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Investigating spatial aspects of the community-based management of a small-scale artisanal grouper fishery

Thesis submitted by
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in September 2016

for the degree of Doctor of Philosophy in Marine Biology
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Excellence for Coral Reef Studies
James Cook University

DEDICATION

I dedicate this dissertation to my advisor, mentor, and friend – Dr Glenn R Almany.

He is deeply missed.

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EXECUTIVE SUMMARY

Fisheries are increasingly understood as complex social-ecological systems (Folke 2006). Fisheries management thus requires an understanding of key processes that underpin both the resource (*i.e.,* fish) and the resource users (*i.e.,* fishers) (Cinner *et al.* 2009b). These processes invariably operate over differing spatial and temporal scales, and one of the primary challenges facing fisheries management is adequately matching the scale of management institutions and actions to all key social and ecological processes (Cumming *et al.* 2006). Failure to adequately match the scale of management to these processes can have severe consequences. For example, regional scale management in the northern Altantic was unable to stop the serial depletion of numerous relatively discrete spawning stocks of cod and other groundfish leading to catastrophic and sustained population collapses (Wilson *et al.* 2013). Such 'problems of fit' have long been a central concern of fisheries management, most notably through Hardin's (1968) 'tragedy of the commons'. For small-scale artisanal fisheries problems of fit are particularly troubling, as key social processes such as patterns of fishing and marine tenure boundaries often operate over very restricted spatial scales (McClanahan *et al.* 2006). Recognition of this has led to an increasing global proliferation of community-based management of small-scale fisheries (Govan *et al.* 2006, 2009). However, critics suggest that problems of fit with the spatial scales of key ecological processes may drastically diminish the ability of community-based management to achieve conservation goals (Foale and Manele 2004; Mills *et al.* 2010).

This thesis examines potential problems of fit for community-based management, through the case study of two vulnerable grouper species, *Epinephelus polyphekadion* and *E. fuscoguttatus,* targeted within a multi-species artisanal coral reef fishery in Papua New Guinea. Specifically I ask:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

Many aspects of this study drew upon the local knowledge, advice, and participation of community fishers of Dyual Island, Papua New Guinea. A range of social science and ecological research methods were employed to assess the spatial scales of operation and governance of the local fishery, and key life history processes for the focal species. Local stakeholders were intrinsically involved in the work, with research questions and methods greatly influenced by

community input. Data were collected during extended field seasons within the communities of Dyual Island, Papua New Guinea, and by trained local stakeholders throughout the study period. The specific scientific objectives of this study were to (1) determine the spatial patterns of settlement, clan affiliation, access rights, and fishing effort within the local fishery, and the spatial scales of the governance institutions most relevant to its management; (2) detail the key demographic and reproductive characteristics of the two focal species of grouper; (3) examine changes in the spatial distributions of the focal species throughout their post-settlement life histories (*i.e.,* ontogenetic shift); (4) examine the reproductive migrations of populations of the focal species associated with a multi-species transient fish spawning aggregation; and finally (5) investigate the level of spatial fit between community-based governance institutions and these key social and ecological processes.

The focal fishery of this study was governed through two complementary systems –Papua New Guinea's relatively recent Westminster governance system and the enduring system of customary ownership which has much older origins. The study region was under the state-based jurisdiction of the Leon Village Planning Committee encompassing approximately 45 km^2 of shallow sub-tidal and inter-tidal habitat. The customary ownership of this area was divided between three clan groups, with individual tenure over areas of 7 – 19 km^2. Local inhabitants had access rights across the entire study area, regardless of clan affiliation. However, fishing effort was highly concentrated around human settlements, such that half of fishing effort was concentrated within just 10% of the study area.

Both *E. polyphekadion* and *E. fuscoguttatus* exhibited relatively typical epinephelid life histories which make them intrinsically vulnerable to overfishing. They had long lifespans (with maximum ages of 22 and 27 yrs, respectively), relatively slow grow rates, and relatively late reproductive maturity. Females of both species reached sexual maturity between 4 – 8 yrs of age. *Epinephelus fuscoguttatus* reached greater lengths and exhibited faster growth. As such, female *E. polyphekadion* entered the reproductive population between 278 – 380 mm in length (with 50% mature at 330 mm), whereas female *E. fuscoguttatus* entered the reproductive population between 370 – 480 mm in length (with 50% mature at 430 mm). These ages and sizes at maturity were used to investigate the habitat requirements of these species throughout their post-settlement life histories.

Habitat suitability modelling indicated that ontogenetic shift was similar for both species. Juveniles (*i.e.,* individuals under the age/size at 50% female maturity) were restricted to habitat directly adjacent to land, particularly around mangroves and freshwater inputs. Both species occupied broader ecological niches throughout their post-settlement life histories. Adult (*i.e.,* individuals above the age/size at 50% female maturity) habitat included patch and barrier reef habitats characterised by high live coral cover, as well as the fringing habitat preferred by juveniles.

Acoustic telemetry revealed that the fish spawning aggregation currently under community-based management drew *E. fuscoguttatus* individuals from a 'catchment area' (*i.e.,* the total area inhabited by the entire spawning population throughout the non-spawning season) of at least 16 km^2. Further analysis however, indicated that reproductive migrations were skewed toward shorter distances. As a result, 30 – 50% of the spawning population resided within the 1-2 km^2 directly adjacent to the aggregation site throughout the non-spawning season.

Finally, I brought together all of the key social and ecological scales considered throughout this thesis, and demonstrated that at western Dyual, community-scale governance institutions presented a good spatial fit to manage the artisanal fishery for these commercially valuable grouper. The ecological processes considered here (ontogenetic shift in habitat suitability and reproductive migration to and from fish spawning aggregations) could be effectively managed at the scale of individual tenure areas. Individual spawning stocks would best be managed at this scale to avoid serial depletions. However, social processes were poorly aligned with tenure areas. Common access to resources and variable patterns of settlement resulted in highly variable fishing effort between tenure areas. Management opportunities within the most heavily fished tenure area were particularly restricted. Thus, the larger scale of community-based governance considered here, encompassing approximately 45 km^2, provided a better spatial fit with social processes, primarily due to its alignment with stakeholders (*i.e.,* resource users). However, fishing effort varied at extremely fine spatial scales here. This could produce serial depletion of grouper stocks here, even within these spatially restricted management areas. This thesis demonstrates that community-based management institutions can provide a good spatial fit for managing key social and ecological processes that underpinning the persistence of relatively mobile coral reef fisheries. However, nested governance institutions may be required, even at these restricted spatial scales.

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CHAPTER 1 - GENERAL INTRODUCTION

1.1 Marine fisheries and overfishing

In 1883, Huxley made the now infamous prediction "…that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish". Since then, the global human population has increased fourfold to 7.3 billion, fishing has become heavily industrialised and then globalised, and the fallacy of Huxley's assertion has become utterly irrefutable. During the second half of the 20th century, a number of these 'inexhaustible' great sea-fisheries collapsed, including Atlantic cod *(Gadus morhua),* Atlantic herring *(Clupea harengus harengus),* Pacific herring *(Clupea harengus pallasii),* Pacific mackerel *(Scomber japonicas),* Peruvian anchoveta *(Engraulis ringens),* Pacific sardine *(Sardinops sagax coeruleus),* and Japanese sardine *(Sardinops melanosticta)* (Beverton 1990; Myers *et al.* 1997; Fréon *et al.* 2005). Coastal fisheries stocks also declined markedly during this time, often leading to the dramatic collapse of associated ecosystems (Jackson et al. 2001).

The most common driver of fisheries decline and collapse is overfishing (Reynolds *et al.* 2005). Global marine fisheries face many serious stressors, including habitat destruction from development, pollution, eutrophication and sedimentation from terrestrial runoff, invasive species and increased major disturbances and changes in ocean chemistry from anthropogenic climate change. However, overexploitation has been implicated in the majority (55%) of local, regional, and global scale extinctions of marine populations (Dulvy *et al.* 2003). The industrialisation and globalisation of the marine fishing sector led to rapid increases in global fishing effort. According to statistics collected by the Food and Agriculture Organization of the United Nations (FAO), during the second half of the 20th century world marine capture fisheries production increased more than fivefold, from 16.7 million tonnes in 1950, to 87.7 million tonnes in 1996 (FAO 2014), considerably outstripping global population growth. Recent 'catch reconstruction' data suggests that actual production figures may be as much as 50% higher (Pauly and Zeller 2016). Changes in maritime law, increasing the jurisdiction of coastal states to 12 nautical miles in the 1960s and then 200 nautical miles in the late 1970s, encouraged governments to heavily subsidise the creation of larger fishing fleets. Simultaneously, technological advances greatly increased vessel range, size and efficiency, so that they could exploit stocks which were formerly unreachable or uneconomical. This steady increase in production masked the fact that stocks were being exploited at unsustainable levels. While global annual production reported by the FAO has declined by around 10 – 16%

from 1996 peak levels (FAO 2014; Pauly and Zeller 2016), the proportion of assessed stocks which are exploited at unsustainable levels (*i.e.,* overfished) has increased from 10% in 1974, to 26% in 2011. Meanwhile, the proportion which are still able to be further developed sustainably (*i.e.,* underfished) has fallen from 40% to 10% (FAO 2014). Put simply, increased global marine fisheries production has largely continued through a move toward less sustainable fishing.

The severe decline or collapse of fisheries can have dire ecological consequences. The systemic removal of organisms by fisheries has led to rapid and sustained demographic changes in target species, such as reduced size at sexual maturity and reproductive output, reducing their potential for population recovery (Conover and Munch 2002). The removal of key functional groups from ecosystems has even been implicated in dramatic regime shifts, to alternative stable, less productive states (Hughes *et al.* 2007). Wholesale removal of large herbivorous fishes from coral-dominated ecosystems throughout the Caribbean led to rapid shifts to algal-dominated states during the 1980s and 1990s (Hughes 1994). Similarly, the selective exploitation of larger, predatory species has led to near ubiquitous changes to the trophic dynamics of ecosystems, termed ‘fishing down the food web’ (Pauly *et al.* 1998; Pauly and Palomares 2005). Removal of predators of grazing urchins from kelp forests and seagrass ecosystems has precipitated catastrophic shifts to low productivity ‘urchin barren’ systems (Eklöf *et al.* 2008; Ling *et al.* 2009). The extensive removal of large, predatory fishes from coral reefs has produced ‘trophic cascades’, whereby prey species released from predatory control increase in abundance, producing flow-on effects onto their prey and so on (Dulvy *et al.* 2004). Such trophic cascades have been implicated in considerable restructuring of faunal assemblages on coral reefs, and significant declines in live coral cover (Graham *et al.* 2003; Dulvy *et al.* 2004; Boaden *et al.* 2015).

Fisheries declines can also have serious socio-economic consequences for the humans who rely on them. Fisheries are vital for global food and nutrient security – directly contributing 17% of global animal protein consumed by humans, and importantly 25% of animal protein consumed in low-income food deficit countries (Kawarazuka and Béné 2010; FAO 2014). Fisheries also directly provide livelihoods for tens of millions worldwide, the vast majority of whom work in small-scale fisheries in low and middle income countries (FAO 2014). Thus, although small-scale fisheries contribute less than 25% of total global fisheries production, they employ over 90% of the world’s fishers and directly or indirectly support over 200 million largely impoverished, vulnerable and marginalised people worldwide (FAO 2014; Pauly and Zeller 2016). The disproportionate reliance of disadvantaged people on small-scale fisheries makes their sustainable governance particularly important. However, balancing the provision of viable livelihoods and food security to such people, while simultaneously ensuring environmental sustainability of such fisheries, is often exceedingly difficult.

1.2 Small-scale fisheries governance

Effective governance of small-scale fisheries is intrinsically challenging. Fish stocks are common-pool resources, and the ‘tragedy of the commons’ suggests that unmanaged common property under sufficient exploitation will be inevitably depleted, as each stakeholder gets the full benefit of exploiting the resource, while costs arising from misuse or over-exploitation are shared among all stakeholders (Hardin 1968). Widespread acceptance of this theory has led to a tendency towards increasingly centralised control of fisheries. However, attempts to apply prescriptive, centralised techniques to small-scale fisheries management have met with widespread failure, for numerous reasons. First, due to heavy reliance of vulnerable people on small-scale fisheries for food security and livelihoods, management actions that limit people’s access to food, even for short periods of time are ethically unconscionable. Second, each small-scale fishery is unique; they target a broad assemblage of species, occur across a range of ecosystems, utilise a diverse set of technologies, and operate within an array of social settings under different official and de facto governance systems. Thus, centralised management tools are often overly prescriptive. Third, this diversity is generally coupled with sparse or non-existent data, making many small-scale fisheries difficult to define, let alone govern. Forth, large numbers of small vessels, operating from small, dispersed, informal landing and processing sites impede effective monitoring and adaptation of management regulations to changing conditions. Fifth, small-scale fisheries are often deeply enmeshed within local communities, characterised by high levels of participation in pre-harvest, harvest, and post-harvest activities. Prescriptive centralised schemes that disregard long-enduring social and cultural practices are often not well received. Sixth, the majority of small-scale fisheries operate in low and middle income countries, with limited resources to allocate to their management.

1.2.1 Customary management systems

Fortunately, many small-scale fisheries are not actually open-access systems. They can have long histories of governance, often pre-dating the centralised, state-based governments that they currently operate within. Increasingly, these customary management (CM) systems are being utilised as governance frameworks for implementing small-scale fisheries management (Govan *et al.* 2009). Customary systems often have a number of features that address some of the challenges facing small-scale fisheries management detailed above. First, as CM systems are integrated within local communities, they are considerate of the food security and livelihoods of local stakeholders. Second, CM systems largely evolved in response to local socio-ecological conditions, and are thus customised to unique local conditions. Third, many CM systems incorporate centuries, or even millennia of local ecological knowledge. While not all CM systems make effective use of local ecological knowledge, and while this knowledge is by no means a replacement for scientific data, it is increasingly being recognised as an important compliment (Hamilton *et al.* 2012). Forth, although formal fisheries monitoring is rare, CM systems are often by necessity highly adaptive to feedback from changing local conditions (Berkes *et al.* 2000; Cinner *et al.* 2005). Fifth, long-enduring CM systems have perceived legitimacy among relevant stakeholders, increasing their inducement for compliance with management rules. Sixth, CM systems often possess existing mechanisms for dealing with conflict and infringement of management rules. Not all CM regimes possess all of these and other key design principles (Cinner 2007). Additionally, CM systems may introduce additional issues such as susceptibility to rapid erosion in response to changing local socio-economic conditions. Nonetheless, there is no viable alternative to CM in many regions (Aswani 2011).

1.2.2 A framework for governance

Recognition of the limitations of centralised governments and the opportunities of localised governance has led to a global proliferation of co-management arrangements, where external organisations partner with local governance bodies, including CM institutions, to govern small-scale fisheries (Govan *et al.* 2006, 2009). This upsurgence of localised management has corresponded with a growing body of theoretical work that adds substantial nuance to the theory of the tragedy of the commons. While recognising the potential for open-access resources to be depleted without centralised control or privatisation of ownership, this work demonstrates that many self-organised, localised governance systems have long histories of sustainably governing common-pool resources (Ostrom 1990). Governance systems here refer to not only *de jure* government, but more broadly “the formal and informal arrangements, institutions, and mores which determine how resources or an environment are utilized; how problems and opportunities are evaluated and analysed, what behaviour is deemed acceptable or forbidden, and what rules and sanctions are applied to affect the pattern of resource and environmental use” (Juda 1999). Additionally, these governance systems are understood to be intrinsically interconnected with the people and natural resources that they seek to govern. This more holistic understanding of exploited natural resource systems as interconnected social-ecological systems (SESs) highlights the complex interactions between humans and the systems that they inhabit. The need to study these complex systems with reductionist scientific methods led to the development of a framework that separates a SES into four interconnected sub-systems – governance, users, the resource system, and resource units (Figure 1.1) (Ostrom 1990). These sub-systems can be further dissected into interconnected components or processes, which can be further dissected, and so on. The SES itself is also nested within a greater social, economic, political, and ecological super-system. This nested model facilitates the investigation of SESs and their components, without losing sight of the additional layers of complexity at both lesser and greater scales.

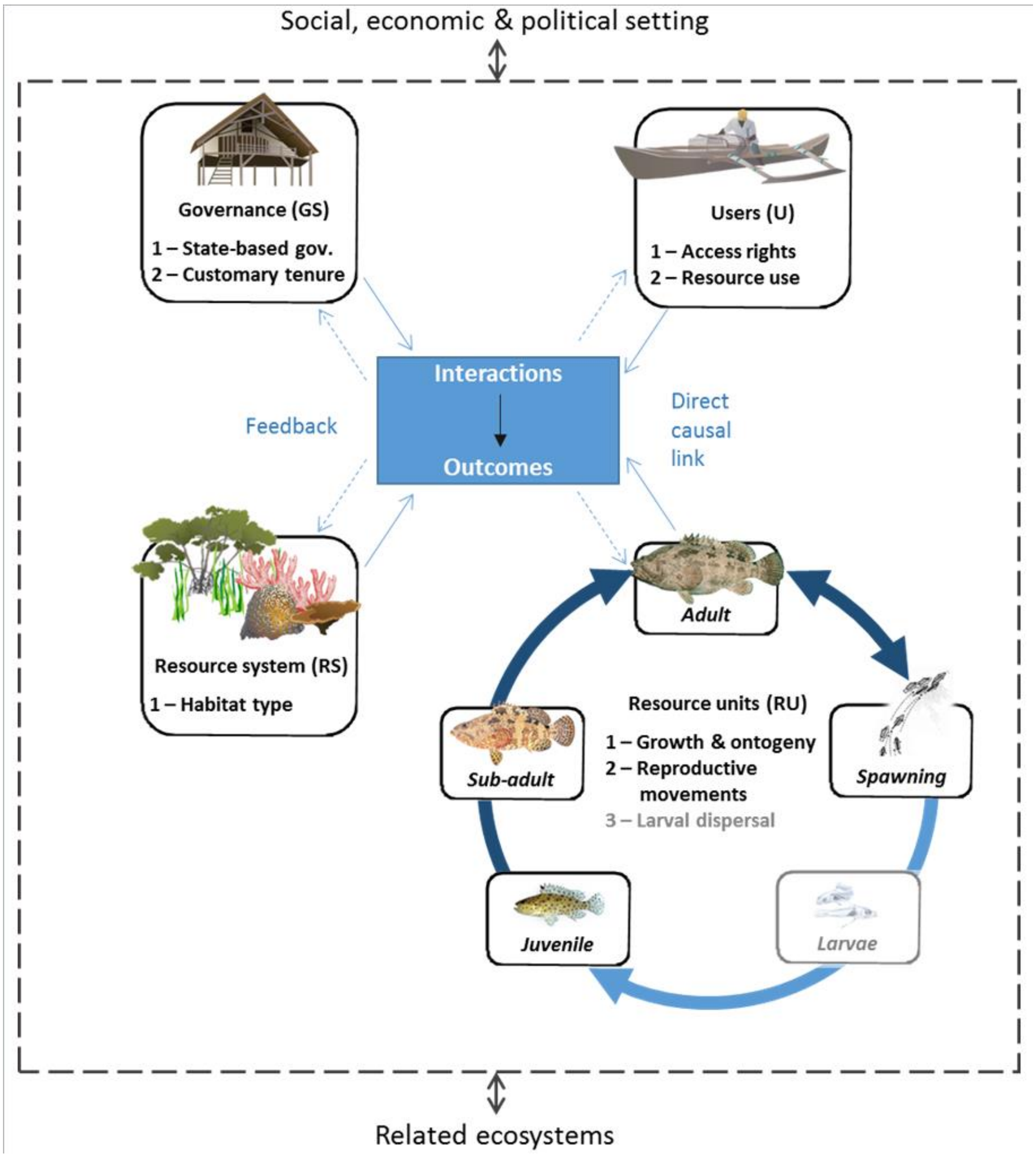

Figure 1.1 - Simplified heuristic framework of the interconnected social-ecological system relating to the Dyual Island grouper fishery, adapted from (Ostrom 2009).

Further, the framework facilitates the investigation of interactions between components of the system as well as interactions with the broader social, economic, political, and ecological setting, and their resulting outcomes (Figure 1.1). Such interactions and their resulting outcomes can help predict the feasibility of the effective implementation of particular management actions (Mills *et al.* 2013). The application of a common framework across various systems facilitates the incorporation of case studies into broader social and ecological contexts, and the advancement of theory. This framework has been applied to develop a set of key design principles for effective common-pool resource governance. These design principles are not intended as prescriptive; not every effectively-managed common-pool resource system will have all of these characteristics, and these characteristics may be substituted or superseded in some cases. Similarly, they are not intended to be exhaustive; additional SES characteristics can certainly play a driving role in common-pool resource governance. However, these principles detail some of the shared characteristics of SESs under robust and long-enduring governance across a broad range of common-pool resource systems (Ostrom 1990).

The design principles are as follows:

1. Clearly defined system boundaries.
2. Congruence of appropriation and provision rules with local conditions.
3. Collective choice arrangements among resource users.
4. An appropriate system to monitor compliance with rules.
5. Graduated sanctions imposed on resource users that violate rules.
6. Rapidly accessible arenas for resolution of conflict between stakeholders.
7. Recognition of the rights of resource users to develop and enforce rules.
8. Governance activities are organised across multiple nested tiers.

These design principles illustrate the primary importance of scale in governing common-pool resources. The first principle highlights the need to clearly understand and define the spatial extent (*i.e.,* scale) of the key processes that underpin the persistence of the resource system. It also highlights the need to clearly understand and define the set of users with rights to access and exploit the resource in question. The second principle highlights the need for governance to adequately match with local conditions. This includes, though is not limited to, matching the scale of governance to the scale of the key processes to be governed. The final principle highlights the need to govern across multiple nested tiers, facilitating governance of processes that act across differing spatial scales. Taken together, the need to govern resources at socially and ecologically appropriate spatial scales is referred to as the ‘problem of fit’.

1.3 The problem of fit

The problem of fit asserts that the effectiveness of governance institutions depends on their spatial, temporal, and functional alignment with the social and ecological systems that they seek to govern (Folke *et al.* 2007). Throughout this thesis I will focus on spatial alignment, and thus 'fit' and 'scale' should henceforth be considered synonymous with 'spatial fit' and 'spatial scale', respectively. The current trend towards co-management of small-scale fisheries at more localised spatial scales has been largely focussed on addressing social problems of fit. Existing socially, culturally, and often legally appropriate governance institutions operate at extremely restricted spatial scales (Govan *et al.* 2006, 2009). Individual fishing grounds are also often spatially restricted, as small-scale fishers generally operate small, unpowered or low-powered vessels. Long-standing customary tenure systems in many places restrict access to resources according to clan or kin groups, further limiting the spatial mobility of fishers. This combination of factors strongly restricts the socially appropriate scale of governance. Throughout the Pacific, this can be seen through the proliferation of small Locally-Managed Marine Areas (LMMAs), which individually cover on average just 22 km^2 (Govan *et al.* 2009). Like larger contemporary Marine Protected Areas (MPAs), various activities may be restricted within LMMA borders, or within a subset of the area. No-take areas, where all forms of extractive activities are prohibited, often make up a small portion of LMMAs – covering less than 1 km^2 on average across the Pacific (Govan *et al.* 2009).

Although the social suitability of community-based management is rarely disputed, substantial debate has arisen over whether fisheries and conservation outcomes can be achieved using such spatially-restricted management areas (Foale and Manele 2004). This fits onto the broader debate about the appropriate size and placement of MPAs. Some scientists argue that to conserve larger, more mobile species and to ensure sustainable levels of larval self-recruitment MPAs need to be large. Precise recommendations vary, but are often in the order of hundreds of square kilometres (Man *et al.* 1995; Walters 2000; Beattie *et al.* 2002). A recent global meta-analysis asserted that small (<100km^2), non-isolated MPAs had to be no-take, well enforced, and 10 years old before they were distinguishable from openly fished sites (Edgar *et al.* 2014). However, earlier meta-analyses had found that the density and biomass of target fish increased within MPAs regardless of size (Côté *et al.* 2001; Halpern 2003). Furthermore, numerous case studies have demonstrated the fisheries and conservation benefits of small MPAs (Alcala *et al.* 2005; Hamilton *et al.* 2011; Harrison *et al.* 2012). This has led to calls for networks of small MPAs, particularly where larger MPAs are socially and politically unfeasible (Roberts *et al.* 2003; Aswani and Hamilton 2004). The effectiveness of such small MPAs depends on the movement patterns of target species. Individual MPAs should ideally be large enough to retain and protect target species within their boundaries. Networks of MPAs should be configured to maximise their larval connectivity, to ensure their mutual replenishment. Information on home ranges, ontogenetic shifts in habitat use, seasonal migrations and larval dispersal are thus vital to inform appropriate size, placement, and spacing of MPA networks (Sale *et al.* 2005; Weeks *et al.* 2016). However, this information is not currently available for many important fishery-targeted species (Green *et al.* 2014).

1.4 Problem statement

The potentially dire consequences of mismatches of scale in the governance of key social and ecological processes that sustain small-scale fisheries are well-established. Despite this, the spatial patterns of habitat use for many relatively mobile, important fishery-targeted coral reef fish species throughout their life cycles are unknown, particularly in the context of the spatial patterns of exploitation and governance of their associated fisheries.

1.5 Study objectives and thesis structure

The broad objective of this thesis is to further understanding of potential problems of fit associated with the governance of small-scale artisanal fisheries. I do this by addressing the primary research question:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

I address this question by applying the diagnostic framework described above (Figure 1.1) to the case study of the small-scale artisanal grouper fishery at western Dyual Island, New Ireland Province, Papua New Guinea. I investigate this fishery through two model target species, *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus.* These two species of grouper represent ideal models for this work for a number of reasons which will be discussed in detail throughout this thesis. First, they are primary targets of fisheries – from small-scale subsistence fishers through the large-scale industrialised Live Reef Food Fish Trade (Sadovy de Mitcheson *et al.* 2012). Second, they are intrinsically vulnerable both demographically, and behaviourally. Third, little is known about their habitat requirements throughout their post-settlement life histories, or the ideal spatial scales at which to apply their management.

Throughout this work I apply a range of research tools and techniques from both social and ecological sciences. Using these, I develop an empirical understanding of the spatial aspects of key social (*i.e.,* governance, access rights, and resource use) and ecological (*i.e.,* ontogenetic habitat shift, and spawning migrations) processes that underpin the study social-ecological system (Table 1.1). Finally, I investigate the spatial interplay between these key processes to empirically address the primary research question.

Table 1.1 – Summary of key research questions covered throughout this thesis, the methods applied, the target species investigated (where applicable), and the sections which address them.

Socio-ecological process		Key research Question(s)	Method / Approach	*Epinephelus polyphekadion*	*Epinephelus fuscoguttatus*	Thesis sections
A. Governance	i.	What are the spatial scales (*i.e.,* jurisdictions) of governance institutions relevant to the community-based fisheries management on western Dyual?	Social surveys /mapping	N/A	N/A	Chapter 2
B. Resource use	i.	What are the spatial patterns of human settlement, clan affiliation, access rights, and fishing effort across western Dyual?	Social & creel surveys /mapping	N/A	N/A	Chapter 2
C. Ontogenetic shift	i.	What are the key age-based demographic characteristics and age- and size-at-maturity for the study species?	Demographic & reproductive biology / Habitat suitability mapping	Yes	Yes	Chapter 3
	ii.	How is suitable habitat distributed throughout the study region for the study species throughout their post-settlement life histories?				Chapter 4
D. Spawning migration	i.	What are the temporal patterns of spawning migration within and between spawning events?	Acoustic telemetry	-	Yes	Chapter 5
	ii.	What are the patterns of movement for reproductively mature individuals during spawning and non-spawning periods?				
	iii.	Do these patterns of movement allow for protection of the stock throughout non-spawning periods?				
E. Social-ecological interaction	i.	Do the spatial distributions of social processes lead to problems of fit with community-based governance institutions?	Spatial analyses	Yes	Yes	Chapter 6
	ii.	Do interactions between fishing effort and suitable habitat for target species lead to problems of fit with community-based governance institutions?				
	iii.	Do stocks of relatively mobile coral reef fishes deliver a sufficient spatial fit for their governance using community-based institutions?				
F. Socio-economic, & political setting	i.	What are the local social, economic, and political characteristics of western Dyual Island that likely affect fisheries sustainability and management?	Social surveys	N/A	N/A	Appendix I
G. Catchability	ii.	What factors affect the catchability by fishers of grouper from the FSA site?	CPUE / UVC	Yes	Yes	Appendix II

1.5.1 Chapter 2 – Spatial scales of governance, and distribution of fishing effort within a small-scale artisanal fishery

This chapter provides detailed empirical information about the key social processes to be considered within this thesis. Here, I use a combination of participatory mapping, and household, key informant, and creels surveys to answer the following research questions:

1. What are the spatial scales (*i.e.,* jurisdictions) of the governance institutions most relevant to the local fishery of western Dyual (the most localised level of state-based government, and the customary tenure system)?
2. How are patterns of human settlement, clan affiliation, access rights, and fishing effort spatially distributed throughout the study region?

The spatial scales of governance institutions and the spatial distribution of social aspects examined within this chapter will provide critical information for the final chapter of this thesis, in the context of examining potential problems and opportunities for the community-based management of small-scale, near-shore fisheries.

1.5.2 Chapter 3 - Age-based demographics and reproductive biology of two co-aggregating epinephelids

Many epinephelids have life history characteristics which make them intrinsically vulnerable to overfishing; they are often long-lived, slow growing, and late to sexual maturity (Craig *et al.* 2011). Understanding such life history characteristics is vitally important to the management of fishery-targeted species (Jennings *et al.* 1999; Choat and Robertson 2002). This chapter begins the examination of the two model species investigated throughout this thesis, with their detailed demographic and reproductive analysis. Specifically, this chapter sought to answer the following research questions:

1. What are the key demographic parameters of *Epinephelus polyphekadion* (camouflage grouper) and *Epinephelus fuscoguttatus* (brown-marbled grouper) including; sex-specific growth rates, longevity, and size and age at sexual maturity?
2. What are the functional sexual patterns of *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus*?

This chapter advances the fundamental biological understanding of these species. Furthermore, this detailed demographic and reproductive work provides ages and sizes at key life history stages. These will be used to partition individuals into biologically meaningful cohorts, to examine ontogenetic shift in habitat suitability in the subsequent chapter of this thesis.

1.5.3 Chapter 4 - Ontogenetic shift in suitable habitat for two large epinephelids

The habitat requirements of individual species often differ across life history stages (Lindeman *et al.* 2000; Wilson *et al.* 2010). Although the protection of juvenile habitat is a key management priority for coral reef fishes, they remain largely unknown for many species. In this chapter I use habitat suitability modelling techniques to assess the ontogenetic shift in habitat use for the two model species. Specifically, this chapter sought to answer the following research question:

1. How is suitable habitat distributed throughout the study region for *E. polyphekadion* and *E. fuscoguttatus* throughout their post-settlement life histories?

This chapter presents the first ever empirical analyses of ontogenetic shifts in habitat requirements for these species. Furthermore, the spatial distributions of suitable habitat across post-settlement life history stages examined within this chapter will be investigated in detail in the final chapter of this thesis, in the context of examining potential problems and opportunities for the community-based management of small-scale, near-shore fisheries.

1.5.4 Chapter 5- Spatial and temporal dynamics of the large epinephelid, *Epinephelus fuscoguttatus*, associated with a transient fish spawning aggregation

Many species of coral reef fish, including high-value species of grouper, form spawning aggregations – where tens to thousands of individuals gather to reproduce (Domeier and Colin 1997). These aggregations are particularly attractive to fishers due to the relatively high densities of target species and their temporal and spatial predictability (Sadovy and Domeier 2005a). Consequently, spawning aggregations are extremely vulnerable to overfishing; a recent meta-analysis found that 79% of worldwide, and 44% of Indo-Pacific coral reef fish spawning aggregations studied were in decline or extirpated (Sadovy de Mitcheson *et al.* 2008). Despite these alarming rates of decline, few spawning aggregations are under effective, scientifically sound management – in part due to a lack of detailed information on the reproductive movement patterns of target species (Sadovy de Mitcheson *et al.* 2008). This chapter focusses on a population of *E. fuscoguttatus* that spawn at a transient aggregation site within the study region, employing acoustic telemetry to answer the following research questions:

1. How much protection does the current no-take LMMA provide to the E. *fuscoguttatus* that have aggregated to spawn?
2. What is the spatial distribution of the *E. fuscoguttatus* population outside of spawning periods?
3. How do local stakeholders perceive the spatial expansion of the current no-take LMMA to include non-spawning areas, relative to other management options?

This chapter provides the most comprehensive information to date on the reproductive movements of this key fishery species. In addition to detailed sex-specific information on visitation to the spawning aggregation site, in this chapter I fit reproductive movement distances with a migration kernel. This kernel provides an estimation of patterns of migration across the reproductive population and facilitates, for the first time, the empirical assessment of where the spawning population resides outside of spawning periods. This in turn facilitates the optimisation of management actions, and represents a major step forward in managing species that aggregate to spawn. Furthermore, the catchment areas (*i.e.,* the areas encompassing different proportions of the spawning population throughout the non-spawning season) calculated within this chapter constitute key ecological scales relevant to their management. These catchment areas will be investigated in the final chapter of this thesis, along with other key social and ecological processes, in the context of examining potential problems of fit for the community-based management of small-scale, near-shore fisheries.

1.5.5 Chapter 6– Comparison of the spatial scales of localised governance institutions and key social-ecological processes relating to small-scale artisanal fisheries

The importance of matching the spatial scales of governance to the scales of key social and ecological processes to be governed is well established (Ostrom 1990). However, for many important fishery-targeted species of coral reef fish these spatial scales have never been directly compared. In this chapter, I return to the primary research focus of this thesis:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

Specifically, through synthesising analyses of the key social and ecological processes considered throughout the previous chapters, I address the following three research questions:

1. Do the spatial distributions of social processes (*i.e.,* settlement, access rights, and fishing effort) lead to problems of fit with community-based governance institutions?
2. Do interactions between the spatial distributions of fishing effort and suitable habitat for target species lead to problems of fit with community-based governance institutions?
3. Do the spatial extents of relatively reproductively isolated adult populations deliver a sufficient spatial fit for the governance of stocks of relatively mobile coral reef fishes using community-based institutions?

This chapter provides compelling evidence that relatively mobile coral reef fishes can be managed at scales that are congruous with community-based management. However, key social processes provided a better spatial fit with the most localised state-based governance institution, whereas key ecological processes provided a better spatial fit with the customary governance institution. Problems of fit would thus arise if either institution exclusively enacted fisheries governance. These results highlight the need to study and manage small-scale fisheries as social-ecological systems, and the need for nested governance institutions, even at extremely restricted spatial scales.

1.5.6 Appendix I – Social, economic, political, and ecological setting of the western Dyual artisanal fishery

This appendix presents and discusses the additional results of key informant, household and creel survey that are not directly relevant to spatial scales of management, but nonetheless affect the management of the western Dyual artisanal fishery.

1.5.7 Appendix II - Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site

This appendix presents the work led by Dr Jan Robinson, investigating how fish and fisher behaviour affects the catchability of *E. polyphekadion* and *E. fuscoguttatus* during aggregation fishing. Data were collected for this work, by Dr Robinson, Tapas Potuku and I at western Dyual during fishing for the tagging study discussed in Chapter 5.

1.5.8 Larval dispersal, and other caveats

Larval replenishment is vitally important for the persistence of populations over generational time-scales (Mora and Sale 2002). Understanding distances of larval dispersal is thus crucial in determining the relative viability of different fisheries management options. Recent advances in genetic techniques now allow the direct empirical analysis of larval dispersal distances

(Jones *et al.* 1999, 2005; Planes *et al.* 2009). These techniques have recently been employed to determine the level of connectivity between MPAs (Harrison *et al.* 2012), and the creation of the first empirically-derived larval dispersal kernel for a fishery-targeted species (Almany *et al.* 2013). I had originally intended to develop similar dispersal kernels for the two species studied here. However, the logistical and political challenges of working in Melanesia intervened. A violent dispute surrounding land tenure necessitated my departure from western Dyual, and stopped access to my field site for approximately 12 months, disrupting this component of the research project. Nevertheless, at the time of writing, sufficient samples have been collected and larval dispersal work is scheduled to continue.

CHAPTER 2 – SPATIAL SCALES OF GOVERNANCE, AND DISTRIBUTION OF FISHING EFFORT WITHIN A SMALL-SCALE ARTISANAL FISHERY

2.1 Synopsis

The vast majority of global coral reef fisheries are small-scale and artisanal in nature, with relatively large numbers of small, unpowered or low-powered vessels making short trips to nearby fishing grounds. Increasingly, community-based systems of governance are being employed to manage these fisheries. Localised governance can address many of the social issues that have previously impeded small-scale fisheries management by centralised governments. Legitimate concerns have been expressed though, that such spatially restricted governance may be mismatched to key ecological processes underpinning the persistence of exploited species. However, scales of governance and resource use are often poorly understood at the fine resolution that they operate. In this chapter, I employ participatory mapping, and household, key informant, and creel surveys to examine the spatial scales of: (1) the governance institutions most relevant to the local fishery of western Dyual, Papua New Guinea (the most localised level of state-based government, and the customary tenure system), and (2) the spatial distribution of fishing effort and access rights throughout the study region. I demonstrate that even light artisanal fishing effort can lead to hotspots of fishing markedly above hypothesised sustainable levels. The scales of governance and ownership here were relatively spatially restricted (7-45 km^2). However, although all fishers had access rights across the entire 43 km^2 study area, the low spatial mobility of fishers meant that half of modelled fishing effort here was concentrated within just 4 km^2. This result demonstrates that the spatial distribution of fishing effort can vary markedly at very fine spatial scales. Due to the growing trend of managing small-scale fisheries at more restricted scales, the spatial scales of governance are increasingly the focus of scientific enquiry. However, this study suggests that the spatial distribution of fishing may in fact be more spatially limiting for low-developed, low-technology artisanal fisheries. In the final chapter of this thesis, the spatial scales of governance institutions and the spatial distribution of fishing effort examined within this chapter will be empirically compared to the spatial scales of key ecological processes (ontogenetic shift and reproductive migrations) to examine challenges and opportunities for the community-based management of small-scale, near-shore fisheries.

2.2 Introduction

A multitude of social and ecological factors contribute to the health and resilience of coral reef systems. Although the overwhelming effects of climate change are emerging as the primary global concern (Gardner *et al.* 2003; Hughes *et al.* 2003), the effects of overfishing remain a primary proximal driver of coral reef degradation globally (Hughes *et al.* 2010). Recently, research into the causes of overfishing have diversified from an almost singular focus on increased human population density (Jennings *et al.* 1995; Jennings and Polunin 1996, 1997; Bellwood *et al.* 2004; Newton *et al.* 2007; Mora 2008), to a more nuanced understanding of a number of interconnected social, economic, and political drivers affecting the magnitude and distribution of fishing effort (Birkeland 2004; Cinner and Kittinger 2015). Access to markets, levels of socio-economic development, access to technology, social characteristics of stakeholders, and characteristics of governance have all been demonstrated to significantly affect long-term fisheries sustainability (Ostrom 1990; Hamilton and Matawai 2006; Cinner *et al.* 2009b, 2016; Brewer *et al.* 2012).

Most coral reef fisheries operate in developing or least-developed nations, with very few resources available for their monitoring and management (Bellwood *et al.* 2004). The challenges of managing dispersed and diverse small-scale artisanal fisheries using their existing, centralised, state-based governance infrastructures are arguably systemic and insurmountable (Govan *et al.* 2009). Target species, fishing methods, available technologies, and socio-economic conditions vary at relatively small scales, such that artisanal fisheries often vary significantly at a community level. Laws enacted at the provincial or national level are thus likely to poorly reflect local conditions (Cinner 2007). Alternative (or complementary) systems of community-based coral reef fisheries governance have recently received a great deal of attention. Co-management approaches – where local communities manage their local resources in partnership with external government, non-government and civil organisations – are now commonly applied to manage small-scale fisheries (Evans *et al.* 2011). This move toward more localised governance has been largely driven by social, economic, and political necessity following the failure of conventional ‘command and control’ management programs (Johannes 2002; Rosenberg *et al.* 2006). Existing customary management systems, particularly where they are robust, are often used as frameworks for such co-management arrangements (Cinner and Aswani 2007; Govan *et al.* 2009). However, these customary management systems generally operate over spatial scales of just a few square kilometres (McClanahan *et al.* 2006). There is legitimate concern that governance at this scale will substantially mismatch with key ecological processes that require management, such as ontogenetic shifts and spawning migrations of target species (Foale and Manele 2004; Mills *et al.* 2010).

Although the vast majority of literature focusses on the magnitude of fishing pressure, the spatial distribution of pressure can also substantially affect fisheries sustainability (Booth 2000; Daw 2008; Ouréns *et al.* 2015). There is increasing interest in understanding spatial behaviour of fishers (Van Putten *et al.* 2012), particularly with the increased application of spatial tools to fisheries management (Lynch 2006). Spatial distribution of fishing effort can be considered as a function of fisher behaviour, as individual fishers seek to optimise the ratio of benefits to costs during resource exploitation (Aswani 1998). Costs presumably increase with increasing distance from home landing sites – through increased risk, travel time, and energy expenditure. Under conditions of relatively homogeneous distribution of benefits (*i.e.,* catch per unit effort [CPUE] of target species), this 'friction of distance' causes fishing pressure to be highest closest to human settlements and landing sites (Lloyd and Dicken 1977; Isard and Liossatos 1979). However, CPUE is linked to the density of target species, and fishing grounds often incorporate a mosaic of habitats, with varying carrying capacities (Caddy 2014). Moreover, current target densities are a function of both these natural carrying capacities and the legacy of past exploitation. Where fishing pressure is unsustainable for prolonged periods, areas proximal to settlements may become serially depleted of site-attached target species, driving fishers to exploit fishing grounds at increasing distances from landing sites (Caddy and Carocci 1999; Huitric 2005; Berkes *et al.* 2006; Cardinale *et al.* 2011). As such the spatial distribution of fishing effort can give a snapshot of current resource use, but also insights into past fishing practices, and future management challenges (Caddy and Carocci 1999).

In this chapter I discuss the results of key informant, household, and creel surveys conducted across western Dyual Island, New Ireland Province, Papua New Guinea in 2014 (Figure 2.1), with the specific aim of answering two research questions;

1) What are the spatial scales (*i.e.,* jurisdictions) of the governance institutions most relevant to the local fishery of western Dyual (the most localised level of state-based government, and the customary tenure system)?
2) How are fishing effort and access rights spatially distributed throughout the study region, and what does this reveal about fishing practices?

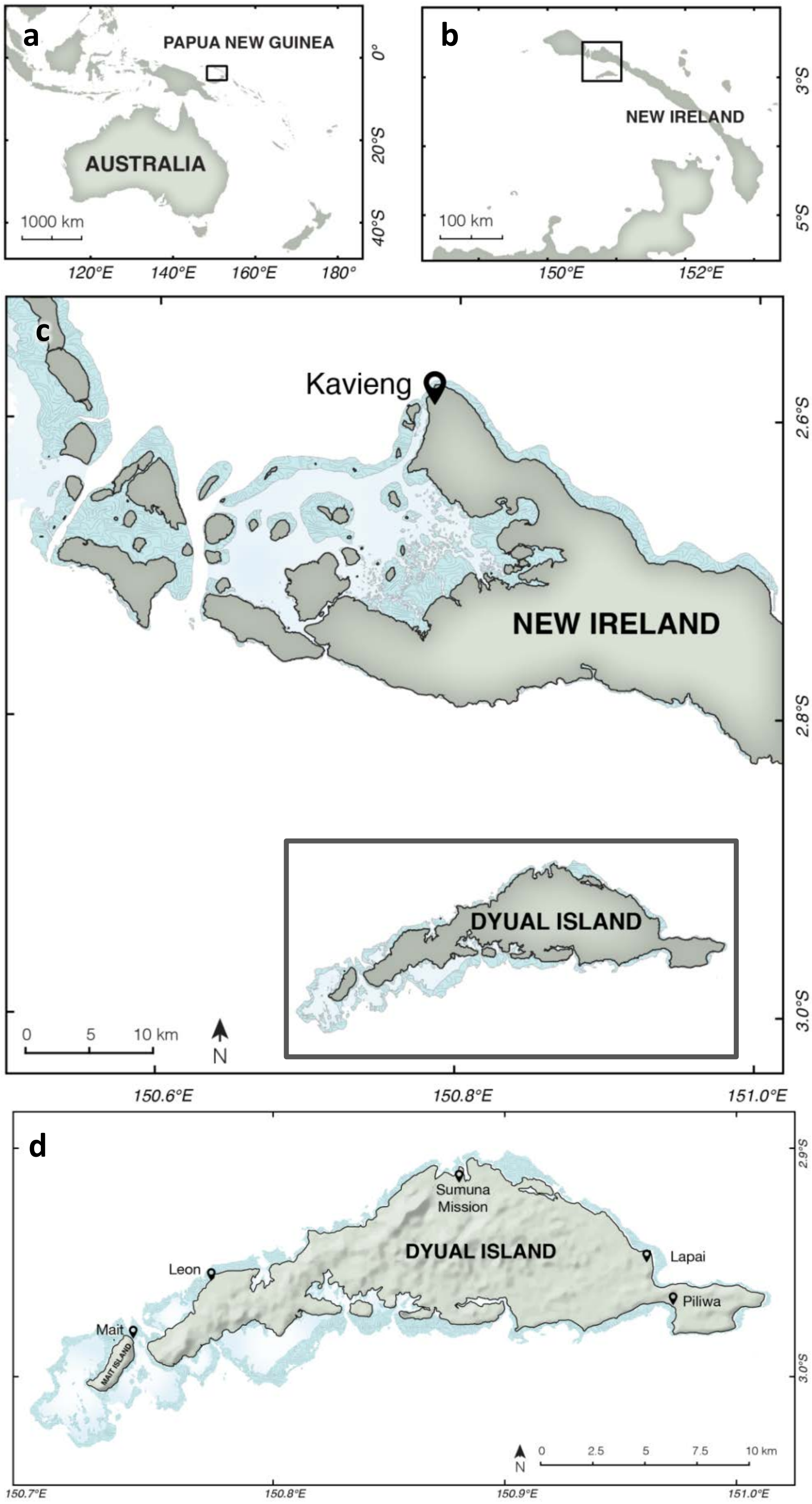

Figure 2.1 - Maps depicting (with increasing map scale, and subsequent maps highlighted in grey rectangles): (a) Oceania, (b) New Ireland Province of Papua New Guinea, (c) Dyual Island relative to the New Ireland Province main island and provincial capital, Kavieng, and (d) Dyual Island. Reef features (textured blue-green), other shallow nearshore habitat (light shaded blue), and major settlements (📍 symbols) are represented.

2.3 Methodology

2.3.1 Study Site

The socio-economic characteristics of the population of western Dyual are relatively typical of rural Papua New Guinea (for more detailed information see Appendix I). Population density is low, with settlements comprised of a few to a few tens of households. Most of the island is covered with thick vegetation and with the exception of foot traffic, all transport is by sea. The majority of the population lives in dwellings made from locally-sourced materials, own paddle-powered dugout canoes for transport, and own few modern possessions. A few more affluent households own motorised vessels (fibreglass boats with outboard motors), live in dwellings constructed of imported materials, and possess items such as generators and televisions.”

Before conducting the surveys detailed below, I resided at the study site for approximately six months, during 2012 and 2013. During this time I lived within a number of households across all surveyed settlements, held discussions at weekly community meetings, shared many informal discussions with local community-members, and participated in resource gathering trips. These activities served numerous purposes, including gaining a deeper understanding of the study system, building relationships and trust across a broad base within the local communities, learning the *lingua franca* Tok Pisin, accessing local ecological knowledge, and addressing issues of positionality (discussed in further detail in section 2.5.5).

Socioeconomic surveys were conducted between 23/02/2014 and 20/03/2014, within settlements situated on the western half of Dyual Island, New Ireland Province, Papua New Guinea and neighbouring Mait Island (Figure 2.2). Surveys were conducted by the author, and the local representative of ‘The Nature Conservancy’, Tapas Potuku. Since 2005, Potuku has represented The Nature Conservancy in a fisheries co-management partnership with the inhabitants of western Dyual. Additional information regarding the local social, economic, and political setting of western Dyual was collected during these surveys, with particular emphasis on factors known to affect small-scale fisheries sustainability and is presented in Appendix I.

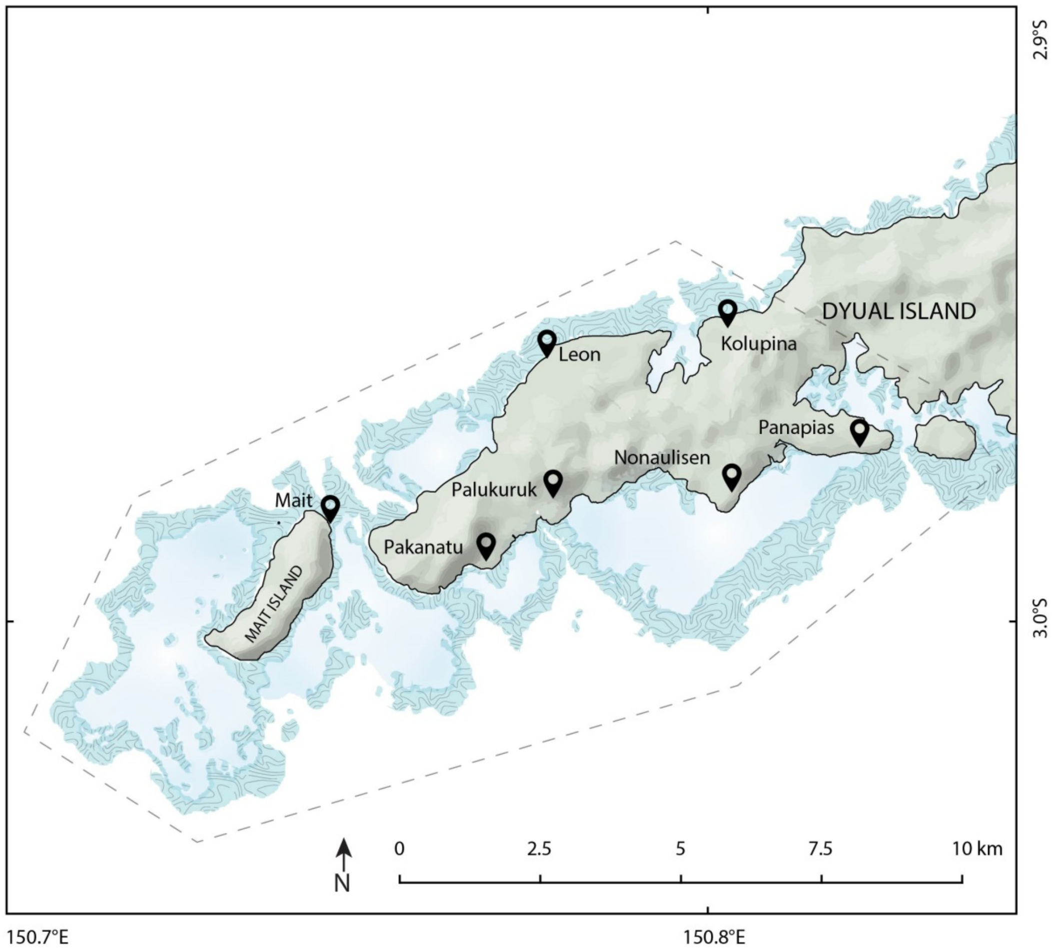

Figure 2.2 - Map of western Dyual including settlements (named and represented by 📍 symbols), reef features (textured blue-green) and other shallow nearshore habitat (light shaded blue). The extent of this map represents the approximate jurisdiction of the Leon Village Planning Committee (VPC). Dashed grey lines delineate the extent of available high-resolution satellite imagery, and the extent of all spatial analyses conducted throughout this thesis (henceforth referred to as the 'study region').

2.3.2 Reference map creation

Laminated, A3 copies of high-resolution Quickbird images of Western Dyual were presented during six key informant interviews with community leaders and locally-renowned fishers, between 23/02/2014 and 20/03/2014. Informants were asked to delineate all known locally-named inter-tidal or sub-tidal areas (henceforth referred to as 'shallow habitat') – using a permanent marker pen on transparent plastic sheets covering the maps. This information was aggregated onto a single map, containing 104 distinct locally-named areas of shallow habitat (henceforth referred to as the 'named reference map', Appendix III). Individual locally-named areas (henceforth referred to as 'named fishing grounds') encompassed a mean 0.12 (± 0.01 SE) km^2. There was no discrepancy between areas named by key informants, although names often had numerous phonetically-similar variants. The named reference map was then separately presented during two further interviews with a fisher and a clan chief deemed by Tapas Potuku to be the most knowledgeable. Both reported that the named fishing grounds delineated on the map were accurate.

The ability of local fishers to accurately identify areas using the named reference map was tested by recording the location during unrelated resource use activities using a handheld GPS unit on 24 occasions, in April-June, 2013. When later presented with the named reference map fishers present during these resource use activities were able to accurately pinpoint the area on all but one occasion, and on all occasions following discussion with other fishers in the vessel.

All spatial analyses were carried out in ArcGIS (ESRI 2014). A georeferenced, high-resolution Quickbird image of Western Dyual was utilised as a basemap. This area was partitioned into planning units (*i.e.,* grid squares) by superimposing a 20*20 m square grid over this image, and clipping this grid to the nearshore habitat features (as described in section 4.3.3). Spatial datasets (named fishing grounds, tenure boundaries, core fishing areas, and management areas) were individually mapped as polygon layers. Each planning unit was then assigned values corresponding to its proportion of intersection with each polygon (*i.e.,* each planning unit received a value of 0-1 for each household's core fishing area, customary tenure area, etc.).

2.3.3 Key informant surveys

Semi-structured key informant surveys were conducted with the clan chiefs, elected village officials, seafood buyers and key resource users that participated in the mapping exercise, as well as the local representative of 'The Nature Conservancy', Tapas Potuku, between 23/02/2014 and 20/03/2014. Initial informants were suggested by Tapas Potuku, based on knowledge gained during over ten years working with the local communities. Further informants were selected using a snowball sampling design, where after each survey was completed, informants were asked to recommend additional informants considered to be particularly knowledgeable about local resource use and management. Additional informants were selected during informal discussions with community members during the study period. Informants were also asked to participate in a mapping exercise. Informants were presented with a copy of the named reference map, and asked to delineate any areas where fishing was prohibited or restricted (hereby referred to as 'management areas'). For each identified management area, informants were asked to provide information on the following: the operational rules in place; the age of the management initiative; the parties involved in managing the area; any ongoing monitoring of resources, users, and overseers of the management area; and any systems in place to address infringement of management rules. Where the management area at the spawning aggregation Site A was identified (Figure 2.3), respondents were also asked to estimate the proportion of resource users aware of the management. Informants identified as being involved in the organisation of management areas were also asked how often they had contact with the following groups: community leaders; donors; financial institutions; non-government and scientific organisations; and local, district and government officials. Informants were then asked to delineate tenure boundaries onto the satellite images, and asked to identify the tenure holders, and any groups of resource users who were excluded from exploiting resources within the boundaries (Figure 2.3). Finally, informants were asked to highlight any areas of disputed tenure.

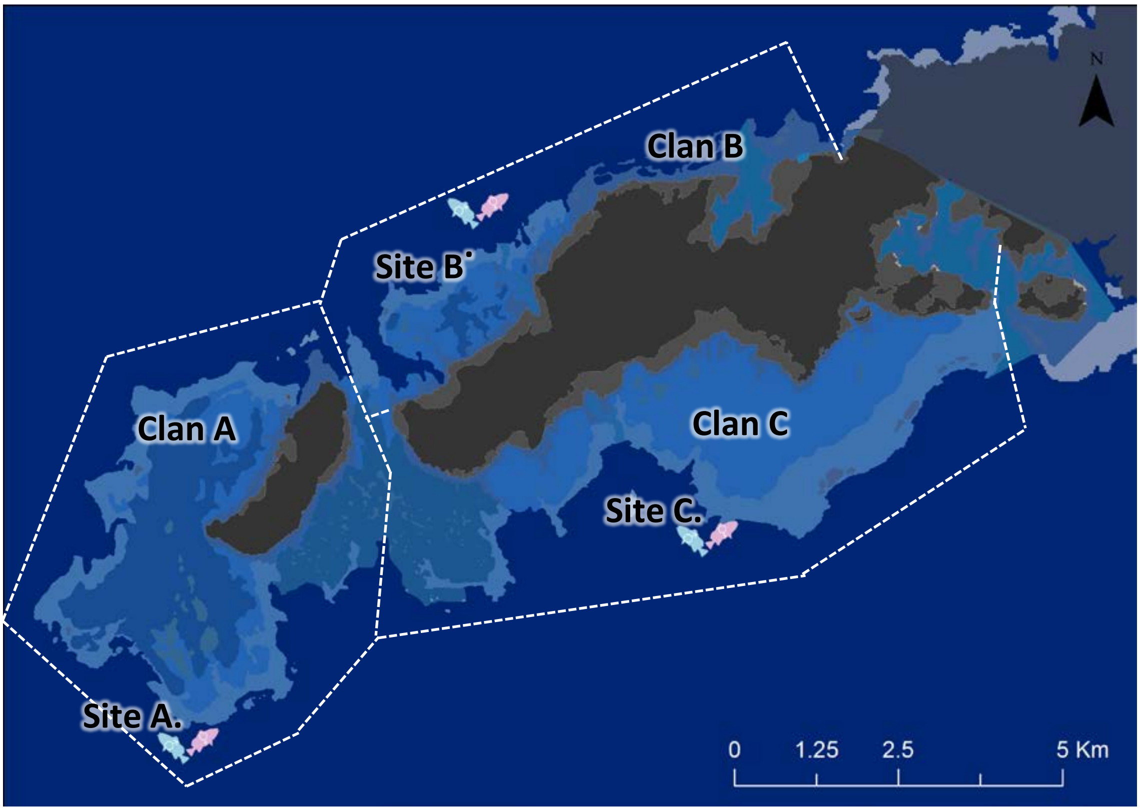

Figure 2.3 – Map depicting customary marine tenure areas for western Dyual Island; white dashed lines depict approximate tenure boundaries. Note that tenure lines are only conceptual boundaries and not definitive. Approximate locations of the reported *tambu* areas protecting grouper spawning aggregation sites, are represented by fish symbols (🐟🐟) with points: Sites A, B, and C. Locations depicted have been moved to protect actual locations, although this precaution is likely unnecessary, as locations are well known by local resource users, and robust customary tenure excludes outsiders.

2.3.4 Household surveys

A total of 32 household surveys were conducted at Leon village (15 surveys), the primary settlement in the study area, as well as the smaller settlements of Mait (4), Nonaulisen (2), Kolupina (2), Panapias (2), Yau (1), and Palukuruk (1), and at individual households situated in the bushland in the interior of the island (5) (Figure 2.2). Households, defined as groups living and eating together, were selected for surveying systematically – household members were approached in every third household, and an interview was requested with either the male or female head of the household. Where the heads of the household were unavailable, the household was skipped, and returned to at a later date. Where the heads of the household were still unavailable, the next unsurveyed household was selected in its place. The five surveys conducted at individual households situated in the bushland in the interior of the island were surveyed opportunistically, where houses were visible and only a short walk from the coastline, or when heads of the households were available for interview within settlements. It is likely that such households were underrepresented in the sampling design, however information from key informants suggested that members of households situated relatively large distances from the coastline utilised marine resources only sporadically, and as such were not major targets of this study.

Household surveys took the form of semi-structured interviews, adapted from Cinner *et al.* (2012c). Respondents were asked to list all livelihoods (activities which provided the household with income or food) in order of importance, and how many household members participated in each livelihood. Where some form of marine resource exploitation was listed (e.g. fishing, gleaning, marketing marine products), respondents were asked to list all gear types used by members of the household in order of importance. For each gear type, the respondent was then asked how many resource use trips were conducted in a high-use, and low-use month, how many household members used the gear, and whether the gear was owned by a household member or borrowed from another member of the community. Respondents were then asked to estimate the total number of fishing trips conducted by all members of the household in an average month.

Respondents were also asked to estimate the number of fish they caught, how long they spent fishing, and the approximate value of their catch (in Papua New Guinean Kina, at the closest available market), during a poor day, an average day, and a good day of fishing. Respondents were asked to estimate what proportion of their catch was eaten by members of the household, what proportion was sold, and what proportion was traded or given away.

Finally, respondents were asked to participate in a mapping exercise, to delineate all areas where members of their household fished, and any areas known to them where fishing was prohibited or restricted. Respondents were presented with a copy of the named reference map, and requested to delineate areas where members of their household participated in fishing activities at least once during an average month (henceforth referred to as their 'core fishing area'). Additionally, respondents were asked to delineate any management areas known to them, and to describe the details of management following the questions from key informant surveys.

2.3.5 Creel surveys

Fishing data were collected through creel surveys using methodology adapted from Cinner & McClanahan (2006). Surveys were conducted by two students from the Papua New Guinea University of Natural Resources and Environment, Max Teliwa and Patson John, who were supervised by Tapas Potuka and I. Of the 63 creel surveys conducted during March 2014, 47 were conducted on the foreshore of the Mait settlement, and 16 were conducted at the foreshore of the Leon settlement. The large proportion of landings surveyed at Mait was due to logistic considerations and the presence of a buyer at Mait during part of the survey period. All key informants described the effort and catch as fairly average during the survey period. Fishers were approached on the completion of a resource use trip and asked if their catch could be examined. Catches were then identified (to species level where possible), and length (to 1 mm), weight (to 0.1 g) and gear type utilised were recorded. The location of catches was ascertained from fishers to the scale of named fishing grounds (discussed in 2.3.1 above). Where a single resource use trip was conducted across multiple areas an equal proportion of the catch and effort were attributed to each area.

2.3.6 Data analysis

Households surveyed were selected from a finite population without replacement and the sample size n was not small compared with the total population size N (*i.e.,* greater than 5% of the population was sampled). Standard errors of means calculated for household survey responses were therefore corrected with a finite population correction factor *(fpc)* to adjust the error based on the proportion of the population sampled, expressed as;

$$fpc = \sqrt{\frac{N - n}{N - 1}}$$

Therefore, standard errors of means were calculated as,

$$\sigma_{\bar{x}} = \frac{\sigma}{\sqrt{n}}\sqrt{\frac{N-n}{N-1}}$$

And standard errors of proportions were calculated as,

$$\sigma_{p_s} = \sqrt{\frac{p(1-p)}{n}}\sqrt{\frac{N-n}{N-1}}$$

Distance to fishing sites

Euclidean distances between site of fishing (centre-point of the relevant named fishing ground) and landing site were calculated for each fishing trip using ArcGIS (henceforth termed 'fishing distance') (ESRI 2014). Candidate functions were then fitted to the fishing distance dataset (n = 58) to examine how fishing effort was related to distance from landing sites (*i.e.,* human settlements). I proposed four candidate functions to explain these data; the (1) Weibull, (2) gamma, (3) Gaussian, and (4) exponential. Parameter sets for each distribution were estimated by maximising the likelihood function:

$$L(\theta) = \prod_{i=1}^{n} f(d_i|\theta)$$

where d_i are the *n* observations of distance between fishing and landing sites and θ represents the parameter set of the function. An AIC weighting analysis was performed on the resulting maximum likelihood functions. The exponential decay function (with rate [λ] = 0.44; henceforth referred to as the 'fishing distance function') provided the best fit with an Akaike weight of 0.51, compared with the gamma (with shape [α] = 0.87, and rate [β] = 0.38), Weibull (with shape [k] = 0.96, and scale [λ] = 2.24), and Gaussian (with mean [μ] = 2.28, and standard deviation [σ] = 2.02) functions, with Akaike weights of 0.28, 0.20, and 0.00, respectively. A 95% confidence interval was then calculated for the maximum likelihood exponential function using non-parametric bootstrapping, with 1000 bootsamples (Figure 2.9).

Differences in fishing trip distances between catches destined for sale and consumption was examined using a Mann-Whitney test, with each fishing trip categorised based on whether the majority of fishes caught during the trip were destined for sale or consumption.

Distribution of fishing effort

The data for the core fishing area of each household were separately weighted as follows. Data for each planning unit were weighted for fishing density as estimated by the fishing distance function (Figure 2.9b), by applying the density weighting factor (dw);

$$dw = \ 0.44 * e^{-0.44\mathrm{d}}$$

where d is the Euclidean distance between the centre of the planning unit and the relevant landing site (*i.e.,* the foreshore closest to the relevant household). These density weighted data were further weighted by monthly fishing effort, by applying the effort weighting factor (Ew);

$$Ew = \frac{E}{T_f}$$

where E is the total number of fishing trips conducted by the relevant household in an average month (as estimated by the head of household), and T_f is the total value of density weighted data for that household, across all planning units. The combination of these two weighting factors effectively spreads the estimated fishing effort for each household across their core fishing ground, as predicted by the fishing distance function. Thus the sum of the unweighted data across all households – within each planning unit – provides an estimate of how many households fish there each month, whereas the sum of the corrected data across all households – within each planning unit – provides an estimate of absolute fishing effort within that planning unit (fisher*trips/month). Finally, this absolute fishing effort was multiplied by the inverse of fraction of coastal households surveyed (that is, the inverse of 32/102) to extrapolate the fishing effort to the unsurveyed households. Additionally, totals were multiplied by the mean catch weight across all creel trips, to provide an estimate of the total fishing yields within each planning unit (kg/month).

2.4 Results

2.4.1 Population and pattern of settlement

Dyual Island was sparsely populated, with people living in four major coastal villages, a number of smaller settlements (often based on clan or family groups), and on small subsistence farm plots throughout the island (Figure 2.1). The population of Dyual was split into two political units, and two language groups. The population living east of approximately 150.9° E longitude (hereafter referred to as 'eastern Dyual') was under the jurisdiction of Ward 18 of the Tikana Local Level Government (LLG), and the Lapai Village Planning Committee (VPC), and speak a locally endemic language – Tiang. The population living west of 150.9° E longitude, including Mait Island, were under the jurisdiction of Ward 17 of the Tikana LLG, and predominantly speak the Tigak language which is spoken throughout much of western New Ireland Province. Ward 17 was further divided under the jurisdictions of the Sumuna VPC and the Leon VPC (see 2.4.4 for more detail). The jurisdiction of the Leon VPC (Figure 2.2) is the focus of this study (hereafter referred to as 'western Dyual').

Total population estimates for western Dyual Island were not feasible to obtain, due to the size of the study area and its densely vegetated inland terrain. As such, only households visible and accessible from the coastline were counted and surveyed during this study. The study population here therefore represents the 'coastal population', rather than the total population of western Dyual. It is unlikely that the absence of households situated in the interior of the island significantly impacted this study however, as key informants advised that inland residents infrequently participate in marine resource exploitation.

A total of 102 households were recorded in coastal western Dyual (Figure 2.2). Almost half of these (46%) were situated within the settlement of Leon. Clusters of households, often representing family or clan groups, also formed a number of smaller settlements; Mait (12%), Nonaulisan (6%), Panapias (6%), Pakanatu (5%), Kolupina (4%), and Yau (3%). The remainder (20%) were scattered throughout bushland, less than one kilometre from the coast. Households surveyed comprised an average of 5.1 (± 0.3 SE) individuals; 2.2 (± 0.2) adults and 2.9 (± 0.2) children, resulting in an estimated coastal population of 520 individuals.

2.4.2 Livelihoods

Members of surveyed households participated in between two and seven livelihoods per household (4.5 ± 0.2; mean ± SE) (Figure 2.4). Fishing was the most commonly reported livelihood – undertaken in all but one (97%) household; followed by small-scale farming, and collecting cash crops, each undertaken in 94% of households. Gleaning and salaried employment were also undertaken in a majority of households (in 65% and 52%, respectively).

Figure 2.4 – Household members' participation in livelihoods, ranked by importance to household (darker coloured blue bars represent livelihoods of higher importance to the household).

Farming

Farming was conducted by members of 94% of households and was considered the primary livelihood for 32% of households (Figure 2.4). For households which reported farming as a livelihood, a mean 3.2 (± 0.3) members of the household participated. Households generally cultivated individual small ‘garden’ plots proximal to settlements. The main crops cultivated were varieties of banana, and root vegetables such as sweet potato, cassava and yam. Assorted vegetables such as beans, cucumbers, pumpkins, and assorted leafy greens (collectively referred to as ‘local greens’) are also cultivated. Pawpaw, pomelo, and ton were among the fruits commonly cultivated. Respondents reported that additional fertile land was available to them for farming, either within their existing tenure areas, or through negotiation with other tenure holders.

Cash crops

Cash crops were harvested by 94% of households, and considered the primary livelihood for 16% of households (Figure 2.4). Of those households which reported cash cropping as a livelihood, a mean 2.7 (± 0.3) members of the household participated. Historically the most important cash crop was coconuts, however recently increasing volatility of copra (*i.e.,* dried coconut) prices precipitated a shift to *buai* (the nut of the areca palm; *Areca catechu*) as the primary cash crop.

Gleaning

The mangroves, intertidal zone and reefs of western Dyual were gleaned by 64% of households; however no household reported gleaning as their primary livelihood (Figure 2.4). Among households which participated in gleaning, a mean 1.9 (± 0.3) households members participated. Households conducted a mean of 1.1 (± 0.3) gleaning trips during a low effort week and 3.6 (± 0.5) trips during a high effort week. When extrapolated to the estimated total coastal population, between 77 and 256 gleaning trips are conducted each week throughout western Dyual.

Gleaners typically collected a variety of shellfish, including mud crabs (*Scylla serrata)*, crayfish (*Panulirus* spp.*)*, trochus (*Trochus* spp.*)*, and giant clams (*Tridacna* spp.*)* for consumption and sale*.* Gleaners also collected a number of animals for fishing bait, including *kuma (Clibanarius* sp.*).* Respondents reported that sea cucumbers (*Holothuroidea* spp.) were the primary target of gleaning, for export as *béche-de-mer* to Asian markets, until a nationwide moratorium in 2009 which remained in place in 2016.

Salaried employment

The majority of respondents reported conducting salaried employment. Three respondents reported regular salaried employment; teaching at a primary school in Sumuna, performing contract work for environmental organisations throughout Papua New Guinea, and working for a business in Kavieng. The remaining respondents reported conducting salaried employment sporadically, performing manual labour as required by government and non-government organisations that conducted work at western Dyual, such as clearing land around a lighthouse on Mait Island. Respondents ranked this occasional work as 3rd, 4th, or 5th in livelihood importance and reported that it did not contribute substantially to their annual income.

2.4.3 Fishing

Fishing was conducted by 97% of households and was considered the primary livelihood for 42% of households (Figure 2.4). For households which reported fishing as a livelihood, a mean 2.4 (± 0.3) members of the household participated.

Gear usage

Of the 30 households which listed fishing as a livelihood an average of 2.6 (± 0.2) fishing methods were used per household (Figure 2.5). Bottom fishing using hook and line was the most commonly used fishing method, utilised in 93% of households, and ranked as the primary method for 47% of households (Figure 2.5). Spearguns were utilised in 63% of households, and ranked as the primary method for 30% of households. Other widely used methods included trolling, and hand spear, utilised in 53%, and 40% of households, respectively. Catches from creel surveys were obtained primary using hand lines (57%) and spearguns (40%), with trolling (2%) and other methods making up the remainder.

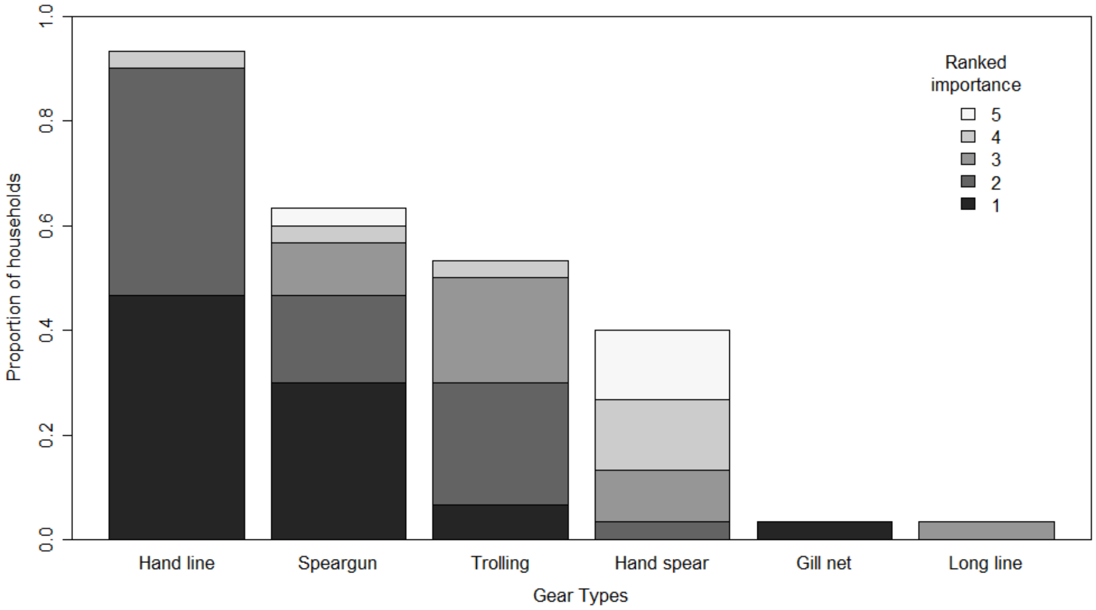

Figure 2.5 - Households' usage of different gear types for fishing, ranked by self-reported importance to the household (darker shaded bars represent gear types of higher importance to households).

Fishing effort

The number of fishing trips per week, as self-reported during household surveys, varied substantially among households. During low effort weeks (particularly during periods of poor weather), households estimated conducting up to 5 fishing trips, however 24% of households reported that they refrained from fishing entirely at such times (1.7 ± 0.3 trips * household^{-1} * week^{-1}). During average effort weeks households estimated conducting between 1 and 13 trips (5.0 ± 0.6).During high effort weeks households estimated conducting between 1 and 20 trips (8.3 ± 1.0).

Mean estimated catches per fisher on poor, average, and good trips were 5.2, 11.8, and 24.0 (± 0.8, 1.3, and 2.6) whole fish, with median estimated values of 5, 15, and 40 Papua New Guinean Kina (PGK), respectively (median values are presented as means were heavily skewed by high-value catches of a few individuals). Mean estimated efforts were 2.5, 2.9, and 4.0 (± 0.3, 0.3, and 0.5 SE) hours * trip^{-1}, respectively. Estimated catch size was positively correlated with estimated value (poor day R^2=0.655, average day R^2=0.61, good day R^2=0.48; all P<0.001).

No correlation was evident between catch size and effort, or catch value and effort (both $P > 0.1$). Mean catch per fisher per trip calculated from creel surveys was 13.3 (± 1.1) pieces, or 3.9 (± 0.6) kg. Mean fishing effort from creel surveys was 2.9 (± 0.2) hours * trip^{-1}.

Extrapolating across the 102 households within the study region an estimated 2.0 tonne (t) of fish is exploited from the region during the average week, or 103.3 t * yr^{-1}. Across the 43.3 km^{2} of shallow nearshore habitat within the study region, this equates to 2.4 t * km^{-2} * yr^{-1}.

Market integration

As self-reported during household surveys, fishers reported consuming smaller fishes, which were less desirable to buyers (mean 42% of catch, ± 6.0% SE). Approximately half (54%) of respondents also gave some smaller fishes to other community members, as unpaid assistance (mean 8% of catch, ± 0.2% SE). The remaining catch was sold (mean 50% of catch, ± 5.9% SE), either smoked or fresh within the community; or fresh to buyers, for transport on ice to Kavieng.

During the study period (2012-2015), four buyers were active in western Dyual. Key informants reported that individual buyers operated sporadically, however one buyer was generally active at any time, when weather permitted. Two residents of Leon, operating since February 2012, each conducted up to one trip per fortnight, carrying 240-420 kg of seafood per trip. As these two buyers did not own motorised vessels, they were required to purchase passage on privately owned vessels. Both reported that the venture was only occasionally profitable. Another resident of Leon began operations in January 2013, and conducted up to two trips per week, carrying 360-420 kg of seafood each trip. A non-resident of Dyual also began operations in January 2014, and conducted up to two trips per week, carrying 100-720 kg per trip. Additionally, a family group residing on Mait Island were awarded a federal grant, and purchased a fibreglass dingy and outboard motor in February 2014. This vessel operated on a cooperative basis, with fishers receiving a proportion of any profits. This vessel conducted up to one trip per week, carrying 260-480 kg of seafood. All buyers reported that the spoiling of catches was an ongoing concern, because ice was not available on Dyual Island.

Buyers purchased fish, directly from fishers, for 3-5 Papua New Guinean Kina (PGK) kg^{-1} (AUD1.40-2.30 kg^{-1}). Buyers then transported the fish on ice in fibreglass coolers, for sale in Kavieng. Several Kavieng-based buyers purchased reef fish for PGK5-7 kg^{-1}. These buyers did not pay premiums for more desirable species; however more desirable species could be sold directly to resorts in Kavieng harbour for higher prices.

Catch composition

With the exception of two green turtles *(Chelonia mydas)*, one mud crab *(Scylla serrata)*, and four crayfish *(Panulirus ornatus),* the surveyed catches consisted of ray-finned fishes. Of the 1003 fishes surveyed, 746 (74%) were identified to species level, with the remainder identified to family level. A total of 101 species were identified, across 21 families. Three-quarters of the surveyed catch (by weight) came from four families: Scaridae, Lethrinidae, Epinephelidae, and Lutjanidae (25%, 18%, 16%, and 15%, respectively). Acanthuridae, Holocentridae, Balistidae, Siganidae, Haemulidae, Carangidae, and Labridae each contributed 2-5%, and the remaining families contributed less than 1% (Figure 2.6). Of the 101 fish species identified in the catch, 36 were represented by a single individual. Approximately two-fifths (39%) of the total catch weight was contributed by ten species, and one tenth of the catch was contributed by a single species – *Lutjanus gibbus* (Figure 2.7).

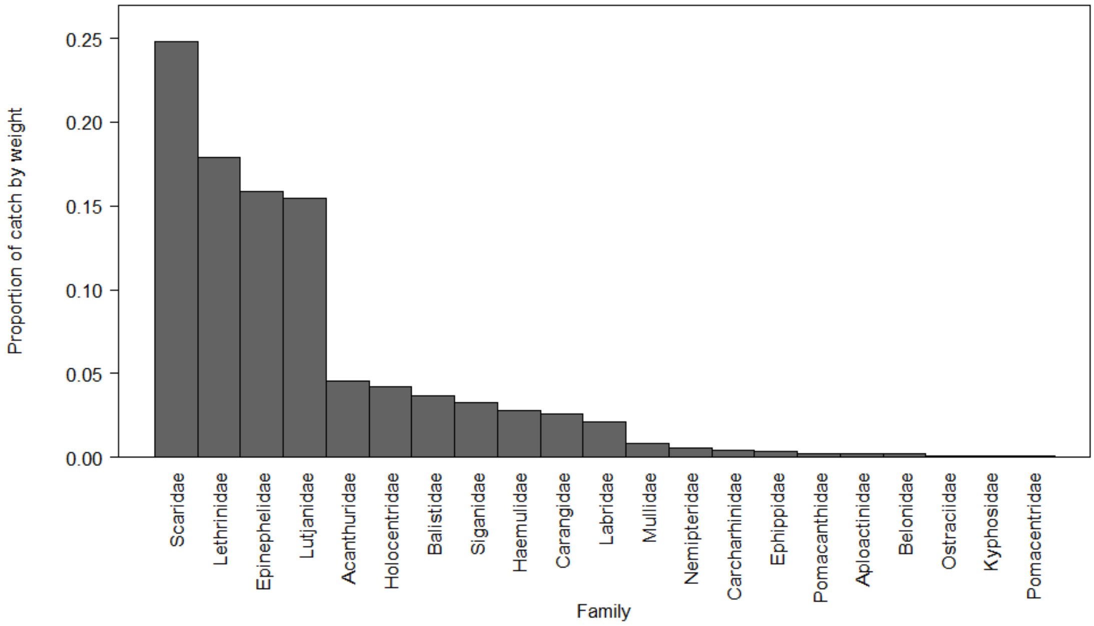

Figure 2.6 – Fish families represented in local artisanal fishery, expressed as proportion of total catch by weight.

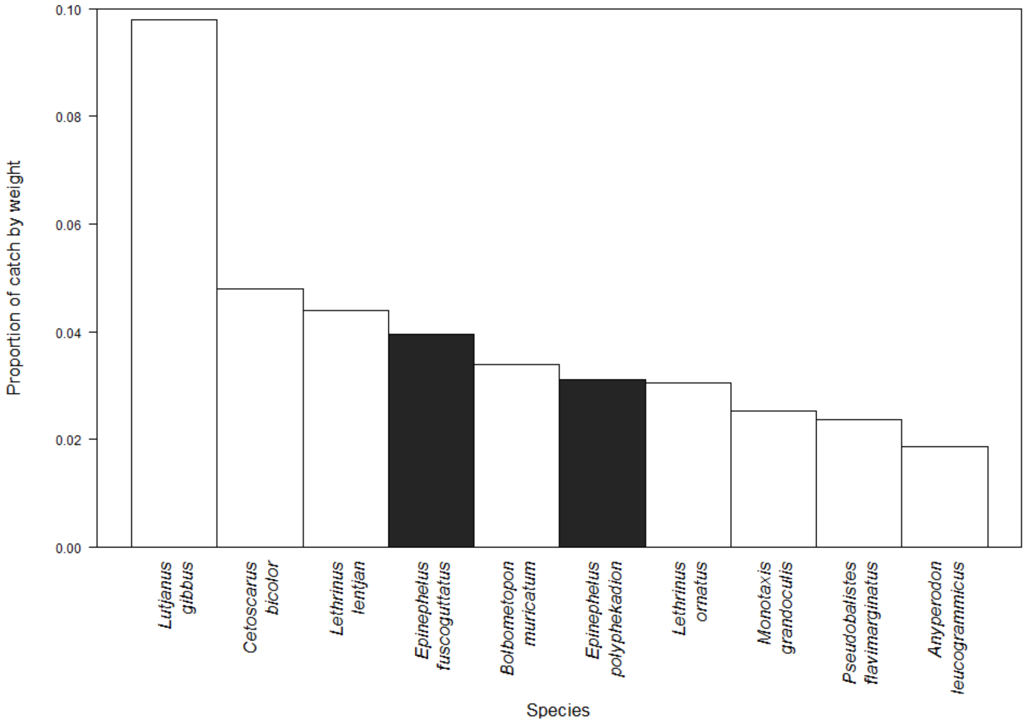

Figure 2.7 - Total landed catch of the top ten species (identified to species level). Focal species *Epinephelus fuscoguttatus* and *E. polyphekadion* are represented with black filled columns.

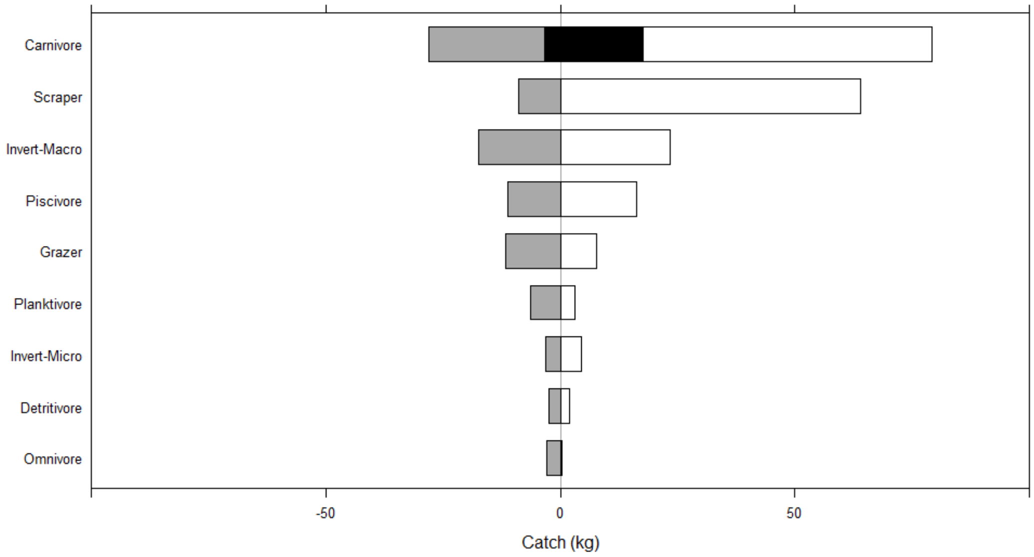

Figure 2.8 – Total landed catch from creel surveys destined for consumption by the fisher's family (grey bars) or sale (white bars), separated by functional group (adapted from Cinner *et al.* [2009c]). Catches of the two study species are emphasized (black bar).

Of the catches examined during creel surveys, approximately half (52%) of the fishes caught were sold with the remainder consumed. Fishes consumed were on average significantly smaller than those sold (198.0g and 383.6g respectively; P<0.001). As such, over two-thirds of the catch, by weight, was sold (69%).

Epinephelus polyphekadion & Epinephelus fuscoguttatus

According to creel survey data, the two focal species of this study, *Epinephelus polyphekadion* and *E. fuscoguttatus,* contributed substantially to the total catch (3 and 4% by weight, respectively) (Figure 2.7). No catches from spawning aggregations were present in the creel sample. Spawning aggregations may be exploited only sporadically, but with greatly increased catches. If substantial proportions of local *E. polyphekadion* and *E. fuscoguttatus* catches are generally exploited from spawning aggregations, their contribution to the total catch may be considerably greater than estimated here. Presumably due to their relatively large size per fish, these catches were predominantly sold (75 and 91% of catch by weight, respectively). The size range of *E. polyphekadion* caught (n = 7) was 188 – 540 mm TL (409 ± 43; mean ± SE). The size range of *E. fuscoguttatus* caught (n = 17) was 195 – 508 mm TL (337 ± 18).

Spatial distribution of fishing effort

Surveyed fishing trips were conducted at distances of up to approximately 8 km from landing sites (*i.e.,* settlements). Fishing effort was significantly skewed toward shorter distances, such that 50% of effort was within approximately 2 km of landing sites (Figure 2.9). A Mann-Whitney test indicated that the distance to fishing grounds was greater for fishing trips catching fishes primarily for sale (Mdn = 2.6 km) than for consumption (Mdn = 1.3 km), W = 225, $p = 0.003$.

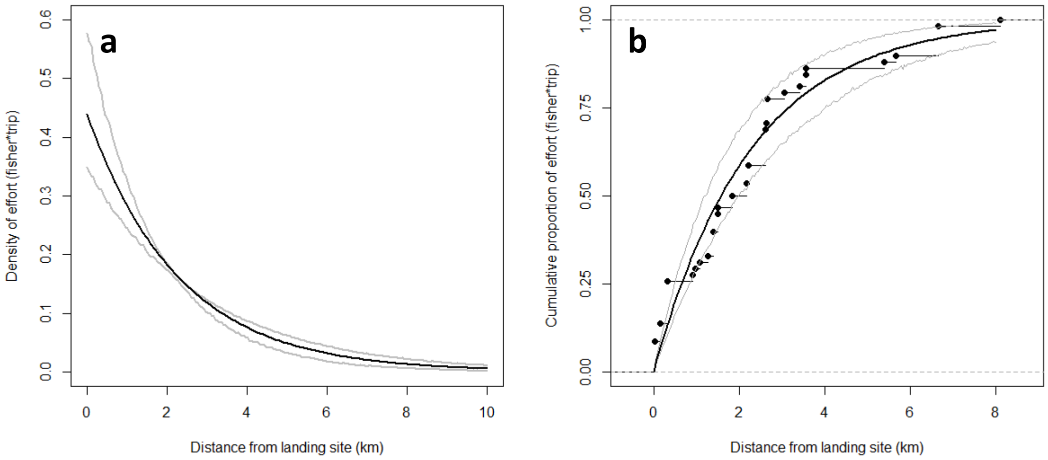

Figure 2.9 – Fishing effort (y-axis) as function of distance from landing site (x-axis) from creel survey dataset (n=58), expressed as (a) probability density of fishing effort $f(d) = \lambda e^{-\lambda d}$; and (b) cumulative distribution of fishing effort $f(d) = 1 - e^{-\lambda d}$ (filled black circles with trailing lines represent recorded distance data). Black lines represent best-fit exponential function (rate [λ] = 0.44), grey lines represent 95% confidence intervals as estimated by boot-sampling (1000 bootsamples).

The size of core fishing grounds (*i.e.,* the area which was utilised for at least one fishing trip during an average month) varied substantially between households, from < 1 km^2 to > 40 km^2 (12.4 ± 2.1 km^2). The near-shore area between Leon and Mait was the most widely utilised, and was reported as core fishing grounds for over half of surveyed households (Figure 2.10).

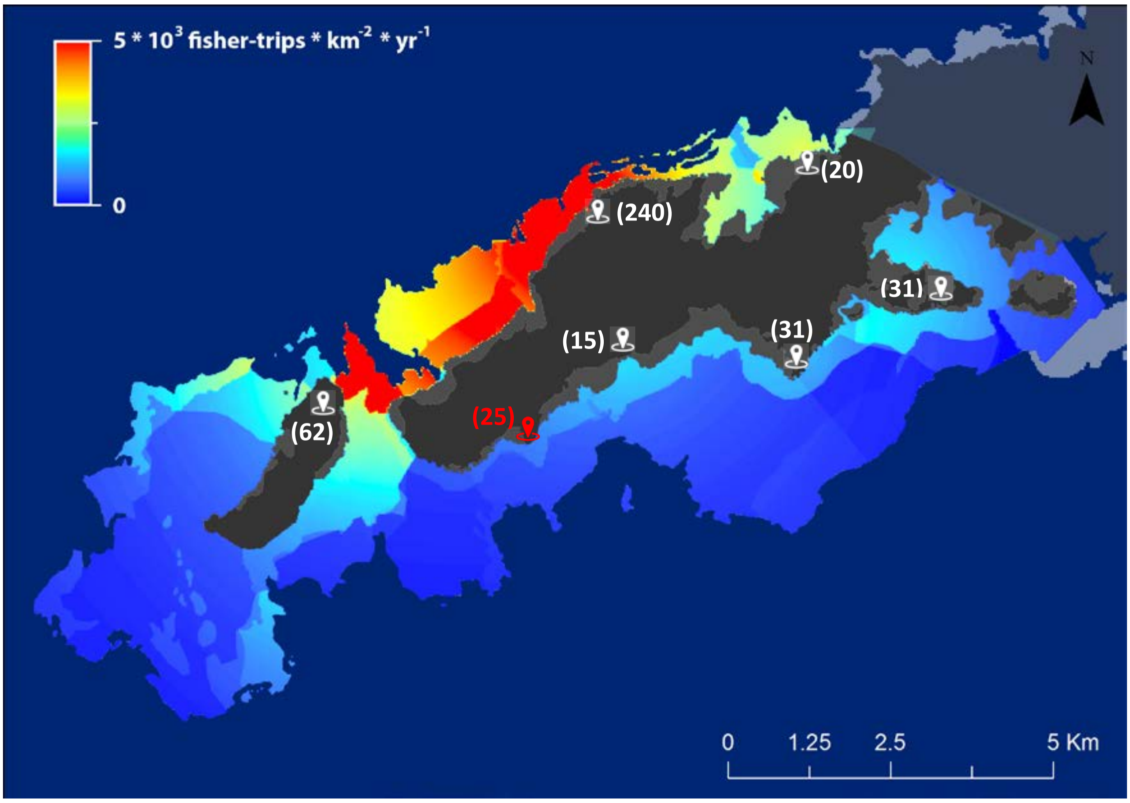

Figure 2.10 – Heat-map depicting the spatial distribution of estimated fishing effort throughout the study region, by residents of western Dyual. Values depicted at a 20 * 20 m grid resolution, representing the self-reported core fishing grounds of households, weighted by distance to landing site closest to the household, and by self-reported number of fishing trips conducted within an average month. Warmer colours represent greater fishing effort, toward a maximum of 4.4 * 10^3 fisher-trips * km^{-2} * yr^{-1}. White place marks (📍) denote settlements with population estimates in parentheses; red place mark represents the settlement burned during a recent land dispute (see section 2.4.4.2).

2.4.4 Governance

Governance within Papua New Guinea was carried out through two complementary systems. State-based governance was nested. The study area was under the jurisdiction of Ward 17 of the Tikana local level government (LLG) area. Tikana was one of the ten LLGs that make up New Ireland Province. Local level government and ward members were individually elected by popular vote by eligible local constituents, for terms of five years. Adult inhabitants of the relative jurisdictions were eligible to run for these positions. Ward and LLG members generally ran as independents and were rarely associated with political parties. The ward member presided over 'community development meetings' with Village Planning Committees (VPCs) within the ward, and presented the resolutions from these meetings at 'ward development meetings', presided over by the relevant LLG member. Ward 17 contained two VPCs; the Leon VPC represented the inhabitants of the primary community of Leon, as well as all smaller settlements within the study region (Figure 2.2), Sumuna VPC represented the inhabitants of Sumuna and its immediate surrounds (Figure 2.1). The Leon VPC was elected by eligible local constituents for terms of five years. Committee members could be replaced at any time by a vote of no confidence by constituents. During the three year study period (2012 – 2015) the Leon VPC chairman was replaced three times by votes of no confidence. Key informants reported that this was common, and that VPC chairmen rarely presided for their full terms.

A complementary, clan-based system of governance also operated within the study region (as throughout much of Melanesia), known as customary tenure, wherein clan or familial groups held use and access rights over land, and coastal areas. These rights were, at least in principle, excludable, transferable, and enforceable (Ruddle *et al.* 1992). In Papua New Guinea, customary tenure rights were recognised by the national government, and hence *de jure* (Hyndman 1993).

Decisions that concerned multiple families or clans within the study region were either made by the Leon VPC, or a council of clan chiefs and elders. Key informants reported that the distinction between these groups' jurisdictions was often unclear, although this did not often result in conflict. In practice, where the VPC claimed ultimate jurisdiction over a matter, key informants reported that decisions were rarely made without the majority support of clan chiefs and elders.

Clan affiliation

The heads of households surveyed on western Dyual reported affiliation with either one or two clans (84 and 16%, respectively), divided among three major (19 – 28% affiliation), and ten minor clans (3 – 6% affiliation).

Land tenure

Land tenure on western Dyual was handed down via a matrilineal system, with tenure devolved to the family level. Landowners often held separate plots for habitation and for cultivation of crops. Key informants reported that community members without local land tenure could be allocated plots of land to inhabit and cultivate, following *kustom* ceremonies and payment to the tenure holders. Disagreement over land tenure was reportedly a major source of dispute within the community. Some claims were extremely complicated and involved tracing linages through numerous generations. Some key informants reported that the outcome of disputes depended somewhat on the relative wealth and social standing of the parties involved. In 2014, one such dispute, relating to the tenure of Mait Island, led to multiple armed conflicts, widespread destruction of property (including the complete destruction of a small settlement), the eviction of a family group from western Dyual, and three deaths.

Marine tenure

Marine tenure on Dyual was also handed down via a matrilineal system, however tenure was held at the clan level. Decisions regarding the use of resources within tenure areas were ultimately made by the most senior male clan member. In practice, decisions were often decided by popular vote involving all adult clan members. Marine tenure disputes within western Dyual were reportedly extremely rare. Tenure holders technically held the right to exclude other community members from exploiting resources within their tenure boundaries, however contrasting with land tenure, this right was rarely exercised, and all inhabitants of western Dyual Island were permitted to fish throughout the entire study area.

The area of shallow habitat under the jurisdiction of the Leon VPC was approximately 45 km^2. Spatial analyses conducted throughout this thesis were restricted to the bounds of available high-resolution satellite imagery. All subsequent analyses thus understate the shallow habitat within the jurisdiction of the Leon VPC by ~ 1.8 km^2 (represented in light grey in Figure 2.10 and hereafter). The Leon VPC jurisdictional area included 22.7 km^2 of coral and seagrass dominated habitats, and 20.6 km^2 of lagoonal and embayment habitat. The majority of this area (95%) was under the tenure of three clans (Figure 2.3). The majority of the local population also reported affiliation with these clans (68%).

Fisheries management

There were few restrictions to fishing within the waters of western Dyual. A nationwide moratorium enacted by the National Fisheries Authority had prohibited the harvest of sea cucumbers since 2009, that remained in place at the time of writing (Hair *et al.* 2016). Locally, fishing with derris root, a locally abundant plant that is highly toxic to fish, was also prohibited in 2005. This ban was enacted and enforced by the Leon VPC. One informant reported that fishers still occasionally used derris root, but that the practice was not widespread. Spatial restrictions on marine resources had been traditionally practiced in western Dyual for generations, in the form of traditional *tambu* areas. Four current *tambu* areas were identified during household surveys, all protecting transient grouper spawning aggregation sites (Figure 2.3). Awareness of the existence of *tambu* areas varied markedly – Site A, 94%; Site B, 3%; Site C, 25%; and Site D (not shown), 34%. All respondents could correctly identify the location of reported *tambus.* When asked to delineate the *tambu* areas, respondents outlined small areas, and conveyed that the fishing closures covered the spawning sites only.

According to 94% of respondents the local abundance of fishes was primarily driven by fishing practices. Half of the respondents (50%) believed that the number of fish had decreased over the past five years, while 19% perceived no change, and 28% believed abundances had increased. The local derris root ban, and the tambu areas were the most commonly reported reasons for perceived increases in abundance (67 and 44%, respectively), while overfishing was blamed for declines in abundance in almost all cases (94%). When asked for suggested changes to local fisheries management, the majority of respondents suggested increasing or strengthening current management, although through a wide variety of differing management measures (Table 2.1).

Table 2.1 – Suggested changes to current fisheries management at Dyual Island, Papua New Guinea, categorised and ordered by percentage of survey respondents (n=32) suggesting the change.

Category	Action	Respondents (%)
Institutional	Strengthen enforcement	37.5
	Increase awareness of management	15.6
	Form management committee	9.4
Spatial / temporal	Expand permanent MPA protection	34.4
	Create periodically-harvested closures	18.8
	Open Site A for periodic harvest	15.6
Other	Size limits	12.5
	Alternative livelihoods	9.4
	Effort restrictions	6.3
	Gear restrictions	3.1
No change		*28.1*

Spawning aggregation Site A closure

This *tambu* was established at the multi-species spawning aggregation Site A in 2004 (Figure 2.3) (Hamilton *et al.* 2011). During the period of 1999 – 2003, the local community entered into a commercial agreement with international operators of the Live Reef Food Fish Trade, to exploit grouper *(Epinephelus polyphekadion, E. fuscoguttatus,* and *Plectropomus areolatus)* from this aggregation (Hamilton *et al.* 2004). Due to perceived declines in the abundance of these species at the aggregation site, and disputes over the volume of mixed coral reef fish harvested to feed the captured fish, the local community cancelled the agreement in 2004. At this time a *tambu* was established through a partnership between The Nature Conservancy and the clan holding tenure over the area. This *tambu* takes the form of a complete ban on all forms of harvest within 0.2 km^2 covering the spawning site, and is thus synonymous with a contemporary no-take marine reserve. In the five years immediately following its closure, abundances of *Epinephelus fuscoguttatus* and *E. polyphekadion* that aggregate to spawn at the site increased markedly (Hamilton *et al.* 2011).

While 94% of respondents were aware of the management area at Site A, 28% of these incorrectly reported that fishing restrictions applied only to the spawning grouper. Some confusion also existed over the party responsible for the management of the aggregation site, with less than a third of respondents (31%) correctly identifying the clan holding customary tenure over the area. The remainder reported that management was the responsibility of either a partnership of the Leon Village Planning Committee (VPC) and The Nature Conservancy (59%), or the National Fisheries Authority (3%).

A majority of respondents (59%) believed that poaching had occurred in the management area within the past 3 years, 18% of respondents reported personally witnessing poaching, and 9% reported participating in poaching within the area. Poachers reported that fishing was conducted by night from motorised fibreglass vessels, catching aggregating grouper for sale in Kavieng. Several spearfishers were reportedly present on poaching trips, filling 2-4 fibreglass coolers per trip. Although respondents did not estimate the total weight of catches, information from fish buyers suggests that this constitutes 140 – 640 kg per poaching event. Although a quarter of respondents (26%) believed that a system existed to punish individuals infringing management rules and to manage conflicts, no respondent could recall a punishment being administered. Key informants confirmed that no punishments had been administered, citing uncertainty regarding the process to administer punishments as the primary reason.

Although a minority (45%) of residents reported initially supporting the closure of spawning Site A to fishing (with the majority neutral), at the time of this study the vast majority believed that the tambu had been beneficial to their household, the community and the environment (80, 93, and 97%; respectively), and all respondents expressed their current support for the *tambu*. A majority of respondents (62%) believed they could influence the management rules at the site through community and VPC (42%), or clan (19%) meetings.

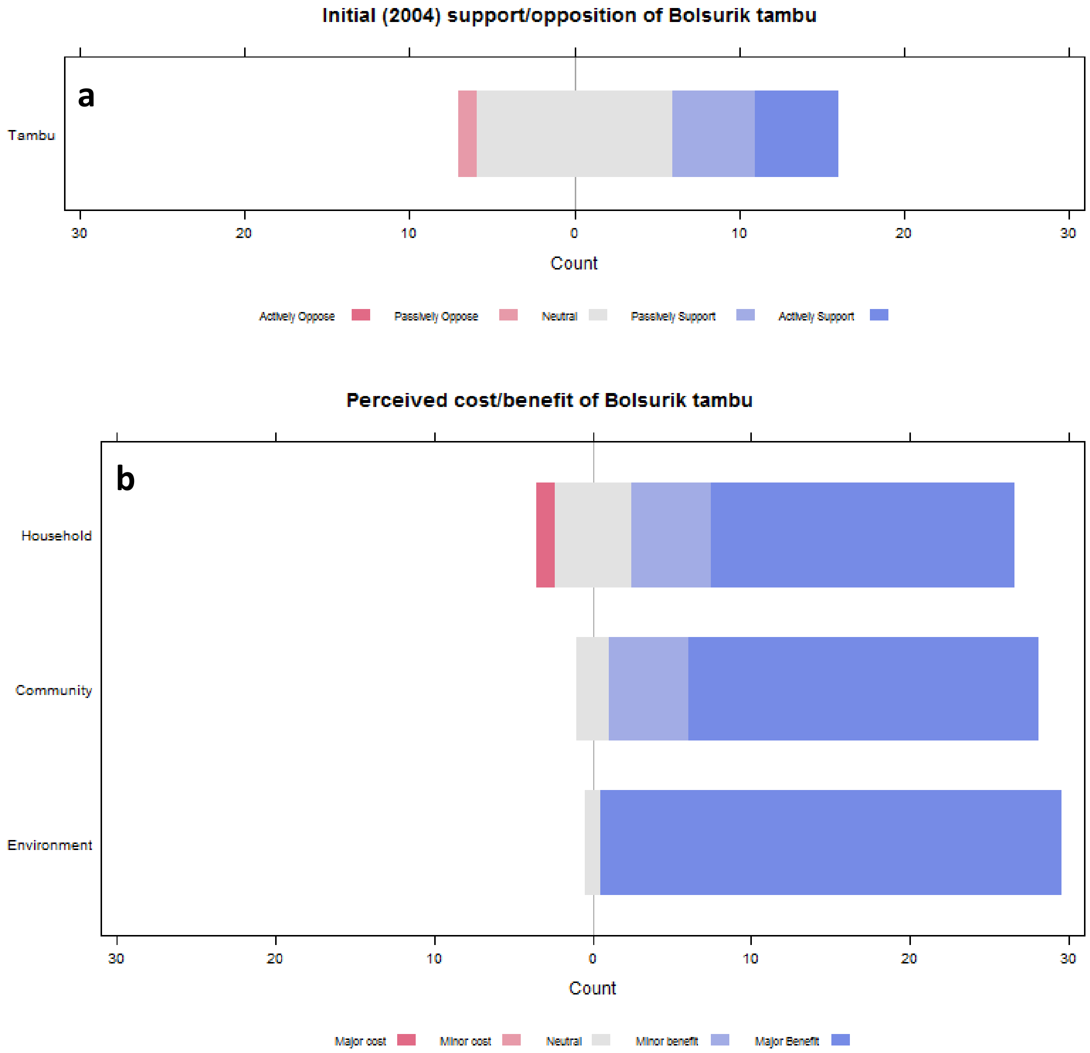

Figure 2.11 - Perceptions relating to the closure of Site A to fishing. (a) Initial support or opposition to the closure of the site in 2004, (b) Perceived costs or benefits of the closure of the site to the household, the community, and the environment.

2.5 Discussion

The local social, economic, and political setting of western Dyual Island was relatively typical of the region, and rural Melanesia more generally (Kaly *et al.* 2005). Household and creel surveys described a low-developed artisanal fishery with largely sustainable levels of exploitation, when considered across the entire study region. A number of factors were present which supported the ongoing sustainable management of this fishery. Population density was low, destructive fishing gears were rare, and the local customary governance was enduring and locally well-respected. Further development of the local fishery was largely impeded by the inaccessibility of regional markets, particularly due to lack of storage infrastructure (*i.e.,* freezers) on western Dyual. The low spatial mobility of fishers – who predominantly operated from unpowered dugout canoes – produced high variability in the distribution of fishing effort across western Dyual. This could potentially lead to localised overfishing in areas directly adjacent to settlements, and ultimately the serial depletion of fishing grounds.

2.5.1 Governance

The critical importance of governance in small-scale coral reef fisheries management is well recognised (Ostrom 1990). The focus of scientific enquiry and management intervention has increasingly shifted toward more localised, sometimes *de facto,* governance systems (e.g. Govan *et al.* 2006; Jupiter *et al.* 2014; Cinner *et al.* 2016). Community-level governance commonly enjoys greater local trust and support (discussed further in Appendix I). Additionally, community-based governance may be more locally relevant, socially and culturally appropriate, and adaptive than more distant and spatially expansive counterparts (McClanahan *et al.* 2006). For many small-scale fisheries, *de jure* or *de facto* access rights and tenure over coastal resources are held at localised scales. In these cases, the engagement of localised governance may be a social, economic, cultural or legal necessity, rather than simply best practice. Across western Dyual, as throughout Melanesia, natural resources were governed through two complementary systems – centralised, state-based government, and a legally-recognised customary tenure (CT) system.

The jurisdiction of the most localised level of state-based governance, represented by the Leon VPC, covered an area of shallow habitat of 45 km^2, including the entirety of the 43 km^2 study region. Local knowledge of state-based restrictions on the western Dyual artisanal fishery was limited to two examples. First, the use of poison to incapacitate fish for capture was prohibited (particularly the local plant – derris root). This restriction was reportedly enacted by the Leon VPC in around 2005 and was still in place at the time of writing. Key informants reported that this restriction was strongly supported by local stakeholders, and that although occasional infringements occurred, no sanctions had been meted out. Second, a nation-wide prohibition of the harvest of sea cucumbers has been in place since 2009 (Hair *et al.* 2016). Sea cucumbers can be dried and stored without refrigeration making them ideal for harvest in rural Papua New Guinean fishing communities, where distance to markets and unavailability of ice limit local supply of fresh seafood to larger regional markets. Prior to its closure, the sea cucumber fishery provided as much as 30% of household income to approximately 200,000 Papua New Guinean artisanal fishers (Kinch *et al.* 2008). The national ban followed repeated failures to arrest declines in sea cucumbers. Catch limits, size limits, closed seasons and gear restrictions were legislated by provincial, and then national governments, but compliance with restrictions in rural communities was extremely low (Kinch *et al.* 2008). Although sea cucumber populations have recovered somewhat during the ban, there is concern that stocks will be quickly depleted on reopening the fishery regardless of management restrictions, as has occurred in other Pacific Island nations (Hair *et al.* 2016). These two examples highlight the reality of centralised state-based governance in Papua New Guinea – unpopular regulations are met with widespread poor compliance. This largely limits the effectiveness of centralised regulations to measures with strong local support, or regulations that are able to be centrally monitored and enforced.

The customary tenure system governing the ownership and governance of natural resources of western Dyual was well developed and robust. Three clans held marine tenure within the study region, with individual areas of 7-20 km^2. However, all inhabitants of western Dyual, including recent migrants, were free to access marine resources across tenure boundaries. This common access was likely important in avoiding intra-community conflict, as a quarter of local fishers held no marine tenure. Conversely, outsiders were expected to request permission to access resources. Inhabitants of eastern Dyual reportedly sporadically fished within the tenure of western Dyual without permission, including at two grouper spawning aggregations under traditional closures (Sites C and D). According to clan leaders and VPC members, attempts to resolve these issues through discussions with their eastern counterparts repeatedly failed. According to the relevant clan leaders (*i.e.,* tenure holders) of these two spawning aggregation sites, these closures remained in place. Despite this, the majority of local resource users did not recognise the closures. These examples highlight the importance to management of clearly defined boundaries of ownership, and the ability to defend these boundaries from incursion (Ostrom 1990; Aswani 2005; Mills *et al.* 2013).

No formal system of monitoring and enforcing fisheries management regulations was present on western Dyual; management regulations were enforced through voluntary coercion and social pressure. The most commonly suggested improvement to fisheries management by local stakeholders was to strengthen current enforcement of regulations – suggested by over a third of respondents. The presence of monitoring and enforcement systems represent key design principles for common-pool resource management (Ostrom 2009; Cox *et al.* 2010). Management has been demonstrated to be more effective where some form of sanctions for infringement of rules is present – particularly ‘graduated sanctions’, where initial costs of infringement are low, but increase with each subsequent offense (Ostrom 1990; Cinner *et al.* 2012a). Compliance with management rules engendered by high levels of social capital has been suggested to replace enforcement mechanisms in limited cases (Aswani 2005; Cox *et al.* 2010; Mills *et al.* 2013). However, as demonstrated by the failure of the customary closures at the transient spawning aggregation sites C and D, social pressure is generally unable to extend to outsiders. Additionally, some poaching by inhabitants of western Dyual occurred within the spawning aggregation Site A closure. This potentially threatened the persistence of these aggregations (Hamilton and Matawai 2006), and the perceived legitimacy of management regulations there. This, in conjunction with high levels of local support, suggests that instating formal monitoring and sanctioning systems should be a priority for local fisheries governance at western Dyual. This is particularly important in the face of increasing market access, which has been demonstrated to erode peoples' willingness to participate in civic duties and their moral attitudes (Falk and Szech 2013).

2.5.2 The role of markets

The role of market access as a driver of fishing pressure, and ultimately ecosystem health is well established (Cinner and McClanahan 2006; Brewer *et al.* 2012; Cinner *et al.* 2013, 2016). Distance to the market is often used as a proxy for market access (Brewer *et al.* 2012), however a number of technological factors may substantially alter these distance effects. For example, availability of storage facilities (e.g. freezers), motorised vessels, or fish buyers have all been demonstrated to dampen these distance effects (Cinner *et al.* 2016). Despite being approximately 50 km from larger regional markets in Kavieng, approximately half of catches landed in western Dyual during this study were intended for sale (50 % as self-reported during household surveys, and 52 % from creel surveys). Due to the tendency to sell larger fish, which fetch a better price, this represented over two-thirds of the catch by weight (69%). Fish destined for sale here were caught twice as far from landing sites, compared with fish for consumption. This suggests that access to markets can substantially impact the spatial distribution, as well as the magnitude, of fishing. For the fishery of western Dyual to supply fresh fish to markets in Kavieng, ice had to be transported from Kavieng, fishing carried out, and the catch returned to Kavieng within a limited time-frame – to prevent catches from spoiling. Transport of fresh fish required access to a motorised vessel, and was generally carried out by fish buyers. Acting as a fisher buyer on Dyual Island was reportedly a profitable though risky enterprise. In poor weather, the safe crossing to Kavieng was not possible and purchased catches routinely spoiled. By reducing such costly spoilage, the reliable availability of ice on Dyual Island would substantially increase the accessibility of markets in Kavieng. Fishers and fish buyers highlighted the unavailability of ice for transport as the primary impediment to increased development of the artisanal fishery.

Due to their large size, the two species of grouper studied in detail throughout this thesis, *Epinephelus polyphekadion* and *E. fuscoguttatus,* were predominantly sold (75 and 91% of catch by weight, respectively). Thus market-related drivers are likely to disproportionately affect fishing practices for these species. The exploitation and subsequent protection of the spawning aggregation at Site A provides an illustrative example of this.

2.5.3 Fish spawning aggregation Site A

The multi-species fish spawning aggregation at Site A has been exploited for subsistence purposes for generations. In the 1980s, fishing pressure increased at the site, with the introduction of sporadic night-time spearfishing to supply markets in Kavieng. Intense commercial fishing was conducted intermittently in 1997-2004, by Live Reef Food Fish Trade (LRFFT) operators in partnership with the local community. At these times, cyanide, traps, and hook and line were employed to capture grouper from the aggregation site. Live fish were kept in ‘holding pens’ in lagoonal areas of western Dyual, and intermittently transported to Kavieng for further transport onto Asian markets. Due to tenure disputes, social conflicts and regulatory issues LRFFT operations were sporadic during this period, however fishing pressure was intense when in operation. For example in 2004, 2-4 t of live grouper (primary *E. polyphekadion* and *E. fuscoguttatus*) were captured from the 16,000 m^2 site in two months. In 2004, reductions in abundances of targeted grouper species, and other coral reef fish taken to feed captive grouper, led to the expulsion of the LRFFT operator by the local tenure holders. At this time, the aggregation site was protected from all forms of fishing with a small (0.2 km^2) customary closure, analogous with a no-take marine reserve. The intense commercial fishing pressure had led to such major declines in the aggregating populations of these species that they were almost entirely absent from the site during the spawning season of 2005. However, following protection abundances recovered within five years (Hamilton *et al.* 2011). Species with similar life history characteristics elsewhere have taken decades to exhibit similar recoveries (Abesamis *et al.* 2014). The rapid recovery rates here may be due to the recruitment of younger cohorts unaffected by the short-term intensive aggregation fishing. If these spawning populations experience levels of self-recruitment similar to those documented for grouper in nearby Manus Province (Almany *et al.* 2013), then prolonged aggregation fishing would have led to substantially longer recovery periods. As such, the swift response to perceived changes in the condition of the fishery, by local governance institutions in partnership with The Nature Conservancy, was likely pivotal in maintaining the sustainable harvest of these intrinsically vulnerable species. Although initial support for the aggregation site closure was modest, the vast majority of local stakeholders reported during surveys that the closure had since yielded individual, community, and environmental benefits. All stakeholders reported their current support for the closure, and over a third suggested expanding the protected area. However, 16% suggested opening the area for periodic harvest by local inhabitants (discussed further in Chapter 5). The substantial increase in local support here suggests that small closures targeting key, spatially-restricted life history events such as spawning aggregations may provide a ‘foot in the door’ for co-management partners, particularly following short-term, intensive harvesting events.

2.5.4 Spatial distribution of fishing effort

As discussed above, low local population density and the relative inaccessibility of larger regional markets in Kavieng mean that fishing pressure across western Dyual remained relatively light. A global assessment of the sustainability of island coral reef fisheries estimated multi-species maximum sustainable yield (mMSY) at 5 tonne * km^{-2} * yr^{-1} (Newton *et al.* 2007). Estimates of fishing yield, when averaged across western Dyual, were less than half of this suggesting that the fishery retains substantial scope for further sustainable development. It is important to note however, that coarse metrics such as mMSY cannot account for the species composition of catches, and even relatively light artisanal fishing pressure can deplete intrinsically vulnerable species such as bumphead parrotfish (Hamilton *et al.* 2016b) and aggregating species of grouper such as *E. polyphekadion* and *E. fuscoguttatus* (Hamilton and Matawai 2006; Hamilton *et al.* 2011), particularly following increased access to markets for these species. Additionally, metrics such as mMSY fail to account for spatial heterogeneity in fishing pressure. Low-development fisheries are often predominantly exploited using unpowered fishing vessels (Cinner *et al.* 2009b). Indeed, nine in ten fishing vessels at western Dyual were small, unpowered dugout canoes. Accessing more distant fishing grounds using such vessels is relatively energy- and time-consuming, and risky in poor weather. Creel data revealed that although fishers exploited areas greater than 8 km from landing sites (*i.e.,* settlements), the majority of effort was focussed within 2 km of landing sites. As such half of the modelled fishing yield was concentrated within the 10% of the study region directly proximal to settlements. The high heterogeneity of fishing pressure across western Dyual resulted in a hotspot between the two largest settlements of Leon and Mait, with estimated fishing yield up to 17.1 t * km^{-2} * yr^{-1} – more than three times mMSY estimates for coral reef fisheries. The exponential distribution of fishing effort relative to landing sites here is consistent with effort allocation modelling of a low-development fishery (Caddy and Carocci 1999). However, if fish stocks within the area proximal to settlements are depleted, the fishery is likely to occupy a broader spatial area over time, as fishers abandon an expanding depleted area (Die *et al.* 1990).

The heterogeneity of fishing pressure at such small spatial scales could have considerable implications for fisheries management and conservation. These patterns of fishing pressure are likely functions of a number of aspects of the local social-ecological system (SES), including but not limited to those discussed in section 2.5.2 above. Variation in the spatial distribution of fishing pressure across differing SES, and across time within individual SES would thus provide valuable information. However, these were not within the scope of this study.

2.5.5 Critiques and caveats

Survey methods employed throughout this chapter are potentially susceptible to issues related to positionality. Positionality refers to the real or perceived position of the researcher within the research setting (Savin-Baden and Major 2013). Issues of positionality are unavoidable when conducting participatory research, and a considerable body of literature exists discussing the differing benefits and challenges across the dynamic and multi-dimensional 'space-between' the researcher and research participants (Muhammad *et al.* 2014). I will address two interrelated issues of positionality here. First, issues of trust could deter participants from sharing information with a rank outsider. This is particularly true of information deemed to be sensitive or privileged. To address this issue, I spent approximately six months living at the study site prior to conducting surveys. During this time, I presented information regarding my work at weekly community meetings. At these meetings I was introduced by various locally respected individuals, including member s of the VPC, clan chiefs, and the church minister. Additionally, I held informal discussions with many individuals and groups at all communities within the study region. As such, I was acquainted with all survey participants before the commencement of the surveys discussed within this chapter. Nonetheless, each semi-structured interview began with a detailed description of the project to minimise any potential confusion. Despite efforts to develop trust, information that is considered particularly sensitive (e.g. undercurrents of conflict that have not resulted in open encounters) may not be shared during interviews. Second, my introduction to the community by a local representative of The Nature Conservancy could bias survey responses. Information could be skewed depending on an individual participant's perception of TNC. For example, participants may be reluctant to volunteer information that they believe could lead to interventions by TNC that they perceived as negative. To address this issue, I presented myself as an independent researcher throughout the study. During the individual and group discussions described above, I explained that although TNC had approached me to conduct the work, I was accountable to the research participants and resource owners/users. I further explained that all information gathered was strictly confidential (between myself and the individual/group that provided it). Although TNC continued to provide logistical support throughout the project duration, I largely interacted with the community independently.

Another limitation of the study design is the restricted period of sampling for both household (two months) and creel (one month) surveys. Individual households were only surveyed on a single occasion. As such, estimations of temporally variable activities relied on the respondents' estimation (e.g. low, average, and high fish catches). Due to the relatively restricted period of creel survey data, seasonal or sporadic fishing is likely to be underrepresented. Methods involving more extensive longitudinal surveys would address these issues somewhat, but would require significantly greater investment of resources. Nonetheless, the methods employed here are well established, including within comparable systems in Papua New Guinea (Cinner 2005; Cinner and McClanahan 2006; Cohen *et al.* 2013).

2.5.6 Summary

A number of social, economic, and political factors supported the continued sustainable management of marine resources at western Dyual. Local population density was low. Local stakeholders were highly reliant on fisheries, and highly engaged in management decision-making. The local customary management system was robust, active and well trusted. Market drivers arguably present the most pressing potential threat to the continued sustainability of local fisheries, as demonstrated by the rapid decline in grouper abundances following the establishment of LRFFT operations in the late 1990s. The introduction of freezers or reliable ice supply to western Dyual would also substantially increase access to regional markets. The spatial scales of governance systems most relevant to community-based management were relatively limited. The most localised level of state-based government, the LLG ward, held jurisdiction over 45 km^2 of shallow habitat. The customary tenure system was more spatially restricted yet, with individual tenure areas covering 7-20 km^2. All local resource users had access rights to fish across the study region, regardless of tenure. However, the spatial distribution of fishing effort was decidedly uneven, such that half of the fishing effort was concentrated within 10% of the study region. The patterns of settlement, clan affiliation, access rights, and fishing effort considered within this chapter represent key social aspects that will impact the local fishery. The two governance systems detailed within this chapter represent the relevant existing community-based governance institutions here. These institutions will be examined for problems of fit with the key social aspects detailed here, along with key ecological processes investigated hereafter, in the final chapter of this thesis.

CHAPTER 3 - AGE-BASED DEMOGRAPHICS AND REPRODUCTIVE BIOLOGY OF TWO CO-AGGREGATING EPINEPHELIDS

3.1 Synopsis

In order to understand when specific reef areas and habitats are preferentially used by fishes during different life history stages (Chapter 4), we first have to determine when these species transition from juveniles to adults. Processes surrounding age, growth, and sexual development are of primary importance to population biology and subsequently to the conservation and management of exploited fishes. Characteristics such as large body size, slow growth, long lives, and late sexual maturity have all been repeatedly demonstrated to increase vulnerability to overexploitation. However, more information on the demographics and sexual function of key fishery-targeted species is still required. In this chapter, I provide key information on the demographic and reproductive biology of two fishery-targeted species of grouper – *Epinephelus polyphekadion* and *E. fuscoguttatus.* Age-at-maturity functions determined that females reached reproductive maturity between 4 – 8 yrs of age for both species. However, *E. fuscoguttatus* exhibited faster growth toward a larger maximum size. As such, female *E. fuscoguttatus* were an average 10 cm larger at sexual maturity. As a result the majority of *E. polyphekadion* harvested within the local fishery were adults, while the majority of *E. fuscoguttatus* were taken as juveniles. Conclusive histological evidence of sexual function was not found. Males of both species were far more prevalent in upper size and age classes, providing demographic evidence of protogynous hermaphroditism. The presence of males from the size and age of first female maturity suggested that *E. polyphekadion* were diandric. These characteristics have repercussions for the management of the species both here and throughout their range. Thus, the age- and size-at-maturity determined for *E. polyphekadion* and *E. fuscoguttatus* within this chapter will be used to partition individuals into biologically meaningful cohorts, to examine their ontogenetic shifts in habitat suitability in the succeeding chapter of this thesis.

3.2 Introduction

Age-based demographics are fundamental to fisheries management (Jennings *et al.* 1999; Choat and Robertson 2002). Stock-recruitment approaches to management intrinsically rely on accurate age information to estimate rates of recruitment and mortality (Beverton and Holt 1957). However, despite their long history of use in temperate, oceanic, and deep-water fisheries, adoption of age-based techniques in tropical coral reef fisheries management has been slow (Choat and Robertson 2002). This reflects the lower levels of attention, funding, and appropriate facilities dedicated to studying less commercially important tropical fisheries, but also the unpromising results of initial examination of tropical fish otoliths (Choat and Robertson 2002). However, over the past three decades thinly-sectioned sagittal otoliths of tropical fishes have been repeatedly and reliably demonstrated to contain observable growth bands. Further, these bands have been validated as annuli for a multitude of species, across a diverse cross-section of phylogenetic groups, environments and geographic locations (Choat *et al.* 2009; Andrews *et al.* 2016). More recent attempts to apply ecosystem-based approaches to management are less directly reliant on age-based demographic parameters than single-species approaches. However, age-based demographic parameters underpin the recovery potential of key species. In the predominantly data-poor coral reef fisheries, age-based demographic parameters can serve as proxies for intrinsic vulnerability to fishing, and can be used to prioritise management action (Abesamis *et al.* 2014). For example, recent comparative modelling of potential management actions targeting species that form transient spawning aggregations indicated that fast-growing, early maturing species are better protected across their non-spawning home-ranges, whereas slow-growing, late-maturing species are better protected at transient spawning sites (Gruss and Robinson 2015).

Variation and plasticity in sexual ontogeny of coral reef fishes also presents unique challenges to fisheries management and conservation. Teleost fishes display remarkable diversity of sexual function (Table 3.1). In addition to gonochorism, hermaphroditism – once considered to be something of a ‘zoological curiosity’ (Atz 1964) – is now know to be widespread, and has been confirmed in at least 27 teleost families across seven orders (Sadovy de Mitcheson and Liu 2008). Diversity of hermaphroditic function is also remarkable, with variations of simultaneous, sequential and serial hermaphroditism confirmed within families and even within species (Wootton and Smith 2014). Within the *Epinephelidae* family alone, species have been confirmed to function as gonochores, simultaneous hermaphrodites, and sequential hermaphrodites (displaying both protogynous and bi-directional sex change), and both monandry and diandry have been confirmed in protogynous epinephelids (Sadovy de

Mitcheson and Liu 2008). In addition to variation in function, recent evidence suggests that hermaphroditic fishes may display substantial plasticity in the timing and direction of sex change between species, populations and individuals in response to local conditions (Munday *et al.* 2006). This variation and plasticity, in conjunction with the lack of morphological distinction of gonad structure between primary and secondary males, makes confirming the sexual pattern of epinephelids particularly difficult (Sadovy de Mitcheson and Liu 2008). Robust confirmation of sexual pattern therefore requires histological examination of gonads across the full range of size and age classes, including juveniles (Sadovy and Shapiro 1987). Additionally, such studies should be carried out in numerous locations, to effectively assess potential variation in sexual pattern across a range of local conditions.

Table 3.1 - Sexual patterns of teleost fishes.

Sexual function		**Description**
Gonochorism		All individuals function exclusively as male or female throughout their reproductive lives. Gonads may either develop from (A) morphologically distinct immature stages, or from (B) 'bipotential' immature gonads, often with female morphological characteristics, through an inactive bisexual stage where germ cells of both sexes are present (sometimes termed 'functional gonochorism', or 'non-functional hermaphroditism') (Figure 3.1).
Simultaneous hermaphrodite		A proportion of individuals function as both males and female at the same time, or within a short space of time.
Sequential hermaphrodite	Monandrous protogyny	All functional males develop from functional females (termed 'secondary males') (Figure 3.1, pathway C).
	Diandrous protogyny	Functional males develop through two pathways – from functional females (*i.e.,* secondary males) (Figure 3.1, pathway C), and directly from a non-functional immature state (termed 'primary males') (Figure 3.1, pathway A and/or B).
	Monogynous protandry	All functional females develop from functional males (termed 'secondary females').
	Digynous protandy	Functional females develop both from functional males (*i.e.,* secondary females), and directly from a non-functional juvenile state (termed 'primary females')
	Bi-directional	Both male to female, and female to male sex change occurs.

The sex ratios of sequential hermaphrodites generally differ across their size range, with the 'terminal' sex skewed toward larger sizes (though this can also be true for gonochoristic species with sexually dimorphic growth rates). Fisheries are almost invariably size-selective – through gear selectivity (e.g. net mesh size), legislated size restrictions, fish behaviour (e.g. ontogenetic shift between areas with varying fishing pressure), fisher behaviour (e.g. targeting larger, more valuable individuals), or some combination of these and other factors. Thus, fisheries targeting hermaphroditic fishes are presumably also often sex-selective. Where sex-selectivity is strong, and fishing pressure is sufficient, this may result in two alternative, non-mutually exclusive outcomes. First, sex ratios may become increasingly skewed. Second, mean size and age of sex change may shift as individuals alter the timing of their sex change to compensate for changing local conditions. A recent literature review of this topic found that, following intense fishing of hermaphroditic species, 58% of studied species had significantly altered sex ratios and 38% had a significantly decreased size or age of sex change (Provost and Jensen 2015).

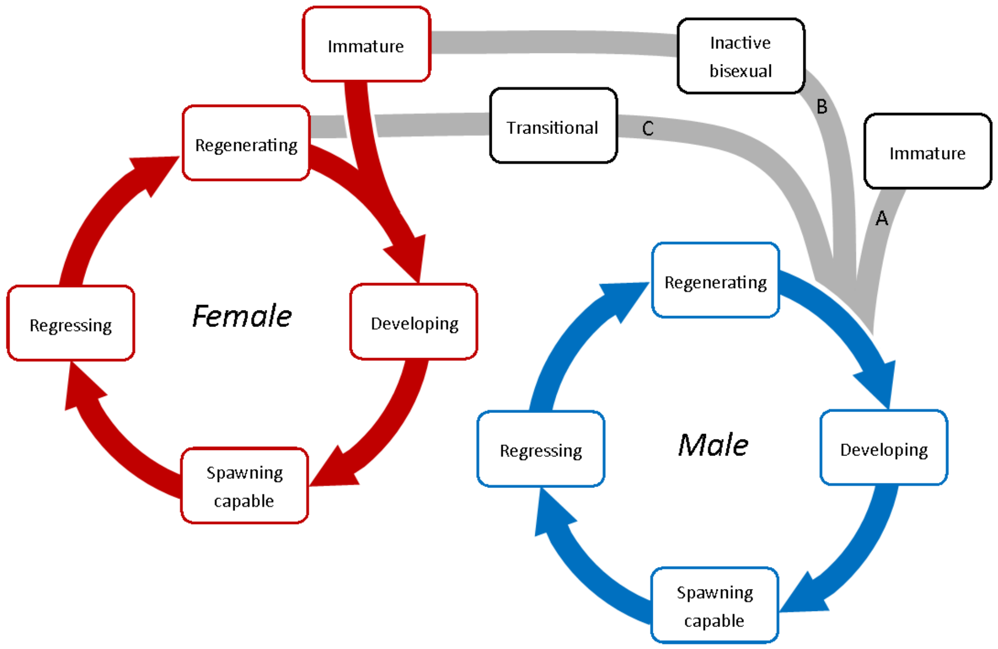

Figure 3.1 - Reproductive life cycle, illustrating the three alternative (although non-mutually exclusive) pathways to male sexual maturity for gonochores and protogynous hermaphrodites. (A) direct development from a morphologically distinct immature stage, (B) development from a 'bi-potential' proto-ovarian gonad through an inactive bisexual stage, and (C) passing through a transitional stage after completing one or more reproductive cycles as a female. See Table 3.1 for descriptions of alternative sexual patterns.

3.2.1 *Epinephelus polyphekadion*

The camouflage grouper *(E. polyphekadion)* displays relative common epinephelid life history characteristics. They are long-lived, with maximum recorded ages of 22 yrs in Pohnpei (Rhodes *et al.* 2011), 31 yrs in New Caledonia (Rhodes 2012), 35 yrs in the Seychelles (Pears 2005), and 36 yrs on the Great Barrier Reef, Australia (Pears 2005). They are reported to reach 90 cm total length (TL) (Craig *et al.* 2011), although maximum sizes of 50-65 cm TL are more common (Johannes *et al.* 1999a; Grandcourt 2005; Pears 2005; Rhodes *et al.* 2011). The sexual pattern of *E. polyphekadion* was originally described as protogynous, following induced sexual transition in the laboratory (Bruslé-Sicard *et al.* 1992). Stronger evidence of protogyny was provided from a tag-recapture study in Palau, where two tagged females were later recaptured as males (Johannes *et al.* 1999a). However, histological examination of gonads from 651 individuals from Pohnpei failed to uncover transitional individuals, but found evidence of two primary males (*i.e.*, spermatogenesis in otherwise morphologically juvenile gonads (Rhodes and Sadovy 2002a)). This histological evidence, combined with the substantially overlapping size distributions between sexes, led to Rhodes and Sadovy (2002) classifying the sexual pattern for *E. polyphekadion* as unresolved. Following inclusion of detailed demographic analysis of individuals from this fishery, Rhodes *et al.* (2011) further reclassified *E. polyphekadion* as a functional gonochore, with the potential for female to male sex change. This classification was based on the lack of sex-specific significant differences in growth, age and size distribution, and the lack of transitional fish among over one thousand individuals examined (Rhodes *et al.* 2011).

3.2.2 *Epinephelus fuscoguttatus*

Brown-marbled grouper *(E. fuscoguttatus)* are one of the largest epinephelids, reaching about 1 m total length (Craig *et al.* 2011). All information on age-based demographics and sexual ontogeny for this species comes from a single study on Australia's Great Barrier Reef (Pears *et al.* 2006, 2007). In that study, 242 individuals ranging from 320 to 970 mm, and from 2 to 42 yrs, were obtained from the local fishery. The mean asymptotic fork length was 806.9 mm, 80% of which was achieved by 10 yrs of age on average. Males were restricted to size and age classes greater than that of 100% female maturity. This, in conjunction with a lack of evidence of primary males suggests that the sexual pattern of *E. fuscoguttatus* is monandric protogynous hermaphroditism, although no evidence of transitional individuals was found.

3.2.3 Study aims

Epinephelus polyphekadion and *E. fuscoguttatus* present biological and behavioural similarities that merit their direct comparison. First, these two species co-aggregate to reproduce in spatially and temporally over-lapping spawning aggregations throughout their Indo-Pacific distributions. As such, they generally face similar fishing pressures (although considerably different in catchability at aggregation sites, as detailed in Appendix II). Second, although *E. fuscoguttatus* attain a larger maximum size, the two species are otherwise relatively similar in appearance. As such, where managed they may be placed under identical fishing restrictions (Pears *et al.* 2007). As such, any significant differences in demographic and reproductive biology could potentially have considerable management implications. Despite this, detailed comparisons of the demographic and reproductive characteristics had not previously been conducted for these species.

To this end, in this chapter I asked;

1. What are the key demographic parameters of *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus* including; sex-specific growth rates, longevity, and size and age at sexual maturity?
2. What are the functional sexual patterns of *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus*?

3.3 Materials and methods

3.3.1 Sample collection

Samples from 575 *E. polyphekadion* and 420 *Epinephelus fuscoguttatus* individuals were collected during the period from February 2014 until November 2015 inclusive, from artisanal fisheries in New Ireland Province, Papua New Guinea; at markets in the provincial capital of Kavieng, which sells catches from the Tigak Islands, and at landing sites throughout Dyual Island (Figure 3.2, Table 3.2). At the time of sample collection, fishers/vendors were asked for the location and method of capture. For samples collected from Kavieng markets, locations of capture were obtained to the scale of individual islands, as fish vendors could rarely specify locations more precisely. For samples collected from landings from the local fishery, locations of capture were obtained to the level of individual areas of habitat (as delineated by their local names). These named fishing grounds were either distinct patches of habitat, or sections of continuous habitat, partitioned using landmarks (Appendix III). Fish were purchased from fishers/vendors, at market price (5 – 60 PGK, dependant on weight). Fishes were weighed (to the nearest 0.1 grams) and measured (total length [TL] to the nearest mm). Total length (TL) and fork length (FL) are equivalent for both *E. fuscoguttatus* and *E. polyphekadion*, due to rounding of the caudal fin. Both sagittal otoliths were removed, cleaned, and catalogued, and where present (fish were often already gutted at market stalls) whole gonads were removed, and stored in a 4% formaldehyde solution. All sample collections were carried out by a local representative of The Nature Conservancy (for Kavieng market samples), or trained local fishers (for Dyual Island samples). Initially, all samples were intended to be collected from Dyual Island; however a violent land dispute in April 2014 largely halted work on the island. At this time Kavieng market collections were initiated in response. These were gradually phased out as Dyual Island collections became possible again in early 2015 (Table 3.2).

Table 3.2 - Number of *E. polyphekadion* and *E. fuscoguttatus* samples collected by month and year from the two sampling regions.

	Epinephelus polyphekadion					*Epinephelus fuscoguttatus*				
	Dyual Island		Tigak Islands			Dyual Island		Tigak Islands		
Month	2014	2015	2014	2015	*Total*	2014	2015	2014	2015	*Total*
January	0	5	0	5	*10*	0	2	0	4	*6*
February	6	10	0	0	*16*	1	7	0	12	*20*
March	85	2	0	4	*91*	33	4	0	10	*47*
April	8	51	22	0	*80*	0	12	26	1	*39*
May	2	51	0	0	*53*	0	41	0	0	*41*
June	2	52	0	0	*54*	1	30	0	0	*31*
July	0	17	30	0	*47*	0	17	13	0	*30*
August	5	29	43	0	*77*	4	25	45	0	*74*
September	5	26	13	0	*44*	1	15	20	0	*36*
October	2	0	45	0	*47*	0	0	39	0	*39*
November	1	0	44	0	*45*	2	0	42	3	*47*
December	2	0	8	0	*10*	3	0	7	0	*10*
Total	**118**	**243**	**205**	**9**	***575***	**45**	**153**	**192**	**30**	***420***

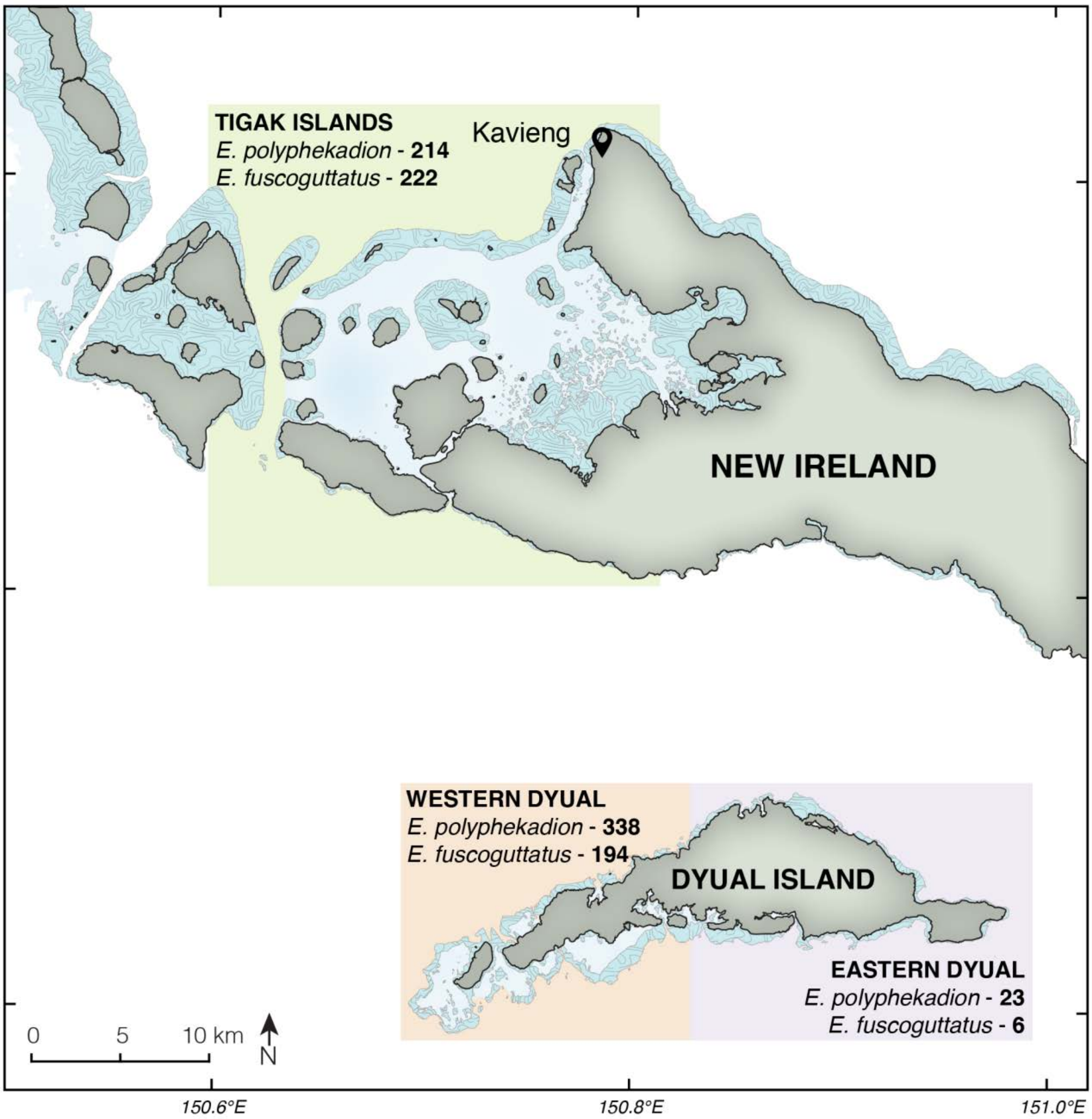

Figure 3.2 - Map of collection sites.

Additionally, 65 *Epinephelus fuscoguttatus* and 479 *E. polyphekadion* individuals were sampled during a tagging study in May – June 2013, at a spawning aggregation located on reef proximal to Dyual Island. These grouper were captured using baited hook-and-line, weighed (to the nearest 0.1 grams) and measured (total length [TL] to the nearest mm). Individuals were also sexed where possible by applying gentle pressure to the abdomen or by inserting a sterile cannula into the gonophore. Age estimates, and histological examination of gonads were unable to be collected for these individuals, as they were non-fatally sampled.

3.3.2 Preparation and analysis of otoliths

Age estimates were obtained and verified using otolith aging techniques modified from other otolith-based studies [e.g. Choat & Axe (1996)]. One otolith per individual was weighed (to the nearest 0.1 mg). This otolith was set in thermoplastic adhesive (Crystalbond 509) on the end of a microscope slide. The otolith was then ground down to the nucleus using P1200 grit wet/dry sandpaper on a GEMMASTA GFL8 lapping wheel. The remaining otolith half was then reset in the centre of the slide, with the ground surface against the slide, before being ground down to a section of approximately 300 µm thickness. Finally, this section was coated in adhesive to aid microscopic examination (Figure 3.3 a-b). A subset of smaller otoliths (n = 10) for each species hand ground with lapping film and polished with alumina powder by hand, to a thickness at which daily growth rings were visible (Figure 3.3c).

Otolith sections were then examined under transmitted light (under a high-power microscope for annual counts, and a compound microscope for daily counts) linked to an image capture device. An experienced reader counted opaque bands on three separate occasions, separated by at least two weeks (Figure 3.3). For annual counts, final age was assigned where two or more readings matched, or where all counts were within one year of the median. If this criterion was not met, the otolith was excluded from analysis. For daily counts, final age was assigned as the mean of three counts, when all counts were within 10% of the median. If this criterion was not met, the otolith was excluded from the analysis.

3.3.3 Validation of otolith ageing techniques

Interpretation error was minimised by establishing a consensus of age estimates by two experienced readers using a subset of 30 otoliths across the studied age range (Campana 2001). The most robust method to validate whether opaque bands represent annuli involves marking individuals in the wild with oxytetracycline (OTC), which leaves a distinct mark on the otolith that is visible under ultraviolet illumination (Cappo *et al.* 2000). Although validation via OTC marking has not been successfully applied in the wild, captive wild-caught individuals of both study species have been validated (Pears 2005). Finally, the relationship between whole otolith weight and putative age (number of opaque bands) was examined by fitting least-squared regressions to the data. A strong correlation is presumably due to the continued accretion of calcium carbonate to the otolith throughout the lifespan of the fish.

Figure 3.3 – Thin (~300 µm) transverse sections of sagittal otoliths for: *E. polyphekadion* (a) a sexually immature fish (274 mm TL, 4 yrs putative age); and *E. fuscoguttatus* (b) an actively spawning mature male (660 mm TL, 21 yrs putative age), and (c) a sexually immature fish (147 mm TL, 137 days putative age) with inset showing the white rectangle area in detail. Dark blue rectangles indicate opaque bands, denoting annuli (for a & b), or daily growth bands (for c).

3.3.4 Preparation and analysis of gonad samples

Gonad samples were blotted dry and then weighed (to the nearest 0.1 mg). A transverse section was cut from the central region of each gonad. Additional transverse sections were cut from the proximal and distal regions for a representative subset of 30 gonads. Each section was dehydrated in a series of increasing grades of ethanol, set in paraffin wax, sectioned to a thickness of 5 µg, and then mounted to a microscope slide and stained with Mayer's Haematoxylin and Young's eosin–erythrosin. Sections were examined under a high-powered microscope under transmitted light. Individuals were classified into reproductive categories based on the presence and state of development of germinal cells (Brown-Peterson *et al.* 2011). Of the 443 *E. polyphekadion* gonads that were histologically examined, sex was able to be determined for 402 individuals, and maturity was able to be estimated for 393 individuals. Additionally, 46 individuals were classified as mature females and 185 individuals were classified as mature males following macroscopic examination during the tagging study (Chapter 4). Of the 294 *E. fuscoguttatus* gonads that were histologically examined, sex was able to be determined for 177 individuals, and maturity was able to be estimated for 173 individuals. Additionally, 9 individuals were classified as mature females and 40 individuals were classified as mature males following macroscopic examination during the tagging study (Chapter 4).

Table 3.3 – Phases of sexual development as distinguished by histological examination of gonads, modified from (Brown-Peterson *et al.* 2011). Cell stages: OM – oocyte maturation, PG – primary growth, CA – cortical alveolar, Vtg1 – primary vitellogenic, Vtg2 – secondary vitellogenic; Vtg3 – tertiary vitellogenic, GVM – germinal vesicle migration, GVBD – germinal vesicle breakdown, POF – postovulatory follicle complex, Sg1 – primary spermatogonia, Sg2 – Secondary spermatogonia, Sc1 –primary spermatocytes , Sc2 – secondary spermatocytes, St – spermatids, Sz – spermatozoa, GE – germinal epithelium.

Sex	Reproductive phase	Histological features
Female	Immature	No evidence of prior spawning. Only oogonia and PG oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes.
	Developing	PG, CA, Vtg1, and Vtg2 oocytes present. No evidence of POFs or Vtg3 oocytes. Some atresia can be present.
	Spawning capable	Vtg3 oocytes present or POFs present in batch spawners. Atresia of vitellogenic and/or hydrated oocytes may be present. Early stages of OM can be present. *Actively spawning subphase:* oocytes undergoing late GVM, GVBD, hydration, or ovulation.

	Regressing	Atresia (any stage) and POFs present. Some CA and/or vitellogenic (Vtg1, Vtg2) oocytes present.
	Regenerating	Only oogonia and PG oocytes present. Muscle bundles, enlarged blood vessels, thick ovarian wall and/or gamma/delta atresia or old, degenerating POFs may be present.
Bisexual	Transitional	Presence of both oocytes and spermatogenic tissue. Evidence of prior spawning requires presence of atresia of vitellogenic oocytes (Vtg) and muscle bundles.
	Inactive bisexual	Presence of both oocytes and spermatogenic tissue. No evidence of prior spawning as a female or male. Closely packed previtellogenic oocytes, though no vitellogenic or atretic tissue present.
Male	Immature	Only Sg1 present; no lumen in lobules.
	Developing	Spermatocysts evident along lobules. Sg2, Sc1, Sc2, St, and Sz can be present in spermatocysts. Sz not present in lumen of lobules or in sperm ducts. GE continuous throughout.
	Spawning capable	Sz in lumen of lobules and/or sperm ducts. All stages of spermatogenesis (Sg2, Sc, St, Sz) can be present. Spermatocysts throughout testis, active spermatogenesis. GE can be continuous or discontinuous. Histological subphases based on structure of GE. *Early-GE:* continuous GE in all lobules throughout testes. *Mid-GE:* continuous GE in spermatocysts at testis periphery, discontinuous GE in lobules near ducts. *Late-GE:* discontinuous GE in all lobules throughout testes.
	Regressing	Residual Sz present in lumen of lobules and in sperm ducts. Widely scattered spermatocysts near periphery containing Sc2, St, Sz. Little to no active spermatogenesis. Spermatogonial proliferation and regeneration of GE common in periphery of testes.
	Regenerating	No spermatocysts. Lumen of lobule often non-existent. Proliferation of spermatogonia throughout testes. GE continuous throughout. Small amount of residual Sz occasionally present in lumen of lobules and in sperm duct.

3.3.5 Data analysis

All analyses detailed below were separately carried out on data collected for *E. fuscoguttatus* and *E. polyphekadion.*

Longevity was estimated by reporting the maximum recorded ages of sampled populations, termed T_{max} (Choat and Axe 1996). Although T_{max} estimates may over-emphasise the outliers of sampled populations where sample sizes are limited (Gust *et al.* 2002), the commonly used alternative, 10% longevity (the mean age of the oldest 10% of the sampled populations), was not reported here. Differing sample collection strategies limits the direct comparability of 10% longevity between this and previous studies (Pears *et al.* 2006; Rhodes *et al.* 2011). In particular, collections for this study actively targeted smaller individuals (to facilitate analysis of ontogenetic shift; Chapter 4), whereas earlier studies collected samples from commercial and recreational fisheries, which are likely to preferentially target larger individuals. Thus 10% longevity estimates are likely to be unevenly biased between studies.

The relationship between length and weight was calculated for each species from measurements taken during a concurrent tagging study (Chapter 5), and from all ungutted individuals from this study (*E. polyphekadion*, n = 905; *E. fuscoguttatus*, n = 331). Length-weight relationships were then determined by least-squared regression.

Sex-specific length-at-age data were fitted with the von Bertalanffy growth function (VBGF), using non-linear least-squares methods;

$$L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$$

where, L_t is the mean size-at-age t, L_∞ is the mean asymptotic length, K is the growth coefficient that describes the curvature of growth towards L_∞, t is the age of the fish, and t_0 is the theoretical age at which total length (TL) = 0.

Curves were fitted without constraining the y-intercept to an estimated age-at-settlement. Although constraining the y-intercept has been shown to improve precision of parameter estimates (Kritzer *et al.* 2001), it has more recently been demonstrated that slight deviations in the constrained value can cause considerable bias in parameter estimates, and constraint provides no benefit even when matching the true size at settlement (Pardo *et al.* 2013). However, unconstrained parameter estimates are only likely to be accurate if the sample contains juveniles, as with this study (Berumen 2005).

Patterns of growth were also examined by fitting the reparametrised von Bertalanffy growth function (rVBGF) to the age and length data. Although equivalent to the VBGF, the rVBGF contains three parameters; L_τ, L_ω, and L_μ representing mean length at ages τ, ω, and μ. These parameters can be set to biologically meaningful ages, and their inclusion facilitates the direct comparison of mean size-at-age data between sexes, regions, or species. The rVBGF function is as follows (Francis 1988);

$$L_t = L_\tau + \frac{\left(L_\mu - L_\tau\right)\left[1 - r\left(2\frac{t-\tau}{\mu-\tau}\right)\right]}{1 - r^2}$$

where $r = \frac{L_\mu - L_\omega}{L_\omega - L_\tau}$, and L_t is the mean size-at-age t as predicted by the model, provided that $L_\tau < L_\omega < L_\mu$ and $\left(L_\mu - L_\omega\right) \neq \left(L_\omega - L_\tau\right)$.

Size and age at maturity

Sex specific size at sexual maturity was calculated by fitting a logistic function to the proportion of mature individuals in the sample-set, using the following equation;

$$P_S = \left(1 + e^{-\ln\frac{19(S - S_{50})}{S_{95} - S_{50}}}\right)^{-1}$$

where P_S is the proportion of mature individuals in any size class S (*E. polyphekadion:* 20 mm, *E. fuscoguttatus:* 40mm), and S_{50} and S_{95} are sizes where 50% and 95% of the sample-set are mature, respectively (Williams *et al.* 2008). Similarly, sex specific age at sexual maturity was calculated by fitting the function;

$$P_A = \left(1 + e^{-\ln\frac{19(A - A_{50})}{A_{95} - A_{50}}}\right)^{-1}$$

where P_A is the proportion of mature individuals in any age class A (1 yr), and A_{50} and A_{95} are the ages where 50% and 95% of the sample-set are mature, respectively. Equations were optimised for size and age of each sex, for both species, were separately fitted using logistic regression analysis. Corresponding 95% confidence intervals were calculated by bootstrap resampling, with 1000 bootsamples.

3.4 Results

3.4.1 Validation of ageing protocols

Otolith sections had visible alternating transparent and opaque bands that allowed age estimation in 99% of cases for *E. polyphekadion* (n = 483), and 99% of cases for *E. fuscoguttatus* (n = 347). Of these, at least two age estimates were identical in 82% of cases for *E. polyphekadion* (n = 401), and 91% of cases for *E. fuscoguttatus* (n = 316). The index of average percent error was 1% for *E. polyphekadion,* and 2% for *E. fuscoguttatus,* indicating high levels of precision of age estimation for both species.

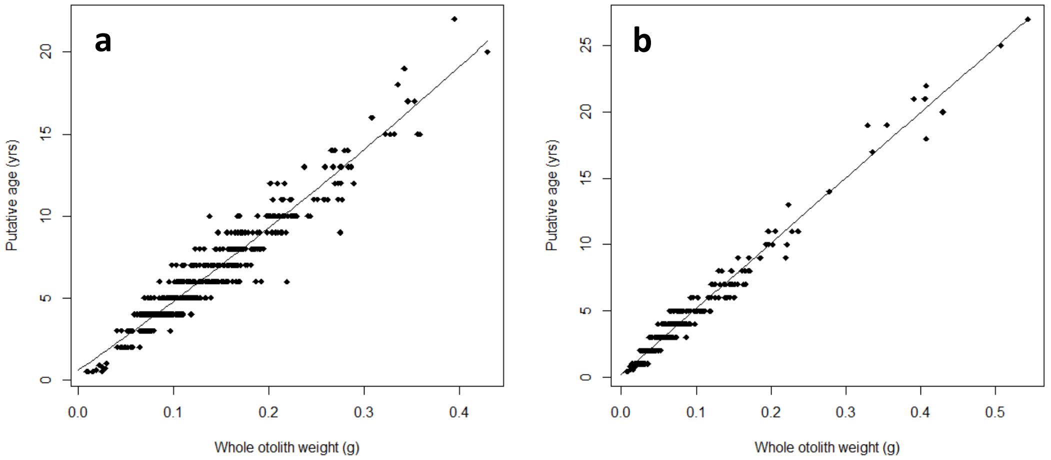

Figure 3.4 - Relationship between whole otolith weight (W [grams]) and putative age (A [years]) for (a) *E. polyphekadion* ($A = 14.1W^2 + 40.7W + 0.6$; $r^2 = 0.91$), and (b) *E. fuscoguttatus* ($A = -0.8W^2 + 49.8W + 0.2$; $r^2 = 0.97$).

3.4.2 Length-weight relationships

Captured *Epinephelus polyphekadion* individuals ranged from 100 to 534 mm TL (383.7 ± 2.5; mean ± S.E.), and from 18.6 g to 2.79 kg (1.04 ± 0.02 kg; mean ± S.E.). *Epinephelus fuscoguttatus* individuals ranged from 110 to 820 mm TL (381.6 ± 9.1; mean ± S.E.), and from 19.9 g to 8.84 kg (1.59 ± 0.10 kg; mean ± S.E.). The length-weight relationship for *E. polyphekadion* was $W = 9.01 * 10^{-6}\ TL^{3.10}$ ($r^2 = 0.97$), and for *E. fuscoguttatus* was $W = 1.72 * 10^{-5}\ TL^{3.00}$ ($r^2 = 0.97$) (Figure 3.5).

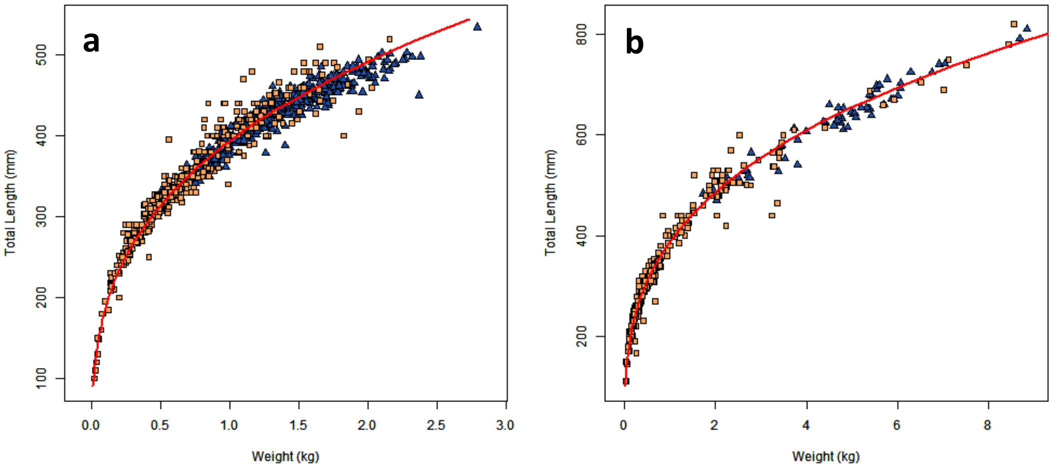

Figure 3.5 - Length-weight relationship for (a) *E. polyphekadion* (n = 892), and (b) *E. fuscoguttatus* (n = 331). Blue filled triangles show fish non-fatally individuals sampled from the spawning aggregation Site A and orange filled squares show individuals sampled from the local fishery. Red line represents the length-weight relationship obtained via 2nd order polynomial regression.

3.4.3 Age and growth analyses

Epinephelus polyphekadion are a long lived species, attaining ages of at least 31 yrs in both the Seychelles (Grandcourt 2005) and New Caledonia (Taylor & Rhodes unpub. data). The oldest individual captured with the fishery here was considerably younger at 22 yrs, as with a previous study in Pohnpei (Rhodes *et al.* 2011). Immature individuals ranged from 100 to 367 mm TL (277.0 ± 5.7 mm; mean ± S.E. [n = 174]). Mature females ranged 278 to 490 mm TL (377.1 ± 3.8 mm [n = 136]). Mature males were on average significantly larger than mature females (t_{610} = -21.8, $p < 0.001$), ranging from 260 to 520 mm TL (428.5 ± 2.6 mm; [n = 274]), although females were present in all but the uppermost size class (Figure 3.6a). Conversely, females were absent from the upper third of the age range (Figure 3.6b). Mature females ranged from 4 to 14 yrs (7.6 ± 0.20 yrs; [n = 87]). Males were on average significantly older than females (t_{111} = 11.5, $p < 0.001$), with ages ranging from 5 to 22 yrs (10.7 ± 0.37 yrs [n = 80]). Ages of immature individuals ranged from 229 days to 8 yrs (4.4 ± 0.13 yrs [n = 174]).

Epinephelus fuscoguttatus are similarly long lived; the only existing study spanning Australia's Great Barrier Reef recorded a maximum age of 42 yrs (Pears *et al.* 2006). The oldest individual captured with the fishery here was considerably younger at 27 yrs. Immature individuals ranged from 145 to 464 mm TL (271.5 ± 7.6 mm [n = 87]). Mature females ranged 431 to 654 mm TL (518.6 ± 7.7 mm [n =409]). Mature males were on average significantly larger than mature females (t_{153} = -17.5, $p < 0.001$), ranging from 400 to 820 mm TL (652.9 ± 11.0 mm [n = 57]), and females were absent from upper size classes (Figure 3.6c). Females were also on average significantly younger than males (t_{17} = 7.0, $p < 0.001$), and were absent from the upper half of the age classes (Figure 3.6d). Mature females' ages ranged from 4 to 14 yrs (4.3 ± 0.25 mm [n = 39]); mature males' ages ranged from 5 to 27 yrs (15.7 ± 1.6 yrs [n = 17]). Ages of immature individuals ranged from 202 days to 7 yrs (2.6 ± 0.17 yrs [n = 103]).

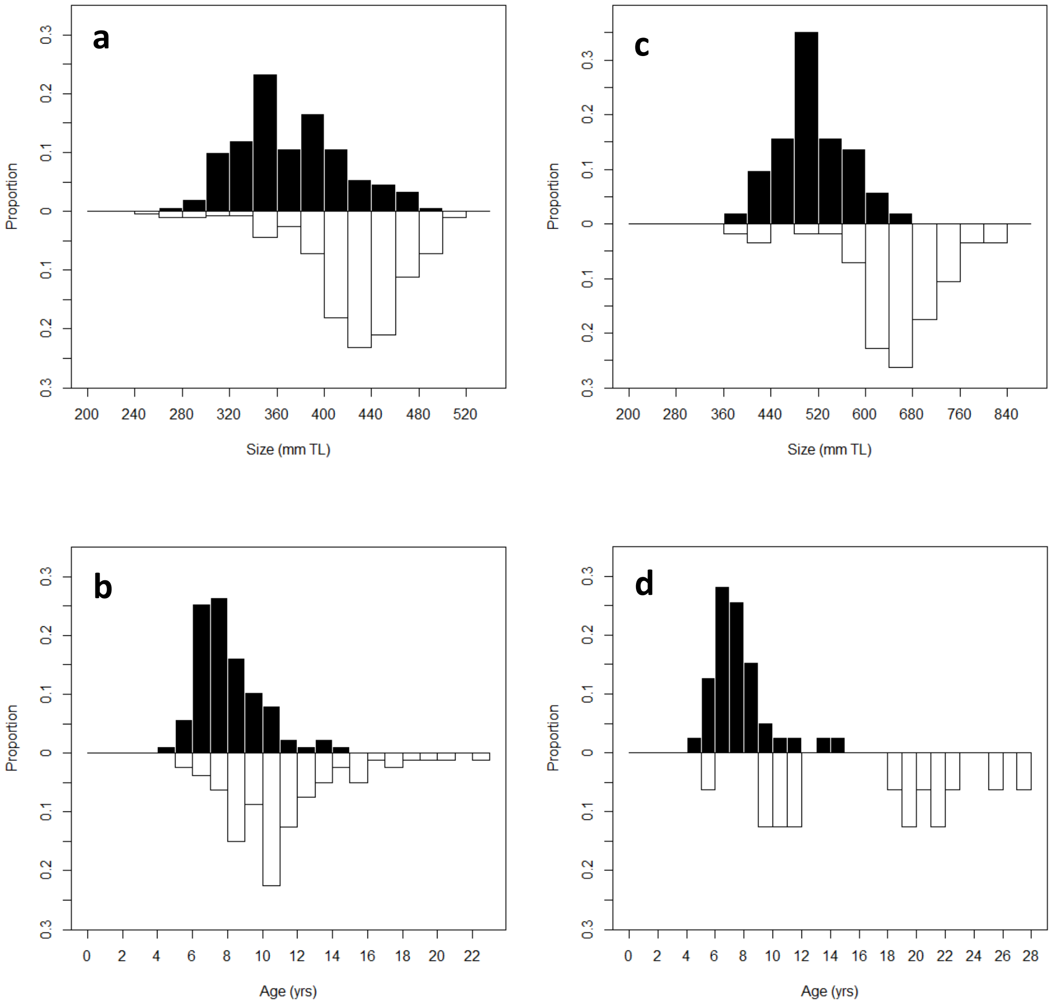

Figure 3.6 – Size and age frequency distribution histograms for *E. polyphekadion* ([a] and [b], respectively), and *E. fuscoguttatus* ([c] and [d], respectively). Black bars represent frequency of females, white bars represent frequency of males.

Epinephelus polyphekadion exhibited an asymptotic growth pattern (Figure 3.7a). Within the first 6.6 yrs of life *E. polyphekadion* exhibited moderate growth – approximately 80% of somatic growth occurred within this period. The growth coefficient and asymptotic length modelled here using the von Bertalanffy growth function (VBGF) (K = 0.23 and L_{∞}= 438.4 mm TL, respectively) were similar to previous work in Pohnpei (K = 0.25 and L_{∞}= 447.1) (Rhodes *et al.* 2011), although *E. polyphekadion* attained significantly greater lengths in the Seychelles (K = 0.18 and L_{∞}= 579).

Epinephelus fuscoguttatus also exhibited an asymptotic growth pattern, with most somatic growth occurring in the first 8.3 yrs, by which time 80% of L_{inf} was reached (Figure 3.7b). *Epinephelus fuscoguttatus* attained maximum and asymptotic sizes (K = 0.19, L_{∞}= 647.5 mm

TL) approximately 50% greater than *E. polyphekadion* here, although grew considerably smaller than their conspecifics at Australia's Great Barrier Reef (K = 0.16, L_∞= 806.9).

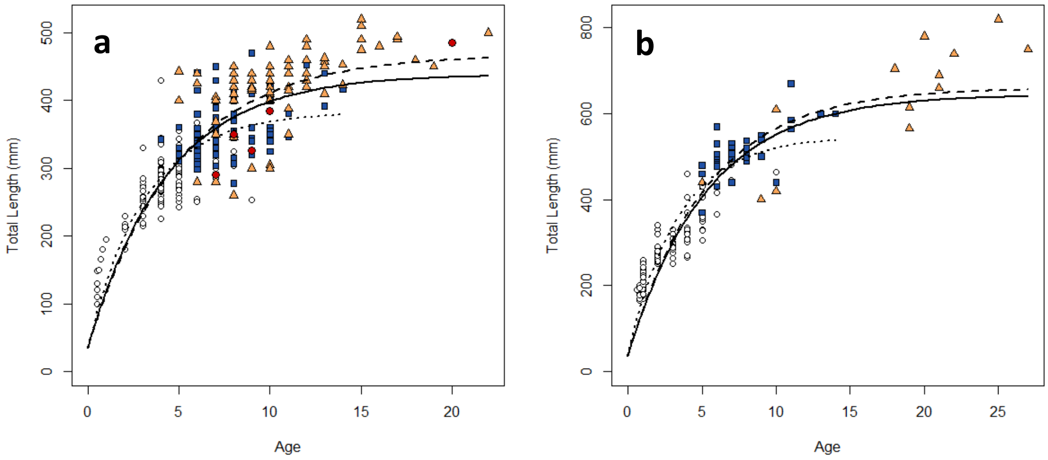

Figure 3.7 – Estimated sex-specific von Bertalanffy growth functions (VBGFs) of the form $L_t = L_\infty\{1 - \exp[-K(t - t_0)]\}$, for (A) *E. polyphekadion:* all samples (solid line) L_∞= 438.4, K = 0.23, and t_0 = -0.36, r^2 = 0.77; males (dashed line, yellow filled triangles) L_∞=467.7, K = 0.20, and t_0 = -0.38, r^2 = 0.80 and; females (dotted line, blue filled squares) L_∞= 382.9, K = 0.32, and t_0 = -0.30, r^2 = 0.69. For (B) *E. fuscoguttatus:* all samples (solid line) L_∞= 647.5, K = 0.19, and t_0 = -0.29, r^2 = 0.74; males (dashed line, yellow filled triangles) L_∞= 659.8, K = 0.19, and t_0 = -0.29, r^2 = 0.75 and; females (dotted line, blue filled squares) L_∞= 546.6, K = 0.29, and t_0 = -0.23, r^2 = 0.86. White filled circles represent immature individuals, and red filled circles represent bisexuals.

3.4.4 Reproductive biology

Analysis of Gonadal Somatic Index (GSI) by month revealed significantly increased GSI for both *E. polyphekadion* and *E. fuscoguttatus,* for both sexes, during May and June (Figure 3.12). This corresponds with the estimated peak aggregation period described using UVC (Hamilton *et al.* 2011) and acoustic telemetry (Chapter 4). However, although only marginally increased GSI was recorded during the months on either side of the peak, when both UVC and acoustic telemetry directly reported aggregations.

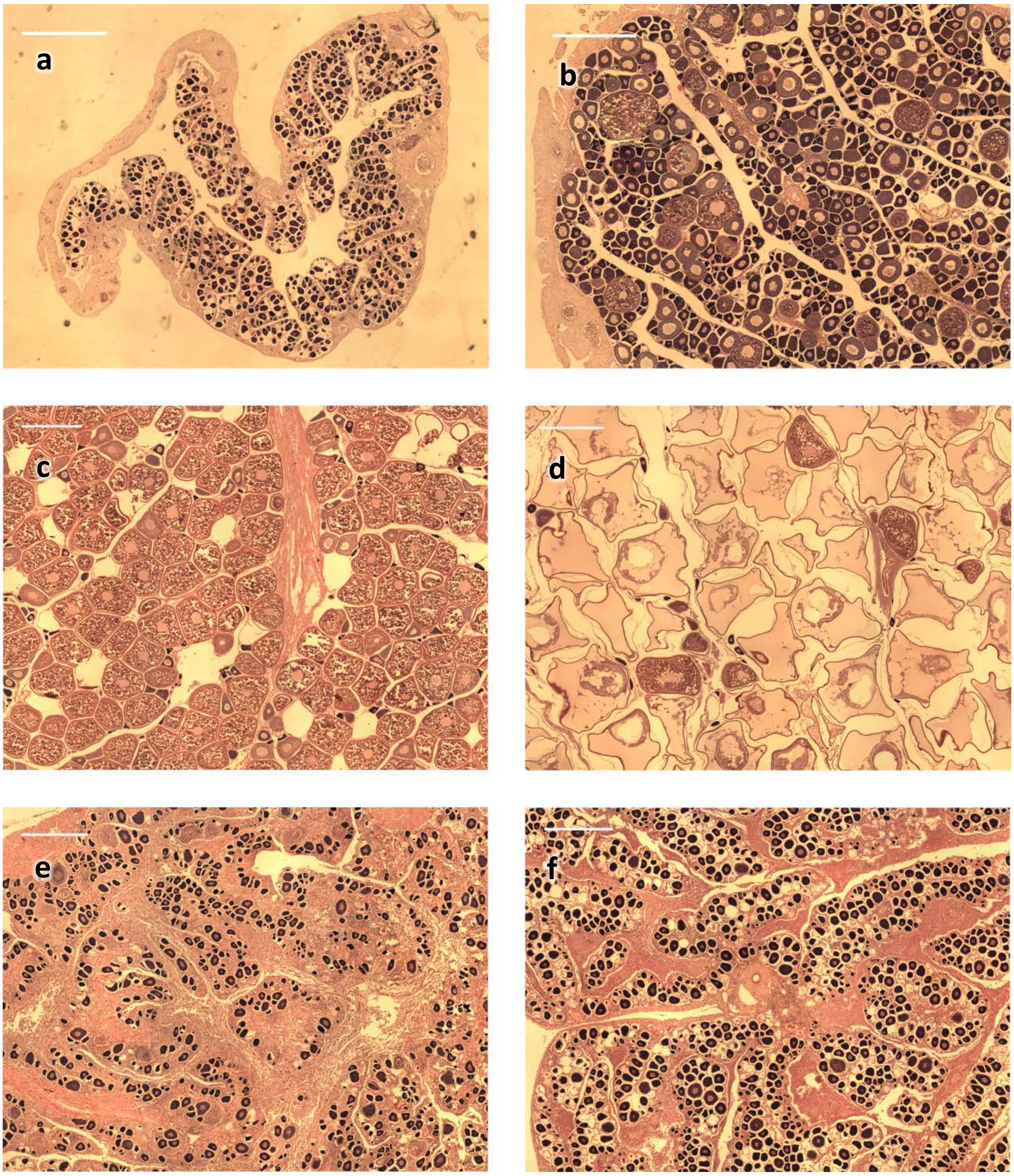

Figure 3.8 - Histological sections of *E. polyphekadion* female gonads - (a) immature (265 mm TL, 4 yrs age): PG cells tightly packed within lobules; (b) developing (355 mm TL, 10 yrs age): PG, CA, Vtg1, and Vtg2 cells throughout, inconclusive evidence of prior spawning with few muscle bundles, and cell wall of moderate thickness; (c) spawning capable (430 mm TL, 7 yrs age): Vtg1-3 cells predominate, large muscle bundle suggests prior spawning; (d) active spawning sub-phase (400 mm TL, 7 yrs age): hydrated cells predominate, some Vtg3 undergoing GVM (note some PG still present); (e) regressing (350 mm TL, 6 yrs age): atresia of vitellogenic cells, and POFs, large amounts of connective tissue and blue macrophage-like cells, some PG and CA; and (f) regenerating (347 mm TL, 7 yrs age): PG predominate, some atresia, muscle bundles, and POFs. White scale bars = 500 µm.

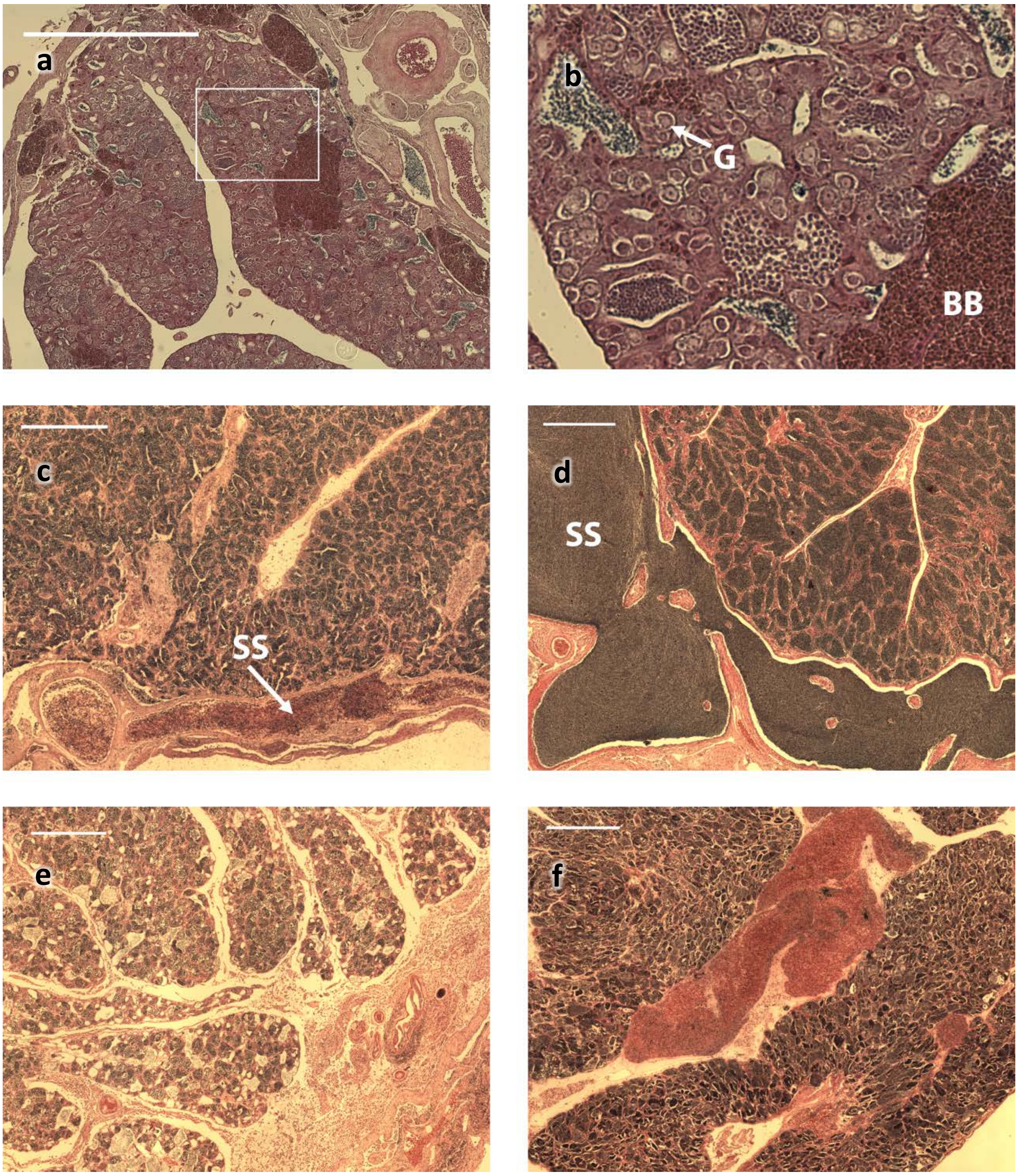

Figure 3.9 - Histological sections of *E. polyphekadion* male gonads - (a) developing (280 mm TL, 7 yrs age): spermatogonia predominates, scattered spermatogenesis and spermatozoa in sperm crypts, none in peripheral sperm ducts, sections of tightly packed brown-bodies [BB]; (b) close-up of white rectangle from (a) showing brown bodies [BB], spermatogonia [G], and pockets of spermatocytes; (c) spawning capable (350 mm TL, 11 yrs age): spermatozoa fills most sperm crypts, peripheral sperm ducts [SS] contain brown-bodies; (d) active spawning (423 mm TL, 14 yrs age): spermatozoa tightly packed in sperm crypts and peripheral sperm ducts [SS]; (e) regenerating (346 mm TL, 8 yrs age): loosely packed spermatozoa and spermatogenesis in sperm crypts, connective tissue throughout; (f) mature uncategorised (440 mm TL, 11 yrs age): sperm crypts filled with spermatozoa, large section of tightly packed brown bodies. White scale bars = 500 µm.

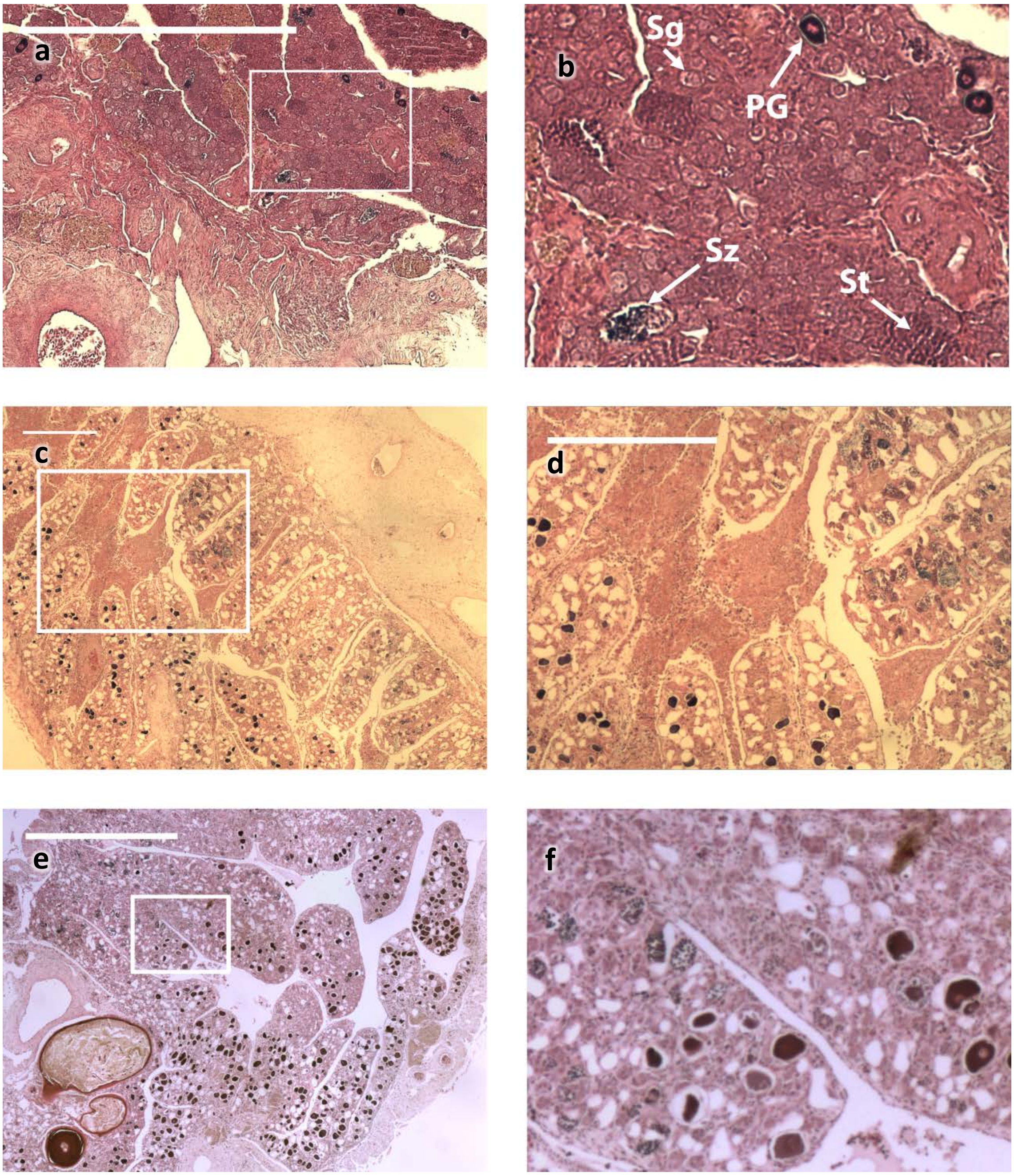

Figure 3.10 - Histological sections of *E. polyphekadion* bisexual gonads – (a) resembling early developing male (290 mm TL, 7 yrs age): small gonad, spermatogonia predominate, large sections of brown bodies; (b) close-up of white rectangle from (a) showing tightly packed spermatogonia [Sg], scattered PG cells, tightly packed spermatids [St] and spermatozoa [Sz] in sperm crypts; (c) resembling regenerating female (384 mm TL, 10 yrs age) scattered PG cells and spermatozoa in sperm crypts, large amount of connective tissue; (d) close-up of white rectangle from (c) showing connective tissue, and small amount of PG cells and spermatozoa; (e) resembling regenerating female (485 mm TL, 20 yrs age): heavily parasitised, scattered PG cells and spermatazoa; (f) close-up of white rectangle from (e) showing scattered PG cells and spermatazoa. White scale bars = 500 µm.

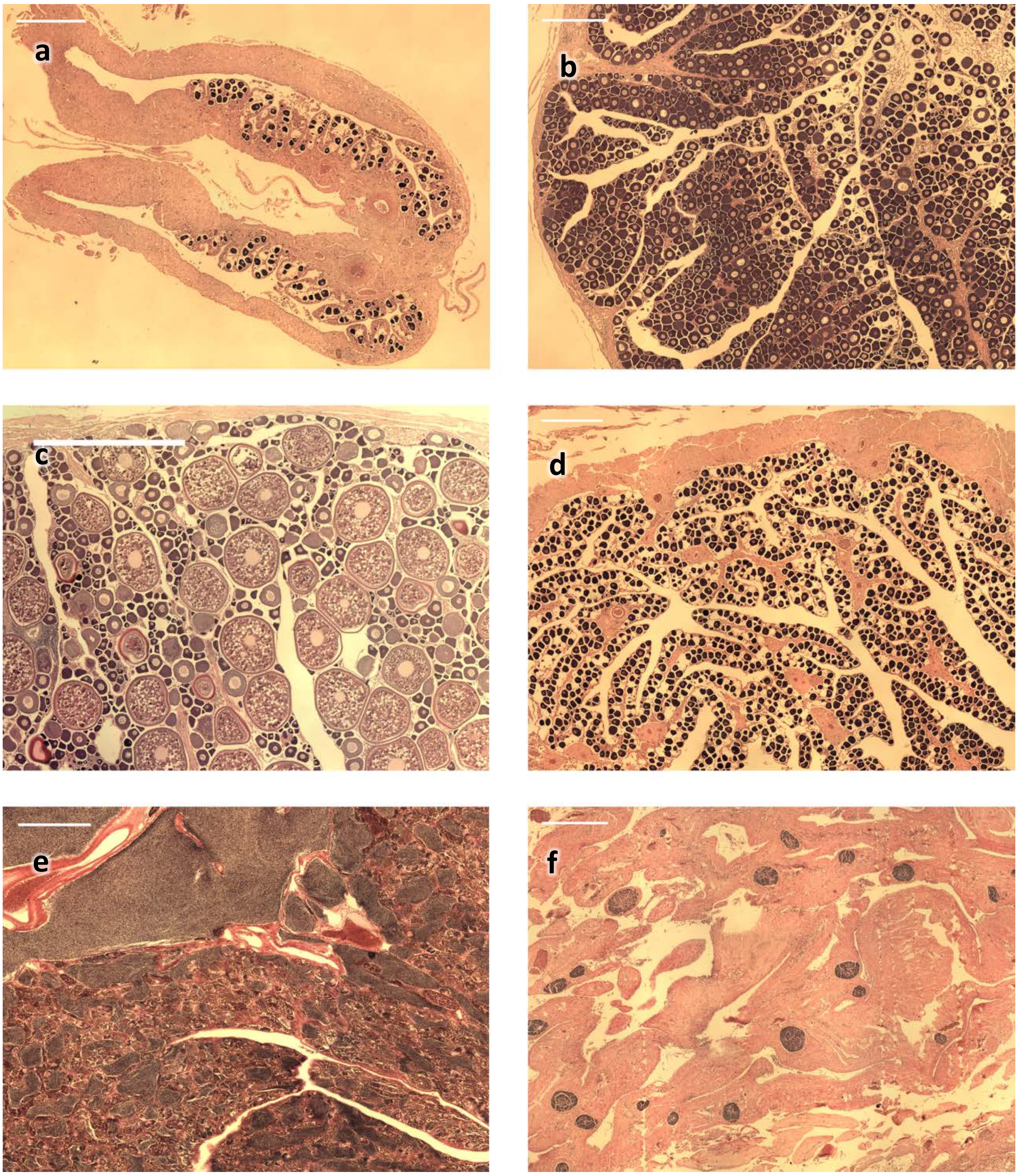

Figure 3.11 - Histological sections of *E. fuscoguttatus* gonads – (a) immature (331 mm TL, 5 yrs age): small gonad cross-section with some developing PG cells; (b) early developing female (450 mm TL, age unknown): PG and CA cells tightly packed within lobules, prior spawning uncertain; (c) late developing female (400 mm TL, 5 yrs age): PG, CA, Vtg1, and Vtg2 cells present, some atresia and POF present (d) regenerating female (550 mm TL, 9 yrs age) PG cells predominate, with scattered POF, muscle bundles and blood vessels; (e) active spawning male (660 mm TL, 21 yrs age): spermatozoa tightly packed in sperm crypts and peripheral sperm ducts; (f) regressing male (820 mm TL, 25 yrs age): large gonad with many empty spaces between thick connective tissue. White scale bars = 500 µm.

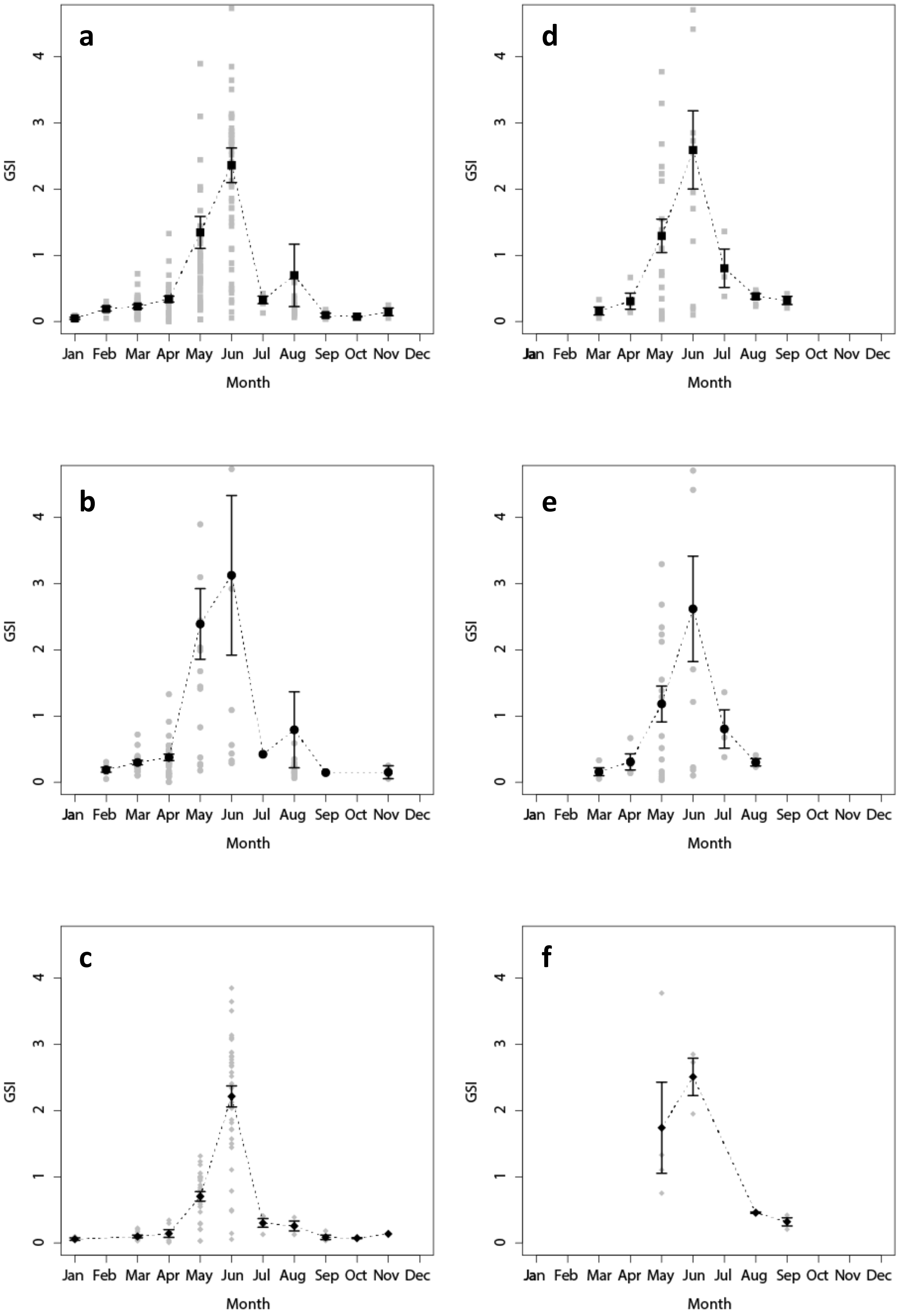

Figure 3.12 - Gonadal somatic index of samples, grouped by month, for *E. polyphekadion:* (a) all, (b) mature females, and (c) mature males; and for *E. fuscoguttatus:* (d) all mature, (e) mature females, and (f) mature males. Grey points represent the GSI of individual samples, black points and error bars represent monthly mean ± standard error.

For *E. polyphekadion,* the youngest mature female (A_F) was observed at 4 yrs of age, the logistic function indicated that half of the female population were mature (A_{50}; dashed line) at approximately 6.8 yrs, and all females were mature A_{100} by 8 yrs of age (Figure 3.13a). The smallest mature female (S_F) was 278 mm TL, the logistic function indicated that half of the female population were mature (S_{50}; dashed line) at approximately 333 mm TL, and all females were mature (S_{100}) over 380 mm TL (Figure 3.13b). The youngest mature males were observed at 5 yrs of age, and 260 mm TL (Table 3.4). These characteristics were similar to those reported from Pohnpei (S_{50} = 352 mm TL; A_{50} = 6.4 yrs) (Rhodes *et al.* 2011).

For *E. fuscoguttatus,* the youngest mature females (A_F) were observed at 4 yrs of age, the logistic function indicated that half of the female population were mature (A_{50}; dashed line) at approximately 5.6 yrs, and all females were mature (A_{100}) by 8 yrs of age (Figure 3.13c). The smallest mature female (S_F) was 370 mm TL, the logistic function indicated that half of the female population were mature (S_{50}; dashed line) at approximately 433 mm TL, and all females were mature (S_{100}) over 480 mm TL (Figure 3.13d). On Australia's Great Barrier Reef females entered the reproductive population younger and smaller, although the age and size at complete female maturity were similar (A_F = 3, A_{50} = 3.7, A_{100} = 7 yrs; S_F = ~290, S_{50} = 433, S_{100} = 480). The youngest mature males here were observed at 5 yrs of age, and 400 mm TL (Table 3.4), considerably younger and smaller than on Australia's Great Barrier Reef (11 yrs and 683 mm) (Pears *et al.* 2006).

Table 3.4 – Species-specific life history stages as described by detailed age-based demographics and sexual ontogeny (Chapter 3).

Life history Stage	Description	Size range (TL mm); Age range (yrs)	
		E. polyphekadion	*E. fuscoguttatus*
Juvenile	Prior to first female maturity	< 278; < 4	< 370; < 4
Early sub-adult	Between first & 50% female maturity	278 – 332; 4 – 6	370 – 436; 4 – 5
Late sub-adult	Between 50 and 100% female maturity	333 – 375; 7 – 8	437 – 481; 6 – 7
Adult	Subsequent to 100% female maturity	> 375; > 8	> 481; > 8
First male maturity	Subsequent to first male maturity	> 259; > 4	> 399; > 5

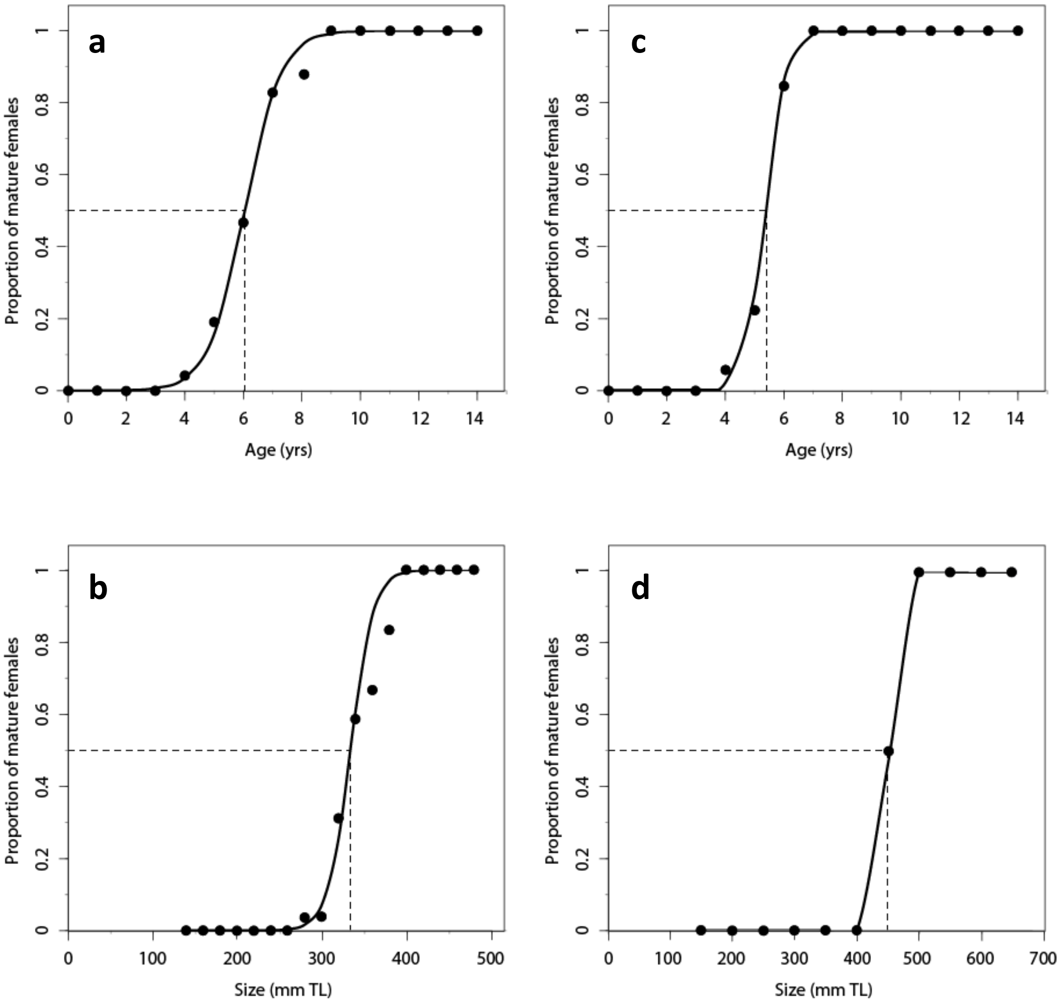

Figure 3.13 – Age and size at female sexual maturity for *E. polyphekadion* (a and b, respectively), and *E. fuscoguttatus* (c and d, respectively).

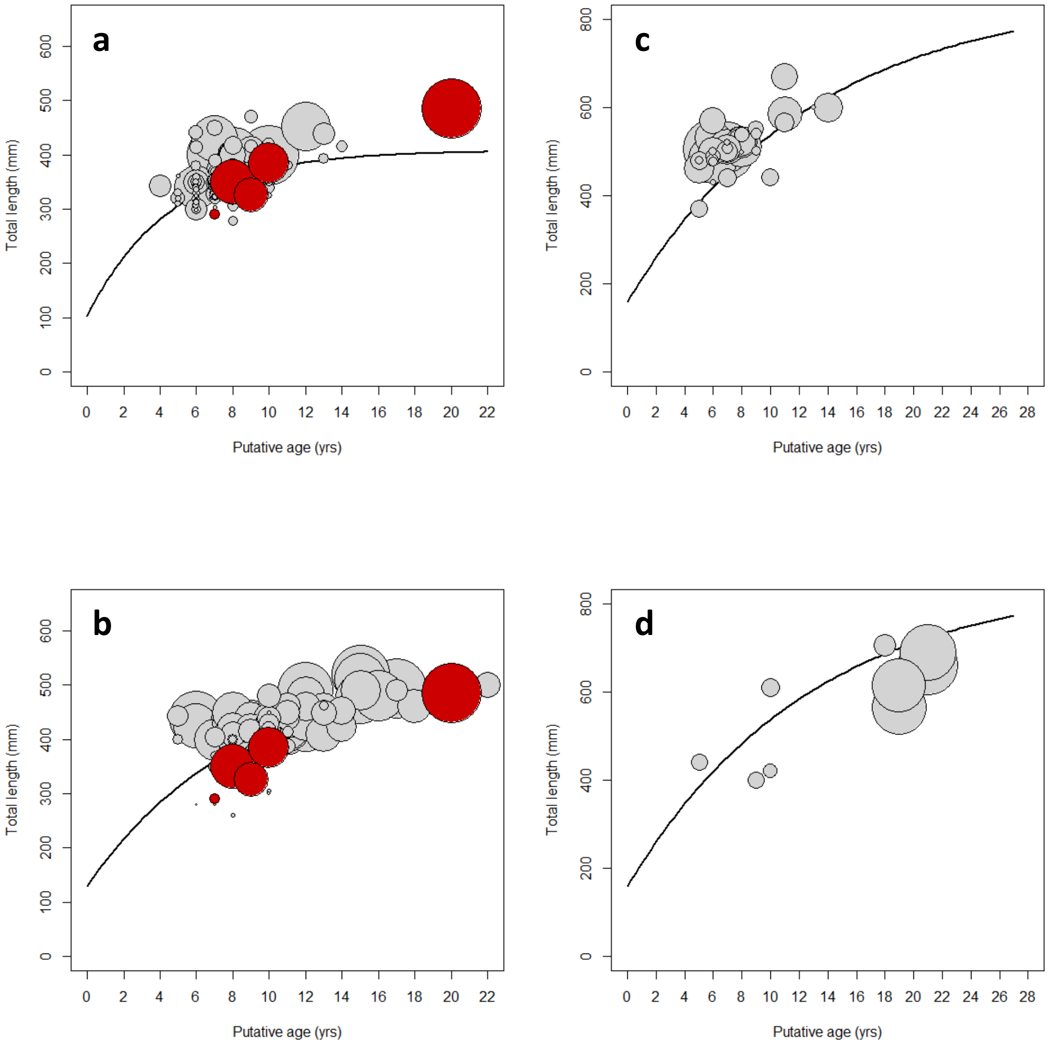

Figure 3.14 – Gonad weights (represented by circle area) for *E. polyphekadion* (a) mature females, and (b) mature males; and *E. fuscoguttatus* (c) mature females, and (d) mature males as a proxy for fecundity mapped onto the sex-specific von Bertalanffy growth functions calculated for that species (black curves). Filled red circles represent gonad weights of bisexuals (included in graphs of both sexes, although excluded from analyses for both sexes)).

3.5 Discussion

Both *Epinephelus polyphekadion* and *E. fuscoguttatus* exhibit demographic characteristics common to epinephelids that make them vulnerable to overexploitation (Craig *et al.* 2011). They are long-lived, moderately slow-growing, late to sexual maturity, and attain a large body size (Jennings *et al.* 1998, 1999; Reynolds *et al.* 2005). Both species recruited to the fishery considerably before size at first sexual maturity. However, *E. fuscoguttatus* were predominantly taken by the fishery before sexual maturity, while the majority of *E. polyphekadion* exploited were sexually mature. Despite the histological examination of a large number of juvenile individuals, sexual function could not be conclusively determined for either species. Sex specific demographic analyses however, suggest that *E. polyphekadion* functions as a diandric protogynous hermaphrodite, and *E. fuscoguttatus* as a monandric protogynous hermaphrodite here.

3.5.1 Age-based demographic characteristics

Due to the indeterminate growth patterns of fishes, demographic characteristics are strongly interrelated (Beverton and Holt 1957). Thus large bodied fishes are generally also relatively slow-growing, long lived, late to sexual maturity, and highly fecund over their reproductive lives. Such fishes have repeatedly been demonstrated to be more vulnerable to overexploitation (Reynolds *et al.* 2005). The specific characteristic or combinations of characteristics that drive this increased vulnerability are difficult to tease out due to their correlation, however recent comparative analyses have identified large body size and late sexual maturity to be the best predictors of vulnerability for coral reef fishes (Reynolds *et al.* 2005; Taylor *et al.* 2014). Vulnerability of a population to overexploitation is a function of the rate of elevated mortality due to exploitation (termed fishing mortality), and the rate at which the population is replenished. Late-maturing species are presumably more vulnerable to overexploitation due to their intrinsically lower rates of replenishment (Cinner and McClanahan 2006). Coral reef fisheries are often extremely size-selective, and larger bodied fishes are more desirable to fishers due their greater economic value. Thus larger body size presumably increases vulnerability due to elevated rates of fishing mortality.

Interestingly, the ages at maturity for *E. polyphekadion* and *E. fuscoguttatus* here were similar; females entered the reproductive population at between 4 – 8 yrs of age for both species. However, *E. fuscoguttatus* reached a maximum length here of 820 mm; 50% larger than the largest *E. polyphekadion*. Although *E. polyphekadion* reached 80% asymptotic length almost 2 yrs before *E. fuscoguttatus,* the latter grew considerably faster in absolute terms. Thus, *E. polyphekadion* reached maturity at much smaller sizes (279 – 368 mm) than *E. fuscoguttatus*

(370 – 480 mm). Creel surveys (see section 2.4.3.5) showed that both species recruit to the fishery before sexual maturity (*E. polyphekadion* – 188 mm; *E. fuscoguttatus* – 100 mm). However due to divergent growth rates, the mean size at capture from creel surveys for *E. polyphekadion* (409 ± 43 mm; mean ± SE) was above its size at 100% sexual maturity, while the mean size at capture for *E. fuscoguttatus* (337 ± 18 mm) was below its size at first sexual maturity. Mean sizes of capture from creel surveys were calculated from relatively low sample sizes (*E. polyphekadion,* n=7; *E. fuscoguttatus,* n=17). However, mean sizes at capture calculated from the larger demographic datasets (*E. polyphekadion,* 384 ± 3 mm, n=575; *E. fuscoguttatus,* 382 ± 9, n=420) produced similar results (although using the demographic data, *E. fuscoguttatus* were captured at a mean size marginally greater than size at first maturity). The latter dataset is not truly representative of the fishery, because smaller individuals were preferentially collected for analysis. However, as sampling bias affected both species equally, the comparison remains valid. Put simply, the majority of *E. polyphekadion* recruited to the reproductive population before the fishery, while the majority of *E. fuscoguttatus* recruited to the fishery before first reproduction. The implications of this differing fishing pressure across life-history stages are potentially profound. However, these will not be explored at length here, as this thesis is primarily concerned with spatial aspects of the fishery. It is worth noting however, that exploiting fish prior to maturity, termed growth overfishing, can dramatically reduce sustainable yields (Noble and Jones 1999). Minimum length limits that attempt to avert this issue are arguably the most common form of fisheries management globally (Coggins *et al.* 2007), and are used for these species elsewhere (Pears *et al.* 2006). However, size limits are uncommon in customary management (Cinner and Aswani 2007). Although directly addressing the capture of juvenile *E. fuscoguttatus* may not be feasible here, their predominance in the catch reinforces the need for other management measures, including the protection of juvenile habitat.

Both *E. polyphekadion* and *E. fuscoguttatus* are long lived, attaining maximum ages of at least 22 and 27 yrs here respectively, and at least 31 and 42 yrs respectively elsewhere within their range (Grandcourt 2005; Pears *et al.* 2006). Thus reproductive lifespans here may exceed 15 yrs for *E. polyphekadion*, and 20 yrs for *E. fuscoguttatus*. These long reproductive life spans in conjunction with high volume of gametes released per spawning event makes larger grouper among the most fecund of reef fishes (Sadovy 2001). Although it has long been proposed that this fecundity may increase the resilience of these large, late-maturing fishes relative to their smaller, less fecund congenerics, recent reviews have found no theoretical or empirical evidence to support this claim (Sadovy 2001; Reynolds *et al.* 2005). There is however substantial evidence that older, larger fishes (particularly females) within populations produce more robust offspring in abundances orders of magnitude higher than their smaller conspecifics (Birkeland and Dayton 2005; Hixon *et al.* 2014). Measures that protect these larger individuals, such as spatial closures, may therefore provide disproportionate management returns.

3.5.2 *Reproductive biology*

Epinephelus polyphekadion

Epinephelus polyphekadion has been variously described as protogynous, unresolved, and functionally gonochoristic with the potential for protogynous sex change (Bruslé-Sicard *et al.* 1992; Johannes *et al.* 1999a; Rhodes and Sadovy 2002b; Rhodes *et al.* 2011). This variety of conclusions highlights the difficulty in resolving the sexual pattern of this species, and epinephelids in general (Sadovy de Mitcheson and Liu 2008). The most recent description of *E. polyphekadion* as a functional gonochore relied heavily on demographic evidence such as non-significant sexual dimorphism in growth, and size and age distributions – in addition to the absence of transitional individuals (Rhodes *et al.* 2011). While these characteristics are certainly similar to other functionally gonochoristic epinephelids (Sadovy and Colin 1995; Posada 1996; Sadovy and Domeier 2005b; Erisman *et al.* 2008; Sadovy de Mitcheson and Liu 2008), this does not exclude diandric protogynous hermaphroditism. This is particularly true as protogynous sex change in this species had been previously supported by laboratory-induced (Debas 1989, Bruslé-Sicard et al. 1992) and field-observed sex change (Johannes et al. 1999). Contrary to the most detailed demographic analysis currently available for this species (Rhodes *et al.* 2011), in this study mature males were significantly larger and older than mature females (Figure 3.6a & b). The majority of males were larger (76%) and older (62%) than the size and length at 100% female maturity. Sexually dimorphic growth rates observed here (Figure 3.7a) could cause males to be larger regardless of sexual function. However excluding sex-specific differences in mortality rates (particularly in older cohorts), the sex-specific difference in age distributions observed here suggests a significant proportion of the population undergo protogynous sex change. The presence of mature males from the approximate age and size of first female maturity (Figure 3.6a & b) suggests the presence of primary males here, particularly as the smallest mature individual was male. This combined support for the presence of both primary and secondary males suggests that *E. polyphekadion* function as a diandric protogynous hermaphrodite here.

This study focused intensive collection and examination of a large number of small individuals to aid in resolving the sexual pattern of *E. polyphekadion.* Other studies that have examined epinephelid juveniles in greater detail have identified primary male development (Adams and Williams 2001; Adams 2003; Liu *et al.* 2016). All early immature *E. polyphekadion* gonads display female morphology (e.g. Figure 3.8a). The ultimate testicular structure of primary and secondary males that develop from such proto-ovarian gonads are generally morphologically indistinct (Sadovy de Mitcheson and Liu 2008). Confirmation of sexual pattern for *E. polyphekadion* therefore requires histological examination of bisexual individuals ('bisexual' here denotes the presence of female and male tissue in the gonad, and does not imply functional hermaphroditism), and identification of developing inactive bisexuals for gonochorism (Figure 3.1B), or transitional individuals for protogynous hermaphroditism (Figure 3.1C) (Sadovy de Mitcheson and Liu 2008). Distinction between these two requires the exclusion or confirmation of prior functioning as females, respectively. In practice, the exclusion of prior function as females is generally not possible, and thus gonochorism may be supported by an overwhelming lack of evidence of hermaphroditism rather than direct positive evidence. Of the 443 gonads histologically examined here, only five contained both female and male tissues. The rarity of bisexual individuals here, despite the large numbers of gonad histologically examined across a broad size and age range suggests a rapid gonadal transition in this species involving the complete removal of female germinal tissue, adding further difficulty to establishing sexual pattern.

No evidence of prior female function (*i.e.,* presence of atretic vitellogenic oocytes, or postovulatory follicle complexes [Sadovy de Mitcheson and Liu 2008; Brown-Peterson *et al.* 2011]) was detected in bisexual individuals, however prior female function could also not be ruled out by histological examination (Figure 3.10). Bisexuals covered a broad range of ages (7-20 yrs) and sizes (290-485 mm TL). The gonad of the smallest/youngest of these (Figure 3.10a, b) otherwise resembled the gonads of immature developing males of similar size and age (Figure 3.9a, b). Each contained spermatogonia, spermatids, and spermatozoa in spermatocysts throughout the lobules. Each also contained large sections of closely packed brown-bodies, which may play a role in rapid restructuring of the gonad. This individual had relatively low size-at-age and gonad weight (Figure 3.14c). The gonad structure of the remaining four bisexuals (Figure 3.10c - f) most closely resembled that of mature regressing males (Figure 3.9e). Sperm crypts throughout the lobules were largely empty, with scattered spermatogenesis and loosely packed spermatozoa. These four bisexuals were above the size and age at 50% female sexual maturity, and one individual was significantly above the size and age at 100% female maturity (Figure 3.13, Figure 3.14).

Taken together, the above evidence suggests that *E. polyphekadion* at western Dyual are diandric protogynous hermaphrodites. The absence of females in the largest and oldest size and age classes, from otherwise overlapping age and size distributions, lends support to diandry. However, the most extensive demographic examination of this species to date, in Pohnpei, found no sex-specific differences in size and age distributions and classified them as gonochoristic. *Epinephelus polyphekadion* may exhibit substantial plasticity in sexual function throughout their range – which would allow for these apparently contradictory results. The examination of large numbers of smaller individuals failed to deliver conclusive evidence of primary males, as it has for other epinephelids. Additional immunological work and behavioural observation of spawning are the likely required next steps to help resolve understanding the ambiguities around germinal elements of sexual transition in this species.

Epinephelus fuscoguttatus

The only previous histological analysis of *E. fuscoguttatus* described them as monandric protogynous hermaphrodites (Pears *et al.* 2007). Pears *et al.* (2007) found no direct histological evidence of transitional individuals. Rather, the classification of protogyny was based on the restriction of males to age and size cohorts substantially above that of 100% female maturity. As with previous work, in this study mature males were significantly larger and older than mature females (Figure 3.6c & d), suggesting the presence of secondary males. In this study, four males were identified smaller than the length at 100% female maturity, one of which was also younger than the age at 100% female reproduction. However, these individuals were all above the size and age at first female reproduction. These individuals could be primary males, but could equally be protogynous hermaphrodites undergoing sex change earlier and smaller, relative to on the Great Barrier Reef. Regardless, the vast majority of males were larger (96%) and older (92%) then the size and length at 100% female maturity. As such, although this study does not refute the possibility of diandry, it provides additional demographic evidence that supports their classification as functional protogynous hermaphrodites. Certainly from a management perspective, the very low numbers of males in lower size and age classes suggests protogyny as their dominant reproductive strategy here.

Implications for management

Classical stock-recruitment models are based on estimates of recruitment, fecundity, and mortality under assumed conditions of static sex ratios, and fail to account for sex-selective fishing (Beverton and Holt 1957; Pauly 1998). Hermaphroditic fishes are often presumed to be more vulnerable to overfishing –due to sperm limitation or Allee effects (Provost and Jensen 2015). However plasticity in sexual pattern, as is hypothesised here for *E. polyphekadion,* may in fact increase their resilience to exploitation under certain conditions (Alonzo and Mangel 2004). Additional reproductive studies are required to assess whether *E. fuscoguttatus* displays similar plasticity. Information on sexual pattern is increasingly being incorporated into stock assessments (Alonzo *et al.* 2008; Provost and Jensen 2015), and ecosystem-based management (Chan *et al.* 2011). Information on plasticity in sexual pattern across different fishery-targeted species represents an important consideration.

3.5.3 Critiques and caveats

The method of sample collection utilised here provided data that were substantially skewed towards smaller, younger individuals. As such, a number of commonly reported demographic metrics have been omitted from the analysis here, including levels of natural and fishing mortality, and '10% longevity'. These metrics were omitted as they are heavily dependent on representative samples of study populations. Conversely, the demographic and reproductive characteristics presented here are minimally affected by skewed samples.

3.5.4 Conclusions

Epinephelus polyphekadion and *E. fuscoguttatus* both exhibit characteristics associated with increased vulnerability to overexploitation; they are both relatively slow-growing, long lived, late to sexual maturity, and attain a large body size. However, *E. fuscoguttatus* grows to maximum lengths approximately 50% greater than *E. polyphekadion,* and reaches sexual maturity at sizes approximately 100 mm larger. Creel survey data from the previous chapter demonstrates that this results in the two species being exploited by the local fishery differently – *E. polyphekadion* primarily as adults, and *E. fuscoguttatus* primarily as juveniles. Despite examination of a large number of gonads across broad size and age ranges, I found no conclusive histological evidence of primary or secondary males in either species. However, demographic evidence led to the classification of *E. polyphekadion* as a diandric protogynous hermaphrodite, and *E. fuscoguttatus* as a monandric protogynous hermaphrodite here. These demographic and reproductive characteristics have implications for the management of these species both here and more broadly throughout their ranges. Importantly, the age- and size- at maturity functions developed here will be employed in the succeeding chapter to examine the ontogenetic shift in habitat use for these species.

CHAPTER 4 - ONTOGENETIC SHIFT IN SUITABLE HABITAT FOR TWO LARGE EPINEPHELIDS

4.1 Synopsis

The life histories of coral reef fish add an additional degree of complexity to managing small-scale, multi-species reef fisheries, with habitat requirements differing not only across species, but also across life history stages of individual species (Lindeman *et al.* 2000; Wilson *et al.* 2010). For example, many coral reef fishes recruit into nearshore habitats before making ontogenetic migrations to outer coral reefs, and these nearshore habitats are often vulnerable to degradation from anthropogenic threats such as land development, which can degrade recruitment habitat and in turn impact adult populations of fish (Beck *et al.* 2001; Mumby *et al.* 2004; McMahon *et al.* 2011, 2012). Despite this, ontogenetic shifts in habitat suitability are currently poorly understood for many coral fishes, including economically important species of grouper. In this study, I used maximum entropy species distribution modelling (MaxEnt) to estimate the location and spatial extent of suitable habitat of *Epinephelus polyphekadion* and *E. fuscoguttatus*, for the first time, throughout their post-settlement life histories. The resulting models indicate that the habitat suitability for the two species was similar. Juveniles (*i.e.,* individuals under the age/size at first female maturity) were restricted to habitat directly fringing the islands. Suitable habitats consisted of mosaics of limestone pavement, coral rubble, seagrass, macroalgal clumps, and live coral heads. Areas of this 'fringing mosaic' habitat adjacent to mangroves and freshwater inputs provided hotspots of highly suitable juvenile habitat. Suitable habitat progressively expanded throughout the groupers' life histories. Adult (*i.e.,* individuals above the age/size at 95% female maturity) habitat included patch and barrier reef habitats characterised by high live coral cover, as well as the fringing mosaics preferred by juveniles. Patterns of ontogenetic shift in habitat suitability were similar whether life-stages were dissected according to fish length or age, however the timing of shifts – relative to reproductive stage – differed somewhat. The spatial distributions of suitable habitat for various post-settlement life history stages examined within this chapter will be investigated in detail in the final chapter of this thesis, specifically to examine how patterns of fishing effort and governance disproportionately affect juvenile versus adult habitat.

4.2 Introduction

The bi-partite life cycle of coral reef fishes enables long-distance movement during the pelagic larval stage, facilitating connectivity between reef systems, but also between spatially segregated habitats. Directly following the larval stage, many coral reef fish settle into benthic habitats that are distinct from those preferred by adults of the same species (Lindeman *et al.* 2000). Subsequent ontogenetic shifts in habitat preference presumably allow individuals to maximise their varying fitness requirements from settlement through to adulthood. This is particularly important during early post-settlement life history, when mortality rates are extremely high. Settlement-stage larvae, may initially settle in first-occupied suitable habitat to avoid predation, then shift through other nursery habitat in a step-wise fashion, as their relative fitness requirements progress (Nagelkerken *et al.* 2015). For example, in the Caribbean, Nassau grouper *Epinephelus striatus* predominantly settle into shallow-water estuarine systems dominated by macroalgal clumps. Within these systems, early juveniles remain within the interstices of macroalgal clumps until approximately 50 mm TL, and remain closely associated with macroalgal clumps until approximately 110-190 mm TL. After this time juveniles move to nearby patch reefs (Eggleston 1995), and ultimately to deeper offshore reefs (Dahlgren and Eggleston 2000). These shifts are consistent with size-mediated optimisation of habitat to minimise the ratio of mortality to growth (Dahlgren and Eggleston 2000). Immediately post-settlement predation risk is extreme, thus micro-habitats offering superior shelter are likely preferable (Almany 2004). In Nassau grouper, the period of close association with macroalgae-dominated habitat coincides with >90% mortality (Dahlgren and Eggleston 2001). As juvenile fish grow and predation risk declines, habitats with superior foraging potential become increasingly desirable, as maximising growth becomes increasingly important to overall fitness.

The importance of protecting early life history habitat is widely recognised (FAO 2014). In most studied grouper species, juveniles settle into nearshore areas such as mangroves, seagrass beds, and estuarine areas (Craig *et al.* 2011). However almost all currently published studies were conducted in the Caribbean, and despite their ecological, commercial, and social importance very little is known about the early life history of Indo-Pacific species of grouper (Craig *et al.* 2011). Juvenile *E. fuscoguttatus* have been observed in seagrass beds (Sommer *et al.* 1996; Gell and Whittington 2002) and in mixed seagrass- macroalgae-dominated habitat, as well as in extensive mangroves systems near tidal flats, river mouths, and other reduced salinity areas (Sadovy 2000). In addition to fishing-related threats, such near-shore habitats risk degradation from land-based activities such as changing land use practices, contamination of freshwater sources, and habitat destruction for development (Bartley *et al.* 2014). Conversely, the limited available evidence suggests that *E. polyphekadion* juveniles are more general in their habitat requirements. In Palau, Tupper (2007) reported capturing recently settled *E. polyphekadion* juveniles of 35-50 mm TL throughout lagoonal habitats, in low branching coral with associated macroalgae, branching coral, massive coral, and coral rubble microhabitats (Tupper 2007), while juveniles of >100 mm TL were caught on hook-and-line in turbid water on rubble patches near mangroves in Pohnpei (Rhodes 2012).

Studies detailing the precise micro-habitat associations of juvenile fishes throughout their early life history are of doubtless importance. However, such information may be of negligible immediate assistance to managers. Mapping the extent of microhabitats such as coral heads and macro-algal clumps, at seascape scales relevant to management is likely to be prohibitively expensive and time-consuming. Additionally, such micro-habitats generally occur in mosaics of varying composition. Juveniles move between specific micro-habitats to shelter and feed, and weighing the relative importance among such habitat mosaics is problematic. The cryptic nature of many epinephelid juveniles further adds to this difficulty. Thus in this study, I employed a habitat suitability mapping approach more relevant to seascape scales.

Species distribution modelling techniques integrate species distribution data (or proxies thereof) and spatially-explicit environmental information to identify combinations of factors that constitute high-value, or essential habitat. These data can then be extrapolated across a broader ‘background’, to identify additional areas of suitable habitat within a region of interest (Le Pape *et al.* 2014). Increased availability of high-resolution remote-sensed data and affordable high-powered computer processors has led to a rapid increase in the application of species distribution modelling techniques. In fisheries, these techniques have been applied to the conservation and management of exploited (Fodrie and Mendoza 2006) and endangered species (Martin *et al.* 2012), and the enactment of spatially expansive ecosystem-based management (Martin *et al.* 2009). These applications often explicitly consider shifting habitat requirements across life history stages of target species (Fodrie and Mendoza 2006; Costa *et al.* 2015). Traditional modelling techniques such as classification and regression trees, and generalised linear models rely on accurate presence and absence data to accurately predict habitat suitability (Elith *et al.* 2011). However, recently developed models such as MaxEnt, are specifically designed to perform well with only georeferenced presence data and ‘pseudo-absences’ (Phillips *et al.* 2006; Phillips and Dudík 2008). The MaxEnt species distribution modelling program uses maximum entropy techniques to estimate the probability of species occurrence across a study area, by respecting a set of environmental constraints derived from the environmental conditions at locations of known species presence (see Elith *et al.* [2011] for a detailed explanation). MaxEnt consistently outperforms other presence-only models, even with limited, biased, presence-only data, and performs well compared with presence-absence techniques (Phillips *et al.* 2006; Pearson *et al.* 2007; Wisz *et al.* 2008; Fourcade *et al.* 2014). The demonstrated predictive accuracy of MaxEnt vastly expands the range of potential data sources for species distribution modelling (e.g. fisheries dependent data, where the absence of catch records do not guarantee the absence of the species in question).

In this study, I used the maximum entropy species distribution modelling program Maxent 3.3.3 (Phillips *et al.* 2006; Phillips and Dudík 2008) to model the probability of distribution of *E. polyphekadion* and *E. fuscoguttatus* of various size- and age-classes (defined by demographic and sexual function information from the previous chapter). Specifically, I investigated the question;

1. How is suitable habitat distributed throughout the study region for *E. polyphekadion* and *E. fuscoguttatus* throughout their post-settlement life histories?

To address this question, I: (1) located juveniles, (2) classified habitat throughout the study area, (3) developed a habitat suitability model to predict the presence of both juveniles and adults of both species.

4.3 Materials and methods

4.3.1 Juvenile collection

Three methods were employed to locate juveniles. The first two methods failed. First, initial attempts to locate juvenile habitat for *E. polyphekadion* and *E. fuscoguttatus* during ~200 hrs of underwater surveys on snorkel throughout April-October 2012, utilising techniques and targeting preferred micro-habitats reported by Tupper (2007), proved unsuccessful. Second, twenty-eight artificial settlement habitats, known as ‘gangos’, were constructed in April-May 2012. Gangos were constructed of loose coral rubble, green mangrove wood, and lengths of bamboo of approximately 2 m diameter (Figure 4.1) used to collect grouper fry for grow-out and sale throughout South-East Asia, including small numbers of *E. fuscoguttatus* (Johannes and Ogburn 1999).

After construction, gangos were left for 3-12 months before harvesting to allow establishment of epibiota (Mous *et al.* 2006). During this time, six gangos were largely destroyed or buried during periods of rough weather. The remaining gangos were individually encircled in a fine-meshed barrier net. Two researchers inside the net thoroughly inspected material and removed it from the encircled area. Once all material had been inspected and removed, the encircling net was brought inwards, until fish could be captured using a scoop net, and transferred into a large container filled with aerated seawater, in a nearby vessel. No juvenile grouper (of any species) were collected from the 22 harvested gangos; therefore this method of collection was discontinued.

Figure 4.1 - Diagram of a gango artificial habitat set-up (from Johannes and Ogburn [1999]).

Due to the failure of the above methods local fishers were paid a daily rate to locate and collect juvenile *E. polyphekadion* and *E. fuscoguttatus.* The involvement of local fishers in specimen collection has been demonstrated to be effective and efficient, including for other species of grouper in Papua New Guinea (Almany *et al.* 2010). A group of eight different fishers were employed to search for juvenile grouper each day, over a period of ten days. Fishers were divided into pairs, and allocated a search region. Due to the previous failure of in-water surveys and traps in locating individuals, fishers used hook-and-line. During these surveys one female fisher proved particularly effective at catching juveniles of interest. On interview, this fisher described a specific technique – fishing in silence from a drifting dugout canoe, using light line and small hooks, casting and waiting for a large strike, with small hermit crabs locally known as *kuma (Clibanarius* sp.*)* as bait. Eight fishers were employed each day, for a further period of ten days to apply this method, again throughout allocated regions to ensure sampling of all habitat types. Following this period, catch rates were judged to be adequate to convert to a per-sample payment method, with samples collected from the local fishery.

4.3.2 Occurrence data

All *E. polyphekadion* and *E. fuscoguttatus* collected during these targeted juvenile collections, and local fishery sampling at Dyual Island for the earlier demographic and reproductive biology study (Chapter 3) were included in habitat suitability modelling. Date and location of capture was recorded from fishers. All presence records (*i.e.,* capture locations for both juvenile and demographic collections) were described to the resolution of locally-named sections of habitat (detailed in section 2.3.1, and Appendix III). Individual areas were relatively small (mean area 0.15 ± 0.02 km^2), and largely encompassed one habitat type, as categorised for this study. As MaxEnt requires precise latitude and longitude coordinates, each capture location was allocated a random position within the area of capture. Date and location of capture was recorded from fishers. Samples were subsequently separately categorised into life history stages by length and by putative age (as determined by otolith analysis), according to species-specific lengths at female sexual maturity calculated in Chapter 3. The model used within the final chapter of this thesis was built using samples separated into two cohorts only – by size at 50% female sexual maturity (Table 4.1).

Table 4.1 – Species-specific life history stages as described by detailed age-based demographics and sexual ontogeny (Chapter 3).

		Size range (total length [TL])	
Stage	Description	*E. polyphekadion*	*E. fuscoguttatus*
Juvenile	Prior to size at 50% female maturity	< 333 mm	< 436 mm
Adult	Subsequent to size at 50% female maturity	> 333 mm	> 436 mm

4.3.3 Environmental data

Habitat types able to be distinguished from high-resolution Quickbird imagery were delineated using ArcGIS (ESRI 2014). Areas within the study region were broadly categorised as; land, mangrove, embayment, river mouth, lagoon, or reef (Table 4.2; Appendix IV). Lagoons were further sub-categorised as; open, enclosed deep, or enclosed shallow with construction. Reefs were further sub-categorised as; fringing, barrier, exposed patch, or sheltered patch. Habitat types that were unable to be distinguished from Quickbird imagery were delineated using participatory mapping techniques. Fifteen residents of western Dyual were presented with laminated A3 copies Quickbird images and asked to mark known areas of; seagrass, macroalgae-dominated habitat, and freshwater input. Freshwater inputs were demarcated as points in ArcGIS (ESRI 2014). Informants reported that all habitats previously categorised as fringing reef were composed of mosaics of limestone pavement, coral rubble, sand/silt, macroalgae, seagrass, and live coral heads in varying compositions. Photographic surveys at haphazardly selected locations confirmed this information (13 haphazardly select locations, 6 photographs/location), and this habitat was re-categorised as ‘fringing mosaic’. All other habitat descriptions were obtained during extensive (> 200 hrs) informal surveys by three individuals. Lagoon depths were obtained using a handheld depth sounder. The resulting habitat map (Appendix IV) was dissected into a grid of 20 * 20 m planning units. Planning unit side length was designated such that the area of each planning unit (400 m^2) was larger than the minimum mappable unit area (167 m^2).

4.3.4 Modelling

Modelling was conducted using MaxEnt 3.3.3 (Phillips *et al.* 2006). Models were built with default parameters [maximum iterations, 500; convergence threshold, 10^{-5}; default prevalence, 0.5], and automatic selection of features. MaxEnt has demonstrated high predictive accuracy with presence-only data using these parameters (Phillips *et al.* 2006; Pearson *et al.* 2007; Wisz *et al.* 2008; Fourcade *et al.* 2014), including from fishery catch records (Brodie *et al.* 2015). Model outputs were presented using the logistic format that estimates the probability of presence within each planning unit ranging 0 to 1 (Phillips and Dudík 2008). Models were built for maturity cohorts based on ages and sizes at first, 50%, and 100% female maturity for both species (results of all models are presented in Appendix V). The final models presented here separated juveniles and adults by length at 50% female maturity. These models were selected for three reasons; (1) ages were only available for a subset of individuals, and thus models based of length-based cohorts were built using larger datasets (2) 50% female maturity is a commonly reported demographic characteristic, increasing the reproducibility of this method, and (3) 50% maturity is less likely to be influenced by the presence of early- or late-maturing outliers.

The gridded study area was described by calculating the shortest Euclidean distance to each categorised habitat type for each planning unit. These rasterised datasets provided the environmental layers for all models. All lagoon habitats and both patch reef habitats were later aggregated, as this had no discernible effect on model performance. Final models contained seven environmental layers – detailing the shortest Euclidean distance (m) to the following habitat types; barrier reef, embayment, freshwater creek, fringing mosaic, lagoon (all sub-categories pooled), mangrove, and patch reef (sheltered and exposed sub-categories pooled). Predictive performance of all models were analysed by examining their receiver operated characteristic curves. The Area Under the receiver operated characteristic Curve (AUC) reflects the overall predictive specificity of the model; values approaching 1 indicate modelled distributions explained more fully by the input environmental variables, and values closer to 0.5 indicate that the modelled distribution is closer to random. Higher AUC values are generally associated with better model performance. However, lower AUC values are also associated with modelling species (or life history stages) with broader ecological niches or species responding to other factors.

Table 4.2 - Habitat categories as discernible from high-resolution satellite imagery, and reported during key informant interviews.

Habitat category	Habitat sub-category	Habitat description	Area (km^2)
Freshwater influenced	Embayment	Large bays characterised by high turbidity, high macroalgae cover, low salinity;	2.7
	Freshwater creek	Freshwater inputs resulting in localised turbidity, low coral cover, low salinity	n/a
Reef	Fringing mosaic	Limestone pavement, coral rubble, macroalgal clumps, seagrass, live coral heads; directly adjacent to land	5.7
	Barrier	Continuous reef structure; characterised by high live coral cover	9.6
	Sheltered patch	Discontinuous reef structure; characterised by high live coral cover; surrounded entirely by land and barrier reef	0.9
	Exposed patch	Discontinuous reef structure; characterised by high live coral cover; completely or partially exposed to open ocean	0.1
Lagoon	Open shallow with construction	Depths < approximately 20 m; discernible by lighter colour on satellite imagery; partially exposed to open ocean; interspersed with scattered coral structures	4.8
	Open deep	Depths > approximately 20 m; discernible by dark colour on satellite imagery; partially exposed to open ocean	0.0
	Enclosed shallow with construction	Depths < approximately 20 m; discernible by lighter colour on satellite imagery; surrounded entirely by land and barrier reef; interspersed with scattered coral structures	11.9
	Enclosed deep	Depths > approximately 20 m; discernible by dark colour on satellite imagery; surrounded entirely by land and barrier reef	6.3
Mangrove forest		Discernible on satellite imagery by darker green colouration, compared with other vegetation.	5.4
Land		All terrestrial habitat	17.6

4.4 Results

4.4.1 Assessing model performance

Model AUC ranged 0.87 – 0.97, suggesting that all models performed well (Phillips and Dudík 2008; Elith and Leathwick 2009). Based on AUC values, there was no discernible difference in performance between models based on age and size cohorts (Appendix V).

4.4.2 Relative contribution of predictor variables

Jackknife comparisons indicate that habitat suitability for both *E. polyphekadion* and *E. fuscoguttatus* juveniles (smaller than size at 50% female maturity; Table 4.1) were strongly influenced by proximity of fringing mosaics and mangrove forests, and were moderately influenced by proximity of freshwater inputs and embayments (Figure 4.4). Adult *E. polyphekadion* were influenced relatively evenly by distance to most habitats. Adult *E. fuscoguttatus* were moderately influenced by distance to fringing mosaic, freshwater inputs, and mangroves (Figure 4.4) however the nature of their influence changed (*e.g.* areas in direct proximity to mangrove forest provided the highest suitability for juveniles, whereas areas approximately 3 km from mangrove forest were most suitable for adults) (Figure 4.2). The similarities in model predictions of suitable adult habitat between species (Figure 4.2), despite substantial differences in the jackknife comparisons (Figure 4.4), further illustrates the dangers of assessing the relative contributions of correlated predictor variables using this method.

4.4.3 Ontogenetic shift in habitat suitability

During early post-settlement life history (*i.e.,* juvenile stage), both *E. polyphekadion* and *E. fuscoguttatus* were largely restricted to shallow reefs that fringe mangrove forested shorelines (Figure 4.2). Within this near-shore habitat, juveniles were caught in greater numbers in areas with freshwater inputs – over 80 and 90% of *E. fuscoguttatus* and *E. polyphekadion* were captured in areas directly adjacent to freshwater creeks, respectively. Two large embayments provided particularly suitable habitat and over 50 and 60% of *E. fuscoguttatus* and *E. polyphekadion* catches, respectively. Both species occupied broader ecological niches through progressive life history stages. Adults of both species were present in all categorised reef habitats, with exposed reef promontories proving particularly suitable (Figure 4.2).

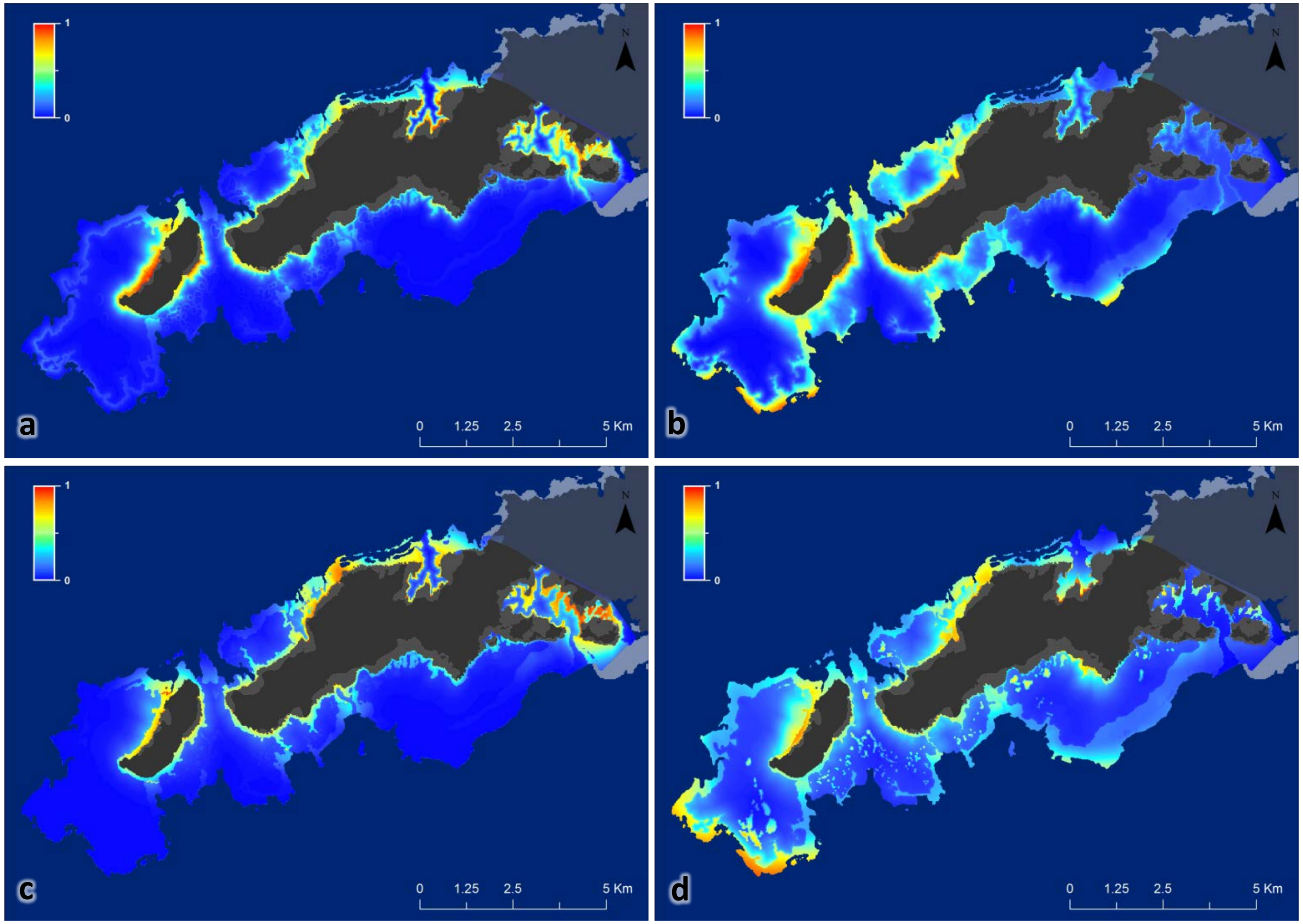

Figure 4.2 – Ontogenetic shift in habitat suitability using life history stages separated according to length for: *E. polyphekadion* (a) juveniles (< total length [TL] at 50% female maturity 333 mm, n = 146); and (b) adults (> TL at 50% female maturity 333 mm, n = 190); and *E. fuscoguttatus* (c) juveniles (< TL at 50% female maturity 436 mm, n = 134); and (d) adults (> TL at 50% female maturity 436 mm, n = 65). Warmer colours represent higher modelled likelihood of presence.

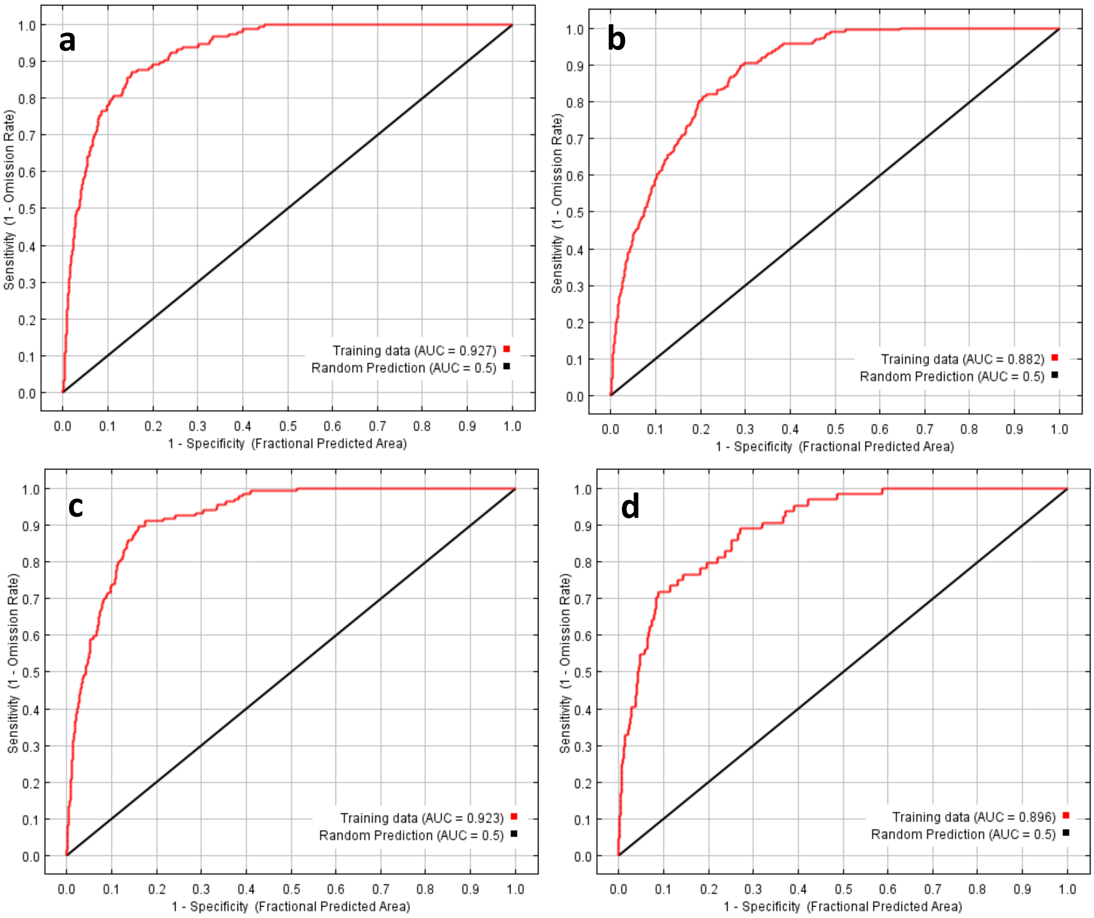

Figure 4.3 – Receiver operating characteristic curves for: *E. polyphekadion* (a) juveniles (< total length [TL] at 50% female maturity 333 mm, n = 146); and (b) adults (> TL at 50% female maturity 333 mm, n = 190); and *E. fuscoguttatus* (a) juveniles (< TL at 50% female maturity 436 mm, n = 134); and (b) adults (> TL at 50% female maturity 436 mm, n = 65).

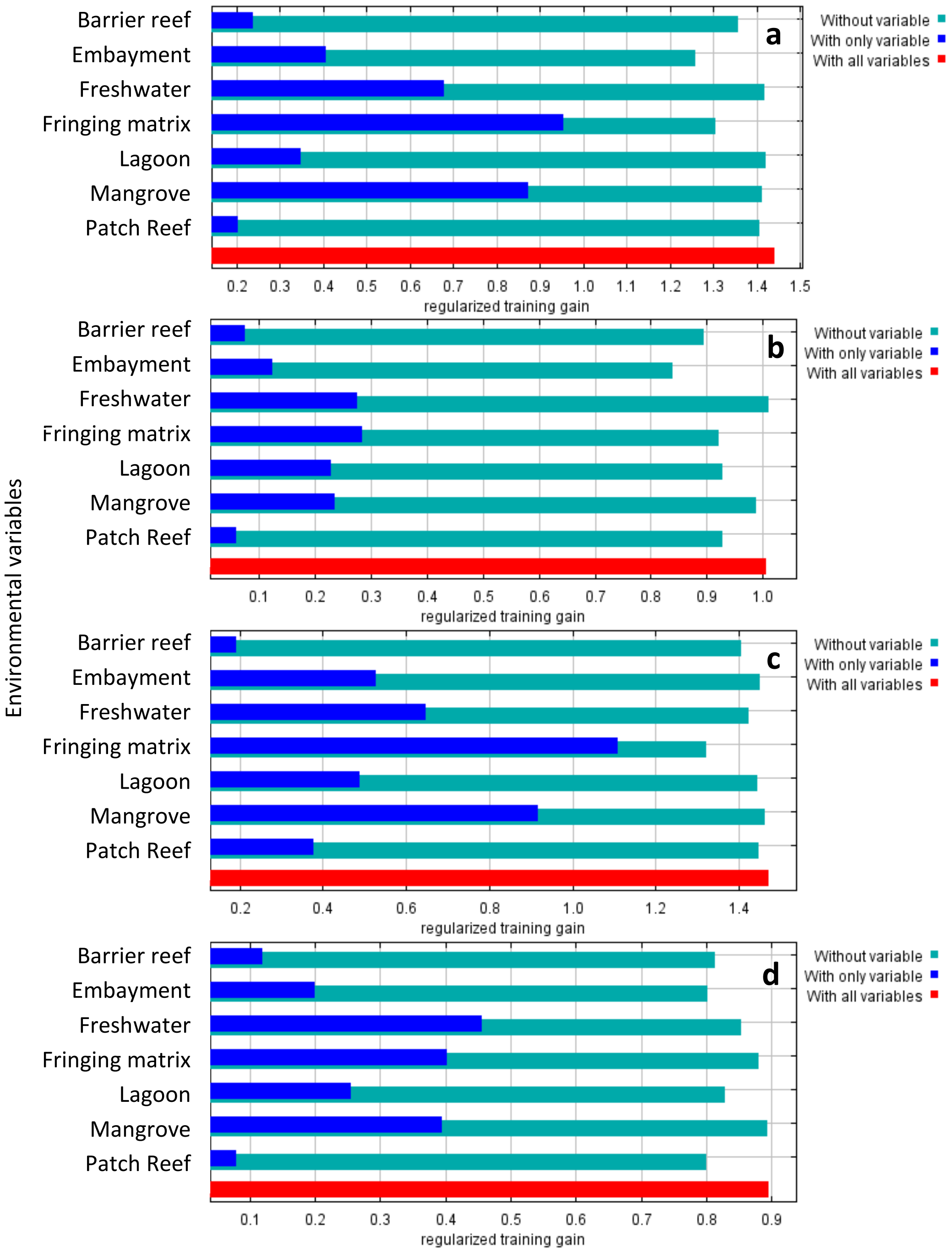

Figure 4.4 - Results of jackknife analysis, assessing relative importance of the seven environmental variables used to predict habitat suitability for: *E. polyphekadion* (a) juveniles (< TL at 50% female maturity 333 mm, n = 146); and (b) adults (> TL at 50% female maturity 333 mm, n = 190); and *E. fuscoguttatus* (c) juveniles (< TL at 50% female maturity 436 mm, n = 134); and (d) adults (> TL at 50% female maturity 436 mm, n = 65). Environmental variables represent minimum distances to (top to bottom): barrier reef, embayment, freshwater input, fringing matrix, lagoon, mangrove, and patch reef.

4.5 Discussion

This study provides the first quantification of ontogenetic shift in habitat suitability for these two important fisheries-targeted coral reef fishes. Habitat suitability modelling reveals that juveniles inhabit very specific habitats, which become more generalised through progressive life history stages. Juvenile habitat is a management priority for nearshore fisheries, and the specialised habitat associations for these species, particularly with freshwater inputs, represents an important consideration in their management.

Juveniles of both species were restricted to near-shore habitat mosaics of limestone pavement, coral rubble, sand/silt, macroalgae, seagrass, and live coral heads, with areas proximal to mangrove forest and freshwater influence providing the most highly suitable habitat. Where predictor variables are likely to be correlated their relative contributions as indicated by jackknife analysis should be interpreted with caution (Phillips and Dudík 2008). This is certainly the case here, due to the close associations among habitat types. However habitat associations, particularly during early post-settlement life history stages, were extremely pronounced supporting the analyses. The majority of juvenile *E. fuscoguttatus* were captured from two large embayments within the study area, and over 80% were captured from areas directly adjacent to freshwater inputs. This confirms existing anecdotal accounts of juvenile *E. fuscoguttatus* habitat, describing seagrass- and macroalgae-dominated habitat, in reduced-salinity areas proximal to mangroves (Sommer *et al.* 1996; Sadovy 2000). Similarly, over 60% of juvenile *E. polyphekadion* were captured within the two embayments, and over 90% were captured adjacent to freshwater inputs. This finding supports observations of smaller individuals captured from turbid water near mangroves (Rhodes 2012), however it differs markedly from the only existing quantitative analysis, which describes *E. polyphekadion* juveniles as generalists, inhabiting a range of microhabitats throughout lagoonal habitats (Tupper 2007). The reasons for the differences reported by Tupper (2007) and those observed here are unknown, but possibly relate to marked geographical variations in habitat suitability between Palau and Papua New Guinea. Size ranges were distinct between this earlier study (35 – 50 mm TL), and here (100 – 277 mm TL), so it is possible that these two studies described distinct life history stages. If so a substantial contraction in suitable habitat occurs between these stages. Early post-settlement contraction in spatial distributions could be driven by two non-mutually exclusive processes – migration or mortality. The former is consistent with theorised stepwise post-settlement life cycle migration (Nagelkerken *et al.* 2015), whereby settlement-stage larvae are expected to occupy their first-encountered suitable habitat (Grol *et al.* 2011), then move through successive suitable juvenile habitats (Cocheret de la Morinière *et al.* 2002). Newly settled individuals may migrate from first-encountered habitats of lower suitability to concentrate in higher densities in more suitable habitat. In this case settlement habitat may represent an additional management priority. Alternatively, *E. polyphekadion* may settle to a range of habitats as predicted, but experience near absolute mortality in sub-optimal habitat. In that case the spatial distribution of *E. polyphekadion* immediately post-settlement will be of little use to management decision-making. Nursery habitats by definition must provide disproportionate biomass to adult populations, rather than simply containing high juvenile densities (Beck *et al.* 2001). Thus the degree to which any early life history contraction in suitable habitat is due to mortality or migration will define the importance of distinct settlement habitat to management. This represents an important avenue of further inquiry (Nagelkerken *et al.* 2015), however it is outside of the scope of the current study.

In contrast to time-consuming and expensive methodologies used in identifying settlement stage habitat (e.g. Nagelkerken *et al.* 2000; Tupper 2007), the current study employs the expertise and effort of local fishers. Such techniques are likely to be far more widely applicable to coral reef fisheries regionally, and globally (Hamilton *et al.* 2005; Almany *et al.* 2010), due to limited funding and expertise available for data collection. Despite being limited to life history stages that can be exploited using existing techniques employed within the local fishery, the current study illustrates the potential for these methods to quantify hitherto unknown juvenile habitat requirements for important, exploited coral reef fishes. However, although relatively financially inexpensive, this approach does require significant investments of human and social capital, and often necessitates longer time-frames to develop understandings of local social and cultural systems, and to develop trust.

The close association of highly suitable juvenile habitat described in this study with terrestrial and mangrove habitats reinforces the importance of understanding their ontogenetic shift. These habitats are likely to be heavily influenced by land-based disturbances such as land-clearing, eutrophication, and sedimentation. Responding to land-based influences requires more holistic management approaches (e.g. ecosystem-based management, ridge to reef, watershed management). However, it is worth noting that human-induced disturbances do not necessarily equate with habitat degradation. One of the most suitable modelled habitat areas (and the site of numerous captures) for both *E. polyphekadion* and *E. fuscoguttatus* was adjacent to a freshwater creek running through the most populous human settlement within the study region, Leon. This area is undoubtedly among the most human-influenced within the study area. Mangrove forests here were noticeably less dense, due to regular harvesting for building materials. Additionally, this area was directly adjacent to a mangrove forest designated for open defecation and thus subjected to human effluent. However, this result should be extrapolated to other areas with extreme caution. These disturbances are likely relatively light, due to low population density, and low socio-economic development here. Indeed, in Isabel Province, Solomon Islands, lagoonal fringing reefs provide critical habitat for juvenile *Bolbometopon muricatum* (bumphead parrotfish). Much of this nearshore habitat has been destroyed in recent decades by runoff from commercial logging on adjacent islands (Hamilton pers. com.). In Isabel Province participatory research on *B. muricatum* has led to a growing appreciation among customary land owners of the importance of preserving remaining nursery habitat, resulting in several commercial logging licences recently being declined (Hamilton *et al.* 2016a,b). Further investigation is required to determine the precise juvenile habitat requirements for these species. Their close association with freshwater and mangroves suggests that activities such as commercial-scale logging and agriculture should be approached with caution.

Habitat suitability for *E. polyphekadion* and *E. fuscoguttatus* shifted towards more generalised associations with hard-bottomed habitats (*i.e.,* fringing mosaic, patch reefs, and barrier reefs) as they progressed through their post-settlement life histories. By the adult stage, individuals were widely distributed throughout the study area. This represented a shift toward more exposed live-coral dominated habitats such as barrier and patch reefs, though adults still remained present within near-shore low-salinity habitats that were highly suitable for juveniles. Areas of high suitability across multiple life history stages are prime candidates for protection, and identifying these areas constitutes an important first step toward recognising and protecting them elsewhere. Mosaic habitat fringing the western and eastern shores of Mait Island were hotspots of suitability across all modelled life history stages. These areas were immediately adjacent to freshwater creeks, relatively small mangrove forests, shallow lagoons, and small patch reefs. The fringing mosaic habitat itself was relatively typical of the area, consisting of limestone pavement, coral rubble, and scattered coral heads, seagrass, and macroalgal clumps.

Additional areas of highest modelled adult suitability included exposed barrier reefs. These included three known sites of current or historic spawning aggregations for these species. The largest spawning aggregation within the study area, Site A (the focus of detailed study in Chapter 5), was modelled as highly suitable habitat for both species. The site of an additional spawning aggregation, on a southward-facing reef promontory was modelled as highly suitable for *E. polyphekadion* adults, though only marginally suitable for *E. fuscoguttatus* adults. This site is only sporadically fished (Figure 2.10), due to its distance from local population centres and was not targeted during this study. This highlights the importance of supplementing species distribution modelling using fishery-dependent data with additional lines of enquiry, such as local knowledge surveys. This is particularly important concerning infrequently or seasonally targeted areas, or transient life history events such as spawning aggregations (Hamilton *et al.* 2005).

Although the general patterns of shifts in habitat suitability were consistent between species, and regardless of whether age or size cohorts were examined, the timing of shifts differed. Where life history stages were separated according to age at maturity, the most dramatic shift in spatial distribution occurred around the age at 50% female maturity for both species. However, where separated according to length *E. polyphekadion* were largely absent from exposed barrier reef habitats until length at 95% maturity. The precise timing of habitat shifts may be of importance where size-limits are a management consideration.

4.5.1 Critiques and caveats

Modelled suitability may be affected by differing levels of catchability between habitats. For example, juvenile fishes may be present in barrier reef habitat, but outcompeted for bait, and thus not represented in the data. Differing catchability did not preclude the capture of adult *E. polyphekadion* and *E. fuscoguttatus* across a range of habitats. The absence of juveniles in the catches from these habitats suggests that catchability must differ between both habitats and life-history stages if it has indeed affected the model. The effects of catchability could be tested by comparing catch data with data obtained from direct observation techniques (as with during aggregation fishing; Appendix II). Despite considerable effort however, no juveniles were observed during underwater surveys, or the deployment of capture devices.

4.5.2 Conclusions

The habitat suitability modelling conducted in this chapter represents an important step forward in our understanding of the spatial requirements of these two important, fisheries-targeted species of grouper, throughout their life histories. This study highlights the restricted distribution of juveniles particularly, to areas which are likely to face additional disturbances of terrestrial origin. This information is in direct contrast to the only previously existing study quantifying juvenile habitat requirements for *E. polyphekadion.* Future studies investigating degrees of connectivity between areas of high suitability would represent a major step forward for fisheries science and management. For example, the degree to which the largest local spawning aggregation (Site A on the south-westernmost reef promontory) seeds the prime juvenile habitats within the two large embayments to the east would inform decisions on the local importance of individual spawning populations, and the recovery potential of areas where spawning aggregations have been heavily fished. Similarly, the degree to which the large embayments are able to contribute recruits to the more distant aggregation at Site A would inform the necessity of protecting more localised juvenile habitats, such as those on the east and west shores of Mait Island. Some of these questions require advanced research techniques carried out in modern research facilities (such as genetic parentage analyses), however as this study demonstrates that critical research questions can be addressed using fisheries-dependent data, with the cooperation and engagement of local stakeholders. Sufficient suitable habitat at all life history stages is required for fish populations to persist, and will thus represent one of the key ecological processes investigated for problems of fit with community-based governance institutions in Chapter 6 of this thesis.

CHAPTER 5 - SPATIAL AND TEMPORAL DYNAMICS OF THE LARGE EPINEPHELID, *EPINEPHELUS FUSCOGUTTATUS,* ASSOCIATED WITH A TRANSIENT FISH SPAWNING AGGREGATION UNDER COMMUNITY-BASED MANAGEMENT

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5.1 Synopsis

Conservation commonly requires trade-offs between social and ecological goals. For tropical small-scale fisheries, spatial scales of socially appropriate management are generally small - the median no-take Locally Managed Marine Area (LMMA) throughout the Pacific is less than 1 km^2. This is of particular concern for large coral reef fishes, such as many species of grouper, which migrate to aggregations to spawn. Current data suggest that the catchment areas (i.e., total area from which individuals are drawn) of such aggregations are at spatial scales that preclude effective community-based management with no-take LMMAs. I used acoustic telemetry and tag-returns to examine reproductive migrations and catchment areas of the grouper *Epinephelus fuscoguttatus*, at a spawning aggregation in Papua New Guinea. Protection of the resultant catchment area of approximately 16 km^2 using a no-take LMMA is socially untenable here, and throughout much of the Pacific region. However, I found that spawning migrations were skewed towards shorter distances. Consequently, expanding the current 0.2 km^2 no-take LMMA to 1-2 km^2 would protect approximately 30 – 50% of the spawning population throughout the non-spawning season. Contrasting with current knowledge, our results demonstrate that species with moderate reproductive migrations can be managed at scales congruous with spatially-restricted management tools. The spatial scales of catchment areas of spawning aggregations examined within this chapter will be investigated in detail in the final chapter of this thesis, in the context of examining potential problems and opportunities for the community-based management of small-scale, near-shore fisheries.

5.2 Introduction

Trade-offs between social and ecological goals are ubiquitous in human-populated ecosystems. For tropical small-scale fisheries management understanding and evaluating these trade-offs is vital. Many coastal communities in developing countries are characterised by low incomes and high reliance on natural resources for livelihoods and food security (Béné *et al.* 2007). Their needs, immediate and on-going, are directly reliant on the sustainable use of surrounding ecosystems, but this cannot come at excessive short-term social costs. In recent decades community-based co-management programs have proliferated throughout the tropics in an attempt to balance the needs of local stakeholders with fisheries management and conservation goals (Govan *et al.* 2009; Cinner *et al.* 2012c; Cinner and McClanahan 2014). These programs utilise existing community governance structures to establish and enforce fisheries management rules, and rely heavily on the support and compliance of local stakeholders. However, community-based fisheries management generally requires significant compromise, between scales of management which are ecologically precautionary and biologically meaningful (Halpern *et al.* 2006), and those which are socially realistic (Foale and Manele 2004; Cinner *et al.* 2012b).

For coral reefs, the most widely used community-based fisheries management tools are Locally Managed Marine Areas (LMMAs), whereby coastal communities limit or prohibit extractive or destructive practices within a defined area (Bartlett *et al.* 2009; Govan *et al.* 2009; Jupiter *et al.* 2014). Although LMMAs are somewhat analogous with contemporary Marine Protected Areas, they generally operate on more limited spatial and temporal scales (Mills *et al.* 2010), potentially reducing their effectiveness for conservation outcomes (Polunin 1984; Foale and Manele 2004; McClanahan *et al.* 2006; Jupiter *et al.* 2012). No-take LMMAs, where extractive and destructive practices are prohibited, are often particularly small; the median size of no-take LMMAs in the Pacific is less than 1 km^2, and no-take LMMAs greater than 10 km^2 are extremely uncommon (Govan *et al.* 2009). Managing large, mobile coral reef fishes with such spatially-limited tools may be problematic. However, evaluating LMMA effectiveness for such fishes has proven difficult, due in part to our limited understanding of their spatial ecology (Green *et al.* 2014). In one notable exception, however, a no-take LMMA prohibited fishing of a multi-species grouper *(Epinephelidae)* spawning aggregation, resulting in increased fish abundances at the site during the first five years of protection (Hamilton *et al.* 2011).

Many large fishes, including many grouper species, form transient fish spawning aggregations (FSAs) where otherwise relatively solitary and sedentary individuals migrate over varying distances to aggregation sites, and amass in markedly increased densities relative to non-reproductive periods (Sadovy de Mitcheson *et al.* 2012). The temporal and spatial predictability of FSAs combined with typically large increases in catchability make them attractive fishing opportunities. Extensive fishing of aggregations has led to the systematic collapse of FSAs globally (Hamilton and Matawai 2006; Sadovy de Mitcheson *et al.* 2012). Emerging evidence that FSAs contribute substantially to the larval supply of local populations (Almany *et al.* 2013) suggests that such FSA failures may result in localised population extinctions. The ecological importance of FSAs, combined with their limited and predicable spatial and temporal extent, make them attractive candidates for a wide range of management action, including community-based management. Conversely, the intrinsic vulnerability of many aggregating species and the potential for long-range migrations to and from FSAs (Rhodes *et al.* 2012; Green *et al.* 2014) suggest that small no-take LMMAs that protect the aggregation site alone may be inadequate for many aggregating species. This is particularly true in scenarios where there is sustained fishing pressure outside of the FSA site, as the spawning population is vulnerable throughout the non-spawning season (Russell *et al.* 2012).

Here I focus on the brown-marbled grouper *Epinephelus fuscoguttatus* (Forsskål, 1775), a coral reef fish that forms FSAs throughout its range and is listed as Near Threatened on the IUCN Red list (Cornish 2004; Pears *et al.* 2006). Analysis from this study site reveals life history characteristics of *E. fuscoguttatus* which are associated with increased vulnerability to overfishing (Abesamis *et al.* 2014); large size (growing to approximately 1 m in length), late-maturity (age at 50% female maturity – 6 years), and longevity (maximum age 27 years) (Chapter 3). *Epinephelus fuscoguttatus* is a highly prized target of subsistence, artisanal, and large-scale commercial fisheries throughout the Indo-Pacific, including Papua New Guinea (Johannes *et al.* 1999b; Robinson *et al.* 2004, 2014; Hamilton *et al.* 2005; Pears *et al.* 2006). Yet, information on the migratory movement of *E. fuscoguttatus* is limited to a single study where the total catchment area (*i.e.*, total area from which all individuals are drawn) of a FSA was estimated at 100-175 km^2 (Rhodes *et al.* 2012). Although protection of the entire catchment of a FSA may be ecologically ideal, a community-based LMMA of this size would be socially untenable. More detailed information on migratory movement is required to effectively evaluate trade-offs between social and ecological conservation goals, and to inform management decision-making (Green *et al.* 2014).

In this study I combined acoustic and tag-returns with social surveys to assess the current effectiveness, and to suggest potential changes to increase the effectiveness, of a small LMMA in Papua New Guinea, established to protect a multi-species grouper FSA in 2004 (Hamilton *et al.* 2011).

Specifically, I sought to answer the following research questions;

1. How much protection does the current no-take LMMA provide to the *E. fuscoguttatus* that have aggregated to spawn?
2. What is the spatial distribution of the *E. fuscoguttatus* population outside of spawning periods?
3. How do local stakeholders perceive the spatial expansion of the current no-take LMMA to include non-spawning areas, relative to other management options?

5.3 Materials and methods

5.3.1 Social context and study site

Our study was conducted on the reefs surrounding Dyual Island, New Ireland Province, Papua New Guinea (Figure 5.1). Here, as in many nations throughout the Asia-Pacific region, a customary tenure system devolves management rights to clan groups (Govan *et al.* 2009). On Dyual Island, the customary tenure system is strong, centuries-old, and enshrined in national law, and thus represents the appropriate governance structure for managing natural resources (McClanahan *et al.* 2006; Cinner and Aswani 2007; Foale *et al.* 2011). A LMMA was established here in 2004 through a partnership between The Nature Conservancy and the local community, to protect a multi-species FSA located along a seaward facing reef promontory. Five years of protection of the FSA, Site A, led to significant spawning population recoveries for two species of large grouper (*Epinephelus polyphekadion* and *E. fuscoguttatus*) that aggregate here (Hamilton *et al.* 2011). *Epinephelus fuscoguttatus* aggregate at the FSA site to spawn (as validated by significantly increased densities, and the presence of gravid females) for approximately one week leading up to the new moon for 4-5 months annually, between March and July, with peak densities generally observed in May (Hamilton *et al.* 2011).

5.3.2 Acoustic range testing

Stationary acoustic range tests were conducted, prior to the deployment of the receiver array, using one Vemco (AMIRIX Systems Inc., Halifax, Canada) VR4-UMW receiver temporarily deployed seaward from the reef wall proximal to the FSA. Four fixed delay tags (V13-1x-A69-

1601, 69 kHz, delay 60s, Vemco) were activated at 15s intervals to avoid signal collisions, attached to dive weights with sub-surface marker buoys for relocation, and deployed along the reef wall at distances of 50, 100, 150 and 200m from the receiver. Over a period of 24 hr, almost all transmissions were successfully detected at 50m and 100m from the receiver (94% and 86%, respectively), however detection success dropped away sharply at greater distances (150m, 46% success; 200m, 3% success). This is consistent with comprehensive range testing of this tag type in reef environments which yielded a mean detection range (distance at 50% probability detection across times and habitat types) of 120m (Cagua *et al.* 2013). Mobile range testing was conducted following deployment of the receiver array (see receiver array deployment, below). A diver carried a fixed delay tag (V13-1x-A69- 1601, 69 kHz, delay 7s, Vemco) during three surveys of the FSA site. The array provided good coverage of the site, with 96% of transmissions successfully detected on at least one receiver, and 64% detected on multiple receivers.

5.3.3 Receiver array deployment

Twenty VR4-UMW receivers were suspended from sub-surface marker buoys, at approximately 10 m depth, with antennae facing downwards, and moored to the reef substrate using stainless steel cables. Four receivers were deployed along the reef wall at the FSA site, with significant overlap in working range (45-54m apart) to ensure complete coverage of the site (Figure 5.1 [circles around receivers indicate working detection range]). Additionally, 16 receivers were deployed across surrounding reefs. Eleven were deployed along the reef wall fringing the Mait lagoon, two receivers were moored proximal to patch reefs in the passage between Mait and Dyual islands, and three receivers were deployed proximal to patch reefs within the Mait lagoon (Figure 5.1). These deployments were made opportunistically (*i.e.,* where suitable attachment points were available in positions which provided good detection coverage of the surrounding areas), targeting areas likely to represent grouper spawning migration pathways (Rhodes *et al.* 2012).

5.3.4 Tagging

Twenty-nine *E. fuscoguttatus* were captured at the FSA site, using baited hook-and-line, during the last quarter lunar phase of two months (May and June) of the 2013 spawning season. Individuals were weighed (to the nearest 0.1 g) and measured (total length [TL] to the nearest mm). If necessary, swim-bladders were deflated by inserting a sterile hypodermic needle posterior to the pectoral fin. Individuals were sexed by stripping (*i.e.*, applying pressure to the abdomen) or by inserting a sterile cannula into the gonophore, to extract eggs or milt.

Individuals were then fitted with passive acoustic random delay-coded tags (V13-1x-A69- 1601, delay 100-140s, 1120-day battery life, Vemco), inserted into the gut cavity through a small incision, which was then closed with non-absorbable sutures and treated with a topical antibiotic. Fish were administered with 50mg/kg fish weight of a saline solution of the broad-spectrum antibiotic oxytetracycline, directly into the muscle tissue of the caudal peduncle, and then returned to the reef, approximately 20m from the aggregation site. Transmitter activity was tested upon release using a VR100 acoustic receiver and VH165 omnidirectional hydrophone (Vemco).

Data were downloaded after a period of two years. Data for visitation to the FSA site were collated, with arrivals and departures expressed in days relative to the new moon. Following arrival at the FSA site, males were detected consistently (using the blanking threshold of 12 hrs) until departure and subsequent migration from the FSA site. Two females each went undetected for periods longer than 12 hours during two visitations. During these periods, these fish either; (1) went undetected despite remaining at the FSA, or (2) departed and returned to the site. Our data are insufficient to conclusively differentiate between these hypotheses. However, these fish were not detected on receivers proximal to the FSA site during these periods, and conversely were detected on proximal receivers during all intra-monthly migrations to and from the FSA site. This suggests that they did not vacate the FSA site during these periods, and these periods were thus not treated as departures from the site. Residence was calculated as the difference between arrival and departure in days. To facilitate comparison among years, aggregation month was expressed as the number of new moons since the preceding southern summer solstice (henceforth lunar month). Data from the tagging month for each individual were excluded from all analyses, to account for the potential short-term behavioural effects of the tagging procedure. All data passed inspections for deviations from homoscedasticity and normality prior to analyses.

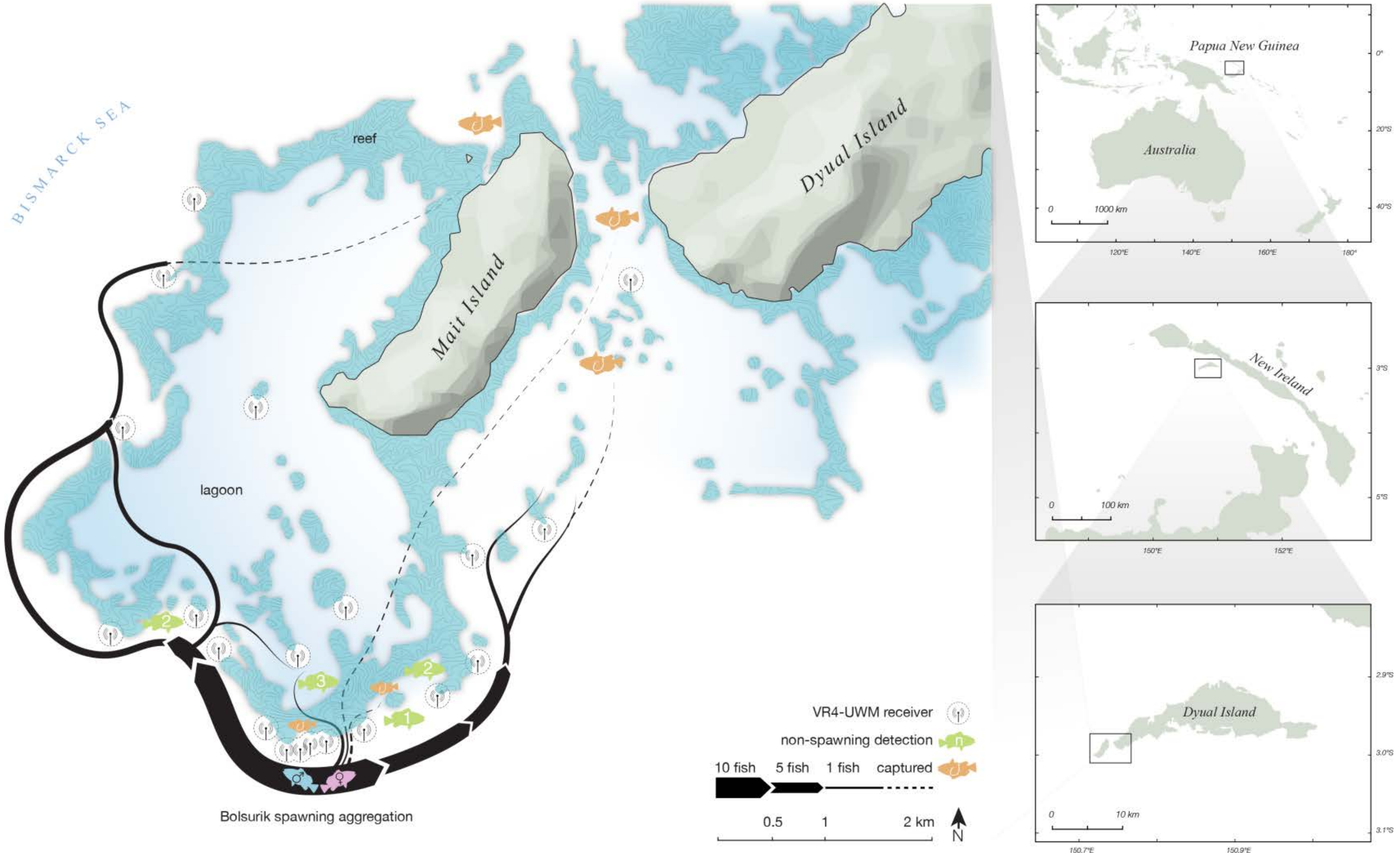

Figure 5.1 - Map of Dyual Island, Papua New Guinea, showing *Epinephelus fuscoguttatus* migrations to and from the FSA Site A. Black lines represent movement of fish; either between acoustic receivers (solid), or between acoustic detection and the point of capture by the local fishery (dashed). Thickness of lines denotes the number of fish moving between points. Fish symbols represent locations of either detections during the non-spawning season (green; numbers denote number of fish detected), or capture by the local fishery (orange; all symbols represent a single fish).

5.3.5 Stakeholder surveys

Thirty-two household surveys were conducted in Tok Pisin (the *lingua franca*) on the western half of Dyual Island, to assess local support for current management measures in comparison to alternative measures. Every third household (defined as a group living and eating together) was surveyed at the primary settlement in the study area (n=15), and at the six smaller coastal settlements (n=12, 1-4 surveys per settlement). Household members were approached in selected dwellings, and an interview was requested with either the male or female head of the household. Where they were unavailable, the household was missed, and returned to at a later date. Five surveys were also opportunistically conducted with heads of households situated in the interior of the island, when heads of these households were available for interview within coastal settlements. It is likely that such households were underrepresented in the sampling design, however information from key informants suggested that members of households situated in the interior of the island utilised marine resources only sporadically, and as such were not major targets of this study. Survey respondents were asked whether they supported the Site A LMMA in 2004 and 2014, using a Likert scale (1-5; actively oppose, passively oppose, neutral, passively support, actively support). They were then asked how the LMMA had affected their livelihood, their community, and the environment, using a Likert scale (1-5; very negative, slightly negative, no effect, slightly positive, very positive). Respondents were then asked to suggest any changes that they felt would improve the current management. Finally, respondents were asked whether they had heard of, witnessed, or participated in poaching activities within the LMMA, whether they recognised the poachers, and whether poachers suffered any consequences.

5.3.6 Statistical analyses

Arrival, departure, and residence data at the FSA were each fitted with linear mixed-effects models (LMEMs) fit by maximum likelihood, with sex and lunar month as fixed factors, and year and individual as random factors. P-values were obtained by likelihood ratio tests of the full model against the model without the effect in question.

The complete FSA catchment area was estimated by fitting the minimum convex polygon which contained all recaptures and acoustic detections, using ArcGIS (ESRI 2014). Maximum recorded migration distance (the greatest Euclidean distance from the FSA site to a point of acoustic detection or recapture) was calculated for each individual, using ArcGIS. To investigate the potential effects of uneven sampling effort, correction factors of 1.5 and 2.0 were individually applied to a subset of these data, such that data from detections or recaptures during the non-spawning season (44%) remained unchanged, while data from acoustic detection during migratory periods (56%) were multiplied by the correction factor. This yielded three permutations of the dataset; (1) 'uncorrected', (2) '1.5 corrected', and (3) '2.0 corrected'. Migration kernels were then separately fitted to these datasets (n = 25). I proposed three candidate migration kernels to explain these data; the (1) Weibull, (2) gamma, and (3) log-normal kernels. Parameter sets for each distribution were estimated by maximising the likelihood function:

$$L(\theta) = \prod_{i=1}^{n} f(d_i|\theta)$$

where d_i are the *n* observations of migration distance and θ represents the parameter set of the function. An AIC weighting analysis was performed on the resulting maximum likelihood functions, fit to the migration data. The log-normal function provided the best fit of the uncorrected data, with an Akaike weight of 0.67, compared with the gamma and Weibull kernels, with Akaike weights of 0.21 and 0.11, respectively. The log-normal function also provided the best fit of the 1.5 corrected data, with an Akaike weight of 0.44, compared with the gamma and Weibull kernels, with Akaike weights of 0.31 and 0.25, respectively. The log-normal, gamma, and Weibull functions provided relatively equivalent fits of the 2.0 corrected data, with Akaike weights of 0.33, 0.35, and 0.33, respectively. A 95% confidence interval was then calculated for each maximum likelihood log-normal function using non-parametric bootstrapping, with 1000 bootsamples.

Pearson product-moment correlation coefficients were computed to assess the relationships between migration distance and number of visits to the FSA, and between migration distance and total residence time at the FSA, over the duration of the study.

All analyses were conducted using the R software package (R Core Team 2015); LMEMs were fitted using the 'lme4' package (Bates *et al.* 2015); functions were fitted to the migration distance distributions using the 'fitdistrplus' package (Delignette-Muller and Dutang 2015).

5.4 Results

Twenty male (578 – 811 mm TL) and nine female (505 – 654 mm TL) *E. fuscoguttatus* were fitted with acoustic transmitters. Four males were removed from all analyses, due to detection patterns suggestive of post-tagging mortality (lack of detections greater than one hour post-tagging) or predation (uncharacteristic repeated, rapid movements along the reef for up to one week immediately post-tagging, with no further detections). Five acoustically tagged male

E. fuscoguttatus were captured by local fishers as part of their regular fishing activity (*i.e*., not part of the study), but these tags were returned and the locations of the captures disclosed. One fish was poached from within the LMMA after 55 days after tagging; the other fish were captured at distances of 0.6, 5.0, 5.4, and 6.0 km from the FSA 442, 623, 116, and 84 days after tagging, respectively.

5.4.1 Visitation to the FSA

Acoustic tagging data revealed that some tagged individuals were present at the FSA site during 13 lunar months of the 24-month study period. Although the number and length of visitations varied substantially between individuals (discussed in detail below), no tagged individuals remained at the FSA site either between spawning months, or between spawning seasons (Figure 5.2). Over the 24-month study period, males spent a mean 35.66 (± 7.48 standard error; range, 6.30-88.66) days at the FSA site (and thus within the LMMA), compared with 11.3 (± 1.11; range, 9.27-13.10) days for females.

Males returned to the FSA more frequently than females over the study period, (t[23] = 2.89, p = 0.008); less than half (44%) of the tagged females were redetected after their tagging month, compared with over three-quarters (78%) of the males. Of those redetected after their tagging month, males were detected at the FSA for a mean 2.64 (± 0.27) lunar months during 2013 and 2.70 (± 0.72) months during 2014, and females were detected at the FSA for a mean 1.75 (± 0.48) lunar months during 2013 and 1.25 (± 0.63) months during 2014. Males visited the FSA for up to six months in one spawning season. One male visited the FSA during 11 lunar months over the 24-month study period. Although data were more limited for females, two females visited the FSA for three consecutive months during a single season.

Males arrived at the FSA a mean 5.48 (± 1.18) days before females ($\chi2[1]= 21.77$, $p<0.001$), and resided a mean 5.76 (± 1.57) days longer ($\chi2[1]=13.51$, $p=0.001$); departures were not significantly affected by sex ($\chi2[1]=0.32$, $p=0.571$) (Figure 5.2). Mean residence time at the FSA steadily increased from 5.84 (± 1.79) days during the first month of the spawning season, to peak at 12.56 (± 1.68) days mid-way through the season, before declining again to 7.53 (± 1.77) days by the last month of the season ($\chi2[6]=96.98$, $p<0.001$) (Figure 5.2). Inter-monthly variation in residence was driven by fish arriving earlier ($\chi2[6]=66.29$, $p<0.001$), and departing later ($\chi2[6]=55.97$, $p<0.001$) mid-way through the season (Figure 5.2). Residence, and arrival and departure time all varied substantially among individuals (explaining 75, 61, and 63% of model variances; respectively), although not among years (explaining 3, 10, and 0% of model variances; respectively).

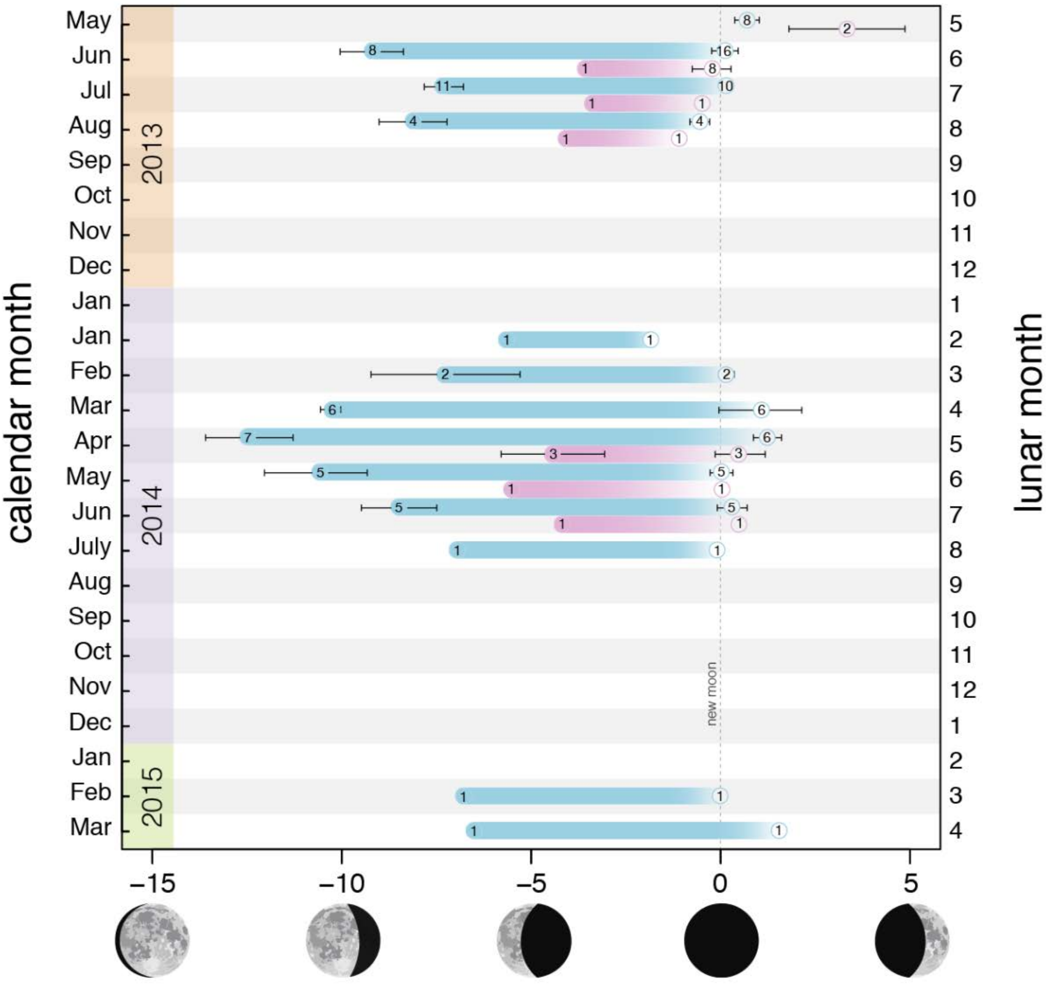

Figure 5.2 - Visitation to the FSA Site A by acoustically tagged male (blue) and female (magenta) *Epinephelus fuscoguttatus*. Days (x-axis) are expressed relative to the new moon (vertical dashed line). Spawning month is expressed as calendar month (left y-axis), and as lunar month (number of lunar cycles following the previous southern summer solstice) (right y-axis). Mean arrival (filled circles), departure (open circles), and residence (filled bar) are displayed for each month. Numbers within circles represent number of tagged individuals present, and error bars represent standard errors.

5.4.2 Reproductive migrations

All tagged individuals were detected moving away from the FSA site (and thus out of the LMMA) between each spawning month, and between spawning seasons. Individuals dispersed from the FSA to the west (44%), east (48%) or directly over the fringing reef and into the lagoon (8%) along common migratory corridors (Figure 5.1). For individuals that made multiple migrations to and from the aggregation site (16 migrations by 3 females; 64 migrations by 13 males), detected migration routes were rarely identical. Two alternative (although not mutually-exclusive) hypotheses could explain this; (1) individuals utilise differing routes between spawning months, or (2) tagged individuals show high fidelity to migration routes but pass some receivers undetected. The data support the latter, as illustrated by the following example. One male was detected on four receivers during migrations across six spawning months. During these 12 unidirectional migrations, the fish was detected on all four receivers once, on three receivers eight times, on two receivers twice, and on one receiver once. Variation in detections followed no apparent pattern, and detections were identical for two consecutive migrations only once. The number of detections on any one receiver during a migration was low (3.4 ± 1.8 detections; mean ± SE) further highlighting the likelihood of passing receivers undetected. Migration routes presented here represent the most complete detected migration for each individual (Figure 5.1).

Table 5.1 – Area required for the protection of percentages of the spawning population of *Epinephelus fuscoguttatus* at Dyual Island, Papua New Guinea. For the complete (100%) population estimates; maximum migration distance is the maximum recorded distance from the FSA to the site of recapture of a tagged fish, and required MPA area is calculated by fitting a minimum convex polygon over all detections and recaptures. For all other (25 – 75%) population estimates – maximum migration distances represent the greatest Euclidean distance from the FSA as predicted by the log-normal migration kernel fit to the uncorrected dataset (maximum likelihood fit), required MPA area represents the intersect of a circle of this radius centred on the FSA, and the complete population catchment (presented in square kilometres and as a percentage of the complete catchment area).

Population (%)	Max. migration (km)		Required MPA area (km^2)		Catchment protected (%)	
	Max. likelihood	Range (95% confidence)	Max. likelihood	Range (95% confidence)	Max. likelihood	Range (95% confidence)
25	0.90	0.62 – 1.24	0.78	0.69 – 1.81	5	4 – 11
50	1.49	1.13 – 1.97	2.12	1.52 – 4.30	13	9 – 27
75	2.45	1.77 – 3.34	8.21	3.44 – 9.61	51	21 – 59
100	6.03	n/a	16.19	n/a	100	n/a

Maximum recorded migration distances reached six kilometres but were skewed toward shorter distances (Table 5.1, and Figure 5.3). There was no correlation either between migration distance and number of visits to the FSA [$r = 0.196$, $n = 24$, $p = 0.348$], or between migration distance and total residence time at the FSA [$r = 0.285$, $n = 24$, $p = 0.168$]. The maximum likelihood fit of the log-normal function fitted to the uncorrected dataset ($\mu = 0.40$, $\sigma = 0.76$), suggested that 50% of *E. fuscoguttatus* that aggregate to spawn at the FSA Site A remain within 1.5 km of the FSA site throughout the non-spawning season (within an area of

2.1 km^2; Table 5.1). The functions fitted to the dataset following application of correction factors of 1.5 (μ = 0.63, σ = 0.79) and 2.0 (μ = 0.79, σ = 0.84), reduce this to 39% and 32%, respectively (Figure 5.3).

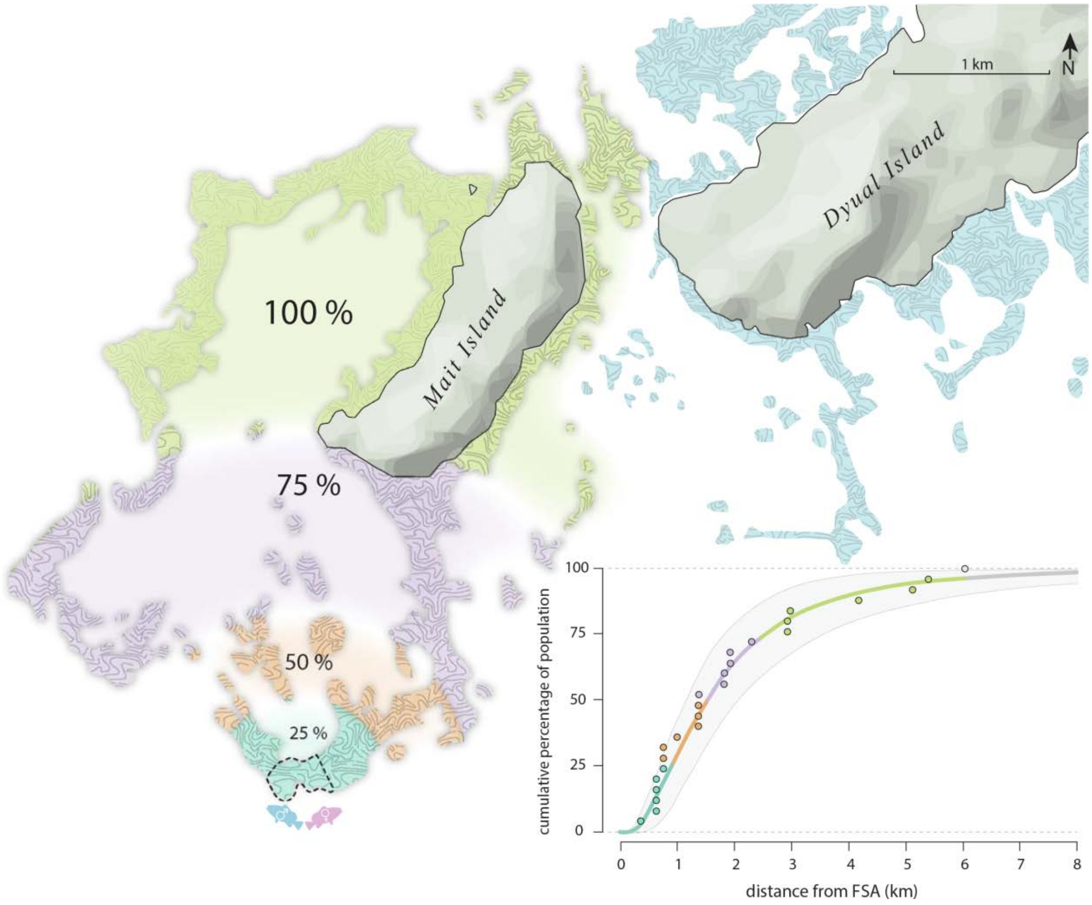

Figure 5.3 - Area of catchment quantiles for *Epinephelus fuscoguttatus* from the FSA Site A, for 25 (aqua blue), 50 (orange), and 75 (purple) percent of the spawning population, as calculated by the migration kernel (inset), and minimum complete catchment (green) calculated using the minimum convex polygon fitted over all locations of acoustic detection or recapture. Dashed line delineates current LMMA. Inset: Cumulative migration kernel. Points represent maximum recorded Euclidean migration distance for each individual, from either acoustic detection or recapture by the local fishery. The maximum likelihood fit of the log-normal function to the uncorrected dataset (μ = 0.40, σ = 0.74) is plotted, coloured to match mapped catchment quantiles. Solid light-grey area represents 95% bootstrapped confidence band.

5.4.3 Detections during non-spawning periods

Excluding detections from migratory movements (within 48 hrs of detection at the FSA), eight individuals (six males, two females) were detected during the non-spawning season. No individual was detected on multiple receivers, and detection frequency varied substantially between individuals, but with one exception was relatively consistent within individuals, suggesting high site fidelity during non-spawning periods. For example, three males were detected on one receiver throughout the non-spawning period of 2013 (September-December inclusive). The first individual was detected 22,524 times, with a mean time between detections of 14.3 minutes (± 0.4) and only one undetected period greater than one day (1.3 days). The second individual was detected 49 times, with 23 undetected periods greater than a day (5.1 ± 0.75 days; mean ± S.E.). The third individual was detected seven times, a mean 18.6 (± 8.5) days apart. Only one individual showed substantial variability in detection over time; female F0056 was detected at receiver E1 for nine days post-tagging, disappeared from the array for 84 days, returned to E1 for 69 days, before disappearing permanently.

5.4.4 Stakeholder surveys

Although less than half (45%) of respondents reported initial support for the Site A LMMA in 2004, most stated that it had subsequently been beneficial to their livelihoods (80%), the community (93%), and the environment (97%), and all respondents expressed their current support for the LMMA in 2014. The majority of respondents (72%) suggested that current fisheries management practices could be improved (Table 5.2). Implementation or improvement of enforcement infrastructure was the most commonly reported management issue (38%). Half of respondents suggested further spatial management, either through expansion of the no-take LMMA (34%) or the creation of new periodically-harvested LMMAs (19%). Sixteen percent of respondents suggested opening the current no-take LMMA periodically for harvest by local fishers. Although a quarter of respondents (26%) believed that a system existed to punish violators, no respondent could recall a punishment being administered. Key informants confirmed that no enforcement system existed. A majority of respondents (59%) reported that poaching had occurred within the LMMA within the past three years, 18% reported personally witnessing poaching, and 9% reported participating in poaching within the LMMA. Respondents reported that all poaching was carried out by members of the communities of western Dyual, who were known to them.

5.5 Discussion

Based on movement patterns evidenced by a combination of acoustic telemetry and tag-return data, the spatial ecology of *E. fuscoguttatus* aggregating to spawn at Site A strongly supports their community-based management. The current LMMA is sized to effectively protect the spawning aggregation site. Additionally, although protection of the entire FSA catchment area is socially unrealistic, a relatively modest expansion of the current spatial protection would protect a substantial proportion of the spawning population through the non-spawning season. Surveys of local stakeholders suggest that such an expansion would be well supported.

Table 5.2 – Potential changes to current fisheries management at Dyual Island, Papua New Guinea, categorised and ordered by percentage of survey respondents (n=32) suggesting the change.

Category	Action	Respondents (%)
Institutional	Strengthen enforcement	37.5
	Increase awareness of management	15.6
	Form management committee	9.4
Spatial / temporal	Expand permanent MPA	34.4
	Create periodically-harvested closures	18.8
	Open Site A FSA for periodic harvest	15.6
Other	Size limits	12.5
	Alternative livelihoods	9.4
	Effort restrictions	6.3
	Gear restrictions	3.1
No change		*28.1*

Our study showed that the current LMMA was highly effective in protecting the spawning stock during spawning events; with two possible exceptions, all tagged *E. fuscoguttatus* that aggregated to spawn at the FSA remained within the LMMA boundaries throughout their visits. However, individuals were protected within the no-take LMMA for a relatively small proportion of the time; males and females spent around 95% and 98% of the two-year study period within the openly fished area, respectively. Notably, one male returned to the FSA during 11 spawning months, yet still resided outside of the LMMA for 88% of the study period. The importance of protecting FSA sites is well established, and cannot be over-stated (Sadovy de Mitcheson *et al.* 2012); however this study further emphasizes the importance of management encompassing, but not limited to, the FSA site.

Maximum recorded migration distances demonstrate that the catchment area of the FSA (*i.e.*, the total area used by the spawning population throughout the year) is at least 16 km^2. This is considerably smaller than the only other catchment area calculated for this species, in Pohnpei (100-175 km^2), suggesting substantial geographic variability in migration distances (Rhodes *et al.* 2012). Nonetheless, a spatial closure of 16 km^2 is almost certainly socially untenable here or elsewhere where fishers with low spatial mobility are highly dependent on coral reef fisheries. The migration kernel illustrates however, that modest spatial expansion of the LMMA could offer relatively large conservation gains. For example, expansion of the current 0.2 km^2 LMMA to the Pacific median size of 1 km^2 would protect approximately 30% of the population during non-spawning periods, and increasing the LMMA to 2 km^2 would protect approximately half of the *E. fuscoguttatus* population throughout the non-spawning season. This is 4.8- and 3.8-fold greater than expected if the population was evenly spread throughout the catchment area, respectively. Importantly, the conservation return on expanding spatial protection diminishes markedly as the full catchment area is approached, such that the area required to protect the quarter of the population furthest from the FSA is 10-fold greater than that required to protect the closest quarter. Although further studies are needed before extrapolating to additional FSAs and species, this result demonstrates that a more detailed understanding of migration patterns is required before rejecting the use of spatially restricted management tools.

It must be noted that all migration data reported here represent minimum distances. This is problematic if migrations distances are significantly underestimated. Underestimation of migration distances may occur through at least two, non-mutually exclusive mechanisms. First, if the number and length of visitations to the FSA were inversely correlated with migration distance (*i.e.*, individuals that reside closer to the FSA spend more time at the FSA), then individuals that migrate shorter distances would likely be overrepresented in the tagged sample. However, no such correlation was observed either here, or in a previous study (Rhodes pers. comm.). Second, migration distance data may be ‘distance weighted’ due to sampling bias (Albanese *et al.* 2003). Specifically, likelihood of acoustic detection was presumably higher proximal to the FSA – due to increased receiver coverage. Ideally, distance weighting could be reduced through design (e.g., with acoustic receivers deployed in a grid formation). However, greater coverage was required proximal to the FSA to accurately determine visitation patterns and to delineate migration corridors. Additionally, receiver placement was considerably constrained by the complex bathymetry and patchy habitat at the site. Thus, limited resources, logistic constraints, and balancing multiple objectives outlined prior to the study limited the feasibility of eliminating distance weighting by design.

Where distance weighting cannot be eliminated through study design, correction factors can be used to assess its effect on observed movement patterns (Albanese *et al.* 2003). However, relatively consistent acoustic detection patterns and the absence of detections across multiple receivers during the non-spawning season, both here, and in a previous study (Rhodes, unpub. data.), suggest high non-spawning site fidelity for *E. fuscoguttatus*. Thus, data from detections or recaptures during the non-spawning season (*i.e.*, excluding individuals with data from migratory movements only) (44%) are likely to represent accurate migration distances. Correction factors of 1.5 and 2.0 were therefore applied to the data from migratory periods only (56%). Uniform correction factors were applied, because more complex distance-dependent correction factors are based on numerous assumptions which are unlikely to be met in this complex system (Albanese *et al.* 2003). Even after applying a correction factor of 2.0 (effectively doubling detected migratory movement distances), the migration kernel suggested that expansion of the LMMA to 2 km^2 would protect 32% of spawning individuals (figure 4). Further, as 32% of all tagged individuals were detected or captured within this area during the non-spawning season, I suggest that this represents a conservative minimum estimate.

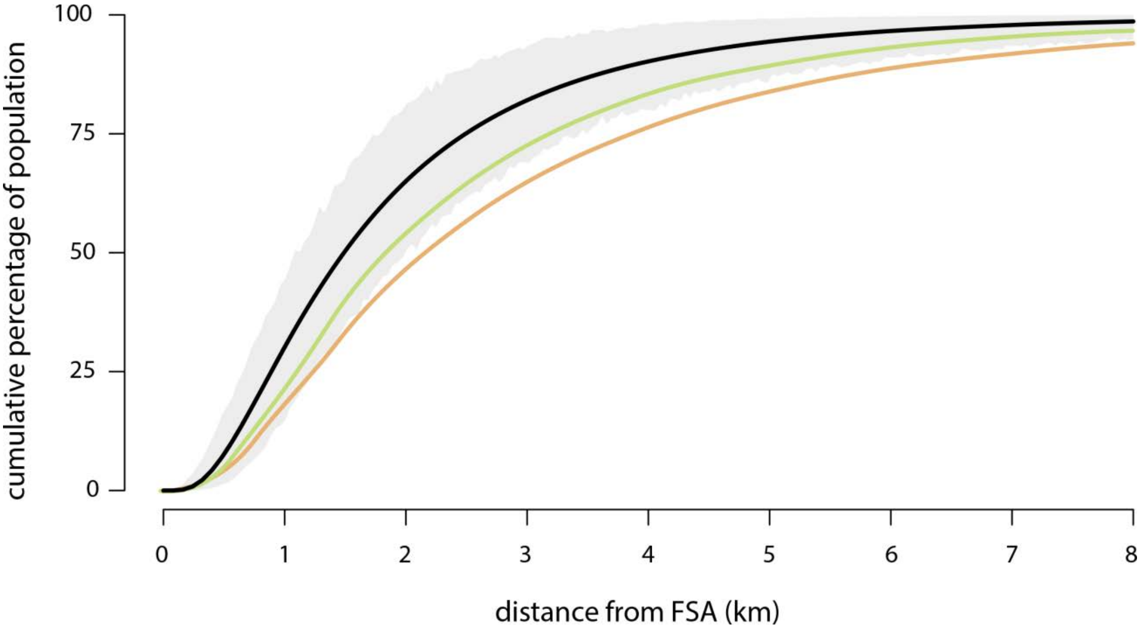

Figure 5.4 - Comparison of maximum likelihood migration kernels (each n=25). The uncorrected dataset maximum likelihood fit of the log-normal function (μ = 0.40, σ = 0.76) is plotted (black line), with 95% bootstrapped confidence interval (grey area). The maximum likelihood fit of the log-normal functions are also plotted for the '1.5 corrected' (μ = 0.63, σ = 0.79; green line) and '2.0 corrected' (μ = 0.79, σ = 0.84; orange line) datasets.

Local stakeholder support for the fishing closure at Site A increased substantially over the decade following LMMA implementation, and all survey respondents reported their current support for the LMMA. Additionally, there was strong support for expanding spatial protection of the current Site A LMMA, with 34% of respondents suggesting this change. However, 16% of respondents suggested that the LMMA be opened periodically for harvest by community members. There is certainly ample opportunity to seasonally harvest the FSA; acoustic data demonstrate that *E. fuscoguttatus* aggregate here during at least seven lunar months annually, substantially more than the 3-4 lunar months recorded elsewhere for this species (Pears *et al.* 2007; Rhodes *et al.* 2012; Bijoux *et al.* 2013). However I do not endorse periodic harvest of this FSA for the following reasons. First, because of the high rates of return by individual fish to the FSA – particularly males – a substantial proportion of the total spawning stock could be removed in a single month. Second, currently no effective mechanism exists for enforcing community regulations, as emphasised by local stakeholders. For this reason it would likely prove difficult to reinstate the closure post-harvest (Jupiter *et al.* 2012). Finally, our limited understanding of recruitment dynamics, temporally variable impacts from fishing, and reproductive output relative to seasonal spawning times, make fine-scale harvest recommendations unjustified at this time. Additional research that improves on our current understanding of these factors may in the future allow recommendations on limited FSA fishing to occur.

Instituting a system of graduated sanctions on violators (increasing in severity with each successive infringement) is one of the key design principles for sustained community-based management success (Ostrom 1990; Cinner *et al.* 2012c), and should thus be prioritised here. Household surveys suggest strong local support for such action. I further advocate that the local community continues to adopt a precautionary approach towards managing their grouper fisheries by continuing the permanent closure of the FSA site while also expanding the LMMA to partially protect the stock throughout the non-spawning period. The migration kernel demonstrates that the current LMMA provides negligible protection during the non-spawning season. While the migration kernel allows for the calculation of the optimal population protection by area, further investigation of population recovery rates and fishery pressure is required to assess the socially and ecologically appropriate LMMA size here. However, in the absence of such data, expansion of the LMMA to encompass 1 – 2 km^2 would protect 30 – 50% of the spawning population year-round, with the additional benefit of protecting common migration corridors (Figure 5.1) – a key management priority for this species (Pears 2012). A spatial expansion of this magnitude is also unlikely to increase the burden of enforcement here, as current and proposed LMMA are equally visible from the surrounding area. Any locally administered system of sanctions is more likely to involve reports by witnesses to infringement, than the apprehension of alleged poachers in the act. According to household surveys, all poaching at the site within the past three years was carried out by members of the local community, and identification of poachers was not difficult.

It should be noted that these recommendations are neither intended to be exhaustive, nor to imply their superiority in achieving social or ecological goals. The establishment of a system of enforcement and the spatial expansion of the current LMMA must be considered among a host of management measures, such as seasonal closures, and restrictions on gear and effort – some of which have some existing stakeholder support (Table 5.2).

5.5.1 Conclusions

This study provides promising evidence that species that are known to migrate moderate distances may still be conserved using community-based spatial management. The diminishing returns as spatial protection approached the entirety of the spawning population highlights the importance of understanding patterns of migration, over simple population boundaries. While direct comparisons with socially acceptable scales of management are still missing, the area required to protect 30 – 50% of the spawning population here is relatively congruous with community-based LMMAs throughout Papua New Guinea, and the wider region. This study thus provides initial evidence that designing LMMAs centred over, but not limited to, FSAs can provide robust conservation benefits, relative to area protected. The catchment areas modelled within this chapter provide an empirically derived representation of where spawning adults reside throughout non-spawning periods. As individuals show high fidelity to spawning sites, these catchment areas represent the spatial bounds of relatively discrete reproductive populations (*i.e.,* stocks), or proportions thereof. These catchment areas thus represent key ecological spatial scales for the management of adults, and will be examined in Chapter 6 in the context of the community-based management of the grouper fishery.

CHAPTER 6 – COMPARISON OF THE SPATIAL SCALES OF LOCALISED GOVERNANCE INSTITUTIONS AND KEY SOCIAL-ECOLOGICAL PROCESSES RELATING TO SMALL-SCALE ARTISANAL FISHERIES

6.1 Synopsis

The spatial scales at which key social and ecological processes operate are of critical importance to fisheries management and conservation. Problems of fit occur when social-ecological systems, such as small-scale fisheries, are governed at spatial scales that are mismatched to the key social and ecological processes that underpin their persistence. Predominantly social and political considerations have led to an increasing tendency to co-manage small-scale artisanal fisheries at relatively restricted spatial scales (e.g. through community-based management and locally-managed marine areas). There is legitimate concern however that governing at this scale creates serious problems of fit. This can have severe consequences, leading to overfishing and serial depletions. However for many important species of coral reef fish, the spatial fit between the scales of their exploitation and governance, and the scales of key ecological processes that sustain them have never been directly assessed. Here, I bring together analyses of the key social and ecological processes considered throughout this thesis, and demonstrate that at western Dyual, community-scale governance that protects critical life history stages of groupers presents a good spatial fit to help ensure the sustainability of the artisanal fishery for these commercially valuable fishes. The ecological processes considered here (ontogenetic shift in habitat suitability [Chapters 3-4]; and reproductive migration to and from transient spawning aggregations [Chapter 5]) demonstrates that grouper can be effectively managed at the scale of individual tenure areas. However, due to the misalignment of tenure boundaries with the social components considered here (patterns of settlement, clan affiliation, access rights, and fishing effort [Chapter 2]), management would best be carried out through nested institutions, incorporating both community-based institutions considered here. This study reinforces the importance of considering social and ecological components when setting the appropriate scales of governance of small-scale fisheries. Further, this study provides compelling evidence that community-based resource management can represent an effective tool for managing mobile coral reef fishes that form spatially defined spawning aggregations.

6.2 Introduction

The problem of fit argues that the effectiveness and robustness of governance institutions are functions their alignment with the scale of both the social and ecological domains in which they operate (Folke *et al.* 2007). To best fit the social domain, a governance institution should include all substantive stakeholders (*i.e.,* users) within its jurisdiction (Ostrom 1990; McKean 2002) , but not so large that the transaction costs of organisation hinder collective action (Agrawal and Goyal 2001). For many small-scale fisheries, users have low spatial mobility; they exploit resources within relatively limited geographic areas. Thus from a social perspective community-based governance, as is common throughout Melanesia (Govan *et al.* 2009), is likely to constitute a good spatial fit. To best fit the ecological domain a governance institution should include the key biophysical processes necessary to the continued function of the SES within its jurisdiction (Cumming *et al.* 2006), but not be so large that, for example, multiple populations of fish are mistaken for single populations leading to serial depletion (Cardinale *et al.* 2011; Srinivasan *et al.* 2012). There is legitimate concern that some key ecological processes that maintain the function of fish communities operate on spatial scales that preclude effective management at local scales. For example, coral reef fish larvae can disperse over scales of 10s or even 100s of kilometres (Planes *et al.* 2009; Cowen and Sponaugle 2009; Harrison *et al.* 2012; Green *et al.* 2014). Localised management institutions thus will almost invariably not offer the best fit for larval dispersal. In reality striving for ‘best fit’ is likely to require a compromise between what is ecologically ideal and what is socially achievable, with a ‘good enough’ fit obtained when adequate proportions of key ecological processes are included within the institution’s jurisdiction. For example, the only empirically derived larval dispersal kernel developed to date for a fishery species of coral reef fish demonstrated that 17 – 25% of juvenile grouper within a community’s tenure area came from spawning aggregations within that tenure area (*i.e.,* self-recruited) (Almany *et al.* 2013). The kernel also demonstrated that the majority of larvae were retained within the tenures of the five neighbouring communities. This was influential in the subsequent creation of a cooperative network of local communities. The network was established around existing socio-cultural boundaries, and ultimately covered an area substantially larger than the best fit estimated by the larval dispersal kernel (Almany *et al.* 2015). This example illustrates the importance that information about ecological spatial scales can have in informing, though not ultimately dictating, appropriate scales of governance. Similarly, some coral reef fish can travel kilometres to 10s of kilometres to transient spawning aggregations to reproduce (Rhodes *et al.* 2012; Nanami *et al.* 2014). Where the catchment areas (*i.e.,* total area from which individuals are drawn) of such aggregations cross institutional boundaries, the costs of the imperfect fit must be weighed against the costs of scaling up governance to the next institutional level.

Further to governing fisheries at the most appropriate institutional level, governance effectiveness also requires that individual management actions are applied over appropriate spatial scales, at appropriate locations within the region of governance. This is important as the social and ecological processes underpinning small-scale fisheries can vary over extremely small spatial scales. In Chapter 2, I documented considerable variation in fishing effort over scales of 100s of metres. In Chapter 4, the suitability of habitat throughout the life histories of *E. polyphekadion* and *E. fuscoguttatus* varied over similarly small spatial scales. Thus the social and ecological outcomes of any management action would vary widely dependent on its scale and location within the study region. These outcomes will depend on the importance of any particular area for both resource users (e.g. fishing effort) and the resource units (e.g. habitat suitability for target species).

Here, I develop a framework that directly compares both the social and ecological importance of particular fishing grounds creating four domains of differing policy implications (Figure 6.1). In the first domain (i), where importance is high to both resource users and to the target species, management actions would displace fishing effort, likely having a negative impact on resource users, but a positive impact on target species (Figure 6.1; i). Impact here refers to the degree of departure that management achieves from 'business as usual'. In the second domain (ii) where areas are of high importance to resource users but low importance to species, management actions that reduce fishing are likely to produce a lose-lose situation, where social costs borne by users are not offset by significant ecological gains for the target species (Figure 6.1; ii). In the third domain (iii), where importance is low to both resource users and target species, management is low-priority and would not appreciably depart from business as usual (Figure 6.1; iii). In the fourth domain, where importance is high to target species, but low to resource users, management actions would have little impact on reducing current fishing mortality, however could be considered precautionary management that protects areas against potential future increases in use (Figure 6.1; iv). To operationalize the framework, I integrate and evaluate the data on resource use, habitat suitability, and governance.

Protecting areas that are not currently heavily used (Figure 6.1; iii-iv), minimises costs and reduces the likelihood of conflict with resource users. Strong socio-political pressure has led to the majority of global terrestrial and marine protected areas being established within areas of high ecological integrity but low human impact (Pressey and Bottrill 2008; Devillers *et al.*

2015). Lively debate exists in the conservation planning literature as to whether conservation efforts should be concentrated within the high impact (i) or precautionary (iv) domains (Knight and Cowling 2007, 2008), (Pressey and Bottrill 2008). These opposing viewpoints may be underpinned by the prioritisation of differing management goals, with high impact intervention prioritising conservation gains, and precautionary management prioritising socio-economic goals. These philosophical debates fail to recognise that the optimal strategy is likely to be a combination of the two, and will certainly be dependent on the specific characteristics of the SES (Spring *et al.* 2007). Certainly at Dyual Island, the more localised socio-economic needs of resource users (e.g. continued food security and financial income) must be effectively balanced with the global conservation-based goals of external partner organisation, The Nature Conservancy (e.g. the conservation of vulnerable species).

While numerous studies have demonstrated that decentralized community based management provides a useful scale of governance for managing tropical fisheries, there remains a dearth of empirical evidence that demonstrates how small scale governance can sustain the key ecological processes for large valuable fishes.

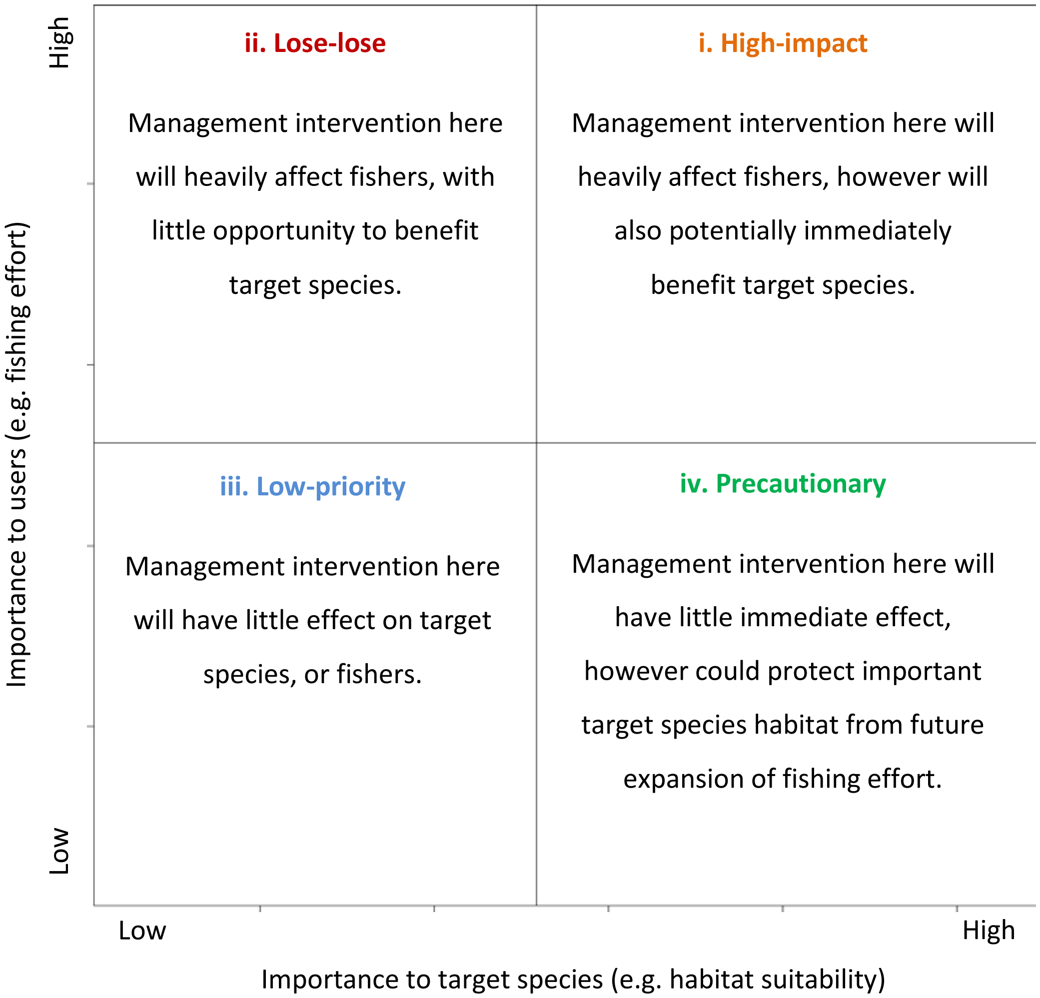

Figure 6.1 – Conceptual framework illustrating the potential of management within domains of varying combinations of importance to stakeholders and importance to target species. The importance of a particular area of habitat to target species is on the X-axis and importance to resource users in on the Y- axis. The quadrants (i-iv) represent domains of different combinations of fisheries and conservation importance. Areas of habitat that are of low importance to target species are of minimal (direct) conservation concern. Areas of high fisheries importance will be most difficult to implement conservation actions in. Different combinations of these traits call for different conservation strategies.

In this chapter, I return to the primary research focus of this thesis to address this gap:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

To answer this, I integrate data examined throughout this thesis to evaluate levels of match or mismatch between the spatial scales of governance in the Dyual grouper fishery, and key components of the social-ecological system (Table 6.1). Specifically, I address the following three research questions in turn:

Q1) Do the spatial distributions of social processes (*i.e.,* patterns of settlement, clan affiliation, access rights, and fishing effort) lead to problems of fit with community-based governance institutions?

Q2) Do interactions between the spatial distributions of fishing effort and suitable habitat throughout the post-settlement life histories of target species lead to problems of fit with community-based governance institutions?

Q3) Do reproductively isolated adult populations (*i.e.,* stocks) of relatively mobile coral reef fishes deliver a sufficient spatial fit for their governance using community-based institutions?

Table 6.1 – Social-ecological components assessed for problems of fit with community-based governance institutions.

Sub-system	Component	Addressed within			
		Q1	Q2	Q3	Chapter
Social	Patterns of settlement	x			2
	Clan affiliation	x			2
	Access rights	x			2
	Patterns of fishing effort	x	x	x	2
Ecological	Juvenile & adult habitat suitability		x		3 & 4
	Spawning aggregation catchments			x	5

6.3 Q1: Do the spatial distributions of social conditions lead to problems of fit with community-based governance institutions?

6.3.1 Methods

All spatial analyses were conducted in ArcGIS (ESRI 2014), using the named reference map divided into 20*20 m planning units used throughout this study (see section 2.3.1). All statistical analyses were conducted using the R software package (R Core Team 2015). The two focal community-based governance institutions were investigated for problems of fit with four social components; patterns of settlement, clan affiliation, access rights, and spatial distribution of fishing effort. For each resource governance area (*i.e.,* individual tenure areas, and the Leon VPC), total fishing effort was calculated by first multiplying estimated fishing effort for each planning unit (as modelled in section 2.4.3.5) by its proportion of intersect with the relevant tenure area (as delineated in section 2.4.4.3), and then summing all of these values. Density of fishing effort was calculated by dividing this total fishing effort by the area of shallow habitat within the relevant governance area (in km^2). The number of local residents that were members of each clan holding marine tenure was calculated by summing the number of people within all surveyed households that reported affiliation to the relevant clan, and extrapolating this to the estimated number of households within the study region (from Chapter 2). Resident populations were estimated by summing all coastal settlement populations within each governance area.

6.3.2 Results

The most localised level of the state-based government – the Leon Village Planning Committee (VPC) – held jurisdiction over the entire study region. Customary tenure over the study region was divided between three clan groups (Figure 6.2). Some shallow habitat within the jurisdiction of the Leon VPC was excluded from analyses throughout this thesis (as discussed in 2.4.4), due to the bounds of available high-resolution satellite imagery. All analyses throughout this thesis were thus conducted with the area of shallow habitat within the jurisdiction of the Leon VPC underestimated by approximately 1.8 km^2. These excluded areas were outside of the tenure of the three clan groups considered within this thesis.

Table 6.2 – Key social conditions summarised for each management area.

	Management areas			
	Clan A	Clan B	Clan C	Leon VPC
Jurisdiction (habitat area [km^2]; % of study region total)	15.7; 36%	6.6; 15%	18.7; 43%	43.3; 100%
Clan affiliation (estimated ppl; % of households)	118; 28%	78; 19%	94; 22%	N/A
Resident population (estimated ppl; % of households)	62; 15%	260; 62%	102; 24%	424; 100%
Total fishing effort (fisher-trips * yr^{-1}; % of total)	5718; 22%	14385; 54%	6385; 24%	26487; 100%
Density of fishing effort (fisher-trips * km^{-2} * yr^{-1})	359	2179	333	615

Clan affiliation was not well aligned with patterns of settlement and fishing. Two-thirds (68%) of the 424 people residing within the Leon VPC management area were affiliated with one of the three clans that held tenure here (Table 6.2). However, only approximately one-third (34%) of surveyed households reported affiliation to the clan that held tenure over the most proximal marine area. The majority of fishers (63%) fished within multiple tenure areas, and 71% fished primarily outside of their own clans' tenure areas. Though all residents of western Dyual had access rights to fish anywhere within the Leon VPC jurisdiction, fishing effort was highly concentrated around population centres (Figure 6.2). Despite being the smallest in terms of habitat area, due to the location of the primary local settlement the majority of fishing was conducted within the tenure of Clan B (Table 6.2).

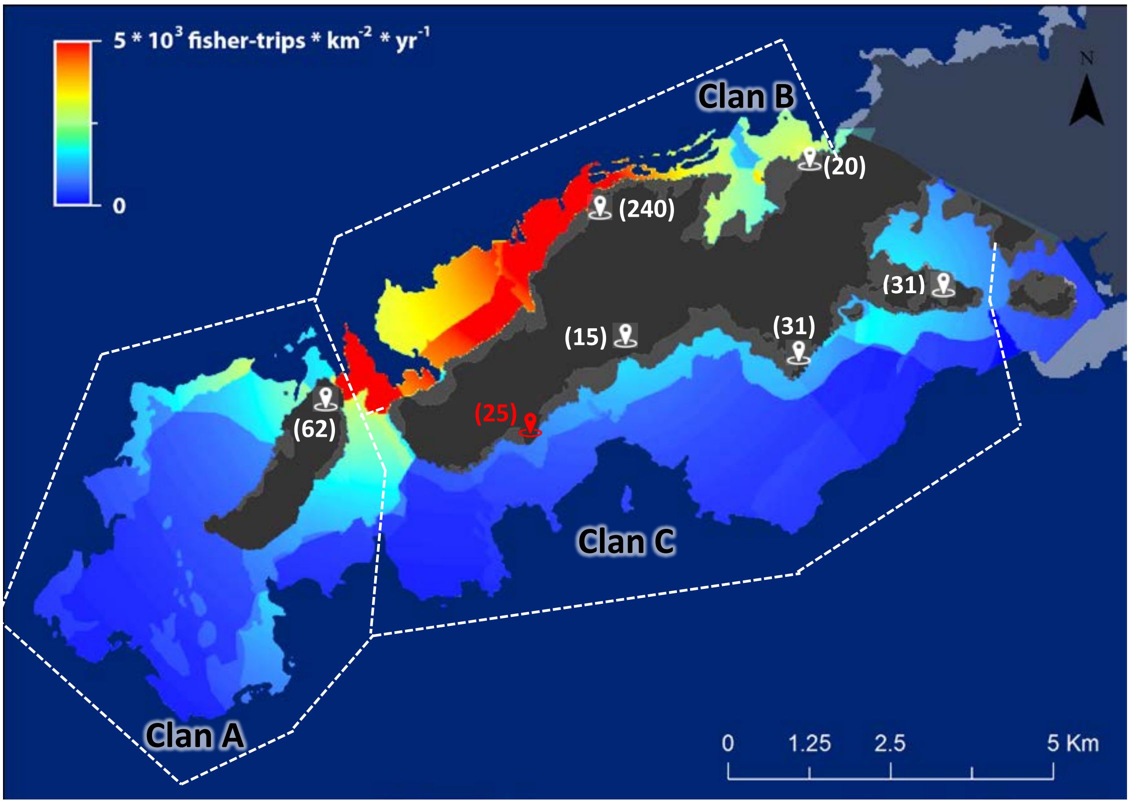

Figure 6.2 –Spatial distribution of estimated fishing effort. Warmer colours denote higher density of fishing effort, toward a maximum 4.4 * 10^3 fisher-trips * km^{-2} * yr^{-1}. White dashed lines denote tenure boundaries, white place marks (📍) denote settlements with population estimates in parenthesises; red place mark represents the settlement burned during a recent land dispute (see section 2.4.4.2). Map extent represents the approximate jurisdiction of the Leon VPC.

6.3.3 Discussion

The Leon VPC provided an appropriate spatial fit for management in the context of the four key social conditions relevant to the small-scale artisanal fishery of western Dyual investigated here (Table 6.1). Although the Leon VPC had legislated few restrictions on fishers, *de facto* governance had been historically conducted at this spatial scale, in the form of restricted access rights to the fishery. Local fishers are free to access marine resources across the entire Leon VPC area, and anyone residing outside of the Leon VPC is required to gain permission before accessing resources here. Fisheries governance conducted at the Leon VPC scale would thus include all relevant stakeholders (*i.e.,* resource users). It is important to note that access rights remain under the jurisdiction of customary tenure holders, not the Leon VPC. Thus the discussion here pertains to the spatial scale of the Leon VPC, not the institution itself.

Conversely, individual tenure areas aligned poorly with relevant stakeholders. This could produce problems of fit through the violation of a key design principle of common-pool resource governance. The principle of collective-choice arrangements states that people who are heavily affected by management rules should have a say in developing and changing those rules (Ostrom 1990). The majority of surveyed resource users resided adjacent to another clan's marine tenure area, fished across tenure boundaries, and primarily fished outside of their own tenure areas. Additionally, one-third of local residents were not affiliated with any clan that held marine tenure here. As such, management decision-making within any individual tenure area excluded the majority of relevant resource users. Where a sub-set of resource users (in this case the relevant tenure holders) manage resources, management rules may disproportionately benefit that group, and disproportionately externalise costs to other resource users. An example of such 'elite capture' of benefits (*i.e.,* where a group of 'local elite' disproportionately appropriate benefits) could be seen during the past operations of the Live Reef Food Fish Trade at spawning Site A. Although all fishers were paid to capture fish from the aggregation, only the tenure holders were paid royalties for the catch (Hamilton pers. comm.). However, the costs of the subsequent resource depletion were shared across all resource users who fished within this area. In instances such as this, where a sub-set of users reap most of the benefits without paying most of the costs, other users are less likely to comply with management rules (Ensminger 2000, 2001).

Population density and fishing effort were also highly variable between tenure areas. Although less than one-fifth of the population of western Dyual held affiliation of Clan B, over three-fifths of the population lived adjacent to their marine tenure area, mostly in the primary settlement of Leon. Due to the low spatial mobility of fishers, all shallow habitat within Clan B's tenure was thus subject to levels of fishing effort substantially above the Leon VPC average. More than half of fishing effort within the Leon VPC was concentrated within the tenure of Clan B, which encompassed just 15% of the study region. This uneven distribution of fishing effort between tenure areas has profound implications for the governance of grouper fisheries here, particularly when considered in conjunction with key ecological processes underpinning their persistence.

6.4 Q2: Do interactions between the spatial distributions of fishing effort and suitable habitat throughout the post-settlement life histories of target species lead to problems of fit with community-based governance institutions?

6.4.1 Methods

The spatial distributions of fishing effort and habitat suitability were individually compared for each life stage of each study species, within each governance area. Comparisons were made by operationalising the framework discussed above (Figure 6.1). Data were analysed to the resolution of individual planning units and presented as density bi-plots, such that darker colours represent a higher density of planning units with that particular combination of habitat suitability (x-axis; modelled probability of presence from Chapter 4, square transformed to aid visual interpretation) and fishing effort (y-axis; modelled fisher-trips from Chapter 2, natural log-transformed to aid visual interpretation) (Figure 6.3). These bi-plots were divided into quadrants; by mean fishing effort across the entire study region (615 fisher-trips * km^{-2} * yr^{-1}; Table 6.2), and by the minimum '10% omission rate' for habitat suitability (0.25). This 10% omission rate is a conservative measure of suitable habitat (Pearson *et al.* 2007) that can be ecologically interpreted at the minimum value that includes at least 90% of all presence locations within the modelled suitable habitat. The spatial distribution of habitat across the study region was also presented (Figure 6.4) with areas of habitat shaded according to categorisation within the four quadrants (i. High-impact, orange; ii. Lose-lose, red; iii. Low-priority, transparent; and iv. Precautionary, green).

6.4.2 Results

Considered at the scale of the Leon VPC, the majority of habitat (*i.e.,* the highest density of planning units) falls into the low-priority quadrant, for both adult and juvenile life history stages (Figure 6.3a-b; iii). The remaining habitat was distributed throughout the other three quadrants, although with limited habitat in the precautionary quadrant (iv) for juveniles (Figure 6.3a; iv).

However, the distribution of habitat throughout the quadrants was highly differentiated between individual tenure areas, particularly in respect to fishing effort (Figure 6.3c-h). Habitat was distributed across all quadrants for both life history stages for Clan A (Figure 6.3c-d; i-iv) and Clan C (Figure 6.3g-h; i-iv). Conversely, although substantially greater proportions of habitat within Clan B's tenure were suitable for both stages of both species (Table 6.3), this habitat was restricted to the lose-lose and high-impact quadrants within the tenure of Clan B (Figure 6.3e-f; i-ii).

Due to their close association with more heavily fished fringing habitats, two-thirds of suitable juvenile habitat experienced fishing effort above the average for the entire Leon VPC. Suitable adult habitat encompassed additional area, and was evenly distributed between areas experiencing greater and lesser than average fishing effort (Figure 6.4; Table 6.3).

Table 6.3 - Suitable habitat within each governance area for *E. polyphekadion*; separated by life history stage (juvenile and adult), and by interaction with fishing effort. Only habitat categorised as suitable is presented here (*i.e.,* high-impact [i], and precautionary [iv]).

		Habitat within management area (km^2; % of tenure area)			
Life history stage	Habitat	Clan A	Clan B	Clan C	Leon VPC
Juvenile	All suitable habitat	1.9; 12%	2.4; 37%	2.0; 11%	6.3; 15%
	High Impact (i)	1.1; 7%	2.4; 37%	0.7; 4%	4.2; 10%
	Precautionary (iv)	0.8; 5%	0; 0%	1.3; 7%	2.1; 5%
Adult	All suitable habitat	5.1; 32%	3.7; 56%	3.2; 17%	11.9; 28%
	High Impact (i)	1.8; 12%	3.7; 56%	0.4; 2%	5.9; 14%
	Precautionary (iv)	3.3; 21%	0; 0%	2.7; 15%	6.0; 14%

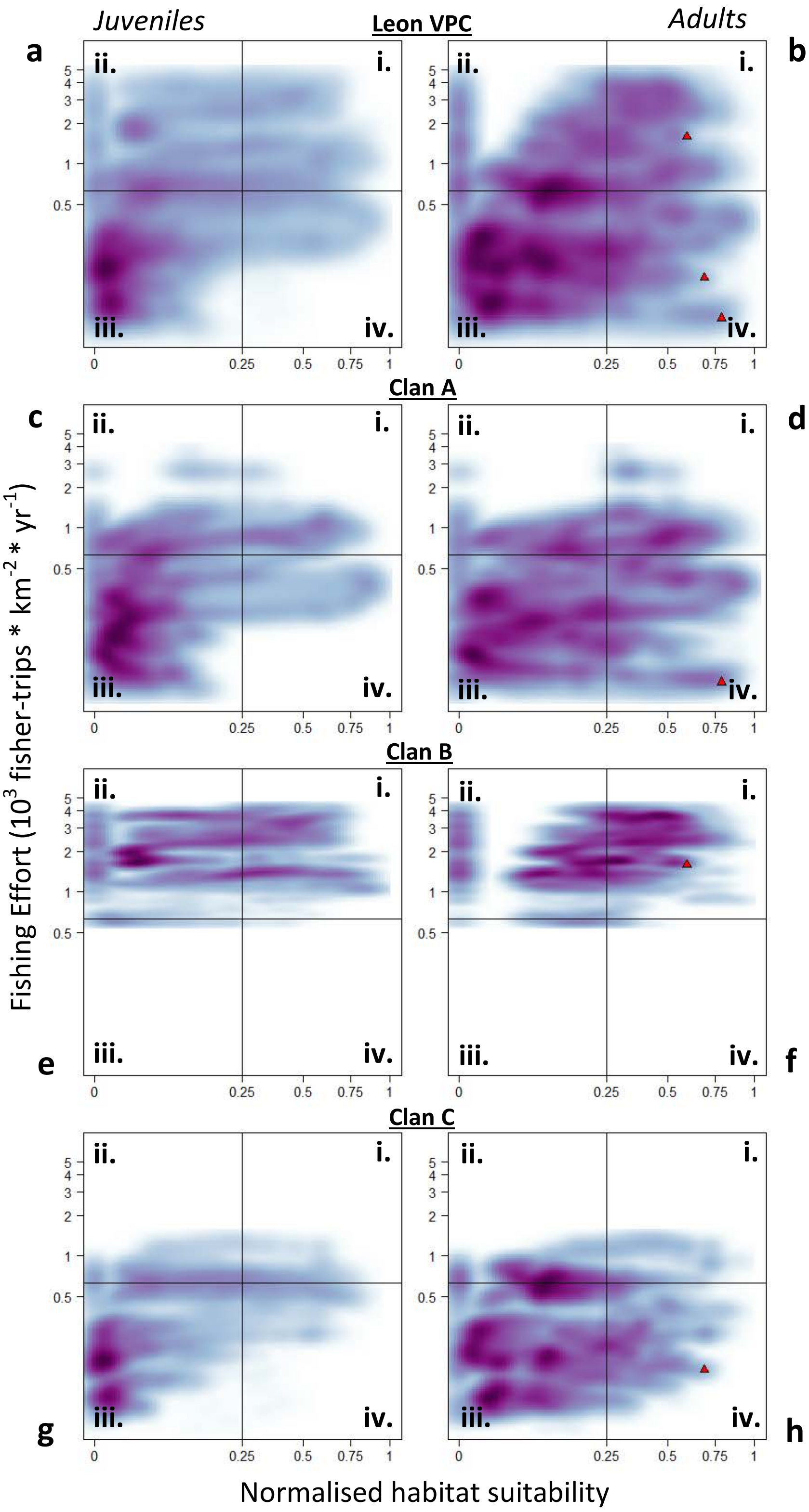

Figure 6.3 – Comparison of habitat suitability (x-axis; square root transformed) for juvenile (n = 146) and adult (n = 190) *E. polyphekadion* (as separated by total length at 50% female sexual maturity; 333 mm) and fishing effort (y-axis; natural log transformed) expressed as a density of planning units separated by management area; darker colours represent higher density of points. Plots on the left are for juvenile habitat and plots on the right are for adult habitat for the Leon VPC (a,b), Clan A (c,d), Clan B (e,f) and Clan C (g,h). Red filled triangles represent spawning aggregations sites. Quadrants represent; i. High-impact, ii. Lose-lose, iii. Low-priority, and iv. Precautionary as discussed in the conceptual framework above (Figure 6.1).

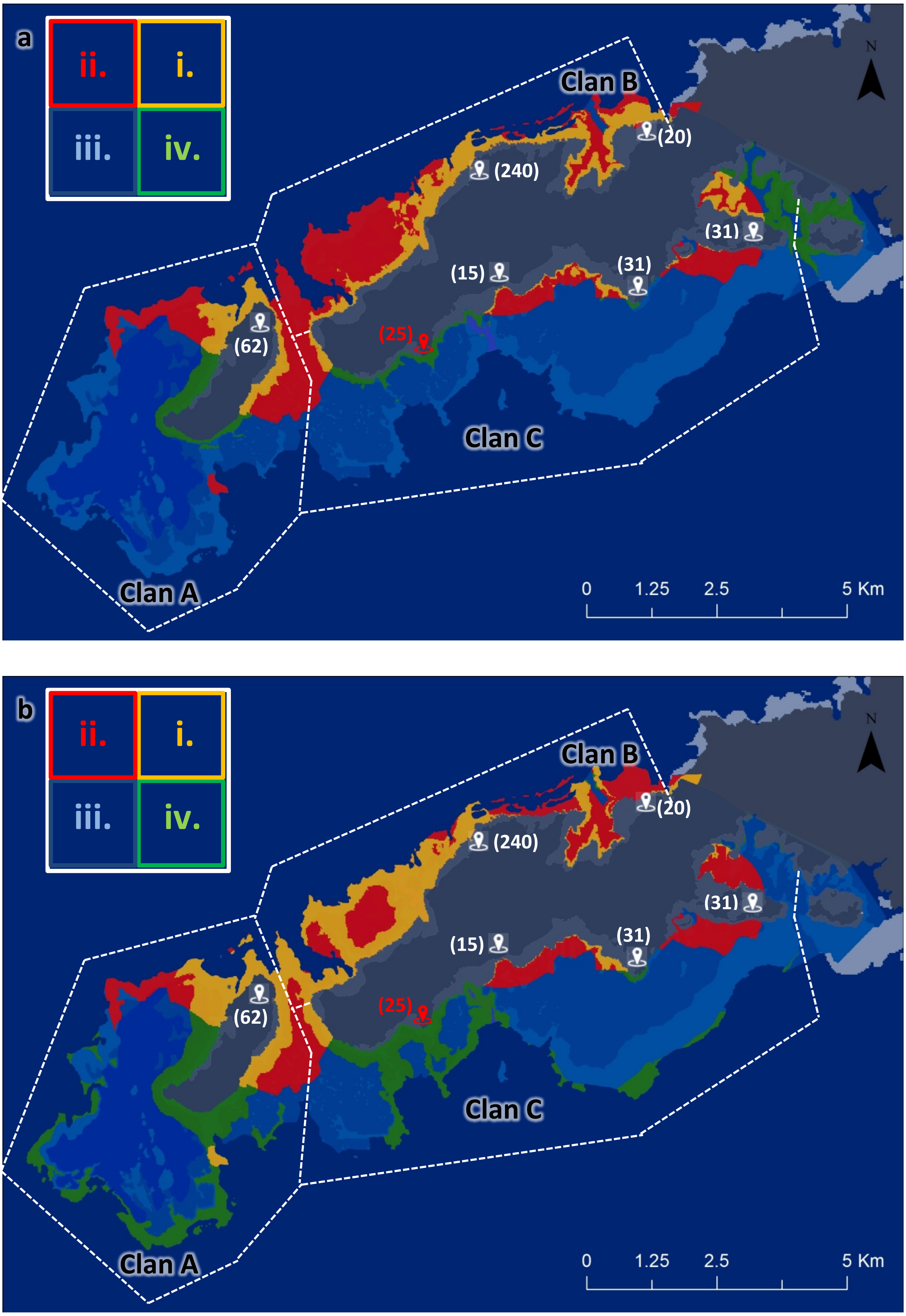

Figure 6.4 – Comparison of habitat suitability for (a) juvenile (n = 146) and (b) adult (n = 190) *E. polyphekadion* (as separated by total length at 50% female sexual maturity; 333 mm) and fishing effort mapped across the study region; colours represent quadrant position from bi-plots above (Figure 6.3): i. High-impact (orange), ii. Lose-lose (red), iii. Low-priority (transparent-blue), and iv. Precautionary (green).

6.4.3 Discussion

Considering the distribution of suitable juvenile and adult habitat across management areas suggests that grouper could be effectively managed at the scale of individual tenure areas, or the Leon VPC. However, due to differences in fishing effort the implications of management were markedly different between tenure areas. Reducing fishing pressure to levels that are sustainable for intrinsically vulnerable species such as grouper within the tenure of Clan B would heavily impact a large proportion of fishers. Conservation plans that examined patterns of resource use and suitable habitat at the spatial scale of the Leon VPC, without considering clan tenure would likely develop plans that either disproportionately targeted or excluded one clan group, contingent on the relative focus on high-impact or precautionary management. Dependant on the perceived costs and benefits of management, this may result in increased social tension among clan groups.

Suitable adult and juvenile habitat for both *E. polyphekadion* and *E. fuscoguttatus* were similarly distributed throughout the study region, and across the three tenure areas. For the sake of brevity, only the analysis for *E. polyphekadion* is presented in the main text (although see Appendix VI for analysis of *E.* fuscoguttatus), although the ensuing discussion could be similarly applied across both species. It is worth noting however, that these two species would prospectively respond to fishing differently. Both species recruited to the fishery as juveniles, although due to faster growth rates *E. fuscoguttatus* were more heavily targeted as juveniles, and thus presumably more vulnerable to fishing pressure at this stage than *E. polyphekadion* (see Chapter 3 for further discussion). Both species occupied more restricted ecological niches as juveniles – limited to areas fringing the coast and strongly associated with mangroves and freshwater sources. As fishing was higher across this fringing habitat, two-thirds of juvenile habitat received fishing effort above the Leon VPC average. Only three areas of suitable juvenile habitat offered precautionary management opportunities within the study region. As adults, the ecological niches of both species broadened to include patch and barrier reefs more distant from the coast. The total area of suitable habitat across the study region for adults was double that of juveniles, encompassing more lightly fished southern reefs. Consequently, more precautionary management options were available for adult habitat, including areas of high conservation value surrounding spawning aggregation sites.

The marked differences in fishing effort between tenure areas here resulted in divergent potential impacts of fisheries management. The tenure area of Clan B particularly contained relatively high proportions of suitable juvenile and adult grouper habitat. However, all of this habitat was heavily fished, largely at levels 2 – 8 times the Leon VPC average, presenting only high-impact management options. Modelled fishing yields within the tenure of Clan B was largely above previously hypothesised multi-species maximum sustainable yields for coral reefs of 5 $Mt*km^{-2}*yr^{-1}$ (Newton *et al.* 2007) (see Chapter 2 for further discussion). Although the value of such coarse metrics is unclear, this level of fishing is likely unsustainable for intrinsically vulnerable groupers. Proponents of high-impact management would thus likely prioritise actions within Clan B's tenure. However, enacting management measures that displace rather than remove fishing pressure, such as spatial closures, would be problematic. The low spatial mobility of fishers here suggests that displaced fishing pressure would be further concentrated into adjacent areas already fished at unsustainable levels. As distance to fishing grounds was significantly lower for subsistence compared with commercial fishing, overall reductions in fishing pressure here would disproportionately affect food security, rather than elite capture (*i.e.,* commercial fishing by wealthier individuals). As such, restrictions aimed at significantly reducing fishing pressure within the tenure of Clan B are unlikely to be appropriate without considerable additional measures that provide alternatives to fishing on shallow habitats (discussed further within section 7.4).

Conversely, the tenure areas of Clans A and C contained much lower proportions of suitable habitat, but encompassed areas under a wider range of fishing effort. Management here presented opportunities for both precautionary and high-impact management. The case for precautionary management often focusses on minimising social barriers to implementation. Restricting fishing within such areas imposes costs on fewer stakeholders and is thus likely to face less opposition and create less conflict from the majority of fishers. Also, larger areas of habitat can be managed with relatively low opportunity costs to fishers (*i.e.,* displaced fishing effort). Two precautionary management opportunities in particular (one each within the tenure areas of Clans A and C) provide suitable habitat for both target species throughout their post-settlement life histories – fringing habitats along the south-western coast of Mait Island, and the southern-facing coast at the western end of Dyual Island. The distribution of fishing effort throughout the study region was highly dependent on the limited spatial mobility of fishers. The mobility of fishers is highly malleable and responsive to changes in fleet technology (e.g. increased numbers of motorised vessels). Additionally, as fishers travelled further to exploit fishes for commercial purposes, increased access to markets (e.g. through increased access to ice, fisher buyers, or transport) would likely increase fisher mobility. Thus precautionary management opportunities at the geographic fringes of more highly exploited areas, such as these, may present particularly attractive prospects.

Due to this disparity in management opportunities between tenure areas, co-management partners are likely to either avoid or focus on management within Clan B's tenure. Either of these may be problematic. Customary management within Melanesian societies is often aimed at achieving a range of broad social goals, such as reinforcing and strengthening customs, asserting access and tenure rights, and gaining resources or status from co-management partnerships (Jupiter *et al.* 2014). Stakeholders are likely to perceive the relative costs and benefits of management actions differently, according to their different goals. Indeed, during interviews numerous respondents expressed jealousy over the perceived increase in status and opportunities that the co-management partnership with The Nature Conservancy had afforded members of Clan A. As such, the concentration or exclusion of management within one clan's tenure area may increase social tension between clan groups.

6.5 Q3: Do stocks of relatively mobile coral reef fishes deliver a sufficient spatial fit for their governance using community-based institutions?

6.5.1 Methods

Catchment areas for 50% of *E. fuscoguttatus* spawning populations were estimated for the three transient grouper spawning aggregation sites within the study area (discussed in Chapter 2). Aggregation sites were buffered with circles of radii of 1.5 km (50% catchment as calculated for the spawning aggregation Site A; Table 5.1). These circles were then intersected with available shallow habitat (discussed in section 4.3.3; Appendix IV); differences in 50% catchment areas (Table 6.4) are thus due to slight differences in available shallow habitat within 1.5 km of each site. Total fishing effort and density of fishing effort were calculated within each of the resulting catchment areas, following the methods within section 2.3.5.2).

6.5.2 Results

Each of the three customary tenure areas contained a transient grouper FSA (Figure 6.5). An additional FSA site was excluded from analyses, as although within the Leon VPC jurisdiction, it was situated outside of the study region. Although, estimated 50% catchment areas were similar across the three FSAs (Table 6.4), fishing effort was 12 and 14 times higher within the 50% catchment of Site B compared with Sites A and C, respectively. More than four in five households reported fishing within the estimated 50% catchment of Site B (Table 6.4).

Table 6.4 - Comparison of fishing activity proximal to FSA sites within western Dyual.

	Fish spawning aggregation site		
	Site A	Site B	Site C
Estimated 50% catchment area (km^2)	2.1 km^2	2.2 km^2	2.3 km^2
Total fishing effort within 50% catchment (fisher-trips * yr^{-1})	385	1418	385
Density of fishing effort within 50% catchment (fisher-trips * km^{-2} * yr^{-1})	183	645	167
Households' fishing grounds intersecting 50% catchment (%)	41%	83%	24%

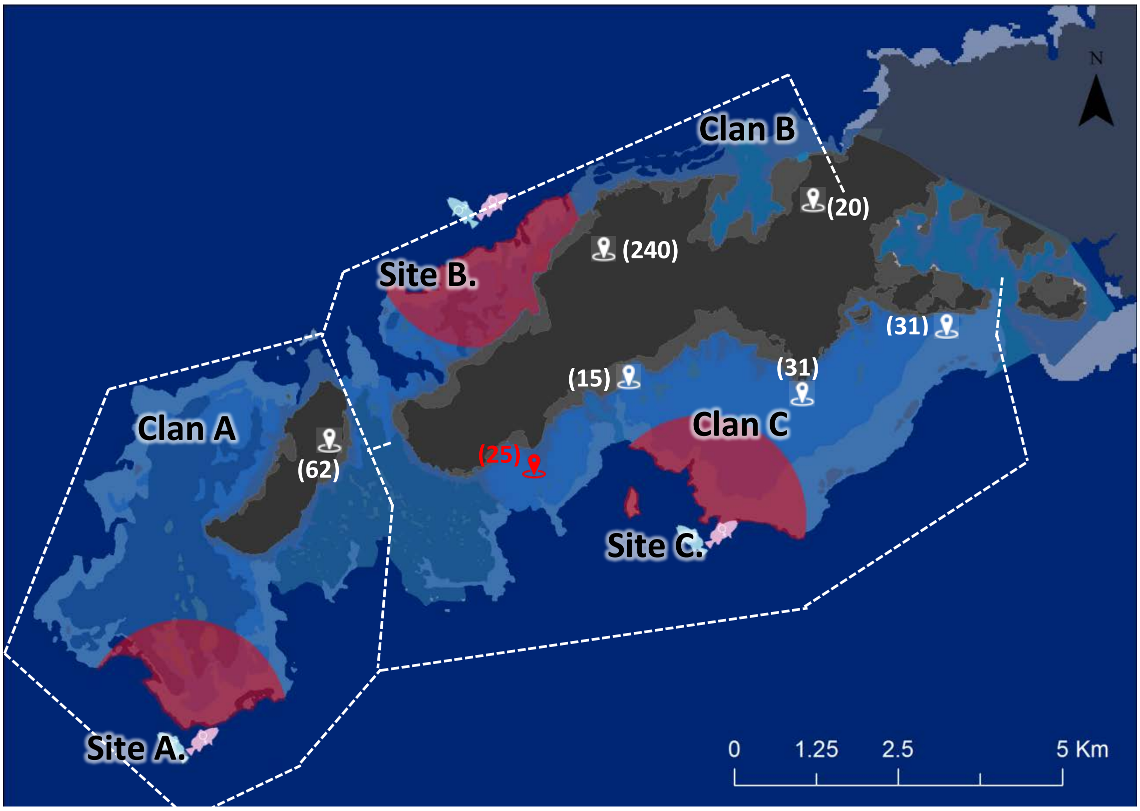

Figure 6.5 – Map depicting approximate locations of transient grouper spawning aggregation sites at western Dyual: represented by fish symbols (🐟🐟) with points: Sites A, B, and C. Red shaded areas represent estimated 50% catchment areas of spawning aggregations.

6.5.3 Discussion

The customary tenure system here provided the best spatial fit for governing individual spawning stocks of grouper. The three tenure areas considered here each contained a transient grouper spawning aggregation site, and the majority of spawning adults from each were likely retained within the relevant tenure boundaries. Conversely, governance at the scale of the Leon VPC introduced the potential for the serial depletion of individual stocks. In fact, the depletion of the stock spawning at Site B had already occurred, due to variation in fishing effort here – a legacy of historic *de facto* governance at the scale of the Leon VPC.

Reproductive migrations recorded for *E. fuscoguttatus* from Site A indicated that few spawning adults resided outside of Clan A's tenure throughout the non-spawning season. Aggregation Site C was similarly relatively distant from tenure boundaries, suggesting similar levels of retention of spawning adults. Aggregation Site B was situated within 3 km of tenure boundaries. As such, significant proportions of the grouper that aggregate to spawn here presumably migrate across tenure boundaries, and reside outside of Clan B's tenure during non-spawning periods. However, modelled migration patterns for *E. fuscoguttatus* at Site A suggest that a significant majority of spawning individuals from Site B would remain within

Clan B's tenure throughout non-spawning periods. It must be noted that the migration model developed for *E. fuscoguttatus* at Site A is the first of its kind. It is therefore currently unknown whether these patterns are representative of other species (including *E. polyphekadion*) or other aggregations (including Sites B and C). Differences including habitat suitability and density-dependent effects could affect patterns of migration and thus catchment areas. As such, analyses and recommendations within this section are intended to be instructive though not prescriptive. Assuming relatively similar patterns of migration however, it is clear that fishing effort was highly concentrated on the reproductive stock that aggregates at Site B. Fishing effort was more than three times greater in the estimated 50% catchment here, relative to Sites A and C. Abundances of spawners at Site B were reportedly extremely low. This concentration of effort can be viewed as the legacy of common access (*i.e., de facto* management) at the spatial scale of the Leon VPC. The patterns of fishing effort observed here would not be possible if access was restricted at the spatial scale of individual tenure areas, according to clan affiliation. Such restrictions are currently socially unconscionable due to food security concerns, however this highlights the consequences of spatial mismatches. The ongoing persistence of spawning grouper at Site B looks uncertain, although would likely minimally require the closure of the aggregation site to fishing.

The restricted spatial scales of aggregation sites makes them ideal candidates for community-based management (Hamilton *et al.* 2011). Due to its proximity to settlements the closure of Site B would directly impact 80% of local fishers. However, a small targeted closure similar to that at Site A would have negligible effects on the overall size of individual fishing grounds. The more significant impact of closing Site A to fishing would likely be the loss of 'windfalls' of profitable fishing during spawning periods. In contrast with the more isolated aggregations, this would potentially disproportionately impact more marginalised fishers with lower spatial mobility. High levels of fishing pressure across this aggregation catchment area also suggest that the closure of the spawning site alone may not be sufficient to produce the recovery of spawning populations. However, as discussed earlier wider restrictions to fishing across the larger catchment area are likely to be problematic. In contrast with Site B, the isolated position of Site C suggests that its closure would present similar opportunities to Site A. Interviews with fishers who reported poaching within Site A suggested that although fishing at isolated aggregations may be sporadic, hundreds of kilograms of grouper could be caught within a single fishing trip. No such trips occurred during the creel surveys conducted here, so fishing pressure was certainly underestimated at these isolated aggregation sites. Thus, although Sites A and C are designated as precautionary management (Figure 6.3), their closure to fishing would presumably have a high impact. Due to their isolation, accessing these sites was reportedly difficult and generally required a motorised vessel. As such, isolated aggregation fishing largely provided for elite capture by a few wealthier fishers, rather than the food security of subsistence fishers. Due to this concentration of benefits, closures of sites providing for elite capture often gain broad community support (Hamilton pers. com.). Spawning aggregations represent a necessary life history event for *E. polyphekadion* and *E. fuscoguttatus,* and their protection is critical for the persistence of these species (Sadovy de Mitcheson *et al.* 2012). Although spawning aggregations can potentially be exploited sustainably, extensive evidence suggests that anything above low-level subsistence use is likely to deplete stocks (Sadovy de Mitcheson 2016). Fishing at spawning aggregations exhibits hyperstability (*i.e.,* catch-per-unit-effort remains steady as abundances decrease) (see Appendix II for details). Therefore, these sites remain lucrative fishing targets even following significant population depletions. Prolonged low abundances at Sites B and C (Hamilton *et al.* 2004, 2011) are therefore concerning, and the closure of these sites to fishing represents a key management priority here.

6.6 Conclusions

In this chapter I addressed the primary research question of this thesis:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

I addressed this through the following three specific research questions:

Q1) Do the spatial distributions of social processes (*i.e.,* patterns of settlement, clan affiliation, access rights, and fishing effort) lead to problems of fit with community-based governance institutions?

Q2) Do interactions between the spatial distributions of fishing effort and suitable habitat throughout the post-settlement life histories of target species lead to problems of fit with community-based governance institutions?

Q3) Do reproductively isolated adult populations (*i.e.,* stocks) of relatively mobile coral reef fishes deliver a sufficient spatial fit for their governance using community-based institutions?

The social components considered here (Q1) provided a good spatial fit with governance at the scale of the most localised level of state-based governance – the Leon VPC. Governance at the scale of individual customary tenure areas introduced problems of fit with these social components. Individual tenure areas aligned poorly with relevant stakeholders, potentially leading to reduced compliance with management measures. Maintaining social cohesion is vital in rural Melanesian societies. As such, potential sources of conflict arising from social problems of fit, including those detailed above, may be implicitly or explicitly considered during management decision-making. However, internal factors such as the death of a local leader, and external factors such as increased access to markets may erode mechanisms that support social cohesion (Cinner *et al.* 2007). Due to the heavy reliance on voluntary compliance with regulations here, social cohesion is crucial for fisheries sustainability. As such, the social problems of fit associated with governance at the scale of individual tenure areas demonstrated here should not be taken lightly.

Conversely, the ecological components considered throughout this thesis provided a good spatial fit with individual customary tenure areas. Governance at the scale of the Leon VPC introduced ecological problems of fit. Marked differences in fishing pressure within suitable juvenile and adult habitat between tenure areas (Q2) would likely lead to management actions being disproportionately concentrated within or excluded from one clan's tenure area, contingent on whether high-impact or precautionary management was prioritised. Additionally, governance at the spatial scale of the Leon VPC introduced the potential for the serial depletion of individual spawning stocks (Q3). The spatial variation in fishing pressure between these stocks, and prolonged low numbers of spawners at the aggregations of more heavily exploited stocks, suggested that serial depletion was already occurring here.

The combination of these results highlights the importance of considering both social and ecological components of small-scale fisheries. Information on either social or ecological components alone would have yielded different recommendations for the appropriate spatial scales of governance. However, as this study demonstrates these recommendations would be incomplete, with potentially serious consequences. When considered as an interconnected social-ecological system, the fishery here would best be governed under nested governance systems. This addresses problems of fit between the key social and ecological scales considered here, allowing for the independent management of stocks (*i.e.,* alignment with ecological scales), and gives stakeholders a voice across tenure boundaries (*i.e.,* social). This work provides compelling evidence that relatively mobile coral reef fishes can be managed at scales that are congruous with community-based management, and further highlights the need to study and manage small-scale fisheries as interconnected social-ecological systems.

CHAPTER 7 – DISCUSSION AND CONCLUSIONS

7.1 General discussion

The study of fisheries as social-ecological systems recognises the inextricable interconnection of humans with the ecosystems that they inhabit and depend on. This interdisciplinary focus is of particular value to the study of small-scale artisanal and subsistence fisheries, where local communities often have long cultural traditions surrounding the use and governance of natural resources. Increasingly, these customary governance systems are being utilised as institutional frameworks for contemporary fisheries management programs (Cinner and Aswani 2007). This often takes the form of co-management partnerships between local fishing communities and external government, non-government, or civil organisations. The trend toward co-management is in clear recognition of the pivotal importance that social, cultural, and political factors play in effective management. However customary governance systems, and as a result co-management programs almost invariably operate over relatively limited spatial scales, and their capacity to effectively manage fisheries is contentious (Foale and Manele 2004; Mills *et al.* 2010). Prior to this thesis however, community-based management institutions had rarely been directly, empirically assessed for spatial mismatches (*i.e.,* problems of fit) with the key social and ecological processes underpinning the fisheries that they seek to manage (but see Almany *et al.* 2013). Within this thesis I sought to address this gap by answering the following overarching research question:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

Addressing this question required an interdisciplinary approach. The social and ecological elements of these fisheries are each formidably complex. Small-scale coral reef fisheries often target a diverse array of species, each forming complex and dynamic connections within the ecosystem as they move through complex life cycles. The management of these fisheries relies on an array of social, economic, and political factors that can form complex feedbacks (Cinner and McClanahan 2006; Cinner 2007; Cinner *et al.* 2009a; Mills *et al.* 2013). Understandably, empirical investigations of small-scale coral reef fisheries have often been conducted with a strong social (Cinner 2007) or ecological (Jones *et al.* 2009; Berumen *et al.* 2012) focus. In this thesis, I applied a combination of research techniques from the social and ecological sciences to the investigation of a small-scale coral reef fishery in Papua New Guinea, focussing on two relatively mobile, exploited species of grouper. By spending a considerable amount of time living in a remote fishing community, I was able develop a detailed understanding of the spatial aspects of key social processes that impact the fishery; patterns of settlement, clan affiliation, access rights, tenure disputes and fishing effort. By building relationships with key stakeholders in this fishery I was also able to adopt a participatory approach to my ecological research that drew on local knowledge and local fishers' participation. This in turn enabled me to develop a comprehensive understanding of the post-settlement life histories of two large, naturally rare, vulnerable, and important fisheries species. Most importantly, by directly assessing the spatial interactions between these key social and ecological processes I was able to empirically address whether community-based governance institutions were spatially capable of managing relatively mobile target fishes. A few specific conclusions of this work and avenues of further enquiry are discussed below.

7.2 Major findings and future directions

Some of the major findings were:

1) Spatial fit – The primary conclusion of this thesis was that community-based institutions provided a good spatial fit for the management of relatively mobile fishery-targeted coral reef fishes. The ecology of the two model species of grouper, *Epinephelus polyphekadion* and *E. fuscoguttatus*, provided a good spatial fit with the most spatially restricted level of governance assessed here – individual tenure areas, encompassing 7 – 19 km^2. Each tenure area contained one transient grouper spawning aggregation site, and reproductive migrations suggested that a substantial majority of spawning adults were likely to remain within the tenure area where they spawn, throughout the non-spawning season. Additionally, each tenure area contained considerable suitable habitat for both species, across their post-settlement life histories. However, when key social conditions were considered, the most localised state-based government scale, encompassing 45 km^2, provided the best spatial fit for their management. Highly variable fishing effort across extremely limited spatial scales was particularly important in considering the most appropriate social scale of governance here. Taken together these findings highlight the need for nested governance, even at these limited spatial scales, and highlights the importance of interdisciplinary approaches

2) Patterns of reproductive migration – During my investigation into the reproductive movements of *E. fuscoguttatus*, I employed a modelling technique that is commonly utilised to assess seed and larval dispersal and the spread of invasive organisms – that is the development of a migration kernel. This technique had not previously been applied to the investigation of reproductive migrations associated with fish spawning aggregations. This function provides an empirically derived estimation of the proportion of the population that can be expected to remain within any given distance of the aggregation site throughout the spawning season. This represents a major step forward in their systematic management, allowing for the estimation of potential conservation returns as increasing areas surrounding the aggregation site are protected. The 'long tail' of migration observed here suggests that methods that exclusively report the 100% catchment (*i.e.,* the total area encompassing all recorded or relocated individuals) may significantly overstate the scale of effective management for species that spawn in transient aggregations. Further study is required to ascertain the extent to which this result is common across populations and species. The high cost of acoustic tagging equipment remains a major limiting factor in applying this approach, as it restricts the number of individuals that can be tagged and the coverage of the surrounding area with passive acoustic receivers.

3) Ontogenetic shifts –This study provided the first empirical examination of ontogenetic shift in habitat suitability for these important fishery-targeted species. Models here demonstrated that the habitat requirements of the two species were similar, though shifted throughout their post-settlement life histories. Juveniles were restricted to habitat directly fringing the land, and were strongly associated with mangroves and freshwater inputs. Adults inhabited a broader ecological niche, and were present across most hard-bottomed habitats, although not uniformly. This directly contradicts the only existing published account for *E. polyphekadion,* which described them as generalists. The close association of juvenile habitat with mangroves and freshwater influences is of particular importance. These habitats are more likely to face disturbances from terrestrial sources, such as increased sedimentation and eutrophication. As such, these habitats may require additional management considerations. Interestingly, the two study species interacted with the fishery differently. Due to divergent growth rates *E. fuscoguttatus* were heavily targeted as juveniles, whereas *E. polyphekadion* were predominantly caught as adults. This has potentially profound implications for their management in general, including the spatial management of these species. Fishing restrictions encompassing juvenile habitats will likely significantly impact *E. fuscoguttatus,* although *E. polyphekadion* to a far lesser degree. This work presents a major step forward in managing critical juvenile habitat for these species. However, the relative importance of juvenile habitat depends on the degree to which it replenishes adult populations (Beck *et al.* 2001). This was not assessed in this thesis. Natural and artificial markers have been used to quantify ontogenetic movements of individuals between juvenile and adult habitats, although

these remain uncommon for coral reef fishes (Gillanders *et al.* 2003). Empirical models of connectivity between juvenile and adult habitats represent a major next step toward understanding the spatial aspects of fisheries.

4) Spatial variation in fishing effort – Although spatial components of fisheries have long been recognised for larger commercial fisheries, they are rarely expressly considered within small-scale artisanal fisheries. A key finding of this work was the high levels of variation in fishing effort at extremely fine spatial scales and highly concentrated around settlements – half of the fishing effort within the study region was concentrated within just 10% of available fishing grounds. This area was fished at more than eight times the average across the study area. This result raises a number of interesting questions, including; (i) Does serial depletion of habitat occur at these extremely limited spatial scales, in low-developed artisanal fisheries? Although serial depletion of fishing grounds is presumed to be common in industrialised fishing, in small-scale multi-species it is generally envisaged in the context of species depletions (*i.e.,* fishing down the food web). The high levels of variation in fishing effort here suggests that serial depletion of fishing grounds may be far more pervasive than previously thought. (ii) To what degree does fish and fisher behaviour compensate for spatial variability in fishing? The depletion of more heavily fished areas may be avoided through substantial spillover of target species from neighbouring habitats that are under lesser pressure. Additionally, fishers may target faster growing, more productive species within these areas. The extent to which these and other processes compensate more heavily fished areas is unknown. (iii) How do intrinsic and extrinsic social and ecological factors affect the spatial patterns of fishing? Fishing for commercial purposes was conducted at greater distances from settlements than fishing for subsistence here. Thus the placement of management areas is important in balancing conservation and food security goals. Additionally, the degree to which commercial and subsistence activities are spatially segregated or overlapping will dictate whether they are largely complementary or competitive, which has clear implications for fisheries management. These results highlight the vital importance of considering spatial aspects of fishing pressure in small-scale fisheries modelling and management. However, currently studies using survey data or modelling techniques using proxies for fishing effort rarely consider such fine-scale variation. Further studies would be beneficial in determining whether such levels of intensely concentrated fishing pressure are common across low developed artisanal fisheries. Additionally, broader examination of spatial patterns of fishing could allow for the development of predictive models, to extrapolate results to unexamined systems and facilitate broader incorporation of finer-resolution spatial aspects of fishing pressure in modelling and spatial planning analyses. Collecting data at such a fine spatial resolution across a broader geographic area presents significant logistical challenges, which can be met at least in part through applying a participatory approach to research.

5) Participatory research – Research into coral reef fisheries has lagged considerably behind industrialised temperate fisheries. The robust science-based management of coral reef fisheries is currently impeded by critical gaps in our understanding of fundamental ecological processes for key fishery-targeted species, and the scarcity of data on fishing effort. The participatory mapping approach applied during this study facilitated the collection of spatial data to a very fine spatial resolution (0.12 ± 0.01 km^2). This participatory approach was applied to the collection of samples for demographic, reproductive, and (future) genetic analysis. The employment of trained local fishers in data and sample collection here provided a low-cost method of collecting samples over a prolonged period. This technique allowed large numbers of samples to be collected directly from the fishery, and as such did not place any extra fishing pressure on these vulnerable species. Additionally, this provided a comprehensive picture of the reproductive cycles of these seasonally-spawning species, across the entire year. This sustainable low-cost sample collection method could assist in filling knowledge gaps, particularly in data-poor, remote, small-scale artisanal fisheries.

Another key benefit of this in-depth participatory approach is the opportunity to obtain local ecological knowledge. Local ecological knowledge is often thought of in terms of community-wide customary knowledge of local ecological conditions, accumulated, refined, and handed down through generations. In addition to this however, local ecological knowledge is personally obtained by individual resource users through decades of interacting with the local ecological system. This latter form of local ecological knowledge may be not widely known throughout the community, and may even be closely guarded. In this study, initial attempts to locate juvenile individuals here involved more than 200 hrs of underwater surveys following methodology published in the scientific literature, the construction of artificial fish-traps (known as gangos) utilised by the aquaculture industry, and the employment of a number of highly-regarded local fishers. All of these methods failed. However during an interview, one local female fisher was able to give precise capture locations for juveniles of both species, and detailed instructions of the most appropriate capture method. This fisher liked to eat small grouper (because of their ‘sweetness’) and had thus honed her technique for their capture. She had not shared this information with the community, and had no previous intention to do so. These methods were subsequently successfully employed to locate juvenile habitat throughout the study region, and highlights the importance of identifying experts and being open to explore various lines of inquiry when utilising local knowledge.

In the interests of balance it is important to note that working closely with communities also presented significant challenges. During this study a long-term land tenure dispute escalated into an armed conflict. This conflict resulted in the deaths of three local community members, and the serious assault of a local representative for The Nature Conservancy. As a result, work at the study site was halted for a period of six months. Significant social, political, or cultural challenges are commonplace in Melanesia, and must be considered as inherent risks involved with intensive, community-based work within the region.

6) Temporal variation in social-ecological systems

It is important to note that this thesis represents a detailed analysis of this social-ecological system at a particular point in time. Due to the enormity of this task, the various causes and effects of temporal shifts in the system were not analysed or discussed in detail. Further study into the effects of internal (e.g. political changes, resource depletion, and changing stakeholder aspirations) and external factors (e.g. increased market access, external management restrictions, interventions by conservation organisations, and introduced technologies) on the spatial aspects of such social-ecological systems would represent a major advancement.

7.3 Caveats and limitations

The most conspicuous omissions from this study are the spatial scales of larval dispersal. Larval replenishment is vital to the persistence of populations over generational time scales. The empirical measurement of larval dispersal distances had long been an elusive goal of fisheries science, however advances in genetic techniques now permit their direct empirical measurement (Almany *et al.* 2007, 2013; Jones *et al.* 2009). These require the sampling of a large proportion of adults from a known reproductive population and the collection of genetic material from a large number of juveniles. As such, the assessment of larval dispersal makes a good companion project to the adult tagging and ontogenetic shift work conducted here. Although I had originally planned to measure the larval dispersal distances of the target species here, a number of logistical challenges, including the violent dispute discussed above, intervened. This work is continuing.

It is also important to note that this study presents in-depth analyses of two key species. The nature of such an approach limits the interpretation of results to similar species. The two study species here were specifically selected for their local and regional importance, and their intrinsic vulnerability, as well as the logistical opportunities presented by their formation of transient spawning aggregations. The depth of understanding generated from the intensive study of individual species is crucial. However, due to the broad multi-species nature of artisanal coral reef fisheries, the trade-off between depth and breadth of research will always be difficult.

Finally, the inclusion of a large number of juvenile samples in this study has allowed the first empirical analysis of early growth rates for these two species (Berumen 2005). Other studies that have examined epinephelid juveniles in greater detail have also identified primary male development (Adams and Williams 2001; Adams 2003; Liu *et al.* 2016). However, despite histologically examining gonads from a large number of individuals, including previously unexamined juveniles, I could not directly confirm sexual function for either species. This suggests that morphological changes in the gonad may be extremely rapid for these species and other methods, such as epidemiology, may be required to confirm their sexual pattern.

7.4 General conclusions on management at western Dyual

The primary purpose of this doctoral work was to progress the scientific understanding of spatial aspects of social-ecological systems – particularly as they apply to the community-based governance of small-scale coral reef fisheries. However, doing so has led to a number of conclusions that have significant importance at western Dyual specifically, and across small-scale fisheries generally, but did not directly contribute to the primary research question.

7.4.1 Appropriate management institutions

Assisting the local communities in forming a nested fisheries management body would greatly increase their capacity to manage local fisheries. There was strong local support for creating an institution specifically tasked with fisheries management broadly across local stakeholders and specifically among clan chiefs and other influential local figures. The customary tenure system of western Dyual has demonstrated past management success, with the closure of the spawning aggregation Site A to fishing (Hamilton *et al.* 2011). However, most fishers incorrectly attributed the closure of Site A to the Leon VPC (59%), rather than the customary tenure holders (31%). Similarly, more fishers believed that they could influence management decisions regarding the closure through the Leon VPC (42%), than through the customary tenure system (19%) (see section 2.4.4.5). These mismatched perceptions of management jurisdiction could potentially contribute to the lack of enforcement of the Site A closure despite widespread local support for strengthening enforcement (Table 2.1). However, members of the Leon VPC and clan chiefs all reported that any spatial closure of fishing grounds was under the jurisdiction of tenure holders. This further highlights the importance of nesting appropriate institutions to enact governance across scales. Any governance institution created at the spatial scale of the Leon VPC should ideally be based around the existing customary tenure system, and incorporate all relevant tenure holders. One such governance network has been recently created in the neighbouring Manus Province, although across a substantially broader spatial scale (Almany *et al.* 2015). This network was created along existing customary tenure, rather than state-based government, boundaries.

7.4.2 Closure of spawning aggregation sites

The existing closure at Site A is widely known to experience poaching. Adding further closures, before enforcing the first may lower their perceived legitimacy, and the authority of management institutions. Key informants reported that customary closures at transient spawning Sites C and D had failed due to high levels of poaching by fishers from eastern Dyual. Enacting a successful system of graduated sanctions is probably a pre-requisite to more restrictive management here.

The locally perceived success of the management at Site A has led to increased local support for the closure, and support for increasing and strengthening fisheries management more broadly throughout the study region. During a key informant interview, the chief of Clan C suggested that with external support, a similar closure would be welcomed at Site C. Despite its relatively isolated location, abundance trends at the site demonstrate that this site is substantially impacted by fishing (Hamilton *et al.* 2011). This is consistent with considerable evidence that even small-scale artisanal fishing pressure can severely deplete vulnerable grouper aggregations (Sadovy de Mitcheson 2016). Closing this site to fishing would likely provide significant conservation returns. However, reported previous poaching by residents of eastern Dyual remains a concern.

In this regard, the proximity of aggregation Site B to major settlements presents an opportunity. If a system of sanctions existed for fishers violating regulations, Site B would presumably be more readily enforced as it is within sight of the settlement of Mait. Conversely however, its proximity to major settlements suggests that the closure of this site would likely disproportionately affect more vulnerable (and thus less spatially mobile) fishers. Due to the restricted size of aggregation sites, the loss of fishing grounds would not be significant. Data collected during the demographic study however, revealed that one spearfisher caught seven grouper (totalling 8 kg) from Site B during a single trip during the spawning season of May

2015. This is twice the average catch as calculated from creel surveys, however an order of magnitude lower than reported catches from poaching at Site A. Such windfalls of more profitable fishing during spawning periods may present opportunities to pay occasional significant expenses, such as school fees. However, the importance of such windfalls was not directly addressed within this thesis.

7.4.3 Closure of spawning aggregation catchments

The displacement of fishing effort represents a key concern when considering using spatial closures to manage a portion of the population during non-spawning periods (*i.e.,* closing FSA catchments to fishing). Closing the estimated 50% catchments for Sites A and C would have little immediate impact on fishers, and represents a good precautionary management opportunity. Conversely, the closure of any significant area of habitat proximal to Site B (which is almost exclusively in the high impact domain; Figure 6.3) would heavily impact fishers. The limited spatial mobility of fishers here suggests that any displaced fishing effort would be further concentrated in surrounding areas that are already heavily fished. I suggest that any such measure should only be considered in conjunction with additional measures designed to reduce total fishing effort on shallow habitat. This could potentially be achieved by deploying a shallow-water fish aggregating device directly in front of the primary settlement here, as has been successfully deployed elsewhere (Hamilton pers. com.).

7.4.4 Managing juvenile habitats

Due to the close association of juvenile habitat with mangroves and freshwater inputs, terrestrial disturbances would likely also impact this habitat. However, these are largely outside of the scope of this thesis. For both target species, the two large embayments (within the tenure of Clan B to the north-east, and within the tenure of Clan C to the south-east) provided the most suitable habitat. Both embayments housed small human settlements, although due to its proximity to the primary settlement of Leon, the bay within the tenure of Clan B experienced considerably higher fishing effort. This suggests that managing juvenile habitats within the tenure of Clans B and C may be a choice between high-impact and precautionary management, respectively. Suitability of juvenile habitat was closely associated with freshwater inputs and mangroves, which can be affected by coastal development and terrestrial disturbances. In the Solomon Islands, species with similar juvenile habitat associations have been severely affected following land clearing for logging and agriculture (Hamilton *et al.* 2016a). No large-scale land clearing was visible proximal to these bays. Conversely, Mait Island had been extensively cleared for agricultural purposes. Large areas of this island have been cleared in the past for copra plantations, and at the time of writing juvenile habitat along the east and west coasts of Mait Island were fringed by relatively small areas of mangrove forest. The degree of connectivity between juvenile and adult habitats across western Dyual is unknown. However, past research demonstrates that juvenile fishes recruit to spawning populations by social means (Warner 1990; Arnold and Metcalfe 1996), such as by following more experienced conspecifics (Mazeroll and Montgomery 1998). As the only substantial juvenile habitat within its catchment, the area fringing Mait Island may be crucial for the replenishment of the spawning stock at Site A. As such, the clearing of the remaining mangrove here could have serious population-scale consequences, including the collapse of the spawning stock (Petitgas *et al.* 2010).

7.4.5 Incorporating larval connectivity

Larval dispersal was not considered within this thesis. Spatial scales of governance that ensure adequate self-replenishment of managed populations, and connectivity between populations are therefore unknown. However, the only existing empirically-derived larval dispersal kernel (Almany *et al.* 2013) suggests that management at western Dyual would likely be well served though inclusion in a larger, nested management network. Such a network was created in response to new information on patterns larval dispersal for another species of grouper in neighbouring Manus Province (Almany *et al.* 2015). This network was created along enduring cultural lines, rather than state-based government jurisdictional boundaries. Significant social barriers exist to similar self-organisation across Dyual Island, as western and eastern populations have distinct cultural identities, speak different languages, and reportedly have little history of co-operation in management.

7.5 Concluding remarks

This thesis investigated the research question:

> *What are the spatial problems of fit between community-based governance institutions, relatively mobile target fishes, and the fishers that target them within small-scale artisanal fisheries?*

This question was investigated using a case study of the small-scale artisanal fishery at western Dyual Island, New Ireland Province, Papua New Guinea, through two model target species, *Epinephelus polyphekadion* and *Epinephelus fuscoguttatus.* The diagnostic framework applied here, adapted from Ostrom (1990), considers the fishery as an intrinsically interconnected social-ecological system. As such, a broad empirical understanding of this model system was developed through the application of a range of research tools and techniques from both social and ecological sciences. First, a combination of participatory mapping and key informant, household, and creel surveys were applied to examine existing institutions relevant to community-based management, and the spatial distributions of human settlement, clan affiliation, access rights, and fishing effort throughout the study region. Second, ontogenetic shifts in habitat suitability were examined for the two target species, through the application of age-based demography, reproductive histology, and habitat suitability mapping. Third, the spatial scales of relatively reproductively-distinct adult populations (*i.e.,* stocks) were examined by investigating the reproductive migrations of adults using acoustic telemetry. Finally, comparative analyses of all of these key social and ecological components delivered the most comprehensive empirical investigation of spatial problems of fit for the community-based management of a small-scale artisanal coral reef fishery.

This thesis concludes that: 1) patterns of fishing in low-developed small-scale fisheries can vary markedly over extremely restricted spatial scales (100s of metres); 2) despite otherwise similar demographic characteristics, faster growth to a larger maximum size likely increases the vulnerability of *E. fuscoguttatus* to growth overfishing; 3) both study species occupied relatively narrow ecological niches as juveniles, within habitats that presumably experience disparate anthropogenic pressures; 4) a more nuanced understanding of reproductive migration patterns can provide spatial management options for species that migrate to spawn; 5) empirical investigation of key social and ecological processes that underpin the persistence of fisheries can individually produce disparate recommendations for ideal spatial scales of governance; and 6) community-based institutions can provide a good spatial fit for the management of relatively mobile coral reef fishes.

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APPENDICIES

Appendix I – Social, economic, political, and ecological setting of the western Dyual artisanal fishery.

Research aim

Numerous interconnected social, economic, and political factors can influence fishing pressure and ultimately the sustainability of fisheries. Within this appendix I discuss the results of key informant, household, and creel surveys conducted across western Dyual Island in 2014. These surveys were conducted and analysed to address the specific research question;

1. What are the local social, economic, and political characteristics of western Dyual Island, that have been previously demonstrated to affect fisheries sustainability and management?

Methods

During key informant surveys (detailed in section 2.3.2), informants were asked to provide a list of items which only wealthy members of the community were likely to possess, as well as the housing materials (floor, roof, and wall) of wealthy and non-wealthy community members.

During household surveys (detailed in section 2.3.3), heads of households were asked to provide their age, sex, years of formal schooling, and clan affiliation, and how many male and female adults, and male and female children resided in their household.

To determine the level of heterogeneity of the local population, respondents were also asked where they were originally from, how long they had lived in the local area, and their reason for moving to the local area. Social capital was investigated by asking respondents whether they were actively or passively involved in any community decisions, and particularly decisions about marine resource management; whether they were members of any community organisations; and whether they had been involved in any community events in the last 12 months, outside of their immediate family. Respondents were also asked to rate their level of trust in the following groups, on a likert scale(1 = trust none, 3 = trust half, and 5 = trust all): other community members, community leaders, police/security, local government, provincial government, and national government.

To provide information on their material style of living, interviewees were asked whether or not they or any other member of their household owned any of the items suggested by key informants to indicate wealth, as well as to provide information on their housing materials, cooking fuels, lighting and methods of transport.

Results

Socioeconomic characteristics

Self-identified heads of households were disproportionately male (72%). This could not be explained by a higher proportion of males in the adult population (54%). Rather this is likely to be due to cultural differences in family roles, and differences in willingness to speak with the male interviewers. Respondents ages ranged from 24 to 72 (42.6 ± 2.0 years; mean ± SE).

Education

The level of education among respondents was relatively low (6.3 ± 0.6 years); 13% had no formal education, less than half had completed primary school, and only 6% had completed high school.

Immigration

Around two thirds (69%) of respondents indicated that they were native to western Dyual. Of the immigrants, one individual (3%) migrated from eastern Dyual, and the remainder migrated from other parts of New Ireland Province (13%), or other provinces within Papua New Guinea (16%). Immigrants had resided locally for between 1 and 38 years (16.6 ± 4.2 years; mean ± SE). Almost all immigration (90%) was for clan or familial reasons, with the remainder for employment purposes.

Material style of living

Most dwellings on western Dyual were primarily constructed with locally sourced materials, such as palm thatch roofing, and woven palm walls, although corrugated iron sheets were commonly incorporated. Almost all households surveyed (93%) owned at least one modern form of lighting (e.g. battery lamp, kerosene lamp, electric lighting). Two-thirds of households (67%) owned no other wealth indicating household items. All households cooked using open wood fires.

A small proportion of dwellings (17%) were constructed entirely from imported materials. These households owned significantly more wealth indicating items, $r = 0.70$, $p < 0.001$; and were more likely to own motorised transport, $r = 0.50$, $p = 0.005$. The remaining dwellings were constructed primarily from locally sourced materials, with sheets of second-hand corrugated iron often incorporated as sections of walls or roofing (41%).

Table A1 - Percentage of surveyed households in western Dyual containing household items, and materials of household dwellings.

Household item	***% of households***	***Household material***	***% of households***
Generator	20.0	*Roofing*	
Solar panel	3.3	Thatch	66.7
Battery	3.3	Corrugated iron	36.7
Electric Fan	0.0	*Flooring*	
Air conditioner	3.3	Dirt / sand	40.0
Television	13.3	Bamboo / palm	6.7
DVD player	13.3	Wooden plank	60.0
Satellite dish	3.3	Cement	10.0
Radio	10.0	*Walls*	
Mobile phone	26.7	Bamboo / palm	73.3
Water tank	6.7	Wooden plank	23.3
Wood stove	0.0	Corrugated iron	20.0
Transport		*Lighting*	
Canoe	83.3	Kerosene lamp	40.0
Fibreglass dinghy	13.3	Battery lamp	53.3
Outboard motor (40 hp)	10.0	Electric	16.7

Social capital

There were various associations within western Dyual, including a women's group, youth group, church group, school fees fundraising group, and the village planning committee. Over three quarters of respondents (77%) reported involvement with at least one association. Respondents were involved with a mean of 1.3 (± 0.2) organisations. Only one respondent reported involvement with an association involved in marine resource management – a local non-government organisation which he had formed.

Almost all respondents reported that they were either actively or passively involved in community-level decision-making (69 and 28%, respectively). For decisions specifically pertaining to marine resource management 56% reported active involvement and 38% reported passive involvement. Passive involvement was defined as attending meetings or discussions, and active involvement was defined as making suggestions, participating in discussions, or voting on decisions.

Most respondents trusted more than half of other community members and community leaders (60 and 59%, respectively), with nearly half of respondents trusting all representatives of both groups (47 and 48%, respectively). Conversely, around half of respondents distrusted most members of the police force, and representative of all levels of government (48 – 54%) (Figure 0.1).

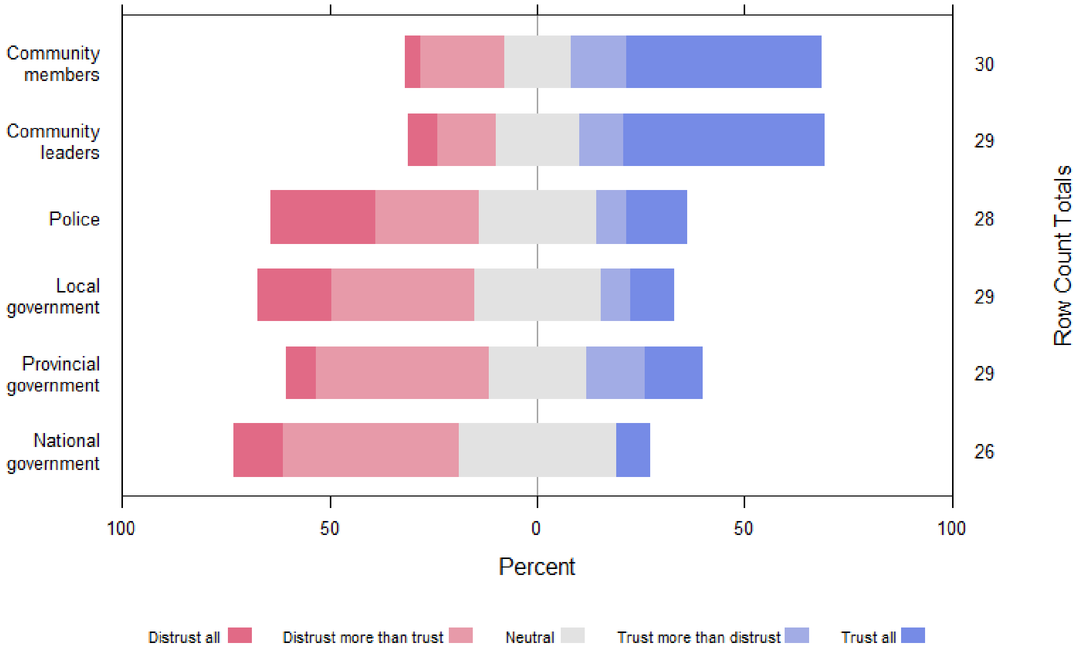

Figure A1 - Percentage of household survey respondents reporting trust or distrust (x-axis) in groups or organisations (left y-axis). 'Neutral' denotes feeling neither distrustful, nor trustful of the relevant group. Where respondents had no contact with a group they were removed from the sample, leading to differing sample sizes between groups (right y-axis).

Infrastructure

Infrastructure on western Dyual Island is very limited (Table 0.2). A medical station staffed by a nurse is available on Dyual Island at Sumuna, 15 km by boat from Leon (Figure 2.1). Any injuries or illnesses requiring a doctor, medical specialist, or hospital facilities require travel to the provincial capital Kavieng, 48 km by boat from Leon. In the case of a medical emergency, the patient is usually carried in one of the privately owned dinghies from Leon or Mait, with the fuel cost borne by the patient's family. Rough sea conditions can delay these journeys, occasionally resulting in the death of the patient. At least three deaths occurred in 2013 and 2014, due to blood loss following delays in reaching medical services.

Two primary schools are available on eastern Dyual Island at Sumuna and Lapai, 15 and 24 km distant by boat from Leon. There are no secondary schools on the island. Secondary students generally attend school in the Kavieng district. Students often reside at boarding houses or with *wantoks* (extended family members) during school semesters and return home during semester breaks and weekends.

No centralised water, sewerage, waste disposal, electricity or telephone infrastructure exists on Dyual Island. Fresh water is either obtained from natural sources (e.g. springs, streams) or from wells available for public use in Leon and Mait. A few households (7%) own rainwater tanks. Mangrove areas proximal to settlements were designated for open defecation. Household waste is generally incinerated or disposed of into the sea. Some households (20%) own solar panels and batteries or petrol-powered generators, and will charge electrical devices such as mobile phones for a small fee. Mobile phone coverage is available in a limited area surrounding Sumuna, however Digicel began construction of a relay tower in 2014, and full coverage of Dyual Island is scheduled for 2016.

A small store located in Leon stocks basic items such as rice, sugar, coffee, tea, and tobacco. Locally harvested goods (e.g. fruit, vegetables and seafood) are generally sold and traded directly between households. More specialised items, such as cooking equipment or clothing, is purchased from Kavieng. No fuel station exists on the island, however fuel can occasionally be purchased from private sellers at a premium rate.

Fish buyers operate intermittently in Leon and Mait. Purchased seafood is transported, on ice, to Kavieng for resale. The operation of seafood buyers is discussed in detail in section 2.4.3, below.

Paths throughout the interior of western Dyual are traversable only on foot. Long distance travel (e.g. between settlements) is predominantly conducted by boat. Passage to the provincial capital, or to settlements on eastern Dyual or the main island, could be purchased on a number of privately owned fibreglass dinghies. These services operated without fixed schedules; based on vessel availability and passenger demand.

Table A2 - Key infrastructure services and facilities available in western Dyual. Where absent, the distance from Leon to the nearest infrastructure is provided, via the shortest navigable route.

Infrastructure (service/facility)	***Present***	***Absent***	***Distance to (km.)***
Hospital		X	46
Medical station		X	15
Pharmacy		X	46
Doctor		X	46
Nurse		X	15
Dentist		X	48
Primary school		X	15
Secondary school		X	48
Piped water		X	48
Sewer pipes/canals		X	48
Sewage treatment		X	48
Septic/settling tanks		X	48
Waste disposal		X	48
Electric service		X	46
Telephone service		X	15
Food market	X		
Seafood buyer	X		
Hotel/inn		X	42
Restaurant		X	42
Fuel station		X	46
Public transportation	X		
Hard-top road access		X	46
Banking service		X	48

Discussion

Local socio-economic factors affecting fisheries sustainability

Human population density is perhaps the most long-recognised driver of fisheries sustainability (Jennings *et al.* 1995; Jennings and Polunin 1996, 1997; Bellwood *et al.* 2004; Newton *et al.* 2007; Mora 2008). Population density on western Dyual was low, however this alone is often a poor predictor of fisheries sustainability; a number of social, economic, and political factors can greatly affect the magnitude, distribution, and nature of interactions with fisheries, and consequently their sustainability (Cinner *et al.* 2016). These effects range from simple and intuitive – such as the negative effects of destructive fishing gears, to complex and indirect – such as the non-linear effects of human development and affluence. Some of the better understood drivers are discussed below.

Local inhabitants of western Dyual were highly reliant on natural resource exploitation, particularly fishing, for both subsistence and income. Nine in ten households reported either fishing, small-scale farming, or cultivating cash crops as their primary source of household income, and over three quarters of households participated in all three livelihoods. Fishing was the primary livelihood in two-fifths of surveyed households, and the primary source of animal protein for all surveyed respondents. As such, the sustainable management of local fisheries are of central importance to the health and prosperity of the local community. High reliance on resources has been associated with increased instance of fisheries management, as well as coral reef ‘bright spots’ (*i.e.,* areas with relatively high fish biomass, given local environmental and socio-economic conditions) (Mills *et al.* 2013; Cinner *et al.* 2016). This is presumably due to higher levels of involvement in collective action where stakeholders are more closely dependent on the sustainable use of natural resources (Agrawal 2001).

Indeed, levels of engagement with management decision-making were also high on western Dyual. The majority of stakeholders reported active involvement in fisheries management decision-making in general, and felt that they could directly influence future decisions regarding the customary closure at Site A in particular. Such collective-choice arrangements are a key design principle of successful common-pool resource management (Ostrom 1990; Cox *et al.* 2010). In practical terms, immediate stakeholders often have access to relevant, first-hand information about the resource, which may be useful in devising appropriate, adaptive management strategies (Berkes *et al.* 2000). Additionally, active participation in decision-making is a key component of social capital. Social capital is positively correlated with the sustainable management of common-pool resources (Agrawal 2001; Ostrom 2007; Cox *et al.* 2010), including Melanesian artisanal fisheries (Mills *et al.* 2013). Another fundamental component of social capital is trust; both between resource users (termed ‘social trust’), and in the individuals and institutions responsible for enacting and enforcing management regulations (termed ‘institutional trust’) (Jones 2010). Compliance with common-pool resource management rules requires that resource users act in the common interest, often at a personal cost. Social trust influences individuals’ perception of whether the majority of other resource users will comply with regulations, and thus whether individuals are willing to incur costs for the common good (ref in Jones 2010). Institutional trust influences the perceived reliability and legitimacy of relevant institutions and thus the willingness to comply associated management recommendation and regulations (Stamieszkin *et al.* 2009). The majority of local stakeholders on western Dyual trusted either most or all other community members and community leaders, with around half of respondents trusting all of both groups. Conversely, around half of local stakeholders distrusted most or all representatives of all levels of state-based government, as well as representatives of the police force. These stark differences in trust suggest that governance at the community level is likely to receive greater local support, and thus greater compliance. In contrast, governance through state-based institutions – at local, provincial, or national levels – is likely to be viewed with some measure of suspicion, and may require increased enforcement to achieve comparable levels of compliance.

Appendix II – Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site

The following appendix is an edited version of the manuscript led by Jan Robinson, and published in the Coral Reefs journal, available at:

Robinson J, Graham NAJ, Cinner JE, Almany GR, Waldie PA. Fish and fisher behaviour influence the vulnerability of groupers (Epinephelidae) to fishing at a multispecies spawning aggregation site. Coral Reefs. 2014. doi:10.1007/s00338-014-1243-1.

Abstract

Targeted fishing of spawning aggregations is a major contributor to extinction risk in numerous species of grouper (Epinephelidae). Marine reserves are often used to protect spawning aggregation sites, including multispecies sites shared by several species of grouper. However, marine reserves may be biologically, socioeconomically or culturally unviable in some fisheries and alternative management actions must be explored. Implementing effective management actions that control rather than prohibit fishing requires an improved understanding of how species vary in their vulnerability to fishing gears and respond to changes in fishing effort. To estimate sources of variability in vulnerability to fishing (i.e. catchability), catch-per-unit-effort (CPUE) and other fisheries data were collected in parallel with underwater visual census-derived estimates of aggregation size at a multispecies spawning site of *Epinephelus fuscoguttatus* and *E. polyphekadion*. Despite having similar abundances, *E. polyphekadion* was 8-fold more vulnerable to capture by hook-and-line gear, clearly outcompeting its congener for bait. Contrasting with the common assumption of a proportional relationship, the CPUE of both species was unrelated to the size of their respective aggregations. Moreover, the CPUE of each species was unrelated to hook size and depth fished. However, *E. polyphekadion* CPUE declined as the density of fishing effort increased at the site, with gear saturation identified as the likely mechanism for this effect. *E. fuscoguttatus* CPUE was negatively related to the size of aggregations formed by its congener, stemming from the superior competitiveness and therefore higher selectivity of the gear for *E. polyphekadion*. Our findings demonstrate that CPUE is an unreliable indicator of spawning aggregation status. The other sources of variation in CPUE that we identify have implications for gear-based management, which must be based

on understanding of gear selectivity for aggregating species, and fishing effort controls, which must consider the potential for effort-dependent patterns in catchability.

Introduction

Many groupers common to coral reef fisheries (Epinephelidae) are highly prized and prone to overfishing, resulting in a high risk of extinction for numerous species (Sadovy de Mitcheson et al. 2013). The prognosis for groupers appears to be worsening given that exploitation rates are increasing in parts of the developing world (Worm and Branch 2012), where the majority of coral reefs are located. Consequently, there has been considerable emphasis on establishing marine reserves to rebuild populations, particularly through the protection of spawning aggregation sites where groupers are typically most at risk from overfishing (Grüss et al. 2013). However, establishing effective marine reserves may be problematic due to a high dependency on reef fisheries for livelihoods, as well as a poor understanding of the non-material benefits (e.g. lifestyle and prestige) derived from accessing traditional resources such as spawning sites (Cinner et al. 2014). Management measures that allow access to spawning aggregations while limiting fishing pressure to levels that rebuild populations may, therefore, offer socially and culturally-preferable alternatives to no-take reserves. Compared to the effects of marine reserves, there is very little evidence regarding the effects of alternative management measures on spawning aggregations and their fisheries (Sadovy de Mitcheson and Erisman 2012; Grüss et al. 2013).

Vulnerability to overfishing in groupers stems from life history characteristics such as longevity, late maturation and spawning aggregation behaviour (Sadovy de Mitcheson et al. 2013). The latter trait poses particular challenges for assessing and managing reef fisheries. Spawning aggregation formation at specific locations and times concentrates fish, and consequently fishers, changing the dynamics of the fishery and typically resulting in a much greater risk of overfishing (Claro et al. 2009; Rhodes et al. 2011). Due to the predictable and often large increase in adult fish density that occurs with aggregation formation, units of fishing effort (e.g. line-fishing hour) can be more efficient at spawning sites, removing a larger proportion of the population than is possible when fish are dispersed (Grüss et al. 2013). Moreover, several species of grouper often aggregate at the same time and location (e.g. *Epinephelus fuscoguttatus*, *E. polyphekadion* and *Plectropomus areolatus*; Sadovy 2005), rendering a significant proportion of grouper biomass on reefs susceptible to overfishing when multi-species spawning sites are known to fishers (Heyman and Kjerfve 2008; Sadovy de Mitcheson et al. 2008).

The dynamics of spawning aggregation fisheries also pose challenges for assessment and management since population declines may go unnoticed by fishers and scientists (Sadovy de Mitcheson and Erisman 2012). Catch rate (i.e. catch-per-unit-effort, CPUE) is used extensively as an index of abundance in stock assessment (Quinn and Deriso 1999), and is one of the main signals that fishers perceive regarding the status of their resources, influencing commercial decisions regarding how much to fish and even whether they will exit or remain in a fishery (Cinner et al. 2011). However, CPUE is usually a poor indicator of fish abundance since catchability, defined quantitatively as the proportion of the population caught by a single unit of effort, is rarely constant (Wilberg et al. 2010). Catchability varies in response to numerous aspects of fish and fisher behaviour, including aggregation formation and the distribution of fishing effort (reviews by Arreguín-Sánchez 1996; Wilberg et al. 2010). As populations decline, densities at spawning aggregation sites often decline at a slower rate than those in the normal residence areas. Consequently, if aggregations are targeted by fishers, fishery-wide and annual CPUE can remain relatively stable in spite of declines in the overall population (an effect known as hyperstability: Rose and Kulka 1999; Harley et al. 2001; Erisman et al. 2011). Moreover, CPUE may be insensitive to declines in the size of a single spawning aggregation over time, as the remaining fish contract into core areas of the site and maintain density (Nemeth 2012). Changes to fisher behaviour, technology and the spatial-temporal distribution and allocation of fishing effort can also cause catchability to vary (termed 'effort dependence'; Gillis and Peterman 1998; van Oostenbrugge et al. 2008; Wilberg et al. 2010). Therefore, by the time declines in CPUE are perceived, whether due to density or effort-dependent catchability, populations may have declined to critical levels (Erisman et al. 2011).

Given that coral reef spawning aggregation fisheries are considered highly susceptible to time-varying catchability, which can cause hyperstability, it is surprising that few studies have assessed these effects and their management implications (Sadovy and Domeier 2005; Wilberg et al. 2010). Rather than the absence of such effects, this situation probably reflects the data-poor context of these fisheries, which often lack catch, effort and fisheries-independent biomass data (Sadovy and Domeier 2005). However, for a number of reasons, spawning aggregation fisheries provide a unique opportunity to collect empirical evidence on these effects and their underlying mechanisms. Fish and fishers are concentrated in a small area at predictable times, facilitating the scale and timing of data collection. Aggregations also vary naturally in size within and among spawning months, providing strong abundance gradients over which patterns in catchability can be assessed (Rhodes and Sadovy 2002; Hamilton et al. 2011). Finally, many species form spatially and temporally overlapping aggregations at multispecies spawning sites (Rhodes and Sadovy 2002; Sadovy 2005; Robinson et al. 2008), which enables the selectivity of gears for different species to be examined.

The aim of this study was to examine aspects of fish and fisher behaviour that influence the vulnerability of groupers to fishing (i.e. catchability) at multispecies spawning aggregation sites. To meet this aim, we posed three specific research questions. Firstly, are species of grouper equally vulnerable to fishing when aggregated at a multispecies spawning site? Secondly, are grouper catch rates proportional to the size of their spawning aggregations? Lastly, what aspects of fish or fisher behaviour influence grouper catch rates and their vulnerability to fishing?

Materials and methods

Site description

The study site is located on an outer reef promontory near Dyual Island in New Ireland Province, Papua New Guinea (PNG), where *Epinephelus fuscoguttatus* and *E. polyphekadion* form overlapping spawning aggregations (Hamilton et al. 2011). The aggregation site extends over a linear distance of approximately 400 m in depths of between 4 and 40 m. From 4 m depth to a seaward reef edge occurring at between 7 and 10 m, the site comprises a relatively flat shelf area ('reef top'). Between the reef top and 40 m, aggregations extend over a precipitous reef slope ('reef wall'). Aggregations of both species are known to form in four to five consecutive months between March and July. Peak densities occur during the last quarter lunar phase and aggregations rapidly disperse after presumed spawning on or around the day of the new moon (Hamilton et al. 2011).

Spawning aggregations at the study site were exploited by local clans for subsistence purposes prior to the mid-1990s. In 1997, a more intensive fishery to supply the live reef food-fish trade was established that, according to local reports, caused major declines in aggregation sizes over the six years that it operated (Hamilton et al. 2011). In 2004, clans holding ownership of the reef established a no-take marine reserve of 0.2 km^2 to protect the entire spawning aggregation site. The reserve is closed to fishing throughout the year and the level of compliance is reportedly high (Hamilton et al. 2011).

Fishery data

In May and June 2013, clan leaders opened the MPA and local communities were engaged to fish spawning aggregations of *E. fuscoguttatus* and *E. polyphekadion* for a tagging project (conventional and acoustic) being conducted in parallel to the present study. All fish caught were tagged and released at the site, with the exception of a small proportion (<3%) that did not survive the procedure. Catch and fishing effort data were collected from this fishery (Table 1).

Fishers operated using baited hook-and-line gear from fibreglass boats that anchored or attached to mooring buoys at the site. Boats fished only the promontory of the site, where densities of *E. fuscoguttatus* and *E. polyphekadion* are highest (Hamilton et al. 2011). Fishing trips were conducted at day and night, sometimes overlapping dusk or dawn (Table 1). The timing of the trips and number of fishers were determined in collaboration with community leaders and depended on factors such as storm activity and sea state, and availability of fishers, boats and bait. The time that each fisher commenced and ceased fishing was recorded and adjusted for any periods of inactivity greater than one hour. In addition to recording fishing time and the number of boats and fishers on a trip (i.e. effort), information on hook size, bait and depth of capture was also collected. Hooks were supplied and the type (j-hooks 4/0-8/0) used by each fisher was recorded at the start of the trip. Bait was typically caught by fishers prior to starting a trip, or bycatch taken during a trip was used. On catching a fish, the depth (to the nearest 0.1 m) under the boat where the fisher was operating was measured using a hand-held depth sounder. Catch was recorded in number of fish.

Catch and effort data were used to calculate CPUE, in terms of number of fish per fisher-trip (no.$^{\bullet}$fisher-trip^{-1}), standardised for trip duration of 10 hrs and rounded to the nearest integer, or in terms of number of fish per boat-hr (no.$^{\bullet}$boat-hr^{-1}) on a trip, with boat fishing time a cumulative function of the time fished by each fisher on the boat. Since the spatial concentration of fishing influences catchability (Wilberg et al. 2010), we also estimated effort density for each trip as a function of the number of fishers and time spent fishing per unit area of the aggregation site (standardised to 100 m^2). However, variation in effort density was driven only by changes in the number of fishers and fishing time since the area fished at the aggregation site did not differ in size among trips, due to boats using fixed moorings or anchoring on only the promontory.

Table 1 Fishing trip and underwater visual census (UVC) survey details and summary of estimated aggregation size and catch by species. DBNM = days before new moon. Start and end times of fishing trips are from when the first fishers arrived at the site to when the last fishers departed. UVC times represent the start of the dive.

Fishing trip details							**UVC survey details**		**Aggregation size and catch**				**DBNM**
Trip No.	Date start	Date end	Time start	Time end	No. of boats	No. of fishers	UVC date	UVC time	*E. fuscoguttatus*	Size	*E. polyphekadion*		
									Catch		Size	Catch	
1	03/05	04/05	16:30	06:00	3	11	03/05	13:15	32	7	24	62	7
2	05/05	06/05	20:00	05:00	4	21	05/05	16:00	70	12	76	52	5
3	07/05	07/05	00:20	05:00	4	19	07/05	15:20	153	8	106	32	3
							08/05	11:20	141		111		2
4	09/05	09/05	09:00	23:00	4	25	09/05	16:20	114	4	60	27	1
							10/05	16:00	52		29		0
5	31/05	31/05	17:15	22:45	2	5	31/05	10:30	76	2	119	32	9
							02/06	10:45	87		130		7
6	03/06	03/05	12:30	17:00	3	25	03/06	11:30	94	1	205	65	6
7	04/06	04/06	12:45	17:00	3	28	04/06	11:40	148	2	233	56	5
8	06/06	07/06	16:45	01:00	3	19	06/06	13:00	108	5	177	27	3

Aggregation density surveys

Fish densities on the reef promontory were surveyed using underwater visual census (UVC) and used to estimate aggregation size. Six and five days were surveyed for the May and June spawning aggregations, respectively (Table 1). Surveys were undertaken between late morning and late afternoon. When fishing occurred in daylight hours, UVC surveys were undertaken during or immediately prior to a trip, with the exception of one survey that occurred approximately 4 hrs before fishing commenced. When fishing occurred at night, the time between surveys and commencement of fishing was longer, ranging from 3 to 12 hrs. As it was necessary to pair aggregation size estimates with CPUE from the nearest fishing trip for data analysis, night fishing was generally conducted every other day to prevent daytime UVC surveys falling intermediately to fishing trips on consecutive nights and presenting problems in pairing the data (Table 1).

UVC surveys followed a specific route through the aggregations of both species, beginning at 15 m depth on the reef wall to the west of the promontory (Hamilton et al. 2011). The 15 m depth contour was followed until the promontory had been rounded, after which divers ascended and surveyed the reef top in depths of 5-8 m. During each survey, fish were counted within 16 point count areas of 7 m radius (count area 154 m^2) divided equally between the reef wall and top. Count areas were orientated on vertical and horizontal planes on the reef wall and reef top, respectively. Consequently, point counts on the reef wall were centred at 15 m but extended from 8 to 22 m in depth.

The aggregation size (N) for each species was estimated by extrapolating mean point count densities to the area of each stratum (wall: 4,200 m^2; reef top: 4,800 m^2), which were then summed. Strata survey areas were approximated from a bathymetry map of the site (Hamilton unpub. data) and GPS coordinates of the survey start and end points in each strata. Since surveys were limited to a depth of 22 m and aggregations may extend to 40 m (Hamilton et al. 2011), estimates are considered a relative index of aggregation size over time rather than absolute aggregation abundance. The areas surveyed were representative of the fish available to the fishery as 96% of the catch was taken in the 5-22 m depth range.

Data analyses

The first research question, concerning the relative vulnerability of each species to hook-and-line gear, was examined using two methods. Firstly, differences between species in aggregation sizes, both within and pooled across spawning months, were examined using a

Wilcoxon Signed Rank test. Catches for each species were then compared qualitatively with the aggregation sizes available to fishers. Secondly, vulnerability to fishing was quantified by estimating the catchability parameter, q, for each species using:

$$q = \frac{Ut}{Nt}$$

where U is CPUE and N is aggregation size at time t (Ricker 1940). For individual boat trips (n = 26; Table 1), q was calculated for both species from mean boat CPUE (no.•boat-hr^{-1}) and aggregation size on that day, and a Wilcoxon Signed Rank test was used to examine the median of differences in this parameter. Boat CPUE was used for estimating q, rather than individual fisher catch rates, under the assumption that variation in fisher skill and targeting preference for particular species would be mitigated by aggregating data. Moreover, since there was less variation in depth and hook size between fishers on a boat than between boats, aggregating CPUE reduced the potential for confounding caused by these parameters.

Analysis of the association between CPUE and aggregation size required matching fishing trips to UVC surveys. Fishery data were collected for eight fishing trips that were split evenly between May and June, whereas eleven UVC surveys were conducted in those months. As three UVC surveys could not be matched to a corresponding fishing trip, eight matched pairs of fishery and UVC data were used for analysis (Table 1).

To answer the second research question, we tested the assumption that fisher CPUE of each species was proportional to their aggregation size using generalized linear models (GLM) . *E. polyphekadion* CPUE was analysed using a negative binomial GLM, from the Poisson regression family. A high percentage of zeros (close to 70%) in *E. fuscoguttatus* CPUE required binary transformation of CPUE data (0 = no catch, 1 = catch) and the fitting of a binomial GLM, which modelled the probability of catch. GLMs were fit using a logit-link, which outperformed other link functions (as determined by the corrected Akaike's Information Criterion, AIC_c).

Given an association, or lack thereof, between species CPUE and aggregation size, the influence of other explanatory variables on fisher CPUE was examined (research question 3). As per the second research question, negative binomial (*E. polyphekadion*) and binomial (*E. fuscoguttatus*) GLMs with a logit-link function were used. Explanatory variables included in the model were effort density (*ED*), depth of capture (*DE*), and hook size (*HK*). Due to the potential effects of species interactions on catchability (i.e. competition among species for baited gear), we also considered the aggregation size (N) of the congener (*E. fuscoguttatus*: N_{Ef}; *E. polyphekadion*: N_{Ep}) as an explanatory variable (i.e. N_{Ef} as an explanatory variable in the model of *E. polyphekadion* CPUE, and *vice-versa*). The aggregation size of a species was not included in the model of its CPUE due to collinearity with aggregation size of the congener (as determined from an analysis of variance inflation factor), and because the association was tested in the previous step (research question 2). Since depth data were only recorded on capture, data substitution was used to assign depth fished to fishers with zero CPUE. For *E. polyphekadion*, depth was missing for around 26.7% of fishers and data were substituted by the mean depth of capture by fishers on the respective boat. Given that *E. fuscoguttatus* was caught by a small percentage of fishers across trips (30%), the mean depth of capture of both species by the boat was used in substitution. Bait was not included in the model as boats utilised up to 6 types of bait per trip, making it problematic to assign any particular bait type to the 30.7% of missing data. Explanatory variables were continuous with the exception of hook size, which was categorical and grouped data into 3 levels due to small samples of hook sizes 4/0 and 8/0 (1 = size 4 and 5 hooks; 2 = size 6 hooks; 3: size 7 and 8 hooks).

GLMs were fit to all combinations of the four explanatory variables plus the intercept-only model. Two-way interactions were initially included, but were removed when found to be non-significant. In the case of the negative binomial GLM, model dispersion was checked using the theta parameter, which is assumed to 1.0. For the binomial GLM, model fit was checked using a Pearson's χ^2 test. Model selection was based on the smallest AIC_c value, and included all other models within two AIC_c units of the best model (Burnham and Anderson 2004). Model importance was assessed using AIC_c weights ($wAIC_c$), while the relative importance of explanatory variables was examined by summing $wAIC_c$ values across subsets of models containing that variable (Burnham and Anderson 2004). We examined the effects of the most important explanatory variables using partial plots, holding others constant at mean levels and hook size at intermediate level.

If effects of effort density are associated with gear saturation, it was predicted that boat CPUE would decline with the number of fishers operating from a boat (i.e. crew size). Pooling data from all 8 fishing trips, the mean boat CPUE was derived for each level of crew size, which ranged from 2 to 11 fishers. Negative correlation between crew size and mean boat CPUE was then examined using a Kendall tau (τ) (1-tailed) test.

Results

Relative vulnerability of grouper spawning aggregations to fishing

Large gradients in relative aggregation size occurred for both species, with *E. fuscoguttatus* aggregations ranging from 32 to 153 fish, while those of *E. polyphekadion* ranged from 24 to 233 fish (Table 1). *E. fuscoguttatus* aggregation sizes (median = 92 fish) were significantly larger than those of *E. polyphekadion* (median = 68 fish) in May (Wilcoxon Signed Rank test: $n = 5$; $p = 0.046$; Fig. 1a). Conversely, *E. polyphekadion* aggregations (median = 177 fish) were larger than those of *E. fuscoguttatus* (median = 94 fish) in June (Wilcoxon Signed Rank test: $n = 6$; $p = 0.043$). There was no difference in aggregation size between species when data were pooled across months (Wilcoxon Signed Rank test; $n = 11$; $p = 0.424$; Fig. 1a).

In spite of the larger *E. fuscoguttatus* aggregation size in May and equivalence in size between species when data were pooled across months, *E. polyphekadion* CPUE was greater than that of its congener in all periods (Fig. 1b). Consequently, the total catch of *E. polyphekadion* was more than 5-fold greater in May and more than 8-fold greater over both months (Table 1). The larger aggregation of *E. polyphekadion* that formed in June (2-fold greater than *E. fuscoguttatus*) resulted in a catch of this species that was 18-fold greater than that of its congener.

Greater vulnerability of *E. polyphekadion* to fishing was confirmed by statistical comparison of the catchability parameter, q (Wilcoxon Signed Rank test: n = 26; $p < 0.001$). The median catchability of *E. polyphekadion* ($q = 0.0027$) was almost 8-fold greater than that of *E. fuscoguttatus* ($q = 0.0004$). This large difference in catchability results from differences in CPUE between the species being much greater than differences between sizes of their aggregations (Fig. 1a, b).

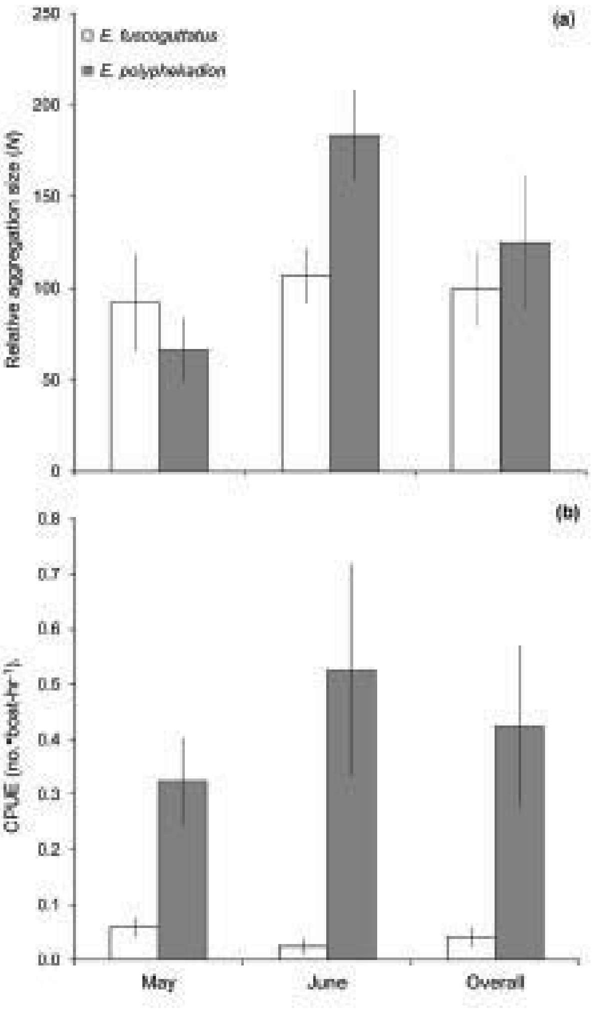

Fig. 1. Comparison of (a) mean ± s.e. relative aggregation size (*N*) and (b) mean ± s.e. CPUE (no.•boat-hr^{-1}) between *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*.

Association of CPUE with aggregation size

In the case of *E. fuscoguttatus*, fisher CPUE was significantly and negatively related to aggregation size (Table 2). However, only 3% of the variability in CPUE was explained by its relationship to aggregation size. For *E. polyphekadion*, there was no relationship between fisher CPUE and aggregation size. On the basis of these results, CPUE was largely disassociated from abundance and did not decline or increase across a large gradient in aggregation sizes.

Table 2 Methods table outlining research questions, their corresponding statistical analyses and variables tested.

Research questions	**Analysis**	**Dependent variable**	**Explanatory variable(s)**
Are species of grouper equally vulnerable to fishing?	Qualitative	Catch, Boat CPUE	Relative aggregation size (*N*)
	Wilcoxon Signed Ranks test	Catchability coefficient (*q*)	Species
Are grouper catch rates proportional to the size of their aggregations?	GLM	Fisher CPUE	Relative aggregation size (*N*)
Which factors influence grouper catch rates?	GLM	Fisher CPUE	*N* (of congener), effort density (*ED*), hook size (*HK*), depth (*DE*)

Factors that influence CPUE

The aggregation size of *E. polyphekadion* (N_{Ep}) was common to both selected models of *E. fuscoguttatus* CPUE (Table 3) and was the strongest explanatory variable in terms of summed $w\text{AIC}_c$ values (Table 4). Effort density (*ED*) was of secondary importance to models of *E. fuscoguttatus* CPUE (Table 4). Consequently, increases in the aggregation size of *E. polyphekadion* had slightly more of a depressing effect on the probability of *E. fuscoguttatus* CPUE (i.e. catch = 1) than did increases in effort density (Fig 2a, b). In terms of *E. polyphekadion* CPUE, five models were selected on the basis of AICc (Table 3). Though depth fished (*DE*) and hook size (*HK*) were present in selected models, the aggregation size of the congener (N_{Ef}) and effort density were again the most important predictors of CPUE (Table 4). However, contrasting with *E. fuscoguttatus*, effort density had a greater depressing effect on *E. polyphekadion* CPUE than aggregation size of the congener (Fig. 3a, b). Evidence for gear saturation as a mechanism for the effects of effort density was mixed, with mean boat CPUE negatively correlated with crew size for *E. fuscoguttatus* ($\tau = -0.597$; $p = 0.01$) but not for *E. polyphekadion* ($\tau = -0.244$; $p = 0.16$).

Table 3 Results of binomial (*E. fuscoguttatus*) and negative binomial (*E. polyphekadion*) GLM models on the relationship between fisher CPUE and aggregation size (*N*). Results in bold are significant at α = 0.05 level. *Z* is the Wald statistic for the slope parameter.

Species	Variables	*Coefficient*	*Z*	*p*
E. fuscoguttatus	Fisher CPUE/aggregation size (N_{Ef})	-0.012	-2.153	**0.031**
E. polyphekadion	Fisher CPUE/aggregation size (N_{Ep})	0.002	1.633	0.102

Table 4 GLM models examining the influence of explanatory variables on fisher CPUE. Explanatory variables are aggregation size of *E. polyphekadion* (N_{Ep}) and *E. fuscoguttatus* (N_{Ef}), effort density (*ED*), hook size (*HK*) and depth (*DE*). Best models are in bold and are based on (corrected) Akaike Information Criteria (AIC_c). Table limited to models with corrected Akaike Information Criterion weight ($wAIC_c$) > 0.01.

Species	Model	ΔAIC_c	$wAIC_c$
E. fuscoguttatus	**N_{Ep} +ED**	**0**	**0.383**
	N_{Ep}	**1.89**	**0.149**
	N_{Ep} +ED+DE	2.11	0.134
	$N_{Ep +}$ED+HK	2.56	0.106
	N_{Ep} +HK	2.99	0.086
	N_{Ep} +DE	3.96	0.053
	N_{Ep} +ED+HK+DE	4.73	0.036
	N_{Ep} +DE+HK	5.09	0.030
E. polyphekadion	**N_{Ef} +ED**	**0**	**0.274**
	N_{Ef} +ED+DE	**0.09**	**0.262**
	N_{Ef} +ED+DE+HK	**1.39**	**0.137**
	N_{Ef} +ED+HK	**1.78**	**0.113**
	ED	**1.84**	**0.109**
	ED+DE	3.37	0.051
	ED+HK	4.14	0.035
	ED+DE+HK	5.28	0.020

Table 5 Summed $wAIC_c$ values that quantify the importance of independent variables in explaining CPUE for E. *fuscoguttatus* and *E. polyphekadion*.

	E. fuscoguttatus	*E. polyphekadion*
Abundance (N_{Ep}, N_{Ef})	0.98	0.79
Effort density (*ED*)	0.66	1.00
Hook size (*HK*)	0.26	0.31
Depth (*DE*)	0.25	0.47

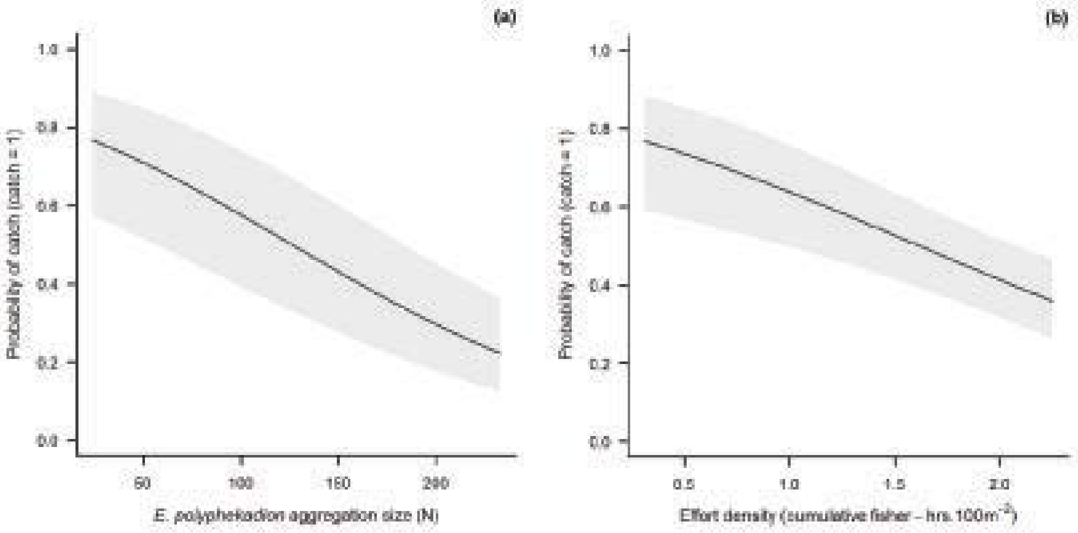

Fig. 2. Partial effect plots of predicted probability of *Epinephelus fuscoguttatus* catch by a fisher (i.e. catch = 1) against (a) the aggregation size of *Epinephelus polyphekadion* and (b) effort density. Line is predicted mean and grey polygon is standard error.

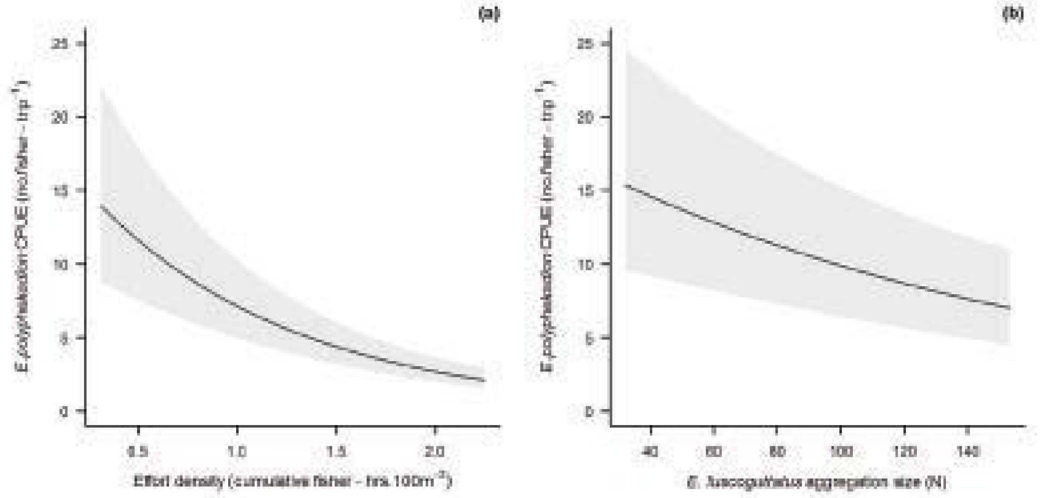

Fig.3. Partial effect plots of predicted *Epinephelus polyphekadion* CPUE (no.•fisher-trip^{-1}) against (a) effort density and (b) the aggregation size of *Epinephelus fuscoguttatus*. Line is predicted mean and grey polygon is standard error.

Discussion

Grouper fisheries pose difficulties for assessment and management. Combined with slow life histories in many species, the formation of spawning aggregations causes profound changes to the distribution and behaviour of fish and fishers. An understanding of these changes is critical for detecting the impacts of fishing on populations (Sadovy de Mitcheson and Erisman 2012). Contrasting with common assumptions regarding proportionality between CPUE and population size (Quinn and Deriso 1999), our study demonstrated that CPUE was disassociated from the size of spawning aggregations, in spite of strong gradients in abundance. CPUE is exhibiting an extreme form of hyperstability when unresponsive to declining abundances, which typically stems from changes in fish or fisher behaviour that cause catchability to increase (Arreguín-Sánchez 1996; Erisman et al. 2011). Exploring changes in fisher behaviour, we found that CPUE was not influenced by hook size and depth fished but, particularly in the case of *E. polyphekadion*, declined with increases in effort density. *E. fuscoguttatus* CPUE was negatively related to the size of aggregations formed by its congener, which clearly stems from the significantly higher vulnerability of *E. polyphekadion* to line fishing. Our findings point to the dynamic role of catchability in conferring vulnerability to hook-and-line fishing among groupers at multispecies spawning aggregation sites.

Dissimilarities in fish behaviour likely underlie the observed difference in catchability between the two species. Interspecific competition for bait is a key factor influencing catchability in multispecies line fisheries and can take the form of exploitative competition, when one species consumes baits more rapidly or efficiently than others, or interference competition, when a species actively prevents other species from accessing bait (Stoner 2004). Previous studies have recognised the links between the vulnerability of *E. polyphekadion* to a wide variety of gear types, its voracity as a predator and propensity to feed throughout the aggregation period (Rhodes et al. 2011). By contrast, *E. fuscoguttatus* is not considered particularly vulnerable to hook-and-line gear at multispecies spawning sites (Mangubhai et al. 2011). If interference competition for bait was occurring, then it would tend to favour the larger (i.e. *E. fuscoguttatus*) rather than the smaller (i.e. *E. polyphekadion*) species (Fernö et al. 1986; Godø et al. 1997). Therefore, exploitative competition is the most likely form of interaction between the species around baited lines, with *E. polyphekadion* exhibiting either an enhanced bait location ability or willingness to attack bait compared to its congener (Stoner 2004).

Competition for bait provides an explanation as to why *E. fuscoguttatus* CPUE declined with increasing aggregation size of its congener. By comparison, the influence of *E. fuscoguttatus* aggregation size on *E. polyphekadion* CPUE was weaker, though still demands an explanation as the effect was influential in the model. Males of both species establish and defend territorial space in aggregations. Given that inter-specific territorial disputes or disruption of territorial behaviour tend to increase with aggregation density (Rhodes and Sadovy 2002;

Robinson et al. 2008), this may lead to a reduction in feeding rates and explain the depressing effect of *E. fuscoguttatus* aggregation size on *E. polyphekadion* CPUE.

Hyperstability is common to fisheries for aggregating species and is typically caused by fishers being able to target dense aggregations in spite of declines in overall population size (Wilberg et al. 2010). We demonstrated that CPUE can also be unresponsive to changes in the size of spawning aggregations, which is indicative of hyperstability at the scale of an aggregation fishery rather than in annual CPUE from a fishery that targets both spawning and non-spawning periods (Erisman et al. 2011). While density-dependent catchability may be common in aggregation fisheries, other mechanisms influenced CPUE in our study fishery. Notably, the CPUE of *E. polyphekadion* was strongly depressed by increases in effort density. A plausible mechanism for this effect is gear saturation since, in the case of *E. fuscoguttatus*, boat CPUE tended to be lower in boats with larger numbers of fishers. However, the fact that crew size and boat CPUE for *E. polyphekadion* were not negatively correlated does not discount gear saturation as a mechanism. Gear saturation is manifested in time as well as space (Groeneveld et al. 2003), so may not be captured by crew size without also accounting for time fished, which was included in the measure of effort density. Effort-dependent catchability has been observed in a few fisheries (review by Wilberg et al. 2010), but not, to the authors' knowledge, in a reef fish spawning aggregation fishery. Since grouper aggregations can attract high levels of concentrated effort (Graham et al. 2008), they are likely susceptible to this source of variation in catchability. There are clear management implications resulting from this result since a negative relationship with CPUE contributed to high levels of catch (i.e. fishing mortality) being observed at low levels of effort density. For example, comparing between trips of similar duration, the five fishers of Trip 5 produced more catch than the 19 fishers of Trip 8, while the 11 fishers of Trip 1 produced more than double the catch of the 25 fishers of Trip 4 (Table 1).

An important assumption of our study was that courtship and territorial behaviour, which change in intensity over the course of aggregation development (Robinson et al. 2008), did not influence feeding behaviour and, therefore, catchability. While Rhodes et al. (2011) report that *E. polyphekadion* feeds throughout the aggregation period, less is known regarding the feeding behaviour of aggregating *E. fuscoguttatus*. Any changes in feeding behaviour are unlikely to have confounded our finding of interspecific difference in catchability, since it occurred on all days, regardless of the state of aggregation development. However, any reductions in feeding behaviour close to spawning, when aggregation sizes of these species are typically at their largest and intra- and inter-specific territorial interactions typically increase (Rhodes and

Sadovy 2002; Robinson et al. 2008; Hamilton et al. 2011), may have affected the relationship of CPUE with abundance or other explanatory variables.

Compared to effort density and congener abundance, both hook size and depth were relatively unimportant predictors of CPUE. A lack of contrast in hook size, with over 95% of effort comprising 5/0-7/0 sizes, likely explains the absence of a strong effect and future studies could utilise a wider range of hooks to examine the importance of this parameter on catchability. Following protection in 2004, both *E. fuscoguttatus* and *E. polyphekadion* aggregations expanded to include deeper and shallower areas on the promontory (Hamilton et al. 2011). Without strong depth stratification in aggregation densities, depth of fishing was unlikely to be influential in the model. While these sources of variation in catchability were accounted for in the model, including bait posed difficulties. The absence of cold storage facilities in the communities meant that bait (species or size) could not be kept constant across the study. However, using a wide variety rather than a single type of bait rendered it less likely that selectivity would be biased towards one of our study species if their preference differs for any particular type.

A further assumption made in examining relative catchability was that UVC based on open circuit (OC) self-contained underwater breathing apparatus (SCUBA) sampled both species with equal efficiency. Possibly resulting from the disturbance caused by bubbles in OC systems, Rhodes et al. (2014) found that this method may considerably underestimate aggregation density of *E. polyphekadion*, by a factor of three, whereas *E. fuscoguttatus* densities were surveyed with similar efficiency on OC and closed circuit re-breather systems. However, if our *E. polyphekadion* aggregation abundance estimates are inflated by a factor of three to account for underestimation, catchability remained significantly higher than that observed for its congener (by a factor of 3.25). Together with the fact that we estimated relative rather than absolute abundance, underestimation caused by diver disturbance likely contributed to the fact that catch on Trip 1 was greater than aggregation size estimated for that day (Table 1).

Other sources of known error or bias in UVC surveys of grouper aggregations were mitigated by maintaining the same observer throughout (J.R), the consistently high visibility at the site (>20 m), avoiding peak tidal currents and dusk and dawn periods, and accounting for the flighty behaviour of *E. fuscoguttatus* by counting that species first (Colin et al. 2003; Robinson et al. 2008). However, in avoiding peak tidal currents, the time of day for surveys varied by up to 6 hours (10:30 am – 16:20 pm; Table 1). While variability in grouper spawning aggregation density during daylight hours may or may not occur, depending on factors such as the timing of arrivals and departures at the sites (Samoilys 1997; Robinson et al. 2008; Bijoux et al. 2013; Rhodes et al. 2014), it clearly warrants further investigation at our study site in order to confirm our results and those of long-term monitoring programs (Hamilton et al. 2011). Coupled with the fact that relative rather than absolute aggregation size was estimated, diel variability in density at the study site, and night-time arrival of fish (Bijoux et al. 2014), may explain why catches were higher or close to aggregation abundance on some night fishing trips (Table 1).

Our findings have clear implications for the conservation and management of groupers that form spatially and temporally overlapping spawning aggregations (Sadovy 2005). Though rarely used compared to closures, gear controls offer potential for managing these fisheries (Sadovy de Mitcheson et al. 2008; Claro et al. 2009). Using these measures at multispecies spawning aggregation sites requires an understanding of gear selectivity and inter-specific differences in catchability. If a single gear is used, sequential fishing effects are likely, with higher rates of depletion initially occurring in species that are most vulnerable to the gear. Consequently, the decline in *E. fuscoguttatus* aggregations to a hook-and-line fishery may involve a threshold, corresponding to the point at which the reduction in *E. polyphekadion* density overcomes the relative difference in catchability. However, *E. fuscoguttatus* is vulnerable to spears (Rhodes and Tupper 2007) and increasing the diversity of gear types at multispecies spawning sites will typically widen the species selectivity of the fishery and increase vulnerability for more co-aggregating species.

Fishing effort controls are also relatively rare in spawning aggregation fisheries (Sadovy de Mitcheson et al. 2008) and may, on the basis of our results, have unintended consequences. Assumptions of constant catchability and linearity in the relationship between fishing effort and mortality can undermine the effectiveness of effort restrictions (van Oostenbrugge et al. 2008). Though this may not preclude effort controls as a measure for managing these fisheries, the relationship of CPUE with a wider range of effort density levels than those observed in our study should be known, especially effort levels from zero to the point at which CPUE asymptotes and starts to decline. However, even if effort levels that yield a sustainable catch were identified, the use of this measure is not without risk since increases in catchability caused by other technological (e.g. bait, hook size) or biological (e.g. size of congener aggregations) factors could result in target catch levels being exceeded.

A range of tools are emerging for adaptive management of fisheries for aggregating groupers to meet both conservation and socioeconomic objectives. For example, no-take marine reserves protecting spawning aggregation can be effective in rebuilding populations and normalising sex ratio (Grüss et al. 2014). Once recovered, management could shift to allowing a limited, sustainable catch of specific species taken annually or periodically, enabling communities to meet subsistence, cultural or other objectives. Specifying the catch (i.e. actual mortality rates) may be preferable to specifying allowable effort due to the dynamic nature of catchability, while specifying the gear would allow species selectivity to be controlled. Using our study site as a hypothetical example, if the goal is to rebuild the *E. fuscoguttatus* population, a limited take of *E. polyphekadion* could be implemented by allowing hook-and-line gear to be used in months when the latter's aggregation numbers are at their peak, which should minimise catch of *E. fuscoguttatus*. Alternatively, if the goal is to rebuild the *E. polyphekadion* population, a spear fishery would be appropriate in obtaining a limited catch of *E. fuscoguttatus,* for which hook-and-line is less selective, while preventing catch of *E. polyphekadion*. Clearly, a combined approach of gear-based management and catch limits could also be used as an alternative to reserves in rebuilding populations of specific species of aggregating groupers at multispecies aggregation sites. Moreover, similar to the use of rotational closures, allowing controlled access to spawning aggregations may promote compliance with management since direct benefits are more easily perceived than those accruing from permanent no-take reserves.

A number of critical gaps or constraints are pertinent to adaptive management of spawning aggregations fisheries to meet multiple criteria. Firstly, catch levels will need to be estimated that consider both productivity of the populations and the non-lethal effects of fishing on spawning aggregations, such as disruption to mating systems and behavioural cues for sex change (Sadovy de Mitcheson and Erisman 2012). The non-lethal effects of fishing spawning aggregations remain poorly known (Dean et al. 2012), but it is clearly risky to set conventional economic objectives based on maximising yield in these fisheries. Consequently, catch limits should be highly conservative and aimed primarily at meeting social and cultural objectives. Monitoring is clearly critical to adaptive management and, due to the sensitivity of CPUE to changes in catchability, should ideally be based on a robust UVC sampling method that takes account of uncertainties and controls for biases in these data. However, conservation initiatives have clearly demonstrated that community-based monitoring programmes can be effective (Hamilton et al. 2012), so the onus or lack of capacity for monitoring should not be construed as a barrier to adaptive management or to advocate for data-less management approaches. Finally, selecting measures for the management of spawning aggregations will involve multiple objectives and trade-offs that are relevant to the local governance context, not least of which is the capacity for enforcement (Grüss et al. 2014). However, enforcing catch limits in spawning aggregation fisheries, which occur over relatively small areas and narrow windows of time, poses less of a constraint than enforcement of annual catch limits for fisheries operating over much larger seascapes.

To conclude, fisheries that target spawning aggregations are complex socio-ecological systems involving shifts in the distribution and behaviour of fish and fishers on lunar, seasonal and annual scales. Consequently, catchability will vary during the build-up and dispersal of aggregations within a month, on the seasonal change in density between spawning and non-spawning habitats, and between years due to changes in aggregation size. Catchability at multispecies spawning sites will also be influenced by the behaviour and aggregation size of co-aggregating species. In addition to these density-dependent sources of variability, fisher behaviour in terms of gears used and effort density will influence catchability. Given the many sources of variation in catchability, it could be argued that permanently closing multispecies spawning aggregation sites to fishing is the most practical approach to management. However, our results highlights that adaptive management need not be overly complex or data-demanding. Should local communities prefer not to lose all opportunities that spawning aggregations provide, gear-based management and highly conservative catch limits could be used to rebuild and allow periodic access to sites, though care should be taken with effort controls due to the effects of effort-dependent catchability. Understanding patterns in catchability will enable a more robust assessment of the costs and benefits of marine reserves and alternative management measures, giving further options for managing complex spawning aggregation fisheries and conserving vulnerable groupers.

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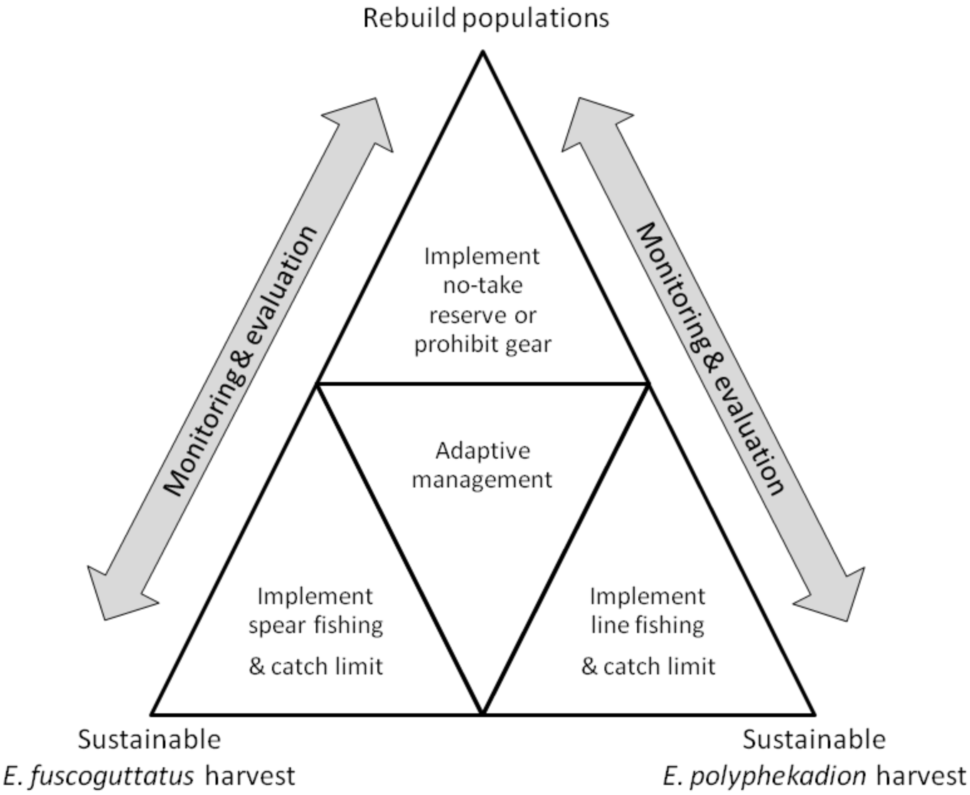
Electronic Supplementary Material:

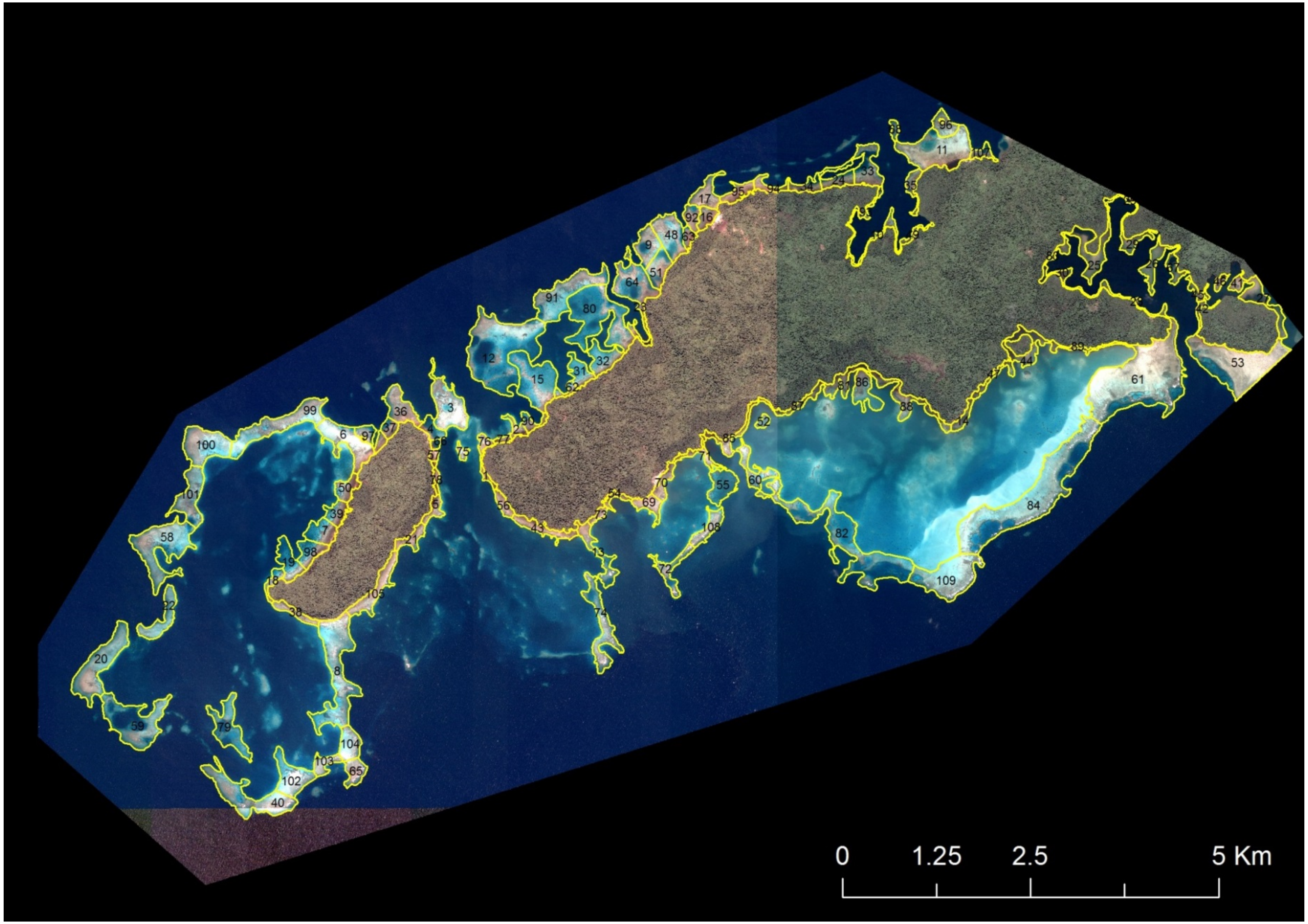
Conceptual scheme highlighting management implications of study findings

Options for implementing adaptive management of spawning aggregation fisheries for the co-aggregating groupers *Epinephelus fuscoguttatus* and *Epinephelus polyphekadion*. No-take reserves (i.e. protecting both species) or prohibiting the relevant gear (i.e. spear fishing that selects for *E. fuscoguttatus*, line fishing that selects for *E. polyphekadion*) can be used to meet the objective of rebuilding aggregation populations. Alternatively, allowing either spear or line fishing in combination with conservative catch limits can meet the objective of a sustainable harvest for the relevant species, reverting to a rebuilding objective if population depletion is detected. Adaptive management is underpinned by monitoring and evaluation of population statusand compliance with the measures.

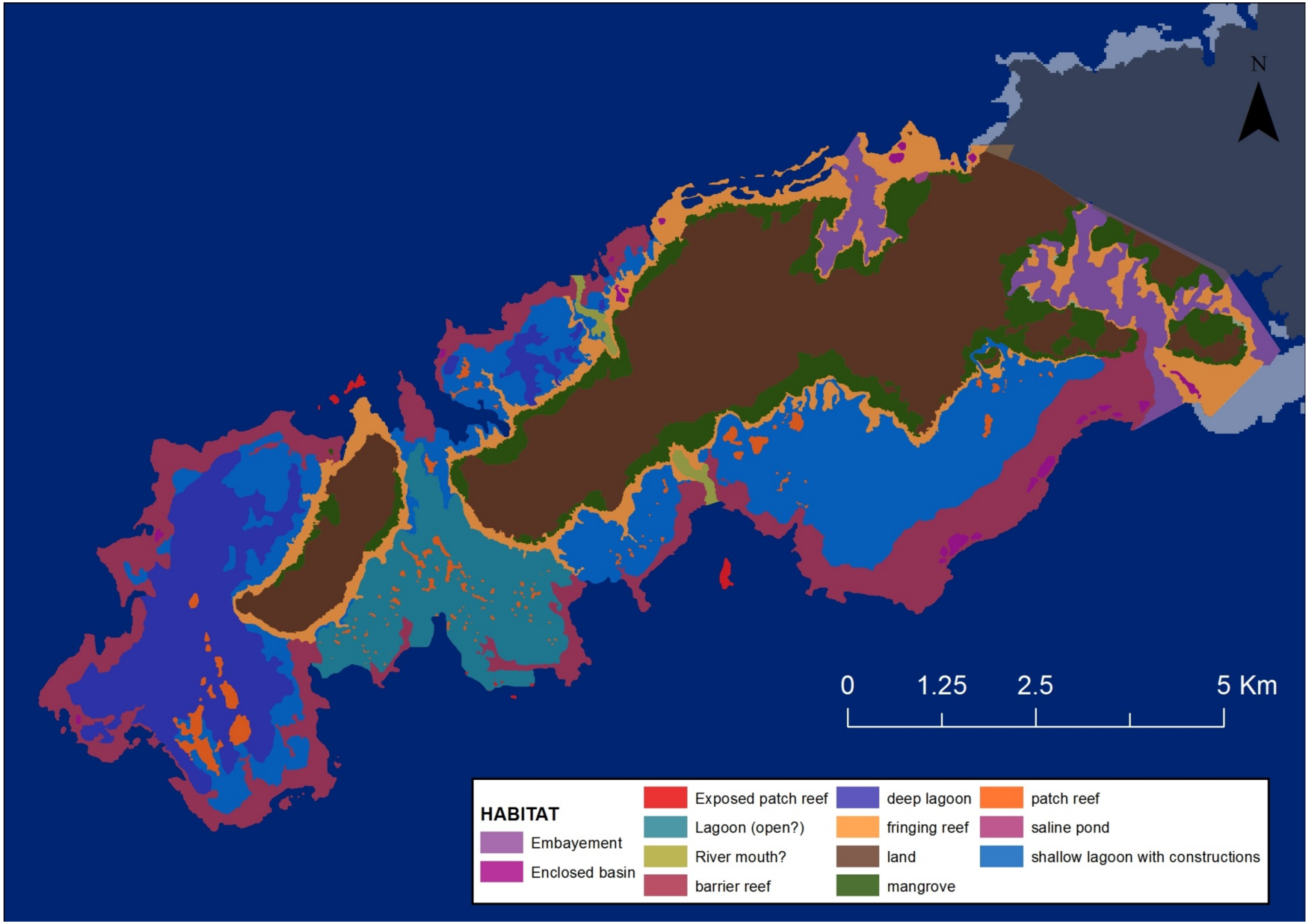


Appendix III – Named reference map.

Yellow lines denote the boundaries of locally-named areas of habitat, as reported during key informant surveys (see section 2.3.1), uniquely identified here with numbers.



Appendix IV – Habitat map



Appendix V –Ontogenetic shift in habitat suitability (additional model outputs)

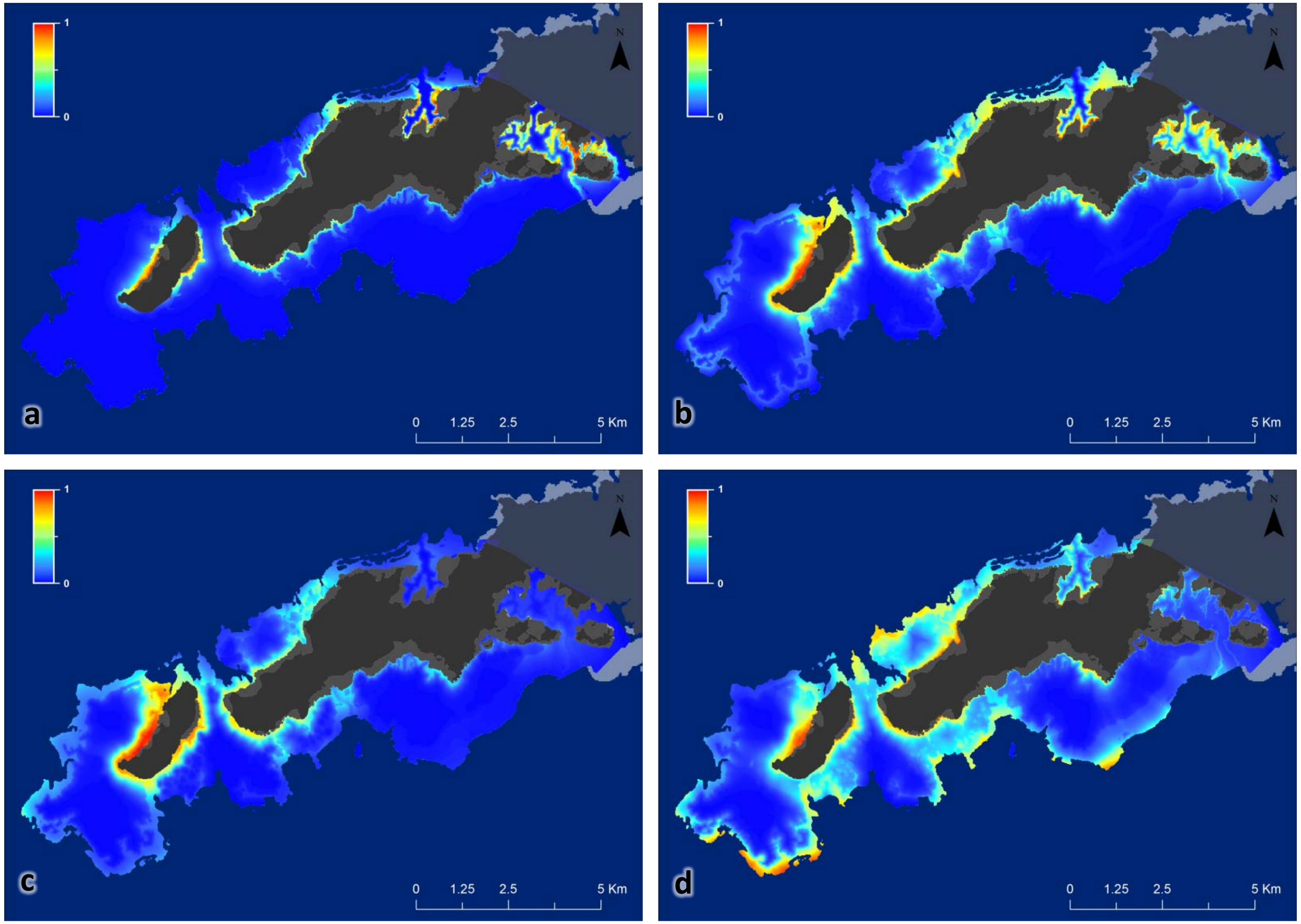


Figure A2 – Ontogenetic shift in habitat suitability for *E. polyphekadion,* using life history stages separated according to length: (a) juveniles (< 278 mm TL, n = 52); (b) early sub-adults (278 - 332 mm TL, n = 96); (c) late sub-adults (333 – 375 mm TL, n = 62); and (d) adults (> 375 mm TL, n = 130). Warmer colours represent higher modelled likelihood of presence.

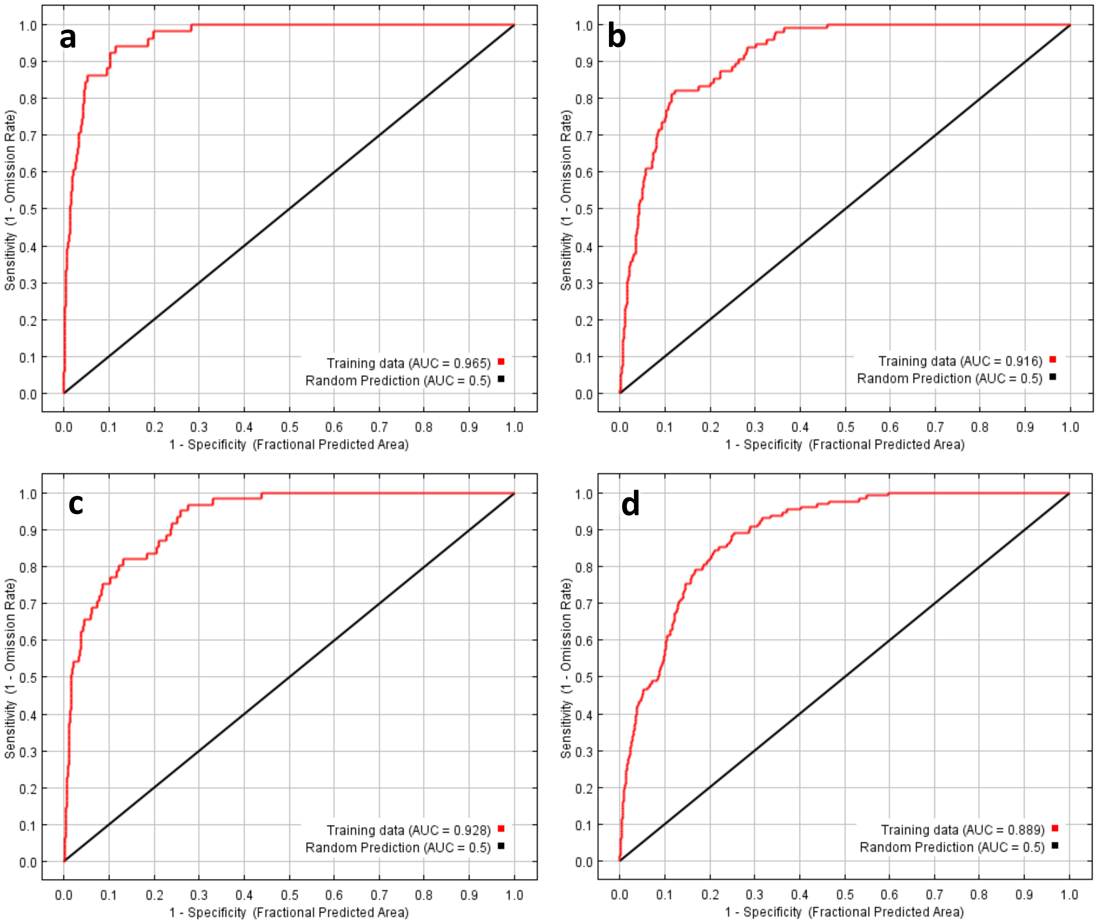


Figure A3 – Receiver Operating Characteristic (ROC) curves for *E. polyphekadion*: (a) juveniles (< 278 mm TL, n = 52); (b) early sub-adults (278 - 332 mm TL, n = 96); (c) late sub-adults (333 – 375 mm TL, n = 62); and (d) adults (> 375 mm TL, n = 130).

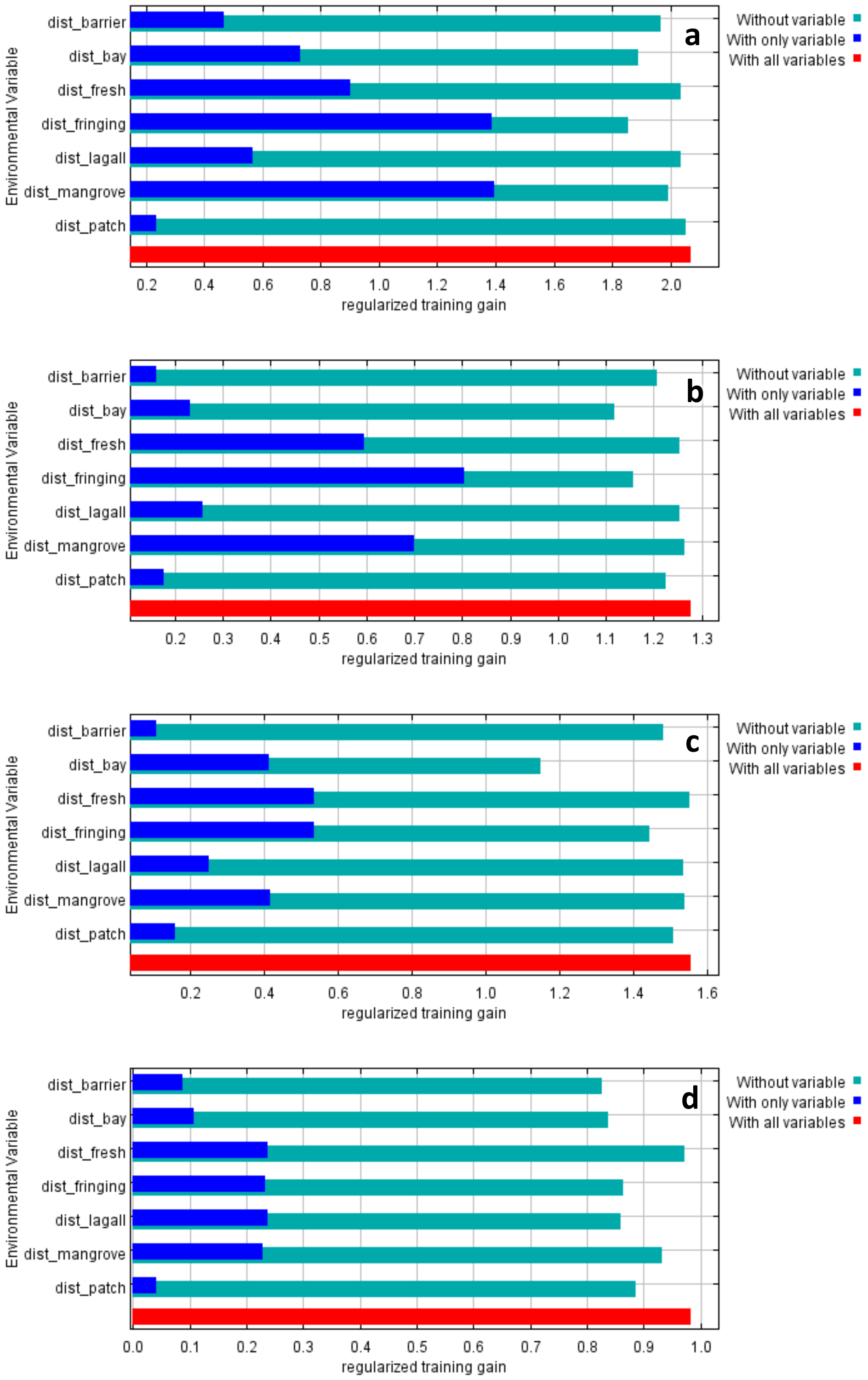


Figure A4 – Results of jackknife analysis, assessing relative importance of the seven environmental variables used to predict habitat suitability for *E. polyphekadion,* over the four modelled life history stages: (a) juveniles (< 278 mm TL, n = 52); (b) early sub-adults (278 - 332 mm TL, n = 96); (c) late sub-adults (333 – 375 mm TL, n = 62); and (d) adults (> 375 mm TL, n = 130). Environmental variables represent minimum distances to (top to bottom): barrier reef, embayment, freshwater input, fringing matrix, lagoon, mangrove, and patch reef.

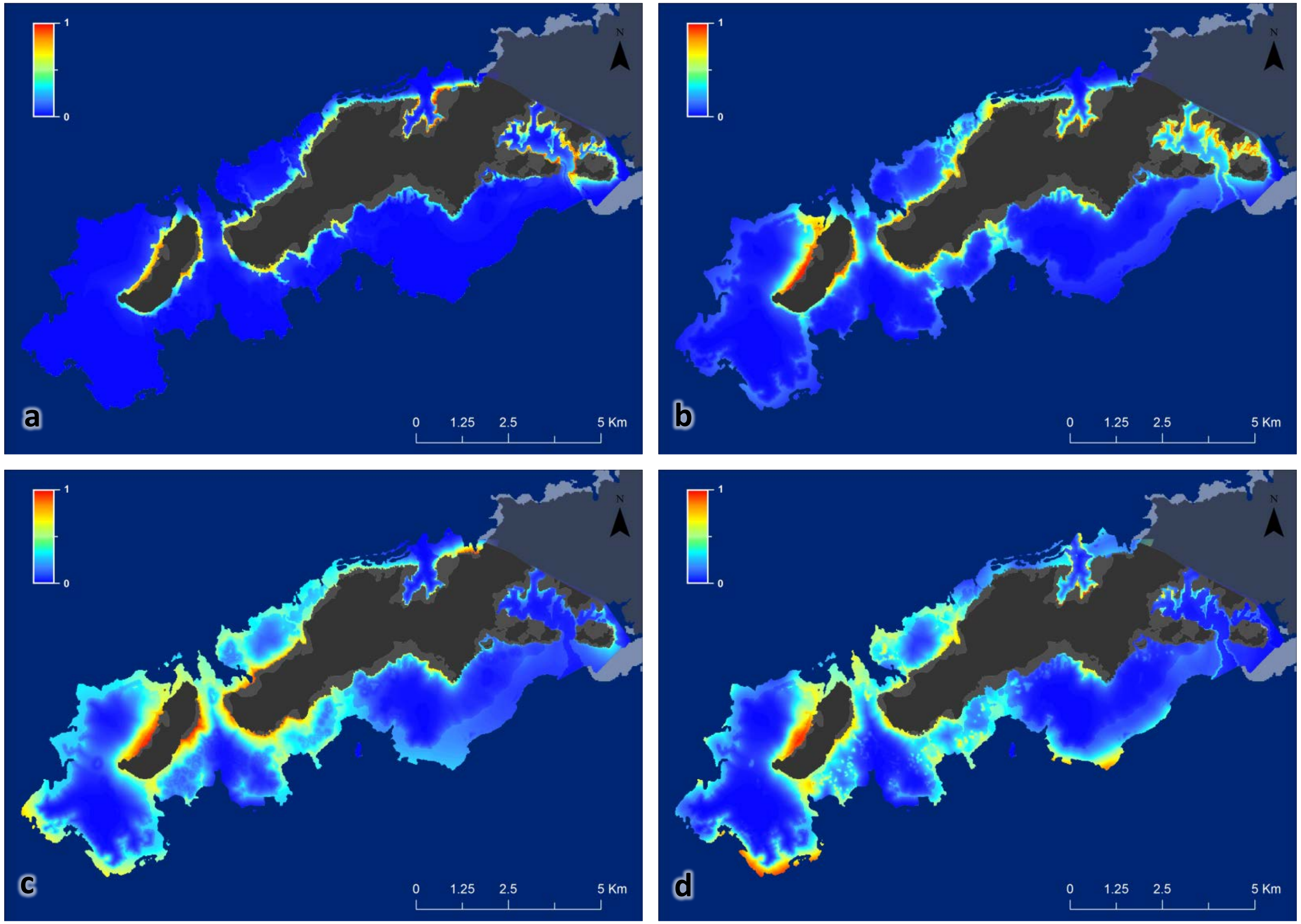


Figure A5 – Ontogenetic shift in habitat suitability for *E. polyphekadion,* using life history stages separated according to age: (a) juveniles (< 4 yrs, n = 28); (b) early sub-adults (4 – 6 yrs, n = 74); (c) late sub-adults (7 – 8 yrs, n = 59); and (d) adults (> 8 yrs, n = 84). Warmer colours represent higher modelled likelihood of presence.

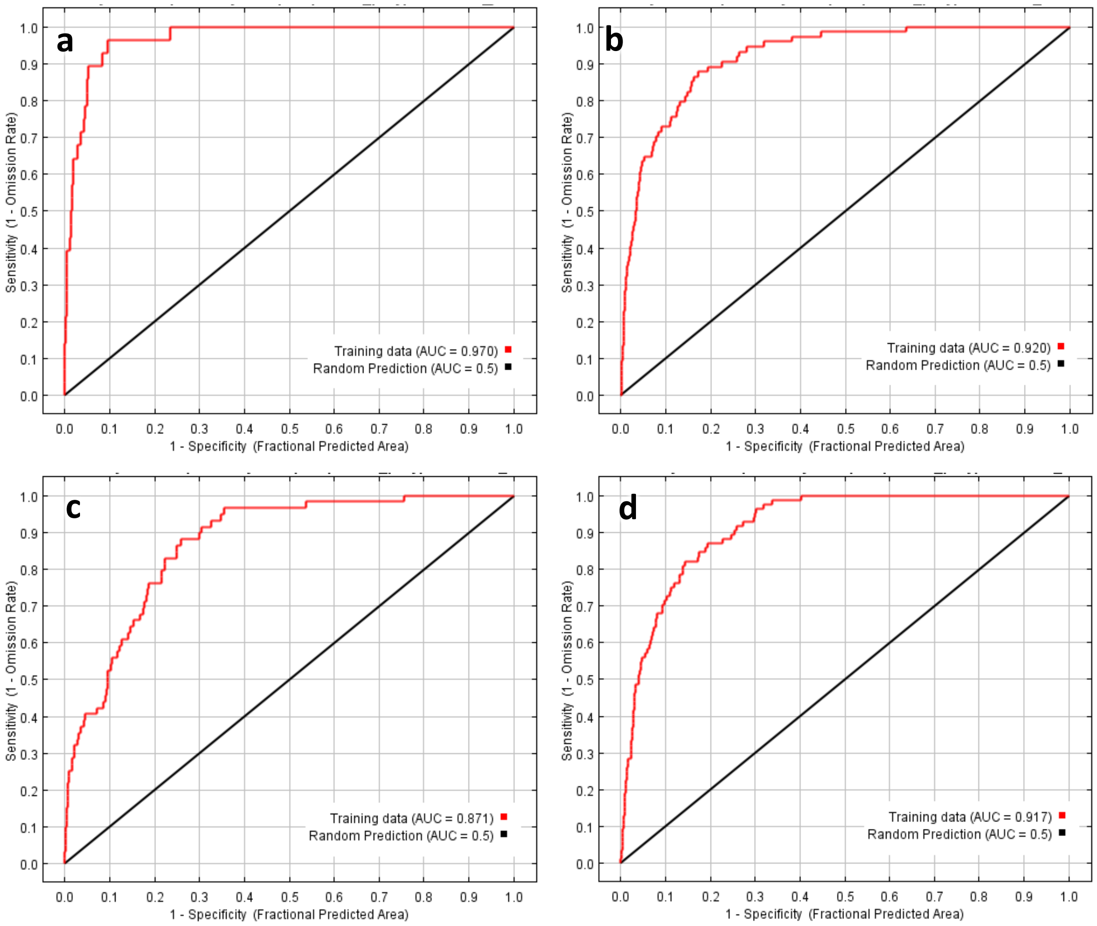


Figure A6 – Receiver Operating Characteristic (ROC) curves for *E. polyphekadion*: (a) juveniles (< 4 yrs, n = 28); (b) early sub-adults (4 – 6 yrs, n = 74); (c) late sub-adults (7 – 8 yrs, n = 59); and (d) adults (> 8 yrs, n = 84).

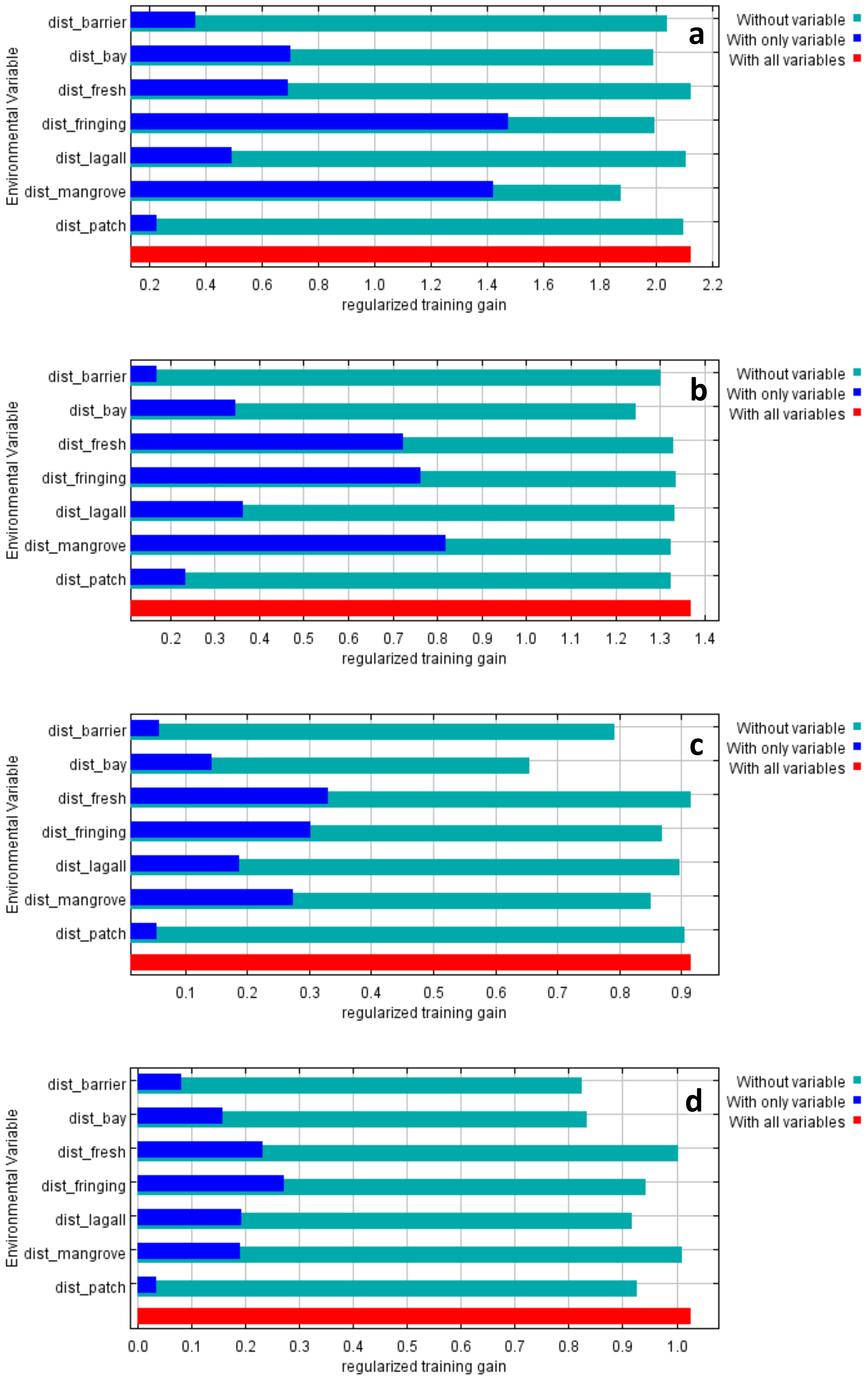


Figure A7 – Results of jackknife analysis, assessing relative importance of the seven environmental variables used to predict habitat suitability for *E. polyphekadion,* over the four modelled life history stages: (a) juveniles (< 4 yrs, n = 28); (b) early sub-adults (4 – 6 yrs, n = 74); (c) late sub-adults (7 – 8 yrs, n = 59); and (d) adults (> 8 yrs, n = 84). Environmental variables represent minimum distances to (top to bottom): barrier reef, embayment, freshwater input, fringing matrix, lagoon, mangrove, and patch reef.

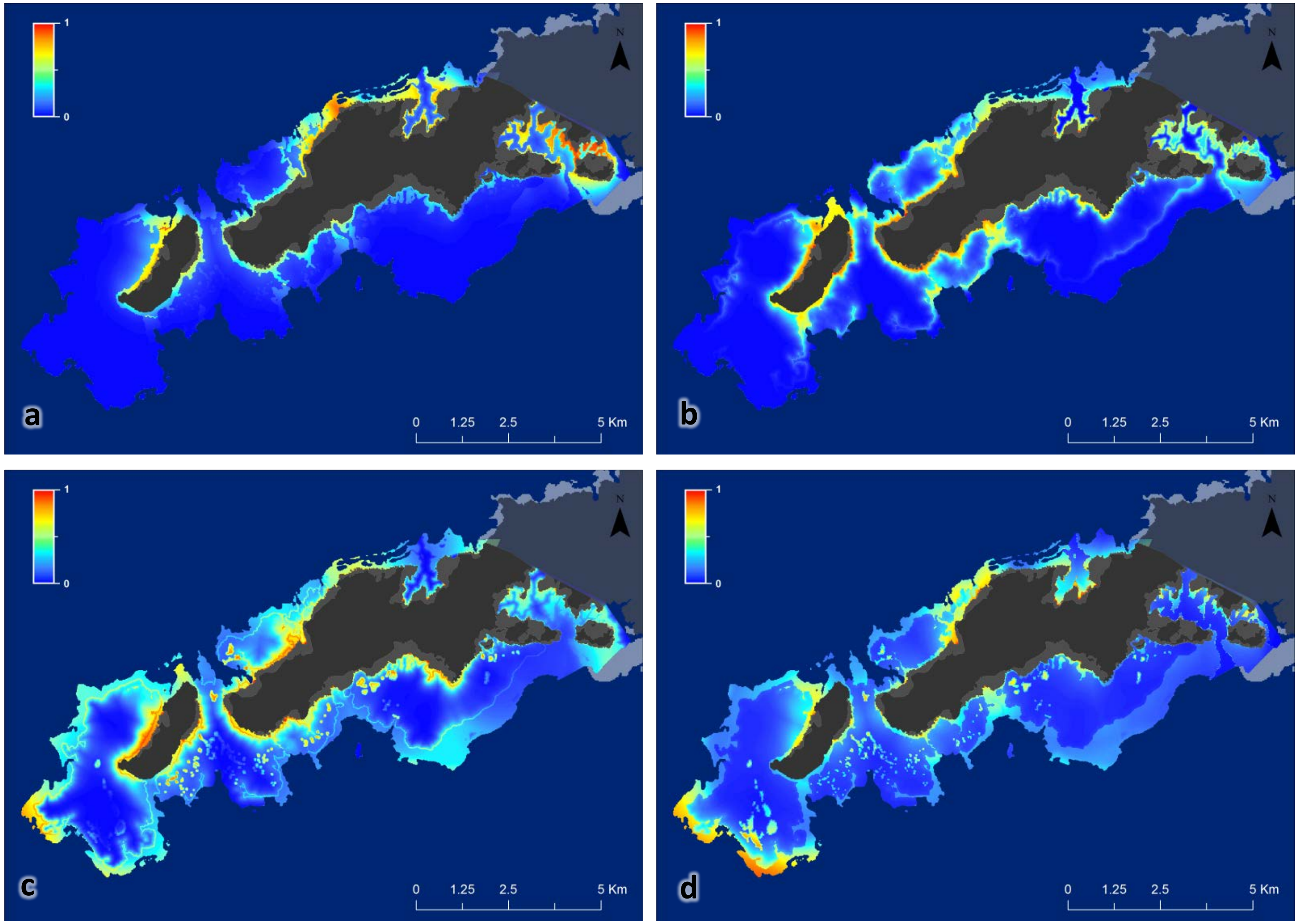


Figure A8 – Ontogenetic shift in habitat suitability for *E. fuscoguttatus,* using life history stages separated according to length: (a) juveniles (< 370 mm TL, n = 122); (b) early sub-adults (370 - 436 mm TL, n = 14); (c) late sub-adults (437 – 481 mm TL, n = 17); and (d) adults (> 481 mm TL, n = 49). Warmer colours represent higher modelled likelihood of presence.

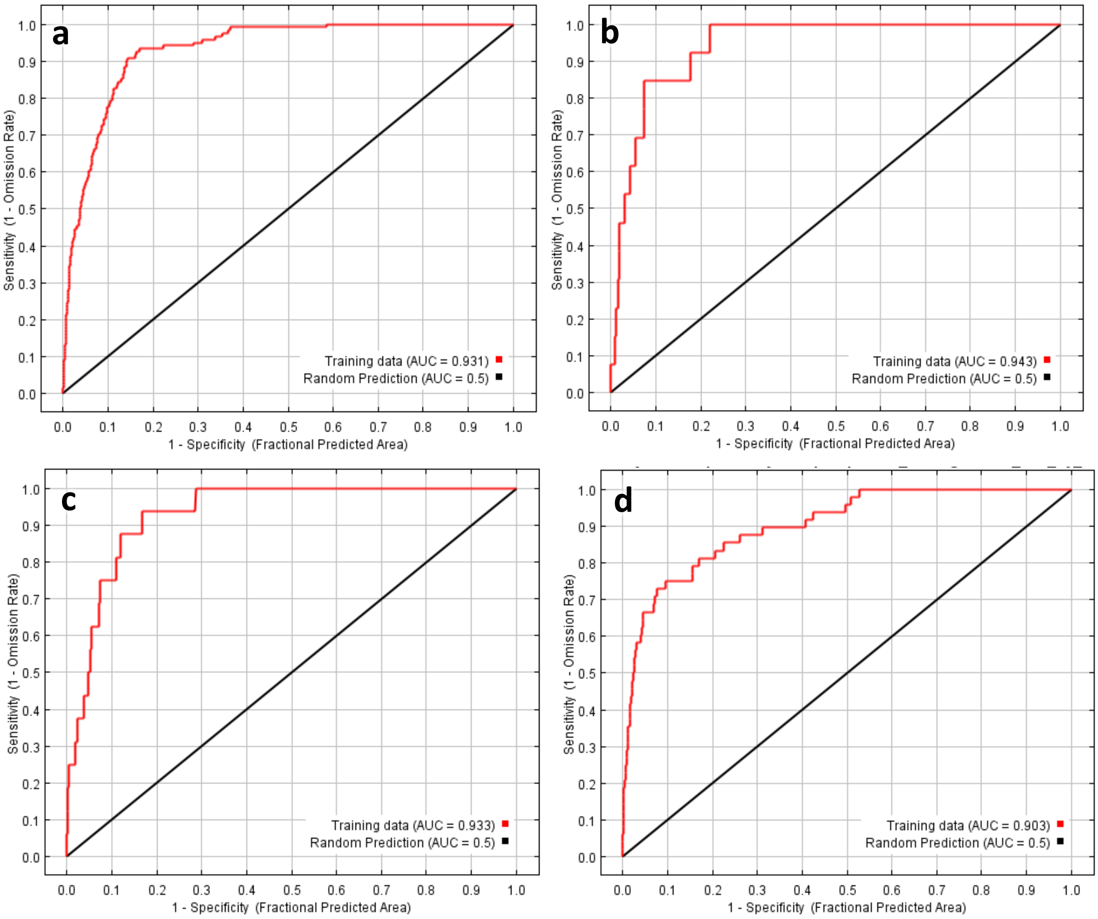


Figure A9 – Receiver Operating Characteristic (ROC) curves for *E. fuscoguttatus*: (a) juveniles (< 370 mm TL, n = 122); (b) early sub-adults (370 - 436 mm TL, n = 14); (c) late sub-adults (437 – 481 mm TL, n = 17); and (d) adults (> 481 mm TL, n = 49).

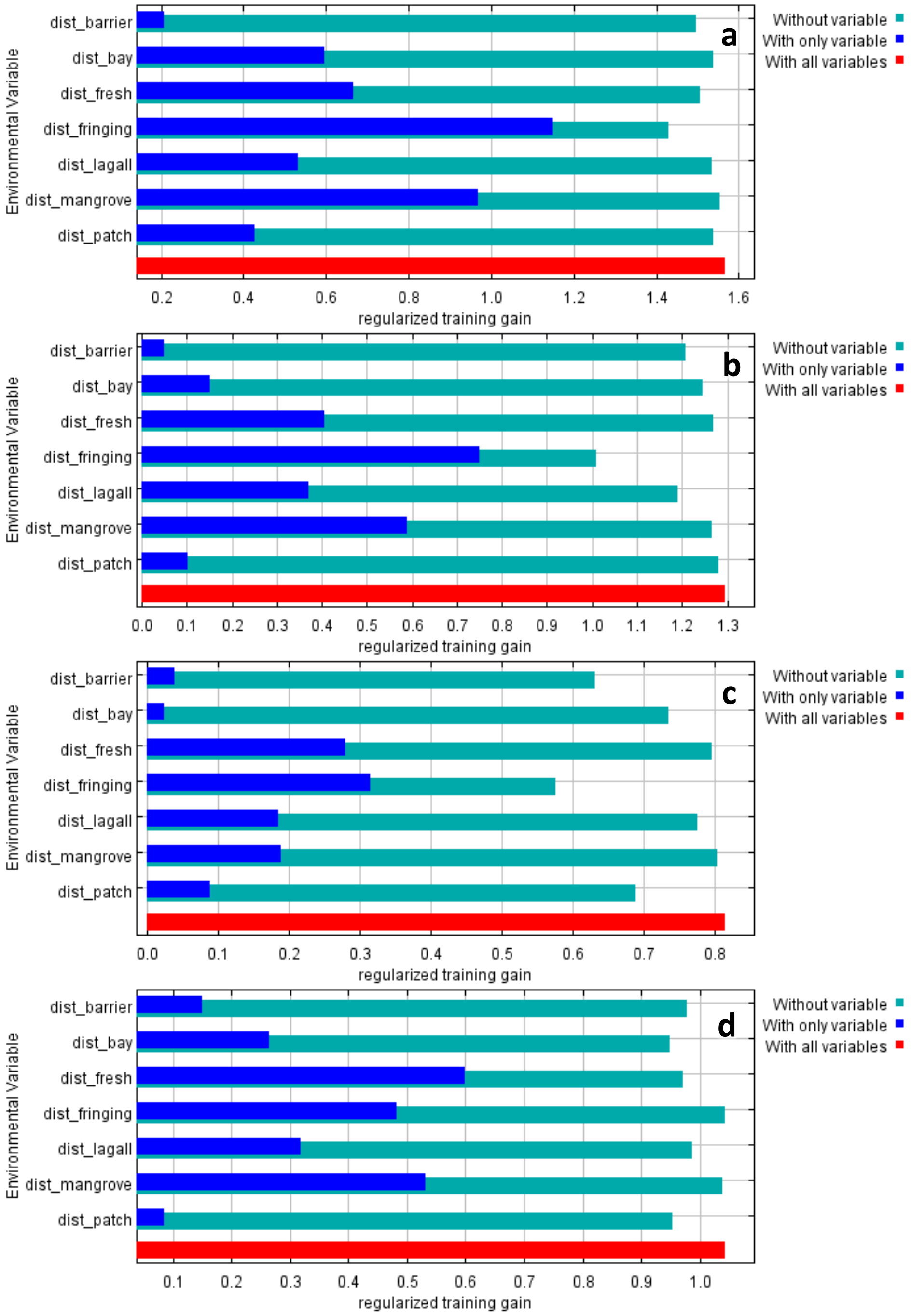


Figure A10 - Results of jackknife analysis, assessing relative importance of the seven environmental variables used to predict habitat suitability for *E. fuscoguttatus,* over the four modelled life history stages: (a) juveniles (< 370 mm TL, n = 122); (b) early sub-adults (370 - 436 mm TL, n = 14); (c) late sub-adults (437 – 481 mm TL, n = 17); and (d) adults (> 481 mm TL, n = 49). Environmental variables represent minimum distances to (top to bottom): barrier reef, embayment, freshwater input, fringing matrix, lagoon, mangrove, and patch reef.

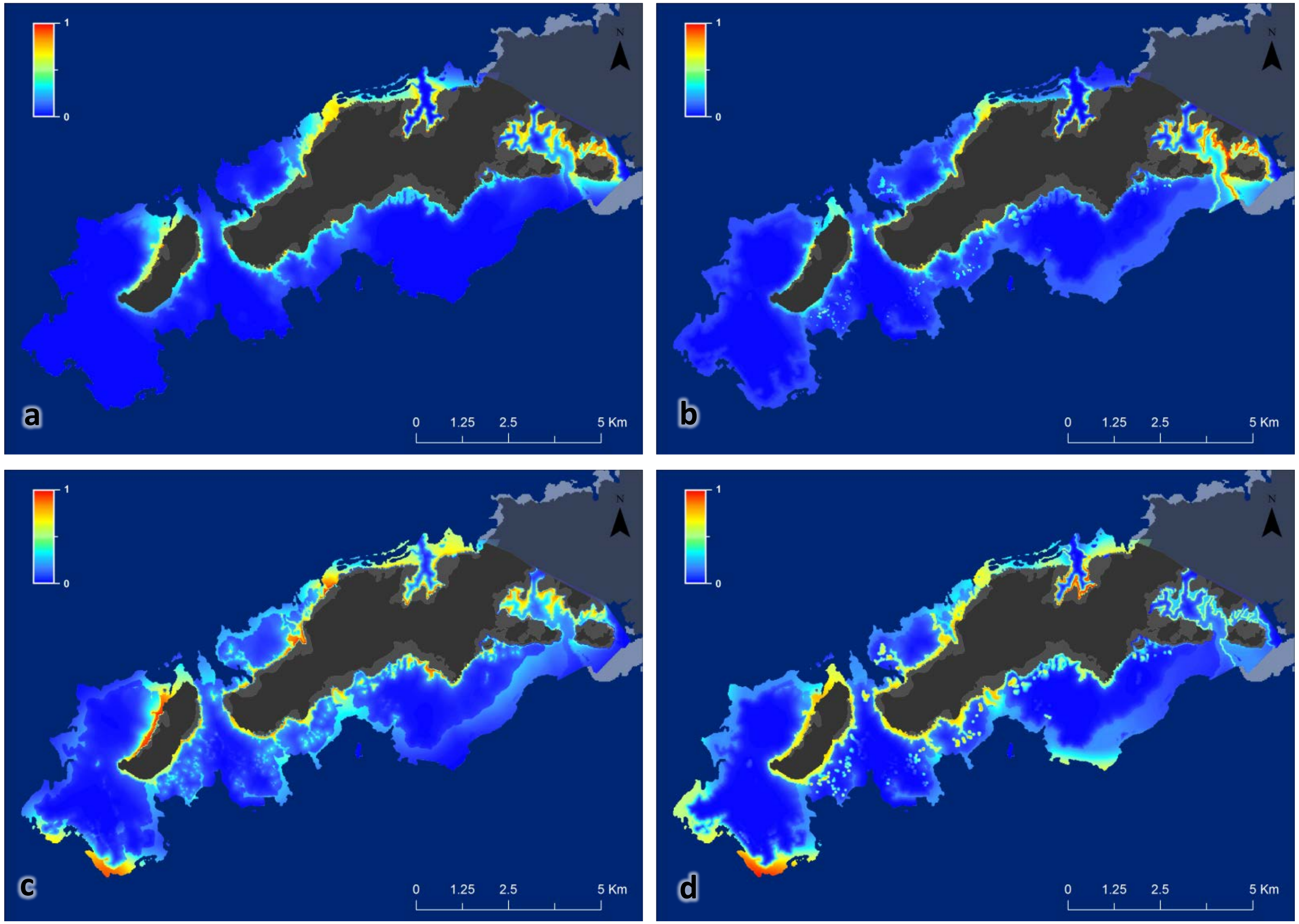


Figure A11 – Ontogenetic shift in habitat suitability for *E. fuscoguttatus,* using life history stages separated according to age: (a) juveniles (< 4 yrs, n = 67); (b) early sub-adults (4 – 5 yrs, n = 24); (c) late sub-adults (6 – 7 yrs, n = 23); and (d) adults (> 7 yrs, n = 23). Warmer colours represent higher modelled likelihood of presence.

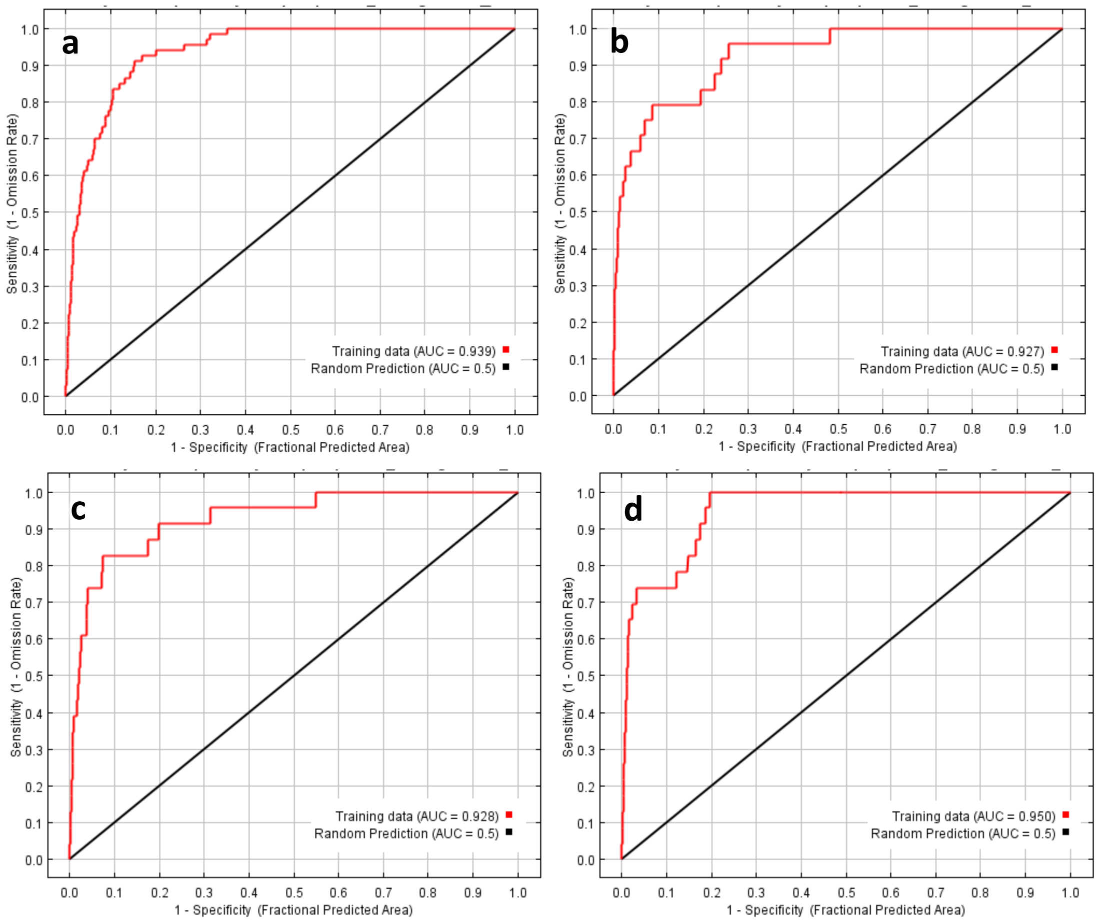


Figure A12 – Receiver Operating Characteristic (ROC) curves for *E. fuscoguttatus*: (a) juveniles (< 4 yrs, n = 67); (b) early sub-adults (4 – 5 yrs, n = 24); (c) late sub-adults (6 – 7 yrs, n = 23); and (d) adults (> 7 yrs, n = 23).

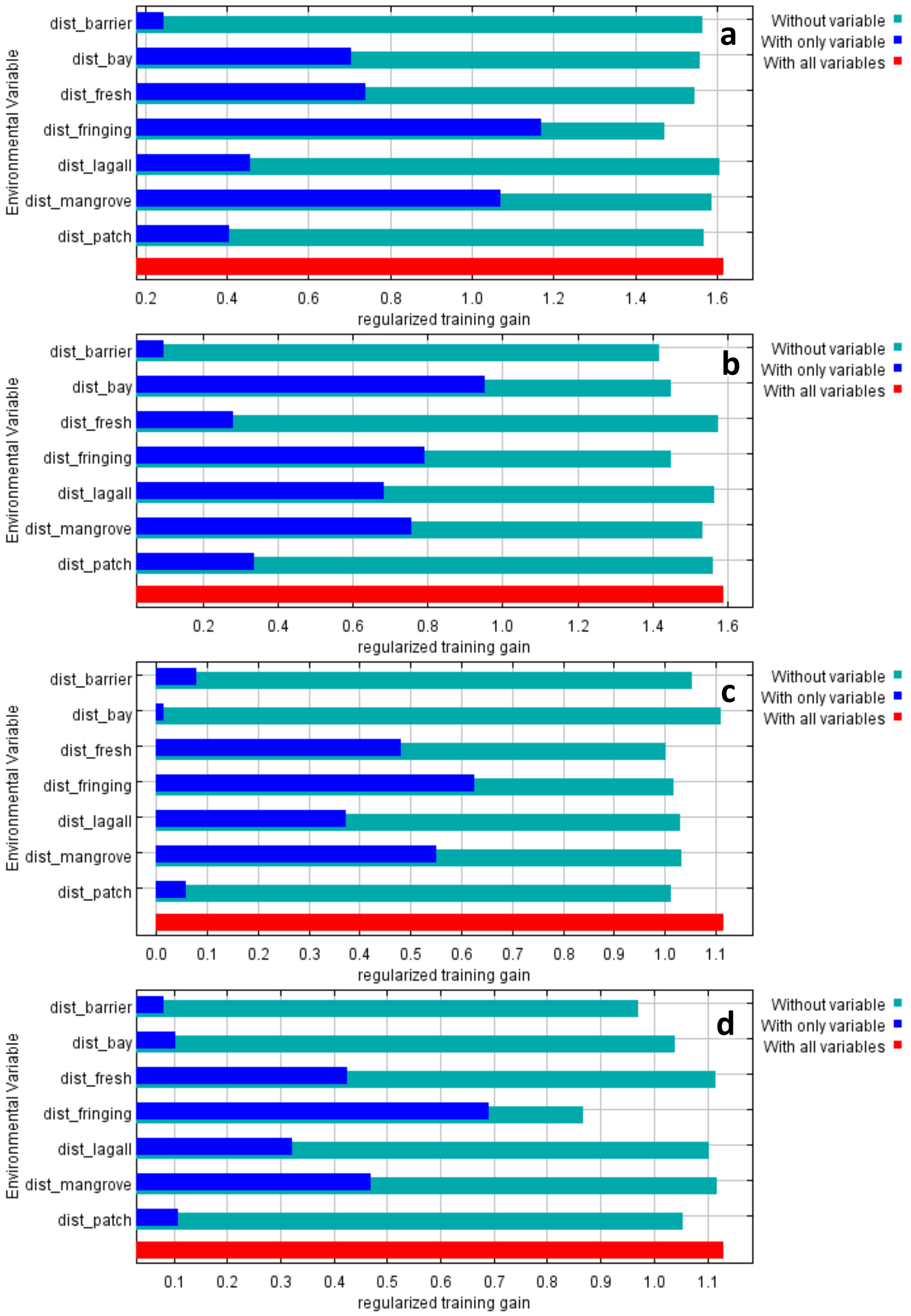


Figure A13 - Results of jackknife analysis, assessing relative importance of the seven environmental variables used to predict habitat suitability for *E. fuscoguttatus,* over the four modelled life history stages: (a) juveniles (< 4 yrs, n = 67); (b) early sub-adults (4 – 5 yrs, n = 24); (c) late sub-adults (6 – 7 yrs, n = 23); and (d) adults (> 7 yrs, n = 23). Environmental variables represent minimum distances to (top to bottom): barrier reef, embayment, freshwater input, fringing matrix, lagoon, mangrove, and patch reef.

Appendix VI – Comparison of suitable *E. fuscoguttatus* habitat and fishing effort

Table A3 - Suitable habitat within each governance area for *E. polyphekadion*; separated by life history stage (juvenile and adult), and by interaction with fishing effort. Only habitat categorised as suitable is presented here (*i.e.,* high-impact [i], and precautionary [iv]).

		Habitat within management area (km^2; % of tenure area)			
Life history stage	Habitat	Clan A	Clan B	Clan C	Leon VPC
Juvenile	All suitable habitat	1.2; 8%	2.5; 38%	1.9; 10%	5.6; 13%
	High Impact (i)	0.8; 5%	2.5; 38%	0.6; 3%	3.9; 9%
	Precautionary (iv)	0.4; 3%	0; 0%	1.3; 7%	1.7; 4%
Adult	All suitable habitat	5.4; 33%	3.3; 50%	3.0; 16%	11.7; 27%
	High Impact (i)	1.7; 11%	3.3; 50%	0.8; 4%	5.8; 13%
	Precautionary (iv)	3.7; 24%	0; 0%	2.2; 12%	5.9; 14%

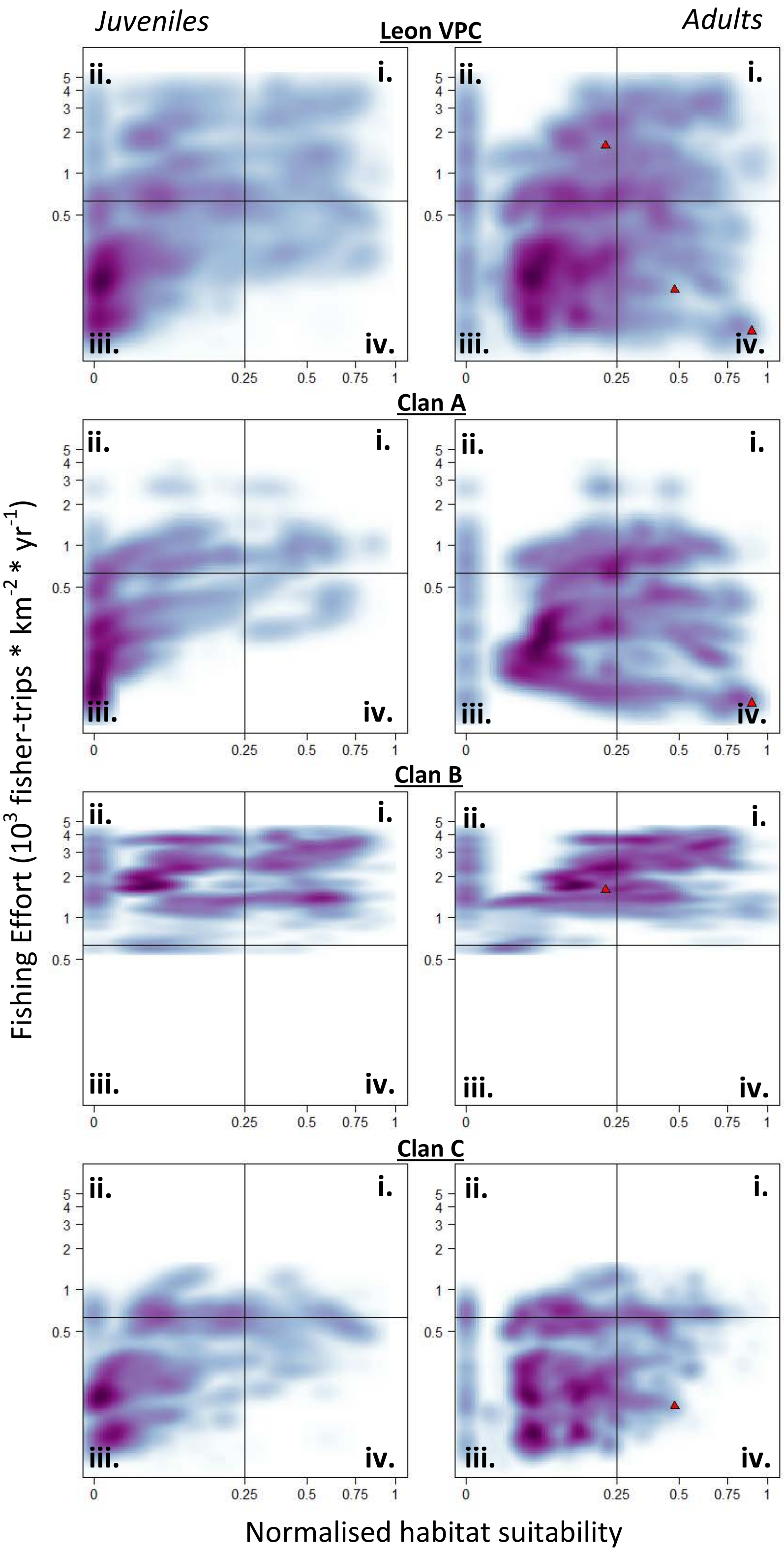


Figure A14 – Comparison of habitat suitability (x-axis; square transformed) for juvenile (n = 136) and adult (n = 66) *E. fuscoguttatus* (as separated by total length at 50% female sexual maturity; 436 mm) and fishing effort (y-axis; natural log transformed) expressed as a density of planning units separated by management area; darker colours represent higher density of points. Red filled triangles represent spawning aggregations sites.

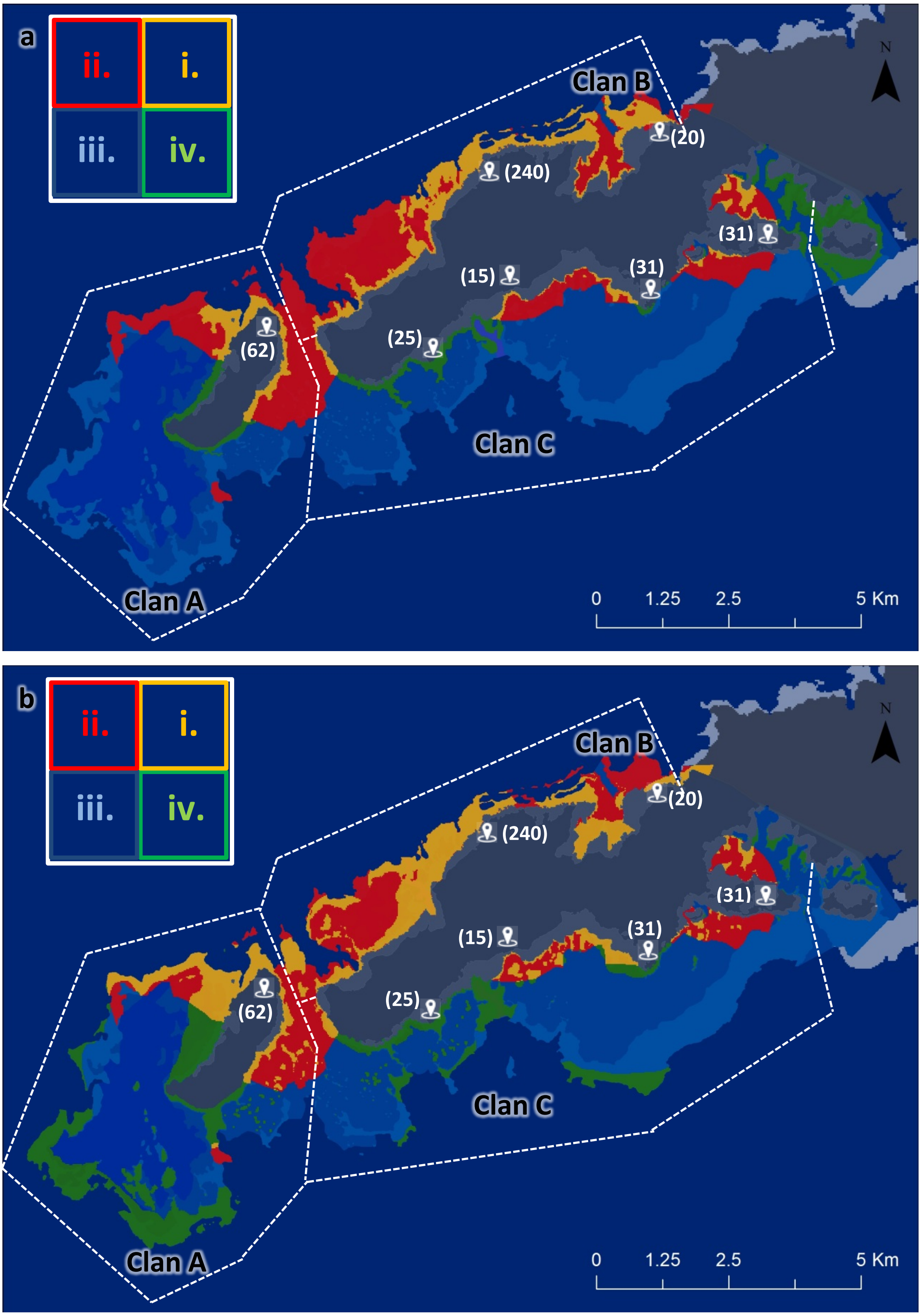


Figure A15 – Comparison of habitat suitability (x-axis; square transformed) for juvenile (n = 136) and adult (n = 66) *E. fuscoguttatus* (as separated by total length at 50% female sexual maturity; 436 mm) and fishing effort fishing effort (y-axis; natural log transformed) mapped across the study region; colours represent quadrant position from bi-plots above (Figure 6.3): i. High-impact (orange), ii. Lose-lose (red), iii. Low-priority (transparent-blue), and iv. Precautionary (green).