Cover Page

Universiteit Leiden

Leiden University Repository

The handle http://hdl.handle.net/1887/20260 holds various files of this Leiden University dissertation.

Author: Becking, Leontine Elisabeth
Title: Marine lakes of Indonesia
Date: 2012-12-04

Marine Lakes of Indonesia

Becking, Leontine Elisabeth

Marine Lakes of Indonesia

Lay-out by René Glas (www.reneglas.com)
Printed by Wöhrmann Print Service, Zutphen

ISBN: 978-94-6203-213-2

2012, ALL RIGHTS RESERVED

De totstandkoming van dit proefschrift werd financieel mogelijk gemaakt door:

- De Nederlandse Organisatie voor Wetenschappelijk Onderzoek (NWO-ALW # 817.01.008)
- Naturalis Biodiversity Center
- National Geographic/Waitt Grant
- De Beukelaar – van der Hucht Stichting
- Koninklijke Nederlandse Akademie Wetenschappen
- INNO/Wereld Natuur Fonds subsidie
- Conservation International & David and Lucile Packard Foundation
- Alida M. Buidendijk Fonds
- Jan Joost Ter Pelkwijk Fonds
- Leids Universiteits Fonds

Marine Lakes of Indonesia

Proefschrift

ter verkrijging van

de graad van Doctor aan de Universiteit Leiden,

op gezag van Rector Magnificus prof. mr. P.F. van der Heijden,

volgens besluit van het College voor Promoties

te verdedigen op dinsdag 4 december 2012

klokke 15:00 uur

door

Leontine Elisabeth Becking

geboren te Amsterdam

in 1978

Promotiecommissie

Promotor	prof. dr. E. Gittenberger (Universiteit Leiden)
Co-promotor	dr. N.J. de Voogd (Naturalis Biodiversity Center)
Overige leden	prof. dr. C.J. ten Cate (Universiteit Leiden) prof. dr. S.B.J. Menken (Universiteit van Amsterdam) prof. dr. G. Wörheide (Ludwig-Maximilians Universität München) dr. B.W. Hoeksema (Naturalis Biodiversity Center) dr. R.W.M. van Soest (Naturalis Biodiversity Center)

To my mother and sister

for their inspiration and support

Table of Contents

SUMMARY 11

THESIS OUTLINE 15

I General Introduction

1 Recently discovered landlocked basins in Indonesia reveal great habitat diversity in anchialine systems 21

II Species Assemblages

2 Sponge community composition in the Derawan Islands, NE Kalimantan, Indonesia 55

3 Sponge species composition, abundance and cover in marine lakes and coastal mangroves of Berau, NE Kalimantan, Indonesia 77

III Taxonomy

4 A new *Suberites* (Porifera: Demospongiae: Hadromerida: Suberitidae) from the Indo-West Pacific 111

5 Revision of the genus *Placospongia* (Porifera: Demospongiae: Hadromerida: Placospongiidae) in the Indo-Pacific 123

IV Phylogeography

6 Phylogeography of the sponge *Suberites diversicolor* in Indonesia: insights into the evolution of marine lake populations 153

7 Are marine lakes cradles or refuges of diversity? A mussel's (*Brachidontes* sp.) perspective 173

REFERENCES 191

SAMENVATTING (DUTCH) 201

RINGKASAN (INDONESIAN) 205

CURRICULUM VITAE 209

PUBLICATIONS 211

I discovered in nature the nonutilitarian delights that I sought in art. Both were a form of magic, both were a game of intricate enchantment and deception.

Vladimir Nabokov, 1951

"Speak, Memory"

The objective of this thesis is to obtain insight into the processes that play a role in biodiversity patterns of tropical marine species by using marine lakes as a model. It has long been hypothesized that marine species in general have large geographic ranges with large population sizes, and face weaker barriers to dispersal than terrestrial organisms. Recent population genetic and phylogenetic studies, however, show a different picture of population differentiation at small spatial scales. This suggests there may be many more barriers for dispersal and consequently more opportunities for allopatric speciation for marine organisms than initially assumed. The marine lake setting with clearly delineated contours provides an opportunity to study species assemblage patterns and early stages of evolution in coastal marine taxa in isolated environments. Marine lakes are little known anchialine habitats. The term anchialine refers to landlocked water bodies that maintain a marine character through narrow submarine connections to the sea. They display a tidal regime that is typically delayed in phase and dampened in amplitude compared to the adjacent sea. The lakes are usually situated in natural inland depressions in between hills; hence they are not visible from the coast. It is unknown exactly how many marine lakes there are worldwide, but the number is estimated at approximately 200 with clusters of ten or more lakes occurring in karstic limestone areas such as Croatia, Bermuda, Vietnam, Palau, and Indonesia. The lakes we see today were formed less than 1500 years ago. Each lake is thus ephemeral on a geological timescale, but the marine lakes ecosystem has probably been present through time. The few studies that focused on the biodiversity of marine lakes, conducted in Palau and Vietnam before the present thesis, portrayed a scenario of isolated populations and a high abundance of species rare or absent elsewhere. These results indicate that marine lakes are remarkable marine ecosystems with an untapped potential for studies on marine biodiversity and evolution, i.e. natural laboratories of evolution.
In this thesis I have studied recently discovered marine lakes in two regions of Indonesia: the Berau region in East Kalimantan (Borneo island) and the Raja Ampat region in West Papua (New Guinea island). The aim was to unveil spatial biodiversity patterns in marine lakes in order to establish to what extent they represent isolated coastal environments. The following questions were addressed:

1. What are the different types of marine lakes in Indonesia?
2. Are the species assemblages in marine lakes distinct from those in the adjacent coastal environments?
3. To what extent are the populations in the lakes isolated?
4. Can marine lakes in Indonesia be considered natural laboratories of evolution?

When I began my PhD in 2007 little was known about marine lakes in Indonesia. As a result much descriptive groundwork (e.g. locating the lakes, describing their geographical and physical characteristics and unraveling the taxonomy of the species residing in these lakes) was a prerequisite before any further analytical studies could be performed. Sponges were chosen as a target group to measure biodiversity, because sponges are one of the most diverse taxa in the lakes and concomitantly constitute important players in reef and mangrove systems outside of the lakes in terms of diversity, biomass and filtering activities. This made them an ideal candidate to compare biodiversity inside and outside the lakes. Three different aspects of isolation

were considered in order to establish whether the lakes in Indonesia are isolated environments:

(a) the physical degree of connection of the water between the lakes and the sea; the amount of exchange of water with the adjacent sea differs per lake and can function as a proxy for the degree of physical isolation of a lake.

(b) the patterns of species assemblages of sponges; variation in species assemblages between localities can provide information on marine area relationships or connectivity, reflecting the processes operating in those areas.

(c) the genetic patterns of populations of two typical species of marine lakes: the sponge *Suberites diversicolor* (Porifera: Demospongiae: Hadromerida: Suberitidae) and the mussel *Brachidontes* sp. (Mollusca: Bivalvia: Mytilidae); molecular markers are well suited to estimate levels of connectivity between natural populations and to estimate levels of diversity and divergence within populations.

If the lakes are in high connection to the adjacent sea and to each other we would expect to find similar species assemblages and little genetic differentiation between populations, particularly between geographically close localities.

1. *What are the different types of marine lakes in Indonesia?*

The results of this thesis show that there is a large diversity in types of marine lakes and many more remain to be documented in Indonesia (CHAPTER 1). There is a gradient in the degree of connection to the sea. The higher the connection the more the lake resembles a lagoon in both water chemistry and biota, while the more isolated lakes have brackish water and contain unique species that are rarely found in the adjacent sea.

2. *Are the species assemblages in marine lakes distinct from the adjacent coastal habitats?*

The spatial variation in sponge species composition of assemblages in marine lakes, coastal mangroves and coral reefs in Berau (East Kalimantan, Indonesia) was systematically and quantitatively measured. These comprehensive studies show that marine lakes are true sponge gardens containing strikingly different assemblage of sponge species with just a subset of the adjacent sea fauna (CHAPTERS 2, 3, 4 & 5). The lake assemblages consist of three groups of sponge species: (a) widespread species known from various coastal locations in Indo-Pacific reefs, (b)lake species that only occur in lake systems, (c) endemic species restricted to a single lake. These marine lakes significantly contribute to the regional diversity due to the presence of lake and endemic species. Over half of the species in these marine lakes do not have a scientific name and need to be described in a taxonomic framework (CHAPTERS 1, 3, 4 & 5).

3. *To what extent are the populations in the lakes isolated?*

In addition to a unique species diversity, lakes can harbor genetic variants not found elsewhere (CHAPTERS 6 & 7). In both *Suberites diversicolor* and *Brachidontes* populations, two highly diverged lineages were detected that may represent cryptic species(CHAPTERS 6 & 7). Furthermore, in both species we see a pattern

emerging of possible recent local diversification in the largest and most isolated marine lake in Indonesia (Kakaban lake in East Kalimantan). The patterns of genetic variation found in the marine lake populations are generally consistent with populations in isolated environments. Isolation of marine lake species assemblages and populations may be the result of strong barriers to dispersal and/or different selective regimes within the lakes.

4. *Can marine lakes in Indonesia be considered natural laboratories of evolution?*

The lakes are no older than 15000 years old, yet much of the species and genetic diversity appears to be restricted to each lake (all CHAPTERS). Given the areal definition of an endemic as spatially restricted species, centers of endemism could be areas where species arise and remain (cradles), and/or the last stand of previously widespread species (refuge). The lakes appear to be cradles of diversity resulting from recent divergence of evolving populations within the lakes (Chapter 6 & 7). The lakes also may serve as refugia for ancient lineages, relicts of marine or older anchialine lake species and populations (Chapter 3, 6 & 7). The role of marine lakes in supporting endemism may thus reflect enhanced survival of endemics, with the possibility of population differentiation that in time may lead to speciation. This thesis only hints at some of the consequences of short term isolation on structuring marine assemblages and populations, but a wealth of information can be gained from studying the interplay of organisms and environments in the marine lakes of Indonesia. Further study of marine lakes will enhance our understanding of some of the physical and ecological processes responsible for diversification in tropical shallow marine environments.

The findings of this PhD research also have important implications for conservation. The marine lakes share characteristics with island systems: they are well-defined geographically (CHAPTER 1), harbor unique biota with a large proportion of endemics and/or an abundance of species rare elsewhere (CHAPTERS 2, 3, 4 & 5), and isolated populations (CHAPTERS 6 & 7). Like island systems marine lakes are vulnerable to anthropogenic threats such as exploitation and alien species introduction. All chapters of this thesis reveal that much species diversity remains to be described. As a result of their many special features, marine lakes should play a prominent role in the marine conservation planning of both Berau and Raja Ampat.

This thesis contains four sections divided into seven chapters.

Section 1: General introduction

Chapter 1 provides a general introduction to anchialine systems and a description of the study sites in Indonesia. Extensive exploration in Indonesia, using local knowledge, a Drifter water plane, and Google Earth satellite images, resulted in the discovery of 23 anchialine systems new to science. This chapter gives a thorough description of these systems. Based on parameters such as bathymetry, size, coastline, salinity, water temperature, pH, degree of connection to the sea, and the presence-absence of selected key taxa, three types of (non-cave) anchialine systems are distinguished in the Indo-Pacific: (a) marine lakes with large and deep basins containing brackish to almost fully marine waters, (b) anchialine pools consisting of small and shallow basins containing brackish water and low diversity of macrofauna, (c) blue pools in chasms that contain water with a clear halocline which are are possibly connected to anchialine caves. Marine lakes show a range in the degree of connection to the sea with the result that the higher the connection the more the lake resembles a lagoon in both water chemistry and biota, while the more isolated lakes have brackish water and contain species that are rarely found in the adjacent sea.

Section 2: Species assemblages

For this section the spatial variation in sponge species composition of assemblages and abundance was systematically and quantitatively measured in the Berau region (East Kalimantan in Indonesia) in the marine lakes Kakaban and Haji Buang, and the adjacent mangroves and coral reefs. The aim was to assess if the assemblages varied between sites and relate the variation to environmental, habitat and spatial variables.
In **Chapter 2** we recorded the sponge species in the reefs of Berau. A total of 168 species were identified in the reefs. Sponge composition varied in relation to distance from the Berau River and water visibility, in addition to sand cover and cover of encrusting corals. Sponges in the Berau reefs appeared to thrive in inshore reefs near the river outlet which is an area with species poor coral communities.

In **Chapter 3** we documented the sponge species diversity in marine lakes and mangroves in the Berau region. A total of 115 sponge species were identified, 33 of which were restricted to Kakaban lake, 18 to Haji Buang lake and 30 to coastal mangroves. Our results show that marine lakes may represent a distinct environment from marine coastal mangroves with significantly higher sponge cover and abundance as well as a markedly different species composition. In both lake and outer coastal mangrove environments there was a pronounced gradient in composition away from the shore with the primary difference being between solid (root or rock) and soft substrates (mud or sand).

Section 3: Taxonomy

Taxonomy is the science of classifying organisms, or put more simply the study of naming and describing species. The marine lakes studied in this thesis are situated in an area known as the Indo-Australian Archipelago which houses the world's largest concentration of marine biodiversity, a large portion of which is yet undescribed. The objective in this section was to produce the taxonomy of the target species that could be used for subsequent population genetic analysis.

In **Chapter 4** the sponge *Suberites diversicolor* sp. n. (Porifera: Demospongiae: Hadromerida: Suberitidae) is described from four marine lakes located in Indonesia and from a brackish inshore area in Singapore. *Suberites diversicolor* sp. n. differs from known shallow water species of the genus *Suberites* in the tropical Indo-Pacific due to its diverse display of color-morphs and the presence of larger tylostyles with a wide size range. This species is typical of marine lake environments in the Indo-Australian Archipelago and the study of its populations allows comparison of multiple lakes with varying degrees of connection to the sea. **Chapter 5** contains a revision of the genus *Placospongia* (Porifera: Hadromerida: Placospongiidae) from the Indo-Pacific was revised. Species of the genus *Placospongia* are common within the tropical Indo-Pacific, occurring in a wide variety of environments from marine lakes, coral reefs and mangroves. There are at least four species of *Placospongia* within the wider Indo-Pacific that can be distinguished by internal skeletal spicule features, but not by external habitus and coloration: *Placospongia anthosigma, Placospongia carinata, Placospongia mixta, Placospongia melobesioides, Placospongia santodomingoae* sp.n.. Two additional, possibly morphologically cryptic, species have been identified by molecular markers.

Section 4: Phylogeography

Phylogeographic studies of taxa inhabiting marine lakes provide excellent opportunities to study biogeographical relationships and population structures of marine species in isolated habitats. Phylogeography is a field of study concerned with the principles and processes governing the geographic distributions of genealogical lineages, especially those within and among closely related species. The discipline focuses on historical and phylogenetic components of population structure. The aim of this section was to estimate levels of diversity and divergence within marine lake populations of two target species and to assess if they are isolated. If marine lakes are isolated environments we would expect to find genetic and/or morphological differentiation between the lake populations.

In **Chapter 6** we studied the phylogeography of the sponge *Suberites diversicolor* (Porifera: Demospongiae: Hadromerida: Suberitidae) in seven marine lake populations and three coastal populations using two mitochondrial and two nuclear markers. We found two divergent lineages (A & B) in populations of *S. diversicolor* that may constitute morphologically cryptic species. There was strong spatial structuring of the genetic populations based on the molecular markers we used. Kakaban lake (Berau, East Kalimantan) housed the highest genetic diversity with genetic variants that were not found in any of the other populations. Kakaban may be an area where multiple putative refugia populations have come into secondary contact, resulting in the high genetic diversity.

In **Chapter 7** the results of chapter 6 are supplemented by studying the phylogeography of a co-distributed but unrelated taxon, the mussel *Brachidontes* sp. (Mollusca: Bivalvia: Mytilidae) in Indonesia and Palau. We sequenced three genes (one mitochondrial and two nuclear) of four populations of *Brachidontes* sp. from

three marine lakes and one coastal mangrove in Indonesia. Subsequently we examined variation in shell shape using a geometric morphometric approach. By combining our data with sequences from *Brachidontes* populations from Palau we detected that the Indonesian populations of *Brachidontes* harbored deeply diverged lineages that were strongly supported by morphological characters. The Indonesian marine lake *Brachidontes* sp. populations are isolated from each other with possible local diversification within the lakes.