Fortschritte der Zoologie · Band 29

Herausgegeben im Auftrag der
Deutschen Zoologischen Gesellschaft
von Martin Lindauer

Polychaete Reproduction

Progress in Comparative Reproductive Biology

Edited by
A. Fischer and H.-D. Pfannenstiel

184 figures and 26 tables

Gustav Fischer Verlag · Stuttgart · New York

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International Symposium Helgoland April 1982

Edited by ALBRECHT FISCHER and HANS-DIETER PFANNENSTIEL

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Gedruckt mit Unterstützung der Ernst-Reuter-Gesellschaft der Förderer und Freunde der Freien Universität Berlin e.V. und des Vereins der Freunde und Förderer der Universität zu Köln.

CIP-Kurztitelaufnahme der Deutschen Bibliothek

Polychaete reproduction : progress in comparative reproduction biology ; internat. symposium Helgoland, April 1982 / ed. by Albrecht Fischer and Hans-Dieter Pfannenstiel. – Stuttgart ; New York : Fischer, 1984. (Fortschritte der Zoologie ; Bd. 29)
ISBN 3-437-30439-9
NE: Fischer, Albrecht [Hrsg.]; GT

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Composed and printed by: Laupp & Göbel, Tübingen 3
Printed in Germany

ISBN 3-437-30439-9
ISBN 0-89574-197-0 NY
ISSN 0071-7991

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Preface

Reproduction in marine invertebrates has been studied from a number of points of view. Many of the facets of reproductive biology are particularly well represented among the polychaetes, upon which many model studies have been carried out. Such investigations have encompassed the following topics:

- studies on sex determination and transformation, and on the development of sexual maturity;
- studies on rhythms in reproduction and their endogenous or exogenous causes;
- cytological and biochemical descriptions of solitary gametogenesis, i.e., gametogenesis outside the confines of a gonad;
- endocrinological studies on especially simple physiological systems for controlling reproduction; and
- characterization of populations on the basis of their mode of reproduction and investigation into the role of reproductive mechanisms in speciation.

As in other scientific disciplines, the refinement of techniques and the growth of our knowledge have fragmented the study of polychaete reproduction into a number of subdisciplines. If growing knowledge of details is to promote the recognition of general principles of reproductive biology – and we are convinced that this is what we are working for and that our efforts will lead us to this goal – then the current state of our knowledge must be periodically summarized and reviewed.

In the past, a number of our colleagues have fortunately made an individual effort to summarize the growth of information in this field and to make it accessible. It seemed to us of even greater value for these specialists and other contributors to the field to participate in a symposium at which their results could be represented and discussed, the contributions to which could be edited and published. Accordingly, the editors of this volume organized such a symposium, which was held at the island of Helgoland in April 1982. Financial support, which we wish to gratefully acknowledge, was provided by the Volkswagen Foundation («Stiftung Volkswagenwerk») and a grant from the German Society for Developmental Biology («Gesellschaft für Entwicklungsbiologie»). It was not by chance that the symposium was held at Helgoland, Germany's most noteworthy marine station. The operators of the station, the «Biologische Anstalt Helgoland», have traditionally supported studies of reproductive and developmental biology, a tradition they have continued with their generous cooperation in providing a site for our symposium.

Following a historical introduction to the topics covered in the volume by C. HAUENSCHILD, the papers may be divided into three groups:

- Control of Sexuality and Reproduction
- Gametogenesis and Fertilization
- Reproductive Mechanisms and Speciation.

Scattered among the 17 review papers will be found five original contributions (GOERKE, ANGER, HOFMANN & SCHIEDGES, BERTOUT and KAHMANN) which tie in directly with the reviews.

The series «Fortschritte der Zoologie», of the Gustav Fischer Verlag, is an ideal vehicle for the publication of our symposium contributions, and the publisher has been most cooperative. Financial support for the publication has been provided by the «Ernst-Reuter-Gesellschaft der Förderer und Freunde der Freien Universität Berlin» and the «Verein der Freunde und Förderer der Universität Köln». This essential support is gratefully ack-

nowledged. The editors also wish to acknowledge the considerable help by Drs. N. Cross (Davis/USA), K. J. Eckelbarger (Fort Pierce/USA), D. I. D. Howie (Dublin/Ireland) and P. J. W. Olive (Newcastle/England) in editing contributions from authors whose first language is not English.

We hope that the publication of the papers presented here will serve to make the works of these specialists accessible to others with more general scientific interests, as suggested by the words of the literary historian Ernst Robert Curtius:

«Spezialismus ohne Universalismus ist blind –
Universalismus ohne Spezialismus ist eine Seifenblase»
(«Specialization without universality is blind –
but universality without specialization is but a soap bubble»)

Köln/Berlin, Spring 1984

A. Fischer
H.-D. Pfannenstiel

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Fortschritte der Zoologie, Band 29 · Fischer/Pfannenstiel (Hrsg.): Polychaete Reproduction
Gustav Fischer Verlag · Stuttgart · New York · 1984

Thoughts on our common theme: reproduction among the polychaetes, a look back on the beginnings

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We owe the appearance of the present volume on polychaete reproduction, which provides a good review of current research in this area, to our colleagues A. FISCHER (Köln) and H. D. PFANNENSTIEL (Berlin). Together these two have provided not only the welcome idea of holding an international symposium on this topic in Helgoland; they also undertook the very considerable task of organizing and successfully running the meeting, and then publishing the collected contributions in this volume of «Fortschritte der Zoologie». Since both of these colleagues began their research careers in my laboratory many years ago, and since studies in my laboratory in the '50's and '60's provided a foundation for work being pursued today, they have asked me to contribute a few words of introduction to the symposium volume.

Even in the late 19th and early 20th century, when descriptive morphological studies were dominating, the diverse and often surprising reproductive processes of polychaetes inspired a number of zoologists to initiate studies of reproduction and development, as well as undertaking the then more usual descriptive morphological studies. Thus *Platynereis* (= *Nereis*) *dumerilii* and *P. massiliensis* were studied by WISTINGHAUSEN (1891), HEMPELMANN (1911), JUST (1914) and HERPIN (1924). MC INTOSH (1907), NUSBAUM (1908) and IZUKA (1908) studied regeneration and reproductive processes in several nereid species. E. B. WILSON (1892) studied the early development of the *Nereis* embryo, building on the early studies of CLAPAREDE and METSCHNIKOW (1869) on the ontogeny of a series of polychaete species. Fertilization as a process, in which the thrust of the analysis was more physiological, was early studied by LILLIE (1912). The first demonstration of neurosecretory cells in the supra-esophageal ganglion of a polychaete was made by SCHARRER (1936) in *Nereis virens* and *N. diversicolor;* supplemental observations were reported by SCHÄFER (1939).

The reproductive biology of the syllids, as well as the nereids, drew the attention of a number of early investigators; the papers of KROHN (1852) on *Syllis* and *Autolytus,* and those of PRUVOT (1890), MALAQUIN (1893) and OKADA (1937) come especially to mind. The startling phenomenon of lunar periodicity in the swarming of the pacific palolo worm was also recorded in detail in the last century by FRIEDLÄNDER (1898) and KRÄMER (1899). The first observations on sex determination and differentiation in two other polychaetes, viz. *Dinophilus gyrociliatus* (= *D. apatris)* and *Ophryotrocha puerilis* also extend far back. The sexual dimorphism in egg size in the archiannelid *Dinophilus* was thoroughly studied by KORSCHELT (1882), followed by BEAUCHAMP (1910) and NACHTSHEIM (1919); more recently TRAUT (1969 a, b; 1970) has added interesting new data to our understanding of this phenomenon. The experiments of M. HARTMANN and his

colleagues (from 1936) on *Ophryotrocha* were based on earlier results published by BRAEM (1893) and KORSCHELT (1894). The studies of HARTMANN on sex determination in *Ophryotrocha* were continued, from a somewhat different point of view, by BACCI and his collaborators (1951 and subsequent papers); recently they have been successfully carried on by PFANNENSTIEL (1973, 1977, this vol.) and most recently by his students. Finally, the work of WHEELER (1896) and JÄGERSTEN (1939) on sexual and reproductive relationships in *Myzostoma* should be mentioned, since the myzostomids are considered to be closely related to the polychaetes.

When I became an assistant at the Kaiser-Wilhelm (later Max-Planck) Institute for Biology, my former teacher MAX HARTMANN, in whose debt I remain to this day for stimulating my thinking and giving me a goal, directed my attention to the polychaetes. He felt them to be particularly suitable and promising for approaching problems of general biological interest. With the studies begun by HARTMANN on laboratory cultures of *Ophryotrocha* as a model, I began to work out culture methods for different polychaetes. With his help, I was first able to show (HAUENSCHILD, 1951) that the reproductive polymorphism assumed for the nereid *Platynereis dumerilii* (DURCHON, 1955) resulted from a mixture of observations on two distinct species, *P. dumerilii* and *P. massiliensis,* which are completely identical morphologically outside of the periods of sexual maturation and embryonic development. The two differ considerably, however, in their sexual differentiation, gamete structure and early development. Such cases, in which a single species appears to reproduce in different ways, but which in reality involve observations on more than one species, have since been found a number of times among polychaetes. Such questions are discussed in this volume from the point of view of the evolutionary biologist by GRASSLE, ÅKESSON and GUÉRIN and KERAMBRUN.

I was also able to culture the syllids *Brania (= Grubea) clavata* and *Autolytus prolifer* continuously for years in our inland laboratory. I have maintained cultures of *Platynereis dumerilii* for many generations in my institute, and subcultures from these are still maintained today in the laboratories of several former students, more than 30 years after the original culture was established from field-collected animals. Continuous culture in the laboratory made readily available specimens whose history was precisely known; this in turn permitted an experimental approach to questions which could scarcely be asked of field-collected animals kept in the laboratory for only a short time, as had been the usual practice until then. At first, I concentrated primarily on the question of sex determination in *Brania clavata,* since this seemed to be influenced by external factors as in *Ophryotrocha.* In contrast to the protandry of *Ophryotrocha*, however, this species turned out to include both protogynous and pure male individuals (HAUENSCHILD, 1953, 1959b). It could also be demonstrated that mature female stages of *Brania* could only spawn in response to a male pheromone released into the water with the sperm (HAUENSCHILD and HAUENSCHILD, 1951). Somewhat later, I discovered that the lunar periodicity in heteronereid swarming, already known from field studies, could be artificially induced or synchronized in the laboratory by an additional periodically applied light, which imitates the full moon (HAUENSCHILD 1955, 1960). This periodicity is based on a corresponding periodicity in the entire sexual development of the animal. Subsequent studies on the brown alga *Dictyota* (BÜNNING and MÜLLER, 1961) and the midge *Clunio marinus* (NEUMANN, from 1963), inspired by the results with *Platynereis*, demonstrated that the previously unknown *Zeitgeber* function of moonlight is a widely distributed phenomenon in nature. These results with *Platynereis* also inspired an attempt, in 1966, to make corresponding observations in Samoa on the pacific palolo worm, *Eunice viridis,* the classical example of strict lunar periodicity in reproduction. This first attempt to analyze the timing mechanism of spawning in the palolo using animals taken from the field at

different seasons and maintained in a sort of laboratory unfortunately failed to produce the desired result. It did, however, produce a promising series of preliminary results (HAUENSCHILD, FISCHER and HOFMANN, 1968) which suggest that continuation of the investigation might produce more definitive answers. Thus, more recently, it has been possible to maintain the closely related Mediterranean species *Eunice siciliensis* in the laboratory so that individuals isolated in small vessels finally reach sexual maturity and release epitokous posterior ends, even after several years of laboratory maintenance (HOFMANN, 1974).

In seeking a means by which photoperiod might intervene in the control of sexual maturation in *Platynereis dumerilii*, I began a series of amputation and reimplantation experiments to explore the endocrine influence, first reported by DURCHON (1952), which the prostomium might have on sexual maturation. In contrast to DURCHON, who at first studied primarily males of *Nereis* and *Perinereis*, I concentrated on female development in *Platynereis* (HAUENSCHILD 1956, 1966, 1974). My own experiments on female *Platynereis dumerilii*, which for the first time utilized oogenesis to delineate the stages of sexual maturation and of demonstrable hormonal effects, were extended in a number of directions by former students (MÜLLER, 1973; HOFMANN, 1975). They also prepared the way for a completely new and extremely promising line of research which FISCHER has established with the in vitro culture of oocytes (HEACOX, FISCHER and FRANGENBERG, 1983) and with the demonstration of a vitellogenin in a nereid (FISCHER, 1979). The *Platynereis* cultures have also produced some interesting observations aside from the direct study of reproduction. Thus FISCHER (1965) found a circadian periodicity in the chromatophores which was further investigated by RÖSELER (1970) in relation to lunar periodicity; furthermore, a mutant appeared spontaneously in the cultures characterized by the lack of an eye pigment, which could be analyzed both genetically and developmentally (FISCHER, 1971), and which was later used for a very elegant analysis of egg development in *Platynereis dumerilii* (FISCHER, this volume).

In addition, I carried out several experiments on the endocrine control of reproduction in the syllid *Autolytus prolifer* (HAUENSCHILD, 1959 a), which were also stimulated by the pioneer observations of DURCHON (1952). This species was cultured for five generations (fed on separately cultured hydroid polyps). Subsequent continuation and completion of this project was undertaken by SCHIEDGES (1979), a doctoral candidate under my former student Hofmann. The very successful studies on *Typosyllis prolifera* which FRANKE (1980, 1981, this volume) began under my direction, approach the same complex of questions and are connected in content and method to both the publications of the DURCHON school and my own 1959 experiments on *Autolytus*. Most recently, two of my students have concerned themselves with the reproductive biology of species outside of the Nereidae and Syllidae; RÖHRKASTEN (1983) studied the influence of the prostomium on oocyte development in *Anaitides mucosa* and KAHMANN (this volume) was concerned with the mode of sperm transfer in the sabellid *Fabricia sabella*, which for this purpose was also bred in the laboratory.

As I was writing the 1953 paper describing the results of my investigations on *Brania clavata*, my review of the literature revealed to me the first two publications of DURCHON (1948, 1950); one of these described the premature production of epitoky and spermatogenesis by prostomium removal in two different nereids; the second, accelerated gametogenesis and stolonization after removal of the proventriculus in *Syllis amica*. With these totally novel discoveries, which were later published in greater detail (DURCHON, 1952; this volume), my esteemed colleague DURCHON earned the distinction of having made the pioneer observations in the field of polychaete endocrinology. Some years later in LILLE, DURCHON assembled a large and very active team of colleagues and students

who, because of their number, cannot all be mentioned here. I would like to mention at least four, namely BOILLY-MARER (from 1962), DHAINAUT (from 1964, this volume), PORCHET (from 1967, this volume) and BERTOUT (from 1973, this volume). In conjunction with his group DURCHON made numerous contributions to reproductive biology and particularly to the endocrinology of nereids and syllids. Among these the application of organ culture and the effort to isolate and chemically identify the nereid brain hormone are perhaps particularly worthy of mention. In the early sixties, effort in the field of polychaete endocrinology, as it had been started by DURCHON and somewhat later by myself, was expanded by the beginning of studies by two further groups, namely HOWIE (from 1961, this volume) in Ireland and CLARK (from 1963) in England. CLARK first studied *Nephtys* and later *Nereis diversicolor* (CLARK and RUSTON, 1963). Later, members of Clark's group investigated the endocrinology of still other polychaetes, such as different aphroditoid families (GOLDING, 1973), as well as *Cirratulus cirratus* and *Eulalia viridis* (OLIVE 1973, 1975, this volume). Toward the end of the sixties, SCHROEDER established a further research group in the USA devoted to the reproduction of nereids and syllids (SCHROEDER, HOFMANN and WALLACE, 1977; HEACOX and SCHROEDER, 1982). Aside from these colleagues, most of whom have been interested in endocrinological problems since 1950, there has of course been a whole series of additional scientists who, starting with different interests, have made important discoveries in the area of polychaete reproductive biology. I recall, for instance, ÅKESSON (1975, this volume) and his multi-faceted studies on different *Ophryotrocha* species; WESTHEIDE (1967, this volume) who, in the course of his taxonomic, morphological and ecological studies of various inhabitants of the mesopsammon, made interesting discoveries with respect to sperm transfer in some hesionids and other polychaetes; or the more morphological studies of gametogenesis, such as those of GIDHOLM (1965 on *Autolytus*), FRANZÉN (from 1974, on spermatogenesis in numerous polychaetes) and ECKELBARGER (from 1975, and this volume) on oogenesis in the terebillid *Nicolea* and several other species. In this connection, the ultrastructural analysis of the acrosome reaction in *Eupomatus* (incorrectly called *Hydroides*) *dianthus* by COLWIN and COLWIN (1960) and the investigation of the fertilization of the *Nereis*-egg by SAWADA (1960) should also be mentioned.

In this short piece it is not my intention to list every zoologist who has contributed in some way to the reproductive biology of polychaetes, nor to provide a complete list of their publications. A more complete account has been prepared by SCHROEDER and HERMANS (1975). I rather hope to have drawn in broad strokes the lines which have been significant in the development of the entire subject to which this symposium volume is devoted. By the very nature of this undertaking, it is natural that those topics in which one has himself been interested, and whose development one has experienced first hand, will be most prominently discussed. Should I have failed to mention any given colleague, it should not be taken to mean that I consider his work objectively less valuable; it has simply been necessary to make a selection, which can only be done somewhat subjectively. I am convinced that the polychaetes will still provide many interesting and perhaps surprising results, some of which may have broad biological significance, to those who now and in the future continue the study of reproduction in this fascinating group of animals. In this spirit I wish all colleagues who can be active in research in this area, good luck in their choice of the right species, and may their labor be crowned with worthwhile results!

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