THE ROLE OF ECOLOGICAL PROCESSES IN STRUCTURING REEF FISH COMMUNITIES IN THE AGULHAS ECOREGION, SOUTH AFRICA

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Abstract

Local, niche-based processes, which arise from the interplay between biotic interactions and abiotic constraints are considered to be important regulators of community structure. However, it is increasingly recognised that patterns of diversity can also be strongly influenced by dispersal-driven processes. While empirical research on the diversity of coral reef fishes on shallow tropical reefs has contributed greatly to the development of general concepts in ecology, there have been considerably fewer studies on the processes which shape the diversity of fish communities on shallow (10 - 30 m) and deep (30 - 75 m) rocky reefs. Consequently, it is less clear at which spatial scales niche partitioning and dispersal limitation contribute most strongly to the structure of reef-associated fish communities within rocky reef ecosystems. To address this caveat, research was conducted at four rocky reef complexes within the warm-temperate Agulhas Ecoregion, South Africa. The diversity of reef-associated fishes was sampled by baited remote underwater stereo-video systems (stereo-BRUVs) to incorporate the range of heterogeneous reef habitat in Tsitsikamma National Park Marine Protected Area (TNP MPA) and Algoa Bay (AB).

To examine how niche-based and dispersal-driven processes influence patterns of diversity among species within the dominant family of resident fishes, the sparids (Sparidae), components of diversity were quantified at several spatial scales. Turnover in the number of species which locally co-occurred was found to be largely driven by the limited dispersal of species over hundreds of kilometres. When relative species abundances were taken into account, sparid communities were characterised by higher than expected rates of compositional turnover among local habitat patches

separated by hundreds to thousands of metres of contiguous reef. Patterns of compositional turnover were associated with the spatial aggregation of conspecifics, particularly at scales which facilitate the post-settlement dispersal of fishes. Niche-based segregation of species along the depth gradient was found to be the primary driver of compositional turnover among both protected and exploited communities. However, spatial structuring within reefs, which was independent of variation in the environment, suggests that compositional differences among communities are also influenced by the limited post-settlement dispersal of resident fishes to adjacent areas during their ontogeny. Together, the results suggest that the diversity of reef-associated sparids is likely to depend both on an adequate diversity of suitable reef habitat and a sufficient degree of spatial connectivity to facilitate ontogenetic habitat shifts.

Taxon-based descriptors of diversity do not adequately account for ecological difference among conspecifics within size-structured populations. To test whether differences in body size facilitated coexistence among sparid fishes, the number of species which coexisted at the local scale was related to variation in the size structure of communities. In communities which have been historically protected from fishing, local coexistence between a greater number of species was promoted by reduced levels of intraspecific variation in size of fishes. This suggests that, among species with similar trophic requirements, further niche segregation along a prey-size and body-size gradient is likely to mitigate the direct impacts of competition for shared food resources. Among exploited communities, size structure did not influence the number of species which coexisted at the local scale. This finding suggests that fishing-induced mortality of larger-bodied fishes is likely to remove some of the constraints to colonisation which arise from asymmetries in competitive fitness between small and large-bodied fishes.

Together, these results highlight the importance of post-settlement processes and population size structure to the maintenance of reef-associated fish diversity within

contiguous rocky reef habitats.

Keywords: Fish; Sparidae; community ecology; rocky reef; diversity; body size; stereo-BRUVs

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Chapter 1

General introduction

Despite decades of empirical research, studies on the ecological drivers which influence patterns of biodiversity remain contentious. Based on the principle that local interactions impose a limit on the number of species that can stably coexist (Gause 1934), competition and predation have been widely recognised as important regulators of community structure (Diamond 1975; MacArthur & Levins 1967; Schoener 1974). According to this view, community membership is governed by predictable assembly rules which determine whether species are sufficiently specialised to occupy specific niches. The opposing view envisions species as functionally equivalent and local communities as largely open systems whose structure is regulated by stochastic processes such as demographic drift and dispersal limitation (Chave 2004; Hubbell 1997, 2001). This view emphasises how limiting dispersal can effectively delay competitive exclusion and allow trophically similar species of arbitrary competitive ability to coexist. Reconciling the relative roles of niche differentiation and dispersal limitation in structuring communities remains central to the study of biodiversity and its management.

1.1 The ecology of reef-associated fishes

Reef-associated fishes are among the most characteristic and diverse groups inhabiting tropical and temperate reef ecosystems. Research on reef fish diversity has contributed widely to the development of general concepts in ecology (reviewed by Hixon 2011; Sale 1991). Following the more widespread use of SCUBA during the 1960's, early in situ observations made by underwater visual census at relatively local scales revealed important differences in spatial habitat use among reef fish species (e.g. Smith & Tyler 1972). As a result, niche diversification and interspecific competition (Anderson et al. 1981; Schoener 1974; Smith & Tyler 1973) remained a central theme of many early studies on reef fish (reviewed by Ebeling & Hixon 1991). An alternative perspective which arose from early studies of territorial damselfishes (Sale 1977, 1978) suggested that while species do compete, coexistence is more often attributable to a competitive lottery for vacant living space: The "lottery hypothesis" proposed that random mortality events and the unpredictable gain and loss of living space would lead to the formation of communities comprised of species with arbitrary competitive abilities. Subsequently, attempts to reconcile the two opposing perspectives stimulated research into the importance of larval recruitment (Doherty & Fowler 1994a,b), density-dependent interactions (Jones 1984a, 1987), and the persistence of long-lived adults (the "storage effect", Chesson & Warner 1981; Warner & Chesson 1985). Although it is now evident that reef fish communities can be structured by both niche partitioning and dispersal limitation, their relative prevalence is contingent on the spatial extent of available reef area (Ault & Johnson 1998a; Belmaker et al. 2009; Connolly et al. 2005; Lewis 1997) and the level of recruitment success (Jones 1990). For example, communities on isolated patch reefs are strongly influenced by variation in larval settlement rates, whereas, the structure of communities inhabiting habitat patches within contiguous reefs depend more strongly on post-settlement immigration (Ault & Johnson 1998c; Lewis 1997). Thus far, the synthesis of conflicting findings has contributed to an emerging consensus that the structure of reef fish communities is hierarchical and shaped by

processes over several spatial scales (Hixon 2011; Hughes et al. 2005; Sale 1998).

Most species have a bipartite life cycle, which includes a pelagic larval phase and older life stages that, following settlement to the reef, remain largely site-attached (Sale 1991). A typical pelagic larval duration of approximately 30 days provides sufficient time for larvae to disperse anywhere from hundreds of metres to hundreds of kilometres. However, determining the origins of juveniles recruiting to a particular reef and the destinations of larvae produced by adults on that reef remains a major challenge (Mora & Sale 2002). Once settled on the reef, species tend to remain resident; this confines the majority of their daily activities and interactions with other fishes to within the bounds of well-established home ranges which are typically between $<$ 100 m - 1,500 m in diameter, depending on the species (Edgar et al. 2004; Freiwald 2012; Kramer & Chapman 1999). A home range can be defined as a limited patch of preferred habitat which is routinely utilised as a source of food and also shelter. Residency within a home range confers numerous advantages towards the acquisition of resources and predator avoidance by limiting activity to a small core area of familiar habitat. Nevertheless, because most reef-asociated fishes exhibit complex habitat requirements that change with ontogeny, fish home ranges are not necessarily permanent: Juveniles tend to disperse from their nursery grounds to other habitats once they attain a larger body size (Brokovich et al. 2007; Macpherson 1998); resident fish undertake broader roaming movements to marginal areas (Parsons et al. 2003; Topping et al. 2006); and, in some instances, adults migrate over 100's of km to other reefs (Attwood & Bennett 1994; Ferguson et al. 2013). As some areas provide better shelter or foraging opportunities than others, repeated roaming movements can facilitate the opportunistic relocation of fish to new home ranges, termed "home range relocation" (Kramer & Chapman 1999; Robertson 1988).

Episodic, wide-ranging movements among otherwise resident species has stimulated the development of alternative models of fish movement behaviour: According to the tourist model (Craig & Hulley 1994), which was originally applied to describe

sunbird movements, migrant and resident movement behaviours coincide when resident individuals temporarily abandon their core home range to explore marginal areas. On the other hand, the polymorphic model (Attwood & Bennett 1994) proposes that there are two classes of fish within a population; the majority of individuals who remain resident and a small minority who remain nomadic and move unpredictably between favourable areas. Although mark-recapture studies have provided valuable insights into the range of scales at which fish movements can occur, most tend to produce biased estimates of home range size by failing to adequately account for the distribution of sampling effort (but see Attwood & Cowley 2005; Hilborn 1990; Kerwath, Götz, Attwood, Cowley, et al. 2007). Mark-recapture studies also lack the spatial and temporal precision necessary to distinguishing broader roaming movements from fine-scale home range shifts, and therefore do not provide a true reflection of the movement behaviours of resident reef fishes.

Acoustic tagging provides the most detailed information on the short-term movement behaviours of reef-associated fishes. Although most studies tend to be limited in their duration, longer-term acoustic monitoring studies ($\sim$ 1 year) have demonstrated that resident species undertake opportunistic home range shifts during the course of their ontogeny: On temperate reefs in New Zealand, the core home ranges of silver seabream *Pargus auratus* have been documented to shift by up to 300 m within a year, with some individuals alternating between 2 or 3 core areas of activity (Parsons et al. 2003). Over a similar time frame, California sheephead *Semicossyphus pulcher* have been shown to undertake regular roaming movements up to 1 km away from their night-time shelter locations, which, in some instances facilitate home range shifts (Topping et al. 2006). Although home ranges are unlikely to remain permanent during the lifetime of most temperate reef fishes, the estimated proportion of individuals which undertake long-distance movements is considered to be small compared to the resident proportion of the population (reviewed by Freiwald 2012).

1.2 The role of marine protected areas (MPAs)

Despite the planktonic life stages representing an important component of the fish life cycle, they are generally not amenable to management action. As a result, research into the management of exploited reef fishes has largely focused on distribution of the benthos-associated adult life stage (e.g. Attwood & Bennett 1994; Götz et al. 2008; Parsons et al. 2003). Marine protected areas (MPAs) are an increasingly important tool for the management of coastal fisheries and marine biodiversity. The benefits of MPAs (defined here as areas closed to fishing) to exploited reef fish populations are well documented, and typically include an increase in the total biomass, numerical density, and average size of fishes (Babcock et al. 1999; Barrett et al. 2007; Edgar & Stuart-Smith 2009; Lester et al. 2009). Fishing can also have indirect effects on how marine ecosystems function by influencing natural mortality regimes (Audzijonyte et al. 2013; McClanahan et al. 1999) and life history traits such as size-at-maturity and sex-change (Buxton 1993; Götz et al. 2008). As a result, MPAs are also considered to provide a tool for the conservation of marine ecosystem function. Although MPAs are clearly beneficial to fish populations residing within their boundaries, their perceived benefits to fisheries remain contentious (Crowder et al. 2000; Hilborn et al. 2004; Kerwath et al. 2013; Sale, Cowen, et al. 2005). The efficacy of MPAs as a fisheries management tool rests on their ability to protect the spawner populations of target species while replenishing adjacent fishing grounds via the export of larvae and net emigration (i.e. spillover) of adults. Because fish show varying degrees of site-fidelity, all species cannot be afforded equal protection. Highly mobile species that frequently stray beyond the boundaries of reserves will not be fully protected from fishing, which may undermine the positive influence of MPAs on local stocks (Kramer & Chapman 1999).

Acoustic tagging provides a means to quantify the frequency and extent of broader roaming movements in order to assess whether species can be expected to benefit from increases in population biomass associated with MPAs. In the case of the luderick *Girella tricuspidata*, recaptures of conventionally tagged fish docu-

mented pre-spawning migrations of some individuals up to 450 km away from their point of release (Gray et al. 2012). However, despite these long-distance movements, the vast majority of acoustically tagged fish were found to remain highly resident throughout their spawning period (Ferguson et al. 2013). Species which remain highly resident and display weak density-dependence are most likely to benefit from the establishment of MPAs, however, they are also likely to provide smaller spillover benefits to adjacent fisheries due to the limited movement of adults to areas outside the reserve (Kramer & Chapman 1999). If MPAs are to facilitate the long-term recovery of exploited species, reserve boundaries should encompass the range of essential fish habitats necessary to support their recruitment, growth to maturity, and spawning (Rosenberg et al. 2000). Knowledge of home range use and habitat selection therefore have important implications for the design and long-term effectiveness of MPA networks (Grüss et al. 2011; Kramer & Chapman 1999).

1.3 Sparids (family Sparidae)

This thesis concentrates on reef-associated fishes from the sparid family, Sparidae (seabreams). Sparids contribute substantially to the abundance and diversity of reef ichthyofauna within the warm-temperate Agulhas Ecoregion, South Africa (Turpie et al. 2000): They are highly abundant on shallow ($<$ 30 m) and mesophotic (30 - 150 m) rocky reefs and include a high proportion of species which are endemic to southern Africa. Although sparids continue to make up an important component of the commercial and recreational linefisheries, many populations have been heavily depleted since the mid 1900's (Brouwer & Buxton 2002; DAFF 2014; Griffiths 2000; Mann 2013). Susceptibility to overexploitation is partly attributed to their k-selected life history strategy (e.g. long lifespan, slow growth and late maturity; Buxton 1993). Nevertheless, increases in fishing effort and improvements in fishing technology remain a growing concern (Mann 2013).

Like most other reef-associated fishes, sparids tend to be highly resident. Mark-recapture studies suggest that the home range sizes of South African sparids typically

range between 100 - 500 m in diameter (Brouwer 2002; Brouwer et al. 2003; Cowley et al. 2002; Kerwath, Götz, Attwood, Cowley, et al. 2007; Maggs et al. 2013). Although scarce, acoustic telemetry has provided more accurate insights into their home range use; roman *Chrysoblephus laticeps*, for example, have been found to hold home ranges < 100 m in diameter and to rarely venture beyond the shelter of the reef (Kerwath, Götz, Attwood, Sauer, et al. 2007). Due to their common life history strategies, it is likely that most species share similar resident behaviours. Nevertheless, long-distance movements over 10's - 100's of km are occasionally documented in some species (e.g. Brouwer 2002; Brouwer et al. 2003; Griffiths & Wilke 2002; Maggs et al. 2013). The reasons for such movements are unclear, but are, in some species, hypothesised to be triggered by ontogenetic changes: This appears to be the case for carpenter *Argyrozona argyrozona*, whose juveniles appear to move from nearshore nursery grounds to deeper reefs where they remain resident as adults (Brouwer & Griffiths 2005; Brouwer et al. 2003). Other species, such as red steenbras *Petrus rupestris* (Brouwer 2002; Griffiths & Wilke 2002) and slinger *Chrysoblephus puniceus* (Duncan et al. 2015; Maggs et al. 2013) undertake longshore migrations of > 800 km to the east following the onset of sexual maturation, presumably to spawn in warmer waters. The majority of mark-recapture studies support the residency of sparids within small spatial extents, however, the tendency of some individuals to abandon their home ranges and depth-related trends in the ontogeny of some species (Griffiths & Wilke 2002; Heyns-Veale et al. 2016) suggest that home ranges are unlikely to be permanent, particularly at spatial scales which impose the smallest costs to movement.

Preliminary studies of South Africa's warm-temperate reef ichthyofauna conducted via underwater visual census (UVC) and angling support the view that sparids partition resources according to species, habitat, depth and size (Buxton & Smale 1984, 1989; Götz et al. 2014; Lechanteur & Griffiths 2003; Smale 1992): Nevertheless, most species show considerable overlap in their diets (e.g. reef-associated invertebrates, Table A6). In addition to obvious partitioning of habitat and food

resources between small opportunistic species and larger, predatory species, notable intraspecific differences are also evident in most species. Dietary analyses illustrate that shared food resources are often further partitioned according to food size among size classes: The diet of juveniles typically consists of smaller, soft-bodied prey; adults, who benefit from a wider jaw gape and more robust dentition, move on to exploit larger, hard-bodied prey items as they attain larger size (Buxton 1984; Buxton & Clarke 1989, 1991). Habitat is also spatially partitioned among conspecifics with juveniles typically inhabiting shallow subtidal reefs, which may act as nursery grounds, while adults are more frequently encountered on deeper reefs (Buxton 1984; Buxton & Clarke 1986; Buxton & Smale 1984, 1989; Griffiths & Wilke 2002; Smale 1988). Ranging movement behaviours which facilitate home range relocations are likely to provide an adaptive response to changing resource distributions within the competitive milieu. Among sparids, home range shifts among adults have only directly been observed in the silver seabream *P. auratus* via acoustic telemetry (Parsons et al. 2003); the frequency and scale at which fish relocate to more suitable home ranges during their lifetime therefore remains poorly understood. This is partly attributable to a scarcity of acoustic monitoring studies which track movements for a longer duration ($>$ 1 year) of a fish's lifetime. Even so, traditional fish monitoring surveys can provide important insights into the distributions of temperate reef fishes and their ecology, through the documentation of fish-habitat associations (Choat & Ayling 1987; Levin & Hay 1996), temporal changes in community structure (Holbrook et al. 1994; James et al. 2012) and ontogenetic trends in habitat use (Griffiths & Wilke 2002; Macpherson & Duarte 1991; McCormick 1989).

1.4 Research approach

Methods

Thus far, UVC and angling surveys have provided a limited view into the processes which structure South Africa's subtidal reef ichthyofauna. Baited remote underwa-

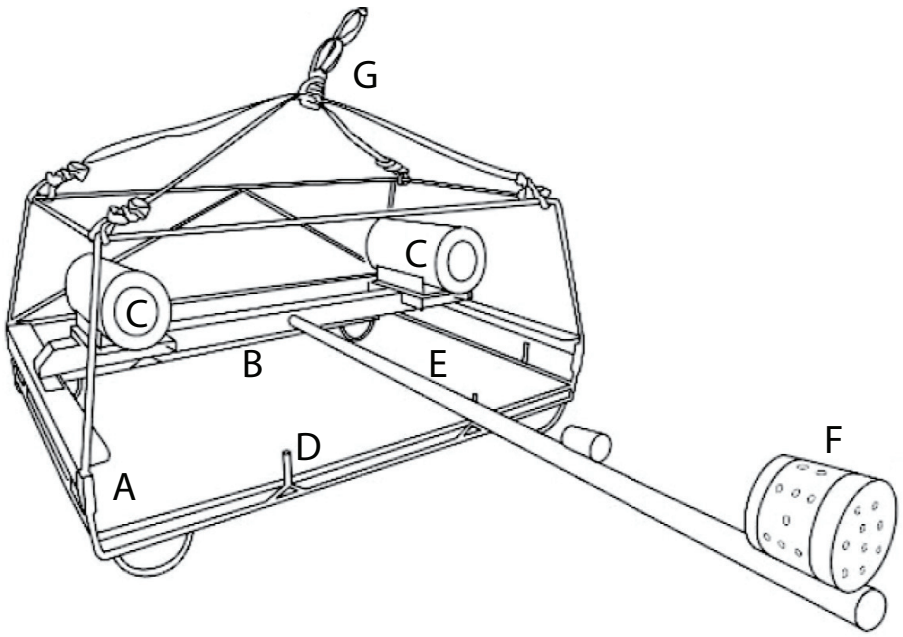


Figure 1.1: Illustration of a baited remote underwater stereo-video system (stereo-BRUVs): The stainless steel frame (A) features a rigid centre bar (B) that holds two camera housings in a stereo configuration (C) and additional weights (not shown) that can be mounted to steel pins (D). A steel bait arm (E) which holds the bait container (F) extends 1.5 m perpendicularly from the centre bar. The system is linked to a surface buoy by a rope system which attaches to the stainless steel frame (G). Image source: Elodie Heyns-Veale

ter stereo-video systems (stereo-BRUVs; Fig. 1.1) can provide fisheries independent information on the relative abundance (Moore et al. 2009; Watson et al. 2007) and length composition of subtidal fish assemblages (McLaren et al. 2015; Parker et al. 2016), and possess numerous advantages over traditional fish monitoring methods: By overcoming many of the limits to sampling depth which usually restrict SCUBA-based UVC to depths shallower than 30 m, stereo-BRUVs provide a more comprehensive representation of fish distribution patterns at scales relevant to their ecology. The use of videography creates a permanent visual record of both fish and the seafloor habitat: This allows observers to consult fish identification guides or experts when analysing samples and makes long-term monitoring programmes using multiple observers easier to standardise, as videos can be re-analysed to account for observer biases (Cappo et al. 2003). The use of bait as an attractant in stereo-BRUVs surveys introduces its own sampling bias towards large predators and scavengers and against herbivores and smaller prey species (Dunlop et al. 2015; Harvey et al. 2007).

Nevertheless, the large field of view and depth of field of horizontally facing baited video assessments is effective at sampling a large proportion of the fish community (Cappo et al. 2004; Willis & Babcock 2000). This is likely to reduce the potential effect of agonistic interactions around the bait (Coghlan et al. 2017). More precise estimates of relative abundance and species richness contribute to a greater power to detect spatial and temporal changes in the fish community (Bernard & Götz 2012; Harvey et al. 2007). As well as being non-destructive, the stereo-video configuration (Figure 1.1C) facilitates the precise and accurate estimation of fish length and biomass (Harvey & Shortis 1995). Length-frequency data estimated from stereo-BRUVs benefits from smaller length-selectivity bias than linefishing (Langlois et al. 2012; Parker et al. 2016), fishtraps (Harvey et al. 2012; Langlois et al. 2015), and UVC (Harvey et al. 2002), and provide important baseline data for the development of size-based indicators of overfishing (Jennings et al. 1999; Shin et al. 2005). Following their increasingly wide-spread use in Australia (e.g. Malcolm et al. 2007; Moore et al. 2009; Watson et al. 2007) and elsewhere (e.g. Bassett & Montgomery 2011; Stobart et al. 2007; Zintzen et al. 2012), BRUVs (Bernard & Götz 2012; De Vos et al. 2014, 2015) and, subsequently, stereo-BRUVs (Heyns-Veale et al. 2016; Parker et al. 2016) have more recently been employed to conduct fish monitoring surveys across the continental shelf of southern Africa (reviewed by Bernard et al. 2014).

Ecological

Unlike the pelagic environment, which is relatively homogeneous, the distribution of reef habitat in the ocean is conspicuously patchy. Whether viewed at the scale of 10's - 100's of m, or 100's of km, the patchy nature of the reef environment imposes spatial structure on the distribution of fish populations and communities over a number of spatial scales. As a result, many reef-associated fishes are considered to exist as metapopulations (i.e. "population of populations") of resident adult fishes which are linked by the dispersal of pelagic larvae (Hixon & Webster 2002; Sale 1998). At the smallest spatial scale (10's - 100's of m), the local habitat

patch, the distribution of resident sparid fishes is expected to be influenced by the rates of larval settlement to the reef and by subsequent post-settlement processes; such as predation, competition, habitat selection, and the immigration of fish from other habitat patches. At the reef-wide scale, sparid populations show varying degrees of connectivity to those on other reefs through the dispersal of pelagic larvae and the occasional movement of adults (see Brouwer 2002; Brouwer et al. 2003). Estimated longshore current velocities in the Agulhas Ecoregion suggest that the eggs and larvae of sparids are potentially capable of being dispersed over distances of 10's - 100's of km within 30 days (time to flexion, Attwood et al. 2002; Brouwer et al. 2003; Davis & Buxton 1996; Davis 1996; Tilney et al. 1996). Because the pelagic larval durations of most reef fishes allow for interpopulation connectivity between distant reefs, most of the recruits on a given reef are unlikely to have been produced by the adults that reside there. The unpredictable rate of larval dispersal can lead to variable fish abundances on a given reef; however, it also acts as a buffer against extinction risk by providing an environmentally resilient source of new recruits (Chesson 1985; Chesson & Warner 1981). Furthermore, it may allow species to persist on reefs which, in isolation, do not support a viable population of reproducing adults. A growing body of recent empirical research indicates that larval dispersal among several coral reef fish families (e.g. Labridae, Pomacentridae, Chaetodontidae, Epinephelidae) frequently takes place over distances of $<$5 - 15 km and that self-recruitment (the proportion of recruits that are produced by parents in the same population) is more common than previously realised (Almany et al. 2007, 2013; Jones et al. 2009). Similar findings of limited larval dispersal among temperate reef fishes would imply that metapopulation structures exist at smaller spatial scales than previously thought (Freiwald 2012). Typically, local populations are distinguished from metapopulations by pooling together conspecifics (juvenile and adult) into groups between which post-settlement movement is considered to be negligible (see Hixon & Webster 2002). Consequently, patches of isolated reef habitat provide a discrete template which is amenable for delineating local populations of

resident fishes. While fish abundances on isolated patch reefs respond strongly to episodic larval recruitment events, studies suggest that fish abundances on larger, contiguous reefs are more strongly influenced by the post-settlement immigration of fish from other areas within the same reef (Ault & Johnson 1998c; Lewis 1997; Robertson 1988). Recruitment limitation is therefore most relevant to populations at the scale of the whole reef. Consequently, the dynamics of local communities of resident fishes on large reefs within the Agulhas Ecoregion may best be described in a context which considers how both post-settlement movements and larval dispersal influence species abundances at the within-reef and between-reef scales, respectively (see Ault & Johnson 1998c; Kritzer & Sale 2010; Lewis 1997).

1.5 General aims and thesis outline

The aim of this thesis is to contribute towards a more comprehensive understanding of how reef-associated fish communities are structured within a warm-temperate rocky reef ecosystem in the Agulhas Ecoregion, South Africa. Non-destructive sampling techniques are employed to investigate the taxonomic diversity and size structure of resident sparid communities to explore how local niche-based processes and dispersal-driven assembly contribute to their diversity. As the processes which contribute to biodiversity maintenance (e.g. environmental heterogeneity, dispersal) are typically scale-dependent (Levin 1992; Sale 1998), it is necessary to assess several spatial scales relevant to the ecology and management of sparid fishes.

Chapter 2 investigates how local environmental (i.e. niche-based) and spatial (i.e. dispersal-based) processes contribute to the community composition of sparid reef fish communities over several spatial scales. Baited remote underwater stereo-video systems (stereo-BRUVs) are deployed to survey local reef-associated fish communities, which are predominantly comprised of resident sparid fishes, across the full depth gradient of four prominent reef complexes. One inshore reef and one offshore reef are included from two locations within the Aghulas Ecoregion: Tsitsikamma National Park marine protected area (TNP MPA), which was established as a 'no

take' MPA in 1964, and Algoa Bay (AB). In order to identify important scales of non-random turnover, a number of studies have explored how total diversity (γ-diversity) is partitioned into mean local diversity (α-diversity) and components of turnover (β-diversity) (Belmaker et al. 2008; Crist et al. 2003; Declerck et al. 2011). Chapter 2 first compares the contribution of different spatial scales to total sparid diversity, by quantifying β-diversity among habitat patches within reefs; between reefs; and between locations. Observed diversity components are compared to those from randomised communities to test whether turnover can be attributed to non-random ecological processes (e.g. niche partitioning, dispersal limitation). Next, compositional variation among communities (β-diversity) is quantified in terms of its relationship to local environmental variation and spatial factors (Cottenie 2005; Peres-Neto & Legendre 2010). Identifying the spatial scales at which β-diversity is related most strongly to environmental or spatial variation provides novel insights into processes which shape the diversity of sparid fishes.

Body size is possibly one of the most fundamental properties of an organism (Peters 1986) which provides an important link between the individual- and population-level species traits and the composition of communities (White et al. 2007; Woodward et al. 2005). Most sparid species are relatively long-lived and slow-growing, and share considerable overlaps in their diet and habitat use during ontogeny. Further niche partitioning according to food size and body size is therefore hypothesised to be important in structuring local communities. Chapter 3 examines how the relationship between species-wide (i.e. intraspecific) and community-wide variance in body length influences the number of sparid species which locally co-occur. This relationship provides a strong test of whether body size-mediated coexistence among sparids is facilitated via niche differentiation between species, neutrality (i.e. chance dispersal), or via individual variation among conspecifics (Violle et al. 2012). Comparisons between near-pristine communities in TNP MPA and exploited communities in AB provide insights into whether body size-mediated competitive coexistence among sparid fishes is likely to be influenced by size-selective fishing mortality.

The long lifespans, large size and high fecundity of many reef-associated fishes is thought to be an evolutionary response to highly variable levels of recruitment success (Murphy 1968; Sale 1977). The same life history traits also make their populations more sensitive to fishing pressure than smaller, fast-growing and early-maturing species (Griffiths 2000; Jennings et al. 1999). Consequently, sparids are considered to be particularly susceptible to the effects of overfishing, and are among the groups most likely to benefit from South Africa's growing network of MPAs (Solano-Fernandez et al. 2012). The persistence of long-lived and highly fecund individuals may also disproportionately contribute to the maintenance of spatially diverse and temporally stable fish communities following adequate lengths of protection from fishing (e.g. TNP MPA: Heyns-Veale et al. 2016; James et al. 2012). This diversity may, in turn, contribute towards a greater stability of biomass and catches (Worm et al. 2009). It is well documented that fishing can, through the removal of fish biomass and truncation of population size-structure, also indirectly affect the abundances of other, non-target, species and thereby the functioning of marine ecosystems (Babcock et al. 1999; Barrett et al. 2007; McClanahan et al. 1999; Watson et al. 2007). The successful implementation of ecosystem-based approaches to sustainable fisheries management therefore needs to be informed through (i) knowledge of the scales and processes which maintain marine biodiversity and (ii) appropriate indicators of exploitation. Analyses of β-diversity (Mouillot 2007) and size-based indicators of exploitation (Shin et al. 2005) provide a complimentary approach towards achieving this end (Pauly et al. 2002).

Chapter 2

Environmental and spatial contributions to patterns of sparid reef fish diversity

2.1 Introduction

The distribution of biodiversity often seems to be highly contingent on idiosyncratic environments and the species interactions that develop within them. Although scale-dependent ecological phenomena will have unique causes and consequences (Levin 1992), patterns of species diversity and abundance, and the structure of communities are the result of only four high level processes: Selection, ecological drift, dispersal and speciation (Vellend 2010). Selection results from deterministic fitness differences between individuals possessing different functional traits; ecological drift arises due to stochastic fluctuations in relative abundance; dispersal involves the movement of organisms and their progeny across space and mediates the importance of ecological drift; speciation creates new species over evolutionary time scales.

Much of the current debate in community ecology centres around the relative roles of deterministic and stochastic processes in the assembly of local communities (Vellend et al. 2014). On one hand, variation in species composition between sites (β-diversity) arises from the interactions between species' niches and local environmental factors (Chesson 2000; Hutchinson 1957). According to classical niche theory, coexistence of trophically similar species at local scales is facilitated by functional trade-offs which minimise competition for limiting resources (Chase & Leibold 2003;

Chesson 2000). Niche differentiation leads to species turnover (i.e. species sorting) along environmental gradients, and ecological communities whose spatial structure tracks (via dispersal) the distribution of favourable environments. Alternatively, neutral models of community assembly (Chave 2004; Hubbell 2001; Hurtt & Pacala 1995) rely on dispersal limitation and ecological drift to explain patterns of species diversity, without the need for niche differences. The cornerstone of neutral theory is that trophically similar species have equal per-capita vital rates (i.e. birth, mortality and dispersal; Hubbell 1997, 2005). The limited capacity of species to adequately disperse promotes greater compositional turnover among communities with increasing geographic separation (Bell 2001; Hurtt & Pacala 1995). Although niche and neutral theories represent two opposing perspectives, their joint consideration can provide valuable insights into the processes which structure communities and the maintenance of biodiversity (Leibold & McPeek 2006).

It is increasingly recognised that individual communities interact with one another through the dispersal of organisms, and that these spatial linkages can strongly influence the structure of communities at multiple scales. The metacommunity concept (reviewed by Leibold et al. 2004) is among the most relevant concepts for integrating the processes which shape patterns of biodiversity among communities connected by the dispersal of multiple interacting species (Wilson 1992). Based on the relative prevalence of local environmental heterogeneity and dispersal limitation, Leibold et al. (2004) proposed four metacommunity paradigms (Fig. 2.1): 'patch-dynamics', 'species sorting', 'mass effects' and 'neutral'. Patch-dynamics represents a form of niche differentiation that does not rely on habitat associations, but rather on the trade-off between competitive dominance and dispersal ability (Levin & Paine 1974). Species which specialise in their ability as either dominant competitors or opportunistic dispersers promote spatial and temporal turnover among environmentally homogeneous habitat patches. Species sorting is facilitated when species with different niches are able to adequately disperse to suitable habitat patches within a spatially varying environment (Chave et al. 2002). As a result of spatial niche

segregation, community composition tends towards an equilibrium state comprised of species best suited to a site's average environmental conditions. Mass effects take place among habitat patches that differ in environmental conditions, but are sufficiently connected via dispersal to allow populations to be maintained via source-sink dynamics (Pulliam 1988). High rates of dispersal from favourable source habitats to marginal or unfavourable sink habitats overcome the effects of local environmental constraints and species interactions to influence abundance patterns. Finally, the neutral paradigm views all individuals, regardless of their species identity, as ecologically equivalent in their ability to compete and disperse, leading to the formation of dispersal-limited communities with strong spatial structures (Hubbell 2001). This can provide a useful null expectation against which to test empirical data for non-neutral patterns (Bell 2001).

The four metacommunity paradigms differ with respect to two fundamental assumptions: Firstly, whether the environment is spatially homogeneous or heterogeneous; and secondly, whether species occupy different niches or can be viewed as ecologically equivalent. Because niche and neutral processes are not mutually exclusive, natural communities do not necessarily conform to only one of the four metacommunity paradigms (Chave et al. 2002; Cottenie 2005). Accordingly, metacommunities can be considered to fall along a continuum between completely niche structured and completely neutral (Gravel et al. 2006; Leibold & McPeek 2006). This has lead some authors (e.g. Heino et al. 2015; Winegardner et al. 2012) to suggest that the relative roles of species sorting and dispersal limitation are the fundamental principles of metacommunity organisation. In these terms, patch dynamics and mass effects come to represent special cases of the species sorting paradigm with limiting and homogenising dispersal, respectively (Winegardner et al. 2012). The partitioning of total community variation into an exclusive fraction of variation explained by environmental factors and an exclusive fraction explained by spatial factors provides one means by which to explore the relative contributions of species sorting and dispersal-limited assembly (Cottenie 2005; Legendre & Legendre 1998;

Peres-Neto & Legendre 2010).

Fish communities provide an excellent illustration of the continuum that exists between completely closed (niche-structured) and completely open (dispersal limited) communities. Because most reef-associated fishes begin life with a pelagic larval phase, the composition of communities can be highly sensitive to the supply and settlement of larvae to a given reef (Andrews & Anderson 2004; Doherty et al. 2004; Sale et al. 1994). As a result, the unpredictable colonisation of available shelter (Munday 2004; Sale 1977, 1978), or variable larval recruitment success (Doherty & Fowler 1994a,b) may potentially influence patterns of species abundance. When broad-scale dispersal dynamics prevail, abundances tend to fluctuate over time and remain only weakly related to small-scale habitat characteristics and the presence

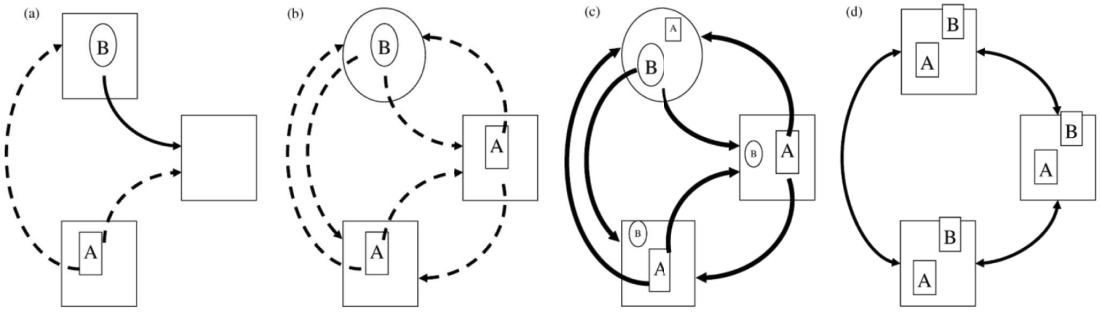


Figure 2.1: Conceptual illustrations of the four paradigms of metacommunity organisation for two competing species with populations A and B (adapted from Leibold et al. 2004): (a) patch-dynamics, (b) species sorting, (c) mass effects and (d) neutral. Habitat patches are illustrated by large rectangles or ovals, representing different habitat types. Whether a species is the dominant competitor in a site is indicated by the matching of the smaller boxes or ovals (denoting its habitat type niche) with the larger site symbol. Arrows represent the strength and direction of dispersal between populations. Solid arrows show higher dispersal rates than dashed arrows and correspond to either unidirectional (single-headed arrows) or bidirectional movements (double-headed arrows). (a) The patch-dynamics paradigm illustrates the competition-colonisation trade-offs which facilitate coexistence between species A, the superior competitor, and species B, the superior coloniser. The vacant habitat patch could be occupied by either species. (b) Species sorting illustrates spatial niche segregation among species which can adequately disperse to suitable habitat types. (c) Mass effects permit the persistence of smaller populations in unfavourable sink habitats through high rates of immigration from favourable source habitats which support larger populations. (d) The neutral paradigm considers species to be ecologically equivalent, and spatial turnover in abundance among communities to be entirely linked to their degree of dispersal limitation. Species which are gradually lost from the metacommunity are replaced by speciation.

or absence of other fishes (Ault & Johnson 1998a; Sale 2004; Sale & Douglas 1984; Sale et al. 1994). On the other hand, depth and habitat structure are known to be important drivers of reef-associated fish distributions on both tropical coral reefs (Brokovich et al. 2008; Fitzpatrick et al. 2012; Malcolm et al. 2011) and temperate rocky reefs (Anderson & Millar 2004; Heyns-Veale et al. 2016; Moore et al. 2009). Within-reef habitat characteristics mediate the outcomes of post-settlement processes such as competition (Almany 2003; Jones 1987), predation (Hixon & Jones 2005), habitat selection (Anderson & Millar 2004; Belmaker et al. 2008; Choat & Ayling 1987), and post-settlement immigration (Belmaker et al. 2009; Lewis 1997; Robertson 1988), and tend to contribute to the maintenance of more spatially predictable fish communities (Ault & Johnson 1998c). This appears to be more prevalent on large, contiguous reefs which facilitate enhanced spatial connectivity and frequency of post-settlement movements of adult fishes to more favourable habitat patches (Ault & Johnson 1998c; Nanami & Nishihira 2002, 2003; Robertson 1988).

Among the characteristic reef fish families which inhabit the warm-temperate reefs of South Africa's Agulhas Ecoregion, sparids (family: Sparidae) are among the most well represented and speciose groups (Mann 2013; Turpie et al. 2000). They are long-lived and highly resident, occupying small home ranges often < 250 m in diameter (Brouwer et al. 2003; Griffiths & Wilke 2002; Kerwath, Götz, Attwood, Cowley, et al. 2007; Kerwath, Götz, Attwood, Sauer, et al. 2007; Maggs et al. 2013). They grow to attain a wide range of adult body sizes (TL: 300 - 2000 mm; Table A6), and show considerable trophic overlap, with diet of most species principally including benthic invertebrates and small epibenthic crustaceans (Table A6). Furthermore, indirect evidence suggests that many species undergo depth-related ontogenetic niche shifts associated with changes in body size, diet and habitat use (Griffiths & Wilke 2002; Heyns-Veale et al. 2016; Macpherson 1998). The structure of local sparid communities is therefore expected to be influenced by the post-settlement immigration of juveniles and adults between habitat patches (Lewis 1997; Robertson 1988) as well as their degree of spatial connectivity (Ault & Johnson 1998c; Fernández

et al. 2008). As a result, sparid communities within sufficiently large, contiguous reef habitats may assume characteristics of a metacommunity at both within-reef and between-reef scales (Ault & Johnson 1998c; Kritzer & Sale 2010).

Both the vagility of species and their spatial setting influence the relative prevalence of species sorting and dispersal-limited assembly (Cottenie 2005). It is therefore necessary to quantify the effects of processes taking place at multiple scales (Levin 1992): At the smallest spatial scale (100's - 1000's of m), within-reef habitat characteristics related to depth, such as the average abiotic conditions (e.g. temperature, light availability, productivity) and macrobenthic structure, have been found to influence fish-habitat relationships (Heyns et al. 2016; Heyns-Veale et al. 2016). At this scale, where home ranges may also overlap, previous studies have reported both inter- and intraspecific partitioning of food size and habitat use among sparid fishes (Buxton 1984; Buxton & Smale 1984, 1989). Post-settlement relocations to more suitable habitats are also likely to predominate at this scale due to the energetic costs and predation risks associated with inter-reef movements (Chapman & Kramer 2000; Kramer & Chapman 1999). Over intermediate scales (10's of km), recruitment rates may vary both between habitats and between locations with similar habitat characteristics (Jones 1984b). Consequently, some areas may consistently recruit higher densities of juvenile fish than others: Reefs with an abundance of shelter in the form of topographic structures or dense macro-algal habitats appear to mitigate early juvenile mortality rates (Connell & Jones 1991; Jones 1984b; Levin & Hay 1996). At broader scales, sparid communities within the Agulhas Ecoregion remain connected by longshore currents which are thought to be capable of transporting pelagic larvae over 10's - 100's of km (Attwood et al. 2002; Brouwer et al. 2003; Tilney et al. 1996).

The aim of this study was to disentangle the contribution of species sorting and dispersal-limitation to the hierarchical structure of reef-associated sparid communities. Communities within the Agulhas Ecoregion were sampled to examine the spatial turnover in the distribution of fishes at three spatial scales: among habitat

patches within reefs (100's - 1000's of m); between reefs (5 - 10 km); and between locations ($\sim$ 200 km). To identify the most important scales of nonrandom species turnover, total species richness and total Shannon diversity (γ-diversity) were decomposed into additive components of α-diversity (average within-site diversity) and β-diversity (average between-site diversity). Observed diversity components were compared to randomised or neutral distributions in which individual fish occupied sites independently of their location and the presence or absence of other fishes (Crist et al. 2003). Similar individual-based randomisations were subsequently used to test whether nonrandom diversity components could be explained by the spatial aggregation of conspecifics. Finally, to estimate the relative influences of species sorting and dispersal limitation to spatial β-diversity patterns, variation in community composition was exclusively related to local environmental factors and spatial structures via variation partitioning analyses.

2.2 Materials and methods

2.2.1 Study area and sampling design

Ichthyofaunal assemblages were sampled at two locations within South Africa's warm-temperate Agulhas Ecoregion (Fig 2.2). Tsitsikamma National Park marine proected area (TNP MPA) and Algoa Bay (AB). TNP MPA is the oldest (established 1964) and largest (320 km^2) 'no-take' MPA in South Africa (Buxton & Smale 1984). Because of this, TNP MPA is considered to host one of the best examples of near-pristine temperate reef communities. Algoa Bay is one of many large crenulated bays along the south-east coast of South Africa, each of which feature a prominent headland. Due to its close proximity to the city of Port Elizabeth, the resident ichthyofauna of Algoa Bay's subtidal reefs has been subject to historical exploitation by both the commercial linefishing and recreational ski-boat fishery (Smale & Buxton 1985). Much of the south coast of South Africa is subject to frequent wind-driven upwelling, which largely occurs off the headlands during the summer

months (Schumann 1999). During the summer months, reefs within 15 km of the southern coastline experience strong thermoclines and short-lived changes in temperature, while winter conditions remain more isothermal (Goschen & Schumann 1995; Hanekom et al. 1989; Schumann et al. 1988).

The depth-stratified random sampling design aimed to capture community variation at multiple spatial scales relevant to the dispersal of adult and larval sparid fishes: Across individual habitat patches within large spatially contiguous reefs (100's - 1000's of m), between reefs (5 - 10 km), and between locations within the Agulhas Ecoregion ($\sim$ 200 km). Within each location, one nearshore and one offshore reef spanning similar depth ranges were surveyed (see Table A1). Large expanses of deep ($>$ 50 m) sandy bottom between nearshore and offshore reefs act as a constraint to the post-settlement movement of most reef-associated fishes (Chapman & Kramer 2000). In TNP MPA, the offshore reef (Middle Bank) is situated approximately 5 km from its nearshore counterpart (Rheeders Reef). The offshore and nearshore reefs in Algoa Bay (Riy Banks and Cape Recife, respectively) are sep-

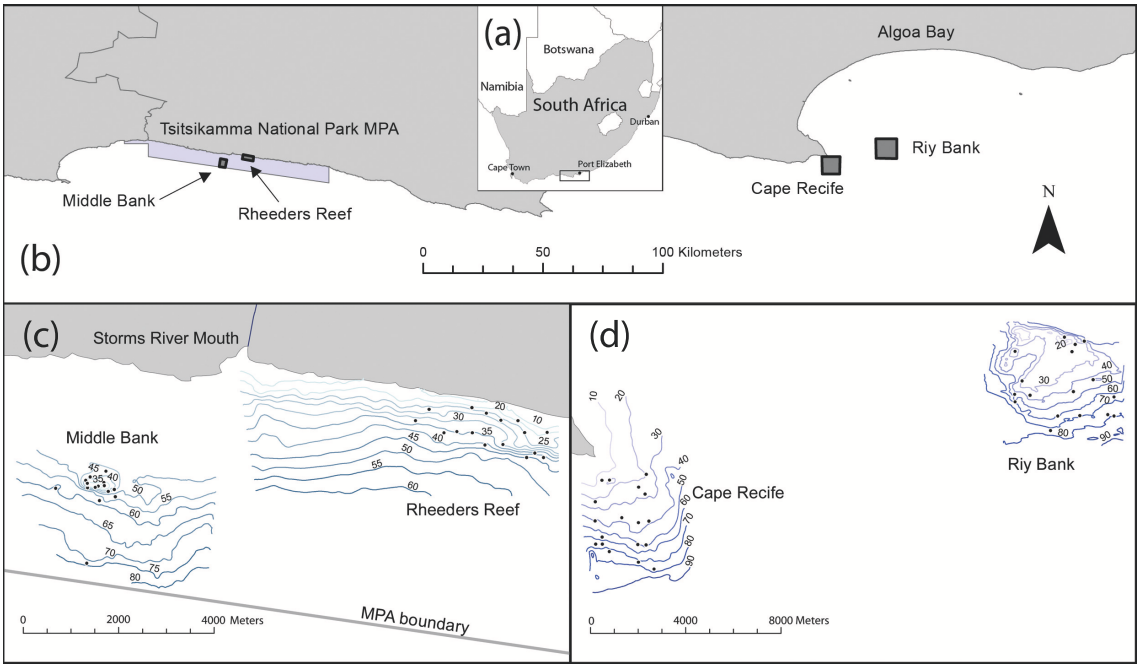


Figure 2.2: A map of South Africa indicating (a) the location of Tsitsikamma National Park marine protected area (TNP MPA) and Algoa Bay (AB), (b) the location of the nearshore and offshore reef complexes within each of the two study areas, and (c, d) bathymetric maps of the two study areas indicating the location and depth of each sampling point.

arated by approximately 10 km of sandy bottom. Within each reef complex, 16-18 sites were stratified across the depth range of available reef in order to adequately represent variation in depth and habitat type (Table A1).

2.2.2 Fish community sampling

Sampling took place during the austral winter months of July 2014 and April 2015 in TNP MPA and Algoa Bay, respectively. In order to sample the full range of available reef habitat, data on reef fish abundance and community composition were collected via baited remote underwater stereo-video systems (stereo-BRUVs). Each system consisted of a pair of high-definition digital camcorders (models Sony HDR-PJ430E and Canon Legria HF-M56) mounted 0.7 m apart within waterproof housings on a stainless steel frame. All systems were fitted with a blue LED light to illuminate the field of view. A perforated PVC container holding 800 - 1000 g of crushed pilchard *Sardinops sagax* was suspended 1.5 m in front of the cameras. Although the use of a bait attractant is known to introduce bias by attracting carnivores and under-representing herbivores, it has been shown to improve the precision of count data and thus provides one of the most efficient methods of surveying the entire fish community (Bernard & Götz 2012; Harvey et al. 2007). Four stereo-BRUVs were deployed consecutively by boat to improve sampling efficiency and then left to film on the seabed for at least 60 minutes. Previous studies have recommended deployment times of 60 minutes to comprehensively survey the warm-temperate reef fish communities (Bernard & Götz 2012; Watson 2006). The geographical coordinates of each stereo-BRUV deployment were recorded by a global positioning system (GPS) receiver. To minimise the overlap of bait plumes and movement of fish between adjacent sites, concurrent deployments were separated by at least 250 m.

Seven attributes were recorded during each replicate stereo-BRUVs deployment (see Table 2.1): (1) Reef type; (2) bottom type; (3) depth; (4) water temperature; (5) water visibility; (6) % visible reef; (7) % obstruction: Reef type was assigned to sites on the basis of whether sites were nested within a nearshore reef (TNP

MPA: Rheeders Reef; Algoa Bay: Cape Recife) or within an offshore reef (TNP MPA: Middle Bank; Algoa Bay: Riy Banks). Six bottom type classifications were inferred from video footage to provide a broad measure of habitat type and complexity (see Table: 2.1). Habitat depth, determined from the boat's echo sounder, provided a proxy for the site's average abiotic conditions (e.g. temperature, light availability, productivity) and turnover in the macrobenthic community (Heyns et al. 2016; Heyns-Veale et al. 2016). The average in-situ water temperature during the deployment was recorded by a submersible temperature logger (Onset HOBO Pro v2) mounted to the stereo-BRUVs frame. In TNP MPA (n = 32), the loss of one temperature logger resulted in seven missing temperature values, spread over several days of sampling. The missing temperature values were approximated to be equal to deployments taken on the same day at similar depth. Water visibility was inferred from the video footage once the system had settled on the seabed by measuring the maximum distance at which all species remained identifiable. The percentage of visible reef within the field of view and the percentage occupied by obstructions took into account sampling artefacts which contributed to observation error.

2.2.3 Video analysis

At the beginning and end of each field trip, stereo-BRUVs were calibrated using the software CAL v2.11 (www.seagis.com.au) according to the procedures detailed in Harvey & Shortis (1995, 1998). This allowed the visible area to be estimated by recording the maximum distance in front of the camera at which fish could accurately be identified under different water visibilities (Harvey et al. 2013, 2002). Upwelling events are common in the warm-temperate waters of the Agulhas Ecoregion and can lead to high temporal variability in water visibility and water temperature. Consequently, samples with a visibility of less than 1.5 m and fish that occurred beyond 5.0 m were excluded from analyses.

The software EventMeasure v4.42 (www.seagis.com.au) was used to annotate

Table 2.1: Site variables recorded during each of the 67 stereo-BRUVs deployments

Variable	**Description**	
Reef type	Nominal:	Inshore; Offshore
Bottom type †	Nominal:	Sand; Sand-inundated reef; Patch-reef low; Reef low; Patch-reef high; Reef high
Depth (m)	Quantitative:	continuous
Water temperature (°C)	Quantitative:	continuous
Visibility (m)	Quantitative:	continuous
% Visible reef	Quantitative:	percentage
% Obstruction	Quantitative:	percentage

† Bottom type classification:
1) Sand; 100% sand
2) Sand inundated reef; reef covered by a thin layer of sand
3) Patch-reef low; mosaic of sand and reef, with visible reef varying by < 1 m in height
4) Reef low; 100% reef varying by < 1 m in height
5) Patch-reef high; mosaic of sand and reef, with visible reef varying by > 1 m in height
6) Reef high; 100% reef varying by > 1 m in height

video footage and record the identity of species and number of individuals sampled. Video analysis commenced once the stereo-BRUVs had settled on the seabed. The focus of this study was on patterns of biodiversity which were representative of resident reef fishes which are known to share a similar capacity for dispersal and might reasonably be expected to interact. Consequently, all analyses were limited to data from the sparid family (Sparidae) with fishes identified to the lowest possible taxonomic level, which was species. For each species, the maximum number of individuals seen within any single frame of the 60 minute recording was recorded as a measure of its relative abundance (MaxN). MaxN avoids repeated counts of the same individual leaving and re-entering the frame. It is considered a conservative estimate of relative abundance, particularly in communities where fish occur in high densities (Cappo et al. 2003, 2004). A schooling sparid (strepie *Sarpa salpa*) was excluded from all analyses as it was only recorded at six sites and included MaxN counts that ranged from a single individual to schools exceeding 100 individuals.

2.2.4 Additive partitioning of diversity across spatial scales

The total measured species diversity (γ) within a set of samples and represented by species richness or abundance-based Shannon diversity was additively partitioned into the average diversity within samples (α) and the average differentiation among samples (β) (see Lande 1996). $\gamma_i = \alpha_i + \beta_i$, for a particular sampling level i. The average β-diversity among samples was then estimated as $\beta_i = \gamma_i - \alpha_i$. This approach was extended across hierarchical sampling scales $i = 1, 2, 3 ... m$, where $i = 1$ represented individual stereo-BRUVs samples (i.e. sites) nested within $i = 2$, and $i = 2, 3, m$ represented stereo-BRUVs samples pooled at the habitat, reef, and location scale, respectively. The habitat scale divided samples within a given reef into two relative depth strata (i.e. habitat) on the basis of whether sites were shallower or deeper than the median sample depth of that reef. Given that $\beta_m = \gamma - \alpha_m$ at the highest sampling scale m (location) can be generalised at each lower sampling scale i as $\beta_i = \alpha_{i+1} - \alpha_i$, the additive partition of diversity across all sampling scales was calculated as

$$\gamma = \alpha_1 + \sum_{i=1}^{m} \beta_i$$

Additive partitioning of diversity ensures that alpha and beta diversity add up to gamma diversity, allowing partitions to be directly compared (Lande 1996). Total diversity (γ) was expressed as the proportional contribution of diversity at each hierarchical sampling scale: α_1: average local site diversity; β_1: differentiation among sites within habitats; β_2: differentiation among habitats within reef complexes; β_3: differentiation among reef complexes within locations; β_4: differentiation among locations.

Given that D_{ij} is the diversity metric recorded for each sample $j = 1, 2, 3 ... n_i$, and n_i is the number of samples within each sampling scale i, the average diversity (α_i) was weighted (following Crist et al. 2003) by the proportional abundance of individuals (q_{ij}) within each sample j of sampling scale i:

$$\alpha_{\mathrm{i}} = \sum_{j=1}^{n_i} D_{ij} q_{ij}$$

2.2.5 Individual-based randomisation tests

Observed α- and β-diversity components at each hierarchical sampling level were compared to expected values generated by a null model in which individual fishes were randomly assigned to samples at the lowest sampling scale (e.g. $i = 1$) from the next-higher scale (eg. $i = 2$) while preserving the original species-abundance and sample-size distributions (Crist et al. 2003). This null model assumes that individual fish colonise habitat patches independent of location and the presence or absence of other fishes. After each randomisation, diversity components were calculated across hierarchical scales by pooling samples from lower sampling scales. As calculated diversity partitions were weighted by sample abundance (q_{ij}) randomisations were relatively robust to variations in the number of individuals recorded. Null distributions for α and β components at each scale of the sampling hierarchy were generated by 999 randomisations of the community data. The proportion of null values greater or smaller than the observed value was used to calculate the probability (p-value) that an observed diversity component was greater or smaller than could be obtained if individuals were randomly distributed within a given hierarchical scale (Gotelli & Graves 1996). This approach allowed insights to be gained about the roles of environmental variation and spatial separation in generating non-random sparid community structure across hierarchical spatial scales.

2.2.6 Intraspecific aggregation

The Morisita Index ($\mathrm{I_M}$) (Morisita 1959, 1962, 1971), which quantifies the dispersion of individuals, was used to test whether the difference between observed and

expected diversity partitions could have arisen due to the non-random spatial aggregation of conspecifics. More specifically, it compares the likelihood that two individuals chosen at random from the population will be from the same sample compared to a population in which individuals are randomly distributed amongst samples:

$$I_{\mathrm{M}} = n\left[\frac{\sum x_j^2 - \sum x_j}{(\sum x_j)^2 - \sum x_j}\right]$$

where n represents the number of sampling sites and x_j equals the number of individuals in sample j = 1, 2, 3 ... n. When rescaled to vary between -1 and 1 (Smith-Gill 1975) using the critical values from a chi-square distribution with n - 1 degrees of freedom, the standardised Morisita Index ($\mathrm{I_{Mstd}}$) is expressed as a likelihood ratio where values > 0 indicate that conspecific abundance is aggregated (i.e. underdispersed), values < 0 indicate a regular (i.e. overdispersed) arrangement in space, and values of -0.5 and 0.5 represent 95% confidence limits around the mean of a randomly dispersed distribution (Veech 2005). Mean values of the index were calculated at each sampling scale for non-singleton species and compared to expected values generated by 999 individual-based randomisations (see 2.2.5).

2.2.7 Spatial variables

Space can either be considered as a factor responsible for ecological patterns, or as a confounding variable which inhibits the interpretation of other processes of interest. A number of methods have been proposed for explicitly incorporating spatial information into ecological models: Legendre & Troussellier (1988) used Mantel and partial Mantel tests with a matrix of geographic distances to explore the spatial structure of ecologial data. Multiple spatial structures have been modelled simultaneously by including geographic coordinates as well as all terms of a polynomial or trend-surface equation as explanatory variables within a linear modelling framework (Borcard & Legendre 1994; Borcard et al. 1992; Legendre 1990). The inclusion of

quadratic and cubic terms of the coordinates and their interactions allows linear gradients in species distributions as well as more complex patterns, such as patches to be detected. Trend-surface analysis is however limited to the identification of coarse spatial structures that can be represented by simple shapes (eg. planes, parabolas or saddles); attempting to model finer structures rapidly leads to over-parameterisation (Borcard & Legendre 2002). Other shortcomings stem from the correlation between spatial variables leading to a lack of statistical independence and the arbitrary choice of degree for the polynomial function (Dray et al. 2006).

A more recent spatial eigenfunction approach, principal coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002; Borcard et al. 2004), identifies and quantifies spatial structures across various scales and addresses many of the shortcomings associated with trend-surface analysis; a set of eigenvectors is generated by principle coordinate analysis (PCoA) from a truncated matrix of geographic distances between sampling sites. Because eigenvectors are orthogonal and therefore linearly independent they can be employed as spatial variables to represent distinct spatial patterns at multiple scales. Dray et al. (2006) demonstrated that the positive and negative eigenvalues produced by the PCNM approach are linearly related to Moran's index of spatial autocorrelation, and thus respectively represent the strength of positive or negative spatial autocorrelation. Eigenvectors associated with the highest eigenvalues correspond to the broadest scales of spatial variability (e.g. global trends), while eigenvectors with eigenvalues closer to zero capture fine-scale trends (e.g. local patchiness) (Griffith & Peres-Neto 2006).

Moran's eigenvector maps (MEMs; Dray et al. 2006) provide a generalised framework within which to generate a variety of orthogonal spatial variables (eigenvectors), of which PCNMs are a particular case. Moran's eigenvector maps are derived from a spatial weighting matrix $\mathbf{W}=[w_{ij}]$ which is defined as the Hadamard (element-wise) product of a connectivity matrix $\mathbf{B}=[b_{ij}]$ by a weighting matrix $\mathbf{A}=[a_{ij}]$. The connectivity matrix $\mathbf{B}$ is binary, with sites i and j defined as either neighbours (1) or non-neighbours (0). Whereas PCNM classifies two sites as neighbours if their

euclidean distance (d_{ij}) is less than the longest distance (t) required to connect all sites by a minimum spanning tree algorithm, MEM generalises this approach by allowing the connectivity matrix to be defined by a variety of connectivity schemes (e.g. Delaunay triangulation, Gabriel graph, relative neighbour, sphere of influence and distance threshold) (see Fortin & Dale 2005; Legendre & Legendre 1998). The PCNM approach weights the connection between neighbours using the function $1 - (d_{ij}/4t)^2$. In the MEM approach, the spatial weighting matrix **W** can be modified by assigning different weighting functions **A** to various types of connections **B** to relate the strength of the spatial process (e.g. dispersal) to various spatial structures (i.e. the neighbourhood).

The distribution of sites within TNP MPA and Algoa Bay deviated from that of a regular sampling design. In such cases, the choice of spatial weighting matrix **W** becomes a critical step, which can greatly influence the outcome of spatial analyses. In the absence of a clear theoretical justification for the form of the spatial weighting matrix, this study adopted the recommendations of Dray et al. (2006) and employed a data-driven approach to test the relative performance of various connectivity schemes and weighting functions. A bias-corrected multivariate analogue of the Akaike Information Criterion (AIC_c; Burnham & Anderson 2002; Godinez-Dominguez & Freire 2003) was used to select from competing spatial models. Due to the linear relationship between MEMs and Moran's I, this approach results in the selection of spatial variables (eigenvectors) which maximise Moran's index of spatial autocorrelation in the response variable.

In order to generate a set of orthogonal spatial variables (MEMs), neighbourhood relationships within locations were first defined by five different connectivity schemes: Delaunay triangulation (del), Gabriel graph (gab), relative neighbour (rnb), sphere of influence (soi) and minimum spanning tree (mst). Based on the neighbourhood relationship, sites were defined as either neighbours (1) or non-neighbours (0). To model the processes of spatial autocorrelation decaying with distance, spatial weights were assigned to neighbourhood links by evaluating three de-

creasing monotonic functions (sensu Dray et al. 2006): linear ($f_1 = 1 - d_{ij}/max(d_{ij})$), concave-down ($f_2 = 1 - (d_{ij}/max(d_{ij}))^a$), and concave-up ($f_3 = 1/(d_{ij})^b$). Following the approach of (Caruso et al. 2012), a sequence of integers between 1 and 10 were considered as parameter values for a and b, where the case of $a = 1$ in f_2 is equivalent to a linear weighting function, thus making f_1 redundant. Alternative sets of spatial variables (MEMs), each represented by a spatial weighting matrix, were generated by combining the five binary connectivity matrices (del, gab, rnb, soi and mst) with alternative weighting functions f_2 and f_3. An additional spatial weighting matrix created using the original PCNM approach of Borcard & Legendre (2002) (pcnm) was also included. Community abundance data (the response matrix) were Hellinger transformed to reduce the influence of rare species and shared absences (Legendre & Gallagher 2001). Because MEM analysis is inefficient in modelling linear spatial trends, community abundance data were detrended by multiple linear regression on X and Y geographical coordinates to remove the effects of linear gradients. (see Borcard & Legendre 2002, for details). The best spatial weighting matrix and subset of MEMs to be used in the final spatial model were selected by identifying the model with the lowest AIC_c score. This model included the subset of spatial variables which maximised spatial autocorrelation in the multivariate response variable.

2.2.8 Environmental variables

Processes directly related to species' niche requirements were summarised as a matrix of local environmental factors (Table: 2.1). Reef type, bottom type, and depth were considered as local environmental factors potentially related to species-specific distribution patterns. The six bottom type classifications were treated as an unordered (nominal) categorical variable and encoded as dummy variables. Although in-situ water temperature was measured during the deployments, it was excluded from the analysis due to its strong correlation with depth. Depth was considered as a more meaningful measure of the average long-term water temperature experienced by resident fishes. Depth was standardised to have a mean of zero and a standard

deviation of one (ie. z-transformed) prior to the analysis. The most parsimonious environmental model to be used subsequently in variation partitioning analyses was constructed using redundancy analysis (RDA; Legendre & Legendre 1998) and a forward selection procedure (Monte Carlo permutations = 999) to retain only the most important variables (Blanchet et al. 2008). The adjusted R^2 of the full environmental model and an alpha level of 0.05 were used as stopping criteria: In other words, environmental variables were only selected if they improved the adjusted R^2 of the model and were found to be significant ($p < 0.005$). To avoid inflated Type I error rates, forward selection was only applied if the global RDA model which included all environmental variables was found to be significant.

2.2.9 Variation partitioning of community abundance data

The relative contribution of local niche processes and dispersal processes to compositional turnover in the sparid community was disentangled using RDA and partial RDA (pRDA), followed by variation partitioning analysis (Borcard et al. 1992; Legendre & Legendre 1998). This was used to quantify the relative contribution of environmental and spatial variables to variation (adjusted R^2) in community composition (using relative abundance data). When both species and the environment independently display spatial structure, as is usually the case in most reef environments, controlling for variation in space is needed to avoid inflated Type-I error rates in tests of species-environment relationships (Peres-Neto & Legendre 2010). It therefore becomes important to distinguish between confounded spatial (S) and confounded environmental (E) effects, and pure spatial (S | E) and pure environmental (E | S) effects. After correcting for covariance in the spatial component (S), a significant fraction of total community variation explained by the environmental component (E | S) can be interpreted as niche-driven turnover in the species composition of communities (i.e. species sorting). Similarly, after accounting for covariation in the environmental component (E), a significant effect of spatial structure (S | E) can be seen as evidence of either dispersal limitation (low dispersal) or

homogenising dispersal (high dispersal). The significance of different components was tested (via RDA and pRDA) using a Monte Carlo permutation procedure (n = 999); the significance of the shared component of spatially structured environmental variation (S ∩ E) - the intersection between (S) and (E) - could not be tested statistically. An important caveat of this approach is that all environmental variables relevant to local community structure have been measured (Cottenie 2005).

To account for the two hierarchical spatial scales within this study (between-location and within-location), dispersal processes within locations were represented by spatial variables (from MEM) describing the spatial configuration of sites within individual locations (S: 100's of m - 10's of km); following the approach of Declerck et al. (2011) and Viana et al. (2015), the identity of the two locations was modelled using a dummy variable. Spatial variables (S) were represented by MEMs which generated individually for each location using the aforementioned (see 2.2.7) data-driven approach of Dray et al. (2006); MEMs were arranged in blocks according to their location to form a staggered matrix representing the spatial relationships among sites within their respective locations.

Variation partitioning was applied separately to RDA and pRDA models at both between-location scales and at within-location scales. This allowed the confounded and unique contributions of the local environmental variables (E) and spatial variables (S), and the shared effect of spatially structured environmental variation (S ∩ E) to be quantified. For the between-location analysis (n = 67), the spatial effect (L) was modelled using location as a dummy variable to highlight compositional differences between communities at the broadest spatial scale. A similar approach was applied for the within-location analysis (n = 67): Here, both the spatial components within locations (S) and the location effect (L) were included to examine spatial processes operating within locations while accounting for between-location differences. To further elucidate the processes structuring sparid communities at the within-location scale, and to control for the possible effects of biogeographic and management differences, TNP MPA (n = 32) and Algoa Bay (n = 35) were also

analysed individually using the aforementioned approach. Analyses were performed on Hellinger transformed community abundance data as this has been shown to provide unbiased estimates of variation partitioning based on RDA (Peres-Neto et al. 2006). Multivariate analyses were performed in R version 3.1.2 (R Core Team 2014) using the vegan (Oksanen et al. 2015), packfor (Dray et al. 2013) and spacemakeR packages (Dray et al. 2006).

2.3 Results

In total, 67 stereo-BRUVs which were deployed across the available depth range of two reefs, each, within TNP MPA and Algoa Bay (Table A1), recorded a total of 4,753 fishes comprising 61 species from 24 families of reef-associated ichthyofauna (summarised in Table A2-5). Of these fishes, 3,588 were represented by 22 species in the family Sparidae [1].

2.3.1 Diversity partitioning

The partitioning of total species richness into its additive components (α_1, β_1, β_2, β_3, and β_4; Fig. 2.3a) revealed that the within- (α_1) and among-site (β_1) scales accounted for 42% and 33% of the total sparid diversity (γ), respectively. Species richness within sites was lower than expected ($p < 0.001$) and associated with higher than expected species turnover ($p < 0.001$) between Algoa Bay and TNP MPA (α_1 and β_4; Fig. 2.3a). On the other hand, the observed differentiation among sites (β_1), between deep and shallow habitats (β_2), and between reefs (β_3) did not deviate from random expectation (Fig. 2.3a).

The largest fraction (73%) of total Shannon diversity (γ) was observed at the smallest sampling scale (α_1). This was followed by 20% among sites (β_1; Fig. 2.3b). Local within-site diversity (α_1) made a larger contribution to Shannon diversity than it did to species richness, but was also significantly lower ($p < 0.001$) than the null

[1] Excluding the schooling species strepie *Sarpa salpa*

expected values in which individuals were randomly assigned to sites. In contrast to the species richness components, all β_{Shannon} components, which also take into account the evenness with which species' abundances are distributed, showed larger values than expected by chance ($p < 0.001$; Fig. 2.3b). The differentiation of diversity among sites nested within the same habitat (β_1) contributed disproportionately to lower than expected levels of within-site diversity (α_1; $p < 0.001$).

These results indicated that while species appeared to be randomly dispersed within a given location, species richness of local communities was most strongly influenced by the absence of some species from locations separated by $\sim$ 200 km. On the other hand, measures of compositional turnover indicated that non-random metacommunity structure largely resided at the smallest spatial scales (i.e. among sites within the same reef).

2.3.2 Intraspecific aggregation

Observed means of the standardised Morisita index (I_{Mstd}) were significantly larger ($p < 0.001$) than expected by chance across all scales, indicating that conspecifics were more aggregated than null model distributions in which individual fish randomly colonised sites (Fig. 2.4). The high degree of intraspecific aggregation corresponded to significantly lower levels of α-diversity and enhanced levels of β-diversity for locations in tests of species richness components (see Fig. 2.3a) which used the same null hypothesis that individual fish colonise local habitat patches independently of their location and the presence or absence of other fishes. It also corresponded to disproportionately lower levels of α-diversity and enhanced levels of β-diversity for sites in analogous tests of nonrandom Shannon diversity components (see Fig. 2.3b).

2.3.3 Variation partitioning

Between-location results

Variation partitioning analyses of species' relative abundances revealed that location identity (L) explained 11.1% (adjusted R^2) of the total variation in species compo-

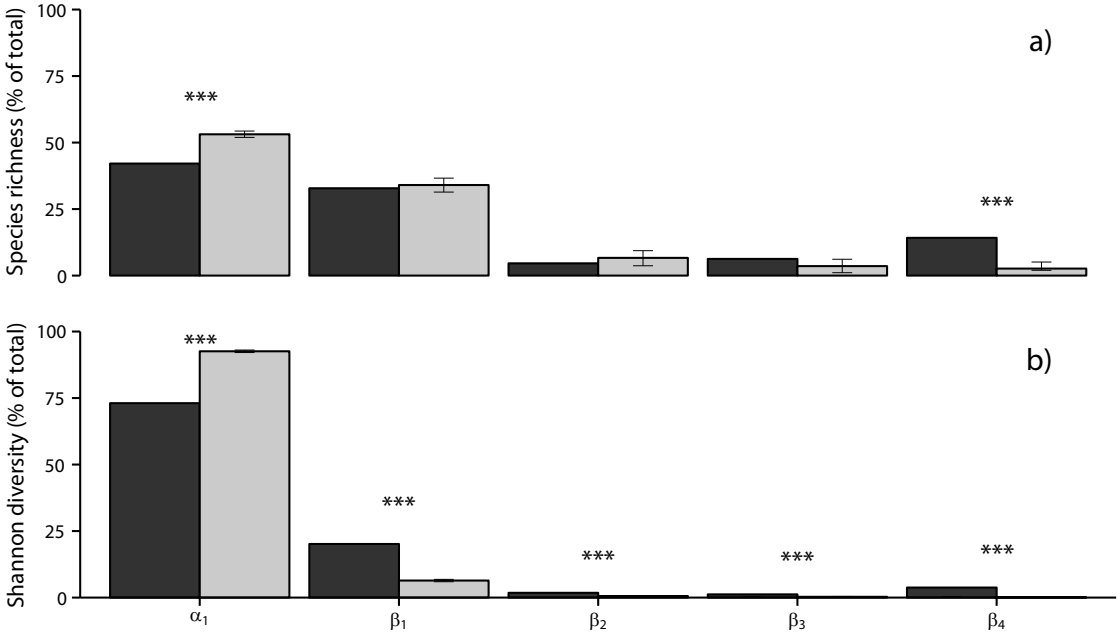


Figure 2.3: Additive diversity partitioning of species richness (a) and Shannon diversity (b) across four nested sampling scales. Values are expressed as the percentage of the total sparid diversity ($\gamma = 22$ species) explained by each hierarchical scale. Observed values (black) are compared to mean expected values (grey) generated by 999 individual-based randomisations. (***) $p < 0.001$; (**) $p < 0.05$; (*) $p < 0.1$. α_1: local site diversity; β_1: β-diversity among sites; β_2: β-diversity among habitats; β_3: β-diversity among reefs; β_4: β-diversity among locations. Error bars represent 95% confidence intervals around the mean of randomised values.

sition (L in Table 2.2a). After correcting for the effect of environmental differences between locations, location identity (L | E) accounted for 10.1% of compositional variation. Environmental heterogeneity was responsible for 32.0% and 33.0% of compositional variation, even after location identity had been accounted for (E and E | L in Table 2.2a, respectively). The most parsimonious environmental model obtained by forward selection included depth, reef type (inshore vs offshore), high profile reef and sandy bottom as variables (Table 2.3). The negligible size of the shared fraction among the location and environmental components indicated that very little of the community variation caused by the location was due to differences in the extent of sampled reef habitat. Nevertheless, biogeographic differences between locations remain confounded by the fact that TNP MPA has been protected from fishing since 1964 while Algoa Bay continues to be heavily exploited.

Table 2.2: Variation partitioning of warm-temperate sparid communities at two spatial scales using RDA and partial RDA on Hellinger transformed relative abundance data. E: environmental model component; S: spatial model component, derived from MEM variables; L: model component representing TNP MPA and Algoa Bay locations; E | [S+L]: pure environmental component corrected for location identity and spatial patterns within locations; S | [E+L]: pure spatial component corrected for location identity and environmental patterns within locations. $_{adj}R^2$ (%): percentage variation in community composition explained by model; $Df_{model, res}$: model and residual degrees of freedom; p-value: significance value generated by Monte Carlo permutation test (n = 999).

	Source	$_{adj}R^2$ (%)	$Df_{model, res}$	p-value
a) Between-location scale (n = 67)				
	E [a]	33.0	4, 62	0.001
	L	11.1	1, 65	0.001
	E | L	32.0	4, 61	0.001
	L | E	10.1	1, 61	0.001
b) Within-location scale (n = 67)				
	E [a]	33.0	4, 62	0.001
	S	10.7	7, 59	0.001
	L	11.1	1, 65	0.001
	E | [S+L]	29.0	4, 54	0.001
	S | [E+L]	9.2	7, 54	0.001
c) Locations				
Algoa Bay (n = 35)				
	E [b]	44.9	2, 32	0.001
	S	13.2	3, 31	0.008
	E | S	42.9	2, 29	0.001
	S | E	11.2	3, 29	0.001
TNP MPA (n = 32)				
	E [c]	27.4	3, 28	0.001
	S	14.8	4, 27	0.001
	E | S [†]	29.8	3, 24	0.001
	S | E [†]	17.2	4, 24	0.001

[a] Depth, Offshore, Sand, Reef High
[b] Depth, Patch-reef Low, Sand
[c] Depth, Offshore, Sand
[†] Unique fractions calculated as greater than their confounded counterparts due to the subtraction of the negative $_{adj}R^2$ value (-2.4 %) of the S ∩ E component (see text for details).

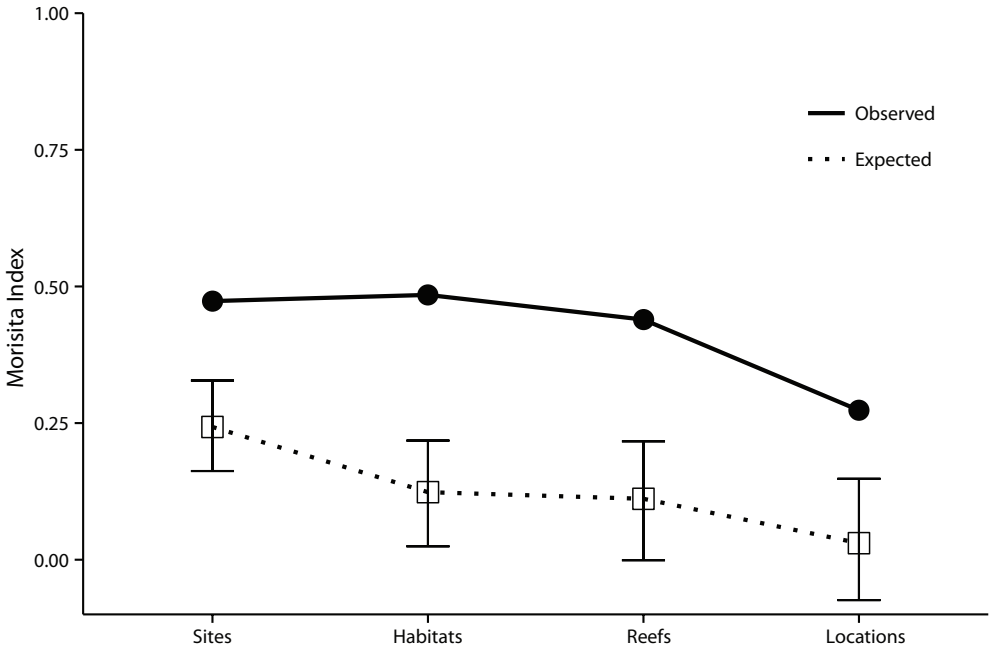


Figure 2.4: Intraspecific aggregation of sparid species across sampling levels. The mean values of the standardised Morisita index (I_{Mstd}) of aggregation for the observed data (solid line) are compared with the mean expected values (dashed line) generated under the null model from 999 randomisations. Values < 0 indicate species are more overdispersed than random, and values > 0 suggest an aggregated distribution. Both observed and expected values were calculated as means of the standardised Morisita index for individuals from non-singleton species. Error bars represent 95% confidence intervals around the mean of randomised values.

Within-location results

Within locations, the spatial variables (MEMs) selected to best explain location-specific patterns of spatial autocorrelation among local sparid communities showed significant trends at both broad (eg TNP MPA: MEM2; MEM3 and Algoa Bay: MEM3) and fine spatial scales (eg TNP MPA: MEM10; MEM16 and Algoa Bay: MEM6; MEM12) at the within-reef scale (Fig. 2.5 and Table A8). Notably, patterns of spatial autocorrelation were confined to areas of spatially contiguous reef habitat (i.e. the within-reef scale); there was no significant spatial turnover between reefs. Regression (RDA) of selected MEMs against the linearly detrended community abundance data explained 12.4% ($p = 0.001$) of the total variance in the sparid community across both locations, with the first two significant canonical axes (RDA1 and RDA2, both $p < 0.002$) capturing 9.7% of the total variance. Multiple

regressions of the two significant canonical spatial axes against the full set of measured environmental variables confirmed that the spatial structure captured by both axes was independent of any local environmental variation (RDA1 and RDA2, both $p > 0.1$). The exclusive environmental model (E | [S+L]) comprised of forward selected environmental variables (depth, offshore reef type, high profile reef and sandy bottom, Table 2.3) and corrected for the conditional effects of location identity and within-reef spatial structures accounted for 29.0% of the compositional variation in the sparid community (Table 2.2b). The confounded (S) and exclusive spatial model components (S | [E+L]) had smaller, but significant relative contributions of 10.7% ($p < 0.001$) and 9.2% ($p < 0.001$), respectively (Table 2.2b).

Location-specific results

Similar results emerged when variation partitioning analyses were applied to each location individually; there was both significant environmental (E | S) and spatial (E | S) structure in the sparid metacommunity (Table 2.2c): The confounded (E) and exclusive environmental components (E | S) had a greater contribution to variation in sparid community composition than the spatial components (both S and S | E), with contribution of spatially structured environmental features (S ∩ E) being negligible (2.0%) or absent (-2.4%) in Algoa Bay and TNP MPA, respectively. Compositional variation in Algoa Bay was however found to be more strongly driven by the spatially confounded (E) and exclusive environmental (E | S) components than in TNP MPA. While the effect of depth alone explained the majority of the environmentally-driven community variation in Algoa Bay, depth and reef type (inshore versus offshore) both made more substantial contributions to the explanatory power of the environmental model within TNP MPA (Table 2.3).

2.4 Discussion

The adopted sampling design allowed the relative contribution of niched-based species sorting and dispersal limitation to compositional variation among of local sparid

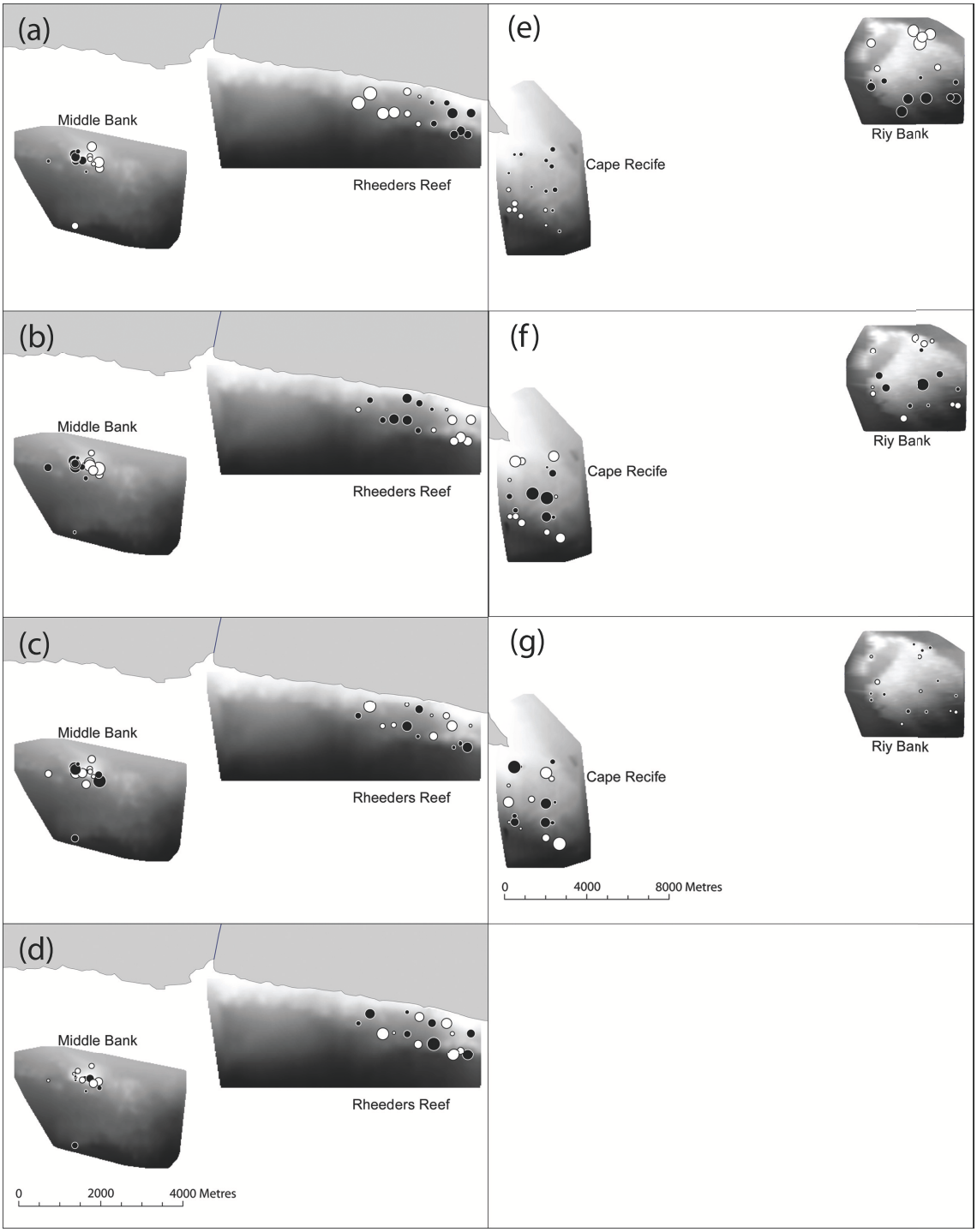


Figure 2.5: Significant Moran's eigenvectors selected to best model spatial autocorrelation in the multivariate distribution of sparid fishes in the TNP MPA (a - d: MEM2; MEM3; MEM10; MEM16) and in Algoa Bay (e - g: MEM3; MEM6; MEM12). Black and white circles correspond to positive and negative values, respectively, while the magnitude is proportional to the size of the circles. Contrasting values can be interpreted as turnover in the community composition between sites, where white circles of similar size represent similar communities and vice versa. Selected spatial variables (MEMs) were those that maximised spatial autocorrelation of community composition within a location (see Table A8 for details). Selected spatial variables reflect processes occurring within individual reef complexes rather than between nearshore and offshore reefs.

Table 2.3: Combinations of selected environmental variables for each globally significant environmental RDA model ($p < 0.05$). Variables are presented in order of importance according to the forward selection procedure of Blanchet et al. (2008).

	Variable	$_{adj}R^2$Cum (%)	F	p-value
All locations (n = 67)				
	Depth	22.6	20.27	<0.001
	Offshore	25.6	3.57	0.001
	Sand	28.2	3.35	0.002
	Reef high	30.0	2.61	0.009
Algoa Bay (n = 35)				
	Depth	42.1	25.70	<0.001
	Patch-reef low	44.9	2.69	0.030
	Sand	46.5	1.95	0.071
TNP MPA (n = 32)				
	Depth	16.6	7.16	<0.001
	Offshore	23.8	3.83	0.001
	Sand	27.4	2.44	0.024

Abbreviations: $_{adj}R^2$Cum (%): adjusted cumulative coefficient of multiple determination; F: F-test statistic; p-value: significance value generated by Monte Carlo permutation test (n = 999).

communities to be investigated. It was also possible to identify the spatial scales at which alternative processes were most likely to prevail. The hierarchical analysis of sparid reef fish diversity revealed that, in terms of species richness, limited alpha diversity at the smallest spatial scale (the local habitat patch) coincided with higher than expected turnover of species between locations. When the spatial scales within reefs were considered, turnover in the number of species conformed to that of a null distribution in which individual fishes colonised local habitat patches independently of their location and the presence or absence of other fishes. This suggests that the intrinsic characteristics of local habitat patches do not impose a significant barrier to occupancy of species whose larvae sufficiently disperse to a location. Rather, differences in species richness arise from the failure of transient species to recruit within a location. When patterns of relative abundance were taken into account, β-diversity

was enhanced at all spatial scales. However, this was most pronounced at the smallest spatial scales - i.e. among sites situated within the same reef. Nonrandom turnover among communities was partly attributed to the aggregated distribution of conspecifics and was particularly evident at spatial scales which favoured the post-settlement movement of fishes (i.e. the within-habitat and within-reef scales). Although conspecific aggregations limit the diverity of species can locally coexist, the spatial partitioning of habitat among species reduces the strength of interspecific competition for shared resources and thereby provides a mechanism whereby species diversity at broader spatial extents can be enhanced (Belmaker et al. 2008; Crist et al. 2003; Veech 2005). The ability of recently-settled juveniles and established adults to disperse to and colonise the most favourable habitat patch is limited by the supply of suitable living space which is often generated by unpredictable events (e.g. predation, disturbance). Due to their limited potential for post-settlment dispersal, the ability of fish to colonise adjacent habitat patches was expected to be limited by spatial proximity and include a significant stochastic component. The greater contribution of the environmental component, which was mainly related to depth, indicated that niche processes played a more important role than dispersal limitation in determining the assembly and dynamics of both protected and exploited sparid communities. Despite most sparids being able to recruit to the reef as juveniles, species sorting along the depth gradient was the most prevalent driver of relative species abundance. This suggests that fish may adequately disperse to reefs, they regularly fail to establish within different reef habitats due to the constraints which are imposed by strong environmental gradients (e.g. average water temperature, productivity). Furthermore, significant patterns of spatial autocorrelation in community composition (represented using MEMs) suggest that the high rates of compositional turnover (i.e. β-diversity) within reefs were also promoted by the limited ability of species to actively disperse to the most favourable habitats.

In the context of the metacommunity framework (Leibold et al. 2004; Winegardner et al. 2012), the results of this study suggest that species sorting is the

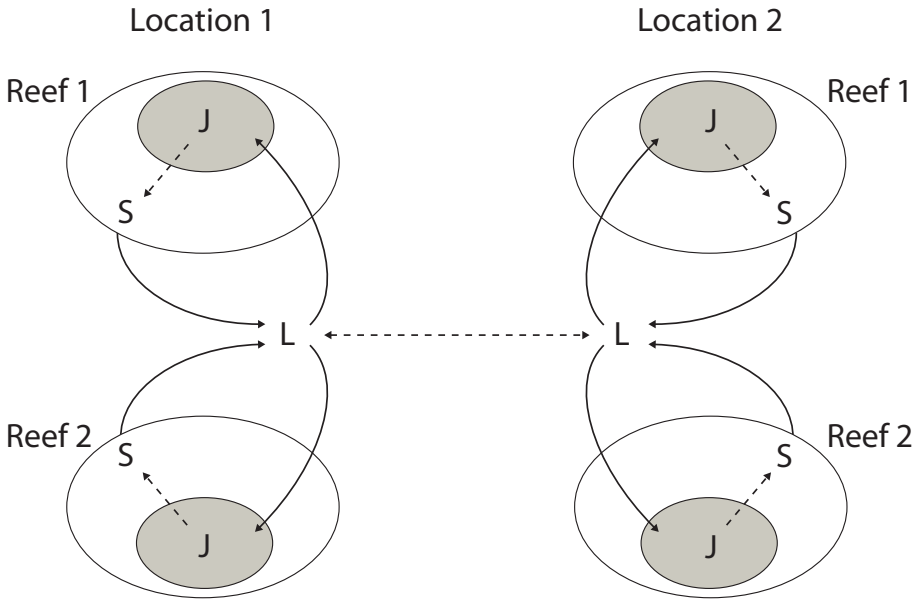


Figure 2.6: Conceptual diagram of the possible arrangement of shallow-water nursery habitat (shaded) relative to deeper reef habitat in TNP MPA and Algoa Bay (adapted from Kritzer & Sale 2010). Nursery habitat within a reef system allows metapopulation structure to exist by preserving a spatial link between the local production of larvae (L) by the adult spawner population (S) and the recruitment of juveniles (J) back to that spawning population. This is, however, contingent on a sufficient degree of self-recruitment necessary for local populations to maintain a degree of demographic independence together with some replenishment from distant reefs. Arrows represent the strength and direction of dispersal between populations. Arrows correspond to either unidirectional (single-headed arrows) or bidirectional movements (double-headed arrows). Solid arrows show a high rate of dispersal whereas dashed arrows indicate limiting dispersal.

predominant driver of high levels of *beta*-diversity among habitat patches separated by 100's - 1000's of m contiguous reef. This was supported by the large contribution of local environmental variation to community compositional variation which mostly related to turnover in depth-related habitat conditions over relatively small spatial scales. Small-scale habitat characteristics (e.g. among transects) appear to be one of the most important drivers of metacommunity structure among shallow-water ($<$ 20 m depth) fishes, both in tropical coral reefs (MacNeil et al. 2009) and on temperate rocky reefs (Anderson & Millar 2004). MacNeil et al. (2009) found that for dispersal potential had a limited role in contributing towards nonrandom patterns of diversity among most tropical reef fishes; however, less specialised functional groups, such as grazers and detritivores, which are less dependent on habitat diversity, were

more prone to be governed by variable dispersal rates. Sparids lack the specialised resource requirements typical of many tropical reef fishes, and may, therefore be expected to more strongly respond to regional spatial processes (Pandit et al. 2009). While this may be true on shallow-water reefs surveyed by UVC, the habitat characteristics on subtidal reefs sampled via stereo-BRUVs extended across a much greater depth range (13 - 76 m depth; Table A1): In TNP MPA, the changes to average abiotic conditions (e.g. light intensity, temperature, current strength and settled particulate matter) which take place across a similar depth gradient contribute substantially towards structural turnover in both the macrobenthic community (Heyns et al. 2016) and resident fish community (Heyns-Veale et al. 2016). This probably explains why niche-based constraints to colonisation success (i.e species sorting) explained a greater proportion of β-diversity than spatial variables, and were made more conspicuous by the presence of deeper reef habitat in Algoa Bay (Table A1).

Although the effect was weaker than that of the depth gradient, the detection of spatial autocorrelation (represented by MEMs) at the within reef-scale suggests that dispersal limitation may still be important in structuring communities at spatial scales which facilitate the active dispersal of fish to new home ranges. Sparids are frequently regarded to be highly resident within small ($<$ 250 m) home ranges (e.g. roman *C. laticeps*; Kerwath, Götz, Attwood, Cowley, et al. 2007; Kerwath, Götz, Attwood, Sauer, et al. 2007). However, longer-term ($\sim$ 1 year) acoustic telemetry studies suggest that home ranges are unlikely to be permanent over the course of a fish's lifetime. On temperate reefs in New Zealand, silver seabream *Pagrus auratus*, one of the largest sparid species, were found to shift their core home ranges by up to 300 m within 1 year of monitoring, with some individuals alternating between multiple transient home ranges (Parsons et al. 2003). Because sparids have lifespans that often exceed 10 years, their home ranges are likely to shift over the course of a lifetime, depending on the availability of resources and presence of competitors. Post-settlement processes are likely to act as a buffer to spatiotemporal variation in larval supply at scales which facilitate the dispersal of adults (Heino et al. 2015).

The contribution of spatial connectivity to compositional turnover at small-spatial scales suggests that, in addition to being constrained by habitat depth, many species may have limited capacity to actively disperse to the most suitable habitat patches. This may have important implications for how strongly niche-based processes or dispersal limitation structure communities at spatial scales which facilitate the post-settlement dispersal of resident fishes.

One of the contributing factors to higher than expected rates of small-scale turnover is likely to be the initially aggregated distribution of juvenile fishes within their nurserry areas. Typically, warmer, more productive, shallow-water habitats provide more suitable settlements sites for reef-associated fish larvae (but see Brokovich et al. 2007). This appears to case for many reef-associated sparids, whose juveniles are conspicuously more abundant in shallow reef habitats (Buxton 1984; Buxton & Clarke 1986; Buxton & Smale 1984). Juvenile densities are also likely to be further concentrated when certain habitat patches support higher recruitment rates than others; an abundant supply of structural shelter mitigates the high rates of juvenile mortality which usually take place within the first weeks of settlement (Connell & Jones 1991) and can promote elevated rates of recruitments success (Andrews & Anderson 2004; Jones 1984b). Shelter from predation and adverse environmental conditions is typically provided by the reef topography (Connell & Jones 1991) and by the structure of the macrobenthic community (e.g. macroalgae; Levin & Hay 1996). Higher juvenile recruitment rates stimulated by an abundance of structural shelter may, in turn, also contribute to higher adult abundances (Hixon & Beets 1989). As a result, some reefs will consistently support higher densities of fish than others. Significant compositional differences between reefs in TNP MPA are likely to be due to the conspicuous presence of habitat-forming kelp *Ecklonia* spp. on Middle Bank's pinnacle. Here, the abundance of structural shelter is hypothesised to mitigate the mortality rates of juvenile fish and thereby support higher densities of small-bodied fishes.

Unfortunately, very little is known about the fate of juvenile fishes within the

first weeks of settlement. Due to their small size and vulnerability to predation, recently-settled sparids are highly cryptic and were only very rarely observed by stereo-BRUVs within habitat patches which featured a high degree of structural complexity. Reef habitats with dense macrobenthic assemblages or which otherwise feature a high degree of structural complexity are likely to provide a spillover of recruits to adjacent areas. In the Western Mediterranean Sea, Macpherson (1998) found that recently-settled juveniles of three sparid species (*Diplodus puntazzo*; *D. sargus*; *D. vulgaris*) remained highly aggregated within their respective nursery areas during the first few months following settlement on the reef. Each species showed a clear preference for different reef habitats, but later dispersed to adjacent areas once they had attained a larger body size (50 - 70 mm). Due to their size, juvenile fish are predicted to have more specialised habitat requirements (e.g. Wilson et al. 2008) and occupy smaller home ranges than adults (Kramer & Chapman 1999). Ontogenetic shifts in habitat use are hypothesised to reflect the trade-offs between mortality risk and growth rate; changes in preferred habitat use and diet; and potentially a mechanism to reduce intraspecific competition among age classes (Dahlgren & Eggleston 2000; Mumby et al. 2004). The hypothesised relocation of fish home ranges to deeper habitats during the course of ontogeny is supported by the general increase in the size of fish with depth (Macpherson & Duarte 1991), a trend which has also been documented among sparids in the Agulhas Ecoregion (Griffiths & Wilke 2002; Heyns-Veale et al. 2016). Home range shifts have already been directly documented among some temperate reef fishes via acoustic telemetry (e.g. Parsons et al. 2003; Topping et al. 2006). However, because sparids frequently live to reach ages of 10 - 30 years, acoustic monitoring studies which track movements over a more ecologically meaningful durations are needed to corroborate a more dynamic view of their home range use.

The long-distance movement of adults is considered to be rare among most resident reef fishes (Freiwald 2012). While most species within the sparid family follow this trend, some individuals are capable of undertaking long-distance migrations

during their lifetime (see Brouwer 2002; Brouwer et al. 2003; Griffiths & Wilke 2002). Nevertheless, connectivity between populations in TNP MPA and Algoa Bay is thought to be largely maintained by the dispersal of pelagic larvae which can remain in the water column for approximately 30 days (Davis & Buxton 1996; Davis 1996), a duration typical of many inshore fishes (Kinlan & Gaines 2003). During this time, longshore currents in the Agulhas Ecoregion are estimated to be capable of transporting larvae over distances ranging from 10's - 100's of km (Brouwer et al. 2003; Griffiths & Wilke 2002; Tilney et al. 1996). This is thought to provide sufficient larval connectivity necessary for protected populations of reproductively active adults in TNP MPA to supplement recruitment rates in Algoa Bay (Brouwer et al. 2003; Tilney et al. 1996). Studies of the genetic stock structure of roman *C. laticpes* (Teske et al. 2010), slinger *C. puniceus* (Duncan et al. 2015) and black musselcrack *Cymatoceps nasutus* (Murray et al. 2014) suggest that these species exists as single well-mixed stocks throughout their core distributions. Despite this degree of genetic connectivity, however, higher than expected species turnover among locations suggests that over ecological timescales, larval connectivity may be sufficiently low to limit the distribution of species near the margins of their core distribution.

Due to historic management differences and unmeasured large-scale oceanographic conditions, differences between TNP MPA and Algoa Bay could not be solely attributed to larval dispersal limitation without additional replicate locations. Overfishing has historically been responsible for reducing the population sizes of many of South Africa's linefish species (Brouwer & Buxton 2002; Griffiths 2000; Mann 2013). Species turnover between locations was, however, not associated with the local extirpation of heavily exploited species such as dageraad *Chrysoblephus cristiceps* and red steenbras *Petrus rupestris*. Instead, the $\sim$ 200 km transition between TNP MPA and Algoa Bay coincided with the edge of the core distributions of sparid species which were notably absent (summarised in Table A6) from TNP MPA (e.g. englishman *C. anglicus*; slinger *C. puniceus*; scotsman *Polysteganus praeorbitalis*) and Algoa Bay (hottentot *Pachymetopon blochii*). Due to the limited dispersal of

larvae and subsequent recruitment rates, some species may only temporarily persist at the margins of their core distribution at small abundances. This is likely to be the case for hottentot *P. blochii*, whose core distribution lies in the colder waters of the Western Cape of South Africa (Pulfrich & Griffiths 1988); the availability of deep-water ($>$ 50 m) reef habitat in TNP MPA is hypothesised to facilitate their distribution further eastward (Heyns-Veale et al. 2016). The absence of sexually immature fish ($<$ 220 mm FL) recorded by this study (Tables A2 and A3) and by Heyns-Veale et al. (2016) suggests that the population of *P. blochii* is likely to be maintained by very episodic recruitment events within TNP MPA. Limited recruitment may, therefore, be an important factor limiting the abundances of some species within locations; after accounting for differences in local environmental factors, the significant location effect did suggest this to be the case for compositional differences in species abundances. However, additional replicate locations are needed to assess the contribution of fishing effort to local fish abundances, as the distribution of the sparid fishes is likely to be conflated by broad-scale limits to larval recruitment rates which arise from the proximity of locations to species' historical core distributions.

In order to protect multiple target species, there has been a call for MPA networks to adequately encompass the full range of essential fish habitats needed by all life stages (Heyns-Veale et al. 2016; Rosenberg et al. 2000). However, the assumption that this approach will necessarily benefit exploited fish populations appears to be contingent on the underlying assumptions about the ecology and life history of the target species. St. Mary et al. (2000) demonstrated that the optimal design and placement of MPAs depends strongly on the timing and strength of density dependence during the life history, and the degree of movement (coupling) between juvenile and adult habitats: If density dependence predominates within the adult life stage, reserves should encompass both adult and juvenile habitats and be positioned to maintain an adequate degree of spatial connectivity to facilitate ontogenetic shifts in habitat use. On the other hand, if density dependence is concentrated among juveniles, the placement of reserves is less critical and the benefits to fish stocks

depend less strongly on the coupling between juvenile and adult life stages. Although there are notable exceptions (e.g. red steenbras *P. rupestris;* Brouwer 2002), most reef-associated sparids remain highly resident within MPAs and appear to display a limited capacity for long-distance movements, especially across areas of non-reef habitat. As a result, coupling between juvenile and adult life stages is likely to take place at spatial scales which are already encompassed by individual MPAs. From a metacommunity perspective (Leibold et al. 2004; Mouillot 2007), the results of this study indicate that spatial niche differentiation occurs predominantly between habitats at different depths. However, among habitats at similar depths, sparid diversity is likely to be maintained by the spatial aggregation of conspecifics and the largely random post-settlement dispersal of individual fish to adjacent habitat patches. This suggests that the management of sparid community diversity within individual MPAs depends both on factors related to the species-sorting perspective (e.g. niche availability, diversity of reef habitat) and on factors which mediate the rates of post-settlement dispersal (e.g. habitat connectivity, juvenile densities). In the context of previous studies which highlight differences in spatial distribution of juvenile and adult sparids (Buxton 1984; Buxton & Smale 1989; Griffiths & Wilke 2002; Heyns-Veale et al. 2016), this illustrates the importance of maintaining spatial connectivity between shallow and deep-water reef habitats at scales which are likely to facilitate ontogenetic niche shifts (i.e. within reefs).

When interpreting variation partitioning results, the unique environmental fraction (E | S) typically represents the effect of environmental selection on community composition while the unique spatial fraction (S | E) captures neutral processes related to the stochastic dispersal of individuals (Cottenie 2005). Dispersal limitation, however, mediates the importance of ecological drift and may thereby influences the relative strength of niche-based and neutral processes. Variation partitioning does not account for this interaction, and therefore cannot always adequately distinguish between alternative assembly processes. Simulated data from communities with known strengths of dispersal limitation and environmental control have been used

to demonstrate that the results of variation partitioning can depend strongly on the spatial structure of the environment variable (Smith & Lundholm 2010): In cases where dispersal limitation and environmental control interact to influence the variation explained by both the pure environmental (E | S) and pure spatial (S | E) fractions, the magnitude of the mixed fraction (S ∩ E) becomes critical to the interpretation of variation partitioning results. Although this was not a prevailing issue for the sparid community data collected by this study, other datasets which feature environmental variables with a much stronger spatial configuration may be unable to disentangle the distinct signatures of niche-based and dispersal-limited assembly. A further limitation of variation partitioning approaches is related to the ability of spatial eigenvector methods such as PCNM and MEM to accurately model known spatial processes. Gilbert & Bennett (2010) found that both methods have a proclivity to overfit known spatial processes and may therefore falsely select spurious spatial variables which overestimate the variation explained by dispersal limitation. Together with the limiting assumption that the environmental model has considered all relevant environmental variables, variation partitioning may be a somewhat limited tool for inferring the precise strength of species sorting and dispersal limitation. Consequently, where estimates of the relative importance of habitat diversity are marred by high levels of uncertainty, managers may risk making spurious decisions for the optimal maintenance of biodiversity. Nevertheless, variation partitioning and spatial eigenvector methods are an informative first step in the analysis of ecological patterns which are likely to be scale-dependent. Future studies would benefit from the inclusion of benthic habitat surveys to disentangle the relative influences of macrobenthic habitat diversity, abiotic constraints such as water temperature, and spatial connectivity, to patterns of fish β-diversity (Heyns-Veale et al. 2016; Pauly et al. 2002). Although there is likely to be some uncertainty surrounding the relative contributions of species sorting and dispersal limitation, the results of this study provide a basis on which to develop more specific models and experimental tests of reef-associated fish distributions.

It is difficult to assess whether reef fish species persist as a network of closed, self-recruiting populations; a single, large, patchy population which recruits from a common larval pool; or as a metapopulation. This will depend on the life history characteristics of the focal species, their spatial setting, and the degree of local population independence which is deemed sufficient to support metapopulation structure. Given their extensive lifespans, the successful long-distance movement of even a few adult reef fishes can have long-term demographic consequences (Gunderson & Vetter 2006). The spatial scales at which populations of adult spawners influence demographic rates will, nevertheless, depend on the distances over which larvae are most frequently dispersed and the degree to which self-recruitment to the natal reef occurs. Although the presence of significant spatial structure which was independent of depth suggests that local community composition is, at least in part, influenced by dispersal limitation, species may not be equally affected. Whether species are dispersal limited at this scale, able to adequately disperse to favourable habitats, or whether they can persist by opportunistically dispersing to vacant habitat patches, may strongly depend on body size-related traits which allow some populations to more rapidly respond to spatio-temporal changes within the reef. Large-bodied reef fish species generally persist at lower population densities than small-bodied species (see Table A2-5 and Ackerman et al. 2004) and may therefore be expected to show a stronger imprint of dispersal limitation (Ng et al. 2009). This may impede the ability of species to actively disperse to suitable habitat patches and thereby limits the strength of species sorting (Leibold et al. 2004). However, because the bipartite lifecycle of fish facilitates their broader dispersal in marine environments, this relationship is likely to be scale-dependent and also depend on the influence of mass effects (Cottenie 2005): The larval output produced by spawning adult populations in favourable "source" habitats may enhance recruitment rates sufficiently for species to overcome the effects of dispersal limitation or niche-based constraints in less favourable "sink" habitats - this is predicted to have a homogenising effect on patterns of β-diversity. The contribution of species sorting and dispersal limitation

which takes place once recruits have settled within reefs should therefore be considered within the broader context in which reefs are connected by larval dispersal (Fig. 2.6). Griffiths & Wilke (2002) considered that carpenter *Argyrozona argyrozona* may exist as a metapopulation on offshore reefs of the Agulhas Bank, due to the post-settlement relocation of some fish between otherwise resident populations. Unfortunately, quantitative estimates of population connectivity, which are needed to ascertain whether metapopulation structure exists using even the loosest definition (i.e. "population of populations linked by dispersal"), are generally lacking for most reef-associated species. Recent advances in larval tagging techniques and parentage analysis have stimulated a number of studies on pelagic larval dispersal which indicate that larval connectivity among coral reef fish populations predominantly takes place over distances of <5 - 15 km, and that populations experience much higher rates of self-recruitment than previously assumed (Almany et al. 2007, 2013; Jones et al. 2009). Similar data about the scales over which temperate reef fish populations maintain spatial connectivity are needed to determine to what degree populations are closed and self-replenishing versus how strongly their dynamics depend on external sources of replenishment from either neighbouring reefs, or a common larval pool. If larval dispersal distances of temperate reef fishes are as limited as they are among many coral reef fishes, metapopulation structures among temperate reef fishes are likely to exist at much smaller scales than previously thought (Freiwald 2012).

2.5 Conclusions

The results of this study illustrated that variation in the composition of resident sparid communities was jointly influenced by local environmental variation and the limited post-settlement dispersal of fishes at relatively small spatial scales. This concords with the view that instead of being mutually exclusive, the relative prevalence of competitive and stochastic exclusion mechanisms positions communities along a continuum which ranges from entirely niche-structured to neutral (Gravel et al.

2006; Leibold & McPeek 2006). Among locations seperated by $\sim$ 200 km, larval dispersal was likely to be limited enough to reduce the number of species within local habitat patches; within locations, the occupancy of species remained largely insensitive to the habitat characteristics at the within-reef scale. Here, the spatial aggregation of conspecifics and high levels of compositional β-diversity coincided with the spatial scales over which the post-settlement dispersal of fishes is likely to accompany ontogenetic changes in habitat use and diet. Consequently, the prevalence of both species sorting and dispersal limitation within reefs suggests that the long-term persistence of sparid reef fishes is likely to depend on both an adequate supply of suitable reef habitat and the appropriate scales of spatial connectivity to facilitate post-settlement immigration among habitat patches (Mouillot 2007). An important aspect of this will be ensuring that MPAs incorporate an adequate degree of connectivity among habits utilised by juveniles and adults of the focal species (Heyns-Veale et al. 2016; Rosenberg et al. 2000). Although scales at which post-settlement dispersal take place are reasonably well documented among species within the sparid family, the processes which structure species abundances within reefs are also likely to depend on the scales at which larval dispersal most frequently takes place. More realistic assumptions about species' dispersal rates, their niche requirements and the range of environmental heterogeneity are therefore key to developing a better understanding of how these communities vary in space (Logue et al. 2011). Trait-based approaches have the potential to provide a more predictive framework for metacommunity ecology by linking organismal traits which influence species' per capita rates of birth, death, and dispersal to the prevailing drivers of metacommunity structure (Cottenie 2005; de Bie et al. 2012). Identifying how body size, and other functional traits, influence the relative fitness and dispersal ability of species, and therefore the spatial scales at which species sorting and dispersal limitation prevail, remains a useful avenue for future research. As the life history characteristics of other linefish species share varying degrees of similarity with those of sparids, it is necessary for the management of subtidal reefs to take place at scales

which appropriately reflect the connectivity of focal fish populations (Gunderson et al. 2008; Kramer & Chapman 1999).

Chapter 3

Body size-driven maintenance of species coexistence in sparid reef fish communities and the role of size-selective fishing mortality

3.1 Introduction

One of the central goals of community ecology, and a key element towards understanding the maintenance of biodiversity, is to understand the mechanisms by which similar species coexist. Among the earliest ideas in ecology is the principle of competitive exclusion which states that two species cannot indefinitely occupy the same niche (Gause 1934). This principle is, however, often contradicted by empirical observations of species-rich communities which feature species with similar ecologies. To resolve this paradox, MacArthur & Levins (1967) identified the quotient of interspecific differences in niche means (d) and intraspecific niche widths (σ) as central to quantifying the minimum degree to which species' niches can overlap while still maintaining coexistence. The minimum value of d/σ imposes a limit on the similarity and number of competing species which can locally coexist (i.e. limiting similarity).

Attempts to explain species coexistence typically highlight how, when biotic interaction are strong, differences between species' functional traits give rise to resource partitioning which facilitates continued coexistence (Chase & Leibold 2003; Hutchinson 1957). On the other hand, evidence of coexistence among ecologically

similar species has challenged the traditional view, and suggested that species coexistence may also be facilitated by ecological similarities (Hubbell 1997, 2006; Lewis 1977). However, these mechanisms are not necessarily mutually exclusive, and may both influence the coexistence of competing species (Adler et al. 2007; Gravel et al. 2006). To reconcile how coexistence can arise from either ecological differences or similarities, Chesson (2000) formalised the view that the magnitude of niche differences required to facilitate long-term coexistence depends on the degree to which species differ in their average fitness: Stabilising mechanisms promote coexistence through species differences that reduce niche overlap, and thereby lessen the impact of fitness inequalities on competitive interactions. By delaying competitive exclusion this mechanism helps species with lower fitness to recover from low abundances. Alternatively, equalising mechanisms promote fitness equivalence among species with respect to their environment. Smaller fitness differences allow coexistence to be maintained via weaker stabilising mechanisms. Local species diversity may therefore be maintained by strong stabilising mechanisms which overcome large fitness inequalities, or by weak stabilising mechanisms which facilitate long-term coexistence among species with similar average fitness. A key question towards understanding the assembly and management of ecological communities is to reconcile under what conditions and to what extent alternative coexistence mechanisms predominate (Leibold & McPeek 2006).

Classical niche theory purports that the number of species which locally coexist is facilitated by interspecific niche partitioning, whereby species contract their resource use and/or use different resources when in the presence of competing species (Leibold & McPeek 2006). Niche partitioning may involve the partitioning of food resources, habitat use (in space or time), and competitive interactions such as territoriality (see Chase & Leibold 2003; Chesson 2000). The continued local coexistence of species relies on stabilising mechanisms which are strong enough to overcome the average fitness inequalities among species. When species in favourable environments experience positive population growth, stabilising mechanisms cause intraspecific

competition to constrain the per capita growth rate of a species more than it limits other species via interspecific competition (Chesson 2000). Consequently, as a species with higher average fitness increase in abundance, intraspecific competition within that species becomes stronger than the competition between species. This mechanism, whereby species with lower average fitness are able to recover from low abundances, can effectively delay competition exclusion.

In contrast, neutral models propose that species are functionally equivalent and have similar average fitness; coexistence occurs via stochastic fluctuations in demographic rates and chance recolonisation events alone, without the need for species to maintain large niche differences (Hubbell 2005). This perspective deviates from the traditional view (sensu Hutchinson 1957) of ecological communities as high-dimensional systems comprised of species which each occupy their own n-dimensional niche space. In the absence of mechanisms which reduce niche overlap, species are considered to be ecologically equivalent: Strictly speaking, the ecological traits which individuals posses do not characterise their prospects of reproduction and mortality (Bell 2001; Chave 2004; Hubbell 2001). Under these assumptions vacant habitat is likely to be colonised by the first available recruit and without displacement from competitively superior species.

Intraspecific variation among individuals within a population (i.e. individual variation; Violle et al. 2012) provides another means by which populations can be released from intra- and interspecific competition or from predation to facilitate species coexistence (see Bolnick et al. 2011): Within populations that display high phenotypic variance, individuals utilise a wider range of resources and thus compete less strongly with conspecifics. This increases the total population niche width whilst simultaneously increasing the amount of overlap with other species' niches. Due to the increased number of species with which a subset of individuals from any single species may overlap (referred to as 'increased degree'), the impact of this overlap is reduced, thereby lessening the effects of interspecific competition. Intraspecific niche variation whereby some individuals within the population adopt different ecological

strategies may, by widening the overall niche of a species, provide an alternative coexistence mechanism for species which interact at local scales (Araújo et al. 2011).

The niche width of a species and its associated patterns of resource use encompasses the balance between the constraining effects of interspecific competition and the diversifying effects of intraspecific competition (Roughgarden 1972; Van Valen 1965). Observed measures of inter- and intraspecific trait variability are therefore often conceptualised as the product of two opposing filters which sort individuals into communities according to their trait values (reviewed by Violle et al. 2012): Constraints imposed by external filters E_J include all processes which take place at broader scales outside the local community J and may include the effects of environmental constraints (e.g. temperature, depth) or that of a generalist predator. Individuals with trait values close to the optimal trait value T_J possess sufficient fitness to pass through the external filter and are likely to establish and reproduce; individuals with trait values far from T_J have zero fitness and do not establish. Internal filters encompass all assembly processes within the local community and are mostly governed by density-dependence, parasitism and microenvironmental heterogeneity. These, mostly biotic filters, select for individuals with traits values which deviate from the optimal trait value T_J. Therefore, when most individuals within a community possess trait values close to T_J, individuals whose traits values deviate from this value have higher relative fitness. The combined effect of external and internal trait filters cause the trait distribution of the local community to be spread around the optimal trait value for external conditions T_J. As a result, trait variance is expected to be small when external filters are strong, and large when internal filters are strong. The relative strength of internal versus external filtering processes can be quantified by considering the relative degree to which trait variation is distributed across four hierarchical levels (see Violle et al. 2012): individual (I), population (P), community (C), and regional pool (R). At the lowest level, trait variation is distributed among members of a species which locally coexist (here defined as a local population). Multiple species (i.e. populations) which can

reasonably be considered to interact at the local scale, via their traits, constitute a local community which supports a subset of all the species within a region.

The maintenance of species diversity within reef fish communities has been attributed to a variety of mechanisms which can broadly be classified as either niche-driven or dispersal-driven. Early explanations of local coexistence among coral reef fishes highlighted the importance of spatial resource partitioning among species (Anderson et al. 1981; Ebeling & Hixon 1991; Smith & Tyler 1972) and the niche diversifying effects of interspecific competition (Roughgarden 1974; Schoener 1974). Strong competitive interactions among dense populations for a limited supply of resources (food or space) was assumed to promote resource partitioning and the evolution of a diverse range of niches. The view that interspecific competition structures reef-fish communities via equilibrium (ie. self-regulating) dynamics and resource partitioning has been scrutinised by dispersal-driven hypotheses. These studies suggested that while reef fish species do compete, coexistence is more often maintained by stochastic patterns of mortality and recruitment which lead to the chance colonisation of vacant habitat (i.e. lottery competition; Sale 1977, 1978). Competitive interactions are also predicted to have little influence on community structure if the supply of larval recruits to the reef is low enough for resources not to become limiting (Doherty 1981). At some spatial scales, populations can be limited by larval recruitment (Doherty & Fowler 1994a,b). Nevertheless, density-dependent regulation via predation or direct competition for living space appears to be the rule rather than the exception for the majority of cases (Ault & Johnson 1998b; Hixon & Webster 2002). Density-dependent interactions and post-settlement dispersal are, however, considered to become increasingly more important within larger, more connected reef habitats (Ault & Johnson 1998c; Robertson 1988) and when recruitment rates are highest (Jones 1990). Although the structure of reef fish communities can, at some scales, be attributed to competitive lotteries (Munday 2004) or recruitment limitation (Doherty et al. 2004), long-term persistence is still thought to depend on population regulation via density dependence at some spatial or temporal scales

(Hixon & Jones 2005; Hixon et al. 2002).

Globally, temperate rocky reefs support fish communities that are characterised by relatively high levels of functional redundancy within trophic groups; roving invertebrate predators, which carry out similar ecological roles within the ecosystem, contribute disproportionately to the species richness of temperate reef ichthyofauna, and are likely to respond similarly to fishing pressure (Micheli & Halpern 2005). The most well-documented effects of fishing include changes to the trophic relationships among species and the truncation of population size structure which follows the removal of large-bodied fishes (Babcock et al. 1999; Edgar & Stuart-Smith 2009; Genner et al. 2010; Watson et al. 2007). Reef-associated fishes from the sparid family (Sparide) contribute substantially to the abundance and diversity of warm-temperate reef ichthyofauna within South Africa's Agulhas Ecoregion (Turpie et al. 2000). Although they continue to form an important component of the commercial and recreational linefisheries, a number of species, including dageraad *Chrysoblephus cristiceps*, red steenbras *Petrus rupestris*, seventy-four *Polysteganus undulosus*, and scotsman *Polysteganus praeorbitalis* have been severely overexploited (Brouwer & Buxton 2002; DAFF 2014; Griffiths 2000; Mann 2013). Their vulnerability to fishing pressure is exacerbated by their longevity, slow growth and hermaphroditic lifestyles (Buxton 1993). Because most species remain highly resident (eg. Brouwer et al. 2003; Griffiths & Wilke 2002; Kerwath, Götz, Attwood, Cowley, et al. 2007; Kerwath, Götz, Attwood, Sauer, et al. 2007; Maggs et al. 2013), spatial management approaches such as Marine Protected Areas (MPAs) are perceived to be one of the most effective tools for ensuring their protection and recovery from overfishing (Barrett et al. 2007; Götz et al. 2009; Kerwath et al. 2013). Most forms of fishing typically target larger or intermediate-sized individuals (reviewed in Kuparinen et al. 2009); protection from fishing may therefore also be useful for conserving trait variation (e.g. size-at-maturity and sex-change; Buxton 1993; Götz et al. 2008) and natural mortality regimes (Audzijonyte et al. 2013).

Reef-associated sparids typically share fairly similar habitat requirements and

a large degree of dietary overlap (Table A6; Buxton & Smale 1984, 1989; Smale 1992). As well as partitioning reef habitats between different stages of their ontogeny (Buxton & Smale 1984, 1989; Griffiths & Wilke 2002), juveniles and adults of most species further partition shared trophic resources according to food size (Buxton 1984; Buxton & Clarke 1989, 1991). Among sparids, depth-related increases in the average body size of many species are thought to coincide with the relocation of fish to deeper, more suitable reef habitats (Heyns-Veale et al. 2016). Allometric relationships between body size and factors such as resource use, growth rates and predation risk are thought to be central to predicting the size-based asymmetries in competitive interactions which favour ontogenetic habitat shifts (Dahlgren & Eggleston 2000; Werner & Gilliam 1984). The size structure of reef-associated fish communities is therefore likely to play an important role in predicting the diversity of species whose home ranges overlap.

The aim of this study was to assess a possible mechanism whereby internal trait filters facilitate species coexistence among sparid fishes, by inspecting the role of body size using the framework of Violle et al. (2012). Estimates of individual fish lengths obtained by stereo-BRUVs from replicate communities were used to quantify body length variation among locally co-occuring conspecifics (i.e. local populations) and within the community as a whole. The relative contribution of individual- and population-level variation to overall community-wide variation provided a relative measure of the strength of internal trait filters with respect to individual body size. The relationship between local species richness, a measure of species coexistence, and the strength of internal community filters provided a strong test of whether species coexistence among sparid fishes was facilitated by niche differentiation, neutral processes (e.g. lottery competition), or by individual variation among conspecifics. Throughout, it is assumed that competitors differ only in their body size, and fish length is used as a measure of body size. The relationships between species richness and the strength of internal filters were compared between historically exploited and near-pristine communities to investigate whether size-selective fishing

potentially mediates size-based coexistence among reef-associated sparid fishes.

3.2 Materials and methods

3.2.1 Data collection

Data were collected from 63 ichthyofaunal communities inhabiting local habitat patches stratified randomly across the depth range of four reef complexes; two unexploited reefs were located within Tsitsikamma National Park marine protected area (TNP MPA), and two exploited reefs were located within Algoa Bay (AB; Fig. 2.2; Table A1). Ichthyofaunal communities were surveyed by baited remote underwater stereo-video systems (stereo-BRUVs) as described in Section 2.2. Stereo-BRUVs footage was analysed in Eventmeasure v4.42 (www.seagis.com.au) to obtain estimates of local species richness and relative abundance (MaxN; see Section 2.2.3). Transient species (strepie *Sarpa Salpa*, giant yellowtail *Seriola lalandi*, and horse mackerel *Trachurus spp.*) which are not closely associated with the local reef habitat were excluded from the analysis. Local environmental variables recorded during stereo-BRUVs deployments included the average in-situ water temperature at deployment depth, water visibility, and the % field of view occupied by visible reef (see Section 2.2.2).

A close to random sample of trait measurements from the population is preferred for questions which concern the roles of intra- and interspecific trait variation (de Bello et al. 2011). The variation in body length of a given species within the community was estimated by measuring the fork lengths (FL; mm) of a random sample of conspecific individuals from each species' MaxN frame. Although the largest individuals of territorial species such as roman (*Chrysoblephus laticeps*) occasionally display instances of bait guarding behaviour, the movement of individuals across the stereo-BRUVs' field of view near the MaxN frame, and thus the ability to measure individuals is independent of their body length. Body lengths followed a log-normal distribution spanning three orders of magnitude at the local commu-

nity scale (Table A2-5). Log-normal distributions of abundance and body size at this scale arise via the multiplicative (or geometric) interaction of random variables associated with compound growth and individual fitness (see Connolly et al. 2005; May 1975). Because absolute differences in body size become biologically less important with increasing size (ie. the difference between a 10 cm and a 20 cm fish is much larger than the difference between a 100 cm and 110 cm fish), body length data were log-transformed to uniformly reflect *relative* variation across the range of observations in a biologically meaningful way (Kerkhoff & Enquist 2009). This places measures of variance within a geometric domain in which proportional length differences between individuals are more consistently reflected.

To relate changes in local species richness to community-wide patterns of intraspecific variation, the body length distributions were normalised to range between 0 and 1. Ratios of species-wide (i.e. intraspecific) versus community-wide variance in body length were quantified by employing the $T_{IP/IC}$-statistic proposed by Violle et al. (2012). The ratio $T_{IP/IC}$ represents the average variance among conspecifics (i.e. populations) within a community relative to the total variance across all species making up that community. $T_{IP/IC}$ quantifies the strength of internal filters, and represents a measure of niche packing between the species within the community (MacArthur & Levins 1967). Internal filters include all assembly processes, such as microhabitat heterogeneity and density-dependence, which regulate species coexistence within the local community. Communities with values of $T_{IP/IC}$ close to 0 display strong interspecific niche packing, while communities with values close to 1 have a high degree of niche overlap among co-occurring species.

3.2.2 Data analysis

Generalised linear models (GLMs) with a gaussian error model were applied to relate the species richness of local communities to the ratio of species-wide (IP) to community-wide (IC) variance in body lengths ($T_{IP/IC}$). The slope of the relationship between species richness and $T_{IP/IC}$ provided a strong test of whether species

coexistence was facilitated by niche processes (negative slope), neutral processes (zero slope) or via individual variation (positive slope) (Violle et al. 2012). To explore the ecological effects of location-wide differences in historical exploitation, two data sets were analysed: (*i*) a subset of the community comprised only of species from the commercially important and heavily-targeted sparid family (Sparidae). (*ii*) the full community of reef-associated ichthyofauna, which is largely comprised of species from 23 families which are not strongly targeted by the linefishery.

Model selection

To address the primary objective of this study, the identification of ecological processes which maintain coexistence among reef-associated species, a two-step AIC-modelling approach was followed whereby two suites of covariates were considered sequentially (sensu Fondell et al. 2008). First, in order to improve the precision of species richness estimates from local communities, a candidate set of models including only covariates related to species' detection probabilities was explored. The following covariates were considered as influential to the ability of Stereo-BRUVs to estimate the species richness of reef-associated ichthyofauna (Table 3.1): (1) Water visibility, which determines the area in which fish can be accurately identified and counted, is expected to reduce the detection rates of non-carnivorous species such as the fingerfins (Cheilodactilidae), cape knifejaw *Oplegnathus conwayi*, and janbruin *Gymnocrotaphus curvidens* (Bernard & Götz 2012). (2) The percentage of the field of view occupied by visible reef was expected to influence the detection of small, cryptic reef fishes (eg. *Cheilodactylus pixi*). (3) The average in-situ water temperature during the deployment was anticipated to influence activity levels of ichthyofauna, and consequently species richness estimates. Resident reef fishes such as roman *Chrysoblephus laticeps* are reported to retreat into caves or crevices and refrain from active feeding during periods of upwelling, possibly as a means to reduce predation risk to more mobile predators (Kerwath, Götz, Attwood, Sauer, et al. 2007). To estimate the relative effect of upwelling-induced variation in ichthy-

ofaunal activity on species richness estimates, while accounting for differences in the average water temperatures of locations, water temperatures were centred to have a mean value of zero within each location. There were 7 possible parametrisations of additive environmental effects related to species' detection probabilities. Candidate models were ranked according to their level of empirical support using the small-sample extension of Aikake's Information Criterion (AIC_c; Burnham & Anderson 2002). AIC_c-based relative-importance weights (ω_i) indicated the level of support for each model, given the data and the other models considered.

An Akaike weight (ω_i) exceeding 0.9 provided a very high degree of confidence that the model in question was the best-supported among those considered. For any well-supported model, however, the addition of an uninformative parameter will yield a new model that falls within 2 AIC units of the well-supported model: Even if the additional parameter contributes no explanatory power toward improving the overall fit of the model (ie. log-likelihood remains unchanged), a 1-unit increase in K only increases AIC by 2 units. In such cases, competitive models falling within <2 ΔAIC of the best model should be examined to evaluate whether additional parameters are informative and improve the log-likelihood (Burnham & Anderson 2002). For model selection based on AIC_c, the boundary somewhat exceeds 2 ΔAIC_c, depending on the values of n/K (Arnold 2010). Among the competitive models ($\omega_i > 0.2$), hierarchically more complex versions of the best model were discarded if they included additional parameters which were biologically uninformative (ie. small β/SE_β) and did not lead to a reduction in AIC_c. Interpretation of parameter estimates is a crucial second step towards distinguishing between competitive models

Table 3.1: Covariates used in analyses of factors affecting detection probabilities of reef-associated fish species sampled by stereo-BRUVs in the warm-temperate Agulhas Ecoregion, South Africa.

Variable	**Description**	**Mean**	**Range**
Temp	Average in-situ water temperature (°C)	15.0	10.4 - 17.1
Vis	Water visibility (m)	3.2	1.5 - 5.0
VisReef	% visible reef within field of view	59.1	0.0 - 100.0

(Guthery 2008), as even AIC-supported variables are subject to a 1 in 6 chance of being admitted on spurious grounds (Arnold 2010).

The detection effects model with the most empirical support formed the base on which to formulate 4 additional candidate models to evaluate the ecological effects of community-wide body length variation ($T_{IP/IC}$) and regional differences in historical fishing pressure. $T_{IP/IC}$ and region were considered as main effects. The interaction between $T_{IP/IC}$ and region was considered to represent the scenario in which exploitation altered the ecological processes maintaining species coexistence. AIC_c-based model selection and an evaluation of parameter estimates identified the best-supported model among the candidate set of ecological models.

Model validation

Plots of residuals against fitted values, normal quantile-quantile plots, and histograms of residuals indicated that the assumptions of a gaussian error model had been met (Fig. A.1).

Testing alternative models of species coexistence

Model predictions from the best-supported ecological models were used to assess the direction and extent to which intra- and interspecific patterns of variance in the body lengths of fishes drive changes in local species richness. The parameter estimates and standard errors of $T_{IP/IC}$ indicated whether the relative ratio of species-wide to community-wide variation in body lengths was associated with either a decrease, no change, or an increase in the number species which co-occured. 95% confidence intervals (CI) around the slope of estimate of the species richness versus $T_{IP/IC}$ relationship were calculated to substantiate either niche-based (negative slope), neutral (zero slope), or individual variation (positive slope) theories of species coexistence. Statistical analyses were performed in R version 3.1.2 (R Core Team 2014).

3.3 Results

In total, the dataset of 63 ichthyofaunal communities included [1] 3956 fishes from 55 species and 21 families. A total of 2692 individual length measurements (68 % of all counted individuals) were obtained from all species' MaxN frames (see Tables A2-5). Local communities spanned the range of subtidal reef habitat between 13 - 74 m depth. There was considerable variation in species richness ($2 < S < 25$) and total ichthyofaunal abundance ($6 < \mathrm{MaxN_{tot}} < 157$). Pearson's (r) and Spearman's (r_s) correlations between depth and S were -0.29 and -0.25, respectively. $\mathrm{MaxN_{tot}}$ showed similar correlations with depth (r = -0.31 and r_s = -0.26).

Species from the family Sparidae had high occupancy rates across the study area, and accounted for a large proportion of the total ichthyofaunal abundance (3439 fishes) and diversity (22 species). A total of 2295 length measurements (67 % of all counted individuals) were obtained from sparid species' MaxN frames (see Tables A2-5). The number of sparid species ($1 < S < 15$) and total sparid abundance ($5 < \mathrm{MaxN_{tot}} < 144$) varied considerably. S was correlated with depth (r = -0.32 and r_s = -0.18); $\mathrm{MaxN_{tot}}$ covaried similarly (r = -0.29 and r_s = -0.25).

3.3.1 Model selection results

Sparid community

For patterns of species richness among sparid communities, the data provided strong support ($\omega_i = 0.662$) for a detection effects model which included water temperature and water visibility. Only one other model, which included the additional parameter % visible reef, fell within 8 $\mathrm{AIC_c}$ of the best-supported model (Table 3.2a). The additional parameter led to a 1.42-unit increase in $\mathrm{AIC_c}$. Further inspection revealed that the larger model's maximised log-likelihood was not noticeably improved by the inclusion of an additional parameter (Table 3.2a). The parameter estimate (β

[1] Transient species (giant yellowtail *Seriola lalandi*; longfin yellowtail *Seriola rivoliana*) and species which aggregate in large schools (strepie *Sarpa salpa* (Sparidae); horse mackerel *Trachurus* spp.; mullet *Chelon richardsonii*) were excluded.

$\pm$ SE_β) for % visible reef (-0.009 $\pm$ 0.009) did not contribute to species richness estimates, and indicated that the larger detection effects model was not supported (Burnham & Anderson 2002).

The full ecological effects model, which included an interaction between $T_{IP/IC}$ and region, had the most AIC-based support (Table 3.2b). A simple main effects model and the ecological null model both fell within 2.00 AIC_c of the full model. The parameter estimate ($\beta \pm SE_\beta$) of the interaction effect proved to be biologically informative (-6.705 $\pm$ 2.956, Table 3.4a), providing support for the full model.

Ichthyofaunal community

When data from all reef-associated ichthyofauna were considered, patterns of species richness were best approximated by a detection effects model which included water temperature, water visibility, and the % of visible reef within the field of view (Table 3.3a). The model received very strong empirical support ($\omega_i = 0.982$; see Table 3.4b for parameter estimates).

The ecological effects model which featured $T_{IP/IC}$ and region as simple main effects received the most AIC-based support ($\omega_i = 0.573$, Table 3.3b). The parameter estimates of both main effects ($T_{IP/IC}$ and region) were biologically informative ($\beta \pm SE_\beta$: -6.030 $\pm$ 2.157 and -1.485 $\pm$ 0.709 in Table 3.4b). A hierarchically more complex model which also included an interaction between $T_{IP/IC}$ and region received a competitive degree of empirical support compared with the best-supported model ($\omega_i = 0.191$, Table 3.3b). The parameter estimate ($\beta \pm SE_\beta$) of the interaction term (-4.465 $\pm$ 7.179) however proved to be uninformative. Consequently, the selection of the more complex ecological model could not be justified, and a simple main effects model was considered to be the best-approximating model.

3.3.2 Coexistence models

Due to the interaction between $T_{IP/IC}$ and location, the best approximating model for the sparid community data made predictions of species richness patterns across

Table 3.2: Models examining the effects of various factors on the species richness of reef-associated sparid communities surveyed by stereo-BRUVs in the Agulhas Ecoregion, South Africa, 2014-2015. Sparid species are target species which comprise an important component of commercial and recreational linefisheries catches (Mann 2013, and references therein). Models are constructed in two stages, with the best model from the first stage (a) serving as the basis for the second stage (b). Models are ranked according to differences in Akaike's information criterion corrected for small sample size (ΔAIC_c). K = number of estimable parameters; *LogLik* = log-likelihood; AIC_c small-sample-size corrected Akaike information criterion; ω_i = Aikake weight. $_{adj}R^2$ (%) = percentage of variance explained by the model.

Model	K	LogLik	AIC_c	ΔAIC_c	ω_i	$_{adj}R^2$ (%)
a) Detection effects						
Temp + Vis	3	-133.357	275.4	0.00	0.662	56.6
Temp + Vis + VisReef	4	-132.887	276.8	1.42	0.325	57.3
Temp	2	-138.871	284.1	8.74	0.008	48.2
Temp + VisReef	3	-138.197	285.1	9.68	0.005	49.3
Vis	2	-144.038	294.5	19.08	0.000	38.9
Vis + VisReef	3	-143.065	294.8	19.41	0.000	40.8
VisReef	2	-157.371	321.1	45.74	0.000	6.3
Null	1	-159.414	323.0	47.62	0.000	0.0
b) Ecological effects						
Temp + Vis + ($T_{IP/IC}$×Location)	6	-128.593	273.2	0.00	0.404	62.8
Temp + Vis + $T_{IP/IC}$	4	-131.319	273.7	0.47	0.319	59.4
Temp + Vis	3	-133.357	275.4	2.18	0.136	56.6
Temp + Vis + $T_{IP/IC}$ + Location	5	-131.315	276.1	2.91	0.094	59.4
Temp + Vis + Location	4	-133.245	277.5	4.32	0.047	56.8

Temp = in-situ water temperature, Vis = water visibility (m), VisReef = % of visible reef within the field of view, $T_{IP/IC}$ = ratio of intraspecific to community-wide variation in body length, Location = TNP MPA (no-take) vs. Algoa Bay (exploited). × denotes interaction effect.

Table 3.3: Models examining the effects of various factors on the species richness of reef-associated ichthyofaunal communities surveyed by stereo-BRUVs in the Agulhas Ecoregion, South Africa, 2014-2015. The majority of surveyed species (excluding sparids) are considered to be non-target species which do not form an important component of commercial and recreational linefisheries catches (Mann 2013, and references therein). Models are constructed in two stages, with the best model from the first stage (a) serving as the basis for the second stage (b). Models are ranked according to differences in Akaike's information criterion corrected for small sample size (ΔAIC_c). K = number of estimable parameters; *LogLik* = log-likelihood; AIC_c small-sample-size corrected Akaike information criterion; ω_i = Aikake weight. $_{adj}R^2$ (%) = percentage of variance explained by the model.

Model	K	LogLik	AIC_c	ΔAIC_c	ω_i	$_{adj}R^2$ (%)
a) Detection effects						
Temp + Vis + VisReef	4	-156.224	323.5	0.00	0.982	61.0
Temp + VisReef	3	-161.688	332.1	8.57	0.014	53.6
Temp + Vis	3	-163.080	334.8	11.35	0.003	51.5
Vis + VisReef	3	-164.148	337.0	13.48	0.001	49.8
Temp	2	-168.419	343.2	19.74	0.000	42.5
Vis	2	-171.261	348.9	25.43	0.000	37.0
VisReef	2	-178.121	362.6	39.15	0.000	21.6
Null	1	-185.778	375.8	52.26	0.000	0.0
b) Ecological effects						
Temp + Vis + VisReef + $T_{IP/IC}$ + Location	6	-148.520	313.1	0.00	0.573	69.6
Temp + Vis + VisReef + $T_{IP/IC}$	5	-150.855	315.2	2.13	0.197	67.2
Temp + Vis + VisReef + ($T_{IP/IC}$×Location)	7	-148.303	315.3	2.20	0.191	70.0
Temp + Vis + VisReef + Location	5	-152.568	318.6	5.56	0.036	65.3
Temp + Vis + VisReef	4	-156.224	323.5	10.42	0.003	61.0

Temp = in-situ water temperature, Vis = water visibility (m), VisReef = % of visible reef within the field of view, $T_{IP/IC}$ = ratio of intraspecific to community-wide variation in body length, Location = TNP MPA (no-take) vs. Algoa Bay (exploited). × denotes interaction effect.

Table 3.4: Maximum-likelihood parameter estimates for the best-fitting models including environmentally-mediated detection effects, and ecological effects associated with community-wide patterns of intraspecific variation in body length of sparid fishes (22 species) and all reef-associated ichthyofauna (55 species).

Parameter [a]	Estimate	SE	95% CI
a) Sparid fishes			
Intercept	4.954	1.199	2.604 to 7.304
Vis	0.947	0.305	0.349 to 1.546
Temp	0.732	0.138	0.461 to 1.004
$T_{IP/IC}$	-0.108	1.189	-3.829 to 3.614
$Region_{(TNP\ MPA)}$	1.156	0.871	-0.162 to 3.253
$T_{IP/IC} \times Region_{(TNP\ MPA)}$	-6.705	2.956	-12.499 to -0.912
a) All ichthyofauna			
Intercept	13.399	1.687	10.092 to 16.706
VisReef	-0.045	0.012	-0.068 to -0.021
Vis	1.261	0.420	0.439 to 2.084
Temp	0.900	0.189	0.530 to 1.269
$T_{IP/IC}$	-6.030	2.157	-10.257 to -1.802
$Region_{(TNP\ MPA)}$	-1.485	0.709	-2.874 to -0.095

[a] Abbreviations correspond to parameters from the best-supported ecological effects models listed in listed in Tables 3.2b and 3.3b. Reference level for the factor location is Algoa Bay.

the $T_{IP/IC}$ gradient which were attenuated by historical differences in exploitation (Fig. 3.1a): At sites within the 'no-take' TNP MPA, species richness of sparid communities was negatively related to $T_{IP/IC}$ ($\beta_{T_{IP/IC}} \pm 95\%$ CI: -6.921 $\pm$ 4.434), conforming to niche-based expectations. For the exploited sparid communities of Algoa Bay, the slope of the relationship between species richness and $T_{IP/IC}$ did not differ from zero (-0.108 $\pm$ 3.721), in line with neutral models of species coexistence. In contrast to results for the sparid fishes, the species richness patterns of all reef-associated ichthyofauna were negatively related to $T_{IP/IC}$ across communities from TNP MPA and Algoa Bay (ie. there was no interaction between $T_{IP/IC}$ and location; see Fig. 3.1b). The negative slope of the relationship between species richness and $T_{IP/IC}$ ($\beta_{T_{IP/IC}} \pm 95\%$ CI: -6.030 $\pm$ 4.228) conformed to expectations from niche theory. Despite limited turnover of species among locations (see Chapter 2, Fig. 2.3a), differences in the slopes of the relationship between species richness and $T_{IP/IC}$ coincided with lower community-wide variation (IC) in the length of sparid fishes from Algoa Bay (Fig. 3.2a). Model residuals for both datasets were homoscedastic and conformed to assumptions of normality (Fig. A.1)

3.4 Discussion

Unexploited sparid communities of TNP MPA displayed species richness patterns consistent with niche-based predictions. Here it is suggested that density-dependent processes within local communities filter individual fishes from the regional pool according to their body length in a way which reduces the overlap among locally coexisting species. In communities that support a large number of species, conspecifics display relatively less size-variation than in communities which support only few species, which would suggest that members of the same species are likely to compete more strongly with each other than they do with other species. This is likely to have a stabilising effect on the relative abundance of the species best adapted to local habitat conditions and allow less fit species to persist at low abundances. This evidence of niche packing along the body size axis was, however, absent from

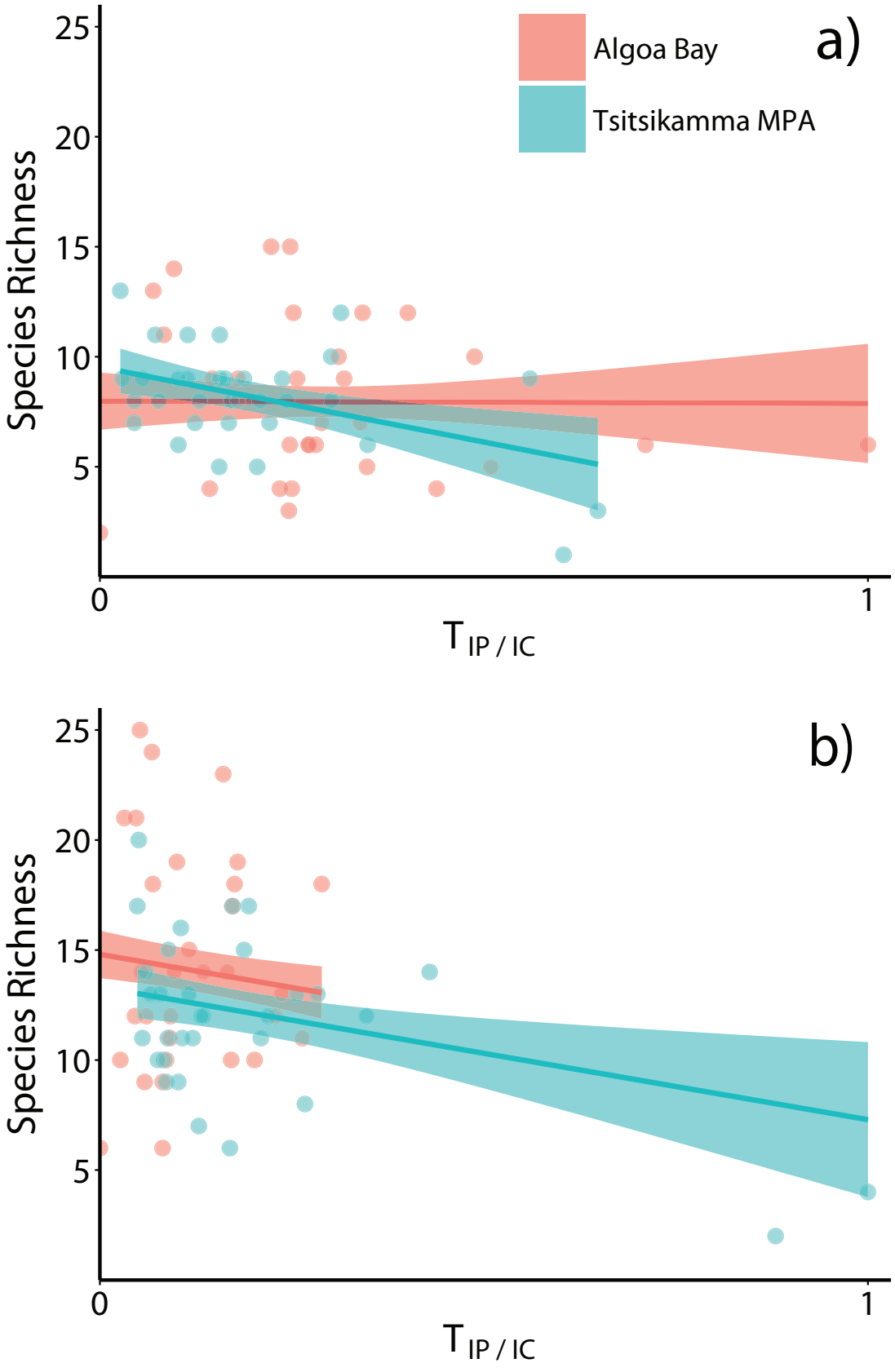


Figure 3.1: Comparisons of the ratio of population-wide to community-wide body length variation ($T_{IP/IC}$) within (a) sparid reef fish communities and (b) ichthyofaunal communities from Algoa Bay (red) and TNP MPA (blue). Species richness estimates predicted by best ecological models (see Table 3.4) represented by solid lines with 95% confidence limits.

exploited sparid communities; sparid communities in Algoa Bay, which have been historically exposed to size-selective fishing mortality, displayed patterns of species coexistence which conformed more closely to trait-neutral expectations. The relative degree of overlap in species' body length distributions remained invariant with respect to the number of locally co-occurring species. In contrast to species from the sparid family, which have historically comprised primary or secondary targets of fishers, most of the remaining reef-associated species recorded in this study do not comprise an important component of commercial and recreational linefisheries catches. Data from the entire ichthyofaunal community, which included 33 additional reef-associated species from 20 families, retained a signature of niche-driven species coexistence, in spite of historical exploitation.

Habitat depth represents one of the principle niche axes along which marine communities are structured. Corresponding to an environmental stress gradient along which a number of important abiotic variables co-vary, water depth influences light attenuation, temperature, sedimentation and hydrodynamic energy (Garrabou et al. 2002). Consequently, habitat depth is one of the principal predictors of species richness and compositional turnover in macrobenthic communities (Heyns et al. 2016; Samaai et al. 2010). Much of the turnover of sessile macrobenthic species along the depth gradient is closely tied to two physical factors: light attenuation and physical disturbance (Bradbury & Young 1981; Wilkinson & Evans 1989). Hydrodynamic activity, which decreases with depth and is an important promoter of physical disturbance, propagule dispersal and suspended particulate matter, also plays a key role in the distribution of sessile macrobenthic species (Gili & Coma 1998). The greater water movement in shallow water habitats promotes higher density and diversity of macrobenthic organisms (Baynes & Szmant 1989; Gili & Coma 1998; Palardy & Witman 2011; Rogers 1990). In contrast, the decrease of strong hydrodynamic events at depth promote elevated sediment loads which favours the establishment of upright, branching growthforms with long life spans (Adjeroud 1997; Linares et al. 2008; Rogers 1990; Wilkinson & Evans 1989). In the warm-temperate Agul-

has Ecoregion, the sessile macrobenthic community transitions from mainly algal and low-growing encrusting ascidians in the shallows (10 - 25m) to a deep water (45 - 75m) community dominated by upright-growing suspension feeders such as gorgonians, sponges and corals (Heyns et al. 2016).

The structure generated by macrobenthic communities provides habitat for many of South Africa's commercially important reef fish species (Brouwer 2002; Brouwer et al. 2003; Griffiths & Wilke 2002; Sink et al. 2006). In addition to maintaining trophic links between the pelagic and benthic environments (Gili & Coma 1998), structural shelter provided by macroalgae and suspension feeders is critical to the recruitment of juvenile reef fishes (Andrews & Anderson 2004; Jones 1984a). Depth-related species richness gradients are a common feature of warm-temperate demersal fish communities in South Africa (Heyns-Veale et al. 2016; Yemane et al. 2010) and eastern Australia (Malcolm et al. 2011). Similar to the patters of species turnover observed within the sparid community (see Tables 2.2 & 2.3), patterns of species richness are likely to be related to the changes in macrobenthic diversity and productivity which occur with depth. Inter- and intraspecific competition for scarce resources such as food and living space are known to be important drivers of spatial variation in the distribution of temperate reef fishes (Jones 1984a,b). For species with similar trophic preferences, further niche segregation with respect to habitat depth and fish body size have been found to be important drivers of coexistence in Mediterranean fish communities (Colloca et al. 2010). Studies which further differentiate species according to size-classes suggest that this form of niche partitioning may also take place between conspecifics, and partly explain the average increase in the body size of fishes with depth (Heyns-Veale et al. 2016; Macpherson & Duarte 1991; McCormick 1989). Macpherson & Duarte (1991) found that the nature of the increase depended on the size range of species, and therefore suggested it reflected a general movement of fish to more favourable, deep water habitats during ontogeny. The relative increase in the intraspecific variance of sparid species' body length distributions with decreasing richness provides strong support for a niche-

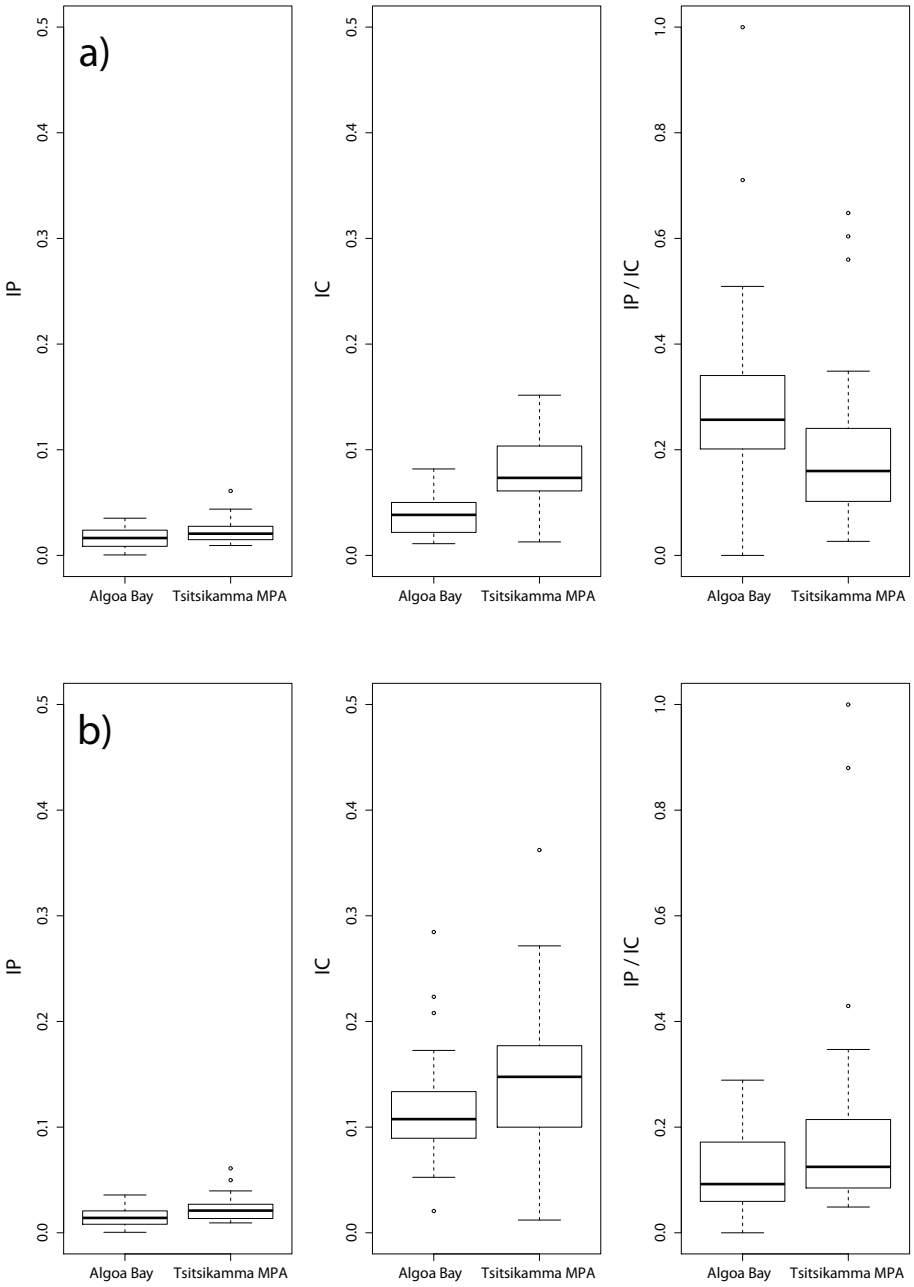


Figure 3.2: Population-wide (IP) and community-wide (IC) body length variation, and their ratio (IP/IC) for communities of (a) sparid reef fishes and (b) all reef-associated ichthyofauna within Algoa Bay and TNP MPA.

driven explanation of species coexistence. Furthermore, the relationship between $T_{IP/IC}$ and depth suggests that deeper habitats impose a stronger external filter on community membership, which excludes smaller-bodied individuals. At least for the unfished habitats within TNP MPA, this result indicates that stabilising mechanisms which arise due to differences in body size are strong enough to overcome the fitness inequalities that exist between sparid species, and thereby allow a greater number of species to co-occur despite the higher fish densities typically observed in shallow-water reef habitats.

In the Agulhas Ecoregion, shallow reef habitats tend to support a greater diversity and density of small-bodied fishes than deep reef habitats, which, typically host less diverse, low-density communities of large-bodied fishes (Heyns-Veale et al. 2016). This conforms to the general trend among sparids, in which small, juvenile fish display a preference for shallow-water habitats (Buxton 1984; Buxton & Clarke 1986; Buxton & Smale 1984, 1989; Griffiths & Wilke 2002; Smale 1988). This is likely to be related to the higher levels of primary productivity in shallow-water habitats, which, in TNP MPA, supported by higher levels of ambient light and dominant algal assemblages (Heyns et al. 2016). Higher abundances of food and warmer average water temperatures are conducive to the recruitment and growth of juvenile fishes (Macpherson 1998). Consequently, population densities are typically higher in shallow waters, and competition for food resources and shelter is likely to be strongest. Juvenile reef fish typically experience the highest rates of density-dependent mortality within the first weeks of settlement (Doherty et al. 2004; Hixon & Jones 2005). Predation rates can be greatly reduced by the abundance and diversity of prey refuges (Andrews & Anderson 2004; Connell & Jones 1991; Hixon & Beets 1989; Levin & Hay 1996). As a result, topographically complex habitats, such as those which host structurally diverse macrobenthic assemblages, are able to support elevated juvenile recruitment rates (Jones 1984a,b) and a greater density and diversity of ichthyofauna (Hixon & Beets 1989; Levin & Hay 1996).

Macrobenthic structure is critical to the early survivorship of small, recently

settled reef fishes, but becomes less important as individuals increase in body size (Choat & Ayling 1987; Connell & Jones 1991; Dahlgren & Eggleston 2000). Body size relationships between predators and prey have long been considered to be important for determining the outcome of competitive interactions (Wilson 1975). The allometric changes which accompany ontogenetic growth influence how fishes interact with each other and the reef environment: Changes which take place during ontogeny facilitate enhancements in sensory acuity (Macpherson & Duarte 1991) and swimming performance (Plaut 2001; Stobutzki & Bellwood 1994; Videler & Wardle 1991) which improve the ability of fish to perform primary functions such as foraging, migration and predator avoidance. Gape size, which linearly increases with body size in many species (Scharf et al. 2000), affords an increase to the sizes of prey items which can be consumed (Juanes & Conover 1994; Persson et al. 1996). However, contrary to predictions from optimal foraging theory, it is generally profitable for larger fish to continue to include small prey items in their diet, due to the prominent role of size-dependent rates of encounter and capture (Scharf et al. 2000). As well as benefiting from an increased foraging ability and wider access to potential prey items, fish also become less vulnerable to predation once they attain a larger body size. Larger individuals, which benefit from lower encounter rates with predators and a reduced susceptibility to capture, face reduced levels of predation risk (Lundvall et al. 1999; Scharf et al. 2000). Conversely, smaller-bodied fishes face higher encounter rates with potential predators and a higher probability of capture, are therefore likely to always remain highly vulnerable to predation from larger-bodied fishes.

Larval and juvenile fishes tend to occur in the shallow, warmer waters in which they recruit, while larger, mature individuals occupy deeper, colder reef habitats (Buxton & Clarke 1986; Buxton & Smale 1984, 1989; Griffiths & Wilke 2002; Heyns-Veale et al. 2016). Within their home range, reef fishes display a preference for refuge sites which match their body size; the attainment of larger body size during ontogeny, however, influences the availability of refuges, and thus, habitat suitability

(Randall, 1963; Robertson and Sheldon, 1979; Shulman, 1984). Several benefits to individual survivorship are associated with the relocation of juvenile fishes from the shallow habitats to deeper water habitats during ontogeny (Macpherson & Duarte 1991): Individuals which have outgrown their juvenile refuges encounter a novel suite of predators and competitors, which may drive them to undergo ontogenetic niche shifts to more suitable habitats (Werner & Gilliam 1984). Ontogenetic niche shifts to deeper habitats (see Heyns-Veale et al. 2016; Macpherson & Duarte 1991; McCormick 1989) provide a means for growing individuals to optimise the trade-off between achieving high growth rates in shallow habitat versus reducing predation risk in deeper, less productive habitats (Dahlgren & Eggleston 2000).

The increased density of fish around the baited system may introduce bias to the estimates of abundance and length-frequency distributions gathered by stereo-BRUVs (Harvey et al. 2007); agonistic interactions between size-classes and among predator and prey species are frequently observed around the bait. Other studies, using downward facing BRUVs, showed that the behaviours of larger predatory species (e.g. silver seabream *Pagrus auratus*) which cause subordinate species and smaller size-classes to leave the field of view are likely to confound comparisons of relative abundance estimates between MPAs and fished areas (Dunlop et al. 2015; Willis et al. 2000). This is exacerbated by the higher densities of fish within MPAs and by the small field of view ($\sim$ 1 m^2) of the downward facing systems. Nevertheless, Cappo et al. (2010) found that with the more widely used horizontal facing BRUVs, which have a larger field of view, small-bodied fishes were also frequently displaced by larger-bodied fishes after the first 15 minutes of a 60-minute deployment, and suggested that, to overcome this bias, length measurements should either be taken at staggered intervals throughout the deployment or from a range of samples of different deployment lengths. More recent research, however, suggests that this may not be necessary: A large enough, horizontal field of view (e.g. $\sim$ 37.2 m^2) is likely to reduce the potential effect of agonistic interactions on sampled length-frequency distributions and abundance estimates by also sufficiently capturing the

presence of smaller-bodied fishes in the background who do not directly interact with dominant individuals around the bait (Coghlan et al. 2017). This suggests that stereo-BRUVs are likely to provide a robust sampling method for comparing the body length distributions of fishes between species, communities and locations.

3.5 Conclusions

Density-dependent mortality in reef fish assemblages arises from the interplay between predation and competition, both of which are contingent upon variable rates of larval recruitment and habitat complexity (Hixon & Jones 2005). The results of this study suggest that body size plays an important role in determining the outcomes of competitive interactions among sparid reef fishes. Asymmetries in resource use related to body size differences between resident individuals appear to be an important predictor of species coexistence. In unfished communities, coexistence among sparid reef fishes was facilitated by niche-based processes along a depth-related species richness gradient. Contraction of species' resource use patterns across the body length axes of local communities appeared to be a promoter of species coexistence. Reduced variance in species' body length distributions may therefore provide a stabilising mechanism which allows individuals with overlapping resource requirements to compete less strongly with members of other species than with conspecifics, thus reducing the impact of size-based fitness inequalities. Size-selective fishing mortality has increased the mortality rate of large, dominant fishes. Among sparids, this has been asocciated with phenotypic changes such as reduced size-at-maturity and earlier sex-change (Buxton 1993; Götz et al. 2008). In addition to showing signs of reduced resource competition (eg. higher condition factor, Götz et al. 2008), the trait-neutral relationship between the species richness of exploited communities and their body length distributions suggests that exploitation may also alter the number of species which can locally coexist. Within this context, size-selective fishing mortality may act as an equalising mechanism which reduces the average fitness of large-bodied species relative to small-boded species, and thereby

facilitates species coexistence via weaker stabilising mechanisms.

Anthropogenic disturbances such as fishing mortality contribute to changes in both the functional traits and relative fitness of individuals; this has the potential to disproportionally alter species' vital rates. MPAs provide an important baseline against which to assess the effects of exploitation by providing essential understanding into how the indirect effects of fishing influence species' vital rates and their distributions. Both in South Africa (Turpie et al. 2000) and globally (Roberts et al. 2002), the management of marine biodiversity has largely focused on mapping patterns of taxonomic diversity in order to focus conservation efforts on biodiversity hotspots. However, because the number of species which coexist within a given area is typically the result of multiple processes acting across different spatial and temporal scales (Scheiner et al. 2011), species richness, evenness, and abundance are often weak quantitative measures of human impacts (D'agata et al. 2014; Villéger et al. 2010). By considering the functional structure of communities, trait-based measures of diversity provide a complimentary, process-based approach for evaluating the sensitivity of communities to different forms of anthropogenic disturbance (Mouillot et al. 2013, 2006). In order to address important knowledge gaps in the management of biodiversity and ecosystem function a more comprehensive understanding is needed of how trait-environment relationships change within the competitive milieu. It is becoming apparent that even in high-diversity systems like coral reefs, the local extirpation of species as a result of fishing pressure may significantly impact ecosystem functioning (Mouillot et al. 2014). Because fishing tends to remove whole functional groups, the effects of species losses on the loss of ecosystem function are likely to be exacerbated in temperate reef fish communities (Micheli & Halpern 2005). By providing a representation of the position of species within a functional space, the additional trait information places a greater emphasis on predicting how species will respond to different forms of competitive interactions, environmental variation, and anthropogenic disturbance (McGill et al. 2006; Mouillot et al. 2013). Most forms of fishing are inherently size-selective and therefore likely to influence the mech-

anisms by which species within size-structured communities coexist. Trait-based approaches which only consider sources of interspecific variation are therefore likely to underestimate the ecosystem effects of fishing at small spatial scales. Body-size distributions are a highly informative alternative to taxon-based descriptors for assessing the status of aquatic ecosystems (Blueweiss et al. 1978; Boudreau & Dickie 1989; Peters 1986). Because size-structure is an important component of marine ecosystem function (Fisher et al. 2010), studies which consider both interspecific and intraspecific sources of trait variation are likely to provide more process-based insights into the effects of fishing.

Chapter 4

General discussion

Sparid fishes (family: Sparidae) constitute one of the most abundant and diverse groups of reef-associated ichthyofauna on subtidal reefs across the Agulhas Ecoregion's (Turpie et al. 2000). Although a number of populations have been heavily depleted since the mid 1900's by overfishing, sparids continue to form an important component of the commercial and recreational linefisheries (Brouwer & Buxton 2002; Griffiths 2000; Mann 2013). This thesis explored the relative contributions of dispersal and local environmental factors to the maintenance of species diversity across spatial scales relevant to the ecology and management of reef-associated sparids within South Africa's Agulhas Ecoregion. Firstly, total regional diversity (γ-diversity) was additively partitioned into mean local diversity (α- diversity) and components of turnover (β-diversity) across hierarchically nested spatial scales. Observed diversity components were compared to those of a null model in which individual fishes colonised sites independently of their location and the presence or absence of other fishes. Next, patterns of compositional turnover (β diversity) between local communities (i.e. sites) were analysed within the metacommunity framework of Leibold et al. (2004). This framework explicitly considers the relative prevalence of niche-based species sorting (i.e. local selection) and dispersal limitation (i.e. dispersal and ecological drift) in promoting compositional differences among local communities. Two spatial scales were analysed to consider the separate dispersal

distances of pelagic larvae and resident fishes: The between-location scale predominantly captured the long-range dispersal of pelagic larvae over 100's of kilometres; the within-location scale encompassed the post-settlement movements of resident fishes among local habitat patches separated by 100's - 1000's of m. Taxon-based descriptors of biodiversity do not fully account for functional differences among conspecifics in size-structured populations. To account for these differences, the ratio of species-wide (i.e. intraspecific) to community-wide variance in body length provided a strong test of whether species coexistence among trophically similar species was facilitated by niche differentiation, trait-neutral mechanisms, or via individual variation. The coexistence framework of Chesson (2000) emphasises the roles of local selection and ecological drift in maintaining species coexistence with respect to internal community filters (eg. microhabitat variation and density-dependent interactions). Comparisons between communities from the Tsistikamma National Park "no-take" marine protected area (TNP MPA) and "exploited" Algoa Bay (AB) highlighted how size-selective fishing mortality potentially alters the processes which mediate competitive coexistence among reef-associated sparid fishes.

Chapter 2 highlighted that species turnover decreased with increasing spatial scale; the highest β-diversity was observed among communities nested within the same depth stratum. The number of sparid species which co-occured at this scale was, however, lower than that expected by chance. This was largely attributed to the non-random turnover of species between TNP MPA and AB: At scales of 100's of km, limits to long-range dispersal (Kiflawi et al. 2006) and habitat area (Bellwood & Hughes 2001) can strongly influence local reef fish diversity (but see Belmaker et al. 2008). The processes which influence broader patterns of diversity among locations were confounded by management differences. Nevertheless, some inferences could be drawn: The exploited status of AB was not associated with the location-wide extirpation of species which have, historically, been heavily exploited (e.g. dageraad *Chrysoblephus cristiceps*, red steenbras *Petrus rupestris*). Rather, species turnover among locations was characterised by small populations

near their biogeographic range margins (eg. englishman *Chrysoblephus anglicus*, slinger *Chrysoblephus puniceus*, hottentot *Pachymetopon blochii*, scotsman *Polysteganus praeorbitalis*). In order to disentangle the joint influence of species' biogeographies and fishing mortality on present patterns of reef fish diversity, a greater number of replicate locations are needed. Given that local diversity patterns can depended greatly on regional species diversity (Belmaker et al. 2008; Cornell et al. 2007; Crist et al. 2003), the influence that local processes have on species' distributions can only be fully understood within the purview of historical factors which have shaped the diversity of marine ecoregions.

While species turnover was highest among sites nested within the same depth stratum, the observed patterns did not differ from those of a null model in which habitat associations and species interactions were absent. This suggests that stochastic factors such as larval dispersal and settlement predominately influence whether species are present or absent at small spatial scales: Unlike crytic reef species, such as clingfishes (Gobiesocidae) and blennies (Blenniidae), whose larvae hatch from benthic eggs, sparid have pelagic larvae which are diffusely distributed within TNP MPA and therefore likely to settle via a largely passive process within the reserve (Tilney et al. 1996). Although late-stage sparid larvae show a limited capacity for directed dispersal (Pattrick & Strydom 2009), stochastic processes linked to pelagic larval connectivity are likely to prevail among nearshore reef fish populations over 100's of km (Siegel et al. 2008). Furthermore, as recruitment fluctuations and early post-settlement mortality tend to dissipate recruit-habitat relationships over small spatial scales, species-specific recruitment patterns are expected to remain invariant with respect to local habitat characteristics (Ault & Johnson 1998a; Sale, Danilowicz, et al. 2005). This view is consistent with predictions from competitive lotteries (e.g. Sale 1977, 1978) in which species coexistence among ecologically similar reef fishes depends on a limited and unpredictable supply of living space alone, rather than fine-scale niche diversification. Within reefs, the number of sparid species which co-occured at the local community scale conformed to this pattern, and could be

adequately represented by a random sample of the species that recruited at reefs within the same location. Nevertheless, patterns of species turnover are contingent on the spatial scale at which observations take place: Stochastic processes, such as recruitment variability, tend to predominate over reef fish communities on isolated habitat patches (e.g. coral heads; patchy reefs). However, they do not necessarily scale up to reflect the diversity of reef fishes at broader spatial scales (Anderson et al. 1981; Sale 1998). Although it not always evident at local scales, direct density-dependence at some spatial or temporal scale remains central to the maintenance of reef fish biodiversity (Ault & Johnson 1998b; Connell & Jones 1991).

When species' relative abundances were taken into account the compositional diversity (i.e. Shannon diversity) of sparid communities was characterised by limited alpha diversity and non-random turnover which was most evident among sites nested within the same depth stratum (Chapter 2). This suggested that ecological processes taking place within reefs contributed disproportionately to the overall compositional diversity of reef-associated sparid fishes within the Agulhas Ecoregion. Non-random turnover among communities was partly attributed to the aggregation of fishes with other conspecifics. In other systems, intraspecific aggregation among coral-dwelling fishes (Belmaker et al. 2008) and arthropod assemblages (Crist et al. 2003; Veech 2005) has been found to significantly limit local α-diversity, while enhancing turnover among sites (but see Stoll & Prati 2001). Although the relative abundances of resident reef fishes may initially be subject to stochastic juvenile recruitment events, post-settlement processes such as resident-juvenile interactions and the establishment of home ranges can modify population densities and the structure of reef fish communities (Almany 2003; Lewis 1997). The perceived degree of spatial connectivity among local communities plays a central role in modulating these processes: Due to their strong aversion to non-reef habitat, post-settlement movements of reef-associated fishes tend to be facilitated on large, continuous reefs, and may, by promoting competitive interactions, buffer some of the variability generated by spatial and seasonal fluctuations in recruitment rates (Andrews & Anderson

2004; Ault & Johnson 1998c; Belmaker et al. 2009; Nanami & Nishihira 2002, 2003). Nevertheless, the results of this study corroborate the view that, while the number of species which locally coexist may largely depend on the chance dispersal of larvae from distant populations, ecological processes which take place within the reef take precedence in shaping patterns of relative abundance (see Sale & Douglas 1984; Sale et al. 1994).

In terms of the compositional differences among communities, species sorting was the most prevalent driver of turnover within both locations (Chapter 2). Species-specific responses to local environmental factors were largely related to habitat depth, in agreement with other studies from tropical (Brokovich et al. 2008), sub-tropical (Malcolm et al. 2011) and warm-temperate reefs (Heyns-Veale et al. 2016; Zintzen et al. 2012). These studies identified depth as a major driver of fish community structure; the transition between shallow and deep reef habitats is accompanied by significant changes in the abiotic environment (Bradbury & Young 1981; Gili & Coma 1998; Wilkinson & Evans 1989) and macrobenthic community (Adjeroud 1997; Garrabou et al. 2002; Heyns et al. 2016). Under conditions where species are able to adequately disperse to favourable sites, variation in environmental conditions is expected to facilitate coexistence via competitive trade-offs in resource use (Leibold et al. 2004). Despite the ability of pelagic larvae to be dispersed over large distances, the dispersal of many reef-associated fishes can still be limited: At the scale of individual reefs, populations may diverge due to spatial and temporal difference in larval recruitment rates (e.g. Doherty 1981; Doherty & Fowler 1994b). This is likely to be exacerbated by the infrequency of post-settlement movements across sandy habitats which prevents fish from colonising neighbouring reefs (Chapman & Kramer 2000; Kramer & Chapman 1999). Consequently, the sand matrix of 5-10 km which separates reefs within TNP MPA and Algoa Bay is likely to be a sufficient barrier to the post-settlement movements of most resident fishes (Ault & Johnson 1998c; Fernández et al. 2008; Lewis 1997). To this effect, dispersal limitation may prevent the best-suited species from establishing at sites favourable to their growth

and survival, and allow less-suited species to persist by chance (Hurtt & Pacala 1995). While long-range larval dispersal between locations may be a limiting factor for regionally rare species, the lack of spatial turnover among reefs within locations (Chapter 2) suggests that, over intermediate distances of 10's of km, reefs are likely to receive recruits from the same source of pelagic larvae. This conforms to the view of Tilney et al. (1996) who found that sparid larvae were diffusely distributed among reefs within TNP MPA. Nevertheless, the importance of habitat structure to the persistence of reef fishes cannot be overstated; the finding that habitat diversity at the smallest spatial scale (e.g. among individual sites) contributes disproportionately to the overall structure of the metacommunity corroborates findings from tropical (e.g. MacNeil et al. 2009) and temperate (e.g. Anderson & Millar 2004) reef fish communities. Consequently, the physical and macrobenthic characterisation of subtidal reef habitats is of considerable importance to the long-term persistence of many of South Africa's demersal linefish species (Griffiths & Wilke 2002; Heyns-Veale et al. 2016; Sink et al. 2006).

At within-reef scales, dispersal limitation also explained a significant portion of compositional turnover (Chapter 2). The detection of spatial structures at this scale, which were independent of local environmental gradients, is likely to be related to the post-settlement dispersal of resident individuals throughout ontogeny. Although many of the proximal causes of post-settlement movements remain elusive, changing ontogenetic requirements and density-dependent interactions favour the adaptive relocation of a fish's home range throughout the course of its lifetime. (Dahlgren & Eggleston 2000; Macpherson 1998). Very little is currently known about the ecology of newly settled fishes on temperate reefs. Recruitment rates are, however, expected to vary widely among different habitat patches within the reef: Topographically complex habitats, such as those with dense macroalgal assemblages and an abundance of structural shelter, mitigate the disproportionately high mortality rates experienced by fishes shorty after settlement and lead to aggregated recruitment patterns (Connell & Jones 1991; Hixon & Beets 1989; Levin & Hay

1996). In the Mediterranean Sea, Macpherson (1998) observed that monospecific aggregations of juvenile sparid fishes tended to disperse away from their respective nursery areas as they attained larger body sizes. This, together with the partitioning of habitat use and food size among different size classes (Buxton 1984; Buxton & Clarke 1986, 1991) and the increase in the average body size of fishes with depth (Heyns-Veale et al. 2016; Macpherson & Duarte 1991; McCormick 1989) supports the view that many sparid species undertake ontogenetic home range relocations during their lifetime.

As the movements of reef-associated fishes away from established home ranges can be highly costly, long-distance movements over non-reef habitat are likely to be rare (Kramer & Chapman 1999). There is currently very little direct evidence documenting the scales or prevalence of ontogenetic niche shifts among resident reef fishes. Acoustic telemetry studies tend to be limited in their duration and do not encompasses a significant portion of the lifespan of long-lived species. While mark recapture surveys have been able to identify long-term residency of fishes within broader areas, their limited ability to provide precise estimates of home range size precludes the detection of small-scale home range shifts. A limited number of acoustic telemetry studies have documented home range shifts among temperate reef fishes: Nevertheless, both silver seabream *Pagrus auratus* (Sparidae) and California sheephead *Semicossyphus pulcher* (Larbidae), have been shown to shift their core home ranges by up to 300 m within a year (Parsons et al. 2003; Topping et al. 2006, respectively). Advancements in the size and lifespan of acoustic tags, which also allow for the recording of fine-scale temperature, depth and tri-axial acceleration, are likely to provide novel insights into the triggers and scales of fish movement behaviour (Stehfest et al. 2015). Although it is often not incorporated into demographic models, the post-settlement dispersal of adult fishes among local communities is likely to have important demographic effects, particularly for sporadically recruiting species whose persistence depends on the survival of long-lived adults (Gunderson & Vetter 2006).

It stands to reason that if reef fish populations are structured by processes which take place throughout the entire life cycle of a fish; the dispersal of eggs and larvae to suitable nursery areas, juvenile recruitment and movements, and the home range use of adults all need to be considered. This requires the consideration of how both local and regional processes contribute to changes in abundance and the long-term persistence of populations. Knowledge of larval dispersal and the potential for self-recruitment remain a long-standing barrier to effectively delineating the scales that will create the local demographic independence characteristic of metapopulation structure (Kritzer & Sale 2010). Recently, the proliferation of larval connectivity studies in tropical coral reefs has demonstrated that larval dispersal frequently takes place over distances of <5 - 15 km, leading to higher rates of self-recruitment than previously thought (Almany et al. 2007, 2013; Jones et al. 2009). Due to their site fidelity, similar findings of less pervasive larval dispersal among temperate reef fishes would lead to metapopulation structures on smaller spatial scales than previously thought (Freiwald 2012). Nevertheless, it may also be necessary to validate the assumptions surrounding the post-settlement movement potential of resident reef fishes over more meaningful timescales. Populations which typically display a high degree of site fidelity often include a small proportion of adults who undertake long-distance migrations to new home ranges. Given their extensive longevity, the successful movement of even a few adult fish can have long-term demographic consequences (Gunderson & Vetter 2006). Despite recent advances in larval tagging and acoustic monitoring techniques, large knowledge gaps still exist in our understanding of demographic connectivity, particularly among temperate reef fishes. A combination of contemporary approaches including parentage analysis, otolith microchemistry, and larval tagging together with longer-term electronic monitoring of adult movements is needed to elucidate the scales at which larval dispersal and home range shifts are likely to influence the demographic parameters of temperate reef fish populations (Gunderson & Vetter 2006; Jones et al. 2009).

When organised into trophic groups, temperate reef fish communities are char-

acterised by high levels of functional redundancy (Micheli & Halpern 2005); in other words, a large proportion of species perform similar functions within the ecosystem. Sparid species share similar average trophic requirements throughout their lifetime (Table A6) and appear to have fairly broad habitat requirements. As a result, much of the partitioning of food resources (via food size) and microhabitat use among resident individuals is likely to be attributable to difference in body size; this was hypothesised to play an important role in determining the number of species that could locally co-occur (Chapter 3): Ratios of intraspecific (i.e. species-wide) to community-wide variance in body length were found to be a good predictor of local species richness among unfished communities within TNP MPA. Here, coexistence among species was promoted by a relative reduction in the ratio of intraspecific to community-wide variance in body length, conforming to predictions from niche theory. This indicated that stablising mechanisms were likely to facilitate species coexistence by causing species to contract their resource use, and thus, compete more strongly with similar-sized conspecifics than they did with other species. This finding also suggests that among species with similar trophic niches, intraspecific differences in body size provide one means of mitigating the direct impacts of competition between juveniles and adults (Colloca et al. 2010; Wilson 1975).

Among exploited sparid communities from Algoa Bay, species richness patterns conformed to neutral expectations. Body size distributions did not appear to influence the number of species which coexist at the local scale. This suggests that constraints to colonisation were not likely to be related to fitness differences between small and large individuals, a feature which would generally be associated with recruitment-limited reefs in which resource limitation and direct density-dependence are absent (Doherty & Fowler 1994b). Patterns of relative abundance that vary with dispersal rate rather than with the density of competitors are the hallmark of recruitment-limited systems (Doherty 1981; Doherty & Fowler 1994a). Although this thesis did not directly address whether larval recruitment rates in Algoa Bay were lower than in TNP MPA, there are a number of reasons why this is unlikely:

Firstly, the relative abundances of sparid fishes was found to vary consistently with local environmental factors in both locations (Chapter 2), and are therefore likely to be fairly stable over time. Secondly, due to the broad scales over which longshore currents are likely to be capable of transporting larvae within the Agulhas Ecoregion (Attwood et al. 2002; Brouwer et al. 2003; Tilney et al. 1996), similar reef habitats separated by approximately 200 km are unlikely to receive disparate larval supplies. Finally, due to the larger reef area of shallow-water habitat, reefs in Algoa Bay are likely to receive a greater supply of larvae, and thus, support a larger number of juvenile fishes.

Fishing-induced truncation of population size-structure is a more likely explanation for what appears to be reduced resource competition: Neutral patterns of species coexistence in Algoa Bay were principally related to a reduction in the community-wide variance (IC) of fish lengths. This is to be expected if fisheries preferentially target large-bodied fish resulting in the size truncation of exploited populations. Because larger fish tend to be more competitively dominant and have access to wider range of trophic resources, their disproportionate removal by fisheries is likely to lead to weaker resource competition if fish compete for limited resources. Other studies in temperate reef systems have cited higher condition factor (Götz et al. 2008) and wider roaming behaviour (Parsons et al. 2010) among resident reef fishes within exploited populations to suggest that the removal of large-bodied fishes by fisheries may weaken competition for limiting resources. There is a growing concern that size-selective mortality rates of fishing gears (reviewed by Kuparinen et al. 2009) may contribute to long-term changes to the phenotypic composition of exploited fish populations (Audzijonyte et al. 2013; Buxton 1993; Götz et al. 2008). As a result, fishing is further hypothesised to exert strong selection on the evolution of earlier maturation and smaller body size (Dunlop et al. 2009; Law 2000).

The metacommunity structure of the Agulhas Ecoregion's reef-associated sparid fauna appeared to be largely driven by species sorting along the depth gradient, and to a lesser extent by the limited post-settlement dispersal of fishes over 100's

Table 4.1: Summary of main factors suggested to influence the diversity of sparid reef fishes in the warm-temperate Agulhas Ecoregion, South Africa. † denotes factors not directly investigated in this thesis.

Spatial scale	**Selection**	**Post-settlement dispersal**	**Larval dispersal**
Within reefs 100's of m	Habitat selection Competition (body size) Fishing mortality	Habitat connectivity Ontogenetic niche shifts	
Between reefs 10's of km	Habitat(depth) variation Nursery habitat †		Reef area †
Between locations 100's of km	Fishing mortality†		Reef area † Stochastic dispersal †

of metres (Chapter 2). The species sorting perspective highlights how the compositional diversity of communities is limited by niche availability. On warm-temperate subtidal reefs niche availability varies most strongly with habitat depth. Dispersal limitation at the within-reef scale emphasises how the relocation of fish home ranges to nearby habitat patches over the course of their ontogeny may contribute to patterns of spatial turnover over 100's - 1000's of m. The presence of both species sorting and small-scale dispersal limitation suggests that the long-term persistence of sparid diversity requires both a diversity of suitable reef habitats as well as a sufficient degree of spatial connectivity to facilitate ontogenetic habitat shifts (Green et al. 2015; Mouillot 2007). While depth is the primary factor influencing reef fish diversity at small and intermediate spatial scales, this study cannot discount composition of the macrobenthic community as a source of essential fish habitat. Because turnover in the macrobenthic community may also be driven by patterns of dispersal assembly which are independent of depth, disentangling the joint influence of macrobenthic diversity and depth-related abiotic factors such as water temperature remains an essential component of better predictive models of demersal fish distributions (Heyns-Veale et al. 2016). The adaptive dispersal of larger individuals to new home ranges provides one avenue by which the spatial overlap between cohorts, and thus, the strength of density-dependent population regulation can be reduced at the reef scale. Most reef-associated fishes have a limited capacity for

post-settlement dispersal, and face an increased energetic cost and risk of predation when undertaking long-distance movements, especially across non-reef habitat (Belmaker et al. 2005; Kramer & Chapman 1999). Although data on the prevalence and scale of home range relocations are limited, resident species should benefit from MPAs which preserve the spatial connectivity between shallow nursery habitats and deeper reef habitats via a continuous distribution of reef (Fernández et al. 2008; Lewis 1997).

While it is evident that size-selective fishing mortality can change the size- and age-structure of exploited fish populations (Edgar & Stuart-Smith 2009; Genner et al. 2010; Hsieh et al. 2010; Shin et al. 2005), it may, consequently, also influence the outcomes of competitive interactions among species, and thus, the species composition of communities (Chapter 3). The spatial aggregation of similar-sized conspecifics provides a likely mechanism whereby trophically similar species can partition their food resources and habitat use at the reef-wide scale. Because competition is most intense between similar sized fishes, ontogenetic niche shifts are likely to contribute towards the maintenance of niche-based coexistence mechanisms in communities following adequate lengths of protection from fishing. Fishing methods which exert their own selective pressure by increasing the mortality rate of fishes with certain traits (e.g. larger body size) have the potential to alter the selection regime in exploited communities. Ecological models which, typically, ignore sources of intraspecific variability will therefore underestimate the uncertainty in the growth of populations (Clark et al. 2001). By accounting for the stabilising effect of intraspecific competition (Chesson 2000), measures of intra- and interspecific variance in fish body size provided additional insights into the ecological processes which structure reef fish communities that were not apparent from species distributions. The results of Chapter 3 contribute toward the growing body of research which supports the applicability of community size structure as an effective indicator of anthropogenic disturbance (Donadi et al. 2015; Mouillot et al. 2006).

4.1 Concluding remarks

Small-scale studies frequently do not scale up to reflect broader scale patterns, due to the scale-dependent nature of ecological processes (Levin 1992; Sale 1998): The widespread phenomenon of age- and size-truncation of exploited populations induced by size-selective fishing frequently reduces the spatial heterogeneity and bet-hedging capacity of populations necessary to buffer short-term environmental variability (Hsieh et al. 2006, 2010). Determining the spatial and temporal scales at which niche processes and dispersal assembly predominate, and whether they are taxon-specific or trait-based, remains a key challenge to the effective protection of exploited reef fish populations (Mellin et al. 2014). The demographic linkages between local populations which are maintained by the dispersal of larvae, juveniles, or adults, are an ecological consideration necessary for the persistence of exploited populations and their recovery within an MPA network (Green et al. 2015): For MPAs to be successfully implemented, it is necessary to ascertain whether (1) populations within individual "no-take" areas are self-sustaining; (2) larval export and adult spillover are sufficient to subsidise exploited populations beyond their boundaries; (3) protected populations are sufficiently connected via larval exchange to support the resiliance of MPA networks. One of the strengths of stereo-BRUVs lies in their ability to non-destructively quantify both the distributions of fishes and degree of trait variation (both morphological and behavioural) among individuals. By overcoming many of the sampling limitations of traditional fish surveys methods, stereo-BRUVs allow this to be undertaken over a range of ecological scales which were previously inaccessible. Traditional ecological theory has largely emphasised interspecific variation; studies which integrate measures of intra- and interspecific trait variation with more traditional measures of taxonomic diversity have the potential to provide a greater understanding of the processes which drive patterns of biodiversity. Future investigations of exploited reef fish communities would benefit from estimates of the spatial and temporal scales at which turnover in taxonomic β-diversity and functional β-diversity correspond to human impacts (McGill et al. 2015). As global

changes threaten both the species composition and functioning of communities, an improved understanding of how the responses of individual species scale up to affect community-level trends is needed in order to proliferate the ecosystem-based management of marine biodiversity.

Appendix A

Supplementary tables and figures

Table A1: Physical characteristics of reefs surveyed by stereo-BRUVs in Tsitsikamma National Park MPA (TNP MPA) and Algoa Bay (AB) within the Agulhas Ecoregion, South Africa.

			Water temperature (°C)			Depth (m)		
Study area	Reef	n	Min.	Max.	Mean	Min.	Max.	Mean
TNP MPA	Rheeders Reef	16	16.5	17.1	16.8	12.5	46.0	28.4
TNP MPA	Middle Bank	16	11.2	16.7	14.9	23.0	72.0	40.7
AB	Cape Recife	18	10.3	17.2	12.0	13.0	76.2	42.0
AB	Riy Bank	17	10.6	16.9	15.2	18.1	73.9	45.0

Table A2: Summary of relative abundances (MaxN) and lengths of all species recorded at Rheeders Reef, Tsitsikamma National Park MPA. $MaxN_{Total}$: Cumulative MaxN of all sites; NA: not applicable (not enough observations); - : not recorded.

				MaxN				‡	Length (FL; mm)				†
Family	Common name	Scientific name	$MaxN_{Total}$	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n
Ariidae	Black seacatfish	*Galeichthys ater*	11	2.20	1.30	1	4	5	256.5	31.6	218	313	9
Carangidae	Giant yellowtail	*Seriola lalandi*	3	1.00	0.00	1	1	3	974.0	374.6	551	1264	3
Centracanthidae	Windtoy	*Spicara axillaris*	9	4.50	3.54	2	7	2	103.0	26.3	87	149	5
Chaetodontidae	Doublesash butterflyfish	*Chaetodon marleyi*	1	1.00	NA	1	1	1	132.0	NA	132	132	1
Cheilodactylidae	Redfingers	*Cheilodactylus fasciatus*	2	1.00	0.00	1	1	2	192.0	NA	192	192	2
Cheilodactylidae	Barred fingerfin	*Cheilodactylus pixi*	5	1.25	0.50	1	2	4	136.7	37.3	95	167	4
Cheilodactylidae	Twotone fingerfin	*Chirodactylus brachydactylus*	12	2.00	1.55	1	5	6	234.3	20.1	211	272	10
Dasyatidae	Short-tail stingray	*Dasyatis brevicaudata* *	1	1.00	NA	1	1	1	562.0	NA	562	562	1
Hexanchidae	Spotted sevengill cowshark	*Notorynchus cepedianus*	4	1.00	0.00	1	1	4	1546.8	195.0	1413	1833	4
Myxinidae	Sixgill hagfish	*Eptatretus hexatrema*	1	1.00	NA	1	1	1	766.0	NA	766	766	1
Oplegnathidae	Cape knifejaw	*Oplegnathus conwayi*	5	1.25	0.50	1	2	4	257.8	54.0	163	294	6
Parascorpididae	Jutjaw	*Parascorpis typus*	1	1.00	NA	1	1	1	190.0	NA	190	190	1
Scyliorhinidae	Puffadder shyshark	*Haploblepharus edwardsii*	2	1.00	0.00	1	1	2	396.0	NA	396	396	2
Scyliorhinidae	Brown shyshark	*Haploblepharus fuscus*	1	1.00	NA	1	1	1	464.0	NA	464	464	1
Scyliorhinidae	Dark shyshark	*Haploblepharus pictus*	2	1.00	0.00	1	1	2	433.5	181.7	305	562	2
Scyliorhinidae	Striped catshark	*Poroderma africanum*	23	1.92	1.31	1	5	12	585.2	81.2	396	775	18
Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	4	1.00	0.00	1	1	4	565.5	7.8	560	571	4
Serranidae	Koester rockcod	*Acanthistius sebastoides*	4	1.00	0.00	1	1	4	205.5	36.7	171	256	4
Serranidae	Yellowbelly rockcod	*Epinephelus marginatus*	4	2.00	0.00	2	2	2	419.5	45.3	362	467	4
Serranidae	Comber	*Serranus knysnaensis*	1	1.00	NA	1	1	1	-	-	-	-	0
Tetraodontidae	Evileye blaasop	*Amblyrhynchotes honckenii*	7	1.17	0.41	1	2	6	181.7	19.0	165	215	7
Triakidae	Smooth-hound shark	*Mustelus mustelus*	2	1.00	0.00	1	1	2	909.0	NA	909	909	2
Triakidae	Spotted gullyshark	*Triakis megalopterus*	2	1.00	0.00	1	1	2	1301.0	NA	1301	1301	2
Sparidae	Carpenter	*Argyrozona argyrozona*	5	2.50	2.12	1	4	2	148.0	2.5	144	151	5
Sparidae	Fransmadam	*Boopsoidea inornata*	190	13.57	8.48	1	33	14	205.8	26.1	139	256	155
Sparidae	Santer	*Cheimerius nufar*	3	1.00	0.00	1	1	3	159.5	24.7	142	177	3
Sparidae	Dageraad	*Chrysoblephus cristiceps*	29	3.22	3.19	1	10	9	373.6	119.5	193	601	23
Sparidae	Red stumpnose	*Chrysoblephus gibbiceps*	6	1.20	0.45	1	2	5	383.5	124.8	193	536	6
Sparidae	Roman	*Chrysoblephus laticeps*	137	9.13	2.95	4	14	15	277.5	65.0	107	416	106
Sparidae	Blacktail	*Diplodus capensis*	54	4.91	3.39	1	11	11	193.4	39.6	90	270	46
Sparidae	Zebra	*Diplodus hottentotus*	5	1.67	0.58	1	2	3	155.8	40.7	121	204	4
Sparidae	Janbruin	*Gymnocrotaphus curvidens*	7	1.00	0.00	1	1	7	278.3	39.6	240	319	7
Sparidae	Blue hottentot	*Pachymetopon aeneum*	79	5.27	3.45	1	12	15	202.0	58.7	119	356	61
Sparidae	Hottentot	*Pagellus bellottii natalensis*	12	4.00	3.00	1	7	3	160.0	32.7	117	213	8
Sparidae	Red steenbras	*Petrus rupestris*	9	1.29	0.49	1	2	7	412.6	46.0	327	477	8
Sparidae	Seventy-four	*Polysteganus undulosus*	1	1.00	NA	1	1	1	291.0	NA	291	291	1
Sparidae	Panga	*Pterogymnus laniarius*	30	4.29	4.11	1	12	7	203.8	47.3	137	329	23
Sparidae	Cape stumpnose	*Rhabdosargus holubi*	7	2.33	2.31	1	5	3	161.8	12.1	148	184	6
Sparidae	Strepie	*Sarpa salpa*	336	112.00	44.80	61	145	3	151.0	23.5	81	273	136
Sparidae	Steentjie	*Spondyliosoma emarginatum*	248	15.50	11.22	2	34	16	181.9	24.6	126	250	179

‡ MaxN estimates from 16 replicate deployments; † Length estimates from 15 replicate deployments; * Disk length measured for skates and rays.

Table A3: Summary of relative abundances (MaxN) and lengths of all species recorded at Middle Bank, Tsitsikamma National Park MPA. $MaxN_{Total}$: Cumulative MaxN; NA: not applicable (not enough observations); - : not recorded.

			MaxN					‡	Length (FL; mm)				†
Family	Common name	Scientific name	$MaxN_{Total}$	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n
Ariidae	Black seacatfish	*Galeichthys ater*	1	1.00	NA	1	1	1	292.0	NA	292	292	1
Carangidae	Horse mackerel	*Trachurus* spp.	5	5.00	NA	5	5	1	-	-	-	-	0
Centracanthidae	Windtoy	*Spicara axillaris*	1	1.00	NA	1	1	1	-	-	-	-	0
Cheilodactylidae	Barred fingerfin	*Cheilodactylus pixi*	5	1.25	0.50	1	2	4	76.7	9.8	71	88	4
Cheilodactylidae	Twotone fingerfin	*Chirodactylus brachydactylus*	9	1.50	0.84	1	3	6	212.2	29.5	172	258	7
Cheilodactylidae	Bank steenbras	*Chirodactylus grandis*	1	1.00	NA	1	1	1	383.0	NA	383	383	1
Dasyatidae	Short-tail stingray	*Dasyatis brevicaudata* *	9	1.29	0.49	1	2	7	1104.1	153.4	871	1368	8
Hexanchidae	Spotted sevengill cowshark	*Notorynchus cepedianus*	4	1.33	0.58	1	2	3	1713.7	267.8	1416	1935	4
Mugilidae	Mullet	*Chelon richardsonii*	176	176.00	NA	176	176	1	140.4	15.0	127	171	8
Odontaspididae	Ragged-tooth shark	*Carcharias taurus*	2	1.00	0.00	1	1	2	1179.0	NA	1179	1179	2
Oplegnathidae	Cape knifejaw	*Oplegnathus conwayi*	1	1.00	NA	1	1	1	234.0	NA	234	234	1
Parascorpididae	Jutjaw	*Parascorpis typus*	1	1.00	NA	1	1	1	384.0	NA	384	384	1
Sciaenidae	Geelbeck	*Atractoscion aequidens*	3	1.00	0.00	1	1	3	780.0	85.9	681	835	3
Scyliorhinidae	Striped catshark	*Poroderma africanum*	19	1.90	1.52	1	5	10	586.8	97.8	400	777	18
Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	2	1.00	0.00	1	1	2	537.5	4.9	534	541	2
Tetraodontidae	Evileye blaasop	*Amblyrhynchotes honckenii*	4	1.33	0.58	1	2	3	179.3	37.6	140	215	3
Triakidae	Smooth-hound shark	*Mustelus mustelus*	5	1.00	0.00	1	1	5	1245.8	150.8	1037	1393	5
Sparidae	Carpenter	*Argyrozona argyrozona*	103	6.87	7.29	1	30	15	356.9	69.4	258	575	62
Sparidae	Fransmadam	*Boopsoidea inornata*	213	17.75	25.44	1	82	12	191.2	28.5	126	247	95
Sparidae	Santer	*Cheimerius nufar*	9	1.50	0.55	1	2	6	268.6	23.5	245	313	9
Sparidae	Dageraad	*Chrysoblephus cristiceps*	2	1.00	0.00	1	1	2	316.5	61.5	273	360	2
Sparidae	Red stumpnose	*Chrysoblephus gibbiceps*	39	3.00	3.42	1	12	13	321.2	75.0	188	417	27
Sparidae	Roman	*Chrysoblephus laticeps*	157	10.47	6.47	2	26	15	305.6	56.8	169	418	110
Sparidae	Blacktail	*Diplodus capensis*	1	1.00	NA	1	1	1	148.0	NA	148	148	1
Sparidae	Zebra	*Diplodus hottentotus*	9	2.25	1.89	1	5	4	237.3	19.2	215	264	8
Sparidae	Janbruin	*Gymnocrotaphus curvidens*	4	1.00	0.00	1	1	4	270.7	57.5	235	337	4
Sparidae	Blue hottentot	*Pachymetopon aeneum*	113	8.69	10.36	1	34	13	198.7	45.4	118	337	66
Sparidae	Hottentot	*Pachymetopon blochii*	24	2.18	1.47	1	6	11	327.7	22.6	285	364	20
Sparidae	Red steenbras	*Petrus rupestris*	36	2.57	1.09	1	5	14	530.3	113.8	241	732	31
Sparidae	Panga	*Pterogymnus laniarius*	46	4.60	3.84	1	12	10	243.9	34.9	186	311	33
Sparidae	White stumpnose	*Rhabdosargus globiceps*	9	3.00	1.73	1	4	3	194.1	16.1	159	207	8
Sparidae	Cape stumpnose	*Rhabdosargus holubi*	1	1.00	NA	1	1	1	142.0	NA	142	142	1
Sparidae	Steentjie	*Spondyliosoma emarginatum*	355	25.36	20.01	3	68	14	192.8	24.7	135	265	200

‡ MaxN estimates from 16 replicate deployments; † Length estimates from 15 replicate deployments; * Disk length measured for skates and rays.

Table A4: Summary of relative abundances (MaxN) and lengths of all species recorded at Cape Recife, Algoa Bay. $MaxN_{Total}$: Cumulative MaxN; NA: not applicable (not enough observations); - : not recorded.

			MaxN					‡	Length (FL; mm)				†
Family	Common name	Scientific name	$MaxN_{Total}$	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n
Ariidae	Black seacatfish	*Galeichthys ater*	57	3.56	1.75	1	7	16	248.1	20.3	207	292	41
Callorhinchidae	Cape elephantfish	*Callorhinchus capensis*	1	1.00	NA	1	1	1	411.0	NA	411	411	1
Carangidae	Horse mackerel	*Trachurus* spp.	3	1.00	0.00	1	1	3	232.0	2.8	230	234	3
Centracanthidae	Windtoy	*Spicara axillaris*	1	1.00	NA	1	1	1	223.0	NA	223	223	1
Cheilodactylidae	Redfingers	*Cheilodactylus fasciatus*	2	1.00	0.00	1	1	2	269.5	6.4	265	274	2
Cheilodactylidae	Barred fingerfin	*Cheilodactylus pixi*	6	1.20	0.45	1	2	5	115.3	11.3	100	127	5
Cheilodactylidae	Twotone fingerfin	*Chirodactylus brachydactylus*	2	1.00	0.00	1	1	2	232.0	NA	232	232	2
Cheilodactylidae	Bank steenbras	*Chirodactylus grandis*	1	1.00	NA	1	1	1	423.0	NA	423	423	1
Dasyatidae	Short-tail stingray	*Dasyatis brevicaudata* *	5	1.67	1.15	1	3	3	965.0	349.3	718	1212	3
Hexanchidae	Spotted sevengill cowshark	*Notorynchus cepedianus*	2	1.00	0.00	1	1	2	1581.5	170.4	1461	1702	2
Muraenidae	Whitespotted moray	*Gymnothorax johnsoni*	1	1.00	NA	1	1	1	-	-	-	-	0
Myxinidae	Sixgill hagfish	*Eptatretus hexatrema*	8	1.14	0.38	1	2	7	460.4	149.3	325	659	7
Odontaspididae	Cape knifejaw	*Carcharias taurus*	1	1.00	NA	1	1	1	-	-	-	-	0
Parascorpididae	Jutjaw	*Parascorpis typus*	1	1.00	NA	1	1	1	303.0	NA	303	303	1
Rajidae	Spearnose skate	*Rostroraja alba* *	7	1.00	0.00	1	1	7	961.0	82.0	903	1019	7
Sciaenidae	Dusky kob	*Argyrosomus japonicus*	1	1.00	NA	1	1	1	-	-	-	-	0
Sciaenidae	Geelbeck	*Atractoscion aequidens*	1	1.00	NA	1	1	1	679.0	NA	679	679	1
Scyliorhinidae	Puffadder shyshark	*Haploblepharus edwardsii*	25	1.67	0.90	1	4	15	363.8	40.7	316	489	21
Scyliorhinidae	Brown shyshark	*Haploblepharus fuscus*	4	1.33	0.58	1	2	3	538.3	39.9	504	593	4
Scyliorhinidae	Striped catshark	*Poroderma africanum*	35	2.92	1.83	1	5	12	689.0	98.2	521	954	23
Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	17	1.42	0.67	1	3	12	536.8	86.6	381	650	16
Serranidae	Koester rockcod	*Acanthistius sebastoides*	6	1.00	0.00	1	1	6	228.0	26.0	200	262	6
Serranidae	Yellowbelly rockcod	*Epinephelus marginatus*	2	1.00	0.00	1	1	2	405.0	NA	405	405	2
Squalidae	Spiny dogfish	*Squalus* spp.	14	1.75	0.71	1	3	8	388.2	32.9	324	437	10
Triakidae	Smooth-hound shark	*Mustelus mustelus*	4	1.33	0.58	1	2	3	757.0	31.1	735	779	4
Sparidae	Carpenter	*Argyrozona argyrozona*	66	6.00	7.10	1	25	11	267.3	46.4	190	362	46
Sparidae	Fransmadam	*Boopsoidea inornata*	292	22.46	15.13	1	46	13	219.4	14.8	189	276	124
Sparidae	Santer	*Cheimerius nufar*	16	1.60	0.84	1	3	10	288.8	23.5	253	337	13
Sparidae	Englishman	*Chrysoblephus anglicus*	2	2.00	NA	2	2	1	384.0	45.3	352	416	2
Sparidae	Dageraad	*Chrysoblephus cristiceps*	9	2.25	1.50	1	4	4	245.5	25.4	211	289	8
Sparidae	Red stumpnose	*Chrysoblephus gibbiceps*	10	1.25	0.46	1	2	8	429.0	81.1	312	536	10
Sparidae	Roman	*Chrysoblephus laticeps*	67	4.47	2.67	1	10	15	271.9	54.1	140	364	53
Sparidae	Blacktail	*Diplodus capensis*	8	2.67	1.53	1	4	3	226.0	18.7	211	247	5
Sparidae	Zebra	*Diplodus hottentotus*	1	1.00	NA	1	1	1	-	-	-	-	0
Sparidae	Janbruin	*Gymnocrotaphus curvidens*	4	1.33	0.58	1	2	3	253.0	36.8	227	279	3
Sparidae	Blue hottentot	*Pachymetopon aeneum*	83	6.92	5.71	1	16	12	266.3	40.5	168	325	40
Sparidae	Red steenbras	*Petrus rupestris*	8	1.60	1.34	1	4	5	439.0	84.7	371	587	7
Sparidae	Seventy-four	*Polysteganus undulosus*	2	1.00	0.00	1	1	2	282.0	NA	282	282	2
Sparidae	Dane	*Porcostoma dentata*	1	1.00	NA	1	1	1	158.0	NA	158	158	1
Sparidae	Panga	*Pterogymnus laniarius*	77	7.00	6.18	1	16	11	296.3	37.4	170	354	40
Sparidae	White stumpnose	*Rhabdosargus globiceps*	9	1.50	0.55	1	2	6	260.4	14.8	244	284	7
Sparidae	Strepie	*Sarpa salpa*	1	1.00	NA	1	1	1	227.0	NA	227	227	1
Sparidae	Steentjie	*Spondyliosoma emarginatum*	33	4.13	3.31	1	9	8	240.0	20.5	210	291	23

‡ MaxN estimates from 18 replicate deployments; † Length estimates from 15 replicate deployments; * Disk length measured for skates and rays.

Table A5: Summary of relative abundances (MaxN) and lengths of all species recorded at Riy Bank, Algoa Bay. $MaxN_{Total}$: Cumulative MaxN; NA: not applicable (not enough observations); - : not recorded.

			MaxN					‡	Length (FL; mm)				†
Family	Common name	Scientific name	$MaxN_{Total}$	Mean	SD	Min.	Max.	n	Mean	SD	Min.	Max.	n
Ariidae	Black seacatfish	*Galeichthys ater*	31	2.21	0.97	1	4	14	253.5	17.1	203	290	28
Carangidae	Giant yellowtail	*Seriola lalandi*	17	5.67	5.69	1	12	3	850.9	164.5	466	993	8
Carangidae	Longfin yellowtail	*Seriola rivoliana*	1	1.00	NA	1	1	1	436.0	NA	436	436	1
Centracanthidae	Windtoy	*Spicara axillaris*	1	1.00	NA	1	1	1	233.0	NA	233	233	1
Cheilodactylidae	Redfingers	*Cheilodactylus fasciatus*	3	1.00	0.00	1	1	3	236.0	14.1	226	246	3
Cheilodactylidae	Barred fingerfin	*Cheilodactylus pixi*	13	1.86	1.21	1	4	7	115.5	18.6	86	133	9
Cheilodactylidae	Twotone fingerfin	*Chirodactylus brachydactylus*	16	2.29	1.38	1	4	7	259.1	36.0	195	334	14
Cheilodactylidae	Bank steenbras	*Chirodactylus grandis*	1	1.00	NA	1	1	1	305.0	NA	305	305	1
Cheilodactylidae	Natal fingerfin	*Chirodactylus jessicalenorum*	1	1.00	NA	1	1	1	474.0	NA	474	474	1
Dasyatidae	Short-tail stingray	*Dasyatis brevicaudata* *	5	1.00	0.00	1	1	5	1001.0	459.5	715	1531	5
Gymnuridae	Butterfly ray	*Gymnura natalensis* *	1	1.00	NA	1	1	1	-	-	-	-	0
Muraenidae	Whitespotted moray	*Gymnothorax johnsoni*	2	1.00	0.00	1	1	2	675.0	NA	675	675	2
Myliobatidae	Common eagle ray	*Myliobatis aquila* *	1	1.00	NA	1	1	1	453.0	NA	453	453	1
Odontaspididae	Ragged-tooth shark	*Carcharias taurus*	4	1.00	0.00	1	1	4	1931.0	299.8	1719	2143	4
Oplegnathidae	Cape knifejaw	*Oplegnathus conwayi*	3	1.00	0.00	1	1	3	228.7	21.5	212	253	3
Rajidae	Spearnose skate	*Rostroraja alba*	6	1.20	0.45	1	2	5	1014.0	79.2	958	1070	5
Scyliorhinidae	Puffadder shyshark	*Haploblepharus edwardsii*	20	1.67	0.89	1	3	12	341.1	55.8	227	491	17
Scyliorhinidae	Striped catshark	*Poroderma africanum*	17	1.70	0.82	1	3	10	680.0	100.9	432	802	11
Scyliorhinidae	Leopard catshark	*Poroderma pantherinum*	23	1.64	1.01	1	4	14	543.5	44.8	458	638	17
Scyliorhinidae	Yellowspotted catshark	*Scyliorhinus capensis*	1	1.00	NA	1	1	1	691.0	NA	691	691	1
Serranidae	Koester rockcod	*Acanthistius sebastoides*	11	2.20	0.84	1	3	5	221.9	23.7	194	256	8
Serranidae	Comber	*Serranus knysnaensis*	3	1.00	0.00	1	1	3	164.0	1.4	163	165	3
Triakidae	Smooth-hound shark	*Mustelus mustelus*	8	1.33	0.52	1	2	6	847.5	193.1	672	1209	7
Triakidae	Spotted gullyshark	*Triakis megalopterus*	1	1.00	NA	1	1	1	-	-	-	-	0
Sparidae	Carpenter	*Argyrozona argyrozona*	85	7.08	5.68	1	18	12	287.3	60.4	183	432	62
Sparidae	Fransmadam	*Boopsoidea inornata*	355	23.67	19.94	2	69	15	199.3	15.3	144	242	176
Sparidae	Santer	*Cheimerius nufar*	21	1.75	0.97	1	4	12	286.9	55.7	245	465	19
Sparidae	Englishman	*Chrysoblephus anglicus*	2	1.00	0.00	1	1	2	210.0	14.1	200	220	2
Sparidae	Dageraad	*Chrysoblephus cristiceps*	5	2.50	0.71	2	3	2	250.8	10.7	242	266	5
Sparidae	Red stumpnose	*Chrysoblephus gibbiceps*	22	1.69	0.75	1	3	13	346.4	57.5	227	462	18
Sparidae	Roman	*Chrysoblephus laticeps*	108	6.35	3.32	1	12	17	253.3	50.9	140	361	89
Sparidae	Slinger	*Chrysoblephus puniceus*	1	1.00	NA	1	1	1	151.0	NA	151	151	1
Sparidae	Blacktail	*Diplodus capensis*	20	2.22	1.39	1	5	9	220.9	19.3	183	249	19
Sparidae	Zebra	*Diplodus hottentotus*	7	1.17	0.41	1	2	6	281.4	26.0	240	301	7
Sparidae	Janbruin	*Gymnocrotaphus curvidens*	9	1.13	0.35	1	2	8	285.3	43.4	231	350	9
Sparidae	Blue hottentot	*Pachymetopon aeneum*	118	6.94	8.65	1	36	17	197.4	40.5	115	286	72
Sparidae	Red steenbras	*Petrus rupestris*	3	1.00	0.00	1	1	3	472.3	30.0	443	503	3
Sparidae	Scotsman	*Polysteganus praeorbitalis*	12	1.33	0.71	1	3	9	310.9	57.3	207	418	12
Sparidae	Seventy-four	*Polysteganus undulosus*	12	1.71	1.11	1	4	7	261.2	27.4	214	298	12
Sparidae	Dane	*Porcostoma dentata*	5	1.25	0.50	1	2	4	168.2	10.9	155	185	5
Sparidae	Panga	*Pterogymnus laniarius*	97	6.93	6.04	1	24	14	245.4	26.9	181	307	70
Sparidae	White stumpnose	*Rhabdosargus globiceps*	2	1.00	0.00	1	1	2	280.0	38.2	253	307	2
Sparidae	Cape stumpnose	*Rhabdosargus holubi*	4	2.00	1.41	1	3	2	205.8	26.0	185	240	4
Sparidae	Strepie	*Sarpa salpa*	62	31.00	42.43	1	61	2	194.1	11.4	172	220	29
Sparidae	Steentjie	*Spondyliosoma emarginatum*	69	6.27	9.61	1	33	11	210.1	14.4	180	254	55
Squalidae	Spiny dogfish	*Squalus* spp.	14	2.33	1.03	1	3	6	391.3	21.4	355	428	13

‡ MaxN estimates from 17 replicate deployments; † Length estimates from 16 replicate deployments; * Disk length measured for skates and rays.

Table A6: Sparid species recorded during stereo-BRUVs survey of warm-temperate reefs in the Agulhas Ecoregion, South Africa.

Scientific name	Common name	Max length (TL; mm)[a]	Min landing size (TL; mm)[a]	Diet[a]	Trophic level[b]
Argyrozona argyrozona	Carpenter	800	350	Small fishes, cephalopods, large mobile invertebrates	3.50
Boopsoidea inornata	Fransmadam	300	No limit	Algae, small mobile invertebrates	3.28
Cheimerius nufar	Santer	750	300	Small fishes, cephalopods, large mobile invertebrates	4.18
Chrysoblephus anglicus[TNP MPA]	Englishman	800	400	Large mobile invertebrates	3.42
Chrysoblephus cristiceps	Dageraad	700	400	Large mobile invertebrates	3.66
Chrysoblephus gibbiceps	Red stumpnose	750	300	Large mobile invertebrates	3.68
Chrysoblephus laticeps	Roman	512	300	Large mobile invertebrates	3.62
Chrysoblephus puniceus	Slinger	643	250	Small fishes, large mobile invertebrates	3.50
Diplodus capensis	Blacktail	471	200	Algae, large mobile invertebrates	2.70
Diplodus hottentotus	Zebra	600	300	Large mobile invertebrates	3.64
Gymnocrotaphus curvidens	Janbruin	500	No limit	Algae, sessile macrobenthic invertebrates	3.40
Pachymetopon aeneum	Blue hottentot	600	No limit	Sessile macrobenthic invertebrates	3.23
Pachymetopon blochii[AB]	Hottentot	540	220	Algae, large mobile invertebrates	3.37
Pagellus bellottii natalensis[AB]	Sand soldier	350	No limit	Algae, large mobile invertebrates	3.34
Petrus rupestris	Red steenbras	2000	400 (600 since 2010)	Small fishes, cephalopods, large mobile invertebrates	4.50
Polysteganus praeorbitalis[TNP MPA]	Scotsman	900	300 (400 since 2010)	Small fishes, cephalopods, large mobile invertebrates	4.50
Polysteganus undulosus	Seventy-four	1000	Restricted (since 1998)	Small fishes, cephalopods, large mobile invertebrates	4.11
Porcostoma dentata[TNP MPA]	Dane	420	No limit	Large mobile invertebrates	3.34
Pterogymnus laniarius	Panga	450	No limit	Large mobile invertebrates	3.59
Rhabdosargus globiceps	White stumpnose	528	250	Large mobile invertebrates	3.28
Rhabdosargus holubi	Cape stumpnose	450	200	Large mobile invertebrates	3.22
Spondyliosoma emarginatum	Steentjie	346	No limit	Algae, small mobile invertebrates	2.76

Sources: [a] Mann (2013) and references therein; [b] Froese & Pauly (2017)

Species not recorded in: Algoa Bay (AB); Tsitsikamma MPA (TNP MPA)

Table A7: Ichthyofaunal species (excluding sparids) recorded during stereo-BRUVs survey of warm-temperate reefs in the Agulhas Ecoregion, South Africa.

Family	Scientific name	Common name	Trophic level[a]
Ariidae	*Galeichthys ater*	Black seacatfish	3.56
Callorhinchidae	*Callorhinchus capensis*	Cape elephantfish	3.45
Carangidae	*Seriola lalandi*	Giant yellowtail	4.20
Carangidae	*Seriola rivoliana*	Longfin yellowtail	4.50
Centracanthidae	*Spicara axillaris* † ‡	Windtoy	3.39
Chaetodontidae	*Chaetodon marleyi*	Doublesash butterflyfish	2.68
Cheilodactylidae	*Cheilodactylus fasciatus*	Redfingers	3.42
Cheilodactylidae	*Cheilodactylus pixi* †	Barred fingerfin	3.07
Cheilodactylidae	*Chirodactylus brachydactylus*	Twotone fingerfin	3.50
Cheilodactylidae	*Chirodactylus grandis*	Bank steenbras	4.10
Cheilodactylidae	*Chirodactylus jessicalenorum*	Natal fingerfin	3.82
Dasyatidae	*Dasyatis brevicaudata*	Short-tail stingray	3.87
Gymnuridae	*Gymnura natalensis*	Butterfly ray	3.89
Hexanchidae	*Notorynchus cepedianus*	Broadnose sevengill shark	4.57
Mugulidae	*Chelon richardsonii*	Mullet	2.38
Muraenidae	*Gymnothorax johnsoni* †	Whitespotted moray	4.11
Myliobatidae	*Myliobatis aquila*	Common eagle ray	3.61
Myxinidae	*Eptatretus hexatrema*	Sixgill hagfish	4.50
Odontaspididae	*Carcharias taurus*	Ragged-tooth shark	4.44
Oplegnathidae	*Oplegnathus conwayi*	Cape knifejaw	2.70
Parascorpididae	*Parascorpis typus*	Jutjaw	3.40
Rajidae	*Rostroraja alba*	Spearnose skate	4.41
Sciaenidae	*Argyrosomus japonicus*	Dusky kob	4.20
Sciaenidae	*Atractoscion aequidens*	Geelbeck	4.50
Scyliorhinidae	*Haploblepharus edwardsii*	Puffadder shyshark	3.90
Scyliorhinidae	*Haploblepharus fuscus*	Brown shyshark	4.04
Scyliorhinidae	*Haploblepharus pictus*	Dark shyshark	4.19
Scyliorhinidae	*Poroderma africanum*	Striped catshark	3.94
Scyliorhinidae	*Poroderma pantherinum*	Leopard catshark	4.06
Scyliorhinidae	*Scyliorhinus capensis*	Yellowspotted catshark	3.95
Serranidae	*Acanthistius sebastoides*	Koester rockcod	4.03
Serranidae	*Epinephelus marginatus*	Yellowbelly rockcod	4.08
Tetraodontidae	*Amblyrhynchotes honckenii*	Evileye blaasop	NA
Triakidae	*Mustelus mustelus*	Smooth-hound shark	3.76
Triakidae	*Triakis megalopterus*	Spotted gully shark	4.21

Source: [a] Froese & Pauly (2017)
† Trophic level of species estimated from average value of genus.
‡ Rare pelagic species, rarely observed on reefs. The family Centracanthidae was recently subsumed into the family Sparidae (Santini et al. 2014).

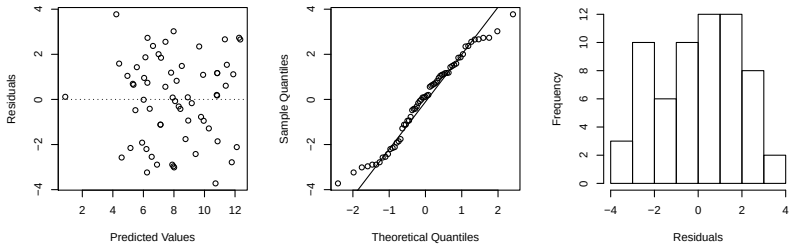
Model	y	AIC_c	No. of MEMs
del.f2	5	-47.76	4
mst.f2	10	-47.33	5
mst	NA	-46.09	3
soi.f2	10	-45.51	3
del	NA	-45.23	4
gab	NA	-45.16	4
soi	NA	-45.16	4
del.f3	2	-44.94	2
soi.f3	1	-44.80	2
rnb.f2	2	-44.75	2
gab.f2	10	-44.62	4
rnb	NA	-44.49	1
gab.f3	2	-44.44	1
rnb.f3	1	-44.00	2
mst.f3	5	-43.65	1
pcnm	NA	-43.28	1

(a) Tsitsikamma National Park MPA

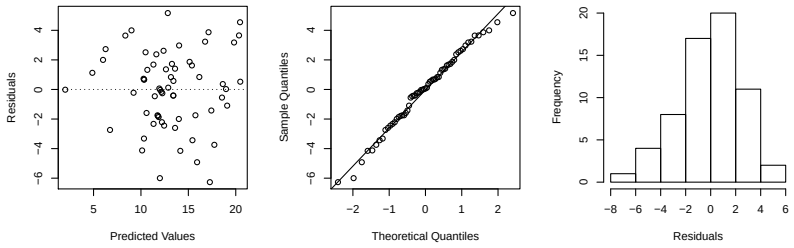
Model	y	AIC_c	No. of MEMs
del.f2	2	-53.11	3
del	NA	-52.55	3
gab.f2	1	-51.51	4
soi.f2	5	-51.06	4
gab	NA	-51.06	4
soi	NA	-50.84	3
del.f3	2	-50.32	4
gab.f3	1	-49.93	3
mst.f3	1	-49.41	3
soi.f3	2	-49.41	4
rnb.f3	1	-48.43	3
mst	NA	-48.41	5
rnb	NA	-48.23	3
rnb.f2	10	-48.02	1
mst.f2	10	-47.61	5
pcnm	NA	-46.81	1

(b) Algoa Bay

Table A8: Tested spatial models for each location ranked in order of AIC_c. Model: names follow Dray et al. (2006) and specify the connectivity scheme (del, gab, rnb, soi, mst, pcnm) and monotonic weighting function (f_2, f_3). y: value of parameter a and b within relevant weighting function (see Section 2.2.7 for details).



(a) Sparid fishes



(b) All ichthyofauna

Figure A.1: Model validation graphs for the best-fitting ecological effects model for (a) reef-associated sparid fishes and (b) all reef-associated ichthyofauna (see Table 3.4a,b and Fig. 3.1a,b). Residuals plotted against fitted values, normal Q-Q plot, and histogram of residuals are shown.

Bibliography

Ackerman, J. L., Bellwood, D. R. & Brown, J. H. (2004) The contribution of small individuals to density-body size relationships: examination of energetic equivalence in reef fishes. *Oecologia*, **139**, 568–571.

Adjeroud, M. (1997) Factors influencing spatial patterns on coral reefs around Moorea, French Polynesia. *Marine Ecology Progress Series*, **159**, 105–119.

Adler, P. B., HilleRisLambers, J. & Levine, J. M. (2007) A niche for neutrality. *Ecology Letters*, **10**, 95–104.

Almany, G. R. (2003) Priority effects in coral reef fish communities. *Ecology*, **84**, 1920–1935.

Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S. & Jones, G. P. (2007) Local replenishment of coral reef fish populations in a marine reserve. *Science*, **316**, 742–744.

Almany, G. R., Hamilton, R. J., Bode, M., Matawai, M., Potuku, T., Saenz-Agudelo, P., Planes, S., Berumen, M. L., Rhodes, K. L., Thorrold, S. R., et al. (2013) Dispersal of grouper larvae drives local resource sharing in a coral reef fishery. *Current Biology*, **23**, 626–630.

Anderson, G. R. V., Ehrlich, A. H., Ehrlich, P. R., Roughgarden, J. D., Russell, B. C. & Talbot, F. H. (1981) The community structure of coral reef fishes. *American Naturalist*, **117**, 476–495.

Anderson, M. J. & Millar, R. B. (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **305**, 191–221.

Andrews, K. S. & Anderson, T. W. (2004) Habitat-dependent recruitment of two temperate reef fishes at multiple spatial scales. *Marine Ecology Progress Series*, **277**, 231–244.

Araújo, M. S., Bolnick, D. I. & Layman, C. A. (2011) The ecological causes of individual specialisation. *Ecology Letters*, **14**, 948–958.

Arnold, T. W. (2010) Uninformative parameters and model selection using Akaike's Information Criterion. *The Journal of Wildlife Management*, **74**, 1175–1178.

Attwood, C. G., Allen, J. & Claassen, P. J. (2002) Nearshore surface current patterns in the Tsitsikamma National Park, South Africa. *African Journal of Marine Science*, **24**, 151–160.

Attwood, C. G. & Bennett, B. A. (1994) Variation in dispersal of galjoen (Coracinus capensis)(Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 1247–1257.

Attwood, C. G. & Cowley, P. D. (2005) Alternate explanations of the dispersal pattern of galjoen Dichistius capensis. *African Journal of Marine Science*, **27**, 141–156.

Audzijonyte, A., Kuparinen, A., Gorton, R. & Fulton, E. A. (2013) Ecological consequences of body size decline in harvested fish species: positive feedback loops in trophic interactions amplify human impact. *Biology Letters*, **9**, 234–243.

Ault, T. R. & Johnson, C. R. (1998a) Relationships between habitat and recruitment of three species of damselfish (Pomacentridae) at Heron Reef, Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology*, **223**, 145–166.

Ault, T. R. & Johnson, C. R. (1998b) Spatial variation in fish species richness on coral reefs: habitat fragmentation and stochastic structuring processes. *Oikos*, **82**, 354–364.

Ault, T. R. & Johnson, C. R. (1998c) Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs*, **68**, 25–50.

Babcock, R. C., Kelly, S., Shears, N. T., Walker, J. W. & Willis, T. J. (1999) Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series*, 125–134.

Barrett, N. S., Edgar, G. J., Buxton, C. D. & Haddon, M. (2007) Changes in fish assemblages following 10 years of protection in Tasmanian marine protected areas. *Journal of Experimental Marine Biology and Ecology*, **345**, 141–157.

Bassett, D. K. & Montgomery, J. C. (2011) Investigating nocturnal fish populations in situ using baited underwater video: with special reference to their olfactory capabilities. *Journal of Experimental Marine Biology and Ecology*, **409**, 194–199.

Baynes, T. W. & Szmant, A. M. (1989) Effect of current on the sessile benthic community structure of an artificial reef. *Bulletin of Marine Science*, **44**, 545–566.

Bell, G. (2001) Neutral macroecology. *Science*, **293**, 2413–2418.

Bellwood, D. R. & Hughes, T. P. (2001) Regional-scale assembly rules and biodiversity of coral reefs. *Science*, **292**, 1532–1535.

Belmaker, J., Shashar, N. & Ziv, Y. (2005) Effects of small-scale isolation and predation on fish diversity on experimental reefs. *Marine Ecology Progress Series*, **289**, 273–283.

Belmaker, J., Ziv, Y. & Shashar, N. (2009) Habitat patchiness and predation modify the distribution of a coral-dwelling damselfish. *Marine Biology*, **156**, 447–454.

Belmaker, J., Ziv, Y., Shashar, N. & Connolly, S. R. (2008) Regional variation in the hierarchical partitioning of diversity in coral-dwelling fishes. *Ecology*, **89**, 2829–2840.

Bernard, A. T. F. & Götz, A. (2012) Bait increases the precision in count data from remote underwter video for most subtidal reef fish in the warm-temperate Agulhas bioregion. *Marine Ecology Progress Series*, **471**, 235–252.

Bernard, A. T. F., Götz, A., Parker, D., Heyns, E. R., Halse, S. J., Riddin, N. A., Smith, M. K. S., Paterson, A. W., Winker, H., Fullwood, L., Langlois, T. J. & Harvey, E. S. (2014) New possibilities for research on reef fish across the continental shelf of South Africa. *South African Journal of Science*, **110**, 01–05.

Blanchet, F. G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623–2632.

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. & Sams, S. (1978) Relationships between body size and some life history parameters. *Oecologia*, **37**, 257–272.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H., Schreiber, S. J., Urban, M. C. & Vasseur, D. A. (2011) Why

intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, **26**, 183–192.

Borcard, D. & Legendre, P. (1994) Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environmental and Ecological Statistics*, **1**, 37–61.

Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling*, **153**, 51–68.

Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, **85**, 1826–1832.

Borcard, D., Legendre, P. & Drapeau, P. (1992) Partialling out the spatial component of ecological variation. *Ecology*, **73**, 1045–1055.

Boudreau, P. R. & Dickie, L. M. (1989) Biological model of fisheries production based on physiological and ecological scalings of body size. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 614–623.

Bradbury, R. H. & Young, P. C. (1981) The effects of a major forcing function, wave energy, on a coral reef ecosystem. *Marine Ecology Progress Series*, **5**, 229–241.

Brokovich, E., Einbinder, S., Kark, S., Shashar, N. & Kiflawi, M. (2007) A deep nursery for juveniles of the zebra angelfish Genicanthus caudovittatus. *Environmental Biology of Fishes*, **80**, 1–6.

Brokovich, E., Einbinder, S., Shashar, N., Kiflawi, M. & Kark, S. (2008) Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Marine Ecology Progress Series*, **371**, 253–262.

Brouwer, S. L. (2002) Movement patterns of red steenbras Petrus rupestris tagged and released in the Tsitsikamma National Park, South Africa. *South African Journal of Marine Science*, **24**, 375–378.

Brouwer, S. L. & Buxton, C. D. (2002) Catch and effort of the shore and skiboat linefisheries along the South African Eastern Cape coast. *African Journal of Marine Science*, **24**, 341–354.

Brouwer, S. L. & Griffiths, M. H. (2005) Stock separation and life history of Argyrozona argyrozona (Pisces: Sparidae) on the South African east coast. *African Journal of Marine Science*, **27**, 585–595.

Brouwer, S. L., Griffiths, M. H. & Roberts, M. J. (2003) Adult movement and larval dispersal of Argyrozona argyrozona (Pisces: Sparidae) from a temperate marine protected area. *African Journal of Marine Science*, **25**, 395–402.

Burnham, K. P. & Anderson, D. R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*, Springer Science & Business Media.

Buxton, C. D. (1984) Feeding biology of the roman Chrysoblephus laticeps (Pisces: Sparidae). *South African Journal of Marine Science*, **2**, 33–42.

Buxton, C. D. & Clarke, J. R. (1986) Age, growth and feeding of the blue hottentot Pachymetopon aeneum (Pisces: Sparidae) with notes on reproductive biology. *African Zoology*, **21**, 33–38.

Buxton, C. D. & Clarke, J. R. (1989) The growth of Cymatoceps nasutus (Teleostei: Sparidae), with comments on diet and reproduction. *South African Journal of Marine Science*, **8**, 57–65.

Buxton, C. D. & Clarke, J. R. (1991) The biology of the white musselcracker Sparodon durbanensis (Pisces: Sparidae) on the Eastern Cape coast, South Africa. *South African Journal of Marine Science*, **10**, 285–296.

Buxton, C. D. & Smale, M. J. (1984) A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park. *Koedoe*, **27**, 13–24.

Buxton, C. D. & Smale, M. J. (1989) Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the southern Cape coast. *Journal of Applied Ecology*, 441–451.

Buxton, C. D. (1993) Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes*, **36**, 47–63.

Cappo, M. M. C., De'ath, G. A. G., Stowar, M. M. J., Johannson, C. C. & Doherty, P. P. J. (2010). *The influence of zoning (closure to fishing) on fish communities of the shoals and reef bases of the Great Barrier Reef Marine Park. Results of repeated surveys of the southern banks and Cardwell shoals, and an overview with regional comparisons. Part 2 - Development of Protocols to Improve Accuracy in Baited Video Techniques Used to Detect Effects of Zoning.* Tech. rep. Townsville, Australia: Marine, Tropical Sciences Research Facility (MTSRF), and Australian Institute of Marine Science (AIMS).

Cappo, M., Harvey, E. S., Malcolm, H. & Speare, P. (2003). Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In: *Aquatic protected areas - what works best and how do we know?* Ed. by Beumer, J. P.; Grant, A. & Smith, D. C. World Congress on Aquatic Protected Areas proceedings. Australian Society of Fish Biology, Cairns, pp. 455–464.

Cappo, M., Speare, P. & De'ath, G. (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *Journal of Experimental Marine Biology and Ecology*, **302**, 123–152.

Caruso, T., Taormina, M. & Migliorini, M. (2012) Relative role of deterministic and stochastic determinants of soil animal community: a spatially explicit analysis of oribatid mites. *Journal of Animal Ecology*, **81**, 214–221.

Chapman, M. R. & Kramer, D. L. (2000) Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes*, **57**, 11–24.

Chase, J. M. & Leibold, M. A. (2003) *Ecological niches: linking classical and contemporary approaches*, University of Chicago Press.

Chave, J. (2004) Neutral theory and community ecology. *Ecology Letters*, **7**, 241–253.

Chave, J., Muller-Landau, H. C. & Levin, S. A. (2002) Comparing classical community models: theoretical consequences for patterns of diversity. *The American Naturalist*, **159**, 1–23.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Rreview of Ecology and Systematics*, 343–366.

Chesson, P. L. (1985) Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology*, **28**, 263–287.

Chesson, P. & Warner, R. R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, **117**, 923–943.

Choat, J. H. & Ayling, A. M. (1987) The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of Experimental Marine Biology and Ecology*, **110**, 257–284.

Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Pizer, W., et al. (2001) Ecological forecasts: an emerging imperative. *Science*, **293**, 657–660.

Coghlan, A. R., McLean, D. L., Harvey, E. S. & Langlois, T. J. (2017) Does fish behaviour bias abundance and length information collected by baited underwater video? *Journal of Experimental Marine Biology and Ecology*, **497**, 143–151.

Colloca, F., Carpentieri, P., Balestri, E. & Ardizzone, G. (2010) Food resource partitioning in a Mediterranean demersal fish assemblage: the effect of body size and niche width. *Marine Biology*, **157**, 565–574.

Connell, S. D. & Jones, G. P. (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. *Journal of Experimental Marine Biology and Ecology*, **151**, 271–294.

Connolly, S. R., Hughes, T. P., Bellwood, D. R. & Karlson, R. H. (2005) Community structure of corals and reef fishes at multiple scales. *Science*, **309**, 1363–1365.

Cornell, H. V., Karlson, R. H. & Hughes, T. P. (2007) Scale-dependent variation in coral community similarity across sites, islands, and island groups. *Ecology*, **88**, 1707–1715.

Cottenie, K. (2005) Integrating environmental and spatial processes in ecological community dynamics. *Ecology Letters*, **8**, 1175–1182.

Cowley, P. D., Brouwer, S. L. & Tilney, R. L. (2002) The role of the Tsitsikamma National Park in the management of four shore-angling fish along the south-eastern Cape coast of South Africa. *South African Journal of Marine Science*, **24**, 27–35.

Craig, A. J. F. K. & Hulley, P. E. (1994) Sunbird movements: A review with possible models. *Ostrich*, **65**, 106–110.

Crist, T. O., Veech, J. A., Gering, J. C. & Summerville, K. S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. *The American Naturalist*, **162**, 734–743.

Crowder, L. B., Lyman, S. J., Figueira, W. F. & Priddy, J. (2000) Source-sink population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science*, **66**, 799–820.

DAFF (2014). *Status of the South African marine fishery resources*. Tech. rep. Cape Town, South Africa: Department of Agriculture, Forestry and Fisheries (DAFF).

D'agata, S., Mouillot, D., Kulbicki, M., Andréfouët, S., Bellwood, D. R., Cinner, J. E., Cowman, P. F., Kronen, M., Pinca, S. & Vigliola, L. (2014) Human-mediated loss of phylogenetic and functional diversity in coral reef fishes. *Current Biology*, **24**, 555–560.

Dahlgren, C. P. & Eggleston, D. B. (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology*, **81**, 2227–2240.

Davis, J. A. & Buxton, C. D. (1996) Larval development of laboratory-reared carpenter, Argyrozona argyrozona (Pisces: Sparidae). *African Zoology*, **31**, 10–14.

Davis, J. A. (1996). Investigations into the larval rearing of two South African sparid species. MA thesis. Rhodes University.

De Vos, L., Götz, A., Winker, H. & Attwood, C. G. (2014) Optimal BRUVs (baited remote underwater video system) survey design for reef fish monitoring in the Stilbaai Marine Protected Area. *African Journal of Marine Science*, **36**, 1–10.

De Vos, L., Watson, R. G. A., Götz, A. & Attwood, C. G. (2015) Baited remote underwater video system (BRUVs) survey of chondrichthyan diversity in False Bay, South Africa. *African Journal of Marine Science*, **37**, 209–218.

De Bello, F., Lavorel, S., Albert, C. H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š. & Lepš, J. (2011) Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, **2**, 163–174.

De Bie, T., Meester, L., Brendonck, L., Martens, K., Goddeeris, B., Ercken, D., Hampel, H., Denys, L., Vanhecke, L., Gucht, K., et al. (2012) Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. *Ecology Letters*, **15**, 740–747.

Declerck, S. A. J., Coronel, J. S., Legendre, P. & Brendonck, L. (2011) Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography*, **34**, 296–305.

Diamond, J. M. (1975). Assembly of species communities. In: *Ecology and evolution of communities*. Ed. by Cody, M. L. & Diamond, J. M., Harvard University Press, Cambridge, Massachusetts, pp. 342–444.

Doherty, P. J. (1981). Coral reef fishes: recruitment-limited assemblages? In: *The Reef and Man*. Proceedings of the 4th International Coral Reef Symposium. Marine Sciences Center, University of the Philippines, Manila, Philippines, pp. 465–470.

Doherty, P. J., Dufour, V., Galzin, R., Hixon, M. A., Meekan, M. G. & Planes, S. (2004) High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology*, **85**, 2422–2428.

Doherty, P. J. & Fowler, A. (1994a) An empirical test of recruitment limitation in a coral reef fish. *Science*, **263**, 935–939.

Doherty, P. J. & Fowler, A. (1994b) Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. *Bulletin of Marine Science*, **54**, 297–313.

Donadi, S., Eriksson, B. K., Lettmann, K. A., Hodapp, D., Wolff, J.-O. & Hillebrand, H. (2015) The body-size structure of macrobenthos changes predictably along gradients of hydrodynamic stress and organic enrichment. *Marine Biology*, **162**, 675–685.

Dray, S., Legendre, P. & Blanchet, G. (2013). *packfor: Forward Selection with permutation (Canoco p.46)*. R package version 0.0-8/r109.

Dray, S., Legendre, P. & Peres-Neto, P. R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, **196**, 483–493.

Duncan, M., James, N., Fennessy, S. T., Mutombene, R. J. & Mwale, M. (2015) Genetic structure and consequences of stock exploitation of Chrysoblephus puniceus, a commercially important sparid in the South West Indian Ocean. *Fisheries Research*, **164**, 64–72.

Dunlop, E. S., Enberg, K., Jørgensen, C. & Heino, M. (2009) Toward Darwinian fisheries management. *Evolutionary Applications*, **2**, 245–259.

Dunlop, K. M., Marian Scott, E., Parsons, D. & Bailey, D. M. (2015) Do agonistic behaviours bias baited remote underwater video surveys of fish? *Marine Ecology*, **36**, 810–818.

Ebeling, A. W. & Hixon, M. A. (1991). Tropical and temperate reef fishes: comparison of community structures. *The ecology of fishes on coral reefs* (ed. by Sale, P. F.). Chap. 18, pp. 509–563. Academic Press, San Diego.

Edgar, G. J., Barrett, N. S. & Morton, A. J. (2004) Patterns of fish movement on eastern Tasmanian rocky reefs. *Environmental Biology of Fishes*, **70**, 273–284.

Edgar, G. J. & Stuart-Smith, R. D. (2009) Ecological effects of marine protected areas on rocky reef communities-a continental-scale analysis. *Marine Ecology Progress Series*, **388**, 51–62.

Ferguson, A. M., Harvey, E. S., Taylor, M. D. & Knott, N. A. (2013) A herbivore knows its patch: luderick, Girella tricuspidata, exhibit strong site fidelity on shallow subtidal reefs in a temperate marine park. *PloS ONE*, **8**, e65838.

Fernández, T. V., D'Anna, G., Badalamenti, F. & Pérez-Ruzafa, A. (2008) Habitat connectivity as a factor affecting fish assemblages in temperate reefs. *Aquatic Biology*, **1**, 239–248.

Fisher, J. A., Frank, K. T. & Leggett, W. C. (2010) Global variation in marine fish body size and its role in biodiversity–ecosystem functioning. *Marine Ecology Progress Series*, **405**, 1–13.

Fitzpatrick, B. M., Harvey, E. S., Heyward, A. J., Twiggs, E. J. & Colquhoun, J. (2012) Habitat specialization in tropical continental shelf demersal fish assemblages. *PloS ONE*, **7**, e39634.

Fondell, T. F., Miller, D. A., Grand, J. B. & Anthony, R. M. (2008) Survival of dusky Canada goose goslings in relation to weather and annual nest success. *The Journal of Wildlife Management*, **72**, 1614–1621.

Fortin, M.-J. & Dale, M. R. T. (2005) *Spatial Analysis: A Guide for Ecologists*, Cambridge University Press, United Kingdom.

Freiwald, J. (2012) Movement of adult temperate reef fishes off the west coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences*, **69**, 1362–1374.

Froese, R. & Pauly, D. (2017). *Fishbase*. URL: `www.fishbase.org`.

Garrabou, J., Ballesteros, E. & Zabala, M. (2002) Structure and dynamics of northwestern Mediterranean rocky benthic communities along a depth gradient. *Estuarine, Coastal and Shelf Science*, **55**, 493–508.

Gause, G. F. (1934) *The struggle for existence*, Williams and Wilkins, Baltimore, USA.

Genner, M. J., Sims, D. W., Southward, A. J., Budd, G. C., Masterson, P., McHugh, M., Rendle, P., Southall, E. J., Wearmouth, V. J. & Hawkins, S. J. (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, **16**, 517–527.

Gilbert, B. & Bennett, J. R. (2010) Partitioning variation in ecological communities: do the numbers add up? *Journal of Applied Ecology*, **47**, 1071–1082.

Gili, J.-M. & Coma, R. (1998) Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology and Evolution*, **13**, 316–321.

Godinez-Dominguez, E. & Freire, J. (2003) Information-theoretic approach for selection of spatial and temporal models of community organization. *Marine Ecology Progress Series*, **253**, 17–24.

Goschen, W. S. & Schumann, E. H. (1995) Upwelling and the occurrence of cold water around Cape Recife, Algoa Bay, South Africa. *South African Journal of Marine Science*, **16**, 57–67.

Gotelli, N. J. & Graves, G. R. (1996) *Null models in ecology*, Smithsonian Institution Press, Washington, D.C.

Götz, A., Kerwath, S. E., Attwood, C. G. & Sauer, W. H. H. (2009) Effects of fishing on a temperate reef community in South Africa 1: ichthyofauna. *African Journal of Marine Science*, **31**, 241–251.

Götz, A., Kerwath, S. E., Attwood, C. G. & Sauer, W. H. H. (2008) Effects of fishing on population structure and life history of roman Chrysoblephus laticeps (Sparidae). *Marine Ecology Progress Series*, **362**, 245–259.

Götz, A., Kerwath, S. E., Samaai, T., Silva, C. d. & Wilke, C. G. (2014) An exploratory investigation of the fish communities associated with reefs on the central Agulhas Bank, South Africa. *African Zoology*, **49**, 253–264.

Gravel, D., Canham, C. D., Beaudet, M. & Messier, C. (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters*, **9**, 399–409.

Gray, C. A., Haddy, J. A., Fearman, J., Barnes, L. M., Macbeth, W. G. & Kendall, B. W. (2012) Reproduction, growth and connectivity among populations of Girella tricuspidata (Pisces: Girellidae). *Aquatic Biology*, **16**, 53–68.

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., Gleason, M. G., Mumby, P. J. & White, A. T. (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, **90**, 1215–1247.

Griffith, D. A. & Peres-Neto, P. R. (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**, 2603–2613.

Griffiths, M. H. (2000) Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *African Journal of Marine Science*, **22**.

Griffiths, M. H. & Wilke, C. G. (2002) Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. *Marine and Freshwater Research*, **53**, 233–244.

Grüss, A., Kaplan, D. M., Guénette, S., Roberts, C. M. & Botsford, L. W. (2011) Consequences of adult and juvenile movement for marine protected areas. *Biological Conservation*, **144**, 692–702.

Gunderson, D. R., Parma, A. M., Hilborn, R., Cope, J. M., Fluharty, D. L., Miller, M. L., Vetter, R. D., Heppell, S. S. & Greene, H. G. (2008) The challenge of managing nearshore rocky reef resources. *Fisheries*, **33**, 172–179.

Gunderson, D. R. & Vetter, R. D. (2006). Temperate rocky reef fishes. In: *Marine metapopulations*. Ed. by Kritzer, J. P. & Sale, P. F., Elsevier Academic Press. Chap. 3, pp. 69–117.

Guthery, F. S. (2008) Statistical ritual versus knowledge accrual in wildlife science. *The Journal of Wildlife Management*, **72**, 1872–1875.

Hanekom, N., Hutchings, L., Joubert, P. A. & Van Der Byl, P. C. N. (1989) Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science*, **8**, 145–153.

Harvey, E. S., Cappo, M., Kendrick, G. A. & McLean, D. L. (2013) Coastal fish assemblages reflect geological and oceanographic gradients within an Australian zootone. *PloS ONE*, **8**, e80955.

Harvey, E. S., Fletcher, D. & Shortis, M. (2002) Estimation of reef fish length by divers and by stereo-video: a first comparison of the accuracy and precision in

the field on living fish under operational conditions. *Fisheries Research*, **57**, 255–265.

Harvey, E. S., Newman, S. J., McLean, D. L., Cappo, M., Meeuwig, J. J. & Skepper, C. L. (2012) Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. *Fisheries Research*, **125**, 108–120.

Harvey, E. S. & Shortis, M. R. (1995) A system for stereo-video measurement of sub-tidal organisms. *Marine Technology Society Journal*, **29**, 10–22.

Harvey, E. S. & Shortis, M. R. (1998) Calibration stability of an underwater stereo-video system: implications for measurement accuracy and precision. *Marine Technology Society Journal*, **32**, 3–17.

Harvey, E. S., Cappo, M., Butler, J. J., Hall, N., Kendrick, G. A., et al. (2007) Bait attraction affects the performance of remote underwater video stations in assessment of demersal fish community structure. *Marine Ecology Progress Series*, **350**, 245.

Heino, J., Melo, A. S., Siqueira, T., Soininen, J., Valanko, S. & Bini, L. M. (2015) Metacommunity organisation, spatial extent and dispersal in aquatic systems: patterns, processes and prospects. *Freshwater Biology*, **60**, 845–869.

Heyns, E. R., Bernard, A. T. F., Richoux, N. B. & Götz, A. (2016) Depth-related distribution patterns of subtidal macrobenthos in a well-established marine protected area. *Marine Biology*, **163**, 1–15.

Heyns-Veale, E. R., Bernard, A. T. F., Richoux, N. B., Parker, D., Langlois, T. J., Harvey, E. S. & Götz, A. (2016) Depth and habitat determine assemblage structure of South Africa's warm-temperate reef fish. *Marine Biology*, **163**, 1–17.

Hilborn, R. (1990) Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 635–643.

Hilborn, R., Stokes, K., Maguire, J.-J., Smith, T., Botsford, L. W., Mangel, M., Orensanz, J., Parma, A., Rice, J., Bell, J., et al. (2004) When can marine reserves improve fisheries management? *Ocean and Coastal Management*, **47**, 197–205.

Hixon, M. A. (2011) 60 Years of coral reef fish ecology: past, present, future. *Bulletin of Marine Science*, **87**, 727–765.

Hixon, M. A. & Beets, J. P. (1989) Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bulletin of Marine Science*, **44**, 666–680.

Hixon, M. A. & Jones, G. P. (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology*, **86**, 2847–2859.

Hixon, M. A., Pacala, S. W. & Sandin, S. A. (2002) Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, **83**, 1490–1508.

Hixon, M. A. & Webster, M. S. (2002). Density dependence in reef fish populations. In: *Coral reef fishes: dynamics and diversity in a complex ecosystem.* Ed. by Sale, P. F., Academic Press, San Diego, California. Chap. 14, pp. 303–325.

Holbrook, S. J., Kingsford, M. J., Schmitt, R. J. & Stephens, J. S. (1994) Spatial and temporal patterns in assemblages of temperate reef fish. *American Zoologist*, **34**, 463–475.

Hsieh, C.-h., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M. & Sugihara, G. (2006) Fishing elevates variability in the abundance of exploited species. *Nature*, **443**, 859.

Hsieh, C.-h., Yamauchi, A., Nakazawa, T. & Wang, W.-F. (2010) Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, **72**, 165–178.

Hubbell, S. P. (1997) A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs*, **16**, S9–S21.

Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography*, Princeton University Press.

Hubbell, S. P. (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional Ecology*, **19**, 166–172.

Hubbell, S. P. (2006) Neutral theory and the evolution of ecological equivalence. *Ecology*, **87**, 1387–1398.

Hughes, T. P., Bellwood, D. R., Folke, C., Steneck, R. S. & Wilson, J. (2005) New paradigms for supporting the resilience of marine ecosystems. *Trends in Ecology and Evolution*, **20**, 380–386.

Hurtt, G. C. & Pacala, S. W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.

Hutchinson, G. E. (1957) Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.

James, N. C., Götz, A., Potts, W. M. & Cowley, P. D. (2012) Temporal variability of a temperate fish assemblage in Africa's oldest marine protected area. *African Journal of Marine Science*, **34**, 15–26.

Jennings, S., Greenstreet, S. P. R. & Reynolds, J. D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology*, **68**, 617–627.

Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., Van Oppen, M. J. H. & Willis, B. L. (2009) Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs*, **28**, 307–325.

Jones, G. P. (1984a) Population ecology of the temperate reef fish Pseudolabrus celidotus Bloch & Schneider (Pisces: Labridae). II. Factors influencing adult density. *Journal of Experimental Marine Biology and Ecology*, **75**, 277–303.

Jones, G. P. (1984b) The influence of habitat and behavioural interactions on the local distribution of the wrasse, Pseudolabrus celidotus. *Environmental Biology of Fishes*, **10**, 43–57.

Jones, G. P. (1987) Competitive interactions among adults and juveniles in a coral reef fish. *Ecology*, **68**, 1534–1547.

Jones, G. P. (1990) The importance of recruitment to the dynamics of a coral reef fish population. *Ecology*, **71**, 1691–1698.

Juanes, F. & Conover, D. O. (1994) Piscivory and prey size selection in young-of-the-year bluefish: predator preference or size-dependent capture success? *Marine Ecology Progress Series*, 59–69.

Kerkhoff, A. J. & Enquist, B. J. (2009) Multiplicative by nature: why logarithmic transformation is necessary in allometry. *Journal of Theoretical Biology*, **257**, 519–521.

Kerwath, S. E., Götz, A., Attwood, C. G., Cowley, P. D. & Sauer, W. H. H. (2007) Movement pattern and home range of roman Chrysoblephus laticeps. *African Journal of Marine Science*, **29**, 93–103.

Kerwath, S. E., Götz, A., Attwood, C. G., Sauer, W. H. H. & Wilke, C. G. (2007) Area utilisation and activity patterns of roman Chrysoblephus laticeps (Spari-dae) in a small marine protected area. *African Journal of Marine Science*, **29**, 259–270.

Kerwath, S. E., Winker, H., Götz, A. & Attwood, C. G. (2013) Marine protected area improves yield without disadvantaging fishers. *Nature Communications*, **4**.

Kiflawi, M., Belmaker, J., Brokovich, E., Einbinder, S. & Holzman, R. (2006) The determinants of species richness of a relatively young coral-reef ichthyofauna. *Journal of Biogeography*, **33**, 1289–1294.

Kinlan, B. P. & Gaines, S. D. (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**, 2007–2020.

Kramer, D. L. & Chapman, M. R. (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, **55**, 65–79.

Kritzer, J. P. & Sale, P. F. (2010). The metapopulation ecology of coral reef fishes. In: *Marine metapopulations*. Ed. by Kritzer, J. P. & Sale, P. F., Elsevier Academic Press, San Diego, California. Chap. 2, pp. 31–68.

Kuparinen, A., Kuikka, S. & Merilä, J. (2009) Estimating fisheries-induced selection: traditional gear selectivity research meets fisheries-induced evolution. *Evolutionary Applications*, **2**, 234–243.

Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos*, 5–13.

Langlois, T. J., Newman, S. J., Cappo, M., Harvey, E. S., Rome, B. M., Skepper, C. L. & Wakefield, C. B. (2015) Length selectivity of commercial fish traps assessed from in situ comparisons with stereo-video: is there evidence of sampling bias? *Fisheries Research*, **161**, 145–155.

Langlois, T. J., Fitzpatrick, B. R., Fairclough, D. V., Wakefield, C. B., Hesp, S. A., McLean, D. L., Harvey, E. S. & Meeuwig, J. J. (2012) Similarities between line fishing and baited stereo-video estimations of length-frequency: novel application of kernel density estimates. *PloS ONE*, **7**, e45973.

Law, R. (2000) Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science*, **57**, 659–668.

Lechanteur, Y. A. R. G. & Griffiths, C. L. (2003) Diets of common suprabenthic reef fish in False Bay, South Africa. *African Zoology*, **38**, 213–227.

Legendre, P. (1990). Quantitative methods and biogeographic analysis. *Evolutionary biogeography of the marine algae of the North Atlantic* (ed. by), pp. 9–34. Springer.

Legendre, P. & Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.

Legendre, P. & Legendre, L. (1998) *Numerical Ecology*. 3rd ed., Elsevier, Oxford, United Kingdom.

Legendre, P. & Troussellier, M. (1988) Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. *Limnology and Oceanography*, **33**, 1055–1067.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters*, **7**, 601–613.

Leibold, M. A. & McPeek, M. A. (2006) Coexistence of the niche and neutral perspectives in community ecology. *Ecology*, **87**, 1399–1410.

Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., Airamé, S. & Warner, R. R. (2009) Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, **384**, 33–46.

Levin, P. S. & Hay, M. E. (1996) Responses of temperate reef fishes to alterations in algal structure and species composition. *Marine Ecology Progress Series*, **134**, 37–47.

Levin, S. A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, **73**, 1943–1967.

Levin, S. A. & Paine, R. T. (1974) Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences*, **71**, 2744–2747.

Lewis, A. R. (1997) Recruitment and post-recruit immigration affect the local population size of coral reef fishes. *Coral Reefs*, **16**, 139–149.

Lewis, W. M. (1977) Net growth rate through time as an indicator of ecological similarity among phytoplankton species. *Ecology*, **58**, 149–157.

Linares, C., Coma, R., Garrabou, J., Dìaz, D. & Zabala, M. (2008) Size distribution, density and disturbance in two Mediterranean gorgonians: Paramuricea clavata and Eunicella singularis. *Journal of Applied Ecology*, **45**, 688–699.

Logue, J. B., Mouquet, N., Peter, H., Hillebrand, H. & The Metacommunity Working Group (2011) Empirical approaches to metacommunities: a review and comparison with theory. *Trends in Ecology and Evolution*, **26**, 482–491.

Lundvall, D., Svanbäck, R., Persson, L. & Byström, P. (1999) Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 1285–1292.

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, **101**, 377–385.

MacNeil, M. A., Graham, N. A. J., Polunin, N. V. C., Kulbicki, M., Galzin, R., Harmelin-Vivien, M. & Rushton, S. P. (2009) Hierarchical drivers of reef-fish metacommunity structure. *Ecology*, **90**, 252–264.

Macpherson, E. (1998) Ontogenetic shifts in habitat use and aggregation in juvenile sparid fishes. *Journal of Experimental Marine Biology and Ecology*, **220**, 127–150.

Macpherson, E. & Duarte, C. M. (1991) Bathymetric trends in demersal fish size: is there a general relationship? *Marine Ecology Progress Series*, **71**, 103–112.

Maggs, J. Q., Mann, B. Q. & Cowley, P. D. (2013) Reef fish display station-keeping and ranging behaviour in the Pondoland Marine Protected Area on the east coast of South Africa. *African Journal of Marine Science*, **35**, 183–193.

Malcolm, H. A., Gladstone, W., Lindfield, S., Wraith, J. & Lynch, T. P. (2007) Spatial and temporal variation in reef fish assemblages of marine parks in New

South Wales, Australia-baited video observations. *Marine Ecology Progress Series*, **350**, 277–290.

Malcolm, H. A., Jordan, A. & Smith, S. D. A. (2011) Testing a depth-based Habitat Classification System against reef fish assemblage patterns in a subtropical marine park. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **21**, 173–185.

Mann, B. Q. (2013) *Southern African Marine Linefish Species Profiles*, Special Publication, Oceanographic Research Institute, Durban.

May, R. M. (1975). Patterns of species abundance and diversity. In: *Ecology and evolution of communities*. Ed. by Cody, M. L. & Diamond, J. M., Harvard University Press, Cambridge, Massachusetts, pp. 81–120.

McClanahan, T. R., Muthiga, N. A., Kamukuru, A. T., Machano, H. & Kiambo, R. W. (1999) The effects of marine parks and fishing on coral reefs of northern Tanzania. *Biological Conservation*, **89**, 161–182.

McCormick, M. I. (1989) Spatio-temporal patterns in the abundance and population structure of a large temperate reef fish. *Marine Ecology Progress Series*, **53**, 215–225.

McGill, B. J., Dornelas, M., Gotelli, N. J. & Magurran, A. E. (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology and Evolution*, **30**, 104–113.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution*, **21**, 178–185.

McLaren, B. W., Langlois, T. J., Harvey, E. S., Shortland-Jones, H. & Stevens, R. (2015) A small no-take marine sanctuary provides consistent protection for small-bodied by-catch species, but not for large-bodied, high-risk species. *Journal of Experimental Marine Biology and Ecology*, **471**, 153–163.

Mellin, C., Bradshaw, C. J. A., Fordham, D. A. & Caley, M. J. (2014) Strong but opposing β-diversity–stability relationships in coral reef fish communities. *Proceedings of the Royal Society of London B: Biological Sciences*, **281**, 20131993.

Micheli, F. & Halpern, B. S. (2005) Low functional redundancy in coastal marine assemblages. *Ecology Letters*, **8**, 391–400.

Moore, C. H., Harvey, E. S. & Van Niel, K. P. (2009) Spatial prediction of demersal fish distributions: enhancing our understanding of species–environment relationships. *ICES Journal of Marine Science*, **66**, 2068–2075.

Mora, C. & Sale, P. F. (2002) Are populations of coral reef fish open or closed? *Trends in Ecology and Evolution*, **17**, 422–428.

Morisita, M. (1959) Measuring of the dispersion of individuals and analysis of the distributional patterns. *Memoirs of the Faculty of Science, Kyushu University, Series E*, **2**, 215–235.

Morisita, M. (1962) I_δ-index, a measure of dispersion of individuals. *Researches on Population Ecology*, **4**, 1–7.

Morisita, M. (1971) Composition of the I_δ-index. *Researches on Population Ecology*, **13**, 1–27.

Mouillot, D. (2007) Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *Journal of Applied Ecology*, **44**, 760–767.

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H. & Bellwood, D. R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology and Evolution*, **28**, 167–177.

Mouillot, D., Spatharis, S., Reizopoulou, S., Laugier, T., Sabetta, L., Basset, A. & Do Chi, T. (2006) Alternatives to taxonomic-based approaches to assess changes in transitional water communities. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **16**, 469–482.

Mouillot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-González, J. E., Bender, M., Chabanet, P., Floeter, S. R., Friedlander, A., Vigliola, L., et al. (2014) Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*, **111**, 13757–13762.

Mumby, P. J., Edwards, A. J., Arias-González, J. E., Lindeman, K. C., Blackwell, P. G., Gall, A., Gorczynska, M. I., Harborne, A. R., Pescod, C. L., Renken, H., et al. (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature*, **427**, 533.

Munday, P. L. (2004) Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. *Ecology*, **85**, 623–628.

Murphy, G. I. (1968) Pattern in life history and the environment. *The American Naturalist*, **102**, 391–403.

Murray, T. S., Gouws, G., Mwale, M., Mann, B. Q. & Cowley, P. D. (2014) Unravelling population structure of black musselcracker Cymatoceps nasutus: evidence for multiple populations in South African coastal waters. *African Journal of Marine Science*, **36**, 493–503.

Nanami, A. & Nishihira, M. (2002) The structures and dynamics of fish communities in an Okinawan coral reef: effects of coral-based habitat structures at sites with rocky and sandy sea bottoms. *Environmental Biology of Fishes*, **63**, 353.

Nanami, A. & Nishihira, M. (2003) Population dynamics and spatial distribution of coral reef fishes: comparison between continuous and isolated habitats. *Environmental Biology of Fishes*, **68**, 101–112.

Ng, I. S. Y., Carr, C. M. & Cottenie, K. (2009) Hierarchical zooplankton metacommunities: distinguishing between high and limiting dispersal mechanisms. *Hydrobiologia*, **619**, 133–143.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. & Wagner, H. (2015). *vegan: Community Ecology Package*. R package version 2.3-1.

Palardy, J. E. & Witman, J. D. (2011) Water flow drives biodiversity by mediating rarity in marine benthic communities. *Ecology Letters*, **14**, 63–68.

Pandit, S. N., Kolasa, J. & Cottenie, K. (2009) Contrasts between habitat generalists and specialists: an empirical extension to the basic metacommunity framework. *Ecology*, **90**, 2253–2262.

Parker, D., Winker, H., Bernard, A. T. F., Heyns-Veale, E. R., Langlois, T., Harvey, E. S. & Götz, A. (2016) Insights from baited video sampling of temperate reef fishes: How biased are angling surveys? *Fisheries Research*, **179**, 191–201.

Parsons, D. M., Babcock, R. C., Hankin, R. K. S., Willis, T. J., Aitken, J. P., O'dor, R. K. & Jackson, G. D. (2003) Snapper Pagrus auratus (Sparidae) home range dynamics: acoustic tagging studies in a marine reserve. *Marine Ecology Progress Series*, **262**, 253–265.

Parsons, D. M., Morrison, M. A. & Slater, M. J. (2010) Responses to marine reserves: decreased dispersion of the sparid Pagrus auratus (snapper). *Biological Conservation*, **143**, 2039–2048.

Pattrick, P. & Strydom, N. A. (2009) Swimming abilities of wild-caught, late-stage larvae of Diplodus capensis and Sarpa salpa (Pisces: Sparidae) from temperate South Africa. *Estuarine, Coastal and Shelf Science*, **85**, 547–554.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T. J., Sumaila, U. R., Walters, C. J., Watson, R. & Zeller, D. (2002) Towards sustainability in world fisheries. *Nature*, **418**, 689–695.

Peres-Neto, P. R. & Legendre, P. (2010) Estimating and controlling for spatial structure in the study of ecological communities. *Global Ecology and Biogeography*, **19**, 174–184.

Peres-Neto, P. R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**, 2614–2625.

Persson, L., Andersson, J., Wahlstrom, E. & Eklov, P. (1996) Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology*, **77**, 900–911.

Peters, R. H. (1986) *The ecological implications of body size*, Cambridge University Press, Cambridge, United Kingdom.

Plaut, I. (2001) Critical swimming speed: its ecological relevance. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **131**, 41–50.

Pulfrich, A. & Griffiths, C. L. (1988) The fishery for hottentot Pachymetopon blochii Val. in the South-Western Cape. *South African Journal of Marine Science*, **7**, 227–241.

Pulliam, H. R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.

R Core Team (2014). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Roberts, C. M., McClean, C. J., Veron, J. E., Hawkins, J. P., Allen, G. R., McAllister, D. E., Mittermeier, C. G., Schueler, F. W., Spalding, M., Wells, F., et al. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295**, 1280–1284.

Robertson, D. R. (1988) Abundances of surgeonfishes on patch-reefs in Caribbean Panamá: due to settlement, or post-settlement events? *Marine Biology*, **97**, 495–501.

Rogers, C. S. (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, **62**, 185–202.

Rosenberg, A., Bigford, T. E., Leathery, S., Hill, R. L. & Bickers, K. (2000) Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science*, **66**, 535–542.

Roughgarden, J. (1972) Evolution of niche width. *American Naturalist*, 683–718.

Roughgarden, J. (1974) Species packing and the competition function with illustrations from coral reef fish. *Theoretical Population Biology*, **5**, 163–186.

Sale, P. F. (1977) Maintenance of high diversity in coral reef fish communities. *American Naturalist*, 337–359.

Sale, P. F. (1978) Coexistence of coral reef fishes—a lottery for living space. *Environmental Biology of Fishes*, **3**, 85–102.

Sale, P. F. (1991) *The ecology of fishes on coral reefs*, Academic Press, San Diego.

Sale, P. F. (1998) Appropriate spatial scales for studies of reef-fish ecology. *Australian Journal of Ecology*, **23**, 202–208.

Sale, P. F. (2004) Connectivity, recruitment variation, and the structure of reef fish communities. *Integrative and Comparative Biology*, **44**, 390–399.

Sale, P. F., Cowen, R. K., Danilowicz, B. S., Jones, G. P., Kritzer, J. P., Lindeman, K. C., Planes, S., Polunin, N. V., Russ, G. R., Sadovy, Y. J., et al. (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution*, **20**, 74–80.

Sale, P. F., Danilowicz, B. S., Doherty, P. J. & Williams, D. M. (2005) The relation of microhabitat to variation in recruitment of young-of-year coral reef fishes. *Bulletin of Marine Science*, **76**, 123–142.

Sale, P. F. & Douglas, W. A. (1984) Temporal variability in the community structure of fish on coral patch reefs and the relation of community structure to reef structure. *Ecology*, **65**, 409–422.

Sale, P. F., Guy, J. A. & Steel, W. J. (1994) Ecological structure of assemblages of coral reef fishes on isolated patch reefs. *Oecologia*, **98**, 83–99.

Samaai, T., Gibbons, M. J., Kerwath, S. E., Yemane, D. & Sink, K. (2010) Sponge richness along a bathymetric gradient within the iSimangaliso Wetland Park, South Africa. *Marine Biodiversity*, **40**, 205–217.

Santini, F., Carnevale, G. & Sorenson, L. (2014) First multi-locus timetree of seabreams and porgies (Percomorpha: Sparidae). *Italian Journal of Zoology*, **81**, 55–71.

Scharf, F. S., Juanes, F. & Rountree, R. A. (2000) Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series*, **208**, 229–248.

Scheiner, S. M., Chiarucci, A., Fox, G. A., Helmus, M. R., McGlinn, D. J. & Willig, M. R. (2011) The underpinnings of the relationship of species richness with space and time. *Ecological Monographs*, **81**, 195–213.

Schoener, T. W. (1974) Resource partitioning in ecological communities. *Science*, **185**, 27–39.

Schumann, E. H., Ross, G. J. B. & Goschen, W. S. (1988) Cold water events in Algoa Bay and along the Cape south coast, South Africa, in March/April 1987. *South African Journal of Science*, **84**, 579–583.

Schumann, E. H. (1999) Wind-driven mixed layer and coastal upwelling processes off the south coast of South Africa. *Journal of Marine Research*, **57**, 671–691.

Shin, Y.-J., Rochet, M.-J., Jennings, S., Field, J. G. & Gislason, H. (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. *ICES Journal of marine Science*, **62**, 384–396.

Siegel, D. A., Mitarai, S., Costello, C. J., Gaines, S. D., Kendall, B., Warner, R. & Winters, K. (2008) The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences*, **105**, 8974–8979.

Sink, K. J., Boshoff, W., Samaai, T., Timm, P. G. & Kerwath, S. E. (2006) Observations of the habitats and biodiversity of the submarine canyons at Sodwana Bay: coelacanth research. *South African Journal of Science*, **102**, 466–474.

Smale, M. J. (1988) Distribution and reproduction of the reef fish Petrus rupestris (Pisces: Sparidae) off the coast of South Africa. *African Zoology*, **23**, 272–287.

Smale, M. J. (1992) Predatory fish and their prey—an overview of trophic interactions in the fish communities of the west and south coasts of South Africa. *South African Journal of Marine Science*, **12**, 803–821.

Smale, M. J. & Buxton, C. D. (1985) Aspects of the recreational ski-boat fishery off the Eastern Cape, South Africa. *South African Journal of Marine Science*, **3**, 131–144.

Smith, C. L. & Tyler, J. C. (1972) Space resource sharing in a coral reef fish community. *Bulletin of the Natural History Museum of Los Angeles County*, **14**, 125–170.

Smith, C. L. & Tyler, J. C. (1973) Direct observations of resource sharing in coral reef fish. *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **24**, 264–275.

Smith, T. W. & Lundholm, J. T. (2010) Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography*, **33**, 648–655.

Smith-Gill, S. J. (1975) Cytophysiological basis of disruptive pigmentary patterns in the leopard frog Rana pipiens. II. Wild type and mutant cell-specific patterns. *Journal of Morphology*, **146**, 35–54.

Solano-Fernandez, S., Attwood, C. G., Chalmers, R., Clark, B. M., Cowley, P. D., Fairweather, T., Fennessy, S. T., Götz, A., Harrison, T. D., Kerwath, S. E., Lamberth, S. J., Mann, B. Q., Smale, M. J. & Swart, L. (2012) Assessment of the effectiveness of South Africa's marine protected areas at representing ichthyofaunal communities. *Environmental Conservation*, **39**, 259–270.

St. Mary, C. M., Osenberg, C. W., Frazer, T. K. & Lindberg, W. J. (2000) Stage structure, density dependence and the efficacy of marine reserves. *Bulletin of Marine Science*, **66**, 675–690.

Stehfest, K. M., Lyle, J. M. & Semmens, J. M. (2015) The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. *ICES Journal of Marine Science*, **72**, 2512–2520.

Stobart, B., García-Charton, J. A., Espejo, C., Rochel, E., Goñi, R., Reñones, O., Herrero, A., Crec'hriou, R., Polti, S., Marcos, C., Planes, S. & Pérez-Ruzafa, A. (2007) A baited underwater video technique to assess shallow-water Mediterranean fish assemblages: Methodological evaluation. *Journal of Experimental Marine Biology and Ecology*, **345**, 158–174.

Stobutzki, I. C. & Bellwood, D. R. (1994) An analysis of the sustained swimming abilities of pre-and post-settlement coral reef fishes. *Journal of Experimental Marine Biology and Ecology*, **175**, 275–286.

Stoll, P. & Prati, D. (2001) Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology*, **82**, 319–327.

Teske, P. R., Forget, F. R. G., Cowley, P. D., Von der Heyden, S. & Beheregaray, L. B. (2010) Connectivity between marine reserves and exploited areas in the philopatric reef fish Chrysoblephus laticeps (Teleostei: Sparidae). *Marine Biology*, **157**, 2029–2042.

Tilney, R. L., Nelson, G., Radloff, S. E. & Buxton, C. D. (1996) Ichthyoplankton distribution and dispersal in the Tsitsikamma National Park marine reserve, South Africa. *South African Journal of Marine Science*, **17**, 1–14.

Topping, D. T., Lowe, C. G. & Caselle, J. E. (2006) Site fidelity and seasonal movement patterns of adult California sheephead Semicossyphus pulcher (Labridae): an acoustic monitoring study. *Marine Ecology Progress Series*, **326**, 257–267.

Turpie, J. K., Beckley, L. E. & Katua, S. M. (2000) Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation*, **92**, 59–72.

Van Valen, L. (1965) Morphological variation and width of ecological niche. *American Naturalist*, 377–390.

Veech, J. A. (2005) Analyzing patterns of species diversity as departures from random expectations. *Oikos*, **108**, 149–155.

Vellend, M. (2010) Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, **85**, 183–206.

Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., Kraft, N. J., Letaw, A. D., Macdonald, A. A. M., Maclean, J. E., et al. (2014) Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, **123**, 1420–1430.

Viana, D. S., Figuerola, J., Schwenk, K., Manca, M., Hobæk, A., Mjelde, M., Preston, C. D., Gornall, R. J., Croft, J. M., King, R. A., Green, A. J. & Santamaria, L. (2015) Assembly mechanisms determining high species turnover in aquatic communities over regional and continental scales. *Ecography*, **38**, 001–008.

Videler, J. J. & Wardle, C. S. (1991) Fish swimming stride by stride: speed limits and endurance. *Reviews in Fish Biology and Fisheries*, **1**, 23–40.

Villéger, S., Miranda, J. R., Hernández, D. F. & Mouillot, D. (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecological Applications*, **20**, 1512–1522.

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. & Messier, J. (2012) The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution*, **27**, 244–252.

Warner, R. R. & Chesson, P. L. (1985) Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist*, **125**, 769–787.

Watson, D. L., Harvey, E. S., Kendrick, G. A., Nardi, K. & Anderson, M. J. (2007) Protection from fishing alters the species composition of fish assemblages in a temperate-tropical transition zone. *Marine Biology*, **152**, 1197–1206.

Watson, D. L. (2006). Use of underwater stereo-video to measure fish assemblage structure, spatial distribution of fishes and change in assemblages with protection from fishing. PhD thesis. University of Western Australia.

Werner, E. E. & Gilliam, J. F. (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics*, **15**, 393–425.

White, E. P., Ernest, S. K. M., Kerkhoff, A. J. & Enquist, B. J. (2007) Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution*, **22**, 323–330.

Wilkinson, C. R. & Evans, E. (1989) Sponge distribution across Davies Reef, Great Barrier Reef, relative to location, depth, and water movement. *Coral Reefs*, **8**, 1–7.

Willis, T. J. & Babcock, R. C. (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Marine and Freshwater Research*, **51**, 755–763.

Willis, T. J., Millar, R. B. & Babcock, R. C. (2000) Detection of spatial variability in relative density of fishes: comparison of visual census, angling, and baited underwater video. *Marine Ecology Progress Series*, 249–260.

Wilson, D. S. (1975) The adequacy of body size as a niche difference. *The American Naturalist*, **109**, 769–784.

Wilson, D. S. (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology*, **73**, 1984–2000.

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. & Sweatman, H. (2008) Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology*, **77**, 220–228.

Winegardner, A. K., Jones, B. K., Ng, I. S. Y., Siqueira, T. & Cottenie, K. (2012) The terminology of metacommunity ecology. *Trends in Ecology and Evolution*, **27**, 253–254.

Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A. & Warren, P. H. (2005) Body size in ecological networks. *Trends in Ecology and Evolution*, **20**, 402–409.

Worm, B., Hilborn, R., Baum, J. K., Branch, T. A., Collie, J. S., Costello, C., Fogarty, M. J., Fulton, E. A., Hutchings, J. A., Jennings, S., Jensen, O. P., Lotze, H. K., Mace, P. M., McClanahan, T. R., Minto, C., Palumbi, S. R., Parma, A. M., Ricard, D., Rosenberg, A. A., Watson, R. & Zeller, D. (2009) Rebuilding Global Fisheries. *Science*, **325**, 578–585.

Yemane, D., Field, J. G. & Leslie, R. W. (2010) Spatio-temporal patterns in the diversity of demersal fish communities off the south coast of South Africa. *Marine Biology*, **157**, 269–281.

Zintzen, V., Anderson, M. J., Roberts, C. D., Harvey, E. S., Stewart, A. L. & Struthers, C. D. (2012) Diversity and composition of demersal fishes along a depth gradient assessed by baited remote underwater stereo-video. *PloS ONE*, **7**, e48522.