ADVANCES IN INVERTEBRATE REPRODUCTION

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Terrance S. Adams
Editors

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ADVANCES IN INVERTEBRATE REPRODUCTION

Proceedings of the Second International Symposium of the International Society of Invertebrate Reproduction (ISIR) held in Davis, California on August 27-31, 1979

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In dedication to the memory of Jean Clark Dan, a friend and inspiration to so many.

PREFACE

In 1975, Dr. Kenneth G. Adiyodi organized an international symposium on the reproductive physiology of invertebrates, which was held at Calicut University, India, September 10 - 12. The proceedings of these meetings, *Advances in Invertebrate Reproduction*, were edited by Dr. Kenneth G. and Dr. Rita G. Adiyodi and published by Peralam-Kenoth in February 1977. This symposium further precipitated the formation of the International Society of Invertebrate Reproduction.

The primary intent of this society is to increase communications among scientists working on various aspects of invertebrate reproduction in traditionally isolated departments such as entomology, nematology, and marine biology, which have classically communicated little with each other. To establish a forum for its members, the society initiated a journal, the *International Journal of Invertebrate Reproduction*, which is issued bimonthly by Elsevier Press.

The present volume represents the proceedings of the Second International Symposium of Invertebrate Reproduction, which was held at the University of California, Davis, August 27-31, 1979. This symposium was organized under the auspices of the International Society of Invertebrate Reproduction and consisted of invited and contributed papers. The invited papers were given by scientists in the forefront of their disciplines and were organized under three main themes: environmental synchronization of reproduction, endocrine control of reproduction, and gamete activation and interaction.

We fervently believe this volume, the second in an open series, will be extremely useful to graduate students and researchers in the broad variety of disciplines related to invertebrate reproduction. The third volume will result from the society's next international symposium in 1983, which will be organized by Dr. Wolf Engels and Dr. Albrecht Fisher and held at Tubingen University in West Germany.

The second symposium and the publication of these proceedings would not have been possible without the assistance of the United States Agency for International Development, the California Sea Grant College Program, and the College of Agricultural and Environmental Sciences, University of California, Davis. The editors wish to take this opportunity to thank the contributors of this volume as well as Lucy Garcia, for her tireless hours spent in the organization of the meeting, and Ann McGuire for her invaluable editorial assistance in the production of this volume.

ADVANCES IN INVERTEBRATE REPRODUCTION

CONTENTS

PART I: ENVIRONMENTAL SYNCHRONIZATION OF REPRODUCTION

W.H. Clark, Jr., and T. S. Adams, eds.
Advances in Invertebrate Reproduction

SYNCHRONIZATION OF SPAWNING IN MARINE INVERTEBRATES BY PHYTOPLANKTON

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INTRODUCTION

The release of gametes is the most striking event in invertebrate reproductive cycles, since it is frequently very abrupt and leads to a dramatic decrease in gonadal size. Entire populations often spawn completely within less than a month, and sometimes within a few days.[1,2,3,4,5,6] For many species, animals are in condition to spawn well before spawning occurs, and the length of the interim before spawning is variable.[1,5,7,8,9,10,11] Moreover, spawning often does not occur when ripe animals are maintained in the laboratory during the spawning period.[10,12,13] These observations, that: (1) entire populations can spawn abruptly and synchronously; (2) the interval from the time that animals reach condition to spawn to the time that spawning actually occurs is variable; and (3) individuals separated from field conditions do not spawn at the time spawning occurs in the field, strongly suggest that spawning is coordinated by external environmental factors. This hypothesis is further supported by the *a priori* reasoning that there must be a mechanism to synchronize gamete release to ensure that fertilization takes place and that the pelagic phase is produced when environmental conditions are favourable.

External factors that might act as spawning stimuli have been suggested by many workers, but there are few species for which the natural spawning cue has been elucidated.[14] There are no experimental studies that verify the correlation between environmental factors and spawning. Our poor understanding of the factors that control spawning is surprising, particularly in the case of abrupt spawners, for which external stimulation is most strongly indicated.

Temperature

Many marine invertebrates, especially in temperate seas, spawn at a particular time of the year at a particular interval of the annual temperature cycle. It is commonly hypothesized that gametes are released when a certain temperature level is reached or when there is a certain temperature change. For a number of species, it has been clearly demonstrated that gonadal maturation is stimulated when the sea temperature increases or decreases to a certain level.[15,16,17,18,19,20,21,22] Further, it has been shown that the temperature that stimulates gametogenesis may vary among populations of a species that lives in different geographical locations.[23,24,25,26,27]

In some lamellibranchs, spawning may not require an external stimulus, but may begin spontaneously after gametogenesis is completed.[19,28] In some invertebrates, the asteroids for example, oocyte maturation occurs rapidly just before spawning, and one external cue probably stimulates both events. In laboratory studies using excised gonads from the scallop, *Pecten yessoensis*, Yamamoto[29] found that a temperature rise caused oocyte maturation and passage of the ova into the oviducts. He also indicated that there is a similar temperature change in the field when *P. yessoensis* spawns.[30] Thus, for this species a temperature change, acting directly on the gonads, appears to synchronize spawning.

In many marine invertebrates, mature gametes are retained for a period of time and are then suddenly released; thus, gonadal maturation and spawning in these species are probably stimulated by separate cues. Although a certain temperature change (different from that which may have stimulated gametogenesis) could stimulate spawning, this has never been demonstrated. In the laboratory, a number of species will spawn in response to a sharp temperature change, usually on the order of 5 to 10°C, but whether such temperature changes occur in nature at the time of spawning is questionable.[31] Despite numerous studies on the influence of temperature on spawning,[6,11,25,32,33,34,35,36,37] there are few species for which it has been established that temperature is the cue for spawning in nature.

Light

During the general reproductive period, a number of ectoprocts, ascidians, and coelenterates are stimulated to spawn by changes in illumination.[38,39] Also, moonlight has been implicated in the regulation of gamete release in some species with lunar spawning rhythms.[40,41,42,43] In some barnacles in boreal seas, gonadal maturation, which normally occurs in the autumn when daylength is decreasing, is strongly inhibited when animals are maintained under constant illumination.[22,44] It is conceivable that photoperiod coordinates annual spawning periods, but this possibility has received little research attention. Spawning variations in different localities and years must be related to other factors.

Chemicals

Many chemicals stimulate spawning in marine invertebrates, but their function in nature is unknown.[45,46,47] Sperm suspension is particularly effective in many species, and the response of individuals to sperm has been used as a criterion to determine if animals are in condition to spawn.[48] This phenomenon undoubtedly is useful in increasing the degree of synchrony of spawning within a population but does not resolve the question of what initiates spawning in the first individuals. The effectiveness of chemical stimulation by sperm and other substances suggests chemical involvement in natural spawning.

Phytoplankton

The synchrony of phytoplankton blooms with spawning and the pelagic phase of marine invertebrates has been recognized for many years.[7] For species with planktotrophic larvae, it is an adaptive necessity that the larvae be produced when there is an adequate supply of food. Although Einarsson[49] and Thorson[7] suggested that phytoplankton blooms might stimulate gamete release, subsequent workers have not pursued this hypothesis.

In an attempt to elucidate the factors controlling spawning, I made observations in several localities and over a number of years to identify the factors that most correlated with spawning. These factors were then tested in the laboratory for their ability to induce gamete release. Under study were two species of sea urchins, *Strongylocentrotus droebachiensis* Muller and *Strongylocentrotus purpuratus* Stimpson, and eight species of chitons, *Mopalia laevior* Pilsbry, *Mopalia ciliata* Sowerby, *Mopalia hindsii* Reeve, *Mopalia lignosa* Gould, *Mopalia muscosa* Gould, *Tonicella lineata* Wood, *Tonicella insignis* Reeve, and *Katharina tunicata* Wood. Because the gonads of urchins and chitons are separate from other body organs, gonadal indices (percentage wet weight of the gonads to total body weight) were easily determined. For the majority of these species, spawning was synchronized within specific populations, and the decrease in the mean gonadal index clearly indicated when spawning occurred.

RESULTS AND DISCUSSION

Correlation between temperature and spawning

The relationship between temperature and spawning in six different invertebrates in the subtidal community at First Narrows, Vancouver, in the Strait of Georgia, British Columbia, Canada, is shown in Fig. 1. *Tonicella lineata, T. insignis, Mopalia laevior, M. ciliata,* and *Strongylocentrotus droebachiensis*

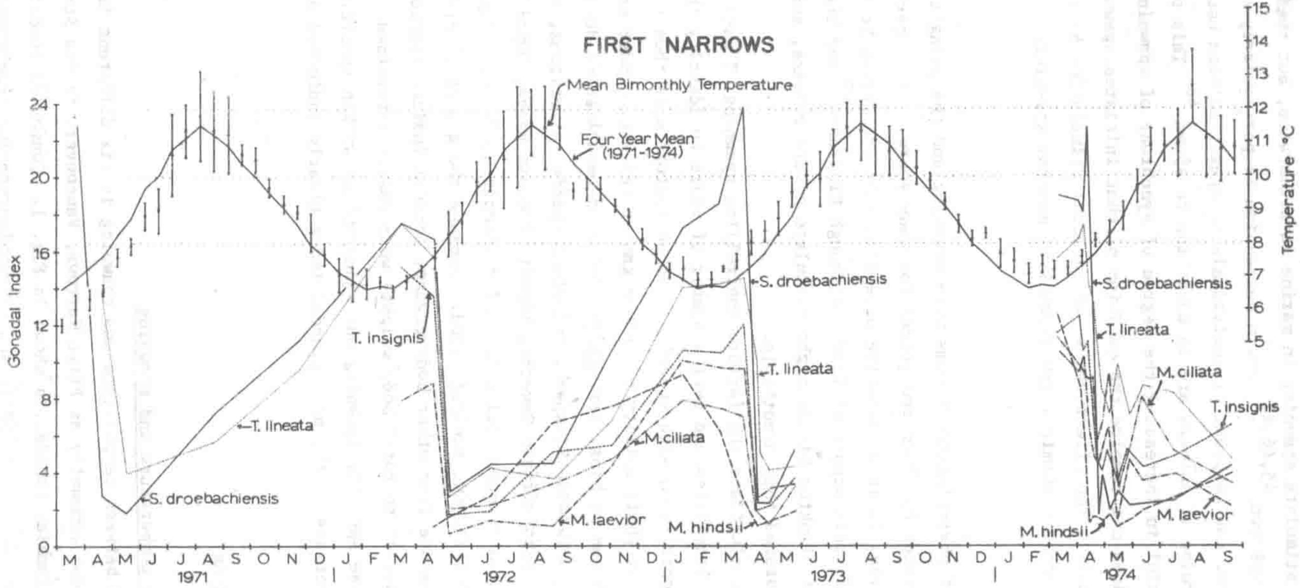

Fig. 1. Mean seawater temperature (± standard deviations) at First Narrows, British Columbia, for first half and second half of each month during period March 1971 to September 1974, compared with 4-year mean (1971-1974) for the first and last half of each month. Mean gonadal index values for *Tonicella lineata*, *T. insignis*, *Mopalia laevior*, *M. ciliata*, *M. hindsii*, and *Strongylocentrotus droebachiensis* superimposed on data show relationship of reproductive cycles to temperature (from Himmelman[52]).

usually spawned together abruptly in the spring. In 1972, this synchronous spawning occurred between 20 April and 8 May, but in 1973 it occurred about two weeks earlier, between 30 March and 17 April. In both years, the temperature at the time of spawning was 7.5 to 8.3°C, thus suggesting that spawning may have been induced when sea temperature reached this level. Furthermore, there was an increase in the rate of warming at the time spawning occurred. In 1974, spawning began as the temperature approached 8°C, but spawning was more prolonged than in 1972 and 1973. There were irregular changes in the mean gonadal indices in April, May, and June 1974, suggesting that spawning was not well synchronized. There appeared to be variations in the degree of spawning in localized areas. The late winter and spring of 1971 was the coldest period during my study, and 1971 was the only year when *S. droebachiensis* and *T. lineata* did not spawn together. *Strongylocentrotus droebachiensis* spawned in early April when the temperature was approximately 6.3°C, whereas *T. lineata* spawned two weeks later when the temperature reached approximately 7.6°C. Thus, while the majority of spawnings at First Narrows took place as the vernal warming approached 8°C, there were no unusual temperature conditions in 1974 that would account for the poorly defined spawnings in that year, and the hypothesis of a critical spawning temperature cannot explain the early spawning of *S. droebachiensis* in 1971.

At Botanical Beach, Vancouver Island, on the open Pacific Ocean, the animals were collected in the low intertidal region. During 80% of the time, these animals are exposed to ambient sea temperature, but during low-tide periods, they are subjected to erratic temperature changes. In this situation, it would be difficult to demonstrate a positive relationship between temperature and spawning, however, a negative relationship was noted.[50,51,52] *Tonicella lineata* and *Katharina tunicata* always spawned together, but sea temperature at the time of spawning varied in different years. It was also noted that sea temperatures at the time of spawning of *T. lineata* and *S. droebachiensis* at Botanical Beach were higher than that at First Narrows.[50,52,53]

At Porteau, in the Strait of Georgia (30 km north of First Narrows), a precise record of temperature was made during the spring of 1973 with a thermograph placed in the subtidal region where the animals were collected. There was an abrupt drop in the mean gonadal indices of *Tonicella insignis, T. lineata,* and *Mopalia laevior* between 27 March and 10 April (Fig. 2). At this time, the temperature was approaching 8°C (Fig. 2), similar to the usual spawning temperature at First Narrows. The stability of the temperature during these abrupt spawnings, however, was notable. If temperature did stimulate spawning, the animals must have had a precise temperature threshold for spawn-