Recently discovered landlocked basins in Indonesia reveal high habitat diversity in anchialine systems

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Abstract In this article, the variability of physical settings of anchialine systems in Indonesia is discussed together with the consequences these settings have for the environment and biota within the systems. Exploration in two karstic areas (Berau, East Kalimantan and Raja Ampat, West Papua) has resulted in the discovery of 20 previously unknown anchialine systems in Indonesia. 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 we distinguish three types of (non-cave) anchialine systems in the Indo-Pacific: (1) Marine lakes with large and deep basins containing brackish to almost fully marine waters. 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 unique species that are rarely found in the adjacent sea. (2) Anchialine pools with small and shallow basins containing brackish water and low diversity of macrofauna. (3) Blue pools in chasms that contain water with a clear halocline and are possibly connected to anchialine caves. Study of the many unique features of anchialine systems will enhance our understanding of the physical and ecological processes responsible for diversification in tropical shallow marine environments.

Keywords Anchialine pools · Marine lakes · Raja Ampat · Berau · Mangroves · Karstic limestone

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Introduction

Anchialine systems are small bodies of landlocked seawater that are isolated in varying degrees from the surrounding marine environment, containing water at sea level in natural depressions, craters, and caves, either in lava or limestone. The marine character of these systems is maintained by subterranean tunnels, fissures, cracks, or small dissolution channels in the surrounding rock, connecting the lakes to the adjacent

sea. This environment has set the stage for small, isolated, rapidly evolving populations, and endemic (sub)species (Tomascik & Mah, 1994; Dawson & Hamner, 2005; Martínez García et al., 2009). Many rare and novel genera and species across a large spectrum of taxa have been found in anchialine systems (Holthuis, 1973; Maciolek, 1983; Tomascik & Mah, 1994; Kott, 1995; Fransen & Tomascik, 1996; Massin & Tomascik, 1996). The anchialine systems that we observe today are thought to be a young phenomenon, having originated during the Holocene, somewhere between 7,000–12,000 years before present (Dawson et al., 2009). In their present location, these systems may be ephemeral in a geological timescale, but anchialine systems have probably always been present through time (Iliffe, 2000; Sathiamurthy & Voris, 2006).

The term anchialine was originally defined by Holthuis (1973) as a system "with no surface connection to the sea, containing salt or brackish water, which fluctuates with the tides". Brock & Kam (1997) subsequently provided a working definition for anchialine pools as "pools isolated from other bodies of water at the highest tides." Since the 1970s, there has been heightened interest in anchialine systems, particularly anchialine caves—systems mostly covered by land with restricted exposure to open air (e.g., Iliffe, 1991; Iliffe, 2000; Humphreys & Eberhard, 2001; Jaume et al., 2009; Martínez García et al., 2009). As a result, the anchialine cave system has been comprehensively defined (Sket, 1996; Iliffe, 2000). In fact, the interest in caves was so great that Stock et al. (1986) proposed to amend the definition of 'anchialine' by adding the phrase "usually with restricted exposure to open air". Their rationale being that the majority of anchialine systems would be cave-like, open lakes being a rare phenomenon. Since then, however, numerous authors have located anchialine lakes, pools, and ponds (i.e., systems exposed to air) from a variety of geographic localities, for example, in the Mediterannean (e.g., Benivic et al., 2000; Katsa-nevakis, 2005), Caribbean (Thomas et al., 1992), Palau (e.g., Hamner & Hamner, 1998; Dawson & Hamner, 2005), Micronesia (Ng et al., 1996), Hawaii (e.g., Brock & Kam, 1997), Vietnam (e.g., Cerrano et al., 2006), and Indonesia (e.g., Tomascik et al., 1997; Hoeksema, 2004; Becking & Lim, 2009). It is evident from this bulk of literature, however, that a variety of terms have been used intermittently for

these systems and with little demarcation between the different types of lakes and pools. Most noteworthy is the term 'marine lake' that has become common place in the scientific literature as well as in popular science for anchialine lakes (Hamner & Carleton, 1979; Hamner & Hamner, 1998; Dawson et al., 2001; Dawson et al., 2009). For the benefit of continuity, we adopt this term, though we would like to stress that marine lakes are to be considered anchialine systems.

Anchialine pools can occur in high abundances in both karstic limestone as well as in irregular porous lava flows (Holthuis, 1973; Iliffe, 2000). Large numbers (over 100) of anchialine pools have been found in the lava-rock of Hawaii (e.g., Holthuis, 1973; Brock & Kam, 1997). The number of marine lakes worldwide is estimated at ~200 based on direct and indirect reports, as well as maps and satellite images (Dawson et al., 2009). Areas where clusters of ten or more lakes occur are located in Croatia, Bermuda, Vietnam, Palau, and Indonesia (Dawson et al., 2009). These areas have karstic settings in common, even though their geologic histories are widely different.

Kakaban lake in East Kalimantan, Indonesia, is one of the largest marine lakes presently known to science and was first scientifically described by Kuenen (1933) during the Dutch "Snellius" expedition to Indonesia from 1929–1930. The lake and its biota were described in more detail by Tomascik & Mah (1994) who called the lake "*Halimeda* lagoon". As a result of their fieldwork many rare and novel genera and species were found across a variety of taxa: a varunine crab (*Orcovita saltatrix* Ng & Tomascik, 1994), two holothurians (*Holothuria* (*Lessonothuria*) *cavans* Massin & Tomascik, 1996 and *Synaptula spinifera* Massin & Tomascik, 1996), and an ascidian (*Styela complexa* Kott, 1995).

A large portion of anchialine taxa have geographically widespread distributions, even though they are adapted to unique niche environments. For example, *Antecaridina lauensis* (Edmondson, 1935) and *Parhippolyte uveae* Borradaile, 1899 are shrimp species with red integumentary pigment and almost only occur in anchialine environments, yet have an extensive (disjunct) geographical distribution from the Red Sea to Hawaii (Holthuis, 1973; Maciolek, 1983; Fransen & Tomascik, 1996). In the Hawaiian archipelago, the small red shrimp *Halocaridina rubra* Holthuis, 1963 typifies the anchialine pools and the

high evolutionary diversification between the various populations was probably driven by population fragmentation and isolation in the aquifers within the islands (Craft et al., 2008; Santos, 2006). A remarkable feature of marine lakes is the vast populations of several subspecies of the jellyfish *Mastigias papua* (Lesson, 1830) that occur enclosed in certain lakes in Palau and Indonesia and most likely radiated from the ubiquitous common ancestor in the sea (Dawson & Hamner, 2005). These subspecies have an adapted morphology compared to the 'ancestral' *M. papua* morphotype from the sea, where a correlation was observed between the presumed age of the lake and the degree of adaptation to the environment (Dawson, 2005).

The physical and chemical characteristics of the lakes and pools have ecological implications for the flora and fauna that reside in them. It is necessary to have a good baseline description of the systems in order to comprehend the distributions and adaptations of the unique anchialine taxa. From 2007 to 2009, we conducted an extensive search and survey of anchialine lakes and pools in Indonesia. In this article, we discuss the variability of the setting in which these systems occur, and the implications for the environments and biota within the systems.

Study areas

We surveyed anchialine lakes and pools on islands in two regions in Indonesia; the islands of Kakaban and Maratua in the Berau region, East Kalimantan Province (Fig. 1A) and the islands Wayag, Urani, Mansuar, and Gam in the Raja Ampat region, West Papua Province (Fig. 1B, C). Monthly precipitation in Berau and Raja Ampat ranges from 200–275 mm with no clear seasonal pattern (Renema, 2006; Prentice & Hope, 2007).

Kakaban island is a trapezoidal shaped island with a maximal (diagonal) length of 7 km and a 40–60 m high Pliocene limestone ridge encircling a large marine lake (Figs. 1A, 2A). The southern coast of Kakaban island has a beach with *Avicennia* mangroves; the remainder of the coast surrounding the island is exposed rock in direct contact with the sea. Steep reef walls surround the island and the maximum depth is ~200 m. A general description of flora and fauna of Kakaban Lake was provided by Tomascik & Mah (1994) and Tomascik et al.

(1997). Maratua is a horse-shoe shaped island with a rim of raised Pliocene limestone that is 0.3–1.4 km wide and 10–120 m high (Fig. 1A). The island hugs a large lagoon of ~29.5 × 6.5 km with a depth of 0.5–5 m at low tide. Tomascik et al. (1997) mentioned the existence of 'anchialine lagoons' on the inner side of the raised rim of Maratua with the presence of *M. papua*, but they gave no further information on the location or characteristics of these lakes. The first records of species and localities of the Maratua lakes were published in a technical report resulting from a KNAW-Naturalis-LIPI expedition to the Berau Region (Hoeksema, 2004). Two lakes, Haji Buang and Bamban, separated by a limestone cliff and a mangrove swamp, were reported on the western arm of Maratua Island.

Raja Ampat constitutes a group of islands at the northern tip of Bird's Head peninsula in West Papua and is an intricate and rugose karst system of late Miocene limestone. Lakes were found on the islands of Mansuar, Gam, Wayag and Urani (Fig. 1B, C). Each of these islands is characterized by a karstic scenery including a complex shaped coastline and frequent occurrence of inland depressions (Figs. 3I and S5A–E). The islands of Wayag and Urani in Northern Raja Ampat are characterized by the scarcity of freshwater sources and as such are practically uninhabited. The lakes and pool on Gam and Mansuar islands were located during the EWIN-LIPI-Naturalis expedition to Raja Ampat in 2007 (Becking et al., 2008. Previous descriptions of biota from lakes on Gam and Mansuar island only include ascidians Monniot (2009).

Methods

Locating lakes

In Berau, the locations of three lakes had been reported in literature: Kakaban lake, Haji Buang lake, and Bamban lake (Kuenen, 1933; Tomascik et al., 1997; Hoeksema, 2004) and the local people from Maratua island were knowledgeable of the anchialine pools present on the island. Many of the islands of Raja Ampat are only sparsely inhabited and we had to use other means than local knowledge to locate the lakes: Google Earth satellite images and a Drifter water-airplane (Fig. S5F).
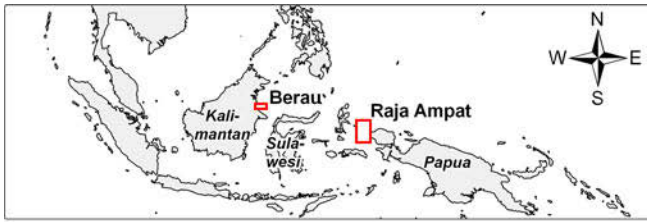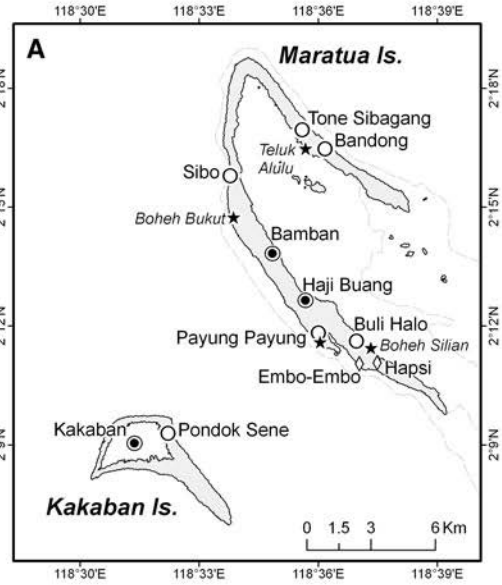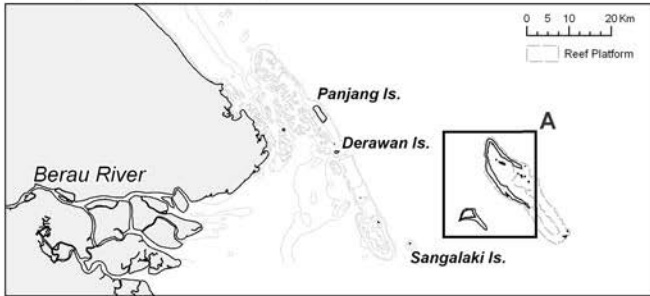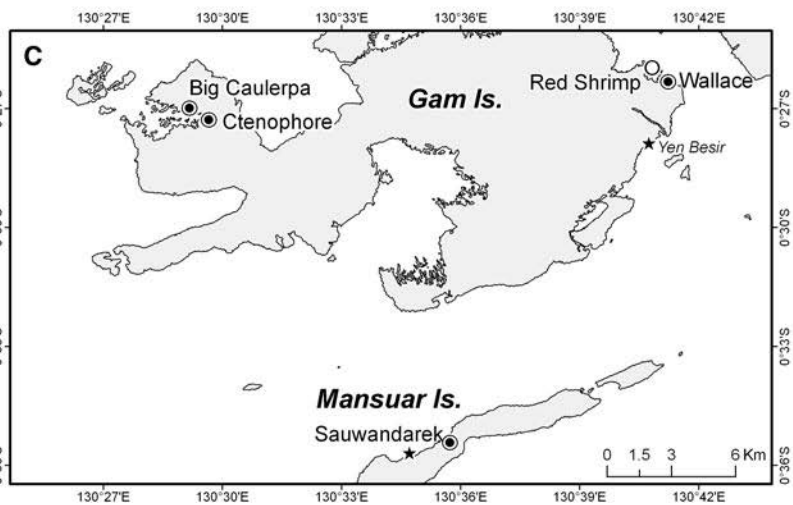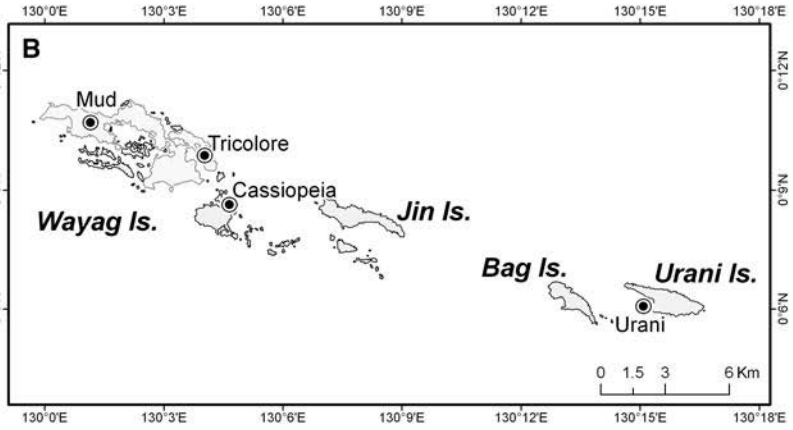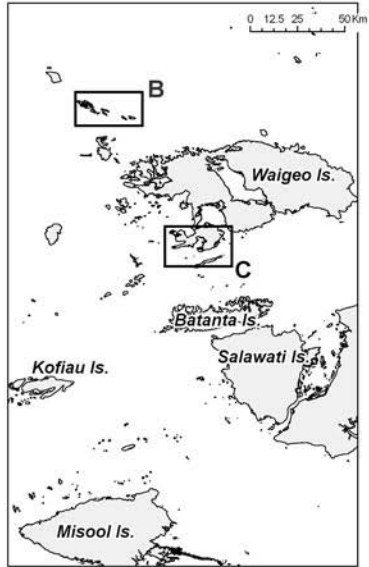
Fig. 1 Study areas in Indonesia. **A** Berau, East Kalimantan, **B** northern Raja Ampat, **C** central Raja Ampat, West Papua. *Filled circles*, *empty circles*, *diamonds*, and *stars* represent lakes, pools, chasms, and villages, respectively. Names of islands, anchialine systems, and villages indicated in the map

Measurements

In Berau salinity, pH and temperature was measured with a handheld multimeter YSI63-50. At least three recordings were made per sample site, unless mentioned otherwise. In Raja Ampat, a STX-3 Salinity Refractometer (Vee Gee Instruments) was used to determine the salinity (in parts per thousand, ppt) and a Waterproof Multimeter Testr35 (Oakton) to determine the pH. Both instruments had been calibrated with the YSI63-50 in salinity and pH. Measurements were made in September 2008 and in May 2009. The

minimal distance to the sea (over land) was measured from the rim of the lake to the nearest outer rim of the surrounding island. The outlines of the lakes were obtained by using the track-option in a handheld GPS device (Garmin GPS 60) walking, swimming or rowing along the perimeter. Satellite images (Berau, Landsat ETM 2001 Path 116/Row58; Raja Ampat, Landsat ETM 1999 Path 108/Row 60) and aerial photographs were used as a reference to adjust the coastline tracks. Depth measurements were made every 10–25 m using a handheld sonar system PX Hawk Eye CE and these measurements were georeferenced along a straight axis from one end to the other of the lake, subsequently zig-zag tracks were made from opposite sides of the lakes crossing the initial straight axis. The obtained perimeter and georeferenced depth-measurements were analyzed
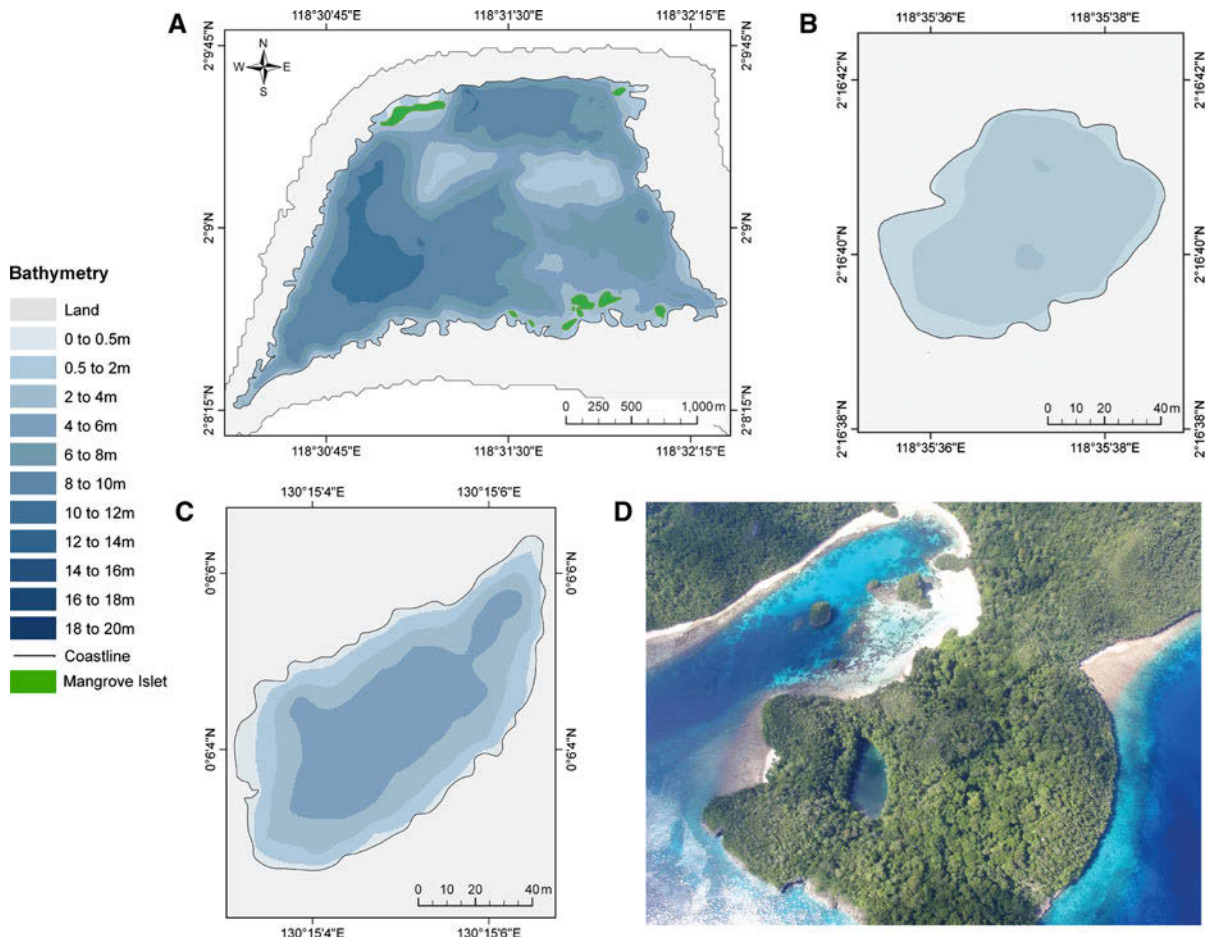

Fig. 2 Bathymetric maps of **A** Kakaban lake, **B** Tone Sibagang pool, **C** Urani lake, **D** aerial view of Urani lake. Note that scale differs per map

in ESRI ArcGIS v9.3 software. Kriging interpolations were used to produce bathymetry maps, where separate models were tested by cross validation (spherical variogram model, small nugget component); the models shown here had mean prediction errors of less than 5%. The tidal fluctuations and temperature were measured with HOBO U20 Water Level Loggers (ONSET Computer Corporation, U.S.A.). The loggers were read out in the software Hoboware Pro version 2.5.0. The dataloggers were deployed for at least 24 h in the lake and in the adjacent sea to obtain tidal measurements simultaneously in both locations with a logging frequency of 10 min. The degree of dampening of the tides was calculated as the relative amplitude of the lake compared to the sea. Relative tide amplitude was calculated as the percentage of tide variation inside the lake ($\Delta Tide_{lake}$) relative to the sea ($\Delta Tide_{sea}$).

The degree of tidal delay and dampening was used a proxy for the variation in the degree of connectivity between the lake and the sea (Hamner & Hamner, 1998; Colin, 2009). Tidal measurements were made in Kakaban lake and Haji Buang lake (East Kalimantan) and Cassiopeia lake and Tricolore lake (West Papua). In all other locations the tidal amplitude was estimated based on the intertidal zone determined at low tide. A Secchi disc was used to estimate vertical visibility around noon (from 11:00 to 14:00 h) in Kakaban lake and Haji Buang lake.

Recording target flora and fauna

Based on preliminary surveys of lakes in Indonesia, Vietnam and Palau (Hamner & Hamner, 1998; Hoeksema, 2004; Cerrano et al., 2006; de Voogd et al., 2006; Becking et al., 2008; Becking & de Voogd, 2008) sponges, algae, molluscs, and mangroves were the most dominant macro-biota in terms of abundance and/or diversity. To provide biological indicators to help demark the different types of anchialine lake systems, the presence of selected taxa was recorded, namely, two sponge species known from anchialine lakes *Suberites diversicolor* Becking & Lim, 2009 and *Darwinella* aff. *gardineri* Topsent, 1905 (de Voogd et al., 2006; Becking & Lim, 2009) (Fig. 3D), two sponge species common in reef flats and lagoons *Spheciospongia vagabunda* (Ridley, 1884) and *Clathria reinwardti* Vosmaer, 1880 (de Voogd et al., 2009); two shrimp species known from

anchialine systems *A. lauensis* (Fig. S2E) and *Parhippolyte uvaea* (Fig. S4G) (Maciolek, 1983); two jellyfish species *M. papua* and *Cassiopeia ornata* Haeckel, 1880 (Fig. 3B) (Dawson, 2005); the algae genera *Caulerpa* spp. and *Halimeda* spp. (Hoeksema, 2004); the mangrove genera *Bruguiera* spp. and *Rhizophora* spp., in more general terms gobies, mussels, oysters, and stony corals. Representative voucher specimens have been deposited at the NCB Naturalis. The size of the fish was estimated in categories: small (<10 cm), medium (10–15 cm), and large (>15 cm). Sponge diversity was categorized as: low (<10 species), medium (10–20 species), and high (>20 species). A detailed description of the sponge fauna of Indonesian marine lakes is in preparation.

Distinction between lakes

A multidimensional scaling (MDS) plot was used to produce a two-dimensional graphical representation of the similarity between the lakes and pools included in this study. IBM® SPSS® Statistics 18 was used to calculate the Euclidean distances and to make an MDS plot with S-stress diminishing by less than 0.0001 during successive iterations, in five trials. Classified abiotic attributes were: connection to sea (high, medium, low), maximum depth at low tide (m: >20/ 10–20/6–10/1–5/<1), maximum length/diameter (m: <100/100–500/>500), salinity (average ppt: 32–34/ 29–31/26–28/23–25/20–22/<20). Classified biotic attributes were: mangrove dominant (yes/no), mussel/oyster presence (mussel, oyster, none), sponge diversity (high/medium/low/absent), fish presence and size (large/medium/small/absent), and the presence or absence of: hard coral, large jellyfish populations, *M. papua*, *C. ornata*, *S. diversicolor*, *Darwinella* aff. *gardineri*, *S. vagabunda*, *C. reinwardti*, *A. lauensis*, *P. uvaea*, and gobies. These attributes were recorded during timed interval surveys of two hours.

Results

A total of 24 anchialine lakes and pools were located of which 20 are new to science. 20 lakes and pools were surveyed for this study, 16 of which are newly cataloged (eight in East Kalimantan and eight in West Papua). None of the lakes and pools in West Papua has been formally named and only one lake had a
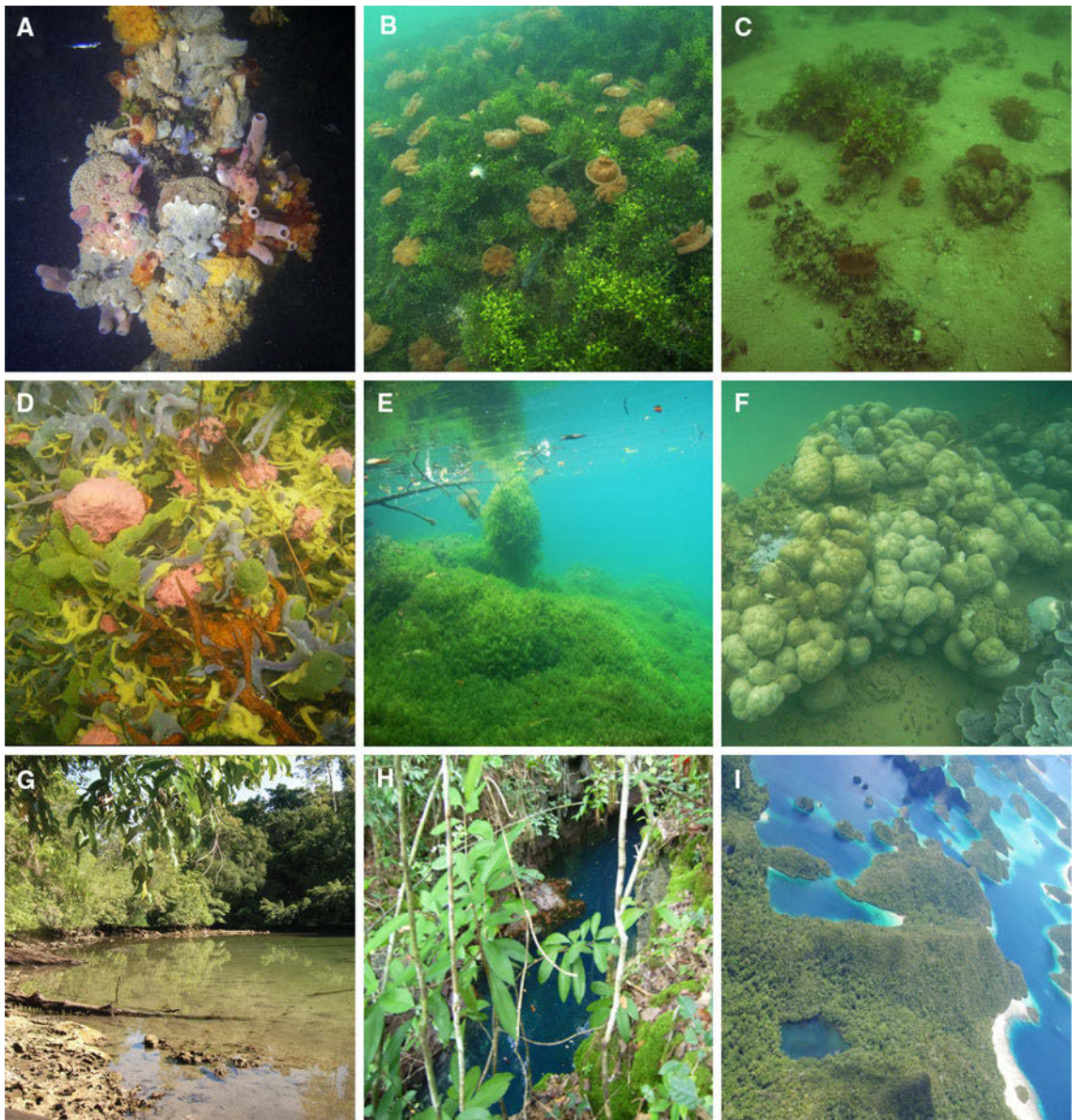
Fig. 3 A mangrove root studded with sponges in Kakaban lake (photograph: B. W. Hoeksema), **B** *Halimeda* algae build-up with *C. ornata*. **C** Kakaban lake floor with patches of mussels, sponges, *Halimeda* algae, and *Cassiopeia* jellyfish, **D** full sponge cover in Haji Buang lake (green sponge *Suberites diversicolor*, pink sponge *Darwinella* aff. *gardineri*), **E** 'blanket' of *Caulerpa* algae in Haji Buang lake, **F** coral in Wallace lake, **G** Buli Halo pool, **H** Embo-Embo blue pool in chasm, **I** aerial view of Mud lake and the surroundings. (all photographs except **A**: L. E. Becking)

local name (Sauwandarek). As such we use our fieldnames where appropriate. All lakes and pools were situated in depressions in karstic limestone, Pliocene reefal limestone in east Berau and late Miocene limestone in Raja Ampat. Geographical, physical, chemical, biological characters are summarized in Table 1A, B.

MDS analysis

The MDS resulted in two clusters representing pools and lakes (Fig. 4), which are primarily distinguished by the features: size, depth and presence of selected crustaceans. Within the lake cluster, there is a gradient primarily determined by the degree of

Table 1 List of all recorded characters of lakes and pools in (A) East Kalimantan, (B) West Papua

(A) East Kalimantan

	Sea	Kakaban	Pondok Sene	Haji Buang	Bamban	Tone Sibagang	Buli Halo	Payung Payung	Sibo	Bandong	Embo-Embo	Hapsi
Code in Fig. 4		Berau01	Berau02	Berau03	–	Berau04	Berau05	Berau06	Berau07	Berau08	Berau09	Berau10
Physical characters												
Island		Kakaban	Kakaban	Maratua	Maratua	Maratua	Maratua	Maratua	Maratua	Maratua	Maratua	Maratua
Latitude		N02°08′57.3″	N02°09′18″	N02°12′31.2″	N02°13′50.0″	N02°16′39.6 ″	N02°11′16.4″	N02°11′ 45.7″	N02°15′47.3″	N02°16′22.3″	N02°11′03.0″	N02°11′04.2″
Longitude		E118°31′26.4″	E118°32′18″	E118°35′46.8″	E118°34′50.7″	E118°35′37.1″	E118°37′06.4″	E118°36′09.9″	E118°33′46.9″	E118°35′55.0″	E118°37′01.9″	E118°37′8.7″
Type	Sea	Lake	Lake	Lake	Lake	Pool	Pool	Pool	Pool	Pool	Chasm	Chasm
Shape		Trapezoidal	Elongated	Elongated	Elongated	Circular	Circular	Circular	Circular	Circular	Elongated	Elongated
Connection to sea		Low	High	Low	Low	High	High	High	High	High	Medium	Medium
Tidal amplitude (m)	1.5–2	0.2	1.5–2	0.9	0.5–1	1.5–2	1.5–2	1.5–2	1.5–2	1.5–2	0.5–1	0.5–1
Tunnel visible		No	Yes	No	No	No	Yes	No	Yes	No	No	No
Max. depth at low tide (m)		12	2	17	n.a.	0.75	<0.5	0	0	<0.5	5	5
Max. length (m)		3850	530	800	600	86	100	80	20	140	30	30
Area (m²)		40 × 10⁵	26500	14 × 10⁴	12 × 10⁴	4900	7295	4800	195	6785	165	105
Min dist to sea (m)		120	20	325	115	50	400	300	60	80	75	200
Salinity range (ppt)	33–34	23–24	33–34	26–28.5	26	20.8–22.6	26	26	20–23	20–23	11	11
pH range	8.2–8.5	7.0–7.8	8.0–8.2	7.3–7.8	n.a.	7.2–7.4	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
Temperature range (°C)	28–30	29–31.5	28–30	29–30	29–30	28–29	n.a.	n.a.	n.a.	n.a.	26–28	26–28
Biota												
Mangrove dominant		Yes	No	No	Yes	No	No	No	No	No	No	No
Sponge diversity		High	High	High	Medium	Low	Low	Absent	Low	Low	Absent	Absent
Fish size		Small	Large	Small	n.a.	Large	Large	Absent	Absent	Absent	Absent	Absent
Hard coral		–	+	–	–	–	–	–	–	–	–	–
S. diversicolor		+	–	+	+	+	–	–	–	+	–	–
Darwinella aff. gardineri		+	–	+	+	–	–	–	–	–	–	–
S. vagabunda		–	+	–	–	–	–	–	–	–	–	–
C. reinwardti		–	+	–	–	–	–	–	–	–	–	–

Table 1 continued

(A) East Kalimantan

	Sea	Kakaban	Pondok Sene	Haji Buang	Bamban	Tone Sibagang	Buli Halo	Payung Payung	Sibo	Bandong	Embo-Embo	Hapsi
Code in Fig. 4		Berau01	Berau02	Berau03	–	Berau04	Berau05	Berau06	Berau07	Berau08	Berau09	Berau10
A. lauensis		–	–	–	n.a.	+	+	–	–	+	+	+
P. uvaea		+	–	+	n.a.	–	–	–	–	–	–	–
Gobies		+	–	+	+	–	–	–	–	–	–	–
Human influence		Tourism, agriculture, sea turtle		Tourism, logging	Consumption mussels, logging	Fishpond, sea turtle	Fishpond, sea turtle	Toilet	Local recreation	Toilet	Local recreation	Local recreation

(B) West Papua

	Sea	Cassiopeia	Tricolore	Mud	Urani	Sawaundarek	Wallace	Ctenophore	Big Caulerpa	Red shrimp
Code in Fig. 4		Raja01	Raja02	Raja03	Raja04	Raja05	Raja06	Raja07	Raja08	–
Physical characters										
Island		Wayag	Wayag	Wayag	Urani	Mansuar	Gam	Gam	Gam	Gam
Latitude		N0°08′36.9″	N0°09′47.9″	N0°10′40.3″	N0°06′03.8″	S0°35′19.6″	S0°26′31.08″	S0°27′17.3″	S0°26′58.9″	S0°25′58.2″
Longitude		E130°04′39.7″	E130°04′05.4″	E130°01′09.3″	E130°15′04.3″	E130°35′48.8″	E130°41′8.04″	E130°29′34.3″	E130°29′10.2″	E130°40′49.7″
Type	Sea	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Lake	Pool
Shape		Circular	Oval	Circular	Oval	Oval	Circular	L-shaped	Circular	Circular
Connection to sea		Medium	Medium	Medium	Medium	Low	High	High	High	n.a.
Tidal amplitude (m)	1–1.5	1.2	0.8	0.5–1	0.5–1	0.1–0.5	1–1.5	1–1.5	1–1.5	1–1.5
Tunnel visible		No	No	Yes	No	No	Yes	Yes	Yes	No
Max. depth at low tide (m)		4	2	2	6	19	n.a.	9	6	0.5
Max. length (m)		125	250	170	140	500	200	230	85	20
Area (m^2)		13×10^3	18×10^3	19×10^3	6800	84×10^3	8640	25×10^3	4100	n.a.
Min. dist to sea (m.)		60	70	270	100	300	50	75	50	n.a.
Salinity range (ppt)	33–34	28–30	31–33	31–33	28–30	28–30	31–33	31–33	31–33	n.a.
pH range	8.0–8.3	7.2–7.8	7.2–7.8	7.2–7.8	7.2–7.8	7.2–7.8	n.a.	7.7–8.0	7.7–8.0	n.a.
Temperature range (°C)	28–29	30–31	29–30	29–30	30–31.5	31–34	29–31	29–31	29–31	n.a.
Biota										
Mangrove dominant		No	Yes	Yes	Yes	Yes	No	No	No	No
Sponge diversity		Medium	High	Medium	High	Medium	High	High	High	Absent
Fish size		Absent	Medium	Medium	Small	Small	Large	Large	Large	Absent
Hard coral		–	–	–	–	–	+	–	+	–
S. diversicolor		+	–	+	+	+	–	–	–	–
Darwinella aff. gardineri		–	+	–	+	+	–	–	–	–

Table 1 continued

(B) West Papua

Code in Fig. 4	Sea	Cassiopeia Raja01	Tricolore Raja02	Mud Raja03	Urani Raja04	Sawaundarek Raja05	Wallace Raja06	Ctenophore Raja07	Big Caulerpa Raja08	Red shrimp
S. vagabunda		–	–	–	–	–	+	+	+	–
Clathria reinwardti		–	–	–	–	–	+	+	+	–
A. lauensis		–	–	–	–	–	–	–	–	+
P. uvaea		–	+	–	+	+	–	–	–	–
Gobies		–	+	+	+	+	–	–	–	–
Human influence		Sea turtle?	Absent	Absent	Absent	Sea turtles, village	Fishpond	Absent	Absent	Absent

n.a., character not recorded; –, absent; +, present. Areas, depths, and maximum lengths are all approximate values. Maximum depths are relative to low tide. See results section for definitions of categories
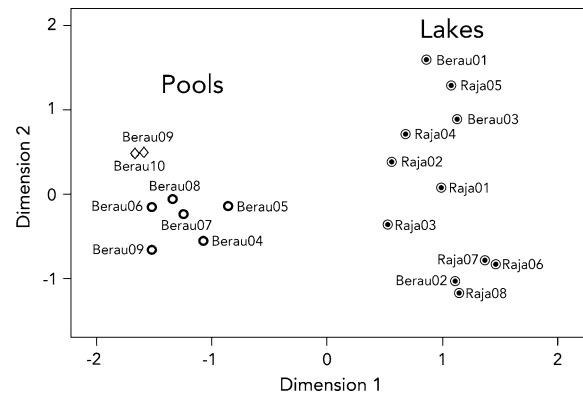
Fig. 4 Multidimensional scaling ordination based on euclidian distances of characters of lakes and pools in Indonesia (Stress: 0.08 and R^2: 0.97). See Table 1A, B for codes. *Filled circles*, *empty circles*, *diamonds* represent lakes, pools, chasms, respectively. *Closer points* indicate a higher similarity in the set of characters

connection, salinity, and the presence or absence of the selected sponge species. Within the pool cluster two subgroups could be recognized: the first one composed by Embo Embo and Hapsi (two blue pools in chasms), and the second one grouping the remaining six pools. The distinction of the two groups is driven by differences in salinity, depth, and presence/absence of fauna.

Marine lakes

Twelve marine lakes were studied in East Kalimantan and West Papua (Fig. 1A–C): Kakaban (Fig. 2A), Pondok Sene, Haji Buang, Bamban, Sauwandarek, Ctenophore, Wallace, Big Caulerpa, Mud (Fig. 3J), Urani (Fig. 2C, D), Tricolore, Cassiopeia. A description of each lake and its biota is provided in the Supplementary Material and Table 1A, B. The majority of the lakes were separated from the sea by high (5–100 m) limestone cliffs or hills (Figs. 2C, 3J, S6A). The smaller lakes had uniform basins with the maximum depth in the central area, while the larger lakes had a heterogeneous bathymetry with multiple depressions (Fig. 2A–C). The lakes have a maximum length of more than 80 m with basins deeper than 2 m at low tide, salinities ranging from 23–33 ppt, and tidal amplitudes ranging from 11% to almost 100% of the adjacent sea amplitudes (Table 1A, B). The shape of the lakes can be circular, elongated or irregular. All lakes had lower salinities

and pH compared to the adjacent sea, while the temperatures were a few degrees higher (Table 1A, B). The connection to the sea is high (90–100% of adjacent sea tidal amplitude and <1 h delay), medium (60–90% relative tide amplitude and 1–2 h delay), or low (<50% relative tide amplitude and >2 h delay). Average tidal amplitude of the sea across all sites is 1.5–2 m (Table 1A, B).

The dominant biota, in terms of abundance, in marine lakes typically consisted of mangroves (e.g., *Bruguiera gymnorrhiza*), algae (*Caulerpa* spp. and *Halimeda* spp.), sponges, ascidians (e.g., *S. complexa*, *Eudistoma* spp.), bivalves (e.g., *Brachydontes* spp.), gastropods (e.g., *Nerita* sp., *Terebralia* sp., *Cerithium* sp.), holothurians (e.g., *Synaptula* sp., *Holothuria* sp.), ophiuroids (*Ophiarachnella* sp.), asteroids (*Echinaster* spp.), fish (e.g., gobies, half-beaks, soldierfish), shrimp (e.g., *A. lauensis*, *P. uvaea*, *Kemponia demani* (Kemp, 1915)), crabs (e.g., *Orcovita saltatrix*), and in many cases also included annelids, and cnidarians (scyphozoans and anthozoans). The lakes with high connection to the sea contained more reef flat species, such as stony corals (e.g., *Porites* sp., Fig. 3F) and the sponges *S. vagabunda* and *C. reinwardti*. The more isolated lakes contained *S. diversicolor*, *Darwinella* aff. *gardineri* (Fig. 3D), and few reef species. All marine lakes had a high cover of bivalves (Fig. 3C), either mussels or oysters were observed but never both in one lake except for in Ctenophore lake (West Papua). In all lakes *Caulerpa* was the dominant algae cover (Fig. 3E), except in Kakaban lake (East Kalimantan) where *Halimeda* was dominant (Fig. 3B) and Sauwandarek lake (West Papua) where both algae were rare. One lake (Haji Buang lake) contained seagrass (*Enhalus* sp.).

Anchialine pools

Five anchialine pools were studied on Maratua, Berau, East Kalimantan (Fig. 1A–C): Buli Halo (Fig. 3G), Sibo, Bandong, Payung Payung, and Tone Sibabang (Fig. 2B); and one on Gam, Raja Ampat, West Papua. A description of each pool is provided in the Supplementary Material. This is the first description of these pools. The anchialine pools were separated from the sea only by sufficient elevation and distance (50–400 m) to prevent waves from entering. The pools are small, typically circular,

basins of 20–100 m maximum width and with gently shelving basins where the maximum depth is located in the central area (Fig. 3G). The depths are less than 0.75 m (the majority less than 0.5 m) at low tide and with a range of salinities of 20–26 ppt. Two types of pools can be distinguished, those where the basin dries entirely at low tide and those where the basins remain minimally submerged depending on depth of the basin.

The dominant biota in anchialine pools consisted of algae (*Caulerpa* spp.), gastropods (e.g., *Nerita* sp, *Terebralia* sp., *Cerithium* sp.), ascidians (e.g., *Eudistoma* sp.), shrimp (e.g., *A. lauensis*), and in some pools cnidarians (anthozoans). Sponges and crabs only occurred in some pools in low abundance and diversity, and jellyfish and corals were never observed.

Blue pool in chasm

Two blue pools (Embo-Embo and Hapsi) were studied on the southern end of the western arm of Maratua island (Fig. 1C) where the only source for fresh water is located (according to inhabitants of nearby villages). The blue pools are located 75–200 m inland, separated by limestone rock from the sea coast. The pools are present in chasms in the ground running parallel to the coastline, with 1–20 m almost vertical walls (Fig. 3H). The depth of the pools is 5–6 m with deep blue color, and a visible halocline at 1–2 m depth. Due to logistical restraints, only samples of surface water (above the halocline) were collected to measure salinity (11 ppt) and temperature (25–28°C). The bottom of the pool consisted of organic detritus, silt, and fallen tree trunks. The only biota observed were shrimp (*A. lauensis* and *Metabetaeus minutus* (Whitelegge, 1897)) and red encrusting algae.

Discussion

The discovery and subsequent survey of 20 lakes and pools in Indonesia has revealed great habitat diversity in anchialine systems. Here, we will discuss the geomorphology, degree of connection to the sea, chemical water parameters, biota, and human influence. We will end with a synthesis of three types of

anchialine systems that are present in the Indo-Pacific.

Connection to the sea and water chemistry

We observed different tidal regimes per location, most of them dampened and delayed compared to the outside sea. Comparing the tidal regime between the anchialine systems and the adjacent sea provided a proxy to estimate the degree of connection to the sea (Hamner & Hamner, 1998). Counter to expectations, there did not appear to be a correlation between the distance of the anchialine system from the sea (i.e., the length of the land barrier) and the degree of connection. Differences in limestone rock porosity, presence of larger channels or tunnels will have a strong effect on the degree of connection to the adjacent sea as well as the residence time of water in anchialine systems (Mylroie & Carew, 1995; Iliffe, 2000). The residence time of the water will be a factor of actual exchange of seawater, the size and the depth of the anchialine system. It must be noted here that the tidal fluctuations are not necessarily only a result of active exchange of sea water, but could in part also be due to isostatic pressure from the surrounding sea. Particularly in the case of Kakaban lake, which is a large lake in a small island, the fluctuation of the damped tides is expected to be largely a result of isostatic pressure and not actual exchange of water with the adjacent sea. The degree of connection has an effect on the water chemistry of the lakes. For example, the salinity and pH were lower within lakes with restricted connection to the sea. However, the pools in contrast had little dampening of the tides, but the salinity was much lower than the sea and than most of the lakes. The shallow basins with a low volume to surface ratio likely allowed for more dilution by groundwater or rainwater.

In this study, all lakes and pools consistently had lower salinities and pH compared to the adjacent sea, while the temperatures were a few degrees higher (see Table 1A, B). The whole spectrum of anchialine systems is typified by a wide range of water qualities. Anchialine cave systems are generally stratified with (meteoric) fresh water or brackish water overlying seawater and separated by a mixing zone. These waters typically have very low concentrations of oxygen at depth, containing hydrogen sulfide and supporting a complex aerobic and anaerobic microbial community (Humphreys, 1999; Iliffe, 2000). The deep marine lakes from Palau similarly show stratification with an increase of salinity and a decrease of oxygen towards the bottom. At the crossover to the anoxic layer a cyanobacterial mat is formed (Hamner et al., 1982; Hamner & Hamner, 1998; Dawson et al., 2009). Though we were not able to measure the oxygen concentration we were able to observe through indirect means (such as the presence of sponges and mussels at the bottom, and the absence of a cyanobacterial mat) that the majority of the presently investigated Indonesian lakes were not stratified. In Kakaban, Tomascik & Mah (1994) had measured lower oxygen levels at greater depth, but not anoxic levels (5.5–5.6 mg l^{-1}). Only Sawaun-darek lake and Cassiopeia lake (West Papua) may have had anoxic layers at the bottom, revealed by changes in temperature (increased), water color (to dark brown-orange), and biota (absence) with depth. In any case, the system was not stable as we observed that the depth of the warmer brown-orange colored water layer changed several meters on different visits, either days or months apart. This change in the position of the anoxic and H$_2$S zone has also been observed in Bundera Sinkhole in Australia (Humphreys, 1999; Seymour et al., 2007).

Biota

The flora and fauna of the anchialine systems are of marine origin, but the lakes and pools harbor only a subset of the adjacent sea flora and fauna. The difference in species assemblages between different lakes and pools can for a large part be attributed to both the nature of the barrier between the lake and sea as well as the various environmental characters within the anchialine systems. First, the biota has to be able to colonize the lake. This colonization process will be different between lakes depending on the external setting which could involve direct connection to the lake or pool from lagoon through a tunnel (e.g., Ctenophore lake), from lagoon through dissolution channels in rock (e.g., Kakaban lake), or from lagoon through mangrove swamp and subsequently through dissolution channels in rock (e.g., Haji Buang lake). In the case of colonization, the environmental barrier to the lake will act as a filter for the faunal composition of the lakes. An extreme

illustration of the effect of the size of connection is that in more restricted lakes only small mangrove associated fish were observed, while in the lakes connected by tunnels to the sea large reef fishes were occasionally observed. Following colonization the taxa have to be able to tolerate the environmental conditions inside the lake. This often includes a broad range of and, in some cases, sudden modifications to environmental parameters. The lower salinities and higher temperatures in all lakes and pools compared to the sea will likely prove a limiting factor for many marine biota. There are taxa that are typically good at colonizing and surviving in anchialine environments, while some groups are only present in highly connected systems. Algae, sponges, molluscs, ascidians, and in many cases mangroves are the most dominant macroorganisms in terms of abundance and/or diversity in the lakes and pools of Indonesia, while corals were absent, except in the most connected marine lakes (Tomascik & Mah, 1994; Hoeksema, 2004a; Becking et al., 2008; this study). The sponge cover and abundance is generally high, but this does not necessarily correspond with high diversity, particularly compared with the numbers of species found in the adjacent reefs (de Voogd et al., 2009). In Vietnam, there is a great variation in the sponge fauna between the different marine lakes, where the local assemblage can vary due to extreme variability of the environment (Cerrano et al., 2006; Azzini et al., 2007).

Types of anchialine systems

Different anchialine systems can be characterized based on environmental gradients, shape, depth, water parameters, and degree of connection to the sea (e.g., Iliffe, 1991). To understand the biological processes within the anchialine systems it is necessary to make a distinction between the different types. The anchialine cave environment has been extensively described in the past (e.g., Sket, 1996; Iliffe, 2000) and is continued in this special issue of Hydrobiologia. There are numerous anchialine caves documented in the Indo-Pacific (e.g., Iliffe, 1991, 2000; Humphrey & Eberhard, 2001; Jaume et al., 2009), yet in this study, we limit our focus to anchialine systems in the Indo-Pacific that are exposed to air, i.e., the lakes and pools. We identified three types of these anchialine habitats: marine lakes,

anchialine pools, and blue pools in chasms. The distinction and spectrum of these systems is evident in Fig. 4.

Marine lakes

Marine lakes are represented by large and deep basins that remain submerged during the whole tidal cycle. Within this category of marine lakes we include the 57 lakes in Palau (from Hamner & Hamner, 1998; Colin, 2009), the eight lakes in Vietnam (from Cerrano et al., 2006; Azzini et al., 2007), as well as the 12 lakes from this study. There is a range of features within marine lakes that is apparent in Fig. 4 where the variation is mostly influenced by the degree of connection to the adjacent sea, which in its turn influences the salinity and the species assemblages in the lakes. In Palau and Vietnam the marine lakes also display a wide variety in the degree of connection to the sea and subsequent environmental regimes within the lakes (Hamner & Hamner, 1998; Cerrano et al., 2006; Azzinni et al., 2007; Colin, 2009). In the marine lakes of Palau the range of tidal dampening (tidal amplitude 8-100% of the adjacent sea) and salinities (20-33.5 ppt) fit within the range that we have observed in Indonesia (Hamner & Hamner, 1998). Hamner & Hamner (1998) and Colin (2009) make a distinction within the marine lakes of Palau between holomictic lakes where the water column is mixed and meromictic lakes where the water column is stratified due to little mixing and low connection to the adjacent sea. Essentially the marine lakes represent a geomorphological gradient starting by 1) lakes that are highly connected to the adjacent sea (through large and apparent tunnels or caves) with tides that are minimally delayed or damped and with well mixed waters with salinities comparable to the adjacent sea, continuing to 2) moderately isolated lakes with at least 1 h delay in tidal phase and reduced salinities compared to the adjacent sea, and extending to 3) highly isolated lakes with tidal amplitudes damped by more than 50% and a delay in phase of more than 2 h compared to the sea and with very low salinity, often meromictic. Beyond this spectrum are lakes that contain saline waters but without any connection to the sea at all, such as Motitoi lake on Satonda island near Sumbawa, Indonesia. Indeed, Motitoi lake is non-tidal and has a very high salinity range of 31.4-41.8 ppt (Tomascik et al., 1997; Pisera et al., 2010).

In this study, the greater the connection to the sea was the more similar the lagoonal and lake assemblages were owing to the presence of, for example, stony corals and the sponges *S. vagabunda* and *C. reinwardti*. The more connected lakes in Palau and Vietnam also contained coral and reef associated species (Azzini et al., 2007; Colin, 2009). The more isolated lakes in Indonesia had unique assemblages that were typified by the presence of the sponges *Darwinella* aff. *gardineri* and *S. diversicolor,* the large red shrimp *P. uvaea,* and in many cases the jellyfish *M. papua* and *C. ornata*. It is remarkable that the sponge species *S. diversicolor* is not only present in more isolated lakes in East Kalimantan and West Papua (de Voogd et al., 2006; Becking & Lim, 2009; this study), but also in marine lakes with reduced salinities and high temperatures in Ha Long Bay in Vietnam (Cerrano et al., 2006; Azzini et al., 2007; Becking & Lim, 2009) and in Palau (pers. comm. L.J. Bell, Coral Reef Research Foundation, Palau). A related species of the genus *Suberites* has even been found in the completely isolated Motitoi lake near Sumbawa (Reitner et al., 1999; Pisera et al. 2010). It is noteworthy that the largest and most isolated lake of this study, Kakaban lake, contained a unique fauna that we did not observe in any of the other lakes in Indonesia, such as two holothurians (*H. (Lessonothuria) cavans* and *S. spinifera*), a jellyfish eating actiniarian (*Entacmaea medusivora*), and an ascidian (*S. complexa*) (Tomascik & Mah, 1994). On a cautionary note with respect to inferring the degree of connection, Cassiopeia lake (West Papua) would be considered a moderately connected lake based on the degree of dampening of the tidal amplitudes, however faunistically this lake would represent a more restricted system with *C. ornata, M. papua,* and *S. diversicolor.* More detailed research on how the variation of the species assemblages relate to the lake characters is required to establish predictors.

Anchialine pools

Anchialine pools are represented by small, circular basins that have a shallow depth (<1 m.) or are dry at low tide. Within the category anchialine pool, we include the pools and ponds as described in Hawaii (Holthuis, 1973; Brock & Kam, 1997), the Philippines (Wear & Holthuis, 1977), Funafuti (Holthuis,

1973), as well as the six pools in this study. On the islands of Hawaii and Maui much smaller anchialine pools than in Indonesia have been found ranging in size from 0.5 to 12 m. in length and in salinities from 8–30 ppt (Holthuis, 1973; Brock & Kam, 1997). The Hawaiian pools are formed in lava rock, while those in Indonesia, the Philippines, and Funafuti are formed in karstic limestone.

In general, the anchialine pools are expected to show great fluctuations in salinity and temperature within a short period within one pool, due to the small size, shallow depth, and the strong influence of the tides. Therefore, they constitute an extreme environment which predominantly euryhaline species can tolerate for longer periods. As a consequence, the diversity in these pools is much lower than the more stable systems of the marine lakes. In Hawaii the small red shrimp *H. rubra* typifies the anchialine pools (Maciolek, 1983; Santos, 2006). Experiments of red shrimp from pools in Hawaii showed that they can survive fresh to hypersaline (50 ppt) water (Holthuis, 1973). In Indonesia and other locations in the Indo-Pacific, the anchialine pools are dominated by another small red shrimp, *A. lauensis* (Holthuis, 1973; Maciolek, 1983; this study). In the Indonesian pools, some individuals of sponges specimens were observed, but sponges are rarely recorded from the other geographic locations.

Blue pools in chasms

We observed two pools with striking blue colored water in chasms in the ground that ran parallel to the coast. Holthuis (1973) described a fissure north of Lohena Rock on Maui where he collected 'red shrimp' which match the chasms presently recorded from Indonesia. Ng et al. (1996) again described the same system at Vaikona chasm and Anatuku chasm in Niue, Polynesia. These blue pools may, in addition, be the same type of systems as the 'grietas' as described by Iliffe (1991) in the Galapagos. As our two observations, do not seem to be singular to the island of Maratua in Indonesia, we have allocated a category to blue pools in chasms. This system is represented by a large brackish water lens which presumable lies above warmer saline water. We have only documented the surface layer of low salinity (11 ppt), whereas Ng et al. (1996) and Holthuis (1973) report salinities ranging from 1.5–8 ppt at the surface

and 31 ppt at depth, the depths ranging from 6–32 m. Possibly, the blue pools are connected to anchialine caves, or may in fact be the exposed part of an anchialine cave systems. These pools only contained shrimp and algae and as such had the lowest biodiversity of all three anchialine systems described in this study.

Conservation

The isolated water bodies of anchialine lakes and pools are, like island systems, vulnerable to anthropogenic influence. Precedence of uncontrolled tourism development and alien species introduction in marine lakes in Palau and Vietnam has resulted in ecological disarray (Dawson et al., 2001; Cerrano et al., 2006; Azzini et al., 2007). While the lakes in Wayag and Urani (West Papua) appeared to be free of human influence, most of the other systems have already been exploited in various ways. For example, in East Kalimantan the lakes are beginning to face an increase in tourism and local exploitation. In Vietnam, the lakes are no longer pristine, having been used for fisheries, mollusk harvesting, and aquaculture (Azzini et al., 2007). In addition, a large number of lakes and pools that we visited had an introduced green sea turtle for various reasons such as consumption and animistic rites. The presence of sea turtles may have a disruptive effect on the anchialine ecosystems, while the impact for the sea turtles may also be negative since there is little food available to ensure their long-term survival.

The two Indonesian regions that contain high abundances of anchialine systems, Berau in East Kalimantan and Raja Ampat in West Papua, are situated in the Coral Triangle, the centre of maximum marine species richness (Hoeksema, 2007). Within this centre, these regions are among the most diverse with regard to species and marine habitats (Hoeksema, 2004a; Renema, 2006). This habitat diversity is partly related to the limestone underground, which is reflected in irregularly shaped coastlines that are fringed by coral reefs that may contain unique benthic species assemblages (e.g., Hoeksema, 2004b; Renema, 2006; de Voogd et al., 2009). Where the karstic limestone emerges above sea level, relatively isolated anchialine biotopes have developed into unique ecosystems, each with its own specific species assemblage. Many species here are rare and even endemic (Tomascik & Mah, 1994; this study). As a result of their many special features, anchialine systems should play a prominent role in the marine conservation planning of both Berau and Raja Ampat.

Conclusions

This study provides the first overview of recently located anchialine systems in Indonesia. These systems vary from each other in terms of size, bathymetry, degree of connection to the sea, salinity, and species composition. Both the various characters within the lakes and pools as well as the nature of the barrier from the sea determine the species assemblages encountered in the systems. To understand the biological processes within the systems, it is necessary to make a distinction between the different types. We propose to distinguish between three anchialine systems, though we caution that these categories are transitional: (1) marine lakes, (2) anchialine pools, (3) blue pools in chasms. We adopt the term marine lakes (sensu Hamner & Hauri, 1981) as a type of anchialine system. Within the marine lakes, there is a clear gradient in characters which is related to the degree of connection to the sea which in its turn affects the salinity, pH, and species present. The discoveries of and continued research in anchialine systems will contribute significantly to a further understanding of the biogeography, connectivity, and genetic divergence of taxa in shallow tropical marine ecosystems.

References

Azzini, F., B. Calcinai, C. Cerrano, G. Bavestrello & M. Pansini, 2007. Sponges of the marine karst lakes and of the coast of the islands of Ha Long Bay (North Vietnam). In Custodia, M. R., G. Lobo-Hajdu, E. Hajdu & G. Muricy (eds), Porifera Research: Biodiversity. Innovation and Sustainability, Rio de Janeiro: 157–164.

Becking, L. E. & N. J. de Voogd, 2008. The sponge fauna of Indonesian marine lakes. In 11th International Coral Reef Symposium—Reefs for the Future, Book of Abstracts, Ft Lauderdale, USA: 556.

Becking, L. E. & S. C. Lim, 2009. A new Suberites (Demospongiae: Hadromerida: Suberitidae) from the tropical Indo-West Pacific. Zoologische Medelingen, Leiden 83: 853–862.

Becking, L. E., L. J. B. Bell, M. N. Dawson, L. E. Martin & S. Patris, 2008. Marine lakes of Raja Ampat. In Hoeksema, B. W. & S. E. T. van der Meij (eds), Cryptic Marine Biota of the Raja Ampat Island Group—Progress Report LIPI–Naturalis Expedition to Raja Ampat, Papua, Indonesia. Naturalis, Leiden: 41–44.

Benivic, A., D. Lucic, V. Onofri, M. Peharda, M. Caric, N. Jasprica & S. Bobanovic-Colic, 2000. Ecological characteristics of the Mljet Island seawater lakes (South Adriatic Sea) with special reference to their resident populations of medusea. Scientia Marina 64: 197–206.

Brock R. E. & A. K. H. Kam, 1997. Biological and water quality characteristics of anchialine resources in Kaloko-Honokohau National Historical Park. PCSU Technical Report. Cooperative National Park Resources Studies Unit, University of Hawaii at Manoa, Department of Botany, Honolulu: 112 pp.

Cerrano, C., F. Azzini, G. Bavestrello, B. Calcinai, M. Pansini, M. Sarti & D. C. Thung, 2006. Marine lakes of karst islands in Ha Long Bay (Vietnam). Chemistry and Ecology 22: 489–500.

Colin, P. L., 2009. Marine Environments of Palau. Indo-Pacific Press, San Diego: 414 pp.

Craft, J. D., A. D. Russ, M. N. Yamamoto, T. Y. Iwai, S. Hau, J. Kahiapo, C. T. Chong, S. Ziegler-Chong, C. Muir, Y.

Fujita, D. A. Polhemus, R. A. Kinzie & S. R. Santos, 2008. Islands under islands: the phylogeography and evolution of Halocaridina rubra Holthuis, 1963 (Crustacean: Decapoda: Atyidae) in the Hawaiian archipelago. Limnology and Oceanography 53: 675–689.

Dawson, M. N., 2005. Five new subspecies of Mastigias (Scyphozoa: Rhizostomeae: Mastigiidae) from marine lakes, Palau. Micronesia Journal Marine Biological Association U.K. 85: 679–694.

Dawson, M. N. & W. M. Hamner, 2005. Rapid evolutionary radiation of marine zooplankton in peripheral environments. Proceedings National Academy of Science 102: 9235–9240.

Dawson, M. N., L. E. Martin & L. K. Penland, 2001. Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451: 131–144.

Dawson, M. N., L. E. Martin, L. J. Bell & S. Patris, 2009. Marine Lakes. In Gillespie, R. & D. A. Clague (eds), Encyclopedia of Islands. University of California Press, Berkeley: 603–607.

de Voogd, N. J., W. H. de Weerdt & R. W. M. van Soest, 2006. The sponge fauna of the anchialine lakes of Kakaban and Maratua (East Kalimantan, Indonesia). In Custodio, M. R. et al. (eds), 7th International Sponge Symposium—Biodiversity, Innovation, Sustainability, Book of Abstracts. Museo Nacional, Rio de Janeiro: 242 pp.

de Voogd, N. J., L. E. Becking & D. F. R. Cleary, 2009. Sponge community composition in Derawan Islands, NE Kalimantan, Indonesia. Marine Ecology Progress Series 396: 169–180.

Fransen, C. H. J. M. & T. Tomascik, 1996. Parhippolyte uveae Borradaile, 1899 (Crustacea: Decapoda: Hippolytidae) from Kakaban Island, Indonesia. Zoologische Mededelingen (Leiden) 70: 227–233.

Hamner, W. M. & J. H. Carleton, 1979. Copepods swarms: attributes and roles in coral reef ecosystems. Limnology and Oceanography 24: 1–14.

Hamner, W. M. & P. Hamner, 1998. Stratified marine lakes of Palau (Western Caroline Islands). Physical Geography 19: 175–220.

Hamner, W. M. & I. R. Hauri, 1981. Long-distance horizontal migrations of zooplankton (Scyphomedusae: Mastigias). Limnology and Oceanography 26: 414–423.

Hamner, W. M., R. W. Gilmer & P. P. Hamner, 1982. The physical, chemical, and biological characteristics of a stratified, saline, sulfide lake in Palau. Limnology and Oceanography 27: 896–909.

Hoeksema, B. W. (ed.), 2004a. Marine Biodiversity of the Coastal Area of the Berau region, East Kalimantan, Indonesia. Progress Report East Kalimantan Program—Pilot phase (October 2003). Naturalis, Leiden: 1–82.

Hoeksema, B. W., 2004b. Impact of budding on free-living corals at East Kalimantan, Indonesia. Coral Reefs 23: 492.

Hoeksema, B. W., 2007. Delineation of the Indo-Malayan Centre of maximum marine biodiversity: the coral triangle. In Renema, W. (ed.), Biogeography, Time and Place: Distributions, Barriers and Islands. Springer, Dordrecht: 117–178.

Holthuis, L. B., 1973. Caridean Shrimps found in land-locked saltwater pools at four Indo-West Pacific localities (Sinai Peninsula, Funafuti Atoll, Maui and Hawaii Islands), with

the description of one new genus and four new species. Zoologische Verhandelingen 128: 1–48.

Humphreys, W. F., 1999. Physico-chemical profile and energy fixation in Bundera Sinkhole, an anchialine remiped habitat in north-western Australia. Journal of the Royal Society of Western Australia 82: 89–98.

Humphreys, W. F. & S. Eberhard, 2001. Subterranean fauna of Christmas Island, Indian Ocean. Helictite 37(2): 59–74.

Iliffe, T. M., 1991. Anchialine cave fauna of the Galapagos Islands. In Jame, M. J. (ed.), Galapagos Marine Invertebrates. Plenum Press, New York: 209–231.

Iliffe, T. M., 2000. Anchialine cave ecology. In Wilkens, H., D. C. Culver, D. C., & W. F. Humphreys (eds), Ecosystems of the World. Subterranean Ecosystems, Vol. 33. Elsevier, Amsterdam: 59–76.

Jaume, D., B. Sket & G. A. Boxshall, 2009. New subterranean Sebidae (Crustacea, Amphipoda, Gammaridea) from Vietnam and SW Pacific. Zoosystema 31(2): 249–277.

Katsanevakis, S., 2005. Population ecology of the endangered fan mussel Pinna nobilis in a marine lake. Endangered Species Research 1: 1–9.

Kott, P., 1995. A new colonial Styela (Ascidiacea: Styelidae) from an isolated marine habitat, Kakaban Island, East Kalimantan, Indonesia. The Raffles Bulletin of Zoology 43: 469–474.

Kuenen, P. H., 1933. Geology of coral reefs. The Snellius-expedition in the eastern part of the Netherlands East Indies 1929–1933. Geological results 5: 1–120.

Maciolek, J., 1983. Distribution and biology of Indo-Pacific insular hypogeal shrimps. Bulletin of Marine Science 33: 606–618.

Martínez García, A., A. M. Palmero, M. del Carmen Brito, J. Núñez & K. Worsaae, 2009. Anchialine fauna of the Corona lava tube (Lanzarote, Canary Islands): diversity, endemism and distribution. Marine Biology 39: 169–182.

Massin, C. & T. Tomascik, 1996. Two new holothurians (Echinodermata: Holothuroidea) from an anchialine lagoon of an uplifted atoll, Kakaban Islands, East Kalimantan, Indonesia. The Raffles Bulletin of Zoology 44: 157–172.

Monniot, F., 2009. Some ascidians from Indonesian marine lakes (Raja Ampat Islands, West Papua). Zootaxa 2106: 13–40.

Mylroie, J. E. & J. L. Carew, 1995. Karst developments in carbonate islands. In Budd, D. A., A. H. Saller & P. M. Harris (eds), Unconformities and Porosities in Carbonate Strata. American Association of Petroleum Geologists Publication, Tulsa: 55–76.

Ng, P. K. L. & T. Tomascik, 1994. Orcovita saltatrix, a new genus and species of anchialine varunine crab (Crustacea: Decapoda: Brachyura: Grapsidae) from Kakaban Island, Indonesia. Raffles Bulletin of Zoology 42: 937–948.

Ng, K. L., D. Guinot & T. M. Iliffe, 1996. Revision of the anchialine varunine crabs of the genus Orcovita Ng & Tomascik, 1994 (Crustacea: Decapoda: Brachyura: Grapsidae), with descriptions of four species. Raffles Bulletin of Zoology 44: 109–134.

Pisera, A., K. Reutzler, J. Kaz'mierczak & S. Kempe, 2010. Sponges in an extreme environment: suberitids from the quasi-marine Satonda Island Crater Lake (Sumbawa, Indonesia). Journal of the Marine Biological Association of the United Kingdom 90: 203–212.

Prentice, M. L. & G. S. Hope, 2007. Climate of Papua. In Marshall, A. J. & B. M. Beehler (eds), The Ecology of Papua: Part One. Periplus, Singapore: 177–196.

Reitner, J., G. Woerheide, G. Arp & J. N. A. Hooper, 1999. An unusual suberitid demosponge from a marine alkaline crater lake (Satonda Island, Indonesia). Memoirs of the Queensland Museum 44: 477–478.

Renema, W., 2006. Habitat variables determining the occurrence of large benthic foraminifera in the Berau area (East Kalimantan, Indonesia). Coral Reefs 25: 351–359.

Santos, S. R., 2006. Patterns of genetic connectivity among anchialine habitats: a case study of the endemic Hawaiian shrimp Halocaridina rubra on the island of Hawaii. Molecular Ecology 15: 2699–2718.

Sathiamurthy, E. & H. K. Voris, 2006. Maps of Holocene sea level transgression and submerged lakes on the Sunda shelf. The Natural History Journal of Chulalongkorn University, Supplement 2: 1–44.

Seymour, J. R., W. F. Humphreys & J. G. Mitchell, 2007. Stratification of the microbial community inhabiting an anchialine sinkhole. Aquatic Microbial Ecology 50: 11–24.

Sket, B., 1996. The ecology of the anchihaline caves. Trends in Ecology and Evolution 11: 221–225.

Stock, J. H., T. N. Iliffe & D. Williams, 1986. The concept "anchialine" reconsidered. Stygologia 2: 90–92.

Thomas, M. L. H., A. Logan, K. E. Eakins & S. M. Mathers, 1992. Biotic characteristics of the anchialine ponds of Bermuda. Bulletin of Marine Science 50: 133–157.

Tomascik, T. & A. J. Mah, 1994. The ecology of "Halimeda lagoon": an achialine lagoon of a raised atoll, Kakaban Island, East Kalimantan, Indonesia. Tropical Biodiversity 2: 385–399.

Tomascik, T., A. J. Mah, A. Nontji & M. K. Moosa, 1997. The Ecology of the Indonesia Seas. Part II. Periplus, Singapore.

Wear, R. G. & L. B. Holthuis, 1977. A new record for the anchialine shrimp Ligur uveae (Borradaile, 1899) (Decapoda, Hippolytidae) In the Philippines with notes on its morphology, behaviour, and ecology. Zoologische Mededelingen (Leiden) 51: 125–142.