

Limitation and Regulation of Ecological Populations: a Meta-analysis of *Tipula paludosa* Field Data

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Abstract. Whether the size of an animal population is environmentally limited or regulated by density dependent negative feedback mechanisms is of ecological interest. Proponents of limitation theory have issued a set of specific challenges which are addressed in this paper using field data for the insect *Tipula paludosa*. This species is known to be subject to population crashes caused by adverse environmental conditions and assumed to be limited. We re-examine published data in support of this hypothesis and show that there is also evidence of negative feedback between generations. Meta-analyses of annual count data from individual fields, and regional surveys provide further evidence of negative feedback and it is concluded that population regulation occurs at both local and regional scales. Evidence from other studies is used to propose that cannibalism is the causative mechanism. Since similar negative feedback responses were apparent under both normal and environmentally limiting conditions when populations crash, a single population model that could simulate the differing regional dynamics observed from the annual surveys was produced. We conclude that the range of annual fluctuations observed in *T. paludosa* populations is the outcome of both limiting and regulating processes, confirming from field observations that these are not exclusive mechanisms.

Key words: *Tipula paludosa*, population limitation, population regulation, population crash, cannibalism, time-discrete model

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1 Introduction

Determination of the mechanisms and factors that regulate fluctuations in animal numbers has long been of interest to ecologists. Early debates were between proponents of density-dependent processes [35,36,37] and those who proposed a greater influence for environmental factors [2,3,7,29,30,31]. Such was the intensity of feelings aroused by the dispute that Milne was still advocating his theory of natural control of insect populations (and decrying those of others) as late as 1984 (A. Milne, personal communication).

Echoes of this dispute continue today and recently Berryman [5] and White [45] have been debating whether populations are limited or regulated. It is White's [44] contention that exogenous variation in a resource constraint such as the availability of food is sufficient to explain population fluctuations whereas Berryman et al. [6] conclude that regulation does exist but that it is an emergent property of particular ecological structures rather than an "a priori fact of life".

The criticism of regulation theory by White [45] is built from empirical evidence that natural populations are not regulated; rather they are limited by the capacity of the environment to support them - with a particular focus on food supply. In his paper, he issues a range of challenges to advocates of regulation theory. Amongst these are to provide evidence: (i) that a population can be regulated below the limits set by its food; (ii) that there is unambiguous experimental and observational evidence of identified mortality factors operating through negative feedback, and (iii) to refute that populations are limited by the availability of food.

In order to address these questions we consider the dynamics of the tipulid species *Tipula paludosa* Mg. The larvae of this species feed on grasses and clovers and are commonly found in agricultural land. Recorded populations in excess of $6 \cdot 10^6 \text{ ha}^{-1}$ have been observed [8], although most populations are considerably smaller than this. Although on occasion feeding by this species can destroy a sward and, hence, eliminate its food supply, this is comparatively rare [11]. In general it is a species that rarely exceeds the food resources available to it and thus contrasts with the examples cited by White [45] in support of his contention that populations are resource limited. In this sense, *T. paludosa* populations exist with excess food as the norm and so provide an example to refute the third challenge of White [45], and to test whether a population can be regulated below the limits set by food.

Larvae of *T. paludosa* are amongst the better studied of temperate soil insects because they are noted agricultural pests. For the purposes of this paper, we are particularly interested in the dynamics of *T. paludosa* populations. Blackshaw and Coll [11] provide a fuller review of the group's biology, impact and control.

Tipula paludosa is a commonly occurring pest of spring cereals and grassland. It is univoltine with adults flying in August/September when eggs are deposited. Larvae (commonly called "leatherjackets") emerge within 2-3 weeks and feed in the soil and at the soil surface throughout the winter, reaching a peak size in June. Fourth instar larvae enter a pre-pupal resting stage and adults emerge from pupal cases that have penetrated the soil surface.

A noted feature of this species is that dispersal is limited because females are gravid at

emergence, poor fliers, and mate and deposit 95% of their eggs within 12 hr of emergence; populations in adjacent fields can differ markedly [11].

Natural enemies of *T. paludosa* have received a lot of attention and it has been demonstrated that larval stages are subject to attack from predators, virus and bacterial pathogens, and parasitoids. However, there is no substantive evidence to date to suggest that these regulate populations other than as occasional and localised epizootics [11].

In contrast, there is a body of published work that postulates populations are limited by weather, especially rainfall. Researchers associated a 'crash' in leatherjacket numbers in 1959 with a dry August/September. In the subsequent study to test this hypothesis Milne et al. [32] exposed eggs and first instar larvae to different simulated rainfall regimes and concluded that "when August/September rainfall drops below 50% of normal, sharp decreases in populations of *Tipula paludosa* will certainly occur".

Further work in Milne's laboratory confirmed effects of soil water tension on egg development [28] and larval growth [27]. Desiccation of eggs and first instar larvae became accepted as the controlling factor: Mayor and Davies [26], for example, used a shortage of rainfall in September/October to explain population crashes observed in leatherjacket populations from annual surveys in south-west England. These results argued a case for density-independent limitation of *T. paludosa* and, incidentally, informed Milne's attitudes [29,30] to his debates with Nicholson [36] and others [e.g. 3] on competing theories of population control. Later studies in Northern Ireland were unable to show a link between population size and rainfall at egg/first instar stages but were able to associate rainfall [8] and temperature [12] at other times of the year with population fluctuations. This work broadened the hypothesis of environmental population limitation but did not challenge it. Since the 1960s, advice to farmers about the likelihood of crop damage caused by leatherjackets has been based on rainfall shortage being the main limiting factor.

However, closer examination of the data presented by Mayor and Davies [26] shows that in order to reach their conclusion about September/October rainfall limiting tipulid populations they omitted data from two out of six counties surveyed in the south-west of England [10]. More importantly, although population crashes did occur when rainfall fell to 50% or less of the long term average, this was only when numbers were high; at low population level declines did not occur and increases were observed (Fig. 1).

The different effects at low and high populations in the Mayor and Davies data [26] suggest that the relationship between rainfall and population changes may not be a simple density-independent function. Indeed, the fact that it operates at high population level rather than low is what would be expected from negative feedback. Plotting these data, from Fig. 3 [26] as annual counts with a time lag of one reinforces this proposition (Fig. 2). The existence of distinct temporal pattern in the data suggests that this population's dynamics do not arise solely as a result of environmental fluctuations which are essentially stochastic.

This re-assessment of these data suggests that *T. paludosa* populations are not necessarily limited by environmental conditions but may indeed be regulated in the sense of Berryman et al. [6]. In this paper we test this hypothesis through analyses of published and unpublished data and show that there is strong evidence for population regulation for this species that

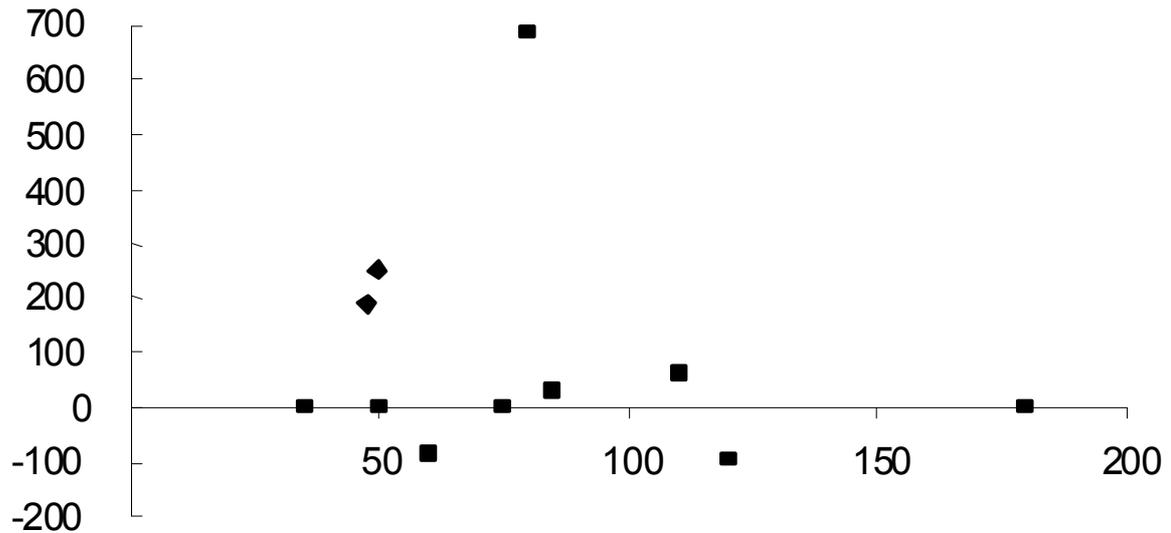


Figure 1: The relationship between the annual change in leatherjacket population size and the proportionate long term average rainfall for September/October in south-west England. Data from Fig. 3 of Mayor and Davies [26]. The diamonds show an increase in the population size observed in cases of low initial population density when average rainfall is at or below the 50% threshold defined by Milne et al. [32].

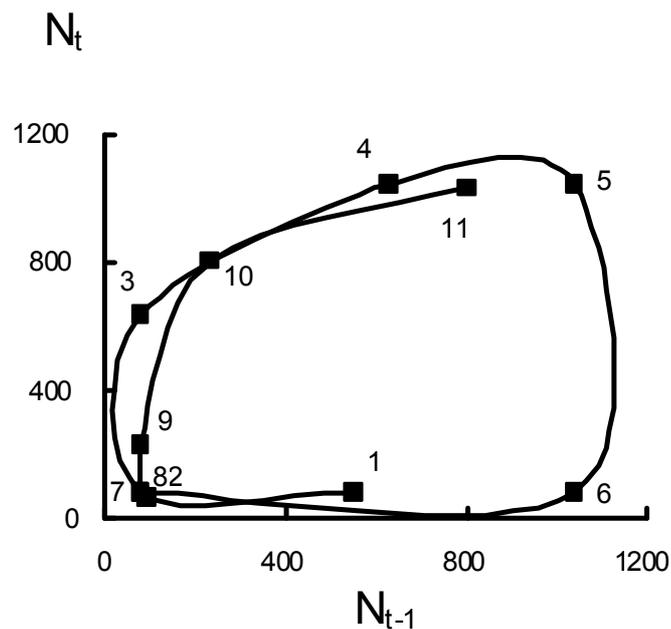


Figure 2: Phase trajectory of annual leatherjacket population ($\cdot 10^3$) changes in south-west England. Each point is a plot of the population in the current year (N_t) against the population in the previous year (N_{t-1}). The line connects points in chronological order with points numbered sequentially. Data from Fig. 3 of Mayor and Davies [26].

operates consistently irrespective of the limiting conditions. A further question is whether such regulatory effects are restricted or can be seen across different parts of *T. paludosa*'s range. We show that a general negative feedback relationship can provide the basis for the simulation of different regional dynamics. Finally, we postulate a behavioural mechanism that can explain these patterns.

2 Methods

2.1 Data

For several years, annual surveys of *T. paludosa* populations were made in grassland in many parts of the United Kingdom as an aid to the prediction of damage to spring cereals. The surveys comprised samples from individual fields and published data exist as annual mean counts for Northern Ireland from 1970 to 1988 [12], south-west England, separable into six counties, from 1963 to 1974 [26], and for northern England from 1948 to 1963 [16,43]. In addition, unpublished data were obtained for south-west Scotland from 1975 to 1994, and north-east Scotland for 17 years from 1987/88 to 2003/04 as individual field counts. Annual means were calculated for the Scottish data to provide count trajectories similar to the other surveys.

Not all these data are directly comparable because of differences in sampling methods. The data from northern England were collected using an expellant mixture (“St Ives Exterminator”) of unknown and variable efficiency, whereas those from Northern Ireland and south-west England were based on wet-sieving 10 cm diameter soil cores. The Scottish surveys used 5 cm soil cores with leatherjackets extracted in a modified Tullgren-type facility that provides equivalent efficiency compared with wet-sieving [13]. For the purposes of this analysis we assume that all data except those for northern England provide absolute estimates of annual population levels (Fig. 3).

2.2 Statistical analysis

With any time series of annual population counts there is the possibility of a Type 1 error resulting in a false conclusion of density dependence [19]. This is particularly true for single datasets. We used a subset of the south-west Scotland database consisting of annual count data from 79 individual fields where there had been continuous sampling for a minimum of 10 (maximum of 20) years, and applied the test described by Pollard et al. [39]. The null hypothesis of this test is that data in a time series are not significantly different from a random walk. The estimated probability of hypothesis rejection was calculated for each time series using 1000 Monte Carlo runs.

The published and unpublished annual survey mean counts were normalised as abundances relative to the regional mean from each source time series to allow for the different sampling method reported by Cohen [16] and White [43]. The annual per capita increase was

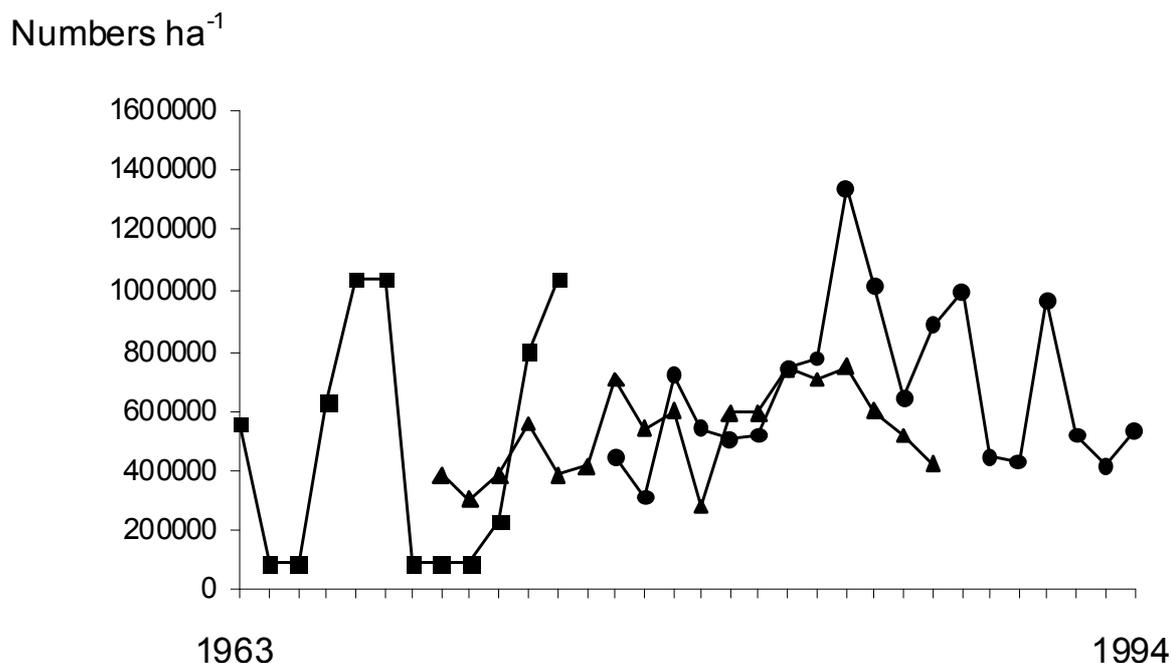


Figure 3: Observed mean annual leatherjacket population trajectories for Northern Ireland (triangles), south-west England (squares) and south-west Scotland (circles).

calculated, and, for all data except north-east Scotland, regressed against the relative abundance for four time lags. A general population model was then developed, verified against the trajectories of the source data, and validated using the data for north-east Scotland.

3 Results

The Pollard test [39] null hypothesis was rejected for 66 out of the 79 tests (83.5 %) showing that at the scale of individual field counts there is evidence of internal pattern in the population time series.

The regressions of $\log(\text{per capita increase} + 1)$ against $\log(\text{relative abundance})$ yielded r^2 values of 0.343, 0.177, 0.016 and 0.047 for time lags of 1 to 4 respectively. The slopes of the regressions for the first two time lags were compared; both were negative with values of -0.672 and -0.425 respectively for time lags of 1 and 2. A multiple regression using population counts at the two time lags resulted in an r^2 value of 0.413. Further analysis lies outside the scope of this paper and subsequent modelling was restricted to a time lag of one.

The per capita rate of increase/ relative abundance data showed strong evidence of negative feedback (see Fig. 4). However it was apparent that the data points in Fig. 4 separated into two discernable relationships so they were analysed independently. The resultant regressions were $\log(\text{per capita increase} + 1) = -0.0252 - 0.8135 \cdot \log(\text{relative abundance})$ ($r^2 = 0.688$), and $\log(\text{per capita increase} + 1) = -2.046 - 0.9236 \cdot \log(\text{relative abundance})$

($r^2 = 0.959$) for the upper and lower data points respectively. There was no significant difference between the slopes ($t = 1.258$, $P > 0.05$). A weighted average slope of 0.822 was calculated.

These two regression lines are shown in Fig. 4 and demonstrate similar density-dependent responses under different conditions. The lower (and smaller) data set consists of growth rates where there is a rapid population decline or 'crash' in the sense of Milne et al. [32]. This set of points therefore represent outcomes when the population has been environmentally limited. The upper (and larger) data set are outcomes when the population is not limited.

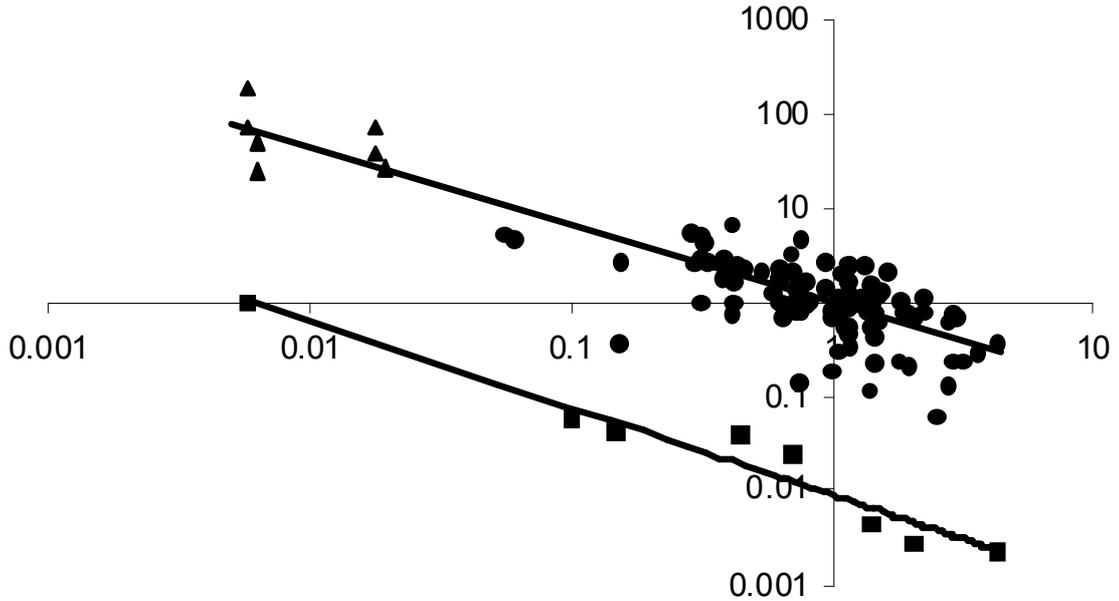


Figure 4: Per capita growth rate and relative abundance for leatherjacket survey data. Data shown are for northern England, Northern Ireland, six counties of south-west England and south-west Scotland. Two separate but parallel relationships are apparent; lower points (squares) concur with population crashes and their associated resurgences (triangles) form the extreme of the relationship that occurs under normal rainfall conditions (circles).

A closer look at the results of the linear regression analysis readily leads to a population dynamics model. Indeed, neglecting fluctuations (which can be taken into account later by means of including environmental noise, see below) it can be written as follows:

$$\log \left(\frac{\Delta N_t}{N_t} + 1 \right) = \alpha - \beta \log \frac{N_t}{\langle N \rangle}, \quad (3.1)$$

where N_t is the average population size at a given year, $\Delta N_t = N_{t+1} - N_t$ is the increase in number over the consequent season, $\langle N \rangle$ is the mean population size over the duration of any particular regional survey time series, α is the intercept and $-\beta$ is the slope (here, for convenience, we have explicitly taken into account that the regression line is descending).

After standard transformations, Eqn. (3.1) turns into

$$\Delta N_t = N_t \left(10^\alpha \left[\frac{N_t}{\langle N \rangle} \right]^{-\beta} - 1 \right), \quad (3.2)$$

which can be written as

$$\Delta N_t = N_t^{1-\beta} \left(K - N_t^\beta \right), \quad (3.3)$$

where parameter $K = 10^\alpha \langle N \rangle^\beta$ is analogous to the population carrying capacity so that the population size remains unchanged between years t and $t + 1$ if $N_t = K^{1/\beta}$.

In a general case, time-discrete models of population dynamics can exhibit rather complicated behaviour such as multi-point cycles and chaos, cf. [21]. However, the properties of the model (3.3) appear to be relatively simple. Indeed, $N_t = \bar{N} = K^{1/\beta}$ is the only steady state of the system. By means of linearizing Eqn. (3.2) in the vicinity of the steady state, it is readily seen that the difference between the actual population size and its steady state value changes with time as

$$n_{t+1} = \Lambda n_t,$$

where $\Lambda = 1 - \beta$ and $n_t = N_t - \bar{N}$ is the deviation of the population size at year t from the steady state value. The steady state is stable for $|\Lambda| < 1$ and unstable for $|\Lambda| > 1$. Restricting our analysis to positive β (which corresponds to negative feedback), it is not difficult to see that the steady state is stable with monotonic damping for $0 < \beta < 1$ and stable with oscillatory damping for $1 < \beta < 2$. For $\beta = 2$ the model exhibits two-point periodic oscillations, and for $\beta > 2$ the system becomes unstable showing oscillations of infinitely increasing amplitude. Note that, since the value of β estimated from the *T. paludosa* field data is between 0 and 1, the steady state appears to be stable in the whole relevant parameter range.

However, models (3.2) or (3.3) do not yet account for any stochastic fluctuations. The importance of stochasticity or noise in field data is obvious: in the absence of stochastic variation, all the points in Fig. 4 would lie on a certain curve (e.g. straight line) rather than them creating a ‘‘cloud’’ around this curve.

There are different ways to include stochasticity into an otherwise deterministic model of population dynamics. One of them is to assume that noise affects the value of some parameters [46]. There are arguments for assigning this variability to any or all of these parameters, and this raises interesting questions about possible resultant differences in model behaviour. In the current study we choose to change α to $\alpha + r$ where r is a certain stochastic factor or an error term, $\langle r \rangle = 0$ because we can assume that β is constant across different values of α (Fig. 4). From Eqn. (3.3), we then arrive at

$$\Delta N_t = N_t \left(10^{\alpha+r} \left[\frac{N_t}{\langle N \rangle} \right]^{-\beta} - 1 \right). \quad (3.4)$$

This general model provides the basis for simulating the different regional dynamics of *T. paludosa* (e.g. those shown in Fig. 3) through varying the mean population and applying a probability function that reflects the frequency with which catastrophic environmental conditions occur; when conditions are reasonable $\alpha = -0.0252$, and when harsh, $\alpha = -2.046$ with $\beta = 0.822$. Note that in order for the model to deliver reasonable results it is necessary to calculate the long term mean population without those annual counts following population crashes [*sensu* 32]; this is subjective but such occasions are relatively easy to determine. Typical simulation trajectories, derived from initial populations, are presented for three regions in Fig. 5 to verify the model. Data for north-east Scotland were used to validate the model (Fig. 6).

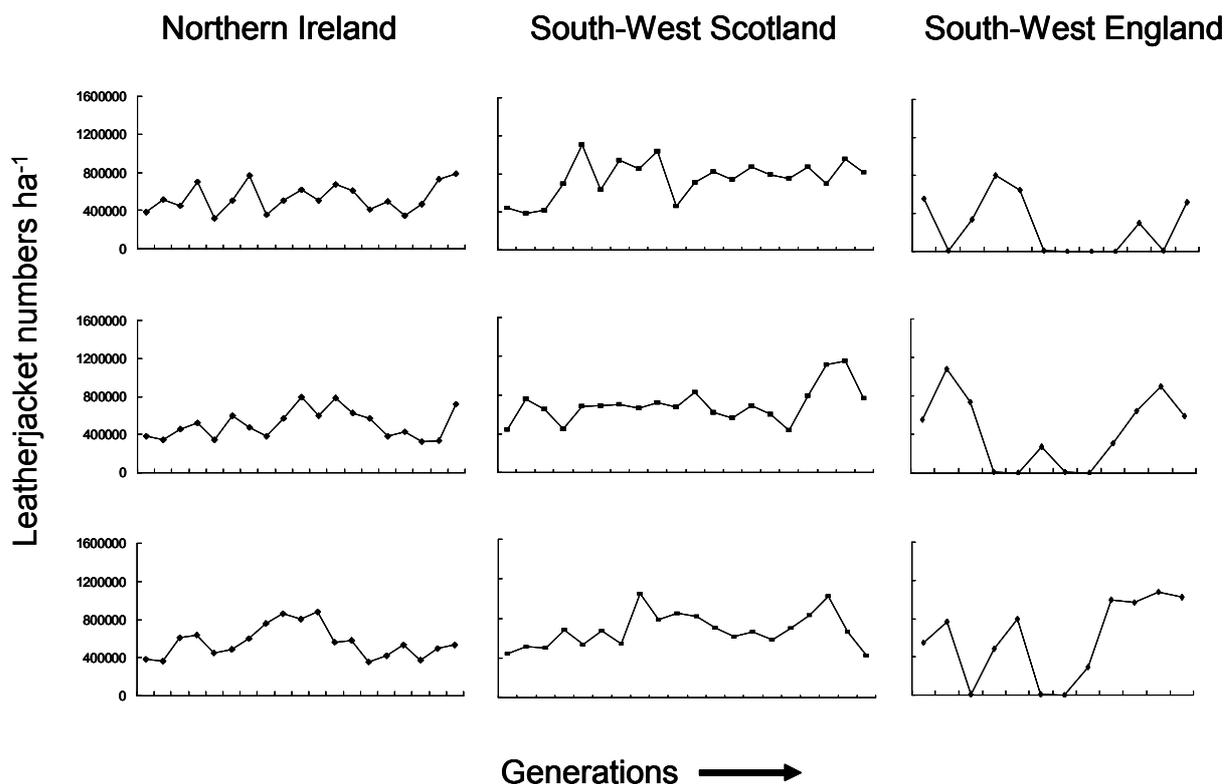


Figure 5: Verification of the simulation model (Equation 5) for three regions of the UK. Parameters used are: $\beta = -0.822$, $\alpha_1 = -0.0252$, $\alpha_2 = -2$. The probability of switching between α_1 and α_2 in any single simulated year was 0, 0 and 0.4167 for Northern Ireland, south-west Scotland and south-west England respectively, and their mean populations were calculated as 522500, 669251 and 766000 ha⁻¹. The latter value excluded the five out of 12 (0.4167) occasions when population crashes were considered to have occurred. The stochastic factor r was randomly selected each generation from a uniform distribution with a maximum $\pm 22.2\%$. Output graphs start with the observed population at the first survey date and show three typical trajectories for comparison with Fig 3.

4 Discussion

4.1 Evidence for population regulation

The Pollard test [39] is a commonly used analysis when trying to determine if populations are limited by density dependent processes, or are alternatively limited by independent factors such as food or weather. Each of the individual field population counts analysed in this way is an estimated mean, potentially subject to the sort of census error described by Freckleton et al. [19]. The probability of attaining 66 outcomes that reject the random walk hypothesis (at $P < 0.05\%$) is exceedingly small and so we conclude that there is a density-dependent effect present in these data.

The annual survey data are means of means. Nevertheless, there is still a strong relationship manifest between the annual per capita rate of population growth and abundance of the population at scales larger than the field (Fig. 4), which implies that there is a significant correlation between the counts in individual fields. Furthermore, the same relationship operates even when there are perceptible population 'crashes' [sensu 32], explaining the apparent anomalies in the data of Mayor and Davies [26] shown in Fig. 1, and the trajectory of these annual census data (Fig 2). Therefore, we conclude that population regulation is apparent at both local (field) and regional population scales.

4.2 Simulation model

The determination of a negative feedback enabled the construction of a population dynamics model. The linear relationship between $\log(\text{per capita increase} + 1)$ and $\log(\text{relative abundance})$ shown by the data (Fig.4) results in a growth model, cf. Eqs. (3.1) to (3.3). The purpose of building this model was to see whether a single model could simulate the different regional dynamics (Fig. 3) and thus provide evidence that the observed negative feedback applied across different regions in a general sense. Clearly setting the carrying capacity of the model to the long term mean of the survey counts (noting that where population crashes occur these data points are omitted from this calculation) will drive its dynamics to return a similar simulation mean. Some stochastic variation is essential to get the model to fluctuate at these rates of population growth [25] but the setting of the stochastic term is subjective. The important point here is that it is possible to approximate the boundaries of all the data (Figs 5 and 6) using a single value, suggesting ecological coherence to the model.

The model was somewhat less good at simulating the extremes of observed data. In particular, simulated crashes tended to result in lower populations than with observed data (Fig. 5, south-west England). We also note that using the selected parameters the model is incapable of delivering the highest observed survey mean population count (1.4m ha^{-1}) from north-east Scotland (Fig. 6). Despite these limitations, the model did provide a reasonable simulation when tested, see Fig. 6, reflecting the fact that the negative feedback in the data is more likely to be a general property of *T. paludosa* dynamics rather than just an occasional or regional phenomenon.

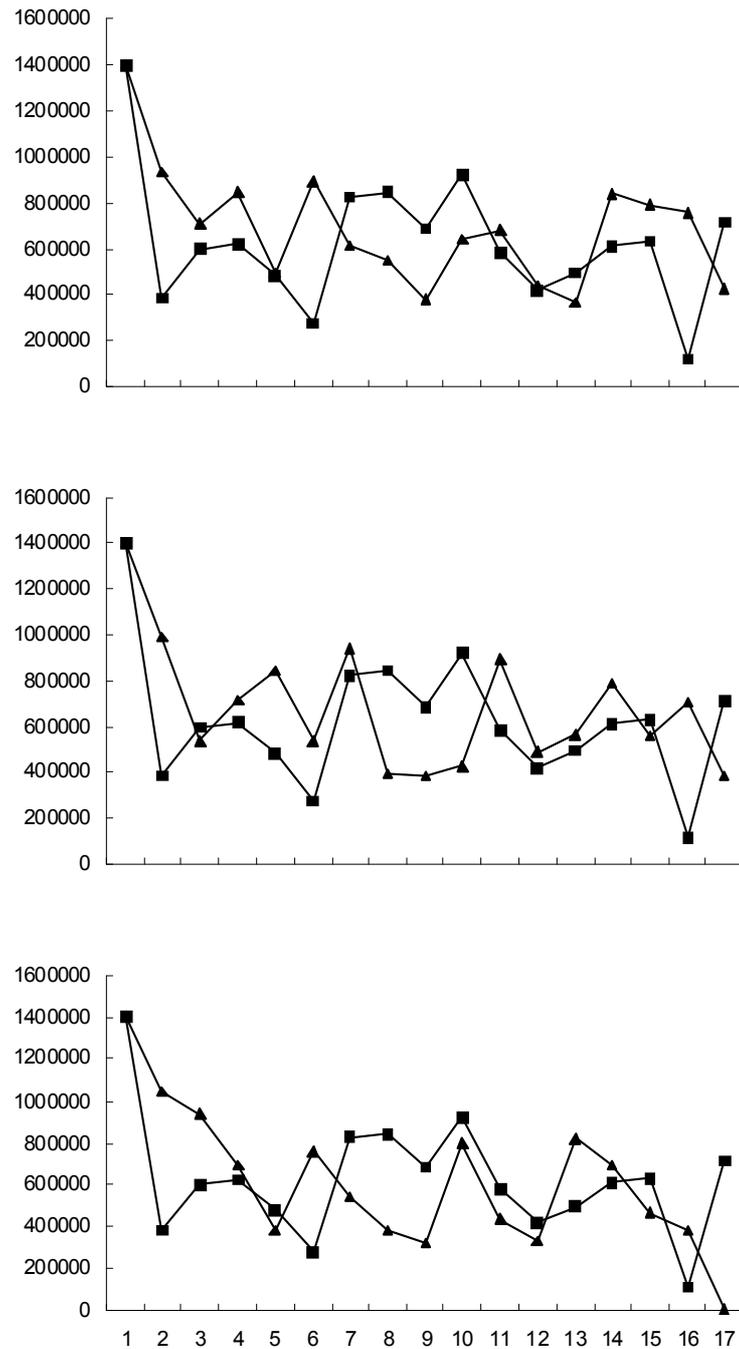


Figure 6: Validation of the simulation model (triangles) using survey data (squares) from north-east Scotland. Model parameters, and degree of stochasticity, are the same as used in Fig. 5, with a mean population of 623750 ha^{-1} and a probability of switching between α_1 and α_2 of 0.0588. Output graphs start with the observed population at the first survey date, and show three examples of typical outputs.

Over the time scales of the published surveys [12,16,26,43] and the unpublished Scottish data, the models are not intended to be predictive. It may be that further exploration of the relationships between annual counts at different time lags will improve predictability. For the purposes of this paper, however, it was sufficient to show that the use of counts with a time lag of two would not have driven the oscillations observed in field data, and that their inclusion in a multiple regression along with time lag one counts only marginally improved the amount of variance explained.

Over shorter timescales, and given an awareness of general population starting levels, these models may be useful in scenario modelling. In particular, it should be possible to model grass-based arable rotations because the effect of cultivations on leatherjacket numbers is known [9]. This is especially relevant to organic farming systems where cultural control provides the only current option for the management of this pest.

We explore a possible regulatory mechanism below that will operate locally but there remains the scaling question of the evident synchrony within the regional survey data. Three primary mechanisms have been proposed to explain this phenomenon: (i) dispersal levelling populations across an area; (ii) trophic interactions with other species that are either more mobile or spatially synchronous; (iii) an exogenous synchronous environmental factor [23]. *Tipula paludosa* has poor powers of dispersal resulting in very localised oviposition, and there is no evidence to suggest that trophic interactions may be important at the regional scale [11]. Thus we contend that the first two of these mechanisms do not apply. Our data show that there is evidence of population regulation even when an exogenous environmental factor is operating. However, this factor (adverse weather) by itself is imperfectly synchronous (for example, it only applied to data from four out of six counties in Mayor and Davies [26]) and does not therefore meet the criteria of Liebhold et al. [23]. It is more probable that *T. paludosa* dynamics exhibit the Moran effect [33]. We suggest that spatial environmental covariation acts at the scale of the regions in this study but breaks down at larger spatial scale. Under these conditions it is possible for population fluctuations to be synchronised even if there is no dispersal-driven exchange of individuals [18].

4.3 Limitation vs regulation

A challenge to population ecologists is not just to determine if density dependence occurs but to establish the mechanism. There is no final experimental proof – as demanded by White [45] – to explain *T. paludosa* dynamics but there is sufficient other evidence to propose an hypothesis.

We postulate that the patterns shown by these data result from outcomes of encounters between individual leatherjackets. Leatherjackets are armed with large mandibles and these have been described not only as tools for feeding but also as weapons of offence. Cannibalism has been identified as a potential regulatory mechanism in a number of species [14], and has frequently been observed amongst leatherjackets [1,4,20] with fatal attacks recorded at the rate of 3% day⁻¹ [20]. It has been argued that cannibalism is an activity for some, though not all, leatherjackets, and that it is probably density-dependent [41]. This was confirmed

in laboratory studies [4].

Laboratory and field studies have shown that *T. paludosa* larvae will move to preferred moisture levels [10] and we postulate that this provides the mechanism that increases direct contact between larvae as soils dry heterogeneously under conditions of reduced rainfall suggested by Milne et al. [31] and Mayor and Davies [26].

Under 'normal' conditions the probability of larval encounters are solely a function of their population density. When rainfall is scarce the availability of desirable refuges declines, and competition ensues for the refuges with resultant mortality. Accordingly, whether a population crashes is dependent upon the competition for refuges, which is a function of population density and environmental harshness. The corollary of this is that when populations are low, encounters are rare and therefore numbers can increase.

It is unlikely that all encounters between larvae result in the death of one or both protagonists because scar tissue is often seen on live larvae. Observation of leatherjackets *in vitro* (R P Blackshaw, unpublished) has revealed a range of individual responses to probing with a mounted needle that includes biting (aggression), retreating (avoidance), and curling (discomfort/passive). The parallel with responses from octopuses to similar probing is strong, and for these animals responses were fixed and ascribed to 'personalities' [24]. Similar individually fixed behavioural responses have been reported for cheetahs [42], fish [15,17,22], and sheep [40].

This raises some interesting questions about leatherjacket behaviours. Under harsh conditions resource will only be competitively secured through aggression and thus an individual being 'aggressive' is the appropriate behaviour. However, the risks of mutual damage between two aggressive individuals is probably greater than for encounters between other behavioural types so under more hospitable conditions it may be desirable to, for example, retreat from a fight.

It is reasonable therefore to expect different behavioural types to be present in a population. Elsewhere, we have explored the theoretical consequences of behaviourally structured populations with individuals expressing either extreme aggression or avoidance under harsh conditions, and concluded that there are survival advantages for the structured population in comparison with unstructured populations [38]. This runs counter to the thesis that competition for a limited resource determines which individuals survive but not how many [34,44].

4.4 Concluding remarks

Berryman et al. [6] described the precise conditions for population regulation. The necessary condition is that the slope of the growth rate should be negative over some part of the population range. They further argued that this condition by itself was insufficient for population regulation to exist; a second condition is that growth rate must be less than zero whilst the first condition is satisfied. The dynamics of *T. paludosa* populations therefore meet the necessary and sufficient conditions for population regulation [6]. Furthermore we have shown that the negative feedback function operates irrespective of the activity of a

limiting factor. That this regulation occurs in a habitat of over-abundant food supply meets the first of White's challenges [45]. We also believe that there is sufficient unambiguous experimental and observational evidence for cannibalism to at least support the contention that this is a real mortality factor. We do, however, acknowledge that we cannot, at this stage, provide convincing proof that this is the case for a soil insect because of the inability to make direct observations. Finally, we can refute the trivial contention that all populations are limited by food, because the evidence for *T. paludosa* is that it is limited by moisture availability in an environment (agricultural grassland) where food is abundant.

On the whole, it seems that a more important problem is not to "choose" between regulation and limitation paradigms but to identify specific scenarios and mechanisms showing how these basically different factors can possibly interplay in nature. Berryman et al. [6] argued that limitation is the result of environmental factors setting the limit to population growth whereas regulation is the process that keeps the population near this limit. The results of this study do, however, fit within the special case "in which populations are regulated by intra-specific interactions (e.g. competition, cannibalism) in response to some limiting factor (e.g. food), provided that the factor is uninfluenced by population density" that he includes under the term limitation [5]. Our study provides field data evidence that *T. paludosa* shows a consistent negative feedback regulatory mechanism under different environmental conditions, and this supports the contention that limitation and regulation are not separate ecological paradigms.

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References

- [1] M. Ahmed. A study of the Tipulidae (Diptera) of agricultural importance in south-east Scotland. PhD Thesis. University of Edinburgh, 1968.
- [2] H.G. Andrewartha. *The use of conceptual models in population ecology*. In: Cold Spring Harbour Symposium on Quantitative Biology 22, 1957, pp. 219-236.
- [3] H.G. Andrewartha, L.C. Birch. *The distribution and abundance of animals*. University of Chicago Press, Chicago, 1954.
- [4] N.M. Barbash. *Improving techniques of rearing Tipula paludosa Mg. (Diptera, Tipulidae) in the laboratory*. Ent. Mon. Mag. 126 (1990), 119-120.
- [5] A.A. Berryman. *Limiting factors and population regulation*. Oikos 105 (2004), 667-670.
- [6] A.A. Berryman, M. Lima, B.A. Hawkins. *Population regulation, emergent properties, and a requiem for density dependence*. Oikos 99 (2002), 600-606.

- [7] L.C. Birch. *The role of weather in determining the distribution and abundance of animals*. In: Cold Spring Harbour Symposium on Quantitative Biology 22, 1957, pp. 203-218.
- [8] R.P. Blackshaw. *The annual leatherjacket survey in Northern Ireland, 1965-1982, and some factors affecting populations*. Plant Path. 32 (1983), 345-349.
- [9] R.P. Blackshaw. *Effects of cultivations and previous cropping on leatherjacket populations in spring barley*. Res. Dev. Agr. 5 (1988), 35-37.
- [10] R.P. Blackshaw. *Behaviour mediated population regulation?* In: Challenges in Applied Population Biology (M.B. Thomas, T. Kedwards, eds.). Aspects of Applied Biology, Vol. 53, 1999, pp.125-130.
- [11] R.P. Blackshaw, C. Coll. *Economically important leatherjackets of grassland and cereals: biology, impact and control*. Int. Pest Man. Rev. 4 (1999), 143-160.
- [12] R.P. Blackshaw, J.N. Perry. *Predicting leatherjacket population frequencies in Northern Ireland*. Ann. Appl. Biol. 124 (1994), 213-219.
- [13] P. Blasdale. *A method of turf sampling and extraction of leatherjackets*. Plant Path. 23 (1974), 14-16.
- [14] J.V. Borre, D. Bonte, J.P. Maelfait. *Interdemic variation of cannibalism in a wolf spider (*Pardosa monticola*) inhabiting different habitat types*. Ecol. Ent. 32 (2006), 99-105.
- [15] S.V. Budaev. *Personality in the guppy (*Poecilia reticulata*): a correlation study of exploratory behavior and social tendency*. J. Com. Psych. 111 (1997), 399-411.
- [16] M. Cohen. *Survey of leatherjacket populations in England and Wales, 1946-1951*. Plant Path. 2 (1953), 80-82.
- [17] K. Coleman, D.S. Wilson. *Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific*. Anim. Behav. 56 (1998), 927-936.
- [18] S. Engen, B.-E. Sather. *Generalisations of the Moran effect explaining spatial synchrony in population fluctuations*. Amer. Nat. 166 (2005), 603-612.
- [19] R.E. Freckleton, A.R. Watkinson, R.E. Green, W.J. Sutherland. *Census error and the detection of density dependence*. J. Anim. Ecol. 75 (2006), 837-851.
- [20] B.E. Freeman. *Cold hardiness and resistance to desiccation in Tipuline larvae*. Agricultural Research Council Conference of Workers on Leatherjackets, 1966, ARC 28A/67.
- [21] M.P. Hassell, J.H. Lawton, R.M. May. *Patterns of dynamical behaviour in single-species populations*. J. Anim. Ecol. 45 (1976), 471-486.

- [22] K. Iguchi, N. Matsubara, H. Hakoyama. *Behavioural individuality assessed from two strains of cloned fish*. Anim. Behav. 61 (2001), 351-356.
- [23] A. Liebhold, W.D. Koenig, O.N. Bjornstad. *Spatial synchrony in population dynamics*. Ann. Rev. Ecol. Evol. Syst. 35 (2004), 467-490.
- [24] J.A. Mather, R.C. Anderson. *Personalities of octopuses (Octopus rubescans)*. J. Comp. Psych. 107 (1993), 336-340.
- [25] R.M. May. *Simple mathematical models with very complicated dynamics*. Nature 261 (1976), 459-467.
- [26] J.G. Mayor, M.H. Davies. *A survey of leatherjacket populations in south-west England, 1963-1974*. Plant Path. 25 (1976), 121-128.
- [27] A. Meats. *The relation between soil water tension and growth rate of Tipula oleracea and T. paludosa (Diptera) in turf*. Ent. Exp. Appl. 10 (1967), 312-320.
- [28] A. Meats. *The relation between soil water tension and rate of development of the eggs of Tipula oleracea and T. paludosa (Diptera: Nematocera)*. Ent. Exp. Appl. 10 (1967), 394-400.
- [29] A. Milne. *The natural control of insect populations*. Can. Ent. 89 (1957), 193-213.
- [30] A. Milne. *Theories of natural control of insect populations*. In: Cold Spring Harbour Symposium on Quantitative Biology 22, 1957, pp. 253-271.
- [31] A. Milne. *On a theory of natural control of insect populations*. J. Theor. Biol. 3 (1962), 19-50.
- [32] A. Milne, R. Laughlin, R.E. Coggins. *The 1955 and 1959 population crashes of the leatherjacket, Tipula paludosa Meigen, in Northumberland*. J. Anim. Ecol. 34 (1965), 529-534.
- [33] P. Moran. *The statistical analysis of the Canadian lynx cycle. II. Synchronisation and meteorology*. Aus. J. Zool. 1 (1953), 291-298.
- [34] B.G. Murray. *On the meaning of density dependence*. Oikos 53 (1982), 370-373.
- [35] A.J. Nicholson. *The balance of animal populations*. J. Anim. Ecol. 2 (1933), 132-178.
- [36] A.J. Nicholson. *The self-adjustment of populations to change*. In: Cold Spring Harbour Symposium on Quantitative Biology 22, 1957, 153-174.
- [37] A.J. Nicholson, V.A. Bailey. *The balance of animal populations*. Proc. Zool. Soc. Lond. (1935), 551-598.

- [38] S.V. Petrovskii, R.P. Blackshaw. *Behaviourally structured populations persist longer under harsh environmental conditions*. Ecol. Lett. 6 (2003), 1-8.
- [39] E. Pollard, K.H. Lakhani, P. Rothery. *The detection of density dependence from a series of annual censuses*. Ecology 68 (1987), 2046-2055.
- [40] D. Reale, B.Y. Gallant, M. Leblanc, M and Festa-Bianchet. *Consistency of temperament in bighorn ewes and correlates with behaviour and life history*. Anim. Behav. 60 (2000), 589-597.
- [41] K. Selke. *Biologische und morphologische Studien an schadlichen Wiesenschnaken (Tipulidae, Dipt.)* Zeit. Wiss. Zool. 148 (1936), 465-555.
- [42] N.C. Wielebnowski. *Behavioral differences as predictors of breeding status in captive cheetahs*. Zoo Biol. 18 (1999), 335-349.
- [43] J.H. White. *Observations on leatherjacket population assessment, forecasting, and control measures*. Proc. 2nd Brit. Ins. Fung. Conf. (1963), 51-58.
- [44] T.C.R. White. *Opposing paradigms: regulation or limitation of populations?* Oikos 93 (2001), 148-152.
- [45] T.C.R. White. *Limitation of populations by weather-driven changes in food: a challenge to density-dependent regulation*. Oikos 105 (2004), 664-666.
- [46] W. Horsthemke, R. Lefever. Noise induced transitions. Springer, Berlin, 1986.