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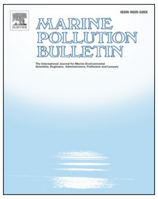

Recognizing peripheral ecosystems in marine protected areas: A case study of golden jellyfish lakes in Raja Ampat, Indonesia

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ABSTRACT

Peripheral marine ecosystems can harbor endemic diversity and attract tourism attention, yet are generally not included in conservation management plans due to their remoteness or inland positioning. A case study in Raja Ampat of seven landlocked marine lakes containing golden jellyfish (*Mastigias* spp.) was conducted to address the lack of fundamental insights into evolutionary, ecological and social contexts of these ecosystems. An interdisciplinary approach was taken towards identifying the jellyfish lakes as distinct management units in order to incorporate them into existing Marine Protected Areas. *Mastigias papua* populations showed strong genetic (ϕ_{ST}: 0.30–0.86) and morphological ($F = 28.62$, p-value $= 0.001$) structure among lakes, with putative new subspecies. Risks arising from rapid increase in tourism to Raja Ampat (30-fold since 2007) warrant restrictions on jellyfish lake use. Recommendations are provided for adaptive management and science-based conservation policies for jellyfish lakes across Indonesia.

1. Introduction

Peripheral marine ecosystems - such as marine lakes, anchialine caves, and cenotes - attract significant attention from tourism due to their relatively pristine environments and propensity to harbor endemic diversity (Dawson et al., 2001; Mercado-Salas et al., 2013; Becking et al., 2015; Gerovasileiou et al., 2016; Lopez-Maldonado and Berkes, 2017; Martínez et al., 2019; Masonjones et al., 2019). Tourism interest can have socio-economic benefits for local communities, can lead to an awareness towards management of the ecosystem and prevent destructive exploitation (Pretty and Smith, 2004; Trave et al., 2017). However, if tourism is not managed effectively, recreational use of peripheral marine ecosystems may have devastating effects, particularly in combination with other stressors such as climate change (Cerrano et al., 2006; Hoegh-Guldberg and Bruno, 2010; Hughes et al., 2017; Trave et al., 2017). Prime examples of peripheral ecosystems that are tourism magnets are “jellyfish lakes”, landlocked marine lakes containing dense populations of golden jellyfish, *Mastigias* spp. (Scyphozoa: Rhizostomae, Lesson 1830). Of the approximately 200 marine lakes known worldwide (Holthuis, 1973; Dawson et al., 2009), 22 contain jellyfish and are located in Indonesia, Palau and Vietnam (Hamner and Hamner, 1998; Dawson and Hamner, 2005; Becking et al., 2015; Swift et al., 2016). Ongeim'l Tketau in Palau, probably the most famous marine lake in the world, attracts thousands of tourists yearly (Dawson et al., 2001). Recently discovered jellyfish lakes in Indonesia are also rapidly becoming tourist attractions (Becking et al., 2015). However, conservation management plans are lacking for peripheral ecosystems in general (Mercado-Salas et al., 2013; Martínez et al.,

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2019; Masonjones et al., 2019), and for jellyfish lakes in Indonesia in particular. Indonesian jellyfish lakes can serve as a case study to formulate an approach towards effectively incorporating peripheral systems into conservation management plans.

The development of effective conservation programs for jellyfish lakes in Indonesia is hampered by incomplete knowledge on local jellyfish evolution and ecology and the unique social context of the lakes. Designating marine lakes as individual management units (MUs) could facilitate their incorporation into governmental management plans (Moritz, 1994; Palsbøll et al., 2007). To be considered an MU sensu Moritz (1994), biological populations should show “significant divergence at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of alleles”, preferably in concordance with non-molecular traits. Marine lakes in Palau are reported to harbor isolated jellyfish populations of unique subspecies with adapted morphology, suggested to be indicative of incipient speciation (Dawson and Hamner, 2005; Swift et al., 2016). The adapted morphology is described to be derived from the ancestral oceanic ecotype (Dawson and Hamner, 2005; Swift et al., 2016). The oceanic ecotype is described to display eight large terminal clubs ($>$ 0.5 times bell diameter), white spots and blue pigmentation, whereas the derived ecotype has fewer and smaller (~0.2 times bell diameter) terminal clubs and no spots or blue pigmentation. The shift from the oceanic towards the derived ecotype in marine lakes is hypothesized to be facilitated by higher turbidity and lower predator presence in isolated lakes (Dawson, 2005; Swift et al., 2016). Demonstrating concordant genetic differentiation and morphological adaptation in Indonesian jellyfish lake populations would provide scientific incentive to view marine lakes as distinct MUs.

Vulnerability of jellyfish lake populations to external stressors has been reported for the marine lake Ongeim'l Tketau in Palau, which suffered severe crashes in jellyfish abundance in 1998, and again in 2016 (Dawson et al., 2001; Howard, 2016). The crashes were associated with changes in lake temperature and salinity following El Niño Southern Oscillation (ENSO) events (Dawson et al., 2001; Martin et al., 2006). In addition, concerns about the impact of sunscreen pollution on jellyfish proliferation have been raised (Bell et al., 2017). Jellyfish are known for boom-bust dynamics, particularly those resulting in harmful blooms (Pitt and Lucas, 2014; Dawson et al., 2015). Here, a ‘boom’ of rapid increase in medusa abundance occurs via strobilation of benthic polyps (scyphistoma) related to potentially seasonal patterns of water temperature increase (Sugiura, 1965; Collins, 2002; Holst et al., 2007). Then, a 'bust' follows by steep declines after a few months due to age or starvation (Pitt and Lucas, 2014). However, in marine lakes of Palau and Indonesia environmental conditions are considered to be relatively stable throughout the year, with no clear seasonal patterns (Hamner et al., 1982; Muscatine et al., 1986). Therefore, strobilation is expected to occur continuously throughout the year, which would preclude boom-bust dynamics. While some natural fluctuation in jellyfish abundance has been recorded for jellyfish lakes in Palau (Dawson et al., 2015), the reported population crashes of 1998 and 2016 suggest severe external perturbation.

There are thirteen jellyfish lakes currently known in Indonesia, located in Berau (East Kalimantan province, 3 lakes), Togean (Central Sulawesi, 1 lake), and Raja Ampat (West Papua, 9 lakes) (Becking et al., 2015; Swift et al., 2016, current study). West Papua lies within one of twelve ecoregions of Indonesia (Spalding et al., 2007), and has by far the most marine lakes documented of any region in Indonesia. West Papua has been the focus of significant Marine Protected Area (MPA) development over the past two decades (Mangubhai et al., 2012), and has become the first “conservation province” in Indonesia (Act No. 522.5/123/6, 2015). As of 2013, Raja Ampat contained seven multiple-use MPAs forming a network of over 1 million hectares (Gaman et al., 2012; Grantham et al., 2013). Two new protected areas (North Misool and Fam MPAs) have been added in the past three years, bringing the total protected marine area to just over 2 million hectares. Development of MPA zonation plans in West Papua is strongly based on the customary tenure rights of local communities, which allow them to control utilization of surrounding natural resources (Kartasapoetra et al., 1985; McLeod et al., 2009). In Indonesia, the special autonomy of West Papua regarding customary tenure rights is recognized nationally (Act No. 21, 2001), and also by local communities and tourism stakeholders. Customary tenure therefore has important bearing on the current and future management of the jellyfish lakes.

Local tenure holders provided significant input on recommendation for the management of jellyfish lakes during the first iteration of the Raja Ampat MPA management plan (Mustaghfirin et al., 2012). However, it was subsequently decided by the Ministry of Marine Affairs and Fisheries (MMAF) to change the classification of Raja Ampat's MPA network from a “coastal and small islands park” to a “marine tourism park”, meaning that only areas below the high tide mark are explicitly managed under the Raja Ampat MPA zonation system (MMAF Ministerial regulation No. 36, 2014). Jellyfish lakes therefore currently are not incorporated in the MPA management plans due to their inland position. Nonetheless, jellyfish lakes in Raja Ampat are actively being promoted as tourist attractions, with jellyfish depicted on the tourism entrance tag in 2019, and advertisement of lakes through homestays. The lack of explicit conservation and tourism management regulations for jellyfish lakes may have implications for the persistence of these fragile ecosystems.

We have conducted an interdisciplinary study with the aim to provide scientific basis to incorporate jellyfish lakes, unique peripheral ecosystems, into conservation management plans. Our objectives were to: 1) determine the phylogenetic position of Raja Ampat jellyfish lake populations in an Indo-Pacific context, 2) quantify variation in jellyfish population genetics, morphometrics and abundance between lakes and over time, and 3) assess lake use, customary tenure and perceived threats. To address these objectives we quantitatively sampled seven jellyfish lakes, held stakeholder interviews, and made direct observations on the use and threats of the lakes throughout Raja Ampat over eleven years. Ultimately, this study provides practical recommendations to aid management agencies in Raja Ampat, and more broadly throughout Indonesia, in implementing biologically sound, science-based conservation policies for peripheral ecosystems.

2. Materials and methods

2.1. Lake profiling and sample collection

We characterized the environment of seven jellyfish lakes in Raja Ampat following the approach of Becking et al. (2011) and Maas et al. (2018), recording temperature (°C), salinity (ppt), pH, depth and connection to sea (Fig. 1, Supplementary material Table 1). The lakes were coded following Maas et al. (2018) and de Leeuw et al. (*in review*). Three of the lakes have local names: Tomolol (Papua2), Lenmakana (Papua4), and Karawapop (Papua5). Two additional lakes in Raja Ampat, Gam mentioned by Swift et al. (2016) (IDWPDAG and IDWPDCG) did not contain jellyfish during our study period. We made direct observations on jellyfish presence, lake use and tourism increase between 2009 and 2019. We sampled 133 *Mastigias* specimens for genetics analyses, and photographed 338 specimens for morphometric analyses between 2013 and 2018 (Supplementary material Table 1).

2.2. DNA extraction and sequencing

Tissue samples were immediately preserved in the field in 96% ethanol or RNAlater and kept at room temperature or at 4 °C throughout the field work period. Upon returning to the lab samples were stored in −20 °C. DNA was extracted using the Qiagen DNeasy Blood & Tissue kit (Qiagen, Germantown, MD, USA). Polymerase chain reaction (PCRs) were performed to amplify mitochondrial cytochrome *c* oxidase subunit I (COI) using dgLCO/HCO primers from Meyer (2003) and LCOjf and MpHCO from Dawson and Hamner (2005). We followed

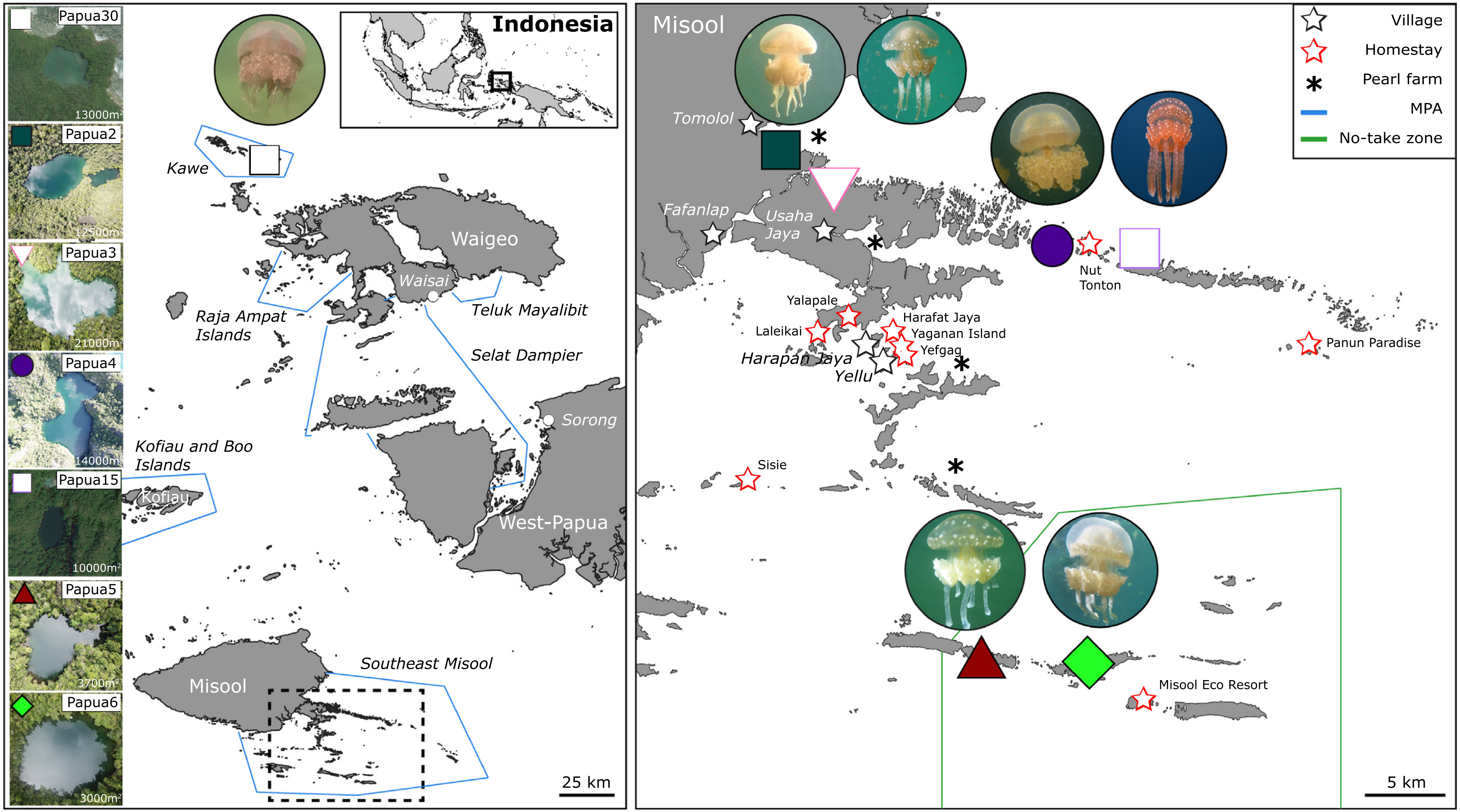


Fig. 1. Sample localities of *Mastigias papua* populations in Raja Ampat, West Papua, Indonesia. Jellyfish were sampled from seven marine lakes (Papua30, Papua2, Papua3, Papua4, Papua15, Papua5, Papua6). Left panel shows overview of Raja Ampat Regency, lake outlines, area, and location of Papua30. Right panel shows zoomed-in map of Misool with locations of Papua2, Papua3, Papua4, Papua15, Papua5 and Papua6.

a protocol as defined in Becking et al. (2016). Briefly, PCR reactions were performed in 25 μL volumes containing 12.5 μL Onetaq Mastermix (2×), 8.5 μL ddH_2O, 2 μL BSA, 0.5 μL of both primers (10 μM), and 1 μL template DNA (10 ng/μL). We used denaturing, annealing and extension temperatures of 94 °C, 45 °C and 72 °C, respectively. Amplicons were purified and Sanger sequenced at Macrogen, Inc. (the Netherlands).

Forward and reverse sequences were aligned and assembled in Geneious (version 10.2.5) and using the Muscle algorithm (Edgar, 2004) in MEGA7 (Kumar et al., 2016). The assemblies were visually inspected and primer-ends were trimmed, resulting in a final fragment size of 542 bp. All sequences had high similarity to *M. papua*, as verified by BLASTn (Altschul et al., 1997). Two datasets were compiled: 1) Only sequences from this study, and 2) including additional samples from Palau, East Kalimantan, Papua New Guinea, Japan, Vietnam (GenBank accession numbers: KU900912-KU901464, (Swift et al., 2016)), and Puerto Rico (GenBank accession numbers: JN215543–JN21551, (Bayha and Graham, 2011)). The sequences are deposited in GenBank (MN107549-MN107722).

2.3. Phylogenetics and population genetics

Using dataset 2, a maximum likelihood phylogenetic tree was constructed and bootstrapped 1000 times in MEGA7 (Kumar et al., 2016), with *M. andersoni* as the outgroup. The Akaike Information Criterion (AIC), calculated in jModelTest v.2.1.5 (Darriba et al., 2012), indicated HKY + I as the best fitting evolutionary model (Hasegawa et al., 1985). The tree was visualized with FigTree v1.4.2. Pairwise sequence divergence between populations (p-distances) was computed in MEGA7. Haplotype networks were constructed using HaploViewer (Salzburger et al., 2011).

Using dataset 1, population genetic structure and diversity was estimated. Nucleotide diversity (π) (Tajima, 1983), haplotype diversity (h) (Nei, 1987), and number of private haplotypes per lake were calculated via the package *pegas* (Paradis, 2010), implemented in R v. 3.5.0 (R Core Team, 2018). Population structure was estimated between lakes and years via ϕ_{ST} using Arlequin with 1000 permutations to estimate significance (Excoffier and Lischer, 2010).

2.4. Morphological measurements

To assess morphological variation, standardized photographs of jellyfish along the longitudinal axis of each specimen with a color chart and scale were taken using a GoPro HERO3 or Olympus TG-3 between 2016 and 2018. Images were analyzed in ImageJ (version 1.5oi). Morphological measurements were corrected for bell diameter to adjust for size effects and rescaled to values between zero and one, following Dawson (2005). Of 13 morphological characteristics measured, nine were concordant with Dawson (2005). The additional 4 variables included total length, bell length, total length of oral arms and terminal club width, and were measured to explore morphology in more depth. We measured continuous and categorical variables. Continuous variables included: total length, bell length, bell width (*f*9 in Dawson, 2005), total length of oral arms, length of unwinged portion of oral arms (*f*11), length of winged portion of oral arms (*f*12), length of terminal clubs (*f*15), and width of terminal clubs. Categorical variables included: bell color (*f*1, categories: orange/brown, white and blue), oral arm color (*f*4, categories same as *f*1), terminal club color (*f*5, categories same as *f*1), shape of terminal clubs (*f*13, categories: Thick end, pointy, straight, wide), and presence/absence of white spots on the bell (*f*6). Morphological characteristics were summarized in bar plots. Kruskal Wallis tests with post-hoc Dunn's tests were performed to assess significant differences among groups, after assumptions for data normality and homogeneity of variances were found to be violated.

Morphological variation between lakes and years was displayed using Principal Component Analysis (PCA) for quantitative data and a Multiple Factor Analysis (MFA) to include categorical data. Multivariate homogeneity of group dispersions were tested to verify the assumption of homogeneous variance distributions. Permutational multivariate analyses of variance using Euclidean distances were performed to assess significant differences between groups (lakes and years). All analyses were performed in R, using *stats*, *car*, *FSA* and *vegan* (Oksanen et al., 2016) packages for statistical tests and *ggplot2* (Wickham, 2016) for visualization.

2.5. Abundance estimations

Quantitative assessments of jellyfish abundance were conducted once every year in May of 2016–2018 for four lakes containing jellyfish most consistently (Papua2, Papua3, Papua4 and Papua15), resulting in 12 assessments in total. A non-invasive method was used by swimming transects with a GoPro HERO3 video camera fixed to a frame (39 × 53.5 cm). Five to eight transects were conducted horizontally with the frame held approximately 50 cm below the surface. One transect was conducted along the longest axis of the lake, and, depending on lake size, four to seven evenly spaced along its perpendicular. Additionally, three vertical transects were performed to estimate the maximum depth jellyfish were present. All transects were swum between 9:00–10:00 AM. Transect videos were processed by counting the number of jellyfish passing the frame every 10 s using a hand counter. Abundance was calculated via the following formula:

$$Abundance\ transect_i = \left(\frac{Transect_i * Frame\ size}{Lake\ area * Max.depth\ jellyfish}\right) * \#\ jellyfish\ transect_i$$

The average of all transects was used as the final estimation of total abundance in the lake. Jellyfish density was graphically displayed in density maps using ESRI ArcGIS (10.4.1), via Inverse Distance Weight (IDW) interpolations. Additionally, we assessed presence/absence and categories of abundance (tens, hundreds, thousands, hundred-thousands) based on own observations and of collaborators from 2009 to 2019.

2.6. Tourist numbers and interviews

To assess trends in tourism visitation in Raja Ampat over time, we obtained the number of tourism entrance tags issued by the Raja Ampat Tourism Department from 2007 to 2018. While permit tags are valid for the whole of Raja Ampat, we assumed a link between increase in the region and increase in visitation to Misool and Wayag, and subsequently the jellyfish lakes. The magnitude of tourist visitation to lakes from 2009 to 2018 was further assessed by 1) means of access to Misool and Wayag, 2) number of homestays, and 3) estimated number of visitors by interviewees.

There is no formal registration on the use and tenure of the jellyfish lakes. Therefore, we conducted semi-structured interviews (Longhurst, 2003), to obtain information from stakeholders involved, in order to collect contextual information based on general discussion items. Specifically, we asked about lake use, tenure and perceived threats. Stakeholder interviews were held in 2017. In total, 28 in-depth interviews were conducted with government officials, homestay owners, liveaboard operators, and locals claiming tenure of the lakes (Supplementary material Table 2). All interviews were anonymous and recorded with prior permission from the interviewees. Perceived threats that were identified by more than two respondents were reported.

3. Results

3.1. Phylogenetic reconstruction and genetic variation

A total of 174 COI sequences of 542 bp were analyzed from seven

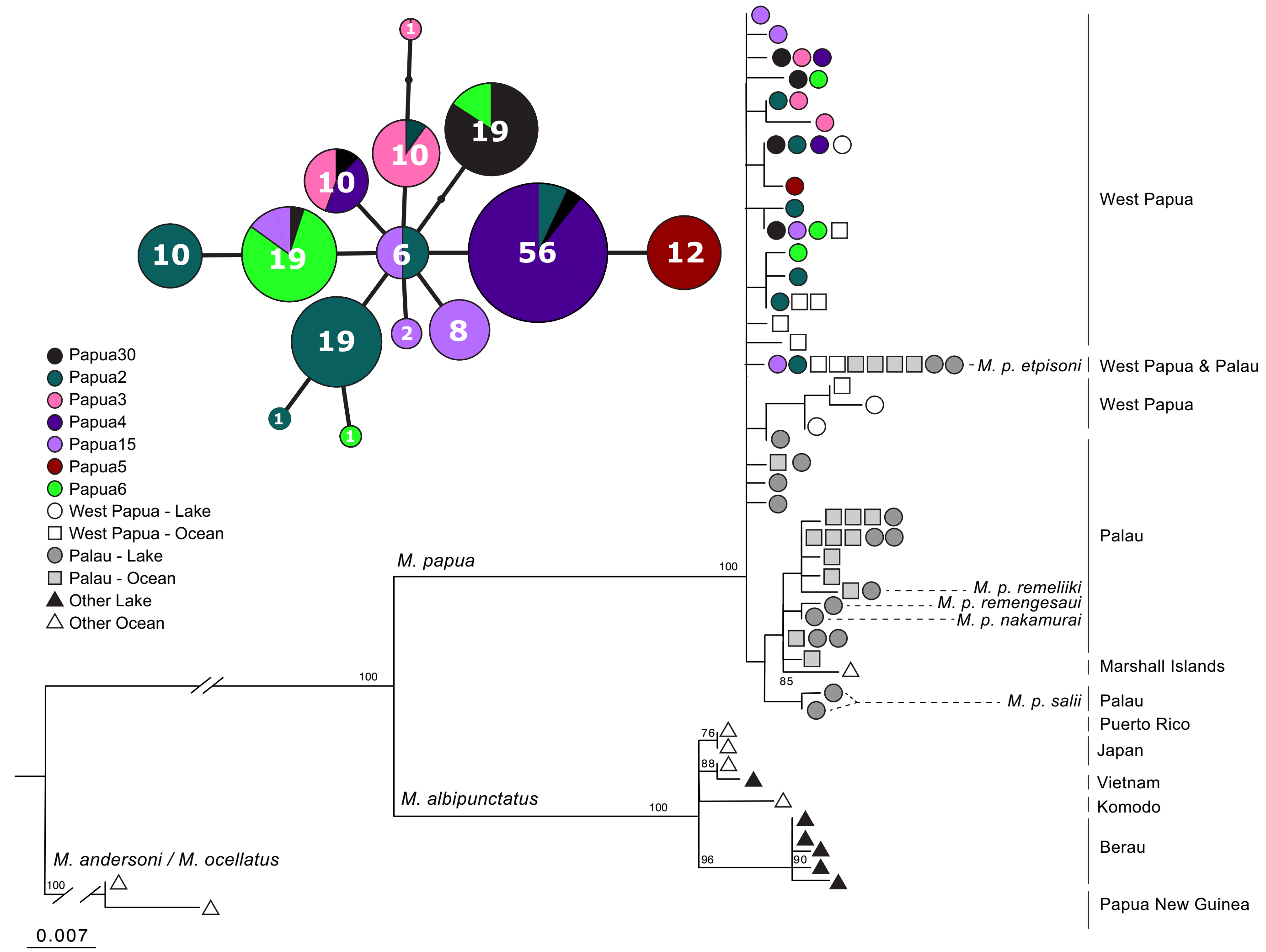


Fig. 2. Phylogenetic relatedness of *Mastigias* spp. from West Papua and other Indo-Pacific locations. Maximum Likelihood Tree (HKY + I model) and haplotype network based on partial Cytochrome Oxidase I marker (542 bp) of *Mastigias* spp. sampled from marine lake and ocean locations. Only maximum likelihood support of > 70% are indicated, based on 1000 bootstraps. Samples from current study are colored according to Fig. 1. Samples were included from Swift et al. (2016) (accession numbers GenBank: KU900912 - KU901464) and Bayha and Graham (2011) (accession numbers GenBank: JN215543 - JN21551). Scale bar indicates substitutions/site. Each circle within the haplotype network represents a haplotype, with size representing number of individuals possessing the haplotype (number specified in circle), coloring according to locations in Fig. 1. Lines connecting haplotypes represent single base substitutions between haplotypes, missing haplotypes are indicated by dots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

jellyfish lakes from Raja Ampat (Supplementary material Table 1). We obtained 14 haplotypes with 15 variable sites, of which six haplotypes were shared by at least two lakes (Fig. 2). The remaining eight private haplotypes were found in Papua2 (3 haplotypes), Papua3 (1), Papua15 (2), Papua5 (1) and Papua6 (1).

Raja Ampat samples fell within the clade of *Mastigias papua*, while samples from jellyfish lakes in Berau, Indonesia are putatively classified as *M. albipunctatus* (Fig. 2) (Souza and Dawson, 2018). Jellyfish populations from Raja Ampat formed a distinct subclade, including some Palau locations. Pairwise sequence divergence among Raja Ampat populations ranged from 0.20% (Papua4 vs. Papua5) to 0.70% (Papua5 vs. Papua30) (Supplementary material Fig. 1). Variable sites are displayed in Supplementary material Table 3, and show lakes Papua2 and Papua15 to contain the same haplotype as subspecies *M. papua etpisoni* as defined by Dawson (2005). Other subspecies defined by Dawson (2005) were not observed.

Next, we estimated within-lake genetic diversity and genetic structure among lakes. Highest genetic diversity was found within lake Papua2 (nucleotide diversity (π) = 0.003, haplotype diversity (h) = 0.723), and lowest in Papua4 (π = 0.001, h = 0.233), and Papua5, which contained only a single haplotype (π = 0, h = 0) (Supplementary material Table 1). We observed significant genetic structure for all pairwise comparisons of jellyfish lakes with ϕ_{ST} ranging from 0.31 to 0.86 (average ϕ_{ST} = 0.63) (Supplementary material Table 4, Supplementary material Fig. 2). Comparisons between years within lakes were not significant with ϕ_{ST} ranging from 0.05 to 0.09.

3.2. Morphological variation

The PCA of quantitative morphometrics showed clustering of morphologies among lakes at the first two Principal Components explaining 61.2% of morphological variation (Fig. 3A). When including categorical morphological measurements consistent patterns were observed (Supplementary material Fig. 3). Multivariate analysis of variance indicated morphometrics were significantly different among lakes ($F_{(4,333)}$ = 25.96, p-value < 0.001), with all pairwise comparisons of lakes being significantly different (p-value < 0.01), apart from Papua3 and Papua15 (p-value = 0.28) (Supplementary material Table 5). Jellyfish from Papua3 and Papua15 displayed the oceanic ecotype as defined by Dawson and Hamner (2005) (terminal club length > 0.5

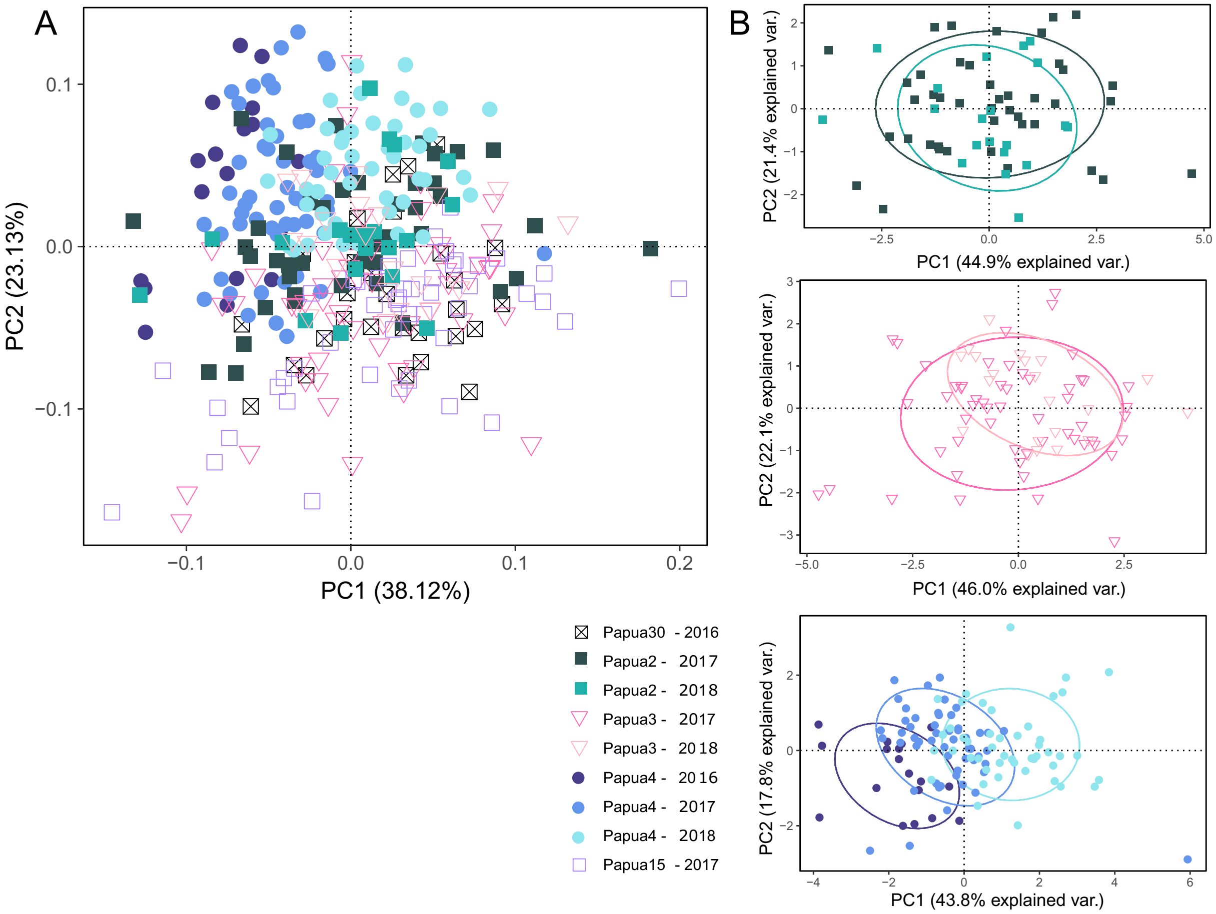


Fig. 3. Spatial and temporal variation in quantitative morphometrics of *Mastigias papua* from marine lakes sampled in Raja Ampat. A) Principal Component Analysis (PCA) of all years sampled (2016–2018). In total, 61.25% of morphological variation is explained by first two Principal Components. B) PCAs subset of lakes. Separate plots for Papua2, Papua3 and Papua4 are displayed for different sampling years. Ellipses indicate samples falling within the standard deviation. Colors and codes correspond with Fig. 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

times bell diameter, spots and blue pigmentation). Jellyfish from Papua4 2016–2017 clearly showed the derived ecotype (loss of spots and pigmentation, terminal club length $<$ 0.2 times bell diameter). Remarkably, Papua4 in 2018 displayed long terminal clubs (0.47 times bell diameter) and some spots, approaching the oceanic ecotype. Papua2 and Papua30 also showed such intermediary states. In 2016–2018, jellyfish were smallest in Papua4 and Papua15 (average bell width: 4.5 cm and 3.3 cm, respectively), and largest in Papua30 (average: 15.0 cm) (Supplementary material Fig. 4A). After correcting for size, differences among groups were most prominently shown by differential unwinged and winged oral arm length (Supplementary material Fig. 4D, E), and terminal club length and width (Supplementary material Fig. 4F, G).

There was no temporal variation in jellyfish morphology between years 2017–2018 for Papua2 ($F_{(1,61)}$ = 0.539, *p*-value = 0.38) or Papua3 ($F_{(1,74)}$ = 4.785, *p*-value = 0.48) (Fig. 3B). Contrastingly, in Papua4 a significant morphological shift was found between years 2016, 2017 and 2018 ($F_{(2,117)}$ = 40.926, *p*-value $<$ 0.001) (Fig. 3B). Here, jellyfish sampled in 2016 and 2017 were significantly different in morphometrics from all other groups (*p*-value: 0.036), whereas jellyfish sampled from 2018 were similar to Papua2 and Papua3.

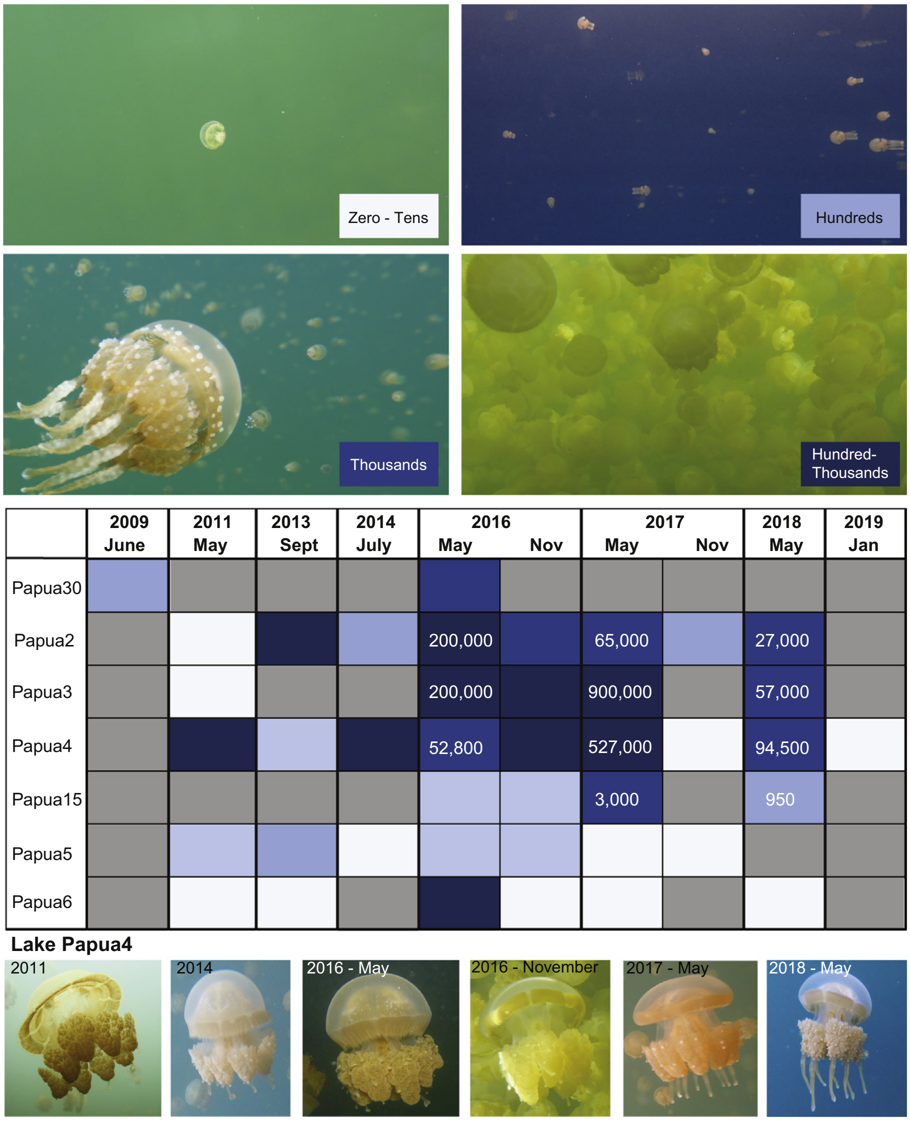
3.3. Variation in abundance

Jellyfish abundance fluctuated in all lakes over eleven years (2009–2019) based on categorical observations (Fig. 4). Fluctuations, including complete disappearance of jellyfish, were present before the onset of tourist visitation in 2012. Periods of jellyfish absence were not synchronised among lakes. Quantitative assessment of jellyfish abundance between years 2017–2018 showed a decrease for all lakes (Fig. 4, Supplementary material Fig. 5). The decrease was most notable in Papua4, where the total estimated number of jellyfish in the lake was 527,000 in 2017 and plummeted to 94,500 in 2018 (Fig. 4).

3.4. Tourism increase and lake tenure, use and perceived threats

In 2007, a total of 998 Raja Ampat tourist entrance tags were sold (domestic and foreign). This increased almost 30-fold to 28,896 tags in 2018 (Fig. 5A). Access to Misool (location of most marine lakes) became organised since 2013 with regular public ferry services, which at the time of publishing run four times per week from Sorong (Fig. 5A). Jellyfish lakes are mainly visited by tourists for snorkelling and photography, although visitation is not spread evenly between lakes (Fig. 5B). The main operators of jellyfish lake tourism are local guides, homestays, and liveaboard dive vessels. In 2018, there were eleven homestays in southeast Misool (Fig. 1). Homestays and liveaboards in southeast Misool offer regular trips to three jellyfish lakes: Papua2 (local name Tomolol), Papua4 (Lenmakana) and Papua5 (Karawapop), of which Papua4 is visited the most frequently (Fig. 5B). Transport to Wayag (location of Papua30) is only possible via chartered tourism vessels. Regulations governing the Wayag MPA do not allow for homestay development, and visitation to this lake is limited to occasional liveaboard guests and private charters from Sorong.

The interviews in 2017 indicated that families from six villages were



	2009 June	2011 May	2013 Sept	2014 July	2016 May	2016 Nov	2017 May	2017 Nov	2018 May	2019 Jan
Papua30										
Papua2					200,000		65,000		27,000	
Papua3					200,000		900,000		57,000	
Papua4					52,800		527,000		94,500	
Papua15							3,000		950	
Papua5										
Papua6										

Fig. 4. Presence-absence and abundance data of *Mastigias papua* in seven marine lakes in Raja Ampat. Colors of boxes in top figure refer to abundance categories used in the table and photos represent visual references. Numbers in table represent quantitative assessments based on video analyses. The main tourist attraction, Lake Papua4 (local name Lenmakana), is highlighted below to show the morphological shift in jellyfish from this lake. Grey values indicate no assessment was done. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

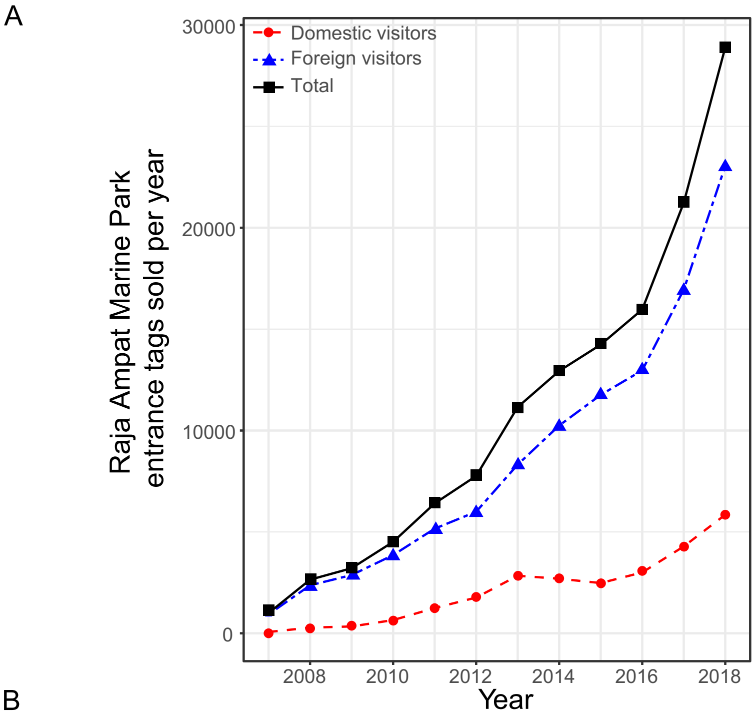
mentioned as customary owners of jellyfish lakes in Misool (Fig. 5B). In 2011, before tourists visited Misool regularly, there were only three villages/families that claimed customary tenure. Some owners collect an entrance fee from visitors to jellyfish lakes, and fees are sometimes also asked by nearby pearl farms. Interviewees identified a range of threats including tenure disputes, conversion of lakes into aquaculture ponds, unregulated tourism, mosquito repellent and sunscreen pollution, lack of garbage handling, building impermanent jetties, and introduced species such as turtles, catfish, and sea anemones (Fig. 5B). Encouragingly, several respondents indicated there is an informal Code of Conduct in place that currently most tourist guides adhere to. This Code of Conduct includes a no sunscreen, no fins and no diving policy for the lakes.

4. Discussion

This is the first study to combine evolutionary, ecological and social approaches to investigate jellyfish lakes in Indonesia, peripheral ecosystems that are increasingly important tourism assets. Focussing on jellyfish lakes in Raja Ampat, we found distinct biodiversity, and indicate the need for specific conservation management plans to cope with the challenges of increasing, and largely unregulated, tourism as well as other stressors. Below, we elaborate on the variation in genetics, morphometrics and abundance of jellyfish, explore the social context of jellyfish lakes, and finally discuss management recommendations and broader implications for jellyfish lakes in Indonesia.

4.1. Genetic and morphological variation indicate isolated populations

Jellyfish populations in Raja Ampat appear to be strongly structured based on genetic and morphological differentiation (Supplementary material Table 1, Figs. 2, 3). Five subspecies were described by Dawson (2005) from marine lakes in Palau, of which only one was observed in the haplotypes from Raja Ampat (*M. papua etpisoni*); all other private haplotypes recorded in Raja Ampat were unique to the region and potentially represent new subspecies. Strong genetic and morphological structure has previously been shown for jellyfish and other marine lake taxa, such as fish and mussels (Dawson and Hamner, 2005; Gotoh et al., 2011; Becking et al., 2016; Swift et al., 2016; Arai et al., 2017; Maas et al., 2018). Despite finding similar degrees of genetic structure as



B

Lake	#Operators	Visits / month	Est. visitors / year	Tenure	Perceived threats
Papua30				Selpele and Saleo	Low threat
Papua2 (Tomolol)	2	2	900	Tomolol and Usaha Jaya	Tourism, invasive species, waste
Papua3				Fafanlap and Usaha Jaya	Invasive species
Papua4 (Lenmakana)	14	50	1500	Fafanlap and Usaha Jaya	Tourism, invasive species, waste
Papua15				Tomolol and Usaha Jaya	Low threat
Papua5 (Karawapop)	3	<1	100	Yellu	Aquaculture, invasive species
Papua6				Yellu	Low threat

Fig. 5. Tourism impact in Raja Ampat, Indonesia. A) Tourism increase in Raja Ampat, based on number of tourist entrance tags sold per year from 2007 to 2018 (Raja Ampat Tourism Department). Lines are drawn for domestic visitors (red circles), foreign visitors (blue triangles) and the total (black squares). B) Estimates of tourist visits, tenure of jellyfish lakes and perceived threats based on interviews with stakeholders in 2017. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

previous studies, we observed fewer private haplotypes when compared to jellyfish populations from Palau (Dawson and Hamner, 2005; Swift et al., 2016). This may result from less strong in situ divergence or smaller population sizes, but could also indicate that marine lakes in Raja Ampat were colonized more recently.

Shifts from the oceanic towards the derived ecotype in marine lakes are thought to be unidirectional and result from local adaptation to lake conditions (Dawson and Hamner, 2005; Swift et al., 2016). Interestingly, we observed a reversed morphological shift in Papua4 over sampling years (2016–2018) from the derived ecotype towards the oceanic ecotype. The shift may be the result of an influx of oceanic jellyfish, although this is not corroborated by genetics. Alternatively, the shift represents a new bloom strobilated from resident polyps showing high morphological plasticity. A shift in morphology was also observed in Palau after the disappearance of jellyfish coinciding with the ENSO events of 1997–1998 (Dawson, 2005). When the jellyfish reappeared they displayed a larger size and differently shaped terminal clubs, but eventually reverted to pre-ENSO derived morphologies. To our knowledge, the genotypes were not published, therefore it is unclear if jellyfish before and after the crash were of the same population. For jellyfish in Papua4, we observed no shift in haplotype diversity. Recorded morphological variation of jellyfish in marine lakes may therefore be the result of phenotypic plasticity and acclimatization to specific local environments rather than evolutionary adaptation. However, phenotypic plasticity may over time facilitate genetic adaptation (Waddington, 1942; Fierst, 2011; Valladares et al., 2014), and as each jellyfish lake environment is unique, protection specific to each lake should be put in place.

4.2. Population dynamics in marine lakes

Jellyfish abundance in marine lakes in Raja Ampat appears to fluctuate greatly, indicating that jellyfish dynamics in these lakes are more heterogeneous than previously observed for lakes in Palau and lake Kakaban in Indonesia (Muscatine et al., 1986; Tomascik and Mah, 1994; Hamner and Hamner, 1998). While jellyfish populations in Palau also show some fluctuation in abundance (Dawson et al., 2015), fluctuations in Raja Ampat appear to be more frequent and severe, with regular occurrences of complete disappearance of jellyfish. Jellyfish lakes in Raja Ampat are five-fold smaller than those in Palau or Kakaban, and have a lower observed total abundance of jellyfish (900,000 vs. ~7 million: Dawson et al., 2001; Cimino et al., 2018). This difference may be conducive to dramatic fluctuations. Larger lakes have more stable environments (Scheffer, 1997), likely resulting in more stable populations and a higher carrying capacity. Remarkably, even for the large lake Ongeim'l Tketau, severe jellyfish population crashes have been observed twice since 1998, related to temperature and salinity change following ENSO events (Dawson et al., 2001; Martin et al., 2006). In Palau, there is no quota system for the number of tourists allowed to visit the lake, which resulted in continued visitation until the total disappearance of jellyfish (Dawson et al., 2001). Tourists possibly exacerbated the decline of jellyfish abundance in Palau or may have led to longer recovery time of populations. It is likely that smaller lakes in Raja Ampat are even less resilient to such external perturbations.

Beyond direct effects on medusae presence, effects of stressors on the benthic polyps likely lie at the basis of jellyfish dynamics. Polyp sensitivity to temperature, salinity, food availability or chemical pollution may influence strobilation patterns (Sugiura, 1965; Prieto et al., 2010; Chi et al., 2019). Furthermore, introduction of invasive species such as fish and sea anemones may result in increased predator presence or competition for space for the benthic polyps (Takao et al., 2014; Patris et al., 2019). Jellyfish dynamics are currently poorly understood (Pitt and Lucas, 2014; Dawson et al., 2015), and a precautionary approach should be taken to avoid detrimental effects of unregulated tourism. Carefully monitoring population abundance in jellyfish lakes is imperative to look for signs of population decline and to better understand jellyfish dynamics in general.

4.3. Lake use, threats and management status

Tourism to Raja Ampat is increasing dramatically, from 998 visitors in 2007 to 28,896 in 2018, representing a 30-fold increase (Fig. 5). While tourism could promote attention to jellyfish lake conservation, currently it is mostly unregulated. There are several threats from tourism towards jellyfish populations in marine lakes. For example, main tourism operators in Raja Ampat tend to ‘follow the jellyfish’, where they simply switch to a different lake when their favored jellyfish lake does not contain jellyfish anymore. This could lead to a cascade of crashes of additional jellyfish populations. Another threat is the introduction of invasive species, intentionally (e.g. fish and turtles for aquaculture, animistic purposes or amusement) or unintentionally (e.g. sea anemones carried in on wetsuits (Patris et al., 2019)). Additionally, disputes in lake tenure rights complicate controlled use and management of the lakes. Full engagement of and participation by local tenure holders in determining the management context and local regulations for any marine ecosystem (including the jellyfish lakes) is imperative for ensuring successful marine conservation in West Papua (McLeod et al., 2009; Grantham et al., 2013). As many of the local tenure holders now have a direct economic stake in tourism development in Raja Ampat, they have a strong incentive for seeking improved management of the jellyfish lakes.

The decision of the Ministry of Marine Affairs and Fisheries (MMAF) to denominate the Raja Ampat MPA network as a “marine tourism park” meant that marine lakes are not included in MPA zonation and conservation (MMAF Ministerial Regulation No. 36, 2014). Fortunately, Indonesian law (No. 5/1990 and No. 31/2004) allows for revision of zonation plans for protected areas based on scientific evidence that indicates a need to better conserve a particular ecosystem. Based on the current and previous studies (Becking et al., 2011, 2015, 2016; Maas et al., 2018), all marine lakes (including jellyfish lakes) are marine ecosystems with marine species, which implies that any marine lake which falls within the boundaries of an MPA should be managed as part of that MPA. The current study provides a strong justification to revise the zonation of the Raja Ampat MPA network to extend protection to marine lakes and include explicit regulations for their management within the Raja Ampat MPA zonation system. The increase in tourism pressure to jellyfish lakes of Raja Ampat and their apparent susceptibility to perturbations, combined with the growing importance of tourism income to local tenure holders, suggests an urgent need to revise the MPA zonation plan of Raja Ampat to ensure the long-term sustainability of tourism to these jellyfish lakes. Below, we emphasize specific policy recommendations that we believe are feasible to implement in the near future.

4.4. Recommendations conservation approach

Jellyfish lakes are important tourism assets across Indonesia, with known lakes in East Kalimantan, Central Sulawesi and West Papua. Tourists visit the lakes for the singular experience of swimming among thousands of jellyfish. Jellyfish lakes of Raja Ampat harbor endemic genotypes and phenotypes of jellyfish, including putative undescribed subspecies. Marine lakes in general have unique local environments and associated organisms (e.g. Becking et al., 2011, 2016; Gotoh et al., 2011; Swift et al., 2016; Maas et al., 2018), indicating that they may provide refuge for ancestral diversity and harbor endemic biodiversity (Gibson et al., 2017). We therefore argue that jellyfish lakes should be viewed as individual management units. The rapid increase in tourism in Raja Ampat is likely already exerting significant stress on its jellyfish lakes, and increased access to remote areas may result in discovery of new jellyfish lakes. Adequate conservation policies need to be in place to efficiently protect known and potential new jellyfish lakes.

Our recommendations for improved jellyfish lake conservation in Raja Ampat are twofold. First, we suggest revising the current Raja Ampat MPA zonation system to explicitly include marine lakes as a sub-zone type within the “Other Zone Types” category (Mustaghfirin et al., 2012). We suggest including all marine lakes in this zonation, as all marine lakes represent unique peripheral ecosystems, and it is moreover possible that marine lakes without current jellyfish populations may be colonized by jellyfish in the future. Designation of a specific 'marine lake' sub-zone type will thereby allow for the formulation of specific regulations for this sub-zone. We suggest that regulations for the marine lake sub-zone should include prohibiting scuba diving, prohibiting sunscreen and mosquito repellent use, requiring the removal of fins and booties, mandatory rinsing of clothing/wetsuits before entering the lake to avoid species introduction, and building permanent jetties as a single-entry point. Formalizing the Code of Conduct currently in use by tourism operators within the management plan will facilitate the acceptance of these regulations. Additionally, numbers of tourists should be limited in any lake at a given time. The actual limits or carrying capacity for each lake will require a productive and respectful collaborative determination including researchers, local tenure holders and marine tourism operators. Furthermore, we recommend that at least some lakes be zoned as ‘core zones’, strictly off limits to any use other than scientific research, in order that they can serve as reference points for lakes that are managed for tourism. Designating such core zone lakes will again require negotiation with local tenure holders, with a likely focus on designating those lakes that are most difficult to access and therefore not currently used by tourism.

Secondly, we strongly urge for the establishment of a collaboration between indigenous communities, local tenure holders, the Raja Ampat MPA Management Authority and Raja Ampat Tourism Department, conservation NGOs, and researchers to develop a specific Raja Ampat Jellyfish Lake Management Plan. By including stakeholders of the indigenous communities, local socio-economic needs can be met in a manner that also ensures adequate conservation. The plan should detail regular monitoring and adaptive management of the lakes to ensure they remain healthy. Monitoring jellyfish abundance and water quality parameters should be done regularly to record trends in abundance fluctuations. A multi-stakeholder working group could be set up including governmental agencies, local tenure holders, tourism operators, NGOs and experts. Such a working group was successfully established in Raja Ampat for the management of manta ray tourism (Kasmidi and Gunadharma, 2017), and jellyfish lakes could follow this model. The working group could meet at least twice yearly to review monitoring results and make any required decisions on tourism management, including potentially (temporary) closure of lakes when jellyfish populations begin showing signs of decline. Ideally, and as a precautionary measure, consideration should be given to a system of rotation of lakes being open to the public and others being closed. Importantly, we note that the recent designation of Raja Ampat as a National Geopark and the government's current bid to gain UNESCO Geopark status could provide a strong impetus for the development of a Raja Ampat Jellyfish Lake Management Plan, given the focus of the Geopark on unique karst habitats of Raja Ampat (of which the jellyfish lakes are certainly one).

We believe these practical applications are feasible at the local level of Raja Ampat and can moreover serve as an excellent model for other areas in Indonesia. Our approach can be followed by conservation managers generally when reconsidering the conservation status of vulnerable peripheral ecosystems, particularly where tourism is currently on the rise or expected to increase considerably in the future.

CRediT authorship contribution statement

Diede L. Maas: Conceptualization, Formal analysis, Investigation, Writing - original draft, Visualization, Funding acquisition. **Agustin Capriati:** Formal analysis, Investigation, Writing - review & editing, Funding acquisition. **Awaludinnoer Ahmad:** Resources, Writing - review & editing. **Mark V. Erdmann:** Resources, Writing - review & editing. **Machiel Lamers:** Writing - review & editing, Supervision. **Christiaan A. de Leeuw:** Formal analysis, Writing - review & editing, Funding acquisition. **Luca Prins:** Formal analysis, Writing - review & editing. **Purwanto:** Resources, Writing - review & editing. **Amanda P. Putri:** Formal analysis, Investigation, Writing - review & editing. **Ricardo F. Tapilatu:** Resources, Writing - review & editing, Supervision. **Leontine E. Becking:** Conceptualization, Investigation, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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