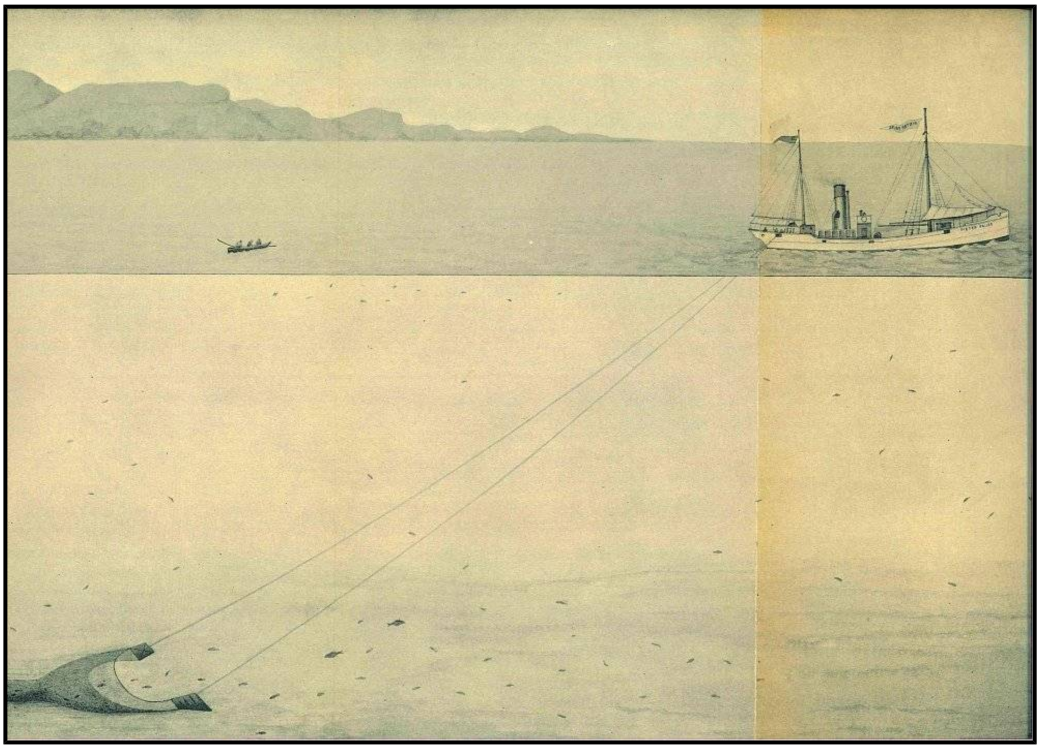
Historical baselines and a century of change in the demersal fish assemblages on South Africa's Agulhas Bank

Jock Carlisle Currie



Thesis Presented for the Degree of Doctor of Philosophy

In the Department of Biological Sciences

University of Cape Town

May 2017

Supervised by Assoc Prof Colin G Attwood, Dr Lara J Atkinson and Dr Kerry J Sink

DECLARATION

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is my own. This thesis has not been submitted in whole or in part for a degree at any other university.

Signed by candidate

Signature: signature removed

Date: 9 May 2017

Acknowledgements

This thesis is the hardest thing I've ever attempted and without huge amounts of support and encouragement, it would never have been completed. I'm sure I will forget to mention some of those who kindly contributed during this journey – thank you and apologies for your omission.

Financial support to make this project a reality is gratefully acknowledged from the Marine Conservation Institute; British Ecological Society; The Explorer's Club; SeaKeys project; SANBI (South African National Biodiversity Institute); the National Research Foundation's Professional Development Programme, SAEON (South African Environmental Observation Network); UCT (University of Cape Town) and the Marine Research Institute at UCT.

The project would never have started without the generous and unwavering support of my supervisors. I won't try to list the many contributions through which they supported my professional and personal development, as I would fail miserably to cover half of them. I dreamt up an unlikely and costly fieldwork approach. Instead of discouraging me from an audacious undertaking, they believed in me, even when I did not. Many times you went far beyond the call of duty. Thank you.

So many other people took the time to help along the way, offering enriching relationships or conversations. Beate Holscher went beyond her duty in making sure I succeeded in navigating red tape, besides her kind encouragement and belief in my abilities. Lance van Sittert and staff at the UCT and Gilchrist Library are thanked for their kind assistance in accessing historical literature. Anne-Flore Laloe (National Marine Biological Library, Plymouth) and Linda Fitzpatrick (Scottish Fisheries Museum) provided fantastic remote assistance. John Pinnegar, Andy Payne and other CEFAS staff generously shared their knowledge. Mandy Roberts was extremely helpful in finding my way around the CEFAS (Lowestoft) library and archives. A huge thank you to Georg Engelhard, who has been generous with his time, friendship and opened his house to me, making collaborative visits to Lowestoft possible. Without Georg's willingness to engage, and interest to help, investigation of the historical trawl gear would have faltered.

Mr Jacobsz from Cape Netting was extremely generous with his time and support of the project. I thank him and his team of net-braiding staff for their hard work in getting the trawl net panels made. Sharon du Plessis and the DAFF fishing gear team (Moses Trimble, John Thomas and Clive Nash) are thanked for invaluable assistance in building the trawl net. As are George du Plessis and Granville Faulmann from the Biological Sciences workshop at UCT, for their help in the construction of trawl doors. Lwandle Technologies generously provided hydrographic sensors to attach to the trawl net during fieldwork.

Peter Bacon, Nico Bacon, the staff at Viking Fishing in Mosselbay and the captain and crew of MFV Leeukop are acknowledged for making the fieldwork possible. A special mention must be made of Noel Less, who taught me more about trawling and trawl gear than I ever expected to know. Noel is a fountain of knowledge on anything trawl or fisheries related. Without his vast experience, careful attention to detail and kind generosity of his time, this project likely would not have happened. Thank you Noel.

A big thank you also to my assistants at sea, who survived the gruelling work and uncomfortable conditions in good humour and provided excellent service. Stewart Norman, Denham Parker, Stephen Lamberth and Colin Attwood, your able assistance was massively appreciated and the fieldwork would have been impossible without it. Thank you also to Garth Kingwill for your enthusiasm and effort to document the project, Dougal Paterson for stepping in when needed (and frequently dragging me into the surf to maintain sanity) and to Tommy Bornman and the SAEON Elwandle staff for their assistance on the Bird Island trip.

The Department of Agriculture, Forestry and Fisheries (DAFF) are acknowledged for making available their invaluable data. Deon Durholtz, Tracey Fairweather and Robin Leslie are thanked for their time and support throughout many discussions, queries and administrative assistance. Thanks also to Rob Cooper, who always had an open door and was ever ready to provide advice or assistance.

The brilliance of many people was tapped for advice. Special mention must be made of Henning Winker, who boggled my mind many times. His infectious enthusiasm and curiosity, together with the generosity of sharing his statistical acumen make him an invaluable colleague and friend. James Thorson is thanked for his friendly, patient and efficient assistance, which enabled me to run his exciting models. The memory-intensive computations were performed using facilities provided by the University of Cape Town's ICTS High Performance Computing team (http://hpc.uct.ac.za). Their staff were very helpful and efficient.

The personal relationships that have nurtured and challenged me throughout the last few years are too many to mention. Thank you to the fantastic people I surround myself with, most of whom I won't mention here. My close friends and family are thanked for their endless support and love. Kerry (J), thank you for your incredible strength, infectious zest for life and loyal support through the hardest of times. Thank you to my Mom for her inspiration, love, strength and never-ending

enthusiasm for everything I tackle. Lastly, thank you to my Dad, Tony, for everything you taught me, your love and gentle kindness, your childlike spirit and joy, and for being an incredible role model. Thank you.

Table of Contents

Thesis abstract

Accurate interpretation of recent variability observed in fish populations, species compositions, distribution ranges or ecological indicators, depends on knowledge of their past dynamics and historical states. The onset of systematic fisheries data collection typically lagged decades or even centuries behind modern fishing exploits. As a consequence, pre-disturbed reference points and descriptions of subsequent change are rarely available. A remarkably detailed set of historical trawl survey data from South Africa provided such a rare opportunity. Government-funded exploration of the Agulhas Bank fishery potential resulted in meticulously-documented trawl survey data from 1897-1904, when prior human impacts on those resources were negligible. Although they used less effective technology, the information recorded and methods used were similar to modern surveys. This thesis investigated change in demersal fish fauna of the Agulhas Bank and documents comparisons between historical trawl surveys and modern re-enactments at the same locations.

In comparing trawl survey catches over multiple decades or among different periods, unquantified changes in fishing power pose a key challenge. The shape, size, materials, mesh sizes and speed at which trawl nets are dragged, interact with the behaviour, size and shape of fish, influencing fishing performance. To accurately compare current catch rates with those of historical trawl surveys, the same trawl gear and methods were carefully replicated in repeat surveys at three sites. An investigation of literature and photographs of the original vessel and equipment were conducted to support the construction of a replica 'Granton' otter trawl net. The net was composed of Manila hemp with a headline length of 27 m (90 ft) and was attached to flat wooden trawl boards. The historical towing speed was estimated as 1.34 m s^{-1} (2.6 knots). Three parts of the shallow Agulhas Bank that were surveyed 111 years prior, were re-surveyed in 2015.

Species composition was contrasted between the historical and re-survey periods by way of unconstrained ordination, permutational multivariate analysis of variance and tests of the homogeneity of multivariate group dispersions. Taxa discerning between periods were identified with similarity percentage analyses. Changes of standardised catch between periods were tested for 27 taxa, using a non-parametric bootstrap approach. Proportions among size-classes, recorded for three taxa, were tested using Fisher's exact test. Results revealed a substantially transformed demersal catch assemblage, where the period effect explained almost half of the measured variance among samples. These changes included the disappearance or heavy depletion of kob (*Argyrosomus spp.*, absent in re-surveys), panga (*Pterogymnus laniarius;* 2.4% of historical catch abundance) and east coast sole (*Austroglossus pectoralis*; 4.6% of historical catch abundance), which had jointly contributed 70-84% of historical catch composition. Average re-survey catches were largely made

up of gurnards (*Chelidonichthys spp.*; 3 792% of historical abundance), horse mackerel (*Trachurus trachurus;* 4 738% of historical abundance), spiny dogfish (*Squalus spp.*; 3 121% of historical abundance), hake (*Merluccius capensis*; 558% of historical abundance) and white sea catfish (*Galeichthys feliceps*; 13 863% of historical abundance).

Analysis of available length information confirmed the expectation that fish sizes (specifically *M. capensis* and *A. pectoralis*) had declined. This implies that comparisons by weight would be more severe for declined abundances and less severe for those that increased, relative to contrasts of numerical abundance. Habitat preferences as well as geographic and depth distribution appeared to separate the taxa that increased from those that declined. These factors, together with reproductive and growth characteristics, as well as indirect trophic impacts, likely shaped the responses of demersal fauna to fishing and other human impacts during the 111 years between trawl surveys.

An assessment of distribution changes of 44 common demersal taxa was undertaken. These analyses were restricted to the last 30 years of trawl survey data as the units and spatio-temporal resolution of prior data were incompatible. Standardised catches were used from annual spring and autumn south coast trawl surveys conducted by the government fisheries department. Geostatistical delta-generalised linear mixed models were used to predict species distribution functions, which were used to calculate annual estimates of latitude/longitude centres of gravity and effective areas occupied by each population. Average trends over the study period (1986-2016) were assessed using a Bayesian state-space model. Of nine species found to have a trend in average location, six moved westward or south-westward, while three moved eastward or north-eastward. Two species showed a trend of contracting spatial extent and one showed an expansion. Across the entire assemblage combined, there was a significant contraction in extent and a westward shift in average location. These assemblage-wide average trends are interpreted to be driven by climate forcing. Fishing impacts are expected to have contributed to the eastward movement in centre of gravity for kob, lesser sandshark (*Rhinobatos annulatus*) and white stumpnose (*Rhabdosargus globiceps*). Interpretation of these distribution shifts is hampered by a lack of knowledge on subsurface hydrographic trends on the Agulhas Bank, which is identified as a research priority.

My research revealed substantial change in demersal fish communities on South Africa's Agulhas Bank and adds novel insight to the history underlying current states of demersal ecosystems. Valuable additions include a) documentation of the extent to which demersal assemblages have transformed during the last century at three representative inshore sites; b) estimates of current abundances relative to pre-disturbed baselines at those sites, which c) highlights drastic local depletion for certain taxa and d) reveals substantial abundance increases of certain species during the post-industrial fishing period; e) novel evidence of distribution trends in south coast demersal

species; and f) identification of trends in the average distribution of the demersal fish assemblage, suspected to be climate-forced. Long-term comparisons, using minimally-disturbed baselines, revealed drastic transformation of the fish assemblage during a century of industrialisation, which points to trawling-induced alteration of benthic habitats and substantial changes in ecosystem structure. Besides the provision of novel historical context for current and future studies and decision-making, this work counters the erosive nature of shifting baselines in South Africa's marine environment.

Chapter 1: General Introduction

Development of South Africa's trawl industry

While pre-colonial exploitation of marine resources in South Africa has a long history that may have been important to human evolution (Parkington 2001), it appears to have been limited to intertidal zones (Griffiths et al. 2004). Compared to many other temperate shelf regions of Europe, Britain and North America, the colonial and industrial impacts were slow to reach South Africa's demersal ecosystems, due largely to a lack of market access that would fuel such expansion. In 1889 the 'Cape of Good Hope' colony (that included the west and south coasts of later South Africa) had a fishing fleet that was estimated to consist of 374 boats crewed by 2 241 fishermen (Lees 1969). Fishing methods at the time consisted predominantly of beach seining or line-fishing, the latter usually from small open boats that caught the majority of their fish within a mile or two from harbours (Lees 1969). As lamented in a speech in parliament in 1890 by a proponent of developing the fishing industry: "...we have not one steam or sailing vessel, small or large, nothing but little open Malay boats hugging the shore, where a great European fleet of vessels and mariners could be employed..." (Lees 1969).

The earliest beginnings of South Africa's trawl industry may be ascribed to a steam tug that experimented with dragging a net outside the Port Elizabeth harbour in 1878 (Lees 1969). These were followed by similar efforts by tugs based in Cape Town (Gilchrist 1914). Only in 1898, however, was the first commercial steam trawler registered at Simon's Town in False Bay (Fig 1; Department of Agriculture 1899), following the evidence of substantial catches made during government-funded trawl surveys. The scientific trawl surveys had commenced the year before, led by Dr John D. F. Gilchrist on a specially-commissioned steam trawl vessel, the Pieter Faure (Department of Agriculture 1898). His primary objective was to demonstrate "what the seas around the coast really contain and the best way of developing them practically" (Department of Agriculture 1896).

The most important fishing grounds during the first two decades of commercial trawling in South Africa were the inshore Agulhas Bank sole grounds (Scott 1949; Botha 1977), where relatively high value catches of east coast sole (*Austroglossus pectoralis*) were targeted. These principal trawl grounds included those off Cape Infanta, which were considered the productive grounds closest to Cape Town (Department of Agriculture 1904), areas around Mossel Bay and the eastern-most grounds near Bird Island (Fig 1; Scott 1949). Initial commercial exploitation of these grounds appears to have started in 1901 at Bird Island (Department of Agriculture 1902), 1903 at Cape

Infanta (after discovery of grounds there in 1902; Department of Agriculture 1904) and as early as 1899 at Mossel Bay. The small Mossel Bay market initially struggled to accommodate the relatively large trawl landings that would flood the market (Department of Agriculture 1900). By 1904 there were nine steam trawlers fishing the Agulhas Bank, most of them registered at Port Elizabeth (Department of Agriculture 1905).

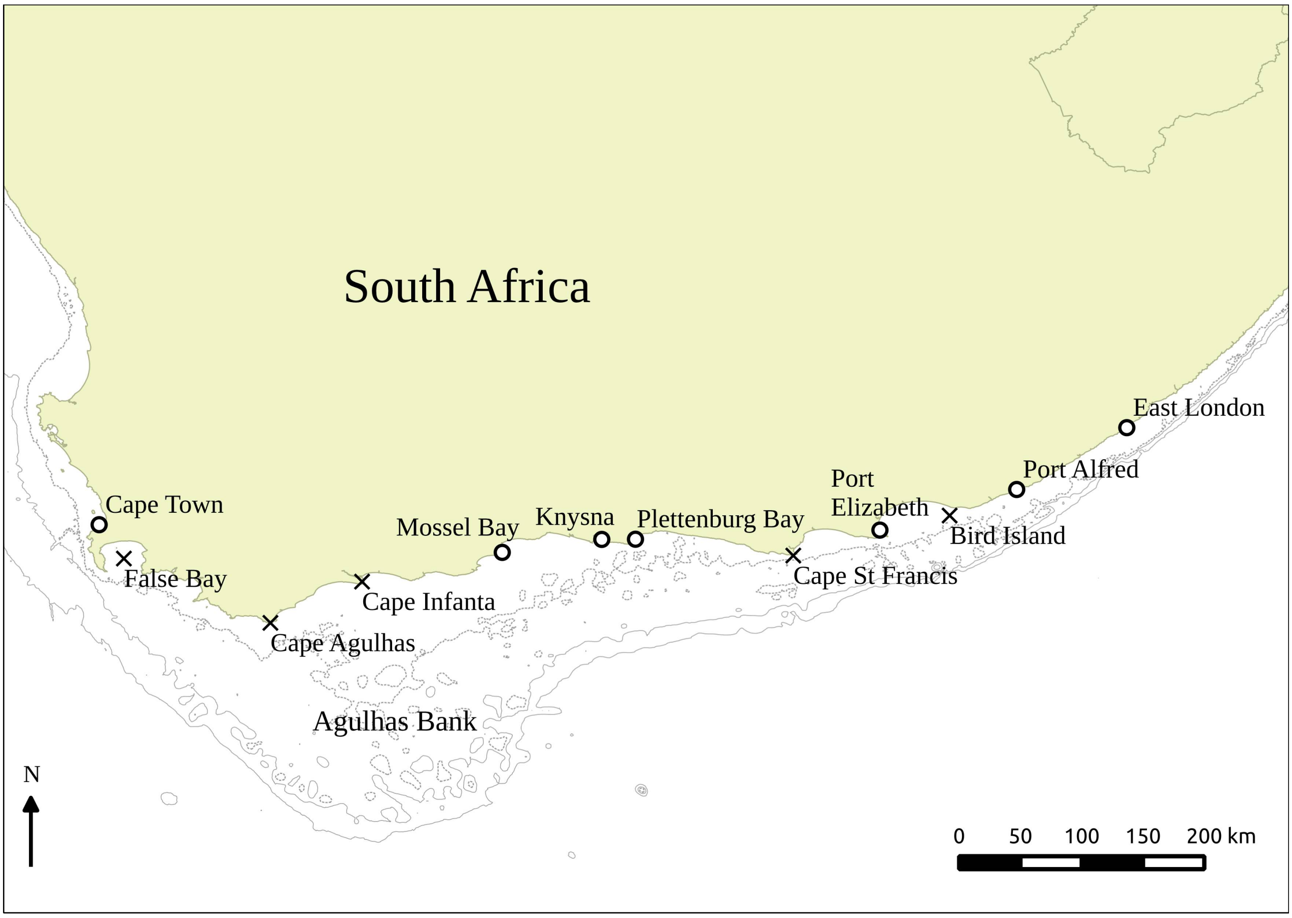


Figure 1. Map of the study region on South Africa's south coast. Names of places used in this or other chapters are shown, including towns/cities (circles) and geographic features (crosses). Bathymetry is indicated by 100-, 200- and 500-m depth contours.

South Africa's trawl industry grew as transportation networks and access to markets developed, after the disruption of the First World War. In 1920, renewed funding and a converted whaling vessel allowed Gilchrist to resume scientific trawl surveys 14 years after they had been abandoned due to financial constraints. In 1922 there were 1 002 boats, of which 17 were steam-driven otter trawlers, registered in the Cape Province (which incorporated both Agulhas Bank and west coast fishing grounds; Lees 1969). The large west coast hake resources were discovered in deeper waters at this time (Scott 1949; Payne and Punt 1995), after which they dominated regional trawl landings as growth in capacity and effort was focused on the west coast. Catches of both shallow-water (*Merluccius capensis*) and deep-water hake (*Merluccius paradoxus*) remained the largest and most valuable part of South Africa's trawl industry, to the extent that their landings provide a proxy for trawl catch and effort over time (e.g. Griffiths et al. 2004).

After the Second World War, technological advances and growing capacity resulted in faster growth of the industry. Hake landings reached approximately 50 000 tonnes in 1950 and 160 000 tonnes by 1960 (Payne and Punt 1995). As news of profitable catches spread, foreign fleets arrived in the 1960s, rapidly escalating fishing effort and catches in the region (Payne and Punt 1995). These included vessels from Japan, Spain, Soviet Union, Poland, Bulgaria, Romania and East Germany (Payne 1989). South African hake landings reached a peak in the early 1970s (~300 000 tonnes), after which they fell steeply due to over-exploitation of the resource (Payne and Punt 1995). In 1972 the International Commission for the Southeast Atlantic Fisheries was formed to try and regulate regional fishing pressures and in 1977 the South African government proclaimed a 200-nautical mile exclusive fishing zone that progressively removed international effort. In the 1980s hake populations started to recover and their catches have subsequently remained relatively stable at ~150 000 tonnes per year (Griffiths et al. 2004; DAFF 2015). An overview of the development, gear and vessel technology, management strategies and fleet structure of South Africa's trawl fishery are provided in Sink et al. (2012b).

The inshore Agulhas Bank plays a relatively minor role in trawl landings compared to large hake catches in deeper waters and on the west coast. Yet a mixed-species trawl fishery has been maintained there since it began at the beginning of the 20th century (Attwood et al. 2011). Inshore trawlers are limited to 30 m vessel length and concentrate their effort in shallower areas (< 110 m) from which larger 'offshore' vessels are excluded (Attwood et al. 2011; Sink et al. 2012b). In recent decades the inshore trawl vessels have focused on east coast sole and hake (*Merluccius capensis*) catches, although horse mackerel (*Trachurus trachurus*), silver kob (*Argyrosomus inodorus*), panga (*Pterogymnus laniarius*), gurnards (*Chelidonichthys spp.*), chokka squid (*Loligo vulgaris*) and multiple other species have added value to landings (Attwood et al. 2011). The number of active inshore trawl vessels was 35 in the early 1990s (Payne and Punt 1995), which declined to 15 in 2015.

Baselines and understanding change

Reconstructing and understanding past dynamics of fishing effort, fish populations and their ecosystems is critical to enable informed management of our oceans. Without knowledge of the historical backdrop that led to them, we lack context in which to interpret current states (Cardinale et al. 2009), whether they describe catch rates or density of a population, the composition of an assemblage or the distribution of a species. Such measures or descriptors of the state of populations, communities or ecosystems at a particular point in the past are commonly referred to as historical reference points or baselines.

In most of the world the initiation of standardised scientific monitoring programs started well after the initiation of fishing and other human impacts (Mackinson 2001; Lotze and Milewski 2004; Lotze and Worm 2009). The majority of our knowledge of trawl ecosystems and their baselines are thus supported by investigations of systems that were already altered by anthropogenic impacts (Rogers and Ellis 2000; Pinnegar and Engelhard 2008; Thurstan et al. 2010). An understanding of the extent and nature in which the already-impacted ecosystems deviated from those prior to human pressures is poorly developed in most cases (but see case study of Lotze and Milewski 2004). This lack of appreciation for historical ecosystem or population states exacerbates the pitfall of shifting baselines (Pauly 1995), whereby successive generations of scientists, fishers and society accept progressively compromised ecosystems. Addressing this knowledge gap is a key focus of marine historical ecology (Lotze and McClenachan 2014). Improving knowledge on historical baselines is a research priority in South Africa and internationally (Sink et al. 2012a; Schwerdtner Máñez et al. 2014).

Climate impacts

Anthropogenic climate change can influence fish populations or communities via an array of direct or indirect effects operating on a range of temporal and spatial scales (Brander 2010). Examples of direct physical and chemical impacts could include changes in temperature, pH, currents, frequency or intensity of mixing events, concentrations of oxygen and nutrients. Such impacts will have direct influence on populations by, for example, causing changes in their distribution, behaviour or productivity, and indirect effects via surrounding ecosystem processes (Harley et al. 2006; Brander 2010). As they can interact with fishing or other anthropogenic impacts in various ways, disentangling climate effects and understanding their implications is challenging in the poorly-sampled marine environment. Expected and documented impacts of climate change in marine ecosystems are provided by Harley et al. (2006), Brander (2010) and Doney et al. (2012).

Much of our knowledge of long-term change in demersal ecosystems stems from assessments of trawl catches over time. Valuable contributions have been made by studying temporal and/or spatial change in commercial catches (e.g. Rijnsdorp and Millner 1996; Klaer 2001; Thurstan et al. 2010; Thurstan and Roberts 2010). An alternative strategy has been to contrast research trawl survey catches over time or among periods. Compared to commercial catches, research surveys usually provide higher resolution data, enable a greater degree of standardisation across effort or gear efficiencies and avoid bias due to market-related changes in discards or targeting strategies.

Research survey data, specifically historical trawl survey data and a repeat experiment thereof, form the basis of this thesis.

Using multiple periods of trawl survey data between 1913 and 2002, Genner et al. (2004) showed that the principal component of community composition was correlated with ocean temperatures in the English Channel. This correlation appeared to be driven by abundances of several taxa increasing during periods of warmer waters. Building on this research, Genner et al. (2010) showed that smaller-sized species had responded to climate fluctuations, whereas there had been persistent fishing-related declines in the sizes and abundances of larger species. Using four periods of varying climate and fishing pressures between 1902 and 2008, ter Hofstede and Rijnsdorp (2011) contrasted changes in species richness and fish size. They suggested that warm periods had favoured taxa that prefer warmer waters and had driven smaller mean body sizes independently of fishing impacts. Engelhard et al. (2011a) assessed changes in the assemblage of demersal fish in 1977-2008 North Sea trawl surveys, having pre-assigned species to ecotypes based on biogeography, habitat preference, body size, trophic guild and level. They concluded that there had been increases of mainly small, warm-water, low- or mid-trophic-level taxa, and declines of mostly large, cold-water, high-trophic-level ecotypes. Responses implicated aspects of both climatic signals and vulnerability to fishing pressures.

Distribution changes are an obvious response that have been linked to climate changes, although direct or indirect effects of fishing may sometimes cause similar responses (Engelhard et al. 2011a). Poleward distribution shifts towards areas of cooler waters have been interpreted as responses to warming waters (e.g. Stebbing et al. 2002; Beare et al. 2004). Using demersal trawl survey datasets across several regions, Pinsky et al. (2013) showed that climate velocity (the rate of geographic isotherm shift over time) explained distribution changes more effectively than taxonomic or biological characteristics of demersal ichthyofauna. Modern statistical techniques are becoming increasingly adept at estimating distribution changes over time, while accounting for potential bias such as non-uniform spatio-temporal sample coverage (e.g. Thorson et al. 2016a).

Fisheries pressures

Contrasting trawl surveys between 1906-1909 and 1990-1995 in the south-east North Sea, Rijnsdorp et al. (1996) showed reduced abundances for the total assemblage and groups within it, as well as reductions in the sizes of fish caught. They also reported lower diversity and greater species dominance in the latter period, as did Greenstreet and Hall (1996) when they contrasted north-west North Sea trawl survey records between the periods of 1929-1953 and 1980-1993. Greenstreet and Hall (1996) noted that assemblage differences between the two periods were mostly driven by relatively subtle changes in the abundances of less-common taxa. These conclusions were supported by follow-up research (Greenstreet et al. 1999) using a dataset expanded in time (1925-1996) and space (addition of central North Sea). Greenstreet et al. (1999) highlighted that decreases in diversity were linked to areas that had been most heavily fished and that community changes were most apparent in the group of species targeted by fishing. They also noted a shift towards a smaller-sized assemblage, consistent with fishing-induced changes in the demersal community. Even though the assemblages separated statistically, both studies emphasized a relatively high degree of similarity among periods and concluded that the trawl-caught communities had not changed drastically over time. A similar conclusion was drawn by Rogers and Ellis (2000), who contrasted trawl survey assemblages between 1901-1907 and 1989-1997 in three coastal regions around the British Isles. They attributed declines of larger (especially elasmobranch) species and increases of smaller non-targeted taxa to the effects of fishing.

In a long-term investigation of the Firth of Clyde (Scotland) trawl fauna, Heath and Speirs (2012) documented the changes that followed the 1962 withdrawal of a trawling ban that had been in place since 1889. The resumption of trawling after 73 years was followed by substantial change in the demersal fish assemblage. Biomass that was previously spread across multiple species, including those of large body size, became concentrated in small-sized fish and predominantly one species (whiting, *Merlangius merlangus*). Once trawling pressure eased due to collapsed fishing yields, the species evenness recovered relatively fast but the curtailed size structure remained 10 years later (Heath and Speirs 2012).

In the Kattegat-Skagerrak region of the north-east North Sea, examination of historical surveys have revealed past abundance and distribution changes critical to the assessment of recent fishery resources. By compiling a series of trawl survey results over time, Cardinale et al. (2009) showed substantial declines in the turbot (*Psetta maxima*) population between 1925 and 2007 that were missing from assessments using only more recent data. Their results suggested that turbot biomass had declined by 86%, that maximum body sizes had decreased by 20 cm and that the population had virtually disappeared from previously-inhabited northern areas. Similarly, Cardinale et al. (2010) used trawl survey data between 1901 and 2007 to investigate past dynamics of plaice (*Pleuronectes platessa*) in the Kattegat-Skagerrak area. The long-term perspective revealed that recent biomass was about 40% of its maximum levels during that time and that mean maximum sizes had declined by about 10 cm during the study period. Bartolino et al. (2012) used a similar dataset to assess spatial estimates of adult cod (*Gadus morhua*) biomass among different periods between 1906 and 2007. They identified two main aggregations within the study area and showed that both had suffered extensive losses as the stocks collapsed after peak fishery landings in the 1960s-1970s.

Large, slow growing predators, with a low intrinsic population growth potential are frequently highlighted as being sensitive to fishing pressures (Myers and Worm 2005; Ferretti et al. 2008). Many elasmobranch species fall into this description and their decline or disappearance from fished waters around the world has been documented (Casey and Myers 1998; Ferretti et al. 2013; Meissa and Gascuel 2015). In an example from the Adriatic Sea, Ferretti et al. (2013) used multiple trawl surveys between 1948 and 2005 to document alarming declines in the elasmobranch community. These included combined catch rate decreases of > 94% and 11 species that had disappeared from survey catches during the studied period. These alarming changes were blamed on the development of excessive fishing effort.

Pre-exploitation baselines

Of the many studies that have investigated trawl survey catches over time or among periods, few have had the opportunity of initial surveys that were conducted prior to or at the very beginning of commercial trawling activity (e.g. Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Kongprom et al. 2003). Although surrounding ecosystems were undoubtedly impacted by human activity to some degree (Pinnegar and Engelhard 2008), such studies likely captured baselines of demersal ecosystems that are closer to their undisturbed or pristine state, relative to the majority of investigations that contain initial data collected decades or centuries after commercial trawling started. A difference between trawled and un-trawled areas may be the state of benthic habitat. Trawls and other mobile fishing gears are associated with reduced habitat complexity via the removal of structure-forming benthic fauna and disturbance or removal of sedimentary structures (Auster et al. 1996; Kaiser et al. 2000). The greatest impacts on benthic communities are considered to be associated with initial trawling activity (Duplisea et al. 2002; Dinmore et al. 2003).

In the shallow, tropical northern Australia Gulf of Carpentaria a prawn trawl fishery developed in the mid-1960s. Using 1964 trawl surveys, prior to the start of the trawl industry, Harris and Poiner (1991) compared the fish fauna with repeat surveys in 1985/1986, using the same trawl gear. Their comparisons revealed substantial changes in the fish assemblage. These included the collapse of one of the previously dominant filefish taxa (*Paramonacanthus spp.*), as well as 17 others that decreased and 12 that had increased between the surveys. They noted that the vertical water-column distribution of fish separated, to some degree, those species that had declined (benthic taxa) compared to those that had increased (pelagic or bentho-pelagic species). Harris and Poiner (1991) attributed these changes to fishing pressure from the prawn trawlers, although suggested that sediment changes, possibly relating to river input, might also have had some influence.

On the trawling grounds of the upper continental slope off New South Wales, a repeat survey was conducted 20 years after the same vessel and similar gear was used to survey areas at early stages of commercial exploitation in 1976/1977 (Andrew et al. 1997; Graham et al. 2001). The majority of targeted and non-targeted taxa declined substantially between survey periods, causing a decrease in total catch rate to 32% of that recorded in initial surveys (Andrew et al. 1997). The decline of elasmobranchs was especially acute. While catch rates of spiky dogsharks (*Squalus megalops*) had remained similar, pooled abundances of the remaining sharks and rays declined to < 10% of the 1970s survey levels (Graham et al. 2001). Almost all species for which size data were available indicated decreases in mean size (Andrew et al. 1997).

Trawl fishing developed relatively late in parts of Asia and as a result further examples exist of documented catch records near the beginning of such industries. Following the initiation of a demersal trawl fishery in 1945 in the Philippines, Silvestre et al. (1986) showed that trawl catch per unit effort in shallow waters (< 100 m) declined between 1947 and 1981 to 31% of initial rates. Commercial trawling was introduced into the Gulf of Thailand in 1960. Using trawl survey data between 1961 and 1995, Kongprom et al. (2003) documented a decline of demersal biomass to 8% of initial levels estimated for 1961. Both Silvestre et al. (1986) and Kongprom et al. (2003) concluded that demersal resources were severely over-exploited by excessive fishing capacity.

Demersal ecosystem changes in South Africa

Demersal trawl research in South Africa has been underpinned by government-led research surveys. In the recent era, from 1983 onwards, these have consisted of annual or bi-annual stratified random surveys conducted separately on the west and south coasts. The data are collected and maintained by the Fisheries Branch of the Department of Agriculture, Forestry and Fisheries (DAFF; formerly Marine and Coastal Management in the Department of Environmental Affairs and Tourism; MCM – DEAT). Badenhorst and Smale (1991) and Smale and Badenhorst (1991) used 1986-1990 survey data to document the distribution and abundances of several demersal species on the Agulhas Bank extending off South Africa's south coast. Multivariate assemblage structures were explored in the same dataset by Smale et al. (1993). They showed consistent groupings of inshore (< 100 m), shelf (90-190 m) and shelf-edge/upper slope fauna (> 200 m), which were theorised to be driven by water-column properties (such as temperature and oxygen) in addition to depth (Smale et al. 1993).

In South Africa, research on temporal changes in demersal fish communities has predominantly focused on the recent era of DAFF surveys, on the south coast (e.g. Yemane et al. 2005, 2008, 2010), west coast (e.g. Atkinson et al. 2011b, 2012; Yemane et al. 2014; Kirkman et al. 2015) or across the region (e.g. Pecquerie et al. 2004; Watermeyer et al. 2016). Whereas regional movement between coasts (Watermeyer et al. 2016) and demersal distribution changes on the west coast of South Africa have been investigated (Yemane et al. 2014), little information exists on distribution dynamics of the south coast Agulhas Bank demersal fauna.

Yemane et al. (2010) examined a range of diversity measures over space and time (1986-2003) in South Africa's south coast trawl survey data. They showed that diversity measures of the demersal community (teleosts, cephalopods, and chondrichthyans) were structured by depth and longitude (alongshore) and that diversity and evenness had increased during the period assessed. The application of abundance-biomass-comparison curves to the same dataset (1986-2003) suggested that the community had been exposed to increasing stress during that period (Yemane et al. 2005). As trawling effort had been in decline, potential causes of the signal of greater disturbance were suggested to be the initiation of a longline fishery in 1994, or perhaps longer-term, cumulative degradation of demersal habitats (Yemane et al. 2005). The finding of a community under increasing pressure was later supported by analysis of size-based indicators over the same period (Yemane et al. 2008).

Few investigations incorporate historical data beyond the recent survey period (1980s onwards) to investigate long-term dynamics in South African fish. Multiple species caught in the inshore trawl fishery are also targeted by line-fishers. Research conducted by Penney et al. (1989) and Van der Elst (1989) were among initial efforts to contrast historical line catch records from the mid- and early-20th century with contemporary data at the time. This research was strengthened by Attwood and Farquhar (1999), Penney et al. (1999) and Griffiths (2000) who confirmed the earlier findings of alarming catch declines amongst several species during the 20th century.

A study of South African trawl-caught assemblages that incorporates historical data beyond the recent era is that by Mussgnug (2013). He combined a variety of south coast trawl survey data (1898-1904; 1922-1948; 1980; 1985-2010) and commercial observer (2003-2006) data to assess changes in the community composition at three inshore areas, focussing on chondrichthyan taxa. Assemblages differed significantly among periods. Contrasting proportional abundances between 1898-1933 and 1985-2010, he found that a suite of species, mostly slow-growing, low-fecundity taxa, had declined, whereas several small, fast-growing generalist species appeared to have increased their proportion over time. The influence of differences in gear technology among different survey periods was challenging to account for and Mussgnug (2013) suggested historical surveys be replicated to overcome this problem.

Thesis aims and overview

The aim of this thesis is to describe historical baselines and investigate temporal and spatio-temporal changes in the demersal fish community on South Africa's Agulhas Bank. The research was inspired by rediscovery and digitisation of a unique historical dataset that sampled trawl-caught fauna prior to substantial anthropogenic impacts. To maximise value from the historical data, they needed to be compared to recent catches at the same locations. Substantial changes in trawl technology and its influence on catchability, meant that the most accurate and meaningful comparison would be achieved by replicating the historical gear and methods in a long-term repeat survey experiment.

Chapter 2 of this thesis aims to document the details of design and methods of operation for the trawl gear used on the historical research vessel, Pieter Faure, to enable replication of its fishing power. Incorporating information from literature, photographs and maps, the materials, design, size and application of trawl gear components are discussed. The evolution of early otter trawls are outlined, as well as consideration of remaining uncertainties of gear size and trawl speeds. This research enabled modern re-construction of the historical gear and re-enactment of 1903/1904 surveys in 2015, providing the data necessary for Chapters 3 and 4.

Chapter 3 investigates changes in assemblage composition between the historical and repeat surveys, using multivariate techniques. Taxa discerning assemblages between periods are explored, as well as species accumulation curves and diversity measures. Besides implications of results, the impacts of key assumptions and logistical constraints of the study are discussed.

Chapter 4 interrogates in more rigorous detail the changes in abundance and sizes of individual taxa between periods. Findings are related to knowledge of the biology, stock size and habitat preferences for common species. Where relevant, management implications are raised and ideas for follow-on research are described.

Spatial distribution changes likely influence species abundances and community composition, besides being an important consideration to fishers, managers and researchers. Chapter 5 investigates temporal changes in distributions of demersal ichthyofauna on the Agulhas Bank. As historical data are incompatible, analyses focus on the last three decades of trawl survey data. Results are interpreted in the context of human pressures, predominantly fisheries and climate/environmental change.

Chapter 6 highlights key findings from Chapters 2-5 and expands on their implications to science, fishers and management. Knowledge gaps and fruitful avenues of future research are key elements outlined in a forward-looking perspective.

Chapter 2: Design and function of the historical Granton otter trawl in South Africa's earliest trawl surveys (1897-1906)

Abstract

The investigation of trawl catch data over time or among different periods is a popular strategy to assess long-term changes in marine environments. Such investigations are challenged by unquantified biases due to advances in gear technology and a lack of knowledge on the fishing power of historical trawl designs. In this context, trawl gear and methods used on board South Africa's first research vessel, from 1897 to 1906, were investigated. The goal was to document the gear and methods to an extent that would allow their reconstruction and use in planned repeat surveys more than a century later. The literature was reviewed for information on the design and function of otter trawls from the relevant period and location (the United Kingdom, Scotland in particular), as gear components employed on the vessel were not documented in sufficient detail. Additional specifics on the materials and dimensions were gleaned from government research reports and photographs of the vessel. The gear consisted of an early 'Granton' otter trawl net, made of Manila hemp and with a headline length of ~27 m. The otter doors were flat wooden boards (with a steal frame) connected directly to the headline and ground-rope of the net. The historical towing speed was estimated to be 1.35 $m{\cdot}s^{-1}$ (2.62 knots). The results of this chapter provided the details necessary to reconstruct trawl gear that functionally imitates those used on the Pieter Faure, enabling the repeat surveys required for Chapters 3 and 4. As similar trawling equipment was used globally during the early 20th century, including in the United Kingdom, United States of America and Australia, this information provides an internationally-relevant foundation for studies aimed at investigating historical trawl records and their associated fishing power.

Introduction

Research trawl surveys are a common approach used globally to monitor fish stocks and their ecosystems (Jennings et al. 2001). Because most demersal ecosystems around the world were subject to exploitation for decades to millennia before they were first scientifically sampled by trawl surveys, knowledge of their undisturbed or ‘pristine’ state is poor (Pinnegar and Engelhard 2008). Uniquely, trawl surveys conducted along the coast of South Africa in 1897-1906, sampled a demersal environment believed to be close to its undisturbed baseline state (Chapter 1). These surveys provide a rare opportunity to quantify historical reference points and measure the subsequent changes in a temperate demersal fish assemblage. Understanding the historical fishing gear and how its technology influenced fishing power is crucial to enable valid comparisons of the historical and contemporary survey data.

As one of the primary objectives of trawl surveys is to compare faunal abundances and sizes over space and time, they require meticulous standardisation to function as replicate samples of the trawled community. Differences in the design of trawl equipment, and in the method that it is fished, influence the sizes and species composition selected for in the catch (Hickling 1931; Margetts 1949; Bagenal 1958; Engås and Godø 1986; Engås and West 1987; Dealteris et al. 1989; Axelsen and Johnsen 2015). As a result, modern trawl surveys are typically accompanied by extensive lists of the gear employed and specifications of their dimensions, design and configuration. Such meticulous gear records were unfortunately not included in South Africa's earliest trawl surveys, which commenced in 1897.

Various components of the trawl design will influence the selectivity of the net. The width of the net gape controls the area of sea floor covered by a demersal trawl and is an important factor in the calculation of swept-area-standardized catch rates (Jennings et al. 2001). In addition, the shape of the trawl net, especially that of its mouth, will influence its selectivity amongst different species or size classes (Engås and Godø 1986; Dealteris et al. 1989; Johnson et al. 2008). Fish that swim above the sea floor or that flee upwards when disturbed, will be captured more effectively by a net with a taller mouth gape. Flatfish and other taxa closely associated with the seabed can be targeted effectively with a net that has a lower headline (Ryer 2008). The degree of contact that the ground-rope has with the sea floor is another critical component that influences the catch rate of organisms closely associated with the benthic substrate (von Szalay and Somerton 2005).

The mesh sizes used to construct a net likely influence the potential escape of organisms as a function of their size and shape (Reeves et al. 1992; Sparre and Venema 1998; Mous et al. 2002). It is the cod-end meshes of a trawl net where the greatest selectivity is believed to act, as this is where the majority of trapped individuals escape (Graham et al. 2009). To quantify the selectivity of a specific mesh, selectivity factors are frequently calculated, usually by way of covered cod-end experiments (MacLennan 1992; Sparre and Venema 1998).

Trawl surveys generally seek to measure a signal in the trawl-caught population or community (over time or amongst areas) and it is therefore vital to minimise any variations that stem from differences in gear or methods. The greatest difficulty in quantifying differences between trawl surveys is to account for potential bias due to variations in gear technology, the effects of which are difficult to estimate. Accounting for technological improvements over time requires a continuous record of catch rates across gear changes and from a spatially-explicit area (e.g. Engelhard 2008). Without the necessary records to account for gear performance, an investigation of catch rates over time requires careful standardisation of gear and methods to keep the fishing power constant.

Revisiting historical survey sites and measuring the changes that have taken place by repeat surveys is not an unusual experiment in ecology (e.g. Dolman and Sutherland 1992; Simkanin et al. 2005). There are only a few cases, however, where it has been performed in the logistically difficult and costly realm of marine trawl surveys.

One such example is that by McHugh et al. (2011), who revisited two sites off the south-east coast of England that had been surveyed during 1913-1922 and repeated trawl surveys in 2008-2009. They used an otter trawl that was of the same size and similar mesh to that of the historical gear. Contrasting the two periods, they investigated changes in community composition and size frequencies of trawl-caught fish. In another example, Andrew et al. (1997) and Graham et al. (2001) report on a 1996/1997 re-survey of the upper continental slope trawling grounds off New South Wales in Australia, 20 years after they were surveyed using the same vessel and similar gear during early stages of commercial exploitation.

In South Africa, detailed descriptions of the Pieter Faure trawl gear in historical government reports is unfortunately lacking. In reference to the 'large otter trawl' employed, Gilchrist mentioned that “The outfit of the boat consists of an otter trawl of the latest pattern with all accessories...” (Department of Agriculture 1898); “The 'spread' or breadth while working of the trawls and dredges are to be taken into consideration in estimation of the relative abundance of animals caught. In the case of the large otter trawl this was about 80 feet...” (Department of Agriculture 1899).

The interest to investigate long-term change in the demersal fish community by repeating the historical trawl surveys led to the obvious question: can one replicate the gear and imitate fishing methods used in these historical trawl surveys, to the point of confidently assigning differences in survey results to changes in the trawl community? The objective of this chapter was to collate the information required to re-build trawl gear of identical size and shape, and which would functionally replicate the catching power and selectivity of the otter trawl used on the Pieter Faure. Accomplishing this would enable the repeat surveys necessary for the assessment of long-term changes in the fish assemblage (Chapter 3) and abundances (Chapter 4). Because similar equipment was used widely (Garstang 1905; Anon 1908; Department of Trade and Customs 1909; Hjort 1914), results should be of interest to investigators studying historical trawl records and past fishing power across the world.

Methods

A review of the literature containing information on past trawling practices was conducted to develop a detailed plan of the historical otter trawl (including gear design, materials, construction and trawling methods). Additional site- and vessel-specific information was obtained from maps and photographs, the methods of which are described below. The photographs were scanned from prints and photographic slides housed by the Department of Agriculture, Forestry and Fisheries (DAFF) Communications Archive Photo Library, Cape Town, South Africa.

To support calculation of historical towing speeds, trawl tracks were examined on maps scanned from the government reports that detailed the trawl survey results (Department of Agriculture 1899). The digital images were geo-referenced using a second order polynomial transformation applied in QGIS (Quantum GIS Development Team, 2014). As coordinates were not included on these maps, prominent landmarks, such as headlands, river mouths or islets were used as control points (a minimum of four per map) and the correct coordinates estimated from a high resolution outline of the South African coastline projected in the World Geodetic System (WGS84). Once the maps were saved as geo-referenced raster images, they were re-projected in the South African Coordinate Reference System, choosing an appropriate reference longitude zone (e.g. 23° E for the Mossel Bay area). The distances of individual trawl tracks were then measured using the distance measure tool in QGIS. Finally the mean speed of tracks was calculated as the distance divided by the duration of the trawl. This process was applied to 12 tracks for which chart tracks and trawl durations were available.

To measure the dimensions of gear components from historical photographs, the images were scaled using three-dimensional (3D) modelling software, Sketchup Make (version 14, 2014). The software allows one to align axes of three orthogonal dimensions with those of an object in a photograph, typically to reconstruct a 3D model of the object. After aligning the dimensions, a known distance/length in the photograph is used to scale the model (image). Since the length of the vessel was known, a correctly-scaled vertical surface could be fit along the centre-line of the vessel. The known vessel width was then used to adjust for the difference in depth between the centre line and the outer edge of the vessel where the trawl boards are attached (assuming that the boards were attached near the widest part of the ship). Following these procedures, the otter boards on the side of the vessel were approximately correctly scaled and their dimensions were measured using the tape-measure tool in Sketchup.

The mesh sizes of the net's cod-end were measured off a photograph, having scaled the image with the approximate heights of crew members in the photograph. Once it was scaled, 10 independent cod-end meshes on the surface of the net facing the photographer were selected. Each of the four sides was measured providing a total of 40 measurements. Although a second photograph of the same cod-end was available (Appendix), it was not used because the legs of the crew members were not included, making it difficult to scale the picture.

The difficulty in applying this method to photographs of (or on) a ship, was the lack of visible edges that represent truly orthogonal lines, which are required to define the dimensions e.g. parallel to the length and width of the vessel. The height of crew members on deck, along with other visible items such as the life-ring, provided diagnostic features to assess whether the vessel and her objects were being (approximately) correctly scaled. Once the heights of the crew members were congruent with the average height of men born in Great Britain between 1860 and 1880 (165-170 cm; Hatton 2013), and the life-ring measured a similar height and width (i.e. was projected to be round), the measured dimensions of the otter boards were deemed to be close to reality.

Results and Discussion

Development of the early otter trawl

Beam trawling was a precursor to otter trawling. The use of beam trawls on sailing smacks (traditional fishing boats) was widespread by the early 1800s and developed rapidly throughout Britain in the 19th century (Robinson 2000; Engelhard 2008). Their fishing power was limited. Firstly, the sailing smacks were completely reliant on the weather (wind) to power their trawling activity. Secondly, the width of the net was limited by the length of beam that could safely be managed and stowed on board vessels (Heape 1887; Edwards 1909).

The swift adoption of steam power on trawl vessels in the late 1880s and early 1890s (Edwards 1909) released the fleets from their reliance on adequate winds and enhanced their fishing performance (Garstang 1900). Yet problems with handling the massive beams on board prevented them from building larger nets to take advantage of the excess power available from steam (Edwards 1909).

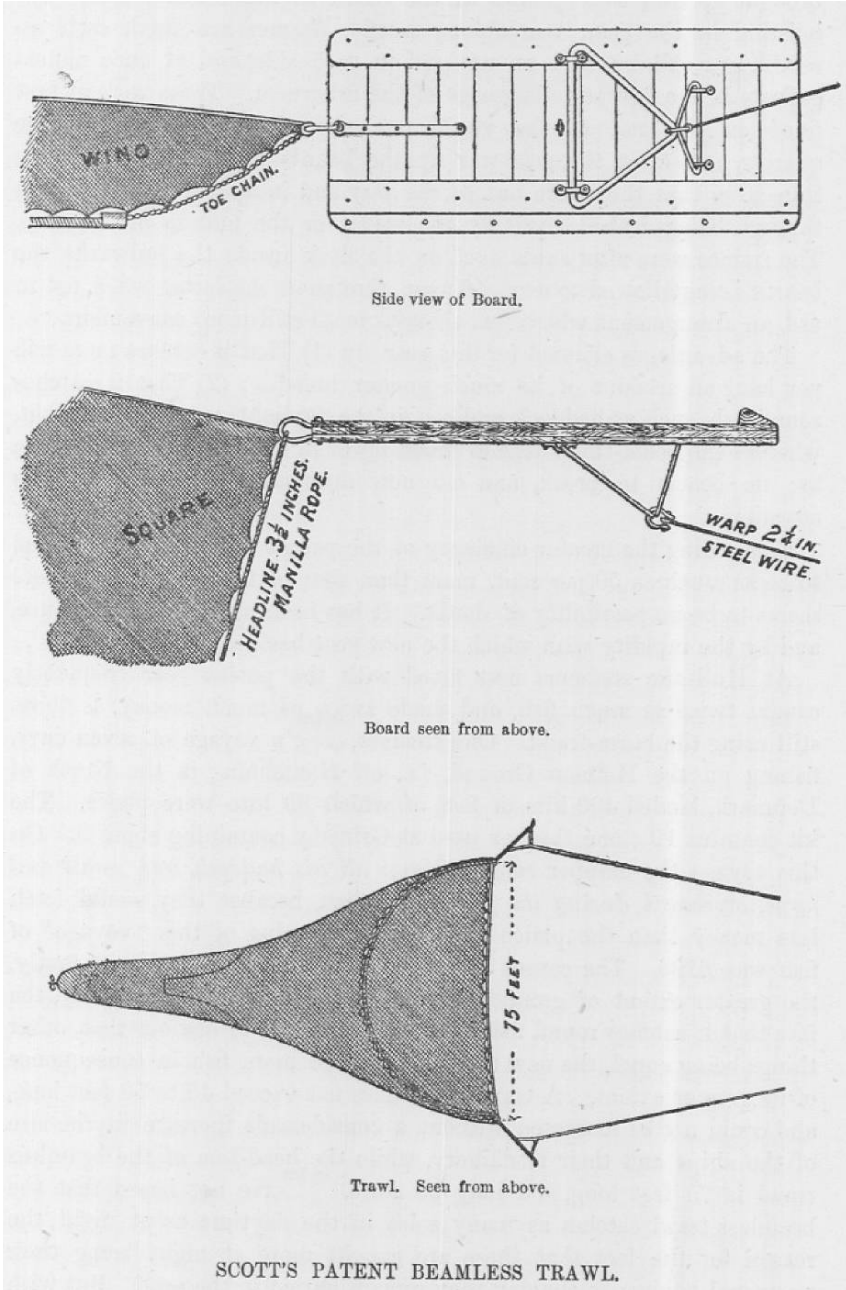


Figure 2. The original otter ('Granton') trawl gear as patented by Mr Scott of Granton in 1894. Adapted from Cunningham (1896).

In 1894 a new set of trawl devices were patented by a Mr Scott of Granton, Scotland, which circumvented the requirement of a beam (Cunningham 1896). Instead a set of rectangular 'otter boards' were used, which resembled a pair of underwater kites, standing upright on their edge and pulling the leading edges of the net outwards as they were towed through the water (Fig 2;

Cunningham 1896). Without a beam, the dimensions of the net could expand to match the towing power available to steam vessels.

The design of the first commercially employed “otter” or “granton” trawls were essentially beam trawl nets attached to otter boards (Fig 2; Cunningham 1896; Kyle 1903; Edwards 1909). One documented improvement was the addition of wings to the square of the net, in order to accommodate the backward curve of the headline when under tow. The addition was made within the first year or two after Scott's granton trawls were introduced (Fulton 1901; Davis 1927).

The greatly augmented catches made by otter trawls were so convincing that their use quickly spread throughout Britain's fishing ports and beyond. Many skippers applied the same concepts but avoided the patented parts and associated royalties (Cunningham 1896). The transformation from beam to otter trawls was so fast that by 1899, when Fulton (1901) wanted to compare the efficiency of beam and otter trawls in Scotland, he struggled to find a working beam trawl to use in his experiment.

The next major innovation in trawling gear took place in the early 1920s in France, with the introduction of Vigneron-Dahl gear, named after its inventors (Le Gall 1931; Hickling 1931). The critical modification was the addition of 'bridles' or 'sweeps', rope or cable extensions that separated the otter boards from the wings of the net. The mud plume and disruption caused by the otter boards and bridles greatly expand the effective width of the net by herding fish inwards toward the mouth. This strategy was highly effective for increasing catches of many 'roundfish' (fish other than flatfish), including cod and hake species (Hickling 1931; Margetts 1949) and quickly spread across the world.

Prior to the Vigneron-Dahl innovation, the design of otter trawls seems to have remained relatively consistent, even though trawlermen undoubtedly made small adjustments to their nets. Beyond the addition of wings, the most significant improvement in fishing power during the pre-Vigneron-Dahl era, was likely the progression in engine technology and greater power output, which allowed progressively larger trawl nets to be employed.

Steam engines and trawl speeds

Once the net sizes could expand beyond the limits set by the beam trawl, engine power became the limiting factor in the size of trawl nets used: larger catches could be made with bigger nets, but the drag of the net and trawl doors had to be kept within the towing power of the vessel.

Trawling speeds vary among different vessels and trawl gear, and the speed of a single vessel can change among substrate types or in varying conditions of weather or current (Dealteris et al. 1989).

Modern trawlers frequently attain speeds of 3-4 knots and faster while towing demersal trawls (Dahm et al. 2002; Weinberg 2003). Early steam trawlers were less powerful and slower towing speeds are recorded. Referring to beam trawls towed by steam vessels, M'Intosh (1895) stated the average speed to be 2.5 knots, though higher speeds were sometimes attained on muddy grounds. Fulton (1901) measured the speed on three otter trawlers in 1900 and calculated an average towing speed of 2.64 knots across the three vessels. Kyle (1903) reported the average speed of a towed otter trawl to be 2.5 knots and that of a beam trawl to be 2 knots. Taking measurements from 135 otter trawl hauls on the SS Huxley, which was a steam trawler of very similar engine and vessel size as the Pieter Faure, Garstang (1905) reported a towing speed range of 2 to 2.9 knots, with an average and mode of 2.30 knots. Thus towing speeds of steam trawlers during the Pieter Faure era typically seem to have ranged about 2-3 knots.

Historically, trawls were frequently towed on a curved or circular track. As a result, comparing start and end locations is not very informative to the calculation of towing speeds. Fortunately Gilchrist provided a handful of detailed maps on which he traced the trawl tracks of the Pieter Faure (Appendix A; Department of Agriculture 1899). Having geo-referenced these maps and measured 12 individual track distances, the mean and median speeds calculated were 2.62 and 2.65 knots respectively (interquartile range of 2.15-3.13 knots). The accuracy of the charted tracks is difficult to ascertain and may include a substantial level of error. However, a bias or error in charting accuracy will most likely add random error (noise) to the track measurements, rather than a systematic bias. This assumption is supported by the fact that the estimated figures are congruent with speeds reported from the literature above. Therefore an average towing speed of 2.62 knots ($1.35\ m\cdot s^{-1}$) will be assumed for the Pieter Faure trawl surveys, but analyses using standardized catch rates will consider the sensitivity of results to using the quartile figures of 2.15 and 3.13 knots.

Net design

The shape, fishing power and selectivity of the net are governed by an interplay of multiple factors. Several components that make up the gear and influence its performance are discussed in separate sections below. However the general shape and behaviour of the net will additionally be affected by the dimensions of the various panels from which it is constructed and the way in which they are connected (to provide slack/taut sections of netting when under tow).

In the absence of design plans for the trawl used on the Pieter Faure, the best alternative was to investigate the designs of trawls from the same era and region. Net plans – design drawings that provide details on the number of meshes and shapes of various panels making up the net – were not found from the initial years of otter trawling. The earliest detailed description and plans of an otter trawl could be located were those of a 'commercial trawl net' by Kyle (1903); Fig 3). It is the same net outlined by Garstang (1905) and used in 1902-1903 surveys on the British research vessel, the SS Huxley.

Unlike modern gear, this historical net included a type of non-return valve ahead of the cod-end, intended to prevent fish from escaping once they were in the cod-end. It consisted of a funnel created by blind-ending pockets laced between the upper and lower surfaces of the net, as well as a loose piece of netting that acted as a lid, called the 'flapper' (Fig 3; Kyle 1903; Garner 1956). The flapper and pockets were present in beam trawls in the 19th century (Holdsworth 1874) and their use continued decades into the era of otter trawling (Davis 1927; Garner 1956).

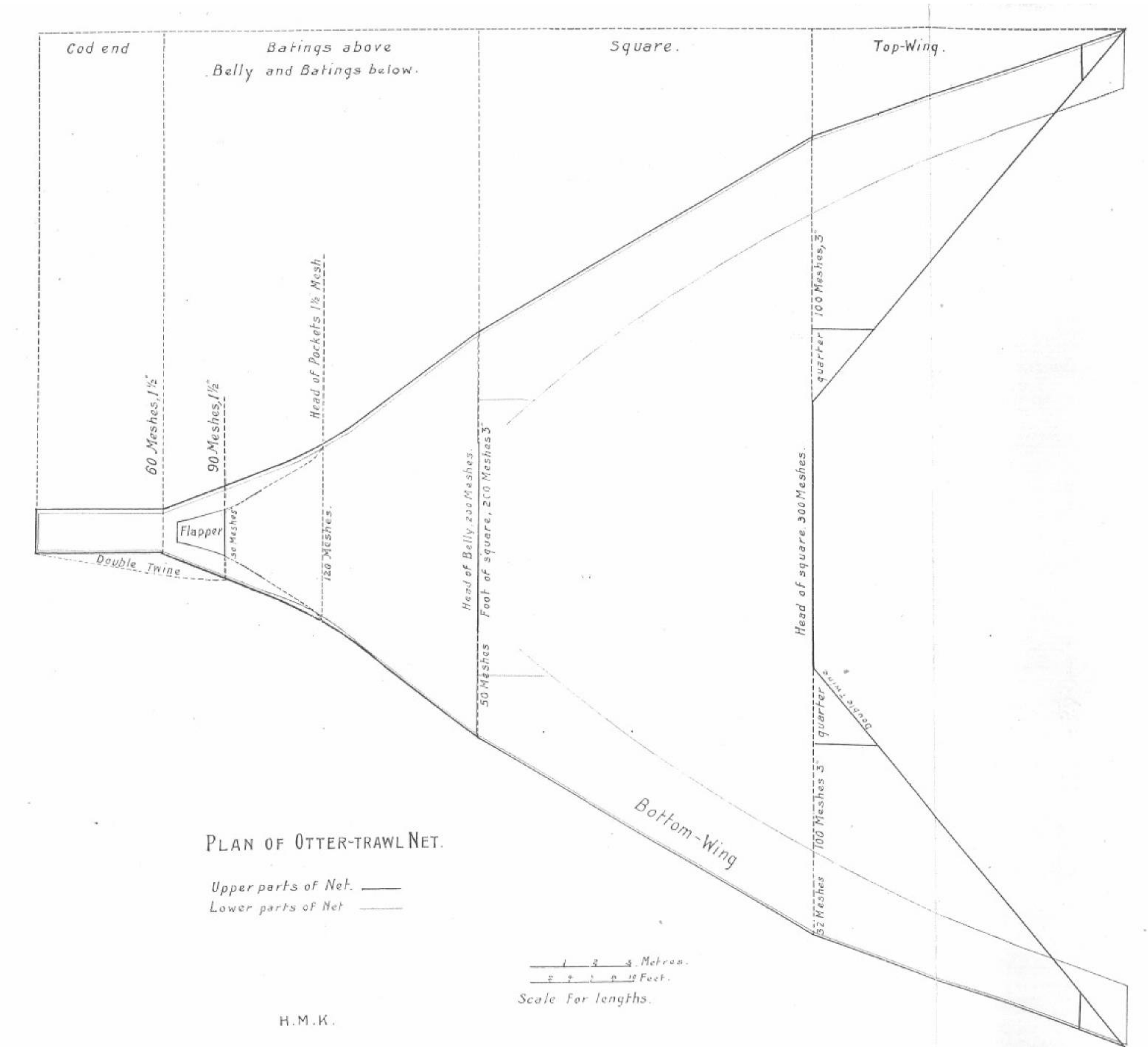


Figure 3. Trawl net plans from Kyle (1903).

A feature of the old nets that is still in use today, is the inclusion of an extra barrier on the underside of the cod-end, to protect the netting from wear as it drags over the sea floor. These 'chafers' or 'rubbers' historically consisted of overlapping sections of old net material (Holdsworth 1874; Kyle 1903). The loose pieces of chafer netting are visible in the photographs of the Pieter Faure cod-end (Fig 4 and Appendix A). Also visible in the same pictures are the ropes that form the belly lines, which are the seams along which the top and bottom halves of the trawl net are laced together (Garner 1956). The photographs indicate these belly lines to be substantially thicker than the 16 mm diameter suggested by Kyle (1903; 2-inch circumference) and instead a 28 mm Manila rope was laced into the net seam.

How much trawl technology might have evolved between the time that the Pieter Faure sailed with her crew from Glasgow in 1897, and 1902/1903, when Kyle (1903) wrote his paper and the SS Huxley was fitted with the net specified in those plans (Garstang 1905), is unknown. The addition of wings took place before this period (Fulton 1901; Davis 1927). Other than that, the literature does not record significant changes in net design prior to the 1920s introduction of Vigneron-Dahl gear (Hickling 1931). Kyle (1903) points out that the industry was in a learning phase and that skippers were constantly innovating small improvements or adjustments. As such, trawl gear of 1902 could have included slight advancements over the net technology brought to South Africa in 1897, but the nature of such improvements are not documented.

Figure 4. A deck scene from the Pieter Faure, showing the full cod-end of the trawl. Mesh sizes and twine thickness were estimated from this photograph.

Nonetheless, the net used on the Pieter Fauretrawl duration and charted tracks were available) were used for the calculation of trawl speeds. I have added two sentences to the discussion of trawl speeds summarising the above reasoning, stating that although we cannot account for or estimate the lack of accuracy of the historical chart tracks, we assume that any errors were likely randomly distributed around the true track lengths and that the mean speed calculated from several tracks is expected to provide an unbiased estimate of the true speed.

must have been very similar to that described by Kyle (1903) and employed on the SS Huxley. The reconstruction of the Pieter Faure net will therefore follow the plans provided by Kyle (1903), adjusting specific components according to the details gleaned from photographs of, and on board, the vessel. The dimensions of various components making up the trawl are discussed further below.

Net materials

In the United Kingdom (UK), the use of hemp (*Cannabis sativa*) twine to construct large trawl nets was largely replaced by the use of Manila hemp (*Musa textilis*) during the latter parts of the 19th century (Kyle 1903; Edwards 1909). Manila was in turn replaced with hardier synthetic twines in the mid 20th century. Materials currently in common use to construct trawl nets in South Africa include polyethylene, polyamide (nylon), polyester and mixtures of these (Jacobsz, personal communication 2014).

Different twines will frequently result in different selectivity factors, believed to be due to properties such as the flexibility (Clark and Jensen 1963; McCracken 1963; Lowry and Robertson 1996) and the extensibility (elasticity) of the fibre used to construct the net (Clark and Fritz 1963; von Brandt 1963). In addition, the specific gravity likely affects the behaviour (and therefore fishing performance) of different net twines, as it will influence the buoyancy of the net panels, thereby the shape of the net and its contact with the sea floor.

Beyond the twine material, its thickness also plays a significant role in the selectivity of a net (Sala et al. 2007). Thicker twines have been shown to have a lower selectivity (retain more fish), likely as a result of less flexibility allowing fewer fish to escape (Lowry and Robertson 1996; Sala et al. 2007; Graham et al. 2009). The twine diameter of the Pieter Faure net was estimated from photographs, as reported in the Mesh section below.

As sufficient Manila rope was not locally available, some parts of the net had to be made from a synthetic alternative. The back end of the net, where most of the selectivity is expected to act (Graham et al. 2009), was prioritised for manufacture from the obtainable Manila rope. The fore-parts of the net, including the belly, square and wings were instead braided from a synthetic polyethylene-polyester alternative.

Unlike the remaining synthetic twines used in trawl nets, which have lower specific gravities in water, polyester has the same as that of Manila (1.38; Appendix A). However polyester fibres are soft compared to the relatively stiff fibres of Manila. Polyethylene fibres produce a far stiffer rope, similar to that of Manila, yet they have a low specific gravity (0.95) and float in water, unlike the heavier polyester (and Manila). Therefore polyethylene and polyester were combined in equal proportions to produce a synthetic rope that was similar in its flexibility and specific gravity to Manila.

In historical trawl construction, the Manila twines were treated with tar to reduce the ingress of sediment, absorption of water and improve their lifespan (Kyle 1903; Davis 1927). The synthetic ropes do not require tarring, however the addition of tar also affects the stiffness of the rope and the specific gravity (as it is lower than that of Manila). As such, the mixed synthetic rope and the Manila were soaked in a bitumen solution (bitumen and petroleum solvent), in order to simulate the effects of the historical tarring process.

Headline

Trawl headlines in Britain were predominantly made of Manila for several decades, starting in the late 1800s (Cunningham 1896; Garner 1956). The diameter of ropes used was typically between 24 and 32 mm (3 and 4 inch circumference respectively; Cunningham 1896; Kyle 1903; Davis 1927; Garner 1956). The headlines were 'marled' (connected) directly to the square and wing meshes (Kyle 1903; Davis 1927) as shown in Fig 5a, which is consistent with the parts of headline visible in Fig 6. Using the scaled photograph (Fig 6), the Pieter Faure headline is estimated to be about 30 mm in diameter, although an accurate measure is precluded by the resolution of the image. Kyle (1903) suggests that headlines varied between 24.3-28.3 mm (3 to 3.5 inches circumference), thus a Manila rope of 28 mm diameter was chosen to make up the headline of the reconstructed net.

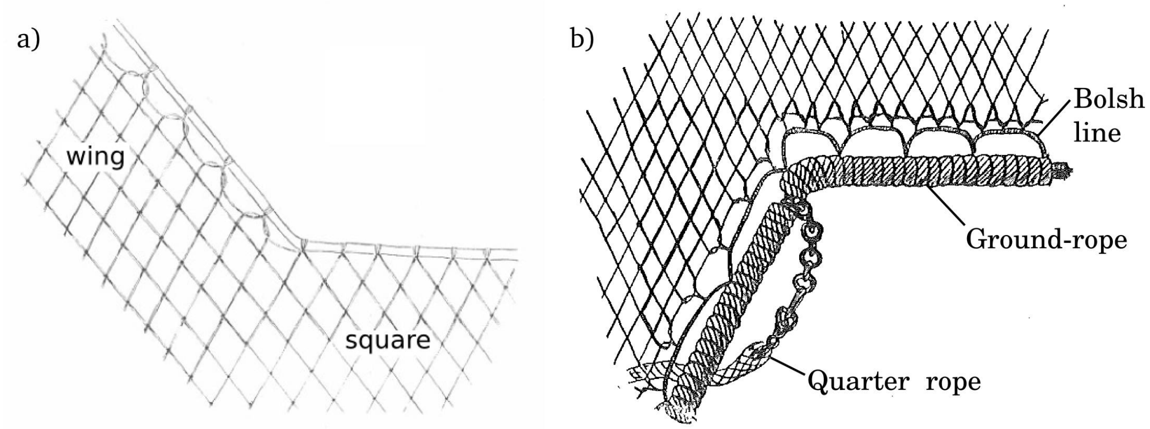


Figure 5. Drawings depicting the method of attachments between net meshes and a) the headline (adapted from Kyle, 1903), and b) the ground-rope, via a bolsh line (Davis, 1927).

Cunningham (1896) reports that Mr Scott's early otter trawls had a headline length of 22.9 m (75 ft). As trawling and steam engine technology progressed, the size of trawl nets increased. Commercial trawlers in Scotland were using headline lengths of up to 42.7 m by 1900 (140 ft; Fulton 1901), yet shorter lengths of between 27.4 and 30.5 m were common well into the 20th century (Todd 1911; Davis 1927).

Even though Gilchrist did not specify the headline length of the Pieter Faure net, he did appreciate the importance of keeping the size of the trawl consistent for comparative purposes and stated that the width of the mouth was 'about 80 feet' (24.4 m; Department of Agriculture 1899). Unfortunately we do not know what assumptions he made when making this statement. The drawing included in the 1898 report (Fig 7) suggests that he was aware that the headline curved backwards while trawling. At the time, however, neither Gilchrist nor his colleagues (nor trawlermen) in Britain appreciated how greatly the headline curved, reducing the width between the wings of a net. Only after Fulton (1901) conducted experiments to answer this question, did scientists (and fishermen) learn that the operational width of otter trawl nets was roughly half the width of the headline length. Without this knowledge, Gilchrist certainly and unwittingly overestimated the width of his net.

Fulton (1901) reported that net-makers allowed for one-third of the headline length to form a curve between doors. If Gilchrist based his estimate of a 24.4 m mouth width in 1898, on the same knowledge that the net-makers of Scotland had in 1901, it would imply a 36.6 m (120 ft) headline, which serves as an upper bound to what the size of the trawl might have been. Assuming that Gilchrist expected a reduction between headline length and mouth width of at least 10%, a lower bound estimate of the headline is 26.8 m. Based on the above reasoning I am confident that the headline length of the Pieter Faure trawl was between 26.8 and 36.6 m (88 and 120 ft respectively).

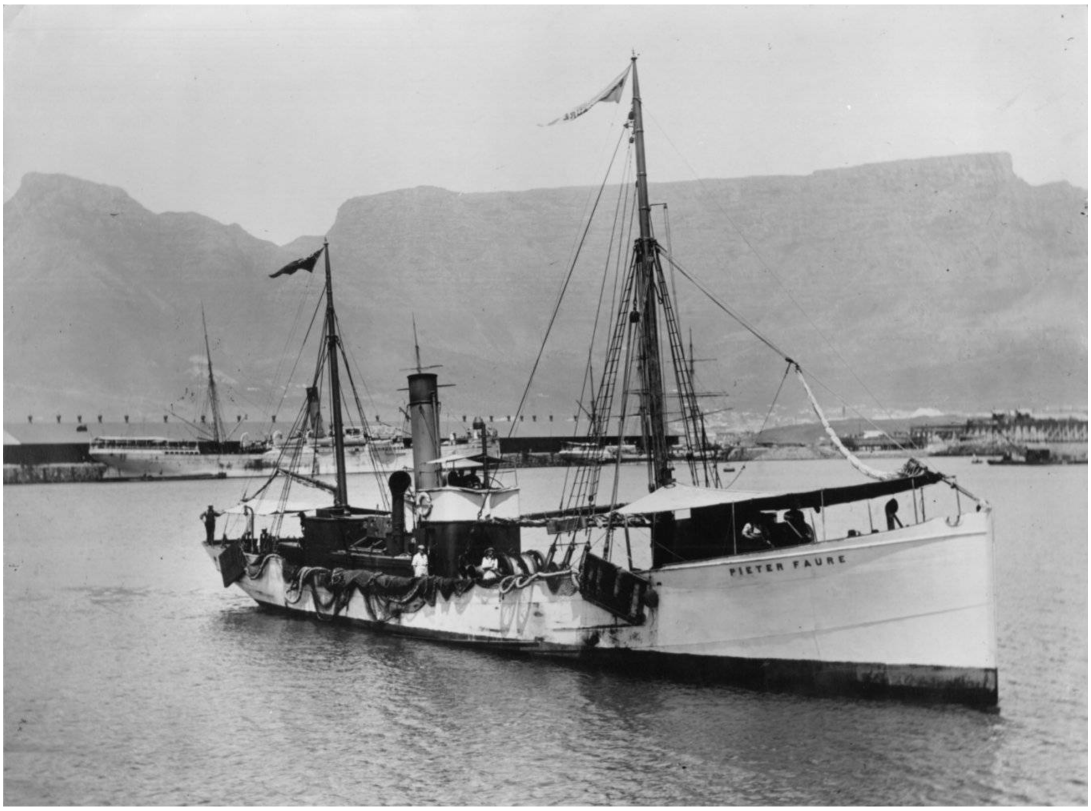


Figure 6. Photograph of the Pieter Faure steaming out of Table Bay in Cape Town. The date is unknown, however some of the crew visible can be matched to another photograph (Fig. 8) that includes John Gilchrist on deck, suggesting that this suite of photographs was taken between 1897 and 1906. DAFF Communications Archive Photo Library.

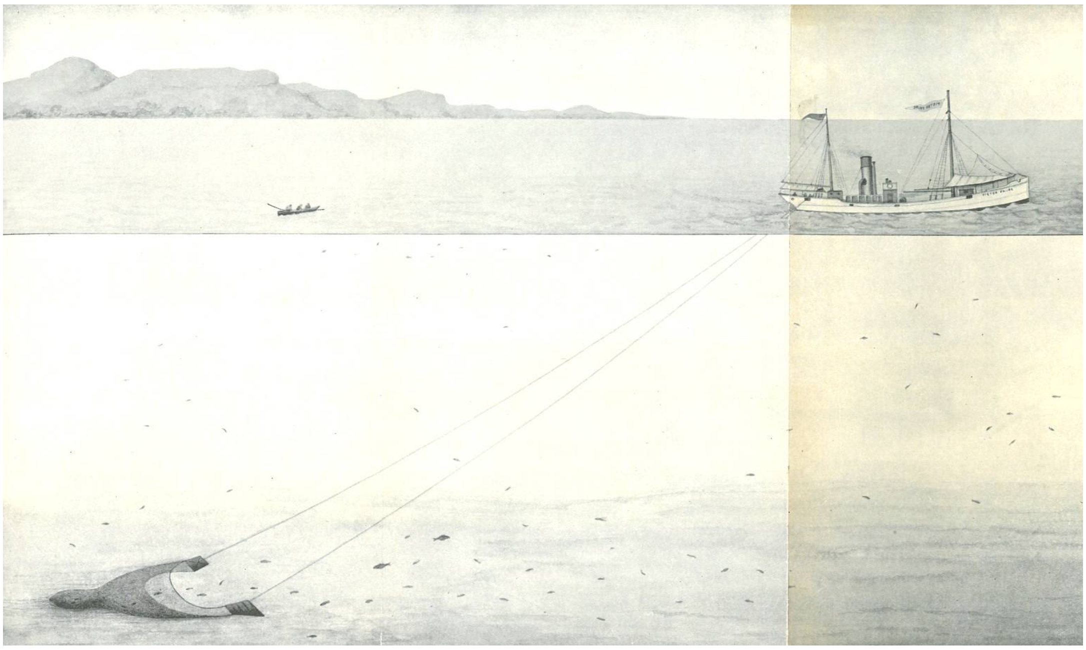


Figure 7. Drawing of the Pieter Faure towing its trawl gear (Department of Agriculture, 1899).

The sizes of nets used by steam trawlers generally grew with the power output of the vessels, as greater power allowed the towing of larger and heavier gear (Fulton 1901; Edwards 1909). As a result, it is informative to investigate the net sizes used on vessels of similar size and engine power as the Pieter Faure. Unfortunately net details are not available for many vessels from the same era. The SS Huxley was a similar size to the Pieter Faure (115.7 ft and 206 gross tons versus 115 ft and 176 gross tons respectively) and both had a similar-sized triple-expansion steam engine (52 nominal Hp versus 50 nominal Hp respectively). The otter trawl used on the Huxley in 1902/1903 was like that described by Kyle (1903) and had a headline that was 90 ft (27.4 m) long (Garstang 1905).

In 1914, the Australian Fisheries Inquiry Officer ordered three new 'deep sea trawlers' from Middlesbrough-on-Tees in the UK (Jacobsen 2010). Two of these vessels (the SS Koraaga and SS Gunundaal) were sister ships and were the same length as the Pieter Faure, but had a heavier gross tonnage of 220 tons. They also had triple-expansion steam engines, the size or power of which does not seem to be recorded, although they would certainly have been as, or more, powerful than those fitted to the Pieter Faure almost 20 years before. The otter trawls on these two vessels had headline lengths of 90 ft (Jacobsen 2010). The fact that slightly larger (and stronger) vessels used otter trawls with a headline length of 90 ft (27.4 m), provides compelling weight to the argument that the Pieter Faure would not have been using a net (much) larger than this.

The longer headlines reported by Fulton (1901) were likely fished from vessels bigger and more powerful than the Pieter Faure. Larger steam trawlers were already in use by 1895: M'Intosh (1895) reported that modern steam trawlers in Scotland at that time were up to 36.6 m 'between the perpendiculars', which implies a total length notably greater than the 30.1-m Pieter Faure built two years later. He also mentions that the engine sizes ranged up to 65 nominal Hp, whereas that of the Pieter Faure was 50 nominal Hp.

For the reconstruction of the trawl gear, the Pieter Faure headline is assumed to have been a Manila rope of 27.4 m (90 ft) length and 28 mm diameter. The sensitivity of the comparative results, which use net-width in the swept-area standardisation of catches, will be investigated using a headline range of 26.8-36.6 m (88-120 ft).

Ground-rope

The ground-rope used on the Pieter Faure is partly visible on the photograph of the vessel (Fig 6). As might be expected from the fact that Gilchrist targeted soft trawl grounds throughout the Pieter Faure surveys, the ground-rope did not include bobbins or chains that were experimented with on hard grounds in the UK (M'Intosh 1895). The standard ground-rope consisted of old wire warp, 16 to 24 mm in diameter (2.5 to 3 inch circumference), covered with old netting material and then rounded with a Manila rope to a diameter of 81 to 97 mm (circumference of 10 to 12 inches; Kyle 1903; Davis 1927). This description is consistent with the ground-rope visible on the picture of the Pieter Faure, the diameter of which is estimated to be about 100 mm from the photograph (Fig 6). Frequently the ground-rope was made of three sections, a bosom of about 6.1 m (20 ft) in the middle and a wing section either side (Kyle 1903; Davis 1927). The ends of the ground-rope on the Pieter Faure look identical to the more central parts visible in the photo (Fig 6), suggesting a uniform ground-rope throughout.

The method of attachment between ground-rope and net (belly and wings) followed on from the traditions of beam trawls. A bolsh-line was used to connect the meshes of the net to the foot-rope, as in Fig 5b (Kyle 1903; Davis 1927). The larger gaps between the bolsh-line and ground-rope (compared to the net mesh) are clearly visible in the shadow cast on the side of the vessel in Fig 6.

Although Gilchrist did not specify the length of the ground-rope, a commonly used commercial trawl at the turn of the century and early 1900s was one with a 27.4 m (90 ft) headline and a 38.1 m (125 ft) ground-rope (Kyle 1903; Garstang 1905; Davis 1927). Ground-ropes of 36.6 m (120 ft) or slightly longer seem to have been common even with earlier and smaller (width) beam (M'Intosh 1895) and otter trawls (Cunningham 1896).

As per the trawl plan by Kyle (1903), a 38.1 m (125 ft) ground-rope was constructed, using a 20 mm fibre-core cable, rounded with 10 mm diameter tarred Manila rope (in place of old Manila netting) and then served with a 28 mm Manila rope. The result was a ~96 mm diameter ground-rope that should be very similar to those used historically on soft grounds.

Mesh size

Alward (1932) reports that fishermen had historically braided nets at sea, using finger-widths to measure the meshes, starting with two fingers at the cod-end, increasing to three, four and five fingers towards the mouth of the net. When nets were later made ashore, often by women who had smaller fingers, standard wooden gauges known as 'spools' were introduced to standardise mesh sizes (Alward 1932). There has been some variation in the way different authors (and fishermen) have referred to mesh sizes, causing potential confusion. The modern convention (in South Africa and many other countries) is to describe the length between opposite knots of a longitudinally stretched mesh. Because it is of importance to fisheries regulations, this measure usually applies to the distance within the mesh, excluding the knots. At the turn of the 20th century, mesh regulations were generally not a concern and meshes were measured between the centres of knots. There was variability, however, in the number of sides included in the measurement (Davis 1927). For example, a '4-inch mesh' could refer to one that was four inches between opposite knots when fully stretched longitudinally (similar to today's convention), or it could imply a mesh of which a single side was four inches (thus eight inches stretched longitudinally), or less frequently, it could even refer to the circumference of a mesh where each side between adjacent knots measured one inch. Fortunately some authors specified which measure they were using, by calling it 3-inch 'bar' for example (Davis 1927), or '3-inch square' (Holt 1895), both of which specify that the length referred to one side between adjacent knots.

Where quoted measurements can be interpreted with certainty in the historical literature, the most commonly referenced cod-end mesh size used in both beam and otter trawls of the United Kingdom, seems to be 76 mm (3 inches or 1.5 inches “bar”; Holdsworth 1874; Heape 1887; Holt 1895; M’Intosh 1895; Kyle 1903; Aflalo 1904; Davis 1927; Alward 1932; March 1953). There is however, some variability around this figure: Alward (1932) suggests that cod-end meshes varied between 76 and 127 mm (1.5 and 2.5 inches 'bar'), whereas Holt (1895) mentions that some cod-end meshes could be as small as 38 mm (0.75 inch 'bar'). Fulton (1901) reported that some cod-ends had meshes of 64 mm (1.25 inch 'bar') and in reference to the period of 1906-1908, Todd (1911) claims that cod-end meshes were about 70 mm (a knot-to-knot length of 35 mm).

Photographs of the Pieter Faure cod-end exist, from which an estimate of the mesh size was made (Fig 4). The mean length between adjacent knots was estimated to be 48 mm (± 0.6 mm SE), which implies a ~96 mm 'stretched' mesh between opposing knots. The diameter of the twine estimated from the same scaled photograph was 6 mm. As the exact location of men standing in the photograph (relative to the surface of the net) and their true height is not known, a level of unquantified uncertainty remains around the scaling of the photograph and these estimates. Nonetheless the historical photographs provide valuable evidence to ensure that gear dimensions are within a close degree to those originally used on the Pieter Faure.

The image in Fig 4 also suggests that the cod-end meshes were made from a single twine, even though some authors report that cod-ends were frequently braided with double twine (Kyle 1903; Todd 1911; Davis 1927; Garner 1956). Based on the evidence from the plan by Kyle (1903) and the photograph in Fig 4, a 6 mm single (Manila) rope was used for the cod-end and extension piece ahead of it. A 5-mm single (synthetic) rope was used for belly number 2 and 4-mm single (synthetic) rope was used in the remaining parts of the net. The mesh sizes were braided as 100 mm between opposing knots for the cod-end and extension piece, whereas the remainder of the net was made of 150 mm stretched meshes, to imitate the plan by Kyle (1903).

Otter boards

The otter boards used historically were flat, rectangular wooden boards, attached to a heavy metal 'shoe' or brace. The initial patented doors introduced by Mr Scott measured 3.66 by 1.52 m (12 by 5 ft) according to M'Intosh (1895) or 3.05 by 1.37 m (10 by 4.5 ft) according to Cunningham (1896), consisted of heavy timber framed with steel and had a ring extending from the back end to which both headline and foot-rope were connected (Fig 2). Also part of the patent were stout triangular metal brackets to which the trawl warps were shackled (Fig 2). Similar designs that avoided the patented parts quickly developed as the concept of otter trawling spread rapidly across the UK, supported by enhanced catches compared to those of beam trawling (Fulton 1901). The triangular brackets persisted, although some fishermen used a set of four chains attached closer to the corners of the trawl doors to avoid Scott's patent (Cunningham 1896; Kyle 1903). The ring at the back of the board was soon discarded and instead the headline and ground-rope were shackled separately to the back edge of the board (Kyle 1903; Gibbs 1922).

The dimensions and weights of otter doors documented by authors during the period relevant to this investigation are listed in Table 1. The sizes of boards varied substantially, though this is perhaps not surprising as the board size had to be matched to the vessel power and net size (Jenkins 1920; Graham 1956). Fortunately the otter boards used on the Pieter Faure are clearly visible in Fig 6 and their dimensions can be estimated by scaling the photograph to the known length of the ship. By doing so, the otter boards were estimated to have a length, height and thickness of 2.42, 1.48 and 0.07 m respectively.

Table 1. Dimensions and weights of otter trawl doors as reported in historical literature from the period relevant to the Pieter Faure era.

Length (m)	**Height (m)**	**Thickness (cm)**	**Weight (kg)**	**Period**	**Reference**
3.05	1.37			1894	Cunningham (1896)
1.83-2.43	1.22			1895/1896	Cunningham (1896)
3.66	1.524			1895	M'Intosh (1895)
3.05-3.20	1.22-1.37			1901	Fulton (1901)
2.74-3.05	1.35-1.37	10.2-12.7	457	1900s	Kyle (1903)
3.05	1.52	7.6-10.2		1900s	Aflalo (1904)
2.44	1.3	6.4		1902	Garstang (1905)
2.44-3.05	1.22-1.52		363-454	1900s	Edwards (1909)
2.44-3.05	1.22-1.52		363-454	1910s	Jenkins (1920)
3.35	1.37		762	1920	Gibbs (1922)

Kyle (1903) reports that there were “three transverse iron bars running across the otherwise smooth front face and bolted through to similar bars on the back” in reference to the trawl doors which employed the patent triangle brackets. He also mentions that the designs using a chain setup instead of the solid brackets, frequently had two long iron bars placed diagonally across the board. The available photograph (Fig 6) shows three transverse bars on the Pieter Faure doors, indicating that they used the patent triangle brackets. Also visible on this photo is confirmation that the headline and ground-rope were shackled separately to the hind edge of the trawl doors.

The angle of attack (between the line of forward motion and the vertical plane of the board) is an important setting for the effectiveness and efficiency of otter doors (Garner 1956; FAO 1974). The point of attachment to the triangular brackets (which influences the angle of attack) is reported to have been about one-third of the length of the board from its front edge (Kyle 1903; Jenkins 1920). The historical angle of attack is quoted to be about 20 degrees (Edwards 1909; Jenkins 1920), although it seems the latter author was reproducing information from the former. More recent literature suggests that the angle of attack used with rectangular flat otter boards is between 35 and 50 degrees, even though the maximum spreading force for such boards is estimated to be at angles less than 30 degrees and their maximum efficiency at even lower angles (FAO 1974; Patterson and Watts 1986).

Flat otter boards were built, taking the above dimensions, angles and weight into account. Imperfect knowledge of the trawl doors on the Pieter Faure, together with the limits of modern components, materials and labour costs, meant that doors were built to be of similar dimensions, weight and functionality compared to the doors visible on the Pieter Faure (Fig 6), yet did not seek to replicate the doors in their materials and structure. Adjustable triangular brackets were created, which will allow modifications of both the angle of attack and the heel angle of the otter boards, should these be found necessary during gear trials. Drawings of the trawl doors that were built for the repeat surveys are shown provided in Appendix B.

Warps

The trawl warps used on the Pieter Faure (and elsewhere) in the late 19th and early 20th century were steel cables similar to fibre-core cables employed today. The cables are captured in photos taken on the deck of the vessel (Fig 8) and are estimated to have a diameter of 17-18 mm, which is close to the thickness of 18.2 mm (2.25 inch circumference) recorded by Cunningham (1896). The diameter of steel warps typically used on current inshore trawlers in South Africa vary between about 14 and 22 mm thick (Less, personal communication 2014). One might expect trawl warps made of different material, or with a drastically different diameter, to behave differently in water (and thereby influence the action of the trawl; Crewe 1964). However slight differences in properties between the wire cables of a century ago and those used now is not expected to have a discernible influence on the shape or efficiency of the trawl.

Figure 8. Deck scene on the Pieter Faure, showing John Gilchrist (front right) and crew taking a break while the trawl is under tow. DAFF Communications Archive Photo Library.

Operation of historical side-trawls

The salient points of shooting and hauling the trawl on a steam-powered side trawler, such as the Pieter Faure, are briefly described below. Edwards (1909), Davis (1927) and Graham (1956) provide greater detail on these gear operations and are the sources from which the below description was gathered. The navigational and fishing operations were completed without any of the electronic devices in use today, but steam-driven winches were employed. The entire process took place off the side of the trawler rather than the stern as in most modern vessels.

Once a decision had been made to shoot the trawl, the ship was brought to a standstill with the trawl doors facing into the wind, so that once the net was released into the water, the vessel would drift away from it. The doors were put over the side and lowered several metres below the surface. Next the net was thrown into the water, first the cod-end, followed by the rest of the net. The ground-rope was put over the side and lastly the headline was released. If the net and boards looked like they were clear and correctly aligned, the engines would be put full speed ahead with the vessel turning in a wide circle towards the side that the trawl was shot (to keep the net clear of the propeller). As the ship picked up speed, the warps were paid out at a rate that kept sufficient tension to spread the trawl doors and avoid fouling the net. Once the correct amount of warp was paid out, the vessel slowed to its towing speed (2-3 knots). The fore (front) warp was pulled in towards the aft (back) warp and side of the vessel, using a messenger wire and winch, where they were both locked into a towing block. In Fig 8, the two warps are locked into the towing block and can be seen leaving the side of the vessel. Markers on the warps are also visible in the picture, which were spaced at set intervals to help ensure that the lengths of warps could easily be aligned.

As with shooting the trawl, the net had to be hauled on the windward side of the vessel. The towing block was knocked open, which released the fore warp. The engine was set to 'dead slow' and the pull on the fore warp turned the vessel side-on to the trailing trawl net. The warps were then wound up by the winch until the trawl doors arrived at the 'gallows', where they were secured. The quarter ropes (ropes on the outside of the net that connected the middle of the ground-rope to the trawl doors) were loosened from the doors and passed to a winch, which brought in the ground-rope. Once the ground-rope was on board, the remainder of the net was pulled in over the side by hand, until the cod-end was reached. A special rope, called a becket, would be looped around the cod-end, and lifted by winch power to heave the cod-end over the side and suspend it above the deck, before it was untied to release the catch.

The historical trawls were typically of multiple (usually 2-4) hours duration (e.g. Department of Agriculture 1904). They could be towed along a straight course if the fishing grounds were known to be clear. In un-chartered grounds, the vessel often towed in a circle or curve, trying to remain near points that had been sounded beforehand and found to consist of soft ground.

Trawlermen historically let out their warps to roughly three times the depth of water, though this ratio was increased in shallower waters and could be less in deeper waters (Gibbs 1922; Davis 1927). This is the same approach used by current trawl skippers (Less, personal communication 2014).

Conclusion

The compilation of information gleaned from different historical sources, including literature, photographs, maps and government reports, demonstrates the feasibility of imitating the trawl gear and trawling methods that were used on the Pieter Faure over a century ago. In addition to these sources, significant input was received via personal communication with individuals working in the trawl and associated industries, underlining the benefits of stakeholder involvement in fisheries research. From the evidence and reasoning presented in this chapter, the component details and plans for a complete trawl net and trawl doors are summarised in Appendix B.

Not all details of the historical gear could be resolved. Some uncertainties remain and certain assumptions are necessary. The headline length of the net and the trawling speed of the vessel are considered amongst the most important factors in the standardisation of historical catches and swept-area analyses will need to consider uncertainty in their values. Plausible bounds of these variables have been identified in the relevant sections above, and their effect on swept-area standardized catch rates can be calculated. If the assumed scenario of a 27.4 m headline length and a trawling speed of 2.62 knots is compared to the outer bounds identified for these variables, the standardised historical catches might have been at most 37% less to 25% more than their assumed level. Despite such uncertainties, the effort to replicate the trawl gear in repeat surveys is expected to attain catches far closer to the true historical fishing power than attempts to adjust modern trawl survey data that were gathered with notably different trawl gear and speeds.

Besides guiding the construction of trawl gear to be used in the re-surveys reported on in Chapters 3 and 4, this research provides a foundation for further studies aimed at investigating historical trawl records and the catching power of historical vessels. Notably, similar trawling equipment was used widely during the first quarter of the 20th century, including on board survey vessels in the UK (SS Huxley; Garstang 1905), the USA (SS Albatross; Alexander et al. 1915; Smith 1921), Norway (SS Michael Sars; Hjort 1914), Netherlands (SS Wodan; Anon 1908; ter Hofstede and Rijnsdorp 2011) and Australia (SS Thetis, FIS Endeavour; Department of Trade and Customs 1909), making this research relevant in a global context.

Appendix A: Supplemental tables and figures

Table A1. Properties of twines that have commonly been used in the construction of trawl nets. Modified from Hanes Supply 2013 (www.hanessupply.com/content/Technical%20Bulletins.asp).

Property	Manila	Sisal	Cotton	Nylon	Polyester	Polyethylene
Breaking tenacity, dry (grams/denier)	5-6.0	4-50	2-3.0	7.8-10.4	7.0-9.5	6
Shock-load absorption ability	poor	poor	poor	excellent	very good	fair
Specific gravity	1.38	1.38	1.54	1.14	1.38	0.95
Elongation percentage at break	10-12%	10-12%	5-12%	15-28%	12-15%	20-24%
Creep (extension under sustained load)	very low	very low	very low	moderate	low	high
Water absorption of fibers	up to 100%	up to 100%	up to 100%	2-8%	<1.0%	none
Resistance to rot, mildew	poor	very poor	very poor	excellent	excellent	excellent
Surface abrasion resistance	good	fair	poor	very good	excellent	fair
Internal abrasion resistance	good	good	good	excellent	excellent	good

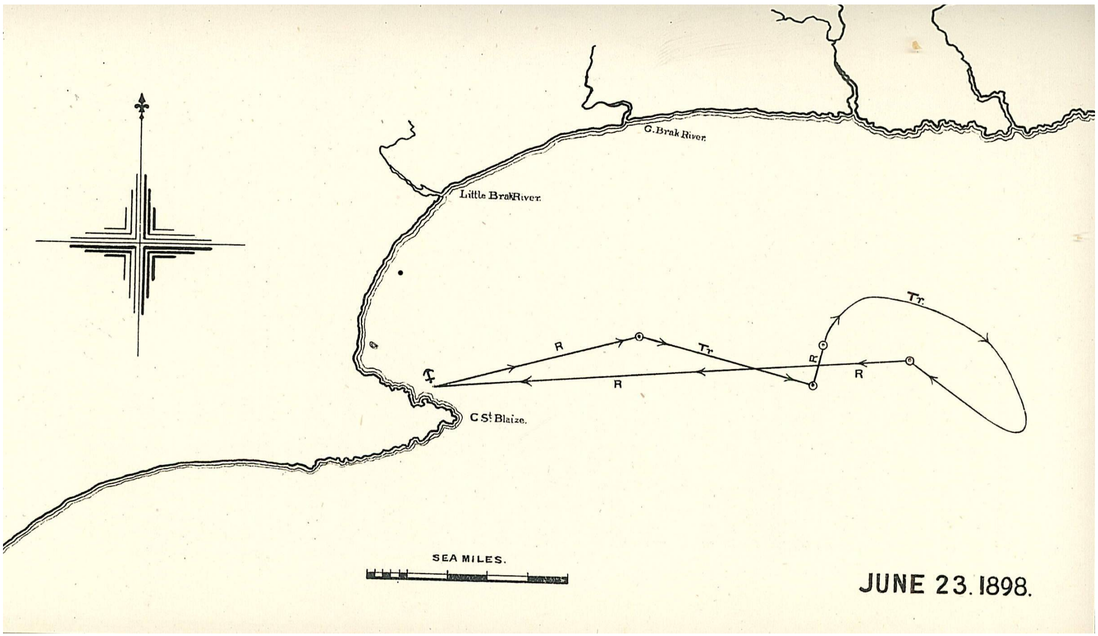


Figure A1. Example of a map of Mossel Bay, from which a trawl track distance was measured after it was geo-referenced with GIS software. The map was digitised from the 1898 government report (Department of Agriculture, 1899). 'Tr' indicates active trawling, 'R' steaming and circles represent start/end points of trawls.

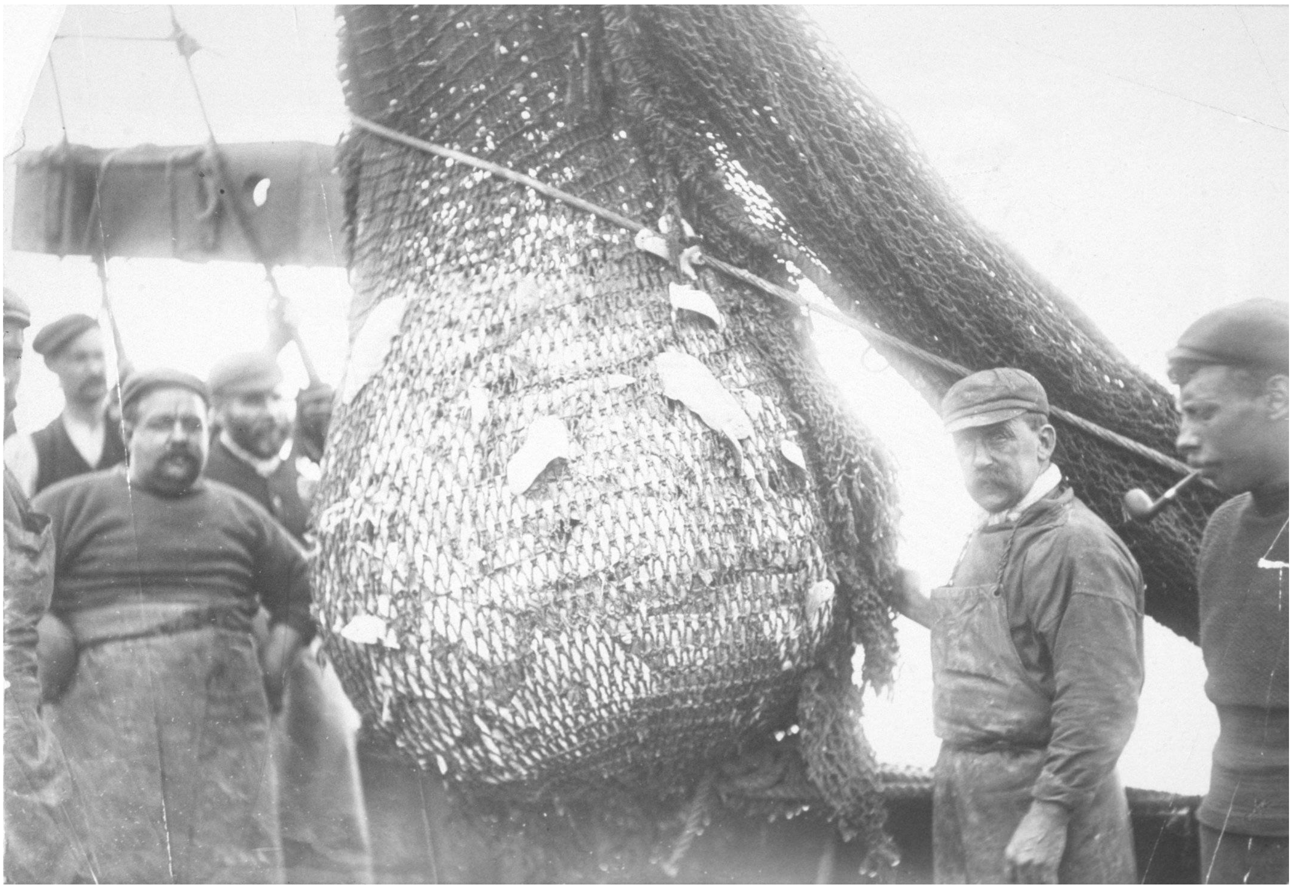


Figure A2. A second photograph taken of the Pieter Faure cod-end. The 'rubbers' and 'belly lines' are clearly visible.

Appendix B: Plans of trawl net and doors

Table B1. Components of the trawl doors depicted in Fig B2. Components a-u are mild steel, with an assumed density of 7 800 kg·m^{-3}. The wooden boards (v) are made of a rot-resistant hard wood, with an approximate density of 900 kg·m^{-3}. The overall board dimensions are 2 700 x 1 400 x 51 mm.

	Component parts	Quantity	Total weight (kg)	Percentage weight of total	Thickness/ Diameter (mm)
	Triangular shackles				
a	Large triangular shackle	1	12.22	3.1%	25
b	Small triangular shackle (2 pieces)	1	12.57	3.2%	25
c	Plates for small triangle	5	6.89	1.8%	8
d	Bolts for small triangle	4	0.39	0.1%	15
e	Tubes holding triangles (45.5 mm)	4	4.34	1.1%	5
f	Tubes locking mechanism (50 mm)	4	0.96	0.2%	4
g	Bolts locking mechanism	4	0.17	0.0%	15
h	Lugs anchoring triangles	8	15.78	4.0%	10
	Central piece with U-shackle				
I	Plates	2	5.86	1.5%	3
j	Square tubes (50.8)	2	4.28	1.1%	3
k	Bolts	6	0.88	0.2%	20
l	U-bolt	1	1.27	0.3%	20
	Frame				
m	U-tube (51 x 57 mm)	1	34.81	8.9%	6
n	Top square plate (55 x 60 mm)	1	14.53	3.7%	6
o	Square tubes (50.8 mm)	6	72.27	18.5%	3
	Shoe				
p	Shoe upper curved plate (80 mm)	1	37.71	9.7%	20
q	Shoe lower (80 mm)	1	24.21	6.2%	20
r	Wear plate - inner lower surface	1	12.97	3.3%	3
	Net attachment point				
s	Plates (50 mm)	4	2.57	0.7%	10
t	Tubes inside door frame (25 mm)	2	0.28	0.1%	4
u	Bolts	4	1.27	0.3%	24
	Wooden boards				
v	Wood (50 mm)	4.6	123.68	31.7%	50
	TOTAL		389.92	100.0%	

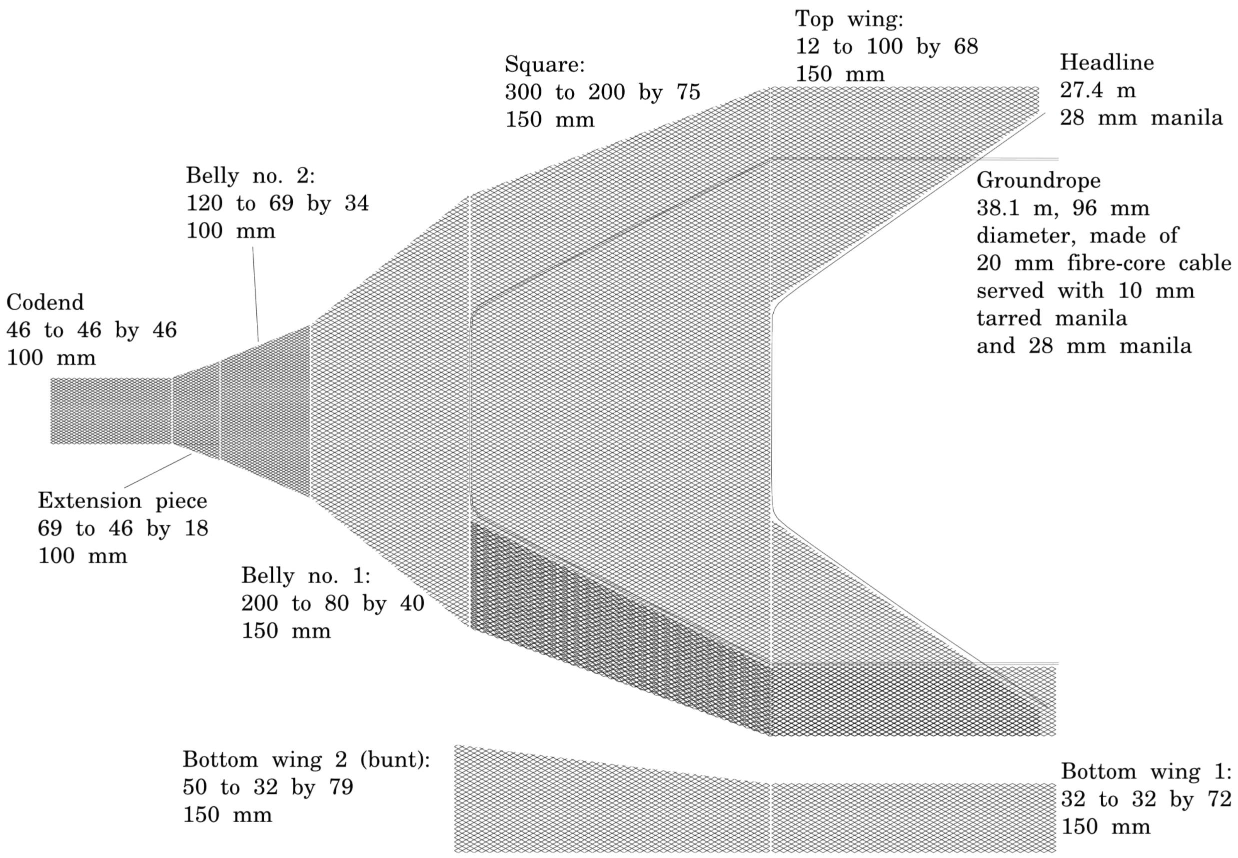


Figure B1. Plan of a trawl net to imitate that used on the Pieter Faure. Lower wings are drawn only on right-hand side. Mesh numbers of individual panels are listed as 'front-width to back-width by depth'. Stretched mesh sizes are indicated in mm. cod-end and extension piece are made of 6 mm single rope, the remaining net panels of 4 mm single rope.

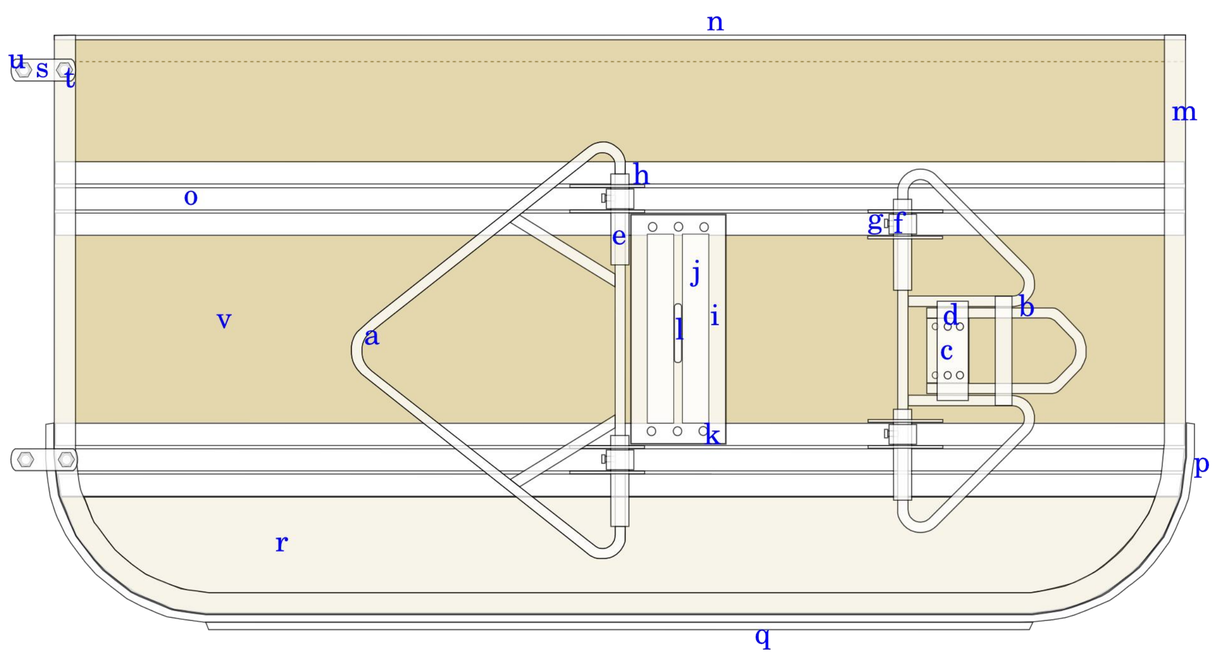


Figure B2. Plan of trawl doors to imitate those used on the Pieter Faure. Brown colour indicates hard wood beams (50 mm), white frame and brackets are made of mild steel.

Chapter 3: Comparison of demersal fish assemblages on the inshore Agulhas Bank between 1903/1904 and 2015

Abstract

Long-term change in the demersal fish assemblage of South Africa's inshore Agulhas Bank was investigated by repeating historical trawl surveys first conducted in the early 20th century. Three sites surveyed in 1903/1904 were revisited in 2015, using replicated gear and methods employed 111 years prior. Patterns in the assemblage were explored with unconstrained ordination, while differences between periods were assessed with permutational multivariate analysis of variance, permutational tests of the homogeneity of multivariate group dispersions and similarity percentage analyses. Species accumulation curves and diversity measures were also examined. Striking changes in the assemblage composition occurred between the historical and re-survey periods, explaining nearly half of the variance among samples and estimated to be >80% dissimilar. The historical catch assemblage was dominated by kob (*Argyrosomus* spp.), panga (*Pterogymnus laniarius*) and east coast sole (*Austroglossus pectoralis*), jointly contributing 70-84% of historical catches. The same taxa contributed a minor component (1.5-5.5%) of re-survey assemblages. Instead recent catches were largely made up of gurnards (*Chelidonichthys* spp.), Cape horse mackerel (*Trachurus capensis*), spiny dogfish (*Squalus* spp.) and shallow-water hake (*Merluccius capensis*). The repeat survey assemblages were characterised by taxa that prefer unconsolidated benthic sediments, whereas historical assemblages included substantial proportions of taxa that associate with reef habitats. Over a century of trawling activity is expected to have altered benthic habitats, likely contributing to the local decline of taxa associated with structure-forming biota and reef-like habitat. Improved management and rebuilding depleted inshore populations will require protection against impacts from multiple fishing sectors, shipping, pollution and climate change, amongst others. Spatial protection, including a representative set of no-take marine protected areas, is a proposed management measure that could provide reference areas for research, safeguard critical habitats and contribute towards resilient demersal assemblages.

Introduction

Effective policy advice on the management of biodiversity, fisheries and the ecosystems that support them requires information about the scale and drivers of past changes in our ocean environment (Schwerdtner Máñez et al. 2014; Engelhard et al. 2016). Without knowledge of historical changes and baseline reference points, recently observed changes within a fishery or ecosystem may have little context for interpretation (Thurstan et al. 2010), which hampers informed decision making.

We know that anthropogenic impacts such as fishing and climate change have altered marine ecosystems (Christensen 1998; Jackson et al. 2001; Genner et al. 2004; Beare et al. 2004; Ward and Myers 2005; Lotze et al. 2006; Stobutzki et al. 2006; Dulvy et al. 2008; Brander 2010; Cheung et al. 2013). Most of our knowledge of these systems is based on research and monitoring efforts that initiated long after such impacts started altering them (Lotze and Worm 2009). In South Africa, some of the most intense trawl fishing pressures developed in the late 1950s, 1960s and 1970s (Griffiths et al. 2004; Sink et al. 2012b; Chapter 1). Yet investigations into periods prior to modern time-series of research survey (1983 to present), commercial catch (1978 to present) and fishery observer (1995 to present) data, are hampered by patchy, discontinuous and incomplete records. Therefore knowledge of pre-disturbed ecosystems and the reference points that describe them are lacking, both in South Africa and across the globe. Strengthening historical baselines is a research priority in South Africa (Sink et al. 2012a) and is considered vital to effective management of ocean spaces.

Assessing ecological change in multispecies samples of 'community data' has received a lot of attention since Field et al. (1982) proposed a simple yet effective framework to do so. Their strategy reduced the complexity of quantities for many species at multiple locations into a similarity matrix among samples. The similarity matrix could be displayed graphically in a number of ways for easy interpretation of patterns and used in statistical tests to gauge group structure and/or relate samples to measures of environment or impact (Field et al. 1982; Warwick and Clarke 1991; Clarke and Ainsworth 1993). The similarity matrix approach has remained central to many multivariate approaches, including methods that allow more rigorous hypothesis testing and the effects of factors to be quantified (Anderson 2001). One of the main advantages of such multivariate analyses is their ability to simplify the complexity of community data into measures that can easily be explored for informative patterns or compared to putative causal factors.

Valuable insight has been gained from studies investigating assemblage changes in long-term comparisons of demersal catches. Periods of warmer water favour greater abundances of certain taxa, specifically smaller, faster-growing species (Genner et al. 2004, 2010; ter Hofstede and Rijnsdorp 2011). Investigating demersal assemblage changes in the North Sea, Engelhard et al. (2011a) concluded that both climatic signals and fishing impacts had resulted in observed patterns, which included higher abundances of warm-water, smaller, lower-trophic-level taxa and declines of mostly larger, cooler-water, higher-trophic-level species.

Fishing impacts are commonly blamed for decreased abundances observed in demersal populations or assemblages (Silvestre et al. 1986; Rijnsdorp et al. 1996; Jackson et al. 2001; Kongprom et al. 2003; Ferretti et al. 2013), as well as declines in larger species or larger sizes within a population (Rijnsdorp et al. 1996; Greenstreet et al. 1999; Rogers and Ellis 2000; Genner et al. 2010). Decreased diversity and greater species dominance in trawl-caught assemblages have also been attributed to the effects of fishing (Greenstreet and Hall 1996; Rijnsdorp et al. 1996; Greenstreet et al. 1999). Greenstreet et al. (1999) showed that areas exposed to the heaviest fishing effort had more pronounced diversity decreases and that catch composition changes were more apparent among species that were favoured fishing targets. Heath and Speirs (2012) had the opportunity to investigate impacts on the demersal community following the resumption of trawling activity after it had been banned for 73 years from the Firth of Clyde in Scotland. They documented substantial change in the demersal assemblage in the decades that followed the resumption of trawling, including reduced evenness, notable reductions in fish sizes and the concentration of biomass in small-sized fish, specifically whiting (*Merlangius merlangus*).

Change in South African demersal communities

Investigations of demersal species composition changes in South Africa have focused predominantly on recent decades. On the west coast, Atkinson et al. (2011b) assessed the demersal fish community composition from trawl surveys conducted between 1986 and 2009. Their findings suggested two temporal shifts in the community assemblage, in 1992-1993 and in the mid-2000s, although the latter might have been influenced by changes in gear. Fishing pressure was the suggested cause of an observed decrease in two larger, slow-growing species and increased catches of three faster-growing, early-maturing taxa, although climate impacts could not be ruled out (Atkinson et al. 2011b). Investigating regime shifts in demersal survey data off the west coasts of South Africa, Namibia and Angola, Kirkman et al. (2015) identified a shift in the South African data in 1994, as well as weaker changes in 1988 and 2006. As the latter two events coincide with previous observations of change in the surrounding ecosystems, they concluded that regional environmental forcing may have been responsible.

Diversity measures and evenness of the Agulhas Bank demersal community appear to have increased over the period of 1986 to 2003 (Yemane et al. 2010), even though abundance-biomass-comparison curves indicated increasing disturbance during the same period (Yemane et al. 2005). The notion of increased stress experienced by the demersal community was supported by analysis of size-based indicators (Yemane et al. 2008). As trawl effort had declined over that time period, explanations proposed for the apparent increase in disturbance included the initiation of longline fisheries and cumulative, long-term trawling impacts on benthic habitats.

Several trawl-caught species are also targeted by South Africa's line fisheries. Griffiths (2000) showed substantial changes in the composition of line catches from similar reef sites sampled on the Agulhas Bank in 1931-1933 and 1987-1993. Several investigations of line-fish catches during the 20th century documented collapses and alarming depletion of species that made up substantial parts of historical catches (Penney et al. 1989, 1999; Van der Elst 1989; Attwood and Farquhar 1999; Griffiths 2000). Such evidence contributed towards the government's decision to declare the line fish resource in a State of Emergency in 2000, leading to substantial curtailment of commercial line fishing effort (Blamey et al. 2015).

To investigate long-term changes in the trawl assemblage, (Mussgnug 2013) combined a variety of datasets from historical (1898-1904; 1922-1948) and recent (1985-2010) trawl surveys and a recent scientific observer program (2003-2006). Contrasts between 1898-1933 and 1985-2010 suggested decreased abundances for several taxa, including panga (*Pterogymnus laniarius*), silver kob (*Argyrosomus inodorus*), east coast sole (*Austroglossus capensis*), carpenter seabream (*Argyrozona argyrozona*), baardman (*Umbrina canariensis*), white stumpnose (*Rhabdosargus globiceps*) and most elasmobranchs. Increased contributions to the catch composition were reported for Cape horse mackerel (*Trachurus capensis*), shallow-water hake (*Merluccius capensis*) and gurnards (*Chelidonichthys* spp.). Mussgnug (2013) concluded that small, fast-growing generalists had withstood expanding fishing pressure better than large, slow-growing, low-fecundity taxa, although exceptions to this pattern were noted.

Repeat surveys and standardisation of fishing gear

As introduced in Chapter 2, the construction (design materials) and methods (including speed) used in trawling operations influence the fishing performance, specifically the selectivity of different species in relation to their size, shape and behaviour (Engås and Godø 1986; Dealteris et al. 1989; Johnson et al. 2008). As a result, it is important to standardise trawl gear and methods in research surveys. When data from different gears are combined, estimation of species-specific selectivity factors may be required for reliable comparisons (Sparre and Venema 1998). Studies contrasting trawl records from different periods generally have to grapple with this potential bias of varying (yet unquantified) selectivity among different gear technologies (Rijnsdorp et al. 1996; Greenstreet et al. 1999; Rogers and Ellis 2000; Mussgnug 2013), which limits confidence in those results. The literature contains relatively few examples of studies that set out to repeat historical trawl surveys and thus had the opportunity to select (or construct) trawl gear to match that used previously.

McHugh et al. (2011) selected two sites off the south-east coast of England that had been surveyed during 1913-1922 and repeated trawl surveys in 2008-2009. They used an otter trawl net of the same size and similar mesh to that of the historical gear. Contrasting the two periods, they documented substantial changes in the assemblage, predominantly in elasmobranch species, which included dramatic declines and an apparent extirpation of angel shark (*Squatina squatina*).

Employing data from 1964 trawl surveys conducted before initiation of a prawn trawl fishery in the Gulf of Carpentaria, Australia, Harris and Poiner (1991) compared the fish assemblage with 1985/1986 repeat surveys that used the same fishing gear. They documented substantial change in the fish assemblage. Of the 82 taxa analysed, 18 had decreased in abundance and 12 had increased significantly. Fishing pressure from the prawn trawlers was considered the likely cause of these changes although environmental variability due to river input and sediment changes also might have had an influence (Harris and Poiner 1991).

Andrew et al. (1997) and Graham et al. (2001) report on a 1996/1997 re-survey of the upper continental slope trawl grounds off New South Wales in Australia, 20 years after they were surveyed using the same vessel and similar gear during early commercial exploitation. Although they did not focus on the assemblage structure, the authors did show that catch rates of both targeted and non-targeted species decreased substantially between survey periods and concluded that fishing pressure was likely responsible for the decline of several taxa. Beyond the use of recent-era DAFF trawl surveys (1980s to present), which provide a valuable sequence of research survey data collected with similar gear, no South African studies have attempted to repeat historical trawl surveys from before this period.

Unique pre-exploitation data from South Africa

Development of a South African trawl industry was prompted by impressive catch records from the government-led exploration of trawl grounds between 1897 and 1906 (Chapter 1). The recent digitisation of detailed survey records from those early research efforts provide an unprecedented view of the demersal ecosystem at a time when human pressures on those grounds are considered to have been negligible. Knowledge of long-term demersal change stems predominantly from investigations reliant on historical data collected after substantial human impacts, as trawl surveys conducted prior to significant exploitation pressures are rare globally (but see Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Klaer 2001; Kongprom et al. 2003; Chapter 1). The early South African trawl survey data therefore provide a valuable opportunity to investigate baselines and subsequent changes from a minimally-disturbed temperate demersal ecosystem.

Despite their qualitative value, quantitative contrasts between the historical records and more modern survey data are difficult due to the substantial changes in trawling technology over time (Rijnsdorp et al. 1996; Rogers and Ellis 2000; Mussgnug 2013). This challenge was addressed by repeating trawl surveys conducted by the Pieter Faure survey vessel more than a century previously. The same sites were revisited with reconstructed trawl gear and methods that imitated the fishing power of historical surveys (Chapter 2). The aim was to quantify and describe long-term changes in the assemblage composition of trawl-caught fish on the inshore Agulhas Bank between 1903/1904 and 2015. Changes in fish composition were investigated and key taxa driving such changes were identified. The ecology of these taxa was examined to reveal potential anthropogenic drivers of change. Besides detection and description of long-term change, this experiment provided a measure of the current state of demersal communities compared to their near-pristine benchmark. Results strengthen historical baselines and offer insights for improved management of demersal ecosystems.

Methods

Selection of data and re-survey sites

Three sites were identified as suitable for repeat surveys, named here as Cape Infanta (Cape Infanta), Mossel Bay (Mossel Bay) and Bird Island (Bird Island; west to east). They were chosen from the historical survey data as spatial aggregations of trawl samples outside of current trawl closures or marine protected areas (MPAs). Individual trawl samples were selected for inclusion in analyses based on the following criteria: 1) they included a start and end time or trawl duration, of which the latter was limited to <200 minutes; 2) they commenced at least 30 minutes after sunrise and ended before sunset; 3) their start locations were positioned outside current MPA or trawl exclusion zones; 4) they were not associated with comments suggesting problems or deviation from normal trawling practices; and 5) for each site the sampling dates were restricted to a defined 3-month season. The location, selection grids and trawl samples are illustrated in Fig 9. All data manipulations and analyses were conducted in the R programming environment (R Core Team 2016), unless specified differently.

Qualifying trawl samples were plotted in geographic information software (QGIS Development Team 2015). A sampling grid was created, the width and height of each cell equal to the approximate length of a standard 30 minute research trawl at a towing speed of 2.6 knots (1.3 nautical miles, ~2.4 km). The survey grid thus defined sampling units from which re-survey cells could be selected. Re-survey targets were chosen by random selection without replacement from those grid cells that contained the start location of at least one historical trawl.

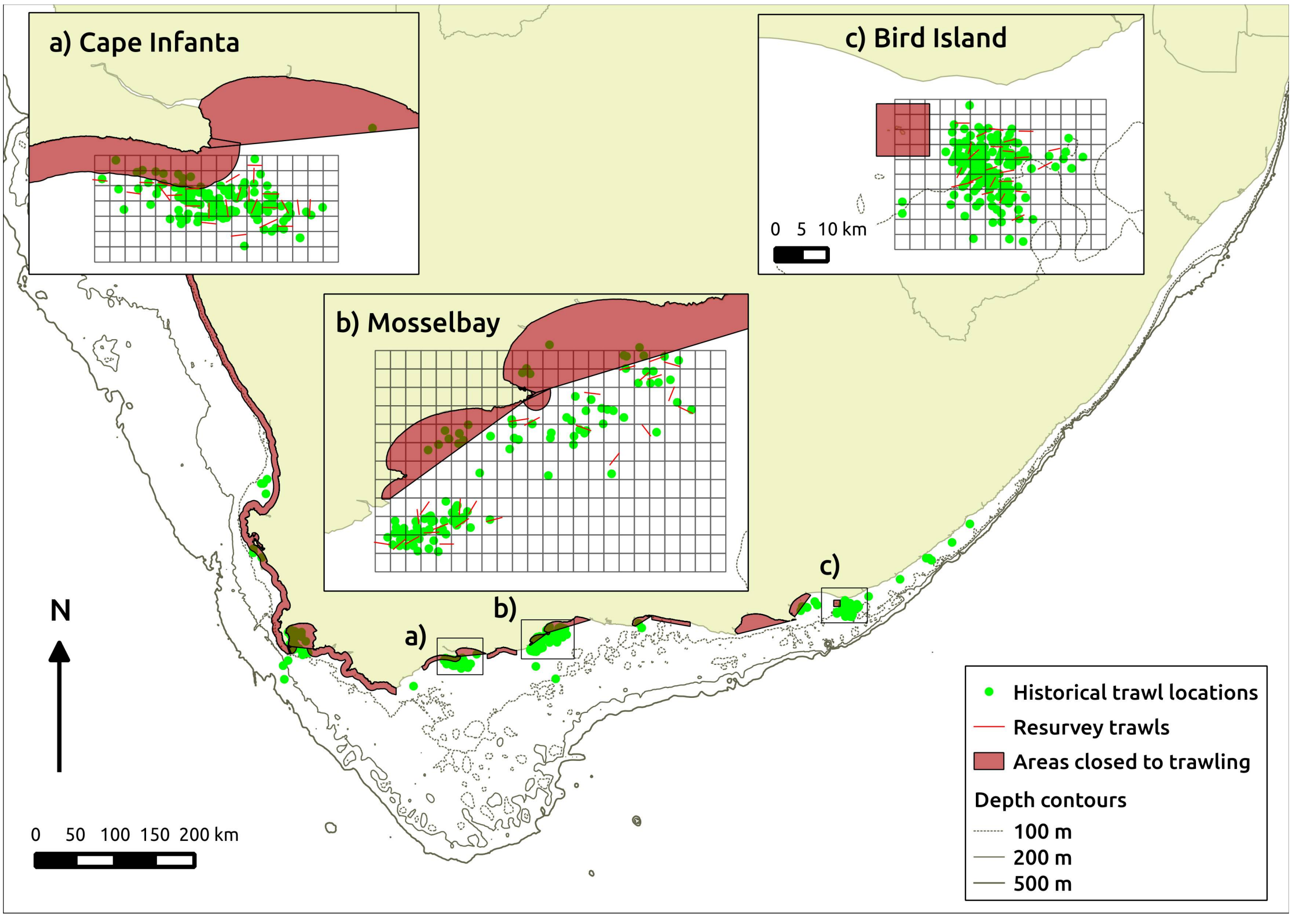


Figure 9. Map showing the location of all historical trawl samples available, together with the sampling grids and re-survey trawl locations at the three chosen re-survey sites. Scale used across the three inserts is consistent. Areas closed to trawling include designated trawl closures and legislated marine protected areas at the time of study. Historical trawls represented by start position of trawl, whereas re-survey trawls are shown as a straight line connecting start- and end-positions.

Prior to fieldwork, the target sample sizes for repeat surveys were considered using univariate (Chapter 4) and multivariate approaches. To assess the impact of increasing sample sizes on multivariate precision, the pseudo multivariate dissimilarity-based standard error (MultSE) was calculated, as provided by (Anderson and Santana-Garcon 2015). The 'MSEgroup.d' function (Anderson and Santana-Garcon 2015) was applied to the historical survey data with site as a grouping factor and using a Bray-Curtis dissimilarity matrix based on square-root transformed catch data that had been standardised by their trawl distance (see below). Profiles of decreasing MultSE with increasing sample size were visually examined

Although recent decades of government-led research trawl surveys were not contrasted directly with historical catches (due to differences in gear technology), they were employed to assess the magnitude of seasonal or interannual variability. These recent (1986-2015) data were obtained from the Department of Agriculture, Forestry and Fisheries and are referred to as DAFF data hereafter. They were collected during annual or bi-annual stratified random surveys of the south coast continental shelf between 1986 and 2015. The sampling protocol for the DAFF data is detailed by Yemane et al. (2010) and is similar to that described below for the repeat surveys. The trawl gear used to collect these data changed in the mid-2000s, as detailed by Atkinson et al. (2011b). Both sets of gear consisted of a 55 m (180 ft) German otter trawl and are similar in many aspects, yet the fishing performance (and selectivity among taxa) may vary between the two. Therefore analyses treated the DAFF 'old gear' (1986-2003; 2006) and 'new gear' (2004-2005; 2007-2015) separately.

Selection of DAFF survey samples used the same spatial grids as described above. Trawls were included in analyses if they had a duration between 20 and 35 minutes, a towing speed of 3-3.5 knots and did not suffer net damage or other disruptions that may have influenced the catch.

Trawl gear

A historical Granton trawl net and flat wooden trawl doors were constructed specifically to imitate those used on the Pieter Faure between 1897 and 1906. Details of the gear are provided in Chapter 2 and only a salient summary is provided here.

The trawl net was based on the plan and descriptions provided by Kyle (1903) and was made from Manila hemp and a mixed polyester-polyethylene alternative with similar properties. The headline consisted of a 28-mm Manila rope, 27.4 m long. The ground-rope consisted of a 20-mm fibre-core cable that was served with a 10-mm tarred Manila rope and thereafter a 28-mm Manila rope to make up a total diameter of 96 mm. The length of the ground-rope was 38 m. Mesh sizes varied from 150 mm stretched mesh in the forward parts of the net, to 100 mm in the trailing parts of the net. The trawl doors were 395-kg, flat, wooden doors with a heavy steel frame and shoe, which were shackled directly onto the net headline and foot-rope.

Repeat fieldwork

Repeat trawl surveys were conducted from a commercial trawler, the MFV Leeukop, owned by the inshore division of Viking Fishing Company (Pty) Ltd. The vessel was built as a side-trawler in

1963, 20.6 m in length and a gross tonnage of 96.26 tonnes, with an indicated engine shaft power of 189.41 kW.

In February, March and May 2015 the repeat surveys were conducted at Mossel Bay, Cape Infanta and Bird Island respectively (Fig 9). Trawling commenced half an hour after sunrise and was completed prior to sunset. If conditions were overcast, a minimum of 30 minutes were added/subtracted to those limits respectively. The tow period, measured between settling of the net on the sea-floor (as observed from vessel speed) and the start of hauling, was intended to be 30 min. This duration was reduced by 5-8 minutes in areas where large catches made processing of the catch difficult. The target towing speed was 2.5 knots. The length of trawl warps was set at ~5.5 times the depth of water after initial attempts with shorter ratios failed to provide good ground contact of the doors and net.

The content of the net was sorted to species level where possible. Reference samples of unidentified fauna and voucher specimens were stored for examination ashore. The catch weight of each species was measured using calibrated marine scales (Marel M1100). Total length was measured to the nearest centimetre, except for pelagic fish, which were measured to the nearest 0.5 cm. The maximum width was measured instead of total length for skates and rays. A representative sub-sample was selected for length-frequency measurement when large catches were encountered. In such cases the number of fish caught was calculated as the mean unit weight from the sub-sample multiplied by the weight of that species' catch.

A field identification error of *Polysteganus coeruleopunctatus* (blueskin) meant that this taxon was recorded with *Pterogymnus laniarius* at Bird Island. *P. coeruleopunctatus* normally occurs further east than Bird Island (Smith and Heemstra 1986). While their catches are not differentiated in analyses, the great majority are expected to have consisted of *P. laniarius* and are referred to as such hereafter.

To monitor the oceanographic environment, water-column variables (salinity, temperature, oxygen concentration) were measured twice daily, before dawn and after dusk. This was done using a hand-held CTD probe (SeaBird SBE 19plus V2 SeaCAT Profiler with SBE 43 dissolved oxygen probe), which was attached to a rope and lowered over the side to the sea-floor. In addition, a compact CTD probe was attached to the headline of the trawl net, about 1.5 m behind the starboard trawl door. During the first survey (Mossel Bay) a RBR TDR-2050 device was employed and during the following surveys a RBR Concerto unit was used. In both cases, the device was set to record the pressure (depth) and temperature every second.

Data preparation

This study was restricted to classes Actinopteri, Elasmobranchii and Holocephali, which are broadly included in the term 'fish' hereafter. Historical records resolved 27 taxonomic groups that could inform analyses (Table 2), the majority of which were at species-level but included five genera, one family, three orders and one mixed group of remaining 'other' fish. Grouped taxa were assigned the lowest taxonomic classification that could be assumed with confidence. In subsequent datasets, catches of taxa were summed within the same groups and comparisons among periods were restricted to taxa that were consistently recorded throughout each of the periods.

Oceanographic data from the hand-held SBE 19plus V2 CTD were processed using SBE Data Processing software (version 7, 23.2). The recorded variables (temperature, salinity, pressure, depth and oxygen concentration) were averaged in 1-m depth bins and the up-cast was used in analyses. Data from the RBR sensors were processed using RBR Ruskin software (version 1.8.14). Profiles of measured variables were exported as text files for further analysis.

The primary unit of measurement in the DAFF trawl survey data is mass (kg). To convert catches into abundances of fish per trawl, the associated length-frequency data were employed. In cases where a sub-sample had been taken for length measurements, those data together with the sub-sample weight were used to calculate a mean weight per individual fish. This figure could then be scaled up to the catch weight (of the relevant species) to estimate the total number of individuals. A few cases existed where no length-frequencies were recorded for a particular species. In such cases, the mean weight per fish was calculated using remaining trawl samples that did contain weight and length data, limited to the same site.

Table 2. The resolution of taxa used in analyses, including their historical and contemporary common names. Identification issues are outlined in the Notes column.

Class	Historical name	Contemporary name	Taxon	Notes
Actinopteri	Stockfish	Shallow water Cape hake	*Merluccius capensis*	Depth of samples precludes *M. paradoxus*.
	Kingklip fish	Kingklip	*Genypterus capensis*	
	Kabeljaauw	Kob/kabeljouw	*Argyrosomus* spp.	
	Pangas	Panga	*Pterogymnus laniarius (and Polysteganus coeruleopunctatus)*	Re-survey included some misidentified *P. coeruleopunctatus*
	Silverfish	Carpenter/silverfish	*Argyrozona argyrozona*	
	Maasbankers	Horse mackerel/maasbanker	*Trachurus trachurus*	
	White stumpnose	White stumpnose	*Rhabdosargus globiceps*	
	Baardman	Baardman	*Umbrina canariensis*	
	Geelbeck	Geelbek/cape salmon	*Atractoscion aequidens*	
	Sandfish	Dragonets	*Paracallionymus costatus*	Assumed historical misidentification of dragonets as *Platycephalus spp.*, which have not been recorded in > 40 years of research trawls.
	Elft	Elf/shad	*Pomatomus saltatrix*	
	Forkbeck	White steenbras	*Lithognathus lithognathus*	
	Seventy-four	Seventy-four	*Polysteganus undulosus*	
	Red stumpnose	Red stumpnose	*Chrysoblephus gibbiceps*	
	Steenbraas	Red steenbras	*Petrus rupestris*	
	Hottentot	(Blue) hottentot	*Pachymetopon* spp.	Assumed to be predominantly *P. aeneum* as *P. blochii* occurs in rocky habitats and very rarely caught in trawls. Re-survey catches exclusively *P. aeneum*.
	Dageraad	Dageraad/daggerhead	*Chrysoblephus cristiceps*	
	Mud soles	Mud sole/east coast sole	*Austroglossus pectoralis*	
	Sand soles	Sand tonguefish	*Cynoglossus* spp.	
	Gurnards	Gurnards (multiple species)	*Chelidonichthys* spp.	
	Barger	White sea catfish	*Galeichthys feliceps*	
Elasmobranchii	Sharks	Shark	Carcharhiniformes	
	Sting rays	Stingray	Myliobatiformes	
	Skates	Skate	Rajidae	
	Dogfish	Spiny dogfish	*Squalus* spp.	
	Electric skate	Electric ray	Torpediniformes	
N/A	Other kinds	N/A	Classes Actinopteri and Elasmobranchii excluding above taxa	
	N/A	All fish (including sharks)	Classes Actinopteri and Elasmobranchii	Entire catch excluding invertebrates.

Comparison of historical and re-survey catches

Most analyses used catches standardised by the distance of the trawl tow, assuming a constant net width across the study:

$$C_{st} = \frac{C}{d} \qquad (1)$$

$$d = r * \bar{v} \qquad (2)$$

where C_{st} is the standardised catch (count·nautical mile^{-1}); C is the summed count for the specified taxon; d is the trawl distance; r is the duration of the haul (in hours); and $\bar{v}$ is the average trawl speed (in knots).

Due to financial and logistical constraints, the re-survey trawl durations (~30 minutes) had to be shorter than those of the historical surveys (60-200 minutes). The trawl duration was recorded historically as 'time trawl down', which was the difference between the 'trawl hauled' time and the 'trawl shot' time. For the re-survey trawls, 'fishing duration' (period that the net is settled on the sea-floor) was estimated using profiles from the temperature-depth sensors attached to the net. The latter method is a more accurate measure of the fishing effort exerted on demersal fish, having removed the sinking time of the gear. In comparison, the 'time trawl down' was exaggerated (mean=3.5 minutes ± 0.3 *SE*) in the re-survey records. Such a bias would have minimal effect on the longer-duration historical samples but proportionally greater influence on the catch rates of shorter re-survey trawls (Battaglia et al. 2006), hence the more accurate 'fishing duration' was used for standardisation of the re-survey samples.

The Pieter Faure trawl speed was assumed to be 1.35 m·s^{-1} (2.62 knots), based on calculations in Chapter 2. The re-survey trawl speed was calculated as the GPS-logged distance over the trawl duration. Trawl distance (duration*speed) was considered a marginally more accurate measure of trawl effort than duration (at least for the re-surveys) and was therefore used preferentially in analyses.

In analyses using recent DAFF survey data, catches were standardised by swept area:

$$C_{sw} = \frac{C}{a} \qquad (3)$$

$$a = d * \frac{w}{1852} \qquad (4)$$

where C_{sw} is the swept-area standardised catch (count·nautical mile^{-2}); a is the area of sea-floor swept by the trawl (nautical mile^{2}); w is the width of the mouth of the trawl net (m).

Multiple analyses (below) were based on a dissimilarity matrix of the community catch data. To down-weight the dominant influence of abundant taxa, all cases that used a Bray-Curtis dissimilarity matrix were based on square-root transformed standardised catches. Ordination of trawl samples was achieved by non-metric multidimensional scaling (NMDS) of a Bray-Curtis dissimilarity matrix. This was applied using the 'metaMDS' function from package 'vegan' (Oksanen et al. 2016).

The null hypothesis that there was no difference in the multivariate community composition between periods was assessed using a permutational multivariate analysis of variance using distance matrices (Anderson 2001); hereafter PERMANOVA). A Bray-Curtis dissimilarity matrix was regressed against covariate depth and categorical variables site, period and a site-period interaction to account for potential depth and between-site influences while testing the period effect:

$$D=\beta_1+\beta_2\,depth+\beta_3\,site+\beta_4\,period+\beta_5\,site*period+\epsilon \qquad (5)$$

where D is the dissimilarity matrix, β_1 represents the intercept, β_2 the estimated coefficient for depth, β_3 the estimated coefficient for the site effect, β_4 the estimated coefficient for the period effect, β_5 the estimated coefficient for the site-period interaction, and ϵ the residual error term.

The 'adonis' function in 'vegan' (Oksanen et al. 2016) was used to run the PERMANOVA models, with 9 999 permutations restricted to within-site levels. The routine used sequential sums of squares, which means the order of terms in the model was consequential. Because the period effect was of main interest, after having accounted for depth and site effects, it was added last in the model structure. As maximum variability is attributed to the other main effects, this approach should provide a conservative estimate of the period effect.

To assess multivariate differences among pairs of surveys, a pairwise PERMANOVA analysis was also conducted among the levels of a combined period-site factor, including depth as a covariate. The Holm adjustment for multiple comparisons (Holm 1979) was applied to avoid an inflated likelihood of obtaining a significant result.

PERMANOVA models are robust in the face of multivariate heterogeneity, but not if the experimental design is unbalanced (Anderson and Walsh 2013). Therefore the results from the unbalanced design were augmented with parameter ranges obtained from 1 000 randomly re-sampled (without replacement), balanced datasets containing 23 trawl samples per site per period.

To ascertain whether there may have been a change in multivariate heterogeneity between periods, a permutation test of the homogeneity of multivariate group dispersions was employed (PERMDISP2; Anderson 2006). The same dissimilarity matrix was used as in the multivariate model and ordination above. Pairwise tests among period-site level combinations were assessed using 9 999 permutations, employing the Holm adjustment of p-values for multiple comparisons (Holm 1979). The multivariate group dispersions were implemented using the 'betadisper' function in package 'vegan' (Oksanen et al. 2016).

A two-way (period*site) similarity percentage analysis (SIMPER; Clarke 1993) was used to investigate taxa that discriminate between periods across sites. Similarly, a pairwise SIMPER was used to identify the taxa discriminating periods for each site. These analyses were based on the same Bray-Curtis matrix described above and conducted in Primer-E (Clarke and Gorley 2006).

Identification of the taxa that were significantly more abundant in either of the two periods was accomplished with a site-group associations test using the 'indicspecies' package (De Cáceres and Legendre 2009). Although the test does not allow a crossed design, permutations (9 999) were restricted to within site levels.

The effects of period and potential covariates on taxonomic richness and diversity were investigated in multiple ways. Species accumulation curves were constructed for historical and re-survey samples at each of the three sites, using untransformed and non-standardised counts. Trawl distance was used as a weight for sampling effort and sites were added randomly during 9 999 permutations, using the 'specaccum' function in the 'vegan' package (Oksanen et al. 2016).

In addition, the influence of covariates (depth, trawl distance and time of day) on diversity and richness was explored. Three measures were plotted against the potential covariates, namely taxonomic richness, Shannon's diversity index and Pielou's evenness index (Hill 1973). Linear relationships were evaluated with a test for association between paired samples, using Pearson's product moment correlation coefficient (Zar 1999). The diversity indices were calculated using the 'vegan' package (Oksanen et al. 2016).

The relationship between the same potential covariates and assemblage composition was assessed using Mantel (Legendre and Legendre 2012) and ENVFIT (Oksanen et al. 2016) tests. The Mantel correlation was performed between a Bray-Curtis dissimilarity matrix of the catch data and a Euclidian distance matrix of the 'environmental' variable, using Pearson's correlation coefficient.

The ENVFIT function uses an ordination of the community data and finds the direction in ordination space that has maximum correlation with the environmental variable (Jongman et al. 1995; Oksanen et al. 2016). Permutation of the environmental variable values is then used to assess significance of the correlation. NMDS was used as the ordination method applied to a Bray-Curtis dissimilarity matrix.

The ENVFIT and Mantel analyses were applied sequentially within period-site level combinations as they would otherwise be confounded with expected between-site and between-period differences.

The Holm adjustment for multiple tests (Holm 1979) was applied to avoid inflated probabilities of a significant result across the 18 tests (three covariates, six period-site levels). Both tests used 99 999 permutations and were performed using the 'vegan' package (Oksanen et al. 2016).

To contrast the magnitude of variability between historical and re-survey samples with that among DAFF samples, a multivariate measure of pseudo variance (MultV) was employed as in Anderson and Santana-Garcon (2015). Consistent with other analyses, MultV was computed from Bray-Curtis dissimilarity matrices derived from square-root transformed, swept-area standardised catches ($count·nm^{-2}$). At each site, 500 pairs of historical and re-survey samples were randomly selected with replacement. DAFF samples were stratified by their temporal proximity to each other, so that the difference between pairs of seasonal (≥2 months and <12 months), interannual (≥12 months and <18 months) and multi-year (≥18 months but ≤60 months) samples could be calculated. As the sample sizes were relatively small for the DAFF pairs, all possible pairwise contrasts were included. The magnitude of MultV values were visually contrasted using their mean and bootstrapped non-parametric 95% confidence intervals on scatterplots.

As uncertainties remained in the length of the historical net headline (affecting the size of the net) and the speed at which it was towed (Chapter 2), the effect of such uncertainties on results was examined. This was accomplished by repeating the full set of analyses on swept-area standardised catches, using the extreme combinations of plausible bounds for headline length and trawl speed. This resulted in two additional sets of results, the one based on the assumption of a 26.8 m (88 ft) headline length and trawl speed of 1.10 $m·s^{-1}$ (2.15 knots); the other on a 36.6 m (120 ft) headline and a speed of 1.61 $m·s^{-1}$ (3.13 knots; see Chapter 2).

In a similar manner, the impact on results of potential biases of trawl distance (duration) and depth were examined. Again the entire set of results was re-generated, using datasets that excluded a) historical Cape Infanta samples with a trawl distance ≥5 nautical miles and b) re-survey Bird Island samples with a depth ≥100 m. Any meaningful differences between these secondary sets of results and the main set presented below were noted.

Results

Investigation of MultSE figures indicated minimal precision increases beyond 20 samples per site (Fig 10). Following these results, and those of univariate power analyses (Chapter 4), a target of 25 trawl samples per site was set. Repeat surveys accomplished 25, 25 and 23 successful trawls at Cape Infanta, Mossel Bay and Bird Island, respectively. These were contrasted with 60, 42 and 54 historical trawls respectively.

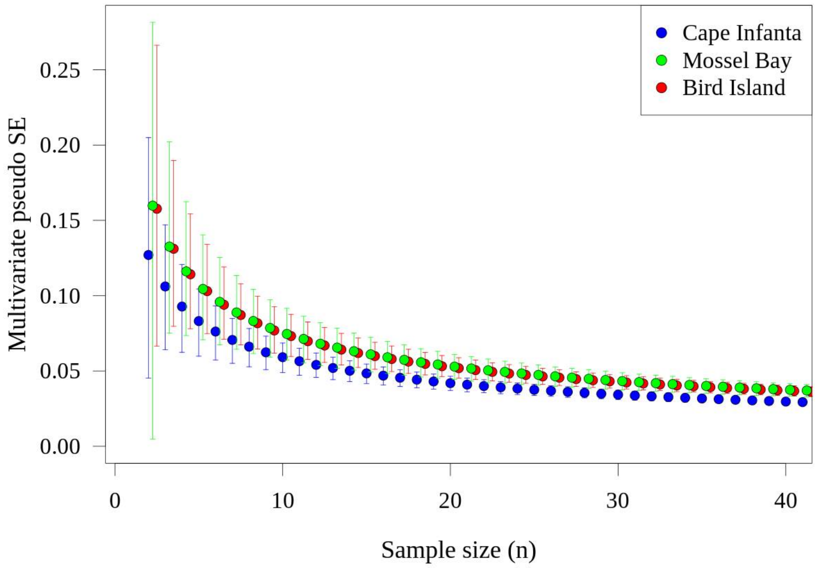


Figure 10. Multivariate pseudo standard error (MultSE) plotted against sample size for the historical trawl samples at each of the three sites. MultSE calculations used Bray-Curtis dissimilarities calculated on square-root transformed, standardised catch data. Error bars represent 2.5 and 97.5 percentiles from 10 000 bootstrap samples.

Ordination of the standardised catches showed a clear separation of historical from re-survey trawl samples (Fig 11), predominantly along the primary x-axis. Site groupings were also discernible in the ordination, partially separating along the secondary y-axis. The large period effect was confirmed by the PERMANOVA results, accounting for 41-47% of the variance explained by the model (Table 3). The highly significant site effect explained 10-13% of the model variance. Together with their interaction, these two variables jointly explained 64-69% of the model variance. The depth of trawls also significantly affected multivariate distances among trawls, but to a lesser extent (6-10% variance). The R^2 estimates from the full (unbalanced) dataset fell within ranges of those estimated by the under-sampled (balanced) models, except for the depth effect, which was underestimated in the full design (Table 3). All terms combined, accounted for 72-76% of total model variance. Results of a pairwise PERMANOVA suggested that all period-site levels were significantly different from each other ($p \leq 0.01$), except for the re-survey samples from Cape Infanta and Mossel Bay.

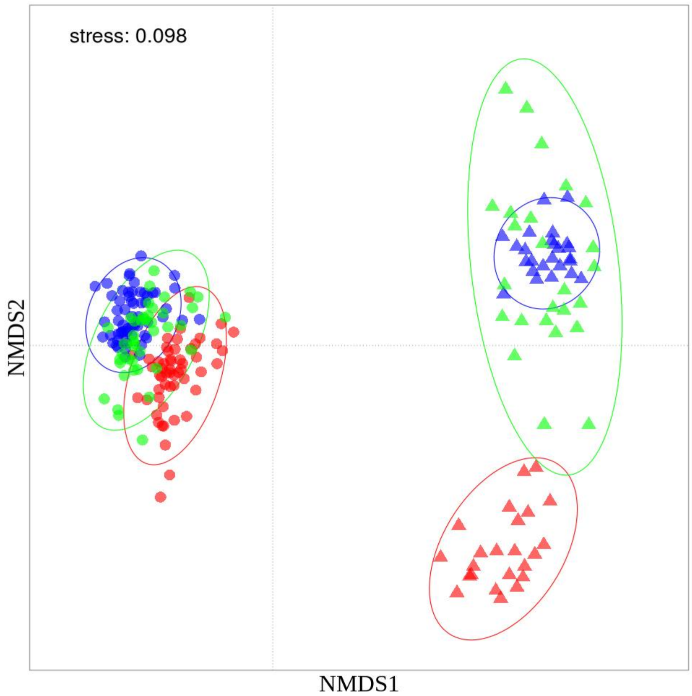


Figure 11. Non-metric multidimensional scaling (NMDS) plot based on Bray-Curtis dissimilarities of square-root transformed standardised catch. Historical and re-survey samples are indicated by circles and triangles respectively, while sites are separated by colour (Cape Infanta blue, Mossel Bay green, Bird Island red). Bounding ellipses represent 95% probability contours estimated for each period-site level.

Table 3. PERMANOVA results shown from the full (unbalanced) dataset as well as ranges from 1 000 under-sampled, balanced datasets. Significance levels remained unchanged. *Df*: degrees of freedom, R^2: proportion variance (sums of square) explained; *F*: pseudo-F statistic; Sign.: significance level, *** $p \leq 0.0001$;

	Unbalanced results			Balanced results			
Variable	***Df***	R^2	***F***	***Df***	R^2	***F***	**Sign.**
Depth	1	0.05	41.9	1	0.06-0.10	31.8-51.4	***
Site	2	0.12	47.2	2	0.10-0.13	24.2-34.4	***
Period	1	0.45	362	1	0.41-0.47	204-252	***
Site:Period	2	0.10	41.3	2	0.09-0.12	23.8-31.6	***
Residuals	222	0.28		131	0.24-0.28		
Total	228	1.00		137	1.00		

Shifting focus to the dispersion among samples (rather than their location), historical trawl samples were clustered closer together than in repeat surveys (Fig 11). The PERMDISP analysis confirmed that the dispersions were different between periods (F=101.3, $p \leq 0.0001$). This difference appears to be caused by the divergence of re-survey Bird Island samples from those of the other two sites, as well as the greater variance (dispersion) among Mossel Bay re-survey samples (Fig 11). Dispersion was significantly different among period-site levels (F=14.7, $p \leq 0.0001$), although a pairwise test revealed that only Mossel Bay differed between historical and re-survey periods (Table 4). The

Mossel Bay re-survey samples were significantly more heterogeneous than all other period-site levels (Table 4, Fig 11).

Table 4. Pairwise significance of PERMDISP analyses. Grey shading identifies period contrasts at the same site. CI Cape Infanta, MB Mossel Bay, BI Bird Island. ns $p>0.05$, ~ $p\leq0.05$, * $p\leq0.01$, with Holm-adjusted p-values for multiple tests.

		Historical		Re-survey		
		MB	BI	CI	MB	BI
Historical	CI	~	*	ns	*	*
	MB		ns	ns	*	ns
	BI			ns	*	ns
Resurvey	CI				*	ns
	MB					*

A large dissimilarity (81.7%) of historical and re-survey assemblages was supported by SIMPER analysis. Of the taxa contributing 90% to between-period dissimilarity, six teleost taxa and Torpediniformes (electric rays) were more abundant historically, whereas four teleost taxa and *Squalus* spp. (spiny dogfish) were more numerous in the re-surveys (Fig 12). *Argyrosomus* spp. (kob), *Pterogymnus laniarius* (panga), *Austroglossus pectoralis* (east coast sole) and *Chelidonichthys* spp. (gurnards) contributed over 50% of the dissimilarity between periods and were relatively consistent in their distinguishing contribution (dissimilarity/SD >1). Abundances of *Argryosomus* spp., *Argyrozona argyrozona* (carpenter seabream) and *Rhabdosargus globiceps* (white stumpnose) contributed a substantial proportion to historical catches (26%, 8%, 4% respectively) but were absent (*Argyrosomus* spp.) or nearly absent in repeat surveys. In addition, large decreases were shown for *P. laniarius* (27% to <1%) and *A. pectoralis* (26% to 3%). *Argyrosomus* spp., *P. laniarius* and *A. pectoralis* dominated the composition of historical catches at each of the three sites, jointly contributing 82%, 70% and 84% of Cape Infanta, Mossel Bay and Bird Island catches respectively. In the re-survey, their summed contribution had dropped to between 1.5% and 5.5%.

Standardised abundances of *Chelidonichthys* spp., *Trachurus capensis* (Cape horse mackerel), *Squalus* spp., *Merluccius capensis* (shallow-water hake) and *Galeichthys feliceps* (white sea catfish) increased between periods, their joint contribution rising from 3% of the historical catch numbers to 85% of the re-survey catches. Inspection of initial years (1986-1990) of DAFF trawl survey data showed that by the late 1980s, the proportional contribution of the same suite of taxa matched more closely the re-survey findings than the historical situation: *Argyrosomus* spp., *P. laniarius* and *A.*

pectoralis contributed a cumulative average of 11% by weight, whereas the five taxa that were most numerous in re-survey catches contributed 75% of the DAFF catches.

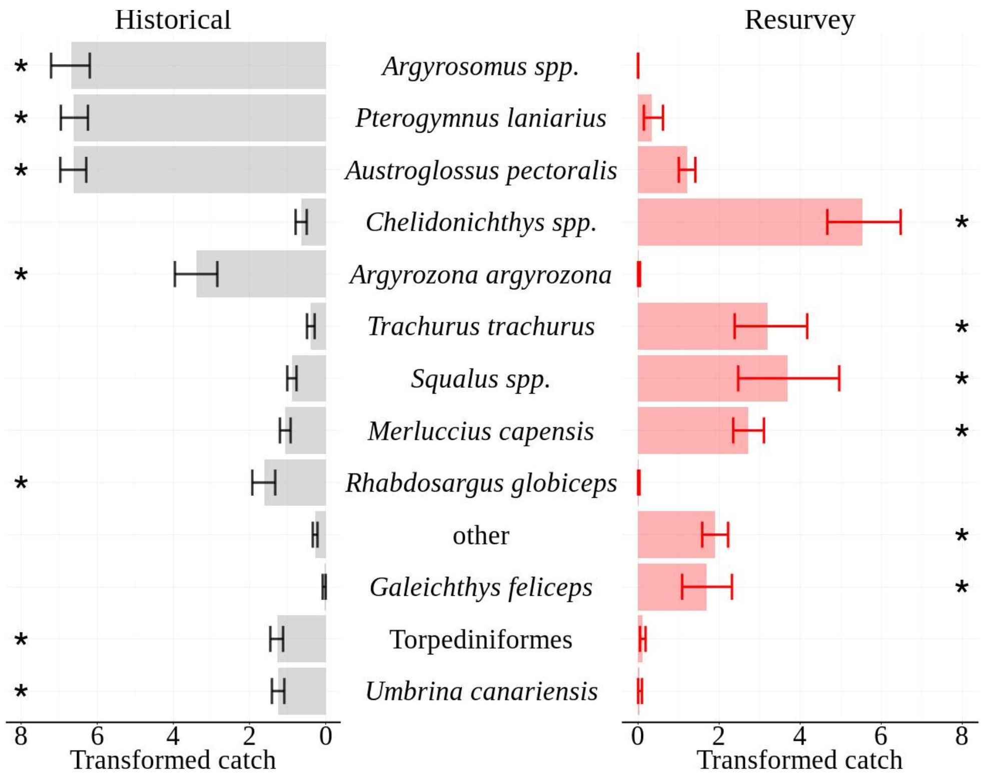


Figure 12. Mean abundances of distinguishing taxa that cumulatively contribute 90% of dissimilarity between periods, as identified by SIMPER analysis. Taxa are plotted in order of contribution to dissimilarity. Standardised abundances (count·nautical mile^{-1}) were square-root transformed prior to analysis and plotting. The SIMPER results for all taxa are tabled in the Appendix. Error bars are non-parametric 95% confidence intervals. * identifies taxa found to be significantly more abundant in one period, using a site-group associations test ($p \leq 0.01$ with Sidak adjustment for multiple tests).

The dissimilarity between periods was driven by relatively few taxa at Cape Infanta compared to other sites, as shown by pairwise SIMPER contrasts (Fig 13). At the two western sites (Cape Infanta, Mossel Bay) the top seven distinguishing taxa were the same, except for *R. globiceps*, which made up 10% of historical Mossel Bay catches but was not encountered there during the re-survey. At Bird Island, the taxa distinguishing most between periods were different to other sites, in that three of the top four distinguishing taxa were more abundant in the re-survey period (*Squalus* spp., *Chelidonichthys* spp. and *G. feliceps*; Fig 13).

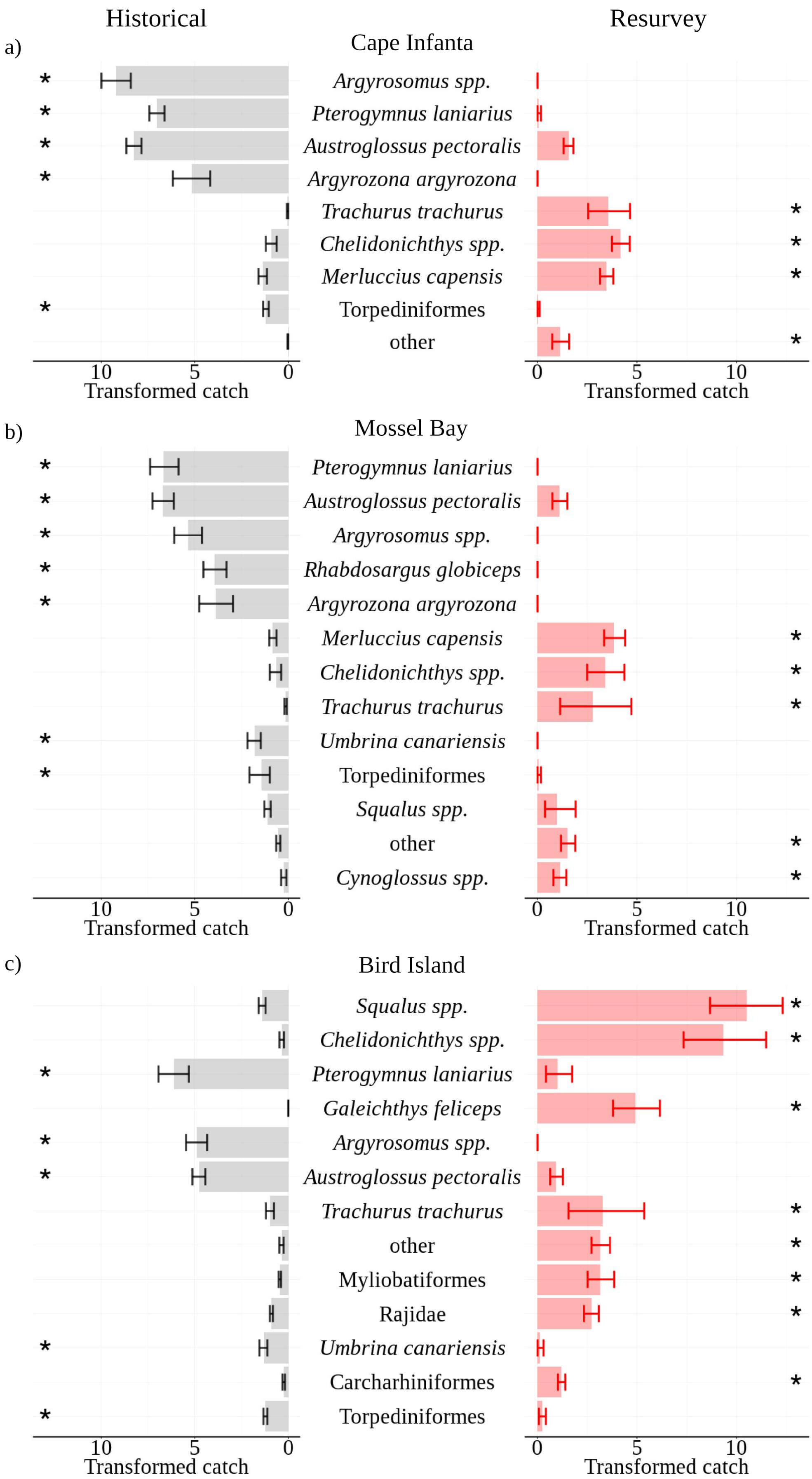


Figure 13. Same as Fig 12, but showing taxa that distinguished between periods for individual sites a) Cape Infanta, b) Mossel Bay and c) Bird Island, using a pairwise SIMPER analysis.

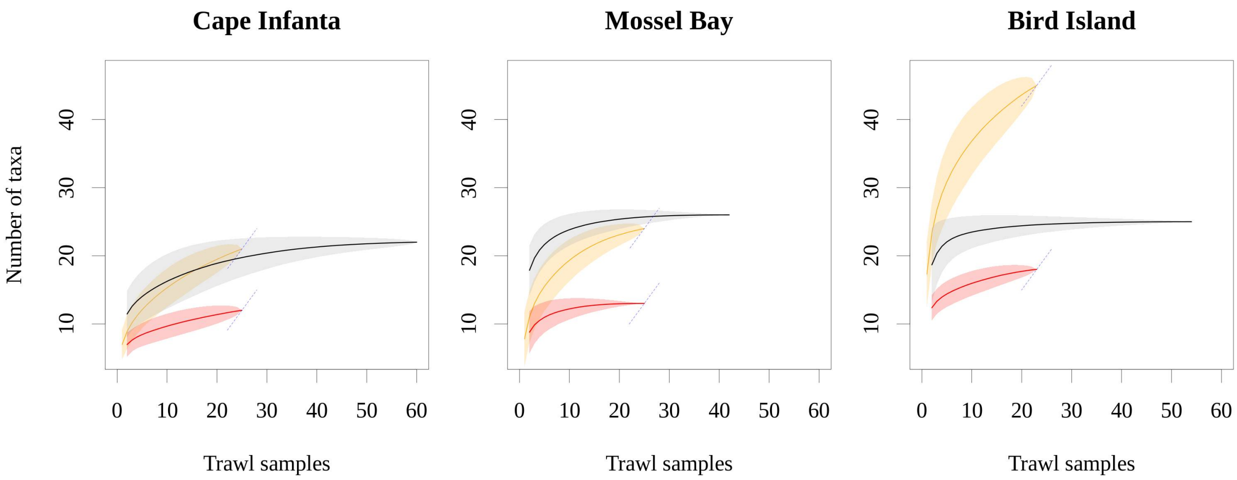


Figure 14. Species accumulation curves for historical (black) and re-survey (red) trawl samples. Included also are the re-survey data disaggregated to species-level resolution (orange; not directly comparable with the other curves). Shaded areas indicate 95 % confidence intervals (2**SE*). Dotted line represents a slope of one taxon per trawl sample.

Species accumulation curves suggested that the trawl-caught fish diversity was not entirely sampled during Cape Infanta and Bird Island repeat surveys (Fig 14). However, the discovery rate of taxa (slope) had decreased to less than one new taxon per trawl sample by the end of the surveys. The shape of historical accumulation curves suggested a higher proportion of common taxa at Bird Island and a greater proportion of rare taxa at Cape Infanta, with Mossel Bay intermediate between the two (Fig 14; Thompson and Withers 2003). Restricted to the taxonomic framework imposed by the historical data, the species accumulation curves showed a notable reduction in richness from historical to re-survey periods at all three sites.

If the full species resolution of the re-survey dataset is used for the same comparison, similar levels of richness are seen between periods at the two western sites (Cape Infanta and Mossel Bay), but far greater richness recorded in re-survey Bird Island samples (Fig 14). Comparing across sites, taxonomic richness was historically lowest at Cape Infanta and similar at Mossel Bay and Bird Island, whereas in the repeat survey the two western sites had notably lower richness than Bird Island (Fig 14).

In comparison to repeat surveys, Shannon's diversity index was higher historically across all three sites, whereas Pielou's evenness index was lower at Cape Infanta but similar at Bird Island and Mossel Bay (Fig 15). Significant linear relationships were revealed between diversity measures and depth, but only in certain cases (period-site levels): Negative relationships were seen between taxonomic richness and depth in the re-survey Mossel Bay data and between Shannon's diversity index and depth in historical Bird Island samples (Table 5). Positive correlations were seen between depth and both Shannon's diversity and Pielou's evenness in historical Cape Infanta samples (Table

5), even though the depth range was narrow (<20 m). Evidence of a relationship between diversity measures and trawl distance was detected only in the historical Cape Infanta survey, by way of a decrease in Pielou's evenness at greater distances (Table 5).

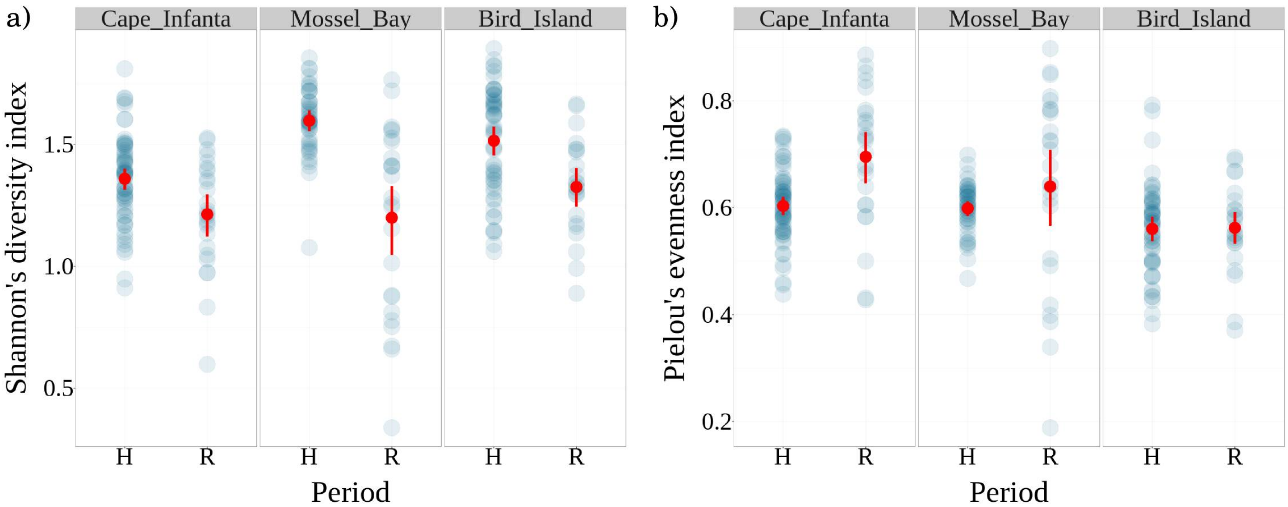


Figure 15. Comparison of a) Shannon's diversity and b) Pielou's evenness indices between historical (H) and re-survey (R) periods for each site. Mean and non-parametric 95% confidence intervals are indicated in red.

Investigation of summed standardised catches with depth and trawl distance showed relationships for some of the same cases as seen in diversity measures: Historical Cape Infanta catches were related significantly to both depth and trawl distance (Table 6). As a result, the two latter variables (depth and trawl distance) were also significantly correlated ($p \leq 0.05$; r=-0.364) in that survey.

Table 5. Correlation coefficients between measures of richness/diversity and depth or distance for both historical (H) and re-survey (R) data. Statistical significance of coefficients indicated by bold ($p \leq 0.05$) or underlined and bold ($p \leq 0.01$) font, following Holm adjustment for multiple tests.

Variables	**Cape Infanta**		**Mossel Bay**		**Bird Island**	
	H	**R**	**H**	**R**	**H**	**R**
Richness vs depth	-0.014	-0.095	-0.165	**-0.599**	-0.298	0.238
Diversity vs depth	**0.388**	-0.162	-0.154	-0.347	**-0.450**	-0.291
Evenness vs depth	**<u>0.440</u>**	-0.126	-0.072	-0.079	-0.269	-0.372
Richness vs distance	0.004	-0.113	0.247	-0.353	-0.018	0.232
Diversity vs distance	-0.340	-0.195	-0.172	-0.241	0.108	0.036
Evenness vs distance	**-0.404**	-0.138	-0.376	-0.096	0.143	-0.047

Statistical relationships between assemblage composition and trawl depth were supported by the Mantel and ENVFIT tests at Cape Infanta (re-survey only) and Bird Island (historical and re-survey; Table 7). Trawl distance was also related to catch composition, but only at the historical Cape Infanta site (Table 7), congruent with the relationship shown in Table 5.

Table 6. Similar to Table 5, but showing correlation coefficients between standardised catch, summed for all taxa, and depth or distance.

Variables	Cape Infanta		Mossel Bay		Bird Island	
	H	**R**	**H**	**R**	**H**	**R**
Catch vs depth	**0.356**	0.175	0.104	-0.462	0.098	-0.023
Catch vs distance	**-0.399**	-0.007	-0.291	-0.321	-0.238	-0.509

Table 7. Mantel and ENVFIT tests exploring relationships between community composition and trawl depth, duration and time of day. *r*: Mantel statistic (Pearson correlation coefficient); r^2: ENVFIT goodness of fit statistic (squared correlation coefficient); Sign: significance of p-values after Holm adjustment for multiple tests; ns $p>0.05$, ~ $p \leq 0.05$, * $p \leq 0.01$, ** $p \leq 0.001$;

Period-site	Depth				Distance			
	Mantel		ENVFIT		Mantel		ENVFIT	
	r	**Sign.**	r^2	**Sign.**	***r***	**Sign.**	r^2	**Sign.**
Historical – CI		ns		ns	0.19	*	0.25	*
Historical – MB		ns		ns		ns		ns
Historical – BI	0.17	~	0.54	**		ns		ns
Re-survey – CI	0.30	*	0.58	*		ns		ns
Re-survey – MB		ns		ns		ns		ns
Re-survey – BI	0.50	*	0.52	~		ns		ns

Comparison of the MultV (multivariate pseudo variance) between periods, with that from seasonal and interannual time-frames in DAFF trawl surveys, showed that mean variability was substantially larger between periods (ranging 2.0-3.3 times the short-term variability; Fig 16). This indicates that the magnitude of mean seasonal and interannual variability among DAFF samples is too small to account for the changes observed between historical and re-survey periods.

Due to the survey design, depths were expected to be similar between periods. This was found not to be the case at Bird Island, however, where a bias towards deeper depths was noted in the re-survey trawls (mean=90 m) relative to historical samples (mean=78 m; Appendix). Repetition of analyses on a dataset that excluded re-survey Bird Island samples with a depth ≥100 m showed no material impact on results, other than to remove the relevant relationship in Table 7. Similarly, a repetition of analyses without historical Cape Infanta samples that had a trawl distance ≥5 nautical miles showed no material change in results other than to remove the relevant (depth and distance) relationships in Tables 5-7.

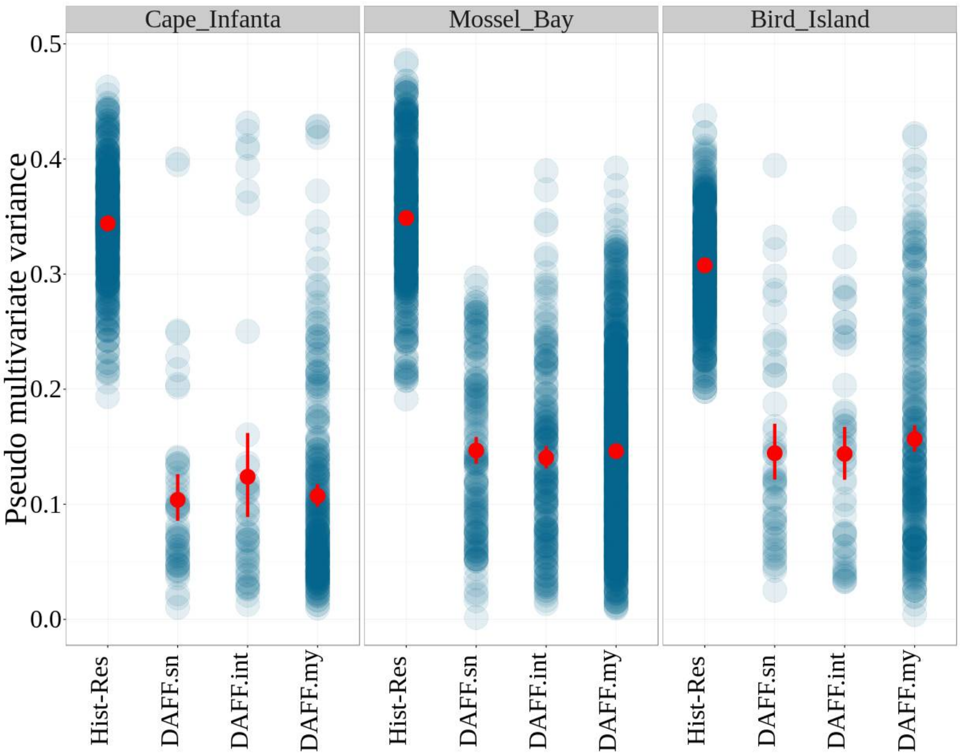


Figure 16. Comparison of MultV calculated between pairs of randomly chosen samples from historical and repeat surveys (Hist-Res; N=500 for each site), as well as all possible combinations of DAFF samples that were separated by ≥2 month but <12 months (DAFF.sn), ≥12 months but <18 months (DAFF.int) and ≥18 months but ≤60 months (DAFF.my). Mean and non-parametric 95% confidence intervals are indicated in red. See Methods for details.

Investigation of oceanographic data collected during the re-survey cruise revealed a correlation between near-bottom oxygen concentrations and depth, only at Mossel Bay (p=0.008; r=0.85). This relationship was due to relatively low dissolved oxygen concentrations (1.5 and 2 $ml \cdot l^{-1}$) at stations shallower than 60 m.

Examination of results that are generated assuming extreme combinations of plausible bounds for the historical net headline length and trawl speed, showed little difference from those presented above. The examined adjustments effectively inflated historical standardised catches by 25% or reduced them by 37%. Effects on results included minor adjustments to the significance of depth effects reported by the Mantel test for Bird Island historical and repeat surveys. In addition, the sequence of species distinguishing between periods (reported by SIMPER and plotted in Figs 12, 13) changed in a few cases. None of these effects had material impact on the interpretations or conclusions drawn from the original results.

Discussion

The contrast of historical and re-survey records convincingly rejected the null hypothesis that there was no difference in assemblage composition between the two survey periods. The separation of periods was the most obvious feature in plots of unconstrained ordination (Fig 11) and the period effect was attributed a dominant proportion (up to 47%) of the variance explained by the multivariate model (Table 3). In addition to the changes between periods, the multivariate model confirmed assemblage differences among sites, as well as an influence of depth on the community.

The striking transformation of the community assemblage was driven by previously dominant species that were absent or rare in the re-survey, as well as a suite of taxa that were numerically sparse in historical surveys but increased to make up the majority of 2015 assemblages (Figs 12, 13). The most severe catch declines were on average seen in *Argyrosomus* spp., *P. laniarius*, *A. pectoralis*, *A. argyrozona* and, at Mossel Bay, *R. globiceps*. *Argyrosomus* spp., *P. laniarius* and *A. pectoralis* dominated the composition of historical surveys at each of the three sites, contributing 70-84% of historical catches. Their relatively consistent proportions (roughly a quarter each) across sites indicates that these three taxa may have been dominant throughout similar habitats in historical, south-coast, inshore areas. If so, they would have had a significant influence on the trophic ecosystem at that time. This may be especially relevant for *Argyrosomus* spp., as their large size and varied diet would have exerted substantial predation pressure on the surrounding community (Smale and Bruton 1985).

The drastic decreases of the above taxa were accompanied by large increases shown in the numbers of *Chelidonichthys* spp., *Squalus* spp., *M. capensis* and *T. capensis* caught in repeat surveys. Whereas the joint historical contribution of these taxa was 5% at Bird Island and 2% at the two other sites, their numbers contributed 73-87% to the re-survey assemblages. Abundances of these taxa were less consistent across re-survey sites, with *M. capensis* more numerous at the two western sites and *Squalus* spp. exceptionally abundant at the eastern site of Bird Island. Inspection of the first five years of DAFF trawl survey data (1986-1990) indicated that the above replacement of dominant taxa had already taken place by the start of the modern-era trawl surveys.

Factors affecting species abundances between periods

Life-history characteristics are frequently cited as determinants of the sensitivity of populations to fishing pressures, including fecundity, age at maturity, spawning strategies, growth rate, longevity and body size (Stevens et al. 2000; Rogers and Ellis 2000; Graham et al. 2001; Genner et al. 2010; McHugh et al. 2011). Declines of elasmobranch taxa, for example, are often explained by their low fecundity, slow growth and/or old age at maturity (Stevens et al. 2000; Graham et al. 2001; Ferretti et al. 2010; McHugh et al. 2011). Yet in the current study, neither life-history characteristics nor taxonomy appeared to effectively separate taxa that had increased from those that had decreased. While abundances of Torpediniformes declined across sites, the numbers of some elasmobranchs, such as *Squalus spp.*, Myliobatiformes and Carcharhiniformes increased overall (Appendix), even though it must be noted that those increases were predominantly due to large catches at one site (Bird Island). Rajidae appeared to decline at the two western sites but were caught in far greater abundances in the Bird Island re-survey.

Habitat preferences may provide insight to the potential drivers of observed assemblage changes. Multiple taxa that declined substantially (*Argyrosomus* spp., *P. laniarius*, *A. argyrozona*, *R. globiceps*) are associated with reef habitats to varying degrees (Mann 2013 and references therein). On the contrary, the majority of species that increased between surveys tend to prefer soft substrates (e.g. *Chelidonichthys* spp., *Squalus* spp., *G. feliceps* and Rajidae) or inhabit both soft and hard benthic substrates (*M. capensis*; Mann 2013). The surveyed sites have remained commercial trawling grounds since the historical surveys took place. Therefore reef-like habitat, consolidated substrate or structure-forming communities that may have been present historically, are likely to have been removed or degraded by over a century of trawling activity (Engel and Kvitek 1998; Auster and Langton 1999; Moran and Stephenson 2000; McConnaughey et al. 2000). Habitat complexity is reduced by trawling in multiple ways (Auster and Langton 1999), including the removal and damage of emergent and high-biomass fauna, which may become replaced by smaller-bodied and infaunal animals (Kaiser et al. 2000). The change from a partially-reef-associated assemblage to a catch composition that is dominated by taxa associated with unconsolidated benthic habitats, supports the expectation that extensive trawl activity has modified the benthic habitats on these inshore trawl grounds. If the sediment structure has been modified by trawling at these sites (Auster et al. 1996), the benthic habitat, together with parts of the fish community dependent on it, may be permanently altered and fail to recover, even if fishing were to cease.

Sainsbury et al. (1993) document a case study in which trawl-related habitat changes appeared to drive fish assemblage changes: The catch composition of the north-west Australian trawl fishery changed markedly over time, even though total catch rates remained relatively stable (Sainsbury et al. 1993). During initial stages of exploitation in the 1960s, two valuable genera (*Lutjanus* spp. and *Lethrinus* spp.) made up about half of a multispecies fishery. Following two decades of escalating trawl pressure, their catch contribution fell to 10% in the mid-1980s. The catches of epibenthic fauna (mainly sponges, alcyonarians and gorgonians) declined over the same period, while two less-valuable fish genera (*Nemipterus* spp. and *Saurida* spp.) increased substantially in their contribution. Further investigation showed that the latter genera preferred areas of open sandy substrate, while the commercially-valuable taxa that had decreased were associated with dense epibenthic cover that was removed by trawling activity (Sainsbury et al. 1993). It is quite conceivable that habitat-related assemblage changes similar to those documented in north-west Australia (Sainsbury et al. 1993) played out during the early years of trawling, both in South Africa and other parts of the world. Trawl intensity has been linked to changes in epifaunal and infaunal communities on South Africa's west coast (Atkinson et al. 2011a), but those changes were relatively recent and from an environment that had been extensively trawled prior to the study. As fishers and scientists generally paid little attention to quantifying catches of invertebrate fauna until relatively recently, evidence of pre-disturbed benthic baselines and their subsequent changes will be hard to come by (Callaway et al. 2007).

Reduced habitat heterogeneity would be expected to diminish the richness and diversity of the demersal fish community, as was shown by results here (Figs 14, 15) and has been found in other long-term studies of trawl-caught assemblages (Greenstreet and Hall 1996; Rijnsdorp et al. 1996; Greenstreet et al. 1999). The fact that *A. argyrozona*, a reef-associated bentho-pelagic species (Brouwer and Griffiths 2005) was abundant at Cape Infanta and Mossel Bay historically, seems to suggest one of two explanations: 1) There used to be patches of reef-like habitat within those trawl grounds, and/or 2) their preference for reef habitat follows a density-dependent basin model (MacCall 1990), whereby they expanded into non-reef areas when abundant, but contracted to reef habitats as their populations declined from exploitation.

Geographic distribution range and depth are additional factors that might separate taxa that increased and decreased during the study period. *Argyrosomus* spp., *P. laniarius*, *A. pectoralis* and *R. globiceps* are restricted to relatively shallow depths (≤120 m), generally close to the coastline. Sought-after fishing targets that are limited to shallower coastal areas will inherently suffer greater fishing pressure, as they are in easy reach of the majority of fishers and fishing gears. The impact of line-fishing sectors (made up of commercial, recreational and subsistence fishers) has certainly played a substantial role in the decline of several taxa shown here (Mann 2013). Most taxa that increased (*Chelidonichthys* spp., *Squalus* spp., *T. capensis*, *M. capensis*) have a substantially wider distribution in terms of distance from the coastline and depth. Besides the fact that their greater distribution may allow larger populations, such taxa are also more likely to have maintained refuges that are inaccessible or uneconomical to exploit. Both proposed explanations pertaining to the observed pattern of assemblage changes, namely habitat preferences and spatial distributions of taxa, implicate fishing pressure as the likely agent of change.

Temporal and spatial differences in assemblage

The variability (dispersion) among recent trawl samples was greater than that observed historically (Fig 11). Two primary reasons appeared to be responsible: 1) The Bird Island samples had diverged from the remaining two sites, and 2) Mossel Bay samples showed far greater variability relative to all other period-site combinations.

Re-survey catches at Bird Island were notably larger than at the other two sites, due to considerable abundances of *Chelidonichthys* spp., *G. feliceps* and a host of elasmobranchs (*Squalus spp.*, Rajidae, Myliobatiformes and Carcharhiniformes). Inspection of the last decade (2006-2015) of DAFF trawl survey data suggested that some of these re-survey catch contributions were unusual (detailed in Chapter 4). Yet the same data do support the finding that Bird Island catches of *Chelidonichthys* spp., *Squalus spp.*, Myliobatiformes and all taxa combined have recently been higher at Bird Island than those of the other two sites. It appears that the Bird Island site may have recently supported a trawl assemblage somewhat different (and richer in overall catches) from those of the other two sites. Although richer in fish abundances, the majority of those greater numbers appear to consist of low-value or discarded taxa and therefore do not necessarily imply economically-richer catches compared to the western two sites.

It is worth noting that summed standardised catches were historically lowest at Bird Island and increased westwards to highest levels at Cape Infanta. This contrasts with recent re-survey and DAFF data, which show Bird Island catches to be larger than at the western two sites. A measure of multivariate variability between historical and re-survey samples indicated that the divergence between periods was lower at Bird Island than at the other sites (Fig 16). These findings imply that current demersal communities have been impacted less severely at Bird Island than at Cape Infanta and Mossel Bay. There may be multiple reasons for this: Relative to the other sites, trawl intensity in recent decades has been lower at Bird Island and declined notably in the few years preceding the repeat survey (detailed in Chapter 5). In addition, the site is adjacent to the Bird Island MPA and in relative proximity to the eastern-most boundary of commercial trawling activities for the last 40+ years (Booth and Hecht 1998). Therefore its location may be influenced by nearby refuges from fishing impacts (including from trawl impacts to the east), which could contribute greater resilience and spillover from such lesser- or unfished areas. It must be acknowledged that the Cape Infanta site is also adjacent to an MPA, which has been shown to benefit surf-zone fish (Bennett and Attwood 1993). The spillover benefits of such MPAs to demersal trawl communities have not been tested in SA. Neither has the effect of bay closures to trawling, some of which were instated as early as 1928 (Sink et al. 2012b). Investigation of habitats and demersal communities inside and outside these protected areas may provide valuable insight on fishing-induced habitat impacts, their recovery and the efficacy of protection to benthos and associated demersal fauna.

The high abundances of *G. feliceps*, Rajidae and Carcharhiniformes encountered in the Bird Island re-survey, together with unusual catches of warm-water species such as sixgill sawshark (*Pliotrema warreni*) and blueskin seabream (*Polysteganus coeruleopunctatus*), suggests that some anomalous faunal abundances were encountered during the repeat survey at this site. The Bird Island bottom waters were well oxygenated and had temperatures ranging 14.1-16.8 °C, which do not appear to be outside of the norm (Goschen and Schumann 1990; Smale et al. 1993; Roberts 2005). Anomalous abundances of certain taxa cannot be explained from the limited environmental data included in the study. Monitoring of future catches in that area, examination of satellite data relevant to the re-survey period, as well as more in-depth investigation of long-term oceanographic data may help shed light on why large abundances of certain taxa were encountered. Although unexplained, such variability, assumed to be environmentally driven, highlights the importance of having included multiple sites in the long-term comparison.

The inflated dispersion seen amongst Mossel Bay samples could conceivably be driven by gradients of environmental variables within the re-survey area (across time or space), which might structure the catch composition and increase variability among samples. An increased range of benthic habitat types is unlikely, as trawling is expected to have reduced rather than enhanced habitat variability (Auster and Langton 1999). However, spatial or temporal gradients in relevant water-column variables might have affected the community. As reported in the Results section, a clear depth-related gradient in near-bottom dissolved oxygen concentrations was found at Mossel Bay, with shallower parts of the re-survey area characterised by relatively low values (1.5-2 $ml \cdot l^{-1}$). While above the level defined as hypoxic (1.43 $ml \cdot l^{-1}$; Diaz and Rosenberg 1995), these concentrations may affect demersal species richness (Breitburg 2002) and catches might be expected to decrease at such low concentrations. Yet contrary to such expectation, larger and more species-rich catches were made at shallower, lower-oxygen stations (Tables 5, 6). Nonetheless, a contribution towards spatial structuring of the community by oxygen or another unmeasured environmental variable cannot be discounted.

A further explanation for the high dispersion seen at Mossel Bay might be degradation of the trawl community due to persistent anthropogenic pressures. Caswell and Cohen (1991) predicted that disturbance would increase heterogeneity within a community. Warwick and Clarke (1993) demonstrated that multivariate variability was associated with stress or degradation across four examples of widely varying marine communities, which prompted them to develop an index to quantify it. Of the three survey sites, Mossel Bay appears to experience the highest level of anthropogenic pressures (Sink et al. 2012a). Human impacts at or near this site include an industrial town and large harbour (including oil and gas terminal), offshore petroleum and gas exploration and production, including pipelines to the onshore refinery, and relatively intense fishing activity in the area. Various fishing and pollution pressures combined, perhaps together with climate stress, may have resulted in a heavily-impacted, sparse demersal fish community at the Mossel Bay survey site. The fact that standardised catches summed for all taxa were slightly lower at Cape Infanta than Mossel Bay, yet did not suggest inflated dispersion among samples there, does not fit this theory. Yet DAFF trawl survey data averaged over the last 10 years do indicate lowest catches at Mossel Bay, where they were 31% and 52% lower than at Cape Infanta and Bird Island respectively.

Substantial differences in the magnitude of standardised catches between Bird Island and the two western sites was similarly reflected in the species richness among sites, with the Bird Island re-surveys recording approximately twice the number of taxa found at the other two sites (Fig 14). Although the taxonomic resolution imposed by historical records requires caution, it appears as if species richness has declined, at least at the two western sites. In Bird Island re-survey samples, the diversity of species included in grouped taxa (especially 'other fish') may equal, or even exceed, the loss of multiple taxa recorded in historic samples there. Taxonomic richness seemed to be greater at Mossel Bay and Bird Island than at Cape Infanta historically, whereas in the re-surveys richness was low at the two western sites and higher at Bird Island. Yemane et al. (2010) indicated that species richness was relatively high between 20° and 22°E (which includes Cape Infanta), then declined to a minimum at about 24°E (approximately half-way between Mossel Bay and Bird Island) before increasing to the highest values in the eastern-most parts of the survey area (near Bird Island). Although those results apply to a far broader shelf area than the inshore parts focused on here, they are congruent with highest taxonomic richness in the eastern area around Bird Island.

Diversity appeared to be suppressed but taxonomic evenness was similar (elevated at Cape Infanta) in re-survey catches, relative to the historical data (Fig 15). Previous studies comparing long-term trawl survey data over time tend to report a decrease in diversity as well as evenness (e.g. Greenstreet and Hall 1996; Rijnsdorp et al. 1996; Greenstreet et al. 1999). However the potential bias caused by the grouped taxonomy inherited from historical records makes such diversity contrasts difficult to interpret and further discussion of these indices is limited to their comparison with depth and trawl distances below.

Comparison with previous studies

McHugh et al. (2011) documented notable changes in the demersal community of the western English Channel between historical (1913-1922) and repeat surveys almost a century later (2008-

2009). Although they did separate statistically, their ordination did not show strikingly disparate periods as seen in Fig 11. In their case, differences were driven predominantly by alterations in the elasmobranch assemblage, which was interpreted as evidence of the loss of larger, slow-growing taxa due to fishing pressures (McHugh et al. 2011). In ordinations of survey data from historical (1929-1953) and more recent (1980-1993) periods, Greenstreet and Hall (1996) found almost orthogonal separations of a period and site effect, which is a commonality with results here. They interpreted it as evidence that the two effects were largely additive with little interaction between them.

Some North Sea studies have shown 20th century demersal assemblage changes to have consisted of relatively subtle abundance changes of mostly less common species (Greenstreet and Hall 1996; Greenstreet et al. 1999; Rogers and Ellis 2000). To illustrate, Greenstreet et al. (1999) noted that the same five dominant species contributed over 50% of similarity across all four periods they examined between 1925 and 1996. The assemblage changes documented in the current study appear to have been substantially more severe.

Few other studies have had access to demersal survey records prior to, or early in the development of a trawl fishery. Of those that did (Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Klaer 2001; Kongprom et al. 2003; Mussgnug 2013), most did not conduct multivariate analyses comparable to those focused on here. However, some commonalities can nonetheless be identified with their results. Klaer (2001) documented strong declines in overall commercial catch rates between 1918-1957 in the south-east Australia trawl fishery, despite substantial technological improvements during that time. Drastic changes in the composition of catches included the virtual disappearance of two species that had been abundant during early years of the fishery. Trawl surveys were conducted on the upper continental slope in 1976/1977, before the fishery expanded into those deeper waters. Twenty years later, when a repeat survey was conducted, the initially dominant taxa of dogsharks (*Centrophorus* spp.) and redfish (*Centroberyx affinis*) had declined to <1% and <5% of initial catch rates, respectively (Andrew et al. 1997). Many other species showed notable declines in size and abundances, with the overall catch rate falling to 32% of that recorded in the pre-fishery survey. On the northern coast of Australia, Harris and Poiner (1991) similarly showed that two decades after the development of prawn trawling in the Gulf of Carpentaria, the combined catch rate of all fish had declined to less than half of initial values. A previously dominant taxon (*Paramonacanthus* spp.) had also collapsed over this time. Their results recorded substantial changes in the fish community during the relatively short duration of the fishery.

Mussgnug (2013) included the same historical data and investigated comparable geographic areas to those of the current study, although he focused predominantly on chondrichthyan taxa and did not have the benefit of repeat survey data used here. He conducted similar ordination and SIMPER analyses to those reported here, therefore agreement between results of the two studies was expected. Mussgnug (2013) also found significant multivariate differences between historical (1898-1933) and recent (1985-2010) periods. Congruent with decreased abundances shown here, he suggested that catch contributions of *P. laniarius*, *A. inodorus*, *A. pectoralis*, *A. argyrozona*, *Umbrina canariensis* and *R. globiceps* had declined between the two periods. He also reported increases in catch contributions for *T. capensis*, *M. capensis* and *Chelidonichthys* spp., in agreement with results from the current study. The main discordance between the two studies pertains to elasmobranch taxa: Mussgnug (2013) emphasised decreases in the contributions of all elasmobranch taxa, whereas average abundances of most elasmobranch taxa (*Squalus* spp., Rajidae, Myliobatiformes, Carcharhiniformes) increased between periods in this study (Appendix). Such a discrepancy might be explained by the point alluded to previously, that unusually high abundances of chondrichthyan taxa (and *G. feliceps*) appeared to be encountered in the Bird Island repeat survey. These apparently anomalous abundances may have biased the comparison between periods for those taxa. As Mussgnug (2013) used multiple datasets spread over many years, his comparisons should be more robust to temporary anomalies. A considerable benefit of the current results over those reported by Mussgnug (2013), however, is that differences in trawl gear and trawl speeds were explicitly examined and effectively removed, thereby addressing a large uncertainty in results and lending them to a greater range of analyses and applications. Nonetheless, most of the results appear to agree between the two studies.

It appears that the few studies with access to records from the beginning of a trawl fishery (or earlier) demonstrate more drastic assemblage changes than those based on initial data collected many years after the development of fishing pressures. This implies that the magnitude of change measured in long-term trawl survey comparisons depends to a large degree on the state of initial communities sampled. If so, this highlights the erosive effect of shifting baselines (Pauly 1995) and the importance of reconstructing pre-disturbed reference points to counter it. The majority of research into long-term demersal assemblage changes has been based in Northern Hemisphere regions, where decades, if not centuries of trawling preceded the earliest available survey records (e.g. Greenstreet and Hall 1996; Rijnsdorp et al. 1996; Greenstreet et al. 1999; Genner et al. 2010; ter Hofstede and Rijnsdorp 2011; McHugh et al. 2011). Those studies provide useful reference points from periods when most anthropogenic pressures were lower, yet the historical systems they document had already suffered substantial exploitation impacts and were not representative of near-pristine ecosystems (Thurstan et al. 2010; McHugh et al. 2011). This study, on the other hand, had access to trawl survey data from relatively pristine demersal communities. If North Sea demersal assemblage data could be reconstructed from 300 rather than 100 years ago, subsequent changes might appear equally striking as in this study.

Examination of assumptions

Factors that might bias comparisons between historical and re-survey trawl catches were accounted for as far as was possible. These included the standardisation of factors such as season, time of day, geographical locations and replication of gear. Nonetheless contrasts of the historical and re-survey catches require examination of certain assumptions. These included that 1) the catches were not biased by different (gear or vessel-related) fishing performances between the two surveys; 2) differences in trawl distance (duration) did not bias catch rates; 3) a depth bias at Bird Island did not impact comparisons; 4) shorter-term interannual variability was not responsible for the changes observed; and (5) the taxonomic resolution imposed by historical records did not confound results or inferences drawn. Each of these was carefully considered and their consequences are discussed below.

Trawl gear performance

The historical trawl gear was carefully imitated in design, materials and function and the resultant gear selectivity and catching power are expected to be closely related to those of the historical trawl gear (Chapter 2). Although the range of realistic values is conscribed, the exact dimensions of the historical trawl net are not absolutely certain. Similarly, there is some uncertainty around the trawling speed attained by the Pieter Faure. In such cases, 'best estimates' had to be made based on available evidence and analyses employ these estimates, assuming that they are representative of historical fishing power. Trawling speeds and net headline lengths are central to the standardisation of catches and incorrect assumptions about them may result in incorrect catch rates. However, assessment of the most extreme bias that might result from the combination of these two variables in the calculation of standardised catches confirmed that they would have negligible effect on the results and interpretations reported here. Therefore even though some uncertainty remains in relation to the replication of the historical trawl gear and methods, the results of analyses appear robust to such uncertainty.

Trawl distances

The trawl duration and resulting distance covered under tow is considered to be the largest operational difference between periods contrasted. The historical trawl samples were of typical commercial duration at that time (~1-3 hours), likely because their surveys were subsidised by sale of the catch, creating incentive for relatively large, commercially-profitable catches. Recent research surveys typically use shorter tows (Walsh 1991; Battaglia et al. 2006; Wieland and Storr-Paulsen 2006) that balance efficiency with attaining ecologically-meaningful samples. Due to economic (time) constraints, the repeat survey employed ~30 minute trawls, similar to the national and some international trawl survey protocols (ICES 2012).

Although there are theories to explain changes in catch rates with changing trawl length, empirical support of such effects seem limited to comparisons of short trawl tows (≤15 minutes). Walsh (1991) and Godø et al. (1990) found greater catch per unit effort (CPUE) for various demersal fish in the shortest (5-minute) trawls, but not when they compared 15- and 30-minute trawls. Wieland and Storr-Paulsen (2006) concluded there was no effect on shrimp or halibut CPUE in their comparison of 15- and 30-minute trawls. Investigating three crab species, Somerton et al. (2002) showed that CPUE was significantly greater in 15-minute tows compared to 30-minute trawls for two of their taxa. None of the above studies found an effect of trawl length on the sizes of individuals caught. Elevated catch rates in short-duration trawls are likely due to a proportionally greater impact of the 'end effect' - catches taken during shooting and hauling of the net, the time of which is frequently excluded from the tow duration (Battaglia et al. 2006). These end effects were removed from the re-survey catches here and were assumed to have minimal effect on the longer-duration historical trawls.

Evidence of a trawl distance effect on catch composition and diversity measures was found, but only in the historical Cape Infanta samples (Tables 5 and 7). The expectation might be that longer trawls would integrate the uneven distribution of fish and result in greater taxonomic evenness. Instead, lower evenness was indicated for longer trawl distances (Table 5). Further investigation of Cape Infanta data showed that both depth (positive) and trawl distance (negative) were correlated with total standardised catch (Table 6) and that there was a correlation between trawl distances and their depth. The observed correlations with trawl distance are attributed towards the behaviour of the fishing master in historical surveys: Trawl distances (durations) appear to have been lengthened when fish were relatively scarce and shortened when fishing was more productive, likely due to the economic incentive to fill the net. This behaviour would act to confound catch variability with an apparent (negative) relationship between catch rates and distance, as was observed (Table 6). For whatever reason, the catch rates were lower in shallower parts of the historical Cape Infanta survey area (Table 6). The lower catches at shallower stations may have resulted in the positive relationships between depth and evenness/diversity in those samples (Table 5). Such depth effects, together with the behavioural response of the fishing master described above, are expected to have produced the observed correlation between evenness and trawl distances (Table 5).

A related assumption implicit in comparison of the historical and re-survey catches is that the magnitude of catches did not bias selectivity or catch rates. It is likely that as a trawl net fills with catch, its geometry and water flow through the net are affected (Somerton et al. 2002; Battaglia et al. 2006), thereby influencing the escapement of fish. The assumption was made that catch rates and selectivity remained approximately constant across different trawl distances and catch sizes. Although an impact of catch size on net performance cannot be discounted, such potential bias is expected to be relatively small in that it likely biased few samples (that had the largest catches) and was most likely to affect only a small proportion of the entire trawl tow (once the net had filled to a capacity where its catch rate was affected). Somerton et al. (2002) found no evidence that differences between 15- and 30-minute catch rates were related to the total catch size.

To verify whether the apparent (historical Cape Infanta) trawl distance effect might bias conclusions in any way, the complete set of analyses were repeated on a dataset that omitted Cape Infanta trawls with a distance greater than five nautical miles. The deductions and conclusions drawn from the reduced dataset did not differ from those of the full dataset.

Bird Island depth bias

As repeat trawl locations were chosen randomly from the grounds surveyed historically, depths were expected to be similar between periods. However a difference in depth distribution was found at Bird Island and an effect of depth on community composition was seen at Bird Island (both periods) and Cape Infanta (re-survey only; Table 7). Impacts of depth on richness and diversity measures were also seen, as has been discussed above. As it was clear that depth did influence catches in some cases, it was included in analyses where possible.

Causes of the unexpected Bird Island bias in depth are unclear but appear to be due to error in historical measurements. The depths recorded for many of the Bird Island historical trawl samples appear to be too shallow compared to nearby re-survey trawls and a 10-m resolution GIS bathymetry layer (not shown). The location of historical trawls may have been estimated inaccurately (with a systematic bias of overestimating the distance to shore), or the depth measurement may have been negatively biased, perhaps due to exaggerated correction of sounder measurements that had been affected by currents and/or wind drift. The currents experienced in this area are generally stronger than at the other two sites (Less, personal communication 2015). In case this bias was real and to assess its impact on results, analyses were repeated with a dataset that excluded seven Bird Island re-survey samples deeper than 100 m. Although the results had reduced statistical power, they did not show material differences to those presented.

Long-term signal vs short-term variability

Trawl catches are potentially affected by multiple sources of variability over relatively short time-frames (Arreguín-Sánchez 1996; and references therein). These could include natural- or anthropogenic-driven abundance changes over interannual time-frames, catchability variation due to changes in weather/oceanography (influencing behaviour of fish or fishing gear), and seasonal changes in their catchability due to altered reproductive or feeding behaviour. An experimental design contrasting long-term changes would therefore be more powerful at isolating long-term differences from such shorter-term variability if it included multiple years of data for each period. Unfortunately neither the historical data nor the repeat surveys allowed use of multi-year data. It might be argued that had the surveys taken place in another year, the results may have differed. To address this point, the magnitude of typical seasonal, interannual and multi-year variability was compared to the variance observed between historical and re-survey periods. Those results (Fig 16) confirmed that the magnitude of change documented between periods was substantially greater than short-term variability captured in DAFF trawl survey data. The sampling of three geographically distinct sites in different months is also expected to reduce the impact of potential short-term bias. The major part of measured between-period differences are therefore attributed towards long-term change that has occurred in the studied assemblages.

Taxonomic limitations

The taxonomic resolution imposed by the historical records (Table 2), requires consideration during interpretation of results. For example, within this taxonomic framework two hypothetical samples with identical species-level richness, diversity or evenness, but a different composition of species, could conceivably exhibit different measures of those indices. Because of this, interpretation of the indices was focused within period-site levels (in relation to depth/distance) or cautiously among sites within a period, assuming that the grouped taxa likely had comparable compositions within a period. Clearly changes in the composition of grouped taxa cannot be resolved here. The 'other' category of fish is especially problematic, as it has almost no taxonomic or ecological meaning to it. Assumedly this group was historically used to pool taxa that were relatively rare and not considered of economic interest. Although included in analyses, interpretation of changes in the 'other' taxon group was therefore not a focus.

The consequence of grouped taxa on comparisons of assemblage composition are expected to dampen differences among samples, because opposing species-level abundance changes within a group would be concealed (Dulvy et al. 2000). It is important to note, therefore, that long-term variability documented here may provide a conservative gauge and that it may have missed important declines or increases within the grouped taxa. Dulvy et al. (2000) document a case where the disappearance or decline of large skates was masked by the increase of two smaller species when skate (Rajidae) catches were not disaggregated. Such an explanation might contribute towards the lack of average declines seen in this study for Rajidae, Myliobatiformes and Carcharhiniformes, despite drastic alterations in several other taxa. Thus results reported here should not necessarily be interpreted as evidence that elasmobranchs in general have escaped fishing or other impacts.

Future research

The contrasts of historical and recent assemblages raise further questions that may identify fruitful avenues of future research. More rigorous examination of abundance changes of individual taxa and the implications of size changes between periods is explored in Chapter 4. Applying indices such as mean temperature (Cheung et al. 2013), mean trophic level (Pauly et al. 1998) or piscivore/zooplanktivore ratios (Caddy and Garibaldi 2000) could add ecological insight to the long-term assemblage comparisons. The use of additional survey and commercial datasets might allow one to isolate the timing and better understand the drivers of some of the observed changes. Together with a comprehensive spatio-temporal reconstruction of fishing effort, such interrogation could go some way in clarifying past relationships between fishing pressures and the responses of taxa or assemblages. Useful insight might also be gained by assessment of the relationships between recent demersal catches and cumulative trawl pressures, as demonstrated by Foster et al. (2015). The inclusion of historical in situ and hindcast environmental data into formal statistical frameworks may similarly clarify the role of temperature and other variables in structuring the demersal communities.

As historical surveys used here do not appear to have consistently reported details of invertebrate catches, it may be difficult to reconstruct a picture of pre-disturbed benthic habitat in areas that have been trawled. Some of the historical records include remarks of the seafloor substrate (ascertained by a sounding lead) and damaged nets or unusual catches of rocks or invertebrates. Collation of those records into a geographic information layer might provide a useful start to address the question of historical habitat distributions.

Conclusion

The historical survey data provide valuable insight into near-pristine, temperate, demersal communities on the inshore Agulhas Bank and how they have changed. Much of this value was unlocked by the replication of surveys in 2015, which enabled quantitative comparisons of recent demersal fish assemblages with their pre-disturbed state in 1903-1904. The comparison showed that these assemblages have undergone striking changes between the beginning of the 20th century and the present.

The severity of the assemblage reorganisation, relative to comparable investigations elsewhere, is interpreted to be due to the near-pristine state of the historical community surveyed. The majority of studies may miss the initial, and perhaps most dramatic, shifts in assemblage composition if they lack baseline data collected prior to substantial exploitation. In the current study, these changes included the depletion or virtual disappearance of previously dominant taxa that were not resilient to exploitation and other human pressures. They were replaced to some degree by opportunist species, frequently smaller, faster-growing generalists that withstood or even benefited from the disturbances. While natural population fluctuations may have partly contributed to observed changes, the majority of severe declines and substantial increases are attributed to fishing and other human pressures.

Habitat preferences, as well as geographic and depth distributions, appeared to separate the taxa that have declined from those that became more numerous. Over a century of commercial trawling is expected to have altered epifaunal communities and reduced structural complexity on the sea-floor (Engel and Kvitek 1998; Auster and Langton 1999), favouring taxa that inhabit unconsolidated 'soft-grounds' over those that prefer reef-like or more heterogeneous habitats. If substantial trawling predates the baseline data, such potential habitat impacts would be (and probably have been) missed in other similar studies.

Additional human impacts, including other fishing sectors, climate change and pollution may have contributed to the state of the demersal assemblages investigated. Improved management of these communities will require interventions that address impacts from multiple sources. MPAs can be an effective management tool to address multiple pressures and safeguard resilient assemblages of non-mobile taxa (Bennett and Attwood 1991; Dayton et al. 2000; Micheli et al. 2012; Mellin et al. 2016), together with their critical habitats (Lindholm et al. 2001; Kritzer et al. 2016).

Appendix: Supplemental tables and figures

Table A2. SIMPER results showing the contribution of all taxa towards dissimilarity between periods. Average dissimilarity between periods was 81.7%. Standardised catches (count·nautical mile^{-1}) were square-root transformed prior to analysis.

Taxon	Historical average	Re-survey average	Dissimilarity (D)	Ratio (D/sd)	Cumulative contribution to D
Argyrosomus spp.	6.68	0.00	12.06	1.89	14.76
Pterogymnus laniarius	6.61	0.34	11.28	2.35	28.56
Austroglossus pectoralis	6.62	1.21	9.94	2.09	40.73
Chelidonichthys spp.	0.64	5.53	8.32	1.46	50.90
Argyrozona argyrozona	3.39	0.02	5.99	0.98	58.23
Trachurus trachurus	0.39	3.20	5.27	0.86	64.68
Squalus spp.	0.89	3.68	5.09	0.78	70.91
Merluccius capensis	1.06	2.72	3.74	1.29	75.49
Rhabdosargus globiceps	1.62	0.01	3.03	0.84	79.20
other	0.28	1.90	2.76	1.35	82.58
Galeichthys feliceps	0.03	1.69	2.61	0.62	85.77
Torpediniformes	1.27	0.11	2.17	0.94	88.43
Umbrina canariensis	1.25	0.03	2.13	1.21	91.03
Rajidae	1.25	1.35	2.12	1.60	93.63
Myliobatiformes	0.25	1.03	1.47	0.66	95.43
Cynoglossus spp.	0.42	0.78	1.17	0.97	96.87
Carcharhiniformes	0.20	0.47	0.77	0.98	97.81
Paracallionymus costatus	0.20	0.06	0.41	0.49	98.31
Atractoscion aequidens	0.29	0.02	0.39	0.51	98.78
Lithognathus lithognathus	0.17	0.00	0.27	0.64	99.11
Pomatomus saltatrix	0.17	0.00	0.26	0.51	99.43
Chrysoblephus gibbiceps	0.05	0.00	0.11	0.26	99.56
Genypterus capensis	0.07	0.00	0.1	0.36	99.69
Petrus rupestris	0.06	0.00	0.1	0.35	99.80
Polysteganus undulosus	0.06	0.00	0.08	0.30	99.90
Pachymetopon aeneum	0.03	0.01	0.07	0.25	99.99

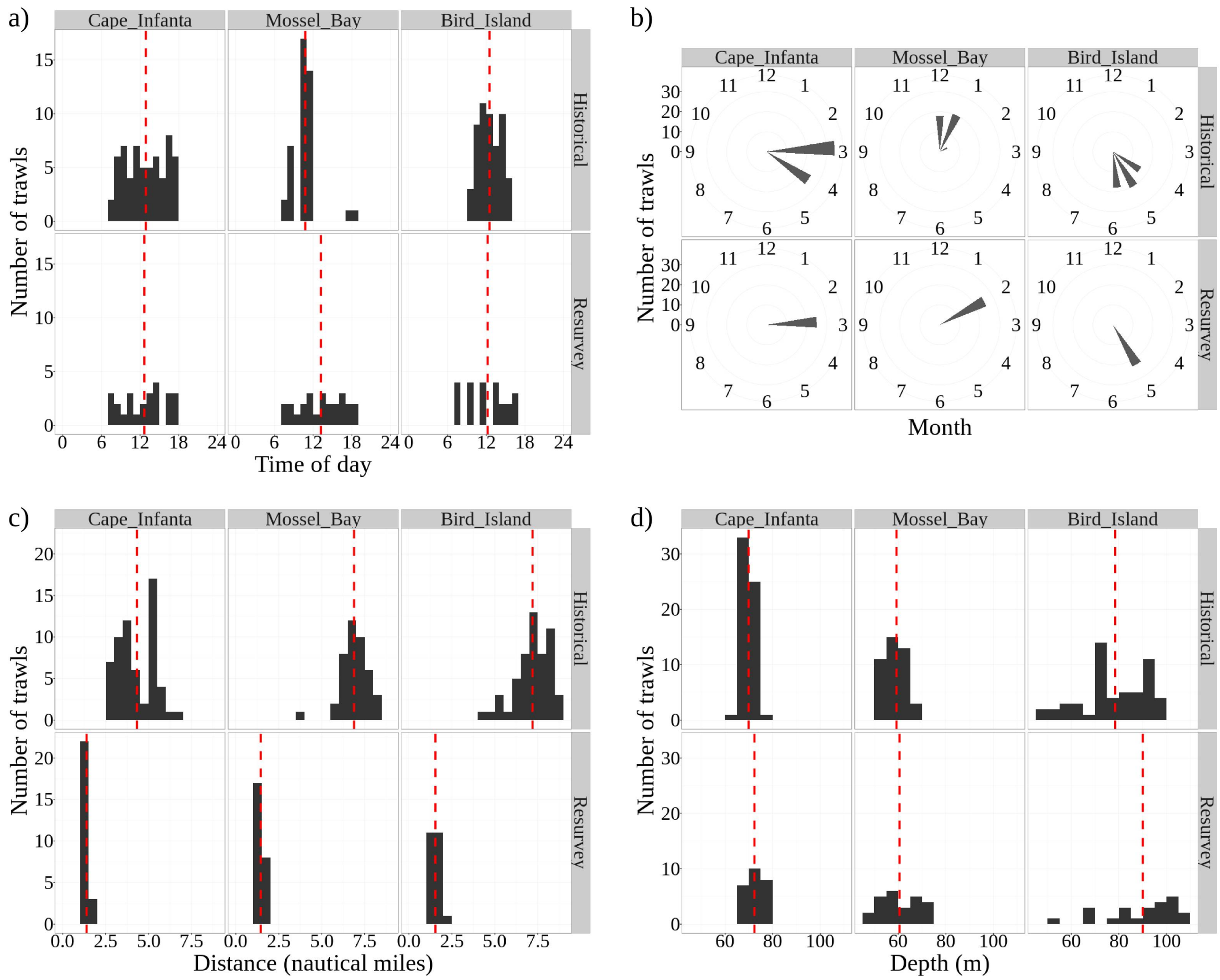


Figure A3. Histograms contrasting historical and re-survey trawl sample a) mid-trawl times, b) months, c) trawl distance and d) trawl depths for the data used in analyses. Vertical red lines indicate mean values.

Table A3. Site-disaggregated summary statistics (mean ± *SD*) for catches of all taxa analysed. CI Cape Infanta, MB Mossel Bay, BI Bird Island.

Taxon	**Historical numbers (count·nautical mile $^{-1}$)**			**Re-survey numbers (count·nautical mile $^{-1}$)**		
	CI	**MB**	**BI**	**CI**	**MB**	**BI**
Argyrosomus spp.	97.15 ± 76.36	35.02 ± 26.85	28.61 ± 25.7	0 ± 0	0 ± 0	0 ± 0
Argyrozona argyrozona	43.88 ± 57.75	24.84 ± 36.21	3.65 ± 7.63	0 ± 0	0 ± 0	0.05 ± 0.26
Atractoscion aequidens	0.12 ± 0.95	0.01 ± 0.04	0.96 ± 1.47	0 ± 0	0 ± 0	0.06 ± 0.21
Austroglossus pectoralis	71.06 ± 27.1	48.99 ± 28.06	24.64 ± 13.44	2.79 ± 2.39	2.23 ± 3	1.58 ± 2.55
Carcharhiniformes	0.06 ± 0.15	0.15 ± 0.17	0.13 ± 0.19	0.02 ± 0.11	0.26 ± 0.55	1.67 ± 1.11
Chelidonichthys spp.	2.09 ± 4.1	1.46 ± 4.76	0.34 ± 0.75	18.8 ± 9.87	16.73 ± 17.98	110.91 ± 92.2
Chrysoblephus cristiceps	0 ± 0	0.01 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Chrysoblephus gibbiceps	0.03 ± 0.16	0.1 ± 0.34	0.01 ± 0.06	0 ± 0	0 ± 0	0 ± 0
Cynoglossus spp.	0 ± 0	0.28 ± 0.67	1.2 ± 0.87	0.39 ± 0.51	2.01 ± 2.26	1.08 ± 1.12
Galeichthys feliceps	0 ± 0	0.24 ± 0.96	0 ± 0	0 ± 0	0.59 ± 1.09	32.16 ± 33.53
Genypterus capensis	0 ± 0.03	0.02 ± 0.05	0.09 ± 0.23	0 ± 0	0 ± 0	0 ± 0
Lithognathus lithognathus	0.03 ± 0.08	0.09 ± 0.14	0.2 ± 0.33	0 ± 0	0 ± 0	0 ± 0
Merluccius capensis	2.75 ± 3.39	1.1 ± 1.18	1.67 ± 2.9	12.67 ± 6.7	16.73 ± 13.17	1.16 ± 1.79
Myliobatiformes	0.01 ± 0.04	0.19 ± 0.33	0.26 ± 0.19	0 ± 0	0.09 ± 0.24	12.86 ± 14.71
Pachymetopon aeneum	0 ± 0	0.03 ± 0.12	0.04 ± 0.12	0 ± 0	0 ± 0	0.03 ± 0.15
Paracallionymus costatus	0.04 ± 0.18	0.69 ± 1.26	0.07 ± 0.27	0 ± 0	0.08 ± 0.22	0.06 ± 0.21
Petrus rupestris	0.02 ± 0.07	0.06 ± 0.13	0.01 ± 0.06	0 ± 0	0 ± 0	0 ± 0
Polysteganus undulosus	0 ± 0	0 ± 0	0.13 ± 0.32	0 ± 0	0 ± 0	0 ± 0
Pomatomus saltatrix	0.01 ± 0.09	0.1 ± 0.19	0.29 ± 0.68	0 ± 0	0 ± 0	0 ± 0
Pterogymnus laniarius	52.55 ± 24.53	51.13 ± 30.62	46.02 ± 39.54	0.06 ± 0.2	0 ± 0	3.57 ± 9.43
Rajidae	2.38 ± 1.68	2.21 ± 1.35	0.91 ± 0.51	0.6 ± 0.76	1.63 ± 2.11	8.22 ± 5.46
Rhabdosargus globiceps	1.91 ± 1.81	19.89 ± 16.38	0.49 ± 1.18	0.03 ± 0.14	0 ± 0	0 ± 0
Squalus spp.	0.23 ± 0.39	1.59 ± 1.9	2.52 ± 2.92	0.09 ± 0.25	4.19 ± 14.49	130.31 ± 116.73
Torpediniformes	1.84 ± 1.53	5.38 ± 14.89	1.68 ± 1.28	0.03 ± 0.16	0.06 ± 0.19	0.24 ± 0.5
Trachurus capensis	0.03 ± 0.13	0.07 ± 0.11	1.71 ± 3.09	19.95 ± 28.34	31.26 ± 87.47	33.28 ± 78.86
Umbrina canariensis	1.59 ± 3.15	4.54 ± 7.81	2.41 ± 4.44	0 ± 0	0 ± 0	0.16 ± 0.67
other	0.01 ± 0.05	0.43 ± 0.46	0.33 ± 0.53	2.5 ± 4.61	3.1 ± 3.22	11.37 ± 7.23

Chapter 4: Comparison of 1903/1904 and 2015 demersal fish abundances on the inshore Agulhas bank

Abstract

Long-term changes in the abundances of 27 demersal fish taxa were investigated on the inshore Agulhas Bank, using the same historical (1903/1904) and repeat (2015) trawl surveys described in Chapter 3. Results focus on 11 taxonomic groups that were common either historically or in the repeat surveys. The null hypothesis, that no difference existed in catch abundances between historical and re-survey trawls, was tested using a non-parametric bootstrap approach. Historically common taxa, most of them commercially valuable, showed large decreases between the historical and repeat surveys. These included kob (*Argyrosomus* spp., absent in re-surveys), panga (*Pterogymnus laniarius;* 2.4% of historical abundance), east coast sole (*Austroglossus pectoralis*; 4.6%), carpenter (*Argyrozona argyrozona*; 0.1%) and white stumpnose (*Rhabdosargus globiceps*; 0.1%). Large increases were shown for other taxa, which included both sought-after and non-targeted species. These included gurnards (*Chelidonichthys* spp.; 3 792% of historical abundance) and horse mackerel (*Trachurus capensis*; 4 738%), while increases in spiny dogfish (*Squalus* spp.; 3 121%), hake (*Merluccius capensis*; 558%) and white sea catfish (*Galeichthys feliceps*; 13 863%) were driven by significantly greater numbers at only one or two of the three sites. Analyses of limited size information available confirmed expectations of reduced fish sizes in repeat surveys. Benthic habitat preferences appear to separate taxa that have declined from those that have increased. Long-term trawling activity likely reduced seafloor habitat complexity and modified energy flow pathways, benefiting certain taxa but costing others. Additional factors that likely influenced the success of populations during a century of exploitation, include their distribution extent, post-capture discard survival, market value and frequently-cited reproductive and life-history characteristics. Impacts of multiple fishing sectors are expected to have contributed to the observed changes at these inshore sites. Disappearance from catches and substantial declines of several taxa, including the iconic and once-dominant kob, and valuable east coast sole, signal substantial ecological consequences and economic losses.

Introduction

Historical reference points contribute a critical component to the development of effective policy advice on fisheries management and biodiversity conservation (Engelhard et al. 2016). Among other benefits, they can provide valuable context to current ecological states or measures, describe the potential productivity of undisturbed ecosystems and provide benchmarks against which long-term change can be measured or the efficacy of management strategies evaluated. Estimates of unfished species abundances provide useful diagnostics and priors to assess or constrain fishery stock assessment models (Hilborn and Walters 2001) and inform the choice of baseline conditions used in ecological models (e.g. Mackinson 2001; Watermeyer et al. 2008; Travers et al. 2010).

Despite the importance of baselines and an understanding of subsequent change, obtaining such information from the sparsely-sampled marine environment is challenging. Historical marine ecology frequently requires innovative strategies to piece together coherent evidence from a divergent range of sources (e.g. Ravier and Fromentin 2001; Lotze and Milewski 2004; Holm 2005; Rosenberg et al. 2005; Lotze et al. 2006; Callaway et al. 2007; Ferretti et al. 2008; Last et al. 2011; Barausse et al. 2014; Jones et al. 2015). This is because the era of systematic and standardised marine surveys typically post-dates widespread fishery and other anthropogenic impacts. It is rare for ecologists to rediscover a cache of historical marine survey records that detail ecological samples in a comparable manner to contemporary practices. It is far more rare that such records capture a snapshot of the marine ecosystem in a relatively undisturbed state, as was the case with the earliest trawl surveys in South Africa.

Baselines prior to extensive fishing pressure

A number of studies have investigated changes in demersal fauna by contrasting historical trawl survey records among or between periods (e.g. Greenstreet and Hall 1996; Rijnsdorp et al. 1996; Greenstreet et al. 1999; Dulvy et al. 2000; Rogers and Ellis 2000; Genner et al. 2004; McHugh et al. 2011; Heath and Speirs 2012), but only a few had access to records from before or during the initial stages of exploitation (e.g. Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Kongprom et al. 2003). The latter studies have generally revealed substantial changes in the abundances and sizes of trawl-caught fauna, markedly more severe than seen in many of the investigations that document changes from areas that had been exposed to previous trawl impacts for decades or centuries.

In a repeat survey 20 years after the development of a trawl fishery off New South Wales, Andrew et al. (1997) and Graham et al. (2001) showed substantial decreases in the catch rates of targeted and non-targeted taxa. The pooled catch rates for sharks and rays had decreased to 20% of their values in the initial survey (Graham et al. 2001), whereas all taxa combined had declined to 32% (Andrew et al. 1997). In some areas, the previously dominant redfish (*Centroberyx affinis*) was <5% of initial catches (Andrew et al. 1997). Most species for which sufficient size data were available showed marked declines in the numbers of larger individuals (Andrew et al. 1997).

In the Gulf of Carpentaria in northern Australia, Harris and Poiner (1991) compared 1985/1986 repeat surveys with initial trawl surveys conducted in 1964, before initiation of a prawn trawl fishery. Overall the catch rate declined by more than half. Eighteen taxa declined, including a previously abundant taxon (*Paramonacanthus* spp.) that had decreased 500 times, whereas 12 taxa increased in abundance (Harris and Poiner 1991).

Although Klaer (2001) did not make use of trawl surveys, he had access to remarkably detailed commercial catch data from the south east trawl fishery in Australia, including early records (1918-1923) collected shortly after commercial trawling started there in 1915. The data resolution included trawl-by-trawl catches and even the quantity of discarded fish during certain periods. Contrasted against later periods in the 1930s, '40s and '50s, the catch rates showed a strong decline over time despite improvements in fishing technology and progressive expansion into deeper and more distant trawl grounds. By the 1950s, two species that had been common in early catches had virtually disappeared and the primary target species, tiger flathead (*Neoplatycephalus richardsoni*), had suffered alarming declines (Klaer 2001). Fishing impacts, both direct (removal of fish) and indirect (modification of benthic habitat), were suggested as likely drivers of the most severe changes.

A trawl fishery developed in the Philippines from 1945 onwards. Silvestre et al. (1986) examined changes in standardised trawl catches between 1947 and 1981. Although individual taxa were not analysed, their results showed that demersal stocks had declined to 31% of those available during early years of the fishery. This was averaged across all areas and was likely far worse in the nearshore traditional fishing grounds where effort was concentrated (Silvestre et al. 1986). The authors concluded that demersal stocks were heavily depleted as a result of over-fishing.

In the Gulf of Thailand, trawling was introduced in 1960. Kongprom et al. (2003) investigated the status of its demersal fishery using trawl survey data collected between 1961 and 1995. Their estimates of demersal biomass had declined to 8.2% of the levels at the start of the time-series, driven by large declines across the dominant species groups. They noted that Dasyatidae, which were the most numerous taxon in 1966 (8.15% of assemblage composition by mass), declined especially quickly (Kongprom et al. 2003). The authors concluded that demersal resources were severely overfished and suggested that fishing capacity was approximately 50% higher than a level that would result in maximum yield.

A reduction in fish sizes is a common indicator of fishing pressure (Andrew et al. 1997; Shin et al. 2005; Yemane et al. 2008; Heath and Speirs 2012). Several studies that have assessed trawl survey catches between or amongst periods have documented declines in the sizes of taxa over time (e.g. Rijnsdorp et al. 1996; Andrew et al. 1997; Cardinale et al. 2009, 2012) or pronounced abundance declines of larger taxa (Dulvy et al. 2000; Rogers and Ellis 2000; Heath and Speirs 2012), both indicative of fisheries impacts.

Long-term change on South Africa's south coast

In South Africa, the few investigations that have examined long-term changes in catch abundances have mostly focused on line-caught species. When contrasting contemporary data with those from the mid- and early-20th century, cases of alarming declines, including virtual disappearance of previously common taxa, were shown on the south and east coasts of South Africa (Penney et al. 1989, 1999; Van der Elst 1989; Attwood and Farquhar 1999; Griffiths 2000). Catch rates from the inshore Agulhas Bank suggested 75-99% declines for several important linefish species during the 20th century (Griffiths 2000). An expectation of the expanding fishing pressures over this period would include a reduction of average sizes of fish (Shin et al. 2005; Yemane et al. 2008). Yemane et al. (2004) showed evidence of decreased sizes for seven out of 12 line-caught fish species contrasted between two historical (1897-1906; 1927-1931) and one contemporary (1986-1998) period on South Africa's south coast.

The investigations in this chapter rely on the same experimental design and datasets introduced in Chapter 3, where the focus was on long-term changes in the composition of the catch. While those multivariate analyses are typically more sensitive to change than univariate methods (Warwick and Clarke 1991), they did not detail abundance changes of individual taxa. The aim of this chapter is to provide a more in-depth and robust assessment of individual taxa, to examine their changes across the three inshore sites and estimate their current states relative to undisturbed baselines. To do so, long-term changes in catch abundances were assessed by testing the null hypothesis that catch abundances remained unchanged. Where possible, changes in size frequencies were also assessed between the historical (1903/1904) and repeat (2015) surveys. Results from these analyses were interpreted in terms of the existing knowledge of the biology, ecology and exploitation history of the relevant taxon.

Methods

To avoid duplication of information from previous chapters, the methods detailed below are predominantly those unique to this chapter. Descriptions of the site and sample selection strategy, fieldwork undertaken, datasets used, data preparation, methods used to standardise catches and taxonomic resolution available for analyses, are detailed in the Methods section of Chapter 3. Described below are the methods used to determine fieldwork sample sizes and analyses conducted in comparisons of abundance and fish sizes between survey periods. All data manipulations and analyses were conducted in the R programming environment (R Core Team 2016).

Determining sample size

Power analyses were used to assess the number of samples needed in repeat surveys. The objective was to estimate the sample size required to statistically detect abundance changes of certain magnitudes between surveys. The historical survey data were used as modern surveys employ substantially different trawl gear and speeds and are thus expected to have notably different fishing performances. The employed approach used generalised linear models (GLMs) in a Monte-Carlo simulation framework, similar to that of De Vos et al. (2014). A GLM was fitted to the historical catches as follows:

$$\ln(\mu_i) = \ln(dur_i) + \beta_0 + \beta_1 * site_i + \beta_2 * depth_i + \epsilon_i \qquad (1)$$

where μ_i represents the catch response variable (count of fish) for trawl sample i, dur_i is the trawl duration included as an offset, β_0 is the estimated intercept, β_1 and β_2 are the estimated coefficients for site and depth effects respectively, and ϵ_i represents the error term (residuals).

The GLM in (1) was initially fitted assuming a Poisson distribution. If the variance of the response was greater than that assumed by the model, as indicated by a test of over-dispersion (Cameron and Trivedi 1990), a quasi-Poisson distribution was fitted instead. A quasi-Poisson distribution essentially adjusts the variance estimates of the model coefficients (and hence p-values) using the estimated dispersion parameter. The over-dispersion test used a 0.05 significance level and was applied using the AER package (Kleiber and Zeileis 2008).

A simulated 're-survey' dataset of N samples at each site was constructed. This included covariates depth, sampled randomly with replacement from the historical data, and duration, consisting of a randomly-generated normal distribution with mean of 30 minutes and standard deviation of three minutes. The simulated covariates and a 'site' category were used together with the fitted model from Equation 1 to predict a set of response values, which were multiplied by a constant that represented an assumed population increase or decrease. Using these adjusted predictions (and the dispersion parameter in quasi-Poisson cases), random Poisson (or quasi-Poisson) deviates were generated during 1000 Monte-Carlo simulations. A second GLM was fitted during each iteration, using the combined dataset of historical and simulated 're-survey' records, this time including a period covariate:

$$\ln(\mu_i) = \ln(dur_i) + \beta_0 + \beta_1 * site_i + \beta_2 * depth_i + \beta_3 * period_i + \epsilon_i \qquad (2)$$

where β_3 is the estimated coefficient of the period effect.

The power of the test was estimated as the proportion of 1000 pseudo-datasets for which the GLM (Equation 2) could detect a period effect with a p-value ≤0.01. These simulations were repeated for a range of plausible population changes (between 1% and 300% of historical catches) and different sample sizes at each site ($N = \{5, 10, 15, \ldots 40\}$). A threshold of adequate power was judged as β =0.8. Results were visually examined on plots of the statistical power versus percentage change in the catch response.

Comparisons of abundance

The analyses of abundance changes focused on taxa that contributed ≥5% to catches at a site during either period. Although statistical results for the remaining taxa are provided, only notable points are highlighted. Comparisons between the historical and recent re-surveys relied on catch data that were standardised by the distance of the trawl tow, as detailed in Chapter 3. Catches were standardised by swept area for the plots that included Department of Agriculture, Forestry and Fisheries (DAFF) survey data from recent decades, as detailed in Chapter 3.

The DAFF data are not directly comparable to the historical and re-survey catches, due to substantial differences in trawl gear and methods used to collect them. Therefore they are used conservatively, predominantly to support interpretation, but not to test hypotheses. DAFF trawl gear was altered in the mid-2000s, as explained in Chapter 3 and detailed by Atkinson et al. (2011b). As that change in gear might have influenced the fishing performance and selectivity among taxa, DAFF 'old gear' (1986-2003; 2006) and 'new gear' (2004-2005; 2007-2015) data were treated separately unless specified otherwise.

Scatterplots were used to contrast the trawl samples and their mean values between periods, by site and for the three sites combined. Combined-site statistics were calculated as means of individual site statistics to avoid bias from unbalanced trawl sample numbers. Non-parametric 95% confidence intervals were constructed as the 2.5th and 97.5th percentile of 10 000 mean values calculated from bootstrap samples that were selected with replacement from the underlying data.

Various statistical approaches were investigated to assess significance of the period effect, including the use of generalised least squares, linear mixed-effects models and generalised linear models. None of these parametric approaches fitted the data of all 27 species (or even the majority) to a satisfactory degree. As there were too many taxa to allow detailed model exploration, selection and diagnostics across multiple approaches, results were limited to a non-parametric bootstrap approach.

For each taxon, an equal-tail bootstrap test (Equation 4 in MacKinnon 2009) was used test the null hypothesis that there was no difference in standardised catch between historical and re-survey periods. The difference between periods (re-survey-historical) was used as the test statistic. A null distribution of the test statistic was constructed from 9 999 pseudo-datasets, in which within-site assignments of 'period' had been randomly shuffled without replacement. This approach estimates the probability of observing a test statistic (mean difference between re-survey and historical catches) as extreme as that observed, assuming that historic and re-survey trawl samples emanate from the same null distribution.

Comparisons of size structure

Historical size information was only available for three taxa (*Argyrosomus* spp., *Austroglossus pectoralis* and *Merluccius capensis*), where their catches were specified to size-categories 'small' and 'large'. Boundaries between the size categories were 33 cm (13 inches) for *A. pectoralis* and 61 cm (24 inches) for the other two taxa. Fisher's exact test was used to test the null hypothesis that summed frequencies of small and large individuals remained the same between periods (Zar 1999).

Attempts were made to use the limited historical size information to convert catches by number into catches by weight. To enable such conversions, length measurements of individual fish are needed, or assumptions have to be made to attain a mean length of fish caught. Published growth equations, length-weight relationships and mortality rates, together with estimated gear selectivity factors were used to estimate a mean weight for each (small/large) size class. However, as those results appeared unlikely and could not be verified, they were not included here but are outlined in Appendix B.

Long-term differences in context of short-term variability

Neither historical nor re-survey datasets included records from multiple years at the same site. Therefore comparisons between periods cannot account for interannual fluctuations in catches. To examine the potential impact of this shortcoming, DAFF survey data were used as a proxy, from which the magnitude of short-term (seasonal/interannual/multi-year) variability was estimated. Contrasted against the change between historical and re-survey periods, an indication is provided of whether the magnitude of long-term differences might be matched or exceeded by typical short-term changes in trawl catches. As the DAFF data are not directly comparable to historical/re-survey data (due to gear differences), this approach was not formalised as a statistical test, but provides a graphical guide to support interpretations.

The absolute difference between pairs of samples were calculated at each site. The historical-re-survey pairs were chosen as 500 randomly selected samples (with replacement) from each period. DAFF samples were stratified by their temporal proximity to each other, so that the difference between pairs of seasonal (>1 month and <12 months), interannual (≥12 months and <18 months) and multi-year (≥18 months but ≤60 months) samples could be calculated. As sample sizes were generally small for the DAFF data, all possible pairwise contrasts were included and data from both 'old' and 'new' trawl gear were combined. Swept-area standardised catches (count.nm^{-2}; values typically ≥1 000s) were log-transformed [ln(x+1)] prior to calculation of differences, to account for abundance-variance relationships that might overwhelm the comparison. Bias due to gear differences are expected to inflate the variability measured from DAFF samples, but in most cases, such an effect is expected to be small relative to the temporal variability among samples. The magnitude of differences were visually contrasted using their mean and bootstrapped non-parametric 95% confidence intervals.

Additional historical data

At the same time as the historical survey data used throughout this thesis were digitised, additional trawl survey records from the 1920s, '30s and '40s were digitised. As these data might add information on the timing of abundance changes, they were included as an additional period in contrasts of abundances among survey periods. Trawl records located within the study areas belonged predominantly to surveys performed by the 'Africana', a government research vessel that conducted surveys around the coast of southern Africa between 1931 and 1949. Different-sized trawl nets were used on board the Africana over time, but analyses were restricted to samples collected by a single set of gear, namely an 18.3 m (60 ft) headline otter trawl net made of Manila hemp. The net was of comparable design, but one-third smaller and used a smaller cod-end mesh size (70 mm vs 96 mm), to that of the early Granton trawl net used in the initial (1897-1906) research surveys. Design details of the Africana net are provided in von Bonde (1933). The selection of trawl samples from survey sites and standardisation of catches followed the same protocol applied to the DAFF trawl survey catches (Chapter 3). The gear restriction and selection of samples resulted in the use of data collected between 1931 and 1934, hence they are referred to as '1930s data/catches' in text and abbreviated to 'H3' in figures.

Results

Examination of power analyses results across all taxa, together with a multivariate assessment of precision with increasing sample sizes (Chapter 3), led to a target of 25 re-survey samples per site. Sample sizes of 20-25 trawls were deemed sufficient to detect catch rate changes in the order of ± 50% for several common taxa. A reduction in power at large catch declines (≥90%) and insufficient power (<0.8) for declines of rare taxa indicated that the GLM might not perform well for species that had many zero catches. Examples of the figures produced during the power analysis are provided in Appendix A.

The sequence of taxa reported in tables (and discussed below) follows the order of their average historical abundance, with explicit focus on taxa that contributed ≥5% of catches at one or more sites during either period. Contrasting average catch abundances between periods showed that eight of the 27 taxa were absent from repeat surveys, eight others were caught in substantially reduced numbers (<20%) compared to historical surveys, and a further eight taxa were caught in substantially greater numbers (>5 times) than historically (Table 8). The bootstrap tests provided convincing evidence ($p<0.0001$) to reject the null hypothesis of equal CPUE between periods for 21 taxa (Table 8). Eleven of those showed a decrease in CPUE between periods and ten had increased. Two rare taxa and the entire chordate catch combined showed no statistical evidence of changes in abundance (Table 8).

Argyrosomus spp. (kob) was the dominant taxon caught historically, both at Cape Infanta and averaged across the three sites (contributing 26% to total abundances). Of the 156 historical samples included in analyses, only one trawl (at Mossel Bay) resulted in a zero catch for this taxon. All 73 re-survey trawls yielded zero *Argyrosomus* spp. individuals (Fig 17a). A large proportion (91%) of the historical *Argyrosomus* spp. catch consisted of large fish (≥61 cm; Fig 18a).

Re-survey catches of *Pterogymnus laniarius* (panga) were drastically lower than in historical surveys, constituting about 2.4% of historical CPUE on average (Table 8; Fig 17b). This decrease was consistent across sites and highly significant. *P. laniarius* were caught in every historical trawl but occurred in only 13 (17.8%) of the re-survey trawls.

The decrease in standardised catch of *Austroglossus pectoralis* (east coast sole) was comparable to that of *P. laniarius* (Table 8; Fig 17c). Average re-survey CPUE of *A. pectoralis* represented 4.6% of its historical level. Records were differentiated by size only at Bird Island historically, where they were made up of predominantly large individuals (88.4%; ≥33 cm; Fig 18b). The proportion of large fish in the Bird Island re-survey (69.1%) appeared comparable to the historical figure, yet the proportions of small and large individuals were statistically different between periods (Fisher's exact test; $p<0.01$). Re-survey catches at the two western sites were dominated by small individuals, so that averaged across the three sites there were fewer large (27.3%) than small individuals. A clear decreasing west-to-east gradient in *A. pectoralis* numbers was seen in the historical data (Fig 17c).

Table 8. Results of the non-parametric bootstrap approach contrasting historical (H) and re-survey (R) standardised catches (count·nautical mile^{-1}). Lower and upper confidence limits (LCL and UCL respectively) were estimated as 2.5th and 97.5th percentiles of 10 000 bootstrap samples. Taxa were ordered by decreasing historical abundances. An equal-tail bootstrap test (MacKinnon 2009) was used to assess the probability that observed differences between periods were chosen from the same

Taxon	Bootstrap medians (95% confidence limits) H	R	Difference (R-H) LCL	UCL	Remain-ing %	Bootstrap test p-value	
Argyrosomus spp.	53.08 (46.38 - 60.81)	0.00 (0 - 0)	-60.81	-46.38	0.0	< 0.0001	***
Pterogymnus laniarius	49.51 (44.6 - 54.62)	1.16 (0.22 - 2.67)	-53.52	-43.15	2.4	< 0.0001	***
Austroglossus pectoralis	47.85 (44.12 - 51.6)	2.18 (1.64 - 2.82)	-49.45	-41.88	4.6	< 0.0001	***
Argyrozona argyrozona	23.78 (18.18 - 30.34)	0.02 (0 - 0.05)	-30.30	-18.15	0.1	< 0.0001	***
Rhabdosargus globiceps	7.35 (5.8 - 9.07)	0.01 (0 - 0.03)	-9.06	-5.79	0.1	< 0.0001	***
Torpediniformes	2.85 (1.68 - 4.57)	0.11 (0.04 - 0.19)	-4.48	-1.57	3.7	< 0.0001	***
Umbrina canariensis	2.78 (2.06 - 3.83)	0.05 (0 - 0.16)	-3.78	-2.00	1.9	< 0.0001	***
Merluccius capensis	1.82 (1.44 - 2.24)	10.14 (8.41 - 12.21)	6.53	10.44	558	< 0.0001	***
Rajidae	1.82 (1.63 - 2.02)	3.47 (2.74 - 4.29)	0.90	2.49	191	< 0.0001	***
Squalus spp.	1.43 (1.14 - 1.77)	44.34 (31.12 - 62.2)	29.68	60.78	3 121	< 0.0001	***
Chelidonichthys spp.	1.26 (0.78 - 1.93)	48.76 (36.79 - 61.63)	35.50	60.31	3 792	< 0.0001	***
Trachurus trachurus	0.59 (0.35 - 0.89)	27.44 (14.15 - 45.7)	13.59	45.06	4 738	< 0.0001	***
Cynoglossus spp.	0.49 (0.39 - 0.59)	1.15 (0.85 - 1.52)	0.34	1.05	238	< 0.0001	***
Atractoscion aequidens	0.36 (0.23 - 0.52)	0.02 (0 - 0.05)	-0.51	-0.21	5.7	< 0.0001	***
Paracallionymus costatus	0.26 (0.15 - 0.4)	0.05 (0.01 - 0.09)	-0.36	-0.09	18.1	0.0032	*
other	0.25 (0.19 - 0.32)	5.65 (4.51 - 6.88)	4.25	6.63	2 225	< 0.0001	***
Myliobatiformes	0.15 (0.12 - 0.19)	4.23 (2.61 - 6.47)	2.46	6.33	2 866	< 0.0001	***
Pomatomus saltatrix	0.13 (0.08 - 0.2)	0.00 (0 - 0)	-0.20	-0.08	0.0	< 0.0001	***
Carcharhiniformes	0.11 (0.09 - 0.14)	0.65 (0.49 - 0.82)	0.38	0.71	586	< 0.0001	***
Lithognathus lithognathus	0.11 (0.08 - 0.14)	0.00 (0 - 0)	-0.14	-0.08	0.0	< 0.0001	***
Galeichthys feliceps	0.07 (0 - 0.19)	10.77 (6.83 - 15.75)	6.75	15.69	13 863	< 0.0001	***
Chrysoblephus gibbiceps	0.05 (0.02 - 0.09)	0.00 (0 - 0)	-0.09	-0.02	0.0	0.0072	*
Polysteganus undulosus	0.04 (0.02 - 0.07)	0.00 (0 - 0)	-0.07	-0.02	0.0	0.0022	*
Genypterus capensis	0.04 (0.02 - 0.06)	0.00 (0 - 0)	-0.06	-0.02	0.0	< 0.0001	***
Petrus rupestris	0.03 (0.02 - 0.05)	0.00 (0 - 0)	-0.05	-0.02	0.0	0.0002	**
Pachymetopon aeneum	0.02 (0.01 - 0.04)	0.01 (0 - 0.03)	-0.04	0.01	46.4	0.3704	ns
Chrysoblephus cristiceps	0.00 (0 - 0.01)	0.00 (0 - 0)	-0.01	0.00	0.0	0.7905	ns
All chordates	196.7 (183.2 - 211.2)	161.9 (136.1 - 189.4)	-64.7	-4.0	82.3	0.0572	ns

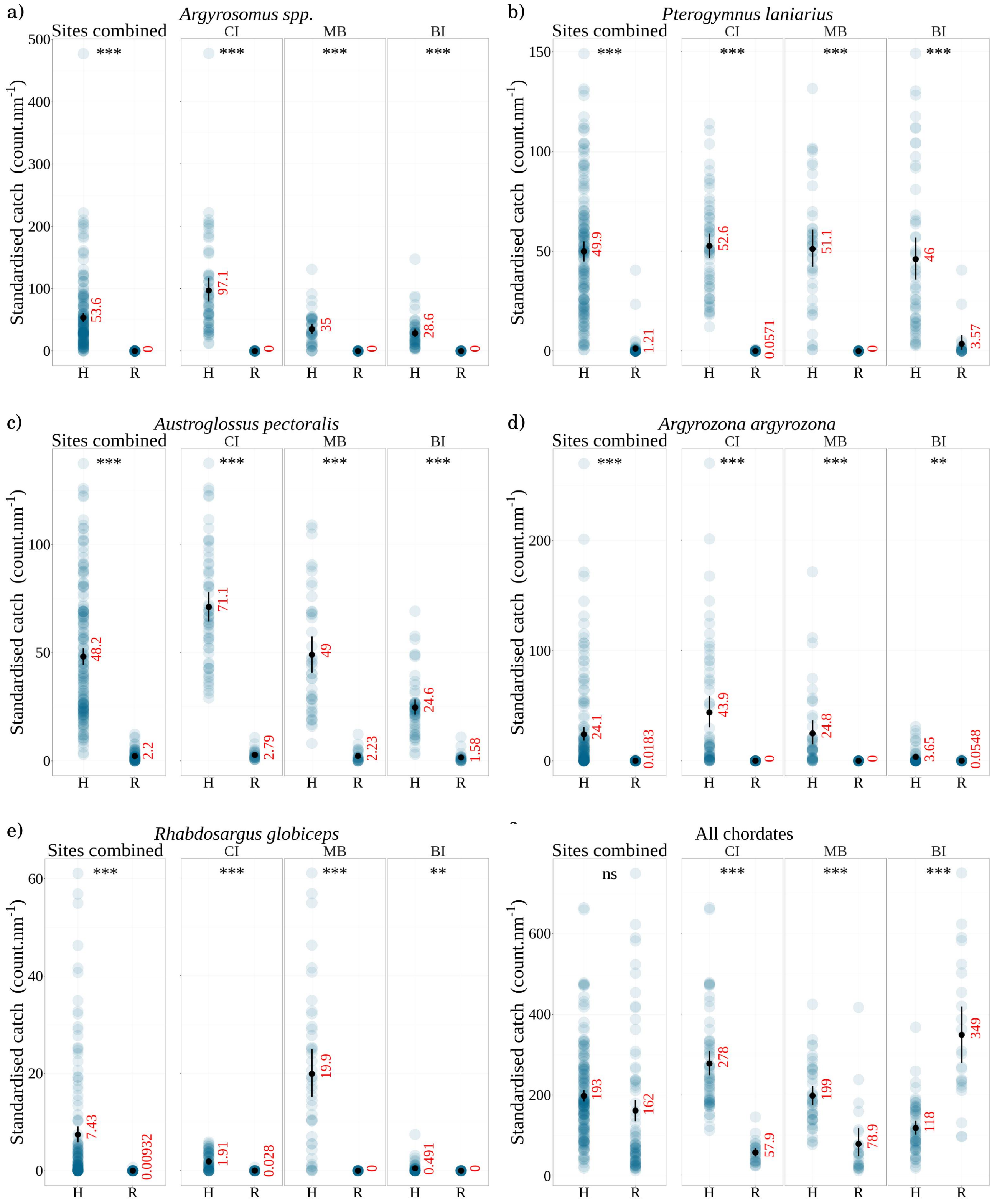


Figure 17. Scatterplots of standardised catches for common taxa that decreased on average between historical (H) and re-survey (R) trawls. The observed mean and 95% confidence intervals (estimated by bootstrap) are indicated in black. The three sites are plotted separately (on right) and combined (on left); CI Cape Infanta, MB Mossel Bay, BI Bird Island. Red numbers indicate the mean. Symbols indicate significance of equal-tail bootstrap tests of period differences. ns $p>0.05$, . $p\leq0.05$, * $p\leq0.01$, ** $p\leq0.001$, *** $p\leq0.0001$

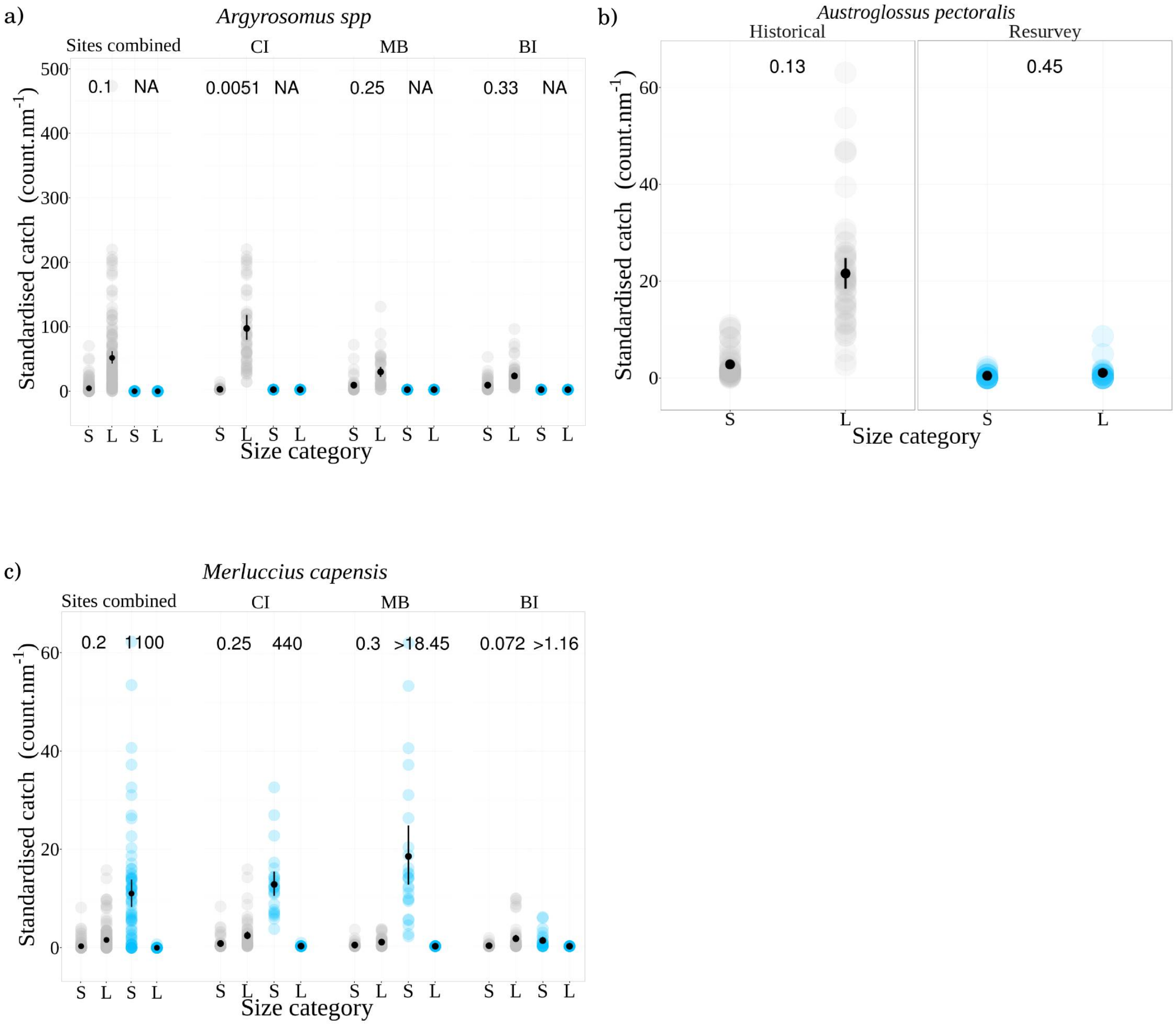


Figure 18. Similar to Fig 17 except that catches were separated into small (S) and large (L) categories for a) *Argyrosomus* spp., b) *A. pectoralis* and c) *M. capensis*. Historical catches are grey, re-survey blue. S/L ratios indicated for each period. S/L boundaries were 33 cm for *A. pectoralis* and 61 cm for the two larger taxa. *A. pectoralis* size data were available only at Bird Island. CI Cape Infanta, MB Mossel Bay, BI Bird Island. Size category frequencies were significantly different between periods (Fisher's exact test; p<0.01) for b) and c), both for individual sites and when combined.

Only three *Argyrozona argyrozona* (carpenter seabream) individuals were caught during repeat surveys, in a single trawl at Bird Island, which represents a highly significant decrease to less than 0.1% of the historical CPUE (Table 8; Fig 17d). As with *A. pectoralis* there was a notable west-to-east decrease in historical standardised catches of *A. argyrozona*.

Rhabdosargus globiceps (white stumpnose) were historically caught in substantial numbers at Mossel Bay, making up 10% of the total catch numbers there (Fig 17e). A single individual was caught throughout the 73 re-survey trawls, indicating a highly significant decrease (Table 8). The

DAFF survey catches indicate that *R. globiceps* is occasionally encountered within the survey sites, but in much lower numbers than were caught during historical surveys (Appendix A).

Standardised catches of *Merluccius capensis* (shallow water hake) increased significantly between historical and repeat surveys at the western two sites and overall (Fig 19d). Historical catches consisted of predominantly 'large' (≥61 cm) *M. capensis* individuals, whereas re-survey catches consisted of substantially smaller individuals (97% of which were <40 cm in length). The proportions of small and large fish were very different between periods at all three sites (Fisher's exact test; $p<0.0001$), as illustrated by the change of mean small:large ratio from 0.20 historically to 1 130 in the re-surveys (Fig 18c).

Catches of *Squalus* spp. (spiny dogfish) were on average 31.2 times higher in the re-survey than in historical surveys. The contrast between periods was driven mostly by large re-survey catches at Bird Island, whereas abundances remained similar at the two western sites (Fig 19b). Contrasting the ratio of standardised catches between Bird Island and the other sites with that of recent DAFF data, indicates that Bird Island re-survey catches of *Squalus* spp. were abnormally high (Appendix A): The 2003-2015 DAFF 'new' net catch rates of *Squalus* spp. averaged 2.9 times higher at Bird Island than the mean of the other two sites, whereas the equivalent ratio for re-survey samples was 61.

Chelidonichthys spp. (gurnards) made up a small proportion (<1%) of the historical catch numbers. Their re-survey catch abundances increased at all three sites, averaging 37.9 times greater than in historical surveys (Table 8; Fig 19a). Inspection of DAFF trawl survey data indicate that high catches of this species at Bird Island (6.3 times the mean of the other two sites) appear not to be a survey-specific anomaly. The recent ('new' net) DAFF catches of *Chelidonichthys* spp. similarly averaged 7.3 times higher at Bird Island than at the two other sites (Appendix A).

Trachurus capensis (Cape horse mackerel) re-survey catches were substantially greater in number than historical catches at all three sites (47.4 times on average), resulting in a highly significant period effect (Table 8; Fig 19c). *T. capensis* made up only 0.4% of the historical abundances, whereas their increased numbers in the repeat surveys contributed a substantial (16.4%) proportion. Considering their maximum size (~52 cm; Hecht 1990) the re-survey catches were mostly made up of relatively small (15-25 cm) individuals, whereas the lengths in historical catches are unknown.

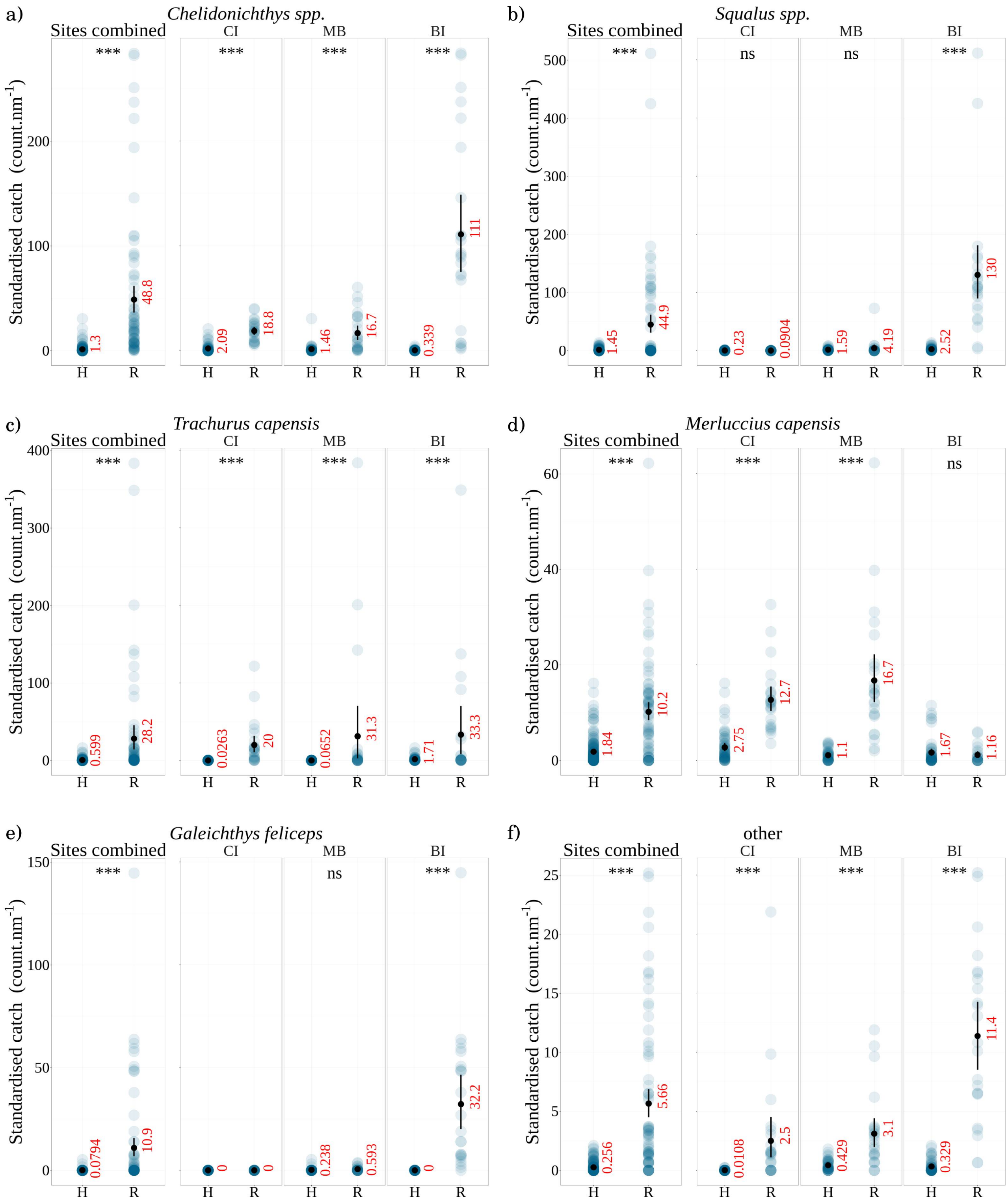


Figure 19. Same as Fig 17, but contrasting common taxa that increased on average between periods. CI Cape Infanta, MB Mossel Bay, BI Bird Island.

Mixed taxa, recorded as the category 'other fish', included species rarely encountered and of no economic interest in the historical period. The standardised catches of this multispecies group increased at each of the three sites (Fig 19f). Whereas this group of taxa contributed an average of 5.1% in the re-surveys, they made up≤0.3% historically. The recent catches were predominantly made up of St Joseph shark (*Callorhinchus capensis*; 51.2%) and the small scalybreast gurnard (*Lepidotrigla faurei*; 19.4%).

In the historical surveys, *Galeichthys feliceps* (white sea catfish) were caught in very low numbers only at Mossel Bay (Fig 19e). Their re-survey standardised catches at Mossel Bay were similar to historical levels, but far greater at Bird Island, increasing average CPUE across sites to a level 139 times higher than the historical average. Examination of DAFF survey catches of *G. feliceps* (Appendix A) suggested that the large re-survey catches at Bird Island were anomalously high.

Of the remaining taxa contributing relatively minor proportions of the catches, abundance decreases were shown for Torpediniformes, the croakers (Sciaenidae) *Umbrina canariensis* and *Atractoscion aequidens*, seabreams *Lithognathus lithognathus*, *Polysteganus undulosus*, *Chrysoblephus gibbiceps* and *Petrus rupestris*, as well as *Paracallionymus costatus*, *Pomatomus saltatrix* and *Genypterus capensis* (Table 8). On average, greater catches were recorded in the re-survey for Rajidae, Myliobatiformes, *Cynoglossus* spp. and Carcharhiniformes (Table 8). Most of these average increases (Rajidae, Myliobatiformes, Charcharhiniformes) were driven predominantly by large catches at Bird Island.

The taxa for which there was no evidence of overall changes in abundance included two rarely-caught seabreams, *Pachymetopon aeneum* and *Chrysoblephus cristiceps* (Table 8). The CPUE of all taxa combined was also similar when averaged over the three sites, but different within each site: the two western sites (Cape Infanta and Mossel Bay) showed depleted re-survey catches (21-40%) relative to historical records, whereas the Bird Island re-survey caught almost three times the historical CPUE.

Contrasting short-term variability among DAFF samples with the long-term changes between historical and repeat surveys, showed that for the majority of cases highlighted above, the magnitude of short-term differences in recent DAFF surveys were smaller than the long-term differences between historical and repeat surveys (Figs 20, 21). For taxa such as *Argyrosomus* spp., *P. laniarius*, *A. pectoralis*, *Chelidonichthys* spp. and *M. capensis*, this was the case across sites. For other taxa, such as *A. argyrozona*, *R. globiceps*, *T. capensis* and *Squalus* spp., the short-term changes were of similar or greater magnitude to the long-term differences at one or two sites. This tended to occur at sites where both historical and re-survey catches were relatively low, resulting in comparatively small differences between periods. An exception was *T. capensis* at Bird Island, where the mean magnitude of seasonal and multi-year changes in DAFF survey data were similar to the long-term differences, despite the highest re-survey catch rate occurring at that site (Figs 19c, 21c).

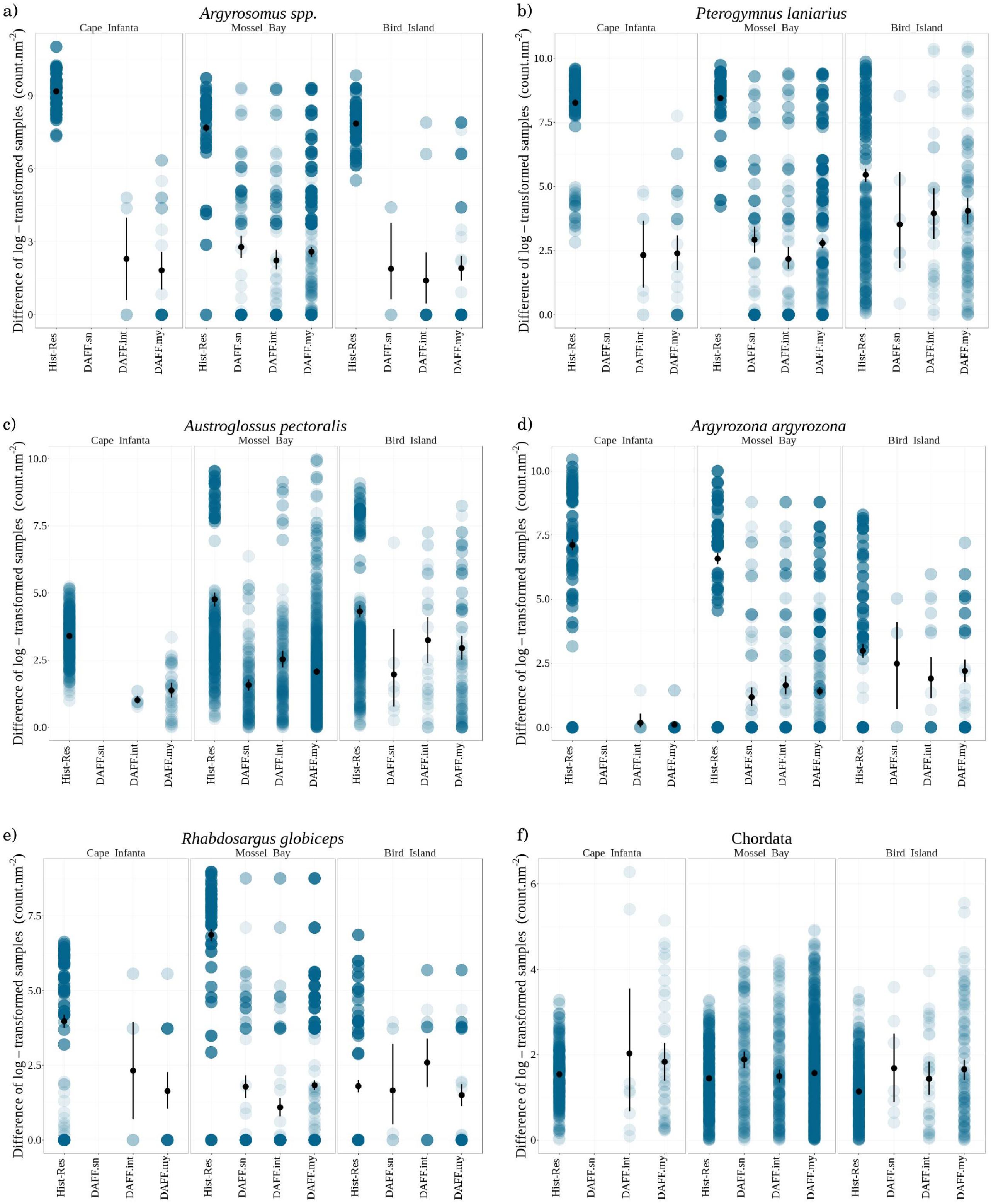


Figure 20. Scatterplot of difference between pairs of randomly chosen samples from historical and repeat surveys (Hist-Res; N=500 for each site) and all possible combinations of DAFF samples that were separated by ≥1 month but <12 months (DAFF.sn), ≥12 months but <18 months (DAFF.int) and ≥18 months but ≤60 months (DAFF.my). Swept-area standardised catches were log-transformed [log(CPUE+1)] prior to calculations. Taxa, colour and symbols same as for Fig 17.

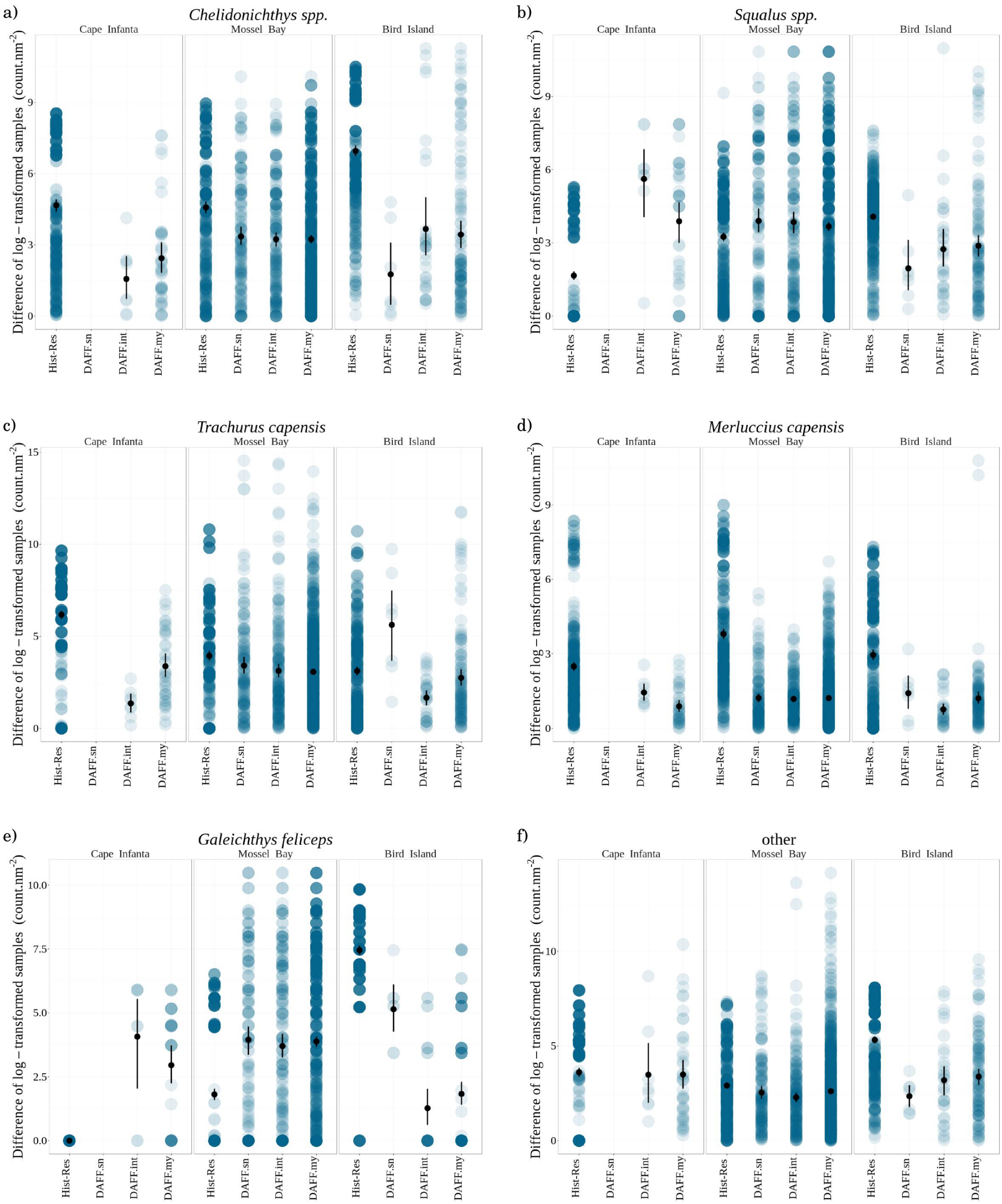


Figure 21. Same as Fig 20, but for the 'increasing' taxa that were included in Fig 19.

Discussion

It is evident that trawl-caught fish abundances changed substantially from 1903/1904 to 2015 and that sizes declined over the same period. Evidence to reject the null hypothesis of equal catch abundances between periods was present for 25 of 27 taxa. Species that historically dominated the research survey catches (*Argyrosomus* spp., *P. laniarius, A. pectoralis*) were reduced to between 0 and 4.6% of their historical catch rates. The abundances of certain other taxa (e.g. *Chelidonichthys* spp., *T. capensis, Squalus* spp., *M. capensis*) increased between periods.

Due to reductions in fish sizes that accompany fishing pressures (Fig 18; Andrew et al. 1997; Bianchi et al. 2000; Yemane et al. 2008; Heath and Speirs 2012), decreases in biomass are expected to be more severe than those by number for most species that have declined. Due to the same expectation of reduced sizes, abundances that have increased are likely exaggerated compared to what a contrast of mass would show. The notable changes in abundance and size have resulted in remarkably different demersal assemblages from those encountered historically, as was shown in Chapter 3.

Argyrosomus spp.

The most striking difference between historical and repeat surveys was the recent absence of previously dominant *Argyrosomus* spp. (Fig 17a). The historical surveys showed that all but one trawl included *Argyrosomus* spp. and that this taxa contributed over a quarter of the catch numbers on average. The vast majority (90%) of those caught were relatively large (≥61 cm in length), suggesting that their contribution to the fish catch was likely greater by mass than by number. Their absence in repeat surveys did not allow comparison of size classes between periods. However, a mean pre-discard length of 43.6 cm reported from the inshore trawl fishery (Attwood et al. 2011), which uses similar mesh sizes on fishing grounds surrounding the survey sites, appears substantially smaller than the historical sizes caught. The consistent, large catches of large-sized *Argyrosomus* spp. caught historically are difficult to imagine for contemporary fishers and scientists, demonstrating the value of historical information to counter shifting baselines (Pauly 1995). Evidence presented here supports previous studies (Griffiths 1997b, 2000) that have highlighted drastic declines of these sought-after, iconic predators. The two other Sciaenidae included in analyses (*Atractoscion aequidens* and *Umbrina canariensis*) also showed significant declines.

The majority of local trawl-caught *Argyrosomus* spp. are assumed to be *A. inodorus* (Griffiths 1997b), although it is uncertain what proportion *A. japonicus* might have contributed to the remarkable historical catches. Using per-recruit models based on data collected on South Africa's south coast in the early 1990s, Griffiths (1997b) estimated spawner biomass per recruit values to be between 2.9 and 12.5% of pristine levels and concluded that *A. inodorus* stocks were heavily over-exploited. While such per-recruit analyses rely on assumptions that are in most cases violated (Attwood 2003), they provide useful first order approximations of stock dynamics in the absence of data required for more detailed stock assessments (Butterworth et al. 1989). Investigation of long-term commercial catch rates supported a substantial decline, suggesting that CPUE towards the end of the 20th century was <10% of historical levels (Griffiths 2000). Donovan (2010) showed a continued decline of *A. inodorus* CPUE between 1985 and 2007 in the Port Alfred line fishery, suggesting that their overexploitation had persisted despite management interventions aimed at curbing it. Examining broader areas of the south-eastern and southern Cape, Winker et al. (2012) showed relatively stable or slightly increasing CPUE values over the period of 1986-2011 and, with the use of age-structured production models, estimated spawner biomass to be between 18-21% of pristine levels. The most recent update from a Bayesian surplus production model (BSPM), estimated the *A. inodorus* spawner biomass in 2015 as 9.8% (6-15.8% confidence interval) of its pre-exploited level (Winker, personal communication 2017).

Percentage reductions of *Argyrosomus* spp. could not be calculated here due to its absence in the repeat surveys, yet the situation at the study sites appears to be distinctly worse than figures quoted above. Some areas may be less depleted than the survey areas, as *A. inodorus* still contributes important landings to local fisheries (approximately 300 t caught by commercial line and trawl fisheries combined in 2015; Winker et al. in prep). However the virtual absence of these fish in areas where their catches used to dominate the assemblage composition is concerning. If these areas are representative of the broader stock they may indicate that pristine biomass estimates and subsequent decreases have been underestimated. The state of these populations clearly requires management attention.

Although the differences in gear technology (and hence catchability) require caution, swept-area standardised catches from the 1930s suggest that *Argyrosomus* spp. abundances had already declined substantially by that time (Appendix A). A similar pattern is evident in a figure of hook and line CPUE from comparable historical and recent periods (Griffiths 2000), although not in commercial trawl catches (Griffiths 2000). Smale (1985) showed that inshore trawl landings of *A. inodorus* decreased substantially between the mid-1960s and early 1980s, which may have reflected part of a long-term decline. A large decrease in the *Argyrosomus* spp. population in the first half of the 20th century could indicate that early fishing pressures, even though they were light compared to later in the century, removed a large proportion of the pre-disturbed populations of *Argyrosomus* spp. If so, this is a narrative missing from the story of *Argyrosomus* spp. declines in South Africa and may warrant further attention.

Besides an economic loss, the massive decline of *Argyrosomus* spp. from these inshore ecosystems is expected to have had a marked impact on inner shelf ecosystems. Both *A. inodorus* and *A. japonicus* are large (>1 m length) predators that consume a wide range of pelagic and demersal prey, including mysids, squid, pleuronectiformes and many other teleosts as well as their own young (Whitfield and Blaber 1978; Smale and Bruton 1985; Griffiths 1997a). *Argyrosomus* spp. prey selection appears to be density-dependent (Whitfield and Blaber 1978; Smale and Bruton 1985) and selection of prey size is related to predator length (Smale and Bruton 1985). The remarkable numbers of (large) *Argyrosomus* spp. individuals that inhabited these historical inshore trawl areas are thought to have contributed a formidable predatory pressure, the decline of which may have contributed towards the increased numbers observed in some other taxa. Across a wide set of regions globally, Christensen et al. (2014) showed that larger fish species had declined markedly during the 20th century, while smaller species had increased. They concluded that such change was consistent with fishing pressure and suggested that the increase in smaller species was likely due to predation release.

Pterogymnus laniarius

P. laniarius is considered the most common seabream (Sparidae) on the Agulhas Bank and contributes one of the dominant components of inshore trawl landings (Booth and Punt 1998; Attwood et al. 2011), even though its relatively lower economic value has precluded a targeted local fishery. Catches of *P. laniarius* expanded massively with the arrival of Japanese and Taiwanese trawl fleets in 1964, which targeted them in hard-substrate habitats using specialised gear (Booth and Punt 1998). By 1977 the stock was estimated to be over-exploited as a result (Sato 1980). After declaration of South Africa's exclusive fishing zone in 1977, much of the foreign effort was removed and total landings returned to relatively low levels (<1000 t) by the early 1980s (Booth and Punt 1998). The large reduction in effort directed at it allowed recovery of the *P. laniarius* stock, from an estimated 20% in 1976 to 60-70% of pristine biomass in 1995 (Booth and Punt 1998). Recent estimates provided by a BSPM suggest that the 2015 spawner biomass was at 80.6% (59-99.8% Cape Infanta) of its unfished level (Winker, personal communication 2017). Those figures do not reconcile with the massive (97.6%) reductions indicated here, which might be more severe by mass, if the average size of *P. laniarius* has declined.

Two potential explanations are offered, both of which may contribute towards this discrepancy. Firstly, due to their long history as core areas of the sole-directed trawl effort, the sites surveyed in this study comprise some of the most intensely fished trawl grounds in South Africa and the resultant depletion of *P. laniarius* (and other taxa) may be more pronounced here than elsewhere on the Agulhas Bank. Secondly, part of the drastic declines may be related to changes in benthic habitat caused by over a century of demersal trawling at the survey sites (Chapter 3; Auster et al. 1996; Engel and Kvitek 1998; Callaway et al. 2007). *P. laniarius* is predominantly associated with reef habitats and reef-mud or reef-sand interfaces (Booth and Buxton 1997a). The long history of trawling at the survey sites has likely removed or reduced emergent biogenic and reef-like habitat, replacing it with a more homogenous, unconsolidated sediment (Sainsbury et al. 1993; Auster et al. 1996). Some of the lost benthic components may be critical elements of *P. laniarius* habitat. Elsewhere on the Agulhas Bank, in habitats that have not suffered extensive trawling impact, *P. laniarius* abundances may be far higher.

Austroglossus pectoralis

A. pectoralis was the dominant target in early south-coast trawl fisheries in South Africa due to their high market value (Scott 1949). Since 1920 their commercial landings have remained relatively stable, fluctuating between 600 and 900 t most of the time, although catches above and below these figures have occurred on occasion (DAFF 2015). Since 2005, landings remained <600 t and declined substantially after 2009, with a 2013 catch of only 127 t and a sharp decline in CPUE raising concern over the state of the stock (Butterworth and Glazer 2014). An effort limitation program has subsequently been applied within priority distribution areas of *A. pectoralis*.

The results reported in this study indicated an average decrease to 4.6% of the CPUE recorded historically, as well as a reduction in the proportion of large fish (≥33 cm). This indicates a severe decline from their unexploited baseline at the three survey sites, which are situated in core areas of *A. pectoralis* distribution (Zoutendyk 1972). Butterworth and Glazer (2014) and Butterworth et al. (2016) applied a simple dynamic Schaefer model to recent landings of *A. pectoralis*. The pristine biomass implied by their model ranges between 4 571 and 8 000 t, depending on the intrinsic rate of population growth assumed (Butterworth et al. 2016). The authors consider the recent decline to be a result of either a reduction in catchability or a decline in the population. Estimating biomass figures from their plots, the most optimistic (catchability) scenario produces a 2015 biomass estimate ≥87% of pristine levels. The worst-case (population decline) scenario puts that same level between 21 and 37% of pristine biomass. As *A. pectoralis* is closely associated with shallow (<120 m) muddy sediments (Zoutendyk 1972; Le Clus et al. 1994), the majority of which are accessible to the trawl industry, the slump in landings are more likely explained by a population decline than a catchability effect. The catchability hypothesis appears especially unlikely if it were to have been accompanied by a recent population size relatively close to pristine biomass. An explanation more parsimonious with our knowledge of its habitat and behaviour, and how these interact with demersal trawling, seems to be that *A. pectoralis* abundances have suffered substantial declines in recent years. Support for the latter interpretation is provided by a recently applied BSPM, which estimated the 2016 spawner biomass to represent 8.9% (4.8-18.8% Cape Infanta) of its pre-disturbed level (Winker, personal communication 2017). The state of *A. pectoralis* requires further investigation and management attention.

In addition to prolonged fishing pressure, environmental impacts may have influenced *A. pectoralis* abundances in space and time. Similar to the patterns reported for several linefish species on South Africa's east coast (Lamberth et al. 2009), anecdotal reports from fishers have suggested that good *A. pectoralis* catches follow after good rainy seasons and strong river flows. The outflow of major rivers along this coastline has declined in recent decades (Lloyd 2010; Sink et al. 2012a), which would likely result in a decline of sediment and organic matter inputs into the mud habitats that *A. pectoralis* depends on. Over time such reduced input might decrease the extent of muddy habitats and the productivity of organisms closely associated with them, including *A. pectoralis* (Tunley, personal communication 2016).

As with *Argyrosomus* spp., it appears that a substantial decline of *A. pectoralis* from pristine levels may have occurred within the first few decades of trawling activity (Appendix A), which is not documented in the literature. Interrogating commercial trawl catches made off Port Elizabeth in 1967-1975 and 1985-1995, Booth and Hecht (1998) showed that a steep (~85%) decline in landings per vessel occurred during the early 1970s and appeared to stabilise at that lower level thereafter.

Argyrozona argyrozona

A. argyrozona was encountered only at Bird Island in repeat surveys, where it was least abundant historically (Fig 17). Standardised catches were severely depressed (0.1%) relative to historical surveys (Table 8). Considering that exploitation has likely caused a decline in the mean size of *A. argyrozona* (Bianchi et al. 2000; Yemane et al. 2004), decreases in biomass have likely been more drastic than those of abundance.

Brouwer and Griffiths (2005) identified two separate *A. argyrozona* stocks on the western/central Agulhas Bank and the eastern Agulhas Bank near Port Elizabeth. Both stocks were considered to be over-exploited in the application of per-recruit models (Brouwer and Griffiths 2006). Compared to their highest historical levels, Griffiths (2000) estimated that 1986-1998 figures of commercial line-fishing CPUE for *A. argyrozona* had declined to 4.8% in the southern Cape (which includes Cape Infanta and Mossel Bay) and 25.9% for the south-eastern Cape (which includes Bird Island). As with *P. laniarius*, heavy exploitation of this resource likely took place by foreign trawling fleets in the 1960s and 1970s. The release of that pressure and reduction of commercial line fishing effort in 2000 (Blamey et al. 2015) is expected to have allowed steady recoveries during the decade that followed (Winker et al. 2012). Using age-structured production models Winker et al. (2012) estimated that both stocks reached their minimum level in the mid- to late-1990s. By those estimates the western stock declined to ~23% of carrying capacity, whereafter it recovered to ~42% by 2011. The eastern stock dropped as low as 15% and then rebounded to 38% of carrying capacity. A recent BSPM estimated the spawner biomass in 2015 to be 50.4% (29.5-77.8% Cape Infanta) of pristine levels (Winker, personal communication 2017).

The disparity between results here and assessments of *A. argyrozona* stock size might be due to habitat effects, similar to those discussed for *P. laniarius*. *A. argyrozona* frequently concentrates over high-profile reefs (Smale and Badenhorst 1991; Brouwer and Griffiths 2005). The arguments of trawling-induced habitat change and concentrated fishing effort may explain their relative scarcity at re-survey sites compared to other, more rocky habitats outside of the study area.

The hypothesis that local depletions of *A. argyrozona* and *P. laniarius* (and perhaps other species) may be explained by trawl-induced habitat changes, has important implications to the spatial management of such species. If physical aspects of the habitat have been altered or the recovery of biological parts is very slow, then closely-associated fish fauna might not recover in trawled areas, even after cessation of fishing activity. This needs to be considered during placement of spatial management interventions aimed at recovering those fish populations.

Rhabdosargus globiceps **and other seabreams**

R. globiceps was frequently caught in historical trawls and was especially abundant at Mossel Bay, contributing a substantial proportion of the ichthyofauna there. They were virtually absent in repeat surveys, with a single individual caught at Cape Infanta representing 0.1% of historical CPUE.

Four discrete populations of *R. globiceps* were identified by Griffiths et al. (2002), two of which fall within the study area focused on here. Similar to *A. argyrozona*, one population inhabits the broader central Agulhas Bank (including Cape Infanta and Mossel Bay sites), whereas an apparently separate population is located between Cape St Francis and Port Alfred (including the Bird Island site). They inhabit areas of unconsolidated sediments and reef habitat up to about 130 m depth (Griffiths et al. 2002). No stock assessments have been conducted on the south coast populations. A per-recruit analysis suggested that the isolated west coast population (in Saldanha Bay) had collapsed (Arendse 2011) and cases have been reported of contractions or disappearance from sites where historical catches were made (e.g. Hout Bay and Table Bay; Griffiths et al. 2002). Griffiths

(2000) presented evidence that the 1986-1998 line fishing CPUE in the southern Cape (which includes Cape Infanta and Mossel Bay) was ~0.2% of that recorded for *R. globiceps* in commercial catches from 1929-1931. This figure is similar to the findings presented here and supports the suggestion that the substantial *R. globiceps* abundances encountered in historical Mossel Bay surveys have largely disappeared.

The literature seems to indicate an increase in commercial landings of *R. globiceps* in recent decades: Japp et al. (1994) reported that between 1986 and 1991 an average of one tonne was caught annually by the line fishery and 14 t by the inshore trawl fleet on the Agulhas Bank. In contrast, Attwood et al. (2011) reported average annual figures for 2002-2006 of 30 and 83 t respectively for the same fisheries, as well as an estimated 148 t of discards in the trawl fishery. Increased landings might represent greater retention or targeting of *R. globiceps*, due to declined catches of more valuable, larger species. Alternatively, they may represent a partial recovery of Agulhas Bank populations during the 1990s and early 2000s. Either way, the results reported here indicate that *R. globiceps* densities in the study areas are severely depleted relative to those of the historical period and highlight the need for greater scientific scrutiny of the Agulhas Bank populations.

Additional seabreams (Sparidae) that were caught in relatively low numbers historically were not encountered at all in the repeat survey. These consisted of traditionally sought-after, line-caught species that are depleted (Mann 2013), such as *Lithognathus lithognathus*, *Petrus rupestris, Polysteganus undulosus* and *Chrysoblephus gibbiceps* (Table 8). Two seabreams (*Chrysoblephus cristiceps, Pachymetopon aeneum*) did not show significant changes between periods, likely because they are rarely caught by trawls.

Merluccius capensis

The abundance of *M. capensis* increased in standardised catches at the two western sites, but not at Bird Island. The historical catches included fewer *M. capensis* individuals (at Cape Infanta and Mossel Bay), but they were substantially larger than the many small fish caught in the re-survey. Considering the difference in numbers and the potential mass of the larger fish caught historically, it is conceivable that the weight of fish remained similar or even declined, despite their greater abundances at the two western sites. At Bird Island their re-survey mass was certainly less than the historical catches, which consisted of marginally greater numbers of substantially larger fish. Investigation of DAFF survey catches (Appendix A) shows that Bird Island catches have on average been similar to those made at the other two sites, which suggests that the low re-survey catches of *M. capensis* encountered at Bird Island may not be typical for this site.

Rademeyer et al. (2008) estimated that the South African *M. capensis* spawner biomass was 51% of its pristine value in 2006, whereas the latest assessment estimated this percentage to be 73% in 2016 (Rademeyer and Butterworth 2016). Both the stock assessment and the repeat survey results presented here indicate an abundant *M. capensis* population. The sizes of fish, however, have declined substantially. The depth distribution of *M. capensis* has been shown to be related to the size of fish, with larger individuals inhabiting deeper waters (Macpherson and Duarte 1991). It is noteworthy that the historical catches in relatively shallow waters consisted predominantly of fish >61 cm in length, raising the question of whether *M. capensis* sizes were in fact distributed according to depth in an unfished ecosystem. The historical abundance of large predators at these inshore sites, predominantly *Argyrosomus* spp. but including cannibalistic *M. capensis* (Pillar and Wilkinson 1995), likely exerted substantial predation pressure on juvenile *M. capensis*, which may have sought refuge in other habitats.

***Squalus* spp.**

It appears that abundances of *Squalus* spp. have increased between survey periods, yet only at Bird Island was the difference in CPUE significant (Fig 19b). Although the Bird Island re-survey catches appeared to be anomalously large, comparison with DAFF survey data indicated that similar large catches have been encountered frequently in recent decades. *Squalus* spp. are known to form large schools (Compagno 1984) and the Bird Island re-survey appears to have encountered such aggregations. The *Squalus* species in re-survey catches was identified as *S. acutipinnis* (previously referred to as *S. megalops*; Viana and de Carvalho 2016), which is what the historical catches are expected to have been, based on location and depth (Watson and Smale 1999).

Results here, together with those of previous studies, suggest that *Squalus* spp. may be relatively robust to trawling pressure. Following intense fishing pressure on the Georges Bank in the 1960s/1970s, small elasmobranchs such as skates and dogfish largely replaced the previous catches of gadoids and flounder (Fogarty and Murawski 1998). *Squalus acanthias* was estimated to have increased five-fold in the Northwest Atlantic between 1968 and the early 1990s, while species that traditionally supported the Northeast US fisheries had declined to record lows (Rago et al. 1998). The same species was also one of the few that increased in heavily trawled areas of the Adriatic Sea between 1948 and 2005 (Ferretti et al. 2013). Graham et al. (2001) found that *S. megalops* (and to a lesser degree, a catshark species) were the only taxa that maintained similar abundances between trawl surveys at the start of a trawl fishery and 20 years thereafter in SE Australia. It was also one of the only taxa for which size compositions remained similar between the two survey periods (Andrew et al. 1997).

The apparent robustness of *Squalus* spp. is surprising, considering they are K-selected, viviparous elasmobranchs with slow growth, low fecundity and a long life span (Watson and Smale 1998, 1999). Their success may be partly explained by the fact that they give birth to relatively large pups and the females reproduce constantly once they reach sexual maturity (Watson and Smale 1998). Their large young and venomous dorsal spines protect them from predators. In long-term comparisons of trawl surveys in the western English Channel, McHugh et al. (2011) found that the abundance of a catshark species (*Scyliorhinus canicula*) had increased substantially while other elasmobranchs had declined or disappeared from catches. They attributed this increase to the fact that it is a relatively small species, which has little commercial value and a comparatively high survival rate when discarded after trawling (Revill et al. 2005). A similar line of reasoning may be applicable to *Squalus* spp. in South Africa. The results of Mandelman and Farrington (2007) support the expectation that their discard survival is relatively high compared to many teleosts and other elasmobranchs (Broadhurst et al. 2006).

***Chelidonichthys* spp.**

The results presented here indicate substantial increases in the numbers of *Chelidonichthys* spp. caught in 2015 compared to the beginning of the 20th century. None of the gurnard species have undergone stock assessments in South Africa. Investigating the reproduction, population structure, age, growth and mortality of *Chelidonichthys capensis*, McPhail et al. (2001) noted that fishing pressure did not appear to be depressing the resource. Their results indicated that *C. capensis* is a relatively fast growing, r-selected generalist species that has an extended spawning season, a high reproductive rate and is long-lived. *C. queketti*, which made up the majority of re-survey catches, similarly has a fast growth rate, reaches early sexual maturity, spawns throughout the year and is a generalist that feeds on a variety of organisms and inhabits diverse benthic habitats (Booth 1997). These factors, together with their broad distributions over most of the Agulhas Bank (Smale and Badenhorst 1991) likely contribute towards the resilience of *Chelidonichthys* spp. to fishing pressure and allow them to maintain or even increase densities where other species have declined.

Trawl activity may benefit *Chelidonichthys* spp. in terms of food provision. Kaiser and Spencer (1994) found evidence of two gurnard species (*Aspitrigla cuculus* and *Eutrigla gurnardus*) and whiting (*Merlangius merlangus*) increasing their food intake after the passage of a trawl in the Irish Sea. In their investigation of trawl effects on demersal scavengers in the southern North Sea, Groenewold and Fonds (2000) suggested that gurnards might benefit indirectly from trawl activity by preying on scavenging crustaceans. The same authors estimated that 6-13% of the annual macrobenthos production is made available to scavengers and microbes by a single trawl tow, which likely shortens trophic pathways and may increase secondary production (Groenewold and Fonds 2000). Together with the characteristics that may confer robustness to fishing pressures (discussed above), an enhanced access to food may make certain levels of trawling advantageous to Agulhas Bank populations of *Chelidonichthys* spp., especially if those levels depress populations of competitors or predators that might be less robust to fishing pressure.

Trachurus capensis

T. capensis was shown to be more abundant in re-survey catches than it was historically, at all three sites (Fig 19c). The re-survey catches consisted of predominantly small (15-25 cm) individuals compared to the maximum size of *T. capensis* (~52 cm; Hecht 1990). Even if one assumes that historical catches consisted of larger individuals, their mass would likely have been less than that of re-survey catches, as plausible size differences are unlikely to have compensated for the discrepancy in numbers (re-survey catches averaged 47 times greater). It appears that *T. capensis* may have increased in biomass, as well as numbers, at the re-surveyed inshore sites. Reasons for this could be many, including declines of predator abundances (e.g. *Argyrosomus* spp.), reduced competition for food resources and/or environmental forcing that might have made these areas more suitable for *T. capensis*. For example, a shift in South Africa's small pelagic fish resources from the west coast to the Agulhas Bank in the late 1990s (van der Lingen et al. 2002; Fairweather et al. 2006), thought to be driven by the environment, might also have resulted in improved Agulhas Bank habitats for *T. capensis.*

It must be acknowledged that the semi-pelagic nature and high spatio-temporal variability of *T. capensis* (Badenhorst and Smale 1991) imply that these 'snapshot' demersal trawl surveys may not be a reliable measure of the regional *T. capensis* population (Barange et al. 1998). Nonetheless, the consistent pattern across the three inshore sites appears convincing. Previous estimates from an age-structured production model of the regional (west and south coast) population suggested their spawning biomass lay between 40 and 78% of pristine levels, depending on a number of assumptions (Furman and Butterworth 2011)

Galeichthys feliceps

The large re-survey catches of *G. feliceps* at Bird Island, compared to zero recorded there historically, suggests an increase in their numbers. Such large *G. feliceps* catches have not occurred at Bird Island during the past 30 years of DAFF surveys (Appendix A), but have been recorded at Mossel Bay. This supports the suspicion that some anomalous densities of certain taxa were encountered during the 2015 Bird Island fieldwork. Continued monitoring of future DAFF surveys may reveal whether the unusual Bird Island catches might be more than a temporary anomaly.

Tilney (1990) conducted per-recruit analyses using *G. feliceps* catches from the Port Alfred line fishery. His results suggested that the level of spawner biomass per recruit was between 22 and 30% of its pristine state. He concluded that the population was relatively heavily exploited and likely below the recommended management level of 50% of pristine biomass (Tilney 1990). Yet the re-survey catches at Bird Island and Mossel Bay are not congruent with a depleted population and suggest that numbers are similar or greater to those encountered historically. If so, similar arguments to those made for *Squalus* spp. might apply to *G. feliceps:* Their low market value may have helped avoid excessive exploitation, which together with potentially reduced competition and a low (perhaps decreased) predation pressure, may have allowed them to maintain or increase their numbers from pre-disturbed levels. This, despite being a long-lived, slow growing, K-selected species (Tilney 1990). As *G. feliceps* prefers soft sediments (Tilney and Hecht 1990), it may also have benefited from the fishing-associated habitat changes that are expected to have taken place at the survey sites.

Other and all taxa combined

Previous authors have shown evidence of increased *Callorhinchus capensis* (St Joseph shark) catches over time (Booth and Hecht 1998; Mussgnug 2013). As it was included in 'other' fish, this species could not be assessed individually here. However, the group of 'other' fish did increase significantly between periods at all sites and *C. capensis* contributed more than half of the re-survey catches for that group, which appears congruent with the hypothesis of increased abundances over time.

The taxa that appeared to maintain, if not increase, their abundances between periods, included some unlikely species with slow growth, old age-at-maturity and low fecundity. Examples included *Squalus* spp. and *G. feliceps*. *C. capensis* might also be assigned to this group, although its fecundity and growth are greater than those of many chondrichthyans (Freer and Griffiths 1993). Nonetheless, evidence that species with relatively slow growth and low reproductive output have managed to maintain or increase their abundances during a century of exploitation is a point of interest that may warrant further investigation. A further commonality across these species is that they have not been favoured fishing targets.

Long-term, persistent trawling pressures likely have indirect impacts on demersal fauna due to their effects on benthic habitat. Trawl activity reduces both physical and biological habitat complexity which species may rely on (Auster et al. 1996; Engel and Kvitek 1998; Moran and Stephenson 2000; Kaiser et al. 2000; Puig et al. 2012). Juvenile fish have been shown to associate with epibenthic structure (Lindholm et al. 2001; Ryer et al. 2004; Baillon et al. 2012), which likely helps them hide from predators (Tupper and Boutilier 1995). Therefore an expectation might be that a loss of epibenthic structure would have less impact on species that are spiny, or in any other way less palatable to predators, than species that are defenceless and more prone to predation if discovered. The fact that spiny taxa (*Chelidonichthys* spp., *Squalus* spp., *G. feliceps* and *C. capensis*) were prominent amongst re-survey catches and had increased or maintained their catch rates over the last century, appears to support such a hypothesis. Besides their spines, *Squalus* spp. pups have the added advantage of being a relatively large size at birth (Watson and Smale 1998) thereby avoiding predation suffered by smaller size classes. Trawling-induced loss of structural habitat likely reduces juvenile survival rates of demersal species that use epibenthic structure for concealment (Tupper and Boutilier 1995), while taxa that do not rely heavily on concealment from predators may escape this indirect impact of trawling.

Regional productivity

In the historical surveys a consistent pattern among several taxa and the pooled assemblage is a west-to-east decrease in CPUE across the three sites. These patterns suggest that the Cape Infanta site was the most productive fishing area historically and Bird Island the least. This west-to-east abundance gradient was reversed in the repeat surveys for all taxa combined. An inspection of DAFF data indicated that elevated catches at Bird Island, the most easterly site, represents the average condition in recent decades. Further investigation to verify this apparent productivity reversal, assess at which levels of the ecosystem it may manifest and what the potential drivers are, would enhance our understanding of south coast, inshore ecosystem dynamics.

Examination of assumptions

The main assumptions and justifications for methods used in the experimental design and fieldwork were discussed in Chapter 3. Some of those points (gear fishing power; differences in trawl duration and depth) are equally applicable to this chapter but are not repeated here. Instead, points of specific relevance to the univariate contrasts are focused on here.

Fish sizes

It is critical to consider the impact of fish sizes when interpreting results presented here. As a fish mass relates to the approximate cube of its length (Froese 2006), relatively small declines in length could translate to substantial changes in the biomass of a population, unless their numbers increase to compensate for the size reduction. To illustrate, a 61-cm *M. capensis* individual weighs approximately 1 900 g, whereas one of 30 cm would be about 213 g (Froese and Pauly 2016). For some taxa (e.g. *M. capensis*), it is conceivable that an increase in their numbers may have been accompanied by a decrease in biomass. Some effort was spent on unsuccessful attempts to convert the 'small/large' size-categories recorded historically for *Argyrosomus* spp., *A. pectoralis* and *M. capensis* into mean weights that would allow conversion of catch numbers into catch weights (Appendix B). Further research on this problem is identified as a challenging priority.

Long-term signal vs short-term variability

Because the sampling design did not allow multiple years of data (from either period), it was important to examine the context of short-term variability in relation to the observed long-term changes (as in Chapter 3). If the observed contrasts between the historical and repeat surveys are of similar or smaller magnitude than fluctuations among years or between seasons, then it might be argued that long-term signals fall within the bounds of short-term 'noise' and are meaningless. The temporal scale of recent DAFF trawl survey data allowed this question to be examined. Results suggested that the notable long-term changes focused on above, could in most cases, not be explained by the magnitude of short-term variability (Figs 20, 21). As would be expected, the exceptions to this tended to occur in cases where the difference between periods was relatively small.

Ideally, the short-term variability would be estimated from surveys conducted with the same trawl gear as used in the historical and repeat surveys. The magnitude of short-term differences estimated from DAFF survey catches may well be exaggerated for many species, relative to what would be measured if the same data had been collected with the historical trawl gear. Larger catches tended to cause larger differences between samples, consistent with the common finding that variance is related to mean catches in trawl survey data (Maunder and Punt 2004). As the smaller mesh size, faster trawl speed, higher-opening and larger DAFF nets are expected to have greater catching power for most species, their variability among samples is likely inflated relative to that of the less effective historical trawl gear. Irrespective of such an effect, examination of the shorter-term variability tended to confirm that prominent long-term changes could not be explained by the magnitude of seasonal, interannual or multi-year changes.

Similarities with previous research

Few studies have had the opportunity to investigate abundance changes from relatively undisturbed demersal baselines to their state after decades of exploitation. A consistent observation from such investigations appears to be an acute decline of taxa that were a dominant part of the assemblage when fishing started (Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Klaer 2001). Such drastic declines may be missed by long-term trawl survey comparisons if their earliest surveys describe a state that was already substantially impacted (Thurstan et al. 2010). In the current study, the virtual disappearance of *Argyrosomus* spp. and >95% decreases of *P. laniarius* and *A. pectoralis*, three taxa dominating the catches historically, represent a substantial loss from the demersal fish community. It is not surprising that other taxa were able to benefit, likely both from freed-up resources and reduced predation. The finding that some taxa increased or maintained abundances, despite increasing exploitation, is another consistency across the above-mentioned studies (Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Klaer 2001). As Klaer (2001) analysed commercial catches, he attributed the increased landings to altered retention strategies and not increased fish abundances.

Although Booth and Hecht (1998) contrasted two more-recent periods (1967-1975 and 1985-1998) and limited their focus to the commercial trawl fishery operating out of Port Elizabeth (near Bird Island), some similarities appear between their results and those of the current study. Similar to results here, they reported reduced catch rates of *P. laniarius*, *A. pectoralis* and *G. capensis* (kingklip). Their reports of increased contributions of *M. capensis*, *Chelidonichthys capensis*, *Callorhinchus capensis* and *Cynoglossus zanzibarensis* (redspotted tonguefish) are also congruent with findings from the current study (Booth and Hecht 1998). Contrary to results here, they showed a decrease in catch rates of *T. capensis* over their shorter study period. Booth and Hecht (1998) recorded a 35% decline in the overall catch rate (all species), despite technological improvements to fishing gear during the period assessed.

Future research

The findings presented here have a range of implications for ecological and fisheries research and raise many further questions that could be addressed in follow-up studies. Converting the catch abundances into catch weights or estimates of biomass would be a valuable accomplishment as such units would be of great interest to fisheries scientists and ecological modellers. It may be hindered by uncertainty, however, unless relevant data on historical sizes or weights can be found to verify calculated values. Investigation of the baseline conditions and long-term changes in trophic structure, and resultant changes in the transfer of energy through the ecosystem, may be a useful avenue for future work. These unique historical and re-survey datasets contain much potential for further work that will deepen knowledge of how historical baselines were shaped into current demersal states.

This work suggested that the estimated depletion at investigated sites was substantially worse for multiple taxa than has been estimated in regional stock assessment efforts. Further investigations could be valuable in explaining these discrepancies. Models of spatio-temporal trawl effort and benthic habitat dynamics from the Agulhas Bank region might help identify whether the discrepancies could be related to localised depletion or habitat alteration. An investigation of the relevant assessment models, specifically what their assumptions are in relation to the initial or unfished biomass, might also shed light on the identified inconsistencies.

Conclusion

The remarkable differences between historical and re-survey catch rates highlight the magnitude of change undergone by the demersal environment of the inshore Agulhas Bank in 111 years. Once-dominant species were absent or contributed small proportions in repeat survey catches. Their numbers were largely replaced by other, apparently more resilient, and in most cases, less economically valuable taxa. Although they no doubt played a role, the biological (growth and reproductive) characteristics typically invoked as indicators of sensitivity to exploitation did not effectively separate the species that have declined from those that have increased in this study. It appeared that other factors, such as habitat preferences and the magnitude of their geographic and depth ranges (as discussed in Chapter 3) influenced the fate of exploited demersal populations on the inshore Agulhas Bank. Over a century of otter trawling is expected to have driven substantial benthic changes (Auster et al. 1996; Auster and Langton 1999; Callaway et al. 2007) and modified the pathways of energy flow (Groenewold and Fonds 2000), benefiting certain taxa and costing others.

Change in fish sizes is an important indicator of fishing pressure (Bianchi et al. 2000; Shin et al. 2005; Yemane et al. 2008) and critical to considerations of changes in biomass. Although limited size data were available in the historical records, they confirmed the expectation of substantial reductions in lengths of favoured fishing targets. The implication of size reductions to changes in biomass would be to exacerbate decreases and weaken increases of catch abundances. Developing realistic and justifiable estimates of historical fish weights (or lengths) for these data, so that comparisons can be expressed in terms of biomass, is a valuable research avenue.

The historical data investigated here are unique in their ability to provide meaningful quantitative ecological samples from a temperate demersal assemblage that has suffered negligible impact from human activities. Compared to previous studies that have benefited from baseline data collected before or during initial trawling activity (Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Klaer 2001; Kongprom et al. 2003), these historical records are the earliest, and quite likely represent the most pristine demersal ecosystem. Analyses have enabled valuable insight into those pre-industrial, baseline catches and estimates of subsequent abundance changes of the trawl-caught fish fauna. The lessons may be applicable to many similar fisheries globally, most of which lack comparable pre-disturbance baselines. Yet the outcomes of this 111-

year 'experiment' have undoubtedly been shaped by regionally-specific histories of spatio-temporal exploitation patterns and pressures from climate change and pollution. Fisheries other than trawling, particularly the line-fishing components of commercial, recreational and small-scale (previously subsistence) sectors, have contributed to the current state of several taxa investigated here. These results strengthen and add to previous findings of a greatly altered inshore fauna that is denuded of a substantial proportion of once economically and ecologically prominent species (Penney et al. 1989; Attwood and Farquhar 1999; Griffiths 2000). Implementation of management interventions to rebuild these depleted populations clearly warrants attention.

Appendix A: Supplemental tables and figures

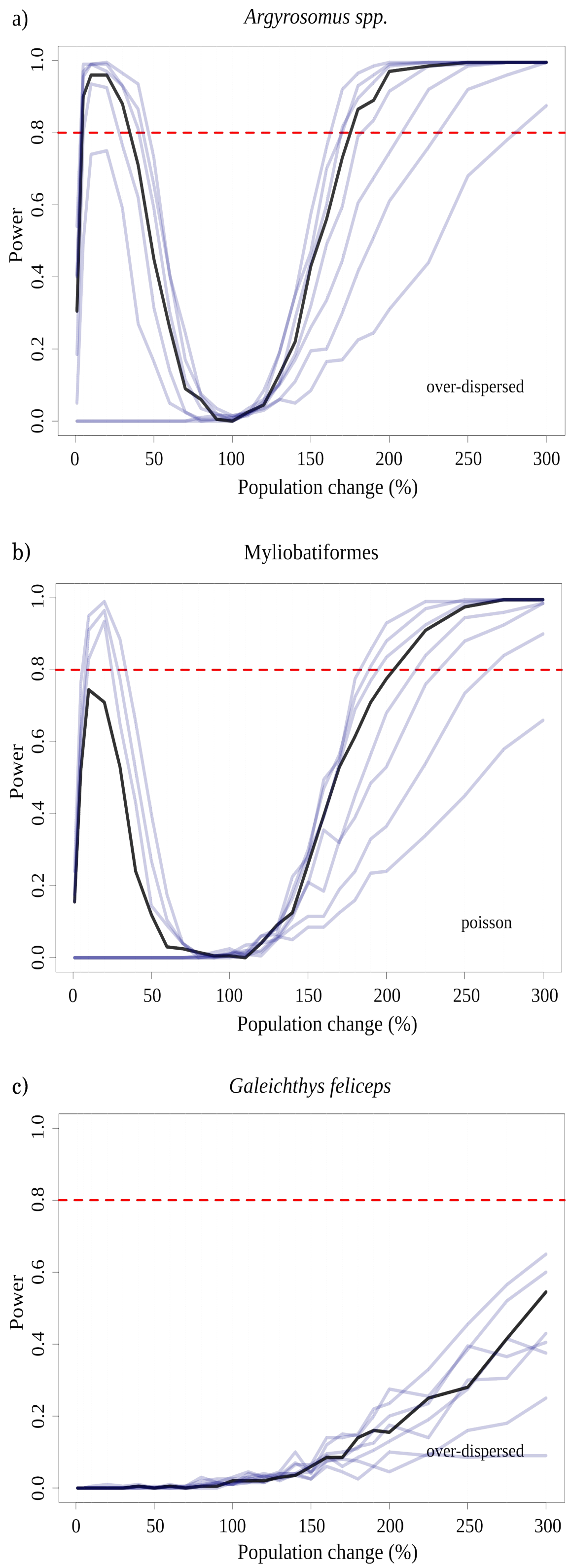


Figure A4. Examples of the power analysis plots visually assessed, for an abundant (a), common (b) and rare (c) taxon. Lines indicate the power of a GLM model to detect a significant ($p \leq 0.01$) effect for prescribed changes in standardised catch. Results were drawn for samples sizes 5 to 40 in increments of 5. Black line indicates N=25 trawls. See Methods section for details.

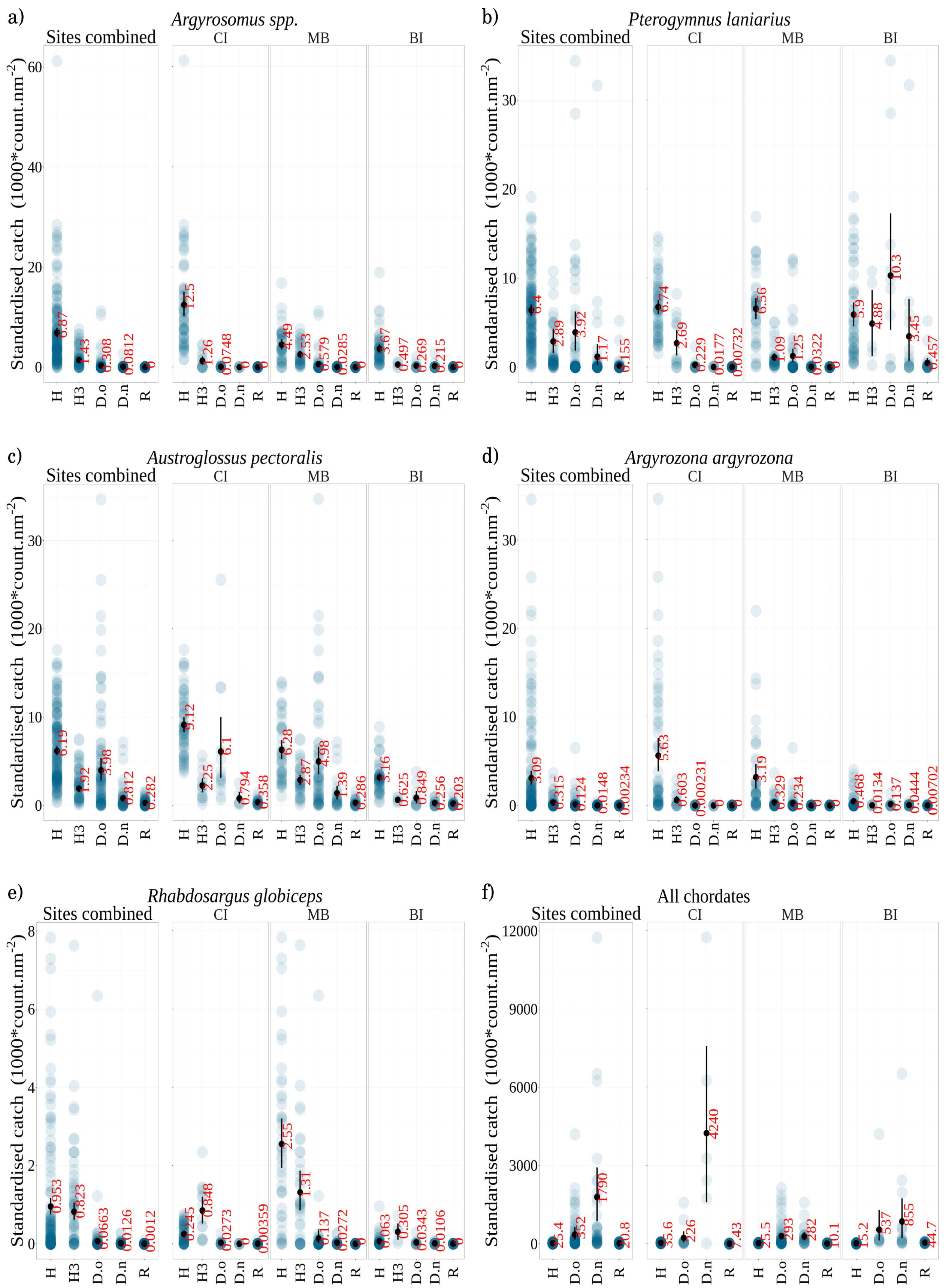


Figure A5. Similar to Fig 17, showing taxa that decreased on average between historical (H) and repeat (R) surveys, but including survey data from 1931-1934 (H3; when available), DAFF 'old' trawl gear (D.o; 1986-2010) and DAFF 'new' gear (D.n; 2003-15).

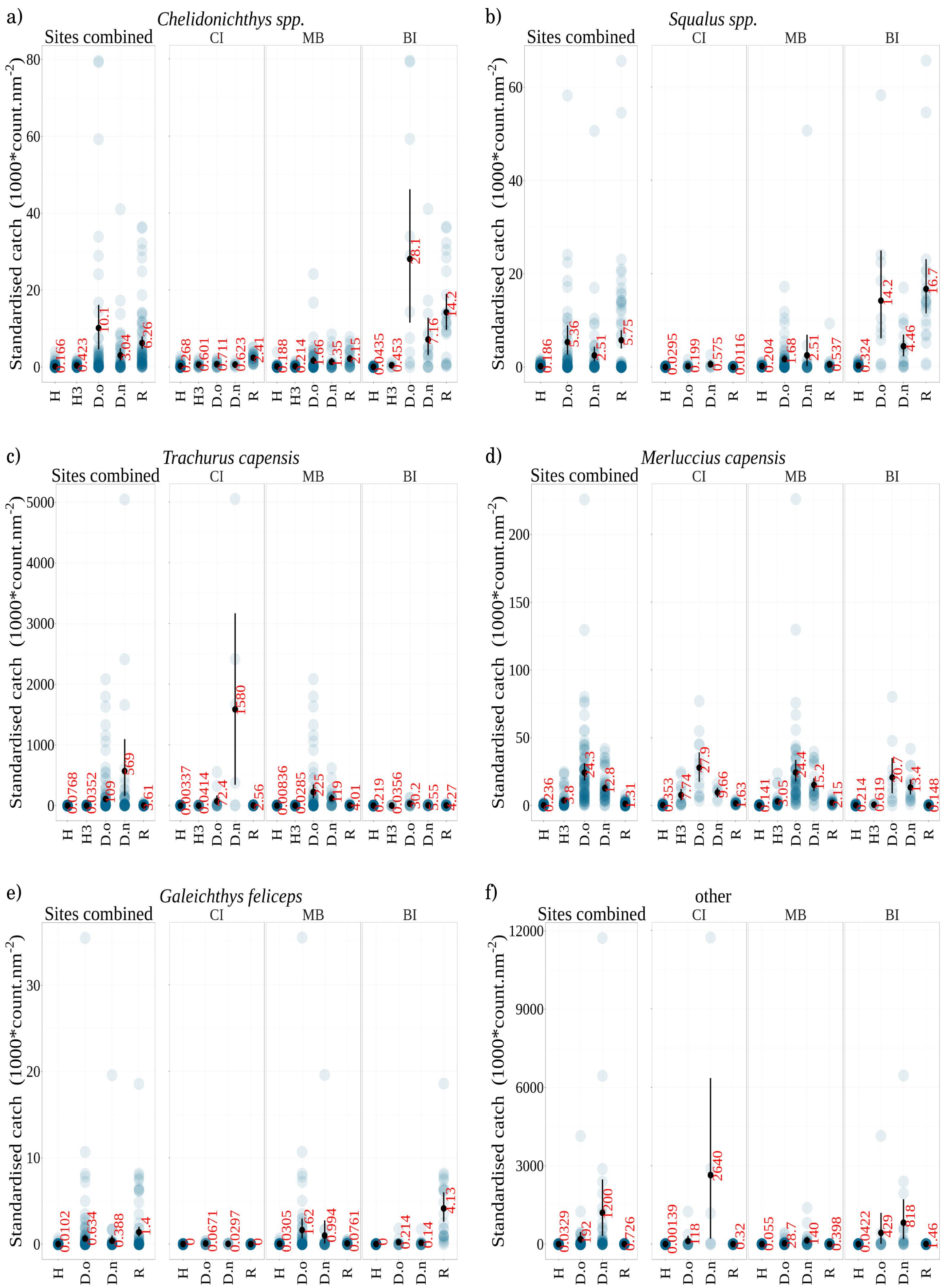


Figure A6. Same as Fig A5, but for the taxa that increased on average between historical and repeat surveys (those included in Fig 19).

Appendix B: Converting size categories into average weights

This appendix describes the procedure followed to estimate a mean mass for size classes (small/large), with the intended objective of converting fish abundances per size class into catches by weight. The results were not used in Chapter 4, but are briefly outlined below in case they might be built upon in future work. The strategy applied was to use established/published growth equations (Von Bertalanffy, 1938), length-weight relationships and mortality rates, together with gear-specific selectivity factors estimated from the repeat survey catches, to calculate the mean weight that a single fish in each (small/large) size class would contribute.

These results were not used further or presented in the chapter because the mean weights they suggested for small/large size classes appeared unlikely. More plausible results could be attained by adjusting parameters such as the natural mortality rate. However, without independent evidence to guide or verify such an adjustment, it would represent unjustified and subjective manipulation of model parameters.

One possible guide to assess whether the modelling procedures might be describing the historical state accurately, was to inspect the ratio of predicted small:large individuals in comparison to the same ratio recorded in historical catches. When parameters (e.g. mortality rate) were adjusted to produce plausible weights for the size categories, the predicted ratio of small:large fish was substantially different to that measured historically. It was therefore concluded that growth and mortality parameters, which were estimated in recent decades from exploited populations, are unable to provide a realistic prediction of the historical pre-disturbed population state. Another explanation for the lack of plausible results might be that the selectivity curves applied do not represent the historical case accurately, as briefly explained below.

Methods

The following steps were taken:

1) Start with creating a vector of theoretical age classes (T). Traditionally, the temporal resolution used is annual (e.g. $T=\{0.5, 1.5, 2.5, \ldots t_{max}-0.5\}$, where t_{max} represents the maximum age of the species), although a higher resolution can be used.

2) Calculate corresponding length-at-age (L_t) values, using published parameters for the growth equation. In this example, the von Bertalanffy growth equation was used:

$$L_t = L_\infty \left(1 - e^{-K(t-t_0)}\right) \qquad (1)$$

where L_∞ is the theoretical asymptotic (maximum) length attained by the species, K the growth coefficient, expressing the rate (1/year) at which the asymptotic length is approached, t the age (years) and t_0 the hypothetical age the fish would have at zero length (years).

3) Calculate corresponding weight-at-age (W_t) values, using the length-at-age values and published parameters for the length-weight relationship:

$$W_t = a * L_t^b \quad (2)$$

where parameters a and b are constants published for the relevant species.

3) Calculate the corresponding population size proportion (N_t) at age t, using the mortality rate (Z). As negligible fishing mortality was assumed for the historical period, the total mortality (Z) was, in this case, assumed to equal natural mortality. Both constant mortality rates and age-specific mortality rates (as suggested by Rademeyer and Butterworth 2014; Ross-Gillespie 2016) were considered. The equation used to model a constant mortality rate was as follows:

$$N_t = e^{-Z*t} \quad (3)$$

4) Calculate corresponding retention probabilities (between 0 and 1), using length-at-age (L_t) figures and the selectivity ogive that was estimated from repeat survey length frequency data (Millar and Fryer, 1999). Two parameters are used to describe the logistic ogive, namely the 50% retention length (L_{50}) and the selection range (δ). These were used to calculate the retention probability $P(L_t)$ of a fish of length L_t as follows:

$$P(L_t) = \frac{1}{1 + e^{-(L_t - L_{50})/\delta}} \quad (4)$$

5) Calculate the 'weight of retained fish' (Wrf_t) at age t, which represents the mass contribution of each age class to the retained (captured) population structure, by multiplying weight-at-age by the population size and the retention probability of the corresponding age t :

$$Wrf_t = W_t * N_t * P(L_t) \quad (5)$$

6) Calculate the average weight for each size class ('small' and 'large') by dividing the summed weight of retained fish (Wrf_t) by the summed proportion of retained population size ($N_t * P(L_t)$) for the ages t that fall within the relevant size class. For example, the limit between 'small' and 'large' *M. capensis* was historically recorded as 61 cm (24 inches). Therefore the mean weight of 'small' fish (W_{small}) would be calculated as:

$$W_{small}=\frac{\sum_{t=1}^{L_t<61} Wrf_t}{\sum_{t=1}^{L_t<61} N_t * P(L_t)} \tag{6}$$

and similarly, the mean mass of a 'large' fish would be:

$$W_{large}=\frac{\sum_{L_t \geqslant 61}^{N} Wrf_t}{\sum_{L_t \geqslant 61}^{N} N_t * P(L_t)} \tag{7}$$

In this way, a mean weight (in grams) for each 'small' and 'large' fish were attained. However, as mentioned above, these figures did not appear plausible. For example, using published growth and length-weight parameters for *M. capensis*, together with selectivity factors estimated from the repeat survey catches, approximate weights of 481 g and 6 473 g were suggested for small and large fish respectively, assuming a uniform mortality rate of 0.3. If the age-specific mortality rates of (Ross-Gillespie, 2016) were used, these figures changed to 433 g and 10 058 respectively. Considering the fact that a 61-cm *M. capensis* individual typically weighs about 1 905 g, the mean weights of large fish appeared to be unrealistically large. Increasing the uniform mortality rate reduces the mean weights estimated, however doing so also increases the ratio of predicted small:large fish and thereby increases the already-large discrepancy between the predicted ratio (3.45) and that measured from historical catches (0.2).

An obvious next step would be to explore application of a dome-shaped selectivity curve to the catches, instead of ogive that was used. Unfortunately, few large fish were caught in the repeat surveys, making it hard to estimate a dome-shaped selectivity curve for the historical gear. This step was not pursued.

Literature cited

Millar RB, Fryer RJ (1999) Estimating the size-selection curves of towed gears, traps, nets and hooks. Reviews in Fish Biology and Fisheries 9:89–116. doi: 10.1023/A:1008838220001

Rademeyer RA, Butterworth DS (2014) Specifications of the South African Hake 2014 Reference Case Assessment. Document MARAM IWS/DEC14/Hake P 2:26pp.

Ross-Gillespie A (2016) Modelling cannibalism and inter-species predation for the Cape hake species *Merluccius capensis* and *M. paradoxus*. PhD thesis, University of Cape Town

Von Bertalanffy L (1938) A quantitative theory of organic growth (inquiries on growth laws. II). Human biology 10:181–213.

Chapter 5: Distribution changes in the demersal fish community of the Agulhas Bank, 1986-2016

Abstract

Anthropogenic climate change and fishery impacts have been predicted and documented to modify the distributions of marine species. An understanding of the direction and velocity of such changes is critical to the adaptation by fishers and the management of fishery resources and biodiversity. Yet detecting trends within the variability inherent in marine data is challenging and few empirical cases have documented distributional trends in South African marine taxa. In this context, the last three decades (1986-2016) of demersal fisheries research survey data from the south coast of South Africa were interrogated using a recently developed method to investigate distributional changes in 44 of the most commonly encountered chondrichthyan and teleost species. Annual estimates were made of the centre of gravity in coordinate space (latitude and longitude) and the effective area occupied by each population, using a species distribution function estimated by a geostatistical delta-generalised linear mixed model. Average trends over the study period were assessed using a Bayesian state-space model. Evidence of a trend in average location was found in nine species, of which six were towards the west or south-west and three were towards the east or north-east. The effective area results showed that two taxa had a decreasing trend in their spatial extent, while one species had increased. At the level of the entire community, average trends were shown as a westward shift in average location and a reduction in the extent of populations. These westward and contracting trends are interpreted as likely signals of climate forcing, whereas the eastward movement in average location for kob (*Argyrosomus spp.*), lesser sandshark (*Rhinobatos annulatus*) and white stumpnose (*Rhabdosargus globiceps*) are likely linked to fishing impacts. A lack of knowledge of subsurface oceanographic changes on the Agulhas Bank challenges interpretation of the distributional changes detected and is identified as a research priority. Disentangling drivers of observed change and projection of trends will provide valuable contributions towards improved ocean management and mitigation of climate impacts on fishers. Future work could reveal additional insights by modelling seasonal variation, the distribution of multiple species or age-classes and incorporating additional historical data. The continuation of multi-decadal ecological time-series, such as the trawl surveys used here, are vital to achieving this research.

Introduction

A consistent theme throughout marine ecology is the dynamic nature of populations in space and time. Understanding the spatial distribution of species is critical to their management, as both impacts and potential interventions are very often spatially structured, whether the focus is on fisheries or biodiversity. Evidence of distribution changes of marine populations, frequently linked to human pressures, are well established (e.g. Garrison and Link 2000; Beare et al. 2004; Perry et al. 2005; Engelhard et al. 2011b; Bartolino et al. 2012; Ferretti et al. 2013; Pinsky et al. 2013). Detecting such distributional changes and understanding aspects such as their scale, direction, speed, and cause, is therefore key to providing management advice. Identifying and predicting spatial distribution trends will also help inform fishers' adaptation and mitigation strategies for climate change impacts, which is a national research priority (DST 2007; Sink et al. 2012a; DAFF 2017).

Fishing and climate influence distributions

Fishing pressure and climate change are expected to be dominant factors altering species distributions in the ocean (Genner et al. 2010; Bell et al. 2015). Fishing is one of the oldest human activities in the sea (O’Connor et al. 2011) and has altered the abundance and distribution of species (Brander 1981; Casey and Myers 1998; Opdal 2010; Engelhard et al. 2011b). Fishing impacts on population sizes may translate to changes in distribution via local extirpation (Brander 1981; McHugh et al. 2011), range contraction or expansion towards or from optimal habitat (Bell et al. 2015; Thorson et al. 2016b), or via the truncation of ages in species that have age-specific distributions (Bell et al. 2015).

The effects of anthropogenic climate change on marine ecosystems may be more gradual than many fishing impacts, yet are likely to be widespread and difficult to reverse (Halpern et al. 2008). Evidence of marine distributional changes linked to climate are well established (e.g. Beare et al. 2004; Perry et al. 2005; Pinsky et al. 2013). Marine species have responded to climate (temperature) changes by adjusting their location, depth or both (Edwards and Richardson 2004; Dulvy et al. 2008; Engelhard et al. 2011b).

The pace of shifting climate is likely critical to the ability for species and ecosystems to adapt or relocate (Loarie et al. 2009). A metric used to assess this, specifically how fast a species would have to move to remain in a constant climate (temperature), is called 'climate velocity'. It expresses the rate of geographic (distance) shift of isotherms, which depends on both the rate of temperature change and existing thermal gradients (Loarie et al. 2009). With a focus on a wide array of demersal species across multiple regions globally, Pinsky et al. (2013) showed that the direction and magnitude of distribution changes were related to climate velocity rather than biological or taxonomic characteristics.

Regional evidence of distribution changes

Changes in marine distributions have been documented from the southern Benguela ecosystem, yet a synthesis of ecosystem change (Blamey et al. 2015) shows that much of the knowledge of physical and ecological change stems from the west coast, whereas dynamics on the Agulhas Bank have received less attention. The most prominently documented distributional shifts have been a southward and eastward movement of small pelagic fish populations (sardine and anchovy) from the west coast to the Agulhas Bank during the late 1990s (van der Lingen et al. 2002; Fairweather et al. 2006). The redistribution of these important prey species is thought to have impacted other parts of the ecosystem, including distributions or abundances of fish, squid (Watermeyer et al. 2016), seabirds (Crawford et al. 2008; Crawford 2009; Blamey et al. 2015) and zooplankton (Huggett et al. 2016).

To assess the ecosystem implications of the small pelagic fish distributional change, Watermeyer et al. (2016) investigated the proportional abundances of key pelagic and demersal species either side of Cape Agulhas (20°E), using three multi-year periods defined as 'before' (1985-1991), 'during' (1997-2000) and 'after' (2003-2008) the shift of small pelagic fish (van der Lingen et al. 2002; Fairweather et al. 2006). Evidence of increased catch proportions of squid (*Loligo reynaudii*), demersal fish (*Genypterus capensis*, *Merluccius paradoxus*) and pelagic fish (*Etrumeus whiteheadi* and *Scomber japonicus*) were shown east of 20°E, following the shifts of small pelagic fish (Watermeyer et al. 2016).

Yemane et al. (2014) assessed the distribution changes in common demersal species in the Benguela ecosystems of South Africa's west coast, Namibia and Angola. Conducting separate analysis for the trawl survey time-series from each country, they calculated a catch-weighted average depth and latitude for each species and year. They also assessed changes in (depth and latitudinal) ranges, by calculating the difference between the maximum and minimum values in each year. Their results suggested that approximately half of the species assessed had changed their mean depth, latitude or range of either variable. While the latitudinal shifts in Angola were poleward and consistent with the expectation from a warming ocean, the shifts in distribution in the other two countries tended to be either north- and south-ward. On the west coast of South Africa, five species shifted in each direction and ten showed evidence of deepening their mean distribution between 1985 and 2010. Yemane et al. (2014) found no evidence that the changes were related to body size or taxonomy and suggested that they were likely predominantly due to changes in climate, although fishing impacts could not be ruled out.

Changes in the distribution of trawl-caught fauna in South Africa have received limited attention beyond the work by Yemane et al. (2014) and Watermeyer et al. (2016). Pecquerie et al. (2004) overlaid multiple fishery and survey datasets to estimate the population distributions of 15 demersal, bentho-pelagic and pelagic species. With a focus on the distributional range, they showed some seasonal differences between two 6-month semesters. Although they also contrasted species ranges between two periods (1985-1989 and 1990-2002), the unequal sample coverage made inferences difficult and their interpretations focused on small pelagic species that had shown notable distribution increases.

Coastal distributional changes that have been documented from South Africa include an eastward shift by rock lobster (*Jasus lalandii*; Cockcroft et al. 2008), an eastward range expansion of kelp (*Ecklonia maxima*; Bolton et al. 2012) and an apparent eastward contraction by the brown mussel (*Perna perna*; Blamey et al. 2015). These changes are congruent with the indication of cooler coastal waters on the south coast (Rouault et al. 2009; Blamey et al. 2015), that may be a result of increased coastal upwelling (Lamont et al. 2016). Further evidence that may signify ecosystem changes on the Agulhas Bank, is the report of decreased abundance of copepods, especially large species, between 1988 and 2011 (Huggett et al. 2016).

Detecting meaningful patterns or trends within the variability inherent in marine data is challenging and relatively few empirical cases have documented distributional changes in South African marine taxa. Despite the efforts of authors such as Pecquerie et al. (2004), Yemane et al. (2014) and Watermeyer et al. (2016), detection and understanding of faunal distribution shifts in demersal and pelagic ecosystems are in their infancy and much more is to be learnt from the decades of research survey data that have been accumulated over South Africa's shelf area. Within this context the last thirty years (1986-2016) of demersal survey data from South Africa's south coast were interrogated to assess whether the spatial distribution of the most common ichthyofaunal taxa have been changing. Recently developed methods were used to assess two questions: a) Are populations changing in their average location? b) Are populations expanding or contracting in their extent? The answers to these questions are interpreted in terms of the state of knowledge of climate signals and regional fishery pressures. Implications for the management of South Africa's demersal communities are raised and likely avenues of future research are outlined. Ideally the distributions from historical data included in previous chapters would be included in these analyses, but their incompatibility in terms of units, survey strategies and gear precluded their inclusion here.

Methods

Study area and data preparation

Trawl survey data and commercial trawl effort data for the south coast of South Africa were obtained from the Department of Agriculture, Forestry and Fisheries (DAFF). The survey data were collected during annual stratified random surveys on the continental shelf. Initially both autumn and spring surveys were conducted, however spring surveys were discontinued after 2008. The surveys span the period 1986-2016 and are bounded by longitudes 20° and 27°E. Prior to 2011, the latitudinal bounds of the survey area consisted of the coastline and the 500 m isobath, whereas sampling was extended to 1000 m depth thereafter. Stations beyond 500 m depth were omitted from these analyses. Table 9 provides a summary of the data used in analyses.

Commercial trawl effort data consisted of the number of trawl hauls reported annually in a 20 by 20 minute spatial grid. Although the coordinates of trawls are recorded in recent years (after 2000), previously only the grid-cell was recorded and analyses were therefore applied at the grid resolution. Data were available from 1983 to 2015.

Species were selected for inclusion in analyses by their rate of occurrence in the survey data, using a cumulative threshold of 80% of total encounters. Analyses were limited to records of teleost and chondrichthyan taxa. Small pelagic fish (*Engraulis encrasicolus*, *Etrumeus whiteheadi*, *Sardinops sagax*) were excluded as they are unlikely to be effectively sampled by the trawl surveys. Samples were included in analyses if they were designated 'abundance' trawls by the authority collecting them. This meant they had a duration between 20 and 35 minutes, a towing speed of 3-3.5 knots and did not suffer net damage or other logistical disruptions that might influence the catch.

Gear changes during the 3-decade survey period were considered in analyses. Most of the survey data were collected by the government research vessel, Africana III. However, in 2000 the survey was performed with the RV Dr Fridtjof Nansen and in 2014-2016 commercial trawl vessels conducted the annual research surveys. During the survey period a change in trawl gear also took place, as detailed by Atkinson et al. (2011b) and Leslie (2008). In 2004, the old trawl gear was replaced with a new net, trawl doors and foot-rope. However, in 2006 and 2010, the old gear was again employed (Table 9). Although they were of similar design and size, these gear changes likely affected the selectivity for some species (Leslie 2008). The trawl gear used on board the RV Dr Fridtjof Nansen (in 2000) provides a third set of gear that likely had different selectivity to both other sets (Axelsen and Johnsen 2015). In addition to the potential effect of gear changes, there were some inconsistencies in the depth (and therefore spatial) coverage of surveys. Whereas most surveys extended to depths of 500 m or more, several spring surveys (1990-1995) were limited to ≤200 m.

Table 9: Summary of the DAFF research trawl survey data used in analyses. Seasons a=autumn, s=spring; gear o='old gear', n='new gear', g=Gissand gear used on the RV Dr Fridtjof Nansen; N=number of trawl samples.

Year	Season	Gear	Depth (m)	N
1986	a			
	s	o	28-485	79
1987	a			
	s	o	17-395	87
1988	a	o	30-450	92
	s			
1989	a	o	32-185	62
	s			
1990	a	o	30-480	57
	s	o	24-224	73
1991	a	o	33-362	91
	s	o	31-144	73
1992	a	o	30-400	82
	s	o	25-124	87
1993	a	o	29-440	108
	s	o	29-186	105
1994	a	o	35-500	87
	s	o	30-200	91
1995	a	o	29-483	92
	s	o	28-193	95
1996	a	o	27-440	77
	s			
1997	a	o	33-426	96
	s			
1999	a	o	30-469	82
	s			
2000	a	g	45-398	87
	s			
2001	a			
	s	o	35-384	80
2002	a			
	s			
2003	a	o	35-441	88
	s	n	35-434	93
2004	a	n	34-444	90
	s	n	40-500	106
2005	a	n	34-463	103
	s			
2006	a	o	38-445	91
	s	o	30-460	103
2007	a	n	35-440	97
	s	n	36-450	79
2008	a	n	37-452	100
	s	n	37-487	95
2009	a	n	36-460	89
	s			
2010	a	o	30-443	63
	s			
2011	a	n	38-446	93
	s			
2014	a	n	36-490	94
	s			
2015	a	n	34-494	98
	s			
2016	a	n	34-482	98
	s			

Mean location and extent of species

Potential changes in the distribution of trawl-caught fauna were assessed using their averaged centre of distribution, hereafter referred to as 'centre of gravity'. This has commonly been calculated as an abundance-weighted average of sample coordinates or depth (e.g. Perry et al. 2005; Engelhard et al. 2011b; Pinsky et al. 2013; Hiddink et al. 2015). Thorson et al. (2016a) demonstrated a novel method to calculate centre of gravity from a species distribution function that is estimated within a statistical model framework. As shown in a simulation study (Thorson et al. 2016a), one of the main advantages over the conventional method is that the species distribution function benefits from the underlying model's ability to account for bias inherent in the survey data. For example, the statistical model can be designed to account for unbalanced sampling effort in space or changes in sampling gear or strategy (Thorson et al. 2016a).

Instead of the conventional strategy of using sample locations to calculate the centre of gravity, weighted averages were calculated from the species distribution function at model-predicted locations. For example, the calculation of latitudinal centre of gravity was as follows:

$$\overline{Latitude} = \frac{\sum_{i=1}^{n_s} \hat{d}(s_i) * Latitude(s_i)}{\sum_{i=1}^{n_s} \hat{d}(s_i)} \qquad (1)$$

where n_s represents the number of grid cells defined in the model, $\hat{d}(s_i)$ is the predicted density at grid cell s_i and $Latitude(s_i)$ the corresponding cell latitude.

To assess whether populations might be expanding or contracting in their spatial distribution, their 'effective area occupied' was investigated (Thorson et al. 2016b). The effective area represents the geographic area (h_t ; km^2) that would be required to contain the total population (b_t ; kg) at its average population density (m_t ; kg/km^2):

$$h_t = \frac{b_t}{m_t} \qquad (2)$$

This simple measure of area occupied does not require parameters to be defined a priori (e.g. X % of the population), the value of which could affect results (Thorson et al. 2016b, supplementary material). It is also not affected by sampling areas of zero or very low density (Thorson et al. 2016b, supplementary material). Calculated for each time-step of the statistical model (annually in most cases), the effective area and centre of gravity results provide a measure over time of the spatial extent and average locality (coordinates) of the population, within the geographic domain surveyed.

Thorson et al. (2016a) estimated the species distribution function using a geostatistical delta-generalised linear mixed model (geoGLMM), which was developed to estimate abundance indices from trawl surveys (Thorson et al. 2015b). Their model is based on the delta approach (Lo et al. 1992; Stefánsson 1996), whereby the probability of encounters (positive catch) and the probability of catch rates given a positive encounter, are modelled separately. In the geoGLMM both probabilities assume spatially correlated errors. The spatial variation is further decomposed into two components – one that is constant among years and another that varies, thereby accounting for changes in spatial distribution over time (Thorson et al. 2016a). As the centre of gravity and effective area statistics are estimated within the geoGLMM, their standard error incorporates estimation uncertainty of model parameters. The mathematical structure of the geoGLMM is detailed by Thorson et al. (2015b).

In this study, the average species locations (latitude and longitude) were calculated using the same methods and geoGLMM as Thorson et al. (2016a), who describe the steps necessary to estimate the species distribution function. The effective area was calculated as in Thorson et al. (2016b). Positive catches were modelled using a gamma distribution, whereas the probability of encounters assumed a Bernoulli process. The geoGLMM was based on a 2.5 by 2.5 minute spatial grid (roughly 2.5 nautical mile^2 per grid-cell). A spatial resolution of 500 'knots' was specified to define the localities within the polygon mesh at which spatio-temporal functions were solved.

The geoGLMM with outputs of effective area and centre of gravity were calculated using the R package SpatialDeltaGLMM (Thorson et al. 2015b; http://github.com/nwfsc-assess/geostatistical_delta-GLMM). It uses the template model builder package (TMB; Kristensen et al. 2016) to invoke Laplace approximation of marginal likelihoods of fixed effects while integrating across all random effects (Skaug and Fournier 2006). Potential bias in the calculation of nonlinear functions of fixed and random effects was avoided by applying the 'epsilon' bias-correction in TMB (Thorson and Kristensen 2016). As the bias-correction routine necessitated substantial computational memory, models were run on a Linux-operated cluster computer at University of Cape Town's High Performance Computing Facility.

Trends were estimated from the centre of gravity and effective area time-series using a Bayesian state-space model framework (Durbin and Koopman 2012). State-space models (SSM) are hierarchical models that decompose a time-series of observations into two parts: 1) the state process that models the dynamics of unobserved state variables (e.g. the 'true' centre of gravity and its trend) and 2) a stochastic observation process or error that is conditional on the underlying state (Simmons et al. 2015).

The unknown 'true' population-level response was treated as the state variable that follows a Markov process (Gilks et al. 1995). The value of the current year ($\mu_{t,i}$) was assumed to be dependent on its value in the previous year ($\mu_{t-1,i}$), an underlying trend component (β) and a process error term ($\eta_{t,i}$) that incorporates variation among years via a random normal walk with mean zero and an estimable variance σ_i^2 . The state process equation was defined as

$$\mu_{t,i}=\mu_{t-1,i}+\beta+\eta_{t,i} \qquad \eta_{t,i}\sim N\left(0,\sigma_i^2\right) \tag{3}$$

and the observation error equation as

$$\hat{y}_{t,i}=\mu_{t,i}+\epsilon_{t,i} \qquad \epsilon_{t,i}\sim N\left(0,SE_{t,i}^2\right) \tag{4}$$

where $\hat{y}_{t,i}$ represents the centre of gravity or effective area values predicted by the geoGLMM and $\epsilon_{t,i}$ the observation error that is normally distributed with mean zero and variance equal to the square of the standard error ($SE_{t,i}$) from the geoGLMM predictions. The subscripts denote years t and species i , where $i=1$ for a single species or $i=\{1,2,...N\}$ for the trend estimated from the combined set of N species. In this way, the underlying trend β represents an estimate of the average rate of change over the time-series, accounting for both observation error (the variance associated with the centre of gravity or effective area estimate) and process error (a measure of the year-to-year variability among centre of gravity or effective area estimates).

Before being passed to the SSM, both time-series were normalised by their mean value for the entire period. In the case of single-species trend estimates, both spring and autumn values were normalised by the mean of autumn, so as to preserve differences between the seasons if they were combined on one plot. In the case of multispecies trend estimates, the values were normalised by the mean of the respective season, so as to centre all series on zero.

Non-informative priors were used for the SSM so that model inference would be based solely on information contained in the data. An inverse-gamma distribution with scale and shape parameters set to 0.001 was used as a prior for the process variance (Chaloupka and Balazs 2007). Expected values of the first year ($\mu_{1,i}$) were drawn from a flat normal distribution with mean equal to $\hat{y}_{1,i}$ and standard deviation of 1 000 000. The prior used for the trend (β) was a flat normal distribution with a mean of zero and a standard deviation of 1 000 000.

Joint posterior probability distributions were estimated using JAGS software (Plummer 2003). The model formulation was passed to JAGS using the R package 'jagsUI' (Kellner 2016), which makes use of the 'rjags' package (Plummer et al. 2016).

Each SSM model was run with 50 000 iterations, removing the first 5 000 results as 'burn-in' and thereafter sampling every 5th iteration to construct the posterior distribution. The mean and 95%

credibility intervals (2.5th and 97.5th percentiles) were used to visualise the model prediction in plots. To assess the probability that the estimated trend component was significantly different from zero (i.e. had a positive or negative slope), the posterior of trend estimates was used as a bootstrap sample to calculate equal-tail p-values as per MacKinnon (2009).

To assess whether emerging trends might be affected by potential sampling bias, the above analyses were repeated on reduced subsets of the data that removed the suspected bias. Firstly, to examine whether a potential depth bias might affect results, an additional set of analyses was performed on the spring survey data while excluding samples with mean depth >200 m. Secondly, to examine whether the trends might be affected by changes in vessel or gear, analyses were repeated on a dataset restricted to the 'old trawl gear' and the RV Africana III. As these curtailed time-series were both shorter and contained far less data, a substantial loss of statistical power was expected and trends were visually compared rather than relying on the same statistical thresholds applied to the entire dataset.

Changes in commercial trawl effort

The commercial trawl effort data were used to assess both spatial distribution and temporal changes in the intensity of trawling effort. The spatial distribution of cumulative commercial trawl pressure in recent decades was mapped as the mean number of trawl hauls recorded in each commercial trawl grid-cell between 1983 and 2015. Change in effort over time was assessed by regressing the annual counts of trawl tows against years. A slope significantly different from zero ($p \leq 0.05$) was inferred as evidence of an increase (positive slope) or decrease (negative slope) in commercial effort over time. The regressions were performed separately for each grid-cell, to assess temporal changes in space.

Summed trawl pressure (number of tows) was also examined for the entire study area, covering most of the Agulhas Bank, and two smaller areas in the western and eastern inshore parts of the study area respectively. The inshore areas were chosen as six commercial grid cells covering areas adjacent to the coastline. The western inshore area stretches between Cape Infanta and the first grid-cell to the east of Mossel Bay. The eastern inshore area extends from the eastern boundary of the study area to between Cape St Francis and Port Elizabeth.

Table 10. Centre of gravity (COG) and effective area results for 44 species and all taxa combined. The first six columns show trend estimates (km.year^{-1} or km^2.year^{-1}). Blue and red figures indicate evidence of trends different from zero ($p \leq 0.1$), signifying negative and positive trends respectively. Underlined figures identify those with $p \leq 0.05$. Bold r^2 values in right-most columns identify species lacking significant correlation ($p > 0.05$) between eastward and northward COG time-series.

Taxa	Eastwards COG		Northwards COG		Effective area		Correlation r^2 E-N	
	Autumn	Spring	Autumn	Spring	Autumn	Spring	Autumn	Spring
All taxa	**-0.26**	-0.16	-0.04	-0.01	**-61.87**	**-58.35**	NA	NA
Galeichthys feliceps	-0.56	1.52	-0.02	0.15	-18.22	-36.14	0.85	0.78
Arnoglossus capensis	0.12	0.26	0.10	0.23	-274.45	-277.47	**0.16**	0.77
Paracallionymus costatus	-0.39	-0.73	-0.23	0.09	-68.37	13.23	0.91	0.83
Callorhinchus capensis	0.52	-0.25	0.07	-0.17	53.95	97.02	0.61	0.37
Trachurus capensis	**-2.61**	**-3.41**	0.88	-1.03	**-487.56**	-314.99	**0.10**	0.73
Congiopodus spinifer	-0.28	-0.11	-0.25	0.04	23.95	-259.45	0.78	0.78
Congiopodus torvus	-0.10	-0.18	-0.09	-0.25	-51.91	-377.07	1.00	0.97
Cynoglossus zanzibarensis	-0.68	0.43	-0.48	0.23	-276.16	-213.97	0.67	0.61
Dasyatis chrysonota	1.25	0.26	0.17	0.07	-71.18	-40.12	0.98	0.95
Thyrsites atun	0.14	-1.12	0.29	-1.23	-9.07	-362.84	0.75	0.76
Gonorynchus gonorynchus	1.08	0.21	0.42	0.06	**430.38**	657.28	0.78	0.58
Lophius vomerinus	-0.86	-0.43	-0.80	-0.30	-164.92	-116.48	0.89	0.98
Merluccius capensis	-0.33	-0.41	0.11	-0.28	-90.70	-19.47	**0.10**	0.50
Merluccius paradoxus	-1.64	-0.30	-0.87	-0.19	17.13	-84.53	0.99	0.99
Myliobatis aquila	-0.10	-1.57	-0.09	-0.57	3.69	263.06	0.89	0.75
Genypterus capensis	-0.49	0.88	-0.45	0.25	-109.08	-69.64	0.89	0.92
Raja miraletus	-0.86	0.52	0.14	0.24	-125.44	-166.00	0.16	0.97
Dipturus pullopunctatus	**-0.68**	-0.30	**-0.38**	-0.24	**-634.69**	-136.54	1.00	1.00
Leucoraja wallacei	-0.27	-0.33	-0.19	-0.33	-376.24	-120.79	1.00	0.90
Rostroraja alba	0.21	0.64	0.45	0.45	-310.94	-460.80	0.55	0.99
Raja straeleni	**-0.94**	-0.87	**-0.51**	-0.29	-537.23	-134.12	0.78	0.53
Rhinobatos annulatus	0.95	-0.05	**0.35**	0.00	-151.67	-173.73	1.00	0.87
Argyrosomus spp.	1.32	1.78	**0.32**	0.37	-140.86	-119.81	0.97	0.53
Scomber japonicus	-1.60	-2.20	0.31	-0.05	1204.13	388.61	**0.08**	0.57
Helicolenus dactylopterus	-0.12	-0.03	-0.10	-0.02	1.03	-8.12	0.85	1.00
Haploblepharus edwardsii	-0.26	-0.26	0.00	0.11	-115.35	-253.34	0.39	0.49
Holohalaelurus regani	-0.52	-0.06	-0.17	-0.07	-168.45	-27.72	0.62	0.98
Scyliorhinus capensis	-0.58	-0.03	-0.60	0.03	-250.88	103.55	0.84	0.50
Halaelurus natalensis	0.25	0.29	0.19	0.16	-171.11	-141.17	0.73	0.94
Austroglossus pectoralis	-0.71	**-2.61**	-0.04	**-0.50**	-89.24	-207.65	0.42	0.84
Argyrozona argyrozona	-0.03	-1.15	-0.12	-0.54	58.70	-52.85	0.51	**0.22**
Pterogymnus laniarius	-0.48	-0.31	-0.17	-0.09	-40.53	0.51	0.93	0.88
Pagellus natalensis	0.61	-1.87	0.13	-0.43	-22.77	3.55	0.99	0.92
Spondyliosoma emarginatum	0.38	0.47	0.03	-0.01	-251.94	-51.64	0.91	0.74
Rhabdosargus globiceps	1.11	**1.94**	0.23	0.31	139.20	157.33	0.66	0.77
Squalus acutipinnis	-0.31	-0.46	**-0.76**	-0.53	-57.63	12.00	0.47	0.88
Mustelus mustelus	0.70	-0.05	0.28	-0.01	-97.41	4.65	0.90	0.99
Mustelus palumbes	0.07	-0.10	-0.16	0.00	-66.52	107.66	0.55	**0.12**
Galeorhinus galeus	-0.45	-0.12	-0.26	-0.11	-279.77	-60.09	0.54	**0.03**
Lepidopus caudatus	**-3.02**	-1.00	-1.26	-0.26	-246.54	-135.27	0.84	0.70
Chelidonichthys capensis	-0.56	-0.14	-0.13	-0.06	-112.28	-34.31	0.67	**0.25**
Chelidonichthys queketti	0.43	0.20	-0.06	0.11	-59.21	-20.82	0.73	0.87
Sphoeroides pachygaster	0.31	0.01	0.11	0.01	6.74	52.67	0.95	0.98
Zeus capensis	0.26	0.63	-0.07	0.23	-56.61	-88.06	0.90	0.76

Results

Of the 44 species investigated, 10 (23%) showed statistical evidence of a trend in distributional changes during the three decades assessed. Of those, nine taxa changed their average locality (centre of gravity) and three changed their extent (effective area; Table 10). The remaining 34 species did not show compelling statistical evidence of trends in their spatial distribution, even though some shorter-term variations and non-significant trajectories appeared to be present.

Of the nine taxa that indicated a trend in their centre of gravity ($p \leq 0.1$), two-thirds have shifted towards the west (or south) over time. Several other species show a non-significant trajectory in the same direction. The entire group of 44 species combined showed a significant negative centre of gravity trend in the autumn survey time-series (Fig 22, Table 10), indicating that the community's average location has shifted towards the west. The corresponding trajectories for the spring surveys and the average latitudinal location of both seasons were also negative, but not significant (Table 10).

Only three taxa showed statistical evidence of a trend in effective area, of which one was increasing (*Gonorynchus gonorynchus*) and two were decreasing (*Dipturus pullopunctatus, Trachurus capensis*; Table 10). Even though they were not significant, the effective area trajectories were negative for many other species. As a result, the autumn (Fig 23) and spring trend components estimated for the entire community showed highly significant reductions in extent (Table 10).

In the case of most species, the longitude and latitude centre of gravity time-series were strongly correlated (Table 10), with eastward (westward) shifts accompanied by northward (southward) shifts, usually of smaller magnitude. Therefore results and their discussion concentrate predominantly on changes in the west-east axis, which is closest to the orientation of the shoreline. Three broad patterns of centre of gravity responses were identified and illustrated with examples below (Figs 24-26). The effective area changes that accompany those patterns are briefly referred to but also treated separately in a section thereafter.

The first category of responses in average location consists of species that showed evidence of a trend towards the west (south). These included examples where the trend appeared to be present in both seasons (though lacking statistical significance in one), as well as cases where the trend seemed stronger in one of the seasons and appeared weak or absent in the other season. These two situations are illustrated by the examples of *Raja straeleni* (thornback skate; Fig 24a) and *Austroglossus pectoralis* (east coast sole; Fig 24b) respectively. Other species that showed similar centre of gravity responses were *Dipturus pullopunctatus* (slime skate) and *Lepidopus caudatus* (ribbon fish; Table 10). The westward trend was accompanied by a contracting (negative) effective area trend for *D. pullopunctatus* (Table 10).

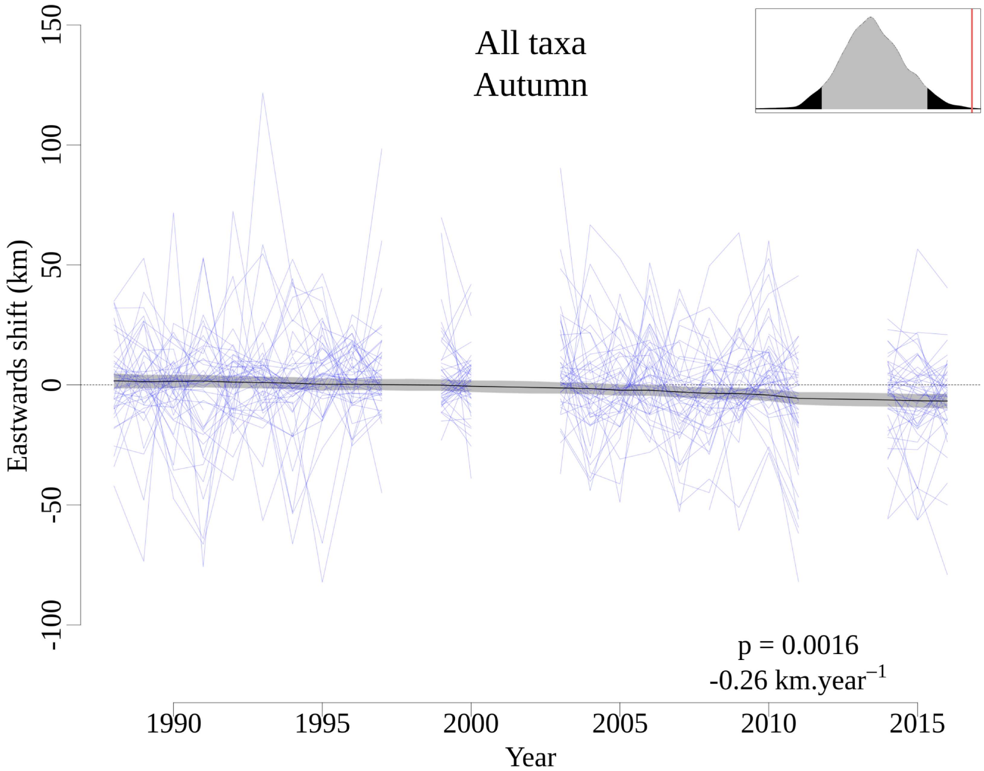


Figure 22. A single trend (black line) with 95% confidence intervals (grey shading) estimated from the longitude centre of gravity time-series of all 44 taxa (thin blue lines) in the Autumn survey. Inset (top right) shows the density distribution of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles darkened. The probability that zero fell within the distribution and the median trend value are shown.

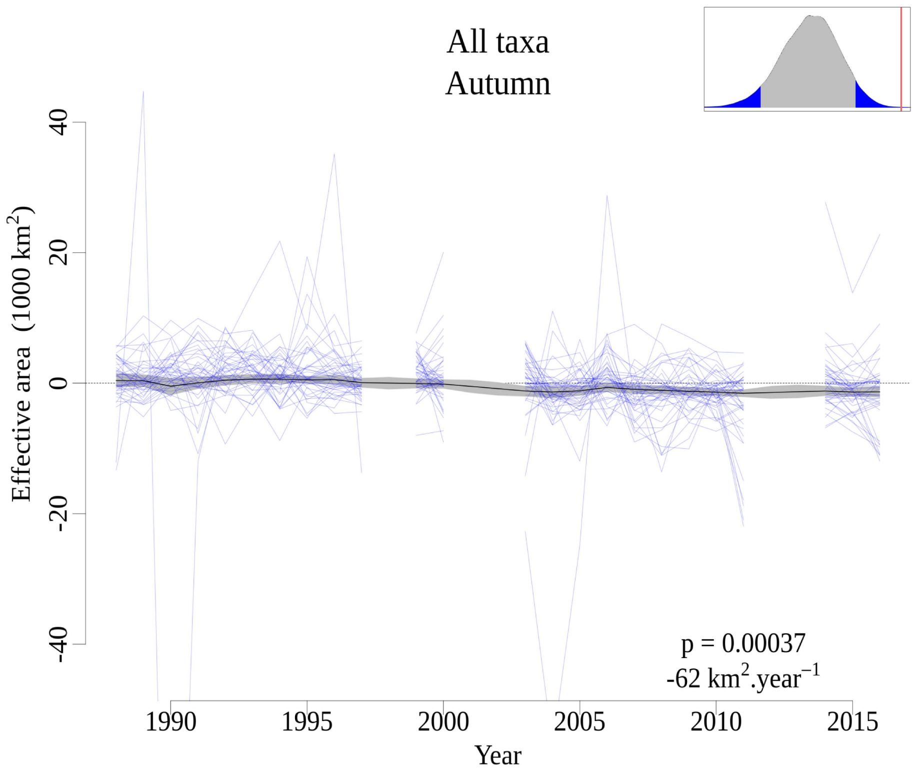


Figure 23. Same as Fig 22, but showing the estimated trend of effective area for all 44 taxa.

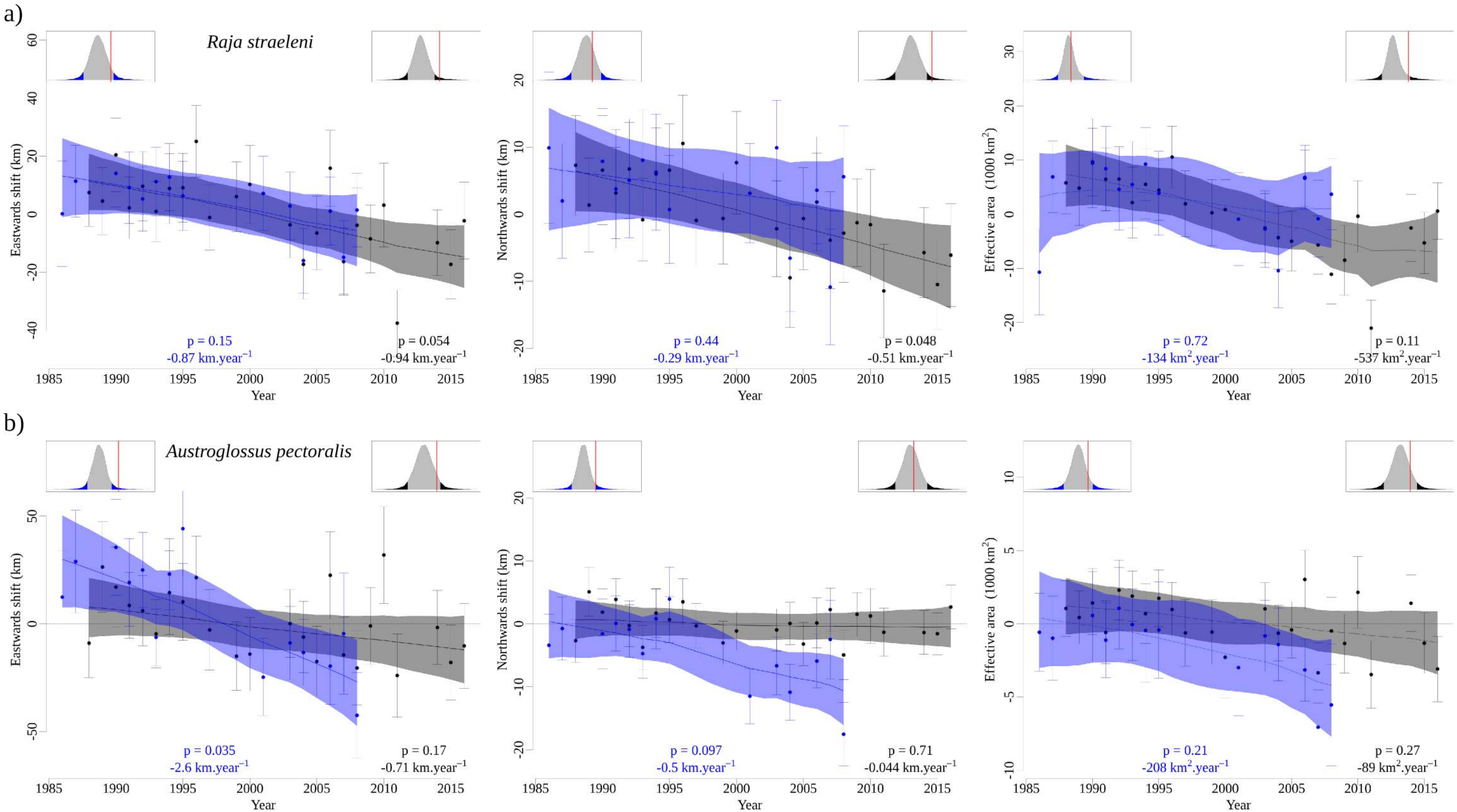


Figure 24. Estimates of longitude (eastward shift; left) and latitude (northward shift; centre) centre of gravity, and effective area (right), shown for autumn (black/grey) and spring (blue) time-series for species a) *R. straeleni* and b) *A. pectoralis*. Trend line and shaded 95% confidence intervals estimated by the SSM method are overlaid. Error bars represent standard error. Inset graphs (top corners) are density distributions of trend estimates, with the origin (zero) marked by a vertical red line and the tails beyond 5th and 95th percentiles highlighted. The probability that zero fell within the distribution and median trend value are shown.

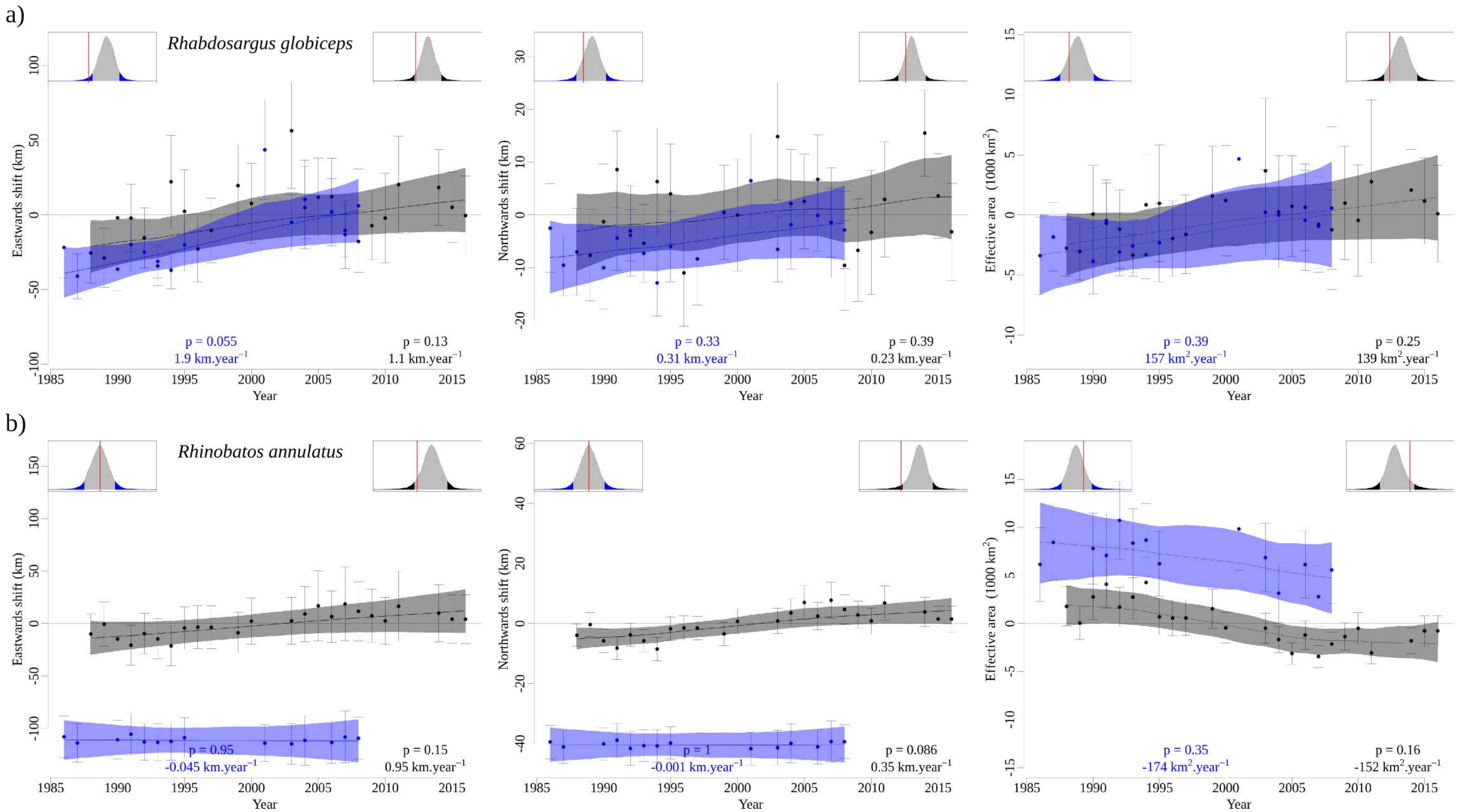


Figure 25. Same as Fig 24, but showing autumn (grey) and spring (blue) centre of gravity and effective area trend estimates for a) *R. globiceps* and b) *R. annulatus*.

The second centre of gravity pattern is similar to the first, but in the opposite direction: evidence of an eastward (northward) trend was seen in average location during either both or only one of the seasons. The two variants of this pattern were illustrated by *Rhabdosargus globiceps* (white stumpnose; Fig 25a) and *Rhinobatos annulatus* (lesser sandshark; Fig 25b) respectively. *Argyrosomus* spp. (kob) also fell into this category. The effective area trajectories for *R. annulatus* and *Argyrosomus* spp. were negative and that of *R. globiceps* was positive, but none of these were significant (Fig 25, Table 10). A notable feature of the *R. annulatus* plot is that its distribution is clearly different between the two seasons. It is centred further east and north and has a smaller extent in autumn than in spring (Fig 25b). Spatial distributions appeared to be disparate for several species, including *Dasyatis chrysonota, Congiopodus torvus, Argyrozona argyrozona, Cynoglossus zanzibarensis, Myliobatis aquila, Genypterus capensis, Argyrosomus* spp., *Leucoraja wallacei, Scyliorhinus capensis, Callorhinchus capensis* and *Spondyliosoma emarginatum*, which jointly make up 25% of the community assessed.

The third centre of gravity pattern is characterised by a trend along one axis (e.g. north-to-south), but lacking evidence of a similar trend along the orthogonal axis (e.g. east-to-west). This can be seen in the case of *Squalus acutipinnis* (spiny dogfish; Fig 26a), which showed a southward trend in its average location but little evidence of a concomitant westward trend. For *Trachurus capensis* (horse mackerel) the westward centre of gravity trend in autumn showed no evidence of an accompanying change southwards, whereas the westward trend in spring does seem to have a southward component (Fig 26b). Unlike those of *S. acutipinnis*, the effective area trend estimates for *T. trachurus* suggest a decrease over time.

Because of the orientation of the depth gradient on this coast, a southward but no westward trend in location suggests an increase in the population's depth distribution. Investigation of the depth centre of gravity of trawl samples revealed significant bias over time (Appendix), precluding the use of that metric to assess depth changes in species. However a comparison of the first and last five years of the autumn records shows that the depth of greatest *S. acutipinnis* catches shifted approximately 30 m deeper during the time-series (Fig 27).

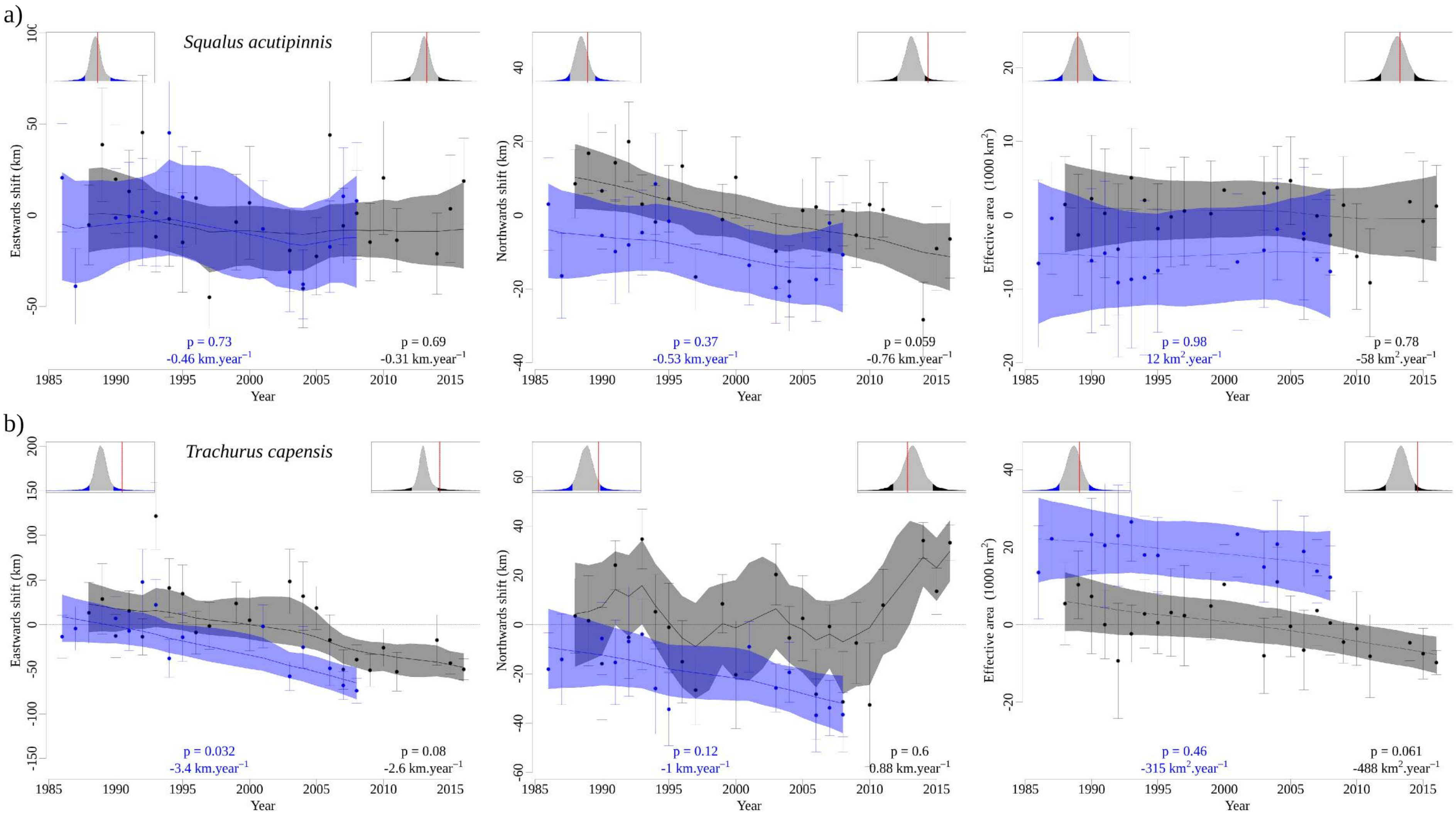


Figure 26. Same as Fig 24, but showing autumn (grey) and spring (blue) centre of gravity and effective area trend estimates for a) *S. acutipinnis* and b) *T. capensis*.

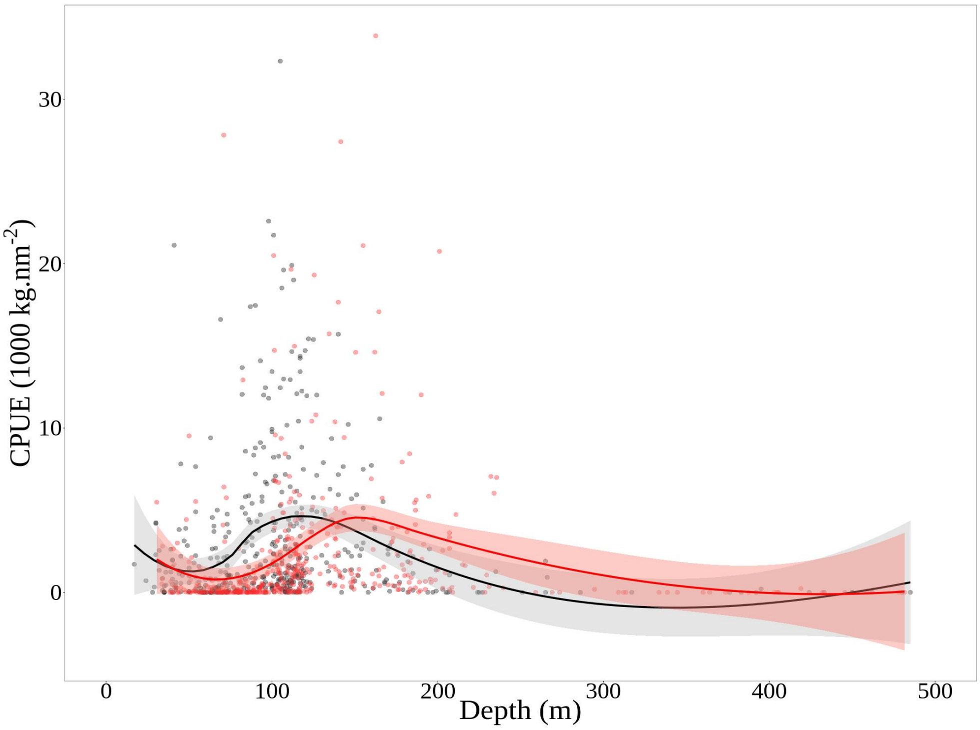


Figure 27. Changes in *S. acutipinnis* catch per unit effort (CPUE) with depth, contrasting the first (black) and last (red) five years of survey data. Plots for each season separately showed similar patterns (not shown). Points represent individual trawls while curves are loess smooths with shaded 95% confidence intervals.

The same centre of gravity and effective area analyses were repeated on subsets of the data. The first was a restriction on depths ≤200 m for the spring survey. The results (not shown) were qualitatively and quantitatively very similar to results based on the full dataset. The second subset of data was restricted to trawls sampled with the old DAFF trawl gear (see Methods). Of the distributional trends identified for 10 species in the full dataset, non-significant trajectories of similar direction were seen in the single-gear time-series for *L. caudatus*, *A. pectoralis*, *T. capensis*, *Argyrosomus* spp., *R. annulatus*, *G. gonorynchus*, *S. acutipinnis* and *R. globiceps*. Only two skates (*D. pullopunctatus* and *R. straeleni*) did not show trajectories similar to the trends identified in the full dataset. To demonstrate these changes, the equivalent plots of Figs 24-26 are presented for the old gear in the Appendix.

When the curtailed old gear dataset was used to estimate the centre of gravity and effective area trends for the entire community, mixed results were evident (Appendix). The general westward (and southward) location trend seen for the full period disappeared. The decreasing effective area trends seen in the full dataset remained in the curtailed dataset, but was significant only for the autumn time-series.

As mentioned above, variability in average latitude and longitude were strongly correlated in most species analysed. These relationships are expected to be due to the orientation of isobaths (the coast) and the depth specificity of taxa. If a species' centre of gravity is displaced (by a significant distance) in this region, it will generally have to include both a longitudinal and latitudinal component if its depth distribution is to remain constant. It is therefore interesting to note the species that suggest a weak or non-significant correlation between the two directions ($p>0.05$, t-test, Pearson product-moment correlation coefficient). These included *T. trachurus*, *Scomber japonicus, A. argyrozona, Merluccius capensis, Arnoglossus capensis, Chelidonichthys capensis, Galeorhinus galeus* and *Mustelus palumbes*. The magnitude of interannual variability for *A. capensis, C. capensis* and *M. palumbes* centre of gravity was negligible, however, which may explain a lack of correlation for these species.

Mapping the average spatial distribution of commercial trawl effort from the last 33 years shows that some of the most intense effort was concentrated in the inshore areas between Cape Infanta and Mossel Bay, extending onto the central Agulhas Bank, as well as east of Bird Island (near Port Elizabeth; Fig 28). In all these areas, the number of trawl tows declined significantly during the period assessed. The only grid-cells that indicate increased fishing pressure in recent decades are those in deeper offshore areas, specifically in the heavily fished Chalk Line grounds offshore of Port Elizabeth and Cape St Francis (Fig 28). Trawl intensity has also increased on the southern and south-eastern edge of the Agulhas Bank during the last three decades.

The number of trawls recorded over the entire survey area has declined during the last three decades, most pronouncedly from 2008 onwards (Fig 29a). In the western inshore areas, between Cape Infanta and Mossel Bay, effort remained relatively high between the 1980s and 2004, after which it declined quite sharply (Fig 29b). In eastern inshore areas, near Port Elizabeth and Bird Island, effort levels were notably lower (than western areas) and declined over most of the three decades, reaching lowest effort values in 2014 and 2015.

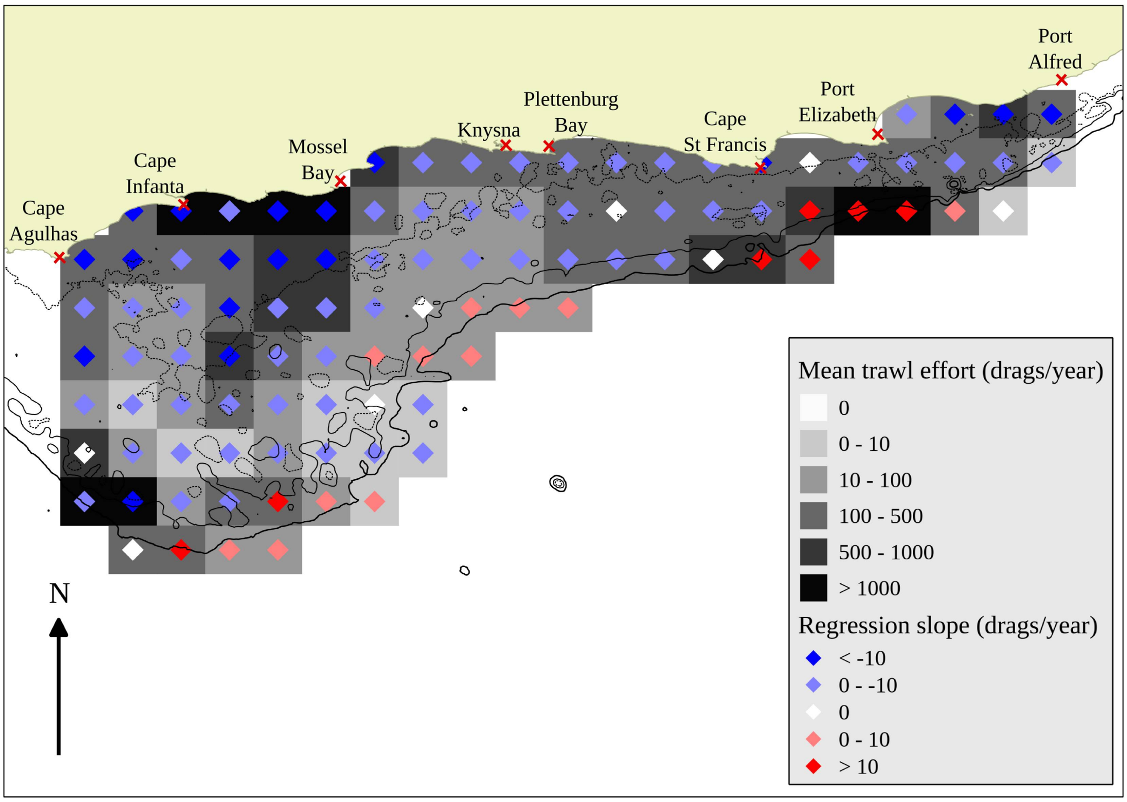


Figure 28. Commercial trawl effort for the period 1983-2015 as recorded to a 20' by 20' resolution grid. Annual mean effort is indicated together with the magnitude of slopes from linear regression fits to the time-series in each cell. A slope different from 0 ($p \leq 0.05$) is indicated with red or blue (increasing or decreasing respectively). Red crosses indicate locations mentioned in the text.

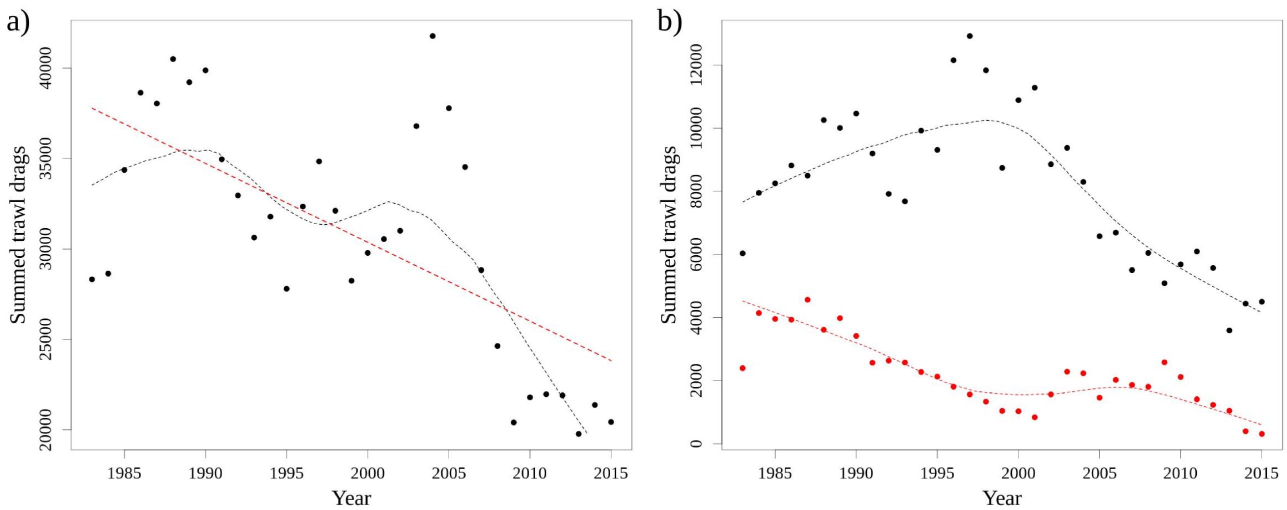


Figure 29. Commercial trawl effort recorded on the Agulhas Bank, summed for a) the entire south coast trawl survey area, and b) for six inshore grid-cells in the western area (Cape Infanta to Mossel Bay; black) and the eastern area (Port Elizabeth to East London; red). Non-linear loess fits are included and a significant linear regression ($p<0.0001$; $r^2=0.42$) is shown in a).

Discussion

Of the trawl-caught fauna assessed on South Africa's south coast, 23% showed evidence of distribution trends over the last three decades. On average across the community, these changes have consisted of predominantly westward movement in average location and a decreasing area occupied. At the level of individual species, trends in location are more apparent (nine taxa) than trends in spatial extent (three taxa). At the level of the community, however, the evidence of a decreasing trend in effective area appears to be stronger than the significant westward centre of gravity trend and remains significant (in autumn) even for a shorter subset of the data that is restricted to a single gear and vessel (Appendix).

The highly significant community-wide average trends of centre of gravity and effective area, even though few individual species showed significant trends, most likely reflects low statistical power. Many of the species appeared to have distributional trends, which were not statistically significant ($p>0.1$). As the power to detect trends is strongly influenced by the length of a time-series (Schlegel and Smit 2016), the number of significant distributional trends is predicted to increase as the survey dataset lengthens in future.

Capturing dynamic signals adequately and identifying drivers in the sparsely-sampled, three-dimensional ocean environment is a challenging undertaking. Beyond the immediate surroundings of large population centres, impacts from fisheries and climate change have likely been the dominant anthropogenic pressures on marine ecosystems. Disentangling their influence is important to building predictions of fishery responses and informing possible interventions. Yet separating the impacts of these two sources involves complexity, much of which may not have been measured. This complexity might include linear and non-linear, direct and indirect effects, as well as cumulative, synergistic or contrary signals and feedback loops across a plethora of organisms making up the ecosystem. A first step in identifying climate and fishery effects is to understand the state of knowledge on these two drivers, from which likely responses can be proposed and against which measured signals can be evaluated. Observations of the existing evidence of fishing effort and (the lack of) knowledge on subsurface oceanographic changes are summarised below.

Agulhas Bank climate/environment

There is little evidence to suggest whether regional demersal ocean waters have warmed or cooled on the Agulhas Bank. Based on global ocean temperature trends (Levitus et al. 2005) and warming of offshore surface waters (Rouault et al. 2009; Wu et al. 2012), one might expect Agulhas Bank waters to have been increasing in temperature. However, the oceanographic dynamics on the bank are complex due to factors such as the variability of the Agulhas Current (including meanders, eddies and filaments), its interaction with the bathymetry and resultant upwelling along its inshore edge, the intermittent coastal upwelling associated with large capes and alongshore winds and subsurface features, such as the cold-water ridge stretching offshore from Tsitsikamma (Schumann and Beekman 1984; Swart and Largier 1987; Largier et al. 1992; Lutjeharms et al. 2000; Roberts 2005).

Looking at surface waters, Rouault et al. (2010) point to evidence of warming offshore but cooling coastal waters on South Africa's south (and west) coast between 1982 and 2009. The coastal cooling signal may be unreliable, however, due to the inaccuracy of nearshore satellite measurements (Smit et al. 2013) and was less apparent in updated, higher resolution data (Blamey et al. 2015). Schumann et al. (1995) suggested that coastal waters in Port Elizabeth were increasing in temperature between the 1960s and early 1990s. This is supported by warming subsurface (10-70 m depth) coastal temperatures in Algoa Bay over the last eight years, although the signal is concentrated mostly in shallower layers (10-30 m; Goschen, personal communication 2016). Recent assessment of multi-decade coastal temperature records spread along South Africa's shoreline indicate warming in most areas, but a cooling trend consistent among sensors located between Betty's Bay and Cape Agulhas (Schlegel, personal communication 2016), which is adjacent to the current study area. The cooling along that coastline is congruent with an eastward extension of kelp (Bolton et al. 2012), an eastward retraction of a warm-water mussel species (Blamey et al. 2015) and may have contributed to the eastward expansion of rock lobsters (Cockcroft et al. 2008). Using NCEP-DOE Reanalysis 2 wind fields to calculate Ekman transport indices between 1979 and 2015, Lamont et al. (2016) suggest increased coastal upwelling on the inshore Agulhas Bank, which supports the evidence of coastal cooling there. Investigation of extreme temperature events in surface waters indicates that the occurrence of cold events has been increasing near Cape St Francis and Port Elizabeth (Schlegel et al. 2017).

Rouault et al. (2009) show warming surface trends on the central and western Agulhas Bank and further offshore, which they attribute to a strengthening of the Agulhas Current. Recent research indicates that the Agulhas Current may be widening, rather than strengthening, and suggests that the meanders associated with the wider current may be causing greater shelf-edge upwelling (Beal and Elipot 2016), which might imply cooler waters over the eastern Agulhas Bank (Chapman and Largier 1989; Lutjeharms et al. 2000).

Subsurface temperature changes have received little scientific attention on the Agulhas Bank, perhaps due to a lack of spatio-temporal resolution of data beyond the surface coverage of satellites. Due to the strong stratification over most of the bank (Largier and Swart 1987), surface temperatures may not provide a good indication of changes below the thermocline. Bottom waters on the eastern Agulhas bank stem from the shelf-edge upwelling of Indian Ocean Central Water, whereas South Atlantic Central Water moves eastward onto the western bank where the two collide and mix in the central and southern parts of the bank at about 20.5°E (Chapman and Largier 1989). It is therefore not clear whether (and if so, how) demersal temperatures have changed on the Agulhas Bank. They may have warmed for the most part, as indicated by surface waters (Schumann et al. 1995; Rouault et al. 2009, 2010; Blamey et al. 2015), or an increase in upwelling activity may have drawn cooler waters onto the bank (Beal and Elipot 2016; Lamont et al. 2016). Considering the oceanographic complexity of the bank, contrasting changes might be taking place in different areas.

In addition to temperature, other variables such as oxygen concentrations and ocean pH are likely to affect populations and their distributions (Rabalais and Turner 2001; Wootton et al. 2008; Gruber 2011). Temporal changes of these important variables have not been investigated on the Agulhas Bank. Roberts (2005) and Grüss et al. (2016) show maps of average bottom-water temperature and oxygen concentrations from in situ oceanographic data collected in 1989-1994 and 2003-2011 respectively. Although their difference in resolution preclude comparison and they provide no information on variability, these maps do show some interesting features in the mean demersal water conditions (Appendix). Bottom waters between Knysna and Cape St Francis are seen to be cooler (~10 °C), compared to warmer temperatures to the west (~11-12 °C; Cape Agulhas to Knysna) and east (≥12 °C; east of Cape St Francis), as has been noted previously (e.g. Le Clus and Roberts 1995). The corresponding dissolved oxygen map shows relatively well-oxygenated waters on average, except for an area centred between Cape Infanta and Still Bay that is lowest inshore (~2.2 $ml{\cdot}l^{-1}$) but extends offshore (south-westwards) to about the 100 m depth contour. The outer bank is again well-oxygenated (≥3.5 $ml{\cdot}l^{-1}$) on average.

Changes in fishing pressure

Fishing pressure on the Agulhas Bank has been dynamic over space and time. As detailed in Chapter 1, fishing effort in South Africa escalated in the 1950s and peaked at unsustainable levels in the 1960s and 1970s (Chapter 1; Payne and Punt 1995; Griffiths et al. 2004). A large proportion of that effort was phased out after South Africa declared an exclusive fishing zone in 1977, although considerable impact had by then been exerted on panga (*Pterogymnus laniarius*) and other Agulhas Bank resources (Japp et al. 1994). Substantial fishing pressure was alleviated from an area known as the 'foreign triangle', located on the central Agulhas Bank between the 110 m depth contour and a line 20 nautical miles from the coast. Although the inshore trawl fleet still fishes on parts of this area, the pressure on much of it has been reduced since the early 1980s and the use of heavy hard-ground gear stopped in 1993 (Sink et al. 2012b). Booth and Hecht (1998) reported that the eastern boundary of demersal trawling contracted from East London to Port Alfred in 1972, due to declining hake catches on the East London grounds. Inspection of commercial effort data confirmed that little trawling has taken place in that area since 1984.

While the number of commercial trawl events has declined overall, especially in some of the most heavily fished inshore areas (Figs 28, 29), they remain exploited and it is not clear whether the reduction in effort may have been sufficient to allow a measurable recovery of those fished communities. There has been a notable increase in trawl effort in some deeper areas near the outer edge of the Agulhas Bank and survey grounds (Fig 28).

Beyond trawling, other human activities impact the marine environment. Sink et al. (2012a) mapped human pressures in South Africa's oceans, including those from the multiple fishery sectors. Overlaying all pressures into one map, their 'total normalised pressure values' suggest that the areas offshore of Port Elizabeth, Cape St Francis and Plettenburg Bay are subjected to substantial human impact, whereas further west the cumulative offshore impacts seem to be lighter (Appendix). Close to shore, there appears to be relatively high pressure along most of the coastline, although particularly so around Port Elizabeth to Cape St Francis and the Mossel Bay area.

Effective area contractions

Although only three species show statistical evidence of a trend in their extent, the majority of species tended to show a negative trajectory. As a result, significantly decreasing effective area trends were estimated for all species combined in both autumn and spring (Table 10). Contraction of the area occupied by a population suggests a stress of some sort (Mace et al. 2008). Whether a result of retraction from a changing environment (e.g. Jones et al. 2010), a reduction in population size towards its core habitat (MacCall 1990), or due to excessive exploitation in certain areas (e.g. Shackell et al. 2005), it will tend to make the population more vulnerable to impacts of environmental calamities and exploitation. Conversely, an increase in the area occupied by a population would suggest an increasingly abundant population or an increasing area of suitable habitat (hence likely also growth of the population).

The only species showing an increasing trend in its spatial extent during the survey period was *G. gonorynchus* (beaked sandfish), which ranges across southern Africa, Australia, New Zealand and the eastern Pacific. Interestingly, this species is recorded to bury itself in the sediment during the day (Paulin et al. 1989), which could conceivably confer a benefit in terms of reducing capture rates by trawl nets. When it does enter a net, its slender shape may enable relatively high escape rates from commercial trawl net meshes. This, together with the fact that *G. gonorynchus* is not caught by line fishers, suggests that it may avoid the majority of direct exploitation pressures. *G. gonorynchus* appears in the diet of predators such as *M. capensis* and *Argyrosomus inodorus* (Smale 1984), and might benefit when the populations and/or sizes of such predators are reduced by fishing pressure. Lastly, certain sediment-dwelling species such as *G. gonorynchus* might benefit from increased food provisioning due to trawl disturbance (van Denderen et al. 2013). The above considerations make *G. gonorynchus* a likely candidate to expand its population size and spatial extent in trawled ecosystems.

Westward community shift

The combined evidence of a community-wide average westward trend in mean location, together with a generally decreasing spatial extent (suggesting populations under stress), yet easing commercial trawl pressure over most of the trawl survey area other than its southern edges (Figs 28, 29), seems to implicate a climate (environmental) rather than a fisheries driver. No pattern of taxonomy or life-history strategies appeared to explain distributional responses. Pinsky et al. (2013) found that climate velocity rather than taxonomic or biological characteristics predicted the distribution changes in demersal fish. Had most of the taxa showed an increase in spatial extent, the westward movement might have been interpreted as a recovery/expansion onto the central Agulhas Bank, following a reduction in trawl pressures there (Fig 28). However, the community-wide decreasing spatial extent is not consistent with such an explanation. As discussed above, there is unfortunately no convincing evidence of whether (or how) the oceanography of demersal waters might have changed on the Agulhas Bank over the last three decades. Without such information, identification of environmental dynamics that might be driving the westward shift in the community would be speculative and likely fruitless, highlighting the need for research into the temporal variability of subsurface Agulhas Bank waters. Without developing an understanding of oceanographic changes, the management of biodiversity, living resources and mitigation of climate change impacts on them will be hampered.

The deeper areas where fishing has increased form an important part of the depth distribution of only a few of the demersal species included here (e.g. *G. capensis, Merluccius paradoxus, Lophius vomerinus, L. caudatus, S. capensis, Zeus capensis*). Of those, only *L. caudatus* showed a significant trend in average location (towards the west) and an apparent decreasing effective area trajectory (though not significant). Judging by the maps of predicted *L. caudatus* density (not shown), the westward centre of gravity trend may be due to decreased abundances on the Chalk Line grounds south of Port Elizabeth, while maintaining densities near the southern edge of the central Agulhas Bank. This could perhaps be due to the increased fishing pressure on the Chalk

Line grounds (Fig 28), or it might be a similar environmental pressure postulated to be causing the general community-wide westward shift in distribution. Yemane et al. (2014) found evidence of a northward movement in *L. caudatus* on the west coast between 1986 and 2010. Their estimated rate of latitudinal shift (~7 km·year^{-1}) appears to be greater than the westward trend recorded here (3 km·year^{-1}).

Studies examining the state of size, population, community or ecosystem indices over periods similar to that assessed here, have found signals of increasing stress or exploitation pressures on the Agulhas Bank (Yemane et al. 2008) or the broader southern Benguela region (Shannon et al. 2009; Coll et al. 2009; Blamey et al. 2015). Such findings appear inconsistent with the significant reductions in trawl pressure over most of the Agulhas Bank (Figs 28, 29). An explanation might be that cumulative fishing impacts remain too large to allow the recovery of species that were likely substantially impacted before the survey period started (Japp et al. 1994; Payne and Punt 1995; Chapter 1). Also, trawl impacts are not the only fishing pressure exerted on these communities. As documented by Sink et al. (2012a), 18 fishing sectors exploit resources in South Africa and several of them overlap in the species and spatial areas that are fished. While trawling pressure on many parts of the Agulhas Bank may have been easing, combined pressures from other fishing sectors, and perhaps climate changes, may have persisted or increased.

Eastward shift of three inshore species

Individual species respond to the drivers of consequence to them and the average community-wide response by no means represents the distributional movements of all taxa. Contrary to the general trend, *R. globiceps, Argyrosomus* spp. and *R. annulatus* show a distribution shifting towards the east (and north). Of these, *R. globiceps* and *Argyrosomus* spp. are traditionally commercial fishery targets, whereas *R. annulatus* is a discarded by-catch species that is sometimes targeted by recreational anglers (Mann 2013). A commonality of *Argyrosomus* spp. and *R. annulatus* is that they inhabit relatively shallow waters, predominantly near the shore, making them more susceptible to shore and boat anglers. While *R. globiceps* is also restricted to relatively shallow depths (≤130 m; Griffiths et al. 2002), its distribution extends onto the central Agulhas Bank (Appendix). Abundance indices and maps of their predicted density from the geoGLMM (not shown) suggest that *Argyrosomus* spp. and *R. annulatus* populations have decreased in the western parts of the survey area and are contracting towards the east. *A. inodorus* is a valuable fishery resource that made up a substantial proportion of historical line and trawl catches on the south coast (Griffiths 1997b, 2000; Chapter 3). The apparent eastward contraction of this commercially important species may represent continuation of a long-term decline of the population and warrants further investigation.

The eastward location shift seen for *R. globiceps* appears to be driven by an expansion that has been more pronounced in the eastern areas near Port Elizabeth (Appendix). This observation is congruent with figures recorded in the literature, which suggest a recent increase in catches of *R. globiceps* on the Agulhas Bank (Japp et al. 1994; Attwood et al. 2011; Chapter 4). While the inshore areas near Mossel Bay may be depleted relative to high historical abundances of *R. globiceps* (Chapter 4), it appears as if the broader population may have expanded since the 1980s, perhaps in response to easing trawl pressure (Figs 28, 29) and the departure of foreign fleets (Japp et al. 1994; Sink et al. 2012b).

Whereas oceanographic forcing cannot be excluded as a causal factor, fishing pressures are thought to be a likely driver of these eastward shifts. Trawling in areas east of Port Alfred reportedly ceased in the early 1980s and was declining before then (Booth and Hecht 1998). This likely allowed recovery in trawl-caught fauna and their habitats in areas adjacent to the eastern edge of the survey area. In addition, trawling intensity has been lower in the area around Port Elizabeth than in western inshore grounds (near Mossel Bay and Cape Infanta) and has been mostly in decline since the 1990s (Fig 29b). The number of trawlers based in Port Elizabeth declined sharply after 1990 as the majority of the fleet moved to Mossel Bay, pushed by market and labour-related factors (Booth and Hecht 1998). The trawl grounds near Mossel Bay and Cape Infanta also experienced a decrease in trawl effort, but only from the mid-2000s onwards, before which trawling pressure was substantially higher there than in the eastern inshore areas (Fig 29b).

It appears that high and sustained trawling pressure in the western areas, up until 2004, may have contributed towards decline (*Argyrosomus* spp. and *R. annulatus*) or slowed recovery (*R. globiceps*) of these three species. In the eastern areas, easing of trawl pressure since the 1990s may have allowed populations to remain relatively stable (*Argyrosomus* spp. and *R. annulatus*) or expand (*R. globiceps*). In this way, trawling pressures appear consistent with the eastward shift in mean location of these populations. It is important to note, however, that these species are also caught by line fishers (commercial, recreational and subsistence), the added impact of which may well be contributing towards the observed distributional changes. Commercial line fishing effort in South Africa was reduced by about 70% in 2000 and has remained relatively low on the west and south coasts (Blamey et al. 2015). The spatial pattern of this substantial effort reduction and the response of recreational fishing effort is not known.

Agulhas Bank climate change scenarios

If a climate-induced, changing environment is putting pressure on Agulhas Bank populations to relocate, some species may be facing a dead-end. If the bank is warming on average, cold-water species could conceivably move into the upwelling ecosystem of the west coast, where cool shelf and inshore waters might be maintained or even strengthened by increased upwelling (Bakun 1990; Rouault et al. 2009). However, if the highly-productive west-coast ecosystem suits their habitat requirements, they should already occur there, as is the case with many of the investigated taxa. The southern edge of the Agulhas Bank and the productivity associated with it will limit poleward expansion for both demersal and pelagic species, signifying a potential dead-end if species are pushed southward by changing environments.

A different scenario might be that bottom waters of the Agulhas Bank are cooling, due to increased coastal upwelling (Lamont et al. 2016) and/or greater shelf-edge upwelling, driven by variability of the Agulhas Current (Rouault et al. 2009; Beal and Elipot 2016). This would likely affect predominantly the eastern (cold ridge; Swart and Largier 1987; Lutjeharms et al. 2000) and/or inshore parts of the bank (coastal upwelling). Species that avoid such cool waters might move further east, towards the warmer bottom waters around Port Elizabeth, or towards slightly warmer inshore areas between Mossel Bay and Cape Agulhas. Both of these areas are narrow compared to the greater (but cooler) Agulhas Bank, which suggest that such distribution changes would likely result in reduced population extents. Increased upwelling would be expected to alter (increase) productivity in certain areas, causing further ecosystem changes (Roberts 2005).

Changes in depth

For those taxa that do show evidence of location changes, the longitudinal shift is most often of greater magnitude and significance than the latitudinal change. This is due to the orientation of the bathymetry (coastline) and species' depth specificity. If a population is loyal to a consistent depth distribution, a change in their spatial distribution is expected to result in a longitudinal change more pronounced than that of latitude, as the depth gradient is predominantly orientated north-south over most of the study area. In fact a significant trend in average latitude, without evidence of a longitudinal change, strongly suggests a changing depth distribution. This was seen in only one species, namely *S. acutipinnis*. The depth of greatest average *S. acutipinnis* catches shifted deeper by about 30 m between the first and last five years of trawl survey data (Fig 27), supporting the centre of gravity evidence of a population moving into deeper water. Yemane et al. (2014) also presented evidence of this species shifting to greater depths on the west coast, together with nine other taxa. A concern over correct separation of *S. acutipinnis* and *Squalus mitsukurii* in DAFF trawl surveys was resolved from 2008 onwards (Leslie, personal communication 2017). Although such species identification issues could affect detected distribution changes, the centre of gravity trend appears to be evident well before 2008 (Fig 26a) and relatively small numbers of *S. mitsukurii* caught on south coast surveys are not expected to have contaminated the signal substantially. The cause of a shift of *S. acutipinnis* to deeper water requires further investigation. It is consistent with a response to warming bottom waters, but could be due to several other factors.

The strong correlations between latitudinal and longitudinal variability seen amongst the majority of species are not surprising, considering that they are mostly demersal species closely associated with seafloor habitat. The species which showed a lack of such a correlation point to distributional variability that is independent of depth. It is not surprising that this situation was associated with pelagic species (*T. trachurus*, *S. japonicus*), as they are likely not directly dependent on seafloor habitat and bathymetric depth. Yet other species also showed a lack of this relationship, including *A. argyrozona* (carpenter), *G. galeus* (soupfin shark) and *M. capensis* (shallow-water hake; Table 10). The spatial distributions appear distinctly different between seasons for all three of these species. A potential explanation is that their distribution during one of the seasons is affected by a behaviour or habitat requirement independent of their usual depth preferences (e.g. due to spawning). A similar explanation might apply to *Raja miraletus* (twinspot skate), which showed strong correlation in spring but weak correlation in autumn (Table 10). The three remaining species that lacked significant correlation between longitude and latitude changes (*A. capensis*, *C. capensis*, *M. palumbes*) had little interannual variability in one or both of the relevant centre of gravity time-series. Thus a lack of correlation is likely not meaningful as the small interannual variability may be approaching the precision with which centre of gravity is estimated by the model.

Comparison with previous distribution change studies

The regional investigation by Yemane et al. (2014) focused on the west coast, the South African component of which comprises a strongly-seasonal coastal upwelling system. Several of the species studied here have a range that encompasses both coasts, enticing comparison of results from the current study with those of Yemane et al. (2014). This, despite the fact that the differences in coastline orientation and oceanographic regimes challenge interpretation of such comparisons. Besides the species already mentioned above (*L. caudatus* and *S. acutipinnis*), Yemane et. al. (2014) also detected a northward latitudinal shift of *R. straeleni* (~4 km·year^{-1}) and a southward shift of *T. capensis* (~5 km·yr^{-1}). In the present study, *R. straeleni* showed a trend towards the south-west (~1 km·yr^{-1}) and *T. capensis* towards the west (~3 km·yr^{-1}).

The method used by Yemane et al. (2014) does not account for potential sampling bias in the depth or spatial distribution of survey effort, although they reduced such bias by removing years in which the distribution of these variables deviated notably from the norm. Assessing the same data using the methods used here would be informative as to what effect such bias might have on results, similar to what was done by Thorson et al. (2016a). Repeating the west coast analyses with updated data and interpreting them alongside the south coast results would enable a synoptic view of distributional changes in the southern Benguela. Interrogating the distributional changes, fishing effort and oceanographic variability on both coasts could help identify potential drivers of distributional shifts in demersal fauna. Consequences of species shifting their distribution northwards on the west coast might include reduced genetic interaction with populations remaining on the Agulhas Bank. If so, this could have important implications for management.

Although Watermeyer et al. (2016) included a few of the taxa investigated here, they used a coarser resolution and far larger area, making comparison of results difficult. Focusing on the south coast, the *T. trachurus* and *S. japonicus* maps in Watermeyer et al. (2016) appear consistent with westward trajectories found in the present study. For taxa such as *Argyrosomus* spp. and *Thyrsites atun* (snoek), they used commercial trawl data, which likely contain spatial bias in effort and makes comparison difficult to justify.

Examination of assumptions

One substantial advantage of estimating distributional changes using the species distribution function rather than survey data directly, is that the geoGLMM is able to account for bias in the location of samples by estimating the spatial and spatio-temporal structure within the catch records (Thorson et al. 2016a). Despite this advantage over conventional methods, a concern was that the spring results for species inhabiting deeper depths might be affected by the fact that multiple consecutive spring surveys were limited to depth strata of ≤200 m. Restricting analyses to include only those shallower strata, however, had minimal effects on results (not shown) and no material effects on inferences drawn or interpretations made.

Analyses of changes in depth distribution may have contributed additional insight to this study. The current geoGLMM framework is not structured to estimate a mean depth within the model. The value of implementing this is uncertain as depths can vary substantially within the area (~2.5 nautcal mile^2) of a single model grid-cell. Estimation of mean depths external to the model was considered, using standardised catch samples and their depth measurements, as has been done previously (Dulvy et al. 2008; Engelhard et al. 2011b; Yemane et al. 2014). However, substantial bias (including a deepening trend in the autumn time-series) was present in the survey data (Appendix). Due to the challenge of accounting for such a bias effectively, calculations of mean depths were not presented here. This also meant that depth distributions had to be contrasted in a way that would not be affected by the trend in sampling depths, as was done for *S. acutipinnis* above.

The results of abundance indices can be significantly impacted by changes in fishing power among years (e.g. due to changes in gear; Engås and Godø 1986; Engås and West 1987; MacLennan 1992). The centre of gravity and effective area calculations within the geoGLMM are independent of the absolute magnitude of abundance values, therefore any gear or vessel bias is likely minor. Although expected to be small, a bias might still arise if the change in gear (or vessel) results in spatially-varying catchability that is different among gears, i.e. one gear performs better in certain areas (habitats or depths) relative to another. To assess whether observed trends might be caused by such potential bias, analyses were repeated on a dataset containing only the DAFF 'old' gear. Although lacking significance, most taxa identified as having evidence of a trend in mean location or extent in the complete dataset, showed similar trajectories in the curtailed, single-gear time-series (Appendix). Similar trajectories supported the assumption that observed trends were not caused by a spatially-varying bias of combining trawl gears.

Unlike the majority of taxa that had distributional trends, the centre of gravity trajectories of two skate species (*R. straeleni, D. pullopunctatus*), and for the entire community combined, appeared absent in the curtailed time-series (Appendix). This suggests that the full-period trends were reliant on changes in the latter ('new gear') period of the survey time-series. It is therefore difficult to separate a true distribution trend from a gear-induced trend in these three cases, without waiting to accumulate a substantially longer 'new gear' period. The community combined centre of gravity records limited to the 'new gear' time-series showed westward (and southward) trajectories (not shown), supporting the conjecture that real distribution changes coincided with the period of gear changes. Centre of gravity and effective area are easily estimated for the two single-gear periods separately, via independent runs of the geoGLMM. How to justifiably align the resulting, partially-overlapping time-series, to estimate a single trend from them, remains a challenge that requires further research.

A final consideration that warrants discussion is that the time-series for the autumn and spring surveys are not directly comparable. The spring time-series is six years shorter and is displaced by two years compared to the autumn survey series, starting two years earlier and ending eight years earlier. The temporal mismatch might be expected to cause some difference between the two series, even for taxa that have no distribution or behaviour change between seasons. Yet the two seasons frequently showed similar responses, which adds weight to those response patterns, as both the distribution estimates (by the geoGLMM) and the trend estimates (using the state-space model) were calculated independently for the two seasons. In some cases, a trend/trajectory appeared to be present in only one season (e.g. *R. annulatus*; Fig 25b), suggesting that change in conditions, likely environmental in nature, are altering their distribution predominantly during a certain season.

Future work

This study addressed the question of whether demersal fish have been changing their distribution over the last 30 years and interpreted such changes in light of knowledge of fisheries pressure and climate/environmental change. Future investigations may be able to further isolate and understand the drivers of observed changes. This would likely require comprehensive treatment of species-specific factors (e.g. length-frequencies and life-history considerations), together with available oceanographic and fisheries effort data. Compilation of spatially-explicit fishing effort over time (including fisheries other than trawling) and interrogation of subsurface hydrographic changes would be valuable advances in this effort. Successfully isolating climate change and fisheries impacts is possible with long-term data from both (e.g. Engelhard et al. 2011b) or with comprehensive fisheries and climate data applied in a modelling framework (e.g. Bell et al. 2015).

To gain a longer-term picture of change in the demersal community, it might be possible to incorporate 1897 to 1949 historical survey data, introduced in previous chapters, into the analyses conducted in this study. The recent DAFF trawl survey dataset covers only the last 30 years, subsequent to when some of the most severe fishing impacts likely took place (Japp et al. 1994; Payne and Punt 1995; Chapter 1). Unfortunately the incompatibility between historical and recent survey data precluded such analyses. The units recorded (numbers of fish vs kg for the historical and recent surveys respectively) and the non-random, highly clustered spatio-temporal distribution of historical survey samples were two major concerns. If these might be overcome, this could provide an exciting and valuable avenue of further research. To improve the spatial representation of historical data, it might be feasible to pool records into multi-year periods and restrict analyses to areas with adequate historical coverage. The difference in units might be addressed by normalising the data to their means for each period or vessel, as the centre of gravity and effective area estimates depend on relative values.

The current analyses could likely be improved for some species by modelling the distributions of different size classes explicitly, using the recently developed multivariate VAST package (Thorson and Barnett 2017). This modelling software applies the same methods as the geoGLMM, but to multiple categories, which might be different species (for a community analysis) or different size- or age-classes, taking into account the correlation among the species (or classes). Many species are documented to be segregated by size with depth (e.g. *M. capensis*, *M. paradoxus* and *A. argyrozona*; Macpherson and Duarte 1991; Griffiths and Wilke 2002). Allowing the distributions to vary for different size- or age-classes could add valuable insight, as changes might be impacting the habitats of certain age-classes more or differently to others.

Another improvement which might be achieved is to add a seasonal component to the geoGLMM, allowing the use of all data within one model. A seasonal model would enable explicit assessment of distribution differences between or among seasons. The substantial proportion (25%) of taxa that suggested disparate distributions between the two seasons indicate the importance of considering seasonal variation in investigations of distribution changes and management decisions. Another benefit of a seasonal model would be to estimate distributions for seasons in which surveys were not conducted. Although density (and resulting centre of gravity and effective area) predictions for cases where there had been no sampling would have high imprecision, they might still be useful for researchers or fisheries managers when interpreting historical data. Seasonal models might also be useful when integrating fishery and survey data into a single spatio-temporal model, especially in cases where surveys are conducted predominantly during a single season, yet fisheries operate over a broader period in each year. Continued development of models that integrate fishing information when estimating density, centre of gravity, and effective area (e.g. Kristensen et al. 2014; Thorson et al. 2015a, 2017) are expected to be valuable tools to differentiate climate and fishing impacts using formal statistical frameworks.

Conclusion

The first empirical evidence is presented of distributional trends in demersal species on the Agulhas Bank. Of 44 common teleost and chondrichthyan taxa encountered in trawl surveys, nearly a quarter revealed evidence of systematic distributional changes during the most recent three decades. The majority of average location changes were towards the west, following the direction of depth contours. Emergent trends from the entire community combined showed that on average species are moving westwards and diminishing their spatial extent. These community-wide trends are interpreted to likely be a climate-related change, predominantly because they are inconsistent with knowledge of easing pressure from trawl fisheries over most of the surveyed area. The lack of knowledge on subsurface oceanographic changes in the study area hampers more detailed interpretation and attribution of the identified distributional changes. This knowledge gap is highlighted as a pressing research priority.

Three species showed a trend in their average location towards the east, contrary to the general westward pattern seen in the majority of taxa. A disproportionate reduction in trawling pressure in the areas around Port Elizabeth and further east, relative to that on the central and western grounds, is suspected to play a role. It appears as if *R. globiceps* has expanded into a more eastwards distribution, whereas the two other species (*Argyrosomus* spp. and *R. annulatus*) have contracted towards the east. The apparent eastward contraction warrants further attention as it may have implications for the management of valuable, but diminished *Argyrosomus* spp. stocks, which are in need of management attention (Chapter 4).

Identification of trends from multi-year variability and thereby developing predictability of the implications of climate change, hinge on the availability and continuation of multi-decadal, ecological time-series such as the trawl surveys analysed here. Long-term survey programs using consistent methods are invaluable to building knowledge on the dynamics that drive variability in the marine environment and the continuation of these surveys is vital to improving our management of ocean spaces around South Africa.

Appendix: Supplementary figures

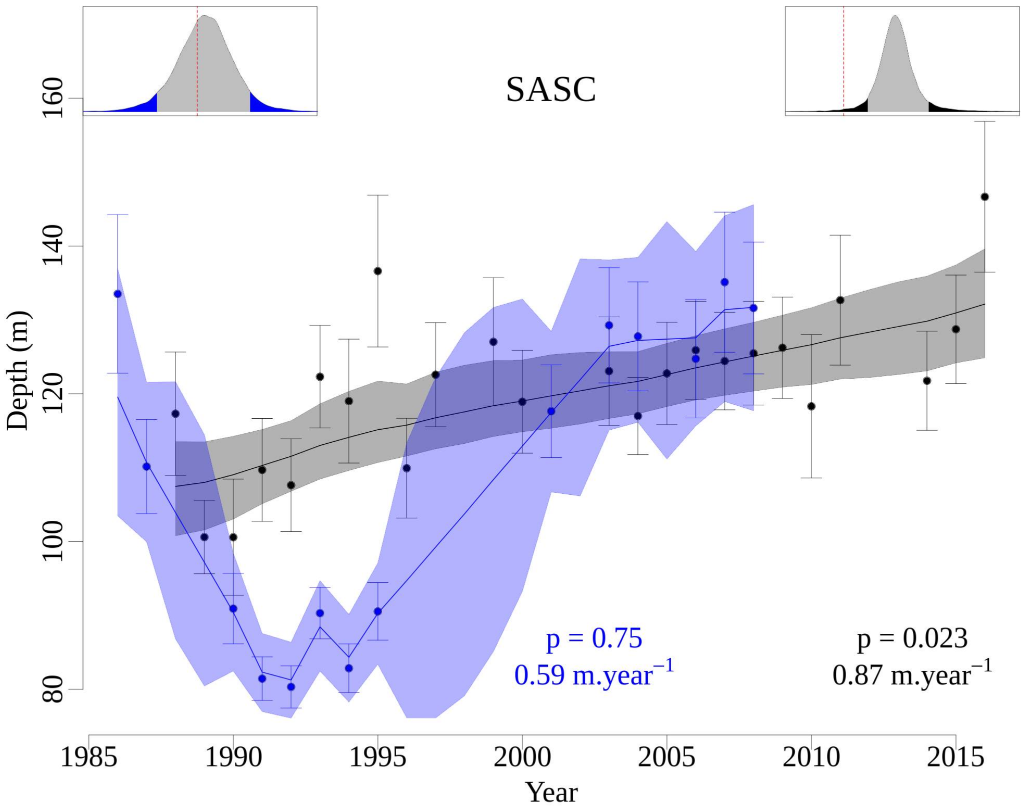


Figure A7. Estimates of the un-weighted depth centre of gravity from trawl survey samples, calculated separately for spring (blue) and autumn (black/grey). Trend line and shaded 95% confidence intervals estimated by the SSM method are overlaid. Inset, p-value and magnitude change same as in Fig 24.

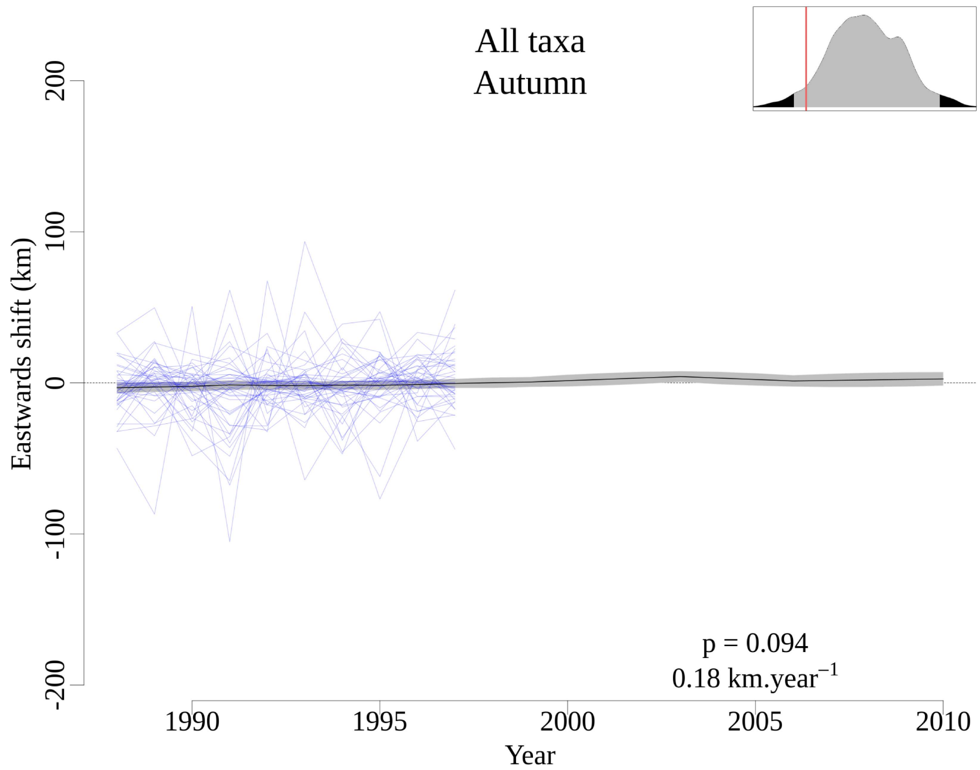


Figure A8. The estimated centre of gravity trend for all 44 taxa, as in Fig 22, but restricted to samples collected with the 'old gear' only. Note the time-series for individual species are only visible when at least two adjacent years were sampled, which did not occur in the latter half of the survey period.

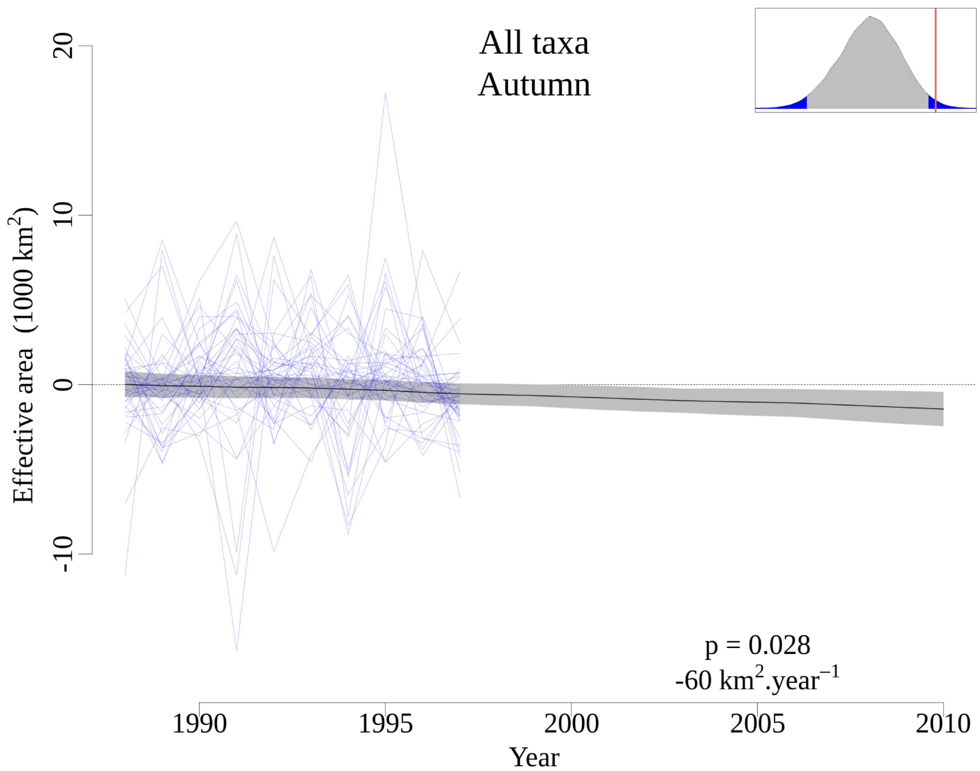


Figure A9. The effective area trend estimated for all 44 taxa, as in Fig 23, but restricted to samples collected with the 'old gear' only. Note the time-series for individual species are only visible when at a)

b)

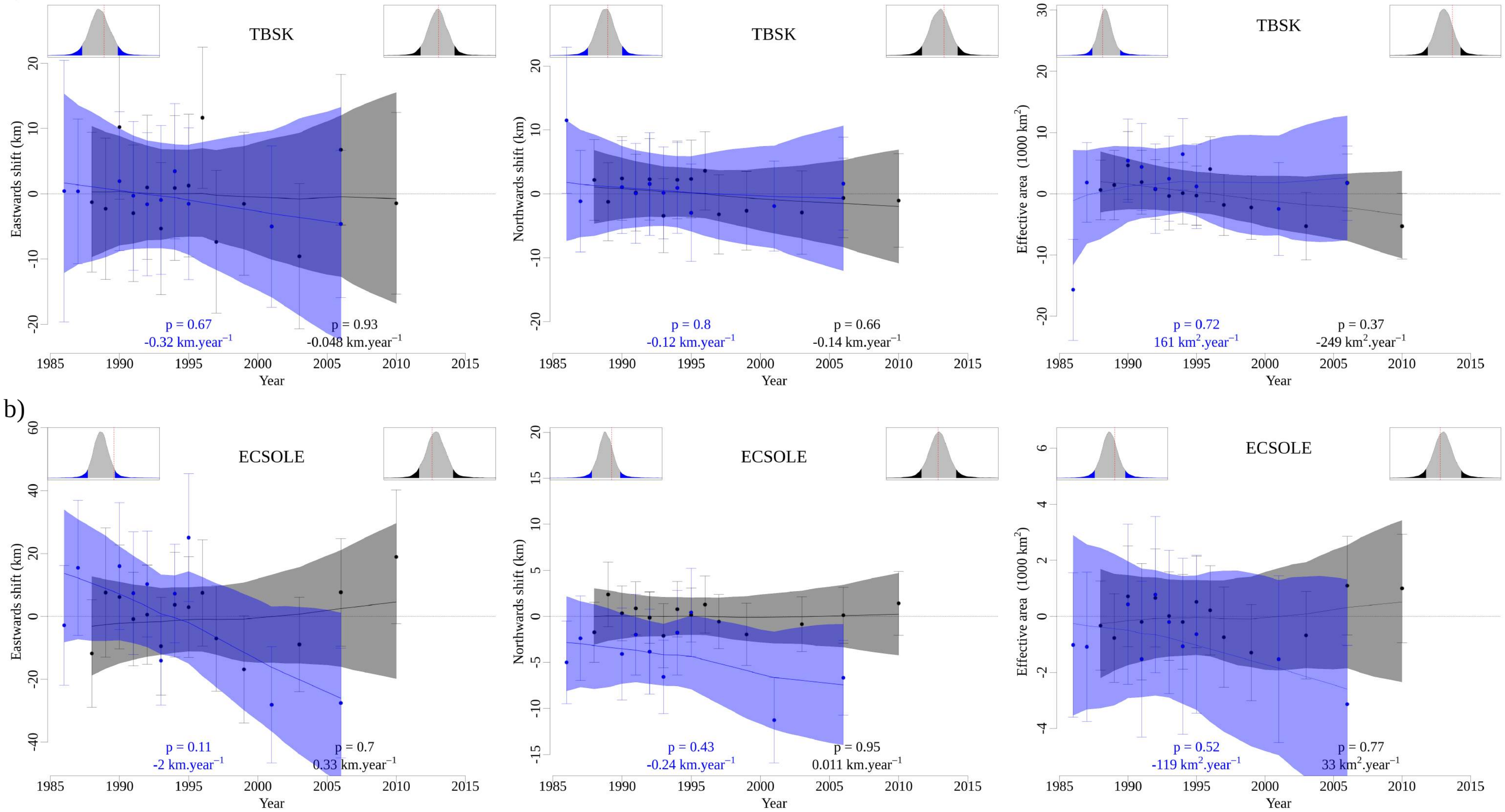


Figure A10. Autumn (grey) and spring (blue) centre of gravity and effective area trend estimates for a) *R. straeleni* and b) A. *pectoralis*, as in Fig 24. but restricted to samples collected with the 'old gear' only.

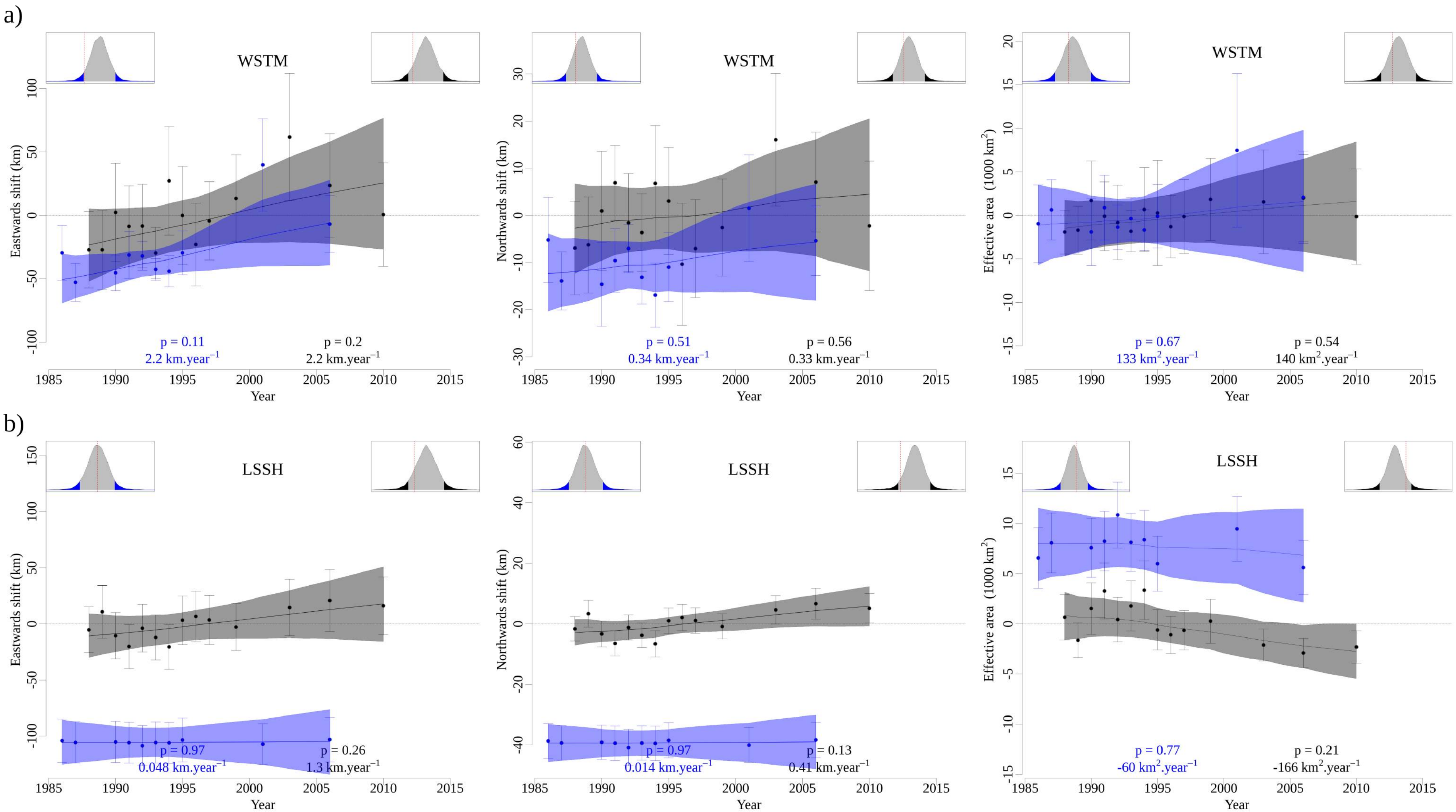


Figure A11. Autumn (grey) and spring (blue) centre of gravity and effective area trend estimates for a) *R. globiceps* and b) *R. annulatus*, as in Fig 25, but restricted to samples collected with the 'old gear' only.

a)

b)

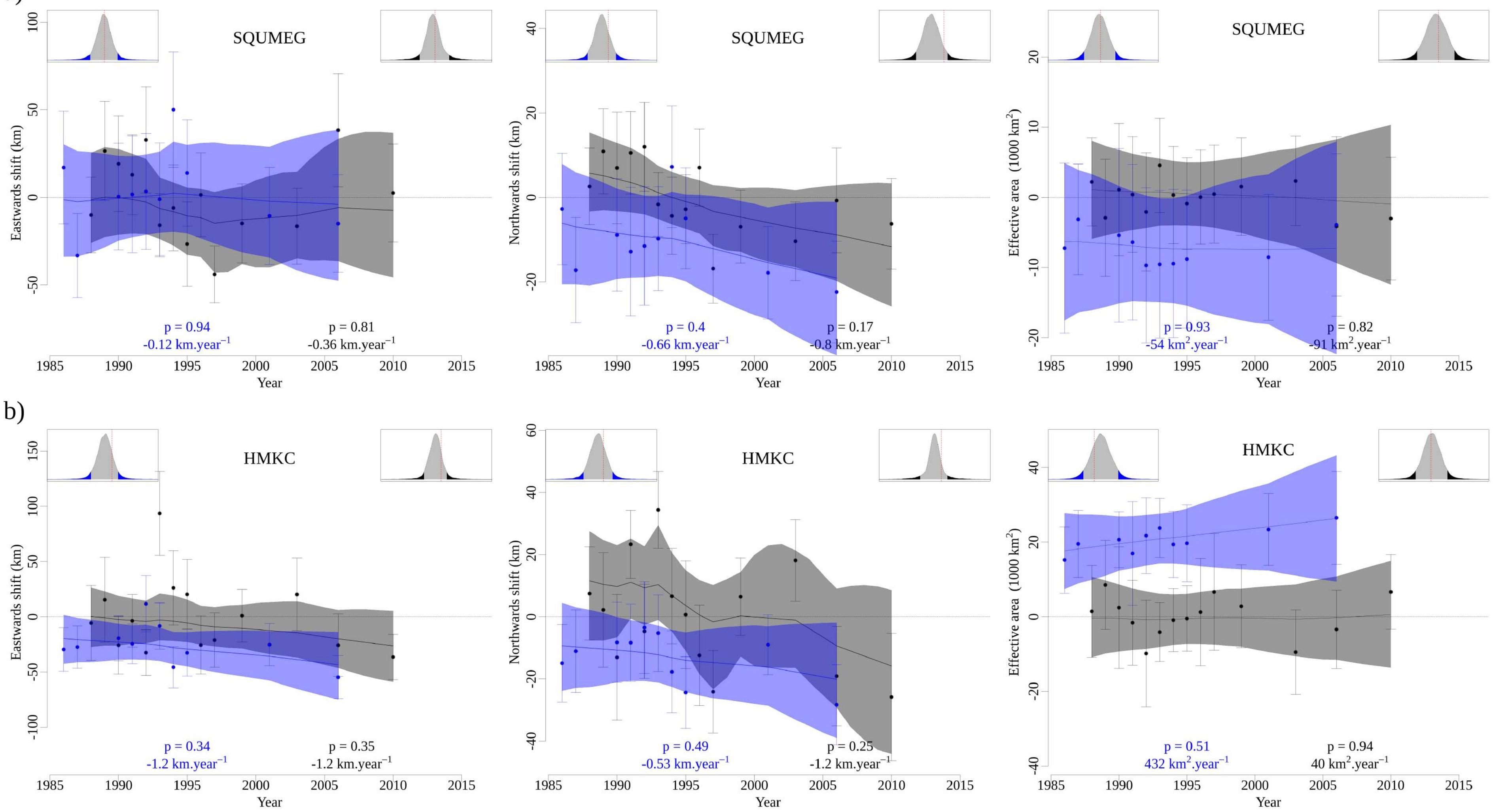


Figure A12. Autumn (grey) and spring (blue) centre of gravity and effective area trend estimates for a) *S. acutipinnis* and b) *T. capensis*, as in Fig 26, but restricted to samples collected with the 'old gear' only.

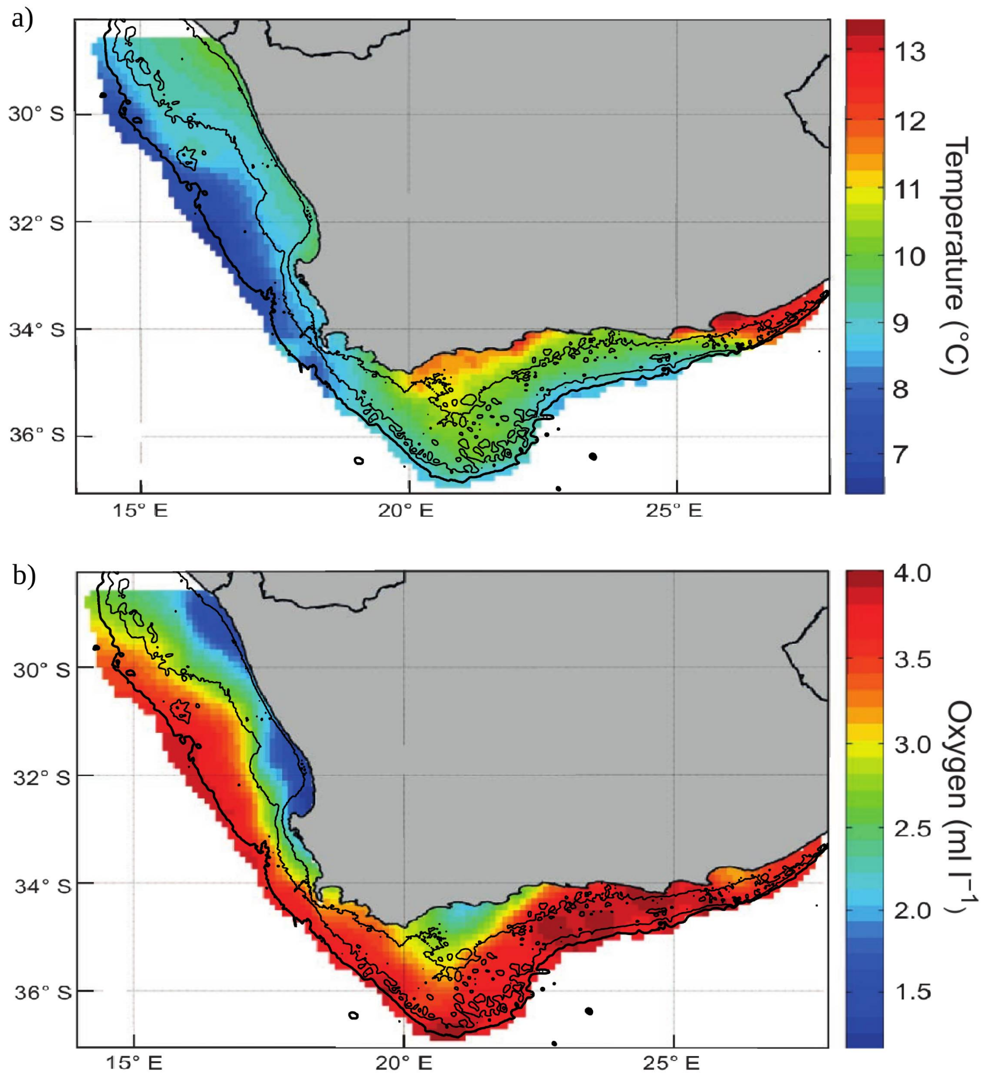


Figure A13. Average bottom water a) temperature and b) dissolved oxygen concentration from in situ records measured between 2003 and 2011. Contour lines represent 100, 200 and 500 m depth. Adapted from Grüss et al. (2016).

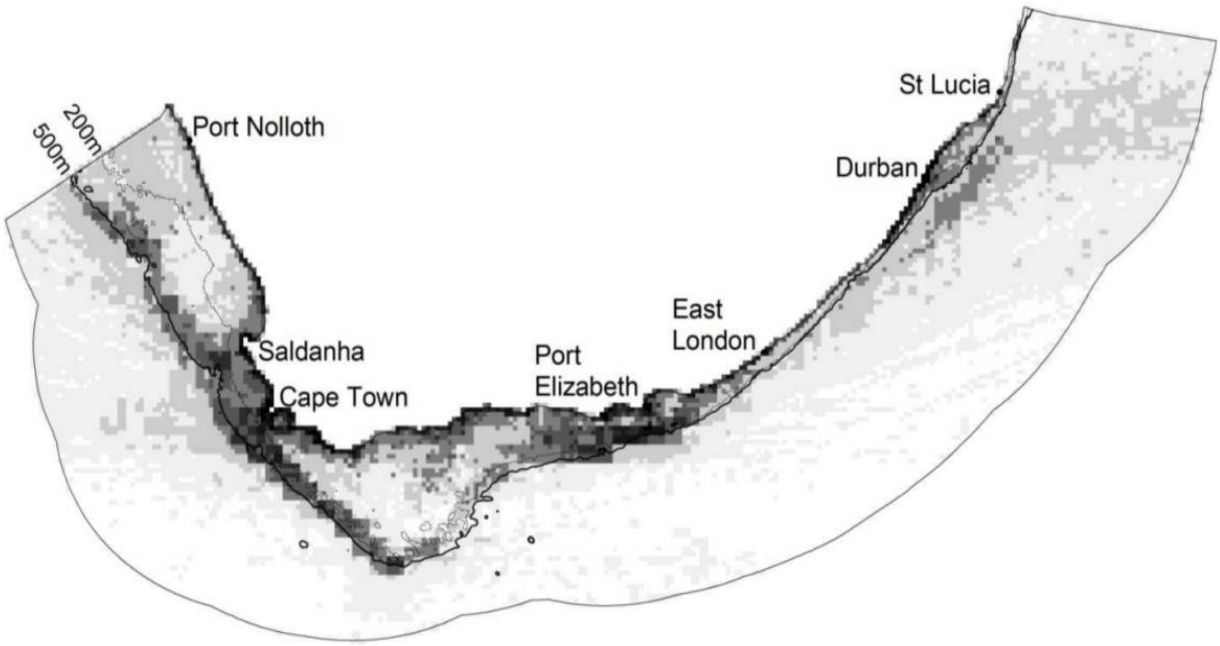


Figure A14. Cumulative normalised anthropogenic pressure values considered in South Africa's 2011 national biodiversity assessment. From Sink et al. (2012a).

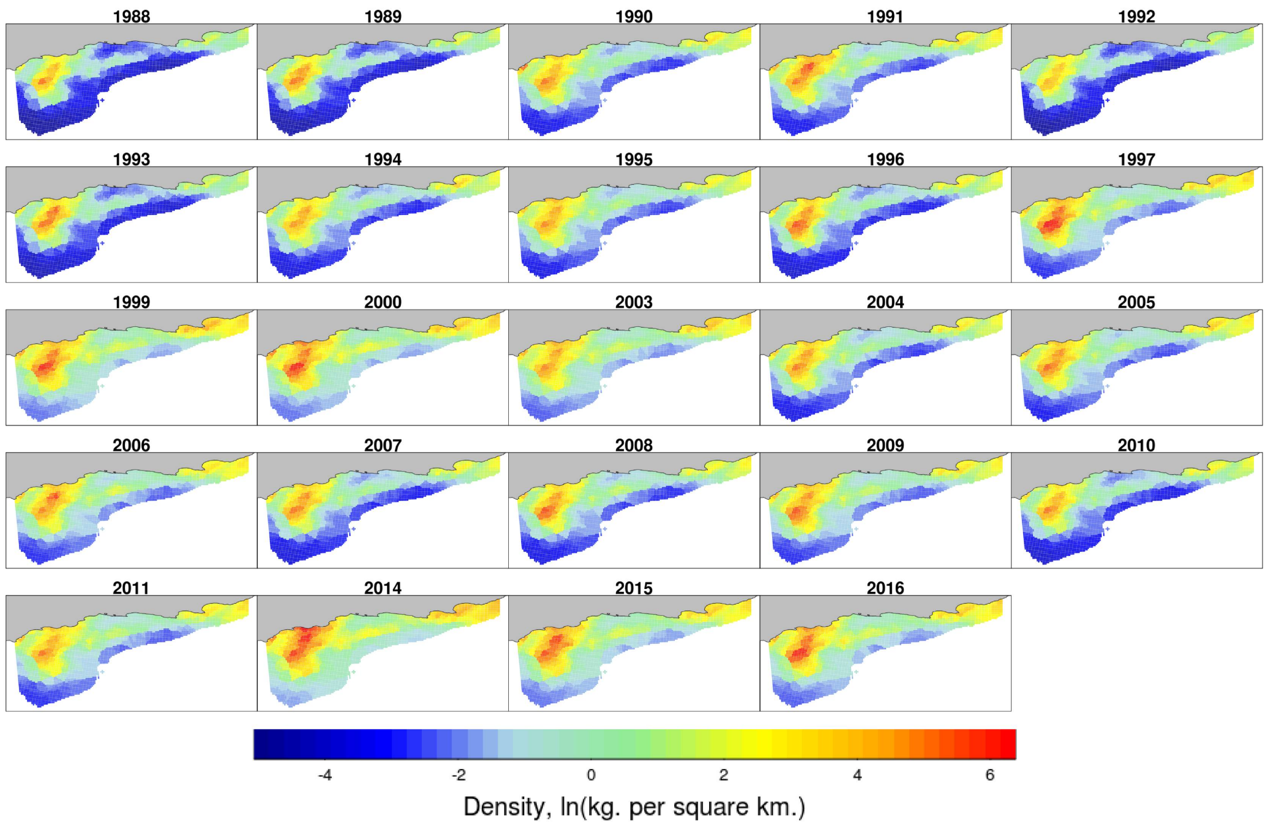


Figure A15. Example of *R. globiceps* density predictions from the geoGLMM. The eastern and western stocks are discernible. The densities of the eastern stock appear to increase over the time-series.

Chapter 6: General Conclusion

South Africa's historical marine biological data

South Africa has a wealth of under-utilised historical marine biological data that can improve our knowledge of past changes in fishery catches, population abundances, species distributions and community assemblages. Studying such changes not only assembles the context that led to current states, but also stimulates new ideas and hypotheses on the causal relationships among physical, ecological or anthropogenic variables. Understanding those relationships is key to predicting the consequences of management interventions or other (e.g. climate-forced) perturbations. The research reported in this thesis has leveraged unique historical trawl data, a long-term repeat experiment and extensive recent survey data from the Agulhas Bank, to quantify changes that have occurred in its demersal fauna and highlight historical reference points that represent its pre-disturbed state.

Due to the socio-economic history along Africa's southern coast and the location of the surveyed trawl grounds (detailed in Chapter 1), these data provide rare snapshots of demersal communities prior to substantial human impacts. Only a handful of other cases were found globally where trawl surveys were conducted prior to development of substantial fishing capacity (Silvestre et al. 1986; Harris and Poiner 1991; Andrew et al. 1997; Graham et al. 2001; Kongprom et al. 2003). Compared to those, the historical data used in this study document samples from the earliest, and likely the most pristine, temperate demersal ecosystem.

Results of this research (Chapters 3 and 4), and continued analysis of these unique historical data, will contribute valuable lessons of relevance to trawled ecosystems globally. While aspects such as the species, timing and specific exploitation history on the Agulhas Bank may be unique, similar narratives of human impacts on demersal ecosystems have replayed across many parts of the world (Jackson et al. 2001). Globally, trawled regions have few quantitative data on their pre-disturbed ecosystems. Therefore research reported here provides a valuable case study of long-term changes that might have taken place in such areas. The results may also contribute to interpretations of limited anecdotal, qualitative or quantitative evidence available in other areas.

Improved knowledge of past change

Chapter 2 collated comprehensive information on the construction and fishing methods used with early Granton otter trawls in the United Kingdom (UK). Together with written and photographic evidence of the SS Pieter Faure vessel and her trawl gear, detailed plans were assembled for the reconstruction of equipment used on the Agulhas Bank over a century previously (1897-1906). The custom-built historical gear enabled the unique long-term repeat experiments to be conducted that were necessary for Chapters 3 and 4. As the use of those early otter trawls spread rapidly from the UK to other trawling countries across the world, the information summarised in Chapter 2 provides a useful understanding of the technology used in early commercial and scientific trawls in many countries, including the UK (SS Huxley; Garstang 1905), Netherlands (SS Wodan; Anon 1908; ter Hofstede and Rijnsdorp 2011), Norway (SS Michael Sars; Hjort 1914), Australia (SS Thetis, FIS Endeavour; Department of Trade and Customs 1909) and the United States of America (SS Albatross; Alexander et al. 1915; Smith 1921).

Chapter 3 demonstrated the extent to which demersal assemblages of the inshore Agulhas Bank were altered between the early 20th century and 2015. Drastic transformations of catch compositions point to substantial modifications of the demersal ecosystem during the 20th century. Changes included large declines of once-dominant taxa and the rise in abundance of species that contributed relatively minor parts to historical assemblages. These results will contribute towards assessments of ecosystem change and evaluation of current states (e.g. van der Lingen et al. 2006; Sink et al. 2012a), thus addressing national research priorities. The lessons and historical context provided by this long-term repeat experiment should be considered in research of more recent dynamics in demersal ecosystems, and by decision-makers in their governance of these resources and ecosystems.

By using directly comparable survey methods, this long-term experiment enabled quantitative estimates of current abundances relative to their pre-disturbance baselines. Examination of key assumptions suggested that results were robust to potential sources of bias and remaining uncertainties. Opportunities to provide such empirical baseline estimates are exceedingly rare. They are expected to be of value to stock assessment scientists as comparisons to their retrospective predictions and to help estimate pristine population levels (e.g. Rosenberg et al. 2005). Results from Chapters 3 and 4 may also be used to inform choices of baseline conditions in ecological models (e.g. Watermeyer et al. 2008).

Investigation of individual taxa in Chapter 4 revealed the magnitude of depletion at these inshore sites for several species known to have declined. This added evidence may reduce uncertainty in the assessment of current population levels, contribute towards setting reference points for stock recovery and help inform conservation priorities. Results could also contribute towards species or population assessments in conservation, consumer awareness and eco-certification programs, such as the IUCN Red List of Threatened Species, the South African Sustainable Seafood Initiative and the Marine Stewardship Council fishery certification program.

Drastic declines of fish species (*Argyrosomus* spp., *Austroglossus pectoralis*, *Pterogymnus laniarius*, *Argyrozona argyrozona*, *Rhabdosargus globiceps*), from areas where they used to contribute large proportions of the assemblage, are a concern. The virtual disappearance of previously-dominant *Argryosomus* spp. highlights the vulnerability of such large, schooling Sciaenidae to fishing pressure. Some of these populations clearly require more effective management interventions to allow their recovery and the improved economic benefits that can be derived from well-managed fisheries. The studied inshore areas are in reach of multiple fishing sectors and may suffer from additional pressures such as pollution, shipping, invasive species and climate change. Improved enforcement of existing regulations, legislating for reduced landings or moratoria for severely depressed species, gear restrictions, lowering market demand for over-exploited species (via consumer awareness and eco-certification programs) and increased spatial protection of areas critical to those taxa, are proposed considerations for improved management. The results shown for *Argyrosomus* spp. and *A. pectoralis* in Chapter 4 are of particular concern, as survey sites covered substantial parts of core distribution areas for these important commercial species.

Novel quantitative evidence, that certain species have increased in number since widespread exploitation of their community started, was presented in Chapter 4. This may be partially due to a decrease in size and replacement of fewer larger individuals with many smaller ones. However for some taxa, notably *Chelidonichthys* spp. and *Trachurus capensis*, the increased numbers were so great that their summed mass is expected to have increased even if sizes decreased. Globally, long-term comparisons of trawl survey data mostly show reduced catches of fauna, although stable or increased catches have been documented (Greenstreet et al. 1999; Branch et al. 2010; Engelhard et al. 2011a; Bell et al. 2014). Evidence of increased abundances from pre-disturbed catches suggest that some species have benefited from the changes to their environment during a century of industrialised fishing, despite the increased mortality that fishing must have caused. Potential reasons for this were discussed in earlier chapters. Ecological models and field experiments involving the increased taxa might help clarify the characteristics that make certain populations robust to exploitation and other human pressures. Encouraging market development for common taxa that have maintained or increased abundances, but are currently discarded, could be considered. Caution should be exercised in the case of slow-growing, low-fecundity taxa, however, such as white sea catfish (*Galeichthys feliceps*) and spiny dogfish (*Squalus* spp.).

The first evidence of distribution trends of demersal ichthyofauna for the south coast of South Africa were presented in Chapter 5. They suggested a general westward shift in average location and a shrinking area occupied by the trawl-caught fish assemblage over the last 30 years, and species-specific distributional changes for nearly a quarter of taxa included in analyses. Changes in distribution will likely have different implications for different species, depending partly on their habitat requirements and the drivers of such change. Both fishers and fishery managers will benefit from understanding distribution trends and the resultant predictions that may be developed. Continued monitoring of these demersal communities in annual trawl surveys will be critical to understand their responses to changing ocean climate and to disentangle that from the effects of fishing.

Habitat impacts

Benthic habitat was a recurring theme in explanations of changes observed over time in Chapters 3, 4 and 5. As demersal fish live on or near the seafloor, most will be influenced by physical and biological aspects of that habitat. Due to its impacts on these habitats, trawl activity has an ecological cost beyond the removal of fish biomass (Auster et al. 1996; Engel and Kvitek 1998; Kaiser et al. 2000). The harm caused to Agulhas Bank fish populations by escalation of national and international fishing efforts in the 1950s-1970s has been documented to a limited degree (Japp et al. 1994; Booth and Buxton 1997b; Sink et al. 2012b). Yet the widespread impacts on benthic communities that assumedly accompanied those expansions have received little attention. The impacted areas included hard grounds, some of which have not been trawled since the departure of international fleets that were phased out between 1977 and the early 1990s (Japp et al. 1994). The slow recovery rates expected of many structure-forming epibenthic organisms (Sainsbury et al. 1993; Rooper et al. 2011; de Moura Neves et al. 2015), and removal or disturbance of rocks and consolidated sediments that many structure-forming species rely on (Auster et al. 1996, 1997), imply that these habitats and their dependent demersal fauna may require multiple decades to recover. In cases where sediments have been altered, recovery might require geological time-scales.

Due to the historical expansion of fishing effort into most areas that could be trawled, researchers are left with few control areas that have escaped trawl impacts but consist of the same habitat (including sediment types) as trawled areas (Auster et al. 1996; Frid et al. 2000; Atkinson et al. 2011a). Without such control sites, the retrospective ecological cost of trawling is difficult to estimate. Major bays on South Africa's south coast have been protected from trawling since between 1928 (False Bay) and the 1980s (Sink et al. 2012b). This may provide opportunity for comparative analyses of benthic habitats inside and outside of protected areas. However, two factors may undermine their value as undisturbed control sites, namely 1) that sediments and habitats inside the bays may not have completely recovered from trawl impacts prior to their closure, and 2) that they may suffer substantial anthropogenic pressures that might include other forms of fishing, pollution, invasive species and climate change.

Knowledge gaps and future perspectives

The value of the historical data and results of Chapters 3 and 4 would be enhanced if they could be converted into mass. Figures of biomass rather than numbers of fish provide a more meaningful ecological metric as they are less affected by fish size and represent the trophic impact of a population. Many users of these historical data, including ecological modellers and stock assessment scientists, might benefit from further research that could enable such a conversion. The confidence in conversion factors may, however, rely on finding additional historical evidence such as size frequencies or mean weights from the relevant era. The difficulty to predict size or weight compositions of unexploited demersal populations with any certainty highlights the problem of missing baselines. The ratios of large to small fish recorded in the historical data for *Argyrosomus* spp. and *Merluccius capensis* appear to be unlike anything encountered in recent decades. Parameters describing growth, mortality and life-history strategies are predominantly based on such recent data and might be inadequate to predict the pristine states of populations.

Certain gaps in our knowledge of the Agulhas Bank environment, fisheries and ecosystem dynamics need to be addressed if we are to disentangle the main impacts of fishing and climate change. While a qualitative understanding of the spatio-temporal development of fisheries effort can be pieced together from literature and various disparate catch datasets, these pieces of information have not been combined into a coherent model of fishing effort over time and space. Such a product, covering the development of trawl and other fisheries, would be valuable to many retrospective investigations, especially if its resolution would enable its inclusion in statistical models.

Another knowledge gap highlighted in Chapter 5 was that of subsurface oceanographic variability on the Agulhas Bank. In situ measurement of variables such as temperature, salinity and oxygen have been a routine part of annual fisheries research surveys on the Agulhas Bank for decades (Hutchings, personal communication 2016). Yet it appears that near-bottom variability over time has not been interrogated from these data. Such analyses are overdue and might reveal a coherent picture of climate-forcing that could contribute to explanations of changes observed in demersal ecosystems. Even if coherent patterns are not obvious, oceanographic covariates could potentially be included in statistical models similar to those used in Chapter 5, to test their effects on distributions or abundances of demersal populations.

Strengthening the rudimentary understanding of South African benthic habitats (beyond shallow coastal areas), including their distribution and ecological functions, is another field deserving greater research attention. Examination of historical records of sediment type and invertebrate catches may provide a start to reconstructing baseline knowledge of pre-trawled benthic habitats. Developing knowledge of spatio-temporal change in benthic communities, and its influence on associated demersal fish populations, will be a valuable, but challenging, contribution.

The economic consequences of observed changes in the demersal assemblage may provide insight on opportunity costs and provide incentive for re-building depleted fish stocks. It appears that the economic yield of these inshore demersal communities has been eroded since the beginning of the 20th century. A large proportion of high-value fish (*Argyrosomus* spp., *A. pectoralis, A. argyrozona,* other Sparidae and Sciaenidae) dominated historical catches, but have largely been replaced by species of lesser or marginal value (*Chelidonicthys* spp., *Squalus* spp., *G. feliceps*). Only increases of *T. capensis* and *M. capensis* (if the latter in fact increased in biomass) would likely be considered of economic benefit. Regaining or retaining the catch rates of un-fished ecosystems is, of course, not realistic. However, economic models, together with the historical and re-survey catch data, may be able to estimate the change in yields brought about by a century of exploitation. Rebuilding some of the depleted stocks and encouraging a more diverse fishery could promote both economic (Cline et al. 2017) and ecological resilience (Garcia et al. 2012).

Recommendations for science and management

The results in this thesis have implications for fished and un-fished species, ecosystem management, environmental monitoring and the ecosystem approach to fisheries management. The basis for these recommendations are outlined above, but in summary, they include:

- Incorporation of historical data into species, ecosystem and stock assessments to improve the understanding of past dynamics prior to relatively data-rich recent periods.
- Further scientific scrutiny to understand discrepancies for species shown to be heavily depleted in repeat surveys, but which have more optimistic regional stock assessments (e.g. *P. laniarius, A. argyrozona*), to enable informed management decisions for these taxa.
- Maintaining and strengthening long-term monitoring programs, such as the annual demersal trawl survey led by the government fisheries department (DAFF). These are critical to detect and adapt to climate change and to enable science-based management action based on the realities of resource abundances.

- Focused research to understand the habitat effects of inshore trawling in South Africa and the effectiveness of current management measures.
- More effective management interventions to enable the recovery of depleted populations investigated here (particularly *Argyrosomus* spp., *A. pectoralis* and *R. globiceps*).
- Improved management could entail greater enforcement, catch reductions or moratoria, reducing market demand for over-exploited species, gear limitations and enhanced spatial management measures, including strengthened/expanded marine protected areas and fisheries management areas.

The value of baselines

The research in Chapters 3 and 4 demonstrated the value of baseline data. Our understanding of fish populations and their ecosystems is typically derived from research in recent decades, without adequate consideration of the historical context or how findings might compare to past baselines (Jackson et al. 2001). Lacking historical perspectives mean that many scientists, fishers, policy makers and laypersons under-estimate the magnitude and extent of change that took place in their marine ecosystems since exploitation began. This is symptomatic of the erosive problem of shifting baselines (Pauly 1995), which can only be countered by improved evidence of historical reference points and effective communication of those findings to society.

The research presented in this thesis has advanced knowledge of historical baselines and subsequent change in demersal fish communities of the Agulhas Bank. Unique historical data were leveraged to describe temperate fish assemblages from a near-pristine demersal ecosystem. Those historical reference points, together with a rigorous repeat experiment, demonstrated the magnitude of changes that have taken place at inshore trawling grounds. A suite of historically-dominant species have been mostly replaced by a different collection of taxa, signifying substantial ecosystem alteration. Evidence of distribution changes in recent decades adds information on more recent dynamics to the findings of long-term change. These contributions provide valuable historical context to contemporary and future research findings, enabling more effective management of ocean resources and ecosystems. Disseminating this information, especially to fishers, other ocean users and decision makers, will be essential to counter societal acceptance of progressively eroded marine ecosystems.

References

Aflalo FG (1904) The sea-fishing Industry of England and Wales. Edward Stanford, London

Alexander AB, Moore HF, Kendall WC (1915) Appendix VI: Otter-trawl fishery. In: Report of the United States Commissioner of Fisheries for 1914. U.S. Government Printing Office, Washington,

Alward GL (1932) The Sea Fisheries of Great Britain and Ireland: A Record of the Development of the Fishing Industry and Its World-wide Ramifications. Albert Gait, Grimsby

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46. doi: 10.1111/j.1442-9993.2001.01070.pp.x

Anderson MJ (2006) Distance-Based Tests for Homogeneity of Multivariate Dispersions. Biometrics 62:245–253. doi: 10.1111/j.1541-0420.2005.00440.x

Anderson MJ, Santana-Garcon J (2015) Measures of precision for dissimilarity-based multivariate analysis of ecological communities. Ecol Lett 18:66–73. doi: 10.1111/ele.12385

Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? Ecol Monogr 83:557–574. doi: 10.1890/12-2010.1

Andrew NL, Graham KJ, Hodgson KE, Gordon GNG (1997) Changes after twenty years in relative abundance and size composition of commercial fishes caught during fishery independent surveys on SEF trawl grounds. Fisheries Research and Development Corporation, NSW Fisheries, Cronulla, NSW

Anon (1908) Overzicht der uitkomsten van visscherijwaarnemingen met het S. S. Wodan: derde stuk: analyse der vangsten met de otter trawl in de jaren 1906 en 1907.

Arendse CJ (2011) Aspects of the early life history and a per-recruit assessment of white stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) in Saldanha Bay with recommendations for future research and monitoring. University of Cape Town

Arreguín-Sánchez F (1996) Catchability: a key parameter for fish stock assessment. Rev Fish Biol Fish 6:221–242. doi: 10.1007/BF00182344

Atkinson LJ, Field JG, Hutchings L (2011a) Effects of demersal trawling along the west coast of southern Africa: multivariate analysis of benthic assemblages. Mar Ecol Prog Ser 430:241–255. doi: 10.3354/meps08956

Atkinson LJ, Jarre A, Shannon LJ, Field JG (2012) Evidence for shifts in demersal fish populations on the west coast of South Africa: 1986 to 2009. Glob Prog Ecosyst-Based Fish Manag Fairbanks Alsk Sea Grant Univ Alsk 45–64.

Atkinson LJ, Leslie RW, Field JG, Jarre A (2011b) Changes in demersal fish assemblages on the west coast of South Africa, 1986–2009. Afr J Mar Sci 33:157–170.

Attwood CG (2003) Dynamics of the fishery for galjoen *Dichistius capensis*, with an assessment of monitoring methods. Afr J Mar Sci 25:311–330. doi: 10.2989/18142320309504020

Attwood CG, Farquhar M (1999) Collapse of linefish stocks between Cape Hangklip and Walker Bay, South Africa. South Afr J Mar Sci 21:415–432. doi: 10.2989/025776199784126150

Attwood CG, Petersen SL, Kerwath SE (2011) Bycatch in South Africa’s inshore trawl fishery as determined from observer records. ICES J Mar Sci J Cons 68:2163–2174. doi: 10.1093/icesjms/fsr162

Auster PJ, Langton RW (1999) The effects of fishing on fish habitat. In: Benaka L (ed) Fish Habitat:

Essential Fish Habitat and Restoration. Bethesda, pp 150–187

Auster PJ, Malatesta RJ, Donaldson CLS (1997) Distributional responses to small-scale habitat variability by early juvenile silver hake, *Merluccius bilinearis*. Environ Biol Fishes 50:195–200. doi: 10.1023/A:1007305628035

Auster PJ, Malatesta RJ, Langton RW, et al (1996) The impacts of mobile fishing gear on seafloor habitats in the gulf of Maine (Northwest Atlantic): Implications for conservation of fish populations. Rev Fish Sci 4:185–202. doi: 10.1080/10641269609388584

Axelsen BE, Johnsen E (2015) An evaluation of the bottom trawl surveys in the Benguela Current Large Marine Ecosystem. Fish Oceanogr 24:74–87. doi: 10.1111/fog.12079

Badenhorst A, Smale MJ (1991) The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. South Afr J Mar Sci 11:377–393. doi: 10.2989/025776191784287565

Bagenal TB (1958) An analysis of the variability associated with the Vigneron-Dahl modification of the otter trawl by day and by night and a discussion of its action. J Cons 24:62–79.

Baillon S, Hamel J-F, Wareham VE, Mercier A (2012) Deep cold-water corals as nurseries for fish larvae. Front Ecol Environ. doi: 10.1890/120022

Bakun A (1990) Global Climate Change and Intensification of Coastal Ocean Upwelling. Science 247:198.

Barange M, Pillar SC, Hampton I (1998) Distribution patterns, stock size and life-history strategies of Cape horse mackerel *Trachurus trachurus capensis*, based on bottom trawl and acoustic surveys. South Afr J Mar Sci 19:433–447. doi: 10.2989/025776198784126917

Barausse A, Correale V, Curkovic A, et al (2014) The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. ICES J Mar Sci J Cons fst222. doi: 10.1093/icesjms/fst222

Bartolino V, Cardinale M, Svedäng H, et al (2012) Historical spatiotemporal dynamics of eastern North Sea cod. Can J Fish Aquat Sci 69:833–841. doi: 10.1139/f2012-028

Battaglia A, Trenkel VM, Rochet M-J (2006) Estimating end effects in trawl catches. ICES J Mar Sci 63:956–959. doi: 10.1016/j.icesjms.2006.03.002

Beal LM, Elipot S (2016) Broadening not strengthening of the Agulhas Current since the early 1990s. Nature. doi: 10.1038/nature19853

Beare DJ, Burns F, Greig A, et al (2004) Long-term increases in prevalence of North Sea fishes having southern biogeographic affinities. Mar Ecol Prog Ser 284:269–278. doi: 10.3354/meps284269

Bell RJ, Fogarty MJ, Collie JS (2014) Stability in marine fish communities. Mar Ecol Prog Ser 504:221–239. doi: 10.3354/meps10730

Bell RJ, Richardson DE, Hare JA, et al (2015) Disentangling the effects of climate, abundance, and size on the distribution of marine fish: an example based on four stocks from the Northeast US shelf. ICES J Mar Sci J Cons 72:1311–1322. doi: 10.1093/icesjms/fsu217

Bennett BA, Attwood CG (1993) Shore-angling catches in the De Hoop Nature Reserve, South Africa, and further evidence for the protective value of marine reserves. South Afr J Mar Sci 13:213–222.

Bennett BA, Attwood CG (1991) Evidence for recovery of a surf-zone fish assemblage following the establishment of a marine reserve on the southern coast of South Africa. Mar Ecol Prog Ser 75:173–181.

Bianchi G, Gislason H, Graham K, et al (2000) Impact of fishing on size composition and diversity of demersal fish communities. ICES J Mar Sci J Cons 57:558–571. doi: 10.1006/jmsc.2000.0727

Blamey LK, Shannon LJ, Bolton JJ, et al (2015) Ecosystem change in the southern Benguela and the underlying processes. J Mar Syst 144:9–29. doi: 10.1016/j.jmarsys.2014.11.006

Bolton J, Anderson R, Smit A, Rothman M (2012) South African kelp moving eastwards: the discovery of *Ecklonia maxima* (Osbeck) Papenfuss at De Hoop Nature Reserve on the south coast of South Africa. Afr J Mar Sci 34:147–151. doi: 10.2989/1814232X.2012.675125

Booth AJ (1997) On the life history of the lesser gurnard (Scorpaeniformes: Triglidae) inhabiting the Agulhas Bank, South Africa. J Fish Biol 51:1155–1173. doi: 10.1111/j.1095-8649.1997.tb01133.x

Booth AJ, Buxton CD (1997a) The biology of the panga, *Pterogymnus laniarius* (Teleostei: Sparidae), on the Agulhas Bank, South Africa. Environ Biol Fishes 49:207–226. doi: 10.1023/A:1007362700687

Booth AJ, Buxton CD (1997b) Management of the panga *Pterogymnus laniarius* (Pisces: Sparidae) on the Agulhas Bank, South Africa using per-recruit models. Fish Res 32:1–11. doi: 10.1016/S0165-7836(97)00045-3

Booth AJ, Hecht T (1998) Changes in the Eastern Cape demersal inshore trawl fishery between 1967 and 1995. South Afr J Mar Sci 19:341–353. doi: 10.2989/025776198784126971

Booth AJ, Punt AE (1998) Evidence for rebuilding in the panga stock on the Agulhas Bank, South Africa. Fish Res 34:103–121. doi: 10.1016/S0165-7836(97)00092-1

Botha L (1977) Assessment of Agulhas sole stocks, Cape Agulhas to East London. South Afr Shipp News Fish Ind Rev 32:39–41.

Branch TA, Watson R, Fulton EA, Jennings S, McGilliard CR, Pablico GT, Ricard D, Tracey SR (2010) The trophic fingerprint of marine fisheries. Nature 468:431–435. doi: 10.1038/nature09528

Brander K (1981) Disappearance of common skate *Raia batis* from. Nature 290:48–49.

Brander KM (2010) Impacts of climate change on fisheries. J Mar Syst 79:389–402. doi: 10.1016/j.jmarsys.2008.12.015

Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries 25:767–781. doi: 10.1007/BF02804904

Broadhurst MK, Suuronen P, Hulme A (2006) Estimating collateral mortality from towed fishing gear. Fish Fish 7:180–218. doi: 10.1111/j.1467-2979.2006.00213.x

Brouwer S, Griffiths M (2006) Management of *Argyrozona argyrozona* (Pisces: Sparidae) in South Africa based on per-recruit models. Afr J Mar Sci 28:89–98. doi: 10.2989/18142320609504136

Brouwer SL, Griffiths MH (2005) Stock separation and life history of *Argyrozona argyrozona* (Pisces: Sparidae) on the South African east coast. Afr J Mar Sci 27:585–595. doi: 10.2989/18142320509504119

Butterworth DS, Glazer JP (2014) A preliminary assessment of the South African east coast sole resource, *Austroglossus pectoralis*. Cape Town

Butterworth DS, Glazer JP, Fairweather TP, Durholtz MD (2016) An updated assessment of the Agulhas sole resource, *Austroglossus pectoralis*. Cape Town

Butterworth DS, Punt AE, Borchers DL, et al (1989) Manual of mathematical techniques for linefish assessment. Cape Town

Caddy JF, Garibaldi L (2000) Apparent changes in the trophic composition of world marine harvests: the perspective from the FAO capture database. Ocean & Coastal Management 43:615–655. doi: 10.1016/S0964-5691(00)00052-1

Callaway R, Engelhard GH, Dann J, et al (2007) A century of North Sea epibenthos and trawling: comparison between 1902–1912, 1982–1985 and 2000. Mar Ecol Prog Ser 346:27–43.

Cameron AC, Trivedi PK (1990) Regression-based tests for overdispersion in the Poisson model. J Econom 46:347–364. doi: 10.1016/0304-4076(90)90014-K

Cardinale M, Hagberg J, Svedäng H, et al (2010) Fishing through time: population dynamics of plaice (*Pleuronectes platessa*) in the Kattegat–Skagerrak over a century. Popul Ecol 52:251–262. doi: 10.1007/s10144-009-0177-x

Cardinale M, Linder M, Bartolino V, et al (2009) Conservation value of historical data: reconstructing stock dynamics of turbot during the last century in the Kattegat-Skagerrak. Mar Ecol Prog Ser 386:197–206.

Cardinale M, Svedäng H, Bartolino V, et al (2012) Spatial and temporal depletion of haddock and pollack during the last century in the Kattegat-Skagerrak. J Appl Ichthyol 28:200–208. doi: 10.1111/j.1439-0426.2012.01937.x

Casey JM, Myers RA (1998) Near Extinction of a Large, Widely Distributed Fish. Science 281:690–692. doi: 10.1126/science.281.5377.690

Caswell H, Cohen JE (1991) Communities in Patchy Environments: A Model of Disturbance, Competition, and Heterogeneity. In: Kolasa J, Pickett STA (eds) Ecological Heterogeneity. Springer New York, pp 97–122

Chaloupka M, Balazs G (2007) Using Bayesian state-space modelling to assess the recovery and harvest potential of the Hawaiian green sea turtle stock. Ecol Model 205:93–109. doi: 10.1016/j.ecolmodel.2007.02.010

Chapman P, Largier JL (1989) On the origin of Agulhas Bank bottom water. South Afr J Sci 85:515–519.

Cheung WWL, Watson R, Pauly D (2013) Signature of ocean warming in global fisheries catch. Nature 497:365–368. doi: 10.1038/nature12156

Christensen V (1998) Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. J Fish Biol 53:128–142. doi: 10.1111/j.1095-8649.1998.tb01023.x

Christensen V, Coll M, Piroddi C, Steenbeek J, Buszowski J, Pauly D (2014) A century of fish biomass decline in the ocean. Mar Ecol Prog Ser 512:155–166.

Clark JR, Fritz RL (1963) Size selection of fish by otter trawls: results of recent experiments in the Northwest Atlantic: E. Escapement of haddock and silver hake through wire meshes. Sel Fish Gear 58–60.

Clark JR, Jensen AJ (1963) Size selection of fish by otter trawls. Results of recent experiments in the Northwest Atlantic: H. Escapement of silver hake through codend meshes. ICNAF Spec Publ 5:81–84.

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143. doi: 10.1111/j.1442-9993.1993.tb00438.x

Clarke KR, Ainsworth M (1993) A method of linking multivariate community. Mar Ecol Prog Ser 92:205–219.

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth

Cline TJ, Schindler DE, Hilborn R (2017) Fisheries portfolio diversification and turnover buffer Alaskan fishing communities from abrupt resource and market changes. Nat Commun 8:14042. doi: 10.1038/ncomms14042

Cockcroft A, van Zyl D, Hutchings L (2008) Large-scale changes in the spatial distribution of South African West Coast rock lobsters: an overview. Afr J Mar Sci 30:149–159. doi: 10.2989/AJMS.2008.30.1.15.465

Coll M, Shannon LJ, Yemane D, et al (2009) Ranking the ecological relative status of exploited marine ecosystems. ICES J Mar Sci J Cons fsp261. doi: 10.1093/icesjms/fsp261

Compagno LJV (1984) Sharks of the world. An annotated and illustrated catalogue of shark species known to date. FAO

Crawford RJM (2009) A recent increase of swift terns *Thalasseus bergii* off South Africa – The possible influence of an altered abundance and distribution of prey. Prog Oceanogr 83:398–403. doi: 10.1016/j.pocean.2009.07.021

Crawford RJM, Underhill LG, Coetzee JC, et al (2008) Influences of the abundance and distribution of prey on African penguins *Spheniscus demersus* off western South Africa. Afr J Mar Sci 30:167–175. doi: 10.2989/AJMS.2008.30.1.17.467

Crewe PR (1964) Some general engineering principles of trawl gear design. In: Modern Fishing Gear of the World II. Fishing News (Books) Ltd., London, pp 165–180

Cunningham JT (1896) North Sea investigations (continued). J Mar Biol Assoc U K 4:97–143.

DAFF (2015) Status of the South African Marine Fishery Resources 2014. Department of Agriculture, Forestry and Fisheries, Cape Town

DAFF (2017) Climate Change Adaptation and Mitigation Plan for South African Agriculture, Forestry, and Fisheries Sectors. Department of Agriculture, Forestry and Fisheries, Cape Town

Dahm E, Wienbeck H, West CW, et al (2002) On the influence of towing speed and gear size on the selective properties of bottom trawls. Fish Res 55:103–119. doi: 10.1016/S0165-7836(01)00301-0

Davis FM (1927) An Account Of The Fishing Gear Of England And Wales, Revised edition. HM Stationery Office, London

Dayton PK, Sala E, Tegner MJ, Thrush S (2000) Marine reserves: parks, baselines, and fishery enhancement. Bull Mar Sci 66:617–634.

De Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. Ecology 90:3566–3574. doi: 10.1890/08-1823.1

de Moura Neves B, Edinger E, Layne GD, Wareham VE (2015) Decadal longevity and slow growth rates in the deep-water sea pen *Halipteris finmarchica* (Sars, 1851) (Octocorallia: Pennatulacea): implications for vulnerability and recovery from anthropogenic disturbance. Hydrobiologia 759:147–170. doi: 10.1007/s10750-015-2229-x

De Vos L, Götz A, Winker H, Attwood C (2014) Optimal BRUVs (baited remote underwater video system) survey design for reef fish monitoring in the Stilbaai Marine Protected Area. Afr J Mar Sci 36:1–10. doi: 10.2989/1814232X.2013.873739

Dealteris JT, Recksiek CW, Fahfouhi A, Liuxiong X (1989) Comparison of the Performance of Two Bottom-Sampling Trawls. Trans Am Fish Soc 118:119–130. doi: 10.1577/1548-8659(1989)118<0119:COTPOT>2.3.CO;2

Department of Agriculture (1899) Report of the Marine Biologist for the Year 1898. Cape of Good Hope, Cape Town

Department of Agriculture (1898) Report of the Marine Biologist for the Year 1897. Cape of Good Hope, Cape Town

Department of Agriculture (1896) Report of the Marine Biologist for January-March, 1896. Cape of Good Hope, Cape Town

Department of Agriculture (1904) Report of the Marine Biologist for the Year 1903. Cape of Good Hope, Cape Town

Department of Agriculture (1902) Report of the Marine Biologist for the Year 1901. Cape of Good Hope, Cape Town

Department of Agriculture (1900) Report of the Marine Biologist for the Year 1899. Cape of Good Hope, Cape Town

Department of Agriculture (1905) Report of the Marine Biologist for the Year 1904. Cape of Good Hope, Cape Town

Department of Trade and Customs (1909) Report by director of fisheries on fishing experiments carried out by the F.I.S. “Endeavour”, for period 12th March to 7th September, 1909. Parliament of the Commonwealth of Australia, Melbourne

Diaz RJ, Rosenberg R (1995) Marine benthic hypoxia: A review of its ecological effects and the behavioural response of benthic macrofauna. Oceanogr Mar Biol Annu Rev 33,:245–303.

Dinmore TA, Duplisea DE, Rackham BD, et al (2003) Impact of a large-scale area closure on patterns of fishing disturbance and the consequences for benthic communities. ICES J Mar Sci 60:371–380. doi: 10.1016/S1054-3139(03)00010-9

Dolman PM, Sutherland WJ (1992) The Ecological Changes of Breckland Grass Heaths and the Consequences of Management. J Appl Ecol 29:402–413. doi: 10.2307/2404509

Doney SC, Ruckelshaus M, Duffy JE, et al (2012) Climate Change Impacts on Marine Ecosystems. Annu Rev Mar Sci 4:11–37. doi: 10.1146/annurev-marine-041911-111611

Donovan B (2010) A retrospective assessment of the Port Alfred linefishery with respect to the changes in the South African fisheries management environment. MSc Thesis, Rhodes University

DST (2007) Innovation towards a knowledge-based economy: Ten-year plan for South Africa (2008-2018). Department of Science and Technology, Pretoria

Dulvy NK, Metcalfe JD, Glanville J, et al (2000) Fishery stability, local extinctions, and shifts in community structure in skates. Conserv Biol 14:283–293. doi: 10.1046/j.1523-1739.2000.98540.x

Dulvy NK, Rogers SI, Jennings S, et al (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. J Appl Ecol 45:1029–1039. doi: 10.1111/j.1365-2664.2008.01488.x

Duplisea DE, Jennings S, Warr KJ, Dinmore TA (2002) A size-based model of the impacts of bottom trawling on benthic community structure. Can J Fish Aquat Sci 59:1785–1795. doi: 10.1139/f02-148

Durbin J, Koopman SJ (2012) Time Series Analysis by State Space Methods: Second Edition. OUP Oxford

Edwards GSF (1909) The origin and growth of British fisheries and deep sea fishing. Smith’s Dock Company, Ltd., Middlebrough-on-Tees

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884. doi: 10.1038/nature02808

Engås A, Godø OR (1986) Influence of trawl geometry and vertical distribution of fish on sampling with bottom trawl. J Northwest Atl Fish Sci 7:35–42.

Engås A, West CW (1987) Trawl performance during the barents sea cod and haddock survey: potential sources of gear-related sampling bias. Fish Res 5:279–286. doi: 10.1016/0165-7836(87)90047-6

Engel J, Kvitek R (1998) Effects of Otter Trawling on a Benthic Community in Monterey Bay National Marine Sanctuary. Conserv Biol 12:1204–1214. doi: 10.1046/j.1523-1739.1998.0120061204.x

Engelhard GH (2008) One Hundred and Twenty Years of Change in Fishing Power of English North Sea Trawlers. In: Payne A, Cotter J, Potter T (eds) Advances in Fisheries Science 50 years on from Beverton and Holt. Blackwell Publishing Ltd., pp 1–25

Engelhard GH, Ellis JR, Payne MR, et al (2011a) Ecotypes as a concept for exploring responses to climate change in fish assemblages. ICES J Mar Sci 68:580–591. doi: 10.1093/icesjms/fsq183

Engelhard GH, Pinnegar JK, Kell LT, Rijnsdorp AD (2011b) Nine decades of North Sea sole and plaice distribution. ICES J Mar Sci J Cons 68:1090–1104. doi: 10.1093/icesjms/fsr031

Engelhard GH, Thurstan RH, MacKenzie BR, et al (2016) ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. ICES J Mar Sci 73:1386–1403. doi: 10.1093/icesjms/fsv219

Fairweather TP, van der Lingen CD, Booth AJ, et al (2006) Indicators of sustainable fishing for South African sardine *Sardinops sagax* and *anchovy Engraulis encrasicolus*. Afr J Mar Sci 28:661–680. doi: 10.2989/18142320609504215

FAO (1974) Otter Board Design and Performance. FAO, Rome

Ferretti F, Myers RA, Serena F, Lotze HK (2008) Loss of large predatory sharks from the Mediterranean Sea. Conserv Biol 22:952–964.

Ferretti F, Osio GC, Jenkins CJ, et al (2013) Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. Sci Rep 3:1057. doi: 10.1038/srep01057

Ferretti F, Worm B, Britten GL, et al (2010) Patterns and ecosystem consequences of shark declines in the ocean. Ecol Lett 13:1055–1071.

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analysing multispecies distribution patterns. Mar Ecol Prog Ser 8:37–52.

Fogarty MJ, Murawski SA (1998) Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. Ecol Appl 8:S6–S22. doi: 10.1890/1051-0761(1998)8[S6:LDATSO]2.0.CO;2

Foster SD, Dunstan PK, Althaus F, Williams A (2015) The cumulative effect of trawl fishing on a multispecies fish assemblage in south-eastern Australia. J Appl Ecol 52:129–139. doi: 10.1111/1365-2664.12353

Freer DWL, Griffiths CL (1993) The fishery for, and general biology of, the St Joseph *Callorhinchus capensis* (Dumeril) off the South-Western Cape, South Africa. South Afr J Mar Sci 13:63–74. doi: 10.2989/025776193784287428

Frid CLJ, Harwood KG, Hall SJ, Hall JA (2000) Long-term changes in the benthic communities on North Sea fishing grounds. ICES J Mar Sci 57:1303–1309. doi: 10.1006/jmsc.2000.0900

Froese R (2006) Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. J Appl Ichthyol 22:241–253. doi: 10.1111/j.1439-0426.2006.00805.x

Froese R, Pauly D (2016) FishBase. World Wide Web electronic publication. http://www.fishbase.org/.

Fulton TW (1901) North Sea Investigations. Part III. Twentieth Annual Report of the Fishery Board for Scotland, pp 73–135

Furman LB, Butterworth DS (2011) Updated assessments and projections under alternative future catch levels for the horse mackerel resource. Cape Town

Garcia SM, Kolding J, Rice J, et al (2012) Reconsidering the Consequences of Selective Fisheries. Science 335:1045–1047. doi: 10.1126/science.1214594

Garner J (1956) Deep sea trawling. Gourock Ropework Company, Glasgow

Garrison LP, Link JS (2000) Fishing effects on spatial distribution and trophic guild structure of the fish community in the Georges Bank region. ICES J Mar Sci 57:723–730. doi: 10.1006/jmsc.2000.0713

Garstang W (1905) Report on the trawling investigations, 1902-3, with especial reference to the distribution of the plaice. In: First Report on Fishery and Hydrographical Investigations in the North Sea and Adjacent Waters (Southern Area). Marine Biological Association of the United Kingdom, London, pp 67–198

Garstang W (1900) The impoverishment of the sea. A critical summary of the experimental and statistical evidence bearing upon the alleged depletion of the trawling grounds. J Mar Biol Assoc U K 6:1–69. doi: 10.1017/S0025315400072374

Genner MJ, Sims DW, Southward AJ, et al (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. Glob Change Biol 16:517–527. doi: 10.1111/j.1365-2486.2009.02027.x

Genner MJ, Sims DW, Wearmouth VJ, et al (2004) Regional Climatic Warming Drives Long-Term Community Changes of British Marine Fish. Proc Biol Sci 271:655–661.

Gibbs WE (1922) The Fishing Industry. Sir Isaac Pitman and Sons Ltd., London

Gilchrist JDF (1914) Marine Biological Report for the Year ending 30th June, 1914. Union of South Africa, Cape Town

Gilks WR, Richardson S, Spiegelhalter D (1995) Markov Chain Monte Carlo in Practice. CRC Press

Godø OR, Pennington M, Vølstad JH (1990) Effect of tow duration on length composition of trawl catches. Fish Res 9:165–179. doi: 10.1016/0165-7836(90)90062-Z

Goschen WS, Schumann EH (1990) Agulhas current variability and inshore structures off the Cape Province, South Africa. J Geophys Res Oceans 95:667–678. doi: 10.1029/JC095iC01p00667

Graham KJ, Andrew NL, Hodgson KE (2001) Changes in relative abundance of sharks and rays on Australian South East Fishery trawl grounds after twenty years of fishing. Mar Freshw Res 52:549–561.

Graham KJ, Broadhurst MK, Millar RB (2009) Effects of codend circumference and twine diameter on selection in south-eastern Australian fish trawls. Fish Res 95:341–349. doi: 10.1016/j.fishres.2008.10.001

Graham M (1956) Sea fisheries: their investigation in the United Kingdom. Edward Arnold, London

Greenstreet SP., Spence FE, McMillan JA (1999) Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. Fish Res 40:153–183. doi: 10.1016/S0165-7836(98)00210-0

Greenstreet SPR, Hall SJ (1996) Fishing and the Ground-Fish Assemblage Structure in the North-Western North Sea: An Analysis of Long-Term and Spatial Trends. J Anim Ecol 65:577–598. doi: 10.2307/5738

Griffiths C, van Sittert L, Best P, et al (2004) Impacts of Human Activities on Marine Animal Life in the Benguela. Oceanogr Mar Biol Annu Rev 42:303–392.

Griffiths MH (2000) Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. South Afr J Mar Sci 22:81–110.

Griffiths MH (1997a) Influence of prey availability on the distribution of dusky kob *Argyrosomus japonicus* (Sciaenidae) in the Great Fish River estuary, with notes on the diet of early juveniles from three other estuarine systems. South Afr J Mar Sci 18:137–145. doi: 10.2989/025776197784161153

Griffiths MH (1997b) The application of per-recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. Fish Res 30:103–115. doi: 10.1016/S0165-7836(96)00552-8

Griffiths MH, Wilke C, Penney AJ, Melo Y (2002) Life history of white stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) off South Africa. South Afr J Mar Sci 24:281–300. doi: 10.2989/025776102784528394

Griffiths MH, Wilke CG (2002) Long-term movement patterns of five temperate-reef fishes (Pisces: Sparidae): implications for marine reserves. Mar Freshw Res 53:233–244.

Groenewold S, Fonds M (2000) Effects on benthic scavengers of discards and damaged benthos produced by the beam-trawl fishery in the southern North Sea. ICES J Mar Sci J Cons 57:1395–1406. doi: 10.1006/jmsc.2000.0914

Gruber N (2011) Warming up, turning sour, losing breath: ocean biogeochemistry under global change. Philos Trans R Soc Lond Math Phys Eng Sci 369:1980–1996. doi: 10.1098/rsta.2011.0003

Grüss A, Yemane D, Fairweather T (2016) Exploring the spatial distribution patterns of South African Cape hakes using generalised additive models. Afr J Mar Sci 38:395–409. doi: 10.2989/1814232X.2016.1218367

Halpern BS, Walbridge S, Selkoe KA, et al (2008) A Global Map of Human Impact on Marine Ecosystems. Science 319:948–952. doi: 10.1126/science.1149345

Harley CDG, Randall Hughes A, Hultgren KM, et al (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241. doi: 10.1111/j.1461-0248.2005.00871.x

Harris AN, Poiner IR (1991) Changes in species composition of demersal fish fauna of Southeast Gulf of Carpentaria, Australia, after 20 years of fishing. Mar Biol 111:503–519. doi: 10.1007/BF01319424

Hatton TJ (2013) How have Europeans grown so tall? Oxf Econ Pap gpt030. doi: 10.1093/oep/gpt030

Heape W (1887) Notes on the Fishing Industry of Plymouth. J Mar Biol Assoc U K 1:45–95. doi: 10.1017/S0025315400073823

Heath MR, Speirs DC (2012) Changes in species diversity and size composition in the Firth of Clyde demersal fish community (1927–2009). Proc R Soc B Biol Sci 279:543–552. doi: 10.1098/rspb.2011.1015

Hecht T (1990) On the life history of Cape horse mackerel *Trachurus trachurus capensis* off the south-east coast of South Africa. South Afr J Mar Sci 9:317–326. doi: 10.2989/025776190784378907

Hickling CF (1931) A comparison of the Vigneron-Dahl Trawling Gear with the Steam Otter Trawl, in the Hake Fishery. J Cons 6:421–431. doi: 10.1093/icesjms/6.3.421

Hiddink JG, Burrows MT, García Molinos J (2015) Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob Change Biol 21:117–129.

Hilborn R, Walters CJ (2001) Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Kluwer Academic Publishers, London

Hill MO (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432. doi: 10.2307/1934352

Hjort J (1914) Fluctuations in the Great Fisheries of Northern Europe, Viewed in the Light of Biological Research. Conseil Permanent International pour L'Exploration de la Mer, Copenhagen

Holdsworth EWH (1874) Deep-sea Fishing and Fishing Boats: An Account of the Practical Working of the Various Fisheries Around the British Islands, with Illustrations and Descriptions of the Boats, Nets, and Other Gear in Use. Edward Stanford, London

Holm P (2005) Human impacts on fisheries resources and abundance in the Danish Wadden Sea, c1520 to the present. Helgol Mar Res 59:39–44.

Holm S (1979) A Simple Sequentially Rejective Multiple Test Procedure. Scand J Stat 6:65–70.

Holt EWL (1895) An examination of the present state of the Grimsby trawl fishery, with especial reference to the destruction of immature fish. J Mar Biol Assoc U K New Ser 3:339–446. doi: 10.1017/S0025315400005129

Huggett JA, Lamont T, Coetzee JC, Verheye HM (2016) Long-term declines in southern Benguela zooplankton during summer: bottom-up or top-down forcing? Cape Town, South Africa,

ICES (2012) Manual for the International Bottom Trawl Surveys, Revision VIII. International Council for the Exploration of the Sea, Copenhagen

Jackson JBC, Kirby MX, Berger WH, et al (2001) Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293:629–637. doi: 10.1126/science.1059199

Jacobsen ALL (2010) Steam trawling on the south-east continental shelf of Australia: an environmental history of fishing, management and science in NSW, 1865-1961. Ph.D. thesis, University of Tasmania

Japp DW, Sims P, Smale MJ (1994) A review of the fish resources of the Agulhas Bank. South Afr J Sci 90:123–134.

Jenkins JT (1920) The Sea Fisheries. Constable and Company Ltd., London

Jennings S, Kaiser M, Reynolds JD (2001) Marine Fisheries Ecology. Wiley

Johnson DD, Rotherham D, Gray CA (2008) Sampling estuarine fish and invertebrates using demersal otter trawls: Effects of net height, tow duration and diel period. Fish Res 93:315–323. doi: 10.1016/j.fishres.2008.05.012

Jones P, Cathcart A, Speirs DC (2015) Early evidence of the impact of preindustrial fishing on fish stocks from the mid-west and southeast coastal fisheries of Scotland in the 19th century. ICES J Mar Sci J Cons fsv189. doi: 10.1093/icesjms/fsv189

Jones SJ, Lima FP, Wethey DS (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis L.*, in the western Atlantic. J Biogeogr 37:2243–2259. doi: 10.1111/j.1365-2699.2010.02386.x

Jongman RH, Braak CJFT, Tongeren OFR van (1995) Data Analysis in Community and Landscape Ecology. Cambridge University Press, Cambridge

Kaiser MJ, Ramsay K, Richardson CA, et al (2000) Chronic fishing disturbance has changed shelf sea benthic community structure. J Anim Ecol 69:494–503. doi: 10.1046/j.1365-2656.2000.00412.x

Kaiser MJ, Spencer BE (1994) Fish scavenging behaviour in recently trawled areas. Mar Ecol Prog Ser Oldendorf 112:41–49.

Kellner K (2016) jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses.

Kirkman SP, Yemane D, Atkinson LJ, et al (2015) Regime shifts in demersal assemblages of the Benguela Current Large Marine Ecosystem: a comparative assessment. Fish Oceanogr 24:15–30. doi: 10.1111/fog.12053

Klaer NL (2001) Steam trawl catches from south-eastern Australia from 1918 to 1957: trends in catch rates and species composition. Mar Freshw Res 52:399–410.

Kleiber C, Zeileis A (2008) Applied Econometrics with R. Springer, New York

Kongprom A, Khaemakorn P, Eiamsa-ard M, Supongpan M (2003) Status of demersal fishery resources in the Gulf of Thailand. In: Silvestre G, Garces L, Stobutzki I, et al. (eds) Assessment, management and future directions for coastal fisheries in Asian countries. Penang, pp 137–152

Kristensen K, Nielsen A, Berg CW, et al (2016) TMB: Automatic Differentiation and Laplace Approximation. J Stat Softw 70:1–21.

Kristensen K, Thygesen UH, Andersen KH, Beyer JE (2014) Estimating spatio-temporal dynamics of size-structured populations. Can J Fish Aquat Sci 71:326–336. doi: 10.1139/cjfas-2013-0151

Kritzer JP, DeLucia M-B, Greene E, et al (2016) The Importance of Benthic Habitats for Coastal Fisheries. BioScience 66:274–284. doi: 10.1093/biosci/biw014

Kyle HM (1903) Fishing nets, with special reference to the otter-trawl. J Mar Biol Assoc U K New Ser 6:562–586. doi: 10.1017/S0025315400072684

Lamberth SJ, Drapeau L, Branch GM (2009) The effects of altered freshwater inflows on catch rates of non-estuarine-dependent fish in a multispecies nearshore linefishery. Estuar Coast Shelf Sci 84:527–538. doi: 10.1016/j.ecss.2009.07.021

Lamont T, Garcìa-Reyes M, Bograd SJ, et al (2016) Upwelling indices for comparative ecosystem studies: variability in the Benguela upwelling system. Cape Town, South Africa,

Largier JL, Chapman P, Peterson WT, Swart VP (1992) The western Agulhas Bank: circulation, stratification and ecology. South Afr J Mar Sci 12:319–339. doi: 10.2989/02577619209504709

Largier JL, Swart VP (1987) East-west variation in thermocline breakdown on the Agulhas Bank. South Afr J Mar Sci 5:263–272. doi: 10.2989/025776187784522252

Last PR, White WT, Gledhill DC, et al (2011) Long-term shifts in abundance and distribution of a temperate fish fauna: a response to climate change and fishing practices. Glob Ecol Biogeogr 20:58–72. doi: 10.1111/j.1466-8238.2010.00575.x

Le Clus F, Hennig HF-KO, Melo YC, Boyd AJ (1994) Impact of the extent and locality of mud patches on the density and geograpidc distribution of juvenile Agulhas sole *Austroglossus pectoralis* (Soleidae). South Afr J Mar Sci 14:19–36. doi: 10.2989/025776194784287166

Le Clus F, Roberts MJ (1995) Topographic and hydrographic effects on catch rates of *Austroglossus pectoralis* (Soleidae) on the Agulhas Bank. South Afr J Mar Sci 16:321–332. doi: 10.2989/025776195784156638

Le Gall J (1931) Les Principales Pêches Maritime de la France: Les Filets et Engins qui y Sont Employés'. Peche Marit 666:181–200.

Lees R (1969) Fishing for Fortunes: The Story of the Fishing Industry in Southern Africa and the Men who Made it. Purnell & Sons

Legendre P, Legendre LFJ (2012) Numerical Ecology, 3rd edn. Elsevier, Amsterdam

Leslie R (2008) Abundance trends for bycatch species taken in the demersal fishery. Cape Town

Levitus S, Antonov J, Boyer T (2005) Warming of the world ocean, 1955–2003. Geophys Res Lett 32:L02604.

Lindholm JB, Auster PJ, Ruth M, Kaufman L (2001) Modeling the Effects of Fishing and Implications for the Design of Marine Protected Areas: Juvenile Fish Responses to Variations in Seafloor Habitat. Conserv Biol 15:424–437. doi: 10.1046/j.1523-1739.2001.015002424.x

Lloyd P (2010) Historical trends in the flows of the Breede River. Water SA 36:329–334.

Lo NC, Jacobson LD, Squire JL (1992) Indices of Relative Abundance from Fish Spotter Data based on Delta-Lognornial Models. Can J Fish Aquat Sci 49:2515–2526. doi: 10.1139/f92-278

Loarie SR, Duffy PB, Hamilton H, et al (2009) The velocity of climate change. Nature 462:1052–1055. doi: 10.1038/nature08649

Lotze HK, Lenihan HS, Bourque BJ, et al (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806.

Lotze HK, McClenachan L (2014) Marine historical ecology: informing the future by learning from the past. Mar Community Ecol Conserv 165–200.

Lotze HK, Milewski I (2004) Two Centuries of Multiple Human Impacts and Successive Changes in a North Atlantic Food Web. Ecol Appl 14:1428–1447. doi: 10.1890/03-5027

Lotze HK, Worm B (2009) Historical baselines for large marine animals. Trends Ecol Evol 24:254–262. doi: 10.1016/j.tree.2008.12.004

Lowry N, Robertson JHB (1996) The effect of twine thickness on cod-end selectivity of trawls for haddock in the North Sea. Fish Res 26:353–363. doi: 10.1016/0165-7836(95)00418-1

Lutjeharms JRE, Cooper J, Roberts M (2000) Upwelling at the inshore edge of the Agulhas Current. Cont Shelf Res 20:737–761. doi: 10.1016/S0278-4343(99)00092-8

MacCall AD (1990) Dynamic geography of marine fish populations. Washington University Press, Washington

Mace GM, Collar NJ, Gaston KJ, et al (2008) Quantification of Extinction Risk: IUCN's System for Classifying Threatened Species. Conserv Biol 22:1424–1442. doi: 10.1111/j.1523-1739.2008.01044.x

MacKinnon JG (2009) Bootstrap hypothesis testing. In: Belsley DA, Kontoghiorghes E (eds) Handbook of Computational Econometrics. Wiley, Chippenham, pp 183–213

Mackinson S (2001) Representing trophic interactions in the North Sea in the 1880s, using the Ecopath mass-balance approach. In: Guenette S, Christensen V, Pauly D (eds) Fisheries impacts on North Atlantic ecosystems: models and analyses. pp 35–98

MacLennan DN (1992) Fishing gear selectivity: an overview. Fish Res 13:201–204. doi: 10.1016/0165-7836(92)90076-6

Macpherson E, Duarte CM (1991) Bathymetric trends in demersal fish size: is there a general relationship? Mar Ecol Prog Ser 71:103–112.

Mandelman JW, Farrington MA (2007) The estimated short-term discard mortality of a trawled elasmobranch, the spiny dogfish (*Squalus acanthias*). Fish Res 83:238–245. doi: 10.1016/j.fishres.2006.10.001

Mann B (ed) (2013) Southern African marine linefish species profiles. South African Association for Marine Biological Research, Durban

March EJ (1953) Sailing Trawlers: The Story of Deep-sea Fishing with Long Line and Trawl. Percival Marshall and Company

Margetts AR (1949) Experimental comparison of fishing capacities of different trawlers and trawls. Rapp Cons Explor Mer 125:72–81.

Maunder MN, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. Fish Res 70:141–159. doi: 10.1016/j.fishres.2004.08.002

McConnaughey RA, Mier KL, Dew CB (2000) An examination of chronic trawling effects on soft-bottom benthos of the eastern Bering Sea. ICES J Mar Sci 57:1377–1388. doi: 10.1006/jmsc.2000.0906

McCracken FD (1963) Selection by codend meshes and hooks on cod, haddock, flatfish and redfish: B. Selection factors for cod and haddock with codends of different materials. ICNAF Spec Publ 5:131–155.

McHugh M, Sims DW, Partridge JC, Genner MJ (2011) A century later: Long-term change of an inshore temperate marine fish assemblage. J Sea Res 65:187–194. doi: 10.1016/j.seares.2010.09.006

McPhail AS, Shipton TA, Sauer WHH, Leslie RW (2001) Aspects of the biology of the cape gurnard, *Chelidonichthys capensis* (Scorpaeniformes: Triglidae) on the Agulhas Bank, South Africa. Vie Milieu 51:217–227.

Meissa B, Gascuel D (2015) Overfishing of marine resources: some lessons from the assessment of demersal stocks off Mauritania. ICES J Mar Sci 72:414–427. doi: 10.1093/icesjms/fsu144

Mellin C, Aaron MacNeil M, Cheal AJ, et al (2016) Marine protected areas increase resilience among coral reef communities. Ecol Lett 19:629–637. doi: 10.1111/ele.12598

Micheli F, Saenz-Arroyo A, Greenley A, et al (2012) Evidence That Marine Reserves Enhance Resilience to Climatic Impacts. PLoS ONE 7:e40832. doi: 10.1371/journal.pone.0040832

M'Intosh (1895) Remarks on Trawling. J Mar Biol Assoc U K 3:307–334. doi: 10.1017/S0025315400000850

Moran MJ, Stephenson PC (2000) Effects of otter trawling on macrobenthos and management of demersal scalefish fisheries on the continental shelf of north-western Australia. ICES J Mar Sci 57:510.

Mous PJ, van Densen WLT, Machiels MAM (2002) The effect of smaller mesh sizes on catching larger fish with trawls. Fish Res 54:171–179. doi: 10.1016/S0165-7836(00)00304-0

Mussgnug RS (2013) An assessment of the long-term changes in chondrichthyan abundance on the inshore trawl grounds of the Agulhas Bank, South Africa. MSc Thesis, University of Cape Town

Myers RA, Worm B (2005) Extinction, survival or recovery of large predatory fishes. Philos Trans R Soc B Biol Sci 360:13–20. doi: 10.1098/rstb.2004.1573

O'Connor S, Ono R, Clarkson C (2011) Pelagic Fishing at 42,000 Years Before the Present and the Maritime Skills of Modern Humans. Science 334:1117–1121. doi: 10.1126/science.1207703

Oksanen J, Blanchet FG, Friendly M, et al (2016) vegan: Community Ecology Package.

Opdal AF (2010) Fisheries change spawning ground distribution of northeast Arctic cod. Biol Lett 6:261–264. doi: 10.1098/rsbl.2009.0789

Parkington J (2001) Milestones: the impact of the systematic exploitation of marine foods on human evolution. Humanity Afr Naiss Coming Millenn 1000–1010.

Patterson RN, Watts KC (1986) The otter board as a low-aspect-ratio wing at high angles of attack; an experimental study. Fish Res 4:111–130. doi: 10.1016/0165-7836(86)90037-8

Paulin C, Stewart A, Roberts C, et al (1989) New Zealand fish. A complete guide.

Pauly D (1995) Anecdotes and the shifting baseline syndrome of fisheries. Trends Ecol Evol 10:430.

Payne AIL (1989) Cape hakes. In: Payne AIL, Crawford RJM (eds) Oceans of Life off Southern Africa. Vlaeberg Publishers, Vlaeberg, pp 136–147

Payne AIL, Punt AE (1995) Biology and fisheries of South African Cape hakes (*M. capensis* and *M. paradoxus*). In: Alheit J, Pitcher TJ (eds) Hake. Springer Netherlands, pp 15–47

Pecquerie L, Drapeau L, Fréon P, et al (2004) Distribution patterns of key fish species of the southern Benguela ecosystem: an approach combining fishery-dependent and fishery-independent data. Afr J Mar Sci 26:115–139. doi: 10.2989/18142320409504053

Penney AJ, Buxton CD, Garratt PA, Smale MJ (1989) The commercial marine linefishery. In: Payne AIL, Crawford RJM (eds) Oceans of Life off Southern Africa. Vlaeberg Publishers, Vlaeberg, pp 214–229

Penney AJ, Mann-Lang JB, van der Elst RP, Wilke CG (1999) Long-term trends in catch and effort in the KwaZulu-Natal nearshore linefisheries. South Afr J Mar Sci 21:51–76. doi: 10.2989/025776199784125890

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate Change and Distribution Shifts in Marine Fishes. Science 308:1912–1915. doi: 10.1126/science.1111322

Pillar SC, Wilkinson IS (1995) The diet of Cape hake *Merluccius capensis* on the south coast of South Africa. South Afr J Mar Sci 15:225–239. doi: 10.2989/02577619509504845

Pinnegar J, Engelhard G (2008) The “shifting baseline” phenomenon: a global perspective. Rev Fish Biol Fish 18:1–16. doi: 10.1007/s11160-007-9058-6

Pinsky ML, Worm B, Fogarty MJ, et al (2013) Marine Taxa Track Local Climate Velocities. Science 341:1239–1242. doi: 10.1126/science.1239352

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A (eds) Proceedings of the 3rd International Workshop on Distributed Statistical Computing. Vienna, Austria,

Plummer M, Stukalov A, Denwood M (2016) rjags: Bayesian Graphical Models using MCMC. https://CRAN.R-project.org/package=rjags

Puig P, Canals M, Company JB, Martín J, Amblas D, Lastras G, Palanques A, Calafat AM (2012) Ploughing the deep sea floor. Nature 489:286–289. doi: 10.1038/nature11410

QGIS Development Team (2015) QGIS Geographic Information System. Open Source Geospatial Foundation. http://qgis.osgeo.org

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rabalais NN, Turner RE (2001) Coastal hypoxia: consequences for living resources and ecosystems. American Geophyical Union, Washington, DC

Rademeyer R, Butterworth D, Plagányi É (2008) Assessment of the South African hake resource taking its two-species nature into account. Afr J Mar Sci 30:263–290. doi: 10.2989/AJMS.2008.30.2.7.557

Rademeyer RA, Butterworth DS (2016) Corrected Reference Case for the South African hake resource.

Rago PJ, Sosebee KA, Brodziak JKT, et al (1998) Implications of recent increases in catches on the dynamics of Northwest Atlantic spiny dogfish (*Squalus acanthias*). Fish Res 39:165–181. doi: 10.1016/S0165-7836(98)00181-7

Ravier C, Fromentin JM (2001) Long-term fluctuations in the eastern Atlantic and Mediterranean bluefin tuna population. ICES J Mar Sci 58:1299–1317.

Reeves SA, Armstrong DW, Fryer RJ, Coull KA (1992) The effects of mesh size, cod-end extension length and cod-end diameter on the selectivity of Scottish trawls and seines. ICES J Mar Sci J Cons 49:279–288. doi: 10.1093/icesjms/49.3.279

Revill AS, Dulvy NK, Holst R (2005) The survival of discarded lesser-spotted dogfish (Scyliorhinus canicula) in the Western English Channel beam trawl fishery. Fish Res 71:121–124. doi: 10.1016/j.fishres.2004.07.006

Rijnsdorp AD, Leeuwen PI van, Daan N, Heessen HJL (1996) Changes in abundance of demersal fish species in the North Sea between 1906–1909 and 1990–1995. ICES J Mar Sci 53:1054–1062. doi: 10.1006/jmsc.1996.0132

Rijnsdorp AD, Millner RS (1996) Trends in population dynamics and exploitation of North Sea plaice (*Pleuronectes platessa* L.) since the late 1800s. ICES J Mar Sci 53:1170–1184. doi: 10.1006/jmsc.1996.0142

Roberts MJ (2005) Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. ICES J Mar Sci 62:33–55. doi: 10.1016/j.icesjms.2004.10.002

Robinson R (2000) Steam power and distant-water trawling. In: Starkley DJ, Reid C, Ashcroft N (eds) England's sea fisheries: the commercial sea fisheries of England and Wales since 1300. Chatham Publishing, Lond, pp 206–216

Rogers SI, Ellis JR (2000) Changes in the demersal fish assemblages of British coastal waters during the 20th century. ICES J Mar Sci 57:866–881. doi: 10.1006/jmsc.2000.0574

Rooper CN, Wilkins ME, Rose CS, Coon C (2011) Modeling the impacts of bottom trawling and the subsequent recovery rates of sponges and corals in the Aleutian Islands, Alaska. Cont Shelf Res 31:1827–1834. doi: 10.1016/j.csr.2011.08.003

Rosenberg AA, Bolster WJ, Alexander KE, et al (2005) The history of ocean resources: modeling cod biomass using historical records. Front Ecol Environ 3:78–84. doi: 10.1890/1540-9295(2005)003[0078:THOORM]2.0.CO;2

Rouault M, Penven P, Pohl B (2009) Warming in the Agulhas Current system since the 1980's. Geophys Res Lett 36:L12602. doi: 10.1029/2009GL037987

Rouault M, Pohl B, Penven P (2010) Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. Afr J Mar Sci 32:237–246.

Ryer CH (2008) A review of flatfish behavior relative to trawls. Fish Res 90:138–146. doi: 10.1016/j.fishres.2007.10.005

Ryer CH, Stoner AW, Titgen RH (2004) Behavioral mechanisms underlying the refuge value of benthic habitat structure for two flatfishes with differing anti-predator strategies. Mar Ecol

Prog Ser 268:231–243. doi: 10.3354/meps268231

Sainsbury KJ, Campbell RA, Whitelaw AW (1993) Effects of trawling on the marine habitat on the north west shelf of Australia and implications for sustainable fisheries management. In: Hancock A (ed) Sustainable Fisheries Through Sustaining Fish Habitat, Australian Society for Fish Biology Workshop. Bureau of Resource Sciences Proceedings, Canberra, pp 137–145

Sala A, Lucchetti A, Buglioni G (2007) The influence of twine thickness on the size selectivity of polyamide codends in a Mediterranean bottom trawl. Fish Res 83:192–203. doi: 10.1016/j.fishres.2006.09.013

Sato T (1980) Reassessment of the panga stock on the Agulhas Bank fishing ground in ICSEAF subarea 2. Colin Sci Pap Int Commn SE Atl Fish 7:315–330.

Schlegel RW, Oliver ECJ, Wernberg T, Smit AJ (2017) Nearshore and offshore co-occurrence of marine heatwaves and cold-spells. Prog Oceanogr 151:189–205. doi: 10.1016/j.pocean.2017.01.004

Schlegel RW, Smit AJ (2016) Climate Change in Coastal Waters: Time Series Properties Affecting Trend Estimation. J Clim 29:9113–9124. doi: 10.1175/JCLI-D-16-0014.1

Schumann EH, Beekman LJ (1984) Ocean temperature structures on the agulhas bank. Trans R Soc South Afr 45:191–203. doi: 10.1080/00359198409519483

Schumann EH, Cohen AL, Jury MR (1995) Coastal sea surface temperature variability along the south coast of South Africa and the relationship to regional and global climate. J Mar Res 53:231–248. doi: 10.1357/0022240953213205

Schwerdtner Máñez K, Holm P, Blight L, et al (2014) The Future of the Oceans Past: Towards a Global Marine Historical Research Initiative. PLoS ONE 9:e101466. doi: 10.1371/journal.pone.0101466

Scott P (1949) Otter-Trawl Fisheries of South Africa. Geogr Rev 39:529–551. doi: 10.2307/210671

Shackell NL, Frank KT, Brickman DW (2005) Range Contraction May Not Always Predict Core Areas: An Example from Marine Fish. Ecol Appl 15:1440–1449. doi: 10.1890/04-0642

Shannon LJ, Coll M, Neira S (2009) Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. Ecol Indic 9:1078–1095. doi: 10.1016/j.ecolind.2008.12.007

Shin Y-J, Rochet M-J, Jennings S, et al (2005) Using size-based indicators to evaluate the ecosystem effects of fishing. ICES J Mar Sci 62:384–396. doi: 10.1016/j.icesjms.2005.01.004

Silvestre GT, Regalado RB, Pauly D (1986) Status of Philippine demersal stocks: inferences from underutilized catch rate data. In: Pauly D, Saeger J, Silvestre GT (eds) Resources management and socioeconomics of Philippine marine fisheries. University of the Philippines in the Visayas, pp 47–96

Simkanin C, Power AM, Myers A, et al (2005) Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. J Mar Biol Assoc U K 85:1329–1340. doi: 10.1017/S0025315405012506

Simmons RE, Kolberg H, Braby R, Erni B (2015) Declines in migrant shorebird populations from a winter-quarter perspective. Conserv Biol 29:877–887. doi: 10.1111/cobi.12493

Sink KJ, Holness S, Harris L, et al (2012a) National Biodiversity Assessment 2011: Technical Report. Volume 4: Marine and Coastal Component. South African National Biodiversity Institute, Pretoria

Sink KJ, Wilkinson S, Atkinson LJ, et al (2012b) The potential impacts of South Africa's demersal hake trawl fishery on benthic habitats: Historical perspectives, spatial analyses, current review and potential management actions. South African National Biodiversity Institute, Cape Town, South Africa

Skaug HJ, Fournier DA (2006) Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. Comput Stat Data Anal 51:699–709. doi: 10.1016/j.csda.2006.03.005

Smale MJ (1984) Inshore small-mesh trawling survey of the Cape south coast. Part 3. The Occurrence and feeding of *Argyrosomus hololepidotus, Pomatomus saltatrix* and *Merluccius capensis*. South Afr J Zool 19:170–179. doi: 10.1080/02541858.1984.11447879

Smale MJ, Bruton MN (1985) Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters of South Africa. South Afr J Zool 20:97–108. doi: 10.1080/02541858.1985.11447921

Smale MJ (1985) Aspects of the biology of *Argyrosomus hololepidotus* and *Atractoscion aequidens* (Osteichthyes: Sciaenidae) in waters of the south-eastern Cape, South Africa. South Afr J Mar Sci 3:63–75. doi: 10.2989/025776185784461199

Smale MJ, Badenhorst A (1991) The distribution and abundance of linefish and secondary trawlfish on the Cape south coast of South Africa, 1986–1990. South Afr J Mar Sci 11:395–407. doi: 10.2989/025776191784287826

Smale MJ, Roel BA, Badenhorst A, Field JG (1993) Analysis of the demersal community of fish and cephalopods on the Agulhas Bank, South Africa. J Fish Biol 43:169–191. doi: 10.1111/j.1095-8649.1993.tb01186.x

Smit AJ, Roberts M, Anderson RJ, et al (2013) A Coastal Seawater Temperature Dataset for Biogeographical Studies: Large Biases between In Situ and Remotely-Sensed Data Sets around the Coast of South Africa. PLOS ONE 8:e81944. doi: 10.1371/journal.pone.0081944

Smith HM (1921) Appendix III: Dredging and Hydrographic Records of the U.S. Fisehreis Steamer "Albatross" 1911-1920. In: Report of the United States Commissioner of Fisheries for the Fiscal Year 1920. U.S. Government Printing Office, Washington,

Smith MM, Heemstra PC (eds) (1986) Smiths' Sea Fishes. Springer Verlag, Cape Town

Somerton DA, Otto RS, Syrjala SE (2002) Can changes in tow duration on bottom trawl surveys lead to changes in CPUE and mean size? Fish Res 55:63–70. doi: 10.1016/S0165-7836(01)00293-4

Sparre P, Venema SC (1998) Introduction to tropical fish stock assessment: Part 1. Food and Agriculture Organization of the United Nations

Stebbing ARD, Turk SMT, Wheeler A, Clarke KR (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). J Mar Biol Assoc U K 82:177–180. doi: 10.1017/S0025315402005325

Stefánsson G (1996) Analysis of groundfish survey abundance data: combining the GLM and delta approaches. ICES J Mar Sci 53:577–588. doi: 10.1006/jmsc.1996.0079

Stevens JD, Bonfil R, Dulvy NK, Walker PA (2000) The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J Mar Sci 57:476–494. doi: 10.1006/jmsc.2000.0724

Stobutzki IC, Silvestre GT, Abu Talib A, et al (2006) Decline of demersal coastal fisheries resources in three developing Asian countries. Fish Res 78:130–142.

Swart VP, Largier JL (1987) Thermal structure of Agulhas Bank water. South Afr J Mar Sci 5:243–

252. doi: 10.2989/025776187784522153

ter Hofstede R, Rijnsdorp AD (2011) Comparing demersal fish assemblages between periods of contrasting climate and fishing pressure. ICES J Mar Sci 68:1189–1198. doi: 10.1093/icesjms/fsr053

Thompson GG, Withers PC (2003) Effect of species richness and relative abundance on the shape of the species accumulation curve. Austral Ecol 28:355–360. doi: 10.1046/j.1442-9993.2003.01294.x

Thorson JT, Barnett LAK (2017) Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. ICES J Mar Sci. doi: 10.1093/icesjms/fsw193

Thorson JT, Ianelli JN, Munch SB, et al (2015a) Spatial delay-difference models for estimating spatiotemporal variation in juvenile production and population abundance. Can J Fish Aquat Sci 72:1897–1915. doi: 10.1139/cjfas-2014-0543

Thorson JT, Jannot J, Somers K (2017) Using spatio-temporal models of population growth and movement to monitor overlap between human impacts and fish populations. J Appl Ecol 54:577–587. doi: 10.1111/1365-2664.12664

Thorson JT, Kristensen K (2016) Implementing a generic method for bias correction in statistical models using random effects, with spatial and population dynamics examples. Fish Res 175:66–74. doi: 10.1016/j.fishres.2015.11.016

Thorson JT, Pinsky ML, Ward EJ (2016a) Model-based inference for estimating shifts in species distribution, area occupied and centre of gravity. Methods Ecol Evol 7:990–1002. doi: 10.1111/2041-210X.12567

Thorson JT, Rindorf A, Gao J, et al (2016b) Density-dependent changes in effective area occupied for sea-bottom-associated marine fishes. Proc R Soc B 283:20161853. doi: 10.1098/rspb.2016.1853

Thorson JT, Shelton AO, Ward EJ, Skaug HJ (2015b) Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES J Mar Sci J Cons fsu243. doi: 10.1093/icesjms/fsu243

Thurstan RH, Brockington S, Roberts CM (2010) The effects of 118 years of industrial fishing on UK bottom trawl fisheries. Nat Commun 1:15. doi: 10.1038/ncomms1013

Thurstan RH, Roberts CM (2010) Ecological meltdown in the Firth of Clyde, Scotland: two centuries of change in a coastal marine ecosystem. PLoS ONE 5:e11767. doi: 10.1371/journal.pone.0011767

Tilney RL (1990) Aspects of the biology, ecology and population dynamics of *Galeichthys feliceps* (Valenciennes) and G. ater (Castelnau)(Pisces: Ariidae) off the south-east coast of South Africa.

Tilney RL, Hecht T (1990) The food and feeding habits of two co-occurring marine catfish *Galeichthys feliceps* and *G. ater* (Osteichthyes: Ariidae) along the south-east coast of South Africa. J Zool 221:171–193. doi: 10.1111/j.1469-7998.1990.tb03990.x

Todd RA (1911) Covered net experiments. In: Third Report on Fishery and Hydrographlcal Investigations in the North Sea and Adjacent Waters (Southern Area). Marine Biological Association of the United Kingdom, London, pp 177–206

Travers M, Watermeyer K, Shannon LJ, Shin YJ (2010) Changes in food web structure under scenarios of overfishing in the southern Benguela: Comparison of the Ecosim and OSMOSE modelling approaches. J Mar Syst 79:101–111.

Tupper M, Boutilier RG (1995) Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Can J Fish Aquat Sci 52:1834–1841. doi: 10.1139/f95-176

van Denderen PD, van Kooten T, Rijnsdorp AD (2013) When does fishing lead to more fish? Community consequences of bottom trawl fisheries in demersal food webs. P Roy Soc Lond B Bio 280:20131883. doi: 10.1098/rspb.2013.1883

Van der Elst RP (1989) Marine recreational angling in South Africa. In: Payne AIL, Crawford RJM (eds) Oceans of Life off Southern Africa. Vlaeberg Publishers, Vlaeberg, pp 164–176

van der Lingen CD, Coetzee JC, Hutchings L (2002) Temporal shifts in the spatial distribution of anchovy spawners and their eggs in the Southern Benguela: implications for recruitment.

van der Lingen CD, Shannon LJ, Cury P, et al (2006) 8 Resource and ecosystem variability, including regime shifts, in the Benguela Current System. In: Shannon V, Hempel G, Malanotte-Rizzoli P, et al. (eds) Large Marine Ecosystems. Elsevier, pp 147–184

Viana ST de F, de Carvalho MR (2016) Redescription of *Squalus acutipinnis* Regan, 1908, a Valid Species of Spiny Dogfish from Southern Africa (Chondrichthyes: Squaliformes: Squalidae). Copeia 104:539–553. doi: 10.1643/CI-14-217

von Bonde C (1933) Fisheries and Marine Biological Survey. Report No. 10 for the Year Ending December, 1932. Union of South Africa, Pretoria

von Brandt A (1963) Selectivity data for synthetic fibres. ICNAF Spec Publ 5:18–23.

von Szalay PG, Somerton DA (2005) The effect of net spread on the capture efficiency of a demersal survey trawl used in the eastern Bering Sea. Fish Res 74:86–95. doi: 10.1016/j.fishres.2005.04.007

Walsh SJ (1991) Effect of tow duration on gear selectivity. Northwest Atl Fish Organ Sci Counc Meet NAFO SCR Doc 91/84:1–9.

Ward P, Myers RA (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. Ecology 86:835–847.

Warwick RM, Clarke KR (1993) Increased variability as a symptom of stress in marine communities. J Exp Mar Biol Ecol 172:215–226. doi: 10.1016/0022-0981(93)90098-9

Warwick RM, Clarke KR (1991) A comparison of some methods for analysing changes in benthic community structure. J Mar Biol Assoc U K 71:225–244.

Watermeyer KE, Hutchings L, Jarre A, Shannon LJ (2016) Patterns of Distribution and Spatial Indicators of Ecosystem Change Based on Key Species in the Southern Benguela. PLOS ONE 11:e0158734. doi: 10.1371/journal.pone.0158734

Watermeyer KE, Shannon LJ, Griffiths CL (2008) Changes in the trophic structure of the southern Benguela before and after the onset of industrial fishing. Afr J Mar Sci 30:351–382.

Watson G, Smale MJ (1999) Age and growth of the shortnose spiny dogfish *Squalus megalops* from the Agulhas Bank, South Africa. South Afr J Mar Sci 21:9–18. doi: 10.2989/025776199784126097

Watson G, Smale MJ (1998) Reproductive biology of shortnose spiny dogfish, *Squalus megalops*, from the Agulhas Bank, South Africa. Mar Freshw Res 49:695–703. doi: 10.1071/MF97255

Weinberg KL (2003) Change in the performance of a Bering Sea survey trawl due to varied trawl speed. Alsk Fish Res Bull 10:42–49.

Whitfield AK, Blaber SJM (1978) Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. J Fish Biol 13:675–691. doi: 10.1111/j.1095-8649.1978.tb03481.x

Wieland K, Storr-Paulsen M (2006) Effect of tow duration on catch rate and size composition of

Northern shrimp (*Pandalus borealis*) and Greenland halibut (*Reinhardtius hippoglossoides*) in the West Greenland Bottom Trawl Survey. Fish Res 78:276–285. doi: 10.1016/j.fishres.2006.01.004

Winker H, Carvalho F, Attwood CG (in prep) Applying Bayesian surplus production models to develop Precautionary Upper Catch Limits (PUCLs) for trawl bycatch species.

Winker H, Kerwath SE, Attwood CG (2012) Report on stock assessments of important South African linefish resources. Cape Town

Wootton JT, Pfister CA, Forester JD (2008) Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. Proc Natl Acad Sci 105:18848–18853. doi: 10.1073/pnas.0810079105

Wu L, Cai W, Zhang L, et al (2012) Enhanced warming over the global subtropical western boundary currents. Nat Clim Change 2:161–166. doi: 10.1038/nclimate1353

Yemane D, Field JG, Griffiths MH (2004) Effects of fishing on the size and dominance structure of linefish of the Cape region, South Africa. Afr J Mar Sci 26:161–177. doi: 10.2989/18142320409504055

Yemane D, Field JG, Leslie RW (2005) Exploring the effects of fishing on fish assemblages using abundance biomass comparison (ABC) curves. ICES J Mar Sci 62:374–379. doi: 10.1016/j.icesjms.2005.01.009

Yemane D, Field JG, Leslie RW (2008) Indicators of change in the size structure of fish communities: A case study from the south coast of South Africa. Fish Res 93:163–172. doi: 10.1016/j.fishres.2008.03.005

Yemane D, Field JG, Leslie RW (2010) Spatio-temporal patterns in the diversity of demersal fish communities off the south coast of South Africa. Mar Biol 157:269–281. doi: 10.1007/s00227-009-1314-y

Yemane D, Kirkman SP, Kathena J, et al (2014) Assessing changes in the distribution and range size of demersal fish populations in the Benguela Current Large Marine Ecosystem. Rev Fish Biol Fish 24:463–483. doi: 10.1007/s11160-014-9357-7

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice Hall, Upper Saddle River

Zoutendyk P (1972) The Biology of the Agulhas Sole, *Austroglossus pectoralis*, Part 1. Environment and Trawling Grounds. Trans R Soc South Afr 40:349–366. doi: 10.1080/00359197209519429