

Temporal variations in English populations of a forest insect pest, the green spruce aphid (*Elatobium abietinum*), associated with the North Atlantic Oscillation and global warming

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Running title: *Elatobium abietinum* and the NAO

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Abstract

Based on an exceptionally long modern ecological dataset (41 years), it has been possible to show that warm weather in England associated with a positive North Atlantic Oscillation (NAO) index causes the spring migration of the green spruce aphid (*Elatobium abietinum*), a pest species of spruce trees (*Picea*) to start earlier, continue for longer and contain more aphids. An upward trend in the NAO index during the period 1966-2006 is associated with an increasing population size of *E. abietinum*. It is important to understand the mechanisms behind the population fluctuations, because this aphid causes considerable damage to *Picea* plantations. Present day weather associated fluctuations in forest insect pests may be useful analogues in understanding past pest outbreaks in forests.

Key words

Rothamsted Insect Survey; *Elatobium abietinum*; *Picea*; North Atlantic Oscillation; phenology.

1. Introduction

Abrupt, sometimes persistent changes in Holocene terrestrial ecosystems are well known: for example the mid-postglacial declines in European elm (*Ulmus* L.) (e.g. Peglar 1993; Parker et al. 2002) and hemlock (*Tsuga canadensis* (L.) Carr.) (Haas and McAndrews, 2000). Both these examples have been linked to insect pests and associated pathogens (e.g. Girling and Greig, 1985; Bhiry and Fillion, 1996; Clark and Edwards, 2004) but there is still uncertainty over what made apparently stable forest populations vulnerable to such pests. Climatic forcing may well be a significant contributing factor, either by directly weakening the trees, or by enhancing insect population growth and dispersal. A more detailed understanding of the relationship between climate change and insect populations is clearly of relevance to palaeoecological studies, and in the context of the current phase of global warming.

Here the response of *Elatobium abietinum* (Walker) (green spruce aphid) to short-term climatic forcing over the last 41 years is examined. Although detailed records of individual climatic variables (temperature, precipitation etc.) are available, the influence of the North Atlantic Oscillation (NAO) is used as a proxy for a range of climatic conditions. In the mid-latitude, temperate, study area of southern England, ecosystems respond to the combined effects of several climatic variables rather than being dominated by a single variable.

The NAO has a considerable influence on the weather in north-west Europe, Scandinavia, the Mediterranean basin, eastern side of North America

and Greenland. The NAO is described by the NAO index, which is calculated from air pressure at two locations. The northern location is usually in Iceland, but the southern location can be in the Azores, Lisbon or Gibraltar, the choice of location being of little importance (Osborn, 2000).

A positive NAO index is associated with depression systems taking a more northerly route across the Atlantic, resulting in warmer autumn and winter weather in the British Isles, whereas a negative NAO index is associated with the depression systems travelling in a more southerly route across the Atlantic (Osborn, 2000). Consequently the NAO index shows a strong, positive association with temperatures at Rothamsted, in Hertfordshire, U.K., between October and March and a weaker association with temperatures in April and May. The NAO has a much weaker control over precipitation, with an almost significant correlation between the January NAO index and January precipitation, but no significant correlations between the winter (January to March) NAO index and precipitation averaged over several months (Table 1).

1.1 NAO and organisms

Weather conditions associated with the NAO have been shown to have an influence on a range of different groups of organisms. Marine Copepod population size in the Eastern North Atlantic and North Sea is influenced by winter temperature and wind speed, with meteorological factors interacting with interspecific competition (Fromentin and Planque, 1996). Cod (*Gadus morhua* L.) recruitment in the North Atlantic increased during the sustained

negative phase of the NAO index in the 1960s and then recruitment decreased during the more positive phase of the NAO index in the 1990s with water temperature as the most likely controlling factor (Parsons and Lear, 2001). Soay Sheep (*Ovis aries* L.) populations on Hirta, part of the St Kilda archipelago, Scotland, appear to be influenced by precipitation in March (Catchpole et al., 2000). Red Deer (*Cervus elaphus* L.) in Norway are affected by the NAO before birth, with warmer winters resulting in smaller birth size than those born following cold winters (Post et al., 1997). Reindeer and Caribou (both *Rangifer tarandus* L.) in Greenland and Russia show synchronous population changes associated with the NAO despite being geographically separated by a minimum of 3300 km (Post and Forchhammer, 2006). Butterflies (Lepidoptera) appear to be influenced in a complex manner by weather, life history characteristics and morphological characteristics associated with partial thermoregulation (Westgarth-Smith et al., 2005a, b and c).

1.2 *Elatobium abietinum* and its hosts

Elatobium abietinum was selected for this study, as high temporal resolution data, extending over 41 years, are available. This species was chosen for study from the range of species caught in a suction trap at Rothamsted, U.K., as it is one of the earliest aphid species to undertake its winged migration each year, and would therefore be flying nearer the time of year when the NAO influences U.K. weather. Also *E. abietinum* has a single, well-defined flight period (Figure 1), which is about two months in duration and

so relatively short compared to many other aphid species. In the U.K., *E. abietinum* is continuously parthenogenetic, over-wintering in the active stages.

Elatobium abietinum lives on *Picea* spp., especially *P. sitchensis* (Bong.) Carr., but also *P. abies* (L.) H. Karst., *P. pungens* Engelm. and less frequently on *Abies* Mill. spp. (Harrington and Pickup, 2005). These tree species are not native to the British Isles. *Picea sitchensis* was introduced into the British Isles in 1831, *P. abies* was probably introduced before 1500 AD, different varieties of *P. pungens* were introduced between 1862 – 1912 and *Abies alba* (Mill.) was introduced in 1603 (Mitchell, 1978).

There is a practical relevance in understanding the ecology of *E. abietinum*, as this species is a significant pest of *Picea* spp. For example, Straw et al. (2000) found that *P. sitchensis*, grown in Wales, suffered 38.5% defoliation and 22.4% reduced height increment when artificially infested with *E. abietinum* at population densities equivalent to a moderate to severe outbreak. Furthermore a high infestation rate can reduce productivity in the following year as the aphids disrupt bud formation, which reduces the quality of foliage and photosynthetic ability, causing 12.2% decrease in the stem diameter increment and 23.8% decrease in the stem volume increment.

Trees in the U.K. are rarely killed by *E. abietinum* (Williams et al., 2005). However *E. abietinum* has been introduced into the south-western USA (Campbell, 2005) where it can cause 24 - 41% mortality of *Picea engelmannii* (Parry) Engelm. and a combined infection with *E. abietinum* and the mistletoe, *Arceuthobium microcarpum* (Engelm.) Hawksworth and Wiens, can cause 70% mortality of *P. pungens* (Lynch, 2004).

Associations between climate and tree pest species are of interest to palaeoecologists. For example, the summer drought related decline of hemlock (*Tsuga canadensis*) in eastern North America which occurred 5700 – 5100 years ago may be due to drought weakened trees being attacked by insect pests (Haas and McAndrews, 2000), especially the hemlock looper (*Lambdina fiscellaria* (Guen.)) and the spruce budworm (*Choristoneura fumiferana* (Clem.)) (Bhiry and Fillion, 1996). Similarly the mid-Holocene elm (*Ulmus*) decline appears to be a combined effect of elm disease which is an infection by the ascomycete fungus, *Ophiostoma* (*Ceratocystis*) *ulmi* (Buisman) carried by elm bark beetles, *Scolytus scolytus* (F.) and *S. multistriatus* (M.), as well as climate change and human activities (Parker et al., 2002).

Insect pest associated changes in tree growth rates are used to identify historical records of pest outbreaks in forests. For example, *Choristoneura occidentalis* (Freeman), another spruce budworm, outbreaks on Douglas-fir (*Pseudotsuga menziesii* var. *glauca* Mirb. Franco) growing in British Columbia, Canada (Campbell et al., 2005) and the larch budmoth (*Zeiraphera diniana* Guénée) defoliation of larch (*Larix decidua* Mill.) in the French Alps (Rolland et al., 2001).

Palaeoecology uses organism population changes as a proxy for meteorological changes, however, butterflies (Lepidoptera) in the U.K. show complex associations between their life history characteristics and the NAO index, such that species that are more positively correlated with the NAO index are more likely to have two generations per year (bivoltine) rather than one generation per year (univoltine) and have a longer flight season. This is

because positive NAO index years tend to be warmer, allowing more time to complete two generations and for a longer flight period. There are also associations with the over-wintering stage such that species of butterfly that hibernate as adults show much less association with the NAO index than species that over-winter as larvae, this is probably because adult butterflies have completed their feeding before the onset of NAO controlled autumn and winter weather, whereas larvae will feed on warm winter days (Westgarth-Smith et al., 2005a, b and c).

Analyses by Westgarth-Smith et al. (2005a, b and c) of the effect of the NAO index on butterfly populations were based on an annual collated index of butterfly population size. We wanted to extend this work to use a daily insect dataset, in particular to examine the influence of the NAO on phenology. Phenology is of particular current interest with biological events reportedly happening earlier in the spring, and also later in the autumn as a response to global warming. For example Roy and Sparks (2000) suggest that climate warming of 1 °C could advance butterfly appearance by 2-10 days.

We hypothesise that there is a correlation between the NAO index and the timing and size of the spring migration of the green spruce aphid, *Elatobium abietinum* (Walker). These associations may be of interest to foresters responsible for spruce (*Picea*) plantations and palaeoecologists investigating the associations between climate, tree population size and insect pests.

2. Materials and methods

Daily counts have been made of aphids since 1966 from a 12.2 m high suction trap (Macaulay et al., 1988) at Rothamsted Research near Harpenden, 30 km north of London, U.K. Air is sucked into the trap at a constant rate every day of the year and the traps operate with a very high level of reliability, such that trap breakdown events are exceptionally rare. With 41 years of data available, this is one of the longest invertebrate ecological datasets available in the World. This trap is one of a network of 16 suction traps distributed throughout England and Scotland, operated by the Rothamsted Insect Survey (Harrington and Woivod, 2007). As part of their life cycle, aphids undergo a period of flight. This winged migration takes place at different times of year depending on the species.

From the daily aphid data it was possible to calculate a total number of *E. abietinum* caught per year and to obtain the first and last date of capture. The dates were recorded as Julian calendar dates, where, for example, 1 January is day 1 and 1 June is day 152. The flight period is the inclusive number of days between the first and last date of capture.

The mean flight day number was calculated by multiplying the number of aphids caught each individual day by the Julian date. These numbers were then summed for each year and divided by the total number of aphids caught in that year.

Monthly NAO indices were obtained from the Climate Research Unit (2004) and Osborn (2006). This NAO index is based on atmospheric pressures in Iceland and Gibraltar and is available in a monthly form. The winter NAO index was calculated as a mean of the January, February and March NAO indices and an autumn and winter (October to March) NAO index,

used in Table 1 only, was calculated from the mean of all monthly NAO indices from October to March.

Monthly mean temperature data and monthly precipitation data were obtained from the Rothamsted meteorological station.

The generalised linear equation $y=mx+c$ was used to describe the trend lines for first flight day number and mean flight day number, when plotted against the winter NAO index. The gradient, m , was used to calculate the change in the day number associated with a change in the winter NAO index. The intercept, c , can be used to estimate the day number for the first day of flight or mean flight day number at Rothamsted for a winter NAO index of zero.

3. Results

The total number of *E. abietinum* caught per year in the Rothamsted suction trap ranged from 5 to 592. \log_{10} total numbers of *E. abietinum* caught per year suggest an upward trend with time, but with considerable oscillations from year to year (Figure 2). There is a significant positive correlation (Pearson correlation coefficient = 0.387, P . = 0.012) between the winter NAO index and the \log_{10} total number of *E. abietinum* caught per year (Figure 3).

There is a significant negative correlation between the winter NAO index and the first date of capture of *E. abietinum* (Pearson correlation coefficient = -0.407, P . = 0.008, Figure 4), but not the date of last capture (Pearson correlation coefficient = -0.034, P . = 0.834, Figure 4). As a result, the flight period is significantly positively correlated with the NAO index (Pearson

correlation coefficient = 0.334, $P.$ = 0.033, Figure 5). Mean flight date is significantly negatively correlated with the winter NAO index (Pearson correlation coefficient = -0.402, $P.$ = 0.009, Figure 6). During the period 1966 to 2006, the first date of capture has advanced by 29.7 days, the mean flight day number has advanced by 17.5 days and the last date of capture by 19.7 days (Figure 7).

There are highly significant positive correlations between the \log_{10} annual total number of *E. abietinum* and the mean October to April temperature (Pearson correlation coefficient = 0.517, $P.$ = 0.001) and with the mean January to April temperature (Pearson correlation coefficient = 0.458, $P.$ = 0.003). However the annual total number of aphids is not significantly correlated with the mean May to June temperature (Pearson correlation coefficient = 0.207, $P.$ = 0.194). There are no significant correlations between the total annual capture of *E. abietinum* and precipitation (Table 1).

The data were tested for 1st order temporal autocorrelations and the only relationship found was a negative association for \log_{10} annual total *E. abietinum* in successive years (Pearson correlation coefficient = -0.371, $P.$ = 0.018).

4. Discussion

The warmer weather associated with a positive NAO index appears to result in *E. abietinum* starting to fly earlier in the year with an earlier peak in flight activity, also as the NAO index has become more positive with time, the flight season for *E. abietinum* has tended to start sooner. The last date of

flight is unchanged by the NAO, so the more positive the NAO index, the longer the flight period. The lack of an association between the last date of flight and the NAO might be due to a much weaker link between weather and the NAO this late in the year, or to the fact that the end date of aphid flight is controlled by some other factor, including possibly a change in the nutritional quality of the phloem sap (Day et al., 2004).

The highly significant correlation between the total annual capture of *E. abietinum* and mean January to April temperatures indicates that temperature during this period is important in controlling the population size of this species. A slight increase in the significance level of the correlation coefficient for mean October to April temperatures, when compared to mean January to April temperatures, might indicate that both autumn and winter temperatures are important. Temperatures in May and June do not appear to affect the population size of *E. abietinum*, which suggests that the population size was determined before the migration and also validates the suction traps as a census method as the number of aphids caught is not a function of temperature determined flight ability. Moreover, precipitation appears to have no effect on *E. abietinum* population size. As the NAO has a much greater influence over temperature rather than precipitation (Table 1), it seems that the mechanism for control of *E. abietinum* population size by the NAO is through temperature rather than precipitation.

These results suggest that the winter NAO index can be used as a proxy for the population size of *E. abietinum* in the Rothamsted area. Furthermore the winter NAO index can be used to predict the timing of the winged migration of *E. abietinum* with an increase of 1.0 in the winter NAO index

resulting in a 4.7 day advance in first flight date and a 2.7 day advance in mean flight day number (Figures 4 and 6). For the Rothamsted area it is possible to calculate the actual date by using the intercept as a reference point. So with a winter NAO index of zero, it would be expected that *E. abietinum* would start flying on about Julian day number 131 (11 May) and the mean flight day number would be day 148 (28 May). The aphid data for Rothamsted is considered to be representative of an area of 80 km radius (Harrington and Woiwod, 2007), so it would be necessary to recalculate this predictive model for different areas. With the winter NAO index predicting the scale and timing of the migration of *E. abietinum*, it may be possible to use the winter NAO index as a proxy for the amount of *E. abietinum* damage to *Picea* populations.

A general upward trend in the number of *E. abietinum* caught per year occurs during the period 1966-2006. During the same period, the winter NAO index has become more positive (Figure 2), the mean annual temperature at Rothamsted increased by 1.46 °C and the mean annual temperature from the Central England Temperature Series increased by 1.19 °C Series (Manley, 1974 and Hadley Centre, 2003). It is possible that the global warming trend will be manifested in the U.K. by an increasingly more positive NAO index, which will in turn be associated with greater flight activity of *E. abietinum* and probably increasing aphid damage to spruce trees. While it is possible that this upward trend in the population of *E. abietinum* in part reflects an increase in the percentage of coniferous forests that has occurred in Great Britain during the period 1950 – 1990, the majority of the increase in sitka spruce has been in Scotland (Forestry Commission, 2005). However the percentage of

conifers has been considerably reduced during the 1990s, but an associated decline in *E. abietinum* is not apparent (Figure 2).

5. Conclusion

The present study has shown a strong link between the winter NAO index and the phenology of the aphid, *E. abietinum*. A positive NAO index is associated with larger populations that start flying earlier in the year and which have a longer flight period. Furthermore there is evidence that global warming is resulting in the winter NAO index becoming more positive, therefore high population sizes of *E. abietinum* may become more common. The winter NAO index has considerable potential as a predictor of the scale and timing of infestations of *E. abietinum* and the associated damage to *Picea*, as well as the potential for use as a proxy in palaeoecological studies of insect pest damage to trees.

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References

- Bhiry, N., Filion, L., 1996. Mid-Holocene Hemlock Decline in Eastern North America Linked with Phytophagous Insect Activity. *Quaternary Research* 45, 312-320.
- Campbell, F., 2005. Gallery of Pests: Established Exotic Insects, spruce aphid – *Elatobium abietinum* (Walker). The Global Invasive Species Initiative. The Nature Conservancy. <http://tncweeds.ucdavis.edu/products/gallery/elaab1.html>. Accessed December 2005.
- Campbell, R., Smith, D.J., Arsenault, A., 2005. Dendroentomological and forest management implications in the Interior Douglas-fir zone of British Columbia, Canada. *Dendrochronologia* 22, 135-140.
- Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S.N., Albon, S.D., 2000. Factors influencing Soay sheep survival. *Applied Statistics* 49, 453-472.
- Clark, S.H.E., Edwards, K.J., 2004. Elm bark beetle in Holocene peat deposits and the northwest European elm decline. *Journal of Quaternary Science* 19, 525-528.
- Climate Research Unit, 2004. North Atlantic Oscillation. University of East Anglia, U.K. www.cru.uea.ac.uk/cru/data/nao.htm. Accessed January 2007.
- Day, K.R., Armour, H., Docherty, M., 2004. Population responses of a conifer-dwelling aphid to seasonal changes in its host. *Ecological Entomology* 29, 555-565.
- Forestry Commission, 2005. Forestry Statistics 2005. www.forestry.gov.uk/website/foreststats.nsf/byunique/woodland.html. Accessed March 2006.

- Fromentin, J.M., Planque, B., 1996. *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series 134, 111-118.
- Girling, M.A., Greig, J., 1985. A first fossil record for *Scolytus scolytus* (F.) (elm bark beetle): its occurrence in elm decline deposits from London and their implications for Neolithic elm decline. Journal of Archaeological Science 12, 347-531.
- Haas, J.N., McAndrews, J.H., 2000. The Summer Drought Related Hemlock (*Tsuga canadensis*) Decline in Eastern North America 5700 to 5100 Years Ago. In: McManus, K.A., Shields, K.S., Souto, D.R., (Editors) 2000. Proceedings: symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. www.treesearch.fs.fed.us/pubs/4141. Accessed January 2007.
- Hadley Centre, 2003. Central England Temperature Series. www.metogov.uk/research/hadleycentre/CR_data/Daily/HadCET_act.txt. Accessed January 2007.
- Harrington, R., Pickup, J., accessed 2005. Rothamsted Insect Survey – Aphid Encyclopedia. www.rothamsted.bbsrc.ac.uk/insect-survey/EncylopaedicInfo/ElatobiumInfo.html. Accessed January 2007.
- Harrington, R., Woivod, I., 2007. Foresight from hindsight: the Rothamsted Insect Survey. Outlooks on Pest Management 18, 9-14.
- Lynch, A.M., 2004. Fate and characteristics of *Picea* damaged by *Elatobium*

- abietinum* (Walker) (Homoptera: Aphididae) in the White Mountains of Arizona. *Western North American Naturalist* 64, 7-17.
- Macaulay, E.D.M., Tatchell, G.M., Taylor, L.R., 1988. The Rothamsted Insect Survey '12-metre' suction trap. *Bulletin of Entomological Research* 78, 121-129.
- Manley, G., 1974. Central England temperatures: monthly means 1659-1973. *Quarterly Journal of the Royal Meteorological Society* 100, 389-405.
- Mitchell, A., 1978. *A Field Guide to the Trees of Britain and Northern Europe*. 2nd Edition. Collins. London.
- Osborn, T., 2000. North Atlantic Oscillation. Climate Research Unit (University of East Anglia, U.K.) Information Sheet, 11.
www.cru.uea.ac.uk/cru/info/nao/. Accessed December 2005.
- Osborn, T., 2006. North Atlantic Oscillation Index Data.
www.cru.uea.ac.uk/~timo/projpages/nao_update.htm. Accessed November 2006.
- Parker, A.G., Goudie, A.S., Anderson, D.E., Robinson, M.A., Bonsall, C., 2002. A review of the mid-Holocene elm decline in the British Isles. *Progress in Physical Geography* 26, 1-45.
- Parsons, L.S., Lear, W.H., 2001. Climate variability and marine ecosystem impacts: a north Atlantic perspective. *Progress in Oceanography* 49, 167-188.
- Peglar, S., 1993. The mid-Holocene *Ulmus* decline at Diss Mere, Norfolk, U.K.: a year-by-year pollen stratigraphy from annual laminations. *The Holocene* 3, 1-13.
- Post, E., Forchhammer, M.C., 2006. Spatially synchronous population

- dynamics: an indicator of Pleistocene faunal response to large-scale environmental change in the Holocene. *Quaternary International* 151, 99-105.
- Post, E., Stenseth, N. Chr., Langvatn, R., Fromentin, J.-M., 1997. Global climate change and phenotypic variation among red deer cohorts. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 264, 1317-1324.
- Rolland, C., Baltensweiler, W., Petitcolas, V., 2001. The potential for using *Larix decidua* ring-widths in reconstructions of Larch Budmoth (*Zeiraphera diniana*) outbreak history: Dendrochronological estimates compared with insect surveys. *Trees, Structure and Function* 15, 414-424.
- Roy, D.B., Sparks, T.H., 2000. Phenology of British butterflies and climate change. *Global Change Biology* 6, 407-416.
- Straw, N.A., Fielding, N.J., Green, G., Price, J., 2000. The impact of green spruce aphid, *Elatobium abietinum* (Walker), and root aphids on the growth of young Sitka spruce in Hafren Forest, Wales: effects on height, diameter and volume. *Forest Ecology and Management* 134, 97-109.
- Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F., 2005a. The North Atlantic Oscillation and U.K. Butterfly Populations. *Biologist* 52, 273-276.
- Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F., Roy, D.B., 2005b. Mechanisms for the control of U.K. Butterfly abundance by the North Atlantic Oscillation. *Antenna* 29, 257-266.
- Westgarth-Smith, A.R., Leroy, S.A.G., Collins, P.E.F., Roy, D.B., 2005c.

The North Atlantic Oscillation and U.K. butterfly life cycles, pigmentation, morphology, behaviour and conservation. *Antenna* 29,186-196.

Williams, D.T., Straw, N.A., Day, K.R., 2005. Performance of the green spruce aphid, *Elatobium abietinum* (Walker) on previously defoliated Sitka spruce. *Agricultural and Forest Entomology* 7, 95-105.

Table and figure legends

Table 1. Pearson correlation coefficients showing the relationships between temperature and precipitation at different times of year and the \log_{10} annual total number of *E. abietinum* caught in the Rothamsted suction trap. An October to March NAO index was used in calculating correlation coefficients with mean October to April temperature and precipitation and the winter (January to March) NAO index was used in calculating correlation coefficients with the mean January to April and mean May and June temperature and precipitation.

Figure 1. Annual migration pattern for *E. abietinum*. Graph of \log_{10} total daily counts for 1966-2006 against day number.

Figure 2. \log_{10} total number of *E. abietinum* caught per year and the winter NAO index for the years 1966-2006.

Figure 3. Relationship between the \log_{10} total number of *E. abietinum* plotted against the winter NAO index. Pearson correlation coefficient = 0.387, P . = 0.012.

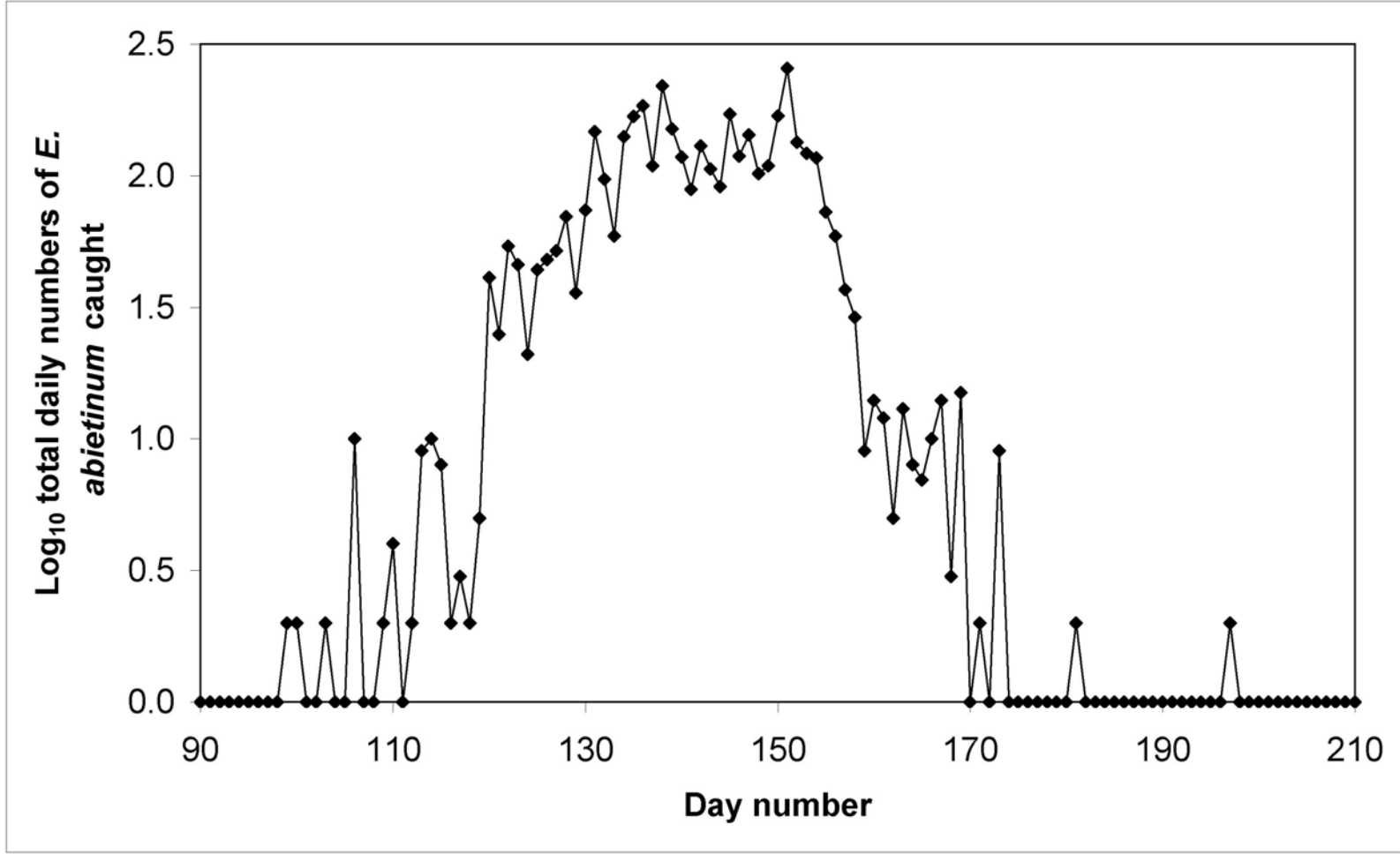
Figure 4. Relationship between first day of capture of *E. abietinum* and the winter NAO index (Pearson correlation coefficient = -0.407, P . = 0.008) and between the last day of capture of *E. abietinum* and the winter NAO index

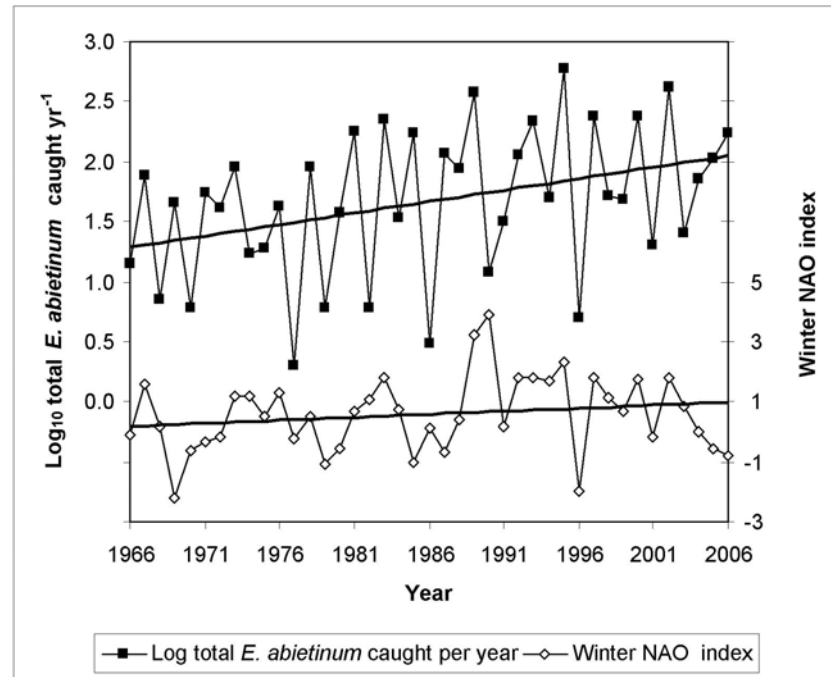
(Pearson correlation coefficient = -0.034, P . = 0.834). The linear equation for the trend line for the first day of capture is $y = -4.7322x + 130.96$.

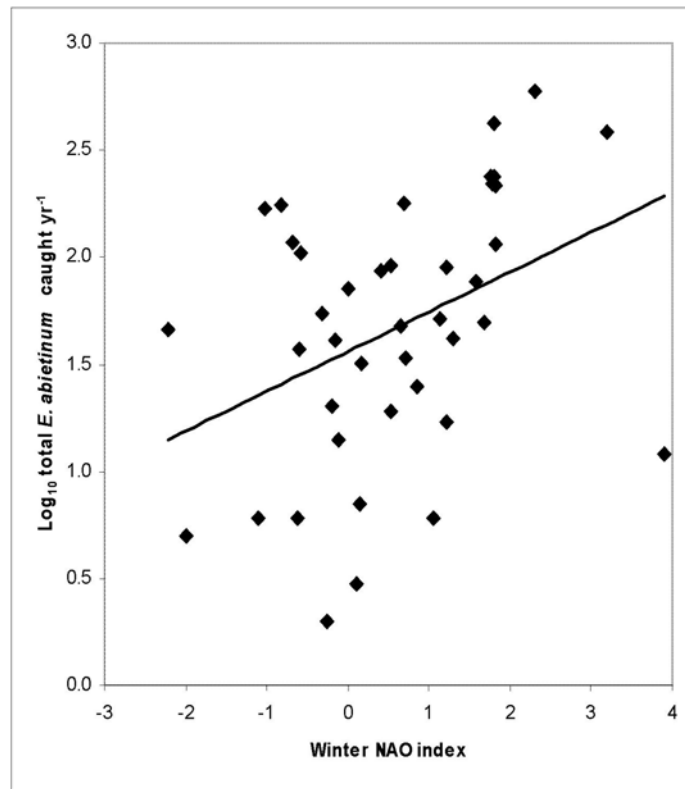
Figure 5. Relationship between the total flight period of *E. abietinum* in each year and the winter NAO index (Pearson = 0.334, P . = 0.033).

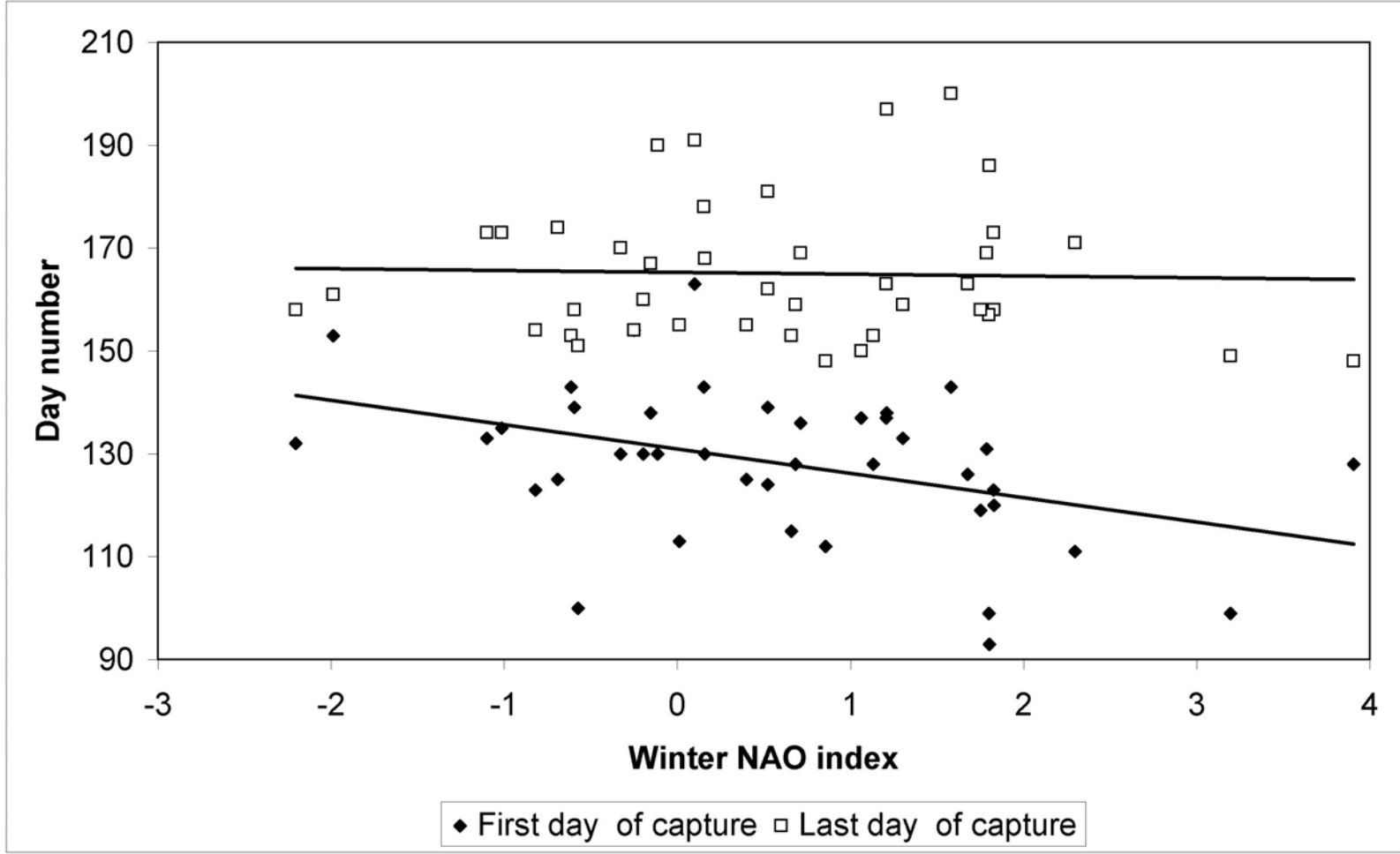
Figure 6. Relationship between the mean flight day number of *E. abietinum* and the winter NAO index (Pearson correlation coefficient = -0.402, P . = 0.009). The linear equation for the trend line is $y = -2.6575x + 147.74$.

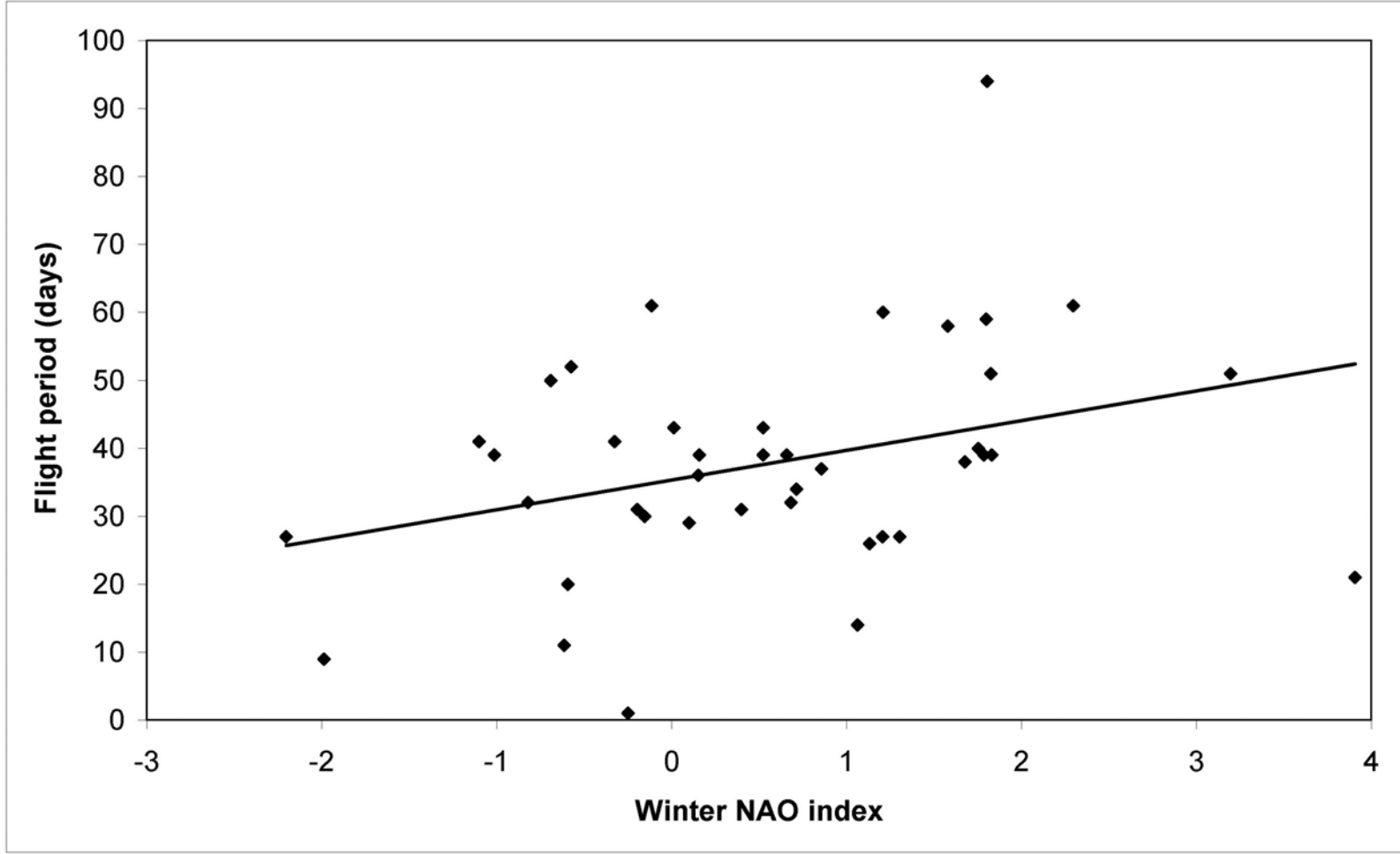
Figure 7. First date of capture, mean flight date and last date of capture of *E. abietinum* for the period 1966-2006.

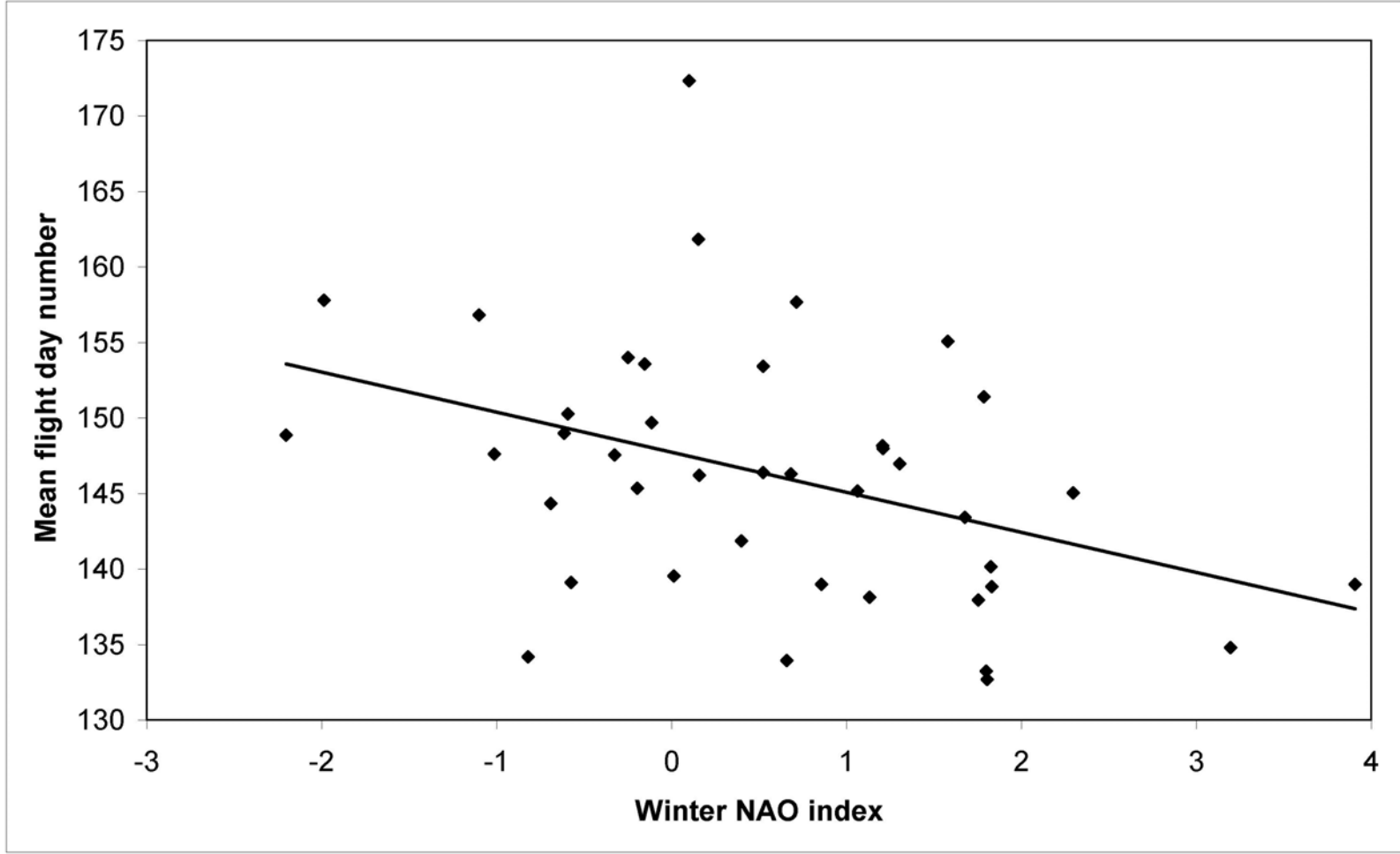


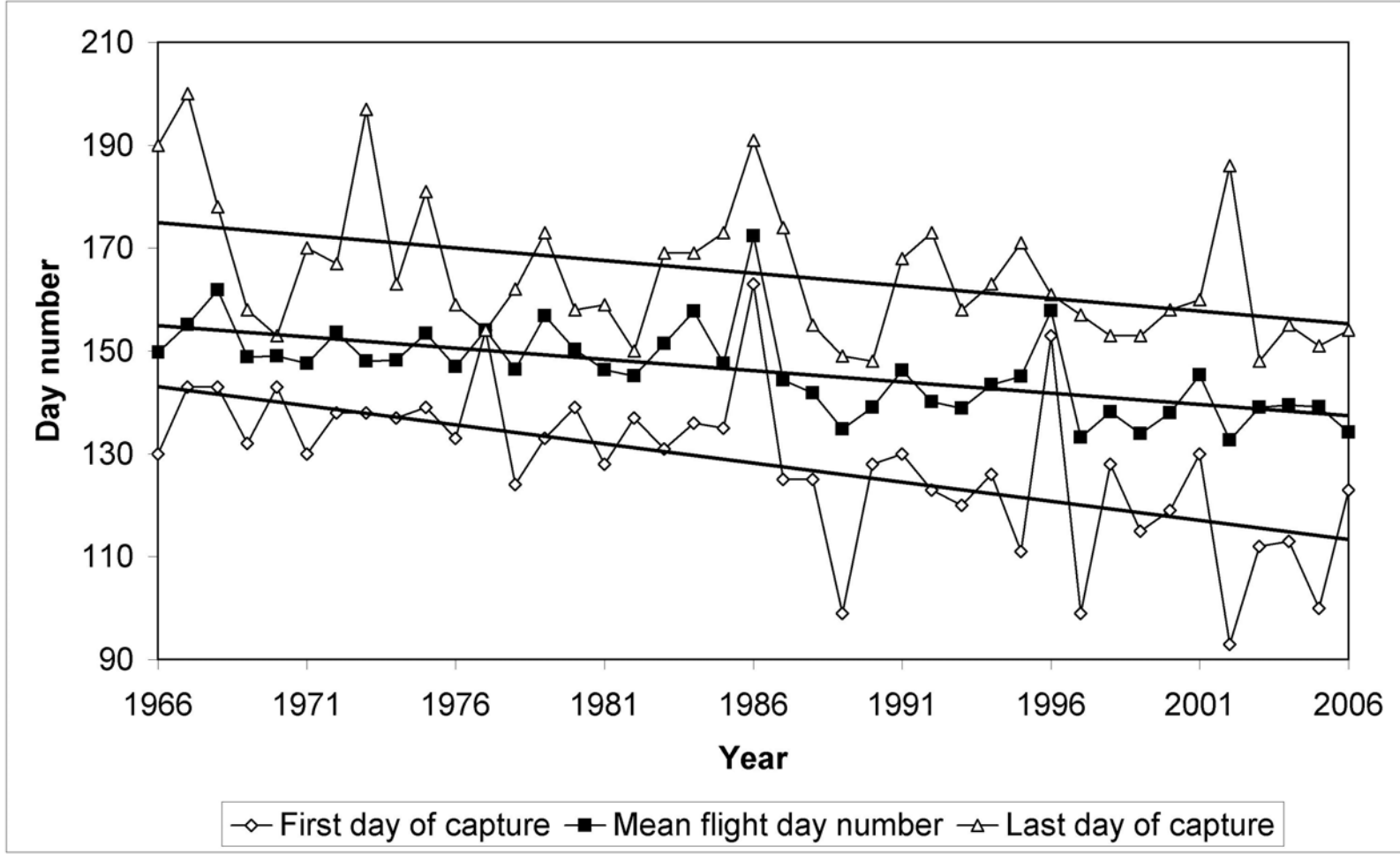












	Winter NAO index		Log ₁₀ annual total <i>E. abietinum</i>	
	Correlation coefficient	Probability	Correlation coefficient	Probability
Mean October to April temperature	0.351	0.024	0.517	0.001
Mean October to April precipitation	-0.023	0.888	-0.241	0.129
Mean January to April temperature	0.646	<0.001	0.458	0.003
Mean January to April precipitation	-0.015	0.927	-0.242	0.127
Mean May to June temperature	0.296	0.060	0.207	0.194
Mean May to June precipitation	-0.110	0.492	0.081	0.615
Winter NAO index			0.387	0.012
October to March NAO index			0.485	0.001