

University of Groningen

Spatial and ecological overlap between coexisting sexual and parthenogenetic Schmidtea polychroa (Tricladida; Platyhelminthes)

Weinzierl, Rolf P.; Beukeboom, Leo W.; Gerace, Letizia; Michiels, Nicolaas K.

Published in:
Hydrobiologia

DOI:
[10.1023/A:1003519418925](https://doi.org/10.1023/A:1003519418925)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
1999

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Weinzierl, R. P., Beukeboom, L. W., Gerace, L., & Michiels, N. K. (1999). Spatial and ecological overlap between coexisting sexual and parthenogenetic *Schmidtea polychroa* (Tricladida; Platyhelminthes). *Hydrobiologia*, 392(2), 179-185. <https://doi.org/10.1023/A:1003519418925>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.



Spatial and ecological overlap between coexisting sexual and parthenogenetic *Schmidtea polychroa* (Tricladida; Platyhelminthes)

Rolf P. Weinzierl¹, Leo W. Beukeboom^{1,2}, Letizia Gerace¹ & Nicolaas K. Michiels^{1,3,*}

¹Max-Planck Institut für Verhaltensphysiologie, P.O. Box 1564, D-82305 Starnberg, Germany

²Institute for Evolutionary and Ecological Sciences, University of Leiden, P.O. Box 9516, NL-2300 RA Leiden, The Netherlands

³Present address: Institut für Spezielle Zoologie, Hüfferstrasse 1, D-48149 Münster, Germany (*author for correspondence)

Fax: [+49] 251 83 24668. E-mail: michiels@uni-muenster.de

Received 5 May 1998; in revised form 16 December 1998; accepted 8 January 1999

Key words: gene flow, population ecology, *Dugesia*, *Schmidtea*, parthenogenesis, coexistence

Abstract

Theoretical models on the costs and benefits of sexual reproduction usually assume that sexual and parthenogenetic individuals coexist and are identical, except for their mode of reproduction. Empirical studies, however, show that conspecific sexuals and parthenogens can differ in ecological preferences and geographical distribution, which complicates the investigation of the costs and benefits of sex. The freshwater planarian *Schmidtea polychroa* exists in a sexual and a sperm-dependent, parthenogenetic form. The latter produce fertile sperm and mate, but received sperm is used only to induce parthenogenetic embryo development. We compared the spatial and ecological distribution between forms within a lake from which both had been reported. Forty samples showed large differences in the relative frequencies of sexuals and parthenogens. Nineteen samples contained both biotypes. All but one of the 13 ecological parameters that we measured, could not explain a significant part of the variance in relative abundance of each type. Only leech abundance had a significant, negative effect on the presence of sexual individuals. The causes of this effect remained unclear. We also estimated the amount of genetic isolation between sites and between reproductive modes, using body coloration as a genetic marker. Large differences were found between sites, suggesting isolation of local populations by migration barriers. There were smaller differences between sexuals and parthenogens within sites, suggesting that genetic exchange between biotypes may be limited. We conclude that there appears to be weak niche differentiation between sexuals and parthenogens in Lago di Caldonazzo in late summer. Fluctuations in relative frequency appears to be a consequence of low dispersal between local populations and stochastic effects within them.

Introduction

Some species consist of sexual and parthenogenetic individuals, and sometimes the two reproductive modes coexist in the same population (Suomalainen et al., 1987; Asker & Jerling, 1992; Mogie, 1992). Such coexistence represents an evolutionary paradox: because of the so called 'cost of sex' (Maynard Smith, 1978), parthenogens should outcompete sexuals within a few generations. The fact that this does not happen in at least some species, shows that the cost of sex must

be balanced by an equally strong benefit of sex. The 'balance argument' (Williams, 1975) makes one implicit assumption: sexuals and parthenogens have to be in direct competition with each other. They should not simply overlap geographically, but form a truly mixed population, also in an ecological sense. This is especially likely in hermaphrodites where sexuals and parthenogens can mate and, hence, even form a common gene pool (Clausen, 1961; Richards, 1973; Jaenike & Selander, 1979; Mogie & Ford, 1988; Menken et al., 1995).

True coexistence is not common. Sexuals and parthenogens often have different geographical distributions (Suomalainen et al., 1987; Asker & Jerling, 1992; Mogie, 1992). Spatial distribution data also suggest ecological differentiation (Christensen, 1960; Levin, 1975; Glesner & Tilman, 1978; Jaenike & Selander, 1979; Bell, 1982; Lynch, 1984). In some cases, niche differentiation could be demonstrated experimentally (Schenck & Vrijenhoek, 1986; Michaels & Bazzaz, 1989; Weeks et al., 1992). Also, genetic differences between parthenogens and their closest sexual relatives can be large (Hedges et al., 1992; Quattro et al., 1992; Spolsky et al., 1992; Foighil & Smith, 1995; Judson & Normark, 1996). Genetic similarity has been found when new parthenogenetic lineages arise regularly (Tomiuk & Loeschcke, 1991; Dybdahl & Lively, 1995), or when genetic exchange between sexuals and parthenogens is possible (Menken et al., 1995).

The hermaphroditic freshwater flatworm *Schmidtea polychroa* Ball (formerly *Dugesia polychroa* Schmidt; Tricladida, Paludicola) occurs as a diploid sexual and several polyploid parthenogenetic forms that produce eggs, either mitotically or meiotically after chromosome duplication (Benazzi, 1957). Diploid parthenogens have not been found. Parthenogenesis is sperm-dependent or 'pseudogamous', i.e. egg development must be stimulated by a sperm cell that does not contribute genetically to the zygote (Benazzi, 1950; Benazzi & Benazzi Lentati, 1976). Parthenogens produce functional haploid sperm that can fertilise eggs of sexuals (Benazzi Lentati, 1970). Gene flow in the opposite direction is also possible, because sexual parents occasionally produce parthenogenetic offspring (Benazzi Lentati, 1966, 1970). Both reproductive modes have different geographical distributions, but coexist in some Italian lakes and streams, e.g. in Lago Maggiore (Benazzi, 1957), in the vicinity of Pisa (Canovai, 1989), and in our study population Lago di Caldonazzo in northern Italy (Beukeboom et al., 1996; Pongratz et al., 1998).

The goal of this study was to reveal whether sexual and parthenogenetic *S. polychroa* share the same ecological niche. First, we examined to what extent they are spatially separated within Lago di Caldonazzo by investigating their relative abundance all around Lago di Caldonazzo. Second, niche differentiation was investigated by relating relative frequencies of both reproductive modes to variation in 13 habitat characteristics. Finally, we investigated genetic similarity between coexisting sexuals and parthenogens

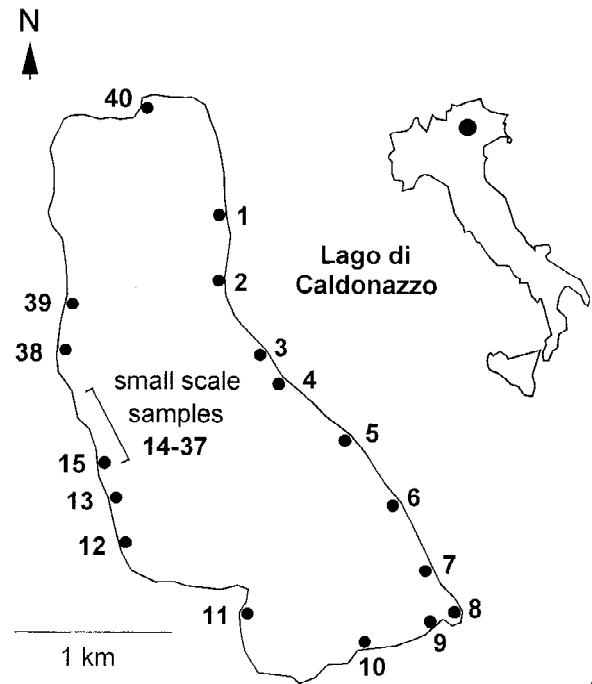


Figure 1. Locations of large (1–13, 15, 38–40) and small scale (14–37) samples along the shore of Lago di Caldonazzo.

within sampling sites. High local similarity is indicative for low dispersal and either local adaptation or matings between individuals of two different reproductive modes, thus providing additional support for ecological overlap. Genetic similarity among sexuals and parthenogens in *L. di Caldonazzo* has already been shown using allozymes (Pongratz et al., 1998). Here, we used body pigmentation as a genetic marker, allowing us to process more samples.

Methods

Sampling techniques

Samples were taken at two scales, reflecting our goal to sample along the whole lake, but with special emphasis on the west shore since, here, sexuals and parthenogens were known to coexist. Seventeen 'large scale samples' (sites 1–13, 15 and 38–40) were distributed all around Lago di Caldonazzo (N-Italy) at intervals of 100–2000 m (Figure 1). A metal frame $1 \times 1 \text{ m}^2$ was placed in shallow water and, if possible, about 25 worms were collected from within it. Using the same method 24 'small scale samples' (sites 14–

37) of about ten worms, each were collected from a 500 m long section along the western shore. Neighbouring samples had an average distance of about 25 m and were selected to represent contrasting types of vegetation. Sample 15 (see Figure 1) was used as a large as well as a small-scale sample. Collection was done in early September 1995.

Ecological parameters

For 15 large scale and 23 small-scale samples, the following parameters were recorded from within the sampling square:

1. Distance of the square from the shore.
2. Water depth in the centre of the square.
3. pH.
4. Coverage with stones (five categories 0%, 1–25%, 26–50%, 51–75% and 75–100%).
5. Median of stone size. For each of twenty stones, length \times width values was calculated. The median was used as the value for the sampling square.
6. Coverage with submersed vegetation, usually green algae. See 4 for categories.
7. Coverage with reeds. See 4 for categories.
8. Overhanging vegetation (seen from above). See 4 for categories.
9. Abundance of isopods (predominantly *Asellus aquaticus*). N individuals on twenty stones of intermediate size (about 10 \times 10 cm²) using five categories 1, 2–5, 6–10, 11–20 and >20. A total estimate was obtained by summing category means of the 20 stones (30 was taken as average of the category >20).
10. Abundance of snails (mostly *Physa* sp.). See 9 for categories and calculations.
11. Abundance of mussels (*Dreissena polymorpha*). See 9 for categories and calculations.
12. Abundance of leeches (Hirudinea). See 9 for categories and calculations.
13. Abundance of leech egg capsules. See 9 for categories and calculations.

Body pigmentation

In *S. polychroa*, body coloration varies from light caramel to black ('polychroa'). This variation is to a large extent genetically determined (Benazzi, 1962, 1965). Worms were kept in 11 pots and starved for minimum 2 weeks to avoid that gut content affected body colour. Individuals were scored while gliding under standardised light conditions in a petri dish placed on page

10YR of Munsell's (1994) soil colour chart. A single person recorded the colour value for all worms (7 categories). Repeatability was 100% in repeated colour scores of 20 worms.

Karyology

S. polychroa can be anything from diploid ($2x=8$) to pentaploid ($5x=20$) and all of these have been found in L. di Caldonazzo (Beukeboom et al., 1996). Diploids are sexual, all others are pseudogamous parthenogenetic. Since external morphology is identical, all individuals were karyotyped using a reliable, standard procedure (Beukeboom et al., 1996) in order to recognise sexuals from parthenogens.

Statistics

Most statistical tests were calculated using SPSS for Windows, release 6.1.2. To perform exact tests and to calculate binomial confidence intervals, we used StatXact-Turbo, version 2.11. If exact P-values could not be determined, Monte Carlo estimates of the exact P-value are given with a 99% confidence interval.

Results

Spatial distribution of chromosomal races

A total of 564 individuals could be karyotyped. Of these, 286 were sexual diploids, 260 parthenogenetic triploids and 18 parthenogenetic tetraploids. In further analyses, triploids and tetraploids have been pooled as parthenogens. Overall, sexuals were more common along the east shore (Figure 2 A, B), but relative frequencies fluctuated drastically among adjacent sites (Figure 2 B, e.g. sites 20–21 and 22–23). No significant correlation between neighbouring small scale samples was found (samples 14–37, samples closer than 10 m pooled, samples with < 5 individuals excluded, Spearman $r_S = 0.376$, $n = 18$, $P = 0.124$), indicating that the composition of neighbouring sites varies in an unpredictable fashion.

Ecological correlates of the distribution of reproductive modes

Ecological parameters varied strongly between samples (Table 1). Using principal component analysis, the 13 variables were combined into two factors. Only the first was correlated with the proportion of sexuals, and

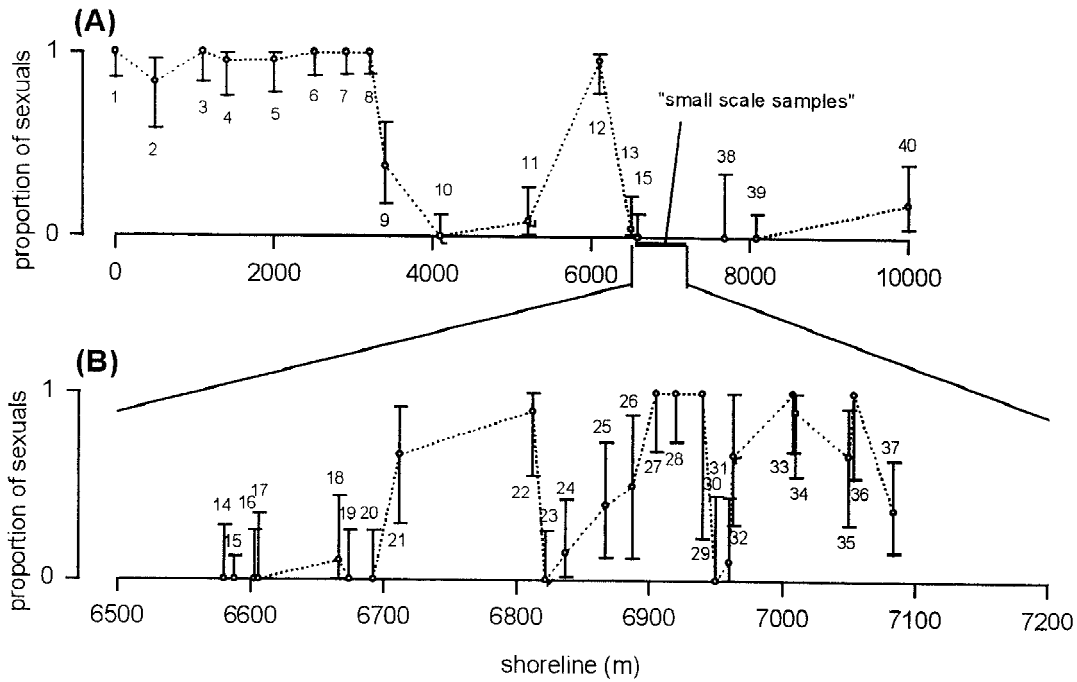


Figure 2. Relative proportions of sexuals in large (A) and small scale (B) samples. Error bars represent binomial confidence intervals and numbers refer to sites. The proportions vary significantly among small scale samples (Fisher's exact test, 99% confidence interval of exact $P = [0, 0.0023]$). Parthenogens were mostly triploid, but included one or two tetraploids at sites 9, 10, 11, 13, 14, 16, 17, 18, 21, 23, 24, 26, 30, 39 and 40.

Table 1. Descriptive statistics of all 13 ecological parameters measured at 38 sampling sites. Missing values are due to an inability to make an unambiguous estimate in the field

Variable	Mean	Std Dev	Min	Max	N
Distance from shore (cm)	56.22	72.76	0	300	37
Water depth (cm)	15.61	8.19	5	35	38
Water pH	6.91	0.39	6.3	8	38
Coverage with stones	3.58	0.65	2	4	36
Median stone size (cm ²)	83.33	51.06	25	200	36
Submersed vegetation	2.03	1.46	0	4	38
Reed	0.58	0.95	0	4	38
Overhanging vegetation	2.30	1.65	0	4	37
Isopods	24.72	38.95	0	238.50	38
Snails	21.57	25.32	0	113.00	38
Mussels	113.43	101.54	0	375.50	38
Leeches	16.46	20.80	0	78.50	38
Leech egg capsules	50.76	63.13	0	254.5	38

Five categories 0: 0%, 1: 1–25%, 2: 26–50%, 3: 51–75%, 4: 76–100%. ²Estimate of absolute number of individuals found on 20 stones (see Methods).

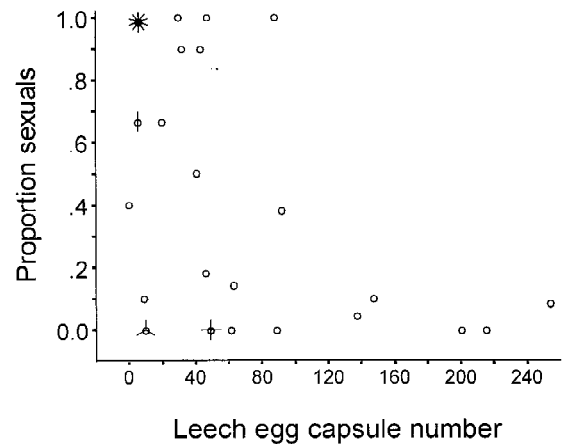


Figure 3. Relationship between the abundance of leech egg capsules and the proportion of sexuals (Spearman $r_S = -0.490$, $n = 38$, $P = 0.023$). Sunflower petals indicate the number of points at that (averaged) location.

it did not explain more of the variance than its leading constituent, the 'abundance of leech egg capsules'. Therefore, principle components were discarded and the analysis was done using the raw data. Of these only 'abundance of leech egg capsules' and 'abund-

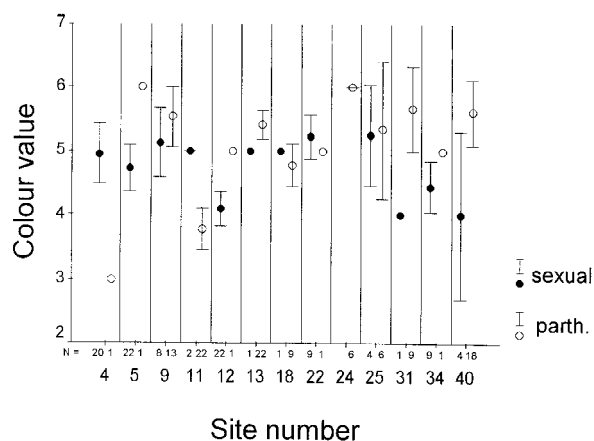


Figure 4. Mean colour values (only samples containing both sexuals and parthenogens and a total of at least 10 individuals). High colour values refer to darker, low values to lighter individuals. Error bars represent 95% confidence intervals. Among site variation in colour value was highly significant (All samples: sexuals: K-W $\chi^2 = 86.8$, d. f. = 25, $n = 247$, $P < 0.0001$; parthenogens: K-W $\chi^2 = 108.4$, d. f. = 26, $P < 0.0001$;). There was also a significant within-site difference between coexisting sexuals and parthenogens (16 mixed samples: stratified Wilcoxon-test, $n = 240$, exact $P = 0.033$).

ance of leeches' were negatively correlated with the proportion of sexuals ('capsules': $r_s = -0.490$, $n = 38$, $P = 0.002$; 'leeches': $r_s = -0.338$, $n = 38$, $P = 0.038$). If P -values are Bonferroni-adjusted for 13 simultaneous comparisons, only the correlation with 'capsules' remains significant ($P = 0.026$; Figure 3).

Genetical isolation between sites and between reproductive modes

There were clear-cut differences in body pigmentation among sampling sites for each reproductive mode (Figure 4), indicating that different sites are genetically isolated to some extent. Overall, sexuals were lighter than parthenogens, but this effect was confounded by colour variation among sites (Figure 4). None of the ecological parameters was able to explain colour variation between sites, suggesting that the differences arise through drift, or through an environmental factor that was not measured.

Discussion

Do sexual and parthenogenetic *Schmidtea polychroa* coexist?

In Lago di Caldonazzo, sexual and parthenogen *S. polychroa* were found together in almost half of all 40

sites investigated. Significant fluctuations in biotype composition occurred over short distances (10 m), but sexuals were particularly common along the east shore, whereas the west shore had mainly mixed or parthenogenetic sites. Overall, L. di Caldonazzo appears to be characterised by a mosaic of many local demes with varying proportions of sexuals and parthenogens. For the balance argument to apply, it is important that the coexistence is stable. However, due to the fact that we present only one extensive sample here, we cannot make reliable conclusions on long-term stability. Repeated sampling at some of the sites in the years preceding and following this study suggests that the composition of local populations is relatively stable (Beukeboom et al., 1996; unpubl. data).

Niche differences

Ecological differences between sexuals and parthenogens have been found in many species (Bell, 1982), and have been invoked as a possible explanation for different geographical distributions of both types in *S. polychroa* (Beukeboom et al., 1996). Within L. di Caldonazzo niche differentiation might explain the observed variation in relative frequencies. The niches of common planarian species are almost exclusively defined by food preference (Reynoldson & Young, 1963; Reynoldson & Bellamy, 1973; Bellamy & Reynoldson, 1974), whereas physical and chemical parameters as well as parasites are supposedly of minor importance (Reynoldson, 1966). Whether food preferences differ between sexual and parthenogenetic *S. polychroa* appears unlikely as the species is known to be a generalist feeder (Reynoldson & Davies, 1970). But these aspects should receive more attention in the future.

We showed that, in late summer, both biotypes can be found in a wide variety of habitats and most ecological parameters were not correlated with their relative frequency. We could only show that sexuals are rare relative to parthenogens when leeches are common. If this relationship is causal, it may indicate differential predation by leeches on sexuals and parthenogens, or differential competition with leeches for prey items. Alternatively, leeches and parthenogens may both be favoured independently by ecological parameters not measured in this study, leading to a spurious relationship. Our study also does not preclude that ecological differentiation between sexuals and parthenogens is more explicit at other times of the year.

Stochastic variation in relative frequencies of reproductive modes

A different explanation for the observed variation between samples could be stochasticity in a spatially structured population. This kind of stochastic variation can arise if migration between demes is low and genetic drift is high, e.g. as a consequence of population bottlenecks in local demes (Hartl & Clark, 1989). In Lago di Caldonazzo, significant fluctuations in body coloration between samples indeed suggest that exchange between sites is limited, as already suggested by Pongratz et al. (1998). The occurrence of bottlenecks in the resultant local populations is suggested by the strong erratic fluctuations in individual number at our sampling sites.

Gene flow between coexisting sexuals and parthenogens

Although sexual and parthenogenetic individuals differ in colour within sites, these differences are small relative to those within reproductive modes and between sites. This lends support to the results by Pongratz et al. (1998), who concluded from allozyme data that some genetic exchange between sexuals and parthenogens takes place within sites.

Conclusion

Lago di Caldonazzo harbours a series of local populations composed of a variable mixture of sexual and parthenogenetic *S. polychroa*. Both types are characterised by large spatial and ecological overlap, and there appears to be only limited dispersal between sites. Most of the variance in relative abundance remains unexplained by ecological parameters, suggesting that erratic fluctuations in local populations are important. Seasonal effects can not be excluded, but would probably not be able to explain the observed mosaic pattern. If ecological differentiation is weak, as suggested by this study, sexuals are in direct competition with parthenogens, and the balance argument applies. The advantages to parthenogens and sexuals in this interaction are published elsewhere (e.g. Weinzierl et al. 1998, 1999).

Acknowledgements

The data presented here were collected during a student practical organised by Leo Beukeboom,

Nico Michiels & Albert Klarenberg at the Ludwig-Maximilians-Universität in Munich. We thank Blanka Bakovsky, Roland Fleißner, Birgit Huber, Florian Karpf, Christian Laforsch, Carsten Schradin & Karin Seidel for their enthusiasm in the field and their tenacity in the laboratory, Tim Sharbel for supervising field work and karyology, Kai Berthold & Connie Schackert for help with collecting the stone-wise samples, and Peter Hammerstein & Tim Sharbel for comments on the manuscript.

References

- Asker, S. & L. Jerling, 1992. Apomixis in plants. CRC Press, Boca Raton, Florida.
- Bell, G., 1982. The Masterpiece of Nature: The Evolution and Genetics of Sexuality. Croom Helm, London.
- Bellamy, L. S. & T. B. Reynoldson, 1974. Behaviour in competition for food amongst lake-dwelling triclads. *Oikos* 25: 356–364.
- Benazzi, M., 1950. Ginogenesi in Tricladidi d'acqua dolce. *Chromosoma* 3: 474–482.
- Benazzi, M., 1957. Cariologia di *Dugesia lugubris* (O. Schmidt) (Tricladida Paludicola). *Caryologia* 10: 276–303.
- Benazzi, M., 1962. L'eredità della pigmentazione nella planaria *Dugesia lugubris*. *Atti della Associazione Genetica Italiana* 7: 213–218.
- Benazzi, M., 1965. Sulle basi genetiche del policromatismo nella planaria *Dugesia lugubris*. *Atti della Associazione Genetica Italiana* 10: 258.
- Benazzi, M. & G. Benazzi Lentati, 1976. Platyhelminthes. In: B. John, (ed.), *Animal Cytogenetics* 1. Gebrüder Borntraeger, Berlin-Stuttgart, 1–77.
- Benazzi Lentati, G., 1966. Amphimixis and pseudogamy in freshwater triclads, experimental reconstitution of polyploid pseudogamic biotypes. *Chromosoma* 20: 1–14.
- Benazzi Lentati, G., 1970. Gametogenesis and egg fertilisation in planarians. *Int. Rev. Cytol.* 27: 101–179.
- Beukeboom, L. W., R. P. Weinzierl, K. M. Reed & N. K. Michiels 1996. Distribution and origin of chromosomal races in the freshwater planarian *Dugesia polychroa* (Turbellaria: Tricladida). *Hereditas* 124: 7–15.
- Canovai, R., 1989. Distribuzione dei tricladi dulcacquicoli dei monti pisani con riferimento ai biotipi cariologici delle diverse specie. *Atti Soc. tosc. Sci. nat. Memorie, Serie B* 96: 107–120.
- Christensen, B., 1960. A comparative cytological investigation of the reproductive cycle of an amphimictic diploid and a parthenogenetic triploid form of *Lumbricillus lineatus* (Oligochaeta, Enchytraeidae). *Chromosoma* 11: 365–379.
- Clausen, J., 1961. Introgression facilitated by apomixis in polyploid Poas. *Euphytica* 10: 87–94.
- Dybdahl, M. F. & C. M. Lively, 1995. Diverse, endemic and polyphyletic clones in mixed populations of a freshwater snail (*Potamopyrgus antipodarum*). *J. evol. Biol.* 8: 385–398.
- Foighil, D. & M. J. Smith, 1995. Evolution of asexuality in the cosmopolitan marine clam *Lasaea*. *Evolution* 49: 140–150.
- Glesner, R. R. & D. Tilman, 1978. Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in parthenogenetic animals. *Am. Nat.* 112: 659–673.
- Hartl, D. L. & A. G. Clark, 1989. *Principles of Population Genetics*, 2nd edn. Sinauer Associates, Sunderland, MA.

- Hedges, S. B., J. P. Bogart & L. R. Maxson, 1992. Ancestry of unisexual salamanders. *Nature* 356: 708–710.
- Jaenike, J. & R. K. Selander, 1979. Evolution and ecology of parthenogenesis in earthworms. *Am. Zool.* 19: 729–737.
- Judson, O. P. & B. B. Normark, 1996. Ancient asexual scandals. *Trends Ecol. Evol.* 11: 41–46.
- Levin, D. A., 1975. Pest pressure and recombination systems in plants. *Am. Nat.* 109: 437–451.
- Lynch, M., 1984. Destabilising hybridisation, general-purpose genotypes and geographic parthenogenesis. *Q. Rev. Biol.* 59: 257–290.
- Maynard Smith, J., 1978. *The Evolution of Sex*. Cambridge University Press, Cambridge.
- Menken, S. B. J., E. Smit & C. M. Den Nijs, 1995. Genetical population structure in plants, gene flow between diploid sexual and triploid asexual dandelions (*Taraxacum* section *Ruderalia*). *Evolution* 49: 1108–1118.
- Michaels, H. J. & F. A. Bazzaz, 1989. Individual and population responses of sexual and apomictic plants to environmental gradients. *Am. Nat.* 134: 190–207.
- Mogie, M., 1992. *The Evolution of Asexual Reproduction in Plants*. Chapman and Hall, London.
- Mogie, M. & H. Ford, 1988. Sexual and asexual *Taraxacum* species. *Biol. J. linn. Soc.* 35: 155–168.
- Munsell, 1994. *Munsell Soil Color Charts*. Macbeth Division of Kollmogoran Instruments Corporation, New Windsor, New York.
- Pongratz, N., T. F. Sharbel, L. W. Beukeboom & N. K. Michiels, 1998. Allozyme variability in sexual and parthenogenetic freshwater planarians: evidence for polyphyletic origin of parthenogenetic lineages through hybridization with coexisting sexuals. *Heredity* 81: 38–47.
- Quattro, J. M., J. C. Avise & R. C. Vrijenhoek, 1992. An ancient clonal lineage in the fish genus *Poeciliopsis* (Atheriniformes: Poeciliidae). *Proc. nat. Acad. Sci. U.S.A.* 98: 348–352.
- Reynoldson, T. B., 1966. The distribution and abundance of lake-dwelling triclads – towards a hypothesis. *Adv. ecol. Res.* 3: 1–71.
- Reynoldson, T. B. L. S. & Bellamy, 1973. Interspecific competition in lake dwelling triclads. A laboratory study. *Oikos* 24: 303–313.
- Reynoldson, T. B. & R. W. Davies, 1970. Food niche and coexistence in lake-dwelling triclads. *J. Anim. Ecol.* 39: 599–617.
- Reynoldson, T. B. & J. O. Young, 1963. The food of four species of lake dwelling triclads. *J. Anim. Ecol.* 32: 175–191.
- Richards, A. J., 1973. The origin of *Taraxacum* agamospecies. *Botan. J. Linn. Soc.* 66: 189–211.
- Schenck, R. & R. C. Vrijenhoek, 1996. Spatial and temporal factors affecting coexistence among sexual and clonal forms of *Poeciliopsis*. *Evolution* 40: 1060–1070.
- Spolsky, C.M., C. A. Phillips & T. Uzzell, 1992. Antiquity of clonal salamander lineages revealed by mitochondrial DNA. *Nature* 356: 706–708.
- Suomalainen, E., A. Saura & J. Lokki, 1987. *Cytology and evolution in parthenogenesis*. CRC Press, Boca Raton, Florida.
- Tomiuk, J. & V. Loeschcke, 1991. A new measure of genetic identity between populations of sexual and asexual species. *Evolution* 45: 1685–1697.
- Weeks S. C., O. E. Gaggiotti, R. A. Schenck, K. P. Spindler & R. C. Vrijenhoek, 1992. Feeding behavior in sexual and clonal strains of *Poeciliopsis*. *Behav. Ecol. Sociobiol.* 30: 1–6.
- Weinzierl, R. P., K. Berthold, L. W. Beukeboom & N. K. Michiels, 1998. Reduced male allocation in a parthenogenetic hermaphrodite (*Dugesia polychroa*, Tricladida, Platyhelminthes). *Evolution* 52: 109–115.
- Weinzierl, R. P., P. Schmidt & N. K. Michiels, 1999. High fecundity and low fertility in parthenogenetic planarians. *Inv. Biol.*: (accepted).
- Williams, G. C., 1975. *Sex and Evolution*. Princeton University Press, Princeton.