THE BIOLOGY OF NODULARIA (CYANOPHYCEAE)

by

RICHARD NELS NORDIN

B.Sc., University of North Dakota, 1970

M.Sc., University of North Dakota, 1971

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the Department

of

BOTANY

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA

MAY, 1974

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the Head of my Department or by his representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of BOTANY

The University of British Columbia
Vancouver 8, Canada

Date May 7, 1974

"The tapers of the gods,

The sun and moon, run down like waxen globes;

The shooting stars all end in purple jellies,

And chaos is at hand."

Dryden's Oedipus, referring to the sudden appearance of Nostoc balls after a rain fall.

Chairman: Professor J. Stein

ABSTRACT

The genus Nodularia [Mertens in Juergens] Bornet et Flahault 1888 is considered with regard to its ecology, distribution, physiology and taxonomy.

Ecology was studied by periodic sampling of organisms and monitoring environmental parameters in four saline ponds in the British Columbia interior, as well as by sampling a variety of brackish, marine and other inland saline water bodies. Nodularia was collected in habitats of alkaline pH 8.2 - 10.0) and medium to high dissolved salts (4 - 60 $^{o}/_{oo}$) and is associated with a specific group of euryhaline bluegreen algae. However, environments in which it grows are usually dominated by species of green algae, with Nodularia only occasionally becoming dominant.

The distribution of Nodularia was examined by reference to herbarium collections and literature reports. Although many bluegreen algae are considered cosmopolitan, Nodularia has a temperate and subtropical distribution with few reports from polar or tropical latitudes.

The growth and physiology was investigated using 16 isolates from Canada, United States, Great Britain and Australia. Isolates were grown in a wide range of conditions of light, temperature, pH and dissolved salts in defined media. Generally, the highest growth rates were obtained with relatively high light intensity (550 - 600 ft-c), temperature of 25 - 30 C, pH near 10 and dissolved salts of 5 - 30 $^{o}/_{oo}$. Highest rates of growth were obtained with NO_3^- as the nitrogen source as opposed to NH_4^+ or urea. Nodularia was found to fix nitrogen in pure culture.

Nodularia was established in 1822 by Mertens, but not validily published until 1888 by Bornet and Flahault. At present there have been 28 taxa described. The validity of these and the variability in nature and of isolates in culture in a variety of chemical and physical conditions was considered. An evaluation of the reliability of the taxonomic characteristics indicates that sheath and akinete characteristics are variable while vegetative cell shape, heterocyst location and aspects of akinete formation are more stable characteristics. On the basis of the observations reported, all the described taxa can be included within two species, *N. spumigena* [Mertens in Juergens] Bornet et Flahault 1888 or *N. harveyana* (Thw.) Thuret 1875, or placed in other genera.

TABLE OF CONTENTS

	PAGE
ABSTRACT	iii
LIST OF TABLES	vi
LIST OF FIGURES	vii
LIST OF APPENDIX TABLES	ix
ACKNOWLEDGEMENTS	x
INTRODUCTION	1
ECOLOGY	3
Methods	4
Results	9
DISTRIBUTION	27
GROWTH AND PHYSIOLOGY	36
Materials and methods	36
Results	45
TAXONOMY	65
DISCUSSION	105
Ecology and Physiology	105
Taxonomy	113
LITERATURE CITED	118
APPENDIX TABLES I - X	138

LIST OF TABLES

TABLE		PAGE
I.	Locations of Nodularia collections, 1971-1973	7
II.	Origin of isolates used in growth and physiology experiments	37
III.	Light intensity used in culture experiments	42
IV.	Microbiological media for checking purity of cultures	44
V.	Comparative morphology of Nodularia in axenic culture, contaminated culture and nature	47

LIST OF FIGURES

FIGURE		PAGE
1.	Study areas in the interior of British Columbia	6
2.	Seasonal changes in saline ponds	12
3.	Seasonal changes in temperature, salinity and organisms for 1972-1973 in Ctenocladus Pond	14
4.	Some features of saline ponds	17
5.	Seasonal changes in temperature, salinity and organisms for 1972-1973 in Wallender Lake	20
6.	Seasonal changes in temperature, salinity and organisms for 1972-1973 in Inks Lake	21
7.	Seasonal changes in temperature, salinity and organisms for 1972-1973 in White Lake	24
8.	North American distribution of N. spumigena	30
9.	North American distribution of N. harveyana	30
10.	European distribution of N. spumigena	32
11.	European distribution of N. harveyana	32
12.	World (exclusive of North America and Europe) distribution of N. spumigena	34
13.	World (exclusive of North America and Europe) distribution of N. harveyana	34
14.	Standard curves of optical density versus cell numbers	40
15.	Quality of light used in culture experiments	42
16.	Comparison of growth of axenic cultures and cultures with bacterial contamination	47
17.	Effect of temperature on isolates of Nodularia	49
18.	Effect of light intensity on growth of Nodularia	52
19.	Effect of pH on the growth of Nodularia	54

FIGURE		PAGE
20.	Effect of salinity on growth of Nodularia	57
21.	Effect of salinities using salts other than NaCl on growth of Nodularia	59
22.	Effect of nitrogen source on the growth of Nodularia	61
23.	Effect of salinity, pH and temperature on acetylene reduction by Nodularia	64
24.	The species of Nodularia described in and since the revision of Bornet and Flahault (1888)	69
25.	Possible explanation for akinete characteristics of N. armorica	86
26.	Comparison of the variability of size of vegetative cells, heterocysts and akinetes of two isolates under a variety of culture conditions	88
27.	Comparison of cell sizes of N. harveyana and N. sphaerocarpa	91
28.	Akinete variability of three British Columbia isolates as related to salinity	94
29.	Comparison of cell sizes of N. spumigena and N. harveyana	96
30.	Cultural variation of Nodularia	99
31.	The morphological variation of N. spumigena	101
32.	The morphological variation of N. harveyana	103

LIST OF APPENDIX TABLES

TABLE		PAGE
I	Procedures used in water analysis	138
II	Water chemistry for Ctenocladus Pond	139
III	Water chemistry for Wallender Lake	140
IV	Water chemistry for Inks Lake	141
V	Water chemistry for White Lake	142
VI	Water chemistry for the lakes irregularly sampled or sampled only once	143
VII	World distribution of *Nodularia*	144
VIII	Medium BG-11 (Stanier *et al.* 1971)	157
IX	Herbarium material of *Nodularia* examined	158
X	Synonomy of *Nodularia*	165

ACKNOWLEDGEMENTS

I would like to thank Dr. Janet R. Stein for help and guidance during the course of this study, and to members of my committee for their comments and criticisms of the thesis. Many persons lent freely of equipment, time and advice and to them I am grateful. The study was supported by funds from NRC A1035 to J.R. Stein.

My gratitude to Carolyn is insufficiently expressed here. She provided help in the field, typed, glued, xeroxed, retyped, worried, ran errands and aided in many other aspects of the study as well as supplying understanding and smiles at even the most difficult of times.

INTRODUCTION

Drouet and Daily's (1956) revision of the coccoid bluegreen algae caused considerable controversy regarding interpretation of taxonomy and morphology of the Cyanophyceae. The variability inherent in bluegreen algal taxa has been subject to a variety of interpretations. Many Cyanophyceae have been described as new species with little justification (Golubic 1969) and every year more taxa are proposed to add to the taxonomic confusion.

Physiological and biochemical characterization are of little value if an incorrect or unacceptable binomial is applied. Anacystis nidulans, a coccoid form, is a case in point. The commonly studied isolate of Kratz and Allen has been shown to be a Synechococcus sp. (Padmaja and Desikachary 1968; Komarek 1970). However Anacystis nidulans is employed by researchers who are apparently unwilling to use the correct binomial.

Taxonomic work is of little value unless variation both in culture and in nature is taken into account. It is important that both field and laboratory studies be coordinated and complementary to give insight into the biology of an alga (Pringsheim 1967). Despite the acknowledged need for this type of an approach for the bluegreen algae (Desikachary 1970), only one study (Kann and Komarek 1970), using ecological observations, cultural study and a critical review of the

literature, has been reported. In light of this, the need for such studies are apparent.

The present investigation of the filamentous, heterocystous genus Nodularia /Mertens in Juergens/ Bornet et Flahault (see Stafleu 1972, p. 240) was undertaken to study the genus and delimit the species. The genus is more manageable than the large genera, such as Nostoc or Anabaena, and appears well-defined in a generic sense. The problem was approached by studying the occurrence and distribution, factors controlling its growth, and its morphological variation. These are considered as three separate chapters; Ecology; Physiology; Taxonomy.

ECOLOGY

Of primary importance in the study of an organism is defining its role in the environment: what organisms it is associated with, and when and why it occurs in a particular place at a particular time.

The primary sampling areas were in the interior of British Columbia near Kamloops and Penticton. These areas are in the ponderosa pine - bunch grass biogeoclimatic zone (Krajina 1965) and the vegetation in the area of the ponds and the lower valleys is dominated by Artemisia tridentata Nutt. Both areas receive relatively low amounts of precipitation, most occuring in the winter. Kamloops has an average of 24.3 cm/yr precipitation, with most snow in December or January and most rain in June. The average daily maximum and minimum July temperatures are 29 C and 13 C and the average daily maximum and minimum January temperatures are -2 C and -9 C. Penticton receives 27.4 cm/yr average precipitation, with most falling as snow in December and as rain in May or June. The average daily maximum and minimum July temperatures are 29 C and 12 C and the average daily maximum and minimum January temperatures are 0 and -6 C (Canada Department of Transport).

Periodic sampling, May-September 1972; April-July 1973, was made of four ponds in which Nodularia regularly occured.

Three of these ponds (Ctenocladus Pond, Wallender Lake, Inks Lake) are located southwest of Kamloops and one (White Lake) located southwest of Penticton (Fig.1). Blinn (1969) has documented some aspects of Ctenocladus Pond and Wallender Lake. In addition to these four habitats, which were sampled periodically, a number of locations were sampled on an irregular basis or only on a single occasion (Table 1).

Methods:

At each sampling the temperature and dissolved oxygen were measured (YSI model 54 oxygen meter-thermistor and a glass thermometer); pH recorded (Metrohm model E280A pH meter); water (duplicate 500 ml samples), plankton and grab samples collected and general observations made (water levels, species present, and estimation of abundance of organisms on a subjective basis since attempts at quantitative measurements proved extremely difficult). The water samples were filtered through Whatman (#1) and Millipore (.45 µm) filters, within six hours of collection and maintained at 5 C for return to the laboratory. In the laboratory the organisms present were identified and Nodularia isolated. Then the samples were fixed with either neutral 4% formalin, Lugol's iodine or 70% ethanol. Analyses of ortho-phosphate, ammonium-nitrogen and nitrate nitrogen were carried out, within 48 hours, according

Figure 1. Study areas in the interior of British Columbia.

scale 1:62,500

a. British Columbia 1 inch = approx. 650 km

b. West of Kamloops British Columbia
1. Inks Lake 2. Wallender Lake 3. Bowers Lake
4. Ironmask Lake 5. unnamed pond 6. Polygon Pond
7. Ctenocladus Pond 8. 'Salt Pond 4' 9. Salsola Pond 10. 'Salt Pond 3' 11. Saltwort Pond

c. South west of Penticton British Columbia
12. White Lake 13. Mahoney Lake 14. Green Lake

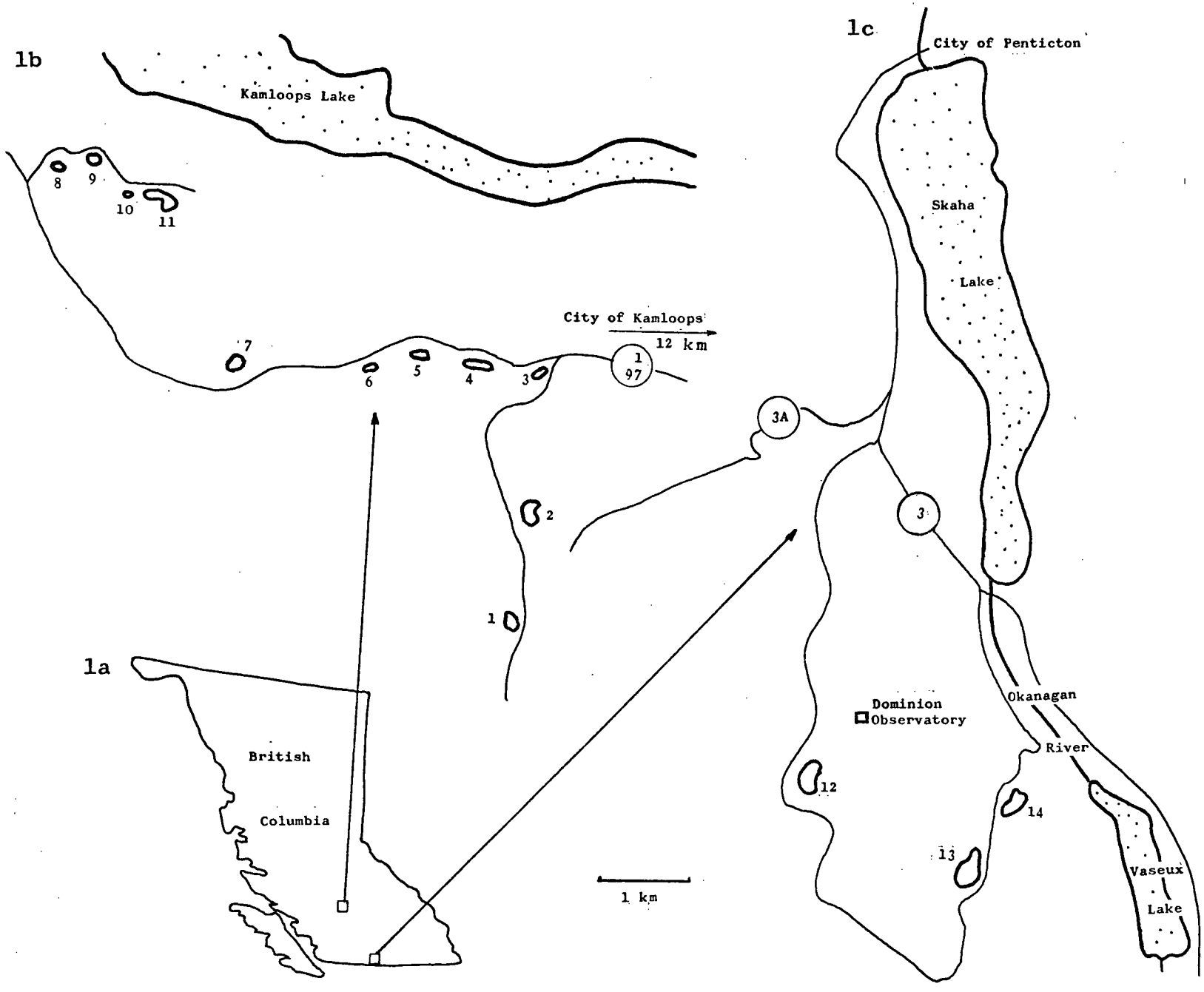

1b
Kamloops Lake
8
9
10
11
City of Kamloops
12 km
7
6
5
4
3
1
97
2
1
1a
British
Columbia
1 km
1c
City of Penticton
Skaha
Lake
3A
3
Dominion
Observatory
Okanagan
River
12
14
13
Vaseux
Lake

Table 1. Locations of Nodularia collections, 1971-1973.

A. Locations regularly sampled

1. Ctenocladus Pond 50°39'N, 120°32'W
North of Trans-Canada Highway (BC Hwy 97), 9 mi west of Kamloops B.C.
Cited by Blinn (1969) as 'Cherry Creek Pond'

2. Wallender Lake 50°38'N , 120°26.5'W
East side of Lac la Jeune Road, 3 mi from its junction with the Trans-Canada Highway (BC Hwy 97)

3. Inks Lake 50°37'N , 120°27'W
West side of Lac la Jeune Road, 4 mi from its junction with the Trans-Canada Highway (BC Hwy 97)

4. White Lake 49°19'N , 119°38'W
One mile south west of the Dominion Radio Astrophysical Observatory and 5 mi south of Penticton B.C.

B. Locations irregularly or singly sampled

5. 'Salt pond 4' 50°40'N , 120°35'W
A small unnamed pond southwest of Salsola Pond (Salsola Pond cited by Blinn as Salt Mine Pond 1)

6. 'Salt pond 3' 50°40'N , 120°34'W
A small unnamed temporary pond between Salsola Pond and Saltwort Pond (Saltwort Pond cited by Blinn 1969 as Salt Mine Pond 2)

7. Big Quill Lake, Saskatchewan 51°30'N , 104°40'W
North of Kandahar on Hwy 14 (Sask.) and 100 mi east of Saskatoon

8. Devils Lake, North Dakota at Camp Grafton 48°N , 99°W

9. San de Fuca, Washington 48°10'N , 122°48'W
Adjacent to Washington Highway 525

10. Riefel Wildlife Refuge 49°08'N , 123°10'W
Near Ladner B.C.

Continued...

Table 1 (Contd.) Locations of Nodularia collections, 1971-1973

C. Cultures were isolated from soil samples collected at the following locations

11. Spotted Lake 49°05'N , 119°34'W
In Richter Pass, 6 mi northwest of Osoyoos B.C. on B.C. Hwy 3

12. Small unnamed pond 119°38'N , 49°09'W
In low area 1 mi south of Richter Lake, 4 mi southwest of Spotted Lake adjacent to Hwy 3

13. Bowers Lake 50°40'N , 120°26'W
At the junction of Trans-Canada Highway (Canada Hwy 1, BC Hwy 97) and Lac la Jeune Road

14. Water hole Simpson's Gap, Northern Territories, Australia 20°45'S , 134'E
Collected by Dr. J.R. Stein, 18 ix 1969

to Standard Methods (A.P.H.A. 1965). The one exception to this treatment of water samples is to be found in the data from August 1972 when the water was not analyzed until two weeks after collection. Analyses of the water for the major cations (Na^+, Mg^{++}, Ca^{++}, K^+) were made with a Perkin-Elmer (model 303) atomic absorption spectrophotometer and for major anions ($CO_3^=$, HCO_3^-, $SO_4^=$, Cl^-) by Standard Methods from water samples stored at 5 C. Details of water analysis are given as Appendix, Table 1.

When reference is made to salinity it is in the broad sense of the amount of dissolved salt contained in the water without any implied ionic content rather than in the narrower oceanographic sense of chlorinity. The term brackish is used in reference to dilute sea water, and the term saline refers to inland water bodies of salt content greater than 0.5 $^o/oo$.

Results:

In the spring (late March and April) the lakes are at their largest volume and contain relatively low amounts of dissolved salts due to the high volume of water resulting from snow-melt and drainage into these depressions. As spring and summer progress, the salinity increases as water volume decreases due to evaporation in excess of rainfall and

runoff. In late summer and fall (late August and September) the ponds reach their minimum volume and in some instances dry up completely (Fig 2).

The dynamics of the ions in saline ponds of this type is described by Blinn (1971). In any interpretation it must be emphasised that there can be a great deal of variation from year to year in water levels of these ponds depending on total precipitation. For example, it was observed that water levels in 1973 were lower than 1972 at corresponding collection dates.

The ponds are characterized by a large amount of autotrophic growth, principally algae, in spring and early summer (April-July) followed by a heterotrophic growth phase, grazing invertebrates and bacteria, from July to September. Maximum diversity of organisms occurs in spring and diversity decreases as the salinity increases. To examine these trends and variations single ponds must be considered.

A. Locations regularly sampled.

1. Ctenocladus Pond has Na^+ and $SO_4^=$ as the dominant ions. The pond normally dries up during the course of the summer and the salinity may vary from 30-50 $^o/oo$ in the spring to more than 400 $^o/oo$ in the fall (Appendix, Table II). The dominant alga is the chlorophyte Ctenocladus circinnatus Borzi.

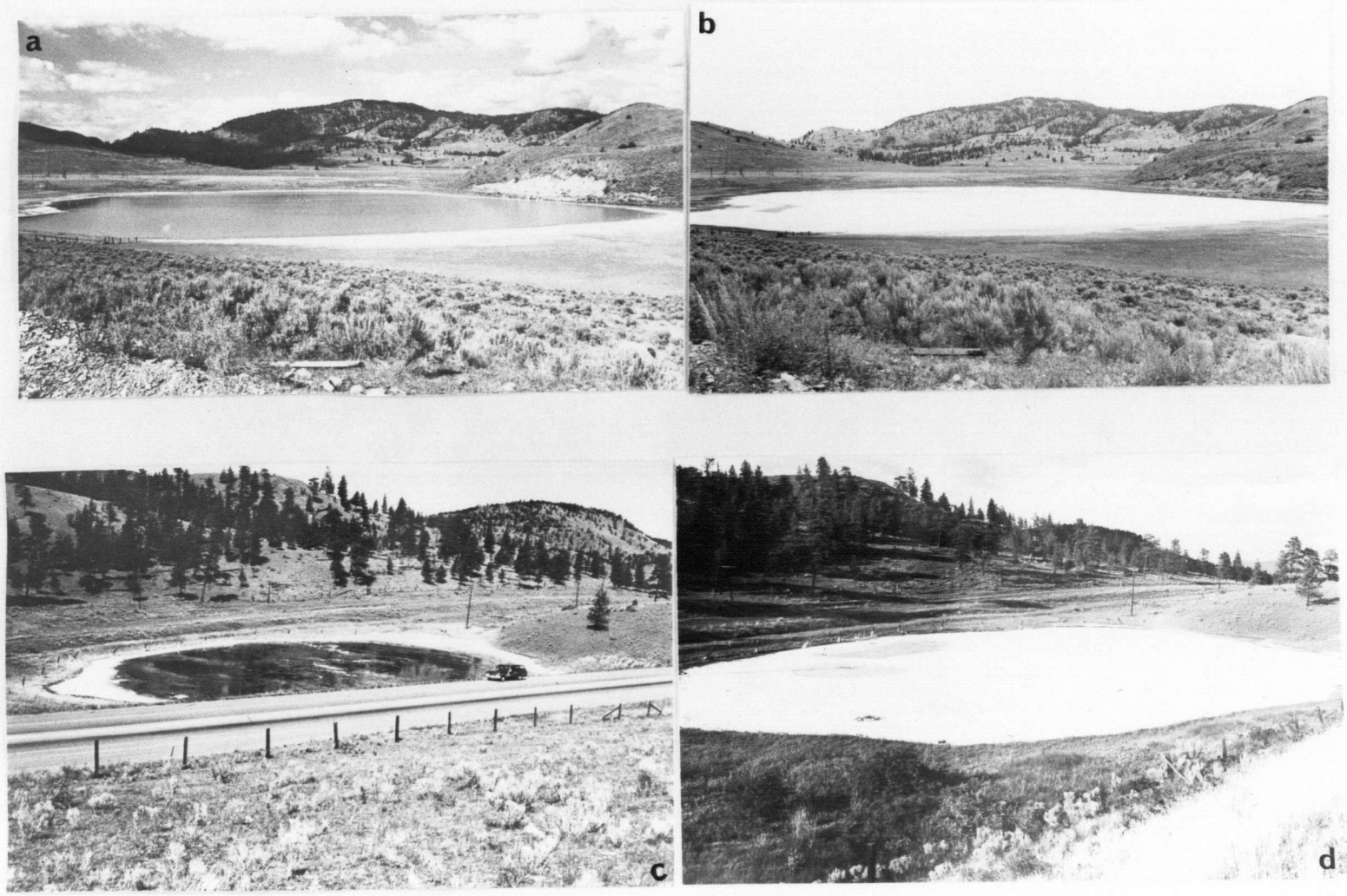
Figure 2. Seasonal changes in saline ponds

a. White Lake, 2 vi 1973

b. White Lake, 22 vii 1973

c. Ctenocladus Pond, 3 vi 1973

d. Ctenocladus Pond, 21 vii 1973


a
b
c
d

Nodularia harveyana was collected only during April and May in small numbers and was absent from June-September. Other algae present were the green algae Spirogyra sp., Ulothrix tenerrima Kützz., Ulothrix sp., Dunaliella salina (Dunal) Teodor. and Cladophora fracta (Dillw.) Kutz; the bluegreen algae Oscillatoria amphibia C.A. Ag., O. brevis C.A. Ag., Anabaena sp., Phormidium tenue (Menegh.) Gomont and Lyngbya nordgaardii Wille; an Euglena sp.; the diatoms Amphora coffeaeformis Ag. and Navicula sp. All but the Dunaliella and Lyngbya were present in their largest numbers in April and May. With increasing salinity during the summer, most species of algae were greatly reduced in numbers or disappeared completely. Dunaliella and Lyngbya reached maximum numbers in June or July, the former in the isolated pockets of open water, the latter as an epiphyte on dead or dying Cladophora and Ulothrix. Ctenocladus remained throughout the summer but in less quantity and hidden under the salt layer deposited by the evaporating water.

Around the shoreline of the pond is a zone of Salicornia rubra Nels. and within the pond itself is a dense growth of Ruppia maritima L. In April and May large numbers of mosquito larvae (Aedes sp.) were observed. In June through August the pond is inhabited by large numbers of brine shrimp, Artemia salina Leach. A mat of purple sulphur bacteria

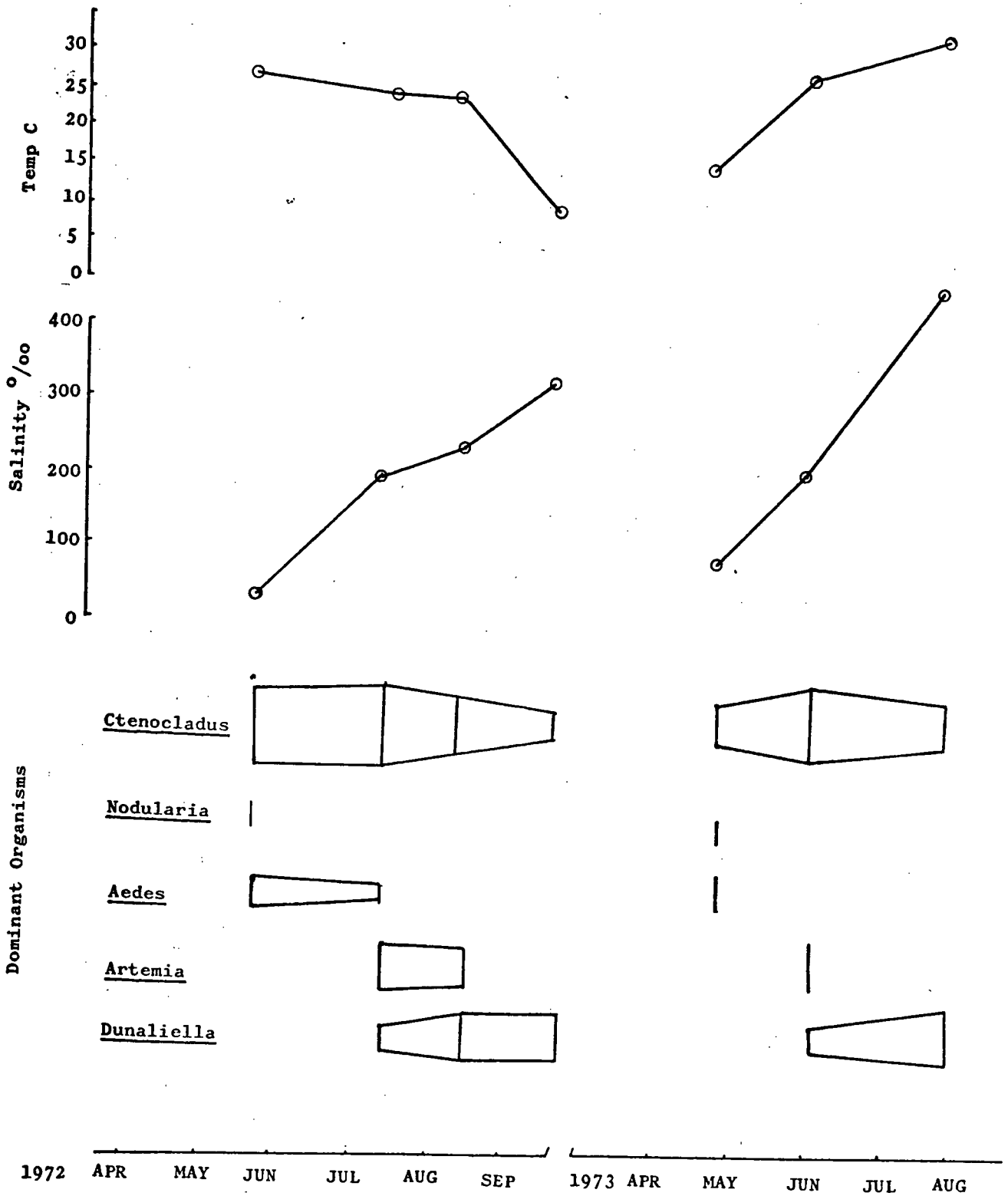


Figure 3. Seasonal changes in temperature, salinity and organisms for 1972-1973 in Ctenocladus Pond.

The relative abundance of the organisms are indicated by the vertical bars

covers a thick, black, anerobic mud. An unidentified ostracod and the rotifer, Brachionus plicatilis Muller, inhabit the pond and egg cases, larvae and adult salt flies (Ephedridae) are around the water's edge. The periodicity and population dynamics of the more important organisms is shown in Fig.3.

2. Wallender Lake is characterized by a lower amount of dissolved salts and less variable salinity range (14-88°/oo) than Ctenocladus Pond. The principal ions are Na^{+}. Mg^{++}, and $SO_4^{=}$ (Appendix, Table III). Probably as a result of these lower levels of dissolved salt, a larger variety of organisms are present. The vascular plants consist of Salicornia rubra and Scirpus maritimus L. around the margin of the lake and Ruppia within the lake itself. The dominant alga throughout the season except for early spring (April and early May), is Cladophora fracta. During May rapid growth of Cladophora results in the formation of a characteristic peripheral mat (Fig.4c). Nodularia (primarily N. harveyana) is present in maximum numbers in May and June and typically occurs associated with the Cladophora mat. During May, Nodularia is primarily vegetative, by June many of the cells have converted to akinetes and by July very few filaments are seen, with nearly all cells as akinetes. Associated with Nodularia is a community of bluegreen algae consisting of Oscillatoria geminata Menegh., O. tenuis C.A. Ag., O. nigroviridus Thwaites,

Figure 4. Some features of the saline ponds studied.

a. Wallender Lake with large numbers of diatoms along the shoreline (iv 1973)

b. A closer view of diatom bloom in a. (pencil is approximately 10 cm long)

c. Peripheral Cladophora mat around the edge of Wallender Lake (vi 1973)

d. Shoreline of Wallender Lake with Cladophora, purple sulphur bacteria and Scirpus (vi 1973)

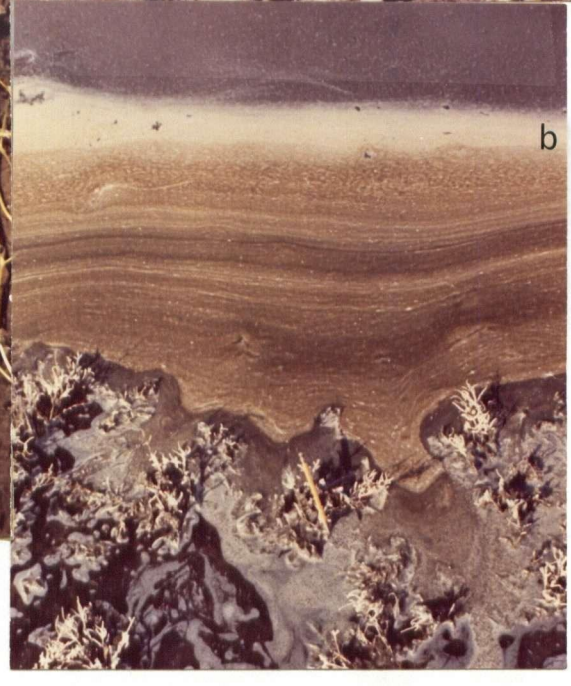
e. Inks Lake showing density of brine shrimp (vii 1973). Also present are Cladophora and Ruppia (thermometer is approximately 35 cm long)

a

c

d

e


b

Spirulina major Kutz. and Phormidium fragile Gamont. Lyngbya nordgaardii appears in July after the decline in numbers of most other bluegreen algae.

During early spring (April) before the growth of the Cladophora mat, a diatom maximum occurs. In April 1973 a remarkable bloom of diatoms occurred (principally Amphora coffeaeformis and Navicula spp.) (Fig.4a,b). These diatoms are present at other times of the year but in much reduced numbers. The diatom maximum is followed by rapid growth of Cladophora and the bluegreen algae associated with Nodularia and two Ulothrix spp., U. tenerrima and U.? aequalis Kütz. In July 1972 a large number of Ceratium hirundinella (O.F.M.) Duj. was observed but not in 1973. Its appearance in such saline (48 ^{o}/oo) waters is interesting since it is normally found in much less saline conditions. At the same time (July 1972) in nearby Inks Lake (see below) a large number of Ceratium were also present. A species of Euglena was found in localized small areas on the shoreline mud throughout spring and summer.

The animal community of the lake is composed of a Moina sp. (Cladocera), Diaptomus sp. (Copepoda), Brachionus plicatilis (Rotatoria) and Chironomidae, all present primarily in the spring. Artemia salina (Branchiopoda) is present in large numbers in late spring and summer (Fig. 4e). Ephidridae

are present around the edges of the lake and the bottom sediment is covered by a mat of purple sulphur bacteria (Fig.4d). The periodicity and dynamics of organisms is shown as Fig.5. The maximum variety of species occurs in the spring or early summer and diversity decreases in response to increasing salinity. By late summer the extreme salinity reduces the number of species to a minimum.

3. Inks Lake is similar to Wallender Lake but differs from Wallender Lake in some details. Inks Lake has slightly less dissolved salts and a slightly higher pH (Appendix, Table IV) but otherwise has similar plant and animal communities (Fig.6). The same distinctive peripheral Cladophora mat and the same plant and animal components (plus Scirpus validus Vahl. and the cyanophyte Anabaena variabilis Kutz.) are present. Both N. harveyana and N. spumigena are present in the spring in large numbers. The same pattern of occurence is noted with greatest growth in spring and disappearance of Nodularia with the water becoming increasingly saline. In both Inks Lake and Wallender Lake most Nodularia disappears at salinities of approximately 60 $^{o}/_{oo}$, the disappearance evidently is related to salinity rather than pH or ionic changes. Evidence is presented in the section on growth and physiology to further support this.

4. White Lake is 100 miles southeast of the other three

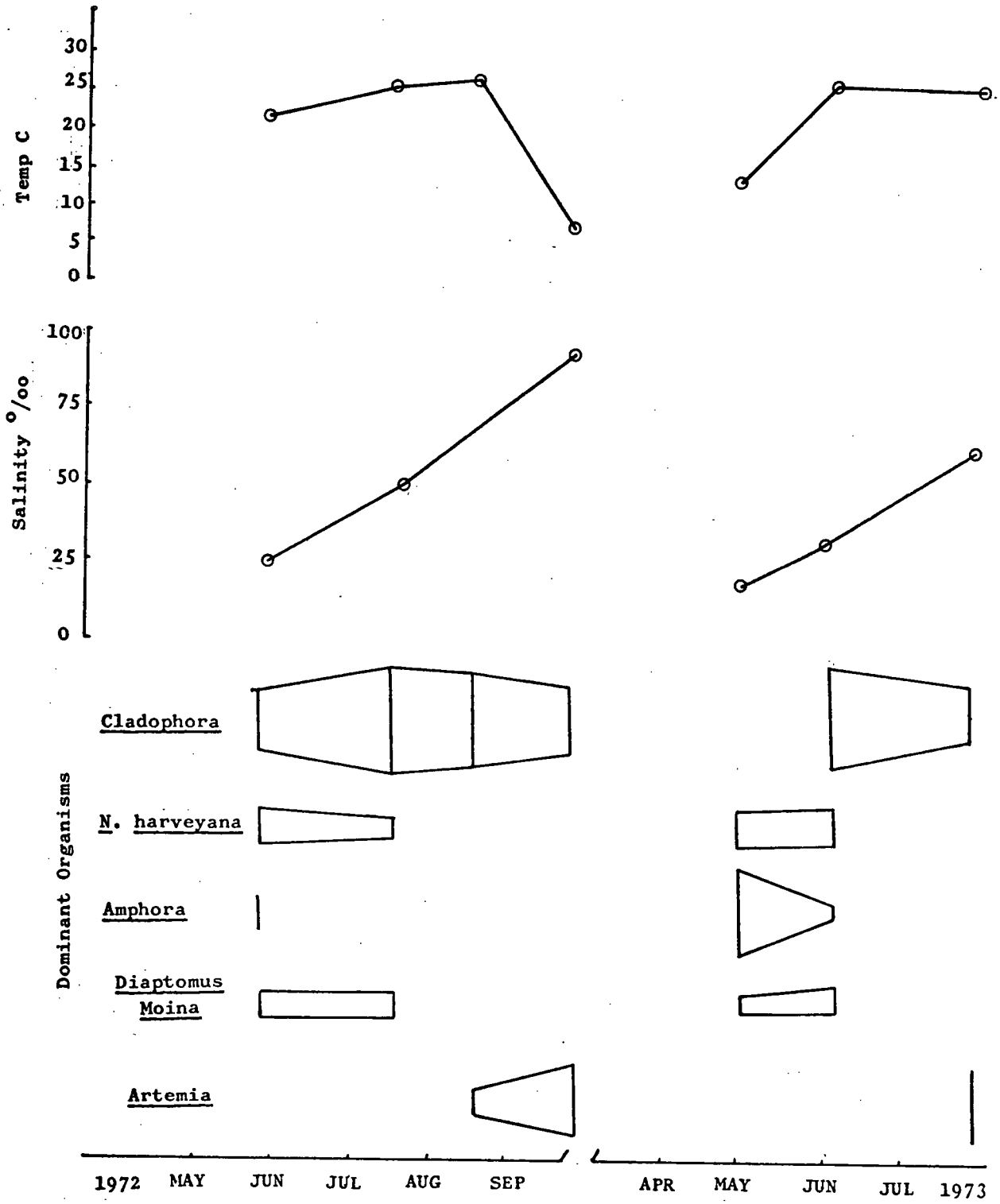


Figure 5. Seasonal changes in temperature, salinity and organisms for 1972-1973 in Wallender Lake

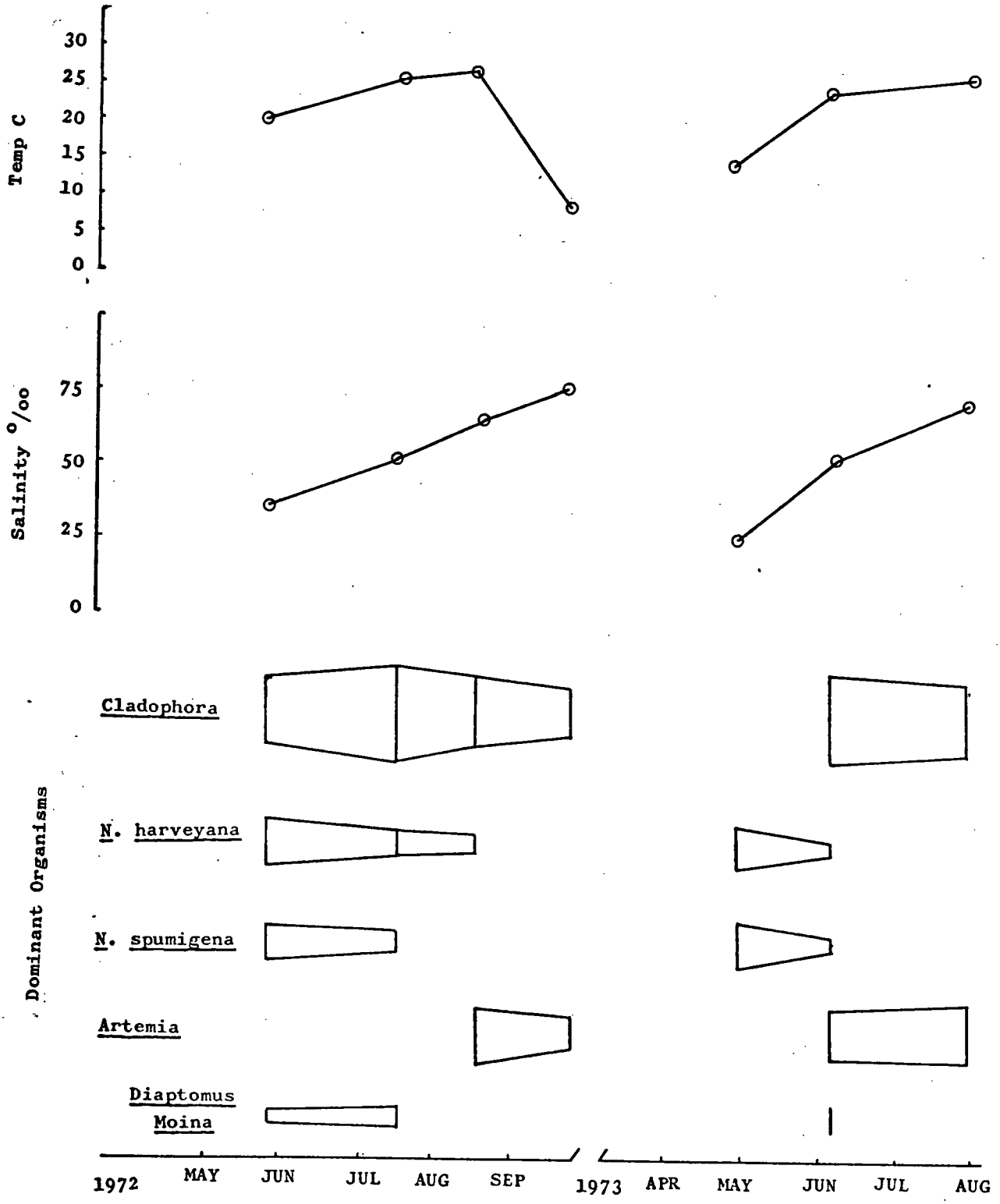


Figure 6. Seasonal changes in temperature, salinity and organisms for 1972-1973 in Inks Lake.

lakes. The dominant ions are Na^{+}, $SO_4^{=}$, and $CO_3^{=}$; the salinity varies from 15-40 °/oo and the pH is 9.4-10.0 (Appendix, Table V). The organisms of White Lake are notably different from the previous three lakes. There is no peripheral mat of algae at the shoreline and no purple sulphur bacteria mat at the mud-water interface as characterizes the other three lakes. Around the margin of the lake is Distichlis stricta (Torr.) Tydb. and Scirpus nevadensis Wats., both at times being emergent from the waterbody itself. Nodularia (both N. harveyana and N. spumigena) occurs on and around the bases of the emergent vascular plants and in hoof prints in a cattle corralling area on the south side of the lake. Nodularia occurs in White Lake in spring to early summer (May-June) and is generally absent the rest of the year. However the salinity, which has a narrow range of fluctuation and relatively low concentration, does not appear to be the limiting factor. The factor responsible for the pattern of growth of Nodularia is the destruction of habitat as the water line recedes beyond the bases of the vascular plants. The presence of Nodularia, as well as most other algae, depends on the level of the water being above the lowest vascular plants. The other algae present with Nodularia are the bluegreen algae Oscillatoria tenuis, O. chalbea Mertens, Phormidium retzi (C.A. Ag.) Gomont, Anabaena sp., Lyngbya aestuarii (Mertens) Liebmann and Spirulina

major; and the green algae Spirogyra sp. and Ctenocladus circinnatus. The preceding bluegreen algae show the same periodicity and limitations as Nodularia. The Spirogyra sp. is present only in April and May and the Ctenocladus in June or July.

In April 1973 the lake contained large numbers of salamanders (Ambystoma sp.). The plankton organisms consist of the diatoms Amphora coffeaeformis and Navicula spp.; the cladoceran Moina sp. and a copepod of the genus Diaptomus. In September 1972 a large amount of Nostoc sp. was floating and washed on shore. The periodicity and population dynamics of White Lake is shown as Fig.7.

B. Locations irregularly sampled or sampled only once.

5. 'Salt Pond 4' contained Nodularia spumigena in May 1972 at a salinity of 47 ^{o}/oo, with the primary ions being Na^{+}, $SO_4^{=}$ and $CO_3^{=}$ (Appendix, Table VI). The dominant alga of this pond was Ctenocladus circinnatus with lesser amounts of Oscillatoria brevis, O. tenuis and Anabaena sp.

6. 'Salt Pond 3' contained N. spumigena as the dominant alga in May 1972 at a salinity of 4 ^{o}/oo (Na^{+}, $SO_4^{=}$, $CO_3^{=}$) (Appendix, Table VI).

7. Big Quill Lake, Saskatchewan, in August 1972, had a salinity of 26 ^{o}/oo of predominantly Na^{+} and $SO_4^{=}$ (Appendix,

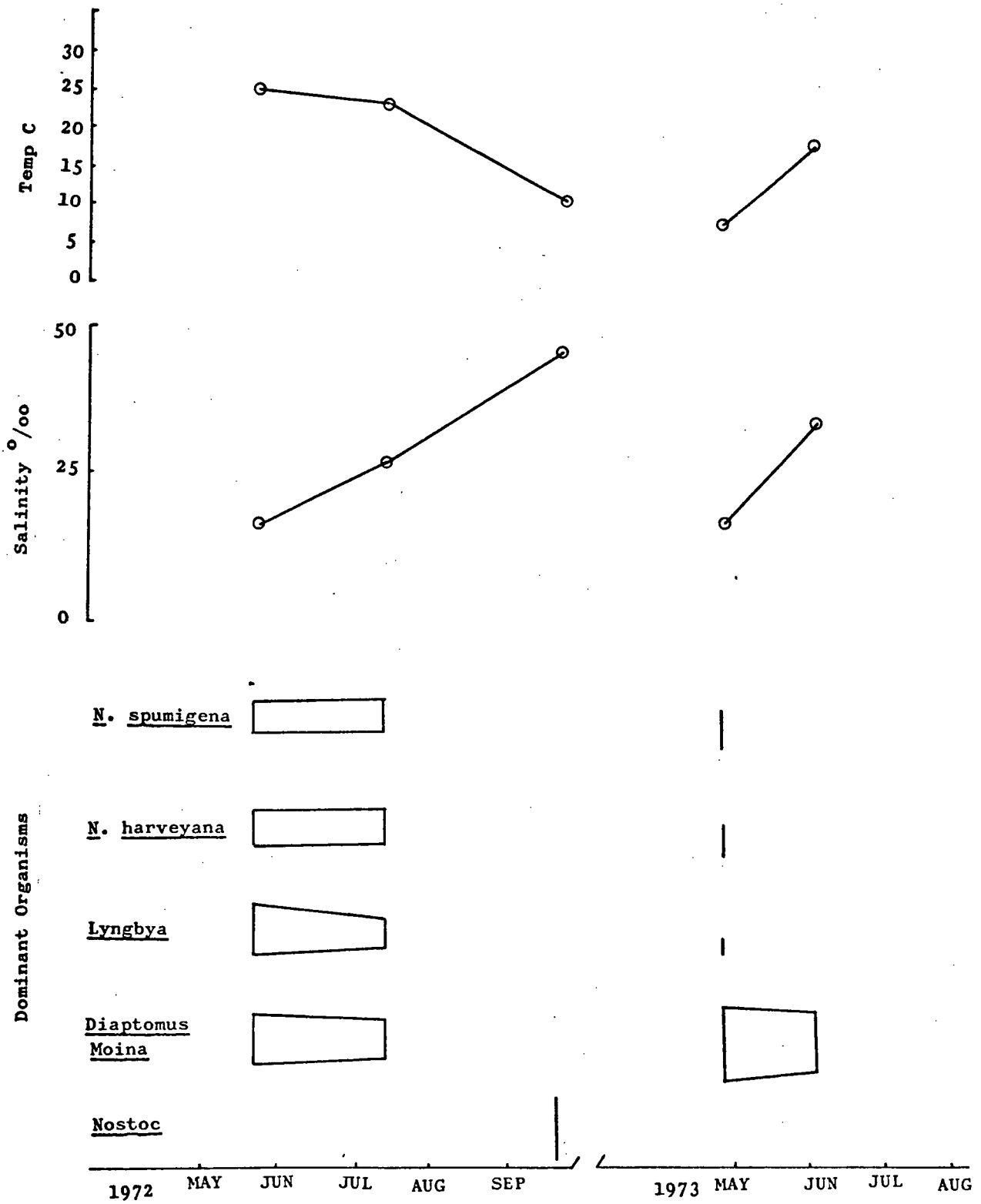


Figure 7. Seasonal changes in temperature, salinity and organisms for 1972-1973 in White Lake.

Table VI). Nodularia spumigena was the principal phytoplankter. Associated with it was the diatom Chaetoceras elmorei Boyer and large numbers of water boatmen (Corixidae) and copepods (Diaptomus sp.). The dominant alga was an Enteromorpha sp. which grew attached to the bottom with large numbers of detached plants blown up on the lee shore.

8. Devils Lake, North Dakota, had a salinity of 12°/oo (Na^+, $SO_4^=$) in August 1972 (Appendix, Table VI). Nodularia spumigena was collected both from open water where it was associated with Aphanizomenon flos-aquae Morren and Microcystis aeruginosa Kutz., and along the shoreline associated with Cladophora sp. and Enteromorpha sp.

9. Near San de Fuca, Washington, in May 1973 Nodularia harveyana was collected from a brackish (Na^+, Cl^-) pond of salinity 18 °/oo (Appendix, Table VI). Associated with the Nodularia was Percursaria percursa (C. Ag.) Rosenvinge and Lyngbya aestuarii.

10. Riefel Wildlife Refuge - a pond near the refuge office had a salinity of 8.4 °/oo (Na^+, Cl^-) (Appendix, Table VI) and contained Nodularia harveyana. The dominant alga was a Mugeotia sp., with Lyngbya aestuarii and an Oscillatoria sp. also being present.

C. Isolates from soil (See also Table I)

Blinn (1969) reports N. spumigena from Wallender Lake,

Ctenocladus Pond, Bowers Lake, Polygon Pond, Ironmask Lake, Salsola Pond and Saltwort Pond. Isolates were obtained from Wallender Lake and Ctenocladus Pond. Bowers Lake was dry from 1971-1973, however microscopic examination of soil and salt from the dry lake bed revealed akinetes. Enrichment techniques (Allen 1973) resulted in an isolate of N. spumigena. Similar observations and techniques resulted in isolates from Spotted Lake and a small pond south of Richter Lake. Enrichment of an Australian soil sample collected near Alice Springs also yielded an isolate of N. spumigena.

Nodularia was never collected from Polygon Pond, Ironmask Lake, Salsola Pond or Saltwort Pond, possibly because when collections were made the salinity was too high (greater than 100 $^{o}/oo$) for Nodularia to be growing. No akinetes were visible in the soil from these sites and enrichment procedures failed to produce any isolates.

DISTRIBUTION

Some authors (Fritsch 1945) regard most bluegreen algae as being cosmopolitan in distribution. However, closer examination of individual genera or species may reveal very discrete distribution. Nodularia illustrates this point. Gietler (1932) and Lindstedt (1943) describe the distribution of N. spumigena as cosmopolitan. Chapman (1955) describes the distribution of N. harveyana as "$\pm$ cosmopolitan" and Umezaki (1961) describes N. harveyana as "subcosmopolitan" without any explanation of the prefix.

However, in a general sense bluegreen algae are very restricted. Cyanophytes are rarely found in acid situations and never below pH 4 (Brock 1973). Dawson (1966) states that many marine species may be differentiated into temperate and tropical. In a specific sense many bluegreen algae are found in restricted habitats (some hot spring species or tropical marine plankton species). Others have more subtle requirements, tolerances or preferences. The nature of these distribution patterns is obscured by misidentification, lack of pertinent data and more particularly the confused taxonomic situation.

The distribution of Nodularia was studied by a critical review of the literature and examination of herbaria material

(Appendix, Table IX). The results of this survey show that the great majority of collections were in temperate and subtropical areas (i.e. 25°-60° north and south of the equator, Figs. 8-13). It may be argued that tropical areas have not been the subject of as extensive collections as more temperate areas; however, there have been sufficient details surveys of tropical areas which would have revealed the presence of Nodularia had it occurred frequently in tropical latitudes (Desikachary 1959; Drouet 1937, 1938; Frémy 1929; Skuja 1949). Some of the tropical reports of Nodularia are from higher more temperate altitudes (Karim 1968; Standey in Field Herbarium; Tilden 1908; West 1914). Others do not contain information regarding altitude (Mobius 1893; Woodhead and Tweed 1957). Collections from the Arctic (Foslie cited in Nordstedt 1897) or the Antarctic (Apstein, collection in Field Herbarium; Fritsch 1912; Fukushima 1959) have been reported but it is obvious from other Arctic and Subarctic surveys (Croasdale 1973; West and West 1911; Wheldon 1947; Wille 1924) that Nodularia is uncommon in polar climates (60°-90° north or south of the equator).

What is more important perhaps in distribution is the type of habitat. Brackish marine habitats (i.e., Baltic Sea, New England coast of North America) and arid or semi-arid inland lakes (i.e., western North America) are areas in which repeated

Fig. 8. North American distribution of N. spumigena

Fig. 9. North American distribution of N. harveyana

● herbarium specimen

o literature report

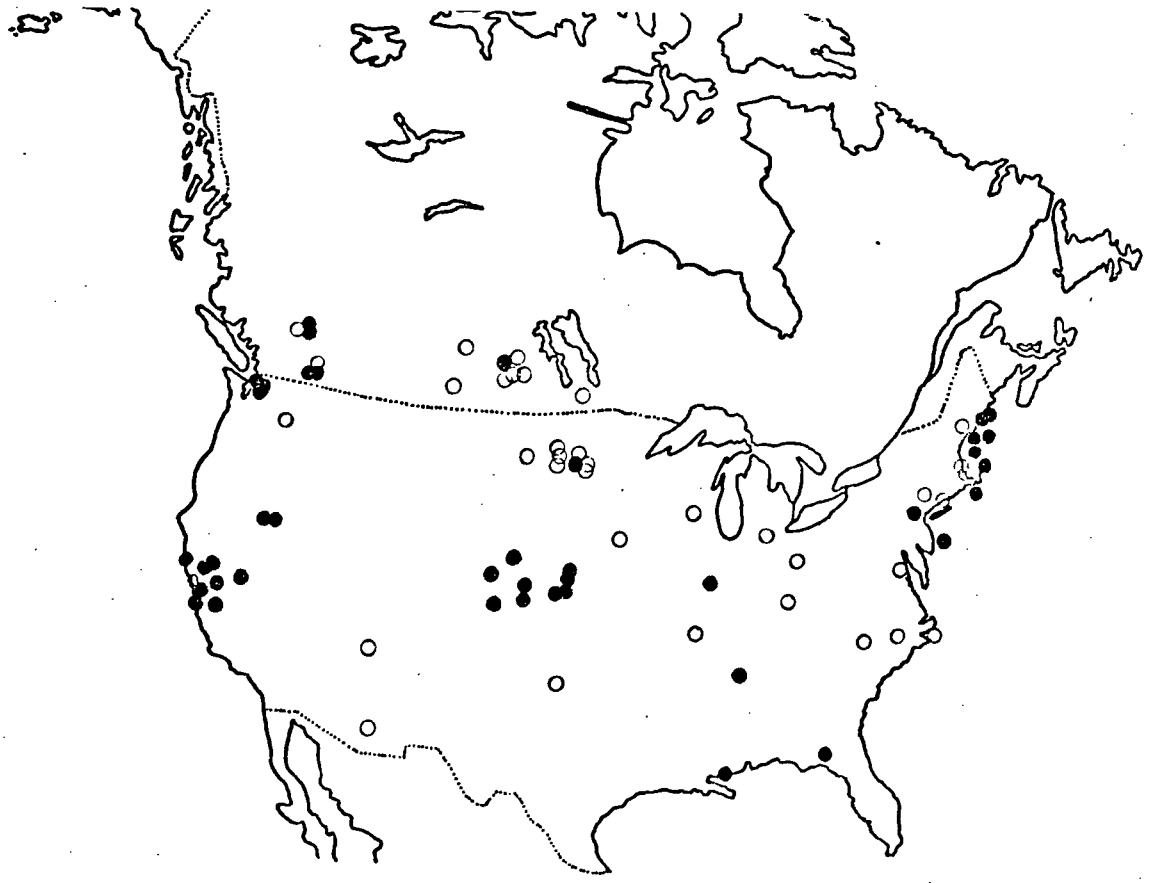


Fig. 10. European distribution of N. spumigena

Fig. 11. European distribution of N. harveyana

● herbarium specimen

o literature report

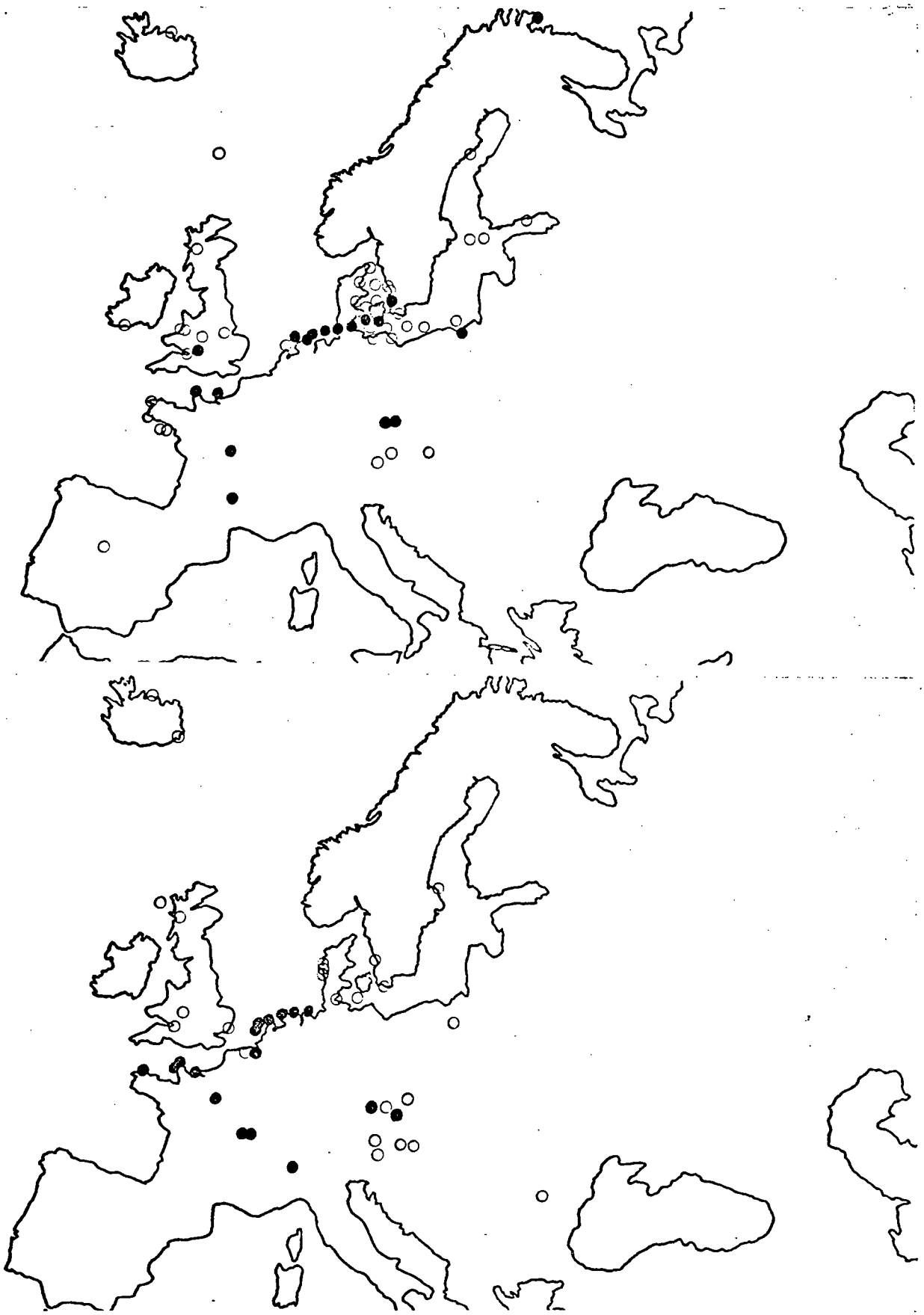
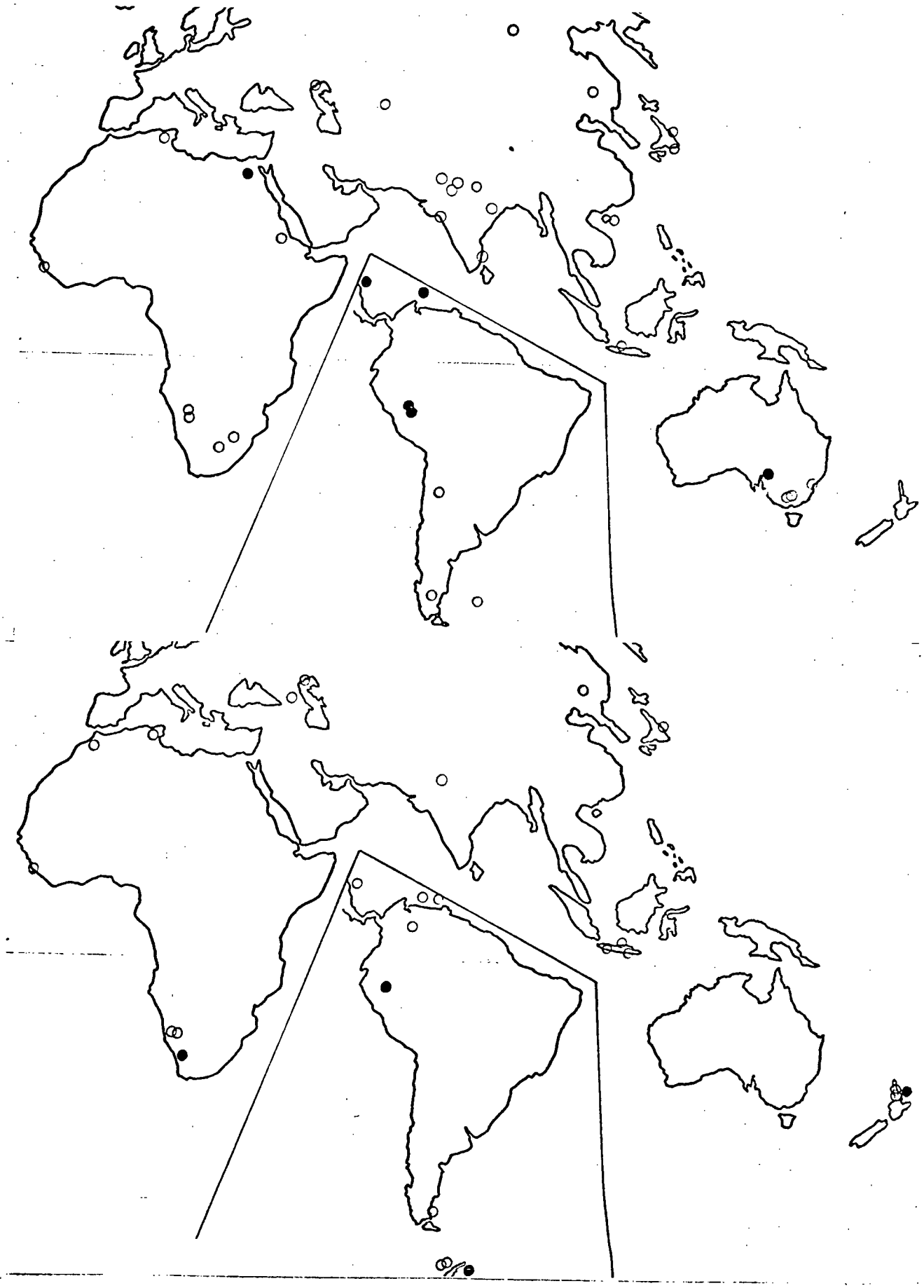


Fig. 12. World (exclusive of North America and Europe) distribution of N. spumigena

Fig. 13. World (exclusive of North America and Europe) distribution of N. harveyana

● herbarium specimen

o literature report



collections have been made. The factors enabling Nodularia to occur in these types of waters is the ability of these algae to grow in a wide range of salinities, ability to resist rapid fluctuations in salinity and resistance to desiccation. Bristol (1919) reported culturing Nodularia harveyana from a dry soil sample stored for 59 years. Laboratory observations indicate that if agar plate cultures are allowed to dry in the culture chamber (15-30 C) and then stored at room temperature, the algal material is viable and growth will resume when a portion of the dried material of any of the isolates is introduced into liquid media after two years storage. Because of this resistance to desiccation, the akinetes are probably distributed by wind as are many other small aquatic organisms (Maguire 1963).

GROWTH AND PHYSIOLOGY

The growth and physiology of a number of Nodularia isolates were studied under laboratory conditions. The sources of the isolates are given in Table II. The purpose of this portion of the study was twofold. First to clarify some ecological observations by growing the isolates in a variety of conditions of temperature, light, pH, and salinity with the hope of obtaining insight into the occurrence and growth patterns of the alga in nature. Second, to aid in the investigation of morphological plasticity by growing isolates under a variety of physical and chemical variables.

Materials and methods:

The medium used was BG-11 of Stanier, Kunisawa, Mandel and Cohen-Bazire (1971), which is a modification from Hughes, Gorham and Zehnder (1958) (Appendix, Table VIII). Several other media were tried but BG-11 proved to be the most satisfactory considering the wide pH range (6-11) used. Isolations of Nodularia spp. were made by streaking the algal material collected in the field on 1% (w/v) agar plates and by manual manipulation and repeatedly restreaking of the filaments. Removal of bacterial contamination was aided by the phototactic response of the hormogonia across the agar surfaces or through the agar. Stock cultures were maintained on agar plates or

Table II. Origin of isolates used in growth and physiology experiments.
Details of locations are given in Table I.

isolate No.	isolated from
1	Alkaline soil from Spotted Lake B.C. (*N. spumigena**)
2	Alkaline soil from near a small pond south of Richter Lake B.C. (*N. spumigena*)
3	White Lake B.C. (*N. harveyana**)
4	'Salt pond 4' B.C. (*N. spumigena*)
5	Ctenocladus Pond B.C. (*N. harveyana*)
6	'Salt pond 3' B.C. (*N. spumigena*)
7	Inks Lake B.C. (*N. spumigena*)
8	Wallender Lake B.C. (*N. harveyana*)
9	Big Quill Lake Sask. (*N. spumigena*, does not form akinetes, has gas vacuoles)
10	Soil collected at Simpson's Gap, Northern Territories Australia by Dr. J.R. Stein (*N. spumigena*)
11	LB-1452/1 from the Culture Collection of Algae and Protozoa Cambridge England, isolated by Butcher (*N. harveyana*, does not form akinetes)
12	Alkaline soil from Bowers Lake B.C. (*N. spumigena*)
13	Inks Lake B.C. (*N. harveyana*)
14	White Lake B.C. (*N. spumigena*)
15	Unnamed pond near San de Fuca Washington (*N. harveyana*)
16	Devils Lake North Dakota (*N. spumigena*)

* The reasons for using these specific names are given in the taxonomy section.

in liquid culture.

Nodularia cultures used for initiating experiments were grown in 500 ml flasks and filaments in the log phase of growth were used. Temperature, light, salinity and nitrogen experiments were done using 20 mm test tubes, containing 25 ml liquid medium in each, with Bellco stainless steel closures. Test tube racks were turned daily to insure homogeneous lighting. For pH experiments cultures were grown in 100 ml liquid medium in 250 ml Erlenmeyer flasks. Growth was measured after a seven day period unless otherwise noted and data based on duplicate cultures replicated three times.

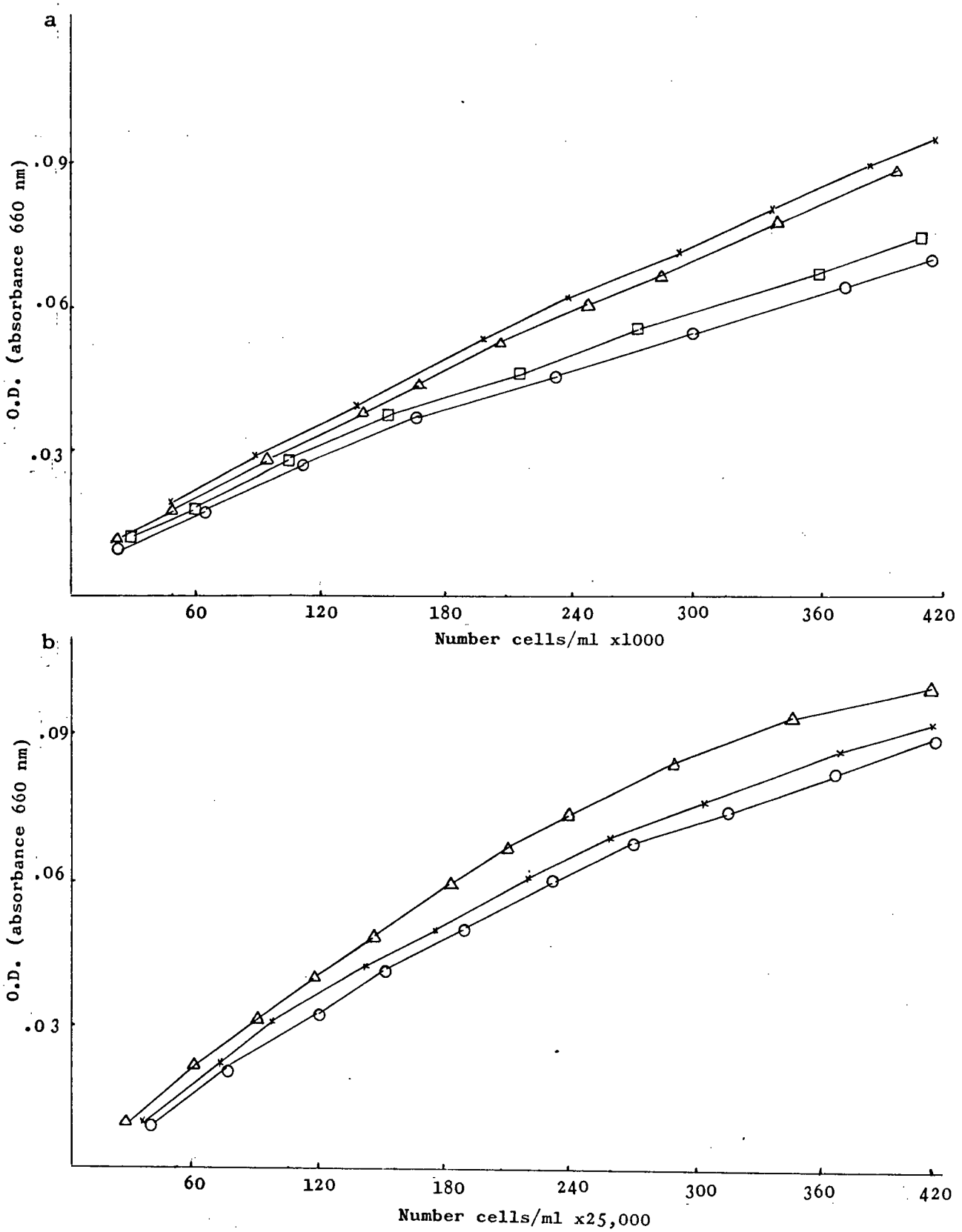
Growth of a 3 to 5 ml aliquot of a culture was measured as the optical density (absorbance) at 660 nm using either a Beckman DBG or a Bausch and Lomb Spectronic 20 spectrophotometer. The optical density was related to the number of cells by preparing standard curves for each isolate. These comparison curves are shown as Fig.14.

Temperatures were varied by growth in controlled environment chambers: reach-in type for 15 C, 25 C, 30 C and 35 C (Sherer Co. Ltd., Marshall, Michigan, model RT-18B-5E; Controlled Environments Ltd., Winnipeg, Manitoba, model T18L; Percival Co. Ltd., Boone, Iowa, model I-36-L) and a walk-in chamber for 20 C (Bell Craft Industries, Surrey, British Columbia, model 2002).

Figure 14. Standard curves of optical density versus cell numbers.

a. The group of isolates with filament widths from 8-12 m (i.e. N. spumigena). The relationship between optical density at 660 nm and cell numbers for isolates 12 (△), 1 (X), 6 (□) and 9 (O). All other N. spumigena isolates (2, 4, 10, 12, 13, 16) relationship lines fell between that of strains 12 and 9.

b. Those isolates with filament widths from 5-7 m (i.e N. harveyana). The relationship between O.D. at 660 nm and cell numbers for isolates 5 (△), 8 (X), and 14 (o). All other isolates of N. harveyana (7, 11, 15) fell between the two extremes (5, 14).


a
O.D. (absorbance 660 nm)
.09
.06
.03
60
120
180
240
300
360
420
Number cells/ml x1000
b
O.D. (absorbance 660 nm)
.09
.06
.03
60
120
180
240
300
360
420
Number cells/ml x25,000

Light was supplied by General Electric 20 and 40 watt cool-white florescent tubes. The spectrum of light from 400-720 nm was measured by using an apparatus similar to the one described by Burr and Duncan (1972). The spectral quality of the light is shown as Fig. 15. The quantity of the light was set at four levels of illumination (Table III) by varying the number of light tubes and the distance of the light tubes from the culture vessel. Light was measured with a Gossen 1.67-873 foot-candle meter and a radiometer (YSI model 60) calibrated in ergs/cm^2/sec. The photoperiod unless otherwise specified was 16 hours:8 hours (light:dark).

Growth in the range of pH 6-11 (in 1.0 unit increments) and 9-11 (in 0.2 unit increments) was investigated. The wide range of pH used was such that no buffer tried was adequate. The use of two or more buffers overlapping in range gave very poor results. For pH experiments the method of Gerloff, Fitzgerald and Skoog (1952) of adjusting the pH every 12 hours with 1 M NaOH or 1 M HCl was used. The pH was measured with a Metrohm E280A pH meter.

The salinity was varied in a range of 1-100 $^{o}/_{oo}$ by adding an appropriate amount of NaCl to the medium. All isolates were grown on the above range of NaCl and in addition, four isolates (Nos 7, 9, 10, 11) were grown with Na_2SO_4, M_gSO_4

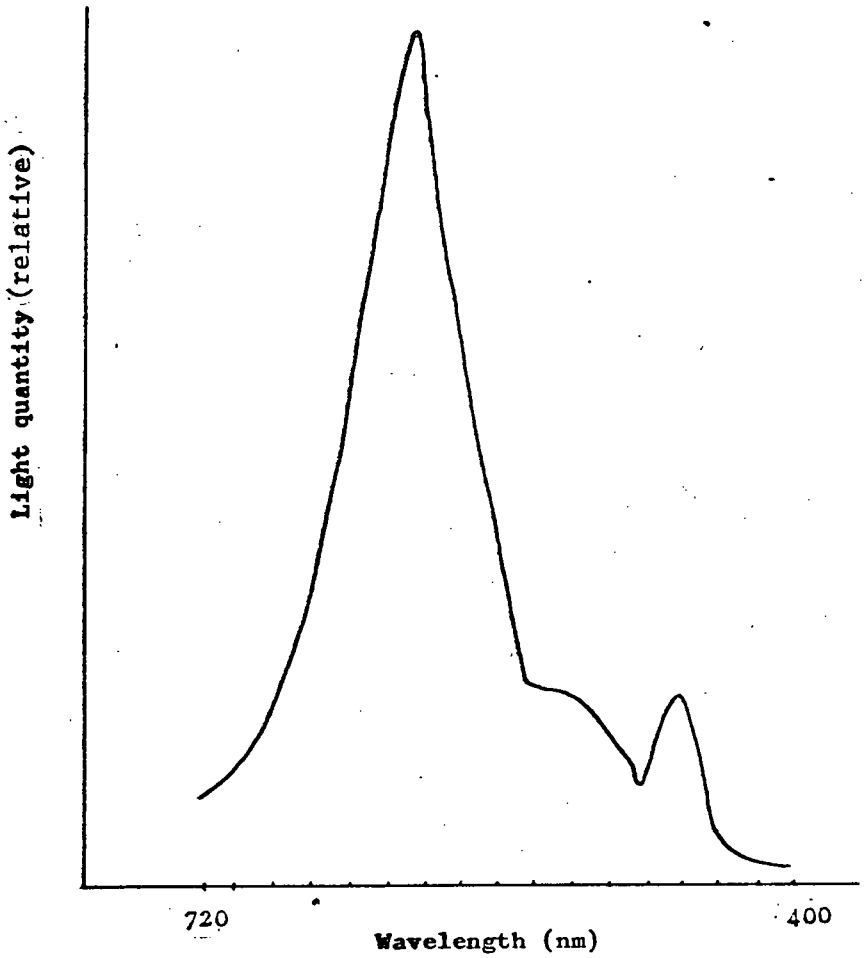


Figure 15. Quality of light used in culture experiments. (see Barr and Duncan 1972)

Table III Light intensities used in culture experiments.

	foot-candles	ergs/cm^2/sec	lux
Light Level 1 (LL1)	550-600	4×10^4	6000-6400
Light Level 2 (LL2)	200	1.8×10^4	2200
Light Level 3 (LL3)	60-75	0.9×10^4	650-800
Light Level 4 (LL4)	25	1.1×10^3	240

and Na_2CO_3 as the dominant salt to discover if different anions or cations had effects on rates of growth or salinity tolerance.

The effect of nitrogen sources on growth was investigated using NO_3^-, NH_4^+ and urea. The concentration of dissolved salts (i.e. osmolality) was kept constant by adding appropriate amounts of NaCl. Inoculation material was grown on BG-11 without nitrogen for 20-30 days before inoculation.

A preliminary consideration was whether growth rates of axenic cultures differed from identical cultures with low level bacterial contamination (less than 5 bacterial cells/ 100 algal cells as measured with phase contrast microscopy). Results (details below) showed that there was little difference in growth patterns and as a consequence all data (except for nitrogen fixation) is based on cultures with the same amount of low level bacterial contamination mentioned above. The purity of axenic isolates No. 1 and No. 6 was checked using a number of bacteriological growth media (Table IV) and phase contrast microscopy.

Nitrogen fixation investigations were studied with field material and under laboratory conditions. Nitrogen fixation was measured by acetylene reduction method (Stewart et al. 1970) at White Lake (May 1972) and Inks Lake (June 1972) when Nodularia was present as a major algal component. Axenic

Table IV. Microbiological media for checking purity of cultures.

1. Nutrient Broth
   beef extract - 3.0 g; peptone - 5.0 g; water - 1.0 l

2. SST Media
   glucose - 1.0 g; tryptone - 1.0 g; yeast extract - 0.5 g; water - 100 ml

3. Peptone - Glucose
   glucose - 1.0 g; peptone - 1.0 g; water - 1.0 l

4. Potato-dextrose agar
   potato - 200 g; dextrose - 20 g; agar - 20 g; water - 1.0 l

5. Thioglycolate
   yeast extract - 5.0 g; casitone - 15 g; dextrose - 5 g; NaCl - 2.5 g; l-cystine - 0.75 g; thioglycolate - 0.3 g; agar - 0.75 g; methylene blue - .002 g; water 1.0 l

6. Sodium caseinate agar
   sodium caseinate - 3.0 g; peptonized milk - 7.0 g; agar - 12 g; water - 1.0 l

cultures were used for laboratory experiments. Analysis of the gas phase was with an Aerograph gas chromatograph (model 600C, Wilkins Instrument and Research Inc. now Varian Co. Ltd.) with a six foot 0.25 in (O.D.) stainless steel column of Porapak R and with hydrogen flame ionization with helium as the carrier gas. The apparatus was set at a temperature of 45 C for all components. Three replicates of each 1 ml sample and three controls for each run were used. The controls consisted of: algae incubated then killed with TCA (trichloroacetic acid, 2% w/v); algae not incubated but fixed with TCA; algae fixed with TCA then acetylene added and sample incubated.

Results:

Comparison of growth rates showed that there was little difference between axenic cultures and cultures with low level bacterial contamination. The Nodularia in the contaminated cultures grew at a slightly higher rate of growth (Fig.16). The contaminated cultures were closer to the morphology in nature than the morphology of axenic cultures (Table V).

1. Temperature. There was some variability among isolates but most grew best (highest O.D.) at either 25 C or 30 C. The maximum temperature tolerance for all isolates was between 30 C and 35 C (Fig.17). The lower limit of growth was apparently less than 5 C, the lowest temperature studied. Growth occurred (although quite slowly) at 5 C for the 5 isolates which

Figure 16. Comparison of growth of axenic cultures and cultures with bacterial contamination.

data at 25 C, 1.6 °/oo and pH 9 for isolate 1 (points are mean of six values. Vertical bar indicates range)

o contaminated

△ axenic

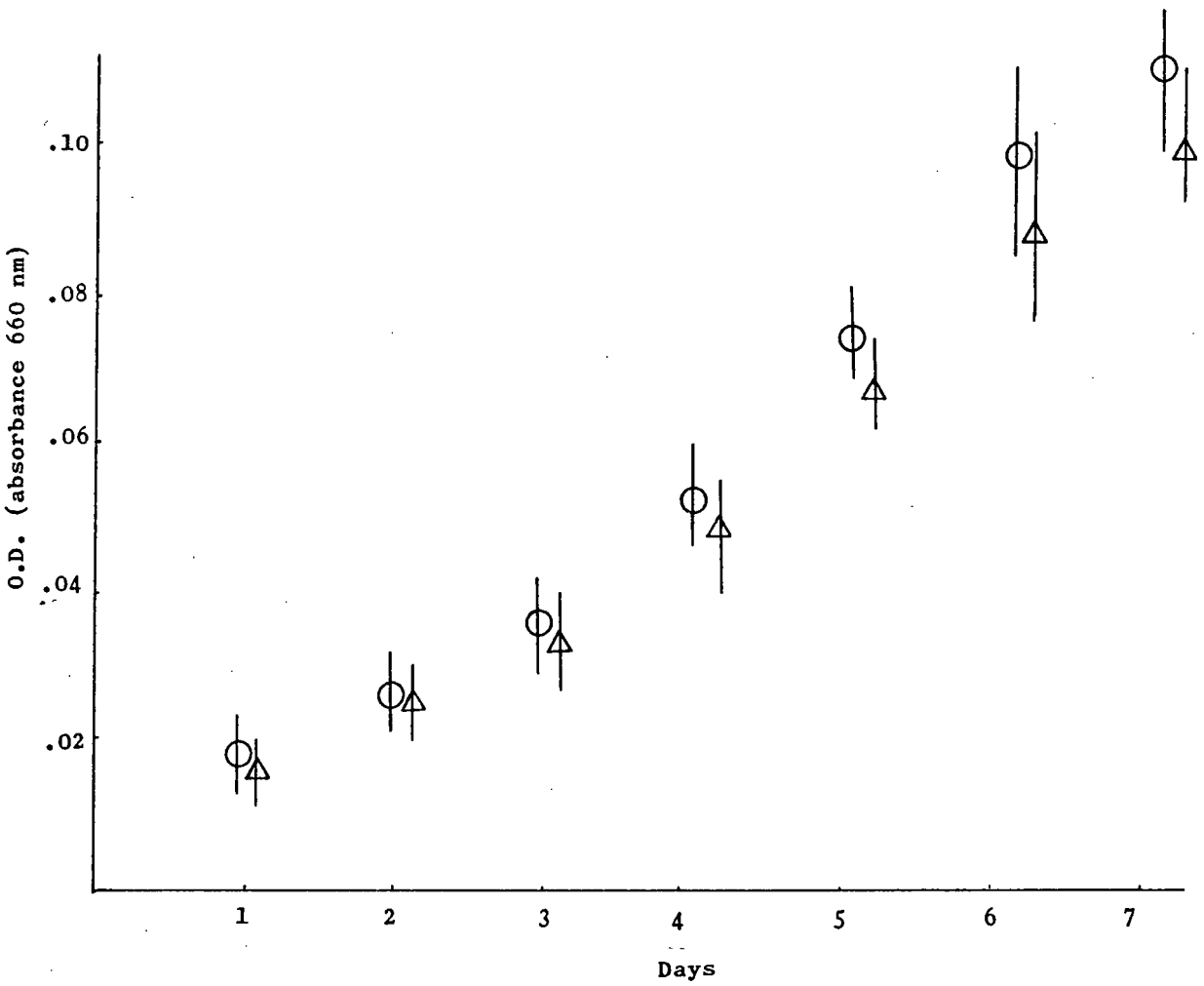


Table V. Comparative morphology of Nodularia in axenic culture, contaminated culture and nature.

	axenic	contaminated	nature
1. autolysis	not uncommon	rare	very rare
2. filament shape	twisted	straight	straight
3. spacing of heterocysts.	irregular	regular	regular

Figure 17. Effect of temperature on isolates of Nodularia.

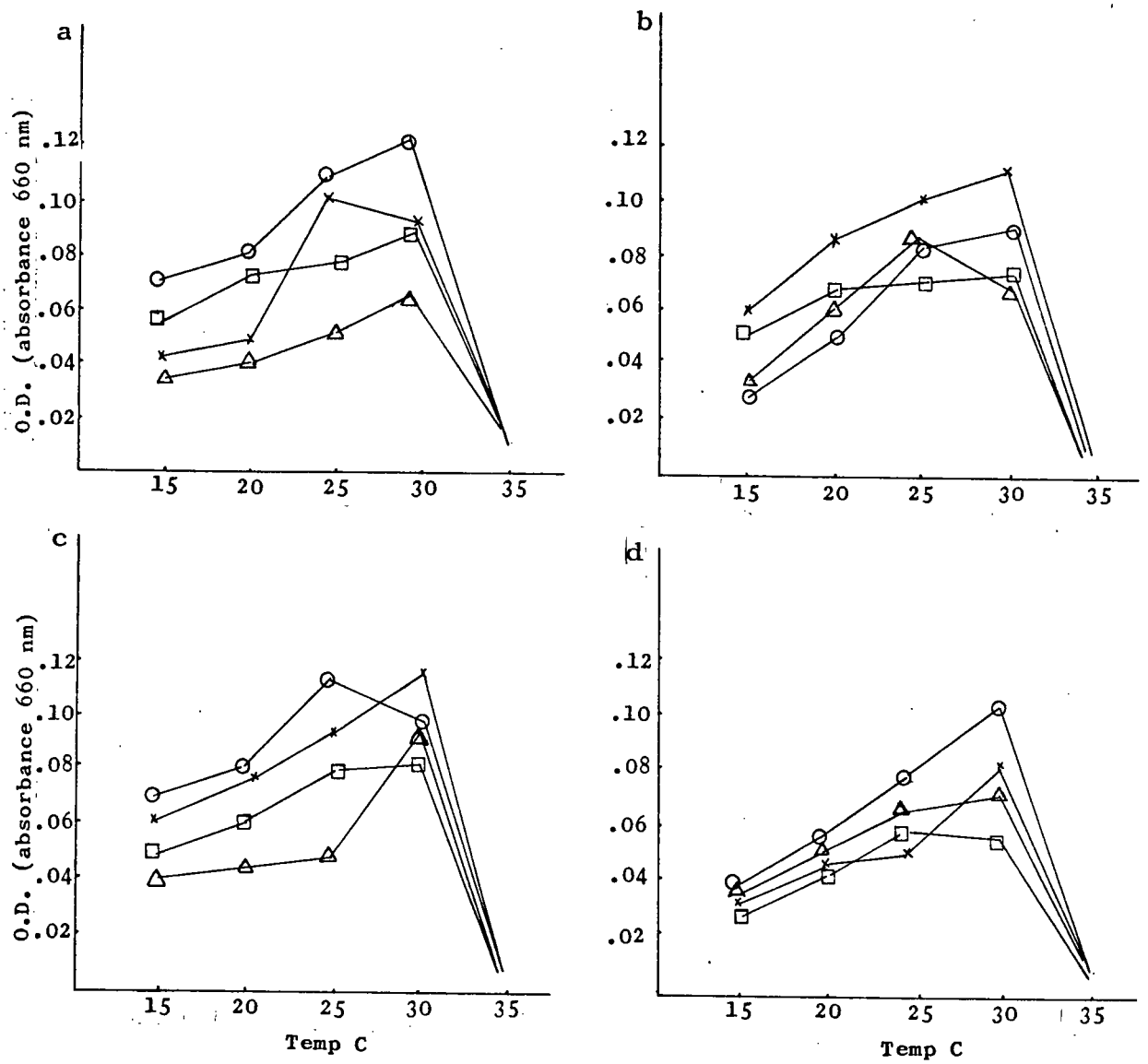
Results shown are for pH 9, LL1 with basal medium (salinity about 1.6 °/oo) after 7 days growth.

a. isolate 1 (o) 2 (X) 3 (□) 4 (△)

b. isolate 5 (o) 6 (X) 7 (□) 8 (△)

c. isolate 9 (o) 10 (X) 11 (□) 12 (△)

d. isolate 13 (o) 14 (X) 15 (□) 16 (△)


a
b
c
d
O.D. (absorbance 660 nm)
.02
.04
.06
.08
.10
.12
15
20
25
30
35
Temp C

were tested.

2. Light. Most isolates grew best at the higher light level, LL1 (Fig.18). Two isolates (Nos. 2, 9) grew best at LL2 and isolate No. 12 grew best at either LL1 or LL2 depending on the temperature. At high temperatures (35 C) the light levels combined with the temperature to inhibit growth to a greater extent than it did at lower light levels. Thus most isolates at 35 C grew very slightly at LL4 but not at all at any other light intensities.

3. pH. The isolates showed optimal growth at or near pH 10 (Fig.19 a-d). Fourteen isolates had pH growth optima between 10.0 and 10.4, whereas isolates No. 2 and No. 8 grew best at pH 9.4 and 9.6 respectively (Fig.19 e,f).

4. Salinity. A wide range of variability was seen among the isolates. Some isolates (Nos. 6, 8, 10, 12) grew in a maximum salinity of 30 ^{o}/oo NaCl. However, most isolates showed an upper salinity tolerance of 60 ^{o}/oo. The salinity of initial isolation affected the upper limit. Cultures initiated from inoculum in normal BG-11 (1.6 ^{o}/oo) had a maximum tolerance in the range of 40-50 ^{o}/oo. However, if cultures were initiated with inoculum grown at 40 ^{o}/oo then the tolerance was increased to 60 ^{o}/oo. Growth of inoculum at 60°/oo and attempts at growing cultures at higher salinities were unsuccessful. The salinity at which

Figure 18. Effect of light intensity on growth of Nodularia

Growth curves for c, d, e, f at 25 C, pH 9 and basal medium (about 1.6 °/oo)

a. growth of isolate 1 at different temperatures - 30 C (X), 25 C (△), 20 C (□), 15 C (o), 35 C (●).

b. growth of isolate 2 at different temperatures - 30 C (X), 25 C (△), 20 C (□), 15 C (o), 35 C (●)

c. isolates 1 (o), 2 (X), 3 (□), 4 (△)

d. isolates 5 (o), 6 (X), 7 (□), 8 (△)

e. isolates 9 (o), 10 (X), 11 (□), 12 (△)

f. isolates 13 (o), 14 (X), 15 (□), 16 (△)

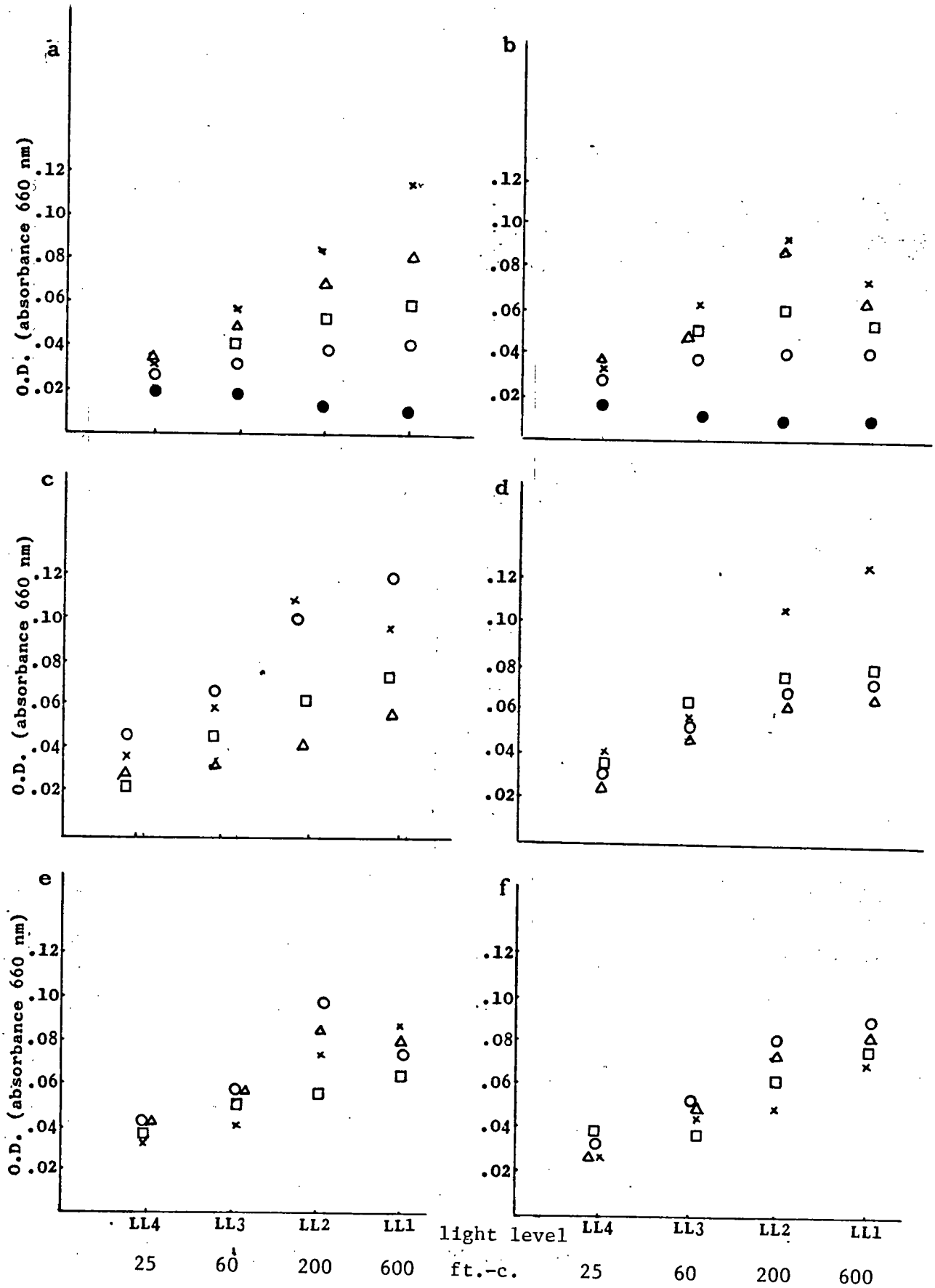

a
b
c
d
e
f
O.D. (absorbance 660 nm)
.02
.04
.06
.08
.10
.12
LL4
LL3
LL2
LL1
light level
25
60
200
600
ft.-c.

Figure 19. Effect of pH on the growth of Nodularia

a. growth at pH 6-11 for isolates 1 (o), 2 (X), 3 (□), 4 (△)

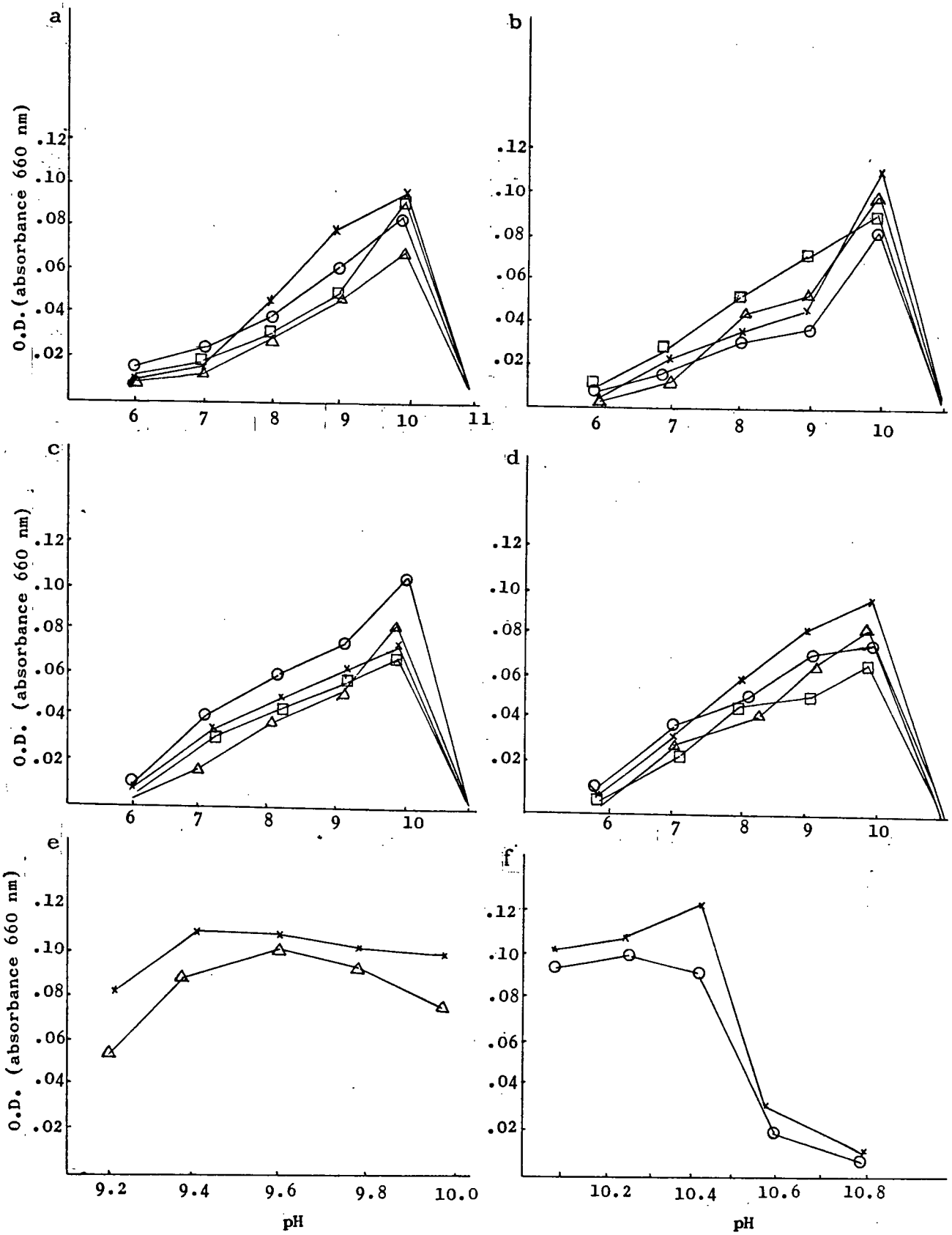
b. growth at pH 6-11 for isolates 5 (o), 6 (X), 7 (□), 8 (△)

c. growth at pH 6-11 for isolates 9 (o), 10 (X), 11 (□), 12 (△)

d. growth at pH 6-11 for isolates 13 (o), 14 (X), 15 (□), 16 (△)

e. growth at pH 9.2-10.0 for isolates 2 (X), 8 (△)

f. growth at pH of 10.2-10.8 for isolates 6 (X), 13 (o)


a
b
c
d
e
f
O.D. (absorbance 660 nm)
.12
.10
.08
.06
.04
.02
6
7
8
9
10
11
9.2
9.4
9.6
9.8
10.0
10.2
10.4
10.6
10.8
pH

optimum growth occured was between 5 °/oo and 20 °/oo NaCl for all isolates (Fig.20).

Use of salts other than NaCl gave essentially the same results. Isolate No. 9 showed better growth at higher salinities but all isolates showed similar levels of tolerance for salts used and highest growth rates were at the same salinities as for NaCl. No differences were evident with Mg^{++} as the major cation nor $SO_4^{=}$ or $CO_3^{=}$ as the major anion (Fig.21).

5. Nitrogen. All isolates grew much better with NO_3^- than with NH_4^+ as the source of nitrogen (compare Fig.22a,b with 22 c,d). Growth was much better in media without added nitrogen than at any level of NH_4^+. Cultures at lower concentrations of NH_4Cl showed some growth, perhaps the high concentration of NH_4^+ used initially was inhibitory. Growth using urea as the nitrogen source gave similar results to growth on NH_4^+ (Fig. 22 e,f).

Acetylene reduction, as a measure of nitrogen fixation, under field conditions (approx. 50,000 cells/liter) was found to be very low (less than 1 nmole/l pond water). In the laboratory, the two axenic isolates, No. 1 and No. 6, were used to investigate the rates of nitrogen fixation and to discover the effect of nitrogen, pH and salinity on rates of nitrogen fixation. Nitrogen in the growth media inhibited

Figure 20. Effect of salinity on growth of Nodularia.

Growth at salinities of 1.6 - 60 °/oo at LL2, pH 9, 25 C, inoculum grown at 1.6 °/oo (normal BG-11)

a. growth for isolates 1 (o), 2 (X), 3 (□), 4 (△)

b. growth for isolates 5 (o), 6 (X), 7 (□), 8 (△)

c. growth for isolates 9 (o), 10 (X), 11 (□), 12 (△)

d. growth for isolates 13 (o), 14 (X), 15 (□), 16 (△)

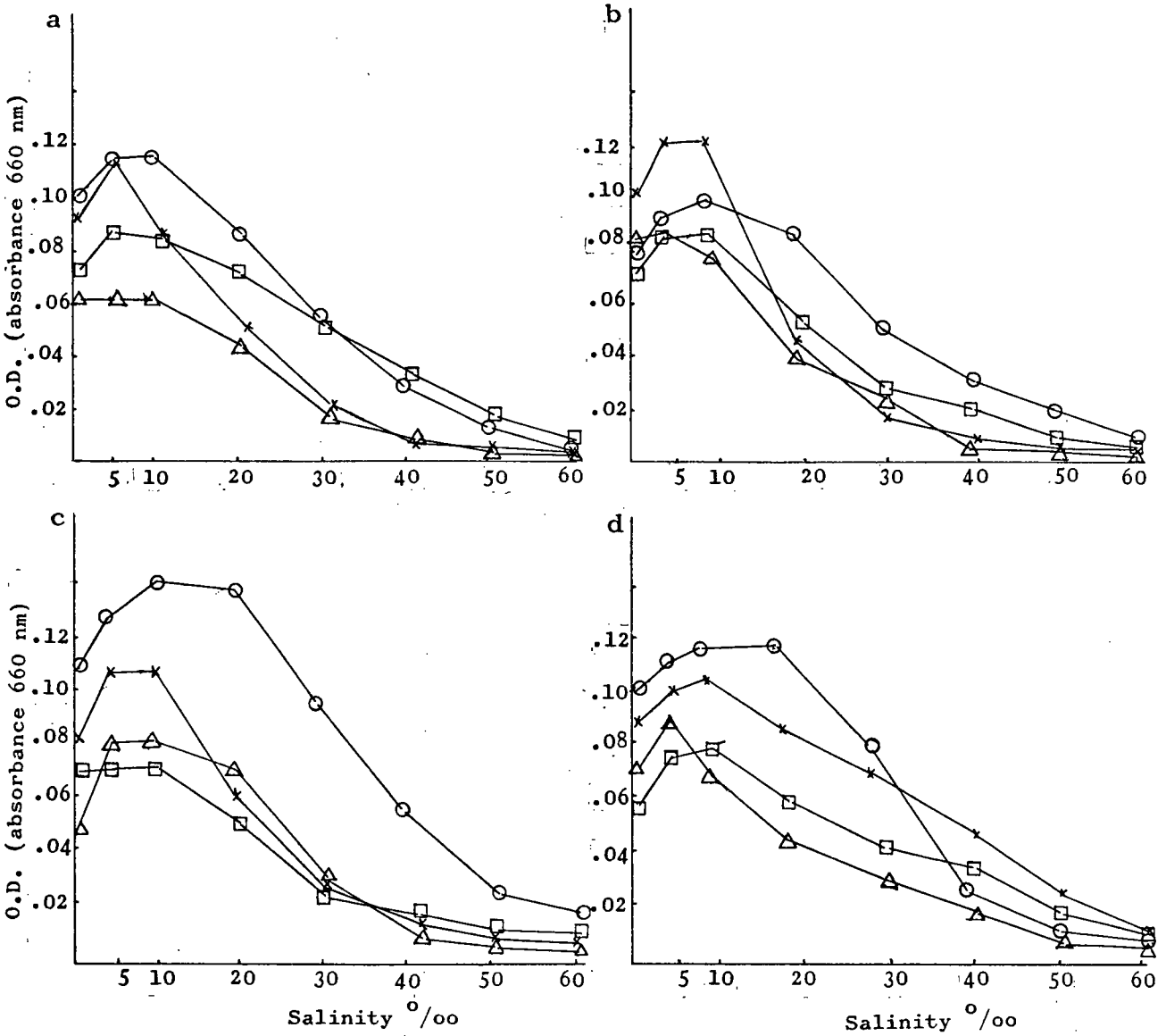

a
b
c
d
O.D. (absorbance 660 nm)
.12
.10
.08
.06
.04
.02
5
10
20
30
40
50
60
Salinity °/oo

Figure 21. Effect of salinities using salts other than NaCl on growth of Nodularia.

Growth at salinities 1.6 - 60 °/oo at LL2, 25 C, pH 9, inoculum grown at 1.6 °/oo BG-11.

a. isolates 10 Na_2SO_4 (△) $MgSO_4$ (□) Na_2CO_3 (○)

b. isolates 9 Na_2SO_4 (△) $MgSO_4$ (□) Na_2CO_3 (○)

c. isolates 7 Na_2SO_4 (△) $MgSO_4$ (□) Na_2CO_3 (○)

d. isolates 11 Na_2SO_4 (△) $MgSO_4$ (□) Na_2CO_3 (○)

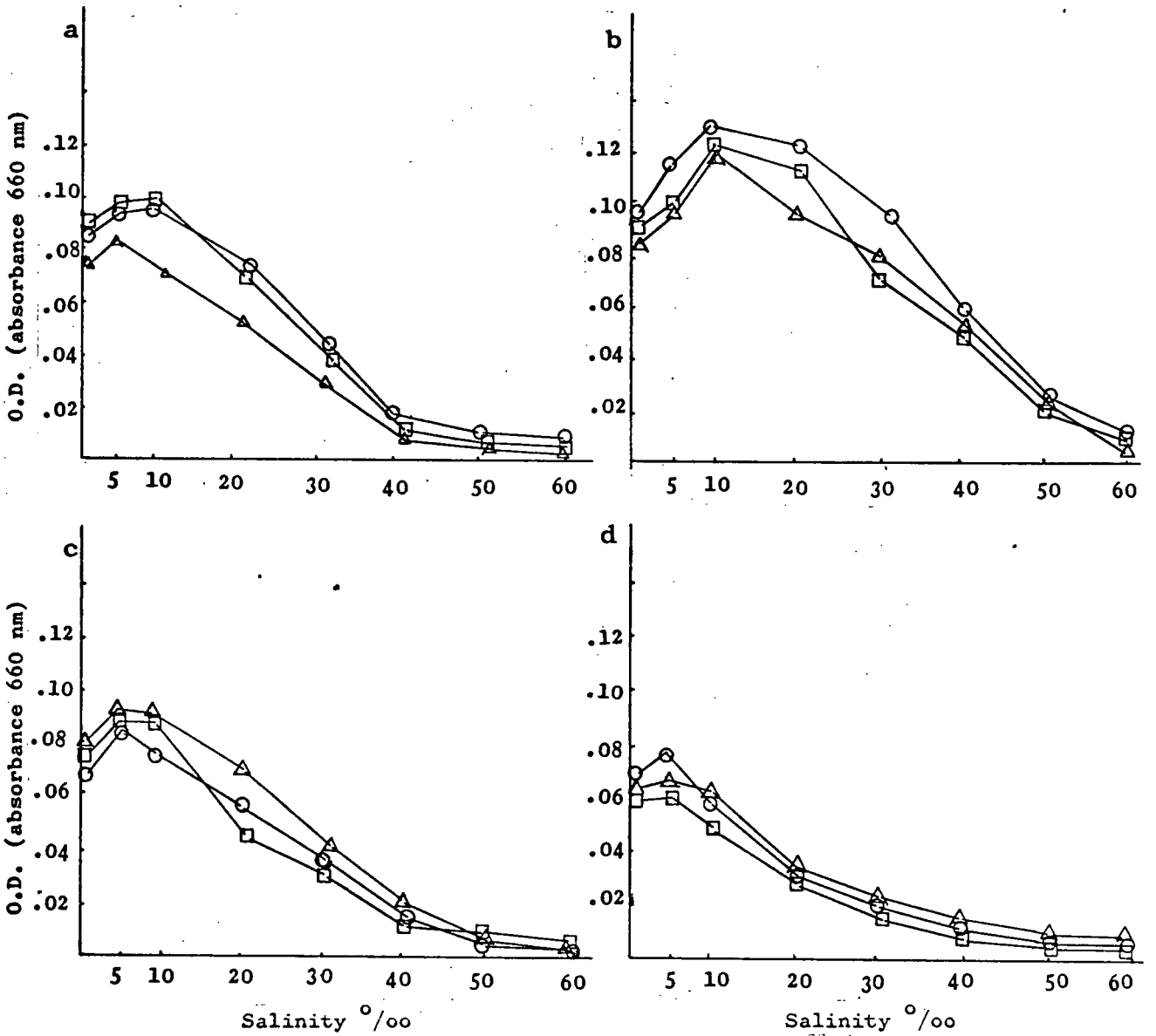

a
b
c
d
O.D. (absorbance 660 nm)
.12
.10
.08
.06
.04
.02
5 10 20 30 40 50 60
Salinity °/oo

Figure 22. Effect of nitrogen source on the growth of Nodularia.

All data at 25 C, LL2, pH 9 and basal medium (salinity about 1.6 °/oo).

a. growth on NO_3 by isolates 1 (o), 2 (X), 3 (□), 4 (△)

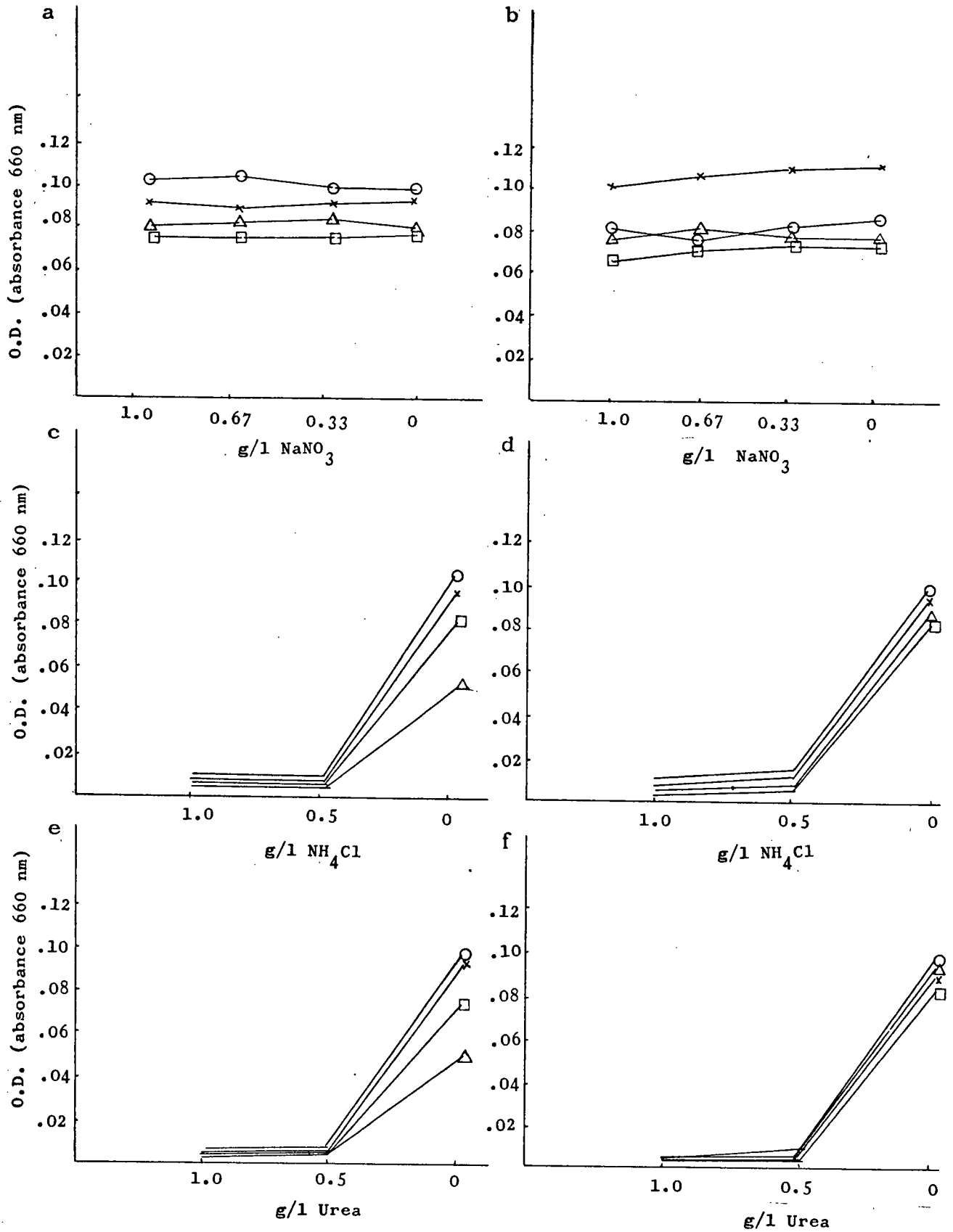
b. growth on NO_3 by isolates 5 (o), 6 (X), 7 (□), 8 (△)

c. growth on NH_4 by isolates 1 (o), 2 (X), 3 (□), 4 (△)

d. growth on NH_4 by isolates 5 (o), 6 (X), 7 (□), 8 (△)

e. growth on urea by isolates 1 (o), 2 (X), 3 (□), 4 (△)

f. growth on urea by isolates 5 (o), 6 (X), 7 (□), 8 (△)


a
b
c
d
e
f
O.D. (absorbance 660 nm)
.12
.10
.08
.06
.04
.02
1.0
0.67
0.33
0
g/l NaNO3
0.5
g/l NH4Cl
g/l Urea

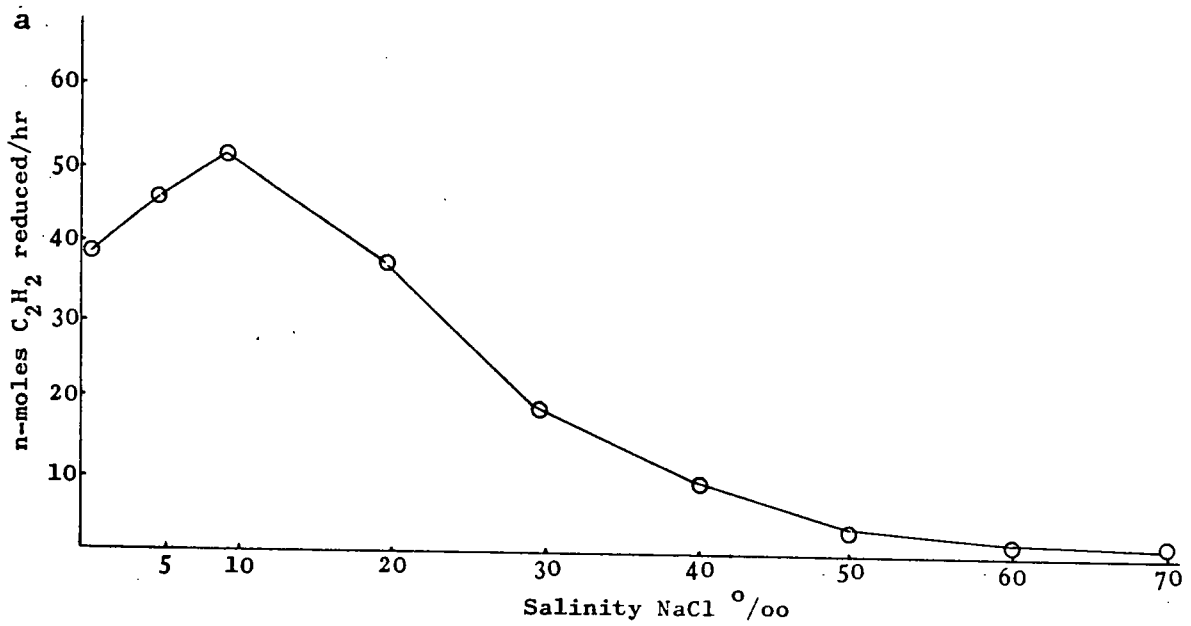
fixation to a level of 0.25 gm/l (about 40 ppm) below which rates increased. Highest rates of acetylene reduction occured at conditions similar to those for maximum growth (pH 10, salinity 5-10 $^{o}/oo$, temperature 30 C) (Fig.23). This perhaps is a reflection of the biochemical link between photosynthesis and nitrogen fixation (photosynthetic phosphorylation supplying the energy requirements of the process, Stewart 1970).

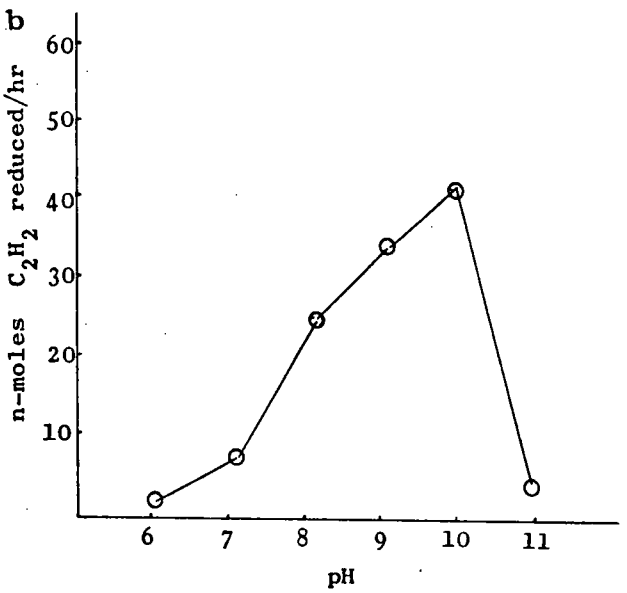
Figure 23. Effect of salinity, pH and temperature on acetylene reduction by Nodularia

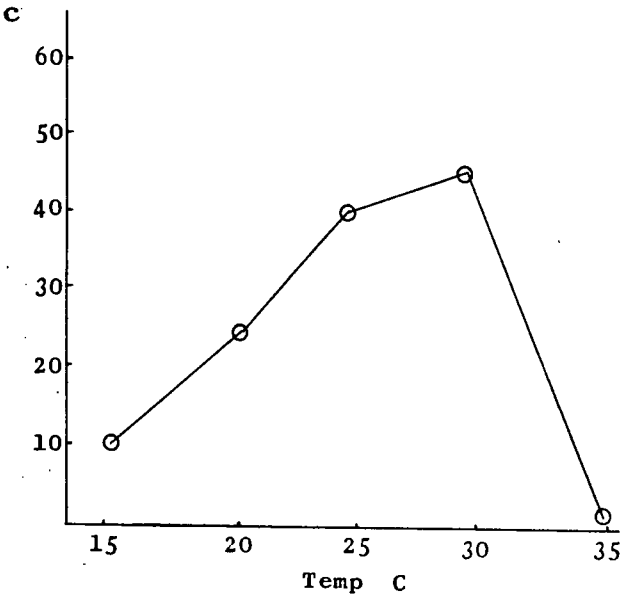
a. Effect of salinity on isolate 1, LL2, pH 10, 25 C, basal media (about 1.6 °/oo)

b. Effect of pH on isolate 1, LL2, 25 C, basal media (about 1.6 °/oo)

c. Effect of temperature on isolate 1, LL2, pH 10, basal media (about 1.6 °/oo)


a
n-moles C_2H_2 reduced/hr
60
50
40
30
20
10
5
10
20
30
40
50
60
70
Salinity NaCl °/oo


b
n-moles C_2H_2 reduced/hr
60
50
40
30
20
10
6
7
8
9
10
11
pH


c
60
50
40
30
20
10
15
20
25
30
35
Temp C

TAXONOMY

The genus Nodularia was established by Mertens in 1822 by distributing specimens of the alga as Decas XV #4 of the exsiccatae Algae Aquaticae of G.H.B. Juergens (1822). The type collection was made in 1821 on the island of Norderney, Germany (53.4°N, 7.0°E). Several specimens of the isotype material of N. spumigena exist (UC 436361, NBV 3925-51, NBV 3925-64, NBV 3925-66, NBV 3925-67, NBV 3925-68, F 951302)*. The last specimen (F 951302) is in very good condition. The generic name was "conserved" by a decision of the International Committee on Botanical Nomenclature (1969), as Link in 1809 used the name to describe a red alga, Lemanea (Stafleu 1972). No published description of Nodularia existed until 1888 when Bornet and Flahault revised the heterocystous bluegreen algae. This work by Bornet and Flahault (1886-1888) has been designated by the International Committee on Botanical Nomenclature as the taxonomic starting point of this group of bluegreen

* Letter initial(s) are standard abbreviations of herbaria (UC - University of California Berkeley; FH - Farlow Herbarium, Harvard University; F - Field Museum of Natural History, Chicago; NBV - Rijksherbarium, Leiden Netherlands; NY - New York Botanical Garden; PC - Cryptogamic Herbarium of the Paris Museum; BM - British Museum, London; UBC - University of British Columbia, Vancouver). The number following the herbarium designation is the accession number of the institution (or loan number in the case of NBV). If no accession number has been designated, a number from 1000-1400 following the name "Nordin" refers to an identification number of the annotation label attached to the herbarium sheet after examination.

algae (Briquet 1935). Bornet and Flahault did an admirable job in reducing the taxonomic confusion that existed at that time. Between 1822 and 1888 several additional species of Nodularia were described and Kützing (1843) established the closely related genus Spermosira. Kützing separated this genus from Nodularia because in Juergen's material akinetes were formed singly whereas in Spermosira the akinetes were formed in groups. Bornet and Flahault did not consider this characteristic to be of signifance and included the genus Spermosira and its accompanying species in the genus Nodularia. They also included a species of Lyngbya, L. annulata Suhr 1834, in the genus. Bornet and Flahault describe the genus as follows (translated from Latin):

> "Filaments free within a sheath. Sterile trichomes exceptionally uniform. Sheath hyaline, close, commonly thin, mucilaginous, sometimes lasting only a short time. Cells short, flattened, disc-shaped. heterocysts compressed. Akinetes spherical, subspherical or disc-shaped, formed in the interval between heterocysts with a smooth epispore."

After examining material from European herbaria, they reduced 16 taxa to 3 species names (one species having 3 varieties). They also described one new species. The species which Bornet and Flahault recognized are discussed below. Their validity is discussed later in this section.

1. N. spumigena [Mertens in Juergens] Bornet and Flahault, Ann. Sci. Nat. Bot. ser. 7. 7 : 243. 1888.

The species has the characteristics of the genus with filaments 8-18 µm wide. Bornet and Flahault described three varieties of this species. The var. genuina had filaments 8-18 µm wide and the akinetes subglobose. The var. litorea had filaments 12-16 µm wide and akinetes spherical-compressed. The var. major (not maior as incorrectly cited by Geitler, 1932) had filaments 12-18 µm wide and akinetes flattened-elliptical. Fig. 24d.

2. N. armorica Thuret, in Bornet and Thuret, Notes Algol. 2, p.122, plate 29, Fig. 12,13, 1880.

This species was first described from material collected near LeCroisic, France. It was separated from N. spumigena by the unique structure of its akinetes which in living plants had biconcave end cell walls, and the ends of vegetative cells fitting into the adjacent akinete like a head into a cap ("pileatae"). The filaments were 10-12 µm wide, the cells compressed and disc-shaped before division; and 3-4 times as wide as long. Fig. 24c.

3. N. harveyana (Thwaites) Thuret, Essai class. Nost., p.378, 1875.

The alga was first described by Thwaites in W.H. Harvey's Phycologia Britannia (1848) as Spermosira harveyana.

Figure 24. The species of Nodularia described in and since the revision of Bornet and Flahault (1888). (Copied or photocopied from originals).

a. N. harveyana drawing of type material from Harvey (1848), see also Fig. 32.x 250

b. N. sphaerocarpa from Frémy (1929). x 500

c. N. armorica drawing of type material from Bornet and Thuret (1880). x 650

d. N. spumigena drawings of Merten's type material from Bornet and Thuret (1880), also see Fig.31. x 650

e. Spermosira atlantica drawing of type material from Dickie (1871). x approx. 500

f. N. paludosa drawing of type material from Wolle (1887). x approx. 250

g. N. turicensis drawing of type material from Hansgirg (1892). x 400

h. N. hawaiiensis drawing from Tilden (1910). x approx. 400

i. N. tenuis drawing from West (1914) on left, x 500 and Fritsch and Rich (1929) on right. x 1400

continued p. 75

a
b
c
d
e
f
g
h
i

Thuret (1875) transferred the species to Nodularia. Bornet and Flahault described the filaments as 4-6 µm wide; akinetes subglobose, 6-8 µm wide; vegetative cells before division not much longer than wide. Fig. 24a.

4. N. sphaerocarpa Bornet and Flahault, Ann. Sci. Nat. Bot. ser. 7. 7 : 245. 1888.

This species was described as new by Bornet and Flahault from several collections: Bory in Belgium; Bornet in France; Meneghini in Italy on soil; Roussel on tree sap in France. The Roussel specimen was examined as a loan from the Paris Museum (PC Nordin 1315). No type specimen was designated by the authors. N. sphaerocarpa was described as being different from N. harveyana by filaments slightly wider in width (6-7 µm), slightly wider width of the akinetes (7-10 µm) and the shape of the akinetes (spherical-compressed). Fig. 24b.

The following species were described after 1888 or were not treated by Bornet and Flahault. Their present status is discussed and the validity of each taxon is considered.

5. Spermosira atlantica Dickie, J. Linn. Soc. Bot. 11 : 458, Fig. 4, 1871.

The material on which the name was based was collected from hurricane debris in the Atlantic, 200 miles off the

African coast. Forti (1907) cited this as being incompletely described. The type collection was the only collection made, no type material could be located and the inadequate description and unconvincing figure suggest that the name should be rejected. Fig. 24e.

6. N. paludosa Wolle, Fresh-water Algae of the U.S. p. 291, plate 198, Fig. 3,4. 1887.

The basis for describing this as a new species was the mistaken impression that european collections of the genus were all made in brackish waters and always occurred in considerable masses. Wolle's material was collected from Colorado and Pennsylvania. The cell dimensions are identical to N. harveyana and from the description and illustration it is possibly a N. harveyana although no akinetes were seen. Drouet (1930) reported that no specimens of this species existed in Wolle's herbarium. Collections identified as N. paludosa have been made by Clements (1896), Ackley (1931), Coyle (1930) and McInteer (1939). Forti (1907) considered it incompletely described and Geitler (1932) did not list it. The species should be rejected because of the inadequate description and lack of type material. Fig.24f.

7. N. mainensis F.L. Harvey, Bull. Torrey Bot. Club 16 : 188, 1889.

This alga was collected from Pushaw Stream near Orono, Maine. It was described as having trichomes 33-38 µm wide and cells 2-6 µm long. No akinetes were reported and no figure was included with the description. The location of the type is unknown and since the original collection, the species has not been reported. The species should be rejected on the basis of being incompletely described.

8. N. turicensis (Cramer) Hansgirg, Prod. Alg. Fl. Böhm. 2 : 74 Fig 27, 1892.

This was originally described as Spermosira turicensis by Cramer (1860). Hansgirg in 1892 transferred the species to the genus Nodularia despite the fact that Bornet and Flahault reduced S. turicensis to synonomy with N. harveyana in 1888 (p.244). Forti (1907) and Geitler (1932) synonomize the taxon with N. harveyana. Examination of herbarium material collected by Cramer (Rabenhorst's Algen Sachsens #994: FH Nordin 1084; NY Nordin 1262; PC Nordin 1236; NBV 3925-1) show it to be identical with N. harveyana. Fig. 24g.

9. N. hawaiiensis Tilden, Hawaiian Almanac and Ann. (1902) p.112, 1901.

Described from Hawaii and distributed in Tilden's American Algae as #484. Examination indicates that isotypes

(UC 740394; NY Nordin 1250; PC Nordin 1339; UBC 2971) and the only other two collections, by Tilden in Tahiti (South Pacific Algae #11; UC 233460; NBV 3925-47; NY Nordin 1257) and that by Crossland from Tahiti (UC 696203), are not Nodularia. Rather they are most likely Hormothamnion (?solutum) Bornet and Grunow. Kahn (1969) reports Hormothamnion from Hawaii, it is apparently common in tropical marine habitats (Phillipines, Velasquez 1962; Florida, Taylor 1928; Dawson 1966). Hormothamnion is superficially similar to Nodularia and can be easily mistaken for it (May 1946, 1951) but differs in having very variable trichome size, irregular spacing of heterocysts, lack of akinetes and a distinctly tropical distribution. Fig. 24h.

10. N. tenuis G.S. West, J. Linn. Soc. Bot. 38 : 171, 1907.

The type specimen from Tanganyika was examined (BM Nordin 1347) and the material has none of the attributes of the genus. It is probably an Anabaena sp. which confirms the suggestion of Geitler (1932). Fig. 24i.

11. N. quadrata Fritsch, Freshw. Alg. Nat. Antarct. Exped. p.45, plate 2, Fig. 109-115, 1912.

The species was described from material collected in the

Antarctic. Fritsch described it as a new species because its trichome is smaller (3-4 μm) than that of N. harveyana (4-6μm) and because some of the heterocysts are square. The material (BM Nordin 1934) was examined and the one akinete observed by Fritsch was not seen. The material lacks one important characteristic of the genus, that of regularly spaced heterocysts. The significance of the square heterocysts is unclear since heterocyst shape is variable in the type material. Iyengar and Desikachary (1944) show a figure of N. spumigena with square heterocysts. Geitler (1932) considered N. quadrata to be a valid species but in his 1942 work considers it to be an Anabaena. Since the species has never been recollected despite detailed (West and West 1911; Wille 1924) and more limited (Holm-Hanson 1964; Fukishima 1959) Antarctic surveys of freshwater algae, its status is questionable. Because of the variability of the heterocyst, irregular heterocyst spacing and lack of akinetes, the alga should be considered an Anabaena sp. rather than a Nodularia. Fig. 24j.

12. N. spumigena var. minor Fritsch, Freshw. Alg. Nat. Antarct. Exped., p.44, plate 2, Fig. 104 - 108, 1912.

This variety was also described from material collected in the Antarctic. The type material (BM 1815) was examined

Figure 24 cont'd.

j. N. quadrata drawing by Fritsch (1912) of the type material. x approx 500

k. N. spumigena var. minor drawing by Fritsch (1912) of the type material. x approx 500

l. N. harveyana var. sphaerocarpa drawing from Skuja (1926). x 820

m. N. epiphytica drawing of type material by Gardner (1927). x approx 300

n. N. willei drawing of type material by Gardner (1927). x approx 500

o. N. fusca drawing of type material by Taylor (1928). x approx 400

p. N. skujae drawing of type material by Gonzalez-Guerro (1928). x approx 500

q. N. spumigena var. vacuolata type material drawn from Fritsch and Rich (1929). x 1000

r. N. spumigena var. zujaris drawing of type material by Gonzalez-Guerro (1930). x approx 400

s. N. aerophila drawing of type material from Brabez (1940). x approx 1750

t. N. spumigena var. aerophila drawing of type material from Brabez (1940). x approx 500

j
k
l
m
n
o
p
q
r
s
t

and is identical to N. harveyana. No other collections of this taxon have been reported but N. harveyana has been collected from the Antarctic by Apfel (F 1299674; F 1299702) and by Fukishima (1959). Fig. 24k.

13. N. harveyana var. sphaerocarpa (Bornet and Flahault) Elenkin, Bull. Jard. Imp. Bot. Pierre le Gr. 16:331, 1916.

Elenkin considered that N. sphaerocarpa was merely an ecological variant of N. harveyana. Evidence from experimental studies is presented below (p.89) to support this. Fig. 24l.

14. N. epiphytica Gardner, Mem. N.Y. Bot. Gard. 7:65, plate 12, Fig.16, 1927.

This species was described from material collected from freshwater in Puerto Rico. The type material (NY Nordin 1254), the isotype material (UC 401800) as well as a second collection (UC 401800a; NY Nordin 1255) were examined. The material is actually juvenile stages of Nostoc sp. Young hormogonial filaments of Nostoc often do not resemble the mature filaments (see Geitler 1932, p. 844 N. muscorum; p.855 N. verrucosum). Geitler seeing only Gardner's diagrams, considered it an Anabaena sp. No subsequent collections of N. epiphytica have evidently been made. Fig. 24m.

15. N. willei Gardner, Mem. N.Y. Bot. Gard. 7:65, plate 12, Fig. 15, 1927.

This species was also described from material collected from freshwater in Puerto Rico. The type and evidently the only collection (NY Nordin 1256) was examined and the material is identical to N. spumigena. Fig. 24n.

16. N. fusca Taylor, Carnegie Inst. Wash., Pap. Tortugas Lab. 25:48, plate 1, Fig.23, 1928.

The species was collected from marine pools in the Tortugas Islands, Florida. The species was placed in the genus provisionally because it lacked both heterocysts and akinetes. Taylor (personal communication) no longer considers this species to be a Nodularia. Its taxonomic position at the present is unclear. It may belong in the genus Johannesbaptistia J. de Toni (Drouet 1938a), it may be synonomous with Cyanothrix willei Gardner (Gardner 1927) or it may be a growth form of Lyngbya (Frémy and De Toni 1940 cited in Drouet and Daily 1956). Nevertheless it is not a Nodularia. Fig. 24o.

17. N. skujae Gonzalez-Guerro, Bol. Real. Soc. Espan. Hist. Nat. 28:435, Fig. 1-3, 1928.

This taxon was described from material collected in tree sap (Ulmus and Populus) at Casa de Compo and Madrid, Spain.

Geitler (1932) lists it in synonomy with N. harveyana. No type material could be located, however from the description and figure the species is identical to N. harveyana. Fig.24p.

18. N. spumigena var. vacuolata Fritsch Trans. Roy. Soc. South Afr. 18:88, 1929.

Fritsch created this variety because of the presence of gas vacuoles. However, material from Baltic collections (i.e. Ostenfeld, NY Nordin 1284, 1285) are collected regularly with gas vacuoles. Lemmerman (1898), Sjostedt (1922) and Lindstedt (1943) have reported gas vacuoles for N. spumigena. This particular attribute is variable and probably does not justify the establishment of a variety. Fig. 24q.

19. N. spumigena var. zujaris Gonzales-Guerro, Bol. Real Soc. Espan. 30:224, Fig. 7-8, 1930.

The alga was collected from Zujar River, Spain. The dimensions of the vegetative cells match those of N. harveyana, however, the akinete size and variation (4-12 µm long; 7-12 µm wide) is very unlike the genus. The figure shown may have been drawn from poorly preserved material or was exhibiting abnormal growth. Most probably it is an Anabaena sp. Geitler (1932) considers it to be an abnormal Anabaena sp. The type material is the only collection reported in the literature and

this variety should be excluded from the genus Nodularia. Fig. 24r.

20. N. fertilissima Randawa, Proc. Ind. Acad. Sci. B. 4:41, 1936.

This species was published from a collection from Northern India. No description was given, thus it is rejected as a nomen nudum.

21. N. aerophila Brabez, Beihefte zum Bot. Zentrablatt 61A:214, Fig.8a, 1941.

This species was reported from Austria and described as a new species on the basis of its soil habitat, short filaments and lack of akinetes. The lack of akinetes is a negative characteristic and the other two characteristics do not justify its separation from N. harveyana to which it is identical in cell size and shape. The type material and only collection was not examined but the published description and figure are that of N. harveyana which has been reported many times from soil. Fig. 24s.

22. N. spumigena var. aerophila Brabez, Beihefte zum Bot. Zentrablatt 61A:215, 1941.

This variety was collected in the same sample as N. aer-

ophila and was separated on similar characteristics (aerial habitat; short filaments; lack of akinetes). It was described from a single filament and by its description is identical to N. spumigena, therefore its separation is completely unjustified. Fig. 24t.

23. N. implexa (Bornet and Flahault) Bourrelly Les Algues d'Eau Douce.III. p.418, Fig.5-6, 1970.

Bourrelly transferred Aulosira implexa to N. implexa and advocated inclusion of part of the genus Aulosira within the genus Nodularia. He maintained that the only difference between the two genera was that the cells of Nodularia were thinner (as compared to their width) and the sheath was thinner (i.e., Aulosira has a thicker sheath and the cells are not as flattened). The genus Nodularia is distinct because the cells are distinctly wider than long (N. spumigena 2-4x as wide as long; N. harveyana 1.5-2x as wide as long and only being as wide as long prior to cell division). In Aulosira the cells have always been considered either as long as wide or longer than wide (except A. schauinslandii Lemm. which resembles a Hormothamnion sp. and A. implexa var. crassa Dixit). Another distinct morphological feature is that akinetes of Nodularia are either round or wider than long and always separate from the heterocyst. The akinetes of Aulosira

are invariably longer than wide and may be either removed from or adjacent to the heterocyst (Desikachary 1959). The heterocysts of Nodularia are regularly spaced along the filament, but Aulosira has random arrangement of heterocysts. This characteristic was used by Thuret (1875) as a major characteristic to define the genus Nodularia. There is also a distinct habitat differentiation. Nodularia is typically found in marine and brackish situations and only occasionally in freshwater or on soil. Aulosira, on the other hand, is primarily a soil and freshwater genus and is only rarely found in brackish or marine environments. The distribution patterns of the two are very different. Nodularia occurs primarily in temperate environments, occasionally in the subtropics and only rarely in the tropics. Aulosira is primarily tropical and subtropical, and less commonly reported from temperate areas. For these reasons the genus Nodularia should not include the genus Aulosira or any part of it.

24. N. spumigena f. crassa (Woronichin) Elenkin.

The original citation of this taxon could not be located. The only reference to it, in Starmach (1966), appears from the description and figure (p. 518-519) to be of an N. spumigena specimen from Siberia with particularly large cell dimensions.

Validity of Bornet and Flahault's Nodularia taxa: The preceding summary indicates that all the species described since 1888 can be shown to be excluded from the genus or can be included within species of Nodularia defined by Bornet and Flahault (1888), it is necessary to establish the validity of the taxa described by Bornet and Flahault. The questions that were considered are: is N. armorica a distinct entity; are the varietal names of N. spumigena justified; is N. sphaerocarpa a distinct species; are N. harveyana and N. spumigena distinct species or merely two halves of a continuum of a single species?

Validity of N. armorica: Bornet and Flahault (1888) state the distinguishing characteristic of this species is the biconcave, truncate akinetes in which the end of an adjacent vegetative cell is hidden by the concave end of the akinete. They note that this characteristic is seen only in living material. Evidently only five collections have been given the specific name armorica. The first was the type collected in France by Thuret in 1873. Three collections were made on the Pacific Coast of North America (1. Gardner 436, UC 100567; 2. Gardner 602, UC 100568; 3. Osterhout and Gardner PBA 1061; FH Nordin 1087, NBV 3925-30, F 980816, NY Nordin 1213, PC Nordin 1302) and the fifth in France (Frémy and Meslin 1924). Of the three North American collections one

(UC 100568) from Whidbey Is. Wash. was in poor condition. The other two did not show the characteristic akinete as would be expected with preserved material and were identical to N. spumigena. The two collections by Gardner (436, 602) were placed in the species armorica "doubtfully" (Setchell and Gardner 1903) since the specimens differed in several details from Bornet and Flahault's (1888) description. The figure shown in Frémy and Meslin's report (1924) is very poor. N. armorica and N. spumigena are identical except for the unique akinete structure. Indeed this characteristic may be a microscopic artifact (Fig. 25a,b). However some herbarium specimens identified as N. spumigena did show biconcave areas between the akinetes (UC 761550; UC 752514) (Fig. 25c,d,e). This is odd since the characteristic supposedly occurs only in living cells (Bornet and Flahault 1888). Studies under varying growth conditions to determine the stability of taxonomic characteristics show that akinete shape, size and wall characteristics are far more variable than size and shape of vegtative cells or heterocysts (Fig. 26). Thus separation of a species on akinete characteristics alone is of doubtful value. With this evidence, N. armorica is considered an ecological variant of N. spumigena and is placed in synonomy with it.

Validity of varietal names of N. spumigena: Examination of a large number of herbarium specimens, observation of the

Figure 25. Possible explanation for akinete characteristics of N. armorica.

a. A simplified representation showing a chain of akinetes in side view, with filament not being horizontal with respect to slide surface.

b. If the filament were not horizontal, then a top view might show the ends of the akinetes visually overlapping to give the appearance of "discs" between the akinetes.

c.d. and e show "disc" areas between akinetes characteristic of N. armorica.

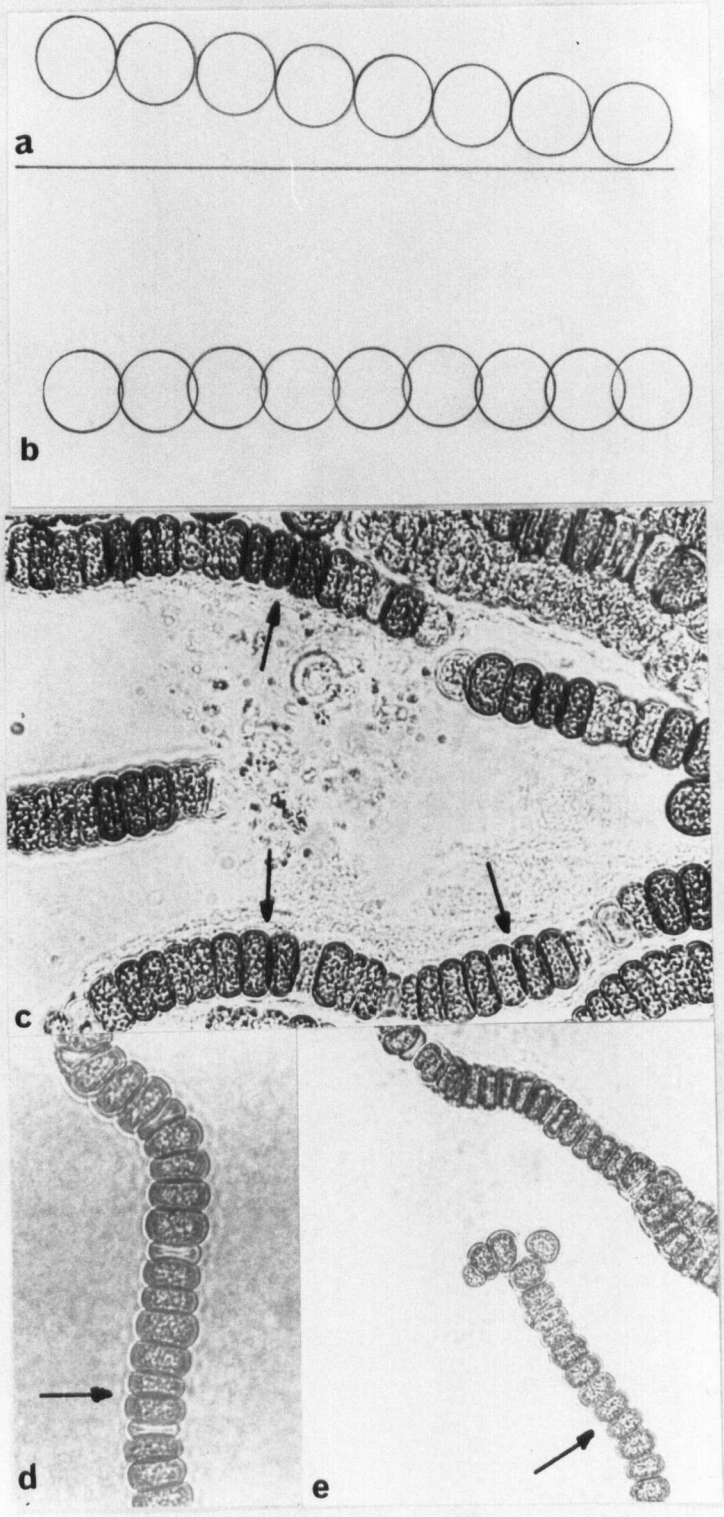
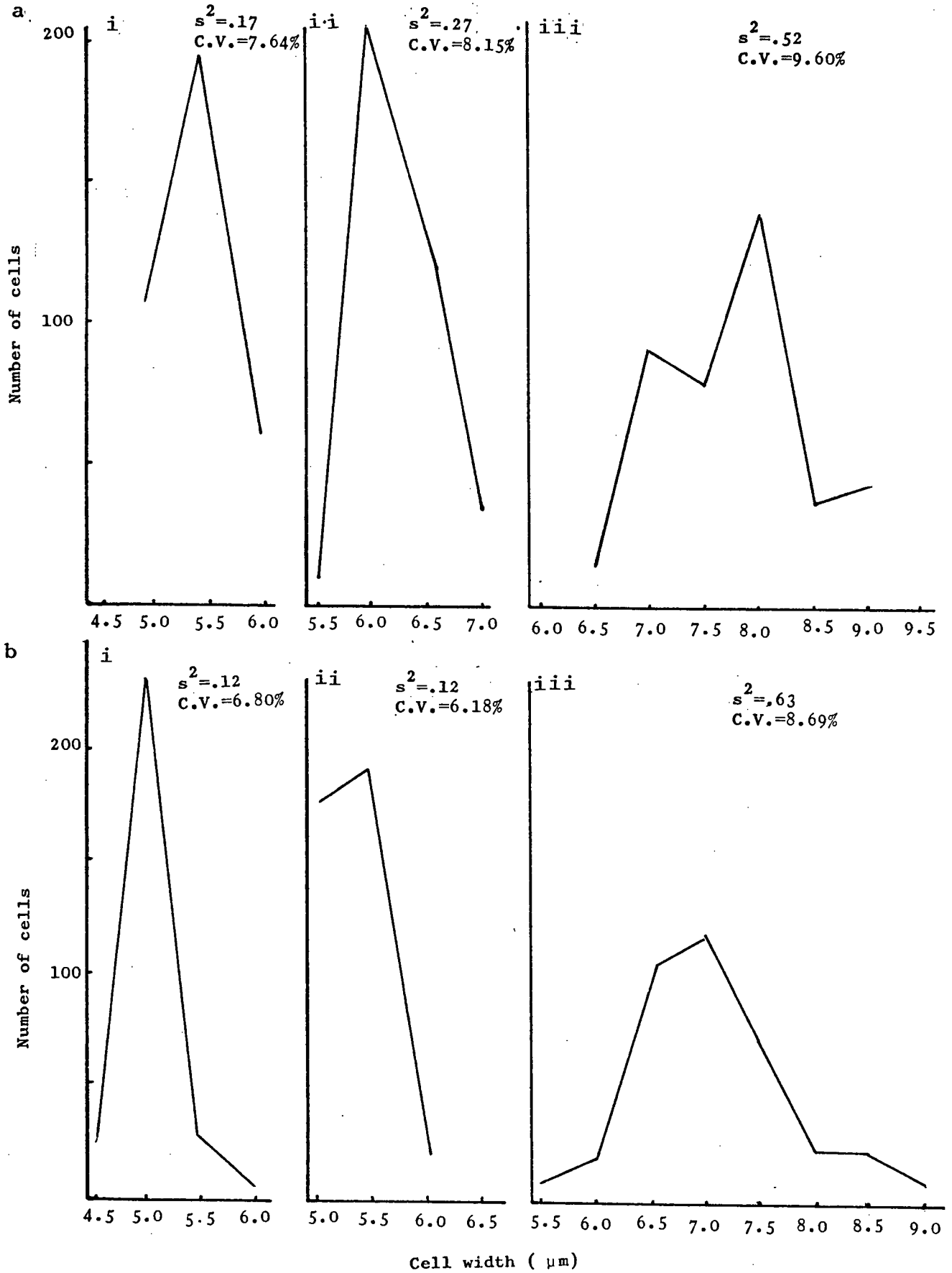

a
b
c
d
e

Figure 26. Comparison of the variability of size of vegetative cells, heterocysts and akinetes of two isolates under a variety of culture conditions.

Count of 20 random cells of each type under variations of pH (8,9,10), temperature (20 C, 25 C) and salinity (1.6 ^{o}/oo, 10°/oo, 20°/oo) n = 360.

a. isolate 7 (i) vegetative cells (ii) heterocysts (iii) akinetes.

b. isolate 3 (i) vegetative cells (ii heterocysts (iii) akinetes.


a
i
s^2=.17
C.V.=7.64%
i i
s^2=.27
C.V.=8.15%
i i i
s^2=.52
C.V.=9.60%
200
100
Number of cells
4.5 5.0 5.5 6.0
5.5 6.0 6.5 7.0
6.0 6.5 7.0 7.5 8.0 8.5 9.0 9.5
b
i
s^2=.12
C.V.=6.80%
ii
s^2=.12
C.V.=6.18%
iii
s^2=.63
C.V.=8.69%
200
100
Number of cells
4.5 5.0 5.5 6.0
5.0 5.5 6.0 6.5
5.5 6.0 6.5 7.0 7.5 8.0 8.5 9.0
Cell width (µm)

variability of several isolates under widely varying culture conditions and a large number of isolates in nature, indicates that there seems little justification for retention of varietal names of N. spumigena. The dimensions were artificially established (the choice is among 8-12 µm, 12-16 µm and 12-18 µm) and akinete shapes are very variable among a clonal population or on the same filament. Developmental stages of akinete formation encompass a variety of shapes during its maturation and categorizing the akinetes as subspherical, spherical-compressed and flattened-elliptical are valueless.

Validity of N. sphaerocarpa: The size and shape of akinetes, heterocysts and vegetative cells of herbarium specimens of N. harveyana and N. sphaerocarpa were compared. Habitat and collection sites were compared to see if habitat differences were significant. The results (Fig. 27) show there is a difference in size of cells of herbarium specimens, with N. harveyana generally being smaller. However, there is no separation into distinct groups, rather merely a gradation. There appears to be a difference in habitat with N. sphaerocarpa collected more frequently from the soil than N. harveyana. Of 68 collections of N. harveyana examined (identification according to collector) 32.3%, 54.4%, and 13.2% were from brackish-marine, "freshwater", and soil habitats respectively. Of 24 N. sphaerocarpa collections (species

Figure 27. Comparison of cell sizes of N. harveyana and N. sphaerocarpa.

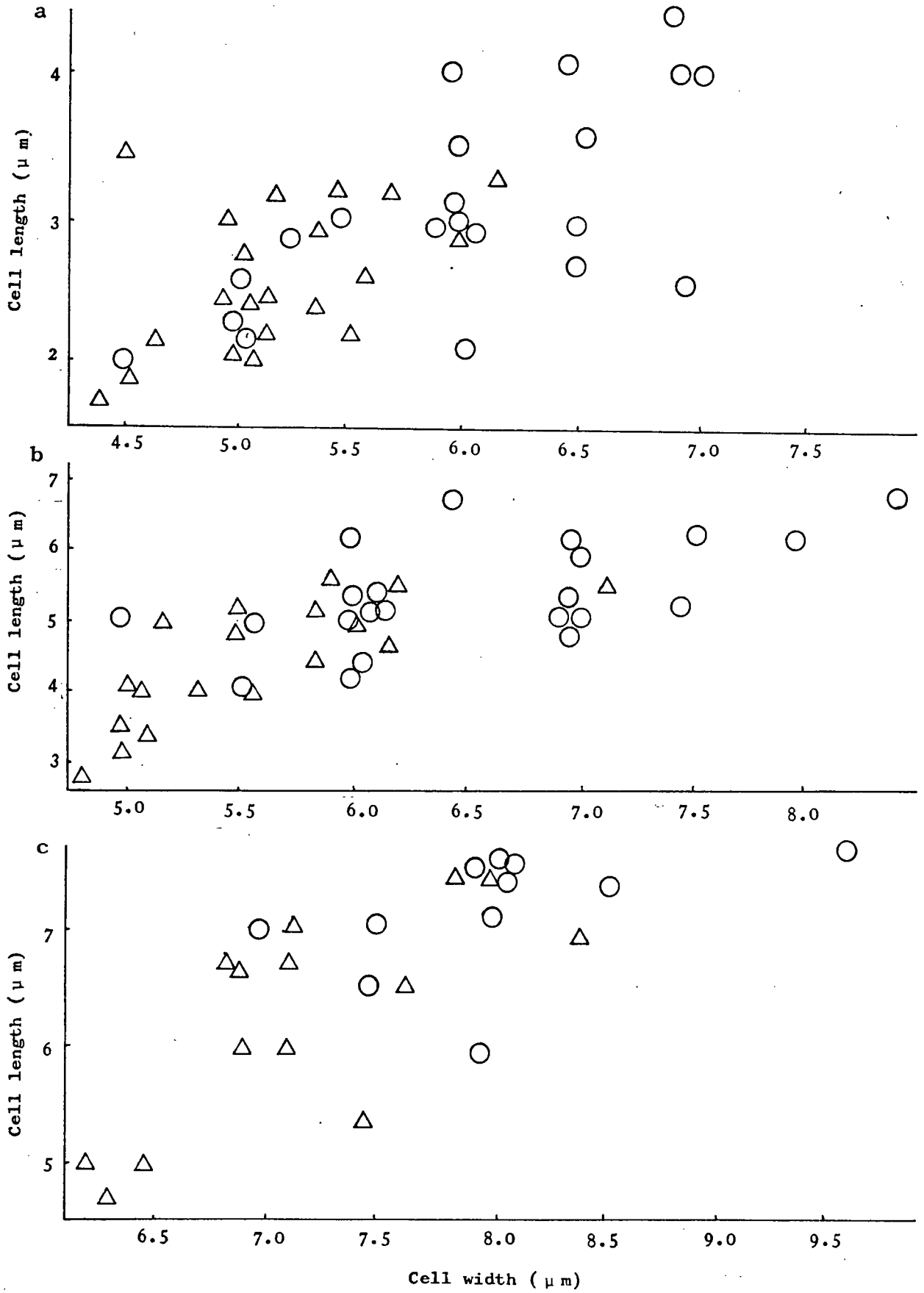
o N. sphaerocarpa (identification on herbarium sheet)

△ N. harveyana (identification on herbarium sheet)

a. vegetative cells

b. heterocysts

c. akinetes


a
b
c
Cell length (μm)
Cell length (μm)
Cell length (μm)
Cell width (μm)
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
2
3
4
5
6
7

identification according to original collector) the respective figures were 22.6%, 52.1% and 25.3%.

An interesting correlation from culture studies is that two of the three isolates identified as N. harveyana, when grown over a wide range of salinities (1-40 °/oo), show a positive correlation between salinity and akinete size (Fig. 28). The higher the salinity in which akinetes are formed, the larger their size. However the third isolate shows no such correlation. Thus, to make a distinction between N. harveyana and N. sphaerocarpa based on akinete size is hard to justify. These observations seem to support Elenkin's (1916) proposal of treating N. sphaerocarpa as that portion of N. harveyana with the largest dimensions.

Validity of N. harveyana and N. spumigena as distinct taxa: This was examined by observation of herbarium material, field collections and growth of material in the laboratory. Scattergrams from herbarium material of akinete, heterocyst and vegetative cell size show a separation into two distinct groups (Fig.29). This contrasts with the view of Bursa (1968) that only a single species of Nodularia should be considered. An obvious support for the maintenance of the two species is the fact that the two are often collected at the same time in the same place and are readily separable into two size classes.

Figure 28. Akinete variability of three British Columbia isolates as related to salinity.

a.	isolate 7	1.6‰ o	10‰△	20‰□
b.	isolate 5	1.6‰ o	10‰△	20‰□
c.	isolate 3	1.6‰ o	10‰△	20‰□

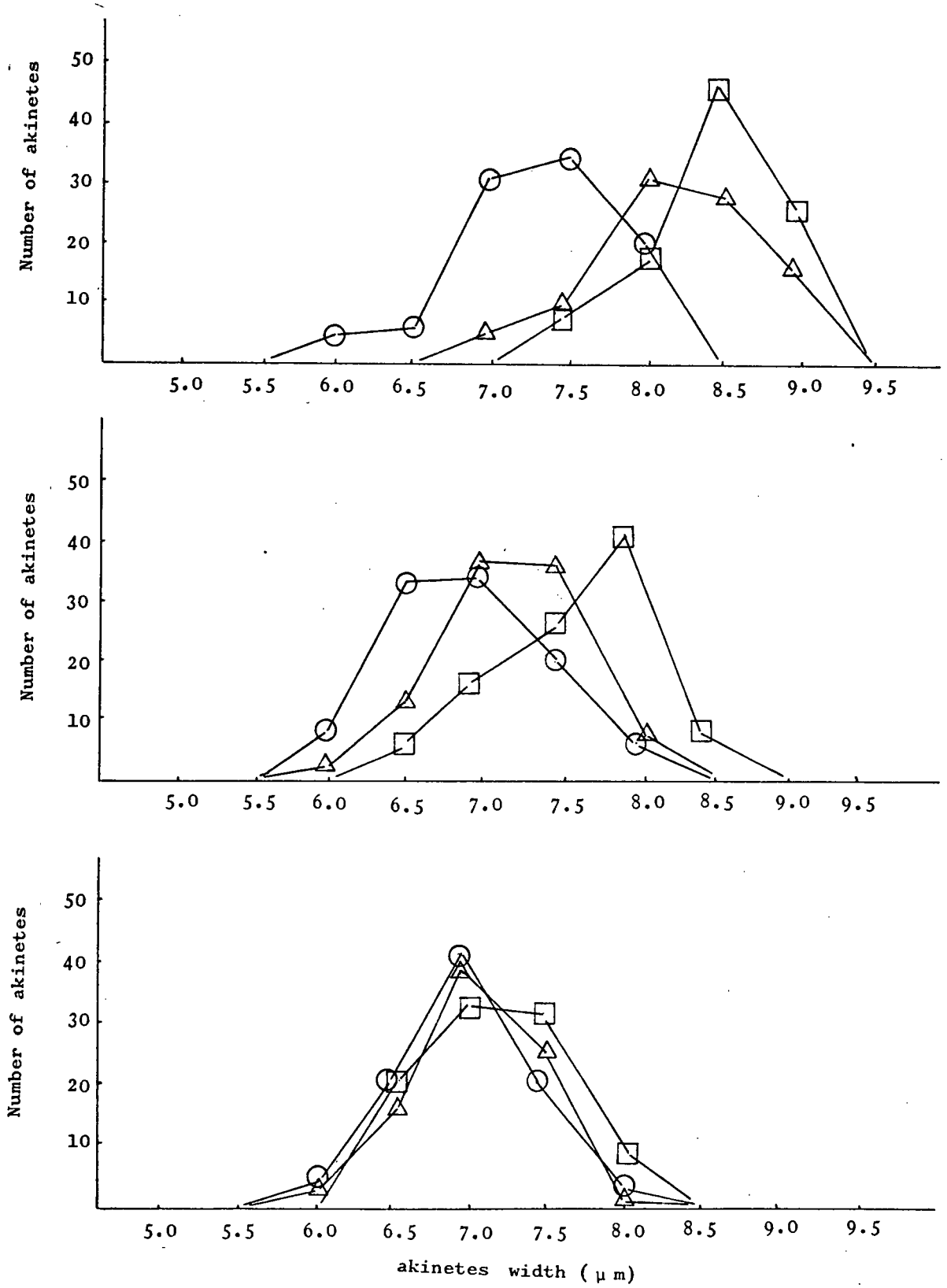

Number of akinetes
50
40
30
20
10
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
Number of akinetes
50
40
30
20
10
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
Number of akinetes
50
40
30
20
10
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
akinetes width (μm)

Figure 29. Comparison of cell sizes of *N. spumigena* and *N. harveyana*.

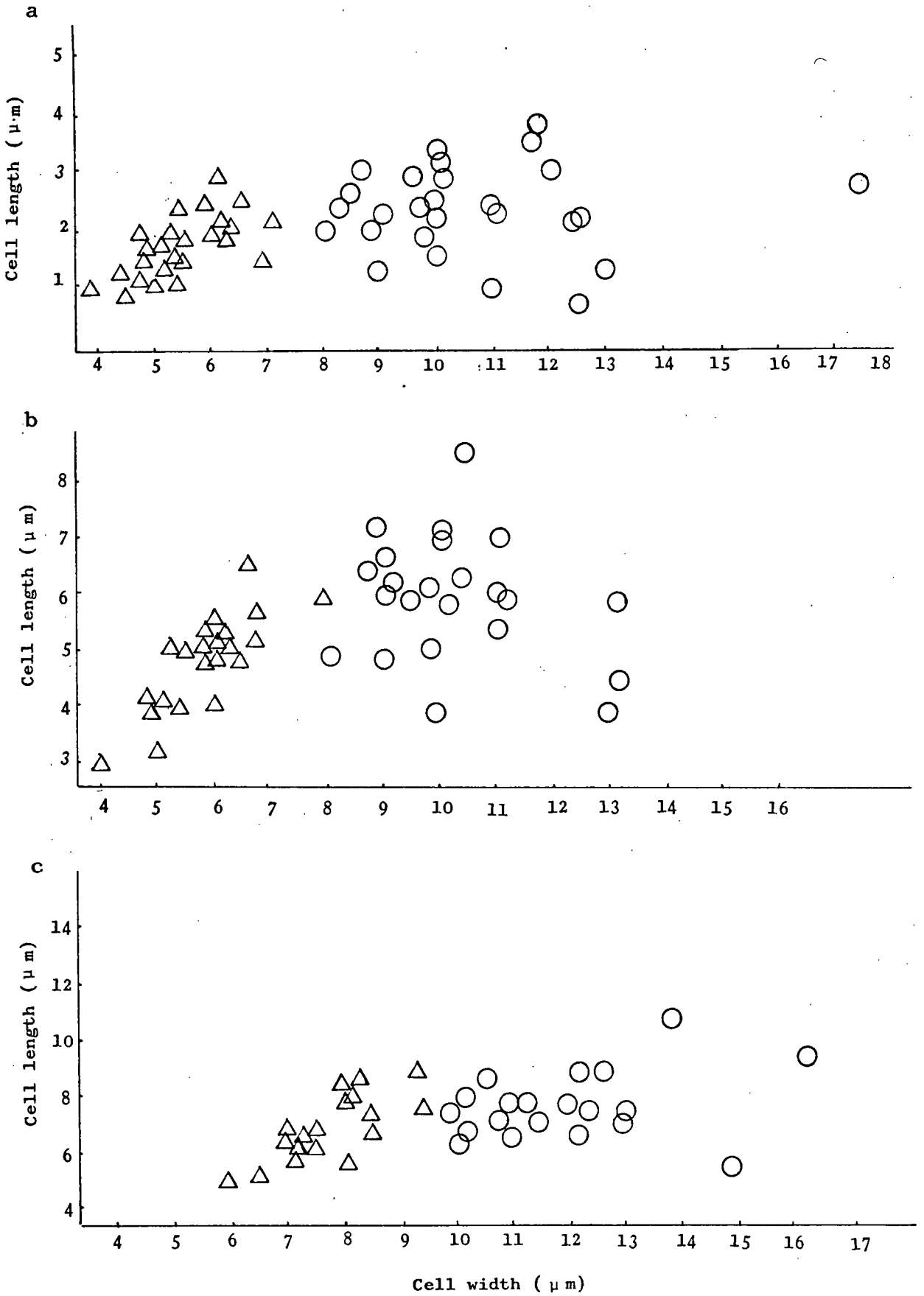
o *N. spumigena* (identification on herbarium sheet)

△ *N. harveyana* (identification on herbarium sheet)

a. vegetative cell size

b. heterocyst size

c. akinete size


a
Cell length (μm)
b
Cell length (μm)
c
Cell length (μm)
Cell width (μm)

One approach used to separate bluegreen algal taxa, that of growth patterns on agar plates (Kantz and Bold 1969, Baker and Bold 1970) proved completely unworkable. Isolates microscopically identical exhibited strikingly different growth characteristics, and recognizing different species or even genera in this manner proved impossible (Fig.30).

The herbarium material considered during this study is shown in Appendix, Table IX.

Thus the genus should contain only two species, N. harveyana (Thw.) Thuret and N. spumigena Mertens.

The genus is distinct and easily separable from other morphologically similar genera. Certain characteristics of the genus (cells being wider than long; regular spacing of the heterocysts; formation of akinete midway between the heterocysts) varied very little under the wide range of growth conditions. Other characteristics were quite variable (sheath presence; filament length; vegetative cell color; akinete shape, texture and color). An illustration of variability in the morphology of the genus is shown in Fig. 31 and 32.

From the investigation presented here an emendation of the generic and species description is as follows:

> Nodularia [Mertens in Juergens] Bornet and Flahault emend. Filaments with cells distinctly wider than long, heterocysts spaced at regular intervals along the trichome. Initiation and formation of akinetes midway between the heterocysts.

Fig. 30. Cultural variation of Nodularia.

Comparison of growth patterns of several isolates after two weeks growth on BG-11 1 % (W-V) agar at 20 C pH 8 and LL1. Identification numbers refer to isolate numbers. "IUCC 583" is a Calothrix sp. which has been mis-identified as Nodularia.

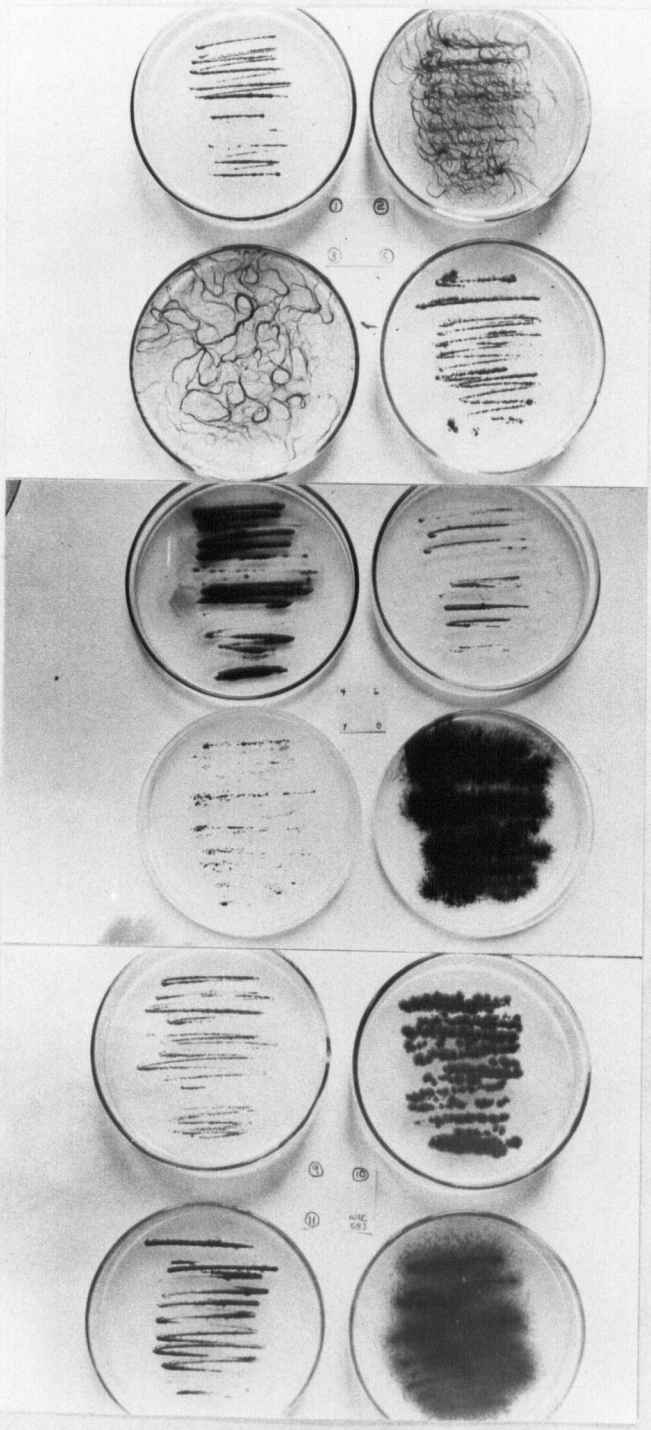


Figure 31. The morphological variation of N. spumigena.

a. from Fritsch 1951 x850, shows terminal and intercalary heterocysts, sheath and location of formation of akinetes.

b. from Bornet and Thuret 1880 x650, vegetative filament.

c. from Bornet and Thuret 1880 x650, filament with akinetes.

d. from Bornet and Thuret 1880 x650, their drawing of Merten's type material, shows a vegetative filament and a filament with a single isolated akinete.

e. from Bharadwaja 1935 x1370, vegetative filament and filament with akinetes.

f. from Playfair 1914 x800, vegetative filament and filament with immature akinetes.

g. from Prescott 1962 x900, vegetative filament and filament with akinetes.

a
b
c
d
e
f
g

Figure 32. The morphological variation of N. harveyana.

a. from Bornet and Thuret 1880 x650, vegetative filament.

b. from Harvey 1848 x250, filament with akinetes (drawing of type material).

c. from Smith 1950 x800, vegetative filament.

d. from Hortobagyi 1959 x1000, vegetative filament and filament with akinetes.

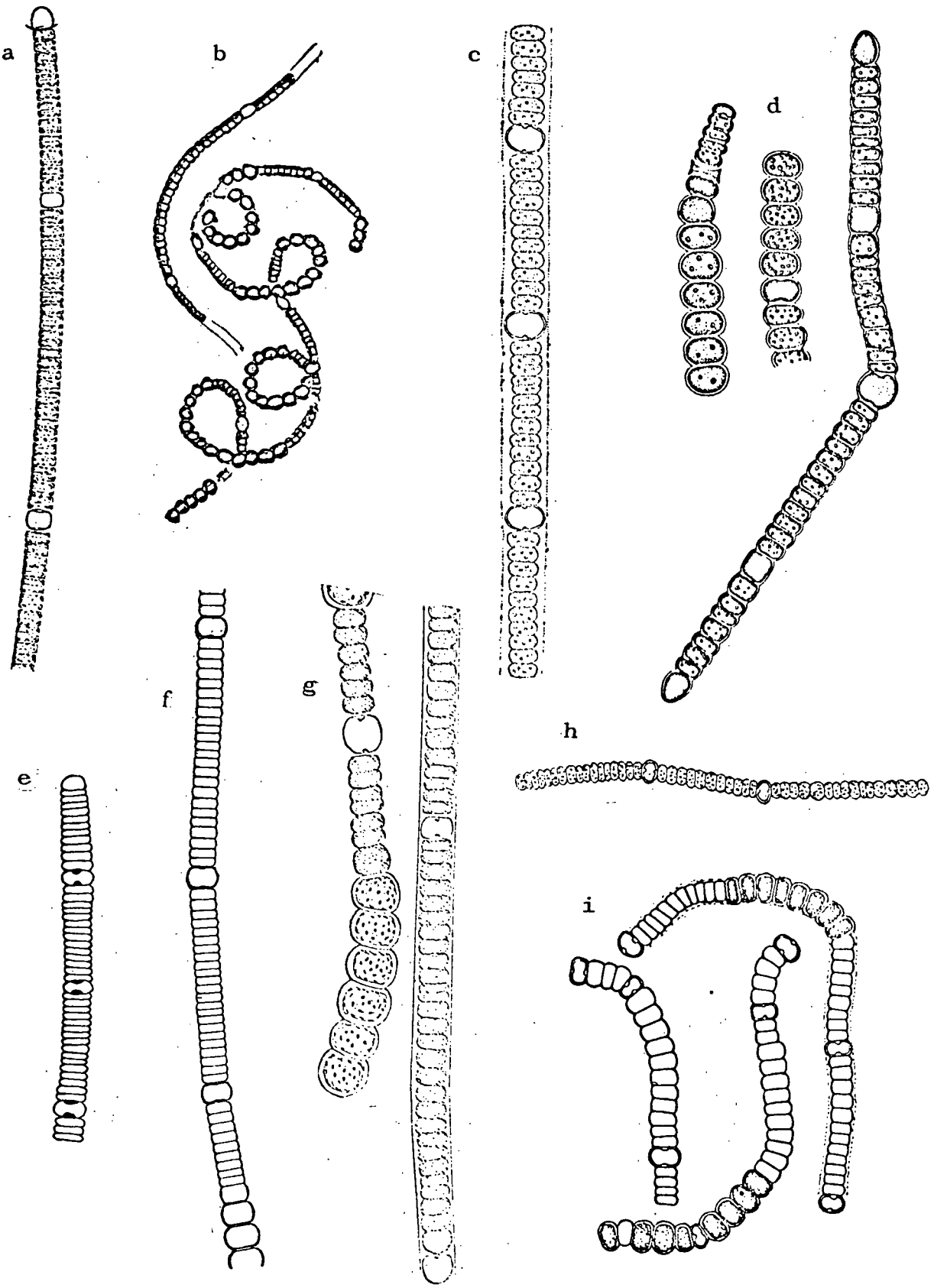
e. from Harding1971 x1000, vegetative filament.

f. from Geitler 1932 x900, vegetative filament.

g. from Mabille 1954 x1000, vegetative filament and filament with akinetes.

h. from Carter 1933 x613, vegetative filament.

i. from Skuja 1926 x820, filaments with immature and mature akinetes.


a
b
c
d
e
f
g
h
i

Vegetative cells 7.5-16.0 µm wide, width/length ratio 2:1 - 10:1; sometimes with gas vacuole. Heterocysts subspherical to disc-shaped; wider than long 8-16 µm wide, 2-10 µm long. Akinetes subspherical to disc-shaped; 8-18 µm wide, 6-15 µm long, usually in a series (occasionally single or in two's). Filaments usually with a thin colorless transparent sheath. Habitat tychoplankton or euplankton; marine, brackish, inland saline, or 'hard' freshwater. Temperate and subtropical in distribution.

N. spumigena [Mertens in Juergens] Bornet and Flahault emend.

Vegetative cells 3.5-7.2 µm wide; wider than long (except just before division when width and length may be equal); width/length ratio 2.5:1 - 1:1. Heterocysts subspherical (wider than long) to spherical; 4.0-7.5 µm wide. Akinete subspherical (wider than long) to spherical 4-9 µm wide, 4-8 µm long. Thin sheath may or may not be present. Habitat tychoplankton or benthic; marine, brackish or inland saline situations; occasionally in freshwater; also found on soil or in tree sap. Temperate and subtropical in distribution.

N. harveyana (Thw.) Thuret emend.

The synonomy of other taxa attributed to Nodularia are shown in Appendix, Table X.

DISCUSSION

Ecology and Physiology:

Few collectors have made quantitative measurements of the environment in which Nodularia spp. were collected and virtually no laboratory work has been done on them. Its occurrence in nature will be considered with reference to ecological observation, literature reports and growth studies in the laboratory.

Temperature: Nodularia was collected during this study at temperatures of 15-30 C. Reports in the literature give a wide range of values from 12.9-33 C (Francis 1878; West 1909; Brannon 1911; Sjostedt 1922; Dellow 1955; Woodson et al.1966; Proshkina-Lavrenko 1968; Toetz 1973). Temperature does not appear to limit growth in some cases since Sjostedt (1922) reports N. spumigena from the Baltic in bloom quantities at 12.9 C. However more typically large numbers occur at high temperatures (20-30 C). N. harveyana has been reported from "hot" springs (Danjoy in Bornet and Flahault 1888) or warm springs (Welch 1964) but no temperatures were given. The only instance in which the temperature of a "hot" spring was measured for any Nodularia collection is 26 C (Groesbeck F 1049304, Mono Co., California), and this is well below the maximum temperature of 30-35 C from laboratory studies (p.45).

The temperature for maximum growth for Nodularia spp. appears to be similar to some other Nostocaceae, i.e., Anabaena variabilis and Nostoc muscorum (Kratz and Meyers 1955a). The restriction of Nodularia to waters of less than 30 C may partially explain its absence from tropical areas.

Light: Light intensity values for growth of Nodularia both under field and laboratory conditions are difficult to assess. In the inland saline ponds, the shallow water and the white salt around the shoreline contribute to the high light intensity, but the light intensity is reduced by shading of other algae (Cladophora or Ctenocladus) and by turbidity of the water in some lakes. The only report of light intensity measured in the field with regard to Nodularia is that of Dellow and Cassie (1955) who describe algal zonation in a sea cave in New Zealand. They note that N. harveyana was restricted to an area with light intensity of 300-750 ft-c. This is the same range of light intensity (200-600 ft-c) which gave maximum growth rates in laboratory experiments (p.50). As in the field studies, difficulties are encountered in assessing the effect of light on bluegreen algal cultures. Because of shading the light intensity at a given distance from the light source is that received only by cells at the surface of the culture vessel. Cells in the center of the vessel receive less light. Some culture work involving bluegreen algae

(i.e. McLachlan and Gorham 1962) used very high light intensities (7500-9000 ft-c) to compensate for high cell densities used. In the growth experiments described previously (p.36) dilute inoculum was used, so that the light intensity differed only slightly from one side of the vessel to the other. The results show that Nodularia spp. grow under a relatively wide range of light intensities (25-600 ft-c) but maximum rates of growth were inhibited by light intensities as high as direct sunlight. Cultures grown with daylight as the energy source grew slower than any of the incubator grown cultures except at the very lowest light level (LL4).

pH: Published reports indicate that Nodularia has been collected where pH values range from 7.0-9.35 (Dellow 1955; Hortobagyi 1959; Bayly and Williams 1966; Serpette and Labbé 1966; Woodson et al. 1966; Ortega 1972; Plinski 1973). The genus is much more commonly reported from habitats of pH greater than 8, with the collections below pH 8 containing only small numbers of Nodularia. When large amounts are present, the pH is invariably above 8. During this study Nodularia was not collected at a pH of less than 8.2, although habitats from pH 5.2 to 10.0 were surveyed. This response to pH is also reflected in the laboratory studies. All isolates of Nodularia showed maximum growth rates at a pH greater than 9, with some isolates as high as 10.4. No growth

occured at pH 6 and very little at pH 7. The only reports of bluegreen algae showing maximum growth at a high pH (10) is by Gerloff et al. (1952) and McLachlan and Gorham (1962) with Microcystis aeruginosa.

Salinity: This aspect of the ecology of Nodularia is the most thoroughly documented quantitatively; however, many reports describe collections in much more general terms, i.e., "especially hard water" (Prescott 1962). In the present study Nodularia isolates were collected at salinities from 3-65 °/oo (Appendix, Tables II-VI). Literature reports show a wide range of salinities for collection of Nodularia, from 0.12-35.7 °/oo (Levander 1900; Moore 1917; Sjostedt 1922; Hutchinson et al. 1932; Trahms 1937; Rawson and Moore 1944; Dellow 1955; Rathsack-Kutzenbach 1961; Kalbe and Tiess 1964; Bayly and Williams 1966; Proshkina-Lavrenko 1968; Ortega 1972; Verch and Blinn 1972; Plinski 1973). Nodularia has been reported from waters with Na^{+} and Mg^{++} as dominant cations and Cl^{-}, HCO_3^{-}, $CO_3^{=}$ and $SO_4^{=}$ as dominant anions. There are no reports of Nodularia collections where the dominant ions are Ca^{++} or K^{+}. This may only reflect the fact that saline lakes of dominant Ca^{++} or K^{+} are uncommon on a world basis. Laboratory observations with different types of dominant ions (p.55) show that growth rate and salinity tolerance are not affected by the dominant anion or cation present.

The maximum level of salinity at which measurable growth occurs appears to be about 60 °/oo. Field observations showed that Nodularia was not present if the salinity rose above approximately 60 °/oo. In culture 60°/oo was the upper limit of growth for most isolates, although some were less tolerant. Hof and Frémy (1933) report that two isolates of Nodularia showed maximum tolerance of 47 °/oo and 58°/oo. On a gradient of salinity Nodularia grows best at 5-20 °/oo, reflecting the most common salinities in which it occurs in nature. Thus, technically the isolates were not "freshwater" organisms. Batterton and van Baalen (1971) noted different patterns of growth of freshwater and marine bluegreen isolates when grown on salinity gradients. The freshwater isolate grew best in the basal medium (1 °/oo) with growth declining with any additional salts. The marine isolates grew better at 10-20°/oo salinity (NaCl) than in the basal medium.

Nitrogen: There is little correlation of nitrogen source or levels with the presence or absence of Nodularia in nature. Sjostedt (1922) stated that the growth of Nodularia was enhanced by sewage outflows but presented no data to support this view. The laboratory results (p.55) show that all isolates grew as well with various levels of NO_3^- (0.25-1.0 g/l) as in medium lacking any combined nitrogen source. The inability of Nodularia to grow with NH_4^+ or urea as nitrogen

source is interesting, however the levels (0.5-1.0 g/l) may have been too high for growth, since the levels in nature are much lower (1.0-6.1 mg/l). Kratz and Meyers (1955a) report that Anabaena variabilis and Nostoc muscorum grew well on similar concentrations (0.5 g/l of NH_4 and urea) to those used with Nodularia in this study.

Stewart (1965) reported that Nodularia presumably fixed nitrogen but because the cultures were impure, definite proof was lacking. The present study shows that the two isolates tested fix nitrogen in pure culture and circumstantial evidence (growth in medium without combined nitrogen) was seen for the ability of the other isolates to fix nitrogen. The only data on the effect of environmental parameters on nitrogen fixation is that reported by Jones and Stewart (1969) for a marine Calothrix isolate. They reported highest rates of nitrogen fixation at 800 ft-c, at 30 C, with a salinity of 5 $^{o}/oo$ (but fixation took place at 1-50 $^{o}/oo$) and pH 8.5. Except for the pH figure these data are nearly identical with the results obtained with Nodularia (pH 10).

Considering the environmental parameters taken into account and laboratory observations made, some generalizations can be made regarding the biology of Nodularia. Salinity (and the related parameter of pH) is probably the most important aspect of the ecology of the genus. The algae, both

species, are typically found in brackish or saline waters (5-30 °/oo) and although they may occur in salinities lower or higher than these values they are usually present in much reduced amounts. Nodularia spp. also seem to tolerate sudden or gradual changes in salinity. This is evident from field observations (in the ponds in the British Columbia interior salinity rose from 15 to 65 °/oo in a few weeks) and laboratory studies (inoculum grown at 1 °/oo grew with only a short lag period when introduced into medium with dissolved salts of 40 °/oo). Some literature reports indicate Nodularia spp. live in conditions where marked salinity changes occur, such as seacoast pools where rainfall and surf alternately affect the salt content of water (Collins 1908 from Maine; Fjerdingstad 1969 from Denmark). Locations where Nodularia has been recorded in bloom quantities, which may be assumed to be favorable conditions (or near favorable), are in waters which are either brackish or saline. Bloom situations reported in the literature where salinity was recorded are Moore (1917) in Devils Lake, North Dakota at 9.5 °/oo; Sjostedt (1922) in the Baltic Sea at 14.5 °/oo; Hutchinson et al. (1932) in South Africa at 21 °/oo; Kalbe and Tiess (1964) from the Baltic Sea at 2.3-2.5 °/oo; and Bayly and Williams (1966) from Lake Corangamite, Australia at 29.1 °/oo. Early records of blooms do not state salinity values, but from the locations

it can be inferred that the waters were brackish: Francis (1878) the tidal Lake Alexandrina, South Australia; Bornet and Thuret at Deauville, France (cited in Sjostedt 1922); Bornet and Flahault (1888) cite bloom reports by Schmitz, Suhr and Hofman-Bang along the Baltic coast. Two blooms (Kalbe and Tiess 1964 on the German Baltic coast; Francis 1878) were toxic and resulted in death of livestock and poultry.

Light and temperature possibly play a lesser role than salinity and pH in controlling growth but a more important role in distribution. The absence of Nodularia spp. from tropical areas could be better explained in terms of light and temperature since Nodularia spp. are absent from inland saline lakes and brackish areas in the tropics. In tropical inland saline situations Arthospira or Spirulina are the dominant bluegreen algae (Armitage 1971; Jenkin 1932; Rich 1932). These two factors would be obvious differences between brackish or saline areas in temperate and tropical areas. Light is a difficult factor to measure in nature since turbidity of the water, shading by other plants, daylength and latitude all affect the amount of light received. The presence of Nodularia spp. at higher altitudes in the tropics indicates that temperature is possibly a more important factor than light.

Taxonomy:

There exists a problem with bluegreen algae in that the term "species" is not applicable in the same sense as in higher organisms since they are prokaryotes. The term has little significance in bluegreen algae other than it surrounds an arbitrary group of organisms with certain characteristics and possessing an undefined amount of variability. Knowledge of the variability is essential to the taxonomy. The variability within a certain "population" is more easily described than the variability among "populations" for bluegreen algae. A population is defined in the sense of a collection of individuals of one species living within a defined area or volume (Hutchinson 1967). The extent of variability in bluegreen algae has been of concern for many years (for example - Crow 1924; Canabaeus 1929; Drouet 1962, 1963; Fjerdingstad 1966, 1969) and without insight into this variability, a workable taxonomic scheme is impossible. It is also apparent observations of natural material is not sufficient and that cultural work is necessary for bluegreen algae (Komarek 1971).

The literature is an often neglected and misused aspect of study. A great deal of data (on variability, ecology, distribution) can be obtained from the accumulated observations of many workers. The literature is misused in the sense that the taxonomic confusion is increased by new species

or variety descriptions with little justification. Also, Nodularia species have been described without type material being retained, or described with incomplete material (without akinetes), or with inadequate material (e.g. N. spumigena var. aerophila, p.80 was described from a single filament lacking akinetes). Another similar problem is improper identification of isolates used in physiological and biochemical investigations. The problem with Anacystis nidulans has already been mentioned (p.1). For example, the strain 11.1.1 of "Nodularia sphaerocarpa" isolated by M.B. Allen and identified by Drouet is evidently not a Nodularia. Material from this original culture (F Nordin 1181) as well as cultures from Indiana University Culture Collection (#583) and the culture collection at the Department of Bacteriology and Immunology Berkeley California (strain 7103) derived from the original culture, were examined. The material shows terminal heterocysts and basal differentiation characteristics of the Rivulariaceae and is a Calothrix sp. This same conclusion was also reached by Kenyon et al. (1972) studying strain 7103. The same isolate (N. sphaerocarpa) has been used in investigations by Edelman et al. (1967), Gorham (1960) and Gorham (1964). The Nodularia sphaerocarpa, (Culture B-1466) in the Gottingen collection is also a subculture of Allen's isolate (Koch 1964). Granhall and Hendrickson (1969)

isolated an alga which they identified as N. spumigena. A subculture of this isolate was examined and has the characteristics of a N. harveyana with filaments 5 μm wide. The isolate using this incorrect specific name was also cited by Granhall and Berg (1972).

The genus Nodularia appears to be a fairly stable taxon morphologically. Studies with other bluegreen algae indicate that generic characteristics may vary and material may have the characteristics of two different genera under different culture conditions (Stein 1963; Pearson and Kingsbury 1966). Certain characteristics of Nodularia vary little under the wide range of growth conditions used (light, temperature, pH, salinity). The cells are always wider than long (except in N. harveyana prior to cell division). The heterocysts are regularly spaced along the filament and fairly close together (every 20-30 cells), a characteristic emphasized by both Thuret (1875) and Fritsch (1951). The akinetes are formed midway between the heterocysts and mature from the center of the trichome towards the heterocyst. Again this characteristic is described in detail by Fritsch (1951).

However other morphological characteristics are variable. The sheath is usually present in field material (more so N. spumigena than N. harveyana); but it is not always present and in culture the presence of the sheath is even more variable,

being absent much more of the time. Foerster (1964) cites Ca^{++} and Mg^{++} hardness as a factor in sheath formation in Oscillatoria limosa (Roth) C.A. Ag. Filament length varies a great deal. In nature filaments may vary from a few dozen cells to several hundred. The latter condition is more prevalent in culture. Vegetative cell color varies a great deal both in nature and in culture. The color is typically a bright blue-green but may be brown, light green or blue.

The akinete as previously mentioned is very variable. Because akinetes are formed from vegetative cells, there are a variety of stages in formation; size, shape, color and texture all depend upon the maturity of the akinete. The size was the only aspect which could be correlated with any physical or chemical parameter.

The multiplicity of species of Nodularia in the literature appears to be more a result of poor judgement in the naming of species and misunderstanding the extent of variability, than any extreme plasticity of the organism. The aptness of generic distinctions of many Cyanophyta (especially the Oscillatoriaceae sensu Geitler) has been questioned (Drouet 1968; Bourelly 1970). Whitton (1962) in evaluating the taxonomic criteria for several bluegreen algae commented that Cylindrospermum species represented a distinct grouping of forms; whereas, Anabaena was a very amorphous group and that genera in the

Oscillatoriaceae were very arbitrary. Nodularia, thus appears to be similar to Cylindrospermum in its distinctiveness. Thus it must be emphasized that the stability and distinctness of the taxa depend to a great extent on selecting the proper taxonomic criteria.

LITERATURE CITED

Ackley, A.B. 1931. Preliminary report of Michigan algae. Mich. Acad. Sci. Art. Let. 15: 1-49.

Ali, S. and Sandhu, G.R. 1972. Blue-green algae of the saline soils of the Punjab. Oikos 23: 268-272.

Allen, M.M. 1973. Methods for Cyanophyceae. In Stein, J.R., ed., Handbook of Phycological Methods Cambridge University Press, Cambridge 448 pp.

American Public Health Association. 1965. Standard Methods for the Examination of Water and Sewage. 12th. ed. A.P.H.A. New York. 769 pp.

Anagnostidis, K. and Schwade, G.H. 1966. Über artenreiche Bestände von Cyanophyten und Bacteriophyten in einem Farbstreifen sandwatt sowie über das Auftreten Gomontiella-Artig deformierter Oscillatoria trichome. Nova Hedwigia 11: 417-441.

Anderson, E.M. and Walker, E.R. 1920 An ecological study of the algae of some sandhill lakes. Trans. Amer. Miscrosc. Soc. 39: 51-85.

Armitage, K.B. 1971. A highly alkaline lake in Nicaragua. Hydrobiologia 38: 437-439.

Arndt, E.A., Pankow, H. and Kell, V. 1966. Über das Phytoplankton der Wismar-Bucht. Int. Rev. ges. Hydrobiol. Hydrogr. 51: 127-146.

Bajkov, A.D. 1935. The plankton of Lake Winnipeg drainage system. Int. Rev. ges. Hydrobiol. Hydrogr. 31: 239-272.

Baker, A.F. and Bold, H.C. 1970. Phycological studies. X. Taxonomic studies in the Oscillatoriaceae. Univ. Texas Publ. No. 7004, Austin. 105 pp.

Bandel, W. 1940. Phytoplankton- und Nährstoffgehalt der Ostsee im Gebiet der Darsser Schwelle. Int. Rev. ges. Hydrobiol. Hydrogr. 40: 249-304.

Batterton, J.C., Jr. and Van Baalen, C. 1971. Growth responses of blue-green algae to sodium chloride concentration. Arch. Mikrobiol. 76: 151-165.

Bayly, I.A.E. and Williams, W.D. 1966. Chemical and biological studies on some saline lakes of Southwest Australia. Aust. J. Mar. Freshwat. Res. 17: 177-228.

Bharadwaja, Y. 1935. The Myxophyceae of the United Provinces of India -I. Proc. India. Acad. Sci. B. 2: 95-107.

Blinn, D.W. 1969. Autecology of Ctenocladus (Chlorophyceae) in saline environments. Ph. D. Dissertation. University of British Columbia. 135 pp.

Blinn, D.W. 1971. Dynamics of major ions in some permanent and semi-permanent saline systems. Hydrobiologia 38: 225-238.

Borge, O. 1901. Süsswasseralgen aus Süd-Patogonien. Bih. Longl. Sv. Vet.-Akad. 27(Afd. 3, No. 10): 1-40.

Borge, O. 1907. Beiträge zue Algenflora von Schweden. Ark. Bot. 6(1):1-88.

Borge, O. 1907a. Algen aus Argentina und Bolivia. Ark. Bot. 6(4): 1-13.

Børgesen, F. 1901. Freshwater Algae, Part I. In Warming, E., ed., Botany of the Faeröes. John Weldon & Co., London. pp. 198-259.

Bornet, E. and Flahault, C. 1886-88. Revision des Nostocacées heterocystées. Ann. Sci. Nat. Bot. 5(19): 314-332, 7(3): 323-381, 7(4): 343-373, 7(5): 51-129, 7(7): 177-262.

Bornet, E. and Thuret, G.A. 1880. Notes Algologiques. Fasc II. G. Masson, Paris. pp. 121-122.

Bourrelly, P. 1970. Les Algues d'Eau Douce. III. Les Algues Bleues et Rouges ,Eugléniens, Peridiniens et Cryptomonadins. N. Boubée & Cie, Paris. 512 pp.

Brabez, R. 1941. Zur Kenntis der Algenflora des Franzenbader und Sooser Thermenbereiches. Beih. Bot. Zentr. 61A: 137-236.

Brannon, M.A. 1911. Factors influencing the flora of Devils Lake, North Dakota. Int. Rev. ges. Hydrobiol. Hydrogr. 4: 291-299.

Brannon, M.A. 1952. Some Myxophyceae in Florida. Quart. J. Florida Acad. Sci. 15: 70-78.

Briquet, J. 1935. International Rules of Botanical Nomenclature. Dritte Asgabe, Jena. 152 pp.

Bristol, B.M. 1919. On the retention of vitality by algae. New Phytol. 18: 92-107.

Bristol, B.M. 1920. On the algal-flora of some dessicated English soils. Ann. Bot. 24: 34-80.

Brock, T.D. 1973. Evolutionary and ecological aspects of the Cyanophytes. In Carr, N.G. and Whitton, B.A., ed., Biology of the Blue-green Algae. Univ. California Press, Berkeley pp. 487-500.

Burr, A.H. and Duncan, M.J. 1972. Portable spectroradiometer for underwater environments. Limnol. Oceanogr. 17: 466-475.

Bursa, A.S. 1968. Epicenoses on Nodularia spumigena Mertens in the Baltic Sea. Acta Hydrobiol. 10: 267-297.

Cameron, R.E. 1963. Algae of southern Arizona I. Introduction - blue-green algae. Rev. Algol. n.s. 6: 282-318.

Canabaeus, L. 1929. Über die Heterocysten und Gasvakuolen der Blaualgen und ihre Beziehungen zueinander. In Kolkwitz, R., ed., Pflanzenforschung, vol. 13. Dahlem, Berlin. 48 pp.

Canada Department of Transport. 1947. Meteorological Division. Climatic summary for selected meterological stations in the Dominion of Canada. Volume I 105 pp. Toronto Ontario.

Carter, N. 1933. Algal flora of two salt marshes. J. Ecol. 21: 128-208.

Cedercreutz, C. 1934. Die Algenflora und Algenvegation auf Aland. Acta. Bot. Fenn. 15: 1-120.

Cedergren, G.R. 1926. Beiträge zue Kenntnis der Susswasseralgen in Schweden. Bot. Notis. 1926: 289-319.

Chacko, P.I. 1972. Blue-green algae of fish ponds. In Desikachary, T.V., ed., Taxonomy and Biology of Blue-green Algae. Univ. Madras. pp.448-454.

Chapman, V.J. 1940. Studies in salt-marsh ecology. J. Ecol. 28: 118-152.

Chapman, V.J. 1955. Revision of the marine algae of New Zealand. Part I - Myxophyceae and Chlorophyceae. J. Linn. Soc. Bot. 55: 333-501.

Clements, F.E. 1896. Additions to the reported flora of the state. Nebraska Univ. Bot. Sem. 1892-1904. Reports of Collections made in 1894-1895. 4: 24-48.

Clements, F.E. 1901. Report on recent collections. Additions to the reported flora of the state. Univ. Nebraska Bot. Surv. 5: 12-27.

Cleve, P.T. 1897. A treatise on the phytoplankton of the Atlantic and its tributaries and on the periodical changes of the plankton of the Skagerak. Upsala.

Cocke, E.C. 1949. The Myxophyceae of North Carolina. J. Elisha Mitchell Soc. 65: 71-89.

Cocke, E. 1967. Myxophyceae of North Carolina. Edwards Bros., Ann Arbor, Michigan. 206 pp.

Collins, F.S. 1884. Notes on New England marine algae IV. Bull. Torrey Bot. Club 11: 130-132.

Collins, F.S. 1900. Preliminary list of New England plants. V. Marine algae. Rhodora 2: 41-52.

Collins, F.S. 1905. Phycological notes of the late Isaac Holden, II. Rhodora 7: 222-243.

Collins, F.S. 1908. Notes on algae IX. Rhodora 10: 155-164.

Coyle, E.E. 1930. The algal food of Pimephales promelas. Ohio J. Sci. 30: 23-35.

Cramer, C. 1860. Über Spermosira turicensis Cramer and Scytonema gracile Kütz. Hedwigia 2: 39.

Croasdale, H. 1973. Freshwater algae of Ellesmere Island, N.W.T. Nat. Mus. Canada, Ottawa. Publ. Bot. No. 3. 131 pp.

Crow, W.B. 1924. Variation and species in Cyanophyceae. J. Genet. 14: 397-424.

Dawson, E.Y. 1966. Marine Botany. Holt, Rinehart and Winston, New York. 371 pp.

Debray, F. 1893. Liste des algues marines et d'eau douce recoltees jusqu'a ce jour en Algerie. Bull. Sci. Fr. Belg. 25: 174-192.

DeHalperin, D.R. 1970. Cianoficeas marinas del Chubut (Argentina). I. Golfo San Jose Galfo Nuevo y Alfrededores de Rawson. Physis 30: 33-96.

Dellow, V. 1955. Marine algal ecology of Hauraki Gulf, New Zealand. Trans. Roy. Soc. New Zealand 83: 1-91.

Dellow, V. and Cassie, R.M. 1955. Littoral zonation in two caves in the Auckland district. Trans. Roy. Soc. New Zealand 83: 321-331.

Desikachary, T.V. 1959. Cyanophyta. Indian Couns. Agr. Res., New Delhi. 686 pp.

Desikachary, T.V. 1970. Taxonomy of blue-green algae - problems and prospects. Schweiz. Z. Hydrol. 32: 490-494.

Dickie, G. 1871. Notes on some algae found in the North Atlantic Ocean. J. Linn. Soc. Bot. 11:456-459.

Drouet, F. 1935. Some Myxophyceae from Nantucket Island Massachusetts Rhodora. 40: 74-76.

Drouet, F. 1937. The Brazilian Myxophyceae I. Amer. J. Bot. 24: 598-608.

Drouet, F. 1938. The Brazilian Myxophyceae II. Amer. J. Bot. 25: 657-666.

Drouet, F. 1938a. Notes on Myxophyceae I-IV. Bull. Torrey Bot. Club 65: 285-292.

Drouet, F. 1939. Myxophyceae of Maryland. Field Mus. Nat. Hist. Bot. Ser. 20: 3-14.

Drouet, F. 1939a. Francis Wolle's filamentous Myxophyceae. Field Mus. Nat. Hist. Bot. Ser. 20: 15-64.

Drouet, F. 1943. Myxophyceae of Eastern California and Western Nevada. Field Mus. Nat. Hist. Bot. Ser. 20: 143-176.

Drouet, F. 1956. Preliminary studies of the algae of Northwest Minnesota. Proc. Minn. Acad. Sci. 22: 116-138.

Drouet, F. 1962. Gomont's ecophenes of the blue-green alga, Microcoleus vaginatus (Oscillatoriaceae). Proc. Acad. Nat. Sci., Philadelphia. 114: 191-205.

Drouet, F. 1963. Ecophenes of Schizothrix calicola (Oscillatoriaceae). Proc. Acad. Nat. Sci., Philadelphia. 115: 261-281.

Drouet, F. 1968. Revision of the classification of the Oscillatoriaceae. Monogr. Acad. Nat. Sci., Philadelphia. 16: 1-341.

Drouet, F. and Daily, W.A. 1956. Revision of the coccoid Myxophyceae. Butler Univ. Bot. Stud. 10: 1-218.

Edelman, M., Swinton, D., Schiff, J.A., Epstein, H.T. and Zeldin, B. 1967. Deoxyribonucleic acid of the blue-green algae (Cyanophyta). Bact. Rev. 31: 315-331.

Elenkin, A.A. 1916. Note sur Nodularia harveyana (Thwaites) Thuret et sur quelques autres espèces de ce genre. Bull. Jardin Imp. Bot. Pierre Grand 16: 325-332.

Elenkin, A.A. 1916a. Note sur le genre Nodularia Mertens suivie de la recherche critique sur la famille Nodulariaceae mihi. Bull. Jardin Imp. Bot. Pierre Grand 16: 333-344.

Fairchild, E.D. and Willson, D.L. 1967. The algal flora of two Washington soils. Ecology 48: 1053-1055.

Farlow, W.G. 1881. The marine algae of New England. Rep. U.S. Comm. Fish. 1879. Government Printing Office, Washington. 210 pp.

Fjerdingstad, E. 1966. Cell dimensions of some numbers of Aphanizomenon Morren. Scheiz. Z. Hydrol. 28: 133-147.

Fjerdingstad, E. 1969. Cell dimensions and taxonomy of Anabaena variabilis Kütz. emend. Schweiz Z. Hydrol. 31: 59-80.

Foerster, J.W. 1964. The use of calcium and magnesium hardness ions to stimulate sheath formation in Oscillatoria limosa (Roth) C.A. Ag. Trans. Amer. Micros. Soc. 83: 420-427.

Forti, A. 1907. Myxophyceae. In DeToni, J.B. ed., Sylloge Algarum, Vol. 5. J.B. DeToni, Padua. 761 pp.

Francis, G. 1878. Poisonous australian lake. Nature 18: 11-12.

Franklin, T. 1972. Blue-green algae of some tropical reservoirs of South India. In Desikachary, T.V., ed., Taxonomy and Biology of Blue-green Algae. Univ. Madras pp. 442-447.

Frémy, P. 1929. Les Myxophycées de l'Afrique Équatoriale Français. Arch. Bot. Caen 3(2): 1-508.

Frémy, P. 1929a. Les Nostocacées de la Normandie. Not. mem. doc. publ. soc. d'Agr. d'Arch. et d'Hist. Nat. Dept. Manche, Saint Lo 41: 197-228.

Frémy, P. 1934. Cyanophycées des côtes d'Europe. Mém. Soc. Nat. Sci. Cherbourg. 41: 1-235.

Frémy, P. and Meslin, R. 1924. Excursion botanique dans la lande de la Meaffe (Manche). Bull. Soc. Linn., Normandie. 7(Ser. 9): 117-130.

Fritsch, F.E. 1912. Freshwater algae. In National Antarctic Expedition Natural History. 6: 1-66.

Fritsch, F.E. 1918. Contributions to our knowledge of the freshwater algae of Africa. Ann. S. Africa, Mus. 9: 483-611.

Fritsch, F.E. 1945. The Structure and Reproduction of the algae. Vol. II. Cambridge Univ. Press, Cambridge 939 pp.

Fritsch, F.E. 1951. The heterocyst: a botanical enigma. Proc. Linn. Soc. London 162: 194-211.

Fritsch, F.E., 1964. Collections of illustrations of algae at Freshwater Biological Association, Ambleside England. On microcards published by International Documentation Center, Tumba Sweden.

Fritsch, F.E. and Rich, F. 1929. Contributions to our knowledge of the freshwater algae of Africa. Trans. Roy. Soc. S. Africa 18: 1-92.

Fukushima, H. 1959. General report on fauna and flora of the Ongul Island Antarctica especially on freshwater algae. J. Yokohama Mun. Univ., ser. C-31, 112: 1-10.

Gardner, N.L. 1927. Myxophyceae of Porto Rico. Mem. New York Bot. Gard. 7: 1-144.

Geitler, L. 1932. Cyanophyceae, vol. 14. In Rabenhorst, L., Kryptogamen-Flora von Deutschland, Österreich und der Schweiz. Acad. Verlagsgesellschaft. Leipzig. 1196 pp.

Geitler, L. 1942. Schizophyta: Klasse Schizophyceae. In Engler, A. and Prantl, K., ed., Die Natürlichen Pflanzenfamilien, 2nd. ed. Ib. W. Englemann, Leipzig. 232 pp.

Gerloff, G.C., Fitzgerald, G.P. and Skoog, F. 1952. The mineral nutrition of Microcystis aeruginosa. Am. J. Bot. 39: 26-31.

Gier, L.J. and Johnson, M. 1954. Algae of Missouri. Trans. Kansas Acad. Sci. 57: 78-80.

Golubic, S. 1961. Entwurf zu einem ökologischen System der Blaualgen. Schweiz. Z. Hydrol. 23: 211-213.

Gonzales-Guerrero, P. 1928. Más datos ficologicos de aqua dulce. Bol. Real. Soc. Espan. Hist. Nat. 28: 435-438.

Gonzales-Guerrero, P. 1930. Algas del rio Zujar (Badajoz). Bol. Real. Soc. Espan. Hist. Nat. 30: 223-227.

Gorham, P.R. 1960. Toxic waterblooms of blue-green algae. Can. Vet. J. 1: 235-245.

Gorham, P.R. 1964. Toxic algae. In Jackson, D.F., ed., Algae and Man. Plenum Press, New York. pp. 307-336.

Granhall, V. and Berg, B. 1972. Antimicrobial effects of Cellvibrio on blue-green algae. Arch. Microbiol. 84: 234-242.

Granhall, V. and Henriksson, E. 1969. Nitrogen fixing blue-green algae in swedish soils. Oikos 20: 175-178.

Grove, W.B., Bristol, B.M. and Carter, N. 1920. The flagellates and algae of the district around Birmingham. J. Bot. 58(supp. III): 1-55.

Guarrera, S.A. and Kühnemann, O. 1949. Catalogo de los "Chlorophyta" y "Cyanophyta" de agua dulce del Republic Argentina. Lilloa n.s. 19(3): 219-318.

Hansgirg, A. 1892. Prodromus der Algenflora von Böhmen, II. Archiv f. Natur. Landes von Böhm (Bot. Abth.) 8: 1-268.

Harding, W.J. 1971. The algae of Utah Lake II. Great Basin Nat. 31: 125-134.

Harvey, F.L. 1889. The fresh water algae of Maine, II. Bull. Torrey Bot. Club. 16: 181-188.

Harvey, W.H. 1846-1851. Phycologia Brittania, London. 4 vols.

Hoek, C van den, Colijn, F., Øortel-Breeman, A.M. and Wanders, J.B.W. 1972. Algal vegetative-types along the shores of inner bays and lagoons of Curaçao, and of the Lagoon Lac (Bonaire), Netherlands Antilles. Akad. Wetenschappen Kon. 61: 1-72.

Hof, T. and Frémy, P. 1933. On Myxophyceae living in strong brines. Rec. Trav. Bot. Neer. 30: 140-162.

Hortobagyi, T. 1959. Adatok Magyarország Moszataihoz IV. Az egri Pedagogiai Föiskola Füzetei 183: 359-391.

Holm-Hanson, O. 1964. Isolation and culture of terrestial and fresh-water algae of Antarctica. Phycologia 4: 43-51.

Hughes, E.O., Gorham, P.R. and Zehnder, A. 1958. Toxicity of a unialgal culture of Microcystis aeruginosa. Can. J. Microbiol. 4: 225-236.

Hutchinson, G.E. 1967. A Treatise on Limnology. Vol.II. John Wiley & Sons, New York. 1115 pp.

Hutchinson, G.E., Pickford, G.E. and Schuurman, J.F.M. 1932. A contribution to the hydrobiology of pans and other inland waters of South Africa. Arch. Hydrobiol. 24: 1-154.

Iyengar, M.O.P. and Desikachary, T.V. 1944. A systematic account of some marine Myxophyceae of the south coast of India. J. Madras Univ. 16(Sect. B): 37-63.

Jabotinsky, A. 1961. Sudden increase of the plankton in the Zohar Reservoir. Bull. Res. Counc. Israel. 10D: 84-89.

Jenkin, P.M. 1932. Reports on the Percy Sladen Expedition to some Rift Valley lakes in Kenya in 1929. I. Introductory account of the biological survey of freshwater and alkaline lakes. Ann. Mag. Nat. Hist., ser. 10. 9: 533-552.

Jones, K. and Stewart, W.D.P. 1969. Nitrogen turnover in marine and brackish habitats III. The production of extracellular nitrogen by Calothrix scopulorum. J. Mar. Biol. Ass. U.K. 49: 475-488.

Jutono 1973. Bluegreen algae in rice soils of Jugjakarta, central Java. Soil Biol. Biochem. 5: 91-95.

Kalbe, L. and Tiess, B. 1964. Entenmassensterben durch Nodularia - wasserblute am Kleinen Jasmunder Bodden auf Rügen. Arch. Exp. Vet. Med. 18: 535-555.

Kamat, N.D. 1968. Algae of Alibag, Maharashtra. J. Bombay Nat. Hist. Soc. 65: 88-104.

Kann, E. and Komarek, J. 1971. Systematisch-ökologische Bemerkungen zu den Arten des Formenkreises Phormidium autumale. Schweiz. Z. Hydrol. 32: 495-519.

Kantz, T. and Bold, H.C. 1969. Phycological studies. IX. Morphological and taxonomic investigations of Nostoc and Anabaena in culture. Univ. Texas Publ. No. 6924, Austin. 66 pp.

Karim, A.G.A. 1968. Studies on the freshwater algae of the Sudan. Hydrobiologia 32: 33-46.

Kenyon, C.N., Rippka, R. and Stanier, R.Y. 1972. Fatty acid composition and physiological properties of some filamentous blue-green algae. Arch. Mikrobiol. 83: 216-236.

Khan, K.R. 1969. Ecology of some littoral blue-green algae of Ohau. Rev. Algol. n.s. 3: 218-230.

Klock, W. 1930. Phytoplanktonuntersuchen im Brackwassergebiet der Unterwarnow. Int. Rev. ges. Hydrobiol. Hydrogr. 23: 305-415.

Koch, W. 1964. Verzeichnis der Sammlung von Algenkulturen am Pflanzenphysiologishen Institut der Universitat Göttingen. Arch. Mikrobiol. 47: 402-432.

Kol, E. 1926. Algák a Lomniczi csúcs tetejéröl (2634 m.). Folia Cryptogamica. 1: 222-224.

Kolkowitz, R. 1910. Die Farbe der Seen und Meere. Deutsch Vierteljarhs. offentiliche Gesundheitspflege. 42: 305-317.

Komarek, J. 1970. Generic identity of the 'Anacystis nidulans' strain Kratz-Allen/Bloom. 625 with Synechococcus Nag. 1849. Arch. Protistenk. 112: 343-364.

Komarek, J. 1971. Benutzung von Kulturen in den Blaualgentaxonomie. Scheiz. Z. Hydrol. 33: 553-565.

Koster, J.T. 1960. Caribbean brackish and freshwater Cyanophyceae. Blumea 10: 323-366.

Krajina, V.J. 1965. Ecology of Western North America. Vol. I. Univ. British Columbia, Vancouver 112 pp.

Kratz, W.A. and Myers, J. 1955. Photosynthesis and respiration of three blue-green algae. Pl. Physiol. 30: 275-280.

Kratz, W.A. and Myers, J. 1955a. Nutrition and growth of several blue-green algae. Am. J. Bot. 42: 282-287.

Kuehne, P.E. 1941. The phytoplankton of south and central Saskatchewan. Can. J. Res. ser. C. 19: 292-322.

Kumar, H. 1970. Cyanophyceae of Sardhana. Phykos 9: 79-85.

Kützing, F.T. 1843. Phycologia generalis oder Anatomie, Physiologie und Systemkunde der Tange. Brockhaus, Leipzig. 458 pp.

Levander, K.M. 1900. Über das Herbst und Winterplankton im finnischen meerbusen und in der Alands-see. Acta Soc. fauna flora Fennica. 18(5): 1-25.

Lewis, I.F. 1924. The flora of Penikese, fifty years after. Rhodora 26: 181-195, 211-220.

Lillick, L.C. and Lee, I.M. 1934. A check-list of Ohio algae with additions from the Cincinnati region. Amer. Mid. Nat. 15: 713-751.

Lindstedt, A. 1943. Die flora der marinen Cyanophyceen der schwedischen Westkuste. Thesis Lund. 121 pp.

Mabille, J. 1954. Quelques Cyanophycées de la Region de Saint-Quentin II. Rev. Algol. n.s. 1: 56-66.

Maguire, B., Jr. 1963. The passive dispersal of small aquatic organisms and their colonization of isolated bodies of water. Ecol. Monogr. 33: 161-185.

Martindale, I. 1889. Marine algae of the New Jersey Coast and adjacent waters of Staten Island. Mem. Torrey Bot. Club 1: 87-109.

May, V. 1946. Studies on Australian marine algae III. Proc. Linn. Soc. New South Wales 71: 273-277.

May, V. 1951. Studies on Australian marine algae. Proc. Linn. Soc. New South Wales 71: 83-87.

McInteer, B.B. 1939. A check list of the algae of Kentucky. Castanea 4: 27-29.

McLachlan, J.L. and Gorham, P.R. 1962. Effects of pH and nitrogen sources on growth of Microcystis aeruginosa Kütz. Can. J. Microbiol. 7: 851-870.

Möbius, M. 1893. Beitrag zür Kenntnis der Algenflora Javas. Ber. Deut. Bot. Ges. 11: 118-139.

Moore, G.T. 1917. Preliminary list of algae in Devils Lake, North Dakota. Ann. Mo. Bot. Gard. 4: 293-303.

Moore, G.T. and Carter, N. 1923. Algae from the lakes in the northwestern part of North Dakota. Ann. Mo. Bot. Gard. 10: 393-421.

Nordstedt, O. 1897. Sammanställing af de skandinaviska lokalerna för Myxophyceae hormogenieae. Bot. Notis. 1897: 137-152.

Nylander, W. 1861. Notula circa Spermosiram et Nodulariam Algarum genera. Ann. Sci. Nat. ser. 4, Bot. 15: 36.

Okada, Y. 1932. The freshwater algae of Botel Tobago Island of Kôtosho Formoas. Bull. Biogeogr. Soc. Japan 3: 36-63.

Ortega, M.M. 1972. Study of the edible algae of the Valley of Mexico. Bot. Mar. 15: 162-165.

Ott, F.B. 1973. The marine algae of Virginia and Maryland including the Chesapeake Bay Area. Rhodora 75: 258-296.

Padmaja, T.D. and Desikachary, T.V. 1968. Studies on coccoid blue-green algae - I. Synechococcus elongatus and Anacystis nidulans. Phykos 7: 62-89.

Palik, P. 1961. Beitrage zür Algenvegation am den betonbauten in der Donau. Ann. Univ. Sci. Budapest, Sect. Biol. 4: 139-150.

Palmer, C.M. 1928. Algae of Indiana - a classified check list of those published between 1875 and 1928. Proc. Indiana Acad. Sci. 38: 109-121.

Pankow, H. 1964. Bemerkungen über die Schädlichkeit von Blaualgenwasserbluten fur Tiere. Naturwissenschaften 51: 146-147.

Pankow, H. 1971. Algenflora der Östsee. Gustaf Fisher Verlag, Stuttgart. 419 pp.

Pearson, J. and Kingsbury, J.M. 1966. Culturally induced variation in four morphologically diverse blue-green algae. Am. J. Bot. 53: 192-200.

Petersen, J.B. 1932. The fresh-water Cyanophyceae of Iceland. In Rosenvinge, L.K. and Warming, E., ed., The Botany of Iceland vol. II. pp. 249-324.

Petersen, J.B. 1935. Studies on the biology and taxonomy of soil algae. Dansk. Bot. Ark. 8: 1-183.

Playfair, G.I. 1914. Contributions to our knowledge of the biology of the Richmond River. Proc. Linn. Soc. New South Wales 39: 93-149.

Pike, N. 1886. Checklist of marine algae based on specimens collected on the shores of Long Island from 1839-1885. Bull. Torrey Bot. Club 13: 105-114.

Plinski, M. 1973. The algae of salt marshes near Leczyca, Central Poland. Monogr. Bot. 34: 1-89.

Prescott, G.W. 1931. Iowa algae. Univ. Iowa Stud. Nat. Hist. 13: 1-235.

Prescott, G.W. 1962. Algae of Western Great Lakes, revised ed. W.C. Brown & Co., Dubuque, Iowa. 977 pp.

Pringsheim, E.G. 1967. Phycology in the field and in the laboratory. J. Phycol. 3: 93-95.

Proshkina-Lavrenko, A.I. 1968. Vodorosli planktona Kaspii-skaga moria. National Academy USSR. 291 pp.

Rabenhorst, L. 1865. Flora europaea algarum aquae dulcis et submarinae. Sect. II E. Kummer, Leipzig. 359 pp.

Raju, N.S. 1972. The blue-green algae from the soils of India. In Desikachary, T.V., ed., Taxonomy and Biology of Blue-green Algae. Univ. Madras pp. 332-352.

Randawa, M.S. 1936. Occurrence and distribution of the freshwater algae of Northern India. Proc. Indian Acad. Sci. B. 4: 36-44.

Rathsack-Kutzenbach, R. 1961. Zur Cyanophyceenflora der Westküte von Rügen I. Int. Rev. ges. Hydrobiol.Hydrogr. 46: 653-663.

Rathsack-Kutzenbach, R. 1961a. Beitrag zur Cyanophyceen-flora der mitteren Ostee. Schweiz. Z. Hydrol. 23: 236-237.

Rawson, S.S. and Moore, J.E. 1944. The saline lakes of Saskatchewan. Can. J. Res. ser. D. 22: 141-201.

Rees, T.K. 1935. The marine algae of Lough Ine (Cork County, Ireland). J. Ecol. 23: 70-131.

Rich, F. 1930. Freshwater phyto-plankton. S.Afr. J. Nat. Hist. 6: 369-374.

Rich, F. 1932. Reports on the Percy Sladen Expedition to some Rift Valley lakes in Kenya in 1929. IV. Phytoplankton from the Rift Valley lakes in Kenya. Ann. Mag. Nat. Hist. ser. 10, 10: 233-262.

Rich, F. 1934. Contributions to our knowledge of the freshwater algae of Africa. 10. Phytoplankton from South African pans and vleis. Trans. Roy. Soc. S. Afr. 20: 149-188.

Richter, P. 1894. Gloiotrichia echinulata P. Richt., eine Wässerblute des Grossen und Kleinen Plöner Sees. Forsch. Biol. Stat. Plon. 2: 31-47.

Riddle, L.C. 1905. Brush Lake algae. Ohio Nat. 5: 268-269.

Rosa, K. 1951. Algen flora von Süd bohmen. Stud. Bot. Czechoslovaca. 12(3): 173-232.

Schmidle, W. 1896. Susswasseralgen aus Australien. Flora. 82: 297-333.

Schmidt, J. 1899. Danmarks blaagrønne Alger (Cyanphyceae Daniae) I. Bot. Tids. 22: 1-283.

Schumacher, G.J. and Muenscher, W.C. 1952. Plankton algae of some lakes of Whatcom County, Washington. Madrõno. 11: 289-297.

Serpette, M. and Labbé, A. 1966. Contribution à l'etude des Cyanophycées de Tunisie. Rev. Algol. n.s. 8: 204-208.

Setchell, W.A. and Gardner, N.L. 1903. Algae of Northwestern America. Univ. Calif. Pub. Bot. 1: 165-418.

Shtina, E.A. 1972. Some peculiarities of the distribution of nitrogen-fixing blue-green algae in soils. In Desikachary, T.V., ed., Taxonomy and Biology of Blue-green Algae. Madras pp. 294-295.

Simons, J. and Vroman, M. 1973. Vaucheria species from the Dutch brackish inland ponds "De Putten". Acta. Bot. Univ. Neer. 22: 177-192.

Sismey, E.D. 1922. A contribution to the algae flora of the Okanagan (B.C.) Can. Field Nat. 35: 112-114.

Sjostedt, L.G. 1922. Biologiskt-botaniska undersökningar av Oresund II. En vegetatims färgning av Nodularia spumigena i Öresund jämte biologisk översikt över övriga marina baltiska planktonfargningar. Lunds Univ. Arssk. N.F. Avd. 2. 18: 1-25.

Skuja, H. 1926. Vorarbeiten zu einer Algenflora von Lettland, II. Acta. Horti. Bot. Univ. Latv. 1: 149-178.

Skuja, H. 1949. Zur Susswasseralgenflora Burmas. Nova Acta Reg. Soc. Sci., Upssala, ser. 4. 14: 1-185.

Skvartozow, B.W. 1927. List of Cyanophyceae from North Manchuria. J. Eot. 65: 195-198.

Smith, G.M. 1924. Ecology of the plankton algae in the Palisades Interstate Park, including the relation of control methods to fish culture. Roosevelt Wild Life Bull. 2: 94-195.

Smith, G.M. 1950. Fresh-water Algae of the United States, 2nd. ed. McGraw-Hill, New York. 719 pp.

Sporring, S.H. 1942. Bitrag til Belysning af Skallingens Cyanophyce-Flora. Bot. Tids. 46: 396-406.

Stafleu, F.A. 1972. International code of botanical nomenclature 1969. A. Oosthaek's Vitgeversmaatschappij N.V. Utrecht, Neth. 426 pp.

Stanier, R.Y., Kunisawa, R., Mandel, M. and Cohen-Bazire, G. 1971. Purification and properties of unicellular blue-green algae (order Chroococcales). Bact. Rev. 35: 171-205.

Starmach, K. 1966. Cyanophyta - Sinice, Glaucophyta - Glaukofity. Flora Slodkow, Polski, vol. 2. Polsk. Akad. Inst. Bot. 807 pp.

Stein, J. 1963. Morphological variation of a Tolypothrix in culture. Brit. Phycol. Bull. 2: 206-209.

Stewart, W.D.P. 1960. Marine blue-green algae from the island of Barra. (Outer Hebrides). Brit. Phycol. Bull. 2: 26-27.

Stewart, W.D.P. 1965. Nitrogen turnover in marine and brackish habitats. I. Nitrogen fixation. Ann. Bot. n.s. 29: 229-239.

Stewart, W.D.P. 1970. Algal fixation of atmospheric nitrogen. Plant and Soil 32: 555-598.

Stewart, W.D.P. and Pugh, G.J.F. 1963. Blue-green algae of developing salt marsh. J. Mar. Biol. Ass. U.K. 43: 309-317.

Stewart, W.D.P., Fitzgerald, G.P. and Burris, R.H. 1970. Acetylene reduction assay for determination of phosphorus availability in Wisconsin lakes. Proc. Nat. Acad. Sci., U.S.A. 66: 1104-1111.

Stockner, J.G., Pomeroy, M. Carney, W. and Findlay, D.L. 1972. Studies of periphyton in the Lakes of the Okanagan Valley. B.C. Okanagan Basin Study Task 122, Preliminary Report No. 133.

Subrahmanyam, A. 1972. Algal flora of Bastar India - Blue green algae of Jagdalpur. Rev. Algol. n.s. 10: 290-296.

Tamas, G. 1958. Beiträge zu der Algenflora des Balaton-Sees. 1. Steiniges Ufer, Sandiges Ufer, Röhricht und Küntliches Substrat. Ann. Biol. Tihany. 25: 353-358.

Tarnavschi, I.T. 1931. Contributii la cunoasterea algelor dia Bucovina II. Bull. Fac. de Stünte din Cernaufi. 5: 135-157.

Taylor, W.R. 1928. Marine algae of Florida with special reference to the Dry Tortugas. Carnegie Inst. Wash., Papers Tortugas Lab. 25: 1-219.

Taylor, W.R. 1928a. The alpine algal vegetation of the mountains of British Columbia. Proc. Acad. Nat. Sci., Philadelphia. 80: 45-114.

Taylor, W.R. and Colton, H.S. 1928. The phytoplankton of some Arizona pools and lakes. Am. J. Bot. 15: 596-614.

Thuret, G. 1875. Essai de classification des Nostochinées. Ann. Sci. Nat. Bot. ser. 6. 1: 372-382.

Tiffany, L.H. and Britton, M.E. 1952. The Algae of Illinois. Univ. Chicago Press, Chicago 407 pp.

Tilden, J. 1901. Collection of algae from the Hawaiian Islands. Hawaii Almanac Ann. for 1902. pp. 106-113.

Tilden, J. 1908. Notes on a collection of algae from Guatemala. Proc. Biol. Soc. Washington 21: 153-156.

Toetz, D.W. 1973. The limnology of nitrogen in an Oklahoma Reservoir: nitrogenous activity and related limnological factors. Am. Midl. Nat. 89: 369-380.

Trahms, O.K. 1937. Zur Kenntnis der Salzverhältnisse und des Phytoplankton der Hiddenseer und Rugenschen Boddengewasser. Arch. Hydrobiol. 32: 75-90.

Trauseau, E.N. 1913. Annotated list of the algae of East Illinois. Trans. Illinois Acad. Sci. 6: 69-89.

Umezaki, I. 1961. The marine bluegreen algae of Japan. Mem. Coll. Agr. Kyoto Univ. 83:1-149.

van Oye, P. 1922. Beitrag zu Myxophyceen-Flora von Java. Hedwigia 64: 174-197.

van Oye, P. 1923. Zweiter Beitrag zur Myxophyceen-Flora von Java. Hedwigia 64: 268-285.

Vasishta, P.C. 1960. A systematic and ecological account of the Cyanophyceae of Hoshiapur. J. Bombay Nat. Hist. Soc. 57: 579-589.

Vasishta, P.C. 1961. More Cyanophyceae of Hoshiapur: I. J. Bombay Nat. Hist. Soc. 58: 135-146.

Velasquez, G.T. 1962. The blue-green algae of the Philippines. Philippine J. Sci. 91: 267-380.

Verch, R. and Blinn, D.W. 1972. Seasonal investigations of algae from Devils Lake North Dakota. Prairie Nat. 3: 67-79.

Villeret, S. 1953. Contributions à la flore algologique d'eau douce des iles d'ouessant (Bretagne). Rev. Gén. Bot. 60: 12.

Vivian, E.L. 1932. Myxophyceae of Nebraska. Trans. Am. Microsc. Soc. 51:79-117.

Waldmann, J. 1959. Qualitative Planktonuntersuchungen in der mittleren Ostsee. Zeit. Fisherei 8: 557-564.

Webber, E.E. 1967. Bluegreen algae from Massachusetts salt marsh. Bull. Torrey Bot. Club 94: 99-106.

Welch, H. 1964. A contribution to our knowledge of the blue-green algae (Cyanophyta,Schizophyceae, Myxophyceae) of South West Africa. Nova Hedw. 7: 15-32.

Welch, H. 1965. A contribution to our knowledge of the blue-green algae of South West Africa and Bechuanaland. Nova Hedw. 9: 131-162.

West, G.S. 1899. The algal-flora of Cambridgeshire. J. Bot. 37: 49-58.

West, G.S. 1904. West Indian freshwater algae. J. Bot. 42: 281-294.

West, G.S. 1907. The freshwater algae of the third Tanganyika Expedition. J. Linn. Soc. Bot. 38: 81-197.

West, G.S. 1909. The algae of Birket Quarun, Egypt. J. Bot. 47: 237-244.

West, G.S. 1912. Fresh-water algae. Ann. S. Afr. Mus. 9: 61-70.

West, G.S. 1914. A contribution to our knowledge of the freshwater algae of Columbia. Mem. Soc. Neuchateloise de Sci. Nat. 5: 1013-1051.

West, W. and West, G.S. 1911. Freshwater algae. In Murray, J., ed., British Antarctic Expedition 1907-1909. Reports on scientific investigations I: 263-304.

Whelden, R.M. 1947. Algae. In Polunin, N., ed., Botany of the Canadian Eastern Arctic, part II. Nat. Mus. Can. Bull 97. Ottawa. pp. 13-232.

Whitford, L.A. 1943. The Fresh-water Algae of North Carolina. J. Elisha Mitchell Soc. 59: 131-170.

Whitford, L.A. and Schumacher, G.J. 1969. A manual of freshwater algae of North Carolina. Tech. Bull. #188, North Carolina Agr. Exp. Stat., Raleigh. 313 pp.

Whitton, B.A. 1962. Morphology-habitat associations in blue-green algae. Br. Phycol. Bull. 2: 167-171.

Wille, N. 1897. Om Faeröernes Ferskvandsalger og om Ferskvandsalgernes Spredningsmaader. Bot. Not. 1897: 1-32.

Wille, N. 1924. Süsswasseralgen von der Deutschen Südpolar-Expedition auf dem Schiff "Gauss". In F. von Drygalski., ed., Deutsche Südpolar - Expedition 1901-1903. 8: 373-445.

Williams, W.D. 1970. Energy transformations in salt lakes. Bull. Aust. Soc. Limnol., 1: 6-8.

Wittrock, V., Nordstedt, O. and Lagerheim, G. 1897. Algae aquae dulcis exsiccatae. Bot. Not. 1897: 75-94.

Wolle, F. 1887. Fresh-water Algae of the United States. Bethlehem, Penn. 364 pp.

Woodhead, N. and Tweed, R.D. 1957. A checklist of tropical West African algae. Hydrobiologia 11: 299-396.

Woodson, B.R., Holoman, V.A. and Quick, A. 1966. Additions to fresh-water algae in Virginia. II. Dinwiddie County. J. Elisha Mitchell Soc. 82: 154-159.

Yondeda, Y. 1937. Cyanophyceae of Japan, I. Acta Phytotax. Geobot. 6: 179-209.

Young, R.T. 1924. The life of Devils Lake North Dakota. Publ. North Dakota Biol. Stat. 116 pp.

Zhadin, V.I. and Gerd, S.V. 1961. Fauna and flora of the rivers, lakes and reservoirs of the U.S.S.R. Israel Prog. Sci. Trans., Jerusalem, No. 1903, 626 pp.

APPENDIX TABLES I - IX

Table I. Procedures Used in Water Analysis

Na^+, K^+, Ca^{++}, Mg^{++}	:	Perkin-Elmer Atomic Absorption Spectrophotometer Model 303.
$SO_4^=$	:	Turbidimetric method (Standard Methods) American Public Health Association, 1965.
Cl^-	:	Argentometric method (Standard Methods) American Public Health Association, 1965.
HCO_3^- and $CO_3^=$	:	Potentiometric titration (Standard Methods) American Public Health Association, 1965.
Ortho-phosphate	:	Stannous Chloride method (Standard Methods) American Public Health Association, 1965.
NH_4^+	:	Nesslerization method (Standard Methods) American Public Health Association, 1965.
NO_3^-	:	Phenoldisulfonic Acid method (Standard Methods) American Public Health Association, 1965.
Total Dissolved Solids	:	Evaporation at 105^oC (Standard Methods) American Public Health Association, 1965.

Table II. Water chemistry for Ctenocladus Pond

	30v72	21vii72	23viii72	24ix72	28iv73	3vi73	21vii73
pH	9.1	9.0	8.8	8.4	8.8	8.9	8.6
temp C	27	24	24	8	14	27	29
Na^{+} mg/l	8100	42500	56000	72000	13700	36000	95000
Mg^{++} mg/l	1800	5200	9700	12600	1200	4200	9200
Ca^{++} mg/l	56	144	172	209	65	87	87
K^{+} mg/l	280	865	1235	1024	193	522	835
$SO_4^{=}$ mg/l	23500	108000	130000	170000	42000	100000	250000
$CO_3^{=}$ mg/l	0	100	480	1240	40	640	620
HCO_3^{-} mg/l	0	40	580	260	330	240	380
Cl^{-} mg/l	650	1750	5000	6400	600	1500	550
NH_4^{+} mg/l	16	12	12	14	10	12	14
NO_3^{-} mg/l	4.1	1.2	3.4	3.0	3.5	3.0	3.0
o-PO_4 mg/l	1.5	2.2	2.0	2.2	2.0	3.1	3.5
TDS g/l	35	180	226	306	48	140	408

Table III. Water chemistry for Wallender Lake

	30v72	21vii72	23viii72	24ix72	28iv73	3vi73	21vii73
pH	8.7	8.65	8.5	8.85	8.5	8.9	8.85
temp C	22	24	25	9	14	24	23
Na^{+} mg/l	3200	6400	7700	9900	3700	7100	8000
Mg^{++} mg/l	2900	3800	4300	2800	600	1600	5600
Ca^{++} mg/l	74	119	250	237	96	151	285
K^{+} mg/l	220	707	570	1031	404	374	921
$SO_4^{=}$ mg/l	20000	31000	41000	46000	12000	22000	43000
$CO_3^{=}$ mg/l	70	160	300	300	0	140	180
HCO_3^{-} mg/l	25	160	220	200	0	150	760
Cl^{-} mg/l	550	650	700	800	300	550	800
NH_4^{+} mg/l	10.2	8.8	8.6	9.5	9.5	8.0	6.3
NO_3^{-} mg/l	2.8	1.9	1.7	0.7	1.9	0.6	0.7
o-PO_4 mg/l	0.4	0.2	0.4	0.1	0.2	0.3	0.2
TDS g/l	25	48	70	88	14	30	64

Table IV. Water chemistry for Inks Lake

	30v72	21vii72	23viii72	24ix72	28iv73	3vi73	21vii73
pH	8.9	8.8	8.8	9.0	8.6	8.8	9.1
temp C	20	25	26	9	15	24	23
Na^{+} mg/l	9800	11300	11800	8400	5500	8800	9800
Mg^{++} mg/l	1600	1950	2400	4000	900	2200	5800
Ca^{++} mg/l	121	148	133	201	60	144	173
K^{+} mg/l	770	1030	1360	1220	390	1260	1390
$SO_4^{=}$ mg/l	27000	35000	37500	44000	14000	34000	46000
$CO_3^{=}$ mg/l	25	70	140	180	0	100	380
HCO_3^{-} mg.l	80	310	550	580	0	240	720
Cl^{-} mg/l	550	650	700	800	300	550	800
NH_4^{+} mg/l	8.8	8.2	7.2	6.0	10.4	8.2	6.5
NO_3^{-} mg/l	3.1	1.9	2.1	1.0	2.1	0.8	0.8
o-PO_4 mg/l	0.3	0.2	0.2	0.1	0.2	0.3	0.1
TDS g/l	35	52	58	66	18	44	65

Table V. Water chemistry for White Lake

	29v72	20vii72	23viii72	23ix73	27iv73	2vi73	22vii73
pH	10.0	9.5	no collection	9.4	9.7	9.75	dry
temp C	25	23		14	11	22	
Na^{+} mg/l	3000	7200		9100	3800	7500	
Mg^{++} mg/l	1050	2000		3980	1400	2100	
Ca^{++} mg/l	455	350		320	0	0	
K^{+} mg/l	131	219		635	420	881	
$SO_4^{=}$ mg/l	11000	21000		32000	10500	23000	
$CO_3^{=}$ mg/l	760	500		340	1380	1500	
HCO_3^{-} mg/l	400	750		280	1050	490	
Cl^{-} mg/l	600	1200		1000	900	1700	
NH_4^{+} mg/l	20.4	15.4		12.0	26.5	12.0	
NO_3^{-} mg/l	2.1	1.0		1.1	2.8	2.2	
o-PO_4 mg/l	0.2	0.3		0.1	0.3	0.3	
TDS g/l	15	27		40	14	27	

Table VI. Water chemistry for the lakes irregularly sampled or sampled only once.

	Salt Pond 4	Salt Pond 3	Big Quill Lake	Devils Lake	Spotted Lake	Riefel Refuge	San de Fuca
	39v72	21vii72	23viii72	24viii72	29v72	24ix73	20v73
pH	9.9	9.3	8.6	9.1	7.8	8.2	8.4
temp C	30	26	25	21	33	19	18
Na^{+} mg/l	11400	2200	10300	1475	34100	2675	5370
Mg^{++} mg/l	41	30	3400	384	17000	320	651
Ca^{++} mg/l	404	0	126	56	6.5	92	200
K^{+} mg/l	128	55	560	175	1610	90	192
$SO_4^{=}$ mg/l	14500	1330	35000	3600	140000	1120	2304
$CO_3^{=}$ mg/l	8300	963	130	120	120	0	10
HCO_3^{-} mg/l	2000	312	320	250	110	29	61
Cl^{-} mg/l	5500	612	5500	650	1200	4620	9690
NH_4^{+} mg/l	2.5	0.9	4.5	0.4	5.0	0.1	0
NO_3^{-} mg/l	3.0	2.2	2.3	6.1	4.0	1.4	0.5
$O\text{-}PO_4$ mg/l	3.5	1.9	0.2	1.2	4.5	0.2	0.1
TDS g/l	47	4	26	12	166	8.4	18

Table VII. World distribution of *Nodularia*

* *N. harveyana*
** *N. spumigena*
*** both
\- identification only to genus

CANADA

British Columbia
**Blinn (1969) Kamloops
**Sismey (1922) no location
*Sismey (1922) Penticton
-Stockner *et al.* (1972) Skaha L. Okanagan L. Vaseux L.

Manitoba
**Bajkov (1935) several locations

Saskatchewan
**Kuehune (1941) 7 locations in south central Sask.
**Rawson & Moore (1944) 8 locations in south central Sask.

U.S.A.

Alaska
*Gardner 3963 Sitka UC 661526 F 1047757

Arizona
*Cameron (1963) Yuma Co. & Gila Co.
**Cameron (1963) Cochise Co.
**Taylor & Colton (1928) Coconino Co.

Arkansas
*Demarree & Thomason 24582 Drew Co. F 1133627

California
**Drouet (1943) Modoc Co.
*Drouet & McBride 4569 Mono Co. & San Bernadino Co. UC 664554 FH Nordin 1076 NBV 3925-43 NY Nordin 1268 F 1101885 (Drouet 1943)
*Gardner 989 (PBA 1063) Marin Co. UC 341420 FH Nordin 1088 NBV 3925-48 F 980816 NY Nordin 1282 PC Nordin 1314
*Gardner 1498 Oakland UC 202866 F Nordin 1182
*Gardner 1604 Berkeley UC 202865 UC 274104
**Gardner 3295 Oakland UC 114844
*Gardner 4151 Oakland UC 661636 FH Nordin 1078 NBV 3925-42 F 1032981 NY Nordin 1266

*Gardner 6552 Berkeley UC 440248
*Gardner 6568 Berkeley UC 661705 FH Nordin 1075 NBV 3925-46 F 1033552 NY Nordin 1264
**Gardner 7231 San Mateo Co. FH Nordin 1081
*Gardner 7670 Berkeley UC 641592 FH Nordin 1080 NBV 3925-40 F 1036391 NY Nordin 1270
**Gardner 7946 Contra Costa Co. UC 661724 NBV 3925-56 FH Nordin 1056 F 1043544 NY Nordin 1293
*Gardner 7963 San Francisco UC 661654 FH Nordin 1077 NBV 3925-41 F 1034223 NY Nordin 1267
*Groesbeck 90 Mono Co. & San Bernadino Co. F 1049304
*Hof & Frémy (1933) Marina
*Hollenberg 1553 Orange Co. UC 634466
**Osterhout 559 Alameda Co. UC 393931 UC 202712 NBV 3925-54 FH Nordin 1066 PC Nordin 1328
**Osterhout & Gardner (PBA 1061) Oakland FH Nordin 1087 NBV 3925-30 F 980816 NY Nordin 1263 PC Nordin 1302
**Setchell 1628 San Benito Co. UC 752513 F 1221362
*Setchell 1679 San Francisco UC 100563
**Setchell & Jepson Stanislaus-Mariposa Co. UC 202713 NBV 3925-53

Colorado
*Louderback 17 Denver F 1235673

Connecticut
**Holden 1458-1461 Bridgeport FH Nordin 1062 NY Nordin 1290 (Collins 1900, 1905)

Florida
*Brannon 141A Gainesville F 1124079 PC Nordin 1329 (Brannon 1952)
*Drouet, Madsen & Crowson 11511 Wakulla Co. F 1324385
*Drouet, Madsen & Crowson 11513 Wakulla Co. UC 912044 F 1324476
*Drouet & Nielsen 11232 Taylor Co. UC 912045 F 1308871
*Drouet & Nielsen 11681 Franklin Co. UC 912043 F 1317616
*Standley 73311 Lee Co. F 1030027

Illinois
*Drouet, Glassman & Chapp 12696 Cook Co. F Nordin 1202
*Drouet, Glassman & Chapp 12711 Cook Co. F Nordin 1203
***Tiffany & Britton (1952) no location
***Transeau 63 Coles Co. NY Nordin 1283
*Velasquez, Richards & Drouet 2507 Cook Co. F 980549

Indiana
**Palmer (1928) Knox Co.
*Palmer et al. 2518 Indianapolis F 980816
**Transeau (1913) Decker

Iowa
**Prescott (1931) Dickenson Co.

Kentucky
*McInteer (1939) no location

Louisiana
*Drouet 8766 Calcasieu Parish UC 910404 NBV 3925-45 F 1332708 PC Nordin 1311

Maine
*Collins[1] (PBA 1062) Casco Bay F 545439 NY Nordin 1280 PC Nordin 1307
*Collins 22 Cape Rosier UC 687705 FH Nordin 1072 NBV 3925-39 F 1209180 NY Nordin 1278 PC Nordin 1310
*Collins 2387 Cape Rosier FH Nordin 1070 FH Nordin 1073 NY Nordin 1275
**Collins 2439 Cape Rosier FH Nordin 1060 NY Nordin 1287
**Collins 3459 Cape Rosier NY Nordin 1289
*Collins 5094 Casco Bay UC 752510 F 1219372 NBV 3925-27
**Collins 5094 Casco Bay UC 752514 F 1219336
**Collins 5526 (PBA 1307) Harpswell UC 693286 F 545467 FH Nordin 1061 NY Nordin 1296a NY Nordin 1288 NBV 3925-55 PC Nordin 1333
**Collins West Brooksister NY Nordin 1276
*Collins 5845 Casco Bay FH Nordin 1069 NY Nordin 1272 (Collins 1908)
***Collins (1908) Casco Bay
*Muxter? Kittery Pt. FH Nordin 1071

Maryland
*Wolle & Drouet 2302 Somerset Co. FH Nordin 1074 NY Nordin 1271 F 939834 UBC 49983 (Drouet 1939)

1 apparently when Collins made a collection with the two species together he made two sheets of the material, calling one for instance Nodularia harveyana and the other Nodularia spumigena. Both sheets show both species contained in them. He usually gave both sheets the same collection number.

Massachusetts
*Chapman (1940) Essex Co.
*Collins Woods Hole UC 752511
*Farlow (1881) Cambridge
**Farlow Woods Hole UC 100562 FH 4555
*Setchell Cambridge UC 100565
**Taylor 3084 Nantucket Island UBC 49982 (Drouet 1935)
*Webber (1967) Essex Co.

Michigan
*Ackley (1931) Livingstone Co., Cheboygan City & Co., Montcalm Co., Washtenaw Co. & Shiawassee Co.
**Ackley (1931) Branch Co.
*Johnson Ann Arbor UC 752512 PC Nordin 1300 F 1157488
**Phinney 23M40 Emmet Co. F 1138192

Mississippi
**Drouet 9844 Hancock Co. F 1310578
*Scott Bay St. Louis F 1085870

Missouri
*Casebolt 167 Clay Co. F Nordin 1198 (Gier & Johnson 1954)

Nebraska
*Anderson & Walker (1920) Cherry Co.
*Clements (1896 & 1901) Lancaster Co. & South Bend
**Kiener 10401a Filmore Co. F 1099262
*Kiener 10466 Red Willow Co. F 1099440
*Kiener 13617 Lancaster Co. F 1127250
**Kiener 13777 Cherry Co. UC 679691 F 1127792
**Kiener 13885 Dodge Co. F 1131624
**Kiener 14139 Lancaster Co. F 1132181
**Kiener 14140 Lancaster Co. F 1132185
*Kiener 15687 Keith Co. F 1139911
**Kiener 16499 Kearney Co. UC 689174 F 1144655
*Kiener 20613a Sheridan Co. F 1219490
**Kiener 21834-21835 Dundy Co. F 1220286 F 1220345
*Kiener 22773a Scott's Bluff Co. F 1249366
*Kiener 22778 Scott's Bluff Co. F 1249569
**Kiener 23130 Garden Co. F Nordin 1184
**Kiener 23602-23604 Lincoln Co. F Nordin 1185-1187

Nevada
**Christiansen 1731 Washoe Co. F Nordin 1169
**LaRivers 616 Washoe Co. F Nordin 1168

New Hampshire
*Collins Hampton NY Nordin 1277
**Collins Hampton NY Nordin 1279 (Collins 1884)
**Collins Hampton NY Nordin 1286 NY Nordin 1292
NY Nordin 1296 F Nordin 1178 FH Nordin 1059
(Collins 1884)

New Jersey
**Peters Atlantic City F 1081208

New York
*Martindale (1889) Staten Island
*Pike (1886) Long Island
**Smith (1924) Bergen

North Carolina
*Cocke (1949) Duplin Co.
**Cocke (1949) Macon Co.
*Cocke (1967) Piedmont & Coastal Plain
**Cocke (1967) Coastal Plain
*Whitford (1943) New Hanover Co.
**Whitford (1943) Craven Co.
*Whitford and Schumacher (1969) Piedmont and Coastal Plain
*Whitford and Schumacher (1969) Coastal Plain

North Dakota
**Brannon (1911) Devils Lake
**Moore (1917) Devils Lake
**Moore & Carter (1923) Ramsay, Nelson, Eddy & McLean Cos.
**Verch & Blinn (1972) Devils Lake
**Young (1924) Devils Lake

Ohio
*Lillick & Lee (1934) Columbus
**Lillick & Lee (1934) Cincinnati
**Riddle (1905) Champaigne Co.

Oklahoma
**Toetz (1973) Payne Co.

Pennsylvania
**Habeeb 3738 Pike Co. F Nordin 1176

Tennessee
**Bold Goodeletsville F Nordin 1174
*Bold B143 Nashville F 1211634

Utah
*Harding (1971) Utah Co.

Virginia
*Louver & Strickland 1130 York Co. UC 680411 F 1109792
*Ott (1973) Yorktown
**Woodson et al. (1966) Dinwiddle Co.

Washington
***Fairchild & Wilson (1967) Grant Co.
*Gardner 335 (PBA 1013) LaConner Skagit Co. UC 100569 NBV 3925-38 F 546279 NY Nordin 1269 PC Nordin 1306 (Setchell & Gardner 1903)
**Gardner 411 (PBA 1012) Whidby Island UC 100566 NBV 3925-72 NY Nordin 1297 F 980816 F 1047781 PC Nordin 1334 (Setchell & Gardner 1903)
**Gardner 436 Port Townsend UC 100567 (Setchell & Gardner 1903)
*Schumacher & Muenscher (1952) Whatcom Co.

Wisconsin
*Prescott (1962) no location
**Prescott (1962) no location

EUROPE

Austria
**Brabez (1941) Franzenbader
*Brabez (1941) Franzenbader
*Forti (1907) cites collection by Beck
**Forti (1907) cites collections made by Loitlesberger, Hansgirg

Belgium
*Beeftink 450 & 451 Fort St. Phillipe NBV 3925-32 NBV 3925-33
*Forti (1907) cites two collections by De Wildemann one by Bory

Czechoslovakia
*Forti (1907) cites a collection by Hansgirg at Carinthiae
*Hansgirg Hermanmestec F Nordin 1233
*Hansgirg Libochovice F Nordin 1234
**Kol (1926) Lomniczi
**Rosa (1951) Bohmen
*Tarnavschi (1931) Bucovina

Denmark
**Cleve (1897) Helleback
***Fjerlingstad (1969) Knudshoved, Sjaelland Island
**Ostenfeld Falster Island NY Nordin 1285
**Ostenfeld Store Beelt NY Nordin 1284
*Schmidt (1899) cites collections by Warming at Skallingen, Th. Mortensen at Nymindegab
**Schmidt (1899) cites collections by Lyngbye & Hofman-Bang at Hofmansgave; Ostenfeld at Taarback, Anhatt, Fyr, Storebaelt; Rosenvinge at Svendborg, Vejlefjord, Faeno-Sund, Limfjorden; Rosenvinge, Ifølge & Ostenfeld at Oresund, Kjerteminde, Fredrideshaven, Groves Flak, Aalborg Bugt, Nordre Rønner, Hirsholmene; Rosenvinge & Th. Mortensen at Nykohing; Schmidt at Bornholm Island
*Sporring (1942) Skallingens
*Wille (1897) Kirkebö, Faeroe Islands (Borgesen 1901)

England
**Berkeley no date Bristol NBV 3925-27
*Bristol (1919 & 1920) Broadbalk
*Carter (1933) Essex
*Grove et al. (1920) Birmingham
**Grove et al. (1920) Birmingham
*Harvey (1848) cites collection by Thwaites at Shirehampton near Bristol
**Harvey (1848) cites collections by Salway at Barmouth, Ralfs at Dolgelley, Thwaites at Shirehampton
**Joshua Cirencester F Nordin 1249
*Petersen (1935) no location
***Stewart & Pugh (1963) Lincolnshire
**Thwaites? Shirehampton PC Nordin 1330
*West (1899) Cambridgeshire

Finland
**Cedercreutz (1934) Alands-Sea
**Forti (1907) cites 2 collections by Elfving
**Levander (1900) Alands-Sea
**Nylander Helsinki PC Nordin 1317-1319 (Nylander 1861)

France
*Bornet & Flahault (W&N 895) Cosne UC 759399 PC Nordin 1309 FH Nordin 1082 NBV 3925-34 NBV 3925-35 F Nordin 1235 NY Nordin 1281
**Frémy (1934) Belle-Ile & Brest
**Frémy & Meslin (1924) La Meaffe

**Gomont Tables de la Loire PC Nordin 1323
*Gomont? Paris PC Nordin 1303
*Gomont Cosne PC Nordin 1304
**Gomont Auvergne PC Nordin 1324
**Gomont (W.N.&L. 1343) Auvergne UC 761550 NBV 3925-49 F 975767 NY Nordin 1294
*Koster 6121 Finistere NBV 3925-31
**Lebel 415 Mont d'Huberville NBV 3925-16 PC Nordin 1337a
**Lebel 580 Negreville PC Nordin 1337b
*Lebel 998 LeHavre PC Nordin 1316
*Mabille Berthenicourt F Nordin 1232 PC Nordin 1299
*Mabille (1954) Berthenicourt
*Roussel Talatus PC Nordin 1315
*Thuret Cherbourg FH Nordin 1083 NBV 3925-36 PC Nordin 1308
*Thuret Cherbourg PC Nordin 1298 PC Nordin 1305
**Thuret Cherbourg FH Nordin 1063 PC Nordin 1327b (Bornet and Thuret 1880)
**Thuret (in Bornet & Thuret 1880) Croisic
*Thuret? Cosne PC Nordin 1313
**Thuret Deauville FH Nordin 1065 NBV 3925-22 NBV 3925-24 PC Nordin 1327 PC Nordin 1331
**Villeret (1953) Bretagne

Germany
*Anagnostidis & Schwabe (1966) Fehmarn Island
**Arndt et al. (1966) Wismar-Bucht
**Bandel (1940) Rostoc
**Bornet & Flahault (1888) cite collections by Braun (var. gen. "in stagnis aquae dulis") (var.lit. "in herb. Thuret")
*Bornet & Flahault (1888) cite a collection by "Hantzsch in herb. Grunow"
**Braun Freiburg NBV 3925-15 PC Nordin 1338
**Braun 1847 Freiburg NBV 3925-25 PC Nordin 1336
**Bursa (1968) Gulf of Gdansk
**Forti (1907) cites collections by Lemmerman, Reinbold, Richter not seen
*Forti (1907) cites collections by Brand, Volk, M. Schmidt not seen
**Frohlich? Schleswig NBV 3925-57 NBV 3925-63 NBV 3925-70 PC Nordin 1326 PC Nordin 1335
**Kalbe & Tiess (1964) Rostoc
**Kleiboden? Wangerooge NBV 3925-13
**Klock (1930) Unterwarnow
**Koch Borkum NBV 3925-17 NBV 3925-26a
**Koch no location NBV 3925-29b

**Kolwitz (1910) Ostsee
*Lindstedt (1943) & Forti (1907) cite collections by Reinke, Reinbold
**Mertens Norderney UC 436361 NBV 3925-15 NBV 3925-59 NBV 3925-64 NBV 3925-66 NBV 3925-67 NBV 3925-68 F 951302
**Pankow (1964) Rostoc
*Pankow (1971) Ostsee, Kieler Forde
*Petersen (1935) no location
**Rathsack-Kutzenbach (1961) Rugen Island
**Rathsack-Kutzenbach (1961a) Mittleren Ostsee
**Richter (1894) Ploner Sea
**Rose Berra (Rabh. Algen 237) NBV 3925-14 F 999057 NY Nordin 1259
**Schmitz (H&R 142) Greifswalder Bodden UC 760936 UC 953542 NBV 3925-58 NBV 3925-65 PC Nordin 1325 PC Nordin 1332
**Trahms (1937) Rugen
**Waldemann (1959) middle Ostsee also cites collections by Merkle, Driver, Hessle and Vallin, Ostenfeld, Brandes, Rothe, Bandel

Hungary
**Fritsch (1964) cites collection by Palik
*Hortobagyi (1959) Lake Szelid
**Palik (1961)
*Tamas (1958) Balaton Sea

Iceland
**Petersen (1932) Einarsnes
*Petersen (1932) Hvalnes & Knararnes & Einarsnes

Ireland
*Bornet & Flahault (1888) cites collection by Harvey
**Rees (1935) Cork Co.

Italy
*Bornet & Flahault (1888) cite collection by Menghini
**Forti (1907) cites collection by Forti

Netherlands
*Beeftink 0-199 & 0-201 Zeeuwsch-Vlaanderen NBV 3925-10 NBV 3925-11
*Bierbräuer Ostvoorne NBV 3925-12
*Bilio 23A Goeree NBV 3925-7
*Bilio 61025-2 Goeree NBV 3925-9
*Bilio 22B Goeree NBV 3925-2

*Bilio 6 Noord-Beveland NBV 3925-4
*Bilio 9 Noord-Beveland NBV 3925-3
*Bilio W Noord-Beveland NBV 3925-5
*Bilio M Noord-Beveland NBV 3925-6
*Bilio M107 Ostvoorne NBV 3925-8
*Forti (1907) cites lists of collections
**Forti (1907) cites collections by Van den Bosch, Surinigar at Leeuwarden
*Simons & Vroman (1973) De Putten
**Van den Bosch Goes PC Nordin 1320

Norway
**Foslie (WN&L 1344) Bugonaes UC 761551 UC 100562 NBV 3925-21 F 975766 NY Nordin 1295

Poland
**Collector unknown Danzig Bay NBV 3925-23
*Plinski (1973) Leczyca
*Starmach (1966) no location
**Starmach (1966) no location

Rumania
*Hof & Frémy (1933) Szovata Siebenburgen

Scotland
*Bornet & Flahault (1888) cite collection by Batters
**Bornet & Flahault (1888) cite collection by Batters at the mouth of the Clyde
*Stewart (1960) Hebrides

Spain
**Gonzalez-Guerro (1928) Madrid

Sweden
**Borge (1907) Väddö, Edeby
*Cedergren (1926) Kolviken
**Cleve (1897) Moseskär Väderöarna
*Granhall & Henriksson (1969)
**Lindstedt (1943) Torekov; Bohuslän: Fiskebückskil Stockevik
*Lindstedt (1943) several locations
**Nordstedt (W&N 198) Lomma FH Nordin 1090 NBV 3925-50 NBV 3925-61 NY Nordin 1298b F Nordin 1250
*Nordstedt (1897) cites collection by C. Ag. in herb Thuret
**Nordstedt (1897) cites collection by C. Ag. at Bastad and Areschoug exsice II #193 from same area
**Sjostedt (1922) Oresund

**Skuja (1924) from Lappland Coast
*Skuja (1926) Staburags
**Skuja (1926) cites collection by Winkler from west Baltic Coast

Switzerland
*Cramer (Rabh. Alg.Sach. 994) Zurich FH Nordin 1084 NBV 3925-1 F 1002450 NY Nordin 1262

EXCLUSIVE OF NORTH AMERICA AND EUROPE

Algeria
*Debray (1893)

Antarctica
*Apfel 51 & 52 Burger Lakes F 1299674 F 1299701
*Fritsch Winter Harbour BM 1815 (Fritsch 1912)
*Fukushima (1959) Ongul Island

Antilles (Dutch)
*Van den Hoek et al. (1972) Curaçao
**Wagenear-Humelinck 641 Aruba NBV 3925-52 (Koster 1960)

Argentina
**Borge (1901) Patagonia
**Borge (1907a) Puna de Atacama
*DeHalperin (1970) Gulfo Nuevo

Australia
**Bayly & Williams (1966) Lake Corangamite
**Francis? Lake Alexandrina FH Nordin 1064 (Francis 1878)
**Playfair (1914) Lismore
**Schmidle (1896)
**Williams (1970)

Barbados
*West (1904) Chancery Lane Estate

China
*Skvartzow (1927) North Manchuria
**Skvartzow (1927) Harbin, North Manchuria

Columbia
*West (1914) Cundinamarca

Egypt
**Fritsch (1964) cites collection by Nayal
**West 393 Birket Quarun BM 302 (West 1909)

Falkland Islands
**Guarrera & Kühnemann (1949) cite collection by Vallentin at Malvinas

Formosa
**Okada (1932) Kotosho

Guatemala
**Standey 65787 Rio Pucal Dept. F 1023960
*Tilden (1908) Lake Amatitlan

India
**Bharadwaja (1935) Benares
-Chacko (1972) Madras
-Franklin (1972) Madras
**Iyengar & Desikachery (1944) Hare Island, South India
**Kamat (1968) Alibag, Maharashtra
**Kumar (1970) Sardhana
*Raju (1972) Kamat
**Raju (1972) Kanpur
**Randawa (1936) N. India
**Subrahmanyam (1972) Bastar, Jagdalpur
**Vasishta (1961 & 1960) Hoshiarpur

Israel
-Jabotinsky (1961) Lake Zohar

Japan
*Umezaki (1961) several locations
**Yoneda (1937) Shinano

Java
*Mobius (1893) Solo
**Van Oye (1922) Batavia
*Van Oye (1923) Tasikmalaja
*Jutono (1973) Jogjakarta

Mexico
*Drouet & Richards 3416 Empalme, Sonora F 1031425
-Ortega (1972) Lake Texcoco
*Patrick Lake Texcoco F Nordin 1241

New Zealand
*Chapman (1955) Stanmore Bay
*Chapman 1b Stanley Bay F 1246844
*Dellow (1955) Hauraki Gulf
*Dellow & Cassie (1955) Whangaparaoa Bay

Peru
**Ibanez Trujillo F Nordin 1238
***Maldonaldo Lago Villa F 1102709 F 1102707

Puerto Rico
**Wille 1817a Laguna Guanica UC 463735 NY Nordin 1256
(Gardner 1927)

Sierra Leone
***Woodhead & Tweed (1957) no location

South Africa
**Fritsch & Rich (1929) Kimberley
**Hutchinson et al. (1932) Transvaal (Rich 1930) (Rich 1934)
*Pearson 26 Orange River BM Nordin 1348 (Fritsch 1918)

South West Africa
*Welch (1964) Swakop River, Rietfontien Spring
**Welch (1964) Gross Barmen, Etosha Reserve
**Welch (1965) Okandu
*West (1912) Little Namaqualand

Sudan
**Karim (1968) Jebel Marra

Tunisia
*Serpette & Labbé (1966) between Rades and Miliane
**Serpette & Labbé (1966) Oasis de Tozeur

U.S.S.R.
*Elenkin (1916) Kislovodsk
*Kosinskaja Tartar Autononous SSR (cited in Fritsch 1964)
*Proshkina-Lavrenko (1968) Caspian Sea
**Proshkina-Lavrenko (1968) Caspian Sea
*Shtina (1972) Khirov S.S.S.R
**Starmach (1966) cites collection by Woronichin in Siberia
**Zhadin & Gerd (1961) Lake Balkash

Table VIII. Medium BG-11 (Stanier et al. 1971)

Compound	Amount (g/l)
$NaNO_3$	1.5
K_2HPO_4	0.04
$MgSO_4 \cdot 7H_2O$	0.075
$CaCl_2 \cdot 2H_2O$	0.036
Na_2CO_3	0.02
Ferric ammonium citrate	0.006
EDTA (disodium salt)	0.001
Trace metal mix A5*	1 ml/l

*A5

H_3BO_3	2.86
$MnCl_2 \cdot 4H_2O$	1.81
$ZnSO_4 \cdot 7H_2O$	0.222
$Na_2MoO_4 \cdot 2H_2O$	0.39
$CuSO_4 \cdot 5H_2O$	0.079
$Co(NO_3)_2 \cdot 6H_2O$	0.0494

notes: The ferric ammonium citrate should be autoclaved separately to eliminate precipitation and added aseptically after cooling.

: the Na_2CO_3 should be autoclaved separately if the desired final pH is above 8, and added aseptically after cooling.

Table IX. Herbarium material of Nodularia examined.

Nodularia spumigena

Berkeley no date Bristol, England NBV 3925-27
Bold 28 iii 1953 Goodeletsville, Tenn. F Nordin 1174
Braun 1847 Freiburg, Germany NBV 3925-15 PC Nordin 1338 (type of Kütz. S. Vriesiana)
Braun 1847 Freiburg, Germany NBV 3925-25 PC Nordin 1336
Brebisson? no date no location NBV 3925-71
Christensen 1731 14 v 1953 Washoe Co., Nev. F Nordin 1169
collector unknown (Kleibaden ?)vii 1839 Wangerooge, Germany NBV 3925-13
collector unknown 5 viii 1887 Danzig Bay, Poland NBV 3925-23
Collins no date West Brooksister, Maine NY Nordin 1276
Collins viii 1884 Rockingham Co., N.H. FH Nordin 1059 F Nordin 1178 NY Nordin 1286 NY Nordin 1292 NY Nordin 1296
Collins viii 1884 Hampton, N.H. NY Nordin 1279
Collins 2439 vi 1892 Cape Rosier, Maine FH Nordin 1060 NY Nordin 1287
Collins 3459 14 vii 1897 Cape Rosier, Maine NY Nordin 1289
Collins 5094 vii 1904 Casco Bay, Maine UC 752514 F 1219336
Collins 5526 (Phycotheca Borealis Americana 1307) 14 vii 1906 Harpswell, Maine UC 693286 FH Nordin 1061 NBV 3925-55 F 545467 NY Nordin 1288 NY Nordin 1296a PC Nordin 1333
Drouet 9844 9 xii 1948 Hancock Co., Miss. F 1310578
Farlow vii 1889 Woods Hole, Mass. UC 100562 FH 4555
Foslie (Wittrock, Nordstedt & Lagerheim, Algae Exsiccatae 1344) 10 viii 1889 Bugonaes, Norway UC 761551 UC 100562 NBV 3925-21 F 975766 NY Nordin 1295
Francis?* 1878? Lake Alexandrine near Adelaide, Australia FH Nordin 1064
Gardner 411 (PBA 1012) vi 1901 Whidbey Island, Wash. UC 100566 NBV 3925-72 F 980816 F 1047781 NY Nordin 1297 PC Nordin 1334
Gardner 436 15 vi 1901 Port Townsend, Wash. UC 100567
Gardner 3295 29 iv 1916 Oakland, Calif. UC 114844
Gardner 7231 14 iv 1933 San Mateo Co., Calif. FH Nordin 1081
Gardner 7946 11 v 1936 Contra Costa Co., Calif. UC 661724 FH Nordin 1056 NBV 3925-56 F 1043544 NY Nordin 1293

*Herbarium sheet FH Nordin 1064 has no collector's name on it but Francis apparently distributed his samples of Nodularia from this site. Bornet & Flahault (1888) report examining material from him.

Gomont? 30 viii 1885 Tables de la Loire, France PC Nordin 1323
Gomont? 15 viii 1894 Auvergne, France PC Nordin 1324
Gomont (Wittrock, Nordstedt & Lagerheim, Algae Exsiccatae 1343) viii 1894 Auvergne, France UC 761550 NBV 3925-49 F 975767 NY Nordin 1294
Habeeb 3738 15 v 1951 Pike Co., Pa. F Nordin 1176
Holden 1458-1461 28 v 1899 Bridgeport, Conn. FH Nordin 1062 NY Nordin 1290
Holden 30 vi 1899 no location NY Nordin 1291
Ibanez 27 x 1952 Trujillo, Peru F Nordin 1238
Joshua no date Cirencester, England F Nordin 1249
Kiener 13777 22 vii 1936 Cherry Co., Nebr. UC 679691 F 1127792
Kiener 10401a 21 vii 1941 Fillmore Co., Nebr. F 1099262
Kiener 13885 23 iv 1943 Dodge Co., Nebr. F 1131624
Kiener 14139 & 14140 6 vi 1943 Lancaster Co. Nebr. F 1132185 F 1132181
Kiener 16499 6 iv 1944 Kearney Co., Nebr. UC 689174 F 1144655
Kiener 21834 27 iii 1947 Dundy Co., Nebr. F 1220345
Kiener 21835 27 iii 1947 Dundy Co., Nebr. F 1220286
Kiener 23130 2 iv 1948 Garden Co., Nebr. F Nordin 1184
Kiener 23602-23604 17 v 1948 Lincoln Co., Nebr. F Nordin 1185 F Nordin 1186 F Nordin 1187
Koch 3 vii 1845 Borkum, Germany NBV 3925-17 NBV 3925-29a
Koch 3 vii 1846 no location NBV 3925-29b
LaRivers 61b 22 ix 1951 Washoe Co., Nev. F Nordin 1168
Lebel 415 14 v 1860 Mont d'Huberville, France NBV 3925-16 PC Nordin 1337a
Lebel 580 12 iv 1862 Negreville, France PC Nordin 1337b
Maldonado 41 i 1942 Lago Villa, Peru F 1102707 F 1102709
Mertens vi 1821 Norderney, Germany UC 436361 NBV 3925-15 NBV 3925-59 NBV 3925-64 NBV 3925-66 NBV 3925-67 NBV 3925-68 F 951302
Nordstedt (Wittrock & Nordstedt, Algae Exsiccatae 198) 11 vi 1877 Lomma, Sweden FH Nordin 1090 NBV 3925-50 NBV 3925-61 F Nordin 1250 NY Nordin 1298b
Nylander 1860 Helsinki, Finland PC Nordin 1317 PC Nordin 1318 PC Nordin 1319
Ostenfeld 5 viii 1901 Falster, Denmark NY Nordin 1285
Ostenfeld 1 viii 1904 Store Beelt, Denmark NY Nordin 1284
Osterhout 559 (not PBA 1061 as marked on UC specimens) 28 vi 1902 Alameda Co., Calif. UC 393931 UC 202712 NBV 3925-54 FH Nordin 1066 PC Nordin 1328
Osterhout & Gardner (PBA 1061) 30 v 1902 Oakland, Calif. FH Nordin 1087 NBV 3925-30 F 980816 NY Nordin 1263 PC Nordin 1302

Peters 14 v 1891 Atlantic City, N.J. F 1081208
Phinney 23M40 8 ii 1940 Emmet Co., Mich. F 1138192
Rose vii 1852 Berra, Germany NBV 3925-14 F 999057 NY Nordin 1259
Schmidt 1899-1900 Siam? PC Nordin 1322
Schmitz, Hauck & Richter (Phykotheca Universalis 142) viii 1886 Greifswalder Bodden, Germany UC760936 UC 953542 NBV 3925-58 NBV 3925-65 PC Nordin 1325 PC Nordin 1332
Setchell 1628 14 iv 1897 San Benito Co., Calif. UC 752513 F 1221362
Setchell & Jepson vii 1896 between La Grange, Stanislaus Co. & Coulterville, Mariposa Co., Calif. UC 202713 NBV 3925-53
Standey 65787 20 ii 1939 Rio Pucal Dept., Guatemala F 1023960
Suhr (Frolich?) vii 1834 Schleswig NBV 3925-57 NBV 3925-63 NBV 3925-70 PC Nordin 1326 PC Nordin 1335 (type of Kützings N. suhriana = N. spumigena Mertens & Suhr's Lyngbya annulata)
Taylor 3084 29 viii 1920 Nantucket Island, Mass. UBC 49982
Transeau 63 14 v 1911 Charleston, Ill. NY Nordin 1283
Thuret 30 viii 1874 Cherbourg, France FH Nordin 1063 PC Nordin 1327b
Thuret? viii 1874 Deauville, France FH Nordin 1065 NBV 3925-22 NBV 3925-24 PC Nordin 1327 PC Nordin 1331
Thwaites? v 1867 Shirehampton, England PC Nordin 1330
Van den Bosch no date Goes, Netherlands PC Nordin 1320
Wagenear-Hummelinck 641 11 v 1955 Aruba, Dutch Antilles NBV 3925-52
West 393 8 xii 1911 Birket Quarun, Egypt BM 302
Wille 1817a Laguna Guanica, Puerto Rico UC 463735 NY Nordin 1256

Nodularia harveyana

Apfel 51 & 52 19 i 1948 Burger Lakes, Antarctica F 1299674 F 1299701
Atkinson 1895 no location PC Nordin 1301
Atkinson 1895 no location PC Nordin 1321
Beeftink 0-199 29 viii 1951 Zeeuwsch-Vlaanderen, Netherlands NBV 3925-10
Beeftink 0-201 29 viii 1951 Zeeuwsch-Vlaanderen, Netherlands NBV 3925-11
Beeftink 450 28 vii 1955 Fort St. Phillipe, Belgium NBV 3925-33

Beeftink 451 28 vii 1955 Fort St. Phillipe, Belgium NBV 3925-32
Bierbrauer 6 vi 1953 Ostvoorne, Netherlands NBV 3925-12
Bilio 61025-2 29 vi 1961 Goeree, Netherlands NBV 3925-9
Bilio M107 24 ix 1965 Ostvoorne, Netherlands NBV 3925-8
Bilio 6 6 ix 1966 Noord-Beveland, Netherlands NBV 3925-4
Bilio 9 6 ix 1966 Noord-Beveland, Netherlands NBV 3925-3
Bilio W 6 ix 1966 Noord-Beveland, Netherlands NBV 3925-5
Bilio M 6 ix 1966 Noord-Beveland, Netherlands NBV 3925-6
Bilio 22B 17 x 1966 Goeree, Netherlands NBV 3925-2
Bilio 23A 17 x 1966 Goeree, Netherlands NBV 3925-7
Bold B143 12 i 1947 Nashville, Tenn. F 1211634
Bornet & Flahault (Wittrock & Nordstedt, Algae Exsiccatae 895) 25 ix 1886 Cosne, France UC 759399 FH Nordin 1082 NBV 3925-34 NBV 3925-35 F Nordin 1235 NY Nordin 1281 PC Nordin 1309
Brannon 141A 5 ii 1943 Gainsville, Fla. F 1124079 PC Nordin 1329
Casebolt 167 5 vi 1950 Clay Co., Mo. F Nordin 1198
Chapman Ib ix 1947 Stanley Bay, New Zealand F 1246844
Collins 4844 no date no location NY Nordin 1273 NY Nordin 1274
Collins vii 1884 Hampton, N.H. NY Nordin 1277
Collins 2387 14 vii 1892 Cape Rosier, Maine FH Nordin 1070 FH Nordin 1073 NY Nordin 1275
Collins 22 vii 1894 Cape Rosier, Maine UC 687705 FH Nordin 1072 NBV 3925-39 F 1209180 NY Nordin 1278 PC Nordin 1310
Collins (PBA 1062) 14 vii 1903 Casco Bay, Maine F 545439 NY Nordin 1280 PC Nordin 1307
Collins 5094 vii 1904 Casco Bay, Maine UC 752510 NBV 3925-37 F 1219372
Collins 16 viii 1904 Woods Hole, Mass. UC 752511
Collins 5845 10 vii 1908 Casco Bay, Maine FH Nordin 1069 NY Nordin 1272
Cramer (Rabenhorst Algen Sachsens 994) vi & vii 1860 Zurich, Switzerland FH Nordin 1084 NBV 3925-1 NY Nordin 1262 F 1002450
Demaree & Thomason 24582 1 viii 1943 Collins, Drew Co., Ark. F 1133627
Drouet 8766 28 x 1948 Calcasieu Parish, La. UC 910404 NBV 3925-45 F 1332708 PC Nordin 1311
Drouet, Glassman & Chapp 12711 2 vii 1957 Chicago, Ill. F Nordin 1203
Drouet, Glassman & Chapp 12696 2 vii 1957 Chicago, Ill. F Nordin 1202
Drouet, Madsen & Crowson 11511 27 i 1949 Wakulla Co., Fla. F 1324385

Drouet, Madsen & Crowson 11513 27 i 1949 Wakulla Co., Fla.
UC 912044 F 1324476
Drouet & McBride 4569 11 x 1941 San Bernardino Co., Calif.
UC 664554 FH Nordin 1076 NBV 3925-43 NY Nordin 1268
F 1101885
Drouet & Nielsen 11232 23 i 1949 Taylor Co., Fla. UC 912045
F 1308871
Drouet & Nielsen 11681 31 i 1949 Franklin Co., Fla.
UC 912043 F 1317616
Drouet & Richards 3416 23 xii 1939 Empalme, Mexico
F 1031425
Fritsch no date Winter Harbour, Antarctica BM 1815
Gardner 335 (PBA 1013) 19 v 1901 La Conner, Wash.
UC 100569 NBV 3925-38 F 546279 NY Nordin 1269
PC Nordin 1306
Gardner 989 (PBA 1063) 29 v 1903 Marin Co., Calif.
UC 341420 FH Nordin 1088 NBV 3925-48 F 980816
NY Nordin 1282 PC Nordin 1314
Gardner 1498 vii 1905 Oakland, Calif. UC 202866
F Nordin 1192
Gardner 1604 xi 1905 Berkeley, Calif. UC 202865
UC 274104
Gardner 3963 vii 1917 Sitka, Alaska UC 661526 F 1047757
Gardner 4151 i 1918 Oakland, Calif. UC 661636
FH Nordin 1078 NBV 3925-42 F 1032981 NY Nordin 1266
Gardner 6552 xii 1930 Berkeley, Calif. UC 440248
Gardner 6568 12 i 1931 Berkeley, Calif. UC 661705
FH Nordin 1075 NBV 3925-46 F 1033552 NY Nordin 1264
Gardner 7670 4 ii 1934 Berkeley, Calif. UC 641592
FH Nordin 1080 NBV 3925-40 F 1036391 NY Nordin 1270
Gardner 7963 7 vi 1936 Lake Merced, Calif. UC 661654
FH Nordin 1077 NBV 3925-41 F 1034223 NY Nordin 1267
Gomont 8 vi 1887 Paris, France PC Nordin 1303
Gomont 11 vii 1892 Cosne, France PC Nordin 1304
Groesbeck 90 12 vi 1940 Mono Co., Calif. F 1049304
Hansgirg vii 1888 Libochovice, Czechoslovakia F Nordin 1234
(Hansgirg 1892)
Hansgirg 1891 Hermanmestec, Czechoslovakia F Nordin 1233
Hollenberg 1553 23 iii 1934 Santa Ana River, Calif.
UC 634466
Johnson 6 v 1893 Ann Arbor, Mich. UC 752512 F 1157488
PC Nordin 1300
Kiener 10466 23 vii 1941 Redwillow Co., Nebr. F 1099440
Kiener 13617 17 xi 1942 Lancaster Co., Nebr. F 1127250
Kiener 15687 24 ix 1943 Keystone, Nebr. F 1139911
Kiener 20613a 23 v 1946 Sheridan Co., Nebr. F 1219490
Kiener 22773a 23 viii 1947 Scott's Bluff Co., Nebr.
F 1249366

Kiener 22778 24 viii 1947 Scott's Bluff Co., Nebr. F 1249569
Koster 6121 16 iv 1957 Penze, France NBV 3925-31
Lebel 791 & 792 no date France NBV 3925-16 NBV 3925-62
Lebel 998 24 vii 1869 LeHavre, France PC Nordin 1316
Louderback 17 22 viii 1947 Denver, Colo. F 1235673
Louver & Strickland 1130 9 v 1942 York Co., Va. UC 680411 F 1109792
Mabille 8 1 xi 1952 France F Nordin 1232 PC Nordin 1299
Muxter? 10 v 1916 Killery Pt., Maine FH Nordin 1071
Palmer, Webster, Prettyman, Webster & Drouet 2518 17 viii 1939 Indianapolis, Ind. F 980816
Patrick 197 24 vii 1947 Xochimilco, Mexico F Nordin 1241
Pearson 26 no date South Africa BM Nordin 1348
Roussel 16 viii 1869 Talatus?, France PC Nordin 1315
Scott 30 iii 1941 Bay St. Louis, Miss. F 1085870
Setchell 1679 no date San Francisco, Calif. UC 100563
Setchell 17 i 1889 Cambridge, Mass. UC 100565
Standley 14 iii 1940 Punta Rossa Lee Co., Fla. F 1030027
Thuret 31 vii 1874 Cherbourg, France PC Nordin 1298 PC Nordin 1305
Thuret 19 viii 1874 Cherbourg, France FH Nordin 1083 NBV 3925-36 PC Nordin 1308
Thuret? vii 1889 Cosne, France PC Nordin 1313
Velasquez, Richards & Drouet 2507 4 viii 1939 Cook Co., Ill. F 980549
Wolle & Drouet 2302 26 viii 1938 Somerset Co., Md. FH Nordin 1074 NY Nordin 1271 F 939834 UBC 49983

The following specimens were in too poor a condition or in insufficient numbers to make a judgement on their identification.

collector unknown ix 1885 Pavia, Germany NBV 3925-26
Drouet & Louderback 5739 21 viii 1946 Salt Lake Co., Utah F 1198553
Drouet & Richards 2709 26 x 1939 Sierra Co., N. Mex. F 1038909
Fan 10130 19 vi 1954 Hubbard Co., Minn. UBC 49981 (Drouet 1956)
Gardner 602 vii 1899 Whidbey Island, Wash. UC 100568
Kiener 13940 23 iv 1943 Dodge Co., Nebr. F 1131688
Runyon & Lillick 609 25 ix 1933 Columbus, Ohio FH Nordin 1058
Stockmayer (Vindobon Kryptogamas Exsiccatus 428) viii 1893 Frankenfels, Austria FH Nordin 1086
Taylor 1923 Purcell Range, British Columbia (Taylor 1928a) uncatalogued material at UBC

West 44 1 viii 1904 Niamkolo, Tanganyika BM Nordin 1344
West 22 23 vi 1904 Nkata Bay, Tanganyika BM Nordin 1346
West 134 10 xi 1904 Komba Bay, Tanganyika BM Nordin 1347
West 208 10 i 1905 Toa, Tanganyika BM Nordin 1345
West 432 10 i 1905 Toa, Tanganyika BM 303

The following material is more properly placed in a genus other than Nodularia

Aavd? 7 vii 1853 Leipzig, Germany FH Nordin 1068 = Scytonema sp.
Allen 5079a 2 iv 1953 from herbarium specimen F Nordin 1181 = Calothrix sp.
Crossland 7292 23 x 1929 Tahiti UC 696203 = Hormothamnion (solutum?) Born. & Grun.
Fritsch 363 no date Winter Harbour, Antarctica BM 1934 = Anabaena sp.
Gardner 3305 9 v 1916 Berkeley, Calif. UC 661514 FH Nordin 1079 NBV 3925-44 F 1033572 NY Nordin 1265 = Anabaena variabilis
Rabenhorst (Algen Sachsens 469) vii 1855 Ultdobern, Germany FH Nordin 1067 NBV 3925-28 NY Nordin 1260 = Scytonema sp.
Rabenhorst (Algen Sachsens 470) vi 1855 Zurich, Switzerland UC 432853 FH Nordin 1089 NBV 3925-60 NBV 3925-69 F 1015345 F 1015346 F 1015349 NY Nordin 1261 = Anabaena sp.
Roussel 4 ix 1851 "Meloduuo", France PC Nordin 1312 = Anabaena sp.
Rrealea x 1857 Attelobern, Germany NBV 3925-19 NBV 3925-20 = Scytonema sp.
Setchell 23 viii 1889 Walite Hill Pond, R.I. UC 100564 = Nostoc (carneum?) Ag.
Tilden (American Algae 484) 22 v 1900 Oahu, Hawaii UC 740394 NY Nordin 1258 PC Nordin 1339 UBC 2971 - Hormothamnion sp.
Tilden (South Pacific Algae 11) x 1909 Tahiti UC 233460 NBV 3925-47 NY Nordin 1257 = Hormothamnion sp.
Wille 282d 6 i 1915 Coamo Springs, Puerto Rico UC 401708 FH Nordin 1085 NY Nordin 1255 = Scytonema sp. Nostoc sp.
Wille 1415a no date Puerto Rico UC 401800 NY Nordin 1254 = Scytonema sp. Nostoc sp.

Table X. Synonomy of *Nodularia* /Mertens in Juergens/ Bornet et Flahault 1888

Nodularia spumigena /Mertens in Juergens/ Bornet et Flahault 1888

- *N. spumigena* var. *genuina* Bornet et Flahault
- *N. spumigena* var. *litorea* Bornet et Flahault
- *N. spumigena* var. *major* Bornet et Flahault
- *N. spumigena* var. *vacuolata* Fritsch
- *N. spumigena* var. *aerophila* Brabez
- *N. spumigena* f. *crassa* (Woronichin) Elenkin
- *N. armorica* Thuret
- *N. willei* Gardner

Nodularia harveyana (Thwaites) Thuret 1875

- *N. harveyana* var. *sphaerocarpa* (Bornet et Flahault) Elenkin
- *N. aerophila* Brabez
- *N. skujae* Gonzalez-Guerro
- *N. sphaerocarpa* Bornet et Flahault
- *N. spumigena* var. *minor* Fritsch
- *N. turicensis* (Cramer) Hansgirg

Species Excludendae

- *N. epiphytica* Gardner = *Nostoc* sp. (juvenile)
- *N. fertilissima* Randawa *nom. nud.*
- *N. fusca* Taylor = conglomerate
- *N. hawaiiensis* Tilden = *Hormothamnion* ?*solutum* Bornet et Flahault
- *N. implexa* (Bornet et Flahault) Bourrelly
  = *Aulosira implexa* Bornet et Flahault
- *N. quadrata* Fritsch = *Anabaena* sp.
- *N. spumigena* var. *zujaris* Gonzalez-Guerro = *Anabaena* sp.
- *N. tenuis* G.S. West = *Anabaena* sp.

continued....

Species Inquirendae

N. mainensis F.L. Harvey

N. paludosa Wolle

Spermosira atlantica Dickie