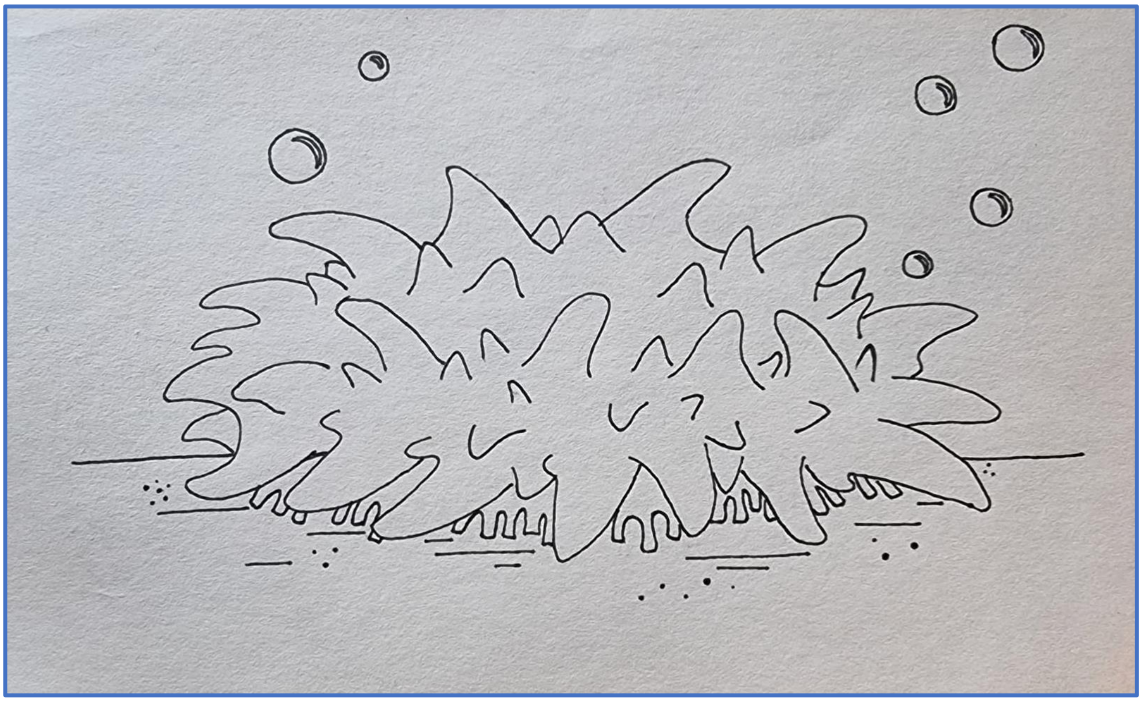
# Supporting sea cucumbers: are seagrass meadows the solution?



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[redacted]

Submitted to Swansea University in fulfilment of the requirements for the Degree of MRes Biosciences.

Swansea University

2022

# Scientific Abstract

Recent years have seen rapid global expansion of sea cucumber fisheries causing two thirds of species to now be considered fully exploited. Such fisheries often occur in areas where communities have restricted livelihoods and there are limited resources for regulation enforcement. Understanding baseline ecology such as habitat preference can allow prioritisation of more effective and focused management strategies. The data presented here was collected by the collaborative research project, the Indo Pacific Seagrass Network. Belt transects were conducted in seagrass and unvegetated habitats at 16 gleaned sites across the Indo Pacific. Sea cucumber community assemblage and seagrass morphometrics were collected. The results demonstrated consistently low sea cucumber abundance and diversity throughout the Indo Pacific compared to historic data with 73% of transects recording zero presence. Exhausted populations have become the new ecological baseline for sea cucumber stocks at gleaned sites. The presence of seagrass supported significantly ($P< 0.001$) higher abundance and diversity than unvegetated transects. 38% of seagrass transects had sea cucumbers present compared to 12% of unvegetated transects. Furthermore, there was a positive relationship between seagrass meadows with a higher percentage of vegetation cover and sea cucumber abundance. Fine scale metrics, such as seagrass life-history trait and benthos type, did not have a significant effect. One site with much lower fishing pressure and pollution sources than the other 15 sites observed no difference in sea cucumber abundance between the seagrass and unvegetated transects. This suggests that seagrass meadows are more critical for supporting the health of sea cucumber populations in heavily harvested systems.

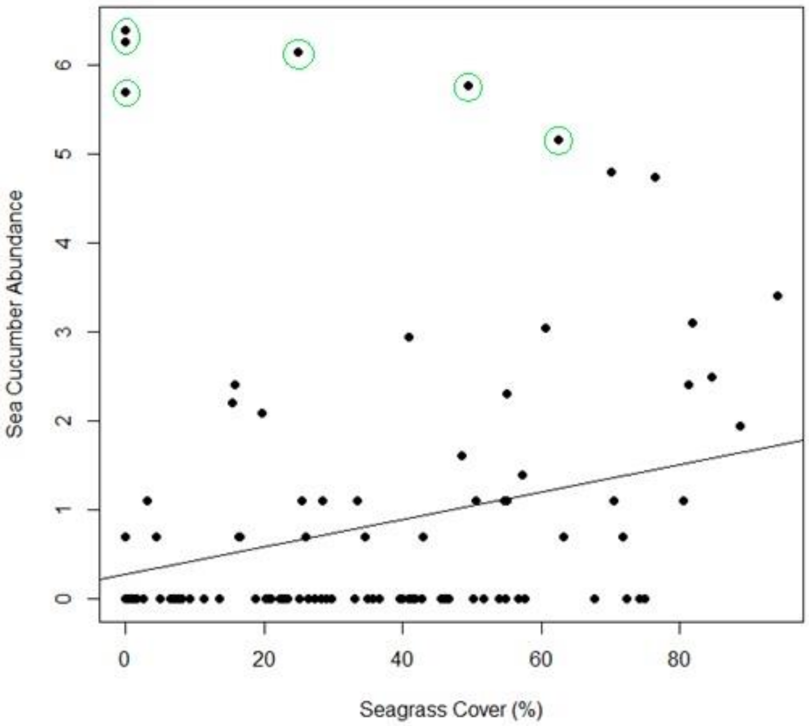
# Summary

Globally, sea cucumbers are under threat and are in high demand. In some cultures they are considered a delicacy, in others they are being sought for medical or cosmetic use. Sea cucumbers are slow to reproduce, making it difficult to maintain healthy populations when fisheries are unregulated. Sea cucumber fisheries are, however, often in areas where livelihood options are restricted making regulation difficult.

Using data collected by the Indo Pacific Seagrass Network, this thesis investigated whether protecting seagrass meadows helps to safeguard sea cucumber populations. Most of our 16 study sites found sea cucumber numbers to be in a poor state. Over 70% of survey points recorded zero presence and there was low diversity throughout.

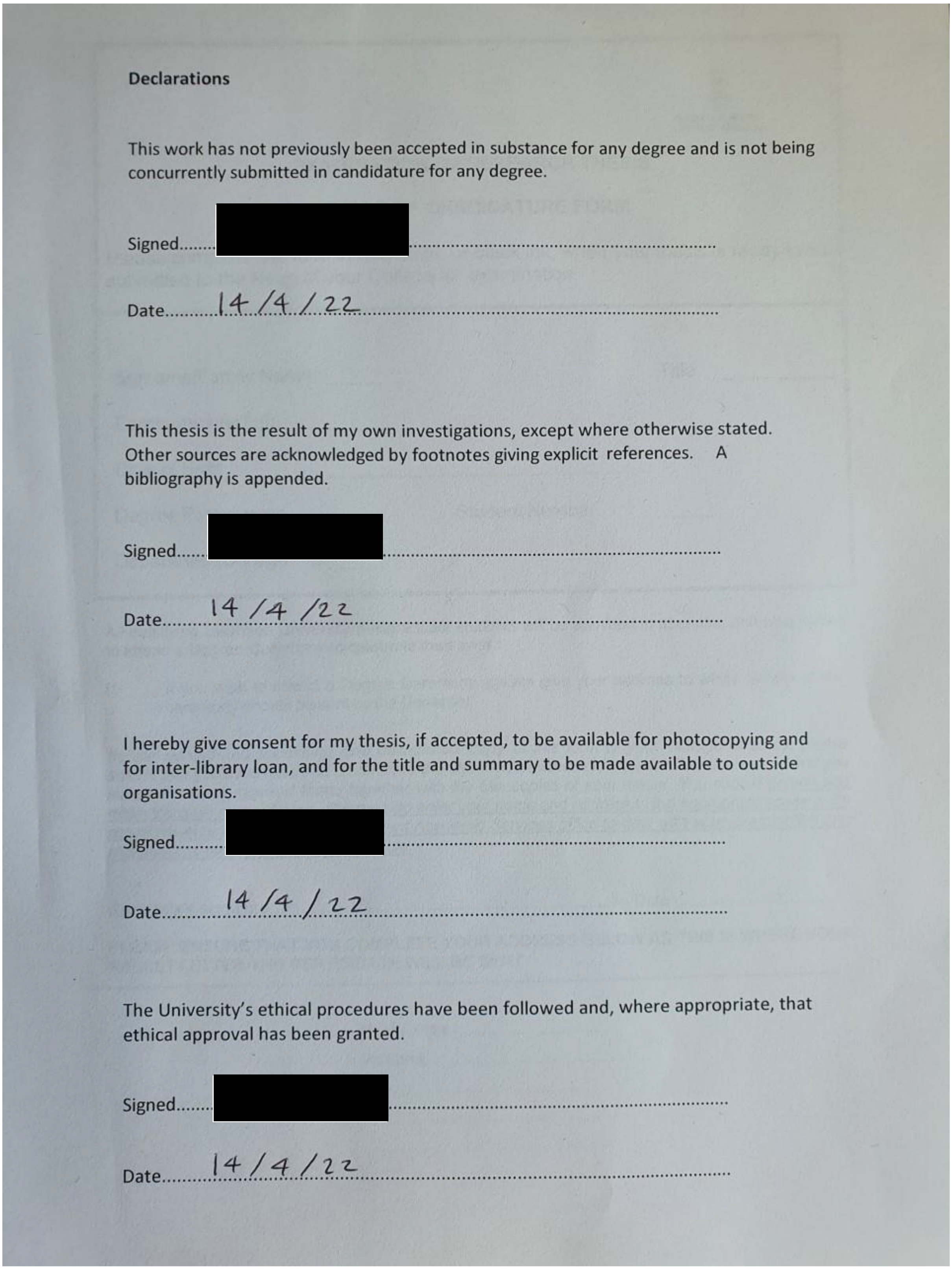
When sea cucumbers were present at a study site then more were found in seagrass meadows than in areas of bare sand or mud. Further to this, when the seagrass was thickly planted more sea cucumbers would be found. This was likely due to the leaves making sea cucumbers harder to spot, hiding them from predators and fishers alike.

The exception to this rule was a study site on a remote island with a small human population and no known sea cucumber trade. At this site sea cucumbers lived in seagrass and bare seabed alike. This leads us to conclude that in a world without human pressure it is likely that seagrass presence would not be crucial for supporting healthy sea cucumber populations. However, when sea cucumber populations are under pressure then protecting seagrass will protect more sea cucumbers, giving them a higher chance of survival.



*The above graph shows higher sea cucumber counts in thicker seagrass meadows. The data points circled in green are from a remote site with a small human population. Here seagrass was less important for sea cucumber populations.*

# Declarations and Statements



**Declarations**

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed........[redacted].................................................................

Date.........14/4/22.......................................................................

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

Signed......[redacted].................................................................

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Date.........14/4/22.......................................................................

## Statement of Expenditure

Student name: Evie Furness

Student number: [redacted]

Project title: Supporting sea cucumbers: are seagrass meadows the solution?

| Category | Item | Description | Cost* |
|---|---|---|---|
| Software | Primer7 | Analytical software. | £570.97 |
| | | | |
| | | Total | £570.97 |

*Including tax and delivery.

I hereby certify that the above is true to the best of my knowledge.

Student: EFurness 14/04/2022

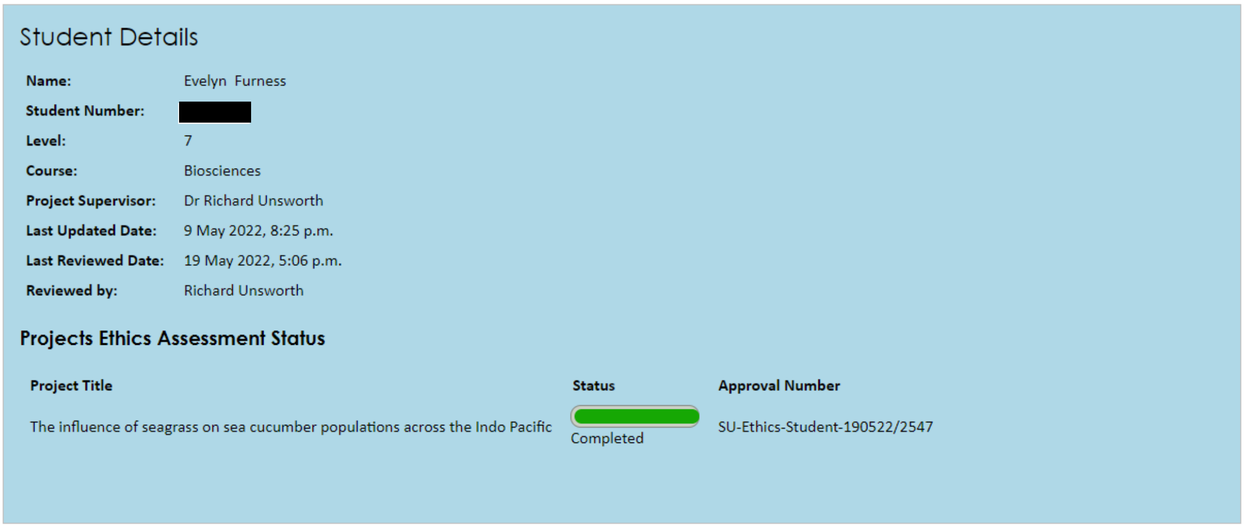
Supervisor: [redacted]/06/2022

## Statement of Contributions

| Contributor Role | Persons involved |
|---|---|
| Conceptualization | Evie Furness, Richard Unsworth, Leanne Cullen Unsworth |
| Data Curation | EF, Maria Eggerston |
| Formal Analysis | EF |
| Funding Acquisition | Indo Pacific Seagrass Network |
| Investigation | IPSN |
| Methodology | IPSN |
| Project Administration | IPSN, EF |
| Resources | IPSN |
| Software | n/a |
| Supervision | RU |
| Validation | n/a |
| Visualisation | EF |
| Writing- Original Draft Preparation | EF |
| Writing- Review & Editing | RU, Fraser Januchowski-Hartley, Johan Elkőf |

# Copy of Ethics Approval

SU-Ethics-Student-190522/2547



## Student Details

| | |
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| **Name:** | Evelyn Furness |
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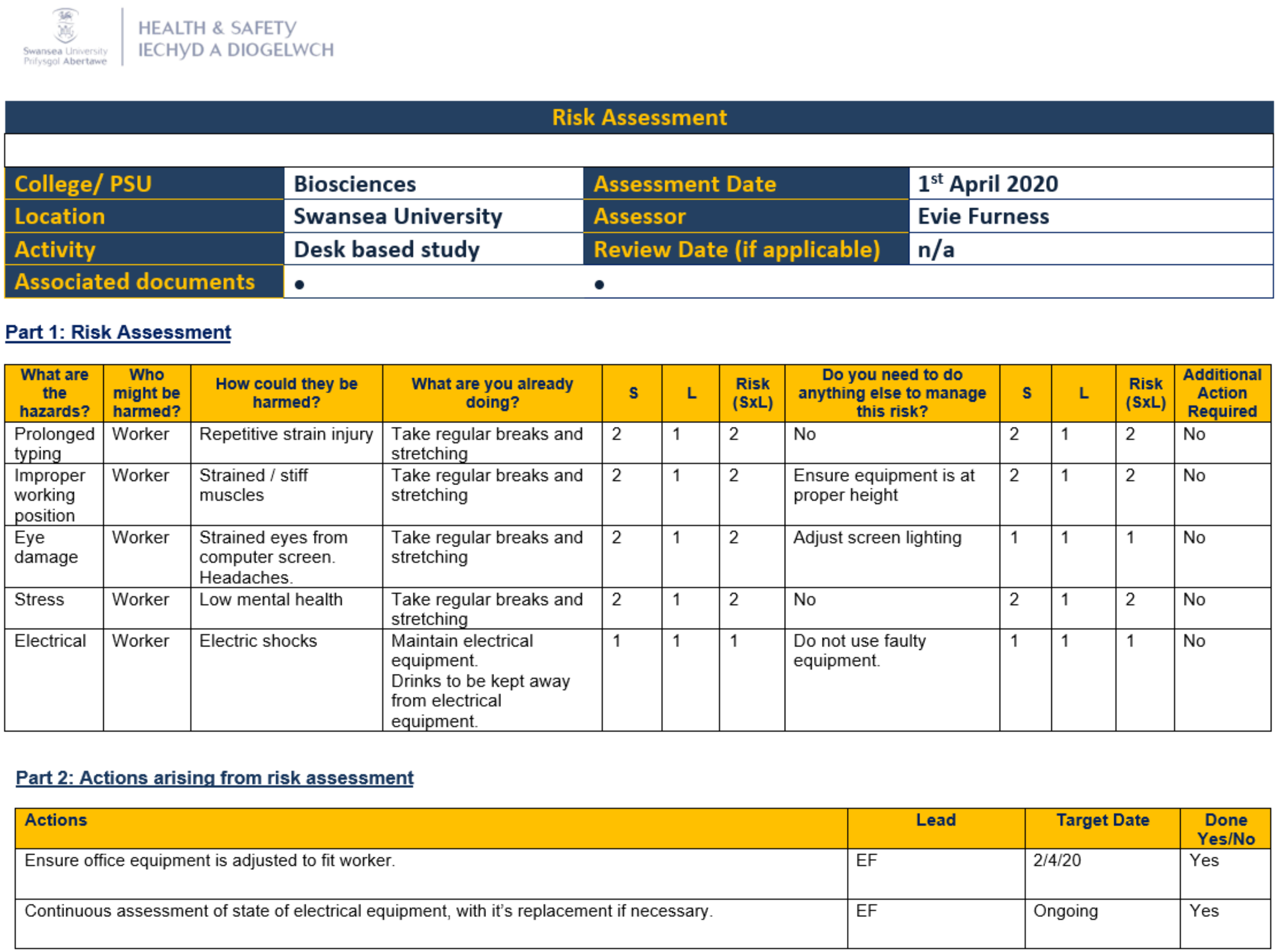
| **Level:** | 7 |
| **Course:** | Biosciences |
| **Project Supervisor:** | Dr Richard Unsworth |
| **Last Updated Date:** | 9 May 2022, 8:25 p.m. |
| **Last Reviewed Date:** | 19 May 2022, 5:06 p.m. |
| **Reviewed by:** | Richard Unsworth |

### Projects Ethics Assessment Status

| Project Title | Status | Approval Number |
|---|---|---|
| The influence of seagrass on sea cucumber populations across the Indo Pacific | Completed | SU-Ethics-Student-190522/2547 |

# Copy of H & S and Risk Assessments



HEALTH & SAFETY
IECHYD A DIOGELWCH

## Risk Assessment

| | | | |
|---|---|---|---|
| **College/ PSU** | Biosciences | **Assessment Date** | 1st April 2020 |
| **Location** | Swansea University | **Assessor** | Evie Furness |
| **Activity** | Desk based study | **Review Date (if applicable)** | n/a |
| **Associated documents** | ● | ● | |

**Part 1: Risk Assessment**

| What are the hazards? | Who might be harmed? | How could they be harmed? | What are you already doing? | S | L | Risk (SxL) | Do you need to do anything else to manage this risk? | S | L | Risk (SxL) | Additional Action Required |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Prolonged typing | Worker | Repetitive strain injury | Take regular breaks and stretching | 2 | 1 | 2 | No | 2 | 1 | 2 | No |
| Improper working position | Worker | Strained / stiff muscles | Take regular breaks and stretching | 2 | 1 | 2 | Ensure equipment is at proper height | 2 | 1 | 2 | No |
| Eye damage | Worker | Strained eyes from computer screen. Headaches. | Take regular breaks and stretching | 2 | 1 | 2 | Adjust screen lighting | 1 | 1 | 1 | No |
| Stress | Worker | Low mental health | Take regular breaks and stretching | 2 | 1 | 2 | No | 2 | 1 | 2 | No |
| Electrical | Worker | Electric shocks | Maintain electrical equipment.<br>Drinks to be kept away from electrical equipment. | 1 | 1 | 1 | Do not use faulty equipment. | 1 | 1 | 1 | No |

**Part 2: Actions arising from risk assessment**

| Actions | Lead | Target Date | Done Yes/No |
|---|---|---|---|
| Ensure office equipment is adjusted to fit worker. | EF | 2/4/20 | Yes |
| Continuous assessment of state of electrical equipment, with it's replacement if necessary. | EF | Ongoing | Yes |

# Contents

# Acknowledgements

Without the support of many this thesis would not have been possible. Firstly, I want to extend my thanks to my supervisor Richard Unsworth for his continuous support and advice. I would like to express my gratitude to all at IPSN for allowing me to use their data when COVID had other plans for my project. A huge thanks to all at Seagrass Ocean Rescue and Project Seagrass who allowed me to have a work-life-MRes balance, in particular to Sam Rees and Eve Uncles for their endless support. Thanks to Josh Mutter for helping me battle with R. A final thanks for the ongoing encouragement from Will Denny.

## List of figures & tables

## Abbreviations

| | |
|---|---|
| **AICc** | Akaike information criterion statistic |
| **FSM** | Federated States of Micronesia |
| **IPSN** | Indo Pacific Seagrass Network |
| **MPA** | Marine protected area |
| **nMDS** | Non-metric multidimensional scaling ordination |
| **PERMANOVA** | Multivariate permutational analysis of variance |

| | |
|---|---|
| **RQR** | Randomised quantile residuals |
| **VIF** | Variance inflation factor |
| **ZINB** | Zero inflated negative binomial |

# Introduction

We have seen repeated degradation and loss of biodiversity to our oceans, from finfish fisheries declining to invertebrate depletion (Pauly et al. 2002, Pauly & Steneck 2019). As global consumption continues to grow, more pressure is being placed on previously less desirable alternative fisheries, such as sea cucumbers (Anderson et al. 2011).

From the class Holothuroidae, sea cucumbers are typically cylindrical or flat, up to a metre in size with soft bodies. They are sessile or low motility detritivores; however, the class is diverse, inhabiting temperate, tropical, deep sea and coastal benthos. Sea cucumbers provide key ecosystem services, such as nutrient recycling, sediment cleaning, bioturbation, prey provision and buffering against localised ocean acidification through alkali production (Wolkenhauer et al. 2010, Purcell et al. 2016a, Wolfe et al. 2018, Williamson et al. 2021).

Strong species-habitat association has been reported in the literature for coastal species, however often with a focus on improving ranching or farming success (Bellchambers et al. 2011, Conand 2018, Eggertsen et al. 2020). These studies have shown up to a two-fold increase in survival rates of juveniles released into seagrass compared to other coastal ecosystems; survival was further improved where a higher percentage cover of seagrass is present (Dance et al. 2003, Altamirano et al. 2017, Ceccarelli et al. 2018).

Seagrasses are marine angiosperms typically associated with sheltered muddy or sandy bays. They provide key fish nursery habitats due to the creation of low energy, complex 3D environments offering protection from predation and high food provision (Heck Jnr et al. 2003, Lilley & Unsworth 2014). Seagrass meadows act as natural filters, trapping suspended solids and plant detritus into the seabed, reducing pollution and sedimentation (Mtwana Nordlund et al. 2016). All these elements improve the conditions for the sea cucumber, a slow moving detritivore, threatened by increased sedimentation from land reclamation (Choo 2008, Tanita & Yamada 2019). Equally, sea cucumbers consume benthic microalgal biomass which enhances seagrass growth (Wolkenhauer et al. 2010, Viyakarn et al. 2020, Arnull et al. 2021).

The tropical seagrass Indo Pacific bioregion, as defined by Short et al. (2007), is globally the most diverse with 24 recorded seagrass species of varying morphology and life history (Coles et al. 2011, Kilminster et al. 2015). Previous studies have found sea cucumber species to have stronger associations with certain seagrass species, such as *Holothuria atra* being associated with *Enhalus acoroides* whilst juvenile, and with *Cymodocea rotundata* once mature (Dissanayake & Stefansson 2012, Setyastuti 2014, Sureshkumar 2017). Given the high diversity in the Indo Pacific then grouping by leaf morph rather than taxonomy may be beneficial as it allows broader management strategies that will be applicable for a wider range of sites.

Since the 1950's sea cucumber fisheries have been subject to rapid global expansion following increasing Asian demand for consumption, medical practices, cosmetic use, and the resulting rising prices (Anderson et al. 2011). It is currently estimated that two-thirds of sea cucumber populations are fully-exploited, over-exploited, or depleted, yet fishing continues to increase (Conand 2018). Sea cucumbers are also threatened by habitat loss, anthropogenic pollution, and a lack of accurate population and fishery data (Choo 2008, Iwalaye et al. 2020).

Coastal dwelling species are easy targets for collection by divers and gleaners, defined as non-specific, opportunistic fishers in the littoral zone, who typically collect with only a stick or knife whilst walking (Grantham et al. 2021). Gleaning is prominent in shallow seagrass meadows, providing key subsistence resources in developing coastal communities (Nordlund et al. 2018). Due to its' unregulated nature, the impact of gleaning is often poorly understood, or excluded from fisheries management strategies, despite accumulative large stock impacts (Purcell et al. 2016a, Kaplan-Hallam et al. 2017). Larger specimens procure a higher monetary value and, thus, are targeted in unregulated fisheries, removing those of sexual maturity, and resulting in boom and bust fishery expansion patterns (Anderson et al. 2011, Eggertsen et al. 2020). Many high value Holothuroidea species are now considered depleted leading to the expansion of the number of species targeted by such fisheries (Purcell et al. 2016b, Govan 2017, Conand 2018).

An understanding of baseline and wider spatial ecology, such as habitat preference and use, is needed to sustainably manage socio-ecological interactions in areas vulnerable to increased food insecurity and poverty, in the face of climate change (Barclay et al. 2019, Grantham et al. 2021). Improving this understanding may reduce the long term implementation (>20 years) of no-take zones currently necessary to positively impact sea cucumber populations (Smith et al. 2000, Uthicke 2004, Castrejón & Charles 2020).

This study aims to provide a current overview of sea cucumber populations and community assemblage structure at gleaned locations across the Indo Pacific. Moreover, it aims to identify effects of morphological diversity of seagrass meadows on sea cucumber communities at a large spatial scale. Thereby, allowing biodiversity management strategies to prioritise protection of seagrass meadows with traits which better support rapidly declining sea cucumber populations.

## Method:

Data on sea cucumbers and their associated habitat were collected as part of the Indo-Pacific Seagrass Network (IPSN), a collaborative research project focusing on seagrass and associated fisheries across the Indo Pacific (Indo-Pacific Seagrass Network (IPSN)). Full protocols can be found on the IPSN website (https://indopacificseagrass.network/research-protocols/).

Assessments utilised for this study were performed during dry season spring low tides between 2018 to 2020 by intertidal belt transects.

### Sites:

The 16 study sites were across six countries within the tropical Indo-Pacific seagrass bioregion at localities where both non-specific gleaning, and seagrass meadows, are known to be present (Fig. 2) (Short et al. 2007).

Sites were in countries known to export sea cucumbers, and to have illegal or unreported sea cucumber fisheries (Appendix A) (Choo 2008, Anderson et al. 2011, Eriksson et al. 2015). Stocks in the Maldives, Mozambique, Philippines and Tanzania were considered depleted, whilst stocks in the Federated States of Micronesia (FSM) and Thailand were considered over exploited (Choo 2008, Prasertcharoensuk et al. 2010, Anderson et al. 2011, Eriksson et al. 2015, Bosserelle et al. 2017).

At Pingelap Atoll (FSM) literature searches found no reference to sea cucumber consumption or export, despite a small local gleaning presence and export trade from Pohnpei town (Bosserelle et al. 2017). The atoll is remote from Pohnpei with a small resident population (<300), few outside visitors, fishers, and cultural restrictions on seagrass fisheries, according to local interviews. Thus, the site was considered to have the most protection with minimal anthropogenic disturbance, despite no formal marine protected area (MPA).

Sitangkai and Tawi Tawi (Philippines), Vilankulos (Mozambique) and Koh Libong (Thailand) are in active marine protected areas (MPA) (Prasertcharoensuk et al. 2010). Nanhimbe (Mozambique), Fumba, Nungwi, Unguja Ukuu and Uroa (Tanzania) are in MPAs with little enforcement. Huraa (Maldives), Sao Sebestiao (Mozambique), Busuanga Island and Ocam Ocam (Philippines) and Chwaka and Nyamanzi (Tanzania) are in unprotected areas.

A literature search was performed to identify previous stock assessments at study sites.

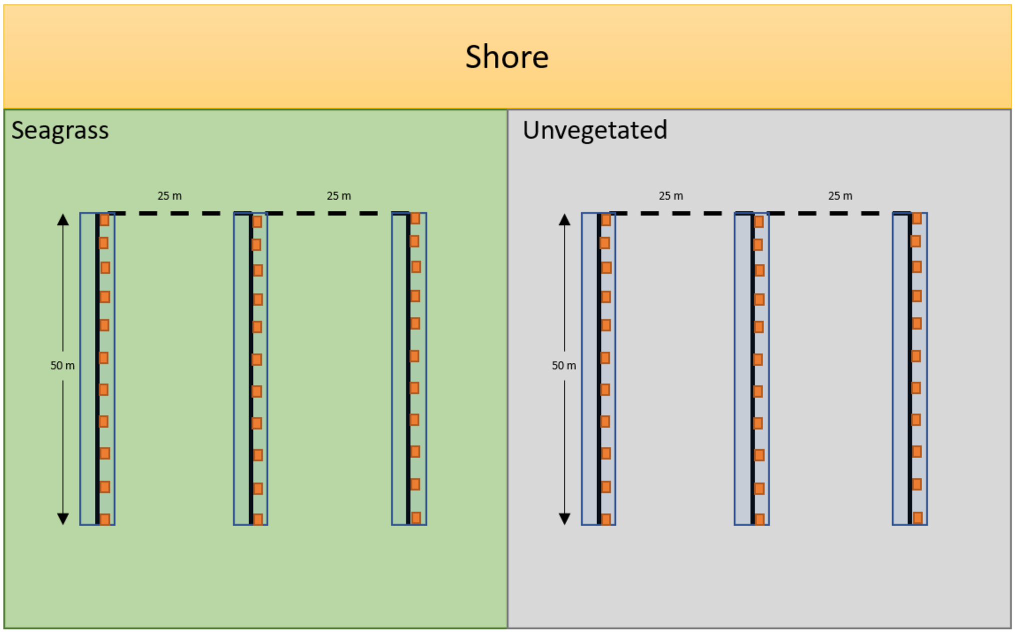


Figure 1. Survey design: three transects were spaced 25 m apart perpendicular to the shore in both seagrass and unvegetated habitats in known gleaning areas. Belt transects for invertebrate assessment were 50 x 2 m (blue) and every 5 m there was a 0.5 m2 quadrat (orange) for seagrass assessment.

## Sea cucumber stock assessment:

Sea cucumbers larger than 5 cm were identified to the lowest taxonomic group possible, along a 50 x 2 m belt transect running perpendicular to the shore (Fig. 1). A minimum of three transects were conducted in seagrass and in adjacent unvegetated sediment. Analysis has grouped to genus or family level.

## Seagrass assessment:

Every 5 m along each transect, a 0.5 $m^2$ quadrat was used to assess seagrass metrics following the SeagrassWatch protocol (Mckenzie 2003): total percent cover, species composition, average canopy height and benthos type (coral, mud, rubble and sand). An average of the quadrats was taken to represent the environmental metrics of the belt transect. Transects having less than 10% average seagrass cover were defined as “unvegetated”.

Benthos type was taken as the most dominant across the quadrats. The most dominant benthos was combined with additional surveyor comments, literature search, and Google satellite imagery to determine the general environment of each site.

The categorisation scheme of Kilminster et al. (2015) was used to group transects by the life trait of dominant seagrass species. The three categories consisted of: ‘colonising’ for fast growing, low canopy species, with rapid recovery post disturbance; ‘opportunistic’ for mid-height and colonisation speed species; and ‘persistent’ for slow growing, high canopy species with low ability to recover from disturbance.

### Statistical analysis:

The sampling design consisted of eight factors: habitat (seagrass and unvegetated), percentage seagrass cover, canopy height (cm), seagrass trait (colonising, opportunistic and persistent), benthos type (mud, sand, rubble and coral), environment (coastal, reef and estuarine), site and country. Due to the nature of collaborative data collection, the study is of an unbalanced design. Unbalanced factors included habitat, seagrass trait, benthos type and environment.

Summary data is presented as mean ± standard deviation and considered per transect (per 100 $m^2$).

Statistical analysis of abundance was conducted in R (V.4.0.3) (R Core Team 2020, RStudioTeam 2020). The count data was heavily right skewed due to overdispersion from zero inflation and high variability in the data, which led to the use of a zero inflated negative binomial (ZINB) model from the ‘pscl’ package to identify drivers (Greene 1994, Martin et al. 2005, Zeileis et al. 2008). Environment was used in the logit part of the model due to its significant effect on the likelihood of false zeros.

From the ‘car’ package, variance inflation factor (VIF) was used to check for multicollinearity between predictors, which were all below 5 and so deemed acceptable (Zuur et al. 2010, Fox & Weisberg 2019).

A lower Akaike information criterion statistic (AICc) and the `lrtest` function from the ‘lmtest’ package were employed to identify the best fitting model (Table 2) (Sakamoto & Ishiguro 1986, Zeileis & Hothorn 2002). Randomised quantile residuals (RQR) were plotted from the ‘MASS’ package to further validate the model (Dunn & Smyth 1996, Feng et al. 2020).

Site was unable to be analysed in the model as a random effect due to nested zero inflation from some sites observing zero sea cucumbers leading to pseudo-replication of transects. Therefore, a Kruskal-Wallis test followed by a pairwise Wilcox test was deployed to identify any significant effects of site on sea cucumber abundance.

Species richness between habitats was analysed using a paired t-Test. Further analysis was not possible due to the high abundance of zero counts.

A zero inflated approach was again adapted to analyse the similarity in assemblages using a Bray-Curtis similarity measure on square root transformed data in the statistics program PRIMER V7 (Clarke et al. 2006, Clarke & Gorley 2015). Non-metric multidimensional scaling ordination (nMDS) was used to visualise the similarities between community compositions.

Permutational analysis of variance (PERMANOVA+) was used to analyse effects of the categorical factors on the uniqueness of assemblages. Factors were nested within site and country and based on 9999 unrestricted permutations under a reduced model.

## Results

### Summary statistics:

Analysis of 186 transects from 16 gleaned sites across the geographic range of the Indo Pacific showed low abundance and species richness of sea cucumbers. The majority of transects (73%) recorded a zero presence. 38% of seagrass transects had sea cucumbers present, with an average abundance of 12.80 ± 56.73 per 100 $m^2$ and 34.66 ±76.65 when zero transects were excluded. In comparison, 12% of unvegetated transects recorded presence, with a higher average abundance and variance at 18.91 ±95.91 per 100 $m^2$ and 157.56 ±79.75 when zero count transects were excluded.

In total, 2,839 individuals were identified across eight taxa, dominated by *Holothuria* spp. (Table 1). Species richness was significantly higher (t test, P< 0.001) in seagrass (1.34 ±0.54) than unvegetated transects (1.11 ± 056). All taxa bar *Opheodesoma* sp. were present in seagrass. Four taxa were present in unvegetated transects, although only one individual was recorded for three of these taxa.

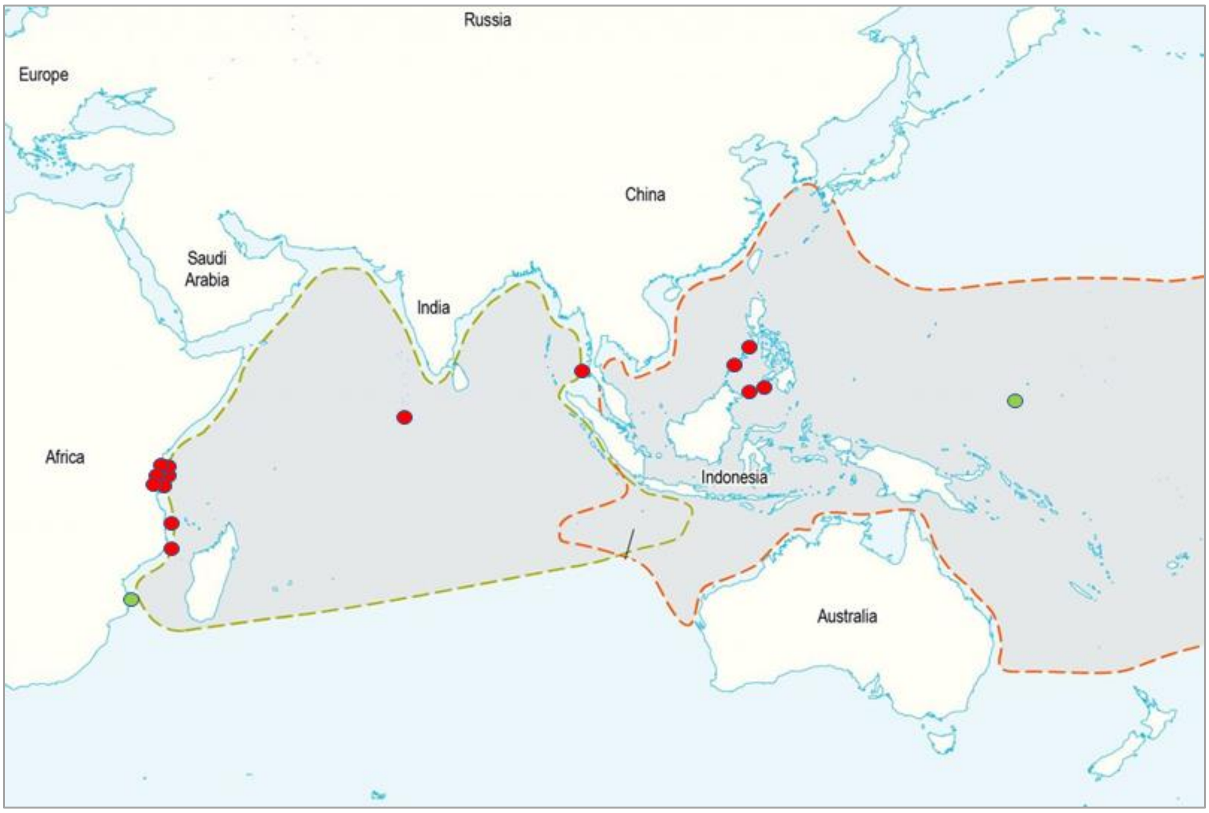


Figure 2. Study sites across the Indo Pacific are indicated; sites with red dots had an average of <3 sea cucumbers per transect and green dots had >10. The shaded area represents the Indian and Pacific oceans.

Table 1. The percent contribution of sea cucumber taxa to sea cucumber community diversity.

| Species | Seagrass diversity (%) | Unvegetated diversity (%) |
|---|---|---|
| *Actinopyga* spp. | 0.42 | 0.00 |
| *Bohadschia* sp. | 0.21 | 0.00 |
| *Holothuria* spp. | 78.18 | 99.79 |
| *Opheodesoma* sp. | 0.00 | 0.07 |
| Phyllophoridae | 17.31 | 0.07 |
| Stichopodidae | 0.21 | 0.00 |
| *Stichopus* spp. | 0.28 | 0.00 |
| *Synapta* spp. | 3.37 | 0.07 |

Table 2. AIC, AICc and likelihood ratio test to identify best fitting model. The final model shows all variables. The chosen model is in bold.

| Included factors | df | AIC | AICc | Likelihood ratio test |
|---|---|---|---|---|
| **Habitat + Seagrass Cover + Benthos + Environment \| Environment** | **12** | **421.30** | **423.92** | **$X^2$=3.55 (df=12, p=0.47)** |

| | | | | |
|---|---|---|---|---|
| Habitat + Seagrass Cover + Canopy + Benthos + Environment \| Environment | 13 | 422.15 | 425.23 | $X^2$=2.40 (df=13, p=0.49) |
| Habitat + Seagrass Cover + Benthos + Environment + Trait \| Environment | 15 | 423.83 | 427.97 | $X^2$=0.07 (df=15, p=0.78) |
| Seagrass Cover + Benthos + Environment + Trait \| Environment | 14 | 425.61 | 429.2 | $X^2$=3.86 (df=14, p=0.15) |
| Habitat + Seagrass Cover + Canopy + Benthos + Environment + Trait \| Environment | 16 | 425.75 | 430.48 | |

## Site comparison:

Figure 3 shows five sites that recorded zero sea cucumber presence across both habitats, and an additional four which recorded presence only in seagrass.

The Kruskal-Wallis test showed site to significantly affect the abundance of sea cucumbers per transect ($P<0.001$), however, this significance was driven by one site Pingelap Atoll. Pingelap Atoll was the only site to show consistent presence and abundance across seagrass (316 ±144.50) and unvegetated (486.67 ±155.72) habitats (Fig. 3). All bar one individual at Pingelap Atoll were *Holothuria* spp., contributing to the dominance of *Holothuria* spp. across all sites (Table 1).

Vilankulos was the only other site with an abundance above 3 per transect. The Vilankulos seagrass transects had an abundance of 38.4 ±41.72, whilst only 0.1 ±0.32 in unvegetated transects.

The highest total species count was found at Sao Sebastiao (0.26 ±0.58) with 4 taxa found in the seagrass transects, however, despite higher inter transect variability, there was consistently more diversity at Vilankulos (2.45 ±3.86). Both sites are in Mozambique.

## Abundance:

The ZINB model including habitat, seagrass cover, benthos and environment showed abundance of sea cucumbers to be significantly higher in seagrass habitats ($P< 0.001$). Furthermore, transects with higher percentage seagrass cover also had a positive impact on the abundance of sea cucumbers ($P<0.001$, $R^2= 0.07$) (Fig. 4).

Coral significantly increased sea cucumber abundance compared to all other benthos types (mud, rubble and sand; all $P<0.001$, Fig. 5). However, coral was only present at Pingelap Atoll where abundance in general was much higher. Further analysis of benthos type with Pingelap Atoll removed, and hence coral removed, showed no significant difference between mud, rubble and sand ($P=0.57$, $P=0.40$ and $P=0.72$ respectively).

When considering the ZINB count model, there was significantly lower abundance in the estuarine environment ($P<0.001$, $Z=-4.23$) than coastal; reef environment also resulted in higher abundance, but it was not significant ($P=0.01$, $Z=2.51$).

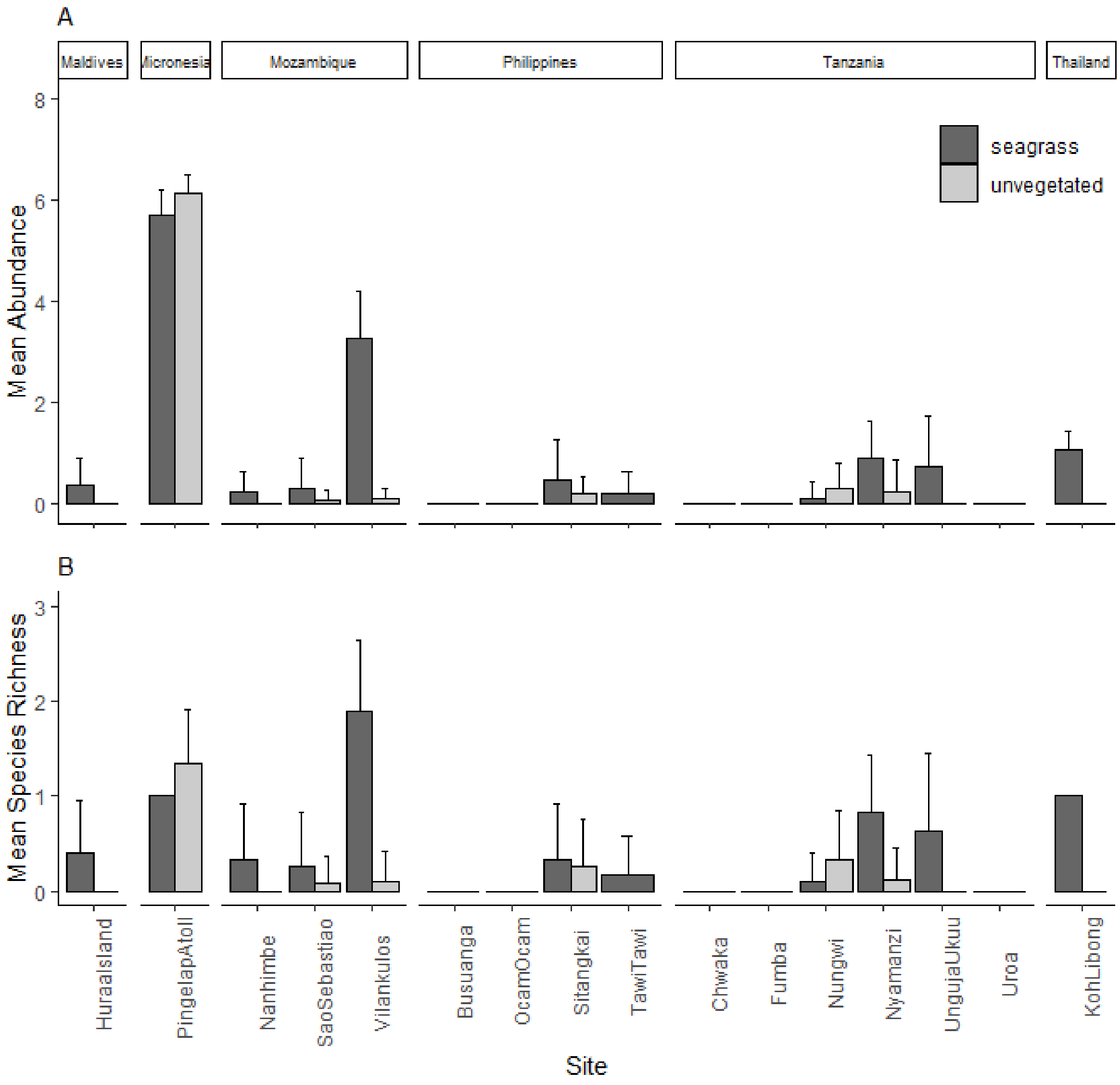


FIGURE 3. A) MEAN ABUNDANCE OF SEA CUCUMBERS PER TRANSECT AT 16 SITES ACROSS THE INDO PACIFIC, IN SEAGRASS AND UNVEGETATED HABITATS, DISPLAYED HERE AS LOG TRANSFORMED FOR VISUAL CLARITY. B) SPECIES RICHNESS FOR THE SAME, BUT NON-TRANSFORMED DATA SET. FLAT LINES REPRESENT ZERO PRESENCE.

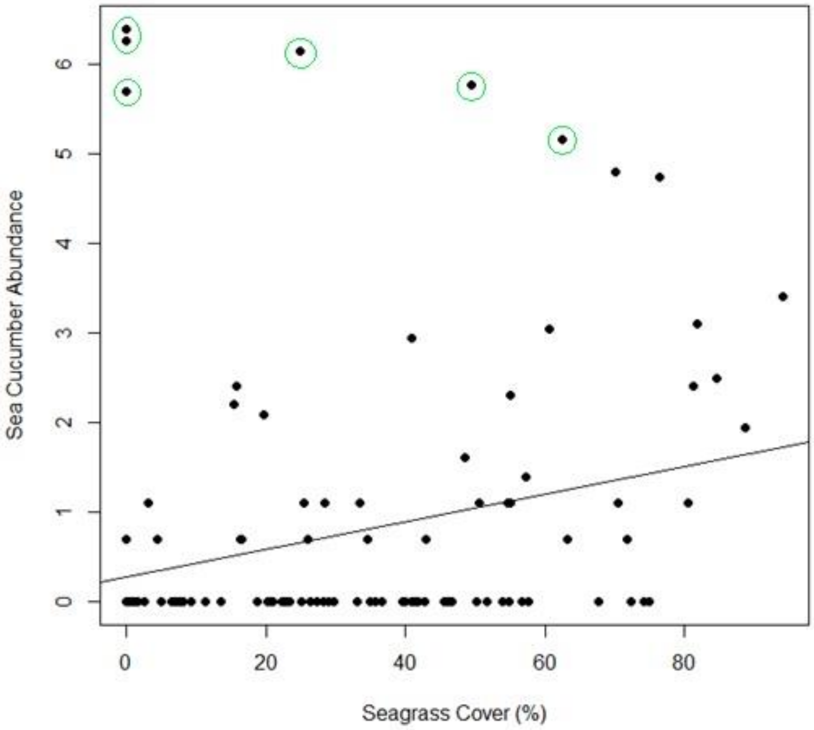


FIGURE 4. LOG TRANSFORMED TOTAL SEA CUCUMBER ABUNDANCE PER 100 M$^2$ TRANSECTS PLOTTED AGAINST THE TRANSECTS AVERAGE SEAGRASS PERCENT COVER, WITH LINEAR REGRESSION LINE ($R^2$= 0.07; $R^2$= 0.11 WHEN PINGELAP ATOLL REMOVED). POINTS CIRCLED IN GREEN ARE THE 6 PINGELAP ATOLL TRANSECTS.

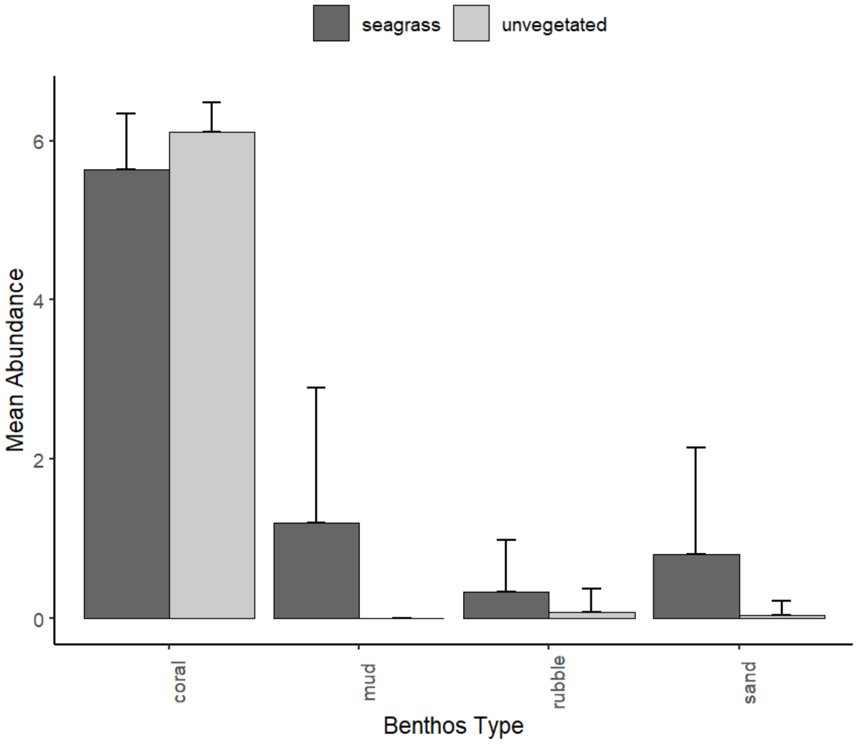


FIGURE 5. MEAN SEA CUCUMBER ABUNDANCE WITH STANDARD DEVIATION ERROR BARS FOR FOUR BENTHOS TYPES ACROSS THE INDO PACIFIC. NOTE THAT CORAL WAS ONLY FOUND AT ONE SITE WHICH HAD ENFORCED TRADITIONAL PROTECTION. DATA WAS LOG TRANSFORMED FOR VISUAL PURPOSES ONLY.

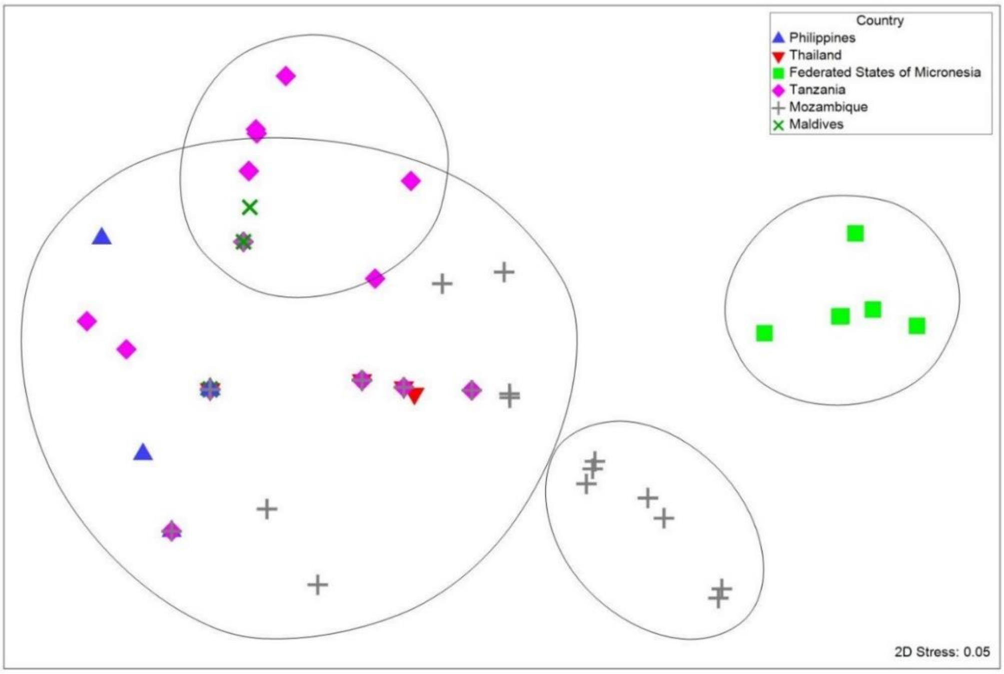


FIGURE 6. NON-METRIC MDS SCALING CONFIGURATION WITH SUPERIMPOSED BRAY-CURTIS SIMILARITY CLUSTERS (50% SIMILARITY) WITH ZERO TRANSFORMATION FOR SEA CUCUMBER ASSEMBLAGES AT GLEANED SITES ACROSS THE INDO PACIFIC.

TABLE 3. PERMANOVA OUTPUT OF ZERO TRANSFORMED SEA CUCUMBER ASSEMBLAGE FROM GLEANED SITES ACROSS THE INDO PACIFIC. ITALICS INDICATES THE REMOVAL OF THE ONLY CORAL SITE, PINGELAP ATOLL.

| Factor | Pseudo- F | P value |
|---|---|---|
| Benthos (Environment) | $F_{7,156}$ 9.86 | P<0.01 |
| Habitat (Site (Country)) | $F_{14,156}$ 6.82 | P<0.01 |
| Site (Country) | $F_{10,156}$ 5.03 | P<0.01 |
| Country | $F_{5,156}$ 7.95 | P=0.13 |
| Trait | $F_{2,156}$ 1.34 | P=0.31 |
| *Benthos (Environment)* | *$F_{6,153}$ 0.92* | *P=0.45* |
| *Environment* | *$F_{1,156}$ 0.75* | *P=0.56* |

TABLE 4. PAST DATA FROM INDO PACIFIC SITES SHOWING AVERAGE ± STANDARD DEVIATION (WHEN AVAILABLE) SEA CUCUMBER ABUNDANCE FOR A 100 M² TRANSECT. INTERTIDAL ASSESSMENTS OF SOFT SEDIMENT, OPEN FISHING AREAS WERE SELECTED WHERE POSSIBLE. WHERE MULTIPLE SPECIES WERE OBSERVED, THE THREE MOST ABUNDANT ONES ARE PROVIDED. 'MIXED' REFERS TO STUDIES THAT WERE NON-DISCRIMINATE ABOUT SPECIES. ABBREVIATIONS INCLUDE FEDERATED STATE OF MICRONESIA (FSM) AND INDO PACIFIC SEAGRASS NETWORK (IPSN).

| Country | Site | Species | IPSN data (2018-2020) | Past data | Reference | Comments |
|---|---|---|---|---|---|---|
| FSM | Pohnpei mainland | *H. atra*<br>*H. scabra*<br>*H. edulis* |  | 75<br>1<br>13 | (Bosserelle et al. 2017) | Mainland known for exporting |
| FSM | Pingelap Atoll | Mixed | 392 ±158 |  |  | Remote from FSM mainland |

| | | | | | | |
|---|---|---|---|---|---|---|
| India | Lakshadweep | *H. atra*<br>*H. hilla*<br>*B. argus*<br>*S. chloronotus* | | 16 ±7<br>2 ±1<br>1 ±1<br>1 ±1 | (Sureshkumar 2017) | Seagrass sites only. |
| Indonesia | Lombok | Mixed | | Significantly decreased | (Syukur et al. 2017) | Local gleaner interviews |
| Indonesia | Wakatobi | Mixed | | 19 ±23 | Robinson 2003 (unpublished) | |
| Tanzania | Fumba | Mixed | 0 | 0.4 | (Eriksson et al. 2010) | All low value species |
| Tanzania | Uroa | Mixed | 0 | 0.2 | (Eriksson et al. 2010) | All low value species |
| Zanzibar | Zanzibar/ Tanzania | Mixed | 0.9 ±2 | 0.1 | (Conand & Muthiga 2013) | Average for country; IPSN Tanzania only |
| Maldives | Vabbinfaru, North Male Atoll | Mixed | | 7 ±5 | (Muthiga 2008) | Functionally protected reef lagoon |
| Maldives | Huraa, North Male Atoll | Mixed | 0.5 | | | |

### Assemblage:

Benthos type had the most significant effect on community composition; however, this became insignificant when the only coral site, Pingelap Atoll, was removed (Table 3). Habitat type and site also had significant effects on the assemblage. Country showed a similar but insignificant strength of influence (Fig. 6). Seagrass trait and environment were insignificant with weak influence on the assemblage.

## Discussion

The current study provides a unique analysis of sea cucumber communities at 16 gleaned sites across the Indo Pacific region. The results provide a bleak reference point for the future management of this economically and ecologically important group of animals. Repeatedly, depleted intertidal communities are evidenced, with low abundance and species richness.

Records of sea cucumber fisheries on a small scale date back beyond the 16th century (Purcell et al. 2013). In that time we have seen many marine species decline due to: anthropogenic degradation of the marine environment, climate change, land reclamation, pollution and overfishing, all of which sea cucumbers are vulnerable to (Choo 2008, Knowlton & Jackson 2008). There is limited historical data on sea cucumber ecology and artisanal fisheries, and these are often forgotten in studies of stock analysis (Nordlund et al. 2018, Furkon et al. 2019). Although research is increasing, the baseline demonstrated in this current study, is that of ecosystems already subject to degradation, a concept noted by Pauly (1995) as the ‘shifting baseline syndrome’. The present study is no different; the sites are all subject to indiscriminate gleaning to various extents and local anthropogenic presence. As a result of this degradation this study cannot confirm that the associations observed are representative of natural sea cucumber ecology, behaviour, and distributions. The results can act as guidelines for best management practices in areas subject to fisheries or other threats, however they cannot be used as recovery targets.

## Site:

The study sites were typically in areas of low fishery regulation enforcement capacity, with small-scale or illegal fishing, stereotypical of gleaning communities (Purcell et al. 2013). In contrast, Pingelap Atoll (FSM) provided a unique study site situated in an area of minimal fishing and anthropogenic pressure (Fig. 3, Appendix A). Despite this, local interviewees from the IPSN surveys commented on decreasing catch size, abundance and diversity of fish and invertebrates, and declining seagrass meadows. In this study Pingelap Atoll is referred to as a 'healthy' sea cucumber community. However, these interviews confirm that the remote Atoll has not escaped from degradation within a generation, and the global shifting baselines syndrome.

The FSM fishery in Pohnpei town is considered depleted, yet continues to export to the Chinese market (Bosserelle et al. 2017). A moratorium on commercial exploitation has been implemented since 1991 following large, unregulated exploitation. The enforced moratorium has seen little difference in recovery between open fishing sites and MPAs; sea cucumber sizes have continued to decrease. In 2017 the abundance was five times lower at Pohnpei than Pingelap Atoll, despite 26 years of apparent fishery closures (Table 4). As access to remote areas improves, and global trade and technology continue to increase, it is important to identify and implement pre-emptive management strategies to areas such as Pingelap Atoll.

FSM echoes a global story of long term closures failing to stimulate recovery of degraded sea cucumber populations (Smith et al. 2000, Uthicke 2004, Castrejón & Charles 2020). Unguja Ukuu (Tanzania) has a minimum Holothuridae catch size of 100 mm, however, 97% of fishers interviewed by Eriksson et al. (2010) were unaware of the restriction. The study observed an absence of breeding groups and considered populations to be fully degraded in 2009. The lack of enforcement led to our study, 10 years later, finding further depletion of Tanzanian sites, regardless of any management measures that may have been implemented (Table 4) (Conand & Muthiga 2013).

Sites with zero sea cucumber presence were all in areas with little or no marine protection, whilst higher abundance and diversity were present at sites with stronger enforcement capacity (Fig. 3, Appendix A). It has been observed that active protection can have, if only small, a positive impact. Muthiga (2008) found seven times more abundance at Vabbinfaru (Maldives), a functionally protected reef neighbouring Huraa, an unprotected and unregulated site (Table 4). Vilankulos (Mozambique), an actively managed MPA with some enforcement capacity, gear restrictions and area closures, showed the highest consistent species richness and second most abundance of all sites (Fig. 4, Table 1, Appendix A) (Conand & Muthiga 2013). MPA's may not be the solution to already depleted populations, yet when actively enforced they can have a positive impact. Furthermore, the sites where comparable historic abundance data was sourced, highlighted that pre-emptive regulations are necessary before a new fishery opens; afterwards is too late to avoid the stock exhaustion associated with growing demand.

## Habitat:

Seagrass meadows support significantly different sea cucumber communities than unvegetated habitats, with significantly higher abundance and species richness (Fig. 3, Table 3). When sea cucumbers were present at a site, they were consistently observed in seagrass transects, but not in unvegetated transects. The complex 3D environment of a seagrass meadow provides predation cover, whilst seagrass detritus provides a food source for juveniles (Mercier et al. 2000, Slater & Jeffs 2010, Dissanayake & Stefansson 2012, Ceccarelli et al. 2018). The leaves decrease wave energy, creating a more benign environment and increasing moisture retention in the meadow, which reduces desiccation stress on sea cucumbers in the littoral zone (Christianen et al. 2013).

The only site where seagrass and unvegetated transects showed similar abundance and species richness was at Pingelap Atoll (Fig. 3). The lower fishing pressure at Pingelap Atoll makes it likely that higher numbers of larger specimens, normally targeted by fishers, were present than at the other more heavily exploited sites (Anderson et al. 2011). It is, therefore, possible that the uniform presence across both habitats at Pingelap Atoll is due to an ontogenetic shift not observed at other sites; larger individuals inhabiting unvegetated areas with higher predator exposure, whilst the smaller, less exploited and hence more abundant juveniles, inhabiting the more protected seagrass meadows (Dance et al. 2003, Eriksson et al. 2012). Fisher habitat preference and sea cucumber size should be evaluated in future studies.

## Seagrass cover and life trait:

Gleaned sites with higher seagrass cover observed higher sea cucumber abundance (Fig. 4). Pingelap Atoll again contradicted this, further suggesting seagrass presence and percentage of seagrass cover to be more critical for over harvested populations, with higher population density negating the risk of predator exposure from sparse seagrass or unvegetated habitats (Dance et al. 2003, Altamirano et al. 2017, Ceccarelli et al. 2018). The presence of coral at Pingelap Atoll again means no definite conclusion can be drawn.

The seagrass life history trait did not significantly affect the abundance or community composition. It was hypothesised that transects with the ‘persistent’ seagrass trait, meadows which are more vulnerable to disturbance, create preferable conditions to support sea cucumber populations (Kilminster et al. 2015). When broader factors such as latitude and annual average temperature have previously been considered, a more significant effect on predation rates have been observed than that of fine scale meadow metrics (Reynolds et al. 2018, Whalen et al. 2020). Focusing on sites not subject to gleaning may present fine and broad scale associations masked here by exploited populations.

## Benthos type:

The depletion observed at the majority of the sites in this study may mask natural behaviours and, therefore, benthos associations. The observed significant effect of coral was biased by its presence at Pingelap Atoll only, additional coral sites are needed to confirm the effect (Fig. 5, Table 3). Certain sea cucumber species have known associations with coral, utilising it for predator protection over diurnal patterns and consuming coral rubble to digest attached organic matter (Shiell et al. 2008, Schneider et al. 2011).

Unvegetated mud offers no 3D environment for cover and unfavourable burial substrate, leading to minimal methods for predator evasion, hence zero presence sea cucumber was observed throughout (Altamirano et al. 2017, Ceccarelli et al. 2018). The mud transects in seagrass, although unfavourable for burrowing, provide obstruction from predator view. Sand and rubble both allow easier burial than mud, reflected in the sea cucumber presence in both unvegetated and vegetated transects (Robinson et al. 2013).

Analysis excluding coral substrate illustrated a lack of significant associations for abundance, species richness and community composition across benthos types (Table 3). Other studies also demonstrate similar non-selectivity at the community level (Muthiga 2008, Tanita & Yamada 2019). Associations with benthos types have, however, been found at the species level; an aversion to mud has been seen for *H. scabra, H. atra* associates with coarse sand, whilst *H. edulis* and *H. leucospilota* associate with rocky shallows (Mercier et al. 2000, Džeroski & Drumm 2003, Dissanayake & Stefansson 2012, Altamirano et al. 2017). Thus, it is inappropriate to prioritise one benthos to support all sea cucumber species.

### Environment:

The significantly lower abundance of sea cucumbers evident at estuarine sites when compared to reef and coastal sites, may reflect the reduced ease of burrowing for sea cucumber when in areas of high sedimentation and silty conditions (Ceccarelli et al. 2018). Coastal or reef sites are likely to offer a more complex habitat-scape, allowing ontogenetic shifts between the habitats. Human settlement is higher near rivers, potentially leading to higher exploitation rates at estuarine sites, as well as higher pollution inputs.

## Conclusion

Sea cucumber fisheries are expanding globally with increasing export volumes and demand (Conand 2018). This study shows depleted stocks at gleaned sites across the Indo Pacific, with exhausted populations becoming the new ecological baseline. At these depleted sites seagrass meadows, and furthermore denser seagrass, support significantly more abundant and diverse sea cucumber communities than unvegetated areas. The exception to this was a site with reduced anthropogenic pressure where sea cucumbers inhabited the seagrass and unvegetated transects alike, suggesting that seagrass may not be crucial for supporting healthy sea cucumber populations. We provide evidence that management strategies should prioritise active protection of seagrass meadows over unvegetated habitats when aiming to protect degraded sea cucumber populations.

# Appendices

## APPENDIX A) DESCRIPTIONS OF SITES AND CORRESPONDING SEA CUCUMBER STATUS ACROSS THE INDO PACIFIC.

| **Country** | **Site** | **Environment** | **MPA** | **Sea cucumber regulations** | **Exports** | **Nation stock state** | **Illegal or unreported fishing** | **Sources** |
|---|---|---|---|---|---|---|---|---|
| Federated States of Micronesia | Pingelap Atoll | Reef | Cultural | Cultural | Mainland | Over exploited | Yes | Bosserelle et al 2017 |
| Maldives | Huraa | Estuarine | No | Species specific | Yes | Depleted | Unknown | Choo 2008, Anderson 2010 |
| Mozambique | Nanhimbe | Reef | Paper park | No | Yes | Depleted | Yes | Choo 2008 |
| Mozambique | Sao Sebastiao | Reef | Unknown | No | Yes | Depleted | Yes | Choo 2008 |
| Mozambique | Vilankulos | Coastal | Yes | No | Yes | Depleted | Yes | Choo 2008 |
| Philippines | Busuanga Island | Coastal | Unknown | No | Yes | Depleted | Yes | Choo 2008 |
| Philippines | Ocam Ocam | Coastal | No | | Yes | Depleted | Yes | Choo 2008 |
| Philippines | Sitangkai | Reef | Yes | No | Yes | Depleted | Yes | Choo 2008 |
| Philippines | Tawi Tawi | Estuarine | Yes | No | Yes | Depleted | Yes | Choo 2008 |
| Tanzania | Chwaka | Reef | No | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |
| Tanzania | Fumba | Reef | Paper park | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |
| Tanzania | Nungwi | Reef | Paper park | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |
| Tanzania | Nyamanzi | Estuarine | No | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Tanzania | Unguja Ukuu | Coastal | Paper park | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |
| Tanzania | Uroa | Reef | Paper park | No | Yes | Depleted | Yes | Eriksson 2015 GOV, Anderson 2011 |
| Thailand | Koh Libong | Estuarine | Yes | Unknown | Yes | Over exploited | Yes | Anderson 2011, Ravadee 2010 MPA report, |

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