Title: Low levels of artificial light at night strengthen top-down control in insect food web

Authors: Dirk Sanders¹*, Rachel Kehoe², Dave Cruse¹, Frank J.F. van Veen², Kevin J. Gaston¹

Affiliations:

¹ Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom

² Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, United Kingdom

*Corresponding author

Lead contact:

Dirk Sanders

Environment and Sustainability Institute,

University of Exeter, Penryn Campus, Penryn,

Cornwall, TR10 9FE, United Kingdom.

Email: d.sanders@exeter.ac.uk
Artificial light has transformed the nighttime environment of large areas of the earth, with 88% of Europe and almost 50% of the United States experiencing light-polluted night skies [1]. The consequences for ecosystems range from exposure to high light intensities in the vicinity of direct light sources to the very widespread but lower lighting levels further away [2]. While it is known that species exhibit a range of physiological and behavioural responses to artificial nighttime lighting [e.g., 3, 4, 5], there is a need to gain a mechanistic understanding of whole ecological community impacts [6, 7], especially to different light intensities. Using a mesocosm field experiment with insect communities, we determined the impact of intensities of artificial light ranging from 0.1 to 100 lux on different trophic levels and interactions between species. Strikingly, we found the strongest impact at low levels of artificial lighting (0.1 to 5 lux), which led to a 1.8 times overall reduction in aphid densities. Mechanistically, artificial light at night increased the efficiency of parasitoid wasps in attacking aphids, with twice the parasitism rate under low light levels compared to unlit controls. However at higher light levels, parasitoid wasps spent longer away from the aphid host plants, diminishing this increased efficiency. Therefore aphids reached higher densities under increased light intensity as compared to low levels of lighting where they were limited by higher parasitoid efficiency. Our study highlights the importance of different intensities of artificial light in driving the strength of species interactions and ecosystem functions.

Keywords aphids, food webs, light pollution, parasitism rate, parasitoids

RESULTS AND DISCUSSION

We assembled replicate plant-aphid-parasitoid communities (see food web in Figure 1 F) in 48 mesocosms in the field and exposed them to different intensities of artificial light at night, ranging from 0.1 to 100 lux, for 10 aphid generations. To understand the mechanisms behind the
impacts of artificial light, we complemented the field experiment with small-scale experiments under more controlled conditions.

In the field experiment, we found that low levels of artificial light at night (0.1 to 5 lux), representing severe skyglow or direct light effects away from the immediate vicinity of typical streetlight sources, had a strong impact on insect communities. The overall abundance of all three aphid species feeding on bean plants (M. viciae, A. pisum, A. fabae) was reduced by 45.5 % under low lighting levels in comparison to the control treatment with natural light levels (Figure 1; treatments 0.1 lux \( t = -3.87, p = 0.0005 \), 1 lux \( t = -2.57, p = 0.0147 \) and 5 lux \( t = -2.75, p = 0.0095 \), \( df = 7,35 \)) whilst the higher levels of lighting (more typical of the immediate vicinity of streetlights and more intense forms of lighting, such as that used in sports stadia and around industrial installations) did not affect their densities \( (p > 0.1) \). The marked impact of low level lighting on aphid numbers was driven by a 56.2% decline of the most abundant aphid species \( (M. viciae) \) in 0.1, 1 and 5 lux treatments, compared to the control (Figure 1; treatments 0.1 lux \( t = -2.97, p = 0.0053 \), 1 lux \( t = -1.95, p = 0.0587 \) and 5 lux \( t = -3.11, p = 0.0037 \), \( df = 7,35 \)). The aphid \( A. pisum \) responded to light treatments with a similar trend to that of \( M. viciae \), though this pattern was not statistically significant compared to the control (overall treatment effect, \( \chi^2 = 5.90, df = 7, p = 0.5511 \)). The aphid \( A. fabae \) had a less predictable response to the treatments, with a negative effect at 10 lux as compared to the control (Figure 1, \( df = 7,35, t = -2.26, p = 0.0304 \)), and a trend to higher densities in the 5 and 100 lux treatments. The grain aphid \( S. avenae \) feeding on barley plants did not respond to the treatments (overall treatment effect, \( \chi^2 = 2.10, df = 7, p = 0.9541 \)).

While we found a strong overall decline in aphid densities under low levels of light compared to control conditions without light, aphid abundance increased from treatments with low lighting to medium and high lighting levels, showing that the negative impact on aphids was alleviated under higher intensity light treatments. Increasing light intensity (including all light treatments from 0.1 to 100 lux) had a positive effect on overall bean aphid numbers (Figure 1; \( df = \))
1,35, $t = 2.65$, $p = 0.0119$, with the model explaining 40% (conditional $R^2$) and the fixed effect explaining 10% of the variation (marginal $R^2$).

To explain the responses of the aphids it is necessary to look at the impact of the artificial light treatments on their resource (the plants), as well as on their top-down control through parasitoids. To test for the impact of light intensity (0, 0.1, 5, 20, 100 lux) on bean plant biomass we conducted an additional experiment under controlled environmental conditions in a greenhouse in the absence of aphids on plants. This revealed a positive correlation between light intensity and plant biomass (Figure 2, df=1,23, $t = 2.23$, $p = 0.0357$). We found a similar trend in the plant biomass data from the field experiment - where aphids were also present - but only in the 20 lux treatment with significantly higher plant biomass than in the control (Figure S2, overall treatment effect: $\chi^2 = 16.56$, df = 7, $p = 0.0205$). The biomass of barley showed no response in the field experiment (Figure S2; overall treatment effect: $\chi^2 = 12.70$, df = 7, $p = 0.080$). In sum, artificial light at night, at least at higher levels has the potential to increase plant biomass, most likely through an increased photosynthesis rate of plants leading to a positive bottom-up effect [8, 9], but this effect is variable between species.

The parasitism rate of *A. megourae* attacking the aphid *M. viciae* in the field experiment increased from 5% in the unlit control treatments to 10% in low light treatments (Figure 3 B, $z = 2.910$, $p = 0.0036$). The parasitism rate of neither of the other host-specific parasitoids, *A. ervi* and *L. fabarum*, responded significantly to light treatments, but that of the latter showed a similar trend to *A. megourae* (Figure 3, C & D). A two-fold increase in parasitism rate is a strong response, especially over multiple generations, and can explain the observed effects of low lighting treatments on aphid numbers. We found a strong decline in the overall parasitism rate (including all parasitoid species) from a low to high level of nighttime lighting (Figure 3 A; linear regression between light intensity and parasitism rate, $z = -2.656$, $p = 0.0079$).

The strong dependence of the strength of host-parasitoid interactions on artificial light intensities in a field experiment under natural conditions is an important result and worthy of further
examination. We first compared the functional response of *A. megourae* under control conditions to medium light levels (20 lux). The relationship between host density and the number of successful attacks by *A. megourae* can be described by a type 2 functional response (Figure 4 A). The fitted curve for the light treatment showed that parasitoid attacks saturated at a much higher level than in the control, demonstrating that the parasitoids can attack more aphids in the 20 lux light treatment - almost doubling attack rate under high host density situations (Figure 4 A). To test whether this effect could explain the increased parasitism rate in the field experiment under low level lighting, we then compared the number of successful attacks by *A. megourae* in control conditions to low intensity (1 lux) and medium intensity (20 lux) treatments (Figure 4 B). This revealed that the number of attacks increased significantly in the 1 lux treatment (t = 3.17, p = 0.0053, df = 2,18) and marginally not significantly under 20 lux (t = 2.07, p = 0.0536, df = 2,18). These results indicate that the activity of these parasitoids is strongly influenced by photoperiod [10]. We then showed that this is indeed the case for the parasitoid *A. megourae*, with the vast majority of parasitoid attacks happening during the day in a 12:12 day:night regime that included no artificial light at night. Parasitism rate was 18% during daylight, dropping to 2.5% during dark hours (Figure S3, z = 7.294, p < 0.0001); this species responds more strongly to photoperiod than has previously been shown for the parasitoid *A. ervi* [11], explaining the stronger response to artificial light in the field experiment. Artificial light at night thus extends the time budget of day-active parasitoids and increases their ability to control aphid populations even at very low intensities of artificial light. This usage of the so-called “nighttime niche” appears to be more widespread with evidence from increased predation rates in ladybirds [12] and changed feeding habits of lizards [13] and birds [14]. However, the overall decline in parasitism rate with increasing light levels suggests that this niche is strongly dependent on light intensity as the parasitoids are more efficient under low level lighting. We tested therefore for the behavioural response of *A. megourae* parasitoids to different light intensities in a setting with a mesocosm that contained a plant with 100 aphids. We found a strong negative linear relationship between the proportion of female parasitoids that stayed on the
plant and light intensity (Figure 4 C, $t = -4.51, p < 0.001, df = 1,13$). Therefore at higher light levels the majority of parasitoids leave the plants with aphids, explaining why the parasitism rate is so strongly dependent on the level of light and the parasitoids most efficient at low light levels.

Overall, despite a potential bottom up effect through increased plant biomass providing more resources for aphids under higher light intensities, we show that the interaction between the aphids and parasitoids is the critical driver for the observed responses in the field experiment. Higher aphid densities were strongly associated with lower parasitism rates under control and high light treatments. Our experiment demonstrates that different intensities of artificial light at night change species interactions and food web dynamics in insect communities. As species interactions are an important building block of ecological communities this can have far reaching consequences for community stability and ecosystem functions. As demonstrated for other environmental stressors, some species respond while others remain unaffected. In our communities, the most abundant species responded, thereby driving the whole community response, and because species are interconnected in food webs even single species responses can drive whole community changes [15].

Host-parasitoid interactions are one of the most common food web interactions in terrestrial ecosystems [16], both natural and agricultural. The mechanisms demonstrated in our experimental communities therefore have major implications for ecosystems exposed to artificial light at night. The ‘broad spectrum’ white’ lights used are typical of those being installed widely across the world for streetlighting and other outdoor purposes, particularly as the economic benefits associated with light-emitting diode (LED) technologies are exploited [17]; our findings may not be relevant to spectra more commonly associated with older lighting types, such as narrow spectrum low pressure sodium lamps. The surprisingly strong community response to low level artificial light is of major concern, because such light intensities are very widespread, and becoming more so with the continued spread in the extent of artificial lighting at 2 % per annum [18].
Our study further demonstrates that it is important to consider that the impacts of artificial light at night are strongly light intensity dependent and within a community context not necessarily possible to predict from single species responses. Prediction of the community response requires knowledge of major pathways, such as the balance between bottom-up and top-down effects. Species interactions are central to understanding the impact of artificial light at night on ecological communities and any resultant effects on ecosystem functions and stability.

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AUTHOR CONTRIBUTIONS

K.J.G. and F.J.F.v.V. conceived the project. K.J.G., F.J.F.v.V. and D.S. designed the experiments. D.S., R.K. and D.C. carried out the experiments. D.S. analyzed the data and wrote the first draft of the manuscript. All authors contributed to the manuscript. K.J.G. and F.J.F.v.V. acquired the funding for the work.

DECLARATION OF INTEREST

The authors declare no competing interests.

REFERENCES


**Figure 1. Aphid densities in the field experiment.**

Boxplots presenting the median, and the lower and upper quartiles 25% and 75% of cumulative aphid densities for (A) all three aphids on *V. faba*, (B) *M. viciae*, (C) *A. pism*, (D) *A. fabae* and (E) *S. avenae*, in mesocosms without light treatments (*c* = control) and in different treatments with increased light intensities at night (0.1, 1, 5, 10, 20, 50 & 100 lux). Each treatment was replicated 6 times. Statistical significance levels for comparison to the control treatment: (*p=0.05, *p<0.05,)
** p<0.01, *** p<0.001. (F) Food web structure of the experimental insect communities, with two plant species: broad bean (*Vicia faba*) and barley (*Hordeum vulgare*), with three aphid species on beans: *Aphis fabae*, *Acyrthosiphon pisum* and *Megoura viciae*. Each of the aphid species was attacked by a specialist parasitoid, these being *Lysiphlebus fabarum*, *Aphidius ervi* and *Aphidius megourae*, respectively. The grain aphid *Sitobion avenae* fed on barley. The generalist parasitoid *Praon dorsale* attacked the aphids *S. avenae*, *A. pisum*, and *M. viciae*. See Figure S1 for population dynamics.

![Figure 2. Plant biomass in greenhouse experiment without aphids.](image)

*V. faba* plant biomass in control (black) and light treatments (0.1, 5, 20, 100 lux). Presented are the median, and the lower and upper quartiles 25% and 75% (based on 6 replicates). See Figure S2 for plant biomass in the field experiment.
Figure 3. Parasitism rate in the field experiment.

(A) Mean and 95% CI for overall parasitism rate (all species) in relation to light intensity (0.1-100 lux). Mean and 95% CI showing the parasitism rate for each of the parasitoid species (B) *A. megourae*, (C) *A. ervi* and (D) *L. fabarum* in control communities without artificial light at night (C) and communities exposed to different light intensities (0.1, 1, 5, 10, 20, 50 and 100 lux) at night (n=6 for each treatment). The parasitism rate for the generalist parasitoid *P. dorsale* is not shown due to the low number of *Praon* aphid mummies detected in the experiment (see Figure S1H).

Statistical significance level for comparison to the control treatment: *p<0.05, **p<0.01.
Figure 4. Parasitoid functional response and behaviour.

(A) Functional response with a fitted Type 2 curve and 95% CI for the parasitoid *A. megourae* attacking its host *M. viciae* under control (no light: black diamonds) and 20 lux at night (medium light intensity: yellow circles). (B) Number of successful attacks in control, 1 and 20 lux treatment (n = 10, 8, 6 respectively) showing the median, and the lower and upper quartiles 25% and 75%, for host density 140-180. (C) Proportion of *A. megourae* parasitoids staying in a plant with aphids under different light intensities (measured for 0, 1, 5, 20 and 100 lux) (D) Overview of the
responses of different trophic levels to increasing ALAN intensities. See Figure S3 for attack rate during day and night.

STAR Methods

Contact for Reagent and Resource Sharing

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Dirk Sanders (d.sanders@exeter.ac.uk).

Experimental Model and Subject Details

The replicate experimental plant-insect communities (see Figure 1F) consisted of two plant species: broad bean (Vicia faba, L., var. the Sutton) and barley (Hordeum vulgare L.), with bean plants as a resource for three aphid species: (1) the black bean aphid Aphis fabae (Scopoli), (2) the pea aphid Acyrthosiphon pisum (Harris), and (3) the vetch aphid Megoura viciae (Buckton). Each of the aphid species was attacked by a specialist parasitoid, these being Lysiphlebus fabarum (Marshall), Aphidius ervi (Haliday), and Aphidius megourae (Stary), respectively. Barley plants were a resource for the grain aphid Sitobion avenae (Fabricius). These separate communities were linked by the generalist parasitoid Praon dorsale (Haliday), which attacked the aphids S. avenae, A. pisum, and M. viciae. Bean and barley seeds were bought from Kings Seeds, UK. Parasitoids were collected in the field (L. fabarum and A. megourae, P. dorsale) and received from Koppert, Netherlands (A. ervi). Aphids were from existing laboratory cultures A. fabae (Silwood Park, Berkshire, U.K), A. pisum (University of Oxford, UK) and M. viciae found on Lathyrus pratensis plants (Penryn, UK). Prior to the experiments, parasitoid and aphid cultures were kept in a controlled environment room at 20 °C, with a 16:8-h light:dark cycle.

Method Details

Field experiment
Experimental communities were established in 47.5 x 47.5 x 47.5 cm Bug Dorm mesocosms (BugDorm-44545F Insect Rearing Cage, Megaview Science, Taiwan), which were secured with a wooden frame and raised slightly above the surrounding vegetation, ensuring that all mesocosms were at a similar height. Mesocosms were located 1.5 meters apart, and the vegetation around them was mown fortnightly. The experiment was conducted in a contained field site at the University of Exeter, Cornwall.

Light level treatments covered a range of light intensities; low light treatments (0.1, 1 and 5 lux) replicating city skyglow levels and levels away from the immediate vicinity of streetlights, medium light treatments (10 and 20 lux) replicating levels in the immediate vicinity of streetlights, and high light level treatments (50 and 100 lux) replicating more extreme lighting, for example stadium or festival lighting. Each of the artificial light level treatments (0.1, 1, 5, 10, 20, 50 and 100 lux), and an unlit control were replicated 6 times and arranged in a randomized block design. Lighting was located at the top of each mesocosm, and consisted of 36 watt ‘Daylight White 5050 SMD LEDs’ (Ledcentre.uk, London, cold white 5000 – 7000 Kelvin, see Figure S4 for spectrum).

The lighting levels were manipulated using a resistor to ensure the correct lux for each treatment. Artificial lights were turned on only at night, by use of a dusk-dawn sensor, switching on at 70 lux and off at 110 lux. Wooden barriers between the cages prevented spillover of light to neighbouring mesocosms and mesocosms further away. Light levels were measured with a lux meter (Delta OHM HD2102- 39 -V2.3 with Illuminance probe LP 471 PHOT/SICRAM module measurement range starting at 0.01 lux with a resolution of 0.01 lux) in every mesocosm to confirm the light levels per treatment. We compared treatment effects against a control treatment without additional light but exposed to the varying influence of moonlight and very low levels of skyglow as there were no direct light sources in the vicinity of the field site. This means the control is not a entirely dark control but a natural nighttime light (as would be experienced in the absence of streetlights) to which each treatment added the artificial light at a certain intensity. Field experiments are important because they indeed include the natural variation as experienced by
natural communities but under more controlled conditions. The field site does experience low levels
of artificial light at night through skyglow (as would be the case throughout much of Europe [1]),
but readings from a Sky Quality Meter regularly reach values of 21 mag\textsubscript{SQM}/arcsec\textsuperscript{2} (lower levels
occur, as would be expected, under moonlight and clouds), which compares favourably with what
has been assumed to be a natural radiance of 21.6 mag\textsubscript{SQM}/arcsec\textsuperscript{2} [19]; note that higher values of
these units mean less illuminance.

The experiment was set up on 29th July 2016, with 3 pots of broad beans and 1 with barley
plants placed in each mesocosm and then a week later completed to a total of 6 pots of broad beans
and 2 pots of barley per mesocosm. Five individuals of each aphid species were placed on the
appropriate plant species and left for 2 weeks to grow in numbers. At weeks 2 and 3, two mated
female parasitoids of each species were released into each mesocosm. Each week, the two oldest
plant pots from each tray were replaced with 2-week-old plants, while leaving the plant matter and
all insects in the mesocosm. This replicates the natural behaviour of aphid colonies, which typically
show cycles of dispersal to fresh host plants.

From week 1 until the termination of the experiment after 9 weeks, all species on half of the
plants were counted on a weekly basis. If no individuals of a particular species were found in a
particular replicate, the entire mesocosm was checked to confirm presence or absence.

Plant biomass without aphids
We used 5 different light treatments to test for the effect of artificial light on plant biomass, in the
absence of aphids: an unlit control, 0.1, 5, 20, and 100 lux. Each of the light treatments was
replicated 6 times and arranged in a randomized block design. For each replicate a single 2 week
old bean plant was placed in a 47.5 x 47.5 x 47.5 cm Bug Dorm cage, in a greenhouse with a 16: 8
hours light: dark period. The experiment ran for 3 weeks, at which point the plants were washed
clean of soil, the aboveground and belowground parts separated, and dried at 50\textdegree C for 48 hours.
They were then weighed to within 0.001 gram.
Parasitoid functional response and attack rate

Third instar *M. vicie* aphid individuals were set onto 2 week old plants at densities varying from 5 to 200, with each plant placed in a 47.5 x 47.5 x 47.5 cm Bug Dorm cage, in the contained field site at the University of Exeter, Cornwall. One female *A. megourae* parasitoid was placed in each cage for a 24-hour period, after which point it was removed. Aphids were then left for 2 weeks before all mummies were counted. We used two treatments: unlit controls and artificial light at night at 20 lux. This experiment ran at the same time as the large field experiment.

We compared parasitoid attack rate between control (no light), 1 lux and 20 lux treatment. 1 female *A. megourae* parasitoid was released on a plant with 150 *M. vicie* aphids, and left for 24 h. This was done in a controlled Temperature room at 20 degrees C and 16: 8 hours light: dark period.

Each treatment was replicated 6 times, and parasitoid mummies were counted after 2 weeks.

Parasitoid activity

To test for the behavioural response of parasitoids to different light intensities, 100 3rd instar *M. vicie* aphids were placed on a 3 week old broad bean (*V. faba* plant) and allowed to settle in a climate chamber with a 16:8 light: dark cycle for 24 hours. This infested plant was then placed in a cage in complete darkness. Different light treatments were then applied over the top of the cage, these being 0 (control) 1, 5, 20, and 100 lux, measureable at the height of the plant (in exactly the same setting as for the field experiment). 20 mated female *A. megourae* parasitoids were then released into the cage, and were left for one hour. After one hour the locations of the parasitoids (on the or away from plant) were noted. Preliminary tests using the artificial light treatments along with red lights showed that there was a period of 20 seconds for counting before the parasitoids changed their location or activity after the counting light was put on.

To test for parasitoid attack rate during day and night, single broad bean plants were infected with 60 3rd star *M. vicie* aphids per plant, and placed in a 20 x 20 x 40 cm cage
constructed of untreated wood and thrip netting. These aphids were left to settle for 1 day before being placed in incubators (Percival Model 1-30 vl) set to 18 degrees C with a 12:12 day night cycle and 75 % humidity. A single, mated female *A. megourae* parasitoid was placed in each cage, and left for 12 hours in either dark or light settings. After 12 hours the parasitoid was removed and placed in another cage, again with 60 3\textsuperscript{nd} instar aphids and left for a further 12 hours at the opposite light treatment. After the removal of the parasitoid, each cage was placed in a controlled temperature room at 18 degrees and a 16:8 day night cycle for mummies to develop. After 2 weeks the number of mummies per cage was counted.

Quantification and statistical analysis

All data were analysed using the open source software R 3.3.2 [20].

Field experiment

The impact of light treatments on plant biomass and aphid populations in the field experiment was analysed with linear mixed effects models using the function `lme` from the package `nlme` [21]. We included treatment (with 8 levels) as a fixed factor, while block was included as a random factor. As response variables we used aphid cumulative numbers (for each of the species the sum of aphids counted per single mesocosm) and plant dry weight (separated for bean and barley plants). We also tested for a linear response of overall aphid numbers to increasing light intensity (0.1 to 100 lux).

Parasitism rate was analysed using generalised linear mixed models assuming a binomial error distribution and using the logit link function. The response variable was the bivariate variable containing ‘cumulative parasitoid mummies of aphid species i’ and ‘cumulative abundance of alive aphids for species i’, where ‘i’ can be the cumulative abundance or mummy number of *A. fabae*, *M. viciae*, or *A. pisum*. The parasitism rate of the generalist parasitoid *P. dorsale* was not analysed due to the low sample size. Block was included as a random factor, and to account for over-dispersion, an additional observation-level random factor was added. For this analysis we used the function
glmer from the package lme4 [22]. To obtain 95% credible intervals for the model predictions, we used the R-package “effects” [23]. We also tested for a correlation between overall parasitism rate in the community (including all parasitoid species) and light intensity (0.1 to 100 lux).

Plant biomass without aphids

The impact of light treatments on plant biomass in the absence of aphids was analysed with linear mixed effects models using the function lme from the package nlme [21]. We included light intensity (0, 0.1, 5, 20, 100 lux) as a continuous explanatory variable, while block was included as a random factor. As response variable we used plant dry weight per single mesocosm.

Parasitoid functional response

The functional response curve for the parasitoid *A. megourae* attacking aphids under unlit control conditions and the treatment with artificial light at night (20 lux) were fitted using the function frair_fit and confidence intervals were estimated with frair_boot from the frair package [24].

Parasitoid attack rate during light and dark period

Parasitoid behaviour under different light intensities (0, 1, 5, 20, 100 lux) and parasitism rate in dark and light periods were analysed using generalised linear models assuming a quasi-binomial error distribution. The response was the bivariate variable containing ‘parasitoids on the plant’ and ‘and parasitoids away from the plant’ in the first and ‘*A. megourae* parasitoid mummies’ and ‘abundance of alive *M. viciae* aphids’ for the latter analysis, which was analysed with treatment (12 h light or 12 h dark period) as explanatory. To obtain 95% credible intervals for the model predictions we used the R-package “effects” [23].

Key resource table (see extra document)
Data and software availability

All data used in this study have been deposited at the Environmental Information Data Centre under the link XXXX.