



# **Patterns of Distribution, Abundance and Community Composition of Rock Pool Fishes in Goukamma Nature Reserve, South Africa**

David Bryce Purchase

Supervisor: Associate Professor Colin Attwood

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Department of Biological Sciences,  
Marine Research Institute,  
University of Cape Town,  
7701, Rondebosch  
Cape Town, South Africa



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# CHAPTER 1

## Introduction and Literature Review

### ABSTRACT

Rock pools can be found in most rocky intertidal marine environments across the globe. Despite the vast body of literature describing the organization of ecological communities and biota inhabiting the greater rocky intertidal, very little effort has been given to rock pools. As a result they are far less understood than the adjacent emergent intertidal, particularly with respect to their fish communities. This is mostly due to the relative small size of rock pool fishes, their cryptic behaviour and morphologies, the relative difficulty in sampling intertidal fish utilizing conventional methods, and the low economic value of rock pool fishes. Rock pool fishes may have significant ecological value, as they are involved in structuring intertidal communities. Due to reduced environmental fluctuations within rock pools, these habitats may serve as crucial refuges from adjacent stressors. Furthermore, rock pools may play an important role in the early life histories of sub-littoral fish species that utilize these habitats as juveniles, some of which are valuable to fisheries as adults. It has been suggested that due to the lack of exposure at low tide, rock pools do not represent a true intertidal habitat, as organisms are not subject to the full range of environmental fluctuations seen in adjacent habitats. There is unequivocal evidence indicating that, like the surrounding emergent substrata, conditions in rock pools are highly regulated by the tidal cycle and that the degree of environmental fluctuations will vary greatly with intertidal height and degree of exposure of individual pools, much like patterns seen in adjacent habitats. Fishes inhabiting rock pools can be broadly categorised into groups based on their major zoographic provinces, life history traits and their behavioural affinities, on top of basic taxonomic categorizations. Global patterns indicate two main rock pool fish communities, those of Gondwanan origin and those of Laurasian origin. South African rock pools are relatively well studied from a taxonomic perspective compared to elsewhere, however, like the rest of the globe, factors influencing their fish communities are far less understood.

## Introduction

The purpose of community ecology is to explain observed distributions and abundances of species and to gain insight into the processes that give rise to these patterns (Begon et al., 1996; Diamond & Case, 1986). The processes that govern most systems include biological interactions such as predation, herbivory and competition, and environmental fluctuations (Metaxas & Scheibling, 1993). To develop suitable ecological models of broad scope and validity, it is important for community ecologists to understand these processes; why they occur, and the wider implications for sustainable management of these ecosystems and the processes that govern them.

## Intertidal Ecosystems

Marine intertidal ecosystems present an ideal model for studies investigating community ecology (White et al., 2015). Intertidal habitats vary from soft substrata such as sandy beaches and estuarine mudflats to hard substrates such as steep cliffs and bluffs or coral reefs and rocky shores, all of which support differing floral and faunal species assemblages. Being the transition zone between both terrestrial and marine influences, the intertidal zone provides community ecologists with a quantifiable natural gradient in physical (abiotic) and biological (biotic) dimensions. Rock pool community assemblages, and as well as their fish assemblages are known to vary in their composition on a number of scales: across continents, latitudinally, among biogeographic regions and within single locations (Gibson, 1982, Bennett, 1984, 1987, Prochazka, 1992, Gibson and Yoshiyama, 1999, Griffiths, 2003, White et al., 2015, Harasti et al, 2016).

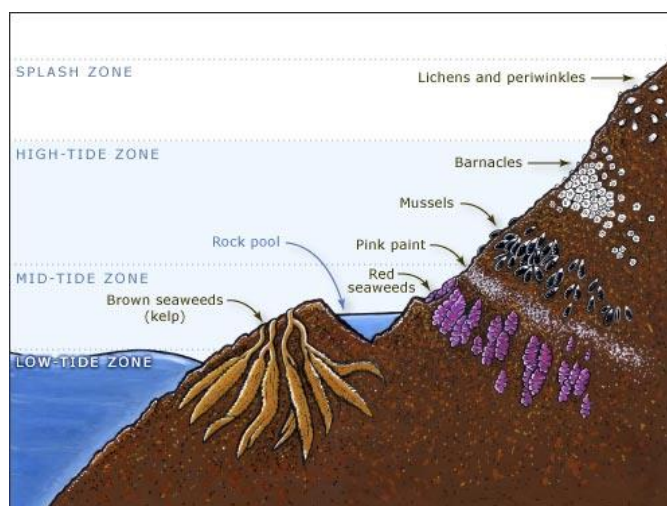


Figure 1: An example of a rocky intertidal ecosystem showing distinct zonation in biota within a highly heterogeneous rock based habitat (Wassilieff, 2006)

The rocky intertidal is a highly heterogeneous habitat (Figure 1). These habitats can range from a few meters (between adjacent open beaches or other soft substrate habitats) to hundreds of kilometres of unbroken rock based substrate (Horn & Martin, 2006). Rock pools (or tidepools

as they are known elsewhere) are found within the greater rocky intertidal and comprise of indentations, gullies and depressions within the rock substrata that retain water at low tide (Figure 2), acting as refuges for inter-tidal organisms (Zander et al., 1999). Rock pools have long been acknowledged as an important and specialized microhabitat within the greater rocky intertidal, however, unlike most of the rocky intertidal, their substrata are not exposed at low tide (Huggett & Griffiths, 1986), and are thus subject to reduced environmental fluctuations in comparison to adjacent exposed substrata. Rock pools are, however, patchily distributed along the rocky intertidal but are still highly variable both spatially and temporally on a number of scales much like the adjacent rocky intertidal (Martins et al., 2008; Firth et al., 2013). Rock pools are highly productive microhabitats and contain a notably diverse range of primary producers, herbivores, omnivores and predators (Horn & Martin, 2006).



Figure 2: Examples of rock pools, varying from semi-open gullies (images: A&B) to deeper pools (image: D) and wave cut depressions (image: C) (from: Griffiths, 2003)

Despite the vast body of literature describing the organization of ecological communities and biota inhabiting the greater rocky intertidal, very little effort has been given to rock pools globally and as a result, they are far less studied and understood than the adjacent emergent intertidal (White et al., 2015). Furthermore, little is known about the fish species assemblages that inhabit these ecosystems and quantitative studies on rock pool fishes are few and far between on a global scale (Griffiths, 2003). Fewer still are studies investigating the spatial and temporal dynamics of rock pool fishes, in particular those species that spend all of their lives within rock pools. This is mostly due to the relatively small size of rock pool fishes, their cryptic behaviour and morphology and the relative difficulty in sampling intertidal fishes utilizing conventional methods such as netting, trapping or hook-and-line methods, and the low economical value of rock pool fish when compared to conventional fisheries (Horn et al., 1998), other than aquarists (ornamental) and recreational fishers.

Rock pool fishes, however, may have significant ecological value, as they are known constituents in structuring intertidal communities (Coull & Wells, 1983, Connell & Anderson,

2000). Furthermore, due to reduced environmental fluctuations within these microhabitats, rock pools may serve as crucial refuges from adjacent stressful conditions (particularly for fishes), or as protection from larger subtidal predators, and may play an important role in the early life histories of sub-littoral fish species that utilize these habitats as juveniles (see later: transient and vagrant species), some of which are commercially valuable to fisheries as adults (Beckley, 1985).

The possible nursery and refuge functions of rock pools may have wide-reaching implications for conservation and fisheries management in light of the degradation of other nursery areas (Griffiths, 2003, Dias et al., 2016). Rock pools may thus act as supplementary recruitment areas where the effectiveness of more suitable nursery areas has been compromised due to anthropogenic activity (Griffiths, 2002).

### **Physical Environments in Rock Pools**

It has been suggested that due to the lack of exposure at low tide, that rock pools “do not represent a true intertidal habitat”, as organisms may be submerged for the full tidal cycle and are therefore not subject to the full range of environmental fluctuations seen in adjacent habitats (Underwood et al., 1991). Regardless, there is unequivocal evidence indicating that, like the surrounding emergent substrata, conditions in rock pools are highly regulated by the tidal cycle and that the degree of environmental fluctuations will vary greatly with intertidal height and degree of exposure (Metaxas & Shiebling, 1993).

Due to the retention of water at low tide, the physical environment of rock pools does not fluctuate as drastically as conditions on emergent substrates. Conditions, however, do fluctuate more drastically than those within subtidal habitats, which are submerged throughout the tidal cycle and thus have a higher degree of water turnover and mixing. The physico-chemical conditions prevailing in a particular pool are highly dependent on the duration for which they are isolated from the adjacent open ocean at low tide as well as the height of the pool and its volume. Pools higher in the intertidal are exposed to greater external changes than those further down and thus the degree of isolation (driven mainly by the tides) is the major factor affecting physical environmental changes in rock pools (Gibson, 1972). Temperature within rock pools can vary daily by up to 15 °C, dependent on intertidal height (isolation from tidal inundation), wave exposure, degree of shading as well as the volume of the pool and its depth reaching as high as 40 °C in summer (at low latitudes) and dropping below freezing during cooler months (at higher latitudes) (Brooker Klugh, 1924, Johnson & Skutch, 1928, Stephenson et al., 1934, Daniel & Boyden, 1975, Huggett & Griffiths, 1986). Changes in daily temperature in pools may also result in thermal stratification of the water column in pools subject to highly reduced turnover of water, generally found high in the intertidal (McGregor, 1965). Salinity fluctuations also occur in rock pools throughout the globe dependent on pool height along the shore as well as fresh water input from adjacent terrestrial habitats, precipitation and evaporation, and have been shown to range between 5 and 35 practical salinity units (psu) (Pyefinch, 1943, Green, 1971, Morris & Taylor, 1983). Other physical changes in water

chemistry (such as carbonate, nitrate and trace metal concentrations) driven by purely physical processes have not been investigated, however, it is widely accepted that temperature and salinity fluctuations are the most important physico-chemical changes controlling fish species composition (Huggett & Griffiths, 1986).

Daily changes in oxygen concentration and saturation, alkalinity and pH have also been noted in rock pools, mainly driven by biological processes making use of, or producing compounds that, alter the chemistry of rock pool water, when isolated at low tides. Huggett and Griffiths (1986) recorded higher oxygen values ( $O_2$ ) during sunlit hours, when photosynthesis occurs and lower oxygen values (at times hypoxic) at night (when alga respire). Fluctuations in pH have been shown to follow much the same pattern, with lower pH values at night due to a higher presence of carbon dioxide ( $CO_2$ ), releasing hydrogen ions ( $H^+$ ) and higher pH values during the day when photosynthesising autotrophs utilise the available carbon (Morris & Taylor, 1983). Changes in alkalinity can also occur when calcifying organisms utilize carbonate ( $CO_3^{2-}$ ) (Truchot & Duhamel-Jouve, 1980).

The physical environment within rock pools fluctuates vertically, horizontally, diurnally and seasonally on a wide range of scales. It is thus almost impossible for two natural pools to be similar in all the above-mentioned characteristics. Indeed each natural rock pool is unique in its particular physical environmental regime (Metaxas & Scheibling, 1993). Few studies have explicitly investigated these characteristics and their effect on community composition, abundance or diversity of fishes (Griffiths, 2003, White et al., 2015).

### **Fishes Inhabiting Rock Pools**

Rock pools play host to a number of different fish species (White et al. 2015). To understand the assemblages present in a particular location, fishes can be broadly categorised into groups based on their major zoographic provinces, life history traits as well as their behavioural affinities on top of basic taxonomic categorizations. Griffiths (2003) provides a suitable review of these categorisations, adapted here for application to the coast of South Africa:

#### **Species Categorisation by Biogeographic or Zoographic provinces**

Biogeographies in South Africa have in the past been split into three main categories, namely the Cool Temperate West Coast, the Warm Temperate South Coast and the Sub Tropical East Coast. It is now accepted that the coast be slit into 5 coastal zones (Griffiths et al., 2010). Furthermore, there is evidence for a further two as “transition” zones: False Bay and the area between Port Elizabeth and East London (Anderson et al., 2016). For the purposes of this study, the three original biogeographic zones (west, south and east) will be used as well as the two transition zones (total: 5 zones, Figure 4).

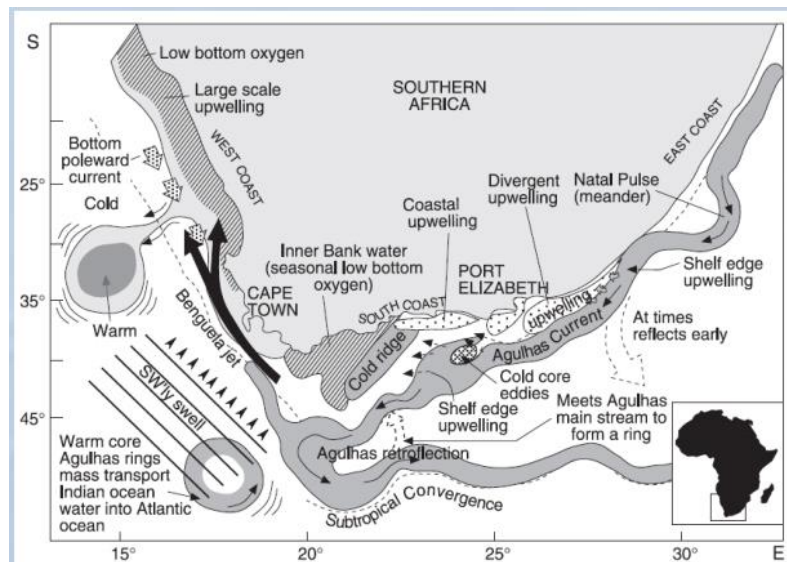


Figure 3: Map showing the major oceanographic features of the South African coastline (from: Roberts, 2005)

- i. **Cold Temperate West Coast Species** are those found along the Benguela Upwelling province on the west coast (Figure 4). This province is not influenced by the warm southward flowing Agulhas current (Figure 3) and environmental conditions are notably different owing to strong year-round upwelling of cooler, nutrient rich waters. (E.g. Klipfishes)
- ii. **Cool Temperate Transition Species** are those found in the cooler waters of the South Western Coast between Cape Agulhas and Cape Point (Figure 4) where influences of the South and West Coasts combine (Figure 3). This Area is characterised by both South and West Coast species. (E.g. Clingfishes and Klipfishes)
- iii. **Cooler Warm Temperate South Coast Species (Agulhas Bank)** are those found in again cooler waters, south of 35°S (Figure 4). Cooler temperate species are generally found between Port Elizabeth and Cape Agulhas. This constitutes the “True South Coast”. (E.g. Clingfishes)
- iv. **Warm Temperate Transition Species** are those found in warmer waters, roughly between 25°S and 35°S (Figure 4), where seasonal fluctuations in environmental conditions (namely seasonal and dynamic upwelling) create unique environmental conditions to prevail due to the divergence of the Agulhas from the shore (Figure 3). In South Africa, warm temperate transition species are found along the south coast from roughly Port Alfred to Port Elizabeth. (E.g. Gobies and Blennies)
- v. **Subtropical to Tropical East Coast Species (Indo-Pacific)** are those which are distributed throughout the tropics (Figure 4) in the warmest waters (0-25°S), however, may also be found further south/ north of this when warm western boundary currents such as the Agulhas displace them pole-ward (Figure 3). In South Africa, sub-tropical species are found northwards of Durban (North East Coast). (E.g. Tropical Wrasses, Gobies)

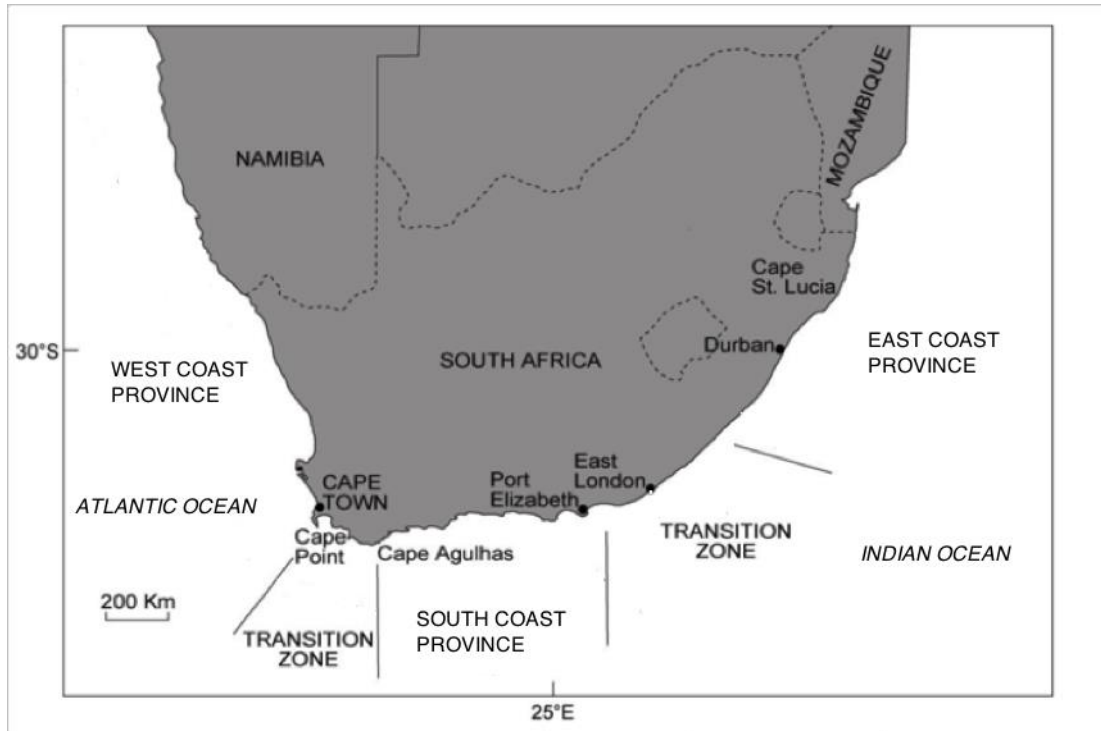


Figure 4: Map of the five major ocean provinces along the South African coast (adapted from Anderson et al., 2016)

### Categorisation of Fishes by Dependency on Rock Pool Habitats

Most inshore coastal fish species make use of rock pools at some stage in their life histories (Griffiths, 2002). Rock pool fishes can be broadly classified into three categories dependent on the proportion of their life histories spent in rock pools (Mahon & Mahon, 1994, Griffiths, 2003) and is most likely reflective of their species-specific tolerances to the environmental conditions and stressors imposed by life within rock pools and the rocky intertidal as a whole (Gibson, 1972, Bennett & Griffiths, 1984; Beckley, 1985; Bennett, 1987; Burger, 1988, 1991, Griffiths, 2002, Griffiths, 2003, White & Brown, 2013, White et al., 2015).

- i. **Primary Resident Species** are those fish species, which spend all, or a large majority, of their lives within the rock pool environment (juveniles to adults). They generally exhibit highly adapted morphological, behavioural and physiological traits for permanent life within the intertidal habitat and within rock pools (e.g. Klipfishes, Clingfishes, Gobies and Blennies). These adaptations include the evolution of “suckers” from pelvic fins (Zander et al., 1999), negative buoyancy, as well as the ability to leave water during unfavourable conditions (Martin, 1993, 1995; 1999; Thyssen et al., 2014). Furthermore, rock pool resident species have also been shown to have higher degrees of ecological cognition and generally exhibit distinct site fidelity (individual rock pool affinity) and homing behaviours (White & Brown, 2013). They are “true rock pool specialists”.
- ii. **Opportunists, or Secondary Resident Species** are those fish species, which make use of rock pools for only part of their life histories. They are generally species that utilise rock pools as juveniles or during high tide feeding. They make use of the refuge and

nursery function of rock pools during their most vulnerable life history stages but generally have few morphological or behavioural adaptations for permanent (juveniles to adults) life within rock pools. They are, however, usually found within the coastal subtidal as they shift into these habitats as adults (e.g. Seabreams). Contrary to residential species, “non-specialist” species such as opportunists or transients (see: below) generally show lower degrees of site fidelity and poor homing abilities (White & Brown, 2013).

- iii. **Transients or Accidental visitors** are those species that are rarely found within rock pools and presence is generally due to stochastic trapping within rock pools during tidal retreat. These species are usually larger individuals or adults of opportunistic species and exhibit few if any adaptations to rock pool stressors. They are usually only found during a when seasonal current changes move them away from their more native habitats, after which they move back into subtidal habitats to which they are more adapted (e.g. Angelfishes)

### Behavioural Categorisation of Rock Pool Fishes

Fishes can also be categorized by behavioural characteristics although these groupings are not mutually exclusive and species may exhibit a combination of more than one or may even shift from between them at different life stages (Griffiths, 2003):

- i. **Solitary Species** are those fish species, which are generally found alone or in pairs but never in schools. (E.g. Clingfishes)
- ii. **Aggregating Species** are those fish that form schools or small congregations. (E.g. Mulletts, Seabreams)
- iii. **Cryptic Species** are those fish species with cryptic morphologies, such as camouflaged colouration or patterning and tend to be exhibit timid behaviours such as hiding in crevices, overhangs or in rock pool macro-algal species. (E.g. Klipfishes, Gobies and Blennies)
- iv. **Territorial Species** are those species, which display aggressive behaviours to defend a home range or a particular area. (E.g. Grouper and Rock cods).

### Factors Influencing the Distribution of Rock Pool Fishes

Despite a distinct lack of explicit research on rock pool fishes, some over-arching conclusions can be made about the factors that influence rock pool fish assemblages and their distributions, at least at relatively large scales. Most marine coastal fish communities are considered to vary greatly owing to temporal variability in recruitment by fishes utilising these habitats (Doherty & Williams, 1988). To the contrary, however, rock pool fish assemblages appear relatively resilient to changes in physical regime at regional scales, even though these fluctuations occur on a range of spatial and temporal scales (Thomson & Lehner, 1976, Prochazka, 1996). This resilience may act over periods of weeks whereas overall community structure may persist for decades (Collette, 1986, Lardner et al., 1993). At intermediate scales, seasonal differences in

assemblages are evident, owing to differential recruitment times of certain rock pool fishes (Willis & Roberts, 1996), movement to other intertidal habitats (Faria & Almada, 2001) and emigration to the subtidal under extreme, unsuitable conditions (Thomson & Lehner, 1976, Moring, 1990). At these scales, however, recruitment differences generally result in changes in size composition rather than overall species composition (Griffiths, 2003).

The presence or absence of rock pool fishes is first and foremost determined by physical environmental constraints imposed by environmental conditions persisting in a given pool as well as the distance between adjacent pools (Brendonck et al., 2015). These impose physiological constraints on inhabitants, which in the long term, will ultimately determine whether a particular species can or cannot survive in a particular area within the intertidal as well as spatial limitations imposing restrictions on recruitment ability into a particular location. Most rock pool species exhibit some degree of parental care, such as viviparity in Klipfishes (DeMartini, 1978, Prochazka, 1994) and limited larval dispersal (benthic eggs in gobies). Thus physical barriers, such as long expanses of sandy shores or differential currents can impose major restrictions on the ability of certain species to inhabit a particular location. At smaller scales, however (10's of meters), fish assemblages may differ due to relative physiological tolerances of each species to environmental conditions such as wave exposure and changes in water chemistry, ultimately determined by degree of water turnover driven by the tidal cycle and vertical height of rock pools in the intertidal (Gibson, 1972). More physiologically adapted species (residential species), that are able to cope with dynamic physical fluctuations, are generally found in less exposed pools, and higher in the intertidal, whereas those less adapted (secondary or transient species) are generally only found in pools lower in the intertidal, where physical environmental (physico-chemical) fluctuations are less drastic.

The community of fishes inhabiting a particular location may also be further regulated by biological factors within pools such as the availability of shelter (Gibson, 1982), the quality of turf, coralline or foliose algal species (Jones, 1984), preferred food availability (Gibson, 1972) and the presence of predators (Paine, 1974). All of these, however, act in concert with physical changes such as absolute pool volume (size), location within the intertidal (height) and the physico-chemical changes associated with these physical characteristics, namely changes in water chemistry (temperature, salinity, oxygen content and pH) (Horn et al., 1998).

Like many other ecosystems, species composition in rock pools can vary greatly owing to habitat complexity and heterogeneity (Horn et al., 1998). Griffiths (2006) considered two main habitat types available to rock pool fishes, both of which vary in their degree of contribution to structural habitat complexity and the degree of shelter available to rock pool fishes.

The fronds or blades of foliose algal species floating within the rock pool water column provide refuge and hiding locations for many species but are mostly utilized by mid water and pelagic fish species. Clinid (Klipfish) species make use of these structures and many exhibit morphological adaptations for camouflage within algal fronds as protection from predators (Kuitert, 1993). Alternatively, the physical and structural complexity of a rock pool such as

crevices, various sized rock, pebbled and sandy bottoms are also likely to have an effect on the species composition of species inhabiting a particular pool (Davis, 2000). Species most common in rock pools of high and heterogeneous rock cover (various rock sizes and crevices etc.) are Gobiidae (Gobies) and Blenniidae (Blennies) species, most of which have adaptations to crypsis within rocky substrates (Thyssen et al., 2014).

The structural complexity of rock pools can also have direct effects on the assemblage and abundance of fish species by affecting the shelter from competition, predation and prey as well as allowing multiple species and feeding guilds to co-exist due to sub-habitat partitioning of limited resources and space (Behrents, 1987, Hixon & Beets, 1993). The utilization of more complex habitats is also likely to increase with the high tide as rock pool fishes become more exposed to subtidal predation (Silbershneider & Booth, 2001) and as mentioned previously, complex habitats provide shelter to inhabitants from physical stressors as well as predation. Overall, the more complex a rock pool is, the higher the abundance and diversity of species living within it (Marsh et al., 1978). Thus rock pools with barren substratum and low structural complexity (straight edges) generally exhibit low species diversity and abundances (Bennett & Griffiths, 1984; Griffiths, 2006).

### **Global Patterns in Rock Pool Fish Assemblages**

Despite the global distribution of inter tidal rock pools; there have been relatively few investigations of their fish composition (Gibson, 1986, Griffiths 2002, 2003). Global necessity and interest in the preservation and sustainable management of marine ecosystems is growing (Sobel, 1993; Jamieson & Levings, 2001), but our knowledge of the community ecology of intertidal fishes (including those of rock pools) and factors driving community composition and distribution is still very much in its infancy. As a result very few overall conclusions can be drawn on the global patterns of rock pool fish communities.

Griffiths (2003), through analysis of rock pool fish species lists throughout the globe, has drawn some over-arching conclusions. Global patterns shown by Griffiths (2003) indicate two main rock pool fish communities, those of Gondwanan origin and those of Laurasian origin. Those of Gondwanan origin, such as France, Portugal, Australia, Chile, New Zealand and South Africa generally play host to families such as Blenniidae, Tripterygiidae, Gobiidae, Gobiessocidae and Clinidae with some species even being shared between countries. On the other hand, rock pools of Laurasian origin such as the United States, Canada and Mexico generally play host to families such as Cottidae, Stichaeidae, Scorpaenidae and Pholidae. It is hypothesised that these differences are due to separation of these landmasses over geological time, which would have had an effect on the ability of species to disperse and colonise certain areas. Rock pool fishes generally exhibit some degree of parental care and thus highly restricted larval dispersal mechanisms (Prochazka, 1993, Marliave, 1986) as well as limited movement as adults and a high degree of rock pool affinity and homing behaviours (Willis & Roberts, 1996; Griffiths, 2003, White & Brown, 2013, Thyssen et al., 2014). Over time these limitations have lead to the presently observed distributions of rock pool fishes globally.

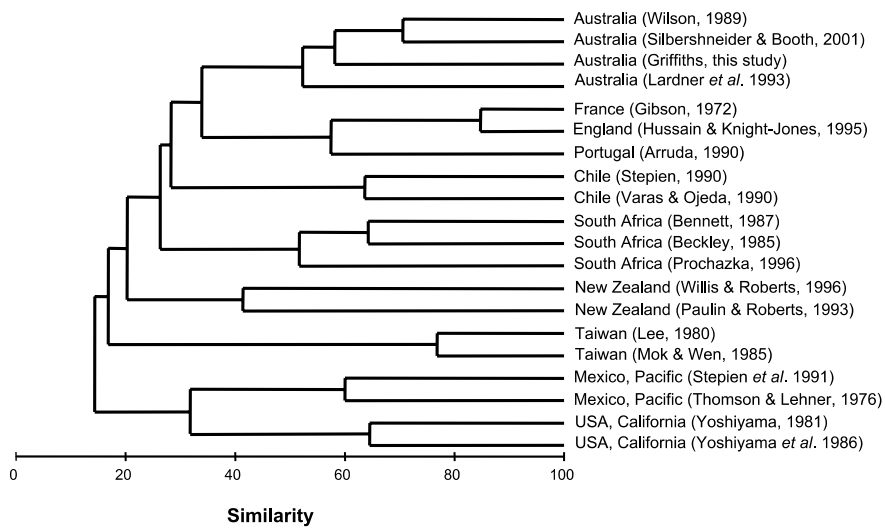


Figure 5: Dendrogram for hierarchical clustering of the communities of fishes utilizing rock pools (using the Bray-Curtis similarity measure), taken from appropriate studies in various countries around the world (from: Griffiths, 2003)

### **Patterns in South African Rock Pools**

Despite the distinct lack of studies investigating rock pool fish assemblages and distributions globally, South Africa has been relatively well studied, at least from a taxonomic perspective. Early studies, conducted in the 1950's, 60's and 70's aimed at being purely descriptive (see: Jackson, 1950; Penrith, 1965, 1970; Penrith & Kensley, 1970a, 1970b; Kensley & Penrith, 1973) where as more recent work has been based upon quantitative sampling methods (see: Marsh et al., 1978, Christensen & Winterbottom, 1981; Bennett & Griffiths, 1984; Beckley, 1985; Bennett, 1987; Burger, 1988, 1991). Only three studies, however, attempted to relate community composition to physical rock pool characteristics such as pool size (Prochazka & Griffiths, 1992) or seasonal patterns (Prochazka, 1996). Few studies (Beckley, 1985; Bennett, 1987) have also investigated the role of rock pool habitats as nursery areas for economically important fish species (mostly secondary residents or transients) although permanent residents were also sampled.

There are several published studies of rock pool fishes from all three major biogeographic zones along the South African coast (The Subtropical East Coast Province, The Warm Temperate South Coast Province and The Cold Temperate West Coast Province) as well as the two transition zones (listed on next page). As a result, and although these studies are relatively out dated, the basal taxonomic knowledge of rock pool fish compositions along the South African coast are relatively well known. Despite this, and given the potential refuge and nursery function of South African rock pools, they are surprisingly poorly included in coastal management frameworks nor do they influence the establishment and design of MPA's or marine zonation generally.

For the purpose of this review, seven studies were used, the oldest being Christensen & Winterbottom (1981) and the most recent Beckley (2000) as all these studies provide suitably comparable species lists for basic along coast and overall patterns to be determined.

Table 1: Listed studies used for determining overall patterns in rock pool fish distributions in South Africa.

Study Site	Biogeographic Province	Method Used	Number of Pools	Length of Study	Year	Reference
Cape St Martin	Cold Temperate West Coast	Ichthyocide (rotenone)	32	January & April	1991	Prochazka & Griffiths(1992)
Groenvlei	Cold Temperate West Coast	Ichthyocide (rotenone)	30	January & April	1991	Prochazka & Griffiths(1992)
Cape Peninsula	Cold Temperate West Coast	Ichthyocide (rotenone)	173	May to May	1992/93	Prochazka (1996)
Cape Peninsula	Cold Temperate West Coast	Ichthyocide (rotenone)	50	July to September	1982	Bennet & Griffiths (1984)
False Bay	Cool Temperate Transition	Ichthyocide (rotenone)	34	July to September	1982	Bennet & Griffiths (1984)
Koppie Alleen	Warm Temperate South Coast	Ichthyocide (rotenone)	61	May to Febuary	1984 to 1986	Bennet (1987)
Port Elizabeth	Warm Temperate Transition	Ichthyocide (rotenone) & Visual Census	22	March to Febuary	1980/81	Beckley (1985)
Port Alfred	Warm Temperate Transition	Ichthyocide (pronoxfish) & Visual Census	2	January to January	1975 to 1977	Christensen & Winterbottom (1981)
Durban	Sub-Tropical East Coast	Ichthyocide (rotenone)	1	July to June	1992/93	Beckley (2000)

Within published studies on rock pool fish assemblages in South Africa a total of 405 individual rock pools have been sampled, playing host to a total of 16484 individual fishes and 27 families. An average of 8 families and 22 species of fish at an average density of 7.67 individuals per square meter of pool surface area (ind.m<sup>-2</sup>) are found at all seven studied sites in South Africa.

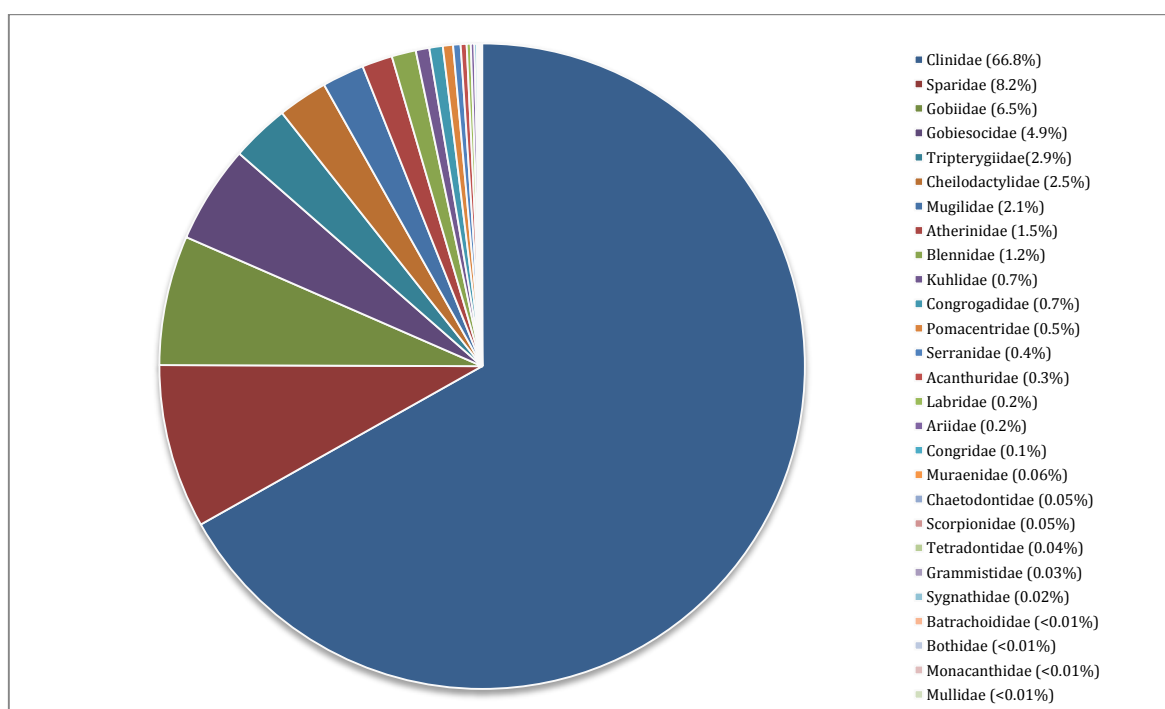


Figure 6: A chart of the percentage composition of fish families to rock pool assemblages in South Africa (from the seven most recent published studies listed previously, number of pools = 405)

At the family level, South African rock pools are distinctly dominated by clinid fishes (klipfishes), which contribute some two-thirds (66.8%) of the species caught to ichthyofaunal communities across all listed study sites along the coast. The second most dominant family include Sparids (Seabreams), which contribute some 8.2% to overall composition, followed by Gobiids (Gobies – 6.5%), Gobiesocids (Clingfishes – 4.9%), Tripterygiids (Triplefins – 2.9%), Cheilodactylids (Finger-fins – 2.5%), Mugilids (Mulletts – 2.1%), Atheriniids (Silversides – 1.5%) and Blenniids (Blennies – 1.2%). The 18 remaining families contribute less than 1% to overall community composition (see: Figure: 6).

### Patterns in South African Rock Pool Fish Assemblages

Before considering patterns at smaller scales (among studies), it is important to note that not all the above listed studies were conducted at equal intensity (Bennett, 1987). The timing of each respective study, the number of pools and size range of pools sampled, as well as the method used to sample fishes (see later), will all have an effect on the outcome of each study. The timing of each study would be influenced by temporal differences in recruitment by both resident and non-resident fish species, which could lead to over or under representation of certain species (Bennett, 1987). As explained previously, however, seasonal changes in community (driven by differential recruitment times) generally have little effect on overall community but rather size composition, with smaller individuals present during times of peak recruitment (Griffiths, 2003). Thus the size compositions were not used for comparisons. The number of pools and size range of pools sampled would be expected to have an effect on the representativeness of each study to the overall area, where more pools across the full range of sizes and intertidal area would be more representative. Studies that investigate a small number of pools, pools of uniform sizes or pools covering only a subset of the intertidal zone would be less representative of the area as a whole.

The methods used also have an effect on the outcome of each study, however, all the listed studies used the same sampling method (the ichthyocide rotenone), as was the practice at the time. The methods used to sample rock pool fishes and their respective efficiencies will be reviewed more extensively later in this study. Despite these possible issues and inconsistencies, for the purpose of this review the studies used were considered of reasonable accuracy and reflected the respective fish communities enough for valid comparisons to be made.

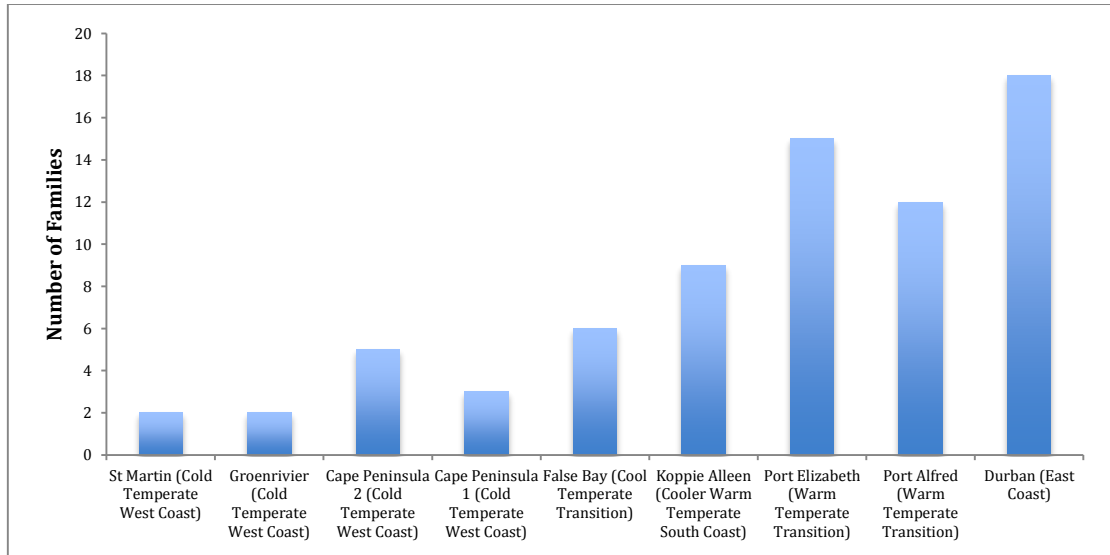


Figure 7: Trends in the diversity of families represented in rock pool fishes along the South African coast

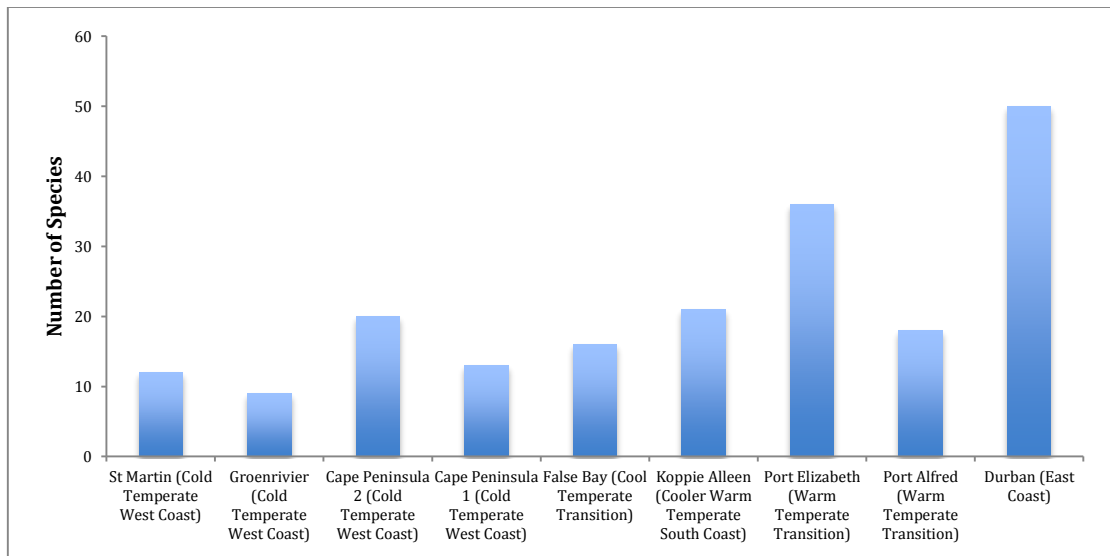


Figure 8: Trends in the diversity of rock pool fishes along the South African coast

Moving from the cold upwelling west coast towards the warm east coast (Figure 4), there is a marked increase in both the number of families and species of fishes within South African rock pools (Figures 7 & 8). Groenvlei, found on the cold west coast has been shown to have the fewest number of species with only 9 species present whereas Durban on the warm sub-tropical east coast has been shown to host some 50 species. At the familiar level, patterns are identical, with two families present on the west coast (lowest) and 18 in the east (highest).

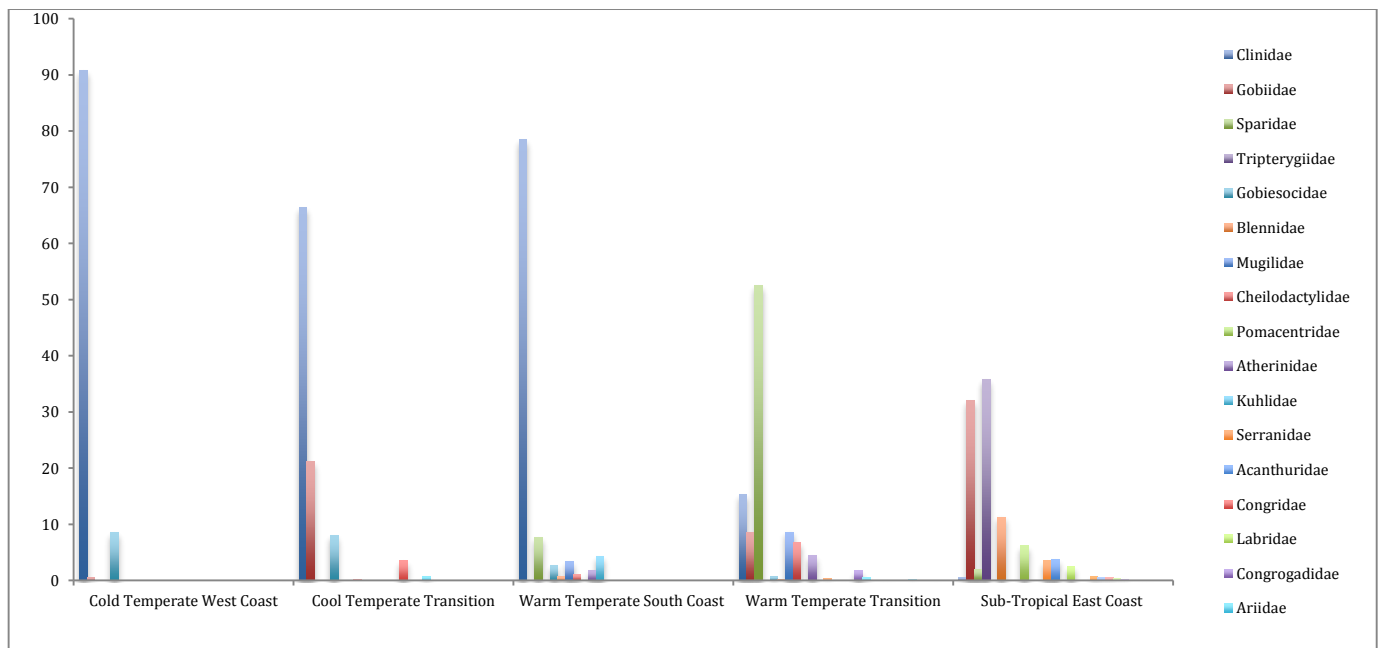


Figure 9: Chart showing the percentage contribution of dominant families in each biogeographic province along the South African coastline

Between each biogeographical province along the South African coast, distinct community changes occur, with clinid and gobiesocid species decreasing in dominance as one moves from west to east. The south coast, whilst still dominated by clinids shows a lower presence of gobiesociids, being replaced by gobiid species. The warm temperate transition zone in the Eastern Cape shows dominance by sparid, clinid, gobiid and mugilid species. The warm east coast province shows few clinids and is rather dominated by tripterygiids, gobiids and blenniids.

The overall pattern (west to east) shows a shift in familial composition from more cryptic dominated to non-cryptic dominated assemblages. The reasons for the shift are unclear (Prochazka & Griffiths, 1992) but are most likely driven by dispersal limitations. Limits to dispersal are highest in the west coast (due to predominantly off shore drift) and lowest in the east due to the warm, pole ward flowing Agulhas Current retaining displaced individuals, larvae and juveniles close to shore. The greater presence of secondary residents and more species rich adjacent sub-littoral habitats in the east may also play a role and would explain the higher diversity of non-cryptic species assemblages.

The unique community shown in the warm temperate transition zone potentially adds evidence to this area as distinct biogeographical region itself. Furthermore, the higher presence of an economically important family, sparidae indicates that rock pools in this area are important refuge areas for these fishes in South Africa. Rock pools in this area may therefore be of conservation importance in the future given the value of these fishes to coastal and inshore fisheries and the unique oceanographic and biological characteristics of this area. This area is both oceanographically as well as biologically distinct from other biogeographical provinces along the coast.

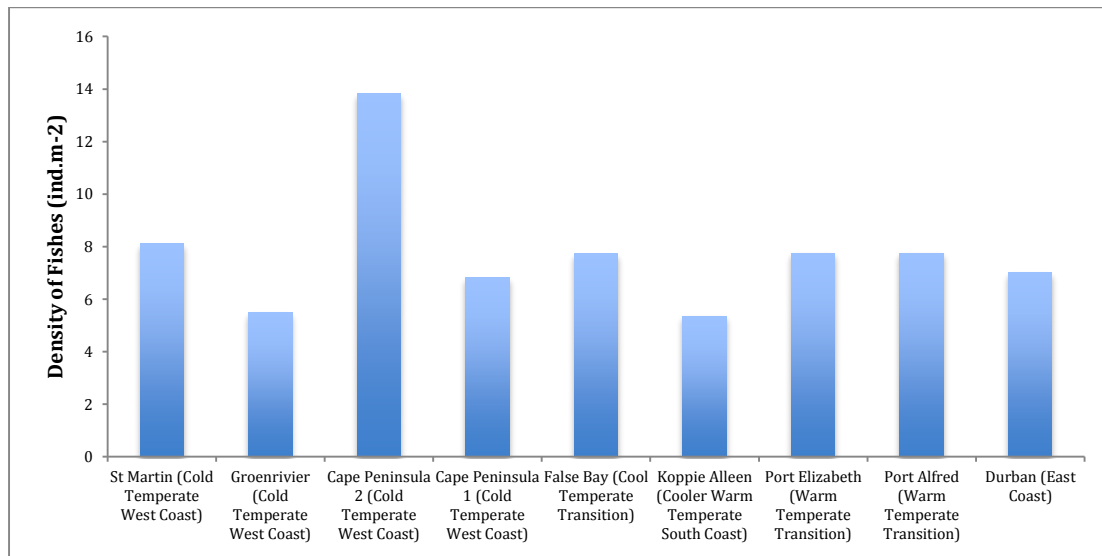


Figure 10: Trends in the density (ind.m<sup>-2</sup>) of rock pool ichthyofauna along the South African coast

Drawing conclusions and comparisons of absolute density of rock pool fishes with locations elsewhere are relatively difficult despite many published studies indicating some form of overall density. Gibson (1982) provides a list of figures of published rock pool fish densities however also discusses the known issues relating to different measures of density used by different authors. Without accurate information describing the characteristics of the study site (number of pools per unit shore area), the characteristics of the pools themselves (size) as well as the communities inhabiting adjacent areas, detailed conclusions are difficult to make. Within South African rock pools though, fish densities tend to follow Gibson (1982) in that “densities rarely exceed a few individuals per square meter of pool surface area” across all sites studied. Densities in all pools sampled in South Africa remain relatively similar despite notable changes in composition (see above) and are roughly 8 ind.m<sup>-2</sup> across all studies.

Table 2: Diversity indices for rock pool fish communities along the South African coast by biogeographic province

Biogeographic Province:	Margalef Species Richness	Shannon-Weiner	Pielou Evenness
Cold Temperate West Coast	1.68	1.89	0.74
Cool Temperate Transition	2.40	3.19	1.01
Cooler Warm Temperate South Coast	2.54	1.49	0.49
Warm Temperate Transition	3.54	2.67	0.75
Sub-Tropical East Coast	6.80	2.25	0.58

Measurements of biological richness and diversity are widely used as they provide more quantitative measures of how many species are present as well as how these species are distributed numerically within a system. It is important, however, to differentiate species richness (number of species present) and evenness (relative species abundances) from species diversity, as well as take into account study duration, seasonality and sampling effort. Systems with many species are considered richer than those with fewer species; however, systems dominated by few species despite high richness are considered less diverse than those with

more evenly distributed species abundances. For the purpose of this review and due to their use in the listed studies, three measures were used. The Margalef Species Richness ( $d$ ) gives a measure of overall richness as a function of the number of species divided by the total number of individuals. The Shannon-Wiener Diversity Index ( $H$ ) gives a measure of overall diversity as it takes into account the evenness of species abundances. The Pielou Evenness ( $e$ ) measure is a measure of overall evenness, calculated as the diversity divided by the number of species present in a system and thus how evenly spread individual species abundances are compared to other species within the system.

Patterns in richness in South African rock pools show that, like the general increase in the number of families and species, richness is highest in the east and lowest in the west (Figure 8). This shows that in the west, rock pools are dominated by high numbers of few species whereas in the east, despite high species numbers few dominate. Comparisons, however, are difficult to make due to the far greater sampling effort in the west. Shannon-Weiner indices of the listed studies show that diversities along the coast are relatively constant, being highest in the cool temperate transition zone, and lowest in the west coast province (Table 2). This is likely due to the contribution of both sub-tropical and temperate species to this assemblage and to few species dominating the systems in the west. Evenness is relatively constant along all studies indicating that the relative spread in abundances of species inhabiting rock pools in South Africa is similar at all sites listed. The overall patterns, however, follow MacArthur (1969) where he shows that in terrestrial systems, dominance decreases with increasing richness as opposed to Birch (1981), who found the opposite trend, likely due to the different types of organisms investigated in each study.

### **Methods Used to Sample Rock Pool Fishes**

Ichthyologists have made a number of methods available to investigate rock pool fishes, each with varying degrees of efficiency. The most common methods used previously include: ichthyocides, anesthetics, bailing or siphoning of pools, hand nets or small seine nets, visual census, hook and line and traps. Each of these has some degree of selectivity and often multiple methods are utilized in tandem. Hand nets have been widely used by recreational intertidal harvesters (including aquarists), however, often under represent small or cryptic species that are better sampled using anesthetics or ichthyocides (Yoshiyama et al., 1986). Traps and angling (hook and line) are often used in subtidal habitats, however, can also be utilized in rock pools. These methods are also selective and limited to certain trophic levels.

Before further investigating the effectiveness of each broad category of sampling method, it is important to describe some measure of effectiveness. Firstly, the main goal of the method used would be to sample every fish in a particular pool irrespective of size or behavioral affinity. That is to say, an ideal sampling method would capture the smallest, most timid and cryptic species as well as the largest, least camouflaged individuals. The capture of a large majority of, if not all, individuals in a pool is crucial for suitable comparisons between different studies as well as for suitable conclusions to be drawn about the site under investigation. The capture of a

large majority of fishes is also important, as any scope for under-representation would draw skepticism to the outcomes of the study. Secondly, due to time constraints of fieldwork, at low tide, as well as the often-distant study locations (often with little or no vehicle access), methods should be efficient and portable. Lastly, the method used should ideally impose little or no threat to neither the safety of both the scientist carrying out the work nor the health of the organisms. The most suitable methods would therefore be able to sample as many pools as possible over a single high tide (quick and easy) as safely and effectively as possible while causing as little damage to the environment as possible.

### Chemical Methods

Chemicals added to rock pools in order to induce anesthesia or kill fishes for later collection by small nets or by hand have been widely used (Griffiths, 2002). The two main types of chemical methods are the use of ichthyocides (Christensen & Winterbottom, 1981) or anesthetics, which temporarily immobilize fishes (Beckley, 2000; Silberschnieder & Booth, 2001; Griffiths, 2002). The ease of use and simplicity of chemical methods have made them some of the most widely used fish collection/ sampling methods for rock pool studies, however, they do have a few drawbacks.

Ichthyocides, namely Rotenone or Pronoxfish have been the most used method for rock pool fish studies (Christensen & Winterbottom, 1981; Yoshiyama et al., 1986). The main negative implication of ichthyocides methods is that fish mortality is high and therefore ethical issues must be justified (Almada & Faria, 2004), although effects on other taxa are minimal. Most countries impose strict regulations on the use of ichthyocides. Other negative effects include potential toxicity to other organisms not under investigation as well as potential harm to researchers (Griffiths, 2000; 2002). Ichthyocides therefore, despite their widespread use in the published literature, are personally considered less desirable over other sampling methods.

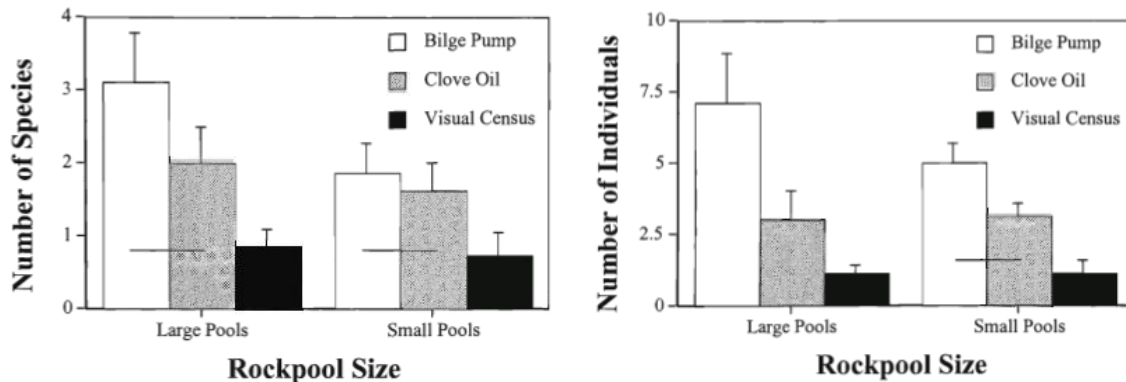
Less destructive sampling methods such as chemical anesthetics have been developed in recent years. The main benefit of anesthetics is reduced fish mortality and reduced harm to other organisms. Anesthetics are applied in much the same way as ichthyocides in that a pool is dosed and after immobilization, fish are captured with small nets or by hand. The benefit is that fishes can then be revived and released back into the wild after observations are recorded. There are a number of anesthetics available to researchers namely: Quinaldine (MS-222), Tricaine Methanesulfonate as well as carbon dioxide although MS-222 is the most widely used in fisheries science. Quinaldine and Tricaine Methanesulfonate have been shown to be effective methods in that they reduce fish mortality, however, these anesthetics are relatively expensive, may pose a health risk to researchers and use in some countries, such as the US, require withdrawal periods of 21 days before affected fishes can be released back into the wild (Anderson et al., 1997). Furthermore, carbon dioxide is relatively slow acting and requires long periods for recovery of anesthetized fishes (Gilderhus & Marking, 1987) and may cause high mortality in certain species due to changes in water pH (Bernier & Randall, 1998).

In recent years, however, alternative anesthetics have gained interest by fisheries scientists. One such chemical is the clove oil, with its active compound eugenol (4-allyl-2-methoxyphenol), derived from the leaves; stems and flowers of clove trees (*Eugenia carophyllata* and *E. aromatic*). Clove oil has a number of useful attributes such as antifungal, antibacterial and antioxidant properties (Karapinar, 1990; Moleyar & Narasimham, 1992; Cort, 1974), as well as use in dentistry as a local anesthetic (Curtis, 1990). Being a natural compound, it has many advantages over other anesthetics posing very little health threats to users, low cost and effectiveness at lower concentrations (Keene et al., 1998). Other benefits include rapid induction and recovery times and effectiveness for both fresh and marine fish species. Furthermore, no withdrawal periods are required for affected fishes, as with the use of MS-222 and costs are far lower than the use of Quinaldine. Considering these benefits, Griffiths (2000) investigated the required concentration needed for use in Australian rock pools and found that 40 mg.l<sup>-1</sup> showed induction and recovery times of <3 and <5 minutes respectively for seven of eight Australian rock pool fish species (see chapter 2 for methods of application of clove oil to rock pools). Cunha & Rosa (2006) also investigated the suitable concentration of clove oil and found that for seven tropical reef fishes, 20 mg.l<sup>-1</sup> was suitable for anesthetic induction and recovery times of <3 and < 5 minutes respectively. This lower concentration was chosen as it imposed less of a threat to fishes in terms of mortality as well as reducing overall stress of sampled specimens.

### Manual Methods

Due to the number of concerns with the use of chemical sampling, many researchers have developed manual means of fish collection in rock pools. These include fish traps (Beja, 1995), visual census (Christensen & Winterbottom, 1981), different net types (Rangley & Kramer, 1995a; 1995b), or draining of pools utilizing battery powered submersible or petrol powered pumps (Griffiths, 2000), siphoning (Davis, 2000a; 2000b) or with bailing with buckets (Hussain & Knight-Jones, 1995). The main benefits of manual methods are that they usually permit rapid census, have little discernable effect on the rock pool biota, however, do tend to under represent secretive or cryptic fish species (Christensen & Winterbottom, 1981; Yoshiyama et al., 1986). The complete emptying of pools is likely the most effective sampling method as it allows for searching within crevices and under rocks (Hussein & Knight-Jones, 1995) as well as imposing little threat to fishes as most are adapted to short periods of aerial exposure (Martin & Bridges, 1999). Emptying of pools, however, does have drawbacks in that large pools take long times to empty (even with the use of bilge pumps) and furthermore, large, heavy batteries needed for powering pumps are not easily transported over rocky shores.

## Comparison of Sampling Methods



Figures 11 & 12: Comparisons of the effectiveness of each sampling method (bilge pumping, clove oil anesthesia and visual census) on the total number of species and number of individuals sampled in large (197-365 liters) and small (8-21 liters) pools in NSW, Australia (from Griffiths, 2000).

Given the different benefits and draw backs of different sampling methods, Griffiths (2000) aimed to compare the effectiveness and efficiency of clove oil against the two most widely used physical methods; visual census and bilge pumping. He found that for small and large pools that bilge pumping was the most effective at capturing both more fish (number of individuals) as well as more species, however, this increase in efficiency was not significantly different from using clove oil in small pools (both number of individuals and species). Bilge pumping was only shown to be significantly better than clove oil at capturing more individuals (not species) in large pools (>197 liters). He showed that clove oil was, for the most part, comparable in efficiency to bilge pumping.

## CHAPTER 2

### **Patterns of Distribution, Abundance and Community Composition of Rock Pool Fishes in Goukamma Nature Reserve, South Africa**

#### **ABSTRACT**

The aim of this study was to determine which, if any, physical and biological rock pool characteristics have any significant influence on the Abundance, Diversity and Community of fishes at Goukamma MPA, South Africa. This site was chosen due to a lack of previous surveys of rock pool fishes at this site and because of a need for an inventory of faunal communities in protected areas in South Africa. The shoreline within the reserve is dominated by sandy shores and interspersed with mixed rock-based habitats. Aelonite platforms form mixed shores and are found along areas west of the Goukamma estuary. Hard, predominantly older Table Mountain Sandstone layers are found along the eastern shore near Buffalo Bay. Rock pools are found at both shore types. Aelonite platforms were formed geologically recently from sand dunes formed during the interglacial periods of the Pleistocene and as a result are relatively flat and easily eroded into circular pools by loose rocks. The hard table mountain sandstone pools formed in cracks and faults caused by geological tilting action, and tend to long and thin rather than circular. Fifty-five rock pools were sampled, to investigate the influence of spatial (*Location and Headland*), temporal (*Season*), abiotic (*Area, Height, Depth, Rugosity*) and biological (*Rock, Algae,*) characteristics of rock pools on the distribution, abundance, diversity and community composition of rock pool fishes. A total of 747 fishes, representing seven families and 16 species were collected, using a non-lethal anesthetic, clove oil. *Clinus cottoides*, *Parablennius cornutus* and *Caffrogobius caffer* were the most dominant species, together making up almost 85% of the fish community. Total fish *Abundance* was not found to significantly change with any of the variables. The *Shannon-Wiener Species Diversity Index* for the whole of Goukamma was 1.64, however, it differed significantly among *Locations*, was greatest in pools of larger *Area*, lower *Heights* and higher cover of *Rock*. Community was found to significantly change with *Location* and was significantly influenced by *Area, Rugosity, Height* and *Depth*. Rock pool fish communities in South Africa show clear biogeographical patterns. These patterns show five distinct bioregions along the South African coastline in that familial distributions tend to be broken by the same oceanographic barriers seen in the distributions of many other marine taxa. The results suggest that rock pool fishes tend to exhibit distinct preferences to pools of certain typology and will seldom move over even small distances in search of new pools. Overall the study followed past findings from studies of similar type, both within South African and elsewhere.

## INTRODUCTION

Despite extensive literature describing the ecology of intertidal zones (Underwood, 2000), relative to other marine habitats, rock pools and their ichthyofaunal communities have received surprisingly little attention (Griffiths, 2003). The reasons for a lack of previous work on rock pool fishes globally are due mostly to the morphologies of the habitat and the fish and fish behaviors, which make them relatively difficult to sample efficiently and effectively using conventional methods (Griffiths, 2000).

Most rock pool fish studies have also only been conducted in the northern hemisphere. Despite the high degree of endemism (Prochazka & Griffiths, 1992) and possible nursery and refuge function of rock pools (Bennett, 1987), little is known about South African rock pools fishes relative to other parts of the world and relative to other groups of fishes in South Africa.

General taxonomic information on the composition of rock pool assemblages from all five major coastal biogeographical regions in South Africa is available (reviewed in Chapter 1). Factors such as pool size, height above the low water mark, habitat complexity and rock and algal cover have all been shown to have some influence on the fish communities inhabiting rock pools. These factors and their influence on rock pool communities are, however, poorly understood, even at the global scale (Gibson, 1982). In contrast to other habitats, seasonal changes in rock pool assemblages are generally weak, and generally result in changes in size composition rather than composition. Rock pools are considered relatively stable in the long term compared to other habitats (Thomson & Lehner, 1976, Prochazka, 1996). None the less there remains paucity in understanding the roles and functions of these ecosystems and the factors that control their community compositions given the lack of work of this type in South Africa and globally.

### Aims

This study aims to describe the rock pool fish community in an area of conservation importance to South Africa, the Goukamma Marine Protected Area. The findings will be compared to other studies of rock pool fishes undertaken elsewhere in South Africa. Furthermore, this study aims to investigate which, if any, physical or biological rock pool characteristics have any influence on community structure and composition.

## METHODS

### Study Site

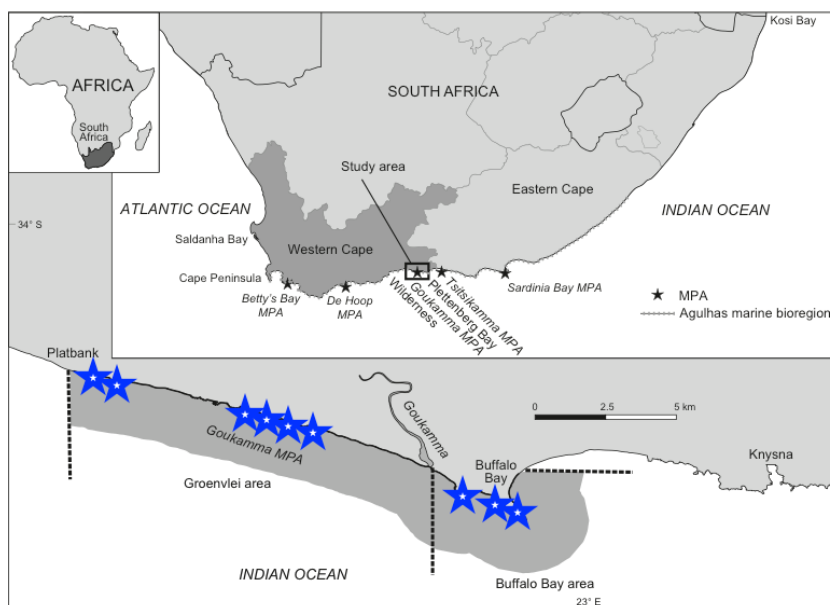


Figure 1: Map showing the location of Goukamma Nature Reserve on the south coast of South Africa and the extent of the MPA (blue stars indicate *headlands*)(from Attwood et al., 2016)

Goukamma Marine Protected Area and Nature Reserve lay approximately 40 km east of George and 25 km west of Knysna. It was proclaimed as a nature reserve in 1960 and subsequently a marine protected area (MPA) in 1990 (Clark & Lombard, 2007). This site was chosen due to a lack of previous work of this type and the distance from any similar survey and because of a need for an inventory of faunal communities in protected areas.

The MPA consists of 18 km of coastline, from Buffalo Bay in the east towards Sedgefield, and 1 nautical mile (1.85 km) out to sea. In the MPA no offshore (boat-based) fishing is permitted, nor is spear fishing, the collection of bait from the rocky shores or night fishing. Fishing with conventional hook-and-line is permitted from shore, subject to countrywide regulations on catch and size limits. These anglers do not target rock pool fishes (Attwood et al. 2016), but the disturbance they create means that the intertidal zone is not entirely protected.

### Intertidal Habitats

The dune system that make up the majority of the reserve was formed during the interglacial periods of the Pleistocene (Illenberger, 1996) and have undergone several phases of formation (dune building) and coastal erosion over the past million or so years. The shoreline within the reserve is dominated by sandy shores and interspersed with mixed rock-based habitats. Sand movement is highly dynamic owing to strong currents and turbulent wave action that cause the coastline to change constantly. Subtidal reefs of aelonite sandstone are found mainly in the eastern portions of the MPA and were formed by coalesced dune sands subsequently eroded by

recent sea level rise. Four main habitat types represent intertidal shores at Goukamma, namely; rocky shores, sandy shores, mixed shores and river mouths (Clark & Lombard 2007).

Two main types of rocky intertidal substrates exist within the reserve. Aelonite platforms form mixed shores (interspersed with sand) and are found along areas west of the Goukamma estuary (see Figure 1: Groenvlei). Hard, predominantly rocky sandstone out crops are found along the eastern shore near Buffalo Bay. Rock pools are found at both shore types, however; the aelonite platform is relatively flat, whereas the rock at Buffalo Bay has a greater height range (see Figure 2).

At Buffels Bay, the hard sandstone does not erode easily and pools were formed in cracks and faults caused by geological action tilting the rock surface and as a result the pools tend to be long and thin. At Groenvlei, the rock substrate is far softer and rock pools form by scouring of loose rocks creating mainly round pools with steep sides. The biota covering the rocks were also different between the two areas, with Buffels Bay being dominated by grazers and Groenvlei being dominated by filter feeders. The rock was therefore relatively bare (few algal or encrusting organisms) at Buffels Bay when compared to Groenvlei, which was predominantly covered by mussels, alga and barnacles (see Figure 3).

### Physical Rock Pool Descriptions

Rock pools at three *Locations*, namely Buffels Bay, Oysterbeds and Platbank (the latter two falling within the Groenvlei section) were described and compared in terms of Benthic Type, *Height*, *Length*, *Width*, *Depth*, *Area*, *Volume* and *Rugosity*. Pools were not randomly selected and therefore differences were not statistically tested among locations.



Figure 2: Photographs of the two rocky intertidal types at each area: Buffalo Bay (sandstone) on the left and Groenvlei (aelonite rock) on the right.



Figure 3: Typical rock pool types seen at each sample area (left – Groenvlei, right – Buffels Bay)

### Climate & Prevailing Environmental Conditions

Lying between South Africa’s winter and summer rainfall areas, yearly rainfall at Goukamma is bimodal, with no clear wet or dry season (Mucina & Rutherford, 2006). Annual rainfall is approximately 757 mm p.a. and is highest in spring and autumn and lowest in summer. Mean air temperatures are 25 °C in summer and 16 °C in winter with prevailing southeasterly and westerly winds respectively with an average of 5-6 knots all year (Windfinder.com).

Average sea surface temperatures range between 20 and 24 °C in summer and 16 to 18 °C in winter. Swells at Goukamma prevail from a southwesterly direction. Swells in summer range between 1 and 3 m in height where as in winter swells range between 2 and 5 m (Surf-forecast.com).

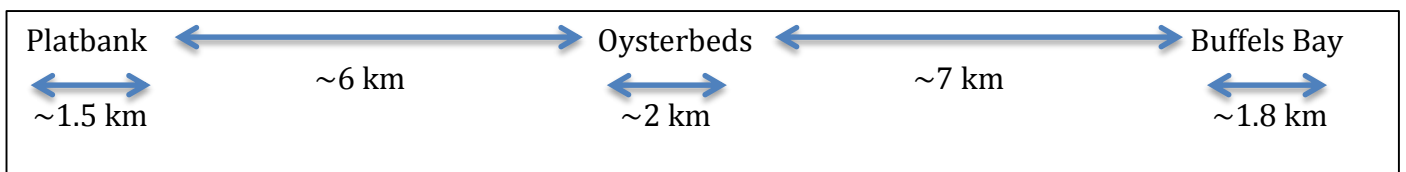


Figure 4: Distances between each of the three sampled locations as well as the maximum distance between *Headlands* within each *Location*

## Sampling Methods

Pools were chosen from three rocky areas called *Locations*. Platbank, on the western part of the reserve; Oysterbeds, west of the Goukamma estuary and Buffels Bay, east of the estuary (Figure 4). On each sampling day a section (*Headland*) of approximately 100 m of shoreline length was chosen for a survey (figure 1). Each section was called a *Headland* and represented rocky outcrops containing rock pools, separate from each other by open sand shores. Each *Headland* was only sampled once overall. Sampling periods were chosen to coincide with spring tides to allow sampling the entire intertidal range.

As it was not possible to sample all the pools in a 100 m stretch in one tidal cycle, a subset of pools were chosen to be representative of the full range of heights above LWM and rock pool sizes (area & volume). Furthermore, only “isolated” pools were chosen, i.e. rock pools that had no visible exchange of water with other pools at low tide and were surrounded on all side by rock.

Peak spring low tides at Goukamma occurred during the morning between 9h00 and 9h15. Sampling began 90 minutes before low tide, and ended 90 minutes after low tide. Sampling took place over three sample trips between August 2016 and February 2017.

## Physical Characteristics (Continuous Variables)

Abiotic and algal assessments of each pool were conducted before fish were sampled. The *Height* of the water surface above LWM of the pool was measured with surveying poles and using the line-of-sight to the oceanic horizon as a horizontal reference. Rock pool dimensions were measured with a tape measure as follows: *Length* (l), the maximum distance along the long axis of the pool; *Width* (w), the average of several (typically 5) equally spaced measures across the long axis; radius (r), in the case of circular pools common at Groenvlei; and *Depth* (d), the average of at least 5 depth measures taken randomly. These measurements were then used to estimate the surface area and volume of the pool by using a formula for shapes most similar to the shape of the pool (e.g. cylindrical= $\pi r^2 d$  or cuboid= $lwd$ ).

## Biological Characteristics (Categorical Variables)

Benthic type in rock pools, sampled at each *Location*, was estimated as the percentage of ground cover of *Rock*, *Algae* and *Sand*. The variable *Rock* refers to the percentage of the pool floor which was either bare rock or rock covered with only crustose or coralline algae. The variable *Algae* refers to the percentage of the pool floor, which was covered by foliose algae. The variable *Sand* refers to the percentage of the pool floor, which was covered by unconsolidated sediment. The combined percentage covered by each substrate type summed to 100%.

*Rugosity* (structural complexity) was determined on a scale of 1-3 with 1 being a very low overall complexity (no overhangs, crevices or ledges) and 3, being highly complex with more than half of the perimeter having overhangs, which could shield fish from sunlight and aerial detection.

To display the similarity among sampled pools at each *Location*, a nMDS plot was constructed on normalized euclidean distances among the following continuous variables; *Height, Length, Width, Depth, Rock, Sand and Algae*.

### Fish Collection

Clove oil was chosen as an anesthetic to aid in the capture of fish. Once the volume of a pool was calculated, a volume of clove oil (dissolved in 70 % ethanol) was added to ensure the optimum concentration for induction of anesthesia. The chosen optimum concentration was  $\sim 30 \text{ mg.l}^{-1}$ , the median recommendation by Griffiths (2000) and Cunha & Rosa (2006). Once anesthetized, the fish were captured with a small hand-held net and transferred to a bucket with fresh seawater to begin recovery. Rock pools were searched repeatedly by removing or overturning loose rocks and removing or shaking foliose algae until it was clear that additional effort would yield no further fish. Pools were also emptied using small buckets and water was also stirred vigorously to dislodge any fish trapped in crevices after anesthesia was induced.

All fish were identified to the lowest taxonomic level possible in the field using: Coastal Fishes of Southern Africa (Heemstra & Heemstra, 2004), Smith's Sea Fishes of South Africa (Smith et al., 2003), and Fishes of the Tsitsikamma Coastal National Park (Smith & Smith, 1966). Once all fish had been identified, they were released into an adjacent, clean pool not earmarked for sampling and left to recover fully. If a fish could not be identified with certainty, it was killed by an overdose of clove oil and preserved in 10% formalin or alcohol for later identification in the lab.

### Statistical Analysis

All statistical data analyses were conducted in R-studio using the 'vegan' package found in the CRAN repository. For all analysis and hypothesis testing, the significance level, alpha ( $\alpha$ ), was set at 0.05.

### Model Design

The influences of the independent variables on the rock pool fish communities were analyzed using PERMANOVA models (MacArdle & Anderson, 2001), analogous to distance based redundancy analysis (db-RDA) using the "Adonis2" routine (vegan package) and visualized, where useful, using non-metric multidimensional scaling (nMDS). PERMANOVA models were used as they allow for whole community analysis (simultaneous responses of many species to several factors) and do not assume multivariate normality (p-values are calculated by

permutation). The community abundance data were square root transformed and a similarity matrix was constructed using the Bray-Curtis similarity coefficient (Clarke & Green, 1988) for running the models.

### Comparisons within Goukamma

The variables used in statistical analysis were: *Season, Location, Headland, Rugosity, Rock, Algae, Height, Depth and Area*. *Sand* was omitted due to numerical dependence on *Algae* and *Rock*.

Due to the small size of the dataset relative to the large number of explanatory variables it was not possible to include all the variables in one model. Two separate, focused PERMANOVA models were developed: A Spatial Model and a Community Model.

### Spatial Model

A spatial model was constructed using *Location* and *Headland* as explanatory variables to compare communities among *Locations* and among *Headlands* within *Location*. *Headland* was nested in *Location*. A nMDS plot was constructed of using the methods explained above to visualize the community similarities within each *Location* and by *Headland*.

### Community Model

A PERMANOVA model was constructed using all the abiotic variables (*Rugosity, Rock, Algae, Height, Depth, Area* and *Season*, to test their influences on fish communities. This was done using a marginal PERMANOVA model (type III), which tested the partial contributions of each abiotic variable in a model with all other variables included (MacArdle & Anderson, 2001). This PERMANOVA model was nested in *Location* by constraining the permutations in the model by *Location* (Warton et al., 2012).

### Linear Models

Although PERMANOVA models are useful models for ecological studies, the results do not indicate how the community responds (i.e. changes in relative abundances of each species or diversity with changes in different variables). Furthermore, they provide no “direction” of any potential change given a change in community.

To determine how the community responded, a linear regression model ('lm' routine) was constructed (Chambers, 1992) for *Location* and for all the abiotic variables, *Location* and *Season*. The response variables tested against the abiotic variables were the *Abundance* (total count of fish) and *Shannon-Wiener Diversity Index*, for in each pool. Coefficients of each abiotic variable in the model provided a direction of changes in the response variables with each.

## Comparisons of Communities at the Bioregional Scale

The rock pool assemblage at Goukamma was compared with other sites in South Africa at the family level using a non-parametric nMDS plot. This was done to determine the influence of *Bioregion* on community composition at the level of family. Data were obtained from all published studies on South African rock pools (listed in Chapter 1) and where possible absolute numbers of each family were used. Where absolute numbers were not given, total numbers of fish caught were scaled according to percentage contributions of each family to total number of fishes caught in the study.

## RESULTS

### Characteristics of Pools Sampled at Goukamma

Pools that were sampled at Buffels Bay were on average located at greater *Heights* on the shore than those at the other two *Locations*, and also showed the greatest variation in pool *Height* (Table 1, Figure 5). Pools at Buffels Bay had on average greater *Volume* than the other two *Locations*, however, *Volume* was most variable at Oysterbeds. Pools at Platbank had the greatest average *Depth*, but *Depth* was most variable at Buffels Bay.

The sampled pools at Buffels Bay had the highest *Rock* cover, whereas those at Oysterbeds the highest cover of *Algae* (Table 1, Figure 5).

Table 1: Physical characteristics of rock pools sampled at each *Location* at Goukamma

Variable	Buffels Bay (n=20)		Oysterbeds (n=16)		Platbank (n= 10)	
	Mean/ Mode	sd	Mean/ Mode	sd	Mean/ Mode	sd
<i>Rock Cover (%)</i>	54.43	31.5	24.71	13.4	25.5	13.0
<i>Algal Cover (%)</i>	11.95	15.0	37.06	19.3	21	15.2
<i>Sand Cover (%)</i>	33.57	27.9	38.24	22.2	53.5	14.9
<i>Height (m)</i>	0.95	0.73	0.84	0.22	0.57	0.14
<i>Length (m)</i>	2.98	1.79	2.11	1.79	1.81	1.15
<i>Width (m)</i>	1.15	0.80	1.06	0.92	0.78	0.16
<i>Depth (m)</i>	0.22	0.13	0.23	0.09	0.26	0.09
<i>Area (m<sup>2</sup>)</i>	2.23	3.42	1.64	5.42	1.8	1.20
<i>Volume (m<sup>3</sup>)</i>	0.44	0.84	0.26	1.34	0.26	0.23
<i>Rugosity (1 - 3)</i>	2	-	1	-	3	-

Taken together these variables portray the pools sampled at Buffels Bay pools as being more variable than those sampled at the other two sites (Figure 5).

*Rugosity* was highest at Platbank with most pools being given scores of either 2 or 3. *Rugosity* was lowest at Oysterbeds with most pools scoring 1 or 2. Pools at Buffels Bay had a modal *rugosity* of 2 (Table 1).

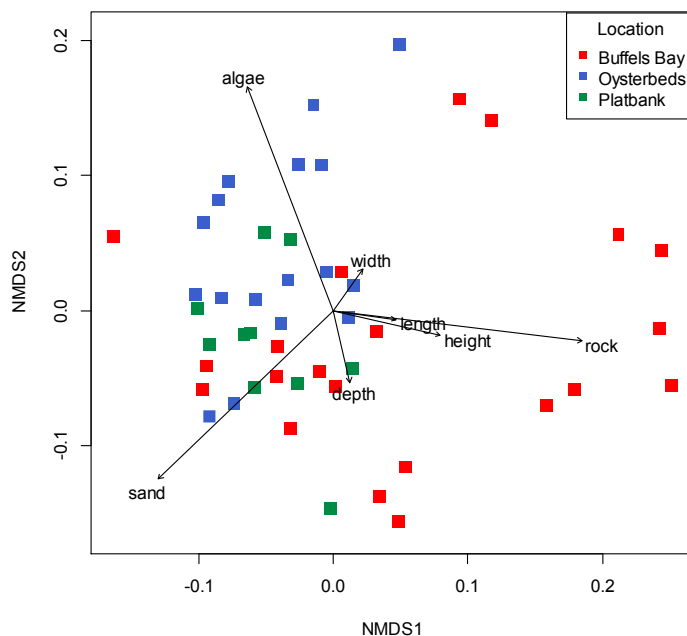


Figure 5: nMDS plot showing physical characteristics of rock pools sampled at three *Locations* in Goukamma

## Diversity

Table 2: The number of species, families and primary and secondary residents caught overall at each *Location* in Goukamma and the Shannon-Wiener diversity index

	Buffels Bay	Oysterbeds	Platbank
<i>Number of Species</i>	14	7	4
<i>Number of Families</i>	7	4	3
<i>Primary Residents</i>	7	6	3
<i>Secondary Residents</i>	7	1	1
<i>Shannon-Wiener Diversity Index</i>	1.89	0.71	0.56

Fifty-five rock pools were sampled at Goukamma of which 48 yielded fish. A total of 747 Fishes representing 16 species and 7 families (Table 2) were caught. The rock pool fish community at Goukamma had an overall *Shannon-Wiener Species Diversity Index* of 1.64.

Pools at Buffels Bay showed the highest diversity of species and families (Table 2). Of the 16 species found during the study, 14 were found at Buffels Bay and all seven families were also found in pools at Buffels Bay. Oysterbeds and Platbank pools had lower familial diversity, with only four and three of the seven families being found at these *Locations* respectively. Species

numbers were also lowest at these *Locations* with only seven and four of the 16 species being found there respectively. Buffels Bay had 7 primary resident species and 7 secondary resident species whereas Oysterbeds and Platbank had only one *Secondary Resident Species* and six and three *Primary Resident Species*, respectively. These differences in diversity were reflected in the *Shannon-Wiener Diversity Index* calculated for each *Location* (Table 2).

Table 3: Results of the linear model of *Shannon-Wiener Diversity Index* against all variables measured at Goukamma

<b>Variable</b>	<b><i>Shannon-Wiener Diversity Index</i></b>
<i>Location</i>	F <sub>(2,32)</sub> = 6.30, p= 0.005**
<i>Area</i>	F <sub>(1,35)</sub> = 5.66, p= 0.023*
<i>Rugosity</i>	F <sub>(2,35)</sub> = 1.28, p= 0.292
<i>Height</i>	F <sub>(1,35)</sub> = 9.95, p= 0.004**
<i>Depth</i>	F <sub>(1,35)</sub> = 0.08, p= 0.780
<i>Rock</i>	F <sub>(1,35)</sub> = 6.83, p= 0.014*
<i>Algae</i>	F <sub>(1,35)</sub> = 0.13, p= 0.718
<i>Season</i>	F <sub>(2,35)</sub> =1.34, p= 0.278

A linear model showed that the *Shannon-Wiener Diversity Index* calculated for pools at each *Location* were significantly different (p=0.005), with lower Indices being calculated for pools at both Platbank and Oysterbeds (coef = - 0.120 & - 0.393 respectively) when compared to Buffels Bay. The results showed that *Shannon-Wiener Diversity Index* significantly (p=0.023) and positively correlated (coef = 0.016) with *Area* and *Rock* (p= 0.014, coef = 0.009), where as negatively correlated (coef = - 0.476) with *Height* (coef = - 1.02, p=0.029). *Season* had no effect on *Diversity*.

### **Species Composition**

The dominant families were Clinidae, Blenniidae, Gobiidae and Sparidae, making up 38%, 34%, 14% and 8% of the total number of fishes caught at Goukamma respectively (Table 4). The most abundant species were *Clinus cottoides*, *Parablennius cornutus* and *Caffrogobius caffer*, making up 36%, 34% and 14% of the total number of fish caught, respectively. Sparid larvae, Mugilid species, *Sparodon durbanesis* and *Chirodactylus brachydactylus* made up 4.4%, 3.5%, 2.3% and 2.1% each. All other species contributed less than 1% to the total number caught.

*Primary Resident Species* made up some 86.1% of the total number of fishes caught at an average density of 4.39 fish.m<sup>-2</sup> whereas *Secondary Resident Species* made up the remaining 13.9% of fishes caught at an average density of 0.11 fish.m<sup>-2</sup>. No transient species were caught in any pools sampled at Goukamma, however, these were seen in small numbers (<5 fish.pool<sup>-1</sup>) in some pools that were too large to sample.

*Clinus cottoides* was found in 41 pools, yielding a frequency of occurrence of 85.1%. Frequency of occurrence of *Parablennius cornutus* and *Caffrogobius caffer* were 54.2% and 37.5%. *Sparodon durbanensis* and *Chirodactylus brachydactylus* were both found in 5 (10.4%) of pools. All other species were found in 3 or less pools (Table 4).

Table 4: The number, percentage, frequency of occurrence and classification as primary or secondary resident of rock pool fish species at Goukamma

Species	Number Caught	% of Numbers	Frequency of occurrence	Residential Status
<i>Caffrogobius caffer</i>	106	14.19	18	Resident
<i>Chirodactylus brachydactylus</i>	16	2.14	5	Secondary
<i>Chrisochismus dentex</i>	6	0.80	3	Resident
<i>Cirriharbus capensis</i>	5	0.67	3	Resident
<i>Clinus agilis</i>	1	0.13	1	Resident
<i>Clinus cottoides</i>	266	35.61	41	Resident
<i>Clinus superciliosus</i>	2	0.27	1	Secondary
<i>Clinus venustris</i>	2	0.27	2	Resident
<i>Muraenoclinus dorsalis</i>	3	0.40	3	Secondary
<i>Pavoclinus laurentii</i>	3	0.40	2	Resident
Sparid larvae	33	4.42	3	Secondary
<i>Sparodon durbanensis</i>	17	2.28	5	Secondary
<i>Diplodus capensis</i>	7	0.94	3	Secondary
<i>Mugilidae spp.</i>	26	3.48	2	Secondary
<i>Parablennius cornutus</i>	253	33.87	26	Resident
<i>Parablennius pilicornus</i>	1	0.13	1	Resident

Table 5: The number and percentage contribution of each species to the total number of fish caught at each Location in Goukamma

Species	Buffels Bay (n=20)		Oysterbeds (n=16)		Platbank (n=10)	
	Number	Percentage	Number	Percentage	Number	Percentage
<i>Caffrogobius caffer</i>	104	30.95	2	1.18	0	0.00
<i>Chirodactylus brachydactylus</i>	10	2.98	6	3.53	0	0.00
<i>Chrisochismus dentex</i>	6	1.79	0	0.00	0	0.00
<i>Cirribharbus capensis</i>	5	1.49	0	0.00	0	0.00
<i>Clinus agilis</i>	0	0.00	0	0.00	1	0.41
<i>Clinus cottoides</i>	103	30.65	131	77.06	32	13.22
<i>Clinus superciliosus</i>	2	0.60	0	0.00	0	0.00
<i>Clinus venustris</i>	1	0.30	1	0.59	0	0.00
<i>Muraenoclinus dorsalis</i>	2	0.60	1	0.59	0	0.00
<i>Pavoclinus laurentii</i>	3	0.89	0	0.00	0	0.00
<i>Sparid larvae</i>	33	9.82	0	0.00	0	0.00
<i>Sparodon durbanensis</i>	17	5.06	0	0.00	0	0.00
<i>Diplodus capensis</i>	6	1.79	0	0.00	1	0.41
<i>Mugilidae spp.</i>	26	7.74	0	0.00	0	0.00
<i>Parablennius cornutus</i>	18	5.36	28	16.47	208	85.95
<i>Parablennius pilicornus</i>	0	0.00	1	0.59	0	0.00
Totals	336		170		242	

Buffels Bay pools were numerically dominated by *Caffrogobius caffer* and *Clinus cottoides* (Table 5), each making up roughly 31% of the total number of fish sampled whereas pools at Oysterbeds and Platbank were dominated by *Clinus cottoides* and *Parablennius cornutus*, however, in opposite fashions. Oysterbeds showed dominance by *Clinus cottoides* (77.1% vs. 16.5%) and Platbank showed dominance by *Parablennius cornutus* (86.0% vs. 13.2%).

### Factors influencing Abundance of Fishes

Table 6: Results of the linear mixed effects model of *Abundance* against variables significantly affecting fish community at Goukamma

Variable	Abundance
<i>Location</i>	$F_{(2,32)} = 2.37, p = 0.110$
<i>Area</i>	$F_{(1,32)} = 0.49, p = 0.488$
<i>Rugosity</i>	$F_{(2,32)} = 2.31, p = 0.115$
<i>Height</i>	$F_{(1,32)} = 0.08, p = 0.780$
<i>Depth</i>	$F_{(1,32)} = 3.59, p = 0.067^\circ$
<i>Algae</i>	$F_{(1,32)} = 2.07, p = 0.160$
<i>Rock</i>	$F_{(1,32)} = 1.69, p = 0.202$
<i>Season</i>	$F_{(2,32)} = 0.01, p = 0.896$

The results of the linear models (Table 6) showed that *Abundance* was nearly significantly ( $p=0.07$ ) positively correlated with *Depth* (coef = 53.7). None of the abiotic variables, nor *Season* had any affect on *Abundance*.

### Comparisons within Goukamma by Location and Headland (Spatial Model)

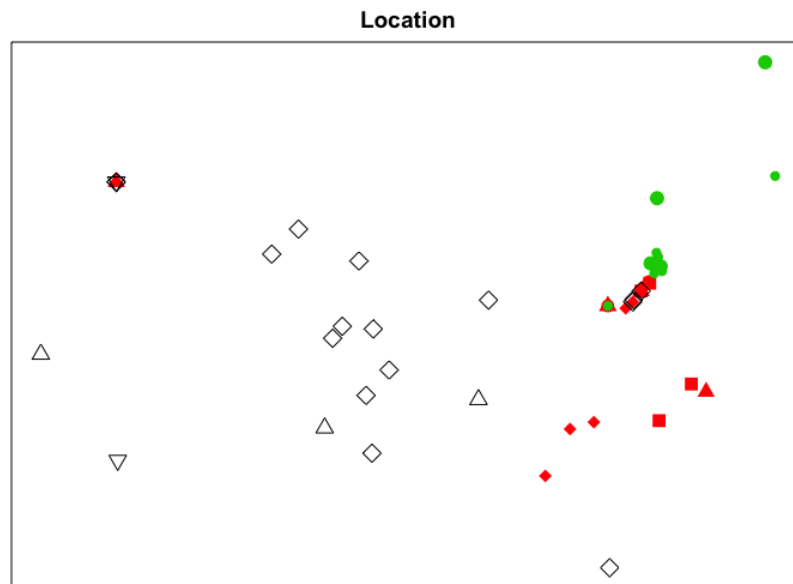


Figure 6: nMDS plots showing rock pool community similarity at Goukamma. Colors represent each *Location* (Buffels Bay – black, Oysterbeds – red and Platbank – green) and the shapes of the points represent different *Headlands*

Comparisons of the communities at the species level among sampled *Locations* at Goukamma showed clear differences (Figure 6). Variation was highest among the Buffels Bay pools

A PERMANOVA model using *Location* as the only explanatory variable showed that *Location* significantly ( $p=0.001$ ) accounted for 21.8% ( $R^2= 0.218$ ,  $F_{(2,45)}=6.27$ ) of the variation in rock pool communities by species. When *Headland* was added as a nested variable within *Location*, the total variation explained increased to 32.3% ( $R^2= 0.323$ ,  $F_{(8,39)}=2.32$ ), however, *Headland* was not a significant factor ( $p=0.392$ ).

The results of the marginal PERMANOVA model (nested by *Location*) for each of the abiotic variables individually showed that *Area*, *Rugosity*, *Height* and *Depth* all had a significant ( $p<0.05$ ) influence on rock pool fish community whereas *Season*, *Algae* and *Rock* did not (Table 7). Each of the significant variables accounted for between 4.1 and 9.2% of the variation in community composition. The overall results show that individually, *Area*, *Rugosity*, *Height* and *Depth* significantly influence rock pool fish community at Goukamma.

## Comparisons within Goukamma by Abiotic Pool Characteristics (Community Model)

Table 7: Results of the Typological PERMANOVA Model of Goukamma Fish Communities

Variable	Marginal PERMANOVA
Area	$R^2 = 0.059$ , $F_{(1,37)} = 3.37$ , $p = 0.0019^{**}$
Rugosity	$R^2 = 0.065$ , $F_{(2,37)} = 1.87$ , $p = 0.028^*$
Height	$R^2 = 0.056$ , $F_{(1,37)} = 3.20$ , $p = 0.0028^{**}$
Depth	$R^2 = 0.041$ , $F_{(3,37)} = 2.33$ , $p = 0.049^*$
Rock	$R^2 = 0.023$ , $F_{(1,37)} = 1.29$ , $p = 0.420$
Algae	$R^2 = 0.018$ , $F_{(1,37)} = 1.04$ , $p = 0.471$
Season	$R^2 = 0.052$ , $F_{(2,37)} = 1.56$ , $p = 0.291$

## Bioregional Patterns in Rock Pool Communities in South Africa

Comparisons of the communities (at the family level) across published studies undertaken in South Africa show clear patterns in rock pool biogeography. The nMDS plots (Figure 7) by *Bioregion* showed distinct grouping of rock pool communities, at least at the family level. Within *Bioregion* and species level analysis was not possible as this data was not available.

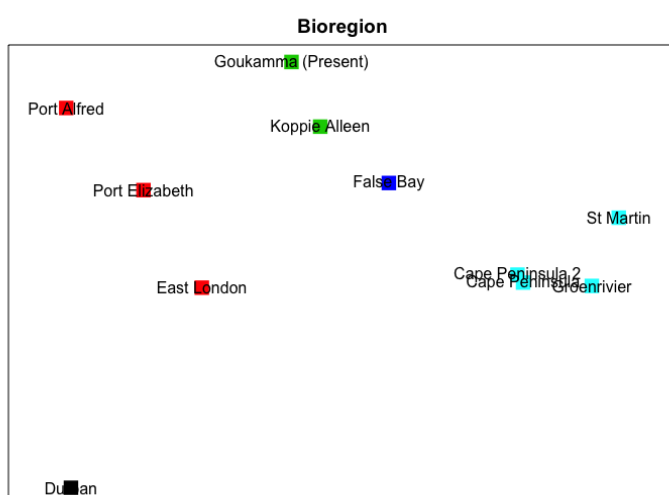


Figure 7: nMDS plot showing similarities in familial composition of rock pool fishes in South Africa. Colors on the represent bioregions (East Coast – black, Warm Transition – cyan, South Coast – red, Cool Transition – green, West Coast – blue)

## **DISCUSSION**

### **Characteristics of Pools Sampled at Goukamma**

The different rock types determined the types of pools available at each location. Pools at Buffels Bay (sandstone) were more variable in physical characteristics than those at Platbank and Oysterbeds (aelonite rock). The differences in these characteristics were reflected in the diversity of fish communities at each location. Platbank and Oysterbeds pools were relatively similar in typology and harbored similar communities in both diversity and species composition. Pool characteristics, irrespective of location, likely influence rock pool fish communities, a conclusion drawn in a number of other studies in South Africa (Bennett & Griffiths, 1984; Huggett & Griffiths, 1986; Prochazka & Griffiths, 1992) and elsewhere (Griffiths, 2003; Griffiths et al., 2006; Godinho & Lotufo, 2010; White et al., 2015). Pool typology is of primary importance in determining community composition.

### **Diversity**

Differences in physical characteristics of rock pools have been shown to play a role in determining rock pool fish diversity (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992; White et al., 2015). Most rock pool fish species have been shown to exhibit distinct preference for certain pool types and characteristics (Marsh et al., 1978; Yoshiyama, 1981; Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992). Where there are more pool types available, fish communities reflect this in being more diverse, as was the case at Buffels Bay.

The effects of area, height and rock found at Goukamma is consistent with conclusions drawn from two past studies conducted in South Africa. Both studies found that cover of rock, height and area all had a significant influence on the number of species in pools sampled in South Africa, on the Cape Peninsula (Bennett & Griffiths, 1984) and West Coast (Prochazka & Griffiths, 1992). Larger pool area influences diversity by increasing the absolute space available for niche partitioning of resources and thus co-existence of multiple species (Griffiths, 2003), whereas increasing height causes a decrease in diversity because conditions in pools high on the shore are more variable and extreme (Gibson, 1969, 1982; Bennett & Griffiths, 1984) to which fewer species are adapted. For species with morphological adaptations for crypsis in rock pools, as is the case for certain rock pool fishes such as Blennies or Gobies, increased rock cover would be beneficial as these species would be afforded more cover from rock substrates over algae or sand (Penrith, 1969, Bennett & Griffiths, 1984).

### **Species Composition**

The dominance of klipfishes, gobies and blennies with some contributions by seabreams and Finger-fins follows the compositions of pools sampled in the bioregion (Bennett, 1987) and elsewhere in South Africa (Jackson, 1950; Penrith, 1965, 1970; Penrith & Kensley, 1970a, 1970b; Kensley & Penrith, 1973, Marsh et al., 1978, Christensen & Winterbottom, 1981;

Bennett & Griffiths, 1984; Beckley, 1985; Burger, 1988, 1991, Prochazka & Griffiths, 1992). Primary resident species also dominated pools sampled at Goukamma over secondary resident species, a pattern that is consistent in rock pools globally (Griffiths et al, 2003; Castellanos-Galindo et al., 2005; Arakaki & Tokeshi, 2006; Tsering et al., 2012; Gozalew-Murchia et al., 2012; Murase, 2013; Arakaki & Tuchiya, 2014; White et al, 2015; Machado et al., 2015).

Species composition differed by location, most likely owing to differences in rock pool characteristics. Rock pools with high cover of rock are often dominated by gobies (Kuitert, 1993) such as in pools sampled at Buffels Bay. Gobies also tend to be better adapted to pools high in the shore by virtue of their physiological adaptations (Kemp, 1990) and likely preferred the greater height ranges of pools at Buffels Bay. Pools with higher cover of algae generally support more klipfishes (Bennett & Griffiths, 1984), as was the case in pools sampled at Oysterbeds, whereas blennies tend to exhibit cryptic behavior and negative buoyancy to avoid predation (Milton, 1983; White & Brown, 2013; Thyssen et al, 2014) and likely prefer the increased cover afforded by deep and structurally complex rock pools, of the type most prevalent at Platbank.

### Factors Influencing Abundance

Rock pool characteristics commonly influence fish abundance (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992; White et al., 2015). Physical pool characteristics influence the abundance of fish as different species have preferences to certain characteristics as mentioned in the previous paragraph. However, none of the pool characteristics measured in the present study had any influence on the abundance of fish in pools at Goukamma, in contrast to studies conducted elsewhere. Past studies have concluded that the number of fishes decreases with increasing pool height, owing to the increased high-shore variation in environmental conditions (Gibson, 1969, 1982, Prochazka & Griffiths, 1992) and pools of larger area provide greater absolute space for niche partitioning of resources, including space, and thus contain a greater abundance of fish (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992).

Two studies (Bennett & Griffiths, 1984; White et al., 2015), however, found no changes in total fish abundance with height, in-line with the present findings. These two studies sampled pools, which were present on flat rock platforms, similar to those at the Groenvlei section of Goukamma. Flatter shores would lead to similar water turnover in both low and high pools as wave action is not attenuated and subsequently reductions in the variation in environmental conditions among pools found at different heights. In contrast, pools found in shores with greater height ranges would exhibit greater variations in conditions between pools at different heights. This was not the case, the lack of influence of height on abundance in pools at Goukamma is therefore likely due to the physical structure of the shore in which they are found and the resultant similarity in conditions prevailing in pools at all heights.

The failure to detect an influence of area on abundance at Goukamma is likely due to a preference of rock pool fishes to smaller pools, to which they are better adapted. Larger pools

would also be more beneficial to predators due to their larger sizes, preferring larger water volumes for effective feeding and so smaller pools would provide greater protection for fishes. Thus whilst there may be greater abundances of fishes in medium over small pools, larger pools are not of preference to most fishes and would host relatively lower densities despite greater overall size.

### Spatial patterns in Rock Pool Fish Community

At scales of greater than 6 kilometers, rock pool fish communities at Goukamma differed significantly but at scales of less than 2 kilometers this was not the case. Past studies show that at small scales, differences in community are attributed to species-specific preferences to microhabitat availability at each shore (Marsh et al., 1978; Yoshiyama, 1981; Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992). At greater distances, however, dispersal limitations, driven by reproductive styles and morphological traits, become more important (Griffiths, 2003; Griffiths, 2006; White & Brown, 2013; Maciera et al., 2015).

The differences in communities between locations sampled at Goukamma and similarity within locations likely reflect this finding. Most rock pool resident fishes (namely Blennies, Gobies and Klipfishes), which make up a majority of the community sampled at Goukamma, exhibit limited reproductive dispersal (Prochazka, 1994), negative buoyancies, cryptic coloration and poor open water swimming abilities (Griffiths, 2003). They are therefore unlikely to selectively swim over any great distances of open or sandy shore in search of more preferential pools as adults. Furthermore, rock pool fishes also been shown to exhibit high degrees of ecological cognition and rock pool affinity or homing behaviors (Griffiths, 2006; White, & Brown, 2013) showing clear preference to certain pool characteristics at smaller scales (Marsh et al., 1978; Yoshiyama, 1981; Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992). The differences in communities likely shows that rock pool fishes at Goukamma are able to, and selectively do, move over relatively small distances (<2 km) in search of pools of their preference but seldom move over distances greater than (>6 km) this by virtue of their preferences to pool characteristics available at their chosen location and potentially, their inability to move over these distances due to morphological adaptations.

### Effects of Abiotic Pool Characteristics on Rock Pool Communities

Even when controlling for location differences, the models of the communities sampled at Goukamma showed that a number of pool characteristics influenced rock pool communities. The influence of area on abundance and diversity of rock pool fish community has been found in past studies and is a result of increased availability of niches and resources (Mahon & Mahon, 1994) and greater absolute swimming space in larger pools (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992). The influence of area on fish community at Goukamma likely reflects a similar result, where larger pools provide more space for more diverse communities. Larger pools are also beneficial to less cryptically colored secondary residents that are also less adapted to changes in physical conditions, particularly as larger pools would offer greater

stability in water conditions (Murase, 2013; White et al., 2015). It is likely that communities shift from those dominated by primary residents in smaller pools to those dominated by secondary residents in larger pools.

Rock pool complexity significantly influences the abundance and diversity of rock pool fish communities in Australia (White et al, 2015) by providing a diversity of micro-niches and increased protection from predators. Habitat complexity is important in a number of marine and terrestrial environments (Telleria & Carrascal, 1994) and for associated communities (Pianka, 1973; Davidowitz & Rosenwieg, 1998; Beck, 2000; Williams et al, 2002; Gratewicke & Speight, 2005). Griffiths et al. (2006), however, highlights that complexity in pools can be derived from both structural rugosity and water column complexity (foliose algae) and concludes that whilst both are utilized by fishes, rugosity is more important to most species. The influence of rugosity rather than algae on community, as was the case at Goukamma, follows this finding.

Height has been shown in a number of studies to affect both the diversity of fish communities (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992) and the abundance and size distributions of single species, and relative abundances of primary and secondary resident species (White et al, 2015). These influences are attributed to differences in water turnover and associated changes in water chemistry driven by wave exposure, height and differential species tolerances to environmental conditions prevailing in each pool (Gibson, 1972). The influence of pool height can therefore also be influenced by absolute pool size (volume), as larger pools would exhibit less fluctuation in water chemistry (Murase, 2013). Height of pools sampled was found to cause a decrease in diversity of pool sampled at Goukamma and shows that this variable causes changes in community due to reductions in diversity up the shore, a finding consistent with a number of intertidal studies in South Africa (Bennett & Griffiths, 1984; Huggett & Griffiths, 1986; Prochazka & Griffiths, 1992) and elsewhere (Castellanos-Galindo et al., 2005; White et al., 2015).

Depth has been shown to also influence fish communities in rock pools (White et al., 2015) due to increased protection from aerial predators. Depth has a significant influence on fish community at Goukamma, following this finding. Furthermore, deeper pools may be preferential to the benthic nature of certain primary resident species, namely Blennies (Griffiths, 2003; Milton, 1983; Thyssen et al, 2014). Deeper pools have also been shown to be beneficial to secondary resident species (White et al., 2015) as more vertical space and potentially volume is found in pools that are deeper. Depth, however, has little effect on diversity (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992). Changes in community but not diversity with depth, likely reflect these findings, where deeper pools are preferential to both primary and secondary residents by providing cover from aerial predation for benthic primary residents and greater swimming area for secondary residents.

## Influence of Season on Rock Pool Communities and Diversity and Abundance of Fishes

Most marine habitats are considered relatively dynamic in time, and show distinct seasonal changes owing to differential recruitment among different species (Doherty & Williams, 1988) and changes in extrinsic pressures. Rock pools, however, have been shown to exhibit little if any changes over the long and short term, showing little change seasonally (Willis & Roberts, 1996) despite the dynamic and physiologically challenges imposed by intertidal life (Thomson & Lenher, 1976; Grossman, 1982, 1986; Prochazka, 1996; Griffiths, 2003; White et al., 2015). This was indeed the case at Goukamma, which showed no significant changes in rock pool fish community, abundance nor Shannon-Wiener diversity, with season, at least over the study period.

## Bioregional Patterns in Rock Pool Communities in South Africa

At the global scale, Griffiths (2003) concluded two main rock pool groups: those of Gondwanan origin (Portugal, France, Australia, South Africa and New Zealand and Chile) and those of Laurasian origin (USA, Canada and Mexico). Those of Gondwanan origin generally play host to blennies, triple-fins, gobies and klipfishes, the latter being a distinct characteristic of South African rock pools. Pools at Goukamma showed dominance by three of these species although triple-fins were not found (but are seen in more tropical areas north of the study area and into Mozambique) adding another line of evidence for these global patterns in rock pool fish communities. As hypothesized by Griffiths (2003), these patterns are likely driven by the inherent dispersal limitations, at these scales, of rock pool fishes which, over geological time would lead to the observed patterns seen today. Indeed, pools at Goukamma are distinctly South African (dominance by Klipfishes) but also follow global patterns, with the exclusion of triple-fins, which are poorly represented in South Africa.

The number of species and families and species composition found in rock pools in South Africa changes as one moves from west to east, evident in the published literature (See Chapter 1- Patterns in South African Rock Pool Fish Communities). Klipfishes and clingfishes dominate pools in the west (Bennett & Griffiths, 1984; Prochazka & Griffiths, 1992) whereas klipfishes, gobies and seabreams dominate those in the south with some contributions by Blennies (Bennett, 1987). Pools in the east show a tropical component not seen elsewhere along the coast, being dominated by Gobies, Blennies and Triple-fins (Beckley, 2000). Whilst there is some overlap in compositions between bioregions, communities found in pools within each bioregion are more similar to those found elsewhere in the bioregion, than to those seen in other bioregions, even when distances between pools in adjacent bioregions are less than between pools within the bioregion. The number of species, families and species compositions found in pools at Goukamma are most similar to those seen elsewhere in the South Coast Bioregion, being most similar to a study by Bennett (1987) conducted further south at Koppie Alleen.

These patterns highlight a general biogeographical pattern in rock pool fish communities along the South African coastline, similar to that seen in other marine taxa (Griffiths et al., 2010). Biogeographical patterns have been shown to be driven by distinct barriers limiting dispersal of organisms between adjacent bioregions, but less so within. Most evident are the southward flowing of the Agulhas in the east, its divergence from the coast, the Cape Point barrier and cold Benguela upwelling cells off the west coast (Roberts, 2005; See Chapter 1: Figure 3). Along with community similarities within bioregions and overall patterns among bioregions, it is likely that the same biogeographical barriers seen to limit other marine taxa also limit the ranges of rock pool fishes, at least at the family level.

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