Seasonal and spatial variability of pelagic fishes in relation to environmental variability in St Helena Bay

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Declaration

I know the meaning of plagiarism and declare that all of the work in this document, except for that which is properly acknowledged, is my own.

Zooplankton data from the St Helena Bay Monitoring Line (SHBML) were provided by, and used with the permission of, Ashley Johnson (Department of Environmental Affairs, DEA) and Dr. Jenny Huggett (DEA).

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I have used a Harvard-UCT (author-date) system for citation and referencing. Each significant contribution to, and quotation in, this report from the work or works of other people has been attributed, and has been cited and referenced.

I participated in research surveys collecting mainly acoustic data used in this project on board research vessels from 2007, when I started working for DAFF.

Signed by candidate

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Student Number: MSHKAN002

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Abstract

The St Helena Bay Monitoring Line (SHBML) stretches 197 nautical miles off Elands Bay on the west coast of South Africa. It is an extensive long term project on environmental monitoring, running from 2000 till 2012 on an almost monthly basis but currently running on a quarterly basis. It extends through the nursery grounds and part of the transport zone for hydrology and productivity in areas that are significant to early life history of small pelagic fish. Environmental, acoustic and zooplankton data have been collected along the SHBML to obtain information on ocean environment, pelagic fish abundance and also zooplankton abundance. This study used an interdisciplinary approach, analysing historical data collected during biannual surveys of small pelagic fish, to investigate seasonal and spatial variability of pelagic fishes in relation to environmental variability in St Helena Bay. Surface values from 2000 to 2010 of temperature, salinity, oxygen and chlorophyll were analysed in relation to zooplankton and fish densities. The results show partial / weak seasonality of SST in offshore and also in coastal stations. Zooplankton, chlorophyll and oxygen show limited seasonality only in nearshore stations. Strong cross-shelf patterns of SST, chlorophyll, salinity, oxygen, zooplankton biomass and fish abundance were noted. These were expected results from a coastal upwelling system where primary productivity during summer is increased in the nearshore zone. There was a positive relationship between salinity and SST ($r = 0.821$, $p<0.0001$) and a negative relationship between chlorophyll and SST ($r = -0.549$, $p<0.001$), as would be expected in a coastal upwelling environment. When other variables were examined (also in pairs), there were no relationships between SST and oxygen, fish and zooplankton, fish and chlorophyll, fish and SST, fish and oxygen, and chlorophyll and zooplankton. A GLM was fitted to the data to investigate the relationship of pelagic fish density with zooplankton biovolume, chlorophyll, SST and oxygen; the GLM results showed a negative relationship between zooplankton abundance and pelagic fish ($t=-1.980$, $p=0.049$). Based on these results, it appears that the SHBML data were not able to pick up seasonal signals but have shown interannual variability and also some inshore-offshore differences.

1. INTRODUCTION

1.1 The Southern Benguela Upwelling Ecosystem

The most productive marine ecosystems of the world are Eastern Boundary Upwelling Systems (EBUS), which occur in the Benguela, Canary, California and Humboldt Currents (Freon *et al.* 2009a). Coastal upwelling in the Benguela ecosystem is forced by Ekman pumping driven by the earth's rotation combined with extreme trade winds, bringing nutrient-rich, cold water from beneath to the surface (Checkley *et al*. 2009; Hutchings *et al*. 2009) where it stimulates primary production, which supports a highly productive food chain (Freon *et al.* 2009b). The southern Benguela (Figure 1) extends from Luderitz to the Agulhas Bank (Hutchings *et al.* 2009), and is affected by physical factors such as fluctuations in bottom topography and alongshore wind stress (Hutchings *et al*. 2012). Upwelling which is locally enhanced results in alongshore disparities in plankton biomass, nutrient concentrations and water temperature (Pitcher *et al.* 1992). The southern Benguela is one of the most productive upwelling regions (Carr 2002) and supports several fisheries (Schwartzlose *et al*. 1999).

Cycles of intense upwelling followed by reduced upwelling, lasting between seven and ten days, are especially evident south of Cape Columbine (Figure 2) on the southern Benguela (South Africa, Hutchings *et al*. 2009). Maximum upwelling intensities in the southern Benguela occur mainly during austral spring and summer months (Hutchings *et al.* 2012; van der Lingen and Huggett 2003). Upwelling systems are variable and unpredictable, with changes in wind strength that can vary on short time scales, causing upwelling strength to vary dramatically (Hutchings *et al*. 2009). Upwelling in the southern Benguela varies on episodic and periodic scales and a frontal zone is typically distinct in temperature distributions, concurring almost with the shelf edge (Barlow *et al*. 2005). Upwelling varies not only on temporal scales but also spatially, with upwelling events concentrated at particular areas along the coast (Hutchings *et al*. 2009).

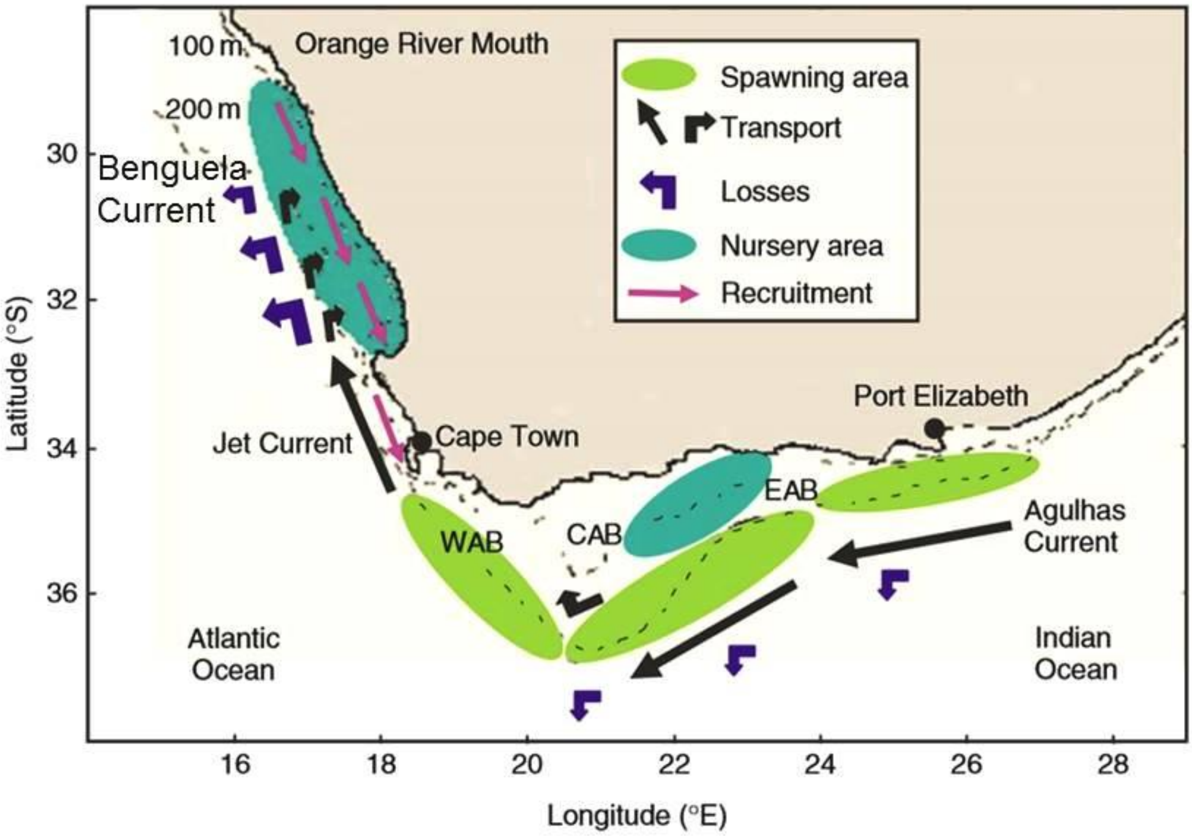


Figure 1: Map of Southern Benguela (off South Africa) showing places of small pelagic fish spawning area, transport, loss processes that influence eggs and larvae and nursery grounds. WAB, CAB, and EAB show the Eastern, Western and Central Agulhas Banks, respectively (modified from Anderson and Lucas 2008).

1.2 St Helena Bay and the St Helena Bay Monitoring Line

Sea surface temperatures (SST) of the southern Benguela ecosystem range between 10°C and 19°C (Figure A1 and A2, Appendix), with seasonal maximum upwelling occurring in austral summer and minimum upwelling in austral winter (Lamont *et al.* 2015). The St. Helena Bay region has the hydrodynamic physical features distinctive of retention areas lying equatorward or downwind from an upwelling cape in eastern boundary current ecosystems. It is influenced by predominantly westerly winds in winter and southeasterly trade winds in summer (Hutching *et al*. 2012), therefore upwelled waters flow north-westward off Cape Columbine. Wind-driven upwelling has a substantial role in regulating the biogeochemical progressions occurring in St Helena Bay (Monteiro and Roychoudhury 2005). Shannon and Nelson (1996) identified St Helena Bay as one of the key upwelling centres in the southern Benguela upwelling ecosystem. Hutchings *et al.* (2012) defined St. Helena Bay (Figure 2) in terms of winds, temperature and phytoplankton production as one of the supreme productive areas of the Benguela Current large marine ecosystem. There has been much emphasis for decades on research in the St Helena Bay region as it has been the centre of the small pelagic fishing industry since its start in the 1940s and it has also been an imperative part of the west coast rock lobster *Jasus lalandii* fishing spots (von Bonde and Marchand 1935).

The nutrient supply to St Helena Bay is affected by the major upwelling centre of Cape Columbine. The St Helena Bay area supports an important small pelagic fishery for anchovy (*Engraulis encrasicolus),* round herring *(Etrumeus whiteheadi),* sardine *(Sardinops sagax)* and horse mackerel (*Trachurus capensis*) (Crawford *et al.* 1987). The upwelled water off Cape Columbine during south easterly wind events in summer is thought to be brought to the St Helena Bay region through a cyclonic gyre (Holden 1985). The steadiness of the structure within the St Helena Bay region facilitates the extreme productivity of the area (Walker and Pitcher 1990). However the water mass outside the bay fluctuates on a time-scale of three to five days whereas the retention time of almost twenty five days within the bay is believed to influence processes there (Waldron 1985).

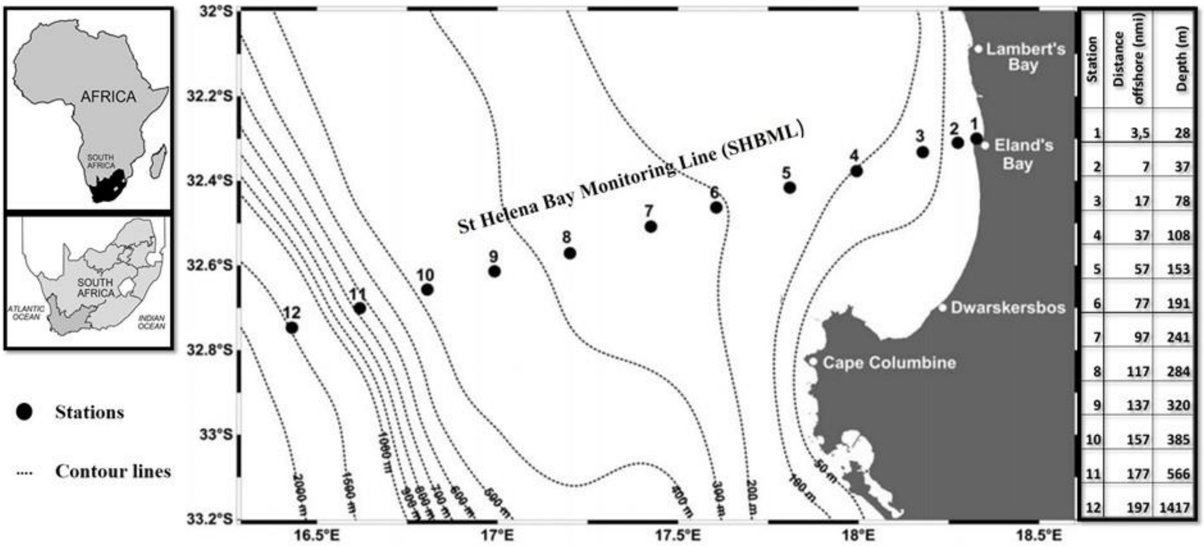
St. Helena Bay is an important small pelagic fish recruitment region within the southern Benguela ecosystem. Small pelagic fish recruits are plentiful in the bay, four to five months after spawning, and grow in size as they migrate south through the bay (Crawford 1980a; Hutchings and Nelson 1985). This semi-enclosed bay obtains nutrient-rich cold water from from the upwelling hub off Cape Columbine, and also from alternating coastal upwelling in a fine band north of St Helena Bay when southerly coastal winds triumph (Armstrong *et al*. 1987).

Brown and Hutchings (1987) reported that this double upwelling, including stratification from sun heating and also a retention time inside St Helena Bay, allow phytoplankton blooms to develop and result in a region of elevated productivity. Mass deaths of rock lobsters and shellfish occurred in the bay periodically, frequently in concurrence with the decline of dense phytoplankton blooms (Pitcher and Weeks 2006; Cockcroft *et al*. 2008). St Helena Bay has differing oxygen concentrations, seasonally and inter-annually. Cockcroft *et al*. (2008) suggested that this variation has led to a shift in west coast rock lobsters southwards and eastwards, although the exact cause has not been confirmed.

In the 1950s a multidisciplinary research programme was devised to investigate the biology, ecology and reproductive behaviour of the South African sardine and Cape horse mackerel, together with extensive hydrological and plankton studies around Cape Columbine (Marchand 1952). A repetitive monitoring grid of 20 hydro-biological and plankton stations was introduced and sampled monthly but in 1967 the routine monthly monitoring was terminated. Another monthly monitoring line comprising 12 stations was implemented in St Helena Bay in April 2000 and ran until 2010 (Hutchings *et al.* 2009). The St Helena Bay Monitoring Line (SHBML, Figure 2), which extends over 100 nautical miles off Elands Bay, was planned as a long term environmental monitoring programme. The distances between stations vary, with the line extending from close inshore (18 m depth) to beyond the shelf edge (1 466 m depth, approximately 187 km offshore) (Hutchings *et al.* 2009). The SHBML was sampled almost every month. In some months, sampling on dedicated cruises was substituted by opportunistic sampling during annual small pelagic recruit and spawner biomass surveys. These surveys also included other sampling, such as acoustic data collection (Hutchings *et al.* 2012). The monthly sampling was done specifically to examine seasonality in variables such as zooplankton density and species composition, and also the presence of low-oxygen water. The SHBML transect encompassed areas of importance for early life phases of small pelagic fishes, such as sardine, round herring and anchovy including a transport (of eggs and larvae) region offshore and nursery grounds inshore (Hutchings *et al.* 2012). Thus, it would be useful to understand whether there is strong environmental seasonality in St Helena Bay matching the seasonality of pelagic fish occurrence in the bay.

1.3 The pelagic food web

An important transitional trophic level exists in upwelling ecosystems; plankton-feeding small pelagic fish occupy that level, which is controlled by one or a limited number of shoaling species (Cury *et al.* 2000). The southern Benguela upwelling ecosystem supports major commercial fisheries based on shoals of anchovy, sardine, round herring and horse mackerel, which are supported by a large quantity of phytoplankton and zooplankton food (Anderson and Lucas 2008). Stock sizes of diverse small pelagic fish species have been variable over the years, suggesting susceptibility of ecosystem structure to climate change or changing sea conditions (Hutchings *et al.* 2009). Understanding the relationship between fish and lower and higher trophic levels, including the environment, is important for understanding variability in these important small pelagic fish resources and ensuring sustainable management (Anderson and Lucas 2008).



Station	Distance offshore (nmi)	Depth (m)
1	3,5	28
2	7	37
3	17	78
4	37	108
5	57	153
6	77	191
7	97	241
8	117	284
9	137	320
10	157	385
11	177	566
12	197	1417

Figure 2: Map of the study area (St. Helena Bay) displaying some important geographical features including the St. Helena Bay Monitoring Line (SHBML). The dots indicate the SHBML stations (1 inshore to 12 offshore).

The relationships between the main components of the pelagic food web (Figure 3) have an important role in defining the dynamics and productivity of the ecosystem. The transfer of energy from primary producers (phytoplankton) to higher trophic organisms occurs via zooplankton and planktivorous fish. Variability in zooplankton communities can influence the population dynamics of exploited species (Lezama-Ochoa *et al.* 2010). Zooplankton provide food for some of the most important commercial small pelagic fish in the southern Benguela, such as sardine, anchovy and round herring (van der Lingen 1994; van der Lingen *et al.* 2006b, Figure 3).

Phytoplankton production is consistently high within St Helena Bay, resulting in high zooplankton abundance (Verheye *et al.* 1998). The dominant zooplankton species from St Helena Bay in the 2000s were principally copepods and euphausiids, along with some hyperiid amphipods, chaetognaths and medusae (Hutchings *et al*. 2012). Zooplankton abundance mostly peaked during summer, dominated by calanoid copepods (Hutchings *et al*. 2009). Small copepod species e.g. *Paracalanus* spp, *Ctenocalanus* spp and *Clausocalanus* spp, are also very abundant in St Helena Bay (Hutchings *et al*. 2012).

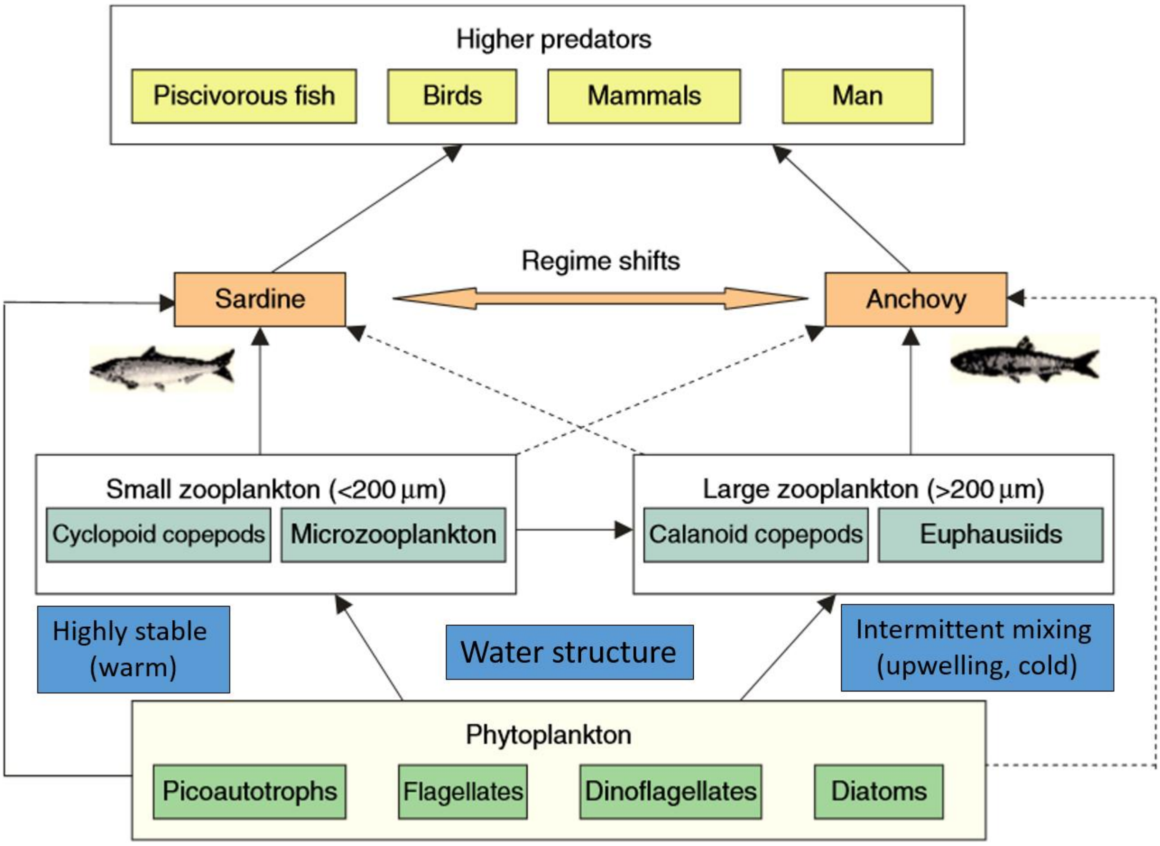


Figure 3: An idealized flow chart for the southern Benguela upwelling ecosystem food web. Physical scenarios (in blue) can lead to environments that support either anchovy or sardine. Dashed arrows indicate weak flows (modified from van der Lingen *et al.* 2006b).

Zooplankton contribute about 60 to 80% of the diet of sardine (James 1988), and 90% of the annual consumption by small pelagic fish in the southern Benguela ecosystem is expected to be derived from meso- and macrozooplankton (Verheye *et al.* 1992).

Fluctuating abundance of zooplankton may limit fish production in the southern Benguela ecosystem (Shannon 1985, Verheye *et al.* 1992). A decrease in zooplankton density in St Helena Bay was observed from 1995 to 2005 (Hutchings *et al.* 2009) and such decrease has been attributed to a number of potential factors, such as change in predation pressure and net selectivity. Other factors included changes in small pelagic fish dominance from filter-feeding sardine to particulate-feeding anchovy, a decrease in overall pelagic fish abundance linked to fishing, increased predation pressure from Cape fur seals *Arctocephalus pusillus pusillus* and snoek *Thyrsites atun*, an increase in upwelling intensity, and increased retention within the semi-enclosed St Helena Bay system (Verheye *et al*. 1998).

The changes over time and space in the abundance and distribution of zooplankton are brought about by changes in both biotic and abiotic factors (Verheye 1991). In St Helena Bay, zooplankton distribution is affected by primary production's seasonal cycle, which in turn corresponds with seasonal fluctuations in upwelling (Verheye *et al*. 1992). During vigorous upwelling, strong winds transport zooplankton offshore (Pillar *et al*. 1992). Offshore, inshore and alongshore advection may lead to significant temporal and vertical changes in plankton communities (Verheye *et al*. 1992). Predation, vertical migration and passive horizontal transport of individuals are biological and physical processes that can result in marked fluctuations within zooplankton populations (Verheye *et al*. 1998).

1.3.1 Relationship between small pelagic fish and zooplankton

Copepods are found to be an important food item for small pelagic fish. Ogawa and Nakahara (1979) indicated high competition for space in zooplankton whereas fish species tend to compete for food. Sardine, round herring and anchovy are all omnivorous, proficient at feeding on both phytoplankton and zooplankton. Zooplankton is the main food source for small pelagic fish species and different size fractions of zooplankton are ingested. Size-selection of zooplankton seems to apply to younger life-history stages of anchovy, round herring and sardine, which school together as pre-recruits or recruits in the southern Benguela, and are in abundance inshore along the west coast of South Africa (van der Lingen *et al.* 2006b).

Many zooplankton undergo diel vertical migration in which animals occupy greater depths (just below the thermocline) throughout the day and ascend into near-surface waters throughout the night (Stuart and Pillar 1990). This kind of behaviour changes with the developmental stage of zooplankton. Anchovy feeding period seems to be linked with vertical migration, with high feeding action during the night coinciding with shoal dispersion in the surface waters, whereas low feeding action during the day matches with shoal aggregation and descent into deeper waters (James 1987). Sardine and anchovy control their swimming speed throughout feeding activity according to diverse properties of the food surroundings; sardine regulate their swimming speed according to prey concentration when feeding on zooplankton and swim faster at higher prey concentrations (van der Lingen *et al.* 2006a), whereas swimming speed of anchovy is controlled by prey size, with larger zooplankton prompting faster swimming speeds (James *et al.* 1989).

1.4 Small pelagic fish abundance

Small pelagic fish species consist of epipelagic and mesopelagic species. Large purse-seine fisheries in South Africa (van der Lingen *et al.* 2006a) and a number of top predator populations (Hutchings *et al*. 2012) are supported by small pelagic fish species. Small pelagic fish are fast-growing, short-lived and are characterized by noticeable fluctuations in their stock size because of variable, environmentally-influenced annual recruitment (Barange *et al*. 2009). The three most exploited species of epipelagic fish on the South African continental shelf are anchovy, sardine and round herring; less exploited mesopelagic species are lanternfish (*Lampanyctodus hectoris*) and lightfish (*Maurolicus muelleri*). The small pelagic fishery is a major component of South Africa's fishing industry with regards to the volume of the landed catch as well as direct and indirect employment (Hampton, 1992). These small pelagic fish species have been exploited off the coast of South Africa since the 1940s. Small pelagic fish biomass can reach several millions of tons, but it fluctuates considerably at different timescales, as does their distribution (Barange *et al.* 2009).

1.4.1 Epipelagic fish

i) Distribution, catches and biomass

Approximately one third of the global fish catches is contributed by epipelagic fish species (Checkley *et al.* 2009) which play an important role in the transfer of energy from low to high trophic levels in the southern Benguela (Cury *et al*. 2000). In South Africa, purse-seine catches of pelagic fish in the 1950s were confined to the St Helena Bay region (Coetzee *et al.* 2008). Since then, pelagic fish biomass in the southern Benguela and catches in St Helena Bay have altered dramatically (van der Lingen *et al*. 2006). Total annual catches of anchovy, sardine and redeye have fluctuated widely in the past years (Checkley *et al*. 2009). In the late 1950s and early 1960s, small pelagic catches were increasingly made south of St Helena Bay towards Cape Agulhas and the proportion of juveniles in the catch increased as good year classes entered the fishery. Peak small pelagic fish catches in St Helena Bay are still taken in autumn/winter, but are composed of predominantly juvenile anchovy, together with a lesser bycatch of immature sardine and round herring (Hutchings *et al.* 2012). Annual combined catches for the pelagic industry have varied between 200 000 and 600 000 t since 1990, with the average catch in the 2000s amounting to 480 000 t per annum (Figure 4).

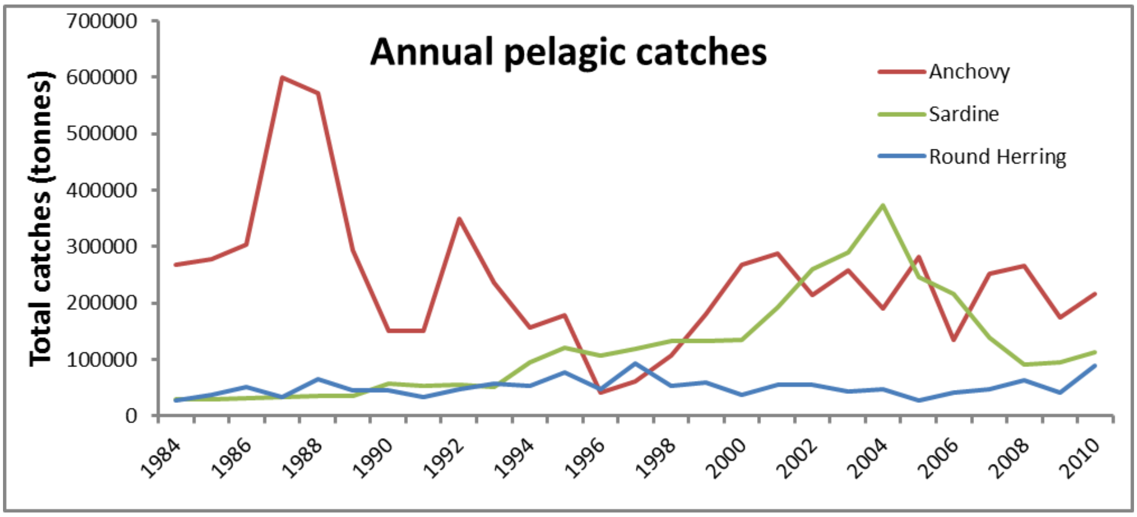


Figure 4: Annual anchovy, sardine and round herring catches from commercial vessel landings from 1984 to 2010 (van der Westhuizen 2011).

The most important target species was sardine, leading to the creation of the small pelagic fishery in the 1940s (Beckley and van der Lingen 1999), before the sardine stock collapsed under extreme fishing pressure. Sardine are largely caught for canning (human consumption), and also as fish meal. Sharply declining sardine catches encouraged the introduction of new technology, such as echosounders (Crawford *et al.* 1987), which allowed effective fishing in daytime and also during moon-light periods. Although most catches of sardine are made around Cape Agulhas recently, some adult sardine are still purse-seined off St Helena Bay, around 30–40 nautical miles offshore in the frontal region (Hutching *et al.* 2012).

Anchovy became the main species of the small pelagic fishery between 1974 and 1995 but sardine catches showed a stable increase from 1995 up to 2000 as a result of a conservative management strategy and favourable environmental conditions (Hutching *et al.* 2012). Figure 5 shows that adult anchovy biomass was at high levels in the early 2000s, generally higher than that observed in the 1980s and 1990s (Hutching *et al.* 2012). Anchovy recruits have continued to dominate anchovy catches in the St Helena Bay area, but adult sardine catches have shifted further to the east (Fairweather *et al.* 2006). Crawford *et al.* (2008) also confirmed the change in sardine distribution in recent years, with increased sardine densities in the east. It is possible that this shift was environmentally induced (Roy *et al.* 2007). Long-term variations in population size of anchovy and sardine are probably driven by decadal variability in climate (Schwartzlose *et al.* 1999), which brings sporadic environmental situations that favour one species (anchovy or sardine) over the other.

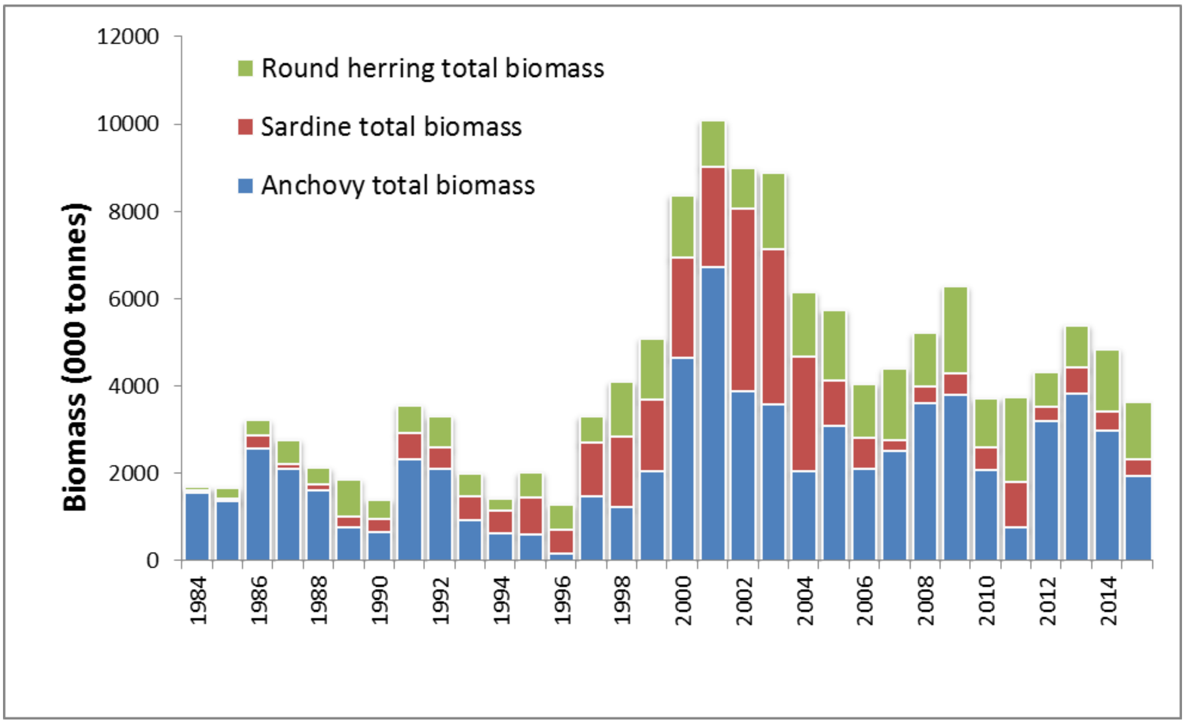


Figure 5: Combined anchovy, sardine and redeye (round herring) biomass from annual spawner biomass surveys conducted by DAFF from 1984 to 2015, covering the South African coast from Hondeklip Bay to Port St Johns (Coetzee *et al*. 2015)

This has resulted in some predator populations, particularly seabirds, migrating to the east and forming fresh colonies on South Africa's south coast. The change in relative abundance has also affected the small pelagic industry, since their processing factories are on the west coast (Hutching *et al.* 2012).

Another important epipelagic species in the St Helena Bay region is round herring, also known as redeye (Roel and Armstrong 1991; Hutching *et al.* 2012). Adult and juvenile round herring make a daily vertical migration during the night. Throughout day time, round herring occur in dense schools in the bottom of the water column and are detected frequently within 15-20 metres from the sea floor. They spawn predominantly on the Agulhas Bank in late winter/spring and the recruits move through St Helena Bay during spring and summer before dispersing offshore on the Agulhas Bank at the onset of maturity (Roel *et al.* 1994). Large round herring are targeted by purse-seiners offshore on the west coast, to the north of St Helena Bay region and between Cape Columbine and Cape Point. Recruits and juveniles round herring aggregate inshore, where they school conjointly with juvenile anchovy and other small pelagic species. The food and distribution of round herring overlap broadly with those of the commercially significant anchovy and sardine populations (Roel and Armstrong 1991).

ii) Spawning

Several small pelagic fish species spawn on the Agulhas Bank, and eggs and larvae are transported by inshore jet currents to the west coast. The west coast serves as a nursery ground (Figure 6). The transportation of larvae and juvenile fish is linked to a resilient thermal front amongst warmer surface water and cold upwelled water flowing north beside the shelf edge of the west coast (Nelson and Hutchings 1983; Shelton and Hutchings 1990; Fowler and Boyd 1998). Sardine and anchovy spawn principally over the Agulhas Bank, although sardine still occasionally spawn offshore along the west coast (Hutchings *et al*. 1998, van der Lingen and Huggett 2003), with eggs and early larvae carried in convergent jet currents from the Agulhas Bank to the west coast.

During much of the acoustic-survey period, the results showed most of the matured and adult small pelagic fish biomass has been restricted to the south of west coast, the Agulhas Bank and on the east coast to Port Alfred (Figure 6). However, fully-grown sardine have been mainly distributed on the western Agulhas Bank during their key spawning season in summer and spring (Crawford 1980; Armstrong *et al.* 1987; Shelton and Hutching 1990; van der Lingen and Huggett 2003), and shifts between primarily south coast spawning and west coast spawning have been common in the past (van der Lingen *et al.* 2001, 2006a). The capability of sardine to spawn in both regions is because they are relatively unspecific in choosing their spawning environment (van der Lingen *et al*. 2001; Twatwa *et al*. 2005).

There is a return migration of juvenile fish south during late summer or early autumn along the west coast, together with recruits to the adult population on the Agulhas Bank during autumn and winter (Hutchings *et al*. 1998, 2002; Barange *et al.* 1999). West coast recruitment remains dominant, with recruits of anchovy, sardine and redeye species still most abundant on the west coast and continuing to move through St Helena Bay during autumn and winter (Armstrong *et al*. 1987). Initially, fish are located far offshore as pre-recruits. Later, as juveniles, they occur in the productive inshore waters from the Orange River (29°S) to Cape Point (34°S). They feed intensively on zooplankton during autumn and winter, growing in length and accumulating energy reserves for their spawning migration in spring back to the south coast (Hutchings *et al*. 1998; Barange *et al*. 1999; van der Lingen and Huggett 2003; van der Lingen *et al*. 2006a; Hutchings *et al*. 2009).

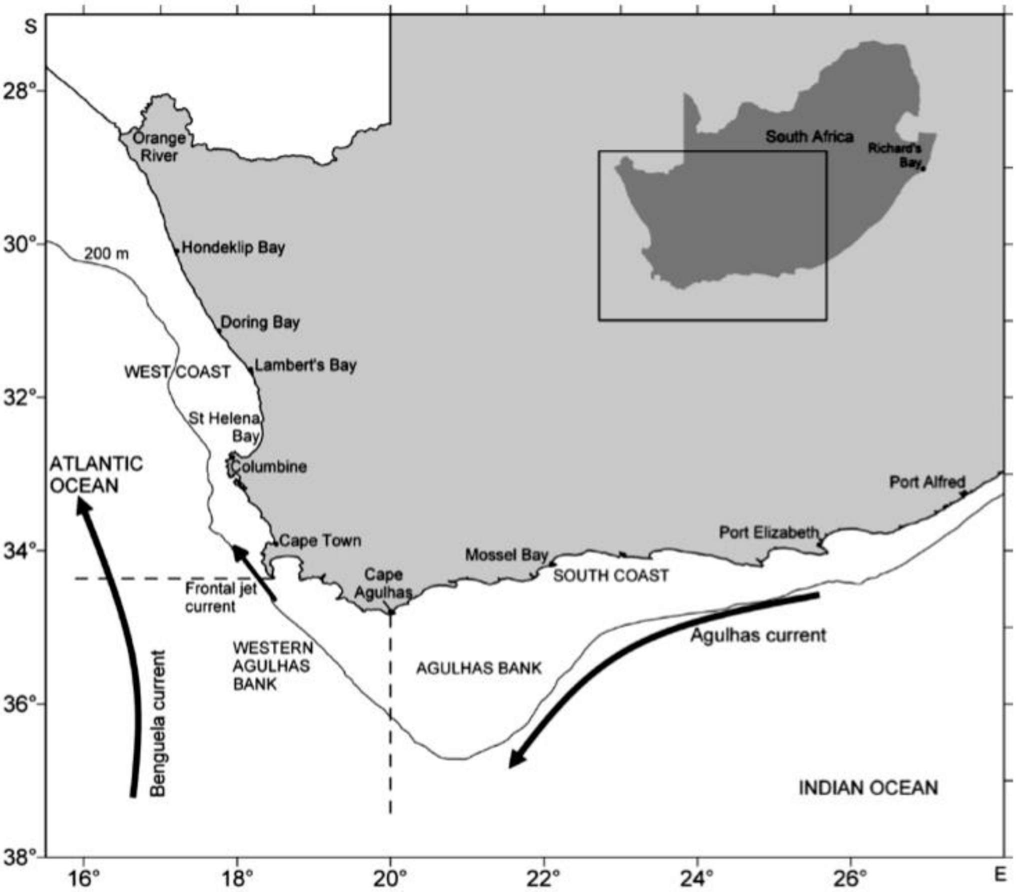


Figure 6: South African map showing St Helena Bay and other positions cited in the text, the 200-m isobath continental shelf, the Benguela and Agulhas Currents are also shown (Coetzee *et al.* 2008).

iii) Feeding

Sardine and anchovy have diverse feeding tactics. Sardine mostly filter feed on phytoplankton, small zooplankton, and small cyclopoid copepods, whereas anchovy practice biting behaviour to selectively eat single particles like larger copepods and euphausiids (van der Lingen 2006b). Van der Lingen *et al* (2006a) reported that intense upwelling promotes diatom growth which supports large zooplankton and therefore should support anchovy. In contrast, the more nutrient-exhausted waters exist during periods of weak upwelling support small phytoplankton and consequently small zooplankton, which are ideal for filter-feeding sardines.

Copepods leave the seafloor at night and migrate up to the surface water column; small pelagic fish do likewise (Barange *et al.* 2005). It is highly likely that small pelagic fish follow the copepods up into the surface water column at night to forage. However, at night the copepods are extensively distributed and extremely difficult to forage on, unlike day time when they can be found in high concentrations. Therefore, it is also contended that small pelagic fish migrate up at night to reduce being preyed on in conditions of reduced visibility by the demersal Cape hake species, *Merluccius capensis* and *Merluccius paradoxus* (Barange *et al*. 2005).

The principal feeding mode of sardine is filter-feeding. Food particles of less than 1 200µm prompt a filter-feeding reaction, whereas larger particles provoke particulate-feeding at low concentrations but filter-feeding at high concentrations (van der Lingen 1994). Sardine exhibit size-selectivity, by eliminating larger prey organisms during particulate-feeding. In contrast to sardine, the primary feeding mode for anchovy is particulate-feeding. Anchovy are highly size-selective, selecting the largest particles available. Filter-feeding by sardine is energetically inexpensive compared to particulate-feeding at a given swimming speed (van der Lingen 1995), whereas particulate-feeding is the energetically inexpensive feeding mode for anchovy (James *et al.* 1989). Barange and Hampton's (1997) study further substantiates the hypothesis that anchovy are primarily particulate-feeders, whereas sardine predominantly filter-feeders. Particulate feeding is also the primary feeding method of round herring. Feeding competition between sardine and anchovy affect their abundance (Hutchings *et al.* 2012).

1.4.2 Mesopelagic fish

Mesopelagic fish are schooling species whose distribution extends over the shelf region. They are caught around the St Helena Bay area with the small-meshed anchovy nets that were introduced in 1966 (Crawford *et al.* 1987). Lanternfish *Lampanyctodes hectoris* and lightfish *Maurolicus muelleri* are opportunistic feeders, although some mesopelagic species seemingly demonstrate a degree of selectivity (Merrett and Roe 1974).

Mesopelagic fish have a significant part to play in the food-web of the Benguela ecosystem, mostly as a linkage between zooplankton communities and particularly larger marine predators, including commercially vital species like hake (Ahlstrom 1969). Mesopelagic fish fall prey to most demersal fish, cephalopods, large horse mackerel, large pelagic fishes such as tuna and snoek, and also to seabirds. Given their importance in the ecosystem, together with the fact that mesopelagic fish are caught as bycatch in the small pelagic purse seine fishery and were successfully caught during a pelagic trawl experiment, the Small Pelagic Scientific Working Group of DAFF has recommended that an annual combined

Precautionary Upper Catch Limit (PUCL) of 50 000 t apply to the two main mesopelagic species (Coetzee 2016).

Lanternfish is the most abundant and narrowly distributed of mesopelagic species in the southern Benguela upwelling area (Hulley 1986). Crawford (1980) has reported that the lanternfish catches are hard to process because of their high oil-content. In contrast, lightfish have an extensive distribution in the southern Benguela upwelling region, and also occur in the traditional commercial fishing regions of Saldanha Bay and St Helena Bay. The biomass of lanternfish and lightfish on the continental shelf area of the west coast of South Africa has been estimated annually during routine hydro-acoustic pelagic research surveys. These biomass estimates suggest a minimum combined biomass for these two species of 550 000 t to 2 000 000 t, with an average of 1 300 000 t per year (Coetzee 2016). Apart from catches taken during a pelagic trawl experiment in the 2010/2011 fishing season, landings of mesopelagic fish species by the purse seine fleet have remained very low.

Despite the high-grade fish meal and fish oil derived from these fish species, the pelagic purse seine fleet has had little success in catching these resources by means of the allowed purse seine gear (Coetzee 2016). An opportunity thus exists for further development of a directed fishery for these resources by means of midwater / pelagic trawl gear. However, because of the challenges, the fishing industry has not yet specifically targeted this species (Coetzee 2016).

1.5 Objectives of this study

St Helena Bay is one of the most studied sites in the Benguela upwelling region. Hutchings *et al.* (2012) used the SHBML data from 2000 to 2010 and included historical data from the 1950s to determine variability and change in temperature, oxygen, chlorophyll, hydrology, wind-forcing, phytoplankton and zooplankton. They reported that the *in situ* temperature measurements did not indicate any warming or cooling trend until 2005, yet satellite-derived temperature measurements suggested a noticeable cooling inshore. Hutchings *et al.* (2012) also reported that zooplankton abundance in St Helena Bay changed in species and size composition, peaking in summer, suggesting that the autumn decrease is a top-down effect of fish predation. The data from the SHBML used in Hutchings *et al*. (2012) were useful as they concluded that long-term trends indicate a climate change response that is subdued.

Lamont *et al*. (2015) used data from 12 stations of the SHBML from April 2000 to December 2011 to investigate the monthly climatology of vertical distributions of different oceanographic variables and different water masses. Lamont *et al*. (2015) assessed average monthly fluctuations of dissolved oxygen and temperature along the SHBML and also the important seasonal and cross-shelf variations in dissolved oxygen and temperature. Indeed, data from the SHBML were useful for addressing the relationship between temperature and dissolved oxygen. Seasonal environmental patterns of nearshore and offshore stations were determined using SHBML data, showing the seasonal nature of upwelling in St Helena Bay (Lamont *et al*. 2015).

Previous findings of long-term fluctuations in environmental variables, using SHBML data, have demonstrated decadal-scale variability in the ecosystem (Hutchings *et al*. 2012; Jarre *et al*. 2015). Hutchings *et al*. (2012) indicated a much reduced zooplankton abundance in autumn compared to summer, which suggests strong predation pressure by pelagic fish recruits on zooplankton. The depletion of oxygen in sub-thermocline waters has restricted epipelagic fish's habitat (recruits of sardine and anchovy), and deep-water hake might also be forced further offshore (Jarre *et al*. 2015). Lamont *et al*. (2015) warned that the 11-year time series along the SHBML was too short and prevented detailed discussion of a low oxygen water signal. Jarre *et al*. (2015) also highlighted the importance of updating oxygen time series published in Cockcroft *et al*. (2008). Therefore, long time series of SHBML data are important and useful for monitoring zooplankton, fish and other environmental variables in St Helena Bay and can also be used to help understand inter-annual and inter-decadal trends in fish species, as highlighted by Hutchings *et al*. (2012).

Hutchings *et al.* (2012) mentioned that intra-annual data of SHBML was needed because the bay is used by different life stages of different organisms, as also mentioned by Jarre *et al.* (2015), who illustrated the importance of bottom-water oxygen conditions that differ spatially and on seasonal, inter-annual and decadal time scales. Jarre *et al.* (2015) also elaborated how the considerable extent of oxygen-depleted bottom water denotes reduced productivity of rock lobster, and extended recovery periods for their population. Blamey *et al*. (2012) also added that the deteriorating oxygen conditions could possibly influence the reduction of rock-lobster growth rates. Additional depletion of oxygen to <0.5 $mL.L^{-1}$ could result in toxic outbreaks and walkouts of rock lobster (Cockcroft *et al.* 2008). Several recent studies, including Hutchings *et al.* (2012) and Jarre *et al*. (2015), have thus concluded that there is no indication of a long-term climatic trend in St Helena Bay, although there are effects of inter-annual variability and decadal-scale change.

This study is aimed at determining seasonal patterns in the density of pelagic fish and zooplankton along the SHBML. Observed seasonal differences in fish abundance will be compared to seasonal variation of zooplankton abundance and oceanographic (environmental) variables in the area. The main objective was to determine the relationship between fish abundance, zooplankton biovolume and environmental variables (SST, chlorophyll and oxygen). The results will be used to infer whether increased zooplankton results in denser schools of small pelagic fish. This is an exploratory study that aims to investigate whether acoustic data collected along the SHBML can be used to define food web purpose and structure on seasonal scales.

2. MATERIALS AND METHODS

The methods below describe the protocols for collecting and processing data from the SHBML; these data were made available to me for analysis in this project. I also participated in some cruises and data collection from 2007.

2.1 Study area

The SHBML is situated between 32°S; 16°E and 32°S; 18°E and was sampled at monthly intervals from offshore (1450 m depth) to inshore (18 m depth) from 2000 to 2009. The vessel in use followed a 100 nautical mile (nm) straight line with 12 environmental stations (Figure 2). Greater emphasis was on environmental than fish sampling; there were no trawls made during sampling for fish identification. An average of 48 hours was typically taken to complete the sampling of this line. The best usable acoustic data for the line were collected during pelagic recruit and spawner biomass surveys because echo sounders were calibrated before, during or after the survey.

2.2 Underway acoustic data collection

Hydro-acoustic data were collected along the SHBML from 2000 to 2009 when monthly environmental sampling was conducted. In this study, acoustic data collected during the autumn pelagic recruit (May/June) and spring spawner biomass (October/November) surveys onboard the fisheries research vessels *FRS Africana* and *FRS Algoa* were analysed. Raw acoustic data were recorded with Simrad ER60 multi frequency split-beam scientific echosounders at 18, 38, 120 and 200 kHz. The system incorporates echoes in real time with a vertical resolution of 1 metre and yields the mean volume back-scattering strength (MVBS) in selected channels at the end of each logging cycle. Primary calibration of the echo-sounders of all research vessels used for data collection was accomplished by calculating the echo received from a 60-mm diameter tungsten or copper sphere with the known target strength at 38 kHz. Secondary calibrations were carried out, when necessary, during or after the cruise.

High resolution acoustic data at 38 kHz (inter-connected to a custom-made digital integration and logging system, logged and analysed using Myriax Echoview® software) were used to evaluate the relative abundance of major epipelagic and mesopelagic fish species (Figure 7). One nautical mile of acoustic data collected before the vessel reached station were added to another nautical mile of acoustic data collected after the vessel left the station; the sum was used as on-station fish biomass. Acoustic data were changed to Nautical Area Scattering Coefficient (NASC – m^2/nm^2), which is a proxy measure representing fish biomass. NASC is the area backscattering coefficient (ABC - m^2/m^2) scaled by 4π and 1 nautical mile squared (MacLennan *et al.* 2002).

2.3 On station bongo net deployment

When the vessel was on station, paired bongo nets were deployed vertically to sample zooplankton. The bongo nets had a diameter of 0.57m fitted with 300 µm meshed nets. The net was hauled through the water column from the maximum bottom depth of 200m to the water surface at a retrieval rate of 1 metre per second. An electronic flowmeter fixed in the centre of the mouth of one net was used to record water volume sampled. Zooplankton samples were condensed and preserved in seawater solution poisoned with buffered 5% formalin for further laboratory analysis. All the samples were labelled with place, date, method and time of collection.

2.4 Laboratory analysis of zooplankton

Zooplankton biomass was estimated as displacement volume or wet weight, and then converted into dry weight using conversion factors (Huggett 2014). In the laboratory, zooplankton samples were transferred into quantifying cylinders and left to settle for 24 hours, and thereafter the settled volume was recorded. Dividing the settled volume by the total volume filtered through the net was the formula used to calculate Biovolume concentration. Zooplankton samples were then separated into two halves using a Folsom splitter, with half used to determine / calculate wet and dry biomass, and the other one half retained for microscopic investigations of taxonomic composition. Wet biomass was confirmed after sample filters were blotted on paper towel to eliminate surplus water. Samples were then dried for 24 hours at 60°C and re-weighed. Zooplankton's wet and dry biomass concentrations were calculated by dividing the sample weights by the volume filtered.

2.5 On-station environmental sampling

A Neil Brown MK 3B conductivity-temperature-depth (CTD) instrument with 12 rosette bottles was lowered vertically at each station from the surface to a maximum depth of 200m or near the bottom to provide profiles of depth (m), salinity (PSU) and temperature (°C). Water samples were also taken to determine dissolved oxygen ($mL.L^{-1}$) at regular depth intervals. Typically, CTD data was calibrated against bottle data. The Winkler method was used to determine the concentration of dissolved oxygen, using acid to counteract the possible presence of nitrites. A Chelsea Instruments Aquatracka submersible fluorometer mounted on a magnum rosette was used to obtain fluorescence profiles. Chlorophyll ($mg.m^{-3}$) was determined by collecting water samples at the surface and at the fluorescence maximum. Chlorophyll samples were immediately analysed or analysed within 6 hours following the method of Parsons *et al.* (1984). Sampling was performed during both the day and night.

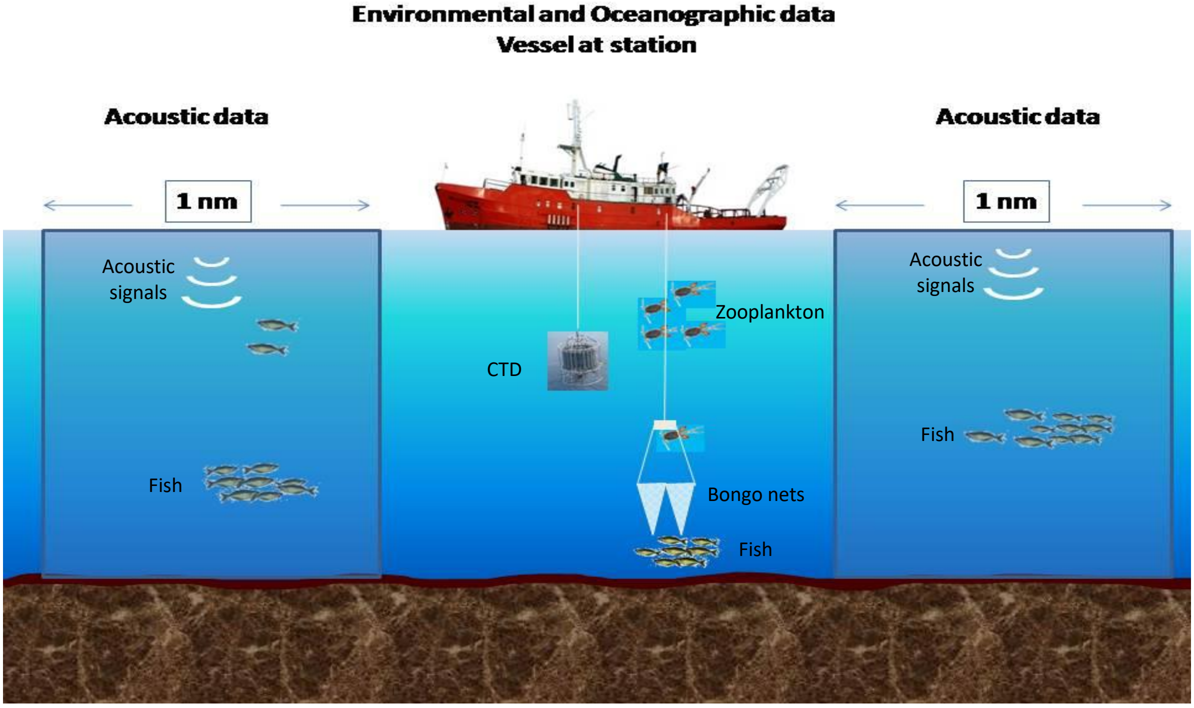


Figure 7: Schematic description of data collection at each station (modified from Lezama-Ochoa *et al.* 2010)

2.6 Data analysis

At times, for some of the SHBML stations, acoustic raw data, zooplankton data or environmental data were not collected due to equipment malfunction or human error. Most errors were experienced during winter surveys, otherwise all 12 stations along the SHBML were sampled correctly and usable data are available. From the acoustic data observations, echograms of fish targets were classified as epipelagic fish or mesopelagic fish, since there were no directed acoustic trawls on the SHBML to allocate fish species accordingly. Closest trawls from the adjacent spawner biomass survey lines, recruit survey lines or commercial vessel trawls were used to define species composition and size distributions of acoustic echogram or targets. For this project, surface environmental data such as oxygen, chlorophyll and temperature were used.

The Ocean Data View (ODV) software package was used for the interactive analysis, exploration, and visualization of all oceanographic time-series data, and also fish and zooplankton biomass time-series. The most common Loess smoothing method was used to smooth volatile oceanographic time series (Cleveland *et al.* 1990). It is a non-parametric method where least squares regression is performed in localized subsets, which makes it a suitable candidate for smoothing. Smoothing was used to remove noise from the data set, allowing important patterns to stand out. The ‘ggplot2, plyr and reshape2’ packages in the R statistical software were used to determine the optimal amount of smoothing. Statistical analysis was performed using a General Linear Model (GLM) approach to model the relationship between fish and zooplankton, and fish and other environmental variables (R Development Core Team 2009). Most variables were log-transformed to get a normal distribution of values.

Pearson product-moment correlation coefficients were used to establish the relationships between small pelagic fish abundance and other variables (zooplankton, chlorophyll, SST and oxygen) collected on station. The Pearson product-moment correlation is a measure of the strength of a linear relationship between two variables (Hinkle *et al.* 2002); the Pearson correlation coefficient *r* measures the strength of the correlation.

3. RESULTS

Out of a possible 120 sampling events, 98 were successfully completed in winter for fish and zooplankton, and 95 for fish and 104 for zooplankton in summer (Table 1). In total, 605 out of a possible 720 environmental samples were successfully completed for the 10-year period (four months of additional environmental data were added to the already-sampled winter and summer data, as summarised in Table 1).

Table 1: Total number of stations out of 12 sampled successfully for fish (and zooplankton in brackets) during winter (May–July) and summer (October–December); and also environmental data during selected months from 2000 to 2009.

	Fish & (Zooplankton)		Environment					
Year	**Winter**	**Summer**	**March**	**April**	**Winter**	**August**	**Sept**	**Summer**
2000	6 (6)	11 (12)	6	12	9	11	10	11
2001	4 (4)	8 (8)	12	10	11	12	7	8
2002	10 (10)	12 (12)	12	12	10		12	12
2003	9 (9)	12 (12)			7	10	12	10
2004	10 (10)	10 (12)	12	11	10	12	12	12
2005	11 (11)	10 (12)	8	8	10	10	12	12
2006	12 (12)	12 (12)	12	6	10	12	10	11
2007	12 (12)	7 (12)	12	12	12	12	9	12
2008	12 (12)	7 (0)	12		12	12	12	12
2009	12 (12)	6 (12)	10	12	12	12	12	12
Total	**98 (98)**	**95(104)**	**96**	**83**	**103**	**103**	**108**	**112**

The majority of offshore stations along the SHBML transect indicated warm SST during winter, and cool SST in summer (Figure 8a). This was opposite to the temperatures at the nearshore stations, particularly the first four stations (stations 1, 2, 3, and 4) which showed coldest temperatures during summer and slightly warmer temperatures in winter. In the summer of 2002 and 2004 both inshore and offshore stations were cooler than normal with the SST of inshore stations <12°C.

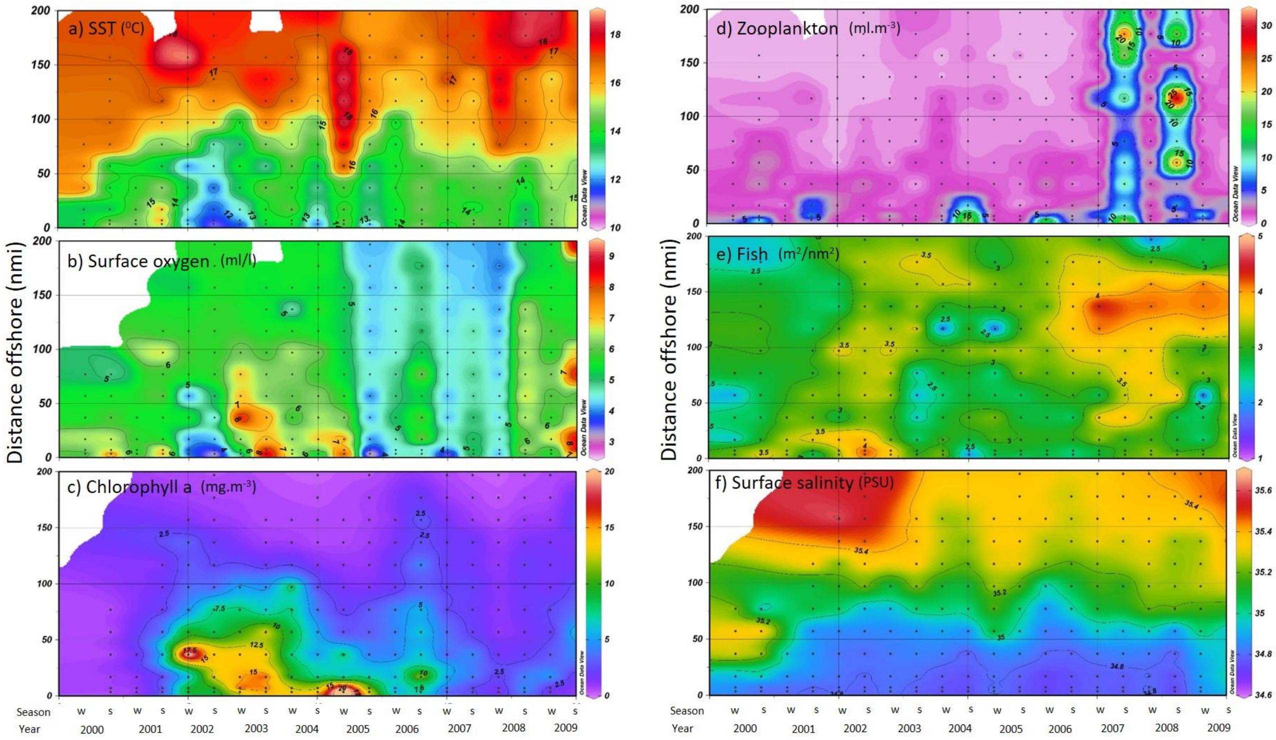


Figure 8: Variability of (a) sea surface temperature, (b) surface oxygen, (c) surface chlorophyll, (d) zooplankton and (e) fish on a seasonal basis at all stations, 2000–2009. Dots indicate SHBML stations; x axis is winter or summer data on the station.

Most stations of the SHBML from 2000 to 2009 have surface dissolved oxygen that is constantly above 4 mL.L^{-1} (Figure 8b), which is suitable for all marine creatures. Seasonal differences of surface dissolved oxygen were apparent between the offshore and coastal stations (Figure 8b); in winter, variations of surface dissolved oxygen between the nearshore and offshore environment were slightly noticeable. Inshore oxygen concentrations were high in a few places and sometimes very low but there was no obvious observed pattern. There is very little noticeable variation in surface dissolved oxygen over an extensive range of temperatures throughout the surface water column in the offshore area, particularly from 2002 to 2004. Some periodic variation in dissolved oxygen was apparent from 2005. The lowest oxygen concentrations were in the offshore warm water region where temperature was above 14°C.

Highest chlorophyll concentrations occurred in the inner shelf (station 1 to 5) during winter, with average chlorophyll concentrations >5mg.m^{-3}. Over the outer shelf, chlorophyll concentrations were generally low (<2mg.m^{-3}) (Figure 8c). Furthest offshore was where the lowest chlorophyll (<0.5mg.m^{-3}) was recorded, coinciding with warm water (>20°C) during both winter and summer. Constant high chlorophyll concentrations generally occurred at the inshore stations, especially between 2002 and 2007, but with occasional low chlorophyll signals.

The largest chlorophyll values at the surface (Figure 8c) coincided with reduced fish biomass (Figure 8e), and increased fish biomass was recorded at low chlorophyll concentrations; there were no obvious patterns. In 2002 chlorophyll and fish abundance were high (Figure 8c and e) whereas in 2004 zooplankton abundance was high (Figure 8d). A consistent high density of zooplankton nearshore during summer was noted (Figure 8d) except in 2007 and 2008 when it also extended offshore. High fish abundance was observed inshore when SST was below 12°C (Figure 8e).

Lowest surface salinity concentrations occurred in the inner shelf during both summer and winter (Figure 8f). Maximum surface salinity coincided with warm SSTs at offshore stations during both winter and summer.

3.1 Cross shelf patterns in environmental variables

The average patterns across the stations from inshore to offshore (Figure 9) indicate that average SST at inshore stations, i.e. the first five stations is below 14.5°C (Figure 9a) during both winter and summer. Maximum surface oxygen concentrations were found at inshore stations during both winter and summer, although oxygen concentrations are very variable (Figure 9b). Reduced surface oxygen concentrations coincide with warm SSTs, at offshore stations during both winter and summer.

Maximum chlorophyll concentrations were found at inshore stations during both winter and summer. During summer, chlorophyll concentration measurements from all stations were close to the summer average while in winter they were more variable (Figure 9c). Lower chlorophyll concentrations coincide with warm SSTs at offshore stations during both winter and summer.

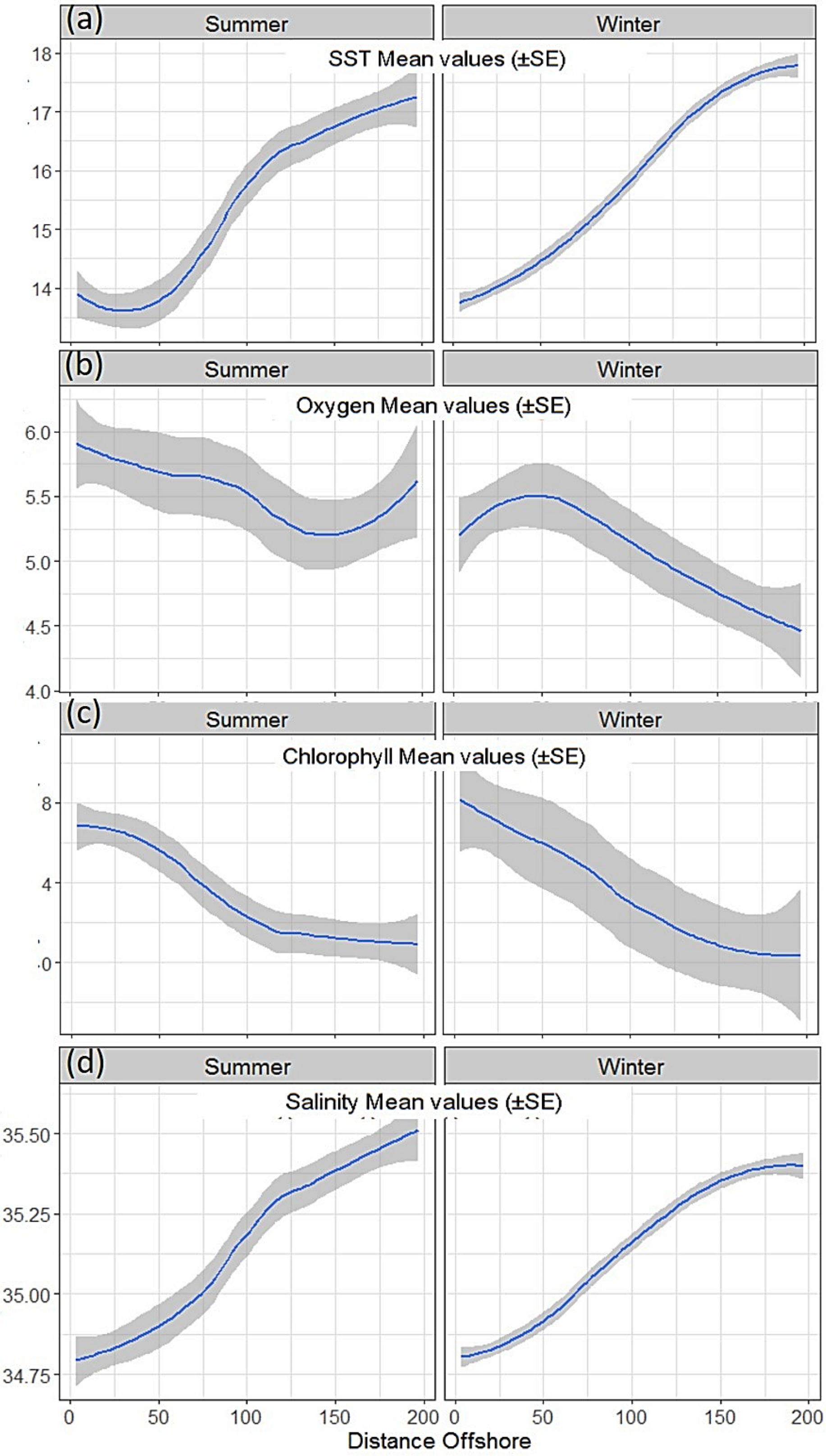


Figure 9: Smoothed winter and summer means (solid lines) and standard errors (shaded areas) are shown for environmental variables, using Loess smoothing functions. (a) SST (°C), (b) Oxygen (mL.L^{-1}), (c) Chlorophyll (mg.m^{-3}) and (d) Salinity (PSU). Estimated smooth functions over distance offshore in nautical miles.

Mean surface salinity distributions indicated higher salinities at offshore stations during summer and winter. The lowest salinity on station 1 was noted in summer 2008 and highest salinity was found in winter 2009 whereas at station 12 lowest was found in winter 2007 and highest was noted in summer 2002. During summer salinity measurements vary about the average summer values contrary to winter salinity data for all stations. Similar salinity measurements were observed for both summer and winter in almost all stations except the last two stations where salinity was slightly lower in winter than in summer (Figure 9d).

Environmental parameters affect one another in many different ways. It is known that evaporation increases salinity while the addition of freshwater decreases salinity. Different measurements of SST along the SHBML show relationships with other environmental parameters, as shown in Figure 10. Figure 10a show a strong positive linear relationship nearshore between SST and salinity during winter. Similarly, Figures 10b and 10h also show a positive linear relationship further offshore between SST and salinity during both winter and summer. There was no correlation between SST and salinity during summer in the nearshore waters (Figure 10g).

Surface oxygen concentrations during winter correlate positively with SST in the nearshore stations (Figure 10c) contrary to the negative correlation that was noticed in summer nearshore (Figure 10i). Surface dissolved oxygen show a strong negative linear relationship with SST further offshore during winter (Figure 10d). There is no relationship between SST and surface oxygen in the offshore stations during summer. The pattern in Figures 10e, 10f, 10k and 10l showed a clear linear relationship between SST and chlorophyll concentrations, with surface chlorophyll concentrations increasing linearly with a decrease in temperature at all stations from winter to summer.

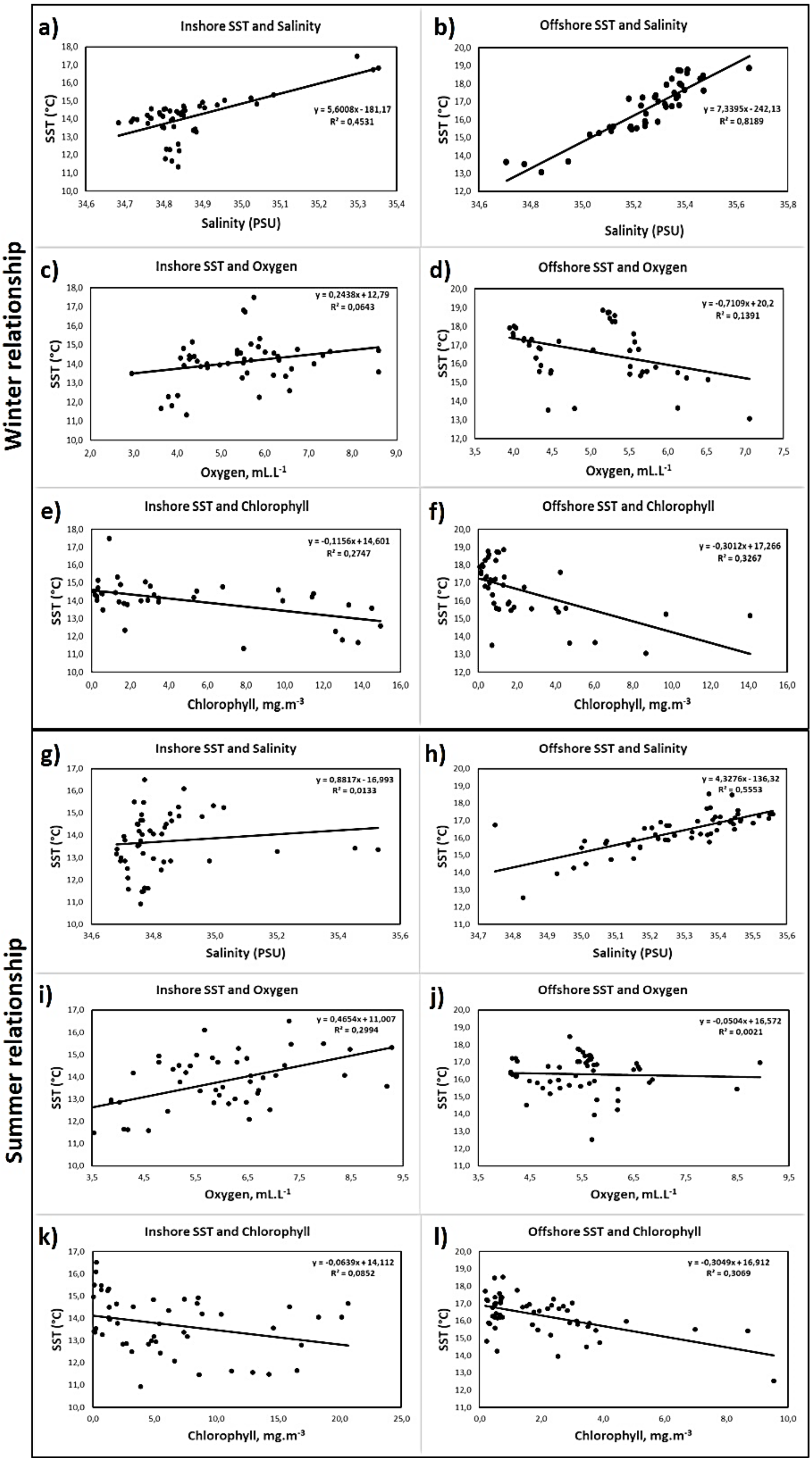


Figure 10: Relationship between SST and three environmental parameters (surface salinity, surface dissolved oxygen and chlorophyll) on the inshore (stations 1 – 5) and offshore stations 6 – 12) during both winter and summer of all stations from 2000 to 2009**.** Regression lines are also shown.

3.2 Relationships between fish and other variables

Small pelagic fish density showed no correlation with zooplankton abundance nearshore stations (1 – 5) in winter and summer. Further offshore stations (6 - 12) there was a noticeable positive linear relationship between fish and zooplankton in winter while a strong negative relationship was observed during summer (Table 2).

Table 2: Summary of regression analyses for relationships between log transformed fish data and other variables (zooplankton, chlorophyll, SST, salinity and oxygen) at 95% confidence level in nearshore and offshore waters during winter and summer.

	Variable	**Winter**			**Summer**		
		df	***r***	***P***	**df**	***r***	***P***
Inshore	Zooplankton	48	-0,051	0,727	49	0,045	0,758
	SST	48	-0,358	0,012	49	0,014	0,922
	Salinity	48	-0,490	0,000	49	-0,018	0,899
	Oxygen	48	-0,031	0,840	49	-0,151	0,295
	Chlorophyll	43	-0,078	0,595	49	-0,323	0,022
Offshore	Zooplankton	44	0,194	0,201	43	-0,104	0,502
	SST	41	-0,195	0,216	41	0,001	0,997
	Salinity	41	-0,179	0,256	35	0,205	0,229
	Oxygen	41	-0,046	0,771	36	-0,284	0,089
	Chlorophyll	41	0,005	0,975	36	0,083	0,624

During winter, pattern showed a clear negative relationship between fish and SST throughout SHBML stations in contrast with no relationship in summer throughout all stations. Similarly a strong negative relationship between fish and salinity was observed in winter throughout SHBML stations. In summer, a clear linear relationship was observed in offshore stations whereas no relation nearshore (Table 2).

Highest oxygen concentration was observed when fish density was low. In winter, there was no relationship observed between fish density and the two parameters (surface dissolved oxygen and chlorophyll) across all stations. The strong negative relationships was observed between fish and the two parameters during summer at both inshore and offshore stations.

3.3 Relationships between chlorophyll and other variables

Substantial variability in chlorophyll concentrations was detected during all surveys. High chlorophyll concentrations occurred nearshore where cooler SST was recorded (Figure 11a). Chlorophyll concentration was at a peak in winter (2002, 2003, 2005, and 2007) and in summer (2008). Chlorophyll maximum concentrations of above 20 mg.m^{-3} were attained when SST was below 15°C. When SST was warm (at offshore stations, SST > 15°C), chlorophyll concentrations were reduced. Higher chlorophyll concentrations were found where zooplankton abundance was very low (Figure 11b).

The warm offshore temperatures (>19°C) also coincide with reduced chlorophyll concentrations (<2.5 mg.m^{-3}). There is a negative correlation between chlorophyll and SST (Figure 12a, df = 193, r = -0.549, $p<0.001$) but no correlation between chlorophyll and zooplankton abundance (df = 211, r = 0.050, $p>0.05$).

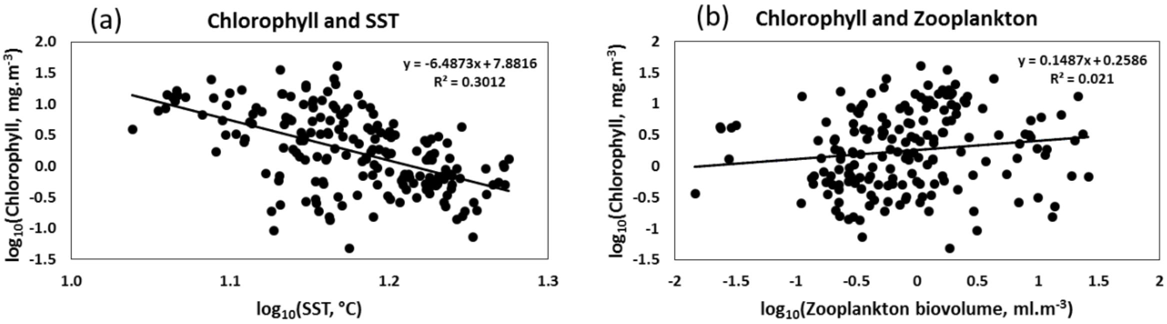


Figure 11: The relationships between log-transformed variables. (a) chlorophyll and SST, (b) chlorophyll and zooplankton biomass. Regression lines are also shown.

Most inshore stations (the five stations closest to the coast) along the SHBML transect had cooler surface temperatures during summer than in winter. Offshore stations showed warm average temperatures in winter, while cool average surface temperatures were observed in summer (Figure 12b).

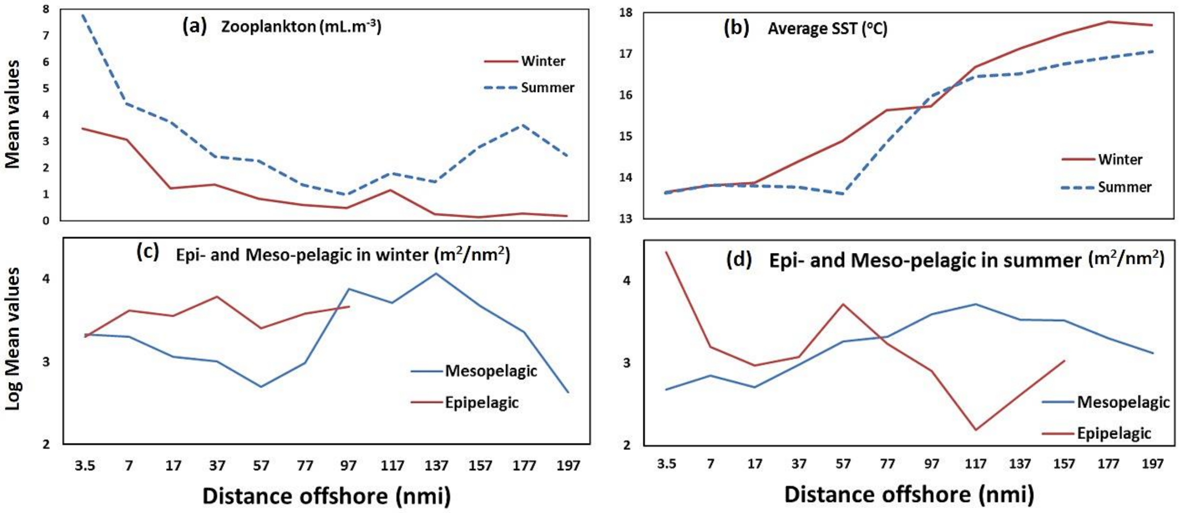


Figure 12: Mean values from 2000 to 2009 in winter and summer of (a) zooplankton biovolume (b) SST. (c) epi- and meso-pelagic fish biomass in winter and (d) epi- and meso- pelagic fish biomass in summer.

Epipelagic fish dominated the inshore stations whereas mesopelagic fish dominated offshore stations during winter and summer surveys (Figure 12c and d). Results also show that the distribution of epipelagic fish was further offshore during summer than winter, most likely with pelagic recruits found close inshore and adult spawners offshore. Mean zooplankton biovolume for all stations was higher in summer than in winter (Figure 12a and also Figure A5, Appendix). Increased zooplankton biovolumes (>2.0 mL.m^{-3}) were associated with cool water (<14°C) inshore whereas low zooplankton biovolumes (<2.0 mL.m^{-3}) were associated with warmer surface temperatures offshore. Zooplankton biovolume was typically highest, but highly variable, at the first two inshore stations (Figure 12a). Mesopelagic fish were found in high abundance offshore where SST was above 16°C during winter and summer (Figure 12c and 12d). The results of the GLM investigating the influence of environmental variables and zooplankton biovolume on pelagic fish biomass showed a significant effect for zooplankton (Table 3).

Table 3: Results of the GLM explaining effects of zooplankton biovolume, chlorophyll, SST and oxygen concentrations on pelagic fish density, with parameter estimates, their standard errors and corresponding t statistics and probabilities.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	3.771	0.643	5.867	2.5e-08
Zooplankton	-0.033	0.017	-1.980	0.049
Chlorophyll	-0.017	0.011	-1.550	0.123
SST	-0.003	0.040	-0.065	0.948
Oxygen	-0.066	0.052	-1.270	0.206

3.4 Horizontal distributions of fish and zooplankton

Sampling the SHBML takes almost 24 hours, providing an opportunity to observe the schooling behaviour of small pelagic fish and zooplankton during the day and also at night. Diel vertical migration of small pelagic fish and zooplankton was particularly noticeable during the night at station 2 (Figure 13). Small pelagic fish and zooplankton are well-known to form schools or aggregations during the day (Figure 13a) and then scatter or disperse during the night (Figure 13b).

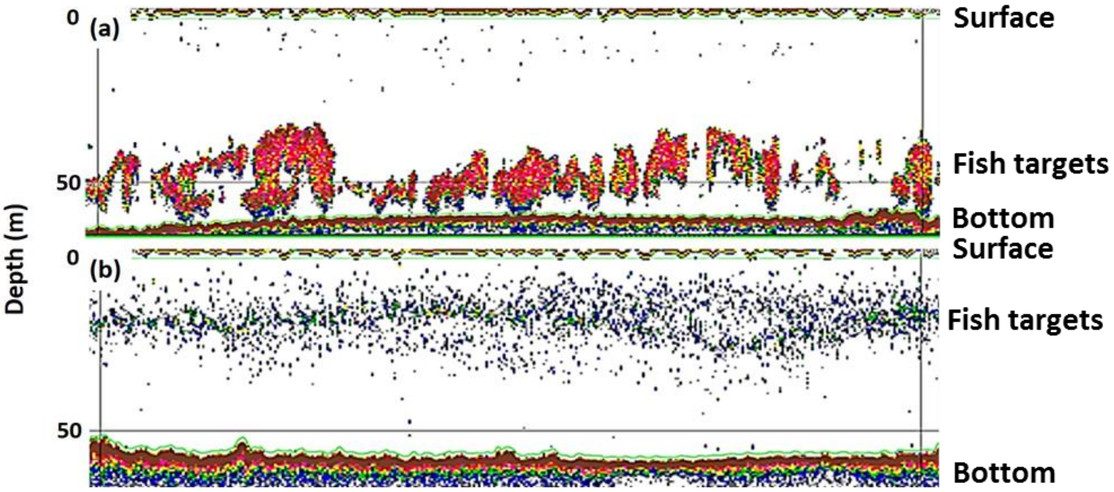


Figure 13: One nautical mile echogram at station 2 during winter sampling of the SHBML (a) in 2003 during the day and (b) in 2004 at night.

4. DISCUSSION AND CONCLUSION

A wealth of research on this productive eastern boundary upwelling ecosystem has been conducted in recent years, like all other upwelling systems that have dramatic quantities of plankton-feeding fish. In contrast to previous studies where data from the SHBML have been used to determine and distinguish only environmental, zooplankton and hydrographic variability in St Helena Bay (Hutchings *et al.* 2012; Lamont *et al.* 2015), fish biomass was also considered in this project.

The SHBML has provided monthly estimates of zooplankton density and in situ data collection of important ocean environment variables. Useful monthly estimates of small pelagic fish biomass in the region were also provided in this study. A constant year-round sampling of small pelagic fish from the same location could offer valuable data in order to observe seasonal variability in a number of fish biological characteristics and also to obtain a time series of epipelagic and mesopelagic fish abundance along the SHBML.

The most important gains of sampling the SHBML have been the direct assessment of abundance of zooplankton and associated accuracy, and also the creation of information on distribution, population structure and migration of zooplankton. In addition, research surveys around St Helena Bay area have also stimulated ocean environment investigations and small pelagic fish migration and abundance research. The major acoustic problems that required attention were lack of consistent acoustic quality data and an improvement of calibration accuracy before or after sampling this important marine ecology line.

Shillington *et al.* (2006) mentioned that the oceanography of St Helena Bay is highly vigorous and multifaceted, displaying greater variability than other upwelling ecosystems. The Bay of Biscay has similar physical factors to St Helena Bay, but displayed differing inshore‒offshore shifts, as zooplankton biomass increased towards deep-sea waters and small pelagic fish biomass decreased (Lezama-Ochoa *et al.* 2010). The Humboldt Current System also displays similar patterns of trends with zooplankton biovolume greater offshore than on the shelf (Ayón *et al.* 2008).

Limited seasonal patterns were determined in the density of pelagic fish and zooplankton along the SHBML (Figure A3, A4 and A6, Appendix). There is a lack of obvious seasonal patterns in Figure 8, therefore some investigations are inconclusive. Observed seasonal differences in fish abundance were compared to seasonal variation of zooplankton abundance and some environmental variables in the area. Fluctuations of environmental data were noticed with no major changes over a decade of SHBML sampling, although there is evidence of episodic events. There were, most often, obvious coastal patterns of cool SST, higher chlorophyll and higher zooplankton biomass. These are the essence of a coastal upwelling ecosystem, as defined by Arístegui *et al.* (2009) for the Canary coastal upwelling ecosystem, as eastern boundary upwelling ecosystems are among the most productive zones of the ocean. High primary productivity is stimulated by nutrient-rich upwelled water appearing as phytoplankton growth, which also sustains higher trophic level species including pelagic fish, birds, seals and whales (Arístegui *et al.* 2009).

The results show partial seasonality of SST in the offshore region and also in coastal stations along the SHBML. Zooplankton, chlorophyll and oxygen show some seasonal signals only in nearshore stations (Figure 8). Strong cross-shelf patterns of SST, zooplankton, chlorophyll, salinity, oxygen and fish density, which are important drivers of oceanic ecology, display a significant disparity across a variety of time and space scales, creating a complex spatial and temporal pattern of trends (Thompson *et al.* 2017) visible in Figures 9 and 12. These patterns are similar to findings that Lamont *et al.* (2015) reported. Contrasting patterns of SST and also surface salinities were detected at nearshore stations. Higher salinity values were found in winter and lower values were recorded during summer. Salinity from the inner five stations in St Helena Bay show a salinity maximum in summer contrary to Hutchings *et al.* (2012) who reported salinity maximum in winter.

Inshore seasonal signals from environmental variables, including SST suggest that the SHBML can be used to detect seasonality. Ayón *et al.* (2008) proposed that zooplankton biovolume is positively correlated with seasonal SST in the Humboldt Current System, and thus persistent upwelling may be an adverse factor for zooplankton abundance. Indeed, strong cross-shelf patterns of SST, zooplankton, chlorophyll, salinity, oxygen and fish indicated that the seasonal signal might be overwhelmed by inter-annual variability and inshore-offshore differences along the SHBML (Figures 9 and 12).

The relationships between fish abundance and environmental variables (SST, chlorophyll and oxygen) and zooplankton biomass were also determined. The spatial surface data of all environmental variables were analysed and compared to temporal scales of fish and zooplankton biomasses. There was no relationship between small pelagic fish biomass and the environmental variables. The results suggest that dense schools of small pelagic fish are associated with decreased zooplankton densities which confirm that the SHBML can be used to define food web purpose and structure on seasonal scales.

When relationships between variables were determined in this study, two pairs of environmental variables show relationships: surface salinity and SST (Figure 10b), and chlorophyll and SST (Figure 11a). The negative correlation of surface salinity and SST in SHBML is similar to one reported by O'Brien (2017) in the Chile-Peru Current System. Conversely, in the western North Pacific, warmer SST was mostly linked to a decrease in surface salinity (Chiba *et al.* 2006). The determined negative relationship between chlorophyll and SST in Figure 12a is similar to one reported by O'Brien *et al.* (2011) in the California Current System. In addition, a few small upwelling regions identified as productive across the Indian Ocean showed areas of declining SST and an increase in chlorophyll (Carr *et al.* 2006). The above environmental variables do not cause the other to increase or decrease but are both driven by an increase in upwelling and powerful winds or are both related to nutrient enrichment.

When all variables were examined in pairs and correlation determined (Figure 10, Table 2 and also Figure 11), then there was no significant relationship between zooplankton and surface chlorophyll at offshore stations. Similarly, the California Current Ecosystem has no significant correlation between zooplankton biovolume and chlorophyll as reported by Ross *et al.* (2017).

Chavez and Messié (2009) found direct relationships between chlorophyll and fish for the California Current Ecosystem and comparisons for the Humboldt Current Ecosystem indicate similar and strong links. Lamont *et al.* (2015) confirmed the relationship between oxygen and SST, revealing two noticeable diverse linear patterns. Firstly, the relationship exhibited very little dissolved oxygen variation over an extensive range of temperatures whereas the second pattern displayed a strong linear relationship, with dissolved oxygen concentrations increasing linearly with a rise in temperature. In contrast, O'Brien (2017) reported that dissolved oxygen generally shows negative correlations with SST in the Humboldt Current System. These positive and negative linear relationships between SST and oxygen mentioned above were not noticed in this project.

The oceanography of the inshore waters in SHBML was expected to have cold surface water as it is dominated by an upwelling system (Barton *et al*. 2013). Average temperatures tended to be cooler during summer months than in winter (Figure 12b). Greatest number of offshore stations along the SHBML transect indicated cool temperatures during summer and warm temperatures in winter (Figure 12b). In contrast, temperatures at the nearshore stations, particularly the first three stations (stations 1, 2 and 3) showed a different pattern, with similar average cold temperatures during both summer and winter. These are expected patterns from a coastal upwelling region where enhanced upwelling is expected during summer.

Most stations of the SHBML from 2000 to 2009 have surface dissolved oxygen that is constantly above 4 mL.L^{-1} (Figure 9d and 9f), which is appropriate for all marine living beings. The Humboldt Current system is the oldest with little publications (Chavez and Messié 2009) and has extremely low oxygen that spreads close to the surface water. This can be contrasted with the high oxygen concentrations found in the Benguela Current system, which also has the highest surface chlorophyll concentrations, followed by the Humboldt and Canary Systems (Chavez and Messié 2009).

Highest chlorophyll concentrations were apparent in the inner shelf (station 1 to 5) during winter and summer, with average chlorophyll concentrations > 5 mg.m^{-3} (Figure 9c and 9g). The observed general trend of high chlorophyll concentration near the coast shifting to smaller concentration offshore reflects the efficiency of high productivity in this upwelling region (Figure 9).

In general, mean zooplankton biovolume for all the years was higher in summer than in winter (Figure 13a). Higher coastal zooplankton biovolume was often noticed in summer in this data set (Figure 13a). Similarly, Ayón *et al.* (2008) also reported higher zooplankton biovolumes during the night and from the shelf break to 100 km offshore; and also in summer than in winter which is in line with improved primary production in austral summer in the Humboldt Current System (Daufresne *et al.* 2009).

Epipelagic fish dominated the inshore stations in winter and summer surveys. In contrast, mesopelagic fish dominated all offshore stations during winter and summer surveys (Figure 12c and 12d). Results also show that the distribution of pelagic fish is further offshore during the summer than winter, while pelagic recruits are found close inshore. Maximum density of small pelagic fish was found nearshore during winter whereas in summer highest abundance is found offshore (Figure A3, Appendix). This was also supported by Hutchings *et al.* (2012), by indicating that recruits and juvenile small pelagic fish occurred in the productive inshore waters of St Helena Bay. Van der Westhuizen (2011) also added that highest pelagic fish catches in St Helena Bay are still made in winter but are consisted of mainly juvenile anchovy with a small bycatch of juvenile sardine and juvenile redeye. Highest peak of small pelagic fish in summer is found offshore of St Helena Bay, Hutchings *et al.* (2012) also indicated that adult small pelagic are widespread offshore of St Helena Bay in summer before moving south to spawn in winter.

GLM results of this study in Table 3 indicate no relationship between fish and zooplankton. Table 2 showed no correlation between fish and zooplankton nearshore stations (1 – 5) in winter and summer but further offshore stations (6 - 12) there was a noticeable positive linear relationship in winter and a strong negative relationship in summer, whereas Lezama-Ochoa *et al.* (2010) found that fish and zooplankton were certainly interrelated at a small scale (<30 nautical miles) and negatively correlated at a bigger scale (> 30 nautical miles) in the Bay of

Biscay. Zooplankton biomass decreased towards offshore stations during both winter and summer. In winter, recruits or juvenile fish biomass decreased towards oceanic waters and spawning fish biomass increased at offshore stations during summer (Figure 13c and 13d). Correa-Ramirez *et al.* (2012) also mentioned that there is a strong relationship between fish and zooplankton along the Humboldt Current System coastlines because of strong wind-induced upwelling results in great phytoplankton blooms, a substantial biovolume of zooplankton, and some of the world's largest annual small pelagic fish catches. In contrast, Winter and Swartzman (2006) demonstrated an inverse relationship between zooplankton biovolume and small pelagic fish near shore of the Pribilof Islands, Alaska.

There are mixed statistically significant relationships between fish and zooplankton including other environmental variables along the SHBLM in this study's results (Table 2 and 3). However unequal coverage of seasonal pelagic, zooplankton and environmental data might have limited the power of the analyses, which also would have been affected by the fact that the overall sample sizes of pelagic fish and zooplankton were relatively small. Indeed, environmental variables affect the distribution of fish. It is known that water temperature is an important factor in the environment of fish. It causes the activity levels of fish to increase or decrease, makes fish move into certain areas while avoiding others and influences feeding and reproductive activities.

The relationship between zooplankton and fish observed along the SHBML in this project illustrates either that small pelagic fish and zooplankton are distributed differently across inshore and offshore stations along the SHBML, or that the fish are negatively impacting the zooplankton. The southward migration of small pelagic fish to spawn on the Agulhas Bank during summer at peak upwelling may also contribute to the negative correlation between zooplankton and small pelagic fish. This negative relationship noticed offshore during summer could also indicate that zooplankton are in low concentrations after being preyed on by pelagic fish. Other studies demonstrated related direct effects of predation on the distribution and abundance of organisms in the marine ecosystem. For instance, Bertrand *et al.* (2004), provided direct indication of substantial predation of zooplankton by the small pelagic fish community in the Humboldt Current System areas. Useful seasonal patterns were determined in the densities of pelagic fish and zooplankton which include spatial surface environmental variables along the SHBML. Lezama-Ochoa *et al.* (2010) also reported that small pelagic fish and zooplankton biomasses displayed contrasting inshore - offshore tendencies, as zooplankton abundances increased towards offshore and pelagic fish density decreased.

The offshore negative correlation between zooplankton and small pelagic fish during summer appears to support Hutchings *et al.*'s (2009) contention that there is top-down control (i.e. predators control their prey) in St Helena Bay. This also supports the findings by Cury *et al.* (2000) who suggested that small pelagic fish exercise top-down control on their zooplankton prey, whereas there is inadequate proof of top-down control of forage fish in the Benguela ecosystem. Similarly, Ayón *et al.* (2008) provided clear evidence of a depletion effect at the local scale on zooplankton biovolume by high local densities of small pelagic fish in the Humboldt Current System. Ayón *et al.* (2008) further mentioned that pelagic fish biomass and zooplankton biovolume appeared to co-vary at a population level. However, zooplankton can exert a bottom up control on the small pelagic fish population, when locally abundant small pelagic fish can also induce local depletion of zooplankton abundance (Ayón *et al.* 2008).

Diel vertical migration of small pelagic fish and zooplankton was noted in this study, similar to the fish behaviour reported by Lezama-Ochoa *et al.* (2010), who conducted an acoustic study on spatial trends and scale-dependent relationships between zooplankton and pelagic fish in the Bay of Biscay. Fréon *et al.* (1996) found that, in the Catalan Sea (Spain), small pelagic fish scattering or dispersion is partial during the night and fish aggregations can still be detected. Fish schools are characterized by a highly irregular distribution of the cross-sectional region while there are only a few schools during the day with restricted real inconsistency, high values of packing density and a more regular shape. Apart from the small pelagic's impact on zooplankton biovolume, Ayón *et al*. (2008) indicated that, due to diel migration or daytime net avoidance, a significant and clearer diel effect on zooplankton biovolume can also be shown.

In conclusion, further temporal analyses of environmental variables is essential to be performed in order to understand significantly the mechanism responsible for the observed trends. Collection of sufficient quality, reliable data on zooplankton, pelagic fish, and all environmental variables should allow us to improve the observed results and better understand the trophic interactions. Ocean observations and monitoring are crucial in the development and substantiation of ocean and climate models used to forecast future ocean conditions. Ship-based biogeochemical data collection and time series yield highest quality biological, physical and chemical measurements that are required to distinguish climate change-driven patterns in the ocean, evaluate related influences on marine food chains and eventually advance our interpretation of changes in marine biodiversity and ecosystems; these parameters can also be measured simultaneously.

Zooplankton abundance and biomass vary substantially between months and years, and are impacted both directly and indirectly by the short- and long-term hydrographic and physical conditions of the marine environment. For example, local water temperatures can greatly influence the community structure and production of zooplankton, which, in turn, can lead to large seasonal, annual, and decadal changes in population size and geographic distribution. Maintaining and increasing the quantity of time series in these regions would improve the ability to recognise and evaluate the impacts of long- and short-term changes on marine ecosystems.

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Appendix

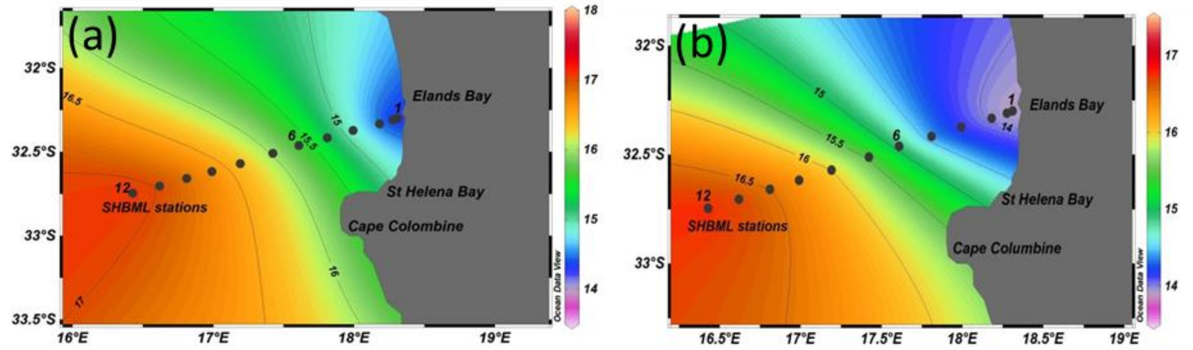


Figure A1: In situ average SST for both (a) winter and (b) summer sampling of SHBML stations. The dots indicate the SHBML stations (1 inshore to 12 offshore).

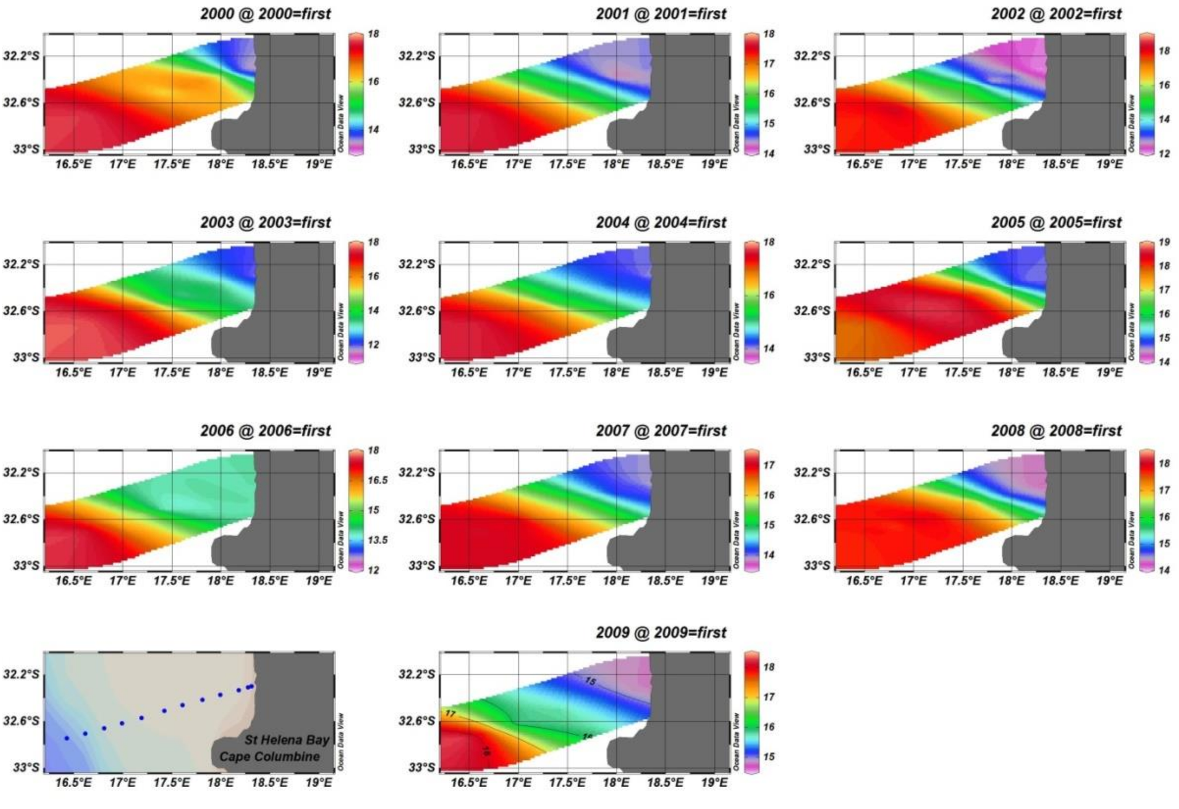


Figure A2: Yearly (2000 – 2009) SST in winter surveys at all stations. The dots indicate the twelve SHBML stations.

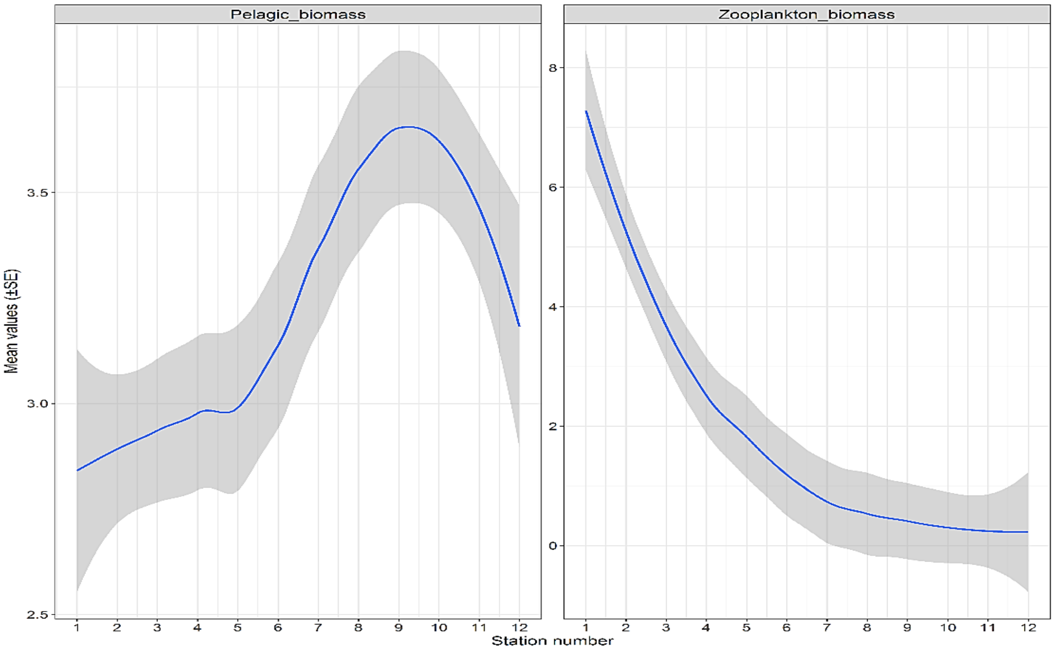


Figure A3: A smoothened average of pelagic and zooplankton biomasses in summer surveys at each station from 2000 to 2009. Grey area indicates standard error (SE).

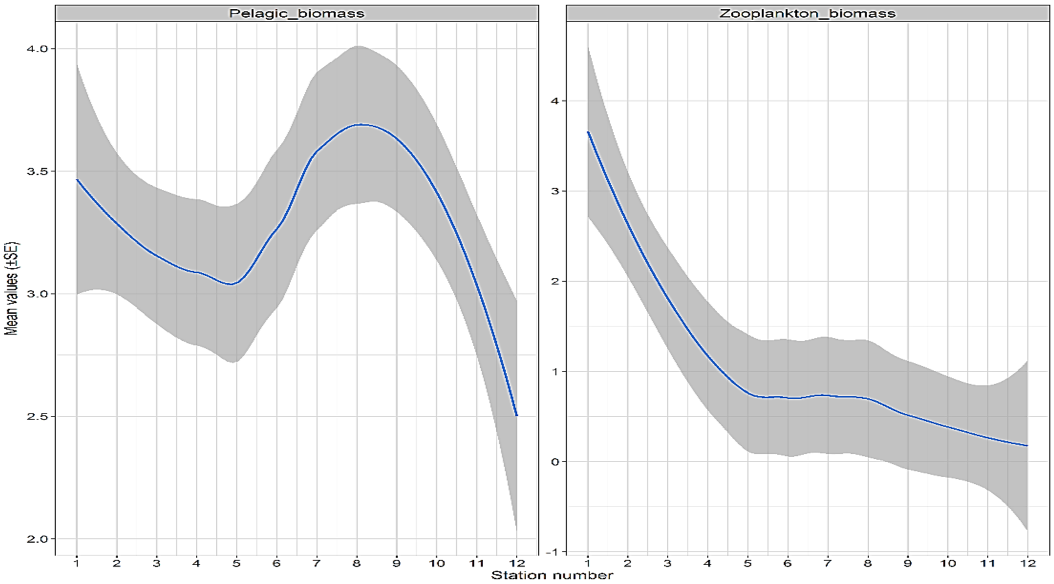
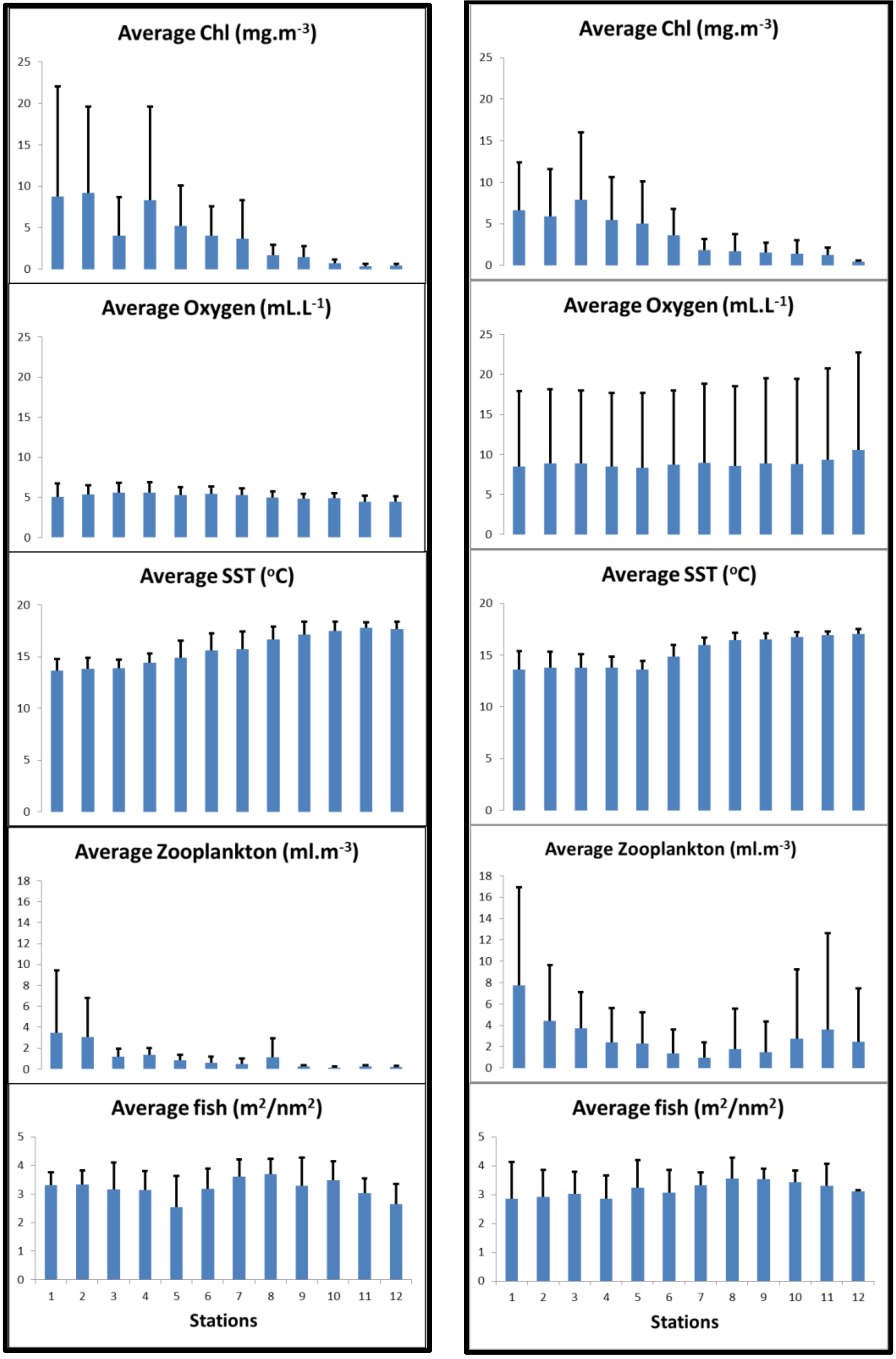


Figure A4: A smoothened average of pelagic and zooplankton biomasses in winter surveys at each station from 2000 to 2009. Grey area indicates standard error (SE).



(a) In winter

(b) In summer

Figure A5: Average values of Chlorophyll, Oxygen, SST, Zooplankton abundance and fish availability along SHBML from station 1 to 12 (a) in winter and (b) in summer. Error bars denote Standard Error

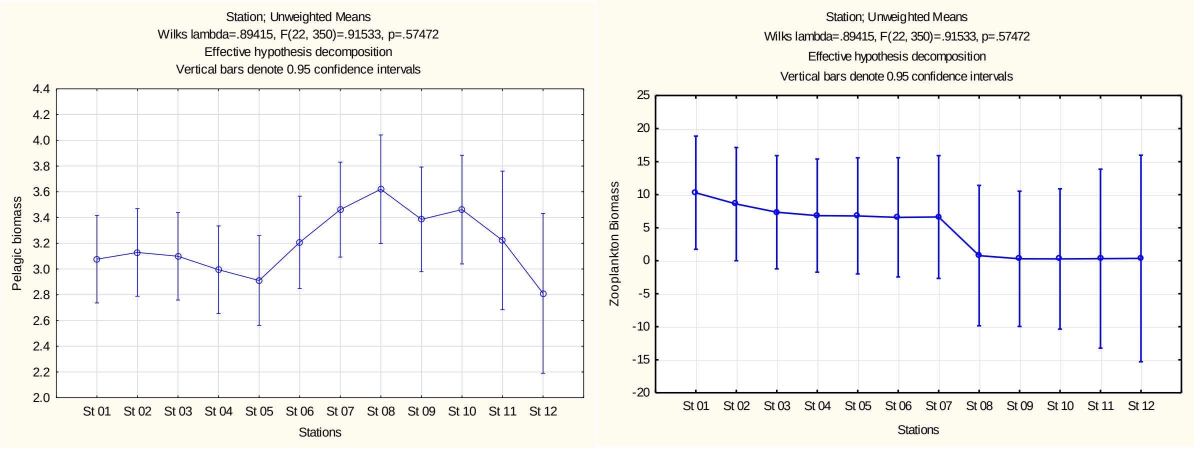


Figure A6: The mean spatial variability of pelagic and zooplankton abundance along SHBML at each station from 2000 to 2009. Vertical bars denote 0.95 confidence intervals.