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

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## Abstract

In this paper 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

## Introduction

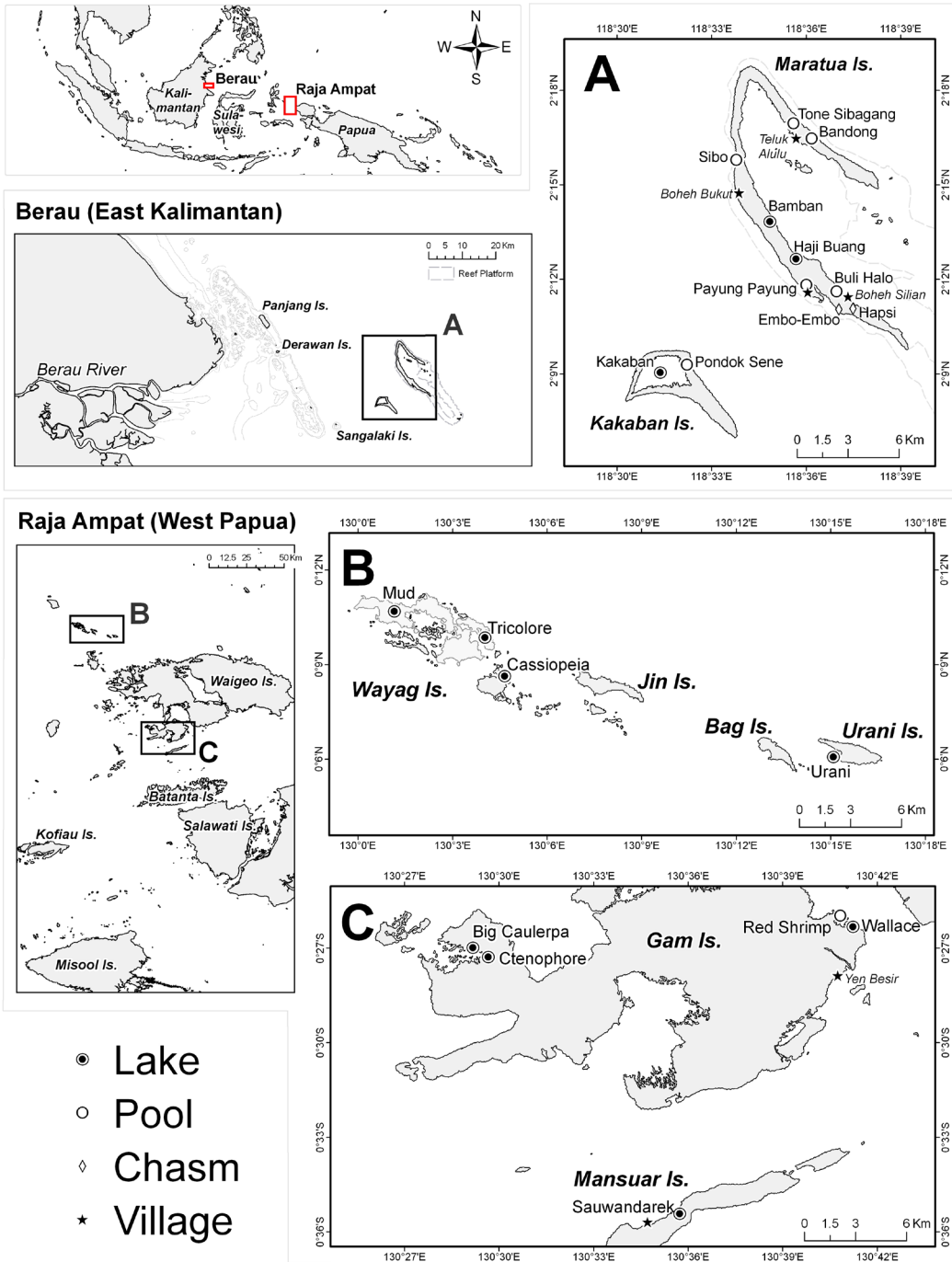
Anchialine systems are small bodies of landlocked seawater that are isolated in varying degrees from the surrounding marine environment, containing water at sea level in natural depressions, craters, and caves, either in lava or limestone. The marine character of these systems is maintained by subterranean 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, Martinez 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 7000-15000 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 1970’s 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, Martinez 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 Mediterranean (e.g. Benivic et al. 2000, Katsanevakis 2005), Caribbean (Thomas 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, *CHAPTER 4*). 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 approximately 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.

A large portion of anchialine taxa have geographically widespread distributions, even though they are adapted





**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

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 paper, we discuss the variability of the setting in which these systems occur, and the implications of these settings for the environments and biota within the systems.

## Study area

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. 1BC). 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 approximately 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 (Figs. 1A & 2A). The island hugs a large lagoon of approximately 29.5x6.5 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 (Figs. 1A & B). Each of these islands is characterized by a karstic scenery including a complex shaped coastline and frequent occurrence of inland depressions (Figs. 5L and 5SE). 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. 2007). 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).

### *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 meters 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 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 hours in the lake and in the adjacent sea to obtain tidal measurements simultaneously in both locations with a logging frequency of 10 minutes. 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 ( $\Delta\text{Tide}_{\text{lake}}$ ) relative to the sea ( $\Delta\text{Tide}_{\text{sea}}$ )

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 hours) in Kakaban lake and Haji Buang lake.

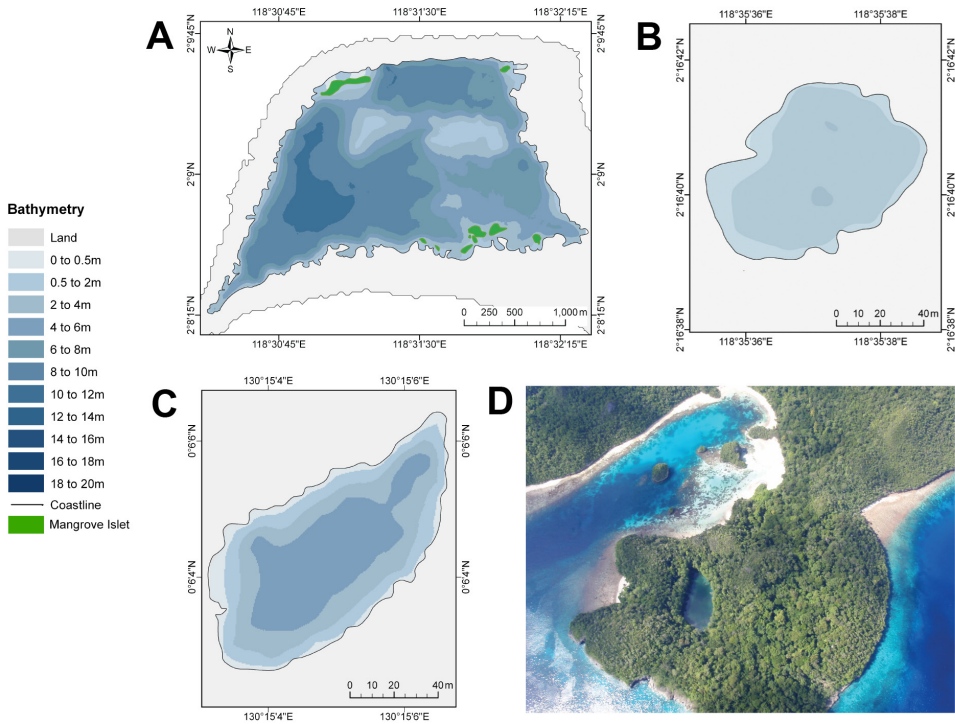


Fig. 2 Bathymetric maps of **A** Kakaban lake, **B** Tone Sibagang pool, **C** Urani lake, **D** aerial view of Urani lake. Note that scale differs per map

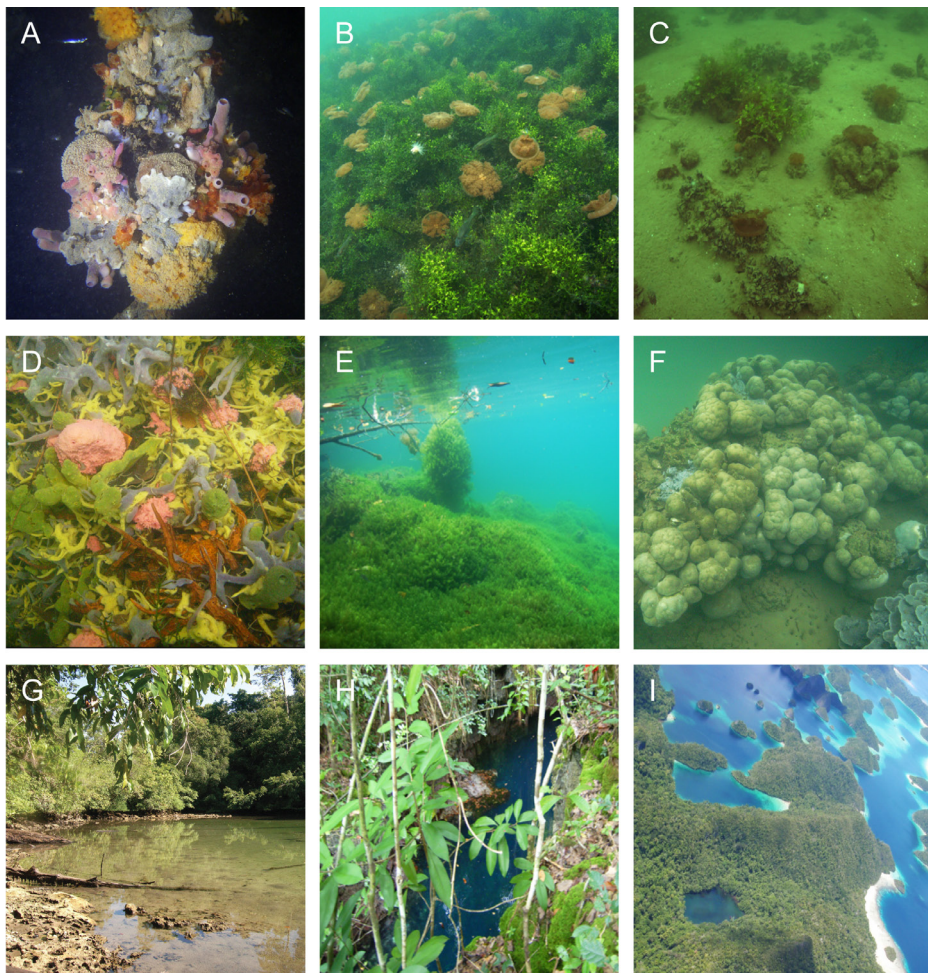
### Recording target flora and fauna

Based on preliminary surveys of lakes in Indonesia, Vietnam and Palau (Hamner & Hamner 1997, 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, CHAPTER 3&4)(Fig. 3D), two sponge species common in reef flats and lagoons *Sphaciospongia vagabunda* (Ridley, 1884) and *Clathria reinwardti* Vosmaer, 1880 (de Voogd et al. 2009); two shrimp species known from anchialine systems *Antecaridina lauensis* (Fig. S2E) and *Parhippolyte uveae* (Fig. S4G) (Maciolek 1983); two jellyfish species *Mastigias 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 Naturalis Biodiversity Center. 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 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, *Mastigias papua*, *Cassiopeia ornata*, *Suberites diversicolor*, *Darwinella* aff. *gardineri*, *Spheciospongia vagabunda*, *Clathria reinwardti*, *Antecaridina lauensis*, *Parhippolyte uveae*, and gobies. These attributes were recorded during timed interval surveys of two hours.



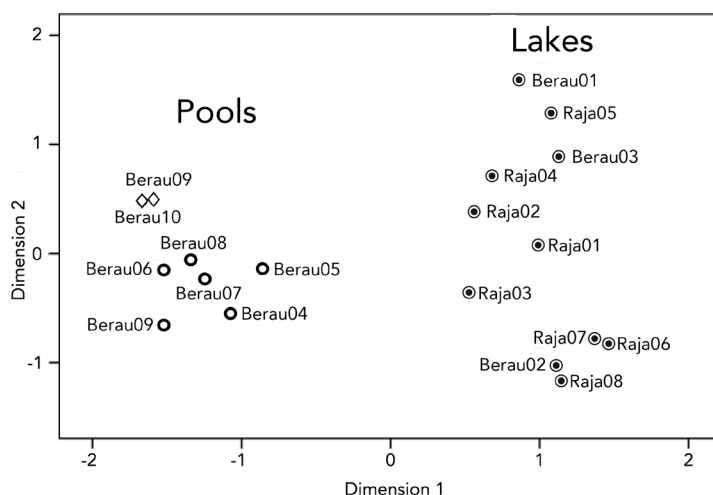
**Fig. 3** **A** mangrove root studded with sponges in Kakaban lake (photograph: B. W. Hoeksema), **B** *Halimeda* algae buildup with *Cassiopeia* jellyfish, **C** Kakaban lake floor with patches of mussels, sponges, *Halimeda* algae, and *Cassiopeia* jellyfish, **D** full sponge cover in Haji Buang 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)

## 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 catalogued (eight in East Kalimantan and eight in West Papua). None of the lakes and pools in West Papua have been formally named and only one lake had a 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 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.



**Fig. 4** Multidimensional scaling ordination based on Euclidian distances of characters of lakes and pools in Indonesia (Stress: 0.08 and R2: 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

### Marine lakes

Twelve marine lakes were studied in East Kalimantan and West Papua (Fig. 1A, B & 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 (Fig. 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, B

& 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 hr delay), medium (60 - 90% relative tide amplitude and 1-2 hrs delay), or low (< 50% relative tide amplitude and > 2hr 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 gymnorhiza*), algae (*Caulerpa* spp. and *Halimeda* spp.), sponges, ascidians (e.g. *Styela 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, halfbeaks, soldierfish), shrimp (e.g. *Antecaridina lauensis*, *Parhippolyte uveae*, *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 *Sphaciospongia vagabunda* and *Clathria reinwardti*. The more isolated lakes contained *Suberites 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, B & C): Buli Halo (Fig. 3G), Sibong, Bandung, 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. *Antecaridina 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, which 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 (*Antecaridina 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 (Myroie & Carew 1995, Illiffe 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 sulphide and supporting a complex aerobic and anaerobic microbial community (Humphreys 1999, Illiffe 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<sup>-1</sup>). Only Sauwandarek lake and Cassiopeia lake (West Papua) may have had anoxic



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

<b>A. East Kalimantan</b>		Sea	Kakaban	Pondok Sene	Haji Buang	Bamban	Tone Sibangang
code in Fig. 4			<i>Berau01</i>	<i>Berau02</i>	<i>Berau03</i>	-	<i>Berau04</i>
<b>PHYSICAL CHARACTERS</b>							
island			Kakaban	Kakaban	Maratua	Maratua	Maratua
latitude			N02° 08' 57.3"	N02° 09' 18"	N02° 12' 31.2"	N02° 13' 50.0"	N02° 16' 39.6"
longitude			E118° 31' 26.4"	E118° 32' 18"	E118° 35' 46.8"	E118° 34' 50.7"	E118° 35' 37.1"
type	sea		lake	lake	lake	lake	pool
shape			trapezoidal	elongated	elongated	elongated	circular
connection to sea			low	high	low	low	high
tidal amplitude (m.)	1.5-2		0,2	1.5-2	0,9	0.5-1	1.5-2
tunnel visible			no	yes	no	no	no
max. depth at low tide (m.)			12	2	17	n.a.	0,75
max. length (m.)			3850	530	800	600	86
area (m2)			40*10 <sup>4</sup>	26500	14*10 <sup>4</sup>	12*10 <sup>4</sup>	4900
min. dist to sea (m.)			120	20	325	115	50
salinity range (ppt)	33-34		23-24	33-34	26-28.5	26	20.8-22.6
pH range	8.2-8.5		7.0-7.8	8.0-8.2	7.3-7.8	n.a.	7.2-7.4
temperature range (°C)	28-30		29-31.5	28-30	29-30	29-30	28-29
<b>BIOTA</b>							
mangrove dominant			yes	no	no	yes	no
sponge diversity			high	high	high	medium	low
fish size			small	large	small	n.a.	large
hard coral			-	+	-	-	-
<i>Suberites diversicolor</i>			+	-	+	+	+
<i>Darwinella aff. gardineri</i>			+	-	+	+	-
<i>Sphaciospongia vagabunda</i>			-	+	-	-	-
<i>Clathria reinwardti</i>			-	+	-	-	-
<i>Antecaridina lauensis</i>			-	-	-	n.a.	+
<i>Parhippolyte uvaea</i>			+	-	+	n.a.	-
gobies			+	-	+	+	-
<b>HUMAN INFLUENCE</b>			tourism, agriculture, sea turtle		tourism, logging	consumption mussels, logging	fishpond, sea turtle
<b>B. West Papua</b>							
<b>B. West Papua</b>		Sea	Cassiopeia	Tricolore	Mud	Urani	Sauwandarek
code in Fig.4			<i>Raja01</i>	<i>Raja02</i>	<i>Raja03</i>	<i>Raja04</i>	<i>Raja05</i>
<b>PHYSICAL CHARACTERS</b>							
island			Wayag	Wayag	Wayag	Urani	Mansuar
latitude			N0° 08' 36.9"	N0° 09' 47.9"	N0° 10' 40.3"	N0° 06' 03.8"	S0° 35' 19.6"
longitude			E130° 04' 39.7"	E130° 04' 05.4"	E130° 01' 09.3"	E130° 15' 04.3"	E130° 35' 48.8"
type	sea		lake	lake	lake	lake	lake
shape			circular	oval	circular	oval	oval
connection to sea			medium	medium	medium	medium	low
tidal amplitude (m.)	1-1.5		1,2	0,8	0.5-1	0.5-1	0.1-0.5
tunnel visible			no	no	yes	no	no
max. depth at low tide (m.)			4	2	2	6	19
max. length (m.)			125	250	170	140	500
area (m2)			13*10 <sup>3</sup>	18*10 <sup>3</sup>	19*10 <sup>3</sup>	6800	84*10 <sup>3</sup>
min. dist to sea (m.)			60	70	270	100	300
salinity range (ppt)	33-34		28-30	31-33	31-33	28-30	28-30
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
temperature range (°C)	28-29		30-31	29-30	29-30	30-31.5	31-34
<b>BIOTA</b>							
mangrove dominant			no	yes	yes	yes	yes
sponge diversity			medium	high	medium	high	medium
fish size			absent	medium	medium	small	small
hard coral			-	-	-	-	-
<i>Suberites diversicolor</i>			+	-	+	+	+
<i>Darwinella aff. gardineri</i>			-	+	-	+	+
<i>Sphaciospongia vagabunda</i>			-	-	-	-	-
<i>Clathria reinwardti</i>			-	-	-	-	-
<i>Antecaridina lauensis</i>			-	-	-	-	-
<i>Parhippolyte uvaea</i>			-	+	-	+	+
gobies			-	+	+	+	+
<b>HUMAN INFLUENCE</b>			sea turtle?	absent	absent	absent	sea turtles, village

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

<b>Buli Halo</b>	<b>Payung Payung</b>	<b>Sibo</b>	<b>Bandong</b>	<b>Embo-Embo</b>	<b>Hapsi</b>
<i>Berau05</i>	<i>Berau06</i>	<i>Berau07</i>	<i>Berau08</i>	<i>Berau09</i>	<i>Berau10</i>
Maratua N02° 11' 16.4" E118°37' 06.4" pool circular high 1.5-2 yes <0.5 100 7295 400 26 n.a. n.a.	Maratua N02° 11' 45.7" E118°36' 09.9" pool circular high 1.5-2 no 0 80 4800 300 26 n.a. n.a.	Maratua N02° 15' 47.3" E118°33' 46.9" pool circular high 1.5-2 yes 0 20 195 60 20-23 n.a. n.a.	Maratua N02° 16' 22.3" E118°35' 55.0" pool circular high 1.5-2 no <0.5 140 6785 80 20-23 n.a. n.a.	Maratua N02° 11' 03.0" E118° 37 01.9 chasm elongated medium 0.5-1 no 5 30 165 75 11 n.a. 26-28	Maratua N02° 11' 04.2" E118° 37' 28.7" chasm elongated medium 0.5-1 no 5 30 105 200 11 NA 26-28
no low large - - - - - + - -	no absent absent - - - - - - -	<b>no</b> low absent - - - - - - -	no low absent - + - - - + - -	no absent absent - - - - - + - -	no absent absent - - - - - + - -
fishpond, sea turtle	toilet	local recreation	toilet	local recreation	local recreation

<b>Wallace</b>	<b>Ctenophore</b>	<b>Big Caulerpa</b>	<b>Red shrimp</b>
<i>Raja06</i>	<i>Raja07</i>	<i>Raja08</i>	-
Gam S0°26'31.08" E 130°41'8.04" lake circular high 1-1.5 yes n.a. 200 8640 50 31-33 n.a. 29-31	Gam S0° 27' 17.3" E130° 29' 34.3" lake L-shaped high 1-1.5 yes 9 230 25*10^3 75 31-33 7.7-8.0 29-31	Gam S0°26'58.85" E 130°29'10.17 lake circular high 1-1.5 yes 6 85 4100 50 31-33 7.7-8.0 29-31	Gam S0°25'58.23" E130°40'49.74" pool circular n.a. 1-1.5 no 0,5 20 n.a. n.a. n.a. n.a. n.a.
no high large + - - + + - - -	no high large - - + + - - -	no high large + - + + - - -	no absent absent - - - - + - -
fishpond	absent	absent	absent

layers at the bottom, revealed by changes in temperature (increased), water color (to dark brown-orange) with depth, and biota (absence). 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<sub>2</sub>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. 2007, 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. Illife 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, Illife 2000) and is continued in this special issue of *Hydrobiologia*. There are numerous anchialine caves documented in the Indo-Pacific (e.g. Illife 1991, Illife 2000, Humphrey & Eberhard 2001, Jaume et al. 2009), yet in the present 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 environments: 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, 1997, Colin 2009), the eight lakes in Vietnam (from Cerrano et al. 2006, Azzini et al. 2007), as well as the 12 lakes from the present 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, Azzini 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 hour delay in tidal amplitude 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 hours 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 the present 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 *Sphaciospongia vagabunda* and *Clathria 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 *Suberites diversicolor*, the large red shrimp *Parhippolyte uveae*, and in many cases the jellyfish *Mastigias papua* and *Cassiopeia ornata*. It is remarkable that the sponge species *Suberites 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 the present study, Kakaban lake, contained a unique fauna that we did not observe in any of the other lakes in Indonesia, such as two holothurians (*Holothuria (Lessonothuria) cavans* and *Synaptula spinifera*), a jellyfish eating actinarian (*Entacmaea medusivora*), and an ascidian (*Styela 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 *Cassiopeia ornata*, *Mastigias papua*, and *Suberites 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 1976), Funafuti (Holthuis 1973), as well as the six pools in the present study. On the islands of Hawaii and Maui much smaller anchialine pools than in Indonesia have been found ranging in size from 0.5-12 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 in 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 *Halocaridina 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, *Antecaridina lauensis* (Holthuis 1973, Maciolek 1983, this study). In the Indonesian pools some individuals of sponge specimens were observed, but sponges are rarely recorded from the other geographic locations.

### *Blue pools in chasm*

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 Illife (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 presumably 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 6-32m. 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 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.

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## Supplementary description

### Berau, East Kalimantan

#### *Kakaban island*

Kakaban is a trapezoidal shaped island with a maximal (diagonal) length of 7 km and a 40-60 m high ridge encircling a large marine lake (Figs. 1A & 2A, and see Tomascik et al. 1997). 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 to a maximum depth of 200 m. Kakaban lake 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) (Fig. S1A), and an ascidian (*Styela complexa* Kott 1995). Since 2001 there is a jetty and walkway towards the lake built for easy access for tourists.

#### *Kakaban lake*

The average depth in the lake is 8m with two deeper areas of 10-12 m in the north and in the southwest separated by a shallow *Halimeda* bank of 0-2 m depth. A large portion of the lake in the center towards the east is very shallow (Fig. 2A). The west and south coasts are bordered by a flat nearshore zone and are fringed by a 1-5 m wide mangrove belt (predominantly *Bruguiera gymnorrhiza* Lam. and *Rhizophora mucronata* Lam.) which results in an irregular coastline with mangrove islets and bays (Fig. 2A, S1D). The eastern part of the south coast contains *Nypa* palm in addition to the other mangroves. The submerged roots of the mangroves are highly intertwined and meshed, providing a wall-like structure (Fig. S1B). In some locations the roots hang above the bottom while in others they are rooted in the bottom. The northern cliff coast is near vertical and mangroves are rare, resulting in a predominantly steep rocky shoreline (Fig. S1C). The east coast consists mostly of exposed rock interspersed by patches of mangroves. There are areas on the east coast with cavern formations 1-2m inland, these are all dead-ended. The bathymetry of the lake is indicated in Fig. 2A. The rocky coast and the submerged mangrove roots were covered with mussels, sponges, ascidians and algae (Fig. 3A), amidst which were holothurians, asteroids, and ophiuroids (Fig. S1A). Sponges had a high abundance and diversity (>40 species) in the lake. Along the upper part of the intertidal area there were high abundances of gastropods (predominantly *Nerita* sp., *Terebralia* sp., *Cerithium* sp.) and bivalves (predominantly *Brachydontes* sp.). The sediment below the roots was dark black-brown scattered with sponges fallen from the roots. The bottom in front of the roots was covered with *Halimeda* where *Cassiopeia ornata* jellyfish, and *Holothuria cavans* sea cucumbers were abundant, with few sponges (Fig. 3B). *Halimeda* spp. were the most dominant algae in terms of biomass. The shallow lake slope was covered by *Halimeda* algae down to a depth of ~5-6 m. The sediment at the lake floor was dominated by dead *Halimeda* thalli. The benthic habitat at >6 m depth was dominated by fine mud where locally patches mussels provided a solid substrate which was usually colonized by sponges (Fig. 3C). The lake housed large swarms of the jellyfish *Mastigias papua*. A detailed description of flora and fauna was provided by Tomascik & Mah (1994) and Tomascik et al (1997). A sea turtle had been released in the lake by humans before 2008 and was in poor health with decomposing flesh in 2009.

Kakaban lake had the smallest measured tidal amplitude (19 cm), which was damped to 11% of the adjacent



sea amplitude (175 cm) and showed the largest delay (3 h 30 min) compared those in the surrounding sea (Table 1A). The water had a vertical transparency of 6-8 m and had a green tinted color which transitioned to a light orange-brown color at depths greater than 5 m.

#### *Pondok Sene*

Outside Kakaban lake, along the eastern coast, separated by a steep cliff from the sea was a second lake. Pondok Sene is enclosed by land, except for a visible and large tunnel by which seawater gushes in and out with wave action and changing tides. At low tide the depth is 2 m in the north and 10-50 cm in the south. The sediment in this lake consisted of light colored carbonate sand. Pondok Sene most resembled a lagoon containing stony coral and the reef flat sponges *Sphaciospongia vagabunda* and *Clathria reinwardti*. Despite its proximity (<100 m) the fauna in this lake was not similar to that of the larger and more isolated Kakaban lake.

#### *Maratua island*

Maratua is a horse-shoe shaped island with a rim of raised limestone that is 0.3-1.4 km wide and 10-120 m high. The island hugs a large lagoon of approximately 29.5x6.5 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 mangrove swamp, are present on the western arm of Maratua Island (Fig. 1C). The mangrove swamp separating the two lakes is dominated by *Bruguiera gymnorhiza* with the presence of gastropods (*Cerithium* sp., *Terebralia* sp., *Nerita* sp.) and algae (*Caulerpa* spp.), but no sponges and mussels. A steep limestone cliff separates Haji Buang lake from this mangrove swamp. We located five anchialine pools on Maratua: Buli Halo, Sibon, Bandong, Payung Payung and Tone Sibabang. This is the first description of these pools and we will describe Tone Sibabang in detail as an example. Additionally, we located two blue pools (Embo-Embo and Hapsi) at the southern end of the western arm of Maratua (Fig. 1C) where the only source for fresh water on Maratua is located (according to inhabitants of nearby villages).

#### *Haji Buang lake*

Haji Buang lake is a large, elongated lake separated from the sea by a steep limestone ridge of ~100 m height to the west and a lower limestone ridge of 20-40 m to the east. Between the western ridge and Maratua lagoon runs a mangrove swamp. The average depth of the lake is 8-10 m with two deeper areas in the north (14 m) and in the south (17 m) (Fig. S6AB). The majority of the coastline of Haji Buang lake is formed by limestone rocks covered in sponges (Fig. 3D). The coastline in the east is rimmed by a shallow plateau extending 1-2 m from the coast which is almost fully exposed to air at low tide (Fig. S1G). This plateau transitions into a steep wall-like slope that ends in the sediment at 3-4 m depth, from which the bottom sediment gently slopes down. The majority of the west coast is a vertical limestone wall which covers inwards at some places at approximately 1 m depth. Along the northern end of the west coast a shallow plateau extends 2-3 m from the coast with a 0.5-1 m depth, followed by a steep slope ending in the sediment at 2-3 m depth. Only the southern coast of Haji Buang lake is fringed by mangroves (predominantly *Bruguiera gymnorhiza*) with a seagrass field (*Enhalus* sp.) in front of it (Fig. S1F). Along and below the intertidal area on the rock there were high abundances of gastropods (predominantly *Nerita* sp., *Terebralia* sp., *Cerithium* sp., *Chicoreus* sp.). Sponges occurred in high abundance and diversity (>30 species) along the coast (Fig. 3D). Along the east coast the sponges were covered by a thick 'blanket' of algae (*Caulerpa* spp.) (Fig. 3E). *Caulerpa* algae were

generally abundant in the lake, and abundance decreased with increasing depth. We observed no *Caulerpa* algae at depths >6 m. *Cassiopeia ornata* was abundant on *Caulerpa* (densities of 5-15 ind. m<sup>-2</sup>). Haji Buang lake contained a dense population of *M. papua*. In the south near the mangroves we observed, in September 2008 and May 2009, swarms of juvenile *M. papua* (0.5-1.5 cm width) (Fig. S1E). A green sea turtle had been introduced to the lake before 2008, but was not observed in 2008 or 2009.

The tidal amplitude in the lake was damped to 48% of that in the sea with a delay of 2 h 30 min (Table 1A). We observed water flowing through the porous limestone rock at high tide. The water had a vertical transparency of 6-7 m and a general color of a milky green which transitioned to more brown-orange in water deeper than 5-6 m. In the southern end of the lake the visibility was lower than in other parts. There are two paths leading to the Haji Buang lake: one from the east, used by tourists from the nearby diversorts, and one from the west, used by people from the nearby village Payung Payung.

#### *Bamban lake*

The second lake on Maratua, located north of Haji Buang lake, is a large, elongated lake (Fig. S1H). On the east coast the rock was covered in patches by mussels interspersed with sponges at a lower diversity and abundance than in Kakaban lake and Haji Buang lake. Small numbers of *M. papua* were present and high numbers of sea urchins. Due to the presence of a saltwater crocodile we were not able to survey this lake comprehensively. One surface water sample was taken for salinity (26 ppt). The lake was accessed from the east along a 150 m pass over a 10 m high ridge.

#### *Tone Sibagang pool*

Tone Sibagang is located in the village Teluk Alulu, approximately 20 m east from the main road and is separated from the sea by low limestone rock (Fig. 1C). The pool is small, circular with a uniform bowl-shaped basin and a maximum depth of 0.75 m at low tide (Fig. 1F, S2A). The pool was fringed by lowland tropical forest vegetation or mangrove associated flora, the *Bruguiera* and *Rhizophora* mangroves were absent. The bottom consisted of a mixture of areas of exposed rock and areas covered with a layer of dead leaves, *Caulerpa* algae, detritus and silt (Fig. S2B). Dense populations of small red shrimp *Antecaridina lauensis* (> 20 ind m<sup>-2</sup>) and gastropods (*Nerita* sp., *Terebralia* sp., *Cerithium* sp.) were present. We observed in total only four individuals of the three sponge species *Suberites diversicolor*, *Spirastrella* aff. *decumbens* Ridley 1884, *Lissodendoryx* aff. *similis* Thiele, 1899. Humans had released large reef fish and one green sea turtle in the pool. Contrary to Haji Buang lake, there was little tidal dampening (pool amplitude 90-100% of adjacent sea amplitude) and the delay was less than one hour. The salinity, however, was significantly lower than in the adjacent sea (Table 1A). The water had a horizontal visibility of 10 m and a green-blue tinted color.

#### *Other pools on Maratua island*

All the other pools on Maratua island represented small, uniform bowl-shaped basins with maximum depths at low tide of <0.5 m. Buli Halo (Fig. 1E, 3G) near the village Boheh Silian contained the red shrimp *Antecaridina lauensis* and *Caulerpa* algae in the central pool. A tunnel connecting the pool to the adjacent sea had a high cover of an assemblage of seven sponge species (*Haliclona* sp., *Geodia* sp., *Placospongia melobesioides* Gray, 1867, *Placospongia mixta* Thiele, 1900, *Higginsia* sp., *Axinyssa* aff. *pitys* (de Laubenfels 1954), *Spirastrella* aff. *decumbens*), gastropods (*Nerita* sp., *Terebralia* sp.), cnidarians (anthozoans), and algae (*Caulerpa* spp.), as well large reef fish. Sibon was covered in *Caulerpa* algae and its basin is dry at low tide (Fig. S2G), except for a small cavern area toward the east side. This cavern contained sponges (*Cliona* aff.

*peleia* (de Laubenfels 1954), *Tethya* aff. *coccinae* Bergquist & Kelly-Borges 1991, *Spirastrella* aff. *decumbens*), ascidians (*Eudistoma* sp.), molluscs (*Nerita* sp, *Terebralia* sp., *Cerithium* sp.). Bandong is located behind the gradeschool in Teluk Alulu and is used as a public toilet (Fig. S2D). This pool had a high cover of *Caulerpa* algae (Fig. S2G) and contained a few individuals of one sponge species (*Suberites diversicolor*), ascidians (*Eudistoma* sp.), and gastropods (*Nerita* sp, *Terebralia* sp., *Cerithium* sp.). Payung Payung pool is located in the village Payung Payung and is heavily used as a public toilet (Fig. S2C) and the flora and fauna in the other pools were not present here.

#### *Embo-Embo*

This blue pool is located 75 m inland, separated by limestone rock from the sea coast that is fringed with *Avecinnia* and *Sonneratia* mangroves. The pool is present in a chasm in the ground running parallel to the coastline which was approximately 1-3 m deep to the water level with almost sheer vertical walls (Fig. 3H). The pool was accessed through a cave to the north of the pool, which opens exposing the pool to air. The depth of the pool is 5-6 m with very deep blue color, and a visible halocline at 1-2 m depth. Only one sample of surface water (above the halocline) was collected to measure salinity (11 ppt) and temperature (25-28 °C). The bottom of the pool consisted of organic detritus, silt, and a tree trunk.

#### *Hapsi*

This pool is located 200 m inland and approximately 500 m from the village Boheh Silian. Similar to Embo Embo, Hapsi is also situated in a chasm with vertical walls of up to 20 m. A portion of this pool is roofed over by rock. The water is deep blue with a visible halocline at 1m depth.

### **Raja Ampat, West Papua**

Raja Ampat represents a group of islands at the northern tip of Bird's Head peninsula in West Papua and is an intricate and rugose karst system. Lakes were found on the islands of Mansuar, Gam, Wayag and Urani (Fig1A&B). Each of these islands is characterized by a karstic scenery including a complex shaped coastline and frequent occurrence of inland depressions (Figs. 5L and S5E). The islands of Wayag and Urani in Northern Raja Ampat are characterized by the scarcity of freshwater sources and as such are practically uninhabited. None of the lakes and pools have been formally named and only one lake had a local name (Sauwandarek). As such we use our fieldnames where appropriate. In total nine lakes and pools were surveyed and here we provide their first description. 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. 2007) in collaboration with researchers from the University of California, Merced and Coral Reef Research Foundation, Palau. Previous biota descriptions from lakes on Gam and Mansuar island are only of ascidians by Monniot (2009).

#### *Sauwandarek lake, Mansuar island*

This lake is located on Mansuar island and is the type locality for the species *Suberites diversicolor*, a sponge frequently found in marine lakes (Becking & Lim 2009). Sauwandarek is a medium sized, oblong shaped lake, separated from the sea to the north by a low pass and to the south by a mangrove swamp and limestone ridge (Fig. S6C). The average depth is 8 m with three deeper areas: one in the center (20 m), one in the southwest (19 m) and one in the south (17 m) (Fig. S6D). The majority of the coastline is fringed by mangroves (predominantly *Bruguiera* sp.) (Fig. S3A). Along the southwestern coast there is a 20-25 m area of exposed limestone rock with a plateau extending 1-3 m from the coast with a depth of 0.25-1 m. In the southern part there is a mangrove islet (Fig. S6CD). The mangrove created an intertwined wall of roots, as

in Kakaban lake. The depth along the coastline ranges from 0.75-1 m and gently slopes down to greater depths. Mussels, sponges, ascidians and algae covered most the coast consisting of mangrove roots, fallen tree trunks, and rock (Fig. S3B). Cover decreased with increasing distance from the coast. There was a high abundance of sponges, but only of moderate diversity (18-20 species). In contrast to the larger lakes in East Kalimantan, neither *Caulerpa* nor *Halimeda* algae were very dominant in biomass. The mangrove roots and epibionts were largely covered by brown-purple filamentous algae. At 1-4 m depth there were patches of mussels, some partly covered by sponges. At least two green sea turtles had been introduced by humans before 2007 and these were still present in 2009. The skin of the turtles had turned a deep yellow color.

The delay in tidal phase was at least two hours and the amplitude appeared to be damped as judged by an intertidal zone in the lake of less than 0.5 m, between 20-50% of the amplitude in the surrounding sea (1-1.5 m). The water turned to a dark brown-orange color at 2-4 m depth in 2007 and at 0.5-1 m depth in 2009. The temperature was up to 34°C at this and greater depth. The lake was accessed from the north side of the island along a path of 500 m in length with little elevation. This path continues towards Sauwandarek village beyond the lake, hence the locals refer to the lake as Sauwandarek.

#### *Ctenophore lake, Gam island*

This lake is located in northern Gam (Fig. 1B) and is a small L-shaped lake that is separated from the sea by high limestone ridges from all wind directions (Fig. S6E). The lake is highly connected to the adjacent lagoon by means of a wide (1-2 m) and low (<0.5 m) tunnel on the western coast (Fig. S3C). Ctenophore lake has a uniform basin with a maximum depth of 8.5 m in the central part of the lake (Fig. S6F). The perimeter of the lake is mostly exposed or mud covered rock with sparsely distributed *Bruguiera* and *Rhizophora* mangroves. The periphery lake floor was covered with shell fragments, but further from the edge the bottom was covered in leaves and silt. Sponges, ascidians, oysters and mussels covered the mangrove roots and rocky coast, the abundance and biomass decreasing from the coasts. There was both a high cover and diversity of sponges (>30 species) that were predominantly reef flat species. We observed high densities of ctenophores and *Aurelia* sp. in the middle of the lake, and fewer than 10 individuals of *Cassiopeia* sp. along the rim. Large reef fish (e.g. *Acanthurus* spp.) rushed in and out of the lake. Judged by the intertidal zone, the tidal amplitude was 90-100% of that of the surrounding sea. After heavy rain a layer of fresh water of 5-25 cm thick remained visible for at least a day. Ctenophore lake was accessed from the west along a 80 m long and 10 m high pass.

#### *Big Caulerpa Lake and Wallace Lake, Gam island*

Two other lakes are present on Gam (Fig. 1B), which are similar to Ctenophore lake with high connection to the sea by means of tunnels, few mangroves, and a high diversity and cover of predominantly reef flat sponges (Fig. S3EF). In contrast to Ctenophore lake, these lakes contained living stony corals (Fig. 3F). Big Caulerpa lake was surrounded by steep cliffs (Figs. S3D & S5C) and contained a high abundance of *Caulerpa* algae with large globular thalli. Wallace lake was designated this name as a reference to the six week stay of Alfred Russel Wallace, during his travels in the “Malay Archipelago”, in the village Bessir (now named Yen Bessir) just south of this lake (Wallace 1869).

#### *Red Shrimp pool, Gam island*

The Red Shrimp pool near Wallace Lake is similar to the small anchialine pools in East Kalimantan, with a uniform, bowl-shaped, shallow basin (<0.5 m at low tide). It is full of small red shrimp *Antecaridina laueensis* and some *Nypa* palms are present.

*Cassiopeia lake, Wayag island group*

This lake is located in the eastern part of the Wayag island group (Fig. 1A) and is a small, almost circular lake that is separated from the sea by a low limestone ridge (<10 m high) from all directions except to the east where there is little elevation (Fig. S5A). The lake has a uniform, bowl-shaped basin with a maximum depth of 4m in the center. The lake is rimmed by a wide (1-4 m) and shallow plateau with a depth of <0.5 m at low tide. In the east there is a shallow bay. The coastline is composed of predominantly exposed rock interspersed with single trees of *Rhizophora* mangrove. Patches of mussels and sponges covered the lake floor amidst which there were bristleworms, red worms and green zoanthids (Fig. 5E, S4B). Fields of *Caulerpa* algae covered the subtidal area until 3 m depth. The lake floor at >3 m depth was covered by light colored sand with occasional occurrence of sponges (predominantly the species *Suberites diversicolor*). In the northern area we observed many dead crabs and bleached or dead sponges (Fig. S4A). There was a high abundance of sponges but only of a moderate diversity (15 species). In the central area there were a small number of *M. papua* jellyfish and along the shallow plateau there were high abundances of large *Cassiopeia ornata* jellyfish (5-15 ind m<sup>-2</sup>). There was a green sea turtle, but it was unknown how it came here. We observed no fish in this lake. The tidal amplitude in the lake was damped to 89% of the sea amplitude, with a 1 h 20 min delay (Table 1B). During one visit the visibility in the lake was highly reduced towards the western coast (horizontally less than 1 m) where the water was a brown-yellow color. During our second visit after a rainstorm, however, the visibility increased in the whole lake (1- 5 m) and we observed the brown-yellow water layer below 2 m depth. The lake was accessed from the east along a 60 m pass with little elevation.

*Tricolore lake, Wayag island group*

This small, shallow, hourglass-shaped lake is located in the central part of the Wayag island group (Fig. 1A). Tricolore lake is separated from the sea by a high limestone ridge (>20 m) to the east and a low (<5 m) ridge to the west. The lake has three basins split by mangrove patches and has four deeper areas of 2m. depth, one each in the west, the northwest, the north and in the central area (Fig. S5B). The lake is fringed by *Rhizophora* and *Bruguiera* mangroves, except along the west side which consists of exposed rock and a 1-2m deep cavern with no visible connection to the sea. The lake bottom was covered with *Caulerpa* algae amidst which there were high abundance of bristleworms and white bullomorph opisthobranch molluscs (Fig. S4C). The deeper part of the lake bottom consisted for a large part of mollusc fragments covered by a thin layer of detritus and of mangrove leaves, especially in the deeper area of the northwest part. The other deeper areas of the basins were covered with *Caulerpa* algae. Contrary to the other investigated lakes, oysters instead of mussels were abundantly attached to all available hard substrates. Sponges and ascidians were attached to mangrove roots in patches in the center of the lake (Fig. S4D), and in the cavern along the west side, but these were notably absent in the southeast part of the lake. In the whole lake the sponge abundance was low compared to other lakes but the diversity was relatively high (>20 species). The tidal amplitude in the lake was damped to 68% of the tidal amplitude of the sea, with a 2hr20 m delay in phase (Table1B). The color of the water was blue-green with a linear visibility 5-6m. The lake is named after its apparent three colors from the air: blue-green, dark brown, and orange-red (Fig. S5B). The lake was accessed from the west along a 70 m pass with little elevation of 2-4m.

*Mud lake, Wayag island group*

This lake is located in the western part of the Wayag island group (Fig. 1A). Mud lake is a small, shallow, oval-shaped lake with a uniform basin with a maximum depth of 2.3m in the central area. The lake is separated from the sea to the north by a high limestone ridge (>20 m high) and to the south by a low one (<5 m high)

and a wide mangrove swamp. The lake coastline is fringed by mangroves (predominantly *Bruguiera* sp.). At the east side of the lake there is a cave which may have a direct connection to the sea. The south coast is muddy and is <0.25 m deep up to 5 m distance from the coast (Fig. S4E). The depth along the rest of the coast ranged between 0.5-1m. All sessile biota was covered with fine mud and filamentous brown algae (Fig. S4F). Translucent shrimp were abundantly present. Sponges and ascidians were sporadically attached to mangrove roots and tree trunks, and had the highest cover in the cave. The degree of connection to the sea is expected to be moderate judged by an intertidal zone of 0.5-1m (70-80% of the adjacent sea amplitude). The color of the water was blue-green and below 0.5-1m depth transitioned to brown-yellow with a high content of flocculent sedimentation. The vertical visibility was 1-2m. The lake was accessed from the south along a 500 m pass through a mangrove swamp and over an elevated limestone ridge of 3-5 m.

#### *Urani lake, Urani island*

This lake, located in the western side of Urani island (Fig. 1A), is a small, tear shaped lake that is separated from the sea in all wind directions by 20-40 m high limestone ridges (Fig. 2C). The lake has a uniform, bowl-shaped basin with a maximum depth of 6m in the central area of the lake (Fig. 2D). A dense mass of *Caulerpa* algae on the lake floor may have biased our handheld sonar measurements, obscuring the actual basin depth. A 1-5 m wide belt of mangroves (predominantly *Bruguiera*) fringes the perimeter of the lake. The west coast is represented by exposed limestone and a cavern with no visible connection to the sea. The depth along the coast ranges from 1-2m and slopes down steeply. Many trees had fallen into the lake (Fig. S5D). There was a mixture of *Caulerpa* and *Halimeda* algae in the lake, but *Caulerpa* was the most abundant. Large portions of the mangrove roots and the lake bottom are covered by *Caulerpa* algae. Sponges, ascidians and mussels were attached to all available substrate, amidst which were orange worms and ophiuroids (Fig. S4H). The large red shrimp *Parhippolyte uveae* appeared abundantly present (Fig. S4G). The degree of connection to the sea was expected to be moderate, judged by an intertidal zone of 0.5-1m (70-80% of the adjacent sea amplitude). The water was tinted a milky blue-green color and the vertical visibility was 4-5 m.

#### *Lakes located by air*

We located seven additional lakes by air, but these are not part of the present survey: WAY05 (Wayag island, N0° 10' 35.9' E130° 01' 18.1"), WAY06 (Jin island, N0° 08' 14.0" E130° 09' 00.7"), WAY07 (Jin island, N0° 08' 10.7" E130° 09' 04.1"), WAY08 (Bag island, N0° 06' 28.6" E130° 12' 57.5"), GAM01 (Gam island, S0° 26' 59.3" E130° 30' 02.3"), GAM02 (Gam island, S0° 26' 57.2" E130° 30' 04.7"), FAM01 (Fam island, S0° 36' 01" E130° 45' 08").



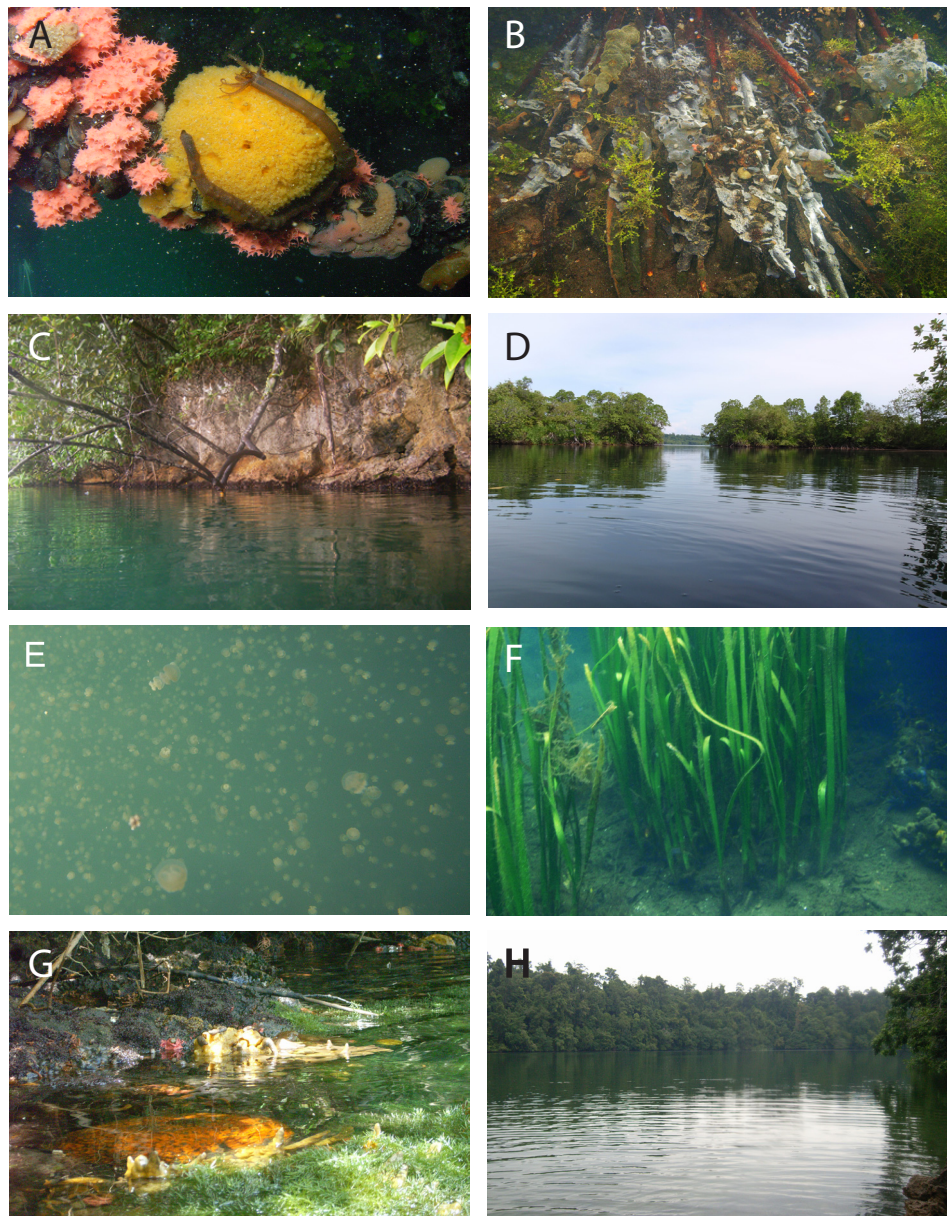
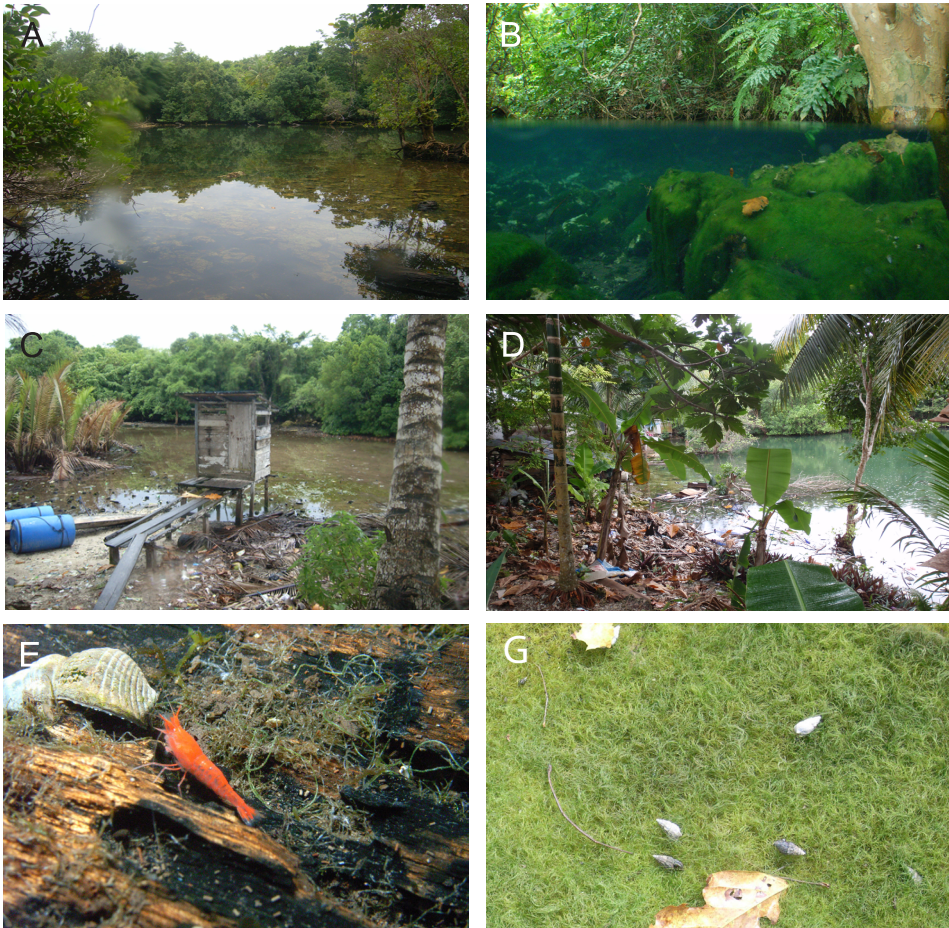


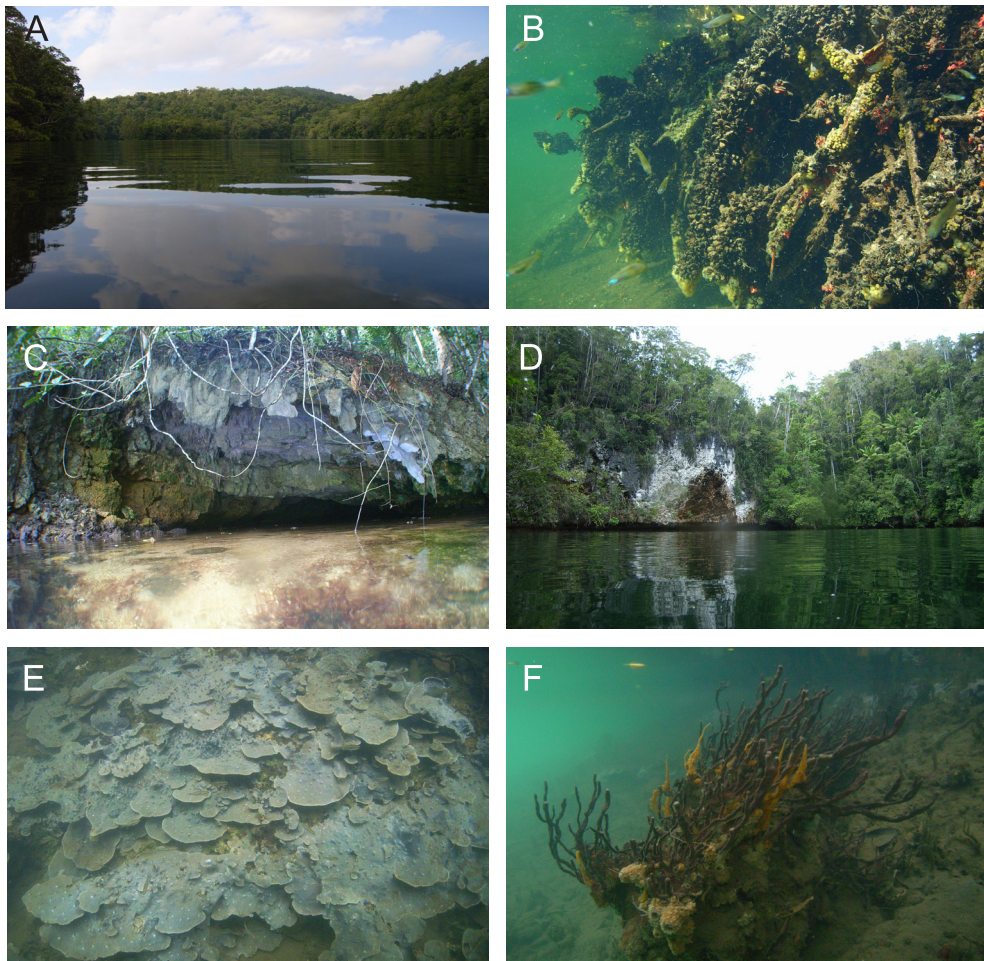
Figure S1. *In situ* photographs of marine lakes in Berau (East Kalimantan, Indonesia): Kakaban lake

A. mangrove root covered in sponges with holothurian, B. mangrove roots intertwined as wall, C. north coast rocky shore, D. mangrove baylet; Haji Buang lake E. swarm of small juvenile *Mastigiaspapa* jellyfish, F. *Enhalus* sp. seagrass, G. sponges and algae along coast exposed to air at low tide, H. overview of Bamban lake. All photographs by L.E. Becking, except F. by N.J. de Voogd.

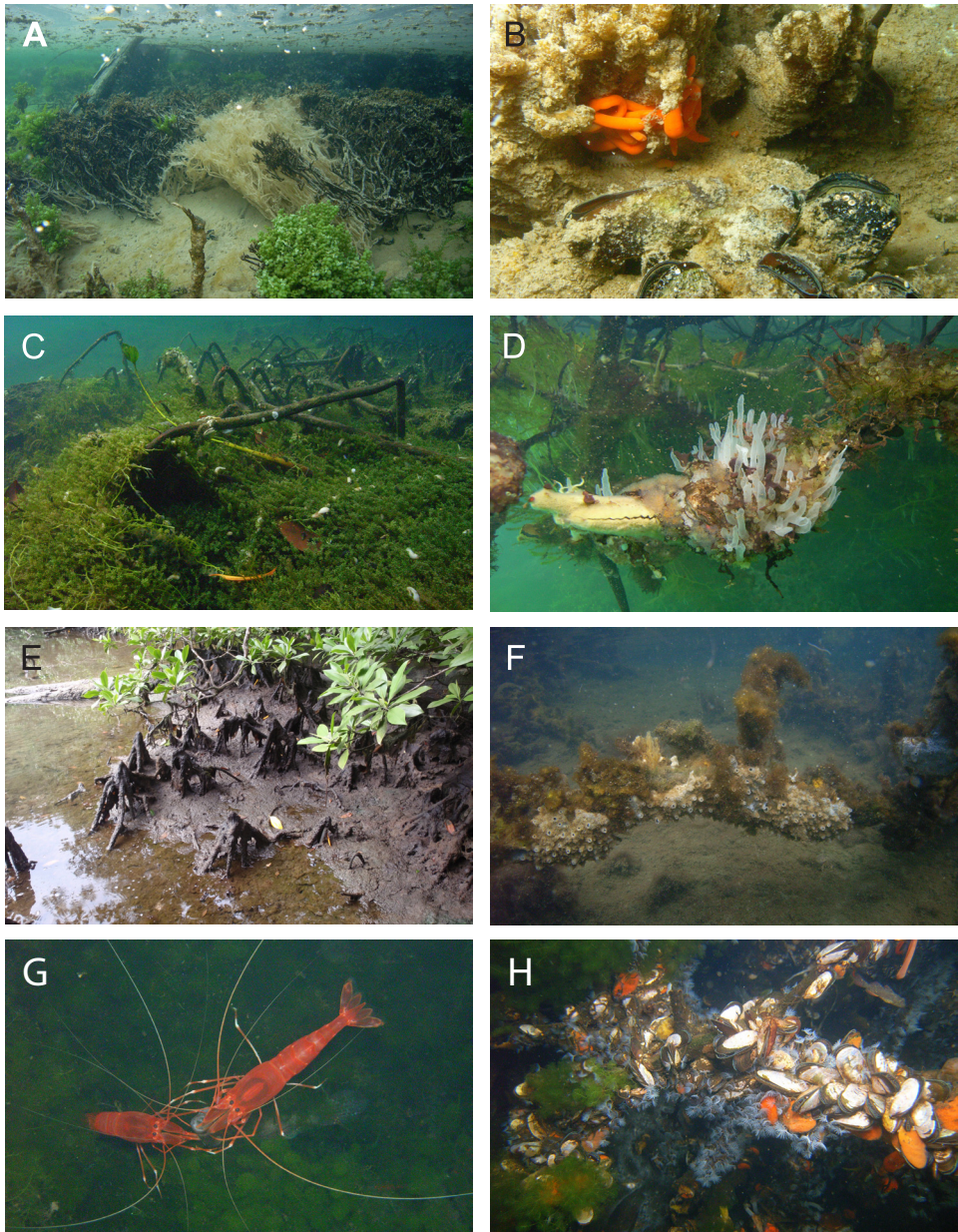


**Figure S2.** *In situ* photographs (by L.E. Becking) of anchialine pools in Berau (East Kalimantan, Indonesia): **A.** Tone Sibagang overview, **B.** Tone Sibagang at high tide, **C.** Payung Payung pool with outhouse, **D.** Bandong pool, **E.** *Antecaridina lauensis*, **F.** algae covering rocks in pools





**Figure S3.** *In situ* photographs (by L.E. Becking) of marine lakes in central Raja Ampat (West Papua, Indonesia): **A.** overview of Sauwandarek lake, **B.** mussels, ascidians and sponges on mangroves in Sauwandarek lake, **C.** tunnel in Ctenophore lake, **D.** cliff in Big Caulerpa lake, **E.** spongereef in Wallace lake, **F.** elongated sponges in Wallace lake.



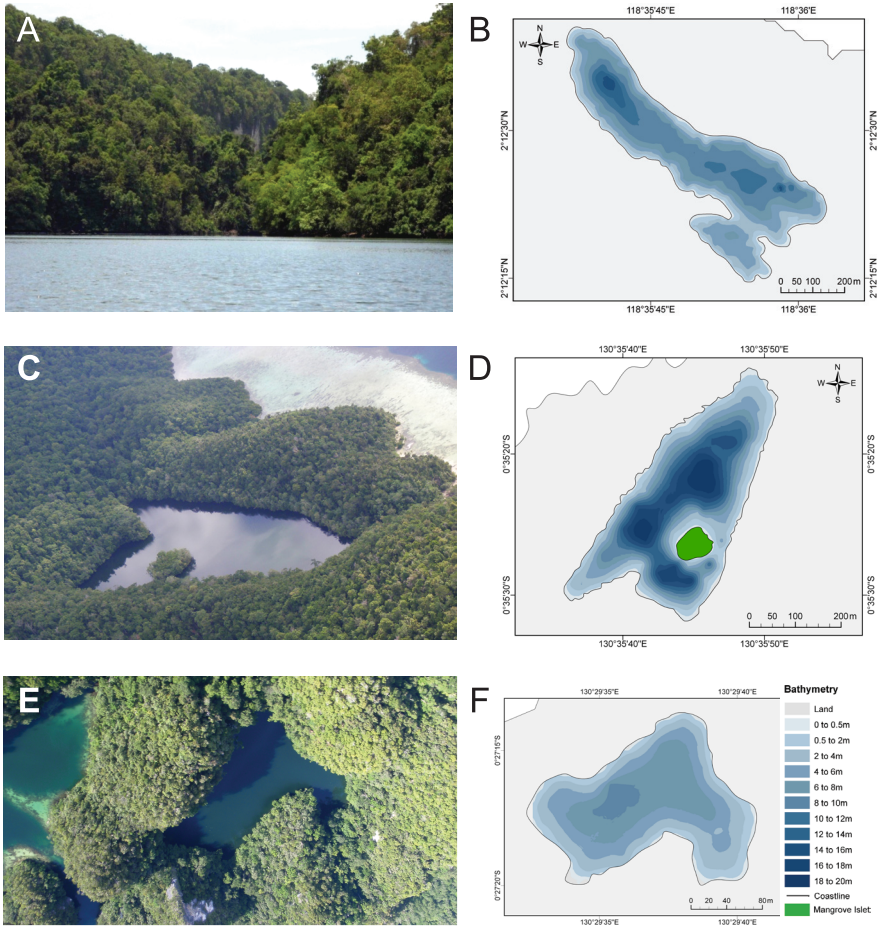
**S4.** In situ photographs (by L.E. Becking) of marine lakes in northern Raja Ampat (West Papua, Indonesia):

Cassiopeia lake **A.** branching brown sponge (*Haliclona* sp.) partially bleached, **B.** red worms and mussels; Tricolore lake **C.** mangrove roots with *Caulerpa* algae, oysters, and bullomorph opisthobranch molluscs (white), **D.** mangrove root with sponges, mussels, ascidians, and algae; Mud lake **E.** muddy coast, **F.** sponge and lake floor covered in silt and algae; Urani lake **G.** *Parhippolyte uveae*, **H.** branch covered in mussels, sponges and tubeworms.





**S5.** Aerial photographs of Raja Ampat (West Papua, Indonesia): **A.** Cassiopeia lake, **B.** Tricolore lake, **C.** Big Caulerpa lake, **D.** close up of Urani lake (note fallen trees on surface), **E.** overview of Wayag island group, **F.** Drifter water aiplane. All photographs by L.E. Becking, except **F.** by E. Dondorp.



S6. In situ photograph (by L.E. Becking) and bathymetric map of **A**, **B**, Haji Buang lake, aerial photographs (by L.E. Becking) and bathymetric maps of **C**, **D**, Sauwandarek lake, **E**, **F**, Ctenophore lake.

