

## LETTER

# Timing and abundance as key mechanisms affecting trophic interactions in variable environments

Joël M. Durant,<sup>1</sup> Dag Ø. Hjermann,<sup>1</sup> Tycho Anker-Nilssen,<sup>2</sup> Grégory Beaugrand,<sup>3</sup> Atle Mysterud,<sup>1</sup> Nathalie Pettorelli<sup>1</sup> and Nils Chr. Stenseth<sup>1,4\*</sup>

## Abstract

Climatic changes are disrupting otherwise tight trophic interactions between predator and prey. Most of the earlier studies have primarily focused on the temporal dimension of the relationship in the framework of the match–mismatch hypothesis. This hypothesis predicts that predator's recruitment will be high if the peak of the prey availability temporally matches the most energy-demanding period of the predators breeding phenology. However, the match–mismatch hypothesis ignores the level of food abundance while this can compensate small mismatches. Using a novel time-series model explicitly quantifying both the timing and the abundance component for trophic relationships, we here show that timing and abundance of food affect recruitment differently in a marine (cod/zooplankton), a marine–terrestrial (puffin/herring) and a terrestrial (sheep/vegetation) ecosystem. The quantification of the combined effect of abundance and timing of prey on predator dynamics enables us to come closer to the mechanisms by which environment variability may affect ecological systems.

## Keywords

Fish, mammals, match–mismatch, plankton, seabirds, vegetation.

*Ecology Letters* (2005) 8: 952–958

## INTRODUCTION

Recent climatic changes have been reported to disrupt tight trophic interactions between predator and prey, in fish–plankton (Cushing 1990; Ottersen *et al.* 2001; Beaugrand *et al.* 2004), insect–plant (Visser & Holleman 2001) and bird–insect systems (Thomas *et al.* 2001; Winkler *et al.* 2002; Sanz *et al.* 2003; Visser *et al.* 2003). However, earlier studies have primarily focused on the temporal dimension – that climate change creates a mismatch between timing of peak breeding of predator and prey (i.e. what might properly be referred to as the temporal match–mismatch hypothesis; Cushing 1990), but typically ignoring variation in food abundance. The match–mismatch hypothesis (Cushing 1990) was first proposed for marine systems and suggest

that the interannual variability in fish recruitment is a function of the timing of the production of their food (Hjort 1914) (Fig. 1a). A similar hypothesis has later been used for other systems (e.g. birds; Nilsson 1998). The match–mismatch hypothesis predict that predator's recruitment will be high if the peak of the prey availability temporally matches the most energy-demanding period of the predators breeding phenology, while a mismatch will lead to poor recruitment. The match–mismatch hypothesis is of great interest today when climate is changing the phenology of several species, changes which may be different for different species within an ecosystem (Forchhammer *et al.* 1998; Stenseth *et al.* 2002). However, by ignoring food abundance component in the trophic interaction, our ability to discover ecological effects of

<sup>1</sup>Department of Biology, Centre for Ecological and Evolutionary Synthesis (CEES), University of Oslo, PO Box 1050 Blindern, N-0316 Oslo, Norway

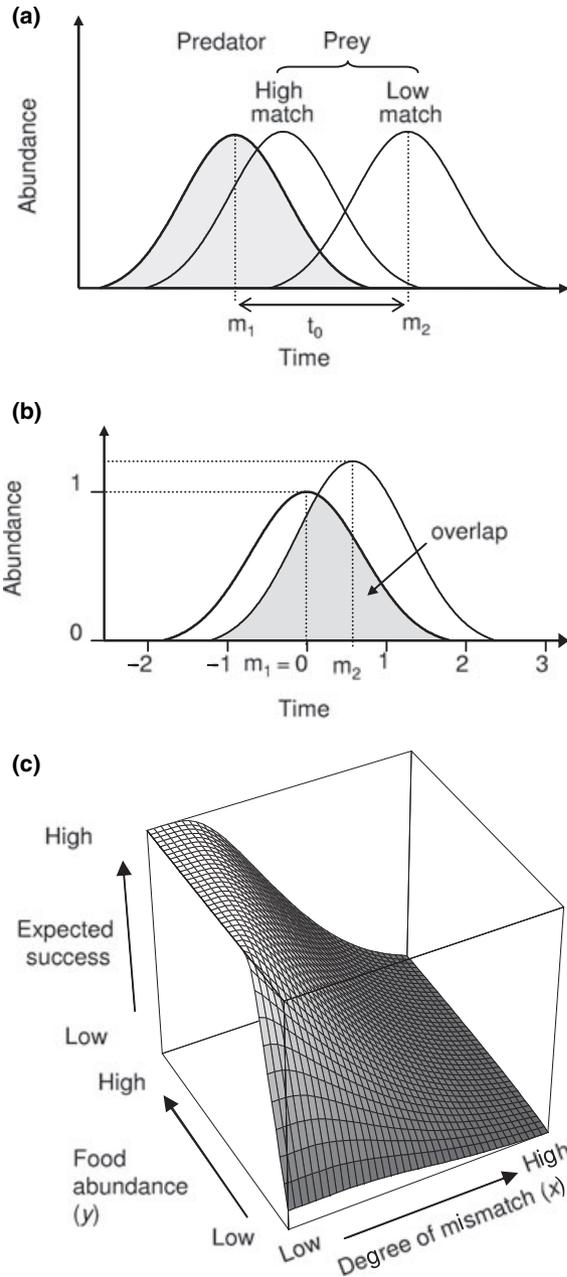
<sup>2</sup>Norwegian Institute for Nature Research (NINA), NO-7485 Trondheim, Norway

<sup>3</sup>Centre National de la Recherche Scientifique (CNRS), UMR 8013 ELICO, Université des Sciences et Technologies de Lille 1,

Station Marine, 28 Avenue Foch, BP 80, F-62930 Wimereux, France

<sup>4</sup>Flødevigen Marine Research Station, Institute of Marine Research, NO-4817 His, Norway

\*Correspondence: E-mail: n.c.stenseth@bio.uio.no



**Figure 1** Interaction between two trophic levels: (a) match–mismatch hypothesis (1). A high match is represented by a temporal overlap of the predator and its prey. An increase of the time-lag ( $t_0$ ) between the two populations leads to a low match: a small or non-existent overlap; (b) determination of the overlap of two normally distributed populations ( $y = 1/\sqrt{2\pi} \cdot s \cdot e^{[-(t - m)^2/(2s^2)]}$ , with  $t =$  time and  $s =$  standard deviation). The higher trophic level distribution ( $n_1 = 1$ ,  $m_1 = 0$  and  $s_1 = 1$ ) is the left curve. The overlap (grey shade) depends on the degree of mismatch ( $m_1 - m_2$ ) and the difference in abundances ( $n_2/n_1$ ); (c) effect on the reproductive success (overlap) of the changes in degree of mismatch and relative abundance of food for the higher trophic level.

climate change will certainly be reduced. Here we extend the match–mismatch hypothesis to also include the food abundance component of food availability.

**MATERIALS AND METHODS**

**The model**

Following the classical match–mismatch graphical representation (Cushing 1990) (Fig. 1a), we assume that the requirement and abundance of the predator and its prey follow a unimodal bell-shaped distribution. These functions are characterized by mean peak time of food requirement and abundance ( $m_1$  and  $m_2$  respectively; Fig. 1a) and the area under the curve ( $n_1$  and  $n_2$  respectively) is a measure of the total food requirement and the total food abundance (Fig. 1b). The ‘success’ of the upper trophic level (e.g. survival or reproduction of the predator) is then proportional to the area of overlap between these curves. This overlap changes as a function of the timing of the peak abundance relative to the requirement (i.e. the degree of mismatch;  $x = m_1 - m_2$ ) as well as the total abundance relative to the total requirement ( $y = n_2/n_1 =$  relative food abundance). Figure 1c shows how the overlap changes as a function of these two variables. If relative food abundance ( $y$ ) is constant, the ‘success’ decreases with increasing mismatch ( $x$ ) following a sigmoid (S-shaped) function, which may be approximated using the logistic function  $\exp(a + bx)/(1 + \exp(a + bx))$ . If mismatch ( $x$ ) is constant, the expected ‘success’ increases linearly with relative food abundance ( $y$ ) until a threshold value  $y_{\text{limit}}$  is reached (Fig. 1c) when the possible overlap is maximum. Thus, taking into account the mismatch as well as the relative food abundance surface, the overlap can be approximated by

$$F(x, y) = \begin{cases} \exp(a + bx)/(1 + \exp(a + bx)) & \text{if } y \geq y_{\text{limit}} \quad (1a) \\ [e^{a+bx}/(1 + e^{a+bx})][1 + c(y - y_{\text{limit}})] & \text{if } y < y_{\text{limit}}, \quad (1b) \end{cases}$$

where  $F(x, y)$  is proportional to the ‘success’ of the upper trophic level. That is, when  $y \geq y_{\text{limit}}$  ‘success’ depends only on the temporal match/mismatch (eqn 1a). If the relative food abundance is lower than this level, the ‘success’ is influenced by both the food abundance and the mismatch component (eqn 1b). The model is to be applied on annual data over many years.

**The data**

We applied the model to time-series data from three systems: Atlantic cod (*Gadus morhua* L.)/zooplankton (*Calanus* spp.) in the North Sea, Atlantic puffin (*Fratercula arctica* L.)/Norwegian spring spawning herring (*Clupea*

*barengus* L.) in the Norwegian Sea and Soay sheep (*Ovis aries* L.)/vegetation on Hirta, Scotland. To estimate the parameters of eqn 1, we needed to have data for the three axes (Fig. 1c) that are the degree of mismatch, the food abundance and the success of the upper trophic level, corrected or not by density, for all the studied systems. Such data are difficult to obtain and we consequently used estimates.

For Atlantic cod we used time-series between 1958 and 1999 (Beaugrand *et al.* 2004) derived from a Virtual population analysis (VPA) (Lassen & Medley 2001) based on the fisheries catch in the North Sea. As reproductive success we used the number of cod at age 1 derived from the VPA. As density index we used the spawning stock biomass of cod in the North-Atlantic. For food abundance, we used the data on *Calanus* spp. abundance collected by the Continuous Plankton Recorder survey 1958–2002 (<http://www.sahfos.org>). The abundance of *Calanus* was estimated by the area below the graph of monthly means for the first 5 months. The timing of the seasonal *Calanus* peak for the first 5 months (the central tendency,  $T$ ) was estimated using the month coordinate of the centre of gravity of this area:

$$T = \frac{\sum_{i=1}^5 Mx_m}{\sum_{i=1}^5 x_m},$$

where  $x_m$  is the mean abundance in month  $M$  (January = 1, ..., May = 5) (Colebrook & Robinson 1965). Assuming a constant hatching date of cod, this peak was used to estimate the mismatch with the yearly *Calanus* bloom.

For Atlantic puffins we used the time-series between 1980 and 2001 collected at Herynken Island (Røst archipelago, Lofoten, Norway) (Anker-Nilssen & Aarvak 2003). As food abundance index we used the average length of herring sampled from food loads brought to the colony by the adults a proxy of the local herring abundance (Anker-Nilssen & Aarvak 2003; Durant *et al.* 2003). To reduce any effects of alternative prey we only used years when Herring composed > 40% of the diet by mass. The mismatch index was calculated using the average dates of Puffin hatch and the estimated date of herring arrival. The latter was estimated using the sea temperature at 75-m depth at station Eggum 120 km north-east of the Røst archipelago (data from the Norwegian Institute Marine Research) assuming it represented an index of the strength of the Norwegian current past Røst from which depends the timing of the herring arrival at Røst if the hatching date is constant (Cushing 1990). The timing of the sea temperature peak, i.e. herring arrival date, was estimated like the timing of the *Calanus* peak, by the month coordinate of the centre of gravity of the area below the graph of monthly temperature mean values for the whole year (Colebrook &

Robinson 1965). As reproductive success we used the average fledging success, i.e. the proportion of chicks surviving to fledging. The Atlantic puffin population density was estimated using annual counts of occupied burrows in study plots distributed evenly throughout the colony (Anker-Nilssen & Røstad 1993; Anker-Nilssen & Aarvak 2003).

For Soay sheep we used time series on lamb survival between 1985 and 2000 (Clutton-Brock & Coulson 2002) for the population of animals ranging within the Village Bay study area (175 ha) on the southeast of Hirta island (St Kilda, Outer Hebrides, Scotland). Most Soay sheep offspring are conceived in November and born in April. The data are the annual average survival of the lamb to 1 year of age. As density index we used the size of the studied population. As a food abundance index for the sheep, we used the integrative Normalized Difference Vegetation Index (Tucker *et al.* 1985) between 1 March and 21 July. NDVI has been shown to correlate with vegetation conditions, phenology and abundance (Goward *et al.* 1987; Myneni *et al.* 1997). NDVI data were collected by the National Oceanic and Atmospheric Administration satellites (<http://eosdata.gsfc.nasa.gov/>). NDVI values are available on a 10-day basis, from 13 July 1981 to 21 September 2001 at a spatial resolution (pixel size) of 64-km<sup>2</sup>. Because of the relative small size of Hirta compared with a pixel, we used NDVI in the Outer Hebrides as a reference (Coulson *et al.* 2001). The mismatch index was calculated using the average Julian date of lamb birth and the estimated date of the start of vegetation growth (assumed to be when the NDVI value surpasses a threshold value of 0.39. This threshold value corresponds to beginning of the spring increase of vegetation growth determined using the curves of NDVI. The choice of another threshold value would have given a very similar result).

We found that the reproductive success was influenced by the density (or abundance) of the consumer in the cases of cod/zooplankton and sheep/vegetation. In the latter, lamb survival was also influenced by the climate the following winter [winter North Atlantic Oscillation index (NAOw) made available by Dr J.W. Hurrell at the NCAR, <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>]. We removed these effects before analysis using a linear model for log(cod spawner abundance) and sheep population size plus NAOw respectively.

### Analysis of the three systems

After verifying that no interaction between parameters can be detected we analysed the different systems. Given the reproductive success ('success'), food abundance ( $y$ ), and the time lag between the peak food requirement and the peak

food abundance ( $x$ ), we estimated the parameters ( $a$ ,  $b$ ,  $c$ ,  $J_{\text{limit}}$ ) for the various equations by minimizing the sum of squared errors of ‘success’ using a parameter search procedure in S-plus (Venables & Ripley 2002). Confidence limits and significance for the parameters were based on estimating the parameters by 1000 bootstrap samples for each of the three systems. To test the significance values we used one-sided tests with the alternative hypothesis being  $b < 0$  and  $c > 0$ , as positive  $b$  and negative  $c$  are biologically non-sensical.

## RESULTS AND DISCUSSION

In the three systems, the food abundance is an important parameter stressing its limiting effect on recruitment (Table 1). If we consider a fixed level of mismatch, the recruitment is a function of the food abundance while in the previous match–mismatch hypothesis one mismatch corresponded to one-recruitment level. The absence of the food abundance component in the previous match–mismatch hypothesis may to some extent explain the occurrence of negative results in the literature.

For the North Sea marine (cod/zooplankton) system (Fig. 2a, Table 1), recruitment is strongly linked to spawner abundance (i.e. population density of the predator), and a large part of the observed decreasing

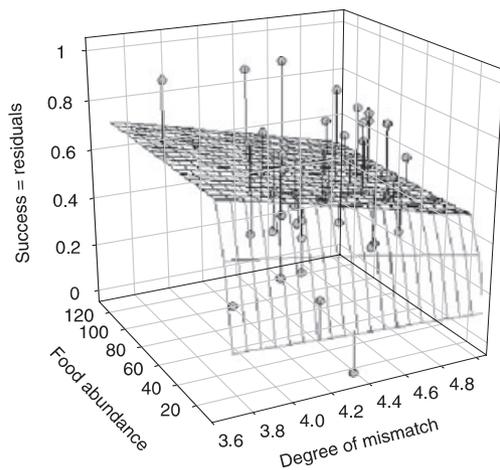
trend in cod recruitment may be explained by decreasing spawner biomass probably linked to over-fishing (Cook *et al.* 1997). After removal of this effect, we found that cod recruitment was affected by both the timing and the total annual abundance of zooplankton. In accordance with the literature (Cushing 1990), this system shows an effect of mismatch; however, it does so in association to food abundance that has an even more important effect below a certain threshold. This seems reasonable as the survival of the cod larvae depends on feeding condition but also on the level of cannibalism by older cod (Bromley *et al.* 1997; Hjermann *et al.* 2004). An increase of the zooplankton availability, which in turn increases the abundance of alternative prey for cod and hence reduces cannibalism, will be doubly beneficial for the young cod.

For the marine–terrestrial (puffin/herring) system (Fig. 2b, Table 1), only herring abundance had a significant influence on chick survival. The abundance of herring is considered to be the most important factor explaining breeding success in puffins in Røst, Northern Norway (Anker-Nilssen & Aarvak 2003; Durant *et al.* 2003). Our model using herring abundance only confirms this assumption. However, when adding a time-component, the model is improved (i.e. an additional 11% of the variability in the breeding success of puffin is accounted for but not

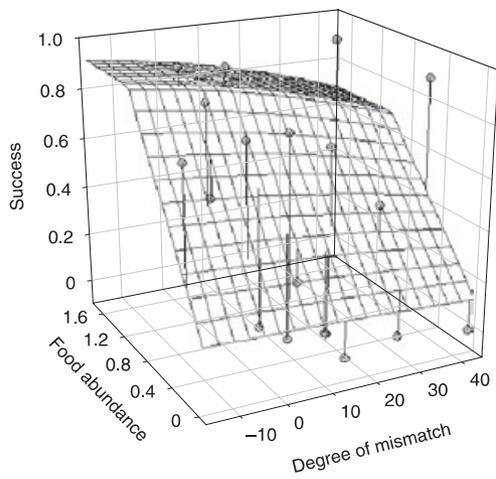
**Table 1** The values of the parameters  $b$  (mismatch),  $c$  (food) and  $J_{\text{limit}}$  (food threshold) as estimated in the three systems

System	$n$	$R^2$	2.5%	Estimate	97.5%	$P$ -value
Cod/zooplankton	44	0.89				
Mismatch			−1.511	−0.729	0.094	<b>0.037</b>
Food						
Slope			0	0.067	0.084	<b>0.038</b>
Threshold			14.754	16.635	54.122	
Atlantic puffin/herring	19	0.31				
Mismatch			−0.148	−0.027	0.028	0.190
Food						
Slope			0.131	0.800	7.615	<b>0.013</b>
Threshold			0.130	1.035	1.597	
Soay sheep/vegetation	17	0.40				
Mismatch			−0.058	0.001	0.056	0.466
Food						
Slope			2.778	4.399	14.956	< <b>0.001</b>
Threshold			0.244	None	None	

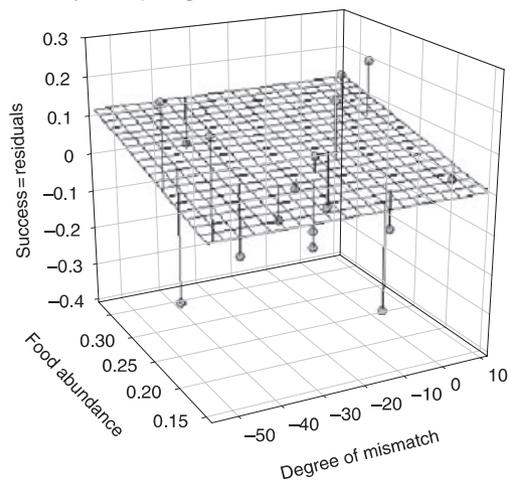
In the case of cod/zooplankton the values of ‘success’ were corrected for the effect of the population size of the upper trophic level before the analysis, and in the case of sheep/vegetation by the population size and the climate during the following winter (winter North Atlantic Oscillation index). For sheep/vegetation the best-fitting model had no food threshold in the range of the data analysed. Confidence limits and significance values are based on 1000 bootstrap samples; the significance values are one-sided tests with the alternative hypothesis being  $b < 0$  and  $c > 0$ .  $R^2$  presented is the deviance for calculated for uncorrected ‘success’. Significant effects are shown in bold. A GAM analysis of the same data confirmed the conclusions (see Table S1).

(a) Cod/*Calanus*

(b) Atlantic puffin/herring



(c) Soay sheep/vegetation



**Figure 2** Application of the theoretical overlap surface model on three different systems: (a) cod/zooplankton, with degree of mismatch ( $x$ ) as month of the year, food abundance ( $y$ ) as the zooplankton (*Calanus*) abundance, and success ( $z$ ) as residuals number of cod at age 1; (b) Atlantic puffin/herring, with degree of mismatch ( $x$ ) as number of days to the optimum match date and food abundance ( $y$ ) as herring length; (c) Soay sheep/vegetation, with degree of mismatch ( $y$ ) as the difference in days between date of birth and date of vegetation start, food abundance ( $y$ ) as the NDVI between 1 March and 21 July, and success ( $z$ ) as residuals of lamb's survival. In all cases the grid represents the model, while the actual data are indicated by dots and their distance from the grid.

significantly). This was expected as the growth of Atlantic puffin nestlings in Røst depends on young herring that drift with the coastal current to Røst from the spawning areas farther south (Durant *et al.* 2003). As such, in the absence of alternative prey, a delayed arrival will affect the growth and survival of nestlings. The breeding success of other seabirds, such as the common guillemot (*Uria aalge*) and Black-legged kittiwake (*Rissa tridactyla*), also seems to be affected by the timing of the phytoplankton bloom, apparently through the abundance of fish prey (Scott *et al.* in press).

For the terrestrial (sheep/vegetation) system (Fig. 2c, Table 1), the survival of Soay sheep lambs in Hirta, Outer Hebrides in Scotland, was significantly affected by the food abundance once taken into account the climate (Catchpole *et al.* 2000; Hallett *et al.* 2004) and density-dependence effects (Coulson *et al.* 2001). However, survival was not affected by temporal mismatch between vegetation peak and the average birth date. Also note that in most of the cases the vegetation starts after the births explaining the general negative values of mismatch. This was not fully unexpected as the Hirta island is only weakly seasonal and vegetation is available all year round (although its quality does vary substantially; Crawley *et al.* 2004). Preparing for the winter, Soay sheep accumulate body reserves (Coulson *et al.* 2001) that are also used to feed the lamb through lactation. During the first part of the year, the lambs' survival is partly depending on energy from lactation. It is then through the mother, and her use of body reserves and/or access to food, that the environment affects lamb survival.

Our theoretical and empirical analyses have extended the discussion on how environment variability affects trophic interactions in contrasting ecosystems. Indeed, by taking into account both the time and quantity components of food availability we improve our ability to detect effects of environmental changes on trophic interactions. The value of our model rests in its ability to separate (without constraints) a within-season temporal shift of trophic synchrony (the match–mismatch hypothesis) from an annual component linked to total food abundance. This

will also improve our ability to predict whether trophic cascades because of climate change are likely in a variety of systems. For example, following our model there is a food abundance threshold in the marine systems under which the recruitment, even during periods of match, can be greatly reduced with consequences on the population. Knowing this threshold will give an easy tool to predict trophic cascades because of climate change.

## ACKNOWLEDGEMENTS

We are indebted to the members of the Hirta Soay Sheep Project, National Centre for Atmospheric Research (NCAR), Sir Alister Hardy Foundation for Ocean Science (SAHFOS), National Oceanic and Atmospheric Administration (NOAA), and Institute of Marine Research in Bergen (IMR, Norway) who kindly gave access to their data. We thank L. Ciannelli, T. Coulson, G. Ottersen and three anonymous referees for helpful comments on the manuscript.

## SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>:

**Table S1** GAM analysis results.

## REFERENCES

- Anker-Nilssen, T. & Aarvak, T. (2003). The population ecology of Puffins at Røst. Status after the breeding season 2002. *NINA Oppdragsmelding*, 784, 1–40.
- Anker-Nilssen, T. & Røstad, O.W. (1993). Census and monitoring of puffins *Fratercula arctica* on Røst, N Norway, 1979–1988. *Ornis. Scand.*, 24, 1–9.
- Beaugrand, G., Brander, K.M., Lindley, J.A., Souissi, S. & Reid, P.C. (2004). Plankton effect on cod recruitment in the North Sea. *Nature*, 426, 661–664.
- Bromley, P.J., Watson, T. & Hislop, J.R.G. (1997). Diel feeding patterns and the development of food webs in pelagic 0-group cod (*Gadus morhua* L.), haddock (*Melanogrammus aeglefinus* L.), whiting (*Merlangius merlangus* L.), saithe (*Pollachius virens* L.), and Norway pout (*Trisopterus esmarkii* Nilsson) in the northern North Sea. *ICES J. Mar. Sci.*, 54, 846–853.
- Catchpole, E.A., Morgan, B.J.T., Coulson, T.N., Freeman, S.N. & Albon, S.D. (2000). Factors influencing Soay sheep survival. *Appl. Stat.*, 49, 453–472.
- Clutton-Brock, T.H. & Coulson, T.N. (2002). Ungulate population dynamics: the devil is in the detail. *Phil. Trans. R. Soc. B*, 357, 1299–1306.
- Colebrook, J.M. & Robinson, G.A. (1965). Continuous plankton records: seasonal cycles of phytoplankton and copepods in the north-eastern Atlantic and the North Sea. *Bull. Mar. Ecol.*, 6, 123–139.
- Cook, R.M., Sinclair, A. & Stefánsson, G. (1997). Potential collapse of North Sea cod stocks. *Nature*, 385, 521–522.
- Coulson, T.N., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H. *et al.* (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, 292, 1528–1531.
- Crawley, M.J., Albon, S.D., Bazely, D.R., Milner, J.M., Pilkington, J.G. & Tuke, A.L. (2004). Vegetation and sheep population dynamics. In: *Soay Sheep: Dynamics and Selection in an Island Population* (eds Clutton-Brock, T.H. & Pemberton, J.M.). Cambridge University Press, Cambridge, pp. 89–112.
- Cushing, D.H. (1990). Plankton production and year-class strength in fish populations – an update of the match mismatch hypothesis. *Adv. Mar. Biol.*, 26, 249–293.
- Durant, J.M., Anker-Nilssen, T. & Stenseth, N.C. (2003). Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proc. R. Soc. Lond. B*, 270, 1461–1466.
- Forchhammer, M.C., Post, E. & Stenseth, N.C. (1998). Breeding phenology and climate. *Nature*, 391, 29–30.
- Goward, S.N., Dye, D.G., Kerber, A. & Kalb, V. (1987). Comparison of North and South American biomes from AVHRR observations. *Geocarto Int.*, 1, 27–39.
- Hallett, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B.T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather? *Nature*, 430, 71–75.
- Hjermann, D.O., Stenseth, N.C. & Ottersen, G. (2004). The population dynamics of North-east Arctic cod through two decades: an analysis based on survey data. *Can. J. Fish. Aquat. Sci.*, 61, 1747–1755.
- Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. *Rapp. PV Réun. Cons. Int. Exp. Mer.*, 20, 1–228.
- Lassen, H. & Medley, P. (2001). *Virtual Population Analysis – A Practical Manual for Stock Assessment*. FAO Fish Tech. Pap. 400, Rome.
- Myneni, R.B., Keeling, C.D., Tucker, C.J., Asrar, G. & Nemani, R.R. (1997). Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature*, 386, 698–702.
- Nilsson, J.-Å. (1998). Fitness consequences of timing of reproduction. In: *Proceedings of the 22nd International Ornithology Congress*. (eds Adams, N.J. & Slotow, R.H.). BirdLife South Africa, Durban, Johannesburg, pp. 234–247.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. & Stenseth, N.C. (2001). Ecological effects of the North Atlantic oscillation. *Oecologia*, 128, 1–14.
- Sanz, J.J., Potti, J., Moreno, J., Merino, S. & Frias, O. (2003). Climate change and fitness components of a migratory bird breeding in the Mediterranean region. *Glob. Change Biol.*, 9, 112.
- Scott, B.E., Sharples, J., Wanless, S., Ross, O., Frederiksen, M. & Daunt, F. (in press). The use of biologically meaningful oceanographic indices to separate the effect of climate and fisheries on seabird breeding success. In: *Top Predators in Marine Ecosystems: their Role in Monitoring and Management* (eds Boyd, I.L., Wanless, S. & Camphuysen, C.J.). Zoological Society of London Conservation Biology Series No. 12, Cambridge University Press, Cambridge, UK.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.-S. & Lima, M. (2002). Ecological effects of climate fluctuations. *Science*, 297, 1292–1296.
- Thomas, D.W., Blondel, J., Perret, P., Lambrechts, M.M. & Speakman, J.R. (2001). Energetic and fitness costs of

- mismatching resource supply and demand in seasonally breeding birds. *Science*, 291, 2598–2600.
- Tucker, C.J., Townshend, J.R.G. & Goff, T.E. (1985). African land-cover classification using satellite data. *Science*, 227, 369–375.
- Venables, W.N. & Ripley, B.D. (2002). *Modern Applied Statistics with S*, 4th edn. Springer, New York, NY.
- Visser, M. & Holleman, L. (2001). Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B*, 268, 289–294.
- Visser, M., Adriaansen, F., Van Balen, J., Blondel, J., Dhondt, A., Van Dongen, S. *et al.* (2003). Variable responses to large-scale climate change in European *Parus* populations. *Proc. R. Soc. Lond. B*, 270, 367–372.
- Winkler, D.A., Dunn, P.O. & McCulloch, C.E. (2002). Predicting the effects of climate change on avian life-history traits. *Proc. Natl. Acad. Sci. USA*, 99, 13595–13599.

Editor, Jordi Bascompte

Manuscript received 4 April 2005

First decision made 12 May 2005

Manuscript accepted 18 May 2005