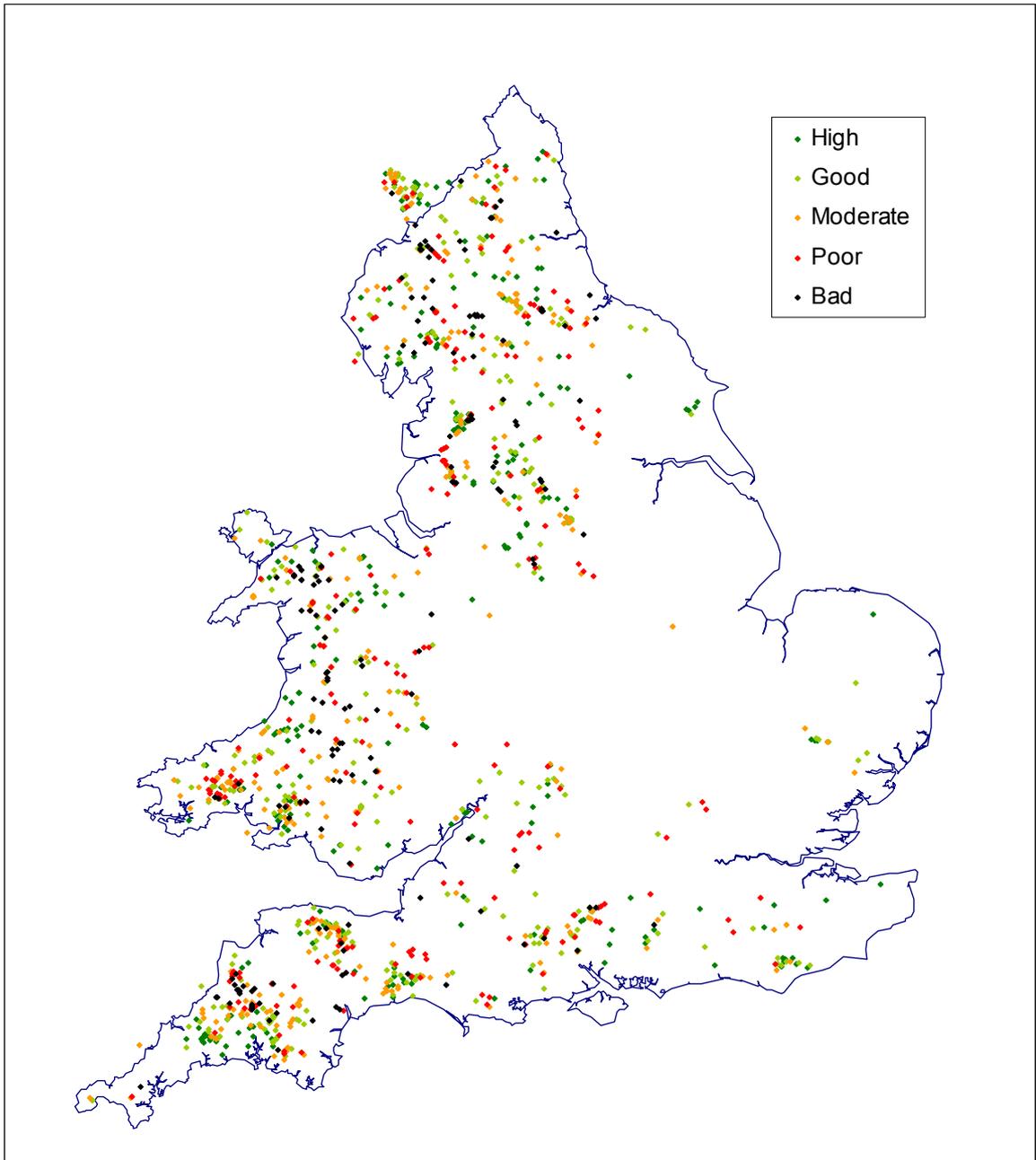


Figure 2.9 Observed:expected ratio for trout abundance (relative FCS) (sites with low habitat quality excluded)

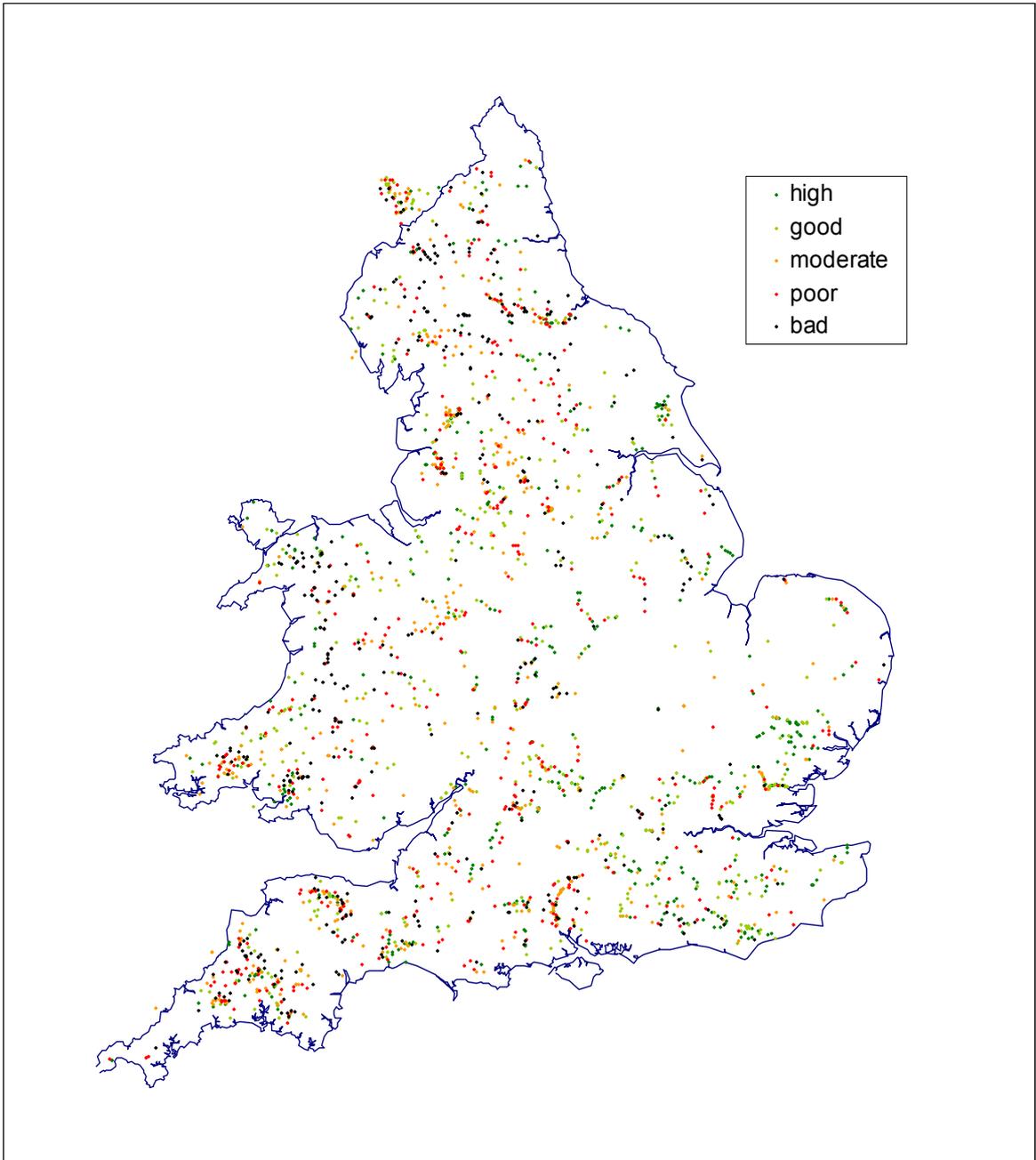


Figure 2.10 Overall relative FCS for the 23 most prevalent species in England and Wales

2.4 Discussion

The original intention for phase 3 of the RFHI project was to include field-based variables from field survey techniques such as the River Habitat Survey (RHS). This would have been particularly important for any applications aimed at physical habitat improvement. However, part way through this project, it became apparent that the outputs from the RFHI project may be used as a tool for reporting fish population status, as required under the WFD. This means that the priority application for the RFHI models will now be to classify observed abundance compared with predicted abundance ('relative' FCS class) for each water body in England and Wales, rather than report the predicted abundance (habitat quality) for each site within a water body.

Further work on the RFHI will now focus on making the models 'as WFD compliant' as possible'. This will include:

- classifying the status of WFD-defined 'water bodies', rather than survey sites;
- setting class boundaries relative to 'reference conditions', as defined by the WFD;
- including the age structure of the population in the assessment;
- reporting classification errors for each water body in terms of the probability of misclassification.

The results presented in this report should therefore be regarded as preliminary and serve only to demonstrate the methodology.

3 Recruitment, survival and growth models (objective 3)

3.1 Introduction

3.1.1 Background

The RFHI provides a statistical link between the numeric abundance of freshwater fish and the values of primary river habitat variables such as width and gradient. The major purpose in defining such relationships is predictive; allowing 'expected' levels of abundance to be estimated, within the bounds of uncertainty, purely from habitat measurements. Extending such predictions across the whole of England and Wales allows an inventory of expected abundance to be created for all species of interest, against which observations may be compared in order to assess the current status.

A single estimate of abundance is a snapshot in time representing the outcome of a highly dynamic set of biological processes, which control the status of all existing cohorts. The contribution of each cohort depends on the reproductive success of the parent stock, recruitment into the 'catchable' population and the rate of survival up to the point of capture. If abundance is measured in terms of biomass, then the rate of growth of the cohort is equally important.

If a population fails to reach its expected abundance, one, some or all of these processes may be below their optima due to limitations in habitat, ecology or water quality. Therefore, the value of fish abundance as an indicator of environmental status will be enhanced by an understanding of the processes that both underlie and determine the outcome. After all, it is these processes that are sensitive to environmental perturbations. This is even more relevant when remedial measures are being contemplated to improve population status. A knowledge of which underlying processes are limiting, and why, is essential if resources are to be targeted effectively.

Although the RFHI is designed to describe spatial patterns of fish distribution, the temporal element is also important. In the wider context, the objective is to establish current population status and compare this with previous assessments, in order to detect changes. Also, the true nature of the current status is better understood in the light of its recent or long-term history, particularly when determining the urgency with which to address a significant decline or deterioration. Thus, the time sequence of changes in fundamental biological processes like recruitment, growth and survival plays an essential role in understanding and interpreting the spatial distribution of fish abundance.

This section describes the application of a statistical Population Dynamics model (PDM), which has been specifically developed to investigate patterns in fundamental biological processes from routine fish population survey data. This analytical tool is a direct complement to the RFHI, because it provides the detailed background information against which RFHI results can be interpreted and allows insights to be gained into the processes that may be affected by environmental impacts.

The PDM was applied to datasets collected from the River Stour catchment (Anglian region) between 1980 and 2003. Data were available from eight sub-catchments and emphasis was placed on the investigation of both spatial and temporal patterns in the recruitment (0+), growth and survival of three common coarse fish species: chub, dace and roach. The patterns that emerged could then be related to long-term estimates of abundance and interpreted in the context of habitat characteristics, local flow and water quality problems, as well as significant events gleaned from the experience of Area Fisheries staff.

3.1.2 The River Stour catchment

The coarse fish populations of the River Stour and its tributaries have been extensively monitored over a long time period. This is primarily because the river attracts a great deal of interest from local anglers and because fish density and health status have long been recognised as valuable indicators of the various water quality and quantity problems that the catchment has suffered.

For hydrological purposes, the main river is divided into three reaches: the Upper Stour, Lower Stour and the Stratford/Flatford reach. There are five major tributaries: the River Glem, the River Box, the River Brett, the Chad Brook and the Belchamp Brook (Figure 3.1).

Essentially, these reaches and tributaries are all lowland watercourses and, in areas experiencing limited rainfall, flows are frequently impoverished. As a consequence and to maintain water levels, there has been considerable management and impounding of extensive sections of the River Stour, leading to the inevitable restriction of fish movement and migration. Low flows are also exacerbated by heavy abstraction for potable supply, particularly from the Lower Stour and Stratford/Flatford reaches. In addition, the catchment receives effluent from several large sewage treatment works, which are located in the Upper Stour, Lower Stour, and Glem and Brett sub-catchments.

The impact of all these pressures was recognised several decades ago and led to the establishment of the Ely–Ouse transfer scheme, which brought water from the north of the region into the headwaters of the Upper Stour. Some of this water is abstracted again, only a few miles downstream, to boost flows in the rivers Pant and Blackwater. The scheme was established in the early 1970s and was intended to support potable supply abstractions, as well as to counteract polluting sewage discharges and alleviate low flows at critical times. A series of weirs and drop structures control the passage of water downstream. The scheme was expected to have both negative and positive impacts, and these are still being evaluated.

In recent years, poor fish survival, particularly of older fish in the lower reaches of the Stour, prompted an investigation into fish health status. This indicated a link between toxins of bacterial origin and high levels of gill hyperplasia in many individuals and suggested that the release of bacterial toxins could be exacerbated by the exposure of riverbed silts during periods of high abstraction.

In spite of these pressures, coarse fish populations thrive along most of the catchment, although their numbers are known to fluctuate quite extensively. The effort and resources directed at monitoring these changes means that their dynamics can be investigated at a level of detail that is unlikely to be possible elsewhere.

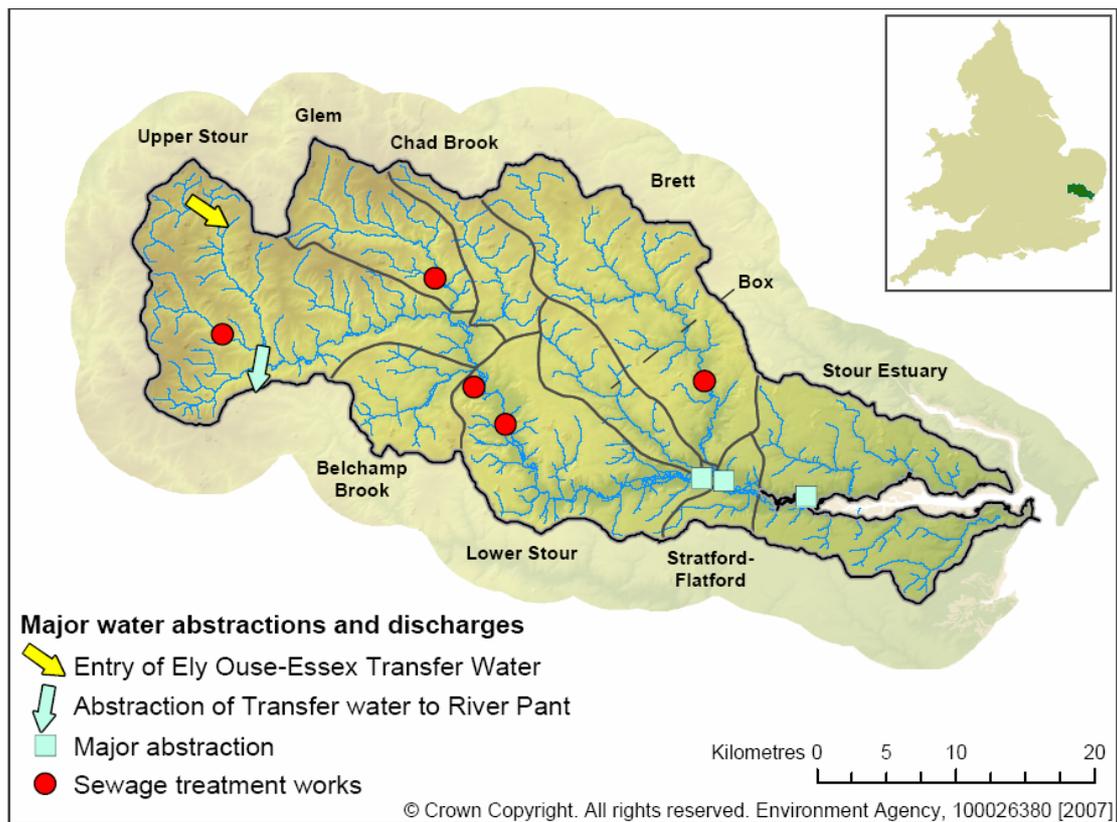


Figure 3.1 General features of River Stour catchment

3.2 Methods

3.2.1 Introduction to the Population Dynamics model (PDM)

The development of the PDM for investigating fish population dynamics has been described in detail elsewhere (Wyatt et al 2007, Science Report SC040014 SR2). Only the salient features that are particularly relevant to the current application are presented briefly here.

Like all statistical models, the PDM relies on the existence of appropriate data to estimate the parameters that govern growth and survival relationships. Long-term time series data from regular routine surveys in the Stour catchment provide the basic information for the model, allowing it to track the progress of individual cohorts as the fish grow in size and decline in numbers. The outputs are produced with estimates of uncertainty to permit realistic interpretation. Since the PDM is probabilistic, all the components are linked and so parameters are estimated by taking all the components into account. Interactive effects can therefore be estimated correctly, and uncertainties associated with all model components are carried through into the estimates, which is something that step-wise models generally fail to do.

The inefficient sampling of juvenile fish, particularly by electric fishing, means that these groups are usually under-represented in the samples. This can cause bias when fitting survival curves and so juvenile fish are frequently omitted from the analysis. The PDM, however, is able to estimate the efficiency of the sampling process from the few data available and adjust the estimates accordingly.

Model parameters can be directly linked with independent estimates of fish abundance at the sites. This means that recruitment, for example, can follow trends in abundance and can be presented in absolute, rather than relative, terms. This feature is of vital importance for interpreting trends and avoiding the pitfalls that often befall some relative methods, such as mistakenly indicating that recruitment is improving when in reality it is declining and vice versa.

Population dynamics relies quite heavily on the correct assignment of age to individual fish, which is usually done on the basis of scale readings. Unfortunately, scale reading is not an error-free process, and becomes more difficult as fish age and the edges of their scales become eroded. Misclassification can have far reaching implications for the analysis, influencing potentially all the estimated parameters. The PDM uniquely addresses this problem by allowing a degree of re-ageing when other data in the model starkly conflict. The extent and propensity for re-ageing is entirely under the control of the operator and can be varied to reflect local knowledge of the species, population and even the skill of the scale reader.

3.2.2 Data requirements and model output

The PDM receives data for each species in the form of individual or grouped fork lengths at age, which are amalgamated over all the sites within a sub-catchment on each sampling occasion. Estimates of population numbers (Carle and Strub (1978)Ref) at each site and on each occasion, together with the area fished, are entered separately. There are many potential outputs from the model, but in this exercise the focus was on annual 0+ recruitment (numbers/100m²), annual survival rate (per cent) and annual growth rate (per cent). 0+ recruitment is estimated at the date of the first survey that includes a particular cohort. Since most of the surveys were undertaken in late summer, the estimate of the annual survival rate does not include the effect of mortality during the first summer. Growth rate was measured as the growth coefficient, which is derived from a fitted von Bertalanffy growth curve (usually denoted *k*) and normally has a negative value. This reflects the declining rate of growth from the initial length (*L₀*) to the ultimate length (*L_{inf}*). For comparative purposes this was expressed as a positive percentage.

Both growth and survival rates were constrained by the model to be consistent across all cohorts within any year and thereby reflect the conditions experienced in that year. This means that the overall growth and survival of an individual cohort depends on the years through which it has existed.

Annual parameter estimates were obtained for all the years where information was available. This spans the period from the birth year of the oldest fish caught in the earliest survey up to the year of the most recent survey. Annual estimates vary around the overall long-term mean for each parameter (known as 'temporal' means), which represents the average achieved over a period of more than 30 years. The temporal means for each parameter and species comprise the basic data used to make spatial comparisons across sub-catchments.

The distribution of annual estimates around the temporal mean generates the temporal variance for each parameter and this variance may contain information reflecting the characteristics of the sub-catchment. In this exercise, temporal variance is expressed in terms of its inverse and called, for the sake of clarity, 'consistency'. It can arise in various ways; either as a result of the relative magnitude of annual fluctuations and/or through the development of temporal trends that persist for different periods of time.

The estimation error is expressed in the 95 per cent confidence intervals around each annual estimate and incorporates all the sources of uncertainty involved in its calculation. This estimation error increases when the sample size is small and at the extremes of the dataset, when the number of fish providing information is limited.

3.2.3 Classification

In order to assist with the spatial comparison of long-term means from each sub-catchment, a classification scheme was sought to assign the values for each parameter from each of the eight sub-catchments to one of three categories: above average, average or below average. The assignment was achieved by fitting a Normal or Log Normal distribution to the dataset of means and then deriving the categories from the form of the distributions. Since this process involved considerable uncertainty due to the small dataset, the categories were not created as equal areas of probability. Instead, the upper and lower boundaries of the categories

were set at the 75 and 25 percentiles, leaving the middle 50 percent to contain the 'average' values. The classification was therefore cautious but appropriate, avoiding over-optimistic discrimination in the face of high levels of uncertainty.

In assigning parameter values to categories (or classes), due regard was taken of the extent of estimation error. Where there was an extensive degree of overlap between the 95 per cent confidence intervals, the class bounds were not rigidly applied and natural groupings were recognised by allowing some transgression. Nevertheless, differences between the members of above average and below average classes were, in general, statistically different ($P < 0.05$). Even so, there were some cases where estimation errors spanned all three classes and interpreting these data required particular caution.

This system of classification has relevance only within the sampled area (the River Stour catchment). As yet there are no external references to judge whether the differences observed have meaning on a wider spatial scale. Furthermore, even when mean parameter values are statistically distinguishable, the differences may be trivial in biological terms.

3.3 Results

3.3.1 Spatial variation in temporal means

For each fish species, the long-term (temporal) mean levels of recruitment, growth and survival varied widely across the sub-catchments. For the purposes of evaluation, the means were assigned to classes and the spatial distributions of the classes are presented geographically in the maps in Figures 3.2 to 3.4. These distributions do not represent the snapshot in time normally associated with a spatial survey, but instead reflect the average performance of each species over a period of some 30 years. They are likely to be influenced more by the physical characteristics of the sub-catchments than by specific events in time, except where the consequences of such events were particularly devastating or persistent. Inset in these figures are similar classifications for the temporal variance or consistency associated with each parameter.

The classification data for recruitment, growth and survival presented in the maps are summarised in matrix form in Figure 3.5a. Figure 3.5b shows the degree of consistency in each parameter for each species and sub-catchment. Sub-catchments with combinations of above average mean and consistency (green/green) and below average mean and above average consistency (red/green) have been separated in Figure 3.6. These sub-catchments occupy opposite ends of the spectrum in terms of a particular parameter and might be expected to provide a contrast in suitable habitat. However, there were no such contrasts among the sub-catchments. For example, there were no sub-catchments in which recruitment was consistently above average or consistently below average. The separation was entirely between the parameters: all the consistently above average parameters were either recruitment or growth rate and the consistently below average parameter was the survival rate. This would imply that issues affecting survival are of more concern within the Stour catchment than those affecting recruitment or growth.

Inspection of Figures 3.2 to 3.6 allows the relative performance of the sub-catchments to be compared. Assessments were made on the basis of the classifications of above or below average. For example, a sub-catchment classed as above average across all parameters for a species would be expected to provide good habitat features (at least within the confines of the Stour catchment) and vice versa.

In the event, there were no such stark differences, but some discernible features did emerge. A crude evaluation can be made by considering the ratio of above average to below average classifications across the sub-catchments. This assessment immediately highlights the River Box, for which only one below average classification was recorded (chub survival) and growth was above average for all species. The mean values for the River Box were also highly consistent over time. In contrast, the Stratford/Flatford reach performed generally worst of all, primarily as a result of below average survival in all species. The River Brett provides an alternative to these sub-catchments, supporting relatively good survival but poor recruitment and including only one average value (roach recruitment). This pattern of contrasts was mirrored in the extent of temporal variance in the Brett, which displayed no high consistency values for any parameter or species.

Within the main River Stour, there was a tendency for the proportion of below average classifications for chub and dace to increase with the distance away from upstream regions (and towards the estuary). Roach classifications, however, followed the opposite trend and recruitment and growth were highest in the Stratford/Flatford reach, despite the overall poor performance. These differences may be related simply to the natural features of the catchment, which favour chub and dace in the upper reaches and roach in the lower, but could also be influenced by the introduction of transferred water into the Upper Stour.

Consistently above average recruitment was observed for roach in the Chad Brook and the Stratford/Flatford reach (Figure 3.4). However, an above average growth rate was maintained for all species in the River Box and for dace in the Upper and Lower Stour. There were no consistently below average values for recruitment or growth. In marked contrast, there were no consistently above average values for survival rate and a consistently below average survival rate for chub in the Chad, Box and Stratford/Flatford reach and for dace and roach in the Lower Stour.

These results suggest a link between recruitment and survival rate. In some cases, good recruitment appears to be associated with poor survival and there are examples of poor recruitment coinciding with good survival, although not necessarily consistently good survival (for example, in the River Brett and Belchamp Brook). This relationship indicates that the influence of density-dependent factors may be more prevalent and have greater effects in small streams. Successful recruitment leads to competition for food resources and attracts predators, whereas low densities, resulting from poor recruitment, may induce less of these pressures, allowing for greater survival. However, these effects are not well documented for coarse fish communities.

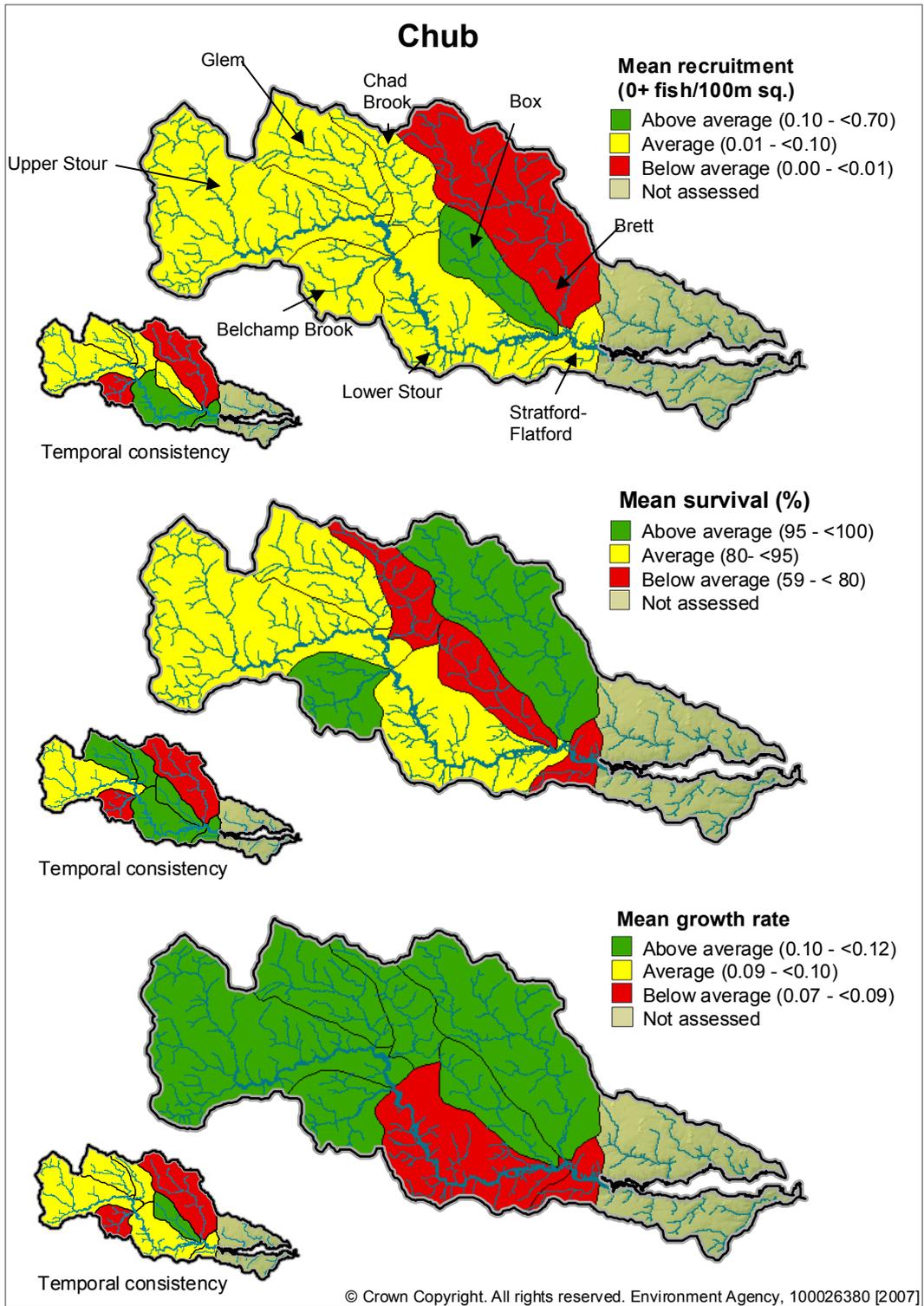


Figure 3.2 Spatial distribution of population dynamics parameters for chub in the River Stour catchment (consistency distribution inset)

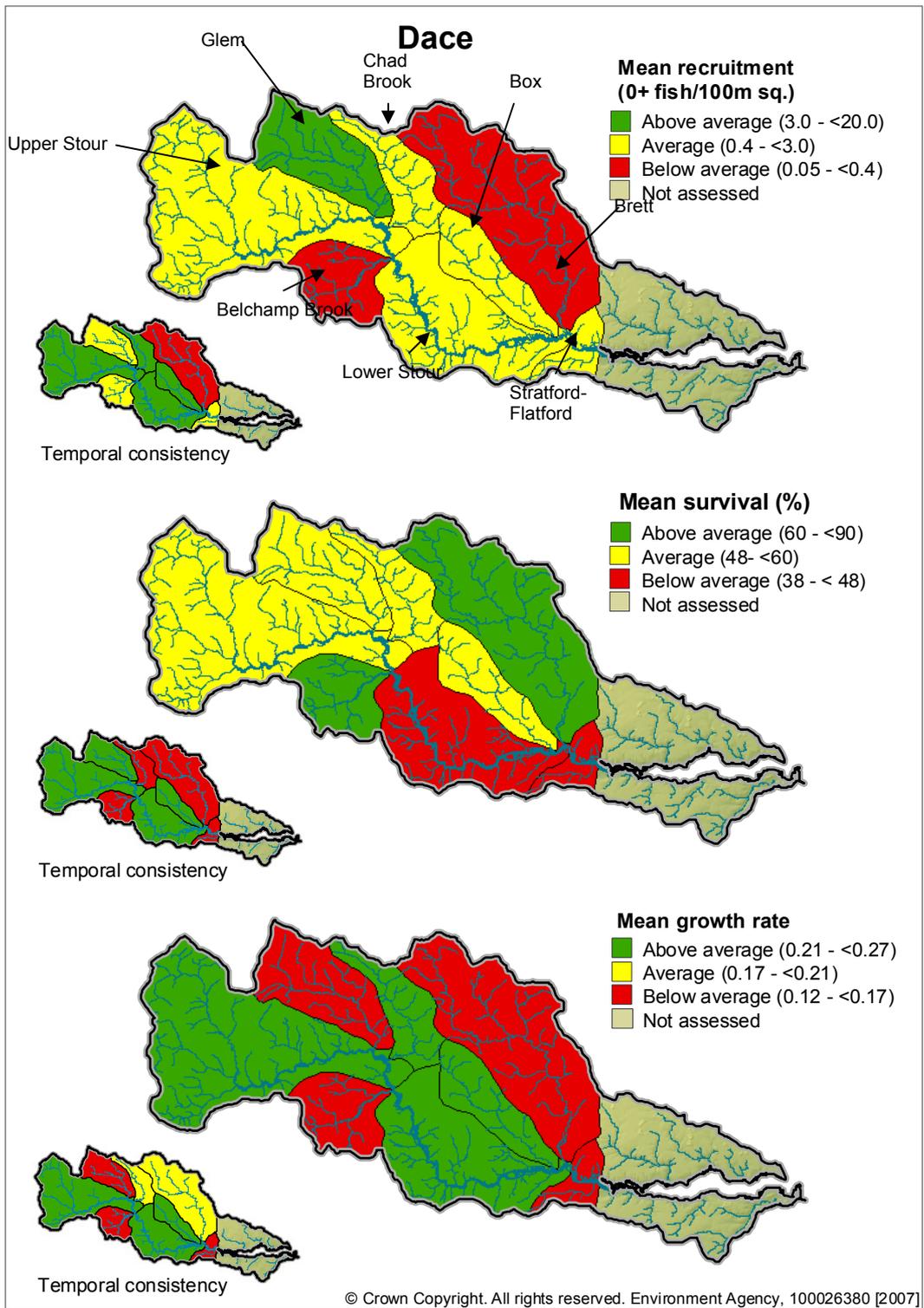


Figure 3.3 Spatial distribution of population dynamics for dace in the River Stour catchment (consistency distribution inset)

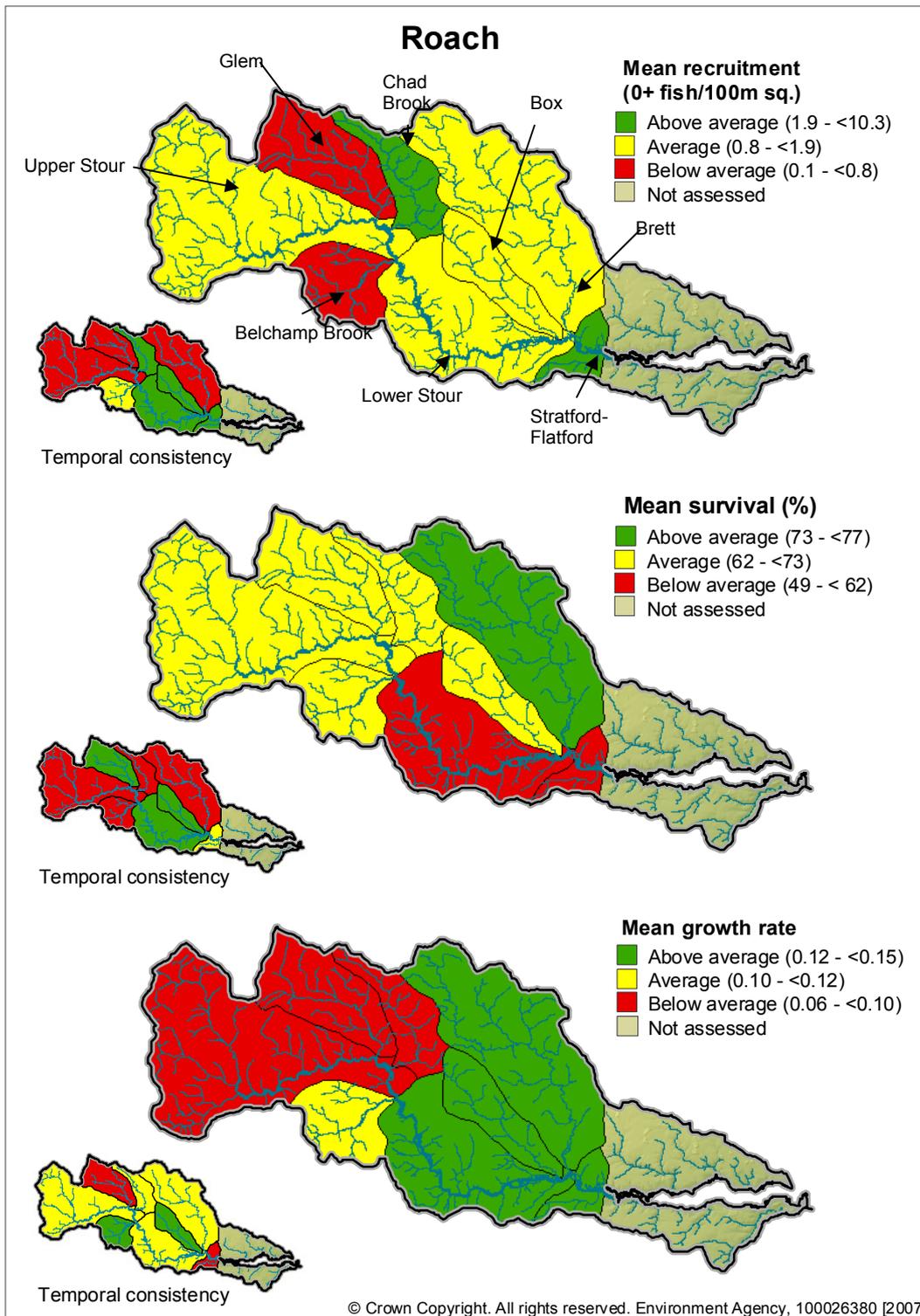


Figure 3.4 Spatial distribution of population dynamics parameters for roach in the River Stour catchment (consistency distribution inset)

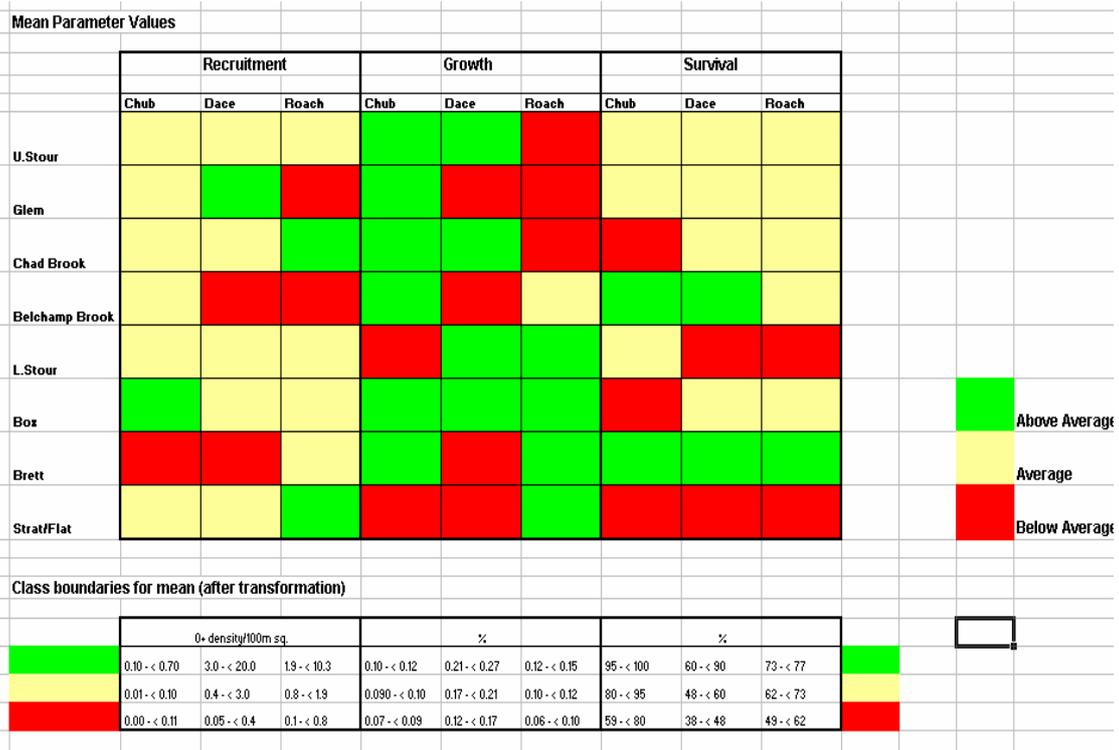


Figure 3.5a Classification matrix for spatial parameter means



Figure 3.5b Classification of consistency in mean spatial parameters

	Recruitment			Growth			Survival			Consistently high	Consistently low
	Chub	Dace	Roach	Chub	Dace	Roach	Chub	Dace	Roach		
	U.Stour					Consistently high					
Glem											
Chad			Consistently high				Consistently low				
Belchamp Brook											
L.Stour					Consistently high			Consistently low	Consistently low		
Box				Consistently high	Consistently high	Consistently high	Consistently low				
Brett											
Strat/Flat			Consistently high				Consistently low				

Figure 3.6 Sub-catchments supporting consistently high and low performance

3.3.2 Species differences

Across all sub-catchments, differences in recruitment, growth and survival were evident between the three species of fish studied (Figures 3.2–3.5). Recruitment of chub was much lower than recruitment of either dace or roach and the survival rate was considerably greater. Indeed, in relative terms, the survival of chub was very high, with little variation between sub-catchments, such that the lower bound of the average category was 82 per cent. Even so, there was no overlap in the 95 per cent confidence intervals for estimation errors between the above average and below average categories.

On average, the growth rate was highest for dace and lowest for chub, although the lowest individual growth rate was found for roach in the Upper Stour and the Chad Brook. With the exception of roach in the Belchamp Brook, all the temporal means for growth rate fell into either the above average or below average categories.

3.3.3 Temporal variation in annual data

The PDM produces annual estimates of recruitment, growth and survival for each species in all the sub-catchments. Plotted sequentially, these data portray the time series that generate the temporal means and embody a vast amount of information that contributes to the spatial patterns. Some of this information is extracted in the

temporal variances, such as the consistency, but closer inspection of the graphics allows greater insights to be gained into the characteristics of the temporal patterns. No attempt is made here to scrutinise all the available graphics, but representative examples are presented in Figures 3.7 to 3.11.

In these graphics, a three-tiered approach to classification was again applied to aid interpretation. However, in this case, the extent of the estimation error (95 per cent confidence intervals) provided the basis for defining the categories. Confidence limits that did not transcend the temporal mean were either significantly above or significantly below the mean and are represented by green or red bars respectively. Those that did transcend the temporal mean were not distinguishable from the mean and are represented by yellow bars.

Figure 3.7 shows the annual recruitment for dace in two sub-catchments with similar patterns of temporal distribution but different degrees of temporal variance. The River Box supported average recruitment overall, with relatively little year-on-year variation. High recruitment in 1976 was followed by more than a decade of mostly low or average recruitment, after which there was a sustained improvement during the mid-1990s. The River Brett displayed essentially the same distribution, but in poor years the recruitment collapsed almost completely while in good years recruitment was exceptional. This chaotic pattern suggests an unstable environment, with dace populations living close to 'the edge'.

Annual growth rates are compared for chub in the upper and lower River Stour in Figure 3.8. The temporal distributions show similar, but not identical, patterns, as may be expected in adjacent river sections. The Upper Stour chub grew significantly faster and were similarly variable, although the extent of the variation in growth was small across all sub-catchments. In recent years, there has been evidence of a decline in the growth of chub in the Lower Stour.

A contrast in the annual survival rates for roach is shown in Figure 3.9. The River Brett again exhibits an unstable pattern over time compared with the River Box, where none of the annual data were significantly different from the overall mean.

Survival and growth rates can be followed and displayed separately for all the cohorts where data are available. Figures 3.10 and 3.11 show fitted curves for roach survival in the Lower Stour and dace growth in the Stratford/Flatford reach respectively. Apparent constriction and separation in the pattern of the lines indicates years when the growth rates were high or low. This demonstrates how mean growth and survival for each cohort depends on the period through which it grows and survives.

A frequent feature of the survival curves is the loss of older fish in more recent years. This is shown in Figure 3.12 for dace in the River Box and for chub in the Stratford/Flatford reach. There appears to be no particular spatial pattern to this phenomenon, which was widely spread across all species and sub-catchments but not consistently. The Stratford/Flatford reach was the most extensively affected, with all three species showing a similarly dramatic decline.

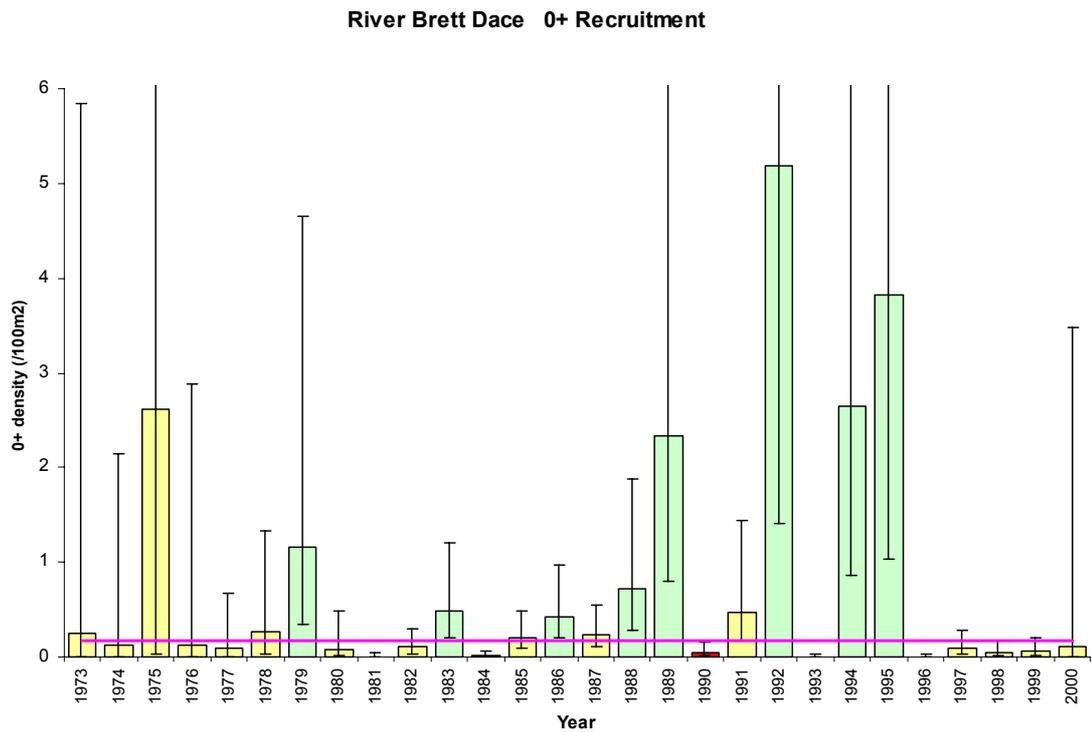
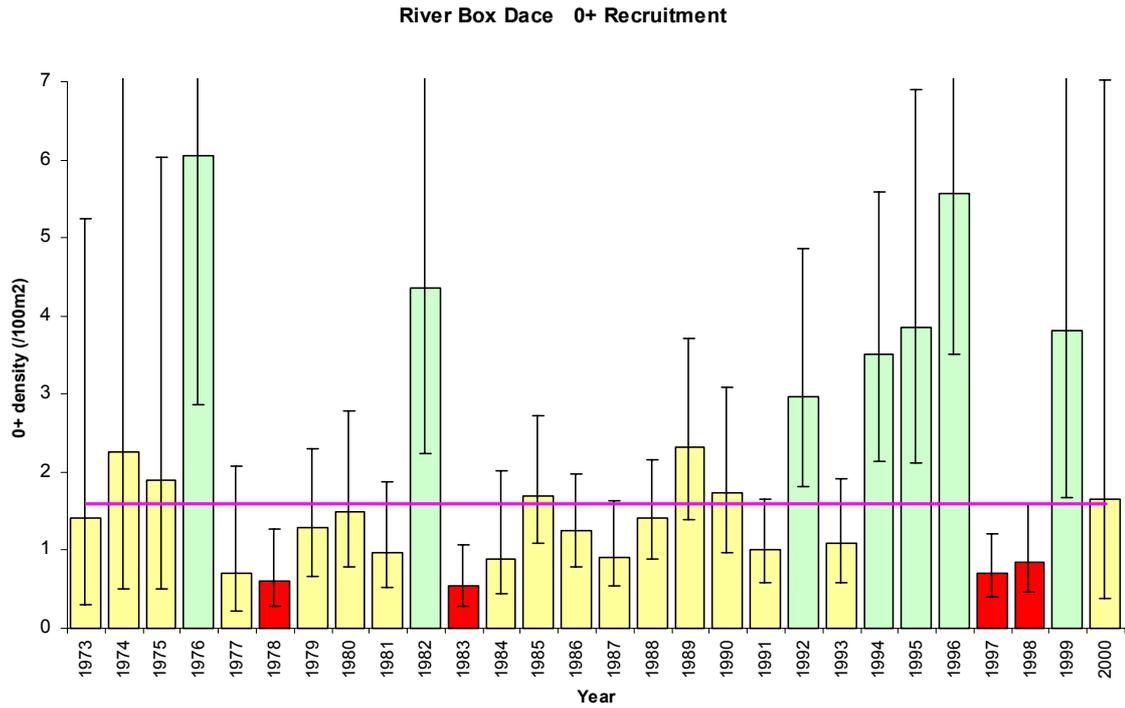
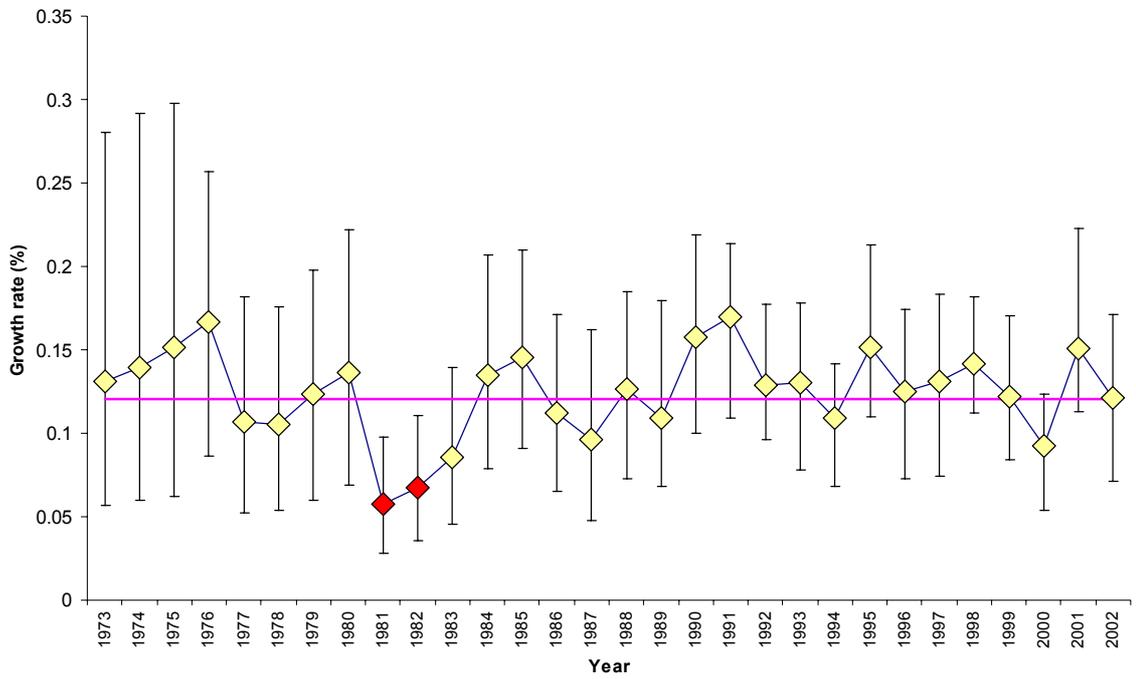


Figure 3.7 Time series of annual recruitment for 0+ dace in the rivers Brett and Box

R.Upper Stour Chub Annual GrowthRate



R.Lower Stour Chub Annual Growth Rate

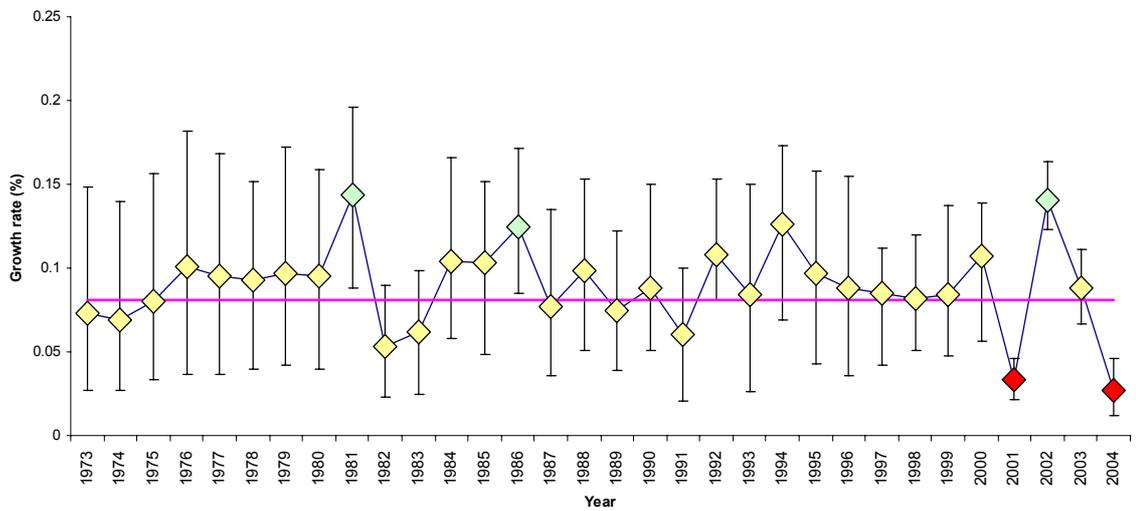


Figure 3.8 Annual growth rate for chub in the Upper and Lower Stour

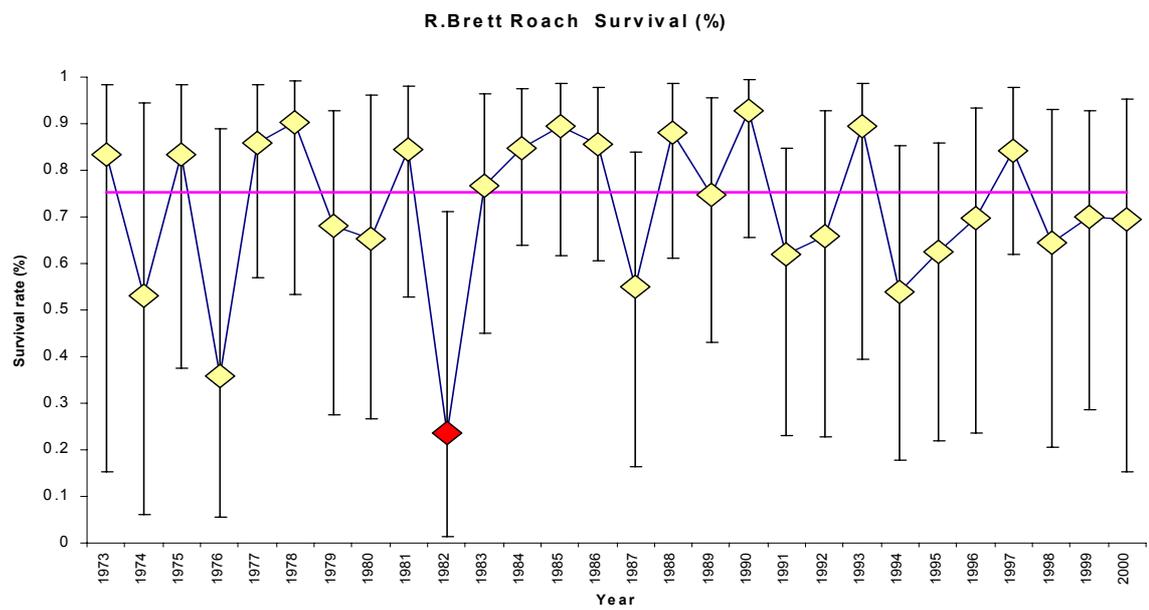
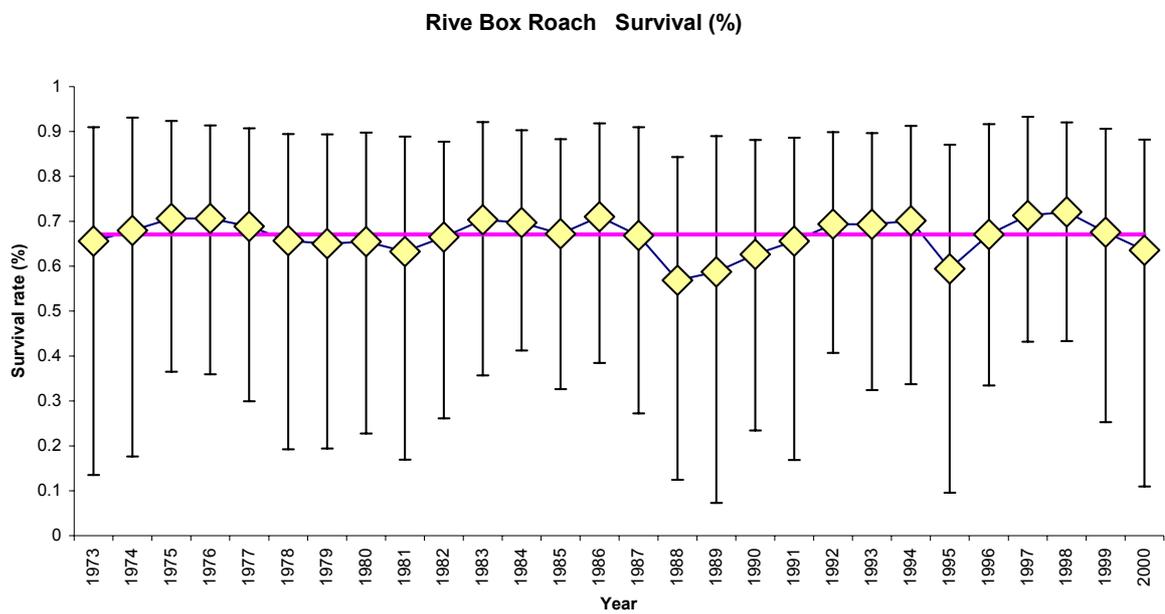


Figure 3.9 Annual survival rate for roach in the rivers Box and Brett

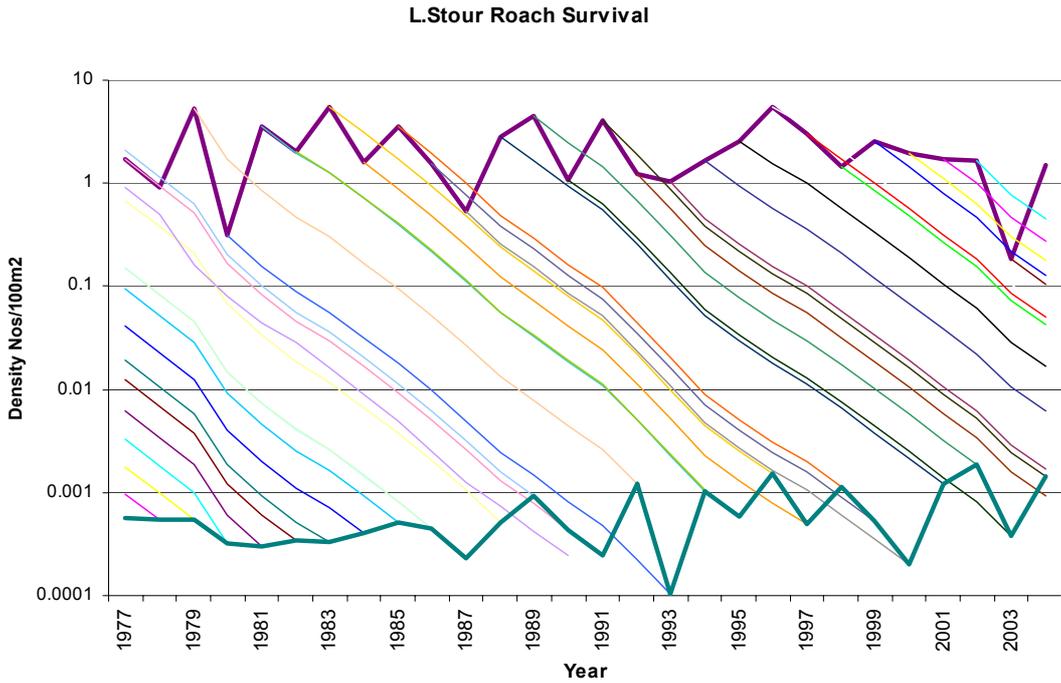


Figure 3.10 Survival curves for roach cohorts in the Lower Stour

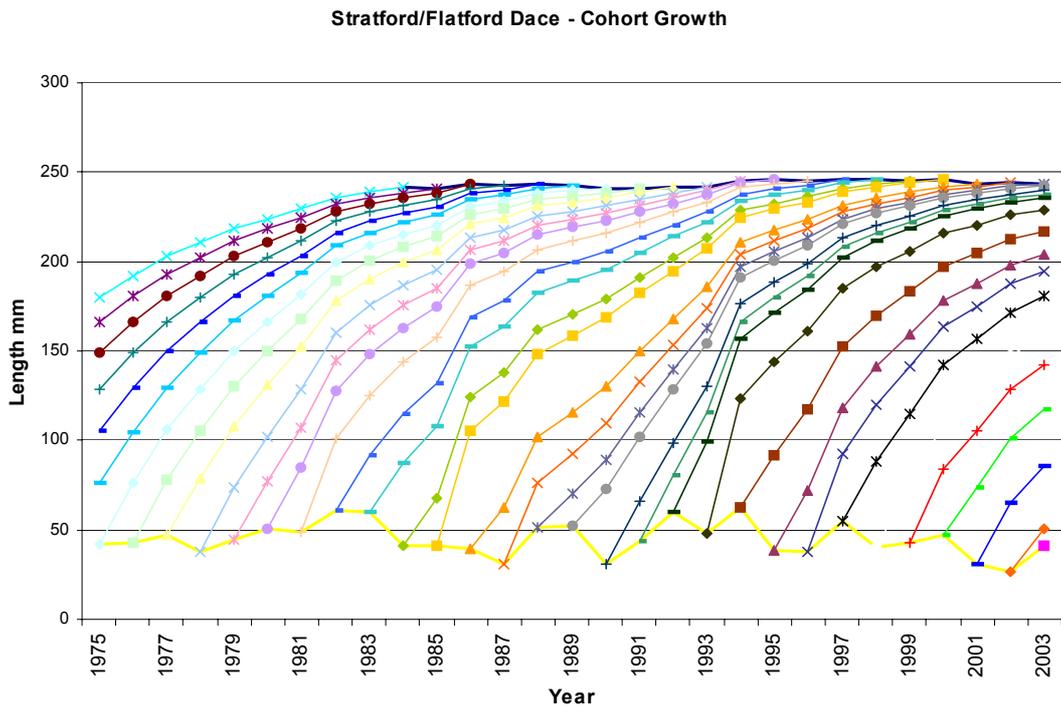


Figure 3.11 Growth curves for dace cohorts in the River Stour (Stratford/Flatford reach)

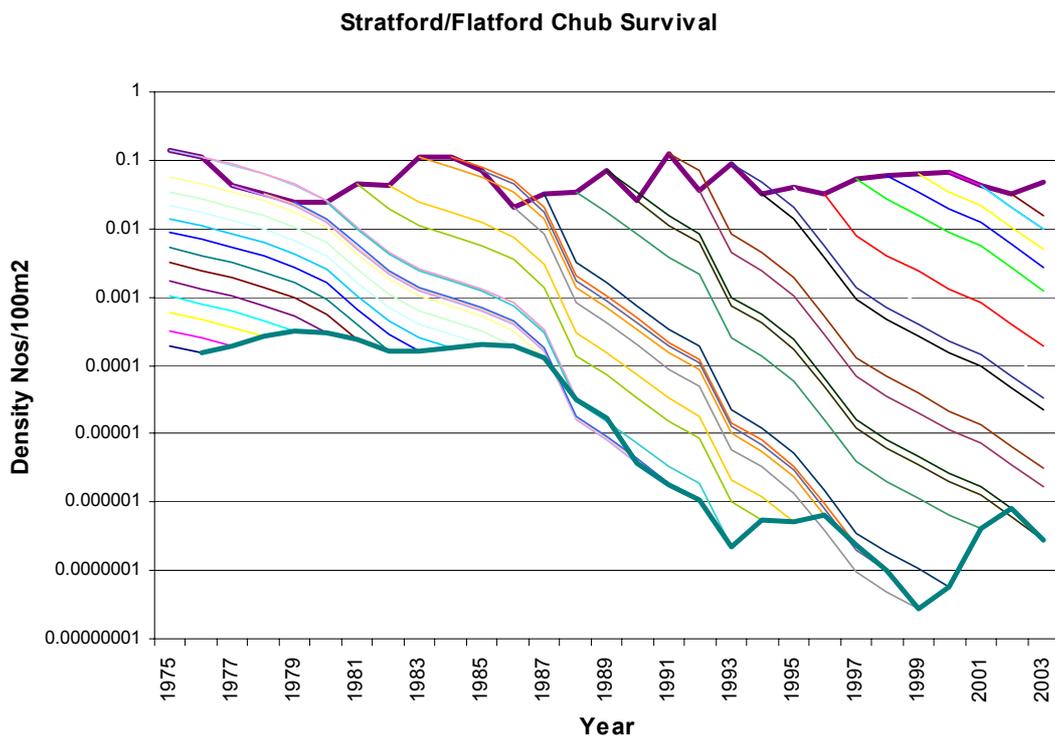
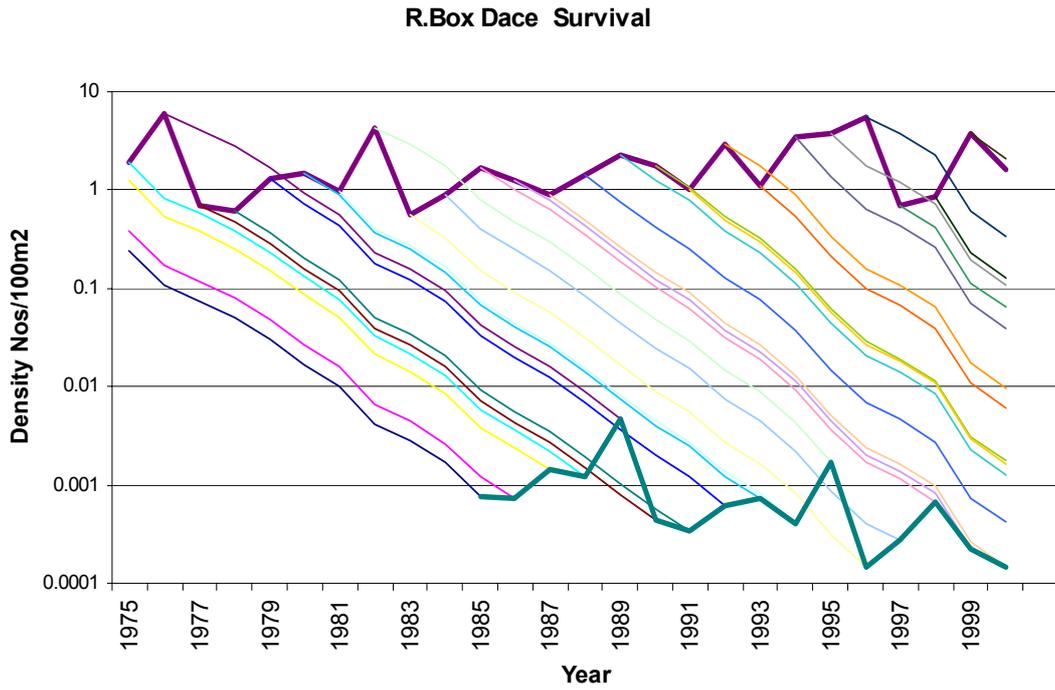


Figure 3.12 Changes in survival in the River Box and the Stratford/Flatford reach of the River Stour

3.3.4 Time series correlations

None of the time series provided evidence of persistent trends extending over long time periods, but short-term trends lasting up to five years or so were commonplace. If these trends reflected changes in climatic conditions then it would be reasonable to expect the fish populations in neighbouring sub-catchments to respond similarly and in synchrony, at least within species. Very influential climatic effects, such as unusually hot and dry years, could affect all species across all parameters.

Temporal correlation analyses, taken over the entire sampling period, were carried out separately for each species and parameter across the sub-catchments. Correlation coefficients and their probabilities are detailed in the half matrices in Tables 3.1 to 3.3.

Significant correlations between sub-catchments occurred rather spasmodically. They were found most frequently for recruitment, less frequently for survival and hardly at all for growth. Also, correlations were more prevalent for chub and dace than for roach. Indeed, no correlations were found for roach survival and growth.

For the most part, correlations occurred too infrequently for any clear patterns to emerge. However, from the results for chub recruitment, it appeared that synchronous annual fluctuations occurred primarily, though not exclusively, between the reaches of the main River Stour and the Belchamp Brook. These findings suggest that local factors exert a much greater influence over population dynamics than climatic conditions, when viewed over the long term. Furthermore, some aspects, such as recruitment, and some species, in this case chub, appear to be more sensitive to climatic conditions than others.

Table 3.1 Temporal correlations for recruitment

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	0.010 <i>0.960</i>						
Box	-0.075 <i>0.703</i>	0.709 <i>0.000</i>				Chub	
Brett	-0.148 <i>0.450</i>	-0.038 <i>0.846</i>	0.141 <i>0.475</i>				
Glem	0.147 <i>0.456</i>	0.595 <i>0.001</i>	0.336 <i>0.080</i>	-0.064 <i>0.748</i>			
Strat/Flat	0.296 <i>0.126</i>	0.407 <i>0.032</i>	0.245 <i>0.209</i>	-0.081 <i>0.683</i>	0.532 <i>0.004</i>		
U.Stour	0.138 <i>0.482</i>	0.764 <i>0.000</i>	0.443 <i>0.018</i>	-0.089 <i>0.654</i>	0.903 <i>0.000</i>	0.619 <i>0.000</i>	
Belchamp Br	0.156 <i>0.4280</i>	0.591 <i>0.0010</i>	0.374 <i>0.0500</i>	-0.071 <i>0.7180</i>	0.955 <i>0.0000</i>	0.543 <i>0.0030</i>	0.857 <i>0.0000</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	0.725 <i>0.000</i>						
Box	0.722 <i>0.000</i>	0.777 <i>0.000</i>				Dace	
Brett	0.227 <i>0.246</i>	0.240 <i>0.218</i>	0.241 <i>0.217</i>				
Glem	0.275 <i>0.152</i>	0.212 <i>0.280</i>	0.201 <i>0.306</i>	-0.078 <i>0.692</i>			
Strat/Flat	0.269 <i>0.167</i>	0.345 <i>0.072</i>	0.222 <i>0.257</i>	-0.102 <i>0.607</i>	0.037 <i>0.845</i>		
U.Stour	0.609 <i>0.001</i>	0.510 <i>0.006</i>	0.683 <i>0.000</i>	0.314 <i>0.104</i>	0.361 <i>0.076</i>	0.121 <i>0.541</i>	
Belchamp Br	0.187 <i>0.346</i>	0.103 <i>0.603</i>	0.055 <i>0.782</i>	0.123 <i>0.533</i>	-0.181 <i>0.929</i>	0.178 <i>0.364</i>	0.131 <i>0.507</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	-0.053 <i>0.790</i>						
Box	-0.222 <i>0.256</i>	0.368 <i>0.054</i>				Roach	
Brett	0.515 <i>0.005</i>	0.203 <i>0.301</i>	0.295 <i>0.128</i>				
Glem	0.613 <i>0.001</i>	0.135 <i>0.493</i>	-0.170 <i>0.389</i>	0.610 <i>0.001</i>			
Strat/Flat	-0.013 <i>0.947</i>	0.365 <i>0.057</i>	0.106 <i>0.592</i>	0.009 <i>0.965</i>	-0.031 <i>0.876</i>		
U.Stour	-0.111 <i>0.574</i>	0.019 <i>0.923</i>	0.009 <i>0.985</i>	-0.089 <i>0.653</i>	-0.146 <i>0.457</i>	-0.078 <i>0.695</i>	
Belchamp Br	-0.13 <i>0.508</i>	-0.18 <i>0.929</i>	-0.07 <i>0.725</i>	-0.129 <i>0.514</i>	0.239 <i>0.222</i>	0.002 <i>0.993</i>	-0.015 <i>0.938</i>

Notes: P values in italics; significant correlations in yellow; grey cells indicate evidence of correlation.

Table 3.2 Temporal correlations for survival

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	0.005 <i>0.979</i>						
Box	-0.009 <i>0.962</i>	0.256 <i>0.188</i>				Chub	
Brett	-0.133 <i>0.501</i>	-0.108 <i>0.585</i>	0.166 <i>0.398</i>				
Glem	0.180 <i>0.360</i>	0.010 <i>0.961</i>	0.509 <i>0.006</i>	-0.039 <i>0.842</i>			
Strat/Flat	0.644 <i>0.001</i>	0.065 <i>0.742</i>	0.051 <i>0.795</i>	-0.182 <i>0.353</i>	0.122 <i>0.536</i>		
U.Stour	0.080 <i>0.686</i>	-0.279 <i>0.150</i>	0.387 <i>0.042</i>	0.201 <i>0.306</i>	0.223 <i>0.254</i>	0.191 <i>0.381</i>	
Belchamp Br	0.08 <i>0.686</i>	0.565 <i>0.002</i>	0.076 <i>0.699</i>	-0.153 <i>0.438</i>	-0.099 <i>0.615</i>	-0.109 <i>0.580</i>	-0.271 <i>0.163</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	0.488 <i>0.008</i>						
Box	0.387 <i>0.042</i>	0.729 <i>0.000</i>				Dace	
Brett	-0.028 <i>0.889</i>	0.045 <i>0.821</i>	0.008 <i>0.968</i>				
Glem	-0.178 <i>0.366</i>	0.008 <i>0.969</i>	-0.200 <i>0.308</i>	0.342 <i>0.075</i>			
Strat/Flat	-0.004 <i>0.985</i>	-0.169 <i>0.391</i>	-0.268 <i>0.169</i>	-0.089 <i>0.651</i>	0.021 <i>0.917</i>		
U.Stour	0.386 <i>0.043</i>	0.627 <i>0.000</i>	0.595 <i>0.001</i>	-0.092 <i>0.642</i>	-0.285 <i>0.141</i>	0.021 <i>0.915</i>	
Belchamp Br	0.18 <i>0.36</i>	0.112 <i>0.572</i>	-0.02 <i>0.921</i>	-0.196 <i>0.317</i>	0.041 <i>0.838</i>	0.104 <i>0.599</i>	0.005 <i>0.98</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	-0.181 <i>0.357</i>						
Box	0.239 <i>0.221</i>	0.044 <i>0.823</i>				Roach	
Brett	-0.153 <i>0.438</i>	0.109 <i>0.579</i>	-0.122 <i>0.536</i>				
Glem	-0.006 <i>0.977</i>	0.257 <i>0.186</i>	0.100 <i>0.611</i>	-0.366 <i>0.055</i>			
Strat/Flat	-0.083 <i>0.675</i>	0.061 <i>0.759</i>	0.050 <i>0.801</i>	-0.063 <i>0.751</i>	0.056 <i>0.779</i>		
U.Stour	-0.114 <i>0.564</i>	-0.155 <i>0.432</i>	0.080 <i>0.684</i>	-0.040 <i>0.838</i>	0.071 <i>0.720</i>	-0.186 <i>0.344</i>	
Belchamp Br	0.24 <i>0.218</i>	0.058 <i>0.771</i>	0.093 <i>0.64</i>	-0.159 <i>0.418</i>	-0.316 <i>0.101</i>	0.14 <i>0.478</i>	-0.244 <i>0.211</i>

Notes: P values in italics; significant correlations in yellow; grey cell indicates evidence of correlation.

Table 3.3 Temporal correlations for growth rate

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	-0.191 <i>0.330</i>						
Box	0.215 <i>0.217</i>	-0.162 <i>0.411</i>				Chub	
Brett	0.235 <i>0.229</i>	0.273 <i>0.160</i>	-0.191 <i>0.331</i>				
Glem	0.340 <i>0.077</i>	-0.476 <i>0.010</i>	0.080 <i>0.686</i>	-0.054 <i>0.785</i>			
Strat/Flat	0.141 <i>0.474</i>	0.193 <i>0.324</i>	0.379 <i>0.047</i>	-0.120 <i>0.544</i>	-0.210 <i>0.283</i>		
U.Stour	0.019 <i>0.923</i>	-0.163 <i>0.406</i>	0.072 <i>0.714</i>	-0.339 <i>0.078</i>	0.104 <i>0.599</i>	-0.069 <i>0.726</i>	
Belchamp Br	0.29 <i>0.135</i>	-0.215 <i>0.273</i>	0.117 <i>0.553</i>	-0.043 <i>0.828</i>	-0.033 <i>0.866</i>	0.091 <i>0.646</i>	0.003 <i>0.987</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	0.040 <i>0.840</i>						
Box	-0.019 <i>0.923</i>	-0.126 <i>0.521</i>				Dace	
Brett	-0.023 <i>0.906</i>	0.021 <i>0.914</i>	-0.138 <i>0.482</i>				
Glem	-0.208 <i>0.289</i>	0.132 <i>0.503</i>	0.069 <i>0.725</i>	-0.045 <i>0.823</i>			
Strat/Flat	0.224 <i>0.252</i>	0.229 <i>0.741</i>	0.091 <i>0.644</i>	0.050 <i>0.799</i>	-0.040 <i>0.840</i>		
U.Stour	-0.186 <i>0.344</i>	0.260 <i>0.181</i>	0.004 <i>0.986</i>	-0.172 <i>0.380</i>	-0.300 <i>0.121</i>	-0.177 <i>0.367</i>	
Belchamp Br	-0.315 <i>0.103</i>	-0.135 <i>0.493</i>	-0.065 <i>0.743</i>	0.253 <i>0.193</i>	0.3 <i>0.121</i>	0.11 <i>0.576</i>	-0.092 <i>0.641</i>

	Chad Br	L.Stour	Box	Brett	Glem	Strat/Flat	U.Stour
L.Stour	-0.188 <i>0.377</i>						
Box	0.264 <i>0.174</i>	0.260 <i>0.181</i>				Roach	
Brett	0.052 <i>0.792</i>	0.025 <i>0.900</i>	-0.209 <i>0.284</i>				
Glem	0.149 <i>0.450</i>	-0.207 <i>0.291</i>	0.320 <i>0.097</i>	-0.285 <i>0.141</i>			
Strat/Flat	0.262 <i>0.177</i>	0.260 <i>0.182</i>	-0.106 <i>0.590</i>	-0.079 <i>0.691</i>	-0.063 <i>0.751</i>		
U.Stour	-0.267 <i>0.170</i>	0.077 <i>0.697</i>	-0.054 <i>0.784</i>	0.014 <i>0.964</i>	0.189 <i>0.336</i>	0.273 <i>0.160</i>	
Belchamp Br	0.047 <i>0.813</i>	0.279 <i>0.15</i>	0.406 <i>0.032</i>	-0.023 <i>0.907</i>	-0.142 <i>0.47</i>	-0.042 <i>0.833</i>	0.101 <i>0.609</i>

Notes: P values in italics; significant correlations in yellow.

3.3.5 Parameter estimates and fish abundance

Ultimately, fish abundance measured at any point in time will be the culmination of the processes of recruitment, growth and survival, summed for each cohort, existing at the time of sampling. In principle, it would be advantageous and desirable to be able to predict fish abundance purely from knowledge of these processes, but since they are dynamic, highly complex and interrelated current understanding is insufficient for this to be a realistic possibility. Nevertheless, it should be possible to demonstrate that the processes do have a bearing on abundance and so confirm that the spatial distributions of fish species are governed by the factors that impinge on population dynamics. For example, if recruitment has been consistently suppressed over an extended period, it is inconceivable, in the absence of immigration, for population levels to be sustained. Similarly, if recruitment remains high and survival is consistently good, then, in the absence of emigration, these processes must ultimately give rise to high abundance. Between these extremes, prediction becomes much more tenuous. Even so, evidence of these fundamental relationships would be expected to begin emerging.

In a preliminary investigation, the relationship between the numeric abundance of each species and the parameters of recruitment and survival were explored by correlation analysis. The prospect of detecting a relationship was enhanced by the fact that the PDM estimates are already linked to population survey data in order to track trends in time. There is no guarantee of success, however, because of the compounded uncertainty that results from the number of stages involved in the estimation process. But this process does provide some feedback on the overall fit of the model to the data.

In this exercise, growth rate was not included, because it only affects abundance expressed in terms of biomass and not numeric density. Correlations were sought between long-term temporal means for recruitment and survival and an estimate of the overall mean numeric abundance of each species in each sub-catchment. The mean abundance was obtained by summing the Carle and Strub population estimates for each site over all the sampling years and dividing by the total area fished during that time. The raw datasets are presented in Table 3.4. It was clear that the abundance measure for the Stratford/Flatford reach was heavily weighted by several exceptional catches in the early years of the surveys, such as catches of roach at Brantham Lock in 1985 and of dace downstream of Dedham Mill in 1983.

Correlations with logged numeric abundance were inconsistent (Table 3.5). Both chub and roach recruitment were positively correlated ($P < 0.05$) but dace recruitment was not. Roach survival was negatively correlated with abundance ($P < 0.05$) but neither chub nor dace survival shared any such correlation.

Table 3.4 Abundance and parameters – raw data

Sub-catchment	0+ recruitment nos/100m ²			Annual growth rate %			Annual survival rate %			Abundance nos/100m ²		
	Chub	Dace	Roach	Chub	Dace	Roach	Chub	Dace	Roach	Chub	Dace	Roach
Upper Stour	0.08	1.49	1.85	0.12	0.27	0.06	0.92	0.50	0.67	0.74	2.21	4.66
Glem	0.06	19.61	0.11	0.11	0.13	0.07	0.88	0.48	0.72	0.85	3.62	3.24
Chad	0.03	2.45	5.95	0.12	0.23	0.06	0.79	0.54	0.61	1.72	2.47	4.25
Lower Stour	0.08	1.49	1.79	0.08	0.27	0.13	0.81	0.38	0.55	1.05	1.69	12.39
Box	0.69	1.60	0.97	0.10	0.25	0.14	0.74	0.56	0.67	2.66	10.99	2.55
Brett	0.00	0.17	0.90	0.11	0.15	0.15	1.00	0.71	0.75	0.45	1.11	6.89
Strat/Flat	0.05	0.43	10.01	0.07	0.16	0.12	0.58	0.42	0.49	0.66	17.44/1.77	39.99/16.82
Belchamp Brook	0.01	0.01	0.20	0.12	0.14	0.10	0.98	0.85	0.68	0.68	0.45	2.38

Table 3.5 Correlation coefficients for abundance against recruitment and survival parameters

	Chub	Dace	Roach
Recruitment	0.75 0.03	0.325 0.432	0.756 0.03
Survival	-0.418 0.303	-0.53 0.176	-0.765 0.027

Notes: P values in parenthesis; significant effects in yellow.

The rather loose overall association between the parameters and abundance is unsurprising in view of the uncertainties involved in obtaining the estimates, the degree of averaging over time required to obtain the mean values and the implied assumption that such relationships may be linear. Nevertheless, a cautious interpretation of the outcome fits broadly with intuitive expectations. Clearly, high levels of recruitment can lead to increased abundance, but not necessarily, and low survival will probably result in low abundance, but not always. Inspection of the raw data shows that where recruitment was poorest, such as for chub in the River Brett and Belchamp Brook, the result was low abundance. However, the decline in abundance with increased survival for roach appears counter-intuitive. In this case, recruitment was also correlated negatively with survival ($P < 0.05$). But it seems that even the observed low survival rates were insufficient to overcome the influence of high levels of recruitment, as experienced in the Stratford/Flatford reach and the Lower Stour.

In view of the limited data contributing to the correlations, it would be unwise to extend these interpretations further. The interplay of recruitment, survival and abundance operates fundamentally at the cohort level and so it is at this level that subsequent investigations should be directed.

3.4 Discussion

The primary purpose of the RFHI methodology is to detect and locate areas where observed fish abundance has fallen significantly below expectations, after taking habitat considerations into account. It follows naturally then that the causes of any change should be identified, so that appropriate remedial measures can be put in place. Applying the PDM begins the process of identification, by following the temporal fortunes of the recruitment, growth and survival of all the cohorts within each species. However, gaining an understanding of the way that these factors respond to environmental perturbations and relate to each other in order to investigate a decline in abundance presents a new set of challenges.

Gaining some insights requires information about the physical characteristics of the catchment, and the anthropomorphic pressures placed upon it, and so local knowledge is of paramount importance. As an illustration, an attempt has been made to place the results obtained for the Stour catchment in the context of the known physical characteristics and anthropomorphic pressures.

As a lowland catchment in the east of England, issues regarding water quantity affect all the sub-catchments to a greater or lesser extent. Water quantity directly influences water quality through dilution and solution. In addition, local attempts to counter low flows and maintain water levels by impounding means that much of the habitat is unnatural. The Ely–Ouse

transfer scheme was intended to address these problems by boosting flows but inevitably created its own impacts through sudden and local changes in the flow, level and quality of the water.

By the standards of most of the rest of the country even the upper reaches of the Stour are lowland in character and so it might be expected that there would be little evidence of a natural zonation of fish species along the river gradient. While this is largely the case, some semblance of the natural pattern is still discernible. This is best expressed in the distributions of roach and dace abundance, as estimated from survey data. Apart from the unusually high densities at Stratford/Flatford in 1983, dace abundance tended to decline with distance down the catchment towards the sea, while roach abundance increased quite markedly. This is mirrored to some extent in the recruitment and survival of these species, which showed the same pattern. However, RFHI assessments of expected abundance take these natural habitat variations into account and are only influenced by environmental perturbations instigated by a decline in water quality and habitat degradation.

While differences in recruitment, growth and survival varied between species along the length of the main River Stour, there was also evidence of a general decline in performance in a downstream direction for all species, as reflected in the increasing proportion of low classifications. While this decline appears non-specific, it might indicate the decreasing influence of the Ely–Ouse transfer scheme on water downstream. This effect could be exacerbated by the more localised problems in the Stratford/Flatford reach.

The results from the Upper Stour lend some support to the positive benefits of the transfer scheme, since only one low classification was observed (roach growth) despite the input of two major discharges into the sub-catchment. These discharges include effluent from a meat processing factory at Great Wrattling and from a main sewage treatment works (STW) near Wixoe (Haverhill STW). The impact of abrupt flow changes caused by the transfer would be felt most severely in this sub-catchment, but do not appear to have had significant consequences, except perhaps on the growth of roach. If this is the case, the mechanism behind it is not clear. Within the last two decades, signal crayfish (*Pacifastacus leniusculus*) have invaded and populated this part of the river (F. Eley personal communication). Their aggressive behaviour can make them competitors with and predators on certain species of fish, but there is no evidence of this from the survival results. They do, however, form a favoured prey for larger chub and may contribute to the high growth rate observed for this species.

A stark contrast in performance is provided by the results from the Stratford/Flatford reach. This sub-catchment suffers from the impact of three abstractions, all in quite close proximity. The abstraction at Langham is within the Lower Stour sub-catchment but its effect is predominantly felt further downstream. Together with abstractions at Stratford St Mary and Cattawade, which are closer to the estuary, the combined effect is to cause drastic fluctuations in flow and water level, occasionally leaving areas of river substrate exposed for long periods. Low water levels and almost static conditions can allow temperatures to rise rapidly to exceptionally high levels in the summer. It is unsurprising, therefore, that the survival of all three species and the growth of two species were found to be low. Indeed, the proportion of low classifications was greatest for this sub-catchment.

Roach was the only species to gain some advantage from these conditions and both recruitment and growth were high for this species, perhaps due to increased plankton blooms providing abundant food resources, particularly for younger fish. Despite low survival rates, roach densities ranged from high to exceptional on occasions and far exceeded those in other sub-catchments, even without the 1985 catch. The dace catch in 1983 at Dedham Mill was clearly an anomaly and was not repeated. It distorts the average abundance and so is

misleading in view of the current situation. Excluding this sample, dace abundance, as might be anticipated from the lowland habitat, was low.

In recent years, investigations into poor fish survival in the Stratford/Flatford reach have revealed the influence of bacterial exotoxins, which can cause hyperplasia of the gills and may be responsible for exacerbating fish losses. There is evidence that the exposure of river silts following water level fluctuations promotes the sporulation of Actinomycetes, with the associated release of secondary metabolites that act directly on gill tissue (R Wright personal communication, Lewis and Parry 2005). The relative magnitude of this effect on fish abundance is currently under investigation.

The Lower Stour primarily occupies an intermediate position in the main river, both geographically and in the response of its fish populations. The main feature of the PDM output for the Lower Stour is the low survival rate of roach and dace populations. Since recruitment was not high, this may not be a density-dependent effect. The discovery of gill hyperplasia in some fish suggests that bacterial exotoxins may be involved, particularly in the lower reaches downstream of the Langham abstraction and in close proximity to the Stratford/Flatford reach.

None of the tributaries receive any alleviation from low flows from the Ely–Ouse transfer. The rivers Glem and Brett receive effluent from major STWs in their lower reaches.

The consistently high performance of the River Box, involving all species, is a prominent feature of the PDM output. This watercourse is the least managed of all the sub-catchments and retains more natural features. The results of the PDM analysis are reflected in the long-term high abundance of dace and chub. But this high abundance does not extend to roach, which may be constrained by the more upland, pool-and-riffle character. Brown trout are also supported in the upper reaches of this sub-catchment. Consequently, the relatively low survival of chub is surprising but may be influenced by density dependence due to high recruitment.

The River Glem is a more upland sub-catchment with gravel beds in the upstream reaches, although these can become compacted through siltation. Brown trout are present and so the habitat is more suited to dace and chub than roach. This is evident in the high dace recruitment and low roach recruitment, although siltation may have had a detrimental effect in recent years.

Of all the sub-catchments, the River Brett is most affected by low flows, with the resultant problems exacerbated by areas of permeable riverbed. Although there are suitable gravels, spawning habitat is frequently limited and this probably accounts for the low recruitment of dace and chub. Time series data show very suppressed recruitment with intermittent spikes of high response, which may well coincide with years when flows were sufficient at spawning time for fish to take advantage of the available habitat. This pattern gives rise to a high degree of temporal variation (low consistency), which is a feature of all the data from this sub-catchment. Above average survival of all species may be a consequence of limited recruitment in a small and often diminished environment where density dependence may play an important role.

Both the Chad and Belchamp Brooks are small tributaries where density-dependent effects are probably relevant when recruitment is high. The Chad Brook appears to provide good spawning habitat for roach in spite of its more upland character, whereas recruitment was below average or average and survival was above average for all species in the Belchamp Brook.

The loss of older fish occurs spasmodically across the catchment, but does not seem to be associated with water quality or habitat variations. There may be several, perhaps unrelated, causes. The cumulative effect of exposure to bacterial toxins could be expressed by relatively few individuals attaining older ages. Alternatively, selective predation, perhaps by large pike or piscivorous birds, may result in the loss of older fish in some localities

The PDM analysis carried out here shows how time series data add an extra dimension of understanding and structure to a simple estimate of fish density applied spatially across a catchment. It is obvious that the information gleaned can be used to direct attention to aspects of population dynamics that may be impacted by environmental pressures and so provide direction for remedial management actions.

It is important, however, to place the results of the PDM analysis in context. The relationships between fundamental biological processes and abundance examined here are based on estimates averaged over a long period of time. Correlations are likely to be disturbed by temporal variation and so associations made with the conditions that prevail today will inevitably be tenuous. Consequently, arguments should not be forced and apparent links should be treated with due caution. Future spatial surveys will also be snapshots in time but can be viewed in the context of all the historic surveys, allowing the extent of any change to be properly assessed. It is in providing this background that the PDM fulfils its most useful role, by guiding management decisions on how to expend resources in improving and restoring habitats.

4 References

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Appendix A: Relative and absolute abundance, habitat quality and variation of abundance and prevalence with environmental variables

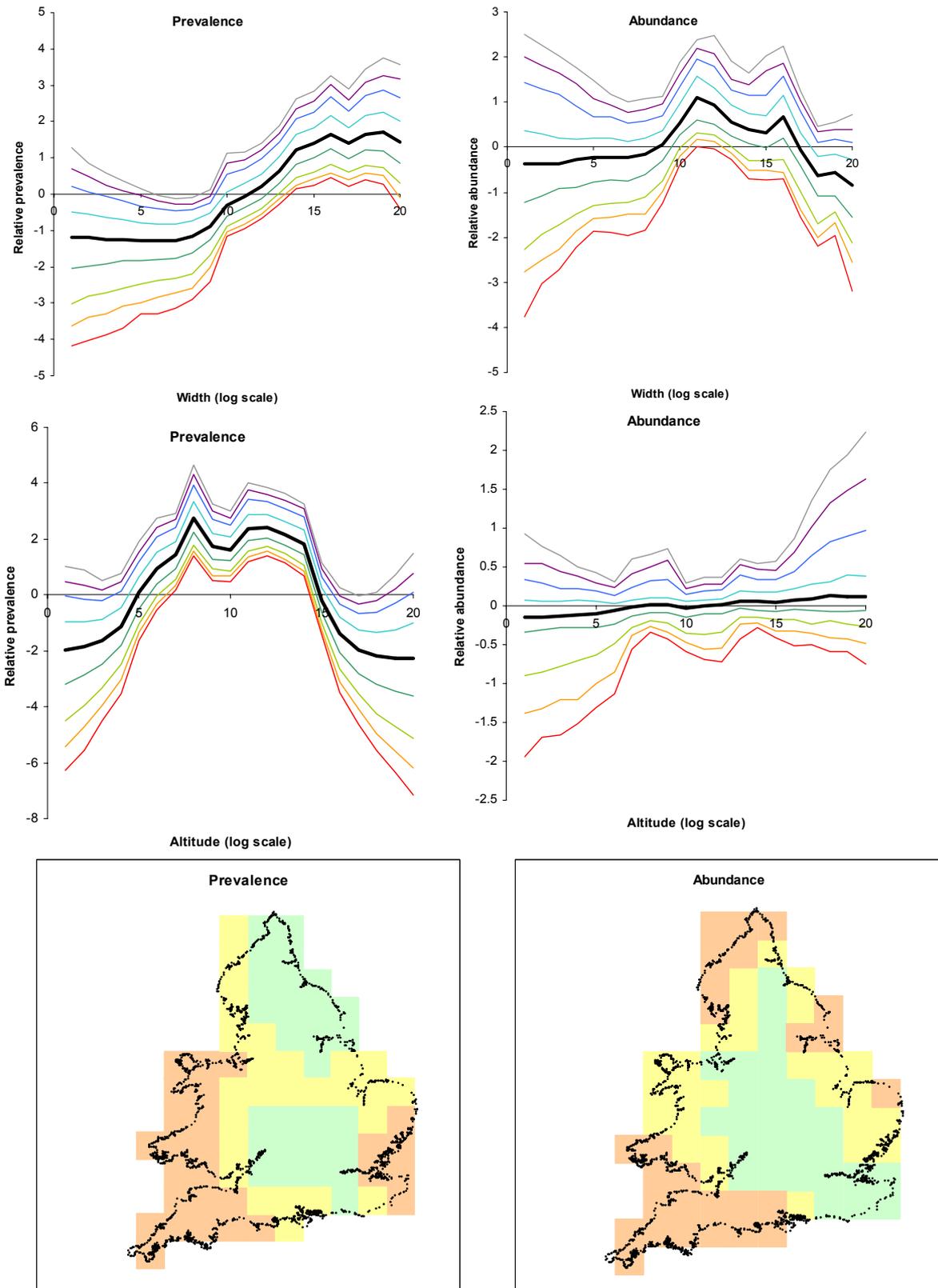


Figure A.1 Variation in abundance and prevalence of barbel with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

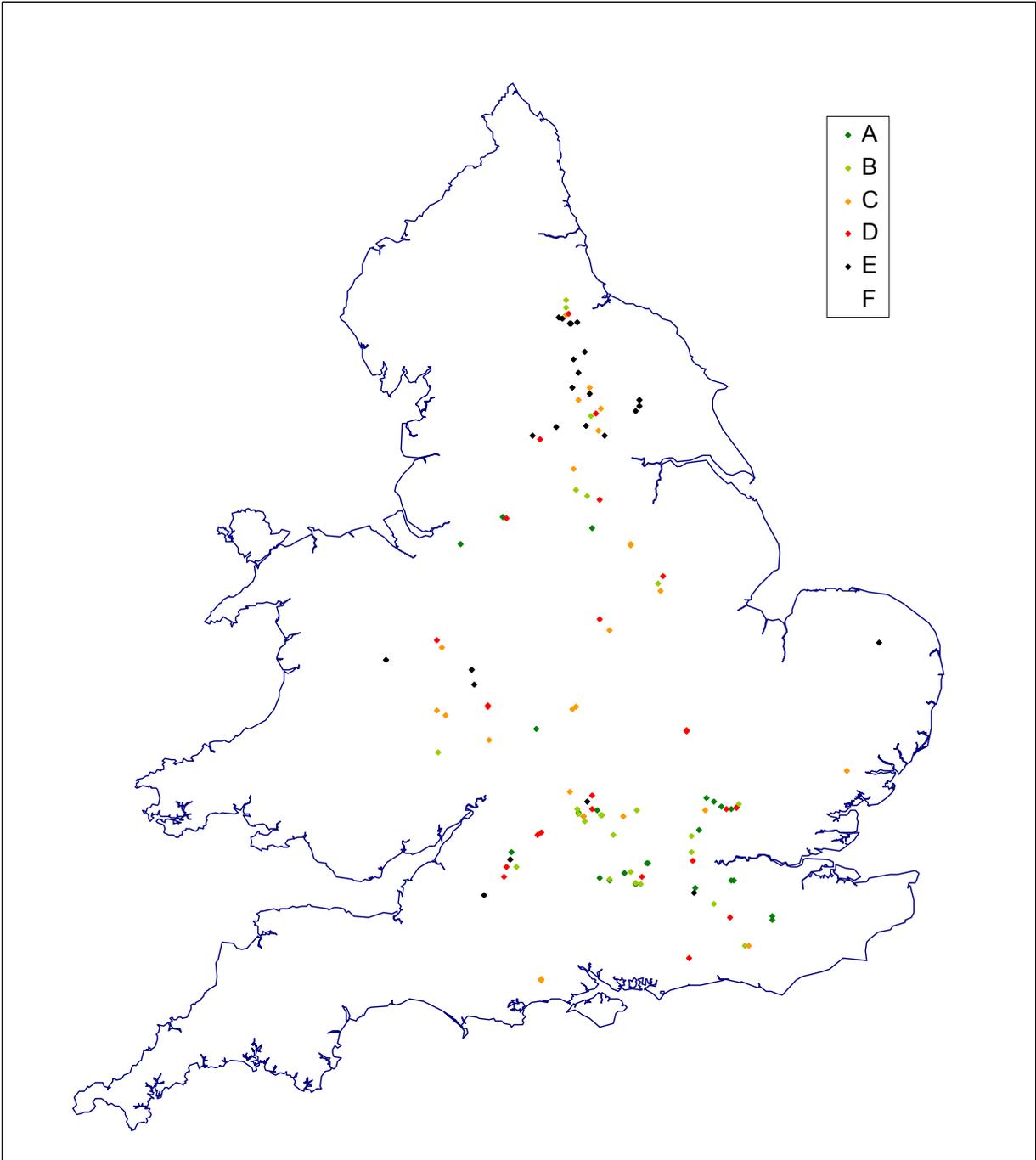


Figure A.2 Classification of barbel abundance (absolute FCS) in 2004

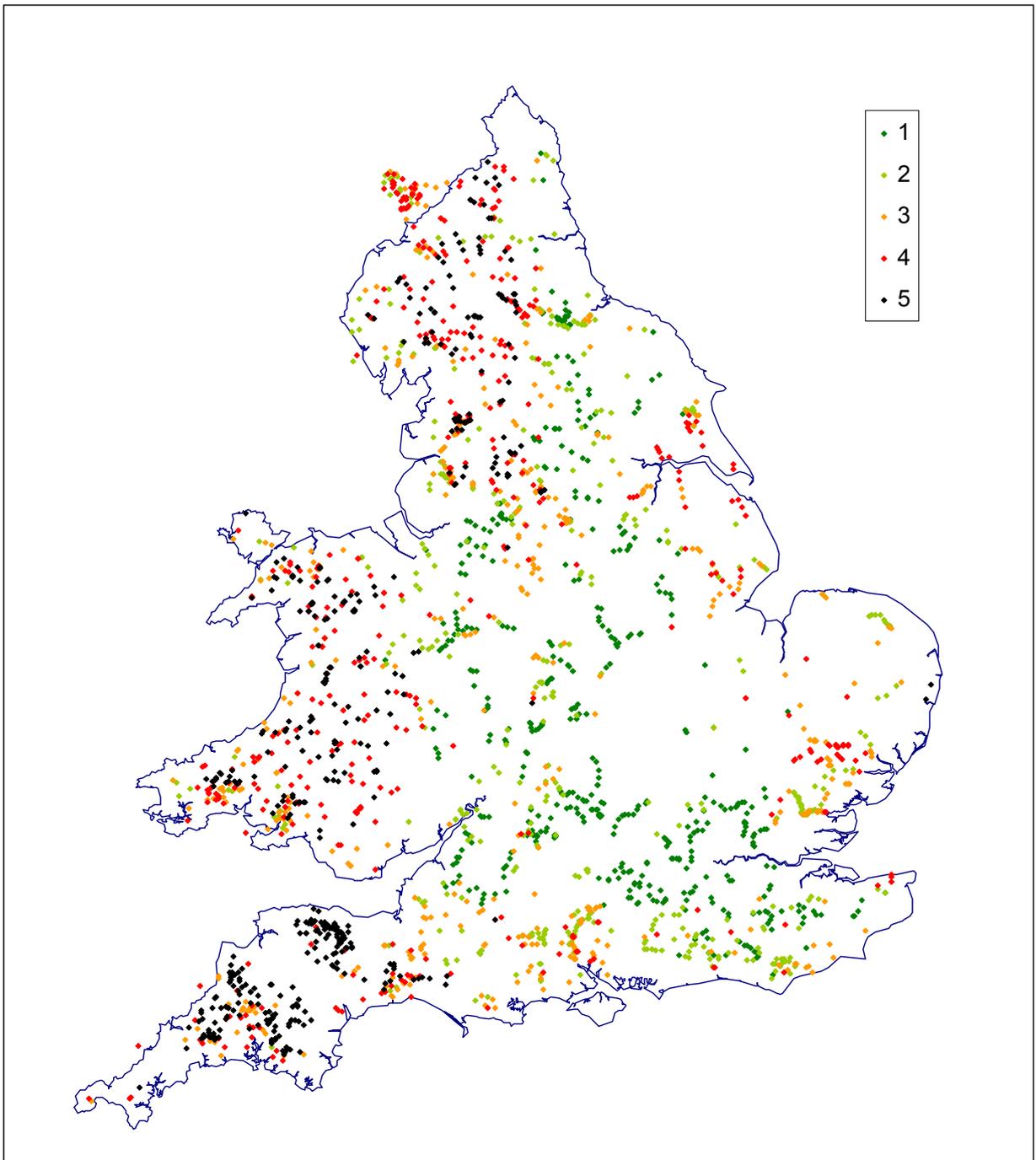


Figure A.3 Expected abundance (=habitat quality) for barbel
Note: 1 (green) is high, 5 (black) is poor.

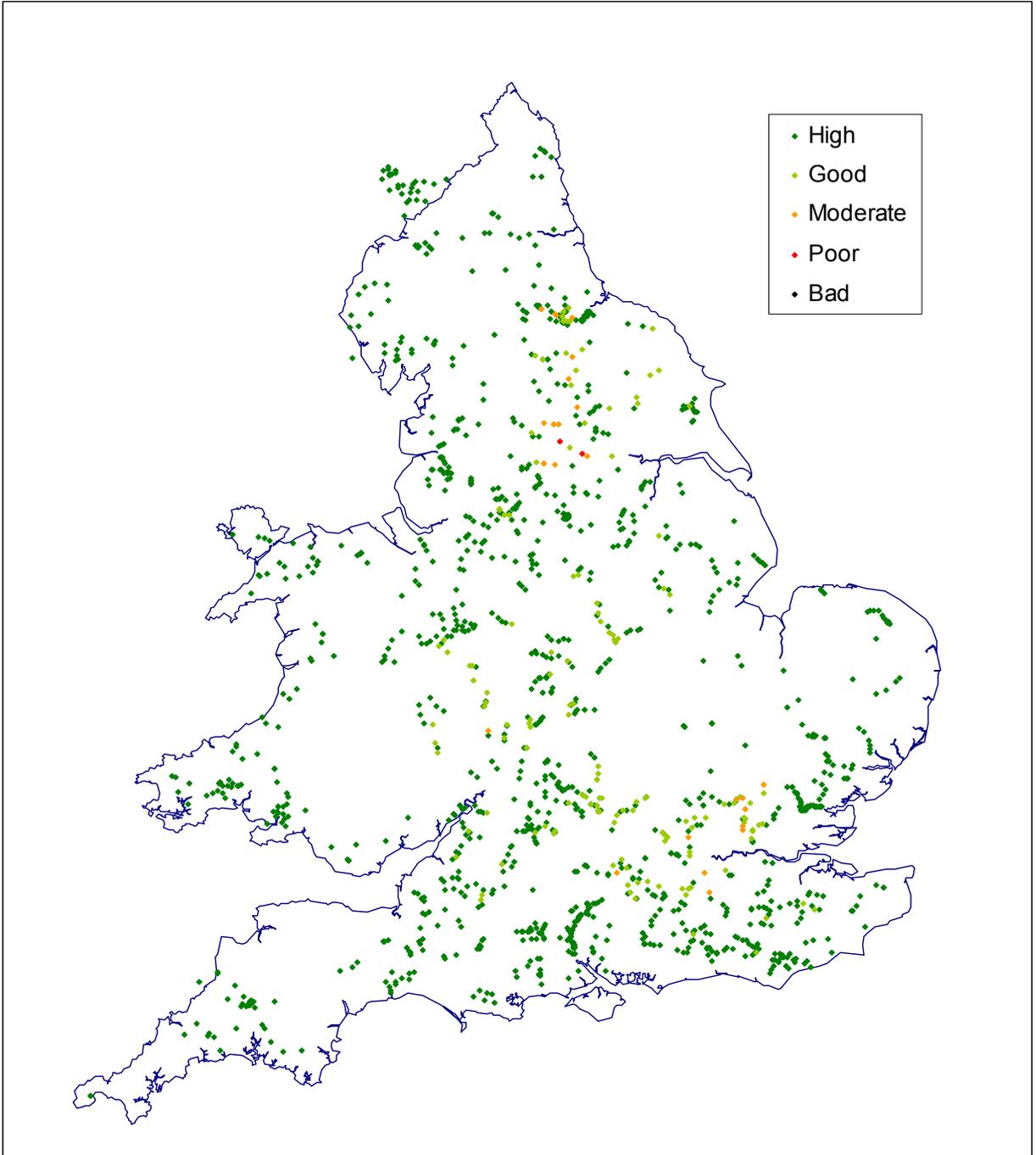


Figure A.4 Observed:expected ratio for barbel abundance (relative FCS) in 2004

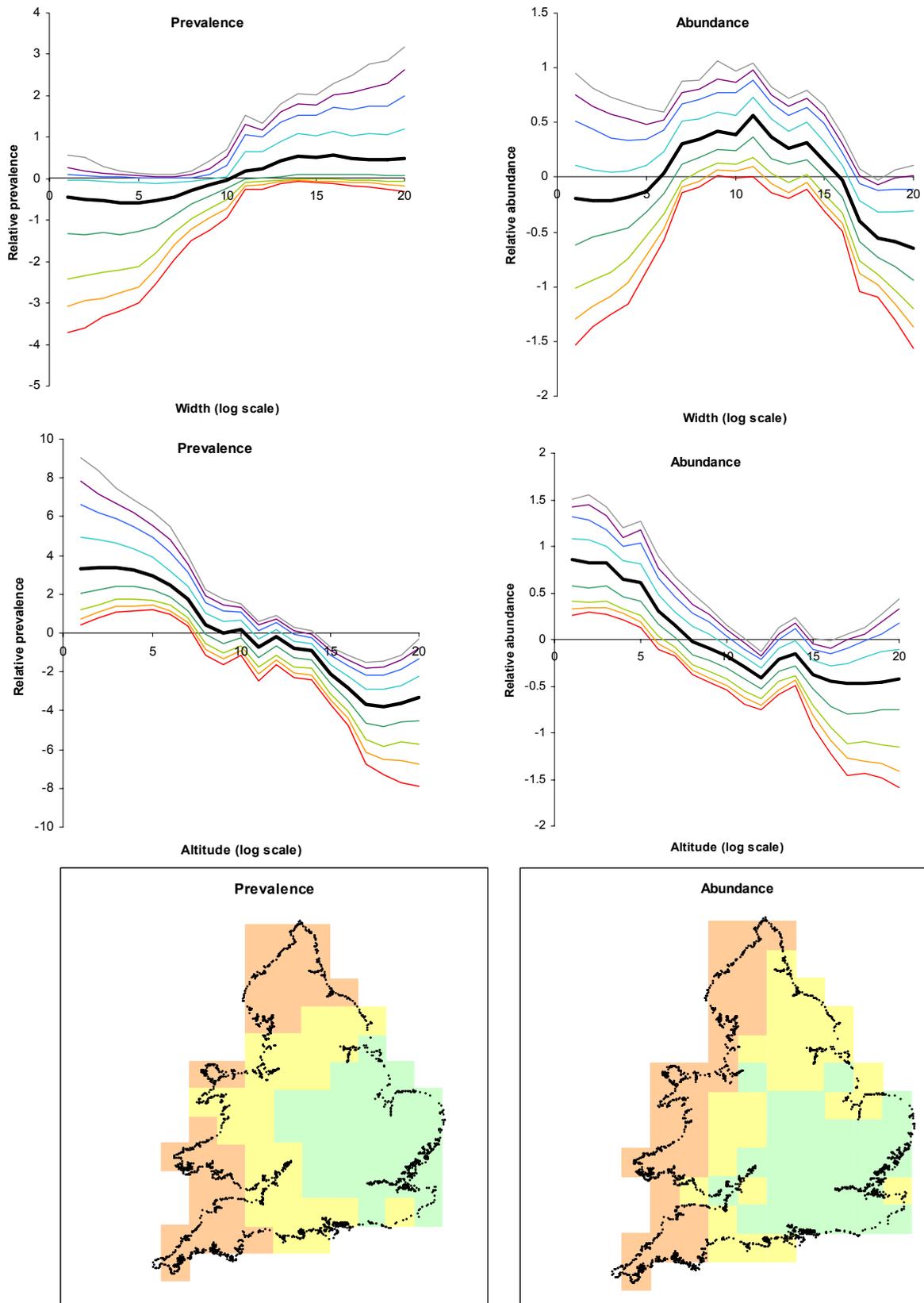


Figure A.5 Variation in abundance and prevalence of pike with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

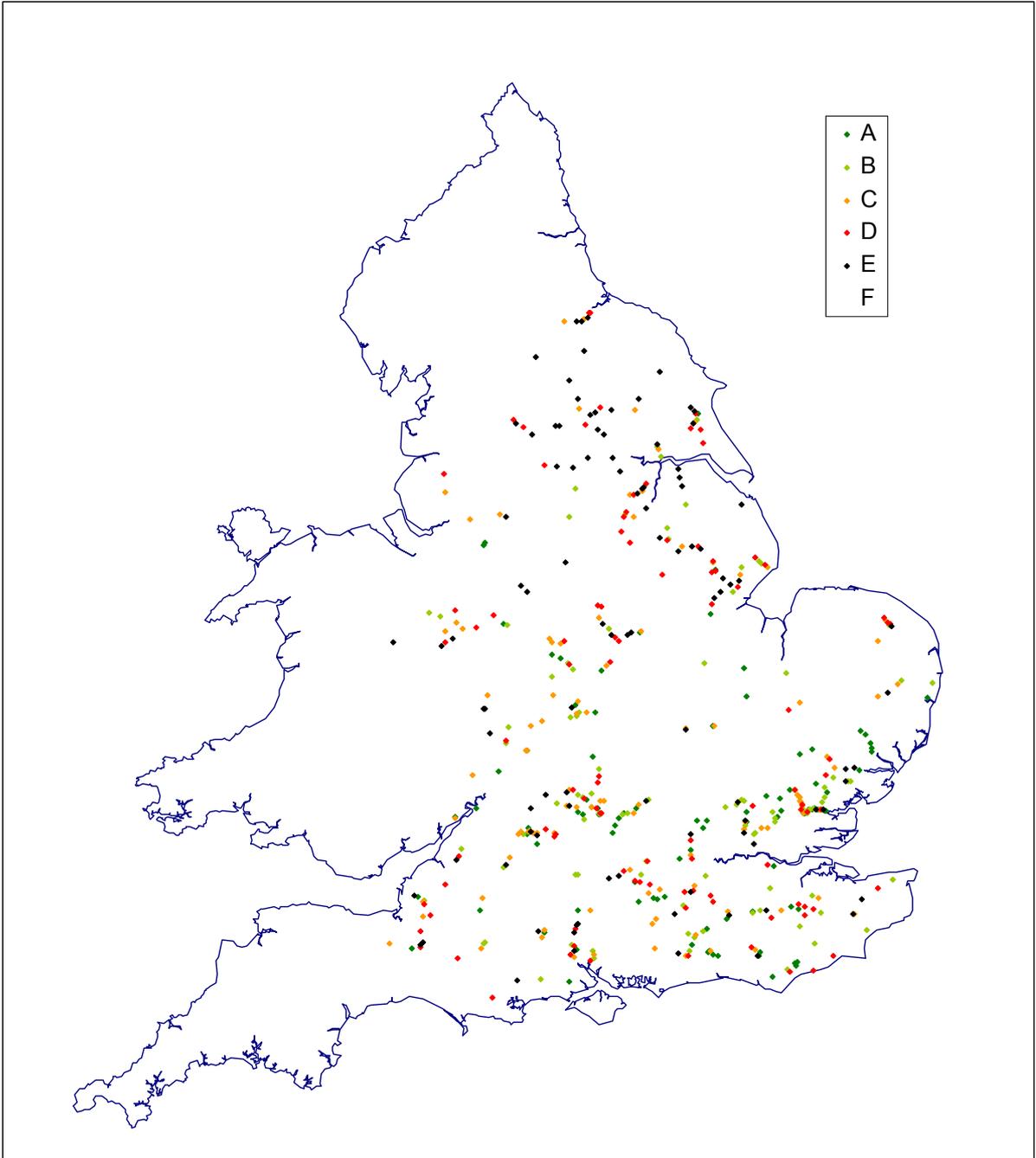


Figure A.6 Classification of pike abundance (absolute FCS) in 2004

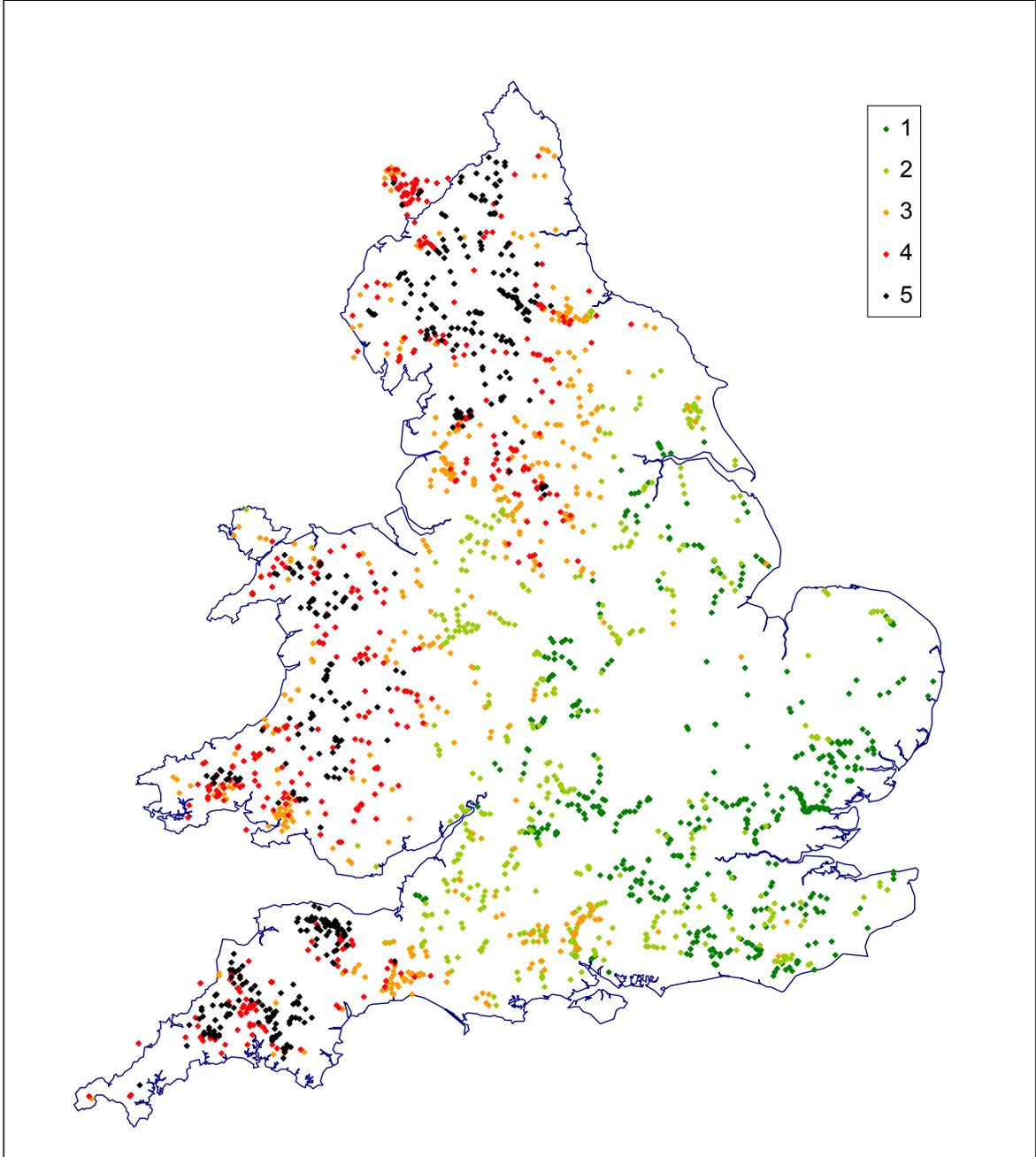


Figure A.7 Expected abundance (=habitat quality) for pike
Note: 1 (green) is high, 5 (black) is poor.

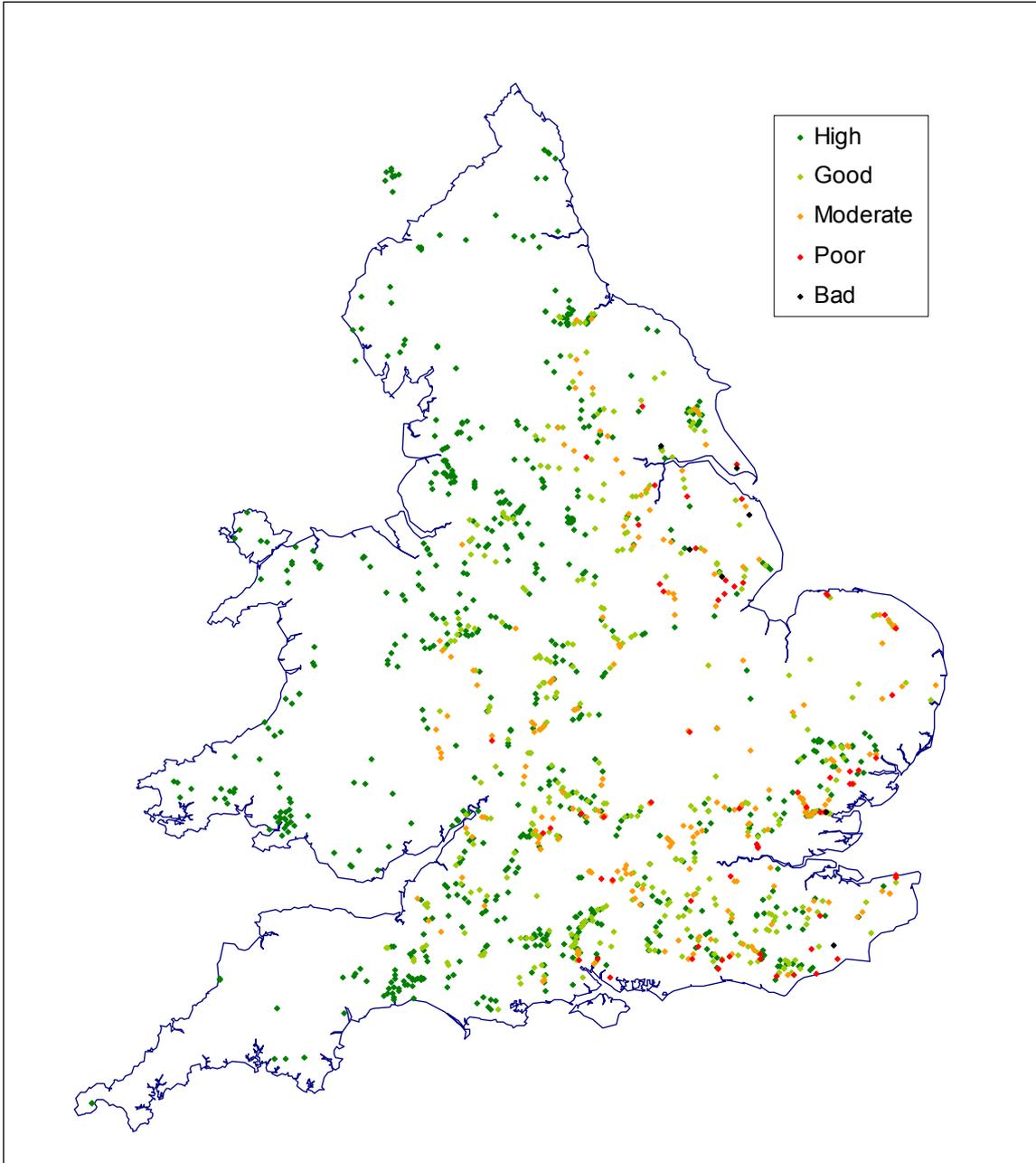


Figure A.8 Observed:expected ratio for pike abundance (relative FCS) in 2004

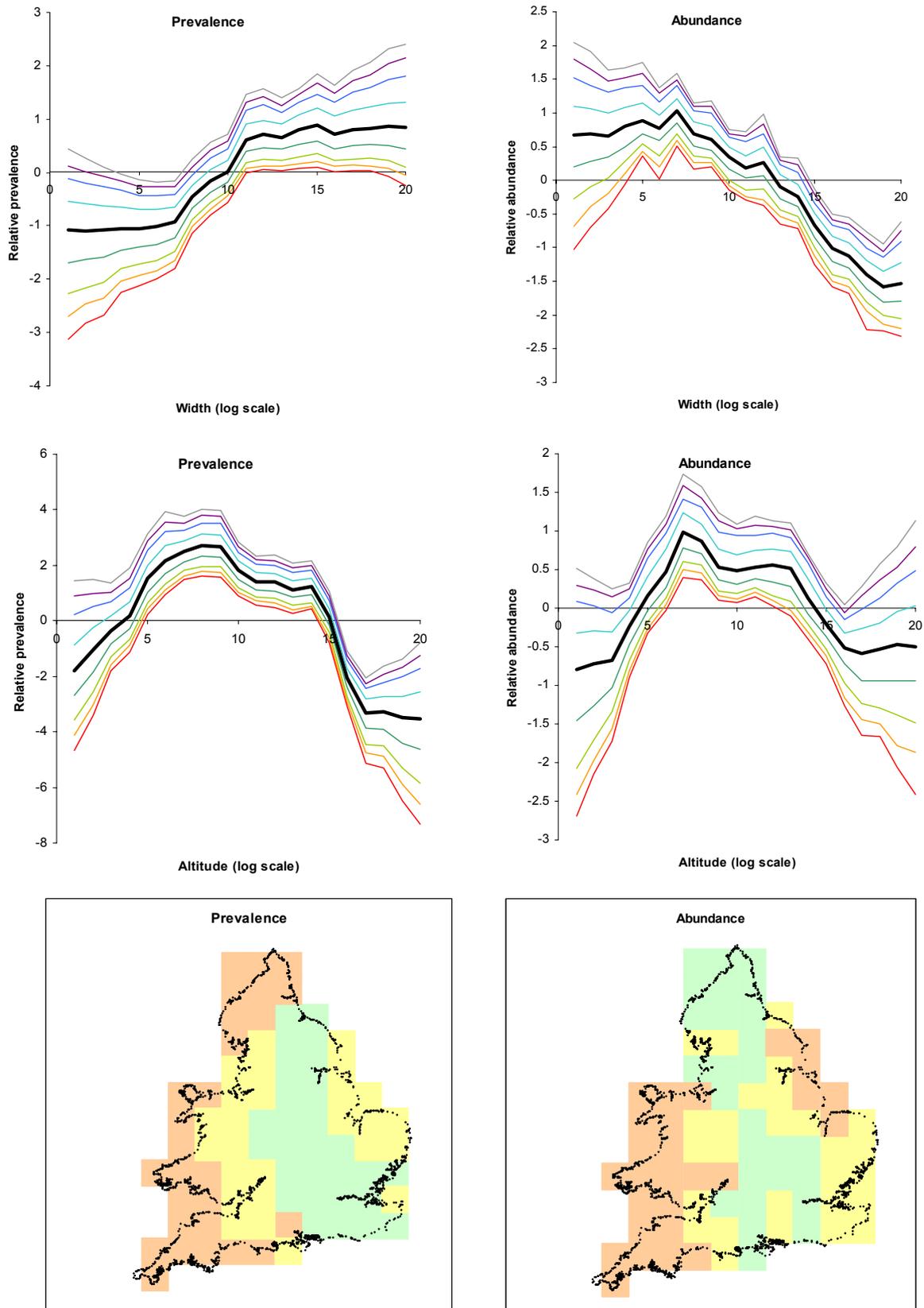


Figure A.1 Variation in abundance and prevalence of chub with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

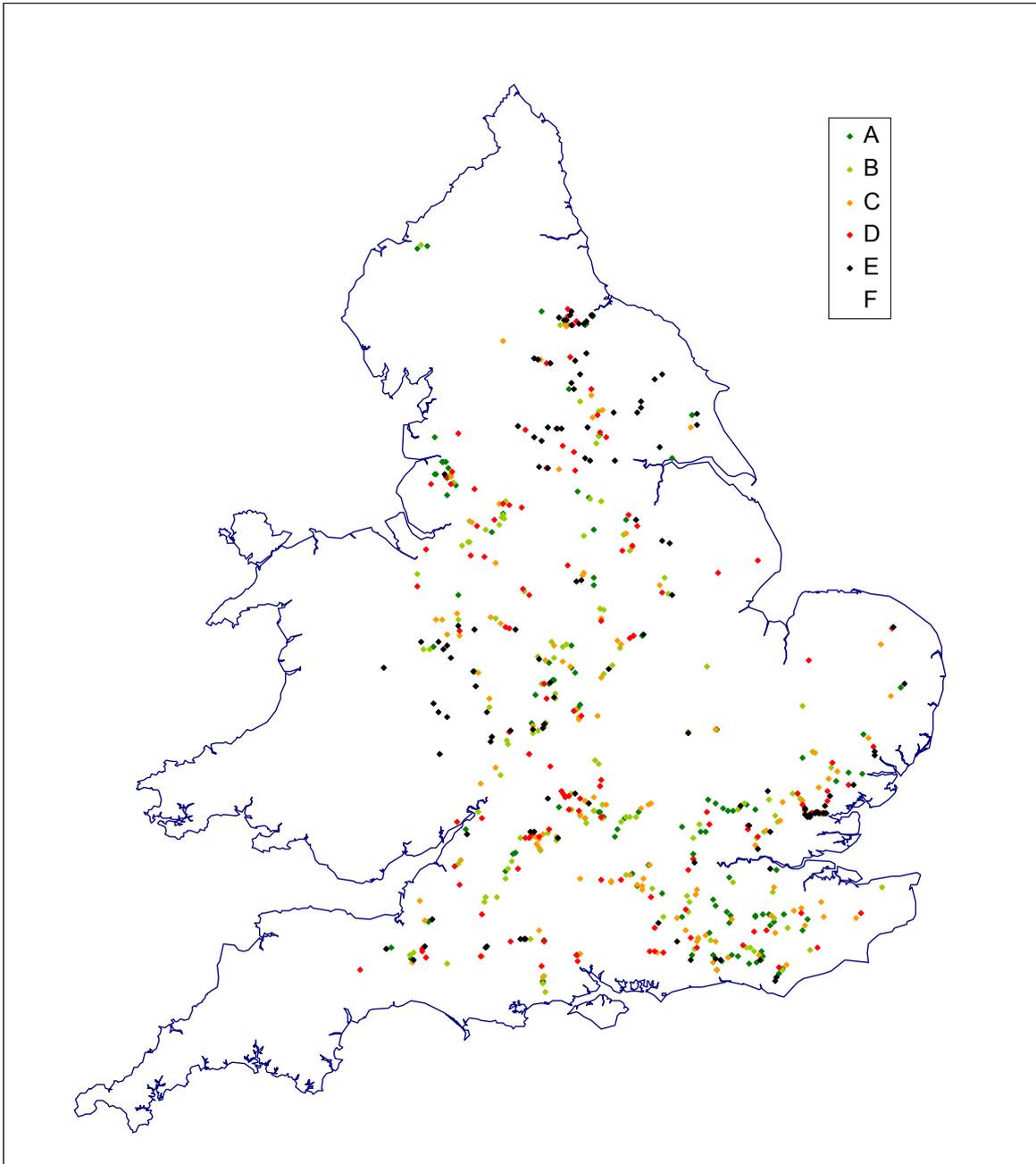


Figure A.10 Classification of chub abundance (absolute FCS) in 2004

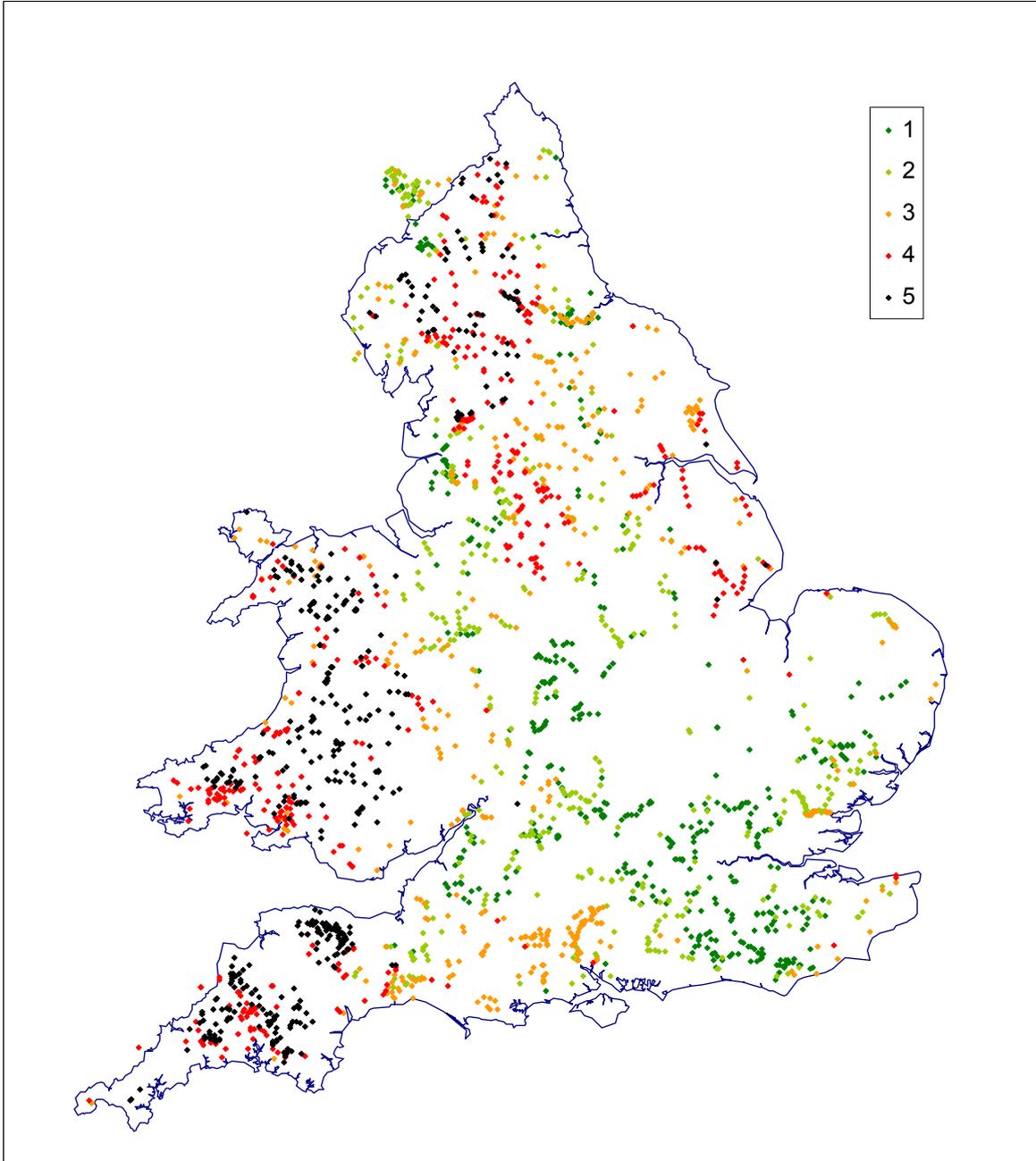


Figure A.11 Expected abundance (=habitat quality) for chub
Note: 1 (green) is high, 5 (black) is poor.

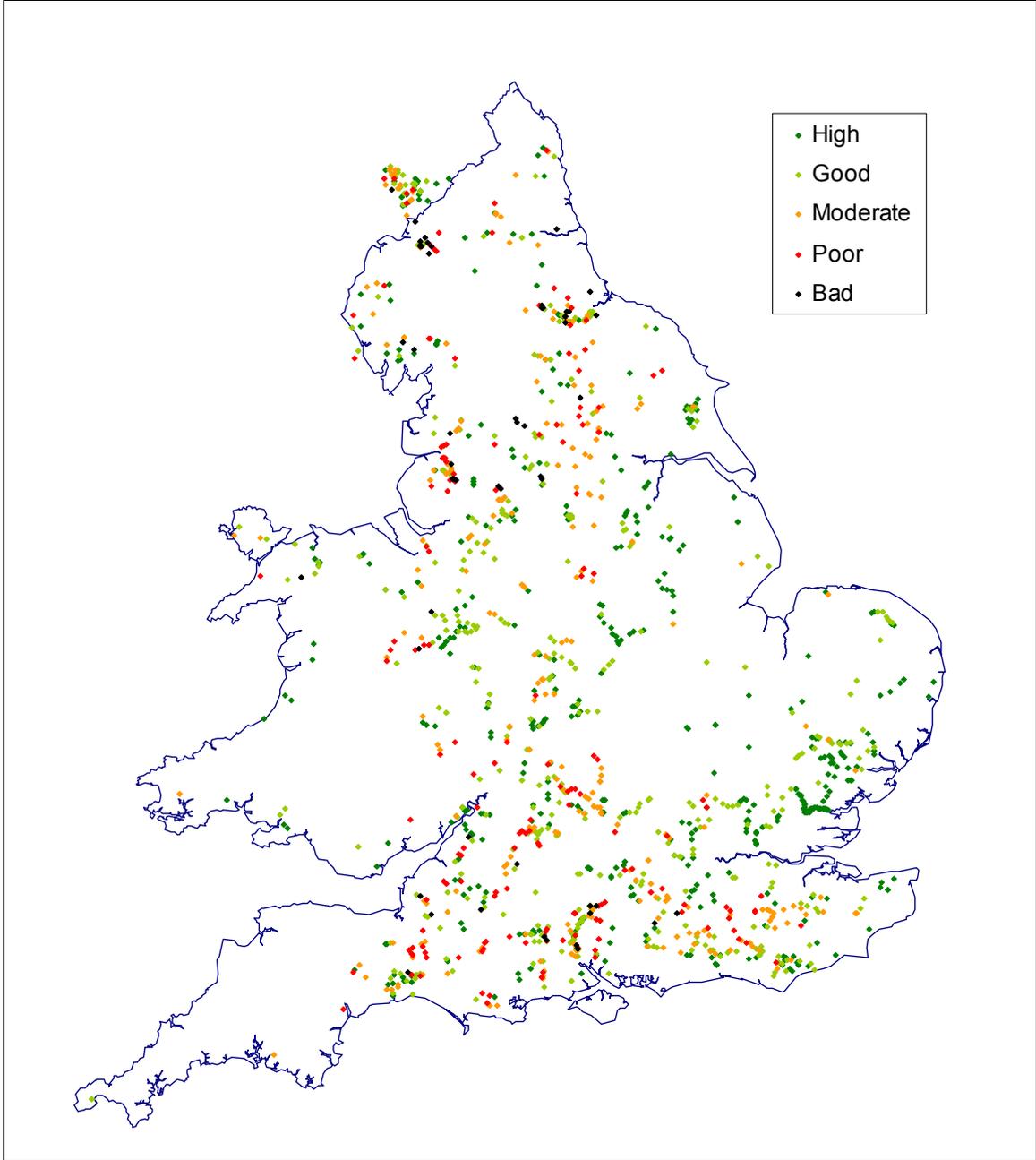


Figure A.12 Observed:expected ratio for chub abundance (relative FCS) in 2004

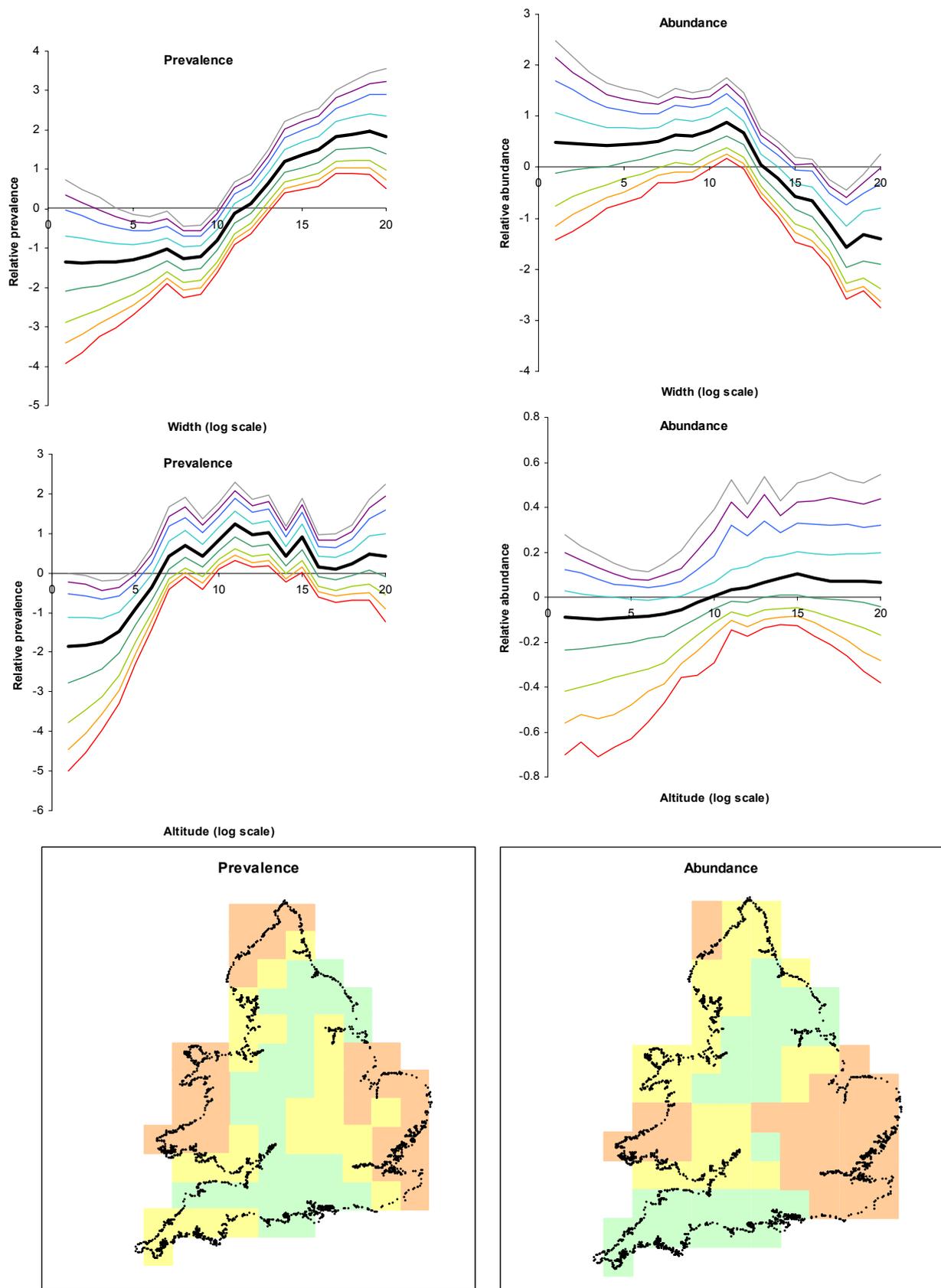


Figure A.13 Variation in abundance and prevalence of grayling with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

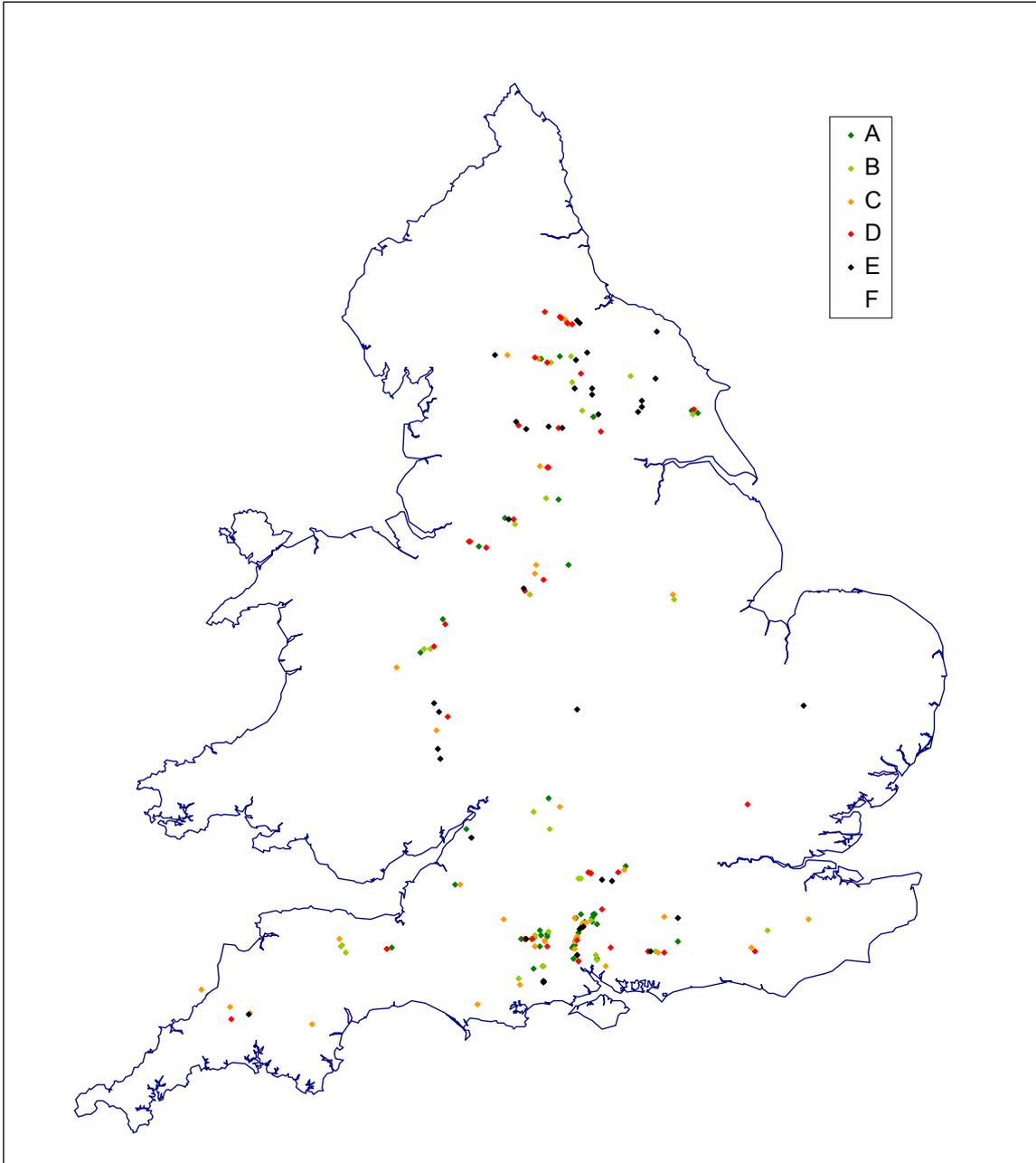


Figure A.14 Classification of grayling abundance (absolute FCS) in 2004

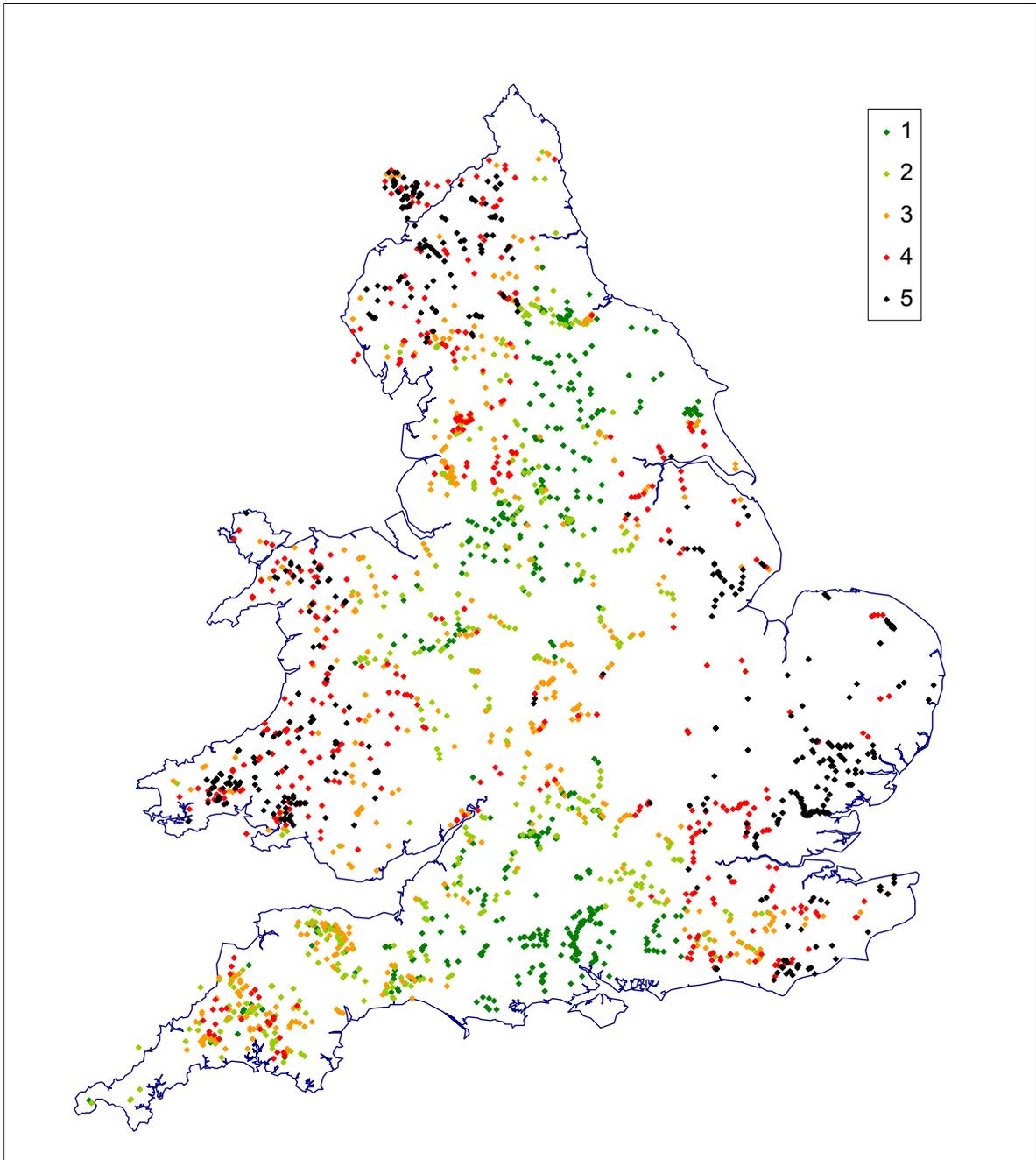


Figure A.15 Expected abundance (=habitat quality) for grayling
Note: 1 (green) is high, 5 (black) is poor.

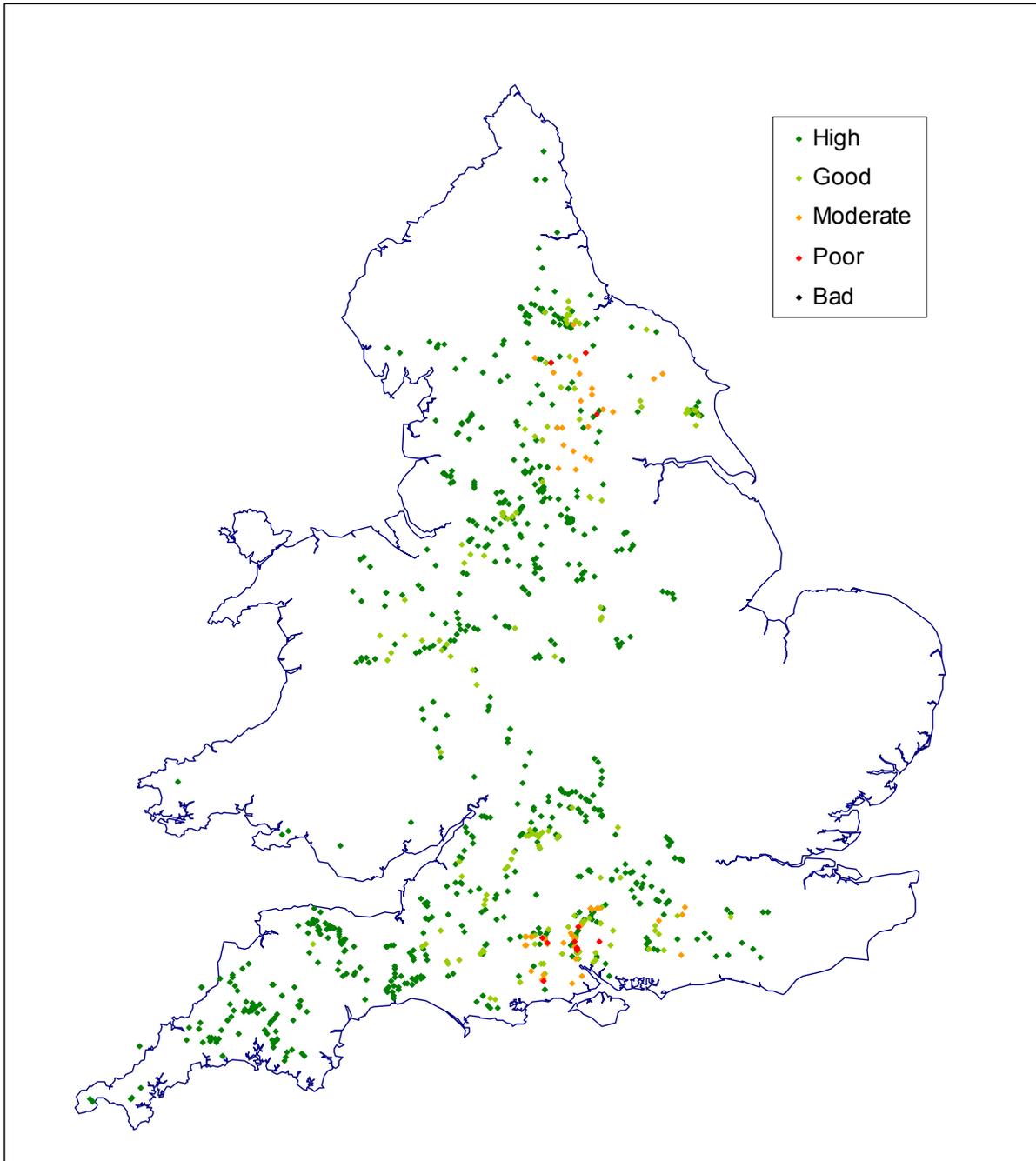


Figure A.16 Observed:expected ratio for grayling abundance (relative FCS) in 2004

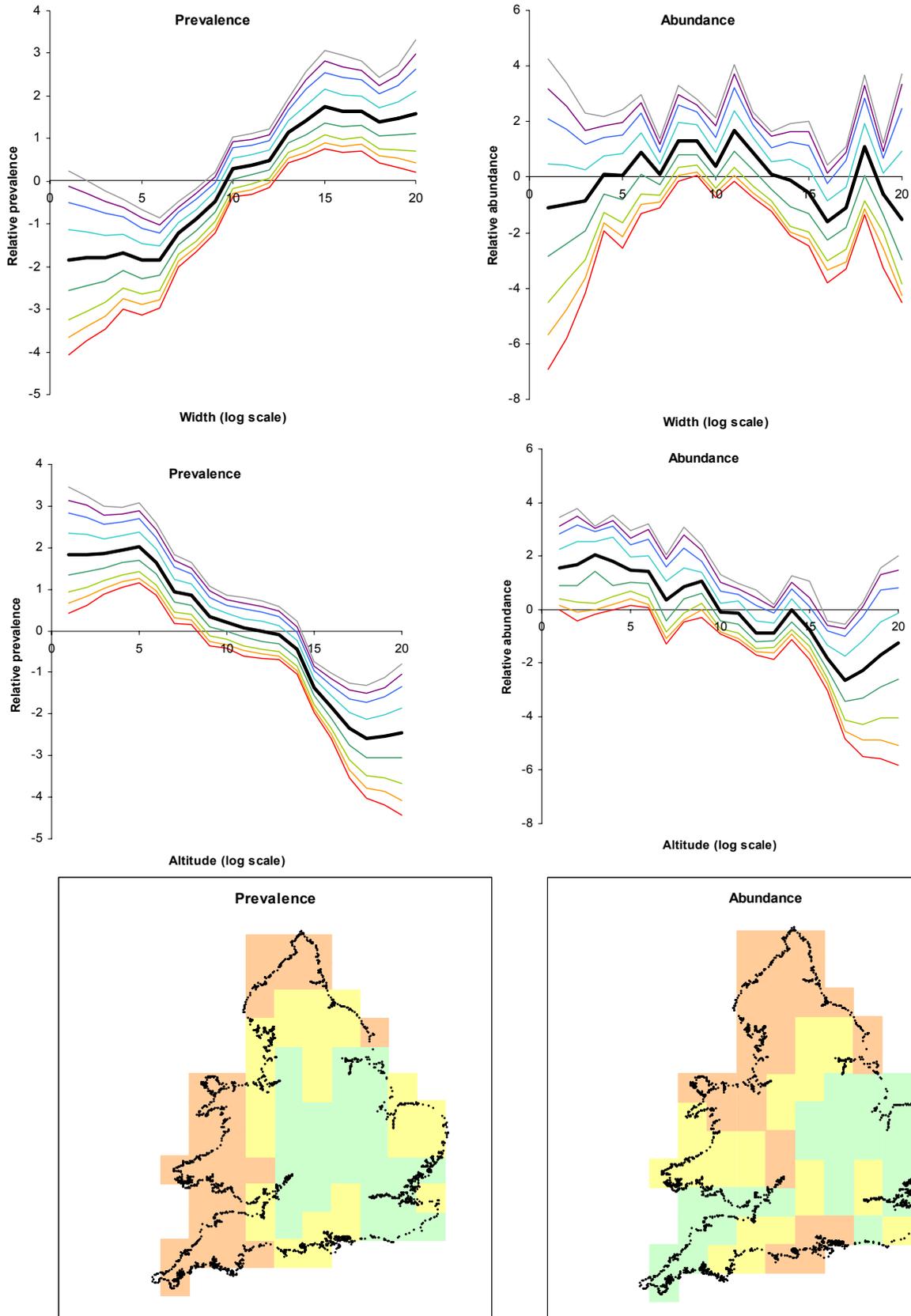


Figure A.17 Variation in abundance and prevalence of roach with width, altitude and geographic location

Note: For the explanatory variables, values of 1, 5, 10, 15 and 20 correspond to altitudes of 0m, 3m, 20m, 96m and 443m, and widths of 0.5m, 1.4m, 4.7m, 15.7m and 53.7m.

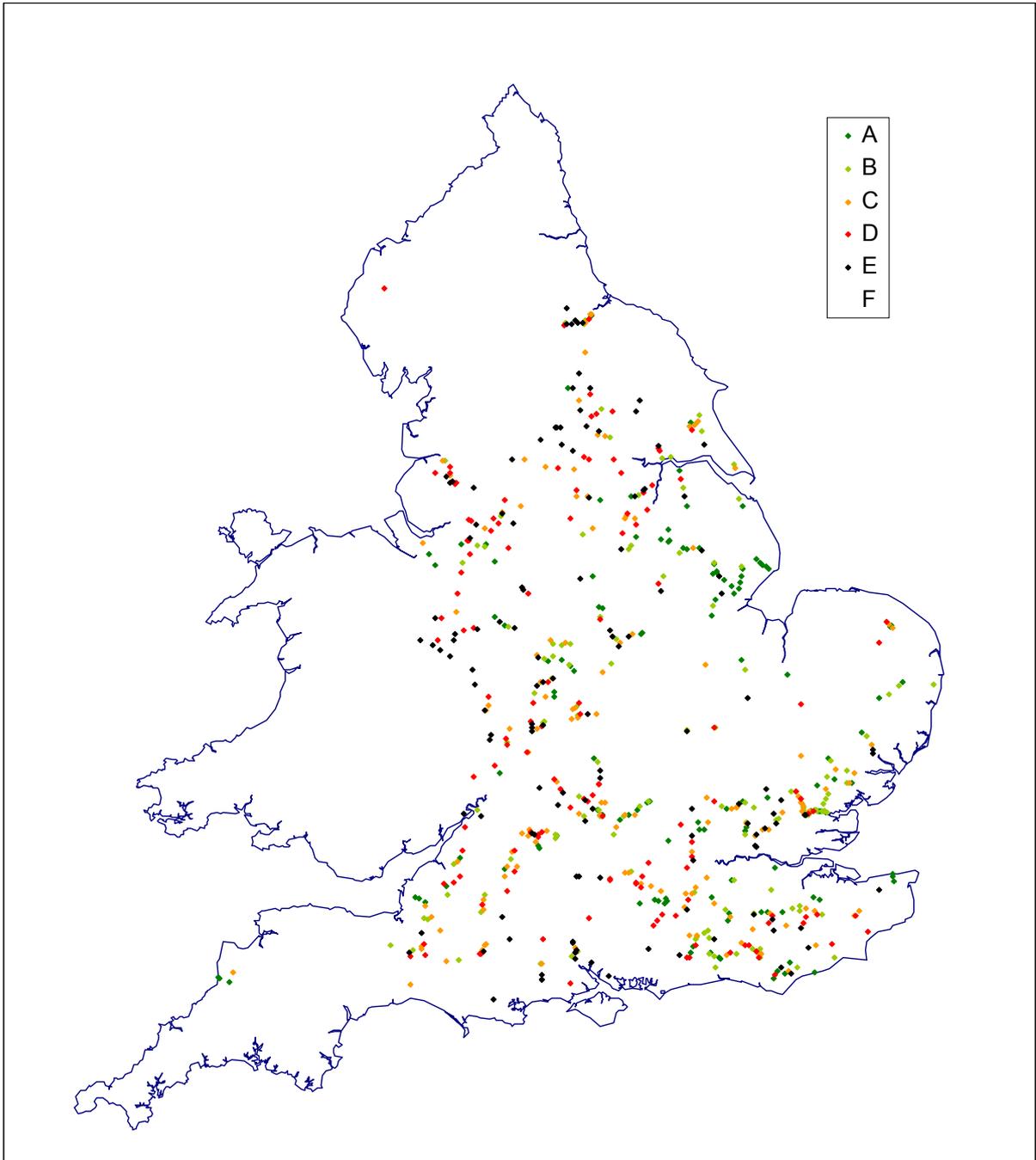


Figure A.18 Classification of roach abundance (absolute FCS) in 2004

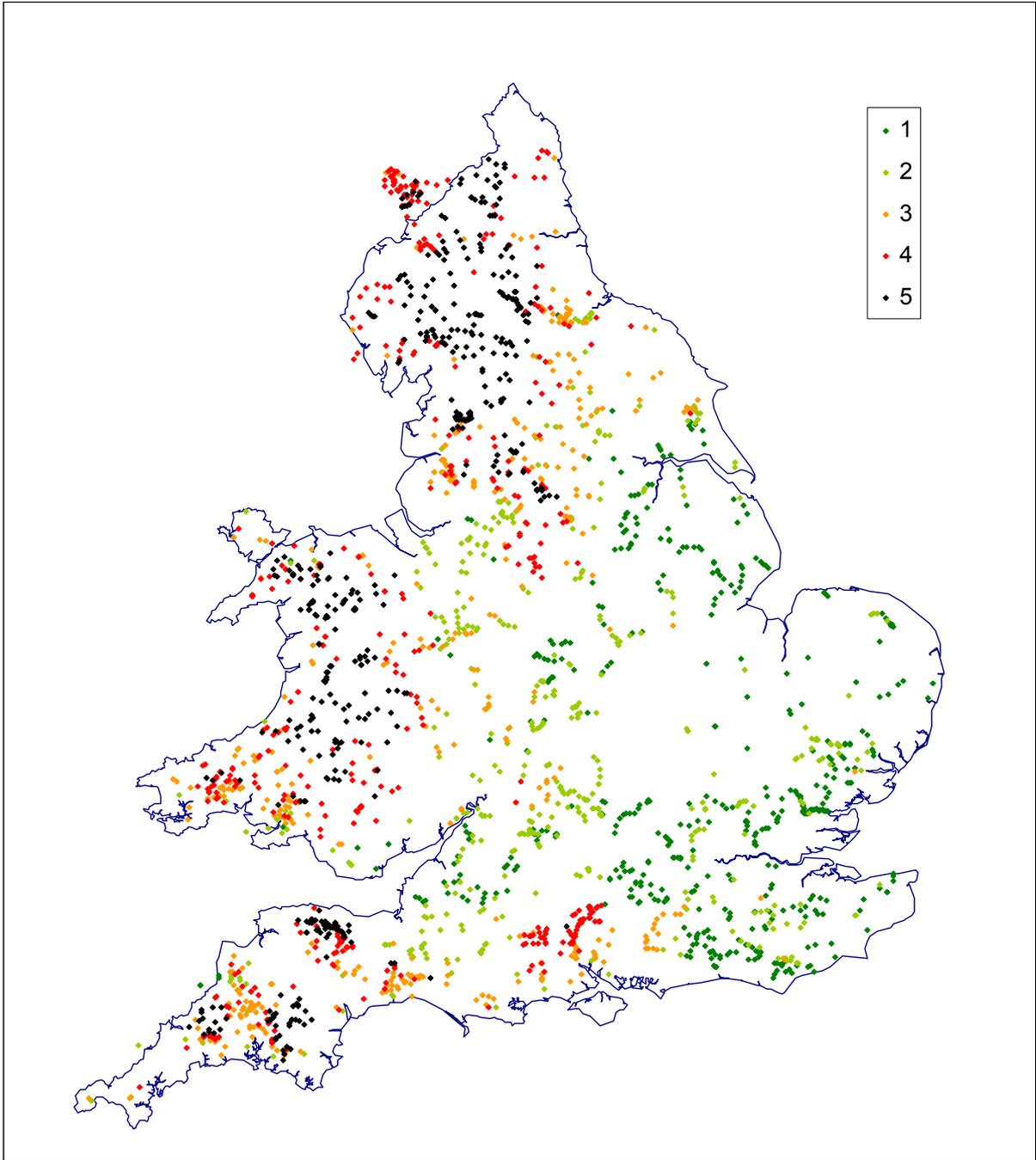


Figure A.19 Expected abundance (=habitat quality) for roach
Note: 1 (green) is high, 5 (black) is poor.

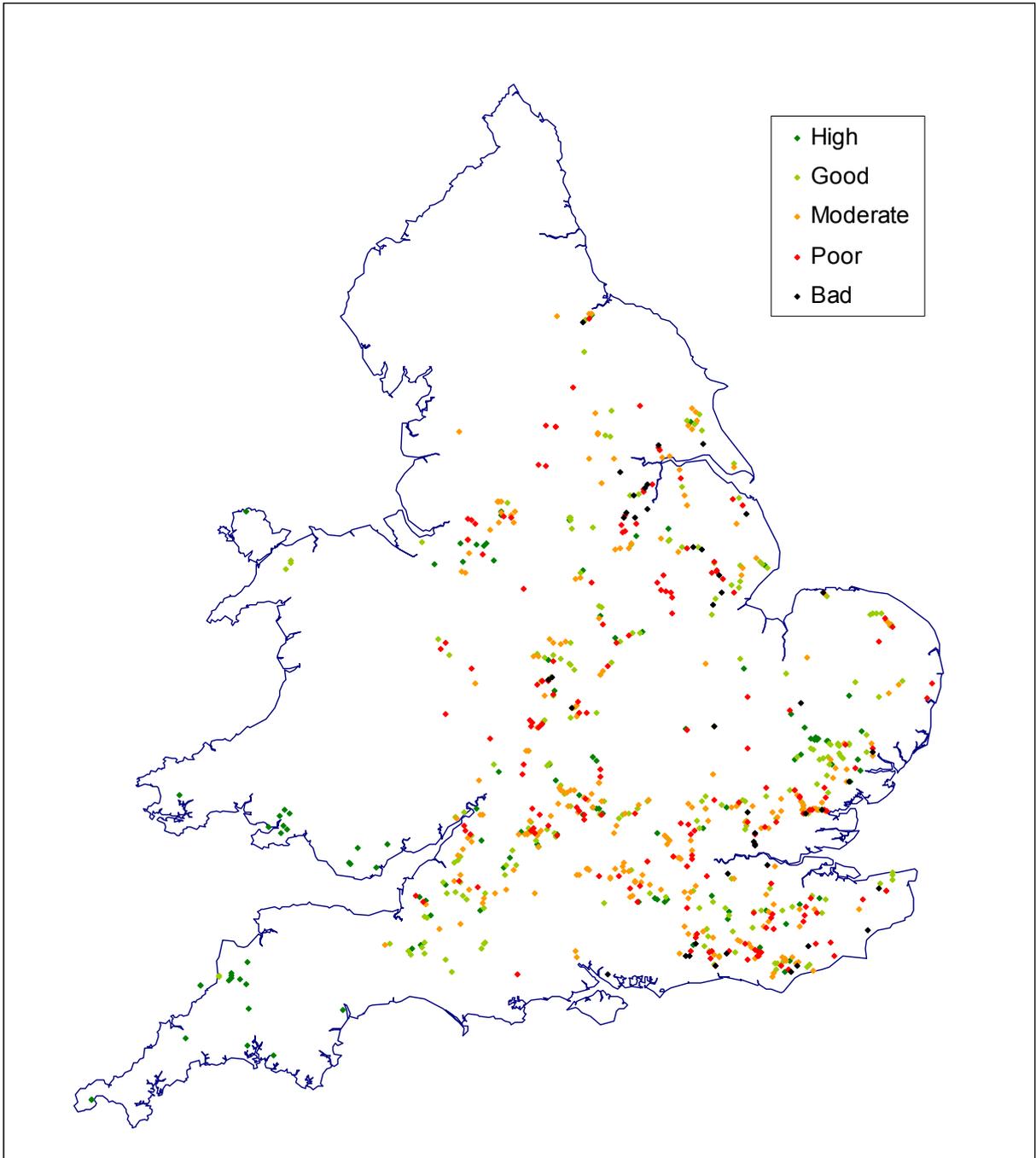


Figure A.20 Observed:expected ratio for roach abundance (relative FCS) in 2004

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