

# Fish nets to nests, from the shallow tropics to bathyal Antarctica.

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A dissertation submitted for the degree of MSc by Dissertation Marine Biology

School of Life Sciences

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Date of submission October 2022

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## **Preface**

Fish are found in all oceans on Earth, compose over half of the world's vertebrates, and exhibit highly differing morphologies (Nelson *et al.*, 2016). They occupy the deep hadopelagic to the shallowest coastal regions. As this group of animals are so diverse, the term 'fish' is not contained within a specific lineage. Fish occupy different ecosystems within the global ocean, being adapted to exploit their specific environments. Zonation occurs between areas of the global ocean due to different environmental conditions, mainly driven by depth; as light levels decrease, and temperatures reduce, species are evolved to exploit these environments. Broadly species diversity is higher in the shallow waters of the global ocean than in the deep sea; however, morphologically, the deep sea hosts greater diversity (Martinez *et al.*, 2021).

Fishes have different life histories that determine their development, and the challenges faced in development are dictated by their environment (Thorson *et al.*, 2017). Species exploit niches which are unique to their specific habitat. A heterogeneous habitat allows for a wider range of niches, and as such, a higher species diversity (Brownscombe *et al.*, 2019; Charton and Ruzafa, 1999). The different morphologies that species of fishes exhibit are specialised for their way of life, for example, fin design and use. Most fishes have some form of locomotion, either by swimming, or using their fins to walk (Lauder, 2000). Movement is widely used by fishes to complete daily and developmental activities such as migration between regions for food.

Fishes, like most animals, are impacted by anthropogenic actions (Pauly *et al.*, 2005). Humans have established fisheries to exploit and extract fishes from their habitats, something undertaken by all coastal countries and communities (Hicks *et al.*, 2019). Fishing can be classed into three overall forms: recreational, commercial, and subsistence fishing

(Cooke *et al.*, 2016; Love, 2006). Fishes are an important source of protein for small island developing states (SIDS) as they have limited space for farming and other agricultural practices (Robinson *et al.*, 2022; Sing Wong *et al.*, 2022). Different types of fishing gear can be used to target different morphologies and movements (Eyo and Akpati, 1995). These fishing gears may be restricted by legislation. There are different levels of governance in place for differing fishing locations. Economic exclusive zones allow coastal countries to have the right to exploit marine resources, within their nation's marine area. Fisheries departments in governments, local enforcements, and international treaties or organisations, such as the United Nations and the Convention on the Conservation of Antarctic Marine Living Resources, can enact levels of restrictions, as can local laws and traditions. Governments and local communities can establish marine protected areas, which have the power to protect marine resources from being extracted by abiding groups. This can offer recovery to a certain stock from stock depletion or provide an area for spill-over effects for fishing to occur beside it (Di Lorenzo *et al.*, 2016; García-Rubies *et al.*, 2013).

This dissertation encompasses and has themes covering the movement, life histories, and governance of fishes. I present data from 1) a tropical island fishery and 2) a unique bathyal cryonotothenioid nesting site in Antarctica in two chapters.

## Chapter 1: Size and length matters; increased juvenile catch by altering artisanal fish fence mesh size and total length.

### **Abstract**

Fisheries are a substantial component of the livelihoods of Indo-Pacific Island nations, providing a key source of potentially sustainable food, essential nutrients, and income. Fishing and gear type investigations have long been used in fisheries science for catch composition analysis. Here, artisanal fish fences were used in the Wakatobi Marine National Park to investigate the use of artisanal fish fences in a temporal study on the finfish community life stage and micronutrient composition in this habitat. Fish fences have proved unsustainable, signalling diminishing catch rates and increases in juveniles caught. This study provides a novel use of artisanal fish fences in a multi-species fishery to investigate the nursery role and fishing intensity in seagrass dominated shallow habitats. The results show seagrass-dominated shallow habitats in the Kaledupan subregion of the Wakatobi are a nursery ground for juvenile fish. Juvenile catch proportions have significantly increased over the final years of the study, reaching up to 59% of a yearly catch, likely due to decreasing mesh sizes and increases in fish fence length. The present study shows that this bioregion, indicates an overall change with troubling trends of Malthusian overfishing within the seagrass dominated shallow habitats. Species richness of juveniles had decreased by 23% during the study period. The composition of juvenile and adult fish catch during the study period was relatively consistent between years; however, due to the significant increase in CPUE, it should not be conflated with the number of individual finfish in this region remaining constant. The micronutrients contained within the individuals of catch over time were largely consistent, with changes to mesh size or fish fence length not significantly affecting the mean muscle mass micronutrient content, although this could be a

consequence of the lack of demography in most micronutrient analyses. Carnivorous coral reef fish were significantly more abundant than any other juvenile feeding guilds studied. By directly reducing the number of juveniles progressing to adulthood and thereby impeding their future restocking ability, there is a potential for long term species composition and life-history trait changes within the mangrove-seagrass-reef continuum.

**Acknowledgements:**

The Fishers of WMNP,

Dr. Michelle L. Taylor,

Dr. Dan Exton and Operation Wallacea,

Dr. Philipp Boersch-Supan,

My family.

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## List of abbreviations:

Wakatobi Marine National Park	WNP
Individuals	Ind.
Catch per unit effort	CPUE
Length at first maturation	Im
Seagrass associated species	SAP
No take areas	NTA

## Introduction

Seagrass habitats are located in shallow coastal regions, and with the exception of Antarctica, they are found on all continents (Hemminga and Duarte, 2000). These habitats are widely estimated to cover 266,562 - 1,646,788 km<sup>2</sup> (Duarte, 2017; Jayatilake and Costello, 2018; McKenzie *et al.*, 2020) and are critically important in carbon fixation, storage, and nutrient cycling of coastal waters (Cullen-Unsworth *et al.*, 2014; Fourqurean *et al.*, 2012). Seagrass beds aid at-risk coastal communities with sediment stabilisation, supporting wave attenuation and preventing erosion (Christianen *et al.*, 2013). These meadows are being planted and restored to support blue carbon strategies that target reducing anthropogenic carbon in the atmosphere, used largely due to their high rate of carbon sequestration and increased longevity in contrast to rainforests (Marbà *et al.*, 2015; McLeod *et al.*, 2011). Seagrass beds are classed as a foundation species as they add structural complexity to habitats, thereby supporting a wide range of organisms, including many economically important invertebrates and finfish species (Blandon and zu Ermgassen, 2014; Hughes *et al.*, 2009). Seagrass beds also host and provide a food source for many endangered species, such as dugongs, manatees and green turtles (Waycott *et al.*, 2009). With all the features and services seagrass beds provide, they are an immensely valuable resource, valued at US\$28,916 ha<sup>-1</sup> yr<sup>-1</sup> (Costanza *et al.*, 2014). As a specific example, the fishery industry in Southern Australia has benefited from an increased commercial fish yield by 0.98 kg m<sup>-2</sup> y<sup>-1</sup>, equating to ~AU\$230,000 ha<sup>-1</sup> y<sup>-1</sup> coming directly from seagrass beds (Blandon and zu Ermgassen, 2014).

### Seascape connectivity

In the Indo-Pacific region, seascape connectivity and location configuration with seagrass beds to adjoining habitats (mangroves and coral reefs) positively influence the level of



diversity of many groups and connectivity in said habitats (Olson *et al.*, 2019; Sheaves, 2009; Unsworth *et al.*, 2008). This connectivity habitat seascape also provides coastal defences to island communities from storms and the impacts of waves. By protecting all three habitats, islands have a higher protection level against extreme weather events than those islands with an individual habitat or any combination of two habitats (Guannel *et al.*, 2016). Seagrass community structure is also altered with diel patterns; typically, coral reef fish, such as the families *Lethrinidae* (Emperors), *Siganidae* (Rabbitfish) and *Scaridae* (Parrotfish) are all known to migrate to seagrass beds for the night for refuge and food (Unsworth and Cullen, 2010; Unsworth *et al.*, 2007c). Mangroves are not continuously submerged due to tidal changes in the Indo-Pacific; individuals must thus migrate in and out of the mangrove swamps to exploit and utilise that habitat during high tides (Marguillier *et al.*, 1997; Unsworth *et al.*, 2009).

#### Threats to seagrass beds

Globally, seagrass beds have been negatively impacted by anthropogenic activities such as coastal development and degraded water quality, leading to declines in area, density, and species richness (Montefalcone *et al.*, 2015; Thorhaug *et al.*, 2017; Unsworth *et al.*, 2018; Waycott *et al.*, 2009). Globally, an average of 1.5% of seagrass area was lost every year from 1879 to 2006 (Waycott *et al.*, 2009). One of these destructive factors is the extraction of patches of seagrass for space to cultivate edible seaweeds (Cullen-Unsworth *et al.*, 2014). Indonesia has increased their production of seaweeds from < 4 million tonnes in the early 2000s to > 11 million tonnes in 2011 (FAO, 2020; Unsworth *et al.*, 2018). The loss of seagrass beds has led and attributed to reductions in fishing yield, with many fisheries reporting decreased catch or biomass (Cullen-Unsworth *et al.*, 2014). Indonesia also ranks second globally on the highest percent of total finfish catches in 2020, with an increased catch from < 4 million tonnes in the early 2000s to > 6.7 million tonnes in 2018; however,

this figure may not include the smaller artisanal fisheries (FAO, 2020). Projections show that by 2030, Indonesia will have increased their export of fish for human consumption by 25.7% (FAO, 2020). Protecting key nursery habitats is therefore essential in maintaining that growth, especially as biodiversity is shown to increase resilience against invasion and disturbance, including climate extremes (Isbell *et al.*, 2015; Stachowicz *et al.*, 2007).

#### Nursery role of seagrass beds

The nursery role of nearshore fisheries is a historical ecological concept that has been defined and investigated for seagrass beds (Beck *et al.*, 2001). The term "juvenile" in the context of finfish, refers to an organism that has left its larval stage and is maturing into a sub-adult or fully adult form. There are four general requirements for a habitat to be classed as a nursery ground, which are: 1) high densities of juvenile organisms occupy an area, or 2) less risk of predation in that area, or 3) juveniles grow faster in that area, or 4) juveniles move out of the area to their adult habitat (Beck *et al.*, 2001; Morinière *et al.*, 2003). The nursery role of seagrass beds has been debated in literature since the early 21<sup>st</sup> century, with largely conflicting conclusions on the true extent of the nursery role of seagrass habitats (Dorenbosch *et al.*, 2005; Dorenbosch *et al.*, 2004; Eggertsen *et al.*, 2017; McDevitt-Irwin *et al.*, 2016; Morinière *et al.*, 2003; Nagelkerken *et al.*, 2002). Whilst many of these papers compare seagrass habitats with other habitats, it is also important to assess the nursery role at the ecosystem level within a region. Seagrass beds have been shown to offer refuge, growth, and nutrition for juvenile development with a low risk of predation (Dahlgren *et al.*, 2006). Recent findings show that 21.5% of the top 25 most landed species can be found as juveniles utilising the seagrass meadows, highlighting the need for further action and research into seagrass conservation and restoration to ensure the security of fish stocks for future generations (Unsworth *et al.*, 2019b).

## Biodiversity of the Wakatobi Marine National Park

The Coral Triangle region of South-East Asia hosts high levels of marine biodiversity and has the highest diversity of seagrasses with 16 species in the bioregion (Short *et al.*, 2011). Inside this bioregion, the Wakatobi Marine National Park (WNP) area of South-East Sulawesi, Indonesia, supports many multi-species fisheries (Exton, 2010). Over half of the fish consumed in the region are seagrass associated and 26% of those caught were juveniles (Unsworth *et al.*, 2014). The seagrass meadows are important for food security in this region; coastal communities within the WNP rely on their marine resources for sustenance and preferentially fish on seagrass beds for the majority, if not all, of their protein (Cullen-Unsworth *et al.*, 2014; Exton *et al.*, 2019; Unsworth *et al.*, 2010). In the Wakatobi, the dominant feeding groups of finfish located on the mangrove-seagrass continuum are carnivores (consume fish and/or invertebrates) and omnivores (Unsworth *et al.*, 2009). Herbivores were the least abundant feeding category within the continuum and are found mainly on the mangrove edge.

## Conservation efforts

Major challenges occur when balancing the economic and social justice requirements of local communities, conservation of biodiversity, seafood availability, and seafood demand (Salomon *et al.*, 2011). Management plans and ocean governance of the WNP and the Wakatobi District should be consistently updated with recent data to ensure an accurate and sustainable future for the seagrass fisheries, whilst emphasising the advantages of preserving these habitats (Adimu *et al.*, 2018). The seagrass beds are one of eight important resources that are under management and targeted by the national park officials during checks and patrols. These seagrass beds can recover from stress when the disturbance is minimal and the suspended sediment rates are low enough for sufficient photosynthetic

growth, allowing for long-term recovery (James *et al.*, 2019; O'Brien *et al.*, 2018; Unsworth *et al.*, 2019a). As the knowledge of the best methods regarding seagrass restoration and conservation in the tropics has not yet been fully developed, understanding the biology and ecology of the local seascape is essential to restore the seagrass beds (James *et al.*, 2019; Wendländer *et al.*, 2020).

### Artisanal fish fences

Artisanal fish fences are an alternative form to modern fishing techniques, such as fyke traps, which are a low-effort, high-reward style of fishing (Exton *et al.*, 2019). These fish fences are not the only form of fishing occurring in the Wakatobi (see Exton, 2010). Fish fences are a type of fyke trap that is secured to the seabed, placed frequently in seagrass habitats (Exton, 2010; Ferry and Kohler, 1987). These fences unselectively catch all motile finfish, exploiting the tidal range and diurnal migration of fish travelling across the mangrove-seagrass-reef continuum (Unsworth and Cullen, 2010; Unsworth *et al.*, 2007c). In contrast to more modern methods, which are used by a wider portion of a fishing community, these fish fences are usually constructed and preserved by an individual or small groups of locals (Exton, 2010). Due to having a 'set and wait' unsupervised approach to fishing and small mesh sizes, fish fences capture individuals regardless of size and catches have been reported to contain up to 59% juveniles (Unsworth and Cullen, 2010). These gear types are difficult to monitor as they are seldom used in areas with good reporting and fisheries enforcement. The removal of early lifestage individuals results in low net biomass, hence, decreasing profitability for fishermen (Exton *et al.*, 2019). When fishing pressure is applied on nursery grounds, limitations are placed on recruitment into the next generation, affecting future assemblages and their life-history traits (Freitas *et al.*, 2009; Kronen *et al.*, 2010).

## Nutritional demands and trends in Indonesia

Globally, 795 million people are estimated to be undernourished, with one in three people being malnourished (Haddad *et al.*, 2016). Food security is a major challenge to developing nations. In 2012, the World Health Organisation recognised the need to create Global Nutrition Targets for 2025 (WHO, 2017). These are a set of six goals to reduce global malnutrition, focusing on a reduction in child stunting, anaemia, low birth weights, child wasting, an increase in breastfeeding and there to be no increase in overweight children. In 2020, 8.35% of Indonesia's population was considered to be undernourished, with 10.06% in Southeast Sulawesi (Republic of Indonesia, 2021). Human populations of Southeast Sulawesi are predicted to rise and have already risen by 392,289 people from 2010 to 2020, thereby placing a greater demand for nutritious food in the region (Statistik and Bappenas, 2018; Statistik and Negeri, 2021). In low-income countries, where malnutrition impacts a large amount of the population, fisheries have been targeted as a pathway to achieve some of the sustainable development goals (Vianna *et al.*, 2020). The focus of confronting undernourishment and malnutrition is more than their nutrient consumption. Studies have investigated broader societal, health, and sanitation factors that play a role in malnutrition and undernourishment, alongside nutrient composition (Haddad *et al.*, 2016; Hanandita and Tampubolon, 2015; Hicks *et al.*, 2019; Miller and Welch, 2013).

The prevalence of malnutrition and undernutrition in Indonesia is disproportionately higher for those whose heads of household are fishermen in 2019, with 37.5% of children being stunted in the country (Republic of Indonesia, 2021). This is also true for children under five who experience wasting at 13%. Reducing this disparity in undernutrition, whilst achieving sustainability, is essential to improve the quality of life of the local islanders and their children.

## Finfish micronutrients

In fisheries, finfish micronutrient analysis and models have been recently investigated in depth to tackle some of the issues surrounding malnutrition and focus on targeted nourishment globally, prioritising developing nations (Hicks *et al.*, 2019; Robinson *et al.*, 2022; Willer *et al.*, 2022). The model developed by Hicks *et al.* (2019) allows fishers to identify the more nutritious species and gives a better understanding of the nutrient profiles eaten by fishing communities. Essential micronutrients identified and modelled include zinc, selenium, vitamin a, calcium, iron, omega 3, and a macronutrient protein. These micronutrients have been chosen as being essential to human health and development, which could help reduce the prevalence of stunting and wasting in children, and anaemia in women. When fishing, the key nutrient targeted has been protein, with local islanders often having fish as their main source of this macronutrient (Exton, 2010; Exton *et al.*, 2019; FAO, 2020). Of the other nutrients, omega 3 polyunsaturated fatty acids aid in promoting neurological and cardiovascular growth and maintenance (Shalders *et al.*, 2022; Tacon and Metian, 2013). The vitamins and minerals, such as vitamin a, zinc, iron, selenium, and calcium, aid the body to maintain its essential functions and carry about proper development including regulating hormones and oxygen transport (Konikowska and Mandecka, 2018; Shalders *et al.*, 2022). A recent study found coral reef fish to contain high levels of selenium and zinc, with comparable levels of omega 3, calcium and iron to terrestrial animal foods (Robinson *et al.*, 2022). The abundance and diversity of finfish in the Wakatobi, therefore, allows for a potential nutritious source of macro and micronutrients that could provide relatively strong food security when fished sustainably. A habitat phase shift from a coral-dominated habitat to one that is macroalgae dominated has shown to increase iron and zinc levels in the harvested finfish, providing hope for the long-term food security of millions of people who rely on the ocean for sustenance (Robinson *et al.*, 2022). So far, no research

has investigated the effect of fishing intensity on a multispecies fishery for community micronutrient content over time.

These finfish are threatened by climate change leading to a cascade of altering environmental factors, including a warmer ocean, and are estimated to become smaller in the tropics, which could reduce their biomass by 20% by 2050 (Golden *et al.*, 2016; Robinson *et al.*, 2022; Shalders *et al.*, 2022). Undernutrition of local human populations could become exacerbated by this decrease in biomass, overfishing, and habitat degradation due to climate change (Exton *et al.*, 2019; Hoegh-Guldberg *et al.*, 2007; Maire *et al.*, 2021). Species-specific responses in micronutrient content have been shown to be caused by changing environmental factors (Shalders *et al.*, 2022). These responses have led to vulnerable and resilient species to environmental changes, and thus, the micronutrient availability to the local human population (Shalders *et al.*, 2022). Further research is needed into the influence of fishing intensity on the micronutrient content of finfish at a community level. It is therefore essential to investigate the fisheries catch content and identify the micro and macronutrients available for human populations from finfish, which will aid the knowledge of required supplements in their diets.

## Hypotheses

It is hypothesised that:

- 1) There is a high proportion of juvenile fish located in seagrass-dominated shallow habitats.
- 2) The proportion of carnivorous fish species caught in the fish fences is higher than any other feeding guild.
- 3) Over the course of this study, the proportion of catch to contain juveniles in fish fences on the seagrass dominated shallow habitats has not changed.

4) Average finfish micronutrient content is not significantly affected by changes to fish fence metrics(e.g., mesh size decrease, fence elongation, number of fences).

## **Materials and methods:**

### Study site

Established in 1996, the Wakatobi Marine National Park is a group of islands in South-East Sulawesi, Indonesia. The coastline is characterised by seagrass meadows, mangrove forests, and coral reefs. The shallow habitats in this bioregion are mainly comprised of the seagrass species *Thalassia hemprichii* and *Enhalus acoro* (Unsworth *et al.*, 2007c). Seagrass coverage varies from 48.8% to 79.5% in the Kaledupa subregion (Unsworth *et al.*, 2008). The island hosts a population of 17,000 people and has a heavy reliance on fishing for protein sustenance and income (Exton, 2010). The 978 fish fences recorded from 2003 to 2016 were located on the seagrass-dominated shallow habitats around the second largest island in the WNP, Kaledupa (Figure 1).



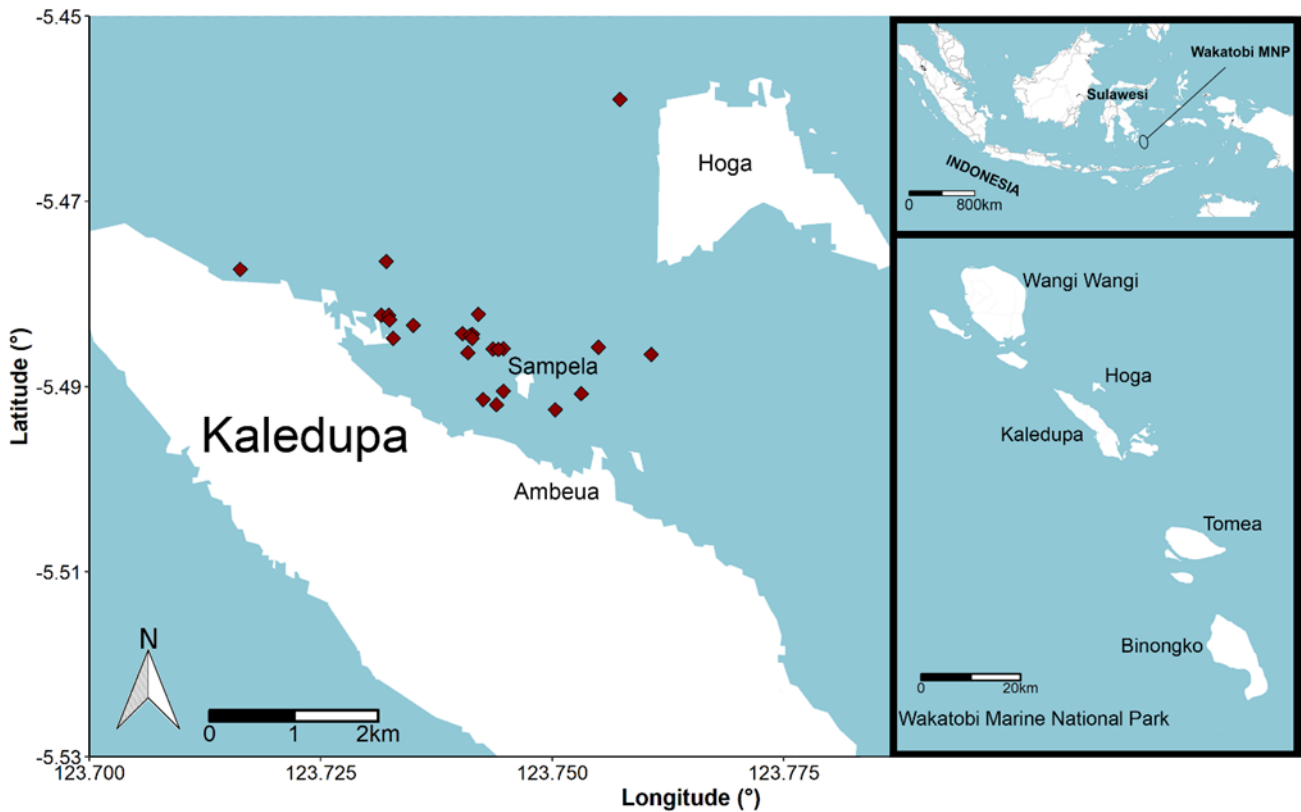


Figure 1: Location of the artisanal fish fence study sites within the Kaledupa subregion of the Wakatobi Marine National Park, South-East Sulawesi, Indonesia. Red diamonds indicate fish fence GPS data, where available.

### Catch composition

Individual fish were caught and sampled using local fishers' artisanal fish fences in a five-week sampling period in July and August biennially from 2003 to 2011, and then annually from 2012 to 2016. Catches were recorded daily at low tide and were identified to species level. The number of individuals of each species caught from the fence was recorded in the field. If the catch was composed of > 20 individuals of the same species, a sub-sample was randomly selected and measured; mean length values were then used for the total number of individuals caught. During the collection, mesh size and total fence length measurements were taken. Physical fence characteristics were unable to be captured at every sampling

event due to logistical constraints. During the survey, GPS coordinates of fish fences were taken when possible. All fences were located in the seagrass dominated shallow habitat.

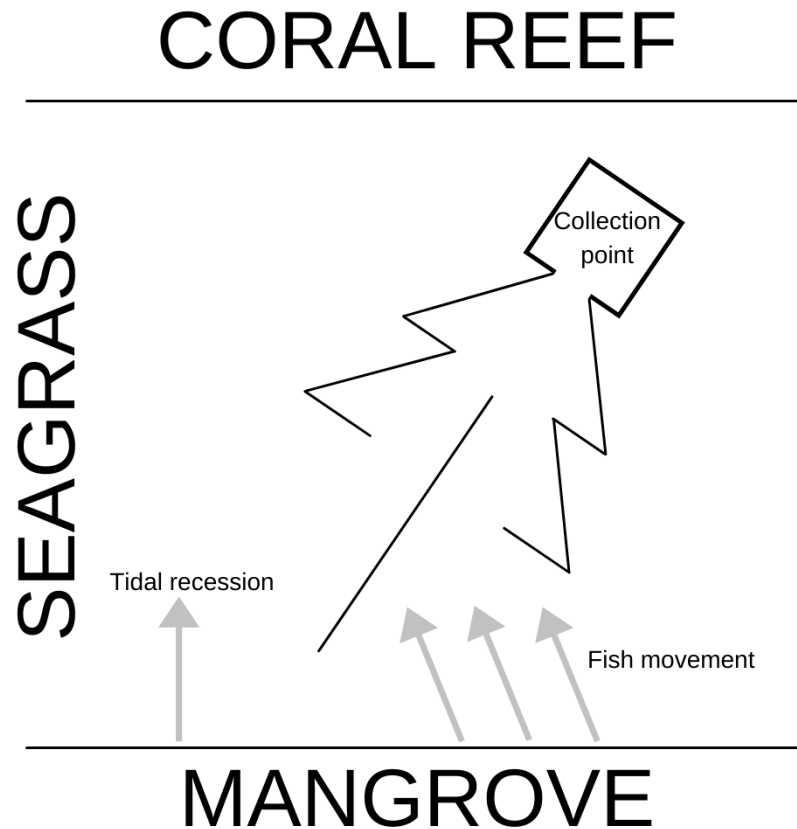


Figure 2: Design and placement of a typical artisanal fish fence used in this study, adapted from (Exton, 2010).

All data collection were completed by Operation Wallacea. The data used in this paper has been published prior, highlighting the threats and challenges artisanal fish fences pose to tropical seascapes on adult finfish compositions (Exton *et al.*, 2019). Some species names have been updated to match accepted nomenclature using Rfishbase (Boettiger *et al.*, 2012; Froese and Pauly, 2020). Certain individuals caught were unable to be identified to species level and were assigned as 'sp.' for analyses. Said individuals were given the most common feeding guild for that genus. Length data were collected to quantify life stages and individuals were assigned as an adult or juvenile per their published species length at first maturation (lm) (Froese and Pauly, 2020). Feeding guilds were assigned using published information on food items and Operation Wallacea's database of local fish feeding guilds

and Rfishbase (D. Exton, pers. comm.). The 15 most abundant juvenile families and species were examined in further detail to explore feeding guilds in the seagrass dominated shallow habitat. Biomass was calculated from the species-specific published length-weight relationships using the formula  $biomass(g) = a * L^b$ , to investigate potential trends in community biomass composition (Froese and Pauly, 2020). Each artisanal fish fence was given a specific ID to calculate catch per unit effort (CPUE), reported here as fence<sup>-1</sup>.

To identify community catch composition by lifestage, mesh size and year, a metacommunity Bray-Curtis nonmetric multidimensional scaling (NMDS) analysis was applied. The *vegan* package containing the function metaMDS in R was used to create the ordination (Oksanen *et al.*, 2013).

#### Finfish micronutrient content

The ‘Nutrient Analysis Tool’ from FishBase was applied to the list of species identified in the fish fences to establish the species’ muscle mass micronutrient content in wet weight per 100 g (Froese and Pauly, 2020; Hicks *et al.*, 2019). The micronutrients included were calcium (mg), iron (mg), selenium (µg), zinc (mg), vitamin a (µg), omega 3 (g), and protein (g). If the species did not have information on micronutrient content available, the genus’ average was used.

Table 1: Mean micronutrient recommended dietary allowances for male and female Indonesians from the age of 10 to 80+ (Moeloek, 2019).

Micronutrient	Recommended dietary allowance (RDA; day <sup>-1</sup> )
Calcium (mg)	1150
Iron (mg)	10.81
Selenium (µg)	26.69
Zinc (mg)	9.44
Vitamin A (µg)	621.88
Omega 3 (g)	1.32
Protein (g)	62.48

All data underwent testing of normality using the Shapiro-Wilk method. A generalised linear negative binomial regression with random sampling event random effects was used to explore potential relationships between juvenile total catch, total fence lengths, and mesh sizes. The differences in feeding guilds as a proportion of catch were tested by one-way ANOVA, using post hoc Tukey-Kramer testing to determine the source of significance. To test for differences within the proportion of adults and juveniles per year, a pairwise Wilcoxon rank-sum test was completed per sampling year and for the overall proportions of juveniles and adults. Generalised gaussian mixed models with nested random effects of date and year were used to explore the effects of mesh sizes and total fence lengths on the finfish micronutrient content. R version 1.3.1093 was used for all statistical analyses (R Core Team, 2017).

## **Results:**

### Overall

In most instances, after attempts to transform the data to confirm to normality, data were not normal. For the temporal investigations, the data were too large to produce a valid normality output. In total, 51,678 individuals across 687 species were sampled in 978 fish fences and identified to a species level with individual lengths recorded; 22,659 (43.8%) of the individuals were juveniles. Overall the average fish abundance was  $26.7 \pm 35.8$  fence<sup>-1</sup>.

## Juvenile catch composition

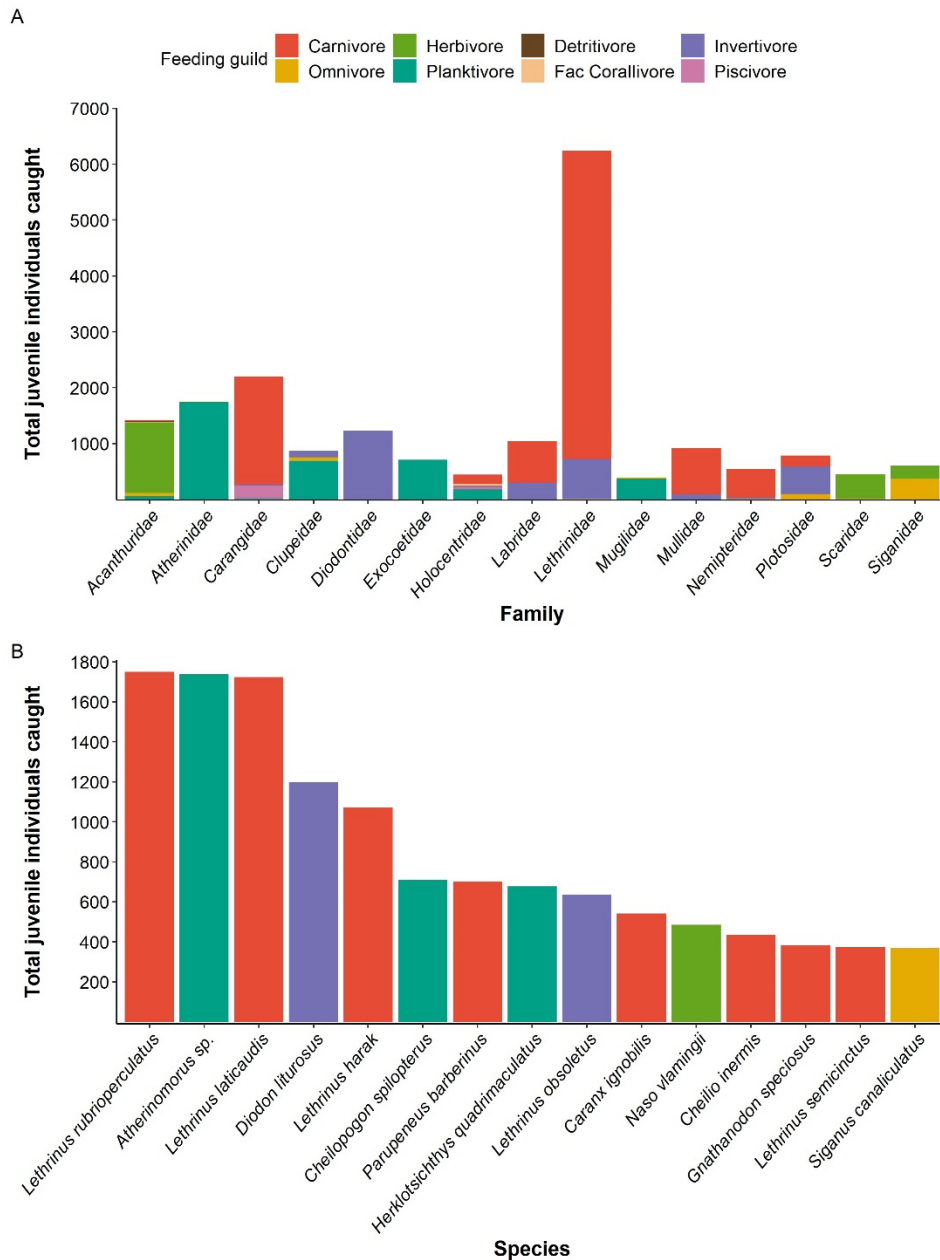


Figure 3: Top 15 most abundant juveniles caught on the shallow seagrass dominated habitat, columns show the total number of juvenile individuals, grouped at (A) family level with stacked feeding guilds and (B) species level with associated feeding guilds.

The adult catch was reported by Exton *et al.* (2019). Throughout the duration of the study, 75 families of juveniles were caught. The most represented family in terms of individuals was *Lethrinidae* (27.6%, 13 species), followed by *Carangidae* (9.7%, 39 species), *Atherinidae* (7.7%, 5 species) and *Acanthuridae* (6.3%, 31 species). The family with the highest biomass caught throughout the study was also *Lethrinidae* (481.8 kg), followed by

*Carangidae* (271.5 kg), *Diodontidae* (147.8 kg) and *Sphyraenidae* (95.6 kg). *Lethrinus rubrioperculatus* (128.65 kg), *Diodon liturosus* (120.25 kg), *Lethrinus harak* (111.45 kg), and *Lethrinus obsoletus* (90.84 kg) were the top four species by biomass and accounted for 25.17% of the juvenile catch by biomass. The family *Diodontidae* is comprised of four species: *Cylichthys orbicularis*, *Cylichthys spilostylus*, *Diodon hystrix*, and *Diodon liturosus*. From 2003 to 2009, less than 20 juveniles were caught in this family per year, all of whom were *D. liturosus*. The total number of *Diodontidae* caught per year after 2009 rose and the other species within this family were also caught, peaking at 613 juveniles in 2013 (55 kg).

A total of 469 species were recorded as juveniles in the fish fences, *Lethrinus rubrioperculatus* (7.71%) was the most common species observed in the fences, followed by *Atherinomorus sp.* (7.67%), *Lethrinus laticaudis* (7.61%), and *D. liturosus* (5.28%). These four species accounted for 17.9% of the total biomass. The highest single species juvenile catch observed in a year was *L. obsoletus*, with 62.2 kg harvested from the seagrass-dominated shallow habitats in 2009.

#### Juvenile feeding guilds

Carnivorous fish were found in the highest abundances, representing over 48% of the juveniles caught. Feeding guild composition in the seagrass habitat differed significantly depending on the proportion of juveniles harvested (ANOVA:  $F_{9,65} = 24.59$ ;  $p < 0.0001$ ). The carnivore feeding guild abundance significantly differed from all other feeding guilds (Tukey test:  $p < 0.05$ ). Obligate corallivores were the smallest feeding guild, with four juvenile individuals observed throughout the study. These obligate corallivores are composed of three species in the family *Chaetodontidae*: *C. oxycephalus*, *C. lunulatus*, and *C. trifascialis*.

## Temporal breakdown of fish harvesting

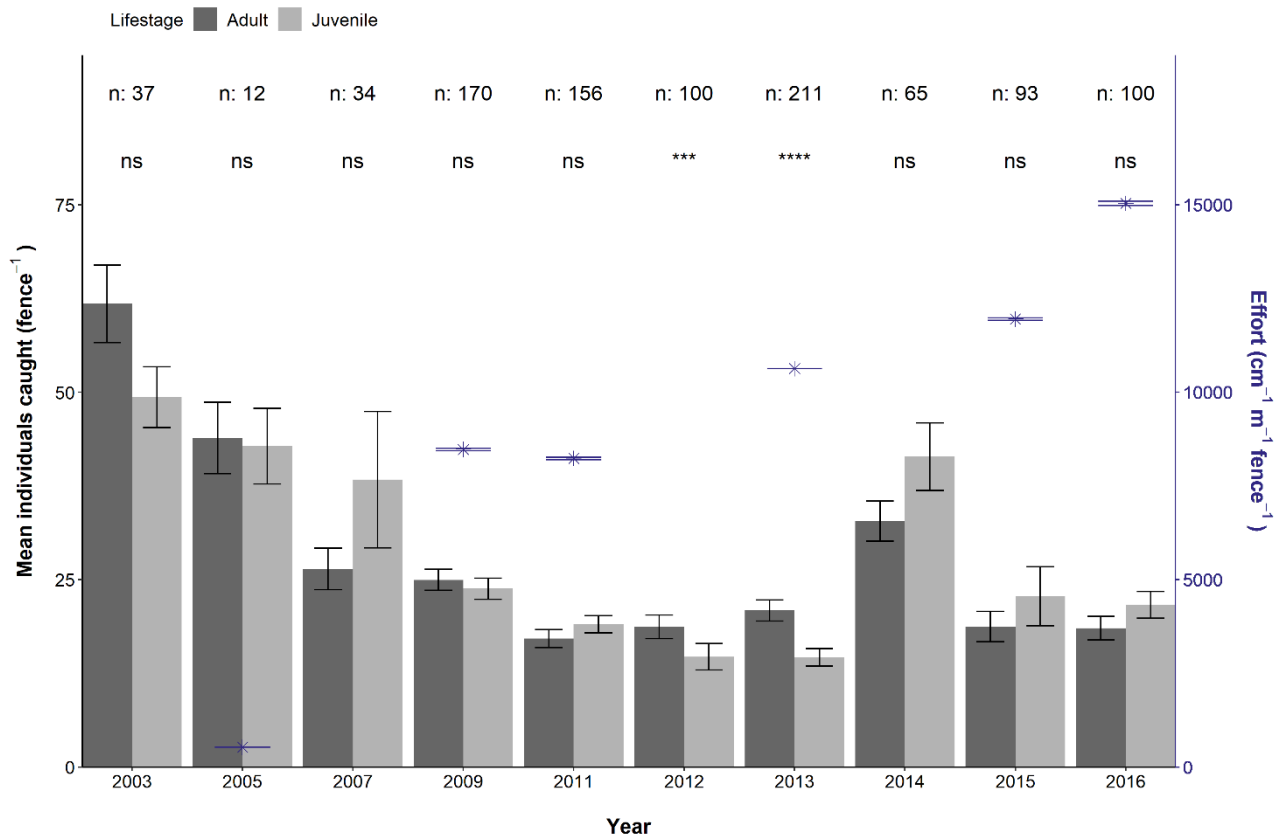


Figure 4: Fish fence effort reported as mean individuals caught per fish fence, with standard error bars between 2003 and 2016 split into adults (dark grey) and juveniles (light grey),  $n$  of fish fences sampled at each time point are noted as  $n: x$ . Effort is reported on the secondary  $y$  axis where available. Pairwise Wilcoxon rank-sum tests are overlaid for differences within the groups on the adult and juvenile proportions, reported as  $ns$  = not significant,  $*** = p < 0.001$ , and  $**** = p < 0.0001$ .

*Herklotsichthys quadrimaculatus*, *Atherinomorus endrachtensis* and *Plotosus lineatus* were removed from the analysis of the catch per fish fence due to their shoaling behaviour, as their high abundances altered any comparative evaluation between the years. There was no difference between most of the life stages per year ( $p > 0.05$ ), with only 2012 and 2013 showing significantly higher numbers of adults than juveniles in the mean catch per fish fence (Wilcoxon rank-sum test:  $W = 6483$ ;  $p < 0.001$  and  $W = 26705$ ;  $p < 0.001$ ), respectively. More juveniles than adults were caught per fish fence in 2007, 2011, 2014, 2015 and 2016, accounting for 59%, 52.6%, 55.8%, 54.8% and 53.9% of the mean yearly

catch, respectively. This can be partly attributed to a significant decrease in mesh sizes over the course of the study; at the start of the sampling period, the mean mesh size was  $2.54 \pm 0.0$  cm and by 2016 had reduced to  $1.24 \pm 0.03$  cm (Figure 5a; LM:  $F_{394} = 940.1$ ,  $p < 0.001$ ). As such, mesh sizes of the fish fence alongside the increased length of artisanal fish fences significantly contributed to the increasing number of juveniles caught (GLMMTMB:  $P < 0.05$ ). For the overall population, the mean species richness fluctuated largely by year, but showed an overall decrease from  $20.59 \pm 1.11$  species per fish fence in 2003, to  $13.6 \pm 0.6$  at the end of the sampling period in 2016 (LM:  $F_{1119} = 56.71$ ,  $p < 0.001$ ). Mesh size changes and total fish fence lengths were found to impact the number of species caught within the artisanal fish fences (GLMMTMB:  $p < 0.05$ ). The mean juvenile species richness also decreased by  $23\% \pm 7.8\%$  from  $9.76 \pm 0.49$  in 2003, to  $7.5 \pm 0.41$  in 2016 (Wilcoxon rank-sum test:  $W = 2597$ ;  $p < 0.001$ ). Using the Shannon-Weaver diversity index, the average diversity H value in 2003 was  $1.81 \pm 0.06$ , which significantly decreased by  $13.2\% \pm 0.15$  to  $1.57 \pm 0.05$  in 2016 (Wilcoxon rank-sum test;  $p < 0.05$ ).



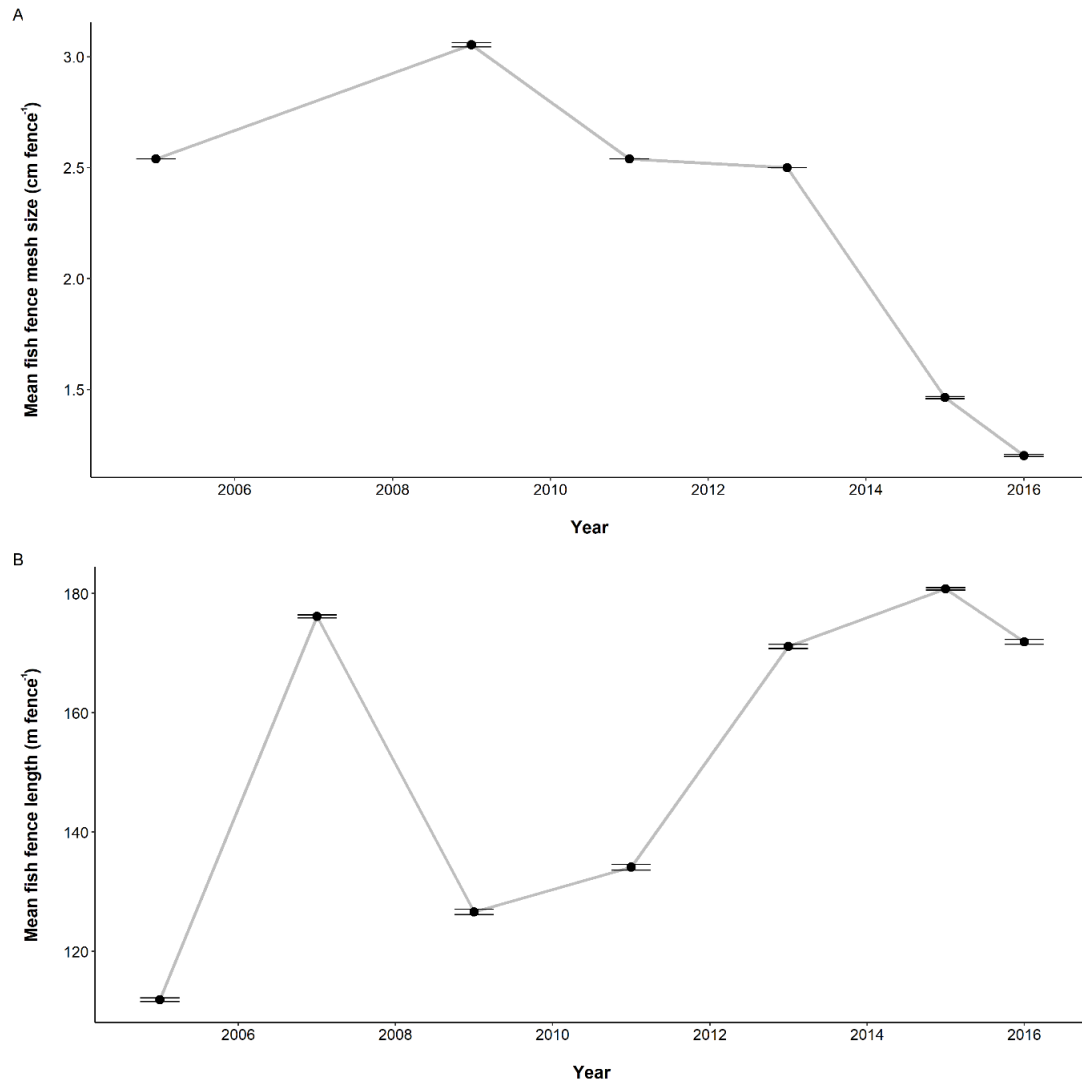


Figure 5: A) Mean mesh sizes of the fish fences per year with standard error bars. B) Mean total length of the artisanal fish fences with standard error bars.

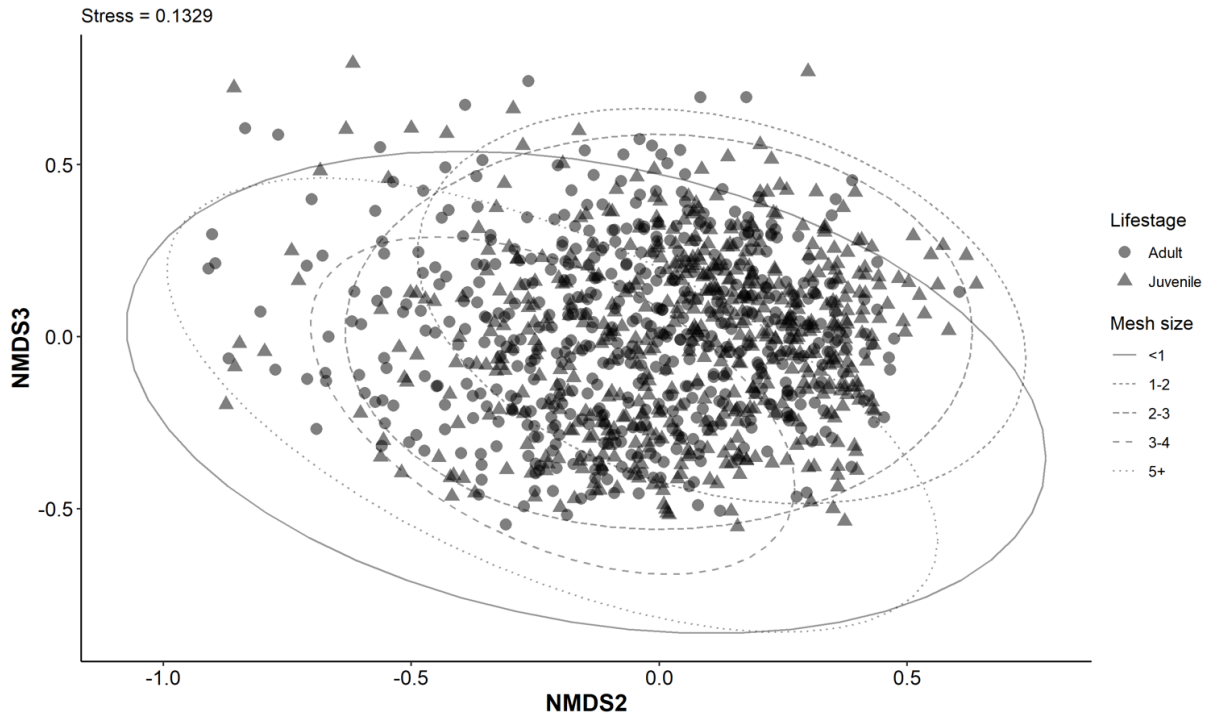


Figure 6: Nonmetric multidimensional scaling (NMDS) of fish species caught between 2003 through to 2016 in artisanal fish fences. Triangles and circles represent juveniles and adults, respectively. Mesh size changes are shown with differing line type ellipses. Individuals that are similar appear closer in proximity.

As the data contain many hundreds of species, a stress value of  $< 0.15$  was accepted as a good representation to allow the evaluation of the community determined by the individual counts of species through mesh size change and lifestage. Analysis of catch diversity through time showed clustering largely within  $\pm 0.5$  of the central 0.0 axes. The smallest mesh size had the largest ellipse surrounding most of the species found, encompassing most of the points in Figure 6, including most juvenile species (Figure 6). The most frequent fish fence mesh size over the course of the study was 2.54 cm, representing 49.54% of the total fences with attributed mesh sizes. The most numerous individuals caught was at a mesh size of 2 - 3 cm at 61.9%, followed by 1 - 2, 3 - 4, 5+, and  $< 1$  cm at 26.7%, 6%, 4%, and 1.33%, respectively. The most numerous species were also harvested at the mesh size of 2 - 3 cm, at 461 species, followed by 1 - 2, 3 - 4, 5+, and  $< 1$  cm at 214, 194, 166, and 65 species, respectively.

The longer fence lengths (> 175 meters) caught the most species; 675 species were reported within this bracket. Species richness decreased in each length bracket thereafter: 150 - 175, 125 - 150, 100 - 125, 75 - 100, and < 75 meters with 633, 503, 423, 121, and 100 species, respectively.

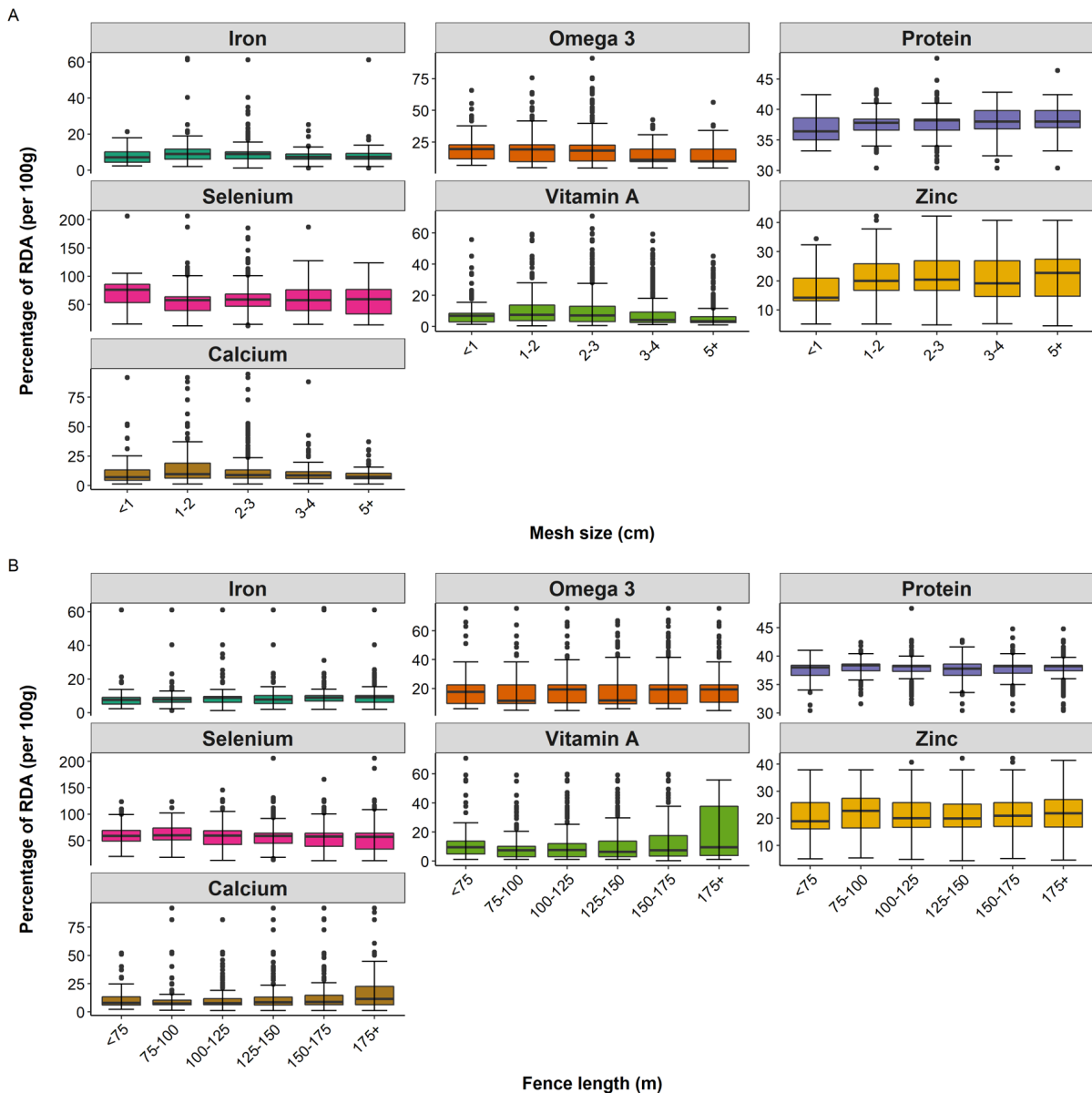


Figure 7: Influence of mesh size in 1cm intervals (A) and total fence length in 25 m intervals (B) on the fish muscle micronutrients iron, omega 3, protein, selenium, vitamin a, zinc, and calcium content, reported as recommended dietary allowance for Indonesians ( $\text{day}^{-1}$ ) per 100 g of wet fish muscle mass.

Micronutrient contents are determined by the species composition of the catch. Overall, throughout the study, an average 100 g of fish muscle tissue contains 0.99 mg of iron, 0.23

g of omega 3 fatty acids, 18.95 g of protein, 38.65 µg of selenium, 81.49 µg of vitamin a, 1.73 mg of zinc, and 85.27 mg of calcium. There was no significant effect between the mesh size of the fish fences or the total length of the fish fence on the concentrations of iron, omega 3, protein, selenium, vitamin a, zinc, or calcium (GLMMTMB;  $p > 0.05$ ) in the average 100 g of fish harvested. Average zinc contents were the most consistent nutrient tested, with a maximum variation of 0.38 mg/100 g between 2012 and 2015 (Figure 9).

Table 2: Mean micronutrient content of finfish caught per year with standard error with 100 g of raw chicken breast as a reference (Tacon and Metian, 2013).

Year	Mean iron (mg/100g)	Mean omega 3 (g/100g)	Mean protein (g/100g)	Mean selenium (µg/100g)	Mean vitamin a (µg/100g)	Mean zinc (mg/100g)	Mean calcium (mg/100g)
2003	0.969 ± 0.0183	0.217 0.00124	18.9 ± 0.0115	37.0 ± 0.202	61.1 ± 0.800	1.72 ± 0.00809	76.3 ± 0.632
2005	0.465 ± 0.0144	0.287 0.00472	19.0 ± 0.0237	39.1 ± 0.396	109.2 ± 3.02	1.84 ± 0.0120	121.7 ± 2.32
2007	0.645 ± 0.0284	0.246 0.00108	19.1 ± 0.0097	32.6 ± 0.204	212.5 ± 1.99	1.87 ± 0.00596	125.9 ± 0.812
2009	0.820 ± 0.00892	0.213 0.00105	19.1 ± 0.0083	39.3 ± 0.118	62.9 ± 0.647	1.72 ± 0.00543	80.5 ± 0.493
2011	0.726 ± 0.0139	0.230 0.00113	18.9 ± 0.0081	39.3 ± 0.108	89.7 ± 0.928	1.81 ± 0.00604	73.3 ± 0.551
2012	1.43 ± 0.0271	0.235 0.00199	18.9 ± 0.0134	40.6 ± 0.179	59.7 ± 0.912	1.52 ± 0.00947	71.7 ± 0.883
2013	1.30 ± 0.0254	0.253 0.00125	18.9 ± 0.0088	39.7 ± 0.0970	71.7 ± 0.690	1.70 ± 0.00480	87.0 ± 0.594
2014	1.00 ± 0.0192	0.197 0.00137	18.9 ± 0.0114	38.3 ± 0.150	55.4 ± 0.740	1.66 ± 0.00676	74.5 ± 0.842
2015	0.641 ± 0.0135	0.287 0.00164	19.0 ± 0.0089	37.8 ± 0.132	85.6 ± 1.21	1.90 ± 0.00803	96.8 ± 0.787

2016	0.985 ± 0.0255	0.226 0.00168	18.8 ± 0.0123	40.7 ± 0.181	62.0 ± 0.830	1.64 ± 0.00655	80.6 ± 0.851
Reference:							
Chicken breast	0.37	0.25	21.23	32.0	9	0.58	5.00

## Discussion:

The high juvenile catch proportions show that the seagrass-dominated shallow habitats in the Kaledupan subregion of the WNP act as a nursery ground for juvenile reef fish (Figure 4). Largely influenced by mesh size reductions and increases in total fence length, juvenile fish were in higher mean abundance per fish fence than adult fish in the final three years of the study. The high abundance of juvenile caught, show that juvenile fish rely on the studied seagrass dominated shallow habitat for their survival and growth, suggesting the seagrass beds fit into the criteria for an essential fish habitat and nursery ground (Beck *et al.*, 2001). Significant reductions in species diversity, in both richness and the Shannon-Weaver index, occurred between the first and last year sampled, potentially due to the effect of overfishing on vulnerable species. Whilst there have been decreases in richness and changes to the harvested community composition, the average finfish micronutrient contents are not affected by the changes to artisanal fish fence mesh sizes, nor the total fence lengths seen across the length of this study.

### Juvenile catch proportions

Findings presented above show that fish fence mesh size and the total length of the fence were influential in the juvenile catch proportions. As mesh sizes decreased and lengths of the fences increased (Figure 5a), there was less chance of juveniles escaping and their harvest increased. Though intuitive we here provide the greatest resolution and detailed analyses of this shift to juvenile catches in this region. In 2009, by-laws were agreed to detail

that the minimum mesh sizes for artisanal fish fences should be no smaller than 2.5 cm (Exton, 2010). The findings from this paper have shown non-compliance to such by-laws, as the average mesh size decreased by 50% to 1.24 cm in the years after the by-law implementation (Figure 5a). No information regarding restrictions to the length of the fish fences could be found. This change may be due to declining catch rates causing fishers to reduce mesh sizes to meet their economic and nutritional demands. There was a higher mean catch in 2014 after years of reducing CPUE. This came directly after 211 fish fences were analysed in 2013, which was the highest number of fences within the duration of the research (Figure 4). These results are indicative of excessive numbers of fish fences exploiting the seagrass beds in the year prior. By installing many fences on the same area of the seagrass dominated shallow habitats, the efficiency of fishing was reduced, and it limited the maximum catch per fish fence.

#### Juveniles harvested

Most of the fish species found in the Coral Triangle exhibit habitat partitioning throughout their life cycles (Ahmadia *et al.*, 2012; Campbell *et al.*, 2011). Many of the species caught in the fish fences are described as seagrass-associated species (SAP) by (Unsworth *et al.*, 2014). Juvenile commercially important coral reef fish, such as the families *Lethrinidae* and *Carangidae* (Jacks), have been found in high abundance in the seagrass dominated habitats studied (Figure 3a). *Lethrinidae* is found to associate with seagrass habitats that have less connectivity and proximity to the coral reefs (Unsworth *et al.*, 2008). Inversely, *Carangidae* is associated with seagrass habitats in closer proximity to the reefs. These juveniles will eventually begin their ontogenetic migration from the protected seagrass habitats to the reef as adults, fitting into the movement criteria for a nursery habitat (Beck *et al.*, 2001). The juveniles will also benefit from the availability of additional resources, such as larger crustacean prey on the reef (Lee *et al.*, 2019; Unsworth *et al.*, 2007c). These fishes serve

ecologically important functions on reefs, for example, the predatory family of *Carangidae* exert high levels of top-down control and thereby maintain biodiversity on the reef (Sudekum, 1991). Of particular interest, is the abundance of the only herbivorous species in the top 15 species harvested, *Naso vlamingii* (Bignose unicornfish, 485 juveniles, Figure 3b). This is a highly abundant species found near both mangroves and reefs in the Kaledupa subregion of the WNP (Unsworth *et al.*, 2008). *Naso vlamingii* accounted for 24.9% of the juvenile herbivores in the fences, an outcome which is lower than that of research from Unsworth *et al.* (2008), which found that > 90% of the juvenile herbivores were of this species. This may be the first indication of a previously common species disappearing from catch analyses.

#### Carnivorous dominance

Consistent with the findings of Unsworth *et al.* (2009), this research found that there was a large juvenile dominance of carnivorous fish in the seagrass dominated shallow habitats in the WNP. Larger piscivores are known to alter the habitat usage of juvenile lethrinids and competition for prey drives them to preferentially inhabit the seagrass beds (Lee *et al.*, 2019). With reduced population control from their predators, carnivorous fish have less predation pressure, and as such, can dominate the habitat. Scarid herbivory was found in seasonally high abundances close to the sites of the fences (Unsworth *et al.*, 2007b). However, as juveniles, this family were not as abundant in the fences. The species *Scarus ghobban* (Blue-barred parrotfish) represented the highest proportion of the family (42.8%; 191 individuals; 72.9 kg). A possible explanation for the low juvenile herbivorous individuals may be the high sediment load in the area near the location of the fish fences (Crabbe and Smith, 2002; Crabbe and Smith, 2005). This sedimentation is potentially heightened by anthropogenic disturbance occurring in the area (Powell *et al.*, 2014). Herbivorous fish, especially scrapers, are known to decrease in abundance with high levels of sedimentation

(Bellwood and Fulton, 2008; Fox, 2007; Moustaka *et al.*, 2018). They would also have a greater preference for algae within hard substrates. For anthropogenic disturbances increasing sedimentation, the fishing communities of the local *Bajo* (sea nomad) and *Pulo* (islander) communities are active within the area studied. Whilst the *Bajo* are informally restricted from owning fences, they have an impact on the fish communities within the seagrass beds, as they use other forms of fishing and offload organic waste into the system (Exton, 2010; Exton *et al.*, 2019; Powell *et al.*, 2014).

### Influence of mangroves

In this study, the effect of mangroves was not investigated, but presumed to positively contribute to the overall diversity of the seagrass dominated shallow habitats. Due to the tidal regime in the Indo-Pacific, the adjacent mangroves are left exposed at low-tide and juvenile fish cannot permanently utilise the habitat, ensuring that the fish studied in this paper were SAP's. As part of the seascape ecology of the Coral Triangle, these habitats are spatially heterogenous and are highly connected, allowing the mixing of individuals between the habitats. When mangroves are in close proximity to seagrass beds, the roots provide refugia for juveniles on the seagrass to shelter from predators (Unsworth *et al.*, 2008). Similarly, mangroves support the overall abundance, richness, and trophic structure of juvenile reef fish on the seagrass beds, supporting up to six times the juvenile abundance in the seagrass habitats than those further away from the mangroves (Laroche *et al.*, 1997; Unsworth *et al.*, 2008). When available to be utilised at high tides, mangroves provide a key feeding ground for juvenile fish due to their large biomass of invertebrate fauna (Robertson *et al.*, 1988). By impeding connectivity within the mangrove-seagrass-reef continuum with fish fences acting as barriers, exacerbated by decreasing mesh sizes, juveniles cannot progress onto the reef to continue their growth into adulthood and serve their ecological functions.



## Diversity changes

In a tropical shallow marine seascape, such as the mangrove-seagrass-reef continuum in the Wakatobi region, there are well-reported high levels of productivity and diversity (Calcinai *et al.*, 2017; Cullen-Unsworth, 2007; Unsworth *et al.*, 2009; Unsworth *et al.*, 2007c). The results highlighted in this paper have shown diversity losses throughout the duration of the study. Overall species richness decline can be a sign of the Malthusian overfishing principle. The reduction of juvenile fish diversity in the seagrass habitats has implications for the functional diversity of the ecosystem, as it may also have cascading effects on the overall resilience to disturbance of the wider seascape. Not all families have decreased species richness, for example, the family *Diodontidae* (Porcupinefish) had increased in species richness in the latter years. This may be due to the decrease in mesh sizes with increases in fence lengths allowing for a wider harvest of the seagrass-associated fauna. An alternative to this is that some species have benefited from the direct removal of their competitors from fishing. These findings, and investigations of what species have not been captured in the final years of the catch composition survey, raise intriguing questions regarding the nature and extent of the loss or gain in species richness.

## Fishing for nutrition - demand for fish and fisheries management

With growing populations in Southeast Sulawesi, comes higher demands for food. The results of this paper indicate a reduction in mesh sizes or increases in fence lengths do not catch the more nutritious finfish. For this gear type, there is no selectivity in the catch composition, meaning fish with all manner of micronutrient profiles are harvested, increasing bycatch. Species caught with the largest mesh sizes and smallest fence lengths were just as nutritious as those caught with the smallest mesh sizes and the largest fence lengths. Regardless of the gear type change, the finfish in this area provide the local human

populations with a valuable, nutritious food source. The average 100 g of an individual finfish in this study contains  $8.43 \pm 0.02\%$  of the recommended Indonesians dietary allowance for iron,  $17.39 \pm 0.03\%$  of omega 3 fatty acids,  $57.25 \pm 0.07\%$  of selenium,  $37.89 \pm 0.007\%$  of protein,  $21.01 \pm 0.03\%$  of zinc,  $12.54 \pm 0.05\%$  of vitamin a, and  $12.18 \pm 0.03\%$  of calcium. These values are for most higher than, or comparable to chicken breast for their levels of micronutrients per 100 g, which can help prevent and reduce under and malnutrition in this region (Figure 9).

The major impact of change to the artisanal fish fences total length and mesh sizes are seen in the lifestage composition, which may ultimately drive declines in the catch in the long-term. Whilst this research shows that the habitat studied supports the conclusion of seagrass dominated shallow habitats playing a nursery role for juvenile fish, there is a worrying trend that Malthusian overfishing is occurring and leading to declines in catch and species diversity (Exton *et al.*, 2019; Pauly, 1994). Due to the indiscriminate nature of this style of fishing, a substantial number of juvenile recruits are removed, potentially causing unforeseen community changes on the reef and within the wider seascape. If the Malthusian principle is to be true for this seascape, juvenile recruitment into adulthood will decrease, and species may become more vulnerable to overfishing, especially given the increasing demand by increasing population. This trend is apparent from studies of Malthusian fishing in the Coral Triangle (Teh and Sumaila, 2007; Unsworth *et al.*, 2014). Evidence for Malthusian fishing can also be seen by the large increase in fish fences in the years 2009, 2011, and 2013 (Figure 3), where locals stated that if diminishing returns were seen, more fences could be erected to supplement these losses from overharvesting, driving a negative impact loop (Exton, 2010). In this region, the locations of seagrass-dominated shallow habitats are relatively close to the shores, which makes fishing reasonably low cost and accessible for many. Given the increase in juvenile fish caught due to significantly

decreasing mesh sizes and increasing fence lengths in the latter years, the conclusion is made that current fisheries management strategies and enforcement are inappropriate for the type and location of fishing gear used.

As is common worldwide, a greater conservation emphasis has been placed on the adjacent coral reefs, whilst fewer protections have been given to seagrass habitats, likely owing to limited biological understanding and seagrasses' lower charismatic appeal (Unsworth *et al.*, 2014). The need for seagrass conservation is compounded further by studies with local fishers' interviews show the main fishing grounds for the *Pulo* communities have preferentially been seagrass habitats (Unsworth *et al.*, 2014). It is important to manage these fisheries at the ecosystem level to preserve the key nursery grounds for a widely diverse fish community. Management may include the enforcement of the mesh size restrictions, a new restriction on the max length of any given fence, and how many fences can be used within a region. This may also require alternative livelihoods for local human populations, potentially allowing for greater advancements in the area. Another potential management strategy involves the use of no-take areas (NTA's) in regions of high juvenile abundance, such as the seagrass dominated shallow habitats revealed in this paper. Similar NTA's have been implemented on the reefs surrounding the neighbouring island of Hoga in 2001, with relatively high success on stock densities (Unsworth *et al.*, 2007a). These NTA's may only be necessary for certain seasons when the highest abundances of juveniles are seen in the seagrass-dominated shallow habitats. This would allow for the facilitation of stock recovery in the seascape and sustainability by offering spill-over effects into the surrounding habitats, whilst still ensuring the food provision of the local populations (Garry *et al.*, 2003; Gell and Roberts, 2003; Mumby and Harborne, 2010). It is important that stakeholders ensure the long-term provision of food and economic security in the Wakatobi, which is ultimately supported by the seagrass dominated shallow habitats. The enforcement of any sort of

restrictions must be agreed upon and continuously adhered to for management to be effective. Combining key ecosystem functions and services into the management strategy, whilst equally ensuring that the needs of the locals are met for sustenance, allows for greater resilience to disturbance, diversity loss, and overall food security in the long term.

#### Limitations and future work

Data were collected from fish fences in one fishing season each year, which could potentially limit the catch composition analysis based on spawning seasons which occur at set times each year, at different times for differing species. Harvesting and sampling of the fishes during this period may have influenced the abundance of species that spawn in the months prior. Nonetheless, as many species were caught in a long sampling timeframe, this should not have made for an unjust comparison. In future studies with larger sampling seasons, there could be investigations into the effect of seasonality on catch composition in the fish fences. With this data, the influences of lunar cycles can be explored, examining the effects of tide and spawning seasons on catch abundances and composition in the seagrass dominated shallow habitats. Further studies may also investigate the claims from *Pulo* fishers that the fish caught have been getting smaller (Unsworth *et al.*, 2014). The effect of lifestage on the micronutrient content has not been able to be investigated due to data unavailability, which if investigated further, could provide this study with more accurate micronutrient contents for the fish sampled in the artisanal fish fences. Micronutrient content models used were sampled from the muscle mass of the fish, which could limit the accuracy of the micronutrient gain from the individual fish if consumed more than just the muscle. This would only increase the micronutrients in each fish, giving a higher percentage estimate of the micronutrients for the recommended dietary allowance.

## Conclusion

To conclude, the use of artisanal fish fences for catch composition analysis in this temporal study provided insight into the community and population level changes occurring within the wider tropical seascape. This research aids stakeholders in better understanding the composition of fish communities in the seagrass dominated shallow habitats, by presenting how critical they are as nursery grounds and essential fish habitats for commercially and ecologically important reef fish in the Kaledupa subregion of the WNP. This study has identified that the seagrass dominated shallow habitats of the Kaledupa subregion in the WNP act as a nursery ground for many commercially important reef fish. One of the more significant findings to emerge from this is that the bylaws regarding mesh sizes have not been obeyed and have alongside increasing fence lengths, significantly affected an increase in the juvenile catch. Whilst an overall assessment of the habitat has not been completed, the decrease in mesh sizes in the latter years of sampling allowed for a close estimate of the true proportion of juveniles in the habitat. Whilst the proportion of juveniles harvested has increased and the fish species diversity harvested has changed, the micronutrient content has not been significantly affected by mesh size or the total fish fence length, which provides hope for the local islanders' nutrition and sustenance. The utilisation of small mesh sizes, increases to the total length, and higher numbers of fences indicates that there is room for improvement in the management of finfish biodiversity and ecology in this area before it can become a concern to human health.

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## Chapter 2: A finding of maintained cryonotothenioid nesting sites in the western Weddell Sea

### Abstract

The Weddell Sea is one of the most remote and least explored regions on Earth. The region around the Larsen C ice shelf studied here has been largely inaccessible due to its remoteness, extreme cold, rough seas, ice cover, and deep waters. Recent advancements in icebreaking ships and technology have made it possible to access these areas. This study describes a new finding of a maintained nesting sites of notothenioid fish (*Lindbergichthys nudifrons*; yellowfin notie) in the Western Weddell Sea. These nesting sites are the first to be described in this area. Nesting sites were found at all locations surveyed during a larger research cruise by the Weddell Sea Expedition 2019 group onboard the *SA Agulhas II* using the remotely operated vehicle, *Lassie*. Nesting patterns, which are groups of nests close to each other, were discernible throughout the expedition's video recordings. It is the first time this type of nest formation, clustering/groups of nests, have been noted in any literature. These nesting patterns are thought to be a form of group predation protection. Unlike other studies that have found marked oceanographic factors such as temperature differences being a possible driver in nest presence, there were no such correlation. These findings help policymakers progress the Weddell Sea Marine Protected Area proposal to protect these and other unique habitats found in this region.

**Acknowledgements:**

Dr. Michelle L. Taylor,

Dr. Lucy Woodall,

Crew of the SA Agulhas II,

My family.

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### List of abbreviations:

Weddell Sea Expedition 2019	WSE
The Weddell Sea MPA	WSMPA
Commission for the Conservation of Antarctic Marine Living Resources	CCAMLR
Remotely Operated Vehicle	ROV
Antarctic Circumpolar Current	ACC
Antarctic Bottom Water	AABW
Ice Shelf Water	ISW
(Modified) Warm Deep Water	(m)WDW
Weddell Gyre	WG
Circumpolar Deep-Water	CDW
High Salinity Shelf Water	HSSW
Seasonal Pack Zone	SPZ
Exclusive Economic Zone	EEZ
Illegal Unregulated and Unreported	IUU
Non-Contracting Parties	NCP
Non-Indigenous Species	NIS



Marine Protected Area	MPA
General Protection Zone	GPZ
Fisheries Research Zone	FRZ

## 1. Introduction

The vast continent of Antarctica, beyond the 60° S ('*Screaming 60s*'), hosts the two icecap masses of East and West Antarctica. East and West Antarctica are separated by the Transantarctic Mountains whose summits are one of the few places in Antarctica not covered by ice (Faucher, 2021). The ice surface and air temperatures of East Antarctica are one of the lowest on Earth, reaching minimum temperatures of  $-98^{\circ}\text{C}$  (Scambos *et al.*, 2018). Ice that covers Antarctica contains 70% of the world's freshwater. The average thickness of the ice is 2.16 km thick, with deepest parts being 4.776 km deep (Crucian, 2013). As a desert, Antarctica has very little rainfall, averaging between 0.9 and 10.21 mm  $\text{y}^{-1}$  (Vignon *et al.*, 2021). Seasonality is composed of four months of no sunlight and four months of 24 hours of sunlight, separated by two transitional months (Tortello *et al.*, 2020).

### 1.1 Oceanographic processes

The Antarctic Circumpolar Current (ACC) transports the Warm Deep Water from the Drake Passage through to the Weddell Sea. The ACC formed over 23 million years ago, as Australia separated from Antarctica with the Drake Passage forming between South America and Antarctica (Pfuhl and McCave, 2005). The ACC drove the cooling of Antarctica's surrounding waters from  $\sim 15^{\circ}\text{C}$  to less than  $0^{\circ}\text{C}$  (Barnes *et al.*, 2006; Katz *et al.*, 2011). This current acts as a barrier and hinders dispersal beyond or into the ACC (Moore *et al.*, 2018; Sanches *et al.*, 2016).

Any research in the Weddell Sea is a challenge for many reasons: its remoteness, the very low air temperatures, low light levels in winter, and the presence of sea ice resulting in the field and remote sensing equipment becoming obstructed (Hutchinson *et al.*, 2020; Vernet *et al.*, 2019). There are many interactions of distinct water masses and flows within the Weddell Sea, including the Antarctic Bottom Water, various Ice Shelf waters, and Warm

Deep Waters (Nachtsheim *et al.*, 2019). The Weddell Sea is an important source in the production of Antarctic Bottom Water (AABW), which is vital for global ocean circulation, gas exchange, and climate regulation (Foldvik *et al.*, 2004; Hutchinson *et al.*, 2020; Vernet *et al.*, 2019). The Ice Shelf Water (ISW), which has temperatures below surface freezing point ( $-1.9^{\circ}\text{C}$ ), is distributed from below the ice shelves surrounding the Weddell Sea and interacts with Warm Deep Water (WDW), contributing to the Antarctic Bottom Water (Nachtsheim *et al.*, 2019; Nicholls *et al.*, 2009). Due to this mixing of water masses, the areas are considered hotspots for biological productivity, activity, and abundance (Nachtsheim *et al.*, 2019). On a greater scale, the Weddell Gyre (WG) encompasses the Weddell Sea and extends further East to the Enderby abyssal plain (Carter *et al.*, 2008). The WG is primarily wind-driven clockwise, and variations can be caused by La Niña and El Niño events (Martinson and Iannuzzi, 2003; Núñez-Riboni and Fahrbach, 2009). As many fish larvae have a pelagic stage during this phase, the WG contributes to the dispersal of the ichthyoplankton. Temperatures in the Southern Ocean are one of the most stable on Earth (Reeves *et al.*, 2011). As such, the main drivers of the minimal differences in water temperatures in the Weddell Sea are depth, proximity to ice shelves, and currents/mixing (Foster and Carmack, 1976). The Weddell Sea has inputs from the High Salinity Shelf Water of the Filchner-Ronne and Larsen Ice Shelves, which increase localised saline flows until mixed at depth (Vernet *et al.*, 2019).

## 1.2 Icefishes

Antarctic fishes, many known as icefish, are a group of species that have adapted to occupy the Southern Ocean, where the marine habitat is often below  $0^{\circ}\text{C}$ , and has a seasonal variation between  $-1^{\circ}\text{C}$  to  $-2^{\circ}\text{C}$ . The suborder Notothenioidei contains 140 species within eight families. Five families (129 species) have an Antarctic distribution, they are collectively known as cryonotothenioids (La Mesa *et al.*, 2021; Near *et al.*, 2015). These species have

evolved a form of antifreeze glycoprotein in their blood that inhibits bodily fluids freezing and enables them to occupy these sub-zero conditions (Chen *et al.*, 1997). Other individuals in the family of *Channichthyidae* lack haemoglobin in their blood as adults, gaining oxygen via plasma instead, at a greatly reduced efficiency (Sidell and O'Brien, 2006; Zummo *et al.*, 1995). As a trade-off, the Channichthyidae have high densities of vascular tissue, allowing for a smaller diffusion distance and thus higher oxygen availability.

Species of Notothenioidei have adapted to lack swim bladders, including *Lindbergichthys nudifrons*. The absence of a swim bladder enables them to have energetic savings as less energy is consumed for buoyancy (Eastman, 2017). This also allows them to occupy a demersal niche at depths of 0 – 1500 m (Eastman, 2013; Eastman and DeVries, 1981). Individuals occupying these depths have had to overcome the extremely low light and pressures associated with depth. Species' eye size is shown to increase with depth around Antarctica and the Weddell Sea (Eastman and Lannoo, 2008; Lombarte *et al.*, 2003); clear light level morphological adaptations. Many cryonotothenioid species are found below 1000 m (26 species), but nothing is currently known about their adaptations to the pressures at these depths (Eastman, 2017).

Cryonotothenioids have been generally characterised by slow maturation, low relative fecundity, and the production of relatively large eggs (Everson, 1984; Gon and Heemstra, 1990). Most species spawn demersally, with some species showing parental care during incubation (La Mesa *et al.*, 2021; Marshall, 1953). There is often a prolonged incubation period of greater than 100 days. After hatching, most species' larvae rise to the epipelagic, develop, and return to the benthos as juveniles (Loeb *et al.*, 1993).

### 1.3 Distribution of icefishes in Antarctica

The Antarctic Convergence, a boundary zone where cold Antarctic water meets warmer sub-Antarctic water, is a critical ecological barrier for many marine species and is thought to be a primary driver of the high levels of endemism found in Antarctic fishes (Ekau, 1991). The distribution of fish in the Weddell Sea has been linked to physical processes, especially the presence and distribution of ice (Clarke and Johnston, 1996). In geological history, the benthic cryonotothenioid radiation has been a result of frequent disturbance events from ice sheet retreats and calvings (Barnes and Conlan, 2007; Thatje *et al.*, 2008). Eastman (2017) suggests that these disturbances caused the cryonotothenioids to seek refugia on the slopes below the ice sheet edges, which in turn gave rise to special barriers for mating to occur and promoted opportunities for speciation to occur. Many cryonotothenioid species exhibit endemism in certain regions, such as island groups, whereas others have a wider distribution across coastal Antarctica (Gon and Heemstra, 1990; White, 1998).

In the Southern Ocean, three major subregions have been classified based on the presence of frontal zones, ice cover, and planktonic distribution: Ice-free Zone, Season Pack-ice Zone (SPZ), and the High Antarctic Zone (Hempel, 1985; Kock, 1992). Species have also been categorised into these regions based on their thermal tolerances and presence or absence in the area (Bilyk, 2011). The Ice-free Zone is represented by meso- and bathypelagic species, the species occupying this zone have a 'broadly Antarctic distribution' (Hulley, 1981). The highest species diversity is found deeper on the Antarctic shelf at 300 – 600 m, and the rest of the world peaks at 100 – 200 m (DeWitt, 1971; Eastman, 2017). The greatest species diversity of cryonotothenioids are found at 500 m depth, due to slope depths and compositions that contain the most energetically feasible niches (Eastman, 2017). The SPZ is more thermally variable, due to the seasonality of the ice cover (Bilyk, 2011). The Pack-

ice Zone consists mainly of notothenioids and has been shown to have greater productivity than the other zones (Kock, 1992; Mesa and Vacchi, 2001). The High Antarctic Zone is characterised by consistent, year-round ice cover; species in the genus *Trematomus* dominate here (Mesa and Vacchi, 2001).

The genus *Lindbergichthys* comprises two species which have polar distributions: between 46° S - 53° S for *Lindbergichthys mizops* and 55° S - 72° S for *Lindbergichthys nudifrons* (Froese and Pauly, 2022). Both species have a benthic lifestyle as adults and reach a maximum length of 15 cm and 19.5 cm for *L. mizops* and *L. nudifrons*, respectively. The latter species occupies a greater depth range of between 3 - 400 m compared to 20 – 220 m for *L. mizops*. Genetic analysis of *L. nudifrons* has shown two distinct lineages - the Antarctic Peninsula and the islands of South Georgia and South Sandwich (Dornburg *et al.*, 2016), a pattern driven by geographical isolation. The Weddell Sea fish fauna has, in recent years, been increasingly studied as greater access due to advancements in technology has been possible. With that said, this is still a relatively unknown field with regards to the community composition of the cryptic species within the Weddell Sea, and a baseline before fishing (Constable, 2004; Dornburg *et al.*, 2016).

#### 1.4 Icefishes in fisheries

Locations of cryonotothenioid habitats are challenging to exploit for commercial or subsistence fishing. The main targets of extraction are the larger species, including the Antarctic toothfish (*Dissostichus mawsoni*), Patagonian toothfish (*Dissostichus eleginoides*), and Mackerel icefish (*Champsocephalus gunnari*). Fisheries extracting *C. gunnari* use trawling gear, whereas the other two species (*D. mawsoni*, and *D. eleginoides*) are caught using longline methods (Kock *et al.*, 2007). *Dissostichus mawsoni* is circumpolar and endemic to the Southern Ocean, with absences in the central Weddell Sea. This species

has been recorded to reach a maximum length of 200 cm and can weigh up to 80 kg (Froese and Pauly, 2022). A total of 3,751 tonnes of *D. mawsoni* was reported to have been extracted in 2020; the USA, China, and Japan were the largest consumer countries (FishStatJ, 2022; Grilly *et al.*, 2015; Xiong *et al.*, 2016). The distribution of *D. eleginoides* is at a higher latitude than that of *D. mawsoni* but still found in Antarctic waters, below 66° S. The maximum length of *D. eleginoides* reaches 215 cm and the maximum published weight is 9.6 kg (Froese and Pauly, 2022). This species is also targeted for food fisheries, and a total of 21,332 tonnes was reported to have been extracted in 2020 by 15 countries and sold under the name “Chilean Sea Bass” (FishStatJ, 2022; Grilly *et al.*, 2015). The other main commercially important icefish, *C. gunnari*, is in the family of *Channichthyidae*, representing the crocodile icefishes (Froese and Pauly, 2022). In comparison to the other commercially important icefishes, *C. gunnari* has the smallest range of distribution – just covering the islands of the Scotia Sea and the northern Antarctic Peninsula (Froese and Pauly, 2022). The catch of this species was reported to be 444 tonnes by 6 countries in 2020 (FishStatJ, 2022). *Champscephalus gunnari* reaches a maximum length of 66 cm and a maximum weight of 2 kg (Froese and Pauly, 2022). Other cryonotothenioids are not commercially important or are not currently exploited by the commercial fishing countries of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR).

Few nations actively exploit the fish stocks in the Southern Ocean and its seas, due to constraints in traveling to such remote locations. Countries that can benefit and exploit these stocks have good access and have an Exclusive Economic Zone (EEZ) either within or nearby the stocks. The main countries that exploited cryonotothenioid stocks in 2020 were France (4342 tonnes), Republic of Korea (2779 tonnes), Argentina (2602 tonnes), Australia (2545 tonnes), Chile (2055 tonnes), and the United Kingdom (1950 tonnes) (CCAMLR, 2021). Although the COVID-19 pandemic was occurring in 2020 and lockdowns were

imposed worldwide, these nations are still representative of countries with high landing reports in prior years. The largest weight in landings from France came from *D. eleginoides* in the sub area 58.5. This species was also the largest fishery catch for the Republic of Korea, with 65.6% of its yearly catch coming from that species in area 41 of the Southern Ocean.

Whilst the krill fishery has been the main exporter and focus to many of the nations in the Southern Ocean (161,085 tonnes in 2012 compared to 10,652 tonnes of toothfish), toothfish landings are however, much more valuable at US\$213,040,000 compared to the Antarctic Krill valued at \$159,050 in 2012 (Brooks, 2013). Antarctic krill's low value can be partly attributed to the fast rate at which it's flesh degrades, meaning less time can be spent at sea before having to process and sell the catch on (Nicol *et al.*, 2012). As of 2012, the value of krill was worth 1/20<sup>th</sup> of the value of toothfish. Icefish are also not as valued as toothfish as their value is worth 1/10<sup>th</sup> of toothfish due to their lack of market value as a food source and generally smaller sizes (Everson, 1992; Kock *et al.*, 2007).

The start of exploration for commercial fisheries began on the Gauss expedition in 1901 - 1903 (Bonner and Walton, 2013). Whaling was a significant driver of research into the marine resources in the Southern Ocean. Fishing in the 1930's – early 1960's was attempted by Argentine, Norwegian, and Japanese companies, but was unsuccessful. Viable commercial fisheries in Antarctica didn't begin until the 1960's. South Georgia's first commercial fishery was recorded in 1969 with the marbled rock cod (*Notothenia rossii*) first species to be targeted (Kock, 1992). Within four years of extraction catch dropped to zero individuals, the fishery collapsed, and nations moved to exploit other regions of the Southern Ocean (O'Brien and Crockett, 2013). By 1977 - 79, the islands of South Shetland and South Orkney were then exploited, with the targets including the Mackerel icefish (*Champscephalus gunnari*), South Georgia icefish (*Pseudochaenichthys georgianus*),



Blackfin icefish (*Chaenocephalus aceratus*) and Spiny icefish (*Chaenodraco wilsoni*) (Ainley and Blight, 2009). As a result of the new exploitation of these fisheries, an international body was formed known as the Commission for the Conservation of Antarctic Marine Living Resources in 1982. Their role was and is to govern marine fauna and ensure the conservation of marine life in the Antarctic (O'Brien and Crockett, 2013). The CCAMLR began to close fisheries in different locations to conserve fish stocks and marine life. Many of these fisheries were fully exploited and were closed in 1990 after reaching significantly low levels of the stock remaining, just ~5 - 10%.

These fish stock losses have also had a wider impact on other species that would naturally predate the cryonotothenioids (Aronson *et al.*, 2011). Populations of Antarctic seals, such as the Southern elephant seals (*Mirounga leonina*) and the Antarctic fur seal (*Arctocephalus gazella*), crashed due to seal hunting in the 1700's and 1800's. Their populations, due to anthropogenic harvesting of their prey, and climate environmental pressures, limit their population sizes (Ainley and Blight, 2009; Aronson *et al.*, 2011; Forcada *et al.*, 2012). The diets of bird species, such as the Gentoo (*Pygoscelis papua*) and Macaroni penguins (*Eudyptes chrysolophus*), are also dominated by commercially targeted finfish, and both have experienced declining populations, which have partly been attributed to the reduction in their prey (Ainley and Blight, 2009).

For other cryptobenthic clades within the cryonotothenioids, species haven't been targeted as much as the species above due to lower market value and the general size of the species. The Grey rockcod (*Lepidonotothen squamifrons*) was targeted in 1971 on the Kerguelen Islands. The peak catch was a year later, at 52,947 tonnes (FishStatJ, 2022). CCAMLR closed this fishery in 1989 with less than 5% of the stock remaining (Ainley and Blight, 2009). Other similar species, such as the Yellowfin rockcod (*Lindbergichthys nudifrons*), have not

been targeted, and only 0.003 tonnes have ever been reported to be extracted (FishStatJ, 2022).

### 1.5 Threats to icefishes

Icefishes are 'K-selected species', meaning their energy goes into long, slow-developing lives with low fecundity, so they are vulnerable to high levels of extraction (Bonner and Walton, 2013; Norse *et al.*, 2012). Both the current commercially targeted species of *D. eleginoides* and *D. mawsoni* rank within the top three for intrinsic vulnerability to overfishing as a result of their long-lifespans and low population growth rates (Norse *et al.*, 2012). Accidental or inadvertent fishing pressure has also been applied to non-target species such as the humped rockcod (*Nototothenia gibberifrons*). This species has been fished as by-catch in the South Georgia fishery and consequently, the mean sizes on extraction were reduced from 41 cm to 30 cm in three years (Bonner and Walton, 2013).

Fishing of Antarctic marine resources has been ongoing since the start of fishing in the Antarctic and is regulated by the CCAMLR; however, there is a large demand for toothfish, which drives the illegal, unregulated, and unreported fishing trade (IUU). IUU had been reported to peak in the 1990's. During 1997 - 2000 CCAMLR estimated that twice the amount of toothfish reported to them were not being reported and as such classified as IUU (Schmidt, 2004). It has been suggested that the motivation behind IUU occurs when there are high opportunity costs of fishing, and the fishers' standard of living is low (Day, 2019). Since the onset of IUU in the Southern Ocean, the reports of IUU fishing have decreased as a result of pressure applied to Non-Contracting Parties (NCPs), which do not co-operate with CCAMLR and do not have a catch documentation scheme (Day, 2019; Miller *et al.*, 2010). Nevertheless, the issue of IUU fishing is still ongoing and threatening the management of cryonotothenioid stocks in the Southern Ocean (Haward, 2020).

The fauna inhabiting Antarctic waters have special physiological adaptations to survive in extremely low temperatures (Hardewig *et al.*, 1999). These physiological adaptations limit their tolerances to higher temperatures, and most are classed as stenothermal (Windisch *et al.*, 2011). A study investigating the respiratory rates of *Lepidonotothen (Lindbergichthys) nudifrons* found that the lethal temperature for most individuals occurs between 8°C – 9°C (Hardewig *et al.*, 1999). Whilst this is the thermal maximum, any increase in temperature has shown to increase the respiratory rate and ventilation frequency, which is a response to attempt to keep tissues well supplied with oxygen, but is energetically demanding. An increase in respiratory rate leads to a higher metabolic demand, which in turn slows growth rates and increases demand for greater food consumption (Montgomery and Wells, 1993). Blackfin icefish (*Chaenocephalus aceratus*) biomass has been shown to have a strong negative correlation with increased temperature (Traczyk *et al.*, 2020). This species' larvae swim away from ice cover and into warmer temperatures, due to the delayed ontogenic onset of the antifreeze proteins (Bilyk, 2011). This migration allows the juveniles to consume krill and other fish to reach maturity and then move deeper into cooler waters (Kock, 1992). As a consequence of global warming, krill populations have declined, especially during warmer years, which may be a longer term seasonal process (Flores *et al.*, 2012; Kawaguchi *et al.*, 2009). Reductions in krill lead to reduced food availability and increased predation pressure on the juvenile *C. aceratus*, thereby reducing their growth rates (Traczyk *et al.*, 2020). This, in turn, can have profound impacts on the population dynamics of the wider ecosystem, which drives yet further cascading changes later in the future.

Indirect human actions, such as global warming increase these risks further. During the twentieth century, the Antarctic Peninsula was one of the most rapidly heating areas of the world; over the past 50 years, roughly 75% of its ice shelves have retreated (Etourneau *et al.*, 2019; Hansen *et al.*, 2010). Warmed circumpolar deep-water (CDW) from an

increasingly warming global ocean circulation is attributed to cause these retreats (Bilyk, 2011). These climatic effects may begin to lead to changing species distributions, important for cryonotothenioids given their poor thermal plasticity (Robinson, 2008).

Natural predation plays a key role in maintaining the Antarctic food webs and the cryonotothenioid populations. Marine birds, such as the Antarctic shag (*Phalacrocorax bransfieldensis*), Gentoo (*Pygoscelis papua*), and Macaroni penguins (*Eudyptes chrysolophus*), have cryonotothenioid fish as their main, or a part of, their diets (Casaux *et al.*, 1997; Coria *et al.*, 2000). These birds, depending on their life histories for the depth at which they can reach, can dive into the water and catch the cryonotothenioids. *Pygoscelis papua* targets demersal species of cryonotothenioids, such as *L. nudifrons* and *G. gibberifrons* (Barrera-Oro, 2002). The feeding habits and stomach content composition of *P. bransfieldensis* show seasonality during the breeding season, in line with their offspring's energetic demands. Smaller and less nutritious fish, such as *L. nudifrons*, were consumed by *P. bransfieldensis* post-fledging, whereas the larger, more nutritious Black rockcod (*Notothenia coriiceps*) is consumed during the main rearing period (Casaux *et al.*, 1997).

Pinnipeds are also active within the Southern Ocean and play their part in maintaining Antarctic food webs. The Southern Elephant seal (*Mirounga leonina*), Leopard seal (*Hydrurga leptonyx*), Weddell seal (*Leptonychotes weddellii*), and the Antarctic fur seal (*Arctocephalus gazella*) all have cryonotothenioids as part of their diet (Barrera-Oro, 2002). *Mirounga leonina* has been recorded to dive down to depths of 1400 m whilst hunting the larger *D. eleginoides* (Slip, 1995).

Cryonotothenioids experience predation by other cryonotothenioids too. The Painted notie (*Nototheniops larseni*) and *L. nudifrons* have their larval stage away from the benthos in the pelagic waters of the Southern Ocean, consuming plankton to develop (Ruzicka, 1996).

Channichthyid larvae, such as *C. aceratus* and *Chionodraco rastrospinosus*, are often present in these waters, and it is suggested that these are predator-prey relationships (Loeb *et al.*, 1993; North and Kellermann, 1990). Recently, spawns of Emerald notothen larvae (*Trematomus bernacchii*) have been reported to be consumed by another sympatric notothenioid species, the Bullhead notothen (*Notothenia coriiceps*), as a result of a lack of effective egg protection (Novillo *et al.*, 2022).

### 1.6 Nesting behaviour of icefishes

One method for increasing the chances of offspring survival involves parental care during spawning until hatching. Worldwide ~ 90 families of bony fishes demonstrate parental care of their offspring (Helfman *et al.*, 2009). Parental care behaviour has been observed in Antarctic icefish, with nesting and egg guarding being the most common forms (Ferrando *et al.*, 2014; Purser *et al.*, 2022). Nesting behaviour has been observed within all cryonotothenioid families (Jones and Near, 2012). For many species, both males and females guard (Daniels, 1978; Hourigan and Radtke, 1989; Moreno, 1980). Nesting can also occur on a harder substrate, as nests with guards have also been seen on top of flat drop stones (Kock *et al.*, 2008). Nesting and guarding have a trade-off between the survival of the eggs and their chance to hatch and develop, and the opportunities for the parent to feed (Kock *et al.*, 2006). The first observations of nesting parental care behaviour from the Antarctic was in 1978 with Plunder fish (*Harpagifer bispinis*) on the Peninsula (Daniels, 1978). The females constructed a nest and were the guardians of that nest for four months. Species in the genus *Lepidonotothen* often exhibit parental care nesting behaviour, as has been seen in *in-situ* and *ex-situ* experiments (Eastman *et al.*, 2013; Konecki and Targett, 1989; La Mesa *et al.*, 2021). Within the genus, the species shares similar morphology, but has temporal niche partitioning and differing early life-history traits (La Mesa *et al.*, 2017).

For *L. nudifrons*, sexual maturity is reached at four to five years and 8 to 9 cm (Hourigan and Radtke, 1989; La Mesa *et al.*, 2017). The females spawn 100 – 3,500 demersal yolky eggs in a nest in late Austral autumn to winter (May to June), usually protected by crevices or rocks (Hourigan and Radtke, 1989). The male guards the nest and eggs for another four months; the female has not been observed to assist in guarding. Guarding also includes deterring egg predators by chasing. The guards observed only move away from the nest to feed in short periods, an activity also seen with *H. bispinis* (Daniels, 1978; Hourigan and Radtke, 1989). Once hatched, between September and May, *L. nudifrons* larvae raise to near the surface to feed on plankton and develop. As juveniles, they return to the benthos the following April (Kellermann, 1989).

Dependent on the species within the cryonotothenioids, nests vary in shapes, sizes, and substratum choice (Jones and Near, 2012). It is not known how many species construct nests (Detrich *et al.*, 2005). *Harpagifer bispinis* nests have diameters ranging between 6 – 10 cm and were seen clumped together as a group of three in one study site at Arthur Harbour (Daniels, 1978). Others, such as *L. squamifrons* and Saddleback plunderfish (*Pogonophryne scotti*), have been photographed using rocky areas and muddy sediments as their nesting sites (Eastman *et al.*, 2013; Jones and Near, 2012).

In a recent survey on the North-Eastern Weddell Sea, the COntinental Shelf MUltidisciplinary flux Study (COSMUS) expedition trawled a camera sled and discovered a large Jonah's icefish (*Neopagetopsis ionah*) breeding colony with 16,160 nests spanning 45,600 m<sup>2</sup> of the seafloor (Purser *et al.*, 2022). The nests were consistent in spacing at ~25 cm between them and none were observed to be having physical contact with another. Depths for these nests ranged between 420 and 535 m, a peak density was seen at 497 m with 1.49 active nests m<sup>-2</sup>. Most nests were occupied and actively guarded, containing 1,735 ±433 eggs. Some nests contained dead and degrading individuals that were being

consumed by opportunistic feeders and covered in a microbial mat. Abandoned nests could be identified by the lack of maintenance from the layer of phytodetritus on top of the nests. Environmental conditions were investigated within the nesting site, and the area is dominated by an inflow of modified warm deep water (mWDW) and had a lower water oxygen concentration. This mWDW was up to 2°C warmer than the surrounding bottom water, which might be a factor in the nest suitability, spawning or egg development.

### 1.7 Weddell Sea Expedition

The Weddell Sea Expedition took place from January to February 2019 with two aims: to explore and survey the Larsen C region in search of Sir Ernest Shackleton's ship, the *Endurance*, which sank in 1915, and to investigate the waters off the Larsen C ice shelf (Dowdeswell *et al.*, 2019). The South African ship *SA Agulhas II* was equipped with Autonomous Underwater Vehicles and a Remotely Operated Vehicle (ROV) was used for the expedition. The sampling locations were chosen due to the recent calving of the Larsen C Ice Shelf, creating the A-68 iceberg, which provided a unique opportunity to investigate the benthos associated with differing levels of time since the breakaway of the A-68. The prospect of studying a recent under ice location, which is now free of ice, is extremely rare, if not a unique chance to study the biology underneath what would usually be covered under ice (Dowdeswell *et al.*, 2019). Five ROV dives were dedicated to the marine biology team throughout the expedition. During the sampling and collection of animals from the ROV, some fish nests were observed.

#### Aims and hypotheses

This study aims to quantify the nests found in the Weddell Sea Expedition, trying to elucidate the species constructing them, the absence or presence of eggs/larvae, and quantifying the grouping patterns seen. From the observations of Purser *et al.* (2022), there was a marked

temperature rise in the areas that contained the nests, so temperature differences between areas of benthos containing and lacking fish nests should show differences. The nests sizes should be the fish length at maturity of the species occupying the nests.

## Materials and Methods

### Study site

The Weddell Sea is an embayment off the coast of Antarctica between the Antarctic Peninsula in the West and Coats Land in the East. Sampling locations were in the North-West Weddell Sea, off the east coast of the Antarctic peninsula.

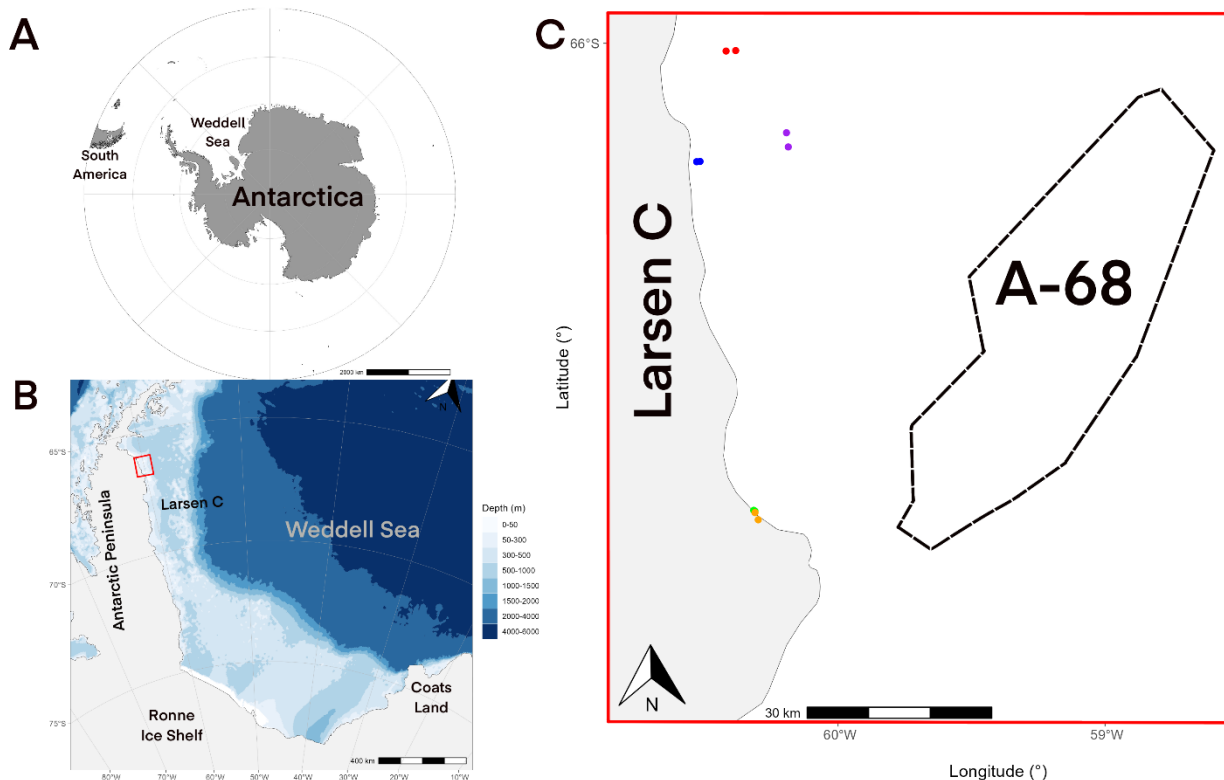


Figure 1: Map of the survey site within the Weddell Sea, Antarctica. A) The landmass of Antarctica. B) Bathymetric Weddell Sea and Antarctic ice shelves with the study site in a red box. C) The study site with the iceberg A-68 in dashed lines. The start and end points for locations sampled are as follows: Purple - Site A, Red - Site B, Green - Site C, Blue - Site D, Orange - Site E.



## Data acquisition and analysis

The Weddell Sea Expedition 2019 (WSE) was conducted between 1 January and 22 February 2019 (Dowdeswell *et al.*, 2019). Five days (14<sup>th</sup> January for Site B, 20<sup>th</sup> January for Site D, 21<sup>st</sup> January for Site C, 22<sup>nd</sup> January for Site E, and 23<sup>rd</sup> January for Site A) were allocated to remotely operated vehicle dives and 27 hours of video data were recorded. The sampling locations were selected due to the calving of part of the Larsen C ice shelf in 2017, creating the A-68 iceberg (losing ~ 11% of the ice shelf) (Etourneau *et al.*, 2019), and exposing marine habitat that had been previously covered in said ice. The four study sites were 5 - 10, 15 - 18, and 50 years clear of permanent ice cover, for Site C, Site D, and Site B, respectively. One site, Site A, has been clear of permanent ice cover for over 50 years. The mean maximum depth across all five sites was  $376.3 \pm 19.07$  m. The deepest depth the ROV achieved was 434 m at Site B.

All video footage was examined and noted for the timestamp, GPS location, depth, abundance of nests, size of nests, general sediment size, and rock presence (with sizes if present). Conductivity, temperature, and depth data (CTD) were also recorded in various locations during the expedition. Two lasers attached to the ROV at 10 cm width enabled the measurements of the nests and any rocks and teleosts to be recorded if present. A temperature logger was also present on the ROV, which measured temperature every 10 seconds for the specific location travelled, although the Site E data was unable to be located and had to be omitted for temperature. Any smaller, more contentious deviations from flat substratum (those below 6.5 cm) were also excluded as they could include pockmarks from gas rises. A large plankton bloom caused flocculent to settle and carpet the seabed, this enabled nests to be classified as 'active' due to the absence of the flocculent inside the nest. Image analysis was conducted using ImageJ, which measured the nests diameter using the

ROV's lasers for calibration (Abramoff *et al.*, 2004). All data analyses and mapping were performed in the open-source software R v.4.2.1 (R Core Team, 2017). The maps were generated using the package ggOceanMaps (Vihtakari, 2022). Data collected underwent normality testing and diameter data had a log transformation to achieve normality. T-test and ANOVA with post hoc Tukey testing were used to compare the temperatures, grouping patterns and sites. Any species identification used Fishbase and the book 'Fishes of the Southern Ocean' (Froese and Pauly, 2022; Gon and Heemstra, 1990)



Figure 2: Comparison of non-maintained, abandoned nests (left) and 'active' maintained nest (right).

After evaluating all the nests in the sites sampled, commonalities were found in nesting patterns. Six groups were described: cluster, crescent, line, oval, sharp u, and singular. The cluster pattern is defined by nests being close to others in no overall shape and structure. Crescent shapes are those that have wider nests at the base and thinner nests on the limbs. The line shape contains nests that are relatively linear with one another. Nests that complete a full oval shape are grouped as an oval pattern. Patterns of sharp u consist of a typical 'U' shape. The singular group are those nests that are not adjacent to or associated with any other nest.

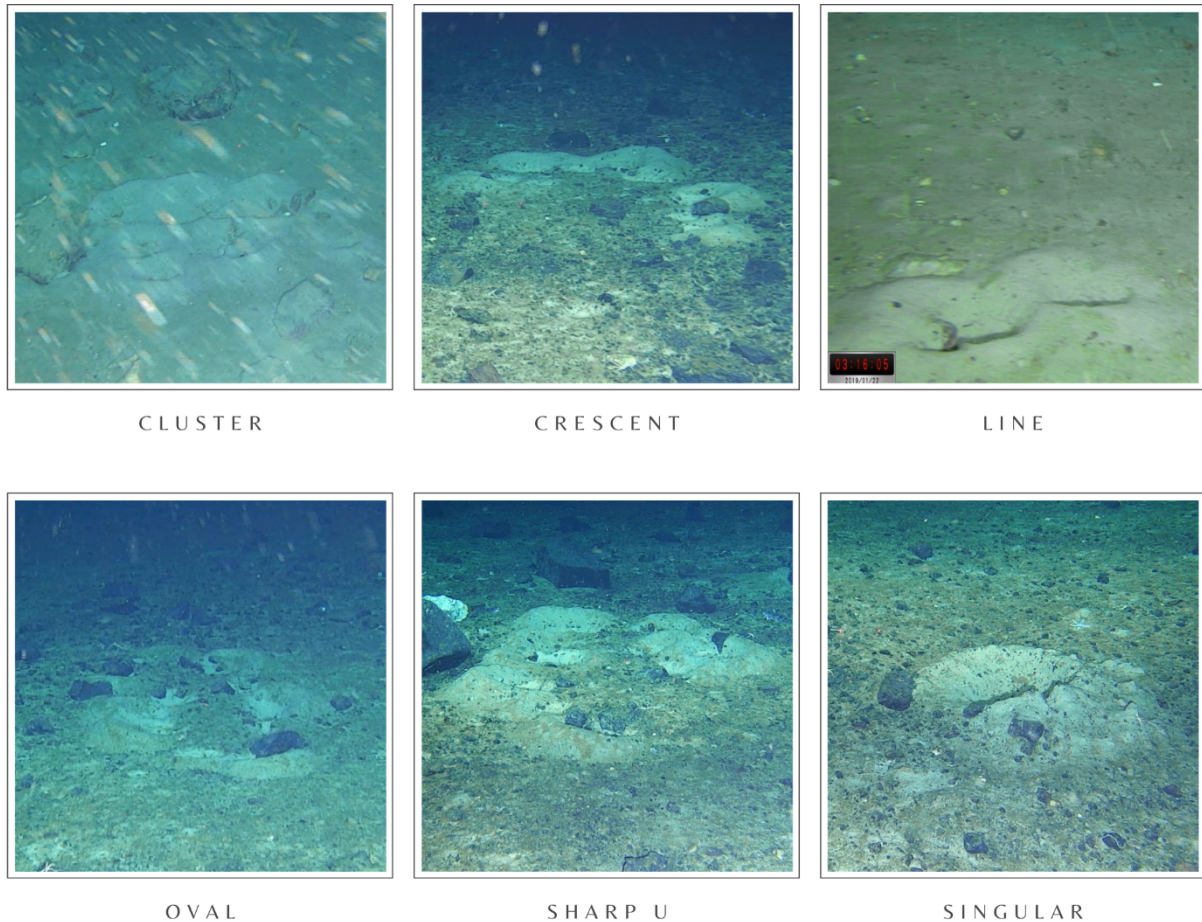


Figure 3: Patterns of cryonotothenioid nests from top left to bottom right; Cluster, Crescent, Line, Oval, Sharp U, and Singular nests.

## Results

A total of 1,036 individual active nests were located within 277 groups on the five ROV dives. 93 nests were classed as inactive nests. Nests were discovered at depths between 290 and 411 meters. A mean of  $3.74 \pm 0.22$  nests per group was found across all the dives. The most abundant nesting group location was found on Site D, with 151 groups of nests, and a mean of 2.3 nests per group. The most abundant location was Site E, with 495 individual nests.

A total of nine cryonotothenioid species were seen, *L. nudifrons* was the most numerically abundant species, 85 individuals were recorded and found adjacent to and within the nests. Other morphotypes included icefish, which contained *Cryodraco antarcticus* and *Hapagifer* sp., but they were never found within any nests. The average nest size (12.9 cm) is larger

than *L. nudifrons* published size at maturity (9.1 to 9.5 cm), especially as other individuals recorded during the data collection were larger and have larger sizes at maturity (Hourigan and Radtke, 1989).

Table 1: The number of groups of nests found per site with their mean nests per group and average depth at which they were found, with standard error.

<b>Site</b>	<b>Number of groups</b>	<b>Mean nest per group</b>	<b>Average depth (m)</b>
<b>SITE A</b>	53	$3.13 \pm 0.44$	$386.13 \pm 0.30$
<b>SITE B</b>	11	$4.5 \pm 0.89$	$399.5 \pm 0.53$
<b>SITE C</b>	2	4.00	$410.88 \pm 0.16$
<b>SITE D</b>	151	$2.3 \pm 0.19$	$298.64 \pm 0.23$
<b>SITE E</b>	60	$7.68 \pm 0.55$	$350.05 \pm 0.37$

## Distribution of nesting sites

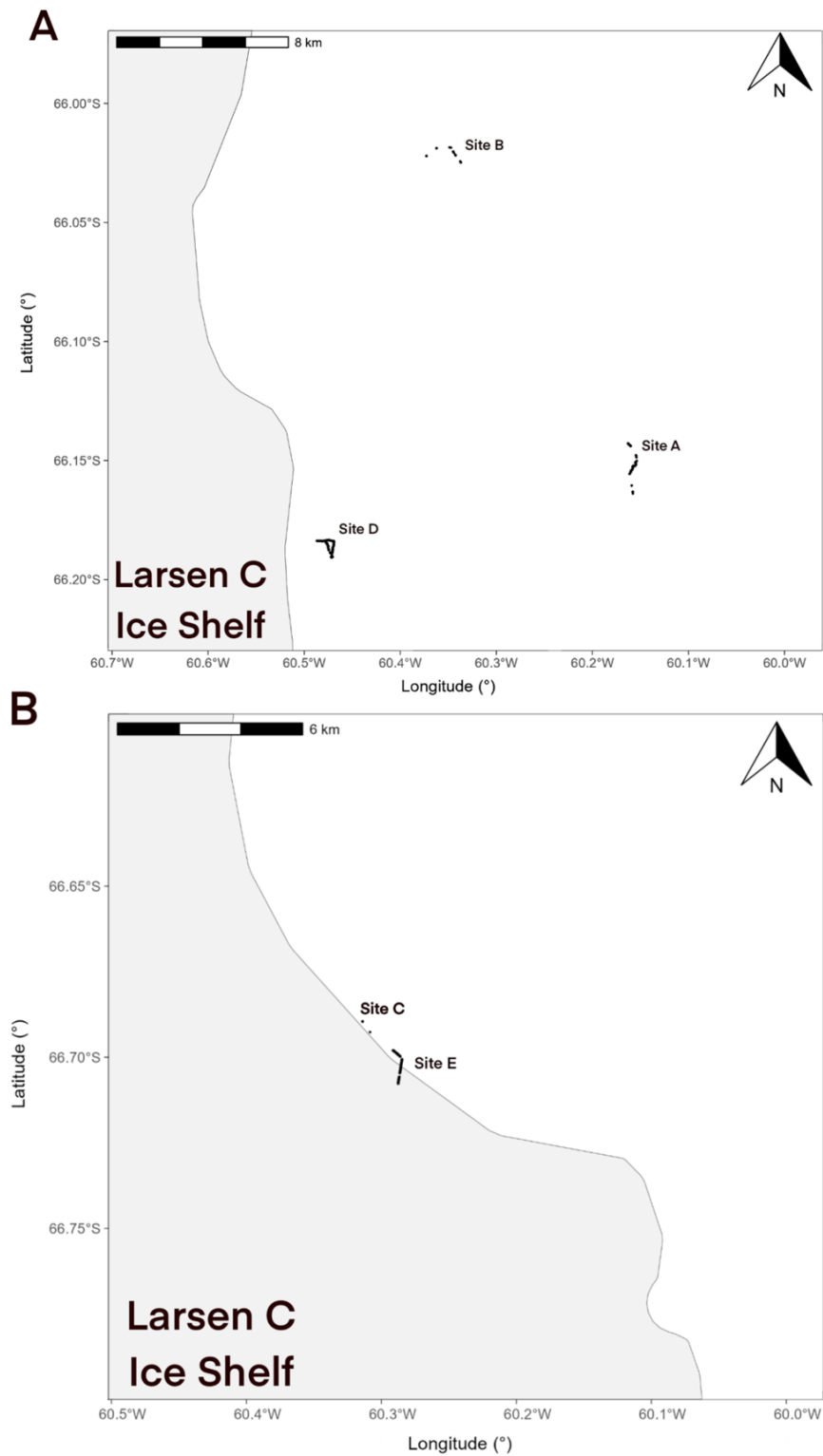


Figure 4: Enlarged map of the study site with the locations of the nests found off the Larsen C Ice Shelf A) Sites A, B, and D. For B) Sites C and E. Nests are represented as black circles.

Different substratum was found between sites. Site B was a lot rockier with a high abundance of invertebrate fauna, such as brittle stars, feather stars, and corals. The other locations (Site D to Site A) had finer sediment, which also contained more nests and fish were observed. 144 nests had large and small pebbles within and around the nests. Nesting sites adjacent to rocks were seen on every sampling location apart from Site C. A total of 193 nests were recorded adjacent to rocks, whilst 843 nests were not directly adjacent to rocks. Mean rock sizes adjacent to the nests were  $27.4 \pm 0.9$  cm. Nesting width diameter ranged between 6.72 to 34 cm, with a mean diameter of  $12.9 \pm 0.14$  cm. Whilst not significant, the nests that were adjacent to rocks were slightly smaller, at a mean diameter of  $12.5 \pm 0.34$  cm in comparison to  $13 \pm 0.15$  cm for those that were not adjacent to a rock ( $p > 0.05$ ).

Local temperature distribution ranged between  $-1.1$  to  $-2.05^{\circ}\text{C}$  across all nesting sites. The coldest nesting sites were on Site D at 304 m deep ( $-1.95$  to  $-2.05^{\circ}\text{C}$ ), whereas the warmest site was on Site B at 418 m deep ( $-1.8$  to  $-1.95^{\circ}\text{C}$ ). The localised nesting temperature in Site C and Site A was  $-1.7^{\circ}\text{C}$ , and  $-1.7$  to  $1.8^{\circ}\text{C}$ , respectively. Localised nesting temperatures did not significantly differ from the surrounding areas ( $p > 0.05$ ), apart from the Site A sampling site, where the nesting sites were colder than the surrounding areas (t-test;  $t_{186.74} = -4.7062$ ,  $p < 0.001$ ).

### Patterns of nesting sites

The cluster pattern was represented in 42.08% of the total nests, followed by singular, sharp u, oval, crescent, and line at 18.82%, 16.8%, 10.14%, 8.41%, and 3.67%, respectively.

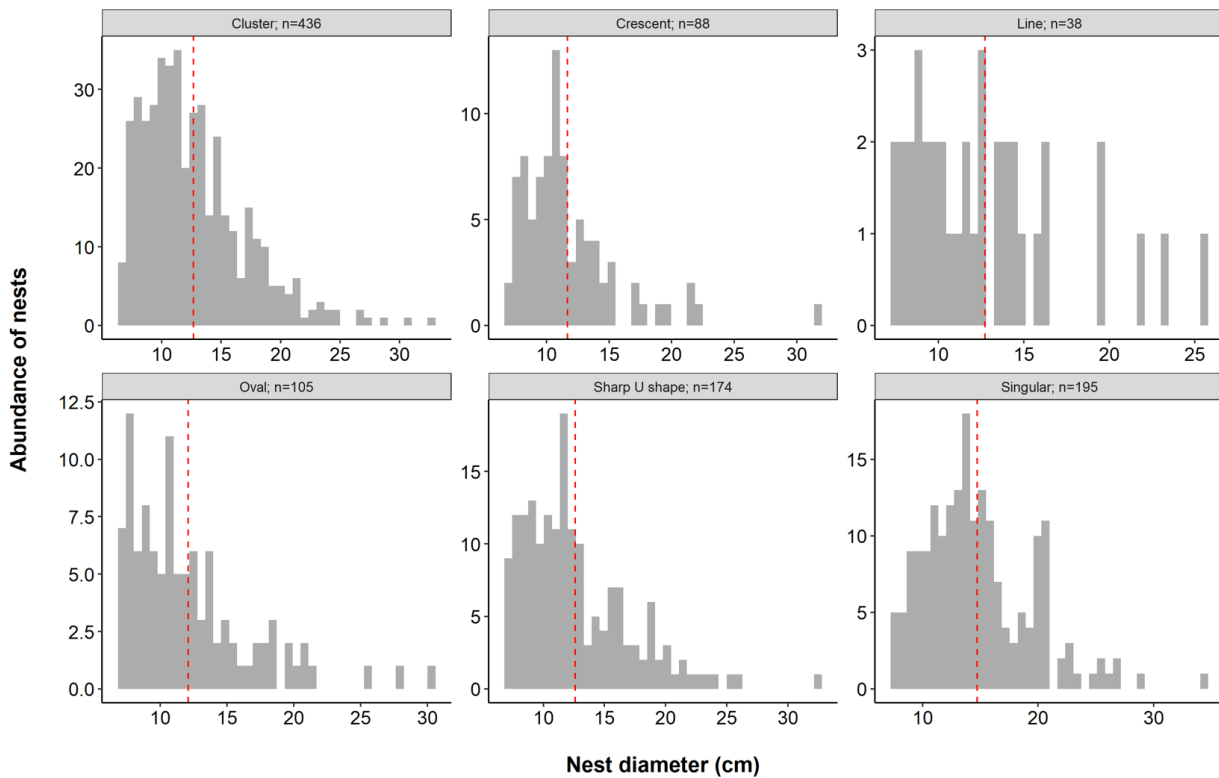


Figure 5: Nesting diameter (cm) abundances faceted by grouping pattern exhibited with their corresponding number of nests found, red dotted line indicates the overall mean nest diameter (cm).

There was a significant difference in the diameter of the different nesting patterns (ANOVA;  $F_{5,1030} = 10.48$   $p < 0.001$ ). Singular nests had a significantly higher average diameter than those within cluster, crescent, oval, and sharp u patterns (Tukey;  $p < 0.001$ ).

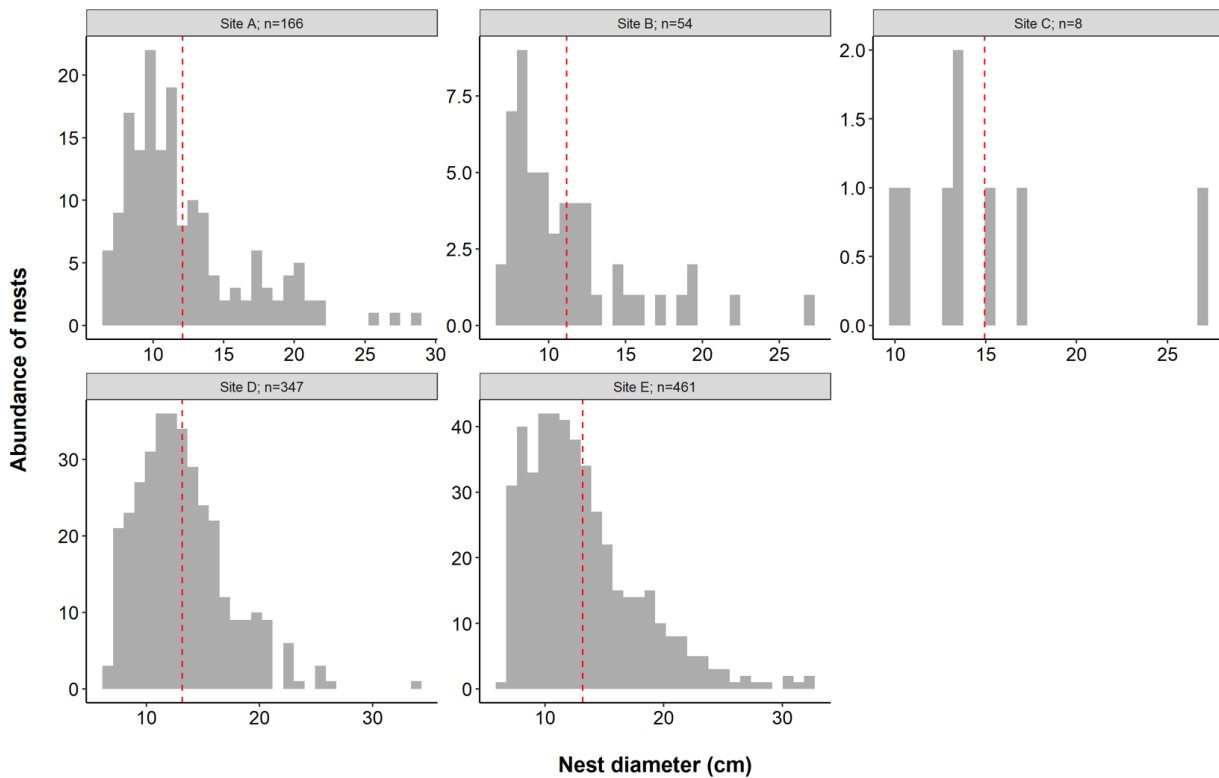


Figure 6: Nesting diameter abundances faceted by site sampled with their corresponding number of nests found, red dotted line indicates the mean nest diameter (cm).

The diameters of the nests were significantly different between the sites studied (ANOVA;  $F_{4,1031} = 4.508$   $p < 0.01$ ). The diameters of the nests found on Site B were significantly lower than those at Site D and E (Tukey;  $p < 0.05$ , and  $0.05$ , respectively).

## Discussion

### Nesting descriptions and patterns

This study shows the first, large-scale nesting group pattern by *L. nudifrons*. Nests were able to be classified as ‘active’ due to the large phytoplankton bloom and this flocculent subsequent settlement on the benthos as phytodetritus (Figure 2). The lack of this flocculent inside nests signifies the nests are being actively maintained. Nests became very distinct in the benthos due to the maintenance of the nests. The depths of the nests varied between the groups, but this was not measured due to the challenge of measuring such a shallow depth using two lasers. The nests were generally circular and shallow parabolic in shape



with the sediment built up on the sides of nests (see Figures 2 and 3). Inside the nests, any larger rocks at the bottom were left, but smaller rocks and shells were pushed aside to the edges of the nests. If the nests were in a group, the sediment built up on the sides tended to be away from the centre of the pattern. In some nests, the larvae could be seen, floating within the circumference of the nest. Only *L. nudifrons* were seen in the nests, suggesting these nests were created by this species, which aligns with the few other studies of this species in nesting and time of hatching seasons (Gon and Heemstra, 1990). This species was also seen to be the most abundant in the area, with eighty-five individuals from this species found nearby to the nesting sites. No eggs were seen within any of the nests, which is explained as the expedition occurred after the typical hatching period of winter to early spring (La Mesa *et al.*, 2017). The presence of larger rocks was also observed beside the nests, which has been noted before, but nests were not always beside such large rocks. These rocks may provide shelter from currents or enhanced refugia from predation.

The nesting groups were classified into six different patterns. Sharp u, oval, and crescent are the most similar in form. Differences within grouping patterns could be attributed to sharp u and crescent incompleteness in forming an oval pattern. The most common pattern, cluster, lacked any distinguishing pattern with the exemption of the accumulation of many nests in a small area. Singular nests had the highest mean nest diameter and were found at all sites (12.67 cm). The line pattern is very distinct, and the least abundant of the patterns seen, which could be justified as a form of community anti-predator adaptation. Previous research has shown that guarding *L. nudifrons* parents will do so up to 25 cm away from their nests (Hourigan and Radtke, 1989), which would encroach on their neighbour's nests in this study. The selfish herd theory for the cluster pattern seen here could offer a reduced risk to the nests in the centre of the cluster (Hamilton, 1971). Alternatively, the opposite could be true and potentially the other closer patterns, bar the singular nests, could provide

a group effort in guarding against predation. Singular nests are significantly larger than those of cluster, crescent, oval, and sharp u patterns, possibly due to the increased space available to the individual or as a form of greater protection, or perhaps these represent a difference in icefish species. Group nesting behaviour is becoming more well defined in the Antarctic, and this study shows more evidence of use of group nesting. One group of three *H. bispinis* nests were demonstrated in Arthur Harbour, Anvers Island, Antarctica, but there was no given reason for this grouping, except for the rubble pile that they were laid upon (Daniels, 1978). It is also not known whether one mating pair created all the nests in the group or whether each nest was attributed to different single mating pair. From previous literature, it is presumed that each nest was for a single mating pair/guard due to the established high risk of predation and energetic costs involving guarding one nest. The reasoning behind these grouping patterns is still not clear or understood. Another study has produced a habitat suitability model prediction based on the current knowledge of nesting sites (Teschke *et al.*, 2016). The nesting sites found within the Teschke *et al.* (2016) study predict that area investigated in the WSE cruise would have the right conditions and is very suitable for nesting sites, which helps validate both studies.

#### Comparison to the Southern Weddell Sea icefish nesting colony

The recent findings from Purser *et al.* (2022) in their expedition to the North-western Weddell Sea, found a large nesting site, with the scale of this nesting colony being  $\sim 240$  km<sup>2</sup>. This research is the only other finding of large-scale Antarctic marine nesting sites in the current literature. Nesting species presented here and in Purser *et al.* (2022) are of differing species: *L. nudifrons* from the Eastern Weddell Sea (data presented here) opposed to *N. ionah* in the West. As *N. ionah* is larger than *L. nudifrons* at the length of maturity, this leads to the nesting sizes being larger for the nests of *N. ionah* at  $\sim 75$  cm, in comparison to the average nest size of this study at 12.9 cm. Both nesting sites had similar maintained bowl/shallow

parabolic shapes as nests. The depths at which these nests are seen also differ, with the *N. ionah* nesting site ranging in depths between 420 to 535 m deep, which is slightly deeper than the *L. nudifrons* nests ranging between 290 to 411 m deep in this study. Nesting sites could nevertheless potentially be seen at differing depths outside the range soupy of this study, as these depths were due to the locations and depths investigated. Spacing between the *L. nudifrons* nesting sites is much more stochastic and neighbouring nests are often touching, whereas, at the *N. ionah* nesting site, they were spaced ~25 cm from each other and did not touch neighbouring nests. The WSE occurred from late January to February 2019, when the nests and individuals encountered had just completed hatching, while the COSMUS expedition occurred from February to April 2021 and still had nesting, eggs, and guards in most of the nests. This suggests that the Weddell Sea is a site where nesting can occur when ice cover has retreated in Austral spring to autumn. The bottom water in the Purser *et al.* (2022) study was dominated by the mWDW, which raised the surrounding water temperature, in contrast to the present study, which found no difference in temperature between nest sites and background waters, with the exception of one site where the surrounding water was colder (-1.76°C); however, this could have been due to sampling restrictions on the ROV.

#### Oceanographic factors

The present study has shown that there is no significant difference between nesting site temperatures and the surrounding waters where nests were absent (with the exception of Site A which was -0.01°C warmer). This may be due to the geographic location of these nests as it is flanked by the Antarctic Peninsula; however, the mWDW has been shown to reach this location, so further investigation is required (Hutchinson *et al.*, 2020). There are four major water flows within this eastern Weddell Sea area: winter water, ice shelf water, high-salinity shelf water, and modified warm deep water. The HSSW and ISW come from

the ice shelves that are hypersaline, and much colder, but readily mix with the mWDW nearby, which is where the nests on Site C were adjacent. Site B was the furthest away from the Larsen C Ice Shelf and in warmer, deeper waters, which accounts for the warmer temperatures seen at deeper depths than the other sites. Potentially, the mixing and combination of the local shelf water masses above from the Larsen C ice shelf and the mWDW allows for a greater level of productivity, meaning a greater abundance of fish, and then a greater abundance of nesting sites; however, this has not been investigated and future research is needed for the oceanographic processes could cause nesting site preferences.

#### Associated fauna with the nesting sites

In all locations visited, typically, the epifauna was visually low in diversity (pers. obsv.). Beside the nests, echinoderms and Cnidaria were the most abundant. Within the echinoderms, brittle stars were the most frequently seen, with feather stars following in abundance. The brittle stars were not seen within nests; however, many individuals were located on the peak rim or edges of the nests. Abundant cnidarians included *Umbellula* and *Leptogorgia*, which were seen further away and not physically touching the nests. Holothurians were seen near nests on Site B, Site D, Site E, and Site A during sampling; these individuals were further away and mainly seen dormant. Other groups of individuals that were noted but were not as abundant included two morphotypes of siphonophore, one morphotype of ribbon worm, *Nemertina*, and an octopus. As noted elsewhere in the literature regarding brittlestars and nesting, it is possible that these brittlestars were predated upon the cryonotothenioid eggs before hatching (Daniels, 1978).

## Temporal and logistical considerations

Visually, the fishes seen during the ROV dives were impacted by the presence of the ROV and most moved away from it, likely causing the abundance of fishes seen to be lower than realistically present with the absence of the ROV. Due to the temporal constrictions of a research cruise, the sampling events were conducted at set times. This meant that the ROV dives were consistent in length; however, the distance covered was not consistent because of the differing velocity of currents.

## Conclusion

To conclude, this study is the first in its kind to discover a large, active, and well-dispersed *L. nudifrons* nesting habitat. These nest sites are also the first to find nesting group patterns, which are thought to be a group predation evasion behaviour. As there was a lack of other species seen in high abundance anywhere near the nests, the nesting sites are attributed to the species *L. nudifrons*. The species also matches the timing of hatching and length at maturity, which the other cryonotothenioids seen in the ROV recordings could not match. This finding also confirms the cryonotothenioid nesting site suitability model accuracy from Teschke *et al.* (2016). The location of this important fish nesting area in the western Weddell Sea beside the Larsen C ice shelf is relevant to future discussions about the protection of this area; it provides additional evidence to support the proposal of the Weddell Sea Marine Protected Area due to the active nesting sites seen.

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## Summary and overall study conclusions

Fisheries are a significant part of the livelihoods of many humans, offering sustainable food, essential nutrients, and income. In this dissertation, two chapters have examined different aspects of fish populations and habitats. The first chapter focuses on artisanal fish fences in the Wakatobi Marine National Park, investigating their impact on the finfish community life stage and micronutrient composition in seagrass-dominated shallow habitats. The study shows that fish fences are proving to be unsustainable, leading to declining catch rates and an increase in the capture of juvenile fish. The seagrass-dominated shallow habitats in the Kaledupan subregion are identified as an essential fish habitat for juveniles, with a significant increase in the proportion of juveniles caught over the study period. However, this increase was accompanied by troubling trends of Malthusian overfishing and a decrease in species richness of juveniles. While changes in mesh size and fish fence length did not significantly affect the micronutrient content of the catch, further investigation considering demographic factors is necessary. The human population on these islands have not been impacted by the changing ecology on the nutrient level.

The second chapter investigates nesting sites of notothenioid fish in the Western Weddell Sea. This study shows the existence of maintained nesting sites of *Lindbergichthys nudifrons* (Yellowfin notie). These nesting sites, characterised by groups of nests in close proximity and with different shape patterns, represent a novel finding not documented in previous literature. The clustering of nests is believed to provide group predation protection. No correlation was found between nest presence and oceanographic factors, distinguishing this study from prior research. These findings contribute to understanding the unique habitats of the Weddell Sea.

Combining the results from both chapters, it is evident that careful management and conservation efforts are necessary to ensure the sustainability of fish populations and their habitats. The use of artisanal fish fences in the Wakatobi Marine National Park highlights the need for alternative, more sustainable fishing methods to prevent overfishing and protect nursery grounds. In the Weddell Sea, the discovery of nesting sites emphasises the ecological importance of preserving these unique habitats. Establishing a Marine Protected Area in the Weddell Sea can contribute to the long-term conservation of nesting sites and other distinct ecosystems in the region.

Several caveats and areas for future research should be acknowledged. In the first chapter, the limitations of using artisanal fish fences as a sampling method, calls for further investigation using alternative sampling approaches to understand the fish community composition. Similarly, in the second chapter, future research should aim to investigate the underlying mechanisms and ecological implications of nesting behaviours and locations in the Weddell Sea. Exploring the drivers behind nest site selection and examining the broader ecological significance within the Weddell Sea ecosystem, would enhance our understanding of these unique habitats.

Overall, these studies provide valuable insights into fish communities and nesting behaviours in specific ecosystems. The findings underscore the importance of sustainable fishing practices, habitat preservation, and the establishment of marine protected areas, to safeguard fish populations and maintain the ecological integrity of marine environments. By pursuing future research, it can further enhance our understanding of these interactions and contribute to effective conservation strategies.