VARIABILITY IN THE PATTERN OF SEXUAL REPRODUCTION OF THE CORAL STYLOPHORA PISTILLATA AT EILAT, RED SEA: A LONG-TERM STUDY

B. RINKEVICH* AND Y. LOYA
Department of Zoology. The George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel

ABSTRACT

Sexual reproduction of the Red Sea coral Stylophora pistillata was followed at Eilat in a long-term study (1974–1984). Field examination of over 9000 colonies through 119 months indicated that S. pistillata had a reproductive season of approximately 8 months (varying from 6 to 9 months). Premature planulae and eggs were aborted following winter storms, resulting in a lowering of the planular index and the number of female gonads per polyp. Histological examinations of tissue from 20 large colonies which were studied for several years, until they were found dead in situ, indicated that either sexuality (reproductive states) and/or fecundity could be completely altered from one reproductive season to the next: i.e., hermaphroditic colonies exhibiting high fecundity in one season became male or even sterile thereafter, and vice versa. In addition, great variability in reproduction between successive years was recorded in sexuality and in the fecundity of shallow water populations. Shallow water colonies (5 m) possessed up to 5 times more female gonads per polyp and shed 5 to 20 times more planulae than deep water colonies (25 to 45 m) in which the reproductive season is 2 to 3 months shorter.

We suggest that the changes in the hermaphroditic, male, or sterile modes of reproduction in S. pistillata are from energy limitations and stress conditions. Since reproductive activity probably involves significant energetic expenditures, any stress or diminution in energy resources affects sexuality or fecundity. This should be considered before formulating any general hypothesis on coral reproduction.

INTRODUCTION

Much information concerning reproductive biology of scleractinian corals has recently become available. Fadlallah (1983) reviewed past studies and provided a list of almost 90 species in which several known reproductive characteristics are presented. More recent studies (Harriott, 1983; Szmant-Froelich et al., 1984; Shlesinger and Loya, 1985; Wallace, 1985; Willis et al., 1985; Babcock et al., 1986; Szmant, 1986) provide information on reproductive patterns of more than 100 additional species of corals.

Although this list of studied species is impressive, data on scleractinian reproduction is still scanty, especially that dealing with their reproductive ecology. These studies evaluated sizes, shapes, and numbers of gonads, and attempted to establish reproductive seasonality, lunar periodicity, mode of reproduction, planula characterizations, and behavior. However, most studies were based on observations and

Received 30 January 1987; accepted 31 July 1987.
* Present Address: Hopkins Marine Station of Stanford University, Pacific Grove, California 93950.
experiments carried out within a period of a year or less. Only a few studies dealt with longer periods ranging from two (Atoda, 1947a, b; Harriott, 1983; Jokiel, 1985; Wallace, 1985) to three years (Kojis and Quinn, 1981a; van Moorsel, 1983; Stoddard and Black, 1985). Consequently, studies on sexual reproduction often fall short in documenting many aspects of coral reproduction (Fadlallah, 1983). Detailed information on coral reproduction could clarify many aspects of their life history patterns and provide a better understanding of the coral reef as a whole.

*Stylophora pistillata* (Esper) is one of the most abundant coral species in the Gulf of Eilat, Red Sea. Some aspects of the reproduction of this species have already been studied in the field and the laboratory. Descriptions of planulae and gonads have been made (Rinkevich and Loya, 1979a). In addition, synchronization in breeding, colony size in relation to fecundity, onset of reproduction, reproduction within a single colony, and seasonality of planulation were also reported (Rinkevich and Loya, 1979b). This paper summarizes results of a ten-year study on the reproduction of *S. pistillata* which elucidate some general conclusions characterizing coral reproductive activities.

**MATERIALS AND METHODS**

Reproductive activity of *S. pistillata* was studied from March 1974 to January 1984 (most intensively from 1976 to 1980). The study area was located in front of the H. Steinitz, Marine Biological Laboratory at Eilat, Gulf of Eilat, Red Sea, and was visited regularly once a month during the ten-year study period. Large colonies (mean geometric radius, \( r > 20 \text{ cm} \)) were sampled from both shallow (3–5 m) and deep water (25–60 m) populations.

Reproduction was studied by two techniques: collections of shed planulae (see below) and examinations of gonads in histological sections (Rinkevich and Loya, 1979a, b). A single branch was sampled from each colony. This branch represents the reproductive state of the entire colony (Rinkevich and Loya, 1979b). The number of female gonads was counted within serial sections for each tested polyp and quantitative data were obtained on the average number of eggs per polyp in a given specimen (6–18 polyps per sample). Male gonads were not counted because of the difficulty of following them in serial histological sections as a result of the irregular shape of a typical male gonad (Rinkevich and Loya, 1979a). Tissue samples were always taken near the bases of branches since few polyps from the tips contain genital cells (Rinkevich and Loya, 1979b; Kojis and Quinn, 1981a).

Early in the study, planulae were collected *in situ* by covering large colonies with plankton nets in the late afternoon and removing the nets at midnight (Rinkevich and Loya, 1979a). However, due to the difficulties with this technique during night diving (especially with the deep-water colonies), planulae were collected from coral branches that were brought into the laboratory. The branches were carefully removed underwater using wire cutters, and transported to the laboratory within 30 min after sampling in closed, separate plastic bags. The water in each bag was checked for the appearance of planulae. Each sample was put separately in a 5 l glass aquarium, containing filtered seawater, and left overnight. Planulae were shed during the night (Rinkevich and Loya, 1979a). Although handling stimulated planula release, it is assumed that these planulae were prepared for shedding. This assumption was supported by the finding that the released planulae were fully developed. Since conditions in all treated samples were similar, we concluded that collection procedures did not affect the results. Planulae were counted by sight and removed by pipettes. The seawater was then filtered through a plankton net (100 \( \mu \text{m} \)) and all remaining planulae were
TABLE I

Some characterizations of recorded southern storms in Eilat

<table>
<thead>
<tr>
<th>Date</th>
<th>No. of storms</th>
<th>Max. height (m)</th>
<th>Max. length (m)</th>
<th>Waves</th>
<th>Winds</th>
<th>General direction</th>
<th>Max. speed (km/h)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feb. 1979</td>
<td>3</td>
<td>2</td>
<td>12</td>
<td></td>
<td></td>
<td>SE</td>
<td>nd</td>
</tr>
<tr>
<td>Apr. 1979</td>
<td>3</td>
<td>1+</td>
<td>nd</td>
<td></td>
<td></td>
<td>S</td>
<td>nd</td>
</tr>
<tr>
<td>Nov. 1979</td>
<td>1</td>
<td>1</td>
<td>6</td>
<td></td>
<td></td>
<td>SE</td>
<td>20</td>
</tr>
<tr>
<td>Dec. 1979</td>
<td>2</td>
<td>2</td>
<td>nd</td>
<td></td>
<td></td>
<td>SE</td>
<td>nd</td>
</tr>
<tr>
<td>Feb. 1980</td>
<td>2</td>
<td>2.5</td>
<td>10</td>
<td></td>
<td></td>
<td>SSE</td>
<td>35</td>
</tr>
<tr>
<td>Mar. 1980</td>
<td>1</td>
<td>nd</td>
<td>nd</td>
<td></td>
<td></td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>Apr. 1980</td>
<td>1</td>
<td>nd</td>
<td>nd</td>
<td></td>
<td></td>
<td>S, SE, SW</td>
<td>25</td>
</tr>
<tr>
<td>Jan. 1981</td>
<td>2</td>
<td>1.5</td>
<td>20</td>
<td></td>
<td></td>
<td>SSE</td>
<td>18</td>
</tr>
<tr>
<td>Feb. 1981</td>
<td>3</td>
<td>1.2</td>
<td>27</td>
<td></td>
<td></td>
<td>S, SE</td>
<td>nd</td>
</tr>
<tr>
<td>Mar. 1981</td>
<td>1</td>
<td>0.5</td>
<td>nd</td>
<td></td>
<td></td>
<td>nd</td>
<td>nd</td>
</tr>
</tbody>
</table>

nd = no available data. (Personal communication, C. Porter, Israel Oceanographic and Limnological Research Ltd., Eilat).

The most severe storms in the sea at Eilat are known as southern storms, which occur during the winter and spring. Some physical parameters of these storms are partly documented from February 1979 (Table I).

RESULTS

Long-term study on seasonality of planulae shedding

Planulation in *S. pistillata* was continuously studied between March 1974 to January 1984 by sampling more than 9000 colonies (Table II). The two questions investigated were whether planulation occurs in the same months from one year to the next and how the planular index in the shallow water population fluctuated during the

...
TABLE II

Monthly planular index in shallow water populations of Stylophora pistillata during 119 months of observations

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1975</td>
<td>+</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>++</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1977</td>
<td>-</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1978</td>
<td>+</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1979</td>
<td>++</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1980</td>
<td>+</td>
<td>-</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1981</td>
<td>+</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1982</td>
<td>++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1983</td>
<td>+</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1984</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* (−), No planulae; (+−), very few; (+), few; (++), intermediate; (+++), large numbers.

119 months of observations. S. pistillata has a long reproductive season (planulae release) lasting approximately 8 months, from December to July (Table II). However, the reproductive season ranged 6 months (in 1976) to 9 months (in 1975). In the three-month period from August to October, no planulation was ever recorded. Only once during the ten-year investigation were very few planulae observed in November (in 1975). A marked variation was noted in the December-January-February index between different years. Although these months represent the beginning of the reproductive season (Rinkevich and Loya, 1979b), this variability might also be the result of the southern storms which are most severe during the winter (Table I). This phenomenon is also demonstrated in another part of the present study: in April 1980 a southern storm interrupted our field sampling. Branch samples were collected before the storm from 10 mature colonies. Nine of them released high numbers of planulae (average of 30 ± 28 planulae, per 100 g skeleton, per colony). One day after the storm samples were collected for histological study from 13 other mature colonies inhabiting the same area and depth. Only eight colonies contained low numbers of female gonads while the others were either sterile or contained only male gonads. The average number of female gonads per polyp, per colony was very low (0.4 ± 0.6), much lower than other April months (for more detail, see Tables VI and IV, respectively).

Long-term study on reproductive states

Two separate sets of experiments followed the long-term state of reproduction in shallow water populations. In the first experiment 20 large colonies (r > 20 cm) were chosen (December 1976) and sampled for histological study two to three times a year e.g., in the beginning, the peak and the end of the reproductive season over four successive reproductive periods, until the deaths of all of them were recorded (February 1980). Since synchronization in the reproduction activity exists between branches (Rinkevich and Loya, 1979b), only one branch was sampled each time from each colony. This sampling procedure did not affect survivorship or reproduction (unpub.). Colony mortality was high (Table III), although colonies were carefully chosen on the basis of their healthy state (without dead branches or tissue damage). One and
two years after the beginning of the study, 60% and 30%, respectively, of the colonies were alive. Only one colony of the 20 samples (5%) remained alive after 3 years (Table III). A decrease in fecundity was repeatedly observed several months prior to the natural death of many of the colonies. In four out of the six dead colonies following a period of high fecundity (colonies 9, 15, 16, 19; Table III), the death was attributed to southern storms. None of the dead colonies during the first 4 months of the study (colonies 8, 11, 12, 17; Table III) contained any genital cells when first sampled.

The results (Table III) also indicate variability in sexuality (reproductive states: male, hermaphrodite, or sterile modes of reproduction) and fecundity of a specific colony in different years. Hermaphroditic colonies which exhibit high fecundity in one reproductive season may differ in the following reproductive season in which they become sterile (colonies 6, 14; Table III), or male (colonies 4, 10; Table III) and vice versa. The changes in colony reproductive patterns are further demonstrated in colonies sampled in three to four consecutive December months (colonies 3, 6, 10, 13, 14, 20; Table III). Sexuality or fecundity of five out of these six colonies were altered in each December month.

In the second set of experiments (Table IV), 155 large shallow water colonies were sampled over 10 successive sampling periods at the beginning and during the peak of 5 reproductive seasons (April 1976–April 1980). Changes among the different seasons
either in sexuality or fecundity were observed. For example, each one of the 4 different December months (years 1976, 1977, 1978, 1979) represented different patterns of reproductive states: 8–56% of the colonies were sterile, 0–25% males and 45–67% were hermaphrodites among the different December months. The same pattern was recorded for sexuality of March to April months: 0–38%, 0–22% and 62–100%, respectively (Table IV). It is concluded that “one year of sampling” is not enough for the characterization of reproductive states in this species.

Reproduction in shallow versus deep water populations

Possible differences in reproduction between shallow and deep water populations were tested in two sets of experiments. In the first, we analyzed serial histological sections of 90 shallow water colonies (from Table IV). The results were compared to those of 77 deep water colonies (25–45 m, Table V) sampled on the same days during three successive reproductive seasons (April 1978–April 1980). Shallow water colonies possessed up to 5 times more female gonads per polyp per colony than deep water colonies ($P < 0.01$, Wilcoxon’s signed rank test; Sokal and Rohlf, 1981). This phenomenon was most clear during the peak of the reproductive season, March to

<table>
<thead>
<tr>
<th>Date</th>
<th>Depth (m)</th>
<th>No. of colonies</th>
<th>Colony reproductive state (%)</th>
<th>Average female gonads (polyp⁻¹ colony⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hermaphrodites</td>
<td>Males only</td>
</tr>
<tr>
<td>Mar. 78</td>
<td>60</td>
<td>1</td>
<td>100</td>
<td>—</td>
</tr>
<tr>
<td>Apr. 78</td>
<td>25–30</td>
<td>15</td>
<td>40</td>
<td>40</td>
</tr>
<tr>
<td>Jun. 78</td>
<td>25</td>
<td>15</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Dec. 78</td>
<td>27–30</td>
<td>15</td>
<td>86</td>
<td>7</td>
</tr>
<tr>
<td>Mar. 79</td>
<td>40–45</td>
<td>11</td>
<td>36</td>
<td>36</td>
</tr>
<tr>
<td>Dec. 79</td>
<td>27–30</td>
<td>9</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Apr. 80</td>
<td>25–30</td>
<td>12</td>
<td>8</td>
<td>50</td>
</tr>
</tbody>
</table>

**Table V**

*Stylophora pistillata: reproductive states of deep water populations*
April (the average female gonad per polyp in April 1980 is lower than other April months because samples were taken immediately after a storm).

In the second set of experiments, planulae were collected in the laboratory from branch samples of 91 shallow water and 88 deep water colonies, on 13 collecting dates (Table VI). Significantly more planulae were shed by shallow water colonies than by deep water colonies ($P < 0.01$; Wilcoxon's signed rank test; Sokal and Rohlf, 1981). At the peak of the reproductive season about 20–80 planulae on average were shed per 100 g skeleton from shallow water colonies during one night. In deep water colonies the number did not exceed four planulae. An additional 55 deep water colonies were sampled during summer and fall (July–November) to examine whether the reproductive season there differs from that of shallow water populations. All histological sections were free of eggs. Moreover, no planulae were shed during a parallel study where branches were carefully broken in situ from an additional 80 colonies. These results indicate that the reproductive season of deep water colonies is probably two to three months shorter than that of shallow water populations.

**DISCUSSION**

The study of coral reproductive biology may be engaged with ambiguous definitions which could lead to wrong interpretations. For example, Fadlallah (1983) indicated that confusion arises from the applications of the term hermaphroditism, which describe two different life history processes: (1) development of monoecy over the lifetime of a specimen and, (2) sequential maturation of female and male products within one breeding period. Thus, it was accepted that *S. pistillata* (Rinkevich and Loya, 1979a, b) and *Goniastrea australensis* (Kojis and Quinn, 1981a, b) were protandrous hermaphrodites over their lifetime, but protogynous hermaphrodites in each single reproductive season. The present study indicates that either sexuality and/or fecundity may be completely altered from one reproductive season to the next. Her-
nfaphroditic colonies which exhibited high fecundity in one season became male or
even sterile thereafter, and vice versa. Small colonies (geometric mean radius \( r < 2 \)
cm) which invest much energy in rapid growth (Loya, 1985), possess only male go-
nads in their first year of reproduction. An increase in colony size correlated with an
increase in percentage of hermaphroditic colonies within the population (Rinkevich
and Loya, 1979b). Reproduction of injured colonies of *S. pistillata* which invested
energy in growth and regeneration was significantly reduced for at least two successive
reproductive seasons after the fracturing event (Rinkevich, 1982). In addition, the
fecundity of dying colonies was reduced several months before their death (Table III
and Rinkevich and Loya, 1986), and dying colonies often changed their sexuality
before their mortality and became male. Field experiments also demonstrated that
the number of female gonads per polyp in *S. pistillata* was significantly reduced in
colonies competing intraspecifically and the typical synchrony in reproduction
among different branches of a given colony was changed and disynchronized (Rin-
kevich and Loya, 1985).

From the above results, we suggest that sexuality and fecundity in *S. pistillata* are
responsive to the general state of health of the colony and its energetic limitations.

Studies also addressed reproduction/energy allocation questions in other coral
reef species. Kojis and Quinn (1985) found lower fecundity in damaged *Goniastrea
favulus* colonies compared to unharmed controls and suggested that this resulted
from reallocation of resources to growth activities that would repair damaged tissue
and cover the broken skeletons. Richmond (1984) indicated that reef corals may
allocate energy into new tissue via budding for colony growth, or via planulation
for production of new colonies. He found that colonies of *Pocillopora damicornis* at
Enewetak atoll, Marshall Islands, allocated the majority of their reproductive energy
into larva production while in the eastern Pacific the same species channels energy
into colony growth. Thus, internal and/or external (see below) determinants may
play a significant role in the expression of sexuality or fecundity in hermatypic corals,
although the mechanisms are not yet understood.

Stimson (1978) proposed that coral species which release planulae are characteris-
tic of shallow water environments such as reef flats, and hypothesized that shallow
water species should planulate to facilitate early settlement in the parental habitat.
Conversely, deep water corals should release eggs and sperm into the water to facili-
tate dispersal. More recent studies, however, suggest that the mode of reproduction
is related to more complex factors than habitat alone (Harriott, 1983; Szmant, 1986).
Thus it is of interest to study the mode of reproduction of the same species in two
different depths. Karlson (1981) found a reduction in reproductive activity with in-
creasing depth in two Jamaican species of *Zoanthus*. Kojis and Quinn (1983) further
indicate that fecundity of *Acropora palifera* decreased with depth. Colonies at depths
greater than 12 m had approximately half the fecundity of surface colonies. These
studies support the results of the present study (Tables IV, V, VI) which indicate high
differences in fecundity between shallow and deep water *S. pistillata* colonies.

The importance of available energy for reproduction is apparent from the de-
crease of fecundity in deep water populations. *S. pistillata* invests photosynthetically
derived energy in reproduction (Rinkevich, 1982; Rinkevich and Loya, 1983). Mc-
closkey and Muscatine (1984) found that the daily CZAR (the percentage contribu-
tion of zooxanthellae-translocated carbon to animal maintenance respiration) in *S.
pistillata* in deep water was less than half of that in shallow water. Mean CZAR at 35
m was 78%, compared to 157% at 3 m. They also found that the decreased carbon
availability to the host animal at 35 m was the consequence of both decreased net
carbon fixation and decreased percentage of net fixed carbon translocated to the host.
Therefore, we suggest, that the generous daily carbon supply in shallow water colonies enables them to channel significantly more energy to reproduction than deep water colonies.

It is hard to separate the two explanations for the differences in reproductive activity between shallow and deep water colonies e.g., energy limitations versus selective pressures. The present results point to energy limitation in deep water colonies rather than to the suggestion of selection pressures which favor high fecundity of shallow water colonies (Stimson, 1978).

This study provides for the first time results of long-term (1974–1984) experiments and observations on reproductive activities in a hermatypic coral. These and earlier (Rinkevich, 1982; Rinkevich and Loya, 1985; 1986) results indicate that sexuality as well as fecundity are determined and regulated by a variety of internal processes (such as the state of health of the colony, regeneration of broken branches, energy limitation, senescence, and death) and external, physical parameters (such as storm activities). The only other relevant papers on external parameters are the recent works of Jokiel (1985) and Jokiel et al. (1985) who suggested that environmental factors including temperature, salinity, tidal cycle, visible, and ultraviolet radiation influence the number of planulae released by Pocillopora damicornis per spawning cycle, as well as the synchronization of lunar release of planula larvae. Therefore it is concluded that reproductive activity in S. pistillata involves significant energetic expenditures that otherwise would be allocated to other physiological pathways such as growth and maintenance. As a result, any significant stress or diminution in energy resources affects at least one of the reproductive characteristics of this species. Physical and biological parameters have often been directly related to the distribution of a given species. However, the present study indicates that even reproduction can be directly altered as a result of the influence of these parameters. The changes in the reproductive activity of S. pistillata colonies in the field may not be a function of a single parameter. The combined effect of several external and internal factors on gravid colonies should be examined experimentally before and during the reproductive season. These should be considered before formulating any general hypothesis on coral reproduction.

ACKNOWLEDGMENTS

We are grateful to A. Shafir and to Y. Shapira for field assistance; to C. Porter for the data presented in Table I; and to Y. Benayahu, Z. Wolodarsky, and Y. Shlesinger for their great help and encouragement throughout the study. We thank L. Fishelson for his help and advice and N. D. Holland, J. Pearse, and K. Ishizuka for their comments on the manuscript. Appreciation is extended to the staff members of the MBL at Eilat for their hospitality and the use of facilities. This study was partly supported by the United States–Israel Binational Science Foundation (BSF) and the Tel Aviv University Fund for Basic Research.

LITERATURE CITED


View This Item Online: https://www.biodiversitylibrary.org/item/17376
DOI: https://doi.org/10.2307/1541546
Permalink: https://www.biodiversitylibrary.org/partpdf/4050

Holding Institution
MBLWHOI Library

Sponsored by
MBLWHOI Library

Copyright & Reuse
Copyright Status: In copyright. Digitized with the permission of the rights holder.
Rights Holder: University of Chicago
License: http://creativecommons.org/licenses/by-nc-sa/3.0/
Rights: https://biodiversitylibrary.org/permissions

This document was created from content at the Biodiversity Heritage Library, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at https://www.biodiversitylibrary.org.

This file was generated 25 August 2023 at 14:13 UTC