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Generation cycles

Robert J. Knell

M any ecologists have their first encounter with complex population dynamics early in their undergraduate career, when a lecturer shows a slide of one of the famous datasets of an animal population undergoing cycles in density. Attending more advanced courses in population ecology, we learn that stable population cycles are only one example of a variety of dynamics which populations are known to exhibit. Many ecologists are fascinated by these phenomena, and attempts to explain the mechanisms behind them have led to many fundamental contributions to modern population ecology.

Many ecologists are unaware, however, of the existence of another category of complex population dynamics. Whereas both the standard examples of cycling populations and the predictions of classical population ecology theory deal with cycles with a period which extends over a number of generations, a series of

Generation cycles are population cycles with a period of roughly one generation. They have been observed in tropical pest populations and in laboratory populations. Theory suggests that they can arise both from intraspecific competition and from the influence of natural enemies, and ecological studies of populations of insects showing these cycles are starting to shed light on the mechanisms that maintain them.

Robert Knell is at the Dept of Zoology, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa (robk@gecko.biol.wits.ac.za).

studies published in the past decade have demonstrated the existence of cycles with a period of roughly one generation; namely 'generation cycles'[1]. These cycles have now been observed in both field (Fig. 1) and laboratory (Fig. 2a–c) populations of insects, and theoretical studies have demonstrated a variety of mechanisms that can cause such cycles, including intraspecific competition[2–6] and the influence of natural enemies[1,7–11].

In temperate climates, the influence of the seasons leads to many insect species, especially univoltine ones, having generations that are synchronized such that most individuals are in the same developmental stage at the same time. Populations of insects that are not affected by strong seasonal pressures, such as those that live in tropical habitats and would therefore be expected to simply breed continuously can also, however, have a synchronized age structure. This leads to peaks in the population of adults at intervals of roughly one generation, the phenomenon which is now referred to as 'generation cycling'[6,7]. Generation cycles arise from the age-structured nature of the populations in question and are therefore a very different phenomenon to the more familiar multi-generation cycles. In fact, generation cycles can be superimposed upon other types of population dynamics, usually oscillations to equilibrium[1,7,11,12].

Generating generation cycles

During the 1960s and 1970s, several laboratory studies were published in which populations of insects showed generation cycles (e.g. Refs 12–15, others cited in Ref. 16). Despite often being the most obvious aspect of a population's behaviour these cycles were largely ignored, or only briefly commented upon when these studies were published. Meanwhile researchers working on tropical insect pests also observed a number of cases in which the pest population appeared to undergo such cycles (see references in Ref. 7), but again these observations made little impact in the general ecological literature.
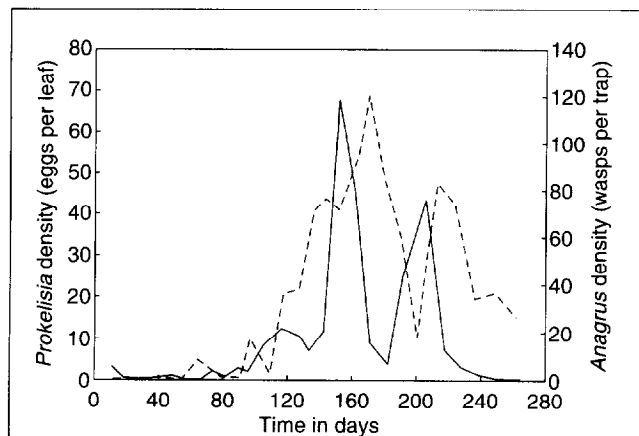

Fig. 1. Generation cycles in the field. Population densities of the plant-hopper *Prokelisia marginata* (solid line) and its parasitoid *Anagrus delicatus* (dotted line) in Florida. *Redrawn from Ref. 10, with permission.*

In the 1970s and early 1980s, models of insect populations with an explicit age structure began to appear, and some of these showed generation cycles under certain conditions[2-6,17]. Most of these concentrated on those situations in which such cycles arise spontaneously in laboratory populations of insects with no natural enemies present[2-5]. Such behaviour is attributed to intraspecific competition between larvae. The crucial point here is that generation cycles will arise only if the consequences of larval competition are expressed immediately, as larval mortality or extended larval development periods. If there is a delay, so that larval competition acts to reduce adult fecundity, for example, then any cycles seen will have a period of between two and four times the length of one generation[3].

Over the past decade the emphasis has shifted, and nearly all of the theoretical work published has addressed the abilities of natural enemies, usually parasitoids[1,7-10,18], to cause host populations to undergo generation cycles (Box 1). A general conclusion is that three features of the host–parasitoid interaction make generation cycles more likely. First, the development time of the parasitoid should be roughly one-half or one-and-a-half times that of the host[1,7-8]. The reasons why this is important are explained in Box 1. Second, the period during which the host is reproductively active should be short compared to its development time[7,8]. This is because if the host is reproductive for a relatively large proportion of its total life, then the peaks in host abundance will tend to overlap. This 'cohort smearing' will damp out any generation cycles[11,18].
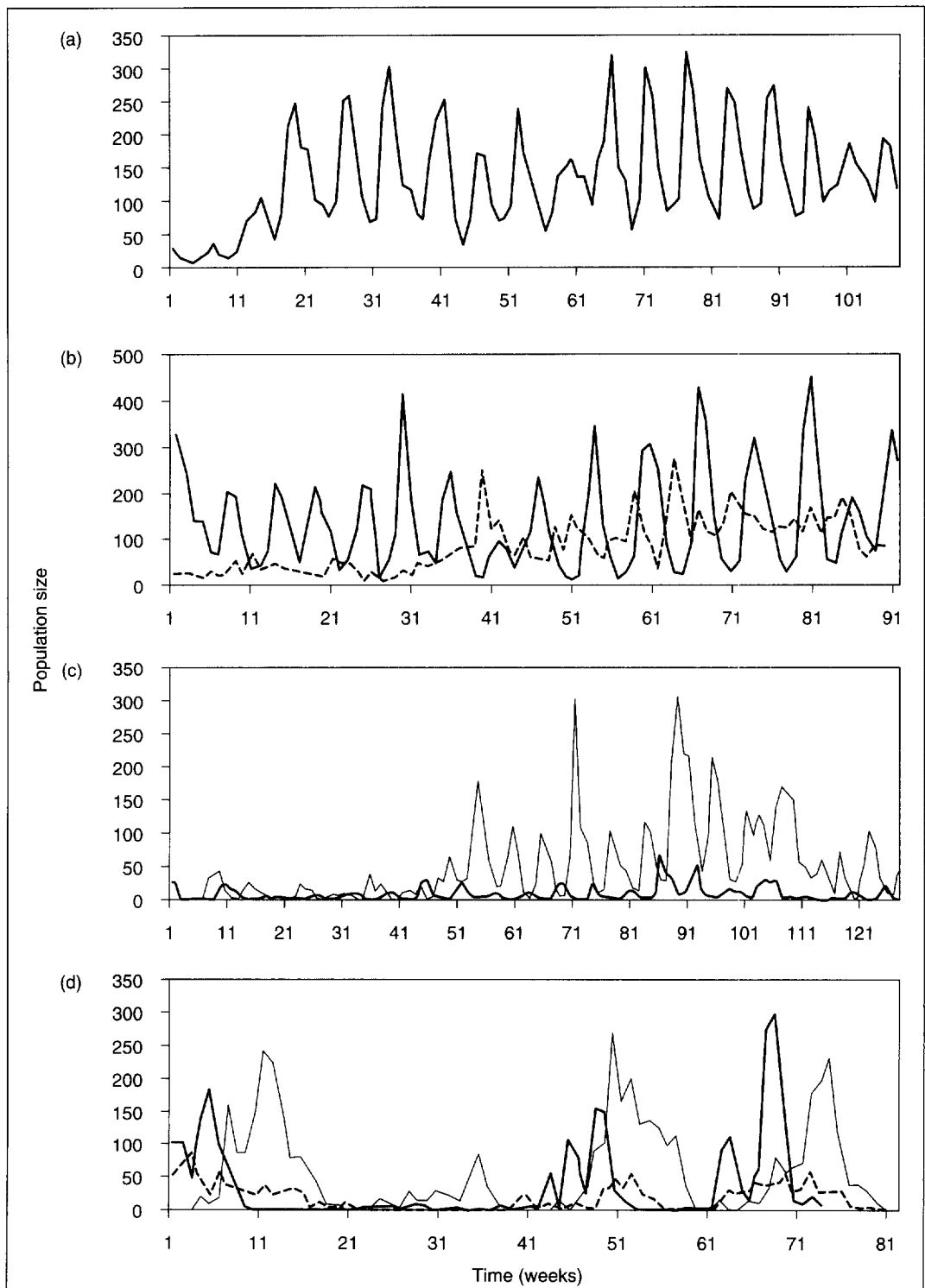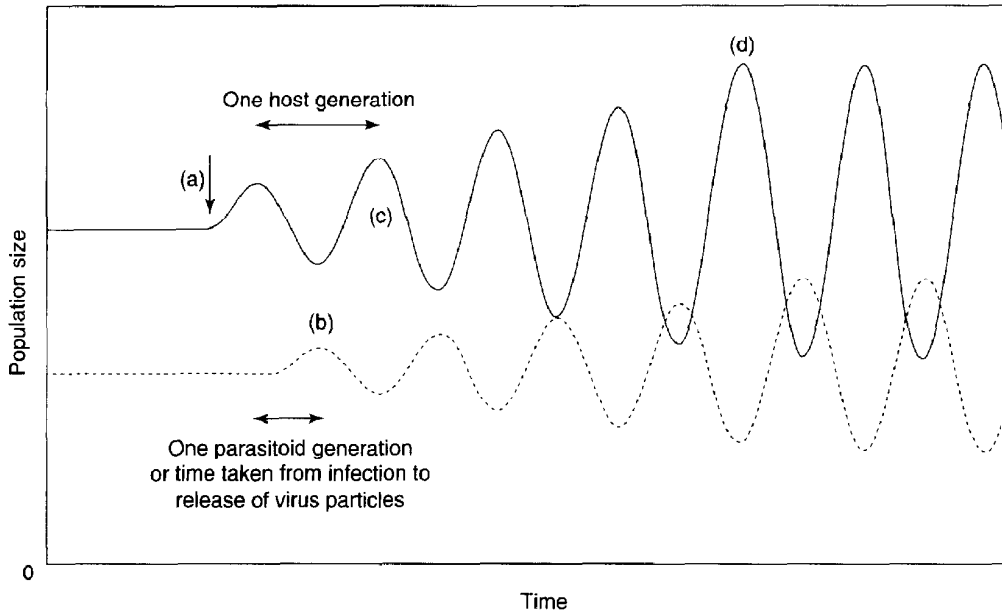
Third, there should be a

Fig. 2. Populations of *Plodia interpunctella* with various natural enemies. Heavy line: population of *P. interpunctella*. Fine line: population of *Venturia canescens*. Dotted line: population of larvae infected with the granulosis virus. (a) *P. interpunctella* alone. The population of adult moths shows clear cycles with a period of 6–7 weeks, roughly one generation. (b) *P. interpunctella* with a granulosis virus. The mean abundance of the moth is reduced, although in this case the period of the cycles is not changed. (c) *P. interpunctella* with the parasitoid *Venturia canescens*. The mean abundance of the moth is drastically reduced, but populations of both the parasitoid and the moth show generation cycles. (d) *P. interpunctella* and the granulosis virus, with *V. canescens* added once the virus was established. Host and parasitoid now show long-term cycles, with a period of 20–25 weeks. *Adapted, with permission, from Ref. 20.*

moderate degree of density dependence in the parasitoid population: in other words, the rate of parasitism should not be linearly related to the density of parasitoids[1,7-9]. This last requirement will dampen out the unstable multigenerational cycles usually seen in predator–prey models, as these are more sensitive to moderate degrees of density dependence in parasitism than are generation cycles[9].

Most modelling efforts have concentrated on host–parasitoid systems, but an age-structured model of insect–virus systems has found that generation cycles can be driven by pathogens as well[11]. Two of the three features of host–parasitoid systems that make generation cycling more likely are mirrored by the conditions under which a virus will lead to such cycles in the host population. The period between

Box 1. How natural enemies can cause generation cycles

Generation cycles arise from a host–parasitoid or host–virus interaction by the same simple mechanism[1,11]. If we consider a population of hosts (shown by the solid line) at equilibrium then any perturbation, say an increase (a), of the host population will lead to a corresponding increase (b) in the population density of the natural enemy (adult parasitoids or free virus particles, shown by the dotted line). This will appear after the parasitoids' developmental time or the time from infection to release of virus. Because of the increase in the number of reproductive individuals in the host population, there will also be a rise in the number of hosts one generation later (c).

If the development time of the parasitoid or the time from infection to release of virus particles is the same as the host development time then the increase in the population density of the natural enemy will coincide with the rise in the host population density. This will cause increased mortality in the host population and so any further changes in the host population will be quickly damped out. If the development time of the natural enemy is roughly half that of the host, the increased mortality caused by the peak in the density of the natural enemy will occur after half a host generation. The natural enemy population will then decline and at the peak in the host population the natural enemy population will be low. This will empha-size the increase in host population one generation after the initial disturbance, and will cause a trough between the two peaks. This process will then continue until the population is showing regular generation cycles (d).

and by direct interference between parasitoids. Moreover, the models predicted that generation cycles should occur in this system. This theoretical work was reinforced by the observations of host and parasitoid in the field (Fig. 1): peaks in the density of *Anagrus* were observed when the density of eggs of *Prokelisia* was at its lowest, which is the pattern of host and parasitoid abundance predicted for a system in which generation cycles are driven by a parasitoid. This study represents the most convincing evidence yet for such a system, although only field manipulation experiments would provide proof.

(28 days and 42 days at 25°C, respectively). The adult planthopper is also relatively short-lived. The host–parasitoid system thus fulfils two of the requirements for parasitoid-induced generation cycling, but previous studies had failed to find any evidence for the density dependence that is also necessary.

Reeve *et al.* used two separate approaches to investigate whether or not the parasitoid was causing the cycles. First, they constructed a detailed model of the host–parasitoid interaction. This included two different mechanisms which had been observed in field populations and which could potentially generate density dependence, namely, variability in the risk of parasitism across patches of hosts and direct interference between searching parasitoids. Secondly, they monitored both host and parasitoid populations over a period of 300 days.

When the models were analysed they found that density dependence in the parasitoid population could be generated by both variability in the risk of parasitism, which led to pseudo-interference,

infection of a host and release of virus particles from it (which is analogous to the developmental time of the parasitoid) must be roughly one-half or one-and-a-half times the developmental period of the host. The reproductive stage of the host must again be short but the requirement for a density dependent response by the natural enemy is relaxed. The finding that a virus can also drive generation cycles implies that they may be a feature of age-structured insect–natural enemy interactions in general.

Generation cycles in real life

The activities of a number of ecologists over the past 15 years have given us a theoretical basis for understanding this phenomenon. Many of the conclusions of these models are, unfortunately, supported by circumstantial evidence at best, since the empirical studies needed to confirm them are lacking. Nevertheless, two sets of empirical work stand out, namely the studies of the Indian meal moth, *Plodia interpunctella* and its natural enemies by Begon, Sait, Thompson and others[19–24], and the study by Reeve *et al.* of a planthopper, *Prokelisia marginata* and its parasitoid, *Anagrus delicatus*[10].

Planthoppers and parasitoids in Florida salt marshes

In the sub-tropical climate of Florida, *P. marginata* is capable of breeding all year round, but populations of the planthopper show distinct generation cycles (Fig. 1). Earlier studies had shown that the eggs of the planthopper are attacked by the parasitoid *A. delicatus*, and that the developmental time of the parasitoid is two-thirds that of its host

Moths, viruses and parasitoids in laboratories

Whereas the populations of *Anagrus* and *Prokelisia* live in salt marshes in Florida, *Plodia interpunctella* and its natural enemies have been studied in an even less seasonal environment, namely laboratory incubators. *Plodia* is becoming something of a standard experimental subject for long-term laboratory population experiments, and can show a wide range of population dynamics under different conditions and with different natural enemies present[2,15,19–24].

Most of the published experiments with *Plodia* have shown that the adult moth population cycles with a period of roughly one host generation, roughly 6–7 weeks. These cycles have been observed in population cages with the moth alone[2,19–21] (Fig. 2a), and in experiments when either a virus[19–21] (*P. interpunctella* – granulosis virus, Fig. 2b) or a parasitoid[15,20,21] (the ichneumonid *Venturia canescens*, Fig. 2c) have been present. With the virus present, the mean

population density of the host may be reduced and the period of the cycles may be increased slightly, although the latter is not always observed[19,21]. With the parasitoid present changes in cycle period are not observed, but the amplitude of the fluctuations increased and mean host abundance decreased[20–22]. The parasitoid may drive the host to extinction if the depth of food for the moth larvae is shallow[20].

Theory predicts generation cycles arising in the absence of natural enemies both from uniform (all larvae compete equally with all others)[3] and from asymmetric larval competition[2]. In *Plodia* they are attributed to asymmetrical competition between different larval age classes causing differential mortality of younger larvae. This leads to the population becoming synchronized so that most animals are in the same developmental stage, giving waves of emerging adults every generation[19]. It is noteworthy that both the parasitoid and the virus fulfil all of the requirements that theory predicts would lead to generation cycles driven by natural enemies[20,21]. If populations of *P. interpunctella* and one of these natural enemies were to be monitored without knowledge of the population dynamics of the host alone then the cycling would probably be attributed to the virus or the parasitoid, whereas in fact it is driven by interactions in the host population. There is only one example of generation cycles that seem to be unequivocally caused by a parasitoid – a laboratory study of the moth *Ephestia kuehniella* with *V. canescens*[12].

When *V. canescens* was added to a population in which the virus was already established, the dynamics of the system changed completely[21,22]. In all cases the host eventually became extinct, leading to the extinction of all three species, but until that time the host and the parasitoid underwent coupled multigenerational cycles in population size (Fig. 2d). Begon *et al.* suggested a possible mechanism to account for this surprising change. The virus infects younger larvae, final instar larvae being immune to the virus, whereas the parasitoid preferentially oviposits in older larvae, and in fact delays development until the host is in its final instar. The effect of the virus killing the younger larvae and the parasitoid killing the older larvae may effectively remove the age structure from the system, in which case the system would come to resemble a classical predator–prey or host–parasitoid system more closely. This could lead to the unstable multigenerational cycles that models of these systems predict, and which the cycles observed closely resemble.

Natural enemies are not the only factors that may change the dynamics of *Plodia* in population cages. If there is only a small amount of food available, or if the food is of low quality, then the moth population will show small, apparently random oscillations around an equilibrium[23,24]. This is seen in experiments with the moth alone, and also when the granulosis virus[24] or the parasitoid[23] is present. Why the generation cycles which are normally observed are absent in these cases is not known, but one explanation may be that the small population sizes make stochastic effects more important. This could cause the population dynamics to become unclear as chance events play a more important role[24].

Future directions

From being a virtually unknown phenomenon a decade ago, generation cycles are now a recognized form of dynamic population behaviour. There is a theoretical background to help us explain likely mechanisms, although the theory is by no means complete, and questions about the generality of this phenomenon still need to be answered. For example, generation cycles have so far only been found in host–pathogen models in which the pathogen kills the host and then disperses infectious particles into the environment[11].

The likelihood of a similar phenomenon arising from, for example, a pathogen spread by close contact with a short infectious period and a latent period of roughly half the host developmental time has not been investigated. More practically, although many of the insects that undergo these cycles are pests there has been little interest in using the theory to help develop control strategies for these animals (Ref. 18 being the only exception).

Empirical studies that take account of the theory are now appearing. The data produced by Reeve *et al.* demonstrate that the generation cycles of *Prokelisia* are probably driven by the parasitoid *Anagrus*. The results from studies of *Plodia* cast some doubt on the role of parasitoids in causing generation cycles but it is not clear how meaningful comparisons between the *Plodia* system, with its extreme resource limitation, and field systems are. The development of new statistical techniques that allow the underlying dynamics behind a time series to be understood in detail[25] points the way forward for future research on such systems.

The population dynamics of *Plodia* are now known under a wide range of conditions, but the mechanisms leading to some of these dynamics are still poorly understood. Further investigation of why it usually shows generation cycles, but may undergo unstable multi-generation cycles, will shed light onto the mechanisms by which generation cycles arise in real biological systems, as will the reasons behind the intriguing effects of differing food availability and quality on the dynamics of the moth populations.

From a broader perspective, the big questions regarding generation cycles in the field still need to be answered: how common is this pattern of population dynamics, and how common are the various mechanisms which can lead to it? Generation cycles arising from intraspecific competition have been demonstrated in the laboratory, but field evidence is entirely lacking. Conversely, many tropical insect pests show generation cycles and suffer heavy mortality from natural enemies, but laboratory studies imply that the natural enemies could simply be tracking cycles which are a consequence of interactions within the host population.

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Archaea and the new age of microorganisms

Rajagopal N. Aravalli, Qunxin She and Roger A. Garrett

In 1977, Carl Woese and coworkers[1] first exploited partial sequences of the 16S-like ribosomal RNA to monitor different phylogenetic types of microorganisms. This RNA molecule had the merits of being present in all living organisms as part of a highly conserved protein synthesis machinery centred on the ribosome and of being relatively easy to isolate. At that time, large RNA molecules were very difficult to sequence. However, by analysing oligonucleotide sequences (in the 8–15 nucleotide size range) that were produced by digestion of 16S rRNA using guanine-specific ribonuclease T_1, Woese *et al.* were able to identify sequences that were common to, and defined, phylogenetic groups. This constituted a major breakthrough in classifying prokaryotes and, at an early stage, it was shown that 16S rRNAs from methanogens exhibited very different oligonucleotide sequences, and nucleotide modification characteristics, from known bacterial and eukaryotic rRNAs. They inferred that the methanogens were not real bacteria (eubacteria) and called them archaebacteria[1]. Later, other organisms isolated from extreme environments, that grew at high temperature or in high salt, were also found to show rRNA sequence similarities to the methanogens (Box 1).

Archaea were, until recently, considered to be confined to specialized environments including those at high temperature, high salinity, extremes of pH and ambients that permit methanogenesis. Recently developed molecular methods for studying microbial ecology, which do not necessitate cell culturing, have demonstrated their presence in a wide variety of temperate and cold environments including agricultural and forest soils, fresh water lake sediments, marine picoplankton and deep-sea locations. These discoveries mark the beginning of a new era for investigating the Archaea and in particular their physiological and metabolic properties and their biological roles in complex microbial populations.

Rajagopal Aravalli, Qunxin She and Roger Garrett are at the Institute of Molecular Biology, University of Copenhagen, Sølvgade 83H, DK-1307 Copenhagen K, Denmark (garrett@mermaid.molbio.ku.dk).

These microorganisms are now grouped as a separate domain of life and have been renamed the Archaea, producing, for the first time, a tripartite tree of life. This tree has received strong support particularly from studies on membrane structure and the informational apparatus for transcription, translation[2] and, more recently, DNA replication[3]. Moreover, it is reinforced by analyses of complete genome sequences, which show that 70% of the identified gene products of *Methanococcus jannaschii* are either bacterial-like (44%), eukaryotic-like (13%) or equally similar to both (13%)[4].

Specialized growth habitats: physiology and metabolism

Archaeal cells, like those of bacteria, exhibit a variety of morphological shapes including rods, discs, spirals and spheres, and many of them grow as clusters or aggregates. In general, they are surrounded by complex and diverse cell envelopes with glyco-protein-containing S-layers and cytoplasmic membranes containing a high proportion of tetraether-lipids[5]. An exception, *Methanopyrus kandleri*, which grows at very high temperatures (up to 110°C), contains 2,3-di-*O*-geranylgeranyl-*sn*-glycerol as the dominating membrane lipid[6]. In addition