ASSEMBLAGE DYNAMICS OF LARVAL FISHES ASSOCIATED WITH VARIOUS SHALLOW WATER NURSERY HABITATS IN ALGOA BAY, SOUTH AFRICA

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by

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Submitted in fulfilment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

to be awarded at the

NELSON MANDELA METROPOLITAN UNIVERSITY

December 2013

Promoter: Dr NA Strydom

GENERAL ABSTRACT

The success of the larval stage in fishes plays a critical role in structuring adult fish populations. It is well understood that juveniles of many marine fish species are closely associated with nearshore and coastal habitats that serve as nursery areas while adult assemblages are more widely distributed. The larval phase however, particularly pertaining to nursery habitat use, remains poorly understood in South Africa. A mixed-method, larval and juvenile fish study was conducted in the warm-temperate shallow coastal waters of Algoa Bay, South Africa. Two years (2010 – 2012) of seasonal sampling at 27 stations at various habitat types revealed distinct spatio-temporal patterns in larval fish composition and abundance. In total, 164 species from 50 families were collected in the nearshore (<30 m), over reef and sand, in the surf zone and large estuarine habitats in Algoa Bay. Engraulidae dominated the larval fish catch in the nearshore (38.4 %) and over the selected reef and sand habitats (37.8 %). Cynoglossidae (28.1 %) and Sparidae (8.4 %) were the second and third most abundant fish families in the nearshore. In subtidal reef and sand habitats, Gobiidae (23.4 %) and Clupeidae (9.2 %) were the second and third most abundant families respectively. Sparidae dominated (71.4%) surf zones followed by Soleidae (10.8 %) and Mugilidae (5.3 %), while in the mouth area of two permanently open estuaries in Algoa Bay, Gobiidae (35.9 %) Sparidae (30.1 %) and Mugilidae (12.4 %) dominated.

Several species from the Blenniidae, Gobiesocidae, Gobiidae, Scorpaenidae and Tripterygiidae fish families complete their pelagic larval phase in the reef habitats in Algoa Bay. These reef habitats therefore serve as important nursery areas for the larvae of benthic species. The sand and nearshore habitats serve as nursery areas for Clupeidae and Engraulidae. Highest densities of Carangidae, Sciaenidae and Sparidae larvae were observed at the subtidal reef habitats indicating that this area is important for accumulation of the early developmental stages of these fishes. The nearshore serves as an important accumulation habitat for species in the Haemulidae and Soleidae families whose juveniles are known to recruit into estuarine nursery areas. The nearshore therefore is a specific area of presettlement buildup of larvae prior to settlement of larvae or juveniles in estuarine nursery areas. Cynoglossidae larvae are also using the nearshore as an accumulation area prior to settlement and recruitment into adult populations occurring in shallow water habitats. In the surf zone, not only are estuary-dependent fish species utilizing this habitat as a nursery area, but marine species whose adults are either associated with rocky shores or surf zones are similarly using these areas as nursery habitats. In addition, estuary-dependent fish species which spawn in the marine environment are actively recruiting into estuarine nursery areas on both tides. Active recruitment against the outgoing ebb tide flow was a conclusive finding in this study. These larvae and juveniles are actively swimming against the ebb tide in the shallower, slower-flowing marginal areas where current flow is reduced.

Strong environmental gradients on multiple temporal and spatial scales occur in Algoa Bay. Seasonal patterns were evident in larval densities, richness and diversity. Peaks in density, richness and diversity occurred during spring and summer (September to February) associated with increasing water temperatures and a high productivity providing a good food environment for larval fishes. Thereafter densities declined steadily as a result of natural mortality, settlement or adult spawning activity, until autumn when numbers dropped suddenly as the surviving larvae moved to settlement habitats. The relationship between larval fish and environmental variables provides information useful to determine distributions. Therefore the Bay is particularly suited for modelling larval fish distributions. Using generalized linear models, larval fish density in the nearshore of Algoa Bay responded to different ocean features to varying degrees. Larval fish density responded positively to both upwelling and when warm water plumes, originating from an Agulhas Current meander, entered Algoa Bay. On subtidal reefs, habitat complexity played an important role in determining larval fish composition and diversity. The less structurally complex, reef-associated sand habitats, yielded higher species richness and diversity than the high and low profile reef habitats. Therefore, it is likely that the importance of less structurally complex habitats has been overlooked relative to other habitats in terms of their function for larval fishes. In the surf zone, wave period and wave height, which can be related to exposure, were the most significant environmental factors influencing larval fish assemblages. Greatest species diversity was observed in the surf zone habitats heavily influenced by wave action in the windward sector of Algoa Bay.

The identification of spawning areas and the mapping of distributions of early developmental stages of fishes are important in providing data pertaining to the protection of these habitats. This is particularly relevant as a new marine protected area (MPA) is planned for the eastern sector of Algoa Bay. Results from retrogressive plots indicate that the spawning locations of several species of coastal and pelagic fishes are occurring outside of the Bay, with the bay therefore serving as an accumulation area. Furthermore, distribution modelling results demonstrate that the early developmental stages of fishes in the shallow coastal habitats of Algoa Bay exhibit high spatial variability in their distributions. Results presented in this thesis help fill the knowledge gaps critical to the understanding of larval fish nursery areas of several economically and ecologically important fish species in Algoa Bay.

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ACKNOWLEDGEMENTS

Acknowledgements are made after each individual chapter but additional thanks and sincere gratitude are extended to the following:

- The South African National Parks (SANParks) for providing funding for all larval fish collections.
- National Research Foundation (NRF) for providing additional funding for the estuarine larval fish collections.
- South African Environmental Observation Network (SAEON) Elwandle Node for technical and logistical support of fieldwork and Acoustic Doppler Current Profiler (ADCP) deployment and measurements and Dr Wayne Goschen in particular for assistance with oceanographic data.
- The Nelson Mandela Metropolitan University (NMMU), the Faculty of Science at NMMU, the Deutscher Akademischer Austausch Dienst (DAAD) and the NRF for financial support.
- Dr Nadine Strydom for supervising this project. Your guidance and mentoring in both my professional and personal life has been invaluable to me. You have been the main source of knowledge, focus, motivation and advice throughout this entire experience. Your positive and calming advice has pulled me through some trying times.
- This dissertation represents a substantial amount of field work that would not have been possible without the help of many people. Special thanks go to Tanja van de Ven, Tim Vink, Kristi Maciejewski and Gavin Rishworth.
- Identifying larvae from these samples was a daunting task and was made easier with help from Dr Tony Miskiewicz who assisted me in confirmation of several of my reference specimens.
- Gordon Marchand for your practical advice and support. It would have been a much harder journey without you by my side.
- It would seem almost destiny that two avid nature conservationists should ‘spawn’ a marine biologist. Having said that however, I would not have made it through this endeavour without the love and support of my parents, Ian and Colleen Pattrick. You have led me to this point in my life with your total faith in my ability to succeed, by driving me to be strong, and to follow my heart.

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CHAPTER 1

GENERAL INTRODUCTION

1. INTRODUCTION

The early life history of marine coastal fishes is complex. A planktonic larval dispersal phase is followed by a period of settlement to nursery habitats that they occupy as juveniles. This bipartite nature of the life history of most fish species has important implications for understanding fish biology and ecology (Leis, 1991; Kingsford *et al.*, 2002). The larval phase of most marine fishes is a critical period in the life cycle, susceptible to many environmental perturbations, but known to have a profound influence on subsequent adult population ecology (Doherty, 1983; Houde, 1987). The structure and persistence of fish populations are strongly influenced by processes during the planktonic stage, settlement or immediately thereafter (Williams, 1980; Sale *et al.*, 1985). Therefore, through studying the larval phase, a better understanding of recruitment variability and population dynamics is achieved (Doherty and Williams, 1988).

The majority of fish species possess a pelagic larval stage that can last from days to months (Leis, 1991), characterized by high egg and larval abundances but severe mortality from predation, starvation and advection (Bailey and Houde, 1989). It is also during this very early developmental stage that eggs and preflexion larvae are dispersed via ocean currents, ultimately determining the population connectivity for many marine fishes (Cowen *et al.*, 2007; Cowen and Sponaugle, 2009). Once larvae have undergone flexion, they are by no means passive particles, with swimming abilities and behaviours that can influence their overall dispersal (Cowen *et al.*, 2000; Fisher *et al.*, 2000; Cowen, 2002; Paris and Cowen, 2004; Pattrick and Strydom, 2009). Physico-chemical variables including temperature, salinity, winds and currents and biotic factors focused on mode of spawning, food availability, predation, pelagic larval duration and larval fish behaviour, play a major role in determining the distribution patterns of fish larvae in the marine environment (Leis, 1991).

Settlement of larvae into nursery habitats involves important morphological, physiological and behavioural transitions (Moser, 1981; Kaufman *et al.*, 1992; Keefe and Able, 1993; McCormick, 1998), and is not necessarily direct but involves substantial habitat selection behaviour on the part of fish larvae (Sponaugle and Cowen, 1996; Wilson, 2001; Lecchini *et al.*, 2005). Shallow coastal marine environments including estuaries, seagrass meadows, marshes, mangrove forests, tidal pools, surf zones and shallow coral reefs are regarded as important nursery habitats for many fish species (Day *et al.*, 1981; Beckley, 1985a; Lasiak, 1986; Thayer *et al.*, 1987; Bennett, 1989; Blaber *et al.*, 1989; Nagelkerken *et al.*, 2000b; Chittaro *et al.*, 2005). In addition, the shallow nearshore (depth between 5 – 7 m) is also known to serve as a nursery area for the juveniles of some species (Blaber *et al.*, 1995). Nursery habitats have generally been defined as areas where juvenile fish species occur at higher densities, avoid predation more successfully or grow faster than in other habitats (Weinstein and Brooks, 1983; Orth *et al.*, 1984; Sheridan, 1992; Jenkins and Wheatley, 1998; Heck *et al.*, 2003). These habitats offer young fishes a measure of protection from predators and a plentiful food supply (Blaber and Blaber, 1980; Shulman, 1985; Parrish, 1989; Cocheret de la Morinière *et al.*, 2002). Although considerable research on the role of shallow coastal habitats as nursery areas for juvenile fishes has taken place, there is still much ambiguity regarding the nursery-role concept particularly pertaining to fish larvae, with no clear definition and no testable predictions, until recently formulated by Beck *et al.* (2001) with additional work expanding on these themes (Dahlgren *et al.*, 2006; Layman *et al.*, 2006). Additional factors in conjunction with density need to be assessed in order to accurately ascertain whether a habitat functions as a nursery area (Beck *et al.*, 2001). Beck *et al.* (2001) has advised that several factors including growth, survival, density and movement must be considered before nursery value can be confirmed. Before processes of settlement into nursery areas can be understood, information on ichthyoplankton density and distributions needs to be gathered. This is especially true for areas such as South Africa where larval fish dynamics are only partially known.

2. LARVAL FISH STUDIES IN SOUTH AFRICA

Larval fish research in South Africa began in the early 1900s with the descriptive work of J. D. F. Gilchrist on the development of eggs and larvae of South African marine fishes collected from the south Cape coastline (Gilchrist, 1903; Gilchrist, 1904; Gilchrist, 1916). Thereafter, the larval stages of several economically important fish species on the west coast of South Africa were described (De Jager, 1955; Haigh, 1972; O'Toole, 1977). From specimens collected during a larval fish survey off the Namibian coastline (O'Toole, 1974) the development of the larval stages of the commercially important, *Sardinops sagax* (Family: Clupeidae), common in South African waters, was described (Louw and O'Toole, 1977). A description on the development of the anchovy, *Engraulis capensis* (Family: Engraulidae), an equally important commercial species in South Africa, occurred in the late

1970's (King *et al.*, 1978). On the east coast of South Africa, information on the identification of marine eggs and larvae, the duration of the incubation period and the laboratory rearing of 40 marine fish species, was investigated around the Cape Peninsula (Brownell, 1979). The eggs and larval development of artificially spawned *Liza richardsonii* (Family: Mugilidae) were later described in the 1980s (Cambray and Bok, 1989). The larval development of laboratory-reared *Argyrozona argyrozona* (Family: Sparidae) and *Dagetichthys marginatus* (Family: Soliedae) followed (Davis and Buxton, 1996; Thompson *et al.*, 2007). The larval development of *Atherina breviceps* (Family: Atherinidae), *Argyrosomus japonicus* (Family: Sciaenidae), *Austroglossus pectoralis* (Family: Soleidae), *Cheimerius nufar* (Family: Sparidae), *Cynoglossus zanzibarensis* (Family: Cynoglossidae), *Dichistius capensis* (Dichistiidae), Gilchristella aestuaria (Family: Clupeidae), *Pagellus natalensis* (Family: Sparidae) and *Spondyliosoma emarginatum* (Family: Sparidae) were described from wild caught specimens (Neira *et al.*, 1988; Beckley, 1989; Beckley, 1990; Haigh and Whitfield, 1993; Leis and van der Lingen, 1997; Connell *et al.*, 1999; Wood, 2000; Leis *et al.*, 2002; Wood, 2003). The larvae from several teleost fishes were described in a comprehensive guide on ichthyoplankton from the south east Atlantic, in the region of the Benguela Current (Olivar and Fortuño, 1991). On the east coast of South Africa, in the region of the Agulhas Current, several Myctophidae larvae were described (Olivar and Beckley, 1995; Olivar *et al.*, 1999).

The estuarine environment, is well known as an important nursery area for larval and juvenile fishes both internationally (Elliott *et al.*, 1990; Potter *et al.*, 1990; Ramos *et al.*, 2010) and in South Africa (van der Elst and Wallace, 1975; Whitfield, 1994a; Strydom *et al.*, 2003). Therefore most larval fish research has taken place in these ecosystems. In South Africa, research assessing the composition, abundance and distribution of larval fishes has been conducted in single (Melville-Smith, 1978; Melville-Smith and Baird, 1980; Melville-Smith, 1981; Whitfield, 1989a; Harrison and Whitfield, 1990; Martin *et al.*, 1992; Harris and Cyrus, 1995; Harris *et al.*, 1995; Harris and Cyrus, 1997; Harris and Cyrus, 1999; Pattrick *et al.*, 2007; Wasserman *et al.*, 2010) and multi-estuary studies (Whitfield, 1994a; Strydom *et al.*, 2003; Montoya-Maya and Strydom, 2009). These studies have mostly been conducted in the warm-temperate estuaries of the east coast of South Africa and have specifically looked at the use of tidal currents by larvae of an estuarine resident fish species (Melville-Smith *et al.*, 1981), tidal exchange (Beckley, 1985b; Whitfield, 1989c; Strydom and Wooldridge, 2005), the effects of altered freshwater input on species occurrence in estuaries (Whitfield, 1994a;

Strydom *et al.*, 2002) and habitat use and preference (Whitfield, 1994b; Strydom, 2003a). In the subtropical region of South Africa on the east coast, larval fish assemblage dynamics have been investigated in the St Lucia Estuary, Kosi Estuary, Durban Bay Harbour and Richards Bay Harbour (Martin *et al.*, 1992; Harris and Cyrus, 1995; Harris *et al.*, 1995; Harris and Cyrus, 1996; Harris and Cyrus, 1997; Harris and Cyrus, 1999). Larval fish assemblages have also been studied in the subtropical-warm temperate boundary region (Pattrick *et al.*, 2007; Wasserman *et al.*, 2010). On the south and west coasts of South Africa larval fish composition and distribution has been investigated in nine estuaries in the cool temperate region of South Africa (Montoya-Maya and Strydom, 2009).

Surf zones, adjacent to estuaries, have been identified as accumulation areas, transient routes and nurseries for several species which arrive at these habitats as actively swimming postflexion larvae (Whitfield, 1989b; Harris and Cyrus, 1996; Strydom, 2003b; Strydom and d'Hotman, 2005). Larval fish studies in South African surf zones have identified this habitat as an interim nursery area for estuary-dependent marine fish species (Whitfield, 1989b; Harris and Cyrus, 1996; Strydom, 2003b). Despite the seemingly rough hydrodynamic environment of the surf zone, larvae accumulate within surf zones before recruiting into estuaries. Larvae actively select areas of reduced turbulence in depressions associated with dissipative beach surf zones (Watt-Pringle and Strydom, 2003). Irrespective of proximity to estuary mouths, continuity in terms of domination by estuary-dependent larvae within warm-temperate South African surf zones was observed (Strydom and d'Hotman, 2005). These accumulations may be related to the wait that accompanies cueing and transport mechanisms into estuaries (Strydom, 2003b). Estuary/river water that enters the surf zone creates an accumulation response by larvae of estuary associated fishes aiding the cueing process (Strydom, 2003b; James *et al.*, 2008). Marine overwash events and estuary breaching serve as important routes of access for fish larvae to recruit into intermittently open estuaries (Cowley *et al.*, 2001; Kemp and Froneman, 2004).

Most larval fishes occurring in estuaries and surf zones originate from nearshore spawned eggs. Larval fish research in the nearshore environment in South Africa has received considerably less attention than the estuarine and surf zone environment. The main focus of research in the marine environment has concentrated on offshore pelagic species of commercial importance, neritic species and those species occurring in Agulhas Current waters (Beckley, 1993; Beckley and Hewitson, 1994; Olivar and Beckley, 1994; Beckley and

Leis, 2000; van der Lingen and Huggett, 2003). Isolated studies assessing the composition of fish larvae in the shallow nearshore have been conducted in the Tsitsikamma National Park marine protected area (MPA) on the warm-temperate south-east coast (Tilney and Buxton, 1994; Wood, 1998). These assessments formed part of a broader study to investigate the role played by the Tsitsikamma National Park MPA in seeding adjacent, fished areas with eggs and larvae (Tilney *et al.*, 1996). Using larval distribution and current-meter information, projected dispersal distances were estimated. Wood (1998) provided the necessary groundwork for the broader study to assess the degree to which eggs and larvae are dispersed from the reserve by describing the early life history stages of several species. In the nearshore waters off the St Lucia Estuary on the subtropical east coast (Harris *et al.*, 1999), larval fish assemblages were assessed along an ocean-estuarine gradient and related to the physical characteristics of each environment (Harris *et al.*, 2001). More recently, a novel jetski-based plankton towing method was used to sample larval fishes in a shallow marine environment in the warm-temperate waters of South Africa (Strydom, 2007). Strydom (2007) observed a size gradient in larval fishes between the surf waters and adjacent nearshore waters with larger individuals occurring in the surf.

Isolated larval fish studies have taken place in the nearshore of Algoa Bay on the south east coast of South Africa within the warm-temperate Agulhas bioregion. Work by Beckley (1986), described the various taxa occurring in the nearshore ichthyoplankton in the western sector of the Bay, in terms of the distribution of adults and juveniles, the breeding biology and available literature on the early life history of these species. Larvae of coastal species with benthic eggs and larvae of pelagic species with pelagic eggs dominated the nearshore (Beckley, 1986). Low abundance of larvae from coastal species that spawn pelagic eggs including Sciaenidae, Soleidae and Sparidae occurred within the study area and Beckley (1986) suggested that spawning and development occurs away from the nearshore region. Over a two-year study period, Pattrick and Strydom (2008) assessed the composition of ichthyoplankton in the nearshore of the eastern sector of the Bay. Preflexion larvae of Sparidae were regularly encountered along the 15 m depth contour (Pattrick and Strydom, 2008) suggesting that spawning was occurring closer to shore than that suggested by Beckley (1986). In addition, the complexity of the nearshore ocean current environment in eastern Algoa Bay and its effect on larval fish ecology has been assessed (Pattrick *et al.*, 2013). Predictions of potential transport from a point source indicate that net displacements were greater during spring and summer, coinciding with peak fish breeding, suggesting that the nearshore currents play a vital role in the transport of eggs and larval stages of fish in Algoa Bay (Pattrick *et al.*, 2013). A host of shallow coastal habitats occur in Algoa Bay, and with larval fish research restricted to the shallow nearshore (15 - 5 m), the potential for alternate habitats to serve as nursery areas for larval fish is virtually unknown in the Bay, thus providing an ideal opportunity to expand existing knowledge.

3. THE PHYSICAL CHARACTERISTICS OF ALGOA BAY

The coastline of southern Africa has a limited number of bays or semi-enclosed seas. Algoa Bay is the easternmost and the largest of several log-spiral shaped bays on the east coast of South Africa, situated centrally within the warm-temperate Agulhas bioregion. The Bay is shallow, with a maximum depth of 73 m at the mouth which is approximately 70 km wide and open to the eastern Agulhas Bank (Harris, 1978). The Bay is enclosed between the Cape Recife rocky headland on the western border (33°53′46′′S; 25°42′08′′E) and the Woody Cape headland consisting of calcareous sandstones of Aeolian origin on the eastern border (33°52′07′′S; 26°17′29′′E). The Agulhas Current, a major western boundary current, flows only 50 km offshore of Algoa Bay along the shelf break of the Agulhas Bank on the 200 m isobath in a southwestwards direction (Lutjeharms, 1981; Gründlingh, 1983). The current plays an important role in influencing the local oceanic conditions in Algoa Bay. Approximately 80 km east of Algoa Bay, the shelf edge widens and it is here where meanders form along the inshore boundary. Warm Agulhas Current water can at times penetrate into Algoa Bay driven by southwesterly winds (Schumann *et al.*, 1988; Goschen and Schumann, 1994). Upwelling occurs predominantly in summer at Woody Cape and Cape Recife (Schumann *et al.*, 1982; Beckley, 1983b; Beckley, 1988; Schumann *et al.*, 1988). Upwelling along the southern shoreline of Cape Recife is mainly wind driven while upwelling at Woody Cape is influenced by both wind and the Agulhas Current (Goschen and Schumann, 2011). Intense thermoclines occur in summer with more isothermal conditions during winter (Schumann *et al.*, 2005). The prevailing wind direction in the Bay is parallel to the large-scale orientation of the coastline, in a west-southwesterly and east-northeasterly direction (Schumann *et al.*, 1991). Surface currents in Algoa Bay are generally in the direction of the wind, parallel to the coastline (Harris, 1978; Roberts, 1990). Variability over both large spatial (kilometres) and temporal (days) scales occurs in the ocean currents in the western sector of Algoa Bay (Schumann *et al.*, 2005). In the shallow eastern sector of Algoa Bay, alongshore currents flow in either an eastward or westward direction (Pattrick, 2008; Pattrick *et al.*, 2013). Westerly winds dominate in speed and frequency throughout the year, with the easterly component varying seasonally, increasing in strength and duration during summer.

The subtidal environment of Algoa Bay consists primarily of soft sediments including coarse sands interspersed with fine silts and clays (Bremner, 1978; Bremner, 1991). Small isolated reef complexes occur throughout Algoa Bay and are frequently inundated during large scale sand movements (McLachlan *et al.*, 1977; Cockcroft and Tomalin, 1987; Chalmers, 2011). The coastline of Algoa Bay is approximately 150 km in length, comprised predominantly of sandy beaches with a beach morphodynamic type exclusively dissipative-intermediate (McLachlan, 1983; Harris *et al.*, 2011) consisting of well sorted fine to medium-sized quartz sands (McLachlan *et al.*, 1977; McLachlan *et al.*, 1981). The Alexandria dune field, within the eastern sector of Algoa Bay, is 50 km long, 2.1 km wide with dunes exceeding 150 m in height and is the third largest active coastal dune field in the world (McLachlan *et al.*, 1982). A south-westerly dominant swell direction within the Bay has led to the formation of sheltered beaches with relatively few rip currents in the western sector, while exposed, dynamic beaches with many semi-permanent rip currents occur in the eastern sector (Talbot and Bate, 1987). The Swartkops (33°51′54″S; 25°38′00″E) and Sundays (33°43′19″S; 25°50′57″E) estuaries are two large permanently open systems which flow into the Bay. The St Croix island group (33°47′58″S; 26°46′20″E) and the Bird Island group (33°52′07″S; 26°17′29″E) are two island clusters located in Algoa Bay and are the only islands found between Cape Agulhas and Maputo (southern Mozambique). In the western sector of the Bay, the St Croix islands, comprised of quartzitic Table Mountain Sandstone, consist of St Croix Island, which is the largest, and Jahleel and Brenton islands, which are small unvegetated rocky outcrops (Beckley and McLachlan, 1979). The St Croix island group was proclaimed as South Africa’s first island marine reserve in 1981 with the marine component extending 500 m in radius around each island (DEAT, 1981). In the eastern sector of the Bay, 10 km offshore of the Woody Cape headland, the Bird Island group, also comprised of quartzitic Table Mountain Sandstone, consists of Bird, Stag and Seal islands and a rocky outcrop, Black Rocks. The Bird Island Marine Protected Area (MPA) was proclaimed in June 2004 (DEAT, 2004).

4. ICHTHYOFAUNAL RESEARCH IN ALGOA BAY

The first comprehensive ichthyological survey in Southern Africa was conducted in the Swartkops Estuary, Algoa Bay at the turn of the 20th Century (Gilchrist, 1918). After a prolonged period, work by several authors followed up on the pioneering work of Gilchrist (1918) and provided information on the biology of individual species in the Swartkops Estuary including several Mugilidae *Mugil cephalus*, *Liza dumerili*, *Liza richardsonii* and *Liza tricuspidens* (Marais and Erasmus, 1977a; Marais and Erasmus, 1977b; van der Horst and Erasmus, 1978; van der Horst and Erasmus, 1981), *Psammogobius knysnaensis* (Family: Gobiidae) (Malan, 1979), *Pomadasys commersonnii* (Family: Haemulidae) (van der Westhuizen and Marais, 1977), *Atherina breviceps* (Family: Atherinidae) (Els, 1979), *Gilchristella aestuaria* (Family: Clupeidae) (Talbot, 1982; Talbot and Baird, 1985) and *Rhabdosargus holubi* (Family: Sparidae) (de Wet and Marais, 1990). The species composition, seasonal abundance and size frequency distributions of the juveniles and adult assemblages in the Swartkops Estuary were conducted during the late 1970s (Marais, 1976; Winter, 1979; Marais and Baird, 1980b; Marais and Baird, 1980a). Species associated with the Eelgrass *Zostera capensis* beds in the lower reaches of the Swartkops were also assessed (Beckley, 1983a). In the Swartkops, larval fish studies commenced in the late 1970s to assess composition in the main channel (Melville-Smith, 1978; Melville-Smith and Baird, 1980) and tidal exchange of fish eggs, larvae and juveniles in the mouth area (Beckley, 1985b). Juvenile fish assemblages have also been assessed in the marine environment immediately off the Swartkops Estuary mouth (Beckley, 1984).

In the Sundays Estuary, juvenile (Beckley, 1984) and adult (Marais, 1981) components of the fish community have been studied. Larval fish research in the Sundays Estuary was initiated in the 1990s where composition, distribution and abundance of larval fish were assessed (Harrison and Whitfield, 1990), followed by a study of the effects of freshwater input on larval and juvenile fishes (Whitfield, 1994a). Trophic studies assessing linkages between larval fish and zooplankton have received some focus in the Sundays Estuary (Wooldridge and Bailey, 1982; Whitfield and Harrison, 1996; Sutherland *et al.*, 2012; Sutherland *et al.*, 2013). Larval fish dynamics in relation to physico-chemical variability in the system have also been assessed (Sutherland *et al.*, 2012). The importance of the Sundays Estuary head waters for young estuary- and marine-spawned fishes has recently been highlighted (Wasserman and Strydom, 2011).

The composition of adult teleost and elasmobranch communities occurring in the surf zones along the sandy beaches of Algoa Bay were also assessed (Lasiak, 1983; Rossouw, 1983; Lasiak, 1984; Romer, 1990). Studies assessing juvenile fish communities in the surf zones of

Algoa Bay have identified this habitat as an important nursery area for several juvenile teleost species (Lasiak, 1981; Lasiak, 1986). In addition, recent work in Algoa Bay has highlighted the importance of the surf zone for larval fishes (Rishworth *et al.*, *In Press*). The fish community of tidal pools in the lower balanoid zone in Algoa Bay was examined (Beckley, 1985a). The utilization of the inshore marine environment of Algoa Bay by juvenile estuary associated fishes has also been assessed (Wallace *et al.*, 1984).

Adult teleost and elasmobranch species have also been identified on the subtidal reefs in the western sector of Algoa Bay (Beckley and Buxton, 1989). The first detailed, fishery independent comparison, of reef fish communities across the full spatial range of Algoa Bay has only recently been completed (Chalmers, 2011). The Sparidae are the most abundant and speciose family in Algoa Bay (Chalmers, 2011). A clear, habitat dependent structuring of reef fish communities occurs in Algoa Bay. Chalmers (2001) also reported on a sheltered western reef community in which non-reef dependent species dominated with several juvenile species of reef dependent species observed. Larger resident reef dependent species dominated the exposed eastern reef community (Chalmers, 2011).

5. RATIONALE

The southern African coastline is one of the least convoluted worldwide and rugged in nature, dominated by strong ocean features on both the west and east coasts. The Agulhas Current, a warm western boundary current, flows close inshore along the eastern seaboard. On the western seaboard, upwelling which creates offshore Ekman drift, is coupled with strong shelf-edge jet currents. Together with westerly cyclones which pass over southern Africa, the coastal environment has notoriously been regarded as a harsh environment. Although estuaries on the south-western coastline of Australia and the south-eastern coastline of South Africa are at similar latitudes, are open to the Indian Ocean and are periodically closed off from the sea by sand bars at their mouths, juveniles of several marine species are restricted to estuaries in South Africa which contrasts the situation in Australia (Potter *et al.*, 1990). It has been suggested by Potter *et al.* (1990) that this difference can be attributed to the presence of a greater area and quality of alternative nursery habitats in the inshore marine environments in south-western Australia than in southern Africa. Hutchings *et al.* (2002) has suggested that due to this, enormous constraints are placed on the reproductive strategies of many fish species occurring within the region. Several important economic and ecologically important species spawn on the edge of current systems where eggs and larvae are transported into productive inshore nursery grounds (Hutchings *et al.*, 2002). Estuaries serve as nurseries for fishes from as early as the larval phase as they are highly productive systems rich in food resources and provide refuge from predators (Roper, 1986; Boehlert and Mundy, 1988; Whitfield, 1994a; Harris and Cyrus, 2000; Strydom, 2003a).

Adjacent to estuaries, coastal habitats are known to play an important role in the early life history of many marine fish species (Ray, 2005). For many species, it is the juvenile phase that is often considered to be the most dependent on coastal habitats for use as nurseries (Blaber *et al.*, 1989; Nagelkerken *et al.*, 2000a; Nagelkerken *et al.*, 2000b). Far less research into “nursery grounds” for larvae has been conducted with the majority of research based on coral reefs (Pearcy and Myers, 1974; Johannes, 1978; Leis, 1986; Colin and Bell, 1991; Leis, 1994; Klumb *et al.*, 2003). Several reef fish have been observed to complete their pelagic larval phase in coral sea atoll lagoons with these habitats serving as important closed nurseries for the larvae of a few coral reef fishes (Leis, 1994). Blaber *et al.* (1995) has speculated that shallow inshore coastal waters may be an important habitat for larvae, with spawning of many species, whose juveniles migrate to estuaries, occurring in the nearshore (Wallace and van der Elst, 1975; Day *et al.*, 1981). Along most of the south-east coast of South Africa, nursery areas for reef and sand associated fish are plentiful within the nearshore zone (Tilney *et al.*, 1996; Wood, 1998). The role however of the nearshore serving as nursery areas for larvae of temperate coastal fishes has not been adequately investigated (Blaber *et al.*, 1995; Wood, 1998).

The importance of the nearshore for the completion of the pelagic larval phase has been highlighted for many coastal species (Tzeng and Wang, 1993; Hernández-Miranda *et al.*, 2003; Azeiteiro *et al.*, 2006; Pattrick and Strydom, 2008). There has been an increasing awareness that nearshore areas serve as accumulation areas for larvae (Warner *et al.*, 2000). Within temperate regions several coastal fish species spawn in the marine environment with the early life history stages entering the estuary from the nearshore marine environment. The accumulation of larvae in the nearshore coastal zone, which have been spawned in the marine environment and are to recruit to estuaries, is the first phase of movement of larval fish (Boehlert and Mundy, 1988). The probability of survival of fish eggs and larvae through the planktonic phase is enhanced when development occurs in a favourable habitat. Some fish species will spawn in or near coastal habitats, providing larvae with accessibility to coastal nursery areas (Boehlert and Mundy, 1988; Potter *et al.*, 1990; Chute and Turner, 2001). The other possibility is that some fish species will spawn at different locations and times and the larvae will accumulate in a ‘holding area’ to await favourable conditions for settlement (Breitburg, 1989; Kingsford and Choat, 1989). Nevertheless, data concerning the functional role of specific habitat types within the nearshore which sustain fish larvae remains fairly ambiguous, largely due to the complexity of larval fish composition and distribution in the nearshore (Young *et al.*, 1986; Doyle *et al.*, 1993; Harris *et al.*, 1999; Gray and Miskiewicz, 2000; Sponaugle *et al.*, 2002; Azeiteiro *et al.*, 2006). Furthermore, the preferential habitat types used by individuals during the various stages in larval fish development remain largely unknown.

A mosaic of coastal habitats exist which are available as nursery areas for larval fishes in the coastal waters of South Africa. The coastal environment between the marine spawning grounds and estuaries include an interconnected mosaic of diverse habitat types such as the nearshore (<30 m), various subtidal reef profile habitat types, reef-associated sand habitats, sand habitats and surf zones. Different habitat types which are found within close proximity to each other, allow for multiple ontogenetic habitat shifts, or occupation of several different habitats types during the same life stage (Eggleston, 1995; Dahlgren and Eggleston, 2001; Serafy *et al.*, 2003). Different habitats vary in the quality and abundance of food and potential predators, therefore, ontogenetic habitat shifts result from conflicting demands of growth and survival, given that resource utilization abilities and predation risk are generally related to body size (Werner and Gilliam, 1984). The importance of estuaries as nursery areas however, has received the most attention, due to ease of accessibility for sampling. The poricity of research on larval fish use of habitats associated with other coastal nearshore habitats in South Africa probably stems from the difficulty of sampling such habitats and coasts.

Nursery areas which are fundamental to the completion of the larval phase are virtually unknown for many species occurring off the South African coast. Furthermore, the incomplete knowledge of the utilization of shallow coastal habitats by fish larvae is coupled with a general lack of information on the environmental drivers of larval fish assemblages in these areas. The complex interactions between biological and physical environmental variables determines the variation in larval supply, which is critical to the maintenance of many marine populations (Roughgarden *et al.*, 1988). The relationship between larval fish and the environment provides information on habitat preferences and predictions of distributions of species. Determining areas of essential fish habitat including spawning, post hatch and recruitment areas are often used to justify conservation prioritization. With approximately 50 % of the growing world populating living within 100 km of the coastline, and with coastal human populations worldwide continuing to increase, coastal habitats are likely to suffer from habitat loss, degradation and overfishing. It has been clearly established that increases in biomass, abundance and diversity of marine organisms occurs as a result of the creation of MPAs, serving as a source of increased production of eggs and larvae. Providing adjacent fished areas with larval recruits is an important objective of MPAs (Leis, 2003). These questions to determine the functioning of coastal habitats for larval fishes are particularly relevant, as a new MPA is planned for the eastern sector of Algoa Bay. The city of Port Elizabeth is located within the western corner of Algoa Bay and is the third largest coastal city in South Africa with a population exceeding one million residents. Therefore, there is a dire need to determine the ecological importance of the coastal region so that appropriate management and conservation measures can be prioritized. By identifying highly productive areas (spawning, post-hatch, recruitment and/or nursery areas), managers are able to target and protect or restore these areas. This important knowledge gap can only be filled by studies that examine the dynamics of larval fish assemblages in association with environmental variables across a wide range of habitat types as presented in the following thesis.

6. AIMS AND OBJECTIVES

The aim of this thesis was to investigate the assemblages of larval fishes, over a period of two years, in various shallow coastal habitats in Algoa Bay in the warm-temperate region of the south east coast of South Africa. This work focussed on quantifying and qualifying larval and early juvenile assemblages to assess the potential nursery functioning of these habitats in conjunction with identifying larval fish sources and sinks. To do this it was imperative to recognize the physico-chemical and other important environmental variables possibly structuring larval fish assemblages within each habitat type respectively. This thesis is comprised of a series of independent studies using mixed-method techniques, to investigate the variations in the spatial and temporal occurrence of fish larvae in relation to environmental variables in Algoa Bay. This thesis contains five content chapters (Chapters 2 – 6) preceded with an introduction and followed by a synthesis and conclusion. The first three content chapters investigate the distribution patterns of fish larvae in potential nursery habitats in the shallow coastal waters of Algoa Bay. These include the nearshore, reef, sand and surf zone habitats. The fourth content chapter investigates the dynamics of recruitment of larval fishes into two permanently open estuarine nursery areas in Algoa Bay. The fifth content chapter uses a novel approach to model the location of spawning areas and the spatial extent of post hatch areas for selected species in Algoa Bay. The objectives of the present study were to assess the:

1. Composition and abundance of larval fish assemblages in the nearshore nursery environment of Algoa Bay and to detect major patterns in relation to ocean features (Chapter 2).
2. Spatial and temporal patterns and the occurrence and abundance of larval and settlement stage fishes on reef habitats associated with islands in the warm-temperate waters of Algoa Bay (Chapter 3).
3. Relative contribution of exposure from winds and waves structuring larval fish assemblages in the surf zone nursery habitats of Algoa Bay (Chapter 4).
4. Influence of the diel and tidal cycle on larval and juvenile fish directional movement in two permanently open estuarine nursery habitats in Algoa Bay (Chapter 5).
5. Location and spatial extent of essential fish habitat including spawning and post hatch areas for several important fish species in Algoa Bay (Chapter 6).

7. THESIS STRUCTURE

The five main content chapters correspond specifically to the five objectives of the thesis. One chapter (Chapter 4) is currently in press in the Journal of Fish Biology and the remaining four content chapters will be submitted for publication. This results in a limited degree of repetition in the methods and study areas for each section. This collective work is preceded by a general introduction and a synthesis and conclusion section follows the content chapters.

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CHAPTER 2

LARVAL FISH VARIABILITY IN RESPONSE TO OCEAN FEATURES IN A NEARSHORE NURSERY AREA

1. ABSTRACT

The relative influence of environmental variables including ocean features on ichthyoplankton assemblages in the warm-temperate nearshore of Algoa Bay, South Africa was assessed. The diverse nearshore ichthyoplankton comprised 88 taxa from 34 families. These were sampled at six stations over a two-year period between August 2010 and July 2012 using a plankton ring net of 750 mm diameter and 500 µm mesh aperture. The majority of larvae collected were in a preflexion stage indicating the importance of the nearshore for newly hatched larvae. The Engraulidae dominated the catch (38.4 %), followed by Cynoglossidae (28.1 %) and Sparidae (8.4 %). *Engraulis encrasicolus*, *Cynoglossus capensis* and *C. zanzibarensis* were the dominant species. Larvae spawned from adults common in the nearshore, dominated catches. Coastal species producing pelagic eggs, particularly those of the Sparidae fish family, made important contributions towards the overall larval fish catch in the Algoa Bay nearshore. Larval fish densities were highest during spring and summer (September to February). Unique patterns in responses of each dominant fish species to ocean features in the nearshore of Algoa Bay, indicate the sensitivity of the early developmental stage to environmental variables. Using generalized linear models, larval fish density responded positively to upwelling and warm water plumes originating from an Agulhas Current meander entered Algoa Bay. Highest densities of anchovy and sardine were observed during Agulhas Plume intrusions into Algoa Bay. Larval fish densities however related negatively to mixed and stratified water column features. The nearshore region of Algoa Bay appears to serve as a favourable environment for the accumulation of larval fishes.

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2. INTRODUCTION

The nearshore serves as an important environment for the early developmental stages of fishes (Lasker, 1975; Lasker, 1978; Myers and Pepin, 1994; Laprise and Pepin, 1995). This region is commonly used as a spawning and/or nursery area by a variety of species (Frank and Leggett, 1983; Doyle *et al.*, 1993; McGowen, 1993). In the nearshore, suitable conditions for larval survival include high food availability, low abundance of predators, suitable physico-chemical characteristics and circulation patterns that promote retention or transport to nursery areas (Brewer and Kleppel, 1986; Boehlert and Mundy, 1988; Laprise and Dodson, 1993; Nishimoto and Washburn, 2002). Larval fish assemblages in nearshore waters are complex (Young *et al.*, 1986; Doyle *et al.*, 1993; Harris *et al.*, 1999; Gray and Miskiewicz, 2000; Sponaugle *et al.*, 2002; Azeiteiro *et al.*, 2006). Spatial and temporal patterns in larval fish distributions and abundance are influenced by biological factors including the location, timing and mode of spawning of adults, pelagic larval duration, larval fish behaviour, predation, feeding and growth (Sherman *et al.*, 1984; Castro and Cowen, 1991; Leis, 1991; Castro *et al.*, 2000; Ward *et al.*, 2003; Leis *et al.*, 2009). Furthermore, physical factors including ocean currents, winds, eddies, upwelling and stratification of the water column are also known to influence larval fish abundance and distribution in the nearshore (Haury *et al.*, 1978; Owen, 1981; Norcross and Shaw, 1984; Kingsford, 1990; Hernández-Miranda *et al.*, 2003).

The successful development and growth of fishes in their early stages therefore largely depends on the surrounding water mass characteristics. Marine systems are highly dynamic environments subject to a variety of physical processes operating on numerous spatial and temporal scales (Haury *et al.*, 1978; Denman and Gargett, 1983). Physical conditions of the water column at the time and location of spawning and hatching will therefore largely determine the fate of eggs and larvae. In highly dynamic nearshore environments, coastal fish species could synchronize their reproduction according to these periods when ocean features persist, to bring largely planktonic larvae to nursery grounds usually found in relatively shallow coastal waters. The coastline of southern Africa has a limited number of bays or semi-enclosed seas. Therefore, potential shallow coastal nursery grounds are limited. Algoa Bay is the easternmost and the largest of several log-spiral shaped bays on the east coast of South Africa. This Bay therefore could serve as an ideal potential nearshore nursery area for larval fishes.

Both international (Borges *et al.*, 2007; Able *et al.*, 2010) and national (Pattrick and Strydom, 2008) literature highlights the importance of the nearshore environment for the early life history of fishes, little is known about how the specific composition as well as the abundance of larval fishes varies spatially and temporally as a result of ocean features in the nearshore. Linkages between water masses and larval fishes have mainly focussed on the offshore continental shelf region (Sabatés, 1990; Dempster *et al.*, 1997; Grothues and Cowen, 1999; Marancik *et al.*, 2005; Muhling *et al.*, 2008b). Few studies have been conducted within the nearshore. Knowledge of these interactions among fish larvae and ocean features of the nearshore environment are important for a greater understanding of overall dynamics of fish populations. In this study, the composition, abundance and distribution of larval assemblages in the nearshore environment of the warm-temperate waters of the Eastern Cape, South Africa was described. The aims were to determine whether larval fish assemblages varied in relation to ocean conditions occurring in the nearshore. Furthermore, considering the large number of potential environmental factors driving larval distributions in the nearshore, the present study would assess which of these (temperature, salinity, prey abundance, *inter alia*) are the most probable within the nearshore waters of Algoa Bay.

3. MATERIALS AND METHODS

3.1 Study site

Algoa Bay (Figure 2.1) is situated on the south east coast of South Africa within the warm-temperate Agulhas bioregion, and is the largest log-spiral bay on the Cape south coast (Goschen and Schumann, 2011). Within the Bay, interactions between the nearshore and the deep-water offshore processes result in a dynamic ocean (Goschen and Schumann, 2011). The Agulhas Current flows south-westwards, along the edge of the continental shelf, approximately 50 km offshore of Algoa Bay and dominates large-scale ocean features in the region (Lutjeharms, 1981; Schumann, 1987; Schumann, 1998). Shear-edge eddies and plumes on the inshore edge of the Agulhas Current frequently penetrate over the shelf and may be driven into Algoa Bay by southwesterly winds (Schumann *et al.*, 1988). Upwelling occurs at the prominent capes driven by easterly-component winds and progress eastwards into Algoa Bay by subsequent westerly winds (Goschen and Schumann, 1995). The prevailing wind directions in Algoa Bay are parallel to the orientation of the coastline, namely west-southwesterly and east-northeasterly with the westerly-component winds dominating throughout the year while the easterly-component winds vary between seasons (Schumann and Martin, 1991).

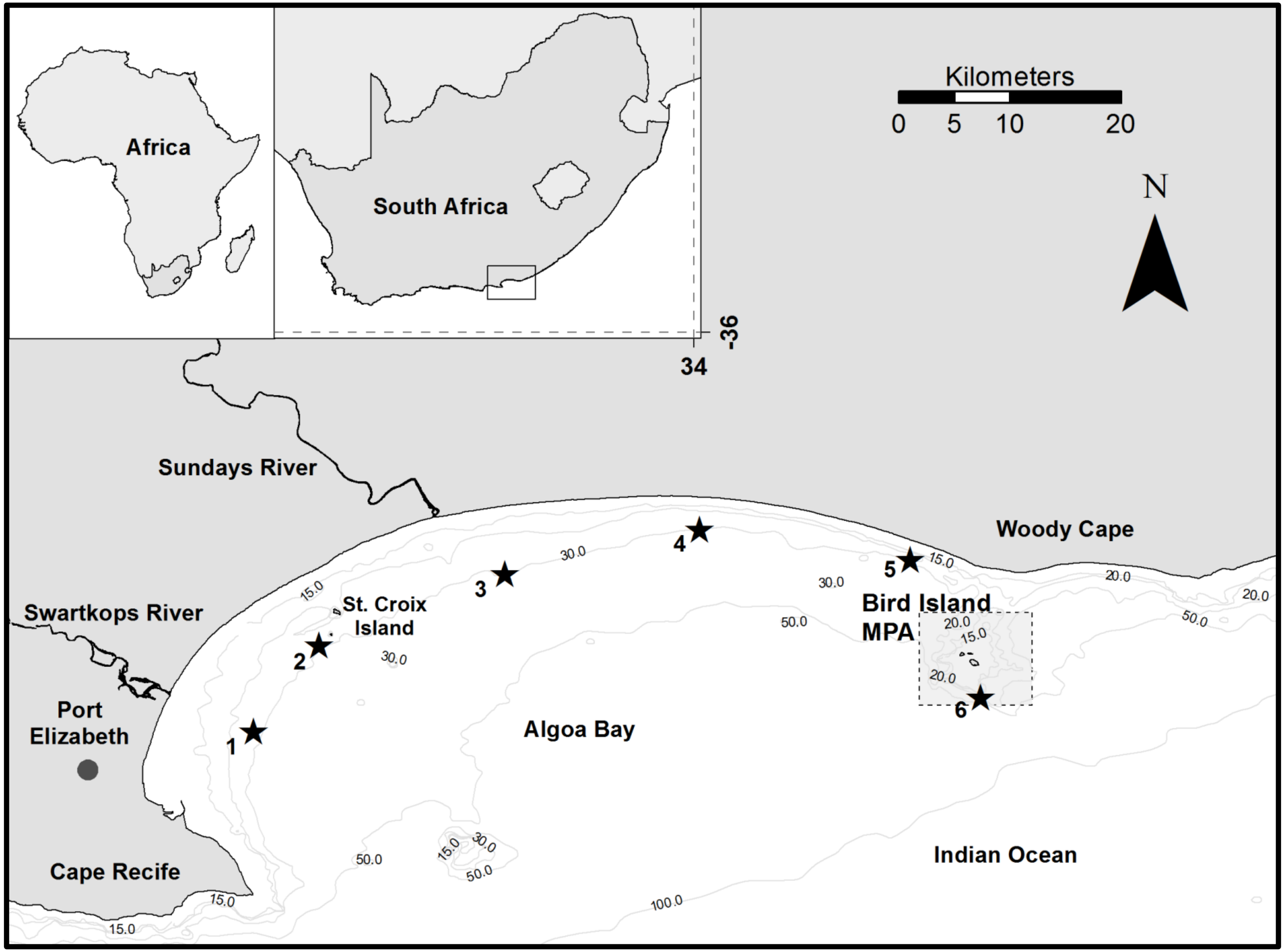

FIGURE 2.1 The geographic position of Algoa Bay, showing the location of the six sampling stations located on the 30 m depth contour in the nearshore

3.2 Field sampling and larval fish identification

The nearshore in the present study is defined at a depth of <30 m as observed in previous ichthyoplankton studies (Brewer and Kleppel, 1986; Roussel *et al.*, 2010). Larval fishes were sampled at six nearshore stations in Algoa Bay between the Port of Port Elizabeth in the western sector of the Bay (33°53′46″S; 25°42′08″E) and Bird Island in the east (33°52′07″S; 26°17′29″E). These stations were situated on the ~30 m depth contour. Collection of larval fishes took place by sampling once per month, weather permitting, for a period of two years. In total, 20 sampling trips took place between August 2010 and July 2012. Summer sampling took place in November, December and January and autumn sampling in February, March and April. Winter and spring sampling took place in May, June and July and in August, September and October respectively. At each station, larvae were collected by means of ski-boat based plankton ring net tows. The net consists of a 12 mm thick stainless steel ring fitted with a 4 m long plankton net and PVC cod-end. The net diameter was 750 mm and the mesh aperture 500 µm. A Kahlsico flowmeter was suspended from the frame at the opening of net and water flow passing through the opening of the net was measured. The ring net was pulled using a stepped oblique tow at a speed of ~2 knots. Three water levels were sampled including the near bottom (30 m), middle (15 m) and near surface (1 m). Each water level was sampled for 2 mins excluding hauling with each tow lasting ~8 mins. The density of larval fishes caught per haul are expressed as the number of larvae per 100 m^3. A total of 120 samples were collected over the study period. The plankton samples were fixed on site in 10 % formalin in seawater. At each station, sea temperature (°C), salinity, pH, dissolved oxygen (mg/L) and turbidity (NTU) were measured from the surface to the bottom four times every second on a single down and up cast using a conductivity-temperature-depth (CTD) profiler (SeaBird 19 plusV2 CTD SBE 55 carousel, Sea-Bird Electronics).

In the laboratory, larval fishes were removed, identified, counted and measured. Species were identified to the lowest possible taxon (Leis, 1991; Leis and Carson-Ewart, 2000; Moser et al., 1984; Neira et al., 1998; Okiyama, 1988; Olivar and Fortuño, 1991; Richards, 2005; Smith and Heemstra, 1995). Notochord length in preflexion and flexion larvae and standard length in postflexion larvae were measured to the nearest 0.1 mm and were referred to as body length (BL).

Microzooplankton biomass (mg/m^3) data and metadata pertaining to main ocean features during each sampling event were obtained from the continuous monitoring of the Elwandle

Node of the South African Environmental Observation Network (SAEON). Wind data were obtained at hourly intervals from three South African Weather Service (SAWS) stations and averaged per day. The three SAWS stations are located on Bird Island, 3 m above sea level (33°50′16.80″S; 26°17′9.60″E), at the Port Elizabeth Airport, 63 m above sea level (33°59′2.40″S; 25°36′36.00″E), and at the Port of Ngqura/Coega, 46 m above sea level (33°59′4.67″S; 25°40′4.80″E). Wind strength (m/s) was assigned a positive sign to indicate a westerly direction and a negative sign to indicate an easterly direction. Rainfall (mm) data which included total rainfall one month preceding sampling was similarly obtained from the three SAWS stations.

3.3 Data analyses

All physical and biological data were tested for normality using a normal probability plot and Shapiro-Wilk test and homogeneity of variance was tested using a Levene’s test with the STATISTICA software package version 11, 2012. All environmental and biological data were not normally distributed, even after appropriate transformations were used, however variances were homogenous. The non-parametric, Kruskal-Wallis (H) ANOVA, was used to assess differences in physico-chemical variables, fish densities and diversity indices between seasons, stations and ocean features.

Diversity indices including total species number (N), Shannon-Wiener diversity (H’), Margalef species richness (d) and Pielou’s evenness (J’) were calculated per station per sampling event, using the PRIMER statistical package version 6.1, 2013 (Clarke and Warwick, 1994). Shannon-Wiener diversity was calculated to one decimal point using $\log_e$. All environmental variables were normalized as they are not on comparable measurement scales by subtracting the mean and dividing by the standard deviation for each variable (Clarke, 1993). The nearshore environmental variations were analysed using principal coordinates (PCO) analysis with physico-chemical, microzooplankton biomass, wind speed, wind direction and rainfall data.

A Bray-Curtis similarity matrix for ocean features and seasons was generated from species density data which were square root transformed. Clusters in a dendrogram format were assessed using group hierarchical sorting and analysis of similarity (ANOSIM) was used to detect differences among groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or difference among seasons and ocean features.

A Poisson generalized linear model (GLM) with a log link function was used to analyse the spatial and temporal patterns in the variability of larval fish abundance in the nearshore of Algoa Bay. The most parsimonious GLM for larval fish density included all environmental variables. The following eight continuous independent environmental variables were included: microzooplankton biomass, sea temperature, salinity, turbidity, pH, dissolved oxygen, wind speed, wind direction and rainfall. Two categorical independent environmental variables were included namely season (winter, spring, summer, autumn) and oceanographic feature (mixed, stratified, Natal Pulse, upwelling, Agulhas Plume, thermocline). Model selection was based on the best subset procedure using Akaike information criterion (AIC).

4. RESULTS

4.1 Environmental variability

Seasonal variability in environmental variables were observed during the present study with a significant difference in turbidity ($H = 33.2$; d.f. = 3; $p < 0.001$), pH ($H = 20.1$; d.f. = 3; $p < 0.001$), dissolved oxygen ($H = 24.1$; d.f. = 3; $p < 0.001$) and rainfall ($H = 10.4$; $n = 114$; $p < 0.05$) occurring among the seasons (Figure 2.2). The mean turbidity and dissolved oxygen levels were highest during spring and lowest in summer. Mean pH values were highest during spring and lowest during autumn. Mean salinity was highest during summer and rainfall was highest during the winter months.

A significant difference in sea temperature ($H = 26.7$; d.f = 5; $p < 0.001$), turbidity ($H = 22.5$; d.f = 5; $p < 0.001$), pH ($H = 31.6$; d.f = 5; $p < 0.001$), dissolved oxygen ($H = 34.9$; d.f = 5; $p < 0.001$), microzooplankton biomass ($H = 25.3$; d.f = 5; $p < 0.001$) and wind ($H = 29.0$; d.f = 5; $p < 0.001$) was observed among the various ocean features identified during the present study (Figure 2.3). Highest mean temperatures (18.2 °C) and lowest mean dissolved oxygen (5.8 mg/L) and turbidity (0 NTU) were recorded when an Agulhas Plume entered Algoa Bay over the shelf. Lowest mean temperatures (15.0 °C) were recorded during upwelling events. Highest mean salinity (35.7), turbidity (2.3 NTU), pH (8.9) and dissolved oxygen (7.3 mg/L) was recorded when the water column was stratified. No significant variation however in sea temperature ($H = 1.5$; d.f = 5; $p = 0.9$), salinity ($H = 8.3$; d.f = 5; $p = 0.1$), turbidity ($H = 4.2$;

d.f = 5; p = 0.5), pH (H = 1.5; d.f = 5; p = 0.9), dissolved oxygen (H = 4.4; d.f = 5; p = 0.5) or wind (H = 1.9; d.f = 5; p = 0.9) was observed alongshore among the six sampling stations.

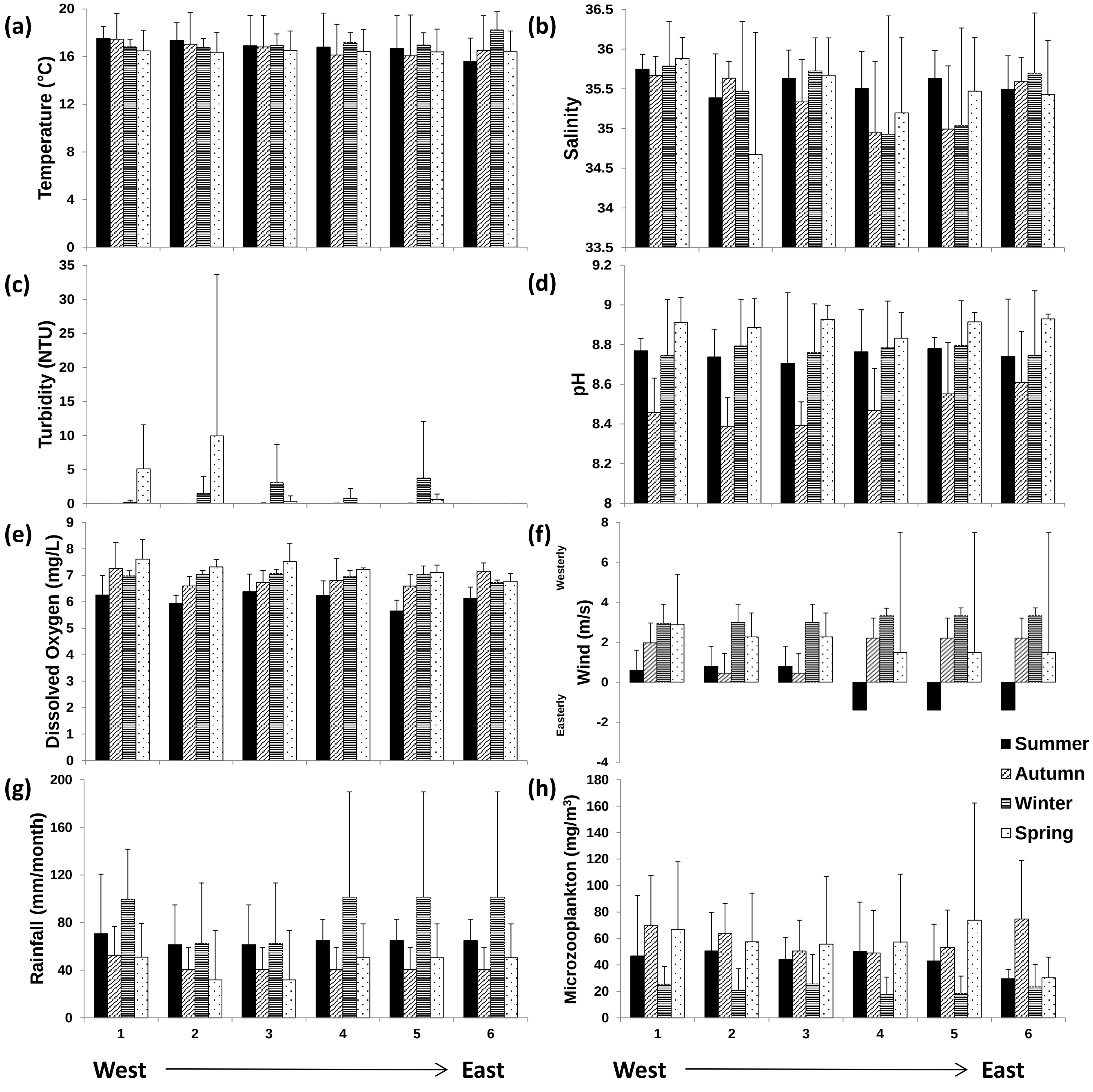

FIGURE 2.2 Mean (n = 5) and maximum of a) sea temperature, b) salinity, c) turbidity, d) pH, e) dissolved oxygen f) wind speed and direction, g) rainfall, h) microzooplankton recorded seasonally at each station in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

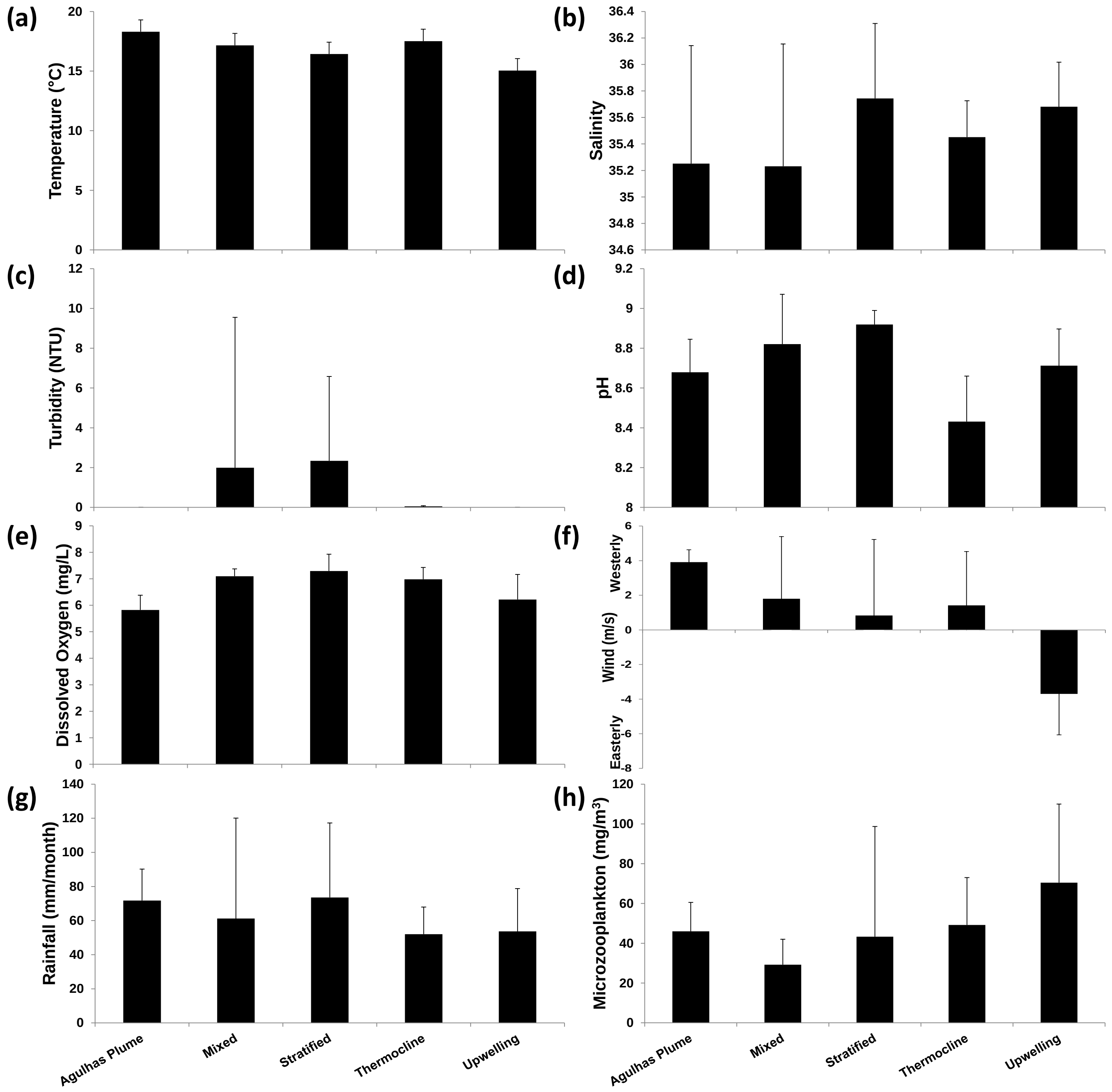

FIGURE 2.3 Mean (n = 24) and maximum of a) sea temperature, b) salinity, c) turbidity, d) pH, e) dissolved oxygen f) wind speed and direction, g) rainfall and h) microzooplankton recorded for each ocean feature during the study (August 2010 – July 2012)

Principal coordinates (PCO) analysis was performed on the environmental variables (Figure 2.4). The eight variables explained 39.8 % of the variation in the first two axes. The first two principal components described 22.5 % and 17.3 % of the nearshore variation respectively. A spatial gradient could be observed defined by the first principal component, which was characterised by a positive relationship with microzooplankton and dissolved oxygen and a negative relationship with wind, rainfall and sea temperature. The second principal component was characterized by a positive relationship with turbidity, salinity and pH.

4.2 Species composition

A total of 3619 larval fishes from 34 families and 88 species were captured using the plankton ring net in the nearshore of Algoa Bay (Table 2.1). The majority of larvae collected were in a preflexion stage. Engraulidae dominated the catch, with *Engraulis encrasicolus*, the only representative species from this family, comprising 38.4 % of the total catch. The second most abundant family was the Cynoglossidae and made a total contribution of 28.1 %, with *Cynoglossus capensis* and *C. zanzibarensis*, contributing 15.1 % and 13.0 % respectively. Sparidae (8.4 %) and Soleidae (7.4 %) made important contributions towards the overall larval fish catch. Smaller contributions towards the larval fish catch were made by the Blenniidae (3.5 %), Clupeidae (3.4 %), Gobiidae (2.2 %), Gobiesocidae (1.7 %), Tripterygiidae (1.5 %) and Haemulidae (1.4 %) fish families. All other fish family contributions were less than 1 % of the total catch.

4.3 Seasonal trends in larval fish density and diversity

A significant difference in larval fish density (H = 21.1; d.f. = 3; p < 0.001) was observed among the seasons with highest densities recorded during spring. With regards to the dominant fish families (Figure 2.5), a significant difference in the densities of Blenniidae (H = 14.1; d.f. = 3; p < 0.01) and Engraulidae (H = 17.0; d.f = 3; p < 0.001) occurred amongst the seasons with highest catches during spring. Similarly, highest densities of Gobiesocidae, Sparidae and Tripterygiidae were observed in spring. Amongst the dominant fish species (Figure 2.6), a significant difference in the densities of *Cremnochorites capensis* (H = 14.4; d.f = 3; p < 0.01) and *Spondyliosoma emarginatum* (H = 38.5; d.f = 3; p < 0.001) occurred among the seasons with highest densities in spring. A significant difference in the densities of Clupeidae (H = 12.1; d.f; p < 0.00) occurred amongst the seasons with highest catches in summer. The highest densities of *Sardinops sagax* (H = 12.1; n = 114; p < 0.01) was observed in summer. The Haemulidae had highest densities in summer. Highest densities of the Soleidae were in autumn with highest densities of *Heteromycteris capensis* (H = 12.1; n = 114; p < 0.01) similarly in autumn. Highest densities of Gobiidae were in winter. Highest densities of *Cynoglossus capensis* (H = 16.7; n = 114; p < 0.001) were observed in autumn while highest densities of *Cynoglossus zanzibarensis* (H = 10.2; n = 114; p < 0.05) was observed in spring.

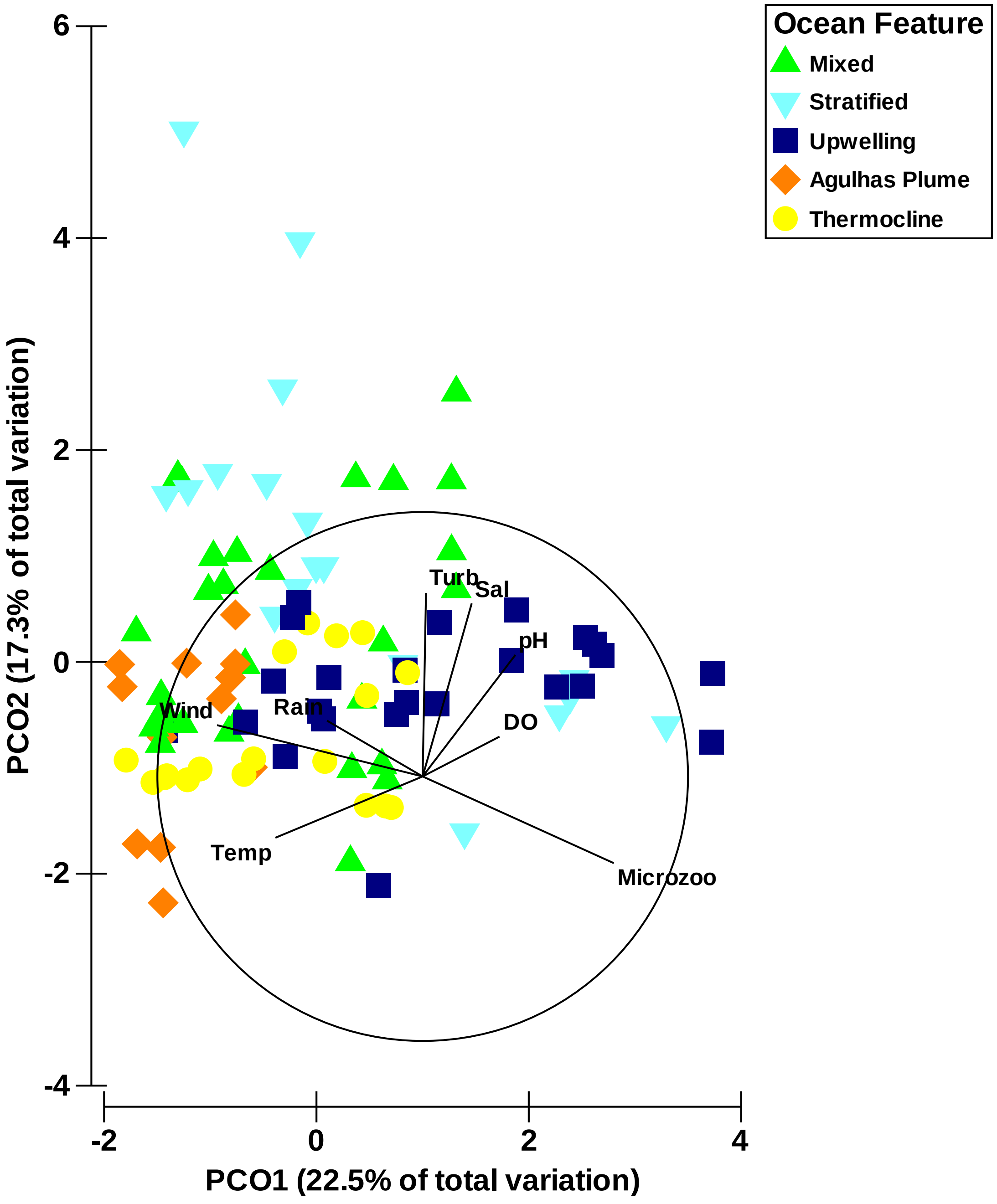

FIGURE 2.4 An ordination plot of the first two principal components illustrating each sampling event in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

TABLE 2.1 Species and taxa composition, mean density (range), total catch, mean body length (range) and developmental stage of larval fishes caught in the nearshore of Algoa Bay. Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile, Le = leptocephalus. Dominant developmental stages bolded

Family	Species	Density (no./100m^3)		Total catch		Body length (mm)		Developmental stage
		Mean	Range	No.	%	Mean	Range	
Ambassidae	Ambassidae sp 1	<0.1	0 – 1.6	1	<0.1	5.4		**F**
Anguillidae	*Anguilla mossambica*	<0.1	0 – 1.6	1	<0.1	55.0		**Le**
Blenniidae	Blenniidae sp 1	0.4	0 – 12.9	27	0.7	6.0	4.0 – 8.5	**Pr**, F
	Blenniidae sp 2	0.2	0 – 3.2	11	0.3	5.4	4.4 – 7.1	**Pr**, F
	Blenniidae sp 3	<0.1	0 – 1.6	2	0.1	4.7	3.2 – 6.7	**Pr**, **F**
	Blenniidae sp 4	0.2	0 – 6.5	15	0.4	7.2	3.2 – 9.7	Pr, **F**
	Blenniidae sp 5	0.1	0 – 6.5	4	0.1	10.4	8.8 – 12.2	**F**
	Blenniidae sp 6	0.3	0 – 6.5	18	0.5	2.8	1.8 – 3.7	**Pr**
	Omobranchus woodi	<0.1	0 – 1.6	1	<0.1	5.9		**F**
	Parablennius sp 1	0.5	0 – 9.7	33	0.9	3.7	2.5 – 6.3	**Pr**, F
	Parablennius sp 2	0.2	0 – 6.5	11	0.3	3.9	2.8 – 5.6	**Pr**
	Parablennius sp 3	0.1	0 – 1.6	4	0.1	7.1	7.0 – 7.3	**F**
Bramidae	*Brama brama*	<0.1	0 – 1.6	1	<0.1	3.8		**Pr**
Callionymidae	Callionymidae sp 1	<0.1	0 – 1.6	2	0.1	1.5	1.4 – 1.5	**Pr**
	Callionymis marlyi	0.1	0 – 4.8	5	0.1	2.1	1.4 – 3.5	**Pr**
Carangidae	*Caranx* sp 1	<0.1	0 – 3.2	2	0.1	2.5	2.2 – 2.8	**Pr**
	Seriola sp 1	<0.1	0 – 1.6	1	<0.1	3.1		**Pr**
	Seriola sp 2	0.1	0 – 3.2	6	0.2	2.4	1.6 – 3.2	**Pr**
	Trachurus trachurus	0.1	0 – 3.2	5	0.1	2.7	2.3 – 3.0	**Pr**
Cheilodactylidae	*Cheilodactylus* sp 1	0.2	0 – 11.3	12	0.3	3.5	3.0 – 4.0	**Pr**
	Cheilodactylus sp 2	<0.1	0 – 1.6	1	<0.1	4.5		**Pr**
Clinidae	*Clinus superciliosus*	<0.1	0 – 1.6	1	<0.1	8.4		**Po**
Clupeidae	*Etrumeus whiteheadi*	<0.1	0 – 3.2	3	0.1	10.4	5.6 – 14.6	**Pr**, F
	Sardinops sagax	1.7	0 – 40.3	119	3.3	4.0	2.0 – 9.5	Yo, **Pr**
Cynoglossidae	*Cynoglossus capensis*	7.7	0 – 153.2	547	15.1	3.2	1.0 – 7.2	**Pr**
	Cynoglossus zanzibarensis	6.6	0 – 377.5	470	13.0	3.2	1.5 – 9.0	**Pr**
Engraulidae	*Engraulis encrasicolus*	19.6	0 – 200.0	1388	38.4	3.3	1.7 – 15.0	Yo, **Pr**, F, Po
Gadidae	*Gaidropsarus capensis*	0.1	0 – 6.5	7	0.2	2.6	2.2 – 3.5	**Pr**
Gobiesocidae	*Chorisochismus dentex*	0.2	0 – 6.5	17	0.5	2.3	1.6 – 3.4	**Pr**
	Diplecogaster megalops	0.6	0 – 59.7	44	1.2	4.8	3.0 – 6.0	Pr, **F**
Gobiidae	*Caffrogobius gilchristi*	<0.1	0 – 1.6	2	0.1	3.3	2.5 – 4.0	**Pr**
	Caffrogobius nudiceps	1.0	0 – 33.9	74	2.0	2.6	1.2 – 4.2	**Pr**
	Gobiidae sp 1	<0.1	0 – 3.2	2	0.1	2.5	2.4 – 2.6	**Pr**
Gonostomatidae	Gonostomatidae sp 1	<0.1	0 – 1.6	1	<0.1	4.3		**Pr**
Haemulidae	Haemulidae sp 1	0.1	0 – 3.2	5	0.1	2.7	2.1 – 3.2	**Pr**
	Haemulidae sp 2	0.1	0 – 4.8	5	0.1	3.2	2.6 – 3.5	**Pr**
	Pomadasys sp 1	0.6	0 – 19.4	42	1.2	2.2	1.7 – 4.0	**Pr**
Kyphosidae	*Kyphosus* sp 1	0.2	0 – 14.5	16	0.4	2.5	2.0 – 3.2	**Pr**
Lutjanidae	*Lutjanus* sp 1	0.1	0 – 1.6	4	0.1	3.4	2.9 – 4.0	**Pr**
Merlucciidae	*Merluccius paradoxus*	<0.1	0 – 1.6	1	<0.1	2.5	2.4 – 2.6	**Pr**
Mugillidae	*Liza* sp 1	<0.1	0 – 1.6	1	<0.1	4.2		**Pr**
	Mugilidae sp 1	<0.1	0 – 1.6	1	<0.1	4.7		**Pr**
	Mugilidae sp 2	<0.1	0 – 1.6	1	<0.1	4.8		**Pr**
Myctophidae	*Benthosema* sp 1	<0.1	0 – 1.6	1	<0.1	4.1		**Pr**
	Diogenichthys atlanticus	<0.1	0 – 1.6	1	<0.1	4.3		**Pr**
	Lampanyctus lepidolychnus	<0.1	0 – 1.6	1	<0.1	3.5		**Pr**
Nomeidae	*Psenes whiteleggii*	<0.1	0 – 1.6	1	<0.1	10.8		**Po**
Pomacentridae	Pomacentridae sp 1	<0.1	0 – 1.6	1	<0.1	3.1		**Pr**
Priacanthidae	Priacanthidae sp 1	<0.1	0 – 1.6	1	<0.1	2.2		**Pr**
Sciaenidae	*Argyrosomus japonicus*	0.1	0 – 3.2	6	0.2	2.1	1.7 – 2.4	**Pr**
	Argyrosomus inodorus	0.2	0 – 6.5	11	0.3	2.9	2.0 – 4.0	**Pr**
	Sciaenidae sp 1	<0.1	0 – 1.6	3	0.1	3.0	2.3 – 3.4	**Pr**
Scorpaenidae	Scorpaenidae sp 1	0.3	0 – 4.8	18	0.5	3.3	2.2 – 4.8	**Pr**, F
Serranidae	Serranidae sp 1	<0.1	0 – 1.6	1	<0.1	4.5		**Pr**
Soleidae	*Austroglossus pectoralis*	0.6	0 – 27.4	45	1.2	2.6	1.1 – 4.6	Yo, **Pr**
	Dagetichthys marginatus	<0.1	0 – 1.6	1	<0.1	5.6		**F**
	Heteromycteris capensis	2.8	0 – 79.0	195	5.4	2.4	1.2 – 6.1	**Pr**, F
	Solea turbynei	0.4	0 – 9.7	28	0.8	2.3	1.3 – 4.3	**Pr**, F
	Soleidae sp 1	<0.1	0 – 1.6	1	<0.1	3.0		**Yo**
Sparidae	*Acanthopagrus* sp 1	<0.1	0 – 1.6	1	<0.1	4.4		**Pr**
	Argyrozona argyrozona	0.1	0 – 9.7	9	0.2	3.5	2.2 – 5.3	**Pr**, F
	Chrysoblephus laticeps	0.4	0 – 16.1	28	0.8	2.2	1.3 – 3.7	**Pr**
	Diplodus capensis	0.1	0 – 1.6	6	0.2	4.3	3.0 – 6.5	**Pr**, F
	Diplodus cervinus hottentotus	<0.1	0 – 1.6	2	0.1	5.8	4.2 – 7.3	**Pr, F**
	Lithognathus sp 1	<0.1	0 – 1.6	2	0.1	2.9	2.7 – 3.1	**Pr**

	Pagellus natalensis	0.4	0 – 8.1	31	0.9	2.8	2.0 – 4.6	**Pr**
	Rhabdosargus sp 1	0.1	0 – 1.6	6	0.2	3.8	2.5 – 5.7	**Pr**, F
	Sparidae sp 1	0.1	0 – 6.5	6	0.2	2.7	2.2 – 3.4	**Pr**
	Sparidae sp 2	0.4	0 – 11.3	30	0.8	2.4	1.6 – 3.3	**Pr**
	Sparidae sp 3	<0.1	0 – 1.6	1	<0.1	2.5		**Pr**
	Sparidae sp 4	0.3	0 – 12.9	20	0.6	3.0	2.1 – 4.2	**Pr**
	Sparidae sp 5	0.2	0 – 12.9	11	0.3	3.2	2.4 – 4.0	**Pr**
	Sparidae sp 6	0.1	0 – 3.2	7	0.2	2.9	2.1 – 3.5	**Pr**
	Sparidae sp 7	0.1	0 – 1.6	4	0.1	3.1	1.9 – 4.2	**Pr**
	Spondyliosoma emarginatum	2.0	0 – 37.1	140	3.9	3.0	1.7 – 6.2	**Pr**, F
Syngnathidae	*Syngnathus temminckii*	<0.1	0 – 1.6	2	0.1	21.5	13.2 – 29.7	**Po**
Teraponidae	*Pelates quadrilineatus*	<0.1	0 – 1.6	1	<0.1	2.8		**Pr**
Tetraodontidae	Tetraodontidae sp 1	<0.1	0 – 1.6	1	<0.1	2.1		**Pr**
	Tetraodontidae sp 2	<0.1	0 – 1.6	1	<0.1	3.9		**F**
Trigilidae	Trigilidae sp 1	0.2	0 – 3.2	11	0.3	2.9	2.0 – 3.5	**Pr**
	Trigilidae sp 2	0.1	0 – 4.8	5	0.1	3.6	3.2 – 4.4	**Pr**
Tripterygiidae	*Cremnochorites capensis*	0.8	0 – 33.9	56	1.5	5.8	3.8 – 8.0	**Pr**, F, Po
Unidentified	Unidentified sp 1	<0.1	0 – 1.6	1	<0.1	2.2		**Pr**
	Unidentified sp 2	<0.1	0 – 1.6	1	<0.1	2.6		**Pr**
	Unidentified sp 3	<0.1	0 – 1.6	3	0.1	3.2	2.9 – 3.5	**Pr**
	Unidentified sp 4	<0.1	0 – 1.6	1	<0.1	2.4		**Pr**
	Unidentified sp 5	<0.1	0 – 1.6	1	<0.1	2.2		**Pr**
	Unidentified sp 6	<0.1	0 – 1.6	1	<0.1	2.9		**Pr**

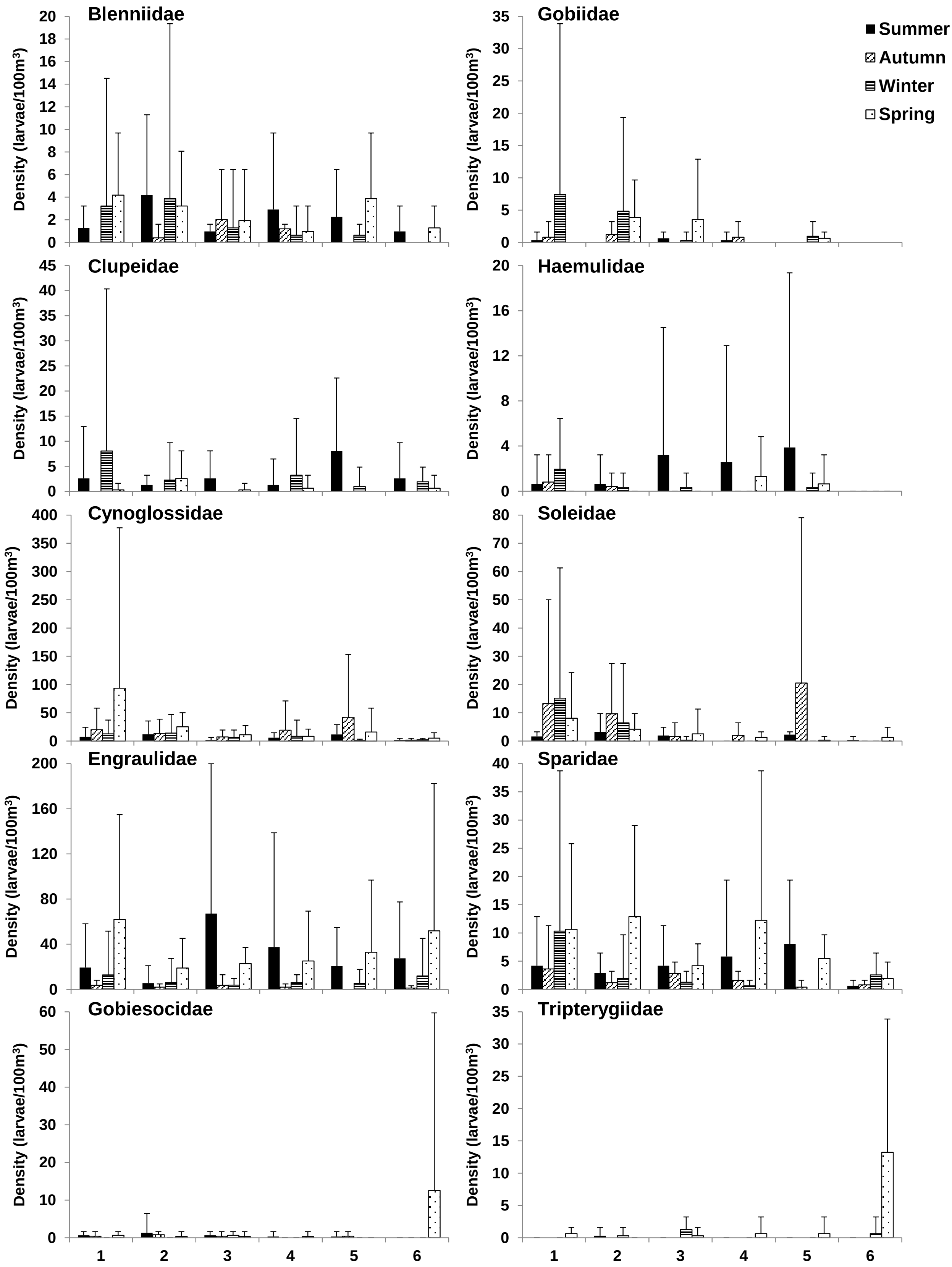

FIGURE 2.5 Mean (n = 5) and maximum density of dominant fish families recorded seasonally at each nearshore station in Algoa Bay during the study (August 2010 – July 2012). Sites run from east to west.

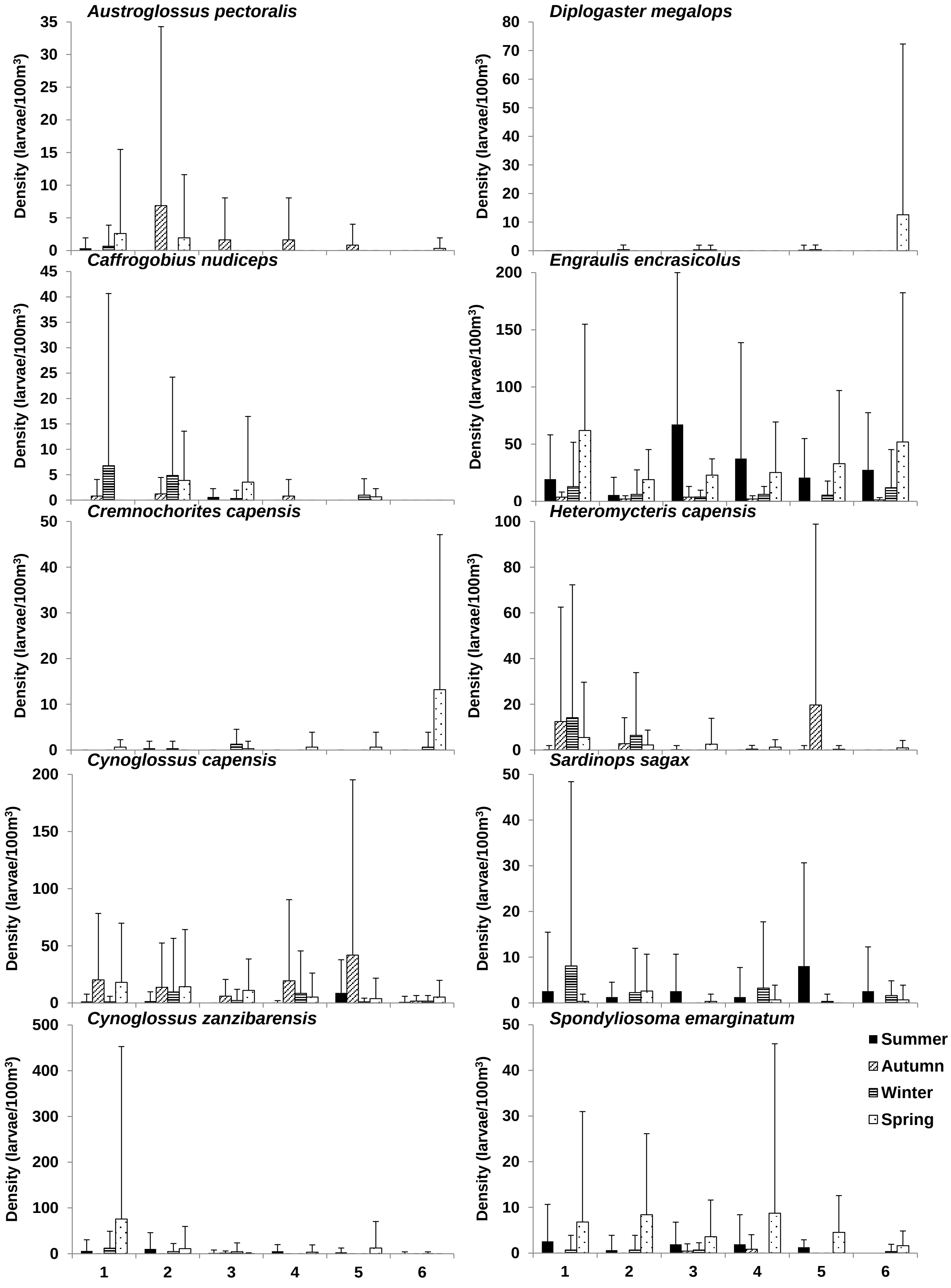

FIGURE 2.6 Mean (n = 5) and maximum density of dominant species recorded seasonally at each nearshore station in Algoa Bay during the study (August 2010 – July 2012). Sites run from east to west.

4.4 Trends in larval fish density and diversity related to ocean features

No significant statistical difference in larval fish density or diversity indices occurred spatially alongshore or among ocean features in the nearshore of Algoa Bay (Figure 2.7). However, significant differences in the densities of several of the dominant fish families were observed (Figure 2.8). The highest densities of Clupeidae (H =11.7; d.f. = 4; $p < 0.05$) and Engraulidae (H = 12.5; d.f = 4; $p < 0.05$) were observed when an Agulhas Plume entered Algoa Bay over the shelf. This trend was observed for the dominant species (Figure 2.9) with densities of *E. encrasicolus* (H = 12.5; d.f = 4; $p < 0.05$) and *S. sagax* (H = 11.7; d.f = 4; $p < 0.05$) highest when an Agulhas Plume entered Algoa Bay. Densities of Gobiidae were significantly (H = 15.6; n = 114; $p < 0.01$) higher when the entire water column was well mixed and that was particularly evident for *Caffrogobius nudiceps* (H = 12.6; d.f = 4; $p < 0.01$). Although not statistically significant, densities of Blenniidae, Cynoglossidae, Gobiesocidae, Sparidae and Tripterygiidae fish families were highest when the water column was stratified. Densities of *S. emarginatum* were significantly (H = 11.8; n = 114; $p < 0.05$) higher when strong thermoclines persisted in the water column. Highest densities of Haemulidae larvae were observed during upwelling events. Although not statistically significant, highest densities of the dominant soleids including *A. pectoralis* and *H. capensis* and the cynoglossid, *C. capensis*, were highest during upwelling events. Densities of *Cremnochorites capensis*, *C. zanzibarensis* and *D. megalops* were highest when the water column was stratified.

4.5 Multivariate analysis of larval fish community structure

Hierarchical classification using Bray-Curtis similarities was used to aggregate the most similar ocean features related to season for further analysis. Six communities were distinguished (Figure 2.10) with upwelling in autumn (Group 1), a mixed water column in summer (Group 2), and a stratified water column in winter (Group 5), forming outliers grouping out at the 27 %, 32 % and 38 % level of similarity respectively. The other ocean features related to season were more similar to each other forming three principal groups with a mostly summer assemblage (Group 3) grouping out at the 52 % level of similarity, a mostly spring mixed water column assemblage (Group 4) grouping out at the 46 % level of similarity and an autumn assemblage (Group 6) grouping out at the 43 % level of similarity. The SIMPER routine showed that in Group 3, four species contributed ~75 % towards the similarity and included *E. encrasicolus* (45.6 %), *Cynoglossus capensis* (13.9 %), *S. sagax* (9.3 %) and *P. natalensis* (6.8 %). Ten species contributed ~75 % towards the similarity in

Group 4 and included *E. encrasicolus* (22.2 %), *H. capensis* (9.0 %), *C. zanzibarensis* (8.8 %), *Cynoglossus capensis* (7.1 %), *Cremnochorites capensis* (6.6 %), *S. emarginatum* (6.2 %), Sparidae sp 2 (4.6 %), *Parablennius* sp 1 (4.0 %), *C. nudiceps* (3.6 %) and Blenniidae sp 2 (3.4 %). In group 6, three species contributed ~75 % towards the similarity and included *Cynoglossus capensis* (38.8 %), *E. encrasicolus* (26.9 %) and *P. natalensis* (11.0 %).

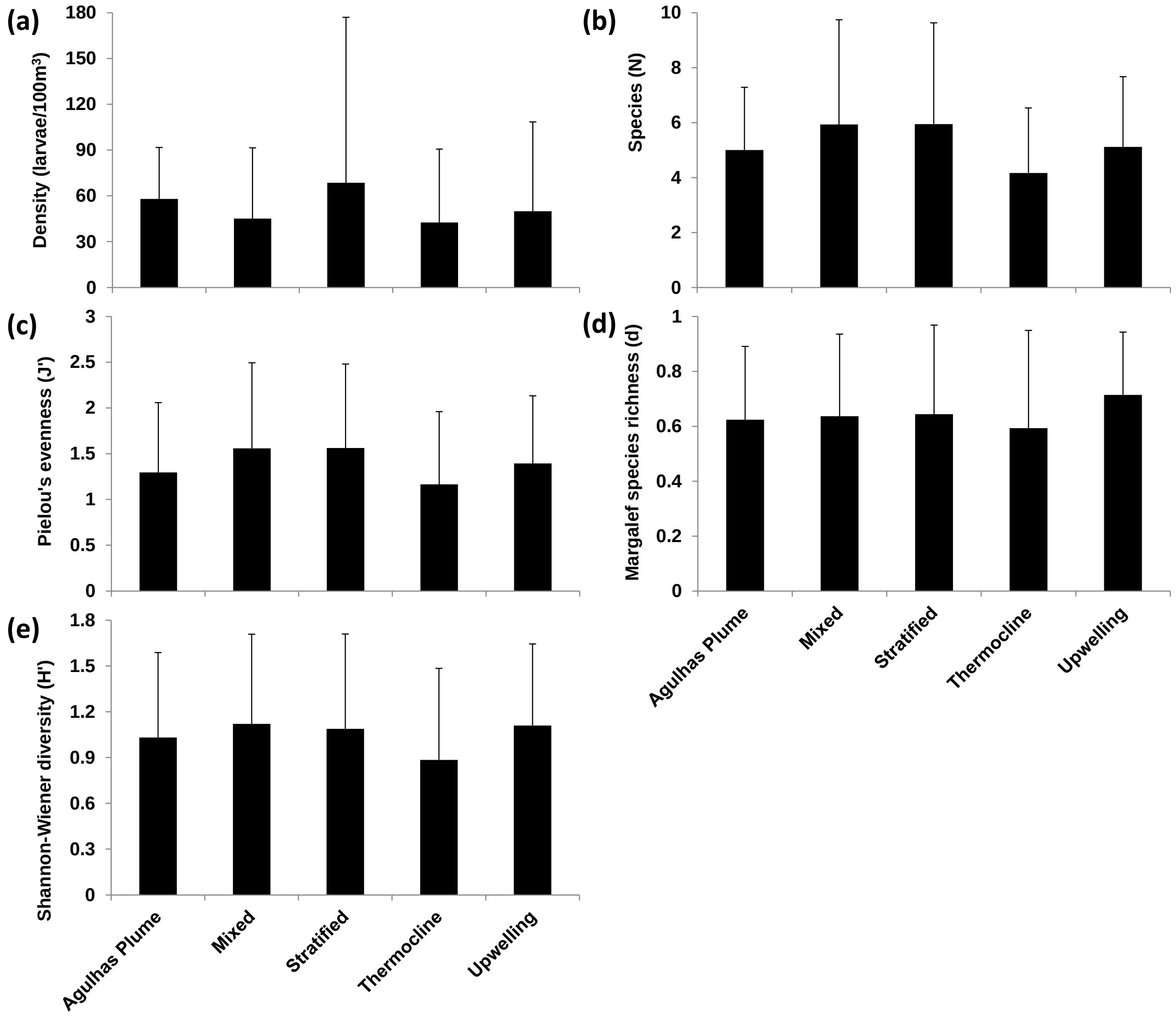

FIGURE 2.7 Larval fish mean (n = 24) and maximum of a) density, b) number of species, c) Pielou's evenness, d) Margalef species richness and e) Shannon-Wiener diversity recorded during each ocean feature occurring in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

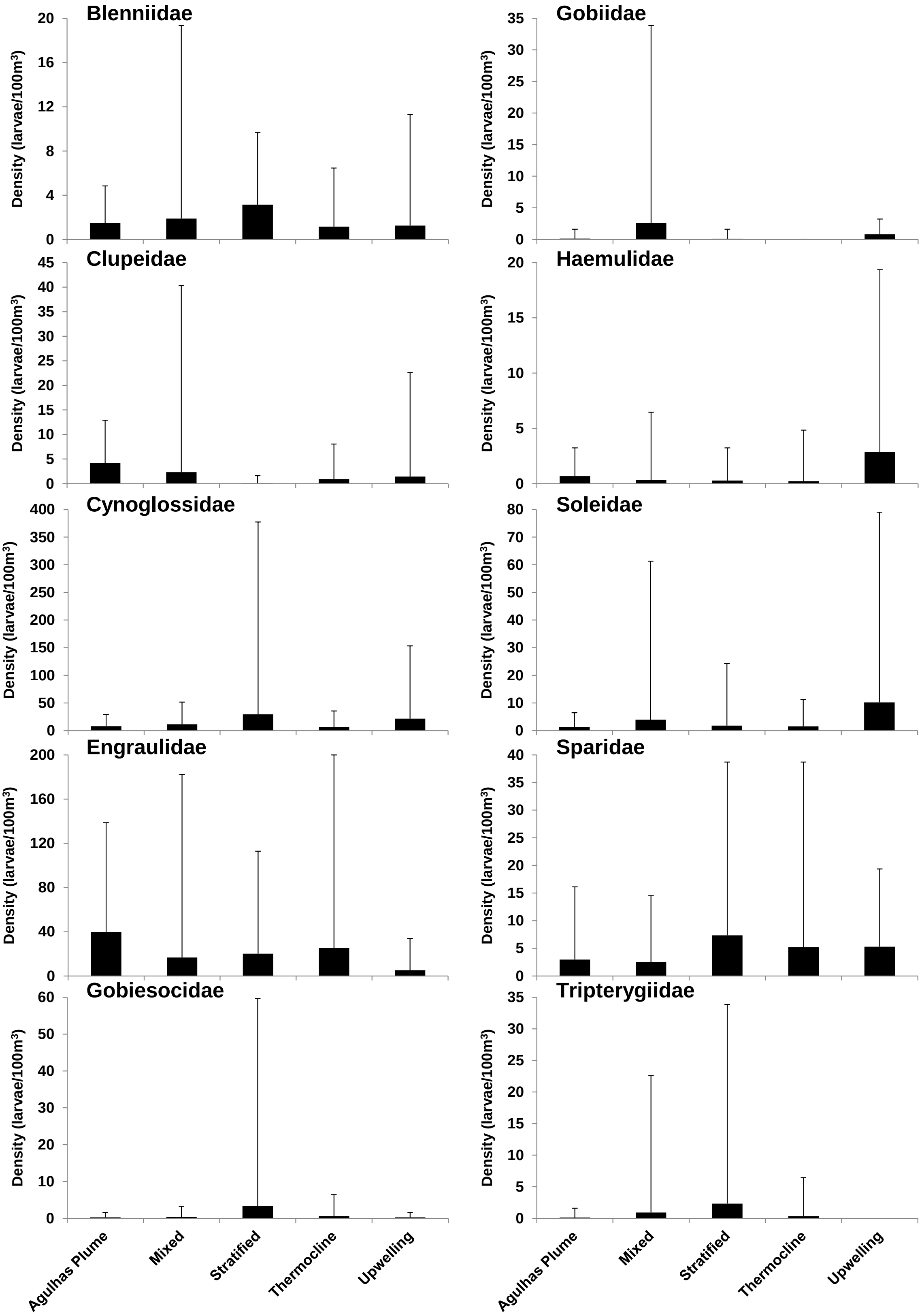

FIGURE 2.8 Mean (n = 24) and maximum density of dominant fish families recorded during each ocean feature in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

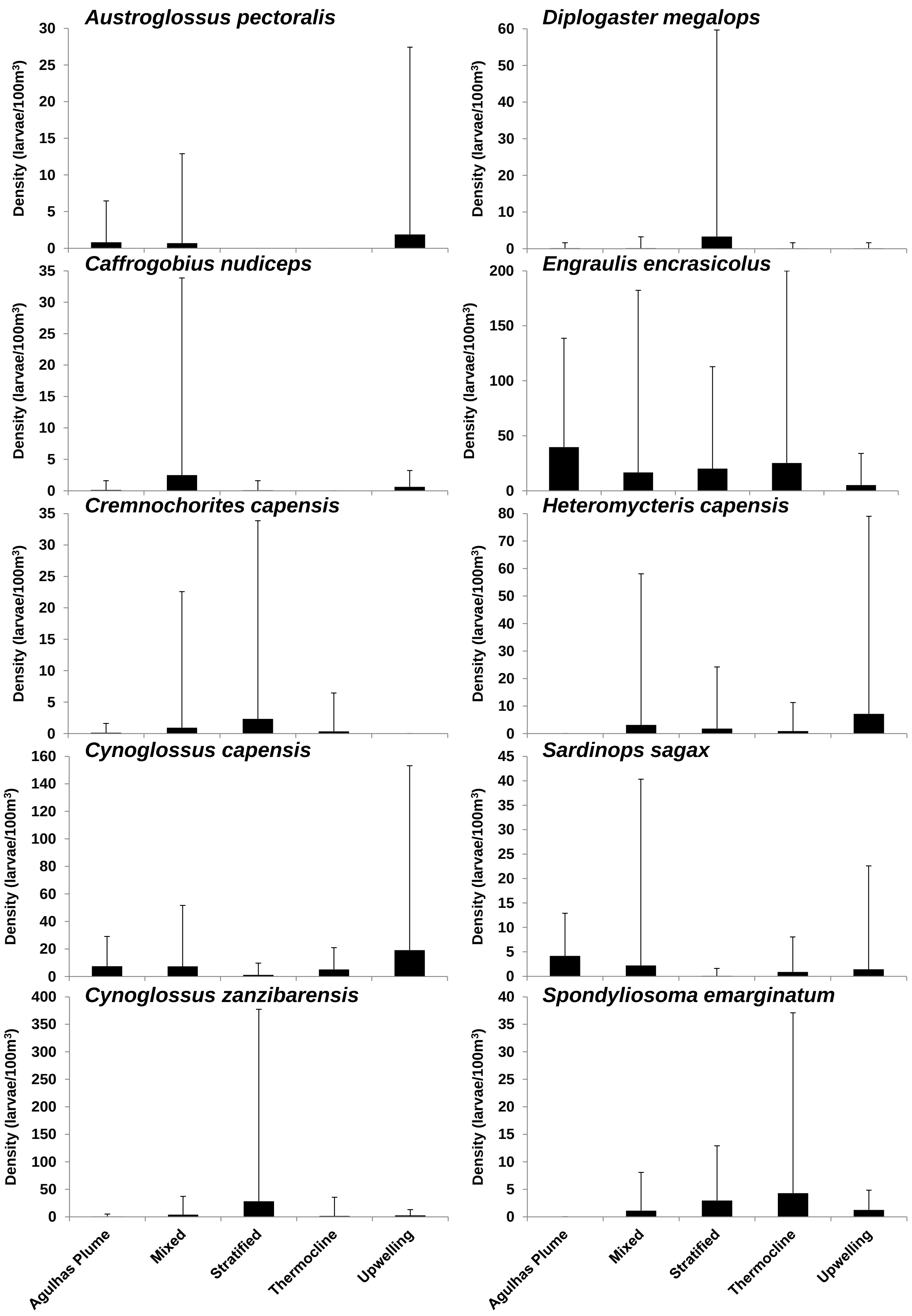

FIGURE 2.9 Mean (n = 24) and maximum density of dominant species recorded during each ocean feature in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

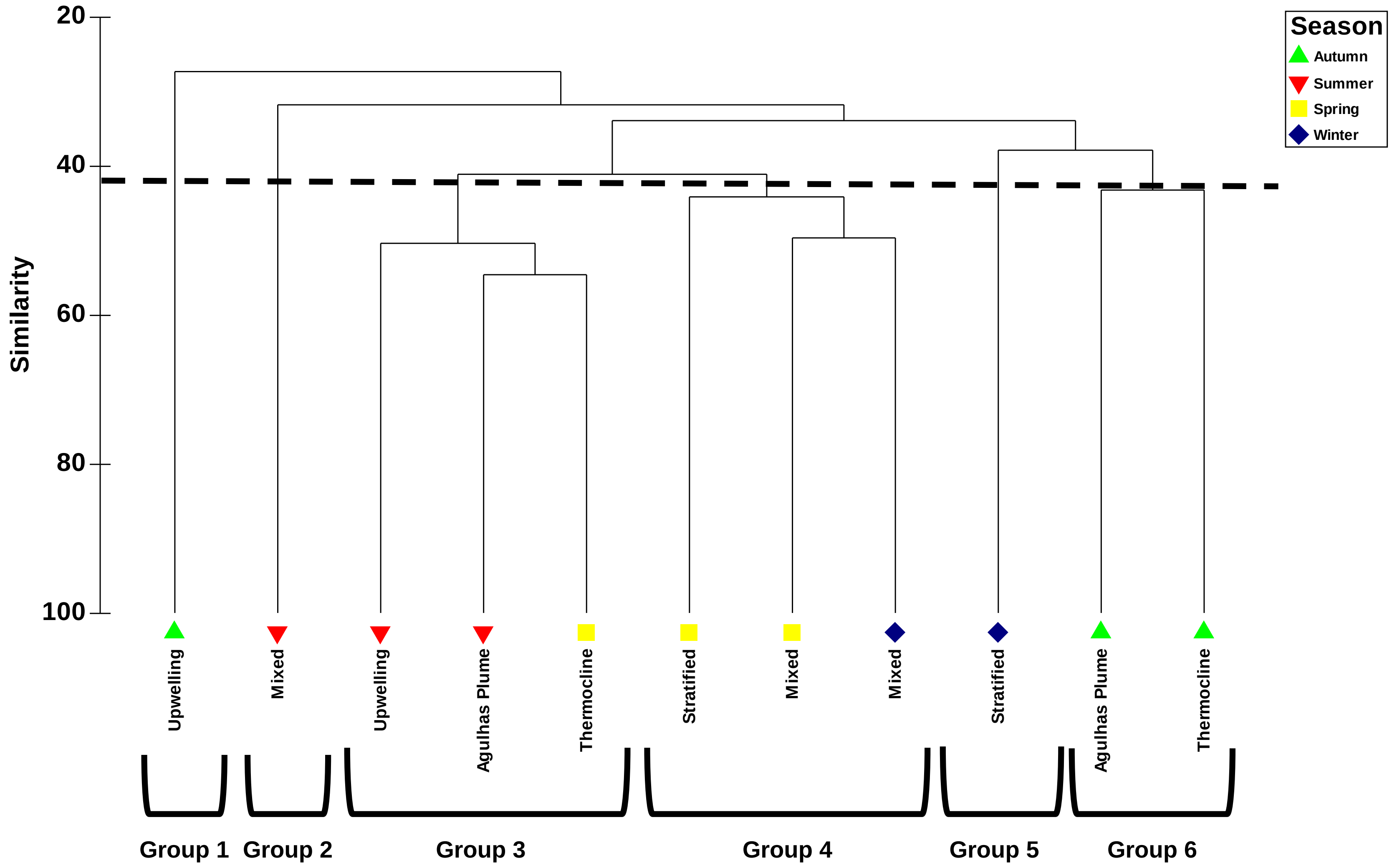

FIGURE 2.10 Bray-Curtis similarity dendrogram showing percentage similarity of samples measured by the square root transformed abundance of species associated with a seasonal ocean feature in the nearshore of Algoa Bay during the study (August 2010 – July 2012)

4.6 Generalized linear models of larval fish abundance

Larval fish density related positively to salinity, turbidity, rainfall, wind speed and wind direction and related negatively to microzooplankton biomass, sea temperature, pH and dissolved oxygen (Table 2.2). Mixed and stratified water column features were negatively related with larval fish density. The influence of the Agulhas Plume and upwelling related positively with larval fish density. Larval fish density related positively to the spring season but negatively to both the autumn and winter seasons. No significant relationships in environmental variables were observed for any of the diversity indices, excluding the number of species where a significant negative response to rainfall and a significantly positive response to the spring season were observed.

TABLE 2.2 Parameters of Poisson generalized linear models fitted to larval fish density and diversity indices. Significant effects ($p < 0.05$) are shown in bold

	Level of effect	Larval fish density	No. species	Evenness	Richness	Diversity
Intercept		**5.55**	-3.51	-8.08	-5.98	-8.16
Microzooplankton		**-0.01**	0.01	0.01	0.01	0.01
Temperature		**-0.27**	0.05	0.11	0.07	0.11
Salinity		**0.09**	0.10	0.14	0.05	0.14
Turbidity		**0.06**	0.01	0.01	-0.01	0.01
pH		-0.04	0.12	0.17	0.22	0.18
DO		-0.04	-0.05	0.04	0.07	-0.01
Wind		**0.10**	-0.01	-0.03	-0.03	-0.02
Rain		**0.01**	**-0.01**	-0.01	-0.01	-0.01
Ocean Feature	Mixed	**-0.17**	0.03	0.09	-0.05	0.08
	Stratified	**-0.94**	-0.01	0.19	0.10	0.14
	Upwelling	**0.62**	-0.01	-0.14	-0.07	-0.10
	Agulhas Plume	**0.72**	0.12	-0.04	0.01	-0.03
Season	Winter	**-0.41**	0.05	0.04	0.16	0.11
	Spring	**1.50**	**0.25**	-0.11	-0.27	-0.13
	Summer	**-0.41**	0.01	0.15	0.11	0.11
Pseudo R^2		0.34	0.36	0.27	0.20	0.26
AIC		4230.0	527.5	255.6	218.1	231.5

Amongst the three dominant fish families and species, various responses to the environmental variables were observed (Table 2.3). The dominant fish family, the Engraulidae represented exclusively by *Engraulis encrasicolus*, related positively to turbidity, dissolved oxygen, wind speed, wind direction and rainfall and related negatively to microzooplankton biomass, sea temperature, salinity and pH. Mixed and stratified water column features were negatively related. Upwelling and the influence of the Agulhas Plume were positively related with Engraulidae density. Furthermore, the engraulids responded positively to both the spring and the summer season but negatively to the winter season. The second dominant fish family, the Cynoglossidae, had several similar relations to environmental variables as the Engraulidae.

These included the positive relationship to turbidity, dissolved oxygen, rainfall, wind speed and wind direction, and the negative relationship to microzooplankton biomass and sea temperature. A positive relationship to salinity and pH however was observed with the cynoglossids. A mixed water column, upwelling and the Agulhas Plume were positively related with Cynoglossidae density and a stratified water column was negatively related with Cynoglossidae density. The cynoglossids related positively to the spring season but negatively to both the winter and summer season. A mixed water column related negatively to the Sparidae densities. When a stratified water column persisted densities of Sparidae related negatively. With regards to upwelling and the Agulhas Plume, the sparids related positively.

TABLE 2.3 Parameters of Poisson generalized linear models fitted to the three dominant fish families and three dominant species occurring in the nearshore of Algoa Bay. Significant effects ($p < 0.05$) are shown in bold

	Level of effect	Cynoglossidae	Engraulidae	Sparidae	*Cynoglossus capensis*	*Cynoglossus zanzibarensis*	*Engraulis encrasicolus*
Intercept		**-13.53**	**41.06**	1.65	-1.59	**-38.51**	**41.06**
Microzooplankton		**-0.01**	**-0.02**	0.00	**-0.00**	**0.02**	**-0.02**
Temperature		**-0.37**	**-0.14**	**0.14**	**-0.38**	**-0.75**	**-0.14**
Salinity		**0.39**	**-0.62**	-0.09	0.08	**1.52**	**-0.62**
Turbidity		**0.13**	**0.12**	**-0.08**	**0.08**	**0.23**	**0.12**
pH		**0.47**	**-1.70**	0.06	**0.57**	**-1.30**	**-1.70**
DO		**0.52**	0.05	0.03	**0.20**	**0.68**	0.05
Wind		**0.21**	**0.11**	0.03	**-0.04**	**0.63**	**0.11**
Rain		**0.01**	**0.01**	**-0.00**	**0.00**	**0.02**	**0.01**
Ocean Feature	Mixed	**0.20**	**-0.86**	**-1.09**	**-0.34**	**1.33**	**-0.86**
	Stratified	**-1.36**	**-1.14**	-0.12	**-3.20**	-0.48	**-1.14**
	Upwelling	**1.51**	0.02	**0.93**	**1.24**	**3.13**	0.02
	Agulhas Plume	**0.58**	**1.32**	0.20	**2.29**	**-1.73**	**1.32**
Season	Winter	**-1.58**	**-0.30**	**0.88**	0.02	**-1.68**	**-0.30**
	Spring	**2.01**	**2.55**	**0.84**	**1.86**	**3.62**	**2.55**
	Summer	**-0.82**	**0.59**	**-0.34**	**-1.97**	**1.20**	**0.59**
Pseudo R^2		0.44	0.69	0.29	0.51	0.80	0.69
AIC		2218.0	1794.8	764.5	1184.5	1223.1	1794.8

5. DISCUSSION

The fish larvae captured in the nearshore of Algoa Bay reflect the highly diverse and endemic fish fauna of the coastal warm-temperate region of South Africa. Conspicuous assemblages of larval fishes from a variety of species with different adult habitats occur in the nearshore (Hernández-Miranda *et al.*, 2003; Koutrakis *et al.*, 2004; Azeiteiro *et al.*, 2006). Engraulids which dominated catches in the nearshore of Algoa Bay also dominate in the nearshore habitats of the northwestern Atlantic (Able *et al.*, 2010), Mediterranean (Olivar *et al.*, 2001; Sabatés *et al.*, 2007) and central Chile (Hernández-Miranda *et al.*, 2003). Horizontal shifts in species assemblages occurs in the nearshore with increasing distance from shore (Leis and Miller, 1976; Richardson and Pearcy, 1976; Leis, 1982; Marliave, 1986; Hernández-Miranda *et al.*, 2003; Borges *et al.*, 2007). The dominance of larvae from benthic spawning adults is a characteristic prevalent among larval fish assemblages close to shore (Young *et al.*, 1986; Sabatés, 1990; Suthers and Frank, 1991). This mode of spawning is a major factor contributing to the retention of larvae in nearshore environments. In the nearshore of Oahu, Hawaii, larvae from oceanic adults and benthic or brooded eggs from reef fishes, dominated catches (Leis, 1982). Larvae of reef fishes with pelagic eggs were thought to probably be found more than 3 km offshore (Leis, 1982). The inshore distribution pattern observed for species that have benthic eggs has been suggested to occur due to the spawning strategy of the adults and the low dispersal due to the non-pelagic nature of the eggs (Hernández-Miranda *et al.*, 2003). Coastal species producing pelagic eggs, including species in the Cynoglossidae, Sparidae and Soleidae fish families, made important contributions towards the overall larval fish catch in the Algoa Bay nearshore. A paucity of coastal species that spawn pelagic eggs occur closer to shore (<15 m) where larvae hatching from benthic eggs dominate catches in the shallower nearshore areas of Algoa Bay (Beckley, 1986; Pattrick and Strydom, 2008). This study support the trend of discrete larval fish assemblages occurring horizontally from shore as observed internationally.

Evidence supporting the importance of the nearshore for the early life history stages of fishes is growing internationally (Sponaugle and Cowen, 1996; Hernández-Miranda *et al.*, 2003; Borges *et al.*, 2007; Able *et al.*, 2010). Preflexion larval fish are common in the nearshore indicating these areas provide important habitat for recently hatched individuals (Able *et al.*, 2010). Similarly, preflexion larvae dominated catches in the nearshore of Algoa Bay signifying the importance of this environment for newly hatched larvae. The importance of this habitat for the very early developmental stages has previously been highlighted within the Bay itself (Pattrick and Strydom, 2008). The shallow (<15 m) nearshore has been identified as an important nursery for several species (Pattrick and Strydom, 2008). The pelagic larval phase of both *E. encrasicolus* and the reef associated tripterygiid *Cremnochorites capensis* is being completed in the nearshore of Algoa Bay. This highlights the importance of the nearshore as a nursery area for these species.

Environmental variability together with ocean features that persist in the nearshore of Algoa Bay, were found to be important in describing larval fish variability. Spawning will often take place close to gyres, upwelling or other directional oceanographic transport systems (Richardson and Pearcy, 1976; Norcross and Shaw, 1984; Sherman *et al.*, 1984; Landaeta and Castro, 2002). This is advantageous for fish larvae, who not only require sufficient and suitable food during their transit to reach nursery areas, but appropriate mechanisms of transport (Norcross and Shaw, 1984). Ocean features serve such a function. Ocean eddies and density fronts for example act as mechanisms for confinement and concentration and play a major role in determining patterns of abundance and distribution of larval fish populations (Lobel and Robinson, 1986; Kingsford, 1990; Grimes and Finucane, 1991; Cowen and Castro, 1994; Sabatés and Olivar, 1996). Mesoscale eddy systems can entrain and entrap larvae, with a sufficient residence time for many species to complete their pelagic developmental phase (Lobel and Robinson, 1986). In the nearshore of Algoa Bay the occurrence of dominant fish species differed in relation to ocean features. Examining patterns of larval abundances in relation to ocean features provides insight into the spawning strategies of coastal fishes to prevailing physical processes. It has been hypothesized that spawning strategies of marine fish populations have evolved in response to prevailing oceanographic conditions (Parrish *et al.*, 1981; Frank and Leggett, 1983; Doyle *et al.*, 1993).

The Engraulidae, which are not only an important economic fishery in South Africa, but play a crucial role in the marine food webs in many ecosystems, were numerically dominant in the nearshore of Algoa Bay. Anchovy in southern Africa spawn in temperatures ranging between 16 – 20 °C (Richardson *et al.*, 1998; Twatwa *et al.*, 2005). It is in these temperature ranges that high copepod production occurs providing a good food environment for larval fishes (Richardson *et al.*, 1998). Therefore it is unsurprising that during the present study, the highest densities of anchovy were observed during Agulhas Plume intrusions into Algoa Bay when mean sea temperatures were highest (~18 °C) and microzooplankton biomass was simultaneously high. The occurrence of *E. encrasicolus* larvae in the Algoa Bay region therefore seems to take advantage of high levels of microzooplankton production that prevail when the Agulhas Plume enters the Bay. Larval anchovy densities were also high when a strong thermocline was evident in the water column. Anchovy spawning is associated with weak winds and therefore stratified, stable water column conditions in southern Africa (Twatwa *et al.*, 2005). Furthermore, anchovy eggs are known to be restricted to the upper-mixed warm layer above the thermocline (Shelton and Hutchings, 1990). The reproductive success of anchovy has also been linked to reduced vertical circulation resulting in a stable water column (Lasker, 1978).

The highest densities of *S. sagax*, similarly an important economic and ecological fish species, occurred when warm water plumes originating from an Agulhas Current meander (Goschen pers. comm.) entered Algoa Bay. Similarly, the Peruvian sardine *S. sagax* spawns in association with relatively warm water with larvae also most abundant at warmer temperatures (Schwartzlose *et al.*, 1999). The Agulhas Current sweeps closely along the shelf break at a depth of ~200 m and only 50 km offshore of Algoa Bay. Several shear-edge eddies bud off the inner edge of the current at frequent intervals and reverse currents within these eddy regions generate a net movement of near-surface waters in a north-east direction (Boyd and Shillington, 1994). This counter flow of water in the opposite direction to the offshore south-westerly flow of the Agulhas Current would allow for eggs and larvae spawned along the shelf-edge to be transported into the Algoa Bay region. Strong winds, particularly westerly winds, were observed during these Agulhas Plume events. Meanders in the Agulhas Current cause Agulhas water to move onto the shelf but wind-forcing drives the water farther over the shelf into Algoa Bay (Goschen and Schumann, 1994). The results therefore suggest that favourable conditions for sardine larvae occur in conjunction with potentially favourable larval retention conditions. This has been observed with sardine larvae in southwestern Australia where eggs and larvae are retained over the shelf due to the presence of the Capes Current, a wind-induced counter-current that flows sporadically northwards (Muhling *et al.*, 2008a). The particular spawning strategy of sardine, which includes year-round spawning, will allow for larvae to hatch during times of favourable retention increasing survivorship (Hutchings *et al.*, 2002).

Densities of coastal species with benthic spawning responded negatively to upwelling events. Should upwelling occur during spawning, its effect would more likely be detrimental as offshore transport of larvae would occur. It appears that coastal species with benthic eggs will avoid spawning during upwelling to avoid the offshore transport of their larvae. Deeper distribution of larvae would render these species liable to shoreward transport in the deep onshore flow that is associated with coastal upwelling (Smith and Suthers, 1999). Similarly, in the temperate regions of the Pacific and Atlantic, spawning patterns of coastal assemblage taxa have been shown to be adapted to prevailing circulation patterns (Doyle *et al.*, 1993). Larvae are scarce in regions associated with upwelling and offshore Ekman transport (Doyle *et al.*, 1993). The coastal species producing benthic eggs tend to spawn during winter and spring, rather than during the summer season when upwelling occurs in the Bay. Coastal fish species in temperate waters similarly spawn during late winter and early spring, when surface drift is generally directed towards the coast, rather than during the more productive upwelling season (Doyle *et al.*, 1993).

Similarly, densities of *E. encrasicolus* were significantly lower during upwelling events. Vigorous upwelling on the coast of northern California has also led to a paucity of larvae with pelagic eggs such as the Californian anchovy, *Engraulis mordax* (Parrish *et al.*, 1981). The early developmental swimming abilities of the clupeiforms are known to be very weak (Fisher *et al.*, 2005), therefore engraulid larvae with near-surface distributions would be more susceptible to transport offshore in the Ekman layers associated with coastal upwelling (Smith and Suthers, 1999). Within the Canaries-African Coastal Transition Zone, the eggs and larvae of anchovy are concentrated near-surface and have been observed to be transported offshore of the African continental shelf within the Ekman layer (Rodríguez *et al.*, 2006). Alternatively, the displacement of fish larvae could arise through active behavioural responses to changes in hydrography as even young larvae could use buoyancy adjustment to allow for considerable vertical and horizontal migration (Smith and Suthers, 1999). Several studies have indicated that plankton distributions are often defined by hydrodynamic boundaries but are maintained by planktonic behaviour (Sameoto, 1984; Boucher *et al.*, 1987).

Three species of flatfishes including *A. pectoralis*, *H. capensis* and *Cynoglossus capensis*, had positive responses to upwelling events which were associated with highest microzooplankton biomass, suggesting that the spawning of these species is timed to maximize food availability for larvae. Upwelling can be favourable serving as a major mechanism for surface nutrient replacement, resulting in a productive environment. If upwelling should occur prior to a species spawning it is therefore likely to aid larval survival

(Parrish *et al.*, 1981). During upwelling events, primary production is high with species succession resulting in the presence of particular desirable food organisms resulting in good larval feeding conditions (Lasker, 1981). Sole larvae are diurnal predators feeding on zooplankton during their pelagic phase (Last, 1978). Upwelling appears to be advantageous for particular species in the nearshore of Algoa Bay.

Results from this study have shed light on the nearshore dynamics of larval fish assemblages in Algoa Bay in association with broad scale oceanographic features. This study identified that larval fish distribution is characterized by high temporal heterogeneity related to ocean features in the nearshore coupled with seasonality. Sharp changes in larval fish assemblages can be attributed to both patterns of adult spawning and changes in water masses. The findings from the present suggest a link between the occurrence of ocean features and larval fish abundance for specific species.

6. ACKNOWLEDGEMENTS

South African Environmental Observation Network (SAEON) Elwandle Node are thanked for technical and logistical support of fieldwork. Fieldworkers are thanked for their valuable assistance. Mr Danie Venter is thanked for statistical advice. Prof. Tony Booth and Dr Ané Oosthuizen are thanked for commenting on a draft copy of this chapter. Mr Tim Vink is thanked for generation of the map in this chapter.

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CHAPTER 3

SPATIAL AND TEMPORAL PATTERNS IN OCCURRENCE OF LARVAL AND SETTLEMENT STAGE FISHES ON REEF HABITATS IN ALGOA BAY, SOUTH AFRICA

1. ABSTRACT

Light traps and a plankton ring net were concurrently used to investigate the larval and settlement stage fish assemblages associated with varying reef habitat types in the warm-temperate waters of Algoa Bay, South Africa. Sampling was conducted over 12 nights spanning a two-year period from June 2010 to February 2012. Four habitat types were sampled namely high profile reef, low profile reef, reef-associated sand and sand. A total of 4084 larvae and settlement stage fishes belonging to 31 teleost families and 84 species were captured in the study area. Three times as many families and five times as many taxa were captured by the plankton net compared to the light traps. Seventy taxa were caught exclusively by the plankton net while six taxa were caught exclusively by the light traps. The present study indicates that reef profile, associated physico-chemical variables, and the start or the end of the spawning period, were important characteristics determining larval fish availability. Larval fishes were abundant at the end of the spawning period. Unique patterns of species assemblages between the various habitats were found. Larval fish abundances, densities and species richness varied depending on the habitat complexity. Reef-associated sand and sand habitats yielded higher species richness and diversity than the high and low profile reef habitats. The importance of sand habitats for larval fish assemblages are highlighted. Significantly greater mean lengths of larvae whose adults are sand associated were observed in the sand habitat. Mean body lengths of larvae whose adults are reef associated were greater at the reef habitats. Results indicate that the light trap samples complemented those taken by the plankton net.

2. INTRODUCTION

The early life history of coastal fishes is complex and includes a pelagic dispersing larval phase in an open water environment followed by a settlement phase where suitable habitat for settlement is targeted (Leis, 1991; Leis *et al.*, 2003). The pelagic larval stage in the early development of temperate fish species has had some research attention (Beldade *et al.*, 2006; Leis *et al.*, 2006; Borges *et al.*, 2007; Pattrick and Strydom, 2008; Álvarez *et al.*, 2012). Information pertaining to the settlement of late stage fishes on tropical coral reefs is gradually accumulating (Doherty, 1987; Brogan, 1994; Milicich, 1994; Milicich and Doherty, 1994; Sponaugle and Cowen, 1996b; Sponaugle and Cowen, 1996a; Öhman *et al.*, 1998; Hendriks *et al.*, 2001; Kingsford, 2001; Wilson, 2001; Kingsford *et al.*, 2002; Paris and Cowen, 2004; Montgomery *et al.*, 2006; Grorud-Colvert and Sponaugle, 2009), however there is very little information available on the settlement of larvae of coastal temperate fishes that live as adults on temperate subtidal reefs or open sand habitats.

Fishes have varying habitat requirements depending on their ontogenetic stage. Juveniles often utilize shallow coastal habitats before moving into adult habitats, with these shallow habitats serving as source areas of juveniles for recruitment (Parrish, 1989; Nagelkerken *et al.*, 2000a; Nagelkerken *et al.*, 2000b; Nagelkerken *et al.*, 2001; Cocheret de la Morinière *et al.*, 2002; Nagelkerken *et al.*, 2002). Research on post-settlement fishes indicates that various migration patterns occur including short and long distance migrations or stepwise migrations using a succession of different habitat types as they grow (Cocheret de la Morinière *et al.*, 2002).

Site selection by late stage larvae may have an effect on the distribution of juveniles (Adams *et al.*, 2006), therefore the need arises for a greater understanding of the habitat characteristics that influence settlement and post-settlement of coastal fishes. The structural complexity of the underlying reef substrate, which ultimately determines the availability of niches, is an important environmental parameter that drives the abundance and distribution of species (Pais *et al.*, 2013). Increased recruitment and survival of fishes has been shown to be influenced by the availability of potential shelter sites, serving as refuge from predators (Steele, 1999). Habitat type is intricately linked with several factors including predation risk and food availability, with species selecting habitats which allow for optimized growth and survival (Dahlgren and Eggleston, 2000). Reef habitats are structurally complex, with the ability to support a variety of microhabitats that contribute to enhancing fish diversity (Angel and Ojeda, 2001; Gratwicke and Speight, 2005). Reef shape and composition influences the space and refuge available for predator avoidance which ultimately influences reef fish community structure (Sherman *et al.*, 2002). Furthermore, high profile reef is known to accommodate more abundant and richer fish assemblages (Pratt, 1994; Jordan *et al.*, 2005; Hackradt *et al.*, 2011). Experimental observations in large outdoor aquaria assessing settlement and post-settlement habitat selection among species of the Pomacentridae fish family, indicate that late-stage larvae can make precise choices regarding settlement habitat (Öhman *et al.*, 1998). Furthermore, settlement stage larvae use a set of strategies which enable them to establish on suitable reef habitats (Sale *et al.*, 1980). However, very little is known of the influence of reef profile type in structuring larval fish communities. Studies assessing larval fish composition and distribution in relation to reef complexity are essential for understanding which reef features are important for supporting larval fish abundance and diversity.

The primary goal of this study was to describe spatial and temporal patterns and the occurrence and abundance of larval and settlement stage fishes on selected reef habitats associated with islands in the warm-temperate waters of Algoa Bay, South Africa. A proportion of the research involved an assessment of the performance of light traps as a method of ichthyoplankton sampling to develop appropriate techniques to assess species composition on varying reef habitat types.

3. MATERIALS AND METHODS

3.1 Study site

Algoa Bay is situated on the south east coast of South Africa and is a wide (~80 km), shallow (<80 m) eastward-facing bay (Figure 3.1). The Bay experiences a warm-temperate climate with a bimodal rainfall pattern (Lubke and de Moor, 1998). The Agulhas Current flows south-westwards, along the edge of the continental shelf, approximately 50 km offshore of Algoa Bay (Lutjeharms, 1981). Water temperatures range between ~11 °C in winter to ~22 °C in summer (Beckley, 1983b). Freshwater inflow from the Sundays and the Swartkops rivers into the Bay is minimal and salinity is stable at an average of 35.2 (Schumann, 1998; Schumann *et al.*, 2005). Two offshore island groups, comprised of quartzitic Table Mountain Sandstone (Beckley and McLachlan, 1979), are located within Algoa Bay and are the only islands located on the east coast of southern Africa between Cape Agulhas and Maputo in southern Mozambique. The St Croix Island group (33°47′58″S; 26°46′20″E) consists of three separate outcrops including St Croix, Jahleel and Brenton islands, and are situated within the western sector of the Bay. The Bird Island group (33°52′07″S; 26°17′29″E) is situated approximately 10 km offshore of the Woody Cape headland in the eastern sector of the Bay and consists of Bird, Stag and Seal islands and a rock outcrop known as Black Rocks. Soft sediments, particularly coarse sands interspersed with fine silts and clays dominate the subtidal environment of the Bay (Bremner, 1978; Bremner, 1991) with small isolated reef complexes occurring in many areas. As a result of large scale sand movements, reef complexes are frequently inundated (McLachlan *et al.*, 1977; Cockcroft and Tomalin, 1987; Chalmers, 2011). Seven areas in Algoa Bay were identified as larval fish sampling stations. These stations included high-profile reef (A and B), low-profile reef (C and D) and reef-associated sand habitats adjacent to reefs (E and F) at Bird and St Croix islands and a sand habitat (G) located on the 20 m depth contour between the Sundays Estuary and Woody Cape.

3.2 Field sampling and fish identification

A mixed method approach was used to sample larval fish over subtidal reef areas and included light traps and a plankton ring net used during night time collections. One light trap, suspended 4 m from the surface, was deployed on a fixed mooring in the water column at each sampling station. Sampling was conducted during the peak spawning period and targeted both the start and the end of spawning of coastal fishes in the Bay. The traps were deployed for a total of 12 nights during the study around the new moon phase in July, August, September, representing the start of the spawning period and November, December and January representing the end of the spawning period. In total, 12 sampling trips took place between June 2010 and February 2012. The traps were deployed before dusk each night and emptied after dawn. All samples were fixed on site in 10 % formalin in seawater.

The light traps, based on a modification of the design of Stobutzki and Bellwood (1997), are cylindrical, 1010 mm high and 470 mm in diameter. The light trap consists of a perspex chamber open to the exterior environment by four vertical slits (270 mm high by 7 mm wide) through which larval and settlement stage fish enter the trap. The catch accumulates in a detachable cod-end with mesh sides (500 µm) at the base of the light trap. The perspex chamber is protected by a stainless steel frame. A 30 cm long, 8 W fluorescent lamp is used as a light source and is placed into a clear perspex tube inserted centrally through the trap.

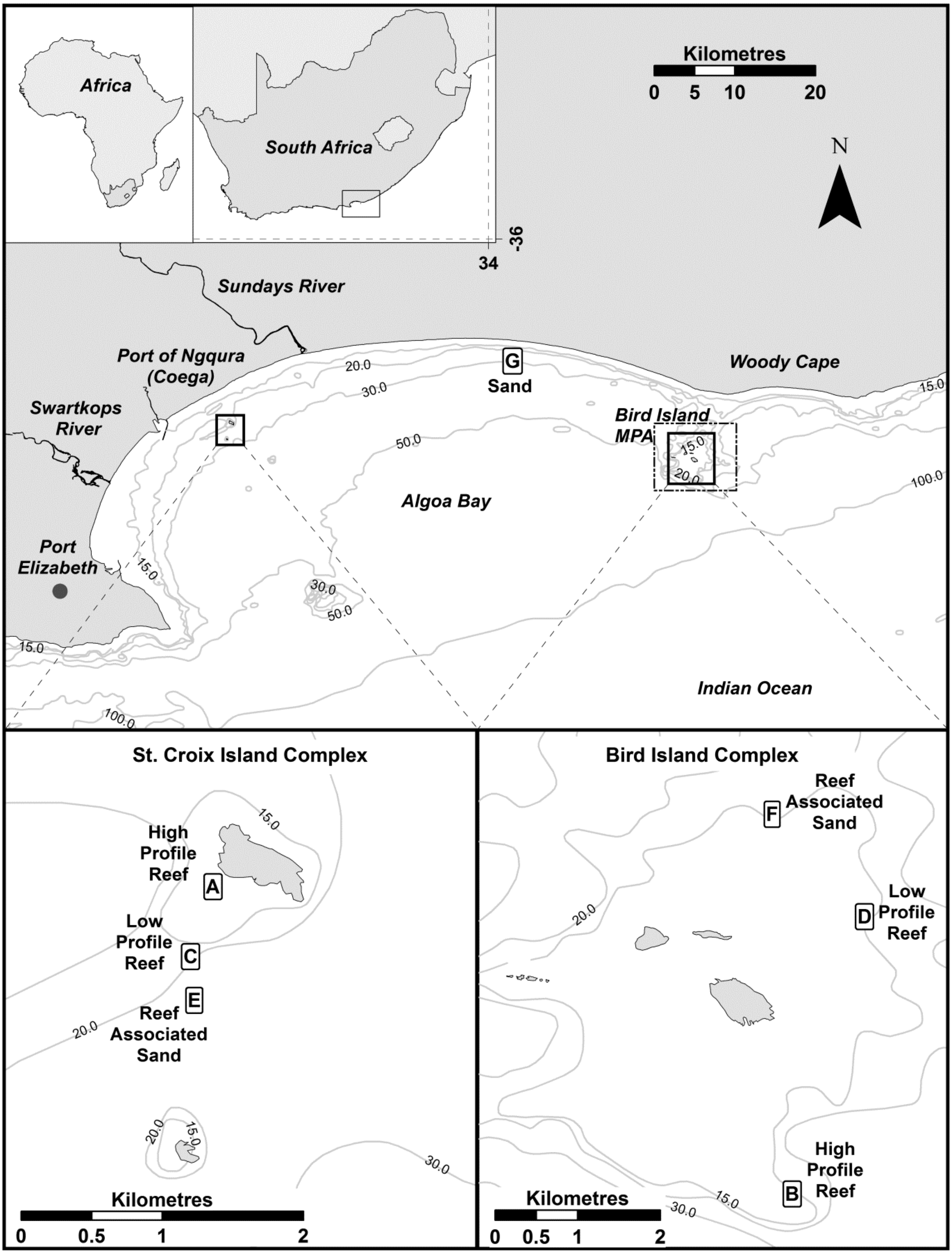

FIGURE 3.1 The geographical position of St Croix and Bird islands in Algoa Bay, showing the location of the sampling stations and the station located on the 20 m depth contour between Woody Cape and the Sundays Estuary

The clear tube is fixed to a water-tight battery box which is attached to the top of the light trap. A rechargeable, sealed, valve regulated lead-acid 12 V, 12 Ah / 20 HR battery is used to power the light source. The light source was switched on and off by a magnetic switch that is triggered by removal or replacement of a magnet on the side of the battery housing. The traps are suspended by a rope harness which is attached to four metal rings secured to the top of the stainless steel. Larval and settlement stage fishes caught in each light trap per night are expressed as CPUE, referring to the number of larval or settlement stage fishes caught per trap, per hour. A total of 84 samples were collected over the study period.

While the light traps were sampling, ski-boat based plankton ring net tows were conducted at each of the seven sampling stations. The ring net consisted of a 12 mm thick stainless steel ring fitted with a 4 m long plankton net with a PVC cod-end. The net diameter was 750 mm and the mesh aperture was 500 µm. A Kahlsico flowmeter was suspended from the frame at the opening of the net and water flow passing through the opening of the net was measured. The ring net was pulled using a stepped oblique tow at a speed of ~2 knots. Three water levels were sampled including the near bottom (~30 m), middle (~15 m) and near surface (~1 m). Each water level was sampled for 2 mins excluding hauling with each tow lasting ~8 mins. The density of larval fishes caught per haul are expressed as the number of larvae per 100 m^3. A total of 84 samples were collected over the study period.

Temperature (°C), salinity, turbidity (NTU), conductivity (µSIEMENS/cm), pH, total dissolved solids (TDS) and dissolved oxygen (%) was measured at each station using a YSI 6600 multi-parameter meter with recordings made at the surface, middle and the bottom of the water column.

In the laboratory, larval fishes were removed, identified, counted and measured. Species were identified to the lowest possible taxon (Moser *et al.*, 1984; Okiyama, 1988; Leis, 1991; Olivar and Fortuño, 1991; Smith and Heemstra, 1995; Neira *et al.*, 1998; Leis and Carson-Ewart, 2000; Richards, 2005). Notochord length in preflexion and flexion larvae and standard length in postflexion larvae and settlement stages were measured to the nearest 0.1 mm and were referred to as body length (BL).

3.3 Data analyses

Diversity indices including total species number (N), Shannon-Wiener diversity (H'), Margalef species richness (d) and Pielou's evenness (J') were calculated per station per sampling event, using the PRIMER statistical package version 6.1, 2013 (Clarke and Warwick, 1994). Shannon-Wiener diversity was calculated to one decimal point using $\log_e$. All physical and biological data was tested for normality using a normal probability plot and Shapiro-Wilk test and homogeneity of variance using a Levene's test with the STATISTICA software package version 11, 2012. All physical data did not conform to parametric test assumptions after appropriate transformations were used, however variances were homogeneous and non-parametric tests were used. For larval fish collected with the plankton ring net, abundance and Shannon-Wiener diversity in the original format conformed to parametric test assumptions. Fish species richness, evenness, density and number of species were square root transformed and conformed to parametric test assumptions. For larval fish collected with the light traps, all data did not conform to parametric test assumptions after appropriate transformations were used, however variances were homogeneous and therefore non-parametric tests were used.

Differences in physical data and light trap catches between the sampling periods were assessed using a Mann-Whitney U-test (U). A Kruskal-Wallis (H) ANOVA test was used to assess differences in physical data and light trap catches among the stations. A 1-way ANOVA test (F) was used to determine differences in plankton ring net catches between the sampling periods and among the stations. To determine if there were trends in occurrence of developmental stages with sampling period an ANOVA Chi-square test was used.

Environmental relationships with larval fish density and CPUE was examined with Principal Component Analysis using the PRIMER statistical package version 6.1, 2013 (Clarke and Warwick, 1994). Community analysis was similarly conducted using the PRIMER statistical package. All biological data were square root transformed to down-weight the most abundant species and allow rare species to contribute. A Bray-Curtis similarity matrix was generated for sampling periods and stations. Clusters in a dendrogram format were assessed using group hierarchical sorting and ANOSIM was used to detect differences among groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or difference among seasons and stations.

4. RESULTS

4.1 Environmental variability

Physico-chemical variables (summarised in Figure 3.2) showed a significant difference temporally during the study period for conductivity ($U = 471.5$; $p < 0.001$), TDS ($U = 476.0$; $p < 0.001$) and salinity ($U = 507.0$; $p < 0.001$) with highest values recorded at the end of the spawning period. Spatial variation in pH ($H = 21.73$; d.f. = 2; $p < 0.001$) and turbidity ($H = 8.91$; d.f. = 2; $p < 0.05$) was observed among the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat with greatest pH and turbidity recorded at the St Croix Island reef habitats.

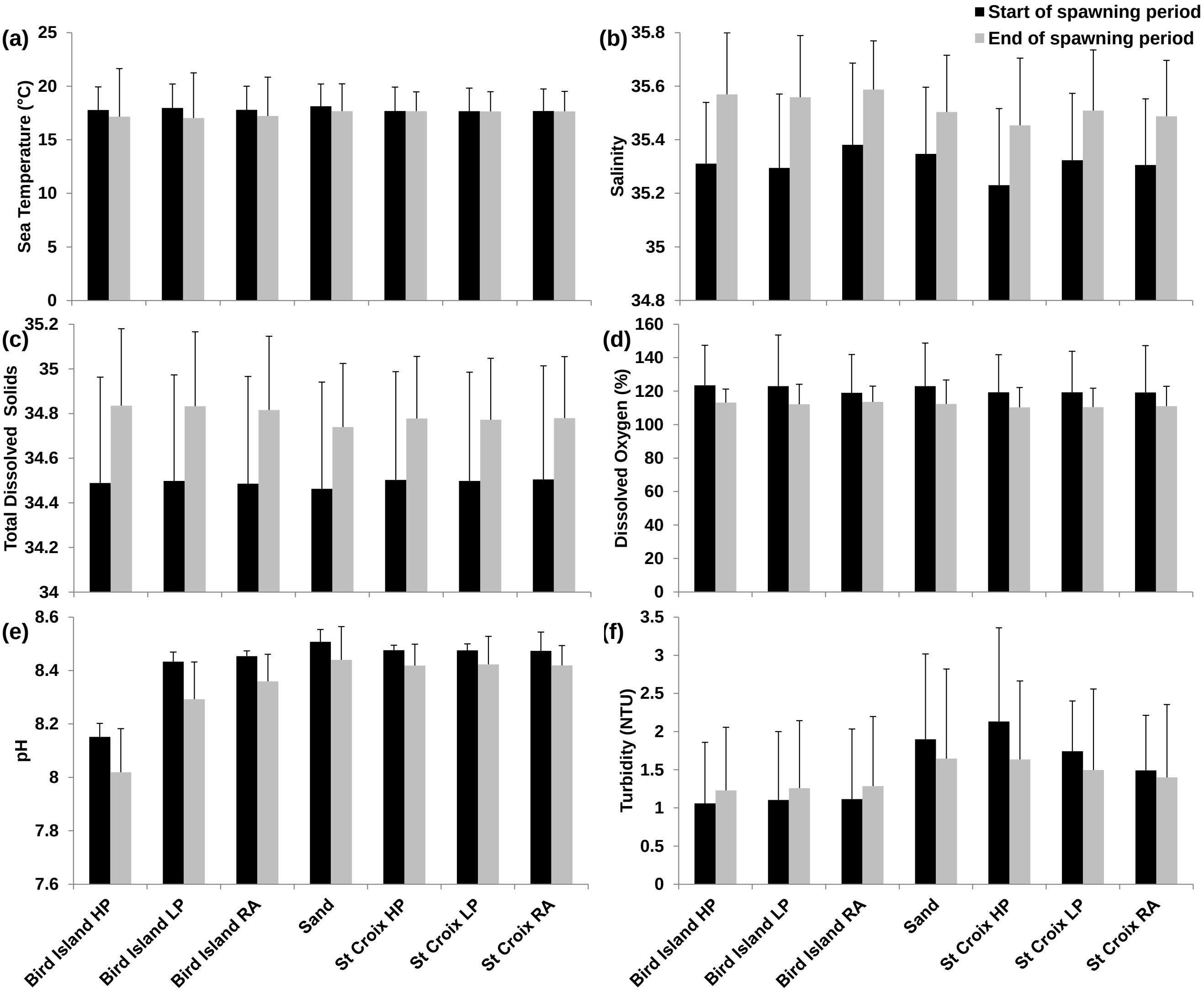

FIGURE 3.2 Mean (n = 6) and maximum of a) sea temperature, b) salinity, c) total dissolved solids, d) dissolved oxygen, e) pH, f) turbidity recorded during each spawning period at each reef and sand habitat station in Algoa Bay during the study (July 2010 – January 2012)

4.2 Species composition

4.2.1 Plankton ring net

Using the plankton ring net, 3961 larval fishes from 29 families and 78 species were captured over the selected reef habitats and the sand habitat in Algoa Bay (Table 3.1). The study area was dominated by the larvae of the Engraulidae fish family, which made a 37.8 % contribution to the total catch. Furthermore Gobiidae (23.4 %) and Clupeidae (9.2 %) fish families made important contributions towards the overall fish catch. Cynoglossidae contributed 8.5 % and Sparidae contributed 8.4 %. Smaller contributions towards the fish catch were made by Gobiesocidae (6.4 %), Blenniidae (2.7 %), Soleidae (2.0 %) and Tripterygiidae (1.9 %).

4.2.2 Light traps

A total of 151 larvae and settlement stage fishes from 10 families and 14 species were captured in the light traps placed over selected reef and sand habitats in Algoa Bay (Table 3.1). The Engraulidae dominated the catch, with anchovy, *Engraulis encrasicolus*, the only representative species from this family comprising 55.3 % of the total catch. The second most abundant family, Clupeidae, made a total contribution of 25.2 %, with the redeye roundherring, *Etrumeus whiteheadi*, the representative species of this family, contributing 21.1 % and the pilchard, *Sardinops sagax*, contributing 4.1 %. The Carangidae contributed 11.4 % of the total catch and a species of Clinidae contributed 1.4 % towards the overall catch. All other species contributions were each less than 1 % of the total catch.

4.3 Temporal trends in fish density and diversity

4.3.1 Plankton ring net

A significant difference in the total number of species ($F = 9.6$; d.f. = 1; $p < 0.01$), richness ($F = 12.6$; d.f. = 1; $p < 0.001$), evenness ($F = 4.7$; d.f. = 1; $p < 0.05$) and diversity ($F = 15.4$; d.f. = 1; $p < 0.001$) of larval fish occurred between the sampling periods (Figure 3.3) with highest values recorded at the start of the spawning period. Significant differences in densities of the dominant species and taxa including *Caffrogobius nudiceps* ($U = 508.0$; $p < 0.001$), *Cynoglossus capensis* ($U = 597.0$; $p < 0.05$), *Etrumeus whiteheadi* ($U = 374.0$; $p < 0.001$), Gobiidae sp 1 ($U = 461.5$; $p < 0.001$) and Gobiidae sp 3 ($U = 504.0$; $p < 0.001$) occurred between sampling periods with peaks in densities at the start of the spawning period with the exception of *C. capensis* (Figure 3.4).

TABLE 3.1 Species and taxa composition, mean density (range), CPUE, mean body length (range) and developmental stage of larval and settlement stage fishes caught by plankton ring net and light traps over selected reef and sand habitats in Algoa Bay. Pre = preflexion, F = flexion, Po = postflexion, Ej = early juvenile. Dominant developmental stages are bolded

		Plankton net					Light trap				
Family	Species	Total catch		Body length (mm)		Developmental stage	Total catch		Body length (mm)		Developmental stage
		No.	%	Mean	%		No.	%	Mean	%	
Blenniidae	Blenniidae sp 1	30	0.8	4.4	3.4 – 6.2	**Pr**					
	Blenniidae sp 2	21	0.5	4.7	4.0 – 6.6	**Pr**, F					
	Blenniidae sp 3	3	0.1	2.9	2.6 – 3.5	**Pr**					
	Blenniidae sp 4	8	0.2	9.5	5.7 – 17.1	Pr, F, **Po**					
	Blenniidae sp 6	36	0.9	3.2	2.1 – 5.0	**Pr**, F					
	Parablennius sp 1	7	0.2	4.8	3.8 – 6.0	**Pr**, F					
Bregmacerotidae	*Bregmaceros atlanticus*	1	<0.1	18.6		**Po**					
Callionymidae	*Callionymis marlyi*	3	0.1	1.9	1.6 – 2.1	**Pr**					
Carangidae	Carangidae sp 1	1	<0.1	4.3		**F**					
	Decapterus macrosoma						2	1.6	33.0	32.5 – 33.5	**Ej**
	Decapterus punctatus						12	9.8	31.6	19.7 – 74.0	Po, **Ej**
	Trachurus trachurus	8	0.2	3.2	2.2 – 3.5	**Pr**					
	Seriola sp 1	7	0.2	2.7	2.0 – 3.0	Yo, **Pr**					
Cheilodacylidae	*Cheilodactylus* sp 2	1	<0.1	3.4		**Pr**					
Clinidae	*Climocoporus navalis*						1	0.8	13.4	–	**Po**
	Clinidae sp 1	2	<0.1	14.0	11.7 – 16.2	**Po**	1	0.8	12.5	–	**Po**
	Clinus superciliosus	1	<0.1	9.0		**Po**					
Clupeidae	*Etrumeus whiteheadi*	174	4.4	15.2	3.7 – 26.2	Pr, **F**, Po	26	21.1	43.4	19.0 – 102.0	F, **Po**, Ej
	Sardinops sagax	191	4.8	4.4	2.0 – 16.4	Yo, **Pr**, F, Po	5	4.1	81.7	20.8 – 109.0	Po, **Ej**
Cynoglossidae	*Cynoglossus capensis*	262	6.6	3.9	1.5 – 10.5	**Pr**, F	1	0.8	4.6	–	**Pre**
	Cynoglossus zanzibarensis	35	1.9	4.5	1.8 – 10.7	**Pr**, F					
Engraulidae	*Engraulis encrasicolus*	1498	37.8	4.4	1.5 – 22.5	Yo, **Pr**, F, Po	68	55.3	46.9	18.8 – 102.0	**Po**, Ej
Gobiesocidae	*Chorisochismus dentex*	4	0.1	2.5	1.9 – 3.4	**Pr**					
	Diplecogaster megalops	117	6.3	4.0	2.4 – 6.4	**Pr**, F, Po					
Gobiidae	*Caffrogobius nudiceps*	327	8.3	3.4	2.0 – 7.0	**Pr**, F, Po					
	Caffrogobius sp 1	1	<0.1	3.5		**Pr**					
	Gobiidae sp 1	499	12.6	8.1	3.4 – 15.2	Pr, F, **Po**	1	0.8		–	
	Gobiidae sp 2	26	0.7	4.0	3.1 – 4.7	**Pr**					
	Gobiidae sp 3	73	1.8	4.3	2.8 – 5.7	**Pr**, F					
	Psammogobius knysnaensis	1	<0.1	15.2		**Po**					

Gonostomatidae	*Cyclothone* sp 1	1	<0.1	4.5		**F**					
	Gonostomatidae sp 1	1	<0.1	4.1		**Pr**					
Haemulidae	*Pomadasys* sp 1	5	0.1	4.0	2.4 – 5.4	**Pr**, F					
	Pomadasys sp 2	4	0.1	3.5	2.9 – 4.5	**Pr**, F					
Kyphosidae	*Kyphosus* sp 1	1	<0.1	3.5		**Pr**					
Lutjanidae	*Lutjanus* sp 1	1	<0.1	3.4		**Pr**					
Merlucciidae	*Merluccius capensis*	6	0.2	2.5	2.2 – 2.7	Yo, **Pr**					
Mugilidae	*Liza macrolepis*	1	<0.1	13.7		**Po**					
	Liza sp 1	1	<0.1	2.5		**Pr**					
Mullidae	Mullidae sp 1	1	<0.1	5.2		**Pr**					
Myctophidae	*Diaphus brachycephalus*	1	<0.1	6.5		**Po**					
Ophidiidae	*Ophidion smitheri*	2	0.1	4.9	4.8 – 4.9	**Pr**					
Pomacanthidae	*Centropyge acanthops*						1	0.8	20.1	–	**Po**
Pomacentridae	Pomacentridae sp 1	2	0.1	2.8	2.7 – 2.9	**Pr**					
Sciaenidae	*Argyrosomus inodorus*	23	0.6	4.4	2.3 – 5.8	**Pr**, F					
	Argyrosomus japonicus	7	0.2	4.4	2.4 – 5.5	**Pr, F**					
	Sciaenidae sp 1	1	<0.1	3.0		**Pr**					
Scombridae	*Euthynnus affinis*						1	0.8	18.2	–	**Po**
Scorpaenidae	Scorpaenidae sp 1	15	0.4	3.3	2.0 – 5.4	**Pr**, F, Po					
Soleidae	*Austroglossus pectoralis*	3	0.1	4.2	1.6 – 7.8	**Pr**, F					
	Heteromycteris capensis	62	1.6	2.8	1.3 – 5.9	Yo, **Pr**, F					
	Solea turbynei	8	0.2	2.9	1.2 – 3.7	**Pr**, F					
	Soleidae sp 1	1	<0.1	1.7		**Pr**					
	Synapturichthys kleini	2	0.1	3.1	1.6 – 4.5	**Pr**					
Sparidae	*Acanthopagrus* sp 1	11	0.5	4.7	4.3 – 5.7	**Pr**, F					
	Cheimerius nufar	1	<0.1	3.0		**Pr**					
	Chrysoblephus laticeps	1	<0.1	4.6		**Pr**					
	Diplodus capensis	10	0.3	4.3	2.2 – 5.5	**Pr**, F	1	0.8	11.1	–	**Po**
	Diplodus cervinus hottentotus	1	<0.1	7.0		**Po**					
	Lithognathus lithognathus	1	<0.1	7.9		**Po**					
	Pagellus natalensis	61	1.5	3.0	2.0 – 5.9	**Pr**, F					
	Rhabdosargus sp 1	6	0.2	4.7	4.1 – 5.9	**Pr**, F					
	Rhabdosargus sp 2	1	<0.1	5.8		**F**					
	Sparidae sp 1	4	0.1	2.5	2.4 – 2.6	**Pr**					
	Sparidae sp 3	21	0.5	2.5	2.1 – 2.9	**Pr**					
	Sparidae sp 5	5	0.1	3.2	2.6 – 4.1	**Pr**					
	Sparidae sp 6	7	0.1	3.4	2.5 – 4.1	**Pr**					
	Sparidae sp 8	1	<0.1	2.0		**Pr**					
	Sparidae yolk sac sp 1	1	<0.1	1.8		**Yo**					

	Spondyliosoma emarginatum	197	5.0	2.7	1.3 – 6.2	Yo, **Pr**, F					
Syngnathidae	*Sygnathus temminckii*	8	0.2	15.6	8.2 – 21.6	**Po**					
Tetraodontidae	*Arothron nigropunctatus*	1	<0.1	8.0		**Ej**					
Trigilidae	Trigilidae sp 1	8	0.2	3.3	2.7 – 4.1	**Pr**					
	Trigilidae sp 2	2	0.1	5.3	3.0 – 7.5	**Pr, F**					
Tripterygiidae	*Cremnochorites capensis*	74	1.9	7.0	4.3 – 16.2	**Pr**, F, Po	2	1.6	11.8	11.5 – 12.1	**Po**
Unidentified	Unidentified Species 1	12	0.3	2.8	2.2 – 3.4	**Yo**					
	Unidentified Species 2	2	0.1	2.8	2.6 – 2.9	**Pr**					
	Unidentified Species 3	1	<0.1	3.6		**Pr**					
	Unidentified Species 4	1	<0.1	3.2		**Pr**					
	Unidentified Species 7	3	0.1	2.6	1.6 – 3.2	**Pr, Yo**					
	Unidentified Species 9						1	0.8	3.9	–	**Pr**
	Yolk Sac Species 1	5	0.1	3.2	3.0 – 3.4	**Yo**					
	Yolk Sac Species 2	2	0.1	3.2	3.1 – 3.2	**Yo**					
	Yolk Sac Species 3	4	0.1	1.8	1.7 – 1.9	**Yo**					

4.3.2 Light traps

The CPUE (U = 618.5; $p < 0.01$), number of species (U = 642.5; $p < 0.05$), abundance (U = 588.5; $p < 0.01$) and species richness (U = 613.5; $p < 0.05$) of larval fishes varied significantly temporally with greatest catches occurring at the start of the spawning period. The highest CPUE of larval fishes was recorded at the start of the spawning period (7.9 larvae/trap/hour). Generally, the CPUE of larvae captured at each station per hour was greater at the start of the spawning period with the exception of the Bird Island reef-associated sand habitat where catches were marginally greater at the end of the spawning period. The dominant species, *Engraulis encrasicolus*, similarly showed a significant difference (U = 616.0; $p < 0.05$) in CPUE between spawning periods with greatest CPUE recorded at the start of the spawning period.

4.4 Spatial trends in fish density and diversity

4.4.1 Plankton ring net

No significant spatial variation in larval fish densities and diversity indices amongst the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat was observed. Greatest mean density of larval fishes was recorded at the St Croix island reef habitats (105 larvae/100m^3), followed by the sand habitat (67 larvae/100m^3) with the lowest mean larval fish density recorded at the Bird Island reef habitats (49 larvae/100m^3). The highest average number of species, species richness and species diversity, was recorded at the sand habitat (N = 9; d = 2.0; H' = 1.5) with the lowest average number of species, species richness and diversity recorded at the Bird Island reef habitats (N = 7; d = 1.7; H' = 1.2).

At the St Croix Island reef habitats the greatest number of species, the species richness and the highest species diversity was recorded at the reef-associated sand habitat (N = 9; d = 2.1; H' = 1.4), followed by the low profile reef habitat (N= 8; d = 1.8; H' = 1.3) with the lowest number of species, species richness and diversity recorded at the high profile reef habitat (N = 7; d = 1.6; H' = 1.2). A similar pattern was observed at the Bird Island reef habitats with species diversity greatest at the reef-associated sand habitat (H' = 1.3), followed by the low profile reef habitat (H' = 1.2) with lowest species diversity recorded at the high profile reef habitat (H' = 1.1).

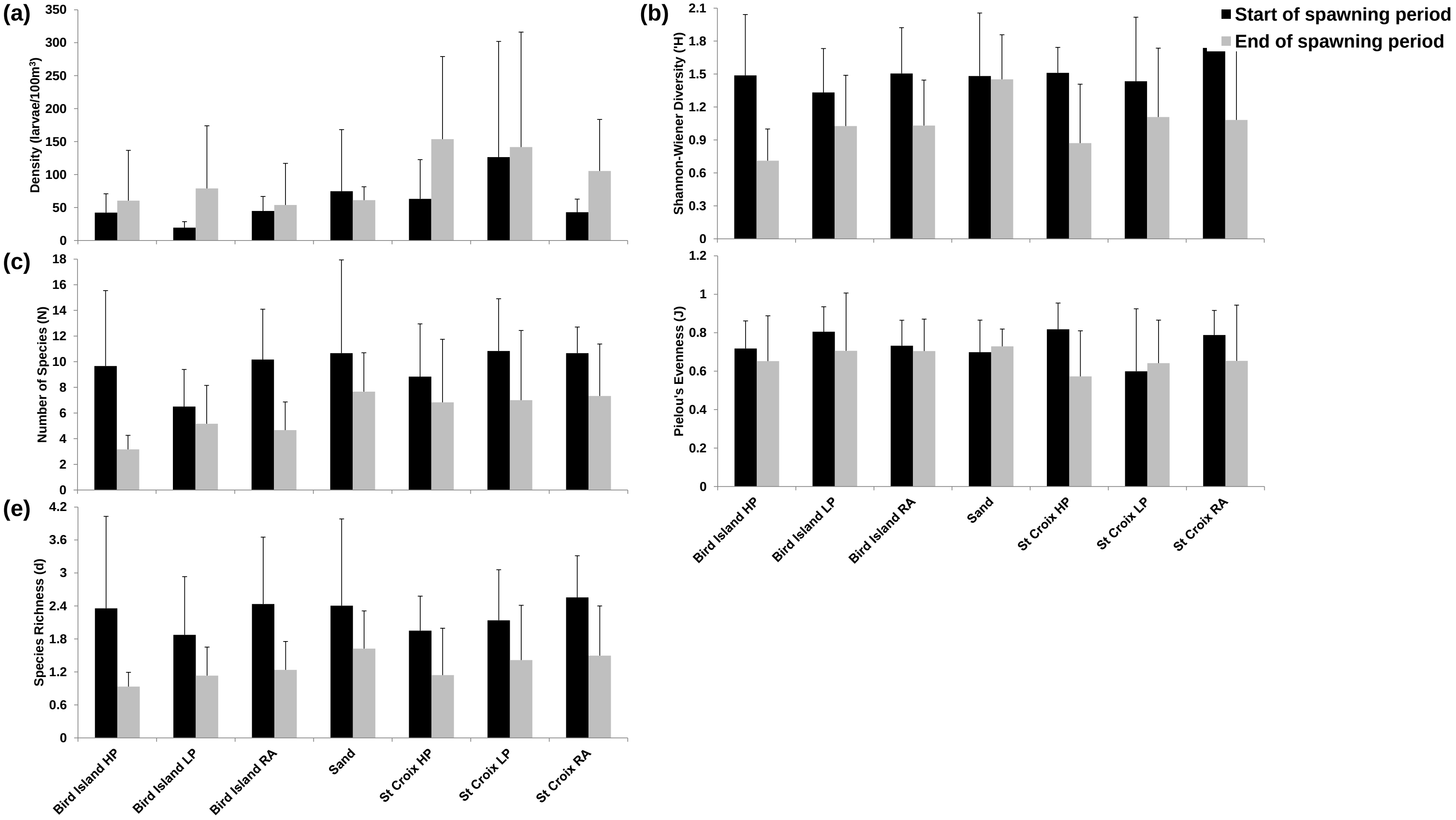

FIGURE 3.3 Larval fish mean (n = 6) and mean error of a) density, b) Shannon-Wiener diversity, c) number of species, d) Pielou’s evenness and e) species richness during each sampling period at each reef and sand habitat station in Algoa Bay during the study (July 2010 – January 2012)

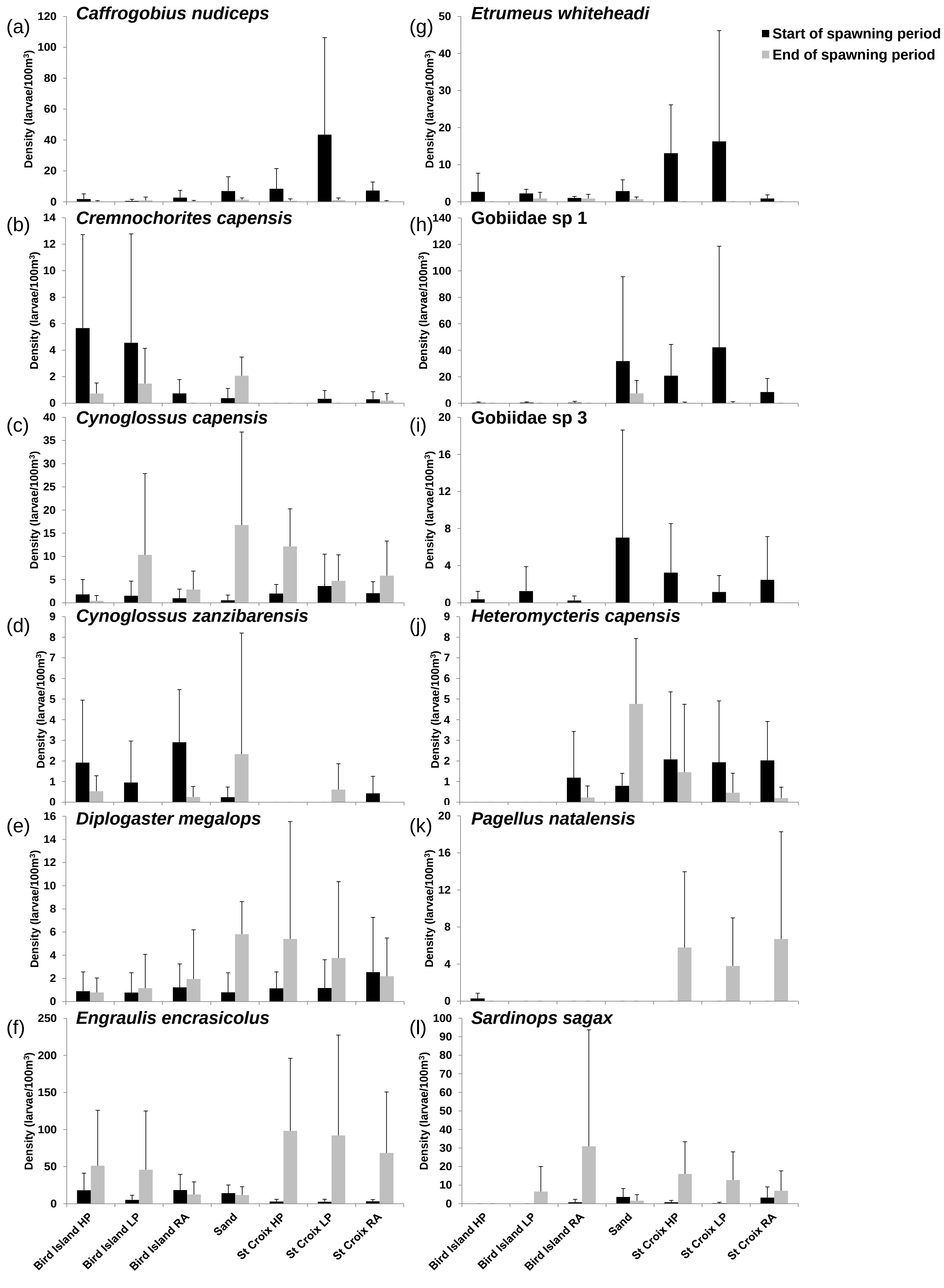

FIGURE 3.4 Mean (n = 6) and maximum density of dominant species (>1 %) during each spawning period at each reef and sand habitat station in Algoa Bay during the study (July 2010 – January 2012)

4.4.2 Light traps

A significant spatial variation in species diversity (H = 8.8; d.f. = 2; $p < 0.05$), evenness (H = 9.4; d.f. = 2; $p < 0.01$) and richness (H = 8.5; d.f. = 2; $p < 0.05$) amongst the Bird Island reef habitats, the St Croix Island reef habitats, and the sand habitat was observed with highest values of these indices occurring at the Bird Island reef complex.

The CPUE of larvae was greater at the Bird Island reef habitats (7.6 larvae/trap/hour) than the St Croix Island reef habitats (3.9 larvae/trap/hour). A significant (H = 8.0; d.f. = 2; $p < 0.05$) spatial variation in *Etrumeus whiteheadi* CPUE was observed among the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat with greatest CPUE at Bird Island.

4.5 Body Length

In the plankton net samples, a significant difference in the lengths of *Caffrogobius nudiceps* (ANOVA Chi Sqr = 14.7; d.f. = 2; $p < 0.01$), *Cynoglossus capensis* (ANOVA Chi Sqr = 21.5; d.f. = 2; $p < 0.001$), *Diplogaster megalops* (ANOVA Chi Sqr = 12.4; d.f. = 2; $p < 0.05$), *Engraulis encrasicolus* (ANOVA Chi Sqr = 60.47; d.f. = 2; $p < 0.001$), *Sardinops sagax* (ANOVA Chi Sqr = 14.3; d.f. = 2; $p < 0.05$) and *Spondyliosoma emarginatum* (ANOVA Chi Sqr = 11.4; d.f. = 2; $p < 0.05$) occurred amongst the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat. Greater means lengths were observed in the sand habitat for the tonguefish, *C. capensis*, the anchovy, *E. encrasicolus*, and the sardine, *S. sagax* as opposed to the reef habitats. Mean body lengths were greatest at the reef habitats for *C. nudiceps*, *D. megalops* and *S. emarginatum*.

Sample sizes from the light traps, were too small for statistical comparison, however, greater mean lengths of the dominant species, *E. encrasicolus* and *E. whiteheadi*, were observed at the Bird Island reef habitats.

4.6 Community analysis

4.6.1 Plankton ring net

Hierarchical classification using Bray-Curtis similarities was used to aggregate the most similar areas for further analysis. Three principal communities were distinguished at the 55 % level of similarity using square root transformed (ANOSIM Global R = 0.98; $p < 0.01$) and presence/absence data (ANOSIM Global R = 0.74; $p < 0.01$). With square root transformed data, the Bird Island high profile reef habitat (Group 1) formed the first group, the St Croix Island reef habitats with the sand habitat formed a second group (Group 2) and the Bird

Island reef-associated sand habitat and low profile reef habitat (Group 3) grouped together (Figure 3.5a). The SIMPER routine showed that 10 species contributed ~50 % of the dissimilarity between the Bird Island high profile reef habitat (Group 1) and the remaining Bird Island reef habitats (Group 3). *Sardinops sagax* (12.4 %), *Spondyliosoma emarginatum* (8.1 %), *Engraulis encrasicolus* (6.0 %) and Sparidae sp 3 (5.1 %) were the major contributors cumulatively contributing 31.7 % to the dissimilarity. The Bird Island high profile reef habitat was characterised by high abundances of *Engraulis encrasicolus*, Sparidae sp 3 and an absence of *Sardinops sagax* and *Spondyliosoma emarginatum*. Ten species contributed 50 % towards the dissimilarity between the Bird Island high profile reef habitat (Group 1) and the St Croix Island reef habitats with the sand habitat (Group 2). Gobiidae sp 1 (9.4 %), *Sardinops sagax* (6.9 %) and *Spondyliosoma emarginatum* (5.9 %) were the major contributors cumulatively contributing 22.2 % to the dissimilarity. Gobiidae sp 1 occurred in higher abundances at the St Croix Island reef habitats and the sand habitat. Thirteen different species contributed approximately 50 % towards the dissimilarity between Group 3 (Bird Island low profile and reef-associated sand habitats) and Group 2 (the St Croix Island reef habitats and the sand habitat). Gobiidae sp 1 (10.5 %) was the major contributor to this dissimilarity followed by *Engraulis encrasicolus* (6.2 %), *Caffrogobius nudiceps* (5.6 %) and *Pagellus natalensis* (4.1 %) which cumulatively contributed 26.4 % to the dissimilarity. Abundances of all four of these species were greater at the St Croix Island reef habitats and the sand habitat. Using presence/absence data, the Bird Island high profile reef habitat and the reef-associated sand habitat grouped together (Group 1), the St Croix Island reef habitats with the sand habitat formed a second group (Group 2) and the Bird Island low profile reef habitat (Group 3) formed the third group (Figure 3.5b). The SIMPER routine showed that 15 species contributed ~50 % of the dissimilarity between the Bird Island low profile reef habitat (Group 3) and the remaining Bird Island reef habitats (Group 1). *Argyrosomus inodorus*, Blenniidae sp 6, *Bregmaceros atlanticus*, *Caffrogobius* sp 1, *Chorisochismus dentex*, Clinidae sp 1, *Cyclothone* sp 1, *Daiphus brachycephalus*, Gobiidae sp 2, *Liza* sp 1 and *Parablennius* sp 1 occurred exclusively at the Bird Island low profile reef habitat.

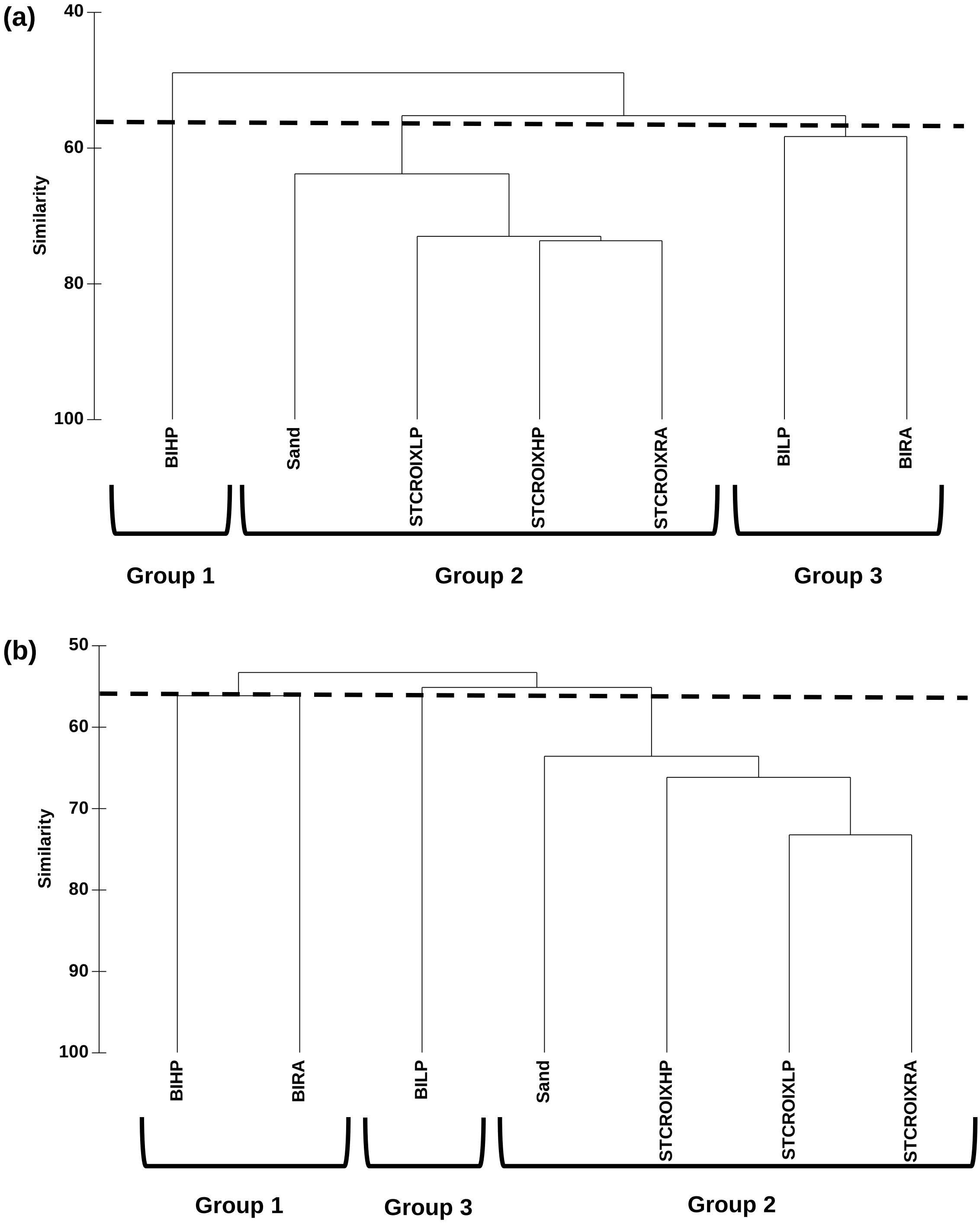

FIGURE 3.5 Bray-Curtis similarity dendrograms showing percentage similarity of habitats measured by the a) square root and b) presence and absence of species collected with a plankton ring net in Algoa Bay during the study (July 2010 – January 2012)

Differences between the three communities are further highlighted by the frequency of occurrence of certain species (Figure 3.6). Only *E. encrasicolus* larvae were recorded at a similar frequency at the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat (63.9 % Bird Island; 66.7 % Sand; 61.1 % St Croix). *Caffrogobius nudiceps* (66.7 %), *Diplogaster megalops* (46.7 %), *E. whiteheadi* (58.3 %), Gobiidae sp 1 (58.3 %), Gobiidae sp 3 (61.7 %) and *Heteromycteris capensis* (71.7 %) larvae were captured more frequently at the reef-associated sand habitat. *Cynoglossus capensis* (62.2 %), *Pagellus natalensis* (22.2 %), *Sardinops sagax* (43.9 %) and *Spondyliosoma emarginatum* (47.2 %) larvae were captured more frequently at the St Croix Island reef habitats. Only *Cremnochorites capensis* (51.7 %) was captured more frequently at the Bird Island reef habitats.

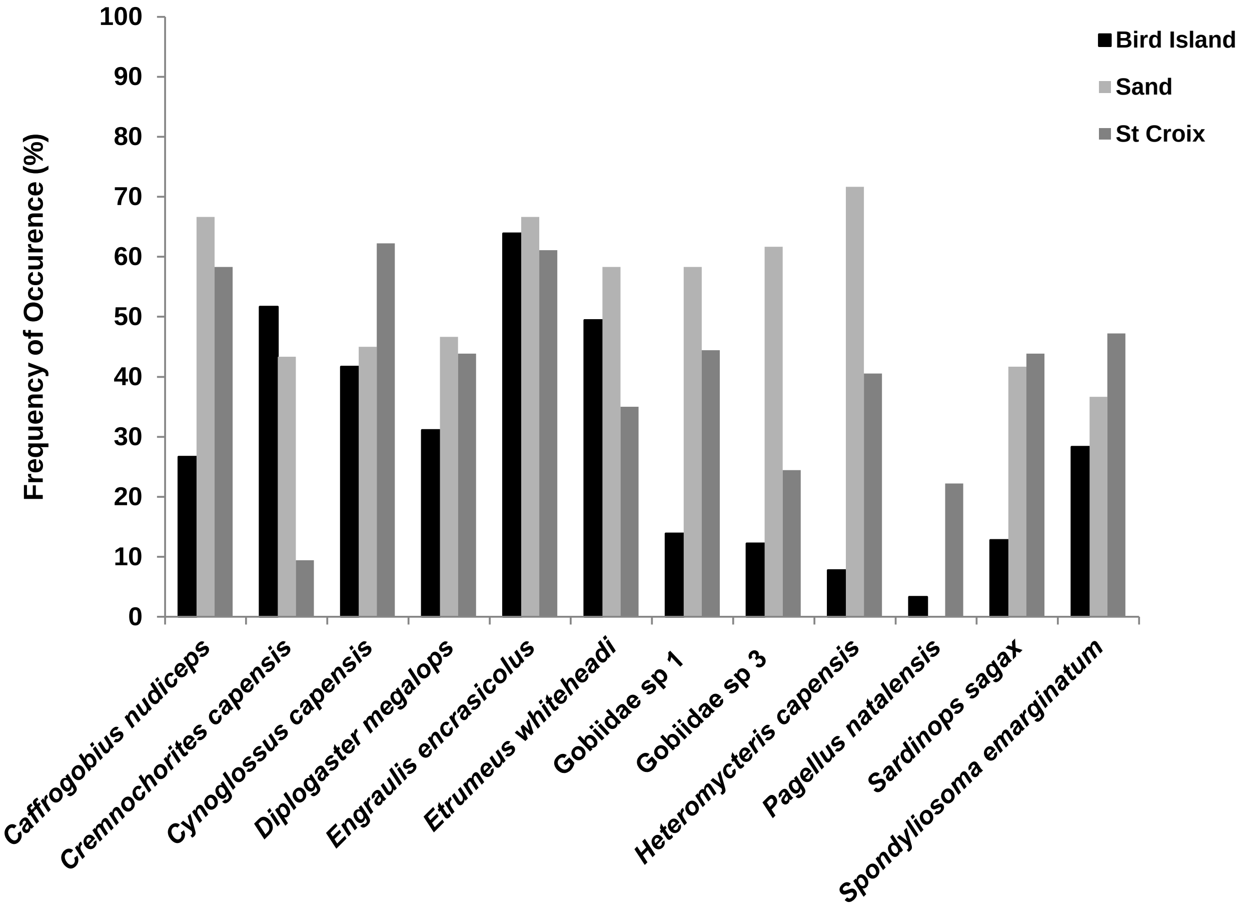

FIGURE 3.6 Frequency of occurence for each dominant species collected during plankton net sampling for the Bird Island reef habitats, the St Croix Island reef habitats, and the sand habitat

4.6.2 Light trap

Four principal communities were distinguished at the 60 % level of similarity. The Bird Island reef-associated sand habitat (Group 1) formed the first group, the St Croix Island high profile and low profile reef habitats (Group 2) formed the second group, the Bird Island high profile and low profile reef habitats formed a third group (Group 3) and the sand habitat and the St Croix Island reef-associated sand habitat grouping together (Group 4) forming the fourth group (Figure 3.7). The SIMPER routine showed that *Cremnochorites capensis* and *Climacoporus navalis* contributed ~45 % of the dissimilarity between the St Croix Island reef-associated sand habitat and the sand habitat (Group 4) and the remaining St Croix Island reef habitats (Group 2). These two species were completely absent from Group 4. Furthermore Gobiidae sp 1 and *Cynoglossus capensis* occurred exclusively at Group 2. Amongst the Bird Island reef habitats, four species contributed ~76 % of the dissimilarity between Group 3 and Group 1. *Decapterus macrosoma*, *D. punctatus*, *Sardinops sagax* and *Centropyge acanthops* were the major contributors, each contributing 19 % to the dissimilarity. The *Decapterus* species were absent from Group 1 where *C. acanthops* occurred exclusively.

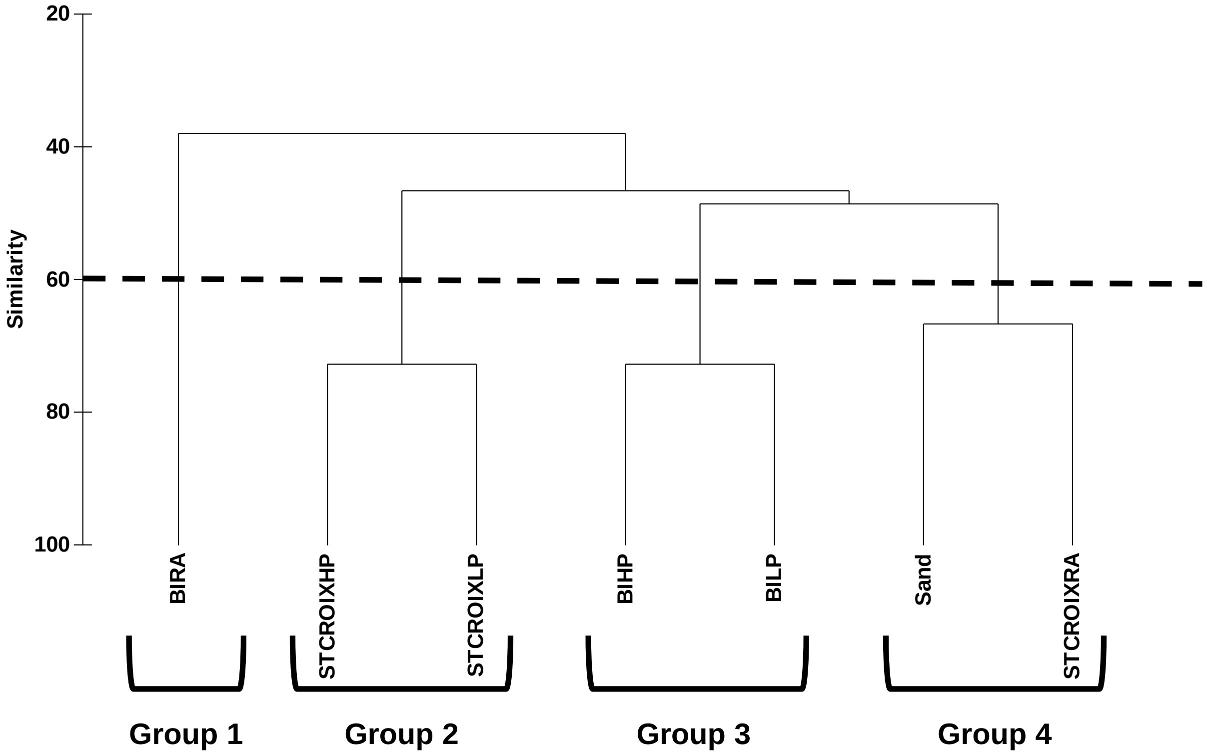

FIGURE 3.7 Bray-Curtis similarity dendrogram showing percentage similarity of habitats measured by the presence and absence of species collected with light traps in Algoa Bay during the study (July 2010 – January 2012)

4.7 Environmental correlation

Spearman's rank order correlation indicated that salinity had a significant positive correlation (r = 0.34; p < 0.05) with larval fish density while dissolved oxygen (r = -0.44; p < 0.05) and pH (r = -0.30; p < 0.05) had significant negative correlations with larval fish density.

Principal Component Analysis indicated that 63.9 % of the variability in larval fish density (Figure 3.8) could be explained by the first eigenvector (PC 1). PC 1 was characterized by a negative correlation with temperature, pH and turbidity and a positive correlation with conductivity, TDS, salinity and dissolved oxygen. The second eigenvector (PC 2) explained 22.4 % of the variability and was associated with a negative correlation with temperature, salinity and dissolved oxygen and a positive correlation with conductivity, TDS, pH and turbidity. These two factorial axes explained 86.3 % of the total variability.

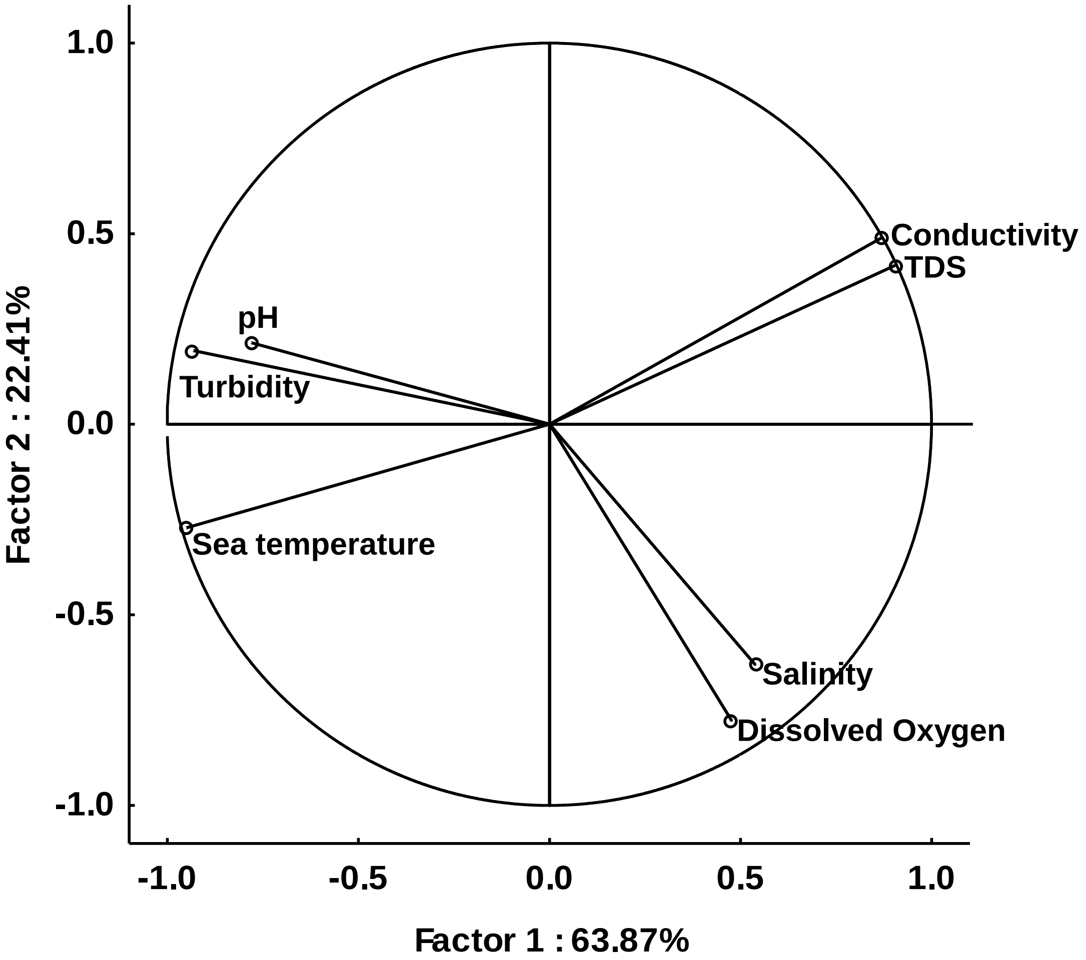

FIGURE 3.8 Representation of eigenvectors determined from PCA for environmental variables influencing total larval fish density

4.8 Gear comparison

A noticeable difference in the taxonomic composition of the samples taken from the light traps and plankton ring net tows, conducted over the various reef and reef associated habitats in Algoa Bay, was evident. The plankton ring net sampled three times as many families and five times as many taxa as the light traps. The plankton ring net captured twenty five more larvae (3961 larvae in total) than the light traps (151 larvae in total). Seventy taxa were exclusively captured in the plankton ring net samples and 6 taxa were captured exclusively by the light traps. Forty-four of the 70 taxa were however considered rare, with each species individually contributing <0.1 % towards the overall catch in the plankton net. Only seven of the remaining taxa (*Caffrogobius nudiceps*, *Cremnochorites capensis*, *Diplogaster megalops*, Gobiidae sp 3, *Heteromycteris capensis*, *Pagellus natalensis*, *Spondyliosoma emarginatum*) however were considered relatively common in the plankton net samples, with each species contributing more than 1 % towards the overall plankton ring net catch (Table 3.1). In both sampling methods, a few abundant taxa dominated catches with the 3 most abundant taxa collected by the plankton net and light traps accounting for 58.7 % and 86.2 % of the catch respectively. The Cape anchovy, *Engraulis encrasicolus*, was the most common taxon in both the plankton net (37.8 %) and light trap samples (55.3 %). *Etrumeus whiteheadi* was the second most common species in the light trap samples (21.1 %) but only the seventh most common in the plankton net samples (4.4 %).

5. DISCUSSION

Reef complexity, associated environmental variables, and the start or the end of the spawning period, were important characteristics determining associated larval fish availability over subtidal reef and sand habitats in Algoa Bay. At the habitat scale, patterns of larval density were complex, with peaks in abundance showing interactive effects with spawning periods. The two sampling techniques detected different patterns in species abundance between the various habitat types with distinct larval fish communities observed between the Bird Island reef habitats, the St Croix Island reef habitats and the sand habitat. Larval fish abundances, densities and species richness varied depending on the habitat complexity. The structural complexity of reef habitats is an important environmental variable that drives the abundance and distribution of species (Pais *et al.*, 2013). Shallow reef areas have been shown to serve as important nursery areas for the juveniles of a select suite of species that utilize microhabitats before the ontogenetic shift to adult habitats on deeper reefs (Beets and Hixon, 1994; Light and Jones, 1997; Nagelkerken *et al.*, 2000b). The structural complexity of mangrove and seagrass beds for example, which are known to serve as ideal habitats for the intermediate life-stages of fishes before moving onto coral reefs, have also been shown to have an effect on the fish abundance and species richness (Heald and Odum, 1970; Bell and Westoby, 1986; Stoner, 1986; Sogard *et al.*, 1987; Rooker and Dennis, 1991).

Sampling using the plankton ring net indicated that the less structurally complex, reef-associated sand habitats, yielded higher species richness and diversity than the high and low profile reef habitats, contradicting those findings often observed for adult and juvenile fish assemblages (Pratt, 1994; Jordan *et al.*, 2005; Hackradt *et al.*, 2011). However, the results from the present study are supported by the finding of Angel and Ojeda (2001) for temperate reef assemblages. Higher species diversity was found to occur at the less structurally complex reef sites on the temperate northern Chilean coast (Angel and Ojeda, 2001). A possible reason described by the authors include an absence of kelp forest at these sites, allowing the rocky and sandy bottoms open to pelagic species commonly found further offshore. Unvegetated sediment adjacent to seagrass has been found to be an important habitat for juveniles of a number of commercial fishery species (Ferrell and Bell, 1991). Caging experiments evaluating the impact of predation by fish on the assemblage structure of small (<10 cm) fishes indicate an increase in abundance of small fishes in areas of unvegetated sand over seagrass when predators were excluded (Hindell *et al.*, 2000). This suggests that juvenile fishes may prefer alternative unvegetated sand habitats, but their distributions are restricted to structurally complex habitats which provide refuge from predation (Levin *et al.*, 1997; Hindell *et al.*, 2000). Larval fishes in the lower reaches of the Swartkops Estuary in Algoa Bay showed preferences for non-vegetated marginal areas as opposed to vegetated areas (Strydom, 2003) which are characteristic of older juvenile fishes in these systems (Beckley, 1983a). This lower affinity for vegetated areas by the early developmental stages of fishes has been observed in temperate Australian estuaries (Hannan and Williams, 1998). Strydom (2003) proposed the lower affinity for vegetated areas displayed by larval fishes may have an advantage in lowering the predation risk from juvenile fishes already associated with the vegetated areas. Therefore, it is likely that the importance of less structurally complex habitats has been overlooked relative to other habitats in terms of their function for larval fishes. While the presence of structure may be sufficient for certain species, some taxa will discriminate amongst habitats based on structural characteristics.

The importance of sand habitats for fish assemblages are commonly ignored as sandy habitats are generally characterised by a lack of cover typically offered by reef habitats with reef areas generally more complex than sandy areas. Despite this, the sand habitat exhibited higher diversity and species richness than most of the reef habitats. Exposed sandy habitats, located only several metres from the main reef are known to exhibit much lower rates of predation than on the main reef itself as they are less frequented by predators (Shulman, 1985). Predation is known to be a major factor influencing juvenile fish abundance (Shulman, 1985; Hixon and Beets, 1993; Sweatman and Robertson, 1994; Beukers and Jones, 1997; Nanami and Nishihira, 2001). The settlement phase is a vulnerable time period during the early life history of fishes as larvae require time to adapt physiologically to the reef environment and are most likely exposed to high predation rates (Leis, 1991; Connell, 1997). The corresponding high species diversity, richness and number of species observed on the reef-associated sand and the sand habitats in the present study could be an artefact of this reduced predation pressure in these habitats.

Spatial variation in larval fish density was observed with greater densities of larvae observed at the St Croix Island subtidal reef habitats. An obvious reason for this discrepancy could be a result of physico-chemical variability. On average, the St Croix Island reef habitats experienced temperatures approximately 1 °C higher than the Bird Island reef habitats. Generally, warmer water masses are associated with higher productivity as primary production increases, ensuring better feeding conditions for larvae (Heath, 1992; Pörtner *et al.*, 2001). Theoretically, warmer temperatures also raise metabolic and growth rates in larvae, reducing the time larvae remain within the plankton, lowering their mortality rates (Houde, 1989). Furthermore, significantly higher turbidity levels were observed at the St Croix Island reef habitats, as this island complex is situated in close proximity to two permanently open estuaries, and two industrial harbours. The higher turbidity has a positive relationship for most species by reducing predation pressure from marine species, in particular visual predators (Martinho *et al.*, 2007).

Ichthyoplankton communities in shallow waters directly above coral reefs sampled with plankton nets within the Florida Keys are dominated by small, schooling fishes in the Atherinidae, Clupeidae and Engraulidae fish families (Sponaugle *et al.*, 2003). Similar findings were observed in the present study where the Engraulidae dominated catches contributing approximately 40 % towards the overall larval fish catch in the plankton net tows. The remaining abundant fish families included larval fishes whose adult assemblages were benthic, reef associated and pelagic including Gobiidae, Clupeidae, Cynoglossidae, Sparidae, Gobiesocidae, Blenniidae, Soleidae and Tripterygiidae. In the shallow (<15 m) nearshore of the eastern sector of Algoa Bay, similar larval fish catches in terms of fish families occur (Pattrick and Strydom, 2008), however changes in rank and abundance were observed. The ichthyoplankton assemblages of oceanic islands are characteristic and consist of larvae from adults who are both demersal and neritic (Leis *et al.*, 1991; Boehlert and Mundy, 1993). The larval fish assemblages in Algoa Bay appear to follow this trend. Similarly in temperate New Zealand, larvae of families with benthic eggs including Gobiescocidae, Acanthoclinidae, Tripterygiidae, Eleotridae and Gobiidae were the most abundant near reefs (Kingsford and Choat, 1989). It appears that some degree of overlap in fish family occurrence associated with reefs occurs internationally.

With regards to the light traps, Engraulidae and Clupeidae larvae and settlement stage fishes largely dominated assemblages in the island-reef habitats of Algoa Bay, as was the case in reef habitats both within the subtropical coastal waters of South Africa (Beckley and Naidoo, 2002) and internationally (Doherty and Carleton, 1997; Carassou and Ponton, 2007). The larvae of adult assemblages which were reef associated, benthic and/or pelagic-oceanic composed the light trap catches in the present study. Similarly, reef resident, benthic and pelagic taxa composed the light trap assemblages in the tropical waters of the Great Barrier Reef (Doherty and Carleton, 1997). The reef habitats associated with islands in Algoa Bay are in relatively close proximity to the Agulhas Current located approximately 50 kms offshore of Algoa Bay (Goschen and Schumann, 1994). The presence of several schooling species including *Decapterus macrosoma* and *D. punctatus* were observed in high abundances in these areas. The adults of these reef associated species are known to group along reef slopes adjacent to deep waters (Smith and Heemstra, 1995). The results of this study show conclusively that the pelagic juveniles of reef associated fish are therefore not randomly distributed in the water column but are in close association with reef habitats during the period of settlement. These species also selectively feed on plankton, therefore their dominance within the light trap samples is unsurprising given that light traps contained several large motile mysids, amphipods and polychaetes. Furthermore, the presence of *Etrumeus whiteheadi*, the redeye roundherring, in the light trap samples can similarly be explained by the selective feeding of this species on macrozooplankton. On one occasion at the Bird Island low profile reef habitat, two species of bathypelagic species, namely *Diaphus* *brachycephalus* and *Cyclothone* sp 1 were collected using the plankton ring net. These lanternfish and lightfish larvae are known to constitute up to 50 % of the total catch of larvae in Agulhas Current waters (Beckley and Van Ballegooyen, 1992). Warm water from the Agulhas Current is known to penetrate over the continental shelf with gale force westerly winds driving the water further into Algoa Bay (Goschen and Schumann, 1994). During the present study, strong (25 knot) westerly winds preceding (6 days) the sampling date, would have assisted in forcing Agulhas Current waters containing bathypelagic larvae into the Bay.

Of the 64 known recreationally and commercially important fish species (Chalmers, 2011) observed in extensive surveys of reefs in the region of the present study area, the early developmental stages of only 26 of these species were caught by either sampling method. Although the abundances of these taxa in the samples were low, they fall within the same range as that recorded by a similar ichthyoplankton survey in the Tsitsikamma National Park marine protected area (MPA) within the same biogeographical region as the present study (Tilney and Buxton, 1994). Comparisons with adult fish catches indicate that the numbers of larval and settlement stage fishes are generally low particularly in the Sparidae fish family. The paucity of sparid larvae in the present study, in relation to adult catches, suggests that spawning and development of these larvae are occurring away from the island regions. In many studies, juveniles of coral reef fish species are found in high densities in non-reef habitats, while the adults occur exclusively on the reefs themselves (Robertson and Duke, 1987; Thayer *et al.*, 1987; Parrish, 1989; Baelde, 1990; Sedberry and Carter, 1993; Laegdsgaard and Johnson, 2001). It is, however, noteworthy that previous reef associated larval fish studies have recorded very few larvae of common reef-dwelling fish (Kingsford and Choat, 1989; Hickford and Schiel, 1999).

The dominant taxa of these island-reef larval fish assemblages differed substantially between the start and the end of the spawning period. A staggered occurrence of larvae during the main spawning period was observed with dominant species showing variations in peak abundance. The dominant gobiids made important contributions towards the overall fish catch at the start of the spawning period, but were virtually absent from catches at the end of the spawning period. Peaks in abundance of *Caffrogobius nudiceps* and *Psammogobius knysnaensis*, which have an obligatory larval marine phase followed by the postflexion larvae and early juveniles entering estuaries, were observed at the start of the spawning season which coincides with maximum rainfall. Algoa Bay is situated centrally within the warm-temperate Agulhas bioregion and falls in the transition zone between winter and summer rainfall regions experiencing an overall winter maximum rainfall (Stone *et al.*, 1998). River flow entering the marine environment may serve as a cue in guiding estuarine-dependent larval fish species into estuary nursery habitats (Strydom and Whitfield, 2000).

Sampling ichthyoplankton in shallow waters close to reefs, which are usually inaccessible to towed plankton nets, has long been a challenge with regards to methodology. Light traps have been used extensively in tropical marine areas to investigate the recruitment of reef fishes by sampling settlement stage larvae as they enter a coral reef area after the completion of the planktonic stage of development (Doherty, 1987; Sponaugle and Cowen, 1996b; Hickford and Schiel, 1999; Fisher and Bellwood, 2002). These devices have been instrumental in understanding larval abundance patterns along the Great Barrier Reef (Doherty, 1987; Thorrold, 1992; Milicich and Doherty, 1994; Stobutzki and Bellwood, 1997). Light traps deployed near Lizard Island, Great Barrier Reef, Australia yielded a catch rate of approximately 4.9 individuals per hour during a 12-day sampling period (Fisher and Bellwood, 2002). A total of 645 individuals of at least 32 species from 11 families were collected. Lower catch rates in the tropics have also been observed averaging 1.9 individuals per hour with 8 families recorded on the Great Barrier Reef (Doherty, 1987). On the temperate coast of North Carolina, U.S.A. an average catch of 0.7 larval fish per hour was recorded (Brogan, 1994). These results fall into the same range of CPUE recorded during the present study.

Taxa that were abundant in the plankton net samples including *Caffrogobius nudiceps*, *Cremnochorites capensis*, *Diplogaster megalops*, Gobiidae sp 3, *Heteromycteris capensis*, *Pagellus natalensis*, *Spondyliosoma emarginatum*, did not occur in the light trap samples. Previous studies comparing light traps and plankton nets in marine waters have found that light traps collect far fewer families than associated plankton tows (Brogan, 1994; Hickford and Schiel, 1999). Similar results recorded by Hickford and Schiel (1999), indicate a likelihood that these taxa may potentially not be positively phototactic. However, the larval specimens captured with the plankton ring net were at a very early stage of development and it is likely that their absence in the light traps could be a result of poor swimming abilities and not phototactic response (Hickford and Schiel, 1999). During the present study, the light traps provided unique collections of carangid larvae and settlement stage fishes never captured with plankton nets.

In conclusion, the abundance of fish larvae in the subtidal reef areas associated with islands in Algoa Bay, South Africa, varies according to both temporal and spatial scales. Multispecies pulses in abundance of larvae were observed at the end of the spawning period linked to known breeding patterns of coastal species including *P. natalensis* and pelagic species including *E. encrasicolus* and *S. sagax*. Large peaks in abundance of Gobiidae larvae occurred at the start of the spawning period, coinciding with winter rainfall with greatest densities observed in the island associated reef habitats in the western sector of the Bay, in close proximity to the permanently open estuaries, suggesting active cueing. Analysis of species contributing most to differences between the various habitats indicate the importance of less structurally complex, reef-associated sand habitats for those larvae belonging to adults both associated with sand and the pelagic-oceanic environment. These species are specifically adapted to sedimentary habitats and will therefore show a preference against structure. The larvae of reef associated adult species occurred abundantly at the complex reef habitats, indicating a close association to settlement habitat during the pelagic larval phase.

6. ACKNOWLEDGEMENTS

This work is based on financial support from the South African National Parks (SANParks), South Africa. Gratitude is expressed to the SANParks. Any opinions, findings and conclusions expressed in this material are those of the authors and therefore the SANParks does not accept any liability in regards thereto. Fieldworkers are thanked for their valuable assistance. Mr Tim Vink is thanked for generation of the map in this chapter.

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CHAPTER 4

SPATIAL VARIABILITY IN SURF ZONE ASSEMBLAGES OF LARVAL FISHES, ALGOA BAY, SOUTH AFRICA

1. ABSTRACT

Sandy beach surf zones occur along approximately 38 % of the South African marine coastline. Wind exposure is known to influence wave energy. There is however a general lack in knowledge whether exposure influences larval fish dynamics within a large bay system with varying exposure along its length. Larval fishes were sampled from two areas with vastly different exposure to waves and wind, namely the windward and leeward sector of Algoa Bay over two years from December 2010 to October 2012. In total, 5702 larval fishes were collected using a modified larval seine net (4.5 x 1.5 m, 500 µm mesh). Of these, 4391 were collected in the lee and 1311 in the windward sector of the Bay, representing a total of 23 fish families and 57 species. Dominant fish families included Clinidae, Engraulidae, Kyphosidae, Mugilidae, Soleidae and Sparidae. Parallels in family occurrence are observed in international studies, highlighting the similarity in composition of larval fish assemblages universally and the utilization of surf zones as a whole by a specific group of larval fishes. Nineteen estuary associated marine species occurred in the surf zones of Algoa Bay and dominated catches (86.7 %) in terms of abundance. Postflexion larvae comprised over 80 % of the catch indicating the importance of the seemingly inhospitable surf zone environment for the early life stages of many fish species. The greatest species diversity was observed in the windward sector of the Bay. Distance-based linear modelling identified wave period as the environmental variable explaining the largest proportion of the significant variation in the larval fish assemblage. The physical environment of the surf zone could create a suitable habitat, sheltered from predators with an abundance of food resources for fish larvae.

2. INTRODUCTION

The physical characteristics of sandy beach surf zones have been well studied around the world with considerably less attention having been paid to the biological aspects of surf zones. Historically, these habitats have been understudied on exposed coastlines, like South Africa, owing to the difficulty of sampling in such a high energy environment. The importance of the surf zone habitat for adult and juvenile fish assemblages has been comprehensively studied internationally (Pearce *et al.*, 1942; Modde and Ross, 1981; Senta and Kinoshita, 1985; Yang and Senta, 1993; Ayvazian and Hyndes, 1995; Santos and Nash, 1995; Gibson *et al.*, 1996; Harvey, 1998; Layman, 2000; Beyst *et al.*, 2001; Able *et al.*, 2003; Gaelzer and Zalmon, 2003; Gomes *et al.*, 2003; Félix *et al.*, 2007b; Inui *et al.*, 2010). Similarly research on the use of surf zone habitats by juvenile fish assemblages in South Africa has had some research attention (Lasiak, 1984; Bennett, 1989; Clark *et al.*, 1994; Clark *et al.*, 1996a; Clark *et al.*, 1996b; Harris and Cyrus, 1996).

The importance of these areas for larval fishes is increasingly being recognized as a nursery habitat (Whitfield, 1989a; Strydom, 2003). In South Africa, isolated studies have assessed larval fish assemblage composition in estuary associated surf zones and non-estuary associated surf zones (Harris and Cyrus, 1996; Strydom and d'Hotman, 2005). Furthermore, recruitment into estuaries during overwash events (Bell *et al.*, 2001; Cowley *et al.*, 2001) and cueing during estuary opening events (Strydom, 2003) have been investigated. Microhabitat selection within surf zones has been observed with larvae actively selecting areas of reduced current flow in depressions associated with dissipative beach surf zones (Watt-Pringle and Strydom, 2003).

Previous studies worldwide on adult and juvenile fish assemblages in surf zones have indicated how wave exposure is one of the main factors affecting the structure of these communities (Romer, 1990; Clark, 1997; Gaelzer and Zalmon, 2003; Félix *et al.*, 2007a). A detailed study on the surf zone juvenile fish communities on an isolated beach in the region of the present study, indicated that a high degree of variability in community structure was observed (Lasiak, 1981; Lasiak, 1986). These dynamics appeared to be largely driven by abiotic factors including exposure and wind which would influence the wave regime. Watt-Pringle and Strydom (2003) indicated the importance of microhabitats such as sheltered trough areas for fish larvae. The early life history stages of fishes therefore have a tendency to seek refuge within surf zones (Watt-Pringle and Strydom, 2003). The influence of larger-scale exposure on larval fish assemblages in the surf zone is not known.

The degree of wave exposure experienced along a coastline depends on the position of the coast relative to the open sea, the prevailing winds and the topography (Lewis, 1964). Algoa Bay is a log-spiral bay with the south-western area of the Bay relatively sheltered behind Cape Recife with exposure increasing north-eastwards to the Sundays River beach (Goschen and Schumann, 2011). Most waves off the south-eastern South African coastline, approach from the south and south-west, generated by storms moving from west to east in the depression belt located to the south of the continent (Darbyshire and Darbyshire, 1964). In Algoa Bay, these southerly swells are deflected to the south east due to refraction of waves by Cape Recife and the shallow Riy Bank subtidal reef complex in the southern extent of Algoa Bay. In the lee of the Bay, sandy beach habitats are situated in close proximity to rocky shores which contrasts with the situation in the windward sector of the Bay where the lack of rocky shore exposes the inshore coastal waters to prevailing weather conditions. Wave heights between 0.5 – 5.0 m (87 % of waves between 1 – 3 m) in summer and between 1.0 – 6.5 m in winter have been recorded in Algoa Bay (McLachlan, 1983; CSIR, 1987). In addition to the regional differences in habitats, shallow water currents are far slower (<10 cm/s) in the western sector of the Bay (Schumann *et al.*, 2005) than current speeds (17.6 cm/s) in the eastern sector (Pattrick *et al.*, 2013). It is therefore hypothesized that the abundance and distribution of fish larvae in the windward and leeward surf zones of Algoa Bay are influenced by varying levels of exposure.

The aim of this study was to investigate larval fish species composition, seasonality and abundance in the surf zones of Algoa Bay and to use these data to test the hypothesis that species abundance and distribution differs between the leeward and windward sectors of the Bay as a result of the influence of wind and wave exposure.

3. MATERIALS AND METHODS

3.1 Study site

Larval fish samples were collected at 10 surf zone stations in Algoa Bay (Figure 4.1), between Cape Recife in the far western sector of the Bay (33°53′46′′S; 25°42′08′′E) and Woody Cape in the far eastern sector of the Bay (33°52′07′′S; 26°17′29′′E). Five sampling stations were located equidistant (~9 km) from each other in the leeward sector of the Bay, and similarly, in the windward sector of the Bay, five sampling stations were located equidistant (~9 km) from each other. Algoa Bay is the easternmost and largest of several log-spiral shaped bays on the temperate south east coast of South Africa (Goschen and Schumann, 2011). Sandy beaches and the associated surf zones comprise the dominant shoreline habitat in Algoa Bay. The beach morphodynamic type in this region is almost exclusively dissipative-intermediate (Harris *et al.*, 2011). The sandy beach habitats are heavily influenced by wave action (Branch and Branch, 1983) and the predominant south-westerly swell direction has led to the formation of sheltered beaches with few rip currents in the western sector (leeward) while in the eastern sector (windward) the shoreline is more dynamic and many semi-permanent rip currents are present (Talbot and Bate, 1987). These rip currents and nutrient rich groundwater originating from coastal aquifers into the surf zone drive the formation of dense aggregations of surf diatoms, *Anaulus australis*, which are the main source of primary production in the windward sector of the Bay (McLachlan and Lewin, 1981; Campbell and Bate, 1991; Campbell and Bate, 1998).

3.2 Field sampling and larval fish identification

During the two-year sampling period, larval fishes were collected by sampling two consecutive months per season during the diurnal spring low tide (December and January are summer months, March and April are autumn months, June and July are winter months and September and October are spring months). In total, 16 sampling trips took place between December 2010 and October 2012. Samples were collected over two sequential days, from the east to west in the windward and leeward sector of the Bay respectively. Seining typically occurred between the two hours before and after the spring low tide for ease of sampling in breaking waves. Samples were collected using a modified beach seine net (Strydom, 2003), with a mesh aperture of 500 µm, operated by two people pulled parallel to shore in depths <1.5 m for a distance of 25 m for each replicate with three replicates collected at each of the ten sampling stations. The net has a width of 4.5 m and a height of 1.5 m. A tapering cone has been fitted at the centre of the net, and the catch is funnelled into this cone during sampling to the cod-end. Larval fishes caught per haul are expressed as CPUE, referring to the number of larval fishes caught in a single 25 m seine haul. Each station was sampled by means of three replicate seine hauls. A total of 480 samples were collected over the study period. The plankton samples were fixed on site with 10 % formalin in seawater. Samples were sorted and analysed in the laboratory where larval fish were removed and identified to the lowest possible taxon (Smith and Heemstra, 1995; Neira *et al.*, 1998; Leis and Carson-Ewart, 2000).

The remaining zooplankton in each sample was placed in to a measuring cylinder and allowed to settle for 15 mins and a settled volume estimate of zooplankton was recorded in millilitres. Larvae and early juveniles were measured to the nearest 0.1 mm body length, which represents notochord length in preflexion and flexion larvae and standard length in postflexion larvae and early juveniles. Larval fish species that were positively identified (n = 51) were grouped into estuary associated categories (Whitfield, 1998). Estuary-resident species belong to category I, estuary-dependent species belong to category II and marine species that are independent of estuaries belong to category III. Temperature (°C), salinity, turbidity (NTU), conductivity (µSIEMENS/cm), pH and total dissolved solids (TDS) were measured at each station using a YSI 6600 multi-parameter meter. Wind speed (m/s) and direction (degrees from North) data were obtained at hourly intervals from two South African Weather Service (SAWS) stations located on Bird Island (3 m above sea level), in the windward sector of Algoa Bay, and at Port Elizabeth Harbour (63 m above sea level) located in the leeward sector of the Bay and averaged daily. Wave height (m) and period (s) data were obtained at three hourly intervals from the Weather Research and Forecasting (WRF) model stations located at Cannon Rocks in the windward sector of the Bay and at Port Elizabeth located in the leeward sector of the Bay and similarly averaged daily. The proximity of each station to the permanently open Sundays Estuary (33°43’20.09”S 25°52’12.85”E) and Swartkops Estuary (33°43’20.09”S 25°52’12.85”E), and the industrial harbours including the Port of Port Elizabeth (33°57’40.30”S 25°38’31.15”E) and the Port of Ngqura (Coega) (33°48’16.40”S 25°21’28.39”E) were calculated using imagery acquired from Google Earth. Surf zone width was calculated following Harris *et al.* (2011) using imagery acquired from Google Earth by measuring the distance between the landward position of the swash edge and the seaward edge of the white water from the outermost breaker at the backline. A frame extending from the high water mark to deepest depth sampled at each station and running parallel to shore for 500 m, was used to determine the area of shore covered by rock representing complex habitat using Google Earth imagery.

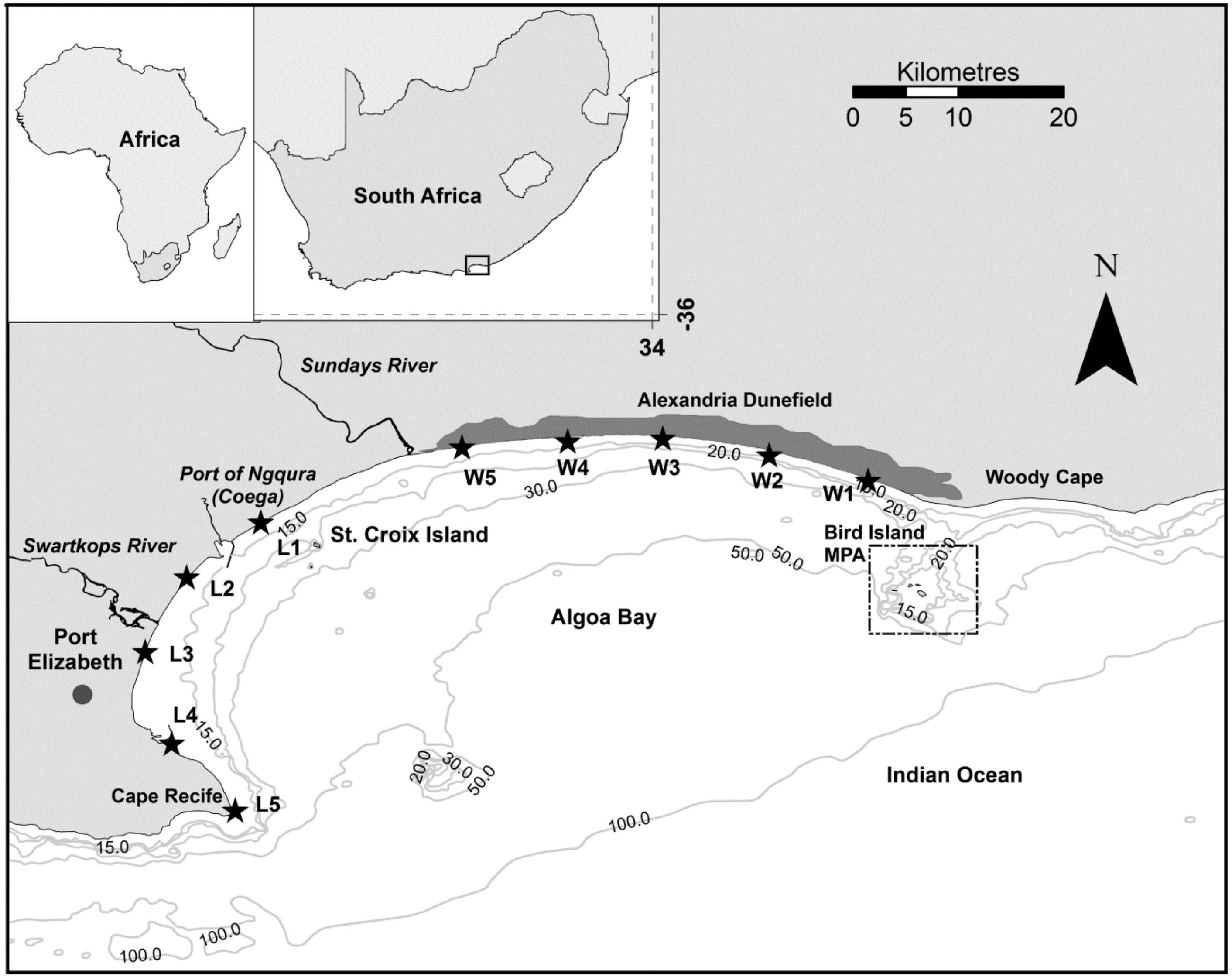

FIGURE 4.1 The geographic position of Algoa Bay, showing the location of the ten surf zone sampling stations located between Cape Recife and Woody Cape

3.3 Data analyses

Diversity indices including total species number (N), Shannon-Wiener diversity (H’), Margalef species richness (d) and Pielou’s evenness (J’) were calculated per station per sampling event, using the PRIMER statistical package version 6.1, 2013 (Clarke and Warwick, 1994). Shannon-Wiener diversity was calculated to one decimal point using $\log_e$. All physical and biological data was tested for normality using a normal probability plot and Shapiro-Wilk test and homogeneity of variance using a Levene’s test with the STATISTICA software package version 11, 2012. All environmental data excluding wave height and wind speed were normally distributed and a 1-way ANOVA test (F) was used to determine variability between the leeward and windward zones, the seasons and the stations and to determine inter-annual variation. Wave height and wind speed data were square root transformed and conformed to parametric test assumptions and similarly a 1-way ANOVA test (F) was used to determine variability between the zones, seasons, stations and years. For the total species number (N) and diversity (H’), data in the original format conformed to parametric test assumptions. Species richness (d) was square root transformed and conformed to parametric test assumptions. For all other larval fish biological and macrozooplankton data, parametric test assumptions were not met, even after appropriate transformations were used and non-parametric tests were conducted. In order to investigate the spatial and temporal patterns of variation in the total species number (N), diversity (H’) and species richness (d) a 1-way ANOVA test (F) was used. Differences in larval fish CPUE and species evenness between the leeward and windward sectors and interannual variation were assessed using a Mann-Whitney U-test (U). A Kruskal-Wallis (H) ANOVA was used to assess differences in larval fish CPUE and species evenness between seasons and stations. Community analysis was similarly conducted using the PRIMER statistical package version 6.1, 2013. Catch per unit effort (CPUE) data were square root transformed to down-weight the most abundant species and allow rare species to contribute. All environmental variables were normalized to account for differences in measurement scales by subtracting the mean and dividing by the standard deviation for each variable. Surf zone environmental variations were analysed using principal coordinates (PCO) analysis with physico-chemical, wave height, wave period, wind speed, wind direction, maximum wind speed, proximity to river and harbour, rocky shore cover and macrozooplankton data. Clusters in a dendrogram format were assessed using group average hierarchical sorting, and ANOSIM was used to detect differences among groups in each analysis. The SIMPER routine was applied to determine the relative contribution of key species to the similarity or difference among leeward and windward stations. Distance-based linear modelling (DistLM) was carried out to assess the relative contributions of environmental variables structuring larval fish assemblages using Pearson correlation R-values using the selection criterion R2 for the model. The significance of the relationship was based on a 999 permutation test. A one-tailed t-test was used to determine whether the mean body lengths of dominant larvae in the windward sector of the Bay were significantly larger than the mean body lengths of dominant larvae in the leeward sector of Algoa Bay. Dominant species were those represented by more than 30 individuals in the total catch.

4. RESULTS

4.1 Habitat variability

A significant difference in water temperature (F = 78.4; d.f. = 3; $p < 0.001$), conductivity (F = 29.5; d.f. = 3; $p < 0.001$), total dissolved solids (F = 48.8; d.f. = 3; $p < 0.001$), salinity (F = 116.2; d.f. = 3; $p < 0.001$), pH (F = 16.3; d.f. = 3; $p < 0.001$), turbidity (F = 5.6; d.f. = 3; $p < 0.01$), wind direction (F = 11.9; d.f. = 3; $p < 0.001$), wave height (F = 1.3; d.f. = 3; $p < 0.001$) and wave period (F = 13.2; d.f. = 3; $p < 0.001$) occurred among the seasons during the study period (Figure 4.2). A general cyclical trend in sea temperatures (Figure 4.2a) was observed during the study period, with temperatures gradually rising to a peak of ~22 °C during summer falling to ~16 °C in winter. Conductivity ranged between ~51.5 µSIEMENS/cm in summer to ~53 µSIEMENS/cm in autumn (Figure 4.2b). Total dissolved solids showed a distinct seasonal trend with highest values recorded during the autumn (34.2) period and lowest values during summer (33.5) (Figure 4.2c). The mean salinity was largely static throughout the study period and spatially within the study area remaining at ~35.5 (Fig. 4.2d). Small fluctuations in pH levels were observed in the study area temporally, however levels remained at ~8 (Figure 4.2e). Similarly, turbidity values fluctuated in the Bay with lowest values of ~5 NTU recorded during spring and highest values of ~10 NTU during summer in the leeward sector of the Bay (Figure 4.2f). Average wave heights (Figure 4.2g) and wind speeds (Figure 4.2h) were greatest during the autumn and winter seasons particularly in the windward sector of the Bay. Wave period was generally longer in the leeward sector of the Bay with greatest period observed in winter and lowest in summer (Figure 4.2i). South westerly winds dominated during the winter and spring months while south easterly winds dominated during the summer and autumn months.

No significant difference in physico-chemical variables, wave height, wave period, wind speed and wind direction was observed spatially between the leeward and windward sector of Algoa Bay. However, a significant difference in macrozooplankton (U = 1280.5; $p < 0.001$) was observed spatially between the leeward and windward sectors with the greatest volumes observed in the windward sector (Figure 4.2j).

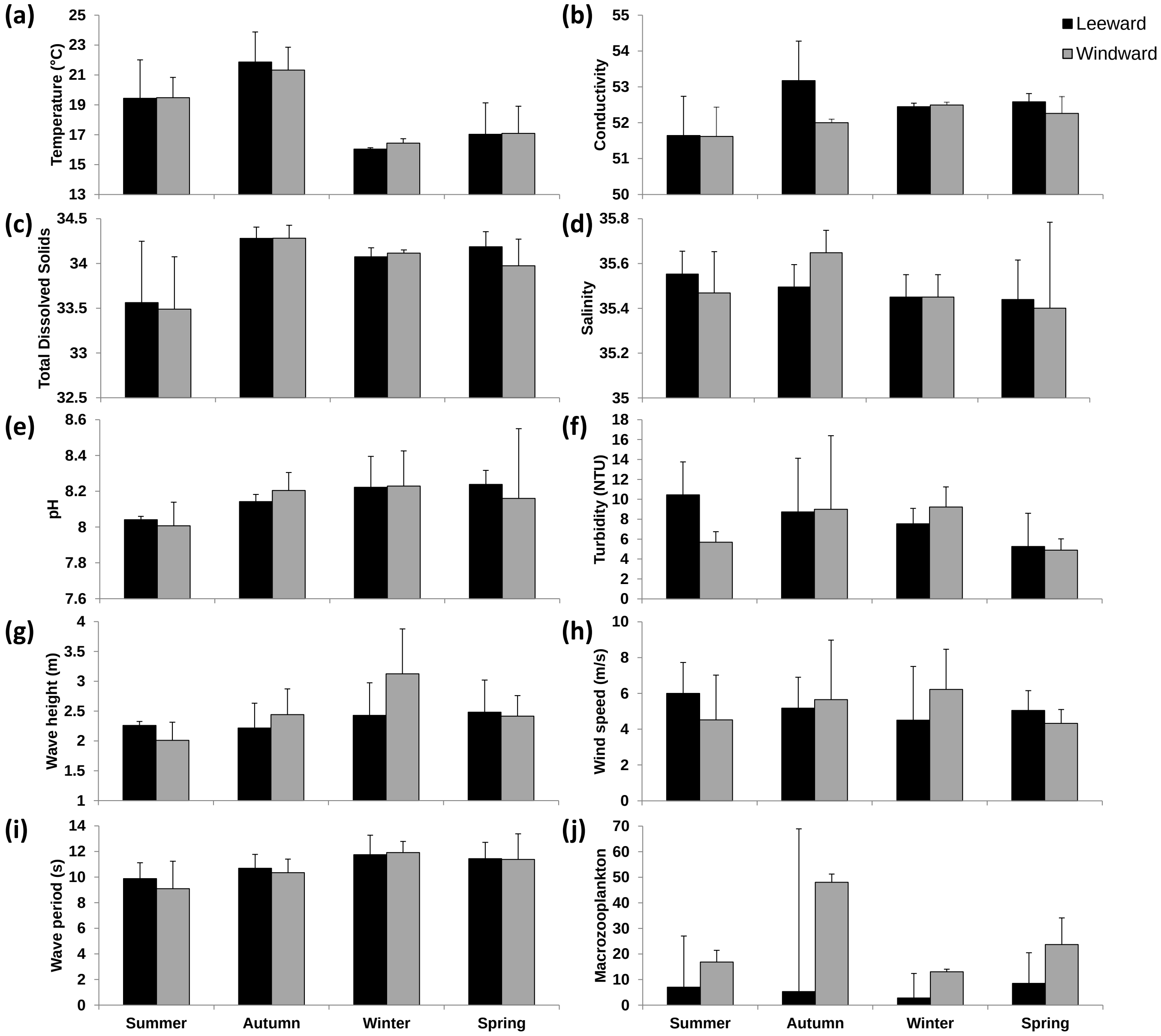

FIGURE 4.2 Mean (n = 20) and mean error of a) sea temperature, b) conductivity, c) total dissolved solids, d) salinity, e) pH, f) turbidity, g) wave height h) wind speed, i) wave period and j) mean and maximum of settled volume of macrozooplankton recorded seasonally at each surf zone station in the leeward and windward sector of Algoa Bay during the study (December 2010 – October 2012)

A significant difference in water temperature ($F = 5.6$; d.f. = 1; $p < 0.05$), conductivity ($F = 8.2$; d.f. = 1; $p < 0.01$), total dissolved solids ($F = 5.1$; d.f. = 1; $p < 0.05$), wind direction ($F = 15.2$; d.f. = 1; $p < 0.001$), wave height ($F = 6.2$; d.f. = 1; $p < 0.05$), wave period ($F = 6.4$; d.f. = 1; $p < 0.05$) and microzooplankton ($U = 1548.0$; $p < 0.001$) occurred inter-annually during the study period with highest observations observed during the second year. No significant difference in turbidity ($F = 2.7$; d.f. = 1; $p = 0.1$), pH ($F = 0.003$; d.f. = 1; $p = 0.9$) and salinity ($F = 0.9$; d.f. = 1; $p = 0.3$) was observed inter-annually during the study period.

Principal coordinates (PCO) analysis ordination was performed on the 18 environmental variables (Figure 4.3). The 18 variables explained 36.4 % of the variation in the first two axes. The first two principal components described 19.1 % and 17.3 % of the total surf zone variation respectively. A clear spatial gradient between the leeward and windward beaches could be observed, defined by the second principal component mainly, mostly evident on windward beaches. The second principal component was characterized by a positive correlation with wave period and percentage rocky shore cover and a negative relationship with macrozooplankton. Furthermore, the second principal component was characterized by a negative correlation with proximity to the Swartkops River Estuary, Port of Port Elizabeth and Port of Ngqura (Coega).

4.2 Catch composition, developmental stages and estuary association

Larval fishes collected in the surf zones over the two year period ($n_{total} = 5702$; $n_{leeward} = 4391$; $n_{windward} = 1311$) represented 23 families ($n_{leeward} = 21$; $n_{windward} = 17$) and 57 species ($n_{leeward} = 49$; $n_{windward} = 34$) (Table 4.1). The Sparidae fish family dominated larval fishes comprising 82.3 % in the leeward sector of the Bay and 60.4 % in the windward sector of the Bay. In the lee of the Bay, Clinidae (6.6 %), Kyphosidae (2.6 %) and Soleidae (2.4 %) made important contributions towards the overall larval fish catch. In the windward sector of the Bay, Soleidae (19.2 %), Mugilidae (9.0 %) and the Gobiidae (3.3 %) made important contributions towards the overall larval fish catch. The sparid, *Diplodus capensis*, was the most abundant species (n = 3814) contributing 66.9 % towards the overall larval fish catch, with more than ten times the number of *Rhabdosargus holubi* (n = 349), the second most abundant species. *Clinus* sp 1, *Clinus superciliosus*, *Engraulis encrasicolus*, *Heteromycteris capensis*, *Liza* sp 1, *Neoscorpis lithophilus*, *Rhabdosargus globiceps*, *Sarpa salpa* and *Solea turbynei* all contributed >1 % towards the total larval fish catch. In the lee of the Bay, *Diplodus capensis* (77.0 %), *Sarpa salpa* (3.5 %) and *Clinus* sp 1 (2.9 %) were the top three most abundant species and in the windward sector, *Diplodus capensis* (32.5 %), *Rhabdosargus holubi* (23.6 %) and *Heteromycteris capensis* (12.1 %) were the most abundant.

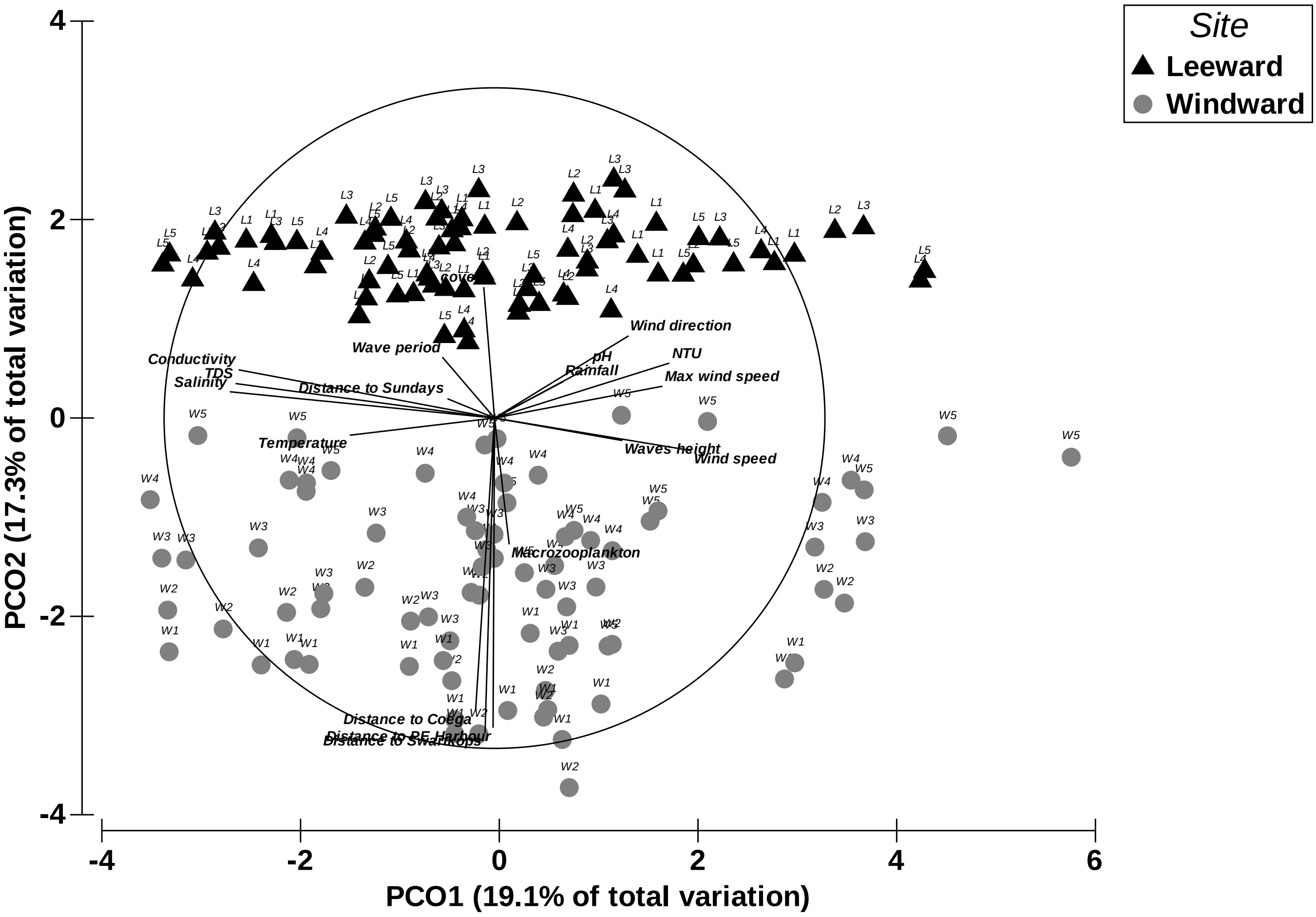

FIGURE 4.3 An ordination plot of the first two principal components illustrating each sampling event in the surf zones within the leeward and windward sector of Algoa Bay during the study (December 2010 – October 2012)

Twelve fish specimens could not be identified past family and five specimens could not be identified past genera. These included representatives from the fish families Atherinidae, Clinidae, Gobiidae, Leiognathidae, Mugilidae and Tetraodontidae with catches rare and each fish family contributing <0.1 % towards the total overall catch.

Postflexion larvae comprised over 80 % of the larval fish catch in the surf zones of Algoa Bay. This developmental stage dominated catches in both the leeward (77.6 %) and windward (87.9 %) sector of the Bay. Larvae in the flexion stage of development contributed 8.4 % towards the total catch in the lee and 6.1 % in the windward sector of Algoa Bay. Only

3.4 % of the total catch in the lee of the Bay consisted of preflexion larvae while this stage only comprised 2.3% in the windward sector. A greater contribution of early juvenile fishes was observed in the leeward sector (10.6 %) than the windward sector (3.7 %) of the Bay.

The total number (21) of marine species (category III), not dependent on estuaries, in the surf zones of Algoa Bay was greater than the number (11) of estuary-resident species (category I) and the number (19) of estuary associated marine species (category II). In terms of abundance however, the estuary associated marine species dominated catches (86.7 %), followed by the estuary-residents (8.0 %) with the marine species contributing the lowest in abundance (5.3 %) towards the overall catch. The total number of estuary associated marine species dominated catches of larval fishes at all ten surf zone stations in the Bay (Figure 4.4). Estuary-resident species however made important contributions towards the larval fish catch particularly at the leeward station 3, 4 and 5. Station 3 is situated close to the permanently open Swartkops Estuary. Station 4 is situated close to the entry of the Port Elizabeth harbour, into which the Baakens River flows. In the windward sector of Algoa Bay, estuary-resident species made important contributions towards larval fish catches as stations from east towards west with the greatest percentage towards the total larval fish catch occurring at station 5 which is located in close proximity to the permanently open Sundays River.

4.3 Spatial trends in larval fish CPUE and diversity

The relative abundance of larval fishes was higher in the leeward sector than in the windward sector of Algoa Bay. A total of 4391 larvae (77.0 % of the total catch), were sampled from the leeward sector while only 1311 larvae (23.0 % of the total catch), were sampled from the windward sector of the Bay. The mean CPUE in the leeward stations was 18.3 larvae/25m haul and ranged from 2.2 larvae/25m to 78.3 larvae/25m. In the windward sector of the Bay the mean was 5.5 larvae/25m and raged from 3.4 larvae/25m to 10.3 larvae/25m (Figure 4.5).

A greater average number of species (3), evenness (0.6) and Shannon-Wiener diversity (0.8) was observed in the windward sector of the Bay compared to that of the number of species (2), evenness (0.5) and Shannon-Wiener species diversity (0.6) in the leeward sector of Algoa Bay. Greatest evenness (0.6) and Shannon-Wiener diversity (0.9) was observed at station number four (King’s Beach) within the lee of the Bay. The lowest degree of evenness (0.3) was recorded at station 5 (Cape Recife) in the leeward sector of Algoa Bay resulting in the lowest Shannon-Wiener species diversity (0.3) observed at this leeward station located at

Cape Recife, a rocky shore associated surf zone. The highest number of species (4) was observed within the windward sector of the Bay at station 2 and the lowest species number (2) was observed in the leeward sector at station 1 (Hougham Park).

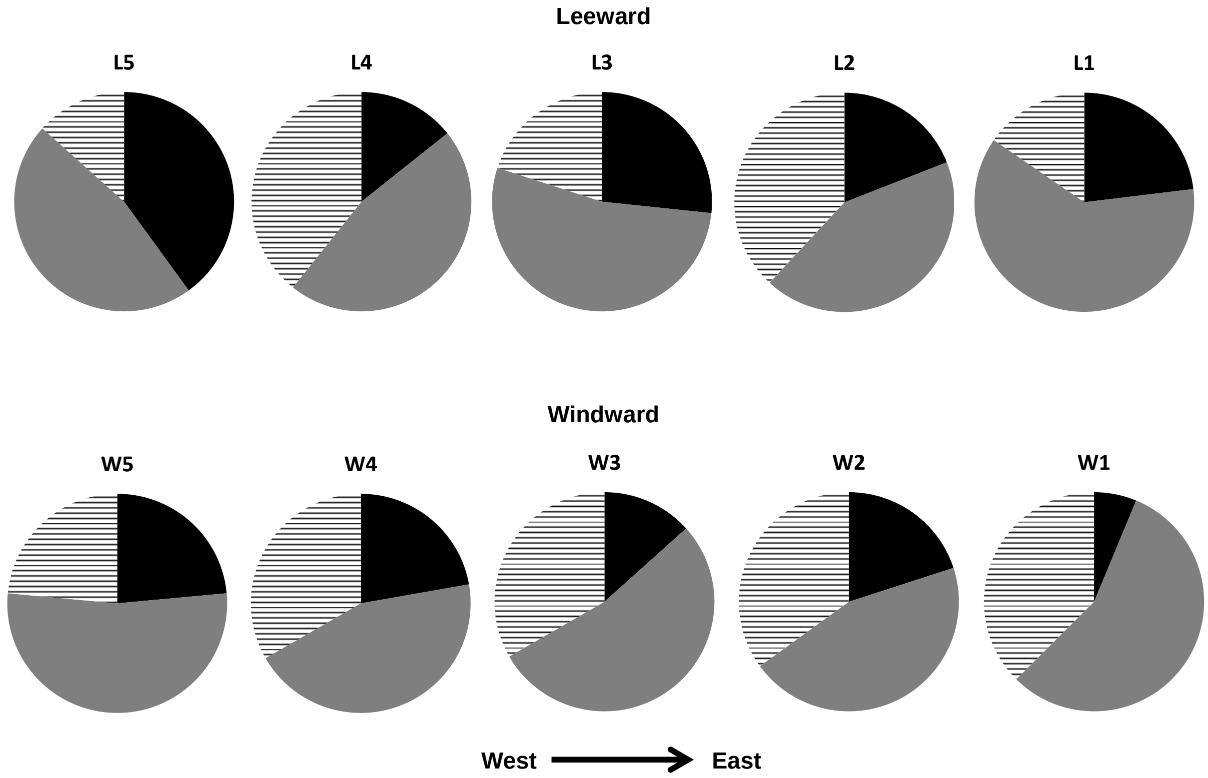

FIGURE 4.4 Percentage contribution of estuary associated species categories towards overall larval fish catch at each surf zone station in the leeward and windward sectors of Algoa Bay during the study (December 2010 – October 2012). Category I defined by black shading, Category II by grey shading and Category III with stripes.

TABLE 4.1 Species and taxa composition, mean CPUE (range), total catch, mean body length (range), developmental stage of larval fishes caught in the leeward and windward surf zones of Algoa Bay. Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile. Dominant developmental stages bolded

		LEEWARD		WINDWARD		LEEWARD		WINDWARD		LEEWARD		WINDWARD	
		CPUE				Total Catch				Length (mm)	Development	Length (mm)	Development
		Mean	Range	Mean	Range	No.	%	No.	%	Range	stage	Range	stage
Atheriniidae	*Atherina breviceps*	0.2	0 – 11.0	0.01	0 – 0.7	47	1.1	3	0.2	58.8 (25.5 – 71.0)	**Ej**	48.3 (42.0 – 55.0)	**Ej**
	Atheriniidae sp 1	0.02	0 – 0.7	0.1	0 – 3.3	5	0.1	14	1.1	6.2 (5.4 – 7.1)	**Pr**	7.8 (6.5 – 9.2)	**Pr**, F
Blenniidae	*Parablennius pilicornis*			0.004	0 – 0.3			1	0.1			14.8	**Po**
Carangidae	*Decapterus macrosoma*	0.004	0 – 0.3			1	0.02			38.5	**Ej**		
Clinidae	Clinidae sp 1	0.2	0 – 10.3	0.01	0 – 0.3	47	1.1	2	0.2	11.0 (8.3 – 15.1)	**Po**	17.3 (15.7 – 19.4)	**Po**
	Clinidae sp 2	0.01	0 – 0.3			2	0.05			15.7 (14.4 – 16.9)	**Po**		
	Clinidae sp 3	0.03	0 – 2.3			7	0.2			18.2 (13.2 – 19.7)	**Po**		
	Clinus sp 1	0.5	0 – 23.0	0.004	0 – 0.3	127	2.9	1	0.1	11.5 (9.8 – 17.4)	**Po**	18.7	**Po**
	Clinus superciliosus	0.4	0 – 34.0			103	2.3			14.3 (12.2 – 32.5)	**Po**, Ej		
Clupeidae	*Etrumeus whiteheadi*	0.004	0 – 0.3			1	0.02			15.4	**F**		
	Gilchristella aestuaria	0.02	0 – 0.7	0.1	0 – 2.3	4	0.1	13	1.0	44.0 (22.0 – 56.0)	Po, **Ej**	20.1 (17.1 – 28.4)	**Ej**
Cynoglossidae	*Cynoglossus capensis*	0.01	0 – 0.3			3	0.1			26.4 (2.4 – 70.0)	**Pr, Ej**		
Engraulidae	*Engraulis encrasicolus*	0.1	0 – 6.7	0.2	0 – 3.0	27	0.6	37	2.8	5.8 (3.0 – 10.3)	**Pr**, F, Po	10.4 (3.9 – 24.2)	Pr, F, **Po**
Gobiesocidae	*Chorisochismus dentex*	0.01	0 – 0.3			2	0.05			2.1 (1.5 – 2.7)	**Pr**		
	Diplecogaster megalops	0.1	0 – 4.0	0.004	0 – 0.3	14	0.3	1	0.1	3.8 (2.8 – 4.9)	**Pr**, F	5.5	**Po**
Gobiidae	*Caffrogobius gilchristi*	0.1	0 – 4.7	0.1	0 – 2.0	16	0.4	15	1.1	19.2 (8.8 – 31.0)	**Po, Ej**	6.9 (3.7 – 10.5)	**F**, Po
	Caffrogobius nudiceps	0.1	0 – 1.7	0.01	0 – 0.3	17	0.4	3	0.2	9.9 (3.5 – 16.5)	Pr, F, **Po**	4.8 (1.3 – 8.6)	**Pr**
	Gobiidae sp 1	0.05	0 – 1.3	0.004	0 – 0.3	11	0.3	1	0.1	10.7 (5.8 – 15.4)	**Po**	6.0	**Po**
	Gobiidae sp 2	0.004	0 – 0.3			1	0.02			4.2	**Pr**		
	Psammogobius knysnaensis	0.04	0 – 1.3	0.1	0 – 2.3	9	0.2	25	1.9	6.5 (5.9 – 7.0)	F, **Po**	6.3 (2.5 – 12.8)	Pr, **Po**
Gonostomatidae	*Cyclothone* sp 1			0.004	0 – 0.3			1	0.1			4.5	**F**
Haemulidae	*Pomadasys commersonnii*	0.004	0 – 0.3			1	0.02			6.0	**F**		
	Pomadasys olivaceum			0.01	0 – 0.3			2	0.2			57.0 (48.0 – 66.0)	**Ej**
Kyphosidae	*Neoscorpis lithophilus*	0.5	0 – 33.3	0.1	0 – 2.0	112	2.6	16	1.2	17.0 (9.4 – 78.0)	F, **Po**, Ej	12.9 (9.8 – 26.0)	**Po**, Ej
Leiognathidae	Leiognathidae sp 1	0.004	0 – 0.3			1	0.02			6.4	**F**		
Lutjanidae	*Lutjanus* sp 1	0.01	0 – 0.3			2	0.05			3.7 (2.7 – 4.6)	**Pr, F**		
Monodactylidae	*Monodactylus falciformis*	0.02	0 – 0.7	0.004	0 – 0.3	4	0.1	1	0.1	5.9 (5.3 – 6.5)	F, **Po**	5.6	**F**
Mugilidae	*Liza dumerili*			0.004	0 – 0.3			1	0.1			25.0	**Po**
	Liza richardsonii	0.1	0 – 10.7	0.1	0 – 3.0	33	0.8	16	1.2	23.0 (11.5 – 35.0)	Po, **Ej**	24.8 (15.8 – 38.0)	**Po**, Ej
	Liza sp1	0.1	0 – 1.7	0.3	0 – 7.0	18	0.4	61	4.7	12.3 (8.7 – 20.0)	**Po**	12.8 (7.9 – 20.5)	**Po**
	Liza sp 2	0.03	0 – 1.7	0.1	0 – 4.7	6	0.1	15	1.1	16.5 (14.9 – 17.2)	**Po**	16.5 (14.5 – 19.0)	**Po**
	Liza tricuspidens	0.004	0 – 0.3			1	0.02			64.0	**Ej**		
	Mugil cephalus	0.01	0 – 1.0	0.01	0 – 0.3	3	0.1	3	0.2	8.1 (7.6 – 8.4)	**Po**	17.5 (13.2 – 20.2)	**Po**, Ej
	Mugilidae sp 1			0.004	0 – 0.3			1	0.1			11.0	**Po**
	Mugilidae sp 2	0.01	0 – 1.0	0.04	0 – 1.7	3	0.1	10	0.8	16.1 (14.8 – 17.2)	**Po**	21.8 (17.9 – 24.0)	**Po**, Ej

	Mugilidae sp 6	0.01	0 – 0.3			3	0.1			18.0 (15.2 – 22.0)	**Po**		
	Mugilidae sp 7	0.004	0 – 0.3			1	0.02			11.0	**Po**		
	Myxus capensis			0.05	0 – 1.0			11	0.8			15.2 (11.3 – 26.4)	**Po, Ej**
Notocheiridae	*Iso natalensis*	0.1	0 – 2.33	0.04	0 – 1.3	18	0.4	10	0.8	12.1 (5.5 – 36.0)	Pr, **F**, Po, Ej	8.5 (6.6 – 12.2)	Pr, **F**, Po
Platycephalidae	*Platycephalus indicus*	0.1	0 – 2.0			14	0.3			18.9 (10.0 – 60.0)	**Po**, Ej		
Pomatomidae	*Pomatomus saltatrix*			0.004	0 – 0.3			1	0.1			90	**Ej**
Sciaenidae	*Argyrosomus inodorus*	0.004	0 – 0.3	0.01	0 – 0.3	1	0.02	2	0.2	2.0	**Pr**	3.2 (2.9 – 3.5)	**Pr**
	Argyrosomus japonicus	0.01	0 – 0.7			3	0.1			5.2 (4.1 – 6.8)	Pr, **F**		
	Umbrina canariensis	0.004	0 – 0.3			1	0.02			6.1	**Po**		
Soleidae	*Austroglossus pectoralis*	0.004	0 – 0.3			1	0.02			3.7	**Pr**		
	Heteromycteris capensis	0.3	0 – 4.0	0.7	0 – 5.0	70	1.6	158	12.1	8.4 (1.8 - 43.5)	Pr, F, **Po**, Ej	6.4 (2.4 – 8.4)	Pr, F, **Po**
	Solea fulvomarginata	0.004	0 – 0.3			1	0.02			3.7	**Pr**		
	Solea turbynei	0.1	0 – 2.0	0.4	0 – 8.7	34	0.8	93	7.1	4.8 (2.8 – 36.0)	**F**, Po, Ej	3.8 (2.8 – 6.8)	F, **Po**
Sparidae	*Diplodus capensis*	14.1	0 – 629.0	1.8	0 – 89.0	3388	77.2	426	32.5	11.8 (4.3 – 31.0)	Pr, F, **Po**, Ej	10.5 (3.7 – 24.7)	Pr, **Po**
	Diplodus cervinus hottentotus	0.01	0 – 0.7			3	0.1			3.8 (9.4 – 19.0)	**Po**		
	Rhabdosargus globiceps	0.1	0 – 2.3	0.2	0 – 8.3	24	0.5	49	3.7	13.0 (10.2 – 17.8)	F, **Po**	14.0 (8.5 – 29.5)	**Po**
	Rhabdosargus holubi	0.2	0 – 4.0	1.3	0 – 26.3	40	0.9	309	23.6	11.3 (9.4 – 14.7)	**Po**	11.3 (8.0 – 22.0)	**Po**
	Sarpa salpa	0.7	0 – 25.3	0.03	0 – 1.3	154	3.5	8	0.6	25.5 (12.9 – 51.0)	Po, **Ej**	14.7 (13.6 – 16.6)	**Po**
	Spondyliosoma emarginatum	0.01	0 – 1.0			3	0.1			7.9 (7.4 – 8.2)	**F**		
Tetraodontidae	*Amblyrhynchotes honckenii*	0.004	0 – 0.33			1	0.02			8.9	**Po**		
	Tetraodontidae sp 1			0.004	0 – 0.3			1	0.1			5.1	**Po**
Tripterygiidae	*Cremnochorites capensis*	0.01	0 – 1.0			3	0.1			4.7 (4.2 – 5.2)	**Pr**		

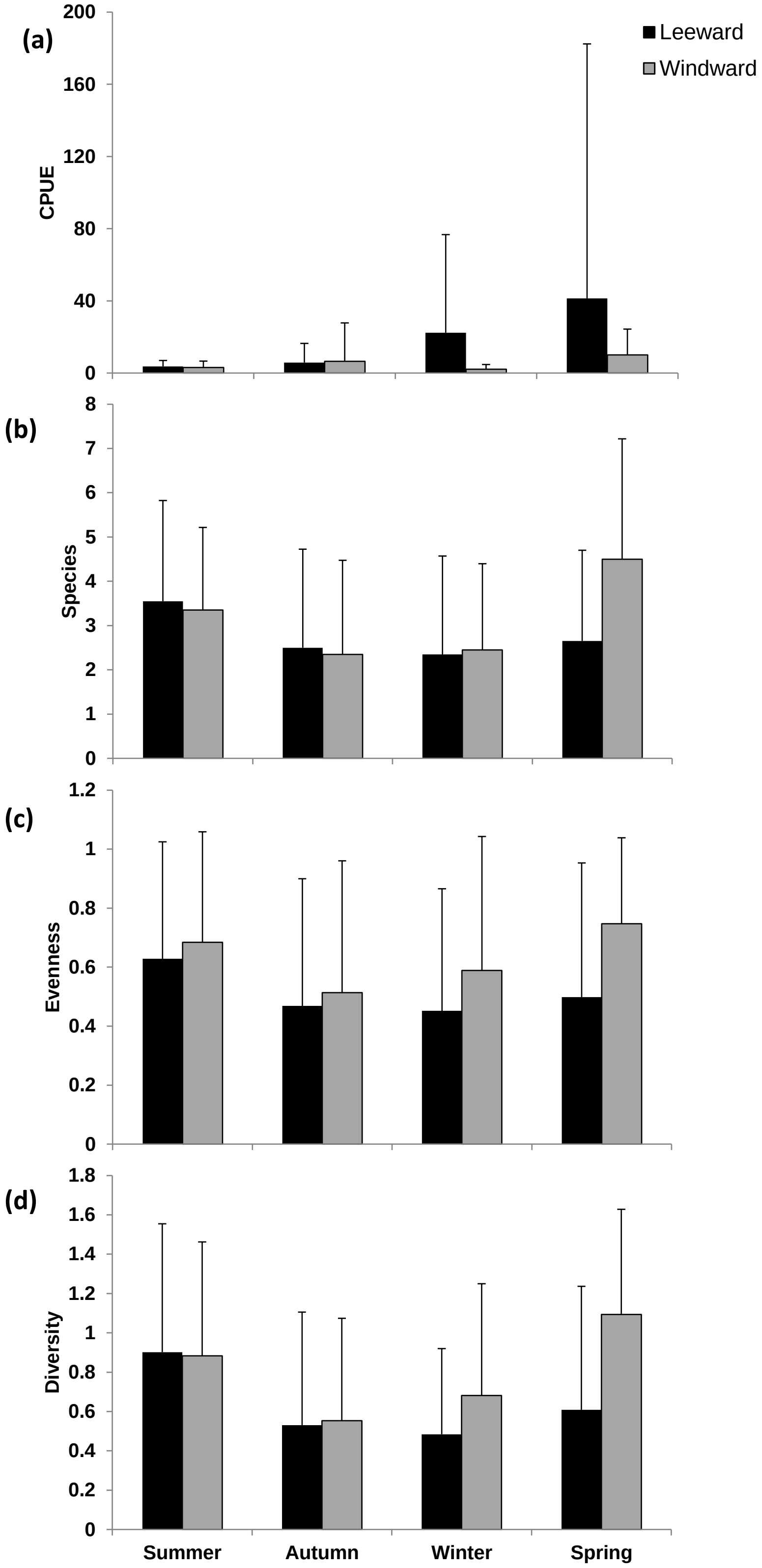

FIGURE 4.5 Larval fish mean (n = 20) and maximum of a) CPUE, b) number of species, c) Pielou's evenness and d) Shannon-Wiener diversity recorded seasonally in the surf zones of Algoa Bay during the study (December 2010 – October 2012)

4.4 Seasonal trends in larval fish CPUE and diversity

Although no statistical significant difference (H = 5.5; d.f. = 3; p = 0.14) in the CPUE of larval fishes was observed among seasons, a significant difference in the number of species (F = 3.3; d.f. = 3; p < 0.05), species richness (F = 4.1; d.f. = 3; p < 0.01) and diversity according to the Shannon-Wiener index (F = 4.0; d.f. = 3; p < 0.001) was observed among the seasons. The highest mean CPUE of 67.0 larvae/25m was recorded during spring in the leeward sector of the Bay (Figure 4.5). Larval fish CPUE declined in winter to 1.3 larvae/25m captured in the windward sector of the Bay. Similar catches in larvae were observed during summer (6.8 larvae/25m) and autumn (6.2 larvae/25m). The highest mean number of species in both the leeward (3.5) and windward (3.4) sectors of the Bay was recorded during summer. Diversity according to the Shannon-Wiener index was highest during spring (0.9) in the leeward sector of the Bay and summer (1.1) in the windward sector of the Bay (Figure 4.5).

No significant difference in the CPUE of larval fishes (U = 2045.0; p = 0.2), the number of species (F = 0.7; d.f. = 1; p = 0.4), species richness (F = 0.9; d.f. = 1; p < 0.4) and diversity according to the Shannon-Wiener index (F = 0.1; d.f. = 1; p = 0.8) was observed inter-annually during the study period.

4.5 Community analysis and environmental correlation

A community analysis approach was used to interpret leeward and windward zones based on species abundance. Three distinct groups could be identified (Figure 4.6). In the leeward sector of the Bay, station 1 and 5 were considered as outliers, as these two stations are associated with rocky shores. The remaining leeward stations were significantly different (p < 0.01; R = 0.651) from the windward stations (ANOSIM) grouping out at the 52 % level of similarity with eight species contributed approximately 50 % to the dissimilarity including *Diplodus capensis* (21.8 %), *Rhabdosargus holubi* (7.7 %), *Sarpa salpa* (4.3%), *Clinus* sp 1 (3.7 %), *Atherina breviceps* (3.4 %), *Clinus superciliosus* (3.2 %), *Liza richardsonii* (2.8 %) and *Caffrogobius nudiceps* (2.7 %). Excluding *Rhabdosargus holubi*, whose abundances were significantly (Z = -2.6; p < 0.001) greater in the windward sector of the Bay, all remaining seven species occurred in higher abundances in the leeward sector of the Bay. A distance-based linear model (DistLM) identified that wave period explained the largest proportion (4.2 %) of the significant (p < 0.01) variation in the larval fish assemblage (Table 4.2). The percentage of shore covered in rocks, representing complex habitat (2.5 %) and wave height (2.3 %) also made significant contributions towards the variation in larval fish assemblages.

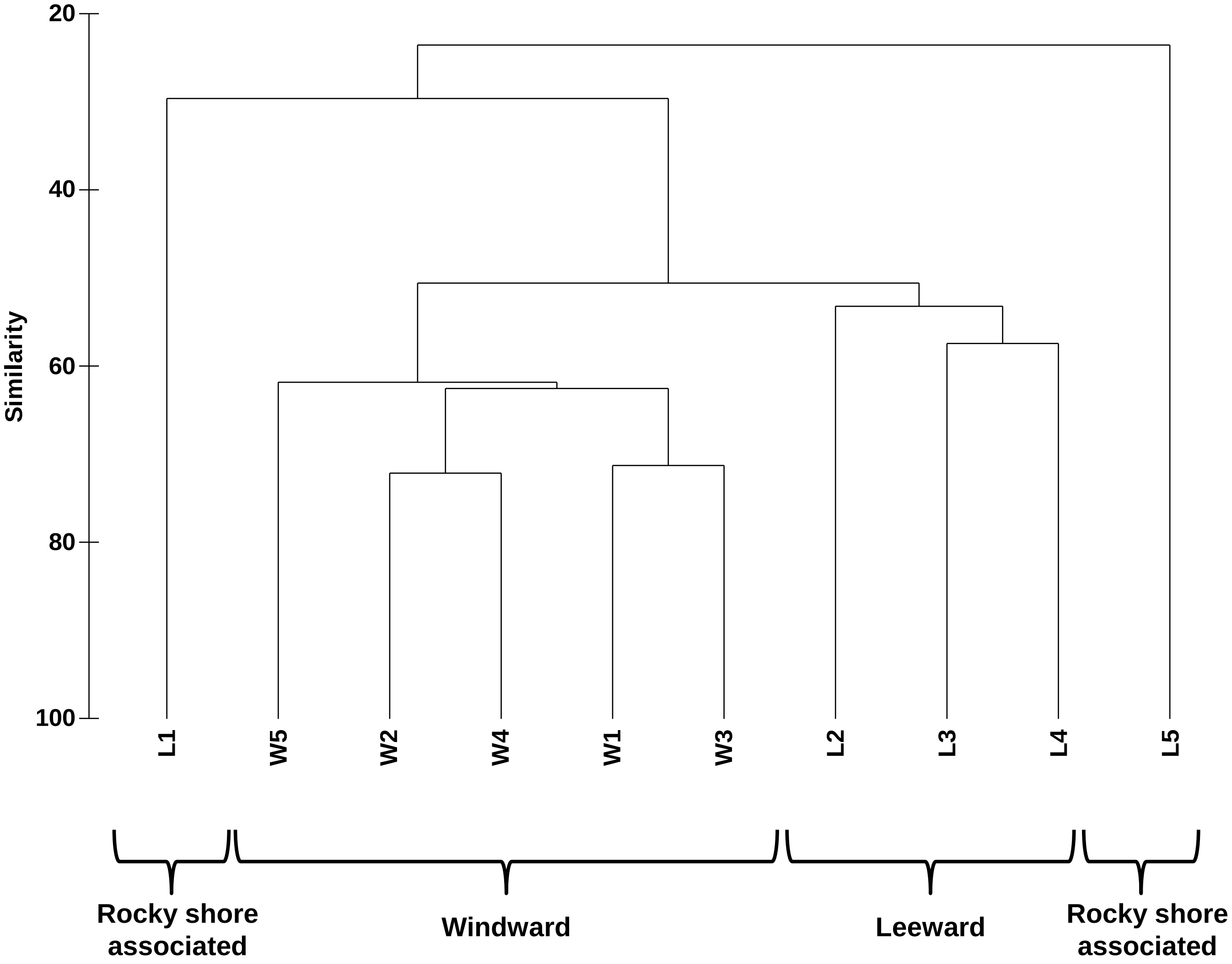

FIGURE 4.6 Bray-Curtis similarity dendrogram showing percentage similarity of samples measured by the square root transformed abundances of species in each surf zone station in the leeward and windward sector of Algoa Bay during the study (December 2010 – October 2012)

TABLE 4.2 DistLM covariate analysis results showing influence of environmental variables on larval fish community composition in the leeward and windward sector of Algoa Bay during the study (December 2010 – October 2012)

Variable	SS (trace)	Pseudo-F	p	Prop (%)	Cumulative (%)
Wave period	13190.0	7.4999	0.001	4.2	4.2
Rocky cover	7927.2	5.3528	0.001	2.5	6.7
Macrozooplankton	4137.6	2.129	0.033	1.3	8.0
Wave height	7292.5	3.8192	0.002	2.3	10.3
Wave height 1 day before	3378.8	1.8185	0.070	1.1	11.4
Wave height 2 days before	2268.5	1.2228	0.248	0.7	12.1
Wave height 3 days before	1554.8	0.83713	0.565	0.4	12.5
Wave height 4 days before	2300.4	1.2406	0.261	0.7	13.2
Wave height 5 days before	4271.1	2.3244	0.026	1.4	14.6
Wind speed	3303.9	1.7385	0.086	1.1	15.7
Wind speed 1 day before	5164.1	2.9852	0.004	1.7	17.4
Wind speed 2 days before	3447.7	2.0071	0.055	1.1	18.5
Wind speed 3 days before	8887.9	5.3331	0.001	2.9	21.4
Wind speed 4 days before	4757.8	2.8935	0.001	1.5	22.9
Wind speed 5 days before	2351.5	1.4346	0.144	0.8	23.7
Max wind speed	2438.5	1.3903	0.172	0.8	24.5
Wind direction	2796.1	1.4757	0.16	0.9	25.4
Wind direction 1 day before	2178.6	1.1509	0.296	0.7	26.1
Wind direction 2 days before	2854.8	1.5132	0.148	0.9	27.0
Wind direction 3 days before	1514.7	0.80184	0.625	0.5	27.5
Wind direction 4 days before	3585.9	1.9097	0.075	1.1	28.6
Wind direction 5 days before	3324.6	1.7797	0.074	1.1	29.7
Sea temperature	2578.3	1.6582	0.097	0.8	30.5
Conductivity	2247.1	1.4501	0.142	0.7	31.2
TDS	890.75	0.57293	0.828	0.3	31.5
Salinity	2178.4	1.4055	0.178	0.7	32.2
pH	1940.3	1.2543	0.242	0.6	32.8
NTU	3542.4	2.3133	0.02	1.1	33.9
Surf zone width	1081.7	0.72886	0.674	0.3	34.2
Rainfall 1 month prior	2873.4	1.9507	0.053	0.9	35.1
Wind direction	2796.1	1.4757	0.16	0.9	36.0
Wind direction 1 day before	2178.6	1.1509	0.296	0.7	36.7
Wind direction 2 days before	2854.8	1.5132	0.148	0.9	37.6
Wind direction 3 days before	1514.7	0.80184	0.625	0.5	38.1
Wind direction 4 days before	3585.9	1.9097	0.075	1.2	39.3
Wind direction 5 days before	3324.6	1.7797	0.074	1.1	40.4

4.6 Body length

To describe the pattern of species utilization, mean body length of the most abundant species was analysed according to season (Figure 4.7). The dominant species, *Diplodus capensis*, occurred during all sampling seasons, but the highest frequencies were observed during spring when postflexion larvae, with mean sizes of 12.2 mm in the lee of the Bay, and 11.1 mm in the windward sector of the Bay, were caught in high numbers. A significant difference (t-value = 7.4; p < 0.001) in the lengths of *D. capensis* larvae between the leeward and the windward sector of Algoa Bay were observed with larger larvae occurring in the lee of the Bay. In the windward sector, the mean size of these individuals increased in successive months from summer. Furthermore, a significant difference in the lengths of *S. salpa* (t-value = 4.62; p < 0.001) and *H. capensis* (t-value = 4.24; p < 0.001) between the leeward and the windward sector of Algoa Bay was observed with larger larvae occurring in the lee of the Bay. Although not statistically significant (t-value = 1.22; p = 0.23), larger larvae of *Neoscorpis lithophilus* occurred in the lee of the Bay. *Sarpa salpa* showed a clear pattern of growing average in the lee of the Bay (21.2 mm to 50.0 mm) with greatest frequencies observed during winter and spring when small larvae (21.2 mm) were caught in high numbers. A reverse pattern in body length was observed in the anchovy, *Engraulis encrasicolus*, where significantly (t-value = -5.01; p < 0.001) smaller larvae were captured in the lee of the Bay. Similarly, although not statistically significant (t-value = -0.23; p = 0.82), smaller larvae of *Rhabdosargus holubi* were captured in the lee of the Bay.

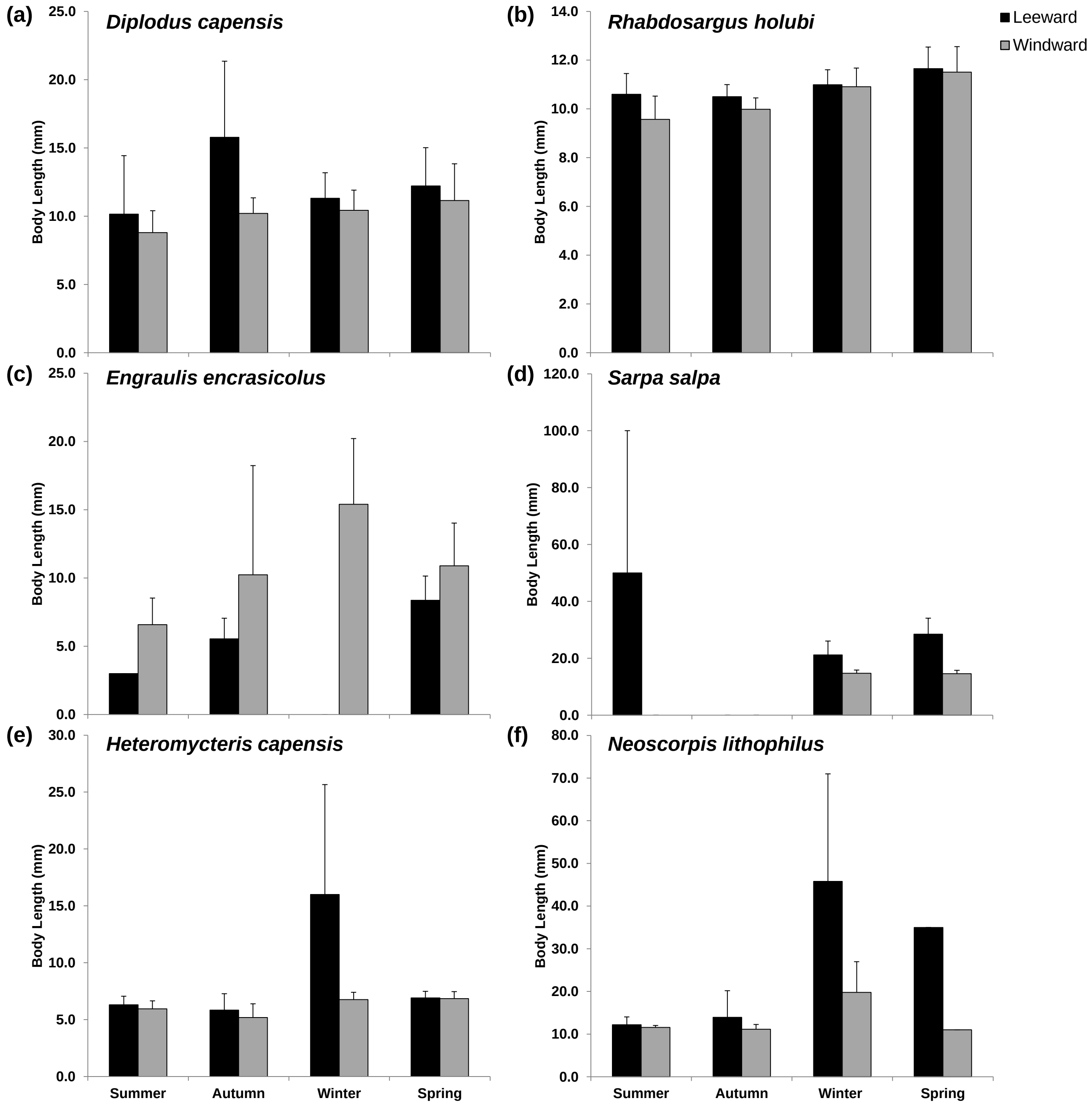

FIGURE 4.7 Seasonal mean and maximum of body length of dominant species including a) *Diplodus capensis*, b) *Rhabdosargus holubi*, c) *Engraulis encrasicolus*, d) *Sarpa salpa*, e) *Heteromycteris capensis* and f) *Neoscorpis lithophilus* collected in the surf zones of Algoa Bay during the study (December 2010 – October 2012)

5. DISCUSSION

The sandy beach surf zones of Algoa Bay possess a diverse larval ichthyofaunal assemblage. A total of 57 species representing 23 fish families, were recorded from the surf zones situated in both the lee and windward sectors of Algoa Bay. The species composition of Algoa Bay includes considerably more species than previous surf zone larval fish studies conducted within the same warm-temperate coastline of South Africa (Whitfield, 1989a; Cowley *et al.*, 2001; Strydom, 2003; Watt-Pringle and Strydom, 2003; Strydom and d'Hotman, 2005). This is probably attributed to a much larger area sampled in the present study and the habitat contribution by proximity to rocky shore in the leeward section of the Bay. However the larval fish community of the Algoa Bay surf zones resembles that of other surf zone habitats within the same geographical province of South Africa. The numbers of species in these assemblages are comparable to those recorded for surf zones of other areas including Japan, 18 (Senta and Kinoshita, 1985) to 100 species (Suda *et al.*, 2002), Taiwan, 47 species (Yang and Senta, 1993), New Jersey, 47 species (Able *et al.*, 2010), Gulf of Mexico, 69 species (Ruple, 1984), Brazil, 29 species (Godefroid *et al.*, 1999), Mauritius, 112 species (Sato *et al.*, 2008) and southwestern Australia, 95 species (Ayvazian and Hyndes, 1995). Several fish families are shared between the present study and these other studies with three fish families namely Engraulidae, Gobiidae and Mugilidae, cosmopolitan to all surf zones studies to date. Representative genera from these families include *Engraulis* spp, *Mugil* spp and *Liza* spp. These parallels in species occurrence highlight the continuity in composition of larval fish assemblages universally and the utilization of surf zones as a whole by a specific group of larval fishes. Surf zones are known productive areas (McLachlan and Lewin, 1981) and due to their turbulent nature serve as ideal interim nursery areas for this specialist group of fishes.

Sandy beach surf zones are typically known to be dominated by a few species (Pearce *et al.*, 1942; McFarland, 1961; Modde and Ross, 1981; Lasiak, 1983; Bennett, 1989; Gibson *et al.*, 1996; Layman, 2000; Wilber *et al.*, 2003; Gaelzer and Zalmon, 2008), specifically those dependent on estuaries in South Africa (Whitfield, 1989a; Cowley *et al.*, 2001; Strydom, 2003). Results from the present study indicate the importance of proximity to estuaries in structuring larval fish assemblages. There were significant contributions of estuary species occurring at the rocky shore associated surf zones. This trend was particularly evident at leeward station 5 which was furthest removed from any estuary, and included the species *Atherina breviceps*, *Caffrogobius gilchristi*, *C. nudiceps*, *Clinus superciliosus* and *Psammogobius knysnaensis*. These species are placed into Category Ib of Whitfield’s (1998) classification of fishes in southern African estuaries and are regarded as estuarine-resident species which also have marine breeding populations (Whitfield, 1998). Therefore the larvae of these species could potentially belong to marine populations occurring on rocky shores associated with surf zones. *Atherina breviceps* is extremely abundant off Eastern Cape sandy beaches where it is known to breed (Lasiak, 1982). *Clinus superciliosus* is the most abundant species observed in tidal pools in Algoa Bay (Beckley, 1985). The gobies including *C. gilchristi*, *C. nudiceps* and *P. knysnaensis* have a marine larval phase achieved by the mass hatching of larvae in estuaries which usually coincides with the nocturnal high tide, with larvae carried passively out of the estuary by the ebb tide, returning as postflexion larvae or early juveniles (Whitfield, 1989b). In the present study, the very early stages within larval fish development were observed for these species at leeward station 5, supporting these findings of a marine larval phase, with rocky shore associated surf zones perhaps serving as the ideal interim nursery habitat. With an increase in localized flooding of estuaries into Algoa Bay occurring over the past two years, catches of *Gilchristella aestuaria* (Category 1a), a resident estuarine species which has not been recorded spawning in the marine or freshwater environment (Whitfield, 1998), has been noted in the surf zone (Strydom, pers. comm.). Furthermore, *G. aestuaria* was the fifth most abundant species observed in the surf zones of False Bay, Western Cape, South Africa (Clark *et al.*, 1996b).

There were also significant contributions of euryhaline marine species from Category II of Whitfield's (1998) classification of fishes in southern African estuaries, particularly found at leeward station 5 and included *Diplodus capensis*, *Heteromycteris capensis*, *Liza richardsonii*, *Rhabdosargus globiceps*, *Sarpa salpa* and *Solea turbynei*. The sparids *D. capensis*, *R. globiceps* and *S. salpa* and the mugilid *L. richardsonii*, usually breed at sea with juveniles occurring in estuaries but are usually more abundant at sea (Whitfield, 1998). Juveniles of *D. capensis*, *S. salpa* and *L. richardsonii* are known to occur in high abundances in tidal pools and subtidal gullies in Algoa Bay (Beckley, 1985; Smale and Buxton, 1989). The two soles, *H. capensis* and *S. turbynei* are marine species with breeding taking place in the nearshore marine environment and larvae and early juveniles recruiting into estuaries with juveniles occurring mainly in estuaries, but are also found at sea (Whitfield, 1998).

The higher index of diversity of fish larvae observed during the present study as opposed to similar studies within the same geographical region (Strydom, 2003; Watt-Pringle and Strydom, 2003), can be attributed to the presence of several marine species not dependent on estuaries but are associated with rocky shores. These include benthic reef associated species in the Gobiesocidae fish family namely *Chorisochismus dentex* and *Diplecogaster megalops*, most Clindae species, the tripterygiid, *Cremnochorites capensis*, and the sparid, *Diplodus cervinus hottentotus*. The larvae and early juveniles of several adult species known to occur in shallow coastal waters were also captured in the Algoa Bay surf zones and included species such as *Argyrosomus japonicus, Argyrosomus inodorus, Pomadasys olivaceus* and *Pomadasys commersonnii*. The larvae of sciaenids and haemulids are documented along beaches of the world (Modde and Ross, 1983; Ruple, 1984; Suda *et al.*, 2002; Gaelzer and Zalmon, 2003; Sato *et al.*, 2008; Able *et al.*, 2010).

Three unique surf environments were identified within the dissipative-intermediate beach morphodynamic type (Harris *et al.*, 2011) occurring in Algoa Bay. These include sheltered beaches with few rip currents in the leeward sector of Algoa Bay, more dynamic beaches in the windward sector of the Bay with many semi-permanent rip currents (Talbot and Bate, 1987) and heavily influenced by the predominantly south-westerly swell, and surf zones associated with rocky shores. The present study provides evidence that the catch of larval fishes varies among these three habitat types, however a select species suite remains present in all surf zones. The number of species ranged from 26 species recorded in the rocky shore associated surf zones, 34 species recorded in the windward sector of the Bay to 41 species recorded in the lee of the Bay. The rocky shore associated surf zones exhibited the lowest species richness, evenness and consequently diversity. However, the greatest abundance of larval fishes was observed at these rocky shore associated surf zones. A similar trend of high abundance of select species particularly sparid larvae associated with rocky shore areas has been observed in temperate South Africa (Strydom, 2008). The relatively high larval fish abundances observed nearest to the rocky shore are similar to the findings of adult and juvenile fish distributions relative to emergent rock in the surf zone of False Bay, Western Cape (Clark *et al.*, 1996a). Furthermore, international studies on adult and juvenile fish assemblages have found greater numbers of individuals in surf zone habitats adjacent to rocky groins (Wilber *et al.*, 2003).

Spatial and temporal instability of surf zones resulting from variable physical features such as wind and wave exposure are known to produce fish assemblages dynamic in abundances (Clark *et al.*, 1996a; Beyst *et al.*, 2001; Gaelzer and Zalmon, 2003; Félix *et al.*, 2007a; Gaelzer and Zalmon, 2008; Inui *et al.*, 2010) particularly regarding juvenile fishes who utilise surf zones seasonally or opportunistically (Lasiak, 1984). Therefore with regards to juvenile fish assemblages, the changing features of the surf zone habitat combined with the mobility of juvenile fishes greatly influences the composition of fish communities in surf zones. A higher species richness and diversity has been observed in sandy beach surf zones with an intermediate level of exposure (Clark, 1997). In the present study, the highest degree of species evenness was observed in the surf zones located in the windward sector of the Bay indicating a high degree of structural homogeneity with an equalitarian distribution in species, resulting in high species diversity. A high evenness value results in a higher diversity which in a naturally disturbed ecosystem can be explained by the Intermediate Disturbance Hypothesis where disturbance prevents competitive exclusion and therefore systems at intermediate levels of disturbance possess highest diversity (Connell, 1978). Wave period in the present study, was the most important environmental variable explaining the largest proportion of the significant variation in the surf zone larval fish assemblage in Algoa Bay. The physical disturbance generated by breaking waves could create a suitable environment, with shelter from predators and an abundance of food resources for fish larvae.

When data from all stations were combined, the overall CPUE of larval fish captured did not vary significantly seasonally. However, seasonal patterns were evident in species richness and diversity. Larval fish assemblages become more speciose with the progression of spawning and an increase in water temperatures during spring. Greatest abundances of fish larvae and the total number of species was found during spring with similar results observed internationally (McFarland, 1961; Modde and Ross, 1981; Gibson *et al.*, 1993; Félix *et al.*, 2007b) suggesting that most fish concentrate their reproductive effort over spring. Therefore seasonality is clearly of considerable importance in the surf zone. Larval fish abundances and number of species peak during the spring and decline steadily as a result of natural mortality until autumn when numbers drop suddenly as the surviving larvae move to settlement habitats.

In summary, three different larval fish assemblages were observed in Algoa Bay surf zones and were linked to both habitat type and exposure. Wave period and wave height, which can be related to exposure, were the most significant factors with regards to correlations with larval fish assemblages. The windward sector of Algoa Bay is subjected to a higher degree of exposure than that in the leeward sector of the Bay. Greatest species diversity was observed in the windward sector. With significantly smaller larvae of several species observed in the windward sector of the Bay, it would appear the very early developmental stages are being swept into this sector of Algoa Bay. Sandy beach habitats represent a significant spatial resource to the early developmental stages of many fish in Algoa Bay, becoming more important during the spring and summer seasons when diversity and abundances increase linked to seasonal reproductive patterns. Since the individuals of several species were primarily dominated by postflexion and early juvenile stages, the importance of the Algoa Bay surf zone habitat as an interim nursery and refuge area for certain species is highlighted. The exposed surf zone habitats provide these larvae and early juveniles with shelter from predators in low visibility shallow coastal water habitats.

6. ACKNOWLEDGEMENTS

This work is based on financial support from the South African National Parks, South Africa (SANParks). Gratitude is expressed to the SANParks. Any opinions, findings and conclusions expressed in this material are those of the authors and therefore the SANParks does not accept any liability in regards thereto. Fieldworkers are thanked for their valuable assistance. Mr Tim Vink is thanked for generation of the map in this chapter.

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CHAPTER 5

RECRUITMENT OF FISH LARVAE AND JUVENILES INTO TWO ESTUARINE NURSERY AREAS WITH EVIDENCE OF EBB TIDE USE

1. ABSTRACT

Many marine fish species are estuarine-dependent, spawning in the marine environment with larvae entering estuarine nursery areas. The objective of this study was to determine the tidal, diel and seasonal variations of larval and juvenile fishes recruiting into two permanently open estuaries in the Eastern Cape, South Africa. Directional swimming of larvae and early juveniles was observed using fyke nets during a 24-hour cycle over two years from December 2010 to October 2012. On either side of each estuary bank, two fyke nets with mouth openings facing opposite directions (i.e. one net facing the incoming or outgoing tide and the other facing the opposing direction) were used to sample fishes. The aims of this study were to determine if 1) on the flood tide, were the nets facing the incoming tide collecting more larvae and early juveniles recruiting into the estuarine nursery area, than the nets facing the opposing direction and 2) on the ebb tide, were the nets facing the sea, and hence the opposing direction of the outgoing ebb tide, collecting more fishes recruiting into the nursery against the ebb tide, than the nets facing the outgoing ebb tide? Larval and juvenile fish CPUE, diversity and richness varied seasonally between estuarine systems and between diel and tidal conditions. Highest catches were recorded on the flood tide which coincided with sunrise in the Swartkops Estuary. Greatest catches of larvae and early juveniles were observed during the ebb tide at night in the Sundays Estuary. On the ebb tide, higher abundances of several dominant species and several important fishery species, occurred in the fyke nets which faced the sea, indicating the early developmental stages of these fish species are not necessarily being lost from the nursery. These larvae and juveniles are actively swimming against the ebb tide in the shallower, slower-flowing marginal areas facilitating recruitment against ebb flow.

2. INTRODUCTION

The importance of estuaries as nursery areas for fishes is well documented, both in South Africa (Harris and Cyrus, 1995; Whitfield, 1998; Strydom and Whitfield, 2000; Strydom *et al.*, 2003) and internationally (Elliott *et al.*, 1990; Berasategui *et al.*, 2004; Aceves-Medina *et al.*, 2008). Several coastal marine fish species are estuarine-dependent and are known to spawn at sea. Their early developmental stages including postflexion larvae, enter estuarine nursery areas that are characteristically sheltered and rich in food resources (Clark *et al.*, 1969; Wallace and van der Elst, 1975; Strydom and Whitfield, 2000). Several estuarine resident Gobiidae species spawn in estuaries, with preflexion larvae undergoing an obligatory marine phase before recruiting back into the estuary as postflexion larvae or early juveniles (Whitfield, 1989c). The recruitment of larvae through an estuarine mouth and subsequent transport up an estuary are critical for successful completion of the life cycle. Recruitment into estuarine nursery areas is challenging as there is a net flow of water from the estuary to the ocean, and often current speeds exceed larval swimming speeds. Larvae and early juveniles recruiting into estuaries must therefore adopt strategies for successful ingress into estuarine nursery grounds (Islam *et al.*, 2007).

The actual process of recruitment into estuaries may either be active via swimming, or passive via drift with tidal currents (Rijnsdorp *et al.*, 1985). Larvae may use either large-scale displacement by major currents or selective tidal stream transport (STST) to enter estuaries (Norcross and Shaw, 1984; Boehlert and Mundy, 1994; Jenkins *et al.*, 1997; Forward *et al.*, 1999; Jenkins *et al.*, 1999). Vertical movement of the very early stages of fish larvae and circadian and tidal rhythms also play an important role in controlling drift, allowing larvae to remain in favourable areas (Melville-Smith *et al.*, 1981; Boehlert and Mundy, 1988; Joyeux, 1999). Selective tidal stream transport, is the process whereby larvae ascend actively in the water column during the flood tide and return to the bottom during the ebb tide (Rijnsdorp *et al.*, 1985; Boehlert and Mundy, 1988; Schultz *et al.*, 2003; Miller and Shanks, 2004; Islam *et al.*, 2007). Larvae can therefore be advected upstream during flood tides, and during the ebb tide, larvae can avoid seaward-moving water layers, thereby facilitating retention within the estuary (Jager, 1999; DiBacco *et al.*, 2001). There appears to be an energetic advantage to selectively occupy tidal currents during recruitment (Metcalfe *et al.*, 1990). Stimuli including salinity, olfactory cues, electric field and pressure changes all serve as possible cues that would allow for preferred current directions to be selected (Miller, 1988; Sulkin, 1990). Diurnal changes in tidal transport have also been observed with increases in flood transport occurring during the night (Forward Jr. and Tankersley, 2001; Islam *et al.*, 2007). This appears to be related to the light level behavioural cue (Luo, 1993). In temperature regions, recruitment is related to water temperature, photoperiod and the seasonal production cycles of zooplankton and phytoplankton. The diel and tidal cycle is also known to influence recruitment (Lyczkowski-Shultz *et al.*, 1990; Doherty and McIlwain, 1996; Power, 1997; Young *et al.*, 1997). Evidence suggests that greater recruitment success and enhanced maintenance within estuarine nursery habitats occurs when larval and juvenile fishes utilize diel and tidal cycles (Melville-Smith *et al.*, 1981; Beckley, 1985; Boehlert and Mundy, 1988).

The dependence of approximately 72 fish species known to utilize South African estuaries as feeding grounds or nursery areas, has been categorized according to the extent juveniles depend on estuaries (Whitfield, 1998). Based on this classification, the import or export of larvae and juveniles to and from estuaries is likely to differ between estuarine association categories (Beckley, 1985). According to Beckley (1985), estuarine resident species that spawn in estuaries are likely to lose early development stages near the estuary mouth when they become entrained on the ebb-tide. Conversely, larvae and juveniles of marine species that spawn at sea are likely to enter the estuary on the flood tide while incidental marine species are likely to show irregular patterns in the export or import of larvae (Beckley, 1985). Strydom and Wooldridge (2005) reported peaks in density of larval fishes after the onset of darkness predominantly associated with the nocturnal ebb tide. High abundances of larvae observed during the ebb tide does not necessarily imply that these larvae are lost from estuarine systems, but using hydrostatic pressure changes (Kingsford *et al.*, 2002) associated with the ebb tide, larvae could be recruiting into estuaries against the ebb tide as was suggested by Strydom and Wooldridge (2005). Juvenile mugilid species have been observed to recruit into a subtropical estuary in South Africa by actively swimming against the strong ebb tide (Harrison and Cooper, 1991).

The present study was undertaken to provide answers to whether larvae could be recruiting into estuary nursery areas against the ebb tide as suggested by Strydom and Wooldridge (2005). In South Africa, isolated studies have assessed the rhythmic activity of larval fishes in estuaries and are linked to either the diel or the tidal cycle (Melville-Smith *et al.*, 1981; Beckley, 1985; Whitfield, 1989a; Whitfield, 1989c; Strydom and Wooldridge, 2005). These studies however, have not assessed larvae and early juvenile swimming direction when sampling a particular tidal state. The present study aimed to investigate the influence of the diel and tidal cycle on larval and juvenile fish directional movement using fyke nets over spring tides in two warm-temperate permanently open South African estuaries. Various movement patterns exhibited by different species could also be analysed as well as the mechanisms of transport resulting from these movements.

3. MATERIALS AND METHODS

3.1 Study site

Larval and juvenile fishes were collected from the permanently open Sundays (33°43′19″S; 25°50′57″E) and the Swartkops (33°51′54″S; 25°38′00″E) estuaries in Algoa Bay, on the south east coast of South Africa (Figure 5.1). The Sundays Estuary is ~21 km long, with a width of ~800 m at its widest point near the mouth, and ~20 m at the head with depths that range from 5 m in the lower reaches to 2 m in the upper reaches (Wooldridge and Erasmus, 1980; Marais, 1981; Whitfield and Harrison, 1996). The Swartkops Estuary is ~16 km long, with a width of ~350 m at its widest point near the mouth and ~90 m in the upper reaches with depths that vary from 2 m in the lower reaches to 3.5 m in the upper reaches (Baird *et al.*, 1986; Baird *et al.*, 1988). The Sundays drains a catchment area of 22 063 km^2 while the Swartkops only 1 354 km^2 (Baird *et al.*, 1986). The Sundays Estuary has continuous freshwater inflow (Jerling and Wooldridge, 1995) supplemented by an inter-basin water-transfer scheme (Pech *et al.*, 1995) and displays a full salinity gradient linked to the inter-basin water-transfer scheme and return flows from the citrus farming practices above the estuary (Wooldridge and Bailey, 1982; MacKay and Schumann, 1990). Although the Swartkops River, which feeds the Swartkops Estuary, is dammed on the main course as well as at the tributaries, there is minimal effect on river flow (Baird *et al.*, 1986; Baird *et al.*, 1988). The lower reaches of the Swartkops Estuary is characterised by extensive intertidal mud flats, islands and saltmarshes (Baird *et al.*, 1986; Baird *et al.*, 1988) while there is an absence of salt marshes or large mud flats in the Sundays Estuary (Beckley, 1984). These estuaries are located in the warm-temperate climatic zone and experience a bimodal rainfall pattern (Lubke and de Moor, 1998). Tides in Algoa Bay are semi-diurnal with a mean spring amplitude of 1.6 m and a maximum of 2.1 m (Talbot and Bate, 1987). The Sundays and Swartkops estuaries are large systems considered in fair and good ecological condition respectively (Whitfield, 2000) and both are of high conservation importance (Turpie *et al.*, 2002).

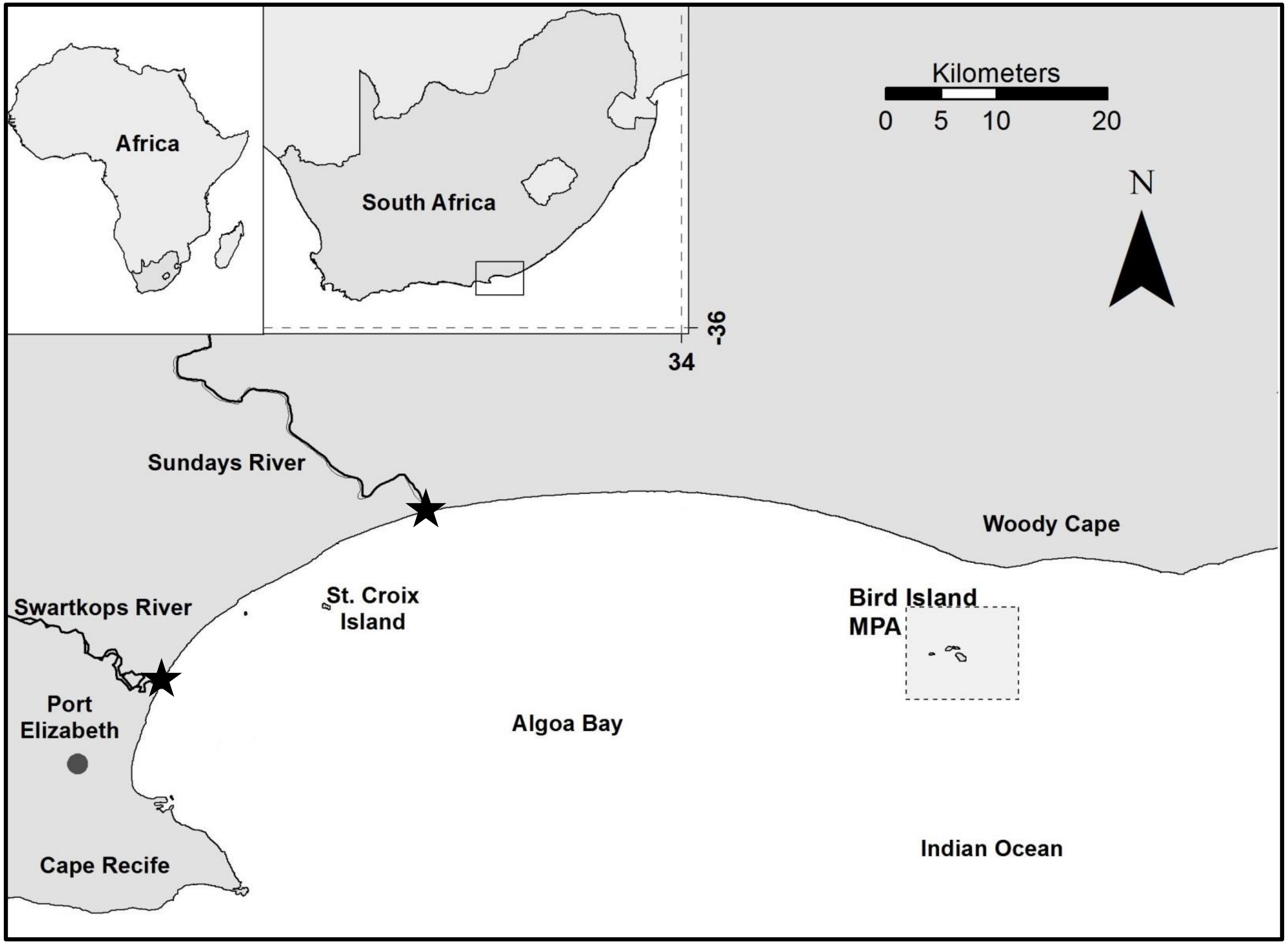

FIGURE 5.1 The geographic position of the Sundays and Swartkops estuaries, showing the location of the sampling stations located at the mouth of each estuary

3.2 Field sampling and fish identification

Samples were collected on two occasions during each season, December and January, and March and April in summer and autumn respectively. Winter and spring sampling took place in June and July and in September and October respectively. Two years of sampling was undertaken, starting in December 2010 and culminating in October 2012 at fixed sampling stations on either bank, in the mouth region of each estuary. In total, 16 sampling trips were conducted and these were all standardized over the new moon period. Each estuary was sampled sequentially. At each estuary, four fyke nets were laid. On each bank, two, double-winged, 6 hooped, 1 mm mesh size fyke nets were set using an anchor attached to the cod end. The opening of one net faced the sea and the other in the opposite direction. The two wings on either side of the opening were stabilised by 1.9 m long iron bars, driven into the sediment. Sampling commenced one hour after the start of the flood tide and culminated 24 hours later. Two tidal cycles or four tide states were therefore sampled. Sampling continuously over a 24 hour period during all seasons provided for an indication of the extent of passive drift or active swimming processes in fish larvae and juveniles to be monitored according to the time of day and tidal phase. The contents from each fyke net were emptied after each tide state sampled. Fish were identified and measured on site. Fish were therefore released alive in most cases. Unidentified individuals and/or very small preflexion larvae were preserved in 10 % formalin and identified in the laboratory to the highest possible taxonomic level (Van der Elst and Wallace, 1975; Smith and Heemstra, 1995; Whitfield, 1998). All fish were measured to the nearest 0.1 mm body length, representing notochord length in preflexion and flexion larvae, standard length (SL) in postflexion larvae and early juveniles and total length (TL) in larger fish. All fyke net catches are expressed as CPUE, referring to the number of fish caught per fyke net per hour of soak time. A total of 512 samples were collected over the study period. Temperature (°C), salinity, turbidity (NTU), conductivity (µSIEMENS/cm), pH and total dissolved solids (TDS) were measured at each site using a YSI 6600 multi-parameter meter.

3.3 Data analyses

Diversity indices namely species number (N), Shannon-Wiener diversity (H’), Margalef species richness (d) and Pielou’s evenness (J’) were calculated per station per sampling event, using the PRIMER statistical package version 6.1, 2013 (Clarke and Warwick, 1994). Shannon-Wiener diversity was calculated to one decimal point using $\log_e$. All physical and biological data was tested for normality using a normal probability plot and Shapiro-Wilk test while homogeneity of variance was assessed using a Levene's test with the STATISTICA software package version 11, 2012. All environmental data at each estuary were not normally distributed, even after appropriate transformations were used. By contrast, variances were homogenous. All biological data excluding CPUE and species evenness data from the Sundays Estuary were not normally distributed, even after appropriate transformations were used, however variances were homogenous. Sundays Estuary CPUE and species evenness data were log transformed and although not normally distributed, variances were equal. A one-tailed t-test was used to determine whether temperature, salinity, turbidity, conductivity, pH and total dissolved solids in the Sundays Estuary were significantly greater from physico-chemical variables in the Swartkops Estuary. The non-parametric Kruskal-Wallis (H) ANOVA was used to assess differences in physico-chemical variables, fish CPUE and diversity indices among seasons and tide states. The Mann-Whitney U-test (U) was used to assess differences in physico-chemical variables, fish CPUE and diversity indices between upstream and downstream facing fyke nets and the east and west banks in each estuary. To assess whether small larvae were being flushed from the estuary during the ebb tide or larger actively swimming larvae were recruiting against the ebb tide, a one-tailed t-test was used to determine whether the mean body lengths of dominant larvae during the ebb tide were significantly larger in the fyke nets facing the sea than the fyke nets facing the opposite direction. Dominant species were those represented by contributing >1 % towards the total catch.

4. RESULTS

4. 1 Environmental variability

In the Sundays Estuary, physico-chemical variables showed a significant difference among sampling seasons (Figure 5.2) for temperature ($H = 183.1$; d.f. = 3; $p < 0.001$), conductivity ($H = 78.7$; d.f. = 3; $p < 0.001$), TDS ($H = 81.7$; d.f. = 3; $p < 0.001$), salinity ($H = 82.3$; d.f. = 3; $p < 0.001$), pH ($H = 38.8$; d.f. = 3; $p < 0.001$) and turbidity ($H = 8.3$; d.f. = 3; $p < 0.05$). A significant difference in pH ($U = 6596.0$; $p < 0.01$) and turbidity ($U = 4206.0$; $p < 0.001$) was observed between the east and west bank in the estuary. A significant difference in only pH ($H = 43.0$; d.f. = 3; $p < 0.001$) was observed among the various tide states (Figure 5.3) in the Sundays Estuary.

In the Swartkops Estuary, a significant difference was shown for temperature ($H = 203.8$; d.f. = 3; $p < 0.001$), conductivity ($H = 97.4$; d.f. = 3; $p < 0.001$), TDS ($H = 86.6$; d.f. = 3; p <

0.001), salinity (H = 127.6; d.f. = 3; p < 0.001), pH (H = 25.1; d.f. = 3; p < 0.001) and turbidity (H = 35.9; d.f. = 3; p < 0.001) among the sampling seasons (Figure 5.2). A significant difference in conductivity (U = 7024.0; p < 0.05), TDS (U = 6518.0; p < 0.01), and turbidity (U = 6608.0; p < 0.01), was observed between the east and west bank. A significant difference in conductivity (H = 7.9; d.f. = 3; p < 0.05) and pH (H = 10.7; d.f. = 3; p < 0.05) was observed among the various tide states (Figure 5.3) in the Swartkops Estuary.

A significant difference between the conductivity (t-value = -16.0; p < 0.001), total dissolved solids (t-value = -16.4; p < 0.001), salinity (t-value = -16.5; p < 0.001), pH (t-value = -3.3; p < 0.001) and turbidity (t-value = 7.3; p < 0.001) occurred between the Sundays and the Swartkops estuaries with higher values of conductivity, total dissolved solids, salinity and pH recorded in the Swartkops Estuary and higher values of turbidity recorded in the Sundays Estuary.

4.2 Species composition

A total of 14 250 larval and juvenile fishes were caught in this study (Table 5.1). The Sundays Estuary comprised 11 587 individuals, 24 fish families and 49 species. The Swartkops Estuary yielded 2 663 individuals, 18 families and 38 species. The Sundays Estuary was dominated by the sparid *Rhabdosargus holubi* (29.6 %), the clupeid *Gilchristella aestuaria* (17.7 %) and the gobiid *Caffrogobius gilchristi* (15.0 %). Other important contributions towards overall fish catch in the Sundays estuary contributing <10 % but >1 % were the sparids *Diplodus capensis* and *Rhabdosargus globiceps*, the gobiids *Caffrogobius nudiceps* and *Psammogobius knysnaensis*, the atherinid *Atherina breviceps*, the haemulid *Pomadasys olivaceus*, the soleid *Heteromycteris capensis*, and the mugilids *Liza richardsonii*, *Liza macrolepis*, an unidentified *Liza* species and an unidentified mugilid. All other fish species contributed <1 % to the total catch. The Swartkops Estuary was dominated by *C. nudiceps* (37.2 %), *D. capensis* (14.8 %) and *P. olivaceus* (11.5 %). Other species making important contributions towards the overall fish catch in the Swartkops Estuary included *C. gilchristi* (8.1 %) and *P. knysnaensis* (4.8 %), the sparids *R. holubi* (5.3 %), *Spondyliosoma emarginatum* (2.4 %) and *R. globiceps* (1.6 %), the soleid *H. capensis* (1.6 %), the clupeid *G. aestuaria* (1.4 %) and the unidentified mugilid *Liza* species (5.3 %).

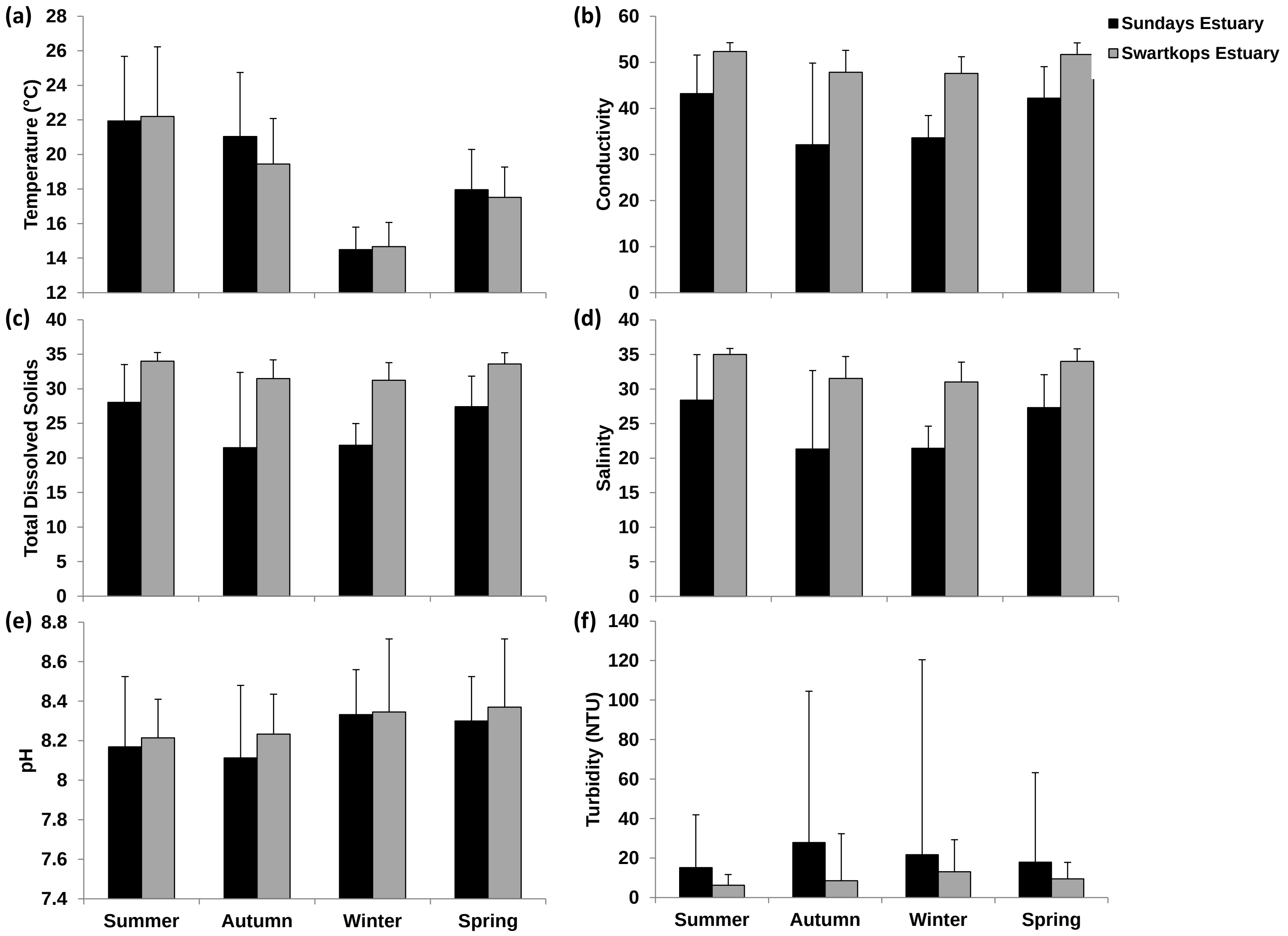

FIGURE 5.2 Mean (n = 64) and maximum of a) temperature, b) conductivity, c) total dissolved solids, d) salinity, e) pH and f) turbidity recorded seasonally at each estuary during the study (December 2010 – October 2012)

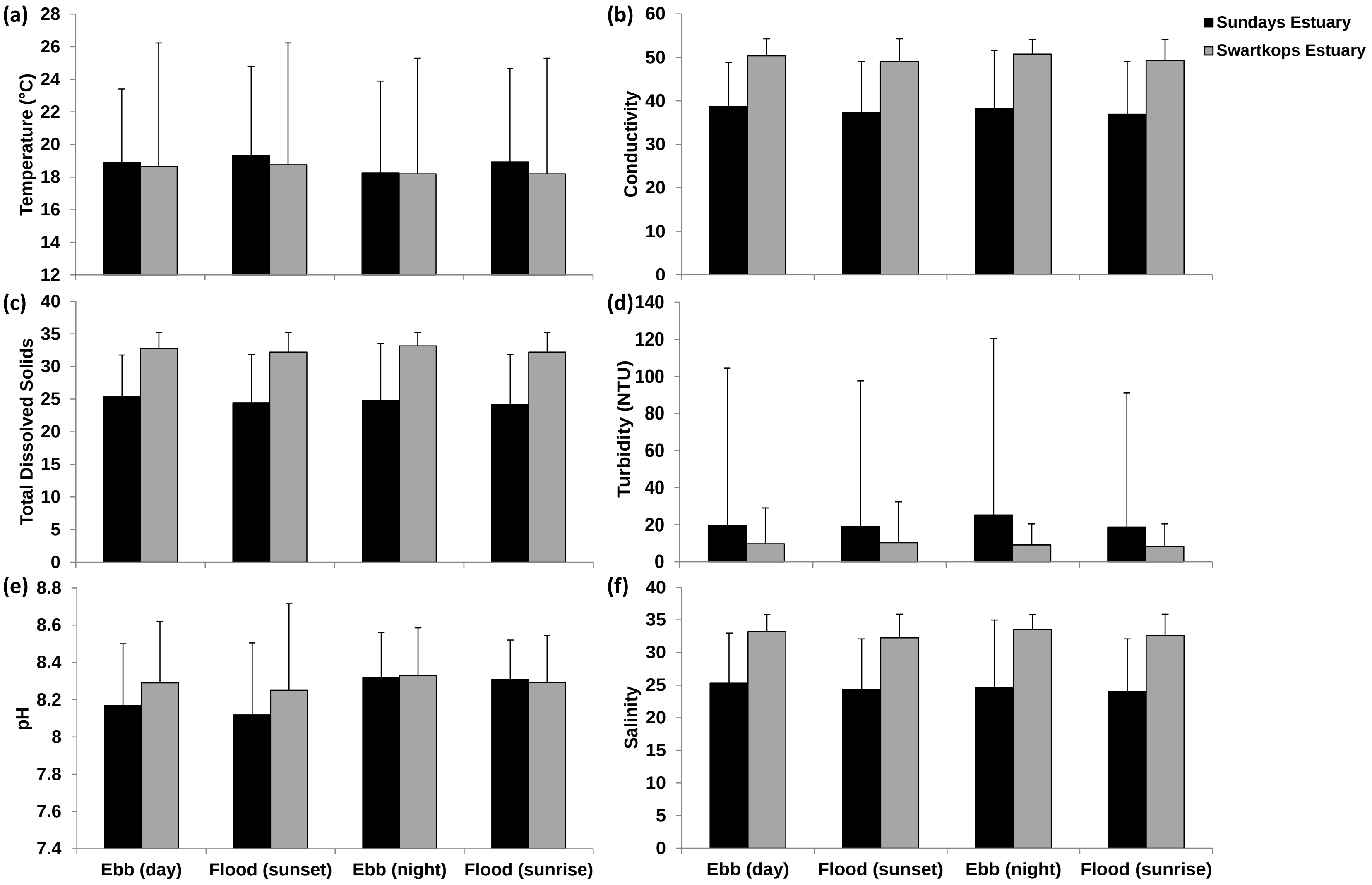

FIGURE 5.3 Mean (n = 64) and maximum of a) temperature, b) conductivity, c) total dissolved solids, d) turbidity, e) pH and f) salinity recorded during each tidal state at each estuary during the study (December 2010 – October 2012)

TABLE 5.1 Species and taxa composition, mean CPUE (range), total catch, mean body length (range), developmental stage of larval and juvenile fishes caught in the mouth region of the Sundays and Swartkops estuaries in Algoa Bay. Pr = preflexion, F = flexion, Po = postflexion, Ej = early juvenile, J = juvenile, A = adult, Le = leptocephalus. Dominant developmental stages bolded

		SUNDAYS						SWARTKOPS					
		CPUE		Total Catch		Length (mm)	Development	CPUE		Total Catch		Length (mm)	Development
		Mean	Range	No.	%	Range	stage	Mean	Range	No.	%	Range	stage
Ambassidae	*Ambassis natalensis*	0.005	0 – 0.4	6	0.1	47.1 (43.0 – 55.7)	**J**						
Ariidae	*Galeichthys feliceps*	0.05	0 – 3.4	64	0.6	50.1 (39.9 – 84.6)	**J**	0.01	0 – 0.2	7	0.2	43.3 (38.6 – 52.5)	**J**
Atherinidae	*Atherina breviceps*	0.2	0 – 13.6	315	2.7	26.6 (4.8 – 68.0)	Pr, F, **Po**, Ej, J, A	0.01	0 – 1.8	17	0.6	9.3 (4.9 – 48.5)	**Pr**, F, Po, Ej, J, A
Blenniidae	*Omobranchus woodi*	0.002	0 – 0.2	3	<0.1	14.4 (14.2 – 14.6)	**Po**	0.001	0 – 0.2	2	<0.1	10.3 (6.6 – 14.0)	**Po**
	Parablennius cornutus	0.002	0 – 0.2	2	<0.1	28.1 (12.2 – 43.9)	Po, **Ej**, J	0.001	0 – 0.2	1	<0.1	14.5	**Po**
	Parablennius pilicornis	0.001	0 – 0.2	1	<0.1	10.7	**Po**						
Carangidae	*Lichia amia*	0.001	0 – 0.2	1	<0.1	31.3	**Ej**						
	Decapterus sp 1							0.002	0 – 0.4	2	<0.1	37 (34.8 – 39.2)	**Po**
Cichlidae	*Oreochromis mossambicus*	0.03	0 – 3.4	39	0.3	58.6 (27.0 – 115.0)	**J**						
Clinidae	*Clinus superciliosus*	0.002	0 – 0.2	2	<0.1	17.9 (15.2 – 20.6)	**Po**	0.01	0 – 0.6	12	0.4	56.5 (11.6 – 147.0)	Po, Ej, **J**
Clupeidae	*Gilchristella aestuaria*	1.6	0 – 60.8	2050	17.7	32.8 (6.5 – 62.0)	F, Po, Ej, J, **A**	0.03	0 – 1.8	36	1.3	17.9 (12.4 – 25.9)	**Po**, Ej
Cynoglossidae	*Cynoglossus capensis*							0.001	0 – 0.2	1	<0.1	5.4	**Po**
Cyprinidae	*Cyprinus carpio carpio*	0.001	0 – 0.2	1	<0.1	18.1	**Po**						
Elopidae	*Elops machnata*	0.001	0 – 0.2	1	<0.1	25.0	**Le**						
Gobiesocidae	*Diplecogaster megalops*	0.002	0 – 0.2	2	<0.1	5.5 (5.3 – 5.6)	**Po**						
Gobiidae	*Caffrogobius gilchristi*	1.4	0 – 60.2	1737	15.0	23.9 (4.2 -86.5)	Po, **J**	0.2	0 – 8.8	216	8.1	22.7 (7.8 – 83.0)	Po, **J**
	Caffrogobius nudiceps	0.3	0 – 29.6	398	3.4	17.6 (8.4 – 103.6)	Po, **J**	0.8	0 – 136.6	990	37.2	16.9 (6.8 – 56.3)	Po, **J**
	Glossogobius callidus	0.04	0 – 3.6	51	0.4	16.8 (4.5 – 99.0)	Po, **Ej**, J	0.01	0 – 0.6	13	0.5	14.5 (7.1 – 16.2)	**Po**
	Psammogobius knysnaensis	0.2	0 – 14.2	254	2.2	18.5 (5.0 – 88.0)	Po, **Ej**, J	0.1	0 – 13.4	128	4.8	39.2 (16.0 61.0)	Po
	Redigobius dewaali	0.02	0 – 4.8	26	0.2	13.6 (9.4 – 10.7)	**Po**						
Haemulidae	*Pomadasys commersonnii*	0.02	0 – 4.0	25	0.2	14.3 (7.5 – 55.6)	**Po**, Ej	0.001	0 – 0.2	1	<0.1	37.8	Ej
	Pomadasys olivaceus	0.1	0 – 15.4	136	1.2	53.5 (12.2 – 83.0)	Po, **Ej**, J	0.2	0 – 21.2	307	11.5	44.4 (11.7 – 97.0	Po, **Ej**
Monodactylidae	*Monodactylus falciformis*	0.06	0 – 3.2	83	0.7	80.0 (5.0 – 115.0)	Po, Ej, **J**	0.005	0 – 0.2	6	0.2	23.4 (4.1 – 61.0)	**Po**, Ej, J
Mugilidae	*Crenimugil crenilabis*	0.001	0 – 0.2	1	<0.1	22.6	**Po**	0.001	0 – 0.2	1	<0.1	34.5	**J**
	Liza dumerili	0.05	0 – 8.8	59	0.5	29.5 (17.8 – 52.5)	**Ej**, J	0.002	0 – 0.4	3	0.1	17.5 (17.0 – 18.0)	**Po**

	Liza macrolepis	0.3	0 – 20.8	411	3.5	28.7 (8.3 – 74.0)	Po, **Ej**, J	0.001	0 – 0.2	1	<0.1	24.1	**Ej**
	Liza richardsonii	0.6	0 – 88.8	771	6.7	30.5 (12.5 – 124.0)	Po, **Ej**, J	0.01	0 – 0.6	11	0.4	25.1 (15.8 – 50.0)	Po, **Ej**, J
	Liza tricuspidens							0.001	0 – 0.2	2	0.1	37.1 (32.7 – 41.5)	**J**
	Mugil cephalus	0.01	0 – 0.4	9	0.1	34.6 (21.0 – 79.5)	**Ej**, J	0.01	0 – 1.2	7	0.3	34.1 (24.5 – 47.2)	**J**
	Myxus capensis	0.001	0 – 0.2	1	<0.1	21.7 (16.5 – 31.0)	**Po**, Ej						
	Valamugil buchanani	0.01	0 – 1.2	9	0.1	19 (13.4 – 35.)	**Po**, Ej	0.001	0 – 0.2	1	<0.1	40.3	**J**
	Liza sp 1	0.6	0 – 47.0	742	6.4	10.7 (6.4 – 20.2)	**Po**	0.1	0 – 17.2	142	5.3	10.4 (8.1 – 13.7)	**Po**
	Liza sp 2	0.002	0 – 0.4	3	<0.1	9.4 (7.6 – 12.2)	**Po**						
	Mugilidae sp 2	0.1	0 – 28.4	145	1.2	14.8 (10.7 – 15.5)	**Po**						
	Mugilidae sp 3	0.001	0 – 0.2	1	<0.1	16.8 (16.5 – 17.0)	**Po**						
Ophichthidae	*Ophisurus serpens*	0.02	0 – 1.2	35	0.3	105.2 (9.0 – 460.0)	Ej, **J**	0.001	0 – 0.2	1	<0.1	90.5	**J**
Pomatomidae	*Pomatomus saltatrix*	0.002	0 – 0.2	2	<0.1	100.5 (62.9 – 138.0)	**J**						
Sciaenidae	*Argyrosomus inodorus*	0.004	0 – 0.4	5	<0.1	5.7 (4.1 – 6.5)	Pr, **F**						
	Argyrosomus japonicus	0.002	0 – 0.2	2	<0.1	14 (5.5 – 19.7)	F, **Po**						
Soleidae	*Dagetichthys marginata*	0.002	0 – 0.2	2	<0.1	6.2 (5.6 – 6.8)	**Po**						
	Heteromycteris capensis	0.1	0 – 13.8	134	1.2	13.3 (4.6 – 81.0)	**Po**, Ej, J	0.03	0 – 5.8	43	1.6	8.6 (4.2 – 38.0)	**Po**, Ej
	Solea turbynei	0.01	0 – 1.0	14	0.1	14.1 (3.6 – 63.1)	**Po**, Ej, J	0.002	0 – 0.4	3	0.1	41. (3.7 – 4.4)	**Po**
Sparidae	*Acanthopagrus berda*							0.001	0 – 0.2	1	<0.1	10.9	**Po**
	Diplodus capensis	0.4	0 – 16.8	450	3.9	21.1 (6.0 – 67.0)	**Po**, Ej, J	0.3	0 – 7.6	395	14.8	46.0 (7.0 – 110.0)	Po, **Ej**, J
	Diplodus cervinus hottentotus	0.003	0 – 0.4	4	<0.1	14.1 (8.4 – 21.8)	**Po**	0.01	0 – 1.0	18	0.7	37.8 (20.7 – 67.0)	**Ej**, J
	Lithognathus lithognathus	0.005	0 – 0.2	7	0.1	30.7 (9.7 – 58.7)	**Po**, **Ej**						
	Rhabdosargus globiceps	0.1	0 – 3.6	131	1.1	13.6 (8.7 – 37.0)	**Po**, Ej	0.03	0 – 1.4	42	1.6	24.3 (9.4 – 90.0)	**Po**, Ej, J
	Rhabdosargus holubi	2.7	0 – 92.4	3434	29.6	47.6 (8.4 – 157.0)	Po, Ej, **J**	0.1	0 – 8.2	142	5.3	33.9 (8.7 – 136.0)	**Po**, Ej, J
	Sarpa salpa	0.004	0 – 0.4	4	<0.1	11.9 (9.9 – 14.0)	**Po**	0.01	0 – 0.4	16	0.6	36.1 (14.0 – 101.0)	Po, **Ej**, J
	Spondyliosoma emarginatum							0.1	0 – 5.6	64	2.4	8.4 (6.4 – 12.7)	**Po**
Syngnathidae	*Syngnathus temminckii*	0.004	0 – 0.2	6	<0.1	97.8 (53.8 – 185.0)	**Ej**, J, A	0.02	0 – 0.8	25	0.9	88.9 (42.3 – 255.0)	Ej, **J**, A
Terapontidae	*Terapon jarbua*	0.001	0 – 0.2	2	<0.1	54.2 (18.3 – 90.0)	**Po**, **J**						
Tetraodontidae	*Amblyrhynchotes honckenii*	0.002	0 – 0.4	3	<0.1	4.9 (3.8 – 6.1)	F, **Po**	0.003	0 – 0.2	3	0.1	8.2 (6.2 – 10.8)	**Po**
Triglidae	*Chelidonichthys capensis*							0.001	0 – 0.2	1	<0.1	7.6	**F**
	Chelidonichthys kumu	0.001	0 – 0.2	1	<0.1	15.7	**Po**						

4.3 Seasonal trends in fish CPUE and diversity indices

The fyke net CPUE in the Sundays Estuary showed a significant difference (H = 22.9; d.f. = 3; $p < 0.001$) among the seasons (Figure 5.4) with greatest mean CPUE in autumn (15.6 fish/net/hour), followed by summer (11.3 fish/net/hour), winter (5.6 fish/net/hour) and spring (3.7 fish/net/hour). Amongst the dominant species (>1.0 %), a significant difference in *Atherina breviceps* (H = 15.7; d.f. = 3; $p < 0.01$), *Caffrogobius gilchristi* (H = 16.3; d.f. = 3; $p < 0.01$), *Diplodus capensis* (H = 8.2; d.f. = 3; $p < 0.05$), *Gilchristella aestuaria* (H = 11.4; d.f. = 3; $p < 0.01$), *Liza macrolepis* (H = 20.1; d.f. = 3; $p < 0.001$), *Liza* sp 1 (H = 23.9; d.f. = 3; $p < 0.001$), *Pomadasys olivaceus* (H = 25.2; d.f. = 3; $p < 0.001$), *Rhabdosargus globiceps* (H = 10.2; d.f. = 3; $p < 0.05$) and *R. holubi* (H = 15.9; d.f. = 3; $p < 0.01$) catches occurred among the seasons. Highest mean catches of *C. gilchristi* (4.1 fish/net/hour) and *G. aestuaria* (4.3 fish/net/hour) were observed in autumn with highest mean catches of *A. breviceps* (0.6 fish/net/hour), *Liza* sp 1 (1.2 fish/net/hour), *P. olivaceus* (0.3 fish/net/hour) and *R. holubi* (5.4 fish/net/hour) in summer. Highest catches of *L. macrolepis* (0.6 fish/net/hour) occurred in winter with highest catches of *D. capensis* (0.9 fish/net/hour) and *R. globiceps* (0.2 fish/net/hour) in spring.

In the Swartkops Estuary, the fyke net CPUE (H = 21.0; d.f. = 3; $p < 0.001$), diversity (H = 18.0; d.f. = 3; $p < 0.001$) and species richness (H = 18.6; d.f. = 3; $p < 0.001$) all showed a significant difference among the seasons (Figure 5.4). Greatest mean CPUE and the total number of species were observed in summer (4.8 fish/net/hour), followed by winter (2.3 fish/net/hour), autumn (0.9 fish/net/hour) and spring (0.4 fish/net/hour). Species diversity and richness peaked in winter (H' = 0.5; d = 1.3), followed by summer (H' = 0.5; d = 0.7), spring (H' = 0.3; d = 0.6) and autumn (H' = 0.2; d = 0.3). Amongst the dominant species (>1.0 %), a significant difference in CPUE of *Caffrogobius gilchristi* (H = 24.5; d.f. = 3; $p < 0.001$), *Caffrogobius nudiceps* (H = 12.4; d.f. = 3; $p < 0.01$), *Diplodus capensis* (H = 19.9; d.f. = 3; $p < 0.001$), *Pomadasys olivaceus* (H = 14.3; d.f. = 3; $p < 0.01$) and *Spondyliosoma emarginatum* (H = 9.9; d.f. = 3; $p < 0.05$) occurred among the seasons. Highest mean catches of *C. gilchristi* (0.2 fish/net/hour) were observed in autumn and highest mean catches of *P. olivaceus* (0.8 fish/net/hour) in winter. Highest mean catches of *C. nudiceps* (2.8 fish/net/hour), *D. capensis* (0.5 fish/net/hour) and *S. emarginatum* (0.2 fish/net/hour) were observed in summer.

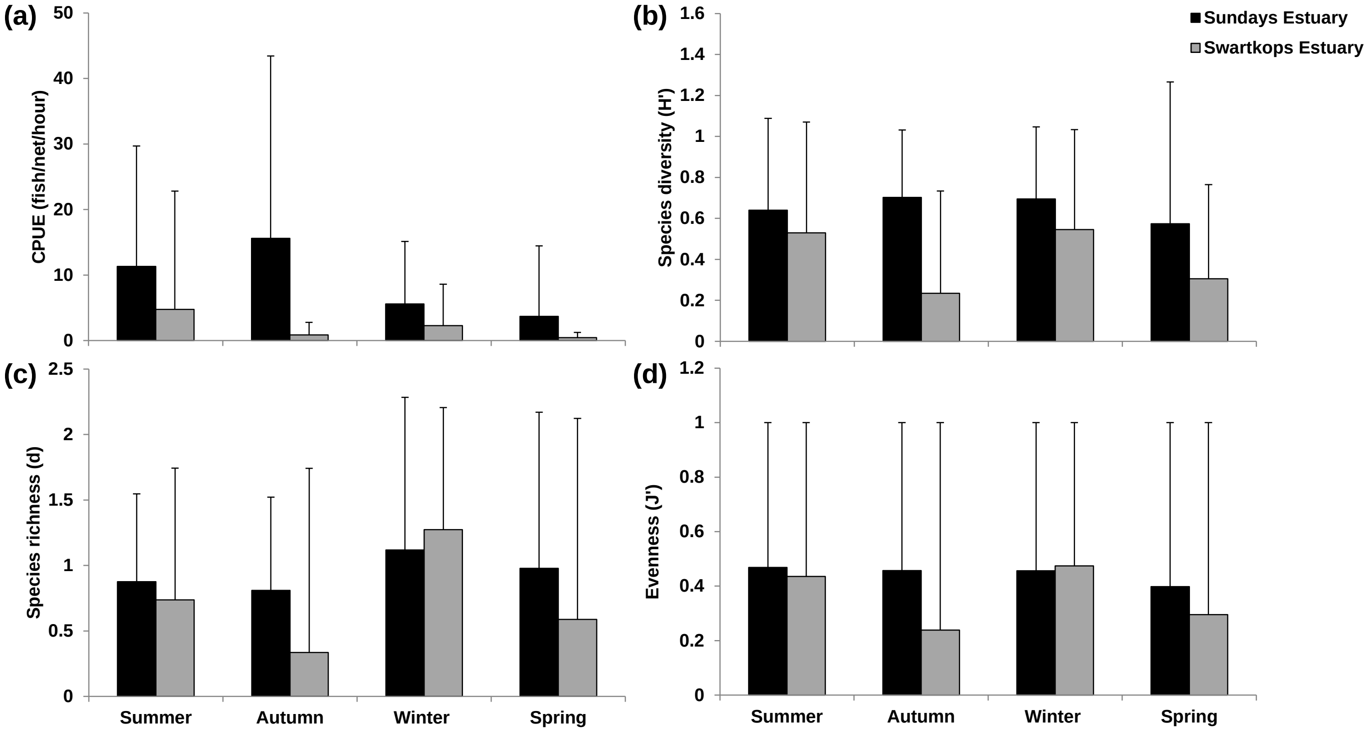

FIGURE 5.4 Larval fish mean (n = 64) and maximum of a) CPUE, b) Shannon-Wiener diversity, c) Margalef species richness and d) Pielou's evenness recorded seasonally in the Sundays and Swartkops estuaries during the study (December 2010 – October 2012)

4.4 Tidal variations in fish CPUE and diversity indices

In the Sundays Estuary, a significant difference in the diversity (H = 9.1; d.f. = 3; $p < 0.05$) and species richness (H = 10.3; d.f. = 3; $p < 0.05$) occurred among the various tide states (Figure 5.5) with greatest mean values recorded on the ebb tide at night (H' = 0.8; d = 1.2), followed by the ebb tide during the day (H' = 0.7; d = 1.1), the flood tide linked to sunrise (H' = 0.6; d = 0.9) and the flood tide linked to sunset (H' = 0.5; d = 0.7). Although not statistically significant (H = 7.7; d.f. = 3; p = 0.05), mean CPUE of larval and juvenile fishes was greatest during the ebb tide at night (11.6 fish/net/hour) followed by the flood tide linked to sunset (11.5 fish/net/hour), the ebb tide during the day (7.6 fish/net/hour) and the flood tide linked to sunrise (5.5 fish/net/hour).

In the Sundays Estuary during the flood tide a significant difference in CPUE (U = 1561.0; $p < 0.05$), diversity (U = 1291.0; $p < 0.001$), richness (U = 1310.0; $p < 0.001$) and evenness (U = 1571.0; $p < 0.05$) was observed in the fyke nets facing the incoming tide and the fyke nets in the opposing direction (Figure 5.6). Highest mean CPUE (10.0 fish/net/hour), diversity (H'

= 0.7), richness (d = 1.0) and evenness (J' = 0.5) was observed in the fyke nets facing the incoming flood tide. No significant difference in CPUE or diversity indices occurred during the ebb tide between the two nets.

The fish CPUE (H = 11.0; d.f. = 3; $p < 0.05$) was significantly higher on the flood tide in the Swartkops Estuary linked to sunrise (4.0 fish/net/hour), followed by the flood tide linked to sunset (2.8 fish/net/hour), the ebb tide during the night (0.9 fish/net/hour) and the ebb tide during the day (0.8 fish/net/hour) (Figure 5.5). Although no significant difference in the diversity (H = 6.0; d.f. = 3; p = 0.11) and species richness (H = 5.6; d.f. = 3; p = 0.13) was observed among the tide states, the highest mean values were recorded on the flood tide linked to sunrise (H' = 0.8; d = 0.5), followed by the flood tide linked to sunset (H' = 0.8; d = 0.5), the ebb tide during the day (H' = 0.7; d = 0.3) and ebb tide at night (H' = 0.7; d = 0.3).

In the Swartkops Estuary during the flood tide a significant difference in CPUE (U = 1294.0; $p < 0.001$), diversity (U = 1230.0; $p < 0.001$), richness (U = 1268.5; $p < 0.001$) and evenness (U = 1335.0; $p < 0.001$) was observed in the fyke nets facing the incoming tide and the fyke nets in the opposing direction (Figure 5.6). Highest mean CPUE (5.7 fish/net/hour), diversity (H' = 0.7), richness (d = 1.1) and evenness (J' = 0.5) was observed in the fyke nets facing the incoming flood tide. No significant difference in CPUE or diversity indices occurred during the ebb tide between the two nets.

In the Sundays Estuary, amongst the dominant species (Figure 5.7), catches of *A. breviceps* (H = 15.9; d.f. = 3; $p < 0.01$), *C. nudiceps* (H = 11.4; d.f. = 3; $p < 0.01$), *D. capensis* (H = 12.5; d.f. = 3; $p < 0.01$), *Liza* sp 1 (H = 9.9; d.f. = 3; $p < 0.05$), Mugilidae sp 2 (H = 15.2; d.f. = 3; $p < 0.01$) and *P. knysnaensis* (H = 12.5; d.f. = 3; $p < 0.01$) were significantly different during the various tide states. Catches of *A. breviceps* (28.8 fish/net/hour), *C. nudiceps* (61.3 fish/net/hour), *D. capensis* (65.0 fish/net/hour), *P. olivaceus* (21.5 fish/net/hour), *R. holubi* (342.5 fish/net/hour) and *S. temminckii* (0.5 fish/net/hour) peaked during the ebb tide at night. During this ebb tide, higher catches of *A. breviceps* and *D. capensis* were observed in the sea facing nets, in the opposing direction of the ebb tide flow. Catches of *C. gilchristi* (157.6 fish/net/hour), *G. aestuaria* (182.3 fish/net/hour), *P. knysnaensis* (24.1 fish/net/hour) were higher during the flood tide linked to sunset.

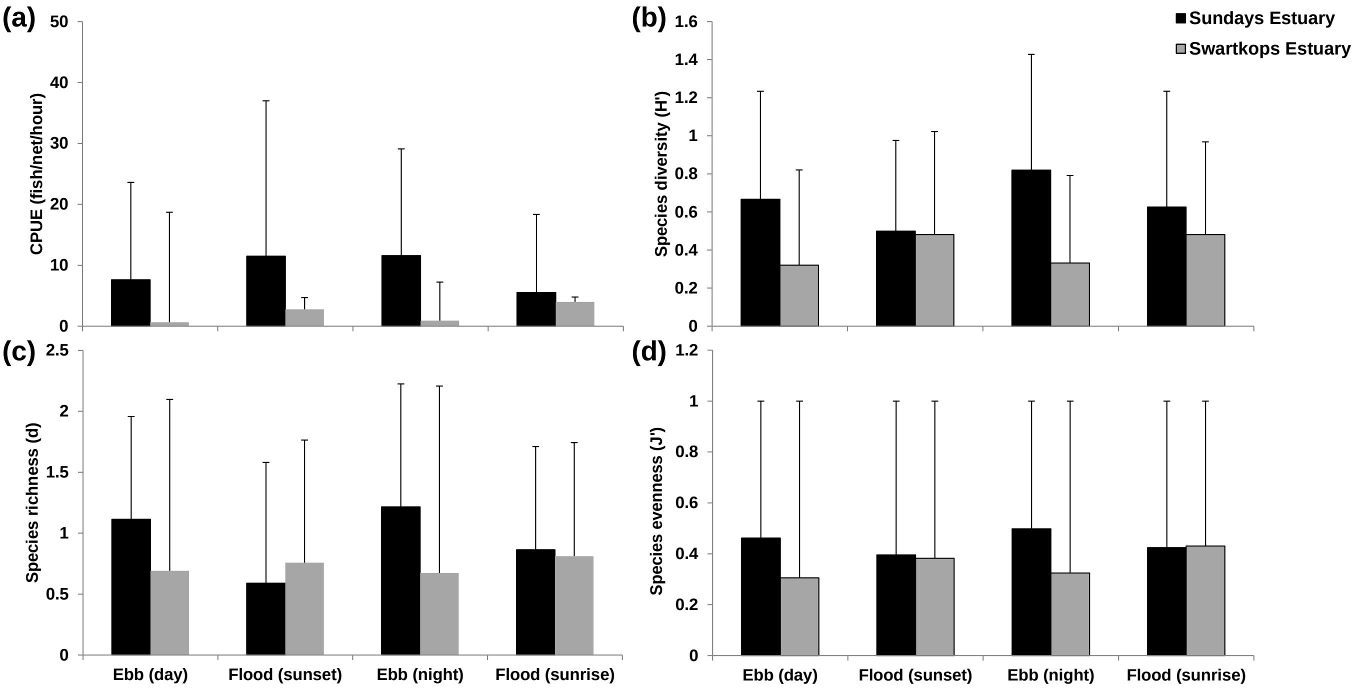

FIGURE 5.5 Larval fish mean (n = 64) and maximum of a) CPUE, b) Shannon-Wiener diversity, c) Margalef species richness and d) Pielou's evenness recorded at each tidal state in the Sundays and Swartkops estuaries during the study (December 2010 – October 2012)

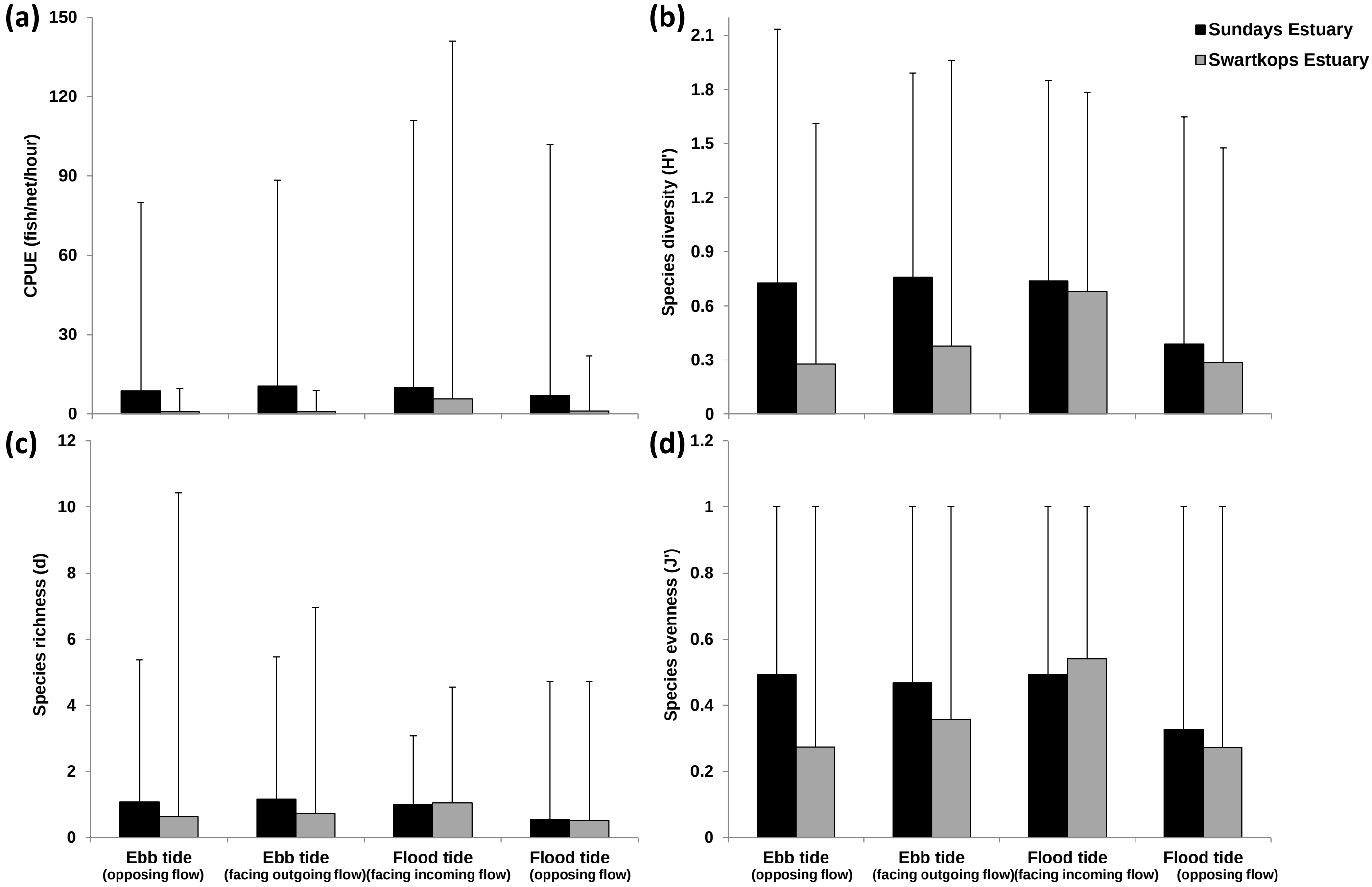

FIGURE 5.6 Larval and juvenile fish mean (n = 64) and maximum of a) CPUE, b) Shannon-Wiener diversity, c) Margalef species richness and d) Pielou's evenness recorded in the fyke nets opposing flow and with flow during the ebb and flood tides respectively in the Sundays and Swartkops estuaries during the study (December 2010 – October 2012)

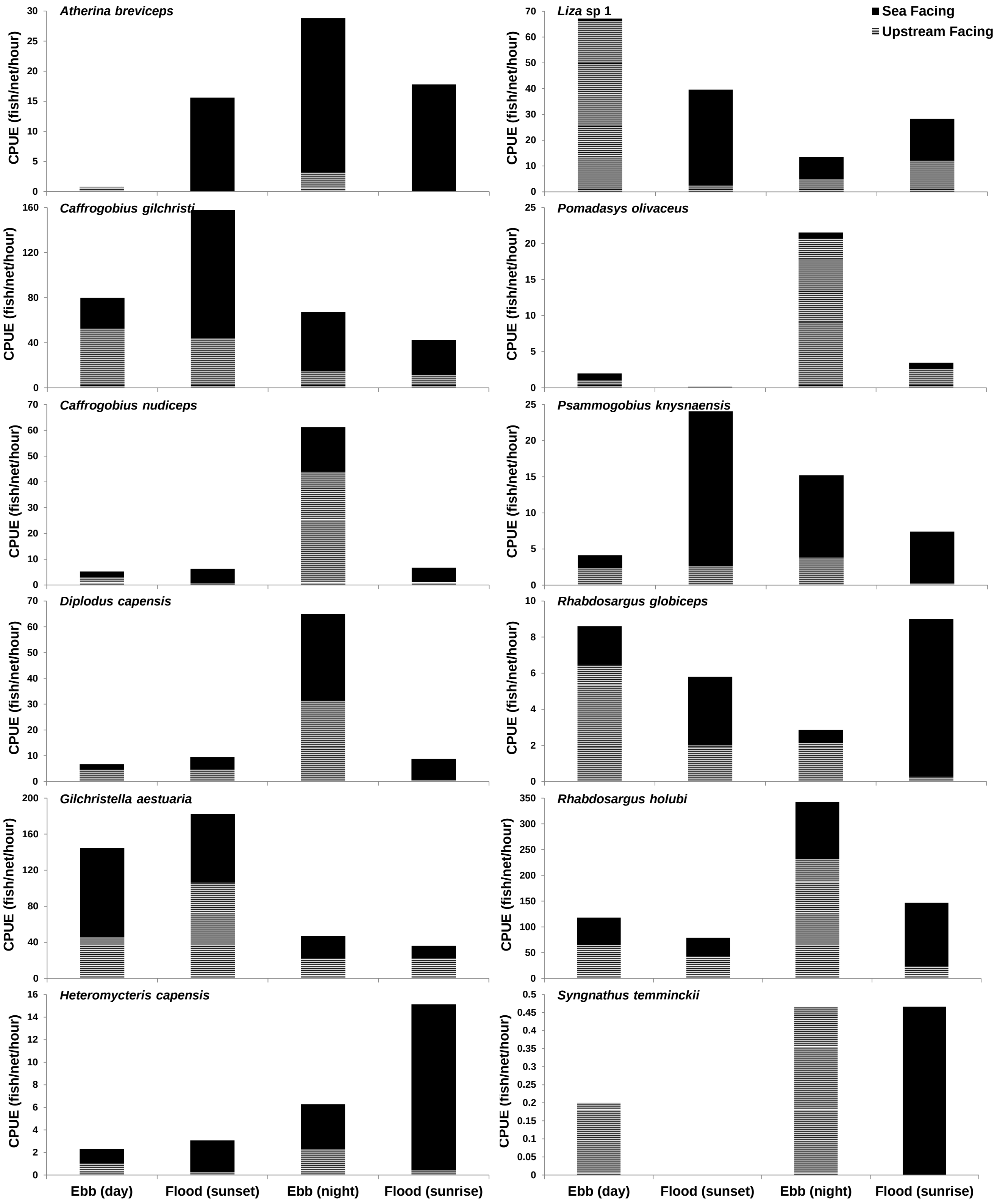

FIGURE 5.7 Mean CPUE of dominant species collected in the Sundays Estuary during the various tide states in the fyke nets which faced the sea and those in the opposing direction, during the study (December 2010 – October 2012)

In the Swartkops Estuary, amongst the dominant species (Figure 5.8), catches of *D. capensis* (H = 12.1; d.f. = 3; p < 0.01) were significantly highest on the flood tide linked to sunrise particularly in the fyke nets facing the incoming tide (23.9 fish/net/hour). Catches of *Liza* sp 1 (H = 8.7; d.f. = 3; p < 0.05) were significantly highest on the flood linked to sunset (23.7 fish/net/hour). Catches of *R. globiceps* (H = 9.7; d.f. = 3; p < 0.05) were significantly highest on the flood tide linked to sunset with a peak (2.3 fish/net/hour) in catches observed in the fyke nets facing the incoming tide. Although not statistically significant, catches of *A. breviceps* and *H. capensis* were highest on the flood tide, specifically in the fyke nets facing the incoming tide with a peak in CPUE occurring on the flood tide linked to sunrise. Catches of *C. gilchristi* (12.3 fish/net/hour) and *P. knysnaensis* (19.4 fish/net/hour) were highest during the flood tide linked to sunset. *Caffrogobius nudiceps* and *R. holubi* catches were similarly highest during the flood tide linked to sunrise specifically in the fyke nets facing the incoming tide. Highest catches of *G. aestuaria* occurring on the flood tide linked to sunset in the fyke nets facing the incoming tide (3.0 fish/net/hour). Peaks in CPUE of *P. olivaceus* were observed on the flood tide linked to sunset in both the nets facing the incoming tide (23.6 fish/net/hour) and the nets facing the opposing flood tide flow (29.1 fish/net/hour). Catches of *S. temminckii* were generally highest during the flood tide in the nets facing the incoming tide.

4.5 Spatial variations in fish CPUE and diversity indices

A significantly greater CPUE (U = 5579.0; p < 0.001), species diversity (U = 5786.0; p < 0.001) and species richness (U = 5680.0; p < 0.001) was observed on the east bank (13.3 fish/net/hour; H’ = 0.8; d = 1.2) of the Sundays Estuary (Figure 5.9) as opposed to the west bank (4.8 fish/net/hour; H’ = 0.5; d = 0.7). Amongst the dominant species, catches of *C. gilchristi* (U = 4559.5; p < 0.001), *G. aestuaria* (U = 6654.0; p < 0.01), *Liza* sp 1 (U = 6997.0; p < 0.05) and *R. holubi* (U = 6077.5; p < 0.001) were significantly greatest on the east bank, and catches of *C. nudiceps* (U = 6310.5; p < 0.01) were significantly highest on the west bank.

No significant difference in CPUE or any of the diversity indices was observed between the east and the west bank of the Swartkops Estuary (Figure 5.9). Amongst the dominant species, only *D. capensis* had significantly (U = 5282.0; p < 0.001) higher catches on the east bank (0.5 fish/net/hour) as opposed to the west bank (0.1 fish/net/hour).

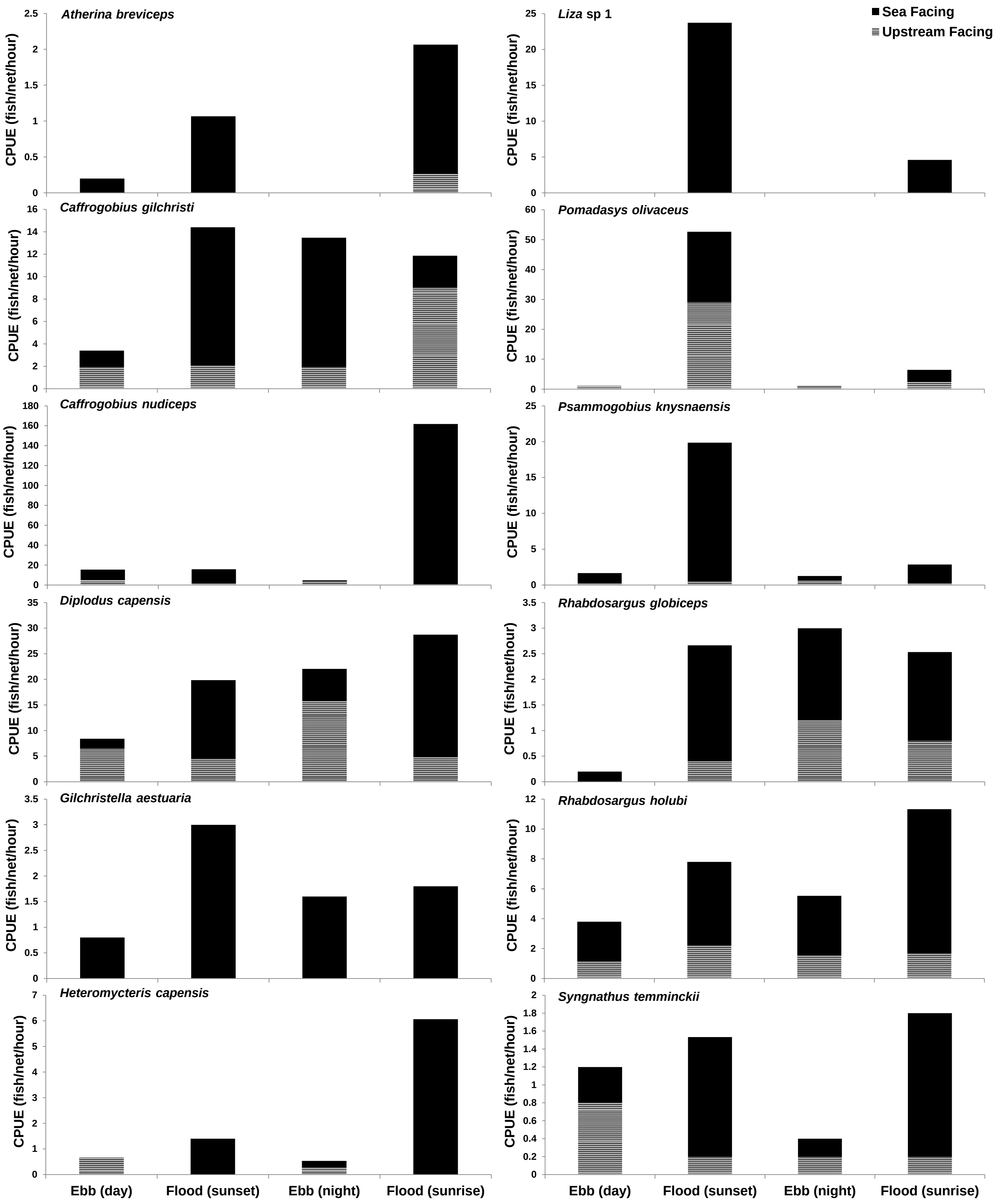

FIGURE 5.8 Mean CPUE of dominant species collected in the Swartkops Estuary during the various tide states in the fyke nets which faced the sea and those in the opposing direction, during the study (December 2010 – October 2012)

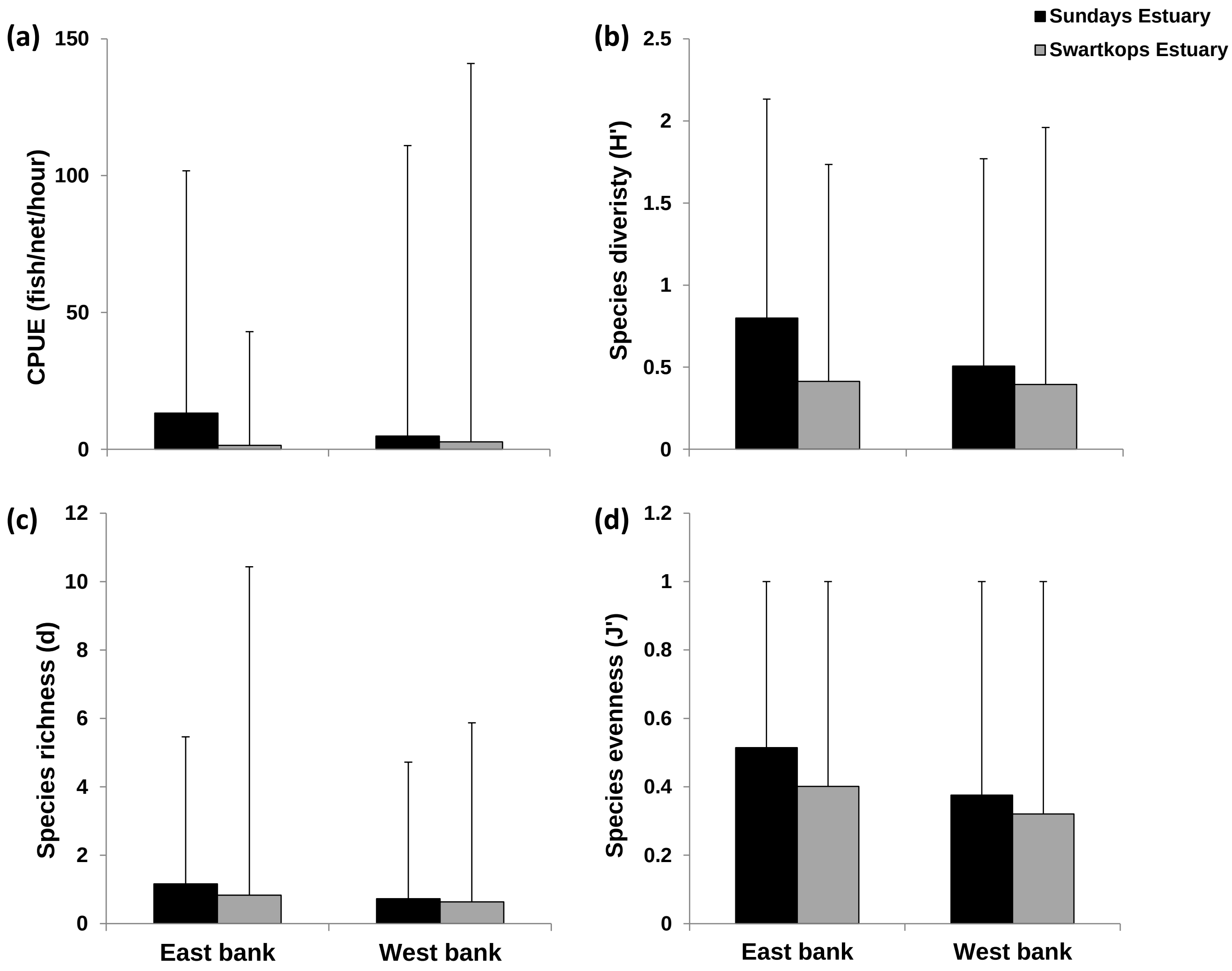

FIGURE 5.9 Larval and juvenile fish mean (n = 128) and maximum of a) CPUE, b) Shannon-Wiener diversity, c) Margalef species richness and d) Pielou's evenness recorded on the east and the west bank in the Sundays and Swartkops estuaries during the study (December 2010 – October 2012)

4.6 Temporal and spatial trends in body length

Amongst the top three most abundant species in the Sundays Estuary, a significant difference in the lengths of *R. holubi* (H = 25.2; d.f. = 3; p < 0.001), *G. aestuaria* (H = 57.8; d.f. = 3; p < 0.001) and *C. gilchristi* (H = 21.3; d.f. = 3; p < 0.001) occurred among the various tide states (Figure 5.10). The largest mean length (63.7 mm) of *R. holubi* was observed on the ebb tide in the fyke nets facing the opposing direction of flow. Smallest mean lengths (31.3 mm) were observed on the ebb tide in the fyke nets facing the outgoing tide. Largest mean lengths of *G. aestuaria* (41.9 mm) and *C. gilchristi* (32.6 mm) were observed on the flood tide in the nets facing the opposing direction of the flow. Similarly the smallest mean lengths of *G. aestuaria* (23.1 mm) and *C. gilchristi* (19.3 mm) were observed on the flood tide in the nets facing the incoming tide.

Amongst the top three most abundant species in the Swartkops Estuary, a significant difference in the lengths of *C. nudiceps* (H = 9.5; d.f. = 3; $p < 0.05$) *D. capensis* (H = 32.5; d.f. = 3; $p < 0.001$) and *P. olivaceus* (H = 15.3; d.f. = 3; $p < 0.01$) occurred among the various tide states (Figure 5.11). The largest (28.9 mm) and smallest (12.1 mm) mean lengths of *C. nudiceps* were observed in the nets facing the outgoing ebb tide during the night and the day respectively. Largest mean lengths of *D. capensis* (55.1 mm) were observed on the flood tide in the nets facing the incoming tide and smallest mean lengths (33.9 mm) on the ebb tide in the nets facing the opposing direction of the flow. Largest mean lengths (55.8 mm) of *P. olivaceus* were observed on the flood tide facing the opposing direction of the incoming tide while smallest mean lengths (34.0 mm) were observed during the ebb tide in the nets facing the opposing direction of flow.

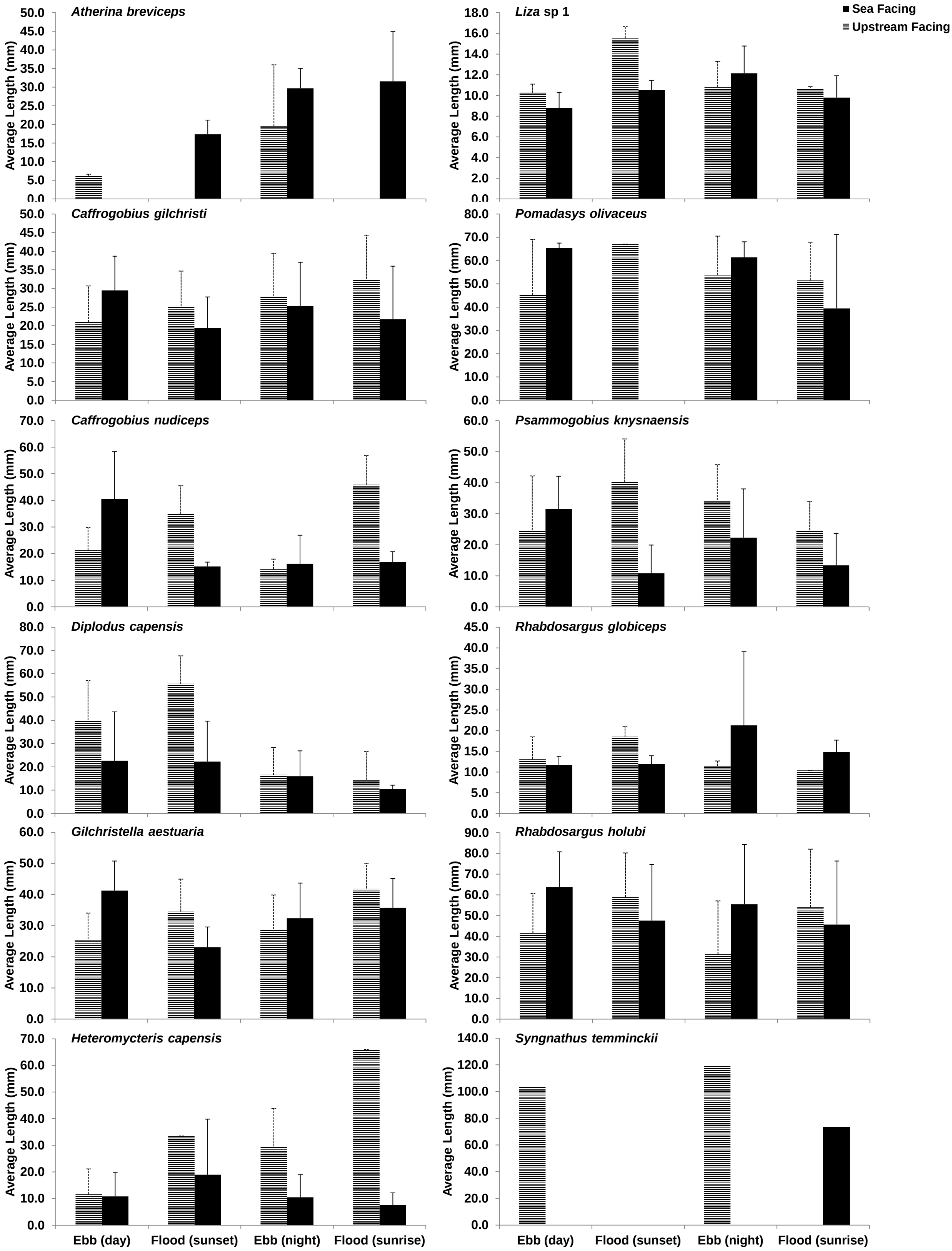

FIGURE 5.10 Mean and maximum body length of dominant species collected in the Sundays Estuary during the various tide states in the facing fyke nets which faced the sea and those in the opposing direction, during the study (December 2010 – October 2012)

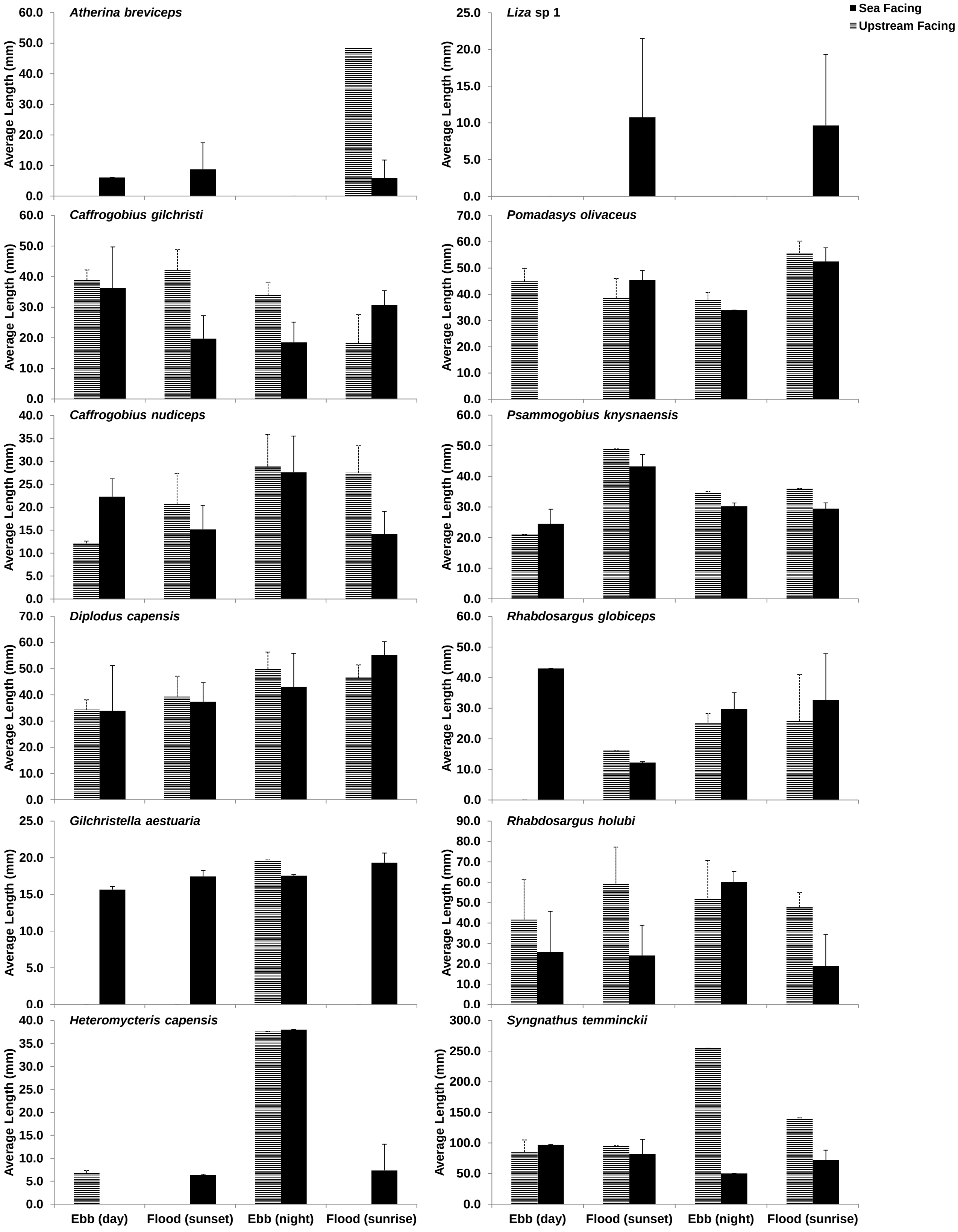

FIGURE 5.11 Mean and maximum body length of dominant species collected in the Swartkops Estuary during the various tide states in the facing fyke nets which faced the sea and those in the opposing direction, during the study (December 2010 – October 2012)

5. DISCUSSION

Physico-chemical properties of the water in the Sundays and Swartkops estuaries exhibited similar seasonal trends following the usual temporal sand spatial patterns observed in warm-temperate estuaries (Strydom *et al.*, 2003; Sutherland *et al.*, 2012). Significantly lower values of conductivity, total dissolved solids, salinity and pH, and significantly higher values of turbidity were however recorded in the Sundays Estuary due to the elevated freshwater supply from an inter-basin water-transfer scheme. Abundances of larval and juvenile fishes were affected by season, with the highest mean CPUE of larvae and juveniles in the Swartkops Estuary recorded in summer. Summer peaks in catches have been observed in similar permanently open estuaries in the warm-temperate regions of South Africa (Strydom *et al.*, 2003), which coincide with recruitment peaks for most fish species. This follows patterns in densities for temperate northern hemisphere estuaries (Pearcy and Myers, 1974; Able *et al.*, 2006; Ramos *et al.*, 2006; Ramos *et al.*, 2010; Primo *et al.*, 2012) and temperate southern hemisphere estuaries (Gaughan *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1994). Highest mean CPUE of larvae and juvenile fishes were however recorded in autumn in the Sundays Estuary, not a typical trend observed in typical warm-temperate estuarine systems in South Africa. These high values correspond to high CPUE of *C. gilchristi* and *G. aestuaria*. Larval abundances of *G. aestuaria* are known to peak however in the autumn months between March and April in subtropical estuaries on the east coast of South Africa (Harris, 1996) and in March on the southern Cape coast (Whitfield, 1989a).

In the Sundays Estuary densities of *G. aestuaria* were high during autumn on both the flood tide, in nets facing the incoming tide and the opposing direction, and on the ebb tide, in nets facing the outgoing tide and the opposing direction. Small larvae (6 – 8 mm) were found in the fyke nets facing the outgoing ebb tide indicating a flushing of underdeveloped larvae with poor swimming abilities unable to maintain their position in the estuary, out of the estuary on the outgoing ebb tide. High densities of larger *G. aestuaria* juveniles and adults were observed in nets facing the opposing direction of flow during both the flood and the ebb tide. *Gilchristella aestuaria* is mainly a zoo- and phyto-plankton feeder and switches feeding strategies from selective feeding in the water column twice daily with peaks in the early morning and late afternoon during summer months (September to March) to filter-feeding in the water-detritus interface throughout the day and night during winter months (April – August) (Talbot, 1982). Furthermore, in turbid waters this species adopts a non-selective zooplankton filter feeding strategy (Blaber, 1979). The elevated freshwater supply from the inter-basin water-transfer scheme in the Sundays Estuary creates a significantly more turbid environment compared to that of the Swartkops Estuary. Therefore it is likely that *G. aestuaria* are adopting a similar filter feeding strategy in the Sundays Estuary, and using the opposing direction of the tides to feed.

Larvae and early juveniles of *C. gilchristi* in the Sundays Estuary, corresponding to lengths between 9 – 20 mm, were observed in high densities during autumn in the nets facing the incoming flood tide, indicating an immigration of larvae on the incoming tide. Several studies have indicated that physico-chemical variables including temperature, salinity and turbidity influence the monthly variation of abundance of larval and juvenile fishes recruiting into estuaries (Martin *et al.*, 1992; Neira *et al.*, 1992; Whitfield, 1994). Mean water temperatures during autumn (21.0 °C) in the Sundays Estuary were almost similar to those recorded in summer (21.9 °C). The present study indicates that recruitment of postflexion larvae and early juveniles of *C. gilchristi* into the Sundays Estuary is protracted occurring mainly in summer and autumn when water temperatures in the estuary are highest. A protracted period of recruitment of *Solea senegalensis* (Family: Soleidae) was observed in the warm-temperate Lima Estuary (NW Portugal) and authors suggested that this may be induced by a prolonged spawning period and by the production of several batches of larvae during the spawning season (Ramos *et al.*, 2010). In addition, similar high densities of larvae and early juveniles of *C. gilchristi* of similar sizes were also observed in the fyke nets facing the opposing direction of the incoming flood tide, indicating emigration against the incoming tide. Newly hatched larvae of *C. gilchristi*, with lengths corresponding to 3 – 4 mm are known to be carried passively out of the estuary by the ebb tide, to complete an obligatory larval phase in the marine environment before entering estuaries at lengths of 8 – 10 mm as permanent residents (Whitfield, 1989c). It appears from the present study that postflexion larvae and early juveniles are indeed entering the system on the incoming flood tide, with the increased freshwater entering the marine environment serving as an important cue for these species. However, due to the faster flowing water in the opposing direction of the flood tide from the elevated freshwater supply from the inter-basin water-transfer scheme, some larvae and juvenile fishes are unable to maintain position and are possibly being swept back out into the marine environment.

The two estuarine species, *C. gilchristi* and *P. knysnaensis*, had similar patterns in temporal abundances in both estuaries. Abundances of these species peaked during the flood tide with the onset of darkness in both estuaries. Noteworthy are the higher abundances of these species in the fyke nets facing the incoming flood tide, indicating an immigration of larvae into the estuarine systems. The larvae of *C. gilchristi* and *P. knysnaensis* hatch from benthic eggs in estuaries and are flushed out of the system on the ebb tide (Beckley, 1985; Whitfield, 1989c). Evidence from the present study supports the work of Whitfield (1989b), where a subsequent return migration of the postflexion larvae and early juvenile of these species back into the estuarine system was observed during the flood tide, particularly during dusk.

The hydrological conditions experienced during the study indicate that the ebb and flood tides presented similar salinity and temperature conditions. An inter-basin transfer scheme provides additional fresh water to the Sundays Estuary, and this lowers salinity values particularly. Consequently, salinity was significantly lower and turbidity levels were significantly higher compared to the Swartkops Estuary. The dominance of *R. holubi* within the Sundays Estuary is therefore not surprising as this species is tolerant of a wide salinity (0.7 – 70) and turbidity range (Blaber, 1973). In the present study, the larvae and juveniles in the Sundays Estuary were dominated by marine and estuarine benthic species (*R. holubi* and *C. gilchristi*) and a marine, freshwater and estuarine pelagic-neritic species (*G. aestuaria*). In the Swartkops Estuary marine and estuarine species (*D. capensis* and *P. olivaceus*) and a marine and estuarine benthic species (*C. nudiceps*) dominated catches. Species composition of the dominant larvae and juveniles collected in the two estuaries had a high degree of overlap with similar studies undertaken in the early 1980s in the Sundays where *G. aestuaria*, *R. holubi* and *Liza dumerili* dominated (Beckley, 1984) and in the Swartkops where *R. holubi*, *Liza richardsonii* and *Etrumeus whiteheadi* dominated (Beckley, 1985). The data are also consistent with other estuaries from the same region with Clupeidae, predominantly represented by *G. aestuaria*, Gobiidae and Sparidae dominating (Strydom *et al.*, 2003; Strydom and Wooldridge, 2005). In northern hemisphere temperate estuaries, dominant fish families include the Atherinopsidae, Blenniidae, Clupeidae, Engraulidae, Gobiidae and Sciaenidae (Martino and Able, 2003; Able *et al.*, 2006; Primo *et al.*, 2012), and in southern hemisphere temperate estuaries dominant fish families include the Blenniidae, Callionymidae, Clupeidae, Engraulidae, Gobiidae and Nemipteridae (Gaughan *et al.*, 1990; Neira and Potter, 1992; Neira *et al.*, 1992; Neira and Potter, 1994).

Larval and juvenile fish abundance relative to the tidal and diel cycle showed a clear preference with greater densities observed during the ebb tide at night and the flood tide linked to sunrise in the Sundays Estuary and in the Swartkops Estuary, larval abundances peaked during both flood tides. Within a permanently open (Strydom and Wooldridge, 2005) and an estuarine lake system (Whitfield, 1989c) in the warm-temperate region of South Africa, in the same biogeographical region as the two estuaries in the present study, the larval fish densities peaked after the onset of darkness, predominantly associated with the nocturnal ebb tide (Strydom and Wooldridge, 2005). Similar observations in estuaries within the Northern (Primo *et al.*, 2012) and Southern (Roper, 1986; Neira and Potter, 1994) hemispheres indicate increased larval density during ebb night time, however, greatest abundance of larvae were caught during rising tides at night in the Newport River Estuary in North Carolina, USA (Forward *et al.*, 1999). This increase in density of larvae and early juveniles indicating extensive movement into and out of estuarine systems during the night could serve as a predator-avoidance strategy (Power, 1997). Furthermore, this extensive movement could be as a result of the nocturnal vertical migration of zooplankton into the surface layers of estuaries which serve as a major food source for larval and juvenile fishes (Whitfield, 1985). Forward *et al.* (1999) suggested light could inhibit swimming during the day to reduce exposure to visual predators. Older larvae of Atlantic menhaden (Clupeidae) larvae have been observed to swim deeper in a column of estuarine water under high light intensities (Forward *et al.*, 1996).

Recruitment of larvae and early juveniles against the outgoing ebb tide was observed in the present study. In both estuaries, amongst the dominant species, *C. gilchristi* (mean lengths of 18 - 36 mm) and *P. knysnaensis* (mean length 22 – 33 mm) were observed in the fyke nets facing the opposing direction of the outgoing ebb tide. In the Sundays Estuary this pattern was observed for *H. capensis*. *Heteromycteris capensis* spawns in the nearshore marine environment (Brownell, 1979) with postflexion larvae observed frequently in surf zones (Whitfield, 1989b; Strydom, 2003; Watt-Pringle and Strydom, 2003; Strydom and d'Hotman, 2005). Larvae and early juveniles recruit into estuaries at lengths between 5 – 15 mm BL (Whitfield, 1998). Mean lengths of ~10 mm BL were observed in the present study, corresponding to the size range of settlement for this species (Whitfield, 1998; Heemstra and Heemstra, 2004). Although not dominant within each estuarine system, fish species important from the recreational fishery in South Africa including *Argyrosomus inodorus*, *Diplodus cervinus hottentotus*, *Lithognathus lithognathus*, *Pomadasys commersonnii* and *P. olivaceus* were observed in the fyke nets facing the opposing direction to the outgoing ebb tide, indicating active recruitment against the ebb tide into the estuarine nursery areas.

Argyrosomus inodorus, *D. cervinus hottentotus*, *P. olivaceus* are categorized as a marine species which occur in the mouth region and lower reaches of estuaries in small numbers but are not dependent on these systems (Whitfield, 1998). *Argyrosomus inodorus* and *D. cervinus hottentotus* spawn in the inshore marine environment while *P. olivaceus* spawns offshore with juveniles common in the lower reaches of estuaries. Larvae as small as ~6 mm in *A. inodorus*, and ~8 mm in *D. cervinus hottentotus,* were observed in these fyke nets facing the opposing direction of the outgoing ebb tide. Larger early juveniles of *D. cervinus hottentotus* ranging between 27 – 45 mm were also observed in the fyke nets facing the opposing direction of the outgoing ebb tide. Lengths of *P. olivaceus* ranging between 34 – 78 mm were observed in the fyke nets facing the opposing direction to the outgoing ebb tide indicating that early juveniles are actively recruiting against the ebb tide into the estuary. *Lithognathus lithognathus* and *P. commersonnii* are marine species which usually breed at sea with the juveniles dependent on estuaries as nursery areas (Whitfield, 1998). *Lithognathus lithognathus* spawns in the marine environment with larval development occurring in the sea and juveniles <50 mm known to enter estuaries (Bennett, 1993). In the present study early juveniles of *L. lithognathus* (~45 mm) and *P. commersonnii* (~50 mm) were observed in the fyke nets facing the opposing direction of the ebb tide.

Coupled with these findings, recruitment on the flood tide was also evident with larvae and early juveniles observed in the fyke nets facing the incoming flood tide. Small flexion and postflexion larvae of *Argyrosomus japonicus,* also a very important recreational fishery species in South Africa, ranging in length between 6 – 19 mm were observed in the fyke nets facing the incoming flood tide. *Argyrosomus japonicus* spawns offshore with small juveniles (30 – 150 mm) restricted to estuaries (Heemstra and Heemstra, 2004). The haemulids *P. olivaceus* and *P. commersonnii* spawn in the marine environment with juveniles of *P. olivaceus* common in the lower reaches of estuaries and juveniles of *P. commersonnii* between 20 – 30 mm BL recruiting into estuaries (Heemstra and Heemstra, 2004). A range in lengths from 11 – 97 mm in *P. olivaceus* and 8 – 55 mm in *P. commersonnii,* were observed during the flood tide in nets facing the incoming tide. It appears that much younger flexion and postflexion larvae of *A. japonicus* and postflexion larvae of *P. commersonnii* are recruiting into estuaries than previously recorded. Most Mugilidae species rely mainly on estuarine nursery areas with spawning occurring at sea and juveniles recruiting at a length of between 20 – 50 mm into estuaries (Wallace *et al.*, 1984). The high abundances of small (9 –

30 mm) mugilid larvae during the flood tide indicate the recruitment of these individuals into the estuarine nursery area.

The dominance of postflexion and early juvenile stages of fishes from both estuaries, corresponds to a size range that would cover settlement in many local species (Heemstra and Heemstra, 2004). The predominance of older larvae and early juveniles within the slower-flowing marginal waters of both estuaries in the present study indicate that postflexion larvae, with definitive fin elements, and early juveniles, both of which have active swimming abilities, are able to select the more favourable margin current regimes for movement within the estuary as observed in previous studies (Beckley, 1985; Whitfield, 1989c; Strydom and Wooldridge, 2005). Results from the present study confirm with results from several studies that larval and juvenile fish assemblages peak during nocturnal ebb tides. However, higher abundances for most dominant species of larvae and juveniles in fyke nets facing the opposing direction of the outgoing ebb tide, indicate that these fish species are not necessarily lost from estuarine systems during the ebb tide, but are actively swimming against the ebb tide in the shallower, slower-flowing marginal areas facilitating recruitment against ebb flow. It must be emphasized that the results presented only reflect littoral fish movements to and from the study estuaries and channel movements of preflexion, flexion and postflexion larvae and early juveniles were not recorded.

6. ACKNOWLEDGEMENTS

This work is based on financial support from the National Research Foundation (NRF), South Africa. Gratitude is expressed to the NRF. Any opinions, findings and conclusions expressed in this material are those of the authors and therefore the NRF does not accept any liability in regards thereto. Fieldworkers are thanked for their valuable assistance. Prof. Tris Wooldridge and Dr Ané Oosthuizen are thanked for commenting on a draft copy of this chapter. Mr Tim Vink is thanked for generation of the map in this chapter.

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CHAPTER 6

PREDICTING SPAWNING LOCATIONS AND THE SPATIAL EXTENT OF POST HATCH AREAS FOR SEVERAL IMPORTANT FISH SPECIES IN ALGOA BAY, SOUTH AFRICA

1. ABSTRACT

A novel approach using the maximum entropy (MaxEnt) machine-learning algorithm was used to model newly hatched larval fish areas in Algoa Bay, temperate South Africa. Coupled with retrogressive plots, potential fish spawning areas were also determined. Temperature, turbidity, pH and wind speed were important predictor variables with contributions of each predictor varying among species. MaxEnt provided ‘very good’ (AUC > 0.9) model predictions according to the classification of Maggini *et al.* (2006) for all species. The results demonstrated that the early developmental stages of fishes in the shallow coastal habitats of Algoa Bay exhibit species specific spatial variability. Results from retrogressive plots indicate that larvae occurring at any location within Algoa Bay, could be hatched and transported extensively within the Bay before reaching a suitable size to swim independently of currents. The spawning of several important fishery species namely the Cape anchovy *Engraulis encrasicolus* (Engraulidae), sardine *Sardinops sagax* (Clupeidae), and silver kob *Argyrosomus inodorus* (Sciaenidae), is occurring locally in Algoa Bay. Eggs and larvae typically remained in close proximity of their spawning origin. Newly hatched larval fish distributions, although variable amongst all the study species, correspond to known adult distributions and potential reef habitats in the study region.

2. INTRODUCTION

The pelagic larval stage plays a critical role in structuring marine fish populations (Werner *et al.*, 2007). Dispersal during the pelagic larval stage is the primary determinant of the geographic size of populations and the connectivity amongst local populations (Roberts, 1997; Cowen, 2002; Kinlan and Gaines, 2003; Sale, 2004). Dispersal of eggs and preflexion larvae is largely passive because the very early stages of fish development have limited behavioural and swimming capabilities (Mora and Sale, 2002). Once larvae have undergone flexion, the prediction of dispersal is impeded by larval fish behaviour, as larvae have sensory and swimming abilities that strongly influence their net dispersal trajectories (Leis, 1991a; Stobutzki and Bellwood, 1997; Stobutzki, 2001; Leis, 2006; Pattrick and Strydom, 2009). Ocean currents therefore play a pivotal role in the distribution of eggs and newly hatched larvae (Leis and Goldman, 1983). Spawning areas can be identified from knowledge of the regional hydrodynamic processes coupled with ichthyoplankton sampling. Eggs and newly hatched larvae can be tracked back to their original spawning location using local oceanographic data. The small size of eggs and preflexion larvae in such a vast and dynamic ocean environment, renders the quantification of dispersal notoriously difficult, however, predicting dispersion is a major goal of population ecology (Roughgarden *et al.*, 1988).

Ultimately, this information is important by providing data pertaining to the location of spawning areas which is important for conservation. Furthermore, knowledge of the distribution of species along environmental gradients is important for understanding population distributions and dynamics. Today, particularly as habitat loss is a major threat to coastal ecosystems, which are important areas in the early development of fishes, the need to map species distributions for nature conservation is increasing dramatically. However, its applicability for fish reproduction habitats is relatively unknown.

Algoa Bay is situated centrally within the warm-temperate Agulhas bioregion along the east coast of South Africa and is the largest log-spiral bay along this section of coastline. Algoa Bay has several biophysical characteristics which contribute to its ecological importance in the Agulhas bioregion. The immense conservation value of Algoa Bay is recognized in the proposal by scientists and managers to expand the existing terrestrial Addo Elephant National Park (AENP), seawards and to develop a large marine protected area (MPA) adjacent to the AENP in Algoa Bay. Several important commercial and recreational fishery species occur in Algoa Bay. Amongst these, and including species selected for the current study, are dusky kob, *Argyrosomus japonicus* (Sciaenidae), silver kob, *A. inodorus* (Sciaenidae), blacktail, *Diplodus capensis* (Sparidae), Cape anchovy, *Engraulis encrasicolus* (Engraulidae), sardine, *Sardinops sagax* (Clupeidae) and Cape sole, *Heteromycteris capensis* (Soleidae). These selected study species were the only species that provided sufficient data to perform distribution analyses at such a fine resolution. As adults, these species are commonly encountered in Algoa Bay (Smale and Buxton, 1985; Chalmers, 2011). The two *Argyrosomus* species are important target species for the recreational and commercial ski-boat fisheries (Smale, 1985). Both species spawn pelagic eggs with juveniles of *A. inodorus* recruiting into shallow bays (Griffiths, 1997) and *A. japonicus* into estuaries (Griffiths, 1996). The Sparidae fish family are important from a recreational linefish fishery perspective in South Africa, with all species, bar *Spondyliosoma emarginatum*, spawning pelagic eggs (Mann, 2000). *Diplodus capensis* serves as a representative of this fish family. Both *E. encrasicolus* and *S. sagax* are pelagic species. Not only are these two species important commercial fishery species, but both occupy crucial positions in the oceans' ecosystems serving as a food source for the upper marine trophic levels. Although *H. capensis* is a benthic fish species, with adults occurring in the marine and estuarine environment, eggs and larvae are pelagic.

In the present study, a broad-scale, larval fish survey in the shallow coastal waters of Algoa Bay was conducted. Results of a mixed-method, multi-habitat, two-year survey of the early developmental stages of important fish species from a fishery and ecological perspective are presented in a spatial model. The aim was to investigate the early life history habitat distributions of certain important ecological and economically important coastal fish species in Algoa Bay, by relating newly hatched larval fish distributions to environmental characteristics.

3. MATERIALS AND METHODS

3.1 Study site

Algoa Bay (Figure 6.1) is the easternmost and largest of several log-spiral shaped bays on the temperate south east coast of South Africa (Goschen and Schumann, 2011). Larval fish samples were collected at 23 stations of various habitat types, in the coastal region of Algoa Bay. Ten surf zone stations (A – J) between Cape Recife in the far western sector of the Bay (33°53′46″S; 25°42′08″E) and Woody Cape in the far eastern sector of the Bay (33°52′07″S; 26°17′29″E), six island associated reef stations (K – P), at Bird (33°50′16.80″S; 26°17′9.60″E) and St Croix (33°48′02.6″S; 25°46′00.1″E) islands, a sand habitat (Q) located on the 20 m depth contour (33°43′5.90″S; 26°5′9.60″E) between the Sundays Estuary and Woody Cape, and six nearshore (30 m) stations (R – W) between the Port of Port Elizabeth (33°53′46.2″S; 25°42′08.2″E) and Bird Island (33°52′7.28″S; 26°17′29.26″E) were selected.

3.2 Field sampling and larval fish identification

The present study relied on data obtained from multiple gear types over a two-year study period to elucidate specific locations, in the coastal environment of Algoa Bay, important for larval fish development namely newly hatched larval fish areas. Larvae at the preflexion stage of development were considered as newly hatched. *Argyrosomus japonicus*, *A. inodorus*, *Diplodus capensis*, *Engraulis encrasicolus*, *Sardinops sagax* and *Heteromycteris capensis* are considered as either important recreational or commercial fishes in southern Africa and thus were selected for predictive spatial modelling.

Surf zone sampling (Chapter 4) comprised seasonal surveys where larval fishes were collected by sampling two consecutive months per season during the diurnal spring low tide (December and January are summer months, March and April are autumn months, June and July are winter months and September and October are spring months). In total, 16 sampling trips took place between December 2010 and October 2012. Samples were collected over two sequential days, from the east to west in the windward and leeward sector of the Bay respectively. Seining typically occurred between the two hours before and after the spring low tide. Samples were collected using a modified beach seine net (mesh aperture 500 µm) operated by two people (Strydom, 2003b) pulled parallel to shore in depths <1.5 m for a distance of 25 m for each replicate with three replicates collected at each of the ten sampling sites. The net has a width of 4.5 m and a height of 1.5 m. A tapering cone has been fitted at the centre of the net, and the catch is funnelled into this cone during sampling to the cod-end. Larval fishes caught per haul are expressed as CPUE, referring to the number of larval fishes caught in a single 25 m seine haul. Each site was sampled by means of three replicate sine hauls. A total of 480 samples were collected.

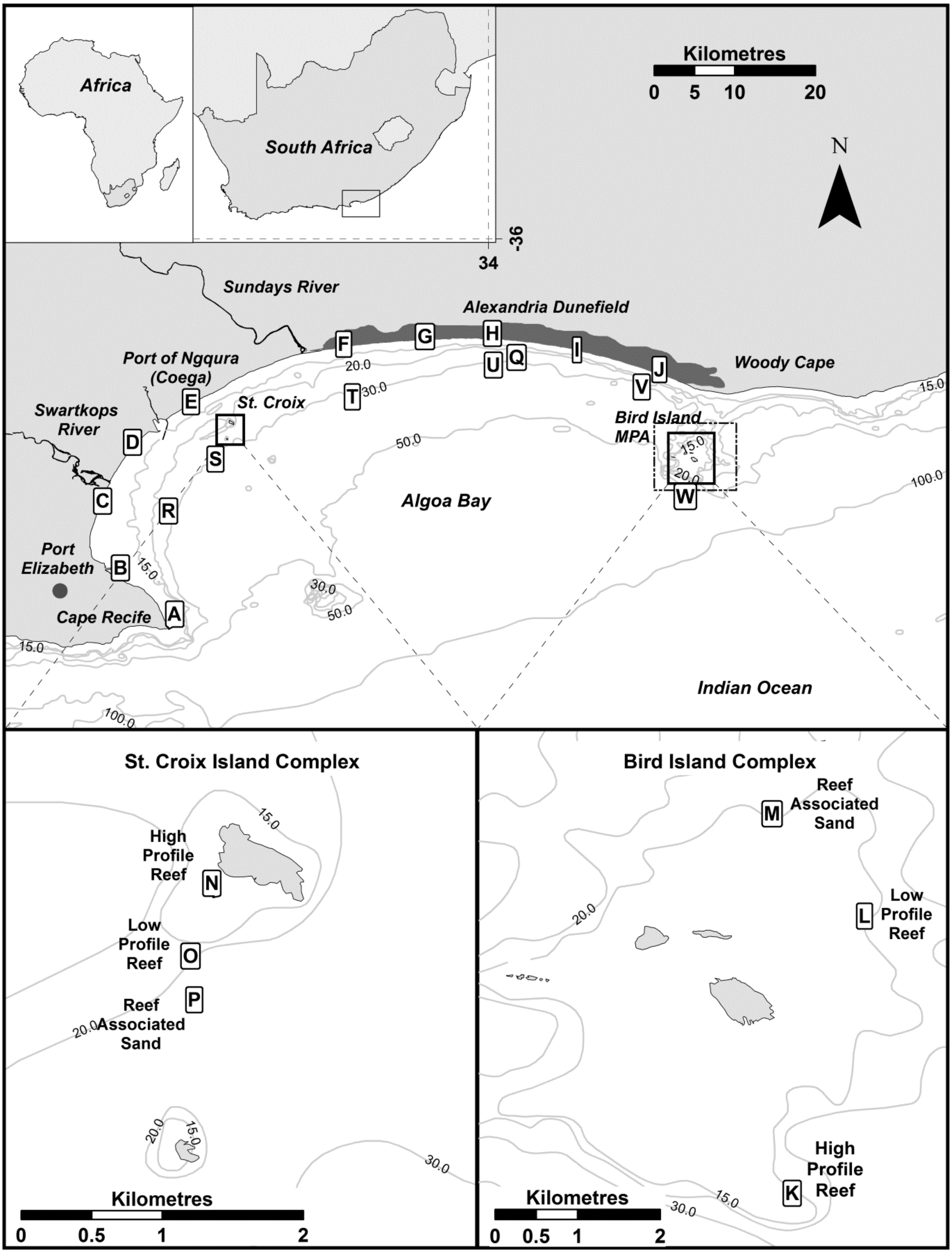

FIGURE 6.1 The geographic position of Algoa Bay, showing the location of the 23 stations sampled for larval fish (August 2010 – October 2012)

Sampling at subtidal reef and sand habitats (Chapter 3) was comprised of summer and winter collections at night, targeting known spawning seasons of coastal and pelagic fishes. In total, 12 sampling trips took place between June 2010 and February 2012 with 84 samples collected over the two-year study period. The sampling in the nearshore (Chapter 2) occurred monthly during the day. Due to arduous sea conditions a total of 20 sampling trips took place between August 2010 and July 2013 with 120 samples collected over the two-year study period. Ski-boat based plankton ring net tows were conducted at all stations. In addition, one light trap, based on a modification of the design of Stobutzki and Bellwood (1997), was deployed on a fixed mooring in the water column at each subtidal reef and sand sampling station. The plankton ring net consisted of a 12 mm thick stainless steel ring fitted with a 4 m long plankton net with a PVC cod-end. A Kahlsico flowmeter was suspended from the frame at the opening of the net and water flow passing through the opening of the net was measured. The net diameter was 750 mm and the mesh aperture was 500 µm. The ring net was pulled using a stepped oblique tow at a speed of ~2 knots. Three water levels were each sampled for 2 mins and including hauling each tow lasted ~8 mins.

All samples were fixed on site with 10 % formalin in seawater. Samples were sorted and analysed in the laboratory where larval fish were removed and identified to the lowest possible taxon (Beckley, 1990; Smith and Heemstra, 1995; Neira *et al.*, 1998; Leis and Carson-Ewart, 2000). Larvae were measured to the nearest 0.1 mm body length, which represents notochord length in preflexion and flexion larvae and standard length in postflexion larvae and early juveniles. Temperature (°C), salinity, turbidity (NTU) and pH was measured at each site using a YSI 6600 multi-parameter meter. Wind speed (m/s) data were obtained at hourly intervals from three South African Weather Service (SAWS) stations located on Bird Island, 3 m above sea level (33°50′16.80″S; 26°17′9.60″E), at Port Elizabeth Airport, 63 m above sea level (33°59′2.40″S; 25°36′36.00″E), and at the Port of Ngqura/Coega, 46 m above sea level (33°59′4.67″S; 25°40′4.80″E) and averaged daily.

3.3 Data analyses

3.3.1 Egg and preflexion larval fish dispersal

The potential transport of fish eggs and preflexion larvae, providing total progressive displacement, was calculated by combining the east-west and north-south current speed and direction components obtained using three 1 200 kHz Acoustic Doppler Current Profilers

(ADCPs) (RD Instruments of San Diego, California) moored in Algoa Bay. Oceanographic data from two of these ADCPs, moored in approximately 30 m of water in the south-east of Bird Island (33°52′7.43″S; 26°18′10.15″E) and south-east of Cape Recife (34°1′44.00″S; 25°43′14.23″E), were obtained from the continuous monitoring of the Elwandle Node of the South African Environmental Observation Network (SAEON). These ADCPs were configured to sample the water column in half metre bins at ten-minute intervals with data spanning the period from December 2008 to present with intermittent gaps when the ADCP was removed for servicing. A third ADCP was deployed on the 20 m depth contour (33°43′32.61″S; 26°7′54.53″E) adjacent to the Alexandria dune field, over a period of one year between May 2006 and May 2007. This ADCP was configured to sample the water column in one metre depth intervals every 30 mins using an ensemble size of 120 pings, with one ping used per second. Data from these instruments were used to construct retrogressive plots. These are similar in principle to reverse particle tracking, whereby particles are tracked backward in time, such that their original location within the ocean environment may be determined. Pelagic larval duration (PLD) is frequently used in modelling to estimate dispersal (Shanks *et al.*, 2003). However, PLD is taxon specific and therefore, dispersal distances can likewise be taxon specific. To acquire estimates of PLD, mean lengths of preflexion larvae of each species were used to estimate age of larvae (Brownell, 1979; Connell, 2007). To obtain estimates of dispersal, the total time spent within the pelagic water column was calculated using the duration of egg incubation and age for each species. Furthermore, PLD is influenced by environmental conditions such as temperature and consequently season plays an important role in determining dispersal distances (Cowen and Sponaugle, 2009). To establish likely spawning period for each fish species, larval fish abundances were calculated per month. Larval fish behaviour, particularly regarding depth selection, differs among species (Leis *et al.*, 2006). Results from *in situ* vertical distribution behaviour of pelagic larvae of marine demersal fishes indicates that larvae were found to move deeper with increasing size, with the smallest larvae (5 – 7 mm) spending the majority of their time in the 2.6 – 5.0 metre depth interval (Leis *et al.*, 2006). Retrogressive plots were therefore modelled according to these depths for individual species.

3.3.2 Distribution modelling

Determining the spatial extent of spawning areas of larval fishes is central to the understanding of population dynamics. Due to the season-driven reproductive biology of these fish species, it would have been ideal to model newly hatched larval fish areas in both space and time. However, with insufficient data to perform the following analyses or other alternatives at such a fine resolution, only spatial patterns were modelled. To this end, data for each of the environmental predictor variables (sea temperature, salinity, turbidity, pH and wind speed) were pooled and represented as the mean, minimum, maximum and range across the sampling period, per station. Data were imported into ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA, USA), interpolating their values across the study area using the *spline with barriers* function in Spatial Analyst. The study area was delineated as a polygon extending along the coast from Cape Recife to Woody Cape, with the seaward boundary approximately following an 8 km buffer around the sampling sites/stations farthest offshore (Figure 6.2). Data were extracted from these interpolated raster layers in a 10" x 10" grid, using the Spatial Analyst function *extract multi values to points*, and served as the background data in the model. Data were subset out of the background dataset based on the respective presence localities of each newly hatched larval fish area per species. This was based on a buffer of 400 m around each station where a newly hatched larval fish area was determined, which represent the total area sampled (6 minute towing at a speed of 2 knots). These data serve as the "species" data in the model.

Species distribution modelling (SDM) was then conducted using the maximum entropy statistical modelling technique, implemented using the software MaxEnt 3.3.3k. (Phillips *et al.*, 2004; Phillips *et al.*, 2006; Phillips and Dudík, 2008; Elith *et al.*, 2011). This software/approach was selected for use in the present study for two reasons. Firstly, MaxEnt is currently one of the most commonly used and popular SDM methods due to its robustness with regards to small samples sizes (Hernandez *et al.*, 2006) and complex scenarios (Elith *et al.*, 2006). Secondly, the response data included information where species absences were uncertain or lacking, as fish larvae are dynamic in both space and time and not observing a species in a particular session would not necessarily mean they are absent, and therefore a presence-only technique is preferred (Elith *et al.*, 2006). MaxEnt is a machine-learning method based on presence-only information, with the principle behind it based on an approximation of an unknown probability distribution, drawn from the environmental background layers. The unknown probability distribution is approximated using maximum entropy, given the constraints that the expected value of each environmental variable equals its empirical average from the presence data (Phillips *et al.*, 2006; Phillips and Dudík, 2008). For the first model run, data were randomly partitioned into a 70 % training set and a 30 %

testing set. The models were evaluated from receiver operating characteristic (ROC) plots which provide an area under the curve (AUC) value ranging between 0.5 and 1. Following the classification of Maggini *et al.* (2006), values below 0.7 are regarded as poor, 0.7 – 0.9 as reasonable, and above 0.9 as very good. ROC plots have recently become a popular approach for evaluating species distribution model performance (Manel *et al.*, 2001; Francis *et al.*, 2005; Maggini *et al.*, 2006; Sundblad *et al.*, 2009). The AUC statistic is known as a robust measure of model performance (Fielding and Bell, 1997; Manel *et al.*, 2001; McPherson *et al.*, 2004). Once the performance of the model was evaluated for accuracy, they were run a second time using all of the data, to obtain the most robust output. The data were entered into ArcGIS 10 and interpolated as continuous raster surfaces using the *spline with barriers* function in Spatial Analyst.

4. RESULTS

4.1 Egg and preflexion larval fish dispersal

Abundance of preflexion stage *Argyrosomus japonicus* and *A. inodorus* larvae were highest during spring in September (Figure 6.3). The abundance of preflexion *Diplodus capensis* peaked during the summer month of January. The anchovy, *Engraulis encrasicolus* peaked in abundance during November. The sardine, *Sardinops sagax* and the Cape sole, *Heteromycteris capensis* both showed peak larval abundances during late summer in February.

Larvae (Table 6.1) were very small ranging in mean length from 2.7 to 3.9 mm and in age from 2 to 13 days (Brownell, 1979; Connell, 2007). With pelagic egg incubation lasting from 24 to 40 hours, the total PLD obtained for the model species ranged from 5 to 14 days.

TABLE 6.1 Study species for analysis including month during dominant spawning, egg incubation including temperature, mean body length (range), age at mean body length and the total dispersal duration in Algoa Bay

Species	Spawning month	Egg incubation (hours)	Temperature at incubation (°C)	Mean (range) length (mm)	Age for mean length (days)	Total dispersal duration (days)
Argyrosomus inodorus	September	25	17 – 22	3.9 (2.0 – 5.8)	13	14
Argyrosomus japonicus	September	30	17 – 22	3.2 (1.7 – 5.5)	5	6
Diplodus capensis	January	40	15 – 24	3.7 (2.2 – 4.9)	5	7
Engraulis encrasicolus	November	30	15 – 19	3.6 (1.5 – 8.9)	4	5
Heteromycteris capensis	February	24	15 - 24	2.4 (1.2 – 6.1)	7	8
Sardinops sagax	February	40	15 – 21	3.9 (3.0 – 9.9)	2	5

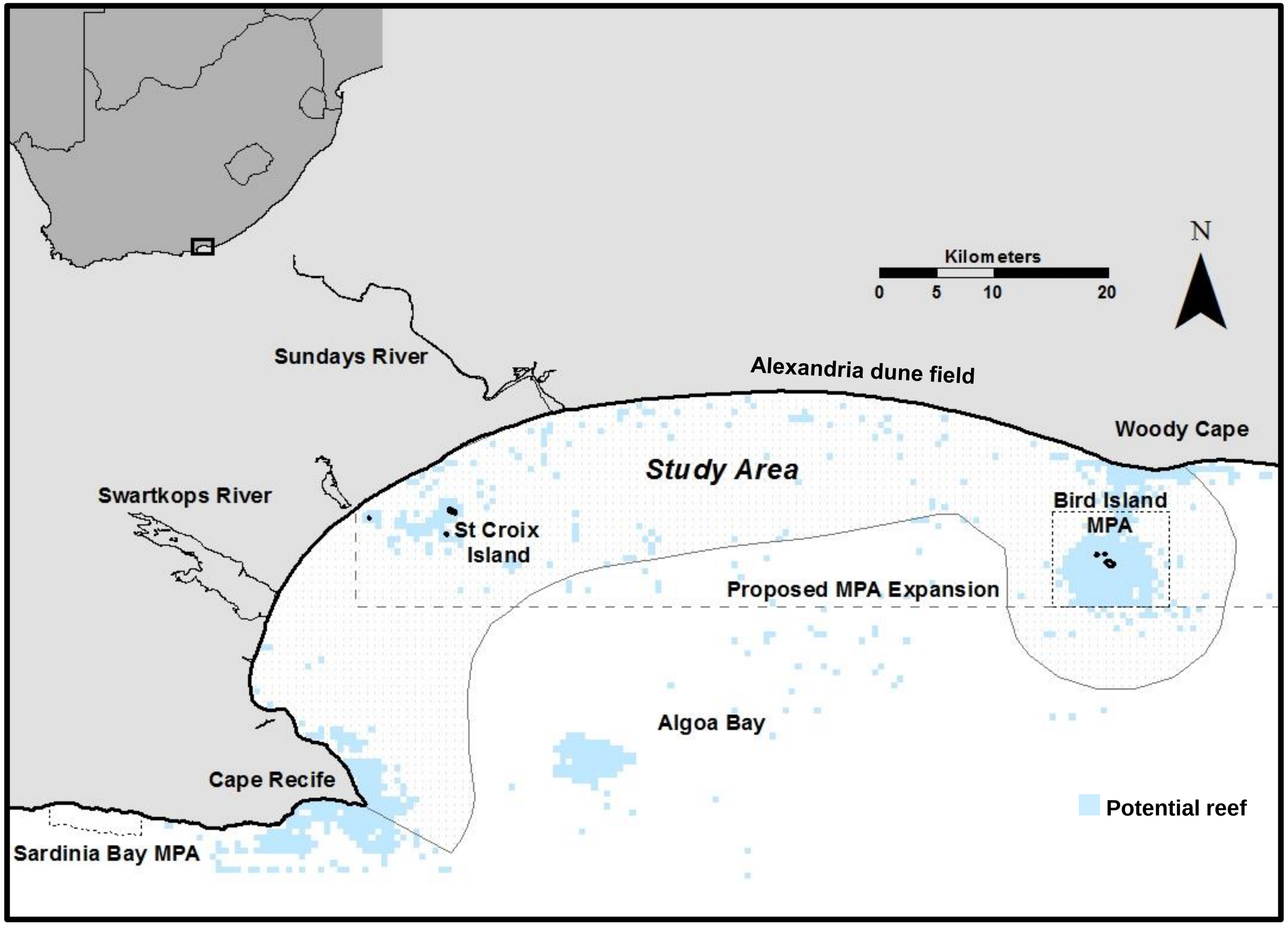

FIGURE 6.2 The study area defined for the distribution modelling in the coastal nearshore of Algoa Bay and the presence of potential reef areas in the Bay obtained from Chalmers (2012)

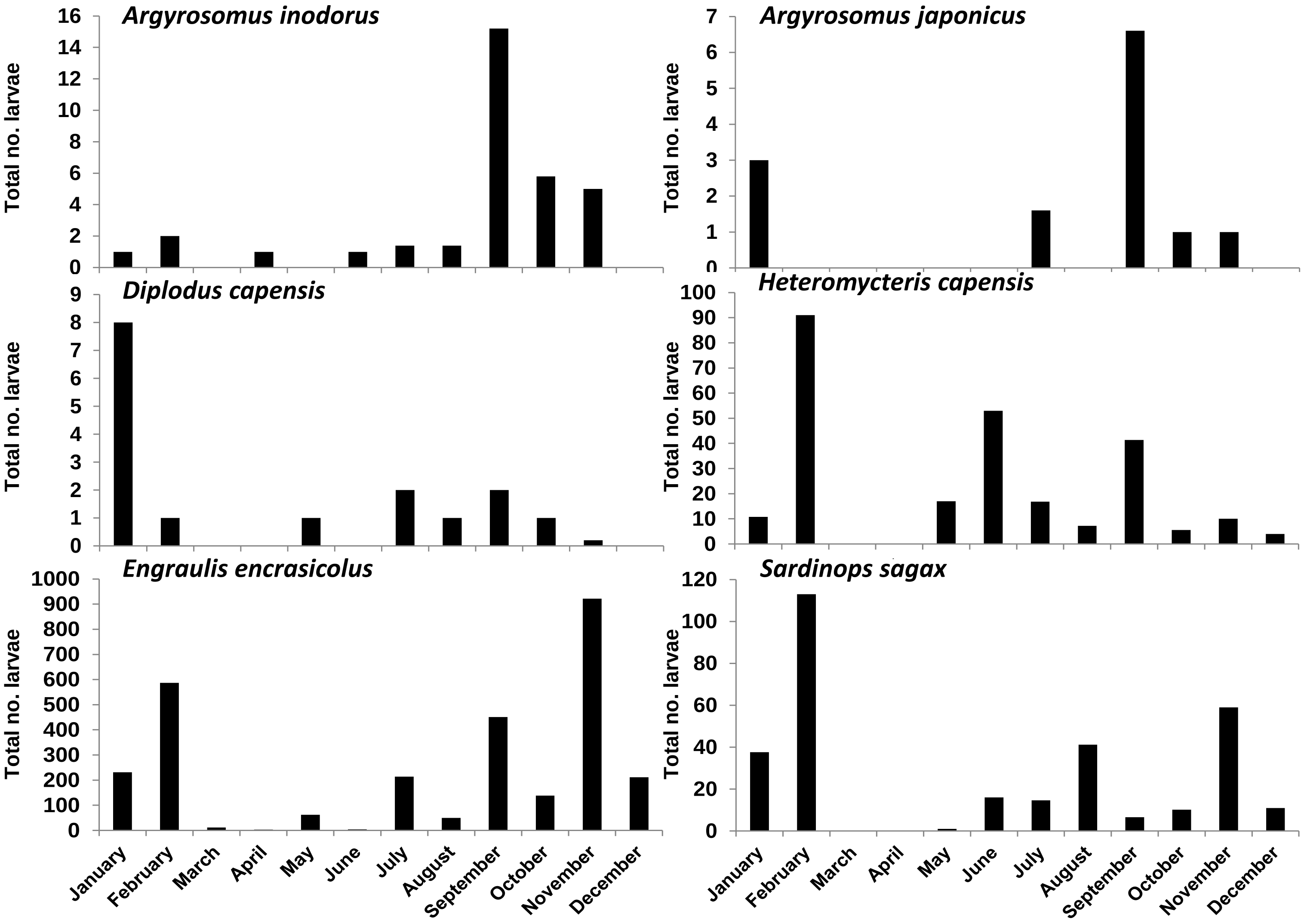

FIGURE 6.3 Abundance per month (August 2010 – October 2012) of study species selected for modelling within the coastal nearshore of Algoa Bay

The results (Appendix 1) from the retrogressive plots not only indicate various patterns of dispersal between locations (Bird Island, Cape Recife, Alexandria dune field), but also between years sampled (2006 – 2013). Generally, greatest dispersal distances were observed at the deeper depths (~5 m) as opposed to the shallower depths near the surface of the water column (~2 m).

According to the retrogressive plots, the origin of spawning for *A. inodorus* and *E. encrasicolus* is occurring predominantly in Algoa Bay. The origin of spawning for *A. japonicus* however, indicates that spawning is occurring outside of the Bay approximately 40 – 100 km north east of Algoa Bay. Although spawning of *D. capensis, H. capensis* and *S. sagax* is occurring in the Bay, isolated spawning locations south and north east of the Bay are also observed.

4.2 Spatial distribution modelling of post hatch areas

Distribution models of newly hatched larval fish areas were created for six fish species. Overall, model performance was very good, with high AUC values (mostly over 0.9) for ROC curves constructed from both the training and testing datasets (Table 6.2).

TABLE 6.2 Statistics evaluating the performance of the species distribution model, based on N presence records per species. AUC_{TRAIN} and AUC_{TEST} = area under the ROC curve of the model created using the training and testing data respectively

Species	N	AUC_{TRAIN}	AUC_{TEST}
Argyrosomus inodorus	35	0.959	0.916
Argyrosomus japonicus	26	0.984	0.986
Diplodus capensis	34	0.972	0.952
Engraulis encrasicolus	64	0.931	0.861
Heteromycteris capensis	39	0.956	0.895
Sardinops sagax	37	0.951	0.847

The strongest environmental predictor providing the greatest contribution to the models varied amongst the study species (Table 6.3). Sea temperature was the strongest predictor for newly hatched *A. inodorus* and *D. capensis*. Specifically, minimum temperature contributed the greatest towards the model in *A. inodorus* (27.2 %) and the variation in temperature contributed the greatest towards the model in *D. capensis* (27.0 %). The variation in turbidity was the strongest environmental predictor for newly hatched *H. capensis* (25.4 %) and *S. sagax* (33.7 %) with minimum turbidity or clearer waters contributing the greatest towards the model in *A. japonicus* (21.9 %). For newly hatched *E. encrasicolus* larvae (30.4 %), variations in pH contributed the greatest towards the model.

The two kob species, *A. inodorus* (Figure 6.4) and *A. japonicus* (Figure 6.5) had different distributions in their newly hatched locations. *Argyrosomus japonicus* was somewhat confined to the western, leeward sector of the Bay in close association with St Croix island, and offshore locations associated with the Alexander dune field in the eastern sector of the Bay. Although *Argyrosomus inodorus* had a close association with St Croix Island in the western sector of the Bay, probability of occurrence of *A. inodorus* was high at Bird Island in the far eastern sector of the Bay. Furthermore, *A. inodorus* occurred at closer inshore locations associated with the Alexander dune field. Newly hatched *D. capensis* (Figure 6.6), *H. capensis* (Figure 6.7) and *E. encrasicolus* (Figure 6.8) larvae were distributed throughout Algoa Bay. *Sardinops sagax* (Figure 6.9) newly hatched larvae had close associations with the islands and the nearshore of the Alexandria dune field.

TABLE 6.3 The relative variable importance in modelling species distributions, quantified by the estimated percentage contribution of each variable to the training models, per species. The most important predictor per species is highlighted in bold

	Argyrosomus inodorus	*Argyrosomus japonicus*	*Diplodus capensis*	*Engraulis encrasicolus*	*Heteromycteris capensis*	*Sardinops sagax*
Temp (max)	6.0	3.1	1.7	1.3	2.8	1.8
Temp (min)	**27.2**	6.2	10.0	11.2	13.9	8.2
Temp (mean)	0	0.3	6.3	3.5	4.8	4.2
Temp (range)	0	0.5	**27.0**	1.1	2.8	0
Turbidity (max)	0.7	0	0	0	0	0.2
Turbidity (min)	8.1	**21.9**	5.1	2.4	3.4	5.3
Turbidity (mean)	14.3	7.2	23.4	14.4	**25.4**	**33.7**
Turbidity (range)	2.8	5.1	0.3	0	0.4	1.6
Salinity (max)	3.5	0.1	7.6	2.6	1.7	0.3
Salinity (min)	0.6	19.2	5.3	1.0	0.6	4.0
Salinity (mean)	1.1	4.1	0.2	5.6	0.2	0.3
Salinity (range)	4.8	7.7	4.9	1.7	7.9	9.5
pH (max)	1.2	0	0	5.0	3.3	0
pH (min)	1.3	5.9	3.2	0.6	1.4	0.2
pH (mean)	0	0	1.1	**30.4**	1.1	3.6
pH (range)	2.7	0.9	0.2	0.1	7.0	3.7
Wind speed (max)	0.1	0.3	0	0.5	2.1	3.9
Wind speed (min)	19.1	15.9	2.5	7.9	14.3	9.4
Wind speed (mean)	6.0	0	1.2	9.2	6.8	6.9
Wind speed (range)	0	1.5	0	1.5	0.1	3.3

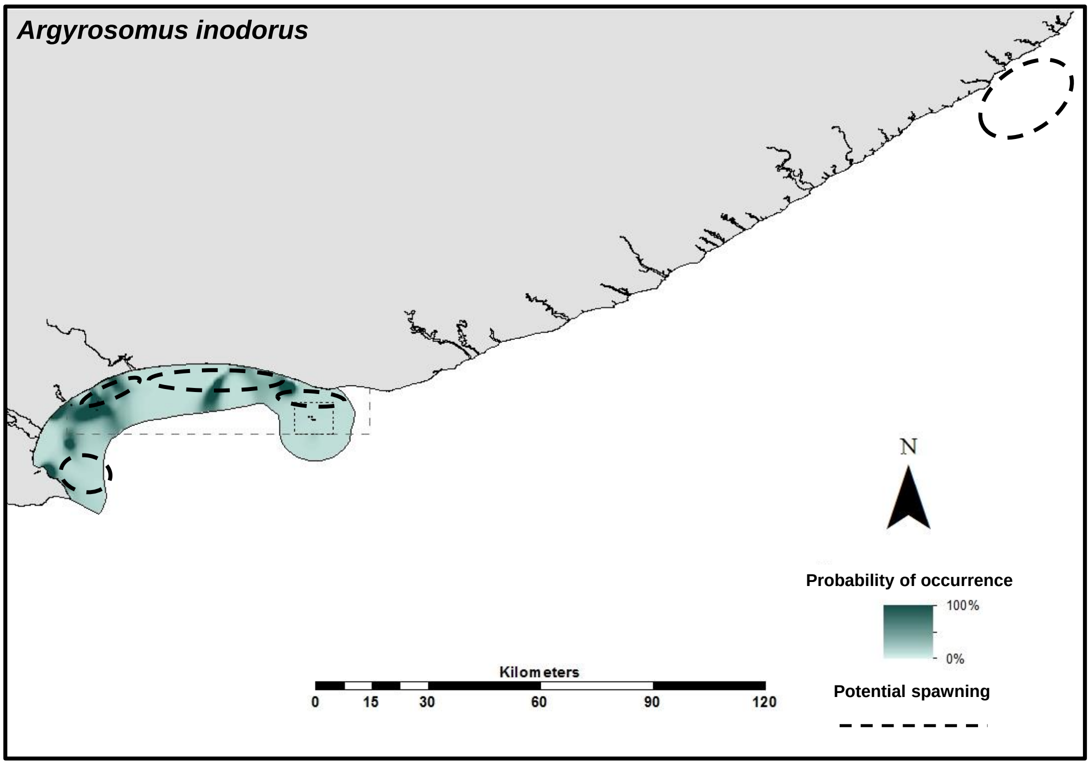

FIGURE 6.4 Distribution models showing probability of occurrence of newly hatched *Argyrosomus inodorus* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

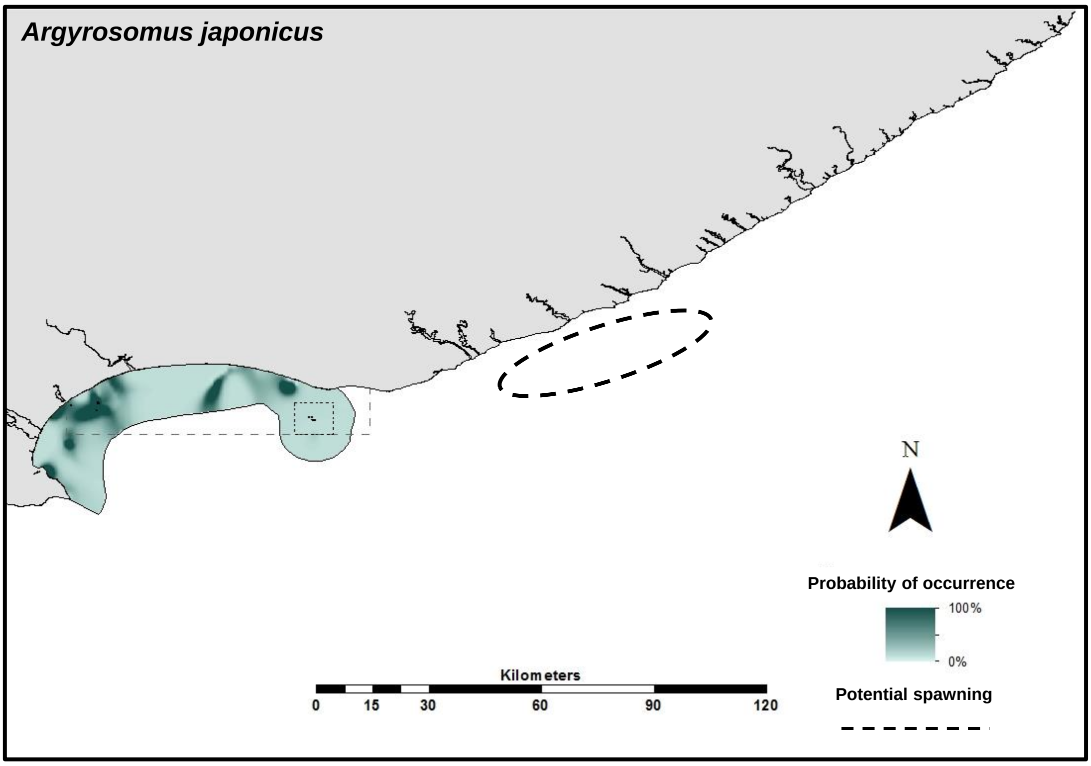

FIGURE 6.5 Distribution models showing probability of occurrence of newly hatched *Argyrosomus japonicus* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

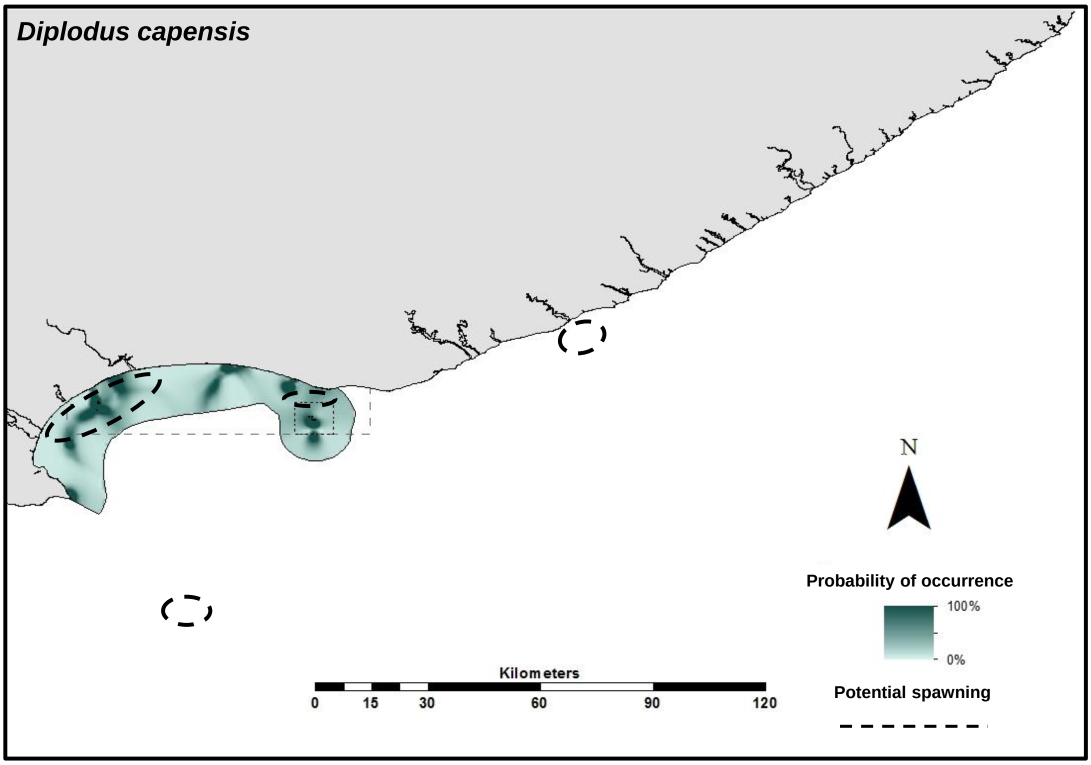

FIGURE 6.6 Distribution models showing probability of occurrence of newly hatched *Diplodus capensis* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

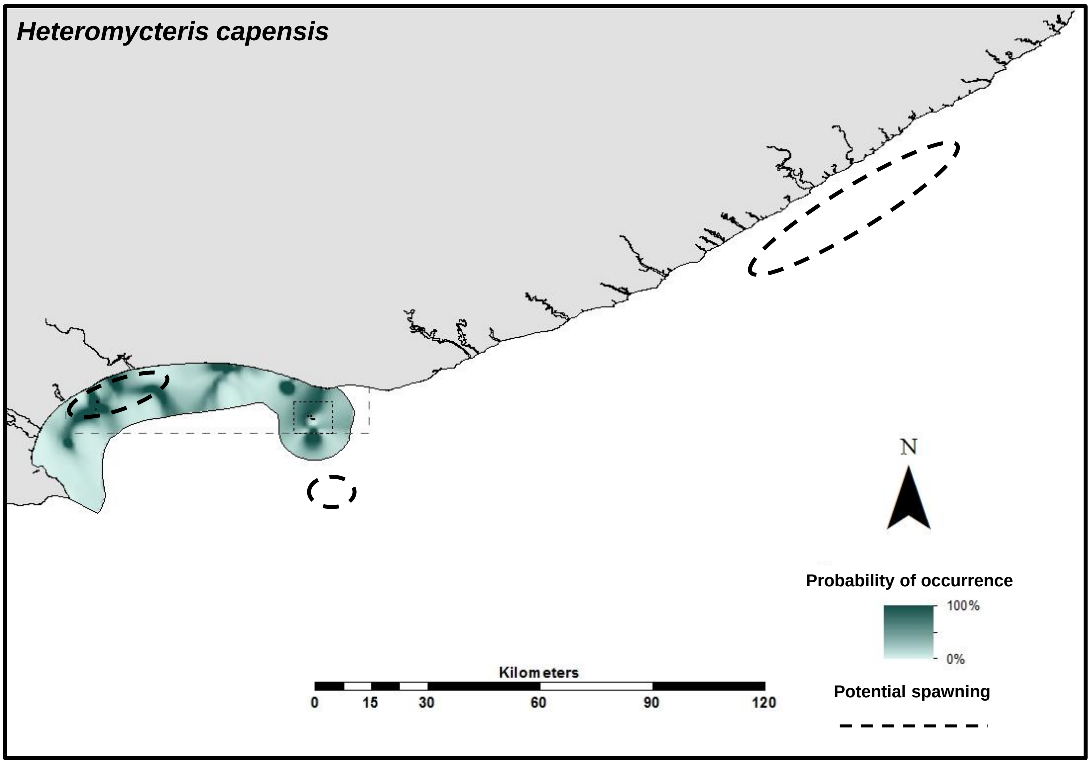

FIGURE 6.7 Distribution models showing probability of occurrence of newly hatched *Heteromycteris capensis* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

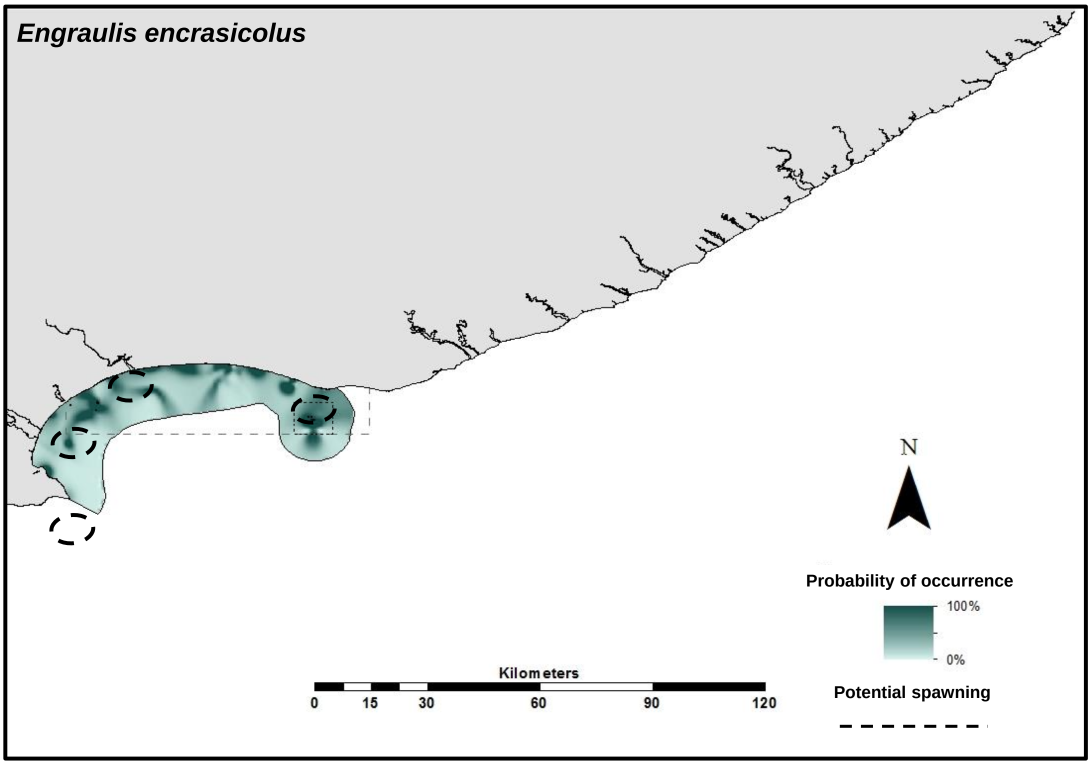

FIGURE 6.8 Distribution models showing probability of occurrence of newly hatched *Engraulis encrasicolus* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

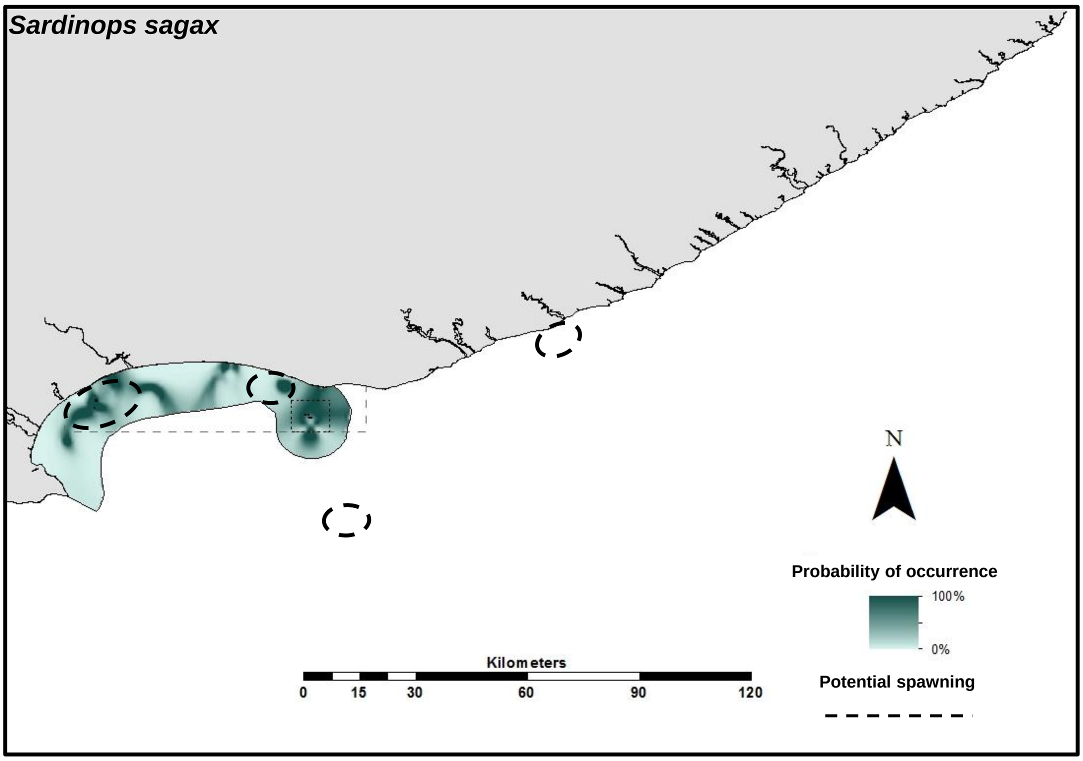

FIGURE 6.9 Distribution models showing probability of occurrence of newly hatched *Sardinops sagax* and the origin of spawning in the study area of the coastal nearshore of Algoa Bay

5. DISCUSSION

Important areas in the early development of six fish species with important ecological and fishery status, in the coastal nearshore of Algoa Bay were described and predicted. Strong environmental gradients on multiple spatial scales renders the coastal zone of Algoa Bay particularly suitable for modelling the early-life stage distribution of fish. The current study presented a widely applicable model of commonly used abiotic factors that explain the distribution of the early developmental stages of six species. The fish species represented utilise different habitats characterised by specific environmental conditions at different life-stages.

The maximum dispersal distances of passive eggs and early stage fish larvae from a point source in the Algoa Bay nearshore were calculated using progressive vector plots (Pattrick *et al.*, 2013). These data included estimates of seasonal dispersal, modelling displacement for three month periods. Predictions of net displacement from a fixed central point in the nearshore, of almost 300 km during spring and early summer were obtained. These trends suggested that eggs and preflexion larvae would be transported out of Algoa Bay. The present study however took into consideration PLD, which for most coastal fish species occurring in Algoa Bay consists only of a few days (Connell, 2007). This allowed for more accurate estimates of dispersal to be calculated. Using retrogressive plots, the location of spawning areas could be determined. The results indicate several locations of spawning areas for species whose larval stages occur in the Bay.

It should be noted that the measurements from the retrogressive plots used in the current study should be used as a guideline for potential dispersal of eggs and preflexion larvae, as information on the vertical distribution of larvae in temperate coastal waters is limited. Furthermore, limited information exists on taxon-specific vertical distribution of preflexion larvae in coastal waters. Therefore efforts to understand dispersal of larvae by ocean currents are difficult. Studies conducted on tropical larvae indicate that specific patterns in vertical distribution occur for related taxa, with strong vertical structure occurring during the day and weak structure at night with most taxa occurring deeper during the day (Leis, 1986; Leis, 1991b). The depth intervals used in the present study, although having been represented in the literature as common areas of accumulation for preflexion larvae and eggs, are still estimates.

The greatest abundance of all study species occurred between September and February. The majority of teleost marine fishes are seasonal breeders, while a few breed continuously with peaks in breeding activity. Marine temperate fishes spawn predominately during spring and early summer. At the onset of spring, an increase in sea water temperatures is observed with associated higher productivity which ensures better feeding conditions for larvae (Heath, 1992; Pörtner *et al.*, 2001). Results indicate that temperature variation, rather than temperature *per se*, was a better predictor of newly hatched *D. capensis* distribution. Similarly, in estuaries, salinity variation has shown to be a better predictor of invertebrate species diversity than salinity itself (Attrill, 2002). Environmental variables that describe both the average conditions experienced by the early developmental stages of fishes, and the variability in those conditions, are important in model development (Francis *et al.*, 2005).

The socio-economic important dusky kob, *Argyrosomus japonicus*, and silver kob, *A. inodorus*, are heavily sought after by recreational anglers, their catches having declined markedly in recent years with stocks currently depleted and catches restricted (Brouwer *et al.*, 1997; Griffiths, 1997; Mann, 2000). Similarly in eastern Australia populations of *Argyrosomus japonicus*, known as mulloway, are reported as overfished (Silberschneider and Gray, 2008; Ferguson *et al.*, 2013b). In South Africa, small-meshed trawl catches in Algoa Bay indicated the abundance of kob to be higher than in other areas along the Cape south coast (Wallace *et al.*, 1984), indicating the importance of Algoa Bay for these species. The inshore distribution of adults in spring and summer (Griffiths, 1996), coupled with the complete absence of any Sciaenidae eggs and larvae offshore in the core of the Agulhas Current (Beckley, 1993) and the occurrence of early stages of kob larvae in the Algoa Bay shallow nearshore (<30 m) and surf zones (Beckley, 1986; Pattrick and Strydom, 2008) suggests that spawning is occurring locally. This hypothesis is confirmed from results obtained from retrogressive plots indicating the origin of passive particles (eggs) of *A. inodorus* in the Bay and in close proximity to both Bird Island and St Croix Island. Within Tampa Bay, a drowned river valley on the west coast of Florida, USA, small (<3.0 mm) sciaenid larvae, *Sciaenops ocellatus*, occurred at the mouth of the Bay with larval size increasing further inshore, suggesting that spawning is occurring near the Bay mouth rather than far offshore (Peters and McMichael Jr, 1987). An increase in length with increasing depth and distance from shore for juvenile *A. inodorus* is also known to occur (Griffiths, 1996). Juveniles move farther offshore as they grow recruiting to adult populations on offshore reefs (Griffiths, 1996).

The two kob species, *A. japonicus* and *A. inodorus*, revealed different distributions in their newly hatched locations. *Argyrosomus inodorus* had a close association with St Croix Island in the western sector of the Bay. The probability of occurrence of *A. inodorus* newly hatched larvae was also high at Bird Island and Woody Cape in the far eastern sector of the Bay. An assessment of adult reef linefish communities in Algoa Bay indicated that *A. inodorus* was the third most abundant species in the St Croix area but was completely absent from catches in the Bird Island area and occurred in low abundance near Woody Cape (Chalmers, 2011). Chalmers (2011) indicated the potential importance of the St Croix area as a nursery ground for *A. inodorus*. Similarly, high abundances of *A. inodorus* have been observed in the shallow inshore regions of Algoa Bay, particularly near Jahleel Island (Smale, 1984). The highest probability of newly hatched areas of *Argyrosomus japonicus* included offshore locations associated with the Alexandria dune field in the eastern sector of the Bay and areas between the Sundays and Swartkops estuaries and St Croix Island. Origins of spawning locations of *A. japonicus* however consistently indicate spawning occurring outside of Algoa Bay, specifically in a north easterly direction which would place spawning at the proximity of Port Alfred. The upwelling of colder water has been detected in this area along a strip of coastline approximately 100 km long and is known to enhance the nutrient concentrations of the surrounding waters substantially (Lutjeharms *et al.*, 2000; Lutjeharms, 2006; Lutjeharms, 2007). Adult dusky kob, *A. japonicus*, comprised a large portion of the retained catch of the recreational shore fishery in the western sector of Algoa Bay and made important contributions at shore localities along the Alexandria dune field in the eastern sector of the Bay (Chalmers, 2011). *Argyrosomus japonicus* was amongst the most abundant species retained by recreational shore fishers at Cannon Rocks (Chalmers, 2011). Cannon Rocks is located outside the proposed MPA of Algoa Bay, approximately 30 kms east of Woody Cape.

Pelagic fish species which occur in the Algoa Bay region include the sardine, *Sardinops sagax*, and the Cape anchovy, *Engraulis encrasicolus*. Sardine is the most abundant and most important pelagic fishery species in the Algoa Bay region. The Cape anchovy is an economically important small pelagic fish found in South African waters targeted by the medium-sized purse-seine fishery. The anchovy is also ecologically important, serving as an important prey source for many piscivorous fish and marine top predators (Cury *et al.*, 2000). Adult anchovy are known to spawn during mid-summer (November to December) on the Agulhas Bank (Hutchings *et al.*, 2002). However, since 1994 there has been a distinct eastward shift in the spawning distribution to the east-central Agulhas Bank with anchovy known to spawn on the shelf on the east coast (Armstrong *et al.*, 1991; Beckley and Hewitson, 1994) and in Algoa Bay (Pattrick and Strydom, 2008). The majority of sardine spawning is known to occur on the west coast with less spawning intensity occurring on the central and eastern Agulhas Bank. There is however sardine spawning on the east coast (Hutchings *et al.*, 2002) and postflexion larvae are regularly encountered in coastal areas of Algoa Bay (Strydom, 2003a; Pattrick and Strydom, 2008). In most cases in the present study, the retrogressive plots indicated an origin of spawning of *S. sagax* in Algoa Bay, specifically in the nearshore region as observed in the distribution modelling of the early hatched larvae. Inshore distribution of spawning of the Pacific sardine, *S. sagax*, has been observed off the southern and central California coastline (Brewer and Smith, 1982; Lynn, 2003). Sardines in Japan and in the Humbolt and California Current systems, have been observed to spawn in near-coastal waters when populations levels and biomass are low, only expanding their spawning range significantly into oceanic mixing areas when population levels are high (Cury *et al.*, 2000).

The distribution of newly hatched Cape sole larvae, *H. capensis*, was confined to the nearshore of Algoa Bay. *Heteromycteris capensis* spawns in the marine environment with larvae and juveniles recruiting into estuarine nursery areas (Whitfield, 1998). Retrogressive plots indicate that spawning of *H. capensis* is occurring locally in the Bay, particularly in the western sector. Postflexion *H. capensis* larvae are commonly observed in surf zones (Cowley *et al.*, 2001; Strydom, 2003b; Watt-Pringle and Strydom, 2003; Strydom and d'Hotman, 2005), where they accumulate before recruitment into estuarine habitats. Two permanently open and smaller estuaries are located in the western sector of the Bay. The close proximity of the estuarine nursery areas could facilitate in determining the distribution of these estuarine-dependent newly hatched larvae within the nearshore.

Diplodus capensis a sparid species, lays pelagic eggs, typical of all the other species within the Sparidae fish family in South Africa, excluding *Spondyliosoma emarginatum*. Newly hatched larval distributions and spawning origins of *D. capensis* follow similar patterns in distribution to potential reef areas identified by Chalmers (2011) in Algoa Bay. Shallow, subtidal bays associated with rocky shores function as preferred nursery habitats for mid to late stage larval and newly settled juvenile *D. capensis* (Strydom, 2008). These rocky shores occur exclusively at Woody Cape in the eastern sector of the Bay and in the western sector of the Bay.

Mapping species distributions, by relating the occurrence of species to environmental descriptors, allows for a better understanding of population dynamics including distribution and the mechanisms regulating these (Guisan and Wilfried, 2005; Kozak *et al.*, 2008). Species distribution modelling (SDM) is based on the concept that certain environmental characteristics of a particular habitat are needed to host specific species. The relationship between the species and the environment provides information on habitat preferences and predictions of distributions of species. Within the terrestrial environment, presence-only modelling of species distributions has been extensively used with only a recent increase in the interest of predicting fish species distribution in the marine environment (Ready *et al.*, 2010). Particularly for marine fish, machine-learning algorithms such as MaxEnt, have proved to consistently outperform more conventional modelling techniques including generalised additive models and linear regression (Knudby *et al.*, 2010). MaxEnt has recently been used to model distributions of marine fishes and invertebrates (Close *et al.*, 2006; Bigg *et al.*, 2008; Cheung *et al.*, 2009; Ready *et al.*, 2010; Pittman and Brown, 2011). Species distribution modelling is a rapidly advancing field and its applicability for fish reproduction habitats is relatively unknown (Sundblad *et al.*, 2009). Many fish species display ontogenetic habitat shifts, with juvenile habitats in shallow coastal areas and adult assemblages more widely distributed. Knowledge of larval habitats however remains poorly understood.

The spatial distribution modelling approach developed in the present study has provided a powerful tool for identification and mapping of the early life stages of ecologically and economically important fish species. Knowledge of spawning and newly hatched larval fish areas is essential for the conservation of fish stocks, whether they be exploited, commercially and economically important, or significant from an ecological point of view. In eastern South Australia, populations of *A. japonicus* have been depleted by habitat loss and overfishing. Management recommendations suggest the identification and preservation of spawning areas will rebuild these populations (Ferguson *et al.*, 2013a). Spatial distribution modelling would therefore serve as a valuable approach to conservation in such cases.

Although the modelling approach employed here may lose precision in assuming that species distributions are dictated by a general and restricted set of environmental variables, the MaxEnt model predictions in the present study have served as a valuable tool to model very complex spatial distributions of fish larvae, for which data and ecological knowledge are often frequently scarce. At the species level, larval fish showed individualistic responses to predictors, however reliable models of species distributions were produced. Furthermore, dispersal distances to determine origin of spawning locations proved to be species specific. Species with longer PLD were dispersed over much greater distances than those with relatively short PLDs. Furthermore, life-history characteristics such as larval vertical and horizontal migration also differ between species and will influence dispersal.

Environmental variables play an important role in determining the distribution of the early life history stages of fish species. Biotic process however need to be incorporated explicitly into species distribution models, as for a substantial portion of the pelagic larval stage, behaviour influences dispersal (Leis, 2006). Therefore, only dispersal of eggs and preflexion larvae were considered, as larvae upon hatching are very small and poorly developed with limited swimming abilities, and with respect to ocean currents, are regarded as close to passive. The results demonstrate that the early developmental stages of fishes within the shallow nearshore of Algoa Bay exhibit high spatial variability in their distributions. These predictions are plausible given what is known of the juvenile and adult ecology of each species. In addition, the modelled distributions corresponded favourably with observations from field sampling. Therefore, the results show that species distribution modelling using species-environment relationships serves as a suitable tool for mapping larval fish distributions. The present study not only indicates that Algoa Bay serves as an important spawning area for several economic and ecological fish species, but also an accumulation area for larvae that are spawned outside of Algoa Bay.

6. ACKNOWLEDGEMENTS

This work is based on financial support from the South African National Parks (SANParks), South Africa. Gratitude is expressed to the SANParks. Any opinions, findings and conclusions expressed in this material are those of the authors and therefore the SANParks does not accept any liability in regards thereto. SAEON Elwandle Node are thanked for technical and logistical support of fieldwork. Dr Linda Harris is thanked for assistance with execution of the MaxEnt programme and the generation of distribution modelling plots in GIS. Dr Wayne Goschen is thanked for generation of retrogressive plots. Dr Ané Oosthuizen is thanked for commenting on a draft copy of this chapter.

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CHAPTER 7

SYNTHESIS AND CONCLUSIONS

One of the present concerns of fish biologists globally, involves defining and identifying nursery habitats in the context of conservation and resource management strategies. Although information exists on the use of nursery habitats by juvenile fishes, there is a general lack in knowledge of the relative value of coastal habitats as nursery areas for fish larvae. Furthermore, seagrasses and wetlands have been the focus of most work on juvenile nursery areas (Robertson and Duke, 1987; Thayer *et al.*, 1987; Baelde, 1990; Ferrell and Bell, 1991; Sheridan, 1992). Although this is justified, a mosaic of coastal habitats exist which are available as nursery areas for larval fishes in coastal waters. For this reason, a two-year study to assess the relative importance of subtidal reef, sand, nearshore, surf and estuarine mouth habitats as larval fish nursery areas was initiated. This effort was accomplished within the framework of community composition, developmental stages and the associated environmental variables of each habitat type structuring the larval fish community.

The presence of numerous habitat types including the nearshore, subtidal reefs, sand habitats and the surf zone in Algoa Bay, contributes to the diverse larval fish communities present. Distinct larval fish communities were identified within each of the coastal habitat types sampled in Algoa Bay. Engraulidae, Cynoglossidae and Sparidae (in descending order) fish families dominated catches in the nearshore (Chapter 2) at depths of ~30 m. Gobiidae, Cynoglossidae and Engraulidae dominate catches in the shallower (5 – 15 m) nearshore of Algoa Bay (Beckley, 1986; Pattrick and Strydom, 2008). Gobiidae, Blenniidae and Tripterygiidae larvae dominate nearshore catches in the northern hemisphere (Sabatés *et al.*, 2003; Beldade *et al.*, 2006). Benthic eggs, such as the Gobiidae, Blenniidae and Tripterygiidae, is a characteristic prevalent among larval fish assemblages close to shore (Suthers and Frank, 1991). Larvae which hatch from benthic eggs are probably not affected by advective processes until they hatch, thus reducing their chances of being transported offshore. This inshore distribution pattern observed for species that have benthic eggs has been suggested to occur due to the low dispersal of the non-pelagic nature of the eggs (Hernández-Miranda *et al.*, 2003). However, Engraulidae, which hatch from pelagic eggs, are the dominant fish family in the nearshore habitats of the northwestern Atlantic (Able *et al.*, 2010), Mediterranean (Olivar *et al.*, 2001; Sabatés *et al.*, 2007) and central Chile (Hernández-Miranda *et al.*, 2003). Most Sparidae species also hatch from pelagic eggs and similarly dominate larval fish catches in the temperate nearshore waters of the Mediterranean (Sabatés *et al.*, 2003; Beldade *et al.*, 2006) and Australia (Gray, 1993). Horizontal shifts in species assemblages occurs with increasing distance from shore (Leis and Miller, 1976; Leis, 1982). It appears that similar horizontal shifts in larval fish assemblages occurs in the nearshore of Algoa Bay, with larvae from benthic eggs occurring predominantly inshore while coastal species that produce pelagic eggs are regularly being encountered in deeper (~30 m) nearshore waters.

Engraulidae, Gobiidae and Clupeidae (in descending order) dominated catches over subtidal reef and sand habitats (Chapter 3). The larval fish assemblages directly above shallow coral reefs in the Florida Keys are similarly dominated by Engraulidae and Clupeidae (Sponaugle *et al.*, 2003). Gobiidae larvae are one of the most abundant fish families found in bays and near reef complexes in temperate New Zealand (Kingsford and Choat, 1989). On the west coast of Portugal, Gobiidae make important contributions towards larval fish catches associated with rocky reefs (Borges *et al.*, 2007). The distribution patterns of presettlement reef fish are known to be influenced by proximity to reefs (Kingsford and Choat, 1989). Gobiidae are benthic fishes associated with structure (Heemstra and Heemstra, 2004), coupled with their production of benthic eggs, their dominance over subtidal reef habitats is not surprising.

In the surf habitats (Chapter 4) of Algoa Bay, Sparidae, Soleidae and Mugilidae dominated catches. The larval fish community of the Algoa Bay surf zones resembles that of other surf zone habitats within the same geographical region of South Africa (Whitfield, 1989a; Strydom, 2003; Watt-Pringle and Strydom, 2003; Strydom and d'Hotman, 2005). Although changes in fish family rank and abundance occur in surf zone habitats internationally, several fish families are shared between the various geographical regions. This highlights the continuity in composition of larval fish assemblages universally and the utilization of surf zones as a whole by a specific group of larval fishes.

In the mouth area of two permanently open estuaries in Algoa Bay (Chapter 5), Gobiidae, Sparidae and Mugilidae dominated. Similar trends are observed with other estuaries from the same region (Strydom *et al.*, 2003; Strydom and Wooldridge, 2005). Larval and juvenile fish abundance relative to the tidal and diel cycle showed a clear preference. Greater densities were observed during the ebb tide at night, with similar findings observed in the same biogeographical region (Whitfield, 1989b; Strydom and Wooldridge, 2005) as the two estuaries in the present study. Internationally, (Roper, 1986; Neira and Potter, 1994; Primo *et al.*, 2012) a similar trend is observed. In addition, active recruitment of larvae and early juveniles into the estuarine nursery areas of Algoa Bay against the outgoing ebb tide was observed. These results indicate that larvae are not necessarily lost from estuarine systems during the ebb tide, but are actively swimming against the ebb tide in the shallower, slower-flowing marginal areas facilitating recruitment against ebb flow as originally suggested by Strydom and Wooldridge (2005).

Coupled with variability in larval fish assemblages between habitat types, the physical environment varied greatly among locations and had a profound influence on larval fish distribution and composition. Larval fish composition and abundance was influenced by prominent ocean features in the nearshore (Chapter 2). Habitat complexity played an important role in structuring larval fish assemblages (Chapter 3). The larvae of reef associated adult species occurred abundantly at complex reef habitats while those larvae belonging to adults associated with sand or the pelagic-oceanic environment dominated less structurally complex reef-associated sand habitats. Exposure from wave action and wind in the surf zone, correlated with a higher diversity of larval fish assemblages (Chapter 4). Coastal habitats such as those occurring in Algoa Bay are highly dynamic environments that are subjected to a variety of physical processes operating on numerous spatial and temporal scales that structure larval fish assemblages.

In addition, these coastal ecosystems are highly productive and serve many important functions, one of which is that of nursery areas. At the end of the planktonic larval phase, the surviving larvae will settle as juveniles into coastal nursery habitats. This period of transition from an open water environment to a structured environment is a vulnerable portion of the fish life history (Kaufman *et al.*, 1992). Larvae that are adapted to the pelagic environment must now alter their behaviour to cue to settlement sites (Leis, 2006; Leis, 2007). Nursery habitats provide an abundance of food, refuge from predators, and shelter for juvenile fishes, resulting in higher growth and survival rates (Laegdsgaard and Johnson, 2001; Cocheret de la Morinière *et al.*, 2002).

The role of coastal ecosystems as nursery areas is a well-established concept. Much research has been focused on defining and identifying juvenile fish nursery areas (Beck *et al.*, 2001; Dahlgren *et al.*, 2006). Historically, nursery areas were defined by higher densities of juvenile fishes that avoided predation more successfully, or grew faster than in a different habitat. Beck *et al.* (2001) recently developed a hypothesis for the nursery-role concept. According to Beck *et al.* (2001), a nursery for juveniles of a particular species was defined “if its contribution per unit area to the production of individuals that recruit to adult populations is greater, on average, than production from other habitats in which juveniles occur”. Furthermore, Beck *et al.* (2001) indicated that for a habitat to be defined as a nursery, any combination of four ecological factors including 1) density, 2), growth, 3) survival of juveniles and 4) movement to adult habitats, must be operating in order to support greater contributions to adult recruitment. This refined definition of the nursery-role concept has greatly improved the evaluation of marine nursery habitats (Heck *et al.*, 2003; Dahlgren *et al.*, 2006). However the definition is somewhat limited with regards to habitats that have a small per unit area contribution to adult recruitment but are also essential for collectively sustaining adult fish populations (Dahlgren *et al.*, 2006). While this nursery definition serves as a powerful approach to identify juvenile nursery habitats, the framework for determining habitats important for larval fish development is often overlooked. This chapter provides a broader framework for evaluating larval fish nursery habitats. This chapter therefore focuses on developing such a framework for evaluating larval habitats based on data from previous chapters to build on the nursery concept. The concept of Effective Larval Nursery Habitat (ELNH) and Effective Larval Accumulation Habitat (ELAH) is introduced.

Several species from numerous families are completing their pelagic larval phase in the coastal habitats of Algoa Bay. Furthermore, several species in the Bay are near the end of their larval phase and recruiting to juvenile nurseries during the larval phase. These results indicate that grow-out of larvae is occurring in the Bay. As growth is one of the ecological factors defining a nursery habitat for juveniles (Beck *et al.*, 2001), coastal habitats in Algoa Bay can therefore be considered as ELNHs. These ELNHs can be described as restricted areas where larvae will spend a limited period, separated from the adult and juvenile habitats, where survival is enhanced through optimal conditions for feeding, growth and protection from predators. The subtidal reef habitats associated with islands in Algoa Bay, serve as ELNHs for several species from the Blenniidae, Gobiesocidae, Gobiidae, Scorpaenidae and Tripterygiidae fish families. The larvae of these benthic and pelagic species are completing their pelagic larval phase in the subtidal reef habitats (Chapter 3). The blenniid, gobiesocid gobiid and tripterygiid larvae hatch from benthic eggs. These taxa are small, substrate or reef associated fishes (Heemstra and Heemstra, 2004). The pelagic larvae of these reef associated adult species are occurring in close association with subtidal reef habitats during their larval phase. Larvae in subtidal reef habitats that hatch from benthic eggs should be better able to participate in their own retention than larvae from pelagic eggs. This is because, on average, larvae that hatch from benthic eggs are larger and have sensory and locomotory abilities that are better developed than larvae hatching from pelagic eggs (Leis, 1991). Furthermore, it is likely that these taxa have predominately closed populations on the subtidal reefs associated with islands in Algoa Bay, in an ecological sense and over ecological time scales. The evolutionary time scales are less clear and not the focus of the present study.

In addition, the sand (Chapter 3) and the nearshore (Chapter 2) habitats in Algoa Bay are similarly serving as ELNHs for the important fishery species *Sardinops sagax* (Clupeidae) and *Engraulis encrasicolus* (Engraulidae). It has been hypothesized that the presence of structure *per se* is more important than the characteristics of the habitat for settling fishes at the end of the planktonic larval phase (Bell *et al.*, 1987; Jenkins and Wheatley, 1998; Heck *et al.*, 2003). Structure provides more protection from predators and thereby allows more time for feeding which increases growth rates (Heck *et al.*, 2003). This may hold true for reef associated species, however pelagic species such as *S. sagax* and *E. encrasicolus* are schooling species and will obviously show a preference against structure.

The surf zone habitats of Algoa Bay, hold a variety of developmental stages from larvae to juveniles indicating that growth is taking place (Chapter 4). Therefore, the

Algoa Bay surf zones are serving as ELNHs for a select suit of species. Typically, surf zone habitats in South Africa are regarded as important nursery habitats for estuary-dependent marine fish species (Whitfield, 1989a; Harris and Cyrus, 1996; Strydom, 2003). Marine species with no association to estuaries whose adults are either associated with rocky shores or the surf zone are also utilizing the surf zone as an ELNH. This trend was particularly evident for *Neoscorpis lithophilus* (Kyphosidae) and *Iso natalensis* (Notocheiridae). Furthermore, the pelagic larval phase of *E. encrasicolus* is being completed in the surf zone and the nearshore, indicating the importance of these habitats as an ELNH for *E. encrasicolus* in the Bay.

Most studies concerning the nursery role of juvenile fish habitats only consider density, and have inferred the importance of certain habitats as nurseries based on density alone. Higher densities do imply the importance of such habitats functioning as an effective habitat for larvae at the ecosystem level. In addition, by surveying several different habitats, as followed in the present study, it is possible to identify and focus on which habitats serve the best as accumulation areas of larvae in various stages of development. This reasoning brings into context the theory of ELAHs, which can be defined as habitats with substantially higher densities of fish larvae. Higher densities of larval fishes in particular coastal habitats will translate to greater export of larvae into adjacent habitats (Heck *et al.*, 2003). Careful scrutiny of the distribution of species in Algoa Bay has shown clearly defined centers of abundance.

Substantial peaks in species abundance occur among the various habitat types. Cynoglossidae, Haemulidae and Soleidae larval densities were highest in the nearshore (Chapter 2). Juvenile Haemulidae and Soleidae utilize estuaries as nursery areas (Whitfield, 1998). The nearshore in Algoa Bay could therefore be defined as an ELAH for Haemulidae and Soleidae, prior to settlement of juveniles in estuarine nursery areas. Cynoglossidae adults are extensively associated with habitats in the coastal environment (Smith and Heemstra, 1995; Heemstra and Heemstra, 2004). Cynoglossidae larvae could therefore be utilizing the nearshore of Algoa Bay as an ELAH before settlement and recruitment into adult populations. Highest densities of Carangidae, Sciaenidae and Sparidae larvae were observed at the subtidal reef habitats (Chapter 3). The adults of these fish families are reef associated (Heemstra and Heemstra, 2004). Furthermore, several coastal habitats in Algoa Bay have been identified as juvenile nursery areas for these fish families. The nearshore of Algoa Bay serves as a nursery for juvenile Sciaenidae (Wallace *et al.*, 1984a; Wallace *et al.*, 1984b). Subtidal reef complexes (Beckley and Buxton, 1989), tide pools (Beckley, 1985), estuaries (Beckley, 1984) and surf zones (Lasiak, 1981) in Algoa Bay have been identified as nursery habitats for a select suite of juvenile sparid species. Therefore, subtidal reefs could serve as specific areas of presettlement buildup of larvae prior to the juvenile settlement in coastal nurseries. Sound is generated and transmitted from reefs with some reef larvae having sensory structures suited to sound reception (Montgomery *et al.*, 2006). Sound has been demonstrated to be a useful orientation cue for some larval reef fishes to guide settlement onto reefs (Montgomery *et al.*, 2006). Similarly, subtidal reef habitats associated with islands in Algoa Bay can be defined as ELAHs.

Internationally, isolated studies on larval fish nursery areas have shown similar results. For ELNHs, Leis (1994) demonstrated that the pelagic larval phase of several species is being completed in atoll lagoons. These semi- to fully-enclosed bodies of water serve as nurseries for the larvae of Apogonidae, Atherinidae, Belonidae, Blenniidae, Bythitidae, Clupeidae, Gobiidae, Hemiramphidae, Lutjanidae, Microdesmidae, Nemipteridaa, Pempherididae, Pomacentridae, Pseudochromidae, Schindleriidae and Tripterygiidae (Leis, 1994). Although during the pelagic larval phase wide dispersal from natal reefs is possible, this work (Leis, 1994) demonstrated that these taxa have predominately closed populations, contrary to the historic paradigm that all coral reef fishes live in predominantly open populations. Recent work has highlighted that several fish populations show a substantial degree of self-recruitment (Sponaugle *et al.*, 2002). Leis's (1994) work indicated that propagules originating from a population of fishes on a given reef would settle back into that same population at the end of the pelagic phase. Self-recruitment is an important mechanisms in controlling the scale of population connectivity in marine populations (Sponaugle *et al.*, 2002). For the ELAHs, nearshore areas both locally (Pattrick and Strydom, 2008) and internationally (Warner *et al.*, 2000; Roussel *et al.*, 2010) have been identified as larval accumulation areas for a select suite of species. Nearshore areas accumulate larvae that will ultimately move into surf zone before swimming actively into estuary nursery areas (Boehlert and Mundy, 1988; Potter *et al.*, 1990). This supports the shoreward movement hypothesis where larvae recruit from offshore spawning areas, swimming towards appropriate coastal nursery habitats (Boehlert and Mundy, 1988).

The coastline of southern Africa has typically been regarded as a rough and harsh environment with few bays and semi-enclosed seas which could serve as nursery areas. Due to the rugged nature of the South African coastline, Hutchings *et al.* (2002) has suggested a spawning strategy adopted by several common fish species in South Africa. This strategy includes one in which spawning is confined to the edge of current systems where physical mechanisms allow for a sufficient number of larvae and juveniles to be retained on the shelf region to replenish adult fish populations (Hutchings *et al.*, 2002). Many coastal species will spawn in or near coastal habitats, providing larvae with accessibility to coastal nursery areas (Wallace and van der Elst, 1975; Day *et al.*, 1981; Boehlert and Mundy, 1988; Potter *et al.*, 1990; Chute and Turner, 2001). The spawning locations of species occurring in Algoa Bay, until now were virtually unknown. Analysis of retrogressive plots (Chapter 6), indicate that certain species are spawning outside the confinement of Algoa Bay, but larvae are accumulating in the Bay. In support of the theory developed by Hutchings *et al.* (2002), the larvae of those species that are spawning outside of the Bay, along the edge of the current systems could be accumulating in Algoa Bay. The Agulhas Current sweeps closely along the shelf break at a depth of ~200 m and only 50 km offshore of Algoa Bay. Several shear-edge eddies bud off the inner edge of the current at frequent intervals and reverse currents within these eddy regions generate a net movement of near-surface waters in a north-east direction (Boyd and Shillington, 1994). This counter flow of water in the opposite direction to the offshore south-westerly flow of the Agulhas Current would allow for eggs and larvae spawned along the shelf-edge to be transported into the Algoa Bay region. The area offshore of Algoa Bay, where the Agulhas Current diverges from the coast has been identified as a zone of major variability (Hutchings *et al.*, 2002) where eddies, intrusions of Agulhas water onto the shelf, and large offshore meanders of the Agulhas Current occur. The present study (Chapter 2) indicated how these mechanisms such as Agulhas plume intrusions into Algoa Bay, are associated with higher abundances of fish larvae, namely sardines and anchovy. In addition, results from this thesis (Chapter 6) also show that spawning of several common economic and ecological fish species is occurring much closer inshore than previously thought. Specifically, spawning is occurring within the sheltered coastal inshore environment of Algoa Bay.

Essential fish habitats such as spawning, hatching and nursery areas are important to sustain the renewal of marine fish populations (Iles and Beverton, 2000; Le Pape *et al.*, 2003; Van de Wolfshaar *et al.*, 2011). The identification of ELNH and ELAH areas are an important link between the early life-history stages and adult populations. Defining essential fish habitats consists not only of obtaining extensive biological data coupled with the relevant descriptors of the coastal environment, but choosing a statistical approach to build a robust spatial distribution model. Data from these models can then be imported into Geographic Information Systems (GIS) for the quantitative identification of key areas for the early developmental stages of fishes. The maximum entropy (MaxEnt) machine-learning algorithm in the present study (Chapter 6), proved to be a powerful tool to identify and map essential fish habitats in Algoa Bay. Previously overlooked habitats serving as important areas in the early developmental stages of fishes in the coastal nearshore of Algoa Bay have been identified during this study. This has significant implications for the identification of habitats for protection and conservation. Determining essential fish habitats including spawning, newly hatched and nursery areas are crucial for conservation and management of fishes e.g. the identification, design and prioritization of effective marine protected area (MPA) networks (Le Pape *et al.*, 2014). By protecting the ecological function of essential fish habitats, conservation targets are met and marine fish populations and fisheries are sustained (Martin *et al.*, 2012). Furthermore, protecting successive fish habitats along their life cycle (i.e. spawning, newly hatched and nursery areas) is of major importance and has considerable influence on the efficiency of fish conservation, especially via MPAs (Kaplan, 2009). Protecting specific areas associated with the early development of fishes has proved to be as effective as securing large parts of the population distribution (Grüss *et al.*, 2011).

A critical area in which knowledge of the linkages between larval fish and environmental processes is lacking, is the coastal environment. It is within coastal ecosystems that spawning, accumulation, retention and settlement of larvae occur (Johannes, 1978; Norcross and Shaw, 1984; Warner *et al.*, 2000; Able *et al.*, 2012). Complex physical oceanography and other environmental variables characterize the coastal environment. Coupled with larval fish behaviour, this introduces an element of complexity of understanding the utilization of coastal habitats by larvae. More consistent testing of the nursery-role hypothesis is needed for the identification of nursery habitats in the coastal nearshore. This will provide a better indication of which species are reliant on particular nursery habitats, and what factors structure nurseries.

A fruitful area for future investigation would be the identification of spawning localities and effective fish nursery areas of several endemic recreationally and commercially important fish species in other parts of the South African coast, particularly those of the reef associated Sparidae fish family. The paucity of data in this area is especially striking. Over 40 species of Sparidae are targeted by both recreational and commercial fisheries on South Africa’s south coast (Tilney *et al.*, 1996). Sparidae are typically long-lived, slow growing, late to mature, and highly resident with several species undergoing a sex reversal during the life cycle, all of which contribute to their susceptibility to overexploitation. The Sparidae stocks have up until recently been poorly managed in South Africa, with several stocks considered collapsed. High levels of fishing contribute to local depletion of these species as they are unable to withstand intense fishing pressure. It has been suggested that by protecting spawner biomass, populations will recover and will reseed surrounding areas and in that way will improve fishery production in exploited areas (Roberts and Polunin, 1991). Therefore, the identification of essential larval fish habitat including spawning, newly hatched and nursery areas of Sparidae is imperative for conservation of these exploited fish stocks. The resolution of the early life history stages of the sparids is seen as a priority for the near future.

It is clear from this thesis and other studies that there is still much work to be done around the world to fully understand the details of the processes of nursery habitat utilization by larval fishes. While species diversity is not accounted for in nursery definitions, the maintenance of a high species diversity is another feature relevant to the perception of coastal habitats as extraordinarily rich. This study greatly contributed to an increase in the scientific knowledge of the early life history of several species occurring in coastal habitats in Algoa Bay. Assessments of ELNHs and ELAHs can use similar approaches to those used for assessing juvenile nursery habitats (Beck *et al.*, 2001). The major advantage of the ELNH and ELAH classification however is that larval habitat specifically is taken into consideration. This study has highlighted the importance of integrating the early pelagic larval phase into traditional nursery studies. By assessing the variability in spawning locations and newly hatched larval distributions, and determining essential larval fish habitats, has added great value to determining the ecological importance of Algoa Bay for larval fishes. This information in turn, has added greatly to our understanding of the dynamic nature of larval fish use of coastal nursery areas in South Africa.

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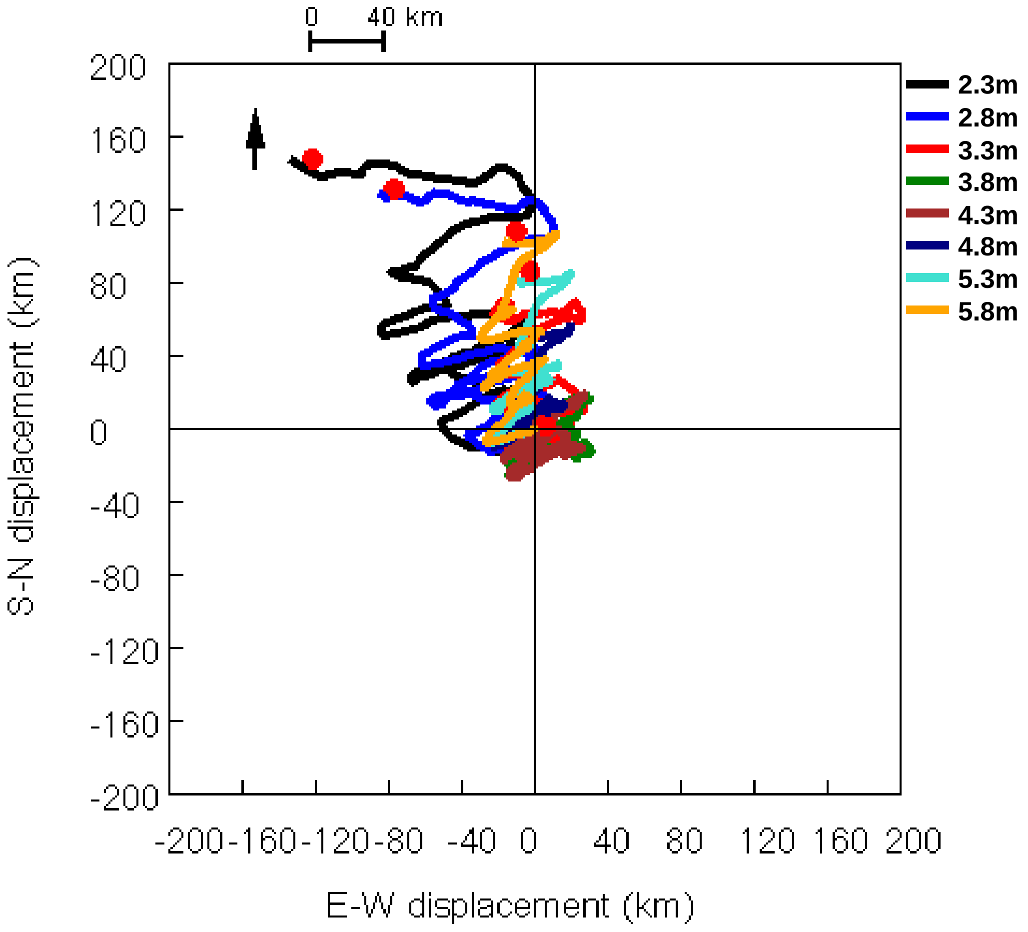
Whitfield, A. K. (1998). *Biology and ecology of fishes in South African Estuaries*. Grahamstown: Ichthyological Monographs of the JLB Smith Institute for Ichthyology, No. 2.

APPENDIX 1: RETROGRESSIVE PLOTS

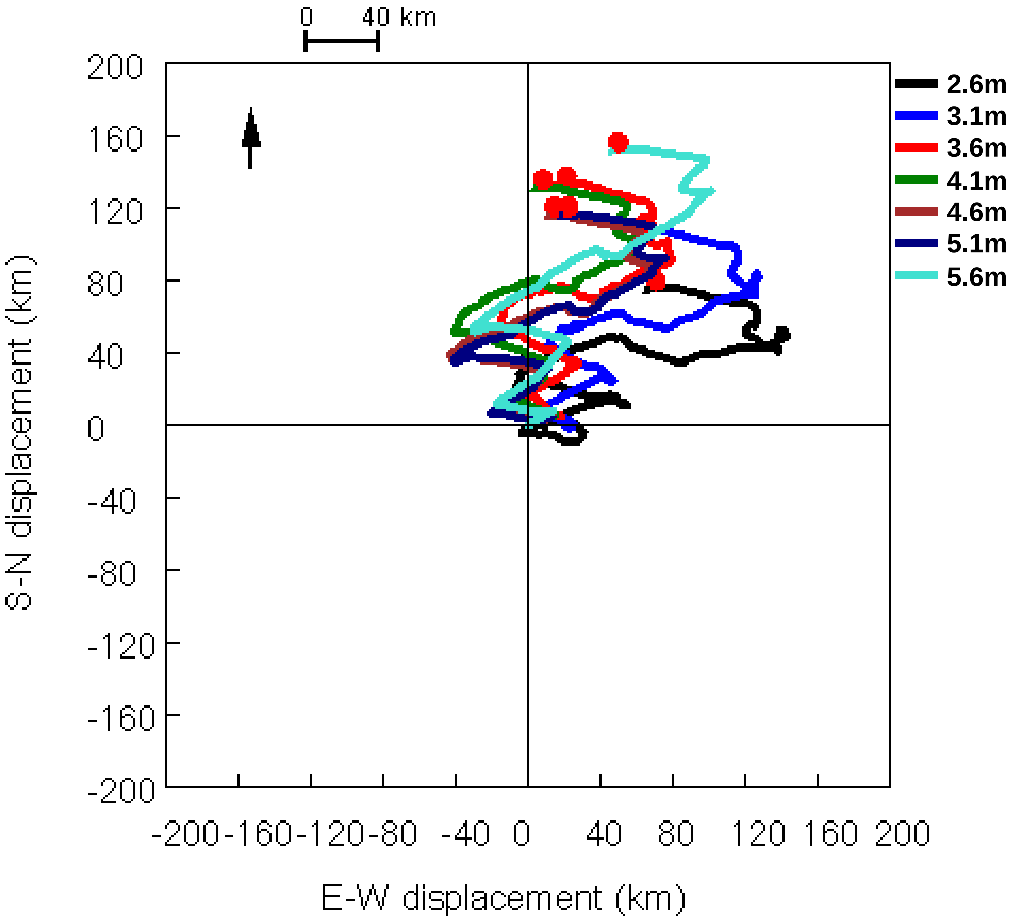
Argyrosomus inodorus
September
14 days PLD
Bird Island
2010



Depth (m)	**Origin Distance (km)**	**Origin Direction (° from N)**	**Average Speed (km/day)**	**Total Distance (km)**
2.3	199.6	317.7	57.0	797.9
2.8	155.2	326.5	49.3	690.4
3.3	68.8	338.8	36.3	508.8
3.8	12.8	146.8	29.4	411.7
4.3	3.5	174.9	25.1	352.5
4.8	48.5	351.3	24.0	337.0
5.3	82.5	354.9	24.8	347.5
5.8	104.9	351.6	25.6	359.0

Black arrow indicated direction of North
Red dot indicated origin

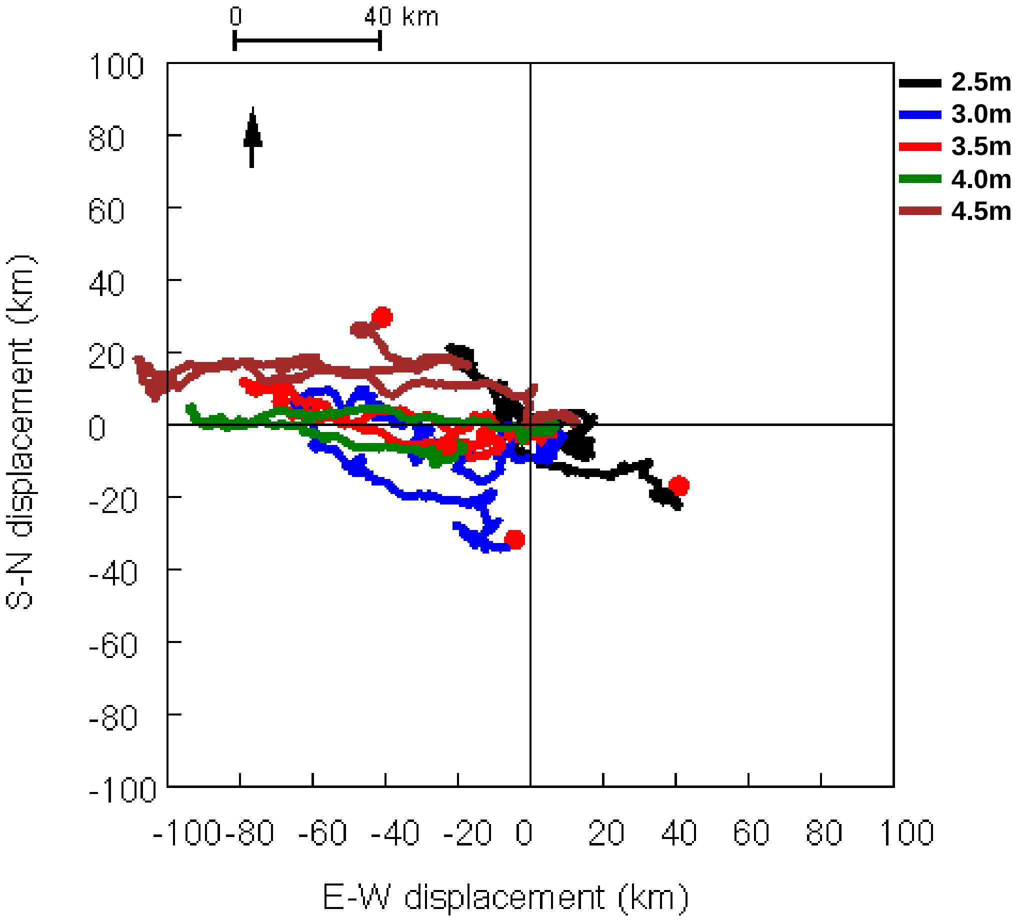
Argyrosomus inodorus
September
14 days PLD
Bird Island
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	98.6	40.2	39.1	547.6
3.1	121.9	29.1	29.3	410.5
3.6	134.2	6.8	25.6	358.6
4.1	131.5	1.0	25.3	354.3
4.6	116.8	4.6	26.0	365.1
5.1	117.4	8.1	26.8	376.3
5.6	158.2	16.2	29.6	414.4

Black arrow indicated direction of North
Red dot indicated origin

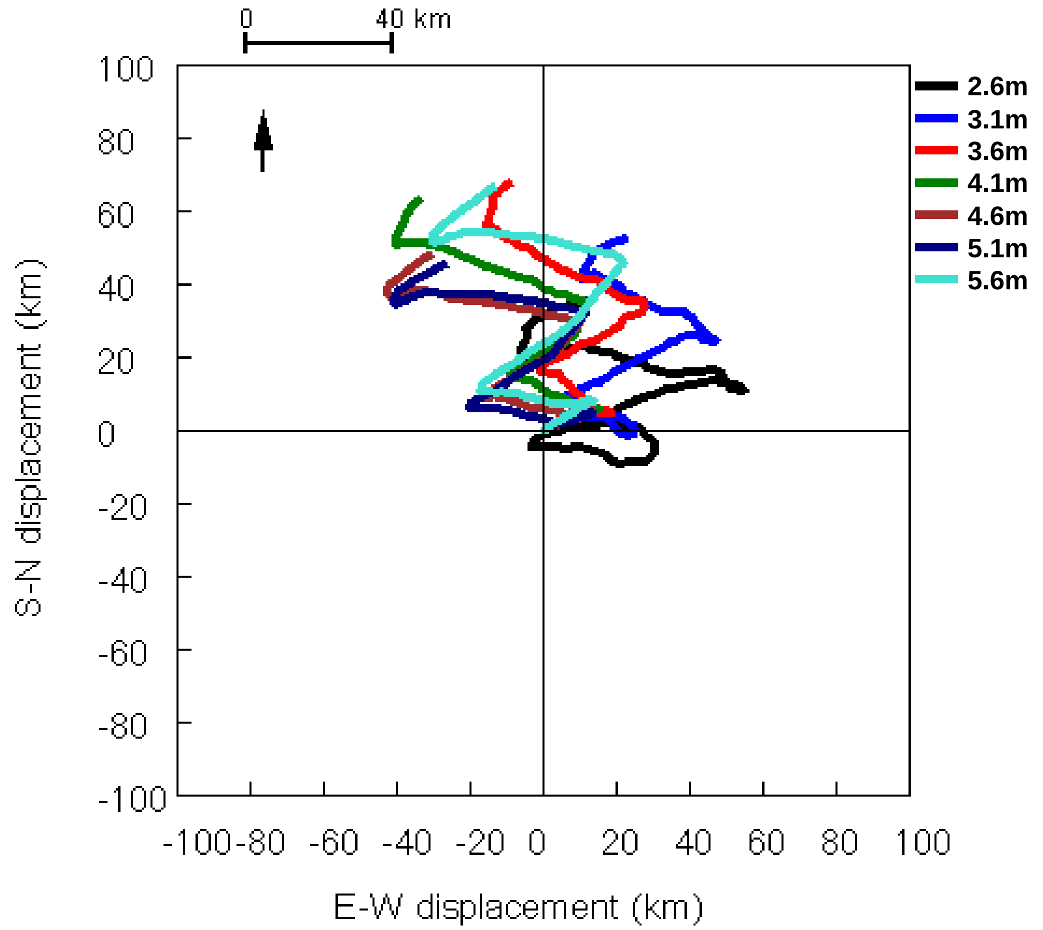
Argyrosomus inodorus
September
14 days PLD
Alexandria dune field
2006



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	43.9	116.0	30.1	421.8
3.0	34.2	189.7	31.9	447.6
3.5	14.4	248.0	22.7	317.8
4.0	25.6	252.0	19.7	276.6
4.5	49.7	303.8	26.6	372.5

Black arrow indicated direction of North
Red dot indicated origin

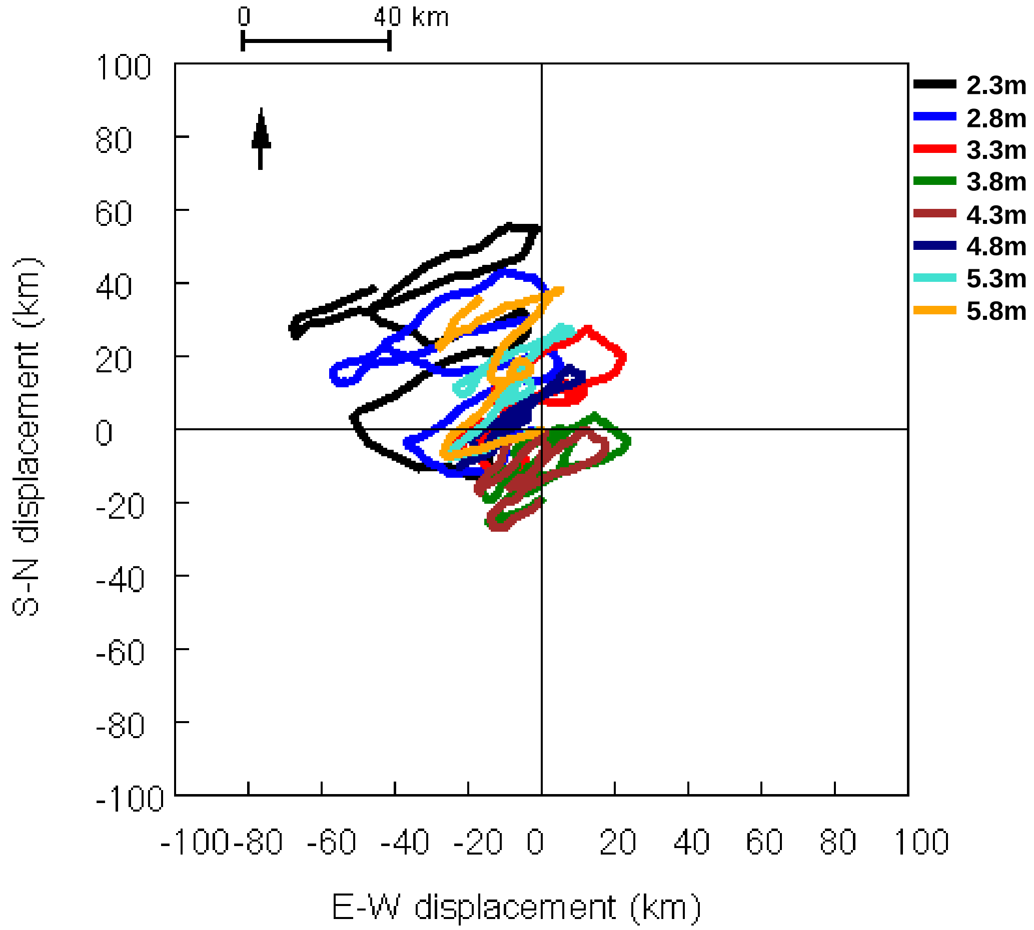
Argyrosomus japonicus
September
6 days PLD
Bird Island
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	38.3	20.0	38.9	233.9
3.1	57.7	23.4	27.3	163.9
3.6	68.5	352.7	24.7	148.3
4.1	71.8	332.3	24.7	148.4
4.6	57.1	327.9	25.9	155.5
5.1	52.8	330.0	27.3	164.3
5.6	68.4	348.9	30.0	180.2

Black arrow indicated direction of North
Red dot indicated origin

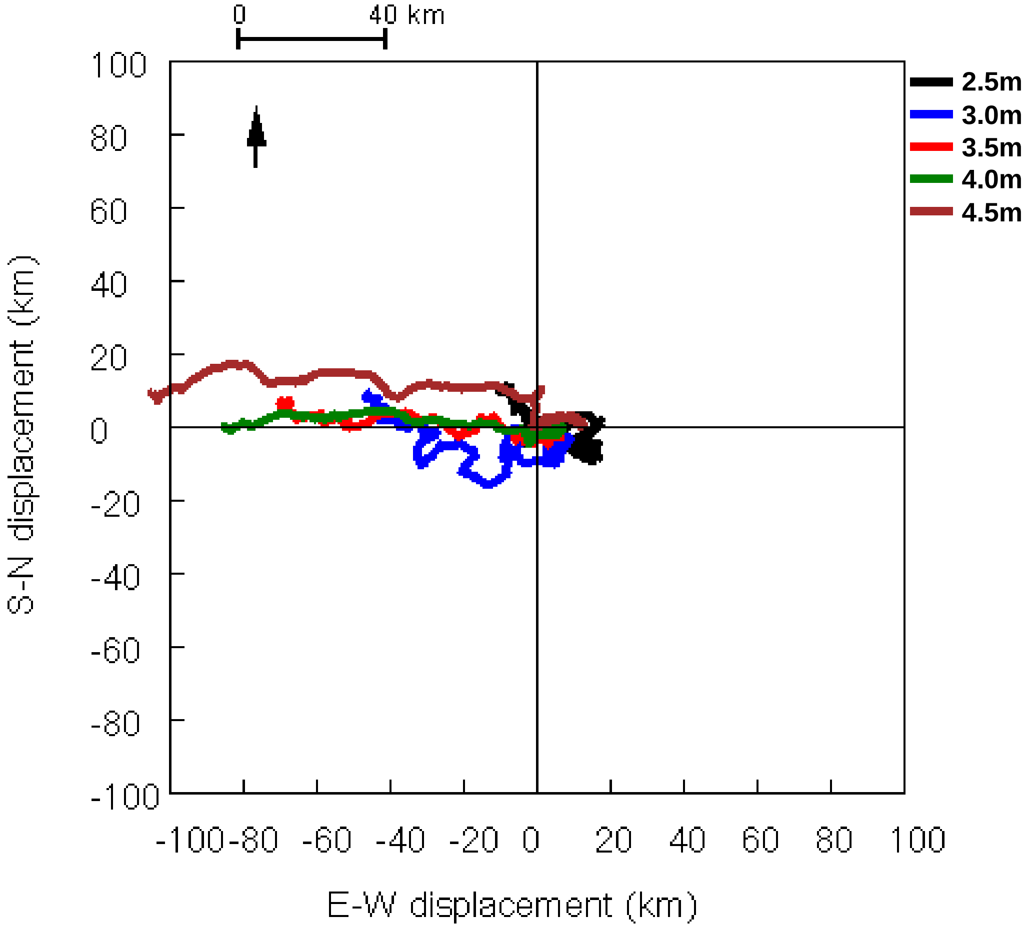
Argyrosomus japonicus
September
6 days PLD
Bird Island
2010



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	59.6	310.8	55.3	331.9
2.8	45.7	304.3	49.7	298.2
3.3	8.2	278.3	38.6	231.7
3.8	18.5	177.8	32.7	196.6
4.3	19.6	179.8	27.9	167.7
4.8	7.7	305.0	26.0	156.3
5.3	23.9	337.2	26.9	161.9
5.8	39.8	335.6	27.8	167.0

Black arrow indicated direction of North
Red dot indicated origin

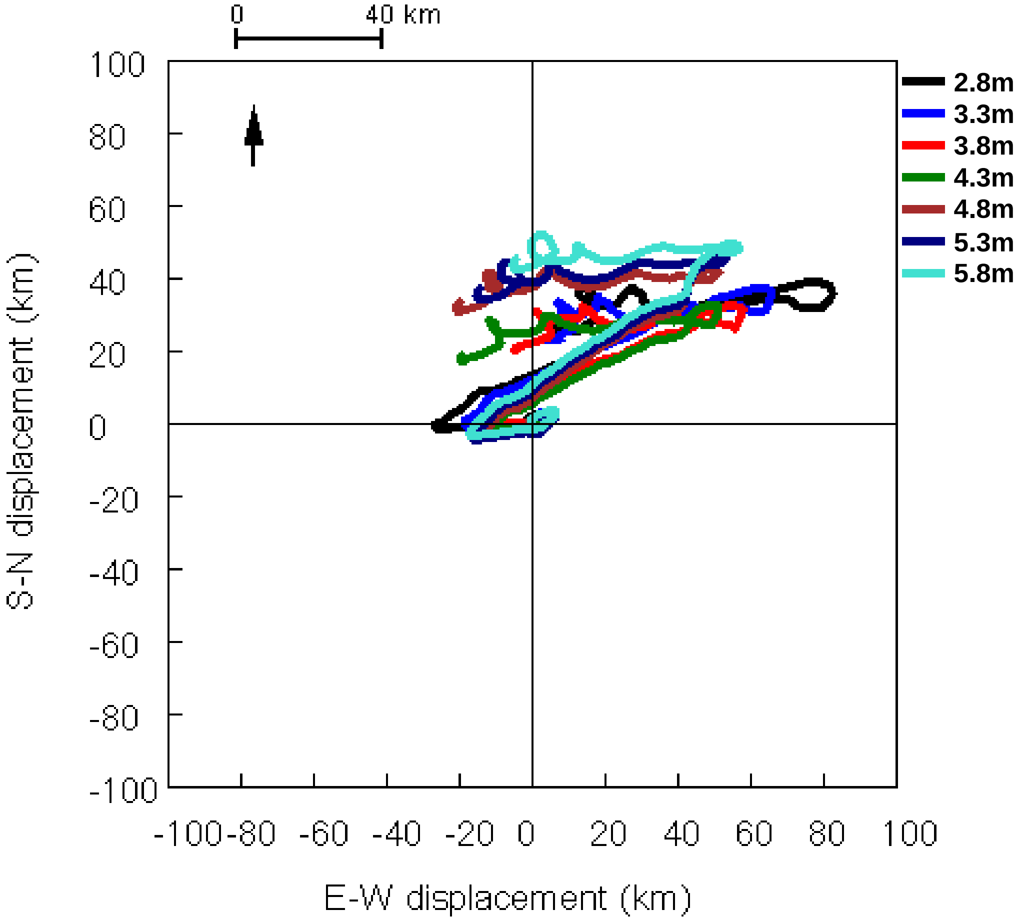
Argyrosomus japonicus
September
6 days PLD
Alexandria dune field
2006



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	14.8	315.6	32.2	193.6
3.0	46.3	282.3	35.4	212.6
3.5	69.7	276.8	24.1	144.7
4.0	84.6	270.5	20.6	123.6
4.5	105.0	275.3	27.9	167.7

Black arrow indicated direction of North
Red dot indicated origin

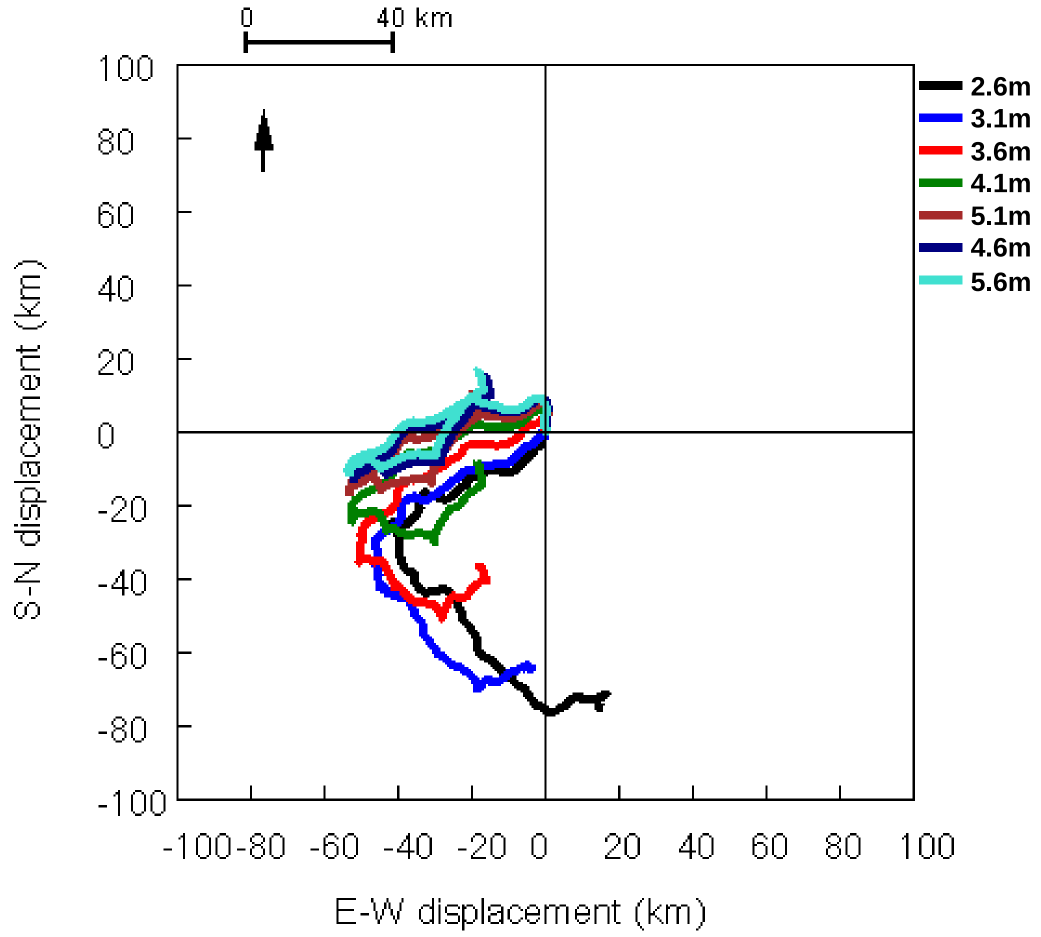
Diplodus capensis
January
7 days PLD
Bird Island
2013



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.8	40.8	65.2	36.1	252.8
3.3	33.4	67.5	29.2	204.9
3.8	17.6	37.9	26.3	184.3
4.3	17.1	316.6	26.1	183.2
4.8	29.4	335.5	26.9	188.6
5.3	31.2	356.2	27.5	192.5
5.8	41.8	15.7	27.5	192.5

Black arrow indicated direction of North
Red dot indicated origin

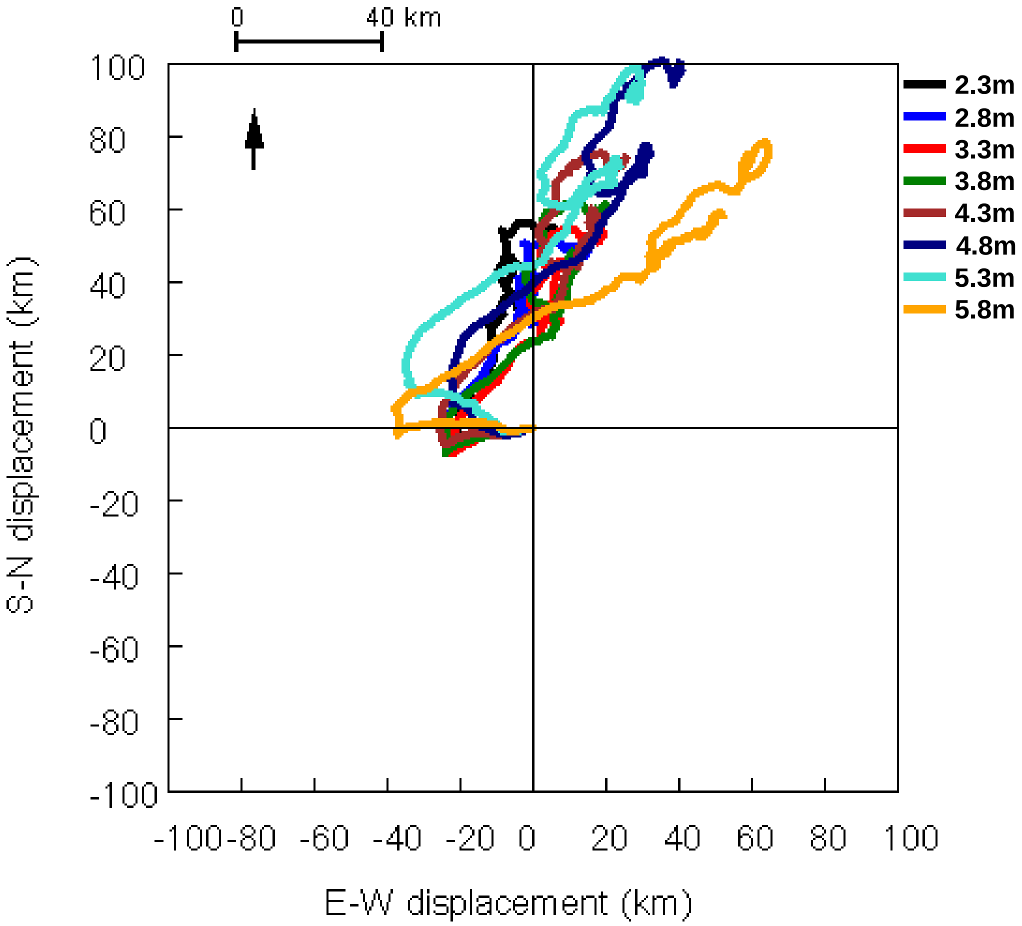
Diplodus capensis
January
7 days PLD
Bird Island
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	46.9	117.6	25.8	181.0
3.1	25.8	80.9	25.2	176.9
3.6	44.0	26.7	27.1	190.0
4.1	61.5	21.2	28.8	202.1
4.6	71.4	19.0	29.7	208.0
5.1	71.8	18.2	29.7	208.0
5.6	70.3	14.0	29.1	204.2

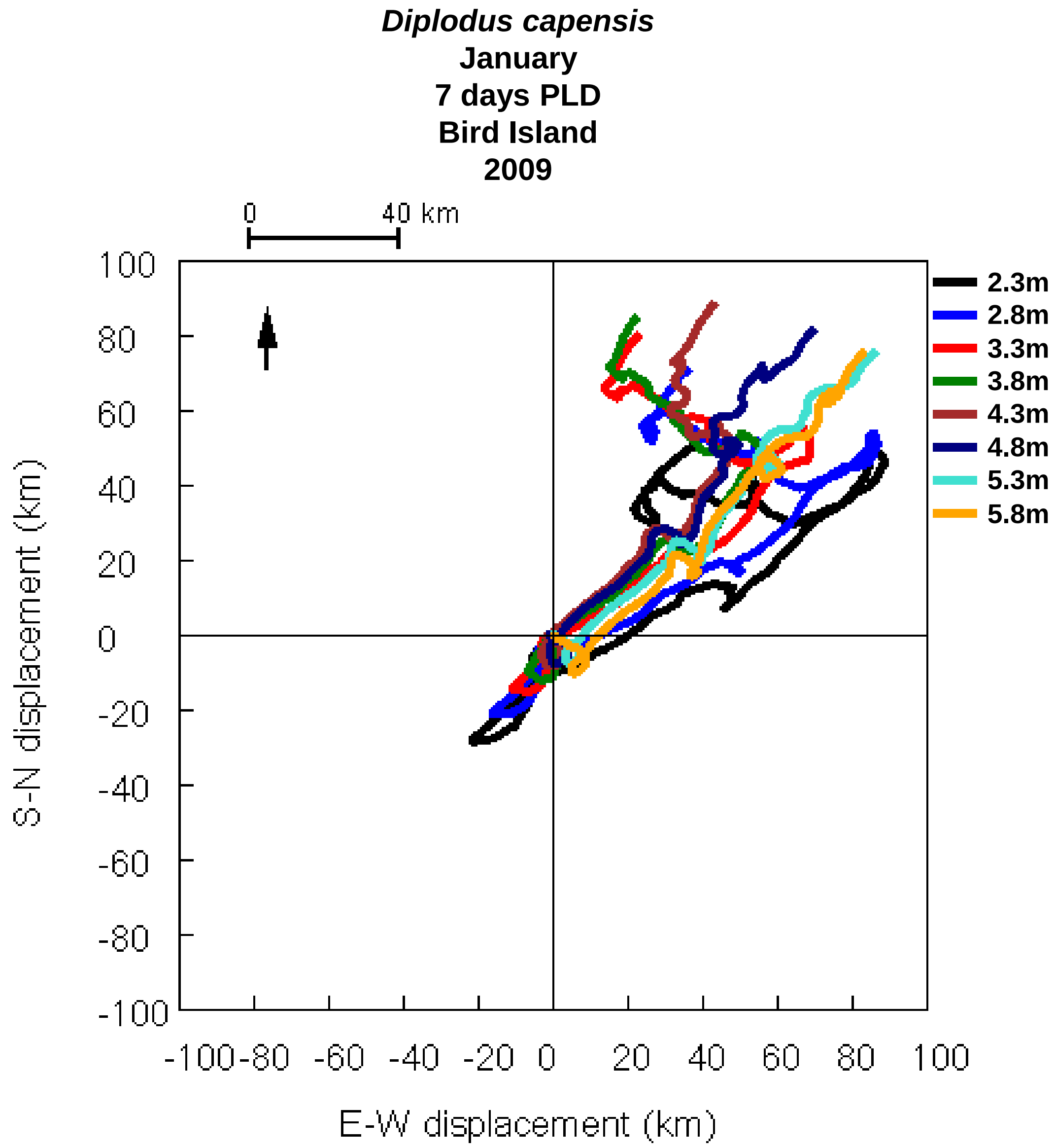
Black arrow indicated direction of North
Red dot indicated origin

Diplodus capensis
January
7 days PLD
Bird Island
2010



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	53.7	4.6	23.1	161.7
2.8	50.6	16.0	24.4	171.1
3.3	56.0	18.7	25.4	178.1
3.8	62.8	17.2	27.1	189.8
4.3	77.9	18.1	29.1	204.0
4.8	109.0	21.7	32.1	224.8
5.3	99.2	16.5	34.9	244.9
5.8	95.6	37.3	38.5	269.6

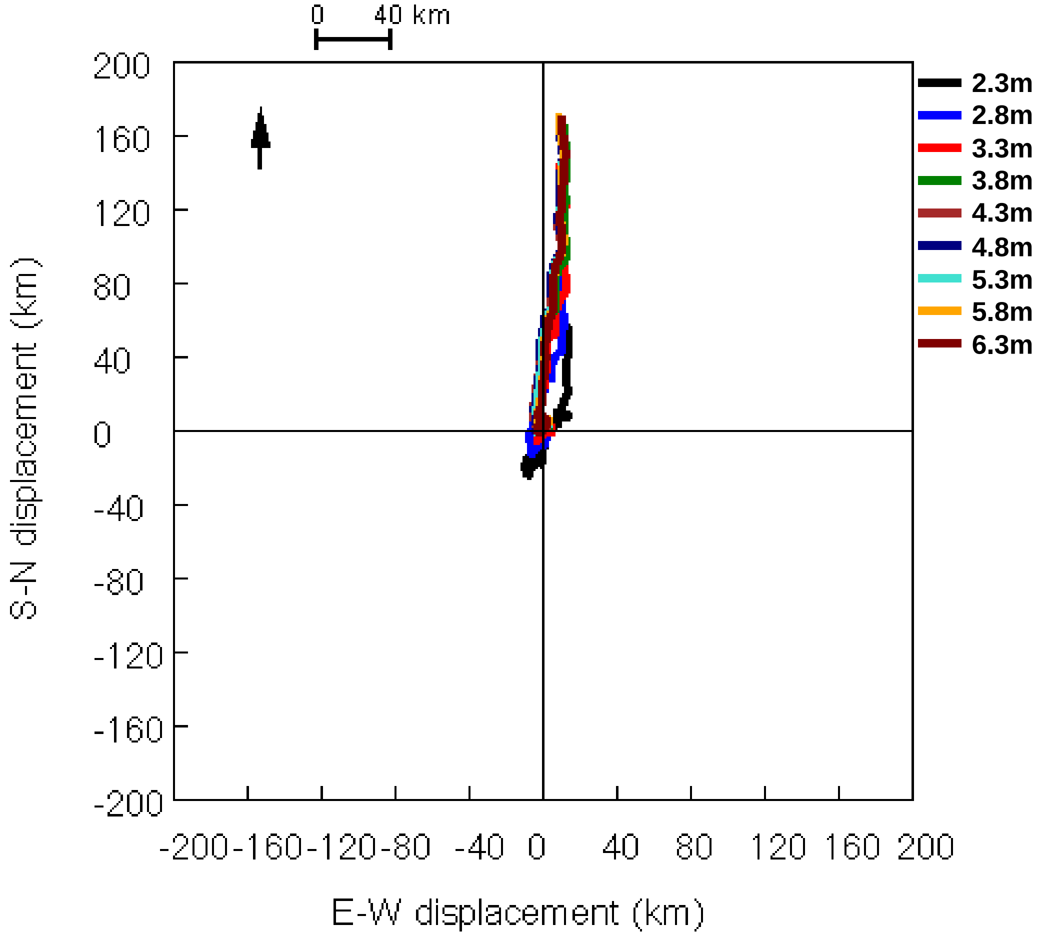
Black arrow indicated direction of North
Red dot indicated origin



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	60.9	35.8	47.5	332.5
2.8	76.7	25.2	41.2	288.8
3.3	81.2	14.2	33.7	235.9
3.8	86.3	13.6	28.2	197.6
4.3	96.6	25.3	24.6	172.6
4.8	105.4	40.0	24.5	171.9
5.3	112.7	48.6	25.0	175.2
5.8	111.0	47.7	25.8	180.6

Black arrow indicated direction of North
Red dot indicated origin

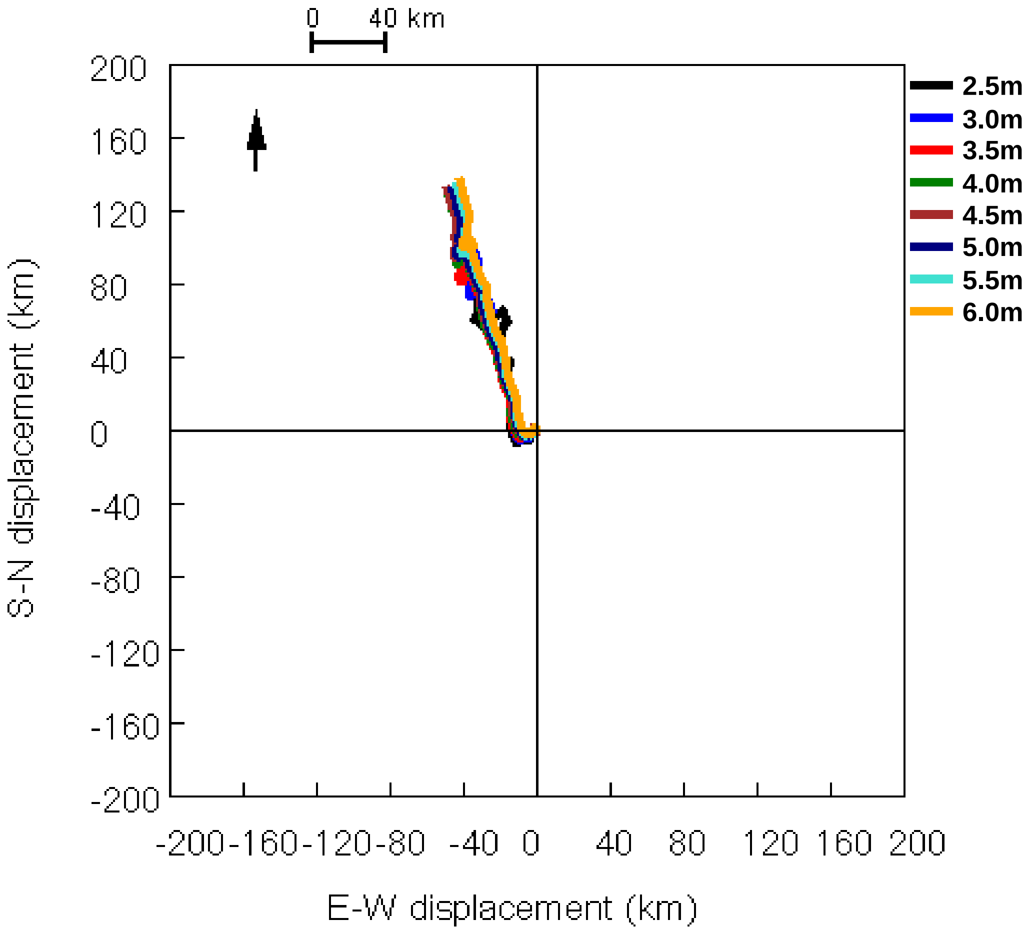
Diplodus capensis
January
7 days PLD
Cape Recife
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	60.2	12.4	23.7	166.1
2.8	102.0	5.8	24.6	172.4
3.3	145.2	3.5	27.4	191.8
3.8	166.3	3.8	29.1	204.3
4.3	168.2	3.1	29.2	205.0
4.8	170.8	2.8	29.6	207.3
5.3	171.8	3.0	29.4	206.3
5.8	172.0	2.9	29.7	207.9
6.3	171.3	3.4	29.7	208.2

Black arrow indicated direction of North
Red dot indicated origin

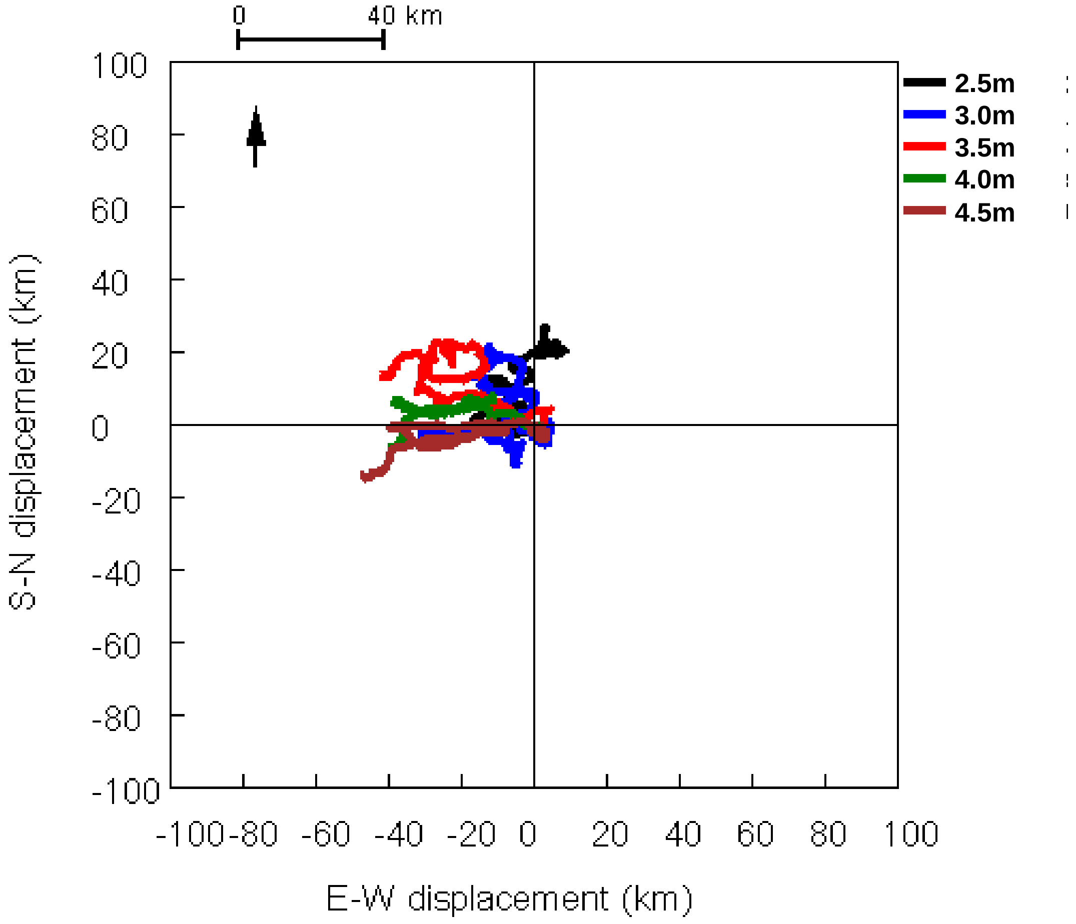
Diplodus capensis
January
7 days PLD
Cape Recife
2009



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	87.6	336.2	22.7	158.9
3.0	110.6	340.8	23.6	165.4
3.5	124.2	338.7	24.8	174.1
4.0	138.5	339.4	26.0	182.3
4.5	142.9	339.6	26.3	184.6
5.0	142.1	340.7	26.2	183.8
5.5	143.1	341.8	26.1	183.1
6.0	144.9	342.8	26.2	183.6

Black arrow indicated direction of North
Red dot indicated origin

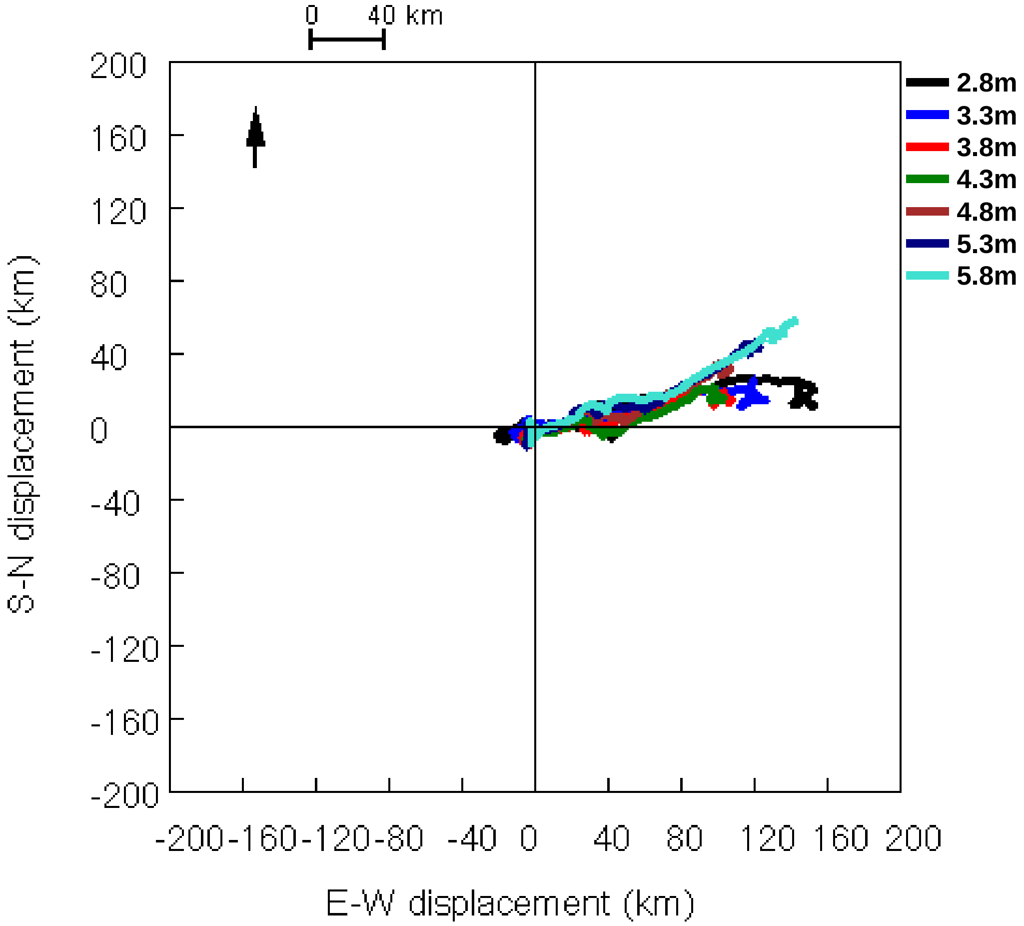
Diplodus capensis
January
7 days PLD
Alexandria dune field
2007



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	19.9	14.1	30.3	212.6
3.0	33.1	280.4	30.3	212.3
3.5	44.2	288.0	26.2	183.3
4.0	40.7	261.3	20.1	140.9
4.5	49.9	253.5	20.8	145.9

Black arrow indicated direction of North
Red dot indicated origin

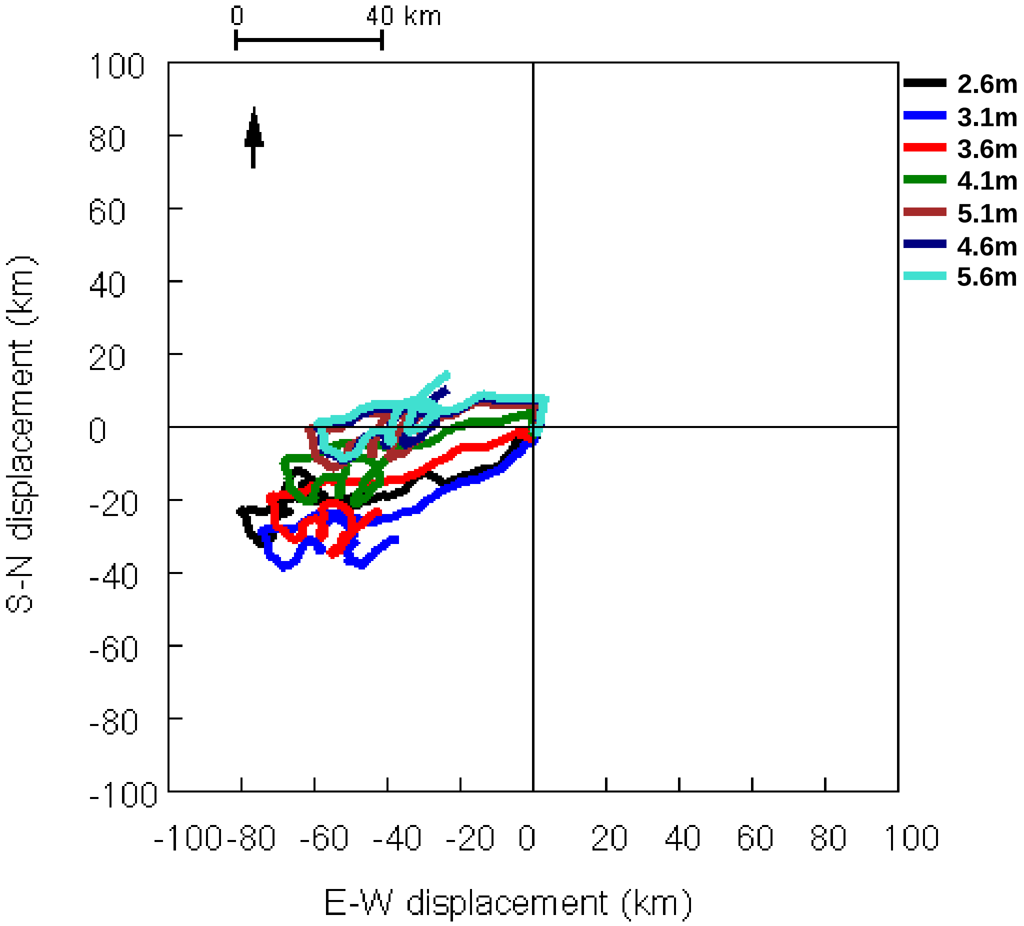
Heteromycteris capensis
February
8 days PLD
Bird Island
2013



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.8	149.4	80.5	38.9	311.2
3.3	124.1	77.7	30.7	245.6
3.8	106.8	79.4	24.5	196.6
4.3	103.2	80.2	23.0	184.7
4.8	113.2	71.9	23.5	188.6
5.3	135.8	69.0	25.3	202.7
5.8	155.0	67.8	26.2	209.5

Black arrow indicated direction of North
Red dot indicated origin

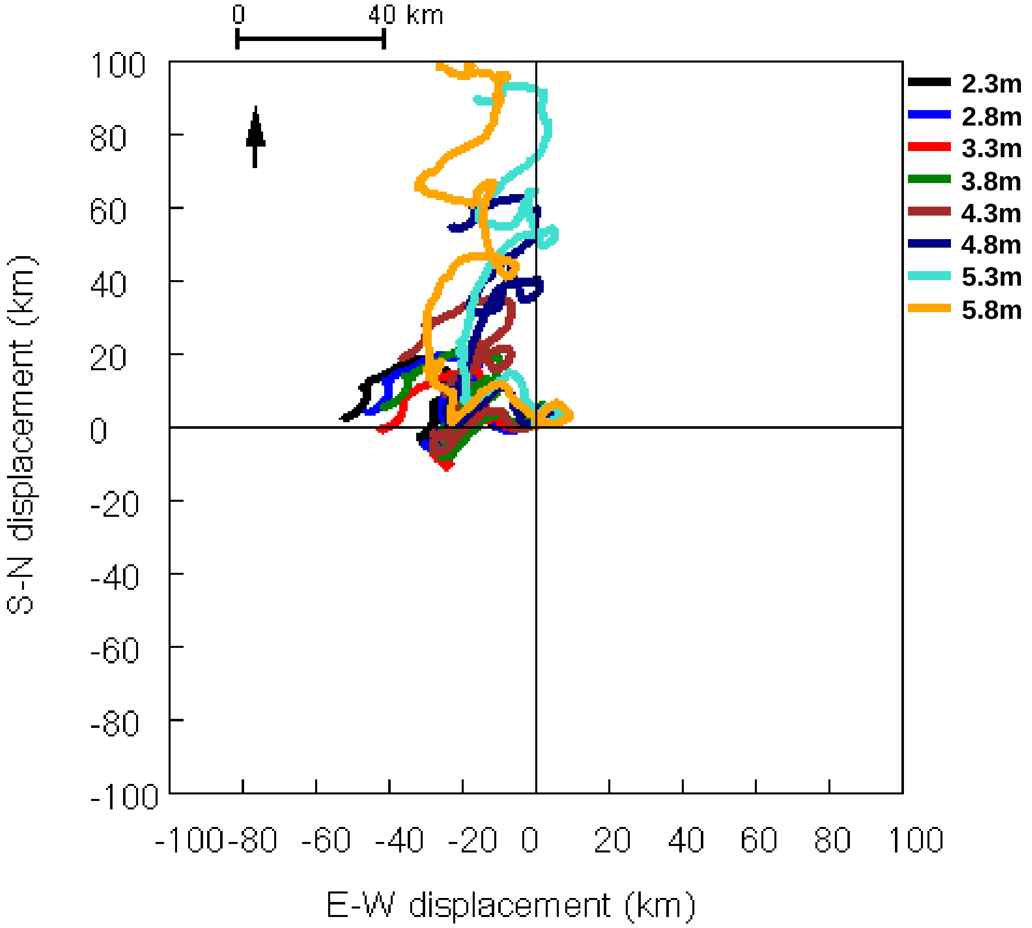
Heteromycteris capensis
February
8 days PLD
Bird Island
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	48.0	248.9	22.8	182.5
3.1	47.9	230.2	20.6	164.9
3.6	47.5	241.1	20.5	164.3
4.1	36.7	261.7	20.9	167.7
4.6	28.1	286.9	20.8	166.6
5.1	25.7	293.7	20.5	164.1
5.6	27.0	303.0	20.4	163.7

Black arrow indicated direction of North
Red dot indicated origin

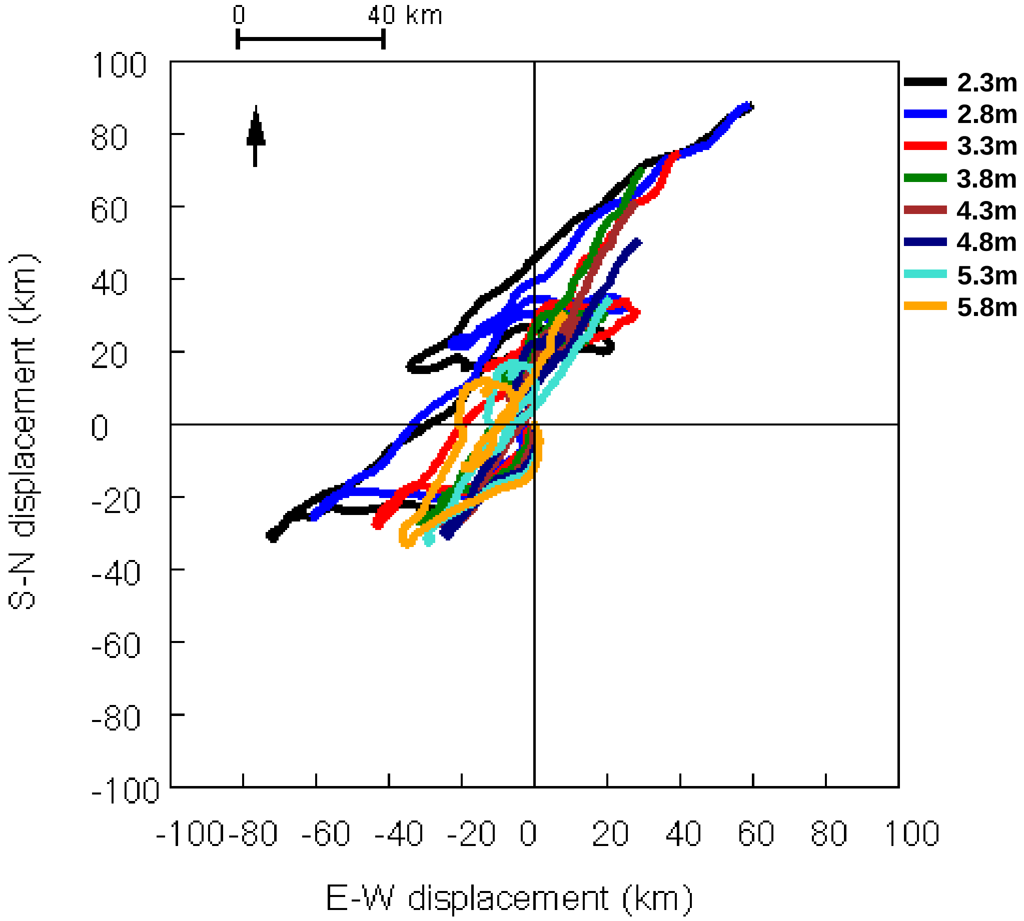
Heteromycteris capensis
February
8 days PLD
Bird Island
2010



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	52.9	273.4	21.2	170.0
2.8	46.3	276.1	22.3	178.3
3.3	42.9	270.2	22.8	182.4
3.8	42.6	278.5	24.4	195.9
4.3	42.1	297.9	25.6	204.9
4.8	60.3	337.2	27.8	222.5
5.3	92.1	349.7	30.8	246.6
5.8	102.2	344.5	34.1	273.3

Black arrow indicated direction of North
Red dot indicated origin

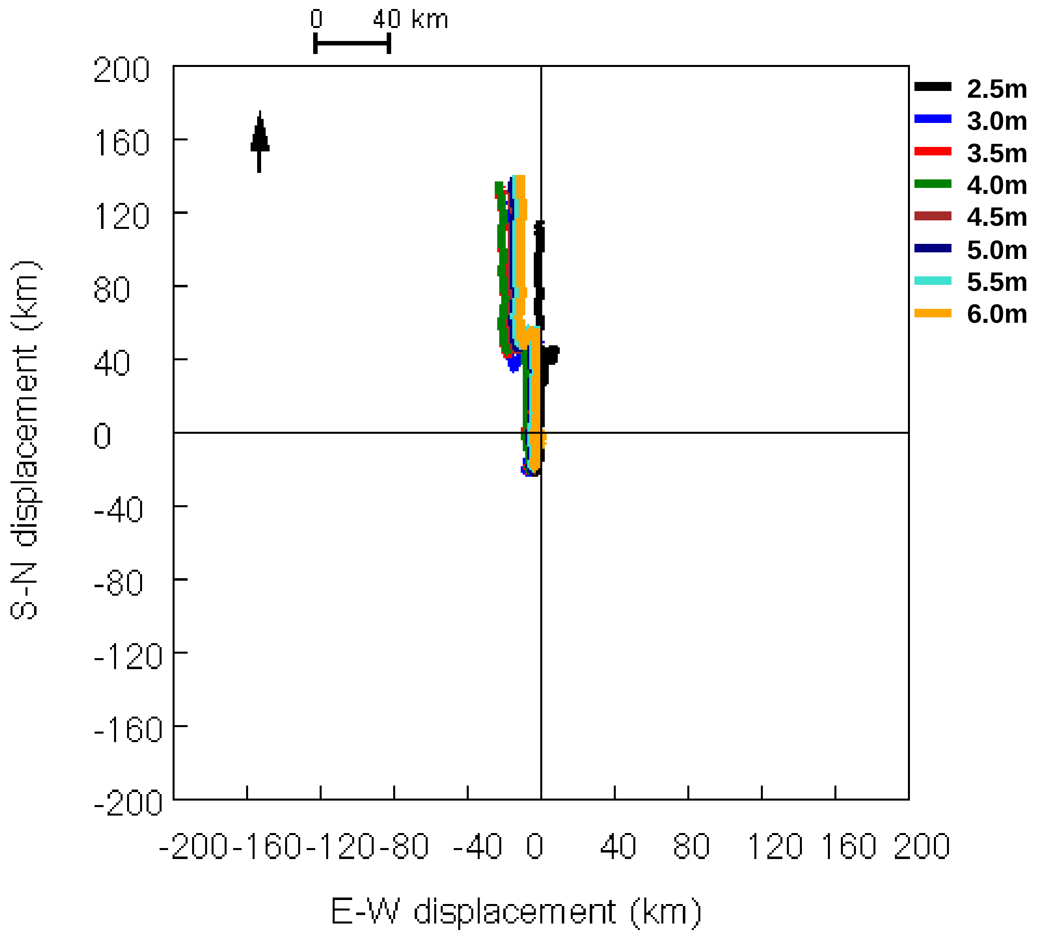
Heteromycteris capensis
February
8 days PLD
Bird Island
2009



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	106.5	34.3	49.8	399.1
2.8	106.1	33.8	44.4	355.6
3.3	84.7	27.9	37.6	300.9
3.8	76.5	22.9	31.2	250.3
4.3	67.2	24.5	27.8	222.6
4.8	58.3	29.3	26.9	215.8
5.3	40.3	31.1	26.2	209.9
5.8	31.8	15.3	25.7	206.0

Black arrow indicated direction of North
Red dot indicated origin

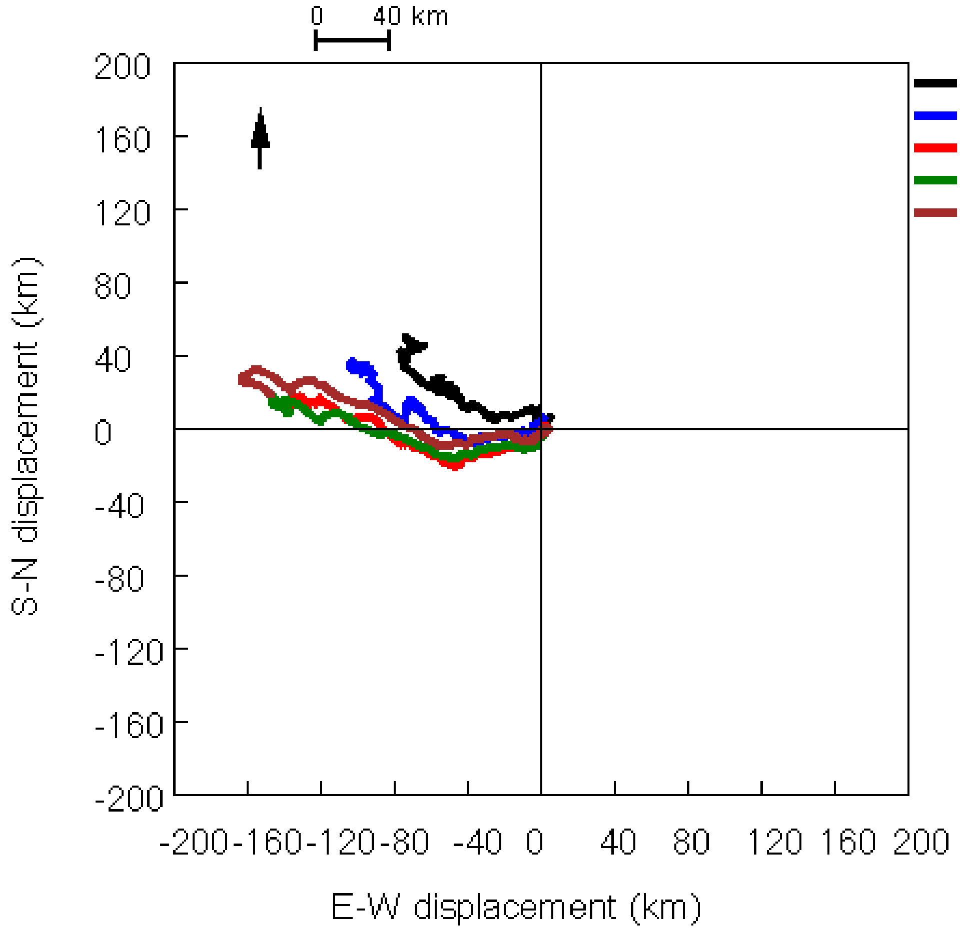
Heteromycteris capensis
February
8 days PLD
Cape Recife
2009



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	115.4	359.4	28.5	228.2
3.0	127.0	352.5	29.0	232.3
3.5	137.1	350.6	29.1	233.3
4.0	139.1	350.7	28.9	231.6
4.5	138.2	353.2	28.6	228.9
5.0	139.9	353.7	28.3	226.8
5.5	141.3	354.3	28.0	224.5
6.0	140.9	355.4	27.8	222.4

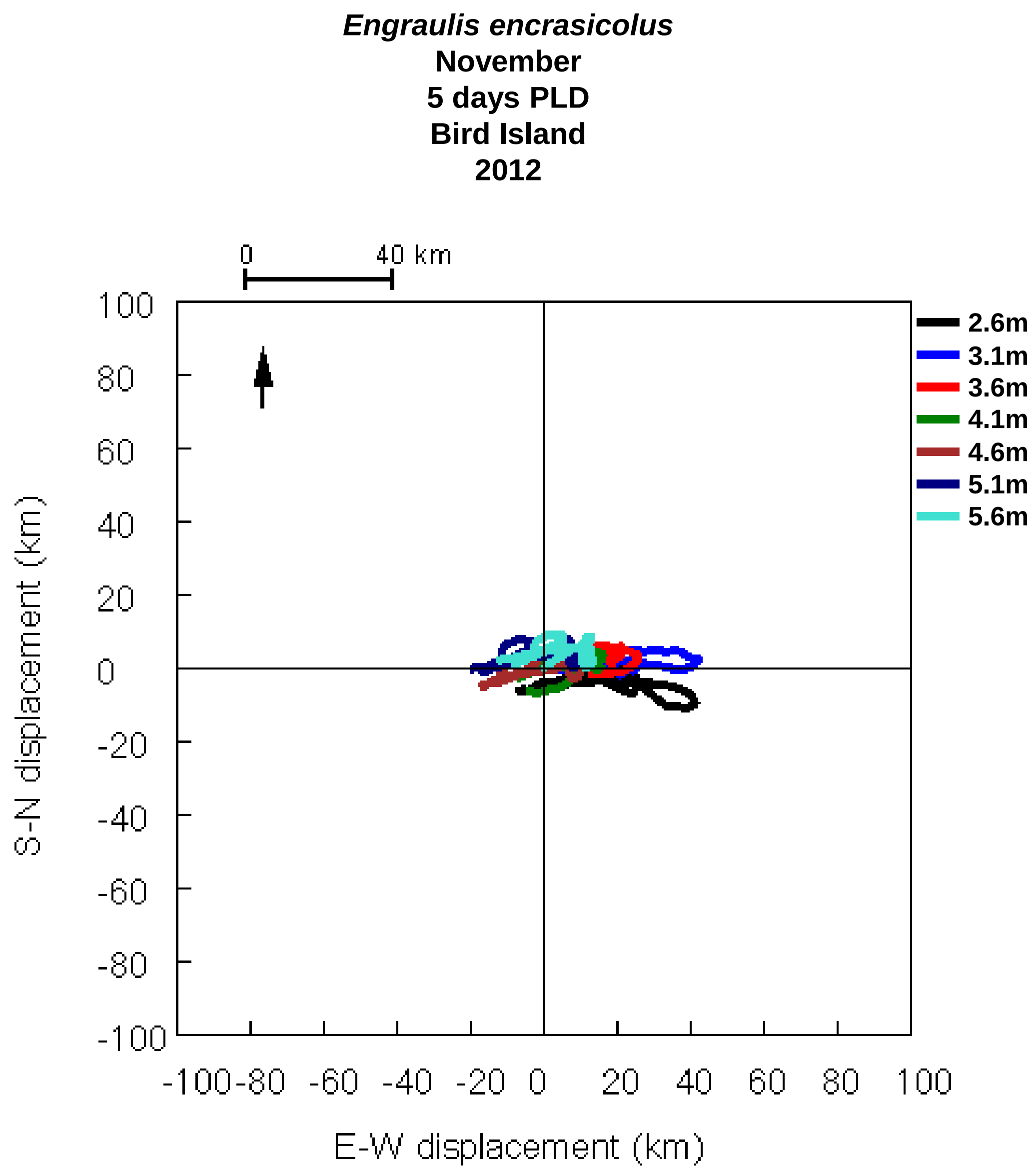
Black arrow indicated direction of North
Red dot indicated origin

Heteromycteris capensis
February
8 days PLD
Alexandria dune field
2007



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	77.6	305.1	32.8	262.9
3.0	106.4	287.6	31.4	251.9
3.5	136.7	275.8	27.8	222.6
4.0	137.6	273.4	27.9	223.6
4.5	148.3	277.3	30.0	240.6

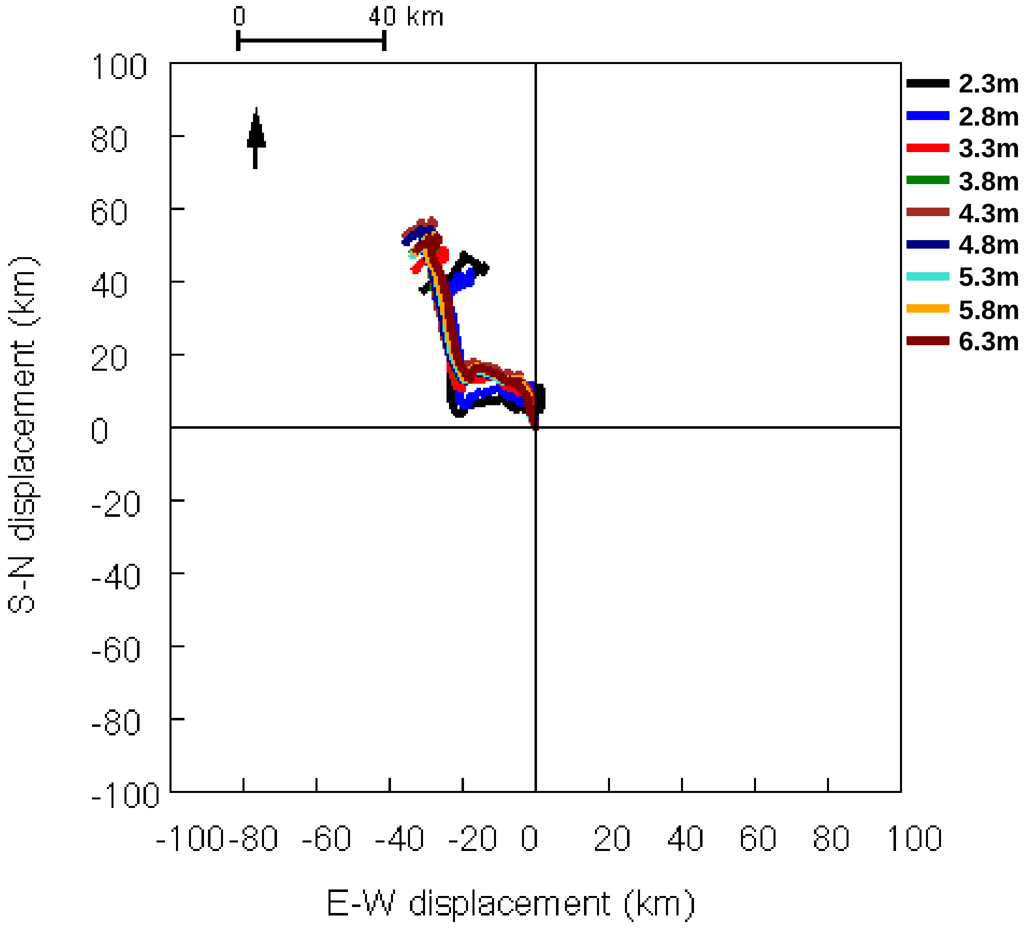
Black arrow indicated direction of North
Red dot indicated origin



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	17.0	98.9	36.9	184.5
3.1	25.0	87.6	27.2	136.3
3.6	12.2	96.7	21.8	109.0
4.1	8.2	218.7	20.4	102.0
4.6	18.3	254.1	20.6	103.2
5.1	20.3	269.3	20.7	103.7
5.6	13.2	279.0	20.3	101.6

Black arrow indicated direction of North
Red dot indicated origin

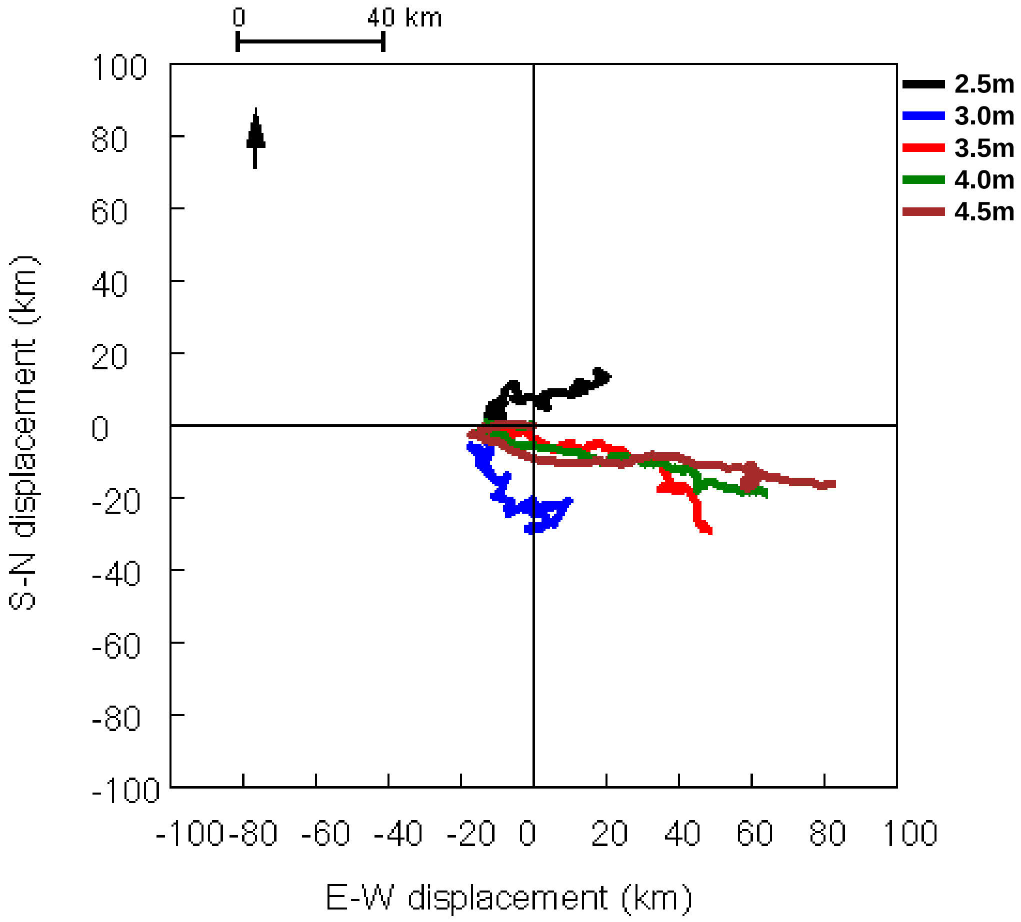
Engraulis encrasicolus
November
5 days PLD
Cape Recife
2010



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	48.6	319.6	23.9	119.7
2.8	44.1	321.4	19.9	99.8
3.3	54.5	321.5	19.3	96.5
3.8	58.4	324.3	18.6	93.3
4.3	63.1	325.3	19.0	95.3
4.8	61.5	324.1	18.6	93.3
5.3	57.4	323.6	18.1	90.8
5.8	58.0	324.7	18.1	90.8

Black arrow indicated direction of North
Red dot indicated origin

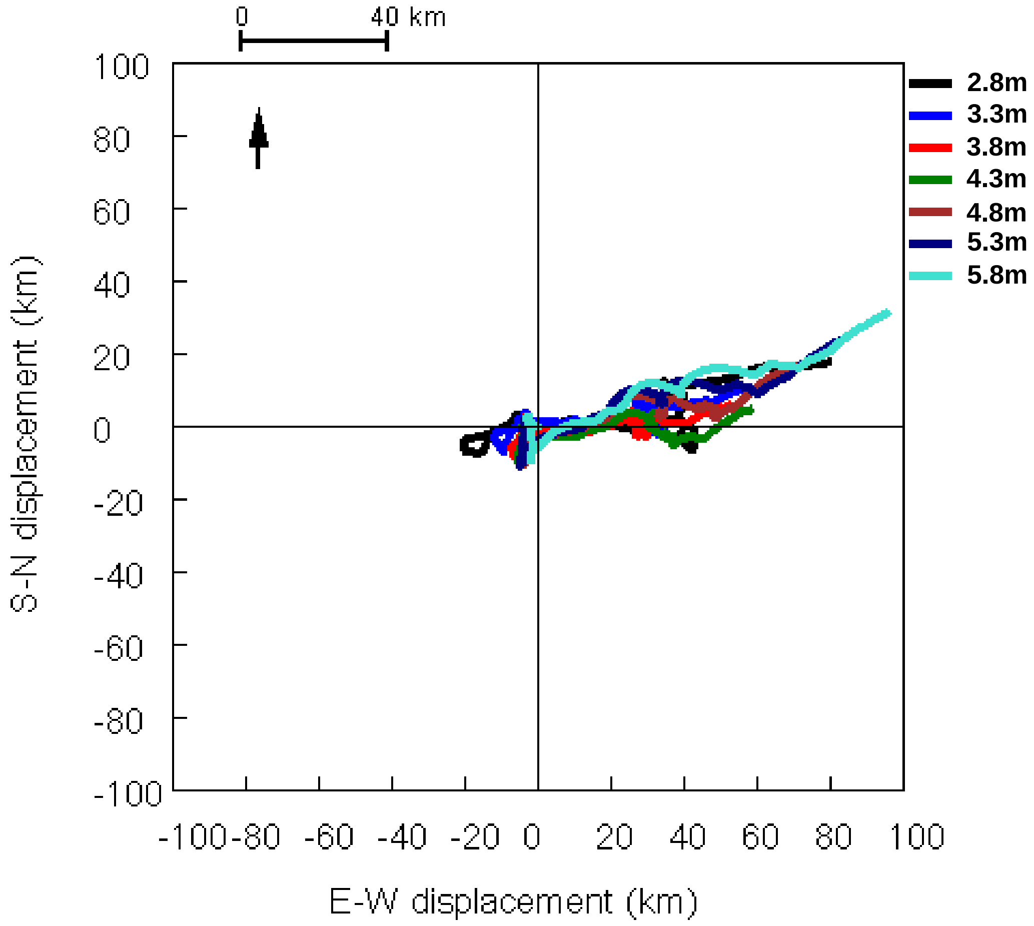
Engraulis encrasicolus
November
5 days PLD
Alexandria dune field
2006



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	24.4	58.9	28.6	143.3
3.0	28.5	166.6	31.6	158.1
3.5	57.2	120.8	25.9	129.9
4.0	67.2	106.3	23.5	117.9
4.5	84.8	101.2	28.8	144.2

Black arrow indicated direction of North
Red dot indicated origin

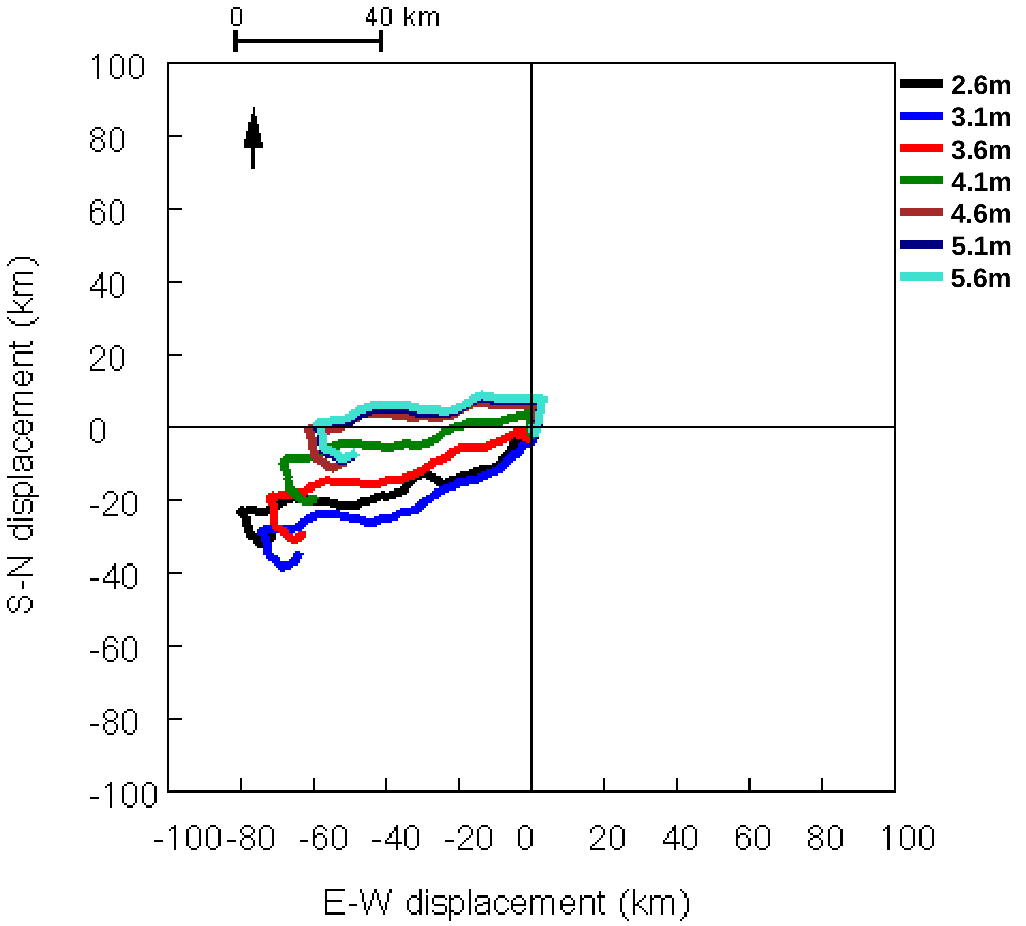
Sardinops sagax
February
5 days PLD
Bird Island
2013



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.8	82.1	77.4	37.1	185.6
3.3	62.3	80.2	28.5	142.5
3.8	53.4	83.3	22.9	114.6
4.3	59.0	85.2	22.5	112.6
4.8	73.0	76.5	24.5	122.7
5.3	87.4	73.7	26.4	132.1
5.8	101.3	71.6	27.6	138.3

Black arrow indicated direction of North
Red dot indicated origin

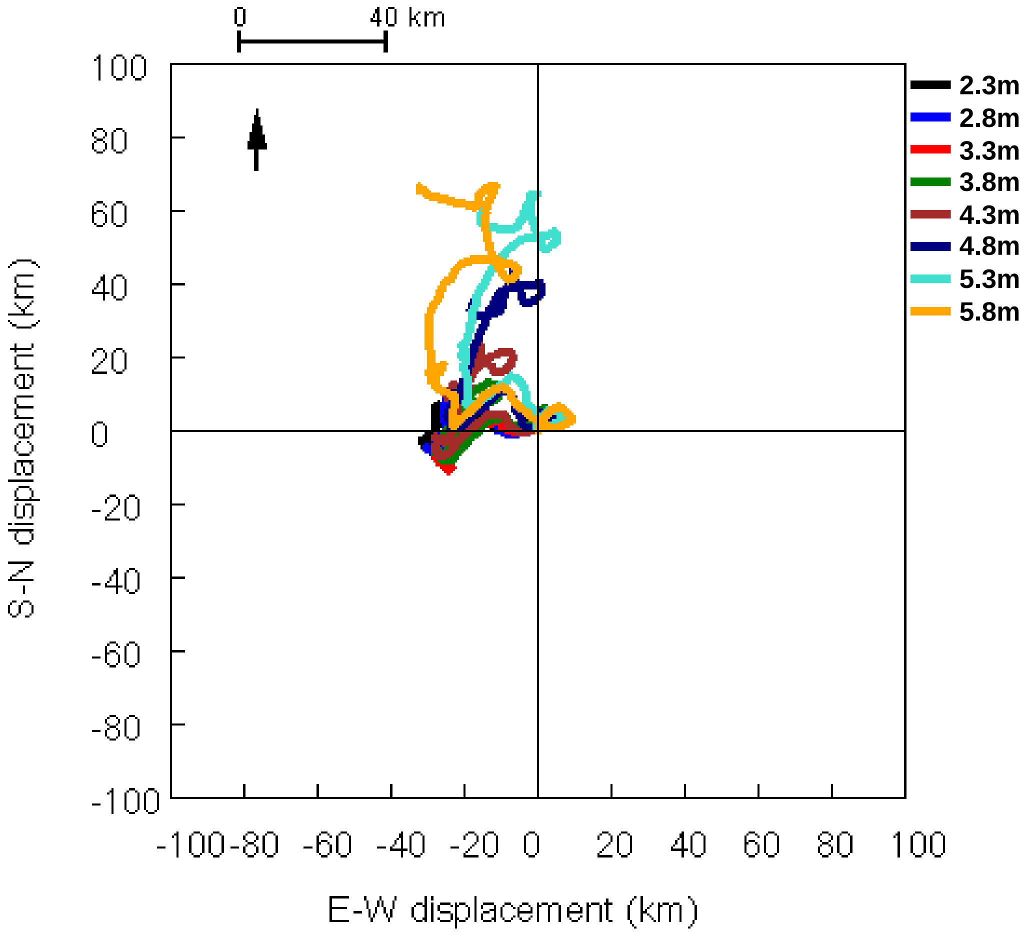
Sardinops sagax
February
5 days PLD
Bird Island
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.6	76.0	249.0	23.7	118.6
3.1	72.2	241.8	21.6	108.0
3.6	69.6	245.7	20.2	100.9
4.1	62.9	252.9	19.6	98.3
4.6	52.6	259.9	18.9	94.8
5.1	49.2	261.4	18.8	94.1
5.6	48.5	262.0	18.9	94.7

Black arrow indicated direction of North
Red dot indicated origin

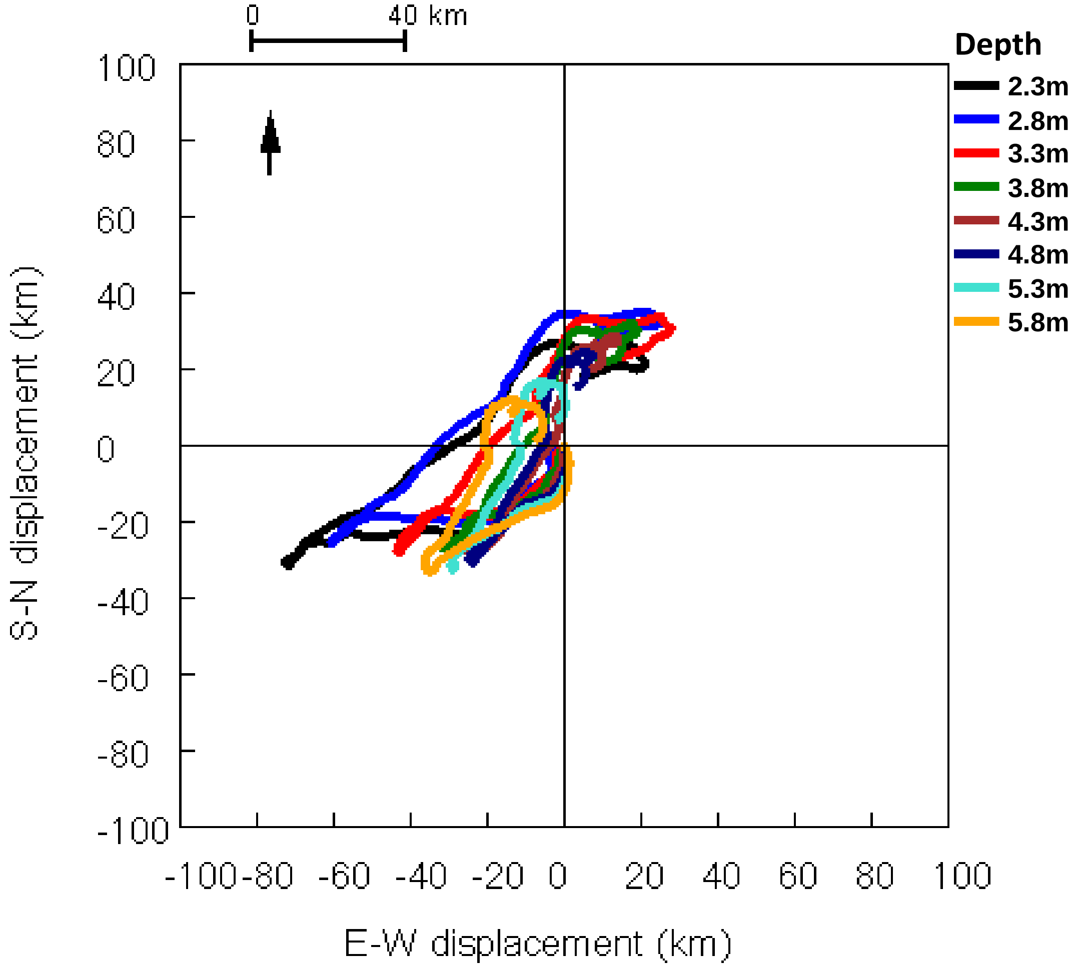
Sardinops sagax
February
5 days PLD
Bird Island
2010



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	29.2	269.0	22.1	110.9
2.8	25.1	270.8	22.8	114.0
3.3	25.3	257.9	23.3	116.8
3.8	23.4	274.2	25.6	128.4
4.3	26.0	301.2	27.3	136.5
4.8	39.8	335.5	31.2	156.0
5.3	63.3	347.3	35.7	178.6
5.8	74.4	334.7	39.4	197.2

Black arrow indicated direction of North
Red dot indicated origin

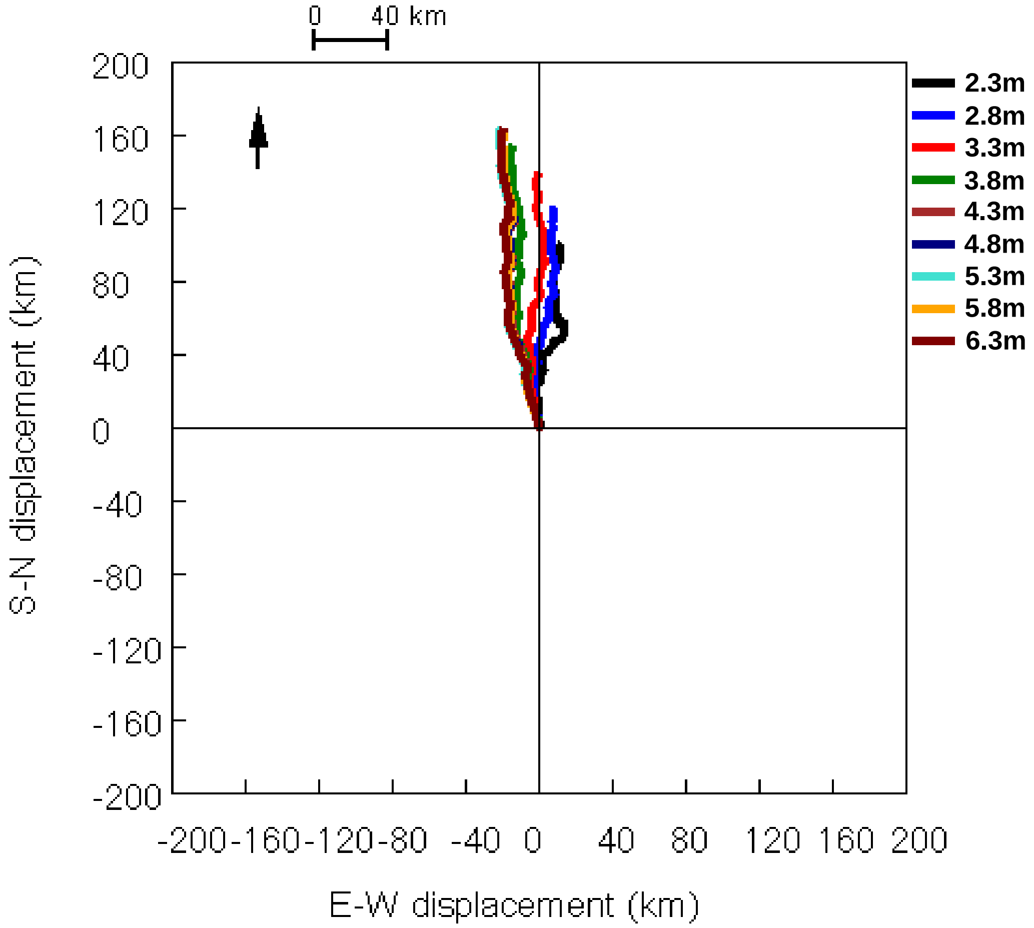
Sardinops sagax
February
5 days PLD
Bird Island
2009



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	18.4	12.7	46.8	234.0
2.8	29.5	15.8	42.1	210.8
3.3	26.6	31.2	37.1	185.7
3.8	23.3	20.5	30.8	154.3
4.3	20.7	15.9	27.0	135.3
4.8	15.2	9.6	26.3	131.5
5.3	6.9	340.8	26.6	133.1
5.8	7.8	277.1	26.6	133.2

Black arrow indicated direction of North
Red dot indicated origin

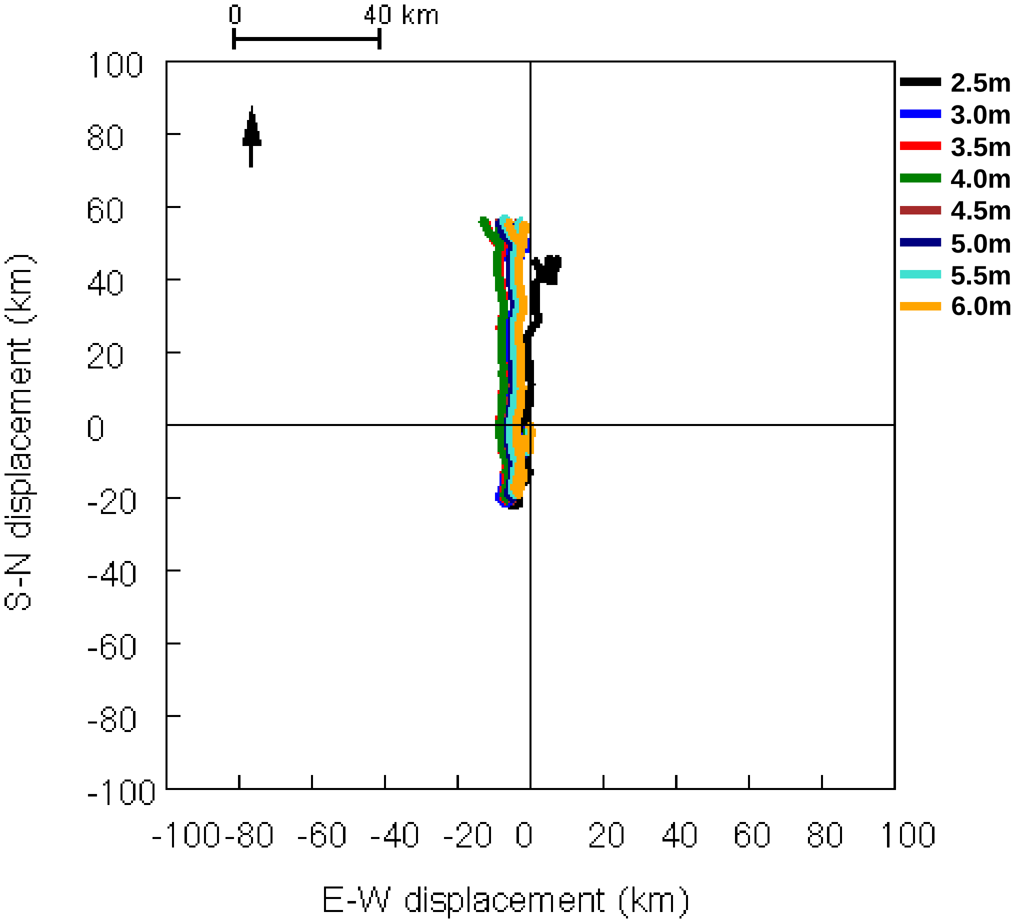
Sardinops sagax
February
5 days PLD
Cape Recife
2012



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.3	46.7	258.9	26.4	132.2
2.8	31.3	265.4	24.6	123.0
3.3	27.3	288.8	24.3	121.9
3.8	28.4	292.1	24.2	121.3
4.3	28.9	293.3	24.5	122.8
4.8	24.3	295.6	23.8	119.0
5.3	22.5	299.6	23.7	118.9
5.8	21.7	303.3	23.4	117.2
6.3	20.0	306.0	23.4	117.0

Black arrow indicated direction of North
Red dot indicated origin

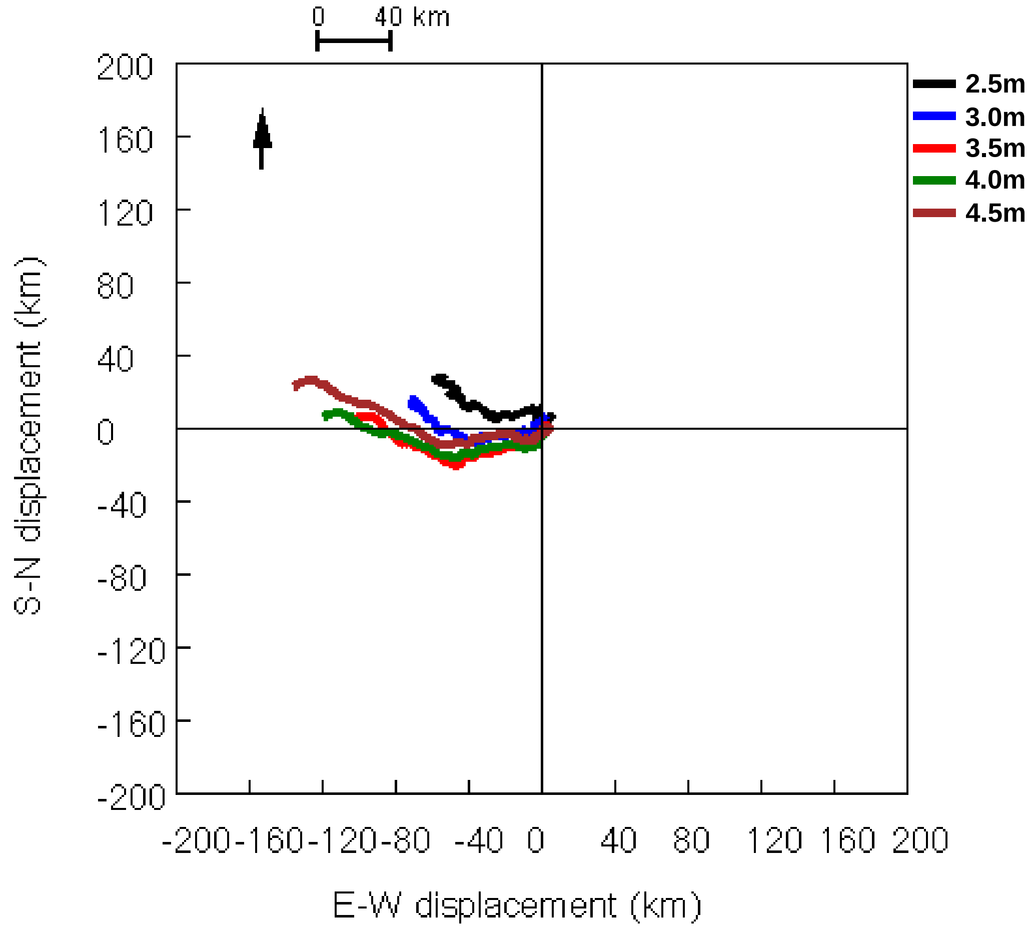
Sardinops sagax
February
5 days PLD
Cape Recife
2009



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	43.4	1.2	24.9	124.5
3.0	48.6	350.4	24.9	124.9
3.5	55.3	347.5	25.0	125.0
4.0	56.9	347.1	24.8	124.2
4.5	55.7	351.7	24.6	123.0
5.0	55.5	351.8	24.2	121.0
5.5	56.5	353.2	23.9	119.4
6.0	55.4	354.7	23.6	118.1

Black arrow indicated direction of North
Red dot indicated origin

Sardinops sagax
February
5 days PLD
Alexandria dune field
2007



Depth (m)	Origin Distance (km)	Origin Direction (° from N)	Average Speed (km/day)	Total Distance (km)
2.5	61.2	295.9	30.8	154.0
3.0	72.8	282.6	27.5	137.9
3.5	102.2	272.4	29.4	147.4
4.0	120.0	272.9	32.2	161.1
4.5	138.2	279.6	35.2	176.0

Black arrow indicated direction of North
Red dot indicated origin