School of Molecular and Life Sciences

Ecology, Value and Threats of Cryptic Marine Benthic Fauna in Southeast Asia

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Doctor of Philosophy

of

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Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgement has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013) and in accordance with the National Health and Medical Research Council National Statement on Ethical Conduct in Human Research (2007) – updated March 2014. The research received animal and human ethics approvals from the Curtin University Animal Ethics Committee and Curtin University Human Research Ethics Committee, Approval Numbers: AEC_2015_02, AEC_2015_03, AEC_2016_3, AEC_2016_19, RDSE-06-15.

This research also received a Fisheries exemption from the Western Australia Department of Fisheries, Exemption number 2798. Research permits in Indonesia were granted by RISTEK, permit number 1316/FRP/SM/V/2015. Finally, research permits in Philippines were granted to Maarten De Brauwer by Dauin municipality mayor Neil B. Credo.

Signature: ________________________ Date: 12/04/2018

“*Travel makes one modest. You see what a tiny place you occupy in the world.*”

-Gustave Flaubert

“*Aut inveniam viam aut faciam*”

-Hannibal

Abstract

Infralittoral soft sediment substrates are the largest global marine habitat. Despite their high value for fisheries and scuba dive tourism they receive limited research or conservation effort compared to other habitats such as coral reefs. In Southeast Asia, a novel type of scuba diving ("muck diving") focuses on cryptobenthic species on soft sediment habitats and attracts visitors to areas that were previously of little interest to tourism. In this thesis I investigated the value of muck dive tourism (Chapter 2), the ecology of cryptobenthic species on soft sediment sites (Chapter 4), and the impacts of dive tourism and flash photography on soft sediment fauna (Chapters 6, 7). Using a novel survey method, I examined which species drive muck dive tourism and critically assessed the research and conservation effort on these species (Chapter 3). Finally, I developed a novel, non-lethal survey method to study cryptobenthic fauna both on reefs and soft sediment habitats (Chapter 5).

Muck dive tourism in Indonesia and the Philippines attracts more than 100,000 dive tourists per year, creating an annual revenue of $152 million, and employing more than 2200 local people (Chapter 2). The species that are most important for muck dive tourism are poorly studied and the conservation status of six of the top ten species remains unknown (Chapter 3).

Species diversity on soft sediment habitats in Indonesia and the Philippines is very high, exceeding the diversity of cryptobenthic fish assemblages on many coral reefs. Abundances, however, are orders of magnitude lower than those on coral reef. Fish assemblages differed strongly between regions, with a limited effect of environmental drivers such as grain size characteristics or benthic cover (Chapter 4).

Biofluorescence is widespread in cryptic fishes, and can be used to non-lethally survey cryptic species such as triplefins. The Underwater Biofluorescence Census (UBC) method developed in this thesis found abundances that were up to three times higher than conventional surveys (Chapter 5).

Scuba divers behave differently when interacting with cryptobenthic fauna than when diving normally, and make more contact with the substrate when diving on soft sediment compared to coral reefs. During interactions such as photographing animals, divers frequently touch or otherwise manipulate marine life (Chapter 6).

Touching animals elicits strong stress responses in animals compared to diver presence or the use of photographic flash. Flash photography does not affect hunting success of seahorses, nor does it have a pathomorphological impact on the retinal structure of seahorses (Chapter 7).

The results of this thesis show that cryptobenthic fauna on soft sediment habitats is highly diverse, very valuable, and strongly lacking in research and conservation attention. Scuba dive tourism can be a sustainable source of income for coastal communities, but negative diver behaviour such as manipulating wildlife should be managed more efficiently. Further research should focus on the entire soft sediment fish assemblage, trophic links between soft sediment habitats and other biomes, and the development of efficient management methods for muck dive tourism.

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Saying that a PhD is a challenging project is an understatement, and this thesis truly would have never happened without the help of many people. While I might have written the final thesis, that would not have been possible were it not for the support of collaborators, supervisors, friends, and loved-ones. I'd like to use this opportunity to thank all of them.

This project started off as a vague dream while I was still working my way around Southeast Asia and Lizard Island as a dive instructor and fieldwork assistant. I will never be able to thank Euan Harvey enough for initially accepting me as an Honours student, which then led to this PhD. He took me in, even if all he knew about me was that my undergraduate studies had been years ago and that I'd spent most of my days since traveling the world as a beach bum. Thank you for your trust Euan.

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Statement of Contributions

Published chapters

<u>**Chapter 2**</u>**:** De Brauwer, M., Harvey, E. S., McIlwain, J. L., Hobbs, J.-P. A., Jompa, J., Burton, M. (Marine Policy 2017). The economic contribution of the muck dive industry to tourism in Southeast Asia.

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Chapter 1 General Introduction

1.1 Background and rationale

1.1.1 Southeast Asia, the centre of marine biodiversity

Southeast Asia is a dynamic region formed by 11 developing countries with large population numbers. While all Southeast Asian countries use marine resources, few are as dependent on the ocean as the island nations of Indonesia and the Philippines. Indonesia and the Philippines support the highest populations in the region (respectively >250 million and >100 million) and combined are made up of close to 20,000 islands (Statistics Indonesia 2014; Philippine Statistics Authority 2015). Approximately 34% of the world's coral reefs are found in the Southeast Asian marine region (Tun et al. 2004). The region is the global centre of coral and fish biodiversity, often referred to as the Coral Triangle (Hoeksema 2007; Allen 2008). These rich marine assemblages are of crucial importance to the livelihoods of local communities, where nearly 70% of the population lives in coastal areas (Bryant et al. 1998; UNEP 2006). More than 140 million people in Southeast Asia reside less than 30 km from the coast, many of whom are reliant on marine ecosystems for fishing, building materials, or aquaculture (Costanza et al. 1998; Barange et al. 2014; Lavides et al. 2016).

The region's high dependence on subsistence and commercial coastal fisheries highlights the importance of healthy marine ecosystems. Current management and conservation efforts in the region are largely focused on protecting coral reef habitats, megafauna or charismatic fish species (McClenachan et al. 2012; Clifton and Foale 2017). However, healthy ecosystems rely on the presence of healthy trophic levels throughout the food chain, especially the small fish species at its base (Pikitch et al. 2012). These fishes are a frequently overlooked part of fish assemblages, particularly those that are hard to detect because of their benthic or cryptic nature, which are referred to as "cryptobenthic fishes".

1.1.2 Cryptobenthic species

Multiple definitions of cryptobenthic species have been proposed by different authors (e.g. Depczynski and Bellwood (2003); Randall (2005); Kovačić et al. (2012); Goatley and Brandl (2017)). For the purpose of this thesis, cryptobenthic fish were defined as fish species that "closely resemble a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral" (Randall 2005) and/or species that are "behaviourally cryptic and are <50 mm total length" (adapted from Depczynski and Bellwood (2003)) (Figure 1.1). Cryptobenthic fish fauna consists of a wide range of diverse fish taxa including *Gobiidae*, *Blennioidei*, *Antennaridae* and *Hippocampinae* (Goatley and Brandl 2017). Despite their small size and cryptic behaviour, they play an important role in ecosystem trophodynamics (Depczynski and Bellwood 2003; Goatley and Brandl 2017).

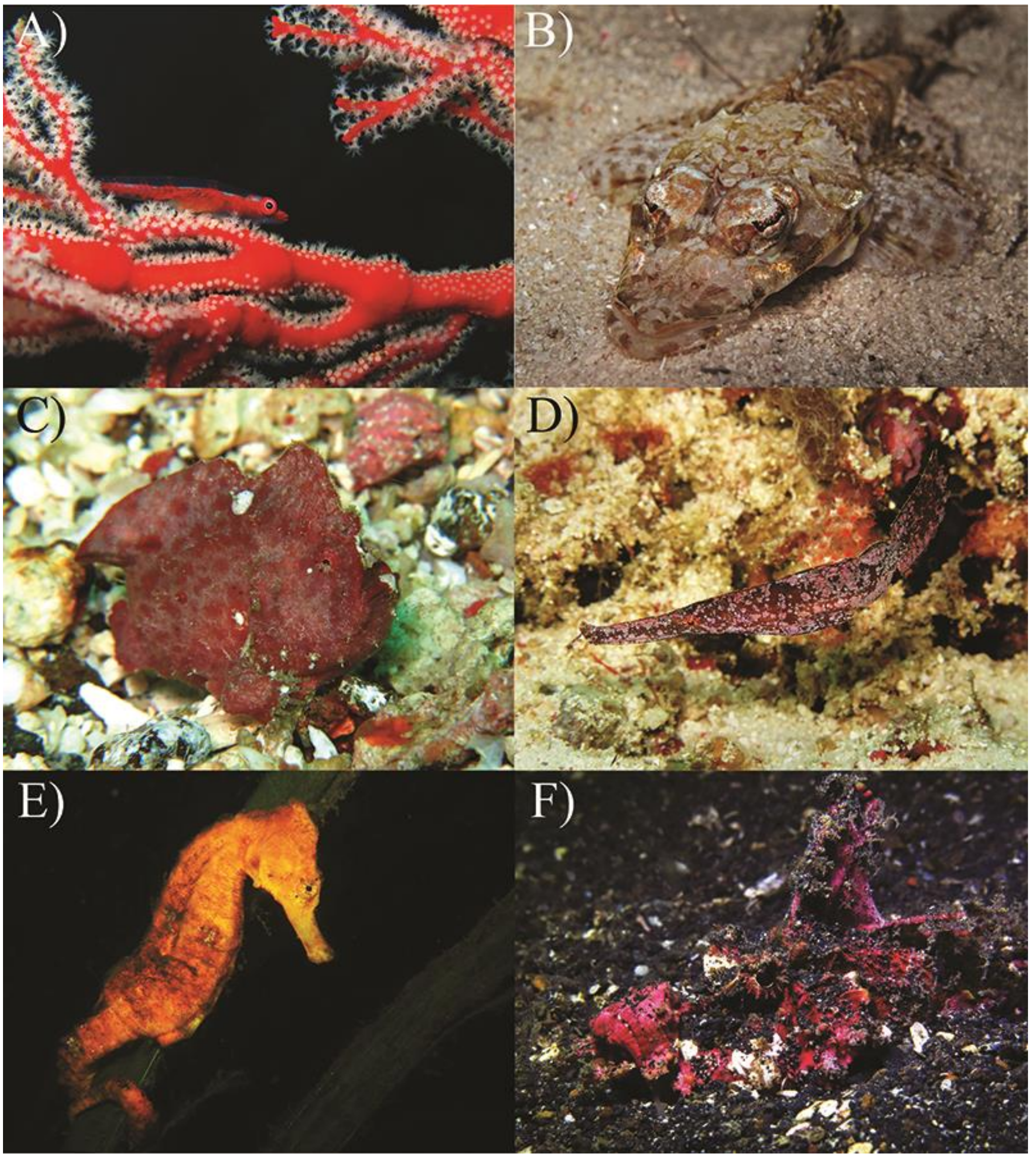


Figure 1.1 Examples of typical cryptobenthic fishes in Southeast Asia. A: Whip goby (*Bryaninops amplus*); B: Crocodile flathead (*Cymbacephalus beauforti*); C: Randall's frogfish (*Antennatus randalli*); D: Robust ghostpipefish (*Solenostomus paradoxus*); E: Common seahorse (*Hippocampus kuda*); F: Spiny devilfish (*Inimicus didactylus*).

Cryptobenthic fauna are numerically dominant on coral reefs and represent highly diverse functional groups (Ackerman and Bellwood 2000; Kovačić et al. 2012). Most species have short life spans, with some *Eviota* goby species having a maximum age of less than 2 months (Goatley and Brandl 2017). Continuous recruitment and rapid maturation prevent potential population bottlenecks caused by short lifespans and high predation mortality (Lefèvre et al. 2016). Collectively, the high growth potential and resulting turnover of biomass of these small, cryptic species can exceed that of other common fish species with far larger body sizes (Depczynski et al. 2007). Via this pathway, the cryptobenthic biomass represents a constant food source for larger predators, contributing a significant energy flux to reef ecosystems. Multiple trophic modes such as detritivores, herbivores and carnivores are present within cryptobenthic fauna, further highlighting their important function in marine ecosystems through nutrient cycling (Depczynski and Bellwood 2003; Goatley et al. 2016).

While the area of highest marine biodiversity in Southeast Asia is called the Coral Triangle, this name is not a correct representation of the dominant habitats in the region. More than 50% of the shallow waters in the Coral Triangle region consists of soft sediment (Hayes 1967). Infralittoral soft sediment habitats in the tropics are often seen as depauparate habitats of little value and have largely been ignored by management and researchers (Alongi 1990). However, ecosystems such as soft sediment habitats or seagrass beds can be more productive and have a higher economic value than coral reefs (Boucher et al. 1998; Costanza et al. 1998). Despite the Western scientific focus on food security through coral reef fisheries, artisanal fishers in the region depend much more on pelagic fishes such as Scads and Sardines (*Decapterus* spp. and *Selar* spp.) than on coral reef fishes for their food security (Clifton and Foale 2017). The trophic structures and energy fluxes in non-reef habitats are poorly understood, but many of the species most important for food security in Southeast Asia depend on soft sediment habitats for spawning and foraging grounds (Stacey and Hourston 1982; Higo 1985). Therefore, understanding the dynamics of soft sediment systems and their associated cryptobenthic fauna is important for continued healthy fish stock and livelihoods of coastal communities.

1.1.3 Cryptobenthic fauna and dive tourism

A high proportion of the population in developing countries in Southeast Asia rely on marine ecosystems through subsistence fishing, extracting building materials, or food production (Barange et al. 2014; Lavides et al. 2016). However, the potential value for soft sediment habitats and cryptobenthic fauna extends beyond reef trophodynamics and fisheries. Livelihoods created by marine tourism are often suggested as sustainable alternatives to extractive activities such as fishing (Wilson and Tisdell 2003; Job and Paesler 2013). The recreational scuba dive industry is an important source of income for many coastal communities in Southeast Asia. When practiced in a responsible manner, dive tourism offers a sustainable income for coastal communities, while simultaneously increasing environmental awareness in those communities and the tourists diving in the region (Wilson and Tisdell 2003; Bottema and Bush 2012; Vianna et al. 2012). Southeast Asia is a growing tourist market and one of the most important scuba dive destinations in the world (Wong 1998; Pascoe et al. 2014). Traditionally, scuba diving in the tropics is undertaken on coral reefs, but with the development of the dive industry, other types of diving are being explored (Dearden et al. 2006; Ince and Bowen 2010).

One of these developing dive tourism niches, especially with underwater photographers, is "muck diving". Muck diving is a distinct type of diving defined as diving in mostly gravel and mud areas with little or no coral reef or rocky outcrops. Frequently sites will also feature man-made structures or natural debris, such as rotting vegetation (Lew 2013). The focus of muck diving is on finding cryptic species such as frogfishes (*Antennariidae*) or seahorses (*Hippocampinae*) that are rarely encountered on coral reefs. Such species can provide special appeal to a dive site, precisely because of their rarity and cryptic nature (Williams and Polunin 2000; Uyarra and Côté 2007). Muck divers often place a strong emphasis on underwater photography, with many divers using high-end dSLR cameras. While muck diving is practiced across the world, the highly diverse marine life in Southeast Asia makes it a particularly popular dive destination.

In Southeast Asia, muck diving has given rise to the development of dive centres in areas previously of little interest to tourism, conservation, or research (e.g. areas with low coral cover). The protection of species or ecosystems often competes with other economic interests, particularly in developing countries (Garrod and Wilson 2004; O'Malley et al. 2013). Determining the monetary value of the dive tourism industry enables comparisons with other industries and with alternative uses of marine resources (Wilson and Tisdell 2003). Diving and snorkelling with marine wildlife has been estimated to have high economic values in many locations (Jones et al. 2009; Clua et al. 2011; Vianna et al. 2012; O'Malley et al. 2013). The muck dive industry is different to these previously studied tourism branches as it seems to attract more experienced divers, who may have different spending potential, which could have implications for the value of the industry.

The core of muck diving is the interest that visiting tourists have in cryptic and rare species. Therefore, it is important to identify which species are most sought after by divers, as they are the ones driving this tourism industry. A decrease in abundance or accessibility of species of interest to tourists is likely to lead to a loss of tourism income, so it is essential to know if key species are vulnerable to extinction or other threats. Considering the potential value of soft sediment associated cryptobenthic fauna to coastal communities, it is important to assess the threats that might face these species.

1.1.4 Potential threats to cryptobenthic fauna

Marine ecosystems are suffering globally from increased anthropogenic impacts such as climate change, pollution and overfishing (Edinger et al. 1998; Wilkinson 2008; Todd et al. 2010; Selig et al. 2014). Impacts that damage the coral reef matrix, such as coral bleaching, destructive fishing practices, or diver-caused damage, can affect cryptobenthic fauna associated with reef structure (Bellwood et al. 2004; Munday 2004). For species that are of interest to dive tourism, large numbers of scuba divers could signify a major threat both on a small and large scale. Poorly managed tourism infrastructure can cause habitat degradation and increased pollution (Wong 1998). Careless diver behaviour has repeatedly been shown to cause damage to corals, and heavily dived sites have higher incidences of coral disease (Hasler and Ott 2008; Lamb et al. 2014). Divers can have direct behavioural and physiological impacts on fishes through feeding or other close interactions such as photography (Shackley 1998; Harasti and Gladstone 2013; Trave et al. 2017). Photographing divers cause more damage on coral reefs (Rouphael and Inglis 2001; Chung et al. 2013), yet it is unclear if these effects are as significant, or potentially stronger on soft sediments. A regularly expressed concern that surrounds fish photography, both underwater and in aquaria, is that flash photography could have an impact on the behaviour of fish and could even damage the eye structure. Laws exist in the UK and at aquaria that prohibit or limit the use of flash when photographing species deemed to be vulnerable, but these are not based on scientific evidence (Smith 2010; MMO 2014).

1.1.5 Research needs

The nature of cryptic species makes surveying them logistically challenging (Schmitt et al. 2002; Smith-Vaniz et al. 2006; Aylesworth et al. 2017). Because of these difficulties, research on cryptic marine species remains under represented, which has significant ramifications from an ecological and conservation management perspective (Ackerman and Bellwood 2000; Jones et al. 2002). Fundamental data on the abundance, distribution, population structure, and conservation status remain unknown for most species (Depczynski and Bellwood 2003; Mobley et al. 2011). The limited research that is conducted on cryptobenthic fishes focuses on families with high abundance found on coral reefs such as blennies, gobies and triplefins (Goatley and Brandl 2017). Little is known about rare cryptic species such as frogfishes, ghostpipefishes, or rhinopias. Rarity further compounds the research issues associated with crypsis, as both cases make accurately surveying species more difficult. Therefore, it is often difficult to answer the question as to whether cryptic species are truly rare, or merely under-sampled. While numerous cryptic species seem to occur in low abundances and have limited mobility, they can simultaneously have very wide distributions (Orr and Fritzsche 1993; Arnold and Pietsch 2012). Without accurate knowledge of their abundance and distribution it remains difficult to determine which cryptic species are most vulnerable to human impacts and in need of conservation management.

1.1.5.1 Value of key tourism species

Common cryptobenthic fishes play an important role in marine ecosystems, but this has so far failed to attract much additional research or conservation attention. Accurately estimating the economic value created by these species through tourism could be a powerful leverage tool when discussing conservation measures with local marine resource managers. Identifying the species responsible for generating the greatest tourism revenue provides a focal point for further research and management attention, especially if the conservation status of these species is unknown.

1.1.5.2 Drivers of distribution and abundance

Despite its reputation as a hotspot for cryptobenthic fauna, so far there have not been any surveys into the cryptic fish diversity and abundance on soft sediment habitats in Southeast Asia. Given their importance, it is crucial to describe the cryptic fish assemblages in these habitats and what drives potential changes within these assemblages. The currently available suite of survey methods are not always suitable, as they either underestimate cryptic fish abundance, or are lethal methods that are not ideal for use on potentially threatened species. For cryptic reef fishes, gaining a full understanding of whether a species is threatened can only be done with an appropriate census technique adapted to the specific challenges involved with these species.

1.1.5.3 Anthropogenic impacts

One of the threats to cryptobenthic fauna is dive tourism. The irony that the people that highly value cryptobenthic species can also pose a significant threat to them requires the attention of resource managers. Diver behaviour is known to have an impact on fragile coral reef structures, but it is yet unknown if diver behaviour changes while muck diving. Likewise, it remains to be tested how species that rely on camouflage rather than a flight response react to close interactions with divers, especially while being photographed. The potential impacts of photographic flashes on fish could have important repercussions on the scuba industry and public aquaria worldwide.

1.2 Research question

The primary goal of this thesis is to increase the knowledge about a valuable, yet poorly studied ecosystem and to improve the understanding of economically important species. The overarching question throughout the thesis is: “How can we best evaluate and conserve cryptobenthic fish communities in Southeast Asia?” (Figure 1.2). This will be achieved through four different steps. Firstly, estimating the value of the muck dive-industry and the species involved, which is likely to lead to an increased interest in the conservation, management and research of these species. Secondly, determining spatial patterns in abundance and diversity of cryptic species on soft sediment habitats to establish baseline data. Thirdly, developing suitable survey methods to create opportunities for more future research on cryptic species. Finally, examining the threats scuba dive tourism poses to cryptic species and suggesting how these risks can be mitigated. Ultimately, this thesis will help in the development of more sustainable dive tourism and contribute to the understanding of cryptobenthic fauna, which is important in providing livelihoods for coastal communities in developing countries.

1.3 Thesis structure

In this thesis, I begin by describing the importance and the challenges of dive tourism focused on cryptobenthic fauna (chapters 2 and 3). I then investigate the ecology of cryptobenthic species on soft sediment habitats and describe a new method to survey cryptic fishes (chapters 4 and 5). In chapters six and seven I examine the anthropogenic threats to cryptobenthic fauna, in particular those caused by scuba divers. In the final discussion chapter (8) I synthesise the research and explore future research needs. The data chapters in the thesis were written and formatted as six journal articles. Chapters two, three, five and six have been published and chapters four and seven have been accepted for publication. An additional paper related to chapter five has been published and has been added to appendices. Since there is considerable overlap between references for each chapter, combined references for all chapters can be found in the Cited Literature section at the end of this thesis.

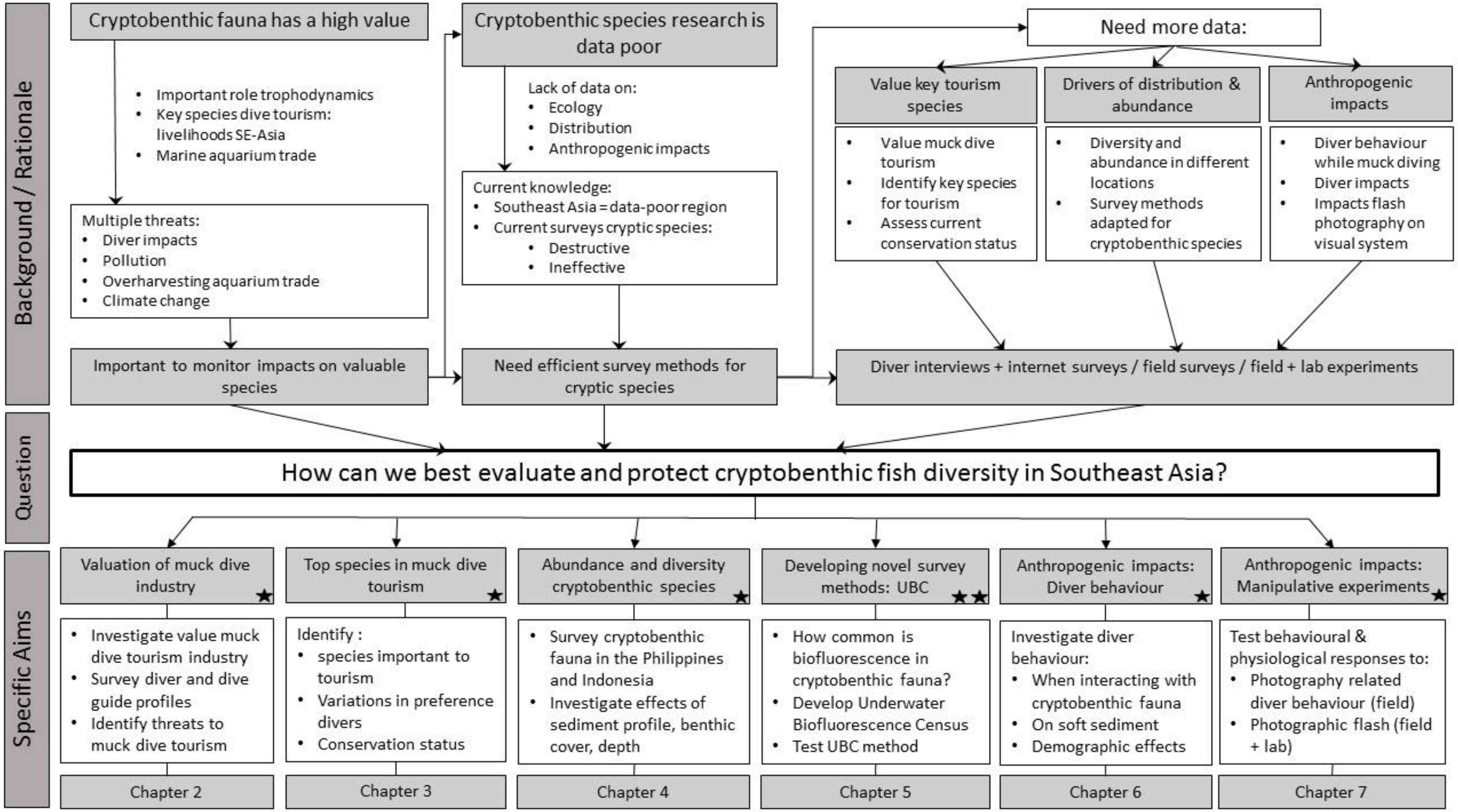


Figure 1.2 Conceptual flow diagram outlining general structure of this thesis. UBC: Underwater Biofluorescence Census; ★ : published papers.

1.3.1 The economic contribution of the muck dive industry to tourism in Southeast Asia (chapter 2)

In chapter two I investigate the socio-economic value of muck dive tourism in Indonesia and the Philippines. The focus of muck diving is on observing and photographing rare cryptobenthic species that are rarely seen on coral reefs. The industry is relatively new compared to traditional diving and anecdotal reports suggest it is growing in popularity. So far, no studies have looked at this tourism niche, its contribution to local economies and the profile of tourists participating in muck dive tourism. Using questionnaires for dive tourists, dive guides, and dive centre operators I investigate the value of the muck dive tourism, the demographic profile of its participants and staff, and the potential threats to the industry. Chapter two has been published in the peer-reviewed journal *Marine Policy* (De Brauwer et al. 2017).

1.3.2 Known unknowns: conservation and research priorities for valuable soft sediment fauna (chapter 3)

In chapter three I identify the species that are crucial to the success of muck dive tourism in Southeast Asia and how much research and conservation interest they currently receive. Cryptobenthic soft sediment fauna supports livelihoods through scuba dive tourism, yet it is unclear which species are most important to attract tourists. Identifying the species most important for muck dive tourism is a crucial first step in developing adequate management, research and ultimately the conservation of soft sediment habitats and their associated fauna. Using a novel method (Best-Worst Scaling) developed in healthcare and marketing research I developed internet surveys to investigate diver preferences. I then examined the research output and conservation status for the ten most important species to assess future research priorities. Chapter three has been published in the peer-reviewed journal *Ocean and Coastal Management* (De Brauwer and Burton 2018).

1.3.3 Drivers of abundance and diversity of soft sediment-associated cryptobenthic species (chapter 4)

Chapter four surveys the cryptobenthic fish assemblages in three locations across Indonesia and the Philippines. Each location is known globally as a site of interest for observing cryptobenthic fauna. However, cryptobenthic fish communities and the factors driving differences in the assemblages in these areas have not yet been investigated. Legal restrictions in both countries prevented the use of ichthyocides to survey cryptobenthic fauna. Two alternative non-destructive methods were used instead: Underwater Visual Census (UVC) and roving diver surveys. To investigate potential drivers of fish assemblages, data were collected on benthic cover, sediment characteristics, and depth. Assemblage data and the relative importance of different factors are compared using PERMANOVA. Chapter four has been published in the peer-reviewed journal *Estuarine, Coastal, and Shelf Science*.

1.3.4 Biofluorescence as a survey tool for cryptic marine species (chapter 5)

In chapter five I investigate the potential of using biofluoresence to survey cryptobenthic fishes. Due to their cryptic nature, traditional surveys methods often underestimate abundance and diversity of cryptic species. Lethal methods specifically designed to sample cryptic species using ichthyocides such as rotenone make their use undesirable for rare species or in sites of high conservation interest. Recent research indicates that biofluorescence is common in coral reef fishes, particularly cryptic taxa. Torches that excite biofluorescence are commonly used to survey coral recruits, but their potential has yet to be tested for use on fishes. I first quantify the prevalence of biofluorescence in cryptic and non-cryptic fishes in the Coral Triangle region to assess the potential suitability of this method on cryptic species. I then develop the Underwater Biofluorescence Census-method (UBC) and compare it with traditional UVC surveys using four different species: two highly cryptic habitat specialists (*Hippocampus bargibanti* and *H. denise*) and two cryptic reef generalists (*Ucla xenogrammus* and *Enneapterygius tutuilae*). Chapter five has been published in the peer-reviewed journal *Conservation Biology* (De Brauwer et al. 2018). An additional paper relevant to this chapter has been published in the peer-reviewed journal *Coral Reefs* (De Brauwer and Hobbs 2016).

1.3.5 Time to stop mucking around? Impacts of underwater photography on cryptobenthic fauna in soft sediment habitats (chapter 6)

Chapter six explores potential human impacts by focussing on the behaviour of divers when they interact with cryptobenthic fauna. Scuba divers have been shown to cause damage to the substrate, particularly when photographing cryptic species on coral reefs (Rouphael and Inglis 2001; Uyarra and Côté 2007). While the impacts of divers in coral reef habitats is well documented, there has been little research into the impacts of divers in other habitats (Hasler and Ott 2008; Lamb et al. 2014). The strong focus on photography in muck diving and divers' perception of soft sediment sites as less vulnerable than coral reefs might change their behaviour and the subsequent impacts. To identify the best predictors for high impact diver behaviour I observed divers on coral reef and muck dive sites across Indonesia and the Philippines. In particular I test if the impacts of diver behaviour change with: the activity divers are engaged in, the habitat divers are in, the complexity of the camera divers are using, and diver certification level, age, and experience. I further investigate how these factors affect the duration of diver interactions with cryptobenthic fauna. Chapter six has been published in the peer-reviewed *Journal of Environmental Management*.

1.3.6 Behavioural and pathomorphological impacts of flash photography on benthic fishes (chapter 7)

Chapter seven is the final data chapter of this thesis and in this chapter I further investigate anthropogenic threats. In this chapter I look at the behavioural and pathomorphological changes in cryptobenthic fauna caused by scuba diver photography. Little is known about the effect of scuba diver interactions on small fishes, but diver presence can disturb spawning aggregations and pygmy seahorses show avoidance behaviour when disturbed by light sources and physical contact by divers (Heyman et al. 2010; Smith 2010). Physical contact by dive guides and photographers to move fish into a more desirable position is a common practice in the dive industry and is likely to disturb and stress animals (Quiros 2007; Roche et al. 2016). Many questions remain about the effects of scuba diver behaviour associated with flash photography, in particular the potential effects on feeding efficiency and other stress responses. Importantly, the question as to whether or not flash photography causes damage to the eye structure of animals has yet to be resolved. To test how fish behaviour changes near photographing scuba divers I conducted behavioural experiments on 12 cryptobenthic fish species in the Philippines. I then ran two tank experiments to assess the behavioural and pathomorphological effects of flash photography on *Hippocampus subelongatus*. Chapter seven has been published in the peer-reviewed journal *Scientific Reports*.

1.3.7 General discussion (chapter 8)

Chapter 8 integrates and synthesises the research from the six data chapters, it relates the new insights stemming from this thesis to potential management solutions and discusses future avenues of research.

1.4 Study area

The research presented in subsequent chapters was conducted across multiple locations in Indonesia and the Philippines (Figure 1.3). Additional data for chapter five was collected in Christmas Island and Cocos Keeling Islands in the Indian Ocean. Surveys for chapters two and three were distributed in 15 divecentres in Indonesia (Bali, North-Sulawesi) and the Philippines (Dauin). Underwater surveys for chapter four were conducted in 20 sites across Indonesia (Bali, North-Sulawesi) and the Philippines (Dauin). A total of 68 sites across the region were visited for chapter five. Observations for chapter 6 were conducted across 33 sites in Indonesia and the Philippines. Experiments for chapter seven were conducted on five sites in Dauin (the Philippines), the seahorses used in the other experiments were collected in the coastal area around Perth (Western Australia).

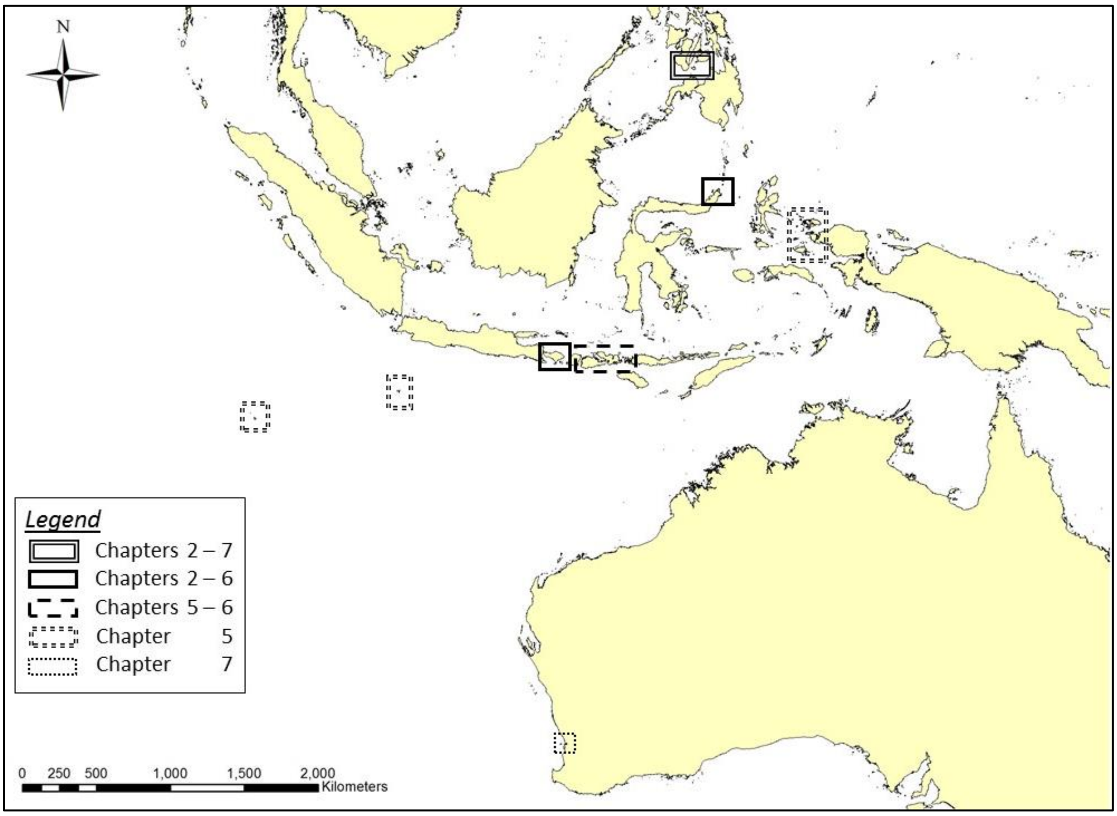


Figure 1.3 Map of study area.

1.4.1 Indonesia

1.4.1.1 Bali

Tourist questionnaires for chapters two and three were distributed to two divecentres in Tulamben. Surveys conducted underwater for chapters four, five, and six focused on the north coast of Bali (Amed, Tulamben, Menjangan). Amed and Tulamben are situated on the east of the island, Menjangan is a small island located in the west of Bali. The sites in Bali are popular scuba dive destinations and receive high numbers of visitors per year.

1.4.1.2 North Sulawesi

Tourist questionnaires for chapters two and three were distributed in four dive centres in Lembeh Strait. Underwater surveys in Lembeh Strait were used for chapters four, five, and six. Data for chapter five were also collected in Bangka and Bunaken. Lembeh Strait is a shallow strait subject to strong tidal currents. Sites in Lembeh consist mainly of black volcanic sand with sparse patch reefs and receives large numbers of divers year round. Bangka and Bunaken are two islands surrounded by coral reefs, the former sloping reefs, the latter steep drop offs. Bunaken is the main dive tourism destination in north-Sulawesi.

1.4.1.3 Nusa Tenggara

Nusa Tenggara consists of multiple islands in central Indonesia, 13 sites in Lombok, Sumbawa, and Komodo were visited to collect underwater survey data for chapters five and six.

1.4.1.4 Raja Ampat

Raja Ampat is considered to be the centre of the Coral Triangle area and has the highest marine biodiversity found in the tropics. 19 sites were surveyed in Raja Ampat for chapter five.

1.4.2 Philippines

All data collected in the Philippines were from Dauin, Southern Negros. The sites in Dauin consist mainly of black volcanic sand slopes, with sparse patch reefs and infrequent seagrass beds in the shallow zones. Questionnaires for chapters two and three were distributed in divecentres in the Dauin area. Underwater surveys for chapters four, five, six, and seven were conducted across eight sites in the area.

1.4.3 Christmas Island and Cocos Keeling Islands

Data for chapter five were also collected in Christmas and Cocos Keeling Islands, two Australian external territories in the east of the Indian Ocean. Two sites were surveyed at Christmas Island and three sites at Cocos Keeling Islands. The sites at Christmas Island were steep walls with high hard coral cover. Two sites at Cocos Keeling were sheltered inshore patch reefs with low hard coral cover, one site was a high current site near a channel, dominated by dead hard coral covered in turf and calcareous algae.

Chapter 2 The economic contribution of the muck dive industry to tourism in Southeast Asia

Preface: This chapter has been published in the journal *Marine Policy* (doi: 10.1016/j.marpol.2017.05.033) and has been formatted according to the journal guidelines. The combined references for all chapters can be found in the Cited Literature section at the end of this thesis.

2.1 Abstract

Scuba diving tourism has the potential to be a sustainable source of income for developing countries. Around the world, tourists pay significant amounts of money to see coral reefs or iconic, large animals such as sharks and manta rays. Scuba diving tourism is broadening and becoming increasingly popular. A novel type of scuba diving which little is known about, is muck diving. Muck diving focuses on finding rare, cryptic species that are seldom seen on coral reefs. This study investigates the value of muck diving, its participant and employee demographics and potential threats to the industry. Results indicate that muck dive tourism is worth more than USD$ 150 million annually in Indonesia and the Philippines combined. It employs over 2200 people and attracts more than 100000 divers per year. Divers participating in muck dive tourism are experienced, well-educated, have high incomes, and are willing to pay for the protection of species crucial to the industry. Overcrowding of dive sites, pollution and conflicts with fishermen are reported as potential threats to the industry, but limited knowledge on these impacts warrants further research. This study shows that muck dive tourism is a sustainable form of nature based tourism in developing countries, particularly in areas where little or no potential for traditional coral reef scuba diving exists.

2.2 Introduction

Nature-based experiences are an integral part of many tourism activities with participation gaining popularity, especially in developing countries (Balmford et al. 2009). Recent estimates of the global revenue created by nature-based visits to wildlife protection areas is as high as USD $6 billion per year (Balmford et al. 2015). If managed correctly, nature-based tourism can lead to increased local incomes and improved standards of living, and decreased dependence on less sustainable livelihoods such as fishing (Wilson and Tisdell 2003; Job and Paesler 2013). In contrast, poor management can lead to conflict between resource users, severe habitat degradation, and leakage of revenue out of the local area (Wong 1998; Walpole and Goodwin 2001; Hall 2010). These challenges highlight the need for a clear understanding of specific drivers of nature-based tourism to enable the development of efficient local management plans.

Participation in nature-based tourism can range from the occasional standardized daytrip during a larger, more general holiday, to entirely customised holidays, focused solely on the nature experience (Arnegger et al. 2010). Nature-based holidays are considered to be a broad tourism niche, which can be divided into multiple narrower categories (Reynolds and Braithwaite 2001; Novelli 2005). One such narrow niche is specialist animal watching with bird watching a classic example, and one that has been steadily increasing in popularity for two decades (Reynolds and Braithwaite 2001; Connell 2009). While fewer visitors participate in niche tourism compared to more general tourism, its specialised attractions appeal to higher spending participants and it has repeatedly been shown to have a high economic value to the local community (Novelli 2005). In Point Pelee, a small national park in Canada, expenditure on bird watching can be as high as USD$5.4 million annually while in Costa Rica, 41% of the total tourism income is estimated to come from bird watchers, a value close to USD$400 million per year (Hvenegaard et al. 1989; Sekercioglu 2002). Demographically, tourists participating in bird watching tend to be middle aged, have relatively high incomes and are well educated (Hvenegaard et al. 1989; Connell 2009).

While research interest in nature-based tourism has focused primarily on the terrestrial environment, a number of recent studies have investigated the value of nature-based marine tourism (Wilson and Tisdell 2003; Brander et al. 2007; O'Malley et al. 2013; Pascoe et al. 2014). When practiced in a sustainable manner, marine tourism offers an alternative income for fishing communities while simultaneously increasing conservation awareness for the local population and tourists visiting the region (Wilson and Tisdell 2003; Bottema and Bush 2012; Vianna et al. 2012). Scuba diving in particular has been shown to be a valuable segment of marine tourism with estimates for Southeast Asia alone as high as USD$4.5 billion per year (Pascoe et al. 2014). An examination of species-specific scuba diving reveals that the annual global value of diving or snorkelling with manta rays, for example, is approximately USD$73 million (O'Malley et al. 2013) and for sharks between USD$5.4 million to USD$18 million per year, depending on the location and shark species (Jones et al. 2009; Clua et al. 2011; Vianna et al. 2012).

Studies that have quantified the valuation of scuba diving mostly focus on regions with coral reefs, or on iconic megafauna such as sharks or whales (Brander et al. 2007; Vianna et al. 2012; O'Malley et al. 2013). Interactions with these species and ecosystems are mostly standardised package tourism and previous studies often do not account for other segments of the scuba diving market (Garrod 2008; Arnegger et al. 2010). When placing a value on diving in tropical destinations, these same studies assume diving activities only happen on or near coral reefs. As the dive industry matures, however, other types of diving in adjacent systems are being explored (Dearden et al. 2006; Ince and Bowen 2010). Inexperienced divers generally visit tropical destinations for a typical coral reef experience, but more experienced divers are often attracted to novel and specialised experiences (Williams and Polunin 2000; Dearden et al. 2006; Cater 2007).

One such novel and yet-unstudied sector in scuba diving tourism is the so-called "muck diving" (sometimes also called "critter diving" or "macro diving") (Lew 2013). Muck diving has previously been defined as "diving in mostly gravel and mud areas with little or no coral reef or rocky outcrops" (Lew 2013) (Figure 2.1). Often sites will also feature man-made or natural debris, such as rotting vegetation (Macaulay 2008), and may be at sites that are adjacent to coral reefs. Understanding what drives this sector requires determining why tourists choose to dive in these less attractive and previously avoided habitats. Muck diving is in many ways the marine equivalent of bird watching, in that it offers a unique opportunity to observe or photograph unusual, rare, or cryptic species that are not usually encountered on coral reefs. The key motivation of muck diving is locating rare species, with greater customer satisfaction recorded when this goal is achieved (MacCarthy et al. 2006). The species of interest are not limited to fishes (e.g. frogfishes, seahorses), but also include molluscs (octopuses, nudibranchs, etc.) and other invertebrates (e.g. harlequin shrimp, bobbit worms).

Figure 2.1 A typical muck diving scene: a sandy bottom with few defining features. In the foreground an estuary seahorse (*Hippocampus kuda*) holding on to algae (Photo by Dragos Dumitrescu).

As with birdwatching, muck diving relies heavily on tourists observing and often photographing cryptic and rare species. The failure to see the animals of interest affects the number of tourists visiting a location, and therefore the incomes of communities dependent on them (Williams and Polunin 2000). The species important to this type of diving are often rare and data deficient, resulting in researchers having little awareness of their population size, distributions, critical habitats or conservation status. Due to this lack of information it is difficult to assess whether threats exist that could affect the abundance and distribution of these species, and the tourism industry that relies on them. Destructive uses of the environment where these species occur, such as trawling, mining, or fishing for the marine aquarium trade could have a significant impact, but data are lacking.

While muck diving is practiced globally, the name originated in Milne Bay, Papua New Guinea (Silcock 2017) and it is currently most practiced in Southeast Asia (Lew 2013). Indonesia is one of the most important dive destinations in the world (Wong 1998; Hampton and Jeyacheya 2015), but the importance of muck diving compared to more general types of scuba diving is unknown. At present, the world’s most popular muck diving sites are in Indonesia and Philippines, often in locations where other tourism activities are limited. Consequently, muck diving might provide a substantial alternative income for communities that otherwise depend on subsistence fishing or other extractive uses of the marine environment (Garrod and Wilson 2004).

Since muck dive tourism is mostly practiced in developing countries, often in areas with limited alternative forms of income, there is a need to define the characteristics of the industry and quantify the value of this type of niche tourism. If muck diving is the marine equivalent of bird watching, it is to be expected that substantially larger revenues will be generated. To evaluate the sustainability of the muck diving industry, it is imperative to determine whether the money spent by dive tourists benefits the local population. Due to the heavy dependence on rare species and the lack of data on their conservation status, it is equally important to define which potential threats exist for the industry. This study has four goals:

1. Describe the demographics and attitudes of divers participating in muck dive tourism.
2. Identify the value of muck dive tourism in Indonesia and Philippines.
3. Describe the demographics and earnings of those employed (dive guides) in muck dive tourism.
4. Describe the main perceived threats to muck dive tourism.

2.3 Methods

2.3.1 Muck Diving

For the purpose of this study, "muck diving" is defined as: Scuba diving in soft sediment habitats with limited landscape features, with the explicit goal to observe or photograph rare, unusual, or cryptic species that are seldom seen on coral reefs. Taking photographs of these rare species is what makes muck diving especially popular with underwater photographers. While Southeast Asia is the region best known for muck diving it is frequently practiced in other regions, albeit without the same intensity (Macaulay 2008).

2.3.2 Study area

The areas surveyed for this study are three of the most popular muck dive destinations in Southeast Asia. Two locations were surveyed in Indonesia and one was surveyed in the Philippines (Figure 2.2).

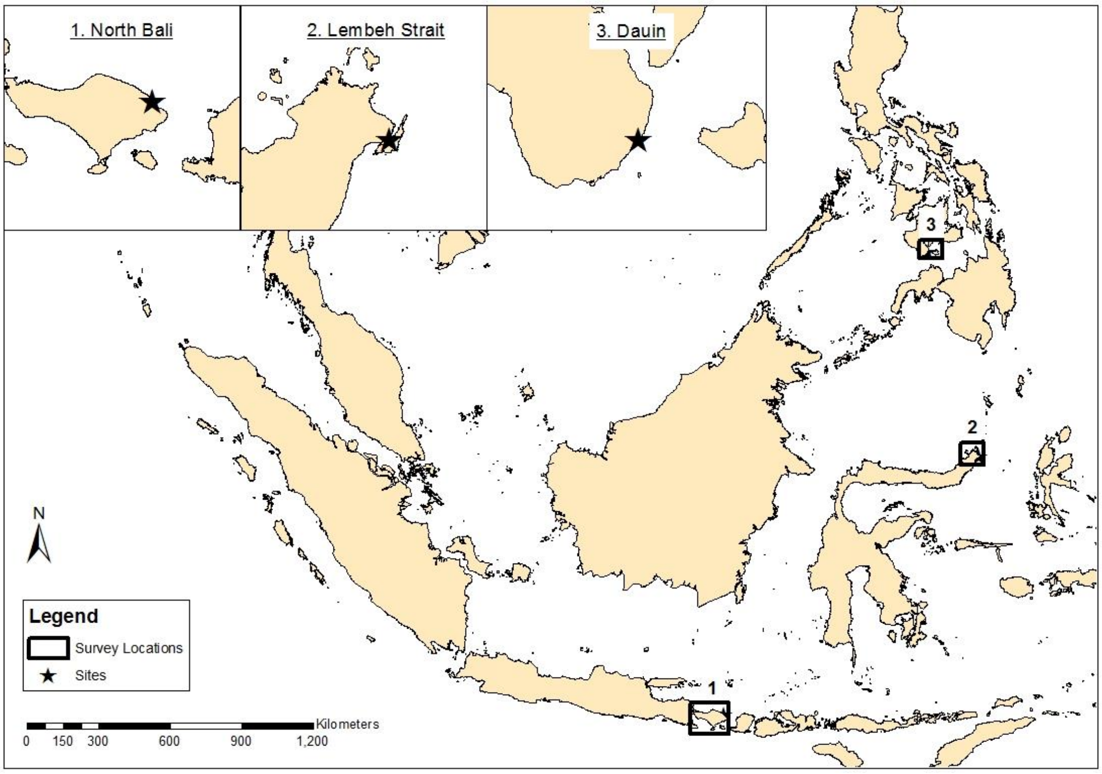


Figure 2.2 Map of surveyed locations across Southeast Asia.

2.3.2.1 Indonesia

North Bali: Bali is Indonesia's most popular tourist destination, it was visited by more than 4 million people in 2015 (Bali Government Tourism Office 2016). The majority of visiting tourists remain in the south and centre of the island, but the north-east coast of Bali is a popular destination for scuba divers. The area with the best established scuba dive infrastructure is based around the village of Tulamben (8° 15' S, 115° 36' E). The population of Tulamben mostly relies on subsistence fishing or tourism for their incomes. Dive tourism in Tulamben has long since been established around the site of the *USAT Liberty*-shipwreck, but in recent years, new dive centres have been built that specialise in muck diving on the nearby black sand slopes. In the high season the popular shipwreck-site can receive up to 300 divers per day (pers. comm. with local authorities). There are an estimated 14 dive centres and resorts in Tulamben, with an additional 40 in nearby villages. The area is also visited by operators from the south which organise daytrips to the wreck.

Unlike the south of Bali, the Tulamben area has few tourist attractions other than scuba diving. Other popular dive destinations around Bali are Menjangan Island in the west of Bali and Nusa Penida, an island situated a short boat ride east of Bali. These locations predominantly offer coral reef diving and limited muck dive opportunities.

Lembeh Strait: Lembeh is an island in North-Sulawesi, opposite the port town of Bitung with a population of 190 000 (1° 27' N, 125° 13' E). The strait between Lembeh Island and the main land is a busy shipping lane, but has also been widely considered an important muck dive location for more than fifteen years (de Vantier and Turak 2004). On Lembeh Island, there are multiple small villages, each with less than 1000 inhabitants. These villages are largely dependent on subsistence fishing and limited agriculture.

There are six dive resorts on Lembeh Island and seven dive resorts on the North-Sulawesi side of the Strait. While dive tourism has been established in Lembeh Strait for more than twenty years, there has been a substantial increase in the last six years, with new resorts and dive centres built each year. Lembeh Strait also receives divers from dive centres and resorts from nearby locations such as Bangka Island and Manado.

The North-Sulawesi region has two other main dive destinations: Bunaken National Park and Bangka Island. Both of these locations are coral reef dive destinations, unlike Lembeh Strait, which is known only for its muck diving. Other tourism activities in the region include visiting the Tangkoko National Park (rainforest), forest hikes, and cultural visits to local markets.

2.3.2.2 Philippines

Dauin: Dauin is a small village in Negros Oriental province, 20 km south of the province capital city Dumaguete (9° 11' 19" N, 123° 16' 10" E). The village has a population of 25,000 people which rely on fishing, agriculture and tourism for their income. Dive tourism in Dauin was originally focused on the coral reefs of nearby Apo Island, one of Philippines oldest and best known marine protected areas. In the last decade diving focus has increasingly shifted to muck diving off the beaches in Dauin, although daytrips to Apo Island are still frequently organised by all dive operators. Tourism in the area is increasing, and plans for the construction of a new international airport have recently been approved. As of late 2015 there were 16 dive centres and resorts operating in Dauin, with an estimated 10 additional operators in Dumaguete and nearby villages. New dive centres and resorts were being built at the time, so this number is likely to increase in the future.

Scuba diving and snorkelling are the main tourist activities in the Dauin region, though there are options for forest hikes, visits to waterfalls and cultural visits to local markets. Other scuba dive destinations are more than a day's travel away, but include coral reef locations such as Bohol, Malapascua, and Cabilao.

2.3.3 Surveys

To determine the value of muck dive tourism, surveys were conducted between May 2015 and November 2015. The surveys consisted of three different questionnaires each designed for specific stakeholders: dive centre operators, dive guides and divers (questionnaires included in Appendices). A pilot survey was conducted with 19 divers in March 2015 to ensure adequacy of the questions, but data were not used in the analysis. Surveys were based on Vianna et al. (2012) and adapted following the pilot study to ensure the goals of this study were addressed. Based on the pilot surveys, questions regarding expenditure and motivations for visiting dive locations were adjusted for clarity. The final surveys were distributed to dive centres and resorts considered representative of the industry. Sampled dive centres included both big and small businesses, locally owned and foreign owned businesses, low cost and high end businesses.

2.3.3.1 Divers

Self-administered, written questionnaires (in Appendices) for divers were distributed by the staff of 15 dive centres, and collected afterwards by the author (MDB). Guidelines for completing the questionnaires were provided with the questionnaire form. These guidelines included the goals of the study, author contact details and ethics information. Diver questionnaires were available in English, Chinese (Mandarin) and Japanese.

Diver questionnaires asked information about an individual's demographic, dive experience, motivation to visit the location, expenditure, and willingness to pay for environmental protection.

2.3.3.2 Dive Guides

Staff surveys were distributed (by MDB) at 15 dive centres and collected a week after distribution. Written dive guide questionnaires were in English only, but explanations were provided to staff upon distributing questionnaire forms. Questions for dive guides focused on demographics, income and personal opinions about tourism in their region.

Wages of dive guides (obtained from questionnaires) were compared with local minimum wages using government data published online (National Wages and Productivity Commission 2016; Statistics Indonesia 2016). If monetary values were not provided in USD in surveys, currencies were converted to USD using the exchange rate (XE 2015) at the time surveys were collected.

2.3.3.3 Dive centre operators

Questionnaires for dive operators were done face to face with the managers of 16 dive centres. Interviews with dive centre operators included questions about visitor and staff numbers, strengths and threats to local dive tourism, prices charged, and costs and incomes of running the operation. For eight interviewed operators, completed surveys were returned by email. An additional email was sent to muck dive operators across Indonesia and Philippines that were not interviewed face to face. Thirty-eight additional operators were located after an internet search for dive centres in the following muck dive destinations: Ambon and Alor in Indonesia and Anilao in Philippines (Table in Appendices). This email asked three targeted questions concerning visitor numbers, staff numbers and the percentage of guests visiting primarily for muck diving. These data allowed for comparisons with the more in-depth surveys in the three focal locations. While attempts were made to survey dive operators who specialise on the Asian market segment, collecting data at any of these dive centres did not succeed.

All surveys were approved by the Curtin University Ethics Committee (RDSE-06-15) and followed the requirements of the Australian National Statement on Ethical Conduct in Human Research.

2.3.4 Estimating revenue

Financial revenue was used as an estimate for the value of muck dive tourism in Indonesia and Philippines (Vianna et al. 2012). The revenue (R) created by tourists visiting muck dive centres was calculated using the formula:

$$R = \left[\sum_{i=1}^{n} Vi \times E \times Pm\right] \times \frac{Nm}{n}$$

- R = Revenue (rounded to nearest USD$1000)
- Vi = Total number of visitors at dive centre i
- E = Average expenditure per visitor
- Pm = Proportion visitors visiting with muck diving as main motivation
- n = Number of dive centres sampled
- Nm = Total number of muck dive centres in Indonesia and Philippines as found in internet search

Costs of airfares were not included in the calculation, since these revenues created by muck dive tourism do not return to local communities. For the same reason the costs of equipment such as underwater cameras or scuba dive gear, were not included in the estimate of expenditure. As these costs are considerable, the amount spent on camera equipment is provided separately from revenue.

The value for R is predicted to be an underestimate of the real value of muck diving in Indonesia and Philippines, as the following assumptions were made which are conservative by nature:

1. Our internet search for dive centres specialising in muck diving (Nm) only showed those dive centres with an online presence. Dive centres without websites are therefore not represented in our results. Some local operators do not have an online presence, but rely on walk-in guests or word of mouth advertising, therefore Nm is very likely to be an underestimation.
2. The number of muck dive centres (Nm) included only dive centres that specialise in muck diving and did not include the many dive centres that are more "general" dive operators. These dive centres usually offer muck dives in addition to normal coral reef dives, and as a consequence still gain income from the muck dives they organise.
3. Exclusive, remote locations such as Ambon or Alor in Indonesia are up and coming muck dive destinations which are generally more expensive than the locations surveyed in this study. Our value for the average expenditure per diver (Ei) is likely to be an underestimate as it does not include data from these high-end locations

2.4 Results

2.4.1 Diver demographics and attitudes

One hundred diver surveys were collected. Diver questionnaires distributed in muck dive centres in Indonesia and Philippines revealed the average age of muck divers was 45.9 years (SE ±4.6 years) old. An estimated 58.1% of respondents were male and 41.9% female. Approximately 79.2 % of visitors held a university degree (Table 2.1) and the mean yearly income of respondents was USD$88,514 (SE ±USD$5,592).

Divers visiting muck dive sites were experienced divers, with 71.7% holding a certification beyond entry level and 22.2% a professional dive certification (equivalent to Instructor or Divemaster). On average, visiting divers had conducted a total of 587 dives (SE ±84 dives) in their life and 58 dives (SE ±6 dives) during the previous year. A third of respondents were returning visitors to the location they were currently diving, though this varied strongly between sites (17.9% in Dauin, 33.9% in Lembeh, 100% in Bali). The majority of divers (73.5%) used some kind of underwater camera, with 41.5% of the cameras being the more expensive dSLR type. The average price of an underwater cameras used was USD$4,296 (SE ± USD$517.2).

Respondents came from 21 countries, of which half were European and an additional 30.6% North-American (Table 2.1). Asian divers made up 10% of visitor numbers, though this number might in reality be much higher and reflect our inability to sample those dive centres focusing on the Asian market.

Muck diving is an important drawcard to the regions that were surveyed, with 53.1% of visitors indicating they would not have visited if there was no muck diving available. This was even higher in Lembeh, where 74.2% of divers visited only because of muck diving. The majority of divers (89.69%) were willing to pay a fee to protect dive sites, although multiple respondents were concerned about possible corruption if such fees would be levied. Divers visiting Lembeh Strait were most willing to pay for such a fee (93.85%), with slightly lower willingness in Bali (83.33%) and Dauin (80.77%). When asked about how much divers would be willing to pay, the average amount was USD$50.9. This number was similar in Lembeh and Bali (USD$56.1 and USD$55.6 respectively), but considerably lower in Dauin (USD$28.6). Dauin is the only location where such a fee is currently in place, although many respondents were not aware of this.

Table 2.1. Education level, diver certification level and origin of scuba divers visiting muck dive locations. All values rounded to nearest whole number (N = 100).

Variable	Dauin	Lembeh	Bali	All
Education Level				
Secondary education	35%	8%	0%	15%
Technical / Vocational Training	12%	5%	0%	6.25%
Bachelor	27%	34%	50%	33%
Master	15%	39%	17%	31%
PhD	12%	14%	33%	15%
Diver Certification Level				
Open Water Diver	32%	20%	17%	23%
Advanced open Water Diver	36%	43%	17%	39%
Rescue Diver	14%	9%	0%	10%
Divemaster	4%	14%	0%	10%
Instructor	11%	9%	50%	12%
Not answered	4%	5%	17%	5%
Origin				
Europe	61%	47%	33%	50%
North-America	29%	30%	50%	31%
Asia	11%	9%	17%	10%
Australia	0%	9%	0%	6%
Africa	0%	3%	0%	2%
South-America	0%	2%	0%	1%

2.4.2 Value of muck dive tourism

One hundred diver surveys and 16 operator surveys were collected. An additional four operators responded to our emailed survey. The visitor numbers from one operator survey showed an outlier with triple the number of visitors compared to similar sized dive centres, this outlier was removed prior to data analysis (summary dive centre statistics in appendices).

In the 19 dive centres for which data were analysed, a total of 35,715 visitors were recorded for the year 2014 (Table 2.2). Extrapolating this number to the total number of dive centres specialising in muck diving (n = 54), amounts to an estimated 101,505 divers visiting Indonesia and the Philippines to participate in muck dive activities. Mean diver expenditure per dive holiday differed between divers who booked a dive package (includes flights, accommodation, food and dives) or those who booked flights and accommodation separately.

Once average cost of flights was subtracted from package deals, expenditure was very similar to the non-package expenditure: USD$2,293.95 compared to USD$2,133.65 after flight adjustments. The former is used in the following estimates. On average, divers spent 9 days (SE ± 1 day) in the dive location and conducted 21 dives (SE ± 1 dive) during their holiday. Operators indicated that an average of 73% of divers visited primarily for muck diving, compared to 67.68% of visitor indicating muck diving as main reason to visit the area. The average of those two numbers (70.3%) was used to calculate total revenue.

The revenue created by muck divers in Indonesia and Philippines is approximately USD$ 152,341,000 annually. Depending on whether diver or operator motivation is used, this can range between USD$ 146,580,000 and USD$ 158,102,000. The total revenue created by muck dive centres when not taking in account the main reason for visits could be as high as USD$ 216,578,000.

Operator surveys indicated 33.7% (SE ±4.3%) of their revenue is spent on wages, which amounts to USD$ 51,339,000 being paid in wages annually across the region. Dive centres and resorts specialising in muck diving employ on average 42 staff (SE ±7 people), the majority of these employees (95%) are local people. This totals to 2289 local people employed in muck dive centres in the study region.

Table 2.2 Key values for muck dive tourism in Indonesia and Philippines in 2015. Values over USD$1 million rounded to nearest thousand, values over 10,000 rounded to nearest ten.

Code	Variable	Value
V	Visitor numbers in surveyed dive centres	35,720
V*t*	Total estimated visitor numbers for all muck dive centres	101,500
E	Average expenditure per diver	$2,133.65
P*m*	Proportion visitors visiting mainly for muck diving	70.3%
n	Number of dive centres sampled	19
T*m*	Total number of muck dive centres	54
R	Total revenue muck dive tourism	$152,341,000
S*m*	Total staff employed	2,290
P*w*	Percentage of dive centre revenue spent on wages	33.7%
R*w*	Total local income in wages	$51,339,000

2.4.3 Dive guide demographics and earnings

Dive guide surveys were collected in Lembeh and Dauin, but not in Bali. Questionnaires distributed to 44 dive guides showed that the average age of dive guides working in muck dive centres was 33.4 years old (SE ±5.1 year). The majority of the dive guides (90.1%) were nationals of the country they were working in, 9.9% of guides were international. In Indonesia none of the dive guides interviewed were foreign nationals. The majority of dive guides were male (90.5%).

Overall, dive guides are extremely experienced divers with an average of 3895 dives (SE ±594 dives) and high diver certification level (Table 2.3). However, the general education level is relatively low with 14% not having completed secondary education (Table 2.3). A frequent comment of dive guides in the surveys was how they are proud to be working in the places they live, having the opportunity to show visitors their marine environment.

Table 2.3 Education level and diver certification level of dive guides in muck dive locations. All values rounded to the nearest whole number (N = 44).

Variable	Dauin	Lembeh	All
Education Level			
No secondary education	15%	11%	14%
Secondary education	38%	56%	45%
Technical / Vocational Training	4%	6%	5%
Bachelor	31%	22%	27%
Not answered	12%	6%	9%
Diver Level			
Open Water	0%	11%	5%
Advanced Diver	0%	6%	2%
Rescue Diver	4%	39%	18%
Divemaster	31%	33%	32%
Assistant Instructor	4%	0%	2%
Instructor	35%	6%	23%
Not answered	27%	6%	18%

Wages were divided into three segments: salary, commission and tips. While dive guides are paid a basic salary, most operators pay extra commission per dive conducted or courses taught. The mean salary for guides was USD$233.6 (SE ± USD$18.9) per month. When including commission and tips, the average income of dive guides in the Philippines and Indonesia was USD$419.1 (SE ± USD$64.8). Mean salaries in the Philippines were higher than in Indonesia, but commission and tips in Indonesia were higher than in the Philippines, resulting in similar monthly incomes (Table 2.4).

Table 2.4 Average monthly income in US dollars of dive guides working in muck dive tourism. "Minimum salary" indicates the legal minimum salary in the region for jobs with a similar education level, "Basic salary" is the average monthly salary for dive guides excluding tips and commission, "Full salary" is the average monthly salary of dive guides including tips and commission. All values rounded to the nearest whole number.

	Dauin (USD$)	Lembeh (USD$)	All (USD$)
Minimum salary	$206	$161	$183
Basic salary	$247	$220	$234
Salary + tips + commission	$404	$435	$419

Basic salaries for dive guides in both the Philippines and Indonesia were higher than the legal minimum income for workers employed in these regions (119.8% and 137.6% respectively). When commission and tips are included, guides employed in the muck dive industry can earn up to double (195.8%) the legal minimum wage of other workers in the Philippines or nearly triple (271.5%) the minimum wage in Indonesia (Table 2.4).

2.4.4 Threats to muck dive tourism

Because the threats to muck fauna have not been documented, dive centre operators and dive guides were asked an open-ended question on what they considered to be the potential pressures that could impact the industry. The three threats most mentioned were: overcrowding of dive sites and associated impacts of diver behaviour, pollution, and negative effects of fishing. Operators and guides in Lembeh were more worried about crowding of dive sites and pollution, whereas dive professionals in Philippines were more worried about the effects of fishing near dive sites and destructive behaviour of divers while interacting with marine life. While questions about threats were not in the diver surveys, informal conversations with divers indicated a similar trend. Most divers seem to be worried about pollution on dive sites and an increase in the numbers of divers on sites.

2.5 Discussion

Nature-based tourism can be a sustainable way to use marine resources and alleviate poverty in developing countries (Job and Paesler 2013, Wilson and Tisdel 2003). This study has shown that the developing niche market of muck diving is a highly valuable tourism industry in

Indonesia and Philippines that attracts experienced divers and employs thousands of local people on a salary well above the national minimum wage. Since this type of diving does not require coral reefs, it offers potential for the development of tourism in areas that were previously considered unattractive to scuba dive tourism.

The tourists participating in muck diving tend to be very experienced, middle aged divers who are well educated and have a high income. The interests of experienced divers tend to differ than those of novice divers. As divers gain experience, they become more interested in smaller or rare animals, and often try to develop new skills such as underwater photography (Ince and Bowen 2010; Cater 2007). The demographic profile of the divers visiting muck dive sites is strikingly similar to that of birdwatchers. The birders described by Hvenegaard et al. (1989), were around 49 years old (46 years in this study), 62.4% had a university degree (79.2% in this study) and their annual income was considerably higher than the national average. Due to various limitations (e.g. language barriers and lack of information received from Asian-based dive centres), it is likely that our study did not adequately survey the growing Asian segment of the muck dive tourism market. Interviews with management indicated a similar demographic profile for the Asian divers. Dive operators consider the Asian market segment as the segment with the largest growth potential for muck dive tourism. Therefore, gaining a better understanding of the demographics and attitudes of this group is important for the future management of muck dive tourism.

The profile of the divers visiting muck divers explains the high value of the industry as a whole. Experienced divers are usually willing to spend more on diving holidays that will guarantee the experience they are looking for (Dearden et al. 2006; Jones et al. 2009). While searching for rare marine species is a highly specialised niche market, it attracts a large number of divers to Southeast Asia. Other well-known, valuable marine tourism destinations such as Bonaire, Moorea, Palau all attract fewer divers on an annual basis (Uyarra and Côté 2007; Clua et al. 2011; Vianna et al. 2012). Furthermore, muck dive tourism is nearly always the dedicated purpose of a holiday, which is why divers stay longer in one location and conduct more dives than divers visiting other destinations, leading to a higher expenditure (Jones et al. 2009). For instance, tourists doing shark diving in Palau and South Africa spent between 4 and 6 days diving (9 days in this study), with shark divers in South Africa doing an average of 2 dives during their stay (21 dives in this study) (Dicken and Hosking 2009; Vianna et al. 2012). Other types of marine tourism have shorter stays as well; 3 to 4 days for turtle and whale watching tourism, and two days or less for tourists visiting dolphin watching sites in in Australia (Wilson and Tisdell 2003; Smith et al. 2006). The specialised nature of muck diving also involves extra equipment such as expensive cameras and necessitates divers to do multiple dives in order to find a maximum of rare species, making it a tourism niche that is only accessible for those with a high expendable income.

Another consequence of the importance of finding rare or cryptic species, is the need for well-trained dive guides to spot the animals. The success of any given muck dive heavily depends on whether or not species were spotted. Therefore, the dive guides working in this industry tend to be highly experienced, strongly service-oriented and comparably well paid. While many of the dive guides working in muck dive centres have had limited education, they frequently make up to twice or more than what is considered to be the local minimum wage. Most guides indicated they were proud to be working in the muck diving industry as they considered it gave their region a good image and it brought employment to their villages. This study did not investigate the magnitude of financial leakage to other countries. While the leakages might be substantial (Walpole and Goodwin 2001), the dive centres surveyed in this study had strong links to the host communities and the benefits of muck dive tourism to local communities meet the social objective of sustainable tourism (Edgell Sr 2016).

While social objectives might be met in muck dive tourism, little is known about the state of the environment and species muck diving depend on. A frequent comment from management, dive guides and divers was the fear of overcrowding on dive sites, and adverse impacts of diver behaviour on popular species and their habitat. Overcrowding is known to make protected areas less attractive to tourists and could potentially lead to declining visitor numbers (Balmford et al. 2009). The high prevalence of cameras, specifically dSLRs might be cause of concern, as photographers are known to cause higher impacts than non-photographers, and flash photography could have a potential impact on animals (Uyarra and Cote 2007; Harasti and Gladstone 2013). Alternatively, the growing popularity of muck diving could be seen as an opportunity to develop muck dive tourism in other locations. Intrusive diver behaviour such as intentionally touching marine fauna was frequently reported, but impacts are unknown. The effects of other potential threats such as climate change, or harvesting of animals for the marine aquarium trade are similarly unknown (Duarte et al. 2008; McClenachan et al. 2012). Our research shows that nearly all divers participating in muck diving are willing to protect the environment, as long as conservation measures are transparent and well communicated. It has previously been shown that entry fees for marine parks have little impact on the total number of divers visiting a site (Pascoe et al. 2014; Bach and Burton 2016). For interactions with wildlife, visitors have been shown to accept management rules that might decrease proximity of wildlife interactions, provided it improved animal welfare (Bach and Burton 2016). It is crucial that management rules are transparent and communicated clearly, as many of the respondents voiced concerns about potential corruption or inefficient management.

For future sustainability of muck dive tourism, the importance of its focal species needs to be emphasized. A large majority of respondents would not have visited the region if muck diving was not possible. This number was even higher than other valuation studies, 21% of scuba divers visiting Palau named sharks as the main reason to visit, compared to 67% that named cryptic species critical for muck diving (Vianna et al. 2012, this study). The importance of muck diving is therefore much higher for local communities than in other types of dive tourism. Rarity of the species observed plays an equally important role for muck diving as it does for birdwatching (Booth et al. 2011). This high reliance on rare species could make muck dive tourism more vulnerable to potential impacts. However, at present it is unknown which species are most important to the industry, and which threats could have the biggest impacts. The inherent problem with rare species is that little is known about their ecology, abundance or conservation status (Kunin and Gaston 1993; Jones et al. 2002; McClenachan et al. 2012). To effectively manage muck diving, more research is needed into the ecology of soft sediment ecosystems, the impacts of diver behaviour and underwater photography, and to determine the diver carrying capacity of popular sites (Barker and Roberts 2004). Future research and management could potentially benefit from the high percentage of camera use in muck diving by establishing citizen science projects. Similar successful initiatives already exist for rare birds, and for marine megafauna and charismatic marine species (Edgar et al. 2016; McFarlane and Boxall 1996; Araujo et al. 2016).

The muck dive sites surveyed in this study were limited to Indonesia and Philippines, however, the real scope and thus value of the industry is much larger. Within the Coral Triangle region, multiple well-known muck dive sites exist in Malaysia and Papua New Guinea (Lew 2013; Macaulay 2008). The total number of specialised muck dive centres in the Coral Triangle area could be as high as 100 dive centres, which would nearly double the value described in this study. In 2013, 8.8 million people visited Indonesia, accounting for USD$49.3 billion in expenditure, or 3.1% of the GDP (Hampton & Jeyacheya 2015; WTO 2014). Scuba diving tourism makes up a small percentage of visitor numbers, but has a high economic value. The non-market use value of scuba dive tourism in Southeast Asia is estimated to be close to USD$4.5 billion per year (Pascoe et al. 2014). Muck diving is a small, yet very valuable niche of this industry that makes an important difference to the livelihoods of the local communities involved in it, especially since it is often practiced in regions where other tourist attractions and industries are limited. The muck diving niche is not limited to Southeast Asia, sites exist across the world, but are often not marketed this way. Therefore, the global value of cryptic, soft sediment species deserves the attention of management and conservation organisations alike. Like birdwatching, viewing and photographing rare or cryptic marine species can be a sustainable form of tourism that benefits local communities, marine conservation and potentially scientific research (Connell 2009).

2.6 Conclusion

Our research has shown that muck diving in Indonesia and Philippines is a very valuable niche tourism industry, combined, it is worth over USD$150 million per year. Muck dive tourism can be a sustainable form of nature based tourism in developing countries, especially in coastal areas where little or no potential for traditional coral reef scuba diving exists. The divers participating in this form of scuba diving tend to be highly experienced, well-educated and have a high annual income. This form of tourism creates thousands of jobs in rural areas where limited other sustainable livelihoods are available. The niche's high dependence on a limited number of rare species makes it vulnerable to future impacts, particularly as very little is known about the major threats to the species important to muck dive tourism. The effects of too many divers was suggested as an important threat to the industry, as was pollution and conflicts with fishermen. At present limited or no protection exists for the species on which this valuable tourism industry depends. However, our results show that muck divers are overall willing to pay for the conservation of the species they come to see, provided management strategies are transparent. The diver's willingness to pay for conservation and the kind of threats facing the industry highlight the possibilities of positive conservation outcomes, if suitable management strategies are employed. More research is needed to guide management policies and in deciding which species are most important and how they would benefit most from conservation actions. The high value of cryptic, soft sediment species illustrates how poorly studied species can support sustainable livelihoods, however, research and conservation efforts on these ecosystems are currently deficient.

Postscript: The next chapter investigates which species are most important for muck dive tourism, and how much research and conservation effort they have received in the past 20 years.

Chapter 3 Known unknowns: conservation and research priorities for soft sediment fauna supporting a valuable scuba diving industry

Preface: This chapter has been published in the peer-reviewed journal *Ocean and Coastal Management* (doi: 10.1016/j.ocecoaman.2018.03.045) and has been formatted according to journal guidelines. The combined references for all chapters can be found in the Cited Literature-section at the end of this thesis.

3.1 Abstract

Wildlife tourism can provide sustainable livelihoods, but can also significantly impact vulnerable species if improperly managed. To manage these impacts whilst continuing to support livelihoods, it is important to know the interests of tourists. Using the Best-Worst scaling method, we identified taxa that were most important to scuba dive tourism on shallow soft sediment habitats in Southeast Asia. We further identified differences in interest between demographic groups. We then investigated the current conservation status and research effort into the fauna driving this branch of tourism. The highest ranked taxa included fishes and invertebrates such as cephalopods and crustaceans. More than 200 respondents indicated that the taxa most important to muck dive tourism are mimic octopus / wunderpus, blue ringed octopus, rhinopias, flamboyant cuttlefish and frogfishes. Diver interests were most influenced by sex, age and dive experience. The extinction risk of six of the top ten taxa has not yet been assessed by the International Union for Conservation of Nature. On average, the taxa driving this multi-million dollar tourism industry had less than one paper published every two years over the past two decades. The lack of research and conservation effort toward these taxa is at odds with their economic and social importance. Considering their high economic tourism value and unknown vulnerability, there is an urgent need for more research on fauna from shallow soft sediment and other habitats important to tourism

3.2 Introduction

Nature-based tourism is an important source of income in both developing and developed countries (Balmford et al. 2009). Tourism can be a sustainable alternative to more destructive uses of the environment, but it can also have considerable impacts such as habitat degradation or conflicts between resource users (Wong 1998; Walpole and Goodwin 2001), and evolving tourist preferences are likely to alter tourism impacts (Reynolds and Braithwaite 2001; Gössling et al. 2012). In recent years, a new niche of scuba dive tourism has developed on soft sediment habitats, which focuses on finding and photographing cryptobenthic species that are rarely found on coral reefs: "muck diving" (Lew 2013).

Muck dive tourism is worth more than US$150 million annually, but the habitats it depends on do not benefit from any formal conservation activities we are aware of (DeVantier and Turak 2004; De Brauwer et al. 2017). To effectively protect biodiversity, it is crucial that natural resource managers have access to accurate data on how resources are used and threatened (Conroy and Peterson 2013). Despite its economic importance, it is unclear which species are most important to attract tourists (De Brauwer et al. 2017).

Little is known on the ecology of soft sediment fauna and even less on the potential threats they face (Alongi 1989). It has been suggested that scuba divers could have a negative impact on soft sediment associated fauna, but the impacts of other common stressors to marine ecosystems (such as overfishing or climate change) remain unknown (DeVantier and Turak 2004). The high dependence of muck dive tourism on a limited number of taxa could threaten the viability of this industry should the taxa driving it disappear. Identifying the taxa most important for muck dive tourism is a crucial first step in developing adequate management, research and ultimately the conservation of soft sediment habitats and its associated fauna.

The public's preference for particular species has traditionally been measured using a variety of survey methods. Rating scales, either ordinal or Likert-scales, (Home et al. 2009; Veríssimo et al. 2009; Schlegel and Rupf 2010) are not always reliable due to individual or cultural differences, introducing multiple potential biases such as extreme responding, social desirability, or acquiescence bias (Paulhus 1991; Cohen 2003). Choice experiments with paired comparisons have been used to test preferences between flagship species for conservation programmes (Veríssimo et al. 2009), but these need for large numbers of questions per option to correctly estimate consumer preferences (Louviere et al. 2013), and if more than two choices are available, asking for the most preferred choice gives no information on any of the other options (Louviere et al. 2013). One of the greatest weaknesses of traditional approaches is the difficulty in differentiating between the preferences of different demographic groups (Cohen 2003; Chrzan and Golovashkina 2006).

Best-worst Scaling (BWS) is increasingly being used to survey consumers' preferences for products or attributes of products and services (Cohen 2003; Flynn et al. 2008; Louviere et al. 2013). BWS is a choice experiment which reveals both the least preferred (Worst) and most preferred (Best) choices (Finn and Louviere 1992). The theoretical basis of BWS is that consumers make the most reliable choices for the most extreme items in a set (Helson 1964; Louviere et al. 2013). The strength of this approach is that stated preferences are more precisely defined. As a result, BWS performs better at estimating preferences than most traditional ratings tasks (Cohen 2003). Muck dive tourism relies strongly on a limited set of taxa which might be more or less preferred by divers, so the BWS method has the potential of being a suitable method to test diver preferences.

This study tests if the BWS method can be used to identify the taxa of greatest interest for dive tourism on the poorly studied soft sediment habitats of Southeast Asia. The Coral Triangle in Southeast Asia hosts the highest marine biodiversity in the world, and is the focus of multiple conservation and research initiatives (Hoeksema 2007; Allen 2008; Hamilton et al. 2011). Current management and conservation efforts in this region are largely focused on protecting coral reef habitats (Scriberras et al. 2013; Clifton and Foale 2017), but this approach ignores a large proportion of the diversity found in the region, as more than 50% of the shallow waters in the Coral Triangle region consists of soft sediment (Hayes 1967). Shallow soft sediment habitats in the tropics are perceived to be of little interest to conservation, and are often seen as depauparate habitats of little value (Alongi 1989). However, the current prioritisation of charismatic species and ecosystems does not necessarily represent those that are most in need of conservation action (Clucas et al. 2008; McClenachan et al. 2012; Clifton and Foale 2017).

The goals of this study were to identify the most important taxa for muck dive tourism industry by using BWS and compare them to those identified using traditional survey methods. To assess future research needs, we investigated the quantity of research and the conservation status of the taxa that drive a multi-million dollar tourism industry in Southeast Asia.

3.3 Methods

3.3.1 Top taxa

3.3.1.1 Best-worst scaling

A shortlist of 21 taxa important to muck dive tourism was compiled after consulting with ten experts (Table 3.1). Experts included dive operators, dive guides and professional underwater photographers active in the area. In some cases, it was not possible to define one single species (e.g. “nudibranchs”), in these cases the most relevant taxonomic clade was chosen. Therefore, we use the term “taxon” when describing important muck diving fauna, depending on what scuba divers perceived as different “species”. Taxon might here refer to a species, a subset of multiple species, a genus, or a family (Table 3.1). The 21 taxa were arranged in 12 subsets of seven taxa using a randomized block design in R, with each taxon occurring four times over the 12 subsets (Flynn et al. 2008; Louviere et al. 2013). The Qualtrics-platform (Qualtrics 2015) was used to create an online survey based on these 12 subsets. Respondents were presented with the subsets one at a time and asked to indicate the taxon they would most and least like to see during a dive (Figure 3.1).

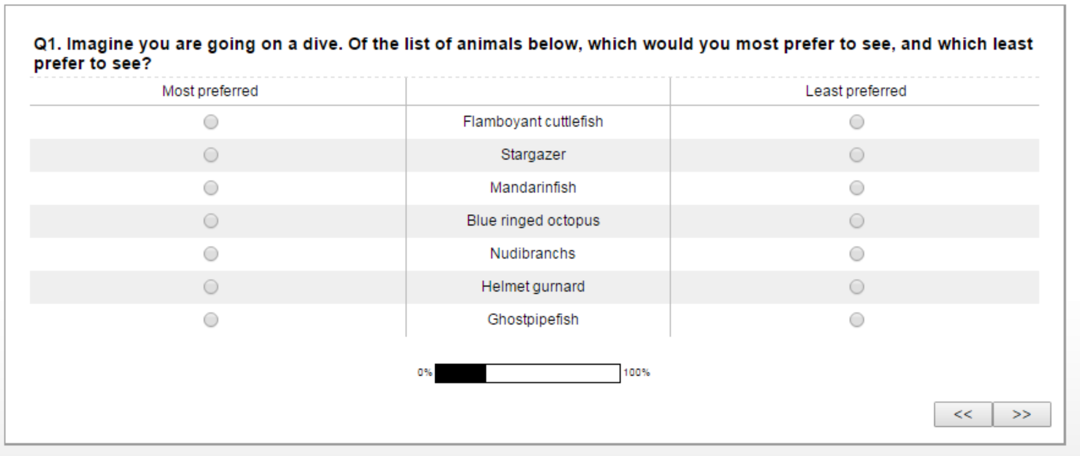


Figure 3.1 Example of a subset in the online Best-Worst Scaling survey.

A design issue was whether to use photos to illustrate taxa. An argument for using photos is that divers may not recognise the taxa names, but be familiar with the taxon when they see it. However, photos may induce a bias in response for those who are not familiar with the taxa, in that the photo itself may be the basis for subsequent rankings i.e. having seen the photo of a previously unknown taxon they may now rate it highly. Avoiding induced values from the survey instrument was deemed more important than overcoming lack of name recognition, and we did not use photos. The order of the 12 subsets was randomized per survey, as was the order of the taxa within each subset. Six additional questions were asked regarding diver experience, sex, nationality and age (Full survey in supplementary materials). Surveys were available in English only and were online from June until November 2015 and respondents were not able to take the survey more than once. Links to the survey were spread by email, posted on various social media (Facebook, blog), on scuba dive forums, websites of dive centres, and scuba diving online newsletters.

BWS survey data were analysed using two methods. First, we used the counts method to calculate the order for attributes in BWS (Finn and Louviere 1992; Louviere and Islam 2008). For each taxon the number of times it was chosen as most and least preferred were totalled. The difference between the best and worst count per taxon gives a measure of importance of the taxon (here denoted Best Worst Scores) (Louviere et al. 2015). For the second method we conducted a conditional logit analysis (Flynn et al. 2008). Using the logit rule, the probability of respondents choosing taxon *i* from the set of taxa *i* through *j* as best or worst was calculated using the formulas (Sawtooth Software 2013):

$Pbi = e^{Ui} / \Sigma\ e^{Uij}$

$Pwi = e^{-Ui} / \Sigma\ e^{-Uij}$

With:

- PBi = Probability of choosing item *i* as best
- Pwi = Probability of choosing item *i* as worst
- Ui = raw logit weight for i
- e^{Ui} = antilog of Ui
- e^{-Ui} = antilog of Ui the negative weight for i

Dummy coding was used to avoid linear dependency, the value of the last taxon (Stargazer (*Uranoscopus spp.*)) was set to zero and the value of the other k-1 taxa was estimated with respect to that final taxon held constant at zero (Sawtooth Software 2013). This dummy variable does not affect the ranking of the taxon that was set to zero (Stargazer), but rather gives values for other taxa relative to that taxon. Results of this model and the counts method are similar, but the logit model allows investigation of heterogeneity in the samples (Flynn et al. 2008; Louviere and Islam 2008). All data were analysed using R, and the "survival"-package was used for estimating conditional logit models.

3.3.1.2 Diver surveys

To afford a comparison with traditional preference survey data, self-administered questionnaires were distributed in 15 dive centres across Indonesia (Bali: 2 dive centres, Lembeh strait: 6 dive centres) and Philippines (Dauin: 7 dive centres) between May 2015 and November 2015. Questionnaires (including information about the goal of the study and guidelines for completing the questions) were distributed to all guests by the staff of the dive centres, and collected at the end of the survey period (survey forms in Appendices). The questionnaires were available in English, traditional Chinese and Japanese. These surveys included a wide range of questions about diver demographics and expenditure (De Brauwer et al. 2017). Of relevance here, divers were asked which 3 species they would most like to see during their diving holiday. Summary statistics were obtained using R to describe which species were most popular with divers (R Core Team 2015).

Surveys were approved by the Curtin University Ethics Committee (RDSE-06-15) and followed the requirements of the Australian National Statement on Ethical Conduct in Human Research.

Table 3.1 List of important muck dive taxa included in online Best-Worst Scaling survey. The common names used in dive tourism do not always represent a single species, and "details" explain how taxa were presented.

Common name	Scientific name	Details
Blue ringed octopus	*Hapalochlaena spp.*	Consists of up to six species, hard to tell apart by non-experts
Bobtail squid	*Euprymna berryi*	Multiple other similar species in genus
Flamboyant cuttlefish	*Metasepia pfefferi*	Sister species in south Japan
Flounder	*Soleichthys spp.*	Multiple species (>30)
Frogfish	*Antennarius spp.*	Multiple species (>20)
Ghostpipefish	*Solenostomus spp.*	Four recognised species, potentially up to nine species
Gobies	*Gobiidae*	Multiple species (>600)
Harlequin shrimp	*Hymenocera elegans*	Sister species in Eastern Pacific, but same common name is used
Helmet gurnard	*Dactyloptena orientalis*	
Mandarinfish	*Synchiropus splendidus*	
Mimic octopus / Wunderpus	*Thaumoctopus mimicus / Wunderpus photogenicus*	Two species, combined in surveys as they are difficult to tell apart by non-experts
Nudibranchs	*Nudibranchia*	Multiple families, representing >3000 species
Octopus (other species)	*Octopus spp.*	Multiple species: e.g. long armed, starry night, algae, etc.
Pipefish	*Syngnathinae*	Multiple species (>40)
Pygmy seahorses	*Hippocampus spp.*	Six species
Rare crabs	*Brachyura*	Multiple families, including Orang-utan crab, Candy crab, Boxer crab
Rhinopias	*Rhinopias spp.*	Three species
Scorpionfish	*Scorpaenopsis spp.*	Multiple species (>20)
Seahorses	*Hippocampus spp.*	Multiple species (>30)
Shrimp (other species)	*Decapoda*	Multiple families including: Coleman shrimp, Bumblebee shrimp
Stargazer	*Uranoscopus spp.*	Two species, hard to tell apart by non-experts

3.3.1.3 Effect of demographics

As well as the initial conditional logit model (= aggregate model), we built new models to test if preferences changed with sex, age, dive experience, certification level, previous muck dive experience, and camera use. This was undertaken using interactions between the attribute dummies and the sociodemographic variables. Sex, previous muck dive experience, and camera use were discreet variables with two levels. Certification level was a discreet variable with five levels (Open Water Diver, Advanced Open Water Diver, Rescue Diver, Divemaster, and Instructor), while different dive organisations have different names for certification levels, we opted to convert levels to PADI levels (largest global dive training organisation). Age and dive experience (expressed as age in years and total number of dives) were continuous variables. For the categorical variables, the probabilities were evaluated for each level. For the continuous variables (age and total dives) the probabilities were evaluated at 3 levels to illustrate the impact of these variables on values. Models were compared to the aggregate model using Loglikelihood tests and AIC-values were calculated for each model. Analyses were conducted in R using the "survival"-package and "lmtest"-package. Results of each model were converted to ratio-scaled probabilities (following Sawtooth Software 2013) to allow for easier interpretation using the formula:

$$e^{Ui} / (e^{Ui} + a - 1)$$

With:

- Ui = raw logit weight for taxon i
- e^{Ui} = antilog of Ui
- a = Number of taxa shown per set

3.3.2 Research and conservation status of important muck dive tourism taxa

Web of Science (webofknowledge.com) was searched for recent research (1997-2017) on the ten most popular soft sediment taxa in Southeast Asia (results from BW-scaling). To compare research effort on popular soft sediment fauna to other marine fauna, the same search was conducted for a charismatic marine mammal (Bottlenose dolphin (*Tursiops truncatus*)), and a damselfish frequently used in research, yet unknown to most recreational divers (Ambon Damsel (*Pomacentrus amboinensis*)). While bottlenose dolphins and Ambon damselfish are not soft sediment-associated species, search results give an indication of the research effort that is possible on marine fauna during the set timescale. The scientific names of taxa were used as search terms. If the name of the animal represented an entire genus or family, the family or genus name that represented the common names in the list closest were used (e.g. *Hippocampus* for "Seahorses"). When taxa represented a limited number of species (<10), searches were done for each species and the counts for each species totalled after duplicate publications were removed. For taxa where confusion might exist due to similar names for different taxa ("*Antennarius*" also represent Crustaceans), Boolean operators were used to ensure results would only be for the target taxon. No filters were used to restrict research domain or geographic area. To assess conservation status, the IUCN red list (www.iucnredlist.org) was searched using the same search terms.

3.4 Results

3.4.1 Top taxa

3.4.1.1 Best-Worst scaling surveys

The online BWS survey was fully completed by 113 respondents. A small minority of respondents were entry level divers (1.8%), 36.3% were divers with additional training (Advanced 21.2%, Rescue 15.0%), compared to 61.9% with a professional diver level (Divemaster 22.1%, Instructor 39.8%). Divers were highly experienced, with a mean of 1242 dives (±SE 113 dives) (median 800 dives). A large proportion of respondents used a camera (83.2%). The mean age of divers was 39 years old (±SE 1 year), 35.4% of respondents were female and 64.6% male. Respondents came from 20 different countries, mostly from Europe and North-America (52.2% and 22.1%), followed by Oceania (15.0%), Asia (8.8%), South-America (0.9%), and Africa (0.9%).

Based on the Best-Worst Scores, the three most popular taxa were mimic octopus (*Thaumoctopus mimicus*) / wunderpus (*Wunderpus photogenicus*), followed by the Blue-ringed octopus (*Hapalochlaena* spp.) and rhinopias (*Rhinopias* spp.) (Table 3.2). The basic conditional logit model reported parameter estimates for each taxa, with the last taxon (stargazer) randomly chosen as the baseline taxon (and hence set to zero) (Table 3.2). The ordered results of the basic conditional logit model were similar to standard Best minus Worst approach, and there were no differences between which ten taxa were considered to be most important. The rank order for all taxa was unchanged for the six taxa considered to be most important and the four least important. There were minor changes of rank order for some of the taxa in the middle. The correlation between the clogit model and the standard Best minus Worst results was very strong ($r = 0.99$) and significant ($p < 0.001$).

3.4.1.2 Diver surveys

One hundred completed surveys were collected in dive centres. Seven percent of divers had entry level certification, 71.7% had received additional training, and 22.2% of divers held a professional dive certification. The average number of dives was 587 dives (SE ±84 dives). A majority of divers used an underwater camera (73.5%). The average age of divers was 46 years old (SE ±5 years), 41.9% of divers were female and 58.1% male. Respondents came from 21 countries, half of which were European, and 30.6% came from North-America. Asian divers made up 10% of respondents, followed by 6% from Australia, 2% from Africa, and 1% from South-America.

The three most popular taxa with divers were frogfishes, nudibranchs and octopuses. Seven out of the ten most popular taxa also occurred in the top 10 of the BWS (Table 3.2). All taxa in the top ten of diver surveys were found in the full BWS list of taxa (Table 3.2).

Table 3.2 Comparison of the most important muck dive taxa using the Best-Worst Scoring approach and traditional surveys. **RBW**: Rank order of animals using Best-Worst Scoring; **RCL**: Rank order of animals using conditional logit model; **RDS**: Rank order of animals using traditional diver surveys; not all species named in these surveys were present in the BW-shortlist, explaining gaps in number order, same rank order indicates species were named equally frequent. **Best**: number of times animal was selected as favourite; **Worst**: number of times animal was selected as least favourite; **B-W:** Best minus Worst scores. Results of basic conditional logit model based on online Best-Worst scaling survey: Stargazer used as baseline, therefore no p-values available. **Para**: parameters from basic conditional logit model.

Species	Ranking			Best-Worst Scoring			Conditional logit model				
	RBW	RCL	RDS	Best	Worst	B-W	Para	SE	P	95% C.I.	
Mimic octopus / Wunderpus	1	1	4	163	4	159	2.56	0.15	<0.001***	2.27	2.85
Blue ringed octopus	2	2	8	167	12	155	2.35	0.15	<0.001***	2.06	2.64
Rhinopias	3	3	13	140	9	131	2.33	0.15	<0.001***	2.04	2.63
Flamboyant cuttlefish	4	4	6	123	10	113	2.16	0.15	<0.001***	1.86	2.46
Frogfish	5	5	1	100	14	86	1.91	0.16	<0.001***	1.61	2.21
Pygmy seahorses	6	6	10	105	22	83	1.76	0.15	<0.001***	1.46	2.06
Octopus (other)	7	8	3	78	13	65	1.52	0.16	<0.001***	1.22	1.83
Rare crabs	8	9	16	77	21	56	1.48	0.16	<0.001***	1.17	1.79
Harlequin shrimp	9	7	14	58	18	40	1.76	0.15	<0.001***	1.46	2.06
Nudibranchs	10	10	2	73	45	28	1.17	0.15	<0.001***	0.87	1.47
Bobtail squid	11	11	16	45	41	4	1.14	0.16	<0.001***	0.84	1.45
Mandarinfish	12	13	9	53	60	-7	0.84	0.16	<0.001***	0.53	1.15
Seahorses	13	14	5	28	42	-14	0.69	0.16	<0.001***	0.37	1.01
Shrimp (other)	14	15	7	44	61	-17	0.61	0.16	<0.001***	0.29	0.93
Ghostpipefish	15	12	15	22	49	-27	0.86	0.16	<0.001***	0.55	1.16
Stargazer	16	17	16	15	87	-72	0.00	-	-	-	-
Scorpionfish	17	16	12	19	102	-83	0.06	0.14	0.70	-0.23	0.34
Gobies	18	18	-	33	139	-106	-0.15	0.15	0.33	-0.45	0.15
Pipefish	19	19	14	8	120	-112	-0.23	0.15	0.13	-0.53	0.07
Helmet gurnard	20	20	-	4	181	-177	-0.78	0.14	<0.001***	-1.05	-0.51
Flounder	21	21	-	1	306	-305	-1.87	0.14	<0.001***	-2.15	-1.60

****: Significant at $p < 0.001$*

3.4.1.3 Effects of demographics

Models were estimated using interaction effects for each demographic variable, individually. Loglikelihood tests showed that each model based on different demographic variables was significantly different to the initial aggregate model (Table 3.3). AIC scores were lowest for age, followed by sex and dive experience and highest for camera use (Table 3.3).

Table 3.3 Results from loglikelihood tests and AIC per model based Best-Worst Scaling surveys.

Model	LogLik	Df	Chisq	P	AIC	ΔAICb
Aggregate model	-4103.1	-	-	-	8246.24	0
Age	-4054.3	20	97.6	<0.001 ***	8188.64	57.60
Sex	-4062.5	20	81.197	<0.001 ***	8205.04	41.20
Total dives	-4071.9	20	62.45	<0.001 ***	8223.79	22.45
Muck experience	-4076.1	20	54.08	<0.001 ***	8232.16	14.08
Level	-4019.3	80	167.56	<0.001 ***	8238.68	7.56
Camera	-4084.9	20	36.47	0.01 *	8249.77	-3.53

*: Significant at $p < 0.05$; ***: Significant at $p < 0.001$

The relative importance of soft sediment fauna changed depending on different models and diver characteristics (Table in Appendices). As divers get older, their interest in rare shrimp increases, while their interest in frogfishes, pygmy seahorses and flamboyant cuttlefish notably decreases. Divers with entry level certifications had less pronounced preferences for most preferred taxa to see, but the strongest preferences against taxa they would least like to see. Entry level divers also had far less interest in the mimic octopus / wunderpus and rare crabs and shrimp than other divers. Instead, the taxa most preferred by starting divers were pygmy seahorses, rhinopias and frogfishes. As divers gain more dive experience, their interest in mandarinfish declines, but shrimp and octopus become more important. Women showed less strong preferences for taxa such as rhinopias, shrimp and different octopus species than men did. Divers without previous muck dive experience held stronger preferences for frogfishes, flamboyant cuttlefish and pygmy seahorses than those with muck dive experience. Divers not using a camera showed less interest in frogfishes and rare crabs than those with a camera, but more in mimic octopus / wunderpus (Figure 3.2, Table in Appendices).

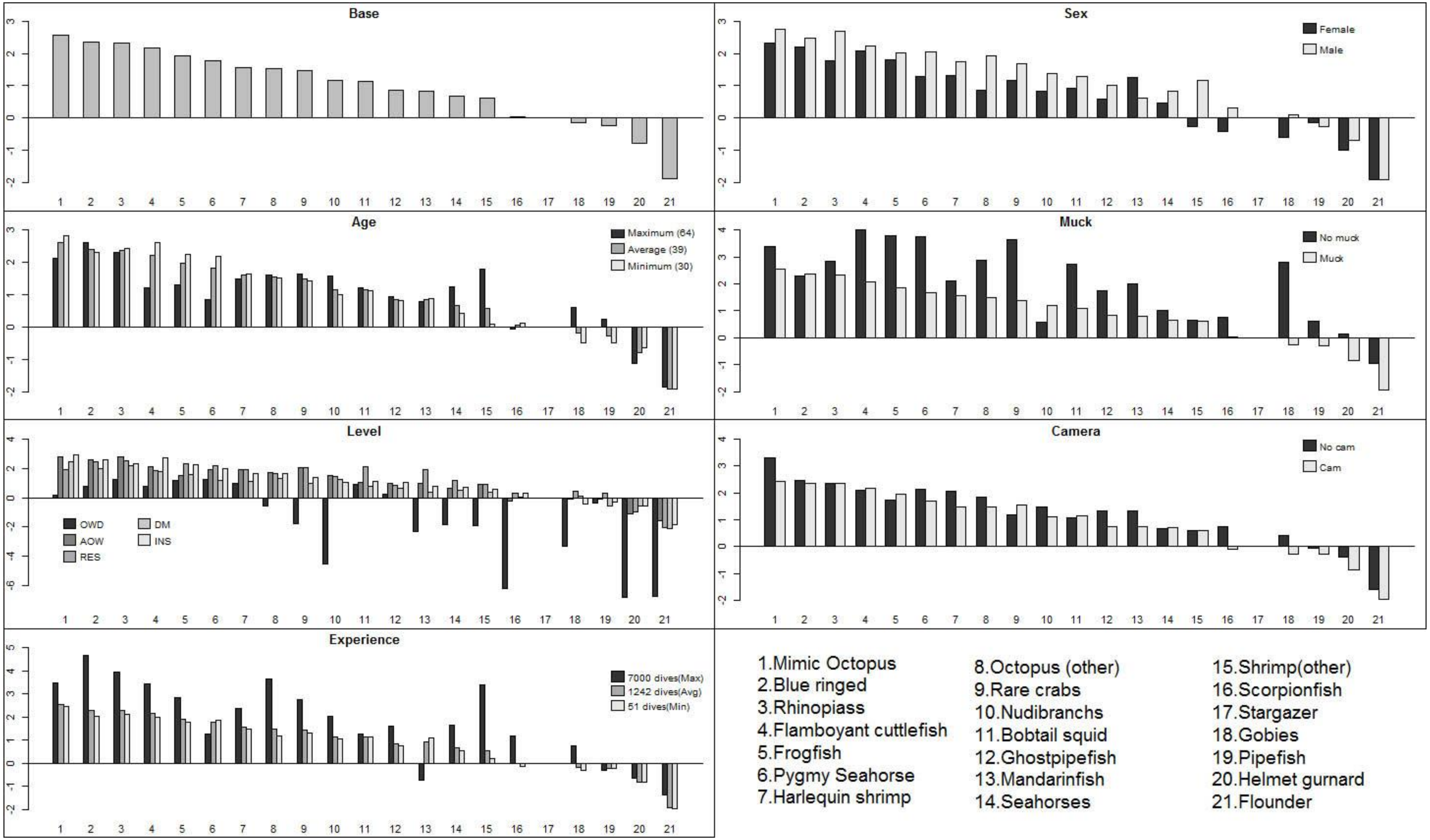


Figure 3.2 Ratio-scaled effects of demographic variables on diver preferences for soft sediment fauna, tested with Best-Worst scaling models.

3.4.2 Research conducted on top taxa

Research effort on the ten taxa that are most important to muck dive tourism has been very limited. Over half of the taxa have featured in less than ten published papers in 20 years. Of the five most important taxa, only one taxon (Blue ringed octopus) has more than an average of one publication per year. The exception is nudibranchs, which have had more than 300 published publications in 20 years. A qualitative look at the publications on the two most researched taxa (nudibranchs, Blue ringed octopus) showed that a majority of publications focused on chemical compounds of the toxins present in these animals, with limited research on their ecological role on soft sediment habitats or potential threats. A total of 108 papers were published on the Ambon damsel (*P. amboinensis*), a coral reef fish species unknown to most divers, in the same time span. The combined research effort on the ten most important taxa for muck dive tourism was just over 10% of the research that has been done on one species of dolphin (*T. truncatus)*.

Table 3.4 Research output and conservation statues of the 10 taxa most important to muck dive tourism. Publications: number of published papers between 1997 -2017; IUCN status: NA: Not Assessed; DD: Data Deficient; LC: Least Concern.

Common Name	Publications	IUCN status
Mimic octopus / Wunderpus	4/8	NA
Blue ringed octopus	33	NA
Rhinopias	4	DD / LC
Flamboyant cuttlefish	1	DD
Frogfish	18	NA / LC
Pygmy seahorses	9	DD
Other octopuses	24	NA
Rare crabs	5	NA
Harlequin shrimp	4	NA
Nudibranchs	331	NA
Ambon Damsel	108	NA
Bottlenose dolphin	3035	LC

More than half of the most important muck dive taxa have not yet been assessed for their extinction risk (Table 3.4). Of those assessed, three taxa are considered to lack enough data to determine their extinction risk ("data deficient"). In only two taxa (frogfishes and Rhinopias) a number of species have been assessed and found to be not in immediate risk of extinction ("least concern") (Table 3.4). The Ambon damsel has not been assessed despite the significant amount of research done on it. Bottlenose dolphins have been assessed, and were found not at risk of extinction.

3.5 Discussion

The results of this study show that Best-Worst Scaling is an appropriate method to identify which taxa are of greatest interest to specific demographic groups. Between the two different methods used, more than 200 respondents indicated that the taxa most important to muck dive tourism are mimic octopus / wunderpus, blue ringed octopus, rhinopias, flamboyant cuttlefish and frogfishes. We further demonstrate that the taxa crucial to a highly valuable branch of marine tourism receive very limited research effort, have not been assessed for their risk of extinction, or the data to do so are lacking.

Best-Worst scaling surveys are uncomplicated to design, can be run cheaply using online survey software, and are easy to understand and answer by respondents. Basic data analysis is quick and straightforward, but can also be expanded to distinguish between multiple variables. Interpretation of results is intuitive and easy to understand for non-experts. These benefits make it a good alternative for organisations that either lack the funding to run extensive face to face surveys or have limited capacity for statistical analysis. Traditional surveys and BWS method resulted in the same top taxa, but data from traditional surveys are often harder to analyse and interpret correctly (Cohen 2003). By forcing respondents to make trade-offs between choices, the BWS method avoids scaling bias (ideal for cross cultural studies), has a strong capacity to differentiate importance between attributes, and has a higher predictive power compared to other ranking tests (Chrzan and Golovashkina 2006; Sawtooth Software 2013).

The validity of the standard Best minus Worst (count) results can be statistically tested with conditional logit analyses. Our study showed that the results of both methods are strongly correlated, indicating the validity of the standard method. Minor differences between the rank order of the conditional regression model and the standard (count) method were only situated in the middle ranking taxa. The most and least preferred taxa followed the same order in both types of analysis, indicating that people have the strongest opinions on those taxa in the top and bottom of the list (Helson 1964; Louviere et al. 2013). Interpretation of parameters should take into account that results are relative interval estimates rather than anchored, fixed scales (Flynn et al. 2008). In other words, individual values are not absolute, but should be compared to how much they differ from the other values. Small differences between taxa in the middle mean less than the large differences between top and bottom, indicating stronger likes or dislikes.

The differences in diver preferences for muck dive taxa were most pronounced for diver age, sex and dive experience. Shifts in preferences between different demographic groups are important for management and conservation organisations, as these could influence where current and future impacts will be. By not using pictures in the online surveys, we measured preferences based on name recognition alone. A useful extension to the current work would be ask for familiarity with taxa *after* the BWS task, or even to present a matching task of taxa names with pictures, so that robustness of preferences can be evaluated. In this study, entry level divers had weaker preferences for top taxa, but made clear choices for taxa they like least. As divers gained experience, their interests changed to lesser-known or rare taxa such as shrimp. This study indicated that the perceived rarity of an animal plays an important role in preferences, confirming existing literature that uniqueness is valued by the general public (White et al. 2001; Eckert and Hemphill 2005; Booth et al. 2011). Alternatively, the interest in certain taxa could be linked to how photogenic they are and how well the taxon or its behaviour translates to images. Regardless of the cause of diver's interests, managers need to be able to predict the public's interest in rare taxa as increased tourism might increase impacts on taxa that are already vulnerable (Sekercioglu 2002; Kelly et al. 2003).

The lack of knowledge about soft sediment fauna is reflected in the research effort into these taxa. Most of the popular soft sediment taxa have an average of one published publication every two years, a stark contrast with bottlenose dolphins which average 300 published papers in the same time period. The research interest in the taxa which had most published papers (blue-ringed octopus, nudibranchs) focuses on their various toxins and potential applications in pharmacology. Research in the ecology or conservation of these taxa is less frequent, however no less needed (McDonald-Madden et al. 2010; Fleming and Bateman 2016). The Ambon damsel, a species which is not of particular interest to tourism, fishing or the marine ornamental trade, has attracted more research than the combined research into the top eight taxa responsible for a multi-million dollar scuba dive industry. In contrast to soft sediment taxa, the Ambon damsel is an abundant species on coral reefs which is easy to collect, observe, and keep in aquaria for experiments (McCormick et al 2016).

The lack of research on soft sediment taxa translates to a limited knowledge of their conservation status. Taxa such as harlequin shrimp and rhinopias are popular in the marine aquarium trade, but are either classed as data deficient or not assessed by the IUCN Red List (Calado et al. 2003). Conservation efforts are mostly focused on well-known large taxa such as cetaceans and sharks, or habitats such as coral reefs (McClenachan et al. 2012; Scriberras et al. 2013), or on large and widely distributed taxa on land (Fleming and Bateman 2016). Unethical diver behaviour such as touching or moving animals to get a better picture can negatively impact cryptic fish species (Chapter 6). If this or other environmental impacts should lead to the disappearance of important taxa from dive destinations, this could have severe consequences on the incomes of local communities dependent on tourism. It is clear that tourists are interested in poorly known taxa, but management, researchers and conservation groups have yet to catch up. This is true for soft sediment fauna, but other poorly studied habitats can have similarly valuable taxa (e.g. bird species in wetlands (Findlay & Houlahan 1997)) that warrant more research and conservation attention.

The most important taxa in this study can be considered to be charismatic fauna, yet it remains unclear which ecological functions these charismatic taxa fulfil in soft sediment ecosystems. Other taxa that are not of interest to dive tourism are likely to have important ecological roles vital to the functioning of soft sediment ecosystems (Alongi 1989). Due to limited research efforts, we still have limited understanding of these ecosystems, the threats that are most likely to impact them, and of which species are most at risk of extinction. These considerable knowledge gaps hamper efficient management and conservation (Scriberras et al. 2013). The most charismatic soft sediment taxa may or may not be of vital importance to ecosystem functioning, and they may or may not be at risk of extinction. They do however, offer the potential to boost public and scientific interest in soft sediment fauna (Home et al. 2009). Charismatic species are widely used as flagship species for conservation management (Verissimo et al. 2009). At present, they offer a valuable opportunity as focal points for soft sediment conservation initiatives.

This study started with a large number of taxa of interest to tourism managers. Similar BWS surveys can be conducted with fewer taxa important to other niches of wildlife tourism, adapting to the needs of the organisation designing the survey. This study gauged the public's interest in a subset of taxa, but BWS surveys can be used to test other aspects of interest to managers. The preferences of local stakeholders in different management approaches could be surveyed using BWS to ensure compliance (Arias et al. 2015; Ruiz-Frau et al. 2015). Alternatively, preferences of tourists for different activities in marine parks can be investigated to estimate the risk to vulnerable habitats or species (Schofield et al. 2015; Stelzenmüller et al. 2018). The strength of BWS is the ease to differentiate between the interests of different demographics, allowing for targeted management (Chrzan and Golovashkina 2006; Sawtooth

Software 2013). Wildlife tourism and its associated pressures may shift over time and between demographics, which can be problematic as tourism depends on the very species it might have an impact on (Reynolds and Braithwaite 2001; Gössling et al. 2012). It is therefore crucial that resource managers have the capability of gauging tourist interests and take appropriate protective measures.

3.6 Conclusion

This study has shown that the taxa supporting a valuable branch of wildlife tourism on soft sediment habitats are poorly studied and lack conservation attention. We further demonstrated that the Best-Worst Scaling method can be applied by tourism managers and conservationists to investigate the public's interests in wildlife. The method's ease of design and analysis might be of particular interest to organisations with limited resources or personnel. Strong tourism markets and associated pressures can develop in poorly studied ecosystems, long before the ecological dynamics of that system are understood by researchers and resource managers. It is crucial to recognize where the strongest tourism pressures occur to ensure sustainability of such niche tourism. In the specific case of the marine soft sediment ecosystems where muck dive tourism occurs, anthropogenic threats remain largely unknown. However, the strong dependence of muck dive tourism on a select few taxa and the impacts of underwater photography on marine fauna could be a cause for concern. We conclude that more research on soft sediment fauna is needed, as thousands of jobs and millions of dollars depend on it.

Postscript: In the next chapter I investigate the drivers of cryptobenthic fish diversity and abundance on marine soft sediment habitats, in particular on sites that are currently of high importance to muck dive tourism.

Chapter 4 High diversity, but low abundance of cryptobenthic fish on soft sediment habitats in Southeast Asia

Preface: This chapter has been published in the journal *Estuarine, Coastal, and Shelf Science* (doi: 10.1016/j.ecss.2018.11.014) and has been formatted according to the journal's guidelines. The combined references for all chapters can be found in the Cited Literature-section at the end of this thesis.

4.1 Abstract

Cryptobenthic fishes play a crucial role in marine ecosystems as trophic links between the base of the food chain and higher-level consumers. Infralittoral soft sediments are the largest marine habitat, yet little is known about fish assemblages in these ecosystems. This study investigates the cryptobenthic fish abundance and diversity on soft sediment habitats in the centre of tropical marine biodiversity. We surveyed 20 sites across three regions in Indonesia (Bali, Lembeh Strait) and the Philippines (Dauin) using Underwater Visual Surveys (UVC) and roving diver surveys. We tested the effects of depth (6m, 16m), benthic cover and sediment grain size characteristics on fish assemblages. Our results showed a high diversity (112 species), but low abundances (mean: 93 individuals/500m2 ± SE: 28 ind.). Benthic cover on surveyed sites consisted for 90.1% (± SE: 0.7%) of unconsolidated sediments, which were predominantly poorly sorted (σ = 0.975 φ), gravelly sand. PERMANOVA analyses showed that fish assemblages and fish diversity were significantly different between regions ($p<0.001$) and depth ($p = 0.002$). Distance based linear Models (DistLM) explained respectively 25% and 33.5% of the variation in fish assemblages and fish diversity. The high cryptobenthic fish diversity found in this study exceeds that of many coral reefs and contradicts the current view of soft sediment fish communities as depauparate ones. Our results provide valuable insights in a poorly studied marine ecosystem and call for more research in these valuable habitats.

4.2 Introduction

One of the foremost challenges in marine ecology is explaining existing patterns in biodiversity. Species-rich habitats such as coral and temperate reefs have received considerable research effort attempting to explain these patterns for fish assemblages. This has led to a good understanding of ecological concepts such as species distribution or abundance, yet questions remain on the drivers of small-scale, community-level processes (Sale 2013). Large scale patterns in distribution and dispersion are strongly affected by biogeographical history (Cowman et al. 2013; Bowen et al. 2016), but also by genetic diversity and ecological plasticity (DiBattista et al. 2015). On a smaller scale, species composition is more affected by environmental variables such as microhabitat (Messmer et al. 2011), depth (Bridge et al. 2016), and reef zonation (Depczynski and Bellwood 2005). On an even finer scale, interactions between species and differing trophic roles are central in structuring fish communities (Griffin et al. 2008; Levine and HilleRisLambers 2009). At this level, cryptobenthic fishes play an important role in shaping the trophodynamics of coral reef systems (Depczynski and Bellwood 2003; Ackerman et al. 2004). These small-sized species provide a crucial link in the base of the food chain through high abundances and rapid generational turnover rates (Depczynski and Bellwood 2006). Therefore, understanding what drives patterns in the composition and distribution of cryptobenthic fish assemblages can help us understand what drives patterns in the entire fish assemblage (Coker et al. 2018).

Cryptobenthic fish are small fishes (typically less than 50 mm Total Length (TL)) that are associated with the seabed, and which are visually or behaviourally cryptic (Goatley and Brandl 2017). On coral reefs they are the most abundant guild of reef fishes and have short life cycles with quick generational turnover rates (Lefèvre et al. 2016). Most species have small home ranges, resulting in a high diversity and big differences in community composition on small spatial scales, as seen in the Red Sea (Coker et al. 2018). Many cryptobenthic species are habitat specialists associated with a preferred microhabitat (Depczynski and Bellwood 2004; Ahmadia et al. 2012). This dependence on microhabitats drives many cryptobenthic assemblages, and habitat associations are phylogenetically conserved over large timescales (Ahmadia et al. 2018). Cryptobenthic fish assemblages are often strongly depth structured (Dalben and Floeter 2012). As a result, cryptobenthic fish assemblages can vary greatly between different reef zones. On the Great Barrier Reef for example, sandy and rubbly habitats had a higher abundance and diversity than open coral reefs (Depczynski and Bellwood 2005). On a biogeographical scale, cryptobenthic fishes show distinct regional assemblages that increase in diversity with decreasing latitude (Brandl et al. 2017).

Biogeographical history affects taxonomic composition of fishes, but the functional composition of fish assemblages is more strongly defined by the habitat they live in (Hemingson and Bellwood 2017). Hemingson and Bellwood (2017) studied three dominant shallow-water marine habitats in the tropics; coral reefs, mangroves, and seagrass beds. Many other studies have investigated species assemblages in these "dominant" habitats, but very few have included one of the most extensive marine habitats in shallow waters: soft sediment (e.g., Travers et al. 2010; Schultz et al. 2012). Because of their close association with the seabed, the composition of cryptobenthic species assemblages are highly dependent on available habitat (Munday 2004; Depczynski and Bellwood 2005; Ahmadia et al. 2012). Therefore, it is expected that cryptobenthic fish assemblages on soft sediment habitats will differ markedly from other, better studied, habitats such as mangroves, seagrass beds, or coral reefs.

Soft sediment habitats (muds, sand, and gravel) make up to 55% of the shallow coastal areas in the coral triangle (Hayes 1967). Faunal assemblages on these habitats have received limited research attention. Research on coral rubble habitats exists; while these resemble gravel habitats, they are typically associated with degraded reefs (e.g., Bellwood and Fulton 2008; Enochs and Manzello 2012; Bailey-Brock et al. 2007). However, not all soft sediment habitats are degraded reefs or seagrass sites (Nyström et al. 2012). The absence of complex biological structures indicates that environmental factors prevent the development of more complex habitats, rather than the disappearance of these habitats by anthropogenic impacts (Gray and Elliott 2009). As such, some soft sediment sites could be considered to be as 'pristine' as untouched coral reefs. The lack of physical complexity typical for soft sediment habitats make them challenging environments for fish to thrive in. In terms of fish fauna, soft sediment habitats have been considered to be 'depauparate' habitats (e.g. Depczynski and Bellwood (2004)), yet they are important as nursery grounds for commercially important species (Hatcher et al. 1989). Since soft sediment habitats differ so strongly from other systems, it has been argued that different paradigms are needed to understand drivers of species assemblages (Wilson 1990).

To date, research on soft sediment habitats has predominantly focused on infaunal invertebrate assemblages (Alongi 1990; Gray 2002; Gray and Elliott 2009). Grain size and related variables such as sorting have been shown to be important environmental factors driving infaunal communities (Gray 2002; Gray and Elliott 2009). Variations in benthic cover or grain size can offer refuge or suitable habitat and has been shown to affect fish assemblages (Langlois et al. 2006; van Denderen et al. 2014; Schultz et al. 2015). Cryptobenthic fish fauna on coral reefs and sub-tropical reefs depends on specific microhabitats for shelter or food (Munday 2004; Ahmadia et al. 2018). Despite extensive work done on invertebrate communities on soft sediment, and cryptobenthic fishes on coral reefs, there is a paucity of data on cryptobenthic fish communities on soft sediment habitats, particularly in the tropics (Alongi 1989, Gray 2002; Schultz et al. 2012).

Our limited knowledge about the most common coastal habitat is a critical knowledge gap, as soft sediment habitats play a vital role in supporting livelihoods of coastal communities. Southeast Asia has the highest marine biodiversity in the world (Hoeksema 2007; Allen 2008), yet less than 25% of the fishery production in Southeast Asia depends on coral reef fishes, but focuses on pelagic or soft sediment associated species such as scad (*Selar* spp.) and sardines (*Clupeidae*) instead (Clifton and Foale 2017). Scuba dive tourism on soft sediment habitat is worth more than USD $150 million year-1 and employs over 2000 people in Indonesia and

Philippines (De Brauwer et al. 2017). The ecology of species driving tourism is poorly understood and their conservation status is often unknown (De Brauwer and Burton 2018).

This study aims to investigate cryptobenthic fish assemblages and diversity on soft sediment habitats in the centre of tropical marine biodiversity, Southeast Asia. This study focusses on sites where local coastal communities are dependent on soft sediment habitats for their livelihoods. In particular we investigated 1) regional differences in fish assemblages and species diversity; and 2) the role of benthic cover, sediment grain size characteristics, and depth in driving differences in fish assemblages.

4.3 Methods

4.3.1 Cryptobenthic fishes

Cryptobenthic fishes on coral reefs have been defined as species that "closely resemble a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral" (Randall 2005), or species that are "typically less than 5 cm long that are visually or behaviourally cryptic, and live near to or within the seabed" (Goatley and Brandl 2017). Recent work further emphasised the importance of small adult size when defining cryptobenthic reef fishes, rather than their benthic position (Brandl et al. 2018). Due to the unique characteristics of soft sediment habitats compared to reefs, we extended this definition to also including larger cryptic species that live in close association with the benthos (e.g. stargazers (*Uranoscopidae*) and frogfishes (*Antennariidae*)), as they form an important part of the cryptobenthic fish communities in these ecosystems.

The two most commonly found cryptobenthic fish families (*Gobiidae*, *Blenniidae*) on coral reefs were not included in surveys despite their abundance on soft sediment habitats. The decision not to include this important group was taken due to the logistical constraints of sampling these families. Soft sediment *Gobiidae* and *Blenniidae* exhibit rapid predator avoidance responses in which they retreat into burrows in the sediment, making reliable species identification during visual surveys nearly impossible. These families are best sampled with ichthyocides (such as rotenone or clove oil), which is prohibited in the majority of the locations surveyed for this research.

4.3.2 Study sites

Surveys were conducted in three regions across Southeast Asia where soft sediment sites are important in supporting local livelihoods through tourism or sustenance fishing: Dauin (Philippines), Lembeh Strait (Indonesia), Bali (Indonesia). Five sites were surveyed in Dauin, seven sites in Lembeh, eight in Bali (Figure 4.1). All sites were slopes (slope angle approximately 40 - 50 degrees), consisting mainly of black or dark brown volcanic sand. Sites were in locations where “muck dive” tourism was present, although three surveyed sites (sites 4, 15, and 16) were not considered to be dive sites by tourism operators, and thus receive limited numbers of divers.

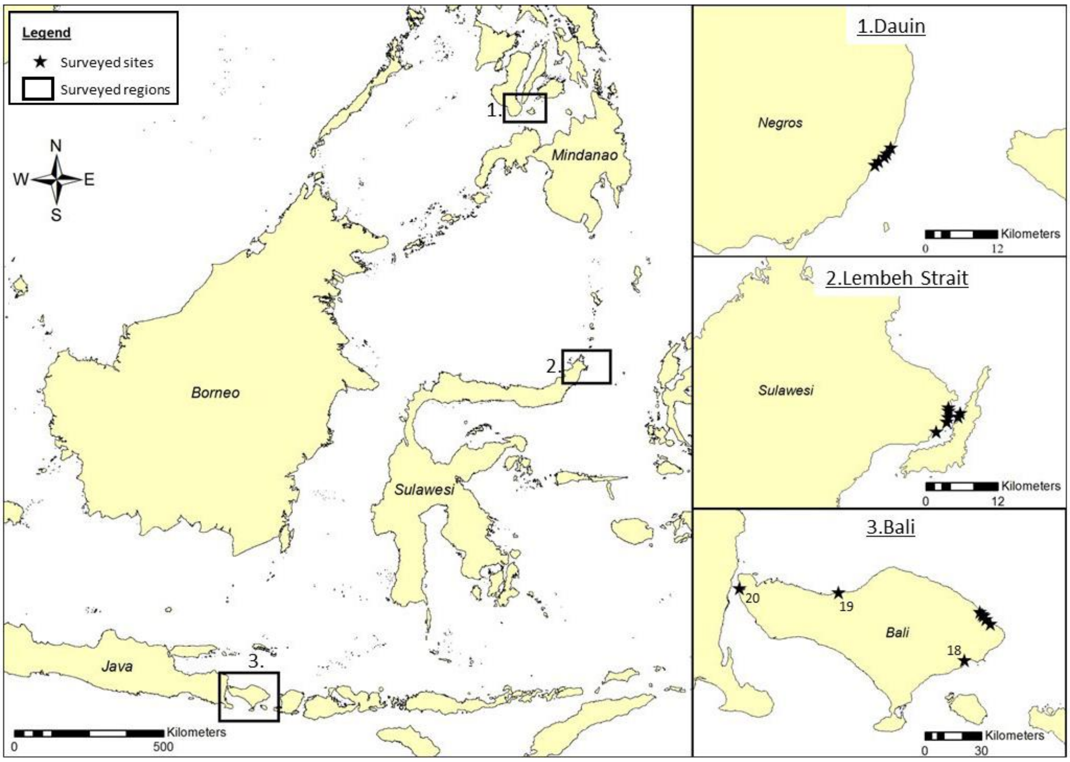


Figure 4.1 Map of survey sites.

4.3.2.1 Dauin

Dauin (9° 11' 22" N, 123° 16' 56" E) is a coastal town in southern Negros, Philippines with a growing dive tourism industry (De Brauwer et al. 2017). The underwater seascape consists mainly of volcanic sand slopes, with occasional widely interspersed small coral reef patch reefs and seagrass growth in some of the shallow areas. Five sites were surveyed in Dauin in May 2015 (Table in Appendices).

4.3.2.2 Lembeh Strait

Lembeh Strait (1° 28' 22" N, 125° 14' 26" E) in North-Sulawesi (Indonesia) is one of the world’s most popular muck dive destinations (De Brauwer et al. 2017). The area is a narrow strait between Lembeh Island and the North-Sulawesi mainland, subjected to strong daily tidal currents. The strait consists of multiple bays with black sand slopes, alternated with small coral reefs on the current-swept capes. A large industrial port city (Bitung) on the mainland is situated in the centre of the strait. Seven sites were surveyed in Lembeh strait in July 2015 (Table in Appendices).

4.3.2.3 Bali

Bali (8° 19' 51" S, 115° 38' 54" E) is Indonesia's most popular tourist destination, with most tourism occurring in the south and centre of the island (Sanders and Willson 2017). Surveys in Bali were done on sites on the northeast coast, one site on the east coast and two sites on the northwest coast. Sites were slopes predominantly consisting of black volcanic sand. One site (site 20) was a protected sandy lagoon, one site (site 18) had a large jetty running through the middle of the surveyed area. Eight sites were surveyed in Bali between August and September 2015 (Table in Appendices).

4.3.3 Surveys

4.3.3.1 Fish assemblages

Underwater Visual Census (UVC) surveys were conducted by two SCUBA divers using 25 m x 2 m belt transects parallel to the shoreline. The width of belt transects was reduced compared to standard 5 m wide UVC belt transects, to more efficiently detect cryptic species (McCormick and Choat 1987; Bozec et al. 2011). At each site, five transects were conducted at 16 m water depth, and five transects at 6 m depth, unless this was not possible due to site topography or weather conditions. The same observer (MDB) surveyed fish fauna for all transects by passing over the transect line twice, recording species and abundance. The initial pass was done while laying out the transect line and detected mobile species with the tendency to flee divers (e.g. *Trichonotidae*, *Callionymidae*). The second pass was at a slower speed and aimed to detect less mobile and smaller species (e.g. *Antennaridae*, *Syngnathidae*).

4.3.3.2 Diversity roving diver surveys

Additional roving diver surveys were conducted on each site to account for rare species that would remain undetected during UVCs (Schmitt et al. 2002). Roving surveys were conducted as a separate third dive after completing the UVC transects at both depths. The site, including the entire area surveyed during UVC transects, was surveyed by descending to 20 m deep and then slowly ascending the site in a zigzag-pattern, scanning for target species. A maximum total dive time of 70 minutes was set as a limit for roving surveys. During the roving diversity surveys species not yet detected during the initial UVC transects were recorded. Presence data only were recorded, no abundance data were recorded during these surveys.

To allow for comparison with other studies, abundance and diversity data was compiled from recently published literature on cryptobenthic fishes. Abundance was standardised to 100 m^2, but diversity was kept for the entire study area as described in each paper.

4.3.4 Environmental variables

4.3.4.1 Benthic cover

To measure benthic cover, a photo was taken of the substrate at every meter of the transect (26 photos per transect) after finishing each UVC transect swim, ensuring the tape measure was visible in each photo. Photos of the substrate were analysed using Coral Point Count (CPCe 4.1) software (Kohler and Gill 2006). Based on the tape measure visible in the photos, 30 cm x 30 cm quadrats were transposed over each photo. Twenty points were randomly placed inside the quadrat and classified into different categories (Description of categories in Appendices). This approach allowed for a benthic cover resolution of 520 points per 50 m^2 transect (5200 per site).

4.3.4.2 Sediment grainsize characteristics

For each transect 100 g of sediment was collected from the top layer (5 cm) of the substrate. Sediment samples were air-dried and organic material removed prior to sediment analyses in Australia (to comply with Australian customs requirements). Dry sediment samples from Dauin were weighed, and then divided into 6 size classes using wet sieving (Syvitski 2007). Each size class oven dried for 48 hours, after which each size class was weighed again. Dry sediment samples from Lembeh Strait and Bali were weighed and then dry sieved to remove the coarse fraction (>2000 µm). The remaining fraction was then analysed using laser diffraction with a Malvern Mastersizer 2000. Both methods have been shown to yield similar results and can be used and compared for the type of sediment in the survey sites (Singer et al. 1988; Loizeau et al. 1994). A full list of all grainsize characteristics that were quantified can be found in supplementary materials (Table in Appendices).

4.3.5 Data analysis

4.3.5.1 Environmental variables

Benthic cover was calculated using CPCe analysis (Kohler and Gill 2006). Grainsize characteristics were analysed using Excel GRADISTAT 4.0 (Blott and Pye 2001). Environmental data were averaged for each depth per site, normalised, and a Euclidean distance resemblance matrix was constructed in PRIMER. Differences between environmental variables were tested using PERMANOVA in Primer, based on a two factor design (Region

(Fixed), Depth (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Pairwise PERMANOVA tests were conducted when the main test showed significant differences.

4.3.5.2 Fish assemblages

Analyses of soft sediment cryptobenthic fish assemblages were conducted with the PRIMER 7 package (Clarke and Gorley 2015). Fish assemblage analyses used UVC data only, as roving diver surveys did not measure abundance. Data for each site were pooled for deep and shallow transects, making site the replication unit for each region. Abundance data met assumptions of homogeneity of variance, so untransformed abundance data were used to construct a zero-adjusted Bray-Curtis resemblance matrix. We tested the differences between assemblages using PERMANOVA based on a two factor design (Region (Fixed), Depth (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Subsequent pairwise PERMANOVA tests were conducted to compare Regions, and Depth differences between and within regions.

Patterns in the data were visualised using Principal Coordinate Analysis (PCO), followed by a constrained Canonical Analysis of Principal Coordinates (CAP) (Anderson and Robinson 2003; Anderson and Willis 2003). PCO is an unconstrained analysis, visualising the largest differences between sites without applying a priori hypotheses, and thus showing broad patterns in abundance data. CAP is a constrained analysis which tests for a specific hypothesis, i.e. differences between regions in this study (Anderson and Willis 2003). Leave-one-out allocation success tests gave an estimate of how samples were allocated to distinct regions. This gave an estimate of how distinct assemblages were at each region (Anderson and Willis 2003). The CAP plots were then overlayed with vectors illustrating the species that were most strongly correlated to the observed difference (Pearson’s correlation value > ±0.5).

Distance based linear models (DistLM) were calculated to test the role of environmental variables in assemblage patterns, using the “best” selection procedure and the Akiake Information Criterion (AIC). Predictor environmental variables were first averaged per site and depth, then normalised. We tested correlations between environmental variables by constructing a draftsman plot. Variables which were strongly correlated (> ±0.8) were excluded, in this case we excluded the predictor variables Skewness, Kurtosis, Median Grainsize, and percent cover of Gravel from analysis. The assemblage was plotted using a distance based Redundancy Analysis (dbRDA) and overlayed with dominant predictor variables (Pearson’s correlation > ±0.4).

4.3.5.3 Fish species diversity

Presence / absence data for species diversity used species lists collated from the combined UVC and roving diver surveys. Using the PRIMER 7 software package (Clarke and Gorley 2015), a Jaccard resemblance matrix was constructed on the presence / absence data. General differences in fish diversity between regions were tested using PERMANOVA (one factor: Region (Fixed)), with a permutation of data under a reduced model, running 9999 permutations. Further pairwise PERMANOVA tests were then conducted to compare the different regions. Data were visualised using PCO and CAP following the same procedure as for the fish assemblages (Anderson and Willis 2003). The CAP plots were then overlayed with species that were most strongly correlated to the observed difference (Pearson's correlation value > ±0.7)

Distance based linear models were calculated to test the role of environmental variables in driving diversity patterns, using the same procedure as described above. For this analysis, the strongly correlated (> ±0.8) variables excluded were Skewness, Kurtosis, and Percent cover of gravel. The results were plotted using a distance based Redundancy Analysis (dbRDA) and overlayed with dominant predictor variables (Pearson's correlation > ±0.4).

4.4 Results

4.4.1 Summary statistics

A total of 187 transects were conducted across 20 sites (Dauin: 5, Lembeh: 7, Bali: 8). In Bali there were two sites where it was only possible to collect data at one depth for two sites (site 20: 6 m, site 18: 16 m). At one site in Bali (site 17) only two transects were possible in the shallow area as the habitat beyond these transects consisted of dense coral reefs and was therefore beyond the scope of this research project (Table in Appendices). During the surveys, a total of 112 different cryptobenthic fish species were observed (Dauin: 48 species, Lembeh: 73 species, Bali: 71 species). The average fish abundance was 93 individuals (± SE: 28) per site (500 m^2) (Dauin: 235 ± SE: 74, Lembeh: 33 ± SE: 6, Bali: 57 ± SE: 27). The most common species in all regions was *Trichonotus elegans* (Full species list in Appendices).

Comparisons with published research showed that cryptobenthic species richness recorded in this study was higher than most surveys on tropical coral reefs, except for one study on the Great Barrier Reef (Table 4.1). Other studies in subtropical or temperate regions similarly reported lower species numbers than this study (Table 4.1). Abundance, however, was up to three orders of magnitude smaller than in previous studies (Table 4.1).

Table 4.1 Comparison of cryptobenthic fish diversity and abundance in different habitats and locations based on published literature. Studies are ranked from highest to lowest diversity (= species richness). Abundance has been standardised to 100m^2 when data was available in the original study.

Country	Location	Habitat	Method	Diversity	Abundance (100m^2)	Reference
Australia	Great Barrier Reef	Coral reef	Clove oil	79	3070	Goatley et al. 2016
Indonesia	Lembeh Strait	Soft sediment	UVC	73	7	This study
Indonesia	Bali	Soft sediment	UVC	71	10	This study
Indonesia	Hoga Island	Coral reef	Clove oil	50	833	Ahmadia et al. 2012
Philippines	Dauin	Soft sediment	UVC	48	47	This study
Australia	Great Barrier Reef	Coral reef	Clove oil	48	N/A	Depczynski and Bellw
Indonesia	Hoga Island	Coral reef	Clove oil	47	1111	Ahmadia et al. 2018
Micronesia	Pohnpei	Coral reef	Clove oil	46	1389	Ahmadia et al. 2018
Australia	Great Barrier Reef	Coral reef	Clove oil	42	N/A	Depczynski and Bellw
Mexico	Baja California	Rocky reef	UVC	40	2560	Galland et al. 2017
Croatia	Cape Silo	Rocky reef	Quinaldine	27	600	Kovačić et al. 2012
French Polynesia	Moorea	Coral reef	Clove oil	22	1667	Ahmadia et al. 2018
Belize	Belizean Barrier Reef	Dock pilings	Clove oil	21	N/A	Brandl et al. 2017
USA	4 locations	Dock pilings	Clove oil	19	N/A	Brandl et al. 2017
Panama	Bocas, Punta Caracol	Dock pilings	Clove oil	14	N/A	Brandl et al. 2017

Benthic cover consisted mostly of unconsolidated sediments (sand, gravel, pebbles, coral rubble), with a mean cover of 90.1% (± SE: 0.7%) across all sites. Marine plants and natural debris were the other principal components of the benthic cover at 5.6% (± SE: 0.5%) and 3.5% (± SE: 0.3%) respectively. Mean coral cover was very low across sites (0.3% ± SE: 0.05%), with little difference between regions (Table and Figure in Appendices).

The sediment was predominantly poorly sorted ($\sigma = 0.975\ \varphi$), gravelly sand (Figure 4.2). Grain size distribution was fine skewed, coarse sand and was platykurtic with a bimodal distribution. The mean grain size was 817.4 μm, and distribution of particles (D10 – D90) ranged from 269.6 μm to 2148.6 μm.

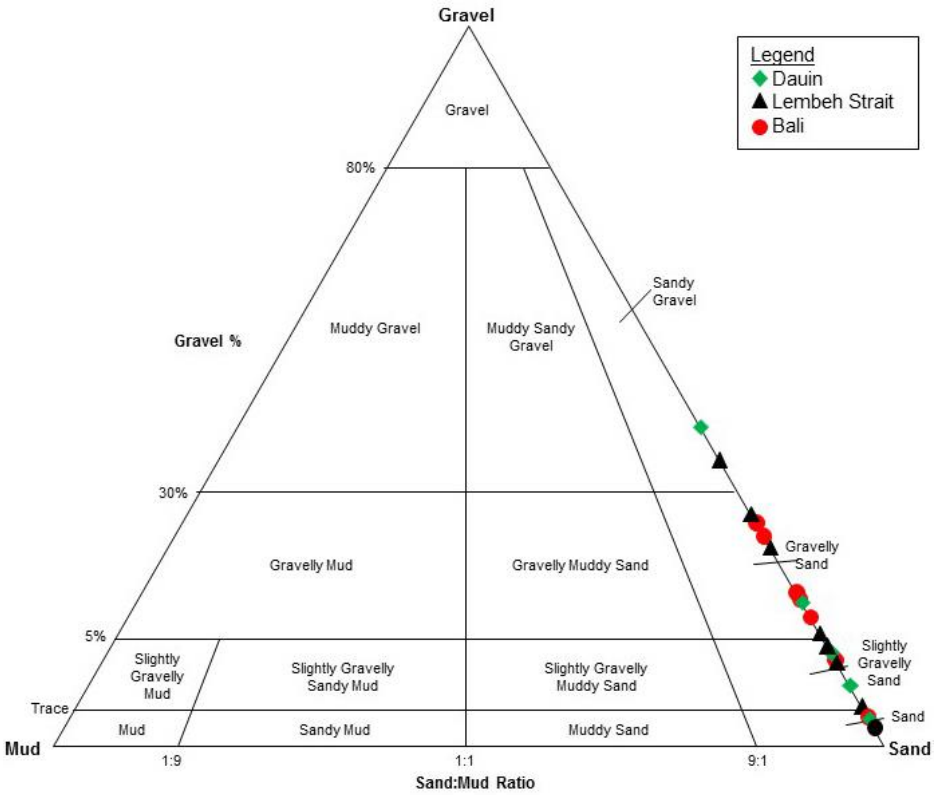


Figure 4.2 Folk sediment classification for 20 soft sediment sites surveyed in Southeast Asia.

Multivariate PERMANOVA analyses indicated statistical differences between environmental variables on the level of region, but not between different depths, nor was there a Region x Depth interaction (Table 4.2). Pairwise analyses for region indicated differences between Lembeh and Dauin ($p = 0.05$, t: 1.5), and Lembeh and Bali ($p = 0.02$, t: 1.6), but not between Dauin and Bali ($p = 0.40$, t: 1.0).

4.4.2 Fish assemblages

PERMANOVA tests of species assemblages and abundance indicated significant differences between the regions, depth, and a region x depth interaction (Table 4.2). Differences in depth were driven by site x depth interactions in Dauin ($p = 0.02$, t: 1.6) and Bali ($p = 0.02$, t: 1.4), but there was no effect of depth in Lembeh ($p = 0.19$, t: 1.2). Pairwise analyses between regions showed that the species assemblages of all regions were significantly different from each other (Dauin – Lembeh: $p < 0.001$, t: 2.2, Dauin – Bali: $p < 0.001$, t: 2.2; Lembeh – Bali: $p < 0.001$, t: 1.7).

Table 4.2 Results of multivariate PERMANOVA analyses of environmental variables, fish assemblages and fish diversity on soft sediment habitats in Southeast Asia. Values in bold show significance at P < 0.05.

Factor	*df*	MS	*Pseudo-F*	*P*
Environmental variables				
Region	2	19.3	1.8	0.04
Depth	1	11.9	1.1	0.32
Region x Depth	2	8.0	0.7	0.72
Fish assemblage				
Region	2	13208	4.0	<0.001
Depth	1	6869	2.1	0.002
Region x Depth	2	5944.1	1.8	0.002
Fish diversity				
Region	2	7251	2.7	<0.001

The principal coordinate analysis illustrated clear patterns in the fish assemblages (Figure 4.3A). The different regions separated out with minor overlap. Shallow sites in Bali and Dauin were different from deep ones, which was not the case in Lembeh. A hypothesis-driven constrained ordination (CAP) was then applied since the PERMANOVA analyses indicated significant differences in regions (Figure 4.3B). The CAP plot indicated a clear separation between regions and a separation between depths in Dauin (Figure 4.3B). Differences seen between sites were mainly driven by *Antennarius pictus*, *Cymolutes torquatus* and *Callionymus superbus* in Dauin (Figure 3B). The allocation success for each region was very high, Dauin (100%), Lembeh (85.7%), Bali (71.4%) (Trace statistic: 1.70; p < 0.001) which confirms that the fish assemblage at each location is distinct (Anderson and Willis 2003).

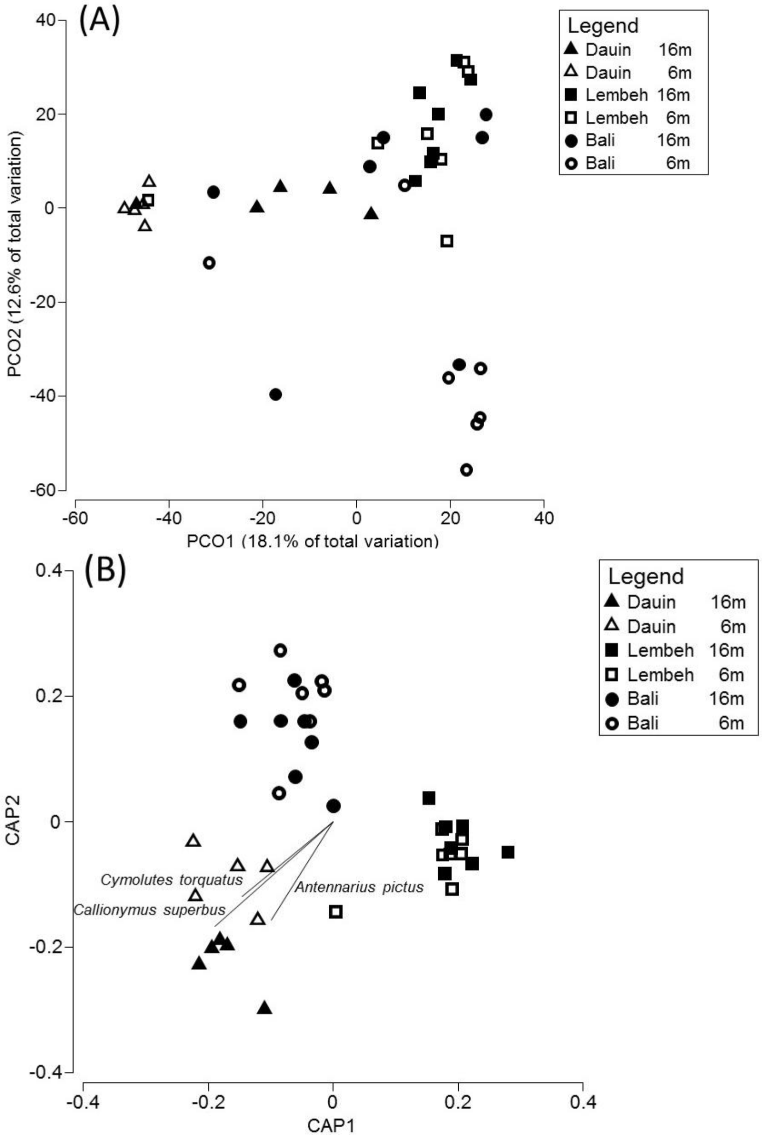


Figure 4.3 A) Principal Component Ordination of fish assemblages at different depths in three regions in Southeast Asia. B) constrained Canonical Analysis of Principal Coordinates (CAP) of these same fish assemblages for the interactions between regions, species overlayed with Pearson R correlation to either axis of value > ±0.5.

The DistLM procedure to test the contributions of different habitat variables resulted in a final model which explained 25% of the variation seen in the assemblage and included five variables. These variables included two components of benthic cover (Sand: 4.9%, Plants: 7.0%) and three sediment grain characteristics (mean grain size: 5.3%, D10: 4.1%, and D90: 4.2%) (AIC = 315.8, R^2 = 0.250) (Table 4.2). D10 and D90 are both measures of the distribution of sediment particle size, indicating that respectively 10% and 90% of the volume of measured sediment is contained below that grainsize. The dbRDA illustrates limited separation of cryptobenthic fish assemblages explained by these environmental variables, indicated by the limited separation between the different depths and regions (25% explained; Figure 4.4).

Table 4.3 Contribution of different habitat variables to cryptobenthic fish assemblages (abundance + diversity) on soft sediment sites in Southeast Asia: results of Distance based Linear model in Primer. Variables in bold were included in final model.

Variable	SS (trace)	Pseudo-F	P	Proportion
AIC = 315.8, R^2 = 0.250, No. of variables = 5				
% Sand	**7322.2**	**1.85**	**0.02**	**0.049**
% Pebbles	6619.2	1.66	0.03	0.044
% Plants	**10510**	**2.71**	**<0.001**	**0.070**
% Artificial objects	2814.5	0.69	0.86	0.019
% Natural Debris	6512.3	1.63	0.01	0.043
% Coral	5231.9	1.30	0.11	0.035
% Sponges	6661.8	1.67	0.03	0.044
Mean grain size	**7931.7**	**2.01**	**0.01**	**0.053**
D10	**6208.3**	**1.55**	**0.05**	**0.041**
D90	**6249.9**	**1.56**	**0.05**	**0.042**
Sorting	3765	0.93	0.53	0.025

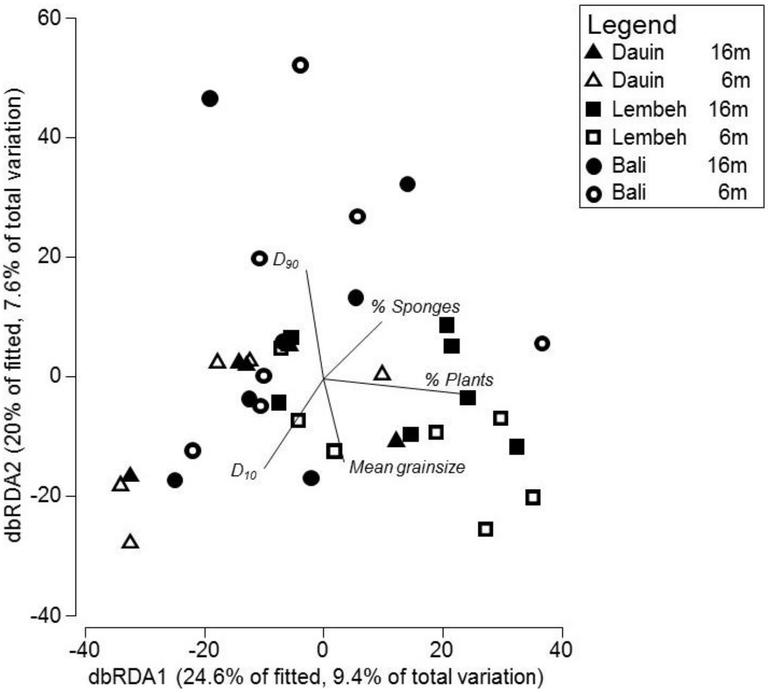


Figure 4.4 Distance based Redundancy Analysis plot of soft sediment fish assemblages (abundance + diversity) in three regions in Southeast Asia, overlayed with environmental variables responsible for changes in the assemblage.

4.4.3 Species diversity

The roving diver surveys detected 34 species that were not observed during the UVC surveys (30.4% increase). The PERMANOVA tests of combined species diversity of UVC transects and roving diver surveys showed significant differences between each of the three regions (Table 4.2). The PCO showed clear differentiation between the different regions, but two sites in Bali (18 and 20) clustered closer to the Lembeh region than to Bali (Figure 4.5A). The hypothesis driven CAP analysis confirmed a strong regional separation in diversity (Trace statistic: 1.78, $p < 0.001$; Figure 5B). There was a very high regional allocation success

(Lembeh: 100%, Dauin: 100%, Bali: 75%), reconfirming the regional distinctness of species richness.

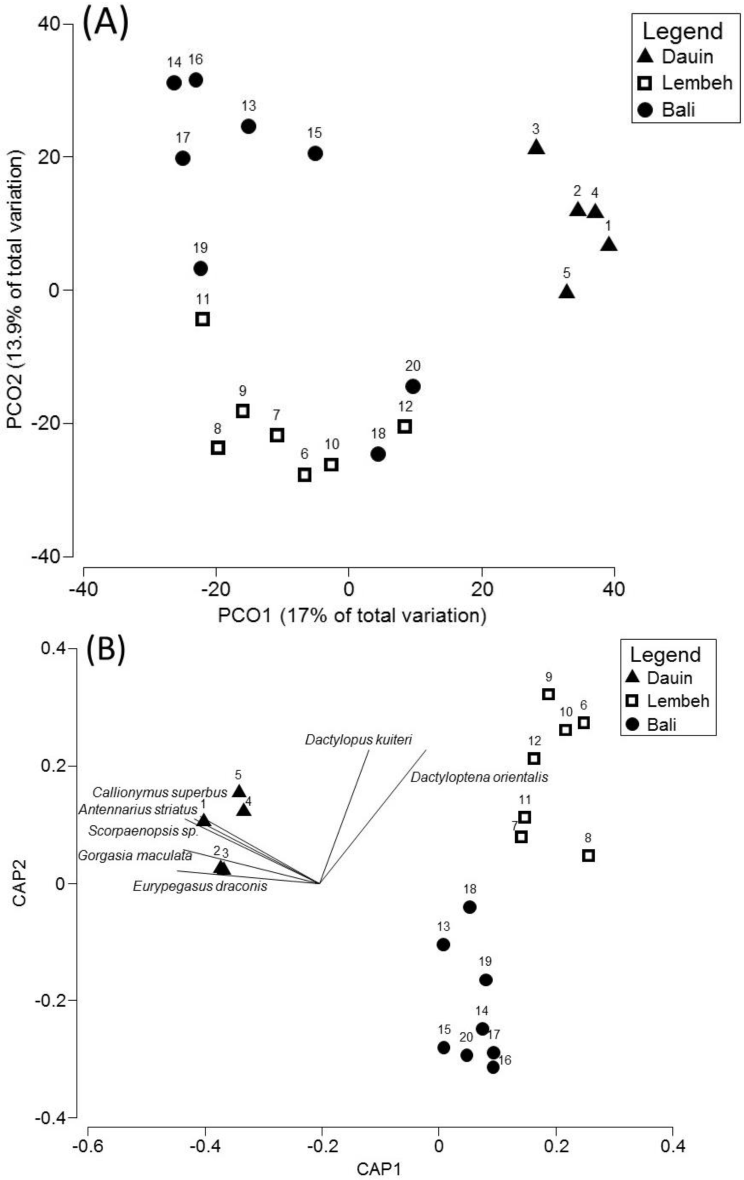


Figure 4.5 A) Principal Component Ordination of fish diversity in three regions in Southeast Asia. B) constrained Canonical Analysis of Principal Coordinates (CAP) of these same fish assemblages for the interactions between regions, species overlayed with Pearson R value > ±0.7.

The best model identified using Distlm explained 33.5% (R2 = 0.335, AIC = 163.7) of species diversity (Table 4.4). The final model included five variables: percent cover of sand (5% variation explained) and plants (9%), mean grainsize (4%), D10 (4%), and D90 (4%) (Table 4.4). The dbRDA plot showed a clear differentiation between the three different regions (Figure 4.6).

Table 4.4 Contribution of different habitat variables to cryptobenthic fish diversity on soft sediment sites in Southeast Asia: results of Distance based Linear model in Primer. Variables in bold were included in final model.

Variable	SS (trace)	Pseudo-F	P	Proportion
AIC = 163.7, R^2 = 0.335, No. of variables = 5				
% Sand	**3022.8**	**0.968**	**0.49**	**0.05**
% Pebbles	3847.8	1.250	0.15	0.06
% Plants	**5147.5**	**1.712**	**0.01**	**0.09**
% Artificial objects	2826.9	0.902	0.60	0.05
% Natural Debris	3225.8	1.04	0.42	0.05
% Coral	3118.8	0.999	0.46	0.05
% Sponges	3110.7	0.998	0.46	0.05
Mean grain size	**2571.4**	**0.817**	**0.76**	**0.04**
D10	**2489.2**	**0.789**	**0.81**	**0.04**
Median grain size	2538.6	0.806	0.78	0.04
D90	**3783.2**	**1.227**	**0.17**	**0.06**

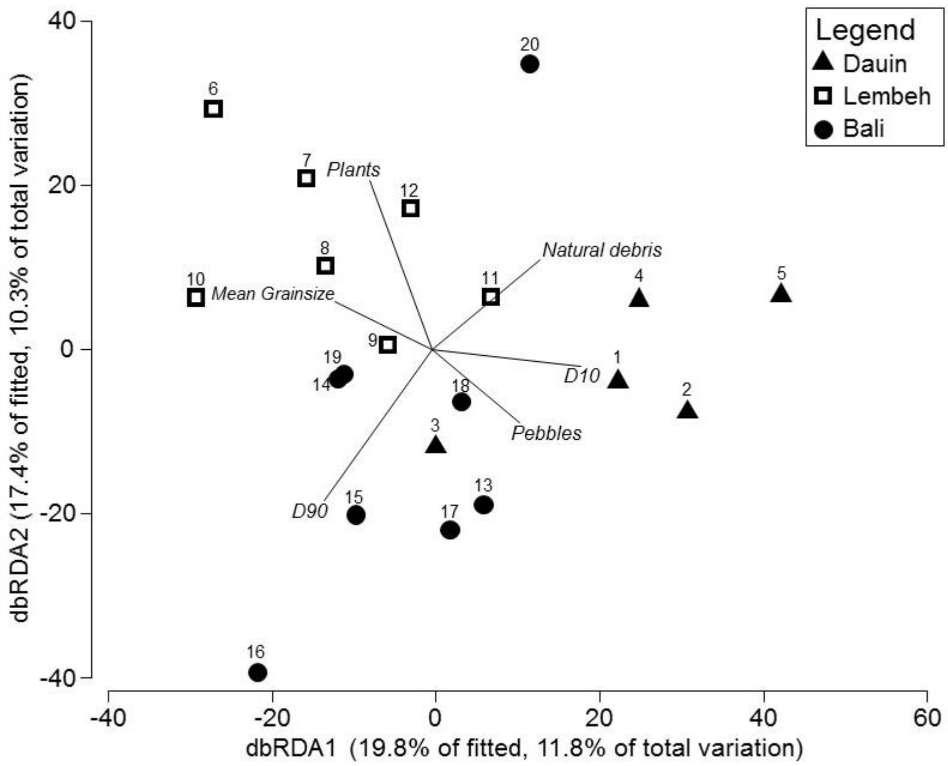


Figure 4.6 Distance based Redundancy Analysis plot of soft sediment fish diversity in three regions in Southeast Asia, overlayed with environmental variables responsible for changes in the assemblage.

4.5 Discussion

Cryptobenthic fishes are highly abundant and play an important role in the trophodynamics of coral reefs, but their assemblage composition on coastal soft sediment habitats is poorly understood. To our knowledge, this study is the first to extensively survey cryptobenthic fish assemblages on tropical infralittoral soft sediments. Our results showed that cryptobenthic fish diversity is considerably higher than what is currently assumed in the literature. Fish abundance, however, was much lower than on coral reefs. Strong regional differences existed in fish assemblages and species diversity, but the environmental variables tested had limited power to explain the observed patterns in fish assemblages. This is likely because similar habitat types were sampled at all of the sites, and there was little variation in sediment characteristics. Overall, these findings suggest that soft sediment habitats in Southeast Asia are far richer in fish diversity than previously assumed, which has important implications for future management.

Despite the current view of soft sediment habitats as depauparate communities, we found strikingly high fish diversity compared to other habitats. Cryptobenthic fish diversity on the sites surveyed in this study was higher than on many coral reefs. Studies on the Great Barrier Reef and Indonesian reefs found either similar or lower diversities (Depczynski and Bellwood 2003; Depczynski and Bellwood 2004; Ahmadia et al. 2012; Goatley et al. 2016). Research across a latitudinal gradient on dock pilings in America found the highest diversity in the tropics, yet the highest recorded number of species was a third lower than this study (Brandl et al. 2017). Studies in subtropical or temperate regions reported lower diversities than this study (Kovačić et al. 2012; Galland et al. 2017). The highest diversity in this study was found in North Sulawesi, the region closest to the centre of the coral triangle, and known to have the highest global fish diversity on coral reefs (Allen 2008). This study suggests that the high fish diversity extends beyond coral reefs and includes different habitats, indicating regional biogeographical drivers of high diversity rather than small-scale local processes (Ahmadia et al. 2018).

While the diversity was higher than most other cryptobenthic fish assemblages across the world, fish abundance much smaller than in previous studies on more complex habitats (e.g. Kovačić et al. 2012; Goatley et al. 2016; Ahmadia et al. 2018). Abundances differed across regions and the region with lowest diversity showing the highest fish abundance. Low abundances were expected as surveyed sites showed very limited physical complexity, making them a fundamentally more hostile environment (Hemingson and Bellwood 2017). Lack of available microhabitat increases predatory pressure by decreasing shelter, thus increasing predation mortality (Depczynski and Bellwood 2004). Furthermore, variations in structural complexity can influence invertebrate prey diversity and abundance, which is in turn likely to affect fish abundance (Kramer et al. 2013; Kramer et al. 2014).

The environmental factors tested to investigate the effect of variations in microhabitat did not explain a large proportion of the variation in assemblages. Grainsize characteristics can directly influence habitat or food availability by increasing complexity and interstitial space (Gray and Elliott 2009), but they can also reflect hydrodynamic energy (e.g. waves, currents) in the water (Trenhaile et al. 1996). Relative to the spectrum of soft sediment habitats (which ranges from mud to sand and gravel), the surveyed locations had little variation in sediment grain characteristics. Despite the small scale of these differences, measurements of particle size did explain variation in the assemblage. D10 and D90 are both measures of the distribution of sediment particle size, indicating that respectively 10% and 90% of the volume of measured sediment is contained below that grainsize, or whether sand is distributed more towards the fine or the coarse end of the spectrum. Their importance in the models highlights the influence of grain size. Larger differences in grainsize, for example on muddy sediments, would be expected to drive a much more significant change in fish assemblage.

Benthic cover on all sites consisted predominantly of sand or gravel. Non-sediment cover was dominated by plant matter (algae or seagrasses in this study) or natural debris (leaves, wood, etc.). Models indicated that plant and sand cover had the strongest effect on fish assemblages. Besides influencing the amount of available shelter, plant growth might be linked to primary productivity and available light level or nutrients (Gray and Elliott 2009). The availability of complex habitat may have both positive and negative influences on soft sediment associated cryptobenthic fishes, depending on the species. Differences in the physical complexity on soft sediment appear limited compared to coral reefs, but can be high enough to make a difference for the small fish species found in these habitats. For sand associated specialist species such as Trichonotus spp. or Callionymus spp., high sand cover might mean a decrease in competition with species less adapted to sandy bottoms (Sogard 1984; Clark and Pohle 1996).

It is likely that other factors drive fish assemblages on soft sediment. Previous studies of cryptobenthic fish on dock pilings showed low predictive power from habitat, but strong regional differentiation (Brandl et al. 2017). Besides biogeographical history, another factor that might play a role is the distance to nearby reefs, or “halo effect” (Langlois et al. 2005). The halo effect predicts that interactions between reefs and soft sediment can cause changes in faunal abundance depending on the distance from reefs. This effect has been observed in temperate regions, but remains to be comprehensively tested for tropical soft sediment fish assemblages (Schultz et al. 2012). The presence of such a halo effect in soft sediment fish fauna might indicate how strongly some coral reef predators rely on soft sediments for prey.

Due to legislations restricting the use of ichthyocides, this study did not use rotenone or other destructive sampling methods which are typically used when assessing cryptobenthic fish fauna (Ackerman and Bellwood 2002; Kovačić et al. 2012; Brandl et al. 2017; Coker et al. 2018). As a result, the species that dominate cryptobenthic fish assemblages on coral or rocky reefs (e.g. Gobiidae) were excluded from this study. The real diversity on soft sediment is therefore higher than described in this study, this is supported by the strong increase in number of species detected during roving diver surveys. Abundances might likewise be higher, though it remains unlikely to approach abundance levels of sites with higher complexity. Non-destructive sampling of cryptobenthic fauna remains a challenge, although alternative methods have been proposed. Absence/presence surveys with increased detection probabilities can be beneficial for conservation planning for rare or cryptic species such as seahorses (Aylesworth et al. 2017). Environmental DNA (eDNA) surveys allow for cost-effective sampling of the entire fish community, yet require more fine-tuning to increase reliability for cryptobenthic species (DiBattista et al. 2017). Alternatively, fluorescence in cryptic fishes has been used to successfully survey triplefins and pygmy seahorses on coral reefs (De Brauwer et al. 2018). It remains to be tested which of the above methods would be most suitable for soft sediment cryptobenthic fish communities, but combining multiple methods might be the most practical option.

This study contributes to the existing literature on cryptobenthic fish fauna, yet it creates many more questions. The locations used for this project were known to have high diversity, and as such were important for dive tourism, it is yet unclear if these sites are anomalies with extreme high diversity, or whether they are representative of soft sediment sites in Indonesia and the Philippines. Similarly, surveyed sites represent a specific sediment type (volcanic, gravelly sand), but the assemblages on different types of sediment might differ strongly from the present study. On coral reefs, more complexity leads to higher diversity and abundance (Graham and Nash 2013). If this paradigm holds for soft sediment, a gradient of increasing diversity and abundance would be expected with increasing grain size. The high diversity found in this study begs the question of how limited structural complexity can support high diversity. In a terrestrial, but comparable system, the high diversity of lizards in Australian deserts can be explained by an abundant food source (termites), combined with lack of competition and predation on species less adapted to arid environments (Morton and James 1988). Similar processes are possible on soft sediment, with high availability of invertebrate prey (e.g. amphipods, caprellid shrimp), and decrease in large predators with distance from reef. Several unanswered questions remain about interactions between soft sediment habitats and other biomes. This is particularly relevant since soft sediment environments are the most extensive infralittoral habitat.

4.6 Conclusion

This study set out to investigate cryptobenthic fish assemblages and diversity on soft sediment habitats in the centre of tropical marine biodiversity. We found a high species diversity comparable or richer than on coral reefs, coupled with very low abundances. Differences in cryptobenthic fish assemblages seem to be principally driven by large-scale regional factors, with smaller site-specific effects of grain size characteristics and benthic cover. The high economic value of soft sediment habitats coupled with the present limited understanding of their ecology calls for more research. This study lays the groundwork for future research into fish assemblages on infralittoral soft sediment habitats and highlights the need for a paradigm-shift when studying fish assemblages on these habitats.

Postscript: In the next chapter I develop a non-destructive survey method specifically adapted to detect cryptic species more effectively than traditional Underwater Visual Census surveys.

Chapter 5 Biofluorescence as a survey tool for cryptic marine species

Preface: This chapter has been published in the journal *Conservation Biology* (doi: 10.1111/cobi.13033) and has been formatted according to the journal guidelines. The combined references for all chapters can be found in the Cited Literature-section at the end of this thesis.

5.1 Abstract

As ecosystems come under increasing anthropogenic pressure, rare species face the highest risk of extinction. Paradoxically, rare species often lack data necessary to evaluate their conservation status, because of the challenges detecting species with low abundance. One group of fishes subject to this under-sampling bias are those with cryptic body patterns. Twenty-one percent of the cryptic fish species assessed for their extinction risk (IUCN) are data deficient. We developed a non-destructive method for surveying cryptically patterned marine fishes based on the presence of biofluorescence. Blue LED torches were used to investigate how widespread biofluorescence is in cryptic reef fishes in the Coral Triangle region. We recorded 95 reef fish species displaying biofluorescence, 73 of which had not been previously described as biofluorescent. Of those fish with cryptic patterns 87% were biofluorescent compared to 9% for non-cryptic fishes. The probability of species displaying biofluorescence was 70.9 times greater for cryptic species compared to non-cryptic species. The effectiveness of our Underwater Biofluorescence Census (UBC) method in generating abundance data was tested on a data deficient pygmy seahorse species (*Hippocampus bargibanti*) and compared to data obtained from standard Underwater Visual Census (UVC) surveys. Almost twice the number of *H. bargibanti* were counted using the UBC compared with UVC. For two triplefin species (*Ucla xenogrammus*, *Enneapterygius tutuilae*), the abundance detected with UBC was triple that detected with UVC. The UBC method is effective at finding cryptic species that are otherwise difficult to detect, reducing inter-observer variability inherent to UVC surveys. Biofluorescence is ubiquitous in cryptic fishes, making this method applicable across a wide range of species. Data collected using UBC could be used with multiple IUCN criteria to assess the extinction risk of cryptic species. Adopting this technique will enhance researchers' ability to survey cryptic species and facilitate management and conservation of cryptic marine species.

5.2 Introduction

Numerically rare species comprise the majority of species in any ecosystem (Gaston 1994), yet comparatively little research is conducted on these species (Kunin & Gaston 1993; Jones et al. 2002; McClenachan et al. 2012). Rare organisms have a higher risk of extinction, and therefore a greater need for data to determine their true conservation status, risk of extinction and changes in abundance and distribution (Diamond 1984; Soulé 1987; IUCN 2014). A taxon-specific problem when assessing fish species' risk of extinction, is the difficulty in adequately assessing population size when applying IUCN criteria (Dulvy et al. 2003). As a result, extinction risk assessments in fishes are frequently based on criteria such as population declines inferred by reduced fisheries catches or by life history characteristics such as geographic range and fecundity (Dulvy et al. 2004). These methods are effective for species exploited by fisheries, but are not as efficient for those species which are not targeted, or otherwise difficult to survey.

While surveying rare species is a challenge, it is more problematic when species are difficult to detect. Many of the species thought to be most threatened are cryptic, which often leads to a classification of "data deficient" when describing their conservation status (Pearson et al. 2007; Chades et al. 2008). In contrast to other reef fishes, cryptobenthic fishes often have small geographic ranges (Goatley and Brandl 2017), which can increase a species' vulnerability to extinction (IUCN 2014). Moreover, survey methods unable to record accurate estimates of a species' abundance can produce false absence data. Consequently, management agencies have difficultly determining if and why a cryptic species is at risk of extinction, and development of an appropriate conservation strategy is a challenge (Mackenzie & Royle 2005; Chades et al. 2008).

A range of solutions have been developed for detecting cryptic species in the terrestrial environment. Auditory surveys are frequently used to survey birds and amphibians (Celis-Murillo et al. 2009; Dorcas et al. 2009), whereas camera traps are increasingly used to monitor cryptic mammals (Tobler et al. 2008). More recently developed, non-lethal methods include infrared digital cameras and hair-sampling to detect rare and cryptic species like the snow leopard and small-bodyweight mammals (Jackson et al. 2006; Paull et al. 2012). These established methods are difficult or impossible to implement in the marine environment, where there are thousands of cryptic species of unknown conservation status that play an important role in ecosystem trophodynamics (Depczynski & Bellwood 2003). Because of these difficulties, research on cryptic marine species remains underrepresented, which has significant ramifications from an ecological and conservation perspective (Ackerman & Bellwood 2000; Jones et al. 2002).

Traditionally, Underwater Visual Census (UVC) has been used as a non-destructive method for measuring the abundance and distribution of reef fishes. However, biases inherent to this method, such as researcher experience and detectability of target species, can cause large inter-observer variability and significantly alter survey outcomes (MacNeil et al 2008; Bernard et al 2013). While UVC is a cost efficient and effective method for larger-bodied, mobile fishes, it is less suitable to detect small and cryptic species (McCormick & Choat 1987; Samoilys & Carlos 2000). Methods that deploy video cameras record less cryptic species than UVC, unless adapted for specific target species (Colton & Swearer 2010; Lowry et al. 2011; Harasti et al. 2014). The popularity of these techniques, designed to enumerate the temporal and spatial patterns of reef fish communities, have led to a poor understanding of cryptic and rare species and their role in the broader ecosystem. While lethal techniques such as rotenone are an effective method to quantify diversity of cryptic species (Brock 1982; Kulbicki 1990), the destructive nature of this method is unsuitable for threatened species (Ackerman & Bellwood 2000; Smith-Vaniz et al. 2006). Clove oil has been proposed as an alternative; however, it has been shown to be less efficient than rotenone (Ackerman and Bellwood 2002). Other techniques such as environmental DNA (eDNA) are rapidly gaining popularity, but these are limited to providing data on presence/absence and require sophisticated laboratory facilities and good reference databases (Thomsen et al. 2012). For cryptic reef fishes, gaining a full understanding of whether a species is threatened can only be done with an appropriate census technique. Unfortunately this is not possible using the current suite of methods, so the question remains which cryptic species are rare and require conservation actions, and which are simply under-sampled?

To sample cryptic coral recruits, researchers increasingly use a method that capitalises on the biofluorescent nature of corals (Baird et al. 2005). Newly settled coral polyps that biofluoresce are detected using fluorescent torches, providing a more accurate method for quantifying coral settlement (Piniak et al. 2005). In reef fish, biofluorescence has only recently been discovered and is phylogenetically widespread (Sparks et al. 2014). While the evolutionary function of fish biofluorescence is unknown, it is particularly common in reef fishes that are cryptically patterned (Sparks et al. 2014). Unlike bioluminescence (an active process whereby light is produced by an organism), biofluorescence is passive and occurs through the absorption of ambient light that is emitted at a different wavelength (Sparks et al. 2014). The work previously done on biofluorescence in fish was mostly descriptive and laboratory-based, and did not attempt to evaluate fish biofluorescence for practical applications (Michiels et al. 2008; Gerlach et al. 2014; Sparks et al. 2014). The recent expansion of “fluorescence” diving in the recreational dive industry has led to the mass production of fluorescence technology such as torches and camera filters. The availability of this technology, coupled with the discovery of widespread biofluorescence in reef fishes led us to investigate, for the first time, its use as a survey method for detecting and quantifying cryptic coral reef fish in their natural environment. To do this we used a fluorescent dive torch to investigate which cryptically patterned fish species emit biofluorescence. We surveyed fishes across multiple locations, and multiple individuals within a species, to determine spatial and taxonomic variability in biofluorescence. We used two seafan-associated pygmy seahorses (*Hippocampus bargibanti* and *H. denise*) and two coral reef habitat generalists (triplefins - *Ucla xenogrammus* (Holleman 1993) and *Enneapterygius tutuilae* (Jordan et al. 1906)) to test the applicability of this technique as a survey method for estimating densities of cryptobenthic fishes.

5.3 Methods

5.3.1 Study sites

This study focussed on coral reef fishes in Indonesia since this region contains the greatest number of marine fish species in the world and is thus a conservation priority. Biofluorescence surveys of reef fishes in general, and pygmy seahorse in particular, were undertaken at 63 sites in four locations in Indonesia (Bali, Nusa Tenggara, North-Sulawesi, Raja Ampat). To determine if the presence of biofluorescence in fishes varied between regions we also surveyed two locations outside of Indonesia - Christmas Island and the Cocos (Keeling) Islands in the East Indian Ocean. Surveys in Indonesia occurred between July and November 2015, and Christmas and Cocos Islands were surveyed in July 2017. Surveyed habitat varied and included fringing coral reefs, coral rubble, drop offs and black sand slopes (Site details in Appendices).

5.3.2 Focal species

The reef fish community was surveyed to determine the prevalence of biofluoresence in cryptic and non-cryptic species. For this study, cryptic fish were defined as species that “closely resemble a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral” (Randall 2005) or species that are “behaviourally cryptic and are <50 mm total length” (adapted from Depczynski & Bellwood 2003).

To test whether the biofluorescence technique could be used to quantify the abundance of a cryptic fish species we did dedicated surveys on four species. We first focused on two pygmy seahorse species (*H. bargibanti* (Whitely 1970, redescribed by Gomon 1997) and *H. denise* (Lourie & Randall 2003)) because pygmy seahorses are highly cryptic fishes that are listed as data deficient on the IUCN Red List (IUCN 2016), making them of considerable conservation interest. Even though highly valued by the tourism sector (Smith 2010; De Brauwer et al. 2017), their distribution, abundance and population size is currently unknown. *Hippocampus bargibanti* is a diminutive seahorse species found in the Coral Triangle and reaches a maximum size of 26.9 mm (SL) (Gomon 1997). It is an obligate symbiont with gorgonian seafans of the genus *Muricella* (Gomon 1997; Reijnen et al. 2011). Individual *H. bargibanti* occur as either yellow or pink colour morphs (Gomon 1997). *Hippocampus denise* reaches a maximum size of 24 mm (SL) (Lourie & Randall 2003) and is known to occupy gorgonian seafans of the genera *Anella* and *Villogorgia* (Lourie & Randall 2003). It also occurs less frequently in *Acanthogorgia spp., Echinogorgia spp. and Subergorgia spp.* seafans (Reijnen et al. 2011). Host gorgonians are usually found in areas of high current, often in depths greater than 14 m (Reijnen et al. 2011 – Table 5.2).

To test if the UBC method could be used to quantify cryptobenthic species commonly found on coral reefs we also examined two habitat generalist species - the largemouth triplefin (*Ucla xenogrammus* (Holleman 1993)) and the highfin triplefin (*Enneapterygius tutuilae* (Jordan et al. 1906)). Largemouth triplefins reach a maximum size of 47 mm (SL) and are distributed from Christmas Island to the central Pacific. They are found in lagoons and outer reefs and on a range of microhabitats including corals, sponges, dead reef, and rubble (Allen et al. 2007). The highfin triplefin reaches a maximum size of 40mm (TL) and is distributed throughout the tropical Indo-Pacific and Red Sea. It occurs on a variety of coral reef microhabitats including tide pools, reef flats, lagoons and outer reefs (Allen et al. 2007).

5.3.3 Survey methods

5.3.3.1 Biofluorescence in cryptic fish species

To detect fluorescence in as many fish species as possible, we used a Sola Nightsea fluorescence torch and yellow barrier filter fitted to a dive mask (http://www.lightandmotion.com/sola-nightsea). A widely available and relatively inexpensive (USD $550) fluorescence torch was chosen to increase accessibility and decrease costs of this method. Fifty-seven night dives were conducted on SCUBA or snorkel at 31 sites across the six locations (Indonesia, Christmas Island, Cocos Islands) to record and photograph fluorescing species. Surveys were conducted between 0 and 30 m and were done at night to increase the observability of biofluorescence. In some cases, multiple dives were done at the same site. Each fish encountered during a dive was classified as either cryptic or non-cryptic, checked for fluorescence and identified to species where possible. Surveys of multiple individuals per species were necessary to test if the presence and pattern of biofluorescence was consistent within a species. In some cases, the same species was surveyed at Indonesia, Christmas Island and the Cocos Islands to test for regional consistency in biofluorescence. At the Indonesian sites, fluorescent fishes were photographed using a Canon G16 with an Isotta underwater housing, combined with a Fisheye FIX M67 Fluo filter fitted to the lens. A Sola Nightsea torch was used as the sole light source.

5.3.3.2 Biofluorescence as a survey method

The applicability of biofluorescence as a survey method was tested by comparing density estimates obtained using UBC to those obtained using traditional UVC. Two pygmy seahorses *(H. bargibanti* and *H. denise*) were surveyed during 84 SCUBA dives, at 63 sites in all four locations in Indonesia and to a maximum depth of 40 m. We did not survey at night, since standard UVC reef fish surveys are always undertaken at daytime. Daylight surveys were appropriate, as biofluorescence can be observed during the day, especially in deeper water where ambient light levels are low (Mazel 2005; Piniak et al. 2005; Schmidt-Roach et al. 2008). As each dive was 35-60 mins, we only surveyed seafans (*Muricella spp*., *Anella spp*. and *Villogorgia spp*.) known to frequently host the pygmy seahorse species (Reijnen et al. 2011; Smith et al. 2012). All visual surveys were done by one observer (MDB), who has more than six years of experience locating pygmy seahorses.

After locating a suitable gorgonian host, a two minute survey was completed covering the entire area of the seafan. This was done either without fluorescence (UVC), or using a fluorescence torch and yellow barrier filter (UBC). The method was assigned randomly to each seafan, resulting in 65 fans surveyed using UBC and 81 using UVC. For biofluorescence surveys, the Sola Nightsea torch was used with the focused beam on the highest light intensity (1700Mw), held no more than 20 cm from the gorgonian seafan. After each observation, we photographed the entire seafan and a close-up of the polyps to allow for identification to genus.

The suitability of the biofluorescence method was then tested on two cryptobenthic species that are habitat generalists found on coral reefs; the largemouth triplefin (*Ucla xenogrammus*) and the highfin triplefin (*Enneapterygius tutuilae*). The largemouth triplefin was surveyed at two sites at Christmas Island and the highfin triplefin at three sites at the Cocos Islands. At Christmas Island surveys were done whilst SCUBA diving at 15 m depth on the outer coral reef slope/wall where the largemouth triplefin was abundant. This species was not present at Cocos Islands, so we surveyed the highfin triplefin at 1 m depth while snorkelling over coral reef habitat located in the lagoon. At each site (both locations) we completed eight replicate 20 × 2 m belt transects. Four transects were conducted either without fluorescence (UVC) or using a fluorescence torch and yellow barrier filter (UBC). The order of the eight transects was randomised. For the biofluorescence surveys, the same Sola Nightsea torch was used with the narrow beam on the highest light intensity (1700Mw) with a yellow barrier filter placed in front of the observer’s mask. All surveys in Cocos and Christmas Island were done prior to sunset (17:00 and 18:15) when the light levels were suitable for UVC and UBC.

5.3.4 Analysis

To test if observed patterns in fluorescence were independent from crypsis, a Pearson's Chi-squared test of Independence with Yates' continuity correction was conducted. Sample odds ratio was calculated following Quinn and Keough (2002) to compare probabilities of biofluorescence in cryptic versus non-cryptic species.

The number of *H. bargibanti* individuals per host seafan were recorded for each method (survey of seafan with (UBC) and without fluorescence torch (UVC)). One-tailed, t-tests were conducted to compare numbers of *H. bargibanti* individuals that were detected using the different methods. One tailed t-tests were used as it was hypothesised that the UBC method would result in an increase in detections. Pearson's Chi-squared and one-tailed, t-tests were conducted using R (R Development Core Team 2010). Data on *H. denise* were not subjected to analysis because of very low sample size (N = 7 across all locations). The mean number of *U. xenogrammus* detected per transect for each method were compared with one-tailed, t-tests using R (R Development Core Team 2010). Data for *E. tutuilae* were square root transformed to meet assumptions of normality, and then compared with one-tailed, t-tests using R (R Development Core Team 2010)

5.4 Results

5.4.1 Biofluorescence of cryptic fish species

During the night surveys, 1528 individuals from 230 species were observed. Ninety-five (95) fish species (887 individuals) showed obvious biofluorescence, of which 73 species were previously unknown to fluoresce (Full list in Appendices). Of the 95 cryptic species encountered, 83 (87.3 %) showed fluorescence (Figure 5.1). In contrast, only 12 (8.9 %) of the 135 non-cryptic species encountered during the night surveys fluoresced (Figure 5.1). The odds of exhibiting biofluorescence were 70.9 times greater for cryptic species compared to non-cryptic species ($\hat{\theta}$=70.9; χ^2 = 138.44, df = 1, $p < 2.2e^{-16}$). A cryptic species was 6.9 times more likely to be fluorescent than non-fluorescent, compared to a non-cryptic species, which was 10.3 times less likely to be fluorescent than non-fluorescent.

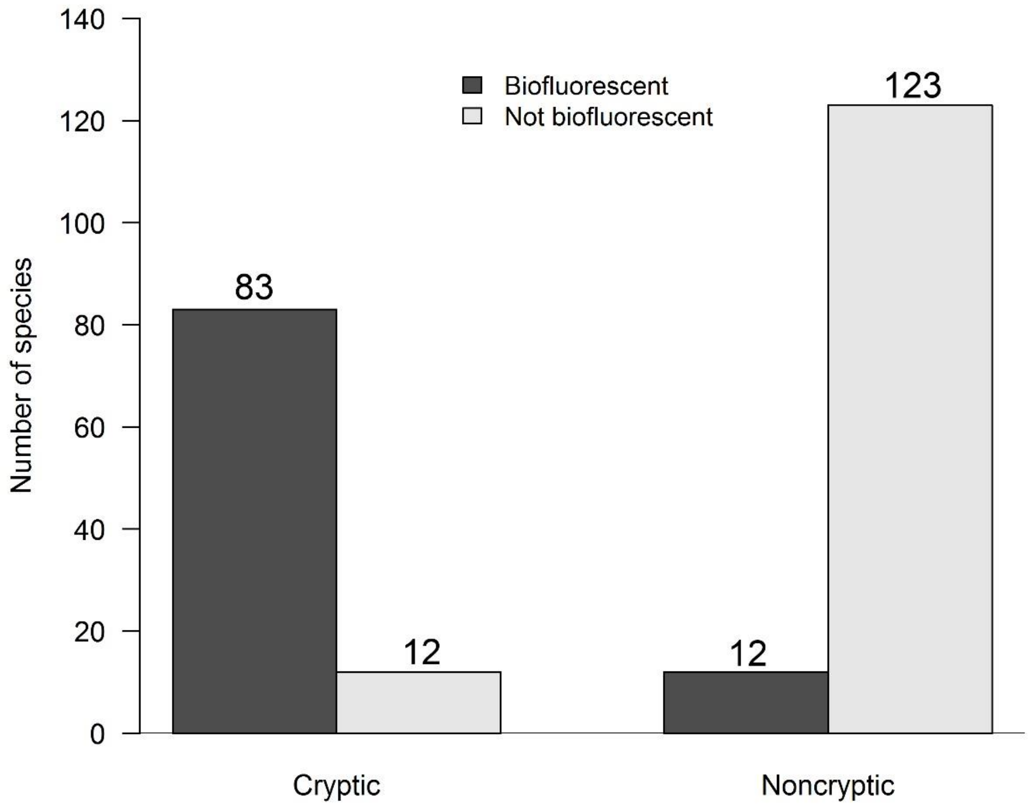


Figure 5.1 Number of cryptic and noncryptic species observed to exhibit biofluorescence.

We observed 49 families of fishes, of which 27 families had at least one biofluorescent species, whereas 22 families did not have any fluorescing species (Complete list in Appendices). Reliable identification to species level was not always possible for *Gobiidae* and *Tripterygiidae*. Therefore these were excluded from further analyses, although more than four different fluorescing species were found in each family (details in Appendices). In the 13 families for which we found more than five species, the families with the highest percentage of cryptic species also contained the highest percentage of fluorescent species (Figure 5.2). From this subgroup, three families comprised only cryptic species, all of which exhibited biofluorescence. In contrast, five families lacked cryptic species, and no species were fluorescent. The *Nemipteridae* family was an exception to this trend: none of the species observed were cryptic, but all showed biofluorescence (N = 5) (Figure 5.2, photos in Appendices).

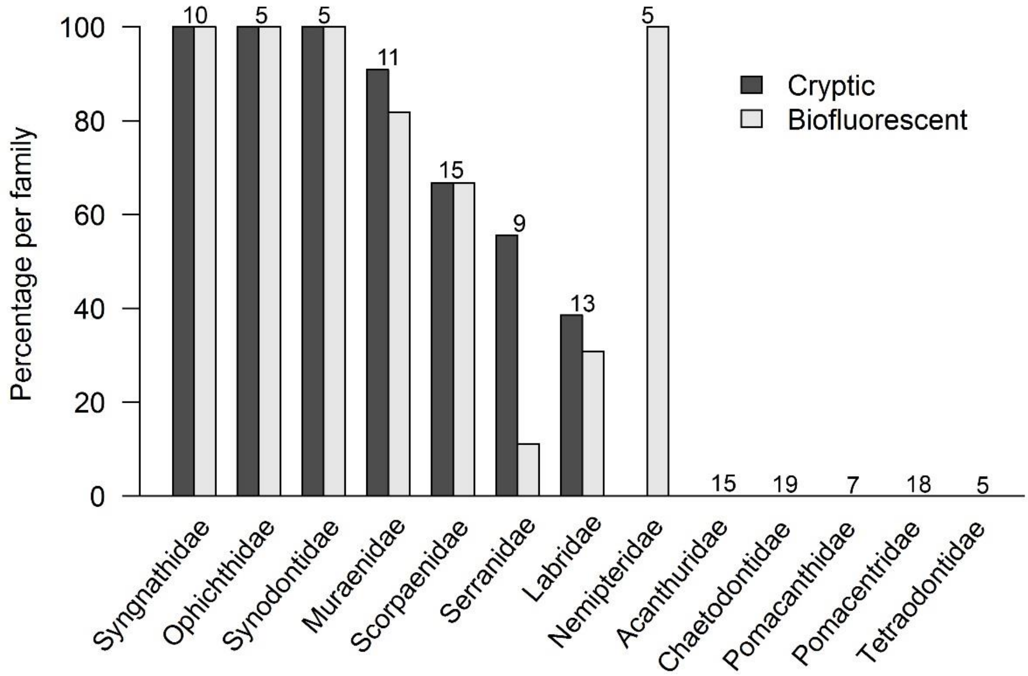


Figure 5.2 Comparison of percentage of species per family exhibiting biofluorescence and crypsis (numbers above bars: number of species surveyed per family).

5.4.2 Biofluorescence as a survey method

To demonstrate the effectiveness of the UBC method on a vulnerable group of cryptic species that are listed as data deficient (IUCN) we focussed on the pygmy seahorses *H. bargibanti* and *H. denise*. Pygmy seahorses were only rarely encountered. Thirty two individuals of *H. bargibanti* and seven individuals of *H. denise* were found during the seafan surveys. All individuals fluoresced in the red and green colour spectrum. Red fluorescence was invariably strongest in the tail of the seahorse with the eyes the only body part to emit green fluorescence (Figure 5.3). The host gorgonian seafans (*Muricella sp.*, *Anella sp.*, *Villogorgia sp.)* were never observed to fluoresce.

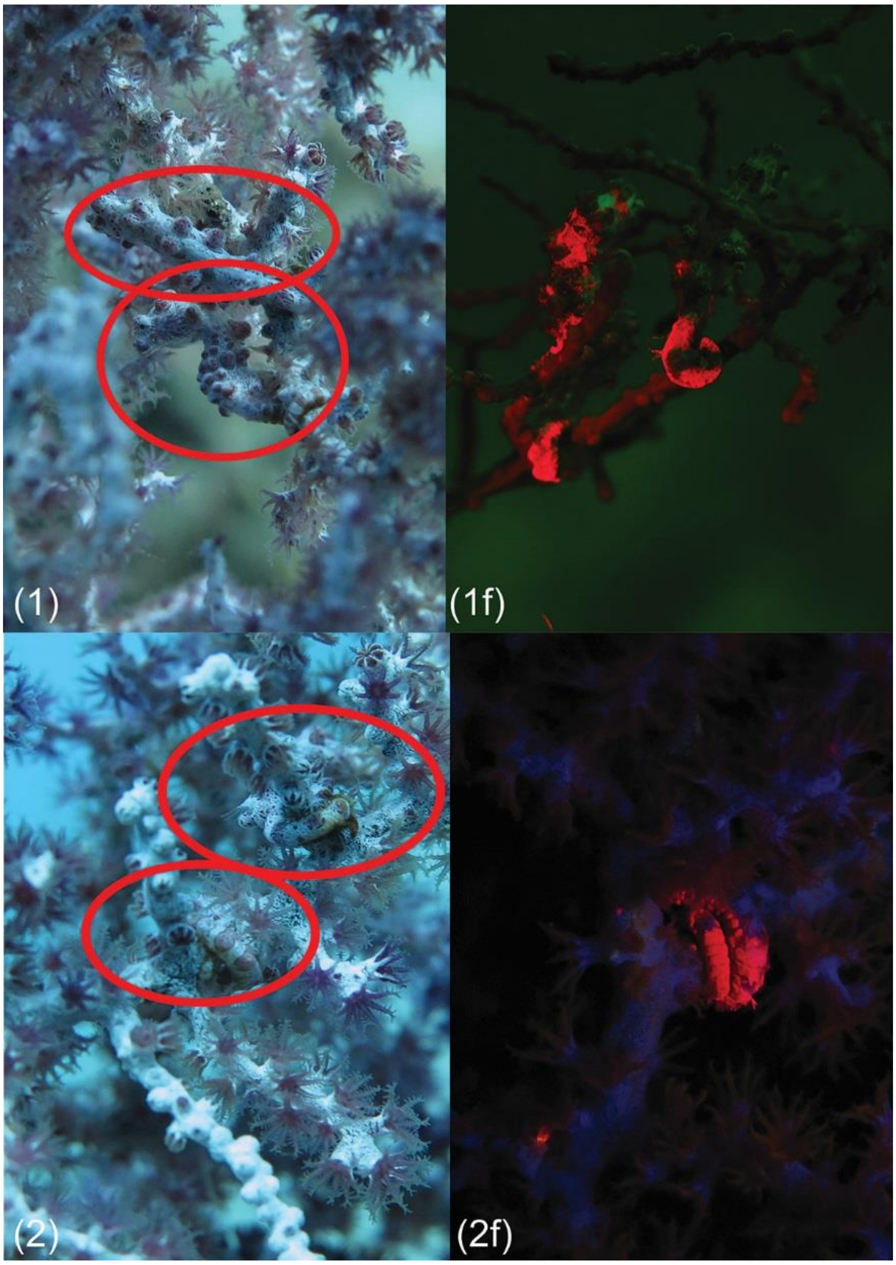


Figure 5.3 Biofluorescence in Bargibant's Pygmy Seahorse (Hippocampus bargibanti). Photos on the left show seahorse under ambient light, photos on the right show seahorses using the UBC-survey method. (1) and (1f) show entire body of the seahorses, (2) and (2f) show close-up of the tails of the seahorses. (1) and (2) taken of the same animals by day using ambient light only, with the individual seahorses (N = 2) circled in red. (1f) taken by day with high intensity blue LED torch and yellow filter, different animals. (2f) taken at night with high intensity blue LED torch and yellow filter, same animal as in (1) and (2).

For *H. bargibanti*, 146 *Muricella sp.* seafans were surveyed, 65 using UBC and 81 using UVC. On average, nearly double the number of *H. bargibanti* were detected using the fluorescence method compared to the non-fluorescent surveys (Figure 5.4) although the difference between survey methods was not statistically significant at $\alpha = 0.05$ for this species (t-test; t= -1.28; p = 0.13). Of the 32 individual *H. bargibanti* observed, 20 were found using the UBC method and 12 individuals were located using only visual surveys. Using the UBC method, an average of 0.31 (SE = 0.07) seahorses were detected per seafan, compared to 0.15 (SE = 0.05) for the UVC method (Figure 5.4). Due to the extremely low abundance, there was insufficient data to statistically analyse *H. denise*.

To test the effectiveness of the UBC method on habitat generalists commonly found on coral reefs, the largemouth triplefin (*U. xenogrammus*) was surveyed in 16 transects at Christmas Island. Nearly three times the number of fish were detected in UBC transects (N = 23) compared to UVC (N = 8). Per transect, UBC surveys found significantly higher numbers (mean = 2.9 individuals per 40 m^2 ± SE 0.5 individuals) than UVC surveys (mean = 1.0 individuals per 40 m^2 ± SE 0.2 individuals) (t-test; t = -2.6112; p = 0.03; Figure 5.4). At the Cocos Islands, 139 highfin triplefins (*E. tutuilae*) were encountered in 24 transects and the mean density detected in UBC transects (mean = 8.8 per 40 m^2 ± SE 1.1 individuals) was more than triple that recorded in UVC transects (mean = 2.8 individuals per 40 m^2 ± SE 0.4 individuals) (t-test; t = -4.258; p < 0.001; Figure 5.4).

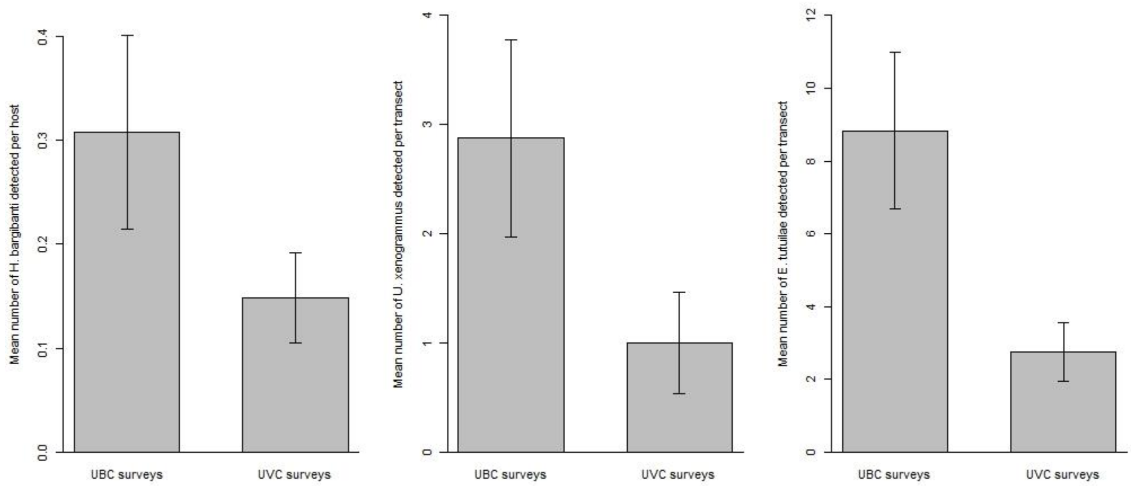


Figure 5.4 Number of detected individuals of *Hippocampus bargibanti* (Indonesia), *Ucla xenogrammus* (Christmas Island), and *Enneapterygius tutuilae* (Cocos Island) with normal visual surveys (UVC) compared with underwater biofluorescence census (UBC) surveys. Detections of *H. bargibanti* are the mean number of individuals found per gorgonian seafan host, and detection of *U. xenogrammus* and *E. tutuilae* are the mean number of individuals found per 40m^2 transect.

5.5 Discussion

The results demonstrate that the UBC method is effective at finding cryptic species that are otherwise hard to detect and quantify. We have shown that biofluorescence is ubiquitous in cryptic species within, and outside of the, centre of reef fish biodiversity (the Coral Triangle), making this method applicable across a wide range of species and geographic locations. We also showed that UBC could be used to gather data on abundance, distribution and habitat use of common (triplefins) and vulnerable (pygmy seahorses) cryptic species. The use of efficient survey methods like UBC could help assess species' extinction risk using IUCN criteria to ensure adequate protection for rare species, shed light on the ecological roles of cryptic species and potentially answer the long-standing question whether cryptic species are indeed rare, or merely under sampled (Jones et al. 2002).

Currently, methods to detect cryptic species are often destructive or inefficient. Destructive methods such as the use of rotenone are efficient at detecting cryptic species, but in the case of rare or threatened species it is counterproductive to kill individuals while surveying them (Ackerman & Bellwood 2000; Smith-Vaniz et al. 2006). Standard Underwater Visual Censuses have repeatedly been shown to underestimate the abundance of cryptic fish species and are affected by species detectability and observer experience (McCormick & Choat 1987; Samoilys & Carlos 2000; Bernard et al. 2013), which might be why cryptic species are rarely included in marine diversity assessments (e.g. Sandin et al. 2008; Osborne et al. 2013; Go et al. 2015). In this study, the UBC method consistently found higher numbers of individuals for three reef fish species compared to traditional UVCs, a result consistent across different locations and depths. Compared to methods using ichthyocides, UBC is non-destructive, making it more suitable for monitoring potentially rare species. The increased detection probability by using the UBC-method is likely to decrease inter-observer variability and will therefore increase the accuracy of surveys (MacNeil et al. 2008). The high incidence of biofluorescence in other cryptic fish means the UBC method could be applicable to a wide host of other cryptic species.

The UBC method was effective for habitat specialists (pygmy seahorses) and habitat generalists (triplefins). Furthermore, we found other cryptic and highly abundant species such as Gobies (*Gobiidae*) displayed stronger fluorescence and would therefore be even more suitable to survey using this method. This is an important discovery as these families are often abundant and ubiquitous on coral reefs yet nearly always ignored during UVC surveys such that their importance to reef ecosystems is grossly underestimated (Depczynksi and Bellwood 2003; Lefèvre et al. 2016). Our surveys across multiple individuals and locations found consistency in which species exhibited biofluorescence (and which did not), highlighting the utility of the UBC approach. Variation in the body location and strength of the biofluorescence was apparent between families of cryptic species. Determining the cause of this variation, and why biofluorescence is more prevalent in cryptic than non-cryptic species, are pertinent questions for future research. Our observations of biofluorescence in numerous invertebrates (*Decapoda*, *Polychaeta*, C*ephalopoda*) suggests the UBC method has considerable potential to be expanded beyond fish taxa when surveying for diversity and conservation reasons.

UBC works best when natural light is low or absent. For this reason, we recommend surveys be conducted during times of low light (e.g. overcast, around dawn or dusk) or at night. UBC surveys can still be effective during the middle of the day in low-light habitats (e.g. shaded walls, deeper water). Biofluorescence is also more obvious particularly against backgrounds that provide maximum contrast. For example, in pygmy seahorses, the contrast between the non-fluorescent host gorgonians and the fluorescent nature of their tails proved to be an effective method to locate and quantify individuals. Thus the optimal approach for surveying cryptic species with UBC will need to consider the light and contrast conditions given the ecology (habitat use, depth range) and behaviour (nocturnal/diurnal/crepuscular) of the study species. Given species' variability in strength of fluorescence, it is advised to assess target species' suitability prior to commencing UBC surveys.

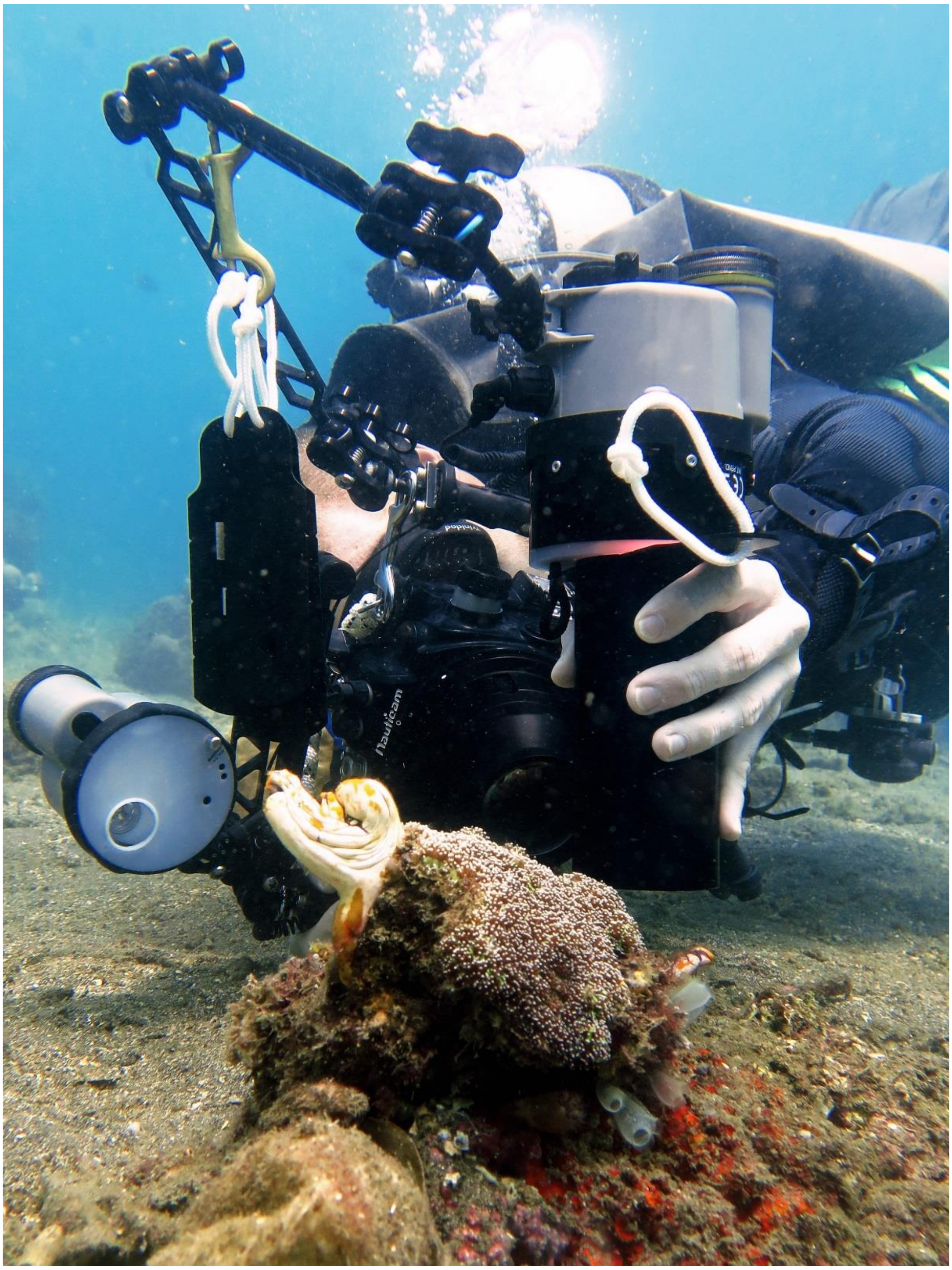
The biggest hurdle to assessing the conservation status of cryptic species is establishing their population size. Many reef fishes are easily observed using UVC, as a result conservation strategies to protect these species are well advanced (Duarte et al. 2008; McClenachan et al. 2012). Conversely, cryptic species are difficult to locate and require experienced observers or complex methods to quantify their abundance (Ackerman & Bellwood 2000; Smith et al. 2012). The lack of efficient survey methods for cryptic species has resulted in a significant data shortage on their extinction. Consequently, the marine environment has double the number of species listed as Data Deficient compared to terrestrial species (Webb & Mindel 2015). Most of those assessed to date belong to a few well-studied taxonomic groups or commercially important fish (McClenachan et al. 2012).

For three large, representative cryptic families (*Gobiidae*, *Scorpaenidae*, *Syngnathidae*), representing more than 2000 species globally, less than 44% have been assessed for their extinction risk (Nelson 1994; IUCN 2017). Twenty-one percent of the species in these families that have been assessed are considered data deficient (IUCN 2017). Since cryptic species represent more than 60% of fish numbers on coral reefs and are crucial for a well-functioning marine ecosystem (Depczynski & Bellwood 2003; Depczynski et al. 2007), it is critical this issue is resolved. The UBC survey method provides a non-destructive way to obtain the abundance and distribution data that is needed when applying IUCN criteria B (Extent of Occurrence and Area of Occupancy) and D (Small or restricted population). Furthermore, repeated UBC surveys can provide data for IUCN criteria A (Population declines) when assessing the conservation status of hundreds of cryptic species.

A sound knowledge of the abundance and distribution of species is crucial in order to implement effective protective measures. We demonstrated that biofluorescence is common in cryptically patterned marine species in the global centre of reef fish biodiversity, and provide a much-needed, non-destructive survey method to identify, quantify and ultimately protect cryptic species for which data is currently lacking. Fluorescent diving torches are widely available, easy to use and inexpensive, opening the way for the UBC survey method to be adopted globally by under-resourced marine conservation groups and for conducting IUCN assessments of extinction risk. Similarly, there is great potential for the UBC method in citizen science for collecting much needed data on rare and endangered species due to the low cost and user-friendly nature of the method (Louv et al. 2012; Edgar et al. 2016). We propose that the use of the UBC survey method is a cost effective tool to detect and count rare and cryptic species, facilitating future research and much needed conservation initiatives globally.

Postscript: The focus of next chapter returns to muck dive tourism and the cryptic species important to it. In the chapter I investigate the behaviour of scuba divers when interacting with cryptic species, and how the impacts of this behaviour change across different habitats, species or diver demographics.

Chapter 6 Time to stop mucking around? Impacts of underwater photography on cryptobenthic fauna in soft sediment habitats



Preface: This chapter has been accepted for publication in the *Journal of Environmental Management* and has been formatted according to the journal guidelines. The combined references for all chapters can be found in the Cited Literature-section at the end of this thesis.

6.1 Abstract

Scuba diving tourism is a sustainable source of income for many coastal communities, but can have negative environmental impacts if not managed effectively. Diving on soft sediment habitats, typically referred to as 'muck diving', is a growing multi-million dollar industry with a strong focus on photographing cryptobenthic fauna. We assessed how the environmental impacts of scuba divers are affected by the activity they are engaged in while diving and the habitat they dive in. To do this, we observed 66 divers on coral reefs and soft sediment habitats in Indonesia and the Philippines. We found diver activity, specifically interacting with and photographing fauna, causes greater environmental disturbances than effects caused by certification level, gender, dive experience or age. Divers touched the substrate more often while diving on soft sediment habitats than on coral reefs, but this did not result in greater environmental damage on soft sediment sites. Divers had a higher impact on the substrate and touched animals more frequently when observing or photographing cryptobenthic fauna. When using dSLR-cameras, divers spent up to five times longer interacting with fauna. With the unknown, long-term impacts on cryptobenthic fauna or soft sediment habitats, and the increasing popularity of underwater photography, we argue for the introduction of a muck diving code of conduct.

6.2 Introduction

The cumulative impacts of fishing, pollution and climate change are causing a decline in the health of oceans habitats across the world (Burke et al. 2011; Alongi 2015; Halpern et al. 2015; Wernberg et al. 2016). The effects of this decline are felt most strongly in countries that depend on ocean resources for people's livelihoods (Burke et al. 2011; Lavides et al. 2016). Developing countries in particular often have a high proportion of their population reliant on marine ecosystems through subsistence fishing, building materials, or food production (Barange et al. 2014; Lavides et al. 2016). Livelihoods created by marine tourism are often suggested as sustainable alternatives to extractive activities such as fishing (Job and Paesler 2013).

Scuba diving is one of the world's fastest growing recreational sports (Musa and Dimmock 2012), estimated to be worth over a billion dollars globally (Garrod 2008). Scuba diving tourism creates thousands of jobs in developing countries which can be sustainable if managed correctly (Vianna et al. 2012; Job and Paesler 2013; De Brauwer et al. 2017). However, scuba diving can also have considerable impacts on fragile fauna living on coral reefs (Hasler and Ott 2008). Poorly managed dive tourism can alter fish behaviour (Shackley 1998), increase pollution, and cause habitat degradation (Wong 1998). Careless diver behaviour has been repeatedly shown to cause damage to corals (e.g. Rouphael and Inglis 2001; Hasler and Ott 2008), with heavily dived sites having a higher incidence of coral disease (Lamb et al. 2014). Divers tend to cause the greatest amount of damage at the start of a dive while they are still adjusting buoyancy (Rouphael and Inglis 2001; Roche et al. 2016). Inexperienced divers with poorly developed technical skills are more likely to cause damage than more experienced divers (Thapa et al. 2006; Chung et al. 2013), while goal orientated diving behaviour such as photography has a higher impact than general dive activities (Uyarra and Côté 2007; Chung et al. 2013).

Divers not only have a potential impact on a reef's structure, they also affect coral-associated fauna. While the effects of divers on habitat forming structures, such as corals have been comprehensively described, less is known about how scuba diving impacts mobile animals (Trave et al. 2017). Studies on megafauna have shown that diver interactions can reduce mobility and change behaviour (Shackley 1998; Clua et al. 2010). For small cryptic fishes, interactions with divers can lead to short-term behavioural changes (Harasti and Gladstone 2013). The presence of divers can also disturb fish spawning aggregations (Heyman et al. 2010), and boat noise can disrupt fish larvae from settling onto coral reefs (Holles et al. 2013).

The literature on diver impacts on coral reefs is extensive (Rouphael and Inglis 2001; Hasler and Ott 2008; Au et al. 2014), but scuba diving is not limited to coral reefs. There has been little research into the impacts of divers in other habitats (e.g. Sala et al. 1996; Bravo et al. 2015). Divers are more likely to touch benthic organisms on artificial reefs than on coral reefs, leading to more damage (Giglio et al. 2016). High numbers of snorkelers can alter the morphology and growth of seagrass (Herrera-Silveira et al. 2010). Understanding these impacts is imperative because ecosystems such as soft sediment habitats or seagrass beds are often more productive than coral reefs and have similarly high economic values (Boucher et al. 1998; Costanza et al. 2014). Considering the millions of active divers in areas without coral and the rise of alternative dive destinations away from coral reefs (Lew 2013), it is important to assess the impacts divers might have on these non-reef environments.

One such alternative type of diving is diving on soft sediment, typically referred to as 'muck diving'. Muck diving is increasingly popular and is valued at over USD$ 152 million per year in Indonesia and the Philippines (De Brauwer et al. 2017). It is estimated that more than 100,000 divers annually visit muck diving destinations in Southeast Asia (De Brauwer et al. 2017). Typical muck dive sites have no or very sparse coral cover, instead consisting mainly of sand with sporadic sponge or algal growth. This specialised diving activity focuses on observing or photographing cryptobenthic species such as frogfishes or seahorses that are rarely encountered on coral reefs. The search for rare species makes this a highly goal-driven type of diving that attracts very experienced divers and large numbers of photographers (De Brauwer et al. 2017). Photographers occasionally use 'muck sticks' to coax animals into better position for photographs, which could lead to stress in animals (Roche et al. 2016). Goal-driven diving activities, such as photography, that focus on cryptic fish causes more damage on coral reefs than diving with a non-cryptic focus (Uyarra and Côté 2007), but it remains unclear if this is the same on soft sediment habitats.

Multiple factors can alter the behaviour of divers. The strong focus on observing cryptic species in muck diving raises the question of whether a diver's behaviour might change depending on the species that is observed. Encountering and photographing animals that are considered rare could lead to decreased compliance to environmental ethics (Uyarra and Côté 2007). The best predictors for high impact diver behaviours have yet to be fully identified.

The aim of this study is to better understand the varying impacts of diver activities in different marine environments. We do this by assessing diver behaviour in both coral reef and soft sediment (muck) habitats, the specific goals of this study are to investigate if the impacts of diver behaviour change with:

1. the activity divers are engaged in,
2. the habitat divers are found in,
3. the type of camera divers are using, and
4. diver certification level, age, and experience.

We also investigate:

5. how these factors affect the duration of divers interaction with cryptobenthic fauna.

6.3 Methods

6.3.1 Location

Diver surveys were conducted between March and May 2016 on 33 sites in three locations in Indonesia (Bali, Nusa Tenggara, Lembeh Strait) and one location in Philippines (Dauin). All locations are important dive destinations with coral reef and soft sediment dive sites, which are visited by divers interested in photography (De Brauwer et al. 2017). Sites were determined independently by the dive centres without the influence of the researchers. At all four locations, divers were observed on both coral reefs (coral, N = 15 sites) and soft sediment slopes (muck, N = 18 sites). Maximum depth for all dives was 30m, topography of coral reef sites were comparable to each other, and soft sediment sites all had a similar, sloping topography. Ten visited dive sites were protected areas where no fishing was allowed, but the majority of sites (N = 23 sites) had no form of official protection.

6.3.2 Diver observations

Divers were observed at eight different dive centres that offered muck and coral reef dives. All dive centres gave pre-dive briefings which outlined dive profile and included advice not to touch fragile marine life. The divers were observed ad hoc, starting with the diver closest to the observer and rotating between divers until all divers in the group had been observed. When limited divers were available over the course of a day, the same divers were observed during multiple dives, which could be on different substrates (N = 30 divers). Two types of observations were conducted: “standard observations” and “interaction observations”, adapted from the methods used by Uyarra and Côté (2007). “Standard observations” were used to gauge normal diver behaviour, whereas “interaction observations” investigated divers’ behaviour close to cryptobenthic fauna. Standard and interaction observations occurred during the same dives. The initial five minute standard observation was conducted for each diver after they had established neutral buoyancy and were swimming normally while watching, or photographing non-cryptic reef fauna. Divers cause more damage in the first phase of a dive (Camp & Fraser 2012), but this study aimed to investigate behaviour during the body of the dive, rather than the initial buoyancy adjusting phase. Interaction observations where conducted when divers observed, photographed or otherwise interacted with cryptobenthic fauna. Interaction observations ran as long as the diver interacted with cryptobenthic fauna. If divers encountered cryptobenthic fauna during standard observations, observations were paused until the diver resumed normal swimming. Both recreational divers (tourists) and professional divers (dive guides) were observed during this study. No observations were made when conditions were suboptimal, such as strong currents or very low visibility (<4m). Observations were conducted from a distance of 2 m – 4m from divers, which was sufficient to observe divers and cryptobenthic fauna. To ensure normal diver behaviour divers were made aware that a marine scientist had joined the dive, but were unaware that the marine scientist would be observing their behaviours.

During interaction observations, we recorded duration of interactions, number of times a diver made contact with the substrate or an animal, and whether contacts were intentional or not (Uyarra and Coté 2007). We further noted which part of the body or equipment touched the substrate or animal and the type of activity the diver was doing during the interaction (observe, photograph, show animal to other diver). If the substrate was damaged by the diver ("breakage, abrasions, detachment of tissue" (Rouphael and Inglis 2001)), this was also recorded. All observations were recorded by one observer (MDB).

After the dive, divers were informed of the purpose of the research and asked to give their permission for researchers to use the data. All divers consented. During this conversation, divers were asked for information about their certification level, total number of dives, gender, and age. Finally, for divers using a camera, the type of camera was recorded (Non specialist point-and-shoot (Compact) or digital Single Lens Reflex (dSLR)). Since it is common practice in muck dive tourism for divers go out in small groups (<4 divers), the number of divers that could be observed daily per dive centre was limited.

6.3.3 Cryptobenthic fauna

As the cryptobenthic species of interest to divers are often rare, we chose to record interactions with any species considered to be cryptobenthic. For this study cryptobenthic fauna were defined as; mobile fish or invertebrate species that "closely resemble a part of a substratum, a plant, or a sedentary animal such as a sponge or soft coral" (Randall 2005), or species that are "behaviourally cryptic and are <50 mm" (adapted from Depczynski and Bellwood 2003). Species were later classified per meaningful taxonomic unit, either as a family or order.

6.3.4 Analysis

To compare if divers behaved differently between standard observations and interactions, observed interaction data were totalled per diver and then standardised. Frequencies of divers touching the substrate or animals were standardised to frequency per 10 minutes. Differences between standard and interaction observations were tested using paired Wilcoxon tests as data did not meet assumptions of normality. Data met assumptions for the paired Wilcoxon test.

For standard observations, the effects of habitat, camera use, and diver demographics (age, gender, diver level, total number of logged dives) on contact frequency were tested using Kruskal-Wallis tests, followed by pairwise rank sum Wilcoxon tests to investigate significant effects. To compare the effect of different variables on contact frequency during interactions with cryptobenthic fauna, touch frequencies were totalled per variable for each diver. Frequencies were then standardised to 10 minutes. Kruskal-Wallis tests were then used to test the effects of activity (observe, photograph, show animal), habitat (coral reef, soft sediment substrate), camera (No, Compact, dSLR), and diver demographics (age, gender, certification level, total number of logged dives) on contact frequency, damage events, and touching animals. Significant effects were further investigated using pairwise Wilcoxon rank sum tests. Sample sizes were too small to test the effects of diver demographics between different habitats and photographer categories.

The duration of diver interactions with animals was summed per family for each diver and then log10-transformed to meet assumptions of normality. A repeated measures ANOVA-design with diver as a random factor was used to test the effects of activity, habitat, camera, and family on the duration of animal-interactions. Observations of dive guides interacting with cryptobenthic fauna were omitted from these interaction duration analyses, as dive guides interactions depend on the time divers spend interacting with animals.

There was a strong correlation between the total number of instances a diver touched the substrate with the number of instances a diver intentionally touched the substrate ($r = 0.83$, $p < 0.001$). Therefore, the observations of divers intentionally touching the substrate were omitted from analyses.

6.4 Results

During 47 dives, we observed the behaviour of 66 divers (50 recreational divers and 16 guides). The average age of divers was 45.6 years old (± SE 1.6 years), and 59.1% of divers were male, 40.9% female. Recreational divers were highly experienced, with an average total of 741 logged dives (± SE 137 dives). Dive guides had an average total of 4053 dives (± SE 960 dives). Three recreational divers (6 %) had entry level certification, compared to 23 divers (46%) with a higher certification and 25 divers (48%) with a professional certification. Twenty recreational divers (40%) did not use a camera, 25 (50%) had a compact camera and six divers (10%) used a dSLR camera.

On coral reefs, the substrates that divers touched most often were sand and corals, compare to sand and sponges on muck sites. Intentional contacts with the substrate were made most often with muck sticks, whereas unintentional contacts occurred most frequently with dive equipment. Damage to the substrate was caused mostly by fins. When divers touched animals, they mostly used muck sticks (Table 6.1).

Table 6.1 Most frequently touched substrates by divers and methods of contacting substrates, causing substrate damage and touching animals.

		%	N
Substrate touched	*Coral Reef*		
	Sand	22.7	93
	Hard coral	20.5	84
	Gorgonian seafans	18.8	77
	Soft sediment		
	Sand	84.7	1432
	Sponges	9.5	161
	Rock	4.5	76
Contact method	*Intentional*		
	Muck stick	45	652
	Fins	23.4	339
	Hand	19.6	284
	Unintentional		
	Dive equipment	42.3	278
	Fins	31.5	207
	Muck stick	11.5	74
Damaged by	Fins	47.8	32
	Dive equipment	14.9	10
	Hand / Muck stick	10.5	7
Animals touched with	Muck stick	65.3	128
	Hand	26.5	52
	Camera	4.6	9

6.4.1 Effect of activity on diver behaviour

We made standard observations for all 66 divers and observed a total of 236 interactions with cryptobenthic fauna. During the standard observations divers touched the substrate 585 times, compared to 1362 times during the interactions (Detailed table of contact frequencies in Appendices). The frequency with which divers touched the substrate was more than three times higher during interactions than during standard observations (W: $p < 0.001$, $V = 103$;

Figure 6.1A). Divers also made three times as many unintentional contacts with the substrate during interactions than during standard observations (W: $p < 0.001$, $V = 187.5$; Figure 6.1A). There was no significant difference between the frequency of damage during interactions and standard observations (W: $p = 0.35$, $V = 43$; Figure 6.1A). As expected, divers touched animals more frequently during interactions than during standard observations (W: $p < 0.001$, $V = 0$; Figure 6.1A).

During interactions, the activity that divers were engaged in had a significant effect on the frequency of unintentional contact with the substrate (KW: $p < 0.001$, $df = 2$, $\chi^2 = 16.2$) and on the frequency of touching animals (KW: $p < 0.001$, $df = 2$, $\chi^2 = 17.6$; Figure 6.1B). Divers made three times more unintentional contacts with the substrate when photographing cryptobenthic fauna than while observing (W: $p < 0.001$, $V = 77$) or showing animals (W: $p = 0.001$, $W = 52$; Figure 6.1B). There was no difference in the number of unintentional contacts between observing and showing animals (W: $p = 0.81$, $W = 150$). Divers touched animals six times more frequently while showing them to other divers than while photographing them (W: $p = 0.02$, $W = 214$), and divers did not touch animals while observing (W: $p < 0.001$, $W = 63$; Figure 6.1B). Photographers touched animals more frequently than divers that were observing animals (W: $p = 0.02$, $W = 157$; Figure 6.1B). Diver activity during interactions had no statistically significant effect on the total instances of substrate being touched (KW: $p = 0.07$, $df = 2$, $\chi^2 = 5.5$) or on instances of damage (KW: $p = 0.97$, $df = 2$, $\chi^2 = 0.1$).

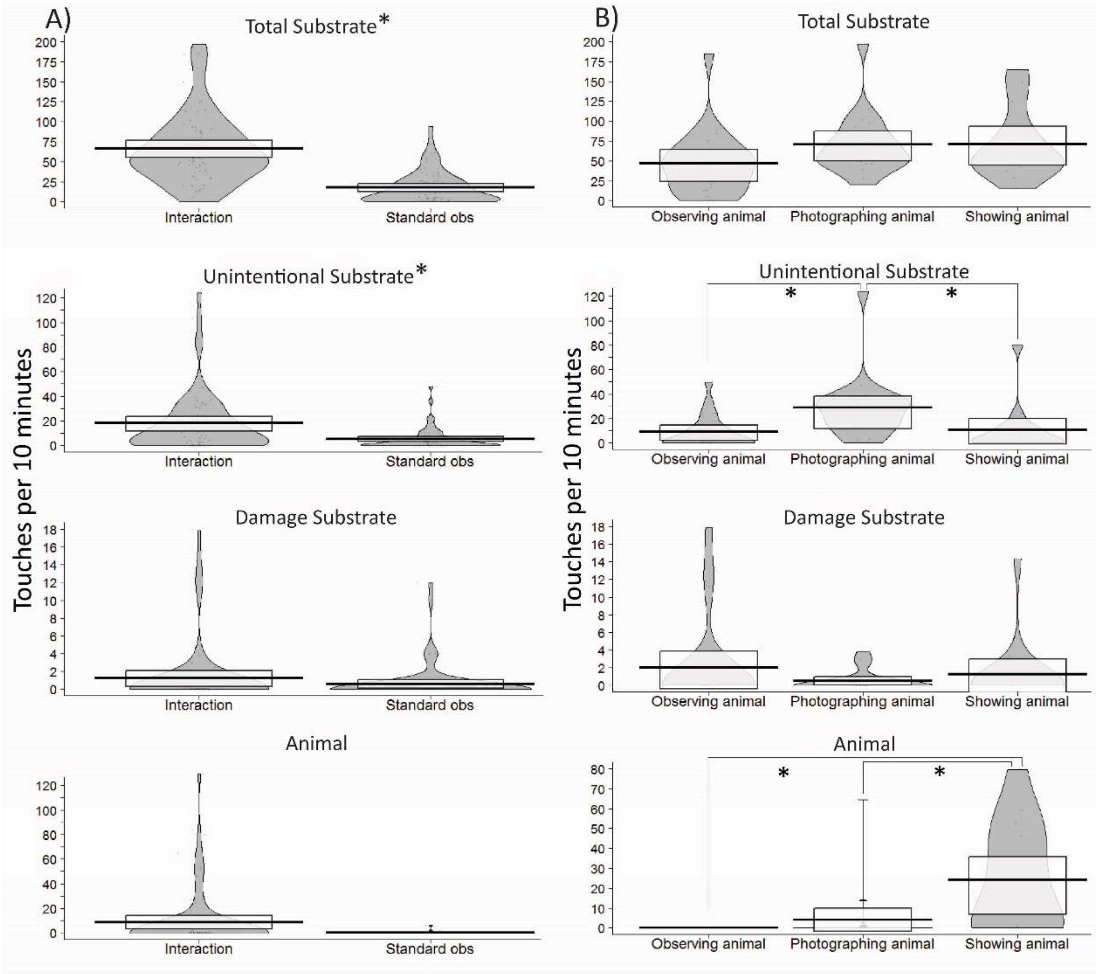


Figure 6.1 Pirate plots of the frequency divers touched the substrate (total and unintentional), caused damage to the substrate and touched animals, * indicates significant differences, black bar indicates mean, white rectangle shows 95% confidence interval, beans represent density. A: Comparison between standard observations and interactions with cryptobenthic fauna. B: Comparisons between diver impacts during different types of cryptobenthic fauna interactions: observing, photographing and showing.

6.4.2 Effect of habitat on diver behaviour

Thirty divers were observed on coral reefs and 49 divers on muck dive sites. During standard observations divers touched the substrate on coral reefs less than half as often than on muck dive sites (W: $p = 0.02$, $W = 315$; Figure 6.2A). There was no effect of habitat on the number of unintentional contacts, damage done or animals touched during standard observations (Figure 6.2A). During interactions with cryptobenthic fauna, the type of habitat had no significant effect on any of the impacts of diver behaviour that we recorded (Figure 6.2B).

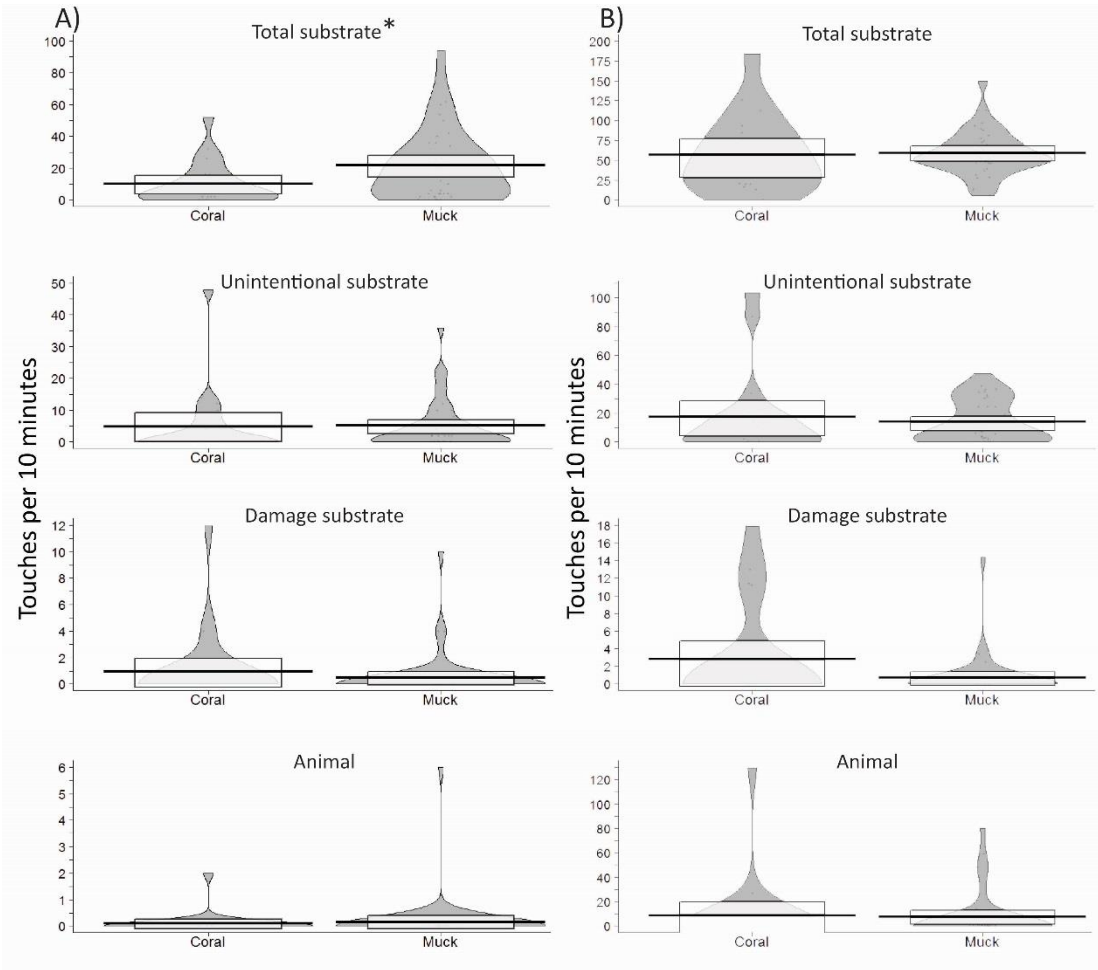


Figure 6.2 Effect of habitat on the frequency divers touched the substrate (total and unintentional), caused damage to the substrate and touched animals, * indicates significant differences, black bar indicates mean, white rectangle shows 95% confidence interval, beans represent density. A: Comparisons between coral reef and muck (=soft sediment) habitats during standard observations. B: Comparisons between coral reef and muck (=soft sediment) habitats during interactions with cryptobenthic fauna.

6.4.3 Effect of camera use on diver behaviour

During standard observations, using a camera had an effect on the number of times divers had unintentional contacts with the substrate (KW: $p = 0.02$, $df = 2$, $\chi^2 = 8.34$), and the number of instances of damage caused (KW: $p = 0.04$, $df = 2$, $\chi^2 = 6.7$). Divers using compact cameras made unintentional contact with the substrate five times more often than divers without a camera (W: $p = 0.006$, $W = 241.5$), but this was not significantly different from those with dSLR cameras. Unintentional contacts or damage were not different between divers without a camera and those with dSLR cameras. The divers with compact cameras caused more damage to the substrate than divers without a camera (W: $p = 0.02$, $W = 324$), but there was no difference between compact or dSLR cameras. There was no effect of camera on total number of contacts with the substrate or on the frequency of touching animals during the standard observations.

When divers interacted with cryptobenthic fauna, the use of a camera had a significant effect on the frequency that divers unintentionally touched the substrate (KW: p = 0.001, df = 2, χ^2 = 13.3), but not on the other variables recorded. Divers without a camera made only one third of the unintentional contacts with the substrate than those with compact cameras (W: p = 0.002, W = 126.5) and half the contacts of divers with dSLR cameras (W: p = 0.01, W = 29). There was no difference between divers with compact or dSLR cameras.

6.4.4 Effects of demographics on diver behaviour

During standard observations, the diver's age or the total number of logged dives had no effect. Gender affected the number of times the substrate was touched, with males contacting the substrate twice as often as females (KW: p = 0.003, df = 1, χ^2 = 8.7). A similar pattern was found with the number of unintentional contacts with the substrate (KW: p = 0.005, df = 2, χ^2 = 7.8). Diver certification level had an effect on the amount of times the substrate was touched (KW: p = 0.01, df = 5, χ^2 = 14.5) and the damage done to the substrate (KW: p = 0.02, df = 5, χ^2 = 13.1), with open water divers causing more damage than higher certification levels (Table 6.2).

During interactions with cryptobenthic fauna, we found no significant effect of diver age or the number of logged dives on any of the variables that were recorded. Male divers touched animals more frequently than female divers (KW: p = 0.02, df = 1, $\chi 2$ = 5.9). Dive level had a significant effect on the frequency that divers touched animals (KW: p = 0.002, df = 5, $\chi 2$ = 16.2). Guides touched animals significantly more often than all other levels, except for Open Water Divers (Table 6.2). There were no significant differences between the other diver levels (Table 6.2).

Table 6.2 Posthoc pairwise Wilcoxon tests for effects of diver certification level on touching the substrate and causing damage during standard observations, and touching animals during diver interactions.

Standard: Touching substrate	Open Water	Advanced	Rescue	Divemaster	Instructor
Advanced	0.13	-	-	-	-
Rescue	0.19	0.80	-	-	-
Divemaster	0.16	0.52	0.26	-	-
Instructor	0.25	0.29	0.38	0.04*	-
Guide	0.40	0.02*	0.02*	0.002**	0.16
Standard: Damage substrate	Open Water	Advanced	Rescue	Divemaster	Instructor
Advanced	0.24	-	-	-	-
Rescue	0.19	1.0	-	-	-
Divemaster	0.007**	0.17	0.18	-	-
Instructor	0.04*	0.45	0.49	0.40	-
Guide	0.001**	0.09	0.11	-	0.29
Interaction: Touching animals	Open Water	Advanced	Rescue	Divemaster	Instructor
Advanced	0.15	-	-	-	-
Rescue	0.40	0.41	-	-	-
Divemaster	0.40	0.41	1.0	-	-
Instructor	0.31	0.45	1.0	0.88	-
Guide	0.26	0.009**	0.01*	0.02*	0.008**

6.4.5 Duration of diver interactions with cryptobenthic fauna

The duration of interactions was most strongly affected by the type of camera the diver was using, divers using dSLR cameras spent more time with animals than those with compact cameras or without a camera ($p < 0.001$; Figure 6.3; Table 6.3). The activity divers were doing during interactions had a significant effect on the duration of interactions, divers who were photographing spent more time with animals than those who were observing ($p < 0.001$; Figure 6.3; Table 6.3). Habitat played a role in the duration of interactions, with longer interactions on muck substrates than on coral reefs ($p = 0.012$; Figure 6.3; Table 6.3). The family of the animal that divers interacted with had no significant effect on the duration of interactions ($p = 0.074$; Figure 6.3; Table 6.3).

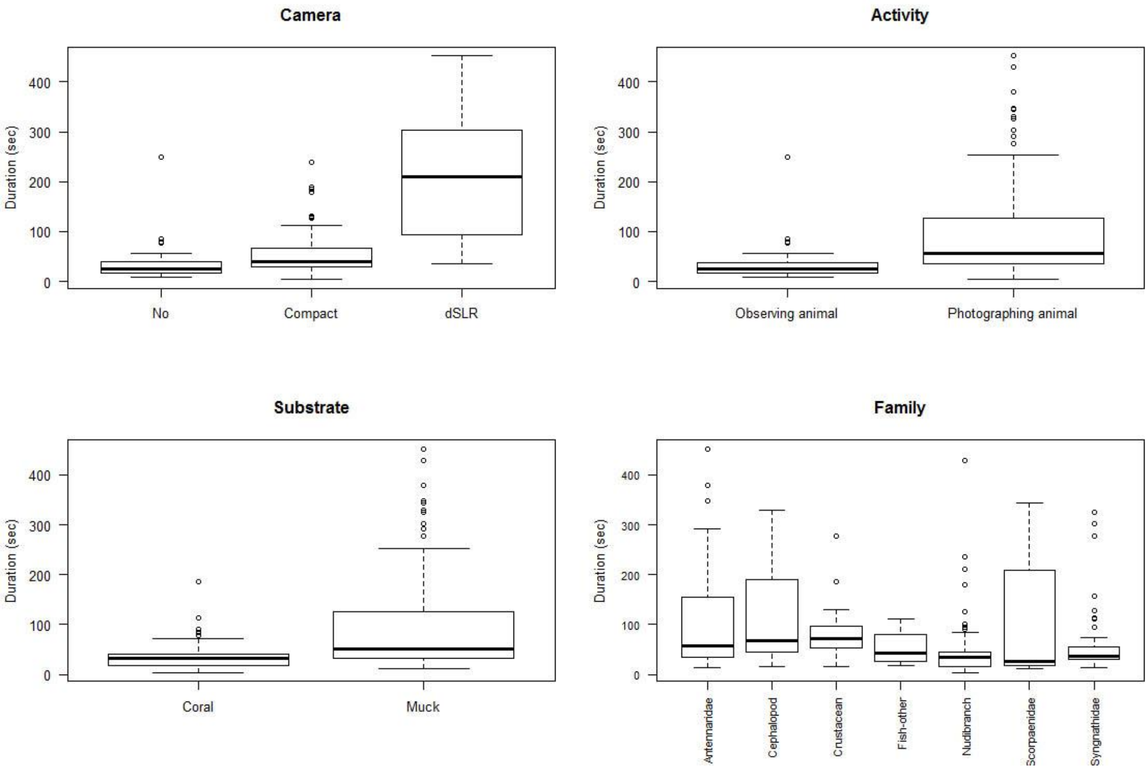


Figure 6.3 Effects of camera, activity, habitat and family on the duration divers interacted with cryptic fauna.

Table 6.3 Results of Repeated Measures ANOVA testing for effects of camera, activity, habitat and family on the duration divers interacted with cryptic fauna, using Diver ID as Random Factor in null model.

Factor	AIC	StdDev (log10)	P-value
Diver ID (null model)	127.6	0.081	
Camera	88.9		< 0.001***
Intercept (None)		1.43	
Compact		0.182	
dSLR		0.819	
Activity	113.7		< 0.001***
Intercept (Observing)		1.466	
Photographing		0.285	
Habitat	123.3		0.012*
Intercept (Coral)		1.512	
Muck		0.188	
Family	128.1		0.074

6.5 Discussion

Scuba dive tourism can be a sustainable source of income for coastal communities, but has potential drawbacks such as increased damage to fragile reef structures. It is important for management agencies to be aware of diver behaviour to minimise detrimental effects on the environment. We demonstrated that normal scuba diver behaviour changes significantly when interacting with cryptobenthic fauna, when diving in different habitats, and when using cameras. Diver certification level and gender also have an effect on behaviour, which should be taken into account when designing management strategies.

The number of divers observed during this study is in line with previously published studies, (see: Chung et al. 2013 (N = 81); Uyarra and Coté 2007 (N = 28); Roche et al. 2016 (N = 100), however the divers in this study were notably more experienced and older than those in other studies (Rouphael and Inglis 2001; Chung et al. 2013; Roche et al. 2016). These high levels of experience are typical for divers participating in muck dive tourism, or interested in cryptobenthic species (Giglio et al. 2015; De Brauwer et al. 2017). Therefore, results of this study are representative for divers in muck dive tourism. The impacts of diver behaviour could be different for less experienced divers on coral reefs, for which a large body of literature already exists (e.g. Chung et al. 2013; Roche et al. 2016).

This study showed that the rate divers make contact with the substrate strongly depends on the type of activity they are doing. When closely observing cryptobenthic fauna, divers approach the substrate more closely than they would during normal dive behaviour. A shift in attention from their surrounding environment to the animal of interest leads to more unintentional contact with the substrate. Divers seemed to be less careful while diving over sand than on coral reefs resulting in significantly more contacts. While this did not result in more observed damage, it is unclear if these disturbances have an impact on soft sediment habitats. The fact that the habitat type of the dive site only affected touch rates during standard observations and not during interactions illustrates the strong effect of diver interactions with cryptic species. Differences between habitats disappeared when divers focused on cryptobenthic fauna, suggesting that divers try harder to avoid fragile coral structures than sand, but that this avoidance behaviour fails when closely approaching small fauna.

These effects were strongest when divers were photographing animals instead of simply observing. Divers made more unintentional contacts with the substrate while photographing, both during interactions and normal dive behaviour. The type of camera a diver used affected how often the diver touched the substrate and how much damage they caused. Divers with compact cameras touched the substrate more often and caused more damage than those with dSLR cameras during normal dive behaviour. This difference could potentially be attributed to the fact that dSLR cameras are used by more experienced divers than compact camera users, allowing them to pay more attention to their environment as well as their camera (Roche et al. 2016; De Brauwer et al. 2017). However, during interactions, differences between camera types disappeared, again highlighting the strong effect of divers' attention being diverted elsewhere. A limitation of this study is the small number of divers using dSLR cameras. Further study focused on the behaviour of photographers using dSLR cameras is therefore suggested.

Photography also had a strong effect on how long divers interacted with wildlife, and was more important than the actual species they were interacting with. Divers with cameras spent up to ten times longer with animals than those who were merely observing. While this did not always result in more damage to the substrate, long interaction times could negatively affect the animals that are observed, particularly when divers also touch the animals. Divers showing cryptic animals to other divers touched animals most frequently, often using muck sticks or hands to coax animals into a better position to take a photograph. Muck sticks are used frequently to avoid injury from potentially dangerous species such as *Scorpaenidae* and blue ringed octopus (*Hapalochlaena* spp.). However, muck sticks can cause considerable damage to animals. On multiple occasions the authors observed crustaceans and crinoids suffering severed appendages from muck sticks. Previous studies have shown that touching animals can be stressful to cryptobenthic fauna and can lead to short-term behavioural changes (Harasti and Gladstone 2013). The continuous manipulations by large numbers of divers (up to 300/day on popular sites in the surveyed regions) are likely to cause chronic stress in slow-moving animals such as seahorses or frogfishes.

Confirming previous studies, divers in this study touched the substrate most frequently and caused the most damage with their fins and loose hanging dive equipment such as submersible pressure gauges or alternate air sources (Barker and Roberts 2004; Roche et al. 2016). During normal dive behaviour, male divers made more contact with the substrate than females and beginner divers caused more damage than experienced ones. This difference could be attributed to males being more prone to taking risks, or less likely to follow dive guide instructions (Luna et al. 2009). Similar trends have previously been reported on the Great Barrier Reef (Rouphael and Inglis 2001), but are different from Uyarra and Côté (2007) which found that female divers caused more damage. Differences between genders or certification levels disappeared when interacting with cryptobenthic fauna, another clear indication that these interactions are strong drivers of diver behaviour. The only diver level-based difference during interactions was that dive guides touched animals more frequently. Dive guides are paid to find and show animals to divers. With this economic incentive, guides undoubtedly feel the pressure of delivering ‘good’ customer service to divers wanting to observe or photograph rare cryptic species.

Divers in this study caused limited damage to the substrate per individual, yet with the high numbers of dive tourists on some sites, the accumulated effects will be significant. Furthermore, potential negative impacts caused by flash photography, remain unknown and should be investigated to assist in management of dive tourism (Harasti and Gladstone 2013). Mitigating the impacts divers have on fauna or substrates is therefore paramount. Adequate buoyancy training is essential to avoid accidental contacts with the substrate, but is not always sufficient in avoiding impacts during interactions. Pre-dive briefings can significantly reduce the impacts of divers on coral reefs (Camp and Fraser 2012). Dive guide interventions during the dive are even more effective at preventing damage than dive briefings (Barker and Roberts 2004; Roche et al. 2016). The question remains whether dive guide interventions are a viable option in the specialised muck dive industry, with its strong emphasis on photography. Cultural differences and a dependence on tips earned by satisfying customer requests to find interesting fauna create strong barriers for dive guides to intervene when their divers are behaving unethically. Dive guides require support from management coupled with education about the potential impacts, empowering them to respond to unethical behaviour. However, it is even more crucial for divers to be educated and made aware of their own impacts, as an awareness of impacts on animals has been shown to increase tourist willingness to make trade-offs that increase animal welfare (Bach and Burton 2017). Alternative regulations such as temporary closures of dive sites or limiting the maximum number of divers per site have been suggested and in some case successfully implemented (Zhang et al. 2016). Effective management is crucial, but is the current regime of self-regulation in dive tourism sufficient to address its impacts?

To ensure efficient management, we suggest the following guidelines:

1. Increased education for recreational divers and dive professionals about the impacts of unethical diver behaviour. This can be achieved during dive briefings or integrated with diver training using specialised programs for dive centres such as Green Fins, but needs the support of dive centre management to be successful (Roche et al. 2016). Education should include scientifically supported evidence explaining why certain behaviour is discouraged (Scott-Ireton 2008; Camp and Fraser 2012; Bach and Burton 2017).
2. Integrating all stakeholders in the development of a region-specific code of conduct. Stakeholders beyond dive tourism should be involved to create a wider support base (Dimmock and Musa 2015). Regional differences need to be taken into account to ensure

successful implementation of codes of conduct and to empower dive guides to take action under water (Wongthong and Harvey 2014).

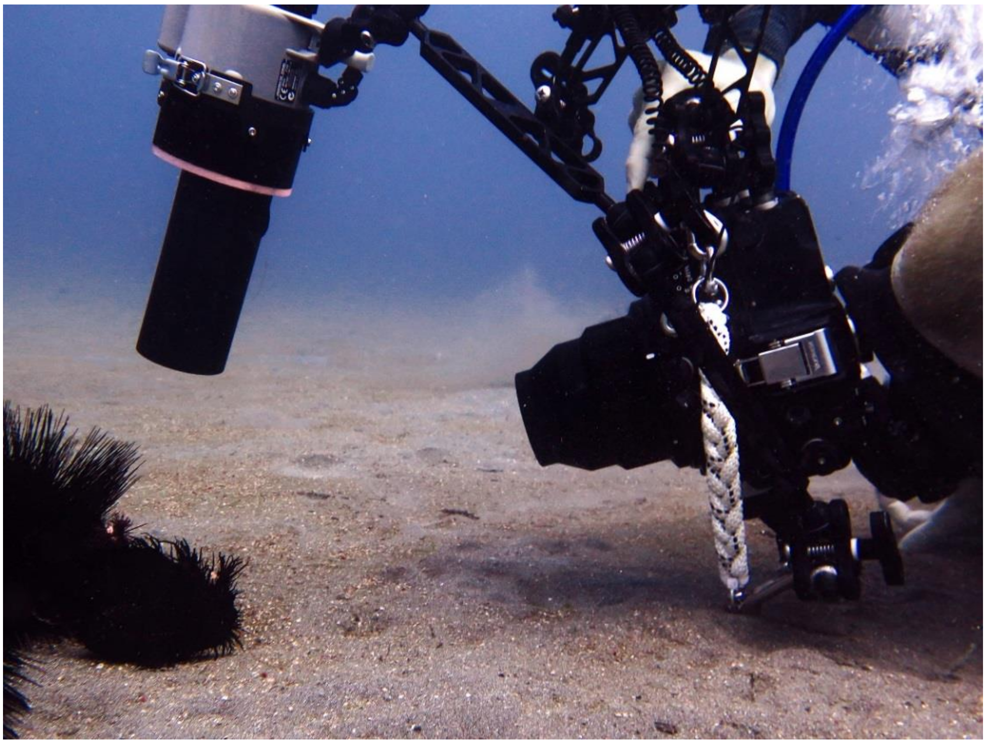
3. Increased awareness of scuba diver and wildlife photography impacts on a global scale. The competitive aspects of photography offers avenues to influence divers' attitudes concerning wildlife photography. Clear rules from the organising committees of photo competitions to no longer accept unethical behaviour would send a powerful signal. Large dive expos, dive magazines and wildlife photography publishing agencies such as National Geographic can fulfil a role-model function by not publishing images that are clearly the result of photographer manipulation.

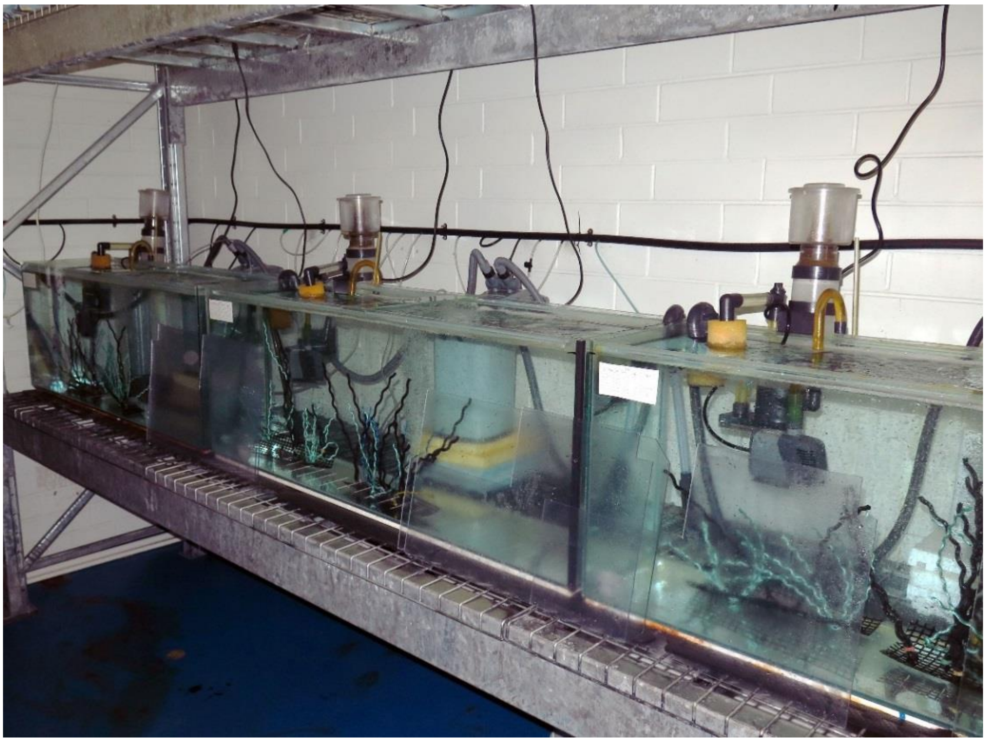
6.6 Conclusion

This research adds to a growing body of literature that explains diver behaviour and its potential impacts on the natural environment. It shows that the activity divers are undertaking underwater has a larger impact on their behaviour and associated environmental damage than their demographic profile. Divers interacting with cryptobenthic fauna, particularly photographers, have a higher impact on the substrate and touch animals more frequently than non-photographers. The frequent touching of animals and often extended periods of time divers spend with individual animals is likely to cause significant stress and requires the attention of management bodies, and targeted research. While underwater photography can be a powerful tool for conservation outreach, care needs to be taken that photography remains sustainable. The increased impacts of divers during interactions with cryptic fauna could be mitigated by increased education, and improved management practices including the development of region-specific codes of conduct. But, strong support from dive certification organisations, publishing houses that specialise in underwater photography, and the tourism industry is essential to ensure successful implementation. While there are significant challenges associated with managing scuba diver impacts, the economic contributions of dive tourism to local communities highlight the importance of striving for increased sustainability of the industry.

Postscript: In the final chapter I further investigate the impacts of diver behaviour on cryptobenthic fauna. In particular, I look into how different aspects of underwater photography affect the behaviour and physiology of seahorses, frogfishes and ghostpipefishes.

Chapter 7 Behavioural and pathomorphological impacts of flash photography on benthic fishes





Preface: This chapter has been published in the journal *Scientific Reports* (doi: 10.1038/s41598-018-37356-2). The chapter has been formatted according to journal guidelines, with one exception: the order in which the Methods and Results sections are presented follow the format of this thesis, rather than the *Scientific Reports* format. The combined references for all chapters can be found in the Cited Literature-section at the end of this thesis.

7.1 Abstract

Millions of people take animal pictures during wildlife interactions, yet the impacts of photographer behaviour and photographic flashes on animals are poorly understood. We investigated the pathomorphological and behavioural impacts of photographer behaviour and photographic flashes on 14 benthic fish species that are important for scuba diving tourism and aquarium displays. We ran a field study to test effects of photography on fish behaviour, and two laboratory studies that tested effects of photographic flashes on seahorse behaviour, and ocular and retinal anatomy. Our study showed that effects of photographic flashes are negligible and do not have stronger impacts than those caused solely by human presence. Photographic flashes did not cause changes in gross ocular and retinal anatomy of seahorses and did not alter feeding success. Physical manipulation of animals by photographing scuba divers, however, elicited strong stress responses. This study provides important new information to help develop efficient management strategies that reduce environmental impacts of wildlife tourism.

7.2 Introduction

Humans are fascinated by animals, and in addition to visiting zoos or aquaria and engaging in wildlife tourism, people spend a significant part of their time and money on observing and photographing wildlife (Gusset and Dick 2011; Newsome and Rodger 2013; Hausmann et al. 2017). An estimated 700 million people visit zoos and aquaria annually, indirectly contributing more than US$350 million to conservation (Gusset and Dick 2011). Wildlife tourism is estimated to be worth approximately £30 billion per annum (≈ US$40 billion) and can provide a sustainable source of income to local communities, benefit conservation practices, and has the potential to educate the general public (Wilson and Tisdell 2003; Job and Paesler 2013; Newsome and Rodger 2013). Tourism and photography are intrinsically linked, where photographs are used both to market destinations and record memories (Garrod 2009; Haller 2014). Where wildlife photography was traditionally the domain of large publishers like National Geographic, social media are now increasingly being used to share billions of wildlife and animal photos (Hausmann et al. 2017). Despite the high number of human-animal interactions, the potential impacts of photography on animals remain unclear (Heyman et al. 2010; Huang et al. 2011; MMO 2014). Animal welfare and ethics in tourism are frequently discussed in both the scientific and grey literature, yet very few studies have examined the behavioural or pathomorphological effects of photography on wildlife (Fennell 2013; Newsome and Rodger 2013; Fennell 2015).

Recreational scuba diving is an important sub-sector of wildlife tourism, with multiple studies highlighting its high economic value to local communities (Vianna et al. 2012; Pascoe et al. 2014; De Brauwer et al. 2017). While scuba diving might indeed be less destructive than extractive activities, such as fishing, it does have potential environmental impacts. The impacts of scuba diving on fragile habitat such as coral reefs have received considerable research interest (Hawkins et al. 1999; Hasler and Ott 2008; Roche et al. 2016). While the effects on habitat forming structures such as hard corals have been firmly established, far less is known about the effects on mobile fauna (Trave et al. 2017). Studies on large-bodied species such as sharks have shown that diver interactions can increase an animals' metabolism, cause behavioural changes, and reduce mobility (Shackley 1998; Clua et al. 2010; Barnett et al. 2016). However, little is known about the effects of scuba diving on smaller teleost fishes, although it has been established that diver presence can disturb spawning aggregations (Heyman et al. 2010) and that touching seahorses can lead to short-term behavioural changes (Harasti and Gladstone 2013).

Overall, goal-oriented diver behaviour, such as photography, has greater impacts on the marine environment than general dive activities (Rouphael and Inglis 2001; Barker and Roberts 2004; Uyarra and Côté 2007). While taking pictures, divers spend more time close to marine life, causing damage to the substrate and often touching animals (De Brauwer et al. 2018). Divers will occasionally carry "muck sticks" to coax animals into a better position for photographs (Roche et al. 2016). The effects of touching or moving marine life has not been studied in detail, but can be expected to cause behavioural changes (Harasti and Gladstone 2013; De Brauwer et al. 2018). The bright photographic strobes used in underwater photography frequently raise questions about potential impacts on animals' behaviour and/or their visual systems, yet thus far, no significant effect of flash photography has been detected on the behaviour of teleost fishes (Heyman et al. 2010; Harasti and Gladstone 2013).

Despite the lack of scientific evidence, a multitude of regulations exist related to photographing marine wildlife, based on the unsubstantiated concern of causing (temporary) blindness in animals, either while scuba diving or visiting aquaria. Public aquaria around the globe prohibit the use of flash while taking photographs, without any scientific evidence to support the ban. Scuba dive resorts in Southeast Asia often restrict the use of flash while photographing pygmy seahorses (Smith 2010) and in the U.K. a ban on using flash while taking pictures of seahorses is in place, despite open acknowledgment of a lack of evidence to support the ban (MMO 2014).

Charismatic and cryptic species such as seahorses (two families within the sub order *Syngnathoidei*) and frogfishes (family *Antennariidae*) are highly popular with underwater photographers and are often displayed in aquaria (Koldewey 2005; Uyarra and Côté 2007). Cryptic species such as these depend on camouflage to avoid predation. Many are slow swimmers and not capable of fleeing from scuba diving photographers. Flash photography does not affect site persistence of seahorses, but touching them elicits, at the very least, short-term stress behaviours (Harasti and Gladstone 2013). Species like seahorses are visual predators that rely on accurate resolving power to catch prey. Any reduction in visual acuity or sensitivity is likely to reduce survivorship (Mosk et al. 2007). The high intensity light of photographic strobe lights could theoretically result in phototoxic retinal damage. This damage could be either short term or permanent retinopathy due to photothermal, photomechanical and/or photochemical effects of high retinal irradiance. Retinopathy has been previously observed in mammals, including humans (e.g. (Organisciak and Vaughan 2010; Youssef et al. 2011)), and also in the photoreceptors of teleosts (e.g. (Taylor et al. 2012; Thomas et al. 2012)). However, a link between flash photography damage to the eye structure of animals has yet to be shown. In addition, questions remain about the effects on fishes of scuba diver behaviour associated with flash photography, in particular the potential effects on feeding efficiency due to temporary reductions in visual acuity and other potential stress responses.

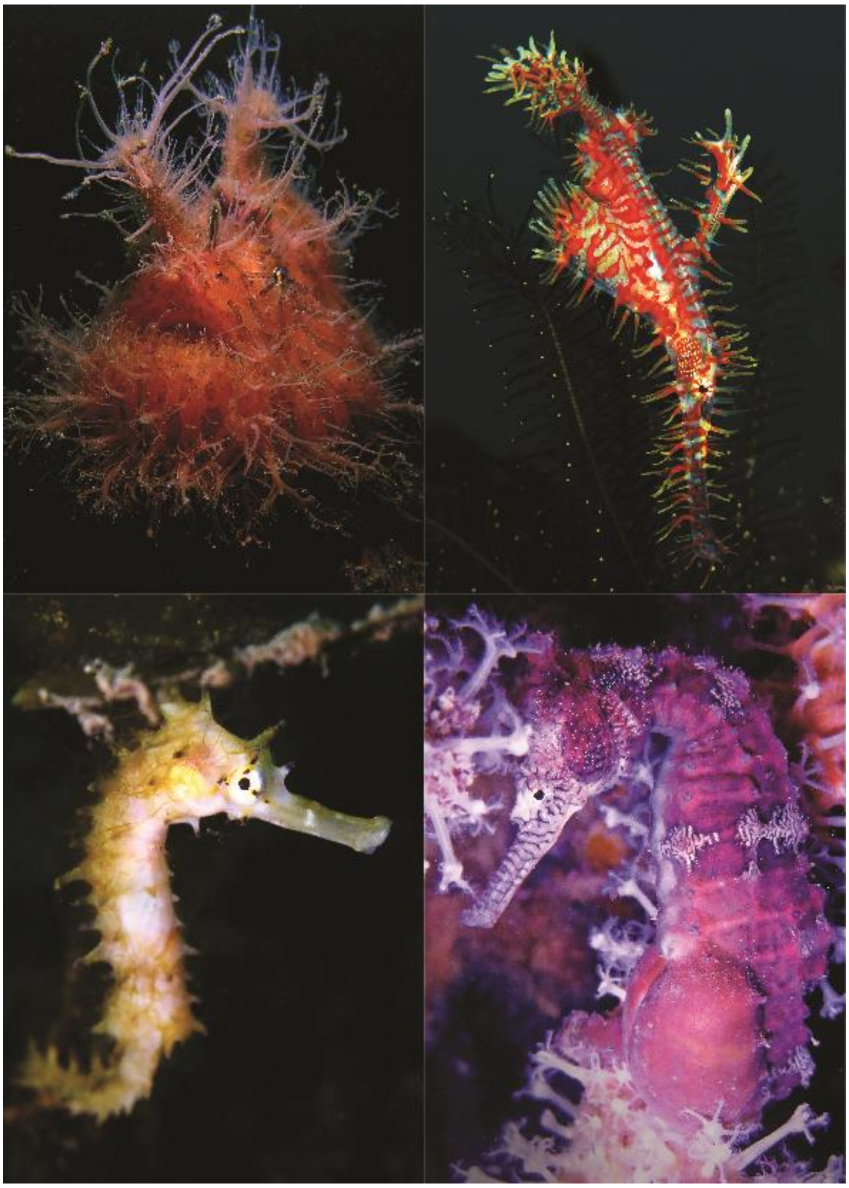


Figure 7.1 Four representative species used in this study (From top left, clockwise: *Antennarius striatus*, *Solenostomus paradoxus*, *Hippocampus subelongatus*, *Hippocampus histrix*).

To answer these questions, we conducted an *in situ* behavioural experiment on 13 species of teleosts from three families (*Syngnathidae*, *Solenostomidae* and *Antennariidae*) commonly found at dive sites throughout Southeast Asia (Figure 7.1). We then ran two controlled aquaria experiments to assess the behavioural and pathomorphological effects of flash photography on a species of seahorse. Specifically we set out to: 1) Quantify the effects of diver behaviour associated with flash photography on slow-moving, cryptic fishes; 2) Assess the effects of photographic flashes on the Western Australian seahorse (*Hippocampus subelongatus*) and 3) Examine the pathomorphological impacts of photographic flashes on the ocular and retinal anatomy of *H. subelongatus*.

7.3 Materials and methods

Ethics statement

All experiments were conducted in accordance with the Animal Ethics Committee of Curtin University (AEC_2016_29) and The University of Western Australia (RA/3/100/1220) in compliance with the Australian Code for the Care and Use of Animals for Scientific Purposes. Seahorse collecting in Western Australia was conducted under Fisheries Exemption Number 2798, approved by the Western Australian Department of Fisheries.

7.3.1 Effects of diver behaviour

7.3.1.1 Site description

To investigate the effects of disruptive diver behaviour *in situ*, a field experiment was conducted in Dauin, Philippines (9° 11' 19" N, 123° 16' 10" E). Dauin is an increasingly popular SCUBA diving destination for observing and photographing cryptobenthic fauna (De Brauwer et al. 2017). Experiments were conducted across five sites spanning 2 km. Bottom composition on all sites was predominantly soft sediment (volcanic sand), with very limited seagrass or coral growth in shallow areas.

7.3.1.2 Species description

For this study, we observed species of *Antennariidae* and *Syngnathoidei*. *Antennariidae* (frogfishes) are ambush predators that use an adapted first dorsal spine to attract prey and occur on shallow coral reefs and soft sediment sites (Pietsch and Grobecker 1987). The sub-order *Syngnathoidei* contains the *Syngnathidae* and *Solenostomidae* families, which are considered to be sister families (Orr and Fritzsche 1993). Both families are visual ambush predators that feed on small invertebrates, ingested through a tubular mouth. The *Syngnathoidei* species used in this study were medium-sized (Range: 50 mm – 150 mm Total Length (TL)) and were found near seagrass, plant debris or rocks.

7.3.1.3 Experimental design

Experiments were conducted by scuba diving in May 2016, opportunistically sampling across five sites. Care was taken to target different depths and areas between different dives to avoid re-sampling the same individuals within the same site, an approach that is possible due to the limited mobility of the target species. Observations were only taken in the daytime (between 9:00 am and 4:00 pm) and no deeper than 27m. When a focal animal was found it was initially observed for three minutes from a minimum 2m distance (Control - C). Preliminary observations showed this distance did not affect individual behaviour, which is in line with previous research that found that small fish are less shy than larger fish (Bozec et al. 2011). After the control observations were recorded, the animals were randomly allocated to one of four experimental treatments conducted by a second researcher and adapted from Harasti et al. 2013: diver presence (TP), diver with flash (T1), diver manipulation without flash (T2), or diver with flash + manipulation (T3). The diver presence treatment (TP) consisted of a diver closely approaching the animal (<30cm), while holding a DSLR camera and remaining at this distance for three minutes without taking pictures or touching the animal. This treatment is considered to be similar to no-flash photography or observing without a camera (Harasti and Gladstone 2013). Flash treatment (T1) consisted of a diver with a DSLR camera approaching the animal closely (<30 cm), remaining near the animal for three minutes, and taking a total of 15 pictures using both flash strobes. During the manipulation treatment (T2) the diver carrying the DSLR camera approached the animal closely (<30 cm) and remained at that distance for three minutes. Instead of taking pictures, the researcher gently nudged the animal 20 times using a 30 cm “muck stick” (a handheld stainless steel or aluminium rod). This type of manipulation is common amongst underwater photographers and is used to reposition an animal in order to get a better picture (Roche et al. 2016). The flash and manipulation treatment (T3) combines T1 and T2, with the researcher staying close to the animal (<30 cm) for three minutes, taking 15 pictures with flash and gently prodding the animal 20 times. This treatment is the equivalent of the behaviour of photographers who take pictures, while manipulating the animal. For each treatment, the researcher who undertook the initial control observation (C) recorded the responses, while staying a minimum distance of 2m away from the focal animal and the second researcher conducting the experimental treatments. The camera used during the experiment was a Canon 7D Mk1, with a Nauticam housing and two external Inon Z240s high power (ISO 100 Guide Number 24) strobes. Strobes were fired at half strength, with a light colour temperature of 5500K.

7.3.1.4 Response categories

Changes in the behaviour of focal animals were recorded continuously and classified as one of three categories: avoidance behaviour, threat displays, and feeding behaviour. Avoidance behaviour was further specified as: turning to face away from observer, moving less than 50cm, and moving more than 50cm. Threat displays were defined as: erecting fins (frogfishes only) and yawning (frogfishes only). Syngnathoidei did not show threat displays. Feeding behaviour was further categorised as: waving lure (frogfishes only) and feeding (striking at prey).

7.3.1.5 Data analysis

Differences in behavioural responses were analysed separately per family as certain responses are family-specific (e.g. *Syngnathidae* are physically incapable of yawning). To ensure behaviour was similar for different taxa, preliminary Kruskal-Wallis tests were conducted comparing the different taxa, taxa which differed significantly from each other in their reactions were analysed separately.

The analysis tested two separate questions: 1) if different diver behaviour caused a behavioural change compared to having no diver present; and 2) if, in the presence of a diver, different treatments caused different reactions. To answer the first question, the control observations (conducted for each individual) were compared to treatments using paired Wilcoxon rank sum tests, as data was non-normally distributed. Kruskal-Wallis rank sum tests were then carried out to answer the second question, i.e. to detect differences in reactions between treatments. The individual control observations were excluded from this analysis, in order to only test the different diver treatments. The four groups of paired control observations were compared using Kruskal-Wallis rank sum tests to check for differences in control groups. Statistically significant effects were investigated using pairwise Wilcoxon rank sum tests. Holm-method p-value corrections were applied and used when testing for significance to reduce the chances of type I errors (McLaughlin and Sainani 2014). Original non-corrected p-values are presented in results for clarity, as non-significant Holm-adjusted p-values commonly resulted in p-value equal to one. All data analyses were conducted using the R software package (R Team 2015).

7.3.2 Behavioural effects of photographic flashes

To test the effects of photographic flashes independent of diver presence, a tank experiment was conducted at the Curtin Aquatic Research Labs in Perth, Australia. The experiment ran for 6 weeks from September to October 2016. The West Australian seahorse (*Hippocampus subelongatus*), a medium-sized seahorse species endemic to Western Australia which is relatively abundant in the waters near Perth (Lourie et al. 1999), was used as a model species. This species was used rather than the species observed in the field experiment, as the latter could only be acquired via the marine aquarium trade without guarantees of sustainability or non-destructive catch methods.

7.3.2.1 Specimen collection and husbandry procedures

Three 192L tanks (122cm x 35cm x 45cm) were set up four weeks prior to collecting seahorses to establish stable water quality conditions. Each tank had its own recirculating system and artificial seagrass made of rope placed to serve as holdfasts for seahorses. The tank room had a regime of 14 hours artificial light per day, mimicking local daylight hours at the time. Water temperature, O_2 saturation, salinity, ammonia, and nitrites were tested daily to ensure optimal conditions. Water temperature was kept between 17°C and 19°C and salinity maintained between 36ppm and 38ppm. Tanks were cleaned twice per week and 25% water changes performed once every three days, or as required. Seahorses were fed three times daily with live *Artemia* enriched with a commercially prepared emulsion of essential fatty acids. Fish were left to acclimatise in the holding tanks for three weeks prior to the start of experiments.

Once conditions in the holding tanks were stable, 37 seahorses of a size range between 110 and 240 mm TL were collected by scuba diving from four different sites along the Perth shoreline. Care was taken not to collect pregnant males or mating pairs. Prior to placing seahorses in holding tanks, each seahorse was tagged using elastomer tags to identify individuals (Woods and Martin-Smith 2004) and TL measured as the sum of head, body and tail length (Lourie 2003). Seahorses were then placed in one of the three tanks independent from treatment, to avoid any potential holding tank effects.

7.3.2.2 Experimental design

Each seahorse was allocated to one of three treatment groups: control (C) (N = 12), low intensity (TL) (N = 12) and high intensity (TH) (N = 12). During the experiment, seahorses were removed from their holding tanks by hand and placed individually in one of two 17L treatment tanks (31cm x 23cm x 25cm), with an artificial holdfast similar to those in the holding tanks placed in the centre. A Sea&Sea YS-250PRO underwater strobes (Colour temperature 5600K; ISO 100 full power guide number 32) was placed on the side of each treatment tank, touching the glass of the tanks (Figure 7.2). A black cloth was hung around each of the treatment tanks to avoid any observer effect and to avoid seahorses seeing each other. Water in the treatment tanks was the same temperature and salinity as water in the holding tanks. A small desk lamp was permanently placed 1.5m above the tanks to provide sufficient light for filming trials. Seahorses were left to acclimatise in the treatment tanks for five minutes prior to commencing treatment. A Sony Handycam HDR-CX12 video camera was placed in front of each treatment tank to record seahorse behaviour. Trials ran in the morning, prior to feeding the seahorses.

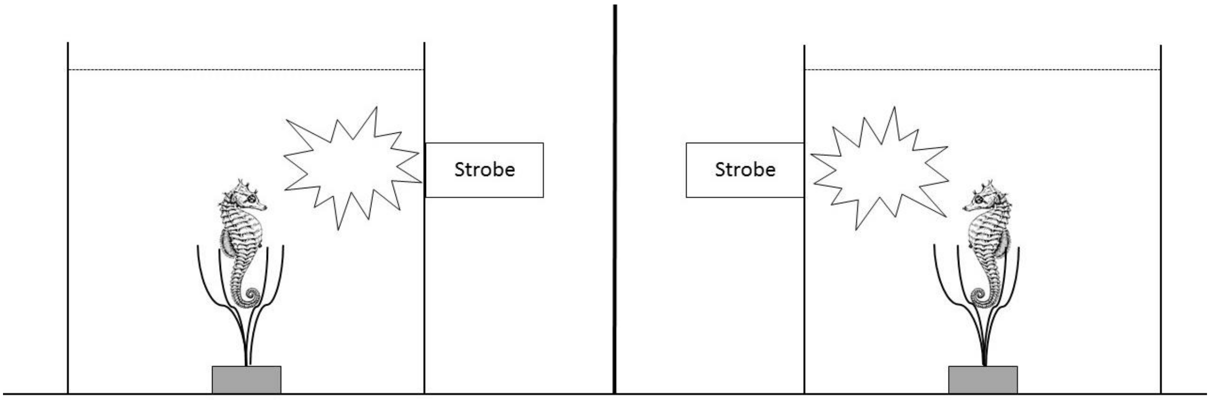


Figure 7.2 Treatment tank setup: two 17L tanks separated by a black cloth, a holdfast consisting of artificial seagrass in the middle of each tank, a Sea&Sea YS-250PRO underwater strobe placed against each tank. A video camera was placed in front of both tanks and a black cloth was hung around the tanks.

Each trial started by releasing 2ml of seawater containing *Artemia* (approx. 25 *Artemia*) into the treatment tank using a pipette, after which trials ran for ten minutes. In control treatments, seahorses were left undisturbed. For low intensity treatments, the strobes were fired at highest strength once every 30 seconds. In the high intensity treatments, strobes were fired at highest strength once every 15 seconds. By using the highest flash strength and placing the strobes against the tank, flash intensity is stronger than in normal scuba dive photography, where animals the size of seahorses are usually photographed with strobes on mid-or one third of maximum strength. The strobes we used were also of much higher intensity than the built-in strobes of cameras frequently by visitors in zoos or aquaria. Strobes were fired remotely by a researcher on the other side of the black cloth, out of view of the seahorses.

After the trials, seahorses were put back into their holding tanks, the water in the treatment tanks was changed and two new seahorses were placed in the treatment tanks. The experiment ran for three consecutive days until each seahorse had received its treatment. Trials were repeated on each subject a total of four times, during which each seahorse remained in its designated treatment group. Between trials, seahorses had a minimum of four days recovery time without exposure to any treatment to minimise stress and avoid any habituation effects. Upon conclusion of the experiment, seahorses of the low intensity treatment group and two seahorses of both the high and control groups were donated to a local public aquarium, as releasing animals back in the ocean was not possible due to permit restrictions.

7.3.2.3 Response categories

Behavioural response categories were adapted from (Faleiro et al. 2008). Four response categories were used: Hunting efficiency, spatial use, activity, and ventilation rate (for definitions see Table 7.1). Hunting efficiency counted the instances of a seahorse striking at food, catching food, and hunting success (ratio of catches to strikes). Spatial use was measured in two ways: the distance of the animal from the side of the tank where the strobe was positioned, and the seahorses' orientation towards the strobe. Activity was the time seahorses spent showing a specific behaviour: inactive, swinging, swimming, hunting, or startled responses. Ventilation rates were used as a proxy for stress and were measured by counting and averaging opercular beats twice for two periods of 20 seconds.

Table 7.1 Definitions of seahorse responses to flash treatments.

Category	Action	Description
Hunting efficiency		
Action	*Strike*	Seahorse attempts to strike at prey.
	Catch	Seahorse catches and swallows prey.
	Success	Ratio of catches to strikes.
Spatial Use		
Position	*Zone 1*	The first vertical quarter of the tank, closest to the strobe.
	Zone 2	The second vertical quarter of the tank relative to the strobe (Holdfast present in this zone).
	Zone 3	The third vertical quarter of the tank relative to the strobe (Holdfast present in this zone).
	Zone 4	The forth vertical quarter of the tank furthest away from the strobe.
Orientation	*Towards*	The seahorse faces in the direction of the strobe.
	Neutral	The seahorse faces towards the camera or away from camera, both eyes are visible (30 degree angle towards or away from camera).
	Away	The seahorse faces away from the strobe.
Activity		
Rest	*Inactive*	The seahorse remains resting, without performing any kind of movement, while attached or unattached to the holdfast.
	Swinging	The seahorse remains attached to the holdfast, with slight movements of the head or body.
Active	*Hunting*	The seahorse swims or tilts the body, head or snout in the direction of prey. Attempted strikes at food irrespective of success.
	Swimming	The seahorse moves horizontally or vertically (through the water or across the bottom of the tank) with undulating pectoral and dorsal fins.
	Startled	The seahorse repeatedly and rapidly contracts and contorts the body, strikes or swims into the tank wall, displays sudden erratic movements.

7.3.2.4 Data analysis

Videos of the trials were analysed twice. During the first analysis, hunting efficiency and spatial use (noted every 10 seconds) were measured. To measure position accurately, treatments tanks were divided in four vertical, equal-sized zones marked by strips on the outside of the aquaria. The second analysis was used to measure seahorse activity (noted every 10 seconds) and ventilation rates (measured at 5 minutes and 10 minutes, then averaged). Video analysis started from the moment *Artemia* were introduced into the treatment tanks and lasted for ten minutes. Videos were analysed in a random order and behavioural definitions reviewed frequently to minimise observer drift effects (Martin et al. 1993; Burghardt et al. 2012).

Data on behavioural responses were transformed to best meet assumptions of normality before statistical analyses that were conducted in R (R Team 2015). We used a repeated measures ANOVA to detect the effects of treatments on behavioural responses, with seahorse ID as a random factor to examine the effect of different repetitions. ANOVA's were followed by Tukey's HSD post hoc tests for significant effects. We further tested for interactions between seahorse sex, size, and origin. Spatial use was tested using χ^2 contingency table tests. All analyses were conducted in R using the lme4 package (Bates et al. 2015) for the repeated measures ANOVA and the multcomp package (Hothorn et al. 2008) for performing the post-hoc tests.

7.3.3 Pathomorphological effects of photographic flashes

To assess the pathomorphological effects of intense flash photography on the visual system of cryptobenthic fauna, seahorses from experiment two were subjected to a second treatment. Ten randomly selected seahorses from both the high intensity treatment (TH) and control (C) groups were retained after concluding experiment 2. Seahorses were held in the same holding tanks as experiment 2 for the duration of this experiment.

7.3.3.1 Experimental design

Seahorses were moved daily into one of two treatment tanks (61cm x 25cm x 31 cm). All seahorses (N = 10) of the control group were placed in a control tank, and all seahorses (N = 10) of the high intensity treatment were placed in a flash treatment tank. Two Sea&Sea YS-250PRO underwater strobe (Colour temperature 5600K; ISO 100 full power guide number 32) were positioned on either side of the flash treatment tank, touching the glass of the tank. No strobes were placed next to the control tank. Both tanks were separated from each other by black cloth to avoid flash reaching seahorses of the control group. Seahorses were kept in the treatment tanks for 150 minutes, during which the strobes of the flash treatment tank were fired a total of 200 times at highest strength. While this strength would not normally be used during underwater photography, this was designed to test the “worst-case scenario”. Strobes were fired remotely by a researcher on the other side of the black cloth, invisible to the seahorses. Over the course of both flash experiments (34 days), seahorses in the highest flash treatment were subjected to a total of 4600 flashes or an average of 135 day^{-1}. The experiment ran for 15 days, after which seahorses were euthanized with a lethal overdose of tricaine methanesulfonate (MS 222).

7.3.3.2 Eye and retina preparation

After euthanasia in MS222, seahorse eyes (both left and right) were enucleated and both the anteroposterior and dorsoventral diameters of the eye were measured with a pair of digital callipers to the nearest 0.01 mm. The anterior segment (cornea, lens and iris) were then dissected free of the scleral eyecup and the lens diameter also measured using the callipers. All ocular and retinal measurements (see below) were performed “blind”, where the experimenter was not aware of which individual belonged to each treatment group.

Each eye was then immersion fixed in 2.5% glutaraldehyde, 2% paraformaldehyde in 0.1 M phosphate buffer (pH 7.2) and stored in fix at 4°C for four weeks. The material was then washed in 0.1M phosphate buffer and post-fixed in 1 to 2% osmium tetroxide. The eyecup was then embedded in Araldite, and semi-thin (1 µm) sections were cut on an ultramicrotome (LKB) using glass knives. Semi-thin sections were stained with Toluidine blue, coverslipped in Entellan, mounting medium and photographed as TIFF images using an Olympus DP30 low noise 12-bit monochrome digital (1360x1024 pixel) camera mounted on a Leica Dialux compound microscope at a magnification between 40 x and 1000x. Semi-thin sections were taken progressively through the eye in order to locate a standardized transverse section of the retina that incorporated the temporo-ventral fovea (Mosk et al. 2007), and both central and dorsal retinal regions. The location of the optic nerve was used as a way of standardizing the location of section to allow for comparative analysis of both treated and control eyes.

Only retinal sections that were deemed to be cut in transverse section (not obliquely) were used for analyses. Defined retinal regions (central and foveal) were examined, where retinal thickness (inner limiting membrane to Bruch’s membrane), photoreceptor length (vitread limit of synaptic terminals to sclerad limit of outer segment), rod inner and outer segment length and width, cone inner segment width, the thickness of the inner and outer nuclear layers, and the thickness of the inner plexiform and ganglion cell layers were analysed (Figure 7.3). Measurements of eye anatomy and retinal layer structure (Table 7.2) were undertaken to identify gross anatomical changes or major histological damage attributable to light exposure. The thickness of the perifoveal retinal region was measured to provide a way of assessing any gross changes specific to the visual axis given this retinal specialization would typically be aligned and fixated on prey during feeding (Easter 1992; Collin and Collin 1999; Mosk et al. 2007). The perifoveal region was targeted due to the difficulty in accurately identifying the central region of the foveal pit and the elongated orientation of the foveal slit in this species.

Table 7.2 Variables measured to test effects of flash photography on the eye anatomy of *Hippocampus subelongatus.*

Variable	Measurements
Anteroposterior eye diameter (Left)	One measurement per eye
Anteroposterior eye diameter (Right)	One measurement per eye
Dorsoventral eye Diameter (Left)	One measurement per eye
Dorsoventral Diameter (Right)	One measurement per eye
Lens Diameter (Left)	One measurement per lens
Lens Diameter (Right)	One measurement per lens
Retinal thickness	Three measurements per retina
Photoreceptor length	Three measurements per retina
Inner plexiform thickness	Three measurements per retina
Inner nuclear layer thickness	Three measurements per retina
Retinal ganglion cell layer thickness	Three measurements per retina
Outer nuclear layer thickness	Three measurements per retina
Perifoveal retinal thickness	Two measurements left and right of fovea
Cone photoreceptor inner segment width	Five measurements per retina
Rod inner segment width	Five measurements per retina
Rod outer segment width	Five measurements per retina

7.3.3.3 Data analysis

We compared 13 variables: three variables of gross anatomy for both the eyes and lenses, and ten variables relevant to retinal anatomy for the right eyes. The sizes of different retinal structures, particularly the thickness of easily differentiated retinal layers, were measured using ImageJ (Schneider et al. 2012). For each retina, we took multiple different measurements for each retinal morphological variable and used the mean of those measurements for testing (Table 7.2, Figure 7.3). All metrics were measured blind; the researchers conducting measurements were unaware which treatment groups each sample belonged to.

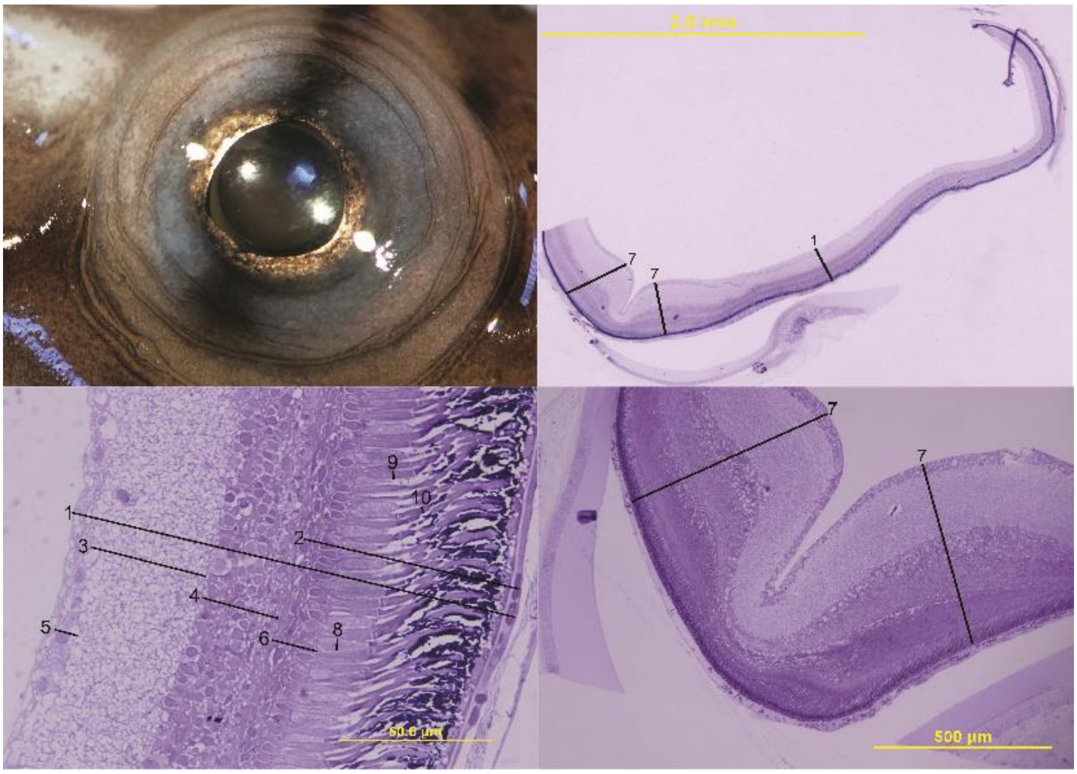


Figure 7.3 Retinal morphology characteristics measured on the eyes of Hippocampus subelongatus. (from top left, clockwise: Eye in situ prior to enucleation; Retina at x4 magnification; Fovea at x10 magnification; Retina at x100 magnification). Variables: 1) Retinal thickness, 2) Photoreceptor length, 3) Inner plexiform thickness, 4) Inner nuclear layer thickness, 5) Retinal ganglion cell layer thickness, 6) Outer nuclear layer thickness, 7) Perifoveal retinal thickness, 8) Cone photoreceptor inner segment width, 9) Rod inner segment width, 10) Rod outer segment width.

Data from ocular gross morphology (eye and retina) and retinal morphology were analysed using the PERMANOVA+ package in Primer 7 to do a multivariate analysis of variance. For both ocular and retinal morphology, data were first normalised to allow for comparisons as measurements were on different scales. We tested correlated variables and removed variables that were strongly correlated ($r > 0.85$) prior to testing. Data met assumptions of normality and heterogeneity, so untransformed data were used to construct a Euclidean distance resemblance matrix. We tested the differences between treatments using PERMANOVA+ based on a one factor design (Treatment (Fixed)), with an unrestricted permutation of raw data, running 9999 permutations.

To compare variables separately, all variables were tested for assumptions of normality and the two treatment groups compared with unpaired t-tests using R (Team 2015). For one variable (photoreceptor length) assumptions did not meet normality, so a Wilcoxon rank test was used to test differences between control and flashed groups. Holm corrections were applied to account for the increased likelihood of false positive Type I errors (McLaughlin and Sainani 2014). Original p-values are presented in results for clarity, as non-significant Holm-adjusted p-values commonly resulted in p-value equal to one.

7.4 Results

7.4.1 Diver effects on fish behaviour

During this experiment, 82 different individual fish were observed (Table 7.3). Fish that responded to the photographing diver by moving away further than 50 cm were not observed frequently enough to include in the analysis. Therefore, all further references to fish movement refers to animals moving less than 50 cm away from the diver.

Table 7.3 Species (N) observed during the diver behaviour effects field experiment. **Syngnathoidei* is a suborder, containing sister-families *Syngnathidae* and *Solenostomidae*. TP: Diver presence treatment; T1: Flash only treatment; T2: Manipulation without flash treatment; T3: Manipulation including flash treatment. Every individual animal was also observed from >2m distance as a control (N = 82).

Family (N)	Genus (N)	Species (N)	TP (N)	T1 (N)	T2 (N)	T3 (N)
Antennariidae (48)	*Antennarius (36)*		**9**	**9**	**9**	**9**
		commersoni (2)	1	1	0	0
		pictus (27)	7	5	8	7
		striatus (6)	1	2	2	2
		sp. (1)	0	1	0	0
	Antennatus (12)		**3**	**3**	**3**	**3**
		sp. (ocellated) (10)	1	3	3	3
		nummifer (1)	1	0	0	0
		sp. (1)	1	0	0	0
*Syngnathoidei** (34)	*Hippocampus (20)*		**5**	**5**	**5**	**5**
		histrix (8)	1	3	2	2
		barbouri (5)	3	1	1	0
		kuda (6)	1	0	2	3
		alatus (1)	0	1	0	0
	Solenostomus (14)		**3**	**4**	**4**	**3**
		paradoxus (4)	0	0	2	2
		cyanopterus (10)	3	4	2	1

7.4.1.1 Antennariidae

Insufficient instances of feeding were observed in individuals of this family of teleosts, so this variable was not included in further analysis. Since no statistically significant effect of genus was found, data were analysed at on only the family level. Diver presence (TP) and flash (T1) treatments had no significant effect on any of the behavioural reactions (Figure 7.4, Table in Appendices). Manipulation (T2) and manipulation + flash (T3) significantly increased the occurrences of movement, turning away from the stressor and erecting fins (Figure 7.4, Table in Appendices). None of the treatments had a significant effect on luring or yawning (Figure

7.4, Table in Appendices). The four groups of paired control observations per treatment were not significantly different from each other.

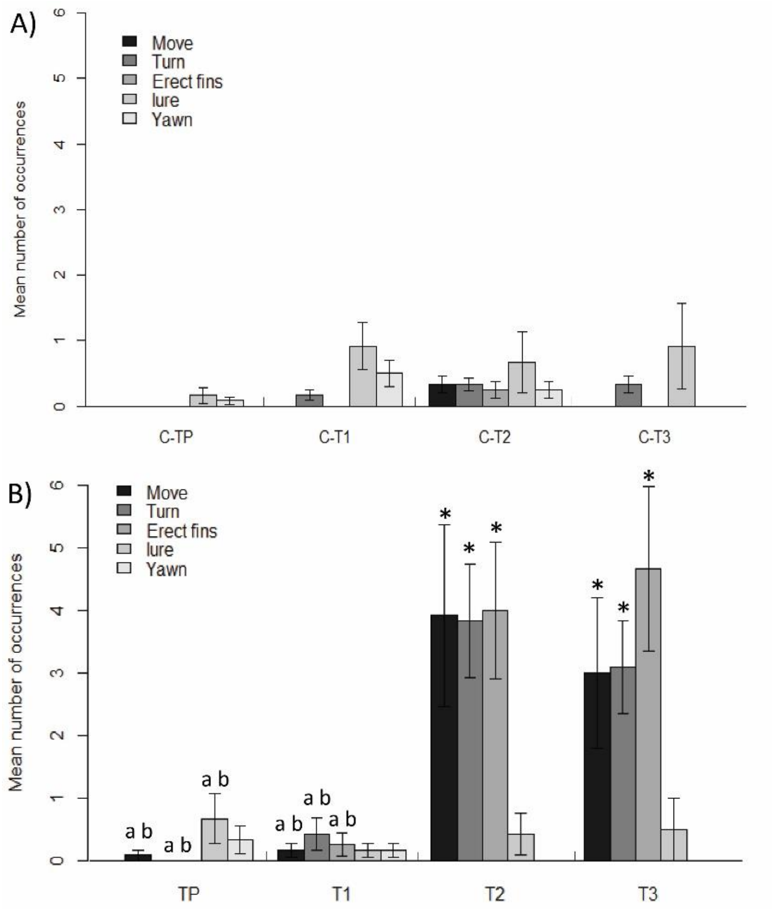


Figure 7.4 Mean number of occurrences of different reactions (±SE) of *Antennariidae* from the central Philippines to diver presence and flash photography. A: Control observations, B: Treatment observations. TP: diver presence (N = 12), T1: flash (N = 12), T2: manipulation (N = 12), T3: manipulation + flash (N = 12). Significance level of treatments compared to control after Holm-Bonferroni corrections: $p < 0.05$, *: different to Control, a: different to T2, b: different to T3.

There were significant differences between the treatments for movement, turning, and erecting fins (Table 7.4). T2 and T3 both had a greater number of occurrences of all of these, and were different from TP and T1, but not from each other (Table 7.4). TP and T1 were never different from each other (Table 7.4).

7.4.1.2 Syngnathoidei

When testing differences between taxa, *Solenostomus* spp. and *Hippocampus* spp. did not react significantly different for turning away ($p = 0.738$) or feeding ($p = 0.075$), but there was a genus-effect for increased movement ($p < 0.001$). Data for movement were therefore analysed at the genus level and data for turning and feeding were analysed on the family level. On the family level, there was no effect of treatments on feeding (Figure 7.5, Table in Appendices). *Syngnathoidei* did show a significant increase in turning for all treatments, except for diver presence (Figure 7.5, Table in Appendices). Kruskal-Wallis tests showed that for *Syngnathoidei, Hippocampus* spp., and *Solenostomus* spp. there were no differences in the reactions to any of the different treatments (Table 7.4). The four groups of paired control observations per treatment were not significantly different from each other.

Table 7.4 Results Kruskal-Wallis rank sum tests comparing different treatments (excluding controls) and for post-hoc pairwise Wilcoxon rank sum tests. For Wilcoxon tests (excluding controls), only significantly different treatments are shown. TP and T1 were never different from each other, neither were T2 and T3. TP: diver presence, T1: flash, T2: manipulation, T3: manipulation + flash. *Significance level after Holm-Bonferroni corrections p<0.05, **p<0.01, ***p<0.001, °p<0.1.

	Kruskal-Wallis			Wilcoxon	
Reaction	X^2	*df*	p	TP (p)	T1 (p)
Antennariidae					
Movement	15.427	3	0.002**	T2 (0.003**)	T2 (0.006**)
				T3 (0.008**	T3 (0.018.)
Turn	25.771	3	<0.001***	T2 (<0.001***)	T2 (<0.001***)
				T3 (<0.001***)	T3 (0.003**)
Erect	23.403	3	<0.001***	T2 (<0.001***)	T2 (0.002**)
				T3 (<0.001***)	T3 (0.002**)
Yawn	4.280	3	0.233	-	-
Lure	1.047	3	0.790	-	-
Syngnathoidei					
Turn	6.364	3	0.095°	T2 (<0.001***)	-
				T3 (<0.001***)	
Feed	4.791	3	0.188	-	-
Hippocampus spp.					
Movement	7.287	3	0.063°	T2 (0.025*)	-
				T3 (0.025*)	-
Solenostomus spp.					
Movement	4.239	3	0.237	-	-

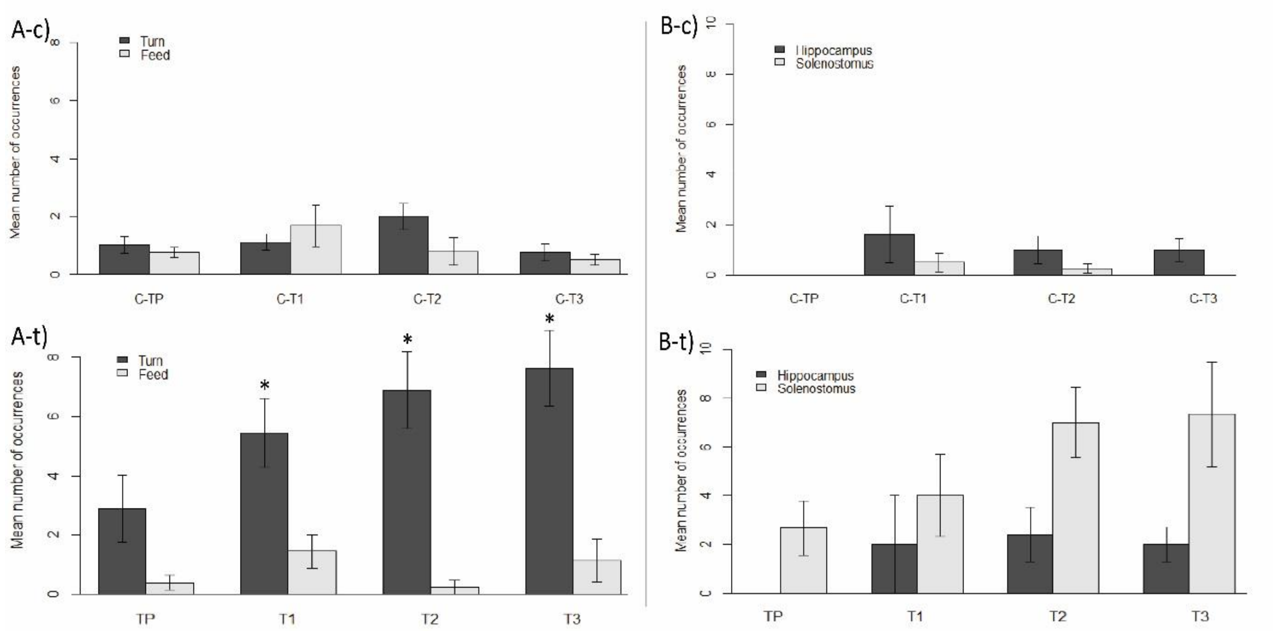


Figure 7.5 A-t: Mean number of turning and feeding reactions (±SE) of *Syngnathoidei* to different treatments; A-c: Paired control observations. TP: diver presence (N = 8), T1: flash (N = 9), T2: manipulation (N = 9), T3: manipulation + flash (N = 8). B-t: Mean number of movement reactions (±SE) of *Hippocampus* spp. and *Solenostomus* spp. to different treatments. B-c: Paired control observations. *Hippocampus*: TP (N = 5), T1 (N = 5), T2 (N = 5), T3 (N = 5). *Solenostomus*: C (N = 14), TP (N = 3), T1 (N = 4), T2 (N = 4), T3 (N = 3). Significance level of treatments compared to control after Holm-Bonferroni corrections: $p < 0.05$, *: different to Control.

7.4.2 Behavioural effects of photographic flashes

A total of 47 control, 48 low intensity, and 46 high intensity trials were analysed. One seahorse in the high treatment group was affected by pouch emphysema after the second repetition and was subsequently removed from analyses as its capacity to swim had become compromised. One video failed to record during the first repetition of the control treatment and could not be analysed. Repeated measures ANOVAs did not show a statistically significant difference between repetitions, sex, or size for any of the variables. Therefore, data of the four different repetitions were combined and analysed together.

7.4.2.1 Hunting efficiency

Flash treatments had no significant effect on the time seahorses spent hunting ($p = 0.796$). The number of strikes at prey was not different between treatments ($p = 0.965$), neither were the catch success rate between treatments ($p = 0.147$).

7.4.2.2 Spatial use

χ^2 tests established that there was no significant effect of treatment compared to the control on the time seahorses spent in different zones of the tanks ($\chi^2_{(6)} = 6.470$, $p = 0.373$). The way seahorses oriented themselves in the tanks did not differ significantly between control and treatments ($\chi^2_{(4)} = 2.180$, $p = 0.701$).

7.4.2.3 Activity

Repeated measures ANOVA confirmed a significant effect of treatment on the time seahorses spent inactive ($p = 0.028$) and showing startled responses ($p < 0.001$). There were no differences in the times spent swinging, hunting, or swimming. The control group spent more time being inactive compared to high treatment ($p = 0.018$) seahorses, but not compared to the low treatment group ($p = 0.770$). Inactivity was not different between low and high treatment groups ($p = 0.106$). Startled responses in control and low treatment groups were not different from each other ($p = 0.119$), but both were different from the high treatment group (C – TH: $p < 0.001$; L – TH: $p = 0.024$) (Figure 7.6).

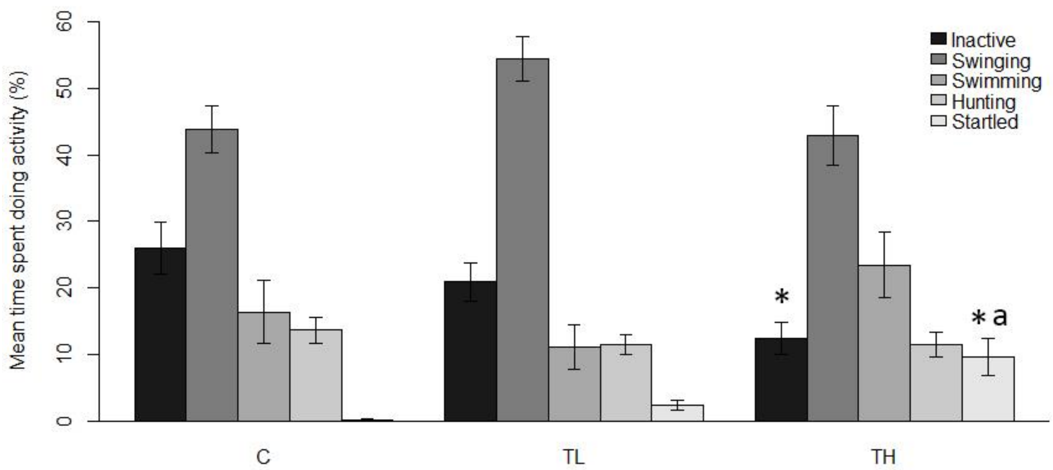


Figure 7.6 Mean time (±SE) seahorses spent doing different activities during different flash treatments. C = Control (N = 47), TL = Low intensity (N = 48), TH = High intensity (N = 46). Significance level of treatments: $p < 0.05$, *: different to C, a: different to TL.

7.4.2.4 Ventilation rate

Treatment had a significant effect on the ventilation rates of seahorse ($p < 0.001$). Ventilation rate of high treatment seahorses (27 beats min^{-1}) were significantly higher than control (15 beats min^{-1}) and low (17 beats min^{-1}) treatment groups (C – TH: $p < 001$; L – TH: $p = 0.006$). There was no difference between control and low treatment groups ($p = 0.439$) (Figure 7.7).

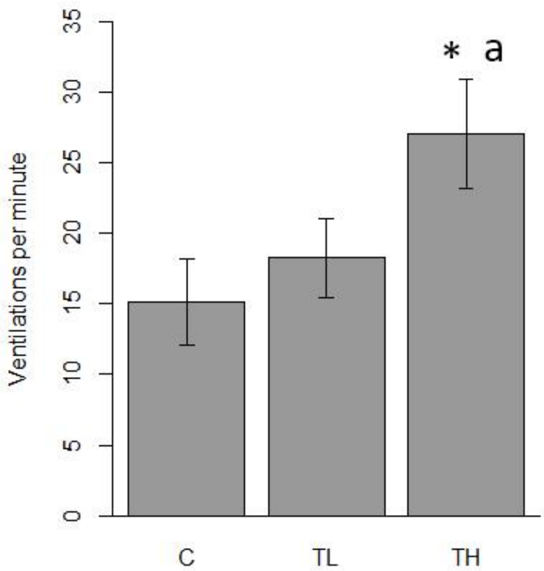


Figure 7.7 Seahorse ventilation rates (±SE) during different flash treatments. C = Control (N = 47), TL = Low intensity (N = 48), TH = High intensity (N = 46). Significance level of treatments: $p < 0.05$, *: different to C, a: different to TL.

7.4.3 Pathomorphological effects of photographic flashes

Multivariate PERMANOVA analysis showed no significant effect from treatment on gross ocular morphology (Pseudo-$F_{(1,18)} = 0.58$, $P = 0.65$) or retinal morphology (Pseudo-$F_{(1,18)} = 0.50$, $P = 0.79$). Individual t-tests showed no significant differences between any variables in the control group and the flash treatment group (Table in Appendices). No lesions, oedema or visible changes were observed in the retina at the light microscopy scale. We found no evidence that photographic strobes result in changes to gross eye anatomy (shape or size of the eye and/or lens) or basic retinal morphology defined here as the thickness of the whole retina or the thickness of each retinal cell layer.

7.5 Discussion

Wildlife tourism is important for supporting livelihoods worldwide, but potential impacts caused by photography or photographer behaviour need to be minimised to ensure sustainability and for best practice in animal welfare. This study showed that repeated photographic flashes delivered over a period of 34 days and involving 4600 exposures to full power flash gun discharges per animal did not cause overt changes in retinal gross anatomy, such as retinal layer thicknesses, in *Hippocampus subelongatus*. More importantly, these flashes had no observable impact on seahorses' foraging behaviour or feeding success rates in a species that is known to rely on vision to capture small moving prey and has relatively high spatial resolving power (Mosk et al. 2007). Manipulation of animals by photographing divers, however, elicited very strong flight and stress responses. These results provide important new information for the development of best-practices photography guidelines for wildlife tourism.

Tourism management bodies including those in government organisations and public aquarium facilities, as well as tourism operators, have developed rules and regulations restricting the use of flash guns or strobes while photographing a range of animals (Smith 2010; MMO 2014). These well-intended preventive measures have not been based on scientific evidence. This experiment demonstrates that repeated photographic flashes do not appear to cause retinal damage in the seahorse *Hippocampus subelongatus*, at least over the duration of this experiment and under these conditions. In this study, we used a strobe at a higher intensity (double to triple) than is usually applied when photographing seahorses *in situ* underwater, and at a much higher intensity than could be reached by compact or phone cameras in an aquarium. In addition, phototoxicity is more frequently associated with extended exposure to intense light sources, in contrast to the very short exposure typical to photographic flashes (Organisciak and Vaughan 2010; Youssef et al. 2011) which suggests that flash exposures may be less likely to cause retinal damage.

Caution remains necessary, as different species may well have different susceptibility to photic damage. The species of seahorse studied here, *Hippocampus subelongatus* inhabits relatively low-light environments (Mosk et al. 2007) so it may be relatively more susceptible to photic injuries when compared to more shallow living species and could therefore be considered a conservative model species for these tests. Fish inhabiting surface waters, for instance, where they are subject to high intensity caustic images of the sun focused by surface waves and wavelets (Čepič 2008) may well be more resistant. This near-surface ‘flicker’ results in short duration (ms) increases in irradiance of 10 fold or more (Loew and McFarland 1990; Darecki et al. 2011). When underwater flicker is considered in terms of a 3-dimensional radiance distribution, fluctuations in intensity can be even higher, up to 100 times (Darecki et al. 2011), and when focussed on the retina highly localised, high intensity illumination will result. Animals with wide fields of view and those inhabiting sunlit shallow waters will therefore be likely to have mechanisms to counter photic retinal damage, whereas other species in less variable and less bright habitats than *H. subelongatus* may be more susceptible.

Our field experiment demonstrated that cryptic fishes are most strongly affected by diver manipulation. The highly significant increase in movement for frogfishes, species which rarely move if undisturbed, implies a considerable energy expenditure which could lead to decreased fitness (Lankford et al. 2005). Movement reactions differed between *Solenostomus* spp. and *Hippocampus* spp., reflecting different defence mechanisms used by each family. Seahorses are less mobile than ghostpipefishes (*Solenostomus* spp.) and rely more on camouflage than on flight response. When divers manipulated animals there was no difference whether or not the diver also used flash. In most cases, flash photography had no more effect than diver presence.

We demonstrated that the argument that flash photography might negatively affect feeding behaviour due to temporary blindness caused by flash photography does not hold up for the species tested in this study. Neither the field nor tank experiment yielded a decrease in the time spent hunting or in feeding efficiency in *H. subelongatus*. Even in the treatments that caused movement reactions, feeding rates were unchanged, indicating that despite potential distress, visual acuity was not impacted. Similar results have been observed when testing the effects of temperature stress on *H. guttulatus* where food intake in seahorses was not decreased despite increased ventilation rates (Aurélio et al. 2013).

High flash treatment caused similar increases in ventilation rates, indicating seahorses might have experienced stress. It remains unclear if this increased ventilation was caused by the observed increase in movement, or how strong this stress reaction was and if the animals were indeed stressed. While ventilation rate can be used as a proxy for stress, it does not always reflect the strength of the stimulus (Barreto and Volpato 2004). However, increased gill ventilation rates in animals experiencing high flash exposure, regardless if caused by stress or through increased movement, suggests increased metabolic rates, which, if sustained, would have consequences for food requirements. In the case of photographic flash, the direct effects seem to be relatively small and were likely exacerbated by seahorses being kept in captivity without the possibility of escaping the stressor. While scuba diving, the reactions seen in the tank study would likely translate to the animal fleeing.

While the tank study indicates that seahorses experience some discomfort caused by photographic flash, the behavioural effects seen during the tank experiment are negligible compared to effects caused by diver presence and manipulation in a scuba diving setting. This is consistent with another study on a similar-sized seahorse species (*H. whitei*), which showed similar short term movement in response to handling and no differences between flash photography and diver presence (Harasti and Gladstone 2013).

It remains unknown if repeated exposure to photography over periods of months or years could lead to chronic stress and associated pathology in cryptobenthic fauna (Pickering 1993; Lankford et al. 2005). Previous studies have found that minimal exposure to photographing divers did not change seahorse site persistence (Harasti and Gladstone 2013), and did not increase stress levels in Rom cichlids or Mozambique tilapia (Leong et al. 2009; Knopf et al.

2018). It does, however, remain unknown what the behavioural or pathomorphological effects would be from being manipulated by up to 50 divers per day, as is the case in popular dive sites (personal observation MDB). Further work, including specific studies of retinal cell apoptosis (e.g. Bejarano-Escobar et al. 2012), transmission electron microscopy studies of photoreceptor and retinal pigment epithelial cell ultrastructure, electrophysiological studies of photoreceptor function, and molecular approaches, would be required to completely eliminate the possibility of light-induced retinal damage in seahorses exposed to underwater strobe lights, but these were beyond the scope of this study.

This study has important implications for dive tourism and public aquaria. It may not be necessary for public aquaria to enforce a ban on flash photography, provided tanks are large enough for animals to move away from the stressor. Popular exhibits might still want to avoid flash photography to prevent animals retreating out of view. For scuba diving, the results of this study clearly show that divers should avoid touching or pursuing animals, rather than focusing on regulations on flash use that have no scientific basis.

7.6 Conclusion

This is the first study to investigate the combined pathomorphological and behavioural impacts of photographer behaviour and photographic flashes on animals. We conclude that the effects of photographic flash alone are minor and do not have a stronger impact than those caused by human presence or photography without flash. However, manipulating animals during photography elicits very strong evasive responses and should therefore be avoided. While feeding efficiency was not negatively impacted in this study, repeated diver manipulation in highly popular dive sites could still have the potential to lead to chronic stress, increased energy requirements, and reduced fitness in photographed animals.

Chapter 8 General Discussion

8.1 Summary of findings

This thesis studied cryptobenthic fauna on infralittoral soft sediment habitats in Indonesia and the Philippines. In this discussion I summarise the main findings of the thesis, discuss the wider role of soft sediment habitats in relation to other biomes and critically interpret how the results can assist, inform, and influence management and conservation. I also identify knowledge gaps and suggest what I believe to be the next steps and important future research directions (Figure 8.1).

This thesis demonstrated that soft sediment habitats and the cryptobenthic fauna that inhabit them are economically valuable, have a high species richness and can contribute to the sustainable use of ocean resources through dive tourism. I have further shown that, despite its high economic value, research and conservation on soft sediments is largely lacking. It is my hope that the outcomes of this thesis will help to lay the groundwork for further study and conservation of both soft sediment habitats and cryptobenthic fauna.

In the first data chapter I investigated the socio-economic value of muck dive tourism in Indonesia and the Philippines. This relatively new type of scuba diving attracts over 100,000 divers per year and is worth more than US$152 million annually (chapter 2). This value is considerably higher than other types of scuba diving such as shark dive tourism (Vianna et al. 2012; Huveneers et al. 2017). At least part of the high value can be explained by the demographic groups that participate in muck dive tourism. Muck divers are highly experienced scuba divers who are well educated and have a high annual income (chapter 2). This high disposable income and high experience level makes divers more willing to spend more time in one place, to do more dives and to do more return visits in order to see, or photograph species of interest, all of which result in a higher economic value (Dearden et al. 2006; Jones et al. 2009). Approximately 2,200 local people are employed directly as staff, often in regions where other options for sustainable livelihoods are limited. Tourism operators, dive guides and staff considered overcrowding of dive sites, pollution, and fishing impacts to be the biggest threats to muck dive tourism in Southeast Asia. If managed correctly, muck dive tourism can be a sustainable alternative to more destructive uses of the marine environment such as dynamite fishing. However, its dependence on a relatively small suite of species combined with a lack of knowledge on their threats could make this tourism niche vulnerable should the species it relies upon disappear.

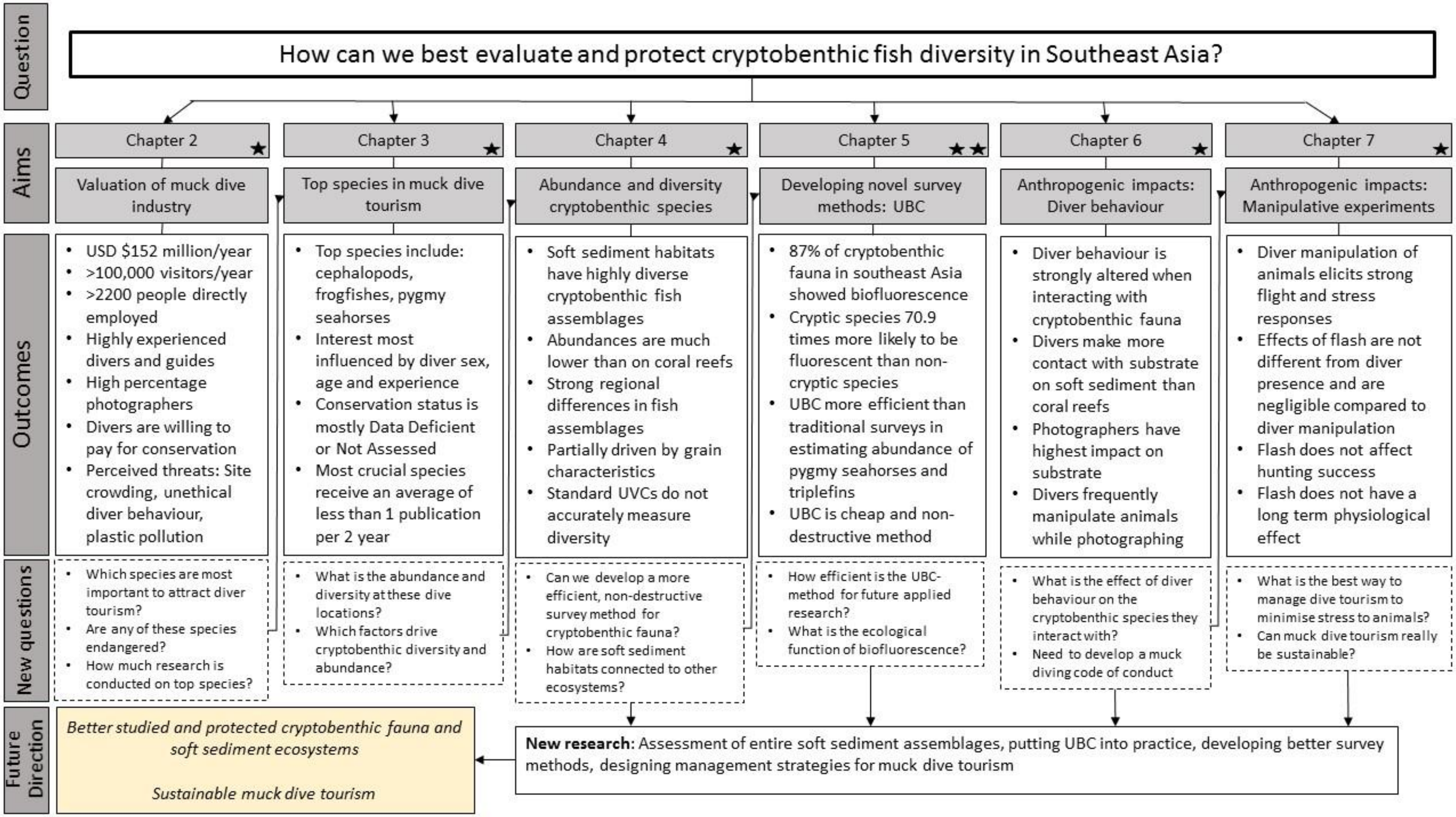


Figure 8.1 Conceptual flow diagram outlining the conclusions from this thesis and avenues of future research.

Chapter three further explored the research and conservation efforts into the species that are most important for attracting tourists to muck dive destinations. To assess divers' interests, I used the Best – Worst Scaling method, a survey method that is increasingly used in food marketing research, but has not yet been used to gauge the general public's interest in wildlife or conservation (Cohen 2003; Louviere et al. 2013). The easy design and interpretation of results of this method make it of interest to conservation and management organisations which might lack funding or skilled staff to conduct other survey methods. The survey indicated that divers are interested in a wide range of taxa, from fishes to molluscs and crustaceans. The ten species that are most important in attracting muck divers have seen very limited research attention in the last 20 years, with on average less than one publication published every two years per species. The extinction risk of eight out of the top ten species is unknown, either because the species have not been assessed yet, or data are lacking to accurately estimate their extinction risk. The public's interest in the conservation of charismatic species is not new, and has in fact been utilised by campaigns that use "flagship species" as a drawcard to protect entire habitats (Clucas et al. 2008; McClenachan et al. 2012). The species driving muck dive tourism are not yet known to the general public, but they have the potential to become flagship species for soft sediment research and conservation (Home et al. 2009; Veríssimo et al. 2009).

Surveys investigating cryptobenthic fish assemblages (Chapter 4) revealed that soft sediment sites can be highly diverse, contradicting the current prevailing idea of soft sediments as species-poor habitats (Alongi 1990; Depczynski and Bellwood 2004). Cryptobenthic species diversity on surveyed sites was higher than cryptobenthic species diversity on most coral reefs, with only one study on the Great Barrier Reef having a similar number of species (Depczynski and Bellwood 2004; Ahmadia et al. 2012; Goatley et al. 2016). Abundances, however, were orders of magnitude lower than those on coral reefs. The three regions surveyed (Dauin, Lembeh Strait, Bali) had significantly different assemblages that could only partially be explained by environmental factors such as benthic cover or grain size characteristics. The strong regional differences and high species richness suggest that the high biodiversity found in the Coral Triangle area extends beyond coral reefs, and indicate that the drivers of diversity on soft sediments act on biogeographical rather than small, local scales (Chapter 4, Ahmadia et al. (2018)). Conventional Underwater Visual Census (UVC), even when area-adjusted for cryptobenthic species, failed to detect the entire cryptobenthic diversity. During the roving diver surveys for chapter 4, I detected 30.4% more species than during the UVC surveys, but it is likely that results still underestimated the real diversity. Lethal survey methods such as the use of rotenone detect more species (Smith-Vaniz et al. 2006), but are not advisable when surveying species that might be rare or endangered.

Chapter five developed a novel method survey method to address the low detection probability of cryptic species during standard UVC surveys. Night-time surveys showed that cryptic fishes are 70.9 times more likely to display fluorescence compared to non-cryptic species. Tests done during day-time compared UVC surveys with Underwater Biofluorescence Census (UBC) surveys and showed that the UBC method detected double the number of pygmy seahorses (*Hippocampus bargibanti*) and triple the number of triplefins (*Ucla xenogrammus*, *Enneapterygius tutuilae*). These results are promising, as the extinction risk of the majority of cryptic fish species remains unknown (Chapter 5). The use of the relatively cheap UBC method opens avenues for citizen science surveys while reducing inter-observer variability inherent to UVC surveys of cryptic fishes.

Having established that soft sediment habitats support high species diversity and developed a method to even better survey this diversity, chapter six returned to muck dive tourism to assess the impacts of scuba divers on soft sediment. While divers touched the substrate more often on soft sediment than on coral reefs, this did not result in more observed damage. The biggest factor determining how strong impacts were, was whether or not divers were closely observing or photographing cryptobenthic fauna. Photographers in particular spent considerably more time interacting with marine life. Across coral reefs and soft sediment habitats, divers frequently touched animals, either to relocate them into a better position for photographs, or to be able observe them more closely. It is to be expected that these interactions cause significant stress to marine life. Repeated exposure might cause behavioural or physiological changes in marine life (Harasti and Gladstone 2013) that would degrade the quality and value of muck dive experiences over time. The majority of global dive training organisations state explicitly that divers should not touch marine life, but the frequent occurrence of animal manipulation indicates that these guidelines are not strong enough. Introducing a muck dive-specific code of conduct might decrease the impacts that divers have on soft sediment fauna, provided this code of conduct is accepted throughout the region and supported by major dive tourism stakeholders such as dive centres, training agencies, and dive magazines.

To further investigate the impacts photographing scuba divers have on cryptobenthic fauna, I conducted three experiments (chapter seven). 1) *In situ* manipulation on dive sites in the Philippines showed that manipulation by divers elicited the strongest stress response in animals. Photographic flash caused minor changes to the behaviour of seahorses and ghostpipefishes, but those were not significantly different than effects caused by diver presence alone. 2) Aquarium experiments showed that hunting success of seahorses was not negatively affected by photographic flash. The highest intensity flash treatment did not affect the spatial use or orientation of seahorses, but did cause increased movement and subsequent breathing rates. 3) Importantly, the final experiment showed no negative effects of long term exposure to photographic flashes on the retinal and gross ocular morphology of *H. subelongatus*. The results of this chapter indicate that while there is a small behavioural impact of flash photography, this effect is negligible compared to the impacts of divers touching cryptobenthic fishes.

In summary, results show that muck dive tourism has a high economic value, but the species driving this tourism are poorly understood. Cryptobenthic fish communities on soft sediment have a higher diversity than previously assumed, and the underwater biofluorescence census method can be used to survey cryptic fishes more efficiently. Scuba divers can have considerable impacts on cryptobenthic species, by touching them, but not by using flash photography. These results can be used to design future research and more efficient management of cryptobenthic fishes on soft sediment habitats.

8.2 Soft sediment ecosystems

Soft sediment substrates are the most extensive infralittoral habitat in tropical seas, yet receive little research and conservation attention compared to other habitats such as coral reefs or seagrass beds. In the scientific literature, soft sediment substrates are habitually studied as being degraded reefs, or as a part of coral reef lagoonal systems (Bailey-Brock et al. 2007; Bellwood and Fulton 2008; Enochs and Manzello 2012). This approach ignores an important fact about soft sediment substrates, i.e. that they are distinct, naturally occurring biomes that provide a habitat for highly adapted fauna and flora (Gray and Elliott 2009). Much like terrestrial desserts, infralittoral soft sediment ecosystems can be pristine and harbour species that are unique and not found in other marine habitats.

While often it is often assumed that soft sediment habitats have depauparate fish communities (Alongi 1990; Depczynski and Bellwood 2004), my research has shown that cryptobenthic species richness is much higher than was previously thought. The low abundances of cryptobenthic fauna, combined with their wide distribution calls into question how rarity should be defined on soft sediment, and how connected populations of rare species are in these extensive habitats. Interestingly, certain species considered to be rare on coral reefs (e.g. *Antennaridae*) were found to be relatively abundant on the sites surveyed during my research. The question remains as to if this relatively high abundance of “rare” species is a general trend on all soft sediment habitats, and for how many species this is the case. The very large area covered by soft sediment could imply that certain “rare” coral reef species which also occur on soft sediment habitats might in fact be highly abundant. These observations challenge the accepted paradigm about soft sediment as habitats of little interest to fish ecologists, but are also relevant to studies of rarity in fishes in other ecosystems.

The importance of soft sediment in providing jobs in the scuba dive industry is clear, but its value extends beyond tourism. The current narrative in much of the conservation work in the Coral Triangle highlights the importance of coral reefs as a source of protein for coastal communities that depend on sustenance fishing (Coral Triangle Initiative 2009). However, recent work has shown that coral reefs provide at maximum 20% of fishing yields in Southeast Asia. The majority comes from pelagic fisheries or aquaculture (Clifton and Foale 2017). Forage fish species such as anchovies or scad are important to pelagic fisheries. These species depend on soft sediment habitats as spawning and feeding grounds (Stacey and Hourston 1982; Higo 1985). This makes understanding the dynamics of soft sediment potentially more important to food security than understanding the dynamics of coral reefs. In short, ignoring soft sediment substrates in a changing world could have big consequences, not only for tourism, but also for food security.

8.3 Limitations of this thesis

The sites used in this thesis were of known importance to muck dive tourism precisely because of the richness in cryptobenthic fauna. The question that needs to be asked is whether or not these sites are exceptional compared to sites where there is no muck dive tourism. There is a reasonable possibility that the regions used for this thesis represent a “best-case scenario” when it comes to cryptobenthic diversity on soft sediment habitats in Southeast Asia. However, two factors make me think that this is not the case.

Firstly, the dive tourism in the three regions I surveyed did not start with a focus on muck diving. Rather, nearby sites of interest initially attracted divers, after which soft sediment species richness was discovered and the focus changed. The first dive resort in Lembeh Strait, one of the world’s primary muck dive destinations, was constructed for its abundance of megafauna (whale sharks, manta rays, etc.). When in 1996 the majority of this megafauna was fished out illegally by Taiwanese fishermen and their so-called “curtains of death” (Cochrane 1997), dive operators discovered the richness in cryptobenthic species, which set Lembeh on its path as the world’s most popular muck dive region (chapter two).

Secondly, new, highly diverse muck dive sites are discovered on a regular basis. During the course of this research project I dived on multiple soft sediment sites that were not used by tourism operators, and found similar species richness as in the sites surveyed in chapter four. These newly discovered sites, however, all had very similar sediment characteristics and benthic cover to the sites I used during my research. Therefore, it is likely that soft sediment sites with different characteristics (such as mud or gravel sites) would show different faunal assemblages. Such differences have already been described for meiofauna (Gray and Elliott 2009), but remain to be tested for fish assemblages on soft sediment habitats.

Another potential limitation of this thesis is the difficulty inherent with studying cryptic species. Despite my best efforts, it is likely that at least some individuals and even species were overlooked during surveys. The lack of accurate data on gobies (Gobiidae) is indicative of the difficulties involved in sampling cryptic species on soft sediment. Gobies are the most abundant cryptobenthic species on coral reefs and are also found on soft sediment substrates, with multiple new species described from the sites used in this thesis (e.g. Allen et al. (2014); Allen et al. (2016)). The highly furtive nature of gobies on soft sediment and the high similarity between species made it impossible to accurately identify species using UVC surveys. Legal restrictions in Indonesia Prohibited the use ichthyocides, which are the preferred method of sampling cryptobenthic fauna on coral reefs (Ackerman and Bellwood 2000; Smith-Vaniz et al. 2006). For this reason I decided to exclude gobies from surveys. On coral reefs, gobies are among the most abundant species and play a vital role in trophodynamics, but until they can be accurately surveyed, their role and importance on soft sediment necessarily remains poorly understood.

Finally, muck dive tourism has a high economic value and provides income to thousands of people, but it is not yet clear how much of the wealth that is generated is retained in local communities. Many, if not most, dive centres in Southeast Asia are owned by people outside the region, which commonly leads to economic leakage and reduced benefits to local communities (Dimmock and Musa 2015). The lack of involvement of host communities reduces the potential positive development of the host community and can in some cases even lead to increased inequality due to inflation of local prices (Walpole and Goodwin 2001; Garrod and Wilson 2004). During socio-economic surveys, considerable effort was made to sample the full market by offering surveys in multiple languages, yet the survey still failed to capture the Asian market. Interviews with operators and dive staff indicated an increase in this market segment, making it important to understand their motivations and expenditure. Cultural differences in expenditures, attitudes towards the environment, and diving style might require different management approaches to ensure effective management.

8.4 Implications for management and conservation

It is clear that dive tourism can play an important role in generating sustainable incomes for coastal communities in Southeast Asia (Pascoe et al. (2014), chapters 2 and 3), but if this tourism is not adequately managed it can cause considerable impacts that would negate the benefits of job creation. A specific muck diving code of conduct (as suggested in chapter 6) would be an important first step towards increasing sustainability of this scuba diving niche. This code of conduct should include strict guidelines prohibiting the manipulation of animals, rather than focusing on limiting flash photography. However, more rules and regulations do not mean anything if they are not supported by the industry and the tourists themselves. Creating more awareness of the issues around the unethical aspects of scuba diving photography and on practical solutions to address these, is therefore crucial. Existing organisations dedicated to sustainable scuba dive tourism, such as GreenFins or Green Bubbles, could help drive this change. Wildlife photography magazines or dive magazines could have a much bigger impact than specialised NGOs, by adapting strict policies that reject photos which are clearly the result of photographer manipulation. Policing behavioural codes is a challenge for scuba tourism management, and the question should be asked if the current regime of self-regulation in dive tourism is sufficient to address its considerable impacts? Alternative measures such as limiting visitor numbers to certain sites, or restricting types of cameras, could be management tools that are easier to implement.

Threats to soft sediment fauna, other than dive tourism, are currently poorly understood. Certain species that are popular with scuba divers, such as frogfishes or seahorses are also coveted by the marine aquarium trade (Calado et al. 2003; Koldewey and Martin-Smith 2010). The marine aquarium trade is notorious for its destructive fishing practices and high mortality during transport (Pet-Soede and Erdmann 1998; Thornhill 2012), but it is unknown if the trade poses a significant threat to cryptobenthic species. Small scale beach seine netting occurs in most of the coastal communities visited during fieldwork (personal observations). While short-term evidence of disturbance was visible after these fishing episodes, it is unclear what the long-term impacts of seine netting are to fish communities in the region. Establishing targeted Marine Protected Areas (MPAs) could be an appropriate management solution for destructive fishing or overfishing (Hilborn et al. 2004; Russ et al. 2004). At local scales, small, unofficial no fishing-zones have been established, but no formal MPAs aimed at soft sediment habitats exist to the best of my knowledge. Moreover, while MPAs might be a solution to some threats, we need to know more about the functioning of soft sediment ecosystems to decide where to establish MPAs to maximise their effect.

Management and conservation of soft sediment habitats is about more than ecosystem value, knowledge of species ecology and the threats to these species. For research to have a real impact and to be translated into efficient management, results need to be clearly communicated to all stakeholders. It is crucial to consider how to reach and educate local coastal communities, scuba divers, and the general public. During this thesis I attempted to do this by a variety of methods. To reach the scuba diving community and general public I used social media, wrote articles for scuba diving magazines, ran a blog dedicated to my research, and did nearly 80 presentations in dive centres and dive expositions. When the opportunities presented themselves, I organised seminars with local researchers, did presentations for community leaders and dive guides. Most of all, I talked to as many local people as possible. What I found were people who cared, people who try to do the right thing if it is possible, people who understand the importance of a healthy ecosystems, but these were also people with many challenges that have a higher priority than saving small fishes on the sand. I strongly believe that if approached correctly, many of the threats to soft sediment ecosystems can be managed. However, effective management will require a higher level of understanding of these habitats and the people that depend on them.

8.5 Moving forward: future research avenues

The current situation of understanding of tropical soft sediment habitats can in many ways be compared to that of mesophotic coral reefs. Both biomes extend over large areas, are poorly studied, but seem to be more important for ocean health than what was assumed until recently. Through the work of dedicated researchers, mesophotic reefs systems are starting to gain more attention (e.g. Fitzpatrick et al. (2012); Bridge et al. (2016); Asher et al. (2017a); Asher et al. (2017b)). A similar movement is possible for soft sediment systems, with many interesting avenues of research possible.

At the smallest scale, we know very little about the cryptobenthic species that drive muck dive tourism. Their life cycles, ecology, in some cases even their taxonomy, remain largely unknown. At present, the extinction risk or even most important threats have not been assessed. One of the main reasons is the difficulty in detecting species in order to study them. I developed a survey method based on biofluorescence that could provide a solution, but new, molecular methods could be useful as well. For example, new environmental DNA (eDNA) techniques have shown promise for coral reef species (DiBattista et al. 2017; Coker et al. 2018), and could potentially be used for soft sediment cryptobenthic fauna as well. Biofluorescence can be used to accurately estimate abundances of certain biofluorescent species, but eDNA has the potential to quickly detect the presence of the entire fish assemblage, including cryptobenthic species. Having better methods to detect cryptobenthic fishes would facility basic biological research (such as age and growth, reproduction, etc.) needed to design appropriate management for these fishes.

Soft sediment substrates provide habitat for more than just cryptobenthic fishes. Scaling up research to investigate the entire faunal assemblage is the next step in understanding these habitats and identifying the processes that allow habitats with seemingly no structural complexity to support such high fish diversity. On habitats with higher complexity, such as rocky and coral reefs, cryptobenthic fishes form a crucial link in the food chain, transferring energy from producers to predatory species (Depczynski and Bellwood 2003). Interestingly, nearly all fish species occurring on soft sediment seem to be predatory species, either preying on small invertebrates or larger fishes (personal observation). The bottom of the soft sediment food chain are the very abundant invertebrate meiofauna and macrofauna, living either in the interstitial spaces in the sediment or on top of the sediment. These organisms are considered to be highly abundant, and could, in theory, provide sufficient nutrients as basal level consumers to support many higher order predators feeding on them (Gee 1989; Schratzberger and Ingels 2018). Despite this apparent abundance of food, fish abundances remain very low. This indicates that other factors than food availability, such as predatory pressure or competition, could play an important role in structuring soft sediment fish assemblages, as is the case for invertebrate assemblages (Peterson 1979; Wilson 1990). A better comprehension of trophic links in soft sediment habitats, from primary producers to top predators, will help to understand what drives change in these systems. The effects of environmental factors such as temperature, salinity, different sediment types, or seasonal changes on fish assemblages remain unclear as well, but need to be understood to anticipate how anthropogenic impacts will affect fauna on different soft sediment habitats (Marshall and Elliott 1998).

On even larger scale, it would be interesting to investigate how soft sediments are linked to other marine ecosystems. In recent years it has become increasingly clear that habitats such as mangroves, coral reefs and seagrass beds are not isolated, but instead influence one another very strongly. This influence can be as nurseries for juvenile species (Galaiduk et al. 2017), trophic linkages (Heithaus et al. 2013), or as refuge for certain species (Wilson et al. 2014). Soft sediments provide an important nursery and foraging ground for commercial species such as *Carangidae* and forage fish species (Edgar and Shaw 1995; Travers et al. 2010). During surveys for this thesis, juvenile coral reef fish of the genus *Haemulidae* and *Lutjanidae* were frequently encountered, as well as abundant schools of unidentified ‘baitfish’. It is unclear how important soft sediments are for adjacent habitats, and how much larval or energy exchange there is with different habitats. But, by ignoring the potential influence of the most widespread marine habitat on other marine biomes, we are essentially studying ocean ecosystems using tunnel vision.

When looking at soft sediments from a vantage point beyond the ocean, the questions of how important these habitats are for humans and how human activities affect soft sediment habitats needs to be asked. It is clear that divers can have a direct effect on individual fish, but the effect of their frequent disturbance of the seafloor is not clear. Soft sediment substrates are highly dynamic habitats, so it is possible that disturbance by divers might not cause a problem. On the other hand, if continuous, diver disturbances could be significant. Since some commercially important species of forage fish depend on soft sediment substrates to deposit their eggs, disturbances to the soft sediment, either by divers or beach seine nets, could impact forage fish abundance, which in turn could affect the rest of the food chain. Mining is common in North-Sulawesi, the location of the most diverse sites surveyed in this thesis, and has already polluted some local waterways with heavy metals (Limbong et al. 2003). During heavy rains the sediments from some of these waterways are deposited in the Lembeh Strait, yet no research has been done to investigate its effects on marine life in the area. Finally, it is beyond doubt that climate change has considerable impacts on marine habitats, but its effects on soft sediment fish fauna has not received much research attention. It is, however, clear that effects on soft sediment meiofauna are substantial, which could have significant knock on effects on the rest of the food chain (Zeppilli et al. 2015).

To improve our understanding of fish assemblages on infralittoral soft sediment habitats, I would propose the following short-term and long-term research and management goals:

Short-term goals:

- Further develop survey methods such as biofluorescence and eDNA to improve detection of cryptobenthic fauna.
- Develop a code of conduct for dive tourism on soft sediment substrates.
- Investigate the impacts of marine aquarium trade on cryptobenthic species.
- Improve understanding of the drivers of cryptobenthic species assemblages on soft. sediment substrates, including those on different types of sediment (such as gravel, mud, carbonate sand)

Long-term goals:

- Clarify the importance of soft sediment habitats to fishing activities in the tropics.
- Improve understanding of the drivers of entire fish assemblages on soft sediment substrates.

- Investigate the trophic roles of soft sediment fauna.
- Investigate how soft sediment habitats interact with different biomes such as coral reefs, mangroves, and seagrass beds.

8.6 Thesis conclusions

Infralittoral soft sediment habitats are the world's largest marine habitat, but despite being so common, very little is known about fish communities living in these habitats. This body of work has challenged the presiding idea that soft sediment communities are of little value to coastal communities and highlighted that they should be a focus for fish ecology researchers. The overarching question in this thesis was how we can best evaluate and protect cryptobenthic fish diversity in Southeast Asia. To do so, I first assessed the high value of muck dive tourism, and showed that the species driving this dive tourism niche are poorly studied. I then demonstrated that soft sediment cryptobenthic fish communities are highly diverse. In the third phase of the thesis I developed a non-lethal survey method to detect cryptobenthic species. During the final phase I discovered that photographing divers frequently touch cryptobenthic fishes, and that this causes strong stress responses in these animals. However, I also showed that flash photography has little impact on cryptobenthic fishes, which is encouraging as much uncertainty exists around this issue in both dive tourism and public aquaria industry. Combined, these results can assist researchers to better study cryptic species, help dive tourism operators to develop guidelines that will increase the sustainability of the dive industry, and help resource managers to make decisions on conservation efforts.

While the focus of this thesis is on cryptobenthic fishes, it became increasingly clear throughout the last three years that the real challenges and research questions extend beyond cryptic fishes. Future research should broaden and investigate infralittoral soft sediment ecosystems as a whole. My work has redefined tropical infralittoral soft sediments as an exciting and valuable field of research. This large habitat ultimately connects all other marine habitats with each other. By only studying the more charismatic, visually appealing habitats in the tropics, we are only covering a small proportion of the true marine biodiversity in the ocean. This lack of understanding of how the marine ecosystem works as a connected whole could have dire consequences for the oceans in a changing world. Ultimately, it is my hope that this thesis will stimulate more research in soft sediment habitats, and that outcomes of this research will help protect valuable marine ecosystems and the livelihoods dependent on them.

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Every reasonable effort has been made to acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

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Appendices

1.1 Copyright statements

Chapter 2: Published in the journal *Marine Policy*. As first author, permission is automatically granted to use the article in a PhD thesis.

To Whom It May Concern I,

Maarten Bernard Yvonne De Brauwer, collected the data, designed the study, conceived and executed the data, and wrote and edited the manuscript for the following publication:

De Brauwer, M., Harvey, E. S., McIlwain, J. L., Hobbs, J.-P. A., Jompa, J., Burton, M. (Marine Policy 2017). The economic contribution of the muck dive industry to tourism in Southeast Asia (doi: 10.1016/j.marpol.2017.05.033)

Date: 6 April 2018

I, as a Co-Author, endorse that this level of contribution by the candidate indicated above is appropriate.

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De Brauwer, Burton, M. (Ocean and Coastal Management 2018). Known unknowns: conservation and research priorities for soft sediment fauna supporting a valuable scuba diving industry.

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De Brauwer, M., Harvey, E. S., Ambo-Rappe, R., McIlwain, J. L., Jompa, J. Saunders, B. J. (Estuarine, Coastal, and Shelf Science, *In Press*). Cryptobenthic fish communities inhabiting soft-sediment habitats in Southeast Asia are characterised by high diversity but low abundance

Date: 6 April 2018

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De Brauwer, M., Hobbs, J.-P. A., Ambo-Rappe, R., Jompa, J., Harvey, E. S., McIlwain, J. L. (Marine Policy 2018). Biofluorescence as a survey tool for cryptic marine species (doi: 10.1111/cobi.13033)

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De Brauwer, M., Saunders, B. J., Ambo-Rappe, R., Jompa, J., McIlwain, J. L., Harvey, E. S. (Journal of Environmental Management, 2018) Time to stop mucking around? Impacts of underwater photography on cryptobenthic fauna found in soft sediment habitats.

Date: 6 April 2018

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To Whom It May Concern I,

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Photos: All photos included in this thesis were either taken by myself, or permission has been sought from the photographers to use the photo (Figure 2.1: Dragos Dumitrescue, Photo cover page Chapter 4: Luke Gordon).

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2.1 List of muck dive centres in Indonesia and the Philippines

Location	Dive centre
Alor	Dive Alor Dive
Alor	Alami Alor
Alor	Alor Divers
Alor	Alor Dive
Alor	La p'tite Kepa
Ambon	Dive into Ambon
Ambon	Diving Maluku
Ambon	Maluku Divers
Ambon	Dive Bluemotion
Ambon	Blue Rose Divers
Ambon	Cape Paperu resort and spa
Anilao	Buceo Anilao Resort
Anilao	Crystal Blue Resort
Anilao	Aiyanar
Anilao	Halo Anilao Dive resort
Anilao	Eagle Point Resort
Anilao	Aquaventure reef club
Anilao	Acacia Resort and Dive centre
Anilao	Planet dive
Anilao	Arthur's Place dive resort
Anilao	Pier Uno Resort
Anilao	Anilao Photo Hotel
Anilao	La chevrerie
Anilao	Balai Sa Anilao
Bali	Villa Markisa
Bali	Seraya Secrets
Bali	Geko Dive Bali
Dauin	Azure
Dauin	Thalatta
Dauin	Sea Explorers
Dauin	Atlantis
Dauin	Chromodoris
Dauin	Dumaguete Divers (Simon)
Dauin	Liquid Divers
Dauin	Bongo
Dauin	Harolds
Dauin	Atmosphere
Dauin	Dive Society
Dauin	Bahura
Dauin	Aquadive
Dauin	Aqualandia

Lembeh	Black Sand Dive Retreat
Lembeh	Bastianos
Lembeh	NAD
Lembeh	Kungkungan
Lembeh	2 Fish Divers
Lembeh	Eco Divers
Lembeh	Yos Dive
Lembeh	Divers Lodge
Lembeh	Froggies
Lembeh	Critters @ Lembeh
Lembeh	Kasawari Lembeh Resort
Lembeh	Lembeh Hills Resort
Lembeh	Dive Into Lembeh @ Hairball resort

2.2 Summary statistics of dive centre staff and visitor numbers

	With outlier			Without outlier
	Dive staff	Resort staff	Visitors	Visitors
mean	14	30	2458	1963
median	11	22	725	650
min	2	0	100	100
max	40	100	13450	7038
Outlier	12	30	13450	

2.3 Survey form: dive guides

Survey Dive guides: Economic valuation muck dive tourism

1. What is your nationality?
2. Please indicate your gender: **Male** – **Female**? *(circle answer)*
3. What is your age?
4. How long have you been guiding dives in Dauin?
5. Which dive certification do you have?
6. How many dives have you done in total?
7. What is the highest level of education you completed?
   - ☐ Did not complete secondary education / high school
   - ☐ Secondary education / high school
   - ☐ Technical / vocational training
   - ☐ Bachelor's Degree
   - ☐ Master's Degree.
   - ☐ Advanced graduate work or Ph.D.
8. For every 100 divers that come to Dauin, how many do you think come specifically for muck diving?
9. In your opinion, which are the 5 most popular muck dive species with divers?
   a. ____________________
   b. ____________________
   c. ____________________
   d. ____________________
   e. ____________________
10. In your opinion, which are the 3 most popular sites in Dauin?
    a. ____________________
    b. ____________________
    c. ____________________
11. When you work as a dive guide, what is your approximate income per month?
    a. Wage:
    b. Commission:
    c. Tips:
12. Do you get higher tips when finding popular species? **Yes** – **No** (circle answer)

   a. If you circled **yes**, which species bring in the highest tips?

13. What is the most positive effect of tourism in Dauin?
14. What is the most negative effect of tourism in Dauin?
15. What do you think are the potential concerns for the future of muck dive tourism in Dauin?

2.4 Survey form: scuba divers

Survey: Economic valuation muck dive tourism

Thank you for taking the time to complete this survey, your answers will assist in scientific research into the value of muck diving to local communities in Southeast Asia. This survey is conducted as part of a PhD project at Curtin University, Australia. It aims to investigate the value of muck dive tourism in Southeast Asia. The information you share is strictly confidential and will be used for research purposes only.

Muck diving is a distinct type of diving defined as "diving in mostly gravel and mud areas with little or no coral reef or rocky outcrops". Frequently sites will also feature man-made or natural debris. The focus of muck diving is on finding small, cryptic species such as frogfishes, seahorses or invertebrates that are rarely encountered on coral reefs. For more information on this project, please refer to the Information Sheet given to you.

Please answer questions truthfully and as accurate as possible. If questions are unclear, feel free to ask Maarten or dive staff to clarify the question.

A. Motivation

1. Is this the first time you visit Lembeh Strait? **Yes – No** *(circle answer)*
    a. If no: how many times did you visit Lembeh Strait previously? ______ times

2. Is this the first time you are on a muck-diving holiday? **Yes** – **No** *(circle answer)*
    a. If no: which other muck diving locations have you visited?

____

____

3. What is the main reason for your visit to Lembeh Strait? *(Please tick one box only)*

    ☐ For general dive activities
    ☐ Mainly for muck diving
    ☐ Specifically for muck diving
    ☐ Snorkelling
    ☐ General tourism activities
    ☐ Other (please specify) ______________________________

4. Would you have visited Lembeh Strait if you could not muck dive there? **Yes – No** *(circle answer)*
    a. If no: where would you have gone instead?

    ____

5. Please list the 3 species would you like to see/photograph/film most?

    ____

6. Are you planning any non-diving related activities during this holiday? **Yes – No** *(circle answer)*
    a. If **yes**: which ones? *(You can tick multiple boxes)*

- ☐ General tourism activities
- ☐ Cultural visits
- ☐ Wellness
- ☐ Nature / trekking
- ☐ Shopping
- ☐ Other (please specify) ______________________________________

7. Do you consider Lembeh Strait to be a "remote" destination? **Yes** – **No** *(circle answer)*
   a. If yes: was this a reason for you to choose it as a holiday destination? **Yes** – **No** *(circle answer)*

B. Dive information

1. Which dive certification do you have? ______________________________________
2. How many dives have you done in total? ______________________________________
3. How many dives did you do in the last year? ______________________________________
4. Do you use an underwater camera? **Yes** – **No** *(circle answer)*
   a. If yes: do you use it mostly for? **Videography - Photography**? *(circle answer)*
   b. Camera type: **SLR - Point-and-shoot**? *(circle answer)*
5. What is the estimated total price of your camera set-up? ______________________________________

C. Demographic information

1. What is your nationality? ______________________________________
2. Please indicate your gender: **Male** – **Female**? *(circle answer)*
3. What's your age? ______________________________________
4. What is the highest level of education you completed?

- ☐ Did not complete secondary education / high school
- ☐ Secondary education / high school
- ☐ Technical / vocational training
- ☐ Bachelor's Degree

☐ Master’s Degree.
☐ Advanced graduate work or Ph.D.

5. What is your yearly income? *(circle value closest to your yearly income)*
   - Please circle your currency: **$** (**US** or **AUS**) **€** **£**

0 - 20,000	60,000 - 80,000	120,000 – 140,000
20,000 - 40,000	80,000 - 100,000	140,000 – 160,000
40,000 - 60,000	100,000 - 120,000	160,000 - Higher

D. Length of stay

1. What will be the total duration of this holiday? ___________________________ days
2. Number of days spent traveling to site (return trip **included**)? ____ days
3. Lembeh Strait*:*
   a. Number of days you intend to stay in Lembeh Strait?_______________ days
   b. How many dives are you planning to do in Lembeh Strait? _________ dives
4. Are you visiting other locations <u>during this holiday</u>? **Yes** – **No** *(circle answer)*
   If you answered **yes**:
   a. Which other locations are you visiting? ____
   b. Number of days you intend to stay in the other locations? ___________ days
   c. How many dives are you planning to do in the other locations? ______ dives
   d. Are you planning to do non-diving activities in the other locations? **Yes** – **No** *(circle answer)*
   e. If yes: which ones? ____
5. How likely are you to make another visit to Lembeh in the future? Please tick one box only.

☐ I won’t make another visit
☐ I’m unlikely to make another visit
☐ I may make another visit
☐ I’m likely to make another visit
☐ I’m definitely planning to make another visit

6. If you “may make”, “likely to make” or “definitely planning to make” another visit to *location:* What is the likely time frame of your next visit? Please tick one box only.
   - ☐ This year
   - ☐ Within the next two years
   - ☐ In the next 3-5 years
   - ☐ In more than 5 years
   - ☐ Can’t say

E. Expenditure

1. Approximately how much did you spend / are you planning to spend on:

Item	Cost
a. **Holiday package** (flights + dives + accommodation + food)	
Costs **NOT included** in any package	
b. Flights	
c. Accommodation	
d. Diving activities	
e. Food and drinks per day	
f. Tips for staff	
g. Non-diving related activities	
h. Other expenses (e.g. souvenirs, entertainment, etc.)	

2. Did you fly to Lembeh Strait? **Yes** – **No** *(circle answer)*
   a. Where did you fly from (airport in home country)?

   ____

3. If you did **NOT** fly to Lembeh Strait, how did you travel here?

   ____

   a. What was the approximate cost?

   ____

4. If you are visiting other locations during your holiday, approximately how much did you spend / are you planning to spend there?

   ____

5. Would you be willing to pay an administrative fee to dive at *location*, provided that fee was used for protection of the local marine environment? **Yes – No** *(circle answer)*
   a. If yes: What is the maximum amount you would be willing to pay? ______________________________

Thanks for participating in this survey. We appreciate your time and the information you have provided.

3.1 Ratio-scaled parameters of important muck dive taxa

Ratio-scaled probability parameters of important muck dive taxa using data from Best-Worst Scaling models for different demographics variables. ‘: Used as baseline model per variable; *: Significant at $p < 0.05$; °: Significantly different from baseline estimate at $p < 0.05$

	Aggregate	Sex		Age			Camera		Total dives			Muck		Level			
Animal	Model	F’	M	64’	39	30	No’	Yes	7000’	1000	<300	No’	Yes	OWD	AOW’	RES	DM
Mimic / Wunderpus	11.47*	11.55*	11.41	8.95*	11.67	12.37	14.83*	10.75°	9.62*	11.55	11.58	9.16*	11.58	6.50	11.72*	6.35	12.62
Blue ringed octopus	10.19*	10.86*	9.78	12.08*	10.19	9.25	9.50*	10.32	15.07*	9.88°	8.95°	4.25*	10.46	8.74	10.45*	9.29	9.50
Rhinopias	10.06*	8.36*	10.92°	10.04*	10.13	9.94	8.85*	10.32	11.96*	10.00°	9.48°	6.41*	10.22	10.30	11.60*	9.40	10.74
Flamboyant cuttlefish	9.05*	10.12*	8.40	4.56*	9.24°	11.18°	7.46*	9.36	9.32*	9.05	8.84	12.55*	8.86°	8.67	8.00*	6.02	8.27
Frogfish	7.66*	8.48*	7.17	4.91*	7.79	8.91	5.76*	8.00	6.55*	7.71	7.72	11.23*	7.48°	10.07	5.11*	8.54	7.50
Pygmy seahorses	6.89*	5.87*	7.43	3.36*	7.01°	8.69°	7.73*	6.71	1.82	7.08	8.05	11.07*	6.66°	10.33	6.81*	7.60	5.34
Harlequin shrimp	5.98*	6.01*	5.88	5.72*	6.04	5.97	7.25*	5.72	4.63*	6.02	6.11	3.64*	6.09	9.44	6.86*	6.35	5.21
Octopus (other)	5.76*	4.19*	6.67°	6.22*	5.73	5.41	6.17*	5.68	10.52*	5.57°	4.95°	6.50*	5.73	3.93	5.83*	5.11	6.05
Rare crabs	5.56*	5.39*	5.61	6.37*	5.51	5.04	3.67*	5.99	6.25*	5.53	5.32	10.52*	5.34°	1.51°	7.63*	7.08	4.61°
Nudibranchs	4.33*	4.09*	4.38	6.13*	4.22	3.54	4.64*	4.25	3.56*	4.34	4.38	0.91	4.55	0.11°	5.11*	4.49	5.64
Bobtail squid	4.24*	4.37*	4.10	4.60*	4.22	3.95	3.40*	4.43	1.82	4.34	4.71	5.97*	4.15°	9.20	3.41*	7.50°	3.87
Ghostpipefish	3.32*	3.33*	3.23	3.63*	3.27	3.03	4.10*	3.16	2.53*	3.31	3.36	2.69*	3.33	6.79	3.21*	2.61	3.40
Mandarinfish	3.28*	5.70*	2.26	3.22*	3.24	3.17	4.13*	3.10	0.27	3.55°	4.60°	3.29*	3.27	0.91	3.21*	6.39	2.73
Seahorses	2.87*	2.97	2.73	4.68*	2.74	2.14	2.34	2.99	2.58	2.85	2.85	1.35	2.92	1.38	2.44	3.49	3.17
Shrimp (other)	2.67*	1.53	3.71°	7.12*	2.53°	1.55°	2.21	2.76	9.22*	2.54°	2.07°	0.96	2.77	1.30	3.07	2.83	2.70
Scorpionfish	1.61	1.32	1.75°	1.45	1.58	1.59	2.51*	1.47°	1.72	1.57	1.54	1.08	1.61	0.02°	1.04	1.65	1.98
Stargazer	1.53	1.94	1.28	1.55	1.50	1.44	1.25	1.58	0.56	1.56	1.72	0.52	1.58	5.85	1.34	1.21	1.96
Gobies	1.33	1.13*	1.42°	2.69	1.26°	0.90°	1.86	1.23	1.17	1.31	1.31	6.19*	1.23°	0.34	1.22	1.86	2.15
Pipefish	1.23	1.72	0.99	1.92	1.16	0.92	1.21	1.23	0.41	1.27	1.41	0.93	1.21	4.60	1.19	1.62	1.13
Helmet gurnard	0.72*	0.76*	0.66	0.53*	0.71	0.78	0.85	0.69	0.29	0.72	0.79	0.59	0.72	0.01°	0.48*	0.47	1.18
Flounder	0.25*	0.31*	0.20	0.26*	0.24	0.22	0.26*	0.24	0.14*	0.25	0.26	0.20	0.24	0.01°	0.29*	0.16	0.26

4.1 List of survey sites

Overview of surveyed sites

Site	Country	Region	Location	# transects	Known dive site	Latitude	Longitude
1	Philippines	Dauin	Dauin	10	Yes	9.186652	123.267944
2			Dauin	10	Yes	9.190997	123.271535
3			Dauin	10	Yes	9.200047	123.277796
4			Masaplod Norte	10	No	9.179328	123.258799
5			Masaplod Norte	10	Yes	9.173982	123.253436
6	Indonesia	Lembeh Strait	Teluk Kembahu 1	10	Yes	1.494576	125.238422
7			Makawide	10	Yes	1.473025	125.235209
8			Makawide	10	Yes	1.480117	125.237211
9			Air Bajo	10	Yes	1.480674	125.252579
10			Teluk Kembahu 3	10	Yes	1.489492	125.238529
11			Air Bajo	10	Yes	1.48638	125.25613
12			Tanderussa	10	Yes	1.45814	125.219792
13	Indonesia	Bali	Amed	10	Yes	-8.333875	115.643954
14			Tulamben	10	Yes	-8.311762	115.623237
15			Tulamben	10	No	-8.294616	115.611725
16			Tulamben	10	No	-8.287445	115.605663
17			Tulamben	7	Yes	-8.276632	115.594556
18			Padang Bay	5 (16m)	Yes	-8.50922	115.519277
19			Seririt	10	Yes	-8.18321	114.914565
20			Gilimanuk	5 (6m)	Yes	-8.1639	114.438816

4.2 Benthic cover categories

Descriptions of benthic cover categories used in CPCe analysis

Category	Definition
CORAL (C)	
Anemones (AN)	Anemone
Hard Coral (HC)	Hard coral
Other Coral (OC)	Other type of coral (e.g. Gorgonian seafan)
Soft Coral (SC)	Soft coral
SPONGES (S)	
Sponge (SPO)	Sponges
PLANTS (P)	
Algae (AL)	Any species of living algae
Seagrass (SG)	Any species of living seagrass
HUMAN OBJECTS (HO)	
Bottles (BO)	Glass bottles
Concrete Structure (CS)	Large concrete structures (e.g. “reef balls”)
Metal Structure (MS)	Large metal debris (e.g. artificial reefs
Other Debris (OD)	Small fragments of other debris (e.g. cans, shoes)
Other manmade structures (OS)	Large structures (e.g. parts of shipwreck_
Plastic Debris (PCD)	Plastic of any kind
Rope (RO)	Mooring lines or discarded ropes
NATURAL DEBRIS (ND)	
Plant Debris (PD)	Wood, dead plants, leaves
Shell Fragments (SF)	Carbonate fragments of mollusc or crustaceans shell
SAND, PAVEMENT, RUBBLE (SPR)	
Coral Rubble (CR)	Unconsolidated coral rubble
Gravel (GR)	Unconsolidated sediment between 2mm and 4mm
Pebbles (PE)	Unconsolidated sediment >4mm
Sand (S)	Unconsolidated sediment <2mm
UNKNOWNS (U)	
Unknown (UNK)	Unidentified
TAPE, WAND, SHADOW (TWS)	
Shadow (SHAD)	Shadow over point, impossible to determine
Tape (TAPE)	Tape measure
Wand (WAND)	Metal rod used to fix tape measure

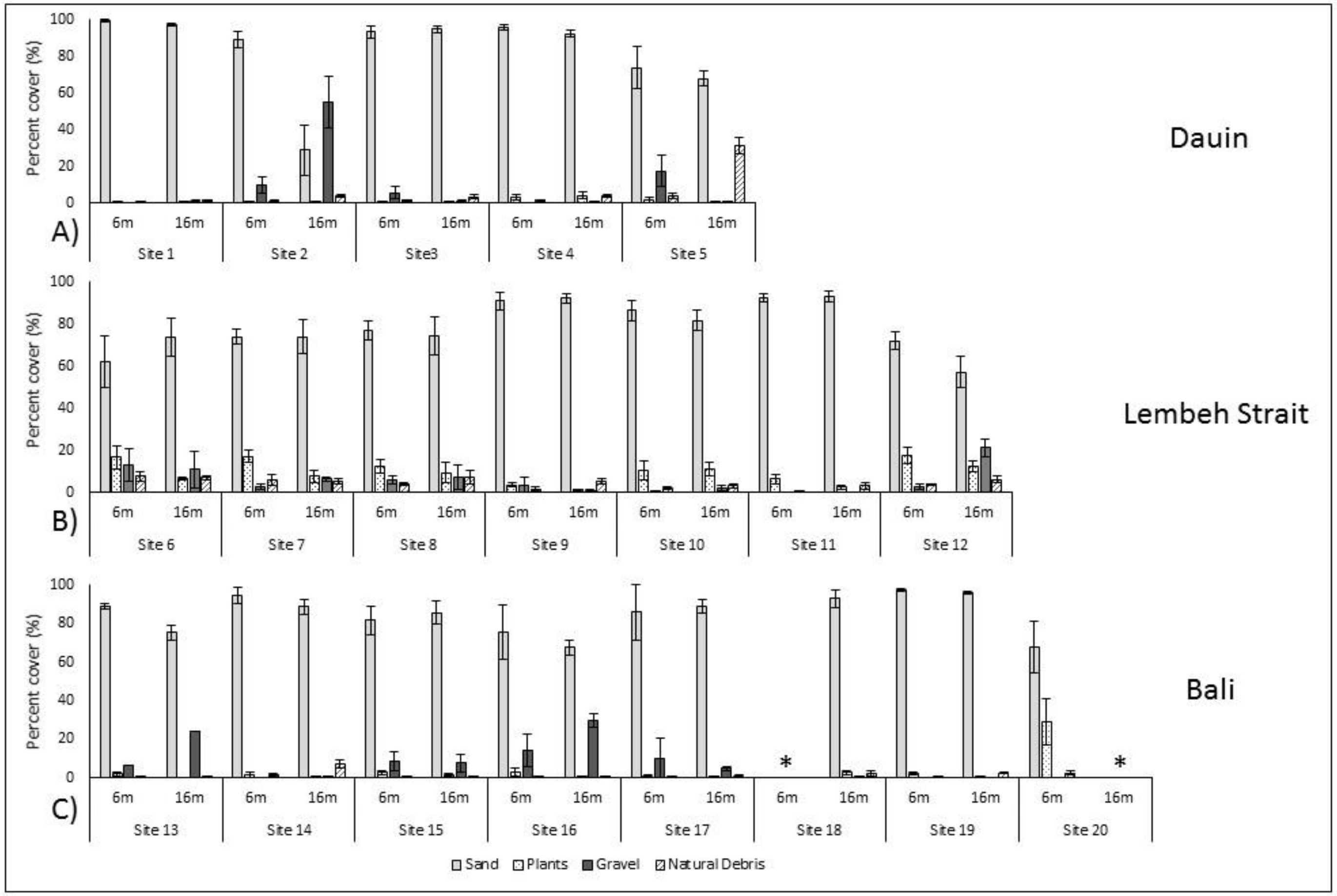
4.3 Species list

Family	Genus	Species
Antennariidae	Antennarius	commersoni
Antennariidae	Antennarius	hispidus
Antennariidae	Antennarius	maculatus
Antennariidae	Antennarius	pictus
Antennariidae	Antennarius	randalli
Antennariidae	Antennarius	striatus
Antennariidae	Antennatus	coccineus
Antennariidae	Antennatus	dorehensis
Antennariidae	Antennatus	nummifer
Antennariidae	Nudiantennarius	subteres
Aploactinidae	Paraploactis	sp.
Bothidae	Asterorhombus	fijiensis
Bothidae	Bothus	juvenile
Bothidae	Bothus	pantherinus
Bothidae	Bothus	sp.
Bothidae	Engyprosopon	grandisquama
Callionymidae	Callionymus	keeleyi
Callionymidae	Callionymus	sp.
Callionymidae	Callionymus	superbus
Callionymidae	Dactylopus	dactylopus
Callionymidae	Dactylopus	kuiteri
Callionymidae	Diplogrammus	goramensis
Callionymidae	Synchiropus	bartlesi
Callionymidae	Synchiropus	sp.
Congridae	Gorgasia	maculata
Congridae	Heteroconger	hassi
Congridae	Heteroconger	perissodon
Congridae	Heteroconger	polyzona
Congridae	Heteroconger	taylori
Congridae	Heteromycteris	hartzfeldii
Congridae	Poeciloconger	fasciatus
Dactylopteridae	Dactyloptena	orientalis
Dasyatidae	Dasyatis	kuhlii
Dasyatidae	Taeniura	lymma
Ephippidae	Platax	batavianus (juvenile)
Labridae	Cymolutes	torquatus
Labridae	Iniistius	aneitensis
Labridae	Iniistius	pavo
Labridae	Iniistius	pentadactylus
Labridae	Iniistius	sp.
Labridae	Iniistius	tetrazona
Labridae	Inimicus	didactylus
Monacanthidae	Acreichthys	sp.
Monacanthidae	Acreichthys	tomentosus

Monacanthidae	Brachaluteres	taylori
Monacanthidae	Chaetodermis	penicilligera
Monacanthidae	Paramonacanthus	japonicus
Monacanthidae	Pervagor	nigrolineatus
Monacanthidae	Pseudalutarius	nasicornis
Monacanthidae	Pseudomonacanthus	macrurus
Monacanthidae	Pseudomonacanthus	tomentosus
Muraenidae	Echidna	nebulosa
Muraenidae	Gymnothorax	fimbriatus
Muraenidae	Rhinomuraena	quaesita
Ophichthidae	Apterichtus	klazingai
Ophichthidae	Brachysomophis	cirrocheilos
Ophichthidae	Brachysomophis	henshawi
Ophichthidae	Callechelys	marmorata
Ophichthidae	Leiuranus	semicinctus
Ophichthidae	Myrichthys	maculosus
Ophichthidae	Ophichthus	bonaparti
Ophichthidae	Ophichthus	cephalozona
Ophichthidae	Ophichthus	melanochir
Ophichthidae	Opistognathus	sp.
Pegasidae	Eurypegasus	draconis
Platycephalidae	Cymbacephalus	beauforti
Plotosidae	Plotosus	lineatus
Samaridae	Samaris	cristatus
Scorpaenidae	Dendrochirus	brachypterus
Scorpaenidae	Dendrochirus	zebra
Scorpaenidae	Parapterois	hetururus
Scorpaenidae	Parascorpaena	picta
Scorpaenidae	Pteroidichthys	amboinensis
Scorpaenidae	Scorpaenopsis	diabolus
Scorpaenidae	Scorpaenopsis	macrochir
Scorpaenidae	Scorpaenopsis	oxycephala
Scorpaenidae	Scorpaenopsis	possi
Scorpaenidae	Scorpaenopsis	sp.
Scorpaenidae	Scorpaenopsis	venosa
Scorpaenidae	Taenianotus	triacanthus
Soleidae	Aseraggodes	kaianus
Soleidae	Aseraggodes	suzumotoi
Soleidae	Brachirus	heterolepis
Soleidae	Pardachirus	pavoninus
Soleidae	Soleichthys	sp.
Solenostomidae	Solenostomus	cyanopterus
Solenostomidae	Solenostomus	paegnius
Solenostomidae	Solenostomus	paradoxus
Synanceiidae	Synanceia	horrida
Synanceiidae	Synanceia	verrucosa

Syngnathidae	Acentronura	breviperula
Syngnathidae	Acentronura	sp. (Longtail pygmy pipehorse)
Syngnathidae	Corythoichthys	ocellatus
Syngnathidae	Doryhamphus	janssi
Syngnathidae	Dunckerocampus	dactyliophorus
Syngnathidae	Dunckerocampus	pessuliferus
Syngnathidae	Hippocampus	alatus
Syngnathidae	Hippocampus	histrix
Syngnathidae	Hippocampus	kuda
Syngnathidae	Micrognathus	andersonii
Syngnathidae	Micrognathus	pygmaeus
Syngnathidae	Phoxocampus	tetrophtalmus
Synodontidae	Trachinocephalus	myops
Tetraodontidae	Torquigener	brevipinnis
Tetrarogidae	Ablabys	spp.
Tetrarogidae	Paracentropogon	longispinus
Tetrarogidae	Richardsonichthys	leucogaster
Trichonotidae	Trachyrhamphus	bicoarctatus
Trichonotidae	Trichonotus	elegans
Trichonotidae	Trichonotus	halstead
Trichonotidae	Trichonotus	sp.
Uranoscopidae	Uranoscopus	sulphureus

4.4 Dominant benthic cover on surveyed sites



4.5 Benthic cover (%) across surveyed sites in Southeast Asia

	Dauin					Lembeh Strait							Bali							
	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15	S16	S17	S18	S19	S20
Sand	97.5	58.7	94.0	94.0	70.6	67.8	73.9	75.6	91.6	84.2	93.0	64.6	82.1	91.4	83.6	71.4	88.2	92.8	96.7	67.6
Gravel	0.5	32.2	3.1	0.0	9.0	12.0	4.6	6.6	2.3	1.1	0.0	12.2	15.2	0.4	8.1	21.9	6.3	0.1	0.0	0.0
Pebbles	0.0	6.2	0.1	0.0	1.7	0.0	0.0	0.4	0.0	0.1	0.0	0.0	0.0	0.0	4.1	4.5	3.7	0.0	0.0	0.0
Coral rubble	0.0	0.0	0.0	0.0	0.0	0.2	0.2	0.5	0.0	0.1	0.1	0.1	0.0	2.3	0.1	0.0	0.0	1.5	0.0	0.0
Coral	0.0	0.0	0.0	0.0	0.0	0.3	2.8	0.2	0.0	0.3	0.2	1.8	0.3	0.1	0.1	0.0	0.0	0.0	0.0	0.0
Sponges	0.0	0.0	0.0	0.0	0.1	0.3	0.4	0.1	0.1	0.2	0.2	0.7	0.1	0.3	0.9	0.0	0.2	0.3	0.0	0.0
Plants	0.4	0.2	0.4	3.4	1.0	11.7	12.5	10.9	2.4	10.8	4.5	15.0	1.0	1.1	2.0	1.8	0.7	2.8	1.3	29.0
Natural debris	1.0	2.4	2.4	2.5	17.5	7.3	5.6	5.6	3.5	2.9	2.0	5.1	0.5	4.3	0.6	0.4	0.7	2.4	1.3	2.5
Artificial objects	0.5	0.3	0.1	0.0	0.1	0.2	0.0	0.2	0.1	0.5	0.2	0.6	0.8	0.0	0.5	0.0	0.1	0.0	0.7	0.9

5.1 Site descriptions

Bali

Underwater surveys were conducted on the north coast of Bali in Amed, Tulamben and Menjangan Island. All sites in Bali are popular scuba dive destinations and receive high numbers of visitors per year. 14 sites were surveyed in Bali. Amed and Tulamben are situated on the east of the island and have sloping volcanic black sand bottoms interspersed with patch reefs. Menjangan is a small island located in the west of Bali. The island is a Marine Protected Area (MPA) and is part of the Bali Barat National park. It has rich coral cover and steep drop offs. Despite of its MPA-status, the reefs around Menjangan have been impacted by stressors like blast fishing and anchor damage (Dustan et al 2013).

Nusa Tenggara

Lombok

One site was surveyed near the island of Gili Meno at the northwest coast of Lombok. Gili Meno Wall is a sloping reef with extensive diver damage. The site receives high numbers of scuba divers year round.

Sumbawa

Surveys in Sumbawa were conducted on six sites in Moyo, Satonda and Sangeang. Sites in Moyo are sloping reefs and walls with dense coral cover. Satonda is a steep reef slope that levels off at 30m. Sangeang is a volcanic island surrounded by sandy slopes with patchy coral cover. Very few divers visit the sites in Sumbawa due to the remoteness of this area.

Komodo

Seven sites were surveyed in the Komodo National Park. The park is a UNESCO World Heritage Site and a Man and Biosphere Reserve (UNESCO 2015). Four sites were pinnacles, the three other sites sloping reefs. Six of the surveyed sites are in the north of the park, one site is in the southernmost area of the park (Nusa Kode), this area is characterised by cold upwellings. Komodo is a popular scuba diving destination, but the south receives few visitors due to its remoteness.

North Sulawesi

Bangka

Bangka Island is surrounded by shallow sloping rocky reefs and has patchy to good coral cover. The surveyed sites are exposed to substantial wave action during windy season (July to September), but are calm during the rest of the year. Surveys were conducted outside windy season with calm conditions. Eight sites were surveyed in Bangka Island. A large iron ore mine has been established on Bangka Island in 2013, mining activities have been suspended since July 2015 after a ruling of the Supreme Court in Jakarta. At the moment of writing it is unclear if mining will recommence in the future.

Bunaken

Bunaken Island is the centre of the Bunaken National Park, which was established in 1991. While the park is an MPA, problems at the management level have impeded full implementation of protective measures. The island is surrounded by deep (>1900m) water and the sites are vertical drop offs with high coral cover. Eight sites were surveyed in Bunaken. Bunaken Island is one of the most popular scuba diving destination in North Sulawesi.

Lembeh Strait

Lembeh Strait is a shallow strait subject to tidal currents. The bottom consists of black volcanic sand with sparse patch reefs. Lembeh Strait receives large numbers of divers year round. Four sites were surveyed in Lembeh Strait

Raja Ampat

Raja Ampat is considered to be the centre of the Coral Triangle area and has the highest marine biodiversity found in the tropics. The area has a network of MPAs which are well policed. 8 sites were surveyed in the north of Raja Ampat and 11 sites were surveyed in the south. Surveyed sites in the north were sloping reefs with moderate to high coral cover, while sites in the south were drop offs and pinnacles with high coral cover.

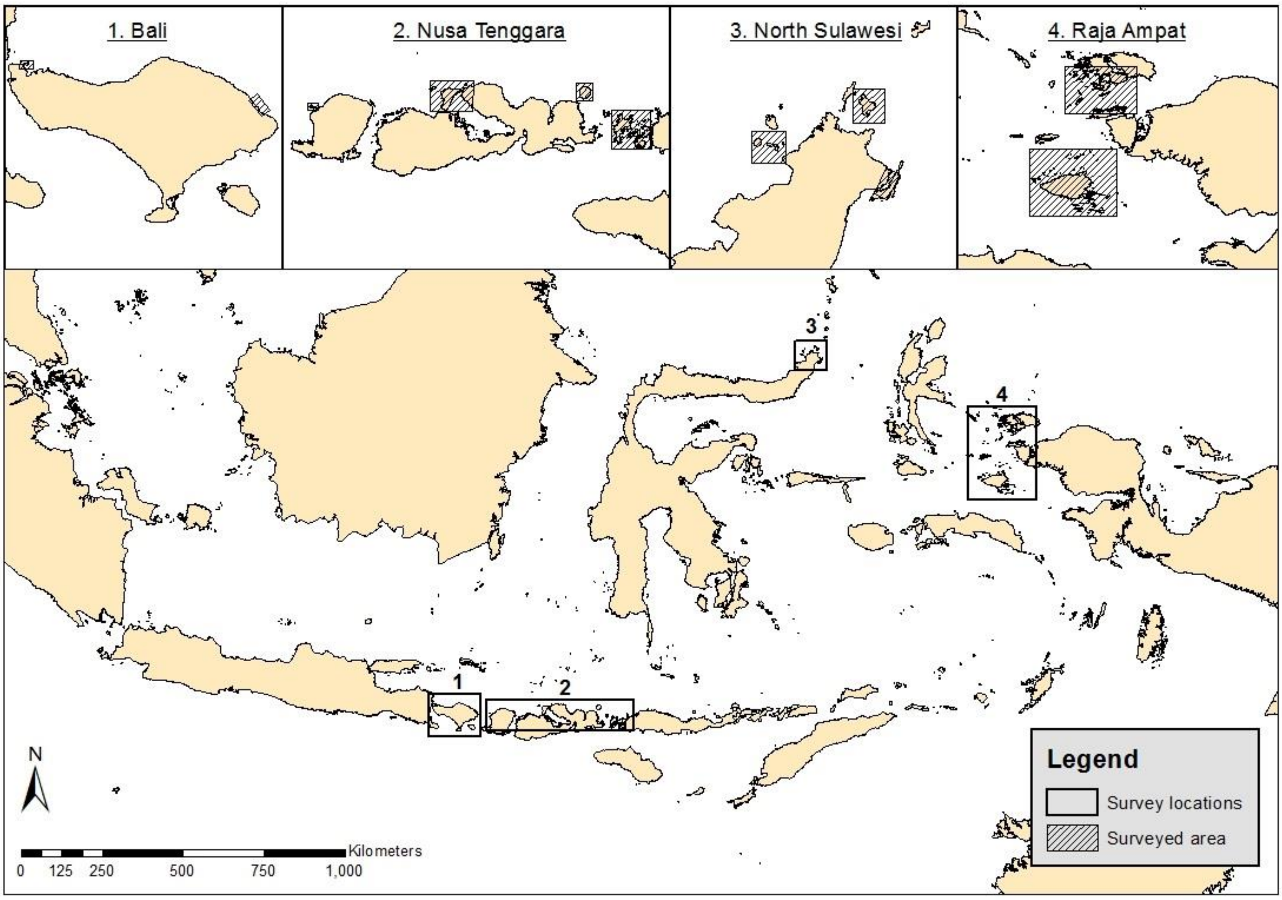
Christmas Island

Christmas Island is an Australian external territory in the east of the Indian Ocean. Two sites were surveyed at 15 m deep; Admin wall and Flying Fish Cove. Both sites have high hard coral cover of around 50%. Admin wall is a steep, almost vertical coral reef drop-off. Flying Fish Cove is a steep outer reef slope.

Cocos Islands

The Cocos Keeling Islands are an Australian external territory in the Indian Ocean. Three sites were surveyed at 1 m deep. Pondok Nek Jamil and Turtle beach are sheltered inshore patch reefs with low hard coral cover (10%-20%), dominated by large massive Porites and rubble with turf and macro algae. Prison Island is a high current site near a channel, the substrate is dominated by dead hard coral covered in turf and calcareous algae, with small massive Porites, Porites branching corals, and encrusting Montipora.

5.2 Map of surveyed sites



5.3 List of Fluorescent species Coral Triangle (nomenclature after Allen et al. 2015)

5.3.1 Fluorescing species

Taxa are listed alphabetically by Family and Species. “C” describes cryptic (C) or non-cryptic (NC) species. “Colour” of fluoresced light is indicated by filled circles corresponding to the observed colour, with “Area” describing the place on the body of the animal that fluoresces. Species previously unknown to fluoresce are marked as “Yes” in the column “New”.

Family	Species	C	Colour	Area	New	N
Antennariidae	*Antennarius pictus*	C	•	Patches on body + eye + esca	Yes	4
Antennariidae	*Antennarius striatus*	C	•	Esca + eye	Yes	4
Apistidae	*Apistus carinatus*	C	•	Entire body	Yes	1
Aploactinidae	*Paraploactis sp.*	C	•	Face	Yes	1
Aulostomidae	*Aulostomus chinensis*	NC	•	Margins dorsal and anal fin	Yes	5
Bothidae	*Bothidae spp.*	C	•	Variable	No	6
Callionymidae	*Synchiropus bartelsi*	C	•	Entire body	Yes	2
Callionymidae	*Synchiropus splendidus*	C	•	Eyes	Yes	2
Fistulariiidae	*Fistularia commersonii*	NC	•	Markings + eye	Yes	3
Gobiescocidae	*Discotrema crinophilum*	C	•	Markings	Yes	2
Gobiidae	*Bryaninops amplus*	C	•	Eyes	Yes	2
Gobiidae	*Bryaninops spp.*	C	•	Eyes	No	120
Gobiidae	*Eviota spp.*	C	•	Variable	No	100
Labridae	*Cheilinus chlorourus*	C	•	Entire body	Yes	1
Labridae	*Cheilinus trilobatus*	C	•	Entire body	Yes	8
Labridae	*Oxycheilinus bimaculatus*	C	•	Entire body	Yes	2
Labridae	*Oxycheilinus digrammus*	C	•	Entire body	Yes	5
Lethrinidae	*Lethrinus lentjan* (juveniles only)	C	•	Dorsal	Yes	3
Mullidae	*Parupeneus macronemus*	NC	•	Dorsal saddle	Yes	2
Mullidae	*Parupeneus multifasciatus*	NC	•	Lateral + eye + pectoral fin	No	4
Muraenidae	*Echidna polyzona*	C	•	Entire body	Yes	1
Muraenidae	*Gymnothorax cfr. flavimarginatus*	C	•	Entire body	No	1
Muraenidae	*Gymnothorax fimbriatus*	C	•	Entire body	Yes	4
Muraenidae	*Gymnothorax flavimarginatus*	C	•	Entire body	Yes	2
Muraenidae	*Gymnothorax richardsonii*	C	•	Entire body	Yes	2
Muraenidae	*Gymnothorax undulatus*	C	•	Entire body	Yes	1
Muraenidae	*Gymnothorax zebra*	C	•	White bands	No	2
Muraenidae	*Gymnomuraena zonipectis*	C	•	Entire body	Yes	10
Muraenidae	*Rhinomuraena quaesita*	NC	•	Yellow dorsal fin	Yes	1
Nemipteridae	*Pentapodus aureofasciatus*	NC	•	Lateral blotches	Yes	2
Nemipteridae	*Pentapodus spp.*	NC	•	Variable	No	20

Nemipteridae	*Scolopsis bilineata*	NC	•	Variable	No	25
Nemipteridae	*Scolopsis xenochrous*	NC	•	Entire body	Yes	1
Octopodidae	*Abdopus aculeatus*	C	•	Eyes + markings arms	Yes	1
Octopodidae	*Hapalochlaena lunulata*	C	•	Body, not rings	Yes	1
Octopodidae	*Octopus marginatus*	C	•	Eyes + markings arms	Yes	1
Ophichthidae	*Brachysomophis henshawi*	C	•	Eyes + head	Yes	2
Ophichthidae	*Callechelys marmorata*	C	•	Snout	Yes	1
Ophichthidae	*Myrichthys colubrinus*	C	•	Tip of tail + snout	No	1
Ophichthidae	*Myrichthys maculosus*	C	•	Entire body	Yes	1
Ophichthidae	*Ophichthus altipennis*	C	•	Head	Yes	2
Pegasidae	*Eurypegasus draconis*	C	•	Entire body	No	2
Platycephalidae	*Onigocia spinosa*	C	•	Entire body	Yes	2
Platycephalidae	*Platycephalidae spp.*	C	• + •	Variable	No	7
Platycephalidae	*Rogadius welanderi*	C	•	Entire body	Yes	1
Scorpaenidae	*Pteroidichthys amboinensis*	C	•	Entire body	Yes	1
Scorpaenidae	*Pterois sp. (juvenile)*	NC	•	Entire body	No	1
Scorpaenidae	*Scorpaenodes varipinnis*	C	•	Variable	No	16
Scorpaenidae	*Scorpaenopsis macrochir*	C	•	Entire body	Yes	6
Scorpaenidae	*Scorpaenopsis oxycephala*	C	•	Entire body	Yes	8
Scorpaenidae	*Scorpaenopsis possi*	C	•	Entire body	Yes	1
Scorpaenidae	*Scorpaenopsis sp.*	C	•	Entire body	No	1
Scorpaenidae	*Scorpaenopsis venosa*	C	•	Entire body	Yes	16
Scorpaenidae	*Sebastapistes mauritiana*	C	• + •	Head + eyes	Yes	2
Scorpaenidae	*Taenianotus triacanthus*	C	•	Entire body	Yes	4
Sepiolidae	*Euprymna berryi*	C	•	Spots on body	Yes	3
Sepiolidae	*Sepia aculeate*	C	• + •	Eyes + dorsal area	Yes	3
Serranidae	*Plectropomus cfr. leopardus*	C	•	Upper half body	Yes	1
Soleidae	*Liachirus melanospilos*	C	•	Eye	Yes	1
Soleidae	*Pardachirus pavoninus*	C	• + •	Variable	Yes	1
Soleidae	*Soleidae spp.*	C	•	Variable	No	3
Solenostomidae	*Solenostomus cyanopterus*	C	•	Entire body	Yes	16
Solenostomidae	*Solenostomus paradoxus*	C	•	Entire body	Yes	23
Solenostomidae	*Solenostomus sp. ("Velvet")*	C	•	Entire body	Yes	1
Synanceiidae	*Inimicus didactylus*	C	•	Entire body	Yes	5
Synanceiidae	*Synanceia horrida*	C	• + •	Entire body	Yes	6
Synanceiidae	*Synanceia verrucosa*	C	•	Entire body	Yes	2
Syngnathidae	*Corythoichthys ocellatus*	C	•	Entire body	Yes	14
Syngnathidae	*Halicampus macrorhynchus*	C	•	Entire body	Yes	1
Syngnathidae	*Halicampus mataafae*	C	•	Body	Yes	8
Syngnathidae	*Hippocampus bargibanti*	C	• + •	Variable	Yes	55
Syngnathidae	*Hippocampus denise*	C	• + •	Variable	Yes	7
Syngnathidae	*Hippocampus histrix*	C	• + •	Entire body	Yes	5
Syngnathidae	*Hippocampus pontohi*	C	• + •	Entire body	Yes	9
Syngnathidae	*Syngnathidae spp.*	C	•	Eye	No	20
Syngnathidae	*Trachyrhamphus bicoarctatus*	C	•	Eye	Yes	2
Synodontidae	*Saurida gracilis*	C	•	Entire body	No	1
Synodontidae	*Saurida nebulosa*	C	•	Entire body	Yes	6

Synodontidae	*Synodus rubromarmoratus*	C	•	Entire body	No	2
Synodontidae	*Synodus spp.*	C	•	Entire body	No	45
Tetrarogidae	*Ablabys sp.*	C	•	Entire body	Yes	1
Tetrarogidae	*Paracentropogon longispinis*	C	•	Entire body	Yes	2
Tetrarogidae	*Richardsonichthys leucogaster*	C	• + •	Head	Yes	2
Tripterygiidae	*Tripterygiidae spp.*	C	•	Entire body	No	30
Uranoscopidae	*Uranoscopus sulphureus*	C	•	Entire body	Yes	3

5.3.2 Non – fluorescent species

Taxa are listed alphabetically by Family and Species. "C" describes cryptic (C) or non-cryptic (NC) species. Species listed as fluorescing in other publications, but not found to fluoresce in this study are marked as "F" in column "Previous".

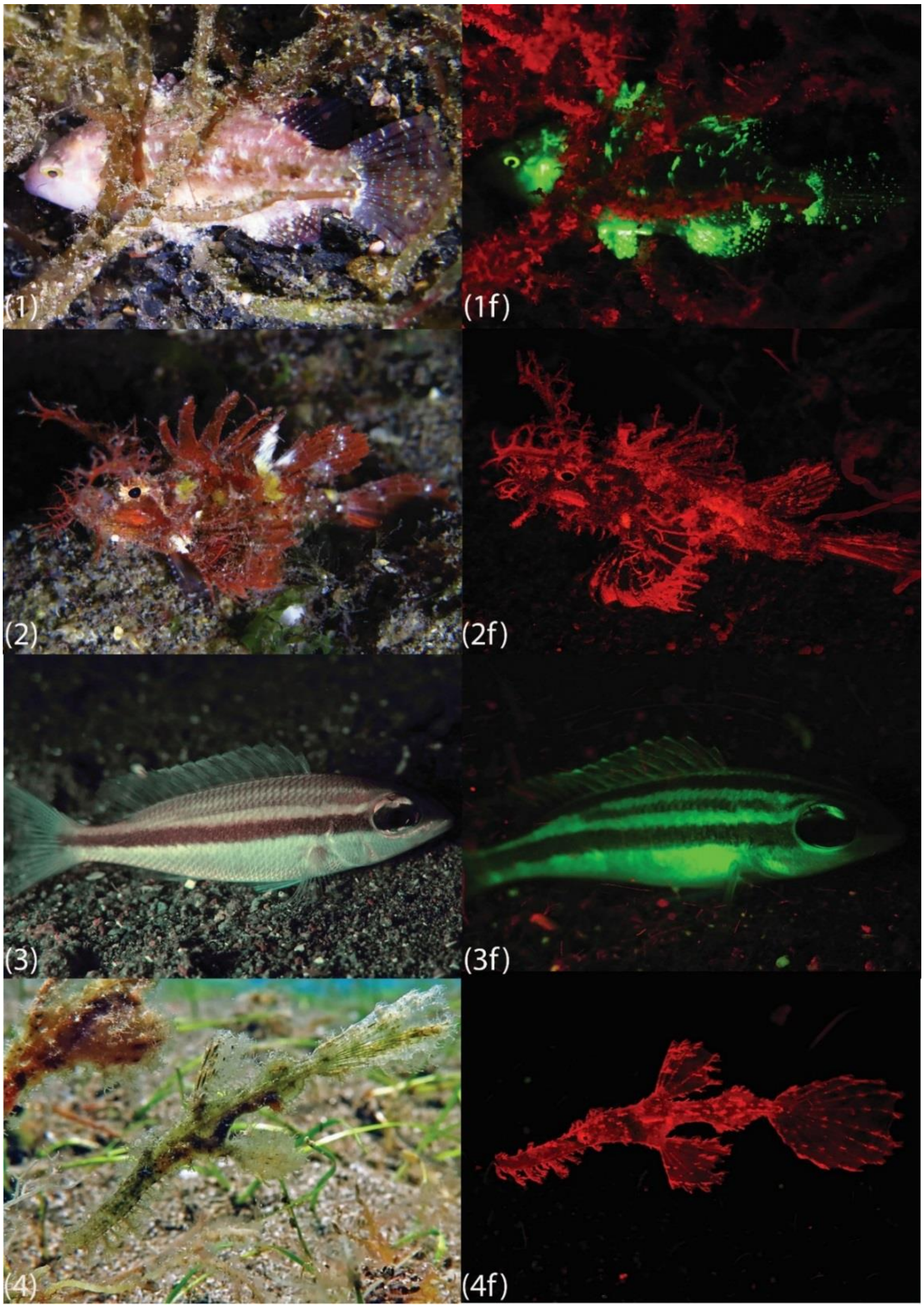
Family	Species	C	Previous	N
Acanthuridae	Acanthurus auranticavus	NC		1
Acanthuridae	Acanthurus leucocheilus	NC		3
Acanthuridae	Acanthurus mata	NC		6
Acanthuridae	Acanthurus nigricans	NC		3
Acanthuridae	Acanthurus olivaceus	NC		1
Acanthuridae	Acanthurus pyroferus	NC	F	2
Acanthuridae	Ctenochaetus striatus	NC		4
Acanthuridae	Naso thynnoides	NC		7
Acanthuridae	Naso vlamingii	NC		3
Acanthuridae	Zebrasoma scopas	NC		15
Acanthuridae	Zebrasoma velifer	NC		1
Apogonidae	Nectamia bandanensis	NC		20
Apogonidae	Cheilodipterus macrodon	NC		1
Apogonidae	Pterapogon kauderni	NC		14
Balistidae	Odunus niger	NC		5
Caesionidae	Pterocaesio tile	NC		3
Chaetodontidae	Chaetodon auriga	NC		2
Chaetodontidae	Chaetodon baronessa	NC		2
Chaetodontidae	Chaetodon citrinellus	NC	F	2
Chaetodontidae	Chaetodon ephippium	NC		2
Chaetodontidae	Chaetodon kleinii	NC		4
Chaetodontidae	Chaetodon lunulatus	NC		5
Chaetodontidae	Chaetodon punctatofasciatus	NC		1
Chaetodontidae	Chaetodon rafflesi	NC		1
Chaetodontidae	Chaetodon semion	NC		1
Chaetodontidae	Chaetodon trifascialis	NC		2
Chaetodontidae	Chaetodon ulietensis	NC		2
Chaetodontidae	Chaetodon unimaculatus	NC		1
Chaetodontidae	Chaetodon vagabundus	NC		4
Chaetodontidae	Heniochus acuminatus	NC		7
Chaetodontidae	Heniochus chrysostomus	NC		1

Chaetodontidae	Heniochus varius	NC	F	5
Cirrhitidae	Cirrhitichthys aprinus	NC		10
Cirrhitidae	Oxycirrhites typus	NC		4
Dasyatidae	Taeniura lymma	NC		11
Diodontidae	Cyclichthys orbicularis	NC		4
Diodontidae	Diodon holocanthus	NC		24
Diodontidae	Diodon liturosus	NC		5
Haemulidae	Plectrorhinchus vittatus	NC		2
Holocentridae	Myripristis sp.	NC		1
Holocentridae	Neoniphon sammara	NC		1
Holocentridae	Sargocentron diadema	NC		32
Lethrinidae	Lethrinus erythropterus	NC		1
Lutjanidae	Macolor macularis	NC		2
Monacanthidae	Aluterus scriptus	NC		1
Monacanthidae	Pseudalutarius nasicornis	NC		3
Mullidae	Parupeneus barberinus	NC		2
Muraenidae	Gymnothorax enigmaticus	C		1
Ostraciidae	Ostracion cubicus	NC		1
Plotosidae	Plotosus lineatus	NC		75
Pomacanthidae	Apolemichthys trimaculatus	NC		1
Pomacanthidae	Centropyge bicolor	NC	F	2
Pomacanthidae	Pomacanthus imperator	NC		2
Pomacanthidae	Pygoplites diacanthus	NC		1
Pomacentridae	Amblyglyphidodon curacao	NC		3
Pomacentridae	Amphiprion clarkii	NC	F	9
Pomacentridae	Amphiprion ocellaris	NC		6
Pomacentridae	Amphiprion perideraion	NC		8
Pomacentridae	Amphiprion polymnus	NC		10
Pomacentridae	Amphiprion sandaracinos	NC		1
Pomacentridae	Dascyllus aruanus	NC		4
Pomacentridae	Dascyllus reticulatus	NC		10
Pomacentridae	Dascyllus trimaculatus	NC		11
Pomacentridae	Plectroglyphidodon lacrymatus	NC		1
Scaridae	Chlorurus microrhinos	NC		1
Scaridae	Hipposcarus longiceps	NC		1
Scorpaenidae	Dendrochirus biocellatus	NC		1
Scorpaenidae	Dendrochirus brachypterus	C		8
Scorpaenidae	Dendrochirus zebra	NC		5
Scorpaenidae	Pterois antennata	NC	F	2
Scorpaenidae	Pterois volitans	NC		3
Serranidae	Belonoperca chabanaudi	NC		1
Serranidae	Cephalopholis argus	NC		2
Serranidae	Cephalopholis cyanostigma	C		2
Serranidae	Cephalopholis sonnerati	NC		1
Serranidae	Epinephelus fasciatus	NC		2
Serranidae	Epinephelus fuscoguttatus	C		1

Serranidae	Epinephelus merra	C		2
Siganidae	Siganus canaliculatus	NC	F	7
Siganidae	Siganus sp.	NC		1
Sphyraenidae	Sphyraena sp.	NC		1
Tetraodontidae	Arothron caeruleopunctatus	NC		1
Tetraodontidae	Arothron manilensis	NC		3
Tetraodontidae	Arothron nigropunctatus	NC		5
Tetraodontidae	Canthigaster compressa	NC		1
Tetraodontidae	Canthigaster valentini	NC		4
Zanclidae	Zanclus cornutus	NC		15

5.4 Additional pictures of fluorescing fish species

Examples of biofluorescence in the same individuals of four different species. (1): *Oxycheilinus bimaculatus* (juvenile), 2: *Pteroidichthys amboinensis*, 3: *Scolopsis affinis* (juvenile), 4: *Solenostomus cyanopterus*. Pictures (1), (2), (3) taken at night using a normal torch for lighting, picture (4) taken by day using ambient light only. Pictures (1f), (2f), (3f), (4f) taken at night with high intensity blue LED torch and yellow filter.



5.5 Additional publication on biofluorescence in cryptic species

Reef sites

Stars and stripes: biofluorescent lures in the striated frogfish indicate role in aggressive mimicry

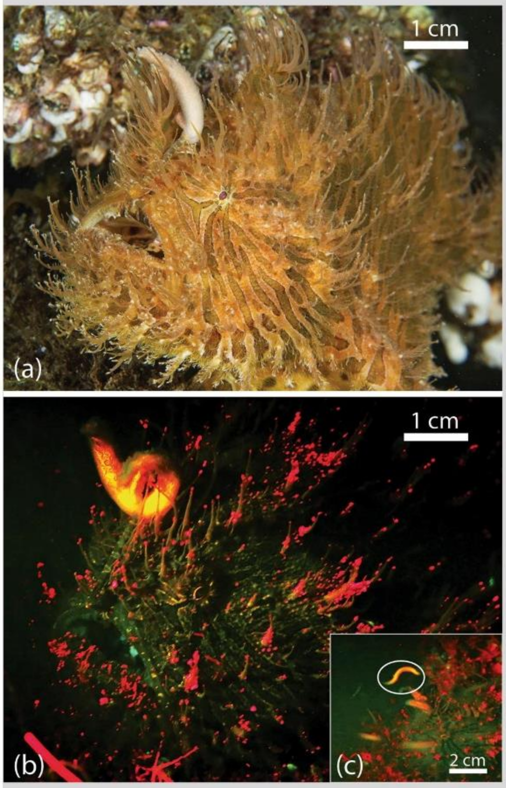


Fig. 1 *Antennarius striatus* under **a** normal light and **b** fluorescent light and **c** worm under fluorescent light

Recent research shows biofluorescence is common in cryptic-patterned coral reef fishes (Sparks et al. 2014). The functional roles of biofluorescence are largely unknown although camouflage and covert intraspecific communication have been hypothesized (Sparks et al. 2014).

Anglerfishes (order Lophiiformes) use an adapted first dorsal spine (esca) as a lure to attract potential prey (aggressive mimicry). Some anglerfishes inhabiting the deep sea (1000 m) use bioluminescent esca to attract prey in dark waters. On coral reefs, anglerfishes are represented by frogfishes (*Antennaridae*), which are cryptic ambush predators whose species-specific esca have evolved to resemble prey such as crustaceans or worms (Pietsch and Grobecker 1987).

Here we report a frogfish (*Antennarius striatus*; Fig. 1a) with biofluorescent esca. Using high-intensity blue LED torches and yellow filters while night diving (depth 5 m) in Dauin, Philippines (9°11′11.64″N, 123°16′4.92″E), we observed three individuals whose worm-shaped esca showed bright orange fluorescence (Fig. 1b). None of the observed fish showed fluorescence on the body, except for limited red fluorescence caused by algal growth. Within 50 cm of the frogfish, we observed free-swimming worms (unidentified species) that were the same size (2 cm) as the frogfish esca and exhibited the same orange fluorescence (Fig. 1c; Electronic Supplementary Material). This suggests biofluorescent esca are used in aggressive mimicry. Bioluminescent bacteria (*Photobacterium leiognathi*) have been reported in the esca of another frogfish (*A. hispidus*) (Ramaiah and Chandramohan 1992) and may serve the same purpose.

These observations indicate a novel function (prey capture) for biofluorescence in coral reef fishes. Given that aggressive mimicry is typical of frogfishes, further research is required to confirm whether biofluorescent esca influence predation success in this genus and to determine the role of biofluorescence in the evolution of reef fishes.

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6.1 Contact frequencies of divers

Mean frequencies of diver contacts per tested variable (frequency = occurrences per min^{-10})

Variable		Mean	SE	N
Total contacts				
	Standard	17.8	1.8	66
	Interaction	66.41	3.8	66
Unintentional contacts				
	Standard	5.1	0.8	66
	Interaction	18.0	2.7	66
Damage				
	Standard	0.6	0.2	66
	Interaction	1.3	0.3	66
Animal contacts				
	Standard	0.1	0.07	66
	Interaction	8.7	2.0	66
Total contacts				
	Observing	47.1	3.6	21
	Photographing	70.5	3.4	20
	Showing animal	70.9	3.9	15
Unintentional contacts				
	Observing	9.1	1.8	21
	Photographing	28.8	3.5	20
	Showing animal	10.7	1.8	15
Damage				
	Observing	2.0	0.5	21
	Photographing	0.5	0.1	20
	Showing animal	1.3	0.3	15
Animal contacts				
	Observing	0.0	0.0	21
	Photographing	4.1	1.9	20
	Showing animal	24.2	3.6	15
Total contacts (Standard)				
	Coral	9.9	1.6	30
	Muck	21.7	2.7	49
Unintentional contacts (Standard)				
	Coral	4.9	1.3	30
	Muck	5.1	0.9	49
Damage (Standard)				
	Coral	0.9	0.3	30
	Muck	0.5	0.2	49
Animal contacts (Standard)				
	Coral	0.1	0.05	30
	Muck	0.1	0.1	49
Total contacts (Interaction)				
	Coral	56.7	5.9	30
	Muck	58.7	3.5	49
Unintentional contacts (Interaction)				
	Coral	17.5	3.6	30
	Muck	13.9	1.8	49
Damage (Interaction)				
	Coral	2.8	0.7	30
	Muck	0.7	0.3	49
Animal contacts (Interaction)				
	Coral	8.4	3.7	30
	Muck	7.5	2.3	49

Total contacts (Standard)			
No camera	15.8	2.4	20
Compact camera	23.7	2.8	25
dSLR camera	10.0	1.4	6
Unintentional contacts (Standard)			
No camera	2.2	0.4	20
Compact camera	10.7	1.6	25
dSLR camera	5.6	0.7	6
Damage (Standard)			
No camera	0.2	0.08	20
Compact camera	1.7	0.4	25
dSLR camera	0.0	0.0	6
Animal contacts (Standard)			
No camera	0.05	0.04	20
Compact camera	0.3	0.2	25
dSLR camera	0.0	0.0	6
Total contacts (Interaction)			
No camera	60.1	6.0	20
Compact camera	79.0	4.7	25
dSLR camera	49.3	1.8	6
Unintentional contacts (Interaction)			
No camera	10.0	2.3	20
Compact camera	29.2	3.9	25
dSLR camera	21.6	1.9	6
Damage (Interaction)			
No camera	1.7	0.6	20
Compact camera	0.2	0.3	25
dSLR camera	0.8	0.06	6
Animal contacts (Interaction)			
No camera	13.7	3.6	20
Compact camera	3.3	1.6	25
dSLR camera	0.3	0.06	6

7.1 Statistical results comparing controls to treatment

Results of paired Wilcoxon rank sum tests comparing controls to treatments, showing original p-values. T: combined mean of all treatments, C: control, TP: diver presence, T1: flash, T2: manipulation, T3: manipulation + flash. Significance level after Holm-Bonferroni corrections *p<0.05, **p<0.01, ***p<0.001, °p<0.1

Reaction	C – TP	C – T1	C – T2	C – T3
Antennariidae				
Movement	1	0.346	0.014*	0.022*
Turn	NA	0.345	0.006**	0.016*
Erect	NA	0.371	0.008**	0.009**
Yawn	0.414	0.345	0.371	NA
Lure	0.361	0.174	1	1
Syngnathoidei				
Turn	0.129	0.0136*	0.014*	0.014*
Feed	0.149	0.832	0.371	0.789
Hippocampus spp.				
Movement	NA	1	0.098	0.269
Solenostomus spp.				
Movement	0.250	0.250	0.098	0.174

7.2 Statistical results of comparisons flash treatment and control group

Differences in morphological variables of the eye anatomy of *Hippocampus subelongatus* between Control group and Flash treatment group. Flash treatment consisted of exposure to ~135 flashes per day for five weeks. SE (C): Control Standard Error; SE (F): Flash Standard Error.

Variable	Control	SE (C)	Flash	SE (F)	t	df	P
Anteroposterior eye diameter (Left) (mm)	3.90	0.12	4.06	0.06	-1.26	13.32	0.23
Anteroposterior eye diameter (Right) (mm)	4.19	0.07	4.12	0.09	0.66	14.64	0.52
Dorsoventral eye Diameter (Left) (mm)	4.06	0.05	4.04	0.07	0.14	17.86	0.89
Dorsoventral Diameter (Right) (mm)	4.22	0.09	4.06	0.06	1.44	12.92	0.17
Lens Diameter (Left) (mm)	1.40	0.04	1.34	0.05	0.86	16.58	0.40
Lens Diameter (Right) (mm)	1.27	0.03	1.26	0.02	0.24	13.23	0.81
Retinal thickness (µm)	200.00	6.36	210.00	10.79	-0.78	14.58	0.45
Photoreceptor length (µm)	75.01	3.84	73.04	1.82	0.46	12.84	0.65
Inner plexiform thickness (µm)	49.36	3.61	55.25	4.97	-0.96	16.42	0.35
Inner nuclear layer thickness (µm)	32.06	3.26	34.94	3.37	-0.61	17.98	0.55
Retinal ganglion cell layer thickness (µm)	5.93	0.55	6.25	0.44	-0.47	17.15	0.65
Outer nuclear layer thickness (µm)	12.03	1.25	12.35	1.38	-0.17	17.83	0.87
Perifoveal retinal thickness (µm)	438.80	30.60	399.30	9.91	1.23	6.04	0.27
Cone photoreceptor inner segment width (µm)	3.14	0.16	2.83	0.16	1.39	17.97	0.18
Rod inner segment width (µm)	2.23	0.13	2.19	0.14	0.22	17.95	0.83
Rod outer segment width (µm)	2.20	0.10	2.10	0.15	0.57	15.49	0.58