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General News

Conservation Scores a Biological Control Success

A recent study in Scotland provides robust evidence for an unusual case of biological control, involving the recovery of two threatened species.[1] The results reinforce findings of a previous study in Ireland.[2] There is now clear evidence from the British Isles that the recovery and range expansion of the pine marten (*Martes martes*), a native mustelid predator, is skewing competition between the invasive North American grey squirrel (*Sciurus carolinensis*) and the native red squirrel (*Sciurus vulgaris*), and facilitating recovery of the native squirrel species from a precipitous decline.

The pine marten was exterminated in large parts of the British Isles in the 19th century through hunting for fur, predator control by gamekeepers and habitat loss. Populations became restricted largely to northern Scotland and western Ireland. Although it remains the second-rarest mammal in the British Isles, reforestation, legislation and conservation activities have facilitated a comeback, and since the 1990s its range has been slowly expanding. Pine marten is now naturally distributed throughout much of Scotland and the Irish midlands, with small populations in parts of Wales and England.

The native red squirrel suffered a steep decline in the 20th century initially through resource competition from the larger North American grey squirrel, which was introduced to Great Britain several times in the 1870s–1920s and to Ireland in 1911. The grey squirrel has replaced the native species through much of its former range: only isolated red squirrel populations remained in England and Wales, and its range otherwise shrank to central and northern Scotland and the west of Ireland. The threat to red squirrel from grey squirrel has been greatly exacerbated in recent decades by squirrel pox virus (SQPV): grey squirrel is an asymptomatic vector but the disease is fatal in red squirrel. First reported in Great Britain in the 1980s, SQPV incidence in grey squirrels was 42–100% by the mid-2000s in England and Wales, although the first record in Scotland was not until 2005, and it was first detected in Ireland as late as 2011.[3] Grey squirrel is not only a threat to red squirrel, but by stripping bark of young trees is also a forestry pest. Its invasive range also includes Italy, from where it could potentially invade a vast region of Eurasia.

Conservation measures for red squirrel remnant populations and at the edge of the grey squirrel invasion rely on heavy (therefore expensive and also not universally supported) culling of grey squirrel populations to below competitive levels. But even this level of culling was insufficient to break transmission of SQPV, and the outlook for the red squirrel seemed bleak. From the 1990s onwards, however, anecdotal reports of red squirrel recovery were emerging in Ireland and Scotland. These coincided with reports of pine marten range expansion, including sightings in areas where the predator had not been recorded for decades. Results of surveys in the Irish midlands showed that by the early 2010s, the pine marten, which had been restricted to west of the River Shannon, now extended throughout the region as far as the east coast.[2]

This study also found that grey squirrel populations had crashed in some 9000 km^2 of its previous range in the Irish midlands and the invasion front had retreated 100 km to the east, leaving it a rare species in much of the central midlands. In contrast, the red squirrel had recolonized 6500 km^2 of its historic range, from which it had been absent for up to 30 years, and it is now common and widespread there. The areas lost by the grey squirrel and regained by the red squirrel lie entirely within the expanded range of the pine marten. Overlap between pine marten and remaining abundant grey squirrel populations was found in the eastern part of the region, where the recently arrived pine marten is at lower density. The study found pairwise correlations between detection of pine marten and red squirrel on a landscape level (strongly positive) and pine marten and grey squirrel on a woodland level (negative). The methodology did not allow conclusions about causality, although factors such as culling and resource limitation were ruled out, and live trapping suggested that the overall status and health of grey squirrels were poorer in the central midlands where pine martens are well established. The authors suggested that pine marten density might be the key factor.

The research in Scotland[1] built on the Irish study. Multi-species sampling by different methods (hair samples from feeders ± trail cameras) allowed differences between species in detectability to be identified and taken into account. The results were used to model red and grey squirrel occupancy for various factors (e.g. region, attributes of habitats, pine marten presence). A key part of the study was identifying individual pine martens from hair samples to provide spatial capture–recapture information, which was used to estimate not only pine marten density but also each individual's use of space ('density-weighted connectivity'), i.e. how 'pine marten rich' a neighbourhood is. This latter estimate allows the likelihood of encounters between pine marten and prey to be assessed as a measure of overall exposure to predation.

Field work was carried out in January–May 2016 in three regions: the northern Scottish highlands, which pine marten recolonized some 45 years ago and grey squirrel has not reached; central Scotland, which pine marten has recently recolonized (8–14 years) and where grey squirrel has been present for some 70 years; and the southern Scottish borders, which pine marten began to recolonize in the past

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few years while grey squirrel has been present for at least 30 years. SQPV is now endemic in central Scotland, but was not detected in the borders until 2017. In the regions where the squirrel species coexist (central and borders), study sites were selected to favour grey squirrel (>30% mixed broadleaf woodland). Although pine marten densities were lower in the borders than in the other two regions, and grey squirrel is not found in the highlands, the authors argue their analysis is valid as it is based on large intra- as well as inter-regional variation.

Results showed a strong relationship between squirrel occupancy and likelihood of encounter with pine marten (density-weighted connectivity). The correlation was negative for grey squirrel and positive for red squirrel. The negative impact of pine marten on grey squirrel occupancy was greater in central Scotland where the species have coexisted for longer than in the borders. The positive relationship between likelihood of encounter with pine marten and red squirrel occupancy included the highlands where there are no grey squirrels.

The authors suggest how behavioural differences may influence squirrel competitiveness in the presence of pine marten. Camera data showed that red squirrels are less likely than grey squirrels to use feeders. The Irish study reported a difference of 15.6% and 2.5% in frequency of grey and red squirrel in pine marten scats, respectively. As a coevolved species, red squirrel may be more wary of feeders (but not otherwise deterred from suitable habitat) if pine marten is in the area, compared with grey squirrel, which has no coevolutionary history with pine marten or similar species, and is thus more prone to direct encounter including predation.

The authors conclude that the results provide "unequivocal support" for the role of the recovering pine marten in modifying competition between the two squirrel species, and skewing it heavily in favour of the native species. As SQPV has been skewing competition heavily in favour of the grey squirrel, the pine marten's impact is particularly striking because it is large enough to outweigh this. The authors do stress that red squirrel is not going to re-appear across the entire British Isles, and certainly not any time soon: it will be a slow process and limited to areas where the shy, elusive pine marten can re-establish. (Separate work by the Vincent Wildlife Trust is focused on restoring pine marten populations in some promising areas.) Nevertheless, it is a welcome example of how conservation and biological control can be synergistic.

An important point the authors make is that a high standard of evidence is a pre-requisite for shaping environmental policy where threatened species are at issue, and they believe that this study provides that. While it confirms that resurgence of pine marten is not having adverse impact on red squirrel even in the absence of grey squirrel, there are other conservation and land management issues. Pine marten is reported to have adverse impact in years of low prey abundance on ground-nesting birds including the capercaillie (*Tetrao urogallus*), whose populations are threatened by climate change. The authors call for rigorous methodology such as they have used in future research in this area. Such research could also help inform a related conflict of interest: the impact of pine marten recovery on the game bird industry. The firm evidence in this paper about the negative impact of the pine marten on grey squirrel may help influence land managers with interests in both commercial forestry and rearing game birds that gains to the former from pine marten presence could outweigh potential losses to the latter.

[1] Sheehy, E., Sutherland, C., O'Reilly, C. and Lambin, X. (2018) The enemy of my enemy is my friend: native pine marten recovery reverses the decline of the red squirrel by suppressing grey squirrel populations. *Proceedings of the Royal Society B* 285, 20172603.

[2] Sheehy, E. and Lawton, C. (2014) Population crash in an invasive species following the recovery of a native predator: the case of the American grey squirrel and the European pine marten in Ireland. *Biodiversity and Conservation* 23, 753–774.

[3] Rushton, S., Lurz, P., Gurnell, J., Nettleton, P., Bruemmer, C., Shirley, M. and Sainsbury, A. (2006) Disease threats posed by alien species: the role of a poxvirus in the decline of the native red squirrel in Britain. *Epidemiology & Infection* 134, 521–533.

Contact: Xavier Lambin, Professor of Ecology, University of Aberdeen, UK.
Email: x.lambin@abdn.ac.uk

Chris Prior: Good Company and an Important Scientist

Dr Chris Prior, born on 27 June 1949, was an internationally renowned biologist: perhaps best known for a discovery leading to the development of effective locust control using a naturally occurring fungus disease. He also did important work in horticulture and on disease management of the cocoa crop. News of his sudden, accidental death has prompted messages of shock and sympathy from six continents.

Chris occasionally mentioned his student days at Cambridge: he was taught by Dennis Garrett (one of the 'pioneers' of plant pathology) and tropical botany by E. J. H. Corner (his last lecture series before retirement) … "Just eight lectures and they changed my life. I had never thought of going and working in the tropics before I heard him, but after I heard them I always thought that was what I should do. After three more years of PhD work, I got a job in Papua New Guinea and so off I went." Apparently Corner didn't actually seem to pay much attention to the real world, it seemed that he had just been brought back from some deep forgotten place to say "Oh really, you want to know about the flora of Socotra, well, I suppose so ... but WHY? Who knows, but here goes, although I'm afraid I can't find my pith helmet." It is perhaps significant that Chris's scientific development somewhat followed Corner's biography: from botany via plant pathology to an interest in insect pathology.

Papua New Guinea (PNG) days focused on cocoa crop pathology at the Lowlands Agricultural Experimental Station (LAES) under the PNG Cocoa Board of the 1980s: in particular, pioneering work on a disease called vascular-streak die-back. Chris's importance in this field is regularly acknowledged by Philip Keane (Latrobe University, Australia), who remembers him as a talented, unique and good-humoured person. He has a clear recollection of the day Chris "arrived in Keravat and unpacked his only two boxes of possessions, consisting entirely of a hi-fi record player, two gigantic speakers and an amazing record collection, mainly classical." They sat at dusk in his house, drinking "a beer" and listening to Julian Bream. Tributes have also come in from other, now very senior, colleagues including Josephine Saul-Maora and John Moxon, repeating words such as "inspirational, talented, industrious, creative, fine intellect, always positive, friendly and cooperative." It was in PNG that Chris had his 'big idea': the rather counter-intuitive one that fungus diseases can be made to control insect pests (in that case a rather spectacular weevil called *Pantorhytes*) more effectively when formulated in oil rather than in water.

After several years in PNG, Chris returned to England, having secured a position with CABI in what was then the International Institute of Biological Control at Silwood Park, Berkshire. Between 'odd jobs' including a rather hazardous field visit to the fledgling Eritrea and assessing potential diseases to control the coconut rhinoceros beetle, Chris started to formulate a project: **the project,** with the help of David Greathead and Jeff Waage. David had assessed natural enemies of locusts for his PhD and concluded that 'standard' parasites and predators were never going to provide more than 10% control; either we would have to continue spraying (the then highly toxic) chemicals, or another approach was needed. A fungus called *Metarhizium* appeared to be highly virulent to locusts in the laboratory: so might this just be combined with the PNG idea? Jeff remembers sitting around a coffee table with Chris and David and seeing this idea slowly take shape in front of their eyes, and that "Aha!" moment. They realised that Chris's idea of a locust pathogen delivered in oil, often sprayed from the air, posed not only a real scientific challenge, but a timely response to a large locust outbreak in the mid-1980s. The donor community was increasingly reluctant to buy chemical pesticides for locust control so a joint paper was written for FAO and a project proposal followed. The first phase of the project was provisionally approved, with one very senior locust control expert saying something along the lines of "I've heard many stupid 'alternative' control ideas, but this one is the least ridiculous."

At the time, Silwood Park contained a unique and eclectic mix of ecologists and biological control scientists, together with a few pesticide scientists and a nuclear reactor. My first recollection of Chris dates from the early summer of 1989 when finishing-off my PhD. One morning, a lean, bearded, softly spoken and obviously very intelligent chap wandered into the International Pesticide Application Research Centre and said "I intend to control locusts using fungi in the semi-arid areas of Africa and need someone who knows a bit about spraying." I thought "using fungi in the Sahel – how can that possibly work?", but needed a job and became one of the first to have the privilege of joining what was to become the LUBILOSA Programme team. Scientists are supposed to delight in being proved wrong (of course, this is only partially true!); the 'Devil's advocacy' had all but gone in a relatively few months, and the job was to convince the rest of the world about the viability of the idea … first in the lab, then in increasingly large-scale field trials. One of the first tasks was to establish field teams in Africa, with the late Chris Lomer starting work at the International Institute of Tropical Agriculture (IITA) in Benin and Christiaan Kooyman in Niger.

All colleagues agree that working with Chris was a very special experience – Nina Jenkins describes what a true pleasure it was: several of us "wouldn't be where [we] are today if it had not been for his mentorship and guidance. We had some wild times with the LUBILOSA team, vivid memories that [we] will cherish forever." Dave Moore adds: "Chris was modest about his extensive knowledge, but very generous with it. [We] all benefited from conversations, often meandering but returning to the point, which led to improvements in the science, and the scientists concerned. He led using his knowledge but never sought the credit, which went to the individuals and the LUBILOSA team. He was very supportive of his colleagues and they flourished under his carefully disguised mentoring. Usually quiet, he was very good and entertaining company, especially one-to-one. He was stoic and tough as he needed to be with some of his overseas trips …" Having had the sheer tenacity to start it up, Chris was Programme Leader for the first two (scientific proving) stages, with this minimalist but effective management style (i.e. giving team members 'enough rope to hang their ideas with' – or otherwise). He often actively participated in lab experiments and field trials, also taking a sabbatical with CSIRO in Australia and helping to set up a similar project for the control of the Australian plague locust. CABI's UK Country Director, Dick Shaw, says "CABI certainly owes a lot to Chris, whose vision, knowledge and ultimately success, gave us international credibility in the field of biopesticides on which we continue to build."

With a strong sense of having 'completed his work' at CABI, Chris joined the Royal Horticultural Society (RHS) at Wisley in 1996 as Senior Plant Pathologist, becoming Head of Horticultural Science from 2001 until his retirement in 2007. Guy Barter (RHS Chief Horticulturist) wrote that Chris was particularly proud of the 2002 RHS publication *Gardening in the Global Greenhouse*, which laid the foundations for subsequent work on climate change. Apparently, Chris was the main instigator of their regular Friday pub meals where they would set the world to rights, discuss vintage cars and listen to his accounts of his adventures in far off places. He particularly liked to 'wind-up' Guy by professing a disdain for horticulture since he regarded plants as "mere substrates for more interesting organisms such as plant diseases". Peter Neuenschwander from IITA, however, remembers above all a visit to the Royal Botanic Gardens at Kew in London and Chris's "infective joy sharing his knowledge of tropical plants" as they compared memories of encountering the same plants in the forests of PNG and West Africa. Although not a gardener at Wisley, it must have had some influence because after retirement to Devon he became an enthusiastic vegetable and 'unusual' flower grower.

I have minimized the technical details here (there are many papers and book chapters), but no one should doubt the important scientific contributions that Chris made – for which many (around the world) are very grateful indeed. He is survived by two sisters and their families.

Compiled by: Roy Bateman.

A version of this obituary also appears in the newsletter of the Society of Invertebrate Pathology.

Eucalyptus Snout Beetle: Early Intervention Pays Dividends

An economic assessment of the eucalyptus snout beetle (*Gonipterus platensis*) biological control programme in Portugal reveals significant benefits from introducing *Anaphes nitens* to control the pest, even though the agent has not been effective in all parts of the country. It also shows the added benefit of acting quickly to implement a control programme.[1] The authors note that they have been selective in the costs they have included and conservative in their estimates, so actual benefits are likely to be even higher.

Gonipterus platensis, first detected on *Eucalyptus globulus* in Portugal in 1995, is one of three Australian species in this genus that have become worldwide pests of eucalypts. The coevolved mymarid parasitoid *A. nitens* was first introduced and successfully controlled a *Gonipterus* species in South Africa nearly a century ago. Since then it has been released in many countries for the same purpose, with widespread although not universal success. It remains the most commonly deployed strategy against *Gonipterus* spp. on eucalypts.

Given the importance of eucalypts in international trade, relatively little is known about the economics of pest impact and control. Portugal's eucalypt wood production is a significant part of world trade: *E. globulus*, used for pulp and paper production, is the most extensively grown plantation species. The country accounts for about half of European and one-quarter of world production of this species.

By the time *G. platensis* was detected in Portugal, it was already the subject of a biological control programme in Spain, where *A. nitens* had been introduced the year before, 1994. There were no geographical barriers to prevent the biocontrol agent dispersing naturally to Portugal. In 1997, however, a programme was initiated to introduce, rear and release *A. nitens* in Portugal to expedite biological control in the country's *E. globulus* plantations. Between then and 2000, some 300,000 parasitoids were released. *Anaphes nitens* was quick to establish and parasitism rates of up to 80% were recorded within the first year. Now, 20 years later, the agent is widely distributed across Portugal. Successful control has been recorded in southern and coastal areas, although it has proved ineffective in northern and central areas with cooler climates.

Annual surveys provided data on the area infested each year by the pest during its dispersion phase (1996–2003). For this study, 85,000 ha of plantation representing all areas of the country were assessed for damage between 2011 and 2014. The recorded distribution of the pest was extrapolated by using annual inventories of areas under plantation to give estimates for the area of pest infestation for each year, 2004–2016. A model developed for analogous conditions in Portugal was used to calculate tradeable wood loss under different levels of defoliation, and from this economic loss was estimated, discounted to present values using recommended methods.

Economic benefits from the biocontrol agent for the years 1996–2016 were assessed by considering a series of scenarios. First, the authors compared current estimated losses (i.e. in the presence of biological control) with an assumed 75% yield loss from *G. platensis* in the absence of the biocontrol agent; the latter loss is probably an underestimate given observations of 100% yield loss in Portugal and South Africa if the pest is not controlled. They also considered three scenarios other than biological control: (i) using less-susceptible *Eucalyptus* species when replanting after harvesting (i.e. not wholesale replacement, so not an additional cost), (ii) using insecticides on 50% of the area only (owing to legal and certification scheme restrictions), and (iii) neither of the above (i.e. no control) with the shortfall in timber for the pulp/paper industry being imported. A benefit–cost analysis of the programme to accelerate biological control by importing the biocontrol agent was also conducted, which assumed a delay of one, two or three years in the establishment of biological control, based on the natural dispersal rate of *A. nitens.*

Results of surveys and extrapolations indicated that 46% of the area planted with *E. globulus* is attacked by *G. platensis*, i.e. biological control is partial. The worst attacks by the pest were in the northern, cool mountainous region where biological control has been ineffective. Actual losses from the pest were estimated to be 648 million euros over 20 years. However, the alternative scenarios to biological control gave net estimated losses of 1803–6516 million euros (i.e. in addition to those actually recorded with biological control in place), meaning that this partially successful biological control programme has had large benefits. Of the alternatives, resorting to importing wood was the most costly, and economic losses would also have been 2–4 times higher with either of the other options. The authors point out, however, that none of these three scenarios is likely to be sustainable on its own, but economic analysis of potential combinations would be difficult. In fact, where biological control has not been successful in the north of the Iberian Peninsula, a combination of replacement with *Eucalyptus nitens* (although not an ideal substitute) and insecticide measures have been implemented. Data from industry reports indicate a sharp increase in timber imports corresponding reasonably well with estimates in this study, so *G. platensis* is likely to have been a major driver.

Fast-tracking biological control by importing agents also proved to have been worth it. The cost of the programme was estimated at 1.1 million euros (present values), which gave benefit–cost ratios of between 67 and 347 to one for preventing the estimated potential delay in biological control of 1–3 years. This indicates the advantages of responding promptly to the arrival of an invasive pest of an economically important species, especially when a tried-and-tested biocontrol agent is readily available.

[1] Valente, C., Gonçalves, G.I., Monteiro, F., Gaspar, J., Silva, M., Sottomayor, M., Paiva, M.R. and Branco, M. (2018) Economic outcome of classical biological control: a case study on the eucalyptus snout beetle, *Gonipterus platensis*, and the parasitoid *Anaphes nitens*. *Ecological Economics* 149, 40–47.

Contact: Carlos Valente, RAIZ – Instituto de Investigação da Floresta e Papel, Aveiro, Portugal.
Email: carlos.valente@thenavigatorcompany.com

Exploring Biological Control: Non-native Comb Jellies in the Black Sea

The accidental introduction of the ctenophore or comb jelly *Mnemiopsis leidyi* from the Gulf of Mexico to the Black Sea in the early 1980s added to what was already an unfolding environmental catastrophe due to anthropogenic activities in and around this semi-enclosed water body. As *M. leidyi* spread throughout the Black Sea it attained high abundance and a huge biomass. Population levels were maintained through the greater part of the year (even winter in warm years). Maximum annual biomass of its zooplankton prey fell by more than an order of magnitude and its biodiversity plummeted to just a few species, with a cascade of other bottom-up and top-down effects on the ecosystem and fisheries. Accidental introduction in 1997 of *Beroe ovata*, a ctenophore that feeds on *M. leidyi*, provided unexpected biological control. Predation by *B. ovata* led to a sharp drop in *M. leidyi* populations, while the period of maximum abundance (when *M. leidyi* inflicts damage to zooplankton populations) shrank to 1–3 months per year. (Also see *BNI* 25(2), June 2004.)

Twenty years on, biological control is still being exerted on an annual basis and zooplankton biodiversity has largely recovered, but *M. leidyi* (and *B. ovata*) populations have varied considerably between years. There is also a perceived trend of lower *M. leidyi* populations in recent years. Drawing on over a quarter of a century of monitoring data from the northeastern and northern Black Sea, scientists have been investigating the mechanisms that underlie these phenomena: how the two non-native ctenophores populations interact, the influence of environmental factors, long-term trends and potential impact of climate change.[1–3]

A paper in *Ecological Modelling* uses 27 years' experimental and field data and a demographic model to explore in- and between-year fluctuations in ctenophore populations in the northeastern Black Sea.[1] The study uses field data collected by the P. P. Shirshov Institute of Oceanology (Russian Academy of Sciences) in Moscow during surveys conducted in the northeastern Black Sea in 1994–2002, and from a 1000-m transect from the shore at one location (Blue Bay, near Gelendzhik) in 2000–2017. An earlier study using the same data sources assessed three linked hypotheses to examine how *B. ovata* controls *M. leidyi* in the Black Sea, and the role of environmental conditions.[2] The model allows the roles of *B. ovata* and environmental conditions in *M. leidyi* annual variation to be further explored by testing different scenarios.

Survey data showed a tight relationship between the two ctenophores, based on the specificity of *B. ovata* for *M. leidyi* in the Black Sea. Sampling revealed seven life cycle steps: adult *M. leidyi* start to reproduce, and reach an annual peak of reproduction; this is followed quickly by the appearance of adult *B. ovata*, which start to reproduce too, and reach their annual peak; at this point, *M. leidyi* larvae disappear (i.e. not found in samples), and then *B. ovata* larvae disappear too. This was a consistent annual pattern across all sampling years (although the timing and duration of the steps varied between years). Moreover, even though maximum annual abundance of both species varied by over an order of magnitude across years, there was always strong covariability between the species. Modelling 'with' and 'without' *B. ovata* scenarios illustrated how the predator limited *M. leidyi*'s maximum population size and precipitated a faster decline, i.e. a shorter period of high abundance, than in the predator's absence (although the authors mention August temperatures above 27°C, the upper threshold for *M. leidyi* reproduction, as potentially limiting too – see also study[3] below).

Assessment of the effects of environmental factors, using experimental/observational data and modelling, indicated that annual maximum abundance of *M. leidyi*, and *B. ovata*, was significantly related to high surface water temperature in spring (March–May, with a threshold of 11.8°C for reproduction), a high zooplankton mass in spring and (especially) early summer (June–July), and wind velocity normal to the coast, which affects ctenophore movement from overwintering to breeding areas. Overall, higher spring zooplankton populations in warmer years were correlated with higher *M. leidyi* and *B. ovata* populations. Modelling scenarios that explored seasonal dynamics demonstrated how variations in maximum spring temperature and the timing and maximum biomass of zooplankton related to abundance of zooplankton and the two ctenophore species over time, and also how higher overwintering populations were related to higher seasonal populations of both ctenophores.

Survey data also revealed that the timing of *M. leidyi* and *B. ovata* life cycles have become more closely coupled in recent years. From about 2005, *M. leidyi* started reproducing and reaching peak reproduction and high abundance earlier than previously, and this was correlated with warmer surface water temperatures in these early months. *Beroe ovata* also started appearing earlier around this period (June–July cf. second half of August), and since 2012 it has been found in May–June (or even earlier), and since then *M. leidyi* has not reached previous levels of maximum abundance. Environmental records, in combination with modelling scenarios for 'cold' and 'warm' years pre-2005, and years representing each of the above periods of observed change (2005–2012 and post-2012), were used to investigate what has been happening. Modelling environmental variables showed *M. leidyi* populations responding to increases in mean spring temperatures above the reproduction threshold, and rising in response to higher maximum zooplankton biomasses. Both factors were similarly correlated with *B. ovata* development. Modelling 'with' and 'without' *B. ovata* scenarios illustrated how closer coupling of the ctenophore life cycles at higher mean spring temperatures and zooplankton populations leads to increased suppression of *M. leidyi* by *B. ovata*.

A separate study by scientists at the Kovalevsky Institute of Marine Biological Research (Russian Academy of Sciences) in Sevastopol draws on data for water temperature and *M. leidyi* and *B. ovata* (reproduction, food consumption, population structure, abundance/biomass) collected since 1999 in northern inshore waters of the Black Sea near Sevastopol.[3] This paper compares data collected in 2013 and 2014 with earlier published data to investigate seasonal and long-term ctenophore populations in this area. It reveals shifts in seasonality and maximum annual populations (abundance and biomass) of *M. leidyi*.

The paper depicts a decline in *M. leidyi* reproduction and abundance in this area between 2004 and 2014, particularly since about 2010, with the average reproductive rate in 2014 being only c. 20% of the rate in 2004, and abundance in 2010–2014 little more than a quarter of the level in 2004–2009. There was between-year variation for 2013 and 2014 in timing of reproduction, as well as abundance and biomass of *M. leidyi* but, mirroring the study above, the ctenophore was found to be reproducing earlier now (the period shifting from late July/early August to late June/early July from 2010), which was attributed to warmer spring water temperatures in the coastal bays where it overwinters. *Beroe ovata* can also reproduce earlier – by about one and a half months in 2009–2013, subject to annual variation. When it appears early, as in 2010, it can reduce *M. leidyi* population abundance. However, the authors suggest that longer periods of high summer water temperatures (>28°C) in recent years are also significant: they could be limiting the feeding rate and thus reproduction of *M. leidyi*. For example, zooplankton half-life was relatively high in 2013 and 2014, which the authors attribute to low feeding pressure from *M. leidyi*. Thus, although *M. leidyi* is reproducing earlier thanks to warmer spring temperatures, a combination of earlier *B. ovata* reproduction and high summer temperatures are currently limiting *M. leidyi* populations.

The studies[1–3] have a wider significance because *M. leidyi* has dispersed much further in the last three decades, either naturally or through anthropogenic influence (ballast water being the principle pathway). A joint Mediterranean Science Commission/International Council for the Exploration of the Sea (CIESM/ICES) meeting in Spain in 2014 synthesized knowledge of *M. leidyi* and *Beroe* spp. in Eurasian waters.[4] Acknowledging the complexity of the marine ecosystems that *M. leidyi* is invading, meeting participants agreed a number of research priorities.

Mnemiopsis leidyi has wide environmental tolerance but presence does not always precipitate outbreaks: better understanding of the role of factors such as temperature, salinity, turbulence, competition and predation on its population dynamics (notably rate of reproduction) is needed. Whether *M. leidyi* has a direct impact on fish stocks is also not yet understood. Areas at risk of *M. leidyi* introduction need to be identified. Germane here is the probable source–sink population dynamics of *M. leidyi* in Europe and the need for better knowledge/mapping of overwintering areas, which provide seed populations each spring.

It is conceivable that *M. leidyi* was present in the Black Sea undetected before the 1980s, and its population explosion was the result of a combination of factors such as rising sea temperatures, eutrophication, other invasive species, and availability of zooplankton prey as overfishing caused fish stocks to collapse. This highlights another key research need: monitoring to better understand what species are present and where – and citizen science could play a part. Research tracing the history of the *M. leidyi* invasion and *B. ovata* introductions, using population genetic analysis, indicates more than one introduction for *M. leidyi* (and potentially *B. ovata*) from different North American populations. But other predatory ctenophores including other *Beroe* spp. also feed on *M. leidyi* in the invaded range, and some of these are following the *M. leidyi* invasion and expanding their ranges. Moreover, there is potential for hybridization for both introduced ctenophore species, while *M. leidyi* has a propensity for morphological variation.

Mnemiopsis leidyi is now found from the Caspian Sea in the east, through the Black Sea and associated water bodies to the Mediterranean, and in the north from the Baltic Sea to the North Sea and the English Channel. Understanding the above questions will help to predict where *M. leidyi* might invade and potential outcomes this vast area.

The situation in the Baltic and North seas is not yet well studied – only largely in fjords, bays and coastal areas. Non-native *B. ovata* was recorded also in the Danish areas[5], but it does not occur continuously owing to changeable conditions in fjords.

The worst situation is in the Caspian Sea where *B. ovata* was not introduced. *Mnemiopsis leidyi* is spreading further into the northeastern part of the north Caspian and its abundance is increasing in the middle and northern Caspian. Impact on all levels of the ecosystem is stronger than in all other recipient seas.[6]

[1] Shiganova, T.A., Alekseenko, E., Moskalenko, L. and Nival, P. (2018) Modelling assessment of interactions in the Black Sea of the invasive ctenophores *Mnemiopsis leidyi* and *Beroe ovata*. *Ecological Modelling* 376, 1–14.

[2] Shiganova, T.A., Legendre, L., Kazmin, A.S. and Nival, P. (2014) Interactions between invasive ctenophores in the Black Sea: assessment of control mechanisms based on long-term observations. *Marine Ecology Progress Series* 507, 111–123.

[3] Finenko, G.A., Anninsky, B.E. and Datsyk, N.A. (2018) *Mnemiopsis leidyi* A. Agassiz, 1865 (Ctenophora: Lobata) in the inshore areas of the Black Sea: 25 years after its outbreak. *Russian Journal of Biological Invasions* 9, 86–93.

[4] CIESM (2015) Report of the Joint CIESM/ICES Workshop on *Mnemiopsis* Science, Corunna, Spain, 18–20 September 2014, co-edited by S. Pitois and T. Shiganova. CIESM Monaco and ICES, Copenhagen, 84 pp.

[5] Shiganova, T.A., Riisgård, H.U., Ghabooli, S. and Tendal, O.S. (2014) First report on *Beroe ovata* in an unusual mixture of ctenophores in the Great Belt (Denmark). *Aquatic Invasions* 9, 111–116.

[6] Shiganova, T.A. (2011) Review of the status of invasive species with special focus on the most invasive species *Mnemiopsis leidyi* (A. Agassiz, 1865) and their effect on the Caspian ecosystem. CASPECO, 123 pp.

Contact: Tamara Shiganova, P. P. Shirshov Institute of Oceanology RAS, Moscow, Russia.
Email: Shiganov@ocean.ru

Galina Finenko, Institute of Marine Biological Research, Sevastopol, Russia.
Email: gfinenko@gmail.com

Rabbit Biocontrol: New Releases in New Zealand

Following releases in Australia in 2017, the Korean strain of the rabbit calicivirus (or rabbit haemorrhagic disease virus) RHDV1 K5 has been released in New Zealand. European rabbits were first introduced to New Zealand in the 1830s, but by the 1870s rabbit 'plagues' leading to abandoned farms were being reported. Today rabbits are a significant agricultural and ecological pest, costing some NZ$50 million annually in lost pasture production despite control measures amounting to over NZ$25 million a year. Prospects for an improved control method have been eagerly anticipated by farmers, but they are complying with official requests to be patient while a national deployment strategy takes effect.

The rabbit calicivirus, which is vectored by flies, was first used as a biocontrol agent in 1996 when a Czech strain (RHDV1) was released in Australia. The same strain was introduced illegally to New Zealand in 1997 after an application for its importation had been declined. It had swift and large impact with more than 70% of rabbits killed as it spread throughout the country and controlled populations in many regions. But in the 20 years since, although outbreaks continue to occur, control has declined. Young rabbits may acquire immunity from mothers, but another cause of immunity emerged after the release of RHDV1. A benign calicivirus (RCV-A1) occurring naturally in wild rabbit populations in both countries provides protection against the introduced strain. Studies in New Zealand revealed evidence of very high incidence of this immunity (≤100%) in some areas.

Researchers in Australia screened an array of virus strains and concluded that the Korean strain has better potential to overcome the immunity than alternative European strains. Assessments in New Zealand, where the Czech strain has evolved somewhat since it was introduced, led to the same conclusion. The Korean strain is not expected to have the dramatic initial impact of the first release, because rabbits are not a naïve population and the new strain will be competing with the existing strain. But it is hoped RHDV1 K5 will provide New Zealand's land managers with an effective and cost-efficient method of rabbit control that could reduce rabbit abundance by up to 40%, especially where mortality from the Czech strain is lowest, and also be integrated with follow-up rabbit management measures for better overall control.

The illegal introduction and uncontrolled releases in New Zealand in 1997 meant the virus was not deployed in a strategic manner, which potentially limited its efficacy. A thread running through communications this time was for patience during what proved to be a lengthy process. Approval to release RHDV1 K5 needed decisions under three pieces of New Zealand legislation: the Hazardous Substances and New Organisms (HSNO) Act, the Agricultural Compounds and Veterinary Medicines (ACVM) Act and (as an 'unwanted organism') the Biosecurity Act. The first hurdle was passed in February 2017 when the Environment Protection Authority decided that because a strain of the virus was already present in the environment, approval of the new strain under the HSNO Act was unnecessary. It was, however, classified as a Vertebrate Toxic Agent under the ACVM Act. The responsible body, the Ministry for Primary Industries (MPI), granted final approval in February 2018 after consulting on and considering potential benefits and impacts of the virus and risks to animal welfare. Permission included conditions to ensure the virus will be securely transported, stored and used in accordance with strict protocols, together with controls on sale and use of RHDV1 K5 to address specific welfare concerns

While the approval process was progressing, a Landcare Research project funded by MPI through the Sustainable Farming Fund developed a release strategy for RHDV1 K5. Key elements included ensuring a high-quality commercial product was available, determining optimum release timing, i.e. periods when vector fly populations are high and numbers of young rabbits (which could potentially acquire immunity) are low, selecting release sites, and honing a method of deploying carrot baits to attract rabbits to the site before releasing the virus. The releases are made by participating regional and district councils, and the strategy aims to help them manage releases in rabbit-prone areas of New Zealand so as to maximize benefits to farmers and the environment. The controlled release strategy also facilitates pre- and post-release monitoring to measure impacts.

Releases of the new strain took place nationwide in March and April 2018, the optimal time to maximize the effectiveness of the virus against wild rabbit populations. The first mortality attributed to the virus was reported by Otago Regional Council in April, but scientists are stressing that more time (and patience) is needed for the strain to establish and become widespread from the controlled release sites.

Further information and sources:
Landcare Research.
Web: www.landcareresearch.co.nz/science/plants-animals-fungi/animals/vertebrate-pests/biological-control-of-rabbits

Ministry for Primary Industries.
Web: www.mpi.govt.nz/news-and-resources/consultations/application-for-approval-of-use-of-rabbit-haemorrhagic-virus-disease-rhdv1-k5/

Duckworth, J. (2018) Rabbit caliciviruses for biological control of rabbits in New Zealand – the good, the bad and the useful. Landcare Research, New Zealand.
Web: www.landcareresearch.co.nz/__data/assets/pdf_file/0015/161142/Rabbit-calciviruses-for-the-biological-control-of-rabbits-in-New-Zealand.pdf

Biological Control of Leafrollers in New Zealand

A paper in *Agricultural and Forest Entomology*[1] describes how leafrollers, once major pests in orchards and vineyards in the Hawke's Bay area of New Zealand, are now uncommon. In the 1980s, 20% of apples in (insecticide) untreated orchards suffered damage, but after 2000 this fell to less than 2%. The authors attribute the reduction in pest populations to biological control by parasitoids introduced in the 1980s together with later changes in insecticide programmes, including a switch to selective insecticides. This is reflected in a 19% rise in parasitism between 1994–1999 and 2008–2011, while immature leafroller numbers fell by 55%.

The paper analyses data for three leafroller species from 40 years of monitoring based on adult bait and pheromone trapping, larval damage to apples, and some host plant searches. While there have been substantial reductions in all species, the endemics *Planotortrix octo* and *Ctenopseustis obliquana*, which dominated in the 1970s, have declined most and are rarely found today, while the non-native *Epiphyas postvittana* is now the dominant leafroller species.

[1] Lo, P.L., Walker, J.T.S., Hedderley, D.I. and Cole, L.M. (2018) Reduction in leafroller (Lepidoptera: Tortricidae) abundance in orchards and vineyards 1976–2016, in Hawke's Bay, New Zealand. *Agricultural and Forest Entomology*, in press. DOI: 10.1111/afe.12283

Biological Control of Wheat Stem Sawfly in the USA

A paper in the *Annals of the Entomological Society of America* summarizes the use of biological control to manage the wheat stem sawfly *Cephus cinctus*, and discusses potential new strategies and research.[1] For over a century, the native sawfly has been a destructive pest of cereal crops in the Northern Great Plains of the USA, with infestation levels of over 70% reported, and economic losses from crop damage in one state (Montana) alone as high as US$80 million annually.

Biological control is an important control measure owing to a lack of effective insecticide treatments, and resistant cultivars that do not reduce pest populations sufficiently. But development of biological control has not been straightforward. Current options are native parasitoids, and entomopathogenic fungi and nematodes. No single agent is likely to be adequate, so the best hope may be focus on improving the efficacy of all three as a strategy to improve control overall.

[1] Portman, S.L., Jaronski, S.T., Weaver, D.K. and Reddy, G.V.P (2018) Advancing biological control of the wheat stem sawfly: new strategies in a 100-yr struggle to manage a costly pest in the Northern Great Plains. *Annals of the Entomological Society of America* 111, 85–91.

Methods in Biological Control

Two recent papers in main biological control journals address methods in classical biological control.

Urs Schaffner and co-authors[1] discuss how the purpose and design of open-field host-range testing has changed over a half-century of using this approach to assess potential non-target impacts of prospective weed biocontrol agents. They argue for a shift to a more hypothesis-driven approach and different experimental designs to facilitate interpretation of results.

Ross Cuthbert and co-authors[2] propose a novel metric, based on functional and numerical responses, to compare and select biocontrol agents, illustrated with reference to the *Culex pipiens* larval agents *Macrocyclops albidus* and *Megacyclops viridis*.

[1] Schaffner, U., Smith, L. and Cristofaro, M. (2018) A review of open-field host range testing to evaluate non-target use by herbivorous biological control candidates. *BioControl* in press. DOI: 10.1007/s1052 6-018-9875-7

[2] Cuthbert, R.N., Dick, J.T.A., Callaghan, A. and Dickey, J.W.E. (2018) Biological control agent selection under environmental change using functional responses, abundances and fecundities; the relative control potential (RCP) metric. *Biological Control* 121, 50–57.